YALE UNIVERSITY   SCHOOL OF FORESTRY

TROPICAL WOODS

CONTENTS

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WOOD ANATOMY OF HELIANTHEAE
(COMPOSITAE)

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In an earlier study the writer (1957a) surveyed the anatomical diversity in woods of the tribe Mutisieae. The present work continues this study to Heliantheae. This tribe is of particular interest both because of the supposed primitiveness of some of its genera (e.g., Cronquist, 1955) and because numerous arborescent or shrubby plants are characteristic of the tribe. Among the genera included in this study which have truly arboreal species are *Fitchia*, *Montanoa*, *Podachaenium*, and *Scalesia*. Most of the remaining genera utilized in this investigation could be classified as shrubby to arborescent. *Wilkesia*, *Espeletia*, and *Coreopsis gigantea* can be called "megaphytes" because of their unbranched stems with terminal leaf rosettes. Certain herbs, such as *Helianthus*, *Argyroxiphium*, *Madia*, and *Grindelia* have been introduced to widen the comparisons and to demonstrate some of the more specialized types of xylem structure.

The tribe Heliantheae is characteristic of the tropical and subtropical portions of the Americas, particularly in the western portions. The subtribe Madiinae, with the exception

of the Hawaiian genera *Argyroxiphium*, *Wilkesia*, and *Dubautia*, is mostly confined to California. *Espeletia* occurs on the high *páramos* of Colombia, *Lipochaeta* on the Hawaiian Islands, *Scalesia* on the Galapagos Islands, and *Fitchia* and *Oparanthus* are endemic to certain islands of southeastern Polynesia. Otherwise, the tribe is found mostly in warmer and drier parts of North, Central, and South America, with a particular concentration of species in Mexico.

An attempt to "monograph" the woods of a given genus is not basic to this study. However, the species diversity in several genera provided an interesting key to diversification in wood structure. Foremost among these is *Dubautia* (construed here as including *Railliardia*), in which many of the woody species were studied. Because a critical problem exists in regard to the relationships of *Dubautia*, certain other genera were included. According to Keck (1936), *Dubautia* bears a relationship to *Argyroxiphium* and *Wilkesia*. These latter genera, in turn, have been traditionally associated with the tarweeds (Heliantheae, subtribe Madiinae), although Keck is dubious of this relationship. Because of similarities in vegetative and floral morphology and anatomy, these three Hawaiian genera are provisionally grouped with the tarweeds here. *Dubautia* has been regarded previously as belonging to Senecioneae (Hillebrand, 1888) or Heliantheae, subtribe Galinsoginae (Hoffmann, 1890). Keck (1936) suggests a relationship of *Dubautia* to two senecionean genera of the Juan Fernandez Islands, *Robinsonia* and *Rhetinodendron*. These latter genera, which will be considered in later studies, seem well placed in Senecioneae, and the writer is skeptical of their relationship to *Dubautia*. Steyermark (1937) has suggested the possibility that *Grindelia* and *Eastwoodia* may not belong to Astereae, in which they have traditionally been placed, but rather are helianthoid. Representatives of these genera have therefore been included. In an earlier study (Carlquist, 1957b) the writer placed *Fitchia* in a new subtribe of Heliantheae, and included *Oparanthus* in the subtribe Petrobiinae. The monotypic genus *Venegazia* seems to the writer best placed

in Heliantheae, subtribe Coreopsidinae, rather than in the tribe Helenieae, although it lacks certain key characters of Coreopsidinae. With the above exceptions, the system of Hoffmann (1890) for the tribal and subtribal arrangement of genera has been followed.

MATERIALS AND METHODS

Wood samples of trunks, or basal portions of larger branches of shrubs, were used almost exclusively. Twigs, approximately three-to five-years old, were used for *Fitchia mangarevensis*, *Dubautia paleata*, *D. linearis*, *Lecocarpus pinnatifidus*, *Scalesia pedunculata*, and *Eastwoodia elegans*. Obviously, with herbaceous species, the amount of wood available was limited, although the basal portion of the stem was utilized in each instance. Wood samples were available either dried or preserved in formalin-acetic acid-alcohol. Dried wood samples were boiled and immersed in commercial-strength hydrofluoric acid for periods varying according to the hardness of the wood. Liquid-preserved wood samples were immersed directly in hydrofluoric acid. Most woods were sectioned on a sliding microtome, although for smaller samples, embedding in paraffin and sectioning on a rotary microtome proved more convenient. Safranin was used as a stain in all instances. Mordanting with tannic acid-ferric chloride proved necessary for adequate staining of wood samples which received only a short treatment with hydrofluoric acid. Duplicates of slides used in this study have been distributed to the wood slide collections of the Yale School of Forestry and of Harvard University. For convenience in referring to growth ring phenomena, all photographs of transverse sections in this paper show the earliest-formed elements below.

ANATOMICAL DESCRIPTIONS

The features of wood anatomy in which significant variation was observed are summarized in table 1. In the second column, the source of each specimen is listed, giving either the Yale (Y) or Harvard (H) accession number or the herbarium specimen documenting a sample or from

which a sample was taken. The herbaria in which these specimens are located are indicated by abbreviations in accordance with Lanjouw and Stafleu, *Index Herbariorum*, ed. 3.

In table 1, the symbol + indicates presence of the indicated character, whereas absence of a symbol indicates that the character does not occur. For certain characters, letter symbols are used to give specific information about the mode of occurrence. The type of apotracheal parenchyma present is indicated by *b*, for bands extending around much or most of the stem, and *pb*, for partial bands which extend the distance between two rays or less. Similarly, if storied structure is present, the elements which are storied are indicated by *f*, fibers, *p*, apotracheal parenchyma, *t*, vascular tracheids, and *v*, vessel elements (if they conformed to the storied pattern of other elements). In no instance were storied rays observed. A figure for average height of uniseriate rays was entered if an appreciable number occurred, i.e., more than about 5 per sq. cm. of a tangential section. The character "rays thin-walled, unlignified" is somewhat arbitrary, although it was apparent that in some taxa, unlignified ray cells, which were sectioned successfully only in paraffin on account of their delicacy, were present (compare fig. 12 and 27 for these techniques). The presence of such rays is indicated by +. Where more than one species of a genus was studied, and little difference could be noted between the two, one is included in the table, and the other mentioned only in the text. Further discussion of characters used in the table is included under the headings below.

VESSELS

Size and shape.—As indicated by Bailey (1957) Compositae is among those families in which the gamut of specialization in vessel elements is relatively small, since the structure of vessel elements is advanced throughout the family. Because of this, as he states, and because differences in growth habit or other features may alter vessel element length or end wall angle, the local variations within the family in these characters may override, and thus negate,

the applicability here of those trends of specialization established in dicotyledons as a whole (e.g., Bailey and Tupper, 1918). Moreover, the significance of such figures in this study is limited by the fact that variations within a plant could not be compared on account of the varied sources of wood samples. Certain features of vessels, therefore, have been treated here statistically because they offer taxonomic characters, not because they are subject to detailed phylogenetic interpretation. It is evident, for example, that vessel element length is much greater in *Verbesina lanata* than in another member of the same subtribe, as *Flourensia cernua*. A glance at the figures for vessel element length reveals considerable variation of this nature, although overall conclusions are not warranted. It is of interest, however, that very short vessel elements occur in species presumed by taxonomists to be highly advanced (e.g., *Hymenoclea salsola*) as well as in some herbaceous taxa (e.g., *Argyroxiphium*; fig. 13–14). Similar considerations obtain for vessel width. In Heliantheae, as in Mutisieae, the great variation in vessel width within a single transverse section prevents an average figure from being meaningful. In addition, the presence of vascular tracheids (which cannot always be distinguished from vessels in a transection) in a number of species results in a gradation between wider vessels, narrow vessels, and vascular tracheids, which are usually as narrow or narrower than the smallest vessel elements. Certain outstanding characteristics, however, are revealed by measuring the widest vessel seen in a slide. To a certain extent, this is a reflection of the overall width of vessels in a given species. For example, the fact that the widest vessels of *Dubautia Menziesii* (fig. 6) are only half as wide as those of *D. Knudsenii* (fig. 1) is correlated with other differences between these species. Likewise, the vessels of *Fitchia speciosa*, which are wider than those of other species, are correlated with larger cell size in other parts of plants of that species, a fact observed qualitatively in an earlier study (Carlquist, 1957b). Many of the herbaceous species studied have narrower maximum vessel diameters than most of the woody species. Relatively wide vessels

Table 1. CHARACTERS IN WOOD ANATOMY OF HELIANTHEAE

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NAME	WOOD COLLECTION OR HERBARIUM NO.	DIAMETER WIDEST VESSEL (μ)	VESSEL ELEMENT LENGTH, AVERAGE (μ)	NO. VESSELS PER GROUP, AVERAGE	VESSELS WITH HELICAL STRIAE	VESSEL PITTING SCALARIFORM-TRANSITIONAL	VASCULAR TRACHEIDS	APOTRACHEAL PARENCHYMA	STORIED ELEMENTS	RAYS THIN-WALLED, UNLIGNIFIED	UNISERIATE RAY HEIGHT, AVERAGE (μ)	MULTISERIATE RAY HEIGHT, AVERAGE (MM.)	RAY CELLS ISODIAMETRIC TO PROCUMBENT	RAY CELLS ISODIAMETRIC TO ERECT
Fitchiinae:														
Fitchia cuneata J. W. Moore	Moore 655 (BISH)	90	318	1.75				b,pb	f,p			1.9		+
F. mangarevensis F. Brown	Quayle 463 (BISH)	78	250	2.36				pb	f,p			1.8		+
F. nutans Hook. f.	Y-26499	84	330	1.73				b,pb	f,p			1.7		+
F. rapensis F. Brown	St. John 15282 (BISH)	96	270	1.76				b,pb	f,p			.7		+
F. speciosa Cheeseman	Carlquist H29 (UC)	120	360	2.00				b	f			2.0		+
Petrobiinae:														
Oparanthus rapensis (F. Brown) Sherff	Y-24310	100	350	2.07					f			1.5		+
Coreopsidinae:														
Bidens hendersonensis Sherff	St. John 15155 (BISH)	100	300	2.13					f			1.9		+
Coreopsis gigantea (Kell.) Hall	Balls 18809 (RSA)	60	210	2.24	+					+	130	2.9		+
Narvalina domingensis Cass.	Leonard 13402 (UC)	66	470	3.84								7		+
Venegazia carpesioides DC.	Carlquist 401 (RSA)	72	240	2.20				?	f		80	3.4		+
Verbesininae:														
Borrichia arborescens (L.) DC.	Stern & Brizicky 232 (Y)	83	183	1.84								1.2	+	+
B. frutescens (L.) DC.	Stern & Brizicky 327 (Y)	77	218	1.52								3.0	+	+
Encelia californica Nutt.	Balls 18822 (RSA)	72	178	2.64			+	b,pb	f,p,t,v		74	1.1	+	
E. farinosa Gray	Balls 18906 (RSA)	108	123	1.60							119	.9	+	
Flourensia cernua DC.	Y-26675	90	121	2.36	+		+	b,pb	p,t,v		190	.7	+	
Helianthus annuus L.	Carlquist 419 (RSA)	122	192	2.60							255	1.4		+
Lipochaeta lavarum (Gaud.) DC.	Y-26675	78	222	2.36								3.3		+
Montanoa bibiscifolia C.Koch	Skutch 1981 (GH)	148	270	1.48							170	1.7		+
Oyedaea boliviana Britton	Metcalf 30652 (UC)	108	239	1.28							187	2.4		+
Perymenium strigillosum R.&G.	H-1523	228	297	1.47		+		b			90	.7		+
Podachaenium eminens (Lag.) Schultz	Turner 238 (RSA)	123	312	1.48	+						133	1.0		+
Scalesia pedunculata Hook. f.	Stewart 687 (CAS)	48	246	1.48							102	.6		+
Verbesina lanata Greenman	Skutch 1778 (GH)	132	426	1.57	+				f		284	.6	+	+
V. sublobata Benth.	Skutch 1982 (GH)	96	402	1.37							240	2.7	+	+
V. vicina Blake	H-1535	84	378	1.47	+						228	1.0		+
Viguiera laciniata Gray	Balls 18838 (RSA)	102	137	3.04				p,b			90	.6	+	
Zexmenia frutescens (Mill.) Blake	Y-10035	100	295	1.18								2.8	+	+

Table 1—Continued

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NAME	WOOD COLLECTION OR HERBARIUM NO.	DIAMETER WIDEST VESSEL (μ)	VESSEL ELEMENT LENGTH, AVERAGE (μ)	NO. VESSELS PER GROUP, AVERAGE	VESSELS WITH HELICAL STRIAE	VESSEL PITTING SCALARIFORM-TRANSITIONAL	VASCULAR TRACHEIDS	APOTRACHEAL PARENCHYMA	STORIED ELEMENTS	RAYS THIN-WALLED, UNLIGNIFIED	UNISERIATE RAY HEIGHT, AVERAGE (μ)	MULTISERIATE RAY HEIGHT, AVERAGE (MM.)	RAY CELLS ISODIAMETRIC TO PROCUMBENT	RAY CELLS ISODIAMETRIC TO ERECT
Madiinae:														
Argyroxiphium Caliginii Forbes	Carlquist H28 (UC)	47	138	2.24			+	b,pb	p,t,v	+		1.0	+	+
A. Grayanum (Hillebr.) Degener	Carlquist H27 (UC)	53	207	3.92			+	pb		+		1.2	+	+
A. sandwichense DC.	Carlquist H19 (UC)	29	114	6.05			+			+		.8	+	+
Blepharizonia plumosa (Kell.) Greene	Carlquist 418 (RSA)	67	153	2.00			+				158	.5		+
Dubautia Knudsenii Hillebr.	Carlquist H15 (UC)	108	413	1.24					f		130	2.8		+
D. laxa H.&A.	Carlquist H12 (UC)	94	306	2.24				b	f,p,v		95	.8		+
D. linearis (Gaud.) Keck	Rock 8123 (BISH)	71	196	1.77				pb	p			3.3		+
D. Menziesii (Gray) Keck	Carlquist H17 (UC)	53	223	4.55			+	pb	f,p,t,v			1.7		+
D. microcephala Skottsberg	Carlquist H14 (UC)	77	336	1.70				b	f,p		210	1.1		+
D. paleata Gray	Forbes 914K (BISH)	61	339	1.65					f			3.3		+
D. plantaginea Gaud.	Carlquist H20B (UC)	65	236	4.65			+	b,pb	f,p,t,v			2.0		+
D. railliardioides Hillebr.	Carlquist H16 (UC)	118	301	1.55							117	1.8		+
Hemizonia Minthornii Jepson	Carlquist 407 (RSA)	71	133	1.60			+	b,pb	p,t,v			.7		+
Madia sativa Mol.	Carlquist 403 (RSA)	77	206	1.65							144	.3		+
Wilkesia gymnoxiphium Gray	Carlquist H10 (UC)	83	336	1.77	+						212	1.6		+
Galinsoginae:														
Bebbia atriplicifolia (Gray) Greene	Bittler VII-28-1957 (RSA)	124	218	2.16					f,v			1.7	+	+
Melampodinae:														
Espeletia Hartwegiana Cuatr.	Y-44409	88	306	1.27	+							1.7	+	+
E. incana Cuatr.	Langenheim 3511 (MIN)	71	201	2.32	+				f	+		.9	+	+
E. pleiochasia Cuatr.	Langenheim 3500 (MIN)	136	282	1.56	+				f,v		133	1.3	+	+
E. Uribei Cuatr.	Langenheim 3677 (MIN)	83	192	1.85							97	1.2	+	+
Lecocarpus pinnatifidus Dec.	Stewart 639 (GH)	61	217	1.80	+							1.0		+
Parthenium argentatum Gray	Y-40997	41	242	2.95	+		+			+	267	.2	+	
Millerinae:														
Clibadium oligandrum Blake	Skutch 1127 (GH)	142	389	1.45			+	b	f			2.0		+
Lagasceinae:														
Coulterella capitata Vasey & Rose	Bittler VII-28-1957 (RSA)	59	218	1.68				b,pb	v,p			1.3		+
Ambrosinae:														
Hymenoclea salsola T.&G.	Munz 17405 (RSA)	100	106	1.70	+		+			+		.5	+	
Grindelia stricta DC. var. *procumbens* (Steyerm.) Keck	Balls 19476 (RSA)	59	147	3.50				b				1.5	+	
Eastwoodia elegans Bge.	Peirson 8405 (RSA)	53	136	2.76	+		+		t,v		135	.7	+	+

were considered to be less specialized than very narrow vessels in the writer's study of Mutisieae (Carlquist, 1957a). This may also be true in Heliantheae. Excessively wide vessels (e.g., *Perymenium strigillosum*, fig. 20) may also represent a derived condition. Webber (1936), in her study of desert and chaparral shrubs, including some Compositae, has noted a correlation of arid habitat with diminished vessel diameter and increased vessel element length. This correlation does not appear to hold for Heliantheae on the basis of the present study.

No figure was given for the number of vessels per sq. mm. because this figure is to some extent correlated with vessel width and the nature of vessel grouping, and did not appear to provide as distinctive expressions of the variation pattern as did these figures. The tendency of vessels in some species to appear angular in transection is not included in the table. This tendency, in Compositae, is probably an expression of specialization rather than primitiveness, a possibility noted by Bailey (1957). Such vessels are shown by several taxa studied, such as *Dubautia Menziesii* (fig. 6) and *Argyroxiphium Caliginii* (fig. 12).

Vessel arrangement.—Tippo (1946) and others have considered that solitary vessels precede aggregations of vessels phylogenetically. Such a correlation appeared justifiable in Heliantheae, so that a figure, the average number of vessels per group (vessels actually in contact with each other) has been calculated. Vascular tracheids were, as much as possible, excluded from this figure, although it is not possible to distinguish a small vessel from a vascular tracheid in transection. This figure may be misleading if vascular tracheids are abundant and vessels rare, therefore. In *Hemizonia Minthornii* (fig. 15), for example, relatively few vessel elements occur in groups, although numerous vascular tracheids are associated with them; had vascular tracheids been included the figure for this species would be extremely high, rather than low. In species having few or no vascular tracheids, however, the figure is a reliable indication of the tendency toward vessel aggregation. Notable differences in

this respect are revealed, so that if we compare three species of *Dubautia*, *D. Knudsenii* (fig. 1), *D. laxa* (fig. 3), and *D. Menziesii*, (fig. 6) we observe marked increase in vessel aggregation within this genus, an interpretation aided by correlation with other wood characters. In Heliantheae at large, the correlation of such characters would seem to justify the generalization that the solitary condition is primitive and larger groupings advanced.

Aggregation of vessels, where present, is usually in the form of groups spread almost equally in tangential and radial directions. Exceptions to this are found in *Narvalina domingensis*, *Venegazia carpesioides*, *Helianthus annuus*, *Lipochaeta lavarum*, *Bebbia atriplicifolia*, and *Grindelia stricta*, in which radial rows of vessels are frequent.

Ring porosity.—According to the Committee on Nomenclature of the International Association of Wood Anatomists (1933), ring porosity includes differences in portions of a wood in number or size of pores. "Pore" is construed as including vascular tracheids. By virtue of this definition, a number of helianthoid woods can be described as ring porous, or having a ring-porous tendency. For example, *Hemizonia Minthornii* (fig. 15) shows bands of thick-walled fibers (fig. 17) alternating with bands in which vascular tracheids and parenchyma predominated (fig. 16). The size of vessels in these two types of bands is not appreciably different. This situation is also present in *Grindelia stricta* and *Eastwoodia elegans*. In *Flourensia cernua* (Carlquist, 1957b) and *Hemizonia clementina*, vessels in the vascular tracheid-parenchyma bands tend to be smaller in diameter. *Clibadium oligandrum* (fig. 25) has, at intervals, bands consisting of vascular tracheids and strand parenchyma; the size of vessel elements, however, is approximately the same from one part of a growth ring to another. In *Blepharizonia plumosa*, a band of vascular tracheids terminates the growth at the end of its growing season. This condition is reminiscent of *Trixis californica* (Carlquist, 1957a), in which short bands consisting of vascular tracheids are intercalated into the wood. *Parthenium argentatum* and *Hymenoclea salsola*

(fig. 27) have smaller vessels and vascular tracheids at the end of a growth ring. Decrease in diameter of fibers toward the end of a growth ring is also seen in *Hymenoclea*. In other taxa which lack vascular tracheids, the situation is simpler. *Perymenium strigillosum* (fig. 20) has large vessels and numerous apotracheal parenchyma cells at the beginning of a growth ring, small vessels surrounded by libriform fibers at the end of a growth ring. *Venegazia carpesioides* has no apotracheal parenchyma, but shows marked increase in vessel and libriform fiber diameter at the beginning of a growth ring. Slight tendency toward ring porosity in *Montanoa hibiscifolia* is indicated by bands of narrower vessels. As with Mutisieae, ring porosity is best considered an advanced character as compared with the diffuse porous condition, in agreement with Tippo (1946) and others. This interpretation is supported by the association with other advanced features in the woods mentioned.

Vascular tracheids.—Table 1 indicates the large number of taxa among Heliantheae studied which possess vascular tracheids. As indicated above, such elements may occur in a certain portion of a growth ring. In other taxa, which lack ring porosity, they are associated with groups of vessels. *Dubautia Menziesii* (fig. 6–7), *Encelia californica* (fig. 22–23), *Argyroxiphium Caliginii* (fig. 12–13) and other species of *Argyroxiphium* show this condition. The presence of vascular tracheids in Heliantheae, as in Mutisieae, is best interpreted as a specialized character, in agreement with their designation as "imperfect or degenerate vessel members" by the Committee on Nomenclature of the International Association of Wood Anatomists (1933). Their occurrence in such a large number of Heliantheae is interesting, particularly in view of their presence in subtribes presumed to be more advanced (Madiinae, Millerinae, Ambrosiinae). Although two genera of Verbesininae possess them, they are lacking in the Fitchiinae, Petrobiinae, and Coreopsidinae examined.

Perforation plates.—Although perforation plates of vessel elements are typically simple in Compositae, numerous thin
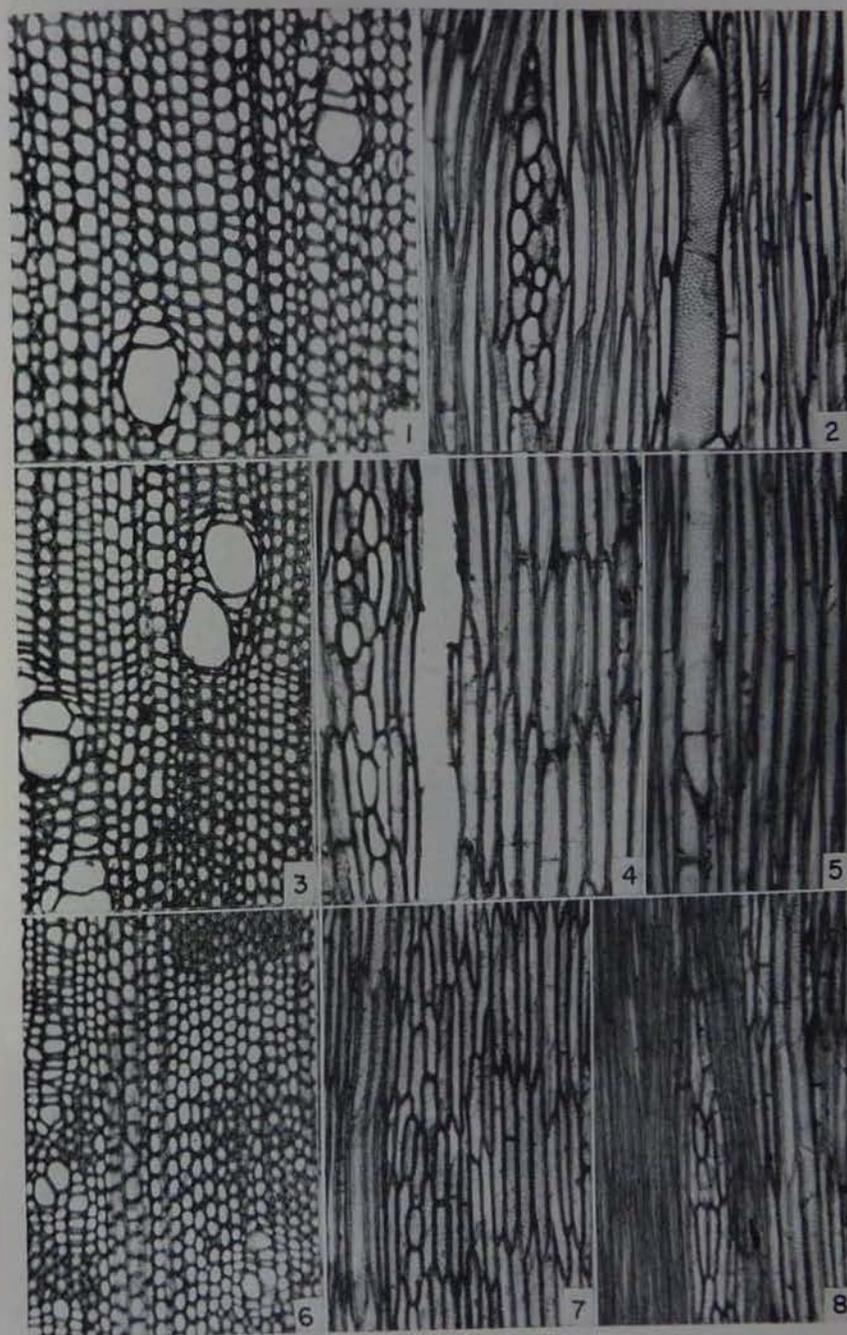

Fig. 1–8: Wood sections of *Dubautia.*—Fig. 1–2. *D. Knudsenii*, transverse, tangential sections.—Fig. 3–5. *D. laxa.*—Fig. 3. tranverse section.—Fig. 4. Tangential section through "apotracheal parenchyma."—Fig. 5. Tangential section through fibers.—Fig. 6–8. *D.*
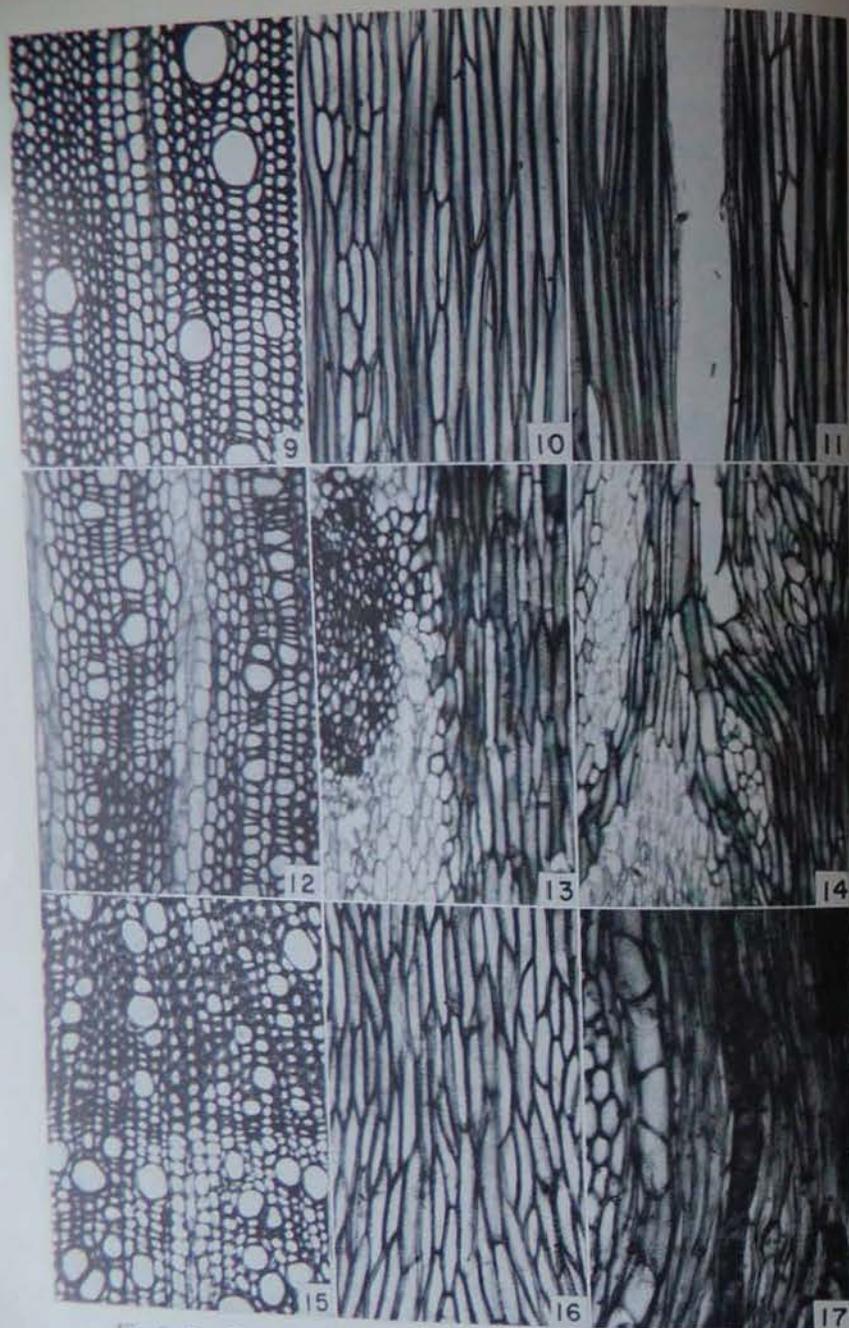
Fig. 9-17.—Fig. 9-11. *Wilkesia gymnoxiphium.*—Fig. 9. Transverse section.—Fig. 10. Tangential section through a zone of shorter fibers, showing portions of two rays.—Fig. 11. Tangential section through a zone of longer fibers.—Fig. 12-14. *Argyroxiphium Caliginii.*—Fig. 12. Transverse section.—Fig. 13. Tangential section, showing foliar ray with sclerenchyma around leaf trace (left) and storied vascular tracheids and...

bars, usually scalariform with some forking of bars, may be seen on occasional perforation plates in woods of Compositae (Metcalfe and Chalk, 1950). Such perforation plates have been figured for *Helianthus* by Smith (1935). Other Heliantheae in which they may be seen include *Fitchia speciosa* (Carlquist, 1957b), *Venegazia carpesioides*, *Verbesina lanata*, and *Espeletia pleiochasia*. It seems reasonable to suppose that these structures may occur in a number of taxa. Their total absence is difficult to demonstrate, because in species in which they occur, only an occasional vessel element can be shown to possess them.

Lateral wall pitting.—Circular bordered pits with elliptical apertures, alternately arranged, are characteristic of vessel walls of Compositae. Such pits may be fewer in number on vessel walls in contact with parenchyma cells. Typical intervascular pitting is figured here for *Dubautia Knudsenii* (fig. 2). In some taxa, bordered pits may be very small and numerous *(Verbesina lanata*, Carlquist, 1957b) or very large and crowded *(Hymenoclea salsola*, fig. 31). Both of these conditions are probably specializations. In some taxa, there is also a tendency toward the production of vessels with scalariform or scalariform-transitional pitting. Although such pitting is not infrequently found on walls of vessels facing parenchyma, certain species characteristically show this type of pitting on all walls, and it is this latter condition which is indicated by + in table 1. Among the species studied which show this are *Coreopsis gigantea*, *Espeletia incana*, *E. pleiochasia* (fig. 19), *E. Hartwegii*, and *Lecocarpus pinnatifidus*. Some tendency toward this type of pitting is shown by *Perymenium strigillosum*. Such pitting has been reported for *Chimantaea mirabilis* (Carlquist, 1957a), a "megaphytic" plant with habit similar to that of *Espeletia* or *Coreopsis gigantea*. As in Mutisieae, this condition seems best interpreted as a retention of metaxylem pitting types throughout the life of the plant. Although *Lecocarpus* is not a megaphyte, the occurrence of this type of pitting in plants of the *Espeletia* habit may indicate that this is one aspect of their growth form, in which a leaf-rosette com-

parable to that of herbs seems to be a protracted juvenile stage.

The occurrence of helical striations in vessel walls of Heliantheae has been reported previously for *Flourensia cernua* (Metcalfe and Chalk, 1950; Carlquist, 1957b). In Mutisieae, the writer suggested that these striations originated as grooves, some of which connect pit apertures (Carlquist, 1957a). A similar interpretation appears possible in Heliantheae, as the photographs of *Wilkesia* (fig. 29) and *Hymenoclea* (fig. 30–31) may suggest. In *Wilkesia*, *Podachaenium*, *Verbesina lanata* and *V. vicina*, these striae appear as numerous very fine lines on vessel walls where few pits occur. In *Flourensia*, *Parthenium*, *Hymenoclea*, and *Eastwoodia* (fig. 28), however, such striae are particularly characteristic of smaller vessels, where they cover the walls, and of vascular tracheids. Some of the larger vessels in these taxa may lack them. In larger vessels, the number of helices is the same or twice as many as the number of helices in which pit apertures (which are connected by the grooves) appear to be arranged. In smaller vessels and vascular tracheids, the number of helical grooves is much greater than the number of helices in which the pit apertures appear to occur. On account of the fact that these striations in all instances appear to be a form of relief in the secondary wall, rather than superimposed thickenings, the term "helical thickening" is not applied to them here. In certain Mutisieae, such as *Flotovia* (Carlquist, 1957a), such thickenings definitely are present, although they may have originated through exaggeration of the type of striations seen in *Flourensia* or *Wilkesia*. As in Mutisieae, the writer believes that these types of vessel wall relief are best interpreted as specializations, in agreement with Frost (1931) and Moseley (1948). In the species in which they are most prominently represented, helical striations occur in association with vascular tracheids, storied wood structure, and other characters which appear to be advanced.

LIBRIFORM FIBERS

Heliantheae have no cells which could be called true tracheids, and the division between vessel elements and libriform wood fibers is quite sharp. Considerable variation in wall-thickness of fibers occurs. Although most species have moderately thick-walled fibers (e.g., *Espeletia pleiochasia*, fig. 18), some, such as *Coreposis gigantea* and *Grindelia stricta*, have very thin-walled, wide fibers. It may be noted that these latter species are herbaceous. Variation in fiber thickness according to growth rings has been discussed above in relation to ring porosity. Consideration is given to differentiation of fibers in respect to length, morphology, and distribution of different types in wood below in connection with vertical wood parenchyma. In *Wilkesia* (fig. 10–11), for example, tangential sections of different portions of the xylem reveal differences in fiber length. Septate fibers were observed in *Zexmenia frutescens*, *Fitchia* spp. (Carlquist, 1957b), and are very frequent in *Lipochaeta lavarum*.

VERTICAL PARENCHYMA

Vertical parenchyma in Heliantheae woods is of two basic types: those parenchyma cells which immediately surround vessels, and those which, in some species, occur in tangential bands. The former type, which is present as scanty vasicentric parenchyma, is basically found in all of the species considered, although the mode of occurrence may be altered by larger groupings of vessels or by the fact that the parenchyma is present in conjunction with vascular tracheids. Vessels or vessel groups are usually jacketed only by a single layer of parenchyma cells; this layer is often incomplete, so that in places a vessel element abuts on libriform fibers. In some species (e.g., *Coulterella capitata*, fig. 24), more than one cell layer may be present in places. Where bands of apotracheal parenchyma contact vessels, however, some difficulty may be encountered in differentiating these from the vasicentric parenchyma, although the two types are usually different in size and morphology. Vasicentric parenchyma cells are typically very narrow and

as long as the adjacent vessel element, although they may be divided into strands of two or three cells (fig. 2, 19, 21). In *Clibadium oligandrum* (fig. 26), the parenchyma cells which occur in bands together with vascular tracheids are present in strands of three to five cells.

The nature and interpretation of apotracheal parenchyma constituted one of the most important problems in analysis of helianthoid woods. As indicated by table 1, a number of species have apotracheal parenchyma either in the form of tangential bands of indefinite extent, or of short bands spanning the space, or part of the space, between two rays, or in both forms. Such parenchyma cells are distinguishable from libriform fibers by their width, wall thickness, shorter length, blunter ends, and (as indicated by liquid-preserved material of some species, such as *Encelia californica*) living contents. Such parenchyma cells may be the same height as short vessels or vascular tracheids (fig. 16). Occurrence of apotracheal parenchyma is clearly demonstrable in woods lacking vascular tracheids, such as *Fitchia, Perymenium strigillosum, Dubautia microcephala*, and *Coulterella*. In the remaining instances, vascular tracheids are present in or adjacent to these bands (*Argyroxiphium Caliginii*, fig. 13; *Hemizonia Minthornii*, fig. 16) so that in a sense, at least some of these cells could be said to be paratracheal. The bands of parenchyma are basically the same in both instances, however, so that they can be considered together.

Although uncertain about the interpretation of these bands of parenchyma in earlier studies (Carlquist, 1957a, 1957b), the writer now believes that such cells are an indication of phylogenetic advancement. This interpretation is based on the fact that they are present in woods having several seemingly advanced features (vascular tracheids, storied wood structure, numerous vessels per group, etc.) and on comparison of species in genera which have parenchyma bands only in certain species. *Dubautia* is the genus in which material permitted this comparison to be made most clearly. In *Dubautia Knudsenii* (fig. 1–2), *D. paleata*, and *D. railliardioides*, which seem less specialized on the
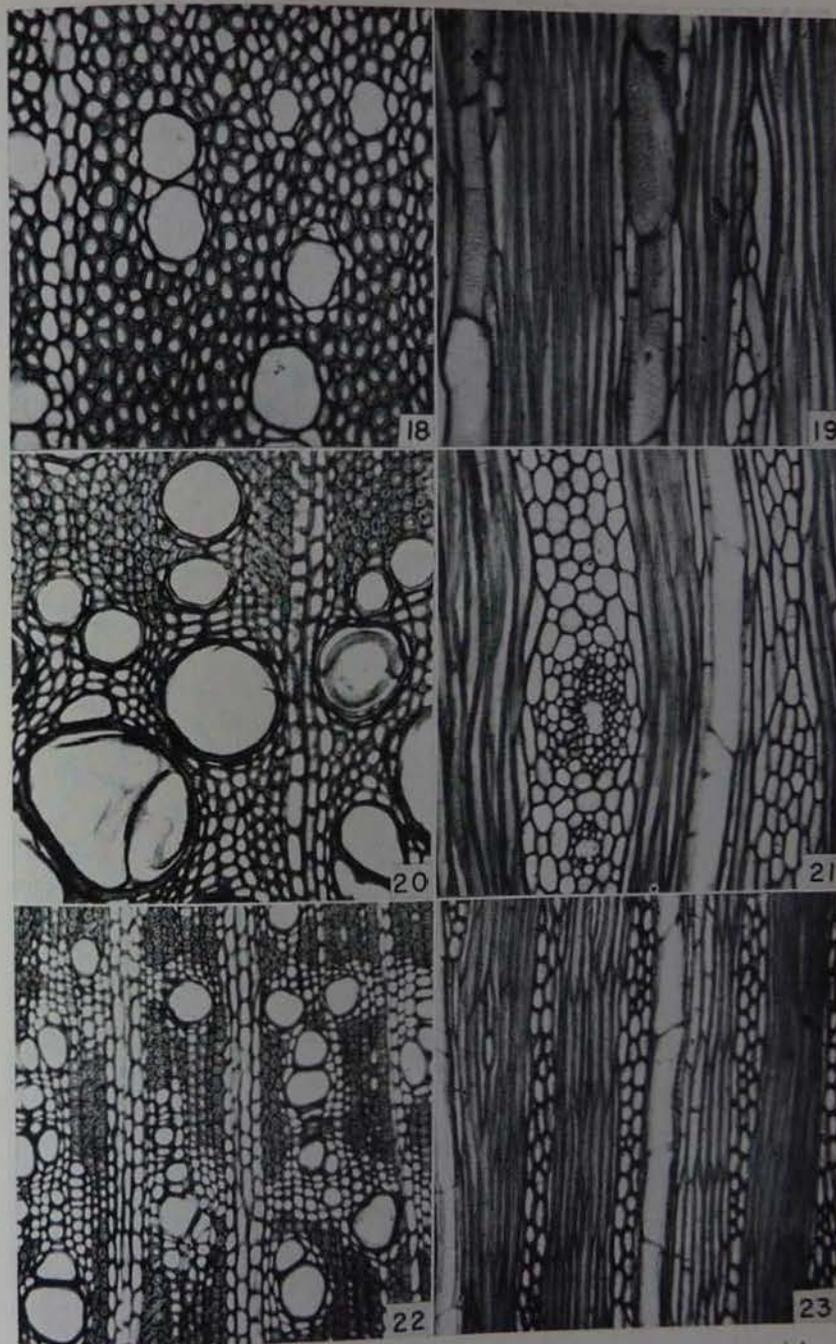

Fig. 18–23.—Fig. 18–19. *Espeletia pleiochasia*, transverse, tangential sections.—Fig. 20. *Perymenium strigillosum*, transverse section.—Fig. 21. *Bebbia atriplicifolia*, tangential section.—Fig. 22–23. *Encelia californica.*—Fig. 22. Transverse section, showing two bands of apo-[...] and below center).—Fig. 23. Tangential
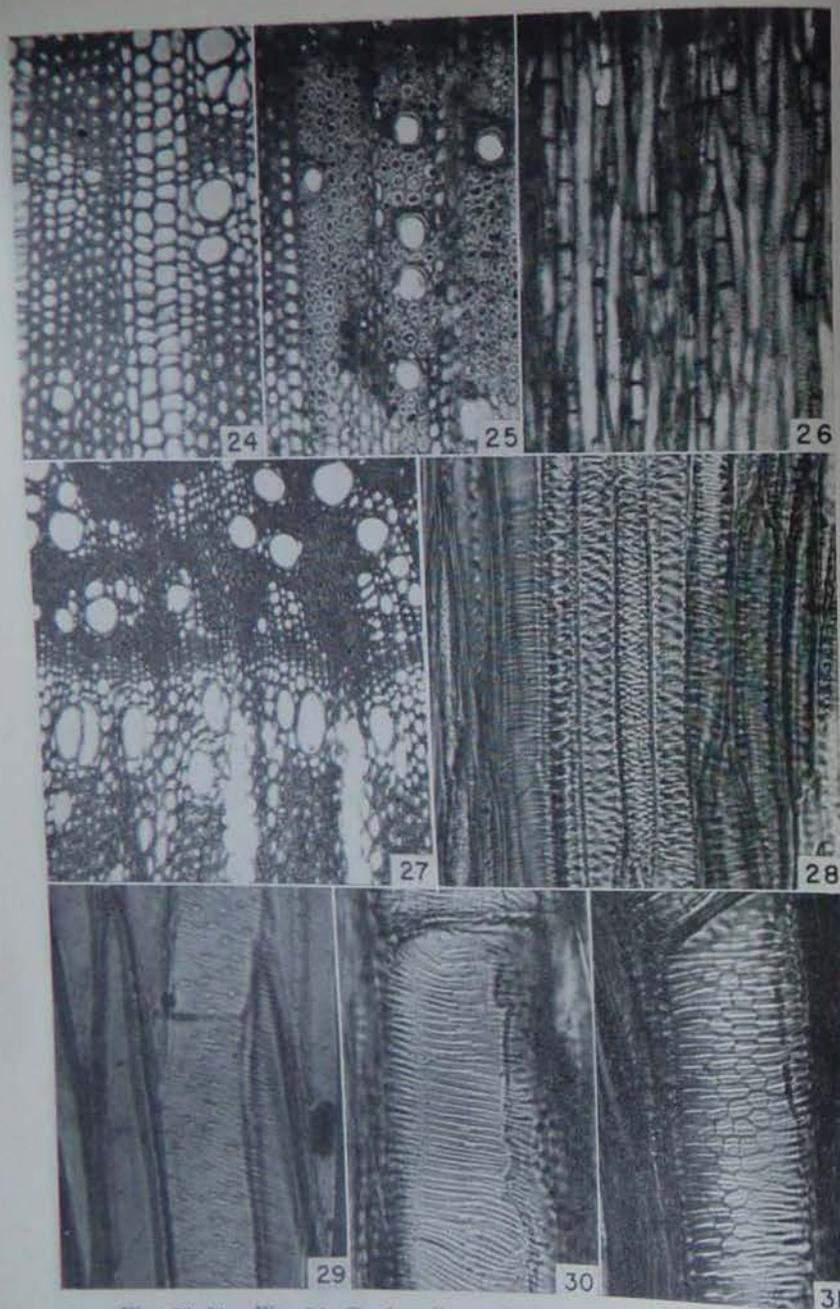
Fig. 24–31.—Fig. 24. *Coulterella capitata*, transverse section, showing apotracheal parenchyma band above center.—Fig. 25. *Borrichia arborescens*, transverse section, showing occlusion of elements by resin.—Fig. 26. *Clibadium oligandrum*, tangential section through a band of vascular tracheids and parenchyma.—Fig. 27. *Hymenoclea salsola*, transverse section; early wood below; soft-walled cells in two rays below have been lost.—Fig. 28. *Eastwoodia* (?) [...]

basis of gross morphology and the lack of particular specializations in wood characters, as well as stem and leaf anatomy, the fibers are relatively uniform in width and length, and more obscurely storied than in the other species. In *D. laxa* (fig. 3–5), there are bands of "fibers" (fig. 4) which are shorter, wider, more frequently septate, and have much more rounded ends than fibers in other portions of the wood (fig. 5). These cells are tentatively termed "apotracheal parenchyma" here. The greater number of vessels per group and the gross morphology of the involucre suggest that *D. laxa* is more advanced than the above species. Like *Dubautia laxa*, a certain degree of differentiation may be seen in *Wilkesia gymnoxiphium*, although the shorter fibers are not considered as "apotracheal parenchyma" in that genus. *Dubautia Menziesii* (fig. 6–8), an alpine shrub specialized in leaf, stem, involucre characters, shows marked differentiation into cells which must definitely be termed apotracheal parenchyma (fig. 7) and libriform wood fibers (fig. 8). The parenchyma cells are very short, wide, thin-walled, and often subdivided by a definite wall rather than inconspicuously septate. The fibers, on the contrary, are long, narrow, thick-walled, and non-septate. *Dubautia Menziesii* shows advanced wood structure in the very narrow vessels, which are numerous in each vessel group, the presence of numerous vascular tracheids and a prominently storied condition. If the above comparisons are valid, it would appear that bands of apotracheal parenchyma have arisen in Heliantheae by differentiation of libriform wood fibers.

VASCULAR RAYS

The Heliantheae studied show a remarkable paucity of uniseriate rays. In only two species, *Verbesina vicina* and *Madia sativa*, could uniseriate rays be designated as frequent. In *Madia sativa*, they are almost as numerous as multiseriate rays. As can be seen in table 1, they are absent in many species. Where present, they are often only one or two cells high, and vertically elongate so that they resemble fibers in some instances. Absence of uniseriate rays,

according to Barghoorn (1941), is phylogenetically advanced. This process he envisions as resulting from elongation of ray initials to form fusiform initials in the cambium, with the resultant products consisting of libriform fibers instead of uniseriate rays. This interpretation seemed tenable in the writer's study of Mutisieae, and the present data do not seem opposed to this thesis. It is of interest, however, to contrast Heliantheae with Mutisieae, in which uniseriate rays were found in all genera except *Chuquiragua* (Carlquist, 1957a). The helianthoid woods in which uniseriate rays were found do not seem particularly specialized in comparison with woods of other members of the tribe.

Multiseriate rays in Heliantheae vary greatly in width and height, and in the nature of cells which compose them. Measurements of ray height could only be an estimate in many instances, because variation within a single tangential section was often extreme. Some species, such as *Coreopsis gigantea, Narvalina domingensis, Borrichia frutescens, Lipochaeta lavarum, Verbesina sublobata*, and *Dubautia linearis*, have extremely high multiseriate rays, almost indefinite in height. None of these could be called truly woody species. Relatively short, discrete multiseriate rays were observed in *Fitchia rapensis, Scalesia pedunculata, Madia sativa, Parthenium argentatum*, and *Hymenoclea salsola*. These species are of such varied habit that no correlation between habit and ray height seems evident. Differences in ray height, however, may be useful as taxonomic characters.

In Mutisieae, the writer observed that ray cells varied between isodiametric and procumbent or between isodiametric and erect, and that in only a few species could both types of cells be found. The occurrence of both procumbent and erect cells in a ray is more frequent in species of Heliantheae, as table 1 indicates. Where this occurs, corresponding to the definition of "Heterogeneous II" by Kribs (1935), the procumbent cells occupy a central position in the ray. Rays consisting of cells varying between isodiametric and procumbent occur in *Encelia farinosa, Flourensia cernua, Viguiera laciniata, Parthenium argentatum, Hymeno-*

clea salsola, and *Grindelia stricta*. Rays in these species would, therefore, correspond most nearly to the definition Homogeneous II by Kribs (1935). The designation of this condition as derived by Kribs seems acceptable in view of the specializations seen in most of the species listed. Most of the Heliantheae studied, however, have ray cells varying between isodiametric and erect. In some species, such as *Wilkesia gymnoxiphium* (fig. 10–11), *Dubautia Menziesii* (fig. 8), *D. paleata*, and *Espeletia pleiochasia* (fig. 19), certain ray cells are nearly as high as the libriform fibers to which they are adjacent. In these species, in fact, it is sometimes difficult to define the precise limits of a ray. Figures 6, 9, and 18 show that both typical thick-walled fibers and vertically elongate thin-walled cells abut on rays, so that a ray may be said to be clothed with parenchyma cells transitional to libriform fibers. The widespread presence of erect ray cells, and the occurrence of rays with marked vertical elongation of cells, such as those just described, are probably phenomena referable to Barghoorn's (1941) statement that, "Extensive vertical elongation of ray initials to produce high-celled multiseriate or uniseriate rays is phylogenetic as well as ontogenetic and is frequently correlated with increasing structural specialization, reduction in cambial activity, and a tendency toward the loss of rays." Although decrease in cambial activity does not seem characteristic of many of the Heliantheae studied which have erect ray cells, and a near ray-less condition was seen in only one species (*Adenothamnus validus*, isotype, GH), the increasing vertical elongation of ray cells may well be an indication of a specialized condition, as Barghoorn suggests.

Variation in cell wall thickness in rays of Heliantheae is quite wide. Ray cells in *Flourensia cernua* are extremely thick-walled, as noted by Metcalfe and Chalk (1950). In contrast, very thin, unlignified walls occur in a number of Heliantheae, indicated in table 1, such as *Argyroxiphium Caliginii* (fig. 12–14) and *Hymenoclea salsola* (fig. 27). With the exception of *Parthenium argentatum* and *Hymenoclea salsola*, which are shrubs possibly of herbaceous origin,

all of the species with such ray cells are perennial herbs. The wood rays of *Argyroxiphium* (fig. 14) are distinguishable from the foliar rays in that species in that they are much smaller and slightly more thick-walled. Very thin-walled rays, then, seem to indicate an herbaceous habit of growth. In a similar manner, the rather thin-walled ray cells, very wide rays, and correspondingly narrow fascicular areas of *Lipochaeta lavarum* suggest a basically herbaceous habit for that plant. Unusually large ray cells were observed in *Dubautia microcephala* and *Coulterella capitata*, whereas unusually small ray cells are characteristic of *Parthenium argentatum* and *Flourensia cernua*.

The sclerification of the central portion of the ray in *Argyroxiphium Caliginii* (fig. 13) applies only to foliar rays, in which such wall-thickenings are developed in the vicinity of a leaf trace.

Secretory canals.—Secretory canals have not previously been reported in vascular rays of Compositae. *Bebbia atriplicifolia* (fig. 21) does have such canals, however. These are not continuous with pith secretory canals, and are originated by the cambium. Some could be traced the entire length of a ray from their point of initiation. As seen in a tangential section of the wood, the canals are small, and lined by a row of epithelial cells which are surrounded by various numbers of small thick-walled procumbent cells. Several such canals may be present in a single ray, and relatively few rays do not possess at least one such canal.

Although secretory canals were not observed in any other woods examined, carbonized resin deposits are characteristic of intercellular spaces of rays in *Hymenoclea salsola*.

STORIED STRUCTURE

The Heliantheae examined are distinguished by the large number of species which exhibit storied wood structure. Storied wood was seen in all the subtribes with the exception of Lagasceinae. In its simplest form, only the libriform fibers are storied, as in *Verbesina lanata* (Carlquist, 1957b, pl. 35d) and *Dubautia Knudsenii* (fig. 2). As might be

expected, transitions from non-storied to storied exist, and only certain portions of the wood in *Dubautia paleata, D. railliardioides,* and *D. microcephala* are storied. *Clibadium oligandrum* and the species of *Verbesina* studied other than *V. lanata* show obscurely storied libriform fibers.

Storied structure in apotracheal parenchyma but not in fibers was observed in *Coulterella capitata* and *Dubautia linearis*. In most of the woods in which storied structure is present, however, this condition tends to extend to all the vertical elements of the wood. In *Dubautia Menziesii* (fig. 7–8) and *Encelia californica* (fig. 23), for example, fibers, parenchyma, vessels, and vascular tracheids all conform to the same pattern of storied structure. Storied wood structure has been reported previously in Heliantheae by Record (1936) for *Hymenoclea salsola* and by Brown (1922) for *Dubautia plantaginea*. In view of the association of storied wood structure with other advanced features, the Heliantheae with storied structure seem good illustrations of the concept of Bailey (1923) that storied wood structure is more specialized than non-storied.

TYLOSES

Striking sclerified tyloses occur in *Fitchia speciosa* (Carlquist, 1957b, pl. 31a) and *Fitchia nutans*. Moderately thick-walled tyloses were observed in *Espeletia incana*. Thin-walled tyloses occur in *Oyedaea boliviana, Perymenium strigillosum* (fig. 20), *Zexmenia frutescens,* and *Clibadium oligandrum*. Thus, tyloses are probably not rare in Heliantheae.

RESIN DEPOSITS[2]

In addition to the resin deposition in rays mentioned above, numerous helianthoid woods show considerable amounts of resin accumulation. Outstanding in this respect are *Flourensia cernua* and *Borrichia arborescens* (fig. 25).

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[2]Although the writer has not analyzed these substances chemically, they probably represent the less volatile residue of an oleoresin such as that described for *Balsamorrhiza sagittata,* a member of Heliantheae, by Faust (Bot. Gaz. 64: 441–479. 1917).

In these woods, all the cells in some portions of the wood are completely occluded with resins. Although resin deposits in some woods are inconspicuous, no helianthoid wood was observed in which such substances were totally absent.

TAXONOMIC IMPLICATIONS

Although some subtribes are represented in this study only by a scattering of genera, sufficient representatives of others have been studied so that evidence from wood anatomy can be discussed in relation to the existing taxonomic system.

FITCHIINAE

The wood characteristics of the only genus in this subtribe, *Fitchia*, have been discussed previously (Carlquist, 1957b). The material given here, however, demonstrates the ways in which species differ. The larger cell size of *F. speciosa*, expressed in increased dimensions of vessels, higher rays, and longer fibers, is evident. In contrast, *F. rapensis* and other species have relatively short fibers, rays, and vessel elements. The figures for *F. mangarevensis* are probably not reliable on account of the small size of the stem from which sections were prepared. In addition, *F. speciosa* has only extensive, not partial, bands of apotracheal parenchyma; these are at more infrequent intervals than in the other species. In *F. speciosa*, apotracheal parenchyma is not storied, whereas it is in the other species. The species of *Fitchia* are rather uniform in respects other than these, however.

PETROBIINAE

Oparanthus is clearly distinguishable from *Fitchia* in lacking apotracheal parenchyma. The wood is more clearly storied, as illustrations in an earlier study (Carlquist, 1957b) indicate. Because of close agreement in other wood characters, the relationship the writer suggested between *Fitchia* and *Oparanthus* seems justified. Although the wood sample of *Petrobium* available was too small to permit any

definite conclusions, there are no marked differences from *Oparanthus*, and the same storied condition of fibers prevails.

COREOPSIDINAE

Members of this tribe, in turn, show affinities to Petrobiinae. *Bidens hendersonensis*, *Narvalina*, and *Venegazia* show no important features not found in *Petrobium* or *Oparanthus*. *Coreopsis gigantea*, although its specializations seem related to its herbaceous habit, exhibits basically the same pattern. *Coreposis gigantea* and *Narvalina* have non-storied xylem, thus differing from *Bidens hendersonensis* and *Venegazia*. *Venegazia* differs from the others in having bands which, in transection, appear to be apotracheal parenchyma. These bands, however, which occur at the beginning of a growth ring, prove to be only shorter, wider fibers, and the condition is reminiscent in this respect of *Wilkesia*. The presence of radial rows of pores is like *Coreopsis* and *Narvalina*; the wide, thin-walled fibers are reminiscent of *Bidens* and *Coreopsis*. The wood of *Venegazia* suggests that it may well be a specialized member of coreopsidinae.

VERBESININAE

Because it is the largest subtribe of Heliantheae, the diversity of this group might be expected to be greater than that of other subtribes. This is, in fact, true, although it is interesting to note that *Borrichia*, *Helianthus*, *Montanoa*, *Oyedaea*, *Podachaenium*, *Scalesia*, and *Zexmenia* lack any obvious specializations other than those characteristic of the tribe at large. Other genera show only one or two features, such as storied fibers (*Verbesina*). Considerable specialization is evident in *Flourensia cernua* and *Encelia californica*. That such specializations are local manifestations in the taxonomic system seems likely; *Encelia farinosa*, for example, conforms to the pattern of the seven genera listed above. Variation in the tendency of ray cells to be erect or procumbent is disregarded in this connection. Such variation, although perhaps significant, does not appear to be corre-

lated with other modifications of xylem. The two types of ray cells most frequent in Heliantheae, isodiametric to erect, and both procumbent and erect, seem rather random-ly distributed among the taxa. *Borrichia frutescens*, for example, lacks procumbent cells in rays, although they are present in *B. arborescens*. The tendency of rays to be wholly composed of procumbent cells *(Flourensia)* seems more clearly an advanced character.

MADIINAE

The apparent diversity of xylem in Madiinae seems caused by the numerous species in which certain specializa-tions are present. As a whole, this subtribe seems more advanced in wood structure than Verbesininae. Certain genera, like *Wilkesia* and *Madia*, have wood similar to the type considered basic in Verbesininae. In Verbesininae, only two species, *Flourensia cernua* and *Encelia californica*, were observed to have an appreciable number of vascular tracheids. In Madiinae, however, these occur in *Argyroxi-phium, Blepharizonia, Dubautia,* and *Hemizonia.* There seems to be no character of wood anatomy which clearly separates Madiinae from Verbesininae. Because the coverage of the Hawaiian genera included in this subtribe is relatively com-plete, more detailed taxonomic comments can be made:

(1) *Argyroxiphium* and *Wilkesia* have quite different types of wood, confirming the writer's opinion that these two genera should remain separate (Carlquist, 1957c). The presence of vascular tracheids, apotracheal parenchyma, and storied wood structure in *Argyroxiphium* are features not found in *Wilkesia. Wilkesia,* on the contrary, appears similar to certain species of *Dubautia,* such as *D. railliardioides.*

(2) The species of *Argyroxiphium* show some diversi-fication among themselves. *Argyroxiphium Caliginii* is dif-ferentiated from the others by its storied xylem, whereas *A. sandwichense* has notably narrower, shorter vessels, more numerous per group, than those of *A. Grayanum.* No apo-tracheal parenchyma was seen in *A. sandwichense.*

(3) The species of *Dubautia* are highly diversified. In consideration of the apotracheal parenchyma, discussed above, a possible line of specialization was indicated:

(a) Vessels are few per group, fibers non-storied or obscurely storied; little or no differentiation of fibers; vascular tracheids absent: *D. Knudsenii, D. railliardioides, D. paleata.* It seems of interest that these three species are all endemic to Kauai (Hawaiian Islands), and are placed next to each other in the monograph of Sherff (1935). They seem, then, to be closely related, although they are separated by distinct characters of gross morphology.

(b) Vessels more numerous per group; fibers differen-tiated into short (apotracheal parenchyma) and long, both storied; vascular tracheids absent or infrequent: *D. laxa, D. linearis, D. microcephala. Dubautia linearis* is transitional to (c) in its sharp differentiation of fibers and apotracheal paren-chyma.

(c) Vessels narrow, numerous per group; conspicuous differentiation into thick-walled, long, narrow libriform fibers and short, wider, thin-walled apo-tracheal parenchyma cells; nearly all vertical ele-ments storied; vascular tracheids abundant: *D. plantaginea, D. platyphylla, D. Menziesii, D. thyr-siflora, D. struthioloides.*

It is noteworthy that the species included in (a) and (b) are, with the exception of *D. linearis,* included in the genus *Dubautia* in the restricted sense (Sherff, 1935); the contents of (c) consist of both species of *Dubautia (sensu stricto)* and *Railliardia.* Because of the great similarity among the woods of (c), the writer agrees with Keck (1936) that a single genus is desirable; no clear lines of demarcation be-tween *Dubautia* and *Railliardia* can be demonstrated in respect to wood anatomy.

In regard to the Pacific Coast members of the Madiinae, similar processes of xylem specialization appear to have

taken place. *Madia sativa* is similar to *Wilkesia*; the species of *Hemizonia* studied show as much, and the same kind of, difference from *Madia* as do the species of *Argyroxiphium* from *Wilkesia*. Consequently, *Hemizonia Minthornii* and *Argyroxiphium Caliginii* look remarkably similar (compare fig. 12–14 with fig. 15–17). *Blepharizonia* is specialized in its vascular tracheids. Whether or not the specializations of Pacific Coast Madiinae and the Hawaiian genera treated here have been totally independent, similar patterns have certainly been followed in both groups. The evidence from wood anatomy is not opposed to the union of these two groups within a single subtribe.

GALINSOGINAE

Because only a single species of this subtribe was studied, no comment concerning relationships can be made. The presence of secretory canals in rays of *Bebbia* is of interest, and the distribution of this character within the subtribe should be studied. The storied xylem of *Bebbia* agrees with the more advanced position of Galinsoginae.

MELAMPODINAE

Espeletia and *Lecocarpus*, although they are plants of remarkably different habit and gross morphology, show similarities in scalariform-transitional pitting, of vessels, presence of both procumbent and erect cells in rays, and also in the fact that wide bands of somewhat shorter, wider fibers alternated with broad bands of narrower, longer fibers. In none of the species studied is the difference between these two types of fibers very great, however. Although some tendency toward storied structure occurs in *E. incana* and *E. pleiochasia*, the basic xylem structure of *Espeletia* is not unlike one of the Verbesininae, such as *Zexmenia*. The occurrence of relatively wide, thin- and soft-walled fibers in *Espeletia* may be related to the "megaphytic" habit of this genus, just as such fibers appear to be related to such a habit in *Coreopsis gigantea* and *Chimantaea* (Carlquist, 1957a). In contrast to the above genera, *Parthenium argentatum* has thin-walled rays composed of

isodiametric to procumbent cells exclusively, vascular tracheids, helically striate vessels, and thick-walled narrow libriform fibers.

MILLERINAE

The only genus studied, *Clibadium*, shows an interesting specialization in its formation of bands containing vascular tracheids and strand parenchyma. Otherwise, this wood is similar to that of *Verbesina*, with which it agrees in having a tendency toward storied structure.

LAGASCEINAE

In view of the strong difference between the two genera of this subtribe in respect to floral anatomy (Carlquist, 1957b), the writer wished to compare xylem of *Coulterella* and *Lagascea*. Although only a limited amount of wood was available on twigs of *Lagascea helianthifolia* from herbarium material, the wood structure of this species appears very similar to that of *Helianthus annuus*, thus agreeing with resemblances to the latter in floral anatomy. *Coulterella*, on the contrary, has bands of apotracheal parenchyma and storied fibers. Although *Lagascea* may well be regarded as a highly specialized genus related to *Helianthus* and its allies, the systematic position of *Coulterella* is quite obscure. The features shown by *Coulterella* can all be found in Heliantheae; one would expect, however, a greater similarity with *Lagascea* if these two genera are indeed related.

AMBROSINAE

Wood of *Parthenium argentatum* is very close to that of *Hymenoclea*. A number of botanists have noted the similarity between advanced members of Melampodinae, such as *Parthenium* and *Parthenice*, and members of Ambrosinae. Certainly the wood of both *Parthenium argentatum* and *Hymenoclea* is highly specialized, so that their advanced position in the tribe and in the family is justified. Because of such close similarity between these two genera, however, treatment of Ambrosinae as a subtribe rather than as an independent tribe seems preferable. The nature of differentiation of Ambrosinae from Melampodinae is an interest-

ing problem, as the results of Wodehouse (1935) indicate, which deserves further study.

Grindelia AND *Eastwoodia*

Steyermark (1937) has suggested that these genera represent outliers of Heliantheae transitional to Astereae. Without detailed evidence on the nature of wood in the latter tribe, little can be said concerning this hypothesis. Both of these genera show derived types of wood structure which, although they do not match any other genus in the tribe, are not outside the range of variability found in Heliantheae. The wood of the *Grindelia* species studied does not appear particularly similar to that of *Eastwoodia*.

GENERAL CONCLUSIONS AND SUMMARY

From the material studied, the following characters would appear to be advanced: very narrow (60 microns or less) vessels; aggregations of numerous vessels; presence of helical striations in vessels and vascular tracheids; presence of vascular tracheids; storied wood structure; rays Homogeneous II; rays composed of thin-walled, non-lignified cells; presence of apotracheal parenchyma. This last character is added to the list on account of the apparent derivation of such parenchyma bands as seen in *Dubautia*.

The problem of dealing with primitive versus advanced in a family of which all the woods are rather specialized—in comparison with dicotyledons at large—is an acute one. As noted by Bailey (1957), the trends established from surveys of dicotyledons as a whole cannot be expected to apply for all wood characters in a family of this nature. The suggestions concerning advanced characters in Heliantheae have, therefore, been made on the basis of established trends only where striking specializations have been clearly demonstrated in other families (e.g., storied wood). For the remainder of the characters, a rather intuitive approach is required, in which the association of hypothetically specialized characters with each other is noted and compared to existing taxonomic, phylogenetic, and anatomical studies in the family. The fallibility of this approach is obvious, and

the writer believes that Compositae demonstrate difficulties in phylogenetic use of wood characters much better than they offer clear instances of their usefulness. Heliantheae serve to illustrate the highly advanced nature of woods in this family.

Because the gamut of characters in which significant variation can be observed in Heliantheae is not large, the value of wood anatomy for taxonomic use in this tribe appears to be restricted mostly to a comparison of species within a genus, or in some instances comparisons of related genera. Delimitation of subtribes or tribes on the basis of wood characters alone is not possible. Comparison of Heliantheae with Mutisieae offers few discrete points of difference. One rather striking feature is the relative absence of uniseriate rays in Heliantheae, whereas wide multiseriate rays are common in this tribe. Uniseriate rays are abundant in Mutisieae, and multiseriate rays, where present, are generally narrow. The tendencies toward the production of vascular tracheids, storied xylem, and apotracheal parenchyma are all more prevalent in Heliantheae studied than in the materials utilized by the writer for Mutisieae, but these hardly afford points of differentiation between the two tribes. Study of other tribes with woody members will be useful in giving perspective to the variation patterns described thus far.

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THE UPPER STORY OF TROPICAL FORESTS[1]

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RELATIONSHIP OF UPPER STORY VOLUME TO TOTAL VOLUME OF FOREST

With the data from table 8 at hand, it is possible to transform the tree counts from the aerial photographs, subdivided into "low" and "high" trees per crown diameter class, into the volume of standing timber for the upper story. As the volume tables for the Amazon trees are not yet ready, the general form factor 0.7 (Gonggryp and Burger, 1948) is used for the calculations. The volume of standing timber in the merchantable bole for the single tree is equal to:

$$D.B.H.^2 \times \frac{11}{14} \times \text{length of merchantable bole} \times 0.7.$$

Table 11 gives the results for the Amazon data with the corresponding data from Surinam in parentheses.

Table 11. VOLUME OF STANDING TIMBER FOR UPPER STORY TREES IN M.^{3}

CROWN DIAMETER CLASS	"LOW TREES"	"HIGH TREES"
I	1.1 (1.5)	2.6 (2.2)
II	1.7 (3.2)	4.4 (4.1)
III	2.5 (4.2)	7.2 (7.0)
IV	4.3 (6.0)	12.0 (9.6)

The forests under consideration were surveyed for commercial purposes. In the samples, all trees from 25 cm. diameter at breast height, or just above the buttresses, and upwards, were enumerated. If there is a demand for pole or timber wood from certain species, it will be possible to present, from the data obtained, the necessary information. Because of recent progress in pulp and paper research, the smaller trees below the 25 cm. d.b.h. limit, were counted on parts of the samples. It is possible that in the future the pulp

[1]Continued from *Tropical Woods* 107: 84.

and paper industry will have a special interest in these smaller trees. It should be clear that interest in these forests is not limited to the upper story alone, but that it includes practically all trees present. In contrast with aerial photographs of most forests in the temperate zone, aerial photographs of tropical forests expose only a fraction of the total number of trees. If complete information about tropical forests is desired from aerial photographs, the relationship between this upper story and the total forest must be established. In Surinam such a relationship was indeed found. The same also proved to be the case for the Amazon forests under survey. Fig. 5 presents the Amazon data; fig. 6 gives the Surinam data (from Publication 13 of the Central Bureau for Aerial Survey in Surinam) and also includes the Amazon curve from fig. 5. The Surinam data are from 419 samples mostly of one hectare each; the Amazon data are from 417 samples of one hectare each.

Both curves show between 170 and 180 m.³ total (or gross) volume per hectare, a typical bend for which at the moment a satisfactory explanation cannot be given. The differences between the curves, which show a higher total volume for Surinam than for the Amazon at the same upper story volume, can be explained to a certain extent by the fact that the total number of trees enumerated per hectare for the Surinam samples was much greater than that for the Amazon samples. This larger number of trees is mainly due to the higher number of trees in the diameter class of 25–34 cm. Table 12 gives a clear picture of these differences.

At the end of table 12 the averages for the total range of the Surinam data and for the corresponding Amazon data are listed. It can be seen from the curves that the greatest differences are in the upper story classes of 40–80 m.³ It will also be seen that the averages for this part are practically the same.

The forests surveyed in Surinam were much denser than those in the Amazon Valley and had roughly 40 trees per hectare more. Half of these were in the diameter class of 25–34 cm. The average number of upper story trees per
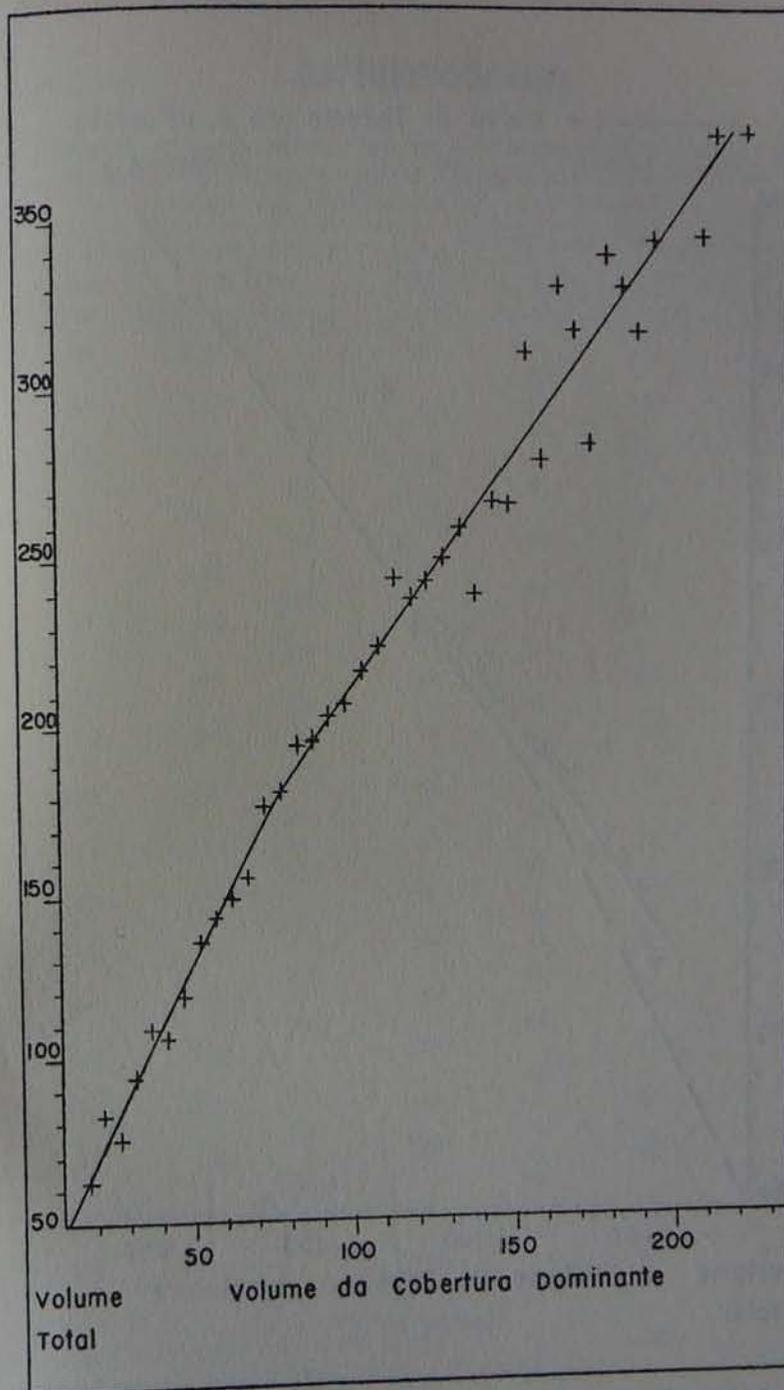

Fig. 5. The graph shows the curve for the relationship of the volume of the upper story (*Volume da cobertura dominante*) to the *total* of the Amazon forests as mentioned in

CONVENÇÕES
——— ++ curva da floresta da G. Holandesa
  "   da   "   "   Amazonia

Fig. 6. The graph shows the curves for the relationship of the volume of the upper story (*Volume da cobertura dominante*) to the total volume (*Volume total*) ...

Table 12. A COMPARISON OF THE TOTAL NUMBER OF TREES PER HECTARE AND THE NUMBER AND VOLUME OF THE TREES FROM DIAMETER CLASS 25–34 CM. FOR THE SURINAM AND THE AMAZON DATA

UPPER STORY volume class	TOTAL NUMBER OF TREES		DIAMETER CLASS 25–34 CM.			
			Number of trees		Volume in m.³	
	Surinam	Amazon	Surinam	Amazon	Surinam	Amazon
40	130	126	72	56	36	29
45	152	94	82	45	43	24
50	159	105	86	51	46	24
55	145	109	72	54	39	30
60	141	106	71	52	38	30
65	152	103	72	50	40	30
70	148	103	68	45	36	26
75	150	113	71	49	41	26
80	147	111	65	50	35	30
85	151	107	67	42	37	29
90	151	107	69	46	38	27
95	152	114	70	52	38	31
100	161	110	69	49	38	29
105	158	111	71	50	35	31
110	158	117	76	55	44	34
115	149	109	65	48	36	30
120	159	115	70	50	40	30
125	164	111	65	47	36	30
Total averages						
All	151	109	73	51	38	29
Averages of upper story volume class of 40–80 m.³						
40–80	148	108	71	50	39	28

hectare for Surinam was approximately 30; for the Amazon 20. There is a strong temptation to attempt an explanation of the differences between the Surinam and the Amazon data for the relationship of crown width to bole diameter and upper story volume to total volume of the forest entirely by this difference in density. For the smaller (younger) upper story trees there is more room for development in the open forests; they can gain rapidly in height. Since there is also more space in the upper story, these trees can better develop the width of their crowns, which, in turn would indicate a smaller bole diameter for the same crown width. The larger (older) upper story trees have less root competition in open forests. Therefore, they can more easily develop into heavy trees. This would mean a greater bole diameter for the same crown width in the more open forests. This last explanation seems to be contrary to expectation. It would appear logical to have a smaller bole diameter corresponding with the same crown width, because the crowns of these trees can more easily develop horizontally. When an upper story tree has a crown completely free from the lower trees it no longer develops upward. These crowns have a denser appearance (more leaves) and some of them start drooping at the periphery. Therefore, it seems that such trees do not gain much more in width. The fact that the curves in fig. 6 meet each other, could only mean, then, that at a certain stage, the difference in volume, caused by the higher number of trees per hectare, is equalized by the rapidly increasing volume of the large trees of the more open forests. We are forced to deal with so many tree species whose characteristics are so little known, that for the time being it is impossible to present more than this suggestion. For practical use by the photo-interpreter, the relationship between the volume of the upper story and the total volume of the forest has been tabulated (table 13).

As can be seen from these data, the Surinam forests surveyed were more uniform in volume than those surveyed in the Amazon Valley. This is partly due to the fact, that in the Surinam data some of the high and the low observations were not included. In reality in the Amazon Valley

Table 13. RELATIONSHIP BETWEEN THE VOLUME OF THE UPPER STORY AND THE VOLUME OF THE TOTAL FOREST IS GIVEN FOR THE AMAZON FOREST AND THE SURINAM FOREST. DATA FOR ESPECIALLY HIGH AMAZON FORESTS, ARE INDICATED IN PARENTHESES.

VOLUME UPPER STORY IN M.³	TOTAL VOLUME FOREST IN M.³ AMAZON	SURINAM	VOLUME UPPER STORY IN M.³	TOTAL VOLUME FOREST IN M.³ AMAZON	SURINAM	VOLUME UPPER STORY IN M.³	TOTAL VOLUME FOREST IN M.³ VOLUME (SURINAM DATA STORY LACKING) IN M.³ AMAZON
10	52	—	90	202 (238)	208	165	304 (347)
15	62	—	95	208 (245)	214	170	311 (354)
20	72	—	100	215 (252)	220	175	318 (361)
25	82	—	105	222 (260)	226	180	325 (368)
30	92	—	110	229 (267)	233	185	332 (376)
35	102	—	115	236 (274)	239	190	339 (383)
40	112	138	120	243 (281)	246	195	346 (390)
45	121	146	125	249 (288)	252	200	353 (397)
50	130 (151)	153	130	256 (295)	—	205	360 (404)
55	140 (163)	161	135	263 (303)	—	210	367
60	150 (175)	168	140	270 (310)	—	215	374
65	160 (187)	176	145	277 (317)	—	220	382
70	170 (199)	183	150	284 (325)	—	225	389
75	179 (211)	189	155	291 (332)	—	230	396
80	188 (223)	195	160	298 (339)	—	235	413
85	195 (231)	201				240	

there were more heavy forests surveyed than in Surinam. The low forests in Surinam occupied comparatively small patches which could easily be mapped with the help of excellent vertical aerial photographs. These patches usually had an outstandingly different composition from those of the surrounding higher forests. This was especially true on sandy soils where there was often an abrupt change from highly mixed, to pure forest stands of *Eperua falcata* or *Dimorphandra conjugata*. In the Amazon forests such changes were not observed. There it appeared more to be a slow degeneration from high to low forest. Some of the tree species disappeared and the growth of the remaining species became very poor. Forest type mapping, especially for the oblique parts of the trimetrogon photographs, had here to be based mainly on the available samples. Therefore, it was also necessary to enumerate the lower forests. With good vertical photographs on hand, the enumeration of this kind of forest can, as long as they do not occupy large areas or are of commercial interest, mostly be avoided (and separated on the forest type map). When during an exploratory survey, small patches of forests are met which show very different composition from that of the surrounding forests, a simple description is sufficient. If they are of commercial interest because of their location and/or composition, subsequently they can be enumerated separately. The question remains however, of whether it is possible to make a reliable estimate of the total volume of the Amazon forests from aerial photographs with the help of the data given in the tables.

Data are available of a systematic forest survey in an area in the Territory of Amapa (C in fig. 1) made in 1956. Enumerated here were trees from a diameter of 45 cm. at breast height, or just above the buttresses, and upwards. Regularly spaced from each other, were 77 forest samples of one hectare each taken from all trees with a diameter at breast height, or just above the buttresses, from 15 cm. and upwards. By extracting the average volume per hectare of all trees from the diameter class of 15-24 cm., the average volume per hectare of all trees from the diameter class of

25-34 cm. and upwards was obtained. Fortunately this part of the forest was covered by the verticals of a trimetrogon flight strip. In this case, it was possible to make plot enumerations from these photographs. Three photo-interpreters, who had never visited this forest area, counted three sets of 36 plots of one hectare each taken at random from the aerial photographs. The following average volumes per hectare were obtained: 177, 172 and 151 m.³, or an average of 167 m.³. The average of the total volume from the actual field enumeration was 165 m.³ per hectare. From forest areas covered by the verticals of trimetrogon flight strips in region B of fig. 1, two sets of 50 plots of one hectare each taken at random from the vertical photographs were counted by two photo-interpreters, who had also visited parts of this area. The results were: 215 and 216 m.³ per hectare. The average of the samples of the exploratory survey was 231 m.³ (real average between 227 and 235 m.³; chance 2 in 3).

In a particular part in region D of fig. 1, 50 plots of one hectare each were counted from the verticals of a trimetrogon flight strip which covered a comparatively small portion of this area. By using the same data as before an average of 250 m.³ per hectare was obtained. In the field, 38 samples of one hectare each were enumerated giving an average total volume of 314 m.³ per hectare (real average between 304 and 324 m.³ per hectare : chance 2 in 3). For the parts of the Amazon forest surveyed up to now, this area was extremely dense, with an average number of 142 trees per hectare. The most remarkable fact was, that this density could be obtained from tree counts of the upper story. The average numbers of upper story trees for regions C and B were both 22 per hectare, whereas in region D the average was 32 per hectare. This is about the average for the Surinam forests. It will be clear that the data in table 13, calculated from forests with an average of 109 trees per hectare, cannot be used for forests of approximately the same composition but with practically all upper story trees in the "high" class and with an average total of 142 trees per hectare. In attempting to correct the deviating results

obtained from the general data in table 13, all observations with an average number of 130 or more trees per hectare, were separated. As has been done for all observations together, these data were put into graphic form, and the total volumes corresponding with the upper story volume classes were abstracted from the curve. These volumes are given in parentheses in table 13. By using these data, the average of the total volume estimates from the aerial photographs rises to 289 m.^{3} per hectare, which is a fairly good result. As only 39 of the 417 Amazon observations had more than 130 trees per hectare, the data in parentheses in table 13 should be regarded as preliminary for the time being.

In region E of fig. 1, a fairly large forest area was found with a uniform low average total volume. Some valuable tree species were present, so this area had to be included in the sampling procedure. Only a part of it was covered by the verticals of a trimetrogon flight strip. In that place 10 samples were enumerated in the field. As close as possible to the location of these samples, 10 plots of one hectare each were enumerated from the vertical aerial photographs. The sampling data in the field were: 72, 110, 101, 110, 118, 117, 116, 139, 63 and 107 m.^{3} per hectare, or an average of 105 m.^{3}. The sampling data from the vertical aerial photographs were: 112, 102, 102, 102, 112, 112, 82, 112, 121 and 140 m.^{3} per plot of one hectare or an average of 110 m.^{3} per hectare. The last two examples are from forest parts which are exceptional and occupy comparatively small areas. The data for these parts are only presented to illustrate the possibilities of volume estimates from aerial photographs.

A forester who has enumerated numerous forest samples, can make excellent ocular volume estimates in the field of forest parts with which he is acquainted. The forester-photo-interpreter can do the same from stereoscopic aerial photographs. To estimate the total volume of *these* tropical forests from aerial photographs is much easier than making similar estimates from forests in the temperate zone, because the range of the total volume of these tropical forests is comparatively small. With a little experience in the field,

combined with proper photo study, the forests with a total volume less than 150 m.^{3} and more than 250 m.^{3} per hectare, can easily be identified on photographs; they are, respectively, usually uniformly low with a smooth crown canopy, or uniformly high and dense with a very coarse crown canopy. To estimate the total volume of tropical forests having a total volume between 150 and 250 m.^{3} per hectare is a little more difficult, since they show a much more varied canopy.

The forest surveyor who has samples of a certain forest area in which he has enumerated in succession, low, high, and higher forests, will seldom think it necessary to make total volume estimates from the vertical aerial photographs used during his survey work. At that time he is much more interested in the composition of the forest than in the total volume. Only in the exceptional cases, as mentioned under PHOTO-INTERPRETATION, and if the aerial photographs were taken when one or some of the upper story trees were in full flower (deduced from observations made in the field), it is possible to obtain valuable additional information about the forest composition through plot counts from the vertical aerial photographs.

With a steadily growing amount of sampling data from the Amazon forests available, it becomes more and more evident, that there is a certain relation between the total volume of the forest and its composition. Practically everywhere groups of tree species are found which grow broader and taller in the heavier forests than in the low forests. Most of the occasionally encountered trees are confined to either the high or the low forests and disappear when these forests change into low or high forests, or at least only occur there as an exception. A good example was found in region B (fig. 1), where the forests on the slopes of a plateau were surveyed. These slopes were mostly covered by oblique photographs, so type mapping became very difficult. It was observed that on the higher parts of the slopes massaranduba (*Manilkara huberi*) grew in reasonable quantities, whereas on the lower parts of these slopes this tree was rarely seen

or tabulated. From the obvious differences in total volume of the forests on the low and the high parts of these slopes, it was necessary to divide the slope forests into a high and a low type, coinciding with the high and steep clayish parts and the lower and flatter sandy parts. As an indicator massaranduba was used. The results were: average of all samples taken on the slopes 132 m.^{3} per hectare; low part (samples *without* massaranduba) 111 m.^{3} per hectare; high part (samples *with* massaranduba) 167 m.^{3} per hectare.

Considering the results obtained of total volume estimates from plots on aerial photographs and the fact that it is impossible or highly speculative to identify tree species from aerial photographs in highly mixed tropical forests, the existing relationship between the total volume of these forests and their composition will be put on a sound statistical base. Without the means to estimate directly the total volume of the Amazon forests from aerial photographs, it would be highly interesting to have data regarding this relationship, but it would not make the survey work easier, more efficient, or less expensive. It would still be impossible to have beforehand (which means before the start of actual field sampling) information which could be checked, instead of all the information being retaken. The forest surveyor will be eager to make plot counts from the vertical aerial photographs to be used during his next survey, if he is convinced that the data obtained will enable him to obtain better, or at least the same results as before with less time in the field.

Conclusions

The timber and veneer wood extractors are interested only in those tropical tree species that can be exploited economically. Usually they can extract larger quantities and more useful timber from the high patches of forests wherein those desirable species are common, but the reverse may also be true. It often happens that the medium-sized trees, which occur more frequently in the lower forest parts, are of better quality, with less heart rot, than the larger trees. Also, they can be handled more easily. But

in general, these extractors will have only slight interest in the total volume of the highly mixed tropical forests.

It is probable that pulp and paper research will reach a stage where it will be possible for the industry to utilize economically, all, or a great number of tree species from these mixed forests. As pulp wood must be cheap in comparison with veneer and timber wood, the production per hectare must be high; probably at least 100 m.^{3} To reach this amount, all, or a group of tree species which are commonly present, will have to be used. In that instance the possibility of making total volume estimates from aerial photographs will become of the utmost importance.

At the time Publication 13 of the Central Bureau for Aerial Survey in Surinam was written, attempts were made to obtain such estimates, but the results were not satisfactory. This was mainly caused by the fact that the differences in the height of the upper story trees was less accentuated in Surinam than those observed in the Amazon. Furthermore, the number of observations on which the relationship between the volume of the upper story and the total volume of the forest was based, was considered insufficient. The typical bend in the curve, which gives a decrease in growth of the total volume per upper story volume class from 180 m.^{3} per hectare and upwards, could not be explained. It is still impossible to explain this bend satisfactorily. The same bend, which is even more accentuated, occurs in the Amazon curve. Therefore this trend must be inherent in the relationship between the volume of the upper story and the total volume of the forest.

Volume estimations from aerial photographs will very probably never reach the same degree of accuracy as similar estimates taken in the field (Spurr, 1952). However, in the initial stage of forest survey work in the Amazon Valley there is no need for great accuracy. What is urgently needed is basic information about the composition of the forests located close to navigable rivers.

According to Ricardo Lemos Froes (Lucio de Castro Soares, 1953) typical Amazon trees occur not only in the

Amazon Valley, but also in the western parts of Maranhao. From east to west in Brazil, the Amazon forests occur over a front of 3,000 km. The parts located close to the navigable rivers are estimated to occupy an area of approximately 100,000,000 hectares, or 25 per cent of the total forest lands. The expectation is, that the composition of the dry land forests close to the Amazon River, will differ only slightly, and will change gradually from east to west. Up to now, samples covering a front of approximately 600 km. justify this expectation.

The Amazon River, and parts of its larger tributaries flowing through Brazil, are navigable to seagoing ships. From the point of view of transportation, the importance of the forests located close to these rivers, is the same for foreign markets as it is for the more populated southern parts of Brazil (Gachot et al., 1953; McGrath, 1955). For this reason, an initial forest survey will have to cover the whole area of 100,000,000 hectares. The least costly, quickest, and also the most desirable way of executing an initial forest survey of this magnitude, would be of course, by pure photo-interpretation. Whether it will ever become possible to obtain reliable information about the composition of the highly mixed tropical forests of the Amazon Valley in this way, is difficult to foresee. At the moment it is not practicable. The survey method used at present, is forest type mapping with the aid of aerial photographs based on samples taken in the field. By employing this means to prepare total volume estimates from aerial photographs, and taking into account the increasing skill of the photo-interpreters in deducing preliminary information about the forest composition with the help of the available sampling data, the progress of the initial forest survey can be increased substantially. The aim is to replace gradually part of the sampling work in the field by photo-interpretation, thereby enabling larger forest areas to be covered in the same number of samples.

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THE ANATOMY OF SOME TIMBERS FORMERLY INCLUDED IN *PIPTADENIA*

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Introduction

As a result of recent work particularly by Brenan (1955), the numerous species formerly included in *Piptadenia* have been reclassified and are now considered to contribute to eight genera. These are *Piptadenia* Benth. *(sensu stricto)*, *Anadenanthera* Speg., *Goldmania* Rose ex Micheli, *Newtonia* Baill., *Pityrocarpa* (Benth.) Britton & Rose and three genera described by Brenan for the first time, *Indopiptadenia*, *Monoschisma* and *Piptadeniastrum*.

The fifteen African species of *Piptadenia (sensu lato)*, described by Baker (1930), are now referred to *Newtonia* except for the important economic species, *Piptadenia africana* Hook.f., which is now known as *Piptadeniastrum africanum* (Hook.f.) Brenan. This species has a wide distribution through West, Central and East Africa and is locally very common. Its timber has been exported to the United Kingdom and other European countries under a number of names according to the country of origin, among them dahoma (adopted as the British Standard name; British Standards Institution, 1955) from Ghana, agboin and

ekhimi from Nigeria, dabéma from the French West African territories and mpwere from Uganda. The name mpwere has also been used in Uganda for the timber of *Newtonia buchanani* (Bak.) Gilbert & Boutique, thought to be similar to that of *Piptadeniastrum africanum*, and for a long time the timbers of the two species were marketed together.

As part of the programme of testing Commonwealth timbers at the Forest Products Research Laboratory, Princes Risborough, six logs of "*Piptadenia africana*," now *Piptadeniastrum africanum*, and seven of "*P. buchanani*," now *Newtonia buchanani*, were received from Uganda in June 1954. From an examination of this material it was clear that the timbers of the two species differed appreciably in general appearance, and it was found subsequently, in certain technical properties. It was of considerable interest, therefore, to determine whether they could be distinguished with certainty on the basis of their wood anatomy.

During the examination of these and other African species of *Piptadenia* Brenan published his revision of the genus. The investigation was then extended to include an examination of wood specimens of as many as possible of the species listed by Brenan in order to determine whether the groups recognized by Brenan and established as genera could be distinguished from an examination of their wood anatomy. So far as is known no comprehensive study of the wood anatomy of the "*Piptadenia*" timbers has been made before.

Wood specimens of all eight genera described by Brenan were available for study but for two of these, *Indopiptadenia* and *Monoschisma*, only a single specimen was available. In the following descriptions a brief account of the physical properties of the timbers is followed by an account of the anatomical features of diagnostic value.

Anadenanthera

As now constituted, *Anadenanthera* comprises four species, *A. colubrina* (Vell.) Brenan, *A. falcata* (Benth.) Speg., *A. macrocarpa* (Benth.) Brenan and *A. peregrina* (L.) Speg. Commercially, the most important of these is *A.

macrocarpa, the cebil colorado or curupay of the subtropical and dry forests of the Argentine and Paraguay. Tortorelli (1948) has given a detailed account of the distribution and importance of this species in the Argentine. *Anadenanthera peregrina* is described by Record and Hess (1943) as *Niopa peregrina*. It is a medium-sized tree occurring from central Brazil, through the Guianas and Venezuela to the West Indies. *A. colubrina* and *A. falcata* are both Brazilian species, the former known as angico and cambuhy ferro.

Descriptions of the wood anatomy of *A. macrocarpa* have been given by Cozzo (1951), Kribs (1950) and Tortorelli (1948), and Pereira (1933) has briefly described the structure of *A. colubrina*. Wood specimens of *A. colubrina*, *A. macrocarpa* and *A. peregrina* were available for study.

The timbers.–The timbers of all three species studied are very hard and heavy. The heartwood is red-brown with darker stripes in *A. macrocarpa*, and dark brown with a reddish tint in *A. colubrina* and *A. peregrina*. The texture is fine, and the grain usually interlocked. The weight[2] of the heartwood is of the order of 60 lb. per cu. ft. in all three species and up to 70 lb. per cu. ft. in *A. macrocarpa*.

Structure.–Vessels solitary and in radial groups of 2–4 and occasionally more; moderately small, 100–160μ mean tangential diameter and moderately numerous, 70–150 per sq. mm.; somewhat larger and less numerous in *A. colubrina* than in *A. macrocarpa* and *A. peregrina*. Vessel–vessel pitting moderately coarse, 7–9μ tangential diameter; ray–vessel pitting similar with mostly 2, occasionally 3 rows of pits per ray–vessel field.

Parenchyma moderately well developed, vasicentric tending to aliform. Scattered strands (diffuse) present, usually containing chambered crystals. Chambered crystals abundant in the vasicentric parenchyma.

Ray tissue homogeneous; multiseriate rays up to 6 but mostly 4 cells wide.

[2]All weight data refer to specimens in the air-dry condition unless otherwise stated.

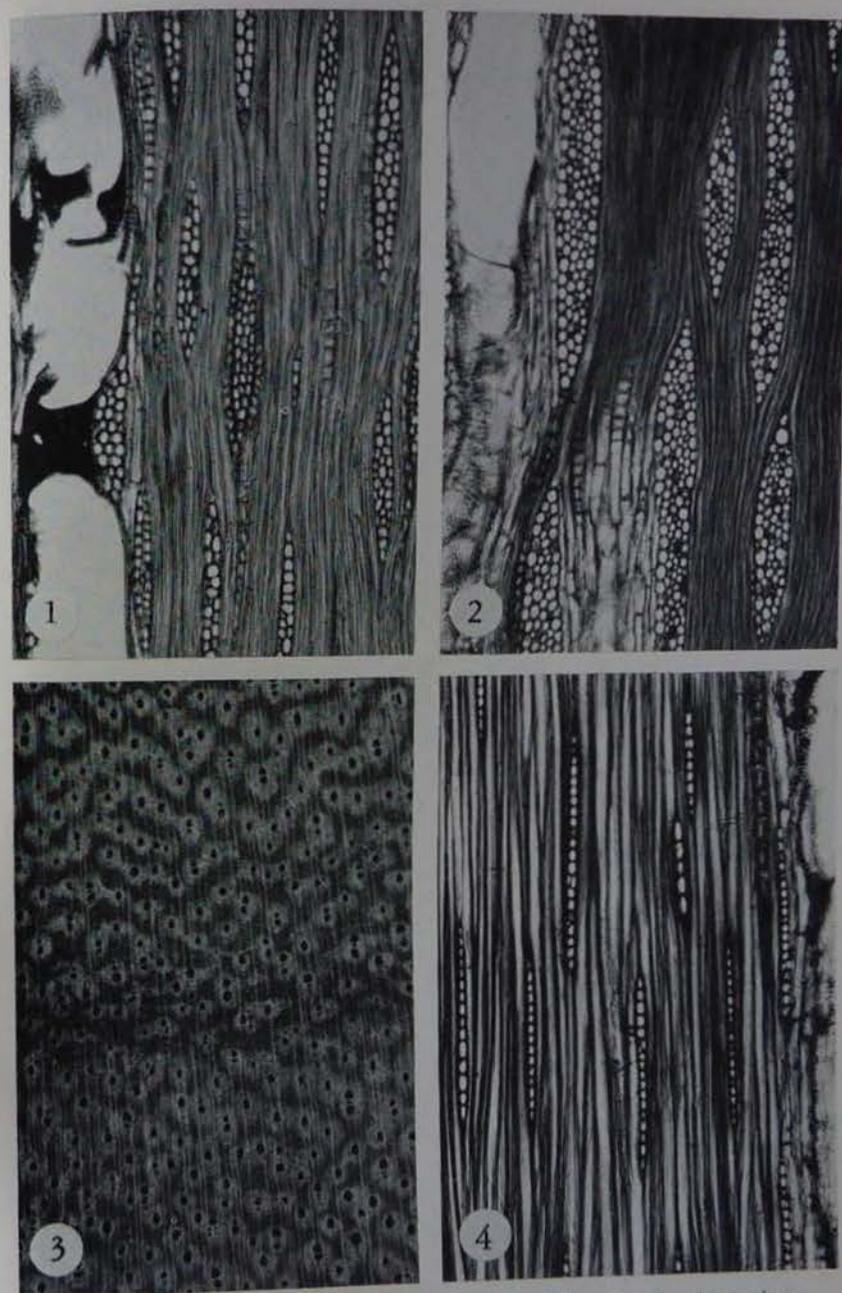
Fig. 1–4.—Fig. 1. *Piptadenia rigida* and Fig. 2. *Anadenanthera macrocarpa*. Note difference in ray widths on these tangential sections. Both × 100.—Fig. 3. *Goldmania paraguensis*, tangential section to show confluent, locally banded parenchyma. × 10.—Fig. 4. *Newtonia suaveolens*, tangential section illustrating uniseriate rays and
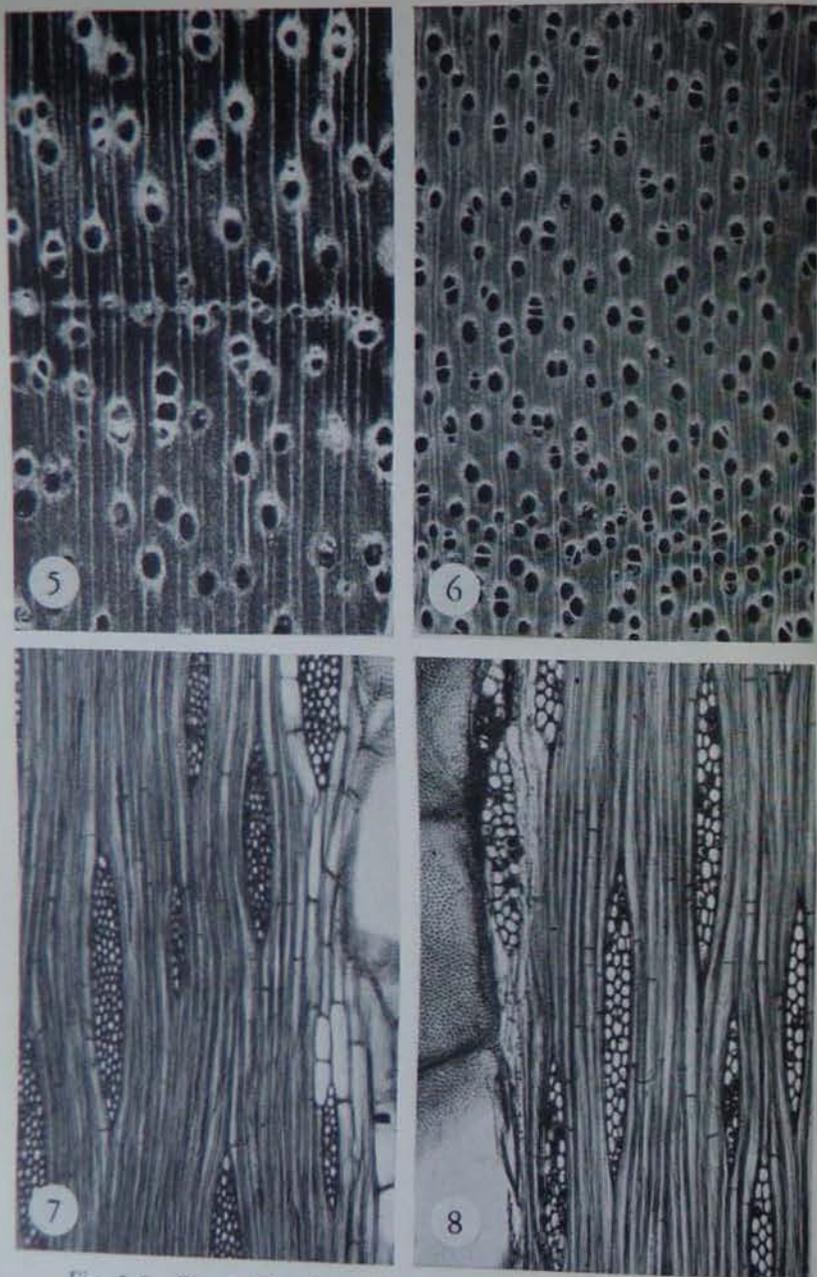
Fig. 5–8.—Fig. 5. *Piptadeniastrum africanum* and Fig. 6. *Newtonia buchanani*, transverse sections. Note fewer, larger pores in *Piptadeniastrum*. Both × 10.—Fig. 7. *Piptadeniastrum africanum* and Fig. 8. *Newtonia buchanani*. Tangential sections to show wider rays in *Piptadeniastrum* and septate fibres in both species. Both × 100.

Fibres thick-walled; septa not observed and not recorded in literature (Cozzo, 1951; Kribs, 1950; Tortorelli, 1948).

Comparison with other species.—In color, texture and weight the species of *Anadenanthera* are similar to *Piptadenia rigida*. Anatomically the timbers of the two genera are readily distinguishable on ray width, the rays in *Piptadenia rigida* being mainly bi- or occasionally triseriate whereas in *Anadenanthera* they are typically 4 and occasionally more cells wide (fig. 1, 2).

Material examined.—*Anadenanthera colubrina* (Vell.) Brenan, two specimens, Brazil; *A. macrocarpa* (Benth.) Brenan, eight specimens, Argentine Republic, Paraguay, Brazil and Florida (cultivated); *A. peregrina* (L.) Speg., two specimens, Brazil and Puerto Rico.

GOLDMANIA

Brenan has listed two species of *Goldmania*, *G. platycarpa* Rose ex Micheli and *G. paraguensis* (Benth.) Brenan. Wood material of the former was not available and, so far as is known, has not been described. The following description refers only to *G. paraguensis*. This is a bush or small tree of the northern Argentine and Paraguay and is known as ibará-né, literally "stinking tree." Tortorelli (1948), who has given an account of the species, says that because of its disagreeable odor the wood is not used.

The wood is of medium weight and a uniform, slightly greenish-yellow color throughout. It has a moderately fine, even texture. The disagreeable odor reported in the green timber is not noticeable when the wood is dry.

Structure (fig. 3).—Vessels solitary and in short radial groups; moderately small, about 100μ mean tangential diameter and moderately numerous, 60–70 per 10 sq. mm.[3] Vessel–vessel pitting moderately coarse, the ray–vessel pit-

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[3]Tortorelli (1948) describes the vessels as numerous to very numerous, 12–30 per sq. mm. Examination of his illustrations shows that *G. paraguensis* has the least numerous pores of the species he describes and, accepting the magnification as given, the number for his illustration of *G. paraguensis* is about 7 per sq. mm.

ting similar and mostly with two rows of pits per ray–vessel field.

Parenchyma well developed, vasicentric, aliform, often confluent and locally forming short, tangential bands. Chambered crystalliferous strands present.

Ray tissue homogeneous; rays not more than biseriate and the majority uniseriate with only occasional biseriate portions.

Fibres moderately thick-walled and apparently non-septate.

Comparison with other species.—In its wood anatomy *Goldmania* is distinguished from all the species studied by the abundance of its parenchyma which, although of the paratracheal type characteristic of the group as a whole, extends laterally often forming an irregular banded arrangement.

Material examined.—*Goldmania paraguensis* (Benth.) Brenan, two specimens, Argentine Republic.

INDOPIPTADENIA

The genus *Indopiptadenia* has been established by Brenan for the Indian species formerly included in *Piptadenia* and now known as *Indopiptadenia oudhensis* (Brandis) Brenan. Little information is available about the species but Gamble (1922) has described it as a moderate-sized tree with a yellowish or reddish, close-grained timber, hard, durable and without color contrast between sapwood and heartwood.

The only material available was a small specimen, not authenticated with herbarium material but from its structure clearly belonging to the *Piptadenia* complex. It has a density of about 47 lb. per cu. ft., but is largely tension wood and this figure may be abnormally high.

Structure.—Vessels mostly solitary but occasionally in pairs and short radial groups; sparse, 40–50 per 10 sq. mm. and moderately small, 100–160μ tangential diameter. Vessel–vessel pitting coarse, mean tangential diameter about 9μ;

vessel–ray pitting similar with 2–3 rows of pits per ray–vessel field.

Parenchyma vasicentric, well developed aliform and in the late wood locally confluent. Diffuse strands, commonly with chambered crystals, present and chambered crystalliferous strands present in the vasicentric parenchyma.

Ray tissue homogeneous; multiseriate rays 2–3 cells wide.

Fibres moderately thick-walled, due, in part, to development of tension wood; apparently non-septate.

Growth rings present but not well marked.

Comparison with other species.—The presence of narrow, predominantly bi- and triseriate rays and the absence of septate fibres serve to distinguish *Indopiptadenia oudhensis* from all other species examined during this survey except those of *Piptadenia (sensu stricto)*.

Material examined.—*Indopiptadenia oudhensis* (Brandis) Brenan, one specimen, India.

MONOSCHISMA

Monoschisma as known at present comprises two species of Brazilian origin, *M. inaequale* (Benth.) Brenan and *M. leptostachyum* (Benth.) Brenan.

The only material available for study was a single specimen of *M. leptostachyum*. It had been cut from a small tree and was sapwood throughout, pinkish white in color and with a moderately fine texture, a shallowly interlocked grain and a density of about 46 lb. per cu. ft.

Structure.—Pores solitary and in groups of 2–4, moderately numerous, about 100 per 10 sq. mm. and moderately small, 90–150μ tangential diameter, average about 115μ. Vessel–vessel pitting moderately fine, 7–8μ tangential diameter, vessel–ray pitting similar, with 3–4 rows of pits per ray–vessel field.

Parenchyma vasicentric, aliform and locally confluent between adjacent pores. Chambered crystals present in the vasicentric parenchyma and abundant as diffuse strands among the fibres.

Ray tissue homogeneous; rays exclusively uniseriate.

Fibres moderately thin-walled; septa not observed.

Comparison with other species.—Anatomically *Monoschisma* is similar to the American species of *Newtonia* and the species described as *Pityrocarpa* A, but pending an examination of more material of *Monoschisma* it is uncertain whether it can be separated from these genera for certain.

NEWTONIA

Baillon's genus *Newtonia* has been re-established and as now constituted comprises fourteen species, eleven of them African and the rest American. Most species are large trees, many producing an attractive timber of potential commercial interest, but so far as is known only *N. buchanani* has been exploited and this on a small scale only. The African species are widely distributed through the tropical regions from Sierra Leone in the west to Somaliland and Tanganyika in the east and Angola and Zululand in the south, although, with the exception of *N. buchanani*, none of the species has a wide geographical range.[4] The American species are imperfectly known; *N. nitida* (Benth.) Brenan occurs in Brazil and *N. psilostachya* (DC.) Brenan has been recorded from the Guianas. Specimens of *N. suaveolens* (Miq.) Brenan have been received from Brazil, British and French Guiana and Surinam.

[4]The African species and their recorded distributions are: *N. aubrevillei* (Pellegr.) Keay, Sierra Leone, Ivory Coast; *N. buchanani* (Bak.) Gilbert & Boutique, Belgian Congo, Angola, Uganda, Kenya, Rhodesia, Tanganyika, Nyasaland, Mozambique; *N. duparquetiana* (Baill.) Keay, (syn. *N. insignis* Baill.), Sierra Leone, Ivory Coast, Ghana, Gabon; *N. ellioti* (Harms) Keay, Sierra Leone; *N. erlangeri* (Harms) Brenan, Somaliland; *N. griffoniana* (Baill.) Bak. f., South Cameroons, Gabon, Portuguese Congo, Mayumbe; *N. glandulifera* (Pellegr.) Gilbert & Boutique, Cameroons, Gabon, Mayumbe; *N. hildebrandtii* (Vatke) Torre var. *hildebrandtii*, Kenya, Tanganyika, Mozambique, Zululand, var. *pubescens* Brenan, Tanganyika, Mozambique; *N. leucocarpa* (Harms) Gilbert & Boutique, Gabon, Mayumbe; *N. paucijuga* (Harms) Brenan, (syn. *Cylicodiscus battiscombei* Bak. f.) Tanganyika; *N. zenkeri* Harms, Cameroons.

Newtonia has attracted little interest so far as its timbers are concerned and there are few published descriptions of the species. Chalk et al. (1932) and Ferreirinha (1955) have described in detail the structure of *N. buchanani* and Scott (1950) has illustrated and given a brief description of this species. Normand (1950) has illustrated and described the timber of *N. duparquetiana*. Wood specimens of ten of the fourteen species listed by Brenan were available for study.

The timbers.—The heartwood of all species of *Newtonia* examined is typically pink or red with sometimes a yellowish tint. In most species it is pale pink with the yellow color well marked in *N. nitida*, *N. suaveolens* and some specimens of *N. buchanani*, but *N. griffoniana* is a medium red-brown and *N. hildebrandtii* a dark red-brown. The texture is mostly fine but moderately coarse in *N. buchanani* and *N. leucocarpa*. The grain is typically interlocked, producing an attractive stripe figure on quartered surfaces. The weight varies from moderately light to heavy. Weight data for the specimens available are as follows:

N. aubrevillei: 36–52 lb. per cu. ft., average of 3 specimens, 41 lb. per cu. ft.

N. buchanani[5]: 26–44 lb. per cu. ft., average of 12 specimens, 36.6 lb. per cu. ft.

N. duparquetiana: (2 specimens), 51 and 57 lb. per cu. ft.

N. glandulifera: (2 specimens), 37.5 and 49 lb. per cu. ft.

N. griffoniana: (1 specimen), 49 lb. per cu. ft.

N. hildebrandtii: (2 specimens), 53.5 and 62.5 lb. per cu. ft.

N. nitida: (2 specimens), 45.5 and 49.5 lb. per cu. ft. (both pieces mostly sapwood).

N. leucocarpa: (1 specimen), 46.5 lb. per cu. ft.

N. paucijuga: 43.5–54 lb. per cu. ft., average of 3 specimens, 48 lb. per cu. ft.

N. suaveolens: 39–55 lb. per cu. ft., average of 5 specimens, 46 lb. per cu. ft.

Structure (fig. 4, 6, 8, 10).—Vessels small to large; small, mean tangential diameter less than 100μ in *N. hildebrandtii*, *N. nitida* and *N. paucijuga*; large, often exceeding 200μ in

[5]Forty-eight pieces, each 5 ft. × 6 in. × 2 in., varied from 29 to 40 lb. per cu. ft. and averaged 36 lb. per cu. ft. at 12 per cent moisture content.

diameter, in *N. buchanani* and *N. leucocarpa*, medium-sized but mostly rather small in the remaining species; variable in number, mostly sparse, 20–70 per 10 sq. mm. in *N. aubrevillei, N. buchanani, N. duparquetiana, N. hildebrandtii, N. leucocarpa* and *N. suaveolens*, exceeding 100 per 10 sq. mm. in the remaining species and occasionally very numerous, 200–400 per 10 sq. mm. as in *N. paucijuga*. Vessel–vessel pitting fine to moderately fine, 4–7μ tangential diameter; vessel–ray pitting similar, commonly with 3, occasionally 4 rows of pits per ray–vessel field (fig. 10).

Parenchyma mostly sparse, vasicentric with tendency to abaxial development in some species, e.g., *N. suaveloens*, and sometimes shortly aliform. Diffuse parenchyma present in *N. buchanani, N. hildebrandtii* and *N. paucijuga*, mostly sparse and containing chambered crystals. Chambered crystals observed in the paratracheal parenchyma of all species except *N. nitida* but sparse in *N. glandulifera* and *N. suaveolens*.

Ray tissue homogeneous; rays mostly 2–3 cells wide, commonly 1- and 2- seriate in *N. aubrevillei* and *N. duparquetiana*, and uniseriate with only very occasional short biseriate parts in *N. nitida* and *N. suaveolens*.

Scattered secretory cavities of indeterminate length and containing a pale brown, gum-like substance are a feature of the rays in the specimens of *N. nitida* studied.

Fibres thin to moderately thick-walled, septa observed in all species except *N. nitida* and *N. suaveolens*, normally well developed and conspicuous but sparse and difficult to see in *N. hildebrandtii*.

Growth rings absent or only poorly developed in most species.

Comparison among species.—The species of *Newtonia* can be divided into two well defined groups, the American species (*N. nitida* and *N. suaveolens*) differing from the African species in ray width and absence of septate fibres.

The African species cover an appreciable range of color, weight, texture and in their anatomy show differences in

ray width, size of vessel–vessel pitting, abundance of chambered crystalliferous strands, etc., which, taken together, may enable a separation of individual species. However, the material at present available is considered inadequate to give a definite opinion on such a separation.

N. buchanani is the only species known to have been exploited. Its timber has been marketed as mafamuti from Mozambique and muchenche from Uganda. In the past it has been sold as mpwere, a name used also for the timber of *Piptadeniastrum africanum* in Uganda. These species can be distinguished with a fair degree of certainty and the salient points of difference are described under *Piptadeniastrum africanum*.

Material examined.—*Newtonia aubrevillei* (Pellegr.) Keay, 3 specimens, Sierra Leone; *N. buchanani* (Bak.) Gilbert & Boutique, 13 specimens, Kenya, Uganda, Tanganyika, Nyasaland; *N. duparquetiana* (Baill.) Keay, 2 specimens, Gabon and Mayumbé; *N. griffoniana* (Baill.) Bak.f., 1 specimen, Belgian Congo; *N. glandulifera* (Pellegr.) Gilbert & Boutique, 2 specimens, Mayumbé; *N. hildebrandtii* (Vatke) Torre, 2 specimens, Tanganyika; *N. leucocarpa* (Harms) Gilbert & Boutique, 1 specimen, Gabon; *N. nitida* (Benth.) Brenan, 2 specimens, Brazil; *N. paucijuga* (Harms) Brenan, 3 specimens, Tanganyika; *N. suaveolens* (Miq.) Brenan, 5 specimens, Br. Guiana, Fr. Guiana, Surinam, Brazil.

PIPTADENIA

Brenan lists only two species for *Piptadenia* Benth. *(sensu stricto)*, viz., *P. rigida* Benth. and *P. pterosperma* Benth. but it is clear from an examination of its wood anatomy that *Piptadenia excelsa* (Gris.) Lillo is correctly placed here. All three species are of South American origin and *P. excelsa* and *P. rigida* are important commercial timbers. Tortorelli (1948) has given a detailed account of the distribution of these species in the Argentine and describes their timbers.

Descriptions of the wood anatomy of *P. excelsa* and *P. rigida* are given by Cozzo (1951) and Tortorelli (1948),

Specimens of *P. pterosperma* were not available for study and the following account summarizes the salient physical and anatomical features of *P. excelsa* and *P. rigida*.

Wood hard and heavy, red-brown in color, moderately fine textured and resembling Cuban mahogany *(Swietenia mahagoni)* in appearance but appreciably heavier, about 60 lb. per cu. ft.

Structure.—Pores solitary and in groups of 2–4, moderately small, 120–130μ mean tangential diameter and moderately numerous, 60–70 per 10 sq. mm. in *P. rigida*, slightly smaller and much more numerous, 150–200 per 10 sq. mm. in *P. excelsa*. Vessel–vessel pitting moderately fine, 6–7μ maximum diameter, and the ray–vessel pitting similar, usually with 2–3 rows of pits per ray–vessel field.

Parenchyma vasicentric, sometimes with a tendency to aliform development particularly in *P. excelsa*. Scattered strands (diffuse) common, usually containing chambered crystals. Chambered crystals abundant in the vasicentric parenchyma.

Ray tissue homogeneous; multiseriate rays 1–3, mostly 2 cells wide.

Fibres moderately thick-walled and apparently non-septate.

Growth rings distinct.

Comparison with other species.—The timbers of *P. excelsa* and *P. rigida* are superficially similar to those of species of *Anadenanthera*. Anatomically they are distinguished by their ray width; in *Piptadenia* the rays are typically 2- or occasionally 3-seriate whereas in species of *Anadenanthera* they are typically 4 and occasionally 5 cells wide (fig. 1 and 2).

Material examined.—*Piptadenia excelsa* (Gris.) Lillo, 4 specimens, Argentine Republic; *P. rigida* Benth., 6 specimens, Argentine Republic, Paraguay, Brazil and Florida (cultivated).

PIPTADENIASTRUM

Piptadeniastrum has been established by Brenan for the African species formerly known as *Piptadenia africana*
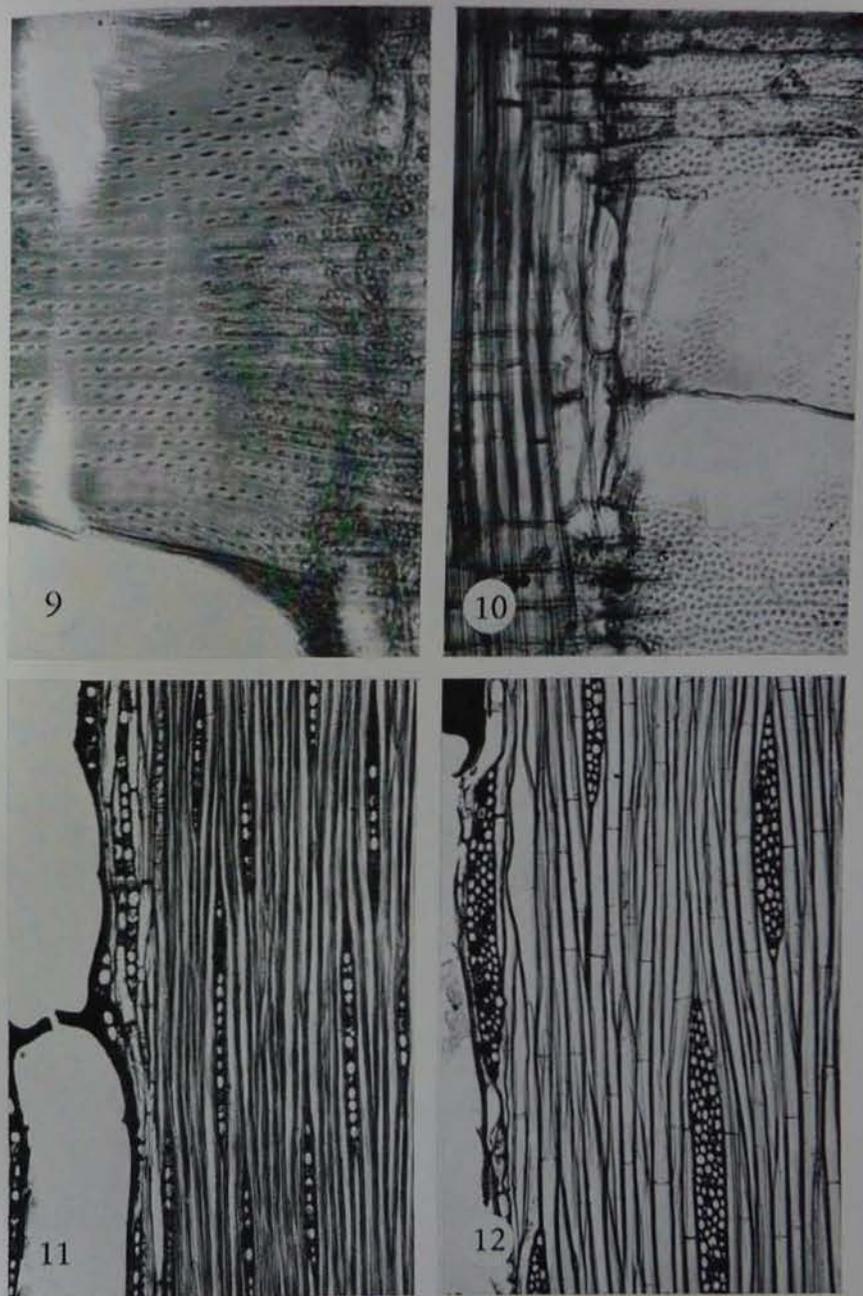

Fig. 9–12.—Fig. 9. *Piptadeniasrtum africanum* and Fig. 10. *Newtonia buchanani*. Radial sections to illustrate size of pits and number of rows of pits per ray–vessel field. Both × 200.—Fig. 11. *Pityrocarpa flava*, tangential section with uniseriate rays and non-septate fibres. × 100.—Fig. 12. *Pityrocarpa gonoacantha*, tangential section showing

Hook.f. and now *Piptadeniastrum africanum* (Hook.f.) Brenan. This species has a wide distribution, from Sierra Leone in the west through Central Africa to Uganda. It has been exploited on a considerable scale and has been exported from Ghana as dahoma, from Nigeria as agboin and ekhimi, from the French West African territories as dabéma and in consignments of mpwere from Uganda.

A number of accounts have been given of the wood and its anatomy (Kribs, 1950; Lebacq, 1954; Normand, 1950; Schmidt, 1949) and the following summarizes only the salient physical and anatomical features.

Wood of medium weight, about 44 lb. per cu. ft.,[6] yellowish brown in color and with a superficial resemblance to iroko *(Chlorophora excelsa)*. It has a very coarse, open texture and a broadly interlocked grain. Freshly sawn the timber has a very strong, unpleasant smell which disappears when the wood is dry.

Structure (fig. 5, 7 and 9).—Pores solitary and in short, radial groups, large, 240–280μ mean tangential diameter, clearly visible to the naked eye, and sparse, 15–30 per 10 sq. mm. Vessel–vessel pitting coarse, 8–10μ maximum diameter, and the ray–vessel pitting similar, usually with 1–2 rows of pits per ray–vessel field (fig. 9).

Parenchyma well developed, vasicentric, often with a tendency to aliform, and confluent towards end of growth zone in some specimens. Scattered strands (diffuse) present, sometimes common and often containing chambered crystals. Chambered crystals present in the vasicentric parenchyma, sparse to moderately abundant.

Ray tissue homogeneous; multiseriate rays 3–7, mostly 4–5 cells wide.

Fibres mostly thin-walled, conspicuously septate.

Growth rings poorly developed.

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[6]Weight range 35–53.5 lb. per cu. ft., average weight 44.4 lb. per cu. ft., based on 24 hand specimens. Sixty-nine specimens, each 5 ft. × 6 in. × 2 in. from 4 trees averaged 45.8 lb. per cu. ft. and varied from 38.8 to 49.7 lb. per cu. ft. at 12 per cent moisture content.

Comparison with other species.—In its anatomical structure *Piptadeniastrum africanum* approaches most closely the species described below as *Pityrocarpa* B and although it can be separated from the species examined, from *P. gonoacantha* and *P. viridiflora* by its larger pores and their smaller number per unit area, and from *P. pteroclada* by the more abundant parenchyma and conspicuous growth rings in the *Pityrocarpa*, the necessity for such separation is unlikely to arise in practice owing to the different geographic distribution of the genera.

Commercially the timber of *Piptadeniastrum africanum* is more likely to be confused with that of the African species of *Newtonia* and reference has already been made to the use of the name mpwere for both *P. africanum* and *Newtonia buchanani* in Uganda. The outstanding differences between African species of *Newtonia* and *Piptadeniastrum* are ray width and the number of rows of pits per ray–vessel field; in *Newtonia* the rays are predominantly bi- and tri-seriate and there are three and sometimes four rows of pits per ray–vessel field, whereas in *Piptadeniastrum* the rays are typically 4- and 5-seriate and the ray–vessel field includes one or at the most two rows of pits.

Material examined.—*Piptadeniastrum africanum* (Hook.f.) Brenan, 27 specimens, Sierra Leone, Ivory Coast, Ghana, Nigeria, Belgian Congo, Uganda.

PITYROCARPA

Eleven species have been included in *Pityrocarpa* by Brenan, all except one South American and mostly Brazilian in origin. The exception, *Pityrocarpa constricta* (Micheli & Rose) Britton & Rose, is a small tree found in Mexico.

The species of *Pityrocarpa* have received scant attention and there are few published descriptions of their timbers. Williams (1936) has described that of *P. pteroclada* (Benth.) Brenan [as *Piptadenia flava* (Spreng.) Benth.], Pereira (1933) has given an anatomical account of the wood of *P. gonacantha* (Mart.) Brenan (as *Piptadenia communis* Benth.)

and Record and Hess (1943) have given a short description of the wood of *Pityrocarpa constricta*.

Ten specimens representing five species were available for study. Anatomically they fall into two distinct groups, viz., 1) those timbers with predominantly uniseriate rays and non-septate fibres, here called *Pityrocarpa* A and comprising *P. constricta* and *P. flava*, and 2) those timbers with multiseriate, commonly 3- and sometimes 4-seriate rays and conspicuously septate fibres, here called *Pityrocarpa* B and comprising *P. gonoacantha*, *P. pteroclada* and *P. viridiflora* (fig. 11 and 12).

Pityrocarpa A

P. constricta. The specimen studied is from the same tree as that described by Record and Hess (1943). The wood is hard and heavy, of the order of 60 lb. per cu. ft., and has a very fine texture. It is a uniform yellowish brown and possibly sapwood throughout.

P. flava. A medium-weight wood, between 40–50 lb. per cu. ft., with a moderately coarse texture and interlocked grain. The heartwood is yellow- to red-brown.

Structure.—Pores solitary and in radial groups of up to 5–6 in *P. constricta;* moderately small, average tangential diameter 140μ and moderately numerous, 65–70 per 10 sq. mm. in *P. flava;* small, tangential diameter $50–90\mu$ and very numerous, exceeding 300 per 10 sq. mm. in *P. constricta.* Vessel–vessel pitting moderately fine, $6–8\mu$ tangential diameter, vessel–ray pitting similar and commonly with 3 rows of pits per ray–vessel field.

Parenchyma sparse, vasicentric with well marked aliform development and locally confluent in *P. flava.* Chambered crystalliferous strands conspicuous.

Ray tissue homogeneous; rays exclusively uniseriate in *P. flava* and predominantly uniseriate but with occasional biseriate parts in some rays of *P. constricta.*

Fibres thick-walled in *P. constricta*, moderately thin-walled in *P. flava* and apparently without septa in both species.

Growth rings present but not well developed in both species.

Pityrocarpa B

Woods light *(P. pteroclada)* to moderately heavy, between 40 and 50 lb. per cu. ft. *(P. gonoacantha* and *P. viridiflora),* coarse-textured and with a straight or slightly interlocked grain. Specimens of *P. gonoacantha* are straw colored or grey with a marked pinkish tint and possibly sapwood throughout. Specimens of *P. pteroclada* and *P. viridiflora* are white or yellow and entirely sapwood; Williams (1936) has described the heartwood of *P. pteroclada* as reddish-brown.

Structure.—Pores solitary and in radial groups of 2, 3 and rarely more; large, in all species the largest exceeding 200μ in tangential diameter and an average size from $130–230\mu$; very sparse, 15–20 per 10 sq. mm. in *P. pteroclada* and sparse to moderately numerous, 30–80 per 10 sq. mm. in *P. gonoacantha* and *P. viridiflora.* Vessel–vessel pitting coarse, $9–12\mu$ tangential diameter but only $7–8\mu$ in *P. viridiflora;* vessel–ray pitting similar with 1–2 rows of pits per ray–vessel field. *P. gonoacantha* has a marked tendency to a semi-ring-porous structure, the size of the early wood pores contrasting with those of the late wood but not forming a distinct pore ring.

Parenchyma paratracheal, vasicentric and with well developed aliform-confluent in *P. pteroclada* and *P. viridiflora.* Chambered crystalliferous strands present.

Ray tissue homogeneous; multiseriate rays commonly three, often four and rarely five cells wide.

Fibres with thin to moderately thick walls and conspicuously septate.

Growth rings poorly developed, marked by a tendency to a ring-porous structure in *P. gonoacantha* and by terminal parenchyma in *P. pteroclada* and *P. viridiflora.*

Comparison with other timbers.—In their anatomy the timbers of *Pityrocarpa* A are similar to those of *Newtonia nitida, N. suaveolens* and *Monoschisma leptostachya,* as all are characterised by the presence of uniseriate rays and absence of septate fibres. They vary in such features as size

and number of vessels, amount and distribution of parenchyma and presence of crystalliferous strands but in the absence of more material, in particular of species of *Pityrocarpa,* it is uncertain how far these features are of diagnostic value for the separation of these timbers.

The species of *Pityrocarpa* B are the only American timbers among those examined with septate fibres. They approach most closely in structure the African timber, *Piptadeniastrum africanum,* and their separation from this timber is discussed under *Piptadeniastrum.*

Material examined.—*Pityrocarpa constricta* (Micheli & Rose) Britton & Rose, 1 specimen, Mexico; *P. flava* (Spreng. ex DC.) Brenan, 2 specimens, Brazil; *P. gonoacantha* (Mart.) Brenan, 4 specimens, Brazil; *P. pteroclada* (Benth.) Brenan, 2 specimens, Peru; *P. viridiflora* (Kunth) Brenan, 1 specimen, Bolivia.

DISCUSSION AND CONCLUSIONS

On the basis of their wood anatomy the species examined can be subdivided into a number of distinct groups, based principally on ray width and the presence or absence of septate fibres as indicated in the following key:

1. Species with septate fibres ....2.
1. Species with non-septate fibres ....3.
2. Species with narrow rays, predominantly 2- and 3-seriate, sometimes commonly 1-seriate; vessel–vessel pitting fine to moderately fine, $4–7\mu$ diameter, vessel–ray pitting similar with commonly 3 and sometimes 4 rows of pits per ray–vessel field ....GROUP I.

    Species examined: *Newtonia aubrevillei, Newtonia buchanani, Newtonia duparquetiana, Newtonia glandulifera, Newtonia griffoniana, Newtonia hildebrandtii, Newtonia leucocarpa, Newtonia paucijuga.*

2. Species with wide rays, commonly 3- and 4-seriate and sometimes 5-seriate; vessel–vessel pitting moderately fine to coarse, $7–12\mu$ diameter, vessel–ray pitting similar with mostly 1–2 rows of pits per ray–vessel field. ....GROUP II, African species.

    Species examined: *Piptadeniastrum africanum.*

....GROUP III, American species.

    Species examined: *Pityrocarpa gonoacantha, Pityrocarpa pteroclada, Pityrocarpa viridiflora.*

3. Species with narrow rays, typically 1-, 2- or 3-seriate ....4.
3. Species with wide rays, typically 4- or 5-seriate ....Group IV.
  Species examined: *Anadenanthera colubrina*, *Anadenanthera macrocarpa*, *Anadenanthera peregrina*.
4. Parenchyma abundant, commonly confluent and locally banded.....
  ....Group V.
  Species examined: *Goldmania paraguensis*.
4. Parenchyma mostly sparse, vasicentric or aliform and rarely confluent except towards end of growth ring...5.
5. Rays uniseriate or practically so ....Group VI.
  Species examined: *Monoschisma leptostachyum*, *Newtonia nitida*, *Newtonia suaveolens*, *Pityrocarpa constricta*, *Pityrocarpa flava*.
5. Rays commonly 2- or 3-seriate ....Group VII, American species.
  Species examined: *Piptadenia excelsa*, *Piptadenia rigida*.
  ....Group VIII, Indian species.
  Species examined: *Indopiptadenia oudhensis*.

It will be seen that the grouping based on anatomical features brings together, for the most part, species which Brenan recognizes as forming distinct genera. The exception to this is Group VI, with representatives of three genera, *Monoschisma*, *Newtonia* and *Pityrocarpa*, characterised by uniseriate rays and non-septate fibres. The species of *Newtonia* represented are those of American origin and are clearly separated from those of African origin which comprise Group I. The uniseriate condition possibly represents an advanced degree of specialisation and it is tempting to link the American species with the more usual bi- and triseriate condition through those African species, e.g., *N. aubrevillei* and *N. duparquetiana*, in which uniseriate rays are common but usually occur with biseriate rays. However, the absence of septate fibres in the American species is in marked contrast to their prominence in all the African species, except the thick-walled *N. hildebrandtii*.

The two species of *Pityrocarpa* included in Group VI, *P. constricta* and *P. flava*, represent the two sections of the genus, section *Pityrocarpa* and section *Orthocraspedon*. These species differ greatly in the size and number of their vessels but otherwise their structure is similar and they are in marked contrast to other species of *Pityrocarpa* examined,

which have rays commonly 3 and 4 and occasionally 5 cells wide and fibres with conspicuous septa.

The presence of *Monoschisma* in Group VI is based on a single specimen of *M. leptostachya*.

It is not intended to imply that the species mentioned above form a distinct natural group but rather that Brenan's classification includes two genera with a greater range of structural variation than is normally associated with that unit, particularly in the Leguminosae. It is possible that *Pityrocarpa* should be recognized as including two distinct types and that the American species of *Newtonia* should be recognized as different from those of African origin and established as a separate section of the genus if the differences are not sufficient to warrant the establishment of a new genus.

A further point of interest is the similarity in structure between species of *Piptadenia (sensu stricto)* and that now known as *Indopiptadenia oudhensis*. These, alone of all the species examined, have bi- and triseriate rays and apparently non-septate fibres. Brenan (p. 179) states that among the genera with exalbuminous seeds, *Indopiptadenia* appears closest to *Piptadenia* itself, and this affinity is fully borne out by the similarity in wood structure of the two genera.

SUMMARY

An anatomical study of the wood of twenty-four species formerly included in *Piptadenia* supports, for the most part, their re-classification into eight genera as proposed by Brenan. A description of each of the eight genera is given together with a key for their separation. Differences between Brenan's classification and that based on wood anatomy occur in *Newtonia* and *Pityrocarpa*, in both of which two distinct types of wood structure can be recognized.

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SOME ASPECTS OF VARIATION IN WOOD

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Anatomists studying the wood of obscure taxa are frequently confronted with a dearth of material both in numbers of samples and sufficiently mature specimens. At times recourse must be made even to the sparse secondary xylem from twigs of herbarium specimens. Results of studies on such limited material are, to be sure, unsatisfactory and inconclusive, and must be qualified with the usual number of modifying adjectives. Rarely is there available to the taxonomic wood anatomist sufficient material (Rendle and Clarke 1934a,b) of little-known taxa to enable him to present anatomical data without also incorporating many qualifications regarding his conclusions.

Several problems beset the anatomist so burdened, chief among which is the question as to the representativeness of the one sample at his disposal. Certainly a single sample, derived from an unknown portion of a plant will not truly represent the variation of anatomical structure in the plant under study. Furthermore, there is undoubtedly variation among different plants in the same taxon (Bailey and Faull, 1934). Rendle and Clarke (1934a) point out the types of variation that may occur in, for instance, vessel diameter: 1) Local variation in a small sample, 2) variations from the pith to periphery, 3) variations from the base of the stem upwards, and 4) variations resulting from changes in external conditions. The latter may be superimposed on the first three types, further complicating the situation. These workers explain that it is possible to eliminate variations of

the second type (effect of distance from the pith) by selecting *adult* material from a *mature* tree. Therein lies one of the most worrisome problems of the anatomist handicapped by limited material. Rendle and Clarke further state that "At any given height in a tree the elements of successive annual rings are progressively larger during what might be called the youthful period, after which the mean size of the elements becomes relatively constant, with small fluctuations due to variations in the external conditions, and the wood is said to be *adult*." These facts were similarly demonstrated many years ago in *Pinus sylvestris* by Sanio (1872) and more recently in *Sequoia sempervirens* by Bailey and Faull (1934). Lately, Youngs (1955) has suggested in his study of *Orthopterygium*, that increase in the size of wood elements with age does not proceed at the same rate for all elements.

The age at which tree species reach maturity doubtlessly varies with the taxon in question (genetic variation), and given his selection of trees, the anatomist, without a tremendous amount of study, can do little more than select the peripheral portions of the wood for his studies and hope that he has chosen mature material. It would be quite impracticable for him first to study radial strips from the woody plants to be considered and to determine in each case whether mature wood is present. The anatomist working with limited material is, therefore, doubly confounded, for often he has no idea of where, radially, his specimens were derived; and if he has peripheral material, the maturity of the tree is still open to question. His best recourse is to qualify his results, making known to readers the limitations of his material and to follow the suggestions given by Rendle and Clarke (1934a,b) for anatomical analyses on limited material.

An example of an anatomical study performed on very limited material is that presented by one of the writers (Stern, 1955). In this work, only a small branch was available for analysis and description. The quantitative data, as may be expected, were subjected to the usual qualifications.

However, after publication of this paper, five more specimens became available. These were analyzed with a view to comparing the results with those presented previously. All of the specimens subsequently available were older than the material studied in the first instance. It should be stated here that material for study was selected from the outer growth ring in all cases.

The species in question, *Gomortega nitida* Ruiz & Pavon, has a restricted range and is known from the vicinity of Concepción, Arauco, Tomé, Collipulli and near the Río Queule in central Chile. The climate here has been recorded (Blair, 1942) as a Mediterranean or subtropical marine type. There is a distinct maximum precipitation from May to August, and the midsummer months of December to February are almost rainless. Thus we can reasonably assume that this marked seasonable variation is responsible, at least in part, for the pronounced growth rings in *Gomortega* and that these are annual in character. In table 1 data are pre

Table 1. SPECIMENS OF *Gomortega nitida* EMPLOYED FOR ANALYSIS

REFERENCE	YALE NUMBER[2]	AGE IN YEARS	DIAMETER IN CM.	COLLECTOR	ORIGIN
A[a]	49370	4	3.0	C. Junge	Concepción
B	49863	13	3.2	L. Rossovsky	Copiulemu
C	49860	15	4.3	L. Rossovsky	Tomé
D	49862	22	3.0	L. Rossovsky	Copiulemu
E	49861	25	9.0	L. Rossovsky	Tomé
F	49846	55	11.0	D. S. Bullock	Tomé

[2]All specimens are housed at Yale University in the Samuel James Record Memorial Collection of the School of Forestry.
[a]Data from Stern, 1955.

sented on the collection, age and diameter of the six specimens under discussion.

For comparison three features possessing phylogenetic significance were chosen: vessel element length, vessel diameter and tracheid length. One hundred measurements on each of these items were made. The results were treated with standard statistical procedures (Rendle and Clarke, 1934b) and the mean, and standard deviation were calculated for each group of data. Range and most frequent range were

also noted and recorded. The results are presented below in tables 2–4.

Table 2. LENGTH OF VESSEL ELEMENTS IN μ

REFERENCE	MEAN	STANDARD DEVIATION	RANGE	MOST FREQUENT RANGE
A	884	168	483–1360	725–975
B	741	110	450–975	600–799
C	762	108	510–990	660–819
D	913	125	600–1230	650–949
E	883	138	600–1230	750–1099
F	971	163	615–1395	850–1099

Table 3. DIAMETER OF VESSELS (TANGENTIAL) IN μ

REFERENCE	MEAN	STANDARD DEVIATION	RANGE	MOST FREQUENT RANGE
A	39	7.0	20–64	35–45
B	36	6.1	22–54	28–44
C	38	8.7	18–61	28–48
D	36	5.9	18–54	28–44
E	42	9.2	22–65	32–56
F	58	13.6	25–79	32–76

Table 4. LENGTH OF TRACHEIDS IN μ

REFERENCE	MEAN	STANDARD DEVIATION	RANGE	MOST FREQUENT RANGE
A	1140	198	629–1615	975–1275
B	991	165	540–1425	750–1149
C	1078	163	675–1425	850–1249
D	1028	183	630–1440	1050–1399
E	1239	199	750–1725	1050–1399
F	1199	190	735–1770	900–1499

Comparison of the morphology of elements was also undertaken. Among the features considered were the nature of the perforation plates, intervascular pitting, vertical parenchyma distribution, pore arrangement, ray type, kinds of imperforate tracheary elements, angle of the vessel element end wall, and pitting between vertical parenchyma and vessels. In only one case was there any pronounced morphological difference among the elements of the different specimens. The single exception was the almost complete absence

of uniseriate vascular rays and the presence of triseriate rays in specimen F. All other specimens showed predominantly biseriate rays and some uniseriate rays. It would appear that in this species, the effect of age on morphology is unimportant, at least after the third year.

The major problem at hand is to determine whether the quantitative data for the sample studied in the first instance, A (Stern, 1955), can be taken as representative for the species. Data such as those presented in tables 2–4 are best analyzed by persons somewhat versed in statistical procedures. However, it is hoped that the simplified analysis presented below will be sufficient to show whether there are significant differences between sample A and each of the other samples.

In order to show this, recourse was made to procedures which would illustrate the significance of the difference between two means; that is, the mean values for specimen A and each of the mean values for the other five samples. It can be demonstrated (Arkin and Colton, 1950) that if the actual difference between two means is larger than 3 standard errors of the difference between these means, the difference is significant and is not caused by chance. The results of these analyses are presented in tables 5–7. Perusal of the signs under the "Significance" column shows rather clearly that in most cases there is a significant difference between measurements in sample A and measurements made on other samples. Therefore we can assume that results previously presented for specimen A were biased and not representative of the total population.

Table 5. SIGNIFICANCE OF THE DIFFERENCE BETWEEN TWO MEANS—VESSEL ELEMENT LENGTH

GROUPS ANALYZED	DIFFERENCE IN μ	STANDARD ERROR OF THE DIFFERENCE	THREE TIMES STANDARD ERROR OF DIFFERENCE	SIGNIFICANCE
A–B	143	20.07	60.21	+
A–C	122	19.97	59.91	+
A–D	29	20.94	62.92	−
A–E	1	21.74	65.22	−
A–F	87	23.41	70.23	+

Table 6. SIGNIFICANCE OF THE DIFFERENCE BETWEEN TWO MEANS—
VESSEL DIAMETER (TANGENTIAL)

GROUPS ANALYZED	DIFFERENCE IN μ	STANDARD ERROR OF THE DIFFERENCE	THREE TIMES STANDARD ERROR OF DIFFERENCE	SIGNIFICANCE
A–B	3	0.928	2.784	+
A–C	1	1.118	3.354	—
A–D	3	0.915	2.745	+
A–E	3	1.158	3.474	—
A–F	19	1.530	4.590	+

Table 7. SIGNIFICANCE OF THE DIFFERENCE BETWEEN TWO MEANS—
TRACHEID LENGTH

GROUPS ANALYZED	DIFFERENCE IN μ	STANDARD ERROR OF THE DIFFERENCE	THREE TIMES STANDARD ERROR OF DIFFERENCE	SIGNIFICANCE
A–B	149	25.77	77.31	+
A–C	62	25.65	76.95	—
A–D	112	26.96	80.88	+
A–E	99	28.07	84.21	+
A–F	59	27.44	82.32	—

It seems evident that what the wood anatomist needs, are some generalizations based on extensive and intensive surveys of anatomical variation which will enable him to interpret more completely and accurately data obtained from restricted material. For instance: Can we generalize as to the age when woody plants reach maturity? How much does this vary among and within species and larger taxa? How do site and other environmental factors influence the size and form of anatomical elements? What are the variations that occur due to proximity to crotches, position on the upper or lower sides of branches? It is true that we have at least partial answers to some of these questions, but for the most part, general rules have not been forthcoming.

Analyses should be designed through the cooperation of anatomists and statisticians which will give us these and other answers upon which generalizations can be based. Studies should be made within species using replicated series to determine the structural variation in *all* parts of the plant. Analyses on different species should be compared and

the whole mass of data treated statistically. This would help in understanding anatomical variation and could lead to the presentation of generalized information on differences within and among woody plants.

SUMMARY

The general problems which face wood anatomists confronted with limited material for study have been discussed. The kinds of variation within wood are shown to be of four kinds, one of which (distance from pith—maturity) is perhaps most influential in determining the size of elements. A brief statistical analysis and comparison of six samples of wood of different ages was made showing that measurements on a single sample are not representative of the population and are biased in that respect. It has been mentioned that observations on these six samples failed to demonstrate any profound morphological differences in anatomy, at least for *Gomortega*. This may be due to the fact that qualitative maturity precedes quantitative maturity (for this species anyway). Suggestions have been advanced for the preparation of exhaustive studies which could result in the presentation of generalizations as regards variation in the anatomical structure of the xylem.

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NOTES FROM THE S. J. RECORD MEMORIAL COLLECTION. I.

GEORGE K. BRIZICKY

Recent examination of material in the S. J. Record Memorial Collection of the Yale School of Forestry, has revealed a number of specimens which seem to be worthy of note. Duplicates of these specimens may occur elsewhere and it will be the purpose of this series to record emendations in the identification of these specimens and/or to bring out interesting features concerning them.

Amphitecna macrophylla (Seem.) Miers (Bignoniaceae). MEXICO: UBERO, OAXACA, *Ll. Williams 9443* (Y 34861). This specimen was previously identified as *Grias fendleri* Seem. On the herbarium sheet, however, Professor Record noted: "Wood different-Leg." The leaf of Williams' specimen is 85 cm. long. The corresponding wood sample is very similar to that of *Enallagma*, and is superficially leguminous in appearance. *Amphitecna macrophylla* is a shrub or tree of restricted occurrence in the montane forests of southern Mexico and Guatemala (Record and Hess. Timbers of the New World. 77. 1943).

Christiana africana DC. (Tiliaceae). E. NICARAGUA: *Shank 118* (Y 46904). The herbarium voucher was previously determined as *Homalium hondurense* J. D. Smith (Flacourtiaceae). The vernacular name was reported by the collector as "palo piedro." Leaves of this sterile collection are fairly large, the biggest being 28 cm. long and 23.5 cm. broad. The basal sinus of the deeply cordate leaves is closed, in which manner Shank's specimen differs from all other herbarium specimens of the species seen by the author. Apparently the collection was taken from a sucker shoot.

Identification of the corresponding wood sample was independent from, and preceded, the determination of the herbarium material. Dr. A. Koehler examined the wood of *Shank 118* and stated: "Does not compare with other *Homalium* spp. from W. Hemisphere. Name on wood

sample is '*Christiana africana* DC.'" (5.15.1952). One can assume that Dr. R. Hess, who was in charge of the Yale Wood Collection at the time Shank's collections were accessioned, identified the wood and wrote the binomial seen by Koehler. Dr. B. F. Kukachka of the U. S. Forest Products Laboratory, while visiting the S. J. Record Memorial Collection, examined the above-mentioned wood sample and marked on the corresponding file card: "Probably *Christiana africana* DC." (9.24.1957). Examination of the herbarium material by the writer has only confirmed the opinion of the wood anatomists.

Shank's collection of *Christiana africana*, made in 1949, seems to be the first known from Nicaragua. Before that, in the Western Hemisphere, the species was reported only from British Honduras in Central America, and British Guiana and northern Brazil in South America. Interestingly enough, in 1926 Standley, reporting on the occurrence of *Christiana africana* in British Honduras, asserted: "This tree is likely to be found along the coast between British Honduras and the Guianas." (Trop. Woods 8: 5).

Qualea cymulosa Schery (Vochysiaceae). COLOMBIA: DEPARTMENT OF BOLIVAR, Lands of Loba, Norosi-Tiquisio trail, *Curran 167* (fr., Y); vicinity of Estrella, Caño Papayal, *Curran 333* (sterile; Y 1539). In his monograph of *Qualea* (Acta Bot. Néerl. 2 (2): 1953) Stafleu cited (p. 202) *Curran 169* as *Qualea cymulosa*. His quotation most likely refers to *Curran 167*, because *Curran 169* from Lands of Loba represents the type collection of *Pithecollobium spinulosum* Pittier (Contrib. U. S. Natl. Herb. 20: 459.1922). The vernacular name of *Curran 167* was reported by the collector as "sabanero."

Swartzia sumorum A. Molina in Ceiba 3: 94. 1952 (Caesalpiniaceae). E. NICARAGUA: *Shank 83* (Y 46873). The collection is represented by several leaves and young inflorescences with flowers in bud. Although *Shank 83* differs from the original description in having 7-foliolate leaves rather than 5-foliolate leaves with mostly more or less obovate leaflets, there is hardly any doubt that it belongs

to Molina's species. Since some details of the floral structure were not mentioned in the original description, it is per- haps useful to add a brief description of the flowers in bud.—Flower buds globose, about 2 mm. in diameter, on pedicels 0.5–1.0 mm. long; calyx entire, closed; petals none (Molina seems to have been somewhat uncertain about the petals for he wrote: *"petala ut videtur nulla."*); stamens about 30 in 2 series; ovary approximately linear, sessile (possibly also subsessile), strongly incurved, dark red- brown, sparsely whitish pubescent at base, stigma small; ovules 9 (in the 2 ovaries seen).—The vernacular name reported by Shank for his specimen is identical with that cited by Molina for *Swartzia sumorum*—"uvillo."

SIGNIFICANT RECENT COLLECTIONS OF *QUERCUS* FROM PANAMA

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In a small collection of *Quercus* collected by Drs. William L. Stern and Kenton L. Chambers from Prov. Chiriqui, Panama, every one proved worthy of note. A full set of their specimens is deposited in the Herbarium of Yale University, School of Forestry (Y) while duplicates are retained in the Muller Collection of the Herbarium of the University of California, Santa Barbara College (SBC). I have added sev- eral specimens bearing upon the same species submitted by Dr. Robert E. Woodson, Jr., of the Missouri Botanical Gar- den (MO) where the originals of these are deposited, with duplicates in my own collection (SBC). I am obliged to Drs. Stern and Woodson for making the specimens available for study.

Quercus corrugata Hook. This species, well known from Chiapas to Costa Rica, has not previously been re- ported from Panama. The material now available is in good condition, accompanied by fruit, and readily recognizable.

Specimen examined: PANAMA, Prov. Chiriqui, north of El Hato, Volcan Baru, at 1570 m. elev., June 5, 1957, *Stern and Chambers no. 47.*

Quercus gulielmi-treleasei C. H. Mull. Although this species was originally described from the same general area, the collection here reported illustrates luxuriant develop- ment of the vegetative characters. Unfortunately, the fruit associated with it is said by the collectors probably to be mixed with that of a neighboring tree of another species.

Specimen examined: PANAMA, Prov. Chiriqui, north of El Hato, Volcan Baru, at 1570 m. elev., June 5, 1957, *Stern and Chambers no. 52.*

Quercus baruensis C. H. Mull. sp. nov. Arbor grandis, ramuli 1.5–3 mm. crassi glabrati vel dense stellato-tomentosi, geminae 2–3 mm. longae rotundo-ovoideae flavae, stipulae caducae, folia decidua (?) integra lanceolata apice acuminata haud aristata subtus circa costa stellato-tomentosa, fructus annuus brevipedunculatus, cupula 13–17 mm. lata, 8–10 mm. alta margine non involuta, squamae appressae omnino puber- ulentae, glans 10 mm. alta, 15 mm. lata circa ⅔ inclusa.

Tree to 30 m. tall, the trunk to 1.8 m. in diameter. Twigs 2 to 3 mm. in diameter, nearly glabrous or densely stellate- tomentulose, soon or tardily glabrate with inconspicuous light lenticels, gray the second year and the lenticels numer- ous and more prominent (this variation occurring as poly- morphism of individual trees). Buds 2 to 3 mm. long, ovoid, apically rounded, dull straw-colored, the scales markedly ciliate or glabrate; stipules quickly caducous (not seen). Leaves deciduous (?), firm and coriaceous, 10 to 15 cm. long, 2.5 to 6 cm. broad, entire, lanceolate or ovate-lanceolate, acuminate, the ultimate apex not aristate, cuneate to obtuse at base, blades dull green and glabrate above or sparingly stellate pubescent along the base of the midrib, very dull beneath, the midrib and veins persistently stellate-tomentose, especially in the axils, margins nearly flat, minutely cartil- aginous; veins about 8 to 10 on each side, obviously branch- ing and anastomosing toward the margin, minutely raised on the upper surface, rather prominently raised on the lower

surface; petioles 8 to 18 mm. long, winged by the decurrent blade, the upper surface flattened, pubescent or glabrate like the twigs. Flowers not seen. Fruit annual, solitary (from short multi-flowered catkins) on short, thick peduncles 3 to 10 mm. long and 3 to 5 mm. thick; cups 13 to 17 mm. broad, 8 to 10 mm. deep, cup-shaped, the bases rounded, the margins not inrolled, the scales tightly appressed, prominently tan-puberulent all over; acorns about 10 mm. long and 15 mm. broad, densely puberulent, about ⅔ included.

Specimens examined: PANAMA, Prov. Chiriqui, north of El Hato, Volcan Baru, at 1570 m. elev., June 5, 1957, *Stern and Chambers no. 55* (type in Y); Cerro Punta, at 1800 m. elev., June 7, 1957, *Stern and Chambers no. 76;* at 2000 m. elev., May 24, 1946, *P. H. Allen nos. 3496* and *3523;* Llano del Volcan, at 1500–1600 m. elev., May 27, 1946, *P. H. Allen and G. Fairchild nos. 3464* and *3467.*

Quercus baruensis is readily distinguished from *Q. seemanni* Liebm. by the pubescence of its twigs, the extensiveness of its leaf pubescence, and the uniformity of the puberulence of its cup scales. The same characters and the annual fruition distinguish it from *Q. esesmilensis* Tucker and Muller. From *Q. gulielmi-treleasei* C. H. Mull. it is distinguished by its rather large fruit, elongate petioles, and thick leaf blades. The addition of *Q. baruensis* to the already confusing assemblage of entire-leaved black oaks is not to be undertaken without a high degree of confidence, for this group constitutes one of the most difficult problems in the genus. The scarcity of material of some species, the intricate pattern of distribution and isolation of populations, and the general similarity and lack of prominent differences among the species combine to complicate the problem. Fortunately, *Q. baruensis* differs so markedly from the previously known species of this assemblage that it is not difficult to recognize.

Fig. 1–2. *Quercus baruensis* C. H. Mull., sp. nov.—Fig. 1. The type, *Stern and Chambers no. 55* (Y).—Fig. 2. A representative specimen, *Stern and Chambers no. 76* (SBC).

CURRENT LITERATURE

What flowering tree is that? A handbook for the tropics. *Edwin A. Menninger*, Southeastern Printing Co., Stuart, Florida. 1–176 and index, 6 plates, 300 illustrations. 1958. Cloth bound $4.00, paper bound $2.50.

This attractively bound volume is designed "to describe outstanding (tropical and subtropical) trees whose flowers are a conspicuous feature of their growth." The title is somewhat misleading, for it implies an all-inclusiveness not evident in the subject matter. Following the author's pretentious introduction (The trees described in this book "are only a fractional part of the flowering trees I am growing for the eventual beautification of all Florida.") is a "Description of the trees" comprising most of the book. Two small chapters, "Description of the vines" and "Flowering calendar of tropical trees in South Florida," as well as enumerations of "wind-resistant trees," "fruit trees," "trees for wet ground," "plants that make good hedges," "fragrant-flowered trees," "good shade trees," and "ornamental foliage trees" are added. A table of contents and index of tree families precede the introduction, and an index of common and scientific names completes the volume. Essentially, the book is a catalogue of about 1000 tropical and subtropical trees and shrubs with high ornamental value, most of them growing in the author's garden at Stuart, Florida. The descriptions are arranged by family, the latter being listed in alphabetical order according to their Latin names. Each tree in the catalogue is provided with a common name, a Latin binomial and an informal description. Nearly 300 excellent black and white photographs illustrate attractive features of the plants under discussion.

There are a few points in the text which the reviewer would like to call to the attention of the author for possible consideration in the preparation of future editions. Latin generic names are abbreviated by their initial letter when the author employs the generic name as a common name,

e. g., "Red Ruttya *(R. fruticosa)*," "Indian Alangium *(A. salviifolium)*." This manner of citation is not in the best form, as readers unfamiliar with generic names might not realize to what name author Menninger refers when he employs an initial letter. To avoid confusion it is suggested that the full generic name always be used, at least where the genus is first mentioned.

In many cases the spelling of Latin specific epithets is not in accordance with the International Code of Botanical Nomenclature, 1956, Recommendation 73 C (b): "When the name ends in a consonant, the letters *ii* are added *(ramondii* from Ramond), except when the name ends in *-er*, when *i* is added (thus *kerneri* from Kerner)." Therefore "*Ruttya scholessi*" must be spelled *Ruttya scholesii*, "*Alangium lamarcki*" should be *Alangium lamarckii*, and so forth.

The author (p. 13) spells "*Rauvolfia*" and states that this is the correct transcription because "there is no 'w' in Latin," nevertheless he writes *Swartzia* and *Brownea*. Article 73 of the International Code of Botanical Nomenclature rules as follows: "The consonants *w* and *y*, foreign to classical Latin, and *k*, rare in that language, are permissible in Latin plant names." Some degree of consistency would be desirable.

According to the author " 'dendron' is Latin for foliage" (p. 72), although in fact, it is Greek for "tree." The common name of the family Caesalpiniaceae is given as "Bean Family." This is likely to be misleading because the true bean, *Phaseolus*, belongs to another taxon, Papilionaceae (Fabaceae). *Tabebuia avellanedae* (not *avellanadae*) and *Tabebuia ipe* are listed as different species, but according to monographer Dugand (Mutisia 25: 12.1956) they are conspecific, and the former binomial is valid. The name applied to the author's "Colombia trumpet," *Tabebuia gaudichaudia* (the correct spelling must be *gaudichaudii* or *gaudichaudiana*), appears to be open to question, for this binomial could not be located in either the *Index Kewensis* or in Dugand's monograph of Colombian tabebuias (Bignoniaceae: El genero *Tabebuia* in Colombia. Mutisia 25: 1–22. 1956).

The native origins of trees as given on pages 170–172 could certainly be emended, e. g., *Gliricidia sepium* and *Cordia alliodora* are not restricted to the West Indies as the author implies. It is hoped that the above notes will bring to the attention of Mr. Menninger a few of the more obvious inconsistencies in his volume.

The cultural recommendations of the author, mostly based on his personal experiences, will be very useful to subtropical gardeners. The tabulations of trees and shrubs according to their hardiness and use in gardens, and for planting in various habitats will guide enthusiasts in the selection of these ornamentals. In general, Menninger has prepared a volume which is admirable, in that it points out many uncommon and strikingly beautiful flowering trees which can be grown in southernmost United States. It is a book which all gardeners will want.—*George K. Brizicky*, S. J. Record Memorial Collection, School of Forestry, Yale University, New Haven, Connecticut.

TROPICAL WOODS

CONTENTS

THE WOODS AND FLORA OF THE FLORIDA KEYS. COMPOSITAE[1]

SHERWIN CARLQUIST

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The fact that Compositae is the largest family of flowering plants is probably related to its wide distribution in both temperate and tropical regions. In his *Flora of the Florida Keys*, Small (1913) lists 40 species. Ledin (1951) records 125 species for the South Florida region. He considers that a low representation of tropical species occurs because frost-free areas are present mostly in shady hammocks where Compositae (which typically occur in sunny locations) are unlikely to grow. Nevertheless, he finds that 48 per cent of the South Florida Compositae represent floristic elements of Mexico, Central America, South America, and the West Indies. The remainder of the species are either typically North American or widespread species. Because many Compositae are adapted to alkaline or disturbed areas, the Florida Keys offer a number of suitable habitats for such weedy species. Many of the species included in this study are of this nature. Twelve species of Compositae form the basis for the present investigation. Although additional species, with relatively small accumulation of secondary xylem could have been added, all the truly woody species of Compositae are represented here. The most woody species of Compositae in the Florida Keys are *Baccharis halimifolia* and *Pluchea odorata*.

Although various authors, such as Small (1913), have divided the Compositae into three families, Ambrosiaceae,

Carduaceae, and Cichoriaceae, this practice has not been accepted by most authors. The group recognized by Small as Ambrosiaceae is more generally treated as a tribe (Ambrosieae), or even a subtribe (Ambrosinae) of Heliantheae. Likewise, the group treated by Small as Cichoriaceae is better regarded as a tribe, Cichorieae, of Compositae. Although it is the most easily defined tribe in the family, members of Cichorieae possess no characters which do not occur also in the other tribes.

TRIBE EUPATORIEAE

EUPATORIUM FRUSTRATUM B. L. Robinson, Proc. Amer. Acad. 47: 193. 1911. *Osmia frustrata* (B. L. Robinson) Small, Fl. Florida Keys 147. 1913.

Eupatorium frustratum is a shrubby perennial, with slender grooved stems 5–10 dm. tall. The leaves are ovate-lanceolate to deltoid-ovate, opposite, up to 6 cm. long and 3 cm. wide. Leaves have three palmately arranged primary veins, dentate margins, and a usually obtuse tip. The herbage is lightly covered with inconspicuous uniseriate trichomes. The heads are oblong-campanulate, 5–8 mm. long. Involucral bracts are elliptic to lanceolate, greenish to greenish-white and bear 5–8 of the linear markings characteristic of involucral bracts in the genus. The heads are discoid and the receptacle convex. Corollas have a bluish or purplish-blue color and are about 4 mm. long. The pappus is composed of numerous capillary bristles about 4 mm. in length. Achenes are black, 4–5 angled, about 4 mm. long. A marked aroma is characteristic of this plant.

General distribution.—Eupatorium frustratum is endemic to the South Florida region (Ledin, 1951).

U. S. distribution.—Ledin (1951) indicates that the species occurs on Cape Sable, Key Largo, and the Ten Thousand Islands. According to Davis (1942) it occurs on the Sand Keys. Therefore, it is more nearly endemic to the Keys than any other Compositae considered here.

ANATOMY[2]

Growth rings are moderately distinct in the specimen studied. Vertical elements of the xylem consist of vessel elements, libriform fibers, and vasicentric parenchyma exclusively.

Pores are somewhat angular in transection. Vessel groupings, where they occur, are mostly radial, with an average of 1.8 pores per group.[3] The range in tangential pore diameter is $15-42\mu$. The most frequent range is $22-30\mu$, and the average diameter is 24μ. Tyloses are absent. Perforation plates are simple and circular in outline. The end walls of vessel elements form an angle which varies between 40 and $75°$ with the horizontal. The average angle is about $45°$. Intervascular pitting consists of alternate circular bordered pits, about 3μ in diameter. Pit apertures are narrow, slit-like, and arranged nearly horizontally. Helical grooves or thickenings are absent. Vessel element length ranges between 84 and 238μ. The most frequent range is $140-190\mu$, and the average length is 157μ.

Libriform fibers are non-storied and average about 350μ in length. They are moderately thick-walled, and possess the simple pits with elongate oblique apertures characteristic of libriform fibers in Compositae.

Ray tissue may be considered as homocellular, because cells are square to upright as seen in radial section. Uniseriate

[2] In this, and the following series of papers, the anatomical methods employed are those in common use and may involve softening in hydrofluoric acid, embedding in celloidin and staining in safranin and Heidenhain's iron-alum haematoxylin. Where several specimens of a species are available, the largest, most mature material is utilized. No attempt is made in this paper, nor in any of the series to follow, to treat measurements statistically, although means, extremes and most frequent ranges, based on samples of 50 measurements each are presented. Except where otherwise stated, nomenclature follows that recommended by the Committee on Nomenclature, International Association of Wood Anatomists in the new *International glossary of terms used in wood anatomy* (Trop. Woods 107: 1–36. 1957).

[3] This measurement, which has been found useful in earlier studies of Compositae (Carlquist 1957, 1958) is defined and discussed by the writer in an earlier paper (1958).

rays are absent or nearly so. Multiseriate rays are difficult to define precisely, as seen in tangential section, because upright cells on the lateral faces and upper and lower tips of rays approximate libriform fibers in shape and size. Rays are mostly 3 or 4 cells wide at their widest point. Although vertical height of rays varies widely, the average height is .54 mm., and few rays exceed 1 mm. in height. The average ray is about 11 cells in height. All ray cells are lignified, and pitting among ray cells consists of abundant, small, simple pits.

Axial parenchyma is present as scanty vasicentric cells which form an incomplete sheath, never more than a single cell in width, around vessels or vessel groups. The walls are relatively thick. As seen in tangential or radial section, vertical parenchyma cells are usually subdivided into strands of two cells.

No resinous deposits nor crystals were observed in any cells.

Discussion of the wood anatomy of this species follows the description of *Eupatorium odoratum* below.

Specimen examined.—LIGNUM VITAE KEY: Erect plant, somewhat woody at base; heads blue-flowered; growing in cut-over area; 22 March 1958, *W. L. Stern & K. L. Chambers 277* (Y; Yale wood no. 51480; RSA).[4]

EUPATORIUM ODORATUM L., Syst., ed. 10. 1205. 1758. *Osmia odorata* (L.) Sch.-Bip., Pollichia 22–24: 256. 1886.

Eupatorium odoratum is a scandent, much-branched shrub, 6–18 dm. in height. The stems are greenish, smooth, and bear a light covering of uniseriate trichomes. Leaf blades are 4–10 cm. long, 2–5 cm. wide, ovate to lanceolate. Leaves are opposite and glabrescent above, but covered with a dense aggregation of uniseriate trichomes on the lower surface. The three primary veins of the lamina are palmately arranged. Leaf margins are variously dentate; the tip of the leaf is acuminate, although bluntish at the apex. Heads are

[4]Herbarium abbreviations are according to Lanjouw & Stafleu, *Index Herbariorum*, ed. 3.

arranged in a corymb at the ends of the branches. Heads are cylindrical, 8–10 mm. in length. Involucral bracts are deltoid to lanceolate, have a darkened tip, and bear 3–5 of the linear markings characteristic of the genus. Heads are discoid and have a flat receptacle. The flowers are about 7 mm. long, the corollas 5 mm. in length, white or sometimes lilac. The pappus consists of capillary bristles, about 5 mm. in length, which turn tawny upon drying. Achenes are black, 4–5 angled, about 5 mm. long. The herbage is aromatic when crushed.

General distribution.—According to Ledin (1951), *Eupatorium odoratum* occurs in the West Indies, Cuba, Central and South America, as well as in South Florida.

U. S. distribution.—Ledin (1951) records the species near Coral Gables, on Cape Sable, and on Key Largo. Small (1913) recorded it from "Upper Keys"; the specimen under study was collected on Plantation Key. Apparently the distribution of this species is limited by frosts. Clearly, it represents a tropical species, the northern limit of which is South Florida. It appears to prefer moist, shady locations, such as hammocks.

ANATOMY

Growth rings are present, although not strongly marked. Vertical elements of the wood consist of vessel elements, fibers, and vertical parenchyma.

Pores are rounded in outline, as seen in transection. Pore groupings are mostly radial; the average number of pores per group is 1.93. Tangential pore diameter varies according to position in growth rings; the range is 28–81μ. The most frequent range is 42–48μ, and the average diameter is 48μ. Tyloses are absent. The perforation plate is simple, and is round or somewhat oval in outline. The perforation plate may be oriented in directions other than strictly radial. The end wall angle of vessel elements is highly variable and ranges between 10 and 60° with the horizontal. The average angle is about 30°. Intervascular pitting consists of alternate circular bordered pits, the cavities of which are about 3μ in diameter. Pit apertures are narrow, nearly horizontal,

and fade into the helical grooves which connect pit aper-
tures on the inner surface of the vessel wall. This is much
like the condition illustrated in the present paper for *Pluchea
odorata* (fig. 7). On vessel walls facing parenchyma, pits
are sparser, and portions of the wall not bearing pits may
show very fine helical striae. The range in vessel element
length is 70–420μ; there is a tendency for vessel elements
to become shorter and wider in the early wood of each
growth ring. The most frequent range in vessel element
length is 266–378μ, and the average length is 278μ.

Libriform fibers are non-storied and approximately 700μ
in length. They are relatively thin-walled, although thicker-
walled fibers occur in xylem laid down near the end of a
season. Pitting of libriform fibers consists of simple pits
with narrow, oblique apertures.

Rays, as seen in tangential section, are fairly abundant,
and may occupy a third of the area of such a section. Rays
may be considered as homocellular because they consist of
cells square to upright in shape, as seen in radial section.
Uniseriate rays are absent or nearly so. Multiseriate rays
vary greatly in vertical height; some are extremely high,
and narrowed at places along the height, giving the appear-
ance of vertically superposed rays. The average ray is 1.9
mm. in height, and about 30 cells high. Most rays have a
maximum width of from 4 to 7 cells. Upright cells are
present along the lateral faces of the rays, and may be pres-
ent at the upper and lower tips. Because these upright cells
are libriform, the precise limits of rays may be difficult to
define, as seen in tangential section. Walls of ray cells are
lignified, although thin, and bear numerous small simple pits.

Axial parenchyma consists exclusively of scanty vasicen-
tric parenchyma. Such cells form only a partial sheath,
never more than a single cell in width, around a vessel or
vessel group. Often, only one or two parenchyma cells are
adjacent to a vessel. As seen in a longitudinal section, verti-
cal parenchyma cells are subdivided into strands of two
cells.

Resinous deposits occlude a few of the vessels. Between
ray cells there are small deposits of resin-like substances
which carbonize. No crystals were observed.

Discussion

The two species of *Eupatorium* described here differ in
vessel diameter and length of vessel elements and libriform
fibers. The figures are greater for *E. odoratum*, and this
fact may be related to the scandent habit of that species.
Other differences occur in respect to ray height and accumu-
lation of resinous deposits.

Metcalfe and Chalk (1950) report the following char-
acters for *Eupatorium:* pores in radial groupings (figured for
E. hiemale); pores mostly less than 50μ in diameter; rays
often exceeding 1 mm. in height; pit apertures of vessel pits
confluent (because of the helical grooves mentioned above
for *E. odoratum*). All of these characters are found in *E.
odoratum,* but only the first two hold true for *E. frustratum.*

Obviously, more data on wood anatomy in this large
genus are needed. However, the fact that *E. frustratum* and
E. odoratum are different in certain respects, although *E.
odoratum* fits descriptions previously given for *Eupatorium,*
suggests that the segregation of the two species from *Eupa-
torium* as *Osmia* (e.g., Small, 1913; Ledin, 1951) does not
seem to be supported.

Specimen examined.—PLANTATION KEY: Shrub,
woody at base; foliage aromatic; fruiting; in hammock; 21
March 1958, *W. L. Stern & K. L. Chambers 257* (Y; Yale
wood no. 51468; RSA).

Tribe Heliantheae

subtribe coreopsidinae

Bidens pilosa L. var. radiata Sch.-Bip., in Barker-Webb &
Berthelot, Hist. Canar. III, 2: 242. 1836–1850. *B. pilosa* var.
alba (L.) O. E. Schulz, in Urban, Symb. Ant. 7: 136. 1911.
B. leucantha (L.) Willd., Sp. Pl. 3: 1719. 1804. For a full
synonymy, see Sherff (1937, p. 430). A detailed discussion
of the nomenclature of this taxon is also given by Sherff
(1937, p. 439).

Bidens pilosa var. *radiata* is an upright, usually annual herb, 4–10 dm. tall. The stems are 4-angled. Simple leaves occur near the base of the plant, although the upper ones are typically trifoliate. Inconspicuous uniseriate trichomes are present on the lower surface of the leaves, along the petioles, and within the joined bases of the pair of opposite leaves at each node. Leaflets have serrate or dentate margins, acuminate tips, and are ovate to lanceolate in shape, up to 6 cm. long and 4 cm. wide. Heads are in groups of 1–3 at the ends of branches. The involucres are campanulate, with the bracts of the outer series green, oblanceolate, united by their bases, and somewhat shorter than those of the inner series. Receptacular bracts are lanceolate and present throughout the head. Three to 6 ray flowers may be present; corollas are whitish, drying yellow, and may be entire or with 2–3 lobes. Disk flowers yellow, corollas 4–6 mm. long. The achenes are crowned by two awns with recurved barbs, and are 5–9 mm. long in fruit.

General distribution.—Bidens pilosa var. *radiata*, originally a native of tropical America, has spread as a weed over warm, dry places in both hemispheres. According to Sherff (1937), New World localities include Mexico, Central America, South America to Chile and southernmost Brazil, Cuba, Haiti, Puerto Rico, Jamaica, and many other West Indian islands. In the Old World, he records it from both North and South Africa, the Canary Islands, China, and Thailand. According to Ledin (1951) it also occurs in the East Indies, the Hawaiian Islands, and other Pacific islands.

U. S. distribution.—Bidens pilosa var. *radiata* is frost-sensitive, but can grow during the warmer portion of the year as far north as Massachusetts (Ledin, 1951). It has been recorded in California, Arizona, and Louisiana (Sherff, 1937) as well as in Georgia and Alabama (Ledin, 1951), but the greatest concentration, according to these authors, appears to be in Florida. Within the Keys, it occurs on both Upper and Lower Keys, and on the Sand Keys (Small, 1913).

ANATOMY

Although an herb, *Bidens pilosa* var. *radiata* is capable of considerable xylem accumulation at its base. Growth rings are present. Vertical elements of the xylem consist exclusively of vertical parenchyma, vessel elements, and libriform fibers.

Pores are rounded in outline, as seen in transection. Pore groupings occur mostly in the form of radial rows, and an average of 1.9 pores is present per group. The range in tangential pore diameter is 30–108μ. The most frequent range is 40–65μ, and the average diameter is 59μ. A few thin-walled tyloses are present. Perforation plates are simple and nearly circular. The end-wall angle ranges between 10 and 60°, and the average angle with the horizontal is 45°. Intervascular pitting consists of alternate oval bordered pits, approximately 6μ at their widest diameter. A few transitional pits occur. Apertures are slit-like, nearly horizontal, and lenticular in face view. A few faint striae are present on some vessel walls. The length of vessel elements is 98–490μ. The most frequent range is from 224 to 350μ, and the average length is 265μ.

Libriform fibers typically occur in a storied pattern, and average 350μ in length. They are relatively thin-walled, although some variation occurs depending on position in growth rings. Pitting consists of small simple pits with narrow oblique apertures.

Rays are homocellular; they consist almost exclusively of upright cells. Horizontal subdivision of some upright cells results in the presence of some square cells, as seen in radial section. A few square cells also originate from cambial ray initials. Uniseriate rays are absent or nearly so. Because upright ray cells are present on lateral faces and on the upper and lower tips of rays, the precise limits of a ray, as seen in tangential section, are sometimes difficult to define. Most rays have a maximum width of 4 cells. Multiseriate rays vary in height between 0.4 and 6.4 mm. The average ray height is 2.4 mm., and such a ray is about 35 cells high. Walls of ray cells are lignified, but rather thin, compared with those of other Compositae.

Axial parenchyma consists of scanty vasicentric paren-
chyma exclusively. This is present as a partial sheath, never
more than a single cell wide, around vessels and vessel
groups. As seen in longitudinal sections, parenchyma cells
are approximately the same length as the vessel element
they accompany, and are typically not subdivided into
strands.

Resinous deposits occlude some vessels and fibers, and are
present in the form of droplets in ray cells and vertical
parenchyma. No carbonization of these substances occurs.
No crystals were observed.

DISCUSSION

In an earlier paper (Carlquist, 1958), the wood anatomy
of several members of Heliantheae, subtribe Coreopsidinae,
was investigated. The resemblance in wood anatomy be-
tween *Bidens pilosa* var. *radiata* and one of these, *Bidens
hendersonensis,* is extremely close both in qualitative and
quantitative characters, and the two species could probably
not be distinguished with regard to wood anatomy. Appro-
priately, the other members of Coreopsidinae differ in vari-
ous respects of wood structure from these two species of
Bidens. Further investigation is needed to determine if the
genus *Bidens* is indeed quite uniform in respect to wood
anatomy.

Specimen examined.—PLANTATION KEY: Semi-shrub,
1 m. high, woody at base; more basal leaves simple, upper
ones compound; heads with white ray flowers and yellow
disk flowers; in hammock; 21 March 1958, *W. L. Stern &
K. L. Chambers 256* (Y; Yale wood no. 51467; RSA).

SUBTRIBE VERBESININAE

BORRICHIA ARBORESCENS (L.) DC., Prod. 5: 489. 1836. *Buph-
thalmum arborescens* L., Sp. Pl. 1273. 1753. *Diomedea glab-
rata* HBK., Nov. Gen. Am. 4: 213. 1820. *Diomedea inden-
tata* Cass., Dict. Sci. Nat. 13: 284. 1826.

Borrichia arborescens is a shrub 2–12 dm. in height. The
bark is smooth and light tan in color. The leaves are oppo-
site, oblanceolate, and succulent, so that the venation is not

obvious on the surface. The leaves are up to 6 cm. in length
and 1 cm. in width. Leaves are glabrous, although the stem
is covered by a dense felt of very short uniseriate trichomes.
The leaf pair, upon dehiscence, leaves a pair of persistent
bract-like pegs which are arranged at right angles to the
midvein of the leaf pair. The heads are solitary, terminal on
branches. Involucres are cup-shaped and have a diameter of
8–12 mm. The involucral bracts are appressed and some-
what succulent at their bases. The outer bracts are acute,
and the inner are rounded at their apices. Receptacular
bracts are oblong and rounded at their apices. The ray
flowers are 8–15 in number. The ray corollas are yellow;
the expanded portion of the corolla is 3–5 mm. long, and
either simple or with a pair of rounded lobes at the apex.
Disk corollas yellow, about 5 mm. in length. Achenes are
black, about 5 mm. in length and crowned by several short
papery calyx teeth. The leaves are aromatic and the stem
often exudes an amber, resin-like substance.

General distribution.—According to Small (1913), the
species occurs in Bermuda, the Bahamas, Cuba, and the
Antilles. Ledin (1951) lists it as also occurring in Central
America. Within the United States, it appears to be re-
stricted to the southern portion of Florida.

U. S. distribution.—A record of the occurrence of *B.
arborescens* on the peninsular portion of Florida is given
by Small (1903). It has, however, been most frequently
collected on the Keys, and Small (1913) indicates that it
occurs on the Upper and Lower Keys as well as on the
Sand Keys. Correlated with its succulent nature are the
alkaline or halophytic locations in which it grows.

ANATOMY

A single growth ring was observed near the periphery of
a stem from the specimen *Stern & Brizicky 232.* Otherwise
growth rings are apparently lacking. This growth ring was
characterized by a narrow band of very narrow vessels
admixed with vertical parenchyma. The band apparently ex-
tended completely around the stem. The vertical paren-
chyma of this band is not distributed in accordance with

the vessels, although some parenchyma cells are in contact with vessels. The parenchyma of these bands is therefore best termed apotracheal. These bands are discussed more fully below for *B. frutescens*, in which they are more frequent. They are illustrated for that species in fig. 3-4.

Pores are not appreciably angular in transection. Grouping of pores is relatively infrequent, and the average number of pores per group is 1.49. The range in tangential diameter of pores is 30–90μ. The most frequent range is 36–47μ, and the average diameter is 45μ. Tyloses are absent. Perforation plates are simple and circular or nearly so. The angle of the end wall of vessel elements varies between horizontal and 50° with the horizontal. The average is about 30°. Intervascular pitting consists of alternate oval bordered pits which measure about 3 by 5μ. Some transitional pitting is also present. Apertures are rather wide and lenticular in shape. Vessel elements have a range in length of 70–238μ. The most frequent range is 154–196μ, and the average length is 164μ. A very few vascular tracheids were observed.

Libriform fibers have an average length of 275μ. They are often septate. Walls of fibers are relatively thick. Pitting consists of small simple pits with slit-like oblique apertures.

Rays are composed of cells square to procumbent in radial section. A few upright cells are present along the upper and lower tips of rays, but not along lateral faces. Uniseriate rays are absent or nearly so. Most multiseriate rays are 4 cells wide at their widest point. Although the variation in ray height is great, the average ray height is 1.1 mm. Such a ray is about 27 cells in height. Walls of ray cells are lignified and bear numerous small simple pits.

Scanty vasicentric parenchyma is present in the form of a partial sheath around vessels and vessel groups. Such parenchyma cells are relatively thick-walled, and are sometimes subdivided into strands of two cells, as seen in a longitudinal section. The apotracheal parenchyma cells mentioned above are subdivided into strands of two cells, as seen in longitudinal section.

The abundant secretion of resin-like compounds was illustrated photographically in an earlier paper (Carlquist, 1958). Such resins may occlude vessels, fibers, and both vertical and ray parenchyma cells. Even in cells where such large deposits are not present, resin-like deposits often occlude pits of all but the most recent cells of the wood. Some of the resinous deposits are carbonized. Crystals were not observed. A discussion of the wood of *Borrichia arborescens* follows the description of *B. frutescens* below.

Specimens examined.—BIG PINE KEY: Succulent woody shrub, 18–24 in. high; flowers yellow; fruits present; in sandy strand at extreme south end of key near sea; 23 June 1956, *W. L. Stern & G. K. Brizicky 232* (Y; Yale wood no. 51076; RSA). Low shrub, 2½ ft. high; leaves fleshy and aromatic; flowers yellow; plant parts exude a sticky, amber-colored sap; at north end of key, edge of hammock; 27 June 1956, *W. L. Stern & G. K. Brizicky 288* (Y; Yale wood no. 51119; RSA).

BORRICHIA FRUTESCENS (L.) DC., Prod. 5: 489. 1836. *Buphthalmum frutescens* L., Sp. Pl. 1273. 1753. *Buphthalmum incanum* Mill., Gard. Dict., ed. 8, 1768. *Diomedea bidentata* Cass., Dict. Sci. Nat. 13: 283. 1826. *Diomedea linearis* Cass., Dict. Sci. Nat. 13: 283. 1826.

Borrichia frutescens is a shrub, 2–7 dm. in height, with smooth, light tan bark. The leaves are opposite and oblanceolate, up to 7 cm. long and 2 cm. wide, or spatulate, up to 5 cm. long and 3 cm. wide. Leaf tips are acuminate or acute, and a few teeth may be present along the margins or they may be altogether lacking. In plants with broader and less succulent leaves, the major venation is visible on both surfaces. Both stems and leaves are densely covered with short, uniseriate trichomes. The pairs of leaves, upon dehiscence, usually leave a pair of persistent bract-like pegs which are arranged at right angles to the midvein of the leaves. Involucral bracts are imbricate, pubescent, not appreciably succulent; the outer bracts are markedly reflexed. Both involucral and receptacular bracts are lanceolate, and the receptacular bracts are terminated by a stout spine. Ray

flowers are 12 to 18 in number. Ray corollas are yellow; the expanded portion is about 5–10 mm. in length, and terminated by three lobes. Disk flowers are yellow, with corollas about 4 mm. in length. Achenes at maturity are about 3 mm. long, and are glabrous, black, and crowned by a cup-like calyx.

General distribution.—Borrichia frutescens is more widespread than *B. arborescens*. It has been reported in Bermuda (Small, 1913) and Yucatan (Ledin, 1951) as well as in the U. S.

*U. S. distribution.—*Small (1903) reports this species as extending from Virginia to Florida and Texas. Within the Keys, Small (1913) reports it on both the Upper and Lower Keys, and on the Lower Sand Keys. As with *B. arborescens*, the number of available localities for this species within that range may be limited, because both species seemingly require littoral or salt-marsh habitats.

ANATOMY

Growth rings are present toward the periphery of stems. These growth rings are demarcated by bands which consist of narrow vessels, a few vascular tracheids, and apotracheal parenchyma (fig. 3, 4). Such bands extend completely around the stem. The parenchyma in them is termed apotracheal parenchyma because it is not distributed primarily with reference to the vessels, although some of the cells may be in contact with vessels. Vertical elements in the earlier-formed xylem of the stem, as well as the xylem between the above-mentioned bands which occur in the later xylem, consist of relatively wider vessels, thick-walled libriform fibers, and vasicentric parenchyma.

Pores are not noticeably angular in transection. The average number of pores per group is 1.8, although grouping of pores increases in the bands mentioned above. Tangential pore diameter ranges from 18 to 60μ. The most frequent range is 30–48μ, and the average diameter is 36μ. Perforation plates are simple and circular. No tyloses are present. The end wall angle of vessel elements varies between horizontal and an inclination of 60° with the hori-

zontal. The average inclination is about 40°. Intervascular pitting consists of alternate oval (5μ by 6μ) bordered pits with nearly horizontal slit-like apertures. Wider apertures occur on walls of narrower vessels, and are lenticular in shape. The length of vessel elements is 112–252μ. The most frequent range is 140–200μ, and the average length is 178μ. Vascular tracheids are infrequent, and represent the furthest extreme in the production of narrow vessels. They occur only in the bands mentioned above, and have an average length of about 180μ.

Libriform fibers are about 420μ in length. Walls are commonly thick, and pitting consists of the usual oblique simple pits with slit-like apertures.

Rays are homocellular, because they consist exclusively of elements square to upright as seen in radial section. Uniseriate rays are lacking or nearly so. Upright cells may be present on the lateral faces of rays, and on the upper and lower tips of rays. Most rays are 5 cells wide at their widest point. Although great variation in ray height occurs, the average ray height is 1.32 mm. Such an average ray is about 40 cells in height. Ray cells are lignified, and pitting between ray cells consists of numerous small simple pits.

Scanty vasicentric parenchyma is present as a partial sheath, never more than a single cell layer in thickness, around vessels or vessel groups. Such parenchyma cells are relatively thick-walled, and, in longitudinal section, may be seen to be subdivided into strands of 2 cells. Apotracheal parenchyma is present in the bands which terminate growth rings. A few tangentially short partial bands may also be present. Apotracheal parenchyma is often continuous with vasicentric parenchyma, although not invariably so. As seen in tangential section (fig. 4), apotracheal parenchyma cells are often septate into a pair of cells. All the vertical cells in the bands—vessels, vascular tracheids, vasicentric parenchyma, and apotracheal parenchyma—conform to a storied pattern.

Resinous deposits were observed in vessels, fibers, vertical parenchyma, and ray parenchyma. Many of these deposits are carbonized. No crystals were observed.

DISCUSSION

A relatively greater amount of material of *Borrichia arborescens* and *B. frutescens* has been studied here than was studied in the writer's earlier survey of Heliantheae (1958). The difference between the species suggested in that paper, in respect to ray cells (square to procumbent in *B. arborescens*; square to upright in *B. frutescens*) appears to be valid. Other differences between the species in wood characters are relatively minor, and perhaps are not constant.

The tangential bands which consist of storied narrow vessels and parenchyma are of considerable interest both in their mode of occurrence and in their significance. In all specimens of both species of *Borrichia*, the earlier portion of the xylem was devoid of such bands. In *B. arborescens*, a single band was seen only in the stem of the collection *Stern & Brizicky 232*. In *B. frutescens*, the stem of *Stern & Brizicky 177* had a single band, whereas three successive bands were observed in the collection *Stern & Chambers 208*. The cause for the production of these bands is not readily apparent. They do not appear to be an annual production. Their formation may rather be induced by some climatic or edaphic extreme.

Whatever the cause of these bands, however, it is interesting to note that they are not without parallel in other Heliantheae. Bands of this nature, although more frequent, were observed in another member of the subtribe Verbesininae, *Encelia californica* (Carlquist, 1958), although none was found in *E. farinosa*. Similarly, *Dubautia Menziesii* (Heliantheae, subtribe Madinae) shows very pronounced bands; other species of *Dubautia* show less extreme stages in differentiation of these bands, as compared to the remainder of the xylem (Carlquist, 1958). In other tribes, such bands occur in *Hecastocleis* and *Proustia* of Mutisieae; the bands of *Baccharis* (Astereae), described below, are somewhat different, but probably represent much the same sort of phenomenon.

Although features of wood anatomy alone are not decisive, data on wood structure would not be opposed to

Fig. 1–7.—Fig. 1–4. *Borrichia frutescens*, Stern & Chambers 208. × 265.—Fig. 1, 2. Transverse and tangential sections of portion of xylem where bands do not occur.—Fig. 3, 4. Transverse, tangential sections showing a band which includes narrow vessels, vascular tracheids, and vertical parenchyma.—Fig. 5. *Ambrosia hispida*, Stern & Chambers 282. Tangential section of wood showing a ray (left) which includes a secretory canal. × 185.—Fig. 6. *Baccharis angusti-folia, Stern & Chambers 250*. Portion of tangential section showing

the supposition that *Borrichia* represents an eastern development from the Mexican-centered verbesininoid complex which has also seemingly given rise to a number of western genera, such as *Verbesina*, *Viguiera*, and *Encelia*.

Specimens examined.—BIG PINE KEY: Single-stemmed shrub, 3 ft. high; leaves fleshy; roadside near Halcyon Beach (Myrtle and Wesley's Place); 21 June 1956, *W. L. Stern & G. K. Brizicky 177* (Y; Yale wood no. 51032; RSA). Same as above. *W. L. Stern & G. K. Brizicky 178* (Y; no wood specimen; RSA). LITTLE TORCH KEY: Shrub, 3 ft. high; west side of key; 29 June 1956, *W. L. Stern & G. K. Brizicky 327* (Y; Yale wood no. 51150, not studied; RSA). NORTH KEY LARGO: Shrub, 2–3 ft. high; flowers yellow; 21 June 1956, *W. L. Stern & G. K. Brizicky 550* (Y; Yale wood no. 51323; RSA). KEY LARGO: Cut-over land on coralline substratum near sea between Tavernier and Key Largo town; 18 March 1958, *W. L. Stern & K. L. Chambers 208* (Y; Yale wood no. 51434; RSA).

MELANTHERA ASPERA (Jacq.) Rendle, in Fawcett and Rendle, Fl. Jamaica 7(5): 232. 1936. *Calea aspera* Jacq., Collect. 2: 290. 1786. *Amellus asper* (Jacq.) O. Kuntze, Rev. Gen. 1: 305. 1891. *Melanthera deltoidea* Michaux (as *Melananthera*), Fl. Bor. Am. 2: 106. 1803.

Melanthera aspera is an upright perennial herb with a woody base. Stems are 4-angled, and often purplish with anthocyanins. Leaves are opposite, on slender petioles 1–6 cm. in length. Leaves are deltoid to hastate or cuneate, 5–12 cm. in length, 2–6 cm. wide. Leaf margins are dentate-serrate, and leaf tips are acuminate. The herbage is hispid with a covering of stiff uniseriate trichomes. Heads are solitary on the ends of branches, or in clusters of two or three. Involucres are cup-shaped, and approximately 1 cm. in diameter. Involucral bracts are elliptic, 3–5 mm. in length, and finely hairy. Receptacular bracts are of the same length, but glabrous or nearly so and longitudinally striate. Heads are discoid, the corollas white and papery, about 5 mm. in length, the anthers black. Achenes measure about 2 mm. in length and have a turbinate shape, widest near the apex.

They are black in color and bear a pair of laterally-arranged capillary awns.

General distribution.—*Melanthera aspera* has been reported (as *M. deltoidea*) by Ledin (1951) to occur in Costa Rica, Yucatan, and other parts of Mexico, as well as in Jamaica, Trinidad, Dominican Republic, Cuba, the Bahamas, and Florida.

U. S. distribution.—Within the United States, *Melanthera aspera*, according to Ledin (1951) occurs in peninsular southern Florida "from Ft. Lauderdale to the Sand Keys" as well as on various of the larger Keys. It appears to be typical of drier disturbed areas, such as roadsides, or sandy beach habitats.

ANATOMY

Growth rings are very indistinct. The vertical elements of the xylem consist of vessel elements, libriform fibers, and vertical parenchyma. Although some very narrow vessels were observed, no vascular tracheids are apparently present.

Pores are distinctly angular in transection. Pores are mostly in groups, and average 2.3 pores per group. The range in tangential pore diameter is 15–48μ. The most frequent range is 27–36μ, and the average diameter is 34μ. Tyloses are abundant and very thin walled. Perforation plates are simple and circular. Although the end walls of vessel elements range between an angle of 30 and 80° with the horizontal, the average angle is 40°. Intervascular pitting consists of alternate circular bordered pits, about 5μ in diameter, with slit-like, nearly horizontal apertures. Pits on walls facing parenchyma cells are more sparse and tend to be elliptical in outline. The length of vessel elements ranges between 112 and 238μ. The most frequent range is 140–195μ, and the average length is 184μ.

Libriform fibers average about 500μ in length, and are non-storied. They are moderately thin-walled and have the typical pitting, consisting of simple pits with oblique, slit-like apertures.

Primary rays on smaller stems occupy a large portion of the xylem, but these are rapidly broken up so that the

amount of ray tissue, as seen in tangential sections of larger stems, is not exceptional. Rays are homocellular; they consist wholly of cells square to upright as seen in radial section. Some upright cells are horizontally subdivided. Upright cells are present along the lateral faces of the rays. Uniseriate rays are absent. Most of the multiseriate rays have a maximum width of 4–5 cells. Rays average 1.35 mm. in vertical height, and an average ray is about 32 cells high. Pitting among ray cells consists of numerous small simple pits, circular in outline.

Axial parenchyma is present in the form of scanty vasicentric cells, relatively few in number. They form a partial sheath around vessels or vessel groups. This sheath is never more than a single cell in width. Vasicentric parenchyma cells are relatively thin walled. As seen in longitudinal section, they are subdivided into strands of 3–4 cells.

Resinous deposits are present in vessels, and droplets of this substance occur in ray cells. Such resinous materials are not carbonized. No crystals were observed.

Specimens examined.—LOWER MATECUMBE KEY: Plant somewhat woody at base; leaves scabrous; heads with white flowers; in sandy strand along ocean side of key, 4 miles north of Craig's Post Office; 23 March 1958, *W. L. Stern & K. L. Chambers 286* (Y; Yale wood no. 51485; RSA). BIG PINE KEY: Plant with woody base; heads with white flowers; sandy spit on southern end of key; 27 March 1958, *W. L. Stern & K. L. Chambers 315* (Y; Yale wood no. 51504; RSA).

SUBTRIBE AMBROSINAE

AMBROSIA HISPIDA Pursh, Fl. Am. Sept. Suppl. 743. 1814.

Ambrosia hispida is a creeping, decumbent perennial herb with a relatively small accumulation of secondary xylem at the base. Leaves are opposite, bi- or tri-pinnatifid, the lobes bluntish or rounded. Leaves are up to 8 cm. in length, 4 cm. in width. A hispidulous covering of uniseriate trichomes is present on young stems and on both surfaces of leaves. Carpellate involucres are accompanied by bracts and congested on short axes axillary to opposite bracteate leaves.

Staminate heads are spirally arranged in the manner of a raceme along the terminal portion of the elongate inflorescence axes which terminate shoots and may bear carpellate branches below. Peduncles of staminate heads are short, 1–3 mm. long and not subtended by bracts. Bracts within the carpellate inflorescences and involucres of staminate heads are hispidulous. Carpellate heads consist of a tuberculate involucral envelope, about 4–4.5 mm. long at maturity. Staminate heads are about 2–4 mm. in diameter, and possess a single series of involucral bracts which are rounded at their apices and more or less united by their bases. Staminate flowers are about 2 mm. in length, with dull white corollas. The plant is aromatic, and small resinous droplets may be seen on leaves and involucres.

General distribution.—Ambrosia hispida occurs in tropical America as a strand plant. It has been reported in South America, Yucatan and other parts of Mexico, Cuba, Haiti, Dominican Republic, Puerto Rico, and Florida.

U. S. distribution.—Within the United States, the species is restricted to southern Florida. It occurs on the Sand Keys and on both the Upper and Lower Keys (Small, 1913). It has been found less commonly in the Miami region. Characteristically it grows on sandy dunes or rocky shores along the coast, where it forms low mats.

ANATOMY

Growth rings are present. The axial portion of the xylem consists of vertical parenchyma, libriform fibers, and vessel elements; vessel elements grade in diameter to quite narrow, however, and a few such elements lack perforations and are therefore vascular tracheids.

Pores are only slightly angular, as seen in transection. The average number of pores per group is 1.7. Tangential pore diameter ranges from 12 to 90μ (the largest pores were observed in the collection *Stern & Brizicky 393*). In the collection *Stern & Chambers 282*, the most frequent range is $20–42\mu$, and the average diameter is 35μ (55μ in *Stern & Brizicky 393*). Tyloses are absent. Perforation plates are simple and tend to be elliptical in smaller vessels, circular in

larger vessels. The end wall angle of vessel elements ranges between horizontal (on wider elements) and vertical (narrower elements). The average inclination ranges between 30–50° with the horizontal. Intervascular pitting consists of oval bordered pits, about 4μ in diameter, with nearly horizontal- slit-like apertures. Some transitional pitting is present. Helical sculpturing is absent on vessel walls. In the specimen *Stern & Chambers 282*, the range in vessel element length is $110–280\mu$. Elements up to 448μ in length were observed in *Stern & Brizicky 393*. The most frequent range in the former is $170–252\mu$, and the average length is 202μ (average, 282μ in *Stern & Brizicky 393*). Vascular tracheids are from $130–150\mu$ in length. They have pits like those of vessels, except that apertures are wider and tend to be the same shape as the pit cavity, although smaller.

Libriform fibers are non-storied and average 280μ in length. They have thick walls and simple pits with oblique, elongate apertures.

Ray cells are typically square to upright, as seen in radial section. A few procumbent cells occur in the central portion of larger rays. Both multiseriate and uniseriate rays are present; uniseriates are relatively infrequent. Multiseriate rays tend to be 2–4 cells wide at their widest point, mostly 2, except where secretory canals (fig. 5) are included within the ray. The average multiseriate ray is about 1 mm. in vertical height and about 15 cells high. The presence of libriform upright ray cells on lateral faces of rays tends to obscure the precise limits of many rays, as seen in tangential section. Uniseriate rays are composed of 1–2 cells and average about 75μ in vertical height. Within perhaps a third of the multiseriate rays, a secretory canal (fig. 5) is present. These secretory canals are surrounded by thin-walled non-lignified cells, although the remainder of the ray in which they occur is composed of thicker-walled, lignified cells. Secretory canals were observed to extend radially much of the length of the ray in which they occur. Similar canals are present opposite them in the rays of the secondary phloem. These canals are initiated from the cambium; they were not observed in the relatively thin xylem cylinder of the collec-

tion *Stern & Brizicky 393*. Pitting between lignified ray cells consists of numerous simple small circular pits.

Scanty vasicentric parenchyma is present as a partial sheath, never more than a single cell in width, around vessels or vessel groups. Cell walls are moderately thick. In longitudinal section, vasicentric parenchyma cells may be seen to be septate into strands of two cells. A few bands of apotracheal parenchyma are present. These are tangentially short, and do not extend the width of an interfascicular area. They are mostly continuous with vasicentric parenchyma. Although some of these cells are transversely septate, most of them are not.

Resin deposits occur in vessels and between ray cells. Some of the latter accumulations are carbonized. No crystals are present.

DISCUSSION

The two specimens of this species differed markedly in the dimension of vessel elements. The largest elements occurred in the collection *Stern & Brizicky 393*, which had a smaller accumulation of xylem.

The presence of secretory canals in rays of *Ambrosia hispida* is of interest, because they have been reported in only one other genus of Compositae, *Bebbia* (Carlquist, 1958). In *Bebbia*, however, the secretory canals are smaller and surrounded by lignified cells. Because *Bebbia* belongs to a part of Heliantheae quite different from subtribe Ambrosinae, and because the nature of canal structure is different, secretory canals have probably arisen independently. The occurrence of secretory canals in *Ambrosia hispida* is perhaps not surprising in view of the abundant internal secretory structures elsewhere in the plant.

The wood of only one other member of Ambrosinae, *Hymenoclea salsola*, has been previously investigated (Carlquist, 1958). Features of *Hymenoclea salsola* different from those of *Ambrosia hispida* include the presence of exclusively non-lignified walls in ray cells, absence of secretory canals, and marked seasonal periodicity in the production of certain elements. Bands containing numerous vascular

tracheids and very narrow vessels terminate growth rings in *Hymenoclea*. The markedly procumbent ray cells and the prominent grooves in vessel walls of *Hymenoclea* offer further differences. Considering the relatively narrow gamut of variation in Compositae wood, the woods of *Ambrosia hispida* and *Hymenoclea salsola* are not particularly similar. An intensive survey of the woods of Ambrosinae is needed.

Specimens examined.—NO NAME KEY: Suffrutescent prostrate plant; leaves aromatic; growing near eastern abutment of No Name–Big Pine Bridge; 5 July 1956, *W. L. Stern & G. K. Brizicky 393* (Y; Yale wood no. 51197; RSA). LOWER MATECUMBE KEY: Plant woody at base, stoloniferous, first erect then scrambling along ground; aromatic; in sandy strand along ocean side of key, 4 miles north of Craig's Post Office; 23 March 1958, *W. L. Stern & K. L. Chambers 282* (Y; Yale wood no. 51482; RSA).

TRIBE HELENIEAE

FLAVERIA LINEARIS Lag., Gen. et Sp. Nov. 33. 1816.

Flaveria linearis is a shrubby perennial, much branched below, which reaches 10 dm. or more in height. Stems are terete and shallowly grooved. Leaves are opposite, lanceolate, and somewhat petiolate. They reach 10 cm. in length and 1 cm. in width. Margins are obscurely dentate and the tips are acuminate. The bases of each leaf pair form a short sheath. The herbage is glabrous. Inflorescences are composed of numerous heads in a corymb. Heads are oblong-campanulate, about 5 mm. long and 2 mm. in diameter. A few scalelike bract leaves subtend each involucre. Involucral bracts are imbricate, 3–5, arranged in 1–2 series, and elliptic. They bear longitudinal brown striae on the outer surface; these are external indications of secretory canals. The expanded portion of the ray corollas is about 3 mm. long, and is elliptic with an entire margin. Disk corollas are about 2–3 mm. long. Corollas of both disk and ray flowers are yellow, with brownish linear markings indicating secretory canals. Achenes are black, terete, 8–10-ribbed, 2 mm. long, and lack pappus.

General distribution.—Flaveria linearis occurs in disturbed, dry, or alkaline areas in Yucatan and other portions of Mexico, Cuba, and the Bahamas, as well as in southern Florida (Ledin, 1951).

U. S. distribution.—The species has been collected in The Everglades of southern Florida. It ranges up the east coast to Brevard County and up the west coast to Sanibel Island (Ledin, 1951). Small (1913) records it on the Sand Keys and on the Lower Keys.

ANATOMY

Growth rings are present, but inconspicuous. The axial portion of the xylem exclusive of vertical parenchyma consists wholly of vessel elements and libriform fibers.

Pores are somewhat angular as seen in transection. The average number of pores per group is 1.7. The range in tangential pore diameter is $21-51\mu$. The most frequent range is $30-39\mu$, and the average diameter is 33μ. Tyloses are absent. Perforation plates are almost exclusively simple. A few plates, which are best termed multiperforate, were observed. These plates had between 10 and 15 scalariform bars, most of which were forked. The end walls of vessel elements range between horizontal and an angle of 60° with the horizontal. The average angle is about 45°. Intervascular pitting consists of circular or slightly oval bordered pits about 5μ in diameter. Apertures are short, oblique, and slit-like. Pits are scarce on walls facing fibers. Helical sculpture is lacking. Vessel element length ranges between 70 and 300μ. The most frequent range is $154-196\mu$, and the average length is 180μ.

Libriform fibers average about 350μ in length. They occur in a storied pattern which conforms to the vessel elements. Walls are relatively thin, although this varies with growth rings. Pits are simple, with apertures oblique and slit-like.

Rays are abundant and occupy perhaps a third of the area of a tangential section, although the material studied suggested active breakup of rays by fusiform cells. Rays are homocellular, and consist of cells square to upright as seen in radial section. Uniseriate rays are absent or nearly so. Up-

right cells occur along the lateral faces and the upper and lower tips of rays; the similarity of these cells to adjacent libriform fibers obscures the exact limits of a ray, as seen in tangential section. Most rays have a maximum width of from 4 to 7 cells. The average ray height is 1.5 mm. An average ray is about 30 cells high. Ray cells are thin-walled, but lignified. Pitting between ray cells consists of numerous somewhat circular simple pits.

Vertical parenchyma is present in the scanty vasicentric condition exclusively. These cells are relatively thin-walled, and form a partial, rarely a complete, sheath around vessels or vessel groups. Such a sheath is never more than a single cell in width.

A few resinous droplets are present in vessels. Such deposits are not carbonized. Crystals were not observed.

DISCUSSION

Flaveria linearis is apparently the only species referred to Helenieae (other than *Venegazia carpesioides*) which has been investigated to date. *Venegazia*, traditionally regarded as helenioid, was considered by the writer (1958) as possibly belonging to Heliantheae, and studied in that connection. Wood anatomy of *Flaveria linearis* is quite similar to that of *Venegazia*. It is equally similar, however, to a number of undoubted Heliantheae, such as *Podachaenium* and *Verbesina*. These similarities correlate well with the very close affinity taxonomists have consistently suggested between Heliantheae and Helenieae.

Specimen examined.—PLANTATION KEY: Shrubby, sprawling, woody at base, about 1 m. high or somewhat higher; flowers bright yellow; 21 March 1958, *W. L. Stern & K. L. Chambers 260* (Y; Yale wood no. 51469; RSA).

TRIBE ASTEREAE

BACCHARIS ANGUSTIFOLIA Michaux, Fl. Bor. Am. 2: 125. 1803.

Baccharis angustifolia is a woody shrub, 5–25 dm. tall. The stems are terete and conspicuously ridged. Leaves are

alternate, linear or somewhat lanceolate, 1–8 cm. in length and up to 5 mm. in width. Leaf margins are entire or with a few teeth. Herbage is glabrous but glutinous, particularly at the shoot tips. Heads are arranged in a bracteate panicle at the ends of branches. Involucres are 4–5 mm. in length and conical in shape. Involucral bracts are numerous, imbricate, and greenish in color (drying tawny) with a darker marking near the center of each. Heads are discoid, dioecious, and with whitish flowers. Corolla lobes of carpellate flowers are filiform, those of staminate flowers lanceolate. Fertile achenes are about 1 mm. in length, whitish and minutely hairy, and crowned by a copious aggregation of capillary pappus bristles. On fertile achenes the bristles are about 8 mm. in length; bristles of the staminate flowers are less numerous and about 2 mm. in length.

General distribution.—*Baccharis angustifolia* is a species characteristic of salt marshes, hammocks, alkaline roadsides, and sand dunes in the southeastern U. S. It has, however, also been recorded for the Bahamas (Small, 1913).

U. S. distribution.—Within the United States, the species ranges west to Texas and north to N. Carolina (Ledin, 1951). It has most frequently been collected in Florida. Within the Keys, Small (1913) records it from the Upper Sand Keys. The specimen under study is from Key Largo.

ANATOMY

Growth rings are indistinct. Bands, which contain vertical parenchyma, narrow vessels, and vascular tracheids are present, but these are scattered equally through all portions of a growth ring. These bands extend across all or part of the distance between two rays, as seen in transection. Some bands extend across several fascicular areas. The remainder of the axial portion of the xylem consists of vessel elements, libriform fibers, and vasicentric parenchyma.

Pores are mostly angular in transection. The average number of pores per group is 1.8. The range in tangential pore diameter is 21–60μ. The most frequent range is 35–49μ, and the average diameter is 41μ. Tyloses are absent. The angle of the end wall of vessel elements varies between 10

and 65° with the horizontal, and the most frequent angle is about 50°. Intervascular pitting consists of alternate bordered pits, circular in outline, with nearly horizontal slit-like apertures. Pit cavities are about 5μ in diameter. Prominent helical grooves connect pit apertures, so that the external portions of apertures of pits in a particular helix may be said to be confluent, like those in *Pluchea odorata* (fig. 7). On either side of such a groove, a ridge may be built up, so that a pair of helical spiral thickenings may accompany a helix of pits. Such a condition is present on many vessels, particularly the narrower ones, as well as on vascular tracheids. This condition is shown in fig. 6. The range of length in vessel elements is 14–160μ. The most frequent range is 154–182μ, and the average length is 164μ. Vascular tracheids average about 180μ in length. They occur in a storied pattern which conforms to that of vertical parenchyma cells and vessel elements in the bands in which they occur. As mentioned above, helical grooves and their accompanying ridges are more prominent in vascular tracheids than in larger vessel elements.

Libriform fibers average about 430μ in length and are not storied. Wall thickness and fiber diameter vary according to position of a fiber in a growth ring. Thin-walled fibers are about 27μ in diameter, whereas thick-walled fibers are about 15μ in diameter.

Rays contain cells square to procumbent, mostly procumbent, as seen in radial section. Procumbent cells exclusively are present in the central portion of multiseriate rays. Both square and procumbent cells occur in uniseriate rays. Multiseriate rays are more frequent than uniseriate rays. Most multiseriate rays have a maximum width of 3 cells. Uniseriates average 117μ in height; such a ray is about 5 cells high. The average multiseriate ray is about 328μ in height, and the average number of cells in height is 20. Upright cells are wholly lacking, and uniseriate wings, which at most contain 2 cells, are rarely present, and inconspicuous. Ray cells are lignified, and pitting consists of numerous simple pits, circular in outline.

Axial parenchyma is present both as vasicentric cells, which usually form a sheath 1–2 cells wide around vessels or vessel groups, and as the parenchyma in bands, which also contain narrow vessels and vascular tracheids. The parenchyma of bands, because it is so intimately associated with tracheary elements, could be termed paratracheal. It appears to be similar to the condition which the writer has termed apotracheal in other Compositae. A few small bands may contain no tracheary elements at all. Consequently, the term apotracheal parenchyma seems defensible here. Banded parenchyma, where it occurs, is continuous with vasicentric parenchyma, as seen in transection. As seen in longitudinal section, vertical parenchyma cells may be non-septate or divided into strands of two or three cells; a strand of two cells is the most common condition.

Large resinous deposits occlude some vessels. In rays and vertical parenchyma, droplets of such substances are present. None of these deposits is carbonized.

Discussion of wood anatomy of B. *angustifolia* follows the description of B. *halimifolia* below.

Specimen examined.—KEY LARGO: All leaves on plant are narrow, broad leaved forms growing nearby; on highway S 905, 6.4 mi. from U. S. 1, south side of road; 19 March 1958, *W. L. Stern & K. L. Chambers* (with G. *Stevenson) 250* (Y; Yale wood no. 51462; RSA).

BACCHARIS HALIMIFOLIA L., Sp. Pl. 860. 1753.

Baccharis halimifolia is a shrub, 15–25 dm. tall, with a trunk up to about 3 in. in diameter. Stems are ridged. Leaves are alternate, petiolate, with margins deeply incised into prominent teeth. Leaf shape varies considerably within the species; the Keys specimens have leaves oblanceolate or obovate in outline, up to 7 cm. in length and 4 cm. in width. Herbage is glabrous and often glutinous, especially near the shoot tips. Inflorescences consist of numerous heads loosely arranged in a bracteate panicle. Heads are discoid and unisexual, with whitish corollas. Involucres measure 5–8 mm. in length and about 5 mm. in diameter. Involucral bracts are numerous, imbricate, and greenish (drying tawny); each

typically bears a darker streak down the center. The pappus of carpellate flowers consists of numerous fine capillary bristles about 8 mm. long. Fertile achenes are minutely hairy, whitish, and about 1 mm. in length. The pappus of staminate flowers consists of fewer bristles, about 3 mm. in length.

General distribution.—*Baccharis halimifolia* is characteristic of maritime localities and disturbed areas near the coast. It is apparently most frequent in somewhat halophytic habitats. In addition to the U. S., it has been recorded in Central America, Mexico, Cuba, and the Bahamas (Ledin, 1951).

U. S. distribution.—This species ranges up along the Atlantic seaboard as far north as Massachusetts. It also occurs on the Gulf Coast from the Keys west to Texas. In Florida, B. *halimifolia* may be found at the edges of hammocks, in salt marshes and swamps, and more rarely in pinelands. Within the Keys, Small (1913) reports it from the Lower Keys only, and the four collections from which wood was studied are from this area.

ANATOMY

Growth rings are rather indistinct. Bands, which contain vertical parenchyma, narrow vessels, and vascular tracheids are present, but these are scattered through all portions of a growth ring. These bands extend across all or part of the growth ring. These bands extend across all or part of the distance between two rays, as seen in transection. Some bands extend across several fascicular areas. The remainder of the axial portion of xylem consists of vessel elements, libriform fibers, and vasicentric parenchyma.

Pores are somewhat angular in transection. The average number of pores per group is 2.2. Tangential pore diameter ranges between 18 and 70μ. The most frequent range is 30–45μ, and the average diameter is 39μ. Tyloses are absent. The end wall of vessel elements is at an angle of from 15 to 50° with the horizontal, and the average angle is 30°. Intervascular pitting consists of circular bordered pits, with cavities about 5μ in diameter. Apertures are slit-like, nearly horizontal, and connected with those of other pits in a par-

ticular helix by a groove. In respect to helical grooves and ridges, the vessels and vascular tracheids are identical to those described above for *B. angustifolia* (see also fig. 6). The range in length of vessel elements is 90–224μ. The most frequent range is 154–210μ, and the average length is 178μ. Vascular tracheids average about 180μ in length, and conform to the storied pattern of vessels and parenchyma in the bands in which they occur.

Libriform fibers average about 380μ in length and are non-storied. They are mostly rather thick-walled, and have simple pits with oblique slit-like apertures.

Rays contain cells square to procumbent, mostly procumbent, as seen in radial section. Procumbent cells exclusively are present in the central portion of rays, and uniseriate rays consist of both procumbent and square cells. Multiseriate rays are more frequent than uniseriate rays. Most multiseriate rays have a maximum width of 3 cells. Uniseriate wings are not present. The average uniseriate ray is 150μ in height and consists of about 7 cells. The average multiseriate ray is 440μ in height and is about 17 cells high. Ray cells are lignified, and pitting consists of numerous simple pits, circular in outline.

Axial parenchyma is present both as vasicentric cells, which form a sheath 1–2 cells wide around vessels, and as parenchyma in bands. The question as to whether the banded parenchyma is truly paratracheal is discussed above in the account of *B. angustifolia*. As seen in transection, banded parenchyma is continuous with vasicentric parenchyma. As seen in longitudinal section, vertical parenchyma cells are usually subdivided into strands of two cells.

Resin deposits occlude a few vessels. Resinous droplets were observed in ray and vertical parenchyma cells of all the collections studied. Such deposits are not carbonized. No crystals were observed.

DISCUSSION

The wood anatomy of *Baccharis halimifolia* has been described previously by Urling and Smith (1953). The

present account differs from the description of those authors in several respects. They apparently overlooked the storied condition of elements in the bands. Resinous droplets occur in all four collections in the present study, in addition to more massive deposits in vessels, although Urling and Smith report them as absent. Numerous multiseriate rays fewer than 25 cells in height were observed in the present study, whereas Urling and Smith report a range of "25–50" cells. The writer was unable to confirm their report of intraxylary cork strands in any of his material. Such cork strands, then, do not appear to be an obligate characteristic of the species. Intraxylary cork strands have, as these authors state, been described in *Artemisia tridentata* by Diettert (1938). They have also been figured by Webber (1936), in the same species. Urling and Smith state that *Artemisia tridentata* belongs to the same tribe as *Baccharis*. This is not true, so the comparison is not a close one in systematic terms.

The similarity in all essential features between wood of *Baccharis angustifolia* and *B. halimifolia* is extremely close. Comparative material of some of the numerous other species of *Baccharis* is needed to lend perspective, but the great similarity between these two species might well suggest a close taxonomic affinity.

The descriptions of Metcalfe and Chalk (1950) in respect to pore diameter, vessel grouping, and vertical parenchyma characteristics of an unspecified species of *Baccharis* (*B. tucumanensis* ?) agree with the data for the two species described above. Although a small amount of variation in pore diameter is correlated with growth rings, there does not seem to be in the two above species the tendency toward ring porosity they mention for *Baccharis* and figure for *B. tucumanensis*. In agreement with the writer's contention that the banded parenchyma may be regarded as apotracheal, they figure bands containing no tracheary elements for *B. tucumanensis*.

Specimens examined.—BIG PINE KEY: Shrub with single stem 5 ft. high, 1 in. in diameter; leaves fleshy; Watson's Hammock; 26 June 1956, *W. L. Stern & G. K. Brizicky 263* (Y; Yale wood no. 51101; RSA). Small tree, 7 ft. high, 1.5

in. in diameter, sterile; leaves somewhat fleshy; north end of key in hammock; 27 June 1956, *W. L. Stern & G. K. Brizicky 292* (Y; Yale wood no. 51122; RSA). Shrub, about 6 ft. high; 10 July 1956, *W. L. Stern & G. K. Brizicky 424* (Y; Yale wood no. 51219; RSA). NO NAME KEY: Robust shrub, largest of the species seen, diameter at base 3 in., several main stems; sterile; along road; 6 July 1956, *W. L. Stern & G. K. Brizicky 398* (Y; Yale wood no. 51199; RSA).

HAPLOPAPPUS PHYLLOCEPHALUS DC. var. MEGACEPHALUS (Nash) Hall, The Genus *Haplopappus* (Carnegie Inst. Wash. Publ. No. 389) 59. 1928. *Eriocarpum megacephalum* Nash, Bull. Torrey Bot. Club 23: 107. 1896. *Eriocarpum floridanum* Gandoger, Bull. Soc. Bot. France 65: 41. 1918. *Eriocarpum glaucum* Gandoger, Bull. Soc. Bot. France 65: 41. 1918. *Haplopappus megacephalus* (Nash) Hitchc., Trans. Kansas Acad. Sci. 16: 131. 1899. *Sideranthus megacephalus* (Nash) Small, Fl. Southeastern U. S. 1185. 1903. *Machaeranthera phyllocephala* var. *megacephala* (Nash) Shinners, Field Lab. 18: 40. 1950.

Haplopappus phyllocephalus var. *megacephalus* is a low shrubby herb with a woody base. The stems branch from near the base, and are lightly striate. Leaves are alternate; middle leaves are 8–12 mm. wide, 3–4 cm. long. Both stems and leaves have both glandular-scabrid and villous or tomentose indument. Leaf margins have prominent teeth, about 2 mm. long, which are terminated in a stout uniseriate trichome. Heads are mostly solitary on the ends of stems or branches; a group of such flowering branches at the end of one of the main stems, however, forms a loose corymb. The involucres are 10–14 mm. high, and consist of numerous imbricate bracts. The bracts are lanceolate, about 8–10 mm. long, greenish with a darkened apex and scarious margins. The receptacle is alveolate. Heads are radiate with yellow flowers. Ray flowers are about 25 to 40 in number, with the expanded portion of the corolla 5–7 mm. long, terminated in two or three lobes. Disk flowers are about 7 mm. in length, the corollas 5 mm. long. Pappus consists of numerous bristles, 5–7 mm. in length. Achenes are dark, but densely covered with minute hairs.

General distribution.—Although the species *Haplopappus phyllocephalus* is wide-ranging, extending into Mexico and as far north as Kansas and Colorado, it is chiefly characteristic of the Gulf Coast (Hall, 1928). The variety under consideration here is much more restricted.

U. S. distribution.—*Haplopappus phyllocephalus* var. *megacephalus* has been recorded from the Gulf coast of Texas, Louisiana, and Florida (Hall, 1928). Although Small (1903) recorded it for Florida, he did not include it in his flora of the Keys. It has been recorded from Big Pine Key as *Sideranthus megacephalus* by Dickson, et al. (1953).

ANATOMY

Growth rings are perceptible, although they do not involve appreciable change in size or distribution of elements. The axial portion of the xylem consists of vertical parenchyma, vessel elements, and libriform fibers; narrow vessels grade into vascular tracheids, a few of which are present.

Various types of pore groupings occur, with an average of 3.6 pores per group. The range in tangential pore diameter is $12–33\mu$. The most frequent range is $18–24\mu$, and the average diameter is 20μ. Tyloses are absent. Perforation plates are simple and circular, or nearly so. End walls of vessel elements range between horizontal and an angle of 75° with the horizontal; the average angle is about 30°. Intervascular pitting consists of oval bordered pits, $3–4\mu$ in diameter, with very small oblique lenticular apertures. Pits are somewhat sparser and more elliptical on walls facing parenchyma cells. Helical sculpturing is absent. In length, vessel elements are $70–154\mu$. The most frequent range is $98–140\mu$, and the average length is 110μ.

Libriform fibers are non-storied and approximately 280μ in length. They have relatively thick walls and simple pits with oblique slit-like apertures.

Ray tissue is not exceptionally abundant. Rays are homocellular, and consist of cells square to upright as seen in radial section. Both multiseriate and uniseriate rays are present, although the latter are relatively infrequent. Multi-

seriate rays are mostly 4 cells wide at their widest point; some are up to 7 cells wide. Upright cells are present on lateral faces of rays. The average uniseriate ray is 3–4 cells high and measures about 100μ in height. Multiseriate rays average .7 mm. in height and are about 32 cells high. Ray cells are lignified, and have abundant small pits with circular apertures.

Scanty vasicentric parenchyma is present as a partial or nearly complete sheath, never more than a single cell in width, around vessels or vessel groups. Cell walls are moderately thin. As seen in longitudinal section, vertical parenchyma cells are in strands of two. Apotracheal parenchyma is absent.

Resinous non-carbonized droplets are present in ray and vertical parenchyma cells. No crystals are present.

DISCUSSION

Metcalfe and Chalk (1950) have studied only one genus belonging to the *Haplopappus* complex. This is *Ericameria*, and the only features they report for it are the presence of crystals, abundant uniseriate rays, and the occurrence of bordered pits in libriform fibers. None of these characters occurs in *Haplopappus phyllocephalus* var. *megacephalus*. Except for the presence of a few vascular tracheids and the high degree of pore grouping, this species exhibits few specialized characters, in contrast to the relatively specialized wood of *Baccharis* described above. This is certainly in accord with the relatively specialized gross morphology of *Baccharis*, which is dioecious.

Shinners' transfer of this taxon to *Machaeranthera* may well prove to be the most acceptable treatment. Because other areas of the *Haplopappus* complex require reassessment before a clear knowledge of the limits of *Machaeranthera* and other genera is obtained, the species is referred to *Haplopappus* here. Both Shinners and Hall agree that the plant should be regarded as an infraspecific entity under *Haplopappus* (*Machaeranthera*) *phyllocephalus*.

Specimen examined.—LITTLE TORCH KEY: Low shrub; leaves aromatic, viscid, fleshy; flowers yellow; 2 July

1956, *W. L. Stern & G. K. Brizicky 342* (Y; Yale wood no. 51162; RSA).

TRIBE INULEAE

PLUCHEA ODORATA Cass., in Dict. Sci. Nat. 42: 3. 1826.

Pluchea odorata is a shrub 1–3 m. high. Leaves are alternate, ovate, with petioles 1–2 cm. long. Leaf blades are typically 3.5–4 cm. wide and 10 cm. long. Margins are entire or with a few obscure blunt teeth. The leaf tip is acute. Leaves are densely puberulent below with uniseriate trichomes intermingled with short glandular trichomes. The upper surfaces of leaves are glabrescent; stems, petioles, and peduncles are densely puberulent. Stems and branches terminate in cymose corymbs composed of numerous heads. Involucres are cup-shaped, about 5 mm. long and 5 mm. in diameter. Outer involucral bracts are ovate, greenish, sometimes with reddish tips, and hairy. The innermost bracts are lanceolate, glabrous, and scarious. Heads are discoid, with central perfect flowers and marginal carpellate ones. Corollas are filiform, lavender, about 3 mm. long. Pappus is composed of numerous capillary bristles, about 3 mm. long. Both heads and foliage are aromatic.

General distribution.—In addition to Florida, the range of the species includes South America, Central America, Mexico, and the West Indies (Ledin, 1951), including such islands as Cuba, the Bahamas, and Bermuda (Small, 1913).

U. S. distribution.—Ledin (1951) regards the species as an introduction to the U. S., although possibly it is native. It is usually found on low ground, at the edges of pinelands, hammocks, or on roadsides. It has been collected as far north in Florida as Miami (Ledin, 1951). Small (1913) records it from Key West. The specimen studied here was collected on Key Largo.

ANATOMY

Growth rings are absent. The axial portion of the xylem consists of vertical parenchyma, libriform fibers, and vessel elements.

Pores are rounded in outline, as seen in transection. Pore groupings are often radial, and the average number of pores

per group is 2.1. The range in tangential pore diameter is 24–87μ. The most frequent range is 51–66μ, and the average diameter is 60μ. Tyloses are absent. Perforation plates are simple and circular. The end walls of vessel elements vary from horizontal to an angle of $50°$ with the horizontal. The average angle is about $30°$. Intervascular pitting consists of alternate bordered pits with circular to oval cavities about 5μ in diameter. Pit apertures are fairly wide, and nearly horizontal. Grooves connect the apertures of pits adjacent in a helix (fig. 7, below). There is, in addition, some transitional pitting present. Vessel elements range in length between 154 and 420μ. The most frequent range is 275–297μ, and the average length is 283μ.

Libriform fibers are non-storied and average about 500μ in length. They are relatively thin-walled, and have simple pits with oblique, slit-like apertures.

Rays consist mostly of cells square as seen in radial section. Procumbent cells are present in the central portion of rays. Uniseriate rays are absent or nearly so. The width of multiseriate rays varies widely; they may have a maximum width of from two to many cells. The average multiseriate ray is about 1.3 mm. in height, and is about 35 cells high. Ray cells are lignified, and bear small simple pits with circular apertures.

Axial parenchyma is present as relatively thin-walled vasicentric cells. These form partial, rarely complete sheaths around vessels or vessel groups; such sheaths are never more than a single cell wide. As seen in longitudinal section, they are subdivided into strands of 2–4 cells, mostly 2.

Resinous deposits are present in a few vessels and vasicentric parenchyma cells. Droplets of such materials occur in ray cells and some fibers. They are not carbonized. No crystals were observed.

DISCUSSION

The only species of *Pluchea* for which any data are available is *P. indica*, in which Coster (1927) reports growth rings. These are lacking in *P. odorata*. Data are given by Metcalfe and Chalk (1950) for other Inuleae, such as *Inula*

and *Anaphalis*, but these are rather different in some characters, and do not seem to provide pertinent comparisons with *P. odorata*.

Specimen examined.—KEY LARGO: Shrub, 5–6 ft. high, spreading; 3 in. in diameter at base; foliage aromatic; on highway S 905, 6.4 mi. from U. S. 1, south side of road; 19 March 1958, *W. L. Stern & K. L. Chambers 249* (Y; Yale wood no. 51461; RSA).

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THE WOODS AND FLORA OF THE FLORIDA KEYS. GOODENIACEAE[1]

WILLIAM L. STERN AND GEORGE K. BRIZICKY

Samuel James Record Memorial Collection, School of Forestry, Yale University, New Haven, Connecticut

The Goodeniaceae are largely confined to Australia and 10 of the 13 genera are restricted to this continent. *Scaevola, Calogyne* and *Selliera* also occur outside of Australia (Krause, 1912). *Scaevola* is the most widespread genus. Of the approximately 300 species in Goodeniaceae, only one, *Scaevola plumieri*, occurs on the Florida Keys. Small (1913, 1933) treats this species under the Brunoniaceae ("Brunoni-aceae. Goodenia Family"). Most botanists today consider the Brunoniaceae to be represented only by *Brunonia australis*, an herbaceous perennial with regular flowers, confined to Australia.

SCAEVOLA PLUMIERI (L.) Vahl, Symb. Bot. 2: 36. 1791. *Lobelia plumieri* L. Sp. Pl. 929. 1753; *Scaevola lobelia* Murr. Syst. ed. 13. 178. 1774.

Scaevola plumieri (fig. 3) is a shrub 3–18 dm. tall. Branchlets are terete, tough, glabrous, greenish or purplish and conspicuously marked with the scars of fallen leaves. The latter are alternate, crowded at the ends of branchlets, 5–9 cm. long and 2–5 cm. wide, thick and fleshy, shining, entire, obovate to spatulate with a rounded apex. Leaf bases are narrowed into winged petioles. Flowers are bisexual, zygomorphic and borne in axillary, 3-flowered cymes. The calyx is small and shallowly lobed. The corolla is gamopetalous, 5-lobed, split to the base on one side, white, 2–2.5 cm. long, glabrous outside and woolly within. The nearly linear corolla lobes are fringed with broad, crisped wings. Stamens number 5, and are included in the corolla tube. The ovary is inferior, bilocular, with 1 ovule in each locule. The stout style is terminated by a stigma subtended by a ciliate, pollen-

collecting cup. The drupe is subglobular, blue-black, juicy, 1–2 cm. in diameter and 2-seeded. Endosperm is corrugated and woody.

General distribution.—*Scaevola plumieri* is almost pantropical, and occurs on sandy and rocky seashores in the tropics and subtropics except Australia and the Pacific Islands. It has been recorded in southern India, Ceylon, Mauritius, Madagascar, east, south and west Africa, and the West Indies. Records also point to *Scaevola plumieri* on the warm eastern coasts of the Americas. Standley (1926) and Johnston (1931) report this species from Clarion Island in the Revillagigedo group, and from Baja California. It is to be noted that the occurrence of *Scaevola plumieri* on the eastern coasts of tropical America appears to be sporadic. As far as we know, the species has only been seen in Mexico (Yucatán Peninsula), Honduras, Colombia, Venezuela and Brazil. Additional reports of *Scaevola plumieri* in tropical America may be expected.

U. S. distribution.—This species inhabits coastal sand dunes of southern peninsular Florida and the Florida Keys. A recent report (Jones, 1957) notes *Scaevola plumieri* on Padre Island in Kleberg County, Texas.

ANATOMY

Growth rings are totally lacking in the Florida Keys specimens under study. Imperforate tracheary elements are tracheids (sensu Bailey, 1936); that is, even though the pits in these elements are small ($3–7\mu$), circular bordered pits in these elements are small ($3–7\mu$), those in the vessels are of correspondingly small size. The pit borders are round and the inner apertures are usually included within the borders. Walls vary from thick to very thick (Chattaway, 1932). Average length of tracheids is 655μ with a range of $398–937\mu$. The most frequent range is $550–800\mu$. In macerations, a high percentage of bizarre cell types is seen: forked ends, sub-terminal branches, "buds," crooks, etc. It was also noted that many tracheids displayed gelatinous inner walls.

Pores are somewhat angular in outline and virtually all solitary, very few pore multiples being noted (fig. 1).

Tangential pore diameters average 41μ and range between 25 and 60μ. The most frequent range is 35–50μ. Tyloses are absent. Both scalariform and simple perforation plates occur in sections. Although scalariform plates are not of rare occurrence, they are not as common as the simple type. Bars in the scalariform perforations are few (1–6) and may be branched. Simple perforations are notable in that they are elliptical; the long axis of the ellipse may be at right angles to the vertical axis of the vessel (fig. 2). The end walls of the vessel elements are mostly oblique varying from 15–65° from the horizontal. Most are about 40–45°. Intervascular pitting is alternate, but quite irregular, with widely separated pits. A tendency to transitional pitting is noted. Pits are small (3–7μ), with somewhat elliptical borders. Vessel elements average 420μ in length and range from 213–639μ. The most frequent range lies between 300 and 500μ.

Ray tissue is irregular when viewed in tangential section (fig. 2). It is quite abundant seemingly occupying half the area of the section. No truly procumbent cells occur and all are either upright or square. Therefore, rays are considered as homocellular. Both multiseriate and uniseriate rays occur. Multiseriate rays range from 2–7 cells in width and may exhibit uniseriate "wings." Uniseriate rays vary from 1–16 cells in height; multiseriate rays from 7–63 cells in height. Ray cells are lignified and thick-walled exhibiting conspicuous pitting between congeneric elements. Pitting between rays cells and vessels is alternate; that between ray cells and tracheids, follows the tracheidal pattern. The division of rays by the growth of imperforate tracheary elements is a conspicuous feature in the wood of *Scaevola plumieri*.

Axial parenchyma is very sparse, and occurs mainly in diffuse distribution. However, some strands are adjacent to vessels producing the scanty vasicentric pattern. Cell walls are thick.

DISCUSSION

Comparative material, in the form of slides, was available from the S. J. Record Memorial Collection of three other
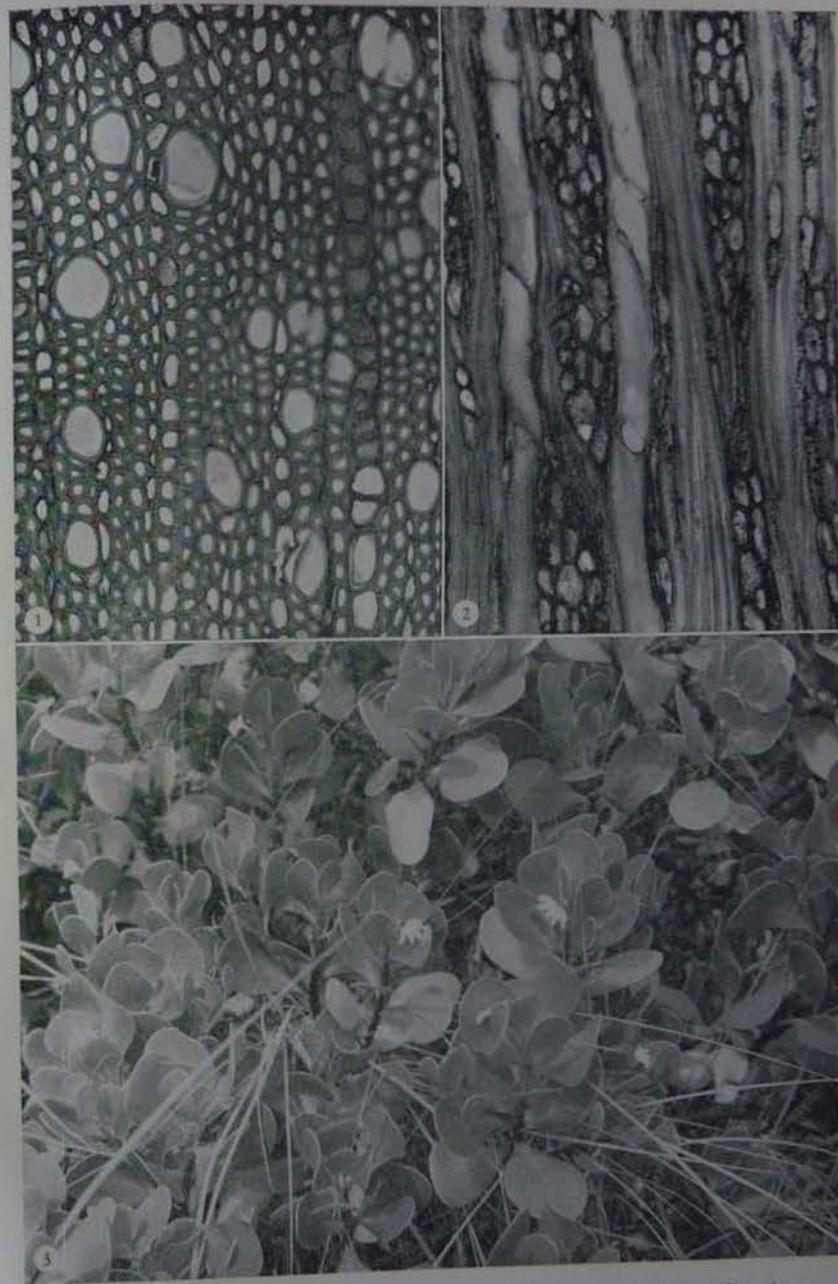
Fig. 1–3. *Scaevola plumieri*. Fig. 1. Transverse section of xylem showing groundmass of tracheids, solitary pores with somewhat angular outlines and squarish cells in vascular rays. × 110.—Fig. 2. Tangential section of xylem illustrating peculiar elliptical simple perforation plates, oblique vessel element end walls and irregular ray tissue. × 100.—Fig. 3. Plants photographed along seacoast on Grassy ... the thick, fleshy, alternate leaves and the zygomorphic,

Table 1. ANATOMICAL COMPARISON OF FOUR SPECIES OF *Scaevola*

SPECIES	IMPERFORATE TRACHEARY ELEMENTS	VESSELS					RAYS		AXIAL PARENCHYMA
		Perforation plates	Intervascular pitting	Tangential diameter (μ)		Distribution	Type	Width (cells)	Distribution
				Average	Range				
S. *plumieri*	tracheids	simple and scalariform	alternate (transitional)	41	25–60	solitary (multiples)	homo-cellular	1–7	diffuse (vasicentric)
S. *floribunda*	tracheids and fiber-tracheids	simple	alternate	60	28–84	solitary (multiples)	Kribs II A	1–2 (1–3)	diffuse and vasicentric
S. *frutescens*	tracheids	simple and scalariform	alternate and transitional	80	38–115	solitary (multiples)	homo-cellular	1–6	diffuse and vasicentric
S. *gaudi-chaudiana*	tracheids and fiber-tracheids	simple and scalariform	alternate and transitional	56	35–84	solitary (multiples)	homo-cellular	1–6	diffuse and vasicentric

species of *Scaevola: S. floribunda, S. frutescens* and *S. gaudichaudiana*. Of the species in table 1, only one, *S. floribunda*, possesses growth rings, and these are poorly defined. All species examined exhibit irregularly arranged, homocellular ray tissue except for *S. floribunda*. In the latter, rays are regular and correspond well with Kribs (1935) heterogeneous type IIA; that is, the multiseriate rays are provided with uniseriate "wings" composed solely of upright cells, the multiseriate portions of the multiseriate rays are composed of procumbent cells and the uniseriate rays are homocellular composed only of upright cells. Ray cells in this specimen contain a reddish, amorphous deposit. Pores in all four species are almost entirely solitary, only a small number of multiples being noted. In all species but *S. plumieri*, the axial parenchyma is fairly abundant. However, only in *S. floribunda* is it conspicuous. Notwithstanding reports to the contrary (Solereder, 1908; Kanehira, 1921; Metcalfe and Chalk, 1950) at least some species of *Scaevola* exhibit scalariform perforation plates. It might be remarked, that the four species of *Scaevola* under discussion are included by Krause (1912) under the section *Sarcocarpaea* G. Don. *S. floribunda*, with its regular ray tissue, lack of scalariform perforations and transitional intervascular pitting diverges markedly from the three other species. An examination of the ray structure and perforation plates in all 14 species of *Sarcocarpaea* might be of taxonomic interest.

Systematic botanists are in agreement that Goodeniaceae are closely allied to Campanulaceae. Goodeniaceae differ from Campanulaceae chiefly in the lack of latex and in the presence of a cup subtending the stigma. The family is highly advanced showing such features as zygomorphic corollas, inferior ovaries and fused carpels. Because of this, the wood of *Scaevola plumieri* is interesting, for it shows a number of primitive features: scalariform perforation plates, diffuse axial parenchyma, a tendency to transitional intervascular pitting and a groundmass of tracheids. This seeming contradictory evolutionary evidence can probably be ascribed to the retention of certain primitive features in the xylem, rather than to the true primitiveness of the

taxon. As Bailey (1957) has emphasized: "It is no longer justifiable to assume . . . that one organ or part of a plant is inherently more conservative and reliable than are all others. . . . Furthermore, the rates of evolutionary modification in different parts frequently are not closely synchronized." Carlquist (1957) has observed similar contradictions between the floral structure of certain woody composites and the anatomy of the xylem.

Although Metcalfe and Chalk (1950) state that vessels are absent from *Scaevola spinescens* according to Krause (1912), we find that Krause asserts that vessels are *"fast völlige Fehlen,"* that is, almost totally lacking. Apparently the vessels in this xerophile are so narrow as to be hardly distinguishable from the imperforate tracheary elements. In general, the woods of Goodeniaceae are extremely poorly known. Other than the xylem description of *Scaevola koenigii (S. frutescens)* by Kanehira (1921) and the description of *Scaevola, Goodenia* and *Dampiera* in Solereder's *Holzstruktur*,[2] no detailed accounts are recorded in the literature.

Specimens examined.—S. plumieri.—FLORIDA KEYS: GRASSY KEY. Shrub, 18 in. high, woody base, succulent upper parts; flowers whitish; in sand south side of key; 1 July 1956, *W. L. Stern & G. K. Brizicky 336* (Y; Yale wood no. 51156). Shrub, 2–3 ft. high; flowers pale purple; 24 March 1958, *W. L. Stern & K. L. Chambers 289* (Y; Yale wood no. 51487).

S. floribunda.—FIJI ISLANDS: VITI LEVU. 1927, *J. W. Gillespie 3188* (Yale wood no. 25584).

S. frutescens.—WEST CAROLINE ISLANDS: PALAU ANGAUR. 29 July 1929, *R. Kanehira 598* (Yale wood no. 20391).

S. gaudichaudiana.—HAWAIIAN ISLANDS: Board of Agriculture and Forestry, Territory of Hawaii *45* (Yale wood no. 21224).

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[2]The writers could not verify Solereder's descriptions as no copy of *Holzstruktur* was available. Interestingly, it is not cited in Metcalfe and Chalk (1950).

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THE WOODS AND FLORA OF THE FLORIDA KEYS. PASSIFLORACEAE[1]

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This predominantly tropical family consists of 12 genera with about 600 species (Killip, 1938). Of the 4 genera which are found in the New World, 3 (*Mitostemma, Dilkea* and *Tetrastylis*) are strictly American. The fourth, *Passiflora*, with about 400 species, is primarily American being represented in the Western Hemisphere by about 360 species. Only the latter genus extends with a few species into the United States. Two species of *Passiflora*, *P. suberosa* and *P. multiflora*, are indigenous to the Florida Keys. Only *P. multiflora* is woody. Passifloraceae are closely related to Malesherbiaceae and Turneraceae (Harms, 1925).

PASSIFLORA MULTIFLORA L.

This species is a woody vine, climbing by axillary tendrils, densely and softly pubescent throughout; young stems striate, old stems more or less conspicuously ribbed (fig. 8), up to 2 inches in diameter; stipules setaceous, 0.2–0.3 cm. long, soon deciduous; petioles 0.3–1.0 cm. long, usually bearing two minute, sessile glands at the apex; leaves oblong, oblong-ovate or oblong-lanceolate, 3.5–12.0 cm. long, 1.5–4.0 cm. wide, apex mostly rounded or retuse, sometimes acutish or mucronulate, rounded or shallowly cordate at the base, tripli-or subtriplinerved, reticulately veined beneath, membranaceous to subcoriaceous; flowers 1.0–1.5 cm. wide in axillary fascicles of 2 to 6; peduncles slender, 0.5–1.0 cm. long, articulated in the lower half; bracts linear-subulate, about 0.2 cm. long, borne near the base of the peduncle; calyx tube patelliform, sulcate; sepals linear-lanceolate, 0.4–0.6 cm. long, greenish-yellow, acutish; petals linear, white, slightly shorter

than the sepals; corona filaments in 2 series, the outer fili-form, 0.2–0.3 cm. long, the inner setaceous, 0.1 cm. long or less; operculum membranous, slightly plicate, less than 0.1 cm. high, incurved; limen annular, closely encircling the ovary; stamens 5, about as long as the sepals, filiments connate at the base, anthers oblong, versatile; ovary globose, sessile, glabrous; styles 3, stigmas capitate; berry subglobose, 0.5–1.0 cm. in diameter, dark blue to purplish-black, glab-rous; seeds arillate, broadly ovate, about 0.3 cm. long, marked with 6–8 transverse grooves having rugulose ridges.

General distribution.—Passiflora multiflora is West Indian in range. It has been recorded from the Greater Antilles and the Virgin Islands. Killip (1938) states that its presence in Costa Rica is probably due to introduction by man. A glabrous form (f. *glabra*) is known from the Bahamas, Cuba and Haiti.

U. S. distribution.—Southern peninsular Florida and the Florida Keys.

ONTOGENY OF THE STEM

Development of the tissues in the stem is at first quite normal. The vascular bundles are discrete and embedded in the fundamental tissue. A continuous vascular cambium develops and formation of secondary xylem and phloem proceeds in regular fashion (fig. 1). Primary xylem elements are conspicuous around the periphery of the pith and are composed of lignified conducting elements surrounded by unlignified parenchyma which is distinguishable from the parenchyma of the pith.

The vascular cambium produces normal tissues in regular quantities until several internodes have been produced. At this time, in older stem portions, five areas in the xylem cylinder become noticeable because of the localized produc-tion of wide vessels (fig. 2). In the intervening areas, no wide vessels occur. The appearance of the xylem cylinder, although still quite regular in outline, is at this stage char-acterized by a sharp difference in pore size in local areas.

The appearance of the xylem cylinder has altered radical-ly in the oldest portions of the stem at the end of a growing

period. A marked irregularity is seen so that xylem produc-tion in the five wide-pored areas has outstripped xylem formation in the intervening areas (fig. 3). In the latter regions, xylem production has been sharply curtailed, and the vascular cambium has formed much more phloem than xylem. The phloem in these areas is composed largely of thin-walled, unlignified parenchymatous cells. The long axis of these cells, as seen on the transverse section, is parallel with the radius of the stem (fig. 6).

A four "year" stem shows a five-armed xylem mass, each arm separated from the other by "rays" of phloem tissue (fig. 4). At this stage the vascular cambium, as seen on the transverse section, is visible at the bases of the phloem "rays," and at the outer margins of the xylem arms. Side walls of the xylem arms are occupied by wide rays which are continuous with the medullary rays (fig. 6).

This scheme is upset as the plant ages and the stem assumes its mature form (fig. 5, 8), as follows: 1) The areas of vascular cambium responsible for xylem production may form patches or "rays" of phloem within the xylem arm. This is caused by the discontinuous formation of phloem (patches), or the more or less continuous production of phloem ("rays"). 2) Within the phloem "rays," a similar phenomenon takes place. The vascular cambium here may lay down few or many lignified xylem cells. These may also occur as patches in the phloem (discontinuous pro-duction), or as "rays" of xylem which may be continuous with the secondary xylem in the original normal part of the xylem cylinder. 3) In old stems, the entire five-armed xylem pattern is completely distorted by the proliferation of the parenchyma cells of the phloem, pith and xylem (?). The vascular cambium is ruptured and torn. Seemingly many separate and disjointed cambia develop at random within the parenchymatous matrix. Wedges of xylem may be formed, or inverted, so that their broadest dimension faces the center of the stem; identifiable fragments of the original parts of the secondary xylem cylinder are found "floating" in the parenchymatous mass oriented at odd angles. All is a disorganized assortment of twisted and dis-

torted cells and tissues. There seems to be little doubt that all living cells in this stem remain totipotent after formation, and that they are capable of dedifferentiation and division to produce other such cells. The wood is soft and pliable and probably offers little resistance to readjustments within the stem brought on through forces set up by the multiplying parenchyma cells.

The development of the stem in *Passiflora multiflora* corresponds closely to Schenck's (1893) *Bignonieentypus*. Schenck describes the development of such a stem as follows:

The wood body maintains more or less regularly arranged furrows as growth in thickness continues. The stem structure then attains the condition where the cambium remains behind in certain longitudinal strips, therefore cutting off relatively more phloem elements than xylem elements in the furrows. The outside cambium becomes split up in this way so that it is narrow in the furrows, and broad at the xylem projections. The side walls of the furrow are lined with broad rays.

In essence, this is the course of stem development in *Passiflora multiflora*. The subsequent irregular behavior of the stem in this species also has parallels in *Bignonia* and in certain Malpighiaceae. This is described and illustrated by Schenck. It is noteworthy, that this complex type of growth has almost exact counterparts in widely different taxa.

There is no evidence from the anatomical literature that the anomalous stem development in *Passiflora multiflora* occurs in any other members of Passifloraceae (Schenck, 1893; Solereder, 1908; Metcalfe and Chalk, 1950). Both Solereder and Schenck state that growth in the stem of Passifloraceae is normal. Although several taxonomists have also studied this species, none remarks on the peculiar stem structure (Harms, 1925; Masters, 1871; Killip, 1938).

Xylem Structure

Although the form of the mature xylem mass as a whole is deeply lobed in transverse section (fig. 8), the elements
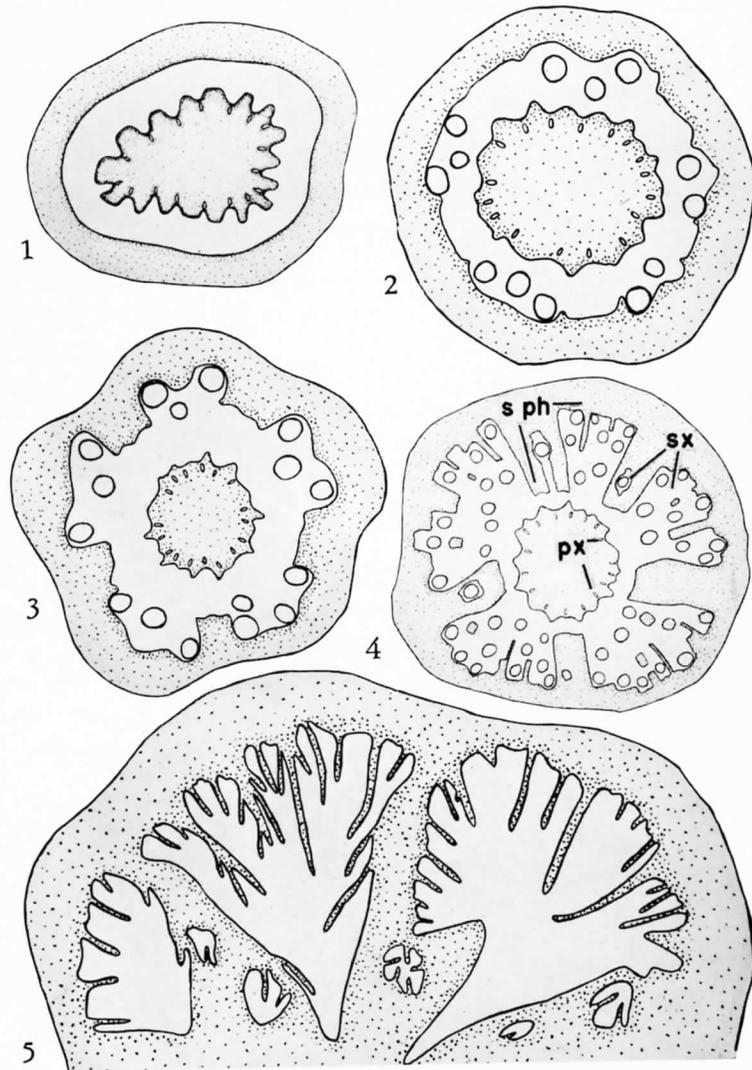
Fig. 1–5. Ontogeny of the stem as seen in transverse sections. Fig. 1. Section through an early internode illustrating the original normal vascular cylinder. × 25.—Fig. 2. A later internode showing the production of large pores in 5 areas. × 30.—Fig. 3. A section through the oldest internode at close of growing period to show the marked irregularity in the production of vascular tissues which culminates in a 5-rayed structure. × 30.—Fig. 4. A stem at the end of 4 growing seasons to illustrate the maximum development of the 5-rayed structure before internal readjustments destroy the configuration; *s ph*=secondary phloem, *s x*=secondary xylem, *p x*=primary xylem. × 12.—Fig. 5. Section from a mature stem exhibiting distorted masses of xylem (unstippled areas) embedded in a matrix of soft tissue (stippled). × 3.
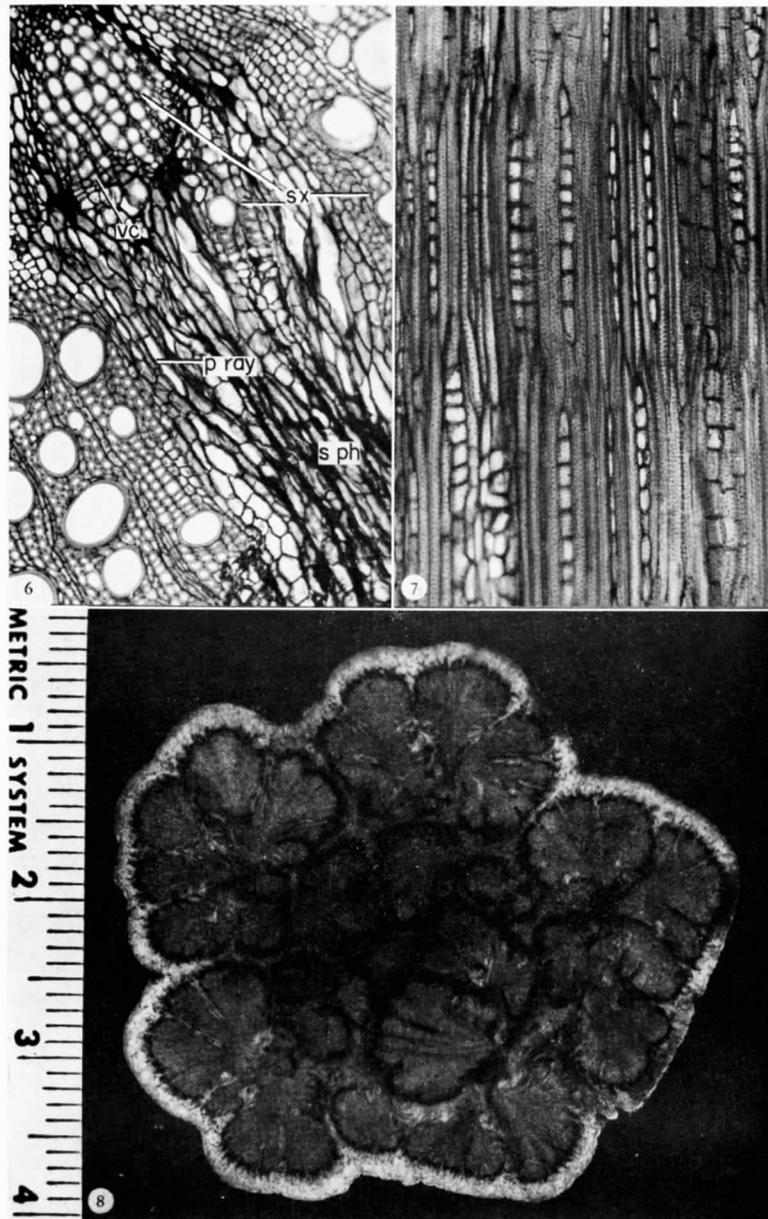
Fig. 6–8.—Fig. 6. Transverse section of 4 "year" stem at the base of a phloem "ray." The vascular cambium, *vc*, can be seen producing much less secondary xylem, *sx*, internally, than secondary phloem, *s ph*, externally. Note the primary rays, *p ray*, bordering the phloem "ray" and the bit of secondary xylem completely surrounded by secondary phloem. × 100.—Fig. 7. Tangential section of wood showing the tendency toward storied structure and the uniseriate vascular rays. × 100.—Fig. 8. Transverse section of the stem to show the lobate, distorted xylem masses. Note that some of the xylem wedges face the center of the axis.

which compose the wood are by and large of quite normal form. As can be seen from the foregoing discussion of the ontogeny, no growth rings are formed, even in the largest stem available for study ($\pm$ 4.0 cm. diameter).

Imperforate tracheary elements are tracheids (sensu Bailey, 1936), the circular bordered pits being equivalent in diameter to those of adjacent vessels (4–7μ). Pits may occur in one or in several rows in tracheid walls. Their borders are rounded and the inner apertures of pit pairs may be crossed. Pit apertures do not extend beyond the borders. In transverse section walls range from thin to very thick (Chattaway, 1932). In table 1, tracheid length measurements are summarized.

Table 1. Lengths of Tracheids in μ

SPECIMEN	RANGE	MOST FREQUENT RANGE	MEAN
Y51303	213–667	300–550	422
Y51318	298–653	350–550	462

Pores are generally circular in outline and are mostly solitary (fig. 6). However, a very few radial multiples were noted; clusters of 2–3 pores are fairly common. Measurements for tangential pore diameters are listed in table 2. Only simple perforation plates have been seen.

Table 2. Tangential Pore Diameters in μ

SPECIMEN	RANGE	MOST FREQUENT RANGE	MEAN
Y51303	26–185	75–150	99
Y51318	40–165	75–150	104

It is probably well to mention here that the fibriform vessel members noted and described by Woodworth (1935) for Passifloraceae, have also been observed in the wood of *Passiflora multiflora*. The cells are tracheid-like in shape, long and narrow with attenuated apices. The perforations, which may be pit-like, apparently lack pit membranes. In the vicinity of the pit-like perforations, the cell wall bulges as if to accommodate this unusual growth. Other times, perforations are more normal, less pit-like, but are very much smaller than those on typical vessel elements. Furthermore, perforations in fibriform vessel members are submore, perforations in fibriform vessel members are terminal, whereas those on typical vessel elements are

always terminal and occupy the horizontal end wall. Wood-worth describes these cells as being of extreme length averaging 1400μ in *Passiflora vitifolia*. Such is not the case in *P. multiflora*, where these cells approximate normal tracheids in length.

Intervascular pitting is alternate. The pits may be widely separated or close, but never is there any evidence of crowded pits. Consequently, borders are rounded in outline or they may approach the elliptical condition. Inner apertures are similarly shaped. On some vessel members, the inner apertures of adjacent pits have coalesced to produce the appearance of transitional pitting.

Vessel element lengths are presented in table 3.

Table 3. Vessel Element Lengths in μ

SPECIMEN	RANGE	MOST FREQUENT RANGE	MEAN
Y51303	57–483	200–400	303
Y51318	185–497	300–450	394

Vascular rays are in large part uniseriate; however, some rays exhibit low, biseriate portions (fig. 7). Most rays are homocellular; that is, they are composed entirely of upright or square cells. Biseriate portions comprise procumbent cells, but the uniseriate "wings" of these rays contain only upright cells (rays heterocellular). Uniseriate rays range between 2 and 15 cells in height; rays with biseriate parts may be up to 22 or more cells high. Rays are very abundant on the transverse section and are sinuous due to the lateral expansion of vessels.

Axial parenchyma is abundant and is conspicuous because the cell walls do not stain as deeply with safranin as do the cell walls of adjacent tracheids and vessels. The arrangement of axial parenchyma on the transverse section is somewhat irregular: 1) It may occur in isolated apotracheal or paratracheal strands, or 2) as irregular clusters of such strands in apotracheal or paratracheal position.

A localized tendency to storied structure involving rays, tracheids and vessel elements has been noted in one specimen, Y51318 (fig. 7). Storying is also evident in the elements of the phloem.

Discussion

The characteristics of the xylem in *Passiflora multiflora* correspond, in general, with those of other members of the family (except *Soyauxia*). The wood is quite highly specialized in several respects: vessel elements have exclusively simple perforations, intervascular pitting is alternate, end walls of vessel elements are horizontal, and there is a tendency to storied structure. As far as is known, this latter phenomenon has never been noted in the Passifloraceae.

Bailey (1920) has demonstrated that during ontogeny, vessel elements elongate but little over their fusiform cambial precursors. It is interesting to note that the lengths of the imperforate tracheary elements (average 442μ) are not much greater than those of the vessel elements (388μ). This indicates that there has been little apical growth of the imperforate elements after their formation from fusiform cambial initials (note in fig. 7 the comparison between tracheid length and the height of the vascular rays). Shortening of cambial initials in dicotyledons is a mark of specialization (Bailey, 1944). That vessel elements and imperforate elements in *P. multiflora* are specialized in this sense, is evident when we see that the mean for vessel element length in 600 species examined by Metcalfe and Chalk (1950) is 649μ, and for imperforate tracheary element length in 534 species is 1317μ. This modification however, may merely be a reflection on the liana habit, and not a true indication of phylogenetic advancement for the species. In any event, "Secondary xylem containing the most highly specialized vessels is formed by a cambium having short initials with abruptly tapered ends and slight overlap" (Bailey, 1957). Judging from the vessel elements in *P. multiflora*, this condition obtains here.

Killip (1938) placed *P. multiflora* in the monotypic subgenus *Apodogyne* and noted that "on the basis of sessile ovary it might perhaps be segregated as a genus." The occurrence of an anomalous stem and the presence of storied structure noted above, seem to favor Killip's remark regarding the possible segregation of this species as a genus. However, a sessile or almost sessile ovary is also known to occur

in *P. apoda* Harms (subgenus *Plecostemma*, sect. *Cieca*) according to Killip. Anomalous wood structure, somewhat similar to that in *P. multiflora*, has been observed by the writers in *P. coccinea* Aubl. (subgenus *Distephana*). In a recent letter from Dr. L. Chalk, he states, "I have examined all my material of Passifloraceae and find that my material of *Crossostemma laurifolia* has the stem broken up into segments by what at first sight appear to be merely large rays, but which on re-examination I find to be clearly not part of the xylem." However, Dr. C. R. Metcalfe has not found any anomalous stem material in the Kew collections of this family.

The observations of the writers and of Dr. Chalk on the occurrence of anomalous stem growth, the presence of storied structure, and the remarks of Killip regarding generic segregation of *P. multiflora* suggest that the classification of this taxon is not a settled matter. However, the solution of this problem, must await further and more comprehensive studies in the comparative anatomy of the Passifloraceae. Judging from the somewhat meagre evidence presented above, a taxonomic re-evaluation of Passifloraceae based on data from comparative anatomy and other botanical disciplines is probably needed.

Specimens examined.—FLORIDA KEYS: UMBRELLA KEY. Coral soil; climbing trees; *A. H. Curtiss 975** (YU). PLANTATION KEY. Vine growing in trees; hammock, north side U. S. 1; 19 July 1956, *W. L. Stern & G. K. Brizicky 522* (Y; Yale wood no. 51303). Vine, 2 in. diameter, clambering in tree tops; hammock; 21 March 1958, *W. L. Stern & K. L. Chambers 255* (Y; Yale wood no. 51466). WINDLEY'S KEY, s. w. end. Vine reaching into tree tops; 20 July 1956, *W. L. Stern & G. K. Brizicky 542* (Y; Yale wood no. 51318).

CUBA: *s. l. C. Wright 2598* (YU).

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ADHESIVES FROM TANNINS IN THE BARK OF BRUGUIERA SPECIES

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Introduction

Bruguiera is one of the important and abundant mangroves. Although mangrove barks are quite rich in tannin content, the utilization of these barks for tannage has always been a problem due to the red color and harsh nature imparted to leather by their tannins. This paper deals with recent attempts to utilize the bark of *Bruguiera* spp. in the preparation of adhesives for plywood manufacture.

According to Pearson (1914), *Bruguiera* species are found in the tidal forests of the Sunderbans, the Andamans, Burma, Ceylon, tropical Africa, Indonesia and Australia and grow into quite large trees. *Bruguiera gymnorrhiza*, in particular, is reported to attain heights of 60 to 80 feet, the yield of dry bark per mature tree averaging about 50 pounds. The tannin content usually ranges from 40 to 45 per cent of the dry weight of the bark (A.M.S., 1914). Paessler (1912), referring to the African species, states that the age of the tree has considerable influence on tannin content which also varies in bark taken from various positions in the tree. The average tannin content is 36 per cent of the weight of the bark. Hooper (1902) remarks that the bark of *Bruguiera gymnorrhiza*, known as "kankra" in the Sunderbans, has a tannin content of 17.5 per cent. Das (1922), however, reports as much as 36 per cent tannins in bark obtained from the Sunderbans. Pilgrim (1924) gives a tannin content of 42.3 per cent of the weight of the inner bark of *Bruguiera* species from Burma. Coombs and Alcock (1913), referring to the *Bruguiera* species of Australia, mention the average percentage of tannin in the bark as 29.1. The results of analysis of tannin in the Australian bark as obtained by Coombs and Alcock are given below:

Bark of *Bruguiera* Species

	TANNIN PER CENT	NON-TANNIN PER CENT
Average	29.1	9
Maximum	36.4	11.8
Minimum	23.6	7.0

According to Brandts (1952), the total area of mangrove forest in Indonesia is approximately 2,500,000 acres. Up to 40 per cent tannin is found in these barks, but they are not much favored as tanning materials. However, being phenolic in nature, they do offer an alternative to phenols in the phenol-formaldehyde type of resin, and thus might become the source of a profitable industry. The tannin contents of Indonesian barks (Brandts, 1952) are as follows:

Tannin Content of Barks and Extracts

SPECIES	TANNIN IN BARK PER CENT	TANNIN IN SOLID EXTRACT PER CENT
Rhizophora conjugata	33	75
Rhizophora stylosa	21	61
Rhizophora mucronata	37	74
Bruguiera gymnorrhiza	30	69
Bruguiera caryophylloides	25	62
Bruguiera parviflora	12	42

Tannin-formaldehyde resins have been suggested for ply-wood and bonding of wood by Dalton (1950, 1953). On account of the high percentage of tannin reported in the bark of *Bruguiera* species, Narayanamurti and Das (1951, 1958 under publication) in their studies on tannin-formaldehyde adhesives, mentioned *Bruguiera* species as a probable source of tannin for adhesive work. They also reported a few tentative results. Narayanamurti, Ramachandra Rao and Rulia Ram (1957, 1958) developed plywood adhesives from the tannins of tamarind seed testae and tea waste. Following this work of investigating tannin-rich raw materials, a solid extract, rich in tannins, has now been prepared from the bark of *Bruguiera* species, and used in the formulation of plywood adhesives.

Experimental

Preparation of tannin.—The bark of *Bruguiera gymnorrhiza* (4 kg.) is cut into small chips and extracted with boiling water in a steam jacketed stainless steel extractor for about two hours. The extract is removed from the bark. The residual bark is further extracted a second and a third time with fresh quantities of water under the same conditions as in the first extraction. The combined extracts are evaporated to dryness. The dry solid extract is scraped and weighed after drying in an air-oven at 100°C. The yield is about 1 kg. An alkaline extract is also prepared in a similar way by extracting the bark with water to which a quantity of sodium hydroxide equal to 0.5 per cent of the weight of the bark has been added. Solid *Bruguiera* bark extracts are powdered and kept for preparation of the adhesive as and when required, since the pot life of the final adhesive is only a few hours.

Preparation of adhesive.—The powdered extract (75 g.) is dissolved in 100 cc. of water while being heated in a steam bath. The thick syrupy liquor is cooled and 3.75 g. of paraformaldehyde (5 per cent of dry weight of the extract) is added and the mixture is then triturated. The adhesive is now ready for use.

Preparation of plywood test panels.—Air-dry veneers, 1/16 inch thick, of *Cedrela toona*, having a moisture content of 10–12 per cent, were employed to make 3-ply panels. Only two sides of the core veneer were painted, by brush, with the adhesive. The face and core veneers were assembled with their grains at right angles, and pressed in a hydraulic hot press at 200 pounds per square inch at 140°C. for 15 minutes. The plywood panels were stacked in the laboratory for about ten days before being cut into specimens and tested.

Testing of plywood panels.—Plywood panels were tested according to the standard procedure mentioned below. Glue shear strength specimens with a shear area of one square inch were cut, each test piece being 3 inches long and 1 inch wide with notches 1 inch apart. Half the shear strength

specimens from each panel were tested in the dry condition and the other half were tested after three hours boiling in water. The tests were carried out in a "Globe Glue Line Tester" (Globe Machine Manufacturing Company, Tacoma, Washington, U. S. A.). The failing load, that is, the maximum load applied to the specimen before failure, and the percentage wood failure in the shear area were recorded (table 1).

The results given in table 1 indicate the possibility of *Bruguiera* bark tannins as being useful in the development of plywood adhesives. Of the three glue formulae tested, glue 3 consisting of 100 parts *Bruguiera* bark extract, 5 parts of para-formaldehyde, 0.5 parts of alkali and 4 parts of wood flour gave the best adhesion. Since formulae 2 and 3 give higher values of glue adhesion than formula 1, it is to be concluded that the addition of alkali to the adhesive improves its strength.

During the preparation of plywood panels of commercial sizes at a temperature of 140°C., the formation of steam pockets within the panels is generally experienced unless the veneers are preconditioned to a suitable moisture content. This difficulty is overcome by the use of adhesives setting at lower temperatures. Therefore, the suitability of *Bruguiera* bark extracts for preparation of adhesives setting at a temperature below 140°C. was investigated. The following three glue formulae were used for making plywood panels at 120°C., the other conditions of pressing being the same as before.

	GLUE I	GLUE II	GLUE III
Powdered alkaline tannin extract	100 g.	100 g.	100 g.
Water	120 g.	120 g.	120 g.
Para-formaldehyde	5 g.	5 g.	5 g.
Wood flour	5 g.	5 g.	5 g.
Phenol	—	5 g.	—
Water soluble phenol-formaldehyde resin	—	—	5 g.

The adhesives and plywood panels from 6 different commercial timbers of India were made according to the procedure already described. Plywood panels were tested according

Table 1. Test Results for Plywood Panels Prepared from Water Extracted Tannin and Pressed at 140°C.

| GLUE FORMULAE | GLUE ADHESION STRENGTH (Shear area: 1 square inch) | | | |
| | Dry | | Hot wet | |
	Failing load in kg. (pounds)[1]	Wood failure in per cent	Failing load in kg. (pounds)[1]	Wood failure in per cent
1. Water extracted tannin + 5 per cent para-formaldehyde	92.1 (203)	42	63.1 (139)	25
2. Glue 1 + 0.5 per cent alkali on the weight of solid extract	108.4 (239)	30	69.0 (152)	0
3. Glue 2 + 4 per cent wood flour on the weight of solid extract	112.5 (248)	36	77.1 (170)	0
4. Standards for commercial plywood in India (1951)	68.0 (150)	—	34 (75)	—

[1]The shear area was 1 square inch. Failing loads refer to this area, but the failing load is not directly proportional to the area.

ing to standard methods described earlier. The values of failing load and wood failure are tabulated in table 2.

Table 2. Test Results for Plywood Panels Prepared from Water Extracted Tannin and Pressed at 120°C.

| SPECIES | GLUE FORMULAE | GLUE ADHESION STRENGTH (Shear area: 1 square inch) | | | |
| | | Dry | | Hot wet | |
		Failing load in kg. (pounds)	Wood failure in per cent	Failing load in kg. (pounds)	Wood failure in per cent
Adina cordifolia	I	83.9 (185)	25	43.1 (95)	0
	II	98.0 (216)	20	65.8 (145)	0
	III	108.0 (238)	38	59.0 (130)	0
Bombax malabaricum	I	103.4 (228)	0	32.7 (72)	0
	II	83.9 (185)	75	42.6 (94)	0
	III	103.4 (228)	72	39.0 (86)	18
Cedrela toona	I	109.8 (242)	28	52.6 (116)	0
	II	113.4 (250)	13	69.0 (152)	0
	III	122.9 (271)	28	88.9 (196)	20
Dysoxylum malabaricum	I	109.8 (242)	0	70.8 (156)	0
	II	114.3 (252)	0	54.4 (120)	0
	III	103.4 (228)	72	57.2 (126)	18
Hardwickia pinnata	I	105.2 (232)	20	73.5 (162)	0
	II	113.4 (250)	13	69.0 (152)	0
	III	120.7 (266)	82	71.7 (158)	0
Holoptelea integrifolia	I	109.8 (242)	28	59.0 (130)	0
	II	108.9 (240)	50	63.5 (140)	0
	III	97.1 (214)	80	64.4 (142)	0

SUMMARY

Bruguiera species are quite abundant in southeast Asia and their bark is rich in tannins. Since these tannins impart a red color to leathers they do not find favor in the leather industry. Alkaline extracts prepared from *Bruguiera* bark have been found to be useful in the preparation of plywood adhesives. Adhesives prepared according to different formulae have given satisfactory results, and plywood panels made with the *Bruguiera* bark adhesives pass the standards laid down in India for commercial plywood.

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A COLLECTION OF WOODY PLANTS FROM PANAMA

GEORGE K. BRIZICKY, WILLIAM L. STERN AND KENTON L. CHAMBERS

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In May and June of 1957, William L. Stern and Kenton L. Chambers traveled to Panama, under the sponsorship of the Office of Naval Research,[1] to assist in a program of wood testing being performed by the Canal Zone Corrosion Laboratory, U. S. Naval Research Laboratory. Their particular task was to locate, in the forest, various species of trees whose wood had been reported to be more or less resistant to attack by marine borers (teredos or shipworms). Timber from these and other species of tropical trees was to be exposed to a series of long-term tests, the goal of which was to measure properties of resistance not only to marine borers but also to decay and deterioration under both aquatic and terrestrial conditions in Panama. To verify scientifically the identity of the woods used in these tests, voucher material and wood specimens were collected for each species. At the same time it was possible to make collections of a number of species of woody plants not directly concerned with the testing program.

The following list is an enumeration of the specimens obtained during the course of these field studies. Although many of the plants collected are of fairly common occurrence, some are more rare and others represent new distribution records for Panama. It has been thought desirable

to record nomenclatural notes, common names, local uses and other supplementary information of interest. No new species are described here, but some of the collections have formed the basis for a recently described new taxon, and others, noted below, appear to represent entities as yet undescribed. All listed specimens are housed in the herbarium of the Samuel James Record Memorial Collection of the Yale School of Forestry. Numbers are those of the collections of Stern and Chambers.

The majority of the specimens was identified by George K. Brizicky; however, certain groups were sent to specialists for determination: *Quercus*, Cornelius H. Muller; Lauraceae, Caroline K. Allen; Melastomaceae, John J. Wurdack; Leguminosae, Richard S. Cowan; *Carapa*, G. K. Noamesi; *Porcelia* and *Cymbopetalum* (Annonaceae), Robert E. Fries; *Sloanea*, C. Earle Smith, Jr.; *Coccoloba*, Richard A. Howard; *Wimmeria*, C. L. Lundell; Verbenaceae, H. N. Moldenke; and *Clibadium*, S. F. Blake.

In general, the localities at which collections were made are as follows (fig. 1): Canal Zone; Volcán Region, Chiriquí Province; vicinity of Almirante, Bocas del Toro Province; Puerto Armuelles, Comarca del Barú; and Bahia de Piñas, Darién Province.

ACTINIDIACEAE

84. SAURAUIA sp. Tree, 8½ in. diameter; fruits with clear mucilage; wood rather soft. Altitude 6000 feet, slopes of Volcán Barú, near town of Cerro Punta. 7 June.

This probably represents a species new for Panama. Leaves are elliptic-ovate, obtuse at apex, cordate at base, up to 35 cm. long and 18 cm. broad.

ANACARDIACEAE

107. CAMPNOSPERMA PANAMENSIS Standl. "orey, orin, auree" Tree, 6 in. diameter; leaves brownish beneath, exuding a clear sap when cut; inflorescence yellowish, spicate. Altitude 150 ft., shores of Laguna de Chiriquí, Bocas del Toro. 11 June.

129. ASTRONIUM GRAVEOLENS Jacq. "sorillo, run run" Tree, 15 in. diameter; leaves from sucker-like shoots at broken apex of tree; wood very hard, sapwood red, riddled by large yellow larvae. Altitude 100 ft., area west of Puerto Armuelles. 15 June.

ANNONACEAE

127. CYMBOPETALUM COSTARICENSE (Donn. Sm.) R. E. Fries. Small tree, 2½ in. diameter; petals creamy yellow, fragile, fleshy, somewhat thicker than the greenish sepals. Altitude 100 ft., area west of Puerto Armuelles. 15 June.

43. PORCELIA MAGNIFRUCTUM (Schery) R. E. Fries. Tree, 30 ft. high; flowers aromatic, with greenish yellow corolla which becomes bright yellow at maturity; carpels separate, cylindrical, about 3 mm. long. Altitude 270 ft., Road K9, Canal Zone. 31 May.

5. XYLOPIA AROMATICA (Lam.) Mart. Small tree; outer surfaces of outer perianth lobes brown, inner lobes and inner surfaces of outer lobes white. Cerra Luisa, Canal Zone. 26 May.

16. XYLOPIA FRUTESCENS Aubl. Small tree; flowers white, aromatic; leaves glaucous beneath, margins slightly revolute; young stems hirsute. Gamboa, Navy Pipeline Road, 10 mi. northeast of Gamboa Bridge, Canal Zone. 29 May.

APOCYNACEAE

33. STEMMADENIA GRANDIFLORA (Jacq.) Miers. Small tree; bark with milky sap; flowers yellow; leaves dark green above, lighter beneath. Naval Ammunition Depot, Group 300 Road, Canal Zone. 31 May.

9. THEVETIA NITIDA (H. B. K.) A. DC. "huevos de gato" Shrub; fruit didymous, scarlet when ripe, with milky juice. Cerra Luisa, Canal Zone. 26 May.

BIGNONIACEAE

130. TABEBUIA cf. CHRYSANTHA (Jacq.) Nichols. "guayacan" Small tree, 6 in. diameter; petioles rusty pubescent. Altitude 100 ft., area west of Puerto Armuelles. 15 June.

BOMBACACEAE

42. OCHROMA PYRAMIDALE (Cav. ex Lam.) Urb. var. bicolor Brizicky comb. nov. *O. bicolor* Rowlee Jour. Wash. Acad. Sci. 9: 165. 1919. *O. lagopus* Swartz var. *bicolor* (Rowlee) Standl. and Steyerm. Field Mus. Nat. Hist. Bot. Ser. 23: 62. 1943. "balsa" Tree, 15 in. diameter, 75 ft. high; leaves with brown tomentum on veins of lower surface; peduncles thick and fleshy; wood soft and brittle. Altitude 270 ft., road K9, Canal Zone. 31 May.

J. H. Pierce (Trop. Woods 69: 1–2. 1942) showed that *Bombax pyramidale* Cav. (in Lamarck, Encycl. 2: 552. 1788), on which Urban's combination is based, apparently has priority over *Ochroma lagopus* Swartz (Prodr. Veg. Ind. Occ. 98. 1788): "The name *pyramidale* then appeared in two publications in April and June 1788, while *lagopus* appeared sometime in 1788 before September." Although an exact publication date for Swartz' *Prodromus* is not known at present (September, 1788, seems to be most probable), there is no basis for

the supposition that it antedates Lamarck's *Encyclopédie* 2(2): 552, which certainly was published in April, 1788. Therefore Pierce's proposal to reduce *Ochroma pyramidale* (Cav.) Urb. to synonymy under *Ochroma lagopus* Swartz is hardly acceptable in view of the publication dates known, or at least assumed, at the present time.

BURSERACEAE

164. TETRAGASTRIS PANAMENSIS (Engl.) O. Kuntze "animé" Tree, 20 in. diameter; flower buds present. Steep hills near the shore, Punta Guayabo Chiquita, 14 miles north of Colombia, Darién. 23 June.

CARYOCARACEAE

161. CARYOCAR COSTARICENSE Donn. Sm. "jenené" Tree, 4–6 ft. diameter, with scaly bark; leaves trifoliolate, with 2 glands (stipels) at base of leaflets. Steep hills near the shore, Punta Guayabo Chiquita, 14 miles north of Colombia, Darién. 23 June.

CELASTRACEAE

57. WIMMERIA sp. "raton rojo" Tree, 16 in. diameter. Altitude 4500 ft., foothills of Volcán Barú, northwest of El Hato. 6 June.

According to C. L. Lundell, this appears to represent a new species.

COMBRETACEAE

150. CONOCARPUS ERECTUS L. "zarragosa" Tree, 11 in. diameter. Mud flats along coast near Farfan, Canal Zone. 20 June.

151. CONOCARPUS ERECTUS L. "zarragosa" Tree. Mud flats along coast near Farfan, Canal Zone. 20 June.

115. TERMINALIA CHIRIQUENSIS Pittier. "guayabo de monte" Tree with multiple trunks, each 16–20 in. diameter; bark conspicuously mottled reddish brown (may resemble *Psidium* spp. which are commonly known as "guayabo"); leaves pale green. Vicinity of Guabito, Bocas del Toro. 12 June.

COMPOSITAE

80. CLIBADIUM LEIOGYNUM Steetz. Small tree, 2½ in. diameter; florets white; fleshy involucral bracts green, becoming blue. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

CORNACEAE

48. CORNUS DISCIFLORA Moc. & Sessé ex DC. "mata hombro" Tree, 50 ft. tall, 24 in. diameter. Altitude 5100 ft., foothills of Volcán Barú, north of El Hato. 5 June.

87. CORNUS DISCIFLORA Moc. & Sessé ex DC. Tree, 24 in. diameter; fruits corky at apex; leaves pale beneath, somewhat stiff and coriaceous. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

CYATHEACEAE

11. ALSOPHILA TRICHIATA Maxon. Tree fern up to 25 ft. tall; fronds up to 24 dm. long, thorny on rachis near base; in dense woods on slopes and along streams. Gamboa, Navy Pipeline Road, 10 mi. northeast of Gamboa Bridge, Canal Zone. 29 May.

188. HEMITELIA sect. CNEMIDARIA. Arborescent fern about 25 ft. tall; base of leaf rachis spiny. Shores of Bahia de Piñas, Darién. 26 June.

This is "a species related to *H. petiolata* Hook. and to *H. Woronovii* Maxon and Morton. I am not able to place it more accurately. Sect. *Cnemidaria* contains the species of *Hemitelia* with broad segments and most of them are not much more than twice pinnate. In addition, most species have a rhizome and do not form a trunk, but a few, as yours, do become trees. Your material is especially distinct from related species in that the terminal segment of the pinnae is stalked, that is, the pinna are imparipinnate." (Abstract from letter of Rolla Tryon, 19 August 1958.)

ELAEOCARPACEAE

65. SLOANEA MEDUSULA Schum. & Pittier. Tree, 13 in. diameter; fruits with 3–5 carpels, spiny, woody. Altitude 4500 ft., foothills of Volcán Barú, northwest of El Hato. 6 June.

EUPHORBIACEAE

31. ACALYPHA MACROSTACHYA Jacq. var. MACROPHYLLA (H. B. K.) Muell. Arg. Small tree; leaves dull on both surfaces. Altitude 1000 ft., Cerro Galero, Road K6, Canal Zone. 30 May.

85. SAPIUM cf. AUCUPARIUM Jacq. (Syn. *S. jamaicense* Swartz). Tree 19 in. diameter, with milky juice in bark and leaves; leaves stiff, with yellow-green veins, bearing 2 glands at base of blade; stamens with bright orange pollen. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

97. SAPIUM cf. BIGLANDULOSUM (L.) Muell. Arg. Tree, 77 ft. high, 14 in. diameter, with thick short branches; milky juice in bark and leaves; leaves clustered at ends of twigs, bearing 2 small glands at base of blade; fruit a 3-seeded tricarpellate capsule, the seeds covered with a white aril. Altitude 6300 ft., slopes of Volcán Barú, near town of Cerro Punta. 8 June.

FAGACEAE

55. QUERCUS BARUENSIS C. H. Mull. Trop. Woods 108: 74–76. 1958. "roble blanco" Tree, 70 ft. tall, 30 in. diameter. Altitude 5100 ft., foothills of Volcán Barú, north of El Hato. 5 June.

76. QUERCUS BARUENSIS C. H. Mull. Tree, 6 ft. diameter, in area partly cut over for grazing. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

47. QUERCUS CORRUGATA Hook. "mamecillo" Tree 70–80 ft. high, 24 in. diameter. Altitude 5100 ft., foothills of Volcán Barú, north of El Hato. 5 June.

52. QUERCUS GULIELMI-TRELEASEI C. H Mull. "roble rojas" Tree, 90–100 ft. high, 30 in. diameter. Altitude 5100 ft., foothills of Volcán Barú, north of El Hato. 5 June.

FLACOURTIACEAE

29. CASEARIA JAVITENSIS H. B. K. Small tree, 6 in. diameter; ovaries bright red; leaves shiny on both surfaces. Altitude 1000 ft., Cerro Galero, Road K6, Canal Zone. 30 May.

35. PROCKIA CRUCIS L. Shrub; stamens numerous, yellow. Naval Ammunition Depot, Group 300 Road, Canal Zone. 31 May.

34. TETRATHYLACIUM JOHANSENII Standl. Small tree; flowers with disagreeable odor; ovary with fleshy white disk; leaves just appearing, lax and very shiny on upper surface. Naval Ammunition Depot, Group 300 Road, Canal Zone. 31 May.

44. ZUELANIA GUIDONIA (Swartz) Britt. & Millsp. Tree 40–50 ft. tall, 8 in. diameter; fruit green, globose, fleshy, splitting into 3 valves when ripe, odor of fruit apple-like, placenta of unripe fruit white when first cut, turning orange on exposure to air; bark produces a clear amber gum when cut. Altitude 260 ft., road K9D, Canal Zone. 2 June.

GUTTIFERAE

60. CALOPHYLLUM BRASILIENSE Camb. var. REKOI Standl. "María" Tree, 18 in. diameter; bark with sticky yellow sap. Altitude 4500 ft., foothills of Volcán Barú, northwest of El Hato. 6 June.

25. CALOPHYLLUM cf. LONGIFOLIUM Willd. "María" Small tree; leaves coriaceous, dark green, shiny. Gamboa, Navy Pipeline Road, 10 mi. northeast of Gamboa Bridge, Canal Zone. 29 May.

105. SYMPHONIA GLOBULIFERA L. f. "sambogum, bogum, cerillo, cerro" Large tree, 40 in. diameter, supported on a mass of heavy stilt roots which extend to about 8 ft. above the ground; sap from bark gummy, yellow; leaves glossy green; flower buds bright red, velvety; fruits 2-seeded, succulent, producing a yellow sap when cut. Altitude 150 ft., shores of Laguna de Chiriqui, Bocas del Toro. 11 June.

36. VISMIA GUIANENSIS (Aubl.) Choisy. Small tree; leaves rusty beneath; petals and sepals persistent at base of fruits, the latter with skunk-like aroma, green, conical, bearing brown seeds 1–2 mm. long on axial placenta. Naval Ammunition Depot, Group 300 Road, Canal Zone. 31 May.

LAURACEAE

95. LICARIA EXCELSA Kosterm. Tree, 24 in. diameter; leaves dark green above, pale green beneath; fruits with red woody cup; cut twigs

aromatic. Altitude 6300 ft., slopes of Volcán Barú, near town of Cerro Punta. 8 June.

169. LICARIA PITTIERI (Mez) Allen. "iigua negro" Tree, 30 in. diameter; wood with cedar-like odor. Slopes of hills bordering Bahia de Piñas, Darién. 24 June.

Known only from Costa Rica heretofore.

186. NECTANDRA FUSCOBARBATA (Mez) Allen. Tree, 8 in. diameter, growing on rocky shore at edge of salt water; flowers white. Bahia de Piñas, Darién. 26 June.

99. NECTANDRA LATIFOLIA (H. B. K.) Mez. Tree 21½ in. diameter; leaves pale green. Altitude 6300 ft., slopes of Volcán Barú, near town of Cerro Punta. 8 June.

111. NECTANDRA RETICULATA (Ruiz & Pavon) Mez. "aguacatillo" Tree, 18 in. diameter. Vicinity of Guabito, Bocas del Toro. 12 June.

111A. NECTANDRA RETICULATA (Ruiz & Pavon) Mez. "aguacatillo" Young stems and backs of leaves densely brown pubescent. Vicinity of Guabito, Bocas del Toro. 12 June.

113. NECTANDRA STANDLEYI Allen. "aguacate" Tree, 15 in. diameter; flowers greenish white. Vicinity of Guabito, Bocas del Toro. 12 June.

50. NECTANDRA WHITEI (Woods.) Allen (?). "sigua" Tree, 90–100 ft. tall, 30 in. diameter. Altitude 5000 ft., foothills of Volcán Barú, north of El Hato. 5 June.

51. NECTANDRA WHITEI (Woods.) Allen. "bambito" Tree, 90–100 ft. high, 15 in. diameter; peduncle and cupule of fruit red. Altitude 5000 ft., foothills of Volcán Barú, north of El Hato. 5 June.

53. OCOTEA cf. VERAGUENSIS (Meissn.) Mez. "sigua canela" Tree, 70 ft. high, 30 in. diameter; cupules of fruit red; wood aromatic. Altitude 5100 ft., foothills of Volcán Barú, north of El Hato. 5 June.

170. OCOTEA sp. "encibe" Large tree with buttressed base; fruit with blue-purple terminal portion and acorn-like cup; fruit, leaves and wood aromatic. Slopes of hills bordering Bahia de Piñas, Darién. 24 June.

56. PERSEA RIGENS Allen. "pizarrá" Tree, 60–70 ft. tall, 30 in. diameter; cupules and peduncles of fruit red. Altitude 5000 ft., foothills of Volcán Barú, north of El Hato. 5 June.

62. PHOEBE BRENESII Standl. Small tree, 14 in. diameter; fruits green with red cupules. Altitude 4500 ft., foothills of Volcán Barú, northwest of El Hato. 6 June.

156. PHOEBE JOHNSTONII Allen. "aguacatillo" Tree, 18 in. diameter; leaves aromatic. Road passing Navy Radio Station, Summit, Canal Zone. 20 June.

32. PHOEBE MEXICANA Meissn. Tree 12–14 in. diameter, of fairly common occurrence; flowers white, attracting a great number of bees; leaves glossy dark green above, pale green beneath; immature

fruits green. Naval Ammunition Depot, Group 300 Road, Canal Zone. 31 May.

173. "vacarita" Tree; wood reddish; leaves with bloom on underside. Slopes of hills bordering Bahia de Piñas, Darién. 24 June.

174. "quiribi or giribi" Tree, 15–18 in. diameter, with small buttresses; leaves somewhat aromatic. Shores of a small river, Ensenada Guayabo between Punta Guayabo Grande and Punta Guayabo Chiquita, Darién. 25 June.

LECYTHIDACEAE

176. ESCHWEILERA sp. "huasca, tuave" Tree, 17 in. diameter; flowers creamy yellow. Shores of a small river, Ensenada Guayabo between Punta Guayabo Grande and Punta Guayabo Chiquita, Darién. 25 June.

141. GRIAS FENDLERI Seem. Tree; leaves up to 10 dm. long, 2 dm. wide, clustered at ends of stout branches; flowers and fruits borne on short lateral twigs. Area near Puerto Armuelles, between Cañazo and Cocos. 17 June.

189. GUSTAVIA RODANTHA Standl. "membrillo" Small tree, about 2 in. diameter; petals pink. Shores of Bahia de Piñas, Darién. 26 June.

Woodson (Ann. Missouri Bot. Gard. 45: 120. 1958) cites petals as 2.5–3.5 cm. long. However, in the original description of *Gustavia rodantha* (conspecific with G. *nana* Pittier), Standley writes (Field Mus. Nat. Hist. Bot. Ser. 4: 230–240. 1929), "*petala . . . c. 6.5 cm. longa et 2 cm. lata.*" Petals in our specimens are up to 7.0 cm. long and 3.5 cm. wide. Standley also mentions that the petioles in his species are 1.0–6.5 cm. long; but the isotype of G. *rodantha* (Y) has petioles up to 12 cm. long. The maximum petiole length in our specimen is 17.0 cm.

G. *nana* has been cited by Woodson as "apparently endemic to Panama." However, a specimen from Colombia *(Lawrance 633)*, presumably identical with G. *nana*, has been observed in the Gray Herbarium.

155. GUSTAVIA SUPERBA (Kunth) Berg. "membrillo" Small tree, 5 in. diameter; leaves clustered at ends of branches, the largest about 1 m. long; fruits resemble a smoking pipe in shape and are borne on short twigs arising from the larger branches; bark (wood?) smells strongly of rotten fish. Road passing Navy Radio Station, Summit, Canal Zone. 20 June.

162. LECYTHIS AMPLA Miers. "coco, salero" Large tree, 30 in. diameter. Steep hills near the shore; Punta Guayabo Chiquita, 14 miles north of Colombia, Darién. 23 June.

163. LECYTHIS AMPLA Miers. "coco, salero" Tree. Steep hills near the shore, Punta Guayabo Chiquita, 14 miles north of Colombia, Darién. 23 June.

165. LECYTHIS cf. AMPLA Miers. "coco, salero" Fruits only, collected from ground. Steep hills near the shore, Punta Guayabo Chiquita, 14 miles north of Colombia, Darién. 23 June.

148. LECYTHIS TUYRANA Pittier. Tree, 24 in. diameter; flowers yellow. Planted across from railroad station near Panama Canal Company administration building, Balboa, Canal Zone. 19 June.

LEGUMINOSAE

19. ANDIRA INERMIS (Swartz) H. B. K. "peronil" Tree, 12 in. diameter, 75 ft. tall; leaves shiny; flowers dark purple, young fruits obovoid, thick and hard. Gamboa, Navy Pipeline Road, 10 mi. northeast of Gamboa Bridge, Canal Zone. 29 May.

45. BAUHINIA EUCOSMA Blake. Woody vine about 1 in. diameter, clambering in *Zuelania guidonia*, No. 44; flowers white, aromatic, lip of corolla short, greenish white. Altitude 260 ft., Road K9D, Canal Zone. 2 June.

167. BROWNEA MACROPHYLLA Linden. "cacique negro" Small tree; bark with red sap; fruits with peculiar truncate-cylindric seeds; heartwood black. Steep hills near the shore, Punta Guayabo Chiquita, 14 miles north of Colombia, Darién. 23 June.

134. DIPHYSA ROBINIOIDES Benth. "macano" Tree, 12 in. diameter; trunk much twisted. Altitude 100 ft., area west of Puerto Armuelles. 15 June.

108. DIPTERYX PANAMENSIS (Pittier) Record. "almendro" Tree, 5 ft. diameter; flowers purple; wood extremely hard (turns edge of axe). Finca 11, Bocas Division of Chiriqui Land Company, west of Almirante. 12 June.

81. ERYTHRINA BERTEROANA Urb. Tree, 19 in. diameter; trunk with broad conical spines; pith in twigs chambered, white; fruits with seeds covered by a bright red aril (testa). Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

157. GLIRICIDIA SEPIUM (Jacq.) Standl. "mata raton" Tree, 10 in. diameter, with greatly contorted trunk; leaves with odor of new-mown grass, red-purple mottling on lower surface. Road passing Navy Radio Station, Summit, Canal Zone. 20 June.

152. HYMENAEA COURBARIL L. "algarrobo" Large tree with 3 main stems each 12–16 in. diameter; flower buds and fruits present. Mud flats along coast near Farfan, Canal Zone. 20 June.

4. INGA HAYESII Benth. Shrubby; stamens white. Cerra Luisa, Canal Zone. 26 May.

138. INGA MARGINATA Willd. Tree; rachis of leaf with green glands on upper side where opposite leaflets are attached; white flowers racemose; wood moderately hard. Rim of deep gorge of Rio Corotú, area west of Puerto Armuelles. 16 June.

137. INGA MULTIJUGA Benth. Tree; leaves with yellowish glands on upper side of rachis where the opposite leaflets are attached; wood

hard. Rim of deep gorge of Rio Corotú, area west of Puerto Armuelles. 16 June.

160. LONCHOCARPUS cf. ATROPURPUREUS Benth. "higuanillo" Tree, 18 in. diameter. Azote de Caballo Road near Madden Dam, before first saddle dam, Canal Zone. 20 June.

110. PENTACLETHRA MACROLOBA (Willd.) O. Kuntze. "gavilán" Tree with hard wood. Vicinity of Guabito, Bocas del Toro. 12 June.

40. PITHECELLOBIUM HYMENAEIFOLIUM (Humb. & Bonpl.) Benth. Shrub, 6 ft. high, ½ in. diameter, the stem unbranched, thorny at nodes; flowers white, very conspicuous. Altitude 270 ft., road K9, Canal Zone. 31 May.

158. PITHECELLOBIUM MANGENSE (Jacq.) Macbr. Tree, about 9 in. diameter, the 10 ft. high trunk supporting a low, greatly spreading crown; branchlets thorny; bark with a sticky, reddish sap. Road passing Navy Radio Station, Summit, Canal Zone. 20 June.

27. PITHECELLOBIUM OBLONGUM (Roxb.) Benth. Small tree with several main stems; spiny branches spreading and drooping; fruits reddish brown. Mud flats along coast near Farfan, Canal Zone. 30 May.

125. PLATYPODIUM MAXONIANUM Pittier. "tigre" Tree with base of trunk bearing sinuate convolute ridges; leaflets readily deciduous from the rachis; seedlings very abundant beneath parent tree. Altitude 100 ft., area west of Puerto Armuelles. 15 June.

114. PRIORIA COPAIFERA Griseb. "cativo" Large tree, 24 in. diameter; wood oozes a green, sticky, water-soluble sap. Vicinity of Guabito, Bocas del Toro. 12 June.

168. PTEROCARPUS OFFICINALIS Jacq. "chuella" Small tree growing close to beach; flowers yellow-orange with red stripe on banner; wood very soft and white. Punta Guayabo Chiquita, 14 miles north of Colombia, Darién. 23 June.

109. PTEROCARPUS sp. "sangre" Tree, 51 in. diameter; bark oozes red sap which hardens in several hours; leaves glossy dark green on both surfaces. Finca 11, Bocas Division of Chiriqui Land Company, west of Almirante. 12 June.

Our specimen, which has nearly mature fruits, is different from all the species known from Central America. It strongly resembles some specimens of Pterocarpus indicus Willd. However, there are no records regarding the introduction of the latter species into this area.

179 SWARTZIA PANAMENSIS Benth. "cutarro" Tree, 7 in. diameter Shores of a small river, Ensenada Guayabo between Punta Guayabo Grande and Punta Guayabo Chiquita, Darién. 25 June.

132. SWARTZIA sp. (?) "sangrillo negro" Tall tree; bark with blood red sap; only fragments of leaves obtainable, the leaflets pale green. Altitude 100 ft., area west of Puerto Armuelles. 15 June.

This sterile specimen, with its 7–11 leaflets arranged alternately (a condition rare in Swartzia), resembles some specimens of Pterocarpus hayesii Hemsl. more than any species of Swartzia known from Central America. However, the corresponding wood sample has been identified by B. F. Kukachka (U. S. Forest Products Laboratory) as probably Swartzia sp. There is another specimen of "sangrillo negro," identical with Stern & Chambers 132, in the Yale collections (Y 45022). This was collected in Chiriquí, Panama, in 1948, and sent to Yale by V. C. Dunlap. A. C. Smith (correspondence, 1948) stated the following regarding Dunlap's sterile specimen: "It is possible that your specimen represents Pterocarpus officinalis Jacq. At least it agrees with some of our South American material (note: in the U. S. National Herbarium) fairly well. I provisionally referred it to P. hayesii Benth. following numerous identifications by Dr. Standley in our herbarium. Actually I am not entirely convinced that it even belongs in the genus." The corresponding wood sample had subsequently been identified by R. W. Hess as Swartzia sp.! The fact that these two different wood samples, representing apparently the same species, had been determined as Swartzia independently by two wood anatomists, makes it probable that a species of Swartzia, unknown from Central America, and possessing leaves with 7–11 alternate leaflets, occurs in Panama. Possibly sterile specimens of this species have already been collected several times but have been referred to Pterocarpus. However, until fruits or flowers of the species are available, its generic position will remain uncertain.

172. VATAIREA sp. (?) "amargo amargo" Large tree, 4½ ft. diameter; buttresses 10–12 ft. high; wood bitter. Slopes of hills bordering Bahia de Piñas, Darién. 24 June.

LORANTHACEAE

76A. PSITTACANTHUS SCHIEDEANUS (Schlechtd. & Cham.) G. Don. Woody parasitic vine, growing high in, and seemingly throughout, the crown of No. 76, Quercus baruensis; leaves succulent, blue-green; flowers with orange-red pedicels, yellow-orange corolla and orange filaments. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

Flowers in our specimen are about 10 cm. long, i. e., somewhat longer than those usually cited for this species (6.5–8.5 cm.).

82. STRUTHANTHUS cf. MARGINATUS (Desv.) Blume ex Schult. "mata palo" Woody parasite; leaves glossy on both surfaces; flowers yellow-green; fruits yellow when ripe. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

MALPIGHIACEAE

191. BYRSONIMA CORIACEA (Swartz) Kunth. "carbonero" Tree, 14 in. diameter; flowers yellow. Shores of Bahia de Piñas, Darién. 26 June.

6. BYRSONIMA CRASSIFOLIA (L). H. B. K. "nancé" Tree; flowers yellow-orange. Cerra Luisa, Canal Zone. 26 May.

106. BYRSONIMA CRASSIFOLIA (L.) H. B. K. Tree, 7½ in. diameter; leaves densely red-brown pubescent beneath, dark green and glabrous above; young twigs red-brown tomentose; flowers yellow, fading to orange. Altitude 150 ft., shores of Laguna de Chiriquí, Bocas del Toro. 11 June.

MALVACEAE

28. HIBISCUS TILIACEUS L. "wild mahoe" Small tree with several, often somewhat decumbent, main stems; young stems pubescent; leaves pale gray-green below; petals bright yellow, fading to reddish. Mud flats along coast near Farfan, Canal Zone. 30 May.

77A. WERCKLEA LUTEA Rolfe. Tree; hairs on fruits stiff, bristle-like. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

The anthers are somewhat unequilaterally horseshoe- or "U"-shaped rather than "oblong" as stated by Rolfe. This corresponds more nearly to the "reniform anther" considered typical for Malvaceae.

MELASTOMACEAE

182. CLIDEMIA PURPUREO-VIOLACEA Cogn. Small shrub; flowers yellow-green. Shores of a small river, Ensenada Guayabo between Punta Guayabo Grande and Punta Guayabo Chiquita, Darién. 25 June.

First record for Panama.

64. CONOSTEGIA CHIRIQUENSIS Gl. Tree, 10 in. diameter; fruits blue when ripe. Altitude 4500 ft., foothills of Volcán Barú, northwest of El Hato. 6 June.

178. CONOSTEGIA SETOSA Triana. Small shrub, ¾ in. diameter; flowers white. Shores of a small river, Ensenada Guayabo, between Punta Guayabo Grande and Punta Guayabo Chiquita, Darién. 25 June.

First report for Panama.

30. MICONIA ARGENTEA (Swartz) DC. Small tree; leaves white beneath, dark green above; mature fruits bluish purple. Altitude 1000 ft., Cerro Galero, Road K6, Canal Zone. 30 May.

37. MICONIA IMPETIOLARIS (Swartz) Don. Shrub, 8 ft. high; leaves dark glossy green above, red pubescent beneath. Naval Ammunition Depot, Group 300 Road, Canal Zone. 31 May.

187. MICONIA ROBINSONIANA Cogn. Small tree; flowers pink. Shores of Bahia de Piñas, Darién. 26 June.

"Stern & Chambers 187 and 193, both from Piñas Bay, Darién, have recently been referred by Wurdack to Miconia robinsoniana Cogn., a species otherwise endemic to the Galapagos Islands. The affinities of M. robinsoniana are with species 40–45 of Cogniaux' familial monograph, as well as with M. curvipetiolata Cogn. & Gl. ex Gl., M. blakeaefolia Gl., and M. transversa Gl. With such an obvious super-

fluity of epithets, no phytogeographic speculations concerning the apparent distributional disjunction of M. robinsoniana would be valid at present." (Extract from letter of J. J. Wurdack, 24 July 1958.)

193. MICONIA ROBINSONIANA Cogn. Small tree; flowers pink; fruits purple, succulent. Shores of Bahia de Piñas, Darién. 26 June.

175. TOPOBEA MEMBRANACEA Wurdack. Woody vine; flowers pink. Shores of a small river, Ensenada Guayabo between Punta Guayabo Grande and Punta Guayabo Chiquita, Darién. 25 June.

First record for Panama.

MELIACEAE

116. CARAPA SLATERI Standl. "batéo, cedro mancho" Small tree, 4½ in. diameter; leaves 6–9 dm. long, even-pinnate, bearing about 14 leaflets per leaf. Vicinity of Guabito, Bocas del Toro. 12 June.

139. CARAPA SLATERI Standl. "cedro macho" Tree; leaves 4.5–6.0 dm. long with 5–6 pairs of leaflets. Area near Puerto Armuelles, between Cañazo and Cocos. 17 June.

166. CARAPA SLATERI Standl. "tangaré" Tree; leaves with 9–11 leaflets. Steep hills near the shore, Punta Guayabo Chiquita, 14 miles north of Colombia, Darién. 23 June.

103. CEDRELA FISSILIS Vell. Tree about 15 in. diameter, bark not aromatic but bitter. Pasture along road between David and El Hato, Chiriqui Province. 9 June.

59. CEDRELA TONDUZII C. DC. "cedro cebolla" Tree, 22 in. diameter; twigs with conspicuous lenticels and solid white pith; leaf scars 12–15 mm. across; bark with sweet odor. Altitude 4500 ft., foothills of Volcán Barú, northwest of El Hato. 6 June.

131. GUAREA LONGIPETIOLA C. DC. "chuchupate" Cut end of stump 24 in. diameter; 2 leaves taken from sucker shoot, one 15 dm. long and still not fully mature but with over 25 pairs of leaflets, the other 10.5 dm. long and with 28 pairs of leaflets, rachis of leaves very woody. Altitude 100 ft., area west of Puerto Armuelles. 15 June.

143. TRICHILIA TUBERCULATA (Triana & Planch.) C. DC. Tree. Area near Puerto Armuelles, between Cañazo and Cocos. 17 June.

146. TRICHILIA TUBERCULATA (Triana & Planch.) C. DC. Tree. Area near Puerto Armuelles, between Cañazo and Cocos. 17 June.

MYRISTICACEAE

112. DIALYANTHERA OTOBA (Humb. & Bonpl.) Warb. "miguelario, wine wood" Small tree, 5 in. diameter; leaves dark green above, blue-green beneath. Vicinity of Guabito, Bocas del Toro. 12 June.

128. VIROLA sp. "bogamani, fruta dorada" Wood sample from tall buttressed tree, herbarium material from apparently identical sapling nearby; leaves with brown pubescence. Altitude 100 ft., area west of Puerto Armuelles. 15 June.

128A. VIROLA KOSCHNYI Warb. "bogamani" Fruits only, collected from ground in forest; pericarp orange, aril bright red with spicy odor. Area near Puerto Armuelles, between Cañazo and Cocos. 17 June.

194. VIROLA SEBIFERA Aubl. "mancha" Tree, growing very near sea; inflorescence orange; flowers and leaves aromatic; bark with red sap. Shores of Bahia de Piñas, Darién. 26 June.

MYRSINACEAE

96. ARDISIA cf. PALMANA Donn. Sm. Tree, 8½ in. diameter; leaves thickish but not stiff, glandular at base; fruit with 1 bony seed, succulent, black at base, blending to red above and yellow-green at apex, borne on a thickened whitish pedicel 2–3 mm. long. Altitude 6300 ft., slopes of Volcán Barú, near town of Cerro Punta. 8 June.

Our specimen seems to belong to this or a very closely related species. Heretofore it has been known only from Costa Rica.

MORACEAE

136. CHLOROPHORA TINCTORIA (L.) Gaud. "mora" Tree; bark with milky sap; heartwood dull yellow, extremely hard and difficult to split, with interlocked grain. Rim of deep gorge of Rio Corotú, area west of Puerto Armuelles. 16 June.

180. SOROCEA AFFINIS Hemsl. Small tree, 2½ in. diameter; flowers small, creamy white. Shores of a small river, Ensenada Guayabo between Punta Guayabo Grande and Punta Guayabo Chiquita, Darién. 25 June.

OLACACEAE

126. HEISTERIA cf. LATIFOLIA Standl. Small, scraggly tree, 3 in. diameter; stems green; flowers greenish yellow; heartwood red. Altitude 100 ft., area west of Puerto Armuelles. 15 June.

ONAGRACEAE

86. FUCHSIA ARBORESCENS Sims. Shrub or small tree, 8–10 ft. tall; flowers magenta; mature fruits blue-glaucous, many-seeded berries with clear yellowish pulp. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

PAPAVERACEAE

79. BOCCONIA FRUTESCENS L. Semishrub, woody at base; the young stems orange; leaves light bluish beneath; fruits succulent, glaucous; seeds with red fleshy aril at base; wood orange with prominent rays. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

PIPERACEAE

32A. PIPER TABOGANUM C. DC. Shrub, 4 ft. tall, ½ in. in diameter, with swollen nodes; flowers white. Naval Ammunition Depot, Group 300 Road, Canal Zone. 31 May.

POLYGONACEAE

181. COCCOLOBA LEHMANNII Lindau. Tree, 8 in. diameter; flowers white. Shores of a small river, Ensenada Guayabo between Punta Guayabo Grande and Punta Guayabo Chiquita, Darién. 25 June.

41. TRIPLARIS SURINAMENSIS Cham. "palo santo" Small tree, 4 in. diameter, 40 ft. high. Altitude 270 ft., road K9, Canal Zone. 31 May.

PROTEACEAE

49. PANOPSIS SUAVEOLENS (Kl. & Karst.) Pittier. "roblecito" Tree, 12–15 ft. tall, 4 in. diameter (said to reach height of 50 ft.). Altitude 5000 ft., foothills of Volcán Barú, north of El Hato. 5 June.

In his monograph of the American Proteaceae (Bot. Jahrb. 76: 139–211. 1954) Sleumer reduced Panopsis costaricensis Standl. and P. murcronata Cuatr. to synonymy under Panopsis suaveolens (Kl. & Karst.) Pittier. The species occurs in Costa Rica, Panama, Ecuador and Colombia.

RHIZOPHORACEAE

149. RHIZOPHORA SAMOENSIS (Hochr.) Salvoza. Small tree, 6 in. diameter; corolla of 4 white, hairy petals. Mud flats along coast near Farfan, Canal Zone. 20 June.

ROSACEAE

133. HIRTELLA TRIANDRA Swartz. "conejo" Small tree, 12 in. diameter; leaves scabrous; fruits pubescent, reddish when mature; heartwood red, fine-textured. Altitude 100 ft., area west of Puerto Armuelles. 15 June.

135. LICANIA ARBOREA Seem. "rasca" Tree, 30 in. diameter; leaves stiff, coriaceous, dark green and smooth above, pale green and finely scabrous beneath. Standing in front of Chiriqui Land Company hospital, Puerto Armuelles. 15 June.

54. PRUNUS ANNULARIS Koehne. "mamey oloroso" Tree, 45 ft. high, 20 in. diameter; fresh wood or bark with strong bitter almond odor. Altitude 5100 ft., foothills of Volcán Barú, north of El Hato. 5 June.

54A. PRUNUS ANNULARIS Koehne. "mamey oloroso" Tree growing near No. 54; fruit present, in loose botryform clusters, perhaps yellow when ripe. Altitude 5100 ft., foothills of Volcán Barú, north of El Hato. 5 June.

RUBIACEAE

153. ALIBERTIA EDULIS (L.Rich.) A. Rich. Shrub, 6 ft. high; flowers white. Mud flats along coast near Farfan, Canal Zone. 20 June.

Wood said to be employed as the vertical members in wattle and daub construction.

39. ALSEIS BLACKIANA Hemsl. Tree, 13 in. diameter, 75 ft. high; flowers white, aromatic; fruits brown and somewhat hard when dry. Altitude 270 ft., road K9, Canal Zone. 31 May.

192. AMAIOUA CORYMBOSA H. B. K. Tree, 6 in. diameter, with fluted trunk; bark very thin; flowers white. Shores of Bahia de Piñas, Darién. 26 June.

18. CEPHAËLIS TOMENTOSA (Aubl.) Vahl. Shrub; brilliant red bracts beneath the inflorescence; flowers 2 mm. across, tubular, yellow; all parts of plant hispid. Gamboa, Navy Pipeline Road, 10 mi. northeast of Gamboa Bridge, Canal Zone. 29 May.

8. GENIPA AMERICANA L. Small tree; fruits brown, erect. Cerra Luisa, Canal Zone. 26 May.

144. HAMELIA AXILLARIS Swartz. Small tree; fruit clusters resemble *Viburnum*; leaves tend to be clustered at ends of branches. Area near Puerto Armuelles, between Cañazo and Cocos. 17 June.

177. HAMELIA ROWLEEI Standl. Small tree, 1 in. diameter; flowers yellow. Shores of a small river, Ensenada Guayabo between Punta Guayabo Grande and Punta Guayabo Chiquita, Darién. 25 June.

2. ISERTIA HAENKEANA DC. Sparsely branched shrub; inflorescence terminal; flowers red at base and yellow at apex. Growing in cut over land, Cerra Luisa, Canal Zone. 26 May.

63. PALICOUREA GALEOTTIANA Martens. Shrub; flowers yellow, on red pedicels; fruits green with yellow stripes. Altitude 4500 ft., foothills of Volcán Barú, northwest of El Hato. 6 June.

61. PALICOUREA sp. Small tree, 10 ft. high, 2 in. diameter; flowers and pedicels of the inflorescence magenta. Altitude 4500 ft., foothills of Volcán Barú, northwest of El Hato. 6 June.

38. PITTONIOTIS TRICHANTHA Griseb. Tree, 12 in. diameter; flowers white, faintly aromatic; fruits green. Naval Ammunition Depot, Group 300 Road, Canal Zone. 31 May.

171. WARSCEWICZIA COCCINEA (Vahl) Klotzsch. "guna" Small tree, leaning on trees along rocky shoreline; striking appearance due to the brilliant red expanded calyx lobes; corolla yellow-orange. Slopes of hills bordering Bahia de Piñas, Darién. 24 June.

Roots said to act as an aphrodisiac.

RUTACEAE

17. ZANTHOXYLUM BELIZENSE Lundell. Small tree; trunk bearing stout spines 1.8 cm. long; leaves 6.0–7.5 dm. long, rachis spiny. Gamboa,

Navy Pipeline Road, 10 mi. northeast of Gamboa Bridge, Canal Zone. 29 May.

The specimen is sterile but it apparently belongs to this species, which heretofore has been known only from Mexico (Oaxaca, Veracruz), British Honduras, Guatemala and Nicaragua.

SABIACEAE

145. MELIOSMA ALLENII Standl. & L. Wms. Tree; flowers in axillary racemes, petals (?) yellow-orange; fruit a drupe. Area near Puerto Armuelles, between Cañazo and Cocos. 17 June.

The type of the species has not been seen. However, it can hardly be doubted that our specimen belongs to this species which has been known before only from Costa Rica.

SOLANACEAE

83. SOLANUM OCHRACEO-FERRUGINEUM (Dunal) Fernald. Small tree with spiny twigs and trunk; youngest leaves with reddish brown tomentum. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

STAPHYLEACEAE

190. TURPINIA OCCIDENTALIS (Swartz) G. Don. Tree, 16 in. diameter; flowers white. Shores of Bahia de Piñas, Darién. 26 June.

STERCULIACEAE

140. THEOBROMA ANGUSTIFOLIUM DC. Tree; leaves somewhat peltate, pale bluish green beneath, petioles not attached at lower margin of blades; fruit resembling a cacao pod. Area near Puerto Armuelles, between Cañazo and Cocos. 17 June.

THEACEAE

46. LAPLACEA SEMISERRATA (Mart. & Zucc.) Cambess. "mangle de monte" Large tree, 70 ft. tall, 27 in. diameter, felled for timber. Altitude 5000 ft., foothills of Volcán Barú, north of El Hato. 5 June.

26. PELLICIERA RHIZOPHORAE Planch. & Triana. "palo de sal" Small tree, 6 in. diameter above the 18 in. high buttresses; leaves coriaceous; fruits with rufous warts. Mud flats along coast near Farfan, Canal Zone. 30 May.

154. PELLICIERA RHIZOPHORAE Planch. & Triana. "palo de sal" Tree, 10 in. diameter; fruits orange-brown to brown, germinating readily on mud beneath tree. Mud flats along coast near Farfan, Canal Zone. 20 June.

THEOPHRASTACEAE

142. CLAVIJA LEHMANNII Mez. Small tree, 5½ ft. high, 2 in. diameter; leaves 10 dm. or more long, clustered at tip of single unbranched

stem; fruits bright orange, also clustered at apex of stem. Area near Puerto Armuelles between Cañazo and Cocos. 17 June.

Although this species was first described from a male specimen only, the above fruiting material seems referable to it. The calyx, persistent on the fruits, indicates the flowers are 4-merous. The dried fruits are somewhat depressed globose, 3.0–3.5 cm. high and 4.0–4.5 cm. broad. The sterile specimen, *Cooper & Slater 191* (Y 10544) from Chiriquí, is identical with our collection.

TILIACEAE

7. APEIBA TIBOURBOU Aubl. Tree; flowers yellow; fruit resembling a sea urchin. Cerra Luisa, Canal Zone. 26 May.

77. HELIOCARPUS POPAYANENSIS H.B.K. Tree, 11 in. diameter; wood white, very soft and light. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

ULMACEAE

58. CHAETOPTELEA MEXICANA Liebm. "cenizo" Tree, 48 in. diameter; buttresses head high, extending out for several feet from the base of the tree; leaves stiff. Altitude 4500 ft., foothills of Volcán Barú, northwest of El Hato. 6 June.

The authors have followed Standley and Steyermark in *Flora of Guatemala* IV. (Fieldiana 24: 5–6. 1946) in choosing the generic name *Chaetoptelea*. However, there appear to be few significant differences between this monotypic genus and *Ulmus*; therefore, *Ulmus mexicana* (Liebm.) Planch. might be preferred.

VERBENACEAE

98. CITHAREXYLUM LANKESTERI Moldenke. Small tree, 8½ in. diameter, of fairly common occurrence; fruits in pendent racemes, bright yellow, succulent, 2-seeded (?), the calyx persistent on old fruit axis. Altitude 6300 ft., slopes of Volcán Barú, near town of Cerro Punta. 8 June.

First record from Panama; previously known only from the original collection of *Lankester 243*, Paso Ancho, Volcán de Irazú in Costa Rica.

88. LIPPIA COSTARICENSIS Moldenke. Tree, 14½ in. diameter; leaves with mint-like aroma, rugose, slightly scabrous; smaller branches square. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

First record from Panama.

78. LIPPIA TORRESII Standl. Tree, 14 in. diameter; leaves with mint-like aroma, rugose and scabrous on upper surface; young stems square; wood very hard, the sapwood light, heartwood dark. Altitude 6000 ft., slopes of Volcán Barú, near town of Cerro Punta. 7 June.

159. VITEX COOPERI Standl. Tree, 12 in. diameter with fluted base. Azote de Caballo Road near Madden Dam, before first saddle dam, Canal Zone. 20 June.

VIOLACEAE

183. RINOREA SQUAMATA Blake. Small tree, 20 ft. high, 2½ in. diameter; fruits green (unripe ?). Shores of a small river, Ensenada Guayabo between Punta Guayabo Grande and Punta Guayabo Chiquita, Darién. 25 June.

VOCHYSIACEAE

104. VOCHYSIA FERRUGINEA Mart. "yemeri mayo" Tree, 18½ in. diameter, abundant and producing great masses of orange-yellow flowers; leaves glossy green above, dull beneath. Altitude 150 ft., shores of Laguna de Chiriquí, Bocas del Toro. 11 June.
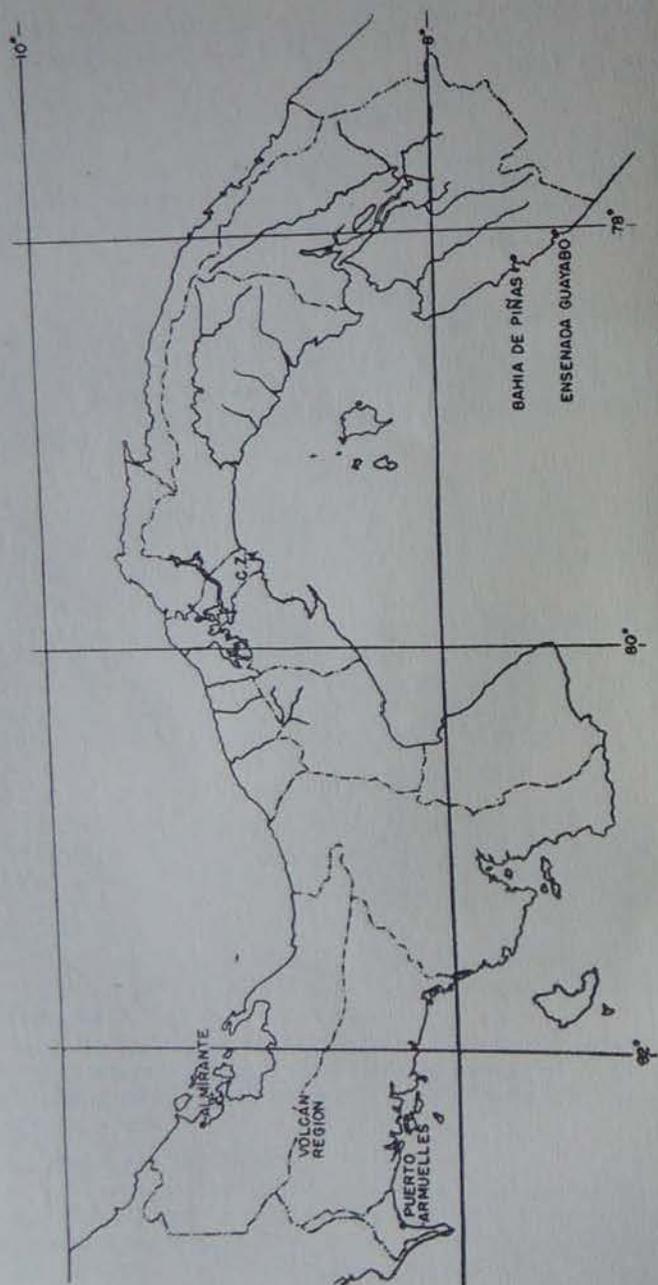
Fig. 1. Republic of Panama. Map showing general areas of collection.

XYLEM STRUCTURE AND ANNUAL RHYTHM OF DEVELOPMENT IN TREES AND SHRUBS OF THE DESERT.

I. *TAMARIX APHYLLA*, *T. JORDANIS* VAR. *NEGEVENSIS*, *T. GALLICA* VAR. *MARIS-MORTUI*

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INTRODUCTION

The fact that plants in desert areas survive long summer periods, after receiving only very limited amounts of rain during the short winter seasons, has been a puzzle to scientists for a long time. Many efforts have been made, and are still being made, to understand the survival mechanism of such plants. A considerable amount of work on this problem has been done in Israel by various scientists (Evenari, 1938; Evenari and Richter, 1937; Shmueli, 1948; Zohary and Orshansky, 1954, 1956, and others). Their views will be discussed in a later article.

Considering the fact that the intensity of cambial activity in the production of new cells and their subsequent differentiation is correlated with many physiological processes taking place in the plant, an investigation of the rhythm of that activity throughout the year may throw some additional light on the ecological behavior of desert plants. For this purpose the anatomical structure of the xylem, and the course of cell differentiation through the year, was studied in seventeen species of trees and shrubs growing in the Negev, the southern part of Israel. Most of these species are representatives of the local desert vegetation, but among

them are also some trees that have been introduced. The species examined were: *Acacia cyanophylla* Lindl., *A. raddiana* Savi, *A. tortilis* (Forsk.) Hayne, *Anabasis articulata* (Forsk.) Moq., *Artemisia monosperma* Del., *Calligonum comosum* L'Hér., *Eucalyptus camaldulensis* Dehn., *Lycium europaeum* L., *Nitraria retusa* (Forsk.) Asch., *Reaumuria palaestina* Boiss., *Retama raetam* (Forsk.) Webb, *Salsola rosmarinus* (Ehr.) Solms-Laub., *Tamarix aphylla* (L.) Karst., *T. gallica* L. var. *maris-mortui* (Gutm.) Zoh., *T. jordanis* Boiss. var. *negevensis* Zoh., *Thymelaea hirsuta* (L.) Endl., and *Zygophyllum dumosum* Boiss. Comparison with data obtained in an earlier, similar investigation on trees and shrubs of the Mediterranean area (Fahn, 1953, 1955), will now be possible.

Studies on some of the species were carried out in collaboration with Miss Carmela Shenkar. The present investigation was begun in November, 1954. As cambial activity in trees and shrubs growing in the desert had not been investigated hitherto, the author's aim was to obtain a general knowledge of a large number of species rather than to collect detailed data from numerous specimens of one or two species only. From the small number of specimens examined in each case, a good general idea of the course of cambial activity throughout the year was thus obtained. The present paper, the first of the series, deals with the three above-mentioned species of *Tamarix*. Nomenclature has been adopted from Zohary (1956).

MATERIAL AND METHODS

Four specimens of *Tamarix aphylla* were examined. Of these, numbers 1 and 2 were trees growing on heavy alluvial soils near Masmiya, in the Mediterranean territory of Israel where the average annual rainfall amounts to 440 mm.; trunks of the trees were about 60 cm. in diameter. The two other specimens, numbered 8 and 9, were located in the Saharo-Sindian territory, some 14 km. south of Beersheba on inland sand dunes, where rainfall amounts to 100 mm. per annum. The trunks of these trees were roughly 10–15 cm. in diameter. Furthermore, two specimens of *Tamarix*

jordanis var. *negevensis*, growing on the same sand dunes south of Beersheba were examined. The trunks of these trees, numbers 10 and 11, were about 10 cm. in diameter. Specimens of *Tamarix gallica* var. *maris-mortui*, numbers 39 and 40, with trunk diameters of approximately 10 cm., grew on a salt marsh near Sdom, where annual rainfall is 50 mm.

Chips of the outermost wood of the trunk were removed with a chisel each month during a period from November 2, 1954, to October 26, 1955, and on several occasions later on. Samples were taken in an alternate fashion, so that the wounds would not affect the interlying areas from which future samples would be taken. Subsequent samples did not, in fact, seem to have been influenced by such wounds. Samples of the two larger trees of *T. aphylla* were taken at chest height, and samples of the other trees were taken at about half a meter above ground. Sections of twigs were also examined. The chips and twigs were both fixed and preserved in formalin-aceto-alcohol. Transverse sections were then cut with a sliding microtome. One set of sections was stained partly in safranin and fast green, and partly in safranin only, and mounted in Canada balsam. In these the number of outermost layers of wood fibres with incompletely thickened or altogether unthickened cell walls, was then determined under the microscope. The other set of sections was treated with I_2KI and mounted in glycerine for starch examination. Radial and tangential sections, as well as macerations, were also prepared from each species for anatomical studies. Other sections stained with carmine acetate were used to determine the existence of nuclei in the wood fibres. The thinnest sections, of which photographs were taken, came from samples embedded in celloidin. As observations made on pieces of twigs were similar to, though less prominent than those made on chips of outermost trunk wood, we shall confine our account to the latter.

TAMARIX APHYLLA (L.) KARST.

Wood anatomy (fig. 1 and 2).—The wood was found to be diffuse-porous to semi-ring-porous. Growth rings are

difficult to distinguish here, especially when examined microscopically. The maximum tangential diameter of the vessels at the beginning of the growth ring was 240μ in the trees growing near Masmiya (no. 1, 2) and 160μ in those growing south of Beersheba (no. 8, 9). Maximum tangential diameter of the vessels at the end of the growth ring was 160μ and 100μ respectively in the two localities. Vessels are either solitary or diagonally placed in multiples of mostly 2 to 3, and sometimes in small clusters. Five to thirty vessels were counted in a square millimeter. (In specimens 1 and 2 the number was smaller than in 8 and 9.) Perforations are simple and mainly transverse. Intervascular pitting is alternate and pits are small, with slit-like openings. Vessel member length was recorded from 90–170μ. No tyloses were found. A transluscent gummose mass appears here and there in a vessel throughout its lumen, or only on its walls. Attention has already been drawn to the occurrence of this substance and its weak tannin reaction by Brunner (1909). Wood parenchyma in the species examined is storied, paratracheal and vasicentric, and is arranged around solitary vessels or vessel groups in single or many-layered sheaths. At the end of the growth ring parenchyma cells are flattened tangentially. All parenchyma cells store starch. Tannin masses were seen in some of the cells.

The heterogeneous rays widen prominently at the borders of the growth rings. Procumbent cells are surrounded by a sheath of square cells in which rhomboid crystals are common. The large rays are sometimes interwoven with narrow strands of fibres, vessels or parenchyma. The majority of rays are 8–20 cells wide, but narrower rays and sometimes even uniseriate rays are also to be seen. Height of rays reaches 1.5 mm. (heights up to 2 mm. have been recorded by Metcalfe and Chalk, 1950, and by Chudnoff, 1956). There are 2–4 rays in a millimeter. The ray cells store starch and scattered cells containing tannins were also observed.

Fibres are of various shapes; sometimes spindle shaped, sometimes with irregular walls and quite often with tail-like ends. Their elongated, steep-diagonal simple pits are almost entirely limited to the radial walls. Fibre walls are

moderately thin. Lengths from 0.37–0.94 mm. were recorded. Fibres contain living protoplasts with nuclei and store starch (fig. 5). Yellowish-brown tannins are also present in some of them.

Rhythm of cambial activity.—From the examination of slides during successive months, it appears that the cambium of *T. aphylla* remains active throughout the year. Judging the intensity of cambial activity from the number of fibre layers with incompletely thickened walls, it was difficult to determine a common course of activity for all species examined (table 1).

Although it is fairly easy to distinguish growth rings macroscopically, difficulties arise on microscopic examination. It was, therefore, difficult to determine the exact point of time at which a new ring began to differentiate. However, in the course of our investigation we came to the conclusion that differentiation of the growth ring began at the end of August in tree 1, and in tree 2 at the end of September. In the sample taken from tree 1 on September 23, 1955, the growth ring had already reached a width of approximately 100 fibres. In a sample taken from tree 2 on the same date, the new growth ring had only just started to develop. Examinations of samples taken from trees 8 and 9 on March 16, 1955 and March 7, 1956, respectively, showed quite clearly that the time of growth ring initiation in the trees is the end of February. There was, however, good reason to conclude that a second growth ring started to develop in tree 8 at the end of October and in 9 at the beginning of September. In all four specimens examined, cambial activity was found to be particularly low about a month prior to new growth ring initiation. This is evident from table 1.

Seasonal changes in starch content of the xylem and cambial activity.—On comparing sections stained with iodine it became evident that the starch content of the xylem undergoes seasonal changes. These changes manifest themselves in the appearance of a starchless zone in the wood bordering the cambium (fig. 6). Figures for the width of that zone, as determined from monthly counts of the fibres, are given in table 1. From table 1 it can be seen that the starchless

Table 1. Intensity of Cambial Activity and Seasonal Changes in Starch Content of the Xylem of *Tamarix aphylla*

Specimen Number	Type of Data	NOV. 2, 1954	DEC. 8, 1954	JAN. 5, 1955	FEB. 9, 1955	MARCH 16, 1955	APRIL 15, 1955	MAY 13, 1955	JUNE 17, 1955	JULY 18, 1955	AUGUST 21, 1955	SEPT. 23, 1955	OCT. 26, 1955
1	Number of outermost layers of fibres with incompletely thickened cell walls	4-10	±15	±5	±25	13-14	20-30	±20	12-18	2-3	±15	10-20	—
1	Width of starchless zone of outer xylem in number of fibres	±40	±25	±10	±25	4-15	35-50	20-30	±20	0-4	5-15	5-10	±130
2	Number of outermost layers of fibres with incompletely thickened cell walls	30-50	8-14	—	15-20	±4	15-20	±20	10-20	4-8	4-8	10-20	15-20
2	Width of starchless zone of outer xylem in number of fibres	—	10-30	—	15-30	7-22	30-60	40-50	±50	6-30	2-5	8-15	±30
8	Number of outermost layers of fibres with incompletely thickened cell walls	±35	8-10	±30	20-30	±20	20-25	35-40	10-15	7-14	20-30	4-8	5-12
8	Width of starchless zone of outer xylem in number of fibres	±40	±40	60-70	±40	25-30	±50	—	30-40	15-20	20-30	30-50	
9	Number of outermost layers of fibres with incompletely thickened cell walls	±40	±20	±40	5-10	10-15	±10	±10	3-4	0	±20	±10	±10
9	Width of starchless zone of outer xylem in number of fibres	±50	±50	±60	20-30	30-40	±30	20-30	40-50	±20	±10	30-40	

*Location of trees 1 and 2: Masmiya; 8 and 9: 14 km. south of Beersheba.

zone reached its minimum width on July 18, 1955 in trees 1 and 9, on August 2, 1955 in tree 2 and on September 23, 1955 in tree 8. It is interesting to note from that table that the starchless zone is narrowest at the time when cambial activity is at its lowest.

Phenology and cambial activity.—Flower buds begin to emerge in the first half of July; sprouting of new shoots occurs in September. In trees 8 and 9, growing south of Beersheba, there seems to be a second wave of shoot development in late February or early March. These periods of emergence of new shoots were found to coincide with the onset of new growth ring development.

TAMARIX JORDANIS BOISS. VAR. NEGEVENSIS ZOH.

Wood anatomy (fig. 3).—In this species, wood was found to be semi-ring-porous. Here it was much easier to distinguish the growth rings microscopically than in the case of *T. aphylla*. The maximum tangential diameter of vessels at the beginning of the growth ring was 160μ, and of those at its end 75μ. On the whole, vessel arrangement resembles that of *T. aphylla* but vessels at the end of the growth ring are embedded in a narrow zone of tangentially flattened fibres and wood parenchyma cells, and are conspicuously smaller in diameter than the neighbouring vessels. Vessel member length was recorded from $60-120\mu$. Pitting, perforations and the presence of starch grains and tannins are as in *T. aphylla*. The paratracheal, vasicentric wood parenchyma was found to be storied. However, in this species there are fewer parenchyma cells than in *T. aphylla*.

Rays are heterogeneous as in *T. aphylla*, but crystals also occur in the procumbent cells. Rays are 8-16 cells wide and up to 1.6 mm. in height, but lower and narrower rays also occur. There are 3 or 4 rays in a millimeter. Fibres are as in *T. aphylla*; lengths from 0.28-0.9 mm. were measured.

Rhythm of cambial activity.—In *T. jordanis* var. *negevensis* outlines of growth rings can easily be distinguished, even microscopically. This is due to the conspicuous zone of tangentially flattened fibres and wood parenchyma at the end of each growth ring in this species in contrast with *T.*

aphylla. In one of the specimens of *T. jordanis* var. *negevensis*, the cambium appeared to have one period of very low activity; in the other specimen two such periods occurred. These periods were observed in samples taken from tree 10 in January and February and again in September, and in tree 11 in December (see table 2). The zone of the flattened fibres was produced in tree 10 during the period between the end of December and the end of February. The new growth ring began to develop in tree 10 at the beginning of April, and in tree 11 at the beginning of March.[3] Examination of a sample from tree 11 on August 21, 1955, gave the impression of the appearance of a false ring.

Seasonal changes in starch content and cambial activity.— As seen from table 2, the starchless zone disappeared or very nearly disappeared in tree 10 during the periods of January– March and September. In tree 11 disappearance of the starchless zone was observed only in the sample taken in December. A correlation between increase in width of the starchless zone and cambial activity is also evident from table 2 (fig. 6).

Phenology and cambial activity.—Vegetative shoots develop from the beginning of March, at about the same period during which the new growth ring begins to form. The development of vegetative shoots continues throughout summer until fall. Inflorescences appear twice yearly, one flowering period starting at the beginning of March and the second in the middle of October, this latter being the main one.

TAMARIX GALLICA L. VAR. MARIS-MORTUI (GUTM.) ZOH.

Wood anatomy (fig. 4).—This was found to be similar to that of *T. jordanis* var. *negevensis*, the only difference being that the procumbent ray cells are shorter and less clearly distinguishable from the square cells of the wood rays.

Rhythm of cambial activity.—Here as in *T. jordanis* var. *negevensis*, growth rings are easily distinguishable. As

[3]In tree 11, ring initiation in 1956 was later than it had been in 1955. On March 7, 1956, there was still no sign of a new ring.

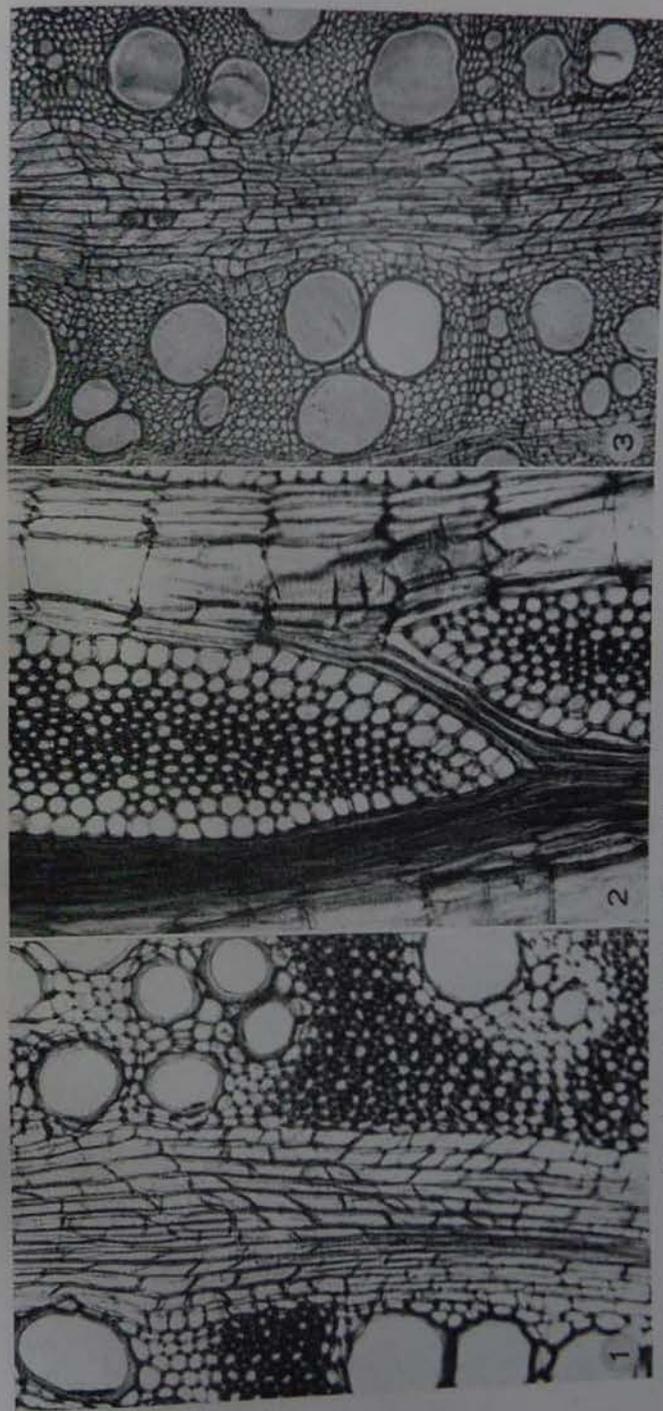Fig. 1–3.—Fig. 1–2. *Tamarix aphylla* (specimen No. 9); Fig. 1. Cross-section of wood on the border of two growth rings, × 115.—Fig. 2. Tangential section of wood, × 117.—Fig. 3. *T. jordanis* var. *negevensis* (specimen No. 10), cross-section of wood, × 90.
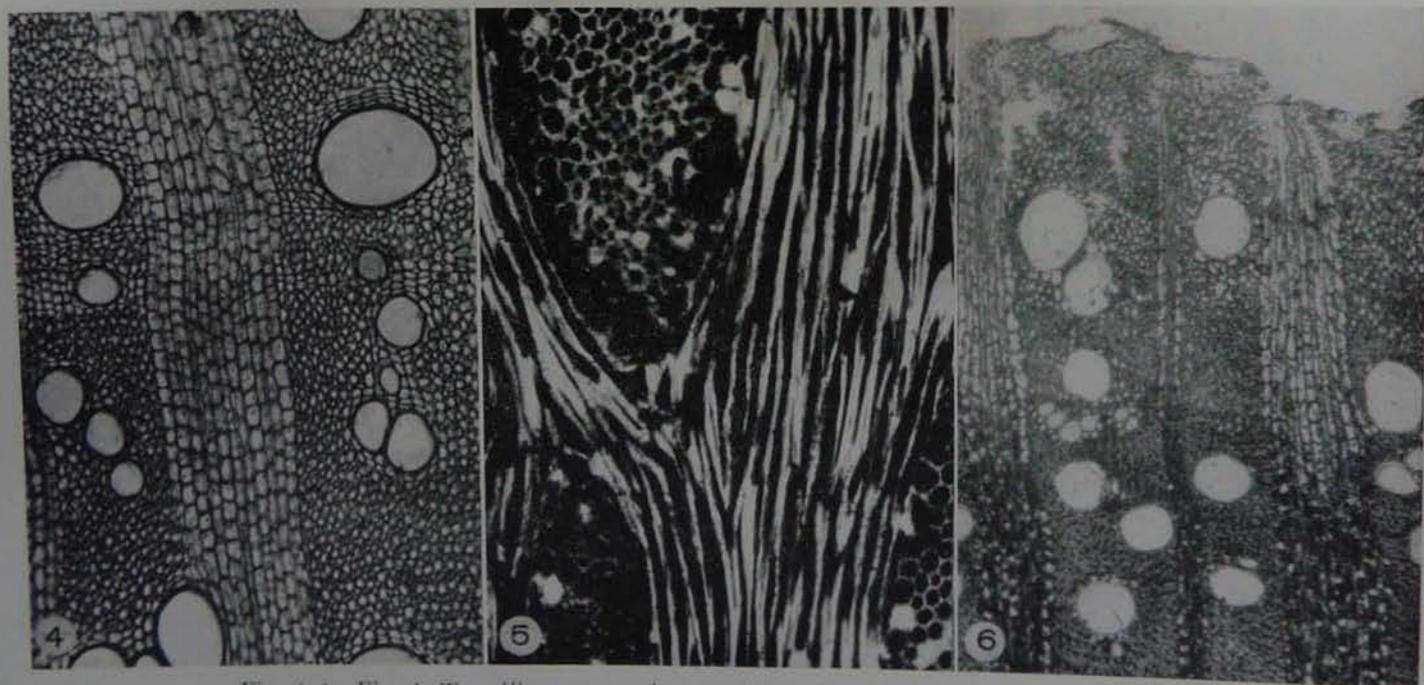
Fig. 4–6.—Fig. 4. *T. gallica* var. *maris-mortui* (specimen No. 39), cross-section of wood. × 96. Fig. 5. *Tamarix aphylla* (specimen No. 2), tangential section of wood stained with I-KI, showing fibres and ray cells containing starch. × 112.—Fig. 6. *T. jordanis* var. *negevensis* (specimen No. 11), cross-section of a sample of the outermost xylem taken on March 16, 1955, stained with I-KI, and showing a starchless zone. × 74.

Table 2. INTENSITY OF CAMBIAL ACTIVITY AND SEASONAL CHANGES IN STARCH CONTENT OF THE XYLEM IN *Tamarix jordanis* VAR. *negevensis* GROWING 14 KM. SOUTH OF BEERSHEBA

SPECIMEN NUMBER	TYPE OF DATA	NOV. 2, 1954	DEC. 8, 1954	JAN. 5, 1955	FEB. 9, 1955	MARCH 16, 1955	APRIL 15, 1955	MAY 13, 1955	JUNE 17, 1955	JULY 18, 1955	AUGUST 21, 1955	SEPT. 23, 1955	OCT. 26, 1955
10	Number of outermost layers of fibres with incompletely thickened cell walls	3–4	2–3	0–1?	0–1?	1–3	1–4	7–20	1–2	4–8	±1	0–1	1–3
	Width of starchless zone of outer xylem in number of fibres	6–10	10–17	0	0	0–1	8–15	±25	—	±60	±7	0	17–20
11	Number of outermost layers of fibres with incompletely thickened cell walls	1–3	0–(1)	±5	1–3	20–25	±30	9–12	±20	8–12	1–3	3–5	1–7
	Width of starchless zone of outer xylem in number of fibres	25–30	0	±5	1–3	±45	±50	±15	±50	50–60	5–15	3–5	30–40

already mentioned, the samples of *T. gallica* var. *maris-mortui* were taken from specimens growing in salt marshes near Sdom. Here the cambium appears to be more or less active throughout the year. In specimen 39 there was a considerable drop in activity during the months of September–February (table 3). In specimen 40 low activity was found at about the same period, but not continuously. As seen from table 3, low cambial activity in that specimen was evident in the sample of August, September, November and February. The zone of tangentially flattened fibres developed during that period. Growth rings started to develop in the first half of March.

Changes in starch content and cambial activity.—In *T. gallica* var. *maris-mortui* and in the previously mentioned species, xylem tissues are filled with starch up to the cambial margins during periods of very low cambial activity, i.e., during the months September–February in tree 39, and during September, November, February in tree 40 (table 3).

Phenology.—New shoots start to develop at the beginning of March, i.e., at the time new growth rings begin to differentiate. The vegetative shoots continue developing until fall. Flower buds appear at the beginning or middle of March.

DISCUSSION

There is a close resemblance in the wood structure of the various species of *Tamarix*, a point already mentioned by Brunner (1909). This similarity is particularly striking in *Tamarix gallica* var. *maris-mortui* and *T. jordanis* var. *negevensis*. The only difference between these two species is in the size of the procumbent ray cells. In *T. gallica* var. *maris-mortui* the procumbent ray cells are considerably shorter than those of *T. jordanis* var. *negevensis* and less easily distinguishable from the square cells. The wood of *T. aphylla* differs from that of the other two species, especially in the end zone of the growth ring. In *T. jordanis* var. *negevensis* and *T. gallica* var. *maris-mortui* that zone is made prominent by several layers of flattened fibres in which narrow vessels are embedded. These small vessels are easily

Table 3. INTENSITY OF CAMBIAL ACTIVITY AND SEASONAL CHANGES IN STARCH CONTENT OF THE XYLEM IN *Tamarix gallica* var. *maris-mortui* GROWING NEAR SDOM

SPECIMEN NUMBER	TYPE OF DATA	NOV. 2, 1954	DEC. 8, 1954	JAN. 5, 1955	FEB. 9, 1955	MARCH 16, 1955	APRIL 15, 1955	MAY 13, 1955	JUNE 17, 1955	JULY 18, 1955	AUGUST 21, 1955	SEPT. 23, 1955	OCT. 26, 1955
39	Number of outermost layers of fibres with incompletely thickened cell walls	±1	1–2	±1	±1	±10	4–7	±15	7–10	±5	2–5	±1	±1
	Width of starchless zone of outer xylem in number of fibres	0	0	0	0	±10	15–20	12–15	±35	±20	±10	0	0
40	Number of outermost layers of fibres with incompletely thickened cell walls	1	2–7	4–5	±1	5–10	15–20	15–20	2–4	2–3	±1	1–3	3–5
	Width of starchless zone of outer xylem in number of fibres	0	2–5	0–5	0–3	>40	±40	±120	±40	8–13	15–20	0	10–15

distinguishable, not only from those at the beginning of the next ring, but also from the neighbouring vessels of the same ring. In *T. aphylla*, on the other hand, the fibres at the ends of the rings, are not as prominently flattened, nor do they produce a many-layered and continuous zone. The vessels of this region are not so strikingly different from neighbouring ones (fig. 1, 3 and 4). The occurrence of crystals only in square cells of the wood rays is another feature which distinguishes the wood of *T. aphylla* from that of the other two species examined.

The cambium of *T. aphylla* was found to be fairly active throughout the year. The intensity of that activity was uneven, and it was difficult to find a common trend for all the specimens examined. The growth rings, too, were found to start their development at different periods of the year. In the specimens which grow near Masmiya, growth rings start to develop at the end of the summer, whereas in the specimens south of Beersheba the main growth ring begins developing at the end of February. Furthermore, it appears that an additional growth ring begins development at the end of the summer or in the autumn.

In *T. jordanis* var. *negevensis* the cambium was found to be scarcely active, or almost dormant for a short period during the winter and at the end of the summer. In *T. gallica* var. *maris-mortui* the drop in cambial activity occurs during the months of September–February. In both, the growth ring begins to develop in spring.

Generally, it may be concluded that almost no real dormant period of the cambium appears to exist in any of the species of *Tamarix* examined. This phenomenon can be explained only by the fact that their root systems are well developed and penetrate deeply into the soil, where sufficient moisture is available even in the late summer months.

The changes in starch content which are influenced by various physiological processes in the plant, show a correlation with the course of cambial activity through the year. This correlation is especially conspicuous during periods of very low cambial activity. During such periods all xylem

tissues up to the cambium, or nearly so, are filled with starch. During periods of greater cambial activity a starchless zone develops in the peripheral part of the xylem. This varies in width, but no parallel can be drawn between changes in the dimensions of that zone and changes in the intensity of cambial activity. Esau (1948) found starch content in grape xylem lowest at the time new xylem was fully formed. After that period starch content began to rise. On comparing her findings with our recordings in *Tamarix* it is seen that in both cases the starch content is highest during the resting period of the cambium, or during periods of subdued activity. The point at which starch content is lowest, however, was not found to occur at any specific time in growth ring formation in the *Tamarix* species examined, but occurred at varying times in the course of development.

SUMMARY

The anatomy of the xylem and annual rhythm of development, as well as the seasonal changes of starch content in *Tamarix aphylla* (L.) Karst., *T. jordanis* Boiss. var. *negevensis* Zoh. and *T. gallica* L. var. *maris-mortui* (Gutm.) Zoh. were examined and described. It was found that wood of the first mentioned species is diffuse-porous to semi-ring-porous, while in the two other species it is semi-ring-porous. Vessel arrangement is solitary, in diagonal multiples, or in small clusters. Perforations are simple. Wood parenchyma is storied and vasicentric. Rays are heterogeneous and flare at the borders of each growth ring. Ray cells, wood parenchyma and fibres store starch. Nuclei were observed in the fibres. The xylem of *T. jordanis* var. *negevensis* and *T. gallica* var. *maris-mortui* was found to differ from that of *T. aphylla* by having the end of each growth ring marked by a more prominent zone of tangentially flattened fibres and more prominent zone of tangentially flattened fibres and parenchyma cells, and in the occurrence of crystals in both procumbent and square ray cells. In *T. aphylla*, on the other hand, crystals were found in the square ray cells only. The wood of *T. gallica* var. *maris-mortui* may perhaps be distinguished from that of *T. jordanis* var. *negevensis* by the less elongated procumbent cells of the wood rays.

In these species of *Tamarix*, the cambium is more or less active throughout the year. In *T. gallica* var. *maris-mortui* and in *T. jordanis* var. *negevensis* growth ring development starts in spring. In *T. aphylla* growth rings in two of the trees examined were found to begin development at the end of summer. In the other two specimens examined, growth rings appear to be formed twice yearly, the development of the first ring starting in early spring, that of the second at the end of summer or in fall.

Changes in starch content of the peripheral xylem were revealed in sections treated with I₂KI. These changes appear to be correlated to a certain extent with seasonal changes in cambial activity.

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NOTES FROM THE S. J. RECORD MEMORIAL COLLECTION. II.

GEORGE K. BRIZICKY AND WILLIAM L. STERN

Colubrina elliptica (Swartz) comb. nov.—*Rhamnus ellipticus* Swartz, Prodr. Veg. Ind. Occ. 50. 1788. *Ceanothus reclinatus* L'Hérit., Sert. Angl. 6. 1788 (1789?). *Colubrina reclinata* Brongn., Ann. Sci. Nat. Sér. 1. 10: 369. 1827.

Recent investigations on the woody flora of the Florida Keys have indicated the need for certain nomenclatural changes. In Rhamnaceae, *Colubrina reclinata* (L'Héritier) Brongniart appears to be invalid as outlined below. This combination, based on *Ceanothus reclinatus* L'Hérit. has been in common use, while Swartz' binomial has been neglected. This is apparently the result of Kuntze's incorrect statement (CXLIV. 1891) that Swartz' *Prodromus* "hat nach Swartz selbst keine Priorität vor Jacquin, Collect. II 1788 und vor L'Héritier, sertum angl. 1788." However, there is hardly any doubt at present that Swartz' *Prodromus* antedates L'Héritier's *Sertum anglicum* (Part 1, i. e., the text).

1. Swartz' *Prodromus* appeared "sometime before September 1788" according to Pierce (2. 1942). Although Pierce does not mention the source of his information, this date of publication seems probable, since a review of the *Prodromus* appeared in the *Göttingische Anzeigen von gelehrten Sachen* (3: 182 Stück. 1820–1823) on 15 November 1788. Apparently Swartz' work was received by the reviewer by the end of October at the latest, and this month should be considered the latest possible publication date for the *Prodromus*.

2. Mez (952. 1896) relates that R. Buser investigated the problem of the priority of Swartz' *Prodromus* over L'Héritier's *Sertum anglicum* and found that the former definitely was published in 1788 while the latter appeared in January 1789. Britten and Woodward (1905) accepted "late 1788" as a publication date for *Sertum anglicum* (cf. Van Steenis-Kruseman and Stearn, CXCVII. 1954).

3. The priority of Swartz' *Prodromus* over L'Héritier's *Sertum anglicum* has already been sanctioned by a botanical congress in conserving "*Pitcairnia* L'Hér. Sert. Ang. 5. 1789" over "*Hepetis* Swartz, Prodr. Veg. Ind. Occ. 56. 1788." (cf. Lanjouw, et al. 225. 1956).

Thus the probable publication date of Swartz' *Prodromus* appears to be September, or October at the latest, 1788, while L'Héritier's *Sertum anglicum* was published in "late 1788," but not before December, or in January 1789. Therefore, Swartz' binomial, *Rhamnus ellipticus*, on which the new combination is based, certainly has priority over L'Héritier's *Ceanothus reclinatus*.

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