

A CONTRIBUTION TO THE WOOD ANATOMY OF SOUTH AMERICAN (CHIEFLY SURINAME) RUBIACEAE. I.*

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SUMMARY

A general description of the structure of the wood of the *Rubiaceae* is given, based on examination of samples from most subfamilies. The results of the author's investigation are compared with the data in the literature. The features of vessels, rays, and parenchyma agree well with those reported by other investigators. When the fibres are divided into libriform fibres and fibre tracheids in the sense of Janssonius, the correlation between the distribution of these organs and recent taxonomic subdivisions of the family is better than when all fibres with bordered pits are regarded as fibre tracheids.

1. INTRODUCTION

In this paper the structure of the wood of the *Rubiaceae* will be discussed, as based upon South American genera. In a next one we will discuss to what degree the differences and agreements in wood structure parallel the divisions of the family as made by Schumann, Verdcourt and Bremekamp. Furthermore a key to the Suriname genera based upon the material studied will be provided.

With regard to the subdivision of the *Rubiaceae* the opinions of the different authors differ widely. Important contributions to the systematics of the family are SCHUMANN's account (in Engler & Prantl "Die natürlichen Pflanzenfamilien", 1897), chiefly based upon observations and classifications of the family by previous authors, and recent papers by BREMEKAMP (1954, 1966), VERDCOURT (1958), and STEYERMARK (1965, 1967). A detailed review of the points of agreement and disagreement with the concepts of the authors cited can be found in the publication by BREMEKAMP (1966).

2. MATERIAL AND METHODS

The investigation is mainly based on material of the woody species occurring in Suriname in so far as they are represented in the wood collection of the Botanical Museum, Utrecht. Some other species from other parts of tropical South America were added. The species studied will be listed in the next paper. Of about 5 Suriname shrubby species no wood was available. The Suriname wood samples have been supplied with herbarium vouchers, which have nearly all been identified by Prof. C. E. B. Bremekamp.

* Dedicated to Professor Dr. C. E. B. Bremekamp.

The anatomy was studied from microtome sections, unstained and stained with saffranine or methyl green, and from macerations. It was often necessary to treat the wood with hydrofluoric acid for several weeks before sectioning could be effectuated.

3. DESCRIPTION OF THE WOOD OF THE RUBIACEAE BASED UPON SOUTH AMERICAN GENERA

Colour sand-yellow to reddish brown; growth rings absent to fairly distinct, formed by zones with more numerous vessels and/or parenchyma bands; rather light and soft, easy to cut, to hard and heavy, difficult to cut; grain straight or interlocked; volume weight 0.7–1.3, mostly 0.8–1.0.

Vessels: often small, diam. less than 40 μ , and very numerous, often more than 40 per sq. mm, to diam. more than 100 μ , and mostly less than 20 per sq. mm; mostly partly in small radial multiples and clusters, sometimes in multiples of more than 4 cells, in some genera (nearly) all solitary; perforations simple, in some species scalariform near the primary wood, in some other species consisting of two large pits in some vessel elements in mature wood (*fig. 41*); intervacular pits 3–6 μ , vested.

Fibre tissue: septate or non-septate; septate fibres mostly present in species without or with scanty parenchyma; pits simple or with small borders, occurring (nearly) exclusively on radial walls or both on radial and tangential walls, or pits with large borders, occurring on radial and tangential walls; walls thin to thick.

Rays: in most species studied 2–4-seriate; in some genera exclusively uniseriate or over a very short distance biseriate; partly 4–6-seriate in some other genera; multiseriate rays generally heterocellular, composed of procumbent and square/upright cells, often one or two uniseriate wings of upright cells, those wings often many cells high; in many species two or more multiseriate rays fused vertically; height often more than 1 mm; in some genera multiseriate and uniseriate parts composed of square/upright cells only; pits between rays and vessels mostly of the same size as the intervacular pits; in some species large and gash-like; in *Retiniphyllum laxiflorum* some large stone cells occur in the ray tissue (*fig. 50*). The number of rays varies between 3–20 per mm.

Parenchyma: absent, diffuse, sometimes forming short uniseriate lines or long, often 2–4-seriate bands, sometimes combined with incomplete narrow vascentric sheaths; seldom exclusively paratracheal.

Crystals: raphides occur in a number of genera in upright or procumbent ray cells or in parenchyma cells (*fig. 52*); in some species rhombic crystals are present in fibres, ray cells or parenchyma cells.

4. DISCUSSION

Vessels: the vessels are small (smaller than 40 μ in diam.) and very numerous (more than 40 per sq. mm) in many *Psychotrieae* (*Cephaelis*, *Naletonia*, *Psycho-*

tria, *Ronabea*, *Rudgea*, *Strempelia*) and some species of *Mapouria*, *Faramea*, *Posoqueria* and *Randia*; in many other genera the diameter is not over 65 μ . METCALFE & CHALK (1950) mention vessels with a diam. of more than 100 μ in species of *Capirona*, *Elaeagia*, *Ferdinandusa*, *Genipa*, *Morinda*, and *Psychotria*; which was observed in the present investigation too; I can add species of *Alibertia*, *Chimarrhis*, *Duroia*, *Hillia*, *Isertia*, *Pagamea*, *Schradera*, and *Uncaria*.

The vessels are mostly arranged in small radial multiples or clusters; (nearly) solitary in *Ixora*, *Pagamea*, *Randia* and *Retiniphyllum*. RECORD & HESS (1944) investigated some species of *Isertia* and did not mention this genus as regards this characteristic, contrary to Metcalfe & Chalk; in our material some small radial multiples were found. According to Metcalfe & Chalk multiples of more than 4 vessels occur in *Alibertia*, *Cephaelis*, *Posoqueria*, *Psychotria*, and *Rudgea*. The results of the present investigation agree with Metcalfe & Chalk's except for *Rudgea* where I observed 4 vessels at the most in one multiple. On the other hand long multiples occur in *Mapouria*.

The faint radial pattern in some species of *Psychotria* described by Metcalfe & Chalk was not observed in the material studied and was not mentioned by JANSSONIUS (1926). The number of vessels was 50–100 per sq. mm, according to Janssonius, whereas in "Anatomy of the Dicotyledons" (1950) the number is stated to be 5–20 per sq. mm. Both numbers occur in *Psychotria paniculata* and *Psychotria hancornioides* (Uw 12342) respectively. In the present investigation only a few species of this very large genus were studied and the difference between the descriptions will be due to the study of different species.

The scalariform perforations of the vessel elements observed by SOLEREDER (1885) were present in *Retiniphyllum laxiflorum*, in the first growth rings near the primary wood. Perforations formed by two large pits in one transverse wall occur in *Retiniphyllum schomburgkii*, *Ronabea latifolia*, and *Rudgea graciliflora* (fig. 41).

The intervascular pits are 3–6 μ wide with enclosed oval apertures. The pits are all vested (fig. 54), but in a number of species this is difficult to observe. According to BAILEY (1933) vested pits are a very good indication of relationship. Within a genus the pits should be vested or non-vested. For taxa of higher rank this should also be considered as a constant characteristic.

Fibre tissue: to distinguish between fibre tracheids and libriform fibres is difficult and opinions differ widely. There is no difference of opinion about the extreme elements: fibre tracheids commonly have thick walls, pits with large borders are frequent on tangential and radial walls between them and between fibres and vessels. Libriform fibres are much elongated, compared with the cambium initials. They are often septate, they have often contents and the pits are simple.

The "Multilingual glossary of terms used in wood anatomy" (1964) accepts the presence or absence of a pit-border as criterion and includes all intermediates between both types in the fibre tracheids. If we apply these definitions to the *Rubiaceae* nearly all investigated samples show fibre tracheids because of the

presence of pit-borders, although these borders are often small and indistinct. An objection seems to be, that fibres of very different type are classified in one group: septate and non-septate, with and (nearly) without pits on tangential walls, whereas fibres which resemble each other (as do the fibres within the *Psychotriaceae*) partly have to be classified in the fibre tracheids because of the presence of small pit-borders, while others which differ in very few features from the former belong to the libriform fibres because of the absence of pit-borders.

The distinction made by Janssonius following Sanio, and described by REINDERS (1935) is:

Fiber tracheid: moderately elongated; commonly with thick and apparently somewhat swollen walls, rarely with mucilaginous layers; hardly ever septate; never containing starch; rather often annularly or spirally thickened; having rather large bordered pits with lenticular to slitlike apertures. The pits are comparatively numerous in the tangential walls, in many instances outnumbering those in the radial. When such fibers constitute the ground tissue the pits toward the vessels usually have borders of much the same size as those of pits in the walls of contact of two vessels.

Libriform wood fiber: much elongated; mostly with relatively thick walls, without swollen appearance and rather often with mucilaginous layers; hardly ever annularly or spirally thickened; sometimes septate by very thin, commonly unpitted partition walls formed after secondary thickening of the fiber walls, the septate and non-septate types often occurring together; often containing starch (in sapwood) or crystals; having simple pits or pits with narrow borders and slitlike apertures (or rarely both kinds). In the tangential walls pits are commonly much less numerous than in the radial and may be entirely lacking; in the parts of the wall adjacent to vessels they are absent or number few. The bordered pits leading toward parenchyma cells are often more numerous and their borders somewhat larger than those toward fibres of the same kind.

JANSSONIUS (1926) using these criteria mentions that all *Rubiaceae* studied by him have fibre tracheids, except for *Guettarda speciosa*, *Morinda citrifolia*, *Morinda tinctoria*, *Psychotria robusta*, *Psychotria aurantiaca* and *Psychotria viridiflora*. However, when the material studied by him is classified in subfamilies and tribes according to the divisions made by Verdcourt and Bremekamp, it becomes evident that he investigated representatives of the *Cinchonoideae* and *Ixoroideae* only, except for the species with libriform fibres mentioned by him, which belong to the *Guettardoideae* and *Rubioideae*.

This result agrees rather well with the descriptions by RECORD & HESS (1944): "wood fibres often septate; walls medium to very thick and gelatinous; pits with slitlike extended apertures and very small to medium sized borders..." and with the observations of METCALFE & CHALK (1950): "fibres either non-septate, with pits with small to very distinct borders, or septate, with simple to slightly bordered pits..."

as well as with the results of the present investigation:

The representatives of the subfamily *Rubioideae* studied have libriform fibres: septate, with pits with small borders or without, chiefly on radial walls. An ex-

ception is *Morinda citrifolia* (the libriform fibres are non-septate). *Pagamea* is of a quite different character because both species have fibre tracheids.

Libriform fibres are also present in the material of the subfamily *Cinchonoideae* studied. JANSSONIUS (1926) described one species of *Cinchona*, the material of which was poor and not identified up to the species name, and *Hymenodiction excelsum*, which have both fibre tracheids. The *Cinchoneae* studied by METCALFE & CHALK (1950) have septate fibres and simple pits or pits with small borders, and they are therefore libriform fibres. This agrees with the presence of libriform fibres in the material of *Capirona* and *Ferdinandusa* studied by me. Janssonius did not study representatives of the *Condamineae*; Metcalfe & Chalk mention libriform fibres in *Pogonopus* and *Pinckneya*. *Wendlandia*, belonging to the *Rondeletieae*, has fibre tracheids, according to Janssonius, whereas the *Rondeletieae* studied by Metcalfe & Chalk have libriform fibres. I agree with Metcalfe & Chalk as regards *Elaeagia* and *Warszewiczia*, of the other genera studied by them no material was available. *Mussaenda* (*Mussaendeae*) has fibre tracheids (JANSSONIUS, 1926), as had the species of *Isertia* studied during this investigation.

The species belonging to the *Gardenieae* and *Ixoreae* (*Ixoroideae*) have fibre tracheids except for two species of *Alibertia* (*Gardenieae*) and *Chomelia tenuiflora* (*Ixoreae*). This agrees rather well with the observations of Janssonius who investigated representatives of the *Gardenieae*, *Ixoreae* and *Vanguerieae*.

BREMEKAMP (1966) has removed some of the genera (reported by Metcalfe & Chalk to have libriform fibres) which had been placed in the *Ixoroideae* by previous authors, among others *Tarena* and *Posoqueria*.

The *Guettardoideae* were represented in the investigation of Janssonius by *Guettarda speciosa*. This species has libriform fibres, like the species included in the present study: *Guettarda acreana*, *Guettarda spruceana*, and *Malanea duckei*; and by Metcalfe & Chalk: *Machaonia* and *Timonius*, such as *Timonius rumphii* DC., described by GRAÇA DE FREITAS (1955).

REINDERS (1935) notes that the correlation between this classification of fibre tracheids and libriform fibres and other systematic classifications is less distinct in the *Rubiaceae* than in many other families. Although I agree, that the correlation is not without exceptions, this division between fibre tracheids and libriform fibres seems to be a more natural one than the division based upon the presence or absence of bordered pits. Therefore the terms "libriform fibre" and "fibre tracheid" are used in the sense Janssonius intended.

Rays: in most species the rays are 2–4-seriate; they are exclusively uniseriate (possibly over a very short distance biseriate) in *Alibertia*, *Ixora* and *Ronabea*. Over 4-seriate rays are found in *Capirona*, *Chimarrhis*, *Coussarea*, *Elaeagia*, *Faramea*, *Ferdinandusa*, *Malanea*, *Mapouria*, *Morinda*, *Retiniphyllum*, and *Warszewiczia*; they are also reported for *Rudgea* (Record & Hess) and *Genipa*, *Guettarda*, *Palicourea*, *Psychotria*, and *Randia* (Metcalfe & Chalk). In *Guettarda*, *Palicourea* and *Psychotria*, however, I observed rays up to 4 cells wide, and in *Genipa*, *Randia* and *Rudgea* 2–3-seriate rays.

The presence of over 4-seriate rays is often correlated with great height (over 1 mm) and sheath cells (*fig. 49*). CHATTAWAY (1933) suggested that sheath cells originate by addition of new ray initials to the sides of the rays, formed from the adjacent fusiform initials. This process of increase in height and width of rays in the *Sterculiaceae* appears to be confined to the subfamily *Sterculieae*, which stands somewhat apart from the rest of the family in other respects too. The combination of great height, great width and sheath cells occurs in the *Rubiaceae* chiefly in the tribes *Coussareeae*, *Psychotrieae*, *Rondeletieae* and *Cinchoneae*; these groups show much agreement also in other features (libriform fibres; parenchyma absent or very scarce paratracheal parenchyma present).

Multiseriate rays are generally heterocellular, composed of procumbent and square/upright cells (*fig. 53*); uniseriate and pluriseriate parts consisting exclusively of square/upright cells (*fig. 51*) occur in the *Psychotrieae* studied except in some species of *Mapouria* and *Palicourea*, which have procumbent and upright cells, and in *Retiniphyllum*.

Procumbent ray cells change frequently in square or upright cells in radial direction, or square/upright cells in procumbent ones. Furthermore, in some species square cells take up the place of procumbent cells by forming the pluriseriate part of a ray, of which the uniseriate parts are formed by upright cells (*fig. 51*), a phenomenon which already has been mentioned by previous authors (see CHATTAWAY 1951 and BRAUN 1955).

In many species the rays have on both sides of the multiseriate parts long uniseriate wings composed of square/upright cells (*fig. 44*). The number of rows is often difficult to count, as parenchyma strands and uniseriate rays may confuse the picture. In many species two or more multiseriate rays are fused vertically, with a total height of often more than 1 mm (*fig. 46*).

Pits between rays and vessels are mostly of the same size and shape as the intervascular pitting; in *Schradera rotundata*, *Faramea occidentalis*, *Posoqueria gracilis*, and *Hillia tubiflora* the pits between rays and vessels are larger, somewhat irregularly shaped. Some by-pass vessel members occur in *Posoqueria gracilis* (*fig. 42*).

Rhombic crystals are found in *Guettarda acreana*, *Guettarda spruceana*, *Ixora orinocensis*, *Ixora surinamensis*, *Hillia tubiflora*, and *Posoqueria longiflora*. Raphides occur in upright or procumbent ray cells of *Coussarea*, *Faramea*, *Hillia*, *Mapouria*, and *Pagamea*, all belonging to the *Psychotrieae* except for *Hillia*.

Parenchyma: absent in all species of the *Psychotrieae* studied. The only genera without parenchyma not belonging to the *Psychotrieae*, *Elaeagia*, *Warszewiczia* and *Guettarda*, are placed in the *Rondeletieae* and *Guettardeae*. The absence of parenchyma in these genera is stated by METCALFE & CHALK (1950), as well as for some other *Rondeletieae*, the *Cinchoneae* and *Hippotis* (belonging to the *Mussaendeae*). The *Cinchoneae*, studied by me, *Capirona* and *Ferdinandusa*, possess scanty vasicentric parenchyma. Besides being absent or present as narrow vasicentric rings, parenchyma can occur apotracheal: diffuse and in short or long bands.

SOLEREDER's statement (1885) that *Retiniphyllum* has much parenchyma could not be confirmed: in *Retiniphyllum schomburgkii* the parenchyma is arranged in short lines, in *Retiniphyllum laxiflorum* diffuse and vasicentric.

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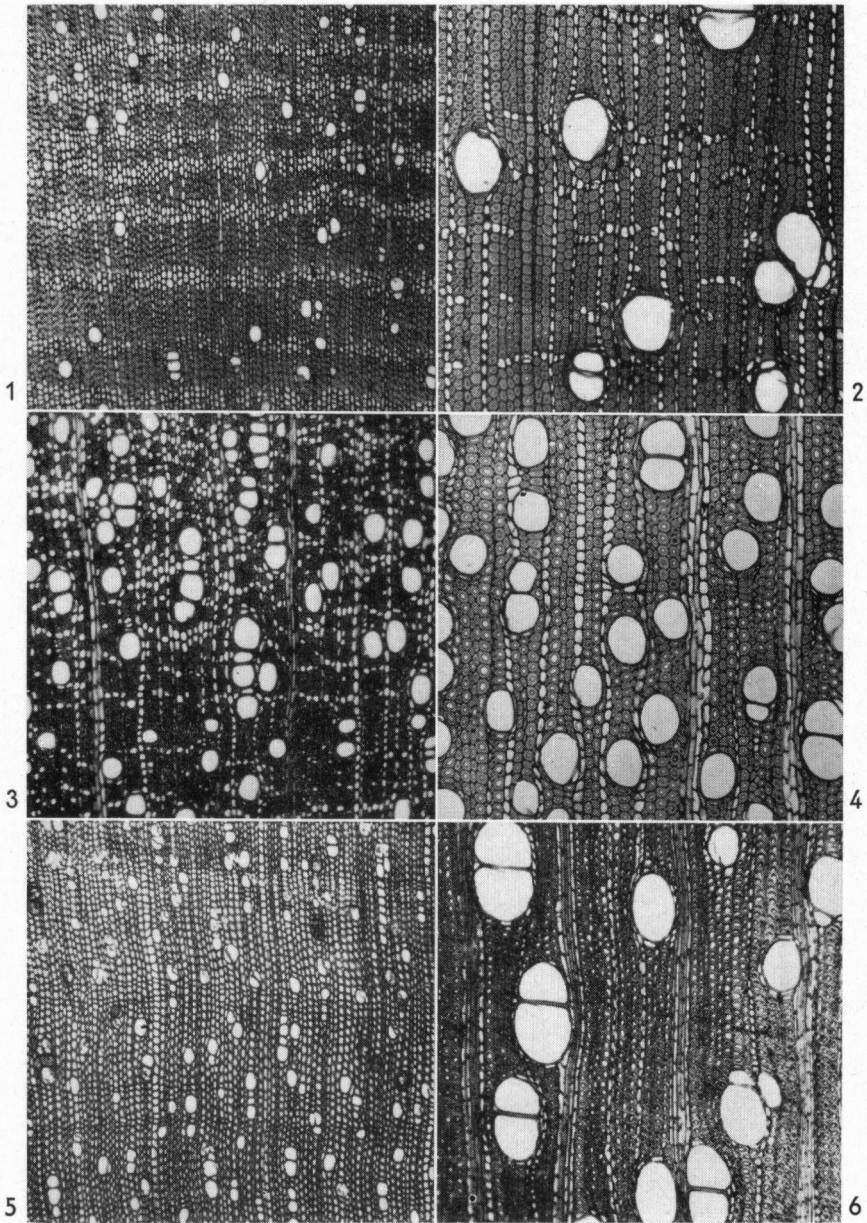


Plate I. Transverse sections, 45 \times .

Fig. 1. *Alibertia myrciifolia* K. Schum. (Uw 8087); fig. 2. *Alibertia edulis* (L. Rich.) A. Rich. (Uw 9062); fig. 3. *Amajoua guianensis* Aubl. (Uw 2970); fig. 4. *Capirona surinamensis* Brem. (Uw 172); fig. 5. *Cephaelis glabrescens* (Müll. Arg.) Standley (Uw 3248); fig. 6. *Chimarrhis longistipulata* Brem. (Uw 207).

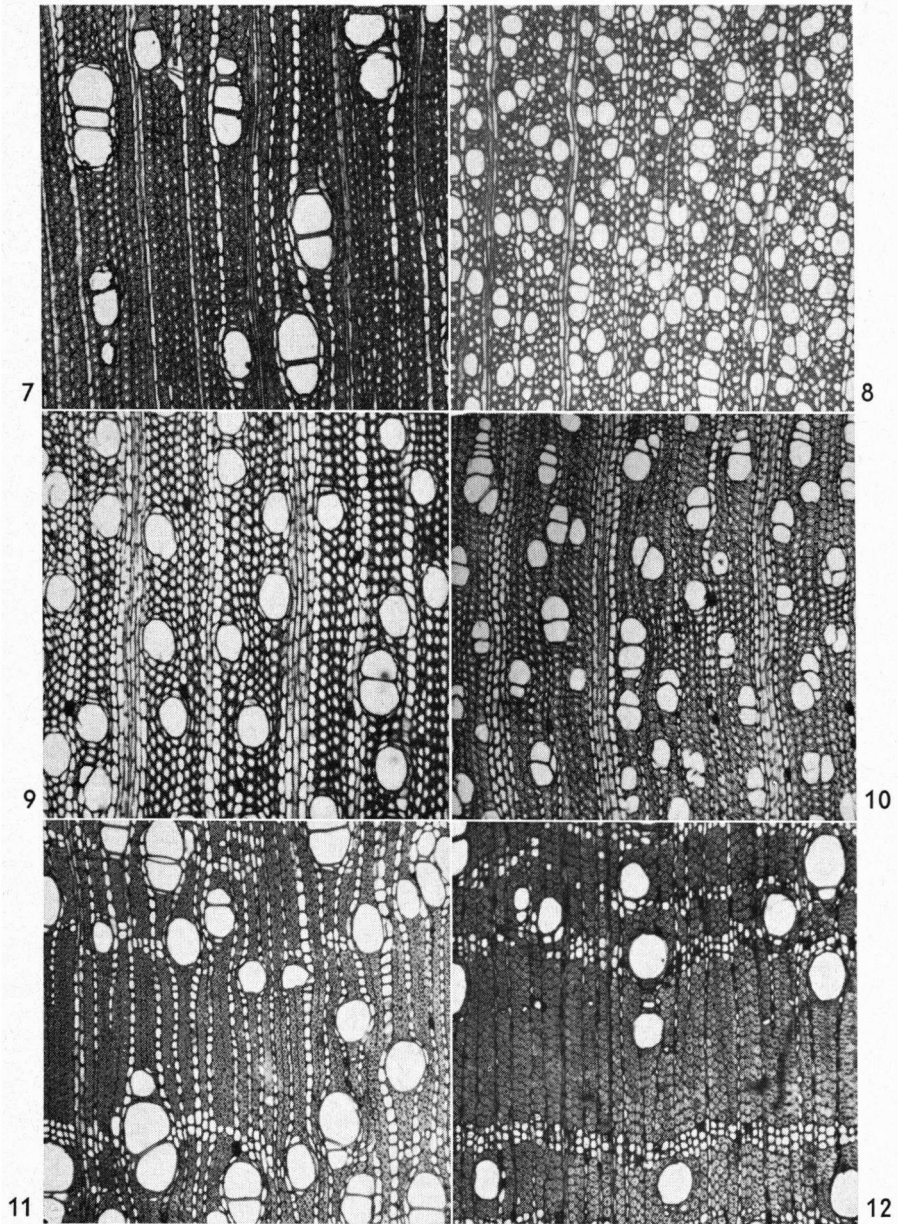


Plate II. Transverse sections, 45 \times .

Fig. 7. *Chimarrhis turbinata* DC. (Uw 261); fig. 8. *Chomelia tenuiflora* Bth. (Uw 378); fig. 9. *Coussarea paniculata* (Vahl) Standley (Uw 4756); fig. 10. *Coussarea racemosa* A. Rich. (Uw 8565); fig. 11. *Duroia aquatica* (Aubl.) Brem. (Uw 2702); fig. 12. *Duroia sprucei* Rusby (Uw 243).

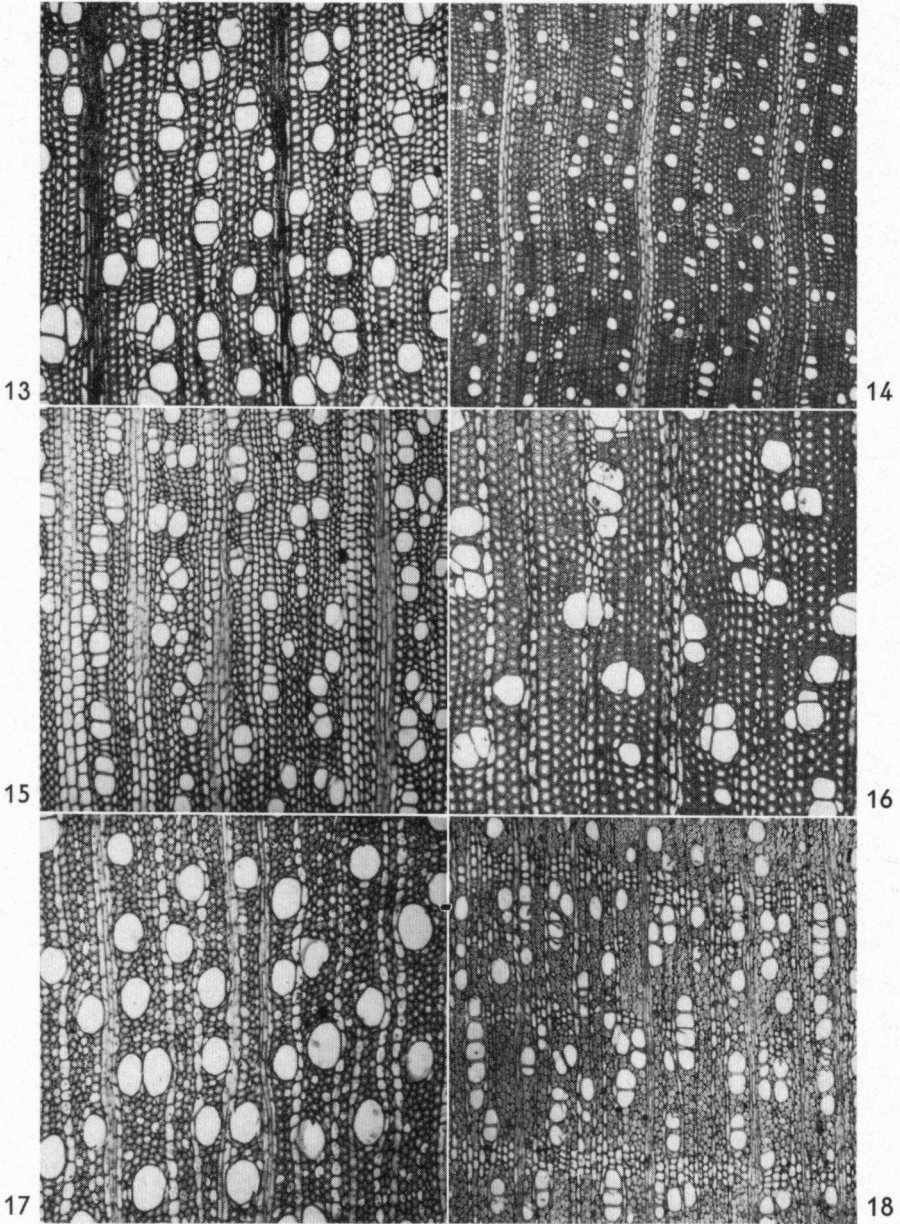


Plate III. Transverse sections, 45 \times .

Fig. 13. *Elaeagia maguirei* Standley (Uw 2552); fig. 14. *Faramea longifolia* Bth. (Uw 3930);
fig. 15. *Faramea occidentalis* (L.) A. Rich. (Uw 3867); fig. 16. *Ferdinandusa rudgeoides* (Bth.)
Wedd. (Uw 1936); fig. 17. *Genipa americana* L. (Uw 193); fig. 18. *Guettarda acreana* Krause
(Uw 1081).

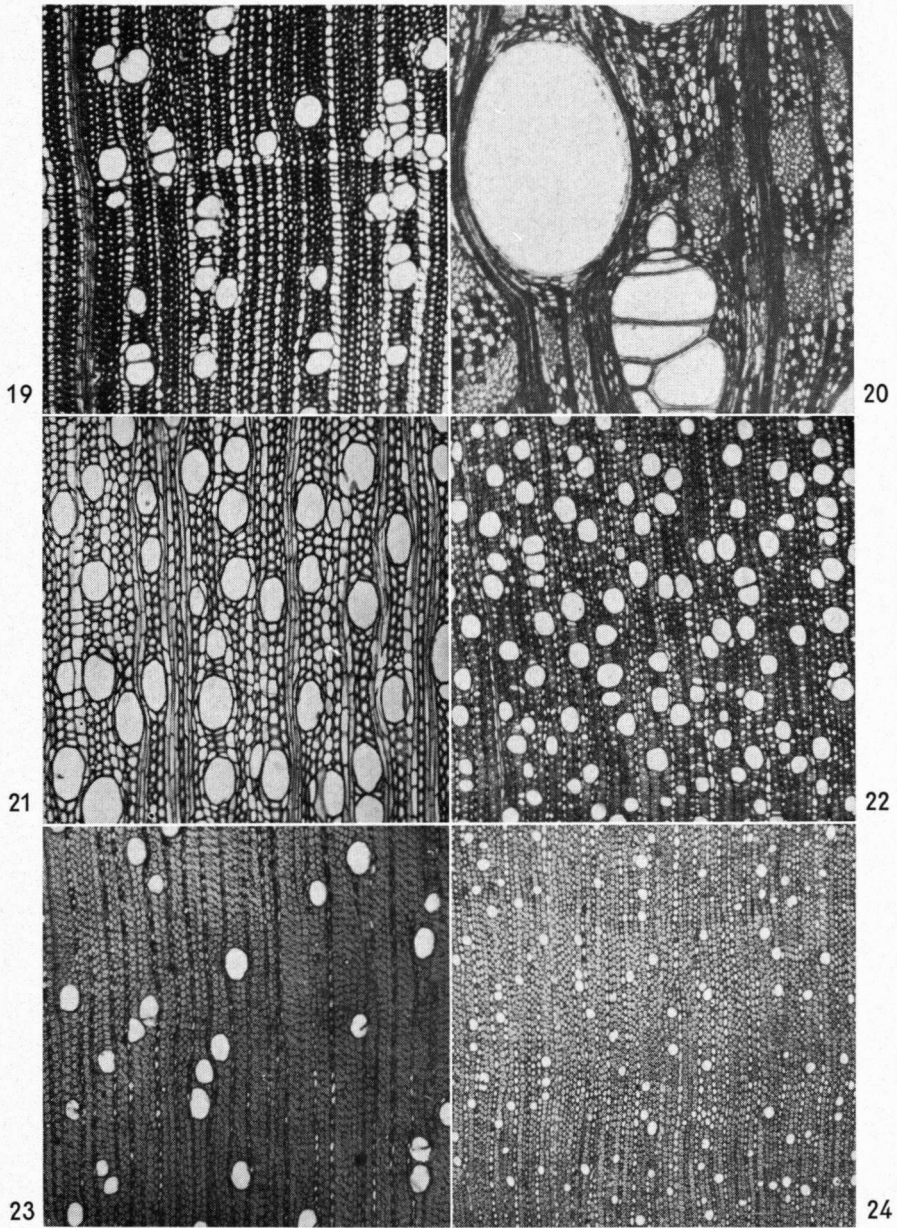


Plate IV. Transverse sections, 45 × .

Fig. 19. *Guettarda spruceana* Müll. Arg. (Uw 4256); fig. 20. *Hillia tubiflora* Cham. (Uw 3510);
 fig. 21. *Isertia hypoleuca* Bth. (Uw 2986); fig. 22. *Isertia parviflora* Vahl (Uw 680); fig. 23. *Ixora*
orinocensis Spruce (Uw 2558); fig. 24. *Ixora surinamensis* Brem. (Uw 3397).

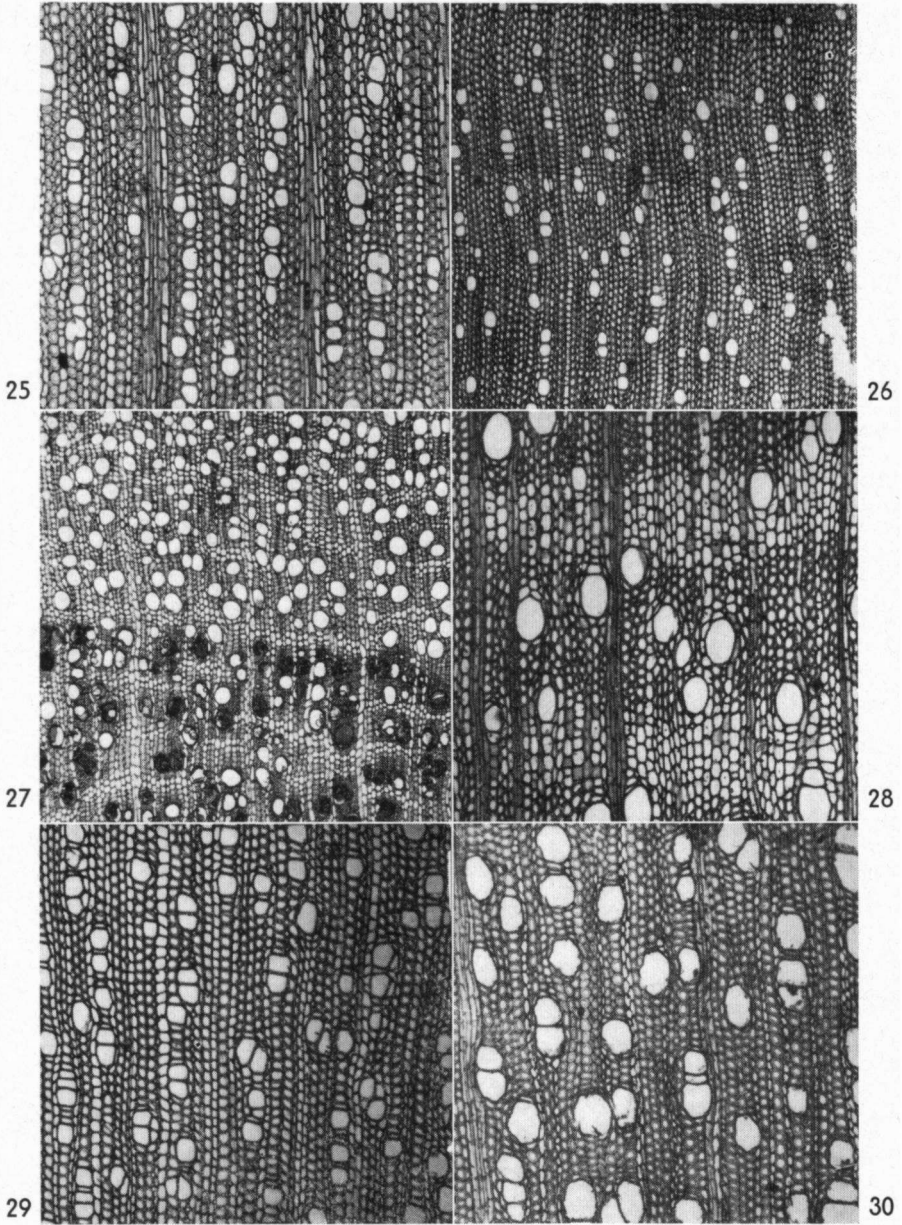


Plate V. Transverse sections, 45 ×.

Fig. 25. *Mapouria chlorantha* (Bth.) Brem. (Uw 4933); fig. 26. *Natelonía violacea* (Aubl.) Brem. (Uw 8531); fig. 27. *Pagamea capitata* Bth. (Uw 2560); fig. 28. *Pagamea guianensis* Aubl. (Uw 8164); fig. 29. *Palicourea crocea* (Sw.) R. & S. (Uw 1481); fig. 30. *Palicourea longiflora* (Aubl.) A. Rich. (Uw 4550a).

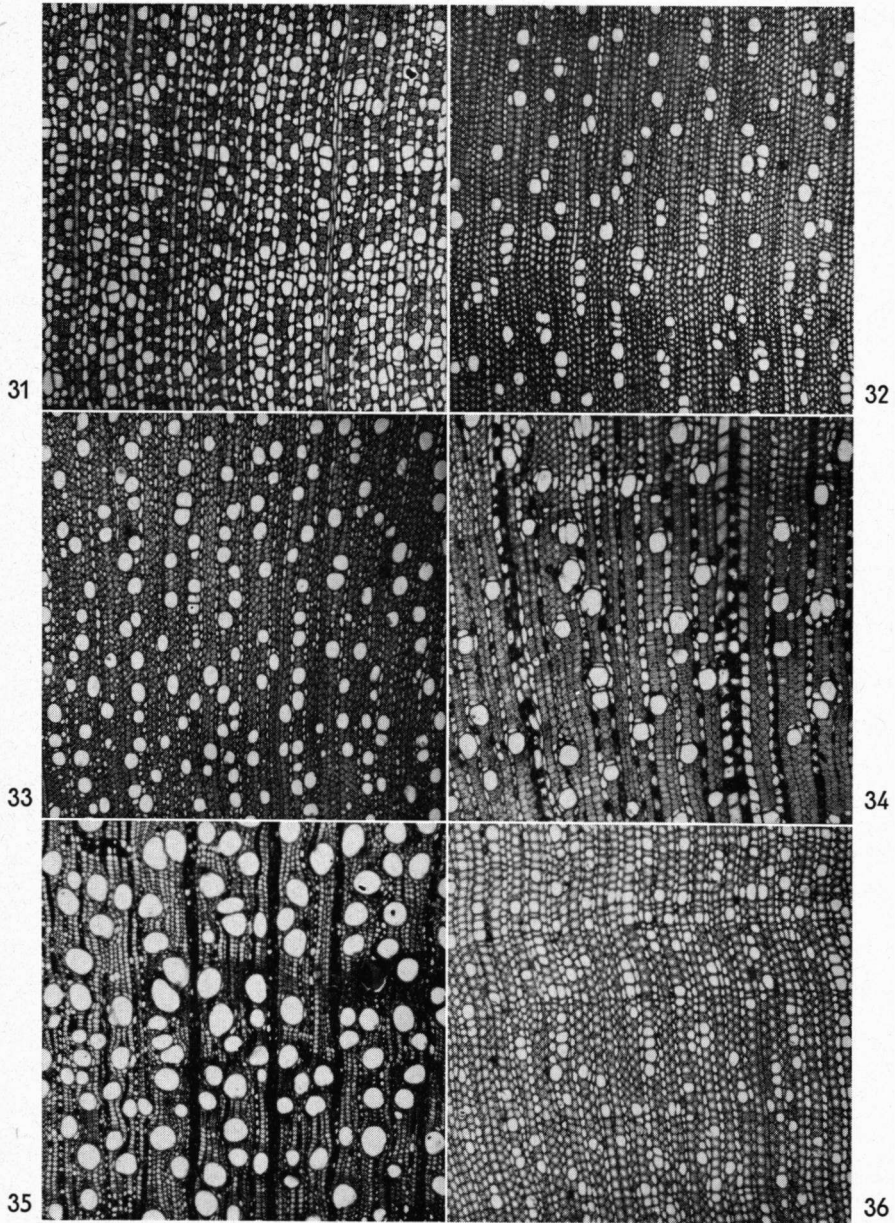


Plate VI. Transverse sections, 45 \times .

Fig. 31. *Posoqueria gracilis* Rudge (Uw 1919); fig. 32. *Psychotria paniculata* (Aubl.) Raensch (Uw 1632); fig. 33. *Randia spinosa* (Jacq.) Karsten (Uw 1656); fig. 34. *Retiniphyllum laxiflorum* (Bth.) N. E. Brown (Uw 2554); fig. 35. *Retiniphyllum schomburgkii* (Bth.) Müll. Arg. (Uw 2598); fig. 36. *Ronabea latifolia* Aubl. (Uw 1888).

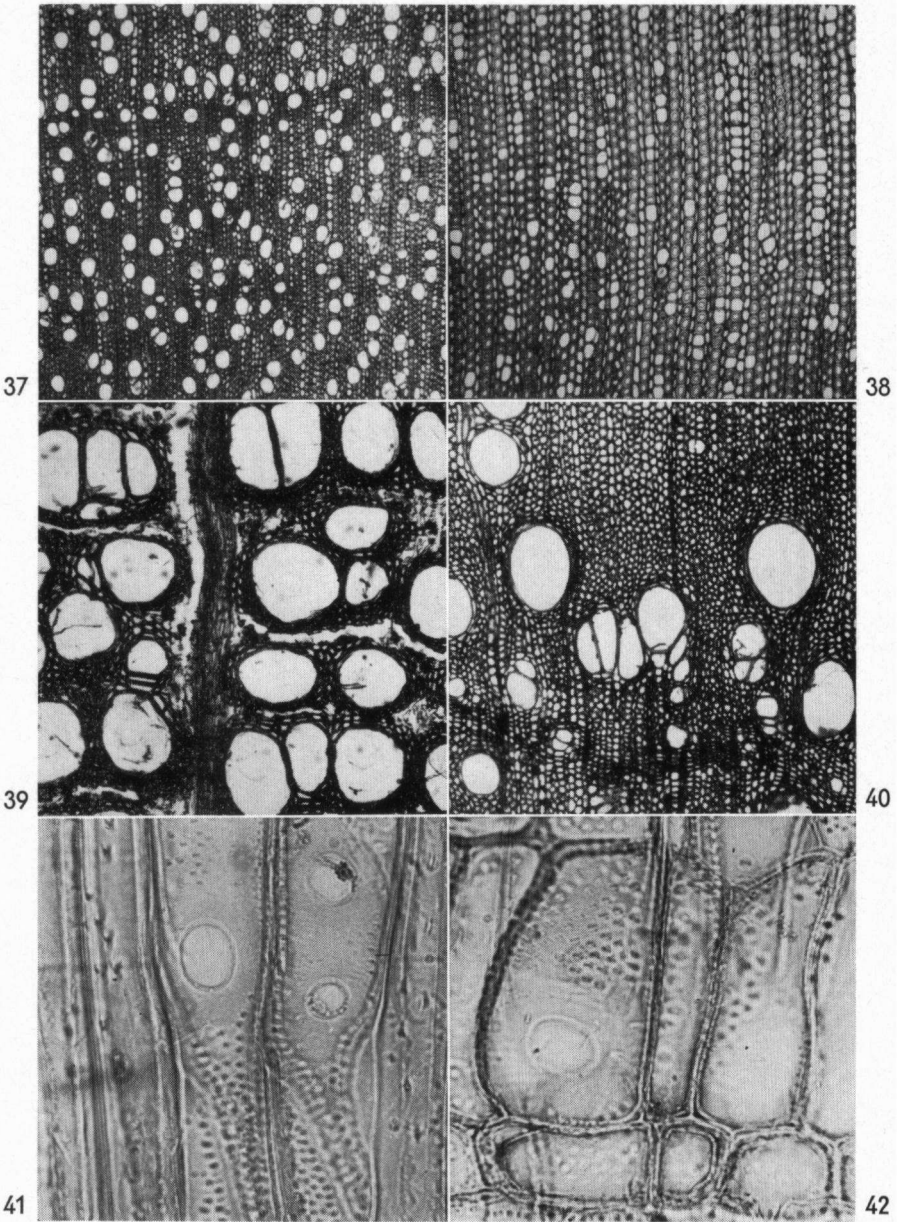


Plate VII.

Fig. 37. *Rosenbergiodendron formosum* (Jacq.) Fagerl. (Uw 1461) transv. sect. 45 ×; fig. 38. *Rudgea hostmanniana* Bth. (Uw 2787) transv. sect. 45 ×; fig. 39. *Schradera rotundata* Standl. (Uw 12437) transv. sect. 45 ×; fig. 40. *Uncaria guianensis* Aubl. (Uw 2550) transv. sect. 45 ×; fig. 41. *Ronabea latifolia* Aubl. (Uw 1888) rad. sect. 450 ×, vessel perforations; fig. 42. *Posoqueria gracilis* Rudge (Uw 1919) rad. sect. 450 ×, ray-vessel perforation.

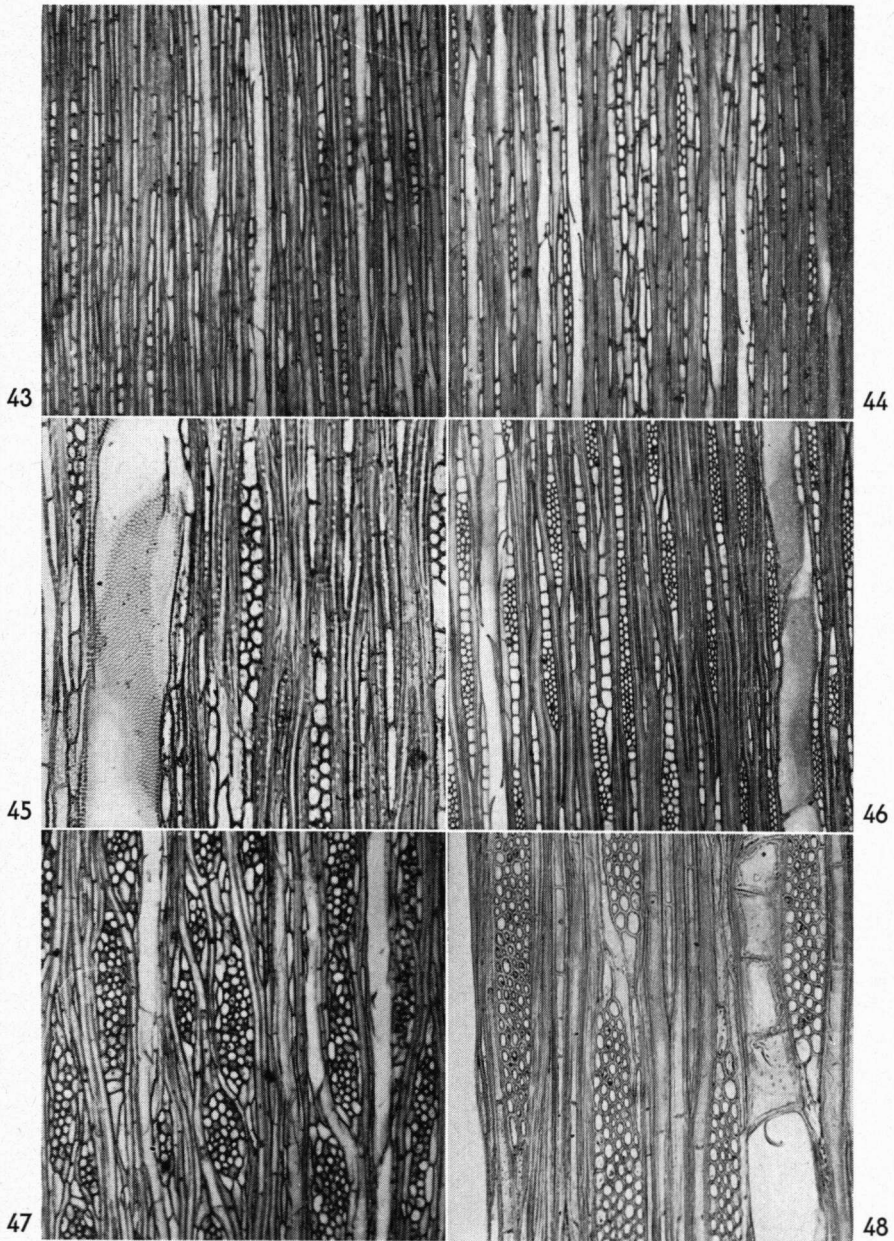


Plate VIII.

Fig. 43. *Ronabea latifolia* Aubl. (Uw 1888) tang. sect. $45\times$; fig. 44. *Posoqueria latifolia* (Rudge) R. & S. (Uw 298) tang. sect. $45\times$; fig. 45. *Duroia aquatica* (Aubl.) Brem. (Uw 2702) tang. sect. $45\times$; fig. 46. *Chimarrhis turbinata* DC (Uw 261) tang. sect. $45\times$; fig. 46. *Faramea occidentalis* (L.) A. Rich. (Uw 3867) tang. sect. $45\times$; fig. 48. *Chimarrhis longistipulata* Brem. (Uw 207) tang. sect. $115\times$.

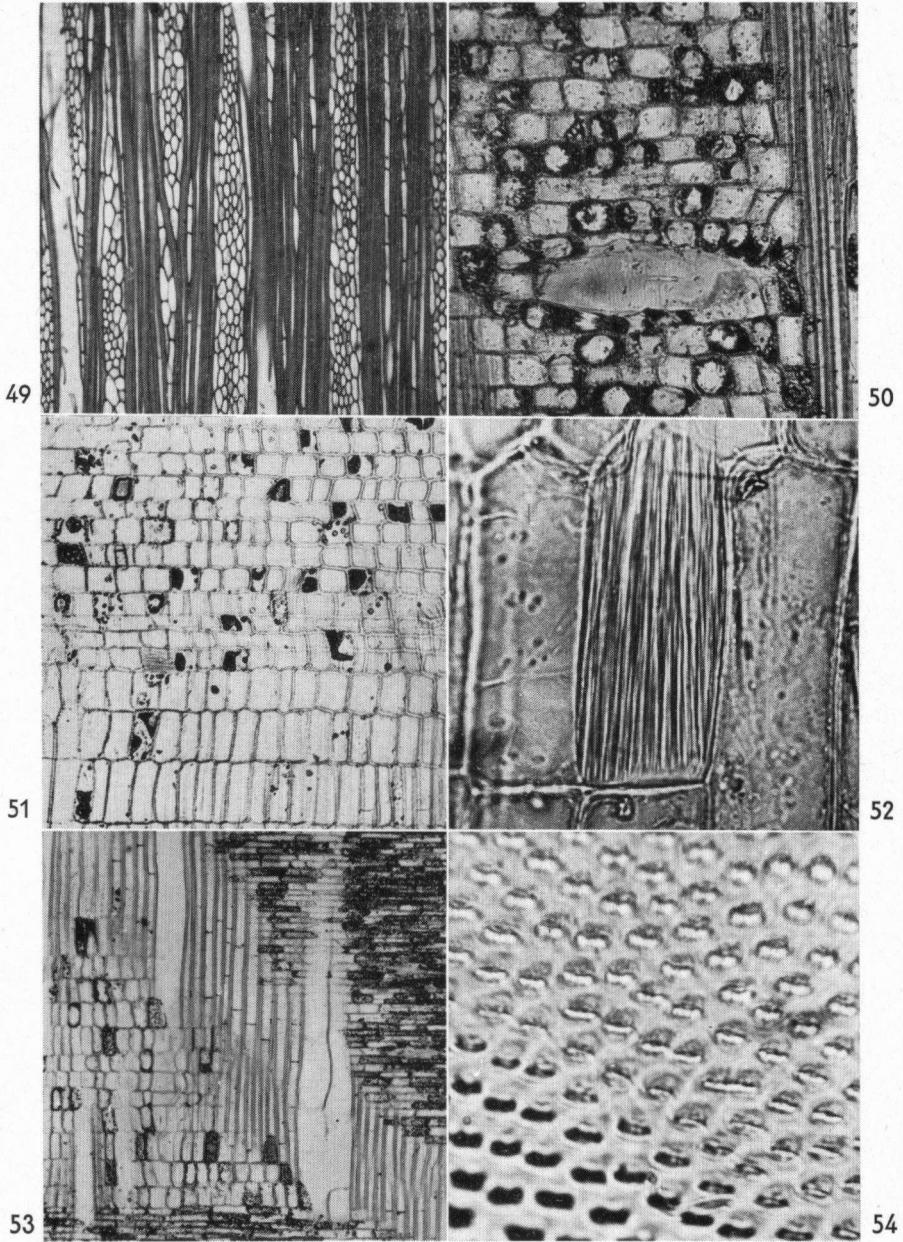


Plate IX.

Fig. 49. *Coussarea surinamensis* Brem. (Uw 280) tang. sect. 45 ×; fig. 50. *Retiniphyllum laxiflorum* (Bth.) N. E. Brown (Uw 2554) rad. sect. 115 ×, ray with sclerotic cell; fig. 51. *Mapouria fockeana* (Miq.) Brem. (Uw 3823) rad. sect. 115 ×; fig. 52. *Coussarea racemosa* A. Rich. (Uw 8565) rad. sect. 700 ×, raphides; fig. 53. *Elaeagia maguirei* Standley (Uw 2552) rad. sect. 115 ×; fig. 54. *Ferdinandusa rudgeoides* (Bth.) Wedd. (Uw 1936) rad. sect. 1150 ×, intervacular pitting.