SYSTEMATIC ANATOMY OF THE WOODS OF THE « BURSERACEAE »

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RESUMEN

Anatomía sistemática del leño de las Burseráceas. — El autor describe la anatomía del leño de las Burseráceas y la compara con la de las Anacardiáceas, Rutáceas, Simarubáceas y Meliáceas. Las semejanzas de la estructura de sus leños sugieren la posibilidad de un origen común ; los de las Meliáceas muestran una mayor especialización que los de las Simarubáceas y Rutáceas, los cuales a su vez son más especializados que los de las Burseráceas y Anacardiáceas.

Las cavidades intercelulares traumáticas de los radios de las Rutáceas y Simarubáceas, parecen sugerir el origen de estas familias a partir de plantas como las Burseráceas y Anacardiáceas, que tienen canales intercelulares normales en sus radios.

The family *Burseraceae* comprises fifteen or sixteen genera and approximately fifty species of tropical woody plants, most of which are large trees. In former times this family and the *Anacardiaceae* were united under the name *Terebinthaceae*. Accounte of the early history and subdivisions of this group are given in the papers of Marchand (1866) (1867 *a*) (1867 *b*), Jadin (1893) (1894), and Guillaumín (1909). The most recent subdivision of the family is that proposed by Lam (1932 *b*) and outlined below. In this outline the number of species comprising each genus is indicated together with its distribution, then the species represented by wood specimens in the present investigation are listed. In this list a number in parenthesis following the species name indicates the available number of specimens of a species represented by more than one specimen. Most of the specimens were obtained from the Yale University Collections through the courtesy of Dean Samuel J. Record, to whom I wish to express my gratitude. For additional material thanks are due Prof. H. P. Brown of New York State College of Forestry, and Mrs. Myrtle Botts of Julian, California.

BURSERACEAE

I. Tribe **PROTIEAE** Engler

1. **Protium** Burm. f. 90 species (81 in tropical America, 4 in Madagascar and Mascarenes, 2 in Indo-China, 1 in Malay Archipelago and Peninsula, and 1 in Australia).

P. asperum Standl., *P. carana* (H. B. K.) March., *P. copal* (S. et C.) Engl. (2), *P. costaricense* (Rose) Engler, *P. crassifolium* (Rich.) Engl.?, *P. cubense* (Rose) Urb. (2), *P. denticulatum* Bl., *P. glaucum* Macbr., *P. guianense* (Aubl.) March. (2), *P. heptaphyllum* (Aub.) March. (2), *P. icicariba* (DC.) March., *P. insigne* (Triana et Planch.) Engl., *P. javanicum* Burm. f., *P. Llewelyni* Macbr., *P. medianum* Macbr., *P. panamense* (Rose) Johnston (2), *P. puncticulatum* Macbr., *P. Schomburgkiana* Engl. (2), *P. serratum* (Colebr.) Engl. (2), *P. sessiliflorum* (Rose) Standl. (3), *P. subserratum* Engler, *P. tenuifolium* Engler (2).

2. **Crepidospermum** Hook. f. 2 species in tropical America.

C. Goudotianum (Tub.) Tr. et Pl.

3. **Tetragastris** Gaertn. 4 species in tropical America.

T. balsamifera (Sw.). O. Kuntze (2), *T. panamensis* (Engl.) Kuntze (2). *T. Stevensonii* Standl. (2).

4. **Trattinickia** Willd. 5 species in tropical America.

T. demerarae Sandw.

5. **Garuga** Roxb. 3 species (1 in Malay Archipelago, 2 in Indo-China).

G. floribunda Decaisne, *G. pinnata* Roxb. (2).

II. Tribe **BURSEREAE** H. J. Lam.

1. Subtribe **Bursereae-Commiphorinae** H. J. Lam.

6. **Aucoumea** Pierre. 1 species in Africa.

A. Klaineana Pierre (2).

7. **Commiphora** Jacq. 139 species (10 in Madagascar and Mascarenes, 121 in continental Africa and Socotra, 8 in Arabia and W. India).

C. Stocksiana Engl., *C. Zimmermannii* Engl.

2. Subtribe **Bursereae-Burserinae** H. J. Lam.

8. **Boswellia** Roxb. 23 species (20 in continental Africa and Socotra, 3 in Arabia and W. India).

B. serrata Roxb.

9. **Triomma** Hook. f. 1 species in Malay Archipelago and Peninsula.

T. malaccensis Hock. f. (3) including *T. macrocarpa* Backer).

10. **Bursera** Jacq. 100 species in tropical America.

B. glabra Tr. et Pl., *B. glabrifolia* (H. B. K) Engl., *B. graveolens* (H. B. K.) Tr. et Pl. (2), *B. microphylla* Gray, *B. Simaruba* (L.) Sarg. (4), *B. tomentosa* (Jacq.) Tr. et Pl.

III. Tribe **CANARIEAE** Engler

11. **Dacryodes** Vahl. 34 species (2 in tropical America, 19 in continental Africa and Socotra, 13 in Malay Archipelago and Peninsula).

D. Buettneri (Engl.) H. J. Lam. (2), *D. excelsa* Vahl, *D. incurvata* (Engl.) H. J. Lam, *D. Letestii* (Pellegr.) H. J. Lam, *D. paniculatus* (Hoyle) H. J. Lam, *D. rostrata* (Blume) H. J. Lam. (2).

12. **Santiria** Blume. 24 species (6 in Africa, 18 in Malay Archipelago and Peninsula).

S. apiculata Benn. (2), *S. Griffithii* (Hook. f.) Engl., *S. laevigata* Bl., *S. oblongifolia* Blume, *S. tomentosa* (2).

13. **Haplolobus** H. J. Lam. 12 species in Malay Archipelago and Peninsula.

14. **Scutinanthe** Thwaites. 1 species in Ceylon.

S. brunnea Thw.

15. **Canarium** L. 109 species (5 in Madagascar and Mascarenes, 8 in continental Africa, 18 in Indo-China, 1 in Ceylon, 66 in Malay Archipelago and Peninsula, 2 in Australia, 9 in Polynesia).

C. album Raeusch, *C. asperum* Bentham (3), *C. Boivini* Engl., *C. Colophania* Baker, *C. commune* L., *C. denticulatum* Blume (2), *C. hirsutum* Willdenow (4), *C. kipella* Miq., *C. littorale* Bl. (2), *C. luzonicum* (Bl.) A. Gray, *C. mafoa* E. Christoph., *C. mehenbethene* Gaertn. (3), *C. occidentale* A. Chev., *C. odontophyllum* Miq., *C. ovatum* Engl., *C. palawense* Laut., *C. rufum* Benn., *C. salomense* B. L. Burtt, *C. Schweinfurthii* Engl., *C. strictum* Roxb., *C. sumatrana* Boerl. et Koord., *C. velutinum* et Guill., *C. vitiense* A. Gray.

16. **Canariellum** Engler. 1 species in New Caledonia, probably should be included in the genus *Canarium*.

C. oleiferum (Baill.) Engler.

Commercially important gum-resing, used in incense and medicine, exude from the bark of various species of the genera *Bursera, Boswellia, Canarium* and *Commiphora*. Some species of *Canarium* and *Dacryodes* are valued for their edible fruits. The timbers of many species are of considerable local importance, but with the exception of *Aucoumea Klaineana*, commonly known as Okumé or Gaboon mahogany, they are seldom exported. The following list indicates where more or less complete descriptions, or notations concerning the general properties or uses of woods of various species may be found in the literature cited at the conclusion of this paper.

Aucoumea Klaineana Pierre. Anonymous (1928); Bertin, A., Chevalier, Aug. et all (1927 & 1928); Collardet, Jean (1929); Dixon, Henry H. (1918); Guillaumin, A. (1909) p. 262; Jentsch, F. and Appel, E. (1936); Lecomte, Henri (1920) (1923) p. 155; Record, S. J. (1926).

Boswellia sp. Pearson, R. S. and Brown, H. P. (1932) p. 217.

Boswellia Carteri Birwdood. Peter, A. (1903).

Boswellia papyrifera Hochst. Solereder, H. (1908) p. 193.

Boswellia serrata Roxb. Foxworthy, F. W. (1909) p. 475; Gamble, J. S. (1922) pp. 137-138; Kanehira, R. (1924*a*) p. 5, Pearson, R. S. and Brown, H. P. (1932) p. 218-220; Troup. R. S. (1909) p. 91-92.

Bursera sp. Moeller, J. (1876) pp. 394-5 (as *Elaphrium* sp.); Pearson, R. S. and Brown, H. P. (1932) p. 217; Record, S. J. (1921) p. 257.

Bursera aloexylon Engl., Solereder, H. (1908) p. 193.

Bursera Simaruba (L.) Sargent, Brush, W. D., Murphy, L. S. and Mell, C. D. (1916) p. 77; Lecomte, H. (1920) (as *B. gummifera* (L.) Jacq.); Piccioli, Lodovico (1919) p. 259; Record, S. J. (1921) p. 257 (as *Elaphrium Simaruba); Record*, S. J. and Mell, C. D. (1924) pp. 33-339; Stepowski, M. (1903) p. 39 (as *B. gummifera).*

Canariellum oleiferum Engl., Guillaumin, A. (1909) p. 250.

Canarium sp. Bargagli-Petrucci, G. (1903*a*), (1903*b*) pp. 315-316 & pl. 7; Berger, L. G. Den and Bianchi, A. T. J. (1931) pp. 897-898; Boorsma (1907) p. 28-29; Lecomte, H. (1920); Pearson, R. S. and Brown, H. P. (1932) p. 217; Record, S. J. (1921) p. 257; Solereder, H. (1908) p. 869.

Canarium acutifolium (DC.) Merr., Lane-Poole, C. E. (1925) p. 98.

Canarium album Raeuschel, Kanehira, R. (1921) p. 59, fig. 68.

Canarium altissimum Blume, Moll, J. W. and Janssonius, H. H. (1908) p. 107.

Canarium asperum Bentham (as *C. villosum* (Bl.) F. Vill.) Bailey, I. W. (1920) p. 361; Kanehira, R. (1924*b*) p. 16; Schneider, E. E. (1916) p. 129.

Canarium bengalense Roxb., Gamble, J. S. (1922) p. 140-141; Troup, R. S. (1909) p. 99.

Canarium Boivini Engl., Lecomte, H. (1923) p. 163.

Canarium brunneum Bedd., Gamble, J. S. (1922) p. 141.

Canarium calophyllum Perkins. Kanehira, R. (1924*b*) p. 16.

Canarium commune Linn., Berger, L. G. Den (1926); Boorsma (1907) p. 31; Foxworthy, F. W. (1909) n° 38; Gamble, J. S.

(1922) p. 141; Moll, J. W. and Janssonius, H. H. (1908) p. 108; Record, S. J. (1918); Svendsen, C. J. (1905) pp. 34-35.

Canarium denticulatum Blume, Moll, J. W. and Janssonius, H. H. (1908) p. 107.

Canarium euphyllum Kurz. Pearson, R. S. and Brown, H. P. (1932) p. 231.

Canarium hirsutum Willdenow, Kanehira, R. (1924*b*) p. 16 (as *C. ahernianum* Merr., and as *C. Radlkoferi* Perk.); Moll, J. W. and Janssonius, H. H. (1908) p. 102 (as *C. hispidum* Blume).

Canarium kipella Miguel., Moll, J. W. and Janssonius, H. H. (1908) p. 108.

Canarium littorale Bl., Moll, J. W. and Janssonius, H. H. (1908) p. 107.

Canarium luzonicum (Bl.) A. Gray. Lecomte, H. (1925) p. 146; Pearson, R. S. and Brown, H. P. (1932) p. 217; Schneider, E. E. (1916) p. 128 and pl. 4 fig. 25.

Canarium maluense Lauterbach, Lane-Poole, C. E. (1925) p. 99.

Canarium mehenbethene Gaertner. Lane-Poole, C. E. (1925) p. 98.

Canarium microcarpum Willd., Boorsma (1907) pp. 30-31.

Canarium nigrum Engl. Lecomte, H. (1925) p. 148 and Atlas pl. 47.

Canarium occidentale A. Chev., Lecomte, H. (1923) p. 155.

Canarium oleosum Engler, Boorsma (1907) pp. 28-32.

Canarium ovatum Engler, Kanehira, R. (1924*b*) p. 17; Pearson, R. S. and Brown, H. P. (1932) p. 217.

Canarium resiniferum Brace., Troup, R. S. (1909) p. 99.

Canarium Schweinfurthii Engl., Lecomte, H. (1923) p. 155.

Canarium sikkimense King, Gamble, J. S. (1922) p. 140; Pearson, R. S. and Brown, H. P. (1932) pp. 228-229; Troup, R. S. (1909) p. 99.

Canarium strictum Roxb. Gamble, J. S. (1922) p. 141; Pearson, R. S. and Brown, H. P. (1932) pp. 229-231.

Canarium tonkinense Engl. Lecomte, H. (1925) pp. 147-148 and Atlas pl. 47.

Canarium zeylanicum Bl. Gamble, J. S. (1922) p. 141.

Commiphora sp. Guillaumin, A. (1909) p. 279.

Commiphora Fischeri Engl., Spiekerkotter, H. (1924) p. 299.

Commiphora glabrata Engl., Spiekerkotter, H. (1924) p. 298.

Commiphora heterozygia A. Peter, Spiekerkotter, H. (1924) p. 307.

Commiphora holosericea Engl., Spiekerkotter, H. (1924) p. 296, fig. 18.

Commiphora holtziana Engl., Spiekerkotter, H. (1924) p. 304.

Commiphora Mildbraedii Engl., Spiekerkotter, H. (1924) p. 303.

Commiphora morogorensis Engl., Spiekerkotter, H. (1924) p. 308.

Commiphora myrrha Engl., Marchand, L. (1866) pp. 262-263, pl. 8. figs. 1-3 (as *Balsamodendrum myrrha* Nees); Pearson, R. S. and Brown, H. P. (1932) p. 217.

Commiphora opobalsamum (Knuth) Engl., Marchand, L. (1867*a*) p. 57 (as *Balsamodendrum opobalsam*).

Commiphora pilosa Engl., Spiekerkotter, H. (1924) p. 300.

Commiphora serrata Engl., Spiekerkotter, H. (1924) p. 309.

Commiphora spinosa A. Peter., Spiekerkotter, H. (1924) p. 306.

Commiphora Stocksiana Engl., Gamble, J. S. (1922) p. 139 (as *Balsamodendron mukul* Hook.); Sabnis (1920) (as *Commiphora mukul* Engl.).

Commiphora subcrenata A. Peter, Spiekerkotter, H. (1924) pp. 297-298.

Commiphora trothae Engl., Spiekerkotter, H. (1924) p. 305.

Commiphora ukolola Engl., Spiekerkotter, H. (1924) p. 300.

Commiphora voensis Engl., Spiekerkotter, H. (1924) p. 304.

Commiphora zanzibarica Engl., Spiekerkotter, H. (1924) p. 302.

Commiphora Zimmermannii Engl., Spiekerkotter, H. (1924) p. 305.

Crepidospermum Goudotianum (Tub.) Tr. et Pl., Williams, L. (1936) p. 232.

Dacryodes sp. Jadin, F. (1893) p. 389; Lecomte, H. (1923) p. 155 (as *Pachylobus* sp.).

Dacryodes excelsa Vahl, Brush, W. D., Murphy, L. S., and Mell, C. D. (1916) p. 77; Record, S. J. and Mell, C. D. (1924) p. 340.

Dacryodes incurvata (Engl.) H. J. Lam (as *Santiria nitida* Merr.) Kanehira, R. (1924*b*) p. 17; Record, S. J. (1918) fig. 5;

Record, S. J. (1921) p. 257; Schneider, E. E. (1916) p. 130.

Garuga sp. Berger, L. G. Den and Bianchi, A. T. J. (1931) p. 898; Guillaumin, A. (1909) p. 283; Pearson, R. S. and Brown, H. P. (1932) p. 217; Record, S. J. (1921) p. 257.

Garuga floribunda Decne., Berger, L. G. Den (1926) pp. 67-68 and Atlas, fig. 45 (as *G. pinnata* Roxb.); Foxworthy, F. W. (1909) p. 476 (as *G. pinnata* Roxb.); Lane-Poole, C. E. (1925) p. 98 (as *Garuga* sp.); Lecomte, H. (1925) p. 146 (as *G. abilo* Merr.); Moll, J. W. and Janssonius, H. H. (1908) p. 93 and fig. 89 (as *G. pinnata* Roxb.); Schneider, E. E. (1916) p. 129 (as *G. abilo* Merr., as *G. Clarkii* Merr., and as *G. littoralis* Merr.).

Garuga pinnata Roxb. Chowdhury, K. A. (1932) p. 13 & pl. 16; Gamble, J. S. (1922) p. 138-139; Pearson, R. S. and Brown, H. P. (1932) pp. 221-224.

Protium sp. Pearson, R. S. and Brown, H. P. (1932) p. 217; Record, S. J. (1921) p. 257.

Protium acuminatum W. et A., Lecomte, H. (1920).

Protium altissimum (Aubl.) L. March., Dixon, H. H. (1918); Hill, L. M. (1902) (as *Icica altissima* Aubl.); Lecomte, H. (1920) (as *Icica altissima* Aubl.); Record, S. J. (1921) p. 257; Record, S. J. and Mell, C. D. (1924) p. 335.

Protium australasicum T. A. Sprague, Dadswell, H. E. and Eckersley, A. M. (1935) p. 45.

Protium carana (H. B. K.) March., Williams, L. (1936) p. 233.

Protium caudatum W. et A. Gamble. J. S. (1922) p. 139 (as *Balsamodendron caudatum* March.); Troup, R. S. (1909) p. 83.

Protium crassifolium (Rich.) Engl., Williams, L. (1936) p. 233.

Protium divaricatum Engl., Stepowski, M. (1903) p. 22.

Protium glaucum Macbr., Williams, L. (1936) p. 233.

Protium grandifolium Engl., Stepowski, M. (1903) p. 22.

Protium heptaphyllum March., Record, S. J. and Mell, C. D. (1924) p. 335; Stepowski, M. (1903) p. 16 & fig. 1; Williams, L. (1939) pp. 12, 15 y 54.

Protium javanicum Burman., Berger, L. G. Den (1926) pp. 68-69 & Atlas fig. 46; Foxworthy, F. W. (1909) p. 476; Moll, J. W. and Janssonius, H. H. (1908) p. 98 & fig. 90.

Protium Llewelyni Macbr., Williams, L. (1936) p. 234.

Protium medianum Macbr., Williams, L. (1936) p. 234.

Protium obtusifolium Marchand, L. (1876*b*) pl. 3, figs. 1-2.

Protium panamensis Rose, Record, S. J. and Mell, C. D. (1924) pp. 336-337.

Protium pubescens Engl., Stepowski, M. (1903) p. 22.

Protium puncticulatum Macbr. Williams, L. (1936) p. 235.

Protium Schomburgkiana Engl., Kribs, D. A. (1928) p. 14 (as *Icica Schomburgkiana* Engler).

Protium serratum (Colebr.) Engler, Chowdhury, R. A. (1932) p. 14 and pl. 21 (as *Bursera serrata* Colebr.); Foxworthy, F. W. (1909) p. 476 (as *Bursera serrata* Colebr.); Gamble, J. S. (1922) p. 140 (as *Bursera serrata* Colebr.); Pearson, R. S. and Brown, H. P. (1932) pp. 224-226 (as *Bursera serrata* Colebr.); Sieck, W. (1895) p. 220 and pl. 7, figs. 24-25 (as *Icica bengalensis*); Stepowski, M. (1903) p. 23 and fig. 7 (as *Icica bengalensis*).

Protium subserratum Engler, Williams, L. (1936) p. 235.

Protium tenuifolium Engler, Williams, L. (1936) p. 236.

Santiria sp. Bargagli-Petrucci, G. (1903*b*) pp. 314-315 and pl. 7; Berger, L. G. Den and Bianchi, A. T. J. (1931) p. 897-898; Guillaumin, A., (1909) pp. 257-260; Pearson, R. S. and Brown, H. P. (1932) p. 217.

Santiria Griffithii (Hook. f.) Engl., Foxworthy, F. W. (1909) p. 476 (as *Trigonochlamys Griffithii* Hook. f.).

Santiria oblongifolia Blume Foxworthy, F. W. (1909) p. 476.

Tetragastris balsamifera (Sw.) O. Kuntze, Brush, W. D., Murphy, L. S. and Mell, C. D. (1916) p. 77; Record, S. J. and Mell, C. D. (1924) p. 339.

Trattinickia burseraefolia Mart., Guillaumin, A. (1909) p. 216.

Trattinickia rhoifolia, Willd., Guillaumin, A. (1909) p. 216.

Triomma malaccensis Hook. f., Guillaumin, A. (1909) p. 268.

The present study of the woods of the *Burseraceae*, in conjuction with the previously published descriptions referred to above, indicates that despite marked differences in texture prevailing between certain specimens, such as those of *Aucoumea* and *Crepidospermum* (Plate 3, figures 3 and 4), there is a fundamental structural similarity between the woods of all genera of the family. This being the case, it would be impossible to construct a satisfactory anatomical key to the woods of the various genera in view of the variations shown to occur within the secondary wood of a single plant (Plate 2, figures 1-5). Accordingly, descriptions of the various species and genera are herein omitted. In the following description of the woods of the family *Burseraceae*, the terms used are those proposed by the Commitee on Nomenclature of the International Association of Wood Anatomists (1933).

Anatomical description of the woods of the Burseraceae

GROWTH RINGS

All of the woods of the *Burseraceae* are diffuse porous, and growth rings are frequently absent. When present, growth rings may be faintly delimited or readily visible, numbering about 5-20 per inch. They are generally marked by but slight differences in number of vessels and diameter of fibers and vessels.

VESSELS

Pores (Plate 2, figs. 1-3 ; Plate 3, figs. 1-4) are mostly solitary or in radial multiples of 2-8, but some irregular clusters of 3-10 are occassionally present. The number per sq. mm. ranges from 5-30, but is commonly about 10-15. The radial diameter of solitary pores ranges from 45 μ (in *Crepidospermum*) to 350 μ (in *Aucoumea*), and is generally about 110-200 μ, while the tangential diameter varies from 40 μ (in *Crepidospermum*) to 205 μ (in *Aucoumea*) and is most frequently about 100-180 μ. Vessel members (Plate 4, figs. 6, 7) vary in form from cylindrical to irregular and in length from 100 μ (in *Crepidospermum)* to 900 μ (in *Canarium ovatum)* but are mostly about 300-500 μ long. Their perforation plates are either horizontal or oblique, and either at the ends of the vessel members or some distance from the ends. The perforations are exclusively simple in all woods of the family that have been examined. Perforation rims are sometimes rather large, and may have pits resembling those of the lateral walls. The lateral walls of the vessels are commonly about 2-4 μ thick and have numerous alternate pits. Intervascular pit-pairs (Plate 1, figs. 2, 5, 6, 7 ; Plate 2, fig. 4) are bordered. The borders are commonly 4-6 angular and more or less crowded, but sometimes the are round. Their diameter ranges from 4,5-17 μ, but is usually about 9-10 μ. The apertures are elliptic or slit-like, commonly oblique, sometimes extended (Plate 1, figs. 6, 7). Ray-vessel and parenchyma-vessel pitting (Plate 1, fig. 1; Plate 4, figs. 8-10) is sometimes unilaterally compound ; when pit-pairs are present they may be half-bordered or simple. Parenchyma-vessel pit-pairs are apparently more often simple than ray-vessel pit-pairs and also attain a larger size; they are often much elongated, sometimes attaining a length of as much as 36 μ; such elongated simple pit-pairs are generally scalariform in arrangement. Although reticulate thickenings on the lateral walls of vessels have been reported in *Commiphora Fischeri* and *Commiphora subcrenata* by Spiekerkotter (1924), in *Canarium littorale* by Moll and Janssonius (1908) and in *Aucoumea Klaineana* by Jentsch and Appel (1936), their absence in the specimens examined by the writer suggests that false spirals due to extended apertures of the vessel pits may have been misinterpreted. Vessels are often more or less completely filled whith thin-walled tyloses wich may contain starch grains, gum, or crystals. Gum deposits are also common in vessels.

WOOD FIBERS

The ground mass of the wood of all species examined consists of libriform wood fibers (Plate 4, figs. 1-4) which are frequently septate and more or less distinctly radially arranged. They vary in diameter from 12-50 μ, and in length from 300-1850 μ. Their walls are about 2-5 μ thick, the radial ones having simple slit-like to roundish pits which may be rather sparse and minute, as in *Aucoumea*, or numerous and quite conspicuous as in *Bursera, Boswellia* and *Commiphora.* In septate libriform wood fibers the number of septa varies from 3-6 per fiber. The cells formed by the septa near the central portion of a fiber are generally shorter than the terminal cells in the same fiber lumen. The fibers may contain starch grains (Plate 2, figs. 1-5), crystals, or brownish gummy masses (Plate 4, fig. 2). In some specimens of *Protium* (Plate 3, fig. 1) gum-filled fibers occur in widely spaced tangential bands 2 or more cells wide. Such bands of fibers with brownish contents are sometimes wider in the vicicinity of pith flecks than elsewhere, and scattered gum-filled fibers are generally most numerous in the vicinity of such bands.

WOOD PARENCHYMA

In all specimens examined, the normal wood parenchyma is sparse and exclusively paratracheal. Usually it completely or partially borders all vessels, forming sheaths 1-3, or rarely more, cells wide, but it may be entirely lacking around some of the vesells of certain specimens. The parenchyma cells occur in strands 2-12, usually 4-8 cells long (Plate 4, fig. 5). They are frequently peripherally flattened, and vary in diameter from 5-40 µ, and in length from 25 to 130 µ. Occassionally the cells are disjunctive. The cell walls are usually about 1 µ thick and have numerous simple pits which are commonly small to moderate size and round or oval when in contact with parenchyma or fibers, but often large and elongated when in contact with vessels. According to Peter (1903), some of the parenchyma cells in *Boswellia Carteri* are septate. Brownish gum frequently is present in the parenchyma cells, and starch grains and crystals (Plate 3, fig. 5) have also been observed. Although Solereder (1908) reported that parenchyma is « more abundant » in *Boswellia papyrifera* Hochst., he did not discuss its distribution in this species. In addition to paratracheal parenchyma similar to that observed in the present study, diffuse parenchyma has been reported by Kanehira (1921) (2924 *a*) (1924 *b*) in *Canarium hirsutum* (syn. *C. ahernianum* and *C. Radlkoferi*). *C. calophyllum*, *C. ovatum*, *C. album*, *Dacryodes incurvata* (syn. *Santiria nitida*), and *Boswellia serrata*, and by Dixon (1918) in *Protium altissimum*; and broken tangential lines or concentric bands of parenchyma from 1-4 cells wide have been reported in *Canarium sikkimense* by Pearson and Brown (1932), in *Commiphora subcrenata*, *C. zanzibarica* and *C. Mildbraedii* by Spiekerkotter (1924), in *Protium* by Williams (1936), in *Protium altissimum* by Dixon (1918) and in *Santiria* sp. by Bargagli-Petrucci (1903 *b*).

PITH FLECKS AND TRAUMATIC VERTICAL CANALS

Vertical traumatic gum ducts have been reported in the secondary wood of *Protium* (Record (1921), Record and Mell (1924), Pearson and Brown (1932)), *Canarium* (Svendsen (1905), Record (1921), Record and Mell (1924), Den Berger and Bianchi (1931), Pearson and Brown (1932)), and *Santiria* (Tav. VII, Bargagli-Petrucci (1903 *b*); and as « Santiara » by Den Berger and Bianchi (1931)). According to Svendsen (1905), in *Canarium commune* L., deep wounding over a large area caused the subsequently formed wood to contain a broad band of traumatic parenchyma in which was embedded a tangential row of vertical, schizolysigenous gum ducts. Following less severe wounding of this species, traumatic parenchyma without ducts was formed.

In the burseraceous wood specimens examined by the writer, no well developed vertical gum ducts were present. Pith flecks, of considerable size and abundance in some specimens, were noted in *Protium panamense*, *P. copal* (Plate 3, fig. 2), *P. tenuifolium*, *P. guianense*, *P. sessiliflorum*, *P. carana*, *P. medianum*, *P. Llewelyni*, *Crepidospermum Goudotianum*, *Tetragastris panamensis*, *Bursera Simaruba*, *Dacryodes rostrata*, *Canarium mafoa*, *C. mehenbethene*, *C. littorale*, *C. Boivini*, *C. Zollingeri* and *C. rufum*. In many of these specimens the traumatic parenchyma cells forming the pith flecks were partially or completely filled with reddish or brownish gum. In some pith flecks of *Protium copal*, *Crepidospermum Goudotianum* and *Canarium mafoa*, short tangential rows of intercellular spaces of very limited extent were observed (Plate 3, fig. 3), suggesting that traumatic vertical canals may be present under certain conditions. According to Peter (1903), pith flecks also occur in *Boswellia Carteri*.

VERTICAL CANALS IN THE PITH AND PRIMARY WOOD

Schizolysigenous vertical intercellular canals were reported by Sieck (1895) to be present in the primary wood of *Protium serratum* (Colebr.) Engler (syn. *Icica bengalensis*) but lacking in his specimens of the secondary wood of this species. Since Solereder (1908) recorded the presence of canals in the pith of this species, although they were reported as lacking by Stepowski (1903) and unobserved by Guillaumin (1909), it is possible that the canals observed by Sieck may have been in the pith adjoining the primary wood rather than in the primary wood itself. This possibility is further suggested by the report of Lam (1932 *a*) of the widespread occurrence in the Canarieae of canals located in the phloem of medullary vascular bundles, some of which adjoin the primary wood.

RAYS

Some uniseriate rays are present in all of the woods examined, and they are the predominant type in some specimens of *Crepidospermum Goudotianum* (Plate 1, fig. 7), *Tetragastris balsamifera, T. Stevensonii* (Plate 1, fig. 6), *Protium Llewelyni, P. subserratum, P. carana, P. puncticulatum, P. Schomburgkiana, P. copal, P. panamense, Santiria tomentosa, S. apiculata, S. laevigata, S. oblongifolia, S. Griffithii, Dacryodes incurvata* and *D. rostrata*. The uniseriate rays are often composed exclusively of upright cells, but sometimes are partially composed of procumbent cells. They vary in width from 11-38 μ, and in height from 1-41 cells or 22-957 μ. In addition to uniseriate rays, there are present, in varying abundance, heterogeneous rays with a maximum width of 2-16 cells or 19-340 μ, and a height of 92-1518 μ. The upright cells of the multiseriate rays are commonly restricted to the margins of the rays (Plate 1, figs. 3, 5, 6, 8), but may be present elsewhere, particularly in rays that appear to be formed by the fusion of several smaller rays (Plate 1, fig. 1). In radial section (Plate 3, figs. 5-7), the upright cells vary in form

from squarish to palisade-like with much greater vertical than radial diameters. Either or both types of upright cells may characterize a given specimen. Occassionally (in *Canarium Boivinii*) the upright cells are irregular in shape. Disjunctive upright cells are sometimes present. According to Solereder (1908), large thin-walled oil cells were reported by Moeller (1897) in *Bursera aloexylon* Engl. Although Solereder does not state the location of these oil cells, and Moeller's article was unobtainable, in view of the usual scarcity of vertical wood parenchyma in the *Burseraceae* their expected location would be among the upright ray cells. Unusually large upright cells, most of which, however, contained large solitary crystals, or rarely several crystals, were irregularly distributed along the margins of rays in *Protium heptaphyllum, P. tenuifolium, P. guianense, P. sessiliflorum, P. Schomburgkiana, P. denticulatum, P. carana, P. crassifolium, P. insigne, Tetragastris panamensis, T. balsamifera, Garuga floribunda, G. pinnata, Commiphora Stocksiana, Bursera simaruba, B. serrata, Triomma malaccensis, Canarium asperum, C. rufum, C. velutinum, C. kipella, C. sumatrana* (Plate 3, fig. 7), *C. salomense, C. littorale, C. denticulatum, C. luzonicum* and *Dacryodes incurvata*.

Procumbet cells of heterogeneous rays vary somewhat in the amount by which their radial diameters exceed their other diameters, and the degree of differentiation between upright and procumbent cells is a widely variable feature in the *Burseraceae* (Plate 3, figs. 5-7). Ray cells often contain starch, gum or crystals. Although the crystals are much commoner in the upright cells (Plate 3, figs. 5, 7) than in the procumbent cells, they are occasionally present in the latter. According to Bargagli-Petrucci (1903 *a*) (1903 *b*), silica bodies are present in all of the ray cells of some species of *Canarium*. The walls of the ray cells are about 1 μ thick, the tangential walls being slightly thicker than the others. They are well provided with simple pits which are small and roundish to elliptic except in contact with vessels. In the latter positions the pits are generally larger, often much elongated and scalariformly arranged.

RADIAL CANALS

Canals were observed in scattered multiseriate rays of the secondary wood of *Protium copal* (Plate 1, fig. 5), *P. guianense* (Plate 1, fig. 8), *P. sessiliflorum, P. Schomburgkiana, P. puncticulatum* (Plate 1, fig. 4), *P. crassifolium, Tetragastris panamensis* (Plate 3, fig. 6), *T. balsamifera, Garuga floribunda, G. pinnata, Boswellia serrata* (Plate 1, fig. 2), *Triomma malaccencis, Bursera Simaruba, B. graveolens, B. glabra, B. glabrifolia, B. tomentosum, B. microphylla* (Plate 2, figs. 1-5), *Commiphora Stocksiana, C. Zimmermanni, Dacryodes incurvata, Canarium vitiense, C. luzonicum, C. mehenbethene, C. odontophyllum, C. commune, C. mafoa, C. rufum, C. littorale* (Plate 1, fig. 3) and *Canariellum oleiferum*. Other species in which similar canals have been reported previously are : *Canarium ovatum* Engl. (Kanehira (1924 *b*), *Protium australasicum* T. A. Sprague (Dadswell and Eckersley (1935), *Protium altissimum* (Aubl.) L. March. and *Protium acuminatum* W. et A. (Lecomte (1920), and *Commiphora serrata* Engl. (Spiekerkotter (1924). Their reported occurrence in the genus *Santiria* (Kanehira (1924*b*), Record (1918) (1921), Record and Mell (1924), Pearson and Brown (1932), Den Berger and Bianchi (1931) is apparently based on their prevalence in the species formerly known as *Santiria nitida*, but now classified as *Dacryodes incurvata*. It is, of course, possible that examination of additional material may reveal their presence not only in *Santiria*, but in other genera of the family in which they have not yet been reported.

The canals are commonly roundish to broad elliptic in tangential section, and in wood of old stems usually vary in diameter from about 40-150 μ. Unusually large canals reaching a maximum diameter of 570 μ were observed in *Protium puncticulatum* (Plate 1, fig. 4). While from one to five canals may occur in a ray, in most species rays containing more than two canals each are comparatively rare. The canals are frequently more or less completely filled with gum. Usually the canal is bordered by one to several layers of ephithelial cells which are smaller in tangential section than ordinary ray cells. The abundance and

degree of differentiation of the epithelial cells is rather variable (Plate 1, figs. 2, 3, 5, 8; Plate 2, fig. 4). Occasionally the canals are more or less completely filled with tylosoids (Plate 1, figs. 5 & 8). In *Bursera microphylla*, and probably the other species of the family also, the intercellular canals in xylem rays are continuous with those in phloem rays (Plate 2, fig. 1). In at least some cases the radial canals in the phloem connect with vertical canals (Plate 2, fig. 1) which, contrary to Solereder (1908), were reported by Guillaumin (1909) to be a characteristic feature of the secondary phloem of all of the *Burseraceae* including *Aucoumea*. As pointed out by Lecomte (1920) in the case of similar intercellular canals in the *Anacardiaceae*, the radial canals of the *Burseraceae* are apparently restricted to the secondary rays. Radial intercellular canals were lacking in numerous sections of one year old stems of *Bursera microphylla*, but were abundant in older stems of the same specimen. In this specimen, the multiseriate xylem rays formed during the second year of growth (Plate 2, fig. 5) are considerably narrower than those formed in older stems (Plate 2, fig. 4), but occasionally contain a single canal. Despite the apparent absence of radial intercellular canals in xylem formed during the first year of growth, such canals occasionally extend to the pith at points where there are leaf gaps (Plate 2, fig. 3). According to Tschirch (1888) and Lecomte (1920), the normal canals in the *Burseraceae* are developed schizogenously.

Discussion

Several investigators have discussed evidences of specialization within the *Burseraceae*. Bews (1927) believed that the ecology of the family indicates that the genus *Commiphora* is a relatively advanced type. Sinia (1938) suggested that greater compounding of the leaves occurs in the more advanced forms. Lam's (1932*b*) extensive studies of the distribution of the family led him to conclude that the primitive *Burseraceae* originated in America and reached the far East via Africa. In addition to presenting his distributional evidence regarding the relative ages of the burseraceous genera, Lams' (1931) (1932*a*) morphological studies enabled him to compare a number of evolutionary tendencies and index the relative specialization of the tribes and some of the genera. His indices show the least specialization in *Protium* and the Protieae and the most in *Canarium* and the Canarieae.

As indicated above, there is no evidence that the wood structure of the Asiatic species of *Protium* is more specialized than that of the American species of this genus, that the woods of species having many leaflets are more specialized than those of species characterized by leaves with few leafles, nor that the woods of *Canarium* or *Commiphora* are of more specialized structure than those of *Protium*. While the relatively advanced feature of metatracheal parenchyma reportedly characterizes a few species of *Canarium* and *Commiphora*, this same feature has also been reported to occur in and American species of *Protium*. The basic similarity in the wood structure of all genera of the *Burseraceae* therefore indicates that in this family specialization in structure of fruits, flowers and leaves has proceeded at a more rapid rate than in the woods.

With regard to the relationships of the *Burseraceae* to other families, it has already been pointed out that the *Burseraceae* were formerly united with the *Anacardiaceae* in the group known as *Terebinthaceae*, but are now generelly considered to be close relatives of the *Rutaceae, Simarubaceae* and *Meliaceae*. Jadin (1894) suggested that the *Simarubaceae* arose along a direct line from the *Terebinthaceae (Burseraceae)* and that the *Meliaceae* and *Rutaceae* were successive off-shoots of this line. Bews (1927), on ecological grounds, regarded the *Burseraceae, Meliaceae* and *Simarubaceae* as relatively primitive, and the *Rutaceae* as more advanced. Sinia (1938), from observations on evolutionary tendencies of compound leaves, considered the *Rutaceae* as relatively primitive among the groups under consideration. Lam (1932*b*) expressed the opinion that the family *Burseraceae*, while undoubtedly closely akin to the *Rutaceae, Meliaceae* and *Simarubaceae*, and not so closely allied to the *Anacardiaceae* as was once believed, is nevertheless closely connected with the *Anacardiaceae*. In his diagram of the supposed phylogenetic relationships of the *Burseraceae*, the *Anacardiaceae* are shown as a branch of the line giving rise to the *Rutaceae*. Immediately above the *Rutaceae* are divergent lines which terminate in the *Meliaceae* and *Simarubaceae*, while the *Burseraceae* stem from the same line as the latter family.

Since similar wood anatomy has been advanced by Lam (1932*b*) as evidence that *Burseraceae* and *Anacardiaceae* are closely related, the existence of certain dissimilarities in the wood structure of the *Burseraceae* and *Anacardiaceae*, as well as the similarities in wood structure of the *Burseraceae, Simarubaceae, Rutaceae* and *Meliaceae* should be considered here. A survey of the accounts of the structure of the woods of the above mentioned families (Chalk (1937), Dadswell and Eckersley (1938), Kribs (1930), Record (1927) (1936) (1939), Record and Hess (1940), Solereder (1908), Webber (1936)) shows that the woods of the *Burseraceae* are by far the least variable, and that each of the diagnostic features of that family occurs in one or more of the others families.

Within each of families *Burseraceae, Anacardiaceae, Simarubaceae, Rutaceae* and *Meliaceae*, some of the woods have, the following characteristic. Diffuse porous woods; with pores solitary, in radial multiples of 2-several, or in small clusters; simple perforations in at least some of the vessels; vessels frequently more or less completely filled with gum or tyloses; vessel-ray pit-pairs in part half-bordered. Parenchyma paratracheal as defined by Chalk (1937), variable in amount, sometimes in crystaliferous strands. Libriform wood fibers, some of which are septate, are the principal element of the wood, and often contain gum. Rays 1-10 cells wide, but generally in parte uniseriate and in part 2-5 seriate, weakly to markedly heterogeneus, frenquently containing crystals.

The woods of the *Burseraceae* and *Anacardiaceae* further resemble each other in that some of the rays of some genera contain normal intercellullar canals: storied structure is absent: and ray-vessel and parenchyma-vessel pit-pairs are frequently simple and much elongated. In comparing these characteristics with those of the *Simarubaceae, Rutaceae* and *Meliaceae*, it is found that normal radial canals are lacking in the latter families, but that short, traumatic, radial gum cavities have been reported by Webber (1938) in the *Simarubaceae* in *Ailanthus, Klainedoxa* and *Odyendea*, and in the *Rutaceae* in *Citrus* : that storied structure, while lacking in many of the members of the *Simarubaceae, Rutaceae* and *Meliaceae,* is present in some species, having been reported in the *Simarubaceae* in *Cadellia, Suriana, Picraena, Picrasma, Simaruba, Samadera, Simaba, Odyendea, Hannoa, Harrisonia, Castela, Brucea, Aeschrion, Ailanthus, Soulamea* and *Amaroria* ; in the *Rutaceae* in *Chloroxylon* and *Esenbeckia* ; in the *Meliaceae* in *Entandrophragma, Xylocarpus, Swietenia, Pseudocedrela, Khaya, Chickrassia, Cedrela, Carapa* and *Guarea* : and that ray-vessel and parenchyma-vessel pit-pairs are simple, although not elongated, in the *Rutaceae* in *Orixa* and *Skimmia.*

The woods of the *Burseraceae* further resemble those of the *Simarubaceae, Rutaceae* and *Meliaceae* in that vertical traumatic canals, similar to those reported in the *Burseraceae* have also been reported in the *Simarubaceae* in *Samadera, Simaruba, Eurycoma, Castela, Picraena, Ailanthus* and *Soulamea* ; in the *Rutaceae* in *Citrus, Balfourodendron, Esenbeckia, Euxylophora, Flindersia, Helietta, Metrodorea, Pilocarpus, Ravenia* and *Zanthoxylum* ; and in the *Meliacea* in *Carapa, Cedrela, Dysoxylon, Entandrophragma, Khaya, Lovoa, Melia, Sandoricum* and *Swietenia.* Apparently no such canals have been reported in the secondary wood of any of the *Anacardiaceae.*

The woods of the *Anacardiaceae, Simarubaceae, Rutaceae* and *Meliaceae,* further resemble each other but differ from those of the *Burseraceae* in that some of the vessels have scalariform perforation plates with few to many bars in the *Anacardiaceae* in *Campnosperma, Micronychia* and *Anaphrenium* : in the *Simarubaceae* in *Ailanthus* ; in the *Rutaceae* in *Adiscanthus, Leptothyrsa, Boenninghausenia, Calodendron, Adenandra, Barosma, Agathosma, Acronychia, Clausena* and *Paramignya* : the woods are ring-porous in the *Anacardiaceae* in *Poupartia, Cotinus, Rhus, Toxicodendron* and *Pistacia* ; in the *Simarubaceae* in *Ailanthus* and *Picraena* ; in the *Rutaceae* in *Evodia, Orixa, Phellodendron* and *Ptelea* ; and in the *Meliaceae* in *Melia, Cedrela* and *Toona.*

In summarizing these comparisons it is evident that the woods of all five families have many structural features in common. However, certain structural features which are absent in the *Burseraceae* are shared by the more variable woods of the *Anacardiaceae, Simarubaceae, Rutaceae* and *Meliaceae,* while among these families other features have been reported only in the *Burseraceae* and *Anacardiaceae* ; or in the *Burseraceae, Simarubaceae, Rutaceae* and *Meliaceae* ; or in the *Simarubaceae, Rutaceae* and *Meliaceae.* Hence it may be concluded that the wood structure of the *Burseraceae,* rather than presenting evidence for grouping this family with the *Anacardiaceae* instead of with the *Simarubaceae, Rutaceae* and *Meliaceae,* is more suggestive of the probable common ancestory of all five families.

With regard to the above outlined concepts of the Phyllogeny of these families, it should be noted that Chalk's (1937) studies of wood parenchyma and storied structure led him to the decision that the woods of the *Anacardiaceae, Burseraceae* and most *Rutaceae* show intermediate specialization, while the *Meliaceae, Simarubaceae* and a small fraction of the *Rutaceae* are highly specialized. The woods of all five of these families are characterized by such specialized structural features as vessels with simple perforation plates, pores multiples, septate, libriform fibers and paratracheal parenchyma ; but they also exhibit such unspecialized features as diffuse porousness, solitary pores, multiseriate and heterogeneous rays. In comparison with the *Burseraceae,* both less specialized structure, such as the presence of scalariform perforation plates in some vessels, and more specialized structure, such as ring-porousness, occur in the *Anacardiaceae, Simarubaceae* and *Rutaceae.* Still further specialization, as evidenced by storied structure, occurs in some of the *Rutaceae, Simarubaceae* and *Meliaceae.* Thus, so far as wood structure is concerned, the *Meliaceae* is obviously the most specialized of the five families under consideration, and somewhat greater specialization occurs within the *Rutaceae* and *Simarubaceae* than within the *Anacardiaceae* and *Burseraceae.* The occurrence of traumatic intercellular cavities in the rays of the *Simarubaceae* and *Rutaceae* suggests the origin of these families from plants with normal intercellular cavities or canals in their rays. Such cavities occur in some *Burseraceae* and *Anacardiaceae.*

Summary. — *Systematic anatomy of the woods of the « Burseraceae».* — The author describes the anatomy of the wood of the *Burseraceae* and compares it with that of the *Anacardiceae, Rutaceae, Simarubaceae* and *Meliaceae.* The similarities in structure of their woods suggest the probability of common extraction of these families. The woods of the *Meliaceae* show the most specialization, and those of the *Simarubaceae* and *Rutaceae* show somewhat more specialization than those of the *Burseraceae* and *Anacardiaceae.* Traumatic intercellular cavities in the rays of the *Simarubaceae* and *Rutaceae* suggest the origen of these families from plants such as the *Burseraceae* and *Anacardiaceae* that have normal intercellular canals in their rays.

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Plate I

1. *Canariellum oleiferum* (Baill.) Engler.
2. *Boswellia serrata* Roxb.
3. *Canarium littorale* Bl.
4. *Protium puncticulatum* Macbr.
5. *Protium Copal* Engl.
6. *Tetragastris Stevensonii* Standl.
7. *Crepidospermum Goudotianum* Tr. et Pl.
8. *Protium guianense* (Aubl.) March.

Tangential sections of burseraceous woods. × 70

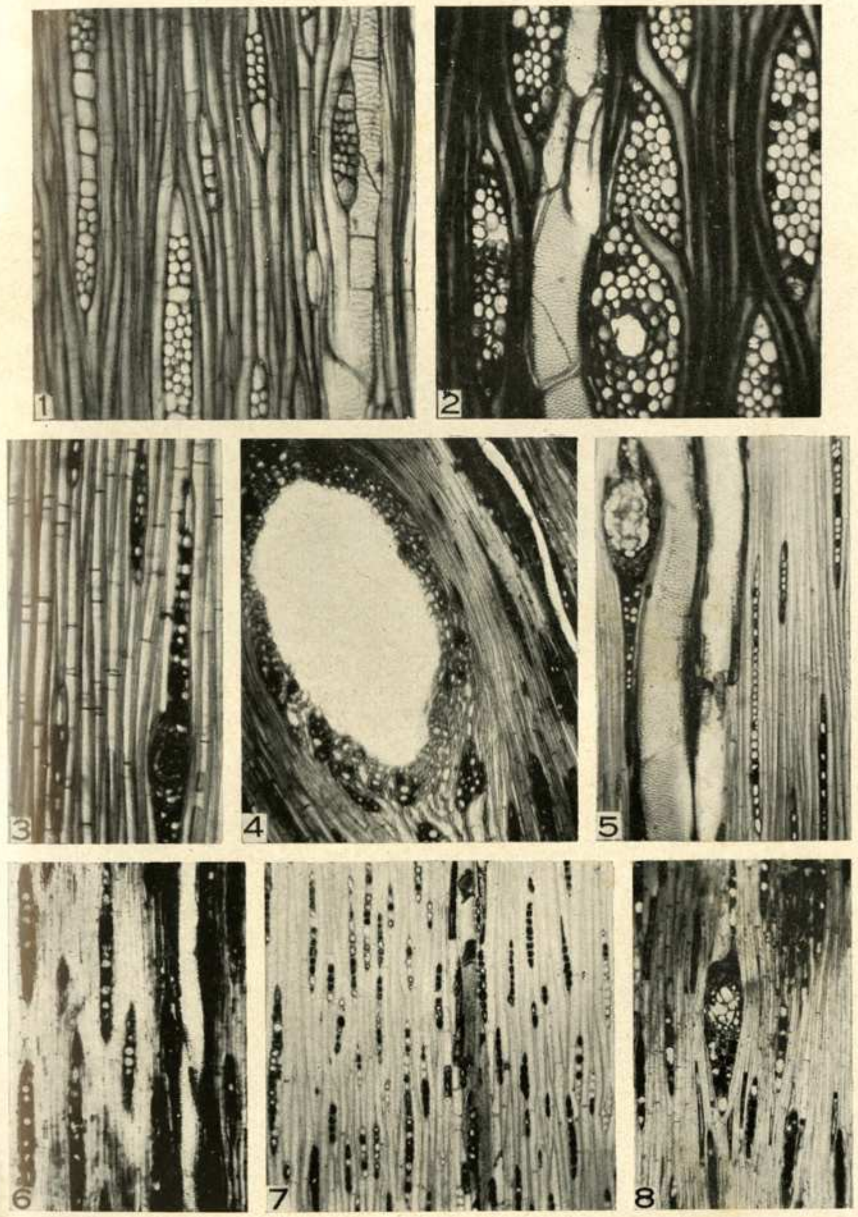

PLATE II

1. Cross section of a portion of a young stem showing radial canal continuous between xylem and phloem where it is united with a vertical canal.
2. Cross section of wood of an old stem.
3. Cross section of portion of a young stem showing a radial canal in the secondary xylem extending to the pith in the vicinity of a leaf gap.
4. Tangential section of wood of an old stem showing portion of a large ray in which four canals are visible.
5. Tangential section of xylem of a two year old stem. This is the youngest wood in which any radial canals were observed.

Bursera microphylla Gray. × 82

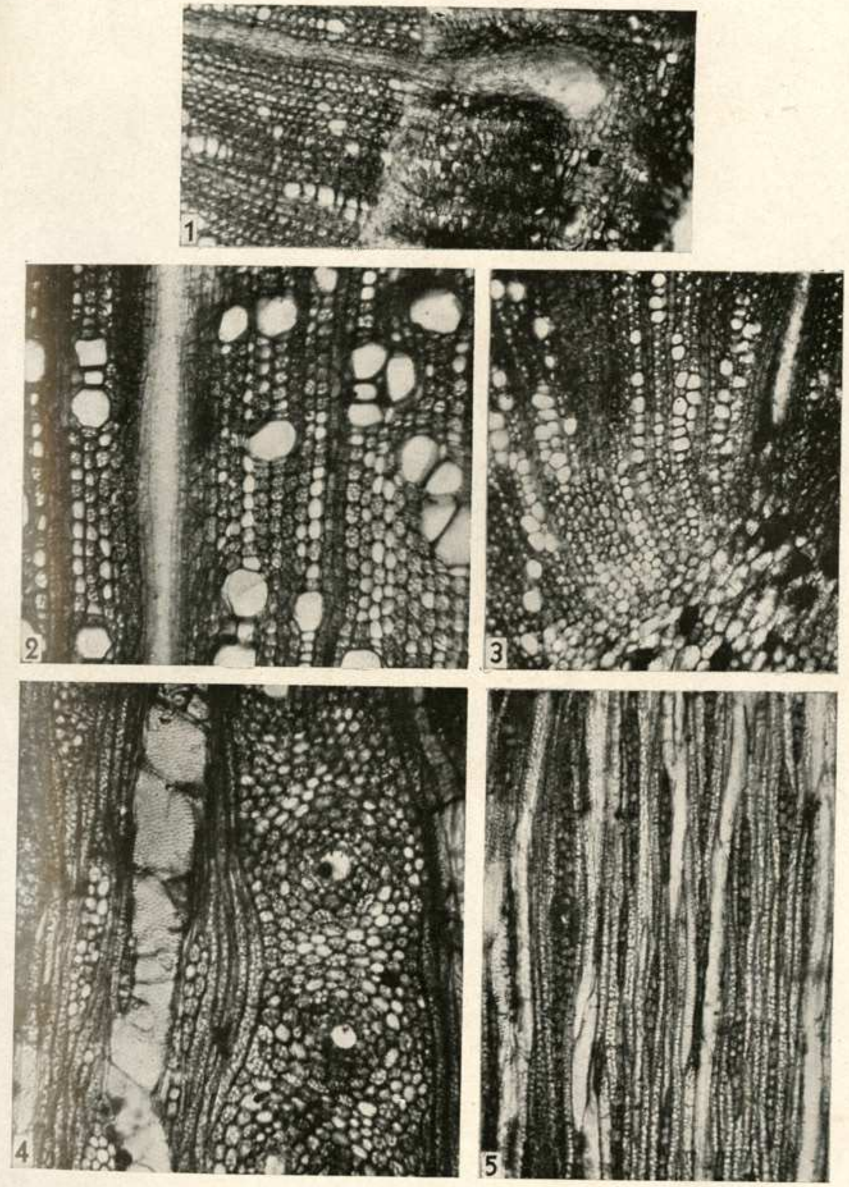

Plate III

1. *Protium Llewelyni* Macbr.
2. *Protium Copal* Engl.
3. *Aucoumea Klaineana* Pierre.
4. *Crepidospermum Goudotianum* Tr. et Pl.
5. *Canarium mehenbethene* Gaertn.
6. *Tetragastris panamensis* Kuntze.
7. *Canarium sumatrana* Boerl. et Koord.

Burseraceous woods. × 70. Figures 1-4 cross sections figures 5-7 radial sections

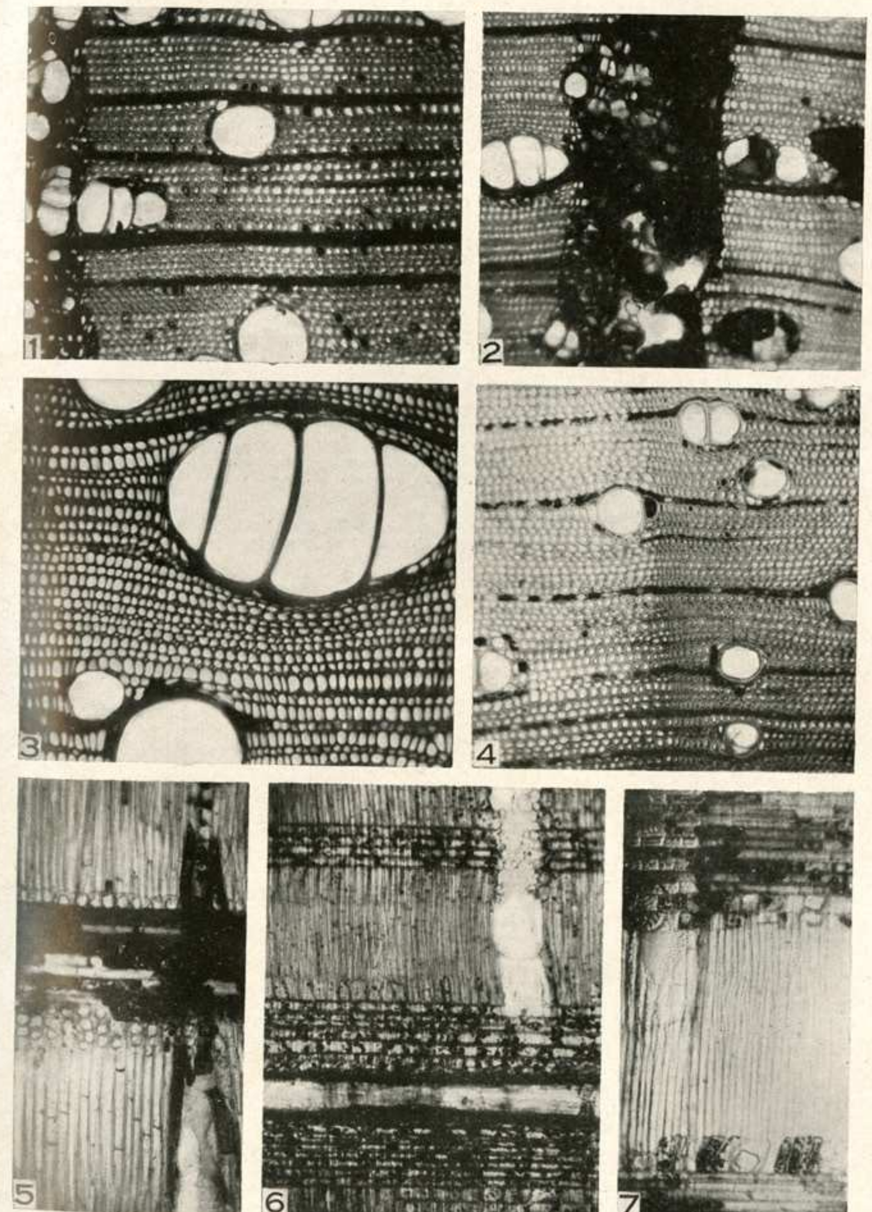

PLATE IV

1. *Aucoumea Klaineana* Pierre, septate libriform wood fiber.
2. *Crepidospermum goudotianum* Tr. et Pl., septate libriform wood fiber.
3. *Santiria Griffithii* (Hook. f.) Engl., libriform wood fiber.
4. *Bursera microphylla* Gray, libriform wood fiber.
5. *Canarium mehenbethene* Gaerth., wood parenchyma strand.
6. *Bursera microphylla* Gray, vessel element.
7. *Aucoumea Klaineana* Pierre, vessel element.
8. *Bursera Simaruba* (L.) Sarg.
9. *Canarium hirsutum* Willdenow.
10. *Crepidospermum Goudotianum* Tr. et Pl.

Figures 1-7 elements of macerated wood. × 104. Figures 8-10 radial sections of burseraceous woods showing ray-vessel pitting. × 547