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Barrett Nelson Rock The Woods and Flora
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“Pinnatae”

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ABSTRACT

Barrett Nelson Rock. The Woods and Flora of the Florida Keys: "Pinnatae." *Smithsonian Contributions to Botany*, number 5, 35 pages, 35 figures, 1972.—The "Pinnatae," comprising six families of woody plants with pinnately compound leaves, is represented on the Florida Keys by at least 16 species. The taxonomic treatment of these families at the ordinal level has been inconsistent. The purpose of this study is to correlate the data derived from intensive study of the xylem anatomy of these 16 species with data from the literature concerning these and other members of the families involved, so that new insight might be gained concerning the taxonomic relationships among these families.

This study indicates that the members of the Pinnatae are anatomically homogeneous. All members possess simple perforation plates, vessel elements having alternate intervacular pitting, fibrous elements with small slitlike simple to vestigially bordered pits, and apotracheal and paratracheal axial parenchyma, or both. Secretory structures, such as crystalliferous idioblasts, parenchymatous cells containing "gum," and intercellular canals, are of wide occurrence within the Pinnatae. In addition, many species possess septate fibers and axial parenchyma arranged in aggregate patterns, with banded arrangements being most frequent.

There is no anatomical basis for the separation of families into distinct orders in my view. The only separation of families within the Pinnatae suggested by a syndrome of several unique characters, in addition to those common to all members, is the formation of an Anacardiaceae-Burseraceae complex. The members of the Pinnatae belong to a taxon corresponding well with Cronquist's Sapindales.

Phylogenetically, the Pinnatae constitutes an advanced taxon, based on xylem anatomy.

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The Woods and Flora of the Florida Keys: “Pinnatae”

Introduction

The Anacardiaceae, Burseraceae, Meliaceae, Rutaceae, Sapindaceae, and Simaroubaceae constitute a group of plant families comprising nearly 6,000 species of pantropical distribution. All are characterized by plants with pinnately compound leaves. These six families are represented on the Florida Keys by at least 15 genera, each has a single species, except for *Zanthoxylum*, which has two species there. This investigation is an intensive study of the secondary xylem of these plants (Table 1). According to Brizicky (1962b, 1963), *Picramnia pentandra* Swartz (Simaroubaceae), *Melicoccus bijugatus* (Sapindaceae), *Amyris maritima* Jacquin, *Zanthoxylum coriaceum* A. Richard, and four naturalized species of *Citrus* in addition to *C. aurantiifolia* (Rutaceae) are also to be found on the Florida Keys but are not included in this study. Of the plants studied, only the familial affinity of the genus *Suriana* has been seriously questioned. The assignment of the other genera to families has been more or less generally accepted. Small (1913) placed the genus *Dodonaea* in his monogeneric Dodonaeaceae. My work has been undertaken to correlate the data derived from the Florida Keys members of these six families with data obtained previously by earlier workers, with the hope that the information gained, although based on a limited number of genera, will give additional insight on the taxonomic relationships of these plants.

The taxonomic usefulness of data derived from study of the secondary xylem of dicotyledons, when correlated with morphological, cytological, palyno-

logical, and other information has been widely acknowledged (Chalk 1944, Heimsch 1942, Keck 1957, Stern 1952, Tippe 1946, and others). Comparative anatomical studies of the secondary xylem of some or all of the genera treated in this investigation (Dadswell and Eckersley 1938, Dadswell and Ellis 1939, Dadswell and Ingle 1948, Hess 1946, Heimsch 1942, Kribs 1930, Record 1939, 1941, Webber 1936, 1941) indicate that, on the basis of wood anatomy, a close interrelationship exists among the members of these six families. Plant taxonomists, using morphological characteristics, have also come to the same conclusion. However, arrangement of these families into orders, based in large part upon such morphological characteristics, has been inconsistent.

Earlier systems of classification, notably those of Linnaeus (1753), de Candolle (1824–1873), and Bentham and Hooker (1862–1883), were not based on concepts of genetic relatedness as we know them today. As such, the arrangement of the six families within these systems is of little interest, other than historical. It is not surprising, however, that these families were closely grouped by de Candolle and

¹ Previous numbers in this series appeared in *Tropical Woods* (Yale University, School of Forestry) under the running title, “The Woods and Flora of the Florida Keys”: “Introduction” by W. L. Stern and G. K. Brizicky, 107:36–65, 1957; “Compositae” by S. Carlquist, 109:1–37, 1958; “Goodeniaceae” by W. L. Stern and G. K. Brizicky, 109:38–44, 1958; “Passifloraceae” by W. L. Stern and G. K. Brizicky, 109:45–53, 1958; and “Wood Anatomy and Phylogeny of Batidaceae” by J. McLaughlin, 110:1–15, 1959. “Capparaceae” by W. L. Stern, G. K. Brizicky, and F. N. Tamolang appeared in *Contributions from the United States National Herbarium*, 34(2):25–43, 1963.

These studies were initiated through a National Science Foundation grant to William L. Stern in 1955.

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TABLE 1.—Wood specimens of the Florida Keys "Pinnatae" examined

Species	Collector and Number	Location and Catalog Number	Herbarium Voucher	Collection Locality
ANACARDIACEAE				
<u>Metopium toxiferum</u> (L.) Krug & Urban	Stern & Brizicky 566	Yw51328 ^a	Y	Key Largo
	Stern 2643 ^b		MARY	Key Largo
<u>Toxicodendron radicans</u> (L.) Kuntze	Stern 2633		MARY	Key Largo
BURSERACEAE				
<u>Bursera simaruba</u> (L.) Sarg.	Stern & Brizicky 171	Yw51027	Y	Big Pine Key
	Stern 1466	USw25391	US	Windley's Key
	Stern 2624		None	Key Largo
MELIACEAE				
<u>Swietenia mahagoni</u> Jacq.	Stern 2616		MARY	Key Largo
RUTACEAE				
<u>Amyris elemifera</u> L.	Stern & Brizicky 477	Yw51260	Y	Key Largo
	Stern 1455	USw25380	US	Key Largo
	Stern 2614		MARY	Key Largo
<u>Citrus aurantiifolia</u> (L.) Swingle	Stern & Brizicky 486	Yw51269	Y	Key Largo
	Stern 2653		MARY	Key Largo
<u>Zanthoxylum fagara</u> (L.) Sarg.	Stern & Brizicky 514	Yw51295	Y	Key Largo
	Stern 2625		MARY	Key Largo
<u>Z. flavum</u> Vahl	Stern, Beaman, Phipps, Rock, & Sweitzer 2764		MARY	Bahia Honda Key
SAPINDACEAE				
<u>Cardiospermum halicacabum</u> L.	Stern 2656		MARY	Key Largo
<u>Cupania glabra</u> Sw.	Stern & Brizicky 419	Yw51215	Y	Big Pine Key
	Stern 1508	USw25431	US	Big Pine Key
	Stern 2691		MARY	Big Pine Key
<u>Dodonaea viscosa</u> (L.) Jacq.	Stern 128	Yw49454	Y	Big Pine Key
	Stern & Brizicky 298	Yw51127	Y	Big Pine Key
	Stern 1513	USw25436	US	Big Pine Key
	Stern, Beaman, Phipps, Rock, & Sweitzer 2735		MARY	Big Pine Key
<u>Exothea paniculata</u> (Juss.) Radlk.	Stern & Brizicky 466	Yw51249	Y	Key Largo
	Stern 1467	USw25392	US	Windley's Key
	Stern 2612		MARY	Key Largo
<u>Hypelate trifoliata</u> Sw.	Stern & Brizicky 526	Yw51307	Y	Windley's Key
	Stern 1468	USw25398	US	Windley's Key
	Stern 2681		MARY	Windley's Key
<u>Sapindus saponaria</u> L.	Stern & Brizicky 552	Yw51325	Y	Key Largo
	Stern 2659		MARY	Key Largo
SIMAROUBACEAE				
<u>Simarouba glauca</u> DC.	Stern & Brizicky 462	Yw51245	Y	Key Largo
	Stern 1497	USw25420	US	Big Pine Key
	Stern 2613		MARY	Key Largo
<u>Suriana maritima</u> L.	Stern & Brizicky 230	Yw51074	Y	Big Pine Key
	Stern 1481	USw25406	US	Grassy Key
	Stern 2666		MARY	Big Pine Key

^aMethod of citation of wood specimens follows that recommended by Stern and Chambers (1960).

^bWood specimens, for which no catalog number is stated, refer to fluid-preserved collections at the University of Maryland.

Bentham and Hooker, for the similarity of gross morphology is striking.

Engler (Engler and Diels 1936) divided these families into two orders: Geraniales and Sapindales. The Rutaceae, Meliaceae, Burseraceae, and Simaroubaceae were placed in the Geraniales; the Anacardiaceae and Sapindaceae were placed in the Sapindales. Assignment of a family to an order was based primarily on the orientation of ovule attachment: family members with epitropous ovules were placed in the Geraniales, while those with apotropous ovules were placed in the Sapindales. The most recent revision of Engler's "Syllabus der Pflanzenfamilien" (Melchior 1964) redistributes the members of the Geraniales into a revised Geraniales and a newly erected Rutales on the basis of histological differentiation and a trend toward zygomorphy in the flowers. The new Geraniales and Rutales are still segregated from the Sapindales on the basis of ovule attachment. The families concerned with in this study which were included in the Geraniales are now placed in the Rutales.

The phylogenetic schemes used by Hutchinson, Hallier, and others, de-emphasized the ovular orientation of Engler. Hutchinson (1926) erected three orders to account for these families, separating them largely on the presence or absence of gland-dotted (pellucid dots) leaves (Figure 5). Those families often having members with gland-dotted leaves were placed in his Rutales (containing the Rutaceae, Simaroubaceae, and Burseraceae), while those families without gland-dotted leaves were placed either in the Meliales or Sapindales. The Meliales (containing the Meliaceae) is characterized by members having a staminal tube which is lacking in members of the Sapindales (containing the Anacardiaceae and Sapindaceae). All of these orders are within Hutchinson's arborescent line of evolution. These three orders plus the order Juglandales were grouped by Hutchinson in the subphylum "Pinnatae." The Juglandales was later dropped from this subphylum (Hutchinson 1959). Hallier's earlier treatment (1905) placed all six families in his large cohort, Rosales, with the note that it would be further subdivided after ". . . more exhaustive examination." Hallier (1912) later combined the members of the Anacardiaceae and Burseraceae into a single family, the Terebinthaceae, which he included in his Rutales, along with Rutaceae, Meliaceae, and Simaroubaceae. The Sapinda-

ceae was placed in his Sapindales. Wettstein (1935) included all six families in his Terebinthales.

A survey of recently proposed phylogenetic systems of classification reveals that the treatment of these families is still not uniform. Cronquist (1968) assigns the six "mutually interrelated" families to his Sapindales, citing Heimsch's work (1942) as a primary reason. Takhtajan (1966) places the Sapindaceae in his Sapindales, moving the remainder of the families into his Rutales. Both orders are placed in the superorder Rutinae (which also includes his Geraniales and Polygalales). Thorne (1968) places all the families in his Rutales, grouping the families into suborders Rutineae (corresponding to Takhtajan's Rutales) and Sapindineae (containing the Sapindaceae). (Table 2 offers a summary of the taxonomic treatment of these six families.)

Suriana maritima Linnaeus, generally considered within the Simaroubaceae, is seen by Gutzwiller (1961), Jadin (1901), Record and Hess (1943), Small (1911), Thorne (1968), Wilson (1911), and others, as constituting a distinct monotypic family, the Surianaceae. Cronquist (1968) accepts Gutzwiller's exclusion of *Suriana* from the Simaroubaceae, but chooses to place this genus with *Stylobasium* in his (Cronquist's) Stylobasiaceae. This family is included in Cronquist's Sapindales. On the basis of wood anatomy, Webber (1936) states that such a separation of *Suriana* from the Simaroubaceae is not justified.

The distribution and habit of each species dealt with in this study vary widely and are listed separately. Data concerning number of species, distribution, and habit were obtained primarily from Brizicky (1962a, 1962b, 1962c, 1963). The species are listed by family. The collection site of each specimen is indicated in Table 1.

ANACARDIACEAE. *Metopium* is a genus of three species, occurring in the West Indies, southern Florida and the Florida Keys, British Honduras, Guatemala, and southern Mexico. *Metopium toxiferum* (L.) Krug and Urban, a West Indian species, is found in the hammocks, pinelands, and coastal dunes in southern Florida and the Florida Keys. It occurs as a large tree in the hammocks and as a shrub in the pinelands throughout the Florida Keys.

Toxicodendron is a largely north temperate zone genus of approximately 15 species of North American and eastern Asiatic distribution. *Toxicodendron ra-*

TABLE 2.—Comparison of taxonomic treatments

Cronquist (1968)	Engler (Melchior 1964)	Hutchinson (1959)	Takhtajan (1966)	Thorne (1968)
Order Sapindales	Order Rurales ^b	Subphylum. Pinnatae ^c	Superorder Rutinae ^d	Superorder. Rutiflorae
Stylobasiaceae ^a	Suborder Rutineae	Order. Rurales	Order Rurales	Order Rurales
Sapindaceae	Rutaceae	Rutaceae	Anacardiaceae	Suborder. Rutineae
Burseraceae	Simaroubaceae	Simaroubaceae	Burseraceae	Rutaceae
Anacardiaceae	Burseraceae	Burseraceae	Simaroubaceae	Simaroubaceae
Simaroubaceae	Meliaceae	Order Meliales	Rutaceae	Surianaceae
Rutaceae	Order Sapindales	Meliaceae	Meliaceae	Meliaceae
Meliaceae	Suborder Anacardiineae	Order Sapindales	Order Sapindales	Burseraceae
	Anacardiaceae	Sapindaceae	Sapindaceae	Anacardiaceae
	Suborder Sapindineae	Anacardiaceae		Suborder. Sapindineae
	Sapindaceae			Sapindaceae

^aIncludes *Suriana*.

^bIn this most recent revision of Engler's system (Melchior 1964) the older Geraniales has been subdivided into a revised Geraniales and a newly erected Rurales (containing those families listed above in addition to others).

^cThis subphylum previously included the order Juglandales (1926).

^dPreviously the superorder Pinnatae.

dicans (L.) Kuntze (Figure 1) is widely distributed in woods, thickets, fencerows, and swamps throughout most of southern Canada, the United States, northern Mexico, and the West Indies.² It occurs as a woody vine throughout its range.

BURSERACEAE. *Bursera* is a genus of approximately 100 species, distributed throughout tropical and subtropical America. *Bursera simaruba* (L.) Sargent (Figures 2, 3) is found in southern Florida and the Florida Keys, the West Indies, southern Mexico, Central America, and northern South America. It occurs as a large tree, primarily in the hammock forests throughout the Florida Keys.

MELIACEAE. *Swietenia*, a genus of at least three species, occurs in southern Florida and the Florida Keys, the West Indies, Mexico, Central America, Colombia, Venezuela, and the upper Amazonian region. *Swietenia mahagoni* Jacquin (Figure 4) is found in the West Indies, southern Florida and the Florida Keys. On the Florida Keys it occurs in the hammock forests. It is a large tree throughout its range.

RUTACEAE. *Amyris* is a genus of approximately 20 species, occurring in southern Florida (including the Florida Keys) and Texas, the West Indies, Central America, and northern South America. *Amyris*

² *Toxicodendron* is recognized as distinct from *Rhus*, primarily on the basis of Barkley's monograph (1937).

elemifera Linnaeus is primarily a West Indian species, occurring also in southern peninsular Florida and the Florida Keys. It ranges in habit from a shrub to a small tree (up to 50 feet tall, with trunks up to a foot in diameter), and occurs in the hammock forests throughout the Keys.

Citrus is a highly polymorphic genus with an uncertain number of species (16 minimum and possibly 145 maximum, Brizicky 1962a), native to southern and southeastern Asia and Malaysia. Several species are widely cultivated and have escaped to all warm regions of the world (Brizicky 1962a). Five species are recorded as more or less naturalized throughout southern Florida and the Florida Keys. *Citrus aurantiifolia* (L.) Swingle, the lime (the single species of *Citrus* collected), is a tree native to the East Indian Archipelago. It occurs on the Florida Keys along roadsides and in secondary woods (hammock forests).

Zanthoxylum, a genus of some 215 species, is mainly pantropical in distribution (Brizicky 1962a), with several species extending into temperate North America and eastern Asia.³ Both of the species en-

³ According to Record and Hess (1943), the genus *Zanthoxylum* comprises only 15 species, all of north-temperate distribution, while the genus *Fagara* comprises approximately 200 pantropical species. Brizicky (1962a) considers *Fagara* as a synonym for the older *Zanthoxylum*.

countered in this study are considered native to the West Indies (Brizicky 1962a). *Zanthoxylum fagara* (L.) Sargent occurs in central and southern Florida, including the Florida Keys, southern Texas, the West Indies, Mexico, Central America, and South America. It occurs as an armed (spined) shrub or small tree throughout its range. *Zanthoxylum flavum* Vahl occurs as an unarmed small tree on the lower Florida Keys (specifically Bahia Honda Key State Park) and the West Indies. Both species occur in hammock forests.

SAPINDACEAE. *Cardiospermum*, a genus of approximately 12 species, is primarily of tropical American distribution, with one species occurring in tropical West Africa and one ill-defined species (*Cardiospermum halicacabum* L.⁴) of pantropical distribution. *Cardiospermum halicacabum* (Figure 8), a woody perennial vine, occurs in the hammock forests on the Florida Keys.

Cupania is a tropical American genus of approximately 45 species and extends from Argentina and Peru north to Mexico and into southern Florida, the Florida Keys, and the West Indies. *Cupania glabra* Swartz (Figure 9) occurs in the West Indies, the Florida Keys, Mexico, and Central America as far south as Costa Rica. It is a small tree of the hammock forests, occurring in Watson's Hammock on Big Pine Key.

Dodonaea is primarily an Australian genus of approximately 60 species. One species occurs in Madagascar, three occur in Hawaii, and one [*Dodonaea viscosa* (L.) Jacquin] is reported as pantropical in distribution. *Dodonaea viscosa*⁵ occurs as a small tree

⁴The treatment of the species *Cardiospermum halicacabum* accepted in this study is as follows: *C. halicacabum* comprises at least three varieties—*halicacabum*, *microcarpum* (syn. *C. microcarpum* H.B.K.), and *corindum* (syn. *C. corindum* L.; *C. keyense* Small)—each of which is considered by some authors (Brizicky 1963) as constituting a separate pantropical species. All three varieties are reported as occurring on the Florida Keys.

⁵Brizicky (1963) refers to the pantropical species as *Dodonaea viscosa* (L.) Jacquin, noting that this species includes *D. jamaicensis* de Candolle and *D. microcarpa* Small, tentatively accepting Sherff's concept of a single species (*D. viscosa*) having three distinct pantropical varieties. Sherff asserts that all of these varieties occur in Florida. Brizicky states, however, that inadequate data make "... impossible any conclusion regarding the nature and delimitation of infraspecific categories of *D. viscosa*." Therefore, throughout this paper, the Florida Keys *Dodonaea* is referred to as *D. viscosa*.

in the hammock forests and adjacent pinelands of the Florida Keys.

Exothea is a tropical American genus of three species, ranging from the West Indies, southern Florida, Mexico and Central America, south to Costa Rica. *Exothea paniculata* (Jussieu) Radlkofer occurs as a small tree in the hammock forests and on calcareous soils and shell mounds in southern peninsular Florida, the Florida Keys, the West Indies, and Guatemala.

Hypelate, a genus comprising a single species, *H. trifoliata* Swartz, occurs as a shrub or small tree in the hammock forests (and rarely the pinelands of Big Pine Key) of the Florida Keys and the West Indies.

Sapindus is largely a tropical genus of approximately 13 species, three of which are distributed in the Americas, with the remainder found in eastern and southeastern Asia, Oceania exclusive of Australia, and Hawaii. At least two of these species are extratropical. The primarily tropical American species, *S. saponaria* Linnaeus (Figures 6, 7), occurs as a tree from Argentina, north into Mexico, the West Indies, southern Florida, and the Florida Keys. It is a member of the hammock forest flora on the Florida Keys.

SIMAROUBACEAE. *Simarouba* is a widely distributed tropical American genus comprising from six to nine species. *Simarouba glauca* DeCandolle (Figure 10) occurs as a tree in southern Florida and the Florida Keys, the West Indies, southern Mexico, Central America, and part of South America. It is an inhabitant of the hammock forests on the Florida Keys.

Suriana is a monotypic genus of pantropical distribution. The single species, *S. maritima* L. (Figure 11) is a small to large shrub (occasionally a small tree) of the strand vegetation, occurring along sea-coasts throughout its range.

Materials and Methods

Specimens studied in this investigation are listed in Table 1. Dried wood specimens were obtained from Dr. William L. Stern. Specimens bearing catalog numbers of the Record Memorial Collection, Yale University School of Forestry (Yw)⁶, and the Na-

⁶The Samuel James Record Memorial Collection, originally housed at the Yale University School of Forestry, was transferred to the U.S. Forest Products Laboratory in Mad-

tional Collection of Woods, Smithsonian Institution (USw), were available as prepared slides. In addition, fluid-preserved specimens bearing Stern collection numbers 2612 through 2764 were utilized (see Table 1). All wood samples were collected from mature stems and are documented with herbarium vouchers, with the exception of *Bursera simaruba* Sargent, Stern 2624.

Microscope slides of specimens bearing Yale or Smithsonian catalog numbers had been previously prepared from unembedded, dried wood samples. The fluid-preserved specimens were embedded in celloidin prior to sectioning. All slides prepared specifically for this study from fluid-preserved material collected by Stern were sectioned on a sliding microtome. All transverse sections were cut at 20μ , while radial and tangential sections were cut at 15μ , 20μ , and 30μ to provide different thicknesses for optimum study of all cells and tissues. The sections were stained in safranin and Heidenhain's iron-alum haematoxylin, dehydrated and cleared following standard microtechnical procedures, and mounted in Canada balsam. Exceptionally hard woods were softened prior to sectioning, either in hydrofluoric acid, as outlined in Sass (1958), or by boiling in Aerosol OT solution in a reflux apparatus (a modification of the procedure outlined by Ayensu 1967).

Macerations were prepared following a variation of Jeffrey's method. The original method, outlined in Johansen (1940), was modified in the following manner: tertiary butyl alcohol was used as the dehydrant and, upon complete dehydration, a small amount of stained cellular material was taken directly from the tertiary butyl alcohol and placed into a watch crystal containing a mixture of xylene and Canada balsam of mounting consistency. The mass of cellular material was then spread throughout the mounting medium by gently mixing with a glass rod. A few drops of this mixture were then placed on a microscope slide and a cover slip added.

Selection of the diagnostic characters to be included in the descriptions of each species was made from those suggested by Tipido (1941). Measurements of the length of both fibrous elements and vessel ele-

ments were made from macerated material. Measurements of pore distribution, pore diameter, and end wall angle were made from sectioned material. All measurements are recorded in microns (μ).

Fibrous elements were measured using a Bausch and Lomb Tri-Simplex microprojector, except in a few cases where, because of cellular breakage, accurate measurement required the higher magnification and resolution available only through the use of a compound microscope. Vessel element lengths were measured with both the microprojector and the microscope, the latter was used when the small size of the vessel elements prohibited accurate measurement on the projector. The total length (tail to tail) of vessel elements was measured, following the suggestions of Chalk and Chattaway (1934, 1935).

Tangential pore diameters were measured from outside wall to outside wall. Only solitary pores were measured except in species where, because of the low percentage of solitary pores, measurement of the tangential diameters of pores arranged in radial multiples was required. Pore distribution was determined from transverse sections, while vessel element end wall inclination was measured on tangential sections.

In measuring the lengths of the fibrous elements and vessel elements, pore diameter, and inclination of vessel element end walls, a total of 50 random measurements of each character was made for each species. From these measurements, a range, a most frequent range (within which at least 50 percent of the measurements made occur; hereafter abbreviated MFR), and a mean (average) were calculated, except for the inclination of end walls, where only a mean was calculated.

Pore distribution was determined by recording the total number of solitary pores, radial multiples, and pore clusters seen in a given field of view. Ten fields were observed, and the total number of pores in each distribution type was converted to a percentage of the total number for all categories. In members of the Rutaceae, pore chains in addition to radial multiples are observed. Because of intergrades between chains and multiples, and the difficulty in distinguishing between each type, the pores of either type are reported only as radially oriented (Table 3).

The terminology used in this investigation generally follows that suggested by the Committee on Nomenclature, International Association of Wood Anato-

ison, Wisconsin, in December 1969. It is distinguished from other wood collections in the Laboratory through the abbreviation SJRw. Original wood collections at the Laboratory bear the abbreviation MADw; the Record Collection formerly carried the abbreviation Yw.

TABLE 3.—*Pore arrangement, diameter, and wall thickness*

SPECIES	PORE DISTRIBUTION (percent)				TANGENTIAL PORE DIAMETER (in μ)		PORE WALL THICKNESS (in μ)	
	Solitary	Multiples	Radially Oriented	Clusters	Avg.	Range	MFR	Range ^b
ANACARDIACEAE								
<i>Metopium toxiferum</i>	67	31(2-8) ^a		2(2-4)	78	40-110	65-90	2-7
<i>Toxicodendron radicans</i>	80	13(2-6)		7(2-7)	52	15-110	20-75	1-5
BURSERACEAE								
<i>Bursera simaruba</i>	70	20(2-4)		10(2-7)	88	45-110	80-105	1-3
MELIACEAE								
<i>Swietenia mahagoni</i>	68	25(2-4)		7(2-7)	136	65-220	100-160	3-8
RUTACEAE								
<i>Amyris elemifera</i>	53		43(2-10) ^c	4(2-5)	53	30-65	45-60	4-8
<i>Citrus aurantiifolia</i>	70		25(2-4)	5(2-5)	78	30-110	65-100	4-8
<i>Zanthoxylum fagara</i>	55		40(2-5)	5(2-6)	63	30-100	45-85	2-12
<i>Z. flavum</i>	42		52(2-9)	6(2-7)	58	40-85	50-70	2-7
SAPINDACEAE								
<i>Cardiospermum halicacabum</i>	75	5(2-5)		20(2-5)	32 ^d	20-50	25-35	4-10
					102	60-145	80-125	
<i>Cupania glabra</i>	35	55(2-5)		10(2-8)	78	30-105	75-95	2-7
<i>Dodonaea viscosa</i>	40	52(2-6)		8(2-9)	72	50-100	60-90	3-7
<i>Exothea paniculata</i>	50	46(2-4)		4(2-7)	71	50-95	60-85	2-8
<i>Hypelate trifoliata</i>	59	38(2-9)		3(2-7)	58	30-80	45-70	3-7
<i>Sapindus saponaria</i>	78	17(2-3)		5(2-7)	99	40-150	85-110	2-5
SIMARUBACEAE								
<i>Simarouba glauca</i>	40	35(2-10)		25(2-14)	175	85-260	140-210	3-12
<i>Suriana maritima</i>	41	55(2-15)		4(2-4)	58	30-85	50-70	2-6

^aNumbers in parentheses indicate the range of the number of pores found in each category.

^bWalls between pores in radial multiples and clusters are the thickest.

^cPore distribution reported as "radially oriented" because of difficulty in differentiating between radial multiples and chains. Only in the case of *Amyris elemifera* are the majority of the radially oriented pores in distinct chains.

^dSmall pores (see description).

mists, *International Glossary of Terms Used in Wood Anatomy* (1957), hereafter referred to as the IAWA Glossary. General terms used in describing relative sizes of structures (e.g., intervacular pit sizes and fibrous element, cell wall thickness) are those suggested by Record and Chattaway (1939).

The terms "fibrous elements" and "imperforate tracheary elements" are used here interchangeably and refer to the prosenchymatous cell types commonly referred to as "fibers."⁷ No attempt was made to designate such fibrous elements as either fiber-tra-

cheids or libriform wood fibers, because of the tenuous nature of the pitting encountered in the species studied.

In describing the simple pits commonly found in the parenchymatous cell types encountered in the woods under study, the term "fenestriform" is used. This term, meaning "windowlike," is used to describe any enlarged, oval to rectangular pit. These enlarged pits are considerably broader than the intervacular pits in the species being described. The fenestriform pits most frequently seen in this study are the enlarged simple components of a half-bordered, vessel to parenchyma pit-pair. In some species both components of vessel to parenchyma pit-pairs are fenestri-

⁷In the parlance of "wood technology" and "forest products," "fibers" also include the tracheids of gymnosperms.

form in nature. Since the simple fenestriform pits are generally larger than the bordered pit of a half-bordered pit-pair, a single fenestriform pit will frequently subtend two or more bordered pits, resulting in unilaterally compound pitting.

Because of the ambiguity, awkwardness, and lack of precision involved in employing only names to categorize vascular rays (Kribs 1935), a description of the ray tissue of each species is given. The terms "homocellular" and "heterocellular" are used in the literal sense. Rays comprising only a single cell type (for example, a ray which consists only of procumbent cells) are referred to as homocellular. A ray containing two or more cell types, even though one type may be of only rare occurrence, is referred to as heterocellular. Since varying degrees of the heterocellular type of ray occur in the woods studied, reference to the predominant cell type or types is given in each description.

In the following anatomical descriptions, characters common to all the species studied are included in an initial description. The descriptions of the individual species which follow this are arranged according to family. The arrangement of both families and the genera within each family is alphabetical. Table 3 contains numerical data concerning the pore distribution, pore diameters, and vessel wall thickness of each species. Table 4 is a summary of pertinent anatomical data obtained from each species and is included in order to facilitate comparison.

Anatomical Descriptions of the Woods of "Pinnatae"

Where growth rings are present, the wood in all specimens studied is diffuse-porous (Figure 16), with the exception of *Toxicodendron radicans*, which is questionably diffuse-porous (Figure 19). All perforations are simple (Figure 32), with the exception of a single multiple perforation observed in *Metopium toxiferum*.

Intervascular pitting is alternate in all species (Figures 30, 31). Scalariform-like intervacular pitting produced by coalescence of adjacent pits and unilaterally compound intervacular pitting (Figure 31) occur to some extent in each species. Fenestriform pits occur in the axial parenchyma and ray parenchyma of each species, while in *Bursera simaruba*, *Metopium toxiferum*, and *Toxicodendron*

radicans both components of vessel to parenchyma pit-pairs are commonly fenestriform (Figure 32). Unilaterally compound vessel to parenchyma pitting occurs in all species.

The fibrous elements of all species studied have oval to slitlike simple or slightly bordered pits predominating on their radial walls (Figures 28, 29). The slitlike inner apertures of any given pit-pair may be either crossed at angles to one another, or directly superposed. Both configurations are frequently observed on a single specimen. Axial parenchyma is present in all species. Vascular tracheids and disjunctive paratracheal parenchyma cells are found in all species.

ANACARDIACEAE

Metopium toxiferum (L.) Krug and Urban: Faint growth rings are present. The pores are angular to rounded, with vessel element walls varying in thickness from 2μ to 7μ .

Vessel element length averages 375μ , with a range of 190μ to 670μ and a MFR of 330μ to 450μ . Perforations are simple, with the single exception of a multiple perforation observed in maceration. The arrangement of perforations in this instance is such that neither the term reticulate nor foraminate is accurately descriptive. It should be noted that because of the fenestriform nature of vessel wall pits involved in vessel to parenchyma pitting, description of this perforation plate as multiple may not be accurate. The structure seen may actually be a collection of such fenestriform vessel wall pits, arranged at the end of the vessel element in such a manner that the impression of a multiple perforation is given. Vessel element end walls are inclined at an average of 44° . In general, the vessels are ligulate.

Intervascular pitting comprises medium-sized pits ranging from 7μ to 10μ in diameter. Pit borders are round to somewhat angular; pit apertures are oval and included within the borders.

Both vessel to axial parenchyma pitting and vessel to ray parenchyma pitting are fenestriform in nature, both members of a vessel to parenchyma pit-pair are oval to somewhat angular and simple.

The imperforate tracheary elements are nonseptate. Fibrous elements are gelatinous in nature (Figure 34), and, as such, two measurements of wall thickness were made. The rigid lignified portion of the sec-

ondary wall is from 1μ to 3μ thick while the combination of rigid and nonrigid secondary walls seldom exceeds 6μ . As such, the wall thickness (combined) ranges from thin to very thick. The average length of the fibrous elements is 683μ , with a range of 330μ to 970μ and a MFR of 560μ to 860μ .

Vascular rays are predominantly bi- and triseriate. Some uniseriates are present and a few rays up to five cells wide are seen. These may contain horizontal intercellular canals. All rays are heterocellular, comprising upright, square, and procumbent cell types. The bi- and triseriate rays frequently possess uniseriate wings of from 2 to 4 rows of square and upright cells, or both, the remainder of the ray comprising procumbent cells. Many of the uniseriate rays appear to be composed largely of square and upright cells, or both. The uniseriate rays range from 1 to 8 or more cells in height, while the bi- and triseriate rays are up to 20 cells (400μ) or more in height. Starch occurs in many of the ray cells.

The horizontal intercellular canals seen in the rays of this species are of infrequent occurrence in *Stern 2643*, but rather frequent in *Stern & Brizicky 556*. The canals are surrounded by an epithelial lining (1 to 2 cells thick) composed of small, square to angular cells with thin isotropic (optically inactive) cell walls. The cells external to the epithelial lining are of similar shape and size, but with somewhat thicker, optically anisotropic cell walls. These cells tend to intergrade with the larger, typical procumbent cells. The canals seen in *Stern 2643* are apparently at an early stage of development, possessing small intercellular spaces or canals, while those seen in *Stern & Brizicky 556* are of a later stage of development, having massive intercellular spaces or canals. Many of these older canals lack any organized epithelial layer (apparently due to lysis). In the latter specimen, the canals are often nearly as wide as the ray in which they occur. In both specimens a dense, rather darkly staining substance is found in many of the canals, in addition to remnants of epithelial cell walls. It is apparent that these canals are secretory in nature.

Axial parenchyma is present in both apotracheal and paratracheal arrangements. Apotracheal parenchyma forms irregularly spaced bands which vary in width from 1 or 2 cells to 10 or more cells wide. Bands are independent of growth rings. Paratracheal parenchyma is aliform to confluent, leading to some

localized banding. All the axial parenchyma cell types frequently contain starch grains. Crystalliferous strands are absent.

Thin-walled tyloses are seen extending into the vessels from both axial and ray parenchyma (Figure 34). In longitudinal section, a high percentage of the fenestriform vessel to ray pits are sites of tylosis formation.

Toxicodendron radicans (L.) Kuntze: The wood is diffuse-porous (Figure 19), although the outer growth rings tend to be ring-porous; faint growth rings are present. The pores are circular to somewhat angular, with walls ranging in thickness from 1μ to 5μ . Tangential pore diameters range from 15μ to 110μ . A study of macerated material, however, reveals a number of smaller vessel elements, having diameters of less than 15μ (as measured on macerated material). These vessels could not be included in the measurements of diameters in transverse section, because they are not readily distinguishable from imperforate tracheary elements.

Vessel element length averages 250μ , with a range of 120μ to 360μ and a MFR of 160μ to 300μ . Vessel element end walls are inclined at an average of 41° . The vessel elements are generally ligulate.

Intervascular pitting comprises small bordered pits ranging in size from 4μ to 6μ in diameter. The pits, generally restricted to the ends of the vessel elements (pitting on the body of the vessel elements is relatively infrequent, because of the high percentage of solitary pores), possess circular to lenticular apertures included within rounded to angular borders.

Vessel to axial parenchyma pitting comprises half-bordered to simple pit-pairs. The component pits of a simple pit-pair, in the vessel element wall and the axial parenchyma wall, are both fenestriform in nature. Half-bordered pit-pairs are rather infrequent, the bordered pit of the vessel element wall generally having large lenticular apertures extending to lenticular borders. These bordered pits are generally larger than the intervacular bordered pits and intergrade with the fenestriform simple vessel element pits. Vessel to ray parenchyma pitting is very infrequent. When present, it resembles the vessel to axial parenchyma pitting.

The imperforate tracheary elements are septate, each cell having a single septum. Fiber walls vary in thickness from 1μ to 5μ and range from very thin to thick. A study of macerated material reveals that

the fibrous elements may have either attenuated or truncate end walls. Fibrous elements contain massive amounts of starch. The average length of the fibrous elements is 374μ , with a range of 230μ to 560μ and a MFR of 300μ to 440μ .

Vascular rays are uniseriate and biseriate, although in some cases, a portion of a biseriate ray may be up to three cells wide. Square and upright cell types occur most frequently, while the procumbent cell type is rare. The cell type found in any given horizontal row is frequently constant, with one row composed entirely of upright cells while another is composed of square cells. The occurrence of two cell types within the same horizontal row is relatively infrequent. Arrangement of cell types does not follow a pattern. The uniseriate rays vary in height from 2 cells to 30 cells or more. Approximately 50 percent of the ray cells contain a dark-staining substance of unknown composition. Ray cells generally contain large amounts of starch.

Axial parenchyma is present in both apotracheal and paratracheal arrangement. Diffuse parenchyma apparently comprises noncrystalliferous strands. Since the fibrous elements of this species are living (septate and store starch), it was difficult to determine whether cells, seen in either transverse or longitudinal section, were axial parenchyma cells or fibers. Since the other parenchymatous cells (paratracheal parenchyma and ray parenchyma) frequently contained a dark-staining substance, this character was used as the distinguishing criterion; cells containing the dark-stained substance, when viewed in transverse section, were interpreted as diffuse parenchyma. The paratracheal parenchyma is scanty vasicentric to vasicentric, and, as mentioned previously, frequently contains a dark-staining substance similar to that seen in the ray tissue.

A large number of small, thin-walled tyloses are present in many of the vessel elements. The tyloses contain the dark-staining substance seen in the paratracheal parenchyma cells. This is to be expected, since tyloses are extensions of parenchyma cells into the vessel lumen.

BURSERACEAE

Bursera simaruba (L.) Sargent: Growth rings are absent. The pores are somewhat angular and have walls 1μ to 3μ thick.

Vessel element length averages 531μ and ranges from 300μ to 770μ ; the MFR is 495μ to 700μ . Vessel element end walls are inclined at an average of 48° . The vessels may be either ligulate or eligulate.

Intervascular pitting comprises medium-sized pits ranging from 7μ to 10μ in diameter. The pit apertures are lenticular and included within polygonal pit borders.

Vessel to axial parenchyma pitting is rare because of the scarcity of paratracheal parenchyma. Where it occurs, it is sporadic and irregular to alternate and larger than the intervacular pitting. Vessel to ray pitting differs from the above in that it is variable in form, ranging from large, generally rectangular fenestriform pits to small, oval pits (Figure 32). Both components of the former type of vessel to ray parenchyma pit-pair are fenestriform in nature. Both vessel to axial parenchyma pitting and vessel to ray parenchyma pitting are half-bordered.

The imperforate tracheary elements are septate, having from 3 to 8 septa per cell, 3 being the most common. Fibrous elements in *Stern 2624* contain massive amounts of starch (Figures 12, 13); starch grains are also seen in *Stern 1466*. Wall thickness of fibrous elements may be classified as very thin, 2μ to 4μ thick. The average length of the fibrous elements is 809μ , the range 440μ to 1160μ and the MFR 730μ to 950μ .

Vascular rays are predominantly multiseriate; some uniseriate and biseriate rays are seen. All rays are heterocellular, although some of the uniseriate rays appear to be homocellular when seen in tangential section. A survey of 10 radial sections, however, did not reveal such homocellular rays. This is apparently related to the nature of cell arrangement. In radial section, there are no horizontal rows consisting of only one type of ray cell. Those rows containing procumbent cells also contain square and upright cells, or both. Tangential sections of the same ray taken at different points would appear to be homocellular at one point and heterocellular at the other. The height of the uniseriate rays is up to 350μ (20 cells). These are far less frequent in occurrence than are the multiseriate rays.

Multiseriate rays are up to 500μ (30 cells) in height and up to 100μ in width. The body of the multiseriate ray is composed of procumbent cells. These rays generally have uniseriate wings, 1 to 3 cells high, composed of upright and square cells, or both. The

rows of procumbent ray cells are uniform, as is generally true of the rows of upright and square cells of the vertical wings. The upright and square ray cells of this ray tissue frequently contain optically anisotropic, prismatic crystals and starch grains.

Horizontal intercellular canals are seen in many of the multiseriate rays (Figure 24). These canals are circular in cross section (as seen in tangential section) and surrounded (lined) with thin-walled epithelial cells. The walls of the epithelial cells are optically isotropic (optically inactive when viewed under crossed nicols).

The arrangement of axial parenchyma is difficult to determine, because of the difficulty in distinguishing between axial parenchyma cells and the thin-walled, septate, living fibrous elements. As mentioned previously, the fibrous elements store starch and, as such, carry on one of the functions of axial parenchyma. Determination of the presence of axial parenchyma was made only through study of macerations. Distinction between fibrous elements and axial parenchyma cells in macerated material was based on the pitting and on the cell wall configuration: the transverse, truncate, horizontal end walls of the parenchyma cells and the septa of the attenuated fibers. The axial parenchyma seen in macerations may be classified as scanty vasicentric. Apotracheal parenchyma may also be present but is not distinguishable in transverse section.

MELIACEAE

Swietenia mahagoni Jacquin: Growth rings are present. Pores are rounded to somewhat angular with vessel element walls varying in thickness from 3μ to 8μ .

Vessel element length averages 437μ , with a range of 200μ to 720μ and a MFR of 390μ to 515μ . Vessel element end walls are inclined at an average of 62° . Vessel elements may be either ligulate or eligulate.

Intervascular pitting comprises minute bordered pits ranging in size from 2μ to 3μ in diameter. Pit borders are rounded to angular; pit apertures are lenticular to oval and are included within the borders.

Vessel to axial parenchyma pitting and vessel to ray parenchyma pitting are very similar in size, shape, and arrangement. Both types of vessel to

parenchyma pitting are half-bordered. The bordered pits of the vessel wall are arranged in an alternate pattern, these pits coinciding in shape and size to intervacular pits. The simple pits of the parenchyma walls are oval to elongate and often fenestriform in nature.

Imperforate tracheary elements are septate, having a wall thickness that varies from 2μ to 7μ , and ranges from thin to thick. Septa are thin and there are two per cell. The average length of the fibrous elements is 981μ , with a range of 650μ to 1250μ and a MFR of 880μ to 1160μ .

The vascular rays are uniseriate to multiseriate, with rays infrequently up to five cells wide; 3- and 4-seriate rays are the most frequent. All rays are heterocellular. The infrequent uniseriate rays are short, ranging from a single cell to eight or more cells in height, and composed almost entirely of square and upright cells, or both. Biseriate rays are longer than uniseriate rays, ranging from 5 to 15 or more cells in height, and composed of the same cell types seen in the multiseriate rays. Multiseriate rays range in height from 10 cells (250μ) to 30 cells (700μ) or more, the longer rays generally resulting from vertical fusion of two rays. Bi- and multiseriate rays comprise procumbent, square, and upright cell types. The procumbent cell type generally makes up the multiseriate portion of a given ray, while the square and upright cell types comprise the one- to many-celled uniseriate wings or margins (Figure 22). Many ray cells contain an opaque, dark-staining substance of unknown composition. Most ray cells contain starch. Marginal cells are frequently crystalliferous idioblasts. The ray tissue is storied.

Axial parenchyma occurs in both apotracheal and paratracheal arrangement. Apotracheal parenchyma is present mainly as marginal bands (initial). Some diffuse parenchyma is also present. Both types of apotracheal parenchyma cells contain starch; either may be crystalliferous, the occurrence of crystalliferous idioblasts is infrequent and random. Crystalliferous strands are not present. The paratracheal parenchyma is scanty vasicentric to vasicentric. Both types of axial parenchyma cells frequently contain the same dark-staining substance reported in the ray cells.

Vessels generally contain this dark-staining opaque substance also. The vessel elements tend to be storied in addition to the rays.

RUTACEAE

Amyris elemifera Linnaeus: Growth rings are present, but not distinct. Pores are rounded in cross section, and have walls 4μ to 8μ thick. Chains are the predominant, radially oriented, pore group.

Vessel element length average 250μ , with a range of 110μ to 350μ and a MFR of 220μ to 330μ . Vessel element end walls are inclined at an average of 55° . The vessel elements are generally ligulate.

Intervascular pitting comprises minute bordered pits ranging from 3μ to 4μ in diameter. Pit apertures are slitlike to oval and included within the circular pit borders. Vessel to axial parenchyma pitting is rare, owing to the scarcity of paratracheal axial parenchyma; where it occurs, it is alternate. Vessel to ray parenchyma pitting is alternate. In both types of vessel to parenchyma pitting, the pit-pairs are half-bordered; the vessel pits are similar in size and shape to the intervacular pits described above, and the parenchyma pits are fenestriform and simple.

Imperforate tracheary elements are nonseptate, having thick cell walls 3μ to 7μ in thickness. The average length of these fibrous elements is 443μ , with a range of 270μ to 660μ and a MFR of 375μ to 530μ .

Vascular rays are uniseriate and homocellular, all cells are procumbent. Although the orientation of individual ray parenchyma cells is horizontal in all cases, cell length varies, and in some instances, some cells in a horizontal row are nearly square. However, since these "square" cells are not a consistent character, either in their occurrence or their arrangement, I feel the designation of "homocellular" is justified. Rays average from 3 to 10 cells in height, rarely up to 19 cells (200μ) high.

Axial parenchyma is present as diffuse and banded apotracheal parenchyma and as scanty paratracheal parenchyma. The banded apotracheal parenchyma is 1 to 3 cells wide and continuous; the diffuse parenchyma is present as crystalliferous strands comprising 2 to 8 cells (as viewed in tangential section). The crystalliferous parenchyma cells (idioblasts) are much enlarged. No starch grains were seen, because of the acid-softening treatment.

Small thin-walled tyloses are present (Figure 33). An amorphous material is seen in some vessels, perhaps because of gummosis of the parenchyma cells forming the tyloses.

Citrus aurantiifolia (L.) Swingle: Growth rings

are present. The pores are circular, with walls ranging from 4μ to 8μ thick. Radial multiples are the predominant, radially oriented, pore group.

Vessel element length averages 273μ , with a range of 150μ to 420μ and a MFR of 235μ to 340μ . Vessel element end walls are inclined at an average of 58° . Vessel elements may be ligulate or eligulate.

Intervascular pitting consists of small pits, ranging from 4μ to 6μ in diameter. Pit apertures are rounded to oval and included within round to polygonal borders.

Vessel to axial parenchyma pitting is alternate. The pits found in the vessel element walls are similar in size to intervacular pits, while those found in the axial parenchyma walls are larger and simple. Vessel to ray parenchyma pitting is alternate and resembles the vessel to axial parenchyma pitting.

Fibrous elements are nonseptate, having thin walls from 2μ to 5μ thick. The average length of the fibrous elements is 752μ , with a range from 400μ to 1150μ and a MFR of 560μ to 890μ .

Vascular rays are uniseriate to triseriate, some rays rarely 4 cells wide. The uniseriate rays range from 1 to 12 cells (150μ) in height and are heterocellular. The biseriate and triseriate rays are up to 40 cells (500μ) in height and are heterocellular, a few having uniseriate wings of from 1 to 4 cells high. In the case of both uniseriate and multiseriate rays, the great majority of cells are procumbent. Very few upright cells were seen in the material studied, arrangement of the cell types follows no pattern, and although the margins of the multiseriate rays may be a mixture of procumbent and square cells, the body of the ray comprises only procumbent cells. The ray cells in contact with vessel elements are frequently disjunctive. Most ray cells contain starch grains.

Axial parenchyma is present in both apotracheal and paratracheal arrangements. The apotracheal parenchyma is banded, diffuse, and diffuse-in-aggregates, some of which comprise crystalliferous strands of from 3 to 20 cells. The banded apotracheal parenchyma is made up of axially elongate parenchyma strand cells, some of which have further subdivided and are crystalliferous (crystalliferous strands). Many of the cells of the diffuse and diffuse-in-aggregates parenchyma are crystalliferous. The crystalliferous idioblasts are generally much enlarged, containing optically anisotropic prismatic

crystals (Figure 25). The bands of axial parenchyma are from 1 to 4 cells wide and are continuous. Paratracheal parenchyma is scanty vasicentric and sometimes aliform. Axial parenchyma cells are frequently disjunctive. Most, if not all, of the axial parenchyma cells contain starch.

The vessels often contain a granular to non-granular, translucent amorphous material aggregated on or near the perforation plates.

Zanthoxylum fagara (L.) Sargent: Faint growth rings are present. Pores are circular, with walls ranging in thickness from 2μ to 12μ . Radial multiples are the predominant radially oriented pore group (Figure 14).

Vessel element length averages 261μ , with a range of 145μ to 465μ and a MFR of 210μ to 310μ . Vessel element end walls are inclined at an average of 64° . Vessel elements may be either ligulate or eligulate.

Intervascular pitting comprises minute bordered pits ranging from 2μ to 3μ in diameter. Pit apertures are oval to lenticular and included within rounded borders.

Vessel to axial parenchyma pitting and vessel to ray parenchyma pitting are similar in size, shape, and arrangement. The pit-pairs are half-bordered, with the bordered vessel element pits similar in size, shape, and arrangement to the intervacular bordered pits described above. The simple parenchyma pits (both axial and ray parenchyma) are generally circular to oval and are either approximately the same size as the bordered pits or large, elongate, and fenestriform.

The imperforate tracheary elements are nonseptate, having walls which range in thickness from 2μ to 6μ and from thin to very thick (lumens entirely occluded). The length of the fibrous elements averages 735μ , with a range of 400μ to 1175μ and a MFR of 600μ to 1000μ .

Vascular rays are predominantly uniseriate and biseriate, with a few triseriate for at least a part of their length. All ray types are heterocellular. Uniseriate rays are frequently short, ranging in height from 2 to 6 cells or more, and are composed of either square or upright cells, or both. A second type of uniseriate ray is generally higher, ranging up to 10 cells or more in height, and consists of procumbent cells in addition to square and upright cells, or both. The biseriate rays are generally higher than the

uniseriates, ranging up to 400μ (30 cells) or more in height, the biseriate portion of the ray is typically composed of only procumbent cells, while the uniseriate margins or "wings" are composed of 1 to 5 or more horizontal rows of square and upright cells, or both. Starch is not present in the ray cells, possibly because of the hydrofluoric acid treatment of the specimen (*Stern 2625*) prior to sectioning.

Axial parenchyma is present in apotracheal and paratracheal arrangement. The apotracheal parenchyma occurs as continuous bands, ranging from 2 to 7 or more cells in width, comprising strand parenchyma. Generally there are two cells per strand, although in some cases, one or both of these cells has further subdivided several times, giving rise to short strands of crystalliferous idioblasts. Scanty diffuse parenchyma comprises the same cell type as described above. The paratracheal parenchyma is scanty vasicentric.

Irregular and continuous periclinal cavities occur throughout the xylem of *Stern 2625* (Figures 26, 27). These cavities are apparently traumatic in origin and contain an evenly staining, homogeneous, opaque to transparent substance. Many of the vessels contain a granular to nongranular (similar in appearance to the homogeneous material seen in the traumatic cavities described above), translucent to transparent material.

Zanthoxylum flavum Vahl: Growth rings are present. Pores are circular to somewhat angular, with the vessel element walls ranging in thickness from 2μ to 7μ . The bulk of the radially oriented pores are intergrades between radial multiples and chains in which at least some pores have flattened tangential walls.

Vessel element length averages 575μ , with a range of 300μ to 750μ and a MFR of 475μ to 650μ . Vessel element end walls are inclined at an average of 44° . The vessel elements are generally ligulate.

Intervascular pitting comprises small bordered pits ranging in size from 4μ to 6μ in diameter. The pit apertures are oval to lenticular and are included within rounded to somewhat angular borders.

Vessel to axial parenchyma pitting and vessel to ray parenchyma pitting is similar in size, shape, and arrangement. The pit-pairs are half-bordered and alternately arranged. The bordered pit of the vessel element wall coincides in size and shape with those of the intervacular pit-pairs. Simple pits of the paren-

chyma wall are round to oval and frequently elongate, the latter fenestriform.

The imperforate tracheary elements are nonseptate, having walls that vary in thickness from 2μ to 5μ and range from thin in early wood to thick and very thick in late wood. These walls are optically inactive and, as such, may indicate that the fibers are actually gelatinous. The average length of the fibrous elements is 1125μ , with a range of 735μ to 1428μ and a MFR of 945μ to 1300μ .

Vascular rays are uniseriate to triseriate, with biseriate rays predominating. The uniseriate rays range from 1 to 7 or more cells high and most frequently comprise only square and upright cells, or both. Some procumbent cells are seen in the uniseriate rays. Bi- and triseriate rays are approximately the same size, ranging from 5 cells to over 25 cells (600μ) in height. In both the bi- and triseriate rays, the multiseriate portion of the ray comprises procumbent cells, while the uniseriate "wings" or margins frequently comprise only square and upright cells or both. The rays are heterocellular, comprising all three cell types. Ray cells contain massive amounts of starch and are frequently crystalliferous.

Axial parenchyma is present in apotracheal and paratracheal arrangements. The apotracheal parenchyma occurs as continuous bands, which are usually, but not necessarily, marginal. When clearly marginal, these bands are initial and are 1 to 2 cells in width. The bands comprise strand parenchyma, many of which, having further subdivided, contain nonenlarged, optically active crystals. Diffusely arranged crystalliferous strands are infrequently seen. The paratracheal parenchyma is exceedingly scanty, not common to every vessel, and never completely vasicentric. All types of axial parenchyma contain massive amounts of starch.

SAPINDACEAE

Cardiospermum halicacabum L.: Faint growth rings are present. Pores are rounded to somewhat angular with walls varying in thickness from 4μ to 10μ thick.

Two distinct sizes of vessel elements are present in this species (Figure 35.) The smaller of the two sizes is generally angular and arranged in radial multiples. These vessel elements are ligulate and have end walls inclined at an average of 45° (the measurement of the end wall angles are made on

macerated material). These small vessel elements intergrade with vascular tracheids.

The larger of the two sizes are rounded and are either solitary or arranged in clusters. The large vessel elements are either ligulate or eligulate, with nearly horizontal end walls.

The average end wall inclination of the combined vessel element types, as measured in tangential section, is 76° . The average vessel element length is 200μ , with a range of 130μ to 290μ and a MFR of 160μ to 250μ .

Intervascular pitting comprises small pits, ranging in size from 4μ to 6μ in diameter. Pit apertures are oval to lenticular. Pit borders are rounded.

Vessel to axial parenchyma pitting and vessel to ray parenchyma pitting, when viewed in section, are similar in appearance. The pit-pairs in both types of pitting are half-bordered. Pits in the vessel element wall are similar in size, shape, and arrangement to intervacular pits. A study of macerations reveals that the simple pits of the ray parenchyma are frequently small and slitlike to oval, while those of the axial parenchyma are large, oval to elongate, and fenestriform.

Imperforate tracheary elements are frequently septate, having walls from 2μ to 4μ thick, ranging from very thin to thick. The average fibrous element length is 533μ , with a range of 350μ to 800μ and a MFR of 440μ to 600μ .

A study of macerations indicates that two distinct types of fibrous elements are present. One type is typically thick-walled, having attenuated ends and infrequent, thin, solitary septa. The second type of fibrous element is generally thin-walled, having truncate end walls. This second type is frequently septate. Septa are thick and range from 1 to 3 or more per cell. Pitting is similar in both types and each may contain starch.

Vascular rays are uniseriate to multiseriate, some rays are 4 or more cells wide. The multiseriate rays frequently have uniseriate margins. The rays range in height from a few cells to over 40 cells (800μ). The ray tissue is heterocellular, comprising upright, square, and procumbent cell types. Upright and square cells are most frequent, while procumbent cells are relatively rare. The arrangement of cell types follows no discernible pattern. Two or more cell types are commonly found in any given horizontal row. Ray cells are often crystalliferous or

contain starch. Some of the ray cells contain a dark-staining, transparent to opaque substance of unknown composition.

Axial parenchyma is present in both apotracheal and paratracheal arrangement. Diffuse parenchyma usually comprises crystalliferous strands. Additional apotracheal parenchyma is present in the form of a discontinuous band that may have been traumatic in origin in my specimen. Cells in these apotracheal parenchyma bands are also frequently crystalliferous. The crystalliferous idioblasts are nonenlarged rectangular cells, each containing a single optically anisotropic prismatic crystal. They are arranged in short vertical strands of from 3 to 10 or more cells. The paratracheal parenchyma is generally scanty vascentric, although a few cases of vascentric are seen. Axial parenchyma cells are frequently disjunctive. Both types of axial parenchyma contain massive amounts of starch and may contain the dark-staining substance seen in ray cells.

Cupania glabra Swartz: Growth rings are present but not distinct. The pores are rounded, having walls from 2μ to 7μ thick.

Average vessel element length is 414μ , with a range from 65μ to 610μ and a MFR from 340μ to 500μ . Vessel element end walls are inclined at an average of 44° . The vessel elements are generally ligulate.

Intervascular pitting comprises minute bordered pits which range from 2μ to 4μ in diameter. Pit borders are rounded; pit apertures are rounded to elliptical and are included within the borders.

Vessel to axial parenchyma pitting is alternate to scattered. Many of the pits in the parenchyma cell walls are large, simple, and fenestriform with irregularly shaped margins. The pits in the vessel walls are slightly to completely bordered. Vessel to ray parenchyma pitting is the same as that described for vessel to axial parenchyma pitting.

The imperforate tracheary elements are septate. Most of the fibrous elements contain 2 or more septa. The cell walls are 2μ to 5μ thick and are thin as compared with the diameter of the lumen. The average length of the fibrous elements is 697μ , with a range of 375μ to 950μ and a MFR of 630μ to 840μ .

Vascular rays are, for all intents and purposes, uniseriate. A few rays possess biseriate segments but these are localized and never extend the length of a

ray. The rays may be up to 20 cells (300μ) or more in height, but generally range from 4 to 10 cells high. Rays are heterocellular, comprising mainly procumbent and square cells, with upright cells occurring infrequently. There is no pattern of arrangement of cell types, although the procumbent cell type makes up the bulk of most rays, while the square cell type frequently occurs in marginal rows. Both square and procumbent cells occur in the same horizontal row. Most of the ray cells contain a dark-staining, transparent to opaque substance of unknown composition.

Axial parenchyma is present in both apotracheal and paratracheal arrangements. Apotracheal parenchyma is mainly diffusely arranged, crystalliferous strand parenchyma. There is continuously banded apotracheal parenchyma 1 to 3 cells wide. The diffuse crystalliferous strands are of frequent occurrence, and range up to 30 cells or more in height. Strand cells, when viewed in longitudinal section, are rectangular, with most of the cells in a given strand being crystalliferous. Apotracheal bands comprise primarily crystalliferous strand parenchyma, but unlike the diffuse strands, the cells of the bands contain the same dark-staining substance seen in the ray cells. The paratracheal parenchyma is scanty vascentric and frequently contains the same dark-staining substance previously mentioned.

Dodonaea viscosa (L.) Jacquin: Growth rings are absent. Pores are circular with walls varying in thickness from 3μ to 7μ .

Vessel element length averages 234μ , with a range of 120μ to 330μ and a MFR of 200μ to 270μ . Vessel element end walls are inclined at an average of 54° . Vessel elements are either ligulate or eligulate.

Intervascular pitting comprises minute bordered pits ranging from 2μ to 4μ in diameter. Pit borders are rounded; pit apertures are lenticular and slightly extended beyond or included within the borders.

Vessel to axial parenchyma pitting and vessel to ray parenchyma pitting are very similar and both fit the following description. The arrangement of pits in the vessel wall is alternate. Vessel to parenchyma (both types) pit-pairs are half-bordered; the bordered pit of the vessel wall coincides in size and shape to the intervacular pits, while the simple pits of the parenchyma wall are generally irregularly shaped, ranging from circular to elongate, and are frequently fenestriform.

Imperforate tracheary elements are nonseptate, having a wall thickness from 3μ to 7μ which ranges from thick to very thick, the lumens of some cells entirely occluded. The average length of the fibrous elements is 525μ , with a range of 250μ to 720μ and a MFR of 440μ to 650μ .

Vascular rays are predominantly uniseriate. Some biseriates are present, either as short biseriate segments in otherwise uniseriate rays or as completely biseriate rays. The rays are heterocellular, comprising procumbent and square cells. Very few upright cells are seen. There is no discernible pattern of cell arrangement and both square and procumbent cell types frequently occur in the same horizontal row. There is a tendency, however, for the main body of a given ray to be composed primarily of procumbent cells. The occurrence of the square cells is sporadic in all cases, their arrangement random.

Uniseriate rays range in height from 2 to 20 cells (300μ) or more, while the biseriates generally range from 5 to 15 cells in height. The ray cells frequently contain a dark-staining, transparent to opaque substance of unknown composition.

Axial parenchyma is present in both apotracheal and paratracheal arrangement. Apotracheal parenchyma is primarily diffuse, consisting mainly of crystalliferous strands. Some continuously banded parenchyma occurs, these bands ranging in width from 1 to 3 or more cells. The diffuse crystalliferous strands are generally short, usually 10 or fewer cells per strand, and composed of slightly enlarged idoblasts, each containing a single optically anisotropic prismatic crystal. The paratracheal parenchyma ranges from scanty vascentric to aliform, with infrequent confluent banding occurring. This banding is local (not continuous) and is definitely associated with the vessel elements. Axial parenchyma frequently contains the dark-staining material seen in the ray cells.

Exothea paniculata (Jussieu) Radlkofer: Growth rings are present. Pores are rounded; the walls are from 2μ to 8μ thick.

Vessel element length averages 428μ , and ranges from 245μ to 560μ , with a MFR of 400μ to 500μ . Vessel element end walls are inclined at an average of 43° . Vessel elements are generally ligulate.

Intervascular pitting comprises minute bordered pits, ranging from 2μ to 3μ in diameter. Pit borders are circular; pit apertures are lenticular and extend

beyond the pit borders.

Vessel to ray parenchyma pitting and vessel to axial parenchyma pitting are very similar in appearance. In both cases, the arrangement of pits in the vessel wall is alternate and the pits are similar in size and shape to intervacular pits. The vessel to parenchyma pit-pairs (both types of parenchyma) are half-bordered, with the simple pits of the parenchyma wall ranging from circular to elongate, and fenestriform.

The imperforate tracheary elements are septate, most having two or more septa per cell. The cell walls are 2μ to 5μ thick, and range from thin in early wood to very thick in late wood. The average length of the fibrous elements is 716μ , and the range is 440μ to 1010μ with a MFR of 630μ to 800μ . The fibrous elements often contain starch.

Vascular rays are uniseriate and biseriate, the latter type predominating. Uniseriate rays are generally low, most are from 2 to 5 cells high. The biseriate rays are somewhat higher, generally ranging from 8 to 15 cells (250μ). Upright cells are rare. Arrangement of these cell types follows no pattern; both procumbent and square cells occur in the same horizontal rows. Procumbent cells predominate and comprise the bulk of most rays. Most ray cells contain a dark-staining, transparent to opaque substance of unknown composition in addition to starch.

Axial parenchyma is present in both apotracheal and paratracheal arrangement. Apotracheal parenchyma is present in diffuse crystalliferous strands and as banded and marginal parenchyma. The crystalliferous strands are of frequent occurrence and range up to 20 cells or more in height. Crystalliferous idoblasts do not appear to be enlarged and each generally contains a single prismatic crystal. Bands of parenchyma may be up to 5 cells wide and are composed of both crystalliferous and noncrystalliferous strands. The bands may or may not be marginal and are unevenly spaced. The arrangement of the paratracheal parenchyma ranges from scanty vascentric to vascentric.

All types of axial parenchyma cells frequently contain starch and the dark-staining substance seen in the ray cells. This dark-staining substance may also occur in the vessels.

Hypelate trifoliata Swartz: Faint growth rings are present. Pores are rounded, with walls varying in thickness from 3μ to 7μ .

Vessel element length averages 319μ , with a range of 200μ to 515μ and a MFR of 275μ to 400μ . Vessel element end walls are inclined at an average of 47° . The vessel elements are generally ligulate.

Intervascular pitting comprises minute pits ranging from 2μ to 4μ in diameter. Pit apertures are rounded to oval and included within rounded to polygonal borders.

Vessel to axial parenchyma pitting and vessel to ray parenchyma pitting are similar in appearance. Both are alternate to scattered in arrangement and half-bordered, the pits in the vessel walls are similar in size and shape to the intervacular pits.

The imperforate tracheary elements are non-septate, having walls which vary in thickness from 3μ to 7μ and range from thick to very thick, the lumens of some cells entirely occluded. The average length of the fibrous elements is 632μ , with a range of 420μ to 850μ and a MFR of 525μ to 780μ .

Vascular rays are uniseriate. The rays are heterocellular, comprising procumbent, square, and upright cells. The main body of most rays is composed of square and procumbent cells, both frequently occurring in the same horizontal row. Upright cells are generally found in the marginal rows. The rays range in height from 2 to 25 cells (350μ) or more, most rays are 10 or fewer cells high.

Axial parenchyma is present in both apotracheal and paratracheal arrangement. Apotracheal parenchyma is diffuse and comprises crystalliferous and noncrystalliferous strands. The crystalliferous strands range from 4 to 30 cells or more per strand, comprising square idioblasts, each containing a single prismatic crystal. Paratracheal parenchyma ranges from vasicentric to aliform, with some confluent present. A few of the paratracheal parenchyma strands contain crystalliferous cells.

Sapindus saponaria Linnaeus: Growth rings are absent. The pores are circular and have walls from 2μ to 5μ thick.

Vessel element length averages 278μ , with a range of 120μ to 390μ and a MFR of 220μ to 330μ . End walls are inclined at an average angle of 62° . In general, the vessel elements are ligulate.

Intervascular pitting consists of minute pits, ranging from 3μ to 4μ in diameter. The pit apertures are oval to lenticular and included within rounded to somewhat angular borders.

Vessel to both axial and ray parenchyma pitting

is alternate and half-bordered in nature. The bordered to slightly bordered pits in the vessel walls are very similar in size and shape to intervacular pits, while the pits in the parenchyma walls are large and simple.

Imperforate tracheary elements are septate, generally having a single thin septum in each cell. Walls vary in thickness from 2μ to 4μ and are thin in comparison with the dimensions of the lumens. The average length of fibrous elements is 911μ , with a range of 650μ to 1180μ and a MFR of 800μ to 1100μ .

Vascular rays are uni- to triseriate, with biserial and triseriate rays predominating. Rays are homocellular, comprising only procumbent cells. The uniseriate rays are generally short, from 2 to 10 or more cells high. A few of the uniseriate rays, when seen in tangential section, appear to be made up of some enlarged square type cells. However, examination of radial sections showed that, although some cells were higher than other cells, they were nevertheless radially elongate and thus procumbent. The biserial and triseriate rays are generally higher than the uniseriates, ranging up to 50 cells (400μ) or more in height. Infrequently, enlarged marginal cells are in the bi- and triseriate rays, but examination of radial sections shows that these cells, although somewhat larger, are still radially elongate. All of the rays frequently contain large amounts of starch (starch grains).

Axial parenchyma is abundant and confluent. Whether this situation represents true confluent, that is, paratracheal, parenchyma is difficult to determine, for the bands of axial parenchyma are frequently so wide as to occupy a large proportion of the ground-mass (Figure 18). These numerous, wide bands thus surround most of the vessels (pores). It would be impossible, without ontogenic studies, to say whether this is fortuitous. The bands comprise two types of strand parenchyma: strands of 2 to 4 axially elongate cells, and strands of many cells, a large number of these crystalliferous. The largely crystalliferous strand parenchyma is commonly found at the margins of the parenchyma bands. These strands were not seen distributed among the fibrous elements. The crystalliferous idioblasts are not enlarged. Distinctly vasicentric parenchyma is also seen in which cells are typically flattened and frequently disjunctive, forming a complete sheath around each vessel or group of vessels. These cells are distinct from the remainder

of the axial parenchyma because they contain the same darkly stained substance found in the vessels. Starch grains often occur in cells of the banded parenchyma, but not in cells of vasicentric parenchyma.

SIMAROUBACEAE

Simarouba glauca DeCandolle: Growth rings are absent. Pores are circular, with walls from 3μ to 12μ thick.

Vessel element length averages 446μ , with a range of 270μ to 560μ and a MFR of 400μ to 500μ . Vessel element end walls are inclined at an average of 60° . Vessel elements are generally eligulate.

Intervascular pitting comprises small bordered pits, ranging in size from 5μ to 7μ in diameter. Pit apertures are oval and included within rounded to somewhat angular borders.

Vessel to axial parenchyma pitting and vessel to ray parenchyma pitting is similar in size, shape, and arrangement. The pit-pairs are half-bordered, the bordered pits of the vessel wall alternate and similar in size to the intervacular pits. The simple pits of the parenchyma are round to elongate, frequently fenestriform.

Imperforate tracheary elements are nonseptate, having walls which range in thickness from 1μ to 3μ and vary from thin to very thin. The average length of the fibrous elements is 794μ , with a range of 550μ to 1110μ and a MFR of 650μ to 950μ .

Vascular rays are uniseriate to multiseriate, with biseriate and triseriate rays predominating. Infrequently, the rays are up to five cells wide. All of the rays are similar in size, although the uniseriates are generally shorter than the bi- and triseriates. The uniseriate rays range from 4 to 10 cells or more high. The bi- and triseriate rays range from 5 to 30 cells (400μ) or more high. Rays are heterocellular, although composed almost entirely of procumbent cells: square cells are seen, but are infrequent in occurrence and random in arrangement. The rays cells frequently contain starch. Rays are storied (Figure 23).

Axial parenchyma is present in paratracheal arrangement as narrow, anastomosing confluent bands. The bands are frequently continuous and range from 3 to 10 cells or more wide. Some of the bands are

discontinuous and, as such, constitute an aliform configuration with long "wings." Axial parenchyma comprises strands generally consisting of four cells each. The strands tend to be storied. (Figure 23). Crystalliferous strand parenchyma is also present, each strand consisting of 5 to 10 or more cells. The crystalliferous idioblasts are rectangular, nonenlarged cells, each containing a single optically anisotropic prismatic crystal. Axial parenchyma cells that are in contact with vessel elements are generally flattened and frequently disjunctive. Cells in strand parenchyma frequently contain starch.

Suriana maritima Linnaeus: Growth rings are absent. Pores are circular, with vessel element walls ranging in thickness from 2μ to 6μ .

Vessel element length averages 173μ , with a range of 45μ to 230μ and a MFR of 165μ to 200μ . Vessel elements are generally eligulate.

Intervascular pitting comprises minute bordered pits ranging in size from 3μ to 4μ in diameter. Pit apertures are lenticular to oval and are included within or are extended slightly beyond the rounded to somewhat angular borders.

Vessel to axial parenchyma pitting and vessel to ray parenchyma pitting are similar in size, shape, and arrangement. The pit-pairs are half-bordered and alternately arranged. The bordered pits of the vessel elements are similar to intervacular pits, while the simple pits of the parenchyma (both ray and axial) are frequently large, oval to elongate, and fenestriform.

Imperforate tracheary elements are nonseptate, having walls which vary in thickness from 2μ to 6μ and range from thin to thick. Some of the fibrous elements in *Stern & Brizicky 230* are gelatinous and in *Stern & Brizicky 230* and *Stern 2666* they contain a darkly staining, translucent to opaque substance of unknown composition. The average length of the fibrous elements is 586μ , with a range of 335μ to 780μ and a MFR of 460μ to 700μ .

Vascular rays are uni- and biseriate, with the uniseriate rays predominating. Rays make up a large portion of the groundmass as viewed in longitudinal section. Rays are heterocellular, comprising mainly upright and square cell types, the procumbent cell type occurs infrequently. Arrangement of the various cell types is random. Both the uniseriate and the biseriate rays are short, generally ranging from 3 to 15 cells or more in height. All of the ray cells con-

tain the dark-staining substance found in the fibrous elements.

Axial parenchyma is present in both apotracheal and paratracheal arrangement. Apotracheal parenchyma is diffuse and diffuse-in-aggregates and comprises noncrystalliferous strands consisting of two cells or more per strand. The paratracheal parenchyma is scanty vasicentric to vasicentric, and frequently comprises disjunctive cells. Both types of axial parenchyma cells contain the same dark-staining substance present in the fibrous elements and the ray cells. An anastomosing arrangement of cells containing this substance is seen in transverse section and comprises primarily the diffuse-in-aggregates apotracheal parenchyma and rays.

Vessel elements frequently contain either this dark-staining amorphous substance, or a granular substance, which is similarly stained. Those vessel elements with empty lumens frequently have their cell walls coated with this dark-staining substance.

Discussion

Since structures which tend to be easily modified in response to environmental changes are of relatively little taxonomic importance, the choice of characters to be studied is critical. In this respect, the components of mature secondary xylem tissue are considered relatively implastic, especially when compared with characters of external morphology (Metcalf and Chalk 1950). Of the large number of anatomical characters discernible from study of mature secondary xylem, however, certain characters appear to be more plastic than others. Characters incorporating dimensions are, in general, more apt to vary with change in environment and growing conditions. The presence or absence of growth rings, the lengths of fibrous elements, and the number of vessels per unit area are examples of plastic characteristics which are usually of little taxonomic significance. On the other hand, characters of form or arrangement are often less plastic and therefore more significant taxonomically. As examples of these, one may cite the arrangement of intervascular pitting, the organization of axial parenchyma, and the configuration of perforation plates.

In addition to the relatively implastic nature of the anatomical characters of wood, the structure of wood tends to be evolutionarily more conservative

than features of external morphology (Metcalf and Chalk 1950). As a result, differences in the wood structure are inclined to be less dramatic than are differences in external morphology. Thus, Metcalf and Chalk state that ". . . this [the implastic nature of wood structure], combined with its more conservative nature, adds to its value for the study of larger groups."

In addition to being taxonomically valuable as a basis of classification, anatomical variations in secondary xylem may reflect the phylogenetic status of plant taxa. Although vessel element length may vary greatly within different plants of the same species and even within the tissues of the same plant, depending upon the age and position of the tissue studied (Bailey and Tupper 1918), vessel element length is the most accurate reflection of the fusiform cambial initial length (Chalk and Chattaway 1934). Bailey and Tupper correlated fusiform cambial initial length, as reflected by the length of vascular elements, with degree of evolutionary development based on both fossil and extant plants. They found that Calamitales, Lepidodendrales, and Cycadofilicales, in addition to extant vascular cryptogams, possessed the longest tracheary elements; gymnosperms, both extant and extinct, possessed tracheary elements of intermediate length; and extant dicots had the shortest vascular elements. From this classic work, based on a large number of plants of wide distribution within the extinct and extant tracheophytes, one is led to conclude that a reduction in length of fusiform cambial initials is associated with evolutionary advance (specialization).

Frost (1930a, 1930b, 1931), Bailey and Tupper (1918), Kribs (1935, 1937), and others correlated the lengths of the fusiform cambial initials with other features of dicotyledonous xylem anatomy. They concluded that definite trends of specialization accompanied the evolutionary reduction in length of the fusiform cambial initials.

Thus, the systematist, if he so chooses, has at hand a tool of great potential taxonomic importance. Using characters derived from the study of wood anatomy as correlative and complementary information, he has an independent means of testing presumptive phylogenetic relationships. These means are not based on the circuitous reasoning commonly encountered in classification based only on morphological characters, e.g., a plant is considered primitive

because it possesses a primitive flower type, which itself is considered primitive because it is characteristic of a "primitive" taxon. The seemingly unrelated characters of perforation type, end wall inclination, intervacular pitting, etc., are now recognized as constituting a syndrome or correlative complex useful in reflecting not only form relationship, but the evolutionary status of the plant. As Bailey (1957) stated, "The chief trends of evolutionary specialization in the cambium and xylem of dicotyledons are now so reliably established (except in the case of certain patterns of wood parenchyma distribution) that they can be utilized to advantage in studying salient problems of phylogeny and classification."

A final point must be made on the value of xylem anatomy in the overall scope of classification. In itself, xylem anatomy is of little inherent value to the taxonomists. Bailey (1953) stated that wood structure, as a collection of internal or endomorphic characters, is ". . . inherently no more conservative or reliable than are exomorphic ones." Any given structure or character is not universally plastic or implastic; a character which may be implastic and thus of taxonomic value within one group of plants, may be quite variable and thus of little use in another. Thus, endomorphic xylem characters of and by themselves, are of no more intrinsic value to the taxonomist than are exomorphic characters. However, when used in conjunction with other data derived from external morphology, in addition to other areas of study, xylem anatomy can be of significant value. When utilized by itself, xylem anatomy best serves the taxonomist as a means of negation of relatedness among taxa (Bailey 1957, Cronquist 1968). Because of the ever-present possibility that similar structures may result through parallel evolution, xylem characters alone cannot be considered as indicative of positive relationship without the strong support of supplemental data.

A brief comparison of the anatomical features of the taxa included in this study follows. In general, these anatomical features conform well with those previously reported in the literature. Some discrepancies are indicated below.

The single observation of an apparent multiple perforation plate in *Metopium toxiferum* is unique in that all other perforations observed in this study are simple. Although at least two genera of Anacardiaceae are reported in the literature (Metcalfe

and Chalk 1950, Heimsch 1942) as having multiple perforations in addition to simple perforations (*Camptosperma* and *Heeria*), *Metopium* is reported as possessing only simple perforations (Heimsch 1940). If the perforation observed is indeed a multiple perforation and not a collection of fenestriform vessel to parenchyma pits clustered at the end of the vessel (as suggested in the description), the occurrence of such multiple perforations is extremely infrequent. Either interpretation leads one to conclude that, for all intents and purposes, the xylem of *Metopium* is characterized by simple perforations.

My observation that *Toxicodendron radicans* has diffuse-porous wood raises some questions. The genus *Toxicodendron* is reported (Heimsch 1942, Metcalfe and Chalk 1950, Record and Hess 1943) as having generally ring-porous wood. Is the diffuse-porous wood of *Stern 2633* (Figure 19) a result of environmental factors, or is it simply a feature of immature tissue? As noted in the description, the outer growth rings exhibit a tendency toward ring porosity. On the Florida Keys, *T. radicans* never has stems that even approach the robust stems of this species growing in northeastern United States. It is possible that the depauperate growth of the stem on the Keys may have some bearing on the formation of ring porosity. The climate of the Keys is probably conducive for plant growth throughout the year. This in itself will have an influence on the formation of growth rings and may seriously affect the expression of typical ring porosity in this species as it occurs on these islands. Spiral thickenings are not present in the vessel elements of *T. radicans*, although all members⁸ of the genus *Toxicodendron* are reported (Record 1939) as having this feature. Heimsch (1940) reports the presence of spiral thickenings in the small vessel elements of only *T. vernix* and the Asiatic *T. trichocarpum*. Heimsch notes, as a possible explanation of this discrepancy, that the portions of the vessel element wall occurring between the slitlike intervacular pits and the fenestriform vessel to parenchyma pits give the impression of spiral thickenings in unstained or poorly stained sections. My observations agree with those of Heimsch to the extent that no spiral thickenings were seen in the specimen of *T. radicans*.

⁸ Record's description of the wood characters of the genus *Toxicodendron* is based on specimens of *T. diversiloba*, *T. radicans*, and *T. vernix*.

Striking similarities occur among *Metopium toxiferum*, *Toxicodendron radicans*, and *Bursera simaruba*. These species have fenestriform vessel to parenchyma pit-pairs (Figure 32). *Metopium toxiferum* and *Bursera simaruba* have medium-sized (in diameter) intervacular pitting. Other species of Pinnatae studied have vessel to parenchyma pitting which is very similar structurally to the intervacular pitting, the intervacular pits ranging in size from small to minute in diameter. *Metopium toxiferum* and *Bursera simaruba* have horizontal intercellular canals in their rays (Figure 24). Record (1939) notes that these canals occur in *Toxicodendron diversiloba*, although Heimsch (1940) did not observe radial canals in any members of the genus. Rays in *Metopium toxiferum*, *Bursera simaruba*, *Swietenia mahagoni*, and the two species of *Zanthoxylum* are so similar as to be hardly distinguishable, except for the occurrence of intercellular canals.

Field collection of the two species of *Zanthoxylum* points up an obvious difference between *Z. fagara* and *Z. flavum*. Although *Z. flavum* is reported in the literature as possessing wood (heartwood) which is ". . . exceedingly hard and heavy" (Small 1933), having ". . . sp. gr. .90, 56 lbs./cu. ft." (Record and Hess 1943), hand sawing showed that, of the two species, *Z. fagara* was much harder. Upon study of the sections of *Z. flavum*, I was surprised to note the presence of thick-walled fibers and a small amount of axial parenchyma (as compared with *Z. fagara*, Figures 14, 15), certainly not what one would expect of the very soft wood *Z. flavum* proved to be on sawing. Observation of transverse sections under crossed nicols reveals, however, that the secondary wall thickenings of the fibrous elements of *Z. flavum* are optically inactive, while those of *Z. fagara* are optically active. This indicated that, although the secondary walls of the fibrous elements of *Z. flavum* are lignified (take up safranin stain readily), the orientation of the cellulose micelles of these secondary walls is such that polarized light is not refracted in the transverse plane of section. Although not typical in appearance, one could refer to these fibrous elements as gelatinous, owing to the apparent noncrystalline nature of the secondary wall thickenings. The wide occurrence of gelatinous fibers could explain the softness of the wood in *Z. flavum*.

A character which separates members of the Rutaceae from the other Pinnatae is the presence in

the rutaceous taxa of at least some radial chain pore arrangement (Figure 15). In other Pinnatae, the radially oriented pore groups comprised only radial multiples (Figure 12). All members of the Rutaceae have banded and diffuse axial parenchyma in addition to some paratracheal parenchyma. *Swietenia mahagoni*, *Metopium toxiferum*, and several members of the Sapindaceae also have this combination of axial parenchyma arrangements. *Amyris* and *Citrus* have enlarged crystalliferous idioblasts (Figure 25), as does *Dodonaea* of the Sapindaceae. The occurrence of crystals in either ray parenchyma or axial parenchyma is a nearly universal character of the species studied. Only *Metopium toxiferum*, *Toxicodendron radicans*, and *Suriana maritima* lack such crystals.

Although the xylem anatomy of *Cardiospermum halicacabum* is not described in the literature (Heimsch 1942, Metcalfe and Chalk 1950, Record and Hess 1943), the xylem of two genera (*Serjania* and *Paullinia*) of sapindaceous lianas are described. The occurrence of two distinct vessel element types in *Cardiospermum* (Figure 35) noted above conforms with the descriptions of vessel elements given for *Serjania* and *Paullinia* (Heimsch 1942, Metcalfe and Chalk 1950). The presence of dimorphic vessel elements is likely related to the lianous habit in this family.

Throughout this investigation, various anatomical characteristics were evaluated, with the hope that a significant set of these could be found which might reflect the present familial arrangement of the 16 species studied. Although certain families did possess anatomical features which served to identify their members, other families did not possess such unifying features. However, all the members of Pinnatae do exhibit many anatomical characters in common to indicate that we are dealing with a remarkably homogeneous group of plants.

Comparison among families of Pinnatae of those anatomical characters considered to be of greatest taxonomic and phylogenetic significance by Metcalfe and Chalk (1950) reveals that (1) all members possess vessel elements having simple perforations, (2) the vessel elements of all members have alternately arranged intervacular pitting, (3) all members possess fibers with slitlike simple to slightly bordered pits, and (4) all members possess at least paratracheal axial parenchyma, with the banded

configuration (paratracheal and apotracheal) the most common. Although anatomical differences exist among the 16 species studied, none of these is great enough to warrant the exclusion of any one of the members from this group. By and large, greater anatomical differences are seen to exist among genera within the same family (e.g., Sapindaceae—Table 4) and even among species of the same genus (e.g., *Zanthoxylum*—Table 4), than exist among the families represented in this group.

Although the ray structure encountered in this study varies in regard to cellular makeup (heterocellular as opposed to homocellular, uniseriate as opposed to multiseriate), the relative sizes of the

rays of each species are similar. The rays of species having only uniseriates are low, rarely exceeding 200μ in height. Those rays in species having multiseriates are also low, rarely exceeding 600μ in height. The widest multiseriate rays do not exceed 10 cells (100μ) in width.

Looking at anatomical characters which vary within the group as a whole, but remain relatively constant at the family level, we find an interesting and significant segregation. The nature of the vessel to parenchyma (both axial and ray) pitting is remarkably consistent among the 15 genera, with the three exceptions of *Bursera*, *Metopium*, and *Toxicodendron*. Only *Bursera* and *Metopium* of the 15

TABLE 4.—Summary of xylem anatomical data in the "Pinnatae"

SPECIES	VESSEL ELEMENTS				FIBERS		PARENCHYMA	
	Average tangential pore diameter in μ	Average vessel element length in μ	Average vessel element end wall angle	Size of intervacular pittings ^a	Average fibrous element length	Septate fibrous element (+ or -)	Axial Al = alliform B = banded C = confluent D = diffuse M = marginal S = scanty vascentric V = vascentric	Ray 1 = uniseriate 2 = biseriate 3 = triseriate m = multiseriate hom. = homocellular het. = heterocellular
ANACARDIACEAE								
<i>Metopium toxiciferum</i>	78	375	44	medium	683	-	B, Al, C	1, <u>2</u> , 3, m, het. ^b
<i>Toxicodendron radicans</i>	52	250	41	small	374	+	D, S, V	<u>1</u> , 2, 3, het.
BURSERACEAE								
<i>Bursera simaruba</i>	88	531	48	medium	809	+	S	1, 2, <u>3</u> , m, het.
MELIACEAE								
<i>Swietenia mahagoni</i>	136	437	62	minute	981	+	B, M, S, V	1, 2, <u>3</u> , m, het.
RUTACEAE								
<i>Amyris elemifera</i>	53	250	55	minute	443	-	B, D, S	1, hom.
<i>Citrus aurantifolia</i>	78	273	58	small	752	-	B, D, S, V, Al	<u>1</u> , 2, 3, m, het.
<i>Zanthoxylum fagara</i>	63	261	64	minute	735	-	B, D, S, V	<u>1</u> , 2, 3, het.
<i>Z. flavum</i>	58	575	44	small	1125	-	B, D, S	1, <u>2</u> , 3, het.
SAPINDACEAE								
<i>Cardiospermum halicacabum</i>	32 102	200	76	small	533	+	B, S, V	1, 2, <u>3</u> , m, het.
<i>Cupania glabra</i>	78	414	44	minute	697	+	B, D, S	1, het.
<i>Dodonaea viscosa</i>	72	234	54	minute	525	-	D, S, V, Al	<u>1</u> , 2, het.
<i>Exothea paniculate</i>	71	428	43	minute	716	+	B, D, S, V	1, <u>2</u> , het.
<i>Hypelate trifoliata</i>	58	319	47	minute	632	-	D, V, Al, C	1, het.
<i>Sapindus saponaria</i>	99	278	62	minute	911	+	C	1, 2, <u>3</u> , hom.
SIMAROUBACEAE								
<i>Simarouba glauca</i>	175	446	60	small	794	-	C, Al	1, 2, <u>3</u> , m, het.
<i>Suriana maritima</i>	58	173	63	minute	586	-	D, S, V	<u>1</u> , 2, het.

^aClassification of intervacular pitting follows that suggested by Record and Chattaway (1939).

^bUnderlined numbers indicate the predominant ray type (3 = triseriate rays most frequent).

*Members having septate fibrous elements which contain starch.

genera possess intervacular pits of medium size, the other 13 genera have either small or minute pits. Four genera possess heterocellular multiseriate rays having uniseriate wings, and among them are *Bursera* and *Metopium*. Add to this the horizontal intercellular canals in the rays of both *Bursera* and *Metopium*, and one recognizes that the members of the Florida Keys Pinnatae may be subdivided on the basis of xylem anatomy so that the genera of Anacardiaceae and Burseraceae are by and large distinguishable from the other genera.

Phylogenetic interpretation of the data derived from this study indicates that the woods of the 16 species exhibit a high degree of specialization. The syndrome of short to medium length vessel elements, simple perforation plates, alternate intervacular pitting, and absence of steeply inclined vessel element end walls shows that the members of the Pinnatae studied are at approximately the same relatively advanced level of specialization. In addition, the storied structure, found in *Simarouba* and *Swietenia* (Figure 23), represents another line of specialization which occurs only in certain Pinnatae. Kribs (1935) considered woods having either homocellular rays (*Amyris* and *Sapindus*) or strictly uniseriate rays (*Amyris*, *Cupania*, and *Hypelate*) as highly advanced. The rays of *Suriana* are, for all intents and purposes, uniseriate. Heterocellular rays which are made up in large part of procumbent cells, with the square and upright cells, or both, occurring only sporadically and infrequently (*Citrus* and *Simarouba*), are also considered as relatively advanced. The common ray configuration (procumbent cells comprising the multiseriate portion with upright and square uniseriate wings or both) seen in *Metopium*, *Bursera*, *Swietenia*, and *Zanthoxylum*, in addition to the low rays found in the remainder of the genera, constitutes an advanced ray situation. The presence of various aggregate arrangements of axial parenchyma, such as banded, aliform and confluent, or both (only *Toxicodendron*, *Bursera*, and *Suriana* lack such arrangements), is accepted as being advanced. The occurrence of fibrous elements lacking distinctly bordered pits is also an advanced characteristic.

The wide occurrence of starch grains in the parenchymatous tissue of the specimens studied probably is of little taxonomic significance. However, specimens of *Toxicodendron*, *Bursera*, *Exothea*, and

Cardiospermum have septate fibrous elements that contain this storage product (Figures 12,13,24,29). This feature may be of some taxonomic import in that it is correlated with a relatively small amount of axial parenchyma in these taxa. This observation is in agreement with those of Harrar (1946).

The occurrence of septate fibrous elements appears to be a local phenomenon and is of little taxonomic significance in this group (the Pinnatae). The only families that have members lacking septate fibers, based on the species in this study, are Rutaceae and Simaroubaceae. Both of these families, however, have other members that have septate fibers (Metcalf and Chalk 1950).

The taxonomic value of diffuse-porosity is also questionable. The effect of environment on the topography of wood is not certain. The great majority of tropical trees having distinct growth rings possess woods that are diffuse-porous, and the occurrence of ring-porosity is largely restricted to woody plants of the North Temperate Zone (Gilbert 1940). The fact that all members, with the possible exception of *Toxicodendron*, have diffuse-porous wood is thus of debatable taxonomic value here.

A survey of the literature (Metcalf and Chalk 1950), concerning both morphological and anatomical characteristics of the families concerned with in this study, shows that the occurrence of secretory structures (Figures 24-27) characterizes members of the Pinnatae. The intercellular canals of anacardiaceous and burseraceous woods, and the intercellular canals in the bark and pith of these families, as well as Simaroubaceae and Sapindaceae, are examples of such structures. Secretory cells are reported as occurring in the pith and cortex of all families. The occurrence of pellucid glands in the leaves of Rutaceae is well known. In addition, traumatic axial canals are reported to occur either frequently or sporadically in some members of all families, with the exception of Sapindaceae and Anacardiaceae. The widespread presence of dark-staining, gumlike substances in the parenchyma and vessels of many of the species seen in this study (Figures 20,22) suggests the secretory potential of these members. The traumatic axial canal observed in *Zanthoxylum fagara* also contained a darkly staining deposit. Crystals, which occur widely in the xylem of Pinnatae are products of idioblasts. These too are considered as secretory cells. Thus, the oc-

currence of secretory structures in most, if not all members, may be of taxonomic value; insofar as it might serve as another indication of the homogeneous nature of Pinnatae.

The data derived from this study indicate that the Pinnatae constitute a homogeneous group, and that no anatomical basis exists for segregation of the various members into separate orders. The traditional Englerian separation of the Sapindaceae and Anacardiaceae from the remainder of the families is not supported by xylem anatomy. Hutchinson's separation of the families into three orders, and Takhtajan's and Thorne's separation of Sapindaceae from the other families, likewise, have no anatomical basis. Cronquist's treatment most nearly reflects the anatomical similarities that exist, with the exception that he removes *Suriana* from the Simaroubaceae and places it into the Stylobasiaceae. There is no anatomical foundation for the separation of *Suriana* from the Simaroubaceae. This conclusion is based both on data derived from this study and the anatomical literature (Webber 1936). Cronquist's (1968) assignment of *Suriana* and *Stylobasium* to his Stylobasiaceae is based on characters of habit and morphology, and a complete study of the anatomy of *Stylobasium* and *Suriana* must be carried out before such an association can be anatomically evaluated. The inclusion of Anacardiaceae and Burseraceae in the single family Terebinthaceae, as proposed by Hallier (1912), is supported by xylem anatomy.

Summary

A study of the wood of 16 species of Florida Keys Pinnatae indicates that the group is anatomically homogeneous. All members possess simple perforation plates, vessel elements having alternate intervascular pitting, fibrous elements with small slitlike, simple to vestigially bordered pits, and axial parenchyma which is both apo- and paratracheal. Crystals are of wide occurrence in the parenchyma cells, and banded and aliform to confluent parenchyma occur in several taxa. Certain families or groups of families have unique characters: radial chain arrangement of pores in the Rutaceae, random arrangement of cells in the heterocellular ray types among members of the Sapindaceae, and fenestriform vessel to parenchyma pit-pairs and intercellular canals in the rays of Anacardiaceae and Burseraceae.

The only separation of families within Pinnatae suggested by a syndrome of several unique characteristics is the formation of an Anacardiaceae-Burseraceae complex. These characteristics, however, when viewed in light of the many common features of the families, are not sufficient bases for the separation of the Anacardiaceae and Burseraceae from the Pinnatae as a group.

There is no anatomical basis for the separation of families into distinct orders as proposed by Engler, Hutchinson, Takhtajan, and others. The system of classification proposed by Cronquist is anatomically feasible except for his exclusion of *Suriana* from the Simaroubaceae. The members of the Pinnatae are seen by this author as belonging to a taxon corresponding well with Cronquist's Sapindales.

Phylogenetically, the Pinnatae constitutes an advanced taxon. Simple perforation plates, short to medium length vessel elements having alternate intervascular pitting, slightly inclined vessel element end walls, advanced ray types, fibrous elements with simple or vestigially bordered pits, and the predominant banded and confluent axial parenchyma mark the Pinnatae anatomically as a highly specialized group. The possession of storied rays in two species is another trend of specialization.

Based on the data derived from this anatomical study and from the literature, the 16 species of Florida Keys Pinnatae are members of a homogeneous, phyletically advanced group. Furthermore, that this group constitutes a genetically related complex of plants is borne out by correlative studies in floral and vegetative morphology, as well as by the substantial anatomical studies of which this investigation is a part. These members belong in the Sapindales as described by Cronquist.

Literature Cited

- Ayensu, E. S.
1967. Aerosol OT Solution—An Effective Softener of Herbarium Specimens for Anatomical Study. *Stain Technology* 42:155–156.
- Bailey, I. W.
1953. The Anatomical Approach to the Study of Genera. *Chronica Botanica* 14:121–125.
1957. The Potentialities and Limitations of Wood Anatomy in the Study of the Phylogeny and Classification of Angiosperms. *Journal of the Arnold Arboretum* 38:243–254.

- Bailey, I. W., and W. W. Tupper
1918. Size Variation in Tracheary Cells: I. A Comparison Between the Secondary Xylems of Vascular Cryptogams, Gymnosperms and Angiosperms. *Proceedings of the American Academy of Arts and Sciences* 54:149-204.
- Barkley, F. A.
1937. A Monographic Study of *Rhus* and Its Immediate Allies in North and Central America, Including the West Indies. *Annals of the Missouri Botanical Garden* 24:265-498.
- Bentham, G., and J. D. Hooker
1862-1883. *Genera Plantarum*. 3 vols. London, England: L. Reeve and Co.
- Brizicky, G. K.
1962a. The Genera of Rutaceae in the Southeastern United States. *Journal of the Arnold Arboretum* 43:1-22.
1962b. The Genera of Simaroubaceae and Burseraceae in the Southeastern United States. *Journal of the Arnold Arboretum* 43:173-186.
1962c. The Genera of Anacardiaceae in the Southeastern United States. *Journal of the Arnold Arboretum* 43:359-375.
1963. The Genera of Sapindales in the Southeastern United States. *Journal of the Arnold Arboretum* 44:462-501.
- Candolle, A. P. de, and A. de Candolle
1824-1873. *Prodromus systemates naturalis regni vegetabilis*. 17 vols. and 4 index vols. Paris, France: Treuttel and Würtz.
- Chalk, L.
1944. The Taxonomic Value of Wood Anatomy. *Proceedings of the Linnean Society of London* 155: 214-218.
- Chalk, L., and M. M. Chattaway
1934. Measuring the Length of Vessel Members. *Tropical Woods* 40:19-26.
1935. Factors Affecting Dimensional Variations of Vessel Members. *Tropical Woods* 41:17-37.
- Committee on Nomenclature, International Association of Wood Anatomists
1957. International Glossary of Terms Used in Wood Anatomy. *Tropical Woods* 107:1-36.
- Cronquist, A.
1968. *The Evolution and Classification of Flowering Plants*. Boston, Massachusetts: Houghton Mifflin Co.
- Dadswell, H. E., and A. M. Eckersley
1938. The Wood Structure of Some Australian Rutaceae with Methods for Their Identification. *The Council for Scientific and Industrial Research, Australia*, 114:1-32.
- Dadswell, H. E., and D. J. Ellis
1939. The Wood Anatomy of Some Australian Meliaceae with Methods for Their Identification. *The Council for Scientific and Industrial Research, Australia*, 124:1-20.
- Dadswell, H. E., and H. D. Ingle
1948. The Anatomy of Timbers of the Southwest Pacific Area: I. Anacardiaceae. *Australian Journal of Scientific Research, Series B., Biological Sciences* 1(4):391-415.
- Engler, A., and L. Diels
1936. *Syllabus der Pflanzenfamilien*. 11th ed. Berlin, Germany: Geb. Borntraeger.
- Frost, F. H.
1930a. Specialization in Secondary Xylem of Dicotyledons: I. Origin of vessels. *Botanical Gazette* 89: 67-94.
1930b. Specialization in Secondary Xylem of Dicotyledons: II. The Evolution of the End Wall of the Vessel Segment. *Botanical Gazette* 90:198-212.
1931. Specialization in Secondary Xylem of Dicotyledons: III. Specialization of the Lateral Wall of the Vessel Segment. *Botanical Gazette* 91:88-96.
- Gilbert, S. G.
1940. Evolutionary Significance of Ring Porosity in Woody Angiosperms. *Botanical Gazette* 102:105-120.
- Gutzwiller, M. A.
1961. Die phylogenetische Stellung von *Suriana maritima* L. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 81:1-49.
- Hallier, H.
1905. Provisional Scheme of the Natural (Phylogenetic) System of Flowering Plants. *New Phytologist* 4: 151-162.
1912. L'origine et le système phylétique des Angiospermes. *Archives Néerlandaises des Sciences Exactes et Naturelles, Séries IIIB*, 1:146-234.
- Harrar, E. S.
1946. Note on Starch Grains in Septate Fibers. *Tropical Woods* 85:1-9.
- Heimsch, C., Jr.
1940. Wood Anatomy and Pollen Morphology of *Rhus* and Allied Genera. *Journal of the Arnold Arboretum* 21:279-297.
1942. Comparative Anatomy of the Secondary Xylem of the "Gruinales" and "Terebinthales" of Wettstein with Reference to Taxonomic Grouping. *Lilloa* 8:82-198.
- Hess, R. W.
1946. Identification of New World Timbers: Part II. Anacardiaceae. *Tropical Woods* 87:11-34.
- Hutchinson, J.
1926. The Phylogeny of Flowering Plants. *Proceedings of the International Congress of Plant Science, Ithaca* 1:413-421.
1959. *The families of flowering plants*. 2nd ed. vol. 1. pp. 353-363. Oxford: Clarendon Press.
- Jadin, F.
1901. Contribution à l'étude des Simarubacées. *Annales des Sciences naturelles; botanique. Paris, Série 8*, 13:201-304.
- Johansen, D. A.
1940. *Plant microtechnique*. New York: McGraw-Hill Book Co.

- Keck, D. D.
1957. Trends in Systematic Botany. *Survey of Biological Progress*, 3:47-97. New York: Academic Press.
- Kribs, D. A.
1930. Comparative Anatomy of the Woods of the Meliaceae. *American Journal of Botany* 17:724-738.
1935. Salient Lines of Structural Specialization in the Wood Rays of Dicotyledons. *Botanical Gazette* 96: 547-557.
1937. Salient Lines of Structural Specialization in the Wood Parenchyma of Dicotyledons. *Bulletin of the Torrey Botanical Club* 64:177-187.
- Linnaeus, C.
1753. *Species plantarum*. 2 vols. Stockholm, Sweden: Laurentii Salvii.
- Melchior, H.
1964. Engler's *Syllabus der Pflanzenfamilien*. 12th ed. Pages 246-284. Berlin, Germany: Geb. Borntraeger.
- Metcalf, C. R., and L. Chalk.
1950. *Anatomy of the dicotyledons*. 2 vols. Oxford, England: Clarendon Press.
- Record, S. J.
1939. American Woods of the Family Anacardiaceae. *Tropical Woods* 60:11-45.
1941. American Timbers of the Mahogany Family. *Tropical Woods* 66:7-33.
- Record, S. J., and M. M. Chattaway
1939. List of Anatomical Features Used in Classifying Dicotyledonous Woods. *Tropical Woods* 57:11-16.
- Record, S. J., and R. W. Hess
1943. *Timbers of the New World*. New Haven, Connecticut: Yale University Press.
- Sass, J. E.
1958. *Botanical microtechnique*. 3rd ed. Ames, Iowa: Iowa State University Press.
- Small, J. K.
1911. Simaroubaceae. *North American Flora* 25:227-239.
1913. *Flora of the Florida Keys*. New York: Published by the Author.
1933. *Manual of the Southeastern Flora*. New York: Published by the Author.
- Stern, W. L.
1952. The Comparative Anatomy of the Xylem and the Phylogeny of the Julianiaceae. *American Journal of Botany* 39:220-229.
- Stern, W. L., and K. L. Chambers
1960. The Citation of Wood Specimens and Herbarium Vouchers in Anatomical Research. *Taxon* 9:7-13.
- Takhtajan, A.
1966. *Systema et phylogenia magnoliophytorum*. "Nauka," Moscow and Leningrad (In Russian).
- Thorne, R. F.
1968. Synopsis of a Putatively Phylogenetic Classification of the Flowering Plants. *Aliso* 6:57-66.
- Tippo, O.
1941. A List of Diagnostic Characteristics for the Description of Dicotyledonous Woods. *Transactions of the Illinois State Academy of Science* 34:105-106.
1946. The Role of Wood Anatomy in Phylogeny. *American Midland Naturalist* 36:362-372.
- Webber, I. E.
1936. Systematic Anatomy of the Woods of the Simaroubaceae. *American Journal of Botany* 23:577-587.
1941. Systematic Anatomy of the Woods of the Burseraceae. *Lilloa* 6:441-465.
- Wettstein, R.
1935. *Handbuch der systematischen Botanik*. 4th ed. Leipzig and Wien: Deuticke.
- Wilson, P.
1911. Surianaceae. *North American Flora* 25:225.



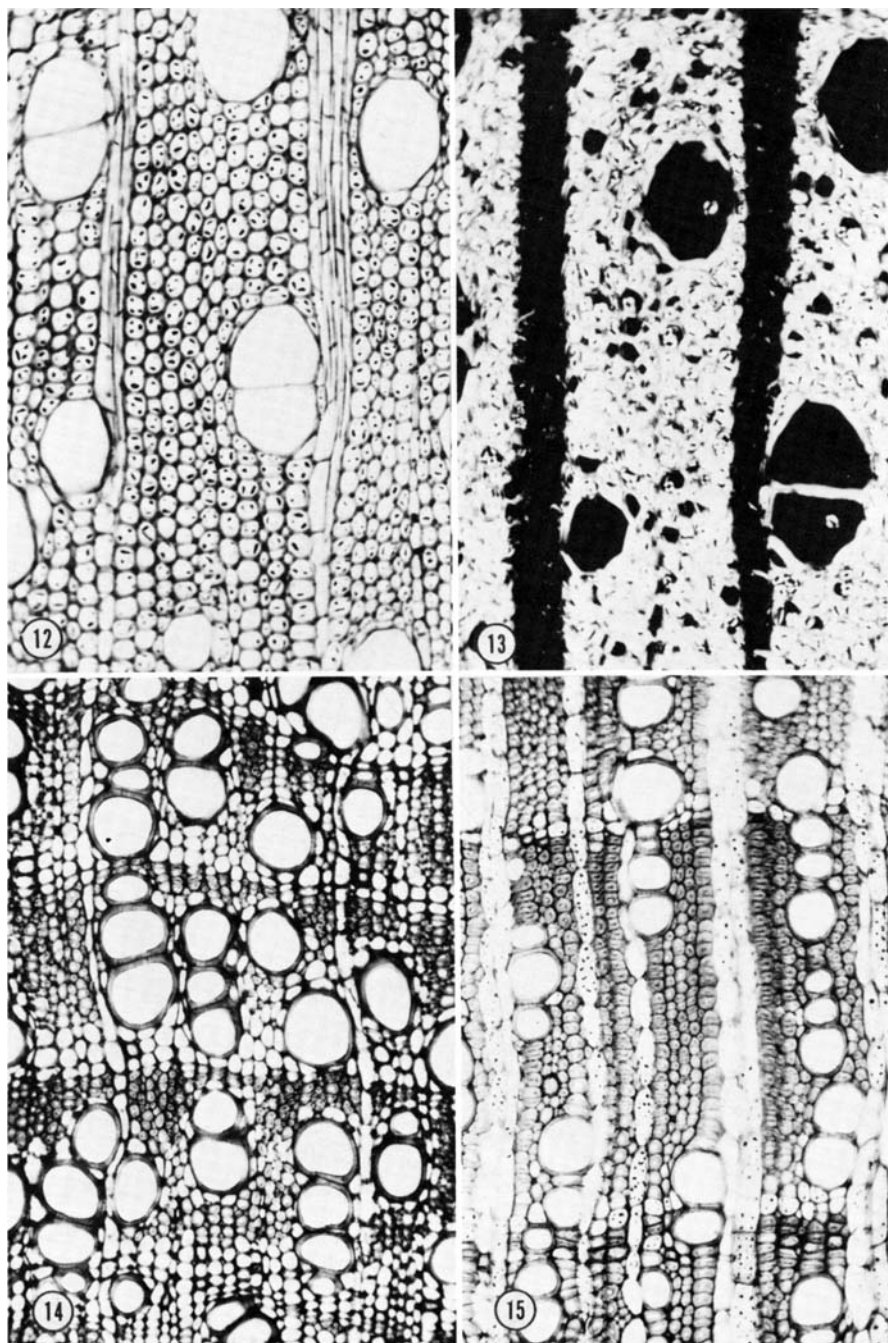
FIGURE 1-4—1, *Toxicodendron radicans*: habit showing flowers; 2, *Bursera simaruba*: habit indicating size of tree; 3, *Bursera simaruba*: leaves and fruit; 4, *Swietenia mahagoni*: habit indicating size of tree.



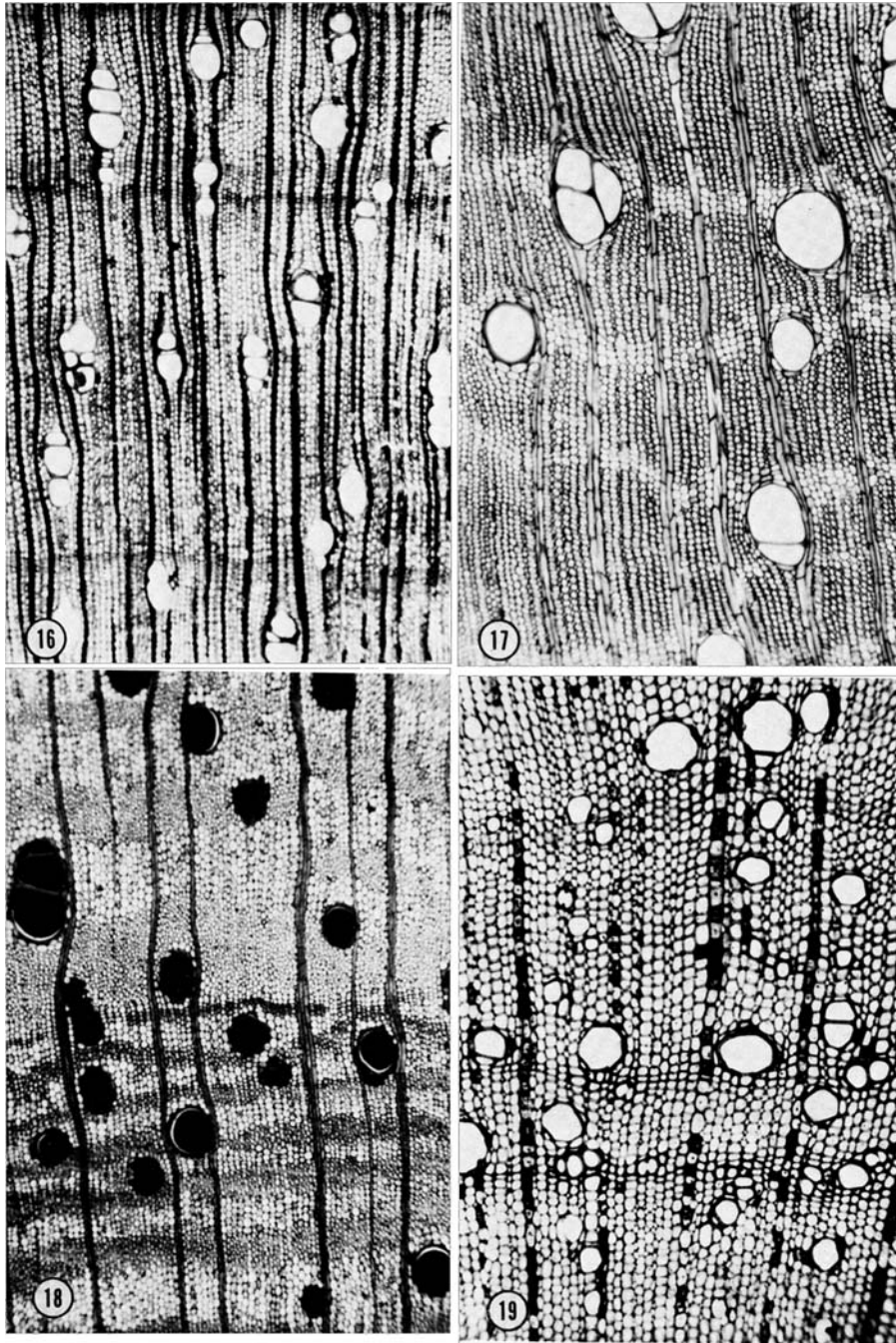
FIGURES 5-8.—5, *Zanthoxylum flavum*: leaf showing glandular dots; 6, *Sapindus saponaria*: habit with fruits and leaves (note winged rachis of pinnately compound leaves); 7, *Sapindus saponaria*: fruits; 8, *Cardiospermum halicacabum*: habit with fruits and flowers.



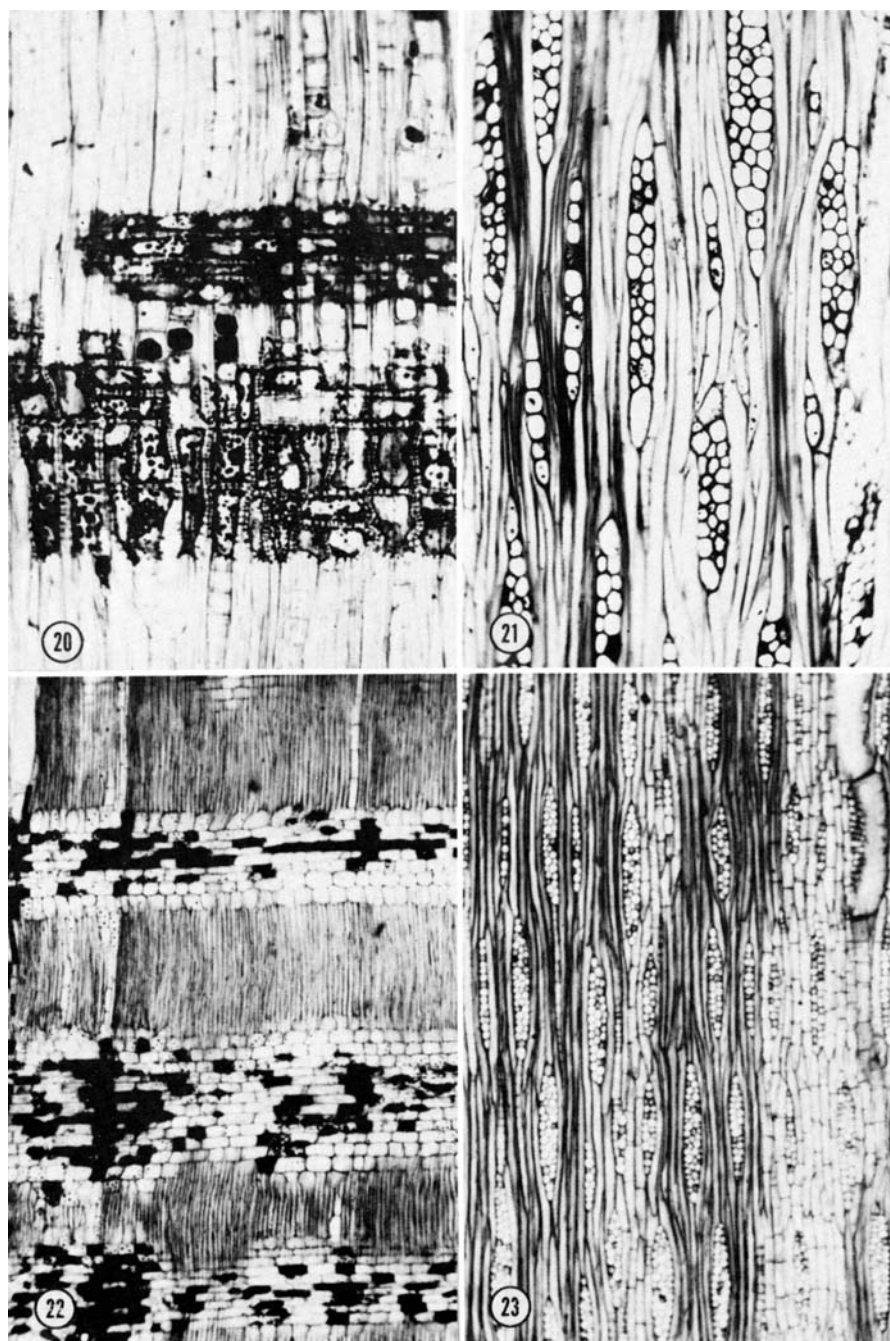
FIGURES 9-11.—9, *Cupania glabra*: fruits and leaves; 10, *Simarouba glauca*: flowers; 11, *Suriana maritima*: flowers (note simple leaves).



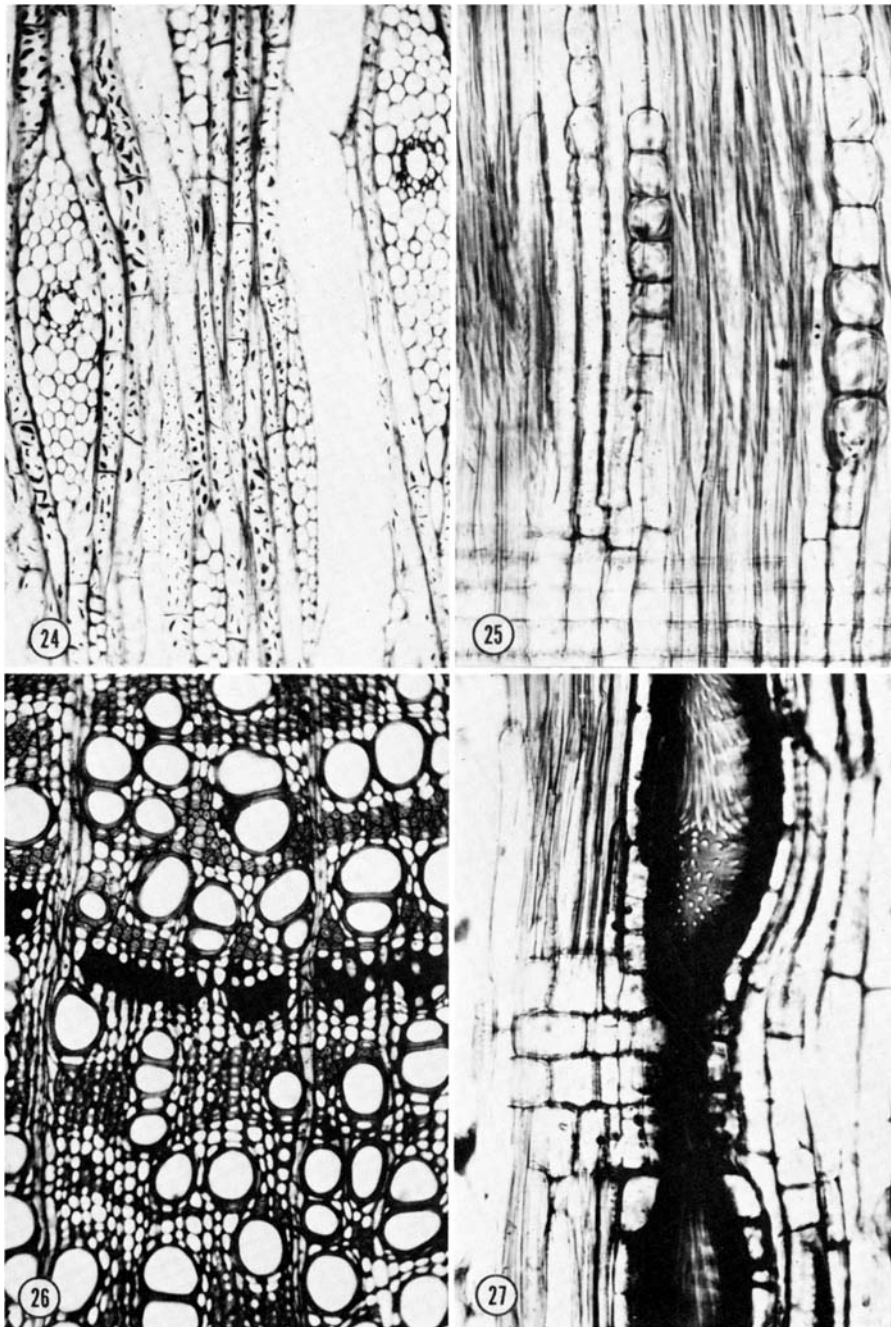
FIGURES 12-15.—12, *Bursera simaruba*: transverse section showing radial multiples and solitary pores (note starch in the fibers), $\times 246$; 13, *Bursera simaruba*: transverse section viewed under crossed nicols (polarized light) showing the birefringent property of the cell walls and starch grains, $\times 269$; 14, *Zanthoxylum fagara*: transverse section showing banded parenchyma and radially oriented pore multiples and chains, $\times 269$; 15, *Zanthoxylum flavum*: transverse section showing large amounts of thick-walled fibers. Banded parenchyma and radially oriented pore multiples and chains are also shown (note the presence of starch grains in both ray and axial parenchyma), $\times 269$.



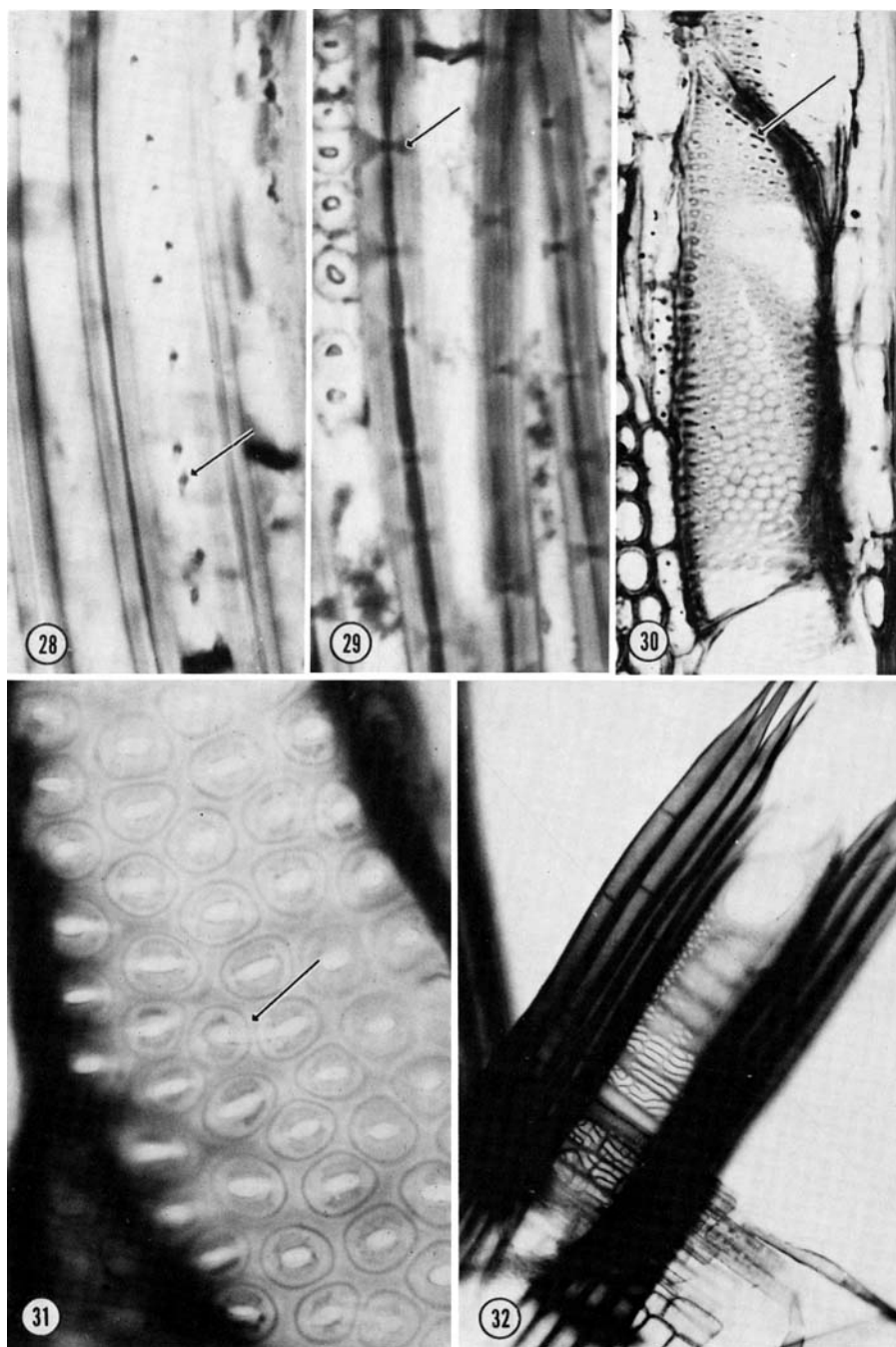
FIGURES 16-19.—16, *Cupania glabra*: transverse section showing growth rings, and solitary, radial multiples, and clusters of pores, $\times 109$; 17, *Simarouba glauca*: transverse section showing aliform and confluent parenchyma arrangement, $\times 97$; 18, *Sapindus saponaria*: transverse section showing confluent bands of parenchyma, $\times 97$; 19, *Toxicodendron radicans*: transverse section showing questionable diffuse-porous distribution of pores, $\times 246$.



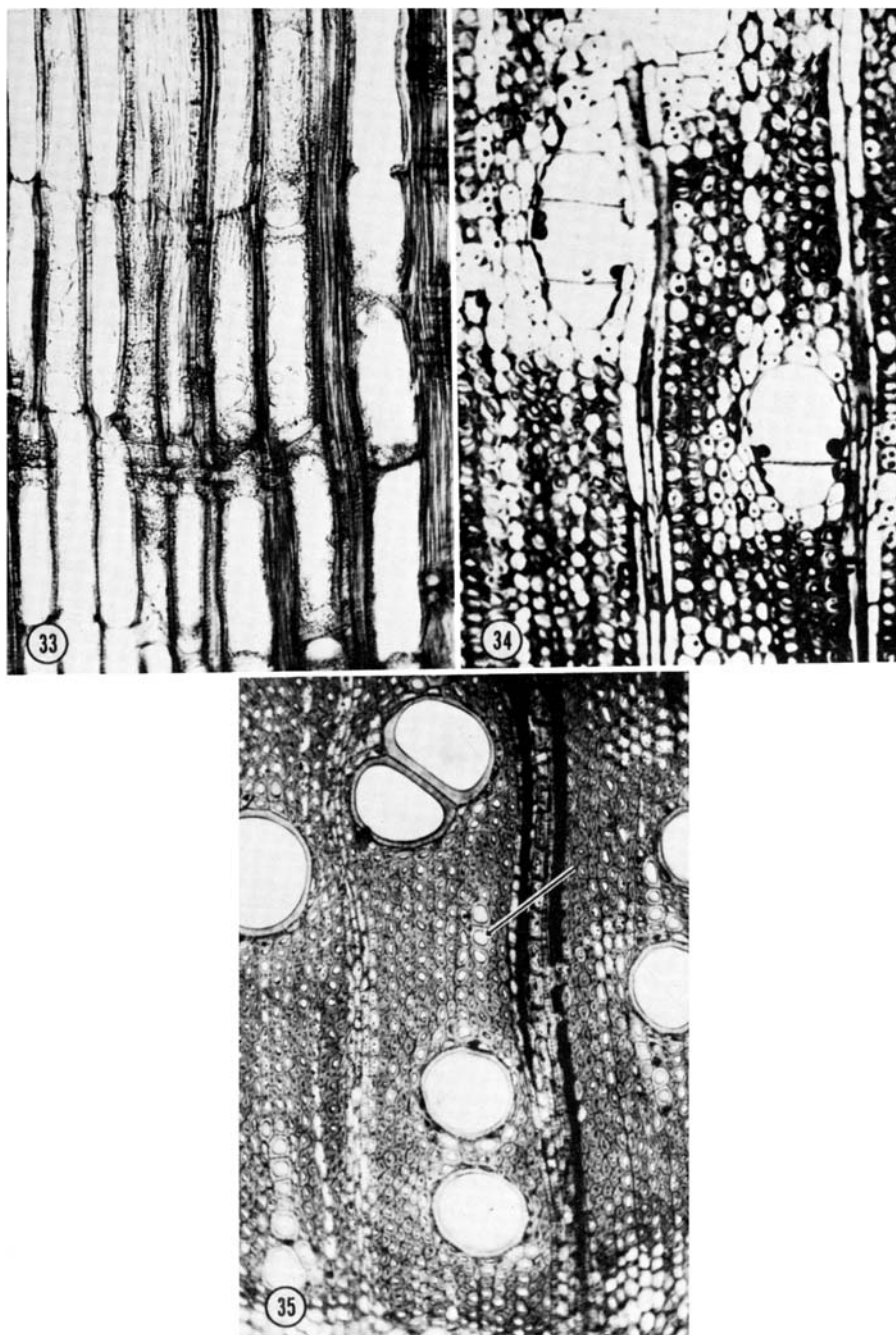
FIGURES 20-23.—20, *Cupania glabra*: radial section showing randomly arranged procumbent, square and upright cells. Note the gumlike substance in ray cells, $\times 390$; 21, *Metopium toxiferum*: Tangential section showing rays having uniseriate "wings," $\times 246$; 22, *Swietenia mahagoni*: Radial section showing rays having square and upright, or both, marginal cells, $\times 97$; 23, *Simarouba glauca*: tangential section showing the storied arrangement of rays and axial strand parenchyma, $\times 97$.



FIGURES 24-27.—24, *Bursera simaruba*: tangential section showing intercellular canals in the rays (note the starch grains in the septate fibers), \times 269; 25, *Citrus aurantiifolia*: radial section showing enlarged crystalliferous idioblasts, \times 539; 26, *Zanthoxylum fagara*: Transverse section showing traumatic intercellular canal, \times 269; 27, *Zanthoxylum fagara*: radial section showing the traumatic intercellular canal in longitudinal section, \times 539.



FIGURES 28-32.—28, *Exothea paniculata*: radial section showing slitlike simple to slightly bordered fiber pits in face view (arrow), $\times 1872$; 29, *Exothea paniculata*: tangential section showing the fiber pits in transverse section (arrow). Note starch grains, $\times 1872$; 30, *Citrus aurantiifolia*: tangential section showing alternate intervascular pitting. Note the coalescence of adjacent pit apertures (arrow), $\times 734$; 31, *Metopium toxiferum*: tangential section showing unilaterally compound intervascular pittings (arrow), $\times 1872$; 32, *Bursera simaruba*: maceration showing the occurrence of fenestriform vessel pitting. These pits occur in the cell walls of both vessel elements and parenchyma. Note the simple perforation plate, $\times 269$.



FIGURES 33-35.—33, *Amyris elemifera*: radial section showing tyloses and granular, translucent material in the vessel elements, $\times 292$; 34, *Metopium toxiferum*: transverse section showing tyloses in vessels and the occurrence of gelatinous fibers, $\times 269$; 35, *Cardiospermum halicacabum*: transverse section showing large solitary pores and radial multiples of small angular pores (arrow), $\times 269$.