GROWTH RINGS IN CERRADO WOODY SPECIES: OCCURRENCE AND ANATOMICAL MARKERS.

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Abstract

Marcati, C.R.; Oliveira, J.S. and Machado, S.R. **Growth rings in cerrado woody species: occurrence and anatomical markers.** *Biota Neotrop.* Sep/Dez 2006 vol. 6, no. 3 http://www.biotaneotropica.org.br/v6n3/pt/abstract?article+bn00206032006 ISSN 1676-0611

Growth ring occurrence was investigated in 48 representative species of cerrado in the state of São Paulo, Brazil. We characterized growth ring markers and described the growth layer structure of the basal portion of the most developed stem branches in woody plants. Growth rings were poorly defined in 33%, well defined in 61% and not discernable in 6% of the species studied. Various anatomical features were used as growth markers, such as: thick-walled latewood fibres; radially flattened latewood fibres; fibre zones; distended rays; marginal bands of axial parenchyma; marginal lines of parenchyma; and closeness of the narrow bands of scalariform parenchyma. In a single species, different growth ring markers often occurred together. Within growth layers, variations in the anatomical features were observed. Variations in the axial parenchyma distribution within growth rings in *Vochysia cinnamomea, Qualea multiflora, V. rufa* and *V. tucanorum*, wood are here reported for the first time. Variation in the distance of the axial parenchyma in narrow bands along the rays within growth layers in *Annona coriacea*, *A. crassiflora*, *Diospyrus hispida* and *Roupala montana* wood is also reported. Phenology and habit of the studied species were important aspects related to both growth ring presence and distinctness as well as to the anatomical features' variations within growth layers.

Key words: *Cerrado, increment zones, habit, phenology, wood anatomy*

Resumo

Marcati, C.R.; Oliveira, J.S. and Machado, S.R. **Camadas de crescimento em espécies lenhosas de cerrado: ocorrência e marcadores anatômicos.** *Biota Neotrop.* Sep/Dez 2006 vol. 6, no. 3 http://www.biotaneotropica.org.br/v6n3/pt/abstract?article+bn00206032006 ISSN 1676-0611

Este estudo investigou a ocorrência de camadas de crescimento em 48 espécies representativas de cerrado no estado de São Paulo, Brasil. Amostras foram obtidas da porção basal de ramos caulinares mais desenvolvidos. Foram caracterizados os marcadores de crescimento, bem como foi descrita a estrutura das camadas de crescimento. As camadas de crescimento apresentaram-se mal definidas em 33% e bem definidas em 61%, sendo ausentes em 6% das espécies analisadas. Várias características anatômicas foram utilizadas como marcadores de crescimento, tais como: fibras de paredes espessas; fibras achatadas radialmente, zonas fibrosas; raios distendidos; faixas marginais de parênquima axial; linhas de parênquima marginal; e proximidade das linhas de parênquima escalariforme. Diferentes marcadores podem ocorrer em uma mesma espécie. Variações na distribuição do parênquima axial nas camadas de crescimento em *Vochysia cinnamomea*, *Qualea multiflora, V. rufa* and *V. tucanorum*, bem como variação na distância das linhas de parênquima axial ao longo dos raios dentro das camadas de crescimento em *Annona coriacea*, *A. crassiflora*, *Diospyrus hispida* e *Roupala montana* são aqui reportadas pela primeira vez. A fenologia e o hábito das espécies foram aspectos importantes relacionados tanto com a presença e nitidez das camadas de crescimento no lenho quanto com as variações dentro dessas camadas.

Palavras-chave: *anatomia da madeira, zonas de incremento, cerrado, fenologia, hábito.*

Introduction

Cerrado plants are characterized by slow secondary growth due to diverse factors including limited water availability during the dry season, high irradiation levels, low fertility and acidic soil, high incidence of herbivores and periodic fires (Coutinho 1990, Franco 2002). Additionally, these plants have small size and genuine morphological characteristics such as scleromorphic leaves, and twisted trunks and branches which give a tortuous aspect to the vegetation; however straight trunks may occur in tall trees (Eiten 1993).

The internal structure of cerrado plants is strongly affected by the environmental factors and most of the studies considering the interaction between these factors and plant anatomy have been conducted with leaf (Morretes & Ferri 1959, Morretes 1967, 1969, Oliveira & Marquis 2002). Regarding to the wood features, which are affected mainly by water availability (Franco 2002), the reports are restricted to a few species and have come mainly from studies on mature wood of the main trunk (Machado & Angyalossy-Alfonso 1995, Ceccantini 1996, Machado et al. 1997, Marcati *et al.* 2001, Machado et al. *in press*). Growth rings occurrence in cerrado plants was reported in a few species by Coradin (2000) and Tomazello et al. (2004). However, growth rings in these plants are very irregular and with poorly defined boundaries (Coradin 2000).

Growth rings studies are of interest to climatology, as a hydrologic register; to dendrochronology, to estimate the age of trees; to ecology, to recuperate data on fire history; to paleoclimatology; to analyze growth dynamics, and to various other practical applications (see Baas & Vetter 1989, Eckstein et al. 1995, Coradin 2000).

The goal of this study was to verify the occurrence of growth rings in 48 representative species of well-preserved remnants of cerrado in the state of São Paulo, Brazil. We characterized growth ring markers and described the growth layer structure. The analyses were conducted in stem branches because destructive methods were not allowed.

Material and Methods

The study was carried out in a well-preserved remnant area of cerrado located in the west central part of the state of São Paulo, Brazil (22° 55' S, 48° 30' W). We studied 48 trees and shrubs species belonging to 27 angiosperm families. Precipitation and temperature data of the region studied were obtained from the Natural Resources Department Agrometeorological Station, São Paulo State University (UNESP). The vouchers and samples of one specimen from all the species are deposited, respectively, in the Herbarium (BOTU) and in the Wood Collection (BOTw) of the Natural Resources Department, University of the State of São Paulo (Table 1). The family classification follows APGII (Souza & Lorenzi 2005).

Discs of 3 cm in thickness were obtained from the basal portion of the most developed branches (three sampled plants, one branch per plant). For macroscopic analyses, the cross sections were polished with sandpaper and analysed under a stereomicroscope. For microscopic analyses, a sliding microtome was used to cut transverse, radial, and tangential sections of 15-20 µm in thickness, which were double-stained with safranin and astra blue (Roeser 1972) and mounted permanently in Entellan synthetic medium.

Due to observation of the entire circumference of the discs, the term "growth ring" was used in this study. The analyses were qualitative and followed IAWA Committee (1989) instructions. The term fibre zone, adapted from IAWA Committee (1989), was used here when a distinct decreasing in frequency of vessels and parenchyma was observed in the entire circumference of the branches. On a macroscopical level, such a zone always appeared darker-colored.

The leaf fall pattern of the studied species were classified into evergreen, semi-deciduous and deciduous, according to phenological observations which were carried out weekly during two years (2002-2004). Habit was classified into shrubs, small trees (seemingly shrubs in size, however with just one slender trunk), trees (with a well-developed trunk and crown) and tall trees (emergents with crown above dossel), adapted from Ribeiro et al. (1999).

Results

The climate diagram shows one annual dry season per year in the studied region (Figure 1).

Growth rings were not discernable in 6% of the species studied, were poorly defined in 33% and were well defined in 61% (Table 1). Among the species with growth rings in their wood, 63% of them are semi-deciduous or deciduous (56,5% semi-deciduous, 6,5% deciduous) against 37% evergreen (Table 1). The figure 2 shows the percentage of species lacking growth rings and with poorly defined and well-defined growth rings, within each phenological category.

Regarding to habit, growth rings are present in 83,3% of the shrubs and small trees and in 100% of the trees and tall trees (Table 1). Figure 3 shows the percentage of species lacking growth rings, species with poorly defined and well-defined growth rings within each habit category.

The growth ring markers and variations within growth rings of each of the studied species (Figures 4a-41b) are described in Table 2. The growth ring markers were observed as follows: thick-walled latewood fibres; radially flattened latewood fibres; fibre zones; distended rays; marginal bands of axial parenchyma; marginal lines of axial parenchyma; and closeness of the narrow bands of scalariform parenchyma. In a single species, different growth ring markers often occurred together. In the species with growth rings, the most common markers were thick-walled and radially flattened fibres and fibre zones (62% of the species),followed

Table 1. Growth rings of the studied species from Brazilian cerrado. ***H*** *= habit. T = tree. ST = small tree. TT = tall tree. S = shrub (Ribeiro, 1999, adapted).* ***PhB*** *= phenological behavior (field observation). E = evergreen. SD = semi-deciduous. D = deciduous.* ***GR*** *= Growth rings: W = well defined; P = poorly defined; A = absent.*

Family	**Species**	**BOT $_W$**	**H**	**PhB**	**GR**
Anacardiaceae	*Tapirira guianensis* Aubl.	1321	T	E	P
Annonaceae	*Annona coriacea* Mart.	1322	ST	SD	W
	Annona crassiflora Mart.	1323	ST	SD	P
Araliaceae	*Didymopanax vinosum* (Cham. & Schlecht.) March.	1324	S	E	P
Asteraceae	*Gochnatia barrosii* Cabrera	1325	S	E	W
	Piptocarpha rotundifolia Baker	1326	S	E	W
Bombacaceae	*Eriotheca gracilipes* (K. Schum.) A. Robyns	1327	T	SD	P
Boraginaceae	*Cordia sellowiana* Cham.	1328	T	SD	W
Caryocaraceae	*Caryocar brasiliense* Cambess.	1331	T	E	P
Chrysobalanaceae	*Couepia grandiflora* (Mart. & Zucc.) Benth & Hook. f.	1332	T	SD	W
	Licania tomentosa (Benth.) Fritsch.	1333	T	E	W
Clusiaceae (Guttiferae)	*Kielmeyera rubriflora* Cambess.	1334	ST	SD	W
Combretaceae	*Terminalia brasiliensis* Raddi	1335	T	D	W
Ebenaceae	*Diospyrus hispida* DC.	1336	S	D	W
Erythroxylaceae	*Erythroxylum suberosum* A. St.-Hill.	1337	S	D	A
	Erythroxylum tortuosum Mart.	1338	S	D	P
Euphorbiaceae	*Pera glabrata* (Schott.) Bail.	1339	TT	E	P
Fabaceae - Caesalpinioideae	*Copaifera langsdorffii* Desf.	1330	TT	SD	W
	Dimorphandra mollis Benth.	1351	ST	SD	P
Fabaceae – Cercideae	*Bauhinia rufa* (Bong.) Steud.	1329	S	SD	W
Fabaceae - Faboideae	*Bowdichia virgiloides* Kunth.	1340	TT	SD	W
	Machaerium villosum Vog.	1341	TT	E	W
	Sweetia subelegans Mohlenbr.	1342	ST	SD	W
Fabaceae - Mimosoideae	*Anadenanthera falcata* (Benth.) Speg.	1350	TT	SD	W
	Stryphnodendron polyphyllum Mart.	1352	ST	SD	W
Lauraceae	*Nectandra* sp.	1343	T	E	W
	Ocotea corymbosa (Meisn.)	1344	T	E	P
Malpighiaceae	*Byrsonima basiloba* A. Juss.	1345	ST	SD	P
	Byrsonima coccolobifolia Kunth.	1346	ST	SD	W
	Byrsonima verbascifolia (L.) DC.	1347	ST	SD	W
Melastomataceae	*Miconia albicans* (Sw) Triana	1348	ST	E	A
	Miconia ligustroides (DC.) Naudir.	1349	ST	E	W
Myrsinaceae	*Rapanea umbellata* (Mart.) Mez.	1353	T	E	P
Ochnaceae	*Ouratea spectabilis* (Mart.) Engl.	1354	T	SD	P
Proteaceae	*Roupala montana* Aubl.	1355	ST	E	W
Rubiaceae	*Alibertia concolor* (Cham.) K. Schum.	1356	S	E	W
Rutaceae	*Zanthoxylum rhoifolium* Lam.	1357	ST	E	W
Sapotaceae	*Pouteria torta* (Mart.) Radlk.	1358	T	SD	W
Styracaceae	*Styrax camporum* Pohl.	1359	ST	E	P
	Styrax ferrugineus Nees & Mart.	1360	ST	E	P
Tiliaceae	*Luehea grandiflora* Mart.	1361	T	SD	A
Verbenaceae	*Aegiphilla sellowiana* Cham.	1362	S	SD	W
Vochysiaceae	*Qualea dichotoma* (Mart.) Warm.	1363	TT	SD	P
	Qualea grandiflora Mart.	1364	T	SD	W
	Qualea multiflora Mart.	1365	T	SD	W
	Vochysia cinnamomea Pohl.	1366	T	SD	P
	Vochysia rufa Mart.	1367	TT	SD	W
	Vochysia tucanorum Mart.	1368	T	SD	W

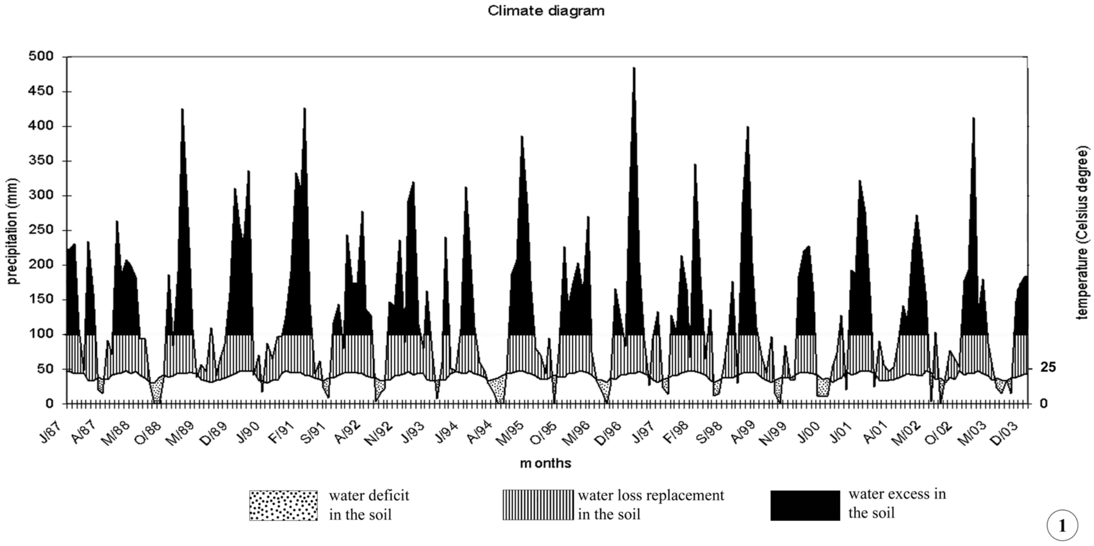
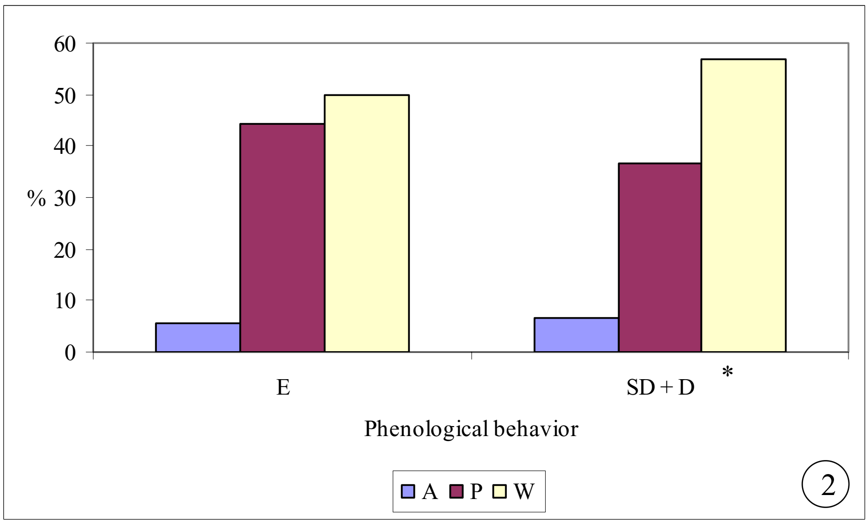


Figure 1. Climate diagram of the west central part of the state of S„o Paulo, according to Walter et al. *(1975) methodology.*



* as the number of deciduous species was small, deciduous and semi-deciduous species were pooled.

Figure 2. Percentage of species lacking growth rings, species with poorly defined and well-defined growth rings within each phenological category. As the number of deciduous species was small, deciduous and semi-deciduous species were pooled. E = evergreen. SD + D = semi-deciduous plus deciduous. A = growth rings absence. P = poorly defined growth rings. W = well defined growth rings.

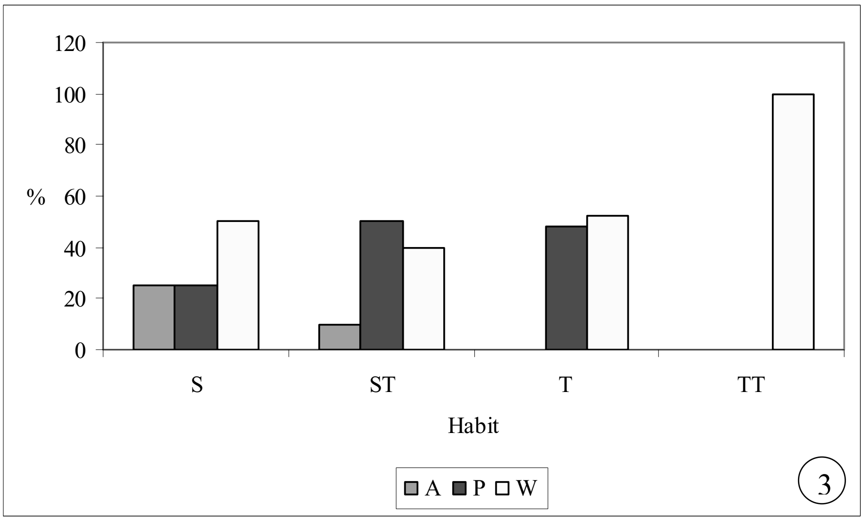


Figure 3. Percentage of species lacking growth rings, species with poorly defined and well-defined growth rings within each habit category. S = shrubs. ST = small tree. T = tree. TT = tall tree. A = growth rings absence. P = poorly defined growth rings. W = well defined growth rings.

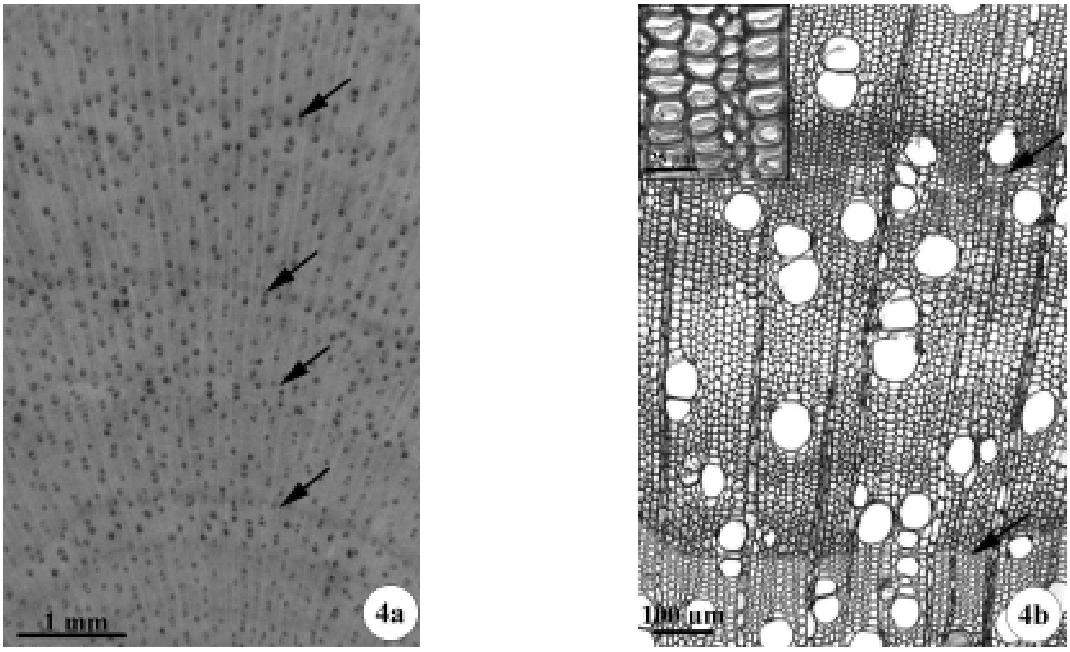


Figure 4. a-b. Transverse section of Nectandra *sp. wood. a) Photomacrograph showing growth layers boundaries (arrows). b) Photomicrograph. Arrows indicate thick-walled and radially flattened latewood fibres. Gelatinous fibres occur along the growth layer and can be noted in detail above in the figure.*

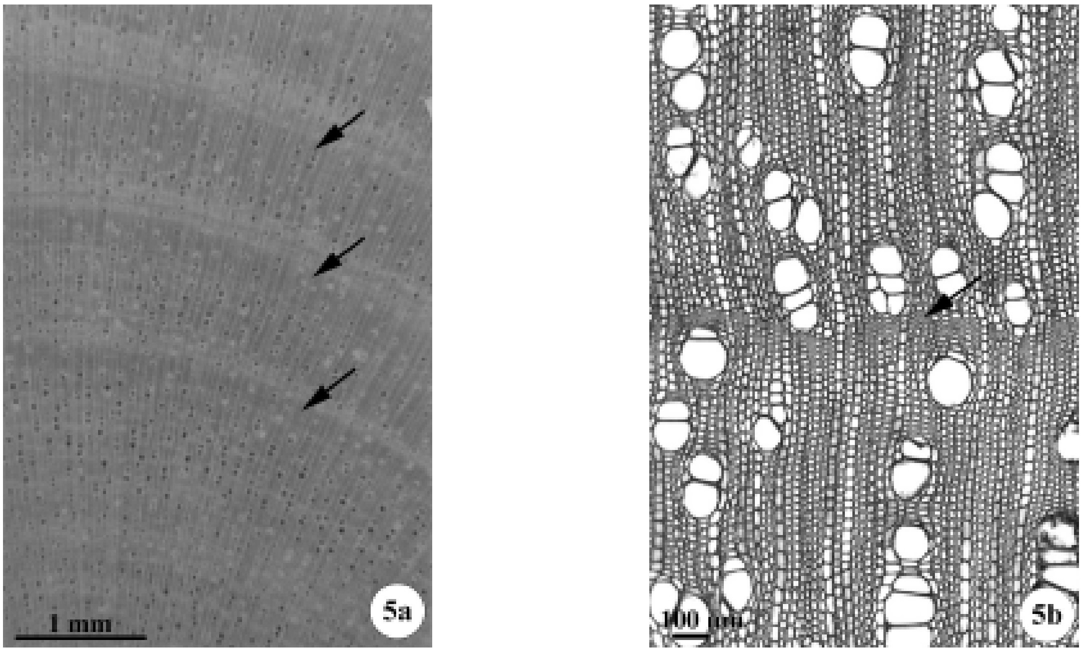


Figure 5. a-b. Transverse section of Miconia ligustroides *wood. a) Photomacrograph. Arrows indicate growth layers boundaries. Parenchyma-like fibre bands can be noted lighter in the figure. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres.*

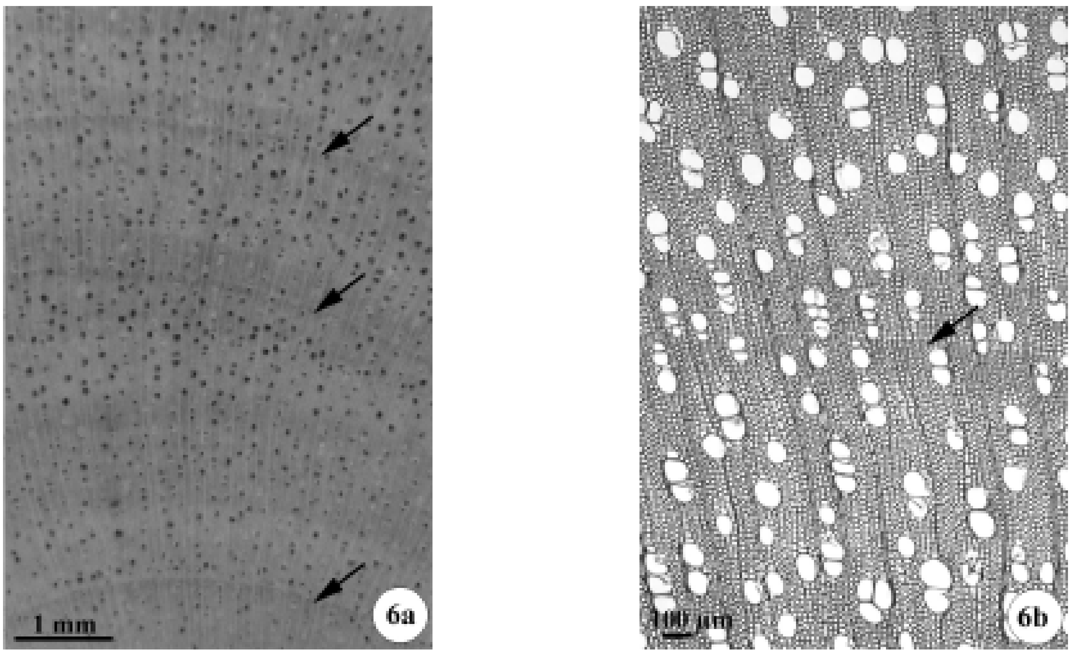


Figure 6. a-b. Transverse section of Zanthoxylum rhoifolium *wood. a) Photomacrograph. Arrows indicate growth layers boundaries. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres.*

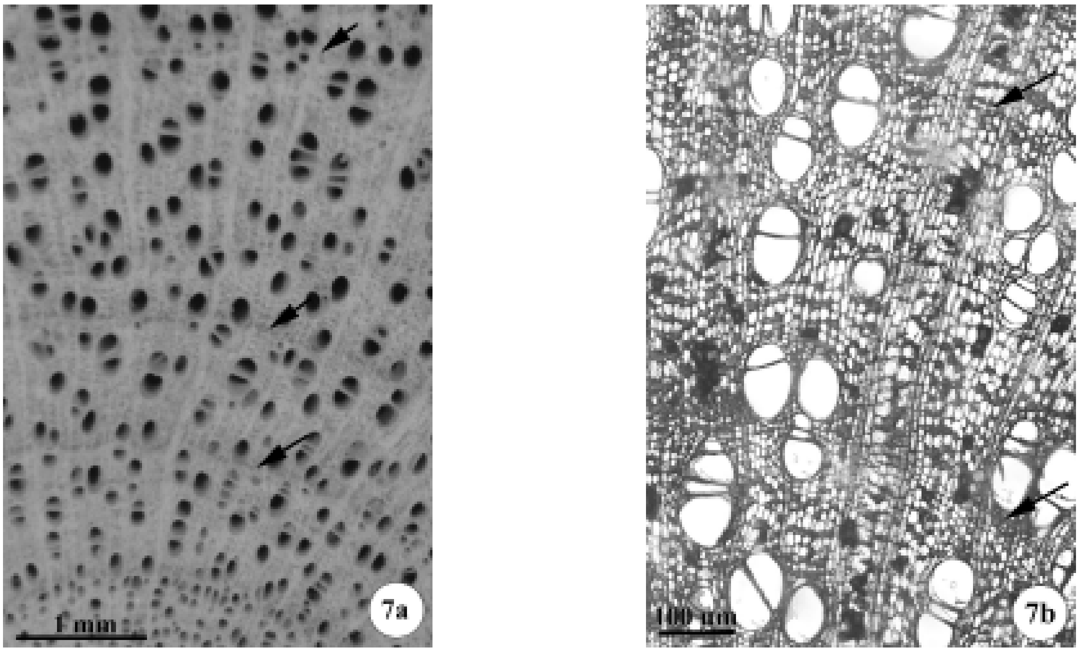


Figure 7. a-b. Transverse section of Eriotheca gracilipes *wood. a) Photomacrograph. Arrows indicate growth layers boundaries. b) Photomicrograph. Arrows indicate thick-walled and radially flattened latewood fibres.*

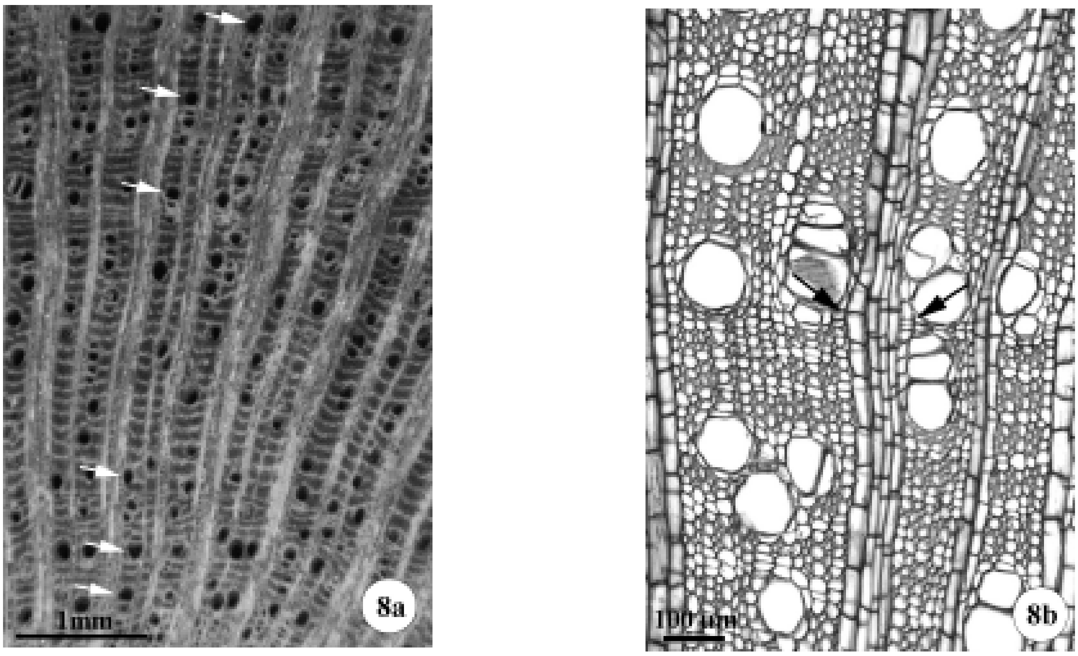


Figure 8. a-b. Transverse section of Annona coriacea *wood. a) Photomacrograph. The arrows indicate the largest vessels in tangential arrangement in earlywood. Note the closeness of the parenchyma narrow bands just before the largest vessels in each growth layer. b) Photomicrograph shows distended rays in the boundary of the growth layers (arrows).*

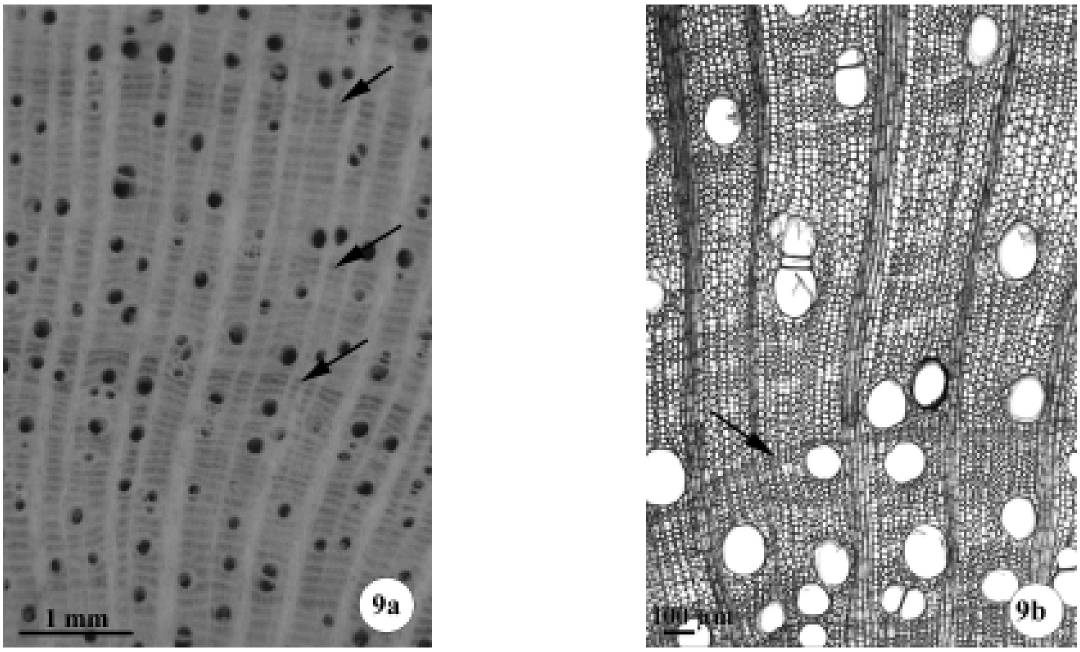


Figure 9. a-b. Transverse section of Annona crassiflora *wood. a) Photomacrograph. The arrows indicate growth layers boundaries. b) Photomicrograph. Arrow indicates thick-walled latewood fibres in the boundary of the growth layers.*

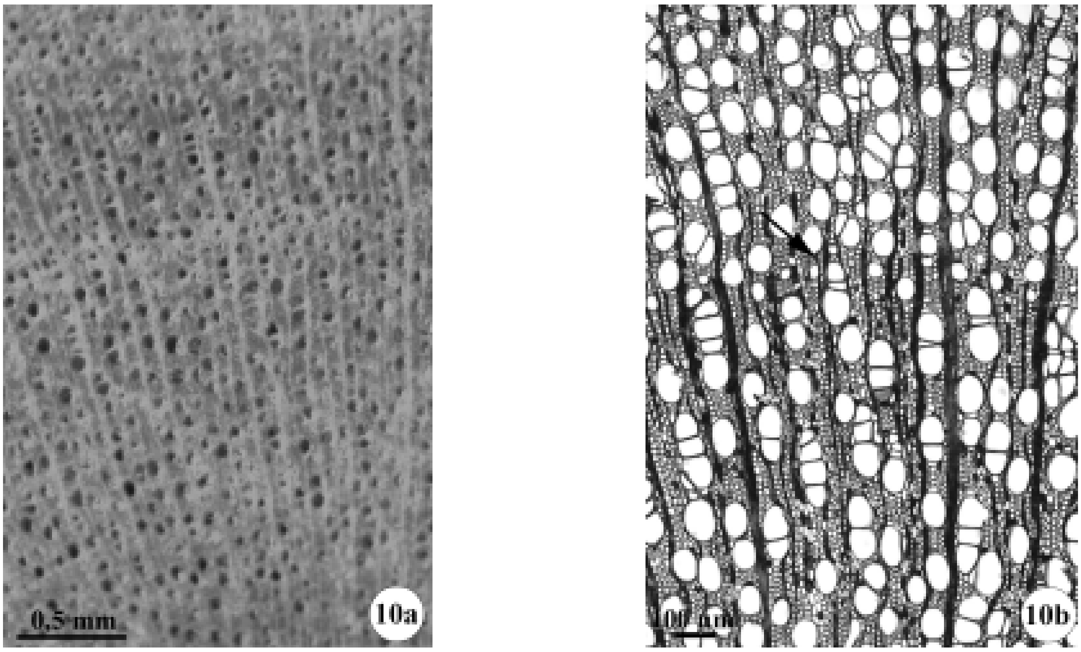


Figure 10. a-b. Transverse section of Erythroxylum tortuosum *wood. a) Photomacrograph. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres and small vessels.*

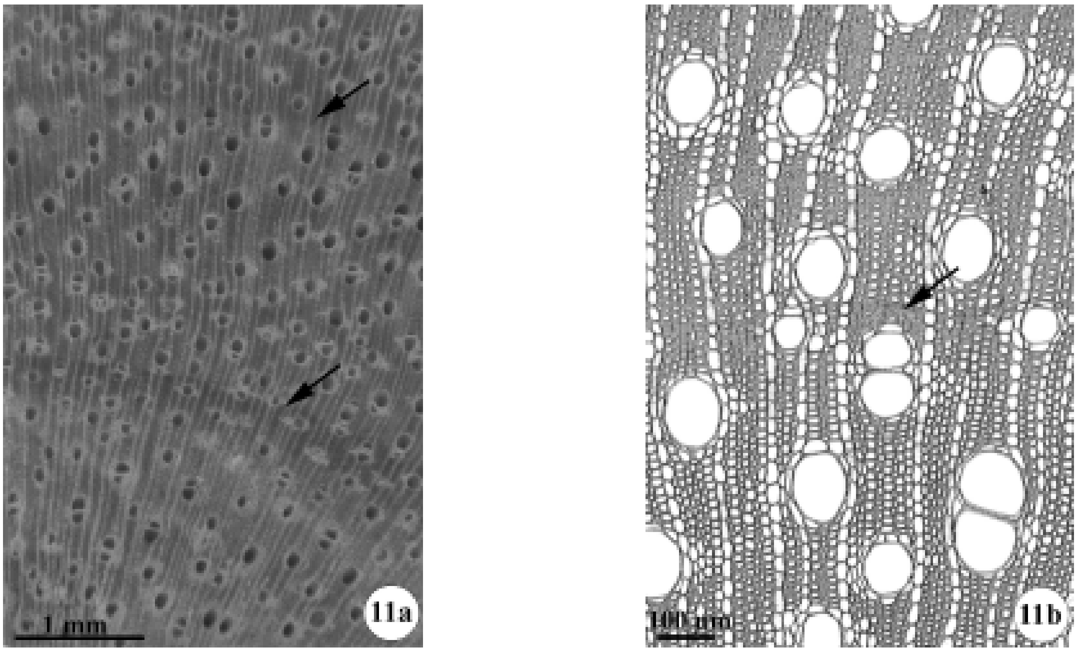


Figure 11. a-b. Transverse section of Terminalia brasiliensis *wood. a) Photomacrograph. Arrows indicate growth layers boundaries. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres.*

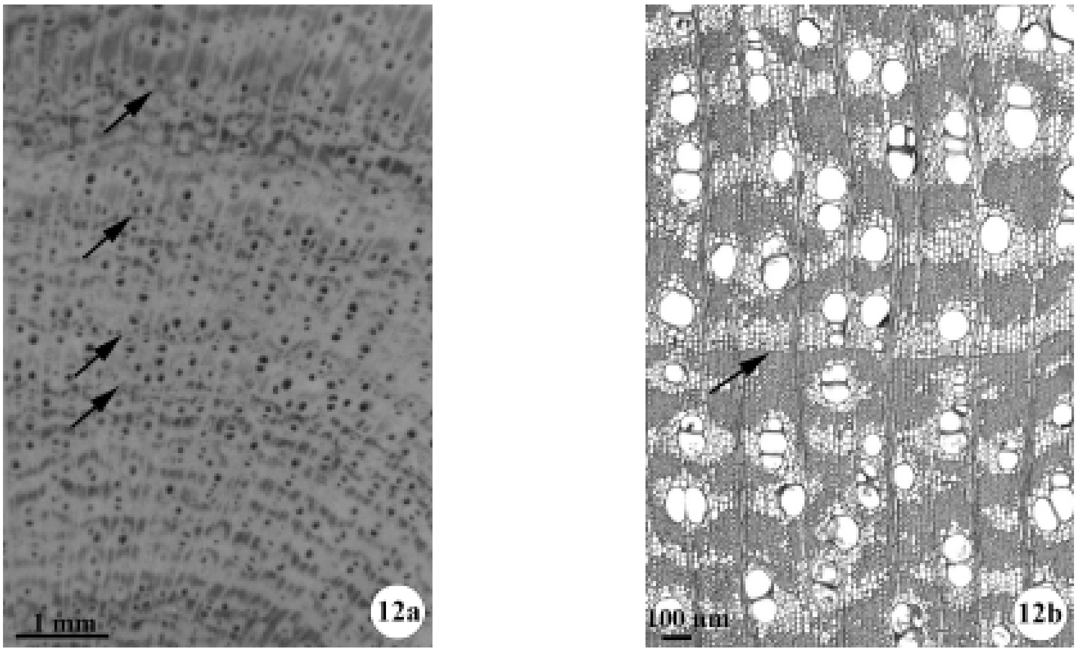


Figure 12. a-b. Transverse section of Qualea grandiflora *wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma marking growth layers boundaries. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres.*

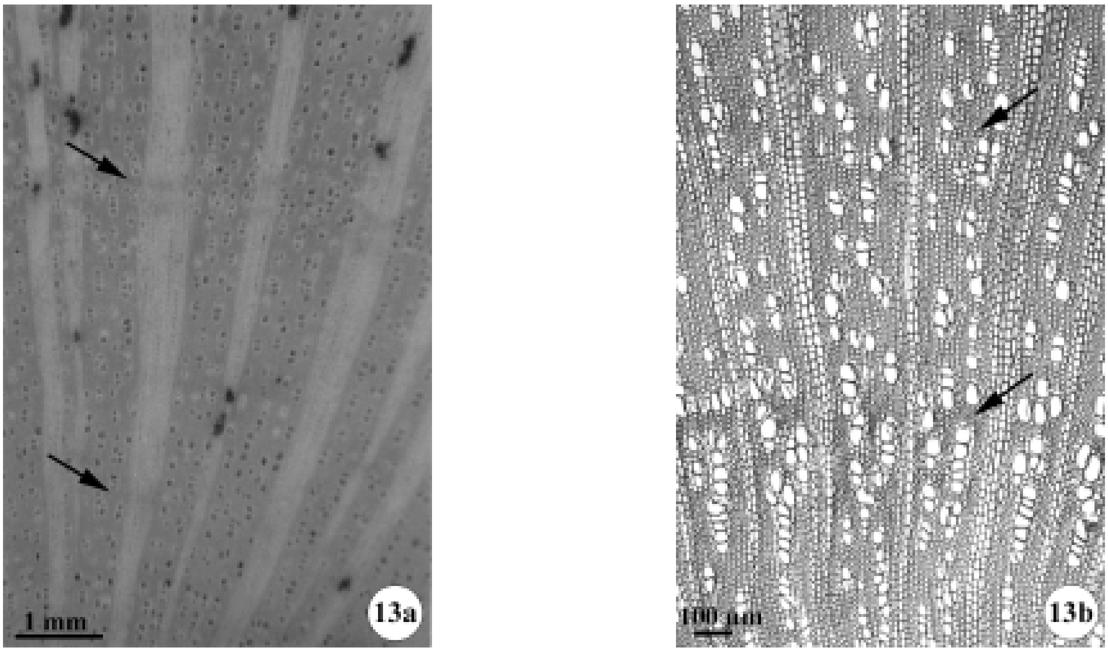


Figure 13. a-b. Transverse section of Rapanea umbellata *wood. a) Photomacrograph. Arrows indicate growth layers boundaries. b) Photomicrograph. Arrows indicate thick-walled and slight radially flattened latewood fibres.*

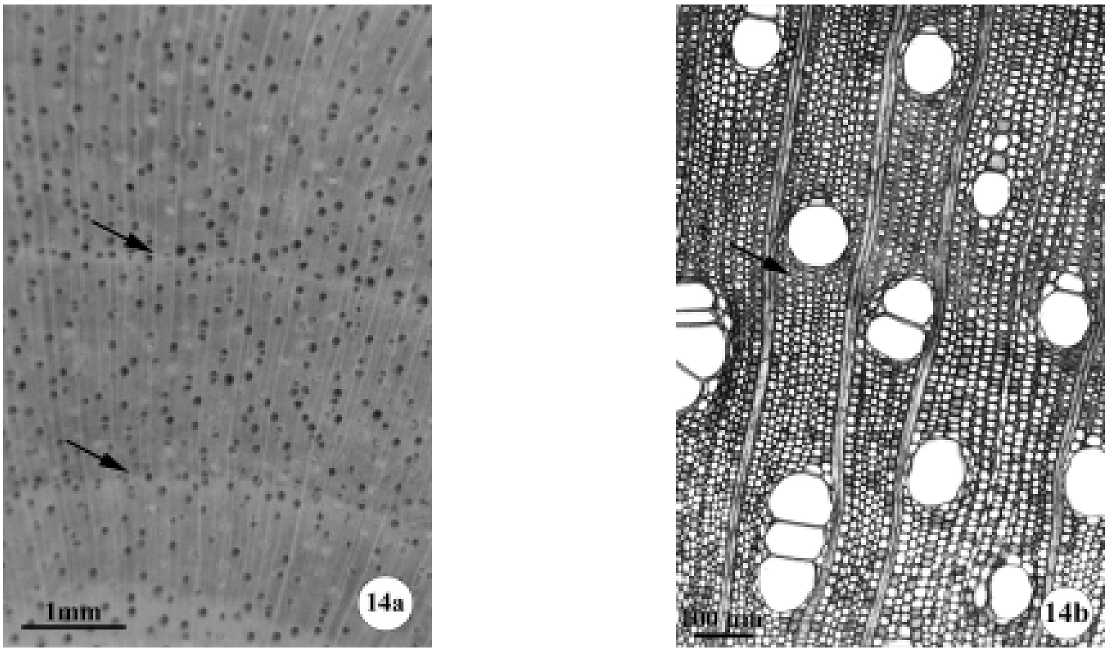


Figure 14. a-b. Transverse section of Tapirira guianensis *wood. a) Photomacrograph. The arrows indicate growth layers boundaries. b) Photomicrograph shows thick-walled latewood fibres (arrow).*

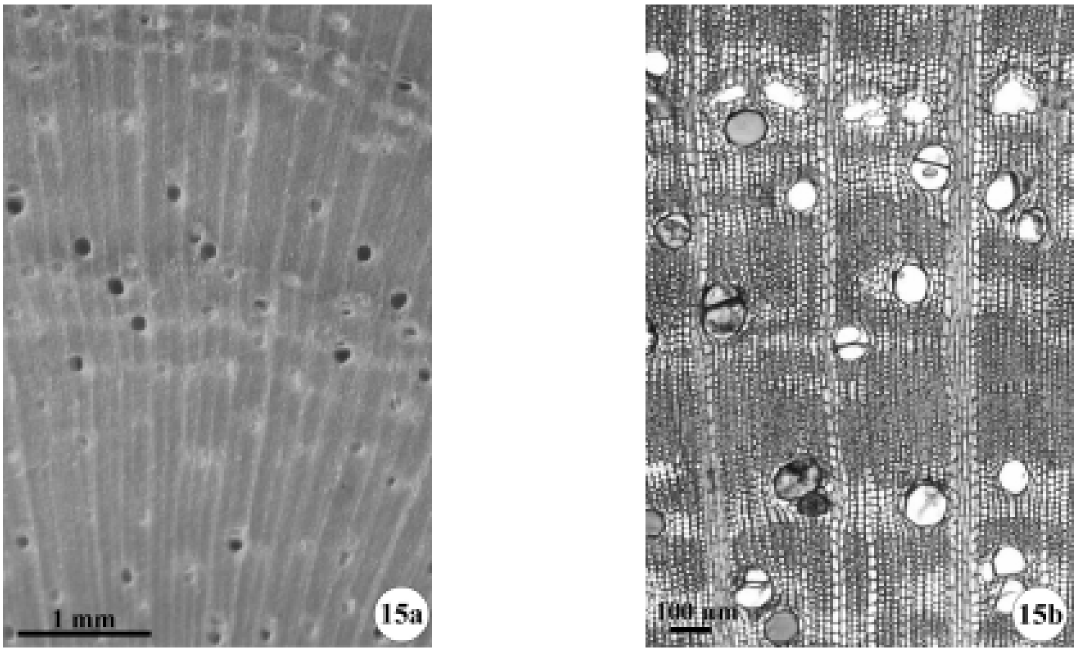


Figure 15. a-b. Transverse section of Vochysia cinnamomea *wood. a) Photomacrograph. Note the variation within growth layers in the axial parenchyma distribution. b) Photomicrograph. Note the variation within growth layers in the axial parenchyma distribution and the tangential arrangement of the traumatic canals above in the figure.*

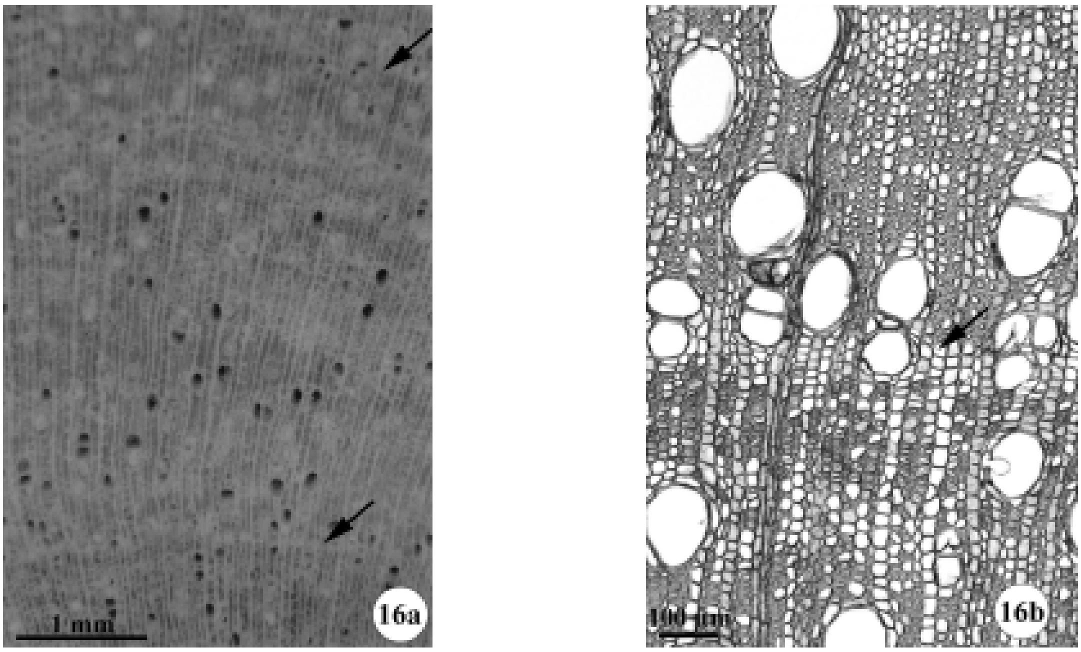


Figure 16. a-b. Transverse section of Caryocar brasiliense *wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. b) Photomicrograph. Arrow indicates marginal lines of axial parenchyma.*

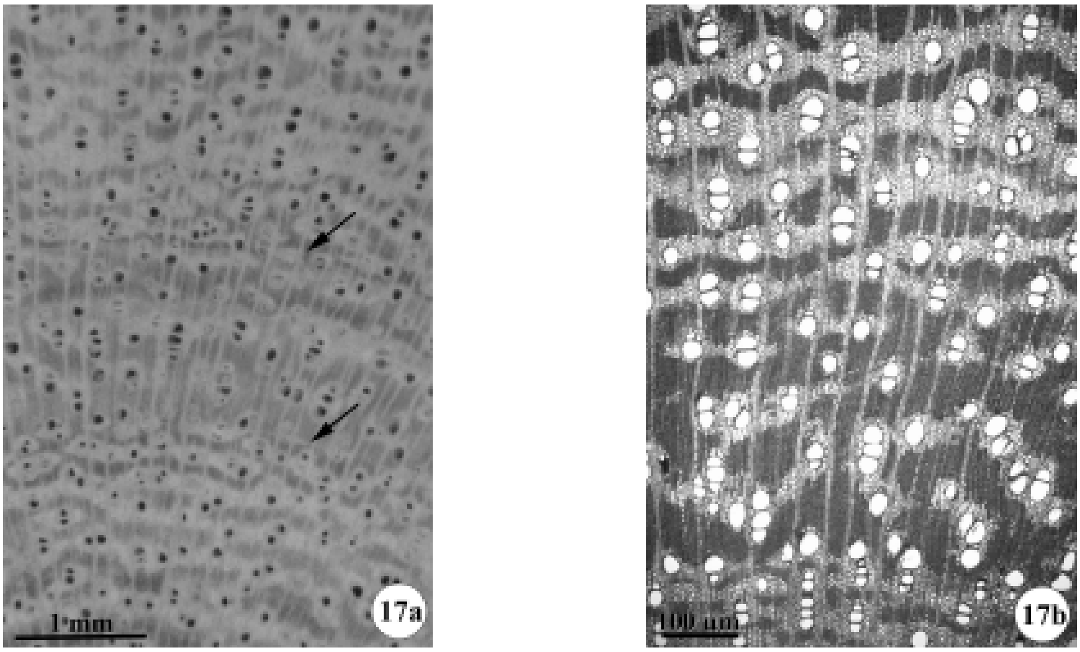


Figure 17. a-b. Transverse section of Qualea multiflora *wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. b) Photomicrograph. Note variation within growth layers in the axial parenchyma distribution.*

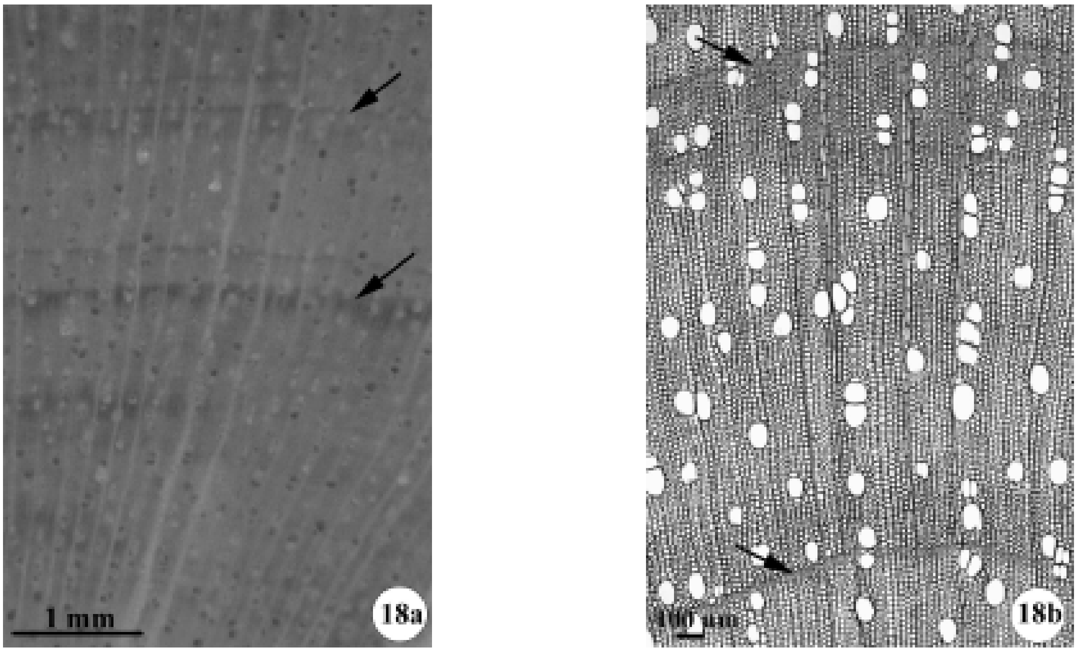


Figure 18. a-b. Transverse section of Didymopanax vinosum *wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Thick-walled and radially flattened latewood fibres in fibre zones (arrows).*

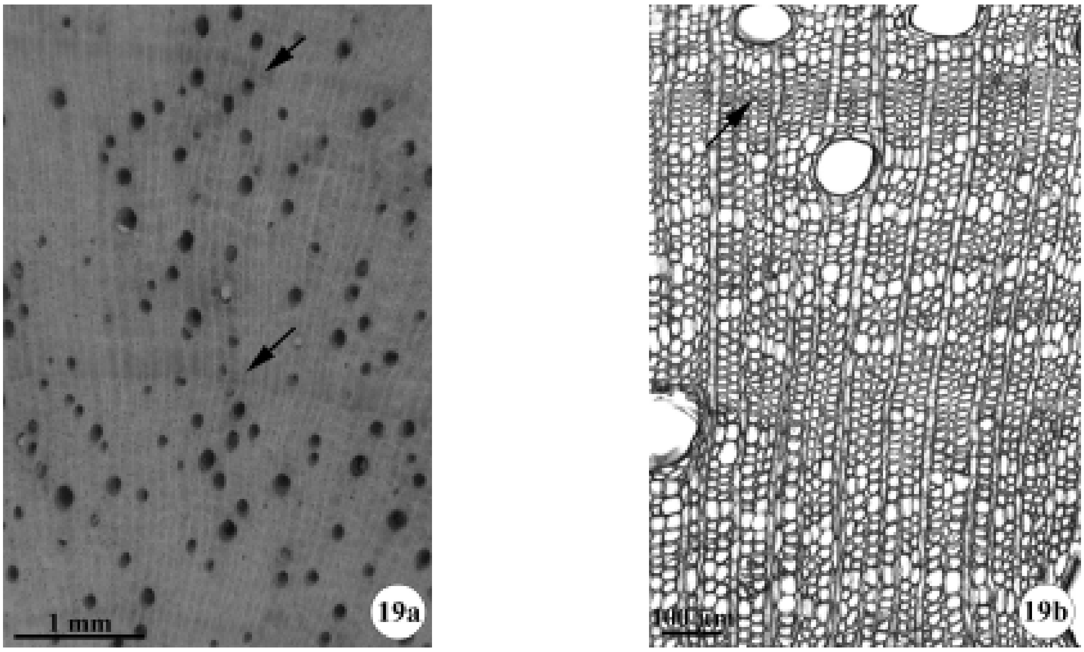


Figure 19. a-b. Transverse section of Couepia grandiflora *wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres in fibre zones.*

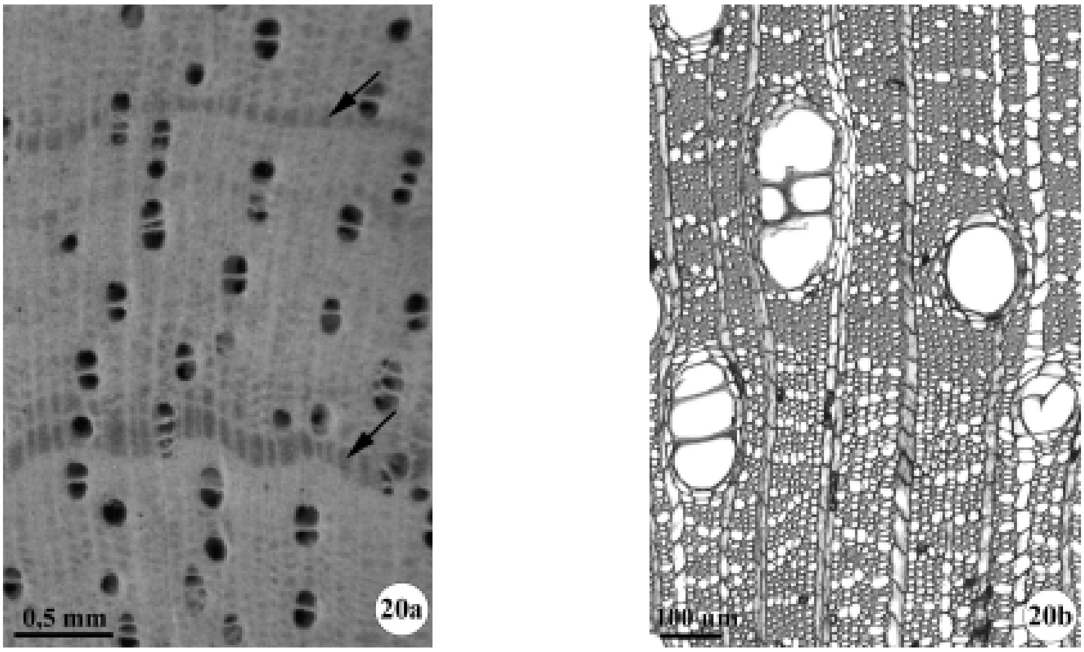


Figure 20. a-b. Transverse section of Diospyrus hispida *wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Note that the narrow bands of axial parenchyma tend to come closer towards the end of the growth ring.*

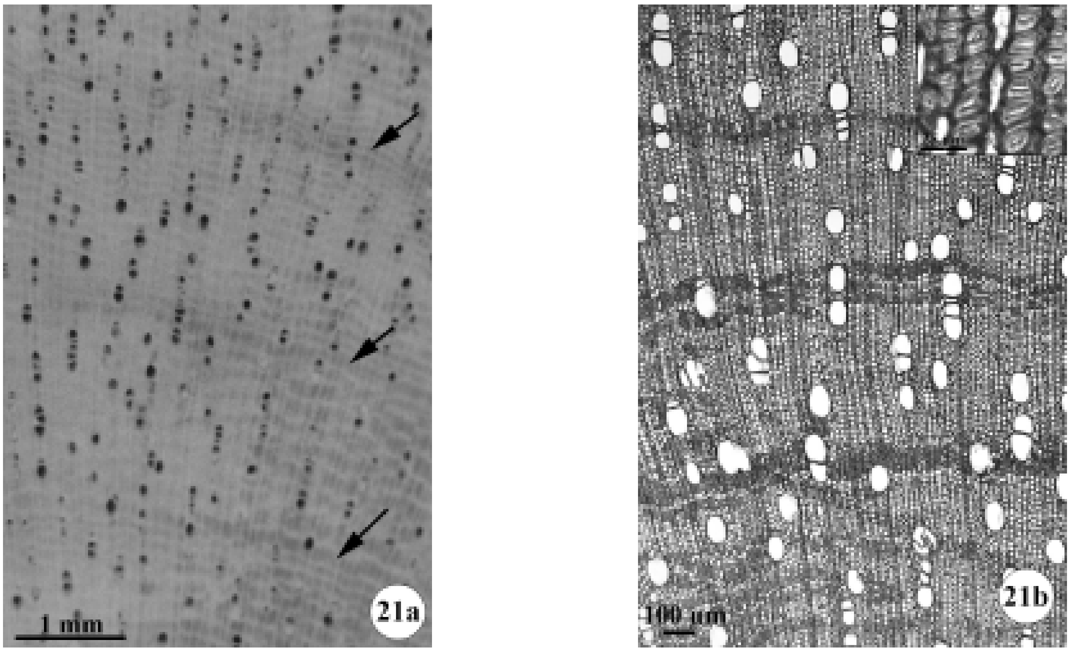


Figure 21. a-b. Transverse section of Pera glabrata *wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Note irregular zones of gelatinous fibres adjacent to the growth layers. Gelatinous fibres in detail.*

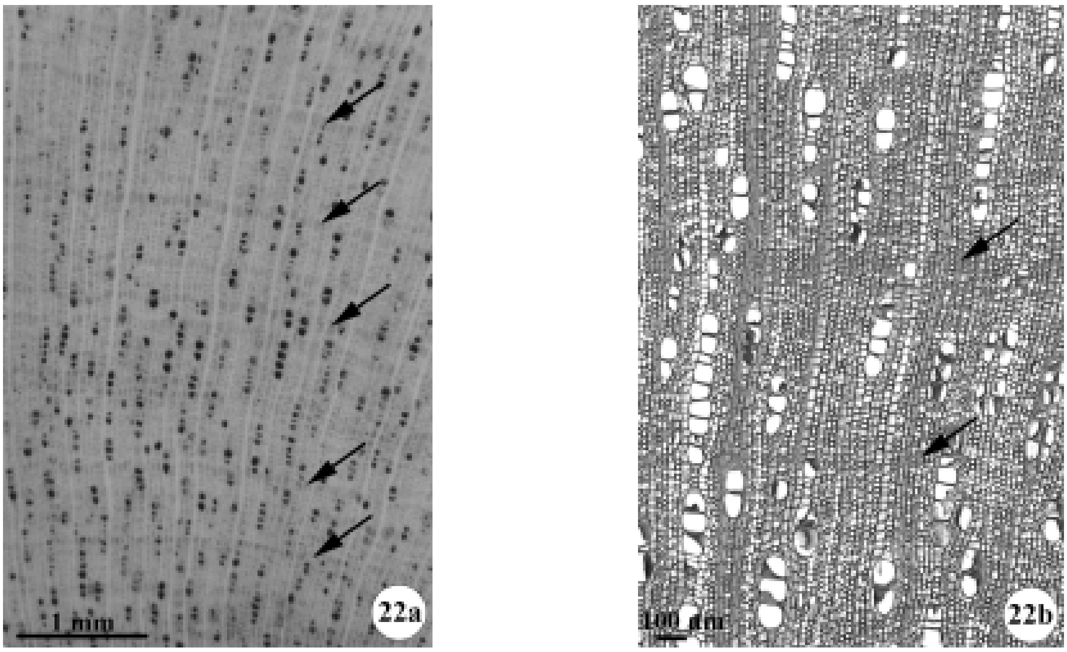


Figure 22. a-b. Transverse section of Styrax ferrugineus *wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Arrows indicate thick-walled latewood fibres in fibre zones.*

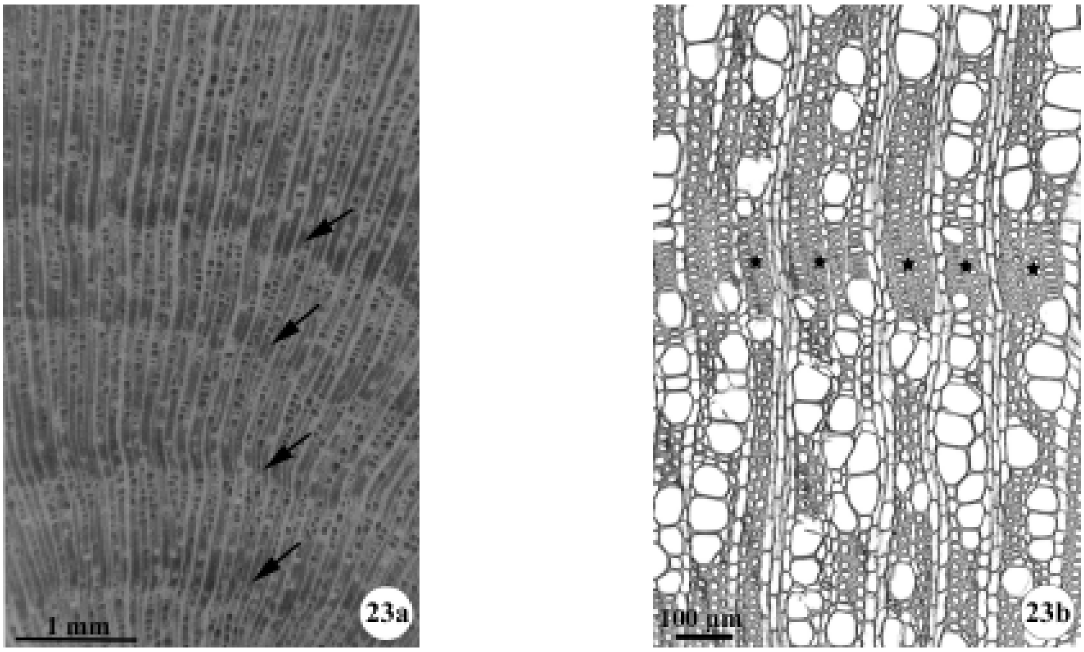


Figure 23. a-b. Transverse section of Byrsonima coccolobifolia *wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Small stars indicate thick-walled and radially flattened latewood fibres in fibre zone. Note that the rays become narrow in this region.*

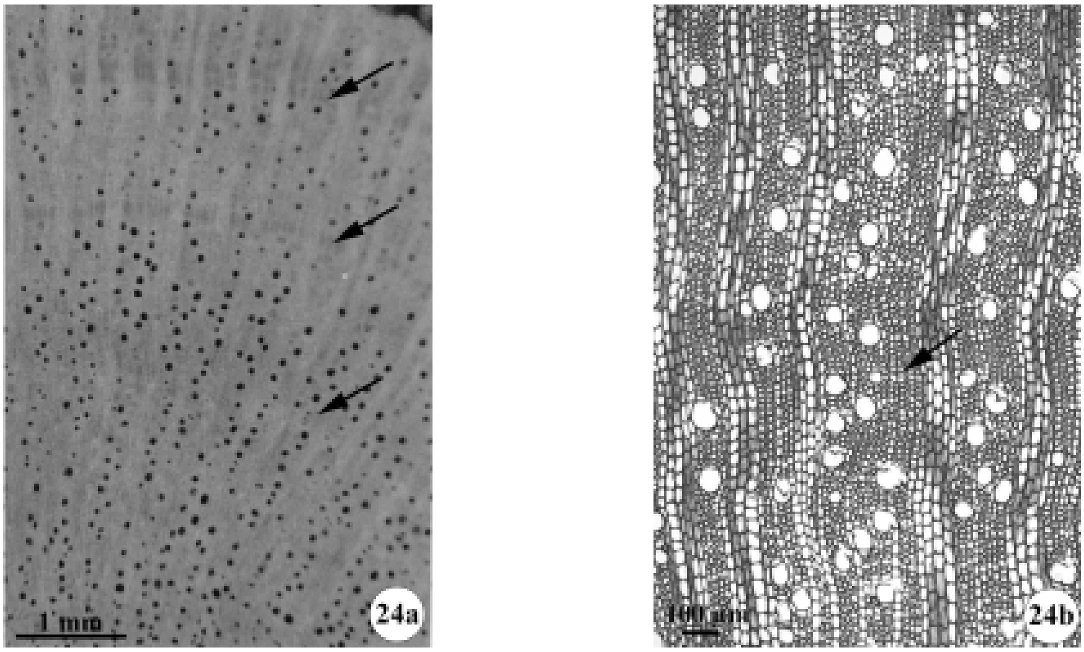


Figure 24. a-b. Transverse section of Ouratea spectabilis *wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Arrow indicates thick-walled and radially flattened latewood fibres in fibre zone.*

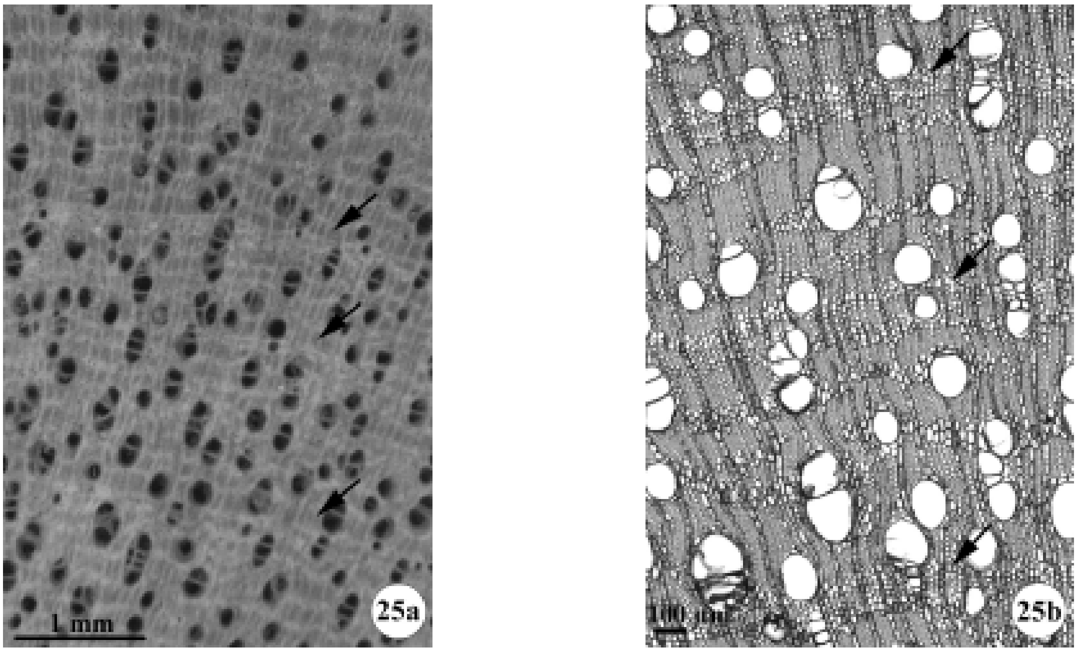


Figure 25. a-b. Transverse section of Kielmeyera rubriflora *wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Arrows indicate straight lines of marginal parenchyma.*

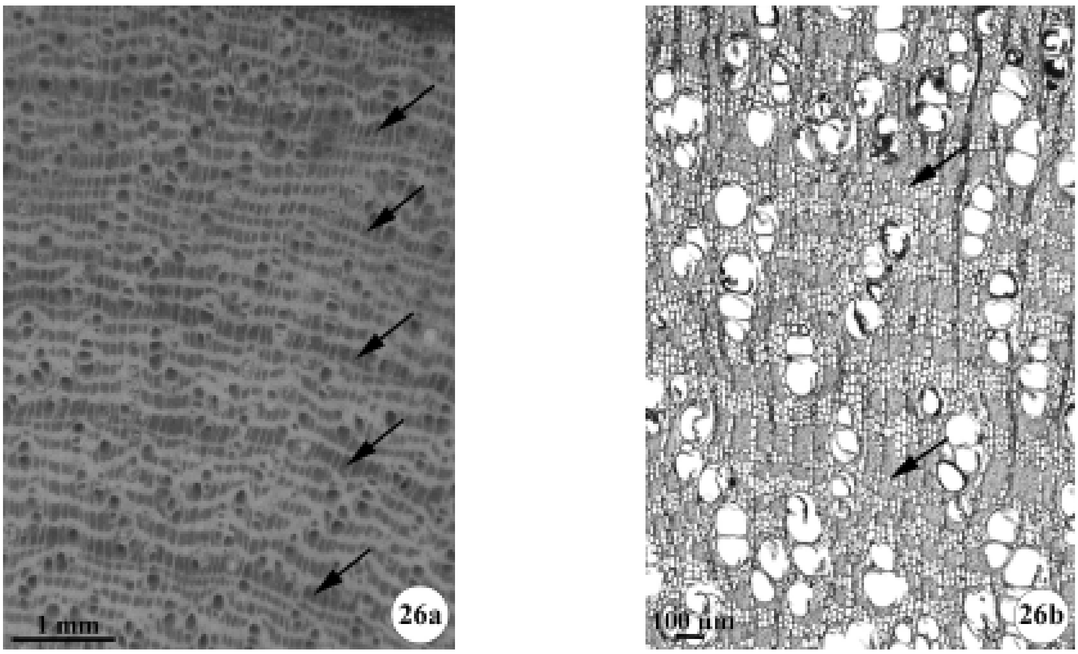


Figure 26. a-b. Transverse section of Pouteria torta *wood. a) Photomacrograph. Arrows indicate fibre zones. b) Photomicrograph. Arrows indicate straighter and thinner lines of marginal parenchyma.*

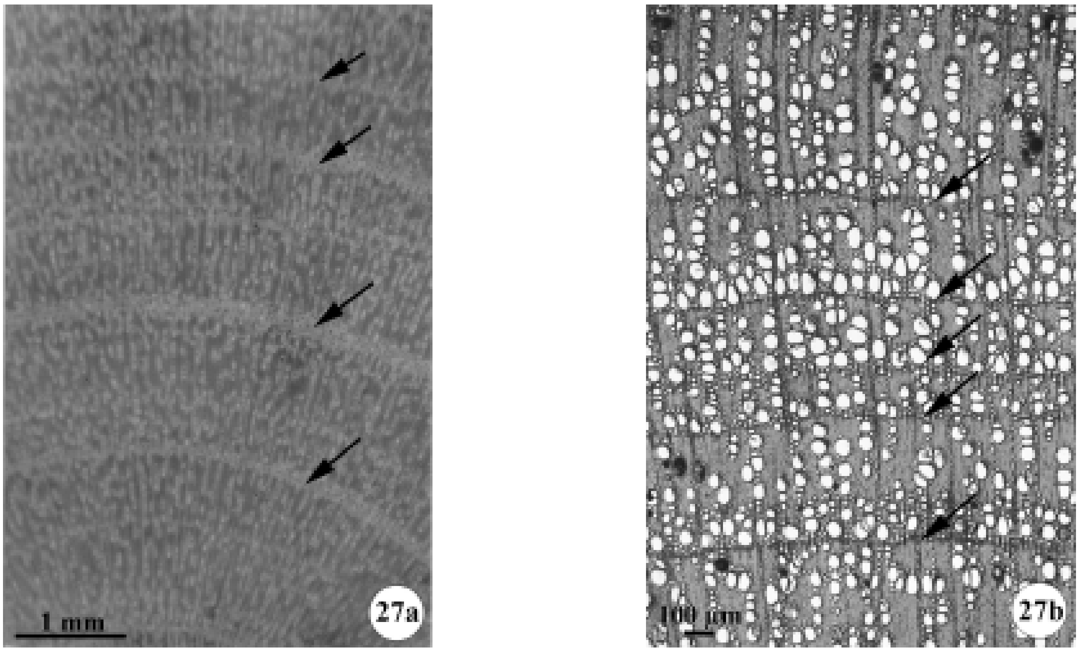


Figure 27. a-b. Transverse section of Gochnatia barrosii *wood. a) Photomacrograph. Arrows indicate marginal bands of axial parenchyma. b) Photomicrograph. Arrows indicate marginal bands of axial parenchyma. Note higher frequency of vessels in earlywood.*

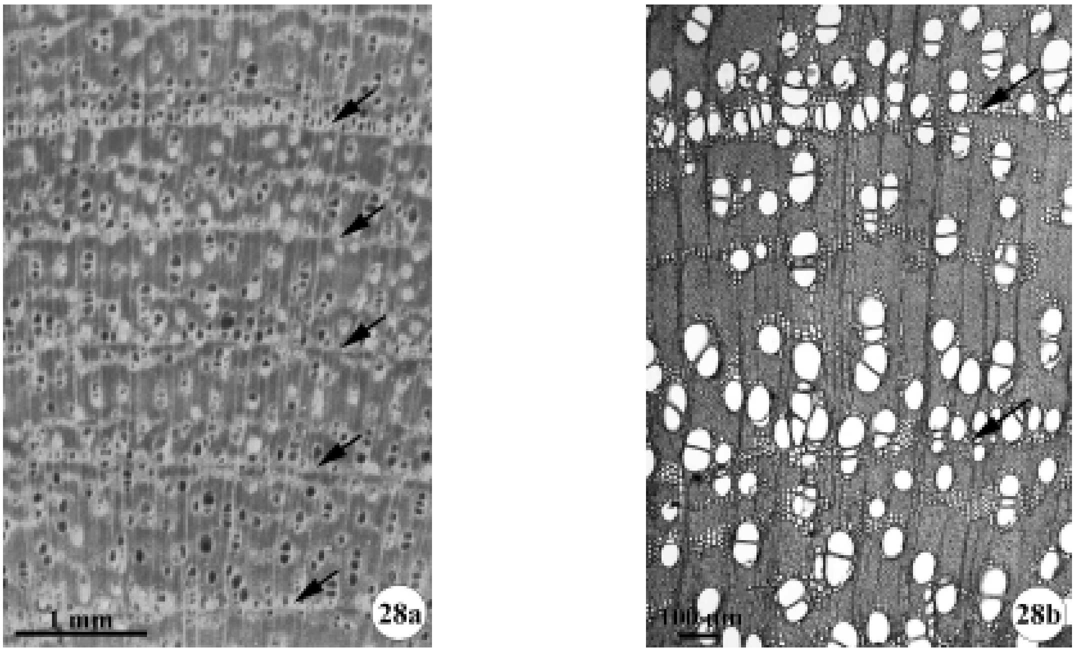


Figure 28. a-b) Transverse section of Bauhinia rufa *wood. a) Photomacrograph. Arrows indicate marginal bands of axial parenchyma. b) Photomicrograph. Arrows indicate marginal bands of axial parenchyma. Note higher frequency of vessels adjacent to the marginal bands.*

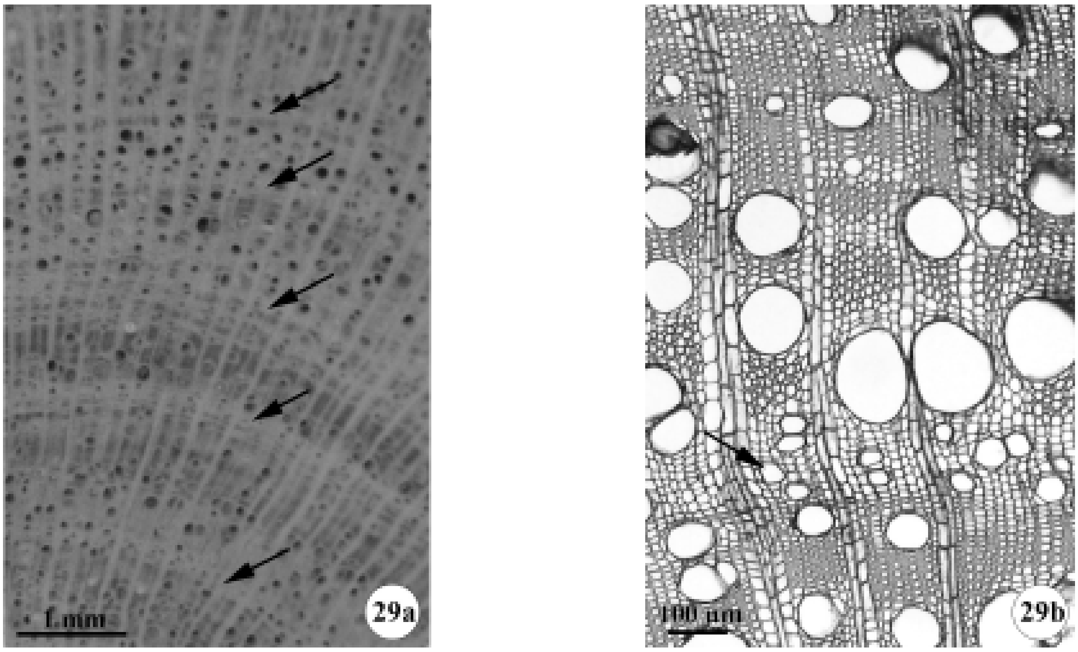


Figure 29. a-b. Transverse section of Cordia sellowiana *wood. a) Photomacrograph. Arrows indicate marginal bands of parenchyma. b) Photomicrograph. Arrow indicates small latewood vessels absorbed in marginal parenchyma.*

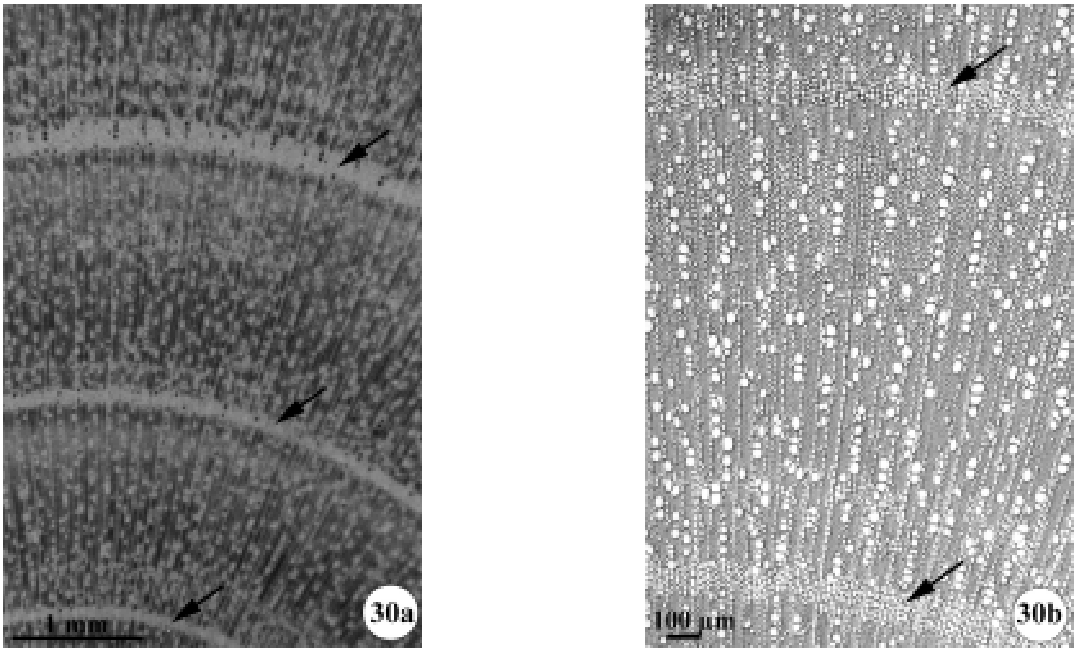


Figure 30. a-b. Transverse section of Alibertia concolor *wood. a) Photomacrograph. Arrows indicate marginal bands of axial parenchyma. b. Photomicrograph. Arrows indicate marginal bands.*

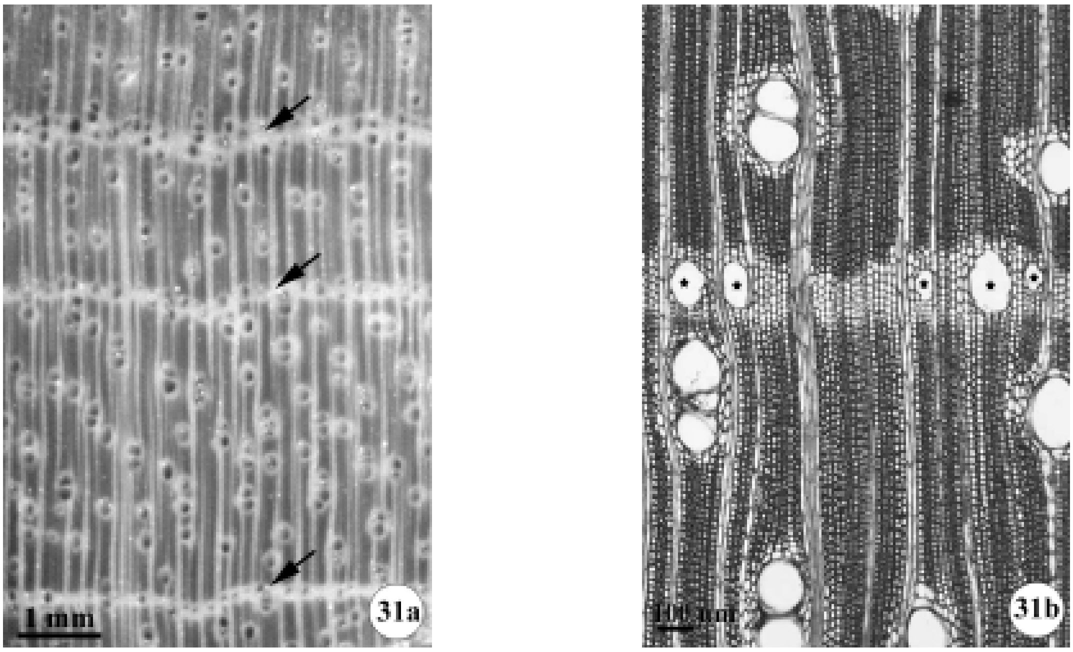


Figure 31. a-b. Transverse section of Copaifera langsdorffii *wood. a) Photomacrograph. Arrows indicate marginal bands of axial parenchyma. b) Photomicrograph. Small stars indicate axial canals in marginal bands of axial parenchyma.*

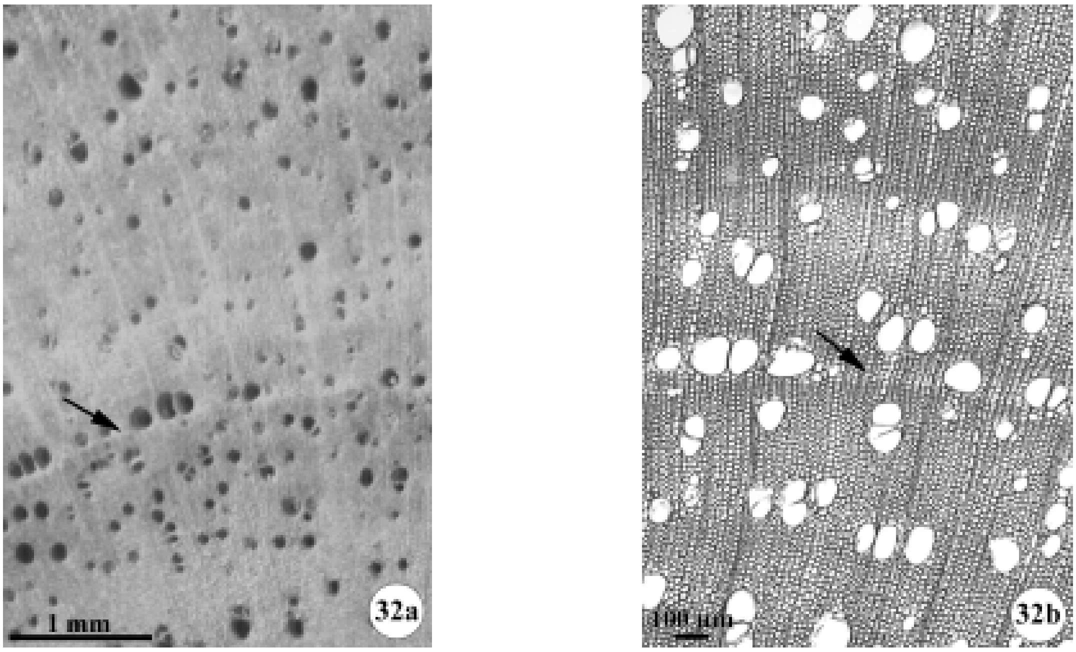


Figure 32. a-b. Transverse section of Aegiphilla sellowiana *wood. a) Photomacrograph. Arrow indicates marginal bands of axial parenchyma. b) Photomicrograph. Arrow indicates marginal band of axial parenchyma.*

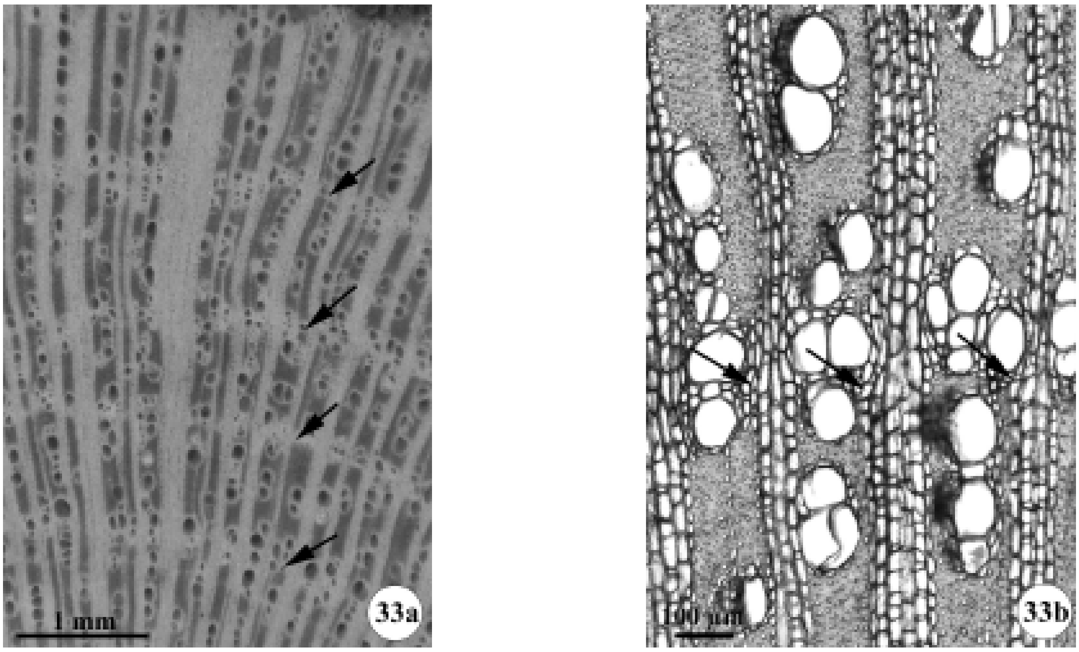


Figure 33. a-b. Transverse section of Piptocarpha rotundifolia *wood. a) Photomacrograph. Arrows indicate marginal bands of axial parenchyma. Note the higher frequency of vessels adjacent to the marginal bands. b) Photomicrograph. Arrows indicate distended rays in the boundary of a growth layer.*

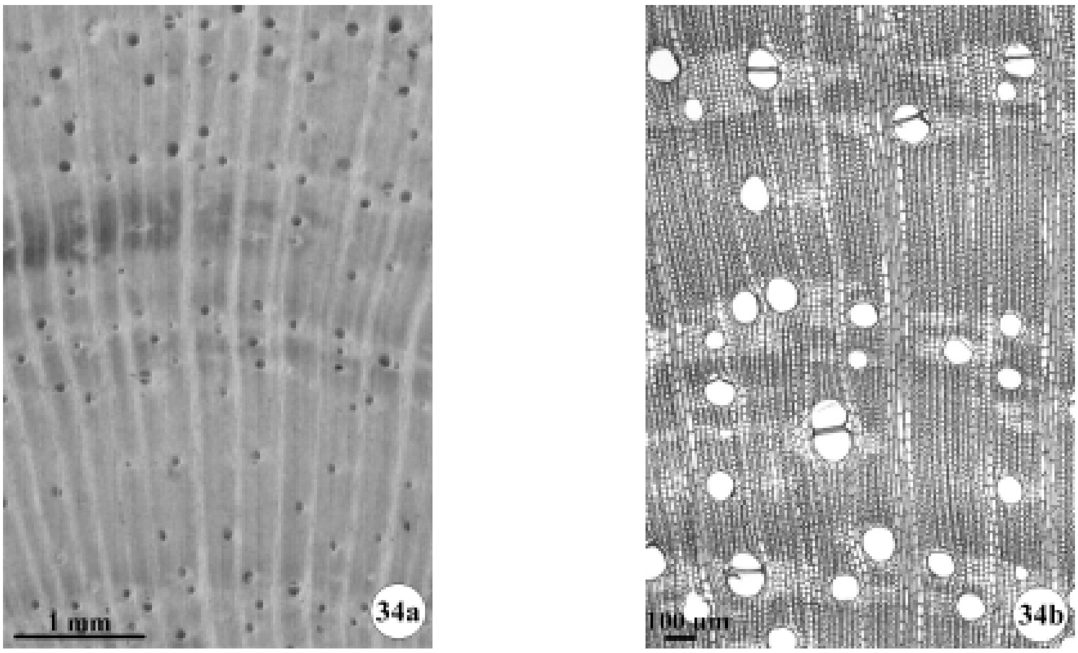


Figure 34. a-b. Transverse section of Vochysia rufa *wood. a) Photomacrograph. b) Photomicrograph. Note axial parenchyma variation within growth layers.*

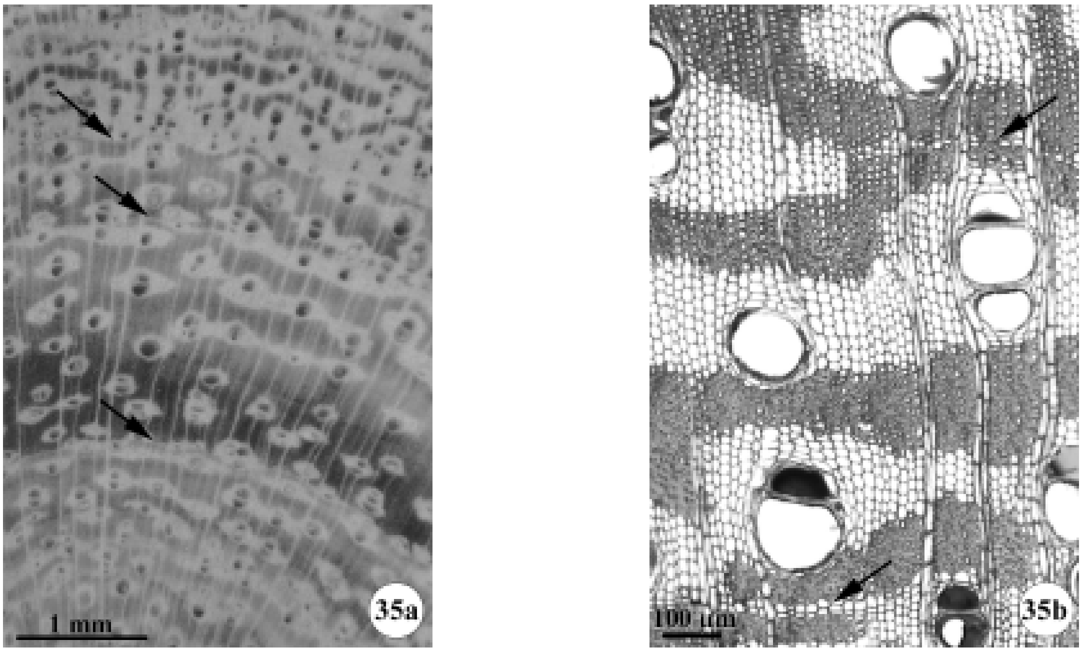


Figure 35. a-b. Transverse section of Dimorphandra mollis *wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. b) Photomicrograph. Arrows indicate marginal lines of axial parenchyma.*

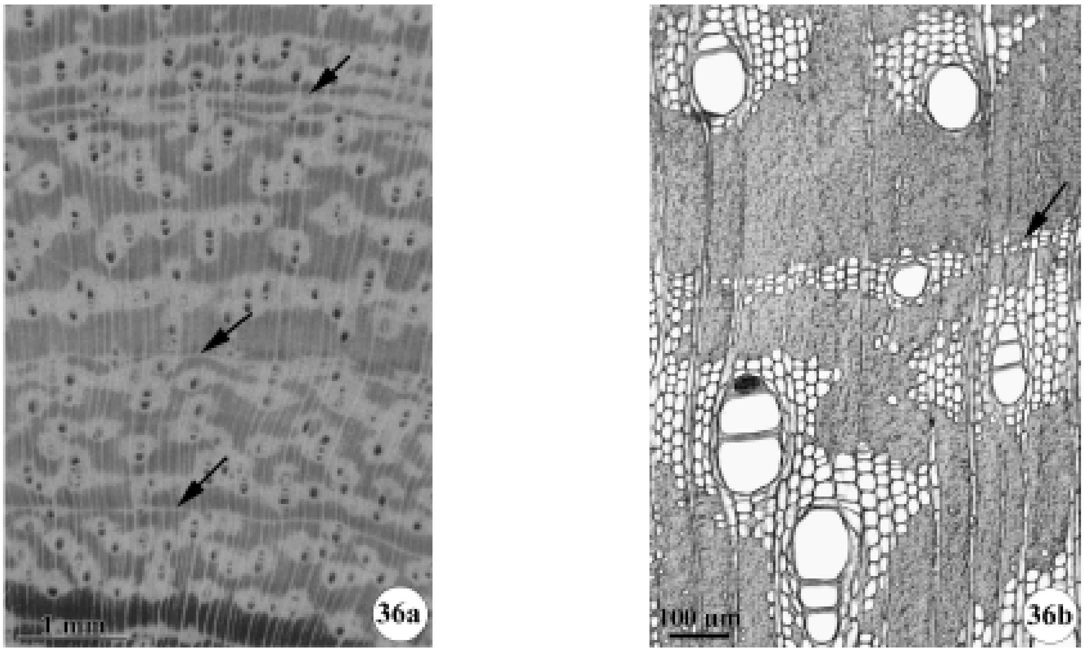


Figure 36. a-b. Transverse section of Bowdichia virgiloides *wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. b) Photomicrograph. Marginal lines of axial parenchyma in detail (arrow).*

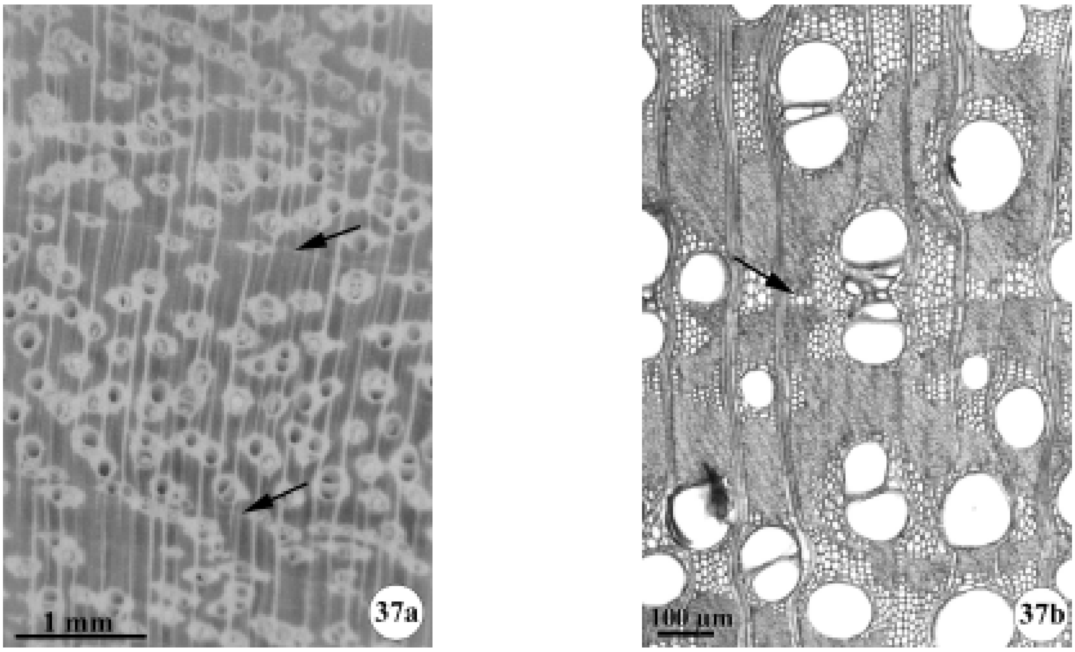


Figure 37. a-b. Transverse section of Anadenanthera falcata *wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. b) Photomicrograph. Arrow indicates marginal lines of axial parenchyma in detail.*

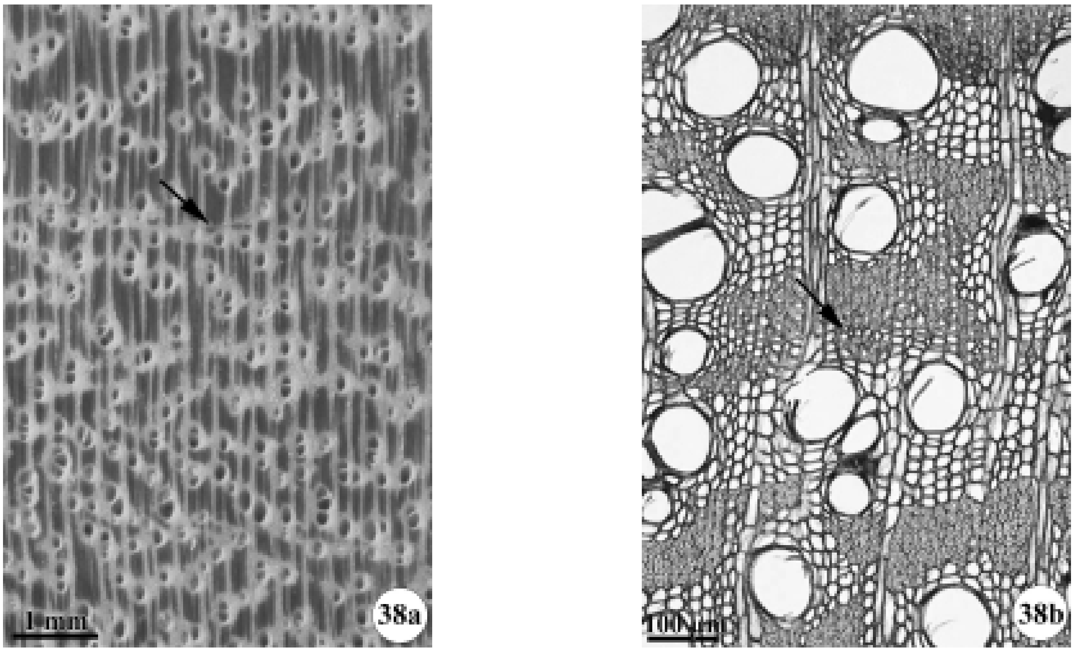


Figure 38. a-b. Transverse section of Qualea dichotoma *wood. a) Photomacrograph. Arrow indicates marginal lines of axial parenchyma. b) Arrow indicates marginal lines of axial parenchyma in detail.*

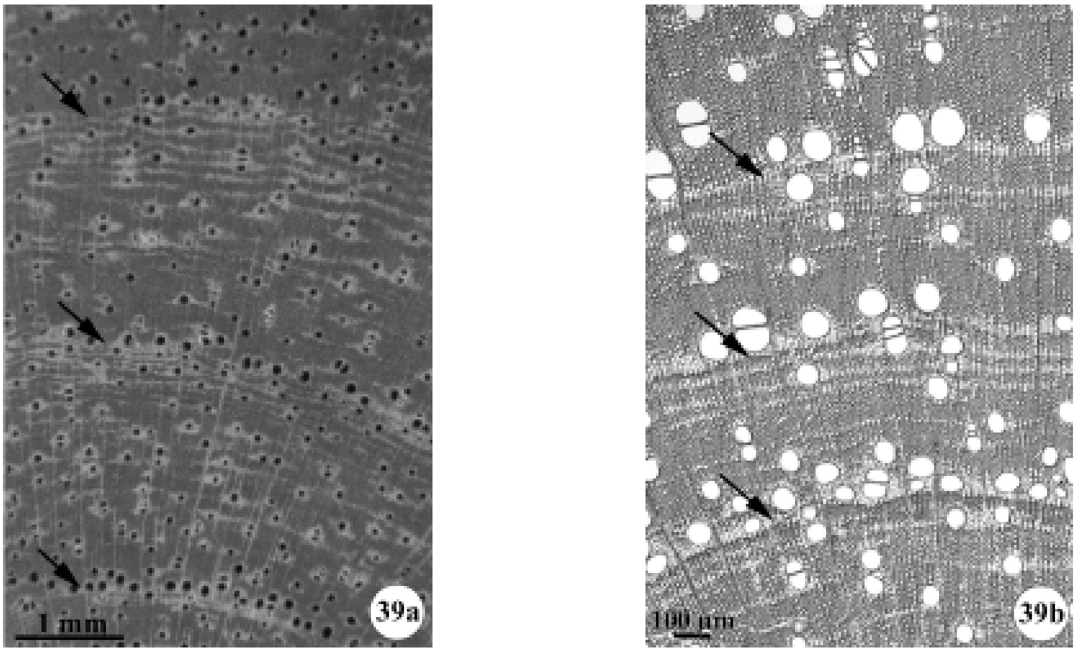


Figure 39. a-b. Transverse section of Machaerium villosum *wood. a) Photomacrograph. Arrows indicate marginal lines of axial parenchyma. Note the variation within growth layers in the axial parenchyma distribution. b) Photomicrograph. Arrows indicate marginal lines of axial parenchyma.*

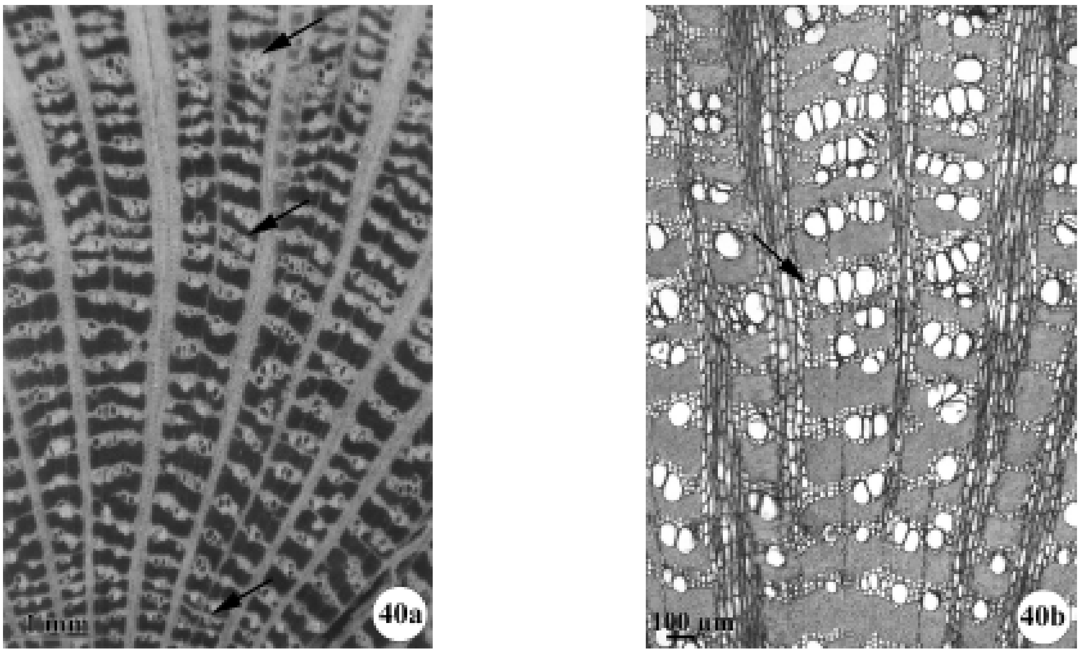


Figure 40. a-b. Transverse section of Roupala montana *wood. a) Photomacrograph. Arrows indicate closeness of the narrow bands of scalariform parenchyma. b) Photomicrograph. Arrow indicates the region of the closeness of the narrow bands of scalariform parenchyma.*

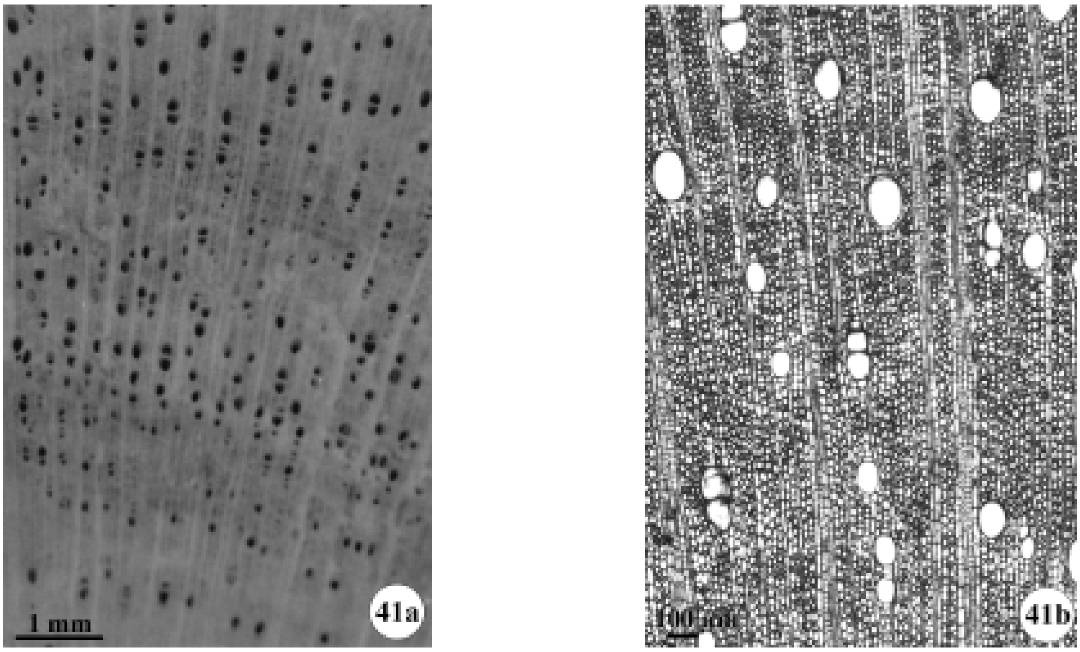


Figure 41. a-b. Transverse section of Luehea grandiflora *wood. a) Photomacrograph. Absence of growth ring markers. b) Photomicrograph.*

Table 2. Growth rings of the studied species from Brazilian cerrado. Growth ring visibility: W = well defined, P = poorly defined, A = growth ring absent.

Growth ring marker	Variation withing growth ring	Species
Thick-walled and radially flattened latewood fibres.	Not observed.	*Nectandra* sp. (W) (Fig. 4a, 4b), *Ocotea corymbosa* (P), *Miconia ligustroides* (W) (Fig. 5a, 5b), *Zanthoxylum rhoifolium* (W) (Fig. 6a, 6b).
Thick-walled and radially flattened latewood fibres.	Within the growth layers there is a higher frequency in the amount of axial parenchyma cells in the earlywood, decreasing to the latewood. In the areas where axial parenchyma is abundant, the fibres seem to be in a diffuse arrangement in relation to the parenchyma cells. Also, there is a variation in the size of axial parenchyma cells, being smaller in the end of the growth ring.	*Eriotheca gracilipes* (P) (Fig. 7a, 7b).
Thick-walled latewood fibres and distended rays.	The wood of species show scalariform axial parenchyma. These narrow bands of parenchyma tend to come closer periodically along the rays. Additionally there is a tangential arrangement of the largest vessels in earlywood.	*Annona coriacea* (W) (Fig. 8a, 8b), *Annona crassiflora* (P) (Fig. 9a, 9b).
Thick-walled and radially flattened latewood fibres. Also, together to these fibres we can note small vessels.	Not observed.	*Erythroxylum tortuosum* (P) (Fig. 10a, 10b).
Thick-walled and radially flattened latewood fibres. Eventually, in some regions, marginal lines of axial parenchyma can be noted.	Not observed.	*Terminalia brasiliensis* (W) (Fig. 11a, 11b).
Thick-walled and radially flattened latewood fibres. Marginal lines of axial parenchyma can be noted tangentially to these fibres.	Not observed.	*Qualea grandiflora* (W) (Fig. 12a, 12b).
Thick-walled and slight radially flattened latewood fibres.	Not observed.	*Rapanea umbellata* (P) (Fig. 13a, 13b).
Thick-walled latewood fibres.	Not observed.	*Tapirira guianensis* (P) (Fig. 14a, 14b).
Thick-walled latewood fibres.	Variation within growth layers in the axial parenchyma distribution were observed: axial parenchyma ranging from simple aliform to short aliform-confluent and finally to long aliform confluent.	*Vochysia cinnamomea* (P) (Fig. 15a, 15b).

Thick-walled latewood fibres and marginal lines of axial parenchyma.	Not observed.	*Caryocar brasiliense* (P) (Fig. 16a, 16b).
Thick-walled latewood fibres. Marginal lines of axial parenchyma can be noted tangentially to these fibres.	Variation within growth layers in the axial parenchyma distribution were observed: axial parenchyma ranging from simple aliform to short aliform-confluent and finally to long aliform confluent.	*Qualea multiflora* (W) (Fig. 17a, 17b).
Fibre zone and thick-walled and radially flattened latewood fibres.	Not observed.	*Didymopanax vinosum* (P) (Fig. 18a, 18b), *Couepia grandiflora* (W) (Fig. 19a, 19b), *Licania tomentosa* (W).
Fibre zone and thick-walled and radially flattened latewood fibres.	The wood shows reticulate axial parenchyma and these narrow bands of parenchyma tend to come closer as they become distant from the fibre zone of the same increment. These narrow bands become very close one to the other, adjacent to the fibre zone of the next layer.	*Diospyrus hispida* (W) (Fig. 20a, 20b).
Fibre zone and thick-walled and radially flattened latewood fibres.	Although gelatinous fibres occur along the growth layers, they seem to be concentric and regular in the fibre zone.	*Pera glabrata* (P) (Fig. 21a, 21b).
Fibre zone and thick-walled and radially flattened latewood fibres.	Not observed.	*Styrax ferrugineus* (P) (Fig. 22a, 22b), *Styrax camporum* (P).
Fibre zone and thick-walled and radially flattened latewood fibres. Also, the rays become narrow in the fibre zone region.	Not observed.	*Byrsonima coccolobifolia* (W) (Fig. 23a, 23b), *Byrsonima basiloba* (P), *Byrsonima verbascifolia* (W).
Fibre zone and radially flattened latewood fibres.	Not observed.	*Ouratea spectabilis* (P) (Fig. 24a, 24b).
Fibre zone and marginal lines. These marginal lines are distinct from the others because they are continuous and straighter.	Not observed.	*Kielmeyera rubriflora* (W) (Fig. 25a, 25b).
Fibre zone and straighter and narrower bands of marginal parenchyma.	Not observed.	*Pouteria torta* (W) (Fig. 26a, 26b).
Marginal bands of axial parenchyma.	There is a variation in the amount of vessels within growth rings, showing a high frequency adjacent to the marginal bands, in the earlywood.	*Gochnatia barrosii* (W) (Fig. 27a, 27b), *Bauhinia rufa* (W) (Fig. 28a, 28b).

Marginal bands of axial parenchyma.	Semi-ring porosity.	*Cordia sellowiana* (W) (Fig. 29a, 29b).
Marginal bands of axial parenchyma.	Not observed.	*Alibertia concolor* (W) (Fig. 30a, 30b).
Terminal bands of axial parenchyma.	Not observed.	*Copaifera langsdorffii* (W) (Fig. 31a, 31b).
Marginal bands of axial parenchyma and radially flattened latewood fibres.	Semi-ring porosity.	*Aegiphila sellowiana* (W) (Fig. 32a, 32b).
Marginal bands of axial parenchyma and distended rays.	There is a variation in the size and amount of vessels within growth rings, being smaller and with a high frequency adjacent to the marginal bands.	*Piptocarpha rotundifolia* (W) (Fig. 33a, 33b).
Marginal bands formed by long aliform confluent.	Variations within growth layers in the axial parenchyma distribution were observed: axial parenchyma ranging from long aliform confluent forming marginal bands to a decreasing in the parenchyma frequency and type, i.e. to the simple aliform.	*Vochysia rufa* (W) (Fig. 34a, 34b), *Vochysia tucanorum* (W).
Marginal lines of axial parenchyma.	Not observed.	*Dimorphandra mollis* (P) (Fig. 35a, 35b), *Bowdichia virgiloides* (W) (Fig. 36a, 36b), *Sweetia subelegans* (W), *Anadenanthera falcata* (W) (Fig. 37a, 37b), *Stryphnodendron polyphyllum* (W), *Qualea dichotoma* (P) (Fig. 38a, 38b).
Marginal lines of axial parenchyma.	Variation within growth layers in the axial parenchyma distribution were observed: axial parenchyma ranging from simple aliform to short aliform-confluent and finally to long aliform confluent.	*Machaerium villosum* (W) (Fig. 39a, 39b).
Closeness of the narrow bands of scalariform parenchyma.	Along the rays the narrow bands of scalariform parenchyma tend to come closer periodically.	*Roupala montana* (W) (Fig. 40a, 40b).
Absent.	Not observed.	*Luehea grandiflora* (A) (Fig. 41a, 41b), *Erythroxylum suberosum* (A), *Miconia albicans* (A).

by marginal bands (20%), marginal lines (16%) and closeness of the narrow bands of scalariform parenchyma (2%).

In *Miconia ligustroides*, parenchyma-like fibre bands (lighter regions in macroscopical view) alternating with ordinary fibres (Fig. 5a) were observed.

Within the growth layers, variations in the anatomical features were observed (Table 2), such as: variation in the amount of gelatinous fibres (Fig 21b); variations in the axial parenchyma distribution (Figures 15, 17b, 34, 39); variation in the distance between the narrow bands of axial parenchyma (Figures 8, 9a, 20, 40a) ; variation in the amount and in the size of axial parenchyma cells (Fig. 7); variation in the size and amount of vessels (Figures 27, 28, 33); semi-ring porosity (Figures 29, 32).

Discussion

For this study we were able to analyse 70% from all wood species that, according to the floristical studies of Bicudo (1987) and Silberbauer-Gottsberger & Eiter (1983), occur in cerrado areas in the west central of the São Paulo state, Brazil. We noticed that more than 60% of all species studied showed clearly defined growth rings. This factor should therefore be accounted for conservation and management programs of cerrado, a much threatened vegetation type. This incidence of growth rings in tropical wood species is comparable with 48% found by Alves & Angyalossy-Alfonso (2000) in stem wood of 491 Brazilian tropical and subtropical wood species. However, the incidence of growth rings in cerrado species is relatively high if it is compared with the study of Mainieri et al. (1983) who found growth rings in approximately 35% of the stem wood of nearly 300 Brazilian tropical and subtropical species (see Alves and Angyalossy-Alfonso 2000). The high occurrence of species with growth rings in cerrado might be related to a distinct annual dry season, lasting about one to four months. According to Worbes (1995), a period of two or three months with precipitation below 60 mm is an environmental condition necessary for species to form growth rings in their wood.

In this study both evergreens and deciduous or semi-deciduous plants had high ratios of species with growth rings. Similar observations were reported by Alvim (1964) and Worbes (1985) on tropical rain forest trees and by Coradin (2000) for deciduous and evergreens species from cerrado of Brazil Central region. In addition, Coradin (2000) observed that species with a single period of flushing, including the deciduous and some of the evergreen species, showed generally distinct growth rings while those evergreen species which showed more than one period of flushing during the year presented indistinct or poorly defined growth rings. The phenological methodology used in the present study does not allow us to relate growth ring distinctness with flushing periods during the year in a species.

We observed clear differences among tree and shrub species related to both growth rings percentage and distinctness, with attention to trees and tall trees with 100% of well defined growth rings. The high frequency of small trees and shrubs in cerrado points out the relevance of habit for the analysis of the growth rings formation in this vegetation type.

All combinations of microscopic anatomical features used to detect the growth layers were already mentioned by other authors (Détienne & Mariaux 1977, Bormann & Berlyn 1981, Worbes 1985, Carlquist 1988, Baas & Vetter 1989, IAWA Committee 1989, Fahn & Werker 1990 and Wheeler & Baas 1991). Thick-walled and radially flattened latewood fibres and fibre zones boundaring the growth rings were the most common features observed in the wood of the branches of the species studied. Extensive analyses are in course to determine if these markers are predominant in the woody plants of cerrado vegetation.

Marginal bands in *Copaifera langsdorffii* had already been described by Mainieri et al. (1983) and Détienne & Jacquet (1993). However, Marcati (2000) studied the formation of these marginal bands and verified that they are terminal since they are formed in the beginning of the dry season, before the cambial dormancy.

The growth ring markers described here agree in general with most of the results obtained by other authors (Mainieri et al. 1983, Détienne 1989, Vetter & Botosso 1989, Boninsegna et al. 1989, Marcati 2000, Callado et al. 2001) studying stem wood of the same genus or species. Although Mainieri *et al.* (1983) have described indistinct growth rings in the stem wood of *Vochysia* spp., *Rapanea* spp., *Qualea* spp., *Tapirira guianensis*, *Didymopanax* spp. and *Roupala* spp., and distinct growth rings in the stem wood of *Luehea* spp., different to our study, it is important to comment that the wood analyzed by Mainieri et al. (1983) were collected from tree stem of different regions of Brazil, so subject to different environmental conditions.

Comparing our results on growth rings markers to those of Coradin (2000) from woody plants from cerrado of Brazil Central region, some differences need further comments. According to this author, *Qualea grandiflora* and *Ouratea hexasperma* wood show differences in vessel frequency as the main feature in the boundary of the growth rings in stem and branches, which was not observed neither in *Q. grandiflora* nor in *Ouratea spectabilis* studied here. Coradin (2000) did not mention the closeness of the narrow bands of scalariform parenchyma in *Roupala montana* wood as noted in our study, but a tangential arrangement of vessels in the boundary of growth rings in stem and branches. *Didymopanax macrocarpum* wood, according to Coradin (2000), shows indistinct growth rings in its branches while in the stem wood the author found a difference in the vessel frequency within growth layers. In *Vochysia elliptica* wood the author observed fibre zones and irregular bands of axial parenchyma in branches and stem wood. The various differences between our study and that of Coradin (2000), listed out above, may be related to the specific environmental conditions of the two cerrados. For instance, unlike the cerrado of São Paulo state, the relative humidity in cerrado from Brazilia can reach very low values during the dry season (see Oliveira & Marquis 2002).

Parenchyma-like fibre bands alternating with ordinary fibres were observed in *Miconia ligustroides* wood and it was already mentioned by Coradin (2000) to genus *Miconia*. These parenchyma-like fibre bands, according to the author, are septate fibres which accumulate starch and so have also a storage function.

Gelatinous fibres, although of common occurrence in most of the studied species, were related to the growth rings, forming a regular pattern, only in *Pera glabrata*, an evergreen species. Callado et al. (2001) observed random zones of gelatinous fibres throughout the rings in the stem wood of the same species that occur on periodically flooded soil. According to Kozlowski & Pallardi (1997), gelatinous fibres often extend throughout both earlywood and latewood in evergreen species. Further studies are required to a better comprehension about the differences in the arrangement of gelatinous fibres in *Pera glabrata* occurring in under different water regime. Gelatinous fibres have been observed in different organs of cerrado plants (Paviani 1978) as a result of reaction wood formation (Kozlowski et al. 1991) and may function as water storage (Paviani 1978, Chalk 1989), as well as giving flexibility to the organ.

Variations in the axial parenchyma distribution in *Vochysia cinnamomea*, *Qualea multiflora*, *V. rufa*, *V. tucanorum*, wood were reported for the first time. For *Machaerium villosum* wood this variation had already been reported by Ceccantini (1996). Although Détienne & Jacquet (1983) have observed long alifom confluent forming bands in the wood of others *Vochysia* species and terminal parenchyma in other *Machaerium* species, they did not mention the variation within growth layers as we observed in this study. Variation in the distance between the narrow bands of axial parenchyma periodically along the rays within growth layers in *Annona coriacea*, *A. crassiflora*, *Diospyrus hispida* and *Roupala montana* wood was also reported for the first time. Variation in the amount of axial parenchyma and in the size of axial parenchyma cells within growth layers in *Eriotheca gracilipes* was already mentioned by Callado et al. (2001) for *E. pentaphylla* wood occurring in swamp forests of Rio de Janeiro, Brazil. Variation in the amount of vessels within growth layers was observed in *Gochnatia barrosii*, *Bauhinia rufa* and *Piptocarpha rotundifolia* as described by Coradin (2000) for other cerrado species. Further studies about cambial activity are necessary to a better comprehension about these variations.

Although growth rings occurrence was verified in different cerrado woody species, additional anatomical wood studies of a larger number of species are necessary to determine if the growth rings are annual, widespread and possess taxonomic and/or adaptive value.

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