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## CONTENTS

- |  |     |
|--|-----|
| THE ANATOMY AND RELATIONSHIPS OF THE ANNONACEAE<br>Raymond W. Vander Wyk and James E. Canright | 1   |
| THE GENUS <i>Tamarix</i> IN ISRAEL<br>M. Zohary  | 24  |
| THE ANATOMY OF THE WATER STORAGE ORGAN OF<br><i>Ceiba parvifolia</i><br>M. F. Moseley, Jr.     | 61  |
| DISCONTINUOUS GROWTH RINGS IN SUPPRESSED SLASH<br>PINE<br>Philip R. Larson                     | 80  |
| CRYSTALS IN WOODY TISSUES; PART II<br>M. Margaret Chattaway                                    | 100 |



## TROPICAL WOODS

*A technical magazine devoted to the furtherance of knowledge of tropical woods and forests and to the promotion of forestry in the tropics.*

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# TROPICAL WOODS

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## THE ANATOMY AND RELATIONSHIPS OF THE ANNONACEAE

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### INTRODUCTION

The Annonaceae are a large natural group, predominantly tropical in distribution, but with one temperate species, *Asimina triloba* (L.) Dunal, extending as far north as southern Ontario, Canada. Among the members of this family, only the genus *Xylopia* has a natural pantropic distribution; the remainder generally occur in one or two of three main centers of distribution: Malaysia, tropical Africa, and the New World tropics. However, various species of *Annona* have long been cultivated throughout the tropics for their edible fruit (cherimoya, soursop, sweetsop, custard apple, illama, etc.), and thus are often found far from their place of origin in the western hemisphere. *Cananga odorata* (Lam.) Hk. f. & Thoms., commonly known as the ylang-ylang, is also widely cultivated in tropical regions for its ethereal oils which are used in perfumes. *Oxandra lanceolata* (Sw.) Baill., lancewood, from the West Indies, is the only timber of commerce of any importance.

The first and only monographer of the Annonaceae (Dunal, 1817) recognized only 9 genera and 103 species. This number gradually increased to 45 genera and 400 species, according to the best estimates of Bentham and Hooker (1862). In 1923 Hutchinson listed 95 genera and 1150 species, and during the past thirty years at least 25

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additional genera have been described and listed in the Index Kewensis. Due to their morphological homogeneity members of this family are normally readily recognizable, yet the inter- and intrafamilial relationships are relatively unknown.

Hallier (1905) grouped the Magnoliaceae (*sensu lato*), Canellaceae, Annonaceae, and Myristicaceae. Engler and Gilg (1924) placed the Annonaceae between the Lactoridaceae and Eupomatiaceae in a suborder of the Ranales which also included the Magnoliaceae, Himantandraceae, Calycanthaceae, Myristicaceae, Gomortegaceae, Monimiaceae, Lauraceae, and Hernandiaceae. Hutchinson (1926) separated the Annonaceae and Eupomatiaceae from other members of the "ranalian complex" and placed them in a new order, Annonales.

More recently, in a series of papers, Bailey and Smith (1942), Bailey, Nast, and Smith (1943), Swamy (1949), and Canright (1952, 1953, 1955) have pointed out the numerous morphological similarities which exist among the Himantandraceae, Degeneriaceae, and Magnoliaceae (*sensu stricto*). They conclude that these are three separate, but closely related, families. Money, Bailey and Swamy (1950) imply that a less compact relationship exists between the three above-mentioned families and the group which includes the Annonaceae, Myristicaceae, Eupomatiaceae, and Canellaceae. Furthermore, it is stated that the Monimiaceae (*sensu lato*), Gomortegaceae, Lauraceae, and Hernandiaceae form another natural grouping of ranalian families.

Therefore, it now seems necessary, by means of comparative morphological surveys of both vegetative and floral organs, to establish the true relationships of the Annonaceae in the ranalian complex. In other words, is there sufficient evidence to warrant the grouping of the Annonaceae with any other families of the Ranales (*sensu lato*), or can it be demonstrated that the Annonaceae and Eupomatiaceae are closely related and sufficiently distinct to allow their inclusion in a separate order, according to the proposal of Hutchinson?

This paper on the wood and general stem anatomy of the Annonaceae is the first of a series which, it is hoped, will provide sufficient evidence to provide a satisfactory answer to these questions. Although it is probable that some concept of the internal organization of the Annonaceae will be gained during the course of this study, this is not the immediate goal, since a monographic treatment of this extremely large family is not feasible at the present time.

#### MATERIALS AND METHODS

A total of 489 species in 79 genera was examined for the study of general stem anatomy. The majority of this twig material was obtained from herbarium specimens belonging to the Arnold Arboretum; the remainder came from the preserved collections of Harvard University. Dried twigs were softened in boiling water, sectioned on a sliding microtome at  $20\mu$ , dehydrated, then mounted unstained in diaphane.

For the survey of the mature wood of the Annonaceae, woods of 61 genera and approximately 400 species were examined from the collections of Harvard University and the Yale University School of Forestry. Blocks of wood were softened in hydrofluoric acid, sectioned in three planes, stained in Delafield's haematoxylin and safranin, and mounted in the usual manner. In addition, for comparative purposes, woods and stems of 31 genera were examined from the following families: Myristicaceae, Magnoliaceae, Eupomatiaceae, Himantandraceae, Degeneriaceae, and Canellaceae.

The authors wish to take this opportunity to thank the curators of the various collections mentioned above for the use of their woods and herbarium specimens. The advice and support of Professor I. W. Bailey is also acknowledged with extreme gratitude.

#### GENERAL STEM ANATOMY

Considering the large size of this family, relatively little information is in the literature concerning its general stem



anatomy. The early observations of Baillon (1871) are the most detailed, and the few lines devoted to this subject in the surveys of Solereder (1908) and Metcalfe and Chalk (1950) add but little to Baillon's findings.

The primary vascular cylinder is a typical eustele, but with the discrete bundles separated by broad medullary rays. Each bundle is capped abaxially by a group of thick-walled fibers (pericyclic?), which remain separate even after the completion of the secondary body, *i. e.*, no complete ring of sclerenchymatous tissue is ever formed in the cortex.

Baillon (*loc. cit.*) was the first to call attention to the septation of the pith in *Annona*, *Artabotrys*, and *Xylopia*. Solereder (*loc. cit.*) also reported the occurrence of this feature in species of *Unona*, *Uvaria*, *Miliusa*, and *Mitrephora*. Metcalfe and Chalk (*loc. cit.*) claim that pith diaphragms of stone cells are present in all 22 genera examined by them, with the exception of species of *Asimina* and *Monodora*. The present authors found these transversely oriented plates of brachysclereids (fig. 2) in all 489 species examined, including species of *Asimina* and *Monodora*. These pith diaphragms are usually more extensive in the nodal region, but are also normally present in the internodal region. The fact that spherical secretory cells were only found in the pith region of slightly over half (276) of the examined species, makes it obvious that this character cannot be relied upon for diagnostic purposes in this group. On the other hand, secretory cells in the cortex are of universal occurrence in examined species of the Annonaceae.

Sclereids of varying number and type are common features of the outer cortical region. These stone cells may be few in number and extremely scattered, but in some cases so numerous as to constitute an almost continuous zone, *e. g.*, *Crementosperma*, *Fusaea*, *Papualthia*, and *Pseudoxandra*. In addition, in many specimens it was found that each stone cell contained in its lumen a single large rhombic crystal of calcium oxalate.

Stratification of hard and soft bast in the phloem region is characteristic for members of this family (fig. 1). The

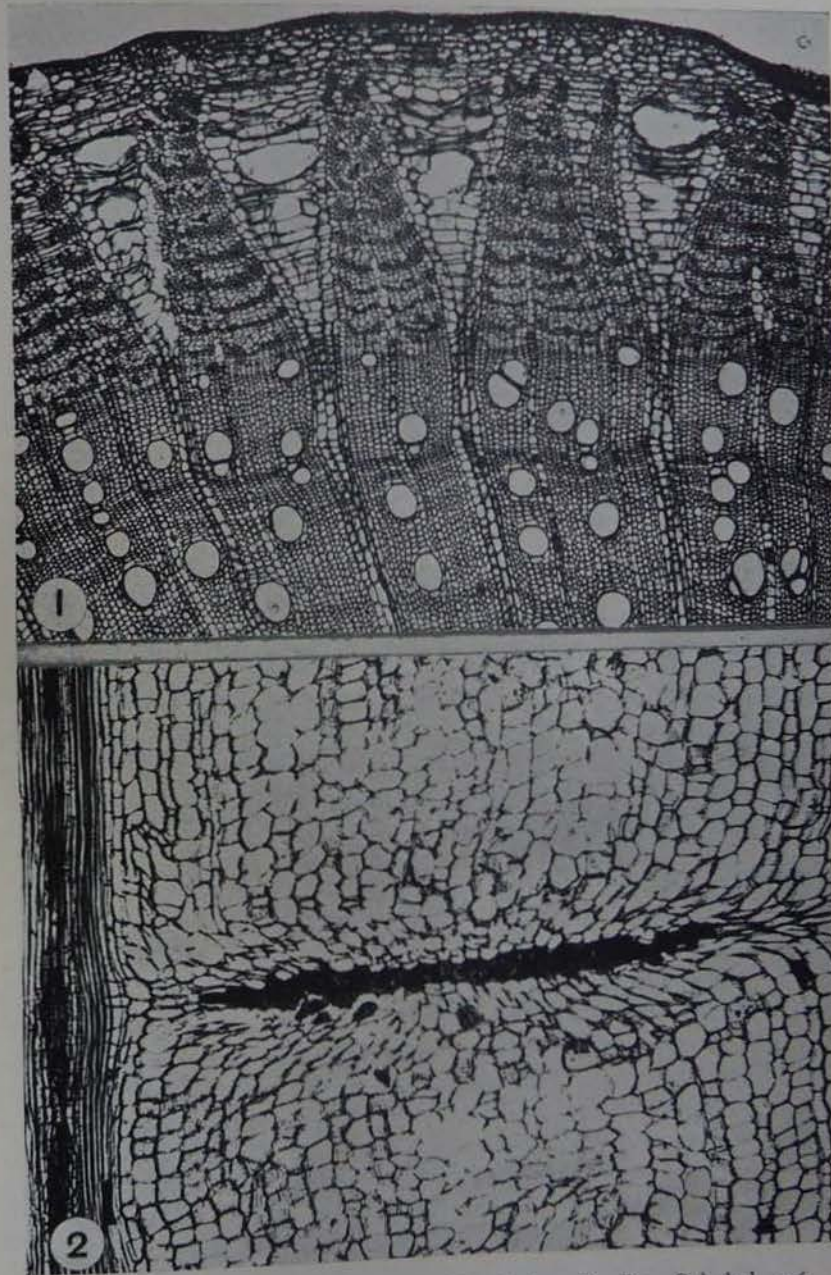


Fig. 1-2.—Fig. 1. *Artabotrys odoratissima* R. Br., Soledad 926. Cross section of stem showing V-shaped rays containing ethereal oil cells, and stratified hard and soft bast.  $\times 50$ .—Fig. 2. *Same*. Median longitudinal section of stem showing pith diaphragm of brachysclereids.  $\times 50$ .



phloem rays are normally V-shaped as seen in transection (fig. 1) and often include large secretory cells.

Calcium oxalate crystals are of regular occurrence in the cortex, ray parenchyma cells, and pith of most species of all examined genera, with the exception of *Brieya*, *Guatterella*, and *Piptostigma*. Crystal types include various sizes and shapes of rhombohedrals, prismatic, and druses. The last-named crystal type is especially numerous, being noted in the cortex of 180 species, the phloem rays of 154 species, and the pith of 147 species. In addition, 32 species showed druses in the young wood rays, including all 12 examined species of *Anaxagorea*, although this feature is comparatively rare in xylem rays of mature woods.

Hairs of five distinct types, ranging from multicellular uniseriates to stellate and peltate forms, are frequently found on stems prior to the formation of periderm. Although these hair types are fairly constant for many genera and thus of diagnostic value, a discussion of their details will be postponed for a subsequent paper on leaf anatomy and pubescence of the Annonaceae. According to Metcalfe and Chalk (1950), periderm development is superficial in species of *Artabotrys*, *Asimina*, *Cananga*, *Monodora*, *Stromia*, and *Uvaria*.

#### WOOD ANATOMY

One of the earliest, and certainly the most detailed, descriptions of annonaceous woods is that of Moll and Janssonius (1906). They found the wood anatomy of 21 species (in 13 genera) of Javanese members of the Annonaceae bore close similarities. Despite this fact, they separated the Javanese species into four groups, meanwhile appending the following remark (p. 110): "*Innerhalb der Gruppen die Unterschiede zwischen den Genera oft fast ebenso gross wie die zwischen den Gruppen selbst.*"

Benoist (1927) described the wood anatomy of three species of *Xylopia* from French Guiana. Record and Hess (1943) refer mainly to the macroscopic characters of the woods of 21 American genera, but Hess later (1946) pub-



lished details of the microstructure of these genera. Upon the completion of his investigation, Hess declared that the woods of all the American genera were so similar that it was impossible to make a workable key for their determination.

Recently, Ingle and Dadswell (1953) have increased our knowledge of the wood anatomy of the Annonaceae by the description of woods of 12 genera from the southwest Pacific area. They conclude that the range of wood characters revealed by the species of some of the larger genera is as great as that between many genera in the family. Nevertheless, they agree with earlier workers that the general features of the woods of the Annonaceae are so homogeneous that woods of this family can readily be recognized from timbers of all other families.

The present investigation of 61 genera and some 400 species of annonaceous woods supports the conclusions of the previous workers, viz., a systematic grouping of this family based solely upon wood anatomy would be meaningless. Therefore, the woods of this family will be treated here as a unit, and individual differences between genera will be commented upon wherever such comment seems necessary.

That the Annonaceae are almost exclusively of tropical distribution is shown in the poor development of growth rings. They are rarely completely absent, but are usually rather indistinct, and the late wood may be demarcated by a narrow zone of slightly thicker-walled fibers. With the exception of temperate species of *Asimina* (fig. 3), vessel distribution is of the diffuse-porous type. The arrangement of vessels is typically solitary or in radial multiples of 2-3 (fig. 5, 6, 8), rarely radial chains of six pores (e. g., *Goniothalamus* and *Hornschruchia*). In cross-sectional outline the pores are nearly circular to slightly oval in a radial direction, rarely angular (*Anaxagorea*, fig. 5, *Asimina*, *Heteropetalum*). The tangential diameter of the largest pores covers a wide range of size, varying in the majority of genera between small (50-100 $\mu$ ) to medium (100-200 $\mu$ ). Those genera having vessel diameters averaging less than 50 $\mu$  are

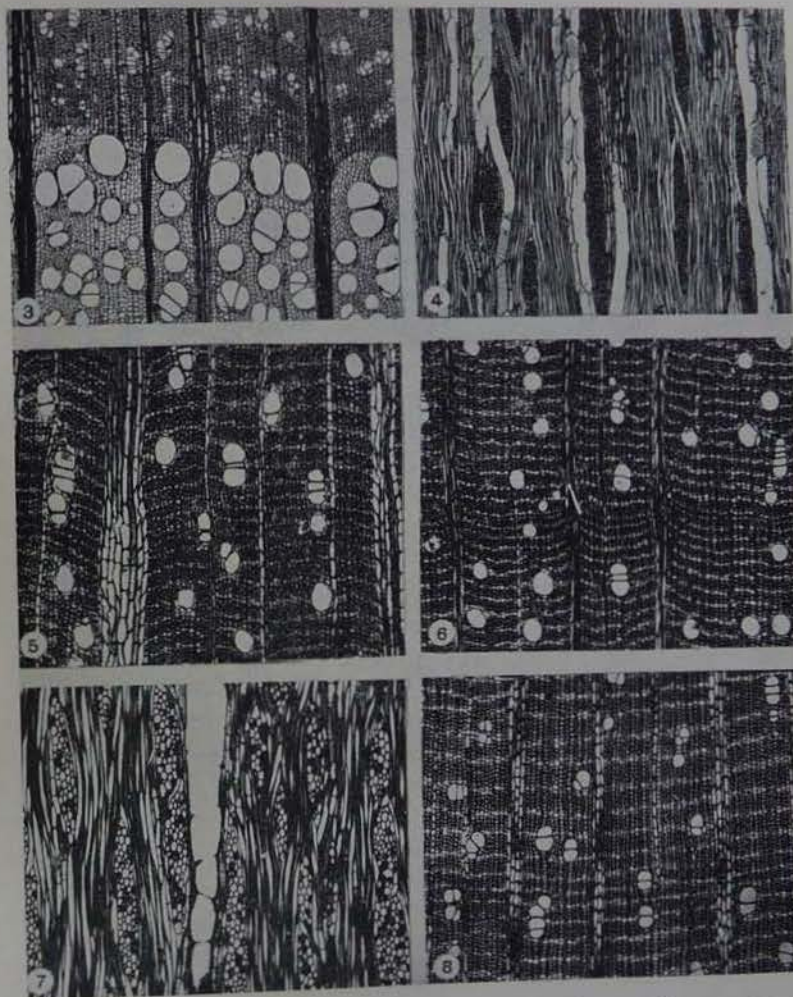


Fig. 3-8.—Fig. 3. *Asimina triloba* (L.) Dunal, H24651. Cross section of wood showing diffuse-porous condition,  $\times 30$ .—Fig. 4. *Same*. Tangential section showing ring-porous condition and size of rays. Note homogeneous character and size of rays. Note short length of vessel elements.  $\times 25$ .—Fig. 5. *Anaxagorea petiolata* R. E. Fries, Y35855. Wood cross section. Note angular outline and distribution of pores; also characteristic narrow-banded parenchyma.  $\times 25$ .—Fig. 6. *Bocageopsis multiflora* (Mart.) Fries, Y36946. Cross section of wood. Pores mainly isolated, but with some radial chains.  $\times 25$ .—Fig. 7. *Cananga odorata* (Lam.) Hook. f. & Thoms. Tangential section of wood. Note slightly oblique end walls in vessel elements and the thin-walled fiber tracheids.  $\times 30$ .—Fig. 8. *Cymbopetalum costaricense* (D. Sm.) Fries, Y12045. Cross section of wood.  $\times 25$ .



*Desmos*, *Desmopsis*, *Guamia*, *Mitrephora*, and *Unona*. Those characterized by vessel diameters averaging over  $200\mu$  are *Drepananthus*, *Guatteria*, *Mezzettia*, *Onychopetalum* and *Pachypodanthium*.

Although the number of vessels per square millimeter is of little phylogenetic import, this character is of some diagnostic value. With this in mind, table 1 gives a complete list of the genera utilized in this study, grouped according to the vessel abundance classification recommended by Record and Chattaway (1939).

The vessel elements in the majority of genera are relatively short, rarely reaching  $500\mu$ , and the perforations are exclusively simple. The angle of the end wall ranges from transverse to slightly oblique, with the latter type being the most common (fig. 4, 7). The intervascular pitting is preponderantly alternate, although a tendency towards opposite pitting has been recorded for some species of *Annona*, *Asimina* (fig. 10), *Diclinanona*, *Anaxagorea*, *Griffithianthus*, *Isolona*, *Malmea*, *Melodorum*, *Mezzettia*, and *Cymbopetalum*. The pits are usually minute to small, mostly  $3-5\mu$ , slit-like, and sometimes with coalescent apertures. The examined genera characterized by pits larger than  $7\mu$  in diameter include *Asimina*, *Artabotrys*, *Cananga*, *Cleistochlamys*, *Diclinanona*, *Drepananthus*, *Mezzettia*, *Popowia*, *Stelechocarpus*, *Unona*, *Unonopsis*, *Uvaria*, and *Uvariastrum*. The pits in the above-listed genera range from  $7-12\mu$  in diameter.

Due to the wide variation of ray type and size, it is difficult to classify the rays of this family according to the strict classification of Kribs (1935). Generally speaking, the rays are either homogeneous or else weakly heterogeneous. Although both uniseriate and multiseriate rays occur in all examined genera, the uniseriates are only sporadic (see e. g., fig. 4), rarely over 12 cells high, and composed of vertically elongated cells. On the other hand, the multiseriate rays of mature wood specimens are composed of cells which are predominantly procumbent (fig. 7), but with radial rows of larger squarish cells sometimes intermixed. The marginal



Table 1. NUMBER OF VESSELS PER SQUARE MILLIMETER

FEW (2-5)	MODERATELY FEW (5-10)	MODERATELY NUMEROUS (10-20)	NUMEROUS (20-40)	VERY NUMEROUS (OVER 40)
<i>Cananga</i>	<i>Aberemoa</i>	<i>Annona</i>	<i>Asimina</i>	<i>Desmopsis</i>
<i>Disepalum</i>	<i>Bocageopsis</i>	<i>Anaxagorea</i>	<i>Artabotrys</i>	<i>Desmos</i>
<i>Drepananthus</i>	<i>Denmettia</i>	<i>Cymbopetalum</i>	<i>Brieya</i>	<i>Guamia</i>
<i>Guatteria</i>	<i>Diclinanona</i>	<i>Fusaea</i>	<i>Cleistochlamys</i>	<i>Isolona</i>
<i>Mezzettia</i>	<i>Fissistigma</i>	<i>Griffithianthus</i>	<i>Duguetia</i>	<i>Mitrephora</i>
<i>Onychopetalum</i>	<i>Goniothalamus</i>	<i>Hexalobus</i>	<i>Enantia</i>	<i>Monodora</i>
<i>Pachypodanthium</i>	<i>Heteropetalum</i>	<i>Hornsbuchia</i>	<i>Lettowianthus</i>	<i>Oxandra</i>
	<i>Xylopa</i>	<i>Malmea</i>	<i>Orophea</i>	<i>Papualthia</i>
		<i>Meiogyne</i>	<i>Polyalthia</i>	<i>Popowia</i>
		<i>Melodorum</i>	<i>Richella</i>	<i>Pseuduvaria</i>
		<i>Oxymitra</i>	<i>Trivalvaria</i>	<i>Sapranthus</i>
		<i>Phacanthus</i>	<i>Unona</i>	<i>Uvaria</i>
		<i>Platymitra</i>		
		<i>Pseudoxandra</i>		
		<i>Rollinia</i>		
		<i>Saccopetalum</i>		
		<i>Sageraea</i>		
		<i>Stelechocarpus</i>		
		<i>Stenanona</i>		
		<i>Stenantha</i>		
		<i>Unonopsis</i>		
		<i>Uvariastrum</i>		

TROPICAL WOODS

1956

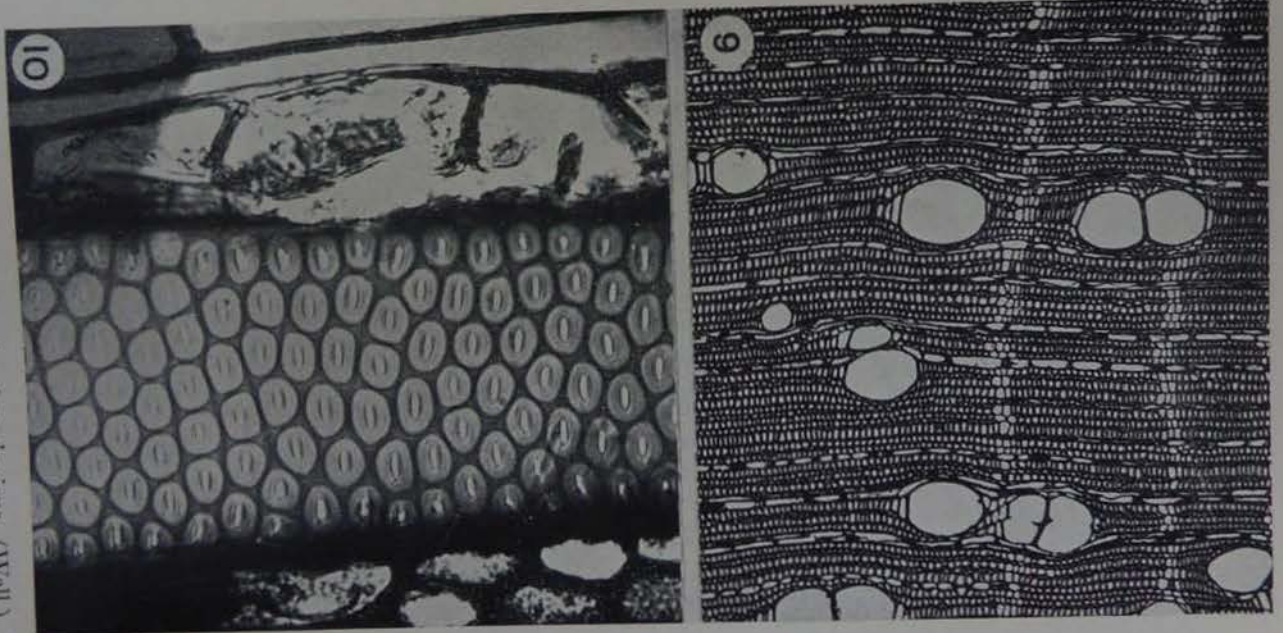


Fig. 9-10.—Fig. 9, *Gymnacrantha farguhariana* (Vall.) Warb., H23598, (Myricaceae). Note general similarity to anonaceous woods.  $\times 50$ .—Fig. 10, *Asimina triloba* (L.) Dunal, H24651, Tan-  
genial section of wood showing opposite interscalar pitting, transitional to alternate.  $\times 375$ .



cells, when they occur, are rarely more than one cell high, and are square to slightly elongate in a vertical direction.

In young wood specimens the rays bordering the pith are definitely of the heterogeneous type, often with several rows of upright marginal cells. Transitions towards a less heterogeneous condition may be observed in the character of these rays more distant from the pith. Such a condition implies an ontogenetic modification of heterogeneous rays to near homogeneity. The ray picture is further complicated by the presence of large oil cells in the rays of several genera, notably *Duguetia*, *Hornschuchia*, *Guatteria*, and *Xylopi*a, in addition to the ten genera reported by Metcalfe and Chalk (1950, p. 49).

It is of interest to note that considerable variation exists between genera in regard to the width, height and cell size of the multiseriate rays. This being true, the width of the rays, as measured by the number of cells, is not a reliable indication of the true ray width when measured in micra. To illustrate this point, the rays of *Orophea* attain a maximum width of 14 cells, whereas the tangential diameter measures only  $145\mu$ . On the other hand, the 14-cell wide rays of *Cananga* (fig. 7) often attain a tangential diameter of  $435\mu$ .

On the basis of the average width of the broadest multiseriate wood rays as measured with an ocular micrometer, it was possible to divide the investigated genera into two fairly evenly divided groups. Those genera possessing rays less than  $100\mu$  wide were considered narrow, and those whose widest rays exceeded this figure were listed as broad. Tables 2 and 3 indicate the results of these measurements, as well as indicating the variations in the number of cells in ray width and length. Examination of the data in tables 2 and 3 reveals that the majority of genera possess rays that are from 1-8 cells wide. However, it should be emphasized in this connection that uniseriate and biseriata rays are relatively rare. The genera characterized by the broadest rays (8-14-seriate) include the following: *Anaxagorea*, *Annona*, *Cananga*, *Cyathocalyx*, *Desmos*, *Mezzettia*, *Onychopetalum*,



*Orophea*, *Stelechocarpus*, *Stenanona*, and *Trivalvaria*. Although it is doubtful at the present time if these groupings based on ray width have much systematic value, a report on correlational studies with other organs and tissues of the Annonaceae will be made in following papers of this series.

The wood parenchyma distribution is an important character for delimiting members of the Annonaceae from other families. The wood parenchyma is essentially all of the apotracheal, narrow-banded (1-2-seriate) type. When viewed with a hand lens, these seriations are especially distinct when in contact with thick-walled fibers (fig. 5, 6).

Table 2. NARROW RAYS (LESS THAN 100 MICRA)

GENUS	WIDTH IN CELLS	WIDTH IN MICRA	MAXIMUM CELLS HIGH
<i>Aberemoa</i>	1-6	75	110
<i>Alphonsea</i>	1-5	85	50
<i>Asimina</i>	1-8	75	120
<i>Brieya</i>	1-6	85	80
<i>Demmettia</i>	1-6	80	50
<i>Diclinanona</i>	1-6	85	115
<i>Disepalum</i>	1-4	80	85
<i>Dugetia</i>	1-6	90	95
<i>Enantia</i>	1-6	60	95
<i>Fissistigma</i>	1-4	55	50
<i>Fusaea</i>	1-8	90	95
<i>Guamia</i>	1-5	80	70
<i>Guatteria</i>	1-8	85	170
<i>Heteropetalum</i>	1-4	80	65
<i>Hexalobus</i>	1-6	95	100
<i>Hornschuchia</i>	1-4	60	80
<i>Lettowianthus</i>	1-6	90	80
<i>Malmea</i>	1-5	85	75
<i>Oxandra</i>	1-6	60	50
<i>Papualthia</i>	1-6	96	65
<i>Platynitra</i>	1-6	84	65
<i>Rollinia</i>	1-4	60	60
<i>Saccopetalum</i>	1-6	60	50
<i>Sageraea</i>	1-6	70	50
<i>Sapranthus</i>	1-6	80	80
<i>Unonopsis</i>	1-5	90	120
<i>Uvaria</i>	1-5	60	275
<i>Xylopi</i>	1-8	96	100

Table 3. BROAD RAYS (MORE THAN 100 MICRA)

GENUS	WIDTH IN CELLS	WIDTH IN MICRA	MAXIMUM CELLS HIGH
<i>Anaxagorea</i>	1-12	330	175
<i>Amnona</i>	1-10	140	200
<i>Artabotrys</i>	1-6	130	100
<i>Bocageopsis</i>	1-8	110	175
<i>Cananga</i>	1-14	435	100
<i>Cleistochlamys</i>	1-8	160	175
<i>Cyathocalyx</i>	1-11	160	160
<i>Desmopsis</i>	1-7	135	95
<i>Desmos</i>	1-9	160	95
<i>Drepananthus</i>	1-8	200	75
<i>Goniothalamus</i>	1-6	160	170
<i>Griffithianthus</i>	1-6	180	60
<i>Isolona</i>	1-6	285	95
<i>Meiogyne</i>	1-6	120	75
<i>Mezzettia</i>	1-12	210	120
<i>Mitrephora</i>	1-8	365	80
<i>Monodora</i>	1-5	140	60
<i>Onychopetalum</i>	1-10	205	180
<i>Orophea</i>	1-14	145	170
<i>Oxynitra</i>	1-8	275	120
<i>Pachypodanthium</i>	1-6	135	100
<i>Phaeanthus</i>	1-8	120	120
<i>Polyalthia</i>	1-6	155	90
<i>Popowia</i>	1-6	120	200
<i>Pseudoxandra</i>	1-8	135	135
<i>Pseuduvaria</i>	1-6	155	160
<i>Richella</i>	1-8	170	120
<i>Stelechocarpus</i>	1-11	175	250
<i>Stenanona</i>	1-12	180	80
<i>Trivalvaria</i>	1-10	235	130
<i>Unona</i>	1-8	170	160
<i>Uvariastrium</i>	1-8	155	100

These parenchymatous bands normally tend to be uniformly spaced, ranging in the different genera from 30-120 $\mu$  apart. Paratracheal parenchyma is sometimes present in the genera with large vessels, but when present, is usually scanty. Some storring of the wood parenchyma has been observed, but it is the exception rather than the rule.

No septate fibers were found in the examined species. The fibers are relatively short; the longest were observed in



woods of *Drepananthus* and *Goniothalamus* (1.5 mm.)<sup>2</sup>, and the shortest were in *Asimina* (0.6 mm.). The fiber walls, for the most part, can be referred to as thick, yet thin-walled fibers were found in 20 of the examined genera (fig. 7). Although pits on the walls of the fibers are relatively numerous and of moderate size, the pit borders, when present, are usually so narrow that they are indistinct. Therefore, it is often difficult to classify these elements definitely as either fiber tracheids or libriform fibers. However, in the cases of *Drepananthus*, *Mezzettia*, *Stenanthera*, *Unona*, and *Unonopsis* the pit borders of the prosenchymatous elements are distinctly visible; thus in these genera these elements are definitely fiber tracheids.

In a summary of the characteristics of the woods of the Annonaceae it is apparent that in almost all features of phylogenetic value a remarkable degree of uniformity exists. Each of the 400 species in the 61 genera examined clearly belongs in the family. The genus least conforming is *Asimina* with its ring-porous wood, distinct growth rings, and spiral thickenings; however, this nonconformity in some wood characters is not surprising in view of the fact that this is the only genus in the family with a temperate distribution.

For the most part uniformity exists in the following characteristics: growth rings absent or indistinct; diffuse porosity; vessels solitary or in short radial chains; vessels rounded in cross section; intervascular pitting mainly alternate and crowded; vessel perforations simple; vessel end walls almost transverse to slightly oblique; rays nearly homogeneous, uniseriate rare; parenchyma in uniseriate or biseriate bands (interrupted by the rays); relatively short fibers, mostly libriform; septate fibers absent.

An examination of the above features indicates that annonaceous woods are not as primitive as one might expect from the phylogenetic position assigned to the family in most

<sup>2</sup>Ingle and Dadswell (1953, Table 3) report four genera of Annonaceae possessing fibers between 1.5-1.87 mm. in length.

systems of classification. On the contrary, the woods of the Annonaceae seem to have attained a moderately high level of specialization. Except for a tendency toward solitary vessel distribution and apotracheal parenchyma, many phylogenetically advanced features are noticed. These include: short vessel elements with almost transverse end walls, simple perforations, and alternate intervascular pitting; homogeneous or weakly heterogeneous rays; evidences of storring in the wood parenchyma; and the short, thick-walled, essentially libriform, fibers.

#### RELATIONSHIPS TO OTHER FAMILIES BASED UPON THE STRUCTURE OF THE YOUNG STEM AND MATURE WOOD

*Magnoliaceae*, *Degeneriaceae*, *Himantandraceae*.—Bailey, Nast, and Smith (1943) and Canright (1955) have pointed out the numerous similarities which exist among the stems and woods of the *Magnoliaceae*, *Degeneriaceae*, and *Himantandraceae*. The following list summarizes the anatomical features of the young stems of these three families:

1. Superficial origin of periderm.
2. Spherical secretory cells in the cortex, phloem rays, and pith.
3. Nests and transversely-oriented plates of medullary sclereids.
4. Stratification of secondary phloem into tiers of hard and soft bast.
5. V-shaped phloem rays.
6. Cortical sclereids, more or less abundant.
7. Eustelic primary vascular cylinder, with each bundle capped externally by thick-walled fibers.

Notably, each of the above-listed characteristics is also common to the stems of the Annonaceae. In addition, this family shares the presence of crystalliferous parenchyma in the cortex, phloem, and pith with both the *Himantandraceae* and *Magnoliaceae*. In *Himantandra*, as well as in many genera of the Annonaceae, rhombohedral crystals jacketed by a thick sheath of lignified cellulose are relatively common.



In comparing the wood anatomy of the Annonaceae to that of the Magnoliaceae-Himantandraceae-Degeneriaceae alliance, the following points are emphasized. The vessel distribution is more or less similar in all four families. The Annonaceae, Himantandraceae, and certain temperate species of the Magnoliaceae possess vessels with simple perforations, although those of *Degeneria* and the majority of the Magnoliaceae possess scalariform perforations. The vessel elements of the Annonaceae are generally shorter and have less oblique end walls than do those of the Himantandraceae, but the intervacular pitting is of a similar type (alternate). The wood parenchyma is of the apotracheal banded type in all four families under consideration (narrow-banded in the Annonaceae and Degeneriaceae, broad-banded in the Himantandraceae, and terminal or initial in the Magnoliaceae). Although the rays of the Annonaceae generally tend to be broader and higher, certain similarities do exist in the four families. The rays of the first-formed secondary xylem are narrow, with a high proportion of uniseriate rays which are decidedly heterogeneous. In mature woods the uniseriate rays become less numerous or are eliminated, while the multiseriate rays approach homogeneity in some cases. In the Degeneriaceae and Himantandraceae the imperforate tracheary elements are thin-walled and possess pits with narrow borders. Fiber tracheids are also characteristic of the woods of the Magnoliaceae, but these may be either thick- or thin-walled types, whereas the annonaceous woods have thick-walled fibers in the majority of cases. In addition, the pit borders are often so reduced that it is difficult to decide whether the imperforate tracheary elements are merely thick-walled fiber tracheids or libriform fibers.

Thus, evidence from young stems and mature woods seems to indicate a close relationship between the Annonaceae, Magnoliaceae, Himantandraceae, and Degeneriaceae. The anatomy of the Degeneriaceae exhibits the most primitive features; that of the Magnoliaceae an intermingling of unspecialized and relatively advanced characters; and that of

the Himantandraceae and Annonaceae a predominance of specialized features. It is of interest in this connection to note that McLaughlin (1933), basing his conclusions on similarities of wood anatomy alone, suggested that the Himantandraceae be transferred from the Magnoliales to the Annonales (of Hutchinson, 1926).

*Myristicaceae*.—Garratt (1933) has reviewed the history of the various taxonomic positions assigned to this family (the nutmegs), and pointed out that various systematists, on the basis of flower, seed, and fruit similarities, have allied the Myristicaceae with the Annonaceae. For this reason, a comparative survey of the important features of the young stem and wood was made by the authors. This survey included all 15 genera and 23 of the species belonging to the pantropical nutmeg family.

As in the case of the Annonaceae, the primary vascular cylinder is a eustele with the individual bundles capped by groups of thick-walled fibers. However, during the formation of the secondary body these sclerenchymatous areas become laterally extended by lignification of the parenchymatous areas on their flanks. Indeed, in *Osteophloem* and *Pycnanthus* an almost continuous ring of sclerenchyma is formed in this manner, a condition which was not observed in any of the annonaceous stems. Although sclerified medullary diaphragms are characteristic of the Myristicaceae, the pith is considerably larger than that seen in annonaceous stems of comparable size. Spherical oil cells are common in both the pith and cortex, and sclereids are also found scattered throughout the latter tissue. Crystalliferous parenchyma occurs in the cortex, and less frequently, in the pith. Although the presence of V-shaped phloem rays and stratified phloem is less conspicuous in young stems than in comparable material of the Annonaceae, both these features are well-developed in older stems. The periderm origin is superficial.

The foregoing summary of myristicaceous stem characteristics indicates that the nutmeg family shares a number of features with the Magnoliaceae, Degeneriaceae, Himan-



tandraceae, and Annonaceae. However, sufficient differences exist to allow a reasonable doubt as to whether this family should be allied with the four previously-mentioned groups.

In summarizing his interpretation of the probable relationships of the Myristicaceae, based solely on wood anatomy, Garratt (1933, p. 42) has gone on record with the following statements: (1) "The structure of the wood of the Annonaceae is so strikingly different from that of the Myristicaceae that it indicates little or no relationship between the two groups"; and (2) "Some affinity is indicated between the Myristicaceae and the families Magnoliaceae and Schizandraceae, of the order Magnoliales, but the relationship is not nearly so marked as with the Lauraceae."

In view of the fact that the present authors have demonstrated a considerable number of important anatomical features which are shared by the Annonaceae and the "magnoliaceous triumvirate," Garratt's statements above seem incompatible. To explain further, if "some affinity" is shown between the Annonaceae and Magnoliaceae (as Garratt states), then it seems improbable that there is "little or no relationship" between the Myristicaceae and Annonaceae. In short, if the Myristicaceae and Magnoliaceae give evidences of relationship, then it seems reasonable to assume that the nutmeg family should show *some* relationship to the annona family as well, since evidence has already been given which definitely links the Magnoliaceae and Annonaceae.

According to Garratt (1933) the outstanding points of distinction between the woods of the Annonaceae and Myristicaceae are found in the nature of the vessel-ray pitting, type of perforation plates, size of rays, arrangement of wood parenchyma, and in the absence of septate fibers in the Annonaceae. Let us examine these "points of distinction" in more detail. Of the differences listed by Garratt, only the size of the rays and the absence of septate fibers in the Annonaceae are constant. On the other hand, similar features in the two families are seen in: (1) growth rings usually indistinct or lacking; (2) pores solitary in distribution,

occasionally in short radial chains; (3) in 7 of the 15 myristicaceous genera examined by the authors the vessel perforations were predominantly simple; the remainder were scalariform, few-barred, with some reticulate types; (4) intervacular pitting usually alternate, but some opposite pitting does occur; (5) ray-vessel pitting of two types in the Myristicaceae, but with one type (similar to intervacular pitting) like that of the Annonaceae; (6) 11 genera of the Myristicaceae were found to possess parenchyma of the banded apotracheal type, mostly 2-4 cells wide (fig. 9); that of the Annonaceae is generally 1-2 cells wide; some scanty paratracheal parenchyma occurs in both families; (7) although the rays of the Myristicaceae are generally narrower and lower than those of the Annonaceae, the ray type is similar in both groups, *viz.*, weakly heterogeneous with a tendency towards homogeneity; (8) oil cells of sporadic occurrence in the rays of both families; (9) thick-walled fibers with either inconspicuously bordered pits or with borders completely absent.

From the above comparisons, it seems evident that the differences between the woods of the Annonaceae and Myristicaceae are not as significant as Garratt has previously indicated. Certainly, it is clear that the woods of the Myristicaceae exhibit a wider expression of their salient structural characteristics than those of the Annonaceae. Furthermore, it is also apparent from an examination of the wood anatomy that the putative genera of the Myristicaceae form a discrete family. Nevertheless, from the viewpoint of comparative anatomy of the young stem and mature woods of the Myristicaceae and Annonaceae, it seems probable that these two families are truly related. It is possible that, because of certain similarities between the woods of the Magnoliaceae and Myristicaceae, *e. g.*, both scalariform and simple perforations in the vessels, that the Myristicaceae may serve as a transitional family between the less specialized Magnoliaceae and the more specialized Himantandraceae and Annonaceae. Naturally, however, this postulate needs an intensive study of floral organs of these ranalian



families to test its validity. In this connection, it is interesting to note that Joshi (1946) on the basis of his studies of pollen morphology and embryology has indicated that his evidence "appears to favor Wettstein's view about the close relationship of the two families Myristicaceae and Annonaceae."

*Eupomatiaceae*.—A small bispecific Australian genus of shrubs, *Eupomatia* has long been treated as a member of the Annonaceae (Baillon, Bentham and Hooker, Engler and Prantl, etc.), due to some superficial resemblances in the flowers. Hutchinson (1926) recognized the individuality of this genus, making it the type of a new family, Eupomatiaceae, which he grouped with the Annonaceae in the order Annonales.

The following description of the general stem anatomy is based on two 8 mm. twigs, *Eupomatia* sp. (Brass 20296) and *E. laurina* R. Br. (Bot. Gard. Melbourne 26193). The only mature wood available for examination was that of *E. laurina* (Y-15903).

The discrete bundles of the primary body are widely separated by broad medullary rays. Each bundle is capped by a group of thick-walled fibers, which retain their identity long after secondary growth has been initiated. Brachysclereids are of sporadic occurrence in the cortex, but medullary diaphragms of sclereids are absent. Although the phloem rays flare slightly, the stratification of hard and soft bast is lacking. Ethereal oil cells were not seen; instead a peculiar type of secretory element consisting of vertical rows of cells or tubes containing an amorphous substance are of common occurrence in the cortex, phloem, and pith. These structures have been previously referred to by Lemesle (1938) as tanniferous tubes, but the present authors have been unable to establish satisfactorily the chemical nature of the contents of these secretory elements.

The vessel members in the examined material are of an extremely primitive type. They are extraordinarily long (over 1000 $\mu$ ), narrow (60-70 $\mu$ ), and the long tapering end

walls are characterized by scalariform perforation plates with from 20 to over 150 bars. The vessels are distributed in fairly long sinuous radial rows. Intervascular pitting varies from strictly scalariform to opposite. The wood parenchyma is sparingly paratracheal or diffuse, but never banded. The rays are mainly narrow, extremely high, and strongly heterogeneous, with upright cells composing the bulk of the ray body as well as the margins. Wood fibers show simple or indistinctly bordered pits, and at times are finely septate.

The numerous striking differences in stem and wood anatomy preclude the alliance of the Eupomatiaceae with the Annonaceae (as proposed by Hutchinson); indeed, the anatomical features of *Eupomatia* are dissimilar to any of the ranalian families considered in the present investigation. Lemesle (1938) has stated his belief that this family represents one of the most primitive in the angiosperms. On the basis of what Eames (personal communication) has recently disclosed concerning the floral morphology of *Eupomatia* (e. g., sporophyllic stamens and carpels with 5-9 traces per sporophyll), Lemesle's views may gain future support from evidence provided from floral morphology and anatomy. However, Ozenda (1949), on the other hand, has reached the conclusion that *Eupomatia* should be allied with *Paeonia*, and that this group is far removed from the Annonaceae.

*Canellaceae*.—The Canellaceae include 5 genera and 11 species from the Caribbean region, east Africa, and Madagascar. Apparently influenced in part by their possession of ethereal oil cells, Hallier (1905) placed this family between the Magnoliaceae and Annonaceae. Later, Hallier (1912) indicated his belief that the Canellaceae also showed alliance to the Myristicaceae. However, in the majority of the other systems of classification this family is situated much higher in the evolutionary scale, e. g., Hutchinson (1926) assigns it to the order Bixales, and Engler and Gilg (1924) to the Parietales.

Young stems of the Canellaceae are characterized by numerous secretory cells in the cortex, pith, and ray paren-



chyma. Although the phloem rays flare outwardly, the remainder of the phloem is unstratified. In addition, cortical sclereids and medullary diaphragms are absent. An examination of the mature wood (based on *Capsicodendron pimenteira* Hoehne, H-23444) reveals the following features: vessels usually solitary, narrow, and with long tapering end walls containing scalariform perforations (10-40 bars); intervacular pits opposite, not numerous; wood parenchyma essentially apotracheal diffuse; extremely long fiber tracheids with large bordered pits; a high percentage of homogeneous uniseriate rays occurs, and the heterogeneous multiseriate are almost entirely only 2-3 cells wide.

An analysis of the above anatomical characters reveals that there are few points of comparison with either the Annonaceae or the magnoliaceous triumvirate of families. Yet certain genera of the Myristicaceae share a number of anatomical features with the Canellaceae. Thus, it may be possible that Vestal (1937) had the correct solution for the proper taxonomic position of this family, when he suggested that it be placed in the woody Ranales near the Myristicaceae. Certainly, evidence from wood anatomy alone is an insufficient basis for major taxonomic realignments of families, since all organs and tissues do not evolve at the same rate. Yet the decidedly primitive nature of all the features in the wood of the Canellaceae make it important that the floral morphology of this family be investigated in detail, due to the fact that the wood anatomy of this family is inconsistent with that of other members of the Bixales or Parietales, where the family is usually placed.

#### SUMMARY

The comparative anatomy of the young stem and mature wood was investigated for 489 species in 79 genera of the Annonaceae. The anatomical features of this family revealed a remarkable consistency, which emphasizes the belief that this is a well-defined natural group. However, there exists a considerable degree of generic overlap for the majority of anatomical features, which, therefore, are of doubtful value

in attempting to understand the intrafamilial relationships of the Annonaceae. Possible exceptions to the above statement may be found in two characteristics, vessel distribution (number/sq. mm.) and ray size, although this surmise needs to be thoroughly tested by means of investigations on the floral morphology of this family (now in progress).

It is clear from the large number of comparative features in the young stems that the Annonaceae are undoubtedly allied to the woody ranalian group, whose relationships to each other have already been well established, *viz.*, the Degeneriaceae, Magnoliaceae, and Himantandraceae. The most important of these stem features shared by these four families are: medullary sclerenchymatous diaphragms, stratified hard and soft bast, V-shaped phloem rays, cortical sclereids, superficial origin of periderm, and ethereal oil cells scattered throughout the parenchymatous tissues.

With reference to the wood anatomy of the Annonaceae, strong affinity is shown to the "magnoliaceous triumvirate" mentioned above, with the closest relationship existing with the Himantandraceae. These two families share such features of phylogenetic import as exclusively porous vessel elements, alternate intervacular pitting, and apotracheal banded parenchyma.

In view of the fact that a number of families have previously been suggested as possible allies of the Annonaceae in various systems of classification, the stem and wood anatomy of 31 genera in the following six families were also re-examined: Degeneriaceae, Himantandraceae, Magnoliaceae, Myristicaceae, Eupomatiaceae, and Canellaceae. Although there exists a wider variability of salient morphological features in the Myristicaceae than the Annonaceae, sufficient points of resemblance were found to allow the tentative conclusion that some relationship is possible between these two families. Furthermore, both the Magnoliaceae and Myristicaceae include genera which possess both scalariform and simple perforations. Thus, on the basis of this and other similar characteristics, it is postulated that these two families may serve as transitional groups between



the more primitive Degeneriaceae on one hand, and the more highly specialized Himantandraceae and Annonaceae on the other.

Both the Eupomatiaceae and Canellaceae exhibit extremely primitive anatomical features, unlike those seen in any other family included in the present study. Certainly no relationship is shown to the comparatively specialized Annonaceae; in addition, not the slightest bit of anatomical evidence was discovered which would favor Hutchinson's inclusion of the Eupomatiaceae with the Annonaceae in his order Annonales. It is therefore recommended that the Annonaceae be transferred to the Magnoliales.

Finally, it is emphasized that the natural positions of the Myristicaceae, Annonaceae, Canellaceae, and Eupomatiaceae cannot be reliably established on evidence from wood and stem anatomy alone. Detailed studies of the various phases of floral morphology, when correlated with that from anatomy, will be necessary to establish ultimately the true relationships of these woody ranalian families.

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### THE GENUS *TAMARIX* IN ISRAEL

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#### INTRODUCTION

The genus *Tamarix* is one of the most intricate genera among the flowering plants. It is one of those in which certain species show a wide range of distribution, and others are "point endemics." Like *Salix*, *Rubus* and others, it displays a high degree of variability and probably also inter-specific hybridization with marked introgression of genes. In the greater European herbaria the identification of a great many species is unreliable, and in many floras there is much divergence as to species delimitation.

A short historical sketch of the investigation of this genus may be in place here. To the fourteen species first enumerated by Desvaux (1825), De Candolle (1828) added four new species, and Ehrenberg (1827) eight new varieties which were later raised to species by Bunge (1852). In his *Tentamen*, Bunge added twenty-one new species to the thirty species then known. Niedenzu (1895) first raised the number to sixty-five species and later (1925) to eighty-seven. Arendt (1926) reduced the number to seventy. Since the start of the present century a considerable number of binomials have been published by Battandier (1907), Maire

(1931, 1935, 1936, 1938), Vierhapper (1907), Gorschikova (1949) and others, and the number of "valid" binomials recorded in the *Index Kewensis* up to 1940 (1895-1947) grew to one hundred and eighteen.

Of the three revisions at hand (Bunge, 1852; Niedenzu, 1895; and Arendt, 1926), Bunge's *Tentamen* still remains the only source of reference in this genus. But the weakness of Bunge's revision lies in the inadequacy of material at his disposal. Despite the comprehensive and very accurate descriptions, some of his species can hardly be kept as such. This is especially true of a whole group of species allied to *T. gallica* on one hand and to *T. nilotica* on the other. The short revision of Niedenzu did not add much to the knowledge of this genus. Not only did he accept all the species included in the *Tentamen*, but raised some of the varieties to species. The diagnostic characters applied in his keys are mostly those used by Bunge, and the changes introduced in the subdivision of the genus do not aid in the delimitation of the species. The paper of Arendt is even less useful to the taxonomist of this genus. This is true not only because of its superficiality in treating the material but also because it is inaccurate in the characterization of many species. Furthermore, the author discards the most pertinent diagnostic characteristics used by his predecessors, and replaces them by characteristics which are mostly inconstant and variable within the species.

As a result of the above, our present knowledge of the genus is very poor, and a modern revision is badly needed. This is particularly urgent because many species of *Tamarix* might readily be utilized in afforestation of marginal and extreme desert regions.

The present paper deals only with the *Tamarix* species of Israel. Although a rather limited area, it is, together with Egypt, Arabia and Iran, one of the main speciation centers of the genus. The study of the local forms and those of the neighboring countries, enabled the author to re-evaluate the diagnostic significance of characteristics within the genus.



*Vernales and Aestivales*.—Contrary to Arendt (1926), the distinction between the *Vernales* and *Aestivales* groups, as emphasized by Bunge (1852), is one of the most reliable characteristics. The presence of a third group of species, the *Vernali-Aestivales*, discerned by Maire (1935), does not invalidate this characteristic. Among the species dealt with here, *T. Meyeri* and *T. deserti* are examples of the *Vernales*, *T. gallica* of the *Aestivales* and *T. jordanis* of the *Vernali-Aestivales* groups.

*The configuration of the staminal disc*.—Arendt (1926), who devoted a considerable part of his paper to the morphology and ontogeny of the disc, came to the conclusion that this characteristic has no diagnostic value. The author examined hundreds of flowers of various species in regard to this characteristic and found it highly constant in certain species, less fixed in others, though not sufficient to separate species from one another. We seldom found any marked change in the disc form after flowering, or variability in the same specimen, as claimed by Arendt. Fig. 1 represents a selection of disc types as observed in the species examined. The following disc types can readily be distinguished after Niedenzu (1895): (a) *Epilophic* insertion; where the mostly broadened base of the filaments gradually merges into the lobes of the disc (fig. 1a, b, c, h). (b) *Confluent epilophic* insertion; where each filament is inserted between two confluent lobes (fig. 1d). (c) The *Epidiscine* insertion represents those cases where there are no apparent discs or disc lobes, and the bases of the filaments meet almost at the center of the torus (fig. 1e, f). (d) *Mesodiscine* insertion is the commonest case where the filaments arise from the sinuses of the 5-lobed, or from the deeper sinuses of the 10-lobed, disc (fig. 1g, h, i, j, k). The distinction between a 10-lobed or a 10-crenate disc, or the distinction between crenate, emarginate or entire lobes, is often very obscure, and should not be used as a differential characteristic.

*Anisandry*.—As already mentioned by Arendt, there are species in which the number of the floral parts is constant, and species in which it is not. In the group with fixed num-

bers of floral parts, one may occasionally find in a few florets of the same raceme, a slight deviation in the basic number. This rarely happens in pentamerous species. In the tetramerous group, a trend toward pentamery is less rare. In the pleiandrous groups the number of stamens varies in the same species and sometimes in the same raceme from 6 to 14, e. g., in *T. passerinoides*, *T. amplexicaulis*, etc. Here it is not the definite number of stamens, but pleiandry as such, which is a most reliable characteristic. In any case, iso- versus anisomery, isandry versus anisandry, pentandry versus tetrandry and pleiandry are diagnostically highly valuable characters.

*Leaf characters*.—Leaf characters are constant both as to size and shape when referred to a definite age of branchlets. Difficulties arise in estimating the degree of clasping. Although one can readily distinguish between vaginant and amplexicaul leaves, it is not always easy to decide between semi-amplexicaul and sessile leaves, particularly, because this characteristic changes with the age of the branch.

*Anther tip*.—Apex of anther is fairly constant and diagnostic.

*Style length*.—Length of styles in relation to length of ovary is a constant characteristic only when referred to a particular stage of flowering, and is best applicable when referred to young flowers at early anthesis. Shape of the styles is another very constant character.

*Persistence of corolla*.—Although in some species (e. g., *T. Pallasii*) this character is fixed, in other species (e. g., *T. chinensis*, *T. ramosissima*, *T. jordanis* var. *brachystachys*) it is less fixed.

*Bract form*.—Form of the bracts is an essential characteristic only when referred to fertile, intact bracts. The size of bracts is also important in some species, but generally small variations may occur in this regard even within otherwise well delimited taxa.

*Petal curvature*.—Direction of the petals proved very constant; deflexed corollas as compared with erect ones is highly diagnostic.



For the subspecific and varietal levels there are a series of other useful characteristics, such as color of petals and anthers, bud form, color of cortex, form and size of fruit, compactness of raceme, etc.

In connection with the present study the author examined about 400 herbarium specimens and many specimens in their natural habitats. A good deal of work has been devoted to determining the relations between *T. gallica* and *T. nilotica*, *T. mannifera* and *T. arborea*, as well as the more recently described *T. maris-mortui* and *T. pseudopallasii*. Some of these species have been reduced to varietal status. Also, four new species, and many varieties, based on clear-cut characteristics, have been described from the Jordan Valley, the southern shores of the Dead Sea and the Arava Valley which is one of the centers of *Tamarix* accumulation in the Near East.

The present investigation considerably alters the list of *Tamarix* species hitherto known from the area under review. Instead of the previously recorded five species, sixteen are given in this paper. But the most conspicuous change in the *Tamarix* list of Israel is the re-inclusion of a series of "species" within *T. gallica* as originally presented by Ehrenberg (1829).

The following is an artificial key to the identification of the species growing in Israel.

KEY TO IDENTIFICATION OF THE ISRAEL *Tamarix* SPECIES

- 1a. Stamens generally 6-15. ....2.
- 1b. Stamens generally 4-5. ....5.
- 2a. All, or at least the vernal, racemes arising from older branches (of the previous year); stamens generally 6-8. *T. syriaca* Boiss.
- 2b. All racemes arising from young branches (of the current year); stamens 10-15, rarely 6-8. ....3.
- 3a. Racemes very short (1-3 cm.) and dense; petals 1-1.5 mm. long, erect, white or pink; capsule 4-5 mm. long; leaves entirely or almost entirely clasping. ....*T. amplexicaulis* Ehrb.
- 3b. Racemes longer; petals 2-7 mm. long. ....4.
- 4a. Leaves less than half clasping, blade much longer than sheath; racemes long (up to 8 cm.), loosely flowered; flowers with

- deflexed pink petals; bracts lanceolate, 2-3 mm. long and less than 1 mm. broad at base. ....*T. arvensis* Zoh.
- 4b. Leaves more than half clasping; racemes more dense than above; petals mostly erect, pinkish, becoming pale at anthesis; bracts shorter and considerably broader at base. ....*T. passerinoides* Del.
  - 5a. Stamens 5. ....6.
  - 5b. Stamens 4. ....13.
  - 6a. Styles generally 4; racemes up to 10 cm. long. *T. tetragyna* Ehrb.
  - 6b. Styles 3. ....7.
  - 7a. Leaves sheathed, without blades. ....*T. aphylla* (L.) Karst.
  - 7b. Leaves not sheathed, with conspicuous blades, erect or spreading. ....8.
  - 8a. Corolla persistent, petals pink or purple, in long, slender racemes; anthers mucicous. Mainly cultivated ornamentals. ....*T. chinensis* Lour.
  - 8b. Corolla deciduous, petals white or pink, in latter case racemes short and corolla deflexed. ....9.
  - 9a. All or at least the vernal racemes arising from older branches (of the previous year) before full foliation of the plant; vernal panicles mostly simple, unbranched; racemes lateral. ....10.
  - 9b. All racemes arising from younger shoots (of the current year); panicles mostly much branched; length of racemes mostly 2-6 cm. ....*T. gallica* L. ssp. *nilotica* (Ehrb.) Maire
  - 10a. Styles longer than half the length of ovary; bracts linear, very long and deflexed; petals deflexed. ....*T. gemessarensis* Zoh.
  - 10b. Styles shorter than above; bracts not deflexed. ....11.
  - 11a. Anthers conspicuously apiculate; racemes rather slender and loosely flowered. ....*T. jordanis* Boiss.
  - 11b. Anthers mucicous. ....12.
  - 12a. Petals white, erect; disc 10-lobed. ....*T. africana* Poir.
  - 12b. Petals pink, deflexed; disc 5-lobed. ....*T. negevensis* Zoh.
  - 13a. Styles of all or most of the flowers 4. ....14.
  - 13b. Styles of all or most of the flowers 3. ....15.
  - 14a. Styles spatulate, much shorter than 1 mm.; racemes 4-8 mm. broad. ....*T. deserti* Boiss.
  - 14b. Styles clavate, about 1 mm. long, racemes broader than above. ....*T. Meyeri* Boiss.
  - 15a. Sepals ovate, almost entirely membranaceous; anthers orbicular with a slight mucro at upper sinus. ....*T. sodomensis* Zoh.
  - 15b. Sepals oblong-lanceolate with a broad green midnerve; anthers ovate, tapering to a long mucro. ....*T. parviflora* DC.



THE *Tamarix* SPECIES OF ISRAEL

*Tamarix tetragyna* Ehrb. in *Linnaea* 2: 247, 257, 258. 1829; Niedenzu, *Diss. gen. Tamarice*. Ind. lect. in lyceo reg. Hosiano Brunbergensi per hiem. 1895-1896: 5. 1895. non *T. tetragyna* in Bunge. *Tentamen* 22. 1852 et Boiss. *Fl. orient.* 1: 768. 1867. fig. nostra 2.

NEAR NEGEV: Wadi Murra (Ein Mur) saline depression, 26 March 1952, M. Zohary, Orshan, De Angeles, *T.* 5006.<sup>1</sup>

This species is very rare in Israel and probably also in Egypt wherefrom it was first described by Ehrenberg (Lake Manzaleh). It closely resembles *T. Meyeri* Boiss. and *T. deserti* Boiss. because of its long and thick racemes and tetragynous flowers, but differs in its predominantly pentamerous calyx and corolla, as well as in its trend towards pleiandry. It has long been confused by several authors of Near Eastern floras with *T. Meyeri*, due to the short description and the very poor authentic material. But it is evident from the description, that Ehrenberg classed this species under the *Decadenia* and the pentamerous group. Boissier (*Diag. plant. orient. sér. 1. 10: 9. 1849*) was probably acquainted with this species when he indicated: "*T. tetragyna* cui cl. Meyer hanc retulera est planta aegyptiaca 5-sepala, 5-petala, decadenia." Nevertheless, in his *Flora orientalis* 1: 768, Boissier also included within this binomial *T. Meyeri* and *T. deserti*. Niedenzu (1895) was the first to rectify this error by classing *T. tetragyna* under his *Anisandrae* group (5 sepals, 5 petals and 5-7 stamens), after examination of the authentic specimen from Lake Manzaleh. In the following I wish to add some details to the description of this species.

Shrub 3-5 m. high, cortex grayish-brown. Leaves of younger shoots lanceolate-linear, sessile, 5-6 mm. long. Racemes arising from older branches, pedunculate, 12-16 cm. long, 8 mm. broad; peduncles loosely beset with deflexed,

<sup>1</sup>All the specimens recorded in this paper are deposited in the Herbarium of The Hebrew University, Jerusalem, and the numbers cited refer to their numbers in that herbarium, the letter *T.* meaning *Tamaricaceae*.

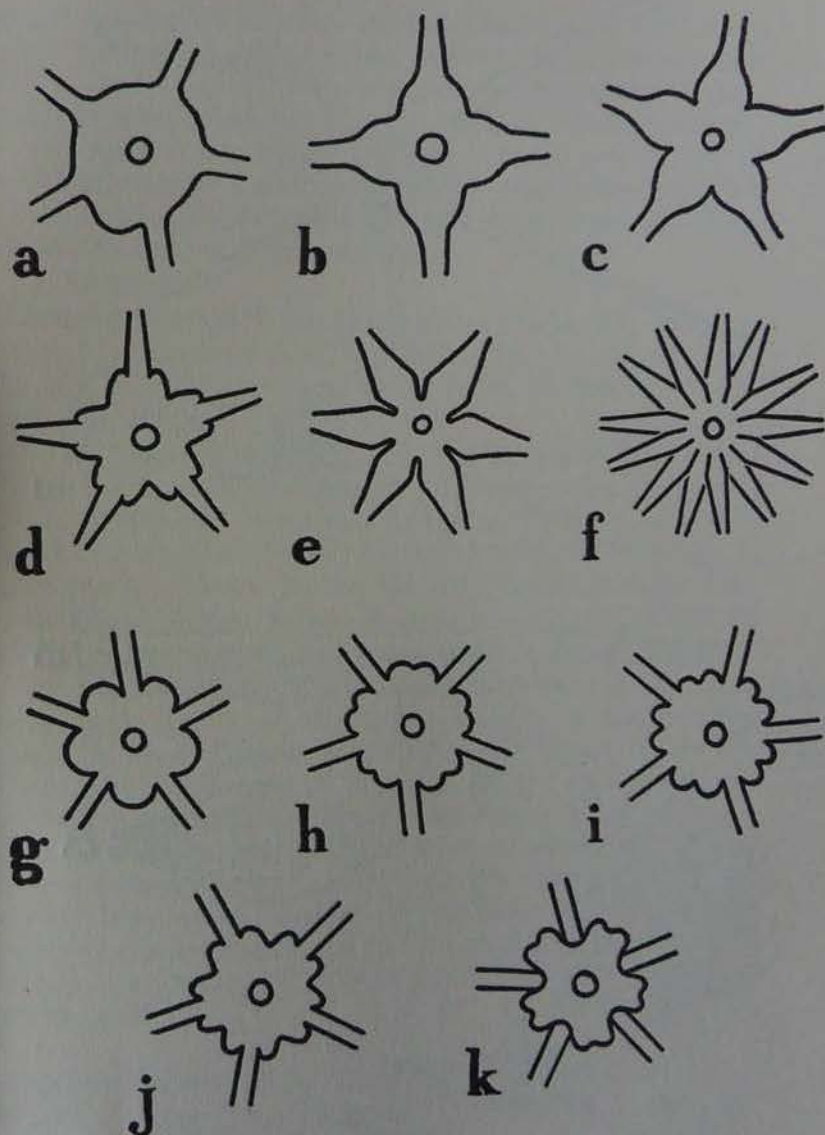


Fig. 1. Configuration of the staminal disc in various species of *Tamarix*.—a, g, b, k. *T. gallica*, b. *T. Meyeri*, c. *T. tetragyna*, d, i. *T. jordanis*, e. *T. passerinoides*, f. *T. arvensis*, j. *T. gennessarensis*.



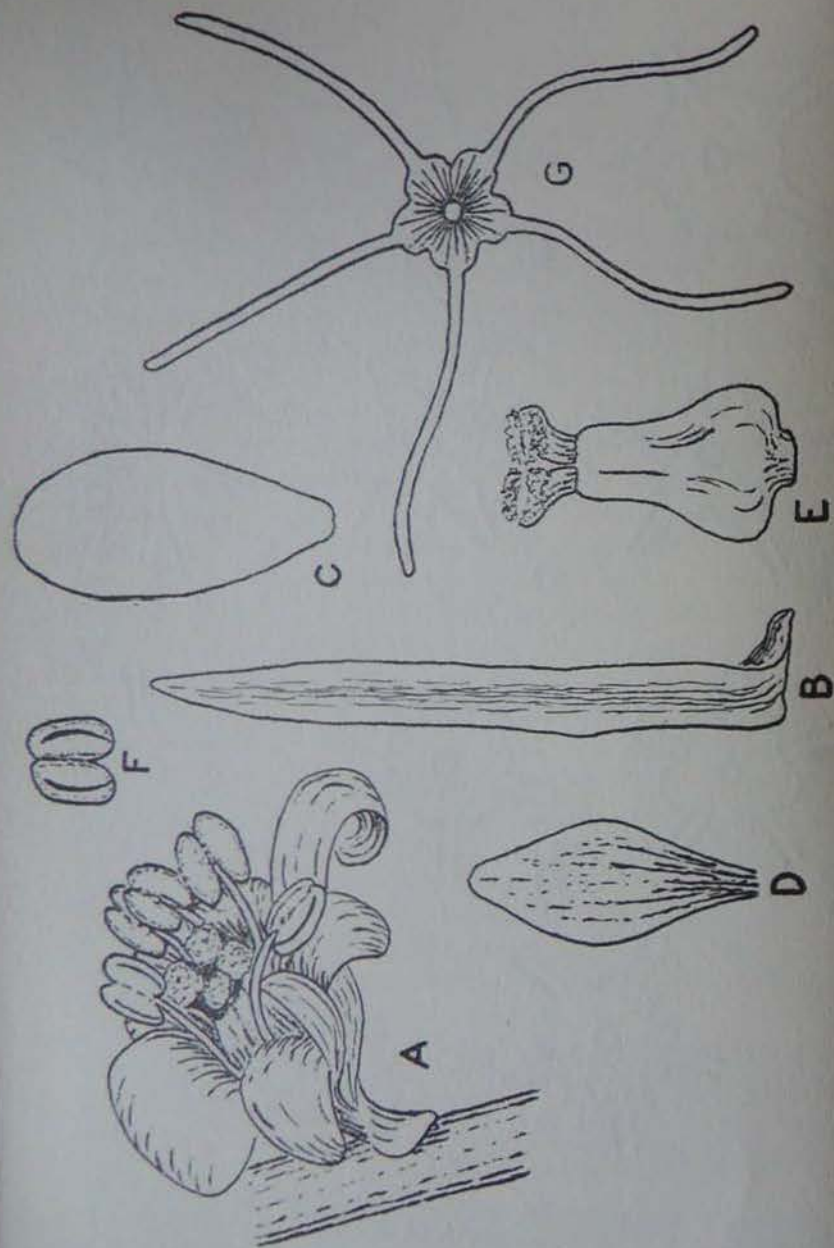


Fig. 2. *T. tetragyna*.—a, flower, b, bract, c, sepal, d, petal, e, pistil, f, anther, g, staminal disc.  $\times 10$ .

sterile bracts; floral bracts linear, deflexed, 7–8 mm. long, 0.8–1 mm. broad, rather acute, pedicels much shorter than calyx; sepals (4) 5 (6), oblong-rhomboid, about 4 mm. long, 1.5 mm. broad; petals (4) 5 (6), pink, obovate-oblong, 4 mm. long, 2 mm. broad, deflexed; stamens 5–7, as long as or slightly longer than corolla, anther exapiculate, insertion of filaments epilophic; pistil 3–4 mm. long; styles spatulate, about one third as long as the ovary.

**Tamarix Meyeri** Boiss. Diag. plant. orient. sér. 1. 10: 9. 1849. *T. tetragyna* C.A.M. Ind. cauc. 165. 1831 in part (non Ehrb.). *T. tetragyna* var. *Meyeri* Boiss. Fl. orient. 1: 768. 1867. fig. nostra 3.

ACRE PLAIN: Marshes of Na'aman River, 6 April 1949, *Feinbrun*, *T. 1017*; same locality, 4 March 1926, *Naftolsky*, *T. 1006*. SHARON: Ma'agan Michael, 10 May 1953, *Grizi*, *T. 1023*. NORTHERN NEGEV: 13 March 1954, *De Angeles*, *T. 1027* (Cult.). UPPER JORDAN VALLEY: Banks of Lake Kinnereth near Jordan River, 18 March 1931, *Naftolsky*, *T. 1016*. Specimens were also observed from Egypt and Iraq.

*T. Meyeri* has originally been described from the environs of Talysch (leg. *C. A. Meyer*). According to the description, the Mediterranean material differs slightly from the Caspian. It differs from *T. deserti* Boiss. by the club-shaped styles, the apiculate anthers, the shorter and thicker racemes, and the narrower bracts. It flowers in early spring, and is very striking because of its large pink-flowered racemes, arising from older branches. It has been introduced into cultivation as an ornamental and for afforestation in extreme salines. It is a highly salt resistant species but requires abundant moisture.

**Tamarix deserti** Boiss. Diag. plant. orient. sér. 1. 10: 9. 1849. *T. Meyeri* Boiss. Fl. orient. 1: 768. 1867. in part. fig. nostra 4.

ARAVA VALLEY: Environs of Sodom salines, 27 April 1953, *M. Zohary*, *T. 1041*; same locality, 18 March 1950, *Tadmor*, *T. 1040*.



*Tamarix deserti* Boiss. var. *microcarpa* Zoh. var. nov.—  
Capsulae (2) 3-4 mm. longae (nec ut in typo 5-7 mm.).  
Flores minores; antherae breviter apiculatae.

ARAVA VALLEY: Environs of Sodom salines, 23 March 1954, *M. Zohary*, *T. 1050*; Ein Yahav salines, 1 May 1954, *Weisel & Litvak*, *T. 1059*. NORTHERN NEGEV: Wadi Murra (Ein Mur), 8 April 1955, *Weisel*, *T. 1060*; Tel Yeruham, depression, 8 April 1953, *Weisel*, *T. 1063*.

*T. deserti* is a leading species of the *Tamaricion* alliance in the salines of the southern shore of the Dead Sea. I have not seen the authentic specimen of *T. deserti*, but our specimens agree well with Boissier's description of this species. The reason why Boissier synonymized this binomial with *T. tetragyna* in his *Flora orientalis* (1867) is no doubt its external resemblance to the latter. *T. deserti* is very close to, and perhaps identical with, *T. Boveana*, described three years later by Bunge (1852) from Algeria. The variety *microcarpa* recorded above clearly intergrades with the type. There are

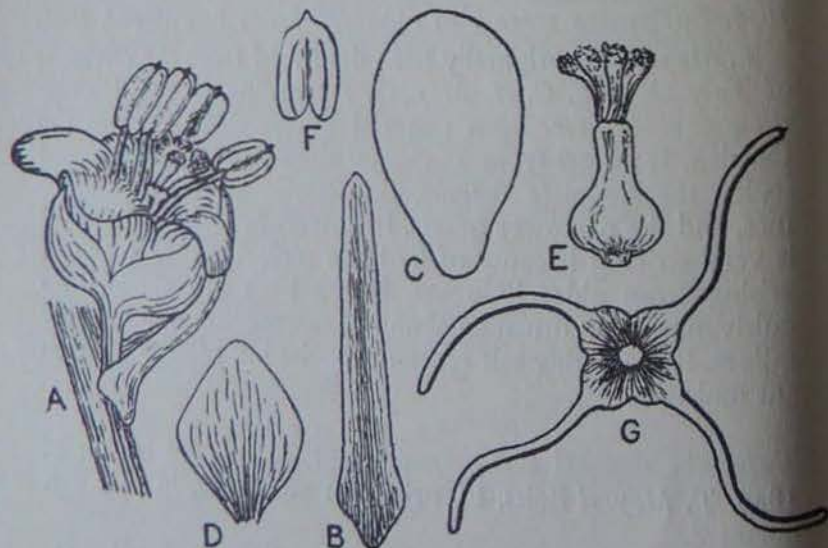


Fig. 3. *T. Meyerii*.—a. flower, b. bract, c. petal, d. sepal, e. pistil, f. anther, g. staminal disc.  $\times 10$ .

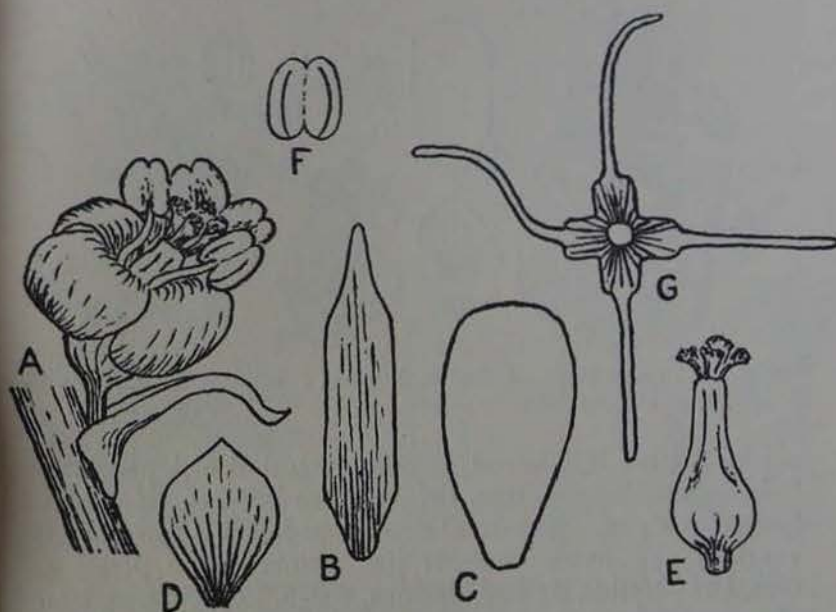


Fig. 4. *T. deserti*.—a. flower, b. bract, c. petal, d. sepal, e. pistil, f. anther, g. staminal disc.  $\times 10$ .

probably also hybrid forms between *T. deserti* and *T. tetragyna* in localities where the two species come together (e.g., Wadi Murra).

*Tamarix parviflora* DC. in Prodr. 3: 97. 1828.

UPPER JORDAN VALLEY: Hule Plain, banks of Jordan River near Neoth Mordekhai, 18 April 1955, *Lamed*, *T. 1078*. SHARON: Giv'ath Hashlosa, 24 March 1952, *Fahn*, *T. 1079* (Cult.).

*Tamarix sodomensis* Zoh. sp. nov. (sect. *Vernales*). fig. nostra 5.—Affinis *T. parviflorae* sed ab ea sepalis ovatis margine latissime membranaceis, petalis deflexis, filamentis basi non dilatatis, antheris truncatis brevissime apiculatis, differt.

Cortex griseo-fuscus. Folia parva, ovato-rhomboidea, acuta, basi breviter decurrentia, apice incurva, semiamplexi-



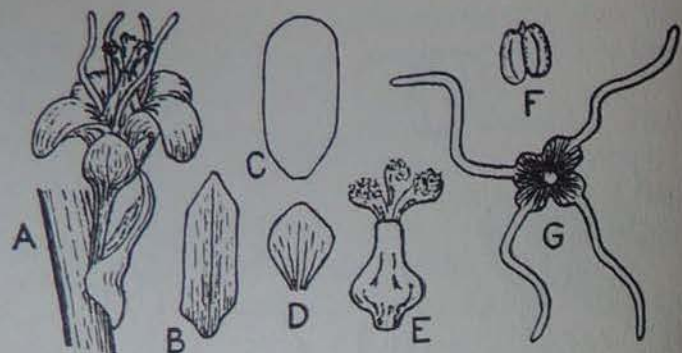


Fig. 5. *T. sodomensis*.—a. flower, b. bract, c. petal, d. sepal, e. pistil, f. anther, g. staminal disc.  $\times 10$ .

caulia. Racemi densiusculi, ex ramis annotinis orti, pedunculati, 2–4 cm. longi, 5 mm. lati; bracteae lineares, 1.5–2 mm. longae, 0.8 mm. latae, acutiusculae; pedicelli 1 mm. longi; sepala 4 (5), ovata, margine late membranacea; petala 4, alba, late elliptica, deflexa, decidua, 2 mm. longa, 1 mm. lata; discus 4-lobatus; filamenta 2.5 mm. longa, antherae truncatae, breviter apiculatae; styli 3, rarissime 4, clavati, dimidio ovario aequales; capsula immatura longe pyramidata, 4–5 mm. longa. Floret Martio.

This species is very near *T. parviflora* DC., but differs from the latter because of its deciduous, deflexed petals, its 4-lobed disc, filaments not dilated at base, and truncate, short-apiculate anthers. It differs from *T. Kotschyi* Bunge by the non-clasping leaves, by the filaments which are narrow at the base, by the apiculate anthers and club-shaped styles.

ARAVA VALLEY: Wadi Um Tarfa, near Sodom, 18 March 1950, *Tadmor*, T. 602 (TYPE).

*Tamarix gennessarensis* Zoh. sp. nov. (sect. *Vernales*).—fig. nostra 6.—Affinis *T. jordani* sed ad ea petalis majoribus, deflexis, stylis conspicue longioribus, racemis majoribus, bracteis longioribus, deflexis, disco majore, foliorum forma distinctissime differt.

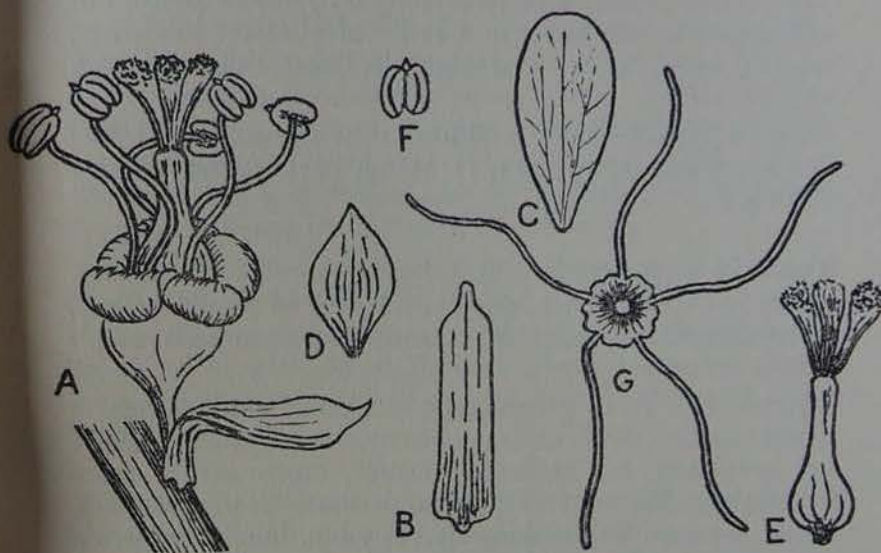


Fig. 6. *T. gennessarensis*.—a. flower, b. bract, c. petal, d. sepal, e. pistil, f. anther, g. staminal disc.  $\times 10$ .

Arbor viridis, glabra. Ramuli elongati, laxi, patentes vel divaricati. Folia sessilia, haud amplexicaulia, etiam ramulorum juniorum distantia, basi decurrentia, lanceolato-oblonga, margine et apice late scarioso-cartilaginea, acuta vel acuminata, apice incurva, 3–5 mm. longa. Racemi laterales, ramis annotinis orti, laxiflori, 6–8 cm. longi, ca. 5 mm. lati, parte inferiore cum bracteis sterilibus ovato-oblongis, margine membranaceis, vestiti; flosculi auximie pedicellati; bracteae lineares, 2.3 mm. longae, 0.6 mm. latae, deflexae, pedicello plus duplo longiores; sepala 5, rhomboidea, 1.5 mm. longa, 0.8 mm. maxime lata, acuta; petala 5, alba, obovato-oblonga, basi angustata, 2.5 mm. longa, 1 mm. lata, primum erecta, demum deflexa; stamina 5, filamenta usque ad basim angusta, longissime exserta, antherae cordatae, apiculatae; discus majusculus, 10-lobus, filamenta ex sinibus profundioribus orta; ovarium anguste lageniforme, sine stylis 2 mm. longum; styli 3, longe clavati, dimidio ovario longiores. Capsula ignota. Floret Martio.



A very handsome tree resembling *T. jordanis* Boiss., but differing from the latter in a series of characteristics, e.g., the long styles, the deflexed petals, the linear, deflexed bracts, etc.

UPPER JORDAN VALLEY: Kinroth district, bank of the Jordan River near Beith Zera, 15 March 1954, *Rimon*, T. 606 (TYPE).

*Tamarix negevensis* Zoh. sp. nov. (sect. *Vernales*). fig. nostra 7.—Affinis *T. jordanis* Boiss. sed ab ea petalis deflexis, roseis, insertione epilophica filamentorum, antheris exapiculatis differt.

Arbor (?). Rami griseo-fusci, elongati. Folia pro genere mediocria, basi longiuscule decurrentia, ovato-oblonga, acuta vel acuminata, vix semiamplexicaulia, erecto-patula, apice cartilaginea. Racemi erecti, ex ramis annotinis orti, 6–7 cm. longi, 4–5 mm. lati, pedunculis 1–1.5 cm. longis, laxiuscule squamatis; bracteae oblongo-lanceolatae, 1.5 mm. longae;

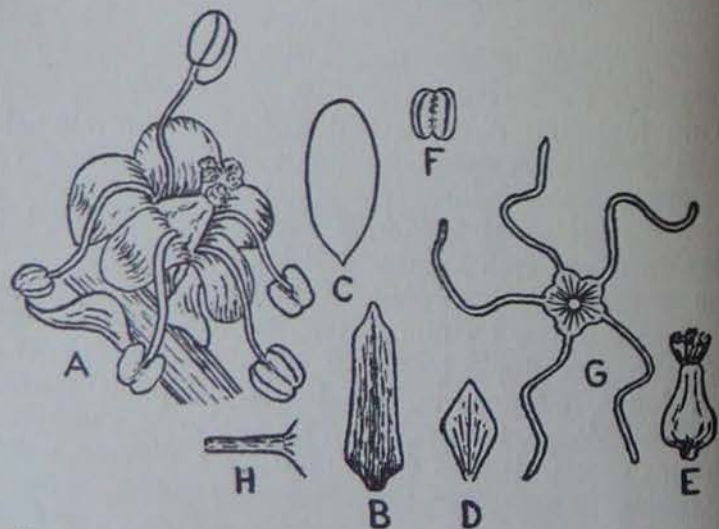


Fig. 7. *T. negevensis*.—a. flower, b. bract, c. petal, d. sepal, e. pistil, f. anther, g. staminal disc.  $\times 10$ .

alabastra obovoidea; flores laxiusculi, pedicellis 1 mm. longis; sepala (4) 5, ovato-rhomboida, margine late membranacea, 1.3 mm. longa, 0.7 mm. lata; petala (4) 5 (6), rosea, elliptica, 2 mm. longa, 1 mm. lata, primum erecta, demum deflexa; stamina (4) 5, filamenta 2.5 mm. longa, antherae exapiculatae; discus 5-lobus, lobi filamenta basi haud dilatata gerentes; styli 3, spathulato-clavati, dimidio ovario breviores. Capsulae juniores pyramidatae. Floret Martio.

ARAVA VALLEY: Ein Hotzev, near spring, 24 March 1950, *D. Zohary*, T. 601 (TYPE).

Greatly resembles *T. jordanis* Boiss., but differs from the latter by its deflexed petals, its epilophic insertion of the filaments, its mucous anthers, etc. Described from a single specimen.

*Tamarix africana* Poir. var. *philistaea* Zoh. var. nov.—Arbuscula. Rami griseo-fusci, elongati. Folia supra basim latiora, semiamplexicaulia, deltoidea, acuminata, apice incurva, margine membranacea. Racemi densiflori, ex ramis annotinis orti, 2–5 cm. longi, 6–7 mm. lati; bracteae supra basim dilatatae, subamplexicaules, membranaceae, ovato-triangularis, acutae, 1.5 mm. longae, 1 mm. latae; alabastra obovata; sepala 5, ovata, obtusa, late membranacea, 1.3 mm. longa, 1 mm. lata; petala 5, alba, oblongo-spathulata, erecta, 2.5 mm. longa, 1.3 mm. maxime lata; stamina 5, filamenta vix exserta, antherae exapiculatae; discus 5-lobus, lobis profunde crenatis; filamenta basi vix dilatata, inter crenis orta; styli 3, clavati, dimidio ovario breviores. Capsula ignota.

COASTAL SHEFELA: Ruins of Ascalon, sandy soil, 15 March 1954, *Jaffe*, T. 1064 (TYPE).

The above detailed description is given here in order to distinguish this species from *T. gallica* with which it has sometimes been confused. Apart from some floral characteristics (configuration of disc, exapiculate anthers, etc.) it is well distinguished by its vernal racemes arising from older branches. I am not clear as to its relation with *T. gallica* var. *hispanica* Bunge; our plant stands near to *T. africana* var.



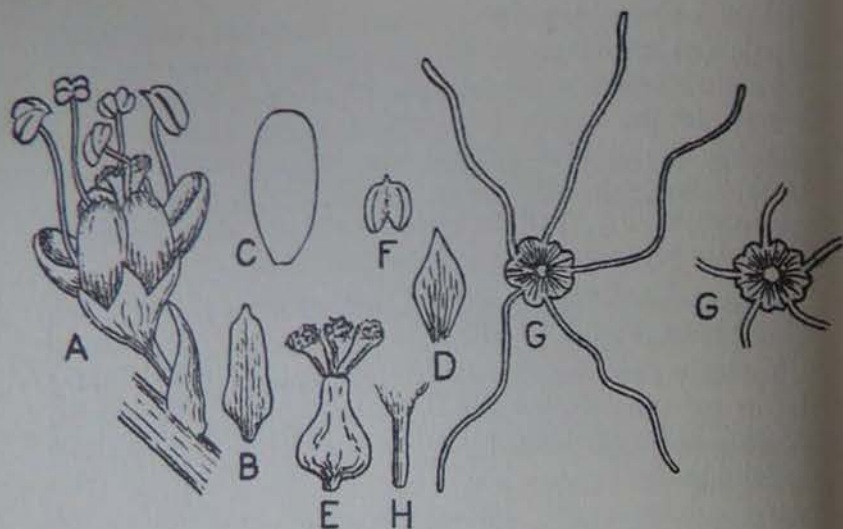


Fig. 8. *T. jordanis* var. *typica*.—a. flower, b. bract, c. petal, d. sepal, e. pistil, f. anther, g. staminal disc.  $\times 10$ .

*brevistylis* Trab. in Maire, *Contrib. fl. Afrique du Nord*, fasc. 17, no. 1784, Bull. Hist. Nat. Afr. Nord 22: 34. 1931 but differs from the latter in its leaves, bracts, shape of sepals and petals, etc.

*Tamarix jordanis* Boiss. Fl. orient. 1: 771. 1867. fig. nostra 8.

This species is nearest to *T. florida*. It is very abundant in the Jordan Valley of Israel and also in the Arava Valley and the Negev. Although described from a single specimen, it is well delimited. Boissier's observation that this species forms vernal and aestival racemes has been confirmed by the present author, so that its inclusion with the section *Vernalo-Aestivales* Maire, as done by Gutman (1947), is fully justified. The two kinds of racemes may be of the same form or of different forms as shown below.

*T. jordanis* is rather variable in certain characteristics and has accordingly been subdivided into the varieties given below.

*Tamarix jordanis* Boiss. var. *typica* Zoh. var. nov. fig. nostra 8.—Plants with biseasonal racemes, the vernal arising laterally from last year's branches, mostly 5–10 cm. long, 3–4 mm. broad, very loosely flowered. The aestival racemes almost of the same form but often somewhat shorter, arising from the current year's shoots; flowers pedicellate, consistently pentamerous and trigynous; anthers prominently mucronate; disc with 10 more or less equal lobes or with 5 clearly notched lobes; filaments inserted in the deeper sinuses; leaves varying from oblong-lanceolate to lanceolate-subulate, often with scarios margins and tip, frequently obscurely or not at all punctate.

Selected specimens: UPPER JORDAN VALLEY: Hule Plain, Neoth Mordekhai, 11 March 1955, *Weisel*, T. 1098; banks of the Jordan River near Kinnereth, 30 March 1955, *R. Bernstein*, T. 1108. LOWER JORDAN VALLEY: Ghuweira, banks of Jordan River near northern shore of Dead Sea, 2 April 1925, *Naftolsky*, T. 1090; Ein Gedi, Wadi Sidr, 4 May 1951, *De Angeles*, T. 1130. NORTHERN NEGEV: Tel Yeruham, depression, 1 May 1954, *Litvak & Weisel*, T. 1265. TYPE in Herbarium Boissier, Geneva.

*Tamarix jordanis* Boiss. var. *brachystachys* Zoh. var. nov.—Racemi vernaes abbreviati, 2–4 cm. longi, 3–5 mm. lati; flosculi plerumque densiores quam in typo; petala paulo majora, plus persistentia; racemi aestivales breves vel longi, cetera ut in typo.

UPPER JORDAN VALLEY: Neoth Mordekhai, 11 March 1953, *Weisel*, T. 1238 (TYPE); Wadi Hindaj, 12 April 1954, *Jaffe*, T. 1229; Lake Kinnereth near Degania, 12 May 1954, *M. Zohary*, T. 1223; same locality, 5 May 1953, *Ziv*, without number. LOWER JORDAN VALLEY: Wadi Areija near Ein Gedi, 8 April 1951, *Tadmor*, T. 1198; banks of Jordan River near Allenby Bridge, 6 April 1941, *Gutmann*, T. 1201.

This variety is well distinguished from the typical form by its shorter, broader and denser racemes; its somewhat larger florets and generally more persistent petals. Some of



the specimens show biseasonal flowering, others only vernal. This variety occurs chiefly in the Hule Plain, but it is also met with elsewhere together with the typical form, and transitions between them are not rare.

*Tamarix jordanis* Boiss. var. *negevensis* Zoh. var. nov.—A typo differt flosculis pleurumque majusculis, rhachidibus rigidioribus, foliis brevioribus, crassiusculis, semiamplexicaulibus, bracteis brevioribus, filamentorum insertione epilophica, racemis tantum vernalibus.

LOWER JORDAN VALLEY: Arnon River, 4 April 1925, Naftolsky, *T.* 1295. NORTHERN NEGEV: Wadi Murra (Ein Mur), 8 April 1955, Weisel, *T.* 1269 (TYPE); between Beersheva and Revivim, sand dunes, 27 April 1953, M. Zohary, *T.* 1311. ARAVA VALLEY: Wadi Fukra, 7 April 1949, Tadmor, *T.* 1307.

This is a rather heterogeneous variety comprising more xerophytic forms and differing from the typical form mainly in its shorter and thicker leaves. In spite of the epilophic insertion of the filaments, it must be classed under *T. jordanis*.

*Tamarix jordanis* var. *sodomensis* Zoh. var. nov.—A typo differt insertione epilophica filamentorum, bracteis linearibus, 2 mm. et ultra longis, racemis rigidioribus plerumque erectis.

LOWER JORDAN VALLEY: Southern shore of Dead Sea, Wadi Um Tarfa near Sodom, 18 March 1950, Tadmor *T.* 1321 (TYPE).

*Tamarix syriaca* (Stev.) Boiss. *Fl. orient.* 1: 767. 1867. *T. Hampeana* Boiss. var. *syriaca* Stev. in Bunge. *Tentamen* 21. 1852.

UPPER JORDAN VALLEY: Hule Plain, Kefar Szold, banks of Banias, 8 April 1954, Jaffe, *T.* 766.

Our specimens differ somewhat from the description by Bunge (1852) and agree more with that of Boissier (1867)

who did not see the specimens of La Billardière. They show closer relation to *T. jordanis* than to *T. Hampeana*, and differ from the former by their larger flowers and pleiandry (stamens 6–8). In the same locality we also collected *T. jordanis* var. *brachystachys* as well as a specimen intergrading between *T. jordanis* and *T. syriaca*. I doubt whether this taxon can be kept as a separate binomial but I would by no means attach it to *T. Hampeana* as Bunge did. The scant material at hand does not allow any further conclusion on this matter.

*Tamarix gallica* L. *Sp. pl.* 1: 386. 1753.

This species is to be considered in its widest sense, so as also to include a series of southern and eastern Mediterranean forms. A part of this series has primarily been described as, or later raised, to species by Bunge (1852) and others. An intensive study of these "species" with the aid of hundreds of living and dried specimens from the eastern Mediterranean littoral, southern Israel and the borders of the Red Sea and Egypt, has led the author to the conclusion that there is no justification for retaining the whole swarm of binomials in the "Formenkreis" of *T. gallica* as autonomous species. In fact, many of them are not clearly distinguishable from one another or from *T. gallica*. Even

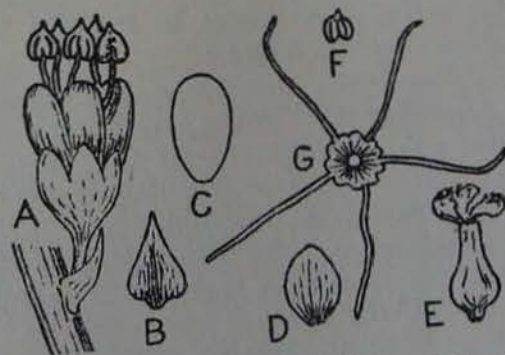


Fig. 9. *T. gallica* var. *maris-mortui*.—a. flower, b. bract, c. petal, d. sepal, e. pistil, f. anther, g. staminal disc.  $\times 10$ .



the character of the staminal disc, which in other groups of species has proved specifically diagnostic, varies in this group from typical epilophic, confluent epilophic to mesodiscic with 5 or 10 lobes. It was this characteristic on which Bunge and other authors based many of their binomials within the *Aestivales* group. In other characteristics too, such as size of leaves, bracts, pedicels, size of inflorescences, etc., I found no adequate support for separating these species from *T. gallica*. Boissier (1867) expressed his doubts as to the specific value of *T. mannifera*, *T. nilotica* and *T. arborea*, first described by Ehrenberg (1827) as varieties of *T. gallica*. Maire (1941) also reduced a series of other "species" of this group to subspecies and varieties of *T. gallica*.

In the following a series of varieties of *T. gallica* in Israel are briefly described. These varieties comprise some of the species described by Bunge. Not all of them, however, could be properly synonymized owing to the inaccessibility and a partial loss of the authentic specimens, notably those of Ehrenberg. Some of them may thus be placed as synonyms by the future monographer of this group. They are tentatively classed under *T. gallica* L. ssp. *nilotica* (Ehrb.) Maire in Emberger and Maire. Tamaricaceae in *Cat. pl. Maroc* 4: 1072. 1941.

*Tamarix gallica* L. var. *maris-mortui* (Gutm.) Zoh. var. nov.—*T. maris-mortui* Gutm. in *Palestine Jour. Bot.* Jerusalem 4: 50. 1947. fig. nostra 9.

Trees or higher shrubs with semiamplexicaul, ovate, deltoid leaves, somewhat decurrent at base. Racemes in diffuse panicles, 2.5–6 cm. long; florets 2–2.2 mm. long; filaments with narrow base arising from the deeper sinuses of the ten-lobed disc. Fruits small, brownish.

Selected specimens: LOWER JORDAN VALLEY: Northern shore of Dead Sea, May 1940, *Gutmann*, *T.* 928 (TYPE); Ein Gedi, Wadi Arija, 8 April 1951, *Tadmor*, *T.* 1425. ARAVA VALLEY: Environs of Sodom, salt marshes, 20 March 1954, *M. Zohary*, *T.* 715; Wadi Fukra, 27 April 1953, *M. Zohary*, *T.* 807; Ein Hotzev, 5 December 1952, *Tadmor*, *T.*

1344. FAR NEGEV: Jebel Tul Napkh, 27 November 1949, *De Angeles*, *T.* 1424.

*Tamarix gallica* L. var. *anisandra* Zoh. var. nov.—Folia semiamplexicaulia. Rami florigeri erecti; racemi breves, laxiusculi; flosculi paulo majores quam in var. praecedenti; bractae 1–1.5 cm. longae; petala post anthesim patentia; discus 5-lobus; stamina (5) 6–7; insertio filamentorum epilophica; styli dimidium ovarium superantes.

This variety is very striking because of its erect flowering branches, its larger florets, etc.

ARAVA VALLEY: Ein Yahav, 24 March 1950, *D. Zohary*, *T.* 895 (TYPE).

*Tamarix gallica* L. var. *longispica* Zoh. var. nov.—Rami saepe efflorescentis salinis quasi albo-pulverulenti. Folia carnosula valde glauca. Racemi rigidissimi, erecti, 6–9 cm. longi, vix 3 mm. lati. Vix varietas.

ARAVA VALLEY: Environs of Eilath, 26 September 1950, *Tadmor*, *T.* 961.

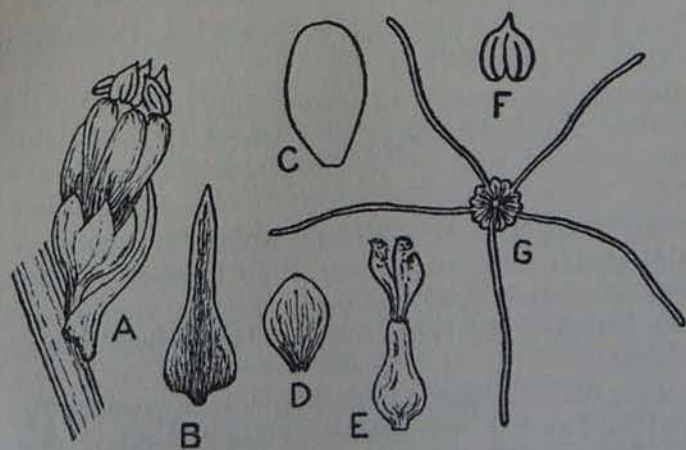


Fig. 10. *T. gallica* var. *ascalonica*.—a. flower, b. bract, c. petal, d. sepal, e. pistil, f. anther, g. staminal disc.  $\times 10$ .



*Tamarix gallica* L. var. *eilathensis* Zoh. var. nov.—*T. mannifera* (Ehrb.) Bunge. Tentamen 37. 1852.

Rami stricti erecti, quasi albo-pulverulenti. Folia carnosula semiamplexicaulia, apice subpatentia. Racemi compacti, rigidi, erecti, 3-4 (5) cm. longi; discus plerumque 5-lobus; insertio filamentorum epilophica vel mesodiscina.

ARAVA VALLEY: Salines near Eilath, April 1949, *Tadmor*, T. 934 (TYPE); outlet of Wadi Jiraffi, 28 September 1953, *Orshan*, T. 955.

This variety fairly well agrees with the description of *T. mannifera* but varies in the configuration of the disc and can by no means be kept as a separate species.

*Tamarix gallica* L. var. *abiadensis* Zoh. var. nov.—Ramusculi erecti, rigidi. Folia deltoidea, acuta, adpressa, crassa, valde glauca vel albo-pulverulenta, apice incurva. Paniculae laxae; racemi floriferi laxi, (2) 3-5 cm. longi, erecti, fructiferi laxissimi, divaricati, remoti cum rhachide rigida; flosculi brevissime pedicellati, vel fere sessiles; bracteae triangulari-lanceolatae; discus 10-lobus; insertio filamentorum mesodiscina.

FAR NEGEV: Wadi Abiad, August 1949, October 1950, *Tadmor*, T. 973 (TYPE).

Reminds one strongly of a form of *T. jordanis* because of its strict panicle bearing almost lateral racemes only, the latter, however, arise from the branches of the current year.

*Tamarix gallica* L. var. *brevispica* Zoh. var. nov.—Valde glauca, albo-pulverulenta. Folia brevissima, deltoidea, semiamplexicaulia. Paniculae paulo-ramosae; racemi laterales, etiam fructiferi brevissimi, 1-2 cm. longi, divaricati; discus 10-lobus.

ARAVA VALLEY: Ein Hotzev, March 1950, *Tadmor*, T. 880 (TYPE). FAR NEGEV: Environs of Ein Shahabia, 6 October 1949, *De Angeles*, T. 887.

*Tamarix gallica* L. var. *pachybotrys* Zoh. var. nov.—Folia deltoideo-lanceolata, acuminata, apice incurva. Paniculae strictae, densae; racemi fructiferi 5-8 cm. longi, 8-10 mm. lati; bracteae (pro specie) longissimae subulatae, 2 mm. longae; discus pentagonus (nec pentalobus); filamenta basi latiora, angulis disci imposita.

ARAVA VALLEY: Ein Hotzev, 5 December 1952, *Tadmor*, T. 899 (TYPE).

Described from a single fruiting specimen which is unlike any other variety of this species. By the shape of the disc and other characteristics this variety agrees well with the description of *T. arborea* Ehrb., but because of the lack of authentic specimens for comparison I am unable to decide upon its identity. From the description of *T. arborea* it is clear however, that the latter can by no means be kept a specific level.

*Tamarix gallica* L. var. *divergens* Zoh. var. nov.—Folia grisea, albo-pulverulenta, ovato-deltoidea, acuta, adpressa. Paniculae laxiusculae, rigidae; racemi 2-3 cm. longi, 4-6 mm. lati, pedunculati, rigidi, fructiferi in angulum amplum (fere horizontaliter) divergentes et remoti; flosculi fertiles cum sterilibus cecidiferibus intermixti; discus 10-lobus; filamentorum insertio mesodiscina.

FAR NEGEV: Wadi Hyani, near crossway to Eilath, December 1949, *Tadmor*, T. 1346 (TYPE).

Readily distinguishable from all other varieties by its very rigid, remote, divaricate racemes, partly beset with sterile flowers transformed to galls.

*Tamarix gallica* L. var. *microcarpa* Zoh. var. nov.—Folia semiamplexicaulia, parte libera lanceolata, acuminata, patentia. Paniculae plus minus densae; racemi tenues, 3-6 cm. longi; bracteae triangulari-lanceolatae; discus 10-lobus, filamentorum insertio mesodiscina. Fructus minutus, maturatus 2-2.5 mm. longus.



ARAVA VALLEY: Ein Hotzev, 3 March 1950, *Tadmor*, T. 1330 (TYPE).

**Tamarix gallica** L. var. *erythrocarpa* Zoh. var. nov.—Folia semiamplexicaulia, parte libera deltoidea vel lanceolata, acuminata vel cuspidata. Racemi tenues, pedunculati, densiusculi; bractae lanceolato-subulatae; discus 10-lobus; filamentorum insertio mesodiscina; fructus 3–4 mm. longus, totus vel parte superiore purpureo-lilacinus. Valde affinis var. praecedenti.

ARAVA VALLEY: Ein (Ghadian) Yotvata near spring, 29 December, 1952, *Tadmor*, T. 662.

**Tamarix gallica** L. var. *ascalonica* Zoh. var. nov. fig. nostra 10.—Ramusculi crassi, valde congesti. Folia deltoidea, brevia, carnosula, valde adpressa. Paniculae strictae, erectae; racemi pedunculati, densiflori, 2–4 cm. longi, 4–6 mm. lati; flosculi breviter pedicellati; bracteae longissime (pro specie) lanceolato-subulatae, calycem aequantes vel superantes; corolla calyce plus duplo longior; discus 10-lobus; filamenta valde exerta, eorum insertio mesodiscina; antherae eximie apiculatae; styli dimidium ovarium superantes vel aequantes.

COASTAL SHEFELA: Ascalon, hedges, 17 October 1954, *M. Zohary*, T. 916.

This variety is conspicuous because of its long styles and bracts as well as by its larger florets.

**Tamarix gallica** L. var. *micrantha* Zoh. var. nov.—*T. pseudo-Pallasii* Gutm. in Palestine Jour. Bot. Jerusalem 4: 51. 1947 in part.

Ramusculi crassi, erecti. Folia ovato-deltoidea, acuta, crassa, basi breviter decurrentia. Paniculae subsimplices, racemis remotis vel ad terminum ramorum congestis; racemi 1.5–4 cm. longi, 3–3.5 mm. lati; flosculi plerumque ante anthesim subsessiles, minuti, 1.5 cm. longi; bracteae deltoideae, acutae; discus 5-lobus, lobi interdum emarginati; insertio filamentorum mesodiscina. Capsula minutissima, 1.5–

2.5 mm. longa. Var. *ascalonicae* valde proxima, ab ea differt floris et fructus magnitudine.

ACRE PLAIN: Sand dunes near refineries, 6 July 1949, *Orshan*, T. 850; Kiryath Motzkin, 30 March 1941, *Gutmann*, T. 860 (TYPE). SHARON: Tantura, hedges, 24 October 1949, *D. Zohary*, T. 853.

**Tamarix gallica** L. var. *subpatens* Zoh. var. nov.—A praecedenti differt foliis longioribus, plus minus patentibus, fructu majore. Vix varietas; forma transitans inter var. *micrantham* et *ascalonicam*.

ACRE PLAIN: Galia, 2 July 1949, *Boyko*, T. 867 (Cult.).

This variety has been collected from the Acre Plain as a cultivated tree; it flowers twice in summer, the early summer (or spring) racemes ripen in July when new racemes start to develop.

**Tamarix gallica** L. var. *tenuior* Zoh. var. nov.—Arbor viridis. Ramusculi tenuissimi, elongati, diffusi. Folia deltoideo-lanceolata, acuta vel acuminata, apice et margine hyalina. Racemi 2–4 cm. longi, laxi, bracteae lanceolato-subulatae; flosculi eximie pedicellati, 2 mm. longi; petala conniventia, valde concavi-naviculiformia; filamenta vix exerta, insertione plerumque epilophica; styli dimidium ovarium aequantes vel superantes.

Readily distinguishable from all other forms of this species by its very thin branchlets, its relatively long pedicels, by the very loosely arranged florets, and by its arborescent habit; flowers rather sparsely in late summer. It is one of the most important trees cultivated by the roadsides and parks of the coastal plain. All our specimens are from cultivated habitats, but the plants have probably been introduced from a local natural habitat.

SHARON: Natanya, 26 November 1952, *M. Zohary*, T. 841 (TYPE).

The high variability of *T. gallica* in Israel tells much of the taxonomic constitution of this species. I am strongly



convinced that the entire series of the above varieties, as well as another series of "species" described by various authors, are to be included within *T. gallica* despite its wide geographical and ecological range. As for the forms described above, although readily distinguishable from each other, some of them must be conceived of as only tentative.

***Tamarix chinensis*** Lour. Fl. Cochinch. 1: 228. 1790. *T. (gallica) chinensis* Ehrb. in Linnaea 2: 267. 1827.

UPPER JORDAN VALLEY: Neoth Mordekhai, May 1955, Lamed, *T.* 499. ESDRAELON PLAIN: Nir David, 26 May 1952, M. Zohary, *T.* 1083. COASTAL SHEFELA: Rishon Le Tsion, 28 May 1954, Ginzburg, *T.* 1080.

Widely cultivated and probably subsponaneous in some localities.

***Tamarix aravensis*** Zoh. sp. nov. fig. nostra 11.—Affinis *T. passerinoidi* Del. sed ab ea differt inter alias floris magnitudine, corolla deflexa, fructu valvis angustis, foliis non amplexicaulis, etc.

Frutex. Rami griseo-fusci; ramusculi divaricati. Folia ovato-deltaidea, basi breviter decurrentia, subsemialexicaulia, acuta vel acuminata, punctata, margine anguste cartilagineo-membranacea, apice incurva. Racemi laxissimi, ex ramis annotinis orti, pedunculati, 5-8 cm. longi, 1 cm. lati, pedunculi bracteis squamiformibus sparsis obsiti; bracteae triangulari-lanceolatae, subsemialexicaules, acuminatae, 3 mm. longae, basi 1 mm. latae; pedicelli 2 mm. longi; sepala (4) 5, obovato-rhomboidea, 2-3 mm. longa, 1.6 mm. lata; petala (4) 5, obovata, 3.5 mm. longa, 2.3 mm. lata, rosea, valde deflexa; discus eglandulosus, in filamentorum basim dilatatum abiens; stamina (5-7) 8-10, cum filamentis 2.5 mm. longa, ex corolla deflexa valde exserta, antherae oblongae, 1 mm. longae, apiculatae; ovarium latelangeniforme, ca. 2.5 mm. longum; styli 3, spathulati, 1 mm. longi. Capsula majuscula, pyramidata, 7-9 mm. longa, basi 2.5-3 mm. lata. Floret Martio-Decembri.

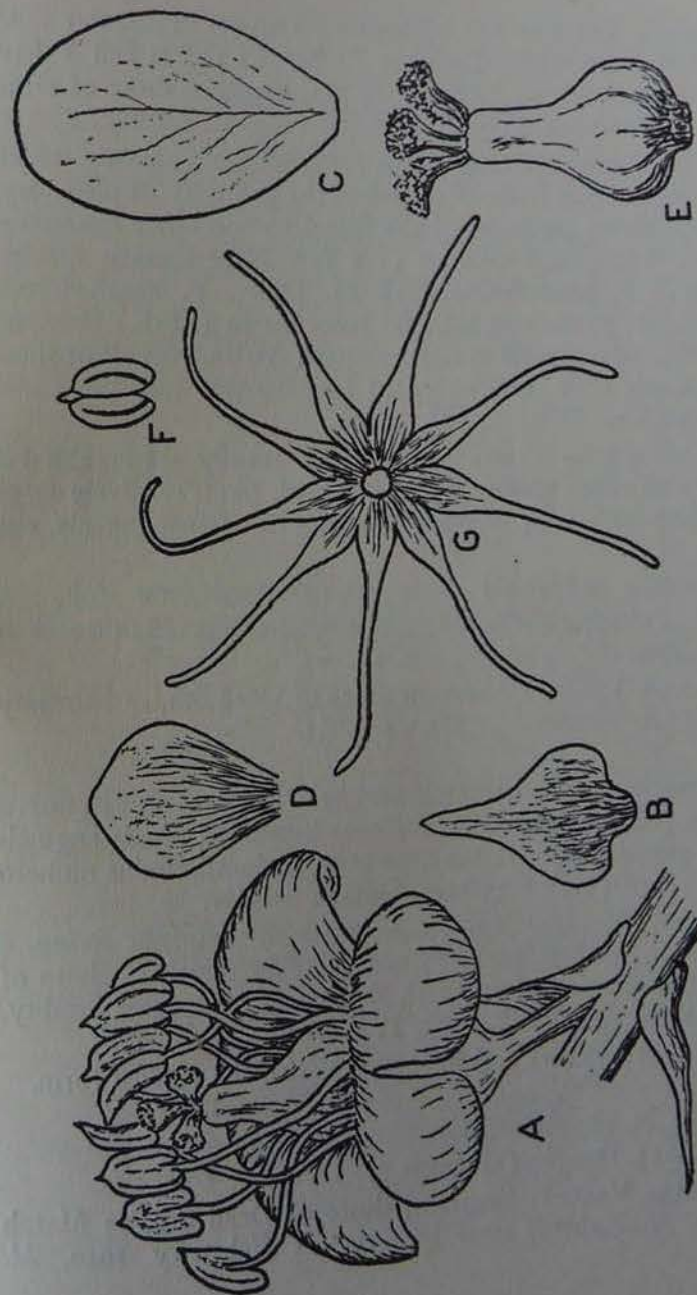


Fig. 11. *T. aravensis*.—a, flower, b, bract, c, petal, d, sepal, e, pistil, f, anther, g, staminal disc.  $\times 10$ .



ARAVA VALLEY: Ein (Ghadian) Yotvata in a water hole, 29 December 1952, *Tadmor*, *T.* 748 (TYPE); Ein Yahav, 23 March 1950, *D. Zohary*, *T.* 755; southern shore of Dead Sea, environs of Sodom, 23 March 1954, *M. Zohary*, *T.* 756.

This species belongs to the "amplexicaulis" group which is distinguished from all others of the genus by its pleiandry, its epidiscine insertion of the filaments and other characteristics. The group consists of a few Near Eastern species, such as *T. passerinoides* Del. ex. Desv., *T. amplexicaulis* Ehrb., *T. pynocarpa* DC., *T. macrocarpa* (Ehrb.) Del. and another two species in northwestern Africa. Not all of these binomials have been accepted by botanists (see Burtt and Lewis, *Kew Bull.*, 3: 388. 1954).

The species described above is readily distinguishable from all other species by its deflexed, pink, relatively large flowers, its bracts, its loose racemes, its narrow capsule, etc.

*Tamarix aravensis* Zoh. var. *patentissima* Zoh. var. nov.—*Folia rigidiora, patentissima. Bracteae angustiores et longiores.*

ARAVA VALLEY: Southern shore of Dead Sea, 17 February 1950, *M. Zohary*, *T.* 765 (TYPE).

*Tamarix aravensis* Zoh. var. *micrantha* Zoh. var. nov.—*Folia plus amplexicaulia. Bracteae breviores; sepala angustiora; petala conspicua, breviora et angustiora; stamina numero 5-7 (8-10); styli breviores. Capsula brevior.*

ARAVA VALLEY: Ein Yahav, banks of brackish spring, 9 April 1950, *D. Zohary*, *T.* 629 (TYPE); southern shore of Dead Sea, 27 April 1953, *M. Zohary*, *T.* 630; same locality, 23 March 1954, *M. Zohary*, *T.* 638.

Grows together and intergrades with the typical form.

*Tamarix passerinoides* Del. ex Desv. in *Ann. Sci. Nat.* 4: 349. 1825, Bunge. *Tentamen* 77. 1852. fig. nostra 12.

ARAVA VALLEY: Southern shore of Dead Sea, 23 March 1954, *M. Zohary*; same locality, 15 February 1950, *M.*

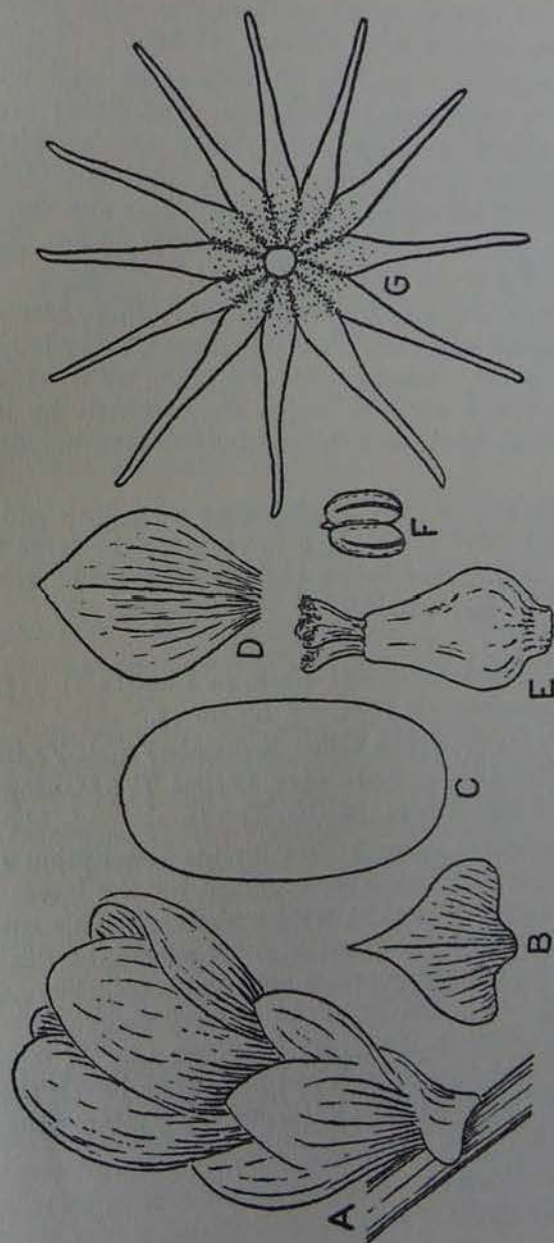


Fig. 12. *T. passerinoides*.—a. flower, b. bract, c. sepal, d. petal, e. pistil, f. anther, g. staminal disc.  $\times 10$ .



Zohary; Ein Yotvata, saline, 29 December 1952, *Tadmor*, T. 601; Eilath, without date, *Tadmor*, T. 613.

Our specimens from Ein Yotvata agree well with the diagnosis as represented by Bunge. The leaves are fully amplexicaul (in *T. amplexicaulis* they are less clasping). The specimens from Eilath differ in appearance from the above but still belong to this species. There also are, in our herbarium, specimens of this species from 94 km. south of Baghdad (Eig & M. Zohary, T. 625).

*T. passerinoides* is well distinguished from *T. arvensis* by its amplexicaul leaves with horizontal apex, by its horizontal, broad and short, almost cupuliform bract, by its very short peduncles which grow in length after anthesis, by its capsules 3–6 mm. broad at base and by its erect, not deflexed, petals.

As to the size of fruit, I fully agree with Burtt and Lewis (1954) that there is no place to consider the large fruited specimen as *T. macrocarpa* (Ehrb.) Bunge, not even as a variety of *T. passerinoides*.

*Tamarix amplexicaulis* Ehrb. in *Linnaea* 2: 275. 1827. Bunge. *Tentamen* 76. 1852. fig. nostra 13.

ARAVA VALLEY: Eilath, saline, September 1949, *Tadmor*, T. 720; same locality, 10 April 1955, *Weisel*, T. 726; same locality, 11 November 1949, *Boyko*, T. 729.

Our specimens agree well with the description of this species as amplified by Bunge, except for the leaves which vary from amplexicaul to semiamplexicaul. This species is readily distinguishable from all other species of this group by its small florets arranged in very short, spikelike racemes, 3 cm. long and 3 mm. broad, by its very short pedicels, 0.5 mm. long (even in fruit), by its petals (1.5 × 0.7 mm.), sepals (1 × 0.7 mm.) and filaments (1 mm. long); the number of stamens varies from 8–10, and the fruits are the smallest in this group.

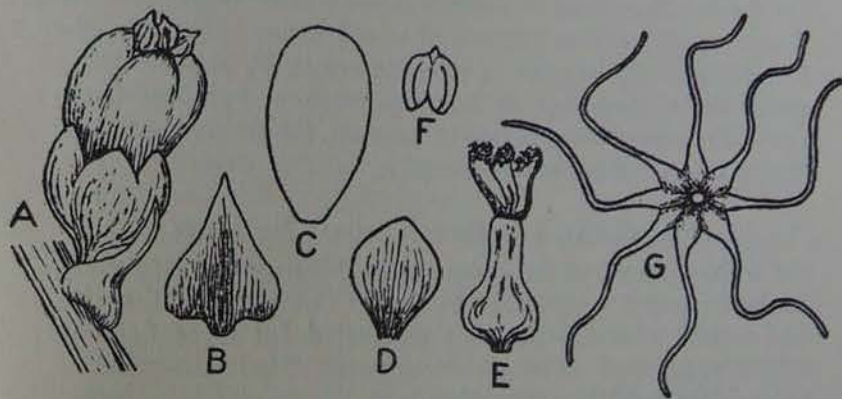


Fig. 13. *T. amplexicaulis*.—a. flower, b. bract, c. petal, d. sepal, e. pistil, f. anther, g. staminal disc. × 10.

*Tamarix aphylla* (L.) Karst. *Deutsch. fl.* 641. 1880–1883. *Thuja aphylla* L. *Cent. pl.* 1: 32. 1755, and in *Amoen. acad.* 4: 295. 1759, and *Sp. pl. ed. 2.* 1422. 1763. *Tamarix orientalis* Forsk. *Fl. aeg. arab.* 206. 1775. *Tamarix articulata* Vahl. *Symb. bot.* 2: 48. *tab.* 32. 1791; Bunge. *Tentamen* 73. 1852.

COASTAL SHEFELA: Environs of Dorothe, 29 September 1949, *Tadmor*, T. 776; Ascalon, 17 October 1954, *M. Zohary*, T. 777. ARAVA VALLEY: Wadi Mahalle, 19 March 1947, *Feinbrun*, T. 794; Wadi Gharandel, 8 May 1950, *Tadmor*, T. 774; Bir Gdeide, 2 December 1949, *De Angeles*, T. 769. NORTHERN NEGEV: Between Beersheva and Revivim, 22 September 1953, *De Angeles*, T. 771; between Kefar Yeruham and Mamshit, September 1953, *M. Zohary*, T. 770. FAR NEGEV: Wadi Hureisha, August 1949, *Tadmor*, T. 781.

This species is one of the commonest in cultivation. It is the only species which reaches a height of 10 m. and can be planted on a commercial scale. It is easily grown from cuttings, and thrives well both in sands and heavy soils. It also grows fairly well in salines. Its wide distribution in the desert sands is probably due to its easy cultivation. But it is



no doubt also native in some wadis of the Negev, and we also observed a few trees within the saline sebkha of the Dead Sea shore. In spite of its wide range, *T. aphylla* shows only slight variation in its vegetative and reproductive parts. Because it flowers late in summer, flowering specimens are rare in most herbaria.

#### ECOLOGICAL AND SILVICULTURAL REMARKS

Of the sixteen species recorded in this paper, *T. chinensis*, is the only one introduced in Israel. The rest are all native and a few of them are also cultivated for dune fixation, afforestation and ornamental purposes. The species below are widely used in cultivation.

*T. aphylla*.—This is very common both as a forest tree in the Negev and as a dune stabilizer in the sands of the coastal plain. It is an Irano-Turano-Saharo-Sindian species and is planted extensively in many Near Eastern countries. The large scattered trees in the dunes of the western Negev are no doubt remnants of ancient cultivation and not native there, since these trees are unable to regenerate from seeds in the dry sand. This has been revealed by the fact that the seeds lose their viability four to six weeks after ripening (October), and the sporadic rains of the first winter months do not moisten the upper layers of the dunes to an extent sufficient for germination and/or development of the extremely slow-growing seedlings. As a matter of fact, not a single seedling has been found by us in the Negev, even in the neighborhood of adult trees. On the contrary, in the wadis of the eastern Negev and Wadi Arava seedling establishment seems to be much more possible, so that specimens collected here are probably native. Planted on bare sand dunes of the Negev, cuttings of *T. aphylla* produce deep roots which enable them to develop rapidly, even under an annual precipitation of 100 mm. But under these extreme conditions the further development of the young tree is strongly determined by the density of the grove. Transpiration measurements have shown that this species consumes high amounts of moisture and may lead to a rapid exhaustion

of the moisture reserves in the dunes, so that under 100 mm. of rain only 15–20 plants per acre can develop to trees of commercial value. Although it is one of the most valuable and easily grown trees of the arid region of the Israel sand deserts, it is almost impossible to grow this tree on loess soil of the Negev without irrigation, not to mention in the Hammada soils of this region.

*T. gallica* L. ssp. *nilotica*.—This species occurs in Israel in a large number of varieties, many of them showing a particular geographic area and ecologic range. Although morphologically readily distinguishable, some of them can hardly be considered as "good" varieties. Among others var. *temuor* of this species attains the size of a tree and is extensively planted on sands, by roadsides and in parks. In the Acre Plain the var. *micrantha* is common in cultivation as an excellent sand binder. Other varieties such as var. *ascalonica* have been successfully planted on the Gaza sand dunes. The growth of this variety is rather rapid but the plant remains shrubby. Both varieties exhibit high rates of transpiration.

Although the above varieties are confined to the coastal sands, there is a group of other varieties confined to the wadis of the Negev, Dead Sea region, and Wadi Arava. Some of these varieties grow on extreme salines with a salt content as high as 10 per cent (as referred to dry matter). Others are confined to wadi beds where the salts are permanently leached out. Most of them are remarkable for their intensive exudation of salts found on the surface of the transpiring organs. Even though var. *maris-mortui* may attain under favorable conditions a tree-like habit, others are shrubby in appearance.

*T. jordanis* Boiss.—This species is confined chiefly to the banks of the Jordan River and its affluents. It is readily distinguishable from *T. gallica* by its vernal inflorescences arising from last year's branches. The var. *typica* forms thickets with the *Tamaricetum jordanis* all along the Jordan River, sometimes intermingled with *Populus euphratica*. In some places it has been taken into cultivation along road-



sides, due to its handsome racemes. This variety, as well as var. *brachystachys*, is well recognizable by its biseasonal flowering, both vernal and aestival, the latter with paniced racemes arising from young shoots. Other varieties of this species have exclusively vernal flowering, and one of them, var. *negevensis*, has been successfully grown on the dunes between Beersheva and Revivim.

*T. tetragyna*, as well as *T. Meyeri* and *T. deserti*, are very ornamental because of their showy racemes. *T. Meyeri* is frequently cultivated as a roadside ornamental in some towns (Naharia, etc.). The other two species may be recommended for the same purpose. All are hydrohalophytes, withstanding soil salinity as high as 10 per cent and requiring a high moisture content of the soil. While *T. Meyeri* is confined mainly to Mediterranean salines, *T. deserti* is Saharo-Sindian and inhabits chiefly the Dead Sea salines; both are accompanied by *Arthrocnemum glaucum*. All of these species are excellent in the afforestation of extreme salines.

*T. chinensis* is one of the most beautiful *Tamarix* species, known in Israel only in cultivation. Here it is probably also subsontaneous. *T. parviflora* is both spontaneous and rarely cultivated.

The *passerinoides* group, including *T. arvensis* Zoh., *T. passerinoides* Del. and *T. amplexicaulis* Ehrh., is confined exclusively to the very extreme salines of the Arava Valley. *T. arvensis*, with its showy pink flowers, may be recommended as an ornamental. The other species mentioned in this paper are rather rare, and not much is known of their ecology and horticultural value.

The occurrence of sixteen species of *Tamarix* in this country, abounding in vast stretches of extreme deserts and salines, is of utmost importance in the problem of the desert afforestation. Thousands of areas of wadi beds in the Hamada deserts and salines of the Dead Sea region as well as sand dunes could perhaps reasonably be afforested with species ecologically suitable to each particular habitat. A

study of the technology and uses of these species would help much in this matter. So far, much of the planting of *Tamarix* in this country has been made in full ignorance of the ecology and the taxonomy of this genus, and this has led to serious failures and ill successes in this field.

## SUMMARY

1. A critical revision of the local species of *Tamarix* has revealed the presence in Israel of sixteen species instead of five previously recorded for this country.
2. Four species new to science and a series of new varieties are described herein.
3. A key to the identification of the local species is also presented.
4. A short discussion on the ecological and silvicultural value of the species under review has been appended.

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THE ANATOMY OF THE WATER STORAGE  
ORGAN OF *CEIBA PARVIFOLIA*

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INTRODUCTION

Ecological observations of *Ceiba parvifolia* Rose (Bombacaceae), which occurs in Puebla, Oaxaca, Morelos, and Guerrero states of Mexico, have been published by Miranda (1942) and Muller (1952). The species is part of the thorn forest which is characterized by a short rainy season followed by a long, extreme drought. Many trees and shrubs of the thorn forest lose their leaves shortly after the onset of the dry season as a response to the drought. In a few species, including *C. parvifolia* (el pochote), this is followed by flowering and the maturation of fruits. Since *C. parvifolia* grows on dry slopes and does not have roots in contact with deep soil water, the plants produce flowers and fruits during a period when the soil obviously lacks an adequate supply of available water.

Muller (1952) discovered large, sub-spherical, soft organs on roots of five individuals of the species. These structures, which may reach 30 cm. diameter, are called locally "camotes." The camotes arise as small fleshy swellings on young roots and remain attached for many years. Gross examination reveals a rough exterior of ordinary cork and a soft parenchymatous interior traversed by fibrous strands. The microscopical study of the mature camote has revealed that it is composed largely of highly parenchymatous secondary xylem. The anatomy of *Ceiba pentandra* (the kapok) has been described to some extent by Calvet (1907), but no detailed anatomical description of *C. parvifolia*, including the camote, has been found.

The camotes, when collected early in the dry season of 1951, contained large quantities of water. Muller (unpublished) found the same organs depleted of water in the late



dry season of 1955. It seems reasonable to suppose that water is stored in the camotes during the rainy season and withdrawn for use during the dry season. Miranda (1942) also noted the water reserve potentialities of these organs.

A record of seasonal fluctuation of water content in the very parenchymatous secondary xylem of the stem of *Ochroma* (balsa), also a member of the Bombacaceae, would lend additional credence to the functional concept of the camote of *Ceiba parvifolia*. Although the cauline secondary xylem of *Ochroma* gradually increases in water content as the tree ages (Greenhouse, 1934; Record and Hess, 1943), no published record has been found in the sparse literature (Carpenter, 1917; Coster, 1927; Greenhouse, 1934; Hyde, 1925; Record and Hess, 1943; Record and Mell, 1924; Rowlee, 1921) of a seasonal fluctuation in water content.

#### MATERIALS AND METHODS

Blocks of tissue from the periphery and interior of a mature camote (30 cm. diameter), three entire, young camotes (2.5 cm. diameter), and one very young camote (0.5 cm. diameter) were fixed in formalin-acetic acid-alcohol (Johansen, 1940), embedded in celloidin (Wetmore, 1932), sectioned, and stained with Heidenhain's haematoxylin and safranin O. Two young unmodified roots, and two young roots with very early developmental stages of camotes were treated similarly. All were collected from one tree in 1951 in Puebla, Mexico.

The diagnostic characters for the description of the secondary xylem of the camote were chosen from Tippon (1941). Further reference and clarification were necessary in several cases: Bailey (1936); Frost (1930a, 1930b, 1931); Hess (1950); Kribs (1935); Metcalfe and Chalk (1950); Normand (1951); Varoissieu (1951). Many descriptive features of the secondary xylem have been omitted because of the singular nature of the organ, lack of comparative anatomical data, and the limited material available for study. The basic terminology used is that approved by the Committee on Nomenclature, International Association of Wood Anatomists (1933).

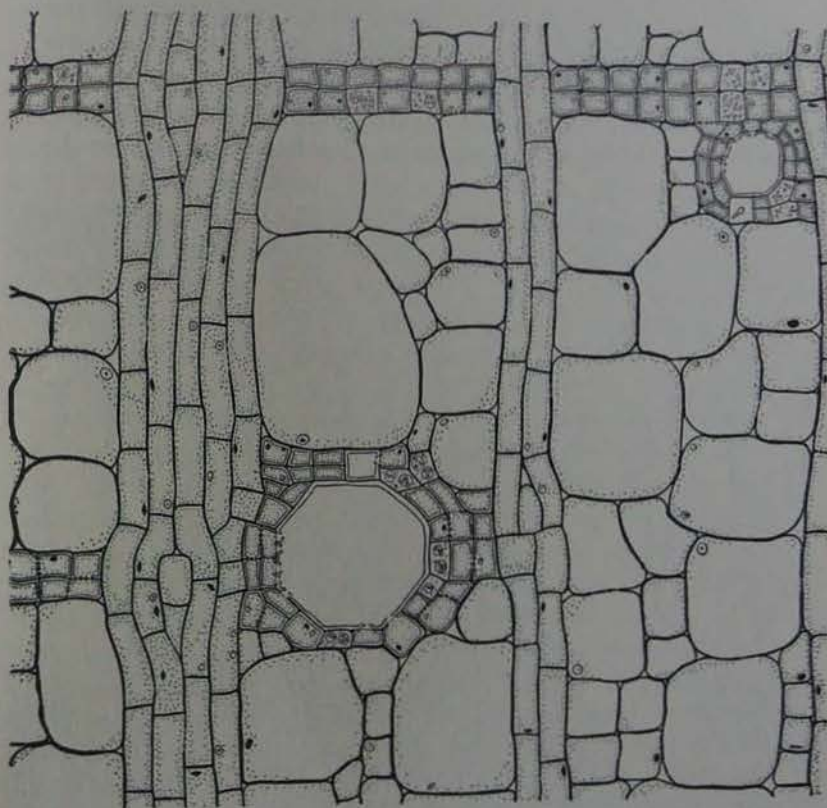


Fig. 1. *Ceiba parvifolia* Rose. Transverse section of the secondary xylem of the camote showing solitary vessels with associated imperforate elements, banded to confluent strand parenchyma, water storage parenchyma, and multiseriate rays.  $\times 100$ .

#### THE MATURE WATER STORAGE ORGAN

*Description of the secondary xylem.*—In transverse section of the mature camote (fig. 1) the secondary xylem demonstrates tangential bands of typical axial wood parenchyma which form a reticulate pattern with the large multiseriate rays. The regions enclosed by the rays and parenchymatous bands are usually filled with very large, irregularly arranged, sub-isodiametric, thin-walled parenchymatous cells. Vessels



are few and are ensheathed by ordinary axial parenchyma. One or two imperforate tracheary elements usually accompany each vessel or small group of vessels.

In tangential section (fig. 2) the vertical system of axial strand parenchyma and vascular elements are seen to be

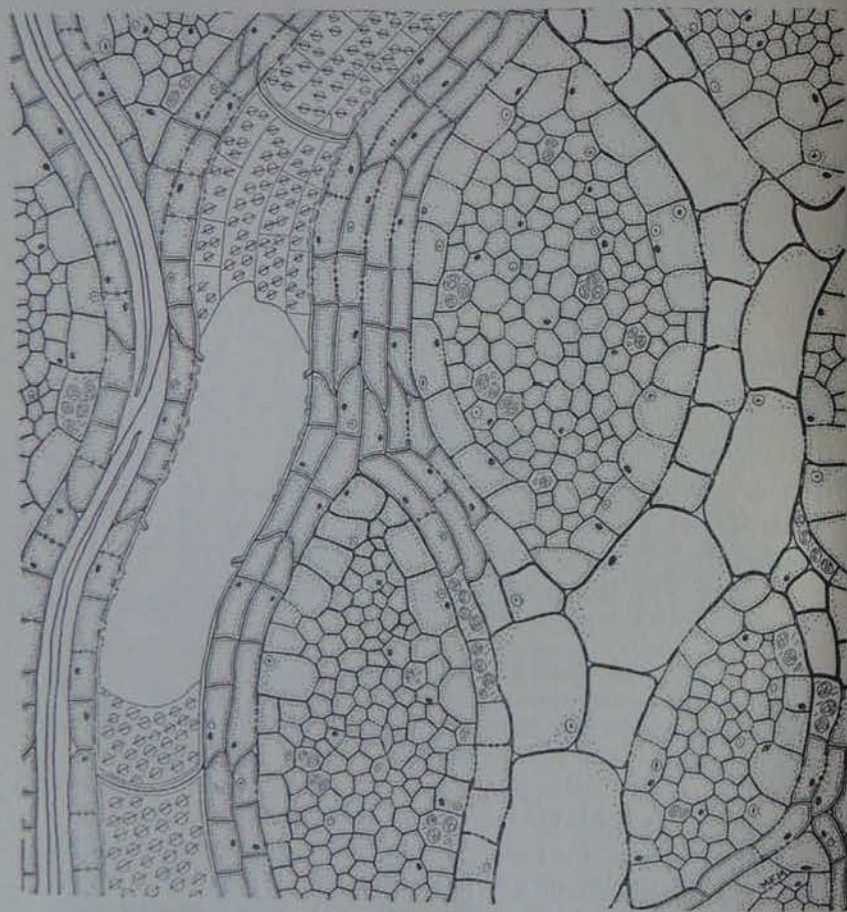


Fig. 2. *Ceiba parvifolia* Rose. Tangential section of the secondary xylem of the camote demonstrating the anastomosing pattern of the vertical system, alternate intervascular pitting, pitting between other element types, vessel element and end walls, strand parenchyma, water storage parenchyma, and multiseriate rays.  $\times 80$ .

contorted and anastomosing. The three-dimensional shape of the intervening large, water-storage parenchyma regions is roughly lens-shaped. Contortion is so great that some vessels lie at right angles to the periphery of the camote. Long, slender imperforate tracheary elements occur in the vicinity of the vessels or are separately enmeshed in the axial strand parenchyma. These elements are fiber-tracheids and libriform wood fibers. The vessels and associated imperforate tracheary elements compose the strands seen in gross observations of the large camotes.

No growth rings were observable. Vessels are so rare that porosity could be determined only with uncertainty; however, the wood is probably diffuse porous. The abundance of vessels is very low, varying from 0 to 4 per square millimeter. Many low-power microscopic fields reveal no pores. Most vessels are solitary (fig. 1), but occasional chains or multiples of two occur. Intervascular pitting is alternate (fig. 2). The intervascular pit-pairs are horizontally elongate and have crossed inner apertures which extend slightly beyond the borders of the pit-cavities.

Pitting between vessels and ordinary axial wood parenchyma is essentially alternate, although rather irregular (fig. 2). The pit-pairs are elongated horizontally and bordered only on the vessel side. Pitting between vessels and the vascular rays is similarly alternate. The pit-pairs are ovoid with elongate half-borders. Vessel element end walls are nearly horizontal to horizontal and bear simple perforations (fig. 2). No spiral thickenings in the vessels are visible.

The vascular rays are multiseriate (fig. 2) varying from 5 to 15 cells (most frequently from 9 to 11) in tangential width. The rays vary from 8 to 70 cells high, most frequently from 25 to 35. Nearly all of the ray cells are long and slender, with their long axes horizontally oriented. Larger cells occur at the apices and also line the sides of some of the rays (fig. 2). Clustered pitting occurs in the walls between ray cells and in the walls between ray and strand parenchyma cells. The rays vary from homogeneous to heterogeneous, and as such do not fit any of the descriptive types. Starch is moderately abundant in the ray cells.



The axial wood parenchyma is apparently of two types: ordinary strand parenchyma and the large-celled water storage parenchyma. The strand parenchyma is distributed largely as wide tangential bands (fig. 1), extending from ray to ray, 1 to 7 (usually 2 to 3) cells in radial width. It is banded (when without vessels) or confluent (when with vessels). Each strand of parenchyma is composed of 3 to 7 cells (fig. 2). Most vessels occur within the bands of strand parenchyma (fig. 1, 2). A few occur embedded in the water storage parenchyma although they are ensheathed by axial strand parenchyma. Starch is fairly common in the strand parenchyma. Pitting is clustered.

The water storage cells (fig. 1, 2) are parenchymatous, sub-isodiametric, loosely and irregularly packed. They are large cells with diameters varying from 50 to 700 $\mu$ , more frequently within the range of 200 to 500 $\mu$ . The cells are often slightly flattened along their tangential axes. The walls are thin and transparent. These cells develop from derivatives of the fusiform cambial initials by great radial and tangential enlargement.

*Description of the secondary phloem.*—The secondary phloem of the water storage organ is fairly typical of many advanced angiosperms. The tissue is composed of phloem rays, which enlarge gradually toward the periphery, and intervening regions which are composed of the other cell types. The longer axis of the ray cells in the inner phloem is vertical. As the vascular rays are pushed out by cambial activity, the ray cells divide and enlarge to form isodiametrically to tangentially elongated cells. The ray cells are originally thin-walled and parenchymatous. About three-quarters of the vascular ray cells store large druse crystals. Some of the other ray cells become filled with opaque mucilages. In outer regions of the rays the cells become sclerotic, often around a druse. Occasionally, all of the cells of a phloem ray became converted into sclerotic or mucilaginous cells. The rays increase in height as well as width in the outer phloem and superposed rays may fuse to become one.

The tissue among the rays is composed of small, compact cells, among which are phloem parenchyma cells and sieve-tube elements. The latter elements are of the advanced type (Hemenway, 1913; Esau, Cheadle, and Gifford, 1953) with end walls which are nearly transverse to transverse and which bear simple sieve plates. The side walls of the sieve-tubes have vestigial, non-functional plates with poorly distinguishable pores or no pores. The phloem parenchyma cells as seen in radial aspect are slender, thin-walled, and about seven times higher than wide. Companion cells were observed in the transverse section.

The tissue among the rays is soon crushed and becomes partly non-functional. Apparently some parenchyma cells remain alive, and very late, perhaps during crushing, give rise to unusually large, thin-walled, living cells which resemble the special water storage cells of the secondary xylem.

*The periderm.*—The phellogen or cork cambium gives rise to phellem or cork to its exterior and to the phelloderm on the interior. The cork is composed of rectanguloid cells with tangential and vertical diameters twice as great as the radial diameter. The walls are but slightly thickened and contain suberin. Mucilage usually fills the lumen of a mature cell.

The phelloderm is apparently produced at a rate of one cell for every fifteen cells of the phellem. The mature cells are essentially similar in shape to the phellem cells. The phelloderm cells become sclerenchymatous and develop ramiform pits. The transverse diameter of the lumen is about 50 per cent of the diameter of the cell. Mucilage fills most cells.

The activity of the phellogen is quite normal. Successive phellogens arise in the secondary phloem and rhytidome is formed.

#### THE UNMODIFIED ROOT

The unmodified or "normal" root differs in no outstanding way from many dicotyledonous roots with secondary



thickening. The primary stele is a hexarch, actinostelic protosteles. The primary xylem is exarch. The secondary xylem becomes continuous around the primary xylem core. The secondary xylem has narrow rays varying from uniseriate to triseriate (no uniseriate rays were observed in the camote). The tissue is compact with large and small tracheids, fiber-tracheids, and occasional septate fiber-tracheids. Axial strand wood parenchyma occurs as banded to confluent distribution types. The secondary phloem and periderm are not extraordinary; but the latter tissue lacks phelloderm. The sieve-tube elements of the secondary phloem have horizontal to nearly horizontal end walls which have simple sieve plates and side walls which show vestigial sieve areas as in the camote.

#### EARLY DEVELOPMENT OF THE CAMOTE

A camote begins development as a lateral outgrowth of a young root (fig. 3). For purposes of clarity, the root which gives rise to a camote is termed the "mother root," although it may be a branch root of a second or higher degree of ramification. In the examples studied, at least one year's increment of secondary xylem and phloem was present in the mother root. Initial growth of the camote appears just outside of, and opposite, a multiseriate ray of the secondary xylem, and opposite a protoxylem pole of the primary stele (fig. 3). The endodermis and pericycle of the mother root were not discernible. The growth stimulus affects more or less simultaneously the phellogen, the secondary phloem, and the vascular cambium. All take part in the formation of the very young camote (fig. 3). Neither an endogenous meristem, as would form a lateral root, nor a well-defined exogenous cauline meristem is formed (fig. 3). Apparently the growth stimulus spreads out laterally around the mother root in both directions. Partly and fully developed camotes often seem therefore, to be essentially parts of the mother root rather than lateral structures of it (fig. 6).

The vascular cambium of the mother root plays a part in the early development of the camote. The rate of divisions

of cambial cells in the region of growth is increased. The cambium bulges outwardly and forms a hemispherical shell of xylary vessels and imperforate tracheary elements (fig. 3). The vascular ray of the mother stele at that region is

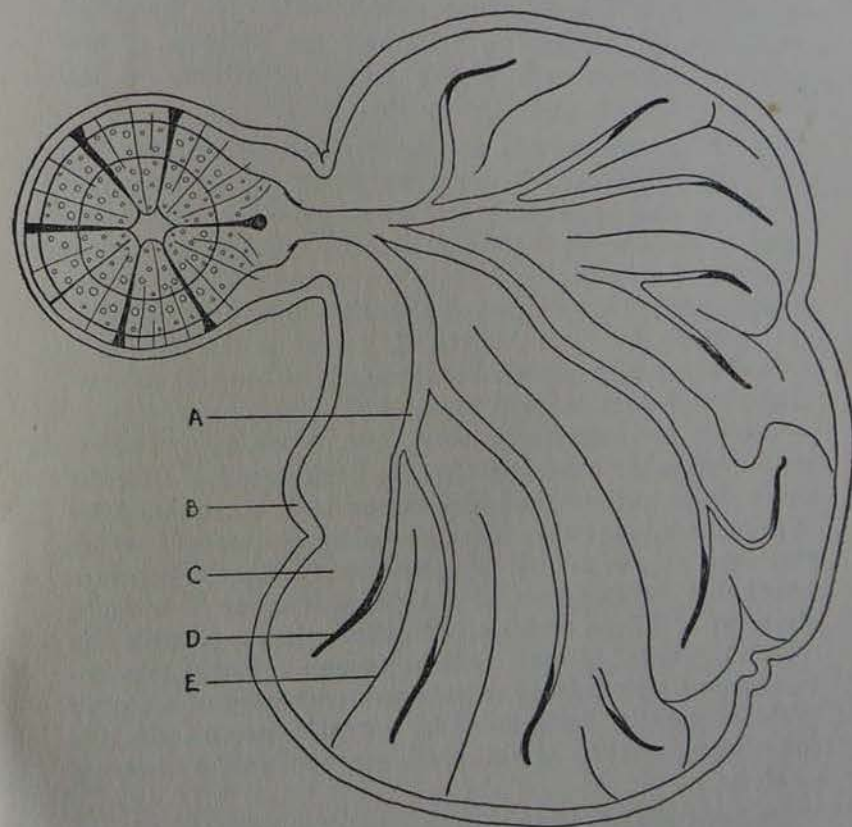


Fig. 3. *Ceiba parvifolia* Rose. A very young camote (5 mm. diameter) and its mother root in transverse section. Note increased production of phelloderm and proliferation of the secondary phloem at the region of initial growth. Also observe the hemispherical shell of xylary tissue formed by the cambium, the "trace" to the camote with its branches ending in procambium-like tissue, the parenchymatous sheaths about each "vascular strand," the lines of mutual compression among adjacent parenchymatous sheaths, the periderm, and the lack of a definite meristem. About  $\times 20$ .



enlarged to fill the central portion of the shell (fig. 3). Conducting cells of this lateral structure in contact with the mother xylary core are oriented parallel with the cells of the core. At a short distance from the mother stele, and still within the hemispherical mass, the conducting cells differentiate perpendicularly to the mother stele. The increased production of phelloderm cells and the division of the secondary phloem cells in the region contribute to the developing camote at this early stage.

Further development is not entirely understood, but certain peculiar features merit description. A very young camote (5 mm. diameter) was examined. Here the hemispherical vascular shell formed by early cambial activity is extended as a short strand of xylem surrounded by poorly differentiated phloem elements and these in turn by cortical-like parenchyma. This cylindrical "trace" to the camote is divided repeatedly into smaller strands of xylem and phloem. Each strand does not end in an apical meristem nor in an advancing meristematic surface, but in its own discrete procambium-like extension (fig. 3). Each strand of vascular tissue or its procambium-like extension is surrounded by radially oriented, rather large, parenchymatous cells which abut upon similar cells of adjacent strands (fig. 3). It is supposed that development of the young camote is brought about by a diffuse division and differentiation of cells but with a tendency of these cells to become oriented into entwined and anastomosing strands each composed of a central "vascular bundle" surrounded by parenchymatous cells. On the surface, activity of the phellogen produces a covering of cork.

Study of slightly older camotes (2.5 cm. diameter) lends some support to the conception of their development described above. A camote of this age (2.5 cm. diameter) consists of a tortuous, anastomosing, three-dimensional network of vascular strands imbedded in a parenchymatous matrix, all enclosed by periderm (fig. 4, 5). No organized meristem is evident, other than the phellogen, which could have given rise to the structure. There is no evidence, such

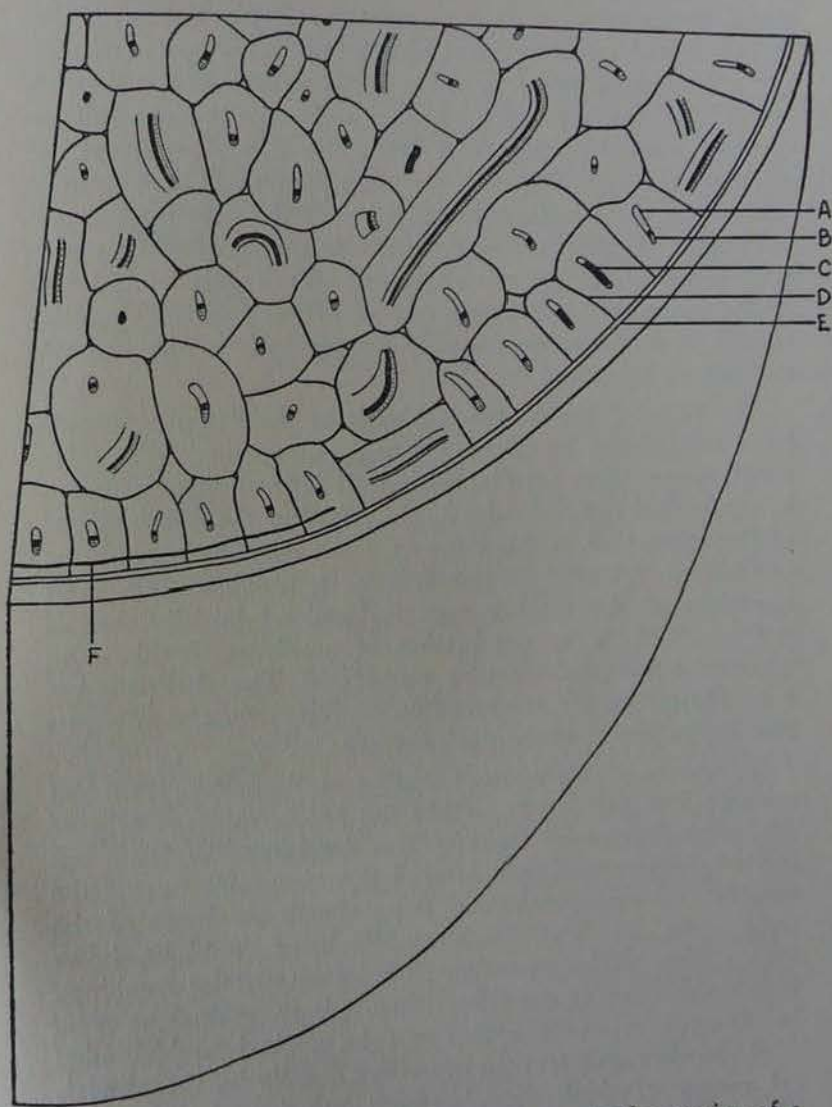


Fig. 4. *Ceiba parvifolia* Rose. Transverse aspect of a portion of a young camote (2.5 cm. diameter). A. xylem, B. phloem, C. procambium-like tissue, D. lines of mutual compression among adjacent parenchymatous sheaths, E. phellogen, F. cambium. About  $\times 4$ .



as an alignment of cells, to indicate that the phellogen produces the camote, except to contribute phelloderm cells during initial development. The parenchymatous matrix is not a continuous mass of cells, but is oriented into sheaths about the vascular strands (fig. 4, 5). There are clear indications of mutual compression along the contact surfaces of adjacent sheaths. This is a puzzling feature. There would seem to be some influence exerted over the development of the matrix by the developing vascular tissue, or some common control over the orientation of all the cells. New links in the reticulum, and extensions of earlier formed vascular strands, must increase the vascular network as the camote expands to this stage.

The vessel elements and tracheids of the vascular strands have scalariform bordered pit-pairs. Occasional spiral elements appear in an exarch position. Ill defined phloem occurs in a collateral position (fig. 4, 5). Whether the development of the camote up to this stage (2.5 cm. diameter) should be considered primary or secondary is problematical. The cambium of the mother root is involved initially, but is not involved in the production of anything to this stage except the proximal vascular connection. The phellogen has a continuous active existence up to this stage and prevents any discontinuity in the cork surface.

In sections of one young camote a cambium-like layer had arisen a few cell layers within the periderm from cells of the parenchymatous matrix. The cambium-like layer extended about one-eighth around the circumference of the camote and was continuous from sheath to sheath of the matrix (fig. 4). This cambium-like layer could be, however, a new phellogen rather than an extra-stelar cambium. If it is the vascular cambium, then it is an anomalous type. It is the opinion of the author that the original cambial bulge of the mother root (fig. 3) opens out distally into a cylindrical structure which then becomes cup-shaped and which advances cell by cell around the periphery of the young camote. It would finally coalesce distally, if this supposition is correct, and assume the shape of the camote. That the

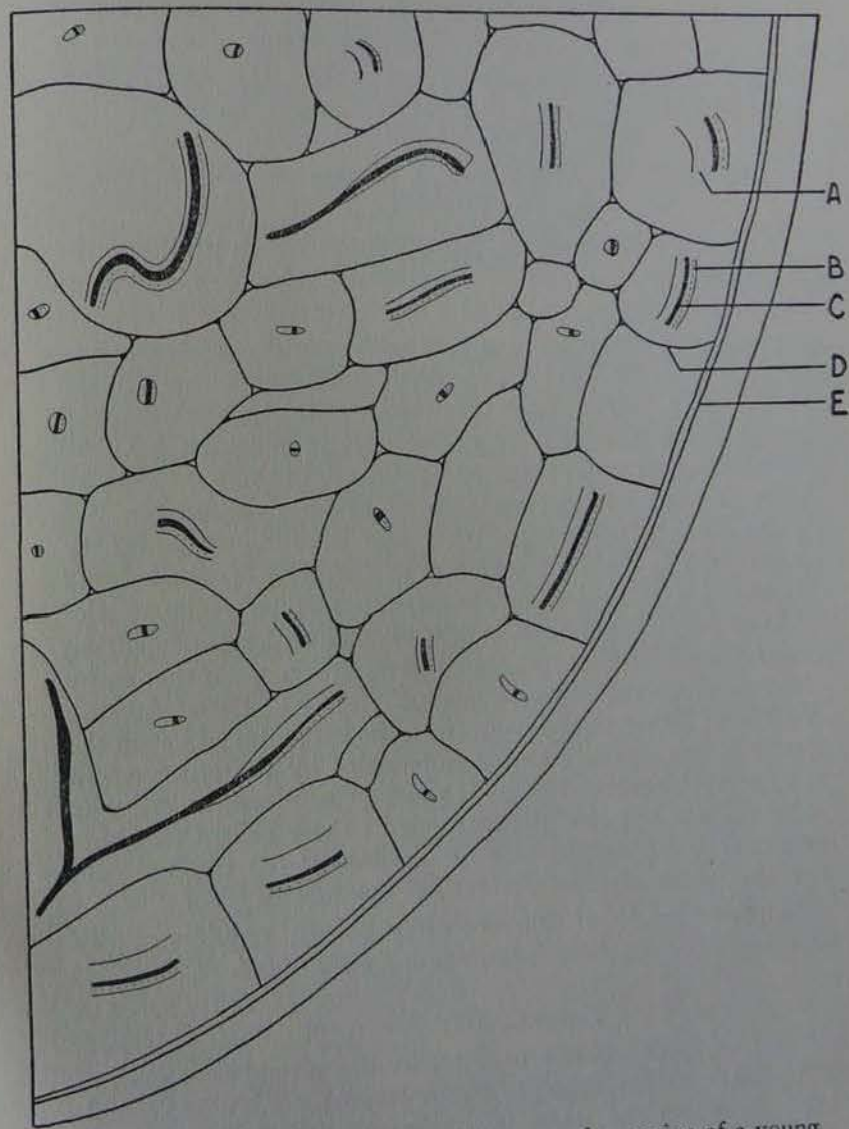


Fig. 5. *Ceiba parvifolia* Rose. Radial aspect of a portion of a young camote (2.5 cm. diameter). A, xylem, B, phloem, C, procambium-like tissue, D, lines of mutual compression among adjacent parenchymatous sheaths, E, phellogen. About  $\times 5$ .



cambium of the more mature camote and the mother root is one continuous structure is obvious from dissections of older stages. Even externally, this would seem to be somewhat obvious (fig. 6).

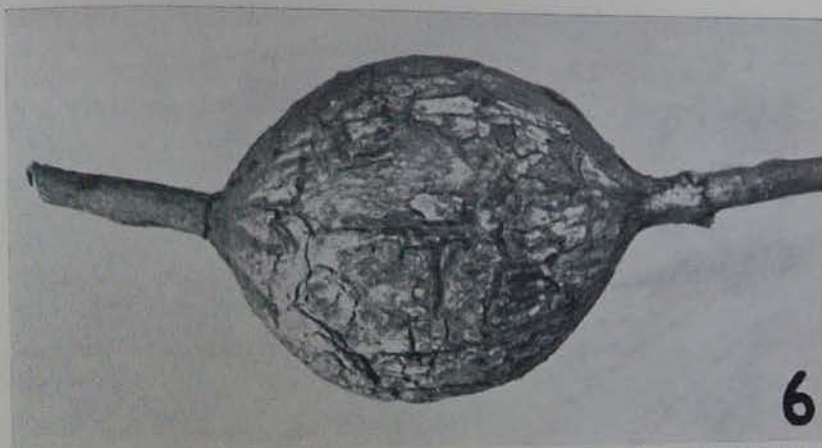
#### THE CAMBIUM AND CAMBIAL REGION OF THE MATURE CAMOTE

Regardless of its origin, the cambium which produces the secondary phloem and the anomalous secondary xylem of the water storage organ is easily distinguishable, appears normal, and behaves in a relatively regular fashion. Ray formation is quite typical. Differentiation of secondary xylary cells merits some discussion. The fusiform cambial initials form small, square to rectangular cells in the xylem differentiation zone. Close to the cambium these cells are all alike (fig. 7) and differentiate to become the various cell types of the mature secondary xylem. Nothing extraordinary is involved in the differentiation of the ordinary axial strand parenchyma, vessel elements, or imperforate tracheary elements. The large, water-storage parenchyma cells arise from fusiform initials; however their growth is so great that many surrounding cells are distorted (fig. 7). Differentiation occurs at about 3 cell layers from the cambium and even the latter is occasionally thrust outwardly by the enlargement of the water-storage cells. It must be assumed, in order to account for the spatial expansion of these cells, that either there is a differential rate of division of the cambial cells or that some cambial derivatives are destroyed.

Differentiation of the secondary phloem requires no discussion since no anomalous features were noted.

#### COMPARATIVE ANATOMY

It is of some interest to compare the secondary xylem of the water storage organ of *Ceiba parvifolia* with the secondary xylem in the stems of *Ceiba* and other Bombacaceae. Basic features of the cauline secondary xylem are fairly constant throughout the family (Metcalf and Chalk, 1950). The imperforate tracheary elements vary from tracheids to



Figs. 6-7.—*Ceiba parvifolia* Rose.—Fig. 6. A partially grown camote (about 10 cm. in diameter) attached to its mother root.  $\times 2/5$ —Fig. 7. The cambial region of a fully grown camote in transverse section. Note the cambium, the differentiation zones of xylem and phloem, and the water storage parenchyma cells.  $\times 104$ .



libriform wood fibers and pits vary from fully bordered to simple. Pores are generally solitary, but a few clusters or multiples occur. Vessel elements have simple perforations, and alternate intervascular pitting. Pitting between vessels and vascular rays or axial wood parenchyma is largely alternate, and in some genera the pits are large, simple, and unilaterally compound.

Axial wood parenchyma in all genera but *Pavonia* is abundant. Commonly the axial wood parenchyma is distributed in regularly spaced, apotracheal, uniseriate to multiseriate bands with intervening bands of imperforate tracheary elements, as in some *Chorisia*, *Montezuma*, and *Bombax*. Vasicentric axial parenchyma is also always present.

The greatest variation among genera is in the relative quantities of axial parenchyma and other elements. In some genera, as *Durio*, *Camptostemon*, and *Coelostegia*, the banded axial parenchyma is radially broad (multiseriate) although the bands of fibers remain narrow. In other genera, as *Ceiba*, some *Chorisia*, and *Ochroma*, the axial parenchyma is continuous (confluent) and the imperforate tracheary elements occur singly or in short discontinuous bands or clusters immersed in a ground tissue of parenchyma.

The strand type of axial wood parenchyma is found in most genera, but in *Hampea*, *Ochroma*, and a few other genera, fusiform axial parenchyma is also common. The cells of the strands have generally greater radial and tangential diameters than the imperforate tracheary elements. Strands seldom have fewer than eight cells (*Boschia*, *Cullenia*, etc.), although four are common in *Ochroma*, *Montezuma*, and a few other genera. The cells have a vertical diameter of about twice the radial or tangential diameter and are roughly rectanguloid.

Vascular rays are typically heterogeneous type IIB, although other types occur. Tile cells and sheath cells are common.

The secondary xylem in the stems of *Chorisia*, *Ochroma*, and *Ceiba* resembles most closely the same tissue in the



camote of *Ceiba parvifolia*. In the stem of *Ceiba parvifolia* the axial wood parenchyma, although abundant, has not become the groundmass of the tissue as in the camote. The regular banded to reticulate axial parenchyma is probably homologous to the ordinary axial strand parenchyma of the camote. The very large, loosely arranged parenchymatous water storage cells of the camote are not found in the stem. In the early wood of each season's increment in the stem of *Ceiba pentandra* (kapok), and throughout the secondary xylem in the stems of *Chorisia* and *Ochroma*, ordinary axial wood parenchyma forms the groundmass or continuous part of the tissue. In the camote of *Ceiba parvifolia* the ordinary axial parenchyma and water storage parenchyma together form the groundmass of the secondary xylem.

In summary, the secondary xylem in the stems of *Chorisia*, and *Ochroma* resembles more closely the secondary xylem of the camotes of *Ceiba parvifolia* than the same tissue in the stem of *Ceiba pentandra* or *C. parvifolia*. The secondary xylem of the camote, indeed, the camote itself, is but a bizarre expression of genomic characters already present in many other members of the family.

#### THE NATURE OF THE CAMOTE

The study of the early developmental stages of the water storage organ reveals anatomical features suggestive of both root and stem. Radial arrangement of xylem and phloem is not present; rather, the vascular strands are essentially collateral vascular bundles characteristic of many stems. Although the first indications of growth occur opposite a protoxylem pole of the mother root and hence are root-like, further development is essentially exogenous and cauline, although no distinct meristem is formed. The xylem strands occasionally reveal an exarch arrangement, a root feature of angiospermous primary xylem.

The structure may be a highly modified lateral root; but it has more stem than root features. It is best to regard the camote as an anomalous organ, rather than to categorize it as a root or stem. In some respects early development is not

unlike differentiation in callus tissue, although more organization is evident in the camote.

#### SUMMARY

1. *Ceiba parvifolia* flowers and fruits during the dry season when soil water is inadequate. Water for flowering and fruiting is apparently provided by the root-borne "camotes" which store water during the rainy season.
2. The mature water storage organ is composed largely of secondary xylem. This tissue is composed of anastomosing sheets of ordinary wood parenchyma oriented in a predominantly tangential direction. The sheets of wood parenchyma are intersected and traversed by multiseriate vascular rays. The intervening regions are filled with very large, irregularly arranged, sub-isodiametric parenchymatous cells—the water storage cells. Rare vessels associated with a few imperforate tracheary elements occur within the ordinary axial wood parenchyma or within the intervening regions of large-celled water storage parenchyma.
3. The secondary phloem of the camote is typical of advanced angiosperms.
4. The periderm of the camote is in no way peculiar; both phellem and phelloderm are formed.
5. The meristematic activity of the secondary phloem, cambium, and phellogen of a small root gives rise to the young camote. An anastomosing system of vascular strands develops concomitantly with surrounding ground tissue. The vascular connection between the camote and the mother root is formed by the cambium of the latter.
6. A cambium eventually produces the bulk of the large (30 cm. diameter) water storage organ. The cambium produces cells in a more or less typical fashion. The origin of the cambium of the camote is not fully understood. The possibility of the extension of the original cambial "bulge" of the mother root into the young camote is discussed.
7. A highly parenchymatous xylem is characteristic of Bombacaceae as indicated by the brief comparative survey in this report.



8. The camote is an anomalous organ with characters suggestive of root, stem, and callus.

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## DISCONTINUOUS GROWTH RINGS IN SUPPRESSED SLASH PINE

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### INTRODUCTION

The determination of tree age based on growth ring counts on increment cores is an almost universally accepted practice in temperate regions. Nevertheless, this method is open to criticism, for it is possible to obtain erroneous estimates of age by failure to recognize certain subtleties of ring structure. These often result from anomalous environmental conditions acting upon a single tree or part of a tree. Overestimates of age may be occasioned by false rings (more than one growth ring per growing season), whereas underestimates result from discontinuous and missing rings.

False rings can generally be identified by a relatively narrow summerwood band in close proximity to a wider summerwood band and by the indistinctness of the springwood–summerwood transition. In true rings the boundary between the summerwood of one year and the springwood of the succeeding year is rather abrupt, whereas in false rings the springwood–summerwood boundary is more gradual. These conditions do not always prevail however, and exceptions can often be found.

The problem of ring identification becomes increasingly difficult with discontinuous and missing rings. Glock (1937) has adequately defined discontinuous (locally present) and missing rings as follows: "A ring locally present is one present only in part on the sample or portion of the tree under study: the ring does not surround the entire stem as a continuous sheath. An absent ring is defined as one wholly missing from the sample or part of the tree under study."

On trees in even-aged stands, the presence of discontinuous rings can be readily detected by means of increment borings, by comparing the observed ages of the suppressed trees with the known ages of the dominant trees. The actual identity of the rings which are discontinuous however, can be determined only by examination of entire cross-sectional discs. A similar procedure, involving examination of a series of cross-sections taken at various stem heights, may be used to identify missing rings, but the task is extremely arduous and not always successful.

Age determination of suppressed trees in uneven-aged stands is seldom unequivocal. True ages can only be verified by exhaustive stem analyses, although some investigators have relied on internode counts in conifers (Hartig, 1871; Lakari, 1915; Topcuoglu, 1940). The latter technique is not applicable to species where multinodal growth is of common occurrence.

Numerous workers have mentioned the occurrence of discontinuous and missing rings and several detailed studies have been made of these phenomena. For the most part discontinuous rings described in the literature have been observed in strongly eccentric stems (Rubner, 1910; Lakari, 1915; Fritz and Averill, 1924; Gassner and Christiansen-Weniger, 1942). One explanation for the occurrence of such rings was that in the case of a one-sided crown the greatest number of rings would occur on the stem side possessing the largest portion of the crown (Hartig, 1871).

In even-aged stands suppressed trees have been found to appear younger than the dominants as a result of missing rings (Flury, 1907; Harris, 1952). When such trees were subjected to complete stem analyses the rings were found to reappear at successive heights above the ground.

Microscopic rings have been described by Bailey and Faull (1934) who noted that in old trees of *Sequoia sempervirens*, growth rings may be reduced to two rows of tracheids—one with thin-walled cells and one with thick-walled cells. Rubner (1910) was of the opinion that if a single cell was laid down it would always be a summerwood cell, but if a



springwood cell was formed it would always be followed by a summerwood cell. No reference has been found in the literature to the condition in suppressed trees where springwood merged with springwood without an intervening band of summerwood. On the contrary, several investigators have described this type of ring structure in trees defoliated during the early part of the growing season (Harper, 1913; Nägeli, 1935).

A large number of investigators have encountered incomplete growth rings in their work. Dendrochronological workers, in particular, have frequently reported atypical growth patterns; many of these papers are cited in the reviews of Glock (1937, 1941, 1955) and Studhalter (1955).

The many reports of discontinuous and missing rings are evidence that incomplete rings are of frequent occurrence in trees where growth has been restricted by suppression, over-maturity, defoliation or other factors. Because of the widespread and frequent occurrence of these ring structures, the actual ages of trees determined from increment cores are often open to question if not verified by cross-checking with other trees in the stand. Incomplete rings may be anticipated in suppressed trees where they are a normal consequence of restricted growth and development; hence, they should not be referred to as "abnormal" rings.

#### METHODS AND RESULTS

Trees selected for this study were suppressed specimens of slash pine (*Pinus elliottii* Engelm.) growing on an old-field site in the flatwoods of northeast Florida. The stand was about 32 years old, of average density (360 trees per acre) and showed evidence of heavy mortality as a result of natural competition. Cattle grazed the area freely and in order to "green up the woods" it had been burned almost annually.

The stand was particularly well suited for a study of discontinuous and missing rings since an exceptionally narrow growth ring was produced on all trees in 1931. By using the 1931 ring as a dating point, it was possible to identify

each succeeding growth ring and to determine whether a tree actually had missing rings or was merely representative of a younger age class. To confirm this point, increment cores were collected from 25 trees representing all size classes on a small area within the stand. In every case the 1931 ring was clearly identifiable. Twenty of the trees possessed the full complement of 23 rings—1931 to 1953 inclusive. Counts of the remaining 5 trees indicated less than the normal number of rings. These 5 trees were all suppressed individuals with long, slender boles topped with very sparse crowns. The average d. b. h. measured outside the bark for the 5 trees was 7.4 inches. Average total height was 71 feet and the average crown length only 14 feet.

The 1931 growth ring is indicated by the arrows in figure 1. The 1930 ring was equally narrow or narrower in many of the trees examined. No explanation can be offered for the unusual thinness of these rings, but the most logical interpretation would be the occurrence of a crown-injuring fire. Drought, although possibly a contributing factor, does not in itself appear plausible, since neighboring stands did not exhibit the same peculiar ring structure. The identity of the 1931 ring as a true rather than a false ring was confirmed by tracing this ring through a series of cross-sections cut at various heights above the ground. In all trees the 1930 and 1931 rings appeared well separated and distinct as they approached the pith in upper parts of the stem.

In July 1954, the 5 suppressed trees were cut flush with the ground. From each of these trees cross-sectional discs, one inch in thickness, were cut at 0, 2, 4, 6, 8, 10, 12, 16, 20, and 24-foot levels and at 6-foot intervals thereafter. The discs were lightly sprayed with pentachlorophenol to prevent blue stain and then air dried.

Prior to examination the discs were dry-sanded and then examined with a low power, wide angle field, binocular microscope. Every growth ring subsequent to 1931 was traced around its entire circumference. This detailed examination revealed that on trees 16, 17 and 22 every ring was complete and distinct from the adjacent rings up to the 1945



ring when discontinuities appeared. Trees 5 and 25 exhibited frequent ring fusions prior to 1945, presumably in response to earlier influences of suppression.

To facilitate the tracing of rings around their entire circumference each disc was divided into eight equiangular sectors. Within each sector every ring was followed clockwise and the point at which ring discontinuity began was noted, as well as the point at which the ring again became clearly identifiable. The resulting annual ring diagrams for 10 years, 1944-1953 inclusive, are shown for tree 22 in figures 2A, 2B, 3A, and 3B for the 0, 4, 8, and 16-foot heights respectively. The inward-pointing arrows indicate that the ring from which the arrow originates merges with the ring to which the arrow points. All discontinuous rings encountered in this study were of the fused summerwood type, that is, a fading out of the springwood and a merging or fusion of the summerwood bands. In constructing the ring diagrams only those ring fusions that resulted in completely inseparable summerwood bands were considered as being discontinuous. The discontinuous rings encountered were not always simple ring fusions but often involved several annual increments (fig. 2, 3).

Ring diagrams for trees 5 and 25 were not constructed since it was impossible to trace the extremely narrow rings around the entire periphery. The discontinuous rings in these trees were of the fused summerwood type as observed on the portions of the cross-sections where the outer rings could be identified. However, in neither tree 5 nor 25 were there actually missing rings, since localized areas could be found on all cross-sections where the full ring complement was present. These areas usually occurred as slight peripheral bulges and often were restricted to a single, small region on the cross-section. This condition may have also existed in certain other studies where missing rings were reported but where the entire cross-section in question was not examined. Lakari (1915) admitted to this possibility in his work.

Many investigators who have studied discontinuous rings have done so on eccentric material (Hartig, 1871; Rubner,

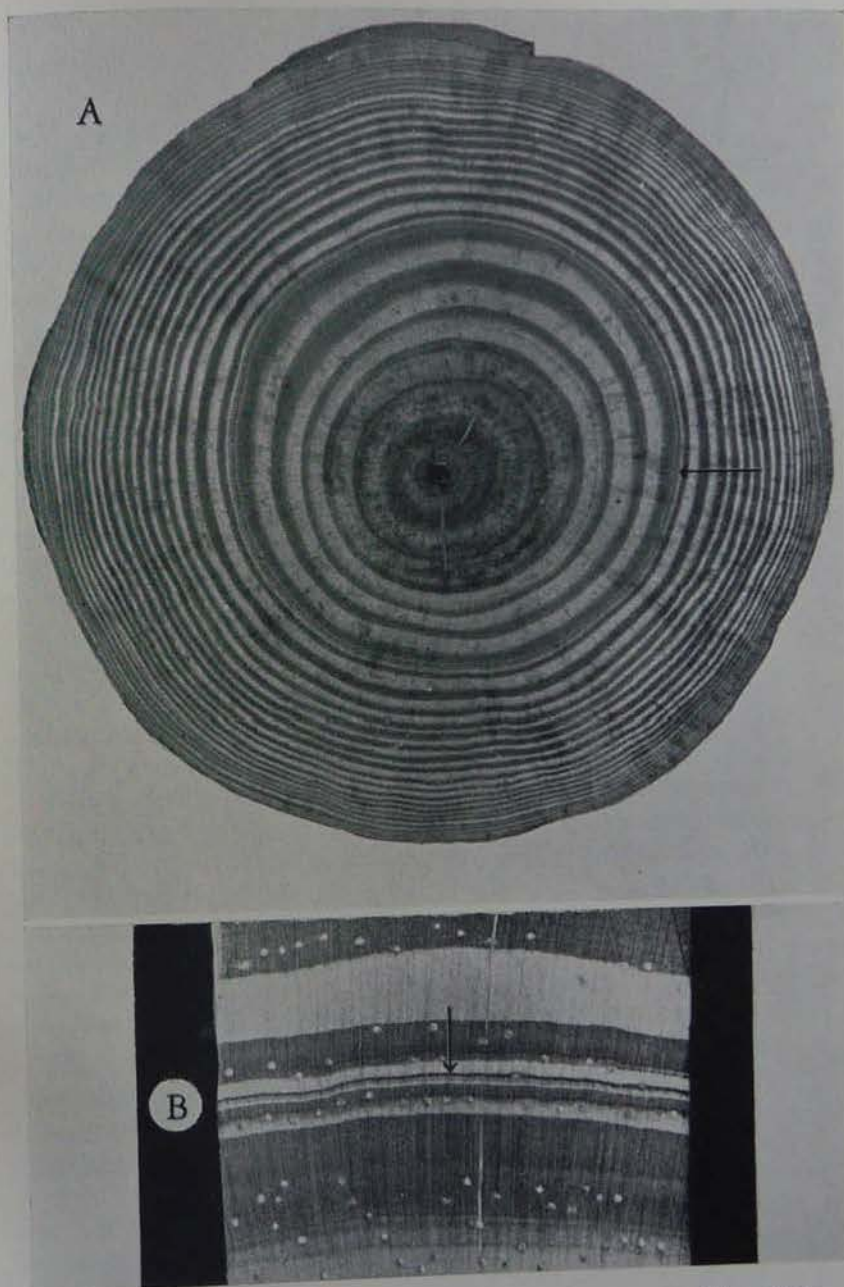


Fig. 1. A. Cross-section of 4-foot level in tree 22. The arrow points to the very narrow growth ring used as a dating point in all trees of the study.  $\times 0.6$ .—B. Enlarged view of the 1931 ring indicated by an arrow.  $\times 8$ .



1910; Lakari, 1915; Fritz and Averill, 1924; Flury, 1926). The eccentric growth pattern generally exhibits a complete complement of rings on the wide radius lying under the major axis of a one-sided crown with the discontinuous rings occurring on the narrow radius below the underdeveloped crown axis. The trees in this study were definitely not eccentric, although compression wood in some of the cross-sections indicated that a slight eccentric condition may have been present in the very early years. Likewise, each crown, although exceedingly small, was fairly well distributed circumferentially with no pronounced one-sidedness at the time of cutting. Presumably as a result of these uniform stem and crown structures, the discontinuous rings occurred more or less at random throughout the suppressed rings as evidenced by the ring diagrams.

Vertical discontinuity appeared to be somewhat more obligate than circuit discontinuity but was traceable through only a few cross-sections. The most obvious example was a very localized fusion of the 1944 and 1945 rings lying between sectors 8 and 1, which could be traced from 0 to 12 feet in tree 22 (fig. 2, 3). The large gap resulting from multiple ring fusions in the upper portions of figures 2 and 3 could also be traced to at least the 8-foot level but with considerable variability in ring structure. The position of this gap appeared to spiral upward in a counter-clockwise direction. Spiral grain is a common phenomenon in trees and it has been previously noted that discontinuous rings may also possess spiral tendencies (Lakari, 1915).

The presence or absence of vertical discontinuity is dependent upon the method of comparison. In figure 5 all fusions between the 1945 and 1946 summerwood bands are diagrammatically presented for all peripheral points with respect to position on the cross-section and height in the tree. This diagram therefore, represents a single annual increment with the solid horizontal lines indicating the actual position on each cross-section where the 1946 springwood failed to form. If vertical discontinuity is measured in a strictly vertical sense, that is, only where a solid line



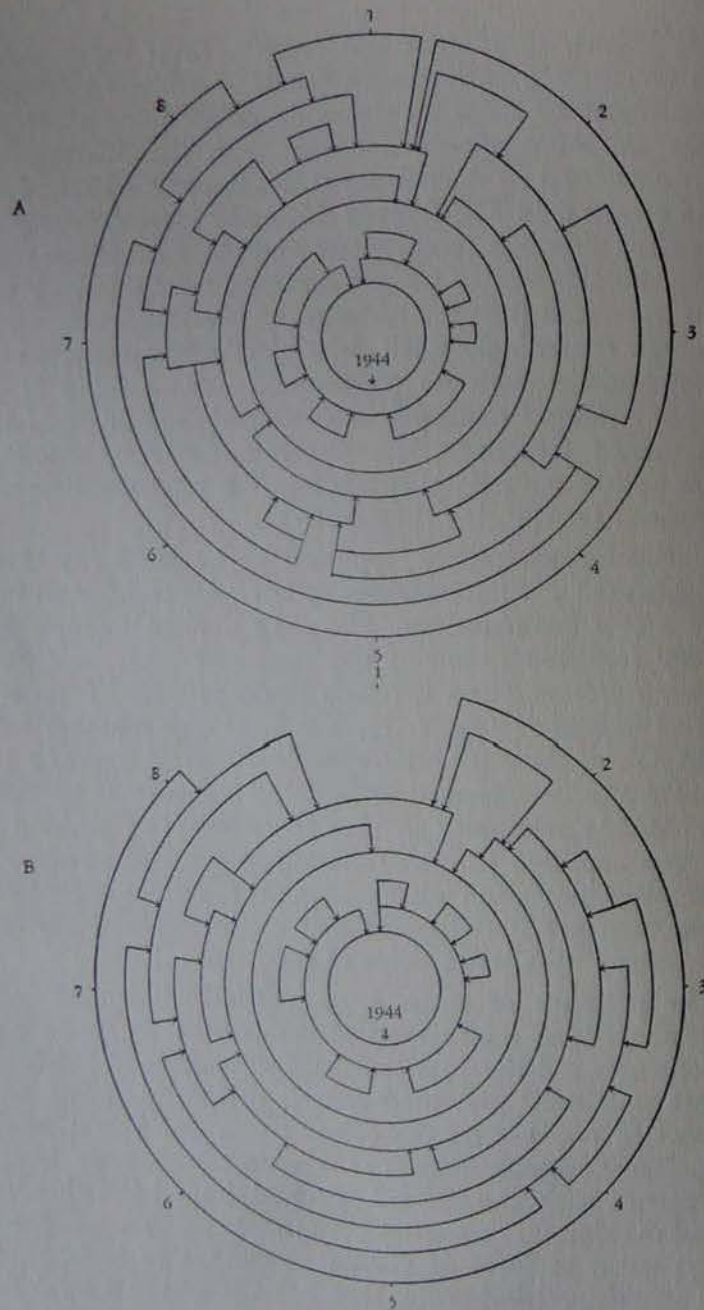


Fig. 2. Annual ring diagrams for the years 1944-1953 inclusive, showing the positions of ring discontinuities on cross-sections of the 0-foot (*A*) and the 4-foot (*B*) levels in tree 22. The inward-pointing arrows indicate that the ring from which the arrow originates merges with the ring to which the arrow points.

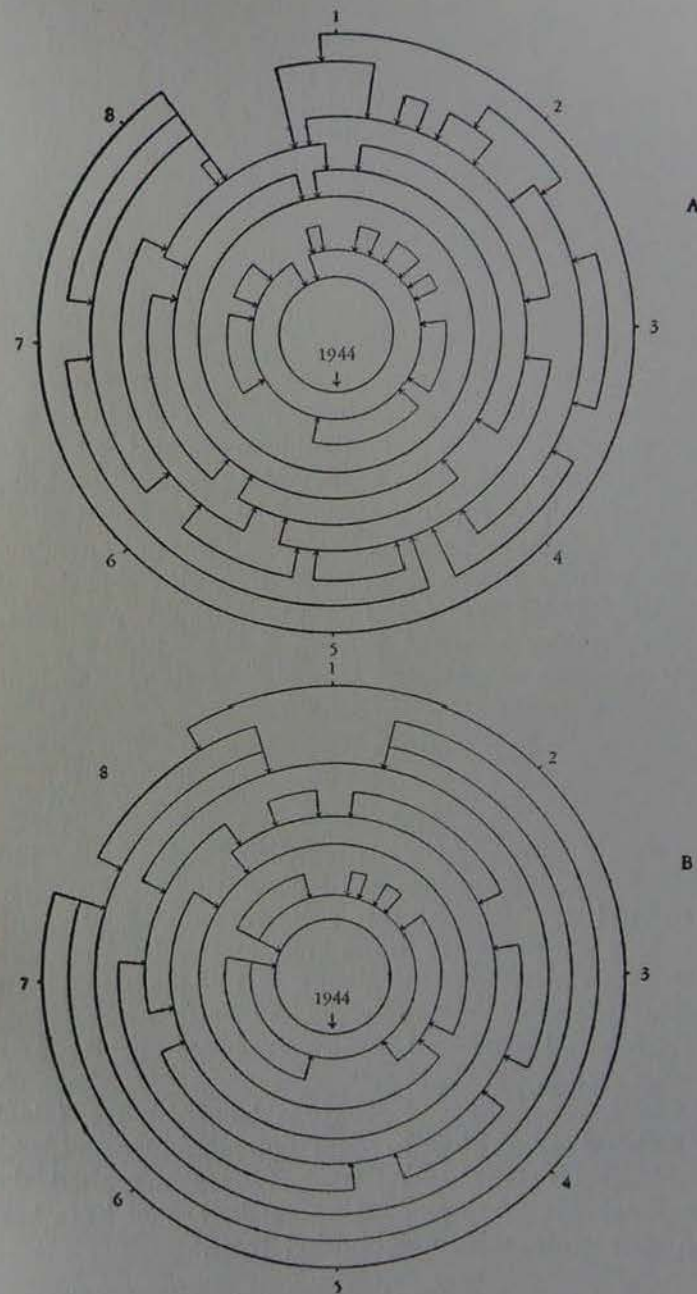


Fig. 3. Annual ring diagrams for the 8-foot (*A*) and the 16-foot (*B*) levels in tree 22.



intercepts a radius, then it will result in a very erratic pattern. On the other hand, if an extensive interconnected series of discontinuities is visualized, as depicted by the dashed lines in figure 5, then the vertical discontinuities will form a fairly regular, although somewhat meandering pattern. The interpretation of this pattern will be discussed later in the paper.

As previously mentioned, all discontinuous rings encountered in this study were of the fused summerwood type. Yet, these occurred in a wide variety of unusual patterns. A number of the most commonly found discontinuities are shown in figure 4. The photographs were made from small blocks cut from the cross-sectional discs. The blocks were surface-smoothed with a sliding microtome and, when dry, the samples were rubbed on a glass plate covered with levigated alumina. The finely powdered alumina filled all cell lumens, resin ducts and radial checks, and not only produced a highly reflective surface but one that also revealed the individual cellular outline. The photographs were made with a vertically-mounted camera fitted with a 32 mm. Micro-tessar lens magnifying about eight times. Maximum contrast was obtained with a Wratten C-5 (blue) filter mounted on the light source.

#### DISCUSSION

The data presented in the preceding sections have indicated an increasing frequency of discontinuous rings from stem top to base. Although this is the most commonly found pattern it is not universal. Some investigators have observed that rings were frequently absent at mid-stem and reappeared at the stem base (Bertog, 1895; Schwarz, 1899), whereas others have noted a more frequent occurrence of incomplete rings in the basal stem parts (Hartig, 1869, 1871; Flury, 1907, 1926; Hine, 1922; Jaccard, 1935; Glock, 1937; Tuberville and Hough, 1939; Topcuoglu, 1940; Harris, 1952). Hartig (1891) and Bertog (1895) suggested that the reappearance of rings at the stem base may have been due to root grafts with neighboring trees.

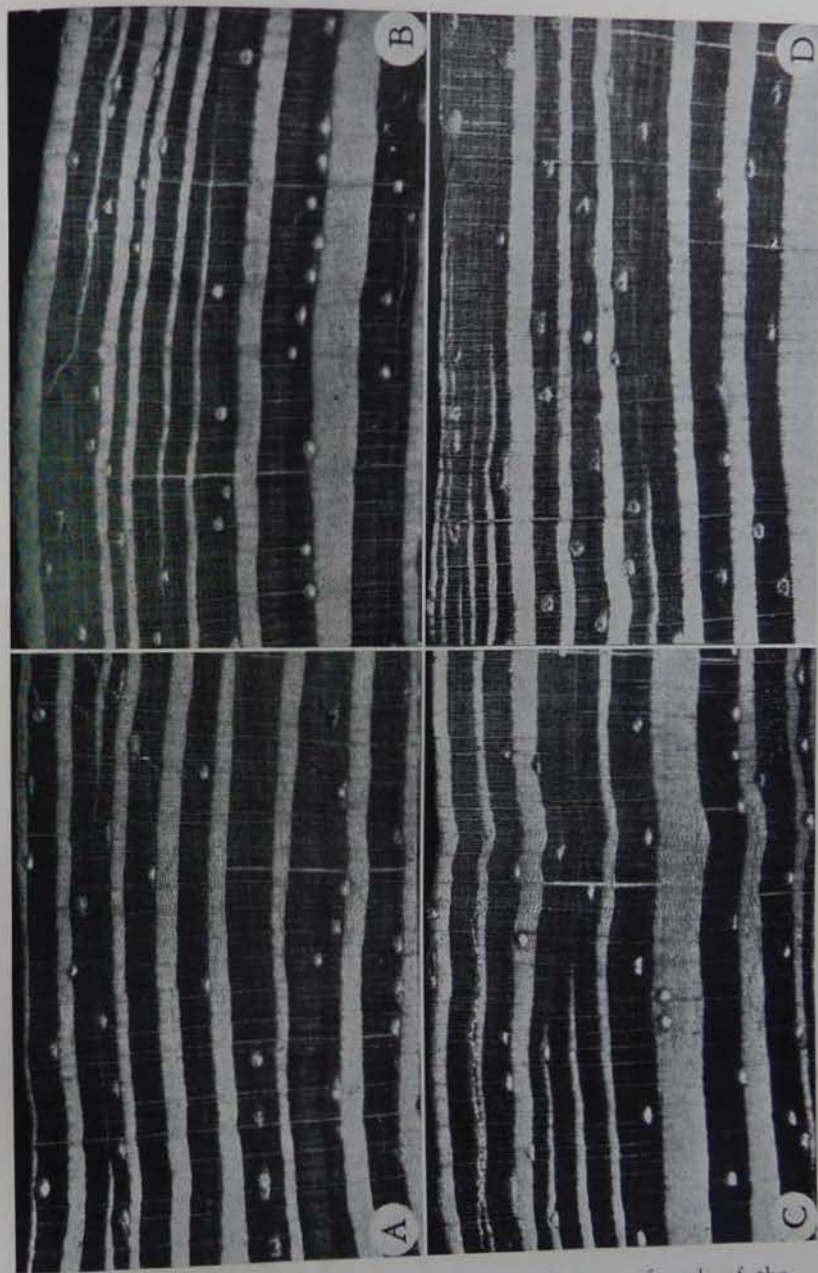


Fig. 4. The 1954 springwood is visible at the top of each of the accompanying photographs; it may be used as a reference for identifying the remaining growth rings. In *D*, the 1954 springwood is discernible as a thin band at the left and center, and is totally absent at the extreme right. *A*. Simple fusion of the 1951-1952 summerwood bands. At the midpoint of the fusion the two rings cannot be distinguished even though the discontinuity extends over a very limited

[Over]



One of the most widely accepted explanations for incomplete rings at the base of suppressed trees has been Hartig's "nutritional theory" which he discussed in numerous publications. He proposed that food materials, elaborated in the crown, would be utilized in the upper stem parts first and would be available to the lower stem parts in progressively decreasing amounts. In presenting this theory in terms of ring width, Hartig (1871, 1891) believed that the growth form of the tree was dependent upon the relationship between crown and stem. If the crown were free and completely developed, then ring width would increase downward in the stem. If the crown were slightly hindered in its development, as in the case of trees in closed stands, then growth in all stem parts would be about equal. However, if the crown were strongly suppressed, ring width would decrease or might be entirely absent in the lower parts of the stem. Although Hartig's nutritional theory has basically had many adherents (Rubner, 1910; Fritz and Averill, 1924; Nägeli, 1935), it has also been modified in various ways to explain certain physiological phenomena (Wieler, 1887; Schwarz, 1899) in addition to peculiar climatic and environmental influences (Haasis, 1933).

The nutritional theory may appear to be a logical explanation for basal missing rings that reappear at progressive heights in the tree and also for discontinuous rings in eccentric stems. Nevertheless, cambial nutrition alone fails to explain the seemingly haphazard year to year distribution of discontinuous rings as observed in the trees under discussion. The radial width of the summerwood bands comprising the ring fusions also casts doubt on the nutritional theory as the causative factor. These summerwood bands were of approximately normal width with respect to closely adjacent portions of the same ring where springwood was present. Thus, the widths of the discontinuous rings were equal to the total widths of the annual rings comprising them less their springwood components.

An alternative hypothesis may be proposed on the basis of our current knowledge of growth hormones. It is known

distance. *B.* To the right the 1948-1949, and to the left the 1949-1950 growth rings, fuse into single summerwood bands. In this case the 1949 ring participates in two simple fusions by crossing over from the 1948 to the 1950 ring. At the upper left the 1952-1953 rings are fused. The lowermost summerwood band consists of a simple fusion of the 1945-1946 rings; several thin points of separation may be seen. *C.* A triple fusion of the 1949, 1950, and 1951 summerwood bands. Note the abrupt fading out of the intervening springwood zones. *D.* Five distinct growth rings, 1949-1953, fuse into a single inseparable summerwood band at the upper right in the photograph. At left center, the 1944 ring is separated from a tightly fused 1945-1946 summerwood band but gradually merges toward the right to form a triple fusion—1944-1946. The four uppermost summerwood bands in the center of the photograph represent the total radial growth for 10 years, 1944-1953 inclusive.



that at the beginning of the growing season cambial activity is initiated just below the expanding buds and progresses downward from this region to all parts of the stem (Priestly, 1930; Priestly, Scott and Malins, 1933; Pessin, 1934; Brown, 1935, 1937; Fraser, 1952). This basipetal extension of cambial activity is preceded in its spread by a growth hormone emanating from the buds, which in some way stimulates cambial divisions (Snow, 1935; Avery, Burkholder and Creighton, 1937; Brown and Cormack, 1937; Söding, 1937). Little, if any, growth hormone can be found in dormant buds but relatively large quantities of readily diffusible auxin can be extracted from developing buds and elongating shoots (Czaja, 1934; Zimmermann, 1936; Mirov, 1941; Gunckel and Thimann, 1949). The movement of this hormone is preponderantly polar (Oserkowsky, 1942; Gregory and Hancock, 1955) and in older twigs it decreases in quantity with increasing distance from the bud (Avery, Burkholder and Creighton, 1937).

The foregoing sequence of events leading to the initiation of cambial activity in normally developed trees is well known, but just where the mechanism could conceivably break down resulting in subnormal cambial development in suppressed stems has received little attention. Investigations have shown that the rapidity with which cambial activity proceeds downward may vary with species, individual tree vigor, certain environmental conditions and position of the buds on the tree. Thus, in old trees and trees with long, clear boles, the resumption of radial growth at the base of the tree may be slower than in young, vigorous trees (Brown, 1912; Priestly, Scott and Malins, 1933; Bannan, 1955) possibly due either to the greater distance or to a weaker intensity of stimulus. The downward spread of cambial activity in conifers progresses with great rapidity and always more rapidly down exposed branches than down shaded branches. In heavily shaded trees this wave of cambial activity advances much more slowly even down the main stem (Priestly, 1932) and may in fact, be too weak to reach the basal stem parts in trees growing under extreme condi-

tions of suppression (Priestly, 1930). These latter facts may be related to the results obtained by Mirov (1941) who found that auxin production was appreciably lower in slow-growing than fast-growing pines and that in slow-growing trees it was also considerably less in the whorl shoots than in the terminals. It is possible that the restricted photosynthetic activity of suppressed trees may further decrease the availability of auxin along the main stem, since it has been suggested (Weintraub and Brown, 1950) that photosynthesis may be necessary for the active transport of growth hormones from the site of production.

On the basis of the forementioned evidence it is conceivable that the abnormal ring structures of suppressed trees may be due to the delayed arrival, or at times to the complete absence, of the growth hormone that initiates cambial divisions. Thus, the delayed stimulation of the cambium in localized areas could result in the initiation of cambial activity during the period of summerwood production, resulting in a growth ring devoid of springwood.

Abnormally low concentrations of auxin in the localized vicinity of ring fusions could be due to its limited production, irregular distribution, or to excessive destruction. In closed stands suppressed trees are continually shaded wholly or in part. This condition, coupled with an under-developed crown which is consequently limited in new bud growth, could seriously retard the production of auxin. The distance over which this limited auxin supply must be transported to reach the lower stem parts is also relatively greater in suppressed trees than in more vigorous individuals due to a smaller crown-length ratio. A similar argument has been used (Hartig, 1869) to support the nutritional theory since it was found that crown reduction as a result of excessive pruning caused radial growth to be shifted upward, whereas it decreased or entirely disappeared at the stem base. Upward and downward displacement of radial growth has also been artificially produced in healthy pines by various debudding experiments (Münch, 1938). However, on the basis of his experiments, Münch rejected the nutritional



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theory and concluded that a hormone produced by the buds, particularly those of the upper crown, regulated the distribution of diameter growth along the stem.

Assuming that the crowns of suppressed trees produce insufficient quantities of auxin to provide for the total requirements of the tree, one must now account for the irregular distribution of this auxin as related to the local failure of the cambium to produce springwood. In pines, bud development progresses from the apex downward and the hormone content of the buds decreases in precisely the same manner (Zimmermann, 1936). The inception of cambial activity originating from these buds parallels this pattern and growth may be proceeding actively on the main stem while the cambium at the base of the lower branches is still dormant (Wight, 1933). In suppressed trees the lowermost branches commonly exhibit an abnormal ring structure which suggests erratic bud development and retarded auxin production. One may thus visualize a downward progression of auxin from the upper crown which would by-pass the lower branches and, being extremely limited in quantity, would result in an elongated area of inactivated cambium below each non-contributing branch. Later production of auxin by these branches would stimulate the cambium for a short distance immediately below them. However, with increasing distance from the crown cambial activity would gradually cease and even in the interjacent areas the over-all pattern would become more disjunctive as more discontinuities arose due to a waning supply of auxin around the entire stem periphery.

Such a hypothetical case is depicted in figure 5. The solid horizontal lines indicate the actual location of fusions between the 1945 and 1946 summerwood bands with respect to position on the cross-section and height in tree number 22. The dashed lines were arbitrarily drawn to illustrate an apparent vertical pattern, although there is no proof that this particular pattern actually existed in the tree. Unfortunately, in this study, the position of branches was not noted and could not be directly related to the occurrence of the vertical discontinuities.

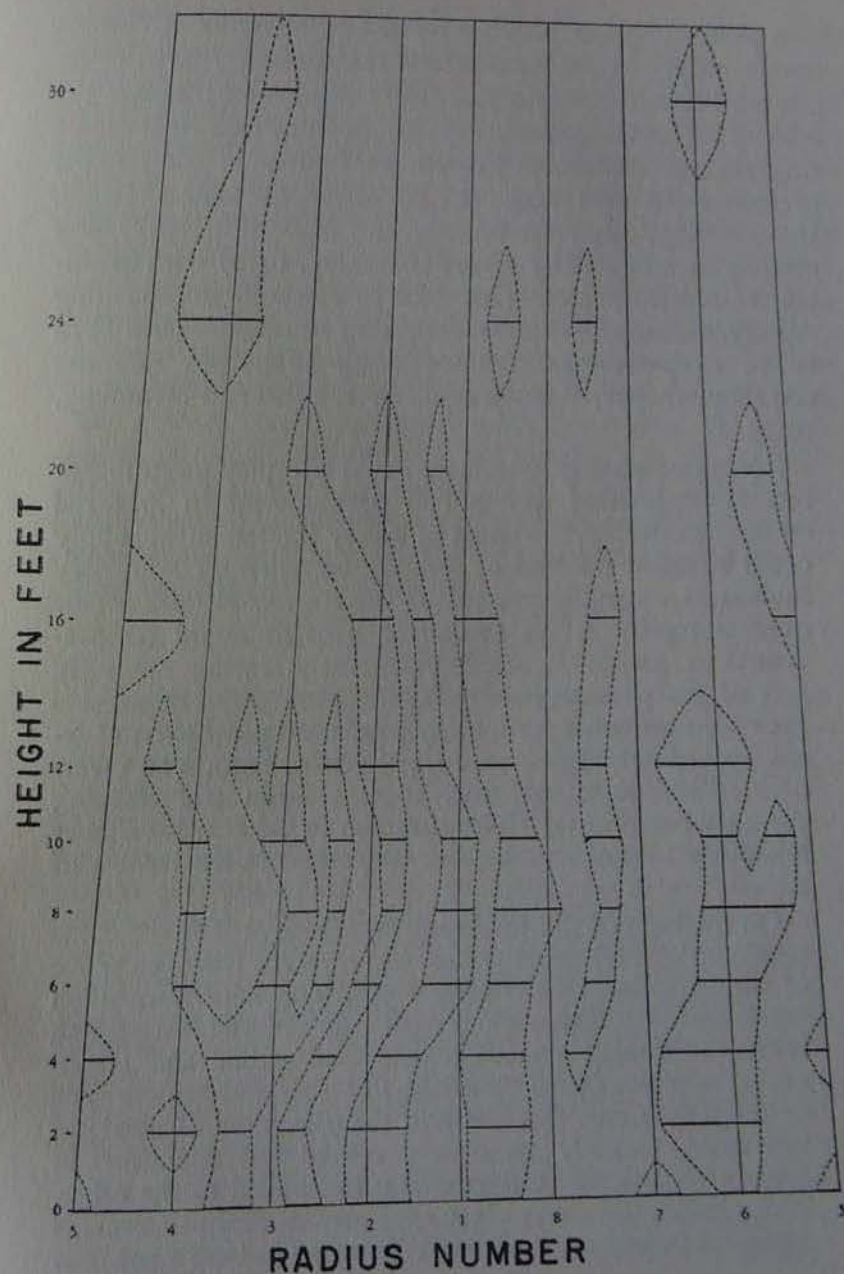


Fig. 5. Vertical distribution of discontinuities for the 1946 ring in tree 22. The solid horizontal lines indicate the actual positions on each cross-section where the 1946 springwood failed to form resulting in



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Assuming that the crowns of suppressed trees produce insufficient quantities of auxin to provide for the total requirements of the tree, one must now account for the irregular distribution of this auxin as related to the local failure of the cambium to produce springwood. In pines, bud development progresses from the apex downward and the hormone content of the buds decreases in precisely the same manner (Zimmermann, 1936). The inception of cambial activity originating from these buds parallels this pattern and growth may be proceeding actively on the main stem while the cambium at the base of the lower branches is still dormant (Wight, 1933). In suppressed trees the lowermost branches commonly exhibit an abnormal ring structure which suggests erratic bud development and retarded auxin production. One may thus visualize a downward progression of auxin from the upper crown which would by-pass the lower branches and, being extremely limited in quantity, would result in an elongated area of inactivated cambium below each non-contributing branch. Later production of auxin by these branches would stimulate the cambium for a short distance immediately below them. However, with increasing distance from the crown cambial activity would gradually cease and even in the interjacent areas the over-all pattern would become more disjunctive as more discontinuities arose due to a waning supply of auxin around the entire stem periphery.

Such a hypothetical case is depicted in figure 5. The solid horizontal lines indicate the actual location of fusions between the 1945 and 1946 summerwood bands with respect to position on the cross-section and height in tree number 22. The dashed lines were arbitrarily drawn to illustrate an apparent vertical pattern, although there is no proof that this particular pattern actually existed in the tree. Unfortunately, in this study, the position of branches was not noted and could not be directly related to the occurrence of the vertical discontinuities.

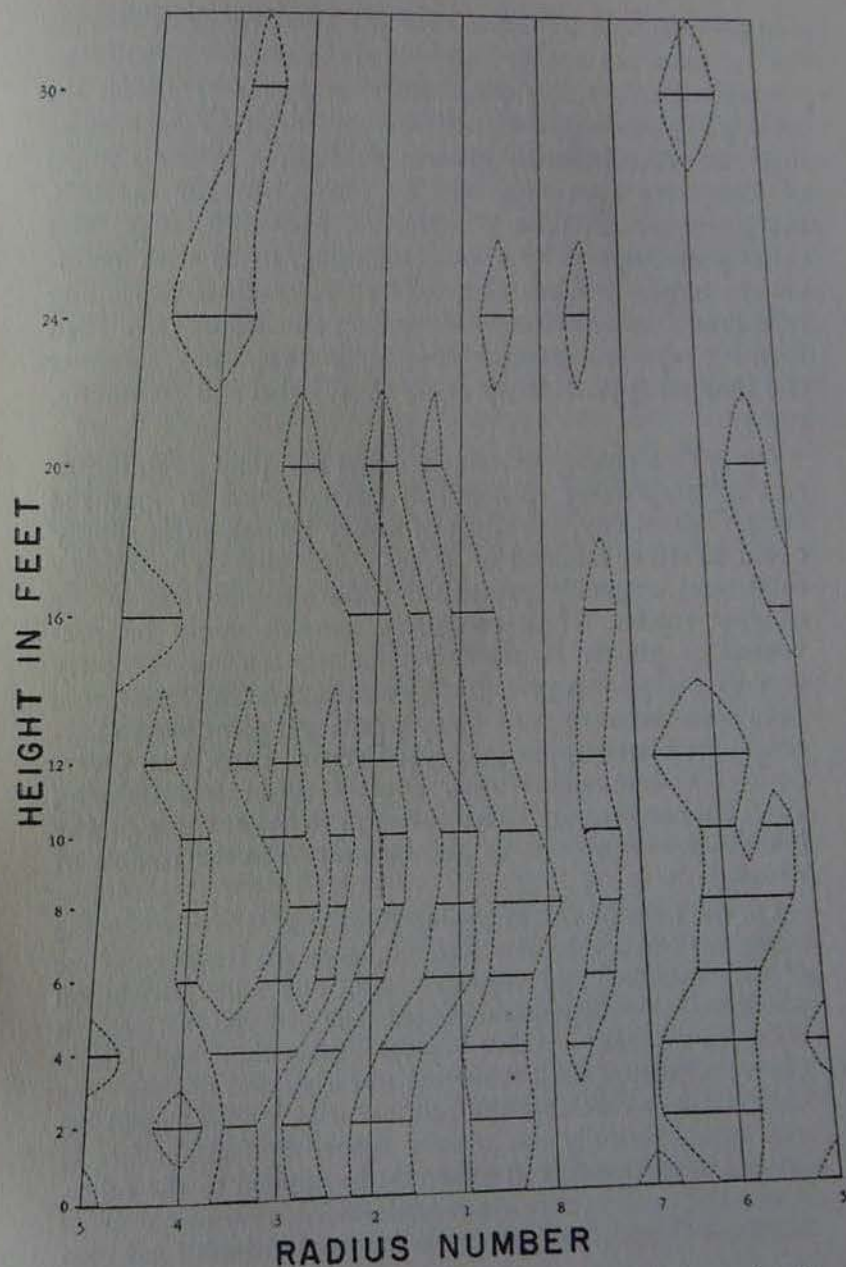


Fig. 5. Vertical distribution of discontinuities for the 1946 ring in tree 22. The solid horizontal lines indicate the actual positions on each cross-section where the 1946 springwood failed to form resulting in fusions of the 1945-1946 summerwood bands. The dashed lines are arbitrarily drawn to illustrate an apparent vertical pattern (see text)



In postulating a hypothesis for the occurrence of discontinuous rings one cannot overlook the possible role of other growth substances that could either augment or inhibit the activity of auxin, particularly in the localized regions of ring fusions. Additional growth substances in the cambium of trees have been suggested by some workers (Münch, 1938; Söding, 1941; Burkholder and McVeigh, 1945) and actively investigated by others (Künning, 1950) with inconclusive results to date. This field of research is expanding rapidly and many naturally occurring substances have been found to possess growth-promoting properties (Bonner and Bonner, 1948; Mauney *et al.*, 1952; Brian and Hemming, 1955).

Growth-inhibiting substances could also play a significant role in suppressing springwood development in localized areas. Conceivably, the effect of a very limited auxin supply could be either nullified or severely curtailed by inhibitory substances originally present or adaptively formed in the cambial region. Thus, secondary growth could be prevented or greatly retarded, particularly during the early part of the growing season. Growth-inhibiting substances have been extracted from many plants and plant parts (Larsen, 1939; Hemberg, 1949, 1954; Evenari, 1949; Van Overbeek, Blondeau and Horne, 1951; Galston and Dalberg, 1954; Libbert, 1955). There is reason to believe that similar inhibitory substances may also be present in the cambium of trees.

On the basis of the foregoing discussion it is felt that the nutritional theory inadequately accounts for the occurrence of discontinuous and missing rings. The same conclusion was reached by Topcuoglu (1940) who believed that growth hormones offered a more logical explanation, and Harris (1952) who suggested "nutrient materials and growth substances." It is true that the two theories, cambial nutrition and auxin, basically are closely related and arguments in favor of one theory can generally be applied to the other. This obtains, since tree vigor expressed in terms of overall bud growth and development is reflected in both food pro-

duction and auxin production. Nevertheless, the cambium must be activated before food materials, whether reserve or otherwise, can be utilized and it is believed that auxin provides this initiating stimulus. Areas of ring discontinuity most probably represent "islands" of auxin deficient cambium during the early part of the growing season, although nutrient materials may be readily available in the adjoining phloem. The factor contributing to the formation of discontinuous rings is therefore suggested as being a localized deficiency of auxin which persists as long as, or longer than, the period of springwood development; activation of the cambium at an earlier date would result in a complete ring but with an underdeveloped springwood zone. In general terms the auxin theory is an old concept, for Jost in 1891 (see Münch, 1938) and other early workers pointed out that even the richest supply of nutrients could not be utilized by the cambium if it was not stimulated to activity by the elongating young buds.

#### SUMMARY

Growth ring counts on increment cores often result in erroneous estimates of tree age. This is particularly true in suppressed trees where discontinuous and missing rings are of frequent occurrence. The discontinuous rings in five slash pine trees from an even-aged stand were traced both circumferentially and vertically on a series of cross-sections taken at frequent intervals of height in these trees. All discontinuous rings encountered were of the fused summerwood type, that is, a fading out of the springwood and a merging or fusion of the summerwood bands; no missing rings were encountered. Annual ring diagrams disclosed very little uniformity in the occurrence of ring discontinuities on the cross-sections but an elongated, meandering pattern of ring discontinuity could be traced in the vertical direction for any one annual ring.

Cambial starvation, as postulated by Hartig's "nutritional theory," is believed inadequate to account for the patterns of discontinuous rings observed in these trees. An alterna-



tive hypothesis is proposed on the basis of evidence accumulated through the years with respect to the effect of auxin in initiating cambial activity at the beginning of the growing season. It is suggested that "islands" of ring discontinuity on the boles of suppressed trees may be due to a localized deficiency of auxin as a result of limitations in bud growth and development in the crowns. The cambia lying within these "islands" would eventually become active later in the growing season during the period of summerwood production; this would account for the fused summerwood type of ring structure. The possible role of additional growth-promoting and growth-inhibiting substances is considered.

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## CRYSTALS IN WOODY TISSUES; PART II

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## INTRODUCTION

In a previous article on the occurrence of crystals in woody tissues (Chattaway, 1955) five different types of crystals were described and their occurrence listed. Such crystals have proved to be of value in wood identification as they are very distinctive in appearance and are of relatively infrequent occurrence. More commonly, however, the crystals found in woody stems cannot be classified in any of these five groups, and the presence of such crystals, although useful in identification, is not of great diagnostic value unless associated with other characters. In a certain number of genera there are modifications of the crystal-containing cells which are sufficiently consistent and infrequent to form useful guides to families and sometimes to genera. These are: 1. the presence of crystals in enlarged cells or idioblasts (fig. 1), 2. changes in the cell wall causing the crystalliferous cell to become sclerosed (fig. 2), 3. the presence of numbers of crystals of variable size and shape in one cell (fig. 3, 4).

## MATERIALS AND DATA

As in the previous paper only genera which were available for examination are given in the main lists; records from literature (Moll and Janssonius, 1906-1936; Metcalfe and Chalk, 1950; Solereder, 1908; etc.) are, as before, listed separately at the end of the paper.

In the rays, crystals may occur in the erect or procumbent cells only, or in both. As this distribution may be of diagnostic value it is listed in two separate columns (1 and 2); if the cells are subdivided this is indicated in a further column (4).

The presence of crystals in the parenchyma is indicated in column 3; subdivision of the strands being added in column 4 when necessary. The subdivision of parenchyma cells by walls or septa is so common that it is seldom a diagnostic feature, but the subdivision of ray cells, though common, is sometimes of great value (fig. 5b). In many genera if both ray and parenchyma cells are crystalliferous, both are subdivided, and for this reason only one column is used for subdivision of crystalliferous cells. Where both ray and parenchyma cells are crystalliferous but only one tissue is subdivided the appropriate letter *r* or *p* in column 4 indicates this fact.

In column 5, headed "Cells enlarged," only those genera are marked in which some crystalliferous cells are considerably larger than other cells of the same tissue (fig. 1); it does not include the rounded cells ("barrel-shaped" of many authors) which are very common in subdivided crystalliferous parenchyma, unless these are accompanied by some cells which are definitely enlarged.

Column 6, headed "Cells sclerosed," includes the genera in which the walls of the crystalliferous cells are thickened so that the crystal fills the entire lumen of the cell, or, as in many Leguminosae, the parenchyma strands are eccentrically thickened. This eccentric thickening is usually found in banded parenchyma, and the thickening is confined to the wall which is contiguous with fibers. It occasionally occurs in parenchyma cells which abut on ray cells. Here, too, the thickening is on the side away from the parenchymatous ray cell and contiguous with the fibers.

Genera in which cells containing many crystals are commonly associated with, or predominate over those containing solitary crystals, are marked in column 7. Often these cells are packed with a mass of crystals of variable sizes; sometimes there will be one crystal which fills a large part of the lumen, the interstices being packed with smaller crystals.



The symbols used in the different columns are to be interpreted as follows:

- = common in all species examined,  
 + = common in 50 per cent or more of the species examined, and  
 - = in less than 50 per cent,  
 × = rare or sporadic.

Numbers in parenthesis following the generic name refer to the number of species examined.

Crystals have from time to time been reported in septate fibers. These will be discussed in a third paper of this series and are not listed here. Crystallographic techniques have not been employed in this survey. The classification followed is that of Bentham and Hooker as modified by Metcalfe and Chalk (1950).

FAMILY	GENERA	1	2	3	4	5	6	7
		RAY: UPRIGHT OR SQUARE CELLS	RAY: PROCUMBENT CELLS	PARENCHYMA	CELLS SUBDIVIDED	CELLS ENLARGED	CELLS SCLEROSED	CRYSTALS VARIABLE IN SIZE AND NUMBER
Acanthaceae	<i>Graptophyllum</i> (1)			□	□			
Aceraceae	<i>Acer</i> (17)		×	×	□			
Akaniaceae	<i>Akania</i> (1)		×					
Alangiaceae	<i>Alangium</i> (5)	□	□	×	×	†		
Aquifoliaceae	<i>Ilex</i> (10)	□	-	×	□			
Anacardiaceae	<i>Astronium</i> (2)	□						
	<i>Blepharocarya</i> (1)	×						
	<i>Bouea</i> (1)	□		□				
	<i>Buchanania</i> (9)	×	×					
	<i>Dracontomelum</i> (2)	□	□					
	<i>Euroschimus</i> (1)	×	×					
	<i>Harpephyllum</i> (1)	□				□		
	<i>Holigarna</i> (1)	×			□			
	<i>Koordersiodendron</i> (1)					□		
	<i>Mangifera</i> (4) <sup>1</sup>	□						×
	<i>Melanochyla</i> (2)	□	□					
	<i>Metopium</i> (1)	□						
	<i>Microstemon</i> (1)	□	□					
	<i>Odina</i> (1)	□	□			×		×

<sup>1</sup>See fig. 3a.

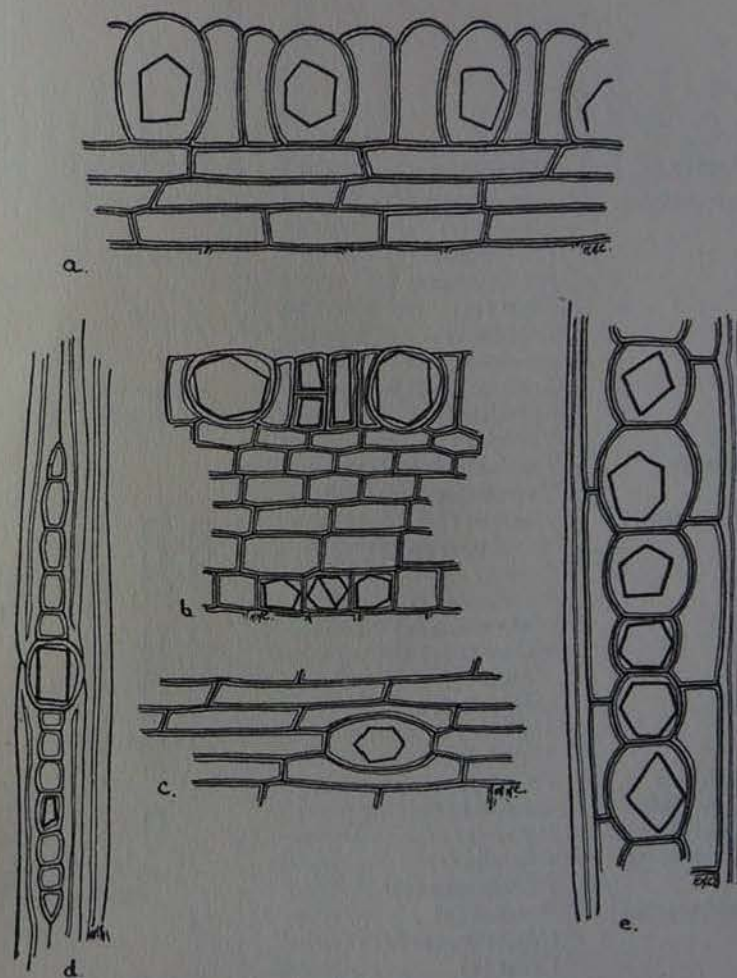


Fig. 1. Enlarged crystal cells. a. *Canarium denticulatum* Bl., enlarged cells on ray margins; b. *Combretum lecananthum* Engl. & Diels, enlarged cells on ray margins; c. *Carpinus carpinoides* Koidz., enlarged procumbent ray cells; d. *Combretum lecananthum* Engl. & Diels, ray cells seen in tangential section; e. *Ceratopetalum apetalum* D. Don, enlarged and subdivided parenchyma cells. × 300.



FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER	
Anacardiaceae	<i>Pentaspadon</i> (2)	□	□					×	
	<i>Pistacia</i> (1)	□	×						
	<i>Pleiogynium</i> (2)	□		□	-p				
	<i>Rhodosphaera</i> (1)	□	□					×	
	<i>Rhus</i> (11)	□	□	-	-p			+	
	<i>Schinus</i> (2)	□	□					×	
	<i>Sclerocarya</i> (1)	□							
	<i>Semecarpus</i> (5)	+		-	-				
	<i>Spondias</i> (3)	□	□	×					
	<i>Tapirira</i> (1)	□							
	Anonaceae	<i>Goniothalamus</i> (1) <sup>2</sup>		□					
		<i>Tetrastemma</i> (1)		□					×
	Apocynaceae	<i>Alstonia</i> (13)		□					×
<i>Aspidosperma</i> (2)				□	□	□			
<i>Cerbera</i> (4)				-	□	□			
<i>Ervatamia</i> (3)		□						□	
<i>Holarrhena</i> (1)				□	□	□			
<i>Kibatalia</i> (1)				□	□	□			
<i>Kopsia</i> (1)		□			□	□			
<i>Occhrosia</i> (1)			□		□	□			
<i>Vallaris</i> (1)				□	□	□			
<i>Wrightia</i> (5)			□		□	□			
Araliaceae		<i>Pseudopanax</i> (1)		□					×
Balanopsidaceae		<i>Balanops</i> (1)	□	□					
Berberidaceae		<i>Berberis</i> (1)	×	□					×
Bignoniaceae	<i>Couralia</i> (1) <sup>3</sup>		×					×	
	<i>Diplanthera</i> (1) <sup>3</sup>		×						
Bombacaceae	<i>Bombax</i> (2)	×	×	□					
	<i>Camptostemon</i> (1)		□	×					
	<i>Ceiba</i> (1)	□		×					
	<i>Coelostegia</i> (1)			×					
	<i>Durio</i> (4)			×	□				
	<i>Gossampinus</i> (1)			×					
	<i>Neesia</i> (1)			□	×			×	
	<i>Salmalia</i> (1)	□		□	×	p			
	Boraginaceae	<i>Bourreria</i> (1)		□					□
		<i>Cordia</i> (5)	□	□	×				

<sup>2</sup>See fig. 5a, crystals rounded and not angular.<sup>3</sup>Similar to fig. 5a.

FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER	
Burseraceae	<i>Boswellia</i> (1)	□	□						
	<i>Canarium</i> (25) <sup>4</sup>	□	-	×	-	-		×	
	<i>Dacryodes</i> (11)	-							
	<i>Garuga</i> (2)	□	□	×	×			×	
	<i>Haplolobus</i> (3)	□	□			+			
	<i>Protium</i> (3)	+				-			
	<i>Trioma</i> (1)	□							
	Casuarinaceae	<i>Casuarina</i> (12)	+	+	□	□			
		<i>Celastraceae</i>							
	Celastraceae	<i>Canotia</i> (1)	×	□	×	□ <sup>p</sup>			
<i>Celastrus</i> (2)		□	□	×	□				
<i>Denhamia</i> (2)		□	□	×	□				
<i>Elaeodendron</i> (2)		□	□						
<i>Gymnosporia</i> (1)		×		□	□				
<i>Lophopetalum</i> (2)				□	□				
<i>Peripterygia</i> (1)				□	□				
<i>Schaefferia</i> (1)		□	×						
<i>Siphonodon</i> (2)		□	□			×			
<i>Solenospermum</i> (1)				□	□				
Cercidiphyllaceae		<i>Cercidiphyllum</i> (1)	×						□
Chenopodiaceae		<i>Kochia</i> (1)	□						□
Combretaceae		<i>Anogeissus</i> (3)	□		+				
	<i>Combretum</i> (3) <sup>5</sup>	-		×		-		×	
	<i>Conocarpus</i> (1)	□						□	
	<i>Macropteranthes</i> (2)			-	□			□	
	<i>Terminalia</i> (33)	-		-	×			□	
Compositae	<i>Olearia</i> (4)							□	
Coniferae	<i>Abies</i> (16)		×						
	<i>Cedrus</i> (2)		×						
	<i>Keteleeria</i> (1)		×						
	<i>Picea</i> (9)		×						
	Connaraceae	<i>Connarus</i> (1)			□	□			
Convolvulaceae	<i>Ipomoea</i> (1)			×				□	
Cornaceae	<i>Curtisia</i> (1)		□						
	<i>Griselinia</i> (2)		+						
	<i>Mastixia</i> (2)		×						
Corylaceae	<i>Carpinus</i> (4) <sup>6</sup>		×		×	×			
	<i>Ostrya</i> (3)		×			×			

<sup>4</sup>See fig. 3a.<sup>5</sup>See fig. 1b, d.<sup>6</sup>See fig. 1c.



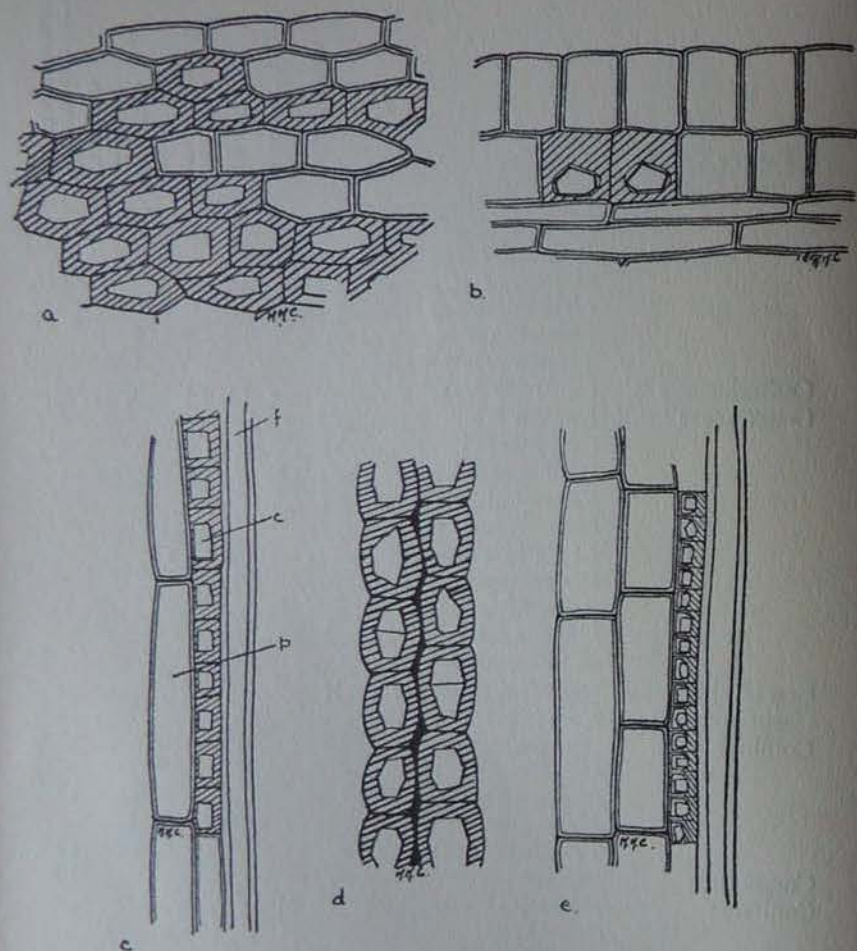


Fig. 2. Thick walled (sclerosed) crystal cells. *a.* *Loranthus dependens* Engl., ray cells; *b.* *Randia exaltata* Griff., ray cells; *c.* *Galbulimima baccata* F. M. Bail., parenchyma cells; *c.*, crystal in eccentrically thickened cell, *p* and *f*, contiguous parenchyma and fiber cells; *d.* *Trochocarpa laurina* R. Br., symmetrically thickened parenchyma cells; *e.* *Archidendron vaillanti* F. Muell., eccentrically thickened parenchyma cells. In *c* and *e* the thickening is regularly on the side contiguous with fibrous tissue.  $\times 300$ .

FAMILY	GENERA	1	2	3	4	5	6	7	
		RAY: UPRIGHT OR SQUARE CELLS	RAY: PROCUMBENT CELLS	PARENCHYMA	CELLS SUBDIVIDED	CELLS ENLARGED	CELLS SCLEROSED	CRYSTALS VARIABLE IN SIZE AND NUMBER	
Corynocarpaceae	<i>Corynocarpus</i> (1)	□							
Cunoniaceae	<i>Ackama</i> (4)			□	□	□			
	<i>Aistopetalum</i> (1)			□	□	□			
	<i>Ceratopetalum</i> (4) <sup>7</sup>	+		□	□	□	□		
	<i>Codia</i> (3)			□	□	□	□		
	<i>Cunonia</i> (3)			□	□	□	□		
	<i>Geissois</i> (7)			□	□	□	□	×	
	<i>Pancheria</i> (3)			□	□	□	□		
	<i>Pseudoweinmannia</i> (1)			□	□	□	□	×	
	<i>Pullea</i> (1)			□	□	□	□		
	<i>Schizomeria</i> (4)	×		×	□	□	□		
	<i>Spiraeopsis</i> (5)			+	□	□	□		
	<i>Weinmannia</i> (6)			□	□	□	□		
	<i>Vesselowskyia</i> (1)			□	□	□	□		
	Davidsoniaceae	<i>Davidsonia</i> (1)			□	□	□		
	Dipterocarpaceae	<i>Balanocarpus</i> (2)	□	×					
<i>Dryobalanops</i> (4)				×	□				
<i>Hopea</i> (15)		+	+	—	—	—			
<i>Parashorea</i> (3)		□	□	—	□	□			
<i>Pentacme</i> (2)		□	□	—	×	—	+		
<i>Shorea</i> (38)		□	□	—	×	—	—		
<i>Vateria</i> (1)		□	□	—	□	—	—		
<i>Vatica</i> (8)		+	×	□	+	—	—		
Ebenaceae		<i>Diospyros</i> (29)	×	+	—	□	—		
		<i>Maba</i> (6)	×	+	+	□	—		
Elaeocarpaceae	<i>Aceratium</i> (1)	□						×	
	<i>Aristotelia</i> (2)	+		+	□	□			
	<i>Dubouzetia</i> (1)	□		□	□	□			
	<i>Elaeocarpus</i> (24) <sup>8</sup>	□	×	×	□	□			
	<i>Sloanea</i> (11)	□	□					×	
Epacridaceae	<i>Leucopogon</i> (1)			□	□				
	<i>Monotoca</i> (2) <sup>9</sup>			+	+		□		
	<i>Trochocarpa</i> (1) <sup>9</sup>			+	□	□	□		
Ericaceae	<i>Oxydendrum</i> (1)			×	□	□		—	
Erythroxylaceae	<i>Erythroxylum</i> (2)			□	□				
Escalloniaceae	<i>Quintinia</i> (2)			+	□				

<sup>7</sup>See fig. 1c.

<sup>8</sup>See fig. 5b.

<sup>9</sup>See fig. 2d; *Monotoca*, similar to *Trochocarpa*.



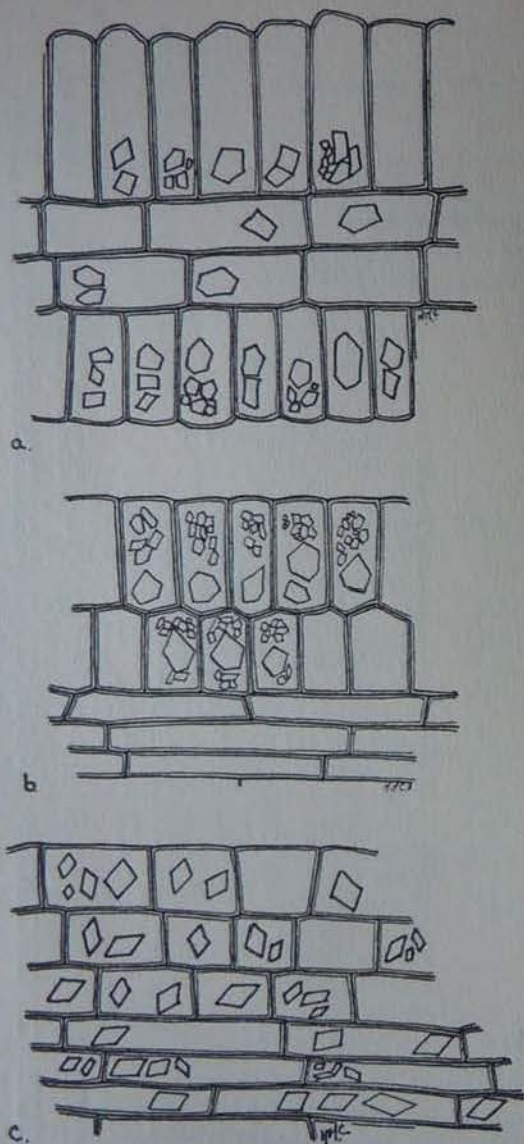


Fig. 3. Crystals variable in size and number, more than one or two per ray cell. *e. Mangifera salomonensis* C. T. White; *b. Ervatamia eriophora* Mgf.; *c. Gnetum costatum* L.  $\times 300$ .

FAMILY	GENERA	1	2	3	4	5	6	7
		RAYS, UPRIGHT OR SQUARE CELLS	RAYS: PROCUMBENT CELLS	PARENCHYMA	CELLS SUBDIVIDED	CELLS ENLARGED	CELLS SCLEROSED	CRYSTALS VARIABLE IN SIZE AND NUMBER
Euphorbiaceae	<i>Acalypha</i>	□						
	<i>Actephila</i> (2)	+			□			
	<i>Aleurites</i> (2)	□		+	□			
	<i>Aporosa</i> (2)	□	□	+	□			
	<i>Baccaurea</i> (3)	+	+	×	×	p		
	<i>Baloghia</i> (1)	□	×	×				
	<i>Beyeria</i> (1)	□	×					
	<i>Bischoffia</i> (1)	□	×	×	×	p		
	<i>Blumeodendron</i> (1)	□		×	×	□		
	<i>Bridelia</i> (2)				□	□		
	<i>Chaetocarpus</i> (1)				□	□		
	<i>Cleidion</i> (1)					□		
	<i>Cleistanthus</i> (1)	×	×					
	<i>Codiaeum</i> (2)	□						
	<i>Croton</i> (4)		□	+				×
	<i>Cyclostemon</i> (1)	□			□	□		
	<i>Dissiliaria</i> (1)				□	□		
	<i>Drypetes</i> (2)	□	×		□	□		
	<i>Elateriospermum</i> (1)	□			□	□	p	
	<i>Endospermum</i> (5)	□			□	□	p	
	<i>Excoecaria</i> (3)		□	×	×	×	r	
	<i>Fontainea</i> (1)	×	×					
	<i>Glochidion</i> (7)	+	×	×			□	
	<i>Hemicyclia</i> (2)	□		×	×			×
	<i>Hevea</i> (1)	□		×	×			×
	<i>Hieronyma</i> (1)	□		□	□	□		
	<i>Hippomane</i> (1)	□		□	□	□		
	<i>Homalanthus</i> (2)	□	×	×	×	×		
	<i>Hura</i> (1)		□	□	□	□		
	<i>Jatropha</i> (1)	□		×	×	×		×
	<i>Joannesia</i> (1)			×	×	×		
	<i>Longetia</i> (1)			×	×	×		
<i>Macaranga</i> (8)	+		+	+	+			
<i>Mallotus</i> (7)	□	-		□	□			
<i>Manihot</i> (1)	×	×		□	□		×	
<i>Melanolepis</i> (1)	×			×	×			
<i>Neoguillauminia</i> (1)	□	□						
<i>Neoscortechinia</i> (2)	□	×	□	□				



FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER
Euphorbiaceae	<i>Ostodes</i> (2)			☐	☐			
	<i>Phyllanthus</i> (4)	☐	☐					
	<i>Pimeleodendron</i> (2)	+		☐	☐			×
	<i>Richeria</i> (2)	+		☐	☐			
	<i>Sapium</i> (3)	×	×	×	☐			
	<i>Securinega</i> (2)	☐	☐					
	<i>Trewia</i> (1)	☐			☐			
Fagaceae	<i>Castanea</i> (7) <sup>10</sup>			+	☐		+	
	<i>Castanopsis</i> (3)			☐	☐			
	<i>Fagus</i> (4)		-			☐		
	<i>Lithocarpus</i> (3)	×	☐	×	☐			
	<i>Nothofagus</i> (20)			+				
	<i>Pasania</i> (4)		+	☐	☐			
	<i>Quercus</i> (35)		+	+	☐			
	<i>Shiia</i> (2)			☐	☐			

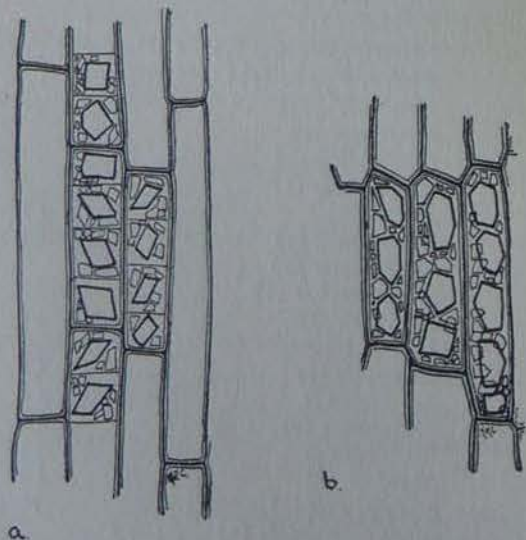
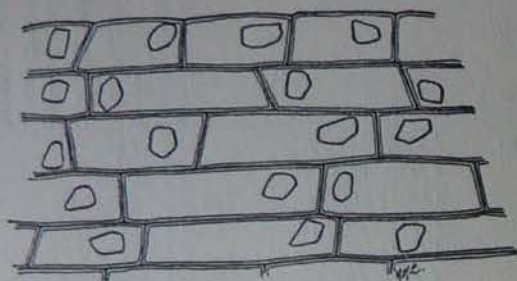
<sup>10</sup>Eccentric thickening.

Fig. 4. Crystals variable in size and number, more than one or two per parenchyma cell. a. cells subdivided, *Eugenia corynantha* F. Muell.; b. *Piliocalyx* sp., cells undivided. × 300.

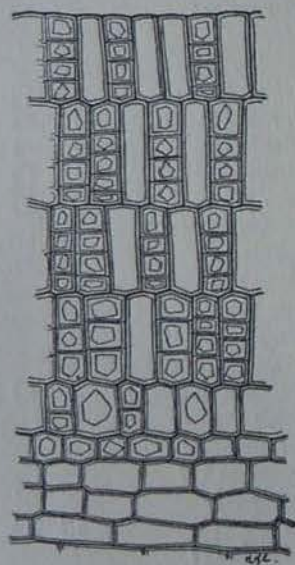
FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER	
Flacourtiaceae	<i>Casearia</i> (7)	☐	☐						
	<i>Flacourtia</i> (2)	☐	☐					×	
	<i>Gossypiospermum</i> (1)	☐	×						
	<i>Homalium</i> (6)	☐	×	×	×				
	<i>Hydnocarpus</i> (2)	×	×						
	<i>Laetia</i> (2)	☐	☐						
	<i>Lindackeria</i> (1)	×	×						
	<i>Pangium</i> (1)	☐		☐					
	<i>Ryania</i> (1)	×							
	<i>Ryparosa</i> (1)	☐	☐			+			
	<i>Scolopia</i> (4)	☐			☐				
	<i>Scottellia</i> (1)	☐	×						
	<i>Trichadenia</i> (1)	☐	☐	×					
	<i>Xylosma</i> (1)	☐	☐						
	<i>Zuelania</i> (1)	☐	☐						
	Gnetaceae	<i>Gnetum</i> (2) <sup>11</sup>		☐					☐
	Gonystylaceae	<i>Gonystylus</i> (2)		☐	×				☐
Guttiferae	<i>Calophyllum</i> (16)			☐	☐				
	<i>Garcinia</i> (10)		×	☐	☐	☐			
	<i>Mannea</i> (1)			☐	☐	☐			
	<i>Mesua</i> (1)			☐	☐	☐			
	<i>Montrouziera</i> (1)			×	☐	☐			
	<i>Ochrocarpus</i> (4)			☐	☐	☐			
	<i>Pentaphalangium</i> (1)		☐	☐	☐	☐			
	<i>Platonia</i> (1)			×	☐	☐			
	<i>Poeciloneuron</i> (1)			☐	☐	☐			
	<i>Symphonia</i> (1)			☐	☐	☐			
	Hamamelidaceae	<i>Altingia</i> (1)	×	×					
		<i>Ostrearia</i> (1)	☐	☐					
		<i>Rhodoleia</i> (1)	×		×	☐			
Himantandraceae	<i>Symingtonia</i> (1)	☐	×		×				
	<i>Galbulimima</i> (1) <sup>12</sup>	×		☐	☐			☐	
Hippocrateaceae	<i>Salacia</i> (2)	☐			-				
Humiriaceae	<i>Saccoglottis</i> (1)			☐	☐				
Icacinaeae	<i>Apodytes</i> (2)	☐	☐		☐				
	<i>Citronella</i> (2)		☐		+			☐	
	<i>Gonocaryum</i> (1)	☐	☐		×				

<sup>11</sup>See fig. 3c.<sup>12</sup>See fig. 2c.





a.



b.

Fig. 5. a. *Goniothalamus grandiflorus* (Warb.) Boerl., crystals with rounded edges; b. *Elaeocarpus pseudosepikanus* O. C. Schmidt, crystals in subdivided ray cells.  $\times 300$ .

FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSH	7 CRYSTALS VARIABLE IN SIZE AND NUMBER
Icacinaceae	<i>Lasianthera</i> (1) <sup>13</sup>		☐	×	☐		☐	
	<i>Medusanthera</i> (1)		×					
	<i>Pennantia</i> (1)		×					
	<i>Rhyticaryum</i> (1)	☐	☐	☐				×
	<i>Stemonurus</i> (3)		—					×
	<i>Tylecarpus</i> (1)	☐	☐					
	<i>Urandra</i> (2)		×					
Juglandaceae	<i>Engelhardtia</i> (3)			+				
	<i>Hicoria</i> (2)			+		×		
	<i>Juglans</i> (6)			+	☐	×		
Lecythidaceae	<i>Barringtonia</i> (10)	☐	☐					×
	<i>Bertholletia</i> (1) <sup>14</sup>			☐			☐	
	<i>Couroupita</i> (1)			☐	☐			
	<i>Eschweilera</i> (8) <sup>14</sup>			+	☐		☐	
	<i>Lecythis</i> (2) <sup>14</sup>			+	☐		☐	
	<i>Planchonia</i> (4)	×	×	×	☐ <sub>p</sub>			
Leguminosae	<i>Acacia</i> (42)		×	☐	☐ <sub>p</sub>	—		
	<i>Acrocarpus</i> (1)	☐						×
	<i>Adenanthera</i> (3)			☐	☐			
	<i>Afzelia</i> (1) <sup>14</sup>			☐	☐		☐	
	<i>Albizzia</i> (14) <sup>14</sup>			+	☐		☐	
	<i>Aldina</i> (1)			☐	☐			
	<i>Andira</i> (1)			×	☐			
	<i>Archidendron</i> (3) <sup>14</sup>			☐	☐		☐	
	<i>Barklya</i> (1)			☐	☐			
	<i>Baubinia</i> (4)			☐	☐			
	<i>Brachystegia</i> (1) <sup>14</sup>			☐	☐		☐	
	<i>Caesalpinia</i> (2)			×	☐			
	<i>Cassia</i> (2)			☐	☐			
	<i>Castanospermum</i> (1)			×	☐			
	<i>Cercidium</i> (2)		×	×	☐			
	<i>Cercis</i> (2)			☐	☐			
	<i>Chloroleucon</i> (1) <sup>14</sup>			☐	☐		☐	
	<i>Cladrastis</i> (1)			×	☐			
	<i>Clathrotropis</i> (2) <sup>14</sup>			☐	☐			
<i>Cynometra</i> (2)	☐	☐	×	☐ <sub>p</sub>				
<i>Dalbergia</i> (6) <sup>14</sup>	×		☐	☐ <sub>p</sub>			×	

<sup>13</sup>Similar to fig. 2b.

<sup>14</sup>Eccentric thickening; see fig. 2e.



FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER
Leguminosae	<i>Daniella</i> (1)	×			□			
	<i>Derris</i> (1)			□	□			
	<i>Desmodium</i> (2)			+	□			
	<i>Dialium</i> (6)			□	□			
	<i>Diploptropis</i> (1)			×	□			
	<i>Dipteryx</i> (1)			×	□			
	<i>Erythrina</i> (3) <sup>14</sup>			—	□		□	
	<i>Erythrophloeum</i> (3)			□	□			
	<i>Fissicalyx</i> (1)			□	□			
	<i>Flemingia</i> (1)			□	□			
	<i>Gleditschia</i> (1)			×	□			
	<i>Gossweilerodendron</i> (1)			×	□			
	<i>Guilandina</i> (1)		□	□	□	p		
	<i>Gymnocladus</i> (1)			×	□	□		
	<i>Hardwickia</i> (1)			□	□	□		
	<i>Hymenaea</i> (1)			×	□	□		
	<i>Indigofera</i> (1)		□	□	□	□		
	<i>Inga</i> (1)			□	□	□		
	<i>Inocarpus</i> (1)			□	□	□		
	<i>Imisia</i> (2)			□	□	□		
	<i>Isoberlinia</i> (2) <sup>14</sup>			□	□	□		□
	<i>Kingiodendron</i> (2)		+	+	□	□		
	<i>Koompassia</i> (3)		—	—	□	□		
	<i>Leucaena</i> (1)			□	□	□		
	<i>Lonchocarpus</i> (1)			□	□	□		
	<i>Maniltoa</i> (1)		□	□	□	□		
	<i>Millettia</i> (1) <sup>14</sup>			□	□	□		□
	<i>Mora</i> (2)			□	□	□		
	<i>Ougeinia</i> (1)			□	□	□		
	<i>Ormosia</i> (1)			□	□	□		
	<i>Pavudia</i> (2) <sup>14</sup>			□	□	□		□
	<i>Parkia</i> (2) <sup>14</sup>			□	□	□		□
	<i>Peltogyne</i> (1)			×	□	□		
	<i>Peltophorum</i> (2)			□	□	□		
	<i>Piptadenia</i> (1) <sup>14</sup>			□	□	□		□
	<i>Pithecolobium</i> (6) <sup>14</sup>			+	□	□		□
<i>Plathymenia</i> (1)			×	□	□			

<sup>14</sup>Eccentric thickening; see fig. 2e.

FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER	
Leguminosae	<i>Podopetalum</i> (1) <sup>14</sup>			□	□			□	
	<i>Pongamia</i> (2) <sup>14</sup>			□	□			□	
	<i>Prosopis</i> (4)		—	□	□	p			
	<i>Pseudosindora</i> (1) <sup>14</sup>			□	□	□		□	
	<i>Pterocarpus</i> (7)			□	□	□			
	<i>Rhynchoscarpa</i> (1)			□	□	□			
	<i>Robinia</i> (2)		□	□	□	p			
	<i>Samanea</i> (1) <sup>14</sup>			□	□	□		×	
	<i>Serianthes</i> (1) <sup>14</sup>			□	□	□		□	
	<i>Sesbania</i> (1)		×	×	□	p			
	<i>Sindora</i> (7) <sup>14</sup>			□	□	□		□	
	<i>Smithia</i> (1) <sup>14</sup>			×	□	□		□	
	<i>Sophora</i> (2)		+	×	□	□		□	
	<i>Stryphnodendron</i> (2) <sup>14</sup>			□	□	□		□	
	<i>Swartzia</i> (3) <sup>14</sup>			□	□	□		□	
	<i>Tamarindus</i> (1) <sup>14</sup>			□	□	□		□	
	<i>Vatairea</i> (1)			×	□	□		□	
	<i>Wallaceodendron</i> (1) <sup>14</sup>			□	□	□		□	
	<i>Xylia</i> (2)			□	□	□			
	Linaceae	<i>Ctenolophon</i> (1)	×		□	□			□
	Loganiaceae	<i>Strychnos</i> (3)		—	□	□			
	Loranthaceae	<i>Loranthus</i> (1) <sup>15</sup>		□	□	□		□	
	Lythraceae	<i>Lagerstroemia</i> (5)			□	□			
Malpighiaceae	<i>Bunchosia</i> (1)	□		×					
Malvaceae	<i>Abutilon</i> (1)	×	×						
	<i>Cephalobibiscus</i> (1)	×							
	<i>Cienfuegosia</i> (1)	×							
	<i>Hibiscus</i> (6)	+		+					
	<i>Kydia</i> (1)	×							
	<i>Lagunaria</i> (1)	□	□	□					
	<i>Malvaviscus</i> (1)	□						×	
	<i>Papuodendron</i> (1)	□		×				×	
	<i>Thespesia</i> (1)	□		×					
Meliaceae	<i>Aglaia</i> (6)			+	□				
	<i>Amoora</i> (4)			×	□				
	<i>Azadirachta</i> (2)			+	□				
	<i>Carapa</i> (2)	×	□	+					

<sup>14</sup>Eccentric thickening; see fig. 2e.<sup>15</sup>See fig. 2a.



FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER
Meliaceae	<i>Cedrela</i> (4)	×	□	+	×			
	<i>Chisocheton</i> (2)			□	□			
	<i>Chukrasia</i> (2)			□	□			
	<i>Dysoxylum</i> (15)			□	□			
	<i>Ekebergia</i> (1)		×	×				
	<i>Entandrophragma</i> (3)		×	+	□	p		
	<i>Guarea</i> (1)				□	□		
	<i>Khaya</i> (3)		×					
	<i>Lansium</i> (1)				□	□		
	<i>Lovoa</i> (1)				×	□		
	<i>Melia</i> (4)				□	□		
	<i>Orwenia</i> (4)				+	□		
	<i>Pseudocarapa</i> (2)				□	□		
	<i>Sandoricum</i> (2)				□	□		
	<i>Soymida</i> (1)		×		□		×	
	<i>Swietenia</i> (2)			×				×
	<i>Syzygium</i> (2)				×	□		
	<i>Toona</i> (3)		×		×	□	p	
	<i>Trichilia</i> (2)				+	□	□	
	<i>Turraeanthus</i> (1)				□	□		
	<i>Vavaea</i> (2)		×		□	□		
	<i>Walsura</i> (1)				×	□		
	<i>Xylocarpus</i> (2)		□		□			
	Monimiaceae	<i>Hedycarya</i> (3)	×	×				×
		<i>Kibara</i> (2)	□	□				□
	Moraceae	<i>Matthaea</i> (1)	□	□				□
		<i>Tetrasyandra</i> (3)	□	□				□
		<i>Allaeanthus</i> (1)	□	□	×			
<i>Antiaris</i> (1)				×			×	
<i>Brosimum</i> (2)		×		×				
<i>Chlorophora</i> (2)		□	×	□	×	p		
<i>Dimerocarpus</i> (1)			□	□	□	p	□	
<i>Ficus</i> (17)		□	□	□	□			
<i>Machura</i> (1)				□	□			
<i>Morus</i> (4)		+	+	+	×	p		
<i>Parartocarpus</i> (2)				×				
<i>Paratrophis</i> (2)		□	□	□	×			
<i>Pseudomorus</i> (1)		×		×	×	r		
<i>Taxotrophis</i> (1)	□	□	×					

FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER
Myrsinaceae	<i>Aegiceras</i> (1)	□	□					
	<i>Discocalyx</i> (1)	□						
	<i>Rapanea</i> (5)	+						
	<i>Suttonia</i> (1)	□	□					
	<i>Tapeinosperma</i> (1)	□	□					
Myrtaceae	<i>Agonis</i> (2)							×
	<i>Angophora</i> (7)				×			
	<i>Backhousia</i> (4)				□			×
	<i>Calyptranthes</i> (3)				□			□
	<i>Eucalyptus</i> (205)				□			□
	<i>Eucalyptopsis</i> (2)				+			□
	<i>Eugenia sens. lat.</i> (62) <sup>16</sup>				+			+
	<i>Feijoa</i> (1)				□		×	
	<i>Kjellbergiodendron</i> (2)				□			×
	<i>Leptospermum</i> (7)				□		×	
	<i>Melaleuca</i> (28)				×			
	<i>Myrciaria</i> (1)				□		×	
	<i>Piliocalyx</i> (1) <sup>17</sup>				□			□
	<i>Psidium</i> (2)				+		□	
	<i>Rhodomyrtus</i> (3)				□			
	<i>Whiteodendron</i> (1)				□			
	Nyssaceae	<i>Nyssa</i> (3)						
Ochnaceae	<i>Lophira</i> (1)				×			
	<i>Ochna</i> (1)						□	
Olacaceae	<i>Testulea</i> (1)							×
	<i>Ochanostachys</i> (1)				□			
Oxalidaceae	<i>Strombosia</i> (3)		×	×	×	r		
	<i>Averrhoa</i> (1)				□			
Pittosporaceae	<i>Sarcotheca</i> (1)				□			
	<i>Citriobatus</i> (1)	×					□	
Platanaceae	<i>Hymenosporium</i> (1)	□					×	×
	<i>Pittosporum</i> (6)	□					+	×
Polygonaceae	<i>Platanus</i> (3)			□				
	<i>Muehlenbeckia</i> (1)	□				×		
	<i>Triplaris</i> (1)				□	□		

<sup>16</sup>See fig. 4a.<sup>17</sup>See fig. 4b.



FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER
Proteaceae	<i>Hakea</i> (14)	—						
	<i>Roupala</i> (5)		×					
	<i>Stenocarpus</i> (5)		×				□	
Rhamnaceae	<i>Alphitonia</i> (8)		□	×	□			
	<i>Ceanothus</i> (2)		□					
	<i>Colubrina</i> (3)	+	+	+	□			
	<i>Enmenosperma</i> (1)	×	×					
	<i>Krugiodendron</i> (1)	□						
	<i>Maesopsis</i> (1)			□	□			
	<i>Reynosia</i> (1)		□					
	<i>Rhamnus</i> (6)	×	×		×			
	<i>Ventilago</i> (1)		□	×	□ <sup>p</sup>			
	<i>Zizyphus</i> (3)	—	—					
Rhizophoraceae	<i>Anopyxis</i> (1)			×	□			
	<i>Bruguiera</i> (6)		□					
	<i>Carallia</i> (4)		□	□	×			
	<i>Cassipourea</i> (2)	□	×	□	×			
	<i>Ceriops</i> (2)		□	×				
	<i>Combretocarpus</i> (1)		×	□	□			
	<i>Rhizophora</i> (4)	□	□	×				
Rosaceae	<i>Amelanchier</i> (2)			□	□			
	<i>Cercocarpus</i> (1)			×	□			
	<i>Crataegus</i> (6)			+	□			
	<i>Heteromeles</i> (1)			□	□			
	<i>Parastemon</i> (1)		×	□	□			
	<i>Raphiolepis</i> (1)			×	□	×		
Rubiaceae	<i>Alseis</i> (1)	□	□				×	
	<i>Coffea</i> (1)		□				×	
	<i>Randia</i> (6) <sup>18</sup>	□			×		×	
Rutaceae	<i>Aegle</i> (1)			□	□	×	×	
	<i>Balfourodendron</i> (1)		×	□	□			
	<i>Bosistoa</i> (1)			□	□			
	<i>Calodendrum</i> (1)	□		□	□			
	<i>Casimiroa</i> (1)			□	□			
	<i>Citrus</i> (3)			□	□			
	<i>Clausena</i> (1)			×	□			
	<i>Eremocitrus</i> (1)			□	□			

<sup>18</sup>See fig. 2b.

FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER
Rutaceae	<i>Fagara</i> (3)			□	□			
	<i>Feronia</i> (1)		□		□			
	<i>Flindersia</i> (14)	×	□	□	□			
	<i>Geijera</i> (2)			□	□			
	<i>Halfordia</i> (3)			×	□			
	<i>Helietta</i> (1)			□	□			
	<i>Lunasia</i> (1)			□	□			
	<i>Melicope</i> (2)			+	□			
	<i>Microcitrus</i> (1)			□	□			
	<i>Micromelum</i> (1)	□			□			
	<i>Murraya</i> (1)		□	□	□			
	<i>Phellodendron</i> (1)	×	×	□	□			
	<i>Vepris</i> (2)			□	□			
	<i>Zanthoxylum</i> (5)			—	□			
Santalaceae	<i>Exocarpus</i> (5)		×	□	□		×	
	<i>Santalum</i> (7)		×	□	□	×	×	
Sapindaceae	<i>Allophylus</i> (1)			□	□			
	<i>Arytera</i> (2)			□	□			
	<i>Atalaya</i> (1)			□	□			
	<i>Castanospora</i> (1)			□	□			
	<i>Cupaniopsis</i> (1)			□	□			
	<i>Dictyoneura</i> (2)			□	□			
	<i>Diploglottis</i> (1)			□	□			
	<i>Dodonaea</i> (3)			+	□			
	<i>Elatostachys</i> (2)	+	+	□	□ <sup>p</sup>			
	<i>Euphoria</i> (1)	×	×	□	□ <sup>p</sup>			
	<i>Exothea</i> (1)			□	□			
	<i>Ganophyllum</i> (1)			□	□			
	<i>Harpullia</i> (1)			□	□			
	<i>Heterodendron</i> (1)			□	□			
	<i>Hypelate</i> (1)			□	□			
	<i>Jagera</i> (2)			×	□			
	<i>Litchi</i> (1)	□		□	□			
	<i>Mischocarpus</i> (5)			□	□			
	<i>Nepbelium</i> (3)			+	□			
	<i>Pometia</i> (3)	□		—	□			
	<i>Sarcopteryx</i> (1)			×	□			
	<i>Schleichera</i> (1)			□	□			



FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER	
Sapindaceae	<i>Talisia</i> (1)			□	□				
	<i>Toeckima</i> (4)			+	□	□			
	<i>Tristiropsis</i> (1)			□	□	□			
	<i>Xerospermum</i> (1)			□	□	□			
Sapotaceae	<i>Archradotypus</i> (2)			×	□	□			
	<i>Chrysophyllum</i> (3)	×		×	×		×		
	<i>Ganua</i> (2)			+	□	□			
	<i>Lucuma</i> (1)			□	□	□			
	<i>Manilkara</i> (2)			□	□	□			
	<i>Mimusops</i> (5)	×		—	×	□			
	<i>Palaquium</i> (10)			—	□	□			
Simarubaceae	<i>Planchonella</i> (3)			+	□			□	
	<i>Ailanthus</i> (3)	×	×	×	□				
	<i>Cadellia</i> (1)			□	□				
	<i>Iringia</i> (1) <sup>19</sup>			□	□		□		
	<i>Klainedoxa</i> (1)			□	□				
	<i>Picramnia</i> (1)		□				□	□	
	<i>Picrasma</i> (1)	□		□				□	
	<i>Duabanga</i> (1)			□				□	
	<i>Sonneratia</i> (3)			□				□	
	<i>Argyrodendron</i> (3)	□		□	□				
Sterculiaceae	<i>Brachyhiton</i> (4)	+		+	×	p			
	<i>Commersonia</i> (1)	□	□	×	□				
	<i>Firmiana</i> (1)	□		×	□				
	<i>Heritiera</i> (1)	×		□	×				
	<i>Kleinbovia</i> (1)	□		×	×				
	<i>Mansonia</i> (1)	□			×				
	<i>Pterocymbium</i> (3)	□		—					
	<i>Pterospermum</i> (4)	□			□	p			
	<i>Pterygota</i> (1)	□		□	×				
	<i>Sterculia</i> (17)	+		□	×				
	<i>Tarrietia</i> (4)	+		+	□	p			
	<i>Triplochiton</i> (1)	+	□	×	□				
	Styracaceae	<i>Styrax</i> (2)	+		□	□			
		<i>Gordonia</i> (9)			×	□			
Theaceae	<i>Schima</i> (2)			□	□				
	<i>Jacquinia</i> (1) <sup>20</sup>			□	□				

<sup>19</sup>Eccentrically thickened; see fig. 2e.<sup>20</sup>In parenchyma surrounding phloem patches.

FAMILY	GENERA	1 RAYS: UPRIGHT OR SQUARE CELLS	2 RAYS: PROCUMBENT CELLS	3 PARENCHYMA	4 CELLS SUBDIVIDED	5 CELLS ENLARGED	6 CELLS SCLEROSED	7 CRYSTALS VARIABLE IN SIZE AND NUMBER
Tiliaceae	<i>Actinophora</i> (1)	□	□					
	<i>Colona</i> (3)	□		□				—
	<i>Diplodiscus</i> (1)	□	□	□	×	p		
	<i>Grewia</i> (2)	□	□					
	<i>Luehea</i> (1)	×						
	<i>Microcos</i> (2)	□	□	□				
	<i>Pentace</i> (2)	×		×				
	<i>Schoutenia</i> (1)	□	□	×	□	p		
	<i>Trichospermum</i> (3)	□	—					
	<i>Ampelocera</i> (1)	□	□					
Ulmaceae	<i>Aphananthe</i> (1)	□						
	<i>Celtis</i> (15)	□		×	×	r		×
	<i>Phyllostylon</i> (1)	□	□					
	<i>Ulmus</i> (6)			—	□			
	<i>Zelkova</i> (1)		□			□		×
	<i>Pipturus</i> (2)	□						
Urticaceae	<i>Vaccinium</i> (1)		×					
Verbenaceae	<i>Avicennia</i> (5)	□	□	×				
	<i>Vitex</i> (14)		+					□
Zygophyllaceae	<i>Bulnesia</i> (1)			□	□			

Crystals have also been reported in the following genera:

Acanthaceae: *Beloperone*.

Anacardiaceae: *Anacardium*, *Comocladia*, *Cotinus*, *Litbraea*, *Mauria*, *Mosquitoxylum*, *Schinopsis*, *Thyrsodium*, *Toxicodendron*.

Apocynaceae: *Cameraria*, *Cerberiopsis*, *Diplorrhynchus*, *Echites*, *Geissospermum*, *Kickxia*, *Macoubea*, *Paralstomia*, *Rauwolfia*, *Tabernaemontana*, *Vallesia*, *Voacanga*.

Araliaceae: *Brassaiopsis*, *Dendropanax*, *Didymopanax*.

Asclepiadaceae: *Leptadenia*.

Berberidaceae: *Mahonia*.

Bignoniaceae: *Dolichandrone*, *Oroxylon*, *Stereospermum*.

Bombacaceae: *Eriodendron*, *Matisia*.

Bonnetiaceae: *Bonnetia*.

Bursaceae: *Balsamodendron*, *Bursera*, *Commiphora*, *Tetragastris*.

Canellaceae: *Canella*, *Capsicodendron*, *Cinnamosma*, *Pleodendron*, *Warburgia*.

Capparidaceae: *Atansiqua*, *Capparis*, *Morisonia*, *Steriphoma*.



- Caryocaraceae: *Anthodiscus*, *Caryocar*.  
 Celastraceae: *Euonymus*, *Microtropis*.  
 Combretaceae: *Guiera*, *Pteleopsis*.  
 Compositae: *Ericameria*.  
 Coniferae: *Pseudolarix*.  
 Connaraceae: *Cnestidium*, *Cnestis*, *Ellipanthus*, *Jollydora*, *Manotes*.  
 Coriariaceae: *Coriaria*.  
 Cornaceae: *Marlea*.  
 Cunoniaceae: *Caldcluvia*.  
 Daphniphyllaceae: *Daphniphyllum*.  
 Dichapetalaceae: *Chailletia*, *Dichapetalum*, *Gonypetalum*, *Tapura*.  
 Dipterocarpaceae: *Cotylelobium*.  
 Elaeocarpaceae: *Crimodendron*.  
 Epacridaceae: *Acrotiche*.  
 Ericaceae: *Arbutus*, *Psammisia*, *Satyria*.  
 Escalloniaceae: *Brexia*, *Carpodetus*.  
 Euphorbiaceae: *Aextoxicon*, *Alchornea*, *Androstachys*, *Aparisthmium*,  
*Breynia*, *Claoxylon*, *Coelodepas*, *Conceveibastrum*, *Daphni-*  
*phyllum*, *Dicoelia*, *Euphorbia*, *Garcia*, *Homonoia*, *Hymeno-*  
*cardia*, *Lingelsheimia*, *Maesobotrya*, *Mischodon*, *Oldfieldia*,  
*Petalostigma*, *Piranhea*, *Podadenia*, *Putranjiva*, *Protomegabaria*,  
*Savia*, *Tetrorchidium*, *Uapaca*, *Wetria*.  
 Flacourtiaceae: *Arechavaletia*, *Azara*, *Banara*, *Bennettia*, *Hasseltia*,  
*Hasseltiopsis*, *Hecatostemon*, *Olmediella*, *Prockia*, *Taraktogenos*,  
*Tetrathylacium*, *Trimenia*.  
 Goupiaceae: *Goupia*.  
 Guttiferae: *Kaya*, *Marila*.  
 Hamamelidaceae: *Distylium*.  
 Hippocastanaceae: *Billia*.  
 Humiriaceae: *Humiria*, *Vantanea*.  
 Hypericaceae: *Vismia*.  
 Icacinaceae: *Calatola*, *Platea*.  
 Julianiaceae: *Juliania*, *Orthopterygium*.  
 Lecythidaceae: *Cariniana*, *Chydenanthus*.  
 Leguminosae: *Abauria*, *Adinobotrys*, *Aeschynomene*, *Amerimnon*,  
*Apoplania*, *Bergeronia*, *Bowdichia*, *Brya*, *Bussea*, *Butea*, *Cal-*  
*pocalyx*, *Cathormion*, *Cedrelinga*, *Centrolobium*, *Cojoba*,  
*Copaifera*, *Cordyla*, *Crudia*, *Cryptosepalum*, *Cylicodiscus*,  
*Dichrostachys*, *Diphysa*, *Englerodendron*, *Etaballia*, *Eysen-*  
*bardtia*, *Genista*, *Harpalyce*, *Havardia*, *Humboldtia*, *Krugio-*  
*dendron*, *Lysiloma*, *Machaerium*, *Martiodendron*, *Muellera*,  
*Myrocarpus*, *Myrospermum*, *Myroxylon*, *Parosela*, *Poinciana*,  
*Poponax*, *Prioria*, *Pseudosamanea*, *Saraca*, *Schotia*, *Senegalia*,  
*Toluifera*, *Ulex*, *Vacbellia*, *Zollernia*, *Zuccagnia*.  
 Linaceae: *Hugonia*, *Lepidobotrys*, *Ochthocosmus*.  
 Loganiaceae: *Nuxia*.  
 Loranthaceae: *Viscum*.

- Lythraceae: *Grislea*.  
 Malpighiaceae: *Banisteria*, *Banisteriopsis*, *Burdachia*, *Byrsonna*,  
*Lophanthera*, *Spachea*.  
 Malvaceae: *Bombycidendron*, *Kokia*.  
 Marcgraviaceae: *Norantea*.  
 Meliaceae: *Cabralea*, *Cipadessa*, *Epicharis*, *Moschoxylum*, *Pseudo-*  
*cedrela*, *Ptaeroxylon*, *Reimwardtiendendron*.  
 Melianthaceae: *Bersama*.  
 Moraceae: *Broussonetia*, *Cudrania*, *Myrianthus*.  
 Moringaceae: *Moringa*.  
 Myristicaceae: *Horsfieldia* p.p., *Iryanthera*.  
 Myrsinaceae: *Conomorpha*, *Myrsine*.  
 Myrtaceae: *Marlierea*, *Myrcia*, *Myrceugenia*, *Myrrhinium*.  
 Ochnaceae: *Cespedesia*, *Elvasia*, *Ouratea*.  
 Octoknemataceae: *Octoknema*.  
 Olacaceae: *Aptandra*, *Anacolosa*, *Chaunochiton*, *Coula*, *Endusa*,  
*Liriosma*, *Minuartia*, *Olax*, *Ongoeka*, *Ptychopetalum*.  
 Oleaceae: *Chionanthus*, *Fraxinus*.  
 Phytolaccaceae: *Gallesia*, *Seguiera*.  
 Polygalaceae: *Carpolobia*, *Phlebotania*.  
 Polygonaceae: *Coccoloba*, *Neomillspaughia*, *Podopterus*, *Ruprechtia*.  
 Quinaceae: *Touroulia*.  
 Rhamnaceae: *Auerodendron*, *Berchemia*, *Colletia*, *Condalia*, *Doerp-*  
*feldia*, *Karwinskia*, *Rhamnella*, *Rhamnidium*, *Sageretia*, *Sar-*  
*comphalus*, *Scutia*.  
 Rhizophoraceae: *Kandelia*.  
 Rosaceae: *Chaenomeles*, *Eriobotrya*, *Eriolobus*, *Malus*, *Pseudocytodonia*.  
 Rubiaceae: *Coutarea*, *Hymenodictyon*, *Hypobathrum*, *Pavetta* p.p.,  
*Petunga*, *Pinckneya*, *Mussaenda*, *Neonauclea*, *Zuccarinia*.  
 Rutaceae: *Aeglopsis*, *Amyris*, *Araliopsis*, *Atalantia*, *Balsamocitrus*,  
*Calodendrum*, *Chloroxylon*, *Esenbeckia*, *Evodia* p.p., *Glycosmis*,  
*Limonia*, *Merrillia*, *Metrodorea*, *Nycticalanthus*, *Oricia*, *Platy-*  
*desma*, *Poncirus*, *Raputia*.  
 Salicaceae: *Populus*.  
 Salvadoraceae: *Salvadora*.  
 Santalaceae: *Acanthosyris*, *Cervantesia*.  
 Sapindaceae: *Aphania*, *Athyana*, *Chytranthus*, *Diatenopteryx*, *Erio-*  
*glossum*, *Euphorianthus*, *Filicium*, *Guioa*, *Koelreuteria*, *Lacco-*  
*discus*, *Lepisanthes*, *Melicocca*, *Otophora*, *Pappea*, *Paranephe-*  
*lium*, *Phialodiscus*, *Ratonia*, *Sapindus*, *Stadmannia*, *Vouarana*,  
*Zanba*.  
 Sapotaceae: *Bassia*, *Bumelia*, *Butyrospermum*, *Mastichodendron*,  
*Nothiopsis*, *Sarcosperma*, *Sideroxylon*.  
 Simarubaceae: *Alvaradoa*, *Hannoa*, *Samadera*, *Suriana*.  
 Solanaceae: *Grabowskya*.  
 Sterculiaceae: *Cola*, *Eribroma*, *Eriolaena*, *Fremontia*, *Helicteres*,  
*Leptonychia*, *Melochia*, *Scaphopetalum*, *Theobroma*.  
 Symplocaceae: *Symplocos*.



Tamaricaceae: *Tamarix*.  
Thymelaeaceae: *Phaleria*.  
Tiliaceae: *Berrya*, *Cistanthera*, *Erinocarpus*, *Grewia*, *Heliocarpus*.  
Trigoniaceae: *Trigoniastrum*.  
Urticaceae: *Urtica*.  
Violaceae: *Alsodeia*.  
Vochysiaceae: *Erisma*, *Qualea*.  
Zygophyllaceae: *Guaiacum*, *Larrea*, *Nitraria*, *Porlieria*.

## SUMMARY

This paper is the second part of a survey of the occurrence of crystals in woody stems. The first part dealt with crystals having a characteristic form of particular value in wood identification; the present paper is concerned with the distribution of the more commonly occurring crystals which cannot be classified in any of the preceding groups. Lists are given of genera in which these crystals have been observed or recorded.

Four modifications of crystal arrangement are noted: 1. subdivision of the containing cell, 2. enlarged cells (idioblasts), 3. sclerosed cell walls of the containing cell, 4. variations in size and number of the crystals occurring in a single cell.

Crystallographic techniques have not been employed in this survey.

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## ACKNOWLEDGMENTS

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## CONTENTS

THE LONGITUDINAL SHRINKAGE OF CATIVO H. O. Fleischer	1
A METHOD FOR ELIMINATING CURL IN WOOD SECTIONS C. L. Lee	3
A NOTE ON THE WOOD ANATOMY OF THE GENUS <i>Corynocarpus</i> H. D. Ingle	8
SURVEY OF AFRICAN WOODS. I. Howard A. Spalt and William L. Stern	13
THE NATURAL MARINE BORER RESISTANCE OF TROPICAL AMERICAN WOODS Frederick F. Wangaard	38
CURRENT LITERATURE	43



## TROPICAL WOODS

*A technical magazine devoted to the furtherance of knowledge of tropical woods and forests and to the promotion of forestry in the tropics.*

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## TROPICAL WOODS

NUMBER 105

OCTOBER, 1956

### THE LONGITUDINAL SHRINKAGE OF CATIVO

H. O. FLEISCHER

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U. S. Department of Agriculture<sup>1</sup>*

#### INTRODUCTION

Recent research at the U. S. Forest Products Laboratory has cast some light on certain contradictory reports about the properties of cativo (*Prioria copaifera* Gris.) wood, particularly with respect to its longitudinal shrinkage and dimensional stability. The information available in the literature (Gerry and Kryn, 1954) on cativo indicates that the wood is characterized by a very low shrinkage and by freedom from warping in drying. It has been compared by various researchers (Wangaard and Muschler, 1952) to yellow-poplar and to butternut. Gerry and Kryn (1954) reported the radial shrinkage to be 2.1 to 2.4 per cent and tangential shrinkage 5.2 to 7.3 per cent. Reports on the longitudinal shrinkage of cativo vary considerably, however. Barbour (1952) found the value for longitudinal shrinkage to be 0.08 per cent, whereas Harrar (1942) found it to be 0.29 per cent.

Some users of cativo in veneer and plywood form state that the wood is very stable and, hence, is suitable for cross-bands in the finest veneered panels or for thick cores in three-ply furniture panels. Yet, there have also been some unfavorable reports regarding the warping of the veneer and even of plywood made with one or more plies of cativo veneer.

<sup>1</sup>Maintained at Madison, Wisconsin, in cooperation with the University of Wisconsin.



OBSERVATIONS AT VENEER MILL<sup>2</sup>

Limited tests at the U. S. Forest Products Laboratory indicate that normal cativo veneer is very stable, with values for shrinkage comparable to the lower values reported in the literature for this species. However, some cativo veneer produced in a mill-run assortment of this material was found to have the characteristics of tension wood (Pillow, 1952) including high longitudinal shrinkage. This veneer had a fuzzy or fibrous surface when cut on the lathe. The veneer usually buckled immediately upon cutting, and the buckling became greatly accentuated upon drying. Some splits extended entirely through the veneer.

Further observations at a commercial veneer plant indicated that the sawn surfaces of the ends of bolts being prepared for veneer cutting usually signalled the presence of tension wood by a rough and fibrous cut in the tension wood areas. These areas frequently were crescent shaped, and they were often restricted to one side of a log. Veneer coming from the lathe with fibrous surfaces and buckling tendencies was traced back to the areas that showed the fibrous saw cut at the ends of the bolt. This same veneer was the material that buckled badly during drying. Portions of veneer logs that show these characteristics are often referred to in the mills as "soft streaks."

## LABORATORY TESTS

Specific gravity and longitudinal shrinkage tests were made on 16 samples of veneer from a single log that appeared to have a severe tension wood streak. Eight of the samples were very flat and appeared to be normal wood that had been cut smoothly. The other samples had cut roughly on the lathe and showed a tendency to buckle. The specific gravity of the smoothly cut wood was 0.37 to 0.38, based on the volume when green and the weight when oven dry. The specific gravity of the roughly cut wood ranged from 0.37

<sup>2</sup>The work described here was done with the cooperation of the Bacon-McMillan Veneer Co., Stockton, Alabama.

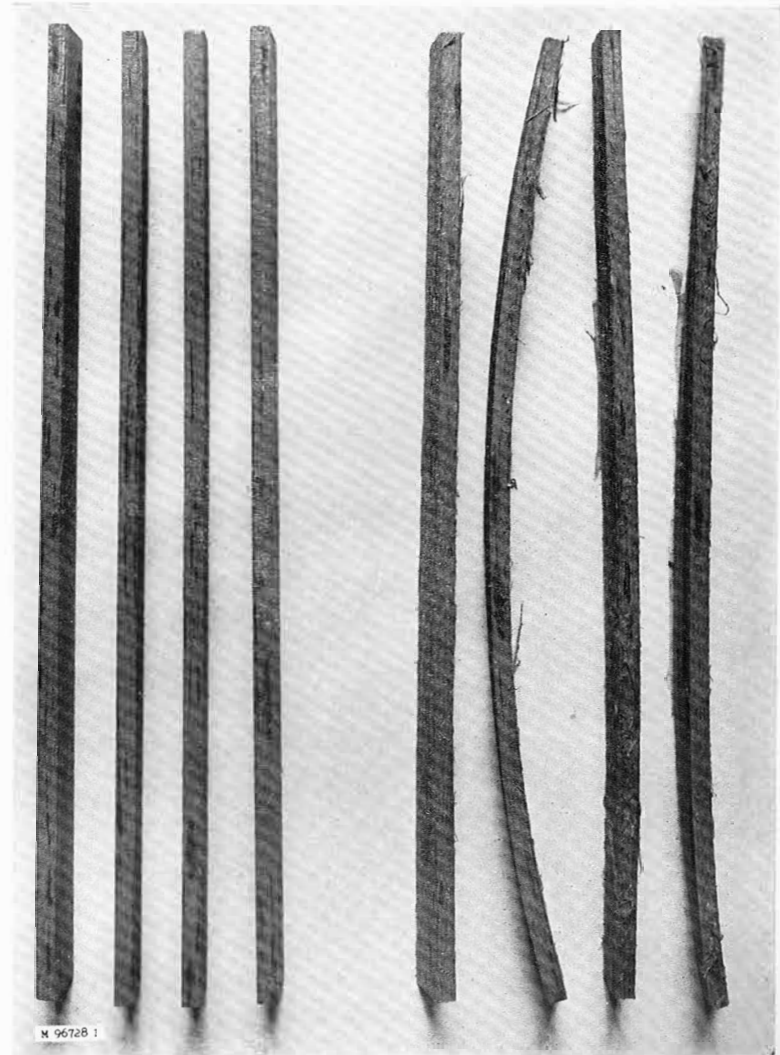


Fig. 2. Typical dry test samples of cativo normal wood (left) and tension wood (right). The samples are nine inches long.



to 0.51. The longitudinal shrinkage of the normal wood based on the length when green, lay between 0.098 and 0.185 per cent, and the longitudinal shrinkage of the roughly cut wood ranged from 0.359 to 0.784 per cent. Widthwise or tangential shrinkage measurements on these pieces indicated an average shrinkage of about 6 per cent for those specimens that shrank least longitudinally and about 10 per cent for those that shrank most longitudinally.

A veneer sample consisting of one complete revolution of veneer cut to a thickness of  $\frac{3}{16}$  inch was chosen from a second log also containing evidence of severe tension wood. The veneer sheet making up this revolution was 4 feet long parallel to the grain and about 5 feet wide across the grain. It was selected from a log at a diameter of slightly less than  $1\frac{1}{2}$  feet and was entirely of sapwood. At equal intervals across the width of the sheet, veneer samples 1 inch wide and 9 inches long were cut from each end of the sheet. Thus, there were two complete sets of samples, each composed of pieces of veneer equally spaced around the circumference of the log.

About one third of the pieces from one segment of the circumference were roughly cut, and they were thought to be tension wood.

The samples were air dried without restraint for two weeks in an atmosphere at 65 per cent relative humidity and then for two weeks at 30 per cent relative humidity. Finally they were oven dried. At each condition, the specimens were measured and weighed.

The longitudinal shrinkage of the pieces from the green to the oven-dry condition and corresponding specific gravity values are shown in figure 1. The samples that showed the greatest longitudinal shrinkage (up to 0.72 per cent) as well as the highest specific gravity (up to 0.50) were those with fuzzy or fibrous surfaces. These samples also warped during drying. The samples with uniformly low longitudinal shrinkage of less than 0.2 per cent and uniform specific gravity of 0.35 to 0.37 were smoothly cut, firm, and flat after drying.



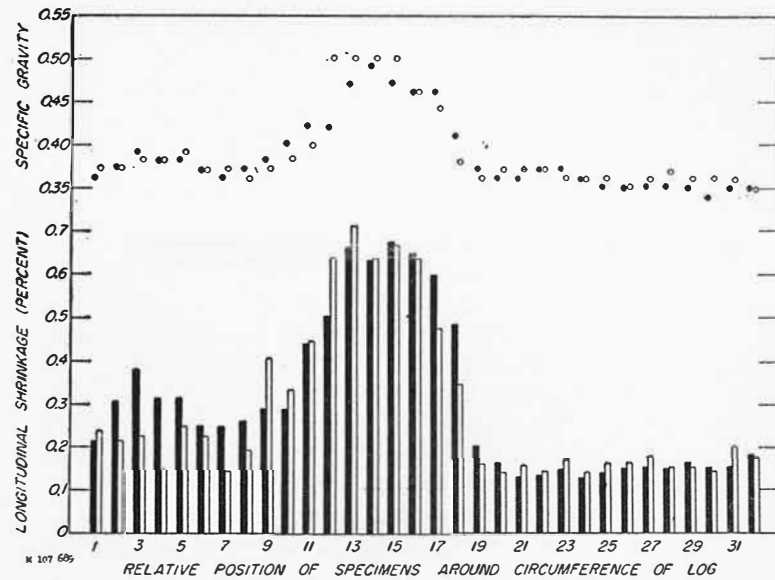


Fig. 1. Specific gravity and longitudinal shrinkage of samples of cativo veneer taken at equally spaced intervals in one revolution around a log. Solid dots and bars represent pieces from one end of sheet, and hollow dots and bars from corresponding positions near the other end.

A comparison of typical normal test pieces and of typical tension wood test pieces is shown in figure 2. Figure 3 shows the relative flatness of larger pieces of normal and tension wood from the same log.

#### CONCLUSIONS

It is concluded that tension wood may occur in cativo and that this characteristic accounts for complaints about the dimensional stability of this wood. Tension wood is characterized by a fuzzy or fibrous saw cut when the log is crosscut, by a fibrous surface on veneer, by the tendency of the wood to buckle when green, by severe buckling or warping and excessive longitudinal shrinkage during drying, and by a higher-than-average density.

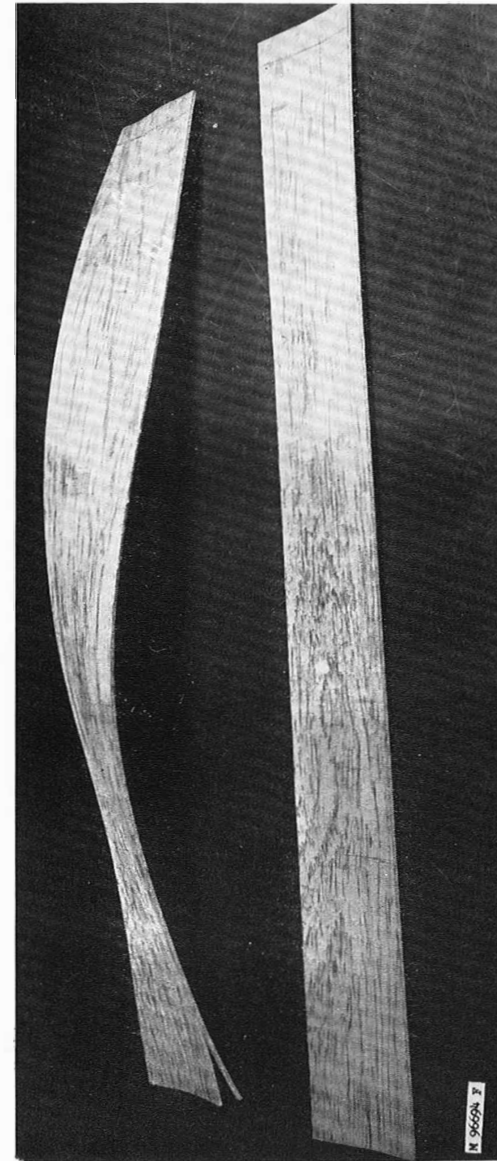


Fig. 3. Samples of cativo veneer, showing the flatness of normal wood (bottom) and the warping of tension wood (top) after drying. The samples are 3/16 by 6 by 24 inches.



At present there is no known method for eliminating or reducing the undesirably high longitudinal shrinkage that characterizes tension wood veneer. For end uses that require a high degree of dimensional stability, such as is displayed by cativo veneer that is free of tension wood, it is necessary to cull out obvious tension wood from the veneer product.

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A METHOD FOR ELIMINATING CURL IN WOOD SECTIONS

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Various methods are currently employed for the preparation of sections of hard woody stems. Of these, the most widely used is the celloidin technique of Duval (1879) which is utilized for many hard tissues (Chamberlain, 1932; Wetmore, 1932). Sectioning by the free-hand method is a convenient and simple technique which requires very little preparation, and yields rapid results, although it demands a variety of individual skills and can not be applied to critical studies. Sectioning of wood imbedded in paraffin is favored by some workers (Hyland, 1941). Steam treatment of material prior to imbedding or sectioning is also followed in some laboratories (Crowell, 1930; Kisser, 1926, 1931).



Even though each system has its merits, none of them eliminates the curling of sections during the cutting procedure. This is particularly true in transverse preparations of hard woods with abundant, thick-walled fibers. Naturally, the use of a new, or very sharp, microtome knife facilitates sectioning of woods (Bailey, 1937), but does not always ameliorate the difficulty. A simple method of handling curled sections while cutting is to press a camel's-hair brush against the section on the microtome blade. If that fails, a dissecting needle or a pair of forceps can be used to uncurl the sections, but this method is tedious and often not satisfactory. A better means of flattening curled sections of wood imbedded in celloidin, or unimbedded, is described in this paper.

Blocks of wood are softened either with hydrofluoric acid or are simply boiled in water. After treatment, they may be imbedded in celloidin if necessary.

It is of utmost importance that the knife be sharp and that the proper cutting angle be maintained. Improper adjustments may produce unsatisfactory sections and decrease the efficiency of the knife. Best results have been obtained by the author with a knife-tilt of  $5^{\circ}$ – $10^{\circ}$  from the horizontal, and with the back edge of the knife producing an angle of  $35^{\circ}$  with the bed of the microtome. As the knife is passed through the block, the section is pressed against the surface of the knife with a camel's-hair brush. The knife should not be drawn through the wood too rapidly, and the movement of the brush should be synchronous with that of the knife. As soon as a section is cut, it is placed in a Petri dish with enough 70 per cent ethyl alcohol to cover it completely. After several sections have been cut and placed into the alcohol, they are transferred to a second Petri dish which has only a few drops of 70 per cent alcohol, or just enough to keep the sections from drying. The sections should then be arranged neatly and flattened by applying gentle pressure with a camel's-hair brush. With the addition of many sections it may be necessary to add more alcohol to keep them immersed. Sections are kept in a covered Petri dish overnight to insure that they remain permanently flattened.

Those not allowed to flatten for a sufficient period of time tend to curl again as they pass through the staining procedures.

After the sections have remained in the Petri dish overnight, distilled water is gently poured into the container; sections will then float on the water. A section lifter and brush can now be used to transfer the sections to a Syracuse watch glass for staining.

Sections may be inadvertently left standing for too long a time (2–3 days) becoming dry and wrinkled. Drying does not affect the stainability of the sections to any great extent, and they can easily be re-flattened simply by the addition of distilled water. Such sections will lay evenly as they float on the water. Any standard method of staining and dehydrating can be followed.

This method introduces an easy, workable system for flattening curled sections of wood. In the opinion of the author much of the difficulty involved in preparation of woody sections can be eliminated through the use of this procedure.

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A NOTE ON THE WOOD ANATOMY OF THE  
GENUS *CORYNOCARPUS*

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INTRODUCTION

Among samples of timber received some few years ago from New Caledonia through the courtesy of the Chef du Service des Eaux et Forêts, M.—P. Sarlin, was one which had no botanical determination. This sample was at first thought to belong to the genus *Sterculia*, and was assigned to "Group B" (Chattaway, 1937). However, recently, some doubt was felt about this determination, though supported independently by the Centre Technique Forestier Tropical, Paris (personal communication from M.—Sarlin).

Although a marked similarity to the timbers of "Group B" of *Sterculia* was apparent, closer inspection and comparison with a wider range of the latter, including nine species kindly supplied by the Imperial Forestry Institute, Oxford, through the courtesy of Dr. L. Chalk, indicated the following differences:

Table 1. COMPARATIVE FEATURES OF UNKNOWN SAMPLE AND *Sterculia* "B"

	UNKNOWN SAMPLE	<i>Sterculia</i> "B"
Parenchyma strands	Fusiform or 2-celled	Almost entirely 4-celled, occasionally 2-celled
Crystal strands	Absent	Frequently present
Mean vessel member length	0.26 mm.	0.30–0.39 mm.
Spiral thickening in vessels	Occasionally present, very fine	Absent
Mean fibre length	1.03 mm.	1.79–2.30 mm.

In such features as the clustering of vessels on transverse section, the broad bands of parenchyma, the appearance of the multiscriate rays and the absence of uniseriate rays, and the storeying of vessel members and parenchyma (fig. 4, 5), the New Caledonian timber comes very close to *Sterculia* "B." However, a genus conforming more closely to the unknown was found in *Corynocarpus* Forst., now considered a separate monogeneric family. Some doubt as to the affinities of this family is evident from the taxonomic literature and it was felt that fuller examination of the wood of the genus might disclose other, closer taxonomic affinities.

Seven samples were available for examination, including *C. laevigatus* Forst. from New Zealand; *C. australasica* C.T. White from north Queensland and New Guinea, and two New Caledonian samples, which are presumed to be *C. dissimilis* Hemsl., and one unassigned species from New South Wales. The distribution of the genus is given in figure 1.

ANATOMICAL DESCRIPTION OF *Corynocarpus* FORST.

*General.*—*Corynocarpus* is a genus of four species: *C. australasica* C. T. White, occurring from New Guinea and Aru Isl. to north Queensland; *C. laevigatus* Forst. in New Zealand and adjacent islands; *C. dissimilis* Hemsl. in New Caledonia, and *C. similis* Hemsl. in the New Hebrides. The wood of *C. laevigatus* and *C. dissimilis* is pale cream to pale yellow-brown, and pinkish-brown in *C. australasica*; moderately light and soft; moderately fine textured but with prominent rays showing on all faces; some figure is evident due to concentric bands of parenchyma. The genus is not of commercial importance as timber since the trees are mainly small. The fruits of *C. laevigatus* are eaten by the Maoris after preliminary treatment by boiling or steeping to remove a toxic glucoside. The fruits of *C. australasica* are larger (2.5 × 3.5 cm.; Steenis, 1951) but apparently are not eaten.

*Structure.*—Growth rings are not evident. Vessels are small and indistinct to the naked eye; maximum tangential diameter 110–153 $\mu$ ; mean member length 0.20–0.34 mm.; moderately numerous, from 11 per sq. mm. in *C. dissimilis* to



25 per sq. mm. in *C. laevigatus*; evenly distributed, often in radial multiples up to 4, or occasionally 6, frequently in clusters; vessel pitting mainly alternate, but with some irregular tendency, the pit borders sometimes horizontally elongated, moderately coarse, borders up to  $10\mu$  in diameter; perforation plates exclusively simple; traces of fine spiral



Fig. 1. Distribution of *Corynocarpus*. *C. australasica* C. T. White,  $\Delta$ ; *C. laevigatus* Forst.,  $\circ$ ; *C. similis* Hemsl.,  $\square$ ; *C. dissimilis* Hemsl.,  $\odot$ ; Unassigned species,  $*$ .

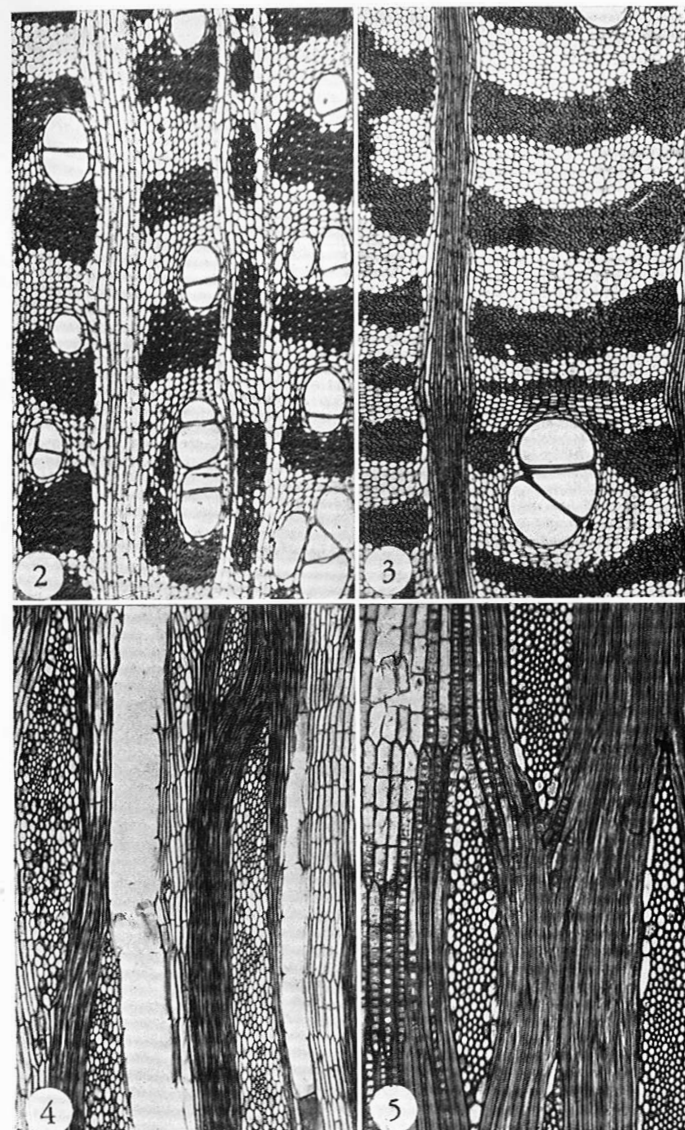


Fig. 2-5.—Fig. 2. *Corynocarpus* sp. unassigned, transverse section, showing broad bands of parenchyma and wide multiseriate rays.  $\times 40$ .—Fig. 3. *Sterculia appendiculata* K. Schum., transverse section showing similar appearance to *Corynocarpus* in rays and parenchyma.  $\times 40$ .—Fig. 4. *Corynocarpus laevigatus* Forst., tangential section showing storeyed fusiform or 2-celled parenchyma and the absence of uniseriate rays.  $\times 40$ .—Fig. 5. *Sterculia elegantiflora* Hutch. & Dalz., tangential section showing storeyed, 4-celled parenchyma, crystal strands and absence of uniseriate rays.  $\times 60$ .



thickening in *C. laevigatus* and *C. australasica*, infrequent in the New Caledonian samples. Rays mainly 6–10 cells wide, occasionally up to 16, uniseriate rays absent; procumbent cells lacking or short, interspersed among square to upright cells; sheath cells common; solitary crystals, sometimes in enlarged cells, common in all species; vessel-ray pitting (usually infrequent), similar to intervessel pitting; pits between ray cells large and numerous; extraneous material sparse to absent. Parenchyma vasicentric, consistently present as a narrow sheath around vessels and vessel groups; predominantly in discontinuous, wavy and anastomosing bands up to 10 cells wide, probably paratracheal; crystals sparse to absent; strands chiefly 2-celled, but frequently fusiform; storeyed; pits large, numerous and conspicuous. Fibres moderately thick-walled, with few simple to indistinctly bordered pits mainly on radial walls; mean length 0.85–1.55 mm.

*Material.*—*Corynocarpus australasica* C. T. White, two samples, north Queensland and Mussau Isl., St. Matthias Grp.; *C. laevigatus* Forst., one sample, New Zealand; *Corynocarpus* sp. unassigned, two samples, New Caledonia, one sample New South Wales.

The following species of *Sterculia* "B" were examined for comparison with *Corynocarpus*: *S. appendiculata* K. Schum. from E. Africa; *S. blancoi* Rolfe from the Philippines; *S. coccinea* Pierre from Indo-China; *S. elegantiflora* Hutch. & Dalz. from W. Africa; *S. oblonga* Mast. from W. Africa; *S. quinqueloba* K. Schum. from E. Africa; *S. rhinopetala* K. Schum. from W. Africa; *S. tomentosa* Guill. & Perr. from the Sudan; *S. urens* Roxb. from India.

In addition nine species occurring in the Australia, New Guinea and the southwest Pacific region, all proved, on examination, to belong to the group *Sterculia* "A."

#### DISCUSSION

Metcalf and Chalk (1950) state, on the examination of one species of *Corynocarpus* (*C. laevigatus*) that the wood has features in common with the Berberidaceae, but none with the Anacardiaceae, as proposed by Hemsley (1903,



1904). The Corynocarpaceae in the Bentham and Hooker (1862) classification is retained in the Sapindales, close to the Anacardiaceae. The present examination reveals no features of similarity between this genus and the Anacardiaceae. It does, however, bear a strong resemblance to the genus *Sterculia* "B," and this resemblance is often of a fundamental character; i.e., in the storeying of the vessel members, their short mean length, and the absence of uniseriate rays.

On sorting in a punched card system covering microscopic characters of families containing woody genera, it was found that the Malvales were predominant in a group of families with features in common with the genus in question; these were the Sterculiaceae (excluding Buettnerioideae), Tiliaceae, Malvaceae and the Ulmaceae. In this latter family the only genera with wide-rayed species are *Celtis* and *Gironmiera*, which genera, unlike *Sterculia* "B" and *Corynocarpus*, both possess uniseriate as well as multiseriate rays. The similar characters of the wood anatomy of these two genera, so unrelated botanically, indicate parallel but independent lines of specialization.

The genera of the Berberidaceae mentioned by Metcalfe and Chalk (1950) as having affinities to *Corynocarpus*, i.e., *Berberis*, *Mahonia* and *Nandina*, are similar in having short vessel members with spiral thickening, wide rays and an absence of uniseriate rays, but differ in lacking parenchyma.

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## SURVEY OF AFRICAN WOODS. I.

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This study of African woods was undertaken in cooperation with the Bureau of Ships, United States Navy, with the objective of compiling information concerning the characteristics of some of the more important species of African timbers. It has previously been demonstrated in this laboratory (Dickinson et al., 1949; Hess et al., 1950; Wangaard et al., 1952, 1954, 1955) that studies of the physical and mechanical properties of tropical American timbers have yielded information useful in appraising the potential suitability of little-known timbers. The authors believed that similar information on African woods should be compiled from the rather extensive, but widely scattered, literature on the subject. An evaluation of African timbers would then be possible, for certainly Africa supports many potentially valuable species as does tropical America.

With this objective in mind, reports on individual species or groups of species were prepared. Each covers the botanical nomenclature as well as many of the common names, the distribution of the species, a description of the tree and the wood, the physical and mechanical properties of the timber and a bibliography of source material. The initial report contains a list of the timbers to be described in subsequent accounts coupled with summary tables describing the mechanical properties, shrinkage and decay resistance of these timbers.

Because of the diverse sources of information, the various methods employed for evaluation and the different means

<sup>1</sup>The authors are indebted to Professor Frederick F. Wangaard of the Yale School of Forestry for his careful perusal and many suggestions pertaining to the original report made to the Bureau of Ships. Dr. George K. Brizicky of the Yale School of Forestry has been kind enough to check on the taxonomic portions of these reports. We should like to express our thanks to both of these men for their help.



used for expressing test results, valid comparisons between and among species cannot always be made readily. However, insofar as possible, the physical data in these reports have been expressed in a uniform manner. Consistency of strength data presented in table 1 has been assured by incorporating only the results available from British and American laboratories which employ uniform test methods.

No claim is made for complete coverage of African timber trees of present or potential commercial importance. Many possibly important timbers have been omitted because of the scarcity or incompleteness of information in the literature. Furthermore, there are undoubtedly many commercially desirable timber trees upon which no studies at all have been conducted. Hence, this series of reports may serve as a starting point by future investigators of African timber species.

*Afrormosia* sp.                      Kokrodua                      Leguminosae

The name kokrodua originated in Ashanti, Gold Coast, and has been applied to commercial consignments of *Afrormosia* timber shipped to England (Jay, 1947). The exact botanical identity of kokrodua is not yet certain. There is some question as to whether or not it is identical with the smaller *Afrormosia elata* Harms of the Ivory Coast, Cameroons and Belgian Congo (Gerry, 1954; Jay, 1947).

Kokrodua is also known as African satinwood, yellow satinwood, ayin, anyesan, elo, duakobin, duabay and makarfo in Nigeria (Lamb, 1950).

The trees attain heights up to 150 feet and diameters of 3-6 feet. The bole is usually straight but somewhat irregularly shaped and slightly buttressed. Larger trees are often free of branches to 100 feet above the ground and have sound heartwood throughout the trunk. The range of kokrodua also includes western Ashanti, Gold Coast, where it is found as the predominant member in some stands (Anonymous, 1953; Flatau, Dick and Company, 1954).

Table 1. MECHANICAL PROPERTIES OF AFRICAN WOODS

Species	Source	Moisture content: per cent	Specific gravity: gr. a.d. vol.	STATIC BENDING				Total work: inch-lb. per cu. in.	Maximum crushing strength: p.s.i.	Hardness: lb. side	Shear: p.s.i.	Cleavage: lb. per in. width	Impact strength: height of drop to failure (50 lb. wt.)
				Modulus of rupture: p.s.i.	Modulus of elasticity: 1000 p.s.i.	Work to maximum load: inch-lb. per cu. in.	Crushing strength: p.s.i.						
<i>Afrormosia</i> sp.	Gold Coast	12	—	—	—	—	—	—	—	—	—	—	—
	Western Africa	12	0.61	19,390	1810	—	43.6	10,350	—	1560	—	—	—
<i>Azalia</i> spp.	Africa	12	—	—	—	—	—	—	—	—	—	—	—
	Western Africa	12	0.73	17,200	2030	11.9	23.2	11,070	1810	1770	2130	260	300
	Western Africa	12	—	—	—	—	—	—	—	—	—	—	—
	Western Africa	12	0.64	15,900	2060	—	—	—	—	—	1950	—	—
<i>Albizia</i> spp.	Africa	12	—	—	—	—	—	—	—	—	—	—	—
	Western Africa	12	0.63	14,400	1650	9.3	15.6	9,030	1510	1390	2130	270	350
	Uganda	123	—	—	—	—	—	—	—	—	—	—	—
	Uganda	12	0.33	4,900	990	4.2	8.0	2,810	460	370	680	190	230
	Uganda	12	0.33	8,200	1280	6.5	7.4	5,050	690	410	850	200	250
<i>Aucoumea klaineana</i>	Western Africa	12	—	—	—	—	—	—	—	—	—	—	—
	Western Africa	12	0.37	7,350	1145	—	—	—	—	—	—	—	—
	Western Africa	12	—	—	—	—	—	—	—	—	—	—	—
	Western Africa	12	0.51	10,120	1430	—	—	—	—	—	—	—	—
	Western Africa	59	—	—	—	—	—	—	—	—	—	—	—
	Western Africa	12	0.64	19,800	2470	18.3	26.9	6,510	1410	1390	—	360	490
	Western Africa	12	0.64	19,800	2470	18.3	31.1	10,180	2020	1680	2260	410	520
	Western Africa	91	—	—	—	—	—	—	—	—	—	—	—
	Western Africa	12	0.54	11,900	1360	—	21.1	4,930	1050	1080	1320	390	460
	Western Africa	12	0.54	11,900	1360	—	15.4	6,950	1340	1100	1710	310	390
<i>Cissambra papaverifera</i>	Gold Coast	78	—	—	—	—	—	—	—	—	—	—	—
	Gold Coast	12	0.62	16,130	1793	12.4	38.9	6,120	1330	1560	1470	540	590
	Gold Coast	12	0.62	16,130	1793	12.4	26.3	9,160	1590	1690	1850	500	600

<sup>2</sup>All specific gravity values based on oven-dry weight.



Table 1—Continued

Species	Source	Moisture content: per cent	STATIC BENDING						Maximum crushing strength p.s.i.	Hardness		Shear p.s.i.	Cleavage		Impact strength: height of drop to failure (50 lb. wt.)
			Specific gravity <sup>2</sup>		Modulus of rupture p.s.i.	Modulus of elasticity p.s.i.	Work to maximum load inch-lb. per cu. in.	Total work inch-lb. per cu. in.		end lb.	side lb.		lb. per in. width	rad. tang.	
			gr. vol.	a.d. vol.											
<i>Cylocodiscus gabunensis</i>	Nigeria	—	—	—	14,000	1980	9.6	26.5	7,930	2470	2530	2130	610	620	—
<i>Cynometra alexandri</i>	Eastern Africa	12	0.79	0.81	19,300	2490	12.9	35.5	11,920	3040	2770	2860	440	590	—
<i>C. ananta</i>	Gold Coast	—	—	0.79	21,450	2341	—	—	11,070	3720	3410	2490	—	—	—
<i>Danilleia ogea</i>	Western Africa	18	—	0.81	19,020	2556	18.5	—	9,650	2630	2530	2105	320	710	—
<i>Distemonanthus benthamianus</i>	Western Africa	—	—	0.44	11,200	1410	10.0	15.5	5,810	670	710	1380	320	380	—
<i>Entandrophragma angolense</i>	Western Africa	74	—	—	7,100	1070	7.4	14.3	3,540	820	770	950	300	350	20
<i>E. cylindricum</i>	Nigeria	52	—	—	9,600	1170	—	—	5,910	1250	1160	—	380	460	33
<i>E. utile</i>	Gold Coast	12	0.54	0.57	9,500	1450	—	—	8,320	1670	1380	—	390	500	23
<i>Gossweilerodendron balsamiferum</i>	Nigeria	50	—	—	10,800	1480	10.3	18.7	5,340	1240	1080	1390	400	440	29
		12	0.55	0.57	14,200	1670	10.1	13.7	8,440	1790	1260	2160	450	500	25
		—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	0.44	11,290	1210	10.8	15.6	5,680	990	700	1375	290	330	25

<sup>2</sup>All specific gravity values based on oven-dry weight.

16

TROPICAL WOODS

1956

Table 1—Continued

Species	Source	Moisture content: per cent	STATIC BENDING						Maximum crushing strength p.s.i.	Hardness		Shear p.s.i.	Cleavage		Impact strength: height of drop to failure (50 lb. wt.)
			Specific gravity <sup>2</sup>		Modulus of rupture p.s.i.	Modulus of elasticity p.s.i.	Work to maximum load inch-lb. per cu. in.	Total work inch-lb. per cu. in.		end lb.	side lb.		lb. per in. width	rad. tang.	
			gr. vol.	a.d. vol.											
<i>Guarea cedrata</i>	Western Africa	99	—	—	10,300	1380	12.1	20.1	4,950	990	870	1390	370	480	29
<i>G. thompsonii</i>	Western Africa	52	—	—	11,800	1640	12.8	26.2	6,030	1100	950	1350	340	310	30
		12	0.54	0.56	14,700	1680	12.1	18.8	8,360	1370	1100	1730	210	170	26
<i>Khaya anthotheca</i>	Uganda	61	—	—	7,300	1150	8.5	22.1	3,540	810	730	1060	340	380	28
		12	0.44	0.46	11,400	1400	9.8	15.5	6,190	1240	860	1600	290	330	25
<i>K. ivorensis</i>	Western Africa	55	—	—	7,600	1180	8.5	—	3,670	570	510	1270	380	—	26
		12	0.43	0.44	10,700	1480	7.8	—	5,680	1080	790	1340	380	—	22
<i>Lophira procera</i>	Gold Coast	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		17.3	—	0.93	22,870	2732	33.5	—	10,450	4310	3810	2490	483	727	—
<i>Lovoa klaineana</i>	Nigeria	61	—	—	7,800	1130	—	—	4,160	780	690	—	330	370	31
		12	0.45	0.49	11,300	1430	—	—	6,730	1130	940	1280	350	410	26
<i>Maesopsis eminii</i>	Uganda	165	—	—	7,600	1250	7.4	13.4	3,990	800	680	950	330	360	27
		12	0.41	0.43	10,400	1430	7.9	16.3	6,420	1020	700	1370	270	330	22
<i>Mansonia altissima</i>	Nigeria	44	—	—	12,300	1490	16.4	33.0	6,160	1330	1210	1610	410	480	40
		12	0.53	0.57	16,800	1690	18.2	30.1	8,190	1680	1290	1980	280	360	45
<i>Mimusops beckelii</i>	Western Africa	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	0.63	12,900	1420	—	—	6,220	1560	1380	—	510	490	—
<i>Mitragyna ciliata</i>	Western Africa	101	—	—	7,500	1260	6.9	13.3	3,810	770	700	—	300	350	27
		12	0.46	0.49	11,500	1440	9.8	15.4	6,490	1160	780	1260	360	450	25

<sup>2</sup>All specific gravity values based on oven-dry weight.

No. 105

TROPICAL WOODS

17



Table 1—Continued

Species	Source	Moisture content: per cent	STATIC BENDING										Impact strength: height of drop to failure (50 lb. wt.)			
			Specific gravity <sup>2</sup>		Modulus of rupture	Modulus of elasticity	Work to maximum load	Total work	Maximum crushing strength	Hardness		Shear		Cleavage		
			gr. vol.	a.d. vol.	p.s.i.	1000 p.s.i.	inch-lb. per cu. in.	inch-lb. per cu. in.	p.s.i.	end lb.	side lb.	p.s.i.		lb. per in. width rad. tang.		
<i>Ocotea bullata</i>	Union of So. Africa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>O. usambarensis</i>	Kenya	59	—	—	8,100	1260	7.3	15.5	4,280	800	760	1110	340	410	25	—
		12	0.51	0.53	12,600	1540	9.5	16.8	7,310	1150	930	1920	340	450	26	—
<i>O. usambarensis</i>	Eastern Africa	56	—	—	8,600	1310	—	18.3	4,370	860	790	1110	340	420	26	—
		12	0.52	0.54	13,300	1550	—	14.8	7,650	1140	970	1920	330	460	31	—
<i>Olea hochstetteri</i>	Eastern Africa	71	—	—	12,700	1780	—	34.1	6,110	1610	1660	1640	600	790	60	—
		12	0.69	0.77	20,400	2300	—	41.3	10,650	2840	2260	2340	350	540	58	—
<i>Parinari excelsa</i>	Uganda	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	0.67	17,000	2080	12.2	23.2	9,160	2190	1720	2330	350	670	32	—
<i>Petersia africana</i>	Western Africa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	0.77	19,300	2250	16.8	28.2	10,460	2430	2180	1970	560	710	—	—
<i>Piptadenia africana</i>	Western Africa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	0.66	13,200	1990	—	—	8,470	1820	1540	—	—	—	—	—
<i>P. africana</i>	Nigeria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		8	—	0.67	16,730	2144	—	—	10,160	—	—	2200	—	—	—	—
<i>Pterocarpus angolensis</i>	Tanganyika	99	—	—	11,300	1270	12.5	34.3	5,750	1280	1070	1280	430	390	41	—
		12	0.50	0.50	13,200	1200	13.8	33.8	7,280	1280	1000	1620	320	300	34	—
<i>P. soyauxii</i>	Western Africa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	0.77	14,720	2290	—	—	8,200	—	1540	—	—	—	—	—

<sup>2</sup>All specific gravity values based on oven-dry weight.

18

TROPICAL WOODS

1956

Table 1—Continued

Species	Source	Moisture content: per cent	STATIC BENDING										Impact strength: height of drop to failure (50 lb. wt.)			
			Specific gravity <sup>2</sup>		Modulus of rupture	Modulus of elasticity	Work to maximum load	Total work	Maximum crushing strength	Hardness		Shear		Cleavage		
			gr. vol.	a.d. vol.	p.s.i.	1000 p.s.i.	inch-lb. per cu. in.	inch-lb. per cu. in.	p.s.i.	end lb.	side lb.	p.s.i.		lb. per in. width rad. tang.		
<i>Sarcocephalus diderrichii</i>	Nigeria	75	—	—	13,000	1840	10.0	22.7	7,210	1650	1520	1680	430	490	32	—
		12	0.63	0.67	16,500	2070	11.7	21.3	10,020	2060	1630	2190	260	280	28	—
<i>Scottellia kamerunensis</i>	Nigeria	65	—	—	11,500	1750	12.7	22.2	5,390	1150	990	1280	370	520	—	—
		12	0.56	0.59	16,000	1990	12.0	16.9	8,880	1620	1090	1910	240	560	—	—
<i>Sterculia rhinopetala</i>	Western Africa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	0.67	16,800	1950	19.5	36.7	8,300	1310	1390	1970	500	590	41	—
<i>Tarrietia utilis</i>	Gold Coast	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	0.50	10,780	1327	8.1	—	5,520	840	840	1260	390	410	—	—
<i>Terminalia ivorensis</i>	Western Africa	42	—	—	8,900	1070	—	—	4,710	—	990	1260	240	290	—	—
		12	0.42	0.41	12,000	1400	—	10.8	6,320	1130	750	1600	250	300	19	—
<i>T. superba</i>	Nigeria	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		10.3	—	0.44	7,968	1272	—	—	5,740	—	—	1340	—	—	—	—
<i>Triplochiton scleroxylon</i>	Nigeria	76	—	—	5,100	700	6.2	14.0	2,580	460	420	670	200	170	24	—
		12	0.31	0.33	7,500	850	6.9	10.9	3,940	690	430	990	230	210	19	—
<i>Turraeanthus africana</i>	Western Africa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	0.51	12,700	1480	9.4	13.1	7,180	1440	1080	2040	370	510	24	—
<i>Juniperus procera</i>	Kenya	78	0.52	—	10,500	1290	11.2	15.8	5,780	1130	930	—	220	250	—	—
		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Podocarpus</i> spp.	Eastern Africa	105	—	—	6,600	940	10.3	18.3	3,090	710	560	810	230	290	24	—
		12	0.43	0.46	11,300	1250	10.7	11.8	6,000	1270	830	1750	230	290	26	—

<sup>2</sup>All specific gravity values based on oven-dry weight.

No. 105

TROPICAL WOODS

19



The sapwood is narrow, about one half inch wide, and slightly lighter in color than the brownish heartwood (Jay, 1947). Upon drying, the heartwood turns from a light brown to a pleasing brownish yellow with darker streaks and a mottled appearance on quartered surfaces. The grain is straight to interlocked; the texture is fine. Growth rings are marked by a scarcity of pores in the late wood. Pores are numerous and either solitary or in radial groups of 2-4. Vertical parenchyma is paratracheal and occurs in wavy tangential bands connecting several pores. On the tangential surface, storied rays can be seen (Jane, 1952).

The weight per cubic foot of the wood at 15 per cent moisture content varies between 40 and 60 pounds with an average of 44 pounds (Gerry, 1954). The specific gravity (oven-dry weight, volume at 15 per cent moisture content) ranges between 0.57 and 0.84 with an average of 0.61.

The wood air seasons and kiln seasons satisfactorily with little tendency toward degrade. Wood is remarkably stable under changes in atmospheric conditions and degrade in the form of distortion should not be a problem (Flatau, Dick and Company, 1954; Jay, 1950).

Strength data (Flatau, Dick and Company, 1954), derived from mechanical tests on air-dry material are reported in table 1. The properties evaluated are static bending, compression parallel to the grain, and side hardness.

In the air-dry condition, kokrodua is superior to teak in all of the static-bending properties except stiffness. It is 30 per cent stronger in maximum bending strength and 80 per cent superior in total work in bending. Kokrodua exceeds teak by 25 per cent in maximum crushing strength and 30 per cent in side hardness. Although the impact strength of kokrodua is not reported, the value for total work in bending indicates that the wood is probably superior to teak in impact strength.

In a paper published by Flatau, Dick and Company (1954) the shrinkage of kokrodua—volumetric 7.8, tangential 5.0 and radial 3.0 per cent—is reported to be almost identical with the shrinkage of teak (table 2). However, a statement

Table 2. SHRINKAGE OF AFRICAN WOODS

Species	Source	Specific gravity <sup>a</sup>	Shrinkage (per cent of green dimension)		
			radial	tang.	volumetric
<i>Afrormosia</i> sp.	Gold Coast	0.61	3.0	5.0	7.8
<i>Afzelia</i>					
<i>africana</i>	Western Africa	0.73	2.0	3.0	5.0
<i>Aucounea</i>					
<i>klaineana</i>	Western Africa	0.37	5.6	6.1	12.6
<i>Berlinia</i> spp.	Western Africa	0.51	6.0	10.0	15.5
<i>Celtis</i>					
<i>soyauxii</i>	Nigeria	0.70	5.6	10.4	15.4
<i>Chlorophora</i>					
<i>excelsa</i>	Western Africa	0.56	2.8	3.8	8.8
		—	3.4	4.8	8.5
<i>Cistanthera</i>					
<i>papaverifera</i>	Gold Coast	0.67	3.6	4.0	8.2
<i>Cylicodiscus</i>					
<i>gabumensis</i>	Nigeria	0.81	4.3	7.3	12.6
<i>Daniellia ogea</i>	Western Africa	0.44	3.0	9.0	11.7
<i>Distemonanthus</i>					
<i>benthamianus</i>	Western Africa	0.60	3.1	5.2	10.7
<i>Entandrophragma</i>					
<i>angolense</i>	Western Africa	0.50	4.6	10.6	15.7
<i>E. cylindricum</i>	Western Africa	0.57	5.9	7.4	14.0
<i>E. utile</i>	Western Africa	0.57	6.0	7.0	12.5
<i>Guarea cedrata</i>	Western Africa	0.49	3.5	6.0	9.8
<i>G. thompsonii</i>	Western Africa	0.56	4.0	6.6	10.3
<i>Khaya anthotheca</i>	Uganda	0.46	3.4	6.4	9.6
<i>K. ivorensis</i>	Western Africa	0.44	4.1	5.8	8.8
		—	3.6	5.0	8.5
		—	5.0	8.4	16.9
<i>Lophira procera</i>	Gold Coast	0.93	9.0	11.0	19.0
<i>Lovoa klaineana</i>	Nigeria	0.49	5.3	8.8	12.1
<i>Mansonia altissima</i>	Nigeria	0.57	2.6	5.2	7.7
<i>Mimusops</i>					
<i>beckelii</i>	Western Africa	0.63	5.3	7.8	13.7
<i>Mitragyna</i>					
<i>ciliata</i>	Western Africa	0.49	5.0	10.4	14.5
<i>Ocotea</i>					
<i>usambarensis</i>	Kenya	0.53	3.0	6.0	9.0
<i>Olea</i>					
<i>hochstetteri</i>	Eastern Africa	0.77	5.2	10.2	14.9
<i>Parinari</i>					
<i>excelsa</i>	Uganda	0.67	6.0	10.0	15.5
<i>Petersia</i>					
<i>africana</i>	Western Africa	0.77	13.0	14.0	25.2

<sup>a</sup>Based on oven-dry weight and air-dry volume.



Table 2—Continued

Species	Source	Specific gravity <sup>8</sup>	Shrinkage (per cent of green dimension)		
			radial	tang.	volumetric
<i>Piptadenia africana</i>	Western Africa	0.66	5.8	10.2	16.4
<i>Pterocarpus angolense</i>	Tanganyika	0.50	1.6	1.8	3.4
<i>P. soyauxii</i>	Western Africa	0.77	3.8	4.4	8.5
<i>Sarcocephalus diderricii</i>	Nigeria	0.67	4.4	7.6	11.7
<i>Scottellia coriacea</i>	Nigeria	0.59	5.0	9.0	13.6
<i>Sterculia oblonga</i>	Western Africa	0.70	7.0	13.0	19.1
<i>Tarrietia utilis</i>	Gold Coast	0.50	5.0	9.0	13.6
<i>Terminalia ivorensis</i>	Western Africa	0.41	4.6	6.2	14.2
<i>T. superba</i>	Nigeria	0.44	5.1	8.1	14.4
<i>Triplochiton scleroxylon</i>	Nigeria	0.33	2.5	5.1	7.8
<i>Turraeanthus africana</i>	Western Africa	0.51	4.0	6.2	10.6

<sup>8</sup>Based on oven-dry weight and air-dry volume.

issued by the Bureau of Ships, United States Navy,<sup>6</sup> indicates that the shrinkage of kokrodua is approximately twice that of teak. The dimensional change between 90 per cent and 60 per cent relative humidity is 1.3 per cent tangentially and 0.7 per cent radially expressed as a per cent of the dimension at 60 per cent relative humidity. Comparable values for teak are 1.3 per cent and 0.8 per cent (Flatau, Dick and Company, 1954; Forest Products Research Laboratory, 1954). With a given variation in moisture content kokrodua exhibits dimensional change similar to teak.

The wood is extremely durable (table 3), even under conditions very favorable to decay. Test pieces submerged in a harbor for two summers were not attacked by teredo borers even though the harbor was badly infested (Flatau, Dick and Company, 1954; Jay, 1947).

<sup>6</sup>Summary of an investigation of kokrodua wood conducted at the Naval Material Laboratory, New York Naval Shipyard, August, 1954.

Table 3. DECAY RESISTANCE OF AFRICAN WOODS

Species	Source	Months of exposure	Loss in weight (per cent) <sup>4</sup>						Average all fungi	Resistance class
			Brown rots		White rots		Average all fungi			
			<i>Merrillius lacrymans</i>	<i>Coniophora cerebella</i>	<i>Lenzites trabea</i>	<i>Polystictus versicolor</i>	<i>Polystictus sanguineus</i>			
<i>Alstonia congensis</i>	Uganda	4	4.9	24.8	21.5	15.8	—	—	Perishable	
<i>Celtis</i>	Nigeria	8	—	36.4	38.3	46.4	—	—	Perishable	
<i>C. soyauxii</i>	Nigeria	8	40.1	39.0	36.1	42.6	47.3	41.2	Perishable	
<i>Chlorophora excelsa</i>	Western Africa	8	nil	nil	neg. <sup>5</sup>	neg.	nil	nil	Very resistant	
<i>Cistambura papaverifera</i>	Gold Coast	8	—	—	—	24.0	32.8	—	Moderately resistant	
<i>Cylicodiscus gabunensis</i>	Nigeria	4	7.2	8.5	—	11.2	—	—	Very resistant	
<i>Entandrophragma angolense</i>	Nigeria	4	nil	nil	—	neg.	nil	neg.	Very resistant	
<i>E. utile</i>	Western Africa	8	10.7	25.3	17.3	54.3	—	26.9	Not resistant	
<i>Gossweilerodendron balsamiferum</i>	Western Africa	8	14.1	13.0	1.3	4.8	—	9.3	Moderately resistant	
<i>Guarea cedrata</i>	Nigeria	4	nil	nil	nil	neg.	—	neg.	Resistant	
<i>G. thompsonii</i>	Western Africa	8	13.9	—	—	20.2	—	—	Not resistant	
<i>Khaya antbotheca</i>	Western Africa	8	—	—	—	7.2	—	—	Moderately resistant	
<i>Khaya antbotheca</i>	Uganda	4	7.0	12.9	—	8.6	—	9.5	Not resistant	
<i>Khaya antbotheca</i>	Uganda	8	15.6	25.1	—	17.3	—	17.3	Not resistant	

<sup>4</sup>See Findlay, 1938.

<sup>5</sup>Negligible.



Table 3—Continued

Species	Source	Months of exposure	Loss in weight (per cent) <sup>a</sup>										Average all fungi	Resistance class
			Brown rots		White rots		White rots		White rots		White rots			
			<i>Merulius lacrymans</i>	<i>Coniophora cerebella</i>	<i>Lenzites itabeca</i>	<i>Polytictus versicolor</i>	<i>Polytictus sanguinis</i>	<i>Polytictus sanguinis</i>	<i>Polytictus sanguinis</i>	<i>Polytictus sanguinis</i>	<i>Polytictus sanguinis</i>	<i>Polytictus sanguinis</i>		
<i>Maesopis emini</i>	Uganda	4	8.0	12.6	19.4	23.2	—	13.3	Not resistant					
<i>Mansonia altissima</i>	Nigeria	8	19.5	23.7	30.3	68.5	—	33.0	Very resistant					
<i>Ocotea usambarensis</i>	Kenya	4	2.2	3.5	1.6	1.7	2.2	2.2	Very resistant					
<i>Olea hochstetteri</i>	Eastern Africa	4	neg.	neg.	neg.	11.2	5.3	neg.	Moderately resistant					
<i>Pterocarpus angolense</i>	Tanganyika	4	neg.	neg.	neg.	2.1	2.9	neg.	Very resistant					
<i>Sarcoccephalus diderrichii</i>	Nigeria	8	neg.	neg.	neg.	3.0	2.5	neg.	Very resistant					
<i>Scottellia coriacea</i>	Nigeria	4	2.2	neg.	2.3	22.2	23.4	10.0	Not resistant					
<i>Terminalia ivorensis</i>	Western Africa	8	neg.	neg.	nil	4.0	5.8	—	Resistant					
<i>T. superba</i>	Nigeria	4	3.3	3.0	—	24.7	30.6	15.4	Not resistant					
<i>Triplochiton scleroxylon</i>	Nigeria	4	6.5	6.4	9.1	8.1	—	7.5	Not resistant					
		8	26.4	19.4	15.8	28.0	—	22.4	resistant					

<sup>a</sup>See Findlay, 1938.<sup>b</sup>Negligible.

The wood works readily and easily with smooth surfaces resulting in all operations if care is taken. A reduced cutting angle is advisable if grain pick-up is to be avoided in planing. Fresh sawdust may be irritating to some workers. The wood takes nails and screws well, turns satisfactorily, and finishes favorably (Gerry, 1954; Jay, 1947).

Kokrodua should prove to be a very serviceable wood where strength, durability and dimensional stability combined with an attractive appearance are desired. It has been installed on ships in decking and railing, doors, winch soles, ladders, etc., and has apparently proven very satisfactory. It is a first-class joinery wood, sufficiently light in color to conform with modern architectural trends. Kokrodua is characterized by abrasion resistance similar to that of teak and is as suitable for flooring. The wood contains tannin which may cause discoloration to take place in the presence of moisture and iron salts. There is some expectation that the wood will prove suitable for most purposes where teak has been used in the past (Flatau, Dick and Company, 1954; Jay, 1947).

*Afzelia* spp.*Afzelia*

## Leguminosae

There are eight species of the genus *Afzelia* recognized in Africa. Of these, *A. africana* J. E. Smith, *A. bipindensis* Harms, *A. caudata* Hoyle, *A. pachyloba* Harms and *A. quanzensis* Welw. are the principal commercial species (Chalk et al., 1932, 1933; Forest Products Research Laboratory, 1951a; Dalziel, 1937).

*A. africana* is identified by numerous local common names probably due to its extensive range. These names include fok, hol, lingué (Senegal); gongo, langué, pau konta (Portuguese Guinea); gbende, kpende-deli (Sierra Leone); kpa-kpa, mboro (Ivory Coast); ahanta, papao, papawu, pepe (Gold Coast); gayohi (northern Nigeria); apa, alinyan, aja (southern Nigeria); balawo-kudu, liwamba, olombi (Belgian Congo); baa (Uganda). Other common names include: *A. bipindensis*, ariyan, ayan, odo (Nigeria); *A. caudata*, apa,



orodo (southern Nigeria); *A. quanzensis*, "Rhodesian mahogany" (Chalk et al., 1933; Dalziel, 1937).

*A. africana* is a moderately large tree attaining a height from 40–60 feet with a straight bole up to fifty feet long and a diameter of approximately three feet. *A. quanzensis* closely resembles *A. africana* in the forest, both having a flat, wide-spreading, umbrella-shaped, crown. *A. bipindensis*, *A. caudata* and *A. pachyloba* attain greater heights and show better timber form than *A. africana* or *A. quanzensis*. *A. africana* is found in Senegal, Sierra Leone, Liberia, French Guinea, Ivory Coast, Gold Coast, Nigeria, Cameroons, Belgian Congo and the Sudan. It occurs in open country, chiefly in savanna regions with rainfall up to forty inches annually, where it is usually the dominant species although stunted in growth. *A. africana* also inhabits the deciduous and monsoon forests (up to 100 inches annual rainfall) where it attains the maximum size. *A. quanzensis* is found in the savanna and coastal forests of east Africa from Kenya and Tanganyika, southward to the Transvaal. *A. bipindensis*, *A. caudata* and *A. pachyloba* grow in the dense evergreen forests of west and central Africa. These three species may have an abundance ranging from 50–300 trees per square mile (Chalk et al., 1933; Forest Products Research Laboratory, 1951).

The woods of the five species are almost indistinguishable from one another. Furthermore, the physical and mechanical properties of the different species are so similar that they will be described as a group.

The wood is yellowish brown when freshly cut, the heartwood darkening to reddish brown upon exposure (*A. caudata* lacks the reddish cast); the thin layer of sapwood (1–2 inches wide) is sharply delineated from the darker heartwood. Grain is straight to moderately interlocked, the latter form producing a fine ribbon figure on the quartered surface. The texture is coarse and the wood is of medium luster. Growth rings are distinct due to evenly spaced concentric bands of terminal parenchyma 1–4 cells wide. The pores are distinct without a lens, not numerous, evenly distributed, solitary or in radial groups of 2–4. The lumina are

filled with a reddish gum. The longitudinal parenchyma is terminal, vasicentric (3–6 cells wide), aliform with blunt wings, and confluent (connecting 2–4 pores). The vascular rays are not distinct on the cross section, but are readily seen on the radial surface. The wood of *A. bipindensis* has markedly storied rays. Other species show only a tendency toward storied structure (Chalk et al., 1932, 1933; Forest Products Research Laboratory, 1951b; Dalziel, 1937; Kribs, 1950).

The seasoned wood ranges from 40–60 pounds per cubic foot with an average density of 52 pounds per cubic foot. The specific gravity based on oven-dry weight and air-dry volume varies between 0.57 and 0.86, averaging 0.74 (Forest Products Research Laboratory, 1951b).

Afzelia kiln seasons satisfactorily, but slowly, from the green condition. Degrade is generally not severe, but distortion, checking, and the extension of splits may occur (Forest Products Research Laboratory, 1951b; Jay, 1947). Careful piling is recommended to minimize distortion. The British Forest Products Research Laboratory (1945) suggests a kiln schedule similar to that used for sugar maple and black walnut.

The strength of the wood (Armstrong, 1953; Forest Products Research Laboratory, 1945) in most categories is proportional to its high specific gravity. Results of mechanical tests conducted at the British Forest Products Research Laboratory are reported for air-dry material only and are presented in table 1. The two different groups of data represent one assemblage with an average specific gravity of 0.64 and another with a specific gravity of 0.73 (oven-dry weight and air-dry volume).

In the air-dry condition, afzelia (sp. gr. 0.64) is approximately as strong in bending as yellow birch (sp. gr. 0.62). Afzelia is 10 per cent stronger in maximum crushing strength and 70 per cent as strong in shear. The denser material of afzelia (sp. gr. 0.73) compares favorably with blue gum (*Eucalyptus globulus*, sp. gr. 0.74) being somewhat stronger in bending, 20 per cent stronger in maximum crushing



strength, slightly harder, and 10–15 per cent stronger in shear. It is approximately 75 per cent as resistant to impact loads as blue gum and falls in a group with sweetgum and red maple. In resistance to splitting, afzelia is exceptionally low and compares equally with yellow poplar.

Afzelia is classified as a poor steam-bending species (Forest Products Research Laboratory, 1951b). Steamed material can be bent to radii of curvature of 32 inches per inch of thickness when supported by a steel tension strap and 44 inches per inch of thickness when unsupported. Unsteamed laminae can be bent to a radius of curvature of 83 inches per inch of thickness.

The shrinkage of afzelia from the green to the oven-dry condition is exceptionally low for a wood of its density (table 2; Forest Products Research Laboratory, 1945). Radial shrinkage is less than one half the radial shrinkage of white oak. Tangential and volumetric shrinkage of afzelia, 3.0 and 5.0 per cent respectively, are only one third as much as white oak. Afzelia exhibits exceptional dimensional stability with moisture content change. A change from 90 per cent relative humidity (14.0 per cent equilibrium moisture content) to 60 per cent relative humidity (9.5 per cent equilibrium moisture content) resulted in 1.0 per cent tangential, and 0.5 per cent radial dimensional change based on per cent of dimension at 60 per cent relative humidity (Forest Products Research Laboratory, 1954). Domestic white oak exhibits 2.8 per cent tangential, and 1.3 per cent radial dimensional change between 90 per cent and 60 per cent relative humidity. Comparable values for teak (*Tectona grandis*) are 1.3 per cent tangential, and 0.8 per cent radial dimensional change—somewhat greater than for afzelia.

Service tests conducted in Nigeria indicate that the wood is very resistant to decay by wood-destroying fungi. In Uganda, test samples were still sound after ten years in the ground. The sapwood of downed trees and logs is susceptible to infestation by powder-post beetles; the heartwood is reported as resistant but not immune to teredo attack. The wood is extremely resistant to impregnation with creosote (Forest Products Research Laboratory, 1951b).

Owing to its hardness and tendency toward interlocked grain, afzelia is difficult to work with hand and machine tools. The wood has a moderate blunting effect on cutting edges and machining of dry material produces an irritating dust. Quartered surfaces tend to show grain pick-up in planing and require a cutting angle of 15°. The timber works well in other operations if cutting edges are kept well sharpened. High resistance to the driving of nails and the tendency to split may require preboring. The wood glues readily, stains and finishes well when properly treated with a grain filler (Forest Products Research Laboratory, 1945, 1951b).

The British Forest Products Research Laboratory (1945) reports that afzelia is suitable for a wide range of purposes where strength, durability and dimensional stability combined with an attractive appearance are desired. In west Africa, the wood is used for indoor and outdoor construction, harbor work, railway ties, cabinet-making, turnery, naval construction, sluice boxes and water conduits. It is suitable for heavy construction but the design of joints must take into account its low resistance to splitting. Afzelia is used as an alternative for teak where its weight is no objection. In England, afzelia was used as a substitute for teak in the manufacture of switchboards and for other exacting purposes during World War II (Forest Products Research Laboratory, 1945). It is recommended for superior joinery such as staircases, paneled doors and counter tops in public buildings (Forest Products Research Laboratory, 1951b).

*Albizia* spp.<sup>7</sup>

Albizzia

Leguminosae

Approximately 30 species of the genus *Albizia* occur in Africa of which *A. ferruginea* (Guill. & Perr.) Benth., *A. gummifera* (Gmel.) C. A. Smith and *A. zygia* (DC.) Macb. are commercially important. The remaining species are small savanna trees (Forest Products Research Laboratory, 1951a; Dalziel, 1937).

<sup>7</sup>See Little (48.1953) for note on spelling.



Albizzia is the trade name applied to the three species which occur within the United Kingdom. Other names include okura (Gold Coast); and nongo (Uganda). Local names for *A. ferruginea* are newei (Sierra Leone); iatandza (Ivory Coast); awiemfo-samina (Gold Coast); sakachi (northern Nigeria); ayinré (southern Nigeria). Native names for *A. gummifera* include bakbwe kapun bongbo (Sierra Leone); bangban, possi (Ivory Coast); pampena (Gold Coast); asihue (Togo); sakachi (northern Nigeria); ayinré, avu (southern Nigeria). Those for *A. zygia* comprise kouket (Senegal); bakbwe, kapun (Sierra Leone); blor-feh (Liberia); koli, wochi (Ivory Coast); kulo, ohura (Gold Coast); kakpara (Togo); sakachi (northern Nigeria); ayinreta (southern Nigeria; Forest Products Research Laboratory, 1951a; Dalziel, 1937).

*A. ferruginea* is the largest of the three species, the tree attaining a height of 120 feet and a diameter of three feet with a clear bole 30-40 feet in length. However, it is the least common, and rarely exceeds twenty-five trees over two feet in diameter per square mile. *A. gummifera* is a smaller tree with a bole commonly twisted and indented. *A. zygia* is a medium-sized tree, heavily buttressed but with a good bole form. It attains a height of 90 feet and a diameter of three feet. The species are widely distributed in the secondary and dry forests of Senegal, Sierra Leone, Liberia, Ivory Coast, Gold Coast, Nigeria, Camerons and eastward to east Africa (Forest Products Research Laboratory, 1951a; Dalziel, 1937; Jay, 1947).

Sapwood of *A. ferruginea* is yellow brown, about two inches wide, and distinct from the dark chocolate-brown heartwood. The wood lacks a distinct taste and odor (Cooper and Record, 1931). The grain is markedly interlocked and often somewhat irregular; the texture is coarse. The sapwood and heartwood of *A. gummifera* are distinct; the former light yellow and about two inches wide; the latter a light brown, sometimes with a greenish tinge. The grain and texture are similar to *A. ferruginea*. Wood of *A. zygia* is distinct from the other two species in that the sapwood is

gray. The heartwood presents a pinkish cast; the grain is straight or more commonly interlocked, and the texture is medium. In *A. ferruginea*, growth rings are indistinct; the pores are visible without a lens, large, scanty and solitary or in radial groups of 2-4. Longitudinal parenchyma can be seen with a lens and is paratracheal. The vascular rays are visible on the cross section with a lens and observable to the naked eye on the radial surface, being darker than the background (Yale wood no. 14476). In *A. gummifera*, the growth rings are indistinct. The pores are large, visible to the naked eye, not numerous and solitary or in radial groups of 2-4. The vertical parenchyma is distinct with a lens and paratracheal. Rays can be seen on the cross section without a lens as fine light lines as they are larger than in *A. ferruginea*. They are visible on the radial surface as dark flecks (Yale wood no. 48258). In *A. zygia*, the growth rings are sometimes distinct. The pores are small, distinct to the unaided eye, fairly numerous and solitary or in radially flattened groups. Parenchyma is indistinct without a lens and paratracheal. The vascular rays are not evident without a lens on the cross section and inconspicuous on longitudinal surfaces.

The density of the wood varies with the species, *A. ferruginea* being very heavy. *A. gummifera* and *A. zygia* are somewhat lighter in weight (Forest Products Research Laboratory, 1951a). *A. ferruginea* ranges in density between 37 and 52 pounds per cubic foot air dry with an average of 45 pounds per cubic foot. The specific gravity (oven-dry weight and air-dry volume) varies between 0.52 and 0.73 averaging 0.63. *A. gummifera* weighs from 27-45 pounds per cubic foot with an average of 36 pounds per cubic foot. This is a specific gravity range from 0.38-0.63 (oven-dry weight and air-dry volume) with an average of 0.50. The weight range of *A. zygia* is from 32-42 pounds per cubic foot with an average of 36 pounds per cubic foot. The specific gravity (air-dry volume) varies between 0.45 and 0.58, averaging 0.50.



*Albizzia* is inclined to dry slowly, particularly in thicker sizes, but with little degrade (Jay, 1947). The British Forest Products Research Laboratory (1951a) suggests a kiln schedule the same as that recommended for sugar maple and black walnut. The schedule employs a maximum dry-bulb temperature of 155°F. and is recommended for lumber up to one and one half inches thick.

The results of strength tests carried out in Great Britain (Armstrong, 1953), on air-dry material are reported in table 1. The identity of the particular species tested is not reported, but the average specific gravity of 0.63 stated for the material suggests *A. ferruginea*. A British Forest Products Research Laboratory report (1951a) states that the material tested was predominantly the heavier wood which would also indicate *A. ferruginea*. The lighter species, *A. gummiifera* and *A. zygia*, are reported as having only 60 per cent of the strength of *A. ferruginea*.

The air-dry material of *A. ferruginea* exhibits strength comparable to American beech of specific gravity 0.64 (air-dry volume). *Albizzia* approximates American beech in maximum bending strength and in stiffness but is considerably inferior to American beech in work to maximum load and total work in bending. Both work values for *albizzia* in bending are approximately one half the comparable work values for American beech. The same relationship is found in the shock resisting properties of the two woods; *albizzia* is only one half as resistant to impact loads as American beech. However, it is 25 per cent stronger in maximum crushing strength, equal in shearing strength parallel to the grain, equally as hard on the end and side grain, and approximately 60 per cent as resistant to splitting.

The wood can be bent, after steaming, to radii of curvature of 20 inches per inch of thickness when supported with a steel strap and 40 inches when unsupported (Forest Products Research Laboratory, 1951a). Thin, unsteamed laminae, bend to radii of curvature of 56 inches per inch of thickness. Considerable variation in bending performance is encoun-

tered and the wood is considered only moderately good for bending purposes.

Shrinkage data are lacking for the species. The dimensional change occurring between 90 per cent and 60 per cent relative humidity (16 per cent and 11.5 per cent equilibrium moisture contents respectively) is 1.2 per cent tangentially based on dimension at 60 per cent relative humidity. No value for radial dimensional change is reported. The tangential variability in dimension is comparable to the 1.3 per cent change exhibited by teak (Forest Products Research Laboratory, 1954) which places *albizzia* in the class of wood with small change in dimension.

*Albizzia* is very resistant to decay (table 3), all three species having similar resistance to decay fungi in laboratory tests. Service tests carried out in Nigeria indicate that *A. ferruginea* is very resistant to decay and *A. gummiifera* and *A. zygia* only moderately resistant. The sapwood of the converted material is susceptible to powder-post beetle damage; the wood is classified as resistant to termites (Forest Products Research Laboratory, 1951a). Impregnation with creosote is extremely difficult and the timber is regarded as impermeable.

Investigations at the British Forest Products Research Laboratory (1951a) indicate that *albizzia* has moderately good working properties, exhibiting ease in cutting with a saw of the light hardwood type. A fine air-borne dust is produced in sawing which irritates the nose. The presence of interlocked grain causes grain pick-up on the radial surface in planing which may be prevented by employing a cutting angle of 15° or less. Clean finishes are produced in other machining operations. *A. ferruginea* tends to split in nailing, but *A. gummiifera* and *A. zygia* exhibit little tendency toward splitting. Satisfactory results are obtained with stains and finishes when a grain filler is used.

In Nigeria, *A. zygia* is used for planks, doors and general house building. *A. gummiifera* is employed in the Gold Coast for carving into household utensils and in the production of charcoal. The heavy timber (*A. ferruginea*) is recommended

as a substitute for oak in construction work where impact strength and splitting resistance are not important. The lighter timbers (*A. gummifera* and *A. zygia*) are recommended for light interior millwork and boxes (Forest Products Research Laboratory, 1951a; Dalziel, 1937).

*Alstonia congensis* Engl.      *Alstonia*      Apocynaceae

The species is known in trade as alstonia, mujwa (United Kingdom) and as emien (French colonies). Local names (Dalziel, 1937) include bantang foro (Senegal); kaiwi (Sierra Leone); emien (Ivory Coast); sindru (Gold Coast); ahun, uhu, uguwa, ebwu, ebo, bokuk (Nigeria); bokuk, wokuka, kanja, kuge (Cameroons).

The tree attains a maximum height of 130 feet and a diameter of three feet. The stem is deeply fluted at the base appearing buttressed for a height of twenty feet. The bole is straight and generally cylindrical for a considerable distance. The species is commonly found in fresh-water swamp forests and inundated forest land, although it is also found on drier sites. In Nigeria, it occurs in both the semi-evergreen and deciduous forests. Its range extends along the coast from Senegal to the Cameroons and eastward across the Belgian Congo to Uganda. *Alstonia* is most abundant in the humid forests of the Cameroons. Mature trees are highly subject to wind damage and decay (Eggeling and Harris, 1939; Jay, 1947).

The wood is yellowish white throughout with no differentiation in color between heartwood and sapwood (Dalziel, 1937; Jay, 1947). Grain is generally undulating or interlocked. The texture is fine to medium (Eggeling and Harris, 1939). Growth rings are indistinct. The pores are barely distinct to the naked eye, numerous, evenly distributed and solitary or in radial groups of 3-5 or more. The longitudinal parenchyma is visible to the naked eye on moist cross sections, abundant and banded. Vascular rays are fine and but visible to the naked eye on the wet end surface. However, on the tangential face rays are indistinct. The tangential surface of the wood often shows lenticular or slot like open-

ings which usually occur in horizontal rows at intervals of 1-3 feet up the stem. These openings, from  $\frac{1}{8}$  inch to 4 inches in height and about 4 inches apart in each row, were laticiferous structures which in the dry wood contain the shrivelled remains of unlignified material.

The air-dry wood ranges from 25-30 pounds per cubic foot with an average of approximately 27 pounds per cubic foot (Jay, 1947). The specific gravity (oven-dry weight, air-dry volume) ranges between 0.36 and 0.43, averaging approximately 0.38.

The wood seasons rapidly and well with a very slight tendency toward degrade in the form of checking or splitting. As mentioned above, the laticifers contract on drying often leaving open passages through the boards (Eggeling and Harris, 1939).

The results of mechanical tests (Armstrong, 1953) on unseasoned and seasoned material are given in table 1. *Alstonia* is considerably stronger than domestic hardwoods of similar specific gravities (such as quaking aspen and black willow) in many strength categories.

The unseasoned wood of *alstonia* is slightly inferior to quaking aspen in modulus of rupture in bending but is superior in stiffness. In work to maximum load, it is approximately 30 per cent below quaking aspen. The value for total work in bending for *alstonia* is one half that for aspen. This is also reflected in resistance to impact, aspen being 70 per cent stronger. In most other properties, *alstonia* exhibits a marked superiority. It is 30 per cent stronger in maximum crushing strength, 250 per cent harder on the end grain, and 30 per cent harder on the side grain. In resistance to splitting, *alstonia* exceeds aspen by 30 per cent. In shearing strength parallel to the grain, *alstonia* is only slightly superior.

With the exception of total work in bending and impact strength, the increases in strength upon drying for both species are quite similar. Increases in modulus of rupture and maximum crushing strength parallel to the grain are appreciable for both woods. Stiffness in bending, work to



maximum load, hardness and shearing strength parallel to the grain exhibit moderate increases—roughly 30–40 per cent. *Alstonia* exhibits very slight increases in cleavage in both the radial and tangential planes. Quaking aspen undergoes a slight increase in total work in bending upon drying, but the total work value for *alstonia* decreases almost 10 per cent. Both woods exhibit decreases in impact strength with *alstonia* showing the more marked loss.

In the air-dry condition, *alstonia* is inferior to aspen in all bending properties except stiffness. The most pronounced difference is in values for total work in which that for quaking aspen is twice the value for *alstonia*. *Alstonia* is only 60 per cent as strong in impact strength. It is 20 per cent stronger in maximum crushing strength, 35 per cent harder on the end grain and 15 per cent harder on the side grain. Both woods are about equal in shearing strength parallel to the grain and resistance to splitting.

No shrinkage data for *alstonia* are reported. The dimensional change with changes in moisture content is very similar in magnitude to that of teak. The dimensional change between 90 per cent and 60 per cent relative humidity (equilibrium moisture contents of 20.5 per cent and 14 per cent respectively) is 1.3 per cent tangentially and 0.9 per cent radially for *alstonia* (expressed as a per cent of dimension at 60 per cent relative humidity) and 1.3 per cent tangentially and 0.8 per cent radially for teak (Forest Products Research Laboratory, 1954).

The results of durability tests conducted at the British Forest Products Research Laboratory are reported in table 3. At the end of a 4-month exposure, the test specimens showed high weight loss due to decay. After an 8-month exposure, the loss in weight due to decay averaged 40.3 per cent of the original weight of the specimens. The wood is therefore classed as perishable and requires preservative treatment for uses where decay is a hazard (Findlay, 1938). The species is also readily attacked by various wood-boring beetles. However, the wood absorbs preservatives very well and can easily be impregnated (Eggeling and Harris, 1939).

The wood is easily worked with hand and machine tools, finishing to a smooth surface in all operations when care is taken to prevent grain pick-up in planing quartered surfaces and chipping-out at tool exits (Eggeling and Harris, 1939). Apparently, the presence of latex deposits does not result in any undue blunting of cutting edges.

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#### THE NATURAL MARINE BORER RESISTANCE OF TROPICAL AMERICAN WOODS

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The principal purpose of this paper is to bring up to date the results of marine exposure tests that were previously discussed by the writer at the Marine Borer Conference held in Miami Beach, Florida in June, 1952. As noted in a report delivered at that conference (Wangaard, 1953), these tests on woods from the American tropics were initiated in 1948 as a cooperative project between the W. F. Clapp Laboratories and Yale University working under the sponsorship of the Bureau of Ships and Office of Naval Research.

Originally installed in 1948 at Kure Beach, the test panels of 2 × 3 × 18-inch heartwood sticks were transferred to Harbor Island, North Carolina in April 1950 where the tests are still continuing. Additional specimens have been added to these tests from time to time until resistance data are now

available for 40 species over exposure periods ranging from 6 to 70 months (Clapp Laboratories, 1952-1955).

Table 1 shows ratings for the most resistant species included in these tests. It will be noted that none of them was completely immune to attack after an exposure period of 16-18 months. This should not be interpreted, however, as an indication of comparable attack in full-size timbers in the same period. Small specimens of this type serve principally to provide values of relative resistance among different species. During the early period of these tests a number of domestic woods were exposed under comparable conditions. Of these, only redwood and bald cypress survived to the end of the first 9-month exposure period. Principal damage at this site has been inflicted by *Bankia*, *Limmoria*, and pholad mollusks.

Gonggrijp (1932) and Bianchi (1932) appear to have first called attention to the significance of silica content in relation to the natural resistance of wood to marine borers. Shortly thereafter van Iterson (1934) noted that the highly resistant manbarklak, *Eschweilera longipes* (Poit.) Miers, contained prominent inclusions of silica in its ray cells.

A striking example of the influence of silica in the Australian turpentine wood (*Syncarpia laurifolia* Tenore), highly reputed for its resistance to marine borers, has been cited by Amos and Dadswell (1948). Comparing typical Australian-grown material with Hawaiian-grown specimens that had been found to lack resistance to marine borers, they discovered that the silica content of the young Hawaiian-grown wood was only 0.091 per cent in contrast to an average of 0.59 per cent for the native Australian material.

In a study of silica content of British Guiana woods, Amos (1951) found percentages of SiO<sub>2</sub> ranging from 0.00 to 2.82. He classed all woods of that group containing more than 0.50 per cent as highly siliceous and, largely on the basis of their reputation, concluded that there is but little doubt that the resistance of such woods to marine borers is attributable to their silica content.



Table 1. TEST RATINGS FOR TROPICAL AMERICAN SPECIES SHOWING SUPERIOR NATURAL RESISTANCE TO ATTACK BY MARINE BORERS AT HARBOR ISLAND, NORTH CAROLINA

Species	Resistance class <sup>1</sup>			Silica content <sup>2</sup> per cent
	16-18 months	24 months	36 months	
Anauerá— <i>Licania macrophylla</i> Benth.	A-B	B	B	1.52
Parinari— <i>Parinari rodolphi</i> Huber	B	B	B	0.804
Burada— <i>Parinari campestris</i> Aubl.	B	B	B	0.902
Manbarklak— <i>Eschweilera</i> <i>subglandulosa</i> (Steud.) Miers	B	B	B	0.688
Acapú— <i>Vouacapoua americana</i> Aubl.	A-B	B	B	0.002
Marishiballi— <i>Licania buxifolia</i> Sandw.	B	B	C	0.432
Matá-matá— <i>Eschweilera odora</i> (Poepp.) Miers	B	B	C	0.619
Castanha sapucaia— <i>Lecythis</i> <i>usitata</i> Miers var. <i>temuifolia</i> Knuth	B	B	C	—
Morrão— <i>Eschweilera blanchetiana</i> (Berg) Miers	B	B	C	—
Aiomoradan— <i>Parinari excelsa</i> Sabine	B	B	D	0.576
Sapucaia— <i>Lecythis paraensis</i> (Huber) Ducke	B	C	C	0.048
Angélique— <i>Dicorynia guianensis</i> Amsh. <sup>3</sup>	B	C	—	0.396
Determa— <i>Ocotea rubra</i> Mez	B	D	—	0.000
Angelim— <i>Hymenolobium excelsum</i> Ducke	C	C	—	0.002
Coco de mono— <i>Eschweilera tenax</i> Miers	C	D	D	0.079
Cumaru preto— <i>Taralea</i> sp.	C	D	D-F	—
Greenheart— <i>Ocotea rodiei</i> (Rob. Schomb.) Mez	C	D-E	D-E	0.01 <sup>4</sup>
Black kakeralli— <i>Eschweilera</i> <i>sagotiana</i> Miers	C-D	D	—	0.221
Fiddlewood— <i>Vitex gaudieri</i> Greenm.	C	E	—	0.025

<sup>1</sup>Marine borer activity: A, None; B, Light; C, Moderate; D, Fairly heavy; E, Heavy.

<sup>2</sup>Except as indicated for greenheart, analysis for silica by Connecticut Agricultural Experiment Station, New Haven, Connecticut.

<sup>3</sup>Previously referred to as *Dicorynia paraensis* Benth. (Wangaard, 1953).

<sup>4</sup>Analysis for silica from Amos (1951).

Edmondson (1955), in a recent thoroughly documented monograph covering extensive studies of marine borer resistance of wood in Hawaiian waters, refers to a rather widely held scientific opinion that 0.50 per cent silica is a minimum for effective marine borer protection by this means. He

concur in the belief that in some timbers, at least, silica provides the principal security against marine borers but points to lack of agreement among investigators (Amos and Dadswell, 1948; van Iterson, 1934) as to whether its protective role is mechanical or physiological. Edmondson concludes that whereas *Teredo* and *Bankia* are inhibited in highly siliceous (or otherwise protected) woods, many such woods may still be vulnerable to attack by *Limnoria* and pholad mollusks (*Martesia* spp.).

Referring again to table 1, the data of the present study lend strong support to belief in the inhibiting effect of silica on all of the molluscan and crustacean organisms—*Limnoria* and pholads as well as *Bankia*—which together were active in the destruction of the less resistant species exposed in these tests. Of the ten species which retained a rating of "B" (light marine borer activity) after 24 months of exposure, analyses for silica are available for eight species and, of these, seven were found to contain in excess of 0.43 per cent silica. Of the five species retaining a "B" rating after 36 months exposure, four show silica contents ranging from 0.688–1.52 per cent. *Vouacapoua americana* was the only exception, and in this case a remarkable one, as chemical analysis of this species has shown it to contain only 0.002 per cent silica. Obviously some other factor is responsible for the resistance of this species. In this connection Edmondson (1955), mentions the possibility of alkaloids, oils, acids, resins, and tannins. Evidence that compactness or high density of a wood does not of itself serve as an appreciable deterrent to marine borer activity is provided by the relatively rapid deterioration in these tests of *Manilkara bidentata* (A.DC.) Chev. (specific gravity 0.85) and *Licaria cayennensis* (Meissn.) Kosterm. (specific gravity 0.96).

The next lower group of species in table 1 includes those which retained a rating of "B" for 16–18 months, but dropped to "C" (moderate borer activity) or lower by 24 months. Of these, only angélique (*Dicorynia guianensis*) contains an appreciable amount of silica. Samples taken from the same logs as the exposure specimens, showed a moderate

silica content of 0.34–0.46 per cent but other determinations on this species are reported to run as high as 2.92 per cent (Edmondson, 1955). The problem of variability is revealed here, as Edmondson reports angélique as showing no infestation by *Teredo* or *Limnoria* after an exposure period of 3 years in Hawaiian waters. *Ocotea rubra*, also in this group, contains no measurable silica and its favorable resistance at 16–18 months must be attributed to some other factor, possibly to the distinctive wax in which this species is exceptionally rich (Wise, 1951).

Among the remaining species listed in table 1, those rated "C" after 16–18 months, interest will perhaps be centered on the well known greenheart (*Ocotea rodiei*). This species is believed to derive its resistance to marine borers from its content of bebeerine, a toxic alkaloid. The relatively heavy damage inflicted upon greenheart in these tests serves to emphasize the severity of the test conditions on such small specimens and the need for cautious interpretation of the results. It is to be hoped that, by correlating these test results with the known performance of round piles and sawn timbers of a number of species, it may be possible to use these and similar data to forecast with reasonable accuracy the service life of timbers in structural sizes.

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## CURRENT LITERATURE

*Osnovi i Methodi Anatomicheskovo Issledovanya Drevesinii* (Foundation and Methods of the Anatomical Investigation of Wood) *A. A. Yatsenko-Khmelevsky*. Academy of Science of U.S.S.R., Moscow. 337 pages. 55 figs. 1954. 22r. 10k.

*Drevesinii Kavkaza* (Caucasian Woods) *A. A. Yatsenko-Khmelevsky*, Armenian Academy of Science, Erevan, Armenia, U.S.S.R. 674 pages. 176 figs. 1954. 24r. 20k.

Although both of these books appear under a single authorship, the preface in the first and the title in the second indicate that parts of each represent a cooperative effort of several workers.

The first text (*Osnovi i Methodi Anatomicheskovo Issledovanya Drevesinii*) is divided into two parts, each containing several chapters. Part I is entitled "Terminology," and Part II "Special Methodology for Anatomical Investigation of Wood." An extensive bibliography of Russian literature, followed by a comprehensive bibliography in the foreign languages, is appended. A final highly useful feature of this



book is a comparative glossary of wood anatomical terms in Russian, English, German and French.

Part I starts with definitions of terms employed in describing the anatomical features of wood. In many instances these are accompanied by further explanatory notes and by drawings. It is notable that only a few of the illustrations are photographs, and these are generally of somewhat inferior quality. It is here that the quadrilingual glossary is of particular assistance. By and large the definitions used correspond closely with those adopted by the International Association of Wood Anatomists. However, repeated references are also made to an earlier glossary by the author.

A brief chapter on the "Technique of Preparing the Material" follows. It is surprising to find that the author is an advocate of the razor blade technique. He sees no advantages for the microtome, except when relatively large cross sections are wanted.

The next chapter, more than 50 pages long, deals with detailed plans for describing the anatomical features of each species. Whether or not one agrees with the emphasis given to this subject, as keyed by the opening sentence in this chapter, "A basic requirement of any investigative work in the sphere of wood technology must be a clear general understanding by the worker of the anatomical structure of wood studied by him," the proposed plan is well conceived and thorough. It is also possible to disagree with the author that the "basic shortcoming of work performed at the Madison Laboratory in the United States . . . is due to frequently very superficial acquaintance with wood structure . . . in consequence of which many findings of such well known representatives of American Wood Technology, as Tiemann, are replete with gross errors and incorrect conclusions."

Chapter IV deals with the techniques of measuring wood elements and reliability of such measurements. The effect of internal and external factors responsible for cell size variations are also discussed.

The second part of the book is introduced by a comprehensive discussion of regional sources of information, both Russian and foreign, dealing with descriptions and identifications of the woody plants. Here considerable emphasis is also placed on the identification of the paleontologic material. The following chapters deal with the place of wood anatomy in systematic botany and with physiological changes occurring in wood after its formation, e. g., formation of tyloses and heartwood, and the possible role living parenchyma may play in fungal attack.

A review of the effect of environmental growth factors on the rate of growth, as indicated by the width of the growth rings, and general characteristics of wood, and a brief discussion of the effects of wood structure on its physical and chemical characteristics and its utilization, conclude the text.

The stated purpose of the book is to bring together all information that can be of interest to specialists concerned with wood structure. It is further stated that the book is aimed at people in technical phases of wood processing, as well as at those interested in botanical aspects of wood technology. In the opinion of the reviewer the former may find the book slanted too much toward the latter. Nevertheless this publication is a real contribution to the technical literature in the field of wood technology. For American workers its chief value may be in the wealth of text references to the publications largely unknown to us, by Russian scientists.

The other volume—*Drevesini Kavkaza*—contains detailed information on the wood of the Caucasian species. The anatomical descriptions follow the plan suggested in the third chapter of the first book. The descriptions in most instances are accompanied by drawings of the cross and tangential sections, at about a hand lens magnification. Some of these drawings are rather inadequate for conveying the desired information. Data on physico-mechanical properties of the more important woods are included, as is the pertinent information on their utilization in the Soviet Union. Fre-

quently, information on the related exotic species is also incorporated.

This volume is a valuable contribution to the regional literature on identification and properties of wood producing species, even though most of those described are not of commercial value either locally or elsewhere.

It is unfortunate, but perhaps unavoidable, that the author should in the preface to this soundly scientific publication engage in Marxist dialectics. In referring to the two well known publications—*Timbers of the New World*, by S. J. Record and R. W. Hess and *Anatomy of the Dicotyledons*, by R. Metcalfe and L. Chalk—he states: "In this way, in both of these works the authors conscientiously avoided even attempting to solve this problem," (The "problem" being that of "genetical comparative wood anatomy.")<sup>1</sup> He continues: "The Soviet science, on the other hand armed with the only correct creative method—method of dialectic materialism, could and must create such comparative wood anatomy."—*A. J. Panshin*, Department of Forest Products, Michigan State University, East Lansing, Michigan.

**Common Exotic Trees of South Florida.** *Mary F. Barrett*. University of Florida Press, Gainesville. xii-414 pages. 178 figs. 1956. \$8.50.

The author states that "The aim of this book is to make the commonest exotic trees intelligible to those who want to learn their names, how they may be recognized, where they came from, some of their uses, where examples can be seen, items of special interest, and where additional information can be obtained." Only exotic dicotyledons growing in the southern half of Florida and on the Keys are represented in this volume. It is apparent upon perusal that this volume has not been written for the trained botanist, but for those with little or no technical training. The introductory chapters are aimed at these people, for they contain

<sup>1</sup>The author uses the term "*drevesinovedenie*" which defies exact translation, but in the context "wood anatomy" appears to be the most apt translation.

simplified explanations of some necessary botanical terms, illustrations of plant structures and a section on the use of keys. The keys which follow are dichotomous and based mainly on easily observable vegetative features. A short chapter lists some of the gardens in South Florida where one can locate specimens of the trees described in the book.

The largest portion of author Barrett's work is concerned with descriptions of the species as well as brief accounts of the plant families involved. A noticeable effort has been made to reduce the amount of highly involved terminology. The arrangement of descriptions in this section is alphabetical according to the scientific name.

Descriptions of each species include the Latin binomial, authority and a common name, as well as a common name for the family to which the species belongs. An attempt is made to illustrate phonetically, the pronunciation of the binomial. A general characterization of each species is presented which may include the aspect of the tree, abbreviated taxonomic notes, flower color, some ecological requirements, shape of leaves and other useful and interesting information. Under "Additional characters" the author summarizes some of the more pertinent features useful to persons seeking to identify species in question. Sections on native distribution, related species, economic uses and literature references are included in most of the species reports. Illustrations (line drawings or halftones) of a leaf or portion of a leaf accompany almost every species description. Following the descriptive portion of the book is a chapter entitled "Sight-seeing Trips in Greater Miami." Here the author lists six trips with the exotic trees that can be seen during each excursion. A list of references is appended and also an index.

Although this book is primarily intended for non-botanists, there is a good deal of useful information for professional botanists. However, the latter should not look for highly detailed nor all-inclusive descriptive taxonomic material. It is to be lamented that some of the line drawings in the explanatory sections are not larger nor more clearly exe-



culated. This is especially apparent in the illustrations of the parts of the twig and the morphology of the flower. Other drawings are well conceived and skillfully reproduced. That merely a single leaf, or part of a compound leaf, is represented for each species is of limited value in many cases, for the systematic botanist knows well the variation that may occur in the leaf morphology of a single species. It should however, be noted that the author is not aware of this shortcoming.

In the author's attempt to reduce technical terminology, she has introduced terms of questionable value even to non-botanists: end bud for terminal bud, side bud for lateral bud, top side bud for false terminal bud, etc.

On reading the author's description of Lauraceae, one gains the impression that sassafras and spice bush (*Sassafras albidum* and *Lindera benzoin*) have been introduced into eastern North America and are not native here. For example, one reads that "Most (species of Lauraceae) are native to tropical and subtropical regions, but Sassafras . . . and Spice Bush . . ., are familiar to residents of the eastern half of North America from Ontario to Florida and west to Texas. These were introduced so long ago that they are considered native." Perhaps these statements would bear closer scrutiny.

*Common Exotic Trees of South Florida* is printed on good quality coated paper in clear, easily readable type. The volume is attractive and well bound. It is a worthwhile addition to the floristic works covering the southern portion of Florida and will be found useful in other warm areas of the United States.—*William L. Stern*, School of Forestry, Yale University, New Haven, Connecticut.