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## 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 112

APRIL, 1960

### THE COMPARATIVE MORPHOLOGY OF THE CANELLACEAE.

#### I. SYNOPSIS OF GENERA AND WOOD ANATOMY<sup>1</sup>

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#### INTRODUCTION

It has often been stated that no truly phyletic classification system of plants can be established until the summation of the evidence provided by the whole plant (both exomorphic and endomorphic) is taken into account. The past ten years or so have seen a number of detailed morphological-anatomical studies on angiosperm families (mainly ranalian), and the conclusions of these studies have been incorporated into several new classification systems (Copeland, 1957; Cronquist, 1957).

Bailey (1953) pointed out that comparative anatomy and morphology can contribute significantly to the elucidation of particularly difficult taxonomic problems. It was with this in mind that the Canellaceae were selected for study. Heretofore no detailed morphological-anatomical study has been made on this family, and there is no comprehensive taxonomic revision in existence.<sup>1a</sup> In addition, the taxonomic

<sup>1</sup>Part of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Indiana University. The author wishes to express his sincere appreciation to Dr. J. E. Canright, Department of Botany, Indiana University, for his guidance and criticism in this study. Publication was aided in part by a Sigma Xi-RESA Grant-in-aid.

<sup>1a</sup>After this paper had already gone to press, the following taxonomic treatment of the Canellaceae appeared: Melchior, H. and W. Schultze-Motel. 1959. *Canellaceae in Engler and Prantl, Die natürlichen Pflanzenfamilien*. ed. 2. 17aII: 221-224.

position of the Canellaceae is not at all clear, the family having at one time or another been allied with the Annonales, Bixales, Guttiferales, Magnoliales, Parietales and Ranales. The problem resolves itself, then, into a comprehensive study of the morphology and anatomy of the Canellaceae, and a comparison of its features with similar ones in supposedly related families. It is hoped that the evidence herein provided will aid in clarifying the phyletic position of this taxon.

In spite of the fact that members of the Canellaceae have been known for some 300 years, its systematic placement is still problematical. Most systematists (e.g., Bentham and Hooker, 1862; Warburg, 1895) placed this family in the Parietales, close to the Violaceae and Bixaceae, mainly because of parietal placentation in these taxa. Lawrence (1957), however, in discussing the Parietales, notes that:

“ . . . available evidence indicates that the order is not a phyletic taxon and the realignment of the families into several orders is to be expected. In some instances this may result in transfer of families to existing orders and in others in the establishment of new orders.”

On the other hand, Baillon (1871) made the canellads the fifth series in the Magnoliaceae based on the presence of a polypetalous or gamopetalous corolla and a slightly convex receptacle. He also noted that the pollen grains of *Canella alba* were very much like those of *Magnolia*. Hallier (1912) followed Baillon and allied the Canellaceae with the magnoliaceous families. Similarly, both Wettstein (1935) and Gundersen (1950) placed the Canellaceae in the Magnoliales, partially because of the spiral arrangement of the petals (although not present in all genera) and the presence of oil cells. Vestal (1937) concluded, on anatomical grounds, that the Canellaceae should be near the Myristicaceae (the latter is generally placed in the Ranales *sensu lato*).

In the past several years several new systematic schemes of the Angiospermae have been published. Boivin (1956), in a new system supposedly based on more recent developments

in taxonomy and morphology, places the Canellaceae between the Samydaceae and the Cistaceae in the Bixales. In this scheme the Bixales are derived from the Dilleniales and the latter in turn from the Magnoliales. These orders are all grouped under the subclass Lignidae of the class Dicopsida (subdivision Angiophytina, division Pterophyta).

Benson (1957) in his recent textbook places the Canellaceae in the Violales because of the following characteristics: fusion of the filaments to form a staminal tube; coalescent carpels, cyclic (rather than spiral) stamens and carpels; and some basal fusion of petals in some of its members. The Violales are included in the Thalamiflorae, the first group in the Dicotyledoneae.

In formulating his system, Copeland (1957) has drawn heavily on microscopic (i.e., anatomical, embryological, and palynological) evidence. In this system the Canellaceae are placed near the Myristicaceae and Monimiaceae in the heteroxylous, monocolpate pollen group of the Multisiliquae. The Multisiliquae in Copeland's system comprise the first order in the dicotyledons (presumably the most primitive) and are a combination of the Englerian orders Piperales and Ranales.

Like Copeland, Cronquist (1957) used anatomical and morphological data (although less extensively) in preparing a new outline of dicotyledonous families and orders. Cronquist (op. cit. 17) makes the Canellaceae the single family in a new order—the Canellales. He states:

“The Canellales, composed of a single small family Canellaceae, are developed from the Laurales or near thereto. The Myristicaceae, a peripheral family of the Laurales which might with some reason be referred to the Ranales instead, are particularly suggestive of the Canellaceae. The similarities between the Myristicaceae and the Canellaceae have been pointed out by Vestal (1937) and others. The Canellaceae retain the monocolpate pollen and ethereal oils of the Laurales, but they have a syncarpous ovary with parietal placentation, and they often have well differentiated petals.”

The Canellaceae, which are small trees of tropical distribution, comprise six well-recognized genera and about twenty-one species. The New World genera include: *Canella*, with two species, ranging from lower Florida, throughout the West Indies, and into northern South America; *Pleodendron*, with two species in Puerto Rico and Haiti; *Cinnamodendron*, with seven species in Brazil, Surinam, and the West Indies; and *Capsicodendron*, with two species in Brazil. The Old World genera consist of *Warburgia*, with four species in eastern Africa (from Kenya to Transvaal), and *Cinnamosma*, with three species endemic to Madagascar.

Figure 1 shows the distribution of the genera.

#### SYNOPSIS OF THE FAMILY

CANELLACEAE Martius, Nov. Gen. et Sp. 3: 170. 1829.

Trees, mostly small (10-15 feet); some species of *Warburgia*, however, may be quite large—up to 90 feet; leaves alternate, simple, entire, exstipulate, short petiolate, thick; flowers bisexual, regular, solitary, or a cyme or raceme; sepals 3, imbricate, fleshy; petals 4-12, free or basally fused or united into a tube; stamens up to 20, connectives fused to form a tube, anthers extrorse, dehiscent by one longitudinal split; pistil 1, ovary superior, unilocular, carpels 2-6, ovules semi-anatropous; style solitary and thick; fruit a berry, seeds with oily endosperm.

#### KEY TO GENERA

- A. Petals 5, in one whorl, free or united.  
 B. Petals free or at most weakly united at base. Anthers 20. \_\_\_\_\_ 1. *Canella*  
 B. Petals united for half their length. Anthers 14-16. \_\_\_\_\_ 4. *Cinnamosma*
- A. Petals more than 5, in two or more whorls.  
 C. Petals 6, in two whorls.  
 D. Stigma 3-lobed. \_\_\_\_\_ 7. *Capsicodendron*  
 D. Stigma 4-5-lobed. \_\_\_\_\_ 4. *Cinnamosma*
- C. Petals more than 6.  
 E. Petals 8-10, free, in two whorls. Stamens 10.  
 F. Petals 8-10, inner whorl shorter than outer and quite thin and membranous. \_\_\_\_\_ 3. *Cinnamodendron*  
 F. Petals 10, inner row of petals similar to outer. \_\_\_\_\_ 6. *Warburgia*
- E. Petals 12, in 4 whorls of 3 each. Stamens 12. ...5. *Pleodendron*

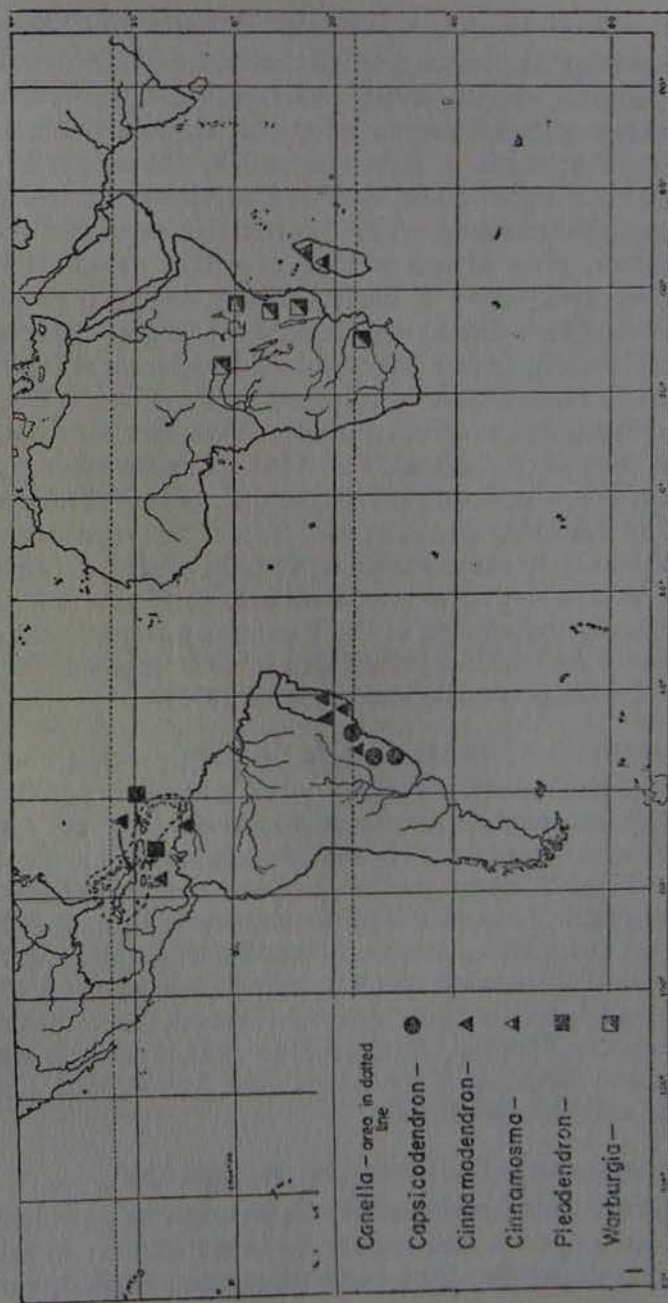


Fig. 1. Map showing distribution of the genera of the Canellaceae.

## 1. CANELLA. P. Browne, Civ. Nat. Hist. Jamaica 275. 1756.

Trees, evergreen; leaves alternate, obovate-oblong, coriaceous, glabrous, simple, entire, short petiolate, exstipulate; inflorescence terminal raceme or cyme; flowers small, bisexual, regular; sepals 3, imbricate, thick, fleshy; petals 5, united at base, rather thick, dark red to violet; stamens 10 united by filaments into a tube, connective protruded beyond anthers, tube almost as long as petals, dehiscent by longitudinal split; ovary 1, conical-oblong, locule 1, carpels 2, ovules 4, almost anatropous; style short, stigma truncate, obsolete, bilobed; fruit a berry, blue-black, seeds 4, endosperm oily. Distribution: southern Florida, Florida Keys, West Indies, northern South America. Two species: *C. alba* Murray, Syst. Veg. 14th ed. 443. 1784. [*C. winterana* (L.) Gaertner, Fruct. et Sem. Pl. 1788] and *C. obtusifolia* Miers, Ann. Mag. Nat. Hist. Ser. 3. 1: 348. 1858. *C. obtusifolia* from Venezuela may be only, according to Gilg (1925), a variety of *C. alba*. The author has not been able to secure material of this species and officials of the Venezuelan Department of Agriculture do not find it recorded in their regional floras (Tobias Lasser, personal communication 1956).

## 2. CAPSICODENDRON Hochne, Ostenia 294. 1933.

Trees, small to medium-sized; leaves alternate, petiole 5 mm. long, exstipulate, entire, oval to obovate, 5-9 cm. long by 2-4 cm. wide; flowers bisexual, regular, axillary, solitary or 1-3 per stalk, large pedicel; sepals 3, large, imbricate; petals 6, imbricate in two whorls; stamens 7-10, united by filaments into a tube, anthers bilocular, longitudinal dehiscence; pistil 1, superior, locule 1, carpels 3-4, ovules 6 (?), style trilobed; fruit a berry (with 2-4 seeds). Two species: *C. pimenteira* Hochne, Ostenia 294. 1933, and *C. dinisii* (Schwacke) Occhioni, Revista Bras. Biol. 3: 484. 1943, both found in southwestern Brazil.

## 3. CINNAMODENDRON Endlicher, Gen. Pl. 1029. 1840.

Trees, evergreen, much branched; leaves ovate or oblong, coriaceous, opposite, entire, short petiolate; flowers in axillary racemes, few-flowered, bisexual, regular; sepals 3, cori-

aceous, persistent, imbricate; petals 8-10, in two whorls, exterior fleshy, oblong, imbricate, interior membranous, spatulate oblong, alternate with exterior and hardly as long; stamens 8, united into narrow tube by filaments, as long as petals, connective produced beyond anthers, 8-lobed, anthers extrorse, longitudinal dehiscence; pistil 1, ovary superior, locule 1, carpels 3-4 (5?), ovules 10 or more, style thick, stigma 3-4-lobed; fruit ovate, fleshy. Seven species: *C. axillare* Endlicher, Gen. Pl. 1029. 1840, southwestern Brazil; *C. corticosum* Miers, Ann. Mag. Nat. Hist. Ser. 3. 1: 350. 1858, West Indies; *C. cubense* Urban, Repert. Sp. Nov. 18: 19. 1922, Cuba; *C. tenuifolium* Uittien, Rec. Trav. Bot. Neerl. 23: 367. 1925, Surinam; *C. angustifolium* Sleumer, Repert. Sp. Nov. 41: 127. 1937, Haiti; *C. ekmanii* Sleumer, Repert. Sp. Nov. 41: 127. 1937, Dominican Republic; *C. sampaioanum* Occhioni, Arq. Jard. Bot. Rio de Janeiro 7: 159. 1947, Brazil; *C. venezuelense* Steyermark, Fieldiana Bot. 28: 402-403. 1952, Venezuela.

## 4. CINNAMOSMA Baillon, Adansonia 7: 219-220. 1867.

Small tree; leaves simple, exstipulate, short petiolate, entire, oval-elongate, base narrow, apex round; flowers solitary, sessile, axillary, bisexual, regular; sepals 3, weakly united at the base; petals 5-6, lower half united into a tube; stamens 8-10, united into a tube, anther dehiscence longitudinal; pistil 1, ovary superior, unilocular, carpels 4-5, placentas 4-5; ovules 8 or more, semi-anatropous; style 4 lobed; fruit a berry. Three species: *C. madagascariensis* P. Danguy, Not. Syst. Paris 1: 236. 1909; *C. macrocarpa* Perrier de la Bathie, Bull. Soc. Bot. Fr. 94: 214. 1947; *C. fragrans* Baillon, Adansonia 7: 219-220. 1867, all of Madagascar. Characterization of genus based mainly on Van Tieghem (1899).

## 5. PLEODENDRON Van Tieghem, Jour. Bot. (Paris) 13: 271. 1899.

Tree; leaves alternate, simple, short petiolate, oval, apex acute, base acute; flowers solitary, axillary, pedicellate; sepals 3, united at base, persistent; petals 12, free, in 4 alternate whorls, external alternate with sepals, large, the others

more narrow; stamens 12, united into a tube, anthers bilocular, dehiscence longitudinal; pistil single, ovary superior, carpels 6, unilocular, placentas 6 parietal, ovules many, style thick with a 6-lobed stigma. Two species: *P. macranthum* (Baillon) Van Tieghem, Jour. Bot. (Paris) 13: 271. 1899 (*Cinnamodendron macranthum* Baillon, 1882), Puerto Rico, and *P. ekmanii* Urban, Ark. Bot. (Stockh.) 22: 75. 1929, Haiti.

6. *WARBURGIA* Engler, Pflanz. Ost.-Afr. Theil C: 276. 1895.

Trees, some quite large, over 33 m., densely branched; leaves short petiolate, subcoriaceous, oblong-spathulate; flowers bisexual, regular, short pedicellate, axillary cymes; sepals 3, free, suborbicular; petals 10, in two whorls of 5 each, the 5 outer twice as long as the sepals, obovate-spathulate, the 5 inner smaller than the outer and spathulate; stamens 10, united by filaments into a tube as long as the petals, connective extended beyond anthers, bilocular, dehiscence longitudinal; pistil 1, superior, carpels 5, unilocular, placentas 5, parietal, ovules 10-15 semi-anatropous, style thick, 5-lobed; fruit a berry, large, fleshy; seeds with oily endosperm. Four species: *W. stuhlmannii* Engler, Pflanz. Ost.-Afr. Theil C: 276. 1895, Kenya and Tanganyika; *W. ugandensis* Sprague, Jour. Linn. Soc. Bot. 37: 498. 1906, Belgian Congo, Uganda, Kenya, Tanganyika, Transvaal (*W. breyeri* Pott, 1917); *W. salutaris* (Bertoloni f.) Chiovenda, Nuovo Gior. Bot. Ital. 3. 44: 680. 1937, Africa; *W. elongata* Verd-court, Kew Bull. 1954: 542. 1954, Tanganyika.

In 1954 Gagnepain described a new genus, *Tardiella*, from Annam (Indochina), and tentatively assigned it to the Canellaceae. *Tardiella* differs from the Canellaceae by having 5 sepals, no petals, fasciated flowers, introrse anthers and stipules. In this connection Steenis (1955) states, "there is no doubt whatsoever that *Tardiella* is synonymous with *Casearia* (Flacourtiaceae)." The present author agrees with Steenis in this conclusion.

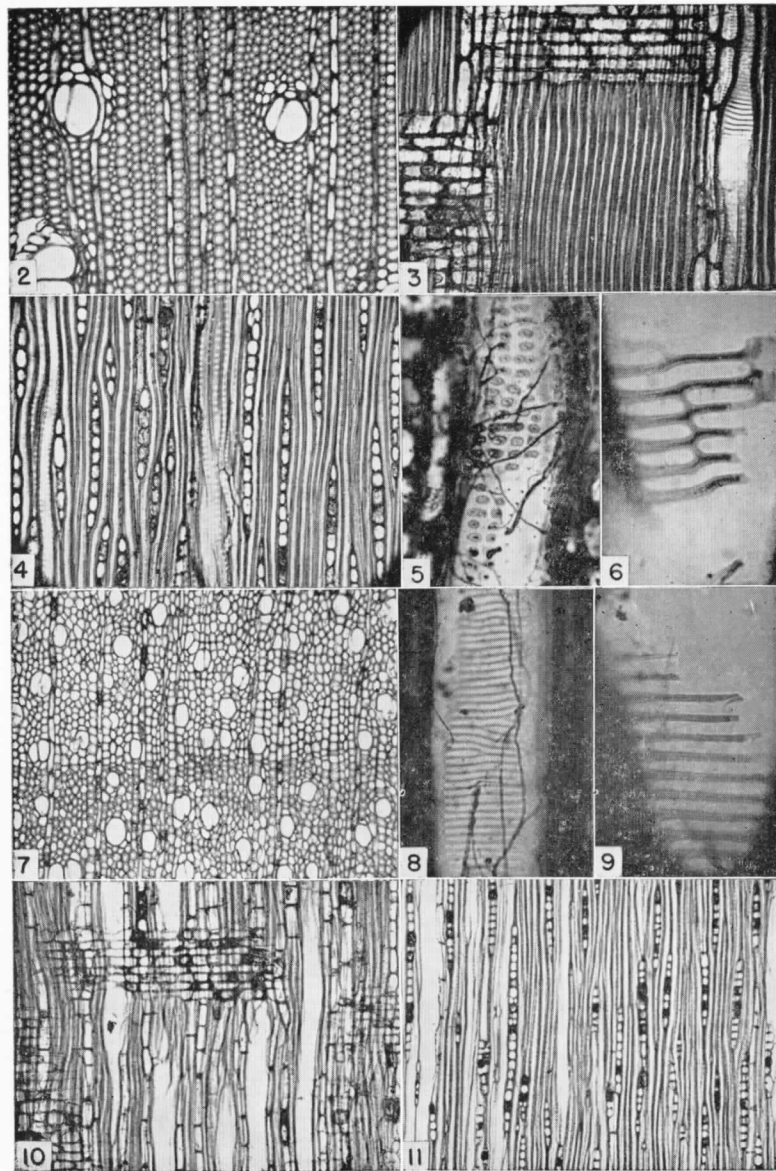


Fig. 2-11.—Fig. 2-6. *Canella alba* Murr.—Fig. 2. Transverse section showing solitary arrangement of vessels and scarcity of axial parenchyma.—Fig. 3. Radial section showing scalariform perforation plate and homocellular character of rays.—Fig. 4. Tangential section showing uniseriate rays.—Fig. 5. Radial section showing intervessel pitting of opposite type.—Fig. 6. Radial section showing perforation plate of scalariform and reticulate type. Notice small borders on perforations.—Fig. 7. *Capsicodendron pimenteira* Hoehne. Transverse section vessel characteristics: small diameter, angular outline, solitary distribution.—Fig. 8. *C. dimistii* Oech. Scalariform-reticulate perforation plate. Radial section.—Fig. 9. *Canella alba* Murr. Radial section showing scalariform perforation plate.—Fig. 10-11. *Capsicodendron pimenteira* Hoehne.—Fig. 10. Radial section showing predominantly homocellular rays.—Fig. 11. Tangential section showing uniseriate rays. Fig. 2-4, 7, 10-11  $\times 64$ . Fig. 5-6, 8-9  $\times 222$ .

## WOOD ANATOMY

Aside from occasional references to oil cells in cortex and leaf, Solereder (1899) seems to have been the first to give any attention to the internal anatomy of the Canellaceae. On the basis of an examination of the wood of two species (*Canella alba* Murr. and *Cinnamodendron axillare* Endl.) Solereder indicates that the Canellaceae may be related to the Magnoliaceae. Van Tieghem (1899) considers briefly the anatomy of the young stem of *Canella*, *Pleodendron* and *Cinnamosma*. Many others investigated the wood anatomy of the Canellaceae merely for descriptive purposes and made no attempt to derive phylogenetic significance from their findings (Lecomte, 1922; Metcalfe, 1933, 1935; Record and Hess, 1943; Occhioni, 1947, 1948).

Garratt (1933b) in investigating the relationships of the Myristicaceae concluded that the Canellaceae, on the basis of wood anatomy, were "rather far removed from the Myristicaceae"; Vestal (1937), on the other hand (again on the basis of wood anatomy), recommended that the Canellaceae be placed near the Myristicaceae.

Metcalfe and Chalk (1950) note that the presence of oil or mucilage in the Canellaceae suggests an affinity with the Magnoliaceae and Lauraceae; further, that vessel-member length and some other characters suggest that the Canellaceae are less specialized than the Lauraceae or even the Magnoliaceae. However, neither Canright (1955) working on the Magnoliaceae, nor Stern (1954) working on the Lauraceae has considered these families to be related to the Canellaceae. Lemesle (1955), from a morphological investigation of the Canellaceae, concluded that this taxon belonged in the Parietales, although he states that the secondary xylem of the canellad members included archaic characters that are not consistent with other advanced features of this group (Lemesle, 1950, 1951, 1955).

Money, Bailey and Swamy (1950) included the Canellaceae in their "Group B" of ranalian families, i.e., families with monocolpate and derived pollen, ethereal-oil cells, and trilacunar or multilacunar nodes.

Recently, Stern (1955) concluded that the similarities between the woods of the Gomortegaceae and the Canellaceae are due to parallel evolution and not to a close genetic relationship. Vander Wyk and Canright (1956) found little comparison between the woods of the Annonaceae and the Canellaceae. The latter investigators conclude that perhaps Vestal was correct in placing this family near the Myristicaceae.

#### MATERIALS AND METHODS

A total of 43 wood specimens representing 10 species in 6 genera was examined. The material was obtained from the following sources: Yale University, School of Forestry (Y); Harvard University (H); Chicago Natural History Museum (CNHM); Jardim Botânico de Rio do Janeiro (JB); Imperial Forestry Institute, Oxford University, England (IFI); Royal Botanic Gardens, Kew, England (K); Museum National d'Histoire Naturelle, Paris, France (MNHN); Department of Agriculture, Division of Botany, Pretoria, Union of South Africa (SA); East African Herbarium, Nairobi, Kenya (EA); and Forest Products Research Laboratory, Princes Risborough, Bucks, England (FPRL).

Small blocks of the samples were boiled in water, softened in one part 70 per cent alcohol and one part hydrofluoric acid for a period of time ranging from one week to several months. After washing, the blocks were either sectioned on a sliding microtome or stored in a solution of one part glycerine and one part 70 per cent alcohol. Even when the blocks of wood were properly softened, the sections had a tendency to curl when they were taken off the microtome. A new technique was developed which has proved successful in all cases tried. If the knife and block being sectioned are continuously bathed in a 1 per cent aqueous solution of a commercially-available detergent, no curling occurs. After sectioning, the sections were washed with tap-water and stained, using a safranin-hemalum combination (Sass, 1951), the celestine blue-iron alum safranin formula of Gray and Pickle (1956), or iron-alum safranin alone described by the same authors.

Slides of macerated wood of most of the above samples were prepared by the method of Wilson and Shutts (1957).

Generally the terms used in describing the anatomy of the wood are those recommended by the Committee on Nomenclature (1957). For terms used to describe the numerical dimensions of wood features, the recommendations of Chattaway (1932), Chalk (1938) and the Committee on Standardization (1937) were followed.

The crystal types of Chattaway (1955) were used to describe those found in the wood of the Canellaceae. In describing the parenchyma recourse was made to the classification of Hess (1950). In interpreting phylogenetic significance of rays, reference was made to the work of Bailey and Howard (1941), Kribs (1935), and Barghoorn (1940).

After examining the wood microscopically, the diagnostic features of the wood were entered onto 5 × 8-inch punch-cards in the method described by Canright (1955). By using this technique, two samples of wood (previously identified as members of the Canellaceae) were discovered whose anatomy was very different from that of the other samples in this family. Although their identity could not be unquestionably determined, further examination established that they were not members of the Canellaceae and had evidently been misidentified. The use of the punch-cards was also helpful in determining ranges of variation within the family as well as relative levels of specialization.

#### OBSERVATIONS

*Canella*.—*Vessels* moderately small in tangential diameter (50–100 $\mu$ ) or sometimes larger; usually almost exclusively solitary with occasionally a few small clusters; 7–10 per sq. mm. with local areas of up to 30 vessels per sq. mm. (fig. 2), perforation plates scalariform, although often the bars anastomose, giving a pseudo-reticulate appearance. The number of bars ranges from 5 to 28, with the mean 15 (fig. 7), and some specimens show vestigial borders on the bars (fig. 6 and 9). Intervascular pitting (fig. 5) generally scarce due to the solitary nature of the vessels, but when present opposite to transitional, with an occasional scalariform pit present;



pits to ray and strand parenchyma similar to intervacular pitting, usually of medium size. Vessel-member length medium to moderately long, to very long (500–1500 $\mu$ ), but most frequently moderately long with acute-angled end walls and a moderately long overlap. *Axial parenchyma* paratracheal, generally confined to one side,<sup>2</sup> but may also surround vessels; also some very scarce, diffuse parenchyma. Some rhombohedral crystals present. *Rays* (fig. 3–4) mostly uniseriate with some biseriate, homocellular to heterocellular; some multiseriate portions of rays seem to be merely local additions to a basically uniseriate ray; rays heterogeneous (Kribs Type I or III), with a few small square marginal cells occurring sporadically. In some samples, the marginal cells showed a slight tendency toward a vertical elongation, but not consistently in all samples studied. Rhombohedral crystals generally present, often abundant. *Imperforate tracheary elements* of the fiber-tracheid type, thick to very thick-walled, pits bordered with medium-sized apertures included; length 800–1800 $\mu$ , most often 1300 $\mu$ . Record and Hess (1943) note that the rays are more or less heterogeneous, and the wood parenchyma is located on the outer side of the pores (abaxial distribution).

Material examined: *Canella alba* Murray [Y49403, Y38276, H21295, H25185, H7633, H21297, H26296, CNHM (*Wilson F-16*), CNHM (*Scott 75188*), FPRL2228, FPRL20382].

*Capsicodendron*.—*Vessels* extremely small to moderately small (25–50 $\mu$  in diameter), usually very small (fig. 7); usually solitary, but some pseudo-pairs due to overlapping ends present; perforation plates exclusively scalariform (fig. 8), the bars frequently anastomosing similar to those in *Canella*, although the bars are much finer and closer together than in *Canella* (the number of bars is usually 46–64); intervacular pitting rare due to solitary nature of vessels, but, when present, opposite to transitional with some scalariform

<sup>2</sup>Due to lack of growth rings it is impossible to decide whether the parenchyma is on the "outer" or "inner" side of vessels, i.e., on the side of the vessels away from the pith or the side toward the pith. However, an abaxial placement of parenchyma is the more common condition.

pits; pits to parenchyma similar with some unilaterally compound pitting to ray cells present in one specimen; vessel-member length moderately long to very long, mostly very long (1100–1500 $\mu$ ). End walls acute (10°–30°), with long overlapping ends.<sup>3</sup> *Axial parenchyma* mostly apotracheal diffuse with some in small groups, occasionally some paratracheal parenchyma present, again occurring as individual cells; oil cells common in parenchyma. *Rays* 1–2(3) cells wide, mostly uniseriate homocellular to heterocellular, very low to low (fig. 11), homogeneous (Kribs Type I or III), although some specimens occasionally show a weakly heterogeneous condition; marginal cells generally horizontally elongated to square (fig. 10), rarely some rays have marginal cells slightly elongated vertically; crystals rarely present in rays, oil cells common.<sup>4</sup> *Imperforate tracheary elements* of fiber-tracheid type, walls thin to very thin, with medium-sized bordered pits and included apertures; length short to long, mostly long (1500–2000 $\mu$ ).

Material examined: *Capsicodendron dimisii* (Schw.) Oech. (JB1914, JB2017, CNHM622864) and *Capsicodendron pimentira* Hoehne (Y23444).

*Cinnamodendron*.—*Vessels* very small to moderately small (50–73 $\mu$  in diameter), mostly moderately small (fig. 12), usually solitary with some pairs due to overlapping ends; very small clusters sometimes present. Perforation plates exclusively scalariform with some anastomosing bars; similar to *Capsicodendron* in size of bars and spacing; 50–100 bars. Intervacular pitting opposite with some transitional (fig. 15); pits to parenchyma similar. Vessel-member length very long to extremely long (1600–2400 $\mu$ ). *Axial parenchyma* apotracheal diffuse, sometimes in short tangential lines. Some rhombohedral crystals present in parenchyma. *Rays* 1–4 cells wide, mostly 1–2 cells, heterocellular, very low to low (fig. 14). Kribs Type heterogeneous I and III. Some samples show a tendency towards a weak homogeneous condition.

<sup>3</sup>Angle of end wall measured from vertical axis of the cell.

<sup>4</sup>Record and Hess (113, 1943) state, "no crystals or oil cells observed."

Marginal cells mostly square, but some specimens have marginal cells that are slightly vertically elongate. *Imperforate tracheary elements* of the fiber-tracheid type with thin walls, and distinctly bordered pits with included apertures; size of pits 10–15 $\mu$ . Fiber length long to very long, mostly long.

Material examined: *C. axillare* Endl. (JB362) and *C. sampaoanum* Occh. (JB1772 from type tree).

*Cinnamosma*.—*Vessels* moderately small to medium, mostly moderately small (50–100 $\mu$  in diameter); mostly solitary with some small clusters (fig. 16). Perforation plates scalariform with anastomosing bars and some reticulate (fig. 19–20), 11–49 (15–30) bars. Intervascular pitting opposite to transitional with some scalariform, pits to rays similar. Vessel-element length moderately long to very long, with very oblique end walls and long areas of overlap; angle of end wall 5°–40°. *Axial parenchyma* paratracheal vasicentric. Rhombohedral crystals present in the parenchyma, and some oil cells. *Rays* 1–2 cells wide, mostly uniseriate homocellular, with some heterocellular (fig. 18); homogeneous, predominantly Kribs Type III and I, and possibly some heterogeneous Type III also; marginal cells horizontally elongated to square with some rare vertically elongate cells (fig. 17). Rhombohedral crystals present. *Imperforate tracheary elements* of the fiber-tracheid type with distinctly bordered pits and included apertures, although some apertures are extended; length short–long (100–1700 $\mu$ ), walls very thick to thick.

Material examined: *C. fragrans* Baillon [Y7367, K19315, K1891, MNHN9819, MNHN (col. by S. J. Record), CNHM (from Yale)]. *C. madagascariensis* P. Danguy (MNHN17, CNHM622578).

*Pleodendron*.—*Vessels* in this sample moderately small (52–94 $\mu$  in diameter), usually exclusively solitary with a few pairs (fig. 21). Perforation plates of the scalariform type with 15–40 bars (fig. 25). The bars resemble those in *Canella*. Intervascular pitting rare due to the solitary nature of the vessels, but when present opposite to transitional. Vessel–ray pitting transitional to opposite with some scalariform arrangement. Vessel-member length moderately long to very

long (900–1300 $\mu$ ). *Axial parenchyma* paratracheal on the outer (abaxial) side of the vessels with some on the inner (adaxial) side. Some diffuse parenchyma present consisting of individual cells or very small groups. *Rays* 1–2 cells wide, mostly uniseriate homocellular to heterocellular (fig. 23); homogeneous Kribs Type III with an occasional ray heterogeneous Type III (fig. 22); marginal cells elongate horizontally and occasionally some elongate vertically. *Imperforate tracheary elements* of the fiber-tracheid type, with distinctly bordered pits. Length short (900–1200 $\mu$ ).

Material examined: *P. macranthum* (Baillon) Van Tieghem (Y35444).

*Warburgia*.—*Vessels* very small to moderately large (42–136 $\mu$  in diameter). Usually solitary, but some pairs and small clusters present (fig. 26). Perforation plates scalariform with some bars anastomosing; 13–52 bars (fig. 29–30). Intervascular pitting opposite to transverse, pitting to rays similar. Vessel-element length very long to extremely long (1100–2300 $\mu$ ). End wall oblique (30°–40°) with moderately long overlap. *Axial parenchyma* mostly apotracheal diffuse and in short concentric lines; occasionally some paratracheal parenchyma, either diffuse or vasicentric, present. Oil cells and crystals sometimes present in parenchyma. *Rays* 1–4 cells wide, mostly 2–3 cells, homocellular to heterocellular (fig. 28). Homogeneous Kribs Type I and III and heterogeneous IIB. Marginal cells horizontally elongate (fig. 27) and some square; occasionally some marginal cells are vertically elongate giving rise to a weak heterogeneous condition. Rhombohedral crystals occasionally present in the rays. *Imperforate tracheary elements* of fiber-tracheid type with distinctly bordered pits with the aperture included, pits large. Fiber length long to very long (1500–2600 $\mu$ ), walls thick.

Material examined: *W. stuhlmannii* Engler (IFI864, IFI12945, IFI13566, FPRL 14027, FPRL 416, FPRL18339) and *W. ugandensis* Sprague [Y24312, IFI2467, IFI11186, Wilson 659 (SA) and 664 (EA), FPRL646, 2717, 10177, 18339].

## SUMMARY OF WOOD CHARACTERISTICS OF THE CANELLACEAE

**Vessels.**—Mostly moderately small ( $50\text{--}100\mu$  in diameter), in *Capsicodendron* very small, and smaller than the average in *Cinnamodendron*. Usually solitary, but with some pairs (due to overlapping ends of vessel elements); occasional small clusters in *Canella*, *Cinnamosma* and *Warburgia*. Perforation plates entirely scalariform; some bars seem to anastomose giving a pseudo-reticulate appearance; in *Cinnamosma* some actual reticulate plates were found; *Canella*, *Pleodendron*, *Cinnamosma* and *Warburgia* had 10–20 bars; *Capsicodendron* and *Cinnamodendron* generally had 50–100 bars. The intervacular pitting is generally opposite to transitional with a few specimens throughout the family showing some scalariform pits. Pits to parenchyma and rays similar: scalariform-opposite. Vessel-member length generally medium to very long in *Canella* ( $500\text{--}1600\mu$ ), moderately long to very long in *Pleodendron* and *Cinnamosma* ( $800\text{--}1400\mu$ ), very long ( $1100\text{--}1500\mu$ ) in *Capsicodendron*, and very long to extremely long (over  $1900\mu$ ) in *Cinnamodendron* and *Warburgia*. The angles of the end walls (measured from vertical axis) in all specimens were generally less than  $45^\circ$  and in some cases approached  $0^\circ$ . The vessel elements in all genera had long overlapping end walls.

**Axial parenchyma.**—Predominantly apotracheal diffuse in *Capsicodendron*, *Cinnamodendron* and *Warburgia*, with occasionally some other arrangements; in *Cinnamosma* there seemed to be an equal amount of apotracheal diffuse and scanty paratracheal parenchyma present; in *Canella* and *Pleodendron* the parenchyma was predominantly vasicentric (abaxial) paratracheal with a few other types sparsely represented. Rhombohedral crystals were present in the parenchyma of *Cinnamosma*, *Warburgia* and occasionally in *Canella* and *Cinnamodendron*. Oil cells were found in the parenchyma of *Capsicodendron* and *Warburgia* and occasionally in *Cinnamosma*.

**Rays.**—Very numerous, 1(2)-cell wide in *Canella*, *Pleodendron*, and *Cinnamosma*; in *Capsicodendron* occasionally triseriate rays are found. In *Cinnamodendron* and *Warburgia* the rays are 1–4 cells wide, mostly 2–3 cells. Rays homo-

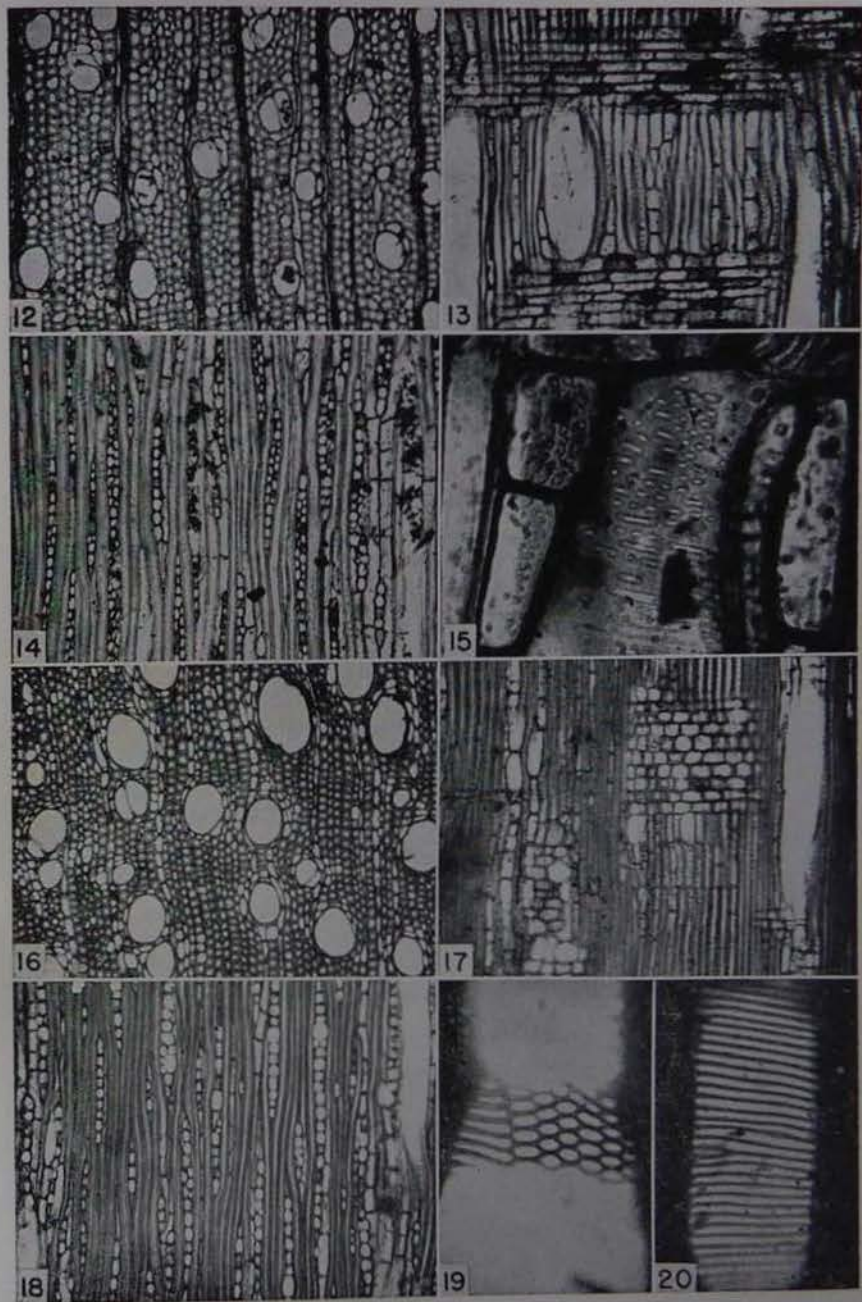


Fig. 12–20.—Fig. 12–15. *Cinnamodendron sampaioanum* Oech.—Fig. 12. Transverse section, showing angular outline of vessels, vessel distribution and uni- and biseriate rays.—Fig. 13. Radial section showing homocellular to weak heterocellular rays and bordered pits on walls of fiber-tracheids.—Fig. 14. Tangential section, showing uni- and biseriate rays and pits on walls of fiber-tracheids.—Fig. 15. Radial section showing scalariform to opposite intervacular pitting grading into a scalariform perforation plate. Fig. 16–18. *Cinnamosma fragrans* Baill.—Fig. 16. Transverse section showing solitary vessel distribution, narrow rays, and scarce vasicentric parenchyma.—Fig. 17. Radial section showing heterocellular rays.—Fig. 18. Tangential section showing uni- and biseriate

geneous Kribs Type I or III with a few weakly heterogeneous in *Canella*, *Cinnamodendron*, *Pleodendron* and *Warburgia*. In *Capsicodendron* and *Cinnamosma* the heterogeneous rays are comparatively rare. The rays are composed of cells horizontally elongate or almost square. The marginal cells may be similar or even slightly vertically elongate, giving rise to the weak heterogeneous condition; however, these are in the minority. The rays range from extremely low to low, most of them being extremely low (20–1500 $\mu$ , averaging 100–500 $\mu$ ). Rhombohedral crystals are found in the rays of *Canella*, *Cinnamosma* and *Warburgia*, and oil cells in the rays of *Capsicodendron*.

*Imperforate tracheary elements.*—All genera have distinctly bordered pits, generally on both radial and tangential walls. The slit-like apertures are included within the pit borders in all species except *Cinnamosma madagascariensis* where some are extended beyond the pit border. The walls of the imperforate tracheary elements are thick in *Canella*, *Pleodendron*, *Cinnamosma* and *Warburgia*; *Capsicodendron* and *Cinnamodendron* have thin-walled imperforate tracheary elements. In *Canella* and *Pleodendron* the imperforate tracheary element length is generally short, short to long in *Cinnamosma*, long in *Capsicodendron*, and long to very long in *Cinnamodendron* and *Warburgia*. The average for the family is long (1500–2000 $\mu$ ).

#### DISCUSSION AND CONCLUSIONS

It is evident that the woods of the Canellaceae show a considerable degree of homogeneity. The vessels are all fairly long with a similar type of intervascular pitting. All genera possess vessels with characteristic many-barred scalariform perforation plates. Some genera have predominantly paratracheal axial parenchyma but with apotracheal parenchyma present also, whereas other genera have predominantly apotracheal parenchyma but with some paratracheal present. The ray types are similar, being in the main quite narrow and low. The imperforate tracheary elements have, likewise, a high degree of similarity, possessing comparatively large bordered pits.

Using this similarity of structure per se as an indication of close generic relationship is hazardous, for it is generally recognized that evidence derived from the examination of vascular tissues is of more value in negations than in confirmations (Bailey, 1949). However, since none of the genera exhibited any radical (*inter se*) anatomical differences, the six genera now recognized for the Canellaceae appear to form a natural group. Nevertheless, the possibility must still be considered that this apparent anatomical similarity may be the result of parallel evolution. Evidence from reproductive and other vegetative parts is needed.

The wood of *Cinnamodendron* and *Capsicodendron* exhibits the most primitive characters in the family. The vessel elements are quite long (maximum observed,  $1500\mu$  in *Capsicodendron* and  $2400\mu$  in *Cinnamodendron*), have an angular outline, very long, sloping end walls and the perforation plates are scalariform, with a large number of bars (up to 100 in both genera) and very narrow openings between the bars. The vessel elements in these two genera come close to meeting the requirements of a primitive vessel as proposed by Frost (1930). In addition, the axial parenchyma of these two genera is predominantly apotracheal-diffuse, the fibers have thin walls, some rays may be 3 or 4 cells wide and tend to be slightly higher than those in the other genera, and the vessels are mostly in a solitary arrangement.

The characters of *Warburgia* also show a degree of primitiveness, but to a lesser extent than the preceding two genera. The vessels range from very long to extremely long, perforation plates with many scalariform bars, and transitional to opposite pitting. However, here the vessels are much larger in diameter and not predominantly solitary in distribution. In addition, the parenchyma is more aggregated and some paratracheal parenchyma is present.

*Pleodendron* and *Cinnamosma* appear to be slightly more advanced. The vessels are shorter than the preceding three genera, and the diameter is larger. The number of bars of the scalariform perforation plates is smaller and the parenchyma is predominantly paratracheal with some apotracheal.

Based on wood anatomy it appears that *Canella* possesses the highest level of advancement. The vessel-member length is the shortest of all the genera ( $832-1250\mu$ ), the scalariform plates have fewer bars, and in cross sectional outline the vessels are round. The rays are mostly uniseriate and predominantly homogeneous. The parenchyma is mostly paratracheal in distribution, with very little apotracheal parenchyma.

In comparing the anatomy of these genera with their geographic ranges a striking correlation emerges. The wood of the most temperate species (*Canella*) shows the greatest number of advanced characters, whereas the genera with the most tropical species (*Capsicodendron* and *Cinnamodendron*) exhibit the most primitive characters. The wood of the species of the other 3 genera are intermediate between these two extremes.

In general, the woods of the Canellaceae exhibit the following specialized structural characteristics: fiber-tracheid walls thick—very thick, cross sectional shape of vessels is round to oval, homogeneous rays almost wholly uniseriate or with a few bi- or triseriate, and unilateral paratracheal parenchyma. Conversely, the woods show the following primitive characteristics: long fiber-tracheids and vessel members, small diameter of vessels, scalariform perforation plates usually with a large number of bars, intervascular pitting and vessel-parenchyma pitting linear (transition from scalariform to opposite) and opposite, very acute end walls of vessel elements, some scalariform perforations show slight borders, thin vessel element walls, some apotracheal parenchyma in each genus, and solitary vessel distribution.

#### COMPARISON OF WOOD OF CANELLACEAE WITH THAT OF PUTATIVELY RELATED FAMILIES

When the anatomy of the secondary xylem of the Canellaceae is compared, via the punch-card method (Canright, 1955) with the anatomy of its supposed allies in the Parietales (or Bixales or Violales), i.e., Violaceae, Bixaceae, Flacourtiaceae, Koeberliniaceae, it becomes apparent that there is no close relationship with any of these families. Although the

Violaceae do possess wood with a few primitive characters, the two distinct sizes of the rays, the septate fibers, and the alternate to opposite intervascular pitting are features quite different from those in the Canellaceae. The wood of the Violaceae does possess some similarity to the Canellaceae in the slightly angular outline of the vessels, in the presence of a few scalariform perforation plates in some members, and in some similarity in pitting. Because these characters are not constant throughout the Violaceae as a whole, the author does not see close relation between this family and the Canellaceae.

There are even fewer similar traits shared by the Bixaceae and Canellaceae than by Canellaceae and Violaceae. The diameter and outline of the vessels are roughly comparable, and the narrow width of the rays (1-4 cells) suggests the Canellaceae. However, these few resemblances probably are of slight phylogenetic significance. These resemblances are opposed by the short vessels and fibers, perforation plates entirely simple, and fibers sometimes septate in the Bixaceae.

The Flacourtiaceae are very similar to the Violaceae, and therefore have little in common with the Canellaceae, aside from the angular outline of the vessels and some scattered scalariform perforation plates.

The Koeberliniaceae possess vessels in a solitary arrangement, and have fiber-tracheids, and are, therefore, similar to the Canellaceae in these two characters. However, this does not seem to be adequate evidence on which to assign any degree of relationship.

As has been reported earlier, the Canellaceae have occasionally been allied with the Ranales (*sensu lato*). Money, Bailey and Swamy (1950) include the Canellaceae in the Ranales because of characteristics other than those provided by wood anatomy, i.e., monocolpate pollen and ethereal oil cells. In view of this fact, it was deemed advisable to investigate the wood anatomy of the woody ranalian families and compare it with the anatomy of the Canellaceae. Wherever possible actual material was examined, augmented by information from the following literature: Bailey (1944); Bailey

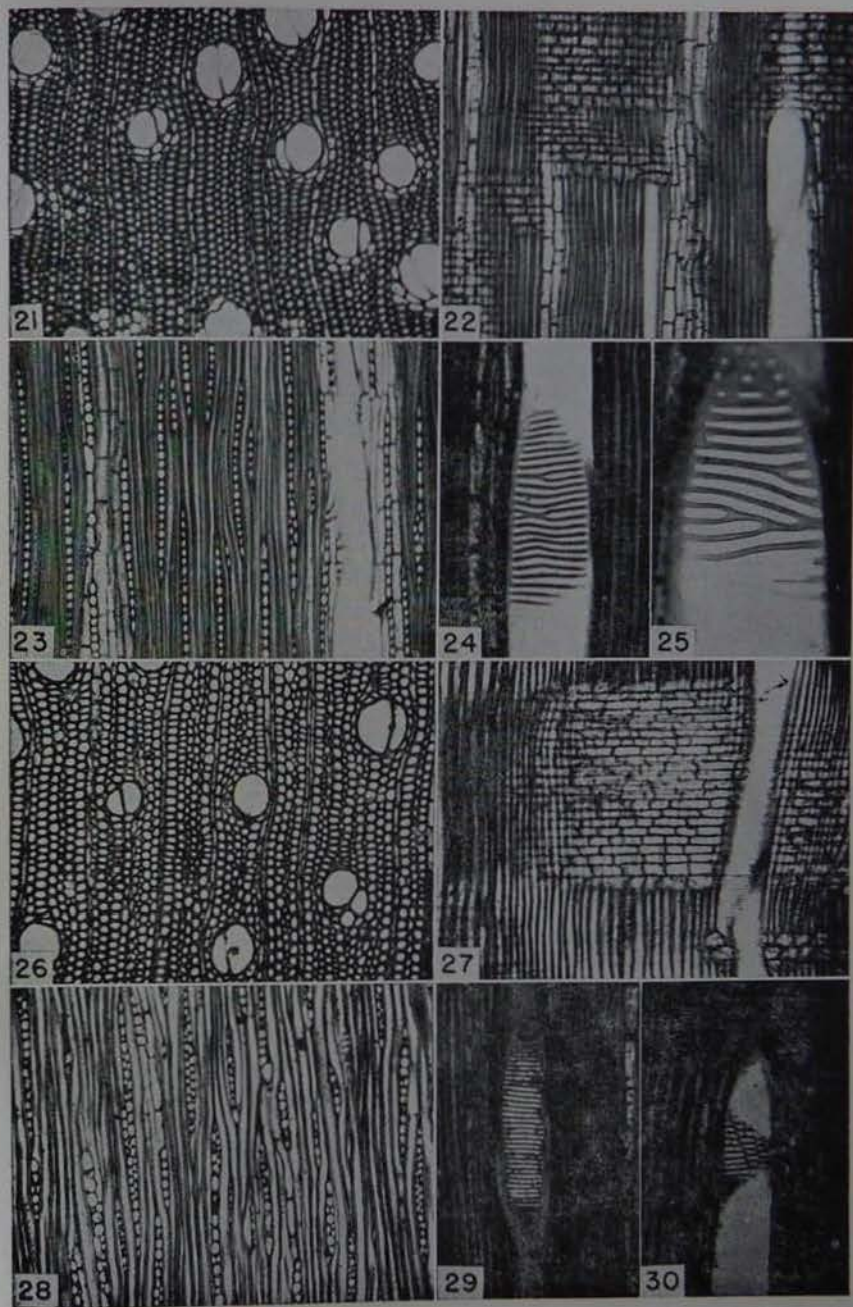


Fig. 21-20.—Fig. 21-25. *Pleodendron macranthum* Van Tiegh.—Fig. 21. Transverse section showing solitary vessel distribution, narrow rays, and unilateral vascentric axial parenchyma.—Fig. 22. Radial section showing heterocellular rays.—Fig. 23. Tangential section showing extremely narrow uniseriate rays.—Fig. 24-25. Portions of scalariform-reticulate perforation plates. Radial section.—Fig. 26-28. *Warburgia ugandensis* Sprague.—Fig. 26. Transverse section showing solitary vessel distribution.—Fig. 27. Radial section showing homocellular to weak heterocellular ray construction.—Fig. 28. Tangential section showing uni- and biseriate rays.—Fig. 29. *W. stuhlmanni* Eng. Complete scalariform perforation plate. Radial section.—Fig. 30. *W. ugandensis* Sprague. Portion of scalariform perforation plate. Radial section.—Fig. 21-23, 26-28.  $\times 64$ . Fig. 24-25, 29, 30.  $\times 100$ .

and Nast (1948); Bailey and Smith (1942); Bailey and Swamy (1953); Bailey and Tupper (1918); Canright (1955); Garratt (1933a, 1934); Howard (1948); Lemesle (1946, 1947, 1950, 1951, 1955); McLaughlin (1933); Metcalfe and Chalk (1950); Money, Bailey and Swamy (1950); Nast and Bailey (1946); and Record and Hess (1943).

The wood of the Canellaceae shows very few similarities to the wood of the vesselless members of the woody Ranales. Of the remaining members of the woody Ranales, the wood of the Canellaceae has little in common with that of the Himantandraceae, Lauraceae, Calycanthaceae, Annonaceae, Piperaceae and Berberidaceae. These conclusions agree with those of other workers. Metcalfe and Chalk (1950) note that some features of the wood of the Canellaceae suggest affinities with the Magnoliaceae and Lauraceae, though they go on to say that other characters lend little support to this conclusion. Stern (1954) did not consider the Canellaceae closely related to the Lauraceae, and consequently did not consider their anatomy.

Bailey, Nast and Smith (1943) note that when all evidence is considered, the Degeneriaceae, Himantandraceae and Magnoliaceae form a group of very closely related families which are only remotely related to the other ranalian families. While the wood anatomy of the Canellaceae shows but few features in common with the Himantandraceae, a number of features are shared with the Degeneriaceae and Magnoliaceae (especially with tropical genera such as *Talauma*). Vander Wyk and Canright (1956) could find no basis for a relationship between Canellaceae and Annonaceae, nor between Canellaceae and the "magnoliaceous triumverate of families." What few similarities do exist between Canellaceae and the Magnoliaceae and Degeneriaceae could possibly be explained on the grounds of equivalent levels of specialization.

As noted above, the Degeneriaceae and Magnoliaceae show more features in common with the Canellaceae than do the Himantandraceae. Also, the Myristicaceae, certain groups of the Monimiaceae, and Chloranthaceae show about

the same number of features in common with the *Canellaceae* as do the *Degeneriaceae* and *Magnoliaceae*.

Vestal (1937), agreeing with Wettstein (1935) and Bessey (1915), has placed the *Canellaceae* next to the *Myristicaceae*. Similarly, Vander Wyk and Canright (20. 1956) state:

“ . . . certain genera of the *Myristicaceae* share a number of anatomical features with the *Canellaceae*. Thus it may be possible that Vestal 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*.”

On the other hand Garratt (1933b) observed “the *Canellaceae* . . . seem rather far removed from the *Myristicaceae*, despite certain points of similarity.” The writer’s own observations are more in line with those of Garratt, in that there seem to be few similar points between these two families.

In wood anatomy the *Chloranthaceae* and *Monimiaceae* in general show little in common with the *Canellaceae*, but certain members of the former families have some points that are similar, e.g., the length of vessel elements, scalariform perforation plates with many bars, and type of intervacular pitting.

By far the greatest degree of agreement in secondary xylem seems to exist between the *Canellaceae* and the following families: *Dilleniaceae*, *Eupteleaceae*, *Eupomatiaceae*, *Illiciaceae*, and *Schisandraceae*. Of these five families, the *Illiciaceae* and *Eupteleaceae* seem to have more features in common with the *Canellaceae* than any of the others. They are quite similar in size and shape of vessels, presence of scalariform perforation plates with many bars, intervacular pitting, vessel arrangement, narrow rays (*Illiciaceae*) and composition (somewhat like *Eupteleaceae*) and length of fibers. All the *Canellaceae* show a characteristic type of perforation plate best described as scalariform with a mixture of a reticulate type (Committee on Nomenclature, 1957).

This same type (scalariform-reticulate) is also found in the *Illiciaceae* and *Eupteleaceae*.

Bailey (1953), Vander Wyk and Canright (1956), and Stern (1954) among others, have warned of the danger of basing phylogenetic conclusions on wood anatomy alone, or for that matter on any one line of evidence. Consequently, the author does not wish to imply that definite relationship exists between the *Canellaceae* and the *Eupteleaceae* or the *Illiciaceae*, but is merely pointing out that these anatomical similarities do exist. However, due to the small number of wood features shared by the *Canellaceae* and *Parietales*, the affinities of the *Canellaceae* do not lie with the *Parietales*. Conversely, because of the abundance of similar features seen in the *Canellaceae* and *Ranales* the affinities of the *Canellaceae* appear to be with certain families of the arborescent *Ranales*. This tentative conclusion will be discussed from other standpoints in succeeding papers in this series.

#### SUMMARY

The *Canellaceae* is here considered to be composed of six genera: *Canella*, *Pleodendron*, *Cinnamodendron*, *Capsicodendron*, *Warburgia* and *Cinnamosma*.

The information gained from studying the secondary xylem of members of the above genera was used to compare the *Canellaceae* with members of the *Parietales* and *Ranales*, orders in which this family has been placed in many taxonomic systems. The anatomy of the wood shows some fairly advanced features in the character of rays, but the other features point to a low level of specialization—a condition which is not in accord with the high rank given this family in most systems of classification. There is more similarity between the wood of the *Canellaceae* and the woody *Ranales* than between the wood of the former and the *Parietales*. Among ranalian families the woods of the *Eupteleaceae*, *Dilleniaceae*, *Eupomatiaceae*, *Illiciaceae* and *Schisandraceae* are most similar to the wood of the *Canellaceae*.



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## FOREST SOILS OF DARIEN PROVINCE, PANAMA

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The arrival in Panamá of a group of botanists<sup>1</sup> from Yale and St. Louis Universities in May 1959, presented an opportunity to obtain more information on the soils of the Province of Darién, Panamá. A previous reconnaissance soil survey prepared by technicians of the United Fruit Company (Smith, et al., 1954) was available and was used as a general guide. The United Fruit Company survey was found to be extremely generalized, and the soils of the Darién are so variable that to attempt a systematized survey in the several classes of vegetation, at different altitudes and along seacoast and rivers, would be a task requiring several years and a large field party. For the purpose of this trip, it was decided to send a soil scientist with the botanists to prepare a soil collection and profile study at each site where plant material was collected. This would serve to check the previous soil survey and provide basic information for a more detailed survey if one were desirable at a later date. It would also provide soil data for possible future correlation in plant ecological studies.

The attached map (fig. 1) shows the location of the generalized soil areas. Sites 1 to 7, 18, 19 and 31 to 35 were in the vicinity of El Real; sites 8 to 17 were taken in the vicinity of the Cuna Indian village of Paya; sites 20 to 30 were obtained between Boca de Cupe and the Cana Valley;

<sup>1</sup>The soils studies described herein were performed in association with floristic investigations of the Darién being carried out partly under the auspices of the National Science Foundation of the U. S. A., and the U. S. Office of Naval Research. The soil scientists worked in close cooperation with botanists W. L. Stern, K. L. Chambers and J. E. Ebinger of Yale University, and J. D. Dwyer of St. Louis University. It is intended to publish a joint paper in an attempt to correlate pedological and botanical observations at a later date.

and sites 36 to 51 near where the Rio Tuqueza meets the Rio Chucunaque, designated on table 1 as "Pandelpet."

Table 1 presents data from field observations while table 2 is devoted to information obtained after laboratory analysis of the soil samples. Reference to figure 1 will show that Darién Province varies from extremely flat river bottom lands to steep mountains. The bulk of the samples collected was from rather flat or rolling lands but this should not be interpreted as meaning that the area is flat.

The column headed "Class" in table 1 indicates the land use capability classification system employed by the U. S. Department of Agriculture, Soil Conservation Service, particularly that of Hockensmith and Steele (1949). The best agricultural land would thus be Class I, with Class VIII the poorest suitable only for recreational purposes. Classes II, III and IV are suitable for cultivation with limitations being imposed by slope, water availability, etc. Classes V, VI and VII are suitable only for pasture or forest. The capital letters immediately following the land class denote a general superficial aspect of the land and may or may not be associated with the factors which influenced the formation of the soil. These are as follows:

- A. alluvial
- C. hilly
- H. rolling
- R. residual soil not otherwise classified
- O. organic

The column headed "survey number" may be interpreted as follows (Hansen and Ah Chu, 1960):

*Alluvial soils (fig. 2)*

- 24 Medium texture: adequately drained not subject to inundation.
- 25 Fine texture: adequately drained and subject to inundation.
- 26 Coarse texture: adequately drained.
- 29 Very fine texture: imperfectly drained.

*Residual soils not latosolic (fig. 3)*

- 30 Coarse texture: adequately drained.
- 40 Medium texture: adequately drained.
- 50 Fine texture: adequately drained.
- 70 Without clay pan: imperfectly drained.

*Latosolic soils* (fig. 4)

75 Without clay pan: imperfectly drained.

82T Rolling with clay pan: imperfectly drained.

550 Land cut sharply: adequately drained.

570 Mountain land: adequately drained.

The latosolic soils are derived largely from basic igneous andesites or basalts (Terry, 1956). Residual soils which are not latosolic are formed largely from parent materials of shales, sandstones, conglomerates and limestones of Eocene to Late Miocene age with some influence of igneous intrusions. The alluvial soils are derived from mixed sediments of both igneous and sedimentary parent materials.

The texture of the soils (table 2) was determined in the laboratory by means of a hydrometer (American Society for Testing Materials, Committee D-18, 1950). In general, the soils contain large amounts of clay, but there is usually sufficient sand and silt so that the soils may be classified as loams. The color of the wet soil was determined by reference to Munsell soil color charts. Most of the soil colors are some shade of brown or red. This may be somewhat misleading because of the presence of a mottled zone in the subsoil. The letter *M* has therefore been placed immediately before the color in order to indicate a mottled zone which is a mixture of red, yellow, black and sometimes green or grey. The latosolic soils usually occur on rolling lands and thus, although they contain a mottled zone in the subsoil, are sometimes listed as having medium drainage if excess water is not a problem. Sites 38, 39, 41 and 51 have a mottled zone which has developed as a result of prolonged flooded periods. The internal drainage is adequate but drainage has been shown as only medium. The pH of the soil was determined by means of a glass electrode using a 1 + 1 soil-water suspension (United States Salinity Laboratory Staff, 1954). There was a wide pH range (3.5 to 7.5). Samples above pH 7.0 are extremely rare and are associated with the calcareous areas. It should be noted however that samples very high in calcium have in some cases a very low pH value.

The fertility levels, that is nitrogen (N), phosphorus ( $P_2O_5$ ) and potassium ( $K_2O$ ), extracted by 10 per cent

Table 1. COLLECTION DATA, SOIL SAMPLES, DARIÉN PROVINCE, 1959

SITE NUMBER	DATE COLLECTED	SLOPE PER CENT	CLASS	SURVEY NUMBER	DRAINAGE	LOCATION <sup>1</sup>
1	June 5	5	II A	25	Good	Yaviza 1 mile west near Río Chucunaque
2	June 6	5	II A	25	Good	Yaviza ¼ mile from Río Tuira
3	June 6	3	II A	25	Good	Yaviza ½ mile from Río Tuira
4	June 6	15	V C	50	Medium	Yaviza 1 mile from Río Tuira
5	June 7	30	VI C	40	Good	Yaviza ½ mile west near Río Chucunaque
6	June 7	40	VI C	50	Good	Site of highway bridge over Río Chucunaque
7	June 7	20	VI C	40	Good	One hundred feet south of site 6
8	June 10	5	III C	75	Poor	Paya 200 feet east on bank of Río Paya
9	June 10	5	II C	75	Medium	Paya ½ mile east 20 feet from Río Paya
10	June 10	5	IV C	75	Poor	Paya ½ mile east 50 feet from Río Paya
11	June 11	1	III C	75	Medium	Paya 1 mile east 500 feet from Río Paya
12	June 11	3	III A	25	Good	Paya ¼ mile south along trail to Palo de las Letras
13	June 11	30	V C	550	Medium	Paya 1 mile south
14	June 12	10	III H	550	Medium	Paya ¼ mile north along trail to Pucro
15	June 12	5	III H	550	Medium	Paya ½ mile north along trail to Pucro
16	June 12	5	III H	550	Medium	Paya ¾ mile north along trail to Pucro
17	June 12	5	II C	550	Medium	Paya 1 mile north along trail to Pucro
18	June 16	1	IV A	29	Poor	El Real ½ mile south near Río Pirre
19	June 16	6	V C	550	Good	El Real 1 mile south near Río Pirre
20	June 23	20	VI C	570	Good	Caná 1 mile north
21	June 23	1	II R	30	Good	Caná 1 ½ miles north
22	June 24	15	VI R	570	Medium	Caná 1 mile south
23	June 24	8	VII R	570	Medium	Caná 2 miles south
24	June 25	3	IV A	25	Good	Caná near Río San José
25	June 26	2	III R	40	Good	Caná 2 miles north

<sup>1</sup>Distances were estimated from town or camp shown in figure 1.

Table 1—Continued

SITE NUMBER	DATE COLLECTED	SLOPE PER CENT	CLASS	SURVEY NUMBER	DRAINAGE	LOCATION
26	June 26	1	II O	30	Good	Cana 3 miles north
27	June 26	1	II A	24	Good	Cana 4 miles north near Río Tuira
28	June 26	12	V R	82 T	Poor	Cana 8 miles north near Río Paca
29	June 27	15	V R	570	Medium	Cana 10 miles north near Río Cupe
30	June 27	3	III R	50	Good	Cana 12 miles north near Río Cupe
31	June 30	5	V C	75	Poor	El Real 1 mile southeast near airport
32	June 30	1	IV C	70	Poor	El Real 300 feet from site 31
33	June 30	1	V H	75	Poor	El Real ¼ mile southeast near airport
34	July 1	1	IV H	70	Poor	El Real south toward Cerro Pirre
35	July 1	1	IV H	50	Good	El Real 300 feet south
36	July 4	1	III A	26	Good	El Real half way to Yaviza on Río Chucunaque
37	July 4	1	III A	26	Good	Site 36 about 150 feet from Río Chucunaque
38	July 4	1	III A	25	Medium	Site 36 about 100 feet from Río Chucunaque
39	July 4	1	IV A	25	Medium	Pandelpet
40	July 4	1	IV C	75	Medium	Pandelpet 60 feet south
41	July 4	1	III A	30	Medium	Pandelpet 100 feet east
42	July 4	10	VI C	550	Medium	Pandelpet 150 feet east
43	July 5	1	VI A	29	Poor	Pandelpet ¼ mile northeast
44	July 5	1	IV A	70	Poor	Pandelpet ½ mile northeast near Río Chucunaque
45	July 5	1	II A	26	Good	Pandelpet 1 mile northeast
46	July 6	1	IV R	70	Medium	Pandelpet 1000 feet northeast
47	July 6	1	IV R	70	Medium	Pandelpet 60 feet from site 46
48	July 7	1	IV R	70	Medium	Pandelpet across Río Chucunaque
49	July 7	15	VI C	75	Poor	Pandelpet 300 feet from site 48
50	July 8	10	IV R	70	Poor	Pandelpet ½ mile northeast
51	July 8	1	III A	26	Medium	Pandelpet 150 feet from site 50



Fig. 2. River margin showing area where alluvial soils are deposited and where agriculture is most promising

Table 2. LABORATORY ANALYSIS OF SOIL SAMPLES COLLECTED IN DARIÉN PROVINCE, 1959

SAMPLE NUMBER	DEPTH IN INCHES	COLOR (WET)	TEXTURE	PH		POUNDS PER HECTARE (8 IN.)			PER CENT ORGANIC MATTER	
				1 + 1	EXTRACT	NO <sub>3</sub>	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O		Ca (EXTRACTABLE BY 10 PER CENT NAAc)
1	0-12	gray brown	clay loam	5.8		160	125	300	14000	6.97
2	0-8	dark gray	silt loam	6.9		160	245	375	14000	6.92
	8-40	yellow brown	clay	5.7		80	245	300	1750	.87
3	0-12	dark gray brown	silt loam	5.6		160	60	300	5000	1.91
	12-36	light yellow brown	clay loam	5.6		80	60	300	7000	.34
4	0-12	pale brown	clay loam	5.6		160	125	300	14000	4.30
	0-6	yellow brown	silt loam	6.4		20	125	300	14000	1.37
5	6-24	pale yellow	sandy loam	6.2		20	60	300	14000	.31
	0-8	dark gray brown	sandy loam	5.7		120	60	300	14000	2.72
6	8-24	dark gray brown	clay	5.6		8	135	300	14000	.95
	0-24	dark brown	sandy loam	5.8		160	60	300	14000	6.05
7	0-24	dark brown	clay	4.7		60	25	600	750	2.16
	24-48	M yellow red	clay loam	4.6		60	25	300	750	1.29
9	0-10	yellow red	clay loam	5.1		20	185	300	5000	2.72
	10-40	M yellow red	clay loam	4.5		20	60	300	350	1.10
10	40-60	M yellow red	clay loam	4.6		8	60	300	1750	.69
	0-10	red brown	sandy loam	5.2		160	60	570	5000	3.33
11	10-20	yellow red	silt loam	4.0		120	60	540	1750	2.34
	20-40	M yellow red	silt loam	4.1		60	60	480	750	1.56
12	0-10	brown	silt loam	5.4		80	120	300	7000	2.37
	10-30	light gray brown	clay	5.2		60	60	300	3500	.83
13	0-4	dark brown	silt loam	5.5		160	125	360	7000	4.20
	4-16	brown	clay	5.5		120	185	300	14000	.68
13	16-36	yellow brown	clay loam	5.4		40	245	360	14000	.75
	0-6	dark brown	sandy loam	5.4		8	125	570	14000	7.32
	12-48	M yellow brown	silt loam	4.2		40	60	780	5000	.77

Table 2—Continued

SAMPLE NUMBER	DEPTH IN INCHES	COLOR (WET)	TEXTURE	pH 1+1 EXTRACT	POUNDS PER HECTARE (8 IN.)				PER CENT ORGANIC MATTER
					NO <sub>3</sub>	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O	Ca	
14	0-6	dark brown	silt loam	4.7	80	25	300	750	3.57
	12-36	M red brown	clay loam	4.6	80	25	300	750	1.01
15	0-6	brown	silt loam	4.2	160	25	540	1750	3.11
	10-15	M dark brown	silt loam	4.2	20	25	420	1750	2.23
16	0-6	yellow brown	sandy loam	6.0	160	60	300	14000	2.71
	6-20	dark brown	clay	4.6	20	60	480	14000	.93
	20-40	M yellow brown	clay	4.7	8	125	360	14000	.90
17	0-6	dark gray brown	sandy loam	6.0	160	60	660	14000	4.82
	12-24	yellow brown	clay	5.4	40	60	300	14000	1.04
	36-48	M yellow brown	clay	5.1	80	185	420	14000	.78
18	0-30	dark gray brown	clay loam	5.3	8	60	660	1750	5.66
	30-60	M dark gray brown	clay loam	5.5	8	60	660	7000	3.49
19	0-16	yellow red	sandy loam	4.7	8	25	360	750	3.16
	16-48	M yellow brown	sandy loam	5.2	8	60	300	14000	.02
	48-60	brown	loam sand	7.3	8	185	300	14000	.09
20	0-6	dark brown	sandy loam	3.6	40	25	360	750	5.3
	6-12	yellow red	clay	4.3	8	60	300	750	2.11
	12-36	very dark brown	sand	4.7	20	25	300	750	.67
	36-54	M light yellow brown	clay loam	4.2	20	25	300	750	.71
21	0-3	dark yellow brown	sandy loam	4.5	40	60	420	1750	11.0
	3-20	light gray brown	sandy loam	4.4	40	60	360	1750	5.00
	20-40	Collected but legend unreadable							
22	40-60	very dark brown	clay	4.8	20	25	300	750	.71
	0-3	red brown	clay	3.5	8	25	300	1750	10.40
	3-12	brown	sandy loam	3.7	80	25	300	750	4.91
	12-40	M yellow red	clay	4.5	8	25	300	750	2.00



Fig. 3. An area being cropped on residual soils which are not latosolic. Such localities occur in mountain valleys and represent places of agricultural potential.



Table 2—Continued

SAMPLE NUMBER	DEPTH IN INCHES	COLOR (WET)	TEXTURE	pH 1 + 1 EXTRACT	POUNDS PER HECTARE (8 IN.)				PER CENT ORGANIC MATTER
					NO <sub>3</sub>	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O	Ca	
	40-50	M yellow red	clay	4.5	8	25	300	750	.81
23	0-3	yellow brown	loamy sand	3.6	80	25	300	750	.14
	3-16	yellow red	sandy loam	4.1	20	25	300	750	3.19
	16-40	M yellow red	clay	4.5	8	185	300	750	1.39
	40-60	M yellow red	clay	4.2	8	25	300	750	1.02
24	0-16	dark red gray	clay loam	4.9	80	60	300	5000	1.66
	16-32	dark yellow brown	sandy loam	5.1	60	60	300	7000	1.14
25	0-12	brown	clay loam	5.5	80	60	540	1750	3.19
	12-24	dark brown	clay	5.1	8	25	360	350	1.62
26	0-8	dark gray brown	loamy sand	6.4	60	185	360	14000	8.24
	8-36	dark yellow brown	sandy loam	6.4	20	125	300	7000	3.07
27	0-16	dark brown	sandy loam	6.1	80	125	300	14000	3.13
	16-40	dark brown	silt loam	6.1	60	185	300	14000	2.41
28	0-12	dark yellow brown	silt loam	5.6	8	125	300	14000	3.37
	12-36	M dark yellow brown	clay loam	5.9	8	185	300	7000	1.66
29	0-16	dark brown	sandy loam	5.7	40	60	300	3500	9.01
	16-24	M dark brown	sandy loam	5.7	20	60	540	14000	2.41
30	0-16	dark brown	sandy loam	5.7	40	60	300	14000	5.72
	20-40	brown	silt loam	7.5	60	185	480	14000	.62
31	0-20	dark red brown	clay loam	5.5	8	185	420	14000	4.16
	20-40	M red brown	sandy loam	4.7	8	60	300	7000	1.87
32	0-10	dark brown	silt loam	6.0	40	125	360	14000	1.69
	10-40	M yellow brown	clay loam	4.5	8	60	300	7000	.71
33	0-8	dark brown	silt loam	5.1	8	60	660	7000	2.41
	8-24	M yellow brown	sandy loam	4.7	8	25	300	750	1.33
	24-40	M yellow red	sandy loam	4.6	8	25	360	5000	.21

Table 2—Continued

SAMPLE NUMBER	DEPTH IN INCHES	COLOR (WET)	TEXTURE	pH 1 + 1 EXTRACT	POUNDS PER HECTARE (8 IN.)				PER CENT ORGANIC MATTER
					NO <sub>3</sub>	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O	Ca	
34	0-3								
	3-18	M brown	silt loam	5.1	8	60	300	14000	1.56
	18-40	M							
35	0-10	gray brown	clay loam	5.7	8	80	660	14000	3.23
	10-40	dark brown	clay loam	5.4	8	185	300	14000	1.91
36	0-3	dark gray brown	sand	5.5	40	60	360	5000	1.91
	3-20	dark yellow brown	silt loam	5.9	80	185	300	7000	1.75
	20-30	dark yellow brown	clay loam	6.6	8	80	300	14000	1.68
37	0-3	very dark brown	loamy sand	7.0	20	245	300	7000	8.60
	3-24	dark brown	sandy loam	7.0	20	185	300	14000	2.16
	24-40	dark brown	sandy loam	6.3	8	185	300	7000	.12
38	0-2								
	2-24								
	24-40	M dark brown	clay	5.1	8	60	300	3500	.83
39	40-60	M brown	clay loam	6.9	60	120	300	750	1.36
	0-2								
	2-18	dark brown	clay loam	5.8	60	185	300	5000	3.58
40	18-40	M dark brown	clay loam	5.3	20	185	300	5000	1.20
	0-2								
	2-20	dark red	clay loam	5.1	40	60	300	750	2.40
41	20-32	M dark red	clay loam	5.0	80	80	300	750	.66
	32-50	M yellow red	clay	4.5	8	125	300	1750	.90
	0-20	dark brown	silt loam	5.7	8	60	300	1750	.96
42	20-30	yellow brown	silt loam	5.7	8	80	300	750	.84
	30-50	M brown	silt loam	6.3	8	125	300	1750	.90
	4-14	dark brown	sandy loam	5.9	60	60	300	14000	5.99



Fig. 4. Steep hillsides where latosolic soils are present. Such areas are best reserved for forest land as their agricultural productivity is low.

Table 2—Continued

SAMPLE NUMBER	DEPTH IN INCHES	COLOR (WET)	TEXTURE	PH 1 + 1 EXTRACT	POUNDS PER HECTARE (8 IN.)				PER CENT ORGANIC MATTER
					NO <sub>3</sub>	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O	Ca	
	14-28	yellow brown	clay	6.2	8	185	300	7000	.45
	28-50	yellow brown	clay	5.9	8	185	300	7000	.75
43	0-10	M dark gray brown	sandy loam	5.7	8	245	420	14000	2.83
	10-50	M brown	silt loam	5.6	20	120	300	7000	1.20
44	0-8	M dark brown	silt loam	6.0	40	40	300	7000	4.91
	8-50	M dark yellow brown	clay	6.1	8	125	300	14000	2.50
45	0-20	Collected but legend unreadable							
	20-48	dark brown	silt loam	6.3	20	185	300	14000	.99
46	0-10	gray brown	clay loam	6.2	8	120	540	7000	3.23
	10-28	M brown	silt loam	5.1	8	60	360	14000	1.74
	28-54	M brown	clay loam	4.9	80	120	360	14000	1.78
47	0-12	dark gray brown	sandy loam	5.5	40	80	660	14000	5.57
	12-30	M brown	clay	4.3	60	80	330	14000	.87
	30-50	yellow brown	clay loam	4.8	20	80	360	7000	.93
48	0-8	dark brown	sandy loam	5.9	40	25	300	750	5.33
	8-26	dark brown	clay	5.4	60	125	300	1750	1.54
	26-50	M dark brown	clay loam	6.0	8	185	300	1750	1.04
49	0-5	dark red brown	sandy loam	6.0	80	125	780	5000	5.66
	5-28	red	clay	4.5	80	25	300	750	1.58
	28-50	M dark brown	silt loam	5.7	40	60	300	1750	.87
50	0-8	dark gray brown	sandy loam	5.9	60	185	420	14000	12.20
	8-26	M dark gray brown	clay	6.0	8	125	330	14000	9.53
51	0-14	Collected but legend unreadable							
	14-28	dark yellow brown	sandy loam	6.6	8	60	420	5000	1.75
	30-50	M dark gray brown	silt loam	6.3	40	185	360	14000	.93

sodium acetate (Lunt, et al., 1950) are very low as would be expected in an area of high rainfall and high temperature. The use of large amounts of fertilizer, particularly high phosphorus application, is indicated by the laboratory analysis. The appearance of the natural vegetation is usually quite vigorous and first impressions are that this land is extremely fertile. This is in error however, and one or two crops will remove the available nutrients resulting in the failure of subsequent crops. This has given rise to the "Rosa" or "slash and burn" system in which the land is cultivated only 1 year of each 5 to 8 years. The alluvial lands, particularly when they contain large amounts of calcium, are however, potentially very productive if fertilized and managed properly.

Organic matter was found to be extremely variable. Areas which have been in tropical forest for many years have large amounts of organic matter in the surface layers, but where an area has been cleared and cultivated, the organic matter is rapidly oxidized under the influence of high temperature and rainfall. Some of the areas of alluvial soils receive an annual deposition of soil and debris and are characterized by a high organic matter content.

#### SUMMARY

The soils of the Darién area may be divided roughly into three groups.

1. The alluvial soil of the lowlands which are subject to inundation by flood waters. Large areas are inundated by high tides which have given rise to the saline mangrove associations not visited on this trip. Nearly all the agricultural activity of the Darién area takes place on the alluvial soils near the major rivers and their tributaries in areas not subject to the influence of seawater. These alluvial soils are potentially extremely productive and offer large regions of valuable agricultural land if protected from flooding and supplied with adequate drainage.

2. The miscellaneous grouping of soils called "residual but not latosolic" occupies locations intermediate between the alluvial and latosolic conditions. It occurs in mountain

valleys which are slightly undulating, and which are of more recent origin than the areas of latosolic soils. Nevertheless, the soils of these valleys are in the process of degradation. The area occupied by this grouping is small but it contains the only soils besides the alluvial kinds which may be successfully cultivated.

3. The latosolic soils which predominate, occupy most of the hilly and mountainous land. These soils are limited to use for pasture or forest production and only very few situations are suitable for cultivation even 1 year in every 5 years.

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## ON THE ORIGIN OF AN UNUSUAL *DIPHOLIS* FROM THE FLORIDA KEYS<sup>1</sup>

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No Name Key is a small island in the Lower Keys of Florida lying just east of Big Pine Key and formerly connected with that larger island by a highway bridge. Prior to 1948, when the bridge was wrecked by a hurricane, No Name Key was permanently inhabited, and its vegetation probably resembled the fire scarred pinelands of neighboring Big Pine Key (Stern and Brizicky, 1957). When Dr. William L. Stern and Dr. George K. Brizicky visited No Name Key in July of 1956, however, they found it was virtually abandoned and evidently had been free from burning for a number of years. An impenetrable growth of palms and young hardwoods was massed below the tall old pines; the unused asphalt road that bisects the island was being encroached upon by grasses, young pine trees, mats of *Acacia farnesiana*, ferns and shrubs from the roadside thicket. The dramatic contrast between the dense vegetation on this uninhabited island and the sparse, open stands of pines and low palms on adjacent, well populated Big Pine Key caused these investigators to suggest that hardwood hammock forests, in the absence of fire, eventually could replace much of the pine forest now present on the Lower Keys.

Among the plants observed by Stern and Brizicky in the lush thickets along the abandoned road on No Name Key was a single small tree, evidently a member of the Sapotaceae, which they tentatively assigned to the genus *Dipholis*. It differed markedly in leaf shape, however, from nearby trees that appeared to be typical of *D. salicifolia* (L.) A. DC., the only species known from Florida. Its leaves, while not noticeably longer than those on adjacent young trees of *D. salicifolia*, were consistently at least twice as broad, giving

<sup>1</sup>Field work necessary for collections on the Florida Keys was accomplished under National Science Foundation grant G-2325 awarded to W. L. Stern.



Fig. 1-4. Two plants of *Dipholis* from No Name Key.—Fig. 1. The broad leaved form, Stern & Chambers 331,  $\times \frac{1}{2}$ .—Fig. 2. Normal *D. salicifolia*, Stern & Chambers 332,  $\times \frac{1}{2}$ .—Fig. 3. Detail of the inflorescence of Fig. 1,  $\times 1\frac{1}{2}$ .—Fig. 4. Detail of the inflorescence of Fig. 2,  $\times 1\frac{1}{2}$ .

quite an unusual aspect to its foliage. All the individuals of *Dipholis* were in fruit at that time of the year, and Stern and Brizicky prepared herbarium specimens of the aberrant, broad leaved tree and of a normal, narrow leaved one growing near it. The broad leaved individual seemed to differ from its neighbors in no other significant morphological features; without further evidence it could only be considered a somewhat atypical form or genetic variant of *D. salicifolia*.

#### MORPHOLOGY

When Dr. Stern and I made a trip to No Name Key in March, 1958, we noticed that the trees of *Dipholis* there had abundant clusters of young flower buds. A second series of pressed specimens of the broad leaved and narrow leaved types was taken, and in addition, buds of the two forms were preserved in Carnoy's 3:1 ethyl alcohol-acetic acid fixative. We hoped that cytological observations on the meiotic behavior of the plants might offer additional clues to the taxonomic problem posed by the variation in leaf shape. The specimens obtained in young bud also revealed distinctive morphological features of the broad leaved variant that were not present in the earlier collections of Stern and Brizicky. The flower clusters were larger and denser, the flower buds were larger, and the pedicels were longer and stouter than the corresponding structures in narrow leaved, "normal" individuals of *D. salicifolia* on No Name Key. The differences in leaf shape and in the appearance of the inflorescences are evident in the accompanying photographs (fig. 1-4). The two plants illustrated grew side by side, and no individuals with leaves or inflorescences of intermediate size were present; the larger buds in figure 3 are not simply older than those in figure 4, since comparable meiotic stages were found in the largest buds of the two plants.

As strikingly different as the leaf shapes may be in the collections from No Name Key, they are readily matched or exceeded in specimens of *D. salicifolia* from elsewhere in the range of that species. The leaf width of the plant in figure 1 varies from 23 to 32 mm.; in the plant in figure 2, it varies from 12 to 17 mm. However, in his monograph of

*Dipholis* Cronquist (1945) states that the leaves of *D. salicifolia* range in width from "1.5 to 4 cm." Some of the variation in leaf shape of *D. salicifolia* is illustrated in figure 5 by leaf tracings made from selected herbarium specimens. The types found on No Name Key are shown at A and B; the remaining sketches are lettered in the order of increasing distance from that island. The plants at C and D are from the tip of peninsular Florida, E and F are from the Upper Keys, G, H and J are from Cuba, and K is from the Dominican Republic (table 1). Even from this small sample of

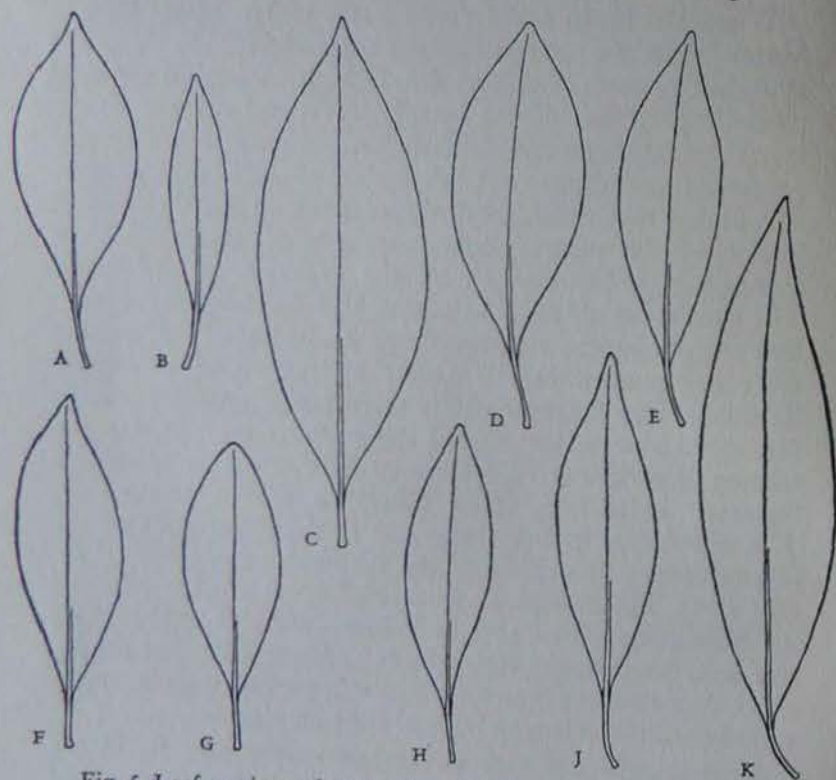


Fig. 5. Leaf tracings of *Dipholis salicifolia* at nine localities.  $\times \frac{1}{2}$ .— A. Stern & Chambers 331, No Name Key; B. Stern & Chambers 332, No Name Key; C. MacDonald 11, Cape Sable; D. Curtiss 1760, Umbrella Key; E. Stern & Chambers 258, Plantation Key; F. W. L. Stern 32, Key Largo; G. Jack 5675, Cuba; H. Wright 1325, Cuba; J. Gill & Whitford 4, Cuba; K. Schiffino 94, Dominican Republic.

leaf types it is evident that the broad leaved individual, A, from No Name Key is not noticeably out of place in *D. salicifolia* as a whole.

To discover whether the samples from No Name Key are within the range of variation of the species as it occurs

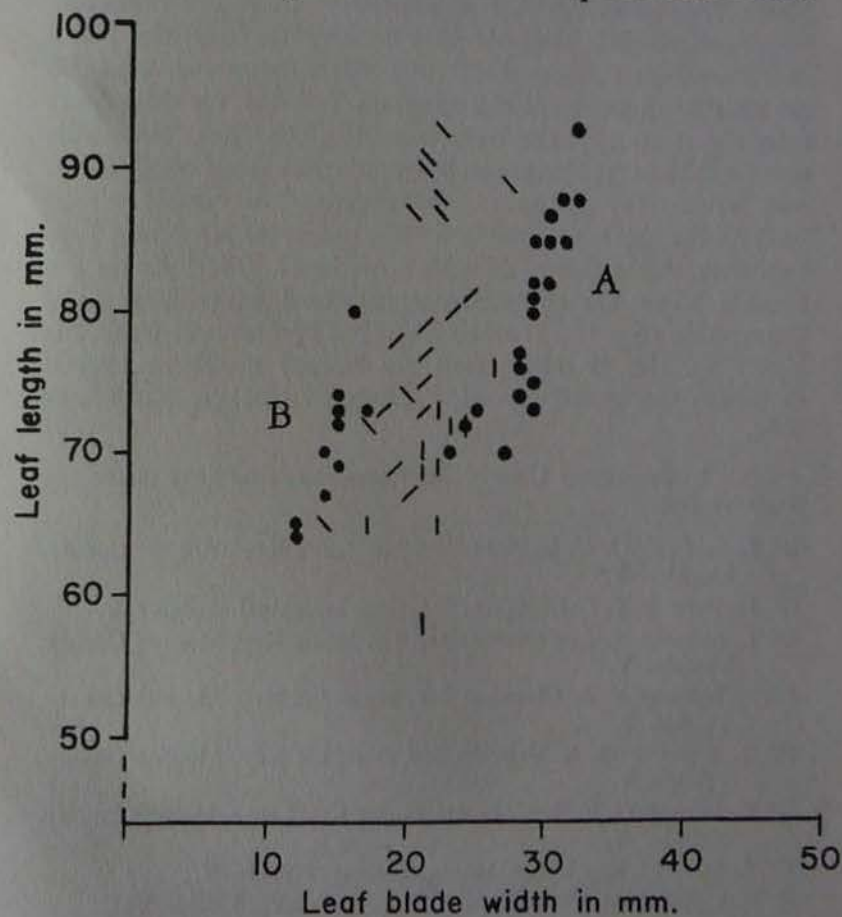


Fig. 6. Scatter diagram of leaf shapes in *Dipholis salicifolia* at four localities in the Florida Keys. Dots at A, No Name Key, Stern & Brizicky 394 and Stern & Chambers 331; dots at B, No Name Key, Stern & Chambers 332; lines slanting to upper right, Big Pine Key, Stern & Brizicky 290; lines slanting to upper left, Plantation Key, Stern & Chambers 258; vertical lines, Key Largo, Stern & Brizicky 460.

on the Florida Keys alone, a scatter diagram was prepared from leaf length-width measurements made on these and three other collections from the Keys (fig. 6). Ten well developed leaves were measured on a single tree from each locality; the 20 leaves diagrammed for the broad leaved No Name Key individual, at A, represent 10 leaves from the Stern and Brizicky sample of 1956 and 10 from the Stern and Chambers collection of 1958. Although trees A and B are clearly distinct on the diagram (as one would expect from fig. 1 and 2), the trees from Big Pine Key (one mile from No Name), Plantation Key (56 miles from No Name), and North Key Largo (75 miles from No Name) rather well fill the gap between them. The plants on No Name Key represent the extremes of leaf shape in *D. salicifolia* on the Florida Keys. On the adjacent mainland, individuals from Cape Sable (fig. 5C, 37 miles from No Name) and Umbrella Key (fig. 5D, 45 miles from No Name) match or exceed in width the broad leaved, "aberrant" tree on No Name Key.

Table 1. SPECIMENS USED IN THE COMPARISONS OF LEAF SHAPE AND STOMATE SIZE.

<i>W. L. Stern &amp; G. K. Brizicky, 394</i> , No Name Key, Monroe County, Florida. Y. <sup>1</sup>
<i>W. L. Stern &amp; K. L. Chambers 331</i> , same individual as above. Y.
<i>W. L. Stern &amp; K. L. Chambers 332</i> , No Name Key, Monroe County, Florida. Y.
<i>W. L. Stern &amp; K. L. Chambers 258</i> , Plantation Key, Monroe County, Florida. Y.
<i>W. L. Stern &amp; G. K. Brizicky 290</i> , Big Pine Key, Monroe County, Florida. Y.
<i>W. L. Stern &amp; G. K. Brizicky 460</i> , North Key Largo, Monroe County, Florida. Y.
<i>W. L. Stern 32</i> , Key Largo, Monroe County, Florida. Y.
<i>A. H. Curtiss 1760</i> , Umbrella Key, Monroe County, Florida. YU.
<i>Gill &amp; Whitford 4</i> , eastern Cuba. Y.
<i>J. G. Jack 5675</i> , Cienfuegos, Cuba. Y.
<i>S. R. MacDonald 11</i> , Cape Sable, Monroe County, Florida. Y.
<i>J. Schiffino 94</i> , Dominican Republic. Y.
<i>C. Wright 1325</i> , Cuba. YU.

<sup>1</sup>Abbreviations for herbaria are taken from Lanjouw and Stafleu (1959).

Despite the equivocal nature of the contrasting leaf shapes found on No Name Key, there remain the clear differences in size of inflorescences and flower buds on the broad leaved and narrow leaved trees there. The number of flowers per axillary cluster in the broad leaved variant, which is in the range of 20 to 48, is not excessive for the species, *D. salicifolia*. The collection, *Stern & Chambers 258*, from Plantation Key, for example, has 8 to 24 flowers in a cluster. However, the size of the flower buds in the robust plants on Plantation Key is the same as that shown in figure 4; the remarkably large buds in figure 3 are unique to the broad leaved individual on No Name Key.

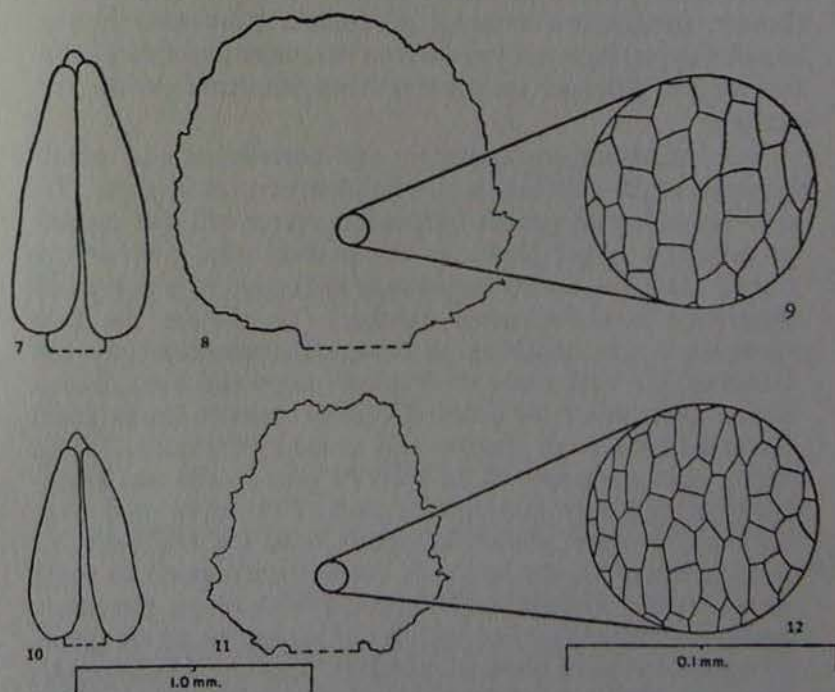


Fig. 7-12. Floral parts and cell size in two plants of *Dipholis* from No Name Key.—Fig. 7-9. *Stern & Chambers 331*.—Fig. 10-12. *Stern & Chambers 332*.—Fig. 7 and 10. Anthers.—Fig. 8 and 11. Petal lobes.—Fig. 9 and 12. Magnified views of petal epidermis.



Preserved flower buds of the collections, *Stern & Chambers 331* and *332*, were sectioned and dissected, and measurements were made of the size and thickness of the floral parts. The largest buds of *331* are 2.5 mm. long and 1.75 mm. wide; the buds of *332* at a comparable stage of development are 1.75 mm. long and 1.25 mm. wide. The sepals and petals of *331* are from one-and-one-fourth to one-and-one-third times as thick as those of *332*, and the anthers and petal lobes are one-and-one-third times as long. The cells of the petal epidermis in *331* are one-third again as wide as in *332*; a microscopic field of view of the former, for example, may show seven rows of cells where one of the latter shows nine rows. Figures 7 to 12 illustrate the differences in anther size, petal lobe size, and cell size just mentioned. Similar, though less striking, differences were seen in the ear-like appendages on the petals, characteristic of *Dipholis*, and in the petaloid staminodes that alternate with the stamens.

Two questions are raised by the correlation just noted between larger cells and larger floral structures in plant *331*, the "broad leaved variant." Does its greater cell size explain its relatively larger leaves, in comparison with the narrow leaved *332*? And are its larger cells indicative of a polyploid difference in chromosome number? To answer the first question it was necessary to compare microscopically the leaves of *331* with those of "typical" large and small leaved plants from other localities. Pieces of mature leaves from six collections were cleared and stained (Carlquist, 1957), and a random sample of 50 pairs of guard cells was examined on the lower epidermis of each. The leaves used were the same as those shown in figure 5; in the tabulation of results, figure 13, the letters at the left correspond to those in the former illustration. In figure 13 the range, the mean, and the standard error of each set of measurements are given. The guard cells of plant A, which is *Stern & Chambers 331*, are very significantly larger than those of the other samples. And the latter plants (with the exception of plant D), though differing in leaf size and in geographical distribution, have essentially the same size guard cells. Why sample

D, from Umbrella Key, varies so greatly from the others in the small size of its guard cells is not clear. However, it seems fair to deduce that plant A, from No Name Key, differs consistently from typical *D. salicifolia* in cell size, even though the shape of its leaves is not abnormal for the species. The contrast in leaf shape between plants A and B (*331* and *332* of fig. 1 and 2) may be due in part to this cellular difference; the similarity in shape between plant A and plant D (fig. 5), on the other hand, is not founded on a similarity in size of cells.

#### CYTOLOGY

Squash preparations of the preserved anthers of the two plants on No Name Key, *Stern & Chambers 331* and *332*, made in aceto-carmin stain, provided satisfactory material for examination of some of the meiotic stages. However, only a few of the largest buds were undergoing meiosis, and

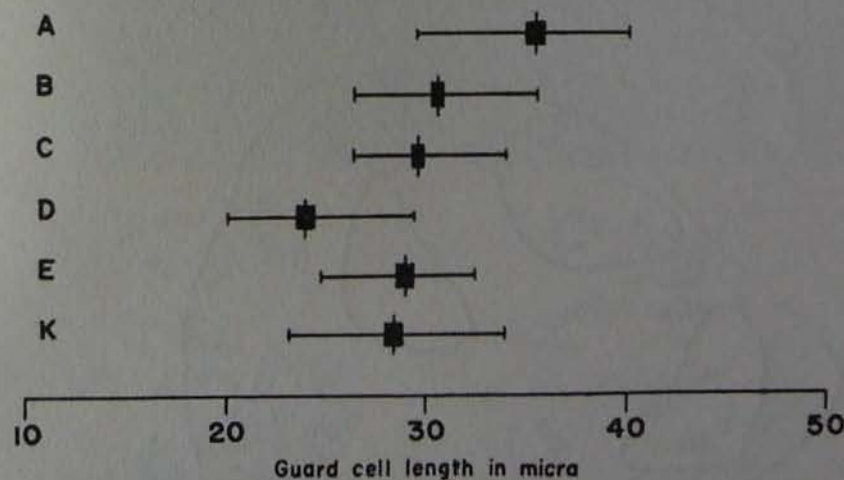


Fig. 13. Size of stomatal apparatus in the leaves of *Dipholis* from six localities. Horizontal line, the range of the measurements; vertical line, the mean; black rectangle, plus and minus one standard error of the mean. A. *Stern & Chambers 331*, No Name Key; B. *Stern & Chambers 332*, No Name Key; C. *MacDonald 11*, Cape Sable; D. *Curtiss 1760*, Umbrella Key; E. *Stern & Chambers 258*, Plantation Key; K. *Schiffino 94*, Dominican Republic.

a relatively small number of cells was available for study. In addition, perhaps because the buds had been stored in 70 per cent ethyl alcohol for several months in a refrigerator, the staining reaction of the chromosomes was relatively weak. Temporary mounts had to be set aside for several days to allow the stain to darken. Phase-contrast microscopy was unsatisfactory because of the numerous inclusions present in the cytoplasm of the sporocytes.

In the narrow leaved, "typical" *D. salicifolia* (332), the only stage seen at which it was possible to obtain a count of the number of chromosomes was second anaphase of meiosis. The haploid number was determined as  $n = 12$ . Figure 14 illustrates a cell at this stage, with the clearest of the four anaphase groups of chromosomes drawn in detail. Very many of the anthers examined had sporocytes that had not yet entered meiotic divisions; the anthers in only a few of the largest buds had completed meiosis and produced quartets of spores. In a preparation showing spore quartets there

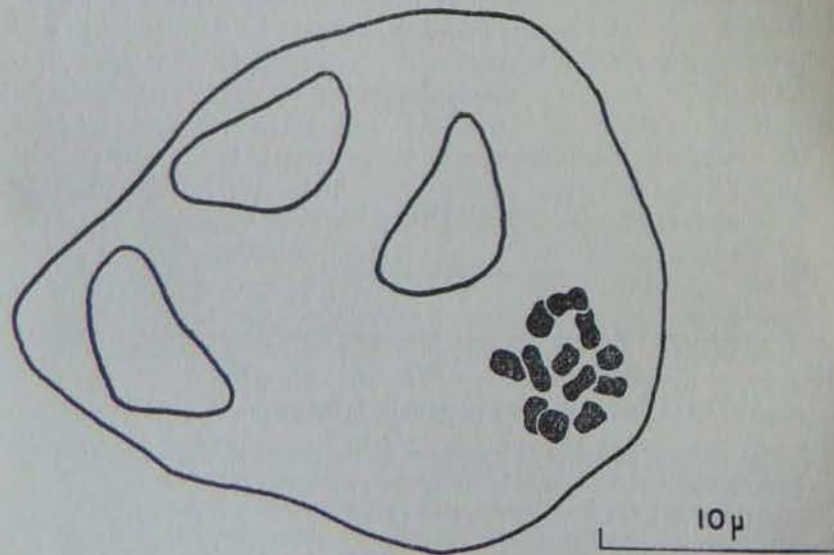


Fig. 14. Second meiotic anaphase in *Dipholis salicifolia*, Stern & Chambers 332, No Name Key.  $n = 12$ .

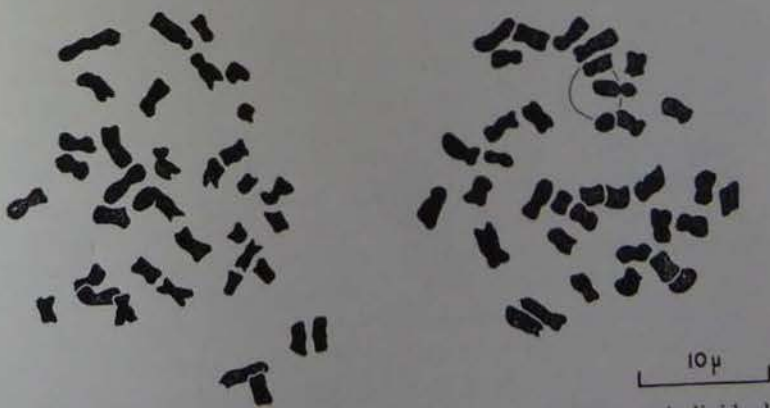
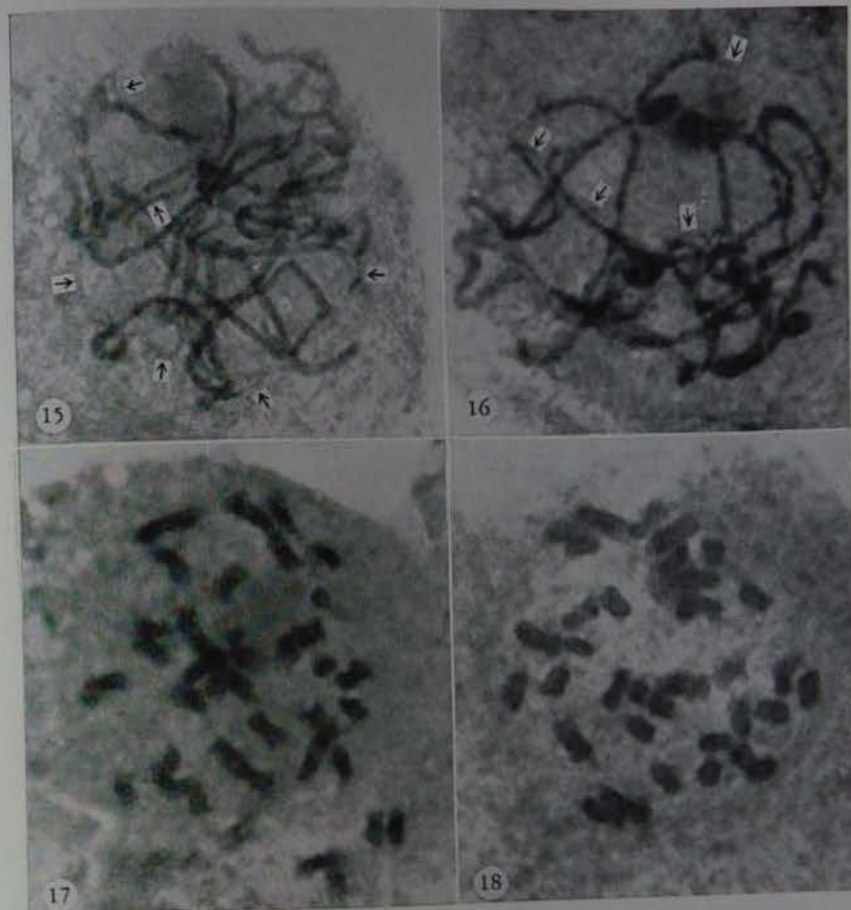


Fig. 15-18. Sporocytes and tapetal cells in the aberrant individual from No Name Key, Stern & Chambers 331.—Fig. 15. Sporocyte in pachynema, with predominantly normal chromosome pairing; arrows indicate some single, unpaired strands.—Fig. 16. Same, but with fewer unpaired strands visible.—Fig. 17. Photograph and drawing of tapetal unpaired strands.—Fig. 18. Same, in later prophase

appeared to be very little irregularity in the meiotic products. Out of 180 quartets studied, only two were abnormal, containing a tiny fifth spore. The percentage of apparently normal quartets was 98.8 per cent.

The preserved material of the broad leaved individual, *Stern & Chambers 331*, had a somewhat more satisfactory staining reaction with aceto-carmin, but in this plant also it was difficult to find many cells in the stages of meiosis intermediate between first prophase and second telophase. While studying a slide containing many sporocytes at pachynema, I noticed three large cells that seemed to be undergoing a mitotic division. Two such cells are illustrated in the photographs and drawings of figures 17 and 18. Of the numerous tapetal cells mixed with the meiocytes on the slide, close to two-thirds were binucleate and one-third were uninucleate. Despite the rarity of division figures, the dividing cells clearly did not resemble meiocytes, and the most reasonable interpretation is that they are part of the tapetum.

Binucleate tapetal cells are known for many genera of plants (Cooper, 1933), and they are usually the result of a normal or nearly normal mitotic division of the diploid nucleus in a uninucleate tapetal cell (Witkus, 1945; Brown, 1949; Nirodi, 1955). A common pattern of development is for the first tapetal division to be mitotic and the later divisions in the daughter nuclei to be endomitotic (Brown, 1949; Nirodi, 1955). The first division in a uninucleate tapetal cell may sometimes be endomitotic, however, producing a single tetraploid nucleus (Witkus, 1945). In tomato and the grass genera studied by Brown and Nirodi, above, the mitotic tapetal division occurred at the time the meiocytes were in earliest prophase, and sporogenous cells at later pachynema were accompanied by completely binucleate tapetum.

The presence of abundant binucleate tapetal cells at the time the sporocytes are in pachynema, in the *Dipholis* plant under discussion, suggests that its tapetum, like that of the genera just mentioned, first undergoes a mitotic division. The cells pictured in figures 17 and 18 would then be interpreted as diploid cells dividing to form binucleate tapetum.

They, and the uninucleate tapetal cells seen on the same slide, may have come from an anther younger than that containing binucleate tapetum and meiocytes in pachynema (two anthers were crushed on the slide). The cells do not show 24 chromosomes, the diploid number that would be assumed from the count of  $n = 12$  made on plant 332, above; rather, they can easily be interpreted as possessing 36 chromosomes, the triploid number. As none of the stages of meiosis, to be discussed below, was satisfactory for verifying this number of chromosomes exactly, these tapetal cells are the best evidence for a significant difference in chromosome number between plants 331 and 332.

It was mentioned that in some genera the first division in a uninucleate tapetal cell may be endomitotic (Witkus, 1945), rather than mitotic. The *Dipholis* tapetum shown in figures 17 and 18 does resemble in appearance nuclei in endoprophase illustrated for *Lycopersicon* (Brown, 1949) and *Coix* (Nirodi, 1955), and endomitotic uninucleate cells in *Spinacia* (Witkus, 1945). However, the essential features of endomitosis—the absence of a spindle, the falling apart of daughter chromosomes at endoanaphase, the pairs of daughter chromosomes in endotelophase—can not be determined on figures 17 and 18. Chromosomes at mitotic prophase and endoprophase in a tapetum often appear quite similar (Brown, 1949, fig. 4 and 10). It would be interesting to know more about the development of the tapetum in the Sapotaceae; however, it is not essential to the present discussion whether the cells illustrated are truly in mitotic prophase or in endoprophase. The somatic chromosome number would be displayed in either case, and the number in this instance is triploid.

An autotriploid origin for plant 331, the "broad leaved variant" under discussion, is clearly indicated by its close morphological resemblance to diploid *D. salicifolia*, the only species of *Dipholis* that occurs in the Florida Keys. Except for the greater size of its flowers, the triploid is perfectly characteristic of the species; it appears unusual only when compared with the particular narrow leaved specimens with which it was growing. The larger floral parts, more numerous flowers, and larger leaves may all be expressions of the

more robust growth and larger cell size attendant upon polyploidy.

Meiotic behavior in the triploid individual, in those stages at which it could be studied, tends to support an hypothesis of autotriploidy. Sporocytes at pachynema stage show a high degree of chromosome pairing. In figures 15 and 16, for example, the paired chromosome strands are visibly double at several places in the photograph. However, accompanying the normal pairing was the consistent presence of single, unpaired strands. Figure 15 illustrates the commonest type of cell observed in pachynema; although most of the strands are broad, double structures, many short or long unpaired segments can be seen. Some of the most obvious such single strands are marked by arrows. In those cells which at first inspection contained only double strands, it was always possible by careful study to locate single threads among the tangled chromosomes (fig. 16). Clear trivalent associations were searched for, and in three favorably spread cells configurations of three strands were seen that suggested a point of exchange in pairing partners. The existence of both paired and unpaired chromosomal segments would be expected in an autotriploid, in which each chromosome is present in triplicate yet only two chromosomes may pair at any one point.

Cells at first metaphase and first anaphase were infrequent and chromosome pairing relationships could not be ascertained. The cell pictured in figure 19 was very irregular, with stickiness, clumping, and fragmentation of chromosomes apparent. In another more normal metaphase cell, bivalents, univalents, and multivalents all seemed to be present on the spindle plate. In a cell at first anaphase, clumping prevented an exact count but the division of chromosomes was clearly unequal; the chromosome number was estimated as 12 in one anaphase group and 24 in the other. Figures 20–22 illustrate the most irregular first telophase configurations that were seen among eight cells at this stage. Micronuclei were common even in essentially normal cells (fig. 23), but chromatin bridges and fragments, as in figures 20 and 21, were infrequent.

Second telophase, or nuclear "quartet," was the most abundant stage obtained in pollen mother cells of plant 331. A careful search was made for irregularities, especially the presence of micronuclei, in 138 such cells. One or more micronuclei were found in 106, or 76.8 per cent of the cells at second telophase; 32 cells, 23.2 per cent, lacked micronuclei. Figures 27-29 illustrate cells with micronuclei, and figure 30 is an apparently normal cell with a quartet of spore nuclei. The high percentage of obviously abnormal quartets is probably a reflection of the upsets in pairing and chromosome segregation that result from triploidy. Micronuclei may form from lagging members of a multivalent at first anaphase, or from univalent chromosomes in either division that fail to move properly on the spindle. Even more extreme abnormalities in meiosis are illustrated by the telophases shown in figures 24-26. Cells with such distinct upsets—numerous and unequal nuclei, bridges, and dumb-bell-shaped nuclei—were rare, however; the three cells illustrated were the only ones seen. The telophase quartets that lacked micronuclei (fig. 30) may nevertheless contain nuclei with unbalanced and abnormal chromosome complements and may thus be inviable. Triploid plants characteristically segregate quite irregularly, and the few observations on early meiotic stages reported above would confirm this type of behavior for the individual under discussion.

Table 2. ABNORMALITIES IN MICROSPORE QUARTETS OF DIPLOID AND TRIPLOID PLANTS OF *Dipholis*, AS MEASURED BY NUMBERS OF SUPERNUMERARY SPORES.

SPECIMEN	NUMBER OF		
	SUPERNUMERARY SPORES PER QUARTET	QUARTETS OBSERVED	PER CENT OF TOTAL
<i>Stern &amp; Chambers 332</i> , $2n=24$	none	178	98.8
	1	2	1.2
	Total	180	
<i>Stern &amp; Chambers 331</i> , $2n=36$	none	219	59.2
	1	107	29.0
	2	39	10.5
	3	3	0.8
	4	2	0.5
Total	370		

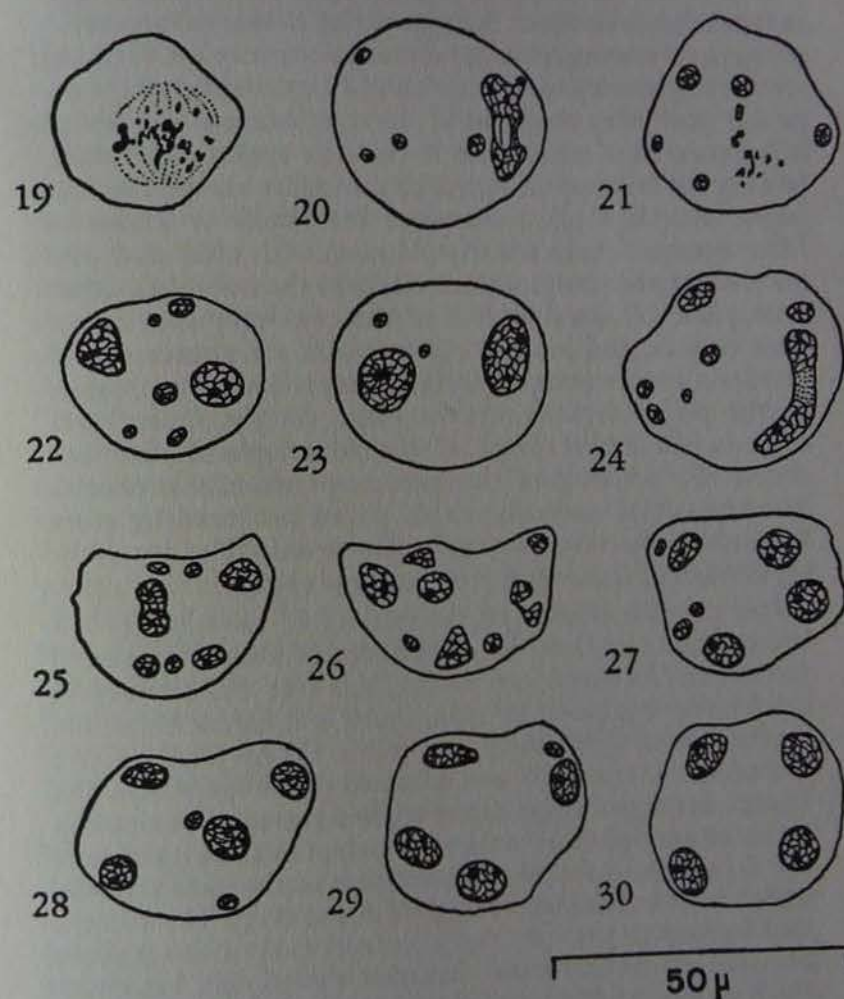


Fig. 19-30. Camera lucida drawings of meiotic stages in pollen mother cells of the triploid plant, *Stern & Chambers 331*.—Fig. 19. Irregular first metaphase.—Fig. 20-23. Abnormalities at first telophase; irregular first telophase, irregular first telophase with micronuclei.—Fig. 24-26. Extreme chromatin bridges, fragments, and micronuclei.—Fig. 27-29. Irregular second telophase; bridges and micronuclei.—Fig. 30. Apparently normal second telophase.

Cells in second telophase that contain micronuclei, as well as those that lack them, may give rise to normal-appearing quartets of microspores. A micronucleus may be included with a larger nucleus in a spore and be overlooked by the person examining the cells. If the micronucleus is enclosed in a separate cell membrane at the time spores are formed, however, it will appear as a fifth tiny spore among the four larger ones. In table 2 are given the results of studies of 370 spore quartets in the triploid plant, 331, compared with the earlier cited study of similar cells in the normal *D. salicifolia*, plant 332. In over half of the cases only four spores were present, and in only 40.8 per cent were there one or more small supernumerary spores. This is not a true measure of the pollen fertility of the plant, on the other hand, since in the earlier stage of second telophase, described above, 76.8 per cent of the quartets possessed micronuclei. The amount of normally viable pollen produced by plant 331 is probably very low, and a similar infertility would be expected in its female gametophytes and egg cells.

One possible measure of the fertility of the triploid, 331, is the number of fruits it forms under conditions of natural pollination. As mentioned earlier, this tree was sampled in the fruiting condition in 1956, under a different collection number, Stern & Brizicky 394 (table 1). An adjacent tree of normal *D. salicifolia* was collected at the same time. On 16 well developed twigs of the triploid there are 24 ripening fruits, an average of 1.5 fruits per twig. On 21 twigs of normal *D. salicifolia* found the same year at the same locality, there are 168 fruits, an average of 8 per twig. The triploid thus formed 19 per cent as much fruit as the normal. If an allowance is made for the fact that the triploid has about twice as many flowers per cluster as the diploid (fig. 3 and 4), its fertility is closer to 9.5 per cent that of the latter. And in addition, fruit set on the triploid probably depends largely on the receipt of normal pollen from nearby diploid individuals.

## DISCUSSION

The chromosome number found in *Dipholis salicifolia*,  $n = 12$ , is not an unusual one for the Sapotaceae. Darlington and Wylie (1956) report numbers of  $n = 12$  and 13 for five genera of the family. Later work, summarized by Cave (1958-1959), brings the total of known base numbers in the Sapotaceae to  $x = 10, 12, 13, 14$  and 18, most of the species being diploid. Of particular interest is the report of Brown and Clark (1940) of the diploid number,  $2n = 24$ , in *Bumelia lanuginosa* (Michx.) Pers. Cronquist, in his monograph of the two genera (1945), considers *Dipholis* and *Bumelia* to be closely related, the latter being "evidently derived from" the former. *Bumelia persimilis* Hemsl., for example, which "may be only slightly removed from the prototype of the genus," is generally similar to *D. salicifolia*. The major difference between the genera is found in the seeds, which contain endosperm in *Dipholis* but lack endosperm in *Bumelia*. The corolla, with its basally appendaged corolla lobes and petaloid staminodes, is similar in both, although four species of *Bumelia* lack lateral appendages on the corolla lobes. Baehni (1938), minimizing the difference in endosperm, united *Dipholis* with *Bumelia* taxonomically. The similar basic chromosome number in the two taxa, implied by the two counts so far reported, supports an hypothesis of close phylogenetic relationship.

The single autotriploid individual found on No Name Key, while apparently not completely sterile, showed extreme meiotic irregularities characteristic of an unbalanced chromosome condition. Although a high degree of normal pairing could be seen in pachynema, chromosome separation at first and second anaphase must have been abnormal, since micronuclei were frequently produced. Chromatin bridges and fragments occurred but were rare. The presence of bridges, fragments, lagging chromosomes and micronuclei is characteristic of many, though not all, autotriploids. Steere (1932) and Smith (1938) reported autotriploids in *Petunia* and *Impatiens* that had a low frequency of abnormalities. It may be significant that, in both genera, trivalents tended to have terminalized chiasmata at first metaphase,

forming mostly simple chains of chromosomes. In autotriploids of *Tulipa*, on the other hand, Woods (1937) described trivalents with interstitial chiasmata; from these, bridges and acentric fragments were produced at anaphase. Sixty per cent of the resulting microspores had one or more "extranuclear chromatic bodies." The products of meiosis in triploid *Dipholis* more closely resemble the example in *Tulipa*; about 77 per cent of the meiocytes at second telophase had micronuclei.

The general morphological similarity between the triploid *Dipholis* and the normal diploids occurring with it—except for the differences in leaf shape, flower size, and cell size—strongly favors an origin through autopolyploidy. All the plants on this portion of No Name Key were part of a young vegetation actively reoccupying a once disturbed locality. A triploid sapling, formed perhaps by the union of an aberrant diploid gamete with a normal haploid one, would be at little disadvantage and might be favored by its more robust growth. Its reproductive fertility is low, however, and dependent perhaps on backcrossing by pollen from its diploid neighbors.

#### SUMMARY

1. An aberrant tree of *Dipholis salicifolia* was discovered that differed in having wider leaves, larger flower clusters and larger flowers than surrounding individuals.
2. Its leaf shape was found to fall within the range of variation of the species as a whole, though the width was extreme among specimens from the Florida Keys.
3. The larger floral parts of the aberrant tree had larger cells than normal plants, and guard cells on its leaves were significantly longer than on samples from five other collections.
4. The chromosome number of normal *D. salicifolia*, determined from meiotic second anaphase, is  $n = 12$ .
5. Tapetal cells of the aberrant individual showed  $2n = 36$  at mitotic prophase. Meiosis was irregular, and micronuclei were common at first and second telophases.

Chromatin bridges and fragments were rare. Small supernumerary spores were seen in 41 per cent of microspore quartets.

6. The aberrant tree was estimated to have a fertility, as measured by fruit set, of slightly less than 10 per cent that of adjacent normal trees. Its origin through spontaneous autotriploidy is suggested.

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A NEW SPECIES OF *PARAMACHAERIUM* FROM  
PANAMA

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In 1925 Ducke (Arch. Jard. Bot. Rio de Janeiro 4: 86) created the genus *Paramachaerium* with a single species *Paramachaerium schomburgkii* (Benth.) Ducke, based on *Machaerium schomburgkii* Benth. In 1935 a second species, *Paramachaerium ormosioides* (Ducke) Ducke, segregated by Ducke from *Pterocarpus*, was added to the genus (Trop. Woods 41: 6). *P. schomburgkii* is known from British Guiana and the State of Amazonas in Brazil; *P. ormosioides* has been collected in the State of Amazonas and also in the State of Pará in Brazil. A third species of the genus can now be established due to the diligence of Mr. Fred Gruber of the United Fruit Company in Puerto Armuelles, Panama, who has presented us with complete herbarium material. Leafy twigs, flowers and fruits were collected from the same tree, but at different times. Because of his efforts, this new species is named in his honor. Sterile specimens are represented in the herbarium of the S. J. Record Memorial Collection: *Dunlap s.n.* 1948 and *Stern & Chambers 132*. Both specimens were collected in Panama, in the Province of Chiriquí and Comarca del Barú, respectively, under the same common name—"sangrillo negro." Because the structure of the associated wood samples suggested that of *Swartzia*, these sterile herbarium vouchers were tentatively identified as belonging to that genus (Trop. Woods 109: 70-71, 1958).

*Paramachaerium gruberi* Brizicky sp. nov.—Arbor inermis ca. 30-metralis trunco recto, 0.9-1.5 m. diametro, basi anteridis robustis ca. 1.8 m. longis fulto. Folia imparipinnata, 21-27 cm. longa foliolis plerumque 9-13 (14), petiolo tereti inconspicue canaliculato 2.0-2.5 cm. longo basi incrassato; stipulae non visae caducae. Foliola alterna, pergamentacea, integerrima, versus folii basim decrescentia,

4.3-13.0 cm. longa et 1.8-4.6 cm. lata, plus minusve oblonga, apicalia saepissime oblanceolata vel obovata, basalia lanceolata vel ovata, apice acuminata et aristata (arista decidua), basi rotundata vel rarius paulo cordata, supra nitidula glabra, subtus opaca pallidiora minutissime parce adpresse pilosa vel glabra (glabrescentia), penninervia nervis lateralibus utrobique 10-14 a costa angulo 50°-60° abeuntibus tenuibus paulo curvatis ante marginem anastomosantibus, venis venulisque reticulatis vix conspicuis; petioluli teretes, 0.2-0.35 cm. longi et 0.06-0.12 cm. crassi, parce pilosi; stipellae minutae subulatae interdum observatae. Spicae densiflorae, ca. 2.5-5 cm. longae (vel verisimiliter longiores) in paniculas terminales erectas dispositae, simplices, rhachibus tenuibus, ca. 0.15 cm. crassis, dense minute fulvo tomentellis, bracteis bracteolisque ad anthesim persistentibus fulvo tomentellis; bractee lanceolatae apice longe attenuatae et plus minusve incurvatae, ca. 0.4 cm. longae et 0.15 cm. latae, bracteolae paulo minores, lanceolatae vel lanceolato-oblongae, apice attenuatae. Calyx tubulato-campanulatus, in alabastro apice paulo incurvatus, ca. 0.7-0.75 cm. longus et 0.3 cm. latus, extus dense fulvo tomentellus, intus parce minute adpresse pilosus, basi obtusus, parte distali bilabiatus labio superiore emarginato lobis duos brevibus oblique lato triangularibus apiculatis ca. 0.1 cm. longis et basi 0.15 cm. latis, labio inferiore trisecto segmentibus subaequalibus ovatis vel triangulari-ovatis apiculatis, ca. 0.23-0.26 cm. longis et 0.14-0.18 cm. latis. Corolla violacea glaberrima; vexillum late unguiculatum ungue 0.35 cm. longo et apice 0.25 cm., basi 0.1 cm. lato, lamina rhomboideo-oblata, 0.65 cm. longa et 1.0 cm. lata, undulata, apice emarginata, mediano canaliculata; alae lamina irregulariter suborbicularis ca. 0.5 cm. longa et 0.25 cm. lata basi inaequali tenuiter unguiculata ungue 0.3 cm. longo; carinae petala dorso breviter connata lamina subobovato-falcata, ca. 0.5 cm. longa et 0.25 cm. lata, basi inaequali tenuiter unguiculata ungue 0.3 cm. longo. Stamina monadelphica, 0.7 cm. longa, tubo 0.45 cm. longo, antheris versatilibus, suborbicularibus ca. 0.05 cm. longis. Discus nectariferus interstaminalis minutus annuliformis. Ovarium minute stipitatum stipite 0.05 cm.



longo, paulo lateraliter compressum, lanceolato-oblongum, dense adpresse fulvo pilosum, ca. 0.45 cm. longum; stylus glaber, 0.3 cm. longus; stigma parvum capitellatum; ovula 4-5 pendula, campylotropa, subtransversalia. Legumen sessile, valde lateraliter compressum, alatum; ala terminalis, pergamentacea, cultriformis, apice rotundata, 7.0-8.7 cm. longa et prope basim 3.8-4.5 cm. lata, margine superiore recto vel basi plus minusve curvato stylo terminali apiculato, margine inferiore valde arcuato, nervis ad marginem superiorem longitudinalibus marginem inferiorem versus transversaliter reticulatis; pars seminifera plus minusve incrassata, reticulata, oblique obovata vel suborbicularis, 3.0-4.4 cm. longa et 2.2-4.0 cm. lata, dura, sublignosa; semina plerumque 4 observata, verisimiliter 1-2 omnino evoluta maturescentia, septis transversalibus crassis lignosis separata, lateraliter compressa, lanceolato-oblonga, ca. 2 cm. longa et prope basim 0.6 cm. lata, apice rotundata, basi oblique rotundata et unilateraliter rostellata, atro-fusca, laevia, glabra; cotyledones fere planae, crassiusculae, lanceolato-oblongae, apice rotundatae, radícula incurvata.

Species *Paramachaerii* speciebus duabus Brasiliensibus valde affinis sed ab eis foliis plerumque 9-13-foliolatis, disco interstaminali minuto annuliformi et leguminibus verisimiliter majoribus differt.

PANAMA: COMARCA DEL BARÚ, area west of Puerto Armuelles, *F. Gruber s. n.* (HOLOTYPUS US, fig. 2; ISOTYPI GH, MO, NY, Y), *Stern & Chambers 132* (MO, US, Y, fig. 1); Provincia de Chiriquí, *Dunlap s. n.* spring 1948 (Y).

A tree about 30 m. high, *P. gruberi* has a straight trunk 0.9-1.5 m. in diameter with strong buttresses about 1.8 m. high; the inner bark exudes a blood-red sap when cut. Leaves alternate, imparipinnate with mostly 9-13 (14) leaflets, which decrease in size toward the base of leaf rachis; petiole 2-2.5 cm. long, incrassate at base; stipules caducous, not seen. Leaflets shortly petiolulate, basically oblong in shape, but the terminal mostly oblanceolate to obovate, and the basal lanceolate to ovate, 4.3-13 cm. long, 1.8-4.6 cm.

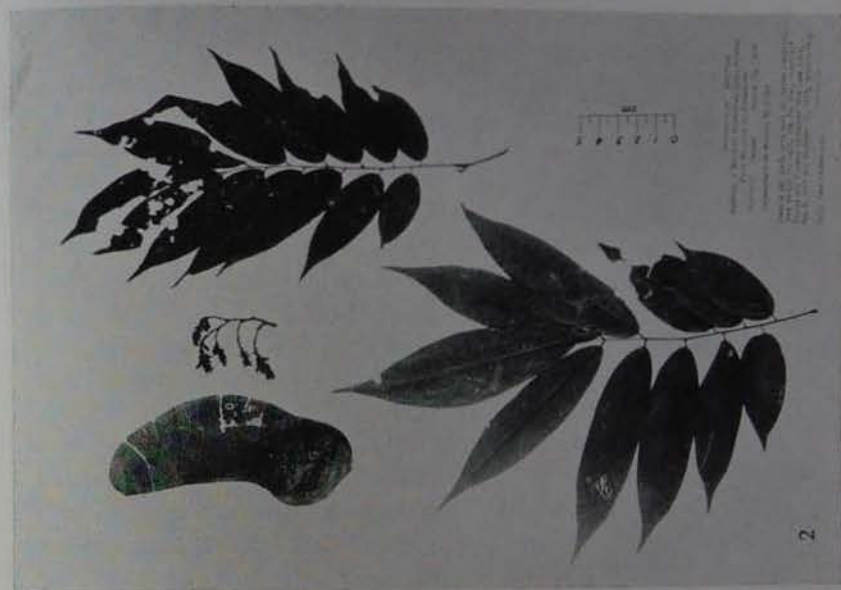


Fig. 1-3.—Fig. 1. *Paramachaerium gruberi* Brizicky, Stern & Chambers 132. Paratype Y.—  
Fig. 2. *P. gruberi* Brizicky, Type US.

broad, tip acuminate and aristate, base rounded or rarely slightly cordate, glabrous above, paler and minutely appressed pilose or glabrous beneath; texture pergamentaceous. Flowers crowded on fairly slender, brownish tomentulose spikes 2.5-5 cm. long arranged in short terminal panicles. Bracts and bractlets (at least in part persistent during blossoming) brownish tomentulose, the former lanceolate, 0.4 cm. long, the latter slightly shorter, lanceolate or lanceolate-oblong. Calyx tubular-campanulate, in bud slightly incurved at apex, 0.7-0.75 cm. long and 0.3 cm. thick, brownish tomentulose outside, sparsely minutely appressed-pilose inside, obtuse at base, bilabiate in the distal half, the upper lip emarginate with short oblique, apiculate lobes, the lower lip 3-parted with ovate or triangular-ovate apiculate segments, 0.23-0.26 cm. long and 0.14-0.18 cm. broad. Corolla dark-violet, glabrous; the standard clawed, about 1 cm. long, with a rhomboidal-oblate, undulate and emarginate lamina and broad-cuneate claw; wings and carinal petals somewhat shorter than the standard, fairly broad with slender claws; nectariferous interstaminal disk minute, annuliform; stamens monadelphous, connate for about two-thirds of their length; ovary minutely stipitate, somewhat laterally compressed, lanceolate-oblong, densely appressed-pilose, style glabrous, stigma terminal, capitellate; ovules 4-5, pendulous, campylotropous, almost transverse. Legume sessile, strongly laterally compressed, winged; wing terminal, pergamentaceous, cultriform, 7.0-8.7 cm. long and 3.8-4.5 cm. broad at the widest point near the base, rounded at apex, ventral margin straight or sometimes curved at the base, crowned by apiculate style remnant, dorsal margin curved; seminiferous portion incrassate, reticulate, obliquely obovate or subcircular in outline, 3.0-4.4 cm. long, 2.2-4.0 broad, hard, more or less woody; seeds blackish-brown, smooth and glabrous, 4-5 (apparently only 1-2 fully developed), separated by lignose septa, laterally compressed, lanceolate-oblong, ca. 2 cm. long and 0.6 cm. broad at base, apex rounded, base obliquely rounded and unilaterally beaked; cotyledons almost flat, thickish, lanceolate-oblong, rounded at apex; radicle incurved.

The new species differs from *Paramachaerium schomburgkii* and *P. ormosioides* in its usually 9–13-foliolate leaves, a minute annular interstaminal disk and larger legumes. (It is not known if the fruits available of the above two species are mature.) According to Ducke (Trop. Woods 41: 6. 1935) the leaves of *P. schomburgkii* and *P. ormosioides* have 3–5 leaflets, subopposite in the former and alternate in the latter species. Ducke did not mention the presence of an interstaminal disk in either of the two Brazilian species. Both, however, possess a conspicuous tubular-cupuliform hypogynous disk around the base of the ovary.<sup>1</sup> Legumes of *P. schomburgkii* have very short wings, the wings on fruits in *P. ormosioides* appear to be only half as long as those in *P. gruberi* (Arch. Jard. Bot. Rio de Janeiro 4: pl. 13, fig. 33. 1925, as *Pterocarpus ormosioides*).

Leaflet shape in *P. gruberi* varies to some degree. Although the type collection is represented by narrow-oblong leaflets, those in the paratypes are broadly oblong to lanceolate- or ovate-oblong. The leaflets of *Stern & Chambers 132* are very similar to those of the Brazilian species of *Paramachaerium*. However, it is probable that all the above-mentioned types of leaflets can be found on the same tree. In some leaves of the type collection the distal interjugum of the rachis is reduced to such a degree that the apical part of these leaves creates the impression of a truly paripinnate leaf. The length of the distal interjugum varies from 0.05–1.0 cm. in the type collection and from 0.4–1.3 cm. in the paratypes.

In some characters, as for example the more or less bilabiate calyces which are apically curved in bud, the ovaries with 4–5 almost transverse ovules, legumes with 4–5 seeds and in the shape of seeds, *Paramachaerium* seems to be fairly close to *Pterocarpus*. The obtuse base of the calyces, the presence of an interstaminal disk and the general appearance

<sup>1</sup>The writer extends his thanks to Dr. Richard S. Cowan of the U. S. National Herbarium for kindly arranging to loan herbarium specimens of *Paramachaerium schomburgkii* and *P. ormosioides* for study.

of the terminally winged legumes might also suggest relationship with *Machaerium*. Although at present any conclusions regarding the relationships of *Paramachaerium* within the tribe Dalbergieae are not possible, it is quite evident that the generic status of Ducke's genus is well-founded.

Whether the great geographic disjunction between our species and the two Brazilian species of *Paramachaerium* exists in fact, must await the results of further exploration in the intervening areas.

#### THE WOOD

(W. L. Stern)

The wood of *Paramachaerium gruberi* is almost identical in anatomical structure to that of *P. schomburgkii* as described by Record in *Tropical Woods* (41: 7. 1935). The brief anatomical description below is based on wood samples accompanying *Stern & Chambers 132*, *Dunlap s. n.* 1948 and two commercial test samples supplied by the Canal Zone Corrosion Laboratory numbered 84A and 84C.

Pores are barely visible to the unaided eye, solitary and in short radial multiples. Vessel elements possess simple perforation plates in the transverse or almost transverse end walls; intervacular pitting is alternate. Axial parenchyma is invisible to the naked eye, and occurs in two dispositions: aliform with narrow extensions and as narrow apotracheal bands; strands of crystalliferous cells are common. Vascular rays are all uniseriate, homocellular (cells procumbent), and usually 7–10 cells high. Imperforate tracheary elements show very minute bordered pits with greatly extended and crossed pit apertures. All elements are regularly storied.

Although the specimen of *P. schomburgkii* on hand (Yw; *Ducke 217*, Y) shows no apparent heartwood, and Ducke has stated that the wood of *P. ormosioides* is white throughout (Arch. Jard. Bot. Rio de Janeiro 3: 155. 1922), wood of *P. gruberi* is marked by a distinct, chocolate-colored heartwood surrounded by a layer of buff-colored sapwood 7 cm. wide in our material. Our specimen of *P. schomburgkii* is rather nondescript, but material of *P. gruberi*

exhibits pronounced striping due to the interlocked grain. The wood of our species is highly lustrous and of fine texture. Ducke (*Trop. Woods* 41: 6. 1935) mentions the wood of *P. schomburgkii* as valueless, and Record and Hess (*Timb. New World* 301. 1943) state that the trees are of small to medium size and exhibit poor form. Our species, however, may be valuable since individual trees are of large size and good form. Furthermore, preliminary results of tests still underway in Panama indicate that the wood shows a high natural resistance to the action of boring organisms in both fresh and salt water environments.

## WOOD ANATOMY OF CICHORIEAE (COMPOSITAE)

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### INTRODUCTION

The tribe Cichorieae is distinctive among Compositae in possessing a high proportion of herbaceous genera, with very few that could be termed woody at all. The woody members of the tribe take on a special significance both because of the localities in which they occur and because of the current controversy over their mode of origin. Either the woody Cichorieae represent vestiges of ancestrally woody Cichorieae, or they represent instances in which herbs have increased production of secondary xylem. The reader must keep in mind that these hypotheses bear no relation to the primitive condition for Compositae as a whole. From the writer's various studies in Compositae, a primitively woody condition for the family as a whole seems more in accord with known observations than does an herbaceous ancestry. Nevertheless, certain groups of Compositae could have evolved from woody to herbaceous, and these herbs could have secondarily acquired increased production of secondary xylem.

Skottsberg (personal communication) believes that the woody Cichorieae of the Juan Fernandez Islands are best interpreted as vestiges of now-extinct mainland woody ancestors. His reasons for this belief seem to stem largely from phytogeographical considerations. This ancestry has been questioned by Stebbins (personal communication), who claims that the Juan Fernandez Cichorieae are best designated, in fact, as herbs. The Juan Fernandez Cichorieae seem relatively advanced in terms of gross morphology

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(Stebbins, 1953), pollen structure (Erdtman, 1952), chromosome number (Stebbins, Jenkins, and Walters, 1953), and floral anatomy. The most primitive floral anatomy described for the tribe occurs in the herbaceous Asiatic genera *Dubyaea* and *Sorosaris* (Stebbins, 1940). The writer, on the basis of independent study in other tribes (1957b, 1957c) arrived at the same general concepts as Stebbins in regard to primitive features of floral anatomy in Compositae.

With respect to Cichorieae at large, the hypothesis that woody Cichorieae are secondarily woody at least in part might be more satisfying because: (1) woody Cichorieae on islands possess many characteristics of herbs (succulence, large pith and cortical regions); (2) woodiness is not present in the genera now regarded as primitive for the tribe, but rather in various relatively advanced genera which are not taxonomically close to each other; (3) woodiness, even in a single genus, is quite different in different species (e.g., *Stephanomeria guadalupensis* acquires secondary xylem in a mode entirely different from that of *S. virgata*); and (4) woody Cichorieae on islands resemble herbs which have been able to continue growth by virtue of release from marked annual cycles in moisture, temperature, or day-length. Nevertheless, the writer does not feel that any interpretation of the mode, or modes, of origin of woody Cichorieae has as yet been supported by decisive evidence. Characteristics of wood anatomy may, however, be examined with regard to this question, and the present paper may be considered a contribution toward resolution of such questions. In addition, wood anatomy of Cichorieae offers a number of features which are of importance to the taxonomic system.

Fourteen species of Cichorieae have been studied here. Additional species of continental herbs, such as several more species of *Lactuca*, could have been included, but the present materials encompass all the "woody" genera of Cichorieae and probably give a representative picture of the gamut of wood characters to be found in the tribe.

Examples of herbs in the present study are species basically annual which, by virtue of a long growing season, may

acquire a woody base. Such species include *Lactuca Serriola*, *Stephanomeria exigua*, and *S. virgata*. *Stephanomeria virgata*, for example, is ideally adapted to the long growing season of southern California, because it germinates and forms a leafy rosette during the winter months, then, as moisture becomes less available, forms a tall (up to 10 feet) inflorescence stem before dying, usually in September.

The two perennial species of *Malacothrix* studied here are distinctive in their maritime habit. *Malacothrix Blairii* is endemic to San Clemente Island, California, whereas *M. saxatilis* occurs on maritime bluffs of southern California and on the southern California islands (Williams, 1957). Most species of *Malacothrix* are annuals, and the perennial habit of the two species may be related to the relatively even maritime climate which they enjoy. The same principle may account for the perennial habit of *Stephanomeria guadalupensis*, an endemic of Guadalupe Island, Mexico. This species possesses a very woody base which annually innovates shoots which terminate in inflorescences.

For whatever reason, predominantly herbaceous families of dicots often include woody insular representatives. This phenomenon is clearly illustrated by the tribe Cichorieae. For example, the Juan Fernandez Cichorieae, represented by *Dendrosaris* and its segregates *Phoenicosaris*, *Rea*, and *Hesperoseris*, are rosette-trees or rosette-shrubs. For taxonomic descriptions and illustrations of these remarkable genera, the reader is referred to the studies of Skottsberg (1922, 1928, 1951, 1953). Information concerning distribution and ecology of the Juan Fernandez Cichorieae is also offered by Kunkel (1957a, 1957b). Although these species may develop a xylem cylinder up to an inch or more in thickness in some instances, they are characterized by relatively wide cortical and pith regions.

The genus *Thamnosaris*, with two species, grows on the low, dry, and thoroughly desolate Desventuradas Islands, located west of northern Chile. *Thamnosaris* is a succulent subshrub, much like *Malacothrix Blairii* (which grows in similar habitats) in habit. For illustrations, taxonomic dis-

cussions, and ecological information, the reader is referred to the works of Skottsberg (1937, 1947) and Johnston (1935).

*Sonchus* is represented by several species (section *Dendrosonchus*) on the Canary Islands. These subshrubs are similar to *Thamnoseris* or *Malacothrix Blairii* in habit, and this habit again may be related to the dry, temperate to subtropical climate of the Canary Islands. For illustrations and phytogeographical discussions, the work of Schenck (1907) on the *Dendrosonchus* species may be consulted. These species are represented in the present investigation by *S. leptocephalus*.

Finally, note should be taken of a group of oriental insular representatives of Cichorieae, the subgenus *Crepidiastrum* of *Ixeris* (Stebbins, 1937), which is not represented in this study. Species of *Crepidiastrum* are notably woodier than other species of *Ixeris*.

Although the Cichorieae are, at least in many genera, well known taxonomically, just as they are cytologically (Stebbins, Jenkins, and Walters, 1953), anatomical studies are relatively few. In addition to this study of wood anatomy in the tribe, the writer is undertaking anatomical studies of other portions of insular Cichorieae to aid in elucidating the problems outlined above. Because wood anatomy represents only one element of such investigation, few conclusions concerning evolutionary and systematic problems can be reached in the present study.

#### MATERIALS AND ACKNOWLEDGMENTS

Because woody Cichorieae occur in such remote localities, the cooperation of a number of individuals was necessary before sufficient material for this study could be accumulated. The writer wishes especially to acknowledge Dr. Carl Skottsberg for sending samples which he and his party collected in the Juan Fernandez Islands in 1955. Wood samples from Dr. Skottsberg's 1917 expedition, located in the Samuel J. Record Memorial Collection at Yale, were made available through the courtesy of Dr. William L. Stern. Thanks are extended to Dr. Reid Moran, of the San Diego Natural His-

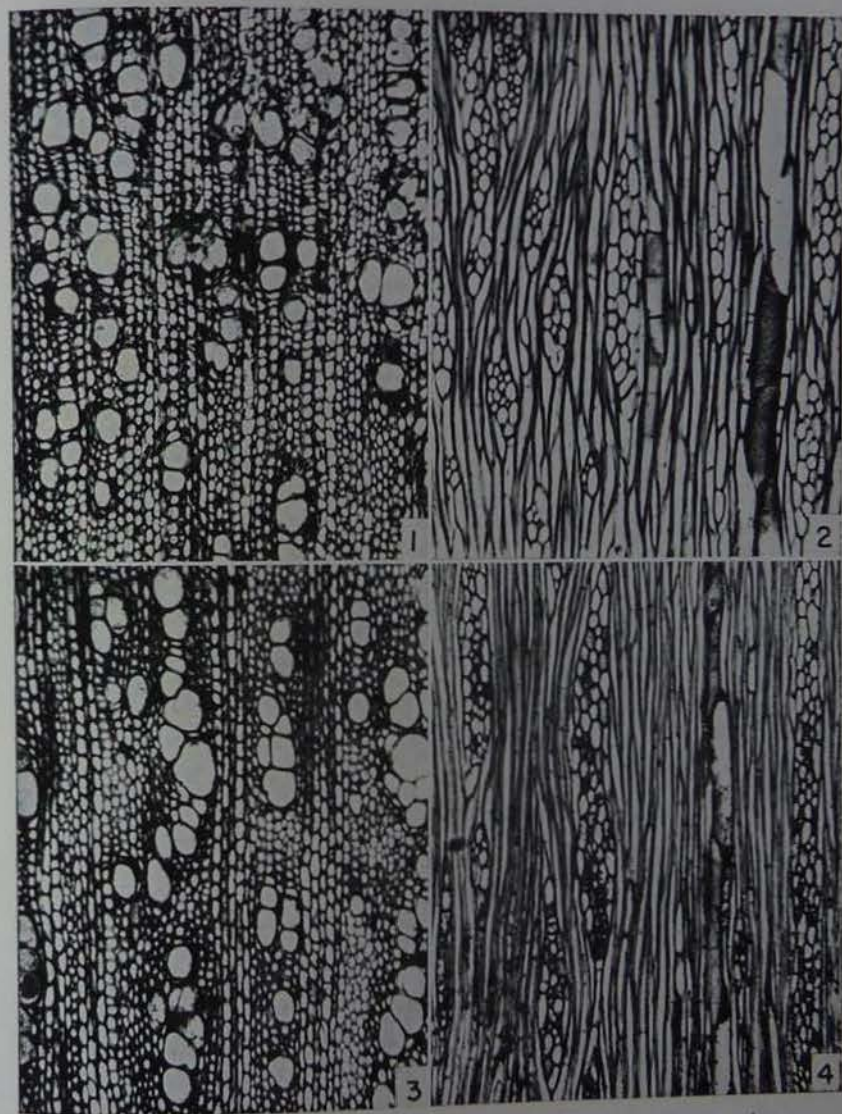


Fig. 1-4.—Fig. 1-2. *Dendroseris litoralis*.—Fig. 1. Transection.—Fig. 2. Tangential section.—Fig. 3-4. *Dendroseris macrophylla* (Yw-27420).—Fig. 3. Transection.—Fig. 4. Tangential section. All,  $\times 65$ .

tory Museum, and to the Scripps Institute of Oceanography, for enabling the writer to visit Guadalupe Island in 1958. Gratitude is expressed to Dr. Roxana S. Ferris of the Dudley Herbarium, Stanford, and to Dr. David D. Keck, formerly of the New York Botanical Garden, for wood samples from herbarium specimens in those institutions, respectively. Dr. William L. Stern and Dr. Carl Skottsberg read the manuscript and offered helpful suggestions. Finally, thanks are due Mr. Alfred G. Diboll for his services in sectioning many of the woods used in this study. Herbarium specimens documenting wood samples, or specimens from which wood samples were taken, are listed in table 1. Herbarium abbreviations are according to Lanjouw and Stafleu (1959). Taxonomic treatment of species collected in California follows that of Munz (1959). Names of the Juan Fernandez Cichorieae are according to Skottsberg (1951).

#### METHODS

Wood samples collected by the writer were fixed in formalin-acetic-alcohol. All other wood samples were dried. For both types of samples the typical methods, described earlier by the writer (1958) were used. In the photographs of wood transections, more recently formed xylem is toward the top of the illustrations.

Table 1. WOOD CHARACTERS IN CICHORIEAE

SPECIES	COLLECTION
<i>Dendroseris litoralis</i> Skottsb.	Skottsberg 20-XII-1954 (SBT)
<i>D. macrophylla</i> D. Don	Kunkel II-1955 (SBT)
<i>D. macrophylla</i> D. Don	Skottsberg, 1917 (NY) (Yw-27420)
<i>Lactuca Serriola</i> L.	Carlquist 617 (RSA)
<i>Malacothrix Blairii</i> (Munz & Jtn.) Munz	Blair, 1923 (Type, POM)
<i>M. saxatilis</i> (Nutt.) T. & G.	Carlquist 496 (RSA)
<i>Phoenicoseris Berteriana</i> (Dcne.) Skottsb.	Sparre 5-III-1955 (SBT)
<i>P. pinnata</i> (Bert. ex Dcne.) Skottsb.	Skottsberg, 1917 (NY) (Yw-27423)
<i>P. regia</i> (Skottsb.) Skottsb.	Skottsberg, 1917 (NY) (Yw-27424)
<i>Rea micrantha</i> Bert. & Dcne.	Skottsberg, 1955 (SBT)
<i>R. micrantha</i> Bert. & Dcne.	Skottsberg, 1917 (NY) (Yw-27421)
<i>Sonchus leptocephalus</i> Cass.	Kuntze 6-I-1888 (NY)
<i>Stephanomeria exigua</i> Nutt.	Munz & Johnston 11258 (POM)
<i>S. guadalupensis</i> Brandegees	Carlquist 457 (RSA)
<i>S. virgata</i> Benth.	Carlquist 616 (RSA)
<i>Thamnosseris lobata</i> Jtn.	Willis 1 (Type, DS)

Table 1. WOOD CHARACTERS IN CICHORIEAE

	DIAMETER WIDEST VESSEL, $\mu$	DIAMETER VESSELS, AVERAGE, $\mu$	VESSELS PER GROUP, AVERAGE	LENGTH VESSEL ELEMENTS, AVERAGE, $\mu$	LENGTH LIBRIFORM FIBERS, AVERAGE, $\mu$	MAXIMUM WIDTH LIBRIFORM FIBERS, AVERAGE, $\mu$	WALL THICKNESS LIBRIFORM FIBERS, RANGE, $\mu$	ELEMENTS DISTINGUISHING RINGS	STORIED ELEMENTS	HEIGHT MULTISERiate RAYS, AVERAGE, IIIII.	HEIGHT UNISERiate RAYS, AVERAGE, $\mu$	RAY CELLS ISODIAMETRIC TO PROCUMBENT	RAY CELLS ISODIAMETRIC TO ERECT
	93	58	2.62	195	377	26.6	2-4	ap		.59	126	+	+
	156	64	1.52	247	373	19.4	1-3			.64	139	+	+
	104	58	2.67	281	390	22.4	1-3			1.06	152	+	+
	93	45	5.13	182	282	18.2	2-3			.61	109	+	
	65	44	2.60	172	416	19.5	3-5	ap,nv, vt	ap,nv, vt	.41	116		+
	104	60	2.03	195	364	26.1	2-3			.58	91	-	+
	104	57	1.42	303	435	23.8	1-3			.70	72		+
	169	79	2.24	338	357	27.5	3-6	wv	ff	.63	85	+	+
	104	69	2.76	259	341	29.5	2-3	nv,vt	ff	1.15	65	+	-
	97	55	2.00	192	346	25.2	2-5			.54	81	+	+
	130	74	1.66	227	343	29.1	1-5	tf	ff	.37	68	+	+
	68	40	1.68	218	204	26.2	2-3	mv,sf	f,vp,v	.83	81	+	+
	66	44	3.00	266	391	24.8	1-3			.46	117	+	+
	104	58	1.86	192	429	29.1	3-5	ap,nv		.41	142	-	+
	91	43	3.30	244	402	23.3	2-3			.44	124	+	+
	91	57	2.58	204	312	33.3	3-6	ap		1.79			+



## ANATOMICAL DESCRIPTIONS

Table 1 contains a summary of characters considered to be significant in comparing species of Cichorieae with each other and with other Compositae. Characteristics which are not easily summarized in chart form, or which occur in a limited number of species, are discussed under appropriate headings below.

## Explanation of symbols in table 1:

- ap = apotracheal parenchyma  
 f = fibers  
 ff = a few, or some, fibers  
 mv = more numerous vessels  
 nv = narrow vessels  
 sf = short fibers  
 tf = thin-walled fibers  
 v = vessel elements  
 vp = vasicentric parenchyma  
 vt = vascular tracheids  
 wv = wide vessels  
 + = presence of characteristic  
 - = presence of characteristic to a limited extent

blank space = absence of characteristic

## VESSELS

*Dimensions, shapes, types.*—Columns 1, 3, and 4 of table 1 give dimensions of vessel elements in woods of Cichorieae. Although species where more than one collection was studied (*Dendroseris macrophylla*, *Rea micrantha*) show that figures for these dimensions are by no means constant, there are some good differences among the taxa. The species which occur in California all have vessels the average diameter of which is  $45\mu$  or less. *Sonchus leptcephalus*, with similarly narrow vessel elements (fig. 17), grows in a similar warm, dry, climate. These species with narrow vessels also have relatively short vessel elements (fig. 15, 18, 20). Notably long vessel elements occur in the close pair of species *Phoebocoseris pinnata* and *P. Berteriana*. This fact may be significant in relation to the tall, single-stemmed, rosette-

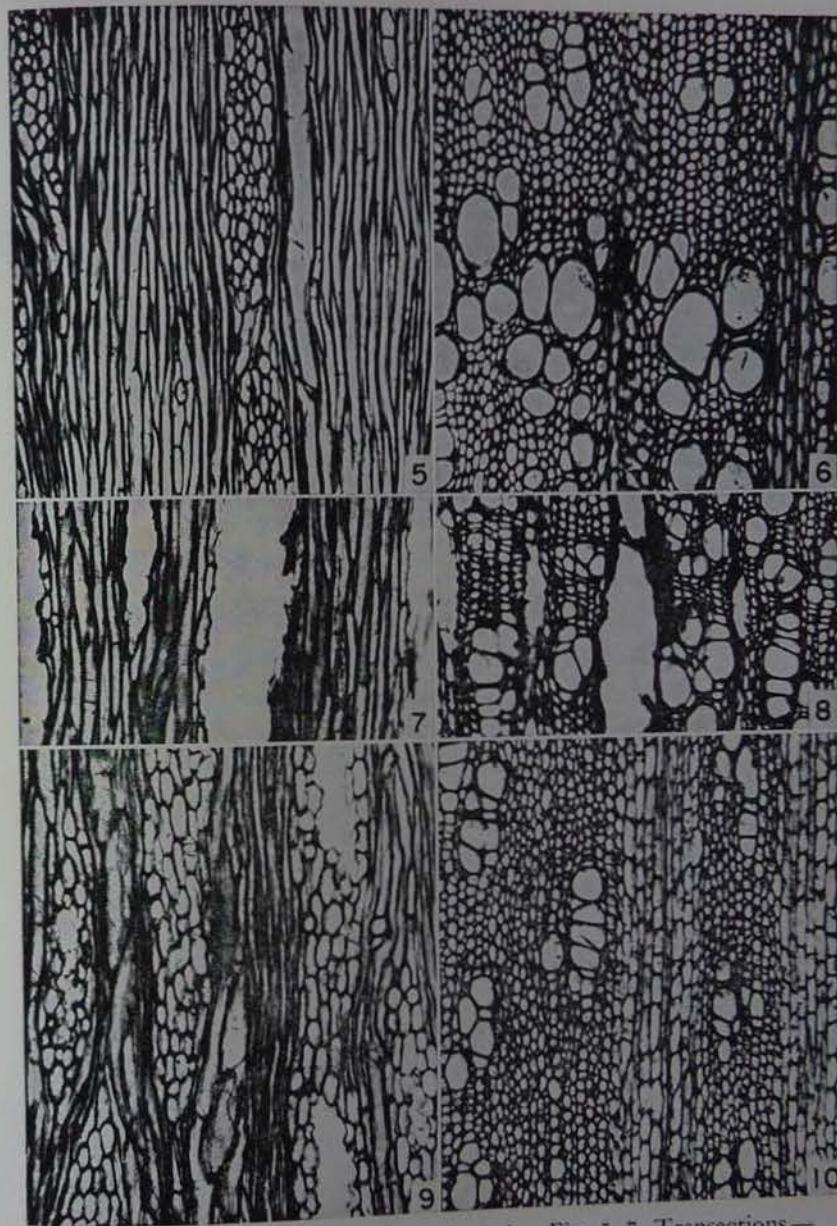


Fig. 5-10.—Fig. 5-8. *Phoebocoseris regia*.—Fig. 5, 7, Transverse sections.—Fig. 6, 8, Tangential sections.—Fig. 5-6 show xylem between specialized bands; fig. 7-8 show bands composed largely of narrow vessels and vascular tracheids.—Fig. 9-10. *Phoebocoseris pinnata*.—Fig. 9, Transverse section.—Fig. 10, Tangential section.—Fig. 5-8,  $\times 65$ ; Fig. 9-10,  $\times 70$ .

tree form of these species. *Phoenicoseris regia*, which has shorter vessel elements, develops a shorter stem. Some variations in vessel-element dimensions may be attributed to relative maturity of wood samples. In the stem of *Stephanomeria virgata* studied, vessels become narrower in later-formed wood (possibly in response to decreasing moisture). The last-formed xylem in the stem of *Malacothrix Blairii* studied contained narrow vessels, some of which, by virtue of their imperforate nature, are vascular tracheids. Such a ring of vascular tracheids may be related to the closing of a season's growth, as seemed to be the case in an annual composite, *Blepharizonia plumosa* (Carlquist, 1958). In *Thammoseris lobata*, on the contrary, wider vessels appear to be formed in the outer portions of a stem.

Markedly caudate vessel elements were observed in *Stephanomeria exigua*. Some tendency toward caudate vessel elements was seen in *S. virgata* and *Thammoseris lobata*.

*Lateral wall pitting*.—Typical alternate bordered pits, circular in outline, were observed in wood of the annual or near-annual species *Lactuca Serriola*, *Stephanomeria exigua*, and *S. virgata*. All the other Cichorieae studied differed to various degrees from this pattern. Although alternate circular bordered pits may be presumed to be basic to the group, all other species possessed at least some pits which were elliptical (elongate tangentially) in outline (fig. 23, 25, 31). Transitions between pits of this shape and decidedly scalariform pits were not infrequent in these species. Three species, *Dendroseris litoralis*, *Phoenicoseris regia*, and *Sonchus leptcephalus*, possessed more scalariform than elliptical pits in vessels. Such pitting is illustrated for *Phoenicoseris regia* in figure 27.

The writer believes that the possession of this type of pitting is of considerable significance. It has been reported in other genera of Compositae, such as the mutisoids *Chimantaea mirabilis*, *Quelchia*  $\times$  *grandiflora*, and *Wunderlichia mirabilis*, as well as a number of Heliantheae, such as *Coreopsis gigantea* and three species of *Espeletia* (Carlquist, 1957a, 1958). The curious fact about all the species mentioned, as well as all the Cichorieae which have abundant

scalariform pitting, is that these species have a growth form which could be termed "rosette tree" or "megaphyte." The writer (1958) has interpreted the occurrence of such pitting in secondary xylem as perhaps being indicative of retention of metaxylem pitting patterns throughout the life of the plant. This may appear to the reader to be merely a form of words, but there can be no doubt, with evidence from three tribes of Compositae, that there is some correlation between growth form and pitting type. Such a correlation might be usable—when more is known about wood anatomy of rosette trees—as a possible indication of derivation from herbaceous ancestry rather than woody. Such pitting, however, should not yet be regarded as the sole criterion for such an evolutionary history in certain groups of Compositae, but it should not be overlooked as having such a possible significance.

Spiral bands or grooves are notably absent in vessels of Cichorieae. The only instance in which this phenomenon was observed to any degree was *Malacothrix saxatilis*. In this species, narrow short grooves extend on either side of apertures in areas where pits are relatively sparse.

*Perforation plates.*—Simple circular or slightly elliptical perforation plates are characteristic of the vast majority of Compositae. There are occasional reports of multiperforate plates in Compositae. A resumé of such occurrences has been given by the writer (46-47, 1957b) and additional instances may be found in subsequent papers (Carlquist, 1958, 1959b). The Cichorieae studied here exhibit a wide variety of such multiperforate plates. However, only the Juan Fernandez species exhibited these plates with any degree of abundance. Plates of *Phoenicoseris Berteriana* (fig. 23-26) show a number of thin bars. In smaller plates, the arrangement of these bars is transverse with relation to the stem, although larger plates (fig. 24, 25) may have bars arranged vertically. If numerous bars are present, many of them are forked. Anastomoses of the bars may be present, so that, as in figure 24, a "fingerprint"-like arrangement is often achieved. In *Phoenicoseris regia* (fig. 28-31), on the contrary, multiperforate plates most frequently give the appearance of round-

ed perforations separated by wider bands of wall material (fig. 29-31). Another interesting phenomenon in this species is the marked elongation of pits surrounding the perforation plate, so that the margin of the plate may appear as an isolated ring (fig. 28). Perforation plates like those illustrated for *Phoenicoseris Berteriana* were observed in small numbers in *P. pinnata* and both collections of *Rea micrantha*. In Cichorieae studied other than the Juan Fernandez species, multiperforate plates were found to be quite uncomplicated and very infrequent. In *Lactuca Serriola*, a single one-bar plate was observed, and in *Stephanomeria virgata*, one two-bar plate was seen. Thus, although multiperforate plates—which are apparently present in only a fraction of the vessels in any wood section of Compositae—cannot definitely be said to be absent in any of the species not mentioned, they are far more abundant in woods of the Juan Fernandez Cichorieae. Interestingly, Sanio (1863) has figured a variety of perforation plates for *Hieracium vulgatum* (Cichorieae), including both the type shown for *Phoenicoseris Berteriana* and that of *P. regia*. Thus there may be no significance in the fact that divergent types were found in the two species.

One fact which does appear to be of some significance—at least morphogenetically—is that in *Phoenicoseris Berteriana* and *P. regia*, which have relatively numerous multiperforate plates, such plates occurred not at random but in radial series. Thus, a cambial initial tends to produce a series of vessels with multiperforate plates, whereas others give rise to vessel elements with simple plates. The writer has not encountered any mention of this mode of occurrence of multiperforate plates in the literature.

*Grouping.*—As in the writer's previous studies on woods of Compositae, a figure is given for number of vessels per group. This figure seems to be significant for the mainland species of Cichorieae, all of which are annuals and have a figure of 3.00 or greater (see fig. 19). The insular species all have an average of fewer than 3.00 vessels per group. The cause of this difference is not readily apparent to the writer. The Cichorieae studied show a strong tendency toward formation of radial rows of vessels (e.g., fig. 3). This tend-

ency is not apparent in some of the species with a very low number of vessels per group, such as *Sonchus leptocephalus* (fig. 17) or *Thamnoseric lobata* (fig. 13).

#### LIBRIFORM FIBERS

The figure for fiber length given in table 1 shows that in most species, libriform fibers are between 300 and 435 $\mu$  in length. The upper extreme is found in *Phoenicoseric Berteriana*, a species which also has relatively long vessel elements. Notably short fibers occur in *Lactuca Serriola*. The lowest average fiber-length, however, occurs in *Sonchus leptocephalus* (fig. 18). In this species, moreover, a fiber dimorphism occurs. As indicated in table 1, the average fiber length is 204 $\mu$ . Shorter fibers (fig. 18, right) occur in bands. Such fibers average 175 $\mu$  in length, whereas fibers between bands average 234 $\mu$  in length. The two types of fibers are otherwise alike in all histological characteristics, and thus the shorter ones do not qualify as apotracheal parenchyma cells. In one collection of *Rea micrantha*, several concentric bands of thin-walled fibers were present (fig. 11, just above center). Because the thinness of walls is the only variation in histology of fibers of this specimen, such fibers cannot be termed apotracheal parenchyma cells. The other collection of *Rea micrantha* showed a single band of only slightly more thin-walled fibers. In both *Sonchus leptocephalus* and *Rea micrantha*, such variation in fiber characteristics is probably related to duration of certain climatic conditions.

In table 1, a figure for range in thickness of fiber walls is given. These figures are intended to demonstrate the relatively thin-walled condition of fibers in almost all of the Cichorieae studied. The only notable exception is *Thamnoseric lobata* (fig. 13), in which some rather thick-walled fibers occur.

An interesting tendency which appears in all of the taxa studied is the radially-widened nature of fibers, as seen in transection.

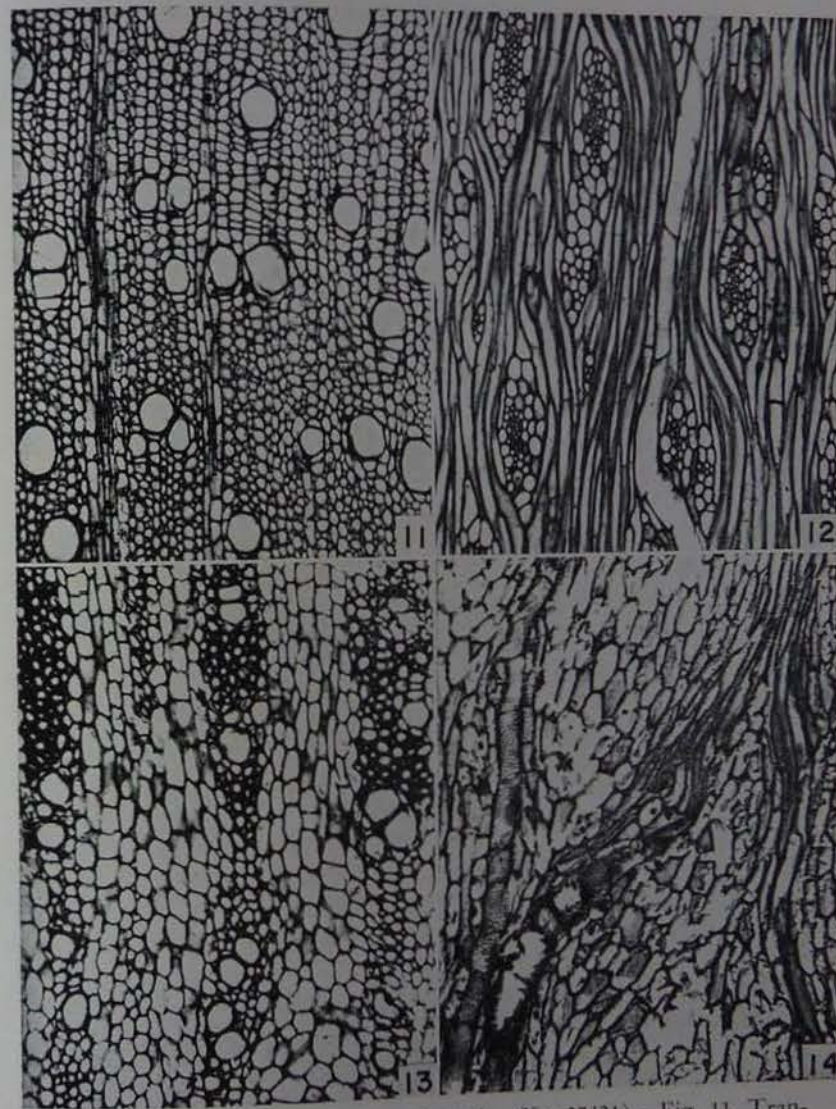


Fig. 11-14.—Fig. 11-12. *Rea micrantha* (Yw-27421).—Fig. 11. Transection.—Fig. 12. Tangential section.—Fig. 13-14. *Thamnoseric lobata*.—Fig. 13. Transection.—Fig. 14. Tangential section. All,  $\times 65$ .

## AXIAL PARENCHYMA

*Apotracheal parenchyma.*—The fact that some fiber dimorphism, mentioned above, is present in certain Cichorieae, may be a similar expression to the presence of actual concentric bands of apotracheal parenchyma cells. Such parenchyma cells are shorter, more thin-walled, and generally richer in latex droplets than are fibers. Examples of such bands may be seen in *Thamnosseris lobata* (fig. 13, just below center) and *Stephanomeria guadalupensis* (fig. 21, two successive bands on lower half of photograph) and, to a lesser extent, *Dendroseris litoralis* (fig. 1, center). In the last-named species, apotracheal parenchyma cells are shorter (ca. 250 $\mu$ ) than fibers. These bands are doubtless related to durations of certain climatic conditions. Such bands have been described in other Compositae, such as *Hemizonia clementina* (Carlquist, 1959a), an insular endemic of southern California. The presence, in the rather short succulent stem of *Thamnosseris lobata*, of wide apotracheal parenchyma bands alternating with thick-walled fibers is curious. Another example of this type of construction may be found in the similar stem of *Wunderlichia mirabilis* (Carlquist, 1957a), however.

*Vasicentric parenchyma.*—The Cichorieae studied here show marked differences with regard to presence of vasicentric parenchyma. Relatively abundant parenchyma, forming a sheath 1–2 cells in width around vessels or vessel groups, occurs in the Juan Fernandez species as well as in *Thamnosseris lobata* and *Sonchus leptocephalus*. Vasicentric parenchyma in *Stephanomeria guadalupensis* is less abundant. It may be present as a sheath, a single layer of cells wide, which is not continuous around a vessel or vessel group, although it may be more abundant, forming a sheath that is two cells in thickness at certain points around the periphery of a vessel or vessel group. *Malacothrix Blairii* has a condition typical for composites: an incomplete sheath, never more than a single layer of cells thick. The three mainland species, *Lactuca Serriola*, *Stephanomeria exigua*, and *S. virgata*, show a minimum of vasicentric parenchyma. In these species, only one or two parenchyma strands may

be present adjacent to a vessel or vessel group. Kribs (1937) has suggested that both loss of vertical parenchyma and abundant vasicentric parenchyma are derived conditions. If this is true, the Juan Fernandez Compositae, together with *Thamnosseris lobata* and *Sonchus leptocephalus* form one extreme of specialization, while the mainland Cichorieae mentioned form another extreme. Vasicentric parenchyma in the former group could not be termed "abundant" compared with that in dicotyldeons at large, but it is abundant when compared to that of other Compositae.

Because the Juan Fernandez Cichorieae form such relatively abundant vasicentric parenchyma, the writer decided to determine the number of cells per strand for each species of Cichorieae. *Lactuca Serriola*, with minimal parenchyma, has mostly two cells per strand. The same number of cells per strand is typical of the two species of *Malacothrix*, *Sonchus leptocephalus*, and *Stephanomeria guadalupensis*. The Juan Fernandez species and *Thamnosseris* have a range of from two to four or five cells per strand. In *Dendroseris macrophylla* four cells were more common, whereas in *Rea micrantha*, two or three cells predominated. In *Phoenicoseris Berteriana* and *P. pinnata*, four or five cells per strand is most frequent, although in *P. regia*, a single cell, rarely two or three, is present per strand.

#### TYLOSES

The only instance of tyloses was seen in *Dendroseris macrophylla*, where thin-walled tyloses were observed in one portion of a transection. As in other groups of Compositae, tyloses are thus of infrequent and sporadic occurrence.

#### VASCULAR RAYS

*Types.*—In comparison with Heliantheae, Cichorieae are distinctive in possessing uniseriate rays in comparative abundance. The only species in which uniseriate rays are absent or nearly so is *Thamnosseris lobata*; they are rare in *Phoenicoseris regia*.

*Dimensions.*—Ray dimensions may be computed in units or in terms of cells. Table 1 gives average ray height for

both multiseriate and uniseriate rays. Notably high rays occur in *Phoenicoseris regia* (fig. 6) and one collection of *Dendroseris macrophylla* (fig. 4). The relatively high rays of *Thamnosseris lobata* (fig. 14) are related to the fact that little alteration of pith rays occurs during secondary growth. Some breakup of rays, as seen in transection, may be observed in this species, however. Relatively short multiseriate rays occur in *Lactuca Serriola*, *Malacothrix Blairii* (fig. 15), *M. saxatilis* (fig. 16), *Rea micrantha* (fig. 12), and the three species of *Stephanomeria* (fig. 20, 22). As measured in number of cells, there is wide variation in width of multiseriate rays among Cichorieae. Juan Fernandez species (fig. 2, 4, 6, 10, 12) and *Thamnosseris lobata* (fig. 14) have notably wide rays, numerous cells in width. In some of these species (e.g., *Rea micrantha*, fig. 12; *Dendroseris litoralis*, fig. 2, upper left) the cells in the central portion of the ray (procumbent cells) are much smaller in diameter than those of the ray margin. Relatively narrow multiseriate rays, rarely more than three and often only two cells in width, occur in *Malacothrix* (fig. 15, 16), *Sonchus leptocephalus* (fig. 18), and *Stephanomeria* (fig. 20, 22). This distinction is certainly a noteworthy one for separating these groups of species. Often, in the latter group of species, multiseriate rays have long uniseriate wings. This character in these species is not related to primitiveness in ray structure but is more likely related to the abundance of uniseriate rays and the narrowness (in number of cells) of the multiseriate rays. Certainly there seems to be a relation, in *Malacothrix*, *Lactuca*, and *Stephanomeria*, between the height of uniseriate rays (note the rather great height of such rays in these taxa) and the fact that they have narrow multiseriate rays. These species also have tall uniseriate rays as measured by number of cells. This correlation is due to the fact that multiseriate rays, which are few cells in width, with uniseriate portions, are closer in construction to uniseriate rays than is the case with species possessing wide multiseriate rays, and thus more numerous and taller uniseriate rays may be expected in species with narrow multiseriate rays. Mention should be made of the fact that uniseriate rays in *Dendroseris macro-*

*phylla* are often three or more cells in height. Two to three cells is the most common condition in uniseriate rays of the species of *Stephanomeria*. In *Phoenicoseris*, *Rea* (fig. 12, center), and *Sonchus leptocephalus*, uniseriate rays are most frequently only a single cell in height.

*Histology.*—Table 1 shows the occurrence of erect and procumbent cells among the various taxa. Cells nearly isodiametric, as seen in radial section, occur in all taxa. These distinctions in pattern of ray-cell shapes are interesting ones, and may be interpreted, in part, as indications of differentiation among the taxa. Erect cells on the margins of rays may be similar to libriform fibers and render precise limits of rays difficult to define in some species, such as *Thammoseris lobata* (fig. 14).

Relative thickness of cell walls varies in rays of Cichorieae. Thin-walled, non-lignified rays occur in *Phoenicoseris regia*. In the regions where bands of narrow vessels and vascular tracheids occur (fig. 7, 8) all ray cells are non-lignified and thin-walled. In regions between these bands (fig. 5, 6) only the central portion of multiseriate rays consists of such cells. Relatively thick-walled ray cells occur in *Dendroseris* (fig. 2, 4) and *Rea* (fig. 12). Because of this thickness of cell walls in these genera, pits, which are rounded in face view, appear prominently. Ray cells of *Phoenicoseris* are thinner, and pitting, consisting of circular to fusiform areas, is less conspicuous. Relatively thin-walled ray cells with inconspicuous pitting occur in the three species of *Stephanomeria* as well as in *Sonchus leptocephalus*, *Thammoseris*, and *Malacothrix* (fig. 15-16). Pitting on the ray cells of *Lactuca Serricola* is relatively prominent, however, despite a thin-walled condition.

*Phoenicoseris Berteriana* and *P. pinnata* are notable in that the ratio of the area of fibers to the area of rays, as seen in transection, is high in comparison with that of the other Cichorieae studied.

#### GROWTH RINGS; RING POROSITY

Variation in the type or nature of elements produced has been mentioned above in relation to fibers and apotracheal

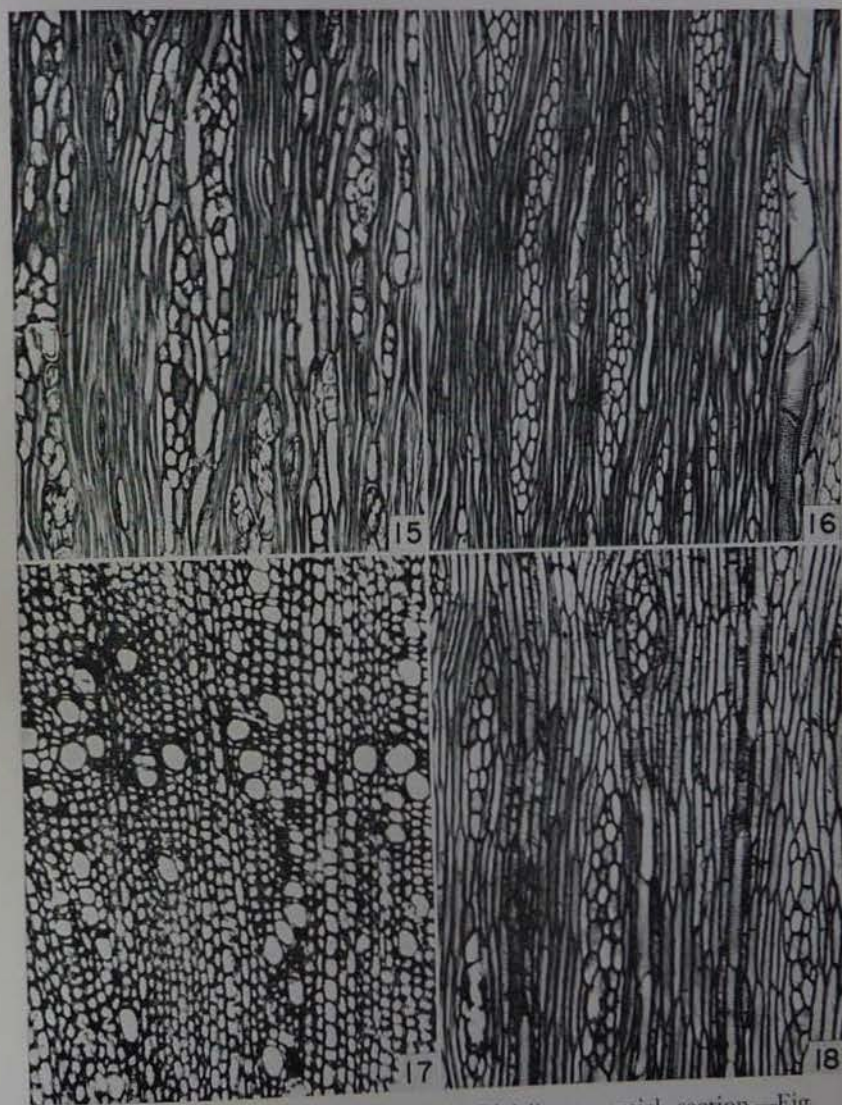


Fig. 15-18.—Fig. 15. *Malacothrix Blairii*, tangential section.—Fig. 16. *Malacothrix saxatilis*, tangential section.—Fig. 17-18. *Sonchus leptocephalus*.—Fig. 17. Transection.—Fig. 18. Tangential section. All,  $\times 65$ .

parenchyma. Thus characteristics of these two cell types are summarized under the heading "ELEMENTS DISTINGUISHING RINGS" in table 1. Vertical elements of the band shown for *Phoenicoseris regia* in figures 7 and 8 are notable because they are narrow vessels and vascular tracheids, with fibers absent. A similar condition was present in the terminal band of the stem examined of *Malacothrix Blairii*. Because variation in vessel diameter and relative abundance characterized bands in these two species, they might be termed ring-porous, or having a ring-porous tendency. Likewise, the presence of wider vessels in a band in *Phoenicoseris pinnata* (fig. 9) or more numerous vessels, combined with presence of shorter fibers in bands in wood of *Sonchus leptocephalus* (fig. 17, just above center) or the combination of apotracheal parenchyma with narrower vessels in *Stephanomeria guadalupensis* (fig. 21, two bands in lower half of photograph) would render these instances also examples of ring-porous tendencies.

#### STORIED STRUCTURE

Despite the presence of patches of obscurely-storied fibers in *Phoenicoseris pinnata* (fig. 10, left), *P. regia*, and *Rea micrantha*, the only prominently and consistently storied condition in the tribe was observed in *Sonchus leptocephalus* (fig. 18), in which all elements except rays conform to the storied pattern. Elements in the terminal band described for *Malacothrix Blairii* are also storied. Examples of storied structure are not infrequent in Compositae and they have been reported in Mutisieceae, Heliantheae, and Heleniceae (Carlquist, 1957a, 1958, 1959b).

#### LATEX DEPOSITORS

Identification of latex deposits in woods of Cichorieae was, to be sure, circumstantial, because no microchemical tests were applied. Such supposed latex deposits, however, do not have the same staining reactions as resin-like deposits in other Compositae. None of the Cichorieae in this study has secretory cavities or canals, whereas the writer's sections of vegetative structures other than wood revealed laticifers clearly in many of the taxa. Indeed, laticifers are considered



a universal feature within Cichorieae. Therefore, the deposition of droplets of latex within xylem elements of Cichorieae is not at all unexpected. The writer does believe, however, that although the presence of numerous small droplets in xylem elements is a genuine characteristic of certain cichorian woods, latex may be infiltrated or soaked into vessels or other elements when a wood sample is cut from a stem. Therefore, the reports below are data the writer believes to represent normal occurrences only. Examples of latex deposition are most apparent in the accompanying photographs as darkish clotted appearances, as for example in figure 1 (center), figure 17 (upper left) and figure 18 (lower left).

*Dendroseris litoralis*: droplets present especially in axial and ray parenchyma, also in fibers and in vessels.

*D. macrophylla* (Kunkel 1955): droplets in rays, tyloses, and especially vasicentric parenchyma.

*D. macrophylla* (Skottsberg 1917): droplets in rays and axial parenchyma.

*Lactuca Serriola*: no appreciable deposits.

*Malacothrix Blairii*: deposits in ray cells (fig. 15); fewer in other cells.

*M. saxatilis*: no appreciable deposits.

*Phoenicoseris Berteriana*: droplets in parenchyma, fibers.

*P. pinnata*: droplets in axial and ray parenchyma.

*P. regia*: droplets in rays, fibers.

*Rea micrantha*: scattered droplets in all cell types.

*Sonchus leptcephalus*: prominent deposits in axial parenchyma; a few droplets in other cell types.

*Stephanomeria exigua*: a few droplets, especially in rays.

*S. guadalupensis*: abundant in apotracheal parenchyma and vasicentric parenchyma, droplets somewhat less abundant in fibers, rays, and axial parenchyma.

*S. virgata*: latex deposits virtually absent.

*Thamnosseris lobata*: scattered droplets in all cells.

The above summary of occurrence shows that latex appears to be more abundant in parenchyma cells than in tracheary

elements. Probably latex in tracheary elements is formed as the element matures and remains when the element dies. The relative abundance of latex in insular species and relative absence in species collected in mainland southern California may be at least in part attributed to the lack of parenchyma cells in the latter species. The difference, in any case, is a rather sharp one.

#### DISCUSSION AND CONCLUSIONS

Analysis of the variation patterns outlined above inevitably involves numerous references to the taxonomic system, to geographical, and to ecological considerations. Summation of relationships of wood anatomy to these factors may be considered under the following headings.

*Variation within a species.*—Two collections were available for two species, *Dendroseris macrophylla* and *Rea micrantha*. Comparison of collections in each of these two species showed a number of differences of a quantitative nature. In *Dendroseris macrophylla*, the collection Kunkel 1955 showed narrower, longer vessel elements, fewer vessels per group, and markedly shorter multiseriate rays than the wood sample Skottsberg 1917. These differences might be attributed to greater maturity of wood characters in the former sample, but the stem from which this was taken did, in fact, show less xylem accumulation. Variations of this sort may be correlated with origin of sample within the stem, or normal variation. No qualitative differences separate the two collections, however.

Comparison of the two collections of *Rea micrantha* reveals that the collection Skottsberg 1955 possesses narrower, shorter vessels, narrower, longer rays, and lack of the prominent bands of thin-walled fibers which characterize the wood sample Skottsberg 1917. These characteristics may indicate a greater maturity in the latter sample, which was obtained from a larger stem. In neither species is there any reason to believe that there was any misidentification. Rather, different growing conditions and different ages of a stem may account for these differences. Such differences, however, do emphasize the unreliability of quantitative char-

acters where source of samples may vary, in agreement with the evidence on this point presented by Stern and Greene (1958).

*Correlations of habit and ecology with anatomy.*—The data presented in this paper suggest that a number of differences exist between the mainland herbs (*Lactuca Serriola*, *Malacothrix saxatilis*, *Stephanomeria exigua*, *S. virgata*) and the insular species. The following contrasts can be offered. These features are not entirely without exception, as reference to the above data will show, but they are generally true.

<i>Mainland Species</i>	<i>Insular Species</i>
Many vessels per group, in radial rows	Fewer vessels per group
Relatively narrow vessels	Relatively wide vessels
Near-circular, alternate pits on vessel walls	Vessel-wall pits elliptical to scalariform
Vasicentric parenchyma scanty	Vasicentric parenchyma more abundant
Multiseriate rays fewer cells in width	Multiseriate rays often four or more cells wide
No bands formed in xylem	Bands of various types formed in xylem
Latex deposits scanty or absent	Latex droplets abundant in parenchyma, other cells

These differences may be attributed at least in part to the rosette-shrub or rosette-tree habit of the insular species, which in turn may have evolved in relation to certain climatic factors characteristic of temperate-zone islands. In addition, these differences may reflect other factors inherent in insular floras. The reader should note that all the "mainland species" are from southern California, and this location may account for some of the differences, although two of the insular species are from the same region.

The peculiar features of rosette-shrubs and rosette-trees are not unique among Compositae. There are parallels in other tribes of Compositae, as well as in other families. For example, xylem of *Thamnoseric lobata* shows similarities to

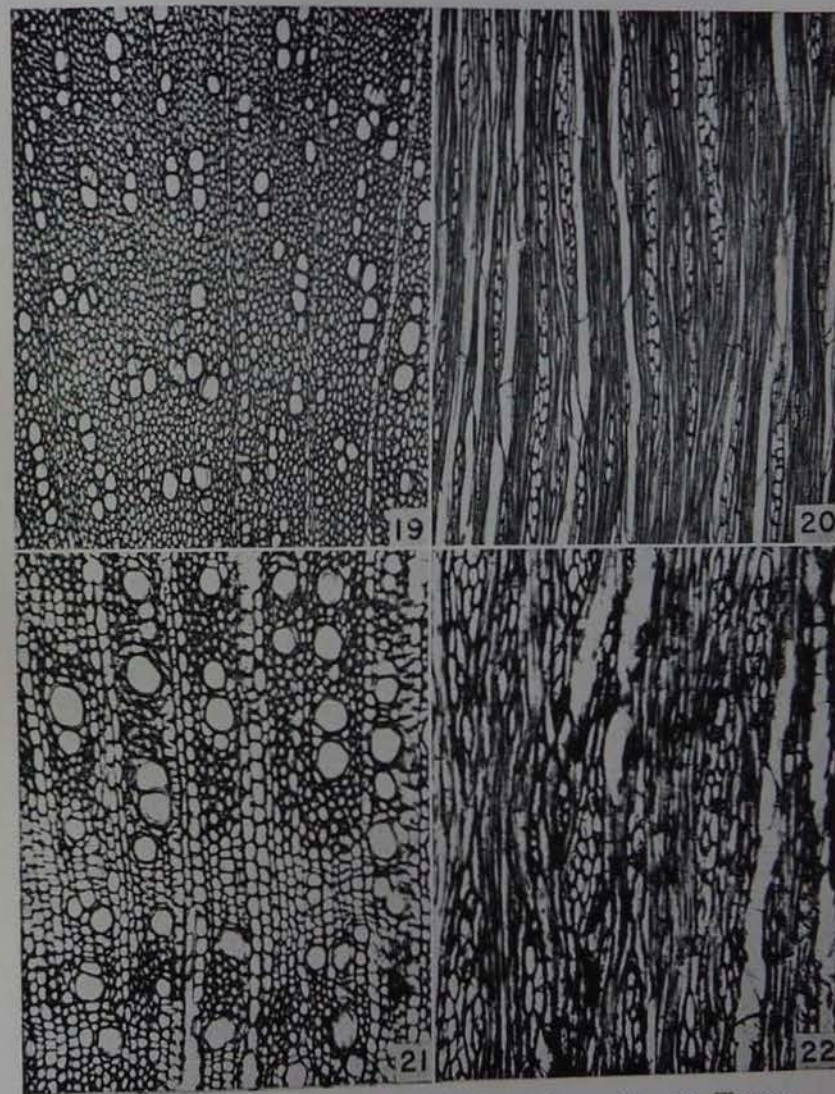


Fig. 19-22.—Fig. 19-20. *Stephanomeria exigua*.—Fig. 19. Transsection.—Fig. 20. Tangential section.—Fig. 21-22. *Stephanomeria guadalupensis*.—Fig. 21. Transsection.—Fig. 22. Tangential section. All,  $\times 65$ .

that of *Hemizonia clementina* (Heliantheae, subtribe Madinae) or *Wunderlichia mirabilis*, as mentioned above. Similar parallels may be found for other Cichorieae. The significance of scalariform pitting of vessels in relation to the rosette-shrub or rosette-tree habit, discussed earlier, has been entertained earlier by the writer (1958). The relatively long vessels in *Phoenicoseris Berteriana* and *P. pinnata* may be related to the peculiar palmiform habit of these species.

The possibility must be noted that the mainland species of Cichorieae may represent just as much adaptation to their locations as insular species do, so that the characteristics of insular species need not be regarded as necessarily derived from the characters listed for the particular mainland species studied.

*Comparisons with the taxonomic system.*—The recent system offered by Stebbins (1953) for the tribe is based on Stebbins' morphological and cytological (Stebbins, Jenkins, and Walters, 1953) studies of that tribe and doubtless represents the best expression of subdivisions within the tribe to date. According to Stebbins' system, the taxa studied here would fall into the following groups:

Subtribe 4. Stephanomerinae: *Thamnosseris*, *Stephanomeria*, *Malacothrix*

Subtribe 5. Dendroserinae: *Dendroseris* and the segregate genera *Phoenicoseris* and *Rea*

Subtribe 6. Crepidinae:

*Launaea-Sonchus* line: *Sonchus*

*Prenanthes-Lactuca* line: *Lactuca*

The genus *Thamnosseris*, on account of its peculiar growth form, geographic location, and certain features of gross morphology, has proved a genuinely anomalous genus within Cichorieae. Skottsberg (1937, 1947) has maintained that the totality of features, including anatomical ones, indicate a relationship to the Juan Fernandez genera of Cichorieae. If this relationship is valid, it perhaps should be placed in the same subtribe. Johnston (1935) was skeptical of this relationship, and Stebbins (1953) has questioned this disposition. Stebbins emphasizes contrasts between *Thamnosseris* and the

Juan Fernandez genera in achene morphology, but Skottsberg (1947), in a paper not cited by Stebbins, seems to have offered close similarities as well as contrasts between the two in respect to achene morphology. Stebbins does not detail his grounds for suggesting affinity between *Stephanomeria* and its allies and *Thamnosericis*. The writer is developing additional anatomical information concerning *Thamnosericis* and the Juan Fernandez Cichorieae, and such data may prove of significance in furthering comparisons and attempting a more definitive statement on the relationships of this genus. At any rate, the present study shows that the secondary xylem, which seems closely related to the peculiar growth form of *Thamnosericis*, offers no close similarities to the secondary xylem of the other taxa considered here.

The grouping by Stebbins of *Stephanomeria* in the same subtribe with *Malacothrix* would seem to be justified on the basis of wood anatomy, although some of these similarities may in fact be due to similar climate and growth form. *Lactuca*, for example, shows much the same features although it is in another subtribe. This accounts for the grouping of *Lactuca* with *Malacothrix saxatilis*, *Stephanomeria exigua*, and *S. virgata* in the *Mainland Species* category above. From the anatomical features which the *Mainland Species* have in common, *Malacothrix Blairii* and *Stephanomeria guadalupensis*, both insular species, depart in similar ways. Such parallelisms need not necessarily indicate any close relationship between these species. Interestingly, *Malacothrix Blairii* was first described by Munz and Johnston (1924) as a species of *Stephanomeria* and later transferred by Munz (1935) to *Malacothrix*. Williams (1957) in a monograph of *Malacothrix* retains the species in that genus, without commenting on the placement, as does Munz (1959). In the opinion of the writer, the affinities of *M. Blairii* have not yet been thoroughly explored, and consideration of other anatomical characteristics is needed to find if more criteria for its placement exist. The chromosome number (Stebbins, Jenkins, and Walters, 1953) of *M. Blairii* is exceptional in the genus *Malacothrix*, but characteristic of

*Stephanomeria*, and on this and other grounds the species has been regarded as a *Stephanomeria* in the paper just cited.

The great similarity of *Stephanomeria exigua* and *S. virgata* in respect to secondary xylem characters is noteworthy, and probably indicates a close relationship.

The placement of the Juan Fernandez genera in subtribe *Dendroseridinae*, which includes no other genera, was originated by Hoffmann (1890) and seems to have been accepted. Skottsberg, after considering all the Juan Fernandez species as *Dendroseris* (1922) recognized four genera in the group (1951), largely persuaded by evidence from pollen morphology developed by Erdtman (see Erdtman, 1952). Stebbins, Jenkins, and Walters (1953) note that two species of Juan Fernandez Cichorieae, placed in separate genera by Skottsberg, have the same distinctive chromosome number and size, and they discount the value of generic distinctions.

The Juan Fernandez Cichorieae could be said to have the following characteristics in common: abundant vasicentric parenchyma, vasicentric parenchyma strands often consisting of four or more cells, relatively wide (four or more cells in width) multiseriate rays, lateral-wall vessel pitting elliptical to scalariform, and relatively frequent, often large multiperforate perforation plates in vessels. These similarities may not seem to be particularly substantial, but attempts to find distinctions corresponding to the segregate genera yielded fewer characteristics. *Dendroseris (sensu stricto)* and *Rea* both possess relatively thick-walled ray cells with fairly prominent pits, whereas in *Phoenicosericis*, the cell walls are thinner, with less conspicuous pitting. Both *Dendroseris (sensu stricto)* and *Rea* have relatively short, wide rays, with narrow procumbent cells in the central portion of the ray. In *Phoenicosericis*, multiseriate rays are somewhat narrower, without smaller cells, and occupy a smaller area in a tangential section, in comparison to fibers, than is the case in *Dendroseris (sensu stricto)* or *Rea*.

The writer has in progress anatomical studies to illumine further degrees of similarity or difference among the groups

of Juan Fernandez species. Meanwhile, the names of segregate genera have been used provisionally.

The wood of *Sonchus leptcephalus* is easily the most distinctive of the Cichorieae studied on account of the short, storied fibers which are shorter in the occasional bands which occur. The xylem of *Lactuca Serriola*, as mentioned above, shows similarity, possibly because of similar ecological conditions, to the mainland species of *Stephanomeria* rather than to *Sonchus leptcephalus*, despite the fact that both *Lactuca* and *Sonchus* are placed in the same subtribe.

*Characteristics and evolution of wood in Cichorieae.*—Relatively few features can be cited as being characteristic of Cichorieae rather than species of tribes studied earlier by the writer. The presence of relatively numerous uniseriate rays and, at least in some species, relatively narrow multiseriate rays is like Mutisieae but unlike Heliantheae and Helenieae. Spirals and grooves in vessels (with the exception of *Malacothrix saxatilis*) are notably absent in Cichorieae, unlike a number of Heliantheae, Helenieae, and Astereae. The tendency toward elliptic to scalariform pitting in vessels and the possession of thin-walled fibers, wider radially than tangentially, are characteristics of many Cichorieae but comparatively few species in other tribes.

The gamut of specialization of characteristics in Cichorieae is small, but certainly, as in other Compositae, the possession of very short, storied fibers (*Sonchus leptcephalus*), large grouping of vessels and very scanty vasicentric parenchyma (*Lactuca*, *Malacothrix saxatilis*, *Stephanomeria exigua*, *S. virgata*) or relatively abundant vasicentric parenchyma (Juan Fernandez species, *Thamnosericis*) seem advanced characteristics.

Certainly some Cichorieae show anatomical adjustment to particular growth forms or ecology. The xylem of *Thamnosericis* seems exemplary of this, as does the formation of bands in this species and others. The species with narrow, short vessel elements and narrow multiseriate rays all occur in Mediterranean-type climates. Thus, suppositions concerning patterns of wood evolution in Cichorieae must untangle the

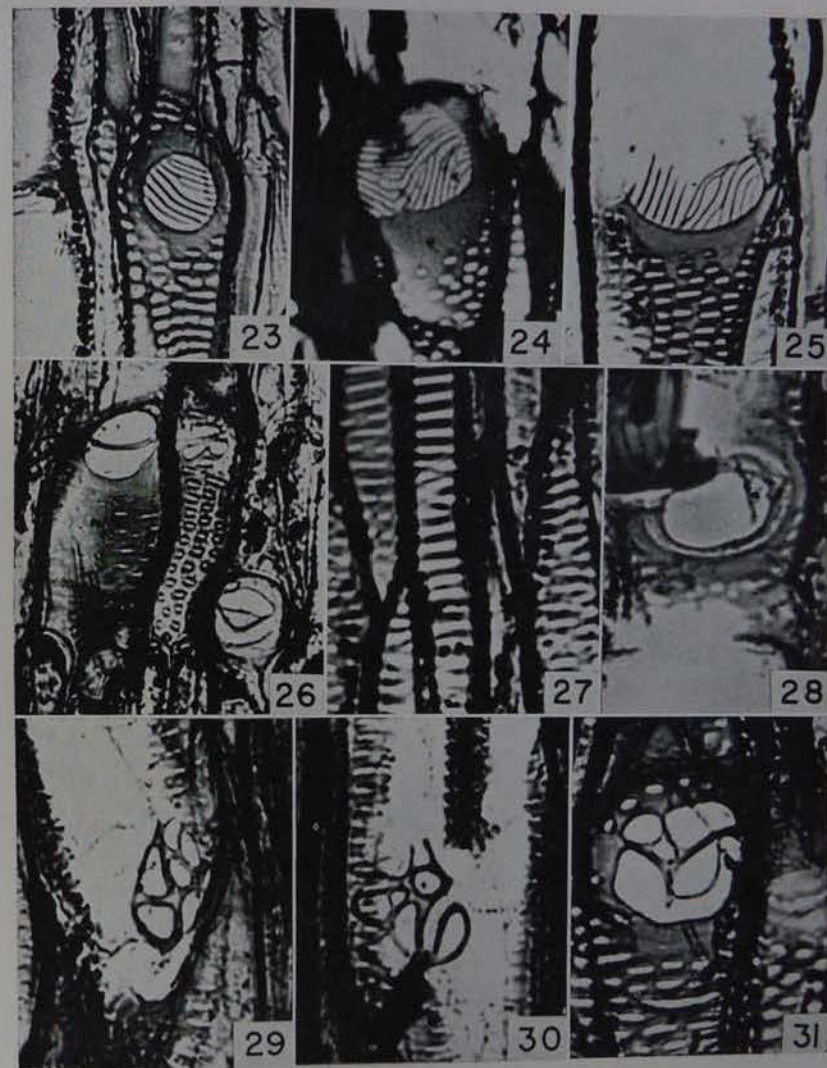


Fig. 23-31.—Fig. 23-26. *Phoenicosericis Berteriana*, perforation plates of vessels from radial sections.—Fig. 27-31. *Phoenicosericis regia*.—Fig. 27. Scalariform lateral-wall pitting from section shown in fig. 8.—Fig. 28-31. Perforation plates of vessels; fig. 28, 31, from radial sections; fig. 29, 30, dislodged plates from tangential sections.—Fig. 23,  $\times$  310; fig. 24,  $\times$  305; fig. 25,  $\times$  347; fig. 26,  $\times$  320; fig. 27,  $\times$  330; fig. 28-31,  $\times$  355.

over-all phylogenetic trends in wood anatomy from changes which may be induced by particular climates or peculiar growth forms. The possibility that these latter considerations might play a relatively important role in attainment of particular wood configurations was explored in Helenieae (Carlquist, 1959b), and this possibility seems equally valid in Cichorieae. If special climatic or ecological factors underlie wood patterns in Cichorieae, the fact that such patterns are different from those described in Helenieae is readily understandable, considering the different habits and habitats occupied by members of the two tribes.

If one were to cite characteristics which could be used in assessing whether or not woody Cichorieae originated from herbaceous ancestors, several might be mentioned. The high proportion of genera with elliptic to scalariform pitting on lateral walls of vessels in Cichorieae seems significant. The presence of thin-walled, radially widened fibers may also be noteworthy in this regard. Woodiness, if it is derived from herbaceousness in Cichorieae, could have originated more than once in Cichorieae. Intensive examination of wood (and other features) of rosette trees throughout Compositae, as well as in other families, is needed before the mode, or modes of origin of such growth forms can be clarified. Cichorieae will undoubtedly prove significant in such further comparisons, however, because of the decidedly herbaceous nature of the tribe, and the striking relation between woodiness and insular habitats.

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## CURRENT LITERATURE

**Know your woods.** *Albert Constantine, Jr.*, Home Craftsman Publishing Corp., New York, N. Y. 1-384 illustrated. 1959. \$5.75.

The book is divided into two parts. Part 1 is entitled "The Wonderful Story of Woods" and consists of fifteen chapters. They include an opening chapter on wood structure and then chapters on identification, nomenclature, logging, veneering, physical appearance, woods of the Bible, state trees, drugs from trees, trees with edible products, poisonous trees, unusual woods, wood collecting, woods in craftwork, and finally a wood quiz. Part 2 is entitled "Woods from Abura to Zebrano," with a color chart and key illustrating 60 woods and a written description of some 300 species. A glossary and index is included.

The jacket states that a dozen experts had a preview of the manuscript and their unanimous opinion was "nothing else like it." Unfortunately, this appears to be true. The author has attempted to boil down complete texts to a single chapter and include a little smattering of many complex subjects. Very little of the subject matter is new or original. The technical subjects have evidently been carefully edited, but the general material is neither carefully edited nor even factually correct.

The wood quiz is truly amazing, a collection of what might be termed "filler material," or culled from the "Believe it or not" columns. For instance, question 122 is: "When is a tree not a tree?", and the answer is: "When it is a papaya tree." It is doubtful if this answer will be considered an advance in education.

The section on woods from Abura to Zebrano is prefaced with the outline of 14 characteristics which are to be given for each wood. However, after making the list, the author proceeds to neglect to follow it in some cases and to change it in others.

The author is in the business of supplying rare woods to craftsmen, and loses few opportunities so to advise the

reader. The chapter on craftwork has some excellent illustrations, and for this reason alone should find a ready sale to the home shop worker, but the book will be of little value outside of the home shop.—*Archie F. Wilson*, 54 Druid Hill Road, Summit, New Jersey.

**Dictionary of economic plants.** *J. C. Th. Uphof*, H. R. Engelmann (J. Cramer), Weinheim, Germany. 1-400 bibliography. 1959. \$9.75 (from Hafner Publishing Co., New York, N. Y.).

Economic botany, in the broad sense, concerns plants which are used by man. The total number of these plants must be in the tens of thousands, and a search for information on any one of them may be accompanied by many hours of arduous library work. Such study is commonly impossible for the interested layman, and may be impracticable for the specialist. For these reasons a comprehensive dictionary of economic plants would provide a highly desirable, simply arranged guide to the plants which man employs. These may have been among the motives which prompted Professor Uphof to prepare his volume on economic plants.

The *Dictionary of economic plants* consists of an alphabetical listing of the scientific names of plants cross-referenced in large part with common names and botanical synonyms. Each species name is followed by the name of the author responsible for the binomial, the family to which the plant belongs, common names and the geographical distribution of the species. For each plant there is a more or less extended explanation of its uses, frequently coupled with a brief description of the plant (or the timber), manufacturing processes, important chemical derivatives and other pertinent notes.

In such a compendium as this, a certain amount of selection must be made. Professor Uphof has drawn his plants from among those used for timber, in horticulture, in medicine and in the manufacture of drugs. Spice yielding plants, toxic plants, fiber and textile producing plants, plants with resins, gums, latices and essential oils, are also included. Many wild plants, used by aboriginals and which are purely



of ethnobotanical interest, have also been considered. One of the useful features of the book is the classified bibliography. Here, under such topics as "Beverages," "Dyestuffs," "Medicinal plants" and "Economic microorganisms," one is introduced to the literature on the plants in any of the many kinds of economic categories.

Generally speaking, and in large part, Professor Uphof's book is very well done. He has brought to bear on the subject his many years of experience and in particular his strong taxonomic background. However, one could wish that the book were composed and printed in an English-speaking country, for the conspicuous typographic, semantic and orthographic errors are no doubt at least partly resultant from the fact that these operations were accomplished in Germany. The typographic errors are particularly disturbing because they sometimes occur in technical words and in scientific names where they may go unnoticed by the lay reader. Certain words are used in a peculiar or at least uncommon manner, e. g., *Celtis australis*, wood used for "blow-instruments" (probably musical wind instruments is intended) and *Cayaponia pedata*, roots contain a "drastic" (probably purgative is meant). The separation of words at the ends of printed lines appears to be random, and is often counter to accepted methods, e. g., "ea-sily" rather than easi-ly, "du-rable" instead of dura-ble and "se-veral" rather than sever-al. Some words as *western*, *species* and *autumn* are divided when they should not be so treated. An English-speaking reader will also wonder at some of the unusual abbreviations employed. It is unfortunate that these rather minor criticisms are so numerous that they detract from the over-all quality of the text.

Even though the classified bibliography constitutes one of the important features of the book, certain highly pertinent works have been omitted in some cases. In other instances, older, out-of-date publications are cited in lieu of newer, more comprehensive literature. A few examples will serve to illustrate these points: Under "Pectic substances, alkaloids and tannins," the author omits the most extensive current work on alkaloids, Manske and Holmes' many vol-

ume series, *The alkaloids*, begun in 1950. In the "Forest products" section, Record and Hess' important *Timbers of the New World* (1943) is lacking. The list of works on "Economic microorganisms" does not mention any of Thom and Raper's significant treatises on the *Aspergilli* and *Penicillia*, nor Waksman's Nobel Prize-winning studies on antibiotic producing microorganisms. Zon and Sparhawk's 1923 *Forest resources of the world* is listed although the recent *A world geography of forest resources* (Haden-Guest, et al., 1956), which covers the same subjects in an extended, up-to-date manner, is omitted. Record and Mell's 1924 publication on the *Timbers of tropical America* is cited rather than the more up-to-date and expansive volume by Record and Hess. Although it is clear that Professor Uphof could not mention all works on economic plants, nevertheless the reviewer feels that his choices are not always of the best.

It is somewhat significant, if not amusing, to note that Professor Uphof, a taxonomist, has added the -aceae familial suffix to the classical Latin roots in Labiatae, Guttiferae, Umbelliferae, Gramineae, Cruciferae, Leguminosae and Palmae, but not in Compositae. Perhaps, even though he states in his introduction that "practically all families end in -aceae," he could not bring himself to overcome this one last remnant of his classical upbringing. No doubt there will be some taxonomic eyebrow-raising among his colleagues, since there are recommended alternative names for these families in the *International code of botanical nomenclature* (e.g., Fabaceae for Leguminosae, Arecaeae for Palmae and Poaceae for Gramineae).

The *Dictionary* is fundamentally a well conceived, factually accurate, highly useful volume which would be a worthwhile acquisition for anyone interested in plants and their relation to man. The 6000 different species of plants which are considered certainly cover most of those commonly to be encountered, and many which will be encountered only by the specialist. The ease of reference, the cross-indexing, the sturdy plasticized binding and the good quality non-reflecting paper all commend this volume to the reader. Professor Uphof's book will doubtlessly take its place on the

book-shelf beside such often consulted botanical compendia as Willis' *A dictionary of the flowering plants and ferns*.—*William L. Stern.*

#### CORRECTION

*TOVOMITA GRANDIFOLIA* L. Wms., nom. nov.

*Tovomita macrophylla* L. Wms. in *Trop. Woods* 111: 16. 1959, non Walp., 1842.

During the time that this plant was being studied it was tentatively placed in three genera. The specific name "*macrophylla*" was used for it in one of these genera and I failed to change it back when I returned the plant to *Tovomita*.—Louis O. Williams.

#### TENTH PACIFIC SCIENCE CONGRESS

The Editor has been asked to announce that the Tenth Pacific Science Congress of the Pacific Science Association will be held at the University of Hawaii, Honolulu, from 21 August to 6 September 1961. A post-session field trip will be held from 2 September to 6 September. All inquiries should be addressed to: Secretary-General, Tenth Pacific Science Congress, Bishop Museum, Honolulu 17, Hawaii, U. S. A.

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# TROPICAL WOODS

## TABLE OF CONTENTS AND INDEX TO AUTHORS, SCIENTIFIC AND COMMON NAMES

NUMBERS 95 TO 111, JUNE 1949 TO OCTOBER 1959

There have been no inclusive indices nor tables of contents published for *Tropical Woods* since the appearance after issue number 94 of a general index and index to scientific names in December 1949, and an index to vernacular and trade names in May 1950. These indices covered all issues published up to that time. However, several incomplete indices and interim tables of contents have appeared since the issuance of number 94: An index and table of contents of numbers 89 through 96 appeared with the latter number; an index to the scientific and common names employed in numbers 95, 97, 98, 99 and 103 appeared as an appendix to issue 103; a table of contents including numbers 97 through 104 was issued with number 104.

In the present index to scientific and common names, a given name will ordinarily be indexed only once for a given article; i. e., the first time it appears in the article.

The Editor would like to acknowledge the assistance of Mrs. Barbara Greenstein and Mrs. Patricia H. Chappell in the tedious and exacting task of preparing these indices.

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