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Contributions to the Wood Anatomy of the Rubioideae (Rubiaceae)

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The secondary xylem of Craterispermeae, Coussareeae, Morindeae s.str., Prismatomerideae, Pauridiantheae, Urophylleae, and Triainolepideae (Rubiaceae, Rubioideae) is described and illustrated in detail. Genera that were previously placed in the Morindeae or Psychotrieae such as *Damnacanthus*, *Lasianthus*, *Saldinia*, and *Trichostachys* are also included. Wood anatomical characters are compared with recent phylogenetic insights into the study group on the basis of molecular data. The observations demonstrate that the delimitation and separation of several taxa from the former Coussareeae/Morindeae/Prismatomerideae/Psychotrieae aggregate is supported by wood anatomical data. The Coussareeae can be distinguished from the other Rubioideae by their scanty parenchyma, septate libriform fibres, and the combination of uniseriate and very high multiseriate rays with sheath cells. Axial parenchyma bands and fibre-tracheids characterise *Gynochtodes* and some species of *Morinda* (Morindeae *s.str.*), but the latter genus is variable with respect to several features (e.g. vessel groupings and axial parenchyma distribution). Wood data support separation of *Rennellia* and *Prismatomeris* from Morindeae s.str.; vessels in both genera are exclusively solitary and axial parenchyma is always diffuse to diffuse-in-aggregates. *Damnacanthus* differs from the Morindeae alliance by the occurrence of septate fibres, absence of axial parenchyma, and the occasional presence of fibre wall thickenings. There are interesting similarities between members of the *Lasianthus* clade and the Pauridiantheae/Urophyleae group such as the sporadic occurrence of spiral thickenings in axial parenchyma cells.

Key words: Rubiaceae — Rubioideae — Systematic wood anatomy

The latest subdivision of the Rubiaceae that was established by Robbrecht (1988, 1993) includes four subfamilies: Cinchonoideae, Ixoroideae, Antirheoideae, and Rubioideae. Several features such as the presence of raphides, valvate aestivation, exotesta cells without perforated thickenings, frequent accumulation of aluminium in woody taxa, and often articulate hairs characterise the subfamily Rubioideae. Earlier relationships among the different tribes of this subfamily are mainly based on the number of ovules, fruit type, and habit. Several authors have emphasized a close association of the tribes Psychotrieae, Morindeae, and Coussareeae, which show fleshy fruits derived from ovaries with one solitary erect ovule in the locules (e.g. Verdcourt 1958, Petit 1963, 1964, Darwin 1979). Robbrecht (1988), who further elaborated Bremekamp's (1966) two series of Rubioideae on the basis of ovule numbers, suggested that the uniovulate Rubioideae (i.e. Psychotrieae and its two satellite tribes Triainolepideae and Lathraeocarpeae, Morindeae, Coussareeae, Paederieae, Anthospermeae, Theligoneae, Spermacoceae, and Rubieae) form a natural entity. The tribes Psychotrieae, Triainolepideae, Morindeae, and Coussareeae are mainly woody, but large herbaceous groups have evolved in the remaining tribes (Spermacoceae, Rubieae, Anthospermeae, Paederieae) which show an herbaceousness index equal to or higher than 50 (cf. Young *et al.* 1996).

Furthermore, the delimitation of the Morindeae has been subject to change. The genus *Damnacanthus* was excluded from the Morindeae s.l., with which it nearly always had been associated. This spiny shrub was found to be closely related to the herbaceous genus *Mitchella* and the two genera were included in a separate and informal *Mitchella* group on the basis of their campylotropous ovules (Robbrecht *et al.* 1991). Igersheim and Robbrecht (1993) restricted the tribe Morindeae to genera having bicarpellate ovaries with biovulate locules (i.e. *Appunia*, *Caelospermum*, *Gynochtodes*, *Morinda*, and *Pogonolobus*), while genera with truly uniovulate locules were placed in the Prismatomerideae.

Recent conclusions from cladistic analyses of sequence data contradict these earlier arrangements since the two groups of uniovulate and multiovulate Rubioideae do not form monophyletic groups (e.g. Bremer *et al.* 1995, Bremer 1996, Bremer and Thulin 1998, Andersson and Rova 1999, Bremer and Manen 2000, Piesschaert *et al.* 2000a). This has led to renewed insights in the phylogenetic relationships

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within Rubioideae (and Rubiaceae in general). For instance monophyly of the Coussareeae is supported by DNA sequences but the tribe is found to take a more basal position than the Psychotrieae-Morindeae alliance to which the Coussareeae have been connected in the past. A remarkable relationship between the tribes Coussareeae and Coccocypseleae was suggested. Morphological evidence for an extended tribe Coccocypseleae, including the shrubby genera *Declieuxia* and *Hindsia*, was recently presented by Piesschaert *et al.* (2000*b*).

The *rbc*L-analysis of Bremer (1996) and the *rps*16-intron analysis of Andersson and Rova (1999) have confirmed the close relationship between Morindeae and Psychotrieae, but macromolecular data contradicted the separation of the *Mitchella* group. This group was found to be the sister group of *Morinda* together with *Gaertnera* (Bremer 1996) or nested within the Morindeae (Andersson and Rova 1999, Bremer and Manen 2000). While *Gaertnera* appears as the sister group of *Morinda* in the analysis of Bremer (1996), the Gaertnereae occurred at the base of the Morindeae and Psychotrieae in the study of Andersson and Rova (1999). The genus *Schradera* also occupies a position close to Psychotrieae, Gaertnereae, and Morindeae (Bremer and Thulin 1998, Andersson and Rova 1999, Bremer and Manen 2000). Futhermore, *rbc*L and *rps*16 intron sequences demonstrated that the genera *Lasianthus*, *Saldinia*, *Ronabea* and *Trichostachys* form a well supported "*Lasianthus*-clade" within the basal Rubioideae; macromolecular data suggest exclusion of these genera from the Psychotrieae or Morindeae, thus eradicating the old problem of the mutual delimitation of these two tribes. Recently, *Lasianthus* and *Trichostachys* are placed in a new tribe Lasiantheae (Bremer and Manen 2000).

While the Rubioideae, Cinchonoideae, and Ixoroideae are supported by various cladistic analyses based on molecular and/or morphological data covering the whole family, a wide circumscription of the subfamily Antirheoideae is now generally abandoned (e.g. Bremer *et al.* 1995, Bremer 1996, Manen and Natali 1996, Bremer and Thulin 1998, Andersson and Rova 1999, Andreasen and Bremer 2000). Accordingly, the Knoxieae and Craterispermeae are now removed from the Antirheoideae to the Rubioideae. The Knoxieae are mainly herbaceous and appear to be related to the Hedyotideae and Spermacoceae, which Bremer (1996) suggested to merge in an extended tribe Spermacoceae s.l. Although Manen and Natali (1996) suggested that *Triainolepis* does not belong to the Rubioideae because it lacks the typical deletion in the *atp*B-*rbc*L-spacer, the presence of raphides indicates that the genus could belong to this subfamily. Verdcourt (1958) noticed similarities in the fruit of *Triainolepis* and the Knoxieae. Interestingly, macromolecular data confirmed a relationship between these taxa (Piesschaert *et al.* 2000a). The taxonomic position of the woody and monogeneric Craterispermeae has been problematic, but macromolecular data as well as the presence of raphides and aluminium accumulation clearly supports Verdcourt's (1958) placement in the Rubioideae (Bremer and Manen 2000, Jansen *et al.* 2000a, b).

In two previous studies we discussed the wood anatomy of Gaertnereae and Psychotrieae (Jansen *et al.* 1996, 1997). The present paper aims to describe the secondary xylem of the remaining 'uniovulate' Rubioideae in order to compare the wood anatomical variation with the new phylogenetic and taxonomic insights based on macromolecular data.

Materials and Methods

Wood samples came from the herbarium of Leiden (L), the wood collection of Tervuren (Tw), Utrecht (Uw), and from the National Botanic Garden of Belgium (mostly from the herbarium BR; only few samples from living collections). A list of the species studied is given below. The diameter (in mm) of each wood sample is included for branch wood; the diameter of mature wood samples is unknown and not reported. Wood samples of *Gentingia* and *Motleya* (Prismatomerideae), as well as *Appunia*, *Caelospermum*, *Pogonolobus* (Morindeae s.str.), and *Schizocolea* (sole African genus of the Coussareeae) were not available. Although we were able to include a light microscopical photograph of a transverse section of *Triainolepis emirensis* (Fig. 46), this species could not be investigated in detail due to lack of material. Accordingly, the wood anatomical description of *Triainolepis* is only based on the African species *Triainolepis africana*. Table 1 summarises the genera and the number of wood samples studied.

Table 1. Taxa examined in the present study

Tribe	Genus	Total number of species	Species/ specimens studied
Coccocypseleae	*Declieuxia*	27	1/1
	Hindsia	8	1/1
Coussareeae	*Coussarea*	ca.100	11/11
	Faramea	125	11/11
Craterispermeae	*Craterispermum*	16	3/4
Mitchella group	*Damnacanthus*	6	1/1
Morindeae	*Gynochtodes*	14	2/2
	Morinda	50	9/10
Pauridiantheae	*Commitheca*	1	1/1
	Pauridiantha	25	3/3
	Poecilocalyx	2	2/2
	Stelecantha	1	1/1
Prismatomerideae	*Prismatomeris*	25	4/5
	Rennellia	10	2/2
Triainolepideae	*Triainolepis*	2	1/2
Urophylleae	*Leucolophus*	3	1/1
	Maschalocorymbus	4	2/2
	Pleiocarpidia	27	2/2
	Praravinia	50	2/2
	Urophyllum	150	4/4
Lasianthus group	*Lasianthus*	150	6/9
	Saldinia	2	1/2
	Trichostachys	10	1/2

Wood blocks were sectioned and macerated according to standard methods (Jansen *et al.* 1998). The specimens were studied with a light microscope (LM; Leica DMLB) and a scanning electron microscope (SEM; Jeol JSM-6400). Vessel element length and fibre length were measured from macerations, 30 elements per sample. The vessel grouping index is used as defined by Carlquist (1988). According to this method, the total number of vessels counted as individuals is divided by the total number of vessel groups. For quantitative features (e.g. the tangential diameter of vessel lumina), the average is given for all specimens studied and the numbers between brackets refer to the total range for all samples. Terminology follows the IAWA list (IAWA Committee 1989).

List of materials studied

Commitheca liebrechtsiana (De Wild. & T. Durand) Bremek., Democratic Republic of Congo, Yangambi, *J. Louis 7992* (BR), 6 mm—*Coussarea* aff. *grandis* Müll.Arg., Venezuela, s. loc., collector unknown (Tw 36177)—*C. contracta* (Walp.) Benth. & Hook. ex Müll.Arg., Brazil, Parama, *Lindeman & De Haas 2956* (Tw 35300)—*C. cuatrecasasii* Standl. ex Steyerm., Colombia, s.loc., *J. Cuatrecasas 16587* (Tw 39561)—*C. hirticalyx* Standl., Peru, Loreto, La Victoria, *L. Williams 2528* (Tw 46671)—*C. leptoloba* (Spreng. ex Benth. & Hook.f.) Müll.Arg., Brazil, Amazonas, SãoPaulo de Olivenga, *B.A. Krukoff 8203* (Tw 38662)—*C. machadoana* Standl., Brazil, Machado River, *B.A. Krukoff 1361* (Tw 34638)—*C. megalocarpa* Standl., Peru, Loreto, Rio Mazan, *L. Williams 8171* (Tw 38704)—*C. ovalis* Standl., Peru, Loreto, Rio Ituya, *L. Williams 3355* (Tw 46672)—*C. surinamensis* Bremek., Surinam, s.loc., *Stahel 280* (Tw 25832)—*C. tenuiflora* Standl., Peru, Loreto, *L. Williams 8152* (Tw 38661)—*C. vallis* Standl. ex Steyerm., Colombia, s.loc., *J. Cuatrecasas 17593* (Tw 39656)—*Craterispermum cerinanthum* Hiern, Democratic Republic of Congo, Kouilou, *H. de Foresta 55* (Tw 48567), 15 mm; Democratic Republic of Congo, *A. Madoux 267* (Tw 41594)—*C. laurinum* (Poir.) Benth., Madagascar, Tamatave, *Thouvenot 26* (Tw 30111)—*C. schweinfurthii* Hiern, Democratic Republic of Congo, Bokoli, *R. Dechamps 8017* (Tw 40317), 18 mm—*Damnacanthus indicus* P. Gaertn., Japan, Nagasaki, *R. Oldham s.n.* (BR-S.P. 802815), 5 mm—*Declieuxia fruticosa* (Willd. ex Roem. & Schult.) Kuntze, Brazil, 25 km N of Alto Paraiso, *W.R. Anderson 6687* (BR), 5 mm—*Faramea amplifolia* Standl., Peru, Pebas, *L. Williams 1946* (Tw 46678)—*F. anisocalyx* Poepp. & Endl., Peru, Iquitos, *L. Williams 1330* (Tw 38657), 38 mm—*F. elegans* Standl. ex Steyerm., Colombia, s.loc., *J. Cuatrecasas 15721* (Tw 39477)—*F. glandulosa* Poepp. & Endl., Peru, San Martin, *L. Williams 6093* (Tw 38696)—*F. neblinae* Steyerm., Venezuela, Amazonas, *B. Maguire et al. 27926* (Tw 36412)—*F. occidentalis* (L.) A. Rich. var. *meridionalis* Steyerm., British Guyana, Moku-moku Creek, *A.C. Smith 3478* (Tw 27351)—*F. parvibracteata* Steyerm., Venezuela, Amazonas, *B. Maguire et al. 28424* (Tw 36315)—*F. quadricostata* Bremek., Surinam, Nickerie, *B. Maguire et al. 54664,* (Tw 37669)—*F. rectinervia* Standl., Peru, La Victoria, *L. Williams 2962* (Tw 38665)—*F. stenopetala* Mart., Venezuela, Amazonas, *B. Maguire et al. 42717* (Tw 36911)—*F. warmingiana* Müll.Arg., Brazil, Para, *B. Maguire et al. 56992* (Tw 38134)—*Gynochtodes* sp., Irian Jaya, s.loc., *M. Jacobs 9670* (L), 17 mm—*G. coriacea* Blume, Sumatra, s.loc., *M. Jacobs 8118* (L)—*Hindsia longiflora* (Cham.) Benth., Brazil, Minas Geraes, *P. Claussen 235 A* (BR), 6 mm—*Lasianthus* sp., Borneo, Bukit Raya, *H.P. Nooteboom 4026*, 10 mm, *4034* & *4189* (L), 13 mm—*L. acuminatus* Wight, India, Cardamom Hills, *C.E. Ridsdale 167* (L)—*L. batangensis* K. Schum., Democratic Republic of Congo, Ngula, affluent Aruwini, *J. Louis 15492* (BR); Democratic Republic of Congo, Yangambi, *J. Louis 11587* (BR), 9 mm; Democratic Republic of Congo, *J. Louis 3042* (Tw 33582)—*L. cinereus* Gamble, India, Walaiyar Estate, Papanasam Tamil Nadu, *C.E. Ridsdale 336* (L), 10 mm—*L. mayumbensis* Good, Democratic Republic of Congo, Kouilou, Les Sara, *R. Dechamps 13165* (Tw 49225), 10 mm—*L. scabridus* King & Gamble, Malaysia, Hutan Simpan Bukit Kesing, Terengganu, *L.E. eo T. & P. 1133* (KL 3633), 12 mm—*Leucolophus* sp., Indonesia, North Sumatra, *W. de Wilde & B. de Wilde-Duyfjes 13721* (L)—*Maschalocorymbus* sp., Borneo, Bukit Raya, *H.P. Nooteboom 4264* (L)—*M. corymbus* (Blume) Bremek., Borneo, Sarawak, *Jacobs 5290* (L)—*Morinda angustifolia* Roxb., Thailand, Chiang Mai, Mae Chan, *J.F. Maxwell et al. 94* (L)—*M. citrifolia* L., National Botanic Garden of Belgium, cultivation number 19592485-6010, 17 mm; India, Andhra Pradesh, *Birla Institute of Scientific Research Amlai (M.P.) nr. 0131* (Tw 46621)—*M. debilis* (Sandwith) Steyerm., Guyana, s.loc., *Stoffers et al. 069* (Uw 27677), 14 mm—*M. geminata* DC., Democratic Republic of Congo, Kasai, R. *Dechamps 7686* (Tw 51575)—*M. lucida* Benth., s.loc., *G. Gilbert 165* (BR), 10 mm—*M. morindoides* (Baker) Milne-Redh., Democratic Republic of Congo, Lieki (Lomani), *J. Louis 3662* (BR), 7 mm; Cameroon, Bretous, *Breteler 747* (Uw 9264), 18 mm—*M. myrtifolia* A. Gray, Society Islands, *Grant 5143* (BISHw 2660)—*M. reticulata* Benth., India, Ponmudi, Kerala, *C.E. Ridsdale 469* (L), 20 mm—*M. umbellata* L., s. loc., *Colonial Museum of Haarlem 1507-32* (L), 14 mm—*Pauridiantha viridiflora* (Schweinf. ex Hiern) Hepper, Angola, d'Uige vers Negage, *R. Dechamps 1545* (Tw 28636)—*P. pyramidata* (K. Krause) Bremek., Democratic Republic of Congo, *R. Dechamps 8082* (Tw 40380), 20 mm—*P. rubens* (Benth.) Bremek., Democratic Republic of Congo, *J. Louis 1254* (Tw 33126), 21 mm—*Pleiocarpidia sandahanica* Bremek., Borneo, Sarawak, *Jacobs 5291* (L)—*P. pilosa* (Ridl.) Bremek., Borneo, Bukit Raya, *H.P. Nooteboom 4473* (L)—*Poecilocalyx schumannii* Bremek., Cameroon, Kribi-Lolodorf km. 16, *Bos 3665* (BR)—*P. stipulosa* (Hutch. & Dalziel) N. Hallé, Liberia, Bassa, *Cooper 205* (Tw 26696), 22 mm—*Praravinia* sp., Indonesia, Sulawesi, Utara, Edwards Camp, Dumoga Nat. Park, *De Vogel & Vermeulen 6775* (L)—*P. suberosa* (Merr.) Bremek., Borneo, North Kalimantan, *Forest Dept. 10,640* (L), 7 mm—*Prismatomeris* sp., Philippine Islands, Palawan, *A.C. Podzorski SMHI 2095* (L)—*P. beccariana* (Baill. ex K. Schum.) J.T. Johanss., Borneo, Bukit Raya, *H.P. Nooteboom 4336* (L), 8 mm; Borneo, Sarawak, *Jacobs 5423* (L)—*P. brachypus* Ridl., Philippine Islands, Surigao, *C.A. Wenzel 2878* (BR), 4 mm—*P. tetrandra* (Roxb.) K. Schum. subsp. *malayana* (Ridley) J.T. Johansson, s. loc., *W. Griffith s.n.* (BR-S.P. 809987), 5 mm—*Rennellia* sp., Borneo, s.loc., *Fuchs 21358* (L)—*R. elliptica* Korth., Borneo, Bukit Raya, *H.P. Nooteboom 4136* (L)

—*Saldinia* sp., Madagascar, E. of Fianarantsoa, Parc National de Ranomafana, *R. Rakoto 301* (BR), 4 mm; Madagascar, Toamasina, E. coast, litoral forest, S. of Amirca-Lemaitso, *Lewis & S. Razafimandimbison 723* (BR), 5 mm—*Stelechantha makakana* N. Hallé, Cameroon, N'Kolandam-N'Koemvome, *J.J.F.E. de Wilde 8009* (BR)—*Triainolepis africana* Hook.f. subsp. *hildebrandtii* (Vatke) Verdc., s.loc., *J.B. Gillet & S.P. Kibuwa 19850* (BR), 4 mm; Kenya, Kwale District, Diani, *J.P.M. Brenan et al. 14512* (BR), 4 mm—*T. emirensis* (Baker) Bremek., Madagascar, Antananarivo, *L.J. Dorr 3273* (Tw 46748)—*Trichostachys microcarpa* K. Schum., s. loc., *R. Devred 7678* (BR), 8 mm, and *R. Devred 2883* (BR), 5 mm—*Urophyllum* cf. *macrophyllum*, Borneo, W. Kalimantan, Danau Sentarum Wildlife Reserve, Belitung River, *W. Giessen 89* (L), 10 mm—*U. corymbosum* Korth., Indonesia, Malaya, Jalan Bukit Tersek, KL 3157, *T. & P. 557* (L)—*U. trifurcum* H. Pearson ex King, Indonesia, Malaya, Pahang, *collectors: T. & P. 781* (L), 9 mm—*U. zeylanicum* Thwaites, Sri Lanka, Kandy distr., Knuckles, from Rangala to Looloowatte, *Nooteboom 3056* (L), 15 mm.

Results

Generic descriptions are given below for each tribe separately. Detailed wood anatomical data of the specimens studied are listed in Table 2.

Coccocypseleae Bremekamp (*sensu* Piesschaert *et al.* 2000b)

The third genus of this tribe, *Coccocypselum*, is entirely herbaceous.

Declieuxia Kunth. (1 species/1 specimen examined)—Fig. 1.

Growth rings are indistinct.—Vessels are diffuse. Vessel grouping index is 1.23. Mean length of vessel elements is 436 (370-510) μm. Tangential vessel diameter is 21 (17-30) μm. The number of vessels per mm^2 is more than 100. Narrow vessel elements that sometimes show a single, very small perforation are frequently found. Vessel elements perforations are simple. Intervessel pits and vessel-ray pits are alternate, minute, and vestured.—Fibre pits are simple or with reduced pit borders. At least some fibres are septate. Mean length of fibres is 585 (500-620) μm.—Axial parenchyma is not observed.—Rays are heterogeneous, uni- to triseriate, and generally more than 1 mm high.—Raphides are present in *D. fruticosa*.

Hindsia Benth. ex Lindl. (1 species/1 specimen examined)—Fig. 2.

Growth rings are absent.—Vessels are diffuse. Vessel grouping index is 1.76. Mean length of vessel elements is 371 (300-450) μm; mean tangential diameter is 20 (17-30) μm. Vessel frequency is high (>100 vessel/mm^2). Fibriform vessel elements are frequently present. Vessel elements perforations are simple. Intervessel pits and vessel-ray pits are alternate, minute, and vestured.—Fibres are septate. Fibre pits are simple or with reduced pit borders. Mean length of fibres is 598 (500-700) μm.—Axial parenchyma is not observed.—Rays are heterogeneous and uni- or biseriate, with usually more than 4 rows of marginal ray cells, and more than 1 mm high. The biseriate rays are wider than the uniseriate rays. - Mineral inclusions are absent.

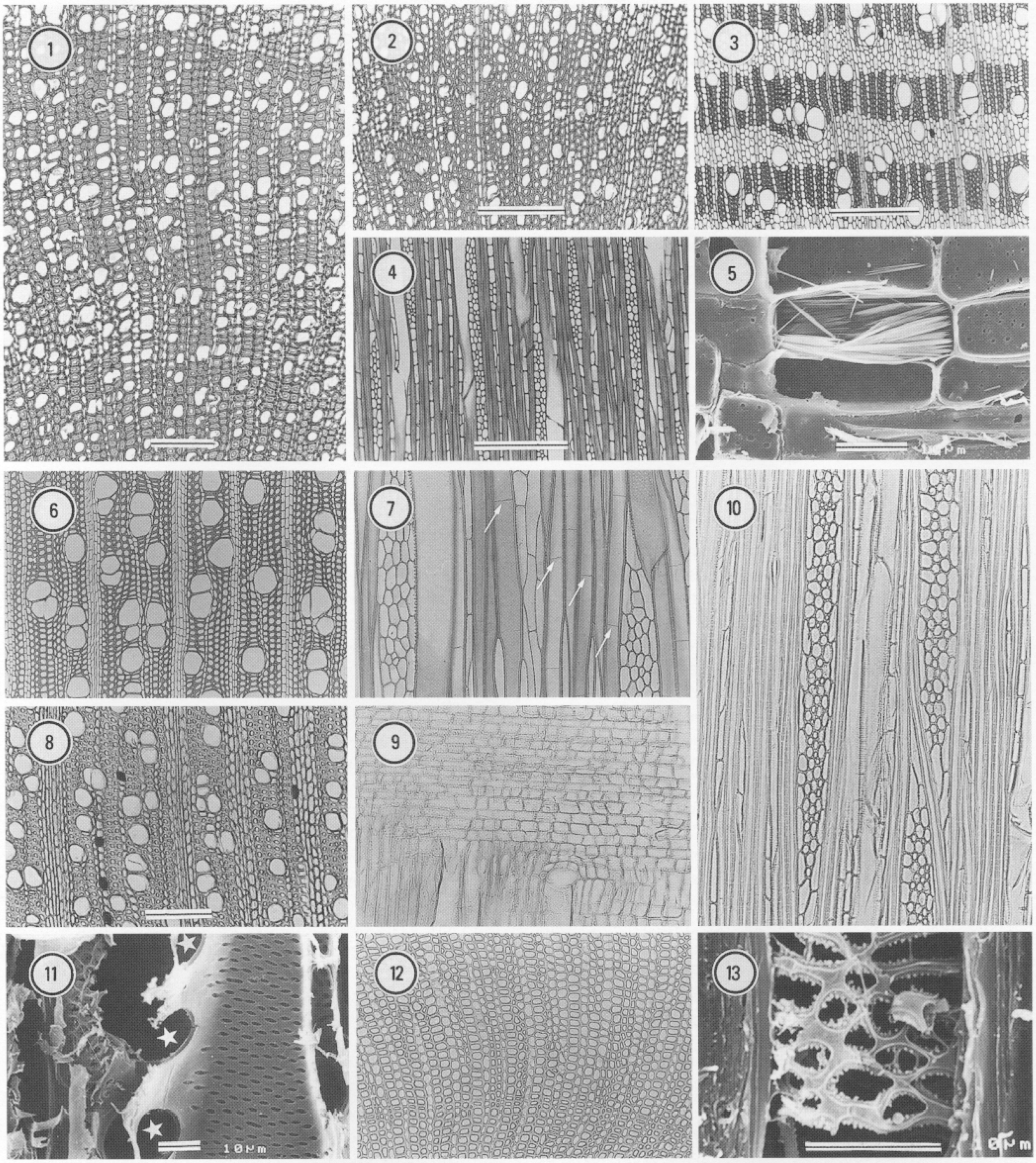
Coussareeae Hook.f.

Coussarea Aubl. (11 species/11 specimens examined)—Figs. 6, 7, 11.

Growth rings are absent or indistinct.—Vessels are diffuse. The vessel grouping index averages 1.65, varying from 1.3 (*C. ovalis*) to 2.16 (*C. leptoloba*). Mean length of vessel elements is 1,023 (600-1,500) μm; mean tangential vessel diameter is 53 (30-150) μm. Vessels about 116 μm wide are found in *C. vallis* only (Fig. 6). Mean number of vessels per mm^2 is 45 (15-120). Vessel element perforations are simple. However, the number of perforations per perforation plate is frequently more than one (Fig. 11); for instance up to five perforations are observed in a perforation plate of *C. machadoana*. Perforated ray cells show simple perforations, but they are sometimes irregular in shape, or irregularly reticulate as e.g. in *C. vallis*. Intervessel pits are alternate or rarely opposite to scalariform, mostly polygonal, and vestured. Intervessel pits are minute (<4 μm), small (4-7 μm), or medium (7, 8 μm) sized. Vessel-ray pits are similar to intervessel pits with distinct pit borders, but enlarged with reduced pit borders in *C. vallis*.—Fibres are septate with simple to minutely bordered pits confined to radial fibre walls (Fig. 7). Septa are not observed in fibres of *C.* aff. *grandis*. Mean length of fibres is 1652 (800-2,400) μm.—Axial parenchyma is scanty paratracheal, very rare and often seemingly absent or lacking. Axial parenchyma strands are composed of 5 to 10 cells.—The heterogeneous rays usually are of two distinct sizes: uniseriate and 4-seriate or wider (up to 10 cells in *C. megalocarpa*). Relatively narrow rays (2-3-seriate) occur in *C. tenuiflora*. The body ray cells are usually procumbent with mostly 2-4 rows of upright and/or square marginal cells. Sheath cells partly surround the rays in most multiseriate rays (except *C. tenuiflora*). Multiseriate rays are very high, on average 2,752 μm, but rays up to 10,100 μm high occur in *C. megalocarpa*. The number of rays per mm is 10 (6-19).—Raphides are abundantly present in the upright/square ray cells of most species studied. Raphides are lacking in C. aff. *grandis*, *C. hirticalyx*, and *C. leptoloba*.

Faramea Aubl. (11 species/11 specimens examined)—Figs. 8-10.

Growth rings are absent or indistinct.—Vessels are diffuse and mean vessel grouping index is 1.62, varying from 1.08 in *F. rectinervis* to 2.76 in *F. parvibracteata*. Vessel outline is oval or slightly angular. Vessel lumina are 46 (18-74) μm wide. Mean number of vessels per mm^2 is 57 (24-110). Vessel element length is 849 (400-1,300) μm. Vessel element perforations are simple and frequently vestured. As in *Coussarea*, however, a single perforation plate is often composed of two or three perforations close to each other. Perforated ray cells show simple (e.g. *F. anisocalyx*) or scalariform (e.g. *F. elegans*) perforations. Intervessel pits are alternate, vestured, and frequently polygonal. Size of intervessel



Figs. 1-13. Wood of Coccocypseleae (1-2), Craterispermeae (3-5), Coussareeae (6-11), and *Damnacanthus* (12-13). 1-4, 6-10, 12: Light micrographs of wood sections. 5, 11, 13: Scanning electron micrographs. 1: *Declieuxia fruticosa*. Transverse section (bar=100 µm). 2: *Hindsia longiflora*. Transverse section (bar=200 µm). 3: Transverse section of *Craterispermum laurinum* showing wide axial parenchyma bands (bar=500 µm). 4: Tangential section of *Craterispermum laurinum* (bar=200 µm). 5: Raphides in ray parenchyma cell (bar=40 µm). 6-7: *Coussarea vallis*. Transverse section (6; bar as in 3) and tangential section (7; bar as in 2) with septate (arrows) libriform fibres. 8: *Faramea occidentalis*. Transverse section with raphides visible as dark spots in the rays (bar=200 µm). 9: Radial section of *Faramea warmingiana* (bar as in 2). 10: *Faramea glandulosa* showing 3-4-seriate rays with sheath cells in tangential section (bar as in 1). 11. *Faramea anisocalyx*. Oblique perforation plate of vessel elements with three simple perforations (stars) (bar=10 µm). 12-13: *Damnacanthus indicus*. Transverse section (12; bar as in 1) and detail of fibre wall thickenings with vestures viewed from the outer surface, the original secondary fibre wall is removed (13; bar=10 µm).

pits is minute, but small intervessel pits (4-7 μm) occur in *F. anisocalyx*. Vessel-ray pits are similar to intervessel pits. —Fibres are septate and show simple to minutely bordered pits (pit diameter 2-3 μm) on radial fibre walls. Fibre length is 1,420 (730-2,000) μm.—Axial parenchyma is scanty paratracheal, with five to ten cells per parenchyma strand. —Rays are heterogeneous, and of two distinct sizes: uniseriate and 4-seriate or wider (Fig. 10). Rays up to 16 cells wide are observed in *F. neblinae*. Rays are not more than three cells wide in *F. elegans* and occasionally 4-seriate in *F. quadricostata* and *F. parvibracteata*. The multiseriate rays are relatively high, on average 1,567 μm, but rays up to 9,620 μm in height are found in *F. quadricostata*. Sheath cells generally form an incomplete sheath around the procumbent cells (Fig. 10). The rays are composed of procumbent body ray cells with usually 2-4 rows of upright/square marginal ray cells (Fig. 9). The number of rays per mm is ca. 10 (6-17). —Raphides are abundantly present in ray cells (Fig. 8), especially in upright/square ray cells of several species.

Craterispermeae Verdc.

Craterispermum Benth. (3 species/3 specimens examined) —Figs. 3-5.

Growth rings are absent.—Vessels are diffuse and the mean vessel grouping index is 1.2. Vessel lumina are on average 55 (25-90) μm wide; mean number of vessels per mm^2 is 36 (11-68). Mean vessel element length is 960 (600-1,500) μm. Vessel element perforations are simple. Perforated ray cells with simple perforations are present. Intervessel pits are alternate, minute, and vestured. Vessel-ray pits show distinct borders and are similar to intervessel pits in size and shape throughout the ray cell.—Fibres are non-septate, with distinctly bordered pits on radial and tangential walls. Diameter of the pit border is ca. 3-4 μm. Mean fibre length is 1,680 (1,000-2,250) μm.—Axial parenchyma bands are continuous, 4-5 cells or 142 (60-280) μm wide (Fig. 3). Parenchyma strands are composed of 5-20 cells. The distance between the parenchyma bands is on average 384 (200-670) μm.—Rays are heterogeneous and usually 2-3-seriate (Fig. 4). Body ray cells are procumbent, with numerous rows of upright/square marginal cells. Rays are on average 1,017 (300-3,300) μm high. The number of rays per mm is ca. 14 (11-20).—Raphides are present in axial parenchyma cells or ray cells of all species studied (Fig. 5).

The Mitchella group

Damnacanthus C.F. Gaertn. (1 species/1 specimen examined) —Figs. 12 and 13.

Growth rings are indistinct and formed by a difference in fibre wall thickness.—Vessels are very narrow and difficult to distinguish from fibres in transverse sections (Fig. 12). Tangential diameter of vessel lumina is 24 (20-27) μm. Vessel element length is 693 (600-900) μm. Vessel element perforations are simple and vestured. The openings of the perforations are elliptical, sometimes irregular or mismatched. Intervessel pits and vessel-ray pits are alternate, minute, and vestured.—Fibres are septate. Fibre pits with pit chambers 2-3 μm in diameter occur on radial and tangential walls. Fibre length is 906 (700-1,000) μm. Occasionally, vesturing is found in association with fibre wall thickenings. The illustration shown in Fig. 13 illustrates the outer surface of the newly deposited fibre thickenings, while the original secondary fibre wall in Fig. 13 is removed by the cutting action during sample preparation. The vestures arise from the thickenings into the depressions which frequently appear just like vestured pits of vessel elements. SEM observations illustrated that the fibre thickenings containing the primary wall were sometimes found to be detached from the inner surface of the secondary wall. Small unbranched vestures also spread out on the inner surface of the thickenings forming narrow lines.—Axial parenchyma is absent. —Rays are heterogeneous, 3-4-seriate, and sometimes 5-6-seriate. The body ray cells are mostly procumbent with 2-4 or more rows of upright/square ray cells. Rays average 1,145 μm high, and more than 15 rays occur per mm. —Mineral inclusions are absent.

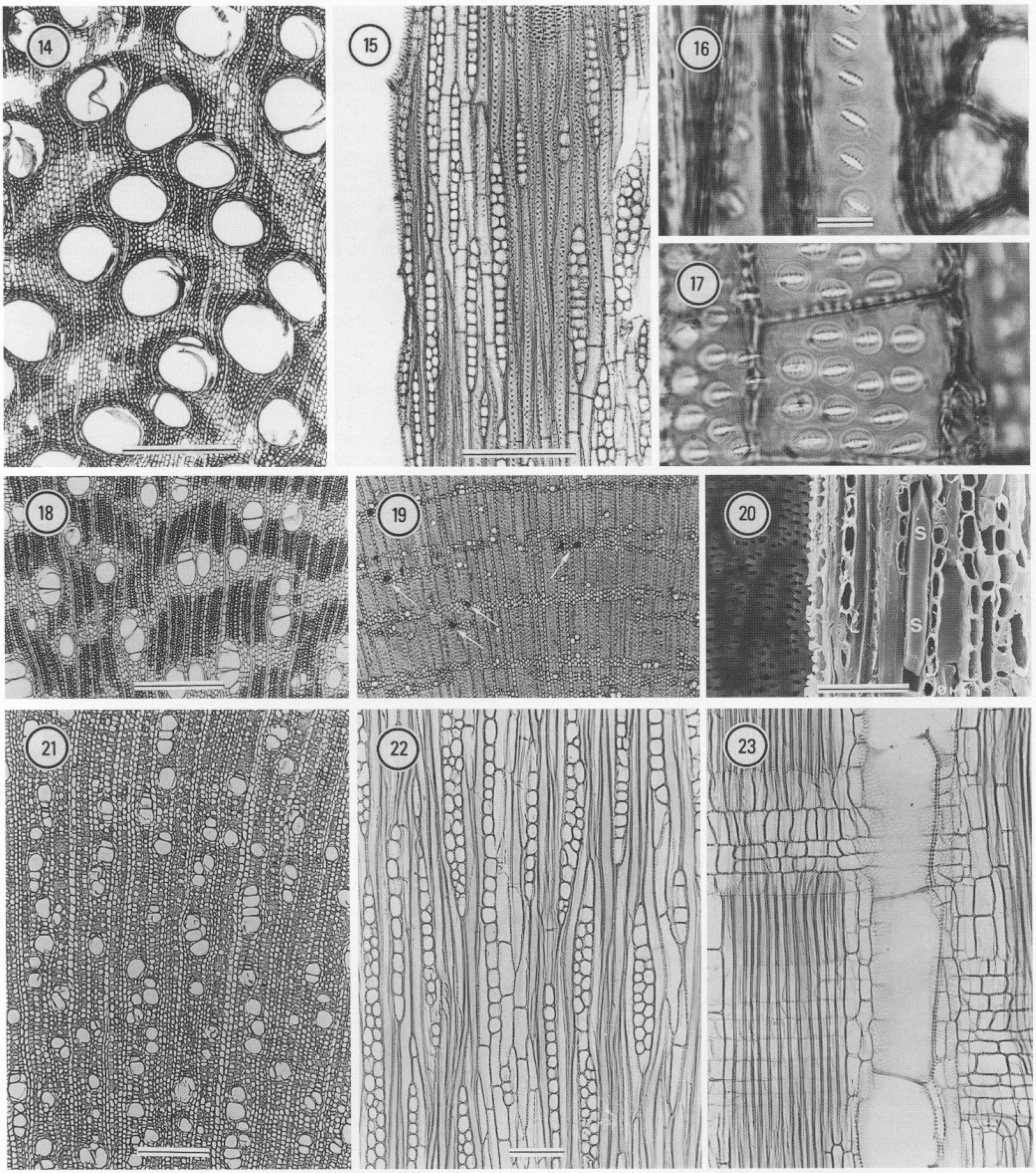
Morindeae Miq.

Gynochtodes Blume (2 species/2 specimens examined) —Figs. 14-17.

Growth rings are absent.—Vessels are exclusively solitary, and round to oval. The tangential diameter of vessel lumina is very wide, on average 247 (150-300) μm; narrow vessels about 40 μm wide are occasionally present. Mean number of vessels per mm^2 is 6 (4-10). Vessel element perforations are simple. Vessel pits are alternate, 7-9 μm in diameter, and vestured. Vessel-ray pits are similar to other types of vessel pits (Fig. 17).—Fibre-tracheids are non-septate, with numerous distinctly bordered and vestured pits on radial and tangential fibre walls (Figs. 15-16). Mean fibre length is 870 (700-1,100) μm.—Axial parenchyma bands are discontinuous, usually more than four cells wide, and the distance between the bands is highly variable (Fig. 14). Axial parenchyma strands are composed of seven to nine cells.—Rays are near homogeneous. They are uniseriate or biseriate in part (Fig. 15). The body ray cells are procumbent, with one row of square or upright marginal ray cells. Rays are 287 (100-630) μm high. The number of rays per mm varies from 11 to 14. —Raphides are present in axial parenchyma cells.

Morinda L. (9 species/9 specimens examined)—Figs. 18-23.

Growth rings are absent or indistinct.—Vessel grouping is variable. Vessels are exclusively solitary in *M. foresteri* and mainly solitary in *M. debilis*, *M. morindoides*, and *M. reticulata*. The vessel grouping index is about 1.5 in *M. citrifolia*, and vessels are predominantly in radial multiples in *M. citrifolia* (Tw 46621), *M. lucida*, *M. geminata*, and *M. angustifolia* (vessel grouping index about 2). Vessels are in radial multiples of more than four in *M. angustifolia* and *M. citrifolia*. Length of vessel elements is 504 (150-1,300) μm. Vessel frequency averages about 25 vessels per mm^2. The mean tangential diameter of vessel lumina is very wide in *M. morindoides* Uw 9,264 (240 μm), and wide in *M. reticulata* (143 μm) and *M. geminata* (110 μm). Narrow vessels of ca. 28 μm occur in *M. debilis*. Other specimens studied show vessels of ca. 70 μm wide. Vessel element perforations are simple. Inter-



Figs. 14–23. Wood of Morindeae. 14–19, 21–23: Light micrographs. 20: Scanning electron micrograph. 14–17: *Gynochtodes* sp. 14: Transverse section showing wide vessels and axial parenchyma bands (bar=500 μm). 15: Tangential section with 1–2-seriate rays, axial parenchyma strands and pitted fibre walls (bar=200 μm). 16: Detail of vestured fibre pits on tangential fibre wall (bar=10 μm). 17: Detail of vestured vessel-ray pits (bar as in 16). 18: *Morinda lucida*. Axial parenchyma bands in transverse section (bar=500 μm). 19: *Morinda debilis*. Transverse section showing narrow vessels and axial parenchyma bands. Raphides are present in axial parenchyma cells indicated by arrows (bar as in 18). 20: *Morinda morindoides* (Breteler 747). Detail of tangential section with styloid (indicated by S) in axial parenchyma cell (bar=60 μm). 21: *Morinda citrifolia* (cultivated at BR). Transverse section showing vessels solitary and in radial multiples. Axial parenchyma distribution is diffuse-in-aggregates (bar=250 μm). 22–23: *Morinda lucida*. Tangential section (22; bar=100 μm) and radial section (23; bar as in 22).

vessel pits are alternate and generally more than 4 µm in diameter. Vessel pits are mostly vestured, but non-vestured vessel pits occur especially in specimens with (very) wide vessels (e.g., *M. morindoides* and *M. reticulata*). Vessel-ray pits are enlarged with reduced pit borders in *M. reticulata* and *M. morindoides*, but similar to intervessel pits in all other species (Fig. 23).—Fibre-tracheids with distinctly bordered pits on radial and tangential walls are present. Fibre pits in *M. geminata*, however, are simple to minutely bordered. Fibre length is 1,086 (500-1,950) µm.—Distribution of the axial parenchyma is variable but parenchyma bands are most common. These are four or five cells wide (Fig. 18), but some species show narrow bands that are two or three cells wide (Fig. 19). *M. geminata* and *M. morindoides* (Uw 9264) show parenchyma bands much more than four cells wide (from 100 to 230 µm). The distance between the bands is variable, e.g. from 50 to 210 µm in *M. debilis* and from 200 to 400 µm in *M. lucida*. Axial parenchyma is diffuse to diffuse-in-aggregates, with small lines 1 or 2 cells wide in *M. angustifolia* and *M. foresteri*, but only diffuse-in-aggregates in *M. citrifolia* (Fig. 21). Scanty paratracheal parenchyma is also found in *M. morindoides*. The axial parenchyma strands are composed of 3 to 12 cells.—Rays are mostly heterogeneous (Fig. 22, 23), but homogeneous rays are found in *M. morindoides* (Uw 9264) and near homogeneous rays occur in *M. geminata* and *M. citrifolia*. The rays are 1-3-seriate, but 4-5-seriate rays occur in *M. geminata* and *M. citrifolia*. Rays in *M. debilis*, *M. foresteri*, and *M. morindoides* are exclusively or predominantly uniseriate. They are mainly composed of procumbent cells with some rows of upright/square marginal cells. Mean height of the rays is 700 (100-2,300) µm. The number of the rays per mm is 11 (7-17).—Raphides are present in axial parenchyma cells of *M. morindoides* (Uw 9264), *M. debilis* (Fig. 19), *M. reticulata*, and *M. citrifolia*. The axial parenchyma cells are distinctly enlarged in *M. debilis*. Styloids (150 to 250 µm long; 15-20 µm wide) occur in parenchyma cells of *M. morindoides* (Uw 9264; Fig. 20).

Pauridiantheae Bremek. ex Darwin

Commitheca Bremek. (1 species/1 specimen examined)

Growth rings are indistinct.—Vessels are diffuse, solitary or in short radial multiples. Vessel grouping index is 1.42. The tangential diameter of vessel lumina averages 39 (30-50) µm. Mean number of vessels per mm^2 is 66 (52-80). Vessel element perforations are simple and sometimes vestured. Intervessel pits are alternate, minute, and vestured. Vessel-ray pits are similar to intervessel pits. Mean vessel element length is 841 (600-1,100) µm.—Fibre-tracheids are non-septate, with numerous distinctly bordered pits on radial and tangential fibre walls. Mean fibre length is 1,273 (800-1,600) µm.—Axial parenchyma is diffuse. Helical thickenings are occasionally present in axial parenchyma cells.—Rays are 2-3-seriate. The ray cells are procumbent, with several rows of square or upright marginal ray cells. Rays are 2,050 (1,500-2,550) µm high. The number of rays per mm varies from 19 to 27.—Raphides are absent.

Pauridiantha Hook.f. (3 species/3 specimens examined)—Fig. 41.

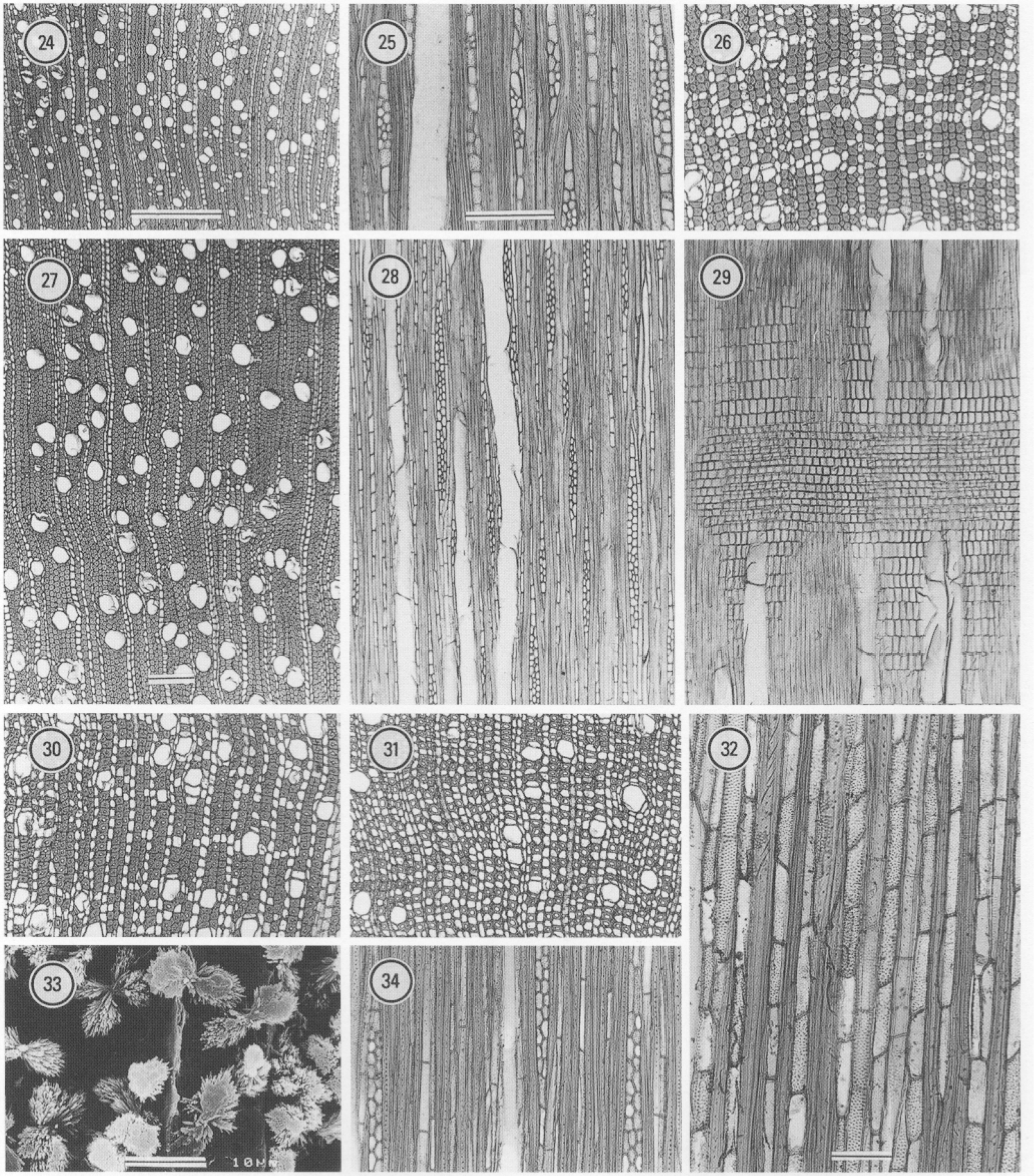
Growth rings are indistinct.—Vessels are diffuse, solitary, or in short radial multiples. Mean vessel grouping index is 2.5 in *P. viridiflora*, but 1.5 and 1.4 in *P. pyramidata* and *P. rubens* respectively. The tangential diameter of vessel lumina averages 47 (30-65) µm. Mean number of vessels per mm^2 is 42 (17-78). Vessel element perforations are simple. Intervessel pits are alternate, minute, and vestured. Vessel-ray pits are similar to intervessel pits. Mean vessel element length is 733 (350-1,100) µm.—Fibre-tracheids are non-septate, with numerous distinctly bordered pits on radial and tangential fibre walls. Mean fibre length is 1,355 (1,000-1,900) µm.—Axial parenchyma is diffuse to diffuse-in-aggregates. Axial parenchyma strands are composed of 8 to 12 cells. Helical thickenings in axial parenchyma cells are rarely observed in *P. pyramidata*.—Rays are 2-3-seriate and up to 5-seriate in *P. viridiflora*. The ray cells are procumbent, with several rows of square or upright marginal ray cells. Rays are 1,304 (200-3,200) µm high. The number of rays per mm varies from 7 to 19.—Raphides are absent in the secondary xylem of the specimens studied.

Poecilocalyx Bremek. (2 species/2 specimens examined)

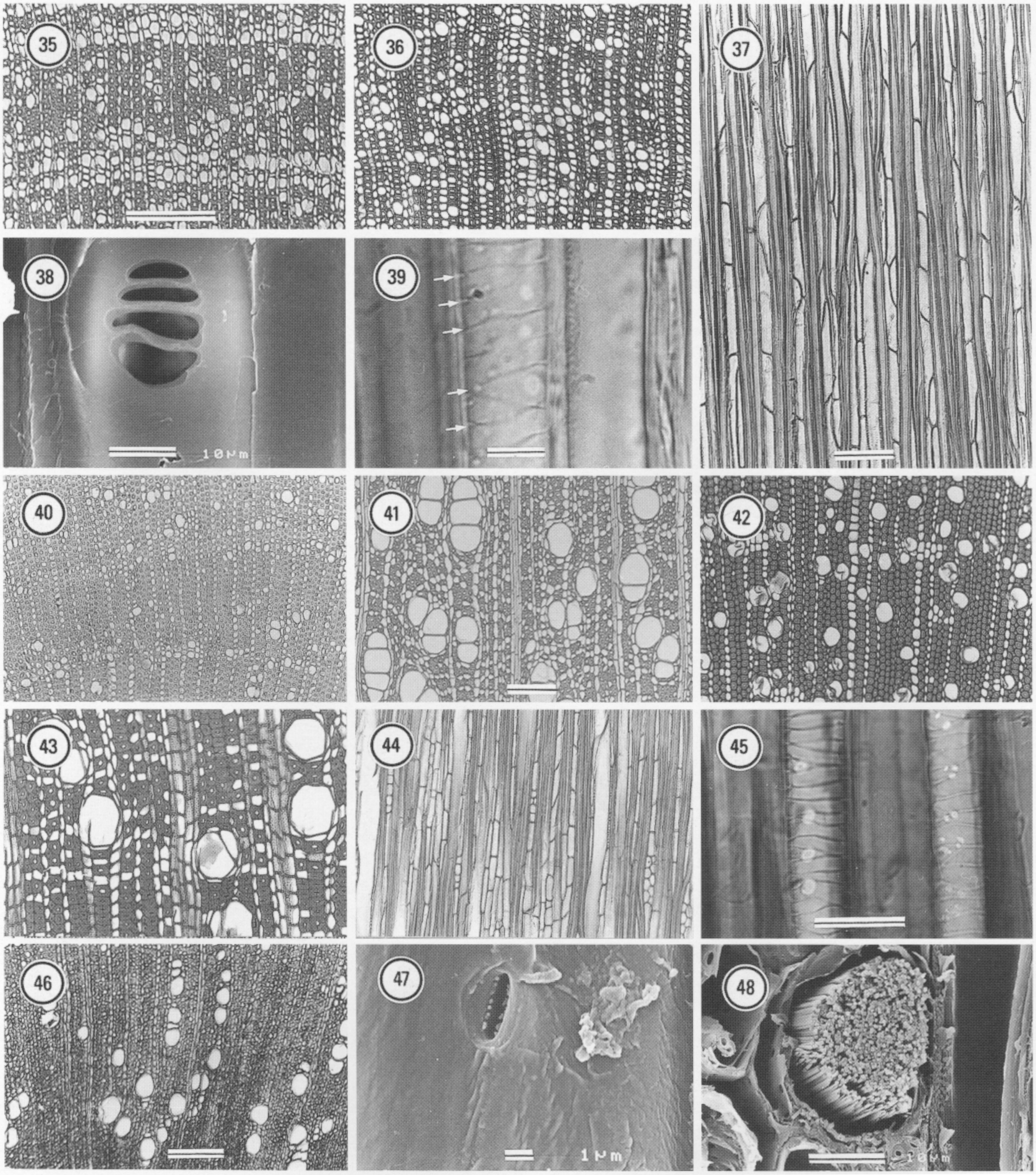
Growth rings are indistinct.—Vessels are diffuse and nearly always solitary. Mean vessel grouping index is 1.15. The tangential diameter of vessel lumina is small, on average 18 (10-25) µm. Mean number of vessels per mm^2 is 105 (50-164). Vessel element perforations are simple. Intervessel pits are alternate, minute, and vestured. Vessel-ray pits are similar to intervessel pits. Mean vessel element length is 719 (500-1,000) µm.—Fibre-tracheids are non-septate, with numerous distinctly bordered pits on radial and tangential fibre walls. Mean fibre length is 1,108 (700-1,600) µm. —Axial parenchyma is diffuse to diffuse-in-aggregates. Helical thickenings in axial parenchyma cells are occasionally found in *P. stipulosa*. Axial parenchyma strands are composed of 6 to 15 cells.—Rays are 2- to 4-seriate. The body ray cells are procumbent, with several rows of square or upright marginal ray cells. Rays average 1,480 (800-2,100) µm high. The number of rays per mm varies from 10 to 24.—Raphides are absent.

Stelechantha Bremek. (1 species/1 specimen examined)—Fig. 40.

Growth rings are indistinct.—Vessels are diffuse, solitary or in short radial multiples. The mean vessel grouping index is 1.5. The tangential diameter of vessel lumina is small, averaging 21 (20-25) µm (Fig. 40). Mean number of vessels per mm^2 is 82 (60-110). Vessel element perforations are simple. Intervessel pits are alternate, minute, and vestured. Vessel-ray pits are similar to intervessel pits. Vessel element length is 850 (650-1,100) µm.—Fibre-tracheids are non-septate, with numerous distinctly bordered pits on radial and tangential fibre walls. Mean fibre length is 1,432 (1,300-1,650) µm.—Axial parenchyma is scanty paratracheal or diffuse-in-aggregates (Fig. 41). Axial parenchyma strands are composed of 6 to 16 cells.—Rays are biseriate. The



Figs. 24-34. Wood of Prismatomerideae (24-29) and *Lasianthus* (30-34). 24-32, 34: Light micrographs. 33: Scanning electron micrograph. 24: *Prismatomeris* sp. Transverse section (bar=500 µm). 25: *Prismatomeris* sp. Tangential section (bar=200 µm). 26: *Rennellia elliptica*. Transverse section with axial parenchyma diffuse to diffuse-in-aggregates (bar as in 25). 27-29: *Rennellia* sp. 27: Transverse section showing solitary vessels (bar=200 µm). 28: Tangential section (bar as in 27). 29: Radial section with procumbent or square body ray cells and several rows of upright/square marginal cells (bar as in 27). 30. *Lasianthus* sp. (*Nooteboom 4034*). Transverse section (bar as in 25). 31. *Lasianthus* sp. (*Nooteboom 4026*). Transverse section with axial parenchyma strands grouped in short tangential lines (bar as in 25). 32: *Lasianthus acuminatus*. Tangential section showing 1(-2)-seriate rays (bar=100 µm). 33: *Lasianthus scabridus*. Detail of raphide-like crystal complexes (bar=10 µm). 34: *Lasianthus* sp. (*Nooteboom 4026*). Tangential section with 2-3-seriate rays and pits on tangential fibre walls (bar as in 25).



Figs. 35-48. Wood of *Saldinia*, *Trichostachys*, Pauridiantheae, Urophylleae, and *Triainolepis*. 35-37, 39-46: Light micrographs. 38, 47, 48: Scanning electron micrographs. 35: *Saldinia* sp. (*Rakoto 301*). Transverse section (bar=200 μm). 36-39: *Trichostachys microcarpa* (*Devred 7678*). 36: Transverse section (bar as in 35). 37: Tangential section with 1(-2)-seriate rays (bar=100 μm). 38: Scalariform perforation plate with three bars (bar=10 μm). 39: Helical thickenings (arrows) in axial parenchyma cell with simple pits variable in size (bar=10 μm). 40: *Stelechantha makakana*. Transverse section (bar as in 35). 41: *Pauridiantha viridiflora*. Transverse section (bar=200 μm). 42: *Urophyllum trifurcum*. Transverse section (bar as in 35). 43. *Maschalocorymbus corymbus*. Transverse section (bar as in 35). 44: *Urophyllum trifurcum*. Tangential section (bar as in 35). 45: *Urophyllum macrophyllum* illustrating helical thickenings in two axial parenchyma cells with simple pits that are variable in size (bar=20 μm). 46: *Triainolepis emirensis*. Transverse section (bar=200 μm). 47-48: *Triainolepis africana* subsp. *hildebrandtii* (*Gillet & Kibuwa 19850*). 47: Bordered fibre pit with minute vestures viewed from the outer surface (bar=1 μm). 48. Raphide bundle in ray parenchyma cell (bar=10 μm).

body ray cells are procumbent, with several rows of square or upright marginal ray cells. Rays are 1,860 (1,500-3,000) μm high. The number of rays per mm varies from 21 to 30. —Raphides are absent.

Prismatomerideae Ruang

Prismatomeris Thwaites (4 species/4 specimens)—Figs. 24, 25.

Growth rings are absent.—Vessels are diffuse and exclusively solitary (Fig. 24). Mean tangential vessel diameter is 36 (15-75) μm and narrow vessel elements that resemble vascular tracheids are common. The number of vessels per mm^2 is 50 (27-85). Vessel element length is highly variable (300-2,300 μm); relatively long in *P.* sp. and *P. beccariana*, but shorter in *P. brachypus* and *P. tetrandra*. Vessel element perforations are always simple. All vessel pits are alternate, minute or small, and vestured.—Fibre-tracheids show bordered pits on radial and tangential walls (Fig. 25). Fibre length is about 2,000 μm, but much shorter in *P. brachypus* (on average 975 μm) and *P. tetrandra* (on average 713 μm). —Axial parenchyma is sparsely diffuse (Fig. 24) to diffuse-in-aggregates. Axial parenchyma strands are composed of ca. seven to ten cells.—Rays are 1-2-(3)-seriate, heterogeneous (Fig. 25), and composed of upright/square ray cells with procumbent body ray cells. Perforated ray cells with simple perforations are present. Rays are more than 1 mm high and on average 14 (9-22) rays occur per mm.—Raphides are found in *P. beccariana* (Jacobs 5423).

Rennellia Korth. (2 species/2 specimens examined)—Figs. 26-29.

Growth rings are absent.—Vessels are diffuse and exclusively solitary (Figs. 26, 27). Vessel outline is round to oval. Vessel diameter averages 67 (33-100) μm and vessel frequency is 25 (12-39) per mm^2. Mean vessel element length is 1,110 (650-1,450) μm. Vessel element perforations are simple. All vessel pits are alternate, minute, and vestured. —Fibre-tracheids are non-septate with distinctly bordered pits on radial and tangential walls. Fibre length is 1,765 (1,500-2,280) μm.—Axial parenchyma is diffuse to diffuse-in-aggregates (Fig. 26), and also scanty paratracheal in *R.* sp. (Fig. 27). Axial parenchyma strands are composed of 7 to 10 cells.—The heterogeneous rays are 2-3-seriate (Fig. 28) and composed of upright/square ray cells with few procumbent cells (Fig. 29). Rays are 1,450 (400-3,700) μm high and about 15 rays occur per mm.—Raphides are observed in *R. elliptica*, while small spiny druses are recorded in *R.* sp.

Triainolepideae Bremek.

Triainolepis Hook.f. (1 species/2 specimens examined)—Figs. 46-48 (*T. emirensis* is illustrated in Fig. 46 but not included in the description below).

Growth rings are indistinct.—Vessels are diffuse, solitary, grouped in relatively long radial multiples, or sometimes with a slight tendency to form a diagonal pattern (Fig. 46). The mean vessel grouping index is 2.7. Tangential vessel diameter averages 38 (20-60) μm and narrow vessel elements with a single, small perforation are common. Vessel density averages 55/mm^2. Vessel element length averages 372 (200-550) μm. Vessel element perforations are simple. Intervessel pits and vessel-ray pits are minute, alternate, and vestured.—Fibres are non-septate. The fibre pits are distinctly bordered, vestured (Fig. 47) and less common on tangential than on radial fibre walls. Fibre length is 666 (250-1,100) μm.—Axial parenchyma is diffuse to diffuse-in-aggregates. Axial parenchyma strands are composed of five to ten cells.—The heterogeneous rays are 2-3-seriate. Ray height is ca. 1,225 μm and the mean number of rays per mm is 16.—Raphides are present in enlarged ray cells (Fig. 48).

Urophylleae Bremek. ex Verdc.

Leucolophus Bremek. (1 species/1 specimen examined)

Growth rings are indistinct.—Vessels are diffuse, exclusively solitary, and round to oval. The tangential diameter of vessel lumina averages 50 (25-70) μm. Mean number of vessels per mm^2 is 29 (24-35). Vessel element perforations are simple. All vessel pits are alternate, minute, and vestured. Mean vessel element length is 881 (650-1,150) μm. —Fibre-tracheids are non-septate, with numerous distinctly bordered pits on radial and tangential fibre walls. Mean fibre length is 2,018 (1,600-2,300) μm.—Axial parenchyma cells are diffuse-in-aggregate. Axial parenchyma strands are composed of 5 to 15 cells. Helical thickenings in axial parenchyma cells are ocassionally present.—Rays are 4-5-seriate with sheath cells partly surrounding the rays. The ray cells are procumbent, with several rows of square or upright marginal ray cells. Rays are 1,954 (900-2,500) μm high. The number of rays per mm varies from 6 to 8. —Raphides are absent.

Maschalocorymbus Bremek. (2 species/2 specimens examined)—Fig. 43.

Growth rings are absent.—Vessels are solitary or in short radial multiples. The mean vessel grouping index is 1.25. The tangential diameter of vessel lumina averages 82 (50-115) μm; narrow vessels about 40 μm wide are occasionally present. Mean number of vessels per mm^2 is 24 (12-37). Vessel element perforations are simple. Intervessel pits are alternate, minute, and vestured. Vessel-ray pits are similar to intervessel pits. Mean vessel element length is 1,273 (600-1,700) μm.—Fibre-tracheids are non-septate, with numerous distinctly bordered pits on radial and tangential fibre walls. Mean fibre length is 2,038 (1,600-2,900) μm. —Axial parenchyma cells are diffuse to diffuse-in-aggregates and scanty paratracheal in *M. corymbus* (Fig. 43). Axial parenchyma strands are composed of 10 to 20 cells. —Rays are relatively homogeneous, 4-5-seriate and up to 6-seriate in *M. corymbus*. The body ray cells are procumbent, with several rows of square or upright marginal ray cells. Rays are 1,948 (900-3,200) μm high. The number of rays per mm varies from 4 to 13.—Raphides are absent.

Pleiocarpidia Schumann. (2 species/2 specimens examined)

Growth rings are absent or indistinct.—Vessels are solitary in *P. sandahanica*, but also in short radial multiples in *P.*

pilosa. The tangential diameter of vessel lumina is relatively wide, on average 95 (45-140) μm. Mean number of vessels per mm^2 is 24 (12-38). Vessel element perforations are simple. Vessel pits are alternate, minute, and vestured. Vessel-ray pits are similar to intervessel pits. Mean vessel element length is 1,300 (800-1,800) μm.—Fibre-tracheids are non-septate, with numerous distinctly bordered pits on radial and tangential fibre walls. Mean fibre length is 1,945 (1,400-2,450) μm.—Axial parenchyma cells are diffuse or scanty paratracheal in *P. sandahanica*. Axial parenchyma strands are composed of 5 to 14 cells. Helical thickenings occur sparsely in axial parenchyma cells of *P. sandahanica*.—Rays are relatively homogeneous. They are 3-4-5-seriate. The ray cells are procumbent, with one row of square or upright marginal ray cells. Rays are 1,568 (600-2,500) μm high. The number of rays per mm varies from 6 to 11.—Raphides are absent.

Praravinia Korth. (2 species/2 specimens examined)

Growth rings are absent or indistinct.—Vessels are nearly always solitary. Mean vessel grouping index is 1.2. The tangential diameter of vessel lumina averages 51 (30-70) μm. Mean number of vessels per mm^2 is 61 (28-120). Vessel element perforations are simple. Intervessel pits are alternate, minute, and vestured. Vessel-ray pits are similar to intervessel pits. Mean vessel element length is 1,077 (700-1,500) μm.—Fibre-tracheids are non-septate, with numerous distinctly bordered pits on radial and tangential fibre walls. Mean fibre length is 1,664 (1,100-2,120) μm.—Axial parenchyma cells are diffuse to diffuse-in-aggregates. Axial parenchyma strands are composed of 6 to 15 cells. Helical thickenings in axial parenchyma cells are observed in the specimens of *Praravinia* studied.—Rays are relatively homogeneous. They are uniseriate or biseriate in *P. suberosa*, but 4-5-seriate in *P.* sp. The body ray cells are procumbent, with several rows of square or upright marginal ray cells. Rays are 1,477 (900-2,800) μm high. The number of rays per mm varies from 4 to 18.—Raphides are absent.

Urophyllum Jack ex Wallich. (4 species/4 specimens examined)—Figs. 42, 44, 45.

Growth rings are absent or indistinctly present.—Vessels are exclusively solitary in *U. trifurcum* (Fig. 42), but also in short radial multiples in the other species studied. Vessel grouping index is 1.5 in *U. zeylanicum*, *U. macrophyllum* and 2.5 in *U. corymbosum*. The tangential diameter of vessel lumina averages 58 (20-70) μm. Mean number of vessels per mm^2 is 57 (30-90). Vessel element perforations are simple. Intervessel pits are alternate, minute, and vestured. Vessel-ray pits are similar to intervessel pits. Mean vessel element length is 1,000 (700-1,500) μm.—Fibre-tracheids are non-septate, with numerous distinctly bordered pits on radial and tangential fibre walls. Mean fibre length is 1,542 (1,000-2,000) μm.—Axial parenchyma is diffuse to diffuse-in-aggregates. Axial parenchyma strands are composed of 4 to 11 cells, with occasional helical thickenings in *U.* cf. *macrophyllum* (Fig. 45) and *U. corymbosum*.—Rays are 2-3-seriate but mainly uniseriate in *U. trifurcum* (Fig. 44). The ray cells are procumbent, with one row of square or upright marginal ray cells. Rays are 1,350 (400-2,600) μm high. The number of rays per mm varies from 10 to 22.—Raphides are absent.

Lasianthus group

Lasianthus Jack (6 species/6 specimens examined)—Figs. 30-34.

Growth rings are indistinct; marked by marginal parenchyma in *L. batangensis* and *L. mayumbensis*.—Vessels are diffuse, mainly solitary, and the mean vessel grouping index is 1.23. Higher vessel grouping indices occur in *L. batangensis* (1.6) and *L. scabridus* (1.4). Vessel outline is circular to oval. Tangential vessel diameter is 33 (20-52) μm; wider vessels 70 (40-100) μm are observed in *L. batangensis*. Vessel density averages 75/mm^2. Vessel element length averages 1,020 (400-1,700) μm. Vessel element perforations are simple. Intervessel pits are minute, alternate, and vestured.—Fibre-tracheids are non-septate and the bordered pits on radial and tangential walls (Fig. 34) are sometimes vestured. Fibre length is 1,612 (1,200-2,300) μm.—Axial parenchyma is diffuse to diffuse-in-aggregates (Fig. 30, 31). Axial parenchyma strands are composed of five to ten cells. Axial parenchyma cells that show helical thickenings with vestured pits are sporadically found in *L.* sp. (4026, 4034, 4189).—The heterogeneous rays are 1-2-seriate with the 2-seriate portion generally not much wider than the uniseriate portions (Fig. 32). Triseriate rays are recorded for *L.* sp. (4026, 4034; Fig. 34) and *L. batangensis* (Tw 33582). Mean height of the rays is 2,000 μm and about 15 rays per mm occur. The rays are composed of procumbent cells with marginal rows of upright/square cells. Perforated ray cells are common. Perforations of perforated ray cells are simple, but scalariform with more than 10 bars in *L. cinereus* and *L. acuminatus*.—Raphides are present in *L. cinereus*, *L. scabridus* (Fig. 33), and *L.* sp. (4189); they are frequently composed of two bundles of needle-like crystals forming raphide complexes. Pith flecks are observed in *L. batangensis* (Tw 33582).

Saldinia A. Rich. ex DC. (1 species/2 specimens examined)—Fig. 35.

Growth rings are indistinct.—The vessels are diffuse, mainly solitary, and vessel grouping index is 1.3. The mean vessel diameter is 22 (20-30) μm and the number of vessels per mm^2 is 215 (200-240). Vessel element length is 1,018 (640-1,350) μm. Vessel element perforations are simple and occasionally scalariform in the specimen collected by Lewis and Razafimandimbison (nr. 723), but entirely scalariform in the other specimen studied (Rakoto 301). Intervessel pits and vessel-ray pits are minute, alternate, and vestured.—Fibres show distinctly bordered pits on tangential and radial walls. Fibres are non-septate. Mean fibre length is 1,583 (900-2,400) μm.—Axial parenchyma is diffuse (Fig. 35).—The juvenile rays are heterogeneous and uniseriate.—Mineral inclusions are not observed in the secondary xylem.

Table 2a. List of wood anatomical features. Numbers in parentheses are averages. 1=vessel grouping index; 2=perforation plates simple; 3=perforation plates scalariform; 4=intervessel pits minute; 5=intervessel pits small (>4 μm); 6=vessel-ray pitting with distinct borders; 7=vessel-ray pitting with reduced borders; 8=tangential diameter of vessel lumina (μm); 9=vessels/mm²; 10=vessel element length (μm); 11=fibre pits simple to minutely bordered; 12=fibre pits distinctly bordered; 13=fibre pits on radial and tangential walls; 14=septate fibres; 15=fibre length (μm); +=present; −=absent; ?=unknown

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Declieuxia fruticosa	1.23	+	−	+	−	+	−	17-(21)-30	120-160	370-(436)-510	+	−	−	+	500-(585)-620
Hindsia longiflora	1.76	+	−	+	−	+	−	17-(20)-30	100-120	300-(371)-450	+	−	−	+	500-(598)-700
Coussarea af. grandis	1.3	+	−	+	−	+	−	50-(61)-70	24-(30)-39	900-(1020)-1250	+	−	−	−	1490-(1634)-2000
C. contracta	1.51	+	−	+	−	+	−	30-(48)-60	36-(47)-56	690-(908)-1000	+	−	−	+	1100-(1490)-1800
C. hirticalyx	2.15	+	−	−	+	+	−	33-(49)-65	24-(36)-48	800-(907)-1100	+	−	−	+	800-(1428)-2090
C. leptoloba	2.16	+	−	−	+	+	−	40-(47)-65	40-(52)-64	870-(1115)-1300	+	−	−	+	1180-(1600)-1900
C. machadoana	1.6	+	−	+	+	+	−	30-(40)-50	42-(46)-52	800-(1158)-1400	+	−	−	+	1700-(2040)-2400
C. megalocarpa	1.54	+	−	+	+	+	−	34-(42)-55	34-(41)-56	700-(884)-1200	+	−	−	+	1200-(1488)-1750
C. ovalis	1.3	+	−	+	−	+	−	37-(52)-59	50-(62)-90	600-(955)-1200	+	−	−	+	1150-(1395)-1800
C. quatracasasii	1.21	+	−	+	−	+	−	30-(43)-65	16-(23)-34	950-(1267)-1500	+	−	−	+	1500-(1912)-2200
C. surinamensis	2.14	+	−	+	+	+	−	35-(46)-60	50-(56)-70	700-(1084)-1300	+	−	−	+	1500-(1734)-1950
C. tenuiflora	1.83	+	−	+	−	+	−	30-(38)-48	60-(85)-120	600-(802)-1100	+	−	−	+	1200-(1372)-1650
C. vallis	1.45	+	−	−	+	−	+	80-(116)-150	15-(17)-22	1000-(1153)-1450	+	−	−	+	1760-(2081)-2400
Faramea amplifolia	1.29	+	−	+	−	+	−	30-(43)-57	40-(48)-54	700-(990)-1200	+	−	−	+	1400-(1713)-1950
F. anisocalyx	1.6	+	−	+	+	+	−	30-(46)-60	24-(35)-50	800-(883)-1000	+	−	−	+	1050-(1280)-1400
F. elegans	1.3	+	−	+	−	+	−	41-(50)-63	43-(47)-52	800-(1033)-1300	+	−	−	+	1400-(1675)-2000
F. glandulosa	1.98	+	−	+	−	+	−	20-(44)-60	70-(81)-100	500-(972)-1120	+	−	−	+	1050-(1600)-1900
F. neblinae	1.5	+	−	+	−	+	−	37-(47)-56	37-(44)-55	800-(970)-1100	+	−	−	+	1200-(1474)-1600
F. occidentalis	1.4	+	−	+	−	+	−	48-(58)-74	38-(48)-59	420-(855)-1250	+	−	−	+	1300-(1590)-2000
F. parvibracteata	2.76	+	−	+	−	+	−	20-(44)-60	80-(93)-110	500-(895)-1300	+	−	−	+	900-(1305)-1600
F. quadricostata	1.4	+	−	+	−	+	−	18-(28)-37	61-(74)-93	650-(767)-1100	+	−	−	+	900-(1205)-1400
F. rectinervis	1.1	+	−	+	−	+	−	37-(50)-60	37-(51)-62	400-(500)-650	+	−	−	+	730-(1006)-1260
F. stenopetala	1.76	+	−	+	−	+	−	40-(52)-70	40-(52)-70	500-(762)-950	+	−	−	+	1100-(1496)-1820
F. warminigiana	1.6	+	−	+	−	+	−	42-(49)-56	42-(49)-56	600-(717)-850	+	−	−	+	1100-(1280)-1500
Craterispermum cerinanthum (*Tw 41594*)	1.18	+	−	+	−	+	−	45-(64)-80	23-(30)-38	840-(914)-1200	−	+	+	−	1600-(1900)-2250
C. cerinanthum (*Tw 48567*)	1.35	+	−	+	−	+	−	35-(48)-65	11-(56)-68	600-(910)-1150	−	+	+	−	1300-(1522)-1700
C. laurinum	1.2	+	−	+	−	+	−	40-(66)-90	20-(21)-23	1000-(1170)-1500	−	+	+	−	1650)-1942)-2200
C. schweinfurthii	1.11	+	−	+	−	+	−	25-(42)-58	58-(39)-50	600-(850)-1180	−	+	+	−	1000-(1356)-1650
Damnacanthus indicus	?	+	−	+	−	+	−	20-(24)-27	?	600-(693)-900	+	−	+	+	700-(906)-1000
Gynochtodes sp.	1.12	+	−	−	+	+	−	160-(248)-340	5-(7)-10	350-(450)-600	−	+	+	−	800-(905)-1100
G. coriacea	1	+	−	−	+	+	−	150-(246)-300	4-(5)-8	300-(410)-500	−	+	+	−	700-(843)-1000
Morinda angustifolia	1.97	+	−	−	+	+	−	20-(53)-85	24-(27)-34	500-(670)-800	−	+	+	−	1100-(1335)-1600
M. citrifolia	1.46	+	−	+	+	+	−	50-(65)-90	27-(40)-52	400-(670)-950	−	+	+	−	1050-(1360)-1600
M. citrifolia (*Tw 46621*)	2.2	+	−	−	+	+	−	50-(89)-120	11-(18)-23	300-(390)-500	−	+	+	−	1100-(1290)-1400
M. debilis	1.19	+	−	+	−	+	−	20-(28)-35	21-(31)-43	300-(405)-500	−	+	+	−	620-(784)-900
M. geminata	1.83	+	−	−	+	+	−	50-(110)-160	3-(10)-15	300-(510)-700	+	−	−	−	1250-(1629)-1950
M. lucida	2	+	−	−	+	+	−	60-(86)-115	11-(19)-24	150-(300)-400	−	+	+	−	580-(750)-900
M. morindoides (*Uw 9264*)	1.1	+	−	−	+	−	+	150-(240)-350	5-(6)-8	150-(278)-450	−	+	+	−	650-(898)-1030
M. morindoides	1.08	+	−	−	+	−	+	35-(68)-120	22-(29)-36	410-(484)-700	−	+	+	−	600-(678)-850
M. myrtifolia	1	+	−	+	+	+	−	50-(64)-80	38-(45)-56	800-(1060)-1300	−	+	+	−	1000-(1345)-1800
M. reticulata	1.28	+	−	−	+	−	+	70-(143)-220	16-(18)-24	200-(415)-550	?	?	?	?	600-(710)-800
Commitheca liebrechtsiana	1.42	+	−	+	−	+	−	30-(39)-50	52-(66)-80	600-(841)-1100	−	+	+	−	800-(1273)-1600

Table 2a. Continued

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Pauridiantha viridiflora	2.5	+	−	+	−	+	−	33-(45)-65	17-(24)-31	650-(866)-1100	−	+	+	−	1300-(1573)-1900
P. pyramidata	1.5	+	−	+	−	+	−	30-(48)-65	60-(66)-78	350-(740)-1000	−	+	+	−	1000-(1285)-1600
P. rubens	1.38	+	−	+	−	+	−	40-(48)-60	31-(38)-46	400-(592)-720	−	+	+	−	1100-(1206)-1500
Poecilocalyx schumannii	1.18	+	−	+	−	+	−	10-(20)-25	136-(146)-164	500-(644)-800	−	+	+	−	700-(850)-1000
P. stipulosa	1.12	+	−	+	−	+	−	12-(16)-25	50-(65)-100	550-(795)-1000	−	+	+	−	1100-(1367)-1600
Stelechantha makakana	1.5	+	−	+	−	+	−	20-(21)-25	60-(82)-110	650-(850)-1100	−	+	+	−	1300-(1432)-1650
Prismatomeris sp.	1	+	−	−	+	+	−	40-(55)-75	41-(47)-55	1100-(1630)-2300	−	+	+	−	2000-(2290)-2700
P. beccariana (*5423*)	1	+	−	+	−	+	−	19-(23)-27	40-(68)-85	600-(925)-1100	−	+	+	−	1600-(1810)-2100
P. beccariana (*4336*)	1	+	−	+	+	+	−	30-(50)-70	46-(53)-62	700-(1100)-1700	−	+	+	−	2000-(2170)-2400
P. brachypus	1	+	−	+	−	+	−	15-(22)-30	?	300-(505)-700	−	+	+	−	800-(975)-1200
P. tetrandra	1	+	−	+	−	+	−	22-(31)-36	27-(33)-44	300-(445)-700	−	+	+	−	470-(713)-920
Rennellia sp.	1	+	−	+	−	+	−	50-(80)-100	24-(33)-39	650-(950)-1200	−	+	+	−	1500-(1640)-1800
R. elliptica	1	+	−	+	−	+	−	33-(53)-100	12-(16)-21	1100-(1270)-1450	−	+	+	−	1500-(1890)-2280
Triainolepis africana 1040 (BR)	3	+	−	+	−	+	−	22-(35)-50	38-(64)-80	200-(305)-350	−	+	+	−	250-(545)-670
T. africana (*Tw 19850*)	2.4	+	−	+	−	+	−	20-(41)-60	320-(440)-550	320-(440)-550	−	+	+	−	620-(788)-1100
Leucolophus sp.	1	+	−	+	−	+	−	25-(50)-70	24-(29)-35	650-(881)-1150	−	+	+	−	1600-(2018)-2300
Maschalocorymbus sp.	1.6	+	−	+	−	+	−	70-(84)-115	28-(31)-37	600-(1246)-1700	−	+	−	−	1800-(2198)-2900
M. corymbus	1.1	+	−	+	−	+	−	50-(79)-110	12-(16)-19	900-(1300)-1600	−	+	+	−	1600-(1879)-2100
Pleiocarpidia sandahanica	1.1	+	−	+	−	+	−	85-(120)-140	12-(17)-21	1100-(1432)-1800	−	+	−	−	1500-(2084)-2450
P. pilosa	1.8	+	−	+	−	+	−	45-(70)-100	26-(31)-38	800-(1163)-1400	−	+	−	−	1400-(1807)-2150
Praravinia sp.	1.2	+	−	+	−	+	−	50-(67)-70	28-(34)-42	900-(1177)-1500	−	+	+	−	1800-(1968)-2120
P. suberosa	1.2	+	−	+	−	+	−	30-(36)-40	70-(88)-120	700-(977)-1400	−	+	+	−	1100-(1360)-1700
Urophyllum cf. macrophyllum	1.5	+	−	+	−	+	−	20-(31)-40	58-(66)-80	700-(857)-1100	−	+	+	−	1200-(1447)-1750
U. corymbosum	2.5	+	−	+	−	+	−	40-(52)-70	34-(37)-40	900-(1014)-1100	−	+	+	−	1000-(1709)-2000
U. trifurcum	1	+	−	+	−	+	−	20-(32)-45	65-(76)-90	700-(908)-1100	−	+	+	−	1200-(1369)-1600
U. zeylanicum	1.52	+	−	+	−	+	−	25-(32)-40	30-(52)-60	1100-(1225)-1500	−	+	+	−	1400-(1642)-1900
Lasianthus sp. (*4026*)	1.33	+	−	+	+	+	−	22-(33)-45	37-(50)-78	700-(1075)-1400	−	+	+	−	1550-(1840)-2200
L. sp. (*4034*)	1.03	+	−	+	+	+	−	25-(36)-47	52-(60)-80	900-(1270)-1450	−	+	+	−	1300-(1730)-2100
L. sp. (*4189*)	1.09	+	−	+	−	+	−	26-(33)-38	45-(60)-70	850-(1280)-1700	−	+	+	−	1650-(2070)-2300
L. acuminatus	1.21	+	−	+	−	+	−	27-(38)-50	52-(71)-88	500-(980)-1340	−	+	+	−	1500-(1800)-2100
L. batangensis	1.6	+	−	+	−	+	−	40-(70)-100	95-(100)-106	400-(722)-1000	−	+	+	−	1000-(1130)-1300
L. batangensis (*Tw 33582*)	1.07	+	−	+	−	+	−	25-(34)-40	55-(64)-85	500-(856)-1200	−	+	+	−	1200-(1496)-1700
L. cinereus	1.1	+	−	+	−	+	−	20-(28)-38	(80)-94	720-(850)-1000	−	+	+	−	1200-(1300)-1600
L. mayumbensis	1.27	+	−	+	−	+	−	21-(27)-33	50-(80)-100	?	−	+	+	−	?
L. scabridus	1.4	+	−	+	+	+	−	30-(38)-52	100-(120)-130	950-(1130)-1400	−	+	+	−	1300-(1535)-1750
Saldinia sp. (*301*)	1.2	+	+	+	−	+	−	15-(21)-30	200-(218)-240	940-(1150)-1350	−	+	+	+	1600-(1883)-2400
S. sp. (*723*)	1.4	+	+	+	−	+	−	20-(23)-30	204-(211)-224	640-(887)-1100	−	+	+	−	940-(1150)-1350
Trichostachys microcarpa (*7678*)	1.21	+	+	+	−	+	−	16-(21)-30	150-(170)-200	670-(856)-1050	−	+	+	+	680-(1070)-1310
T. microcarpa (2883)	1.38	+	+	+	−	+	−	20-(25)-30	125-(150)-170	600-(906)-1050	−	+	+	+	1200-(1330)-1550

Table 2b. List of wood anatomical features. Numbers in parentheses are averages. 16=axial parenchyma scanty paratracheal; 17=axial parenchyma diffuse; 18=axial parenchyma diffuse-in-aggregates; 19=axial parenchyma in narrow bands; 20=axial parenchyma in wide bands; 21=helical thickenings in axial parenchyma cells; 22=ray width in cell numbers; 23=ray height (μm); 24=sheath cells (partly) surrounding rays; 25=rays/mm; 26=raphides; +=present; —=absent; ?=unknown

	16	17	18	19	20	21	22	23	24	25	26
Declieuxia fruticosa	—	—	—	—	—	—	1-3	1300-(1400)-1500	—	12-13	+
Hindsia longiflora	—	—	—	—	—	—	1-2	400-(950)-1700	—	12-(13)-16	—
Coussarea af. grandis	+	—	—	—	—	—	1, 4-6	2000-(3897)-8300	+	7-(9)-10	—
C. contracta	+	—	—	—	—	—	1, 4-5	600-(1166)-1900	+	10-(12)-15	—
C. hirticalyx	+	—	—	—	—	—	1, 5-6	1200-(1945)-3200	+	8-(9)-10	—
C. leptoloba	+	—	—	—	—	—	1, 4-5	1000-(2336)-4100	+	14-(15)-17	—
C. machadoana	+	—	—	—	—	—	1, 3-6	1800-(3127)-5700	+	8-(11)-14	+
C. megalocarpa	+	—	—	—	—	—	1, 4-10	2600-(5113)-10100	+	8-(10)-13	+
C. ovalis	+	—	—	—	—	—	1, 5-8	1110-(2134)-4070	+	6-(6)-7	+
C. quatracasasii	+	—	—	—	—	—	1, 4-5-(6)	2250-(4305)-5700	+	8-(10)-12	+
C. surinamensis	+	—	—	—	—	—	1, 4-5	1050-(3470)-7010	+	7-(8)-10	+
C. tenuiflora	+	—	—	—	—	—	1, 2, 3	300-(1140)-2200	—	15-(17)-19	—
C. vallis	+	—	—	—	—	—	1, 4	800-(1642)-3200	+	7-(8.5)-10	+
Faramea amplifolia	+	—	—	—	—	—	1, 4-5	600-(1500)-2100	+	9, 10	+
F. anisocalyx	+	—	—	—	—	—	1, 4-6	420-(1324)-2200	+	8-(9)-10	—
F. elegans	+	—	—	—	—	—	1, 2, 3	555-(1565)-2775	+	13-(14)-17	—
F. glandulosa	+	—	—	—	—	—	4, 6	1000-(1780)-2600	+	10-(11)-12	+
F. neblinae	+	—	—	—	—	—	1, 5-10 (16)	814-(2371)-5550	+	6-(6)-8	—
F. occidentalis	+	—	—	—	—	—	1, 5-6	555-(1585)-2590	+	6-(7)-8	+
F. parvibracteata	+	—	—	—	—	—	1, 3-4	800-(1413)-4000	+	10-(12)-14	—
F. quadricostata	+	—	—	—	—	—	1, 3-4	370-(1804)-9620	+	9-(10)-12	+
F. rectinervis	+	—	—	—	—	—	1, 4-5(6)	740-(1323)-2405	+	8-(9)-10	+
F. stenopetala	+	—	—	—	—	—	1, 4-7	400-(1284)-2200	+	10-(12)-13	—
F. warminigiana	+	—	—	—	—	—	1, 4-7	600-(1288)-2400	+	11-(12)-13	—
Craterispermum cerinanthum (*Tw 41594*)	—	—	—	—	+	—	1, 2, 3	400-(1553)-3300	—	11-(14)-17	+
C. cerinanthum (*Tw 48567*)	—	—	—	—	+	—	1, 2	300-(1290)-2400	—	14-(16)-17	+
C. laurinum	—	—	—	—	+	—	1, 2, 3	900-(3142)-5010	—	14-(15)-17	+
C. schweinfurthii	—	—	—	—	+	—	1, 2	400-(912)-1500	—	16-(18)-20	+
Damnacanthus indicus	—	—	—	—	—	—	1-(2)	800-(1145)-1500	—	?	—
Gynochtodes sp.	—	—	—	—	+	—	1-(2)	150-(354)-700	—	11-12	+
G. coriacea	—	—	—	—	+	—	1-(2)	10-(227)-350	—	12-(13)-14	+
Morinda angustifolia	—	+	+	+	—	—	2, 3	200-(752)-1700	—	8-(12)-17	—
M. citrifolia	—	—	+	—	—	—	2, 3	700-(1315)-1800	—	8-(10)-12	—
M. citrifolia (*Tw 46621*)	—	—	+	—	—	—	3, 4, 5	250-(564)-1100	—	9-(11)-12	+
M. debilis	—	—	—	+	+	—	1	200-(550)-1400	—	13-(15)-17	+
M. geminata	—	—	—	—	+	—	3, 4, 5	150-(769)-1950	—	9-(10)-11	—
M. lucida	—	—	—	—	+	—	2, 3	100-(654)-1200	—	9-(10)-11	—
M. morindoides (*Uw 9264*)	—	—	—	—	+	—	1, 2	150-(377)-700	—	12-(13)-14	+
M. morindoides	+	—	—	+	—	—	1, (2)	200-(785)-2300	—	7-(9)-13	—
M. myrtifolia	—	+	+	+	—	—	1, (2)	210-(508)-800	—	9-(10)-12	—
M. reticulata	—	—	—	—	+	—	?	?	—	?	+
Commitheca liebrechtsiana	—	+	—	—	—	+	2, 3	1500-(2050)-2550	—	19-(22)-27	

Table 2b. Continued

	16	17	18	19	20	21	22	23	24	25	26
Pauridiantha viridiflora	–	+	+	–	–	–	3, 4, 5	700-(1300)-2500	–	7-(9)-10	–
P. pyramidata	–	+	+	–	–	+	2, 3	200-(1487)-3200	–	12-(17)-19	–
P. rubens	–	+	–	–	–	–	2, 3	600-(1125)-2400	–	8-(11.5)-13	–
Poecilocalyx schumannii	–	+	–	–	–	–	2, 3	1000-(1566)-2100	–	16-(20)-24	–
P. stipulosa	–	+	+	–	–	+	3, 4	800-(1400)-2000	–	10-(13)-15	–
Stelechantha makakana	+	+	–	–	–	–	2	1500-(1860)-3000	–	21-(26)-30	–
Prismatomeris sp.	–	+	–	–	–	–	2, 3	180-(795)-2000	–	9-(11)-13	–
P. beccariana (*5423*)	–	–	+	–	–	–	2, 3	400-(1222)-2550	–	11-(15)-16	+
P. beccariana (*4336*)	–	+	–	–	–	–	2	600-(1265)-2200	–	9-(11)-13	–
P. brachypus	–	+	–	–	–	–	1, 2	?	–	16-(20)-22	–
P. tetrandra	–	+	+	–	–	–	1, 2	900-(1327)-2800	–	15, 16	–
Rennellia sp.	+	+	+	–	–	–	1, 2, 3	400-(1105)-2800	–	13-(14)-16	–
R. elliptica	–	–	+	–	–	–	1, 2, 3	600-(1792)-3700	–	15-(17)-18	+
Triainolepis africana 1040 (BR)	–	+	+	–	–	–	2, 3	1000-(1250)-2300	–	14-(15)-17	+
T. africana (*Tw 19850*)	–	+	+	–	–	–	2, 3	800-(1200)-1700	–	15-(17)-20	+
Leucolophus sp.	–	–	+	–	–	+	4, 5	900-(1954)-2500	+	6-(7)-8	–
Maschalocorymbus sp.	–	+	–	–	–	+	4, 5	900-(1262)-1700	+	4-(5)-6	–
M. *corymbus*	+	+	–	–	–	–	5, 6	1500-(2634)-3200	+	10-(12)-13	–
Pleiocarpidia sandahanica	+	+	–	–	–	+	3, 4	900-(1828)-2500	–	7-(10)-11	–
P. pilosa	–	+	–	–	–	–	4, 5	600-(1309)-1800	–	6-(7)-9	–
Praravinia sp.	–	+	–	–	–	+	4, 5	900-(1538)-2800	–	4-(7)-13	–
P. suberosa	–	+	+	–	–	+	1, 2	1200-(1417)-1900	–	12-(16)-18	–
Urophyllum cf. macrophyllum	–	+	+	–	–	+	2, 3	1100-(1433)-2000	–	10-(12)-15	–
U. corymbosum	–	+	+	–	–	+	1, 2, (3)	800-(1480)-2100	–	12-(13)-15	–
U. trifurcum	–	–	+	–	–	–	1, (2)	400-(710)-1200	–	16-(20)-22	–
U. zeylanicum	–	–	+	–	–	–	3	1500-(1783)-2600	–	13-(14)-16	–
Lasianthus sp. (*4026*)	–	–	+	–	–	+	1, 2, 3	1500-(2511)-3600	–	10-(11)-14	–
L. sp. (*4034*)	–	+	+	–	–	+	2, 3	700-(1466)-2400	–	14-(14)-15	–
L. sp. (*4189*)	–	–	+	–	–	+	1	1100-(2111)-4400	–	14-(17)-18	+
L. acuminatus	–	+	+	–	–	–	1, 2	700-(1970)-3500	–	13-(16)-19	–
L. batangensis	–	+	+	–	–	–	1	1700-(3280)-5600	–	19-(20)-23	–
L. batangensis (*Tw 33582*)	–	+	–	–	–	–	2, 3	300-(809)-2000	–	12	–
L. cinereus	–	+	+	–	–	–	1, 2	?	–	19-(22)-25	+
L. mayumbensis	–	+	+	–	–	–	1, 2	370-(640)-1110	–	8-(9)-10	–
L. scabridus	–	–	+	–	–	–	1	1200-(3220)-4000	–	15-(16)-19	–
Saldinia sp. (*301*)	–	+	–	–	–	–	1	?	–	15-(17)-19	–
S. sp. (723)	–	+	–	–	–	–	1	?	–	20-(23)-26	–
Trichostachys microcarpa (*7678*)	–	+	–	–	–	+	1	1800-(2700)-5800	–	16-(18)-20	+
T. microcarpa (2883)	–	+	–	–	–	–	1	?	–	20-(23)-25	–

Trichostachys *Hook.f.* (1 species/2 specimens examined) —Figs. 36-39.

Growth rings are indistinct and formed by a difference in the fibre wall thickness and vessel frequency.—Vessels are diffuse. The mean vessel grouping index is 1.3. Vessel outline is round to oval. Vessels are 23 (16-30) μm wide. Vessel frequency is 160 (150-200) per mm^2. Vessel element length is 880 (600-1,050) μm. About 80% of the vessel element perforations are scalariform (Fig. 38), with circa three bars; other perforations are simple. Intervessel pits and vessel-ray pits are minute, alternate, and vestured.—Fibres show bordered pits (3-4 μm in diameter) on radial and to a lesser extent on tangential walls. Septa are observed in at least several fibres. Mean fibre length is 1,200 (680-1,550) μm.—Axial parenchyma cells are sparsely diffuse, although they are difficult to distinguish from vessels in transverse sections (Fig. 36). Helical thickenings are occasionally found in axial parenchyma cells of *T. microcarpa* (R. Devred 7678; Fig. 39).—Rays are nearly always uniseriate, heterogeneous, and composed of upright/square ray cells (Fig. 37). Vessel-ray perforations are scalariform. Rays are generally more than 1 mm high, and about 20 rays occur per mm. —Small and mainly navicular prismatic crystals are observed. Raphides are present in ray cells of *T. microcarpa* (7678).

Discussion

The Rubioideae studied in this paper show distinct differences in their wood anatomical characters. A summary of diagnostic features is given in Table 3.

As already recorded by Metcalfe and Chalk (1950) and Koek-Noorman (1969), the Coussareeae stand apart from the other Rubioideae by their scanty axial parenchyma. Our results agree with Koek-Noorman (1969: 386) who stated that *Coussarea* and *Faramea* "are as difficult to distinguish from each other as the woods of the Psychotrieae". The only difference between the two genera we observed is the higher amount of paratracheal parenchyma in *Faramea*. Coussareeae and Psychotrieae share septate libriform fibres and vessel element plates that show two or more simple perforations (Jansen *et al*. 1997). Psychotrieae, however, usually do not possess axial parenchyma and very high multiseriate rays. The presence of two ray sizes with high multiseriate rays that show sheath cells are a diagnostic feature of the Coussareeae. Moreover, vessel pits of Coussareeae are mostly polygonal and especially in *Coussarea* relatively large (5-7 μm). Barros and Callado (1997) described scalariform perforation plates and prismatic crystals for the wood of *Coussarea friburgensis*, but these features were not found in the species studied by us.

As mentioned in the introduction, macromolecular data strongly support a relationship between Coussareeae and Coccocypseleae (e.g., Andersson and Rova 1999). Although the wood samples of *Hindsia* and *Declieuxia* studied are juvenile, the presence of septate fibres may support their relationship with the Coussareeae. Paratracheal parenchyma is not found in these genera, but several species of *Coussarea* also show very few or no axial parenchyma cells. Other differences in wood anatomical features of *Declieuxia* and *Hindsia* are quantitative and thus should not be compared with the mature wood of Coussarea and *Faramea*.

The genus *Craterispermum* is characterised by the presence of continuous parenchyma bands and fibre-tracheids. Our wood data agree with earlier descriptions of *Craterispermum* (Normand and Paquis 1976, Lecomte 1922). Axial parenchyma bands are a relatively rare feature in Rubiaceae, but they are known in the Morindeae and Gaertnereae, which are placed near the Psychotrieae, as well as for *Colletoecema* (Jansen *et al*. 1996, 1997, Piesschaert *et al*. 2000a). These taxa with parenchyma bands also share fibre-tracheids. Based on macromolecular data, Bremer and Manen (2000) found that *Craterispermum* takes a well supported position in the Psychotrieae alliance.

Fibre-tracheids as well as the presence of axial parenchyma bands and solitary vessels in *Colletoecema* support an exclusion from the Psychotrieae (Piesschaert *et al*. 2000a). A position of *Colletoecema* in or near the Craterispermeae is a suggestion that deserves serious consideration. The two genera share habitual similarities (woody plants with congested axillary opposite inflorescences—a feature rare in Rubioideae) and both have drupes (in *Craterispermum* with a derived unilocular stone, in *Colletoecema* with a derived bilocular stone) (Igersheim 1992, Piesschaert *et al*. 2000a). There are also many floral similarities. Moreover, the two genera are strong aluminium accumulators and have similar wood characters.

Morindeae s.str. are characterised by parenchyma bands and fibre-tracheids, which support a close relationship between Morindeae and Gaertnereae as confirmed by molecular data (Bremer 1996), and these features distinguish them from Coussareeae and Psychotrieae. *Morinda* and *Gynochtodes* also share relatively large intervessel pits, which are sometimes up to 9 μm in diameter.

The wood anatomy of *Morinda* is fairly heterogeneous with respect to axial parenchyma distribution, vessel grouping, and ray structure. Normand (1960) described *Morinda geminata* and *M. lucida* with numerous 4-6-seriate parenchyma bands, but remarks that this feature is not constant within the whole genus. He noticed that the Indian *M. citrifolia* can easily be distinguished from the African species *M. lucida* and *M. geminata*. Indeed, the axial parenchyma in *M. citrifolia* is diffuse-in-aggregates (Brown 1922, Janssonius 1926, Pearson and Brown 1932, Desch 1954). Vessels are exclusively solitary in several species, while others show radial multiples of more than four vessels. Most rays are heterogeneous, but in *M. morindoides* (Uw 9264), and to a lesser extent *M. geminata* and *M. citrifolia*, homogeneous rays occur.

The wood anatomical variation in the Morindeae probably can be explained by its different growth forms. *Morinda* and *Gynochtodes* both contain woody climbers; this habit clearly influences the structure of the secondary xylem of taxa such as *Gynochtodes*, *M. morindoides*, and *M. reticulata* (see e.g. Carlquist 1985 for a general survey of the secondary xylem of vines). The vessel diameter in these species is wide, vessel elements are rather short, vessels are almost exclusively

Table 3. Summary of diagnostic wood anatomical characters of the genera studied. VGI=mean vessel grouping index; VP=vessel element perforation; SI=simple; SC=scalariform; IR=irregular; DV=mean tangential diameter of vessel lumina; N=narrow (≤50 μm); M=medium (50-100 μm); W=wide (100-200 μm); VW=very wide (≥200 μm); SF=septate fibres; AP=axial parenchyma; D=diffuse; DA=diffuse-in-aggregates; NB=narrow bands; WB=wide bands; P=paratracheal; HT=helical thickenings in axial parenchyma cells; RW=ray width given in cell numbers; SC=sheath cell; +=present; −=absent.

Tribe Genus	VGI	VP	DV	SF	AP	HT	RW	SC
Coccocypseleae								
Declieuxia	1.23	SI	N	+	−	−	1-3	−
Hindsia	1.76	SI	N	+	−	−	1-2	−
Coussareeae								
Coussarea	1.65	SI	N, M, (W)	+	P, −	−	1, (2-3), >3	+
Faramea	1.62	SI	N, M	+	P	−	1, (2-3), >3	+
Craterispermeae								
Craterispermum	1.20	SI	N, M	−	WB	−	1-2-3	−
Mitchella group								
Damnacanthus	/	SI, IR	N	+	−	−	1-(2)	−
Morindeae								
Gynochtodes	1.0	SI	(W)-VW	−	WB	−	1-(2)	−
Morinda	1-2	SI	(N), M, W, (VW)	−	D, DA, NB, WB	−	1-(2), 2-3-(5)	−
Pauridiantheae								
Commitheca	1.42	SI	N	−	D	+	2-3	−
Pauridiantha	1.8	SI	N, (M)	−	D, DA	+	2-3-(5)	−
Poecilocalyx	1.15	SI	N	−	D, DA	+	2-3-4	−
Stelechantha	1.50	SI	N	−	D, P	−	2	−
Prismatomerideae								
Prismatomeris	1.0	SI	N, M	−	D	−	2-(3)	−
Rennellia	1.0	SI	(N), M	−	D, DA	−	2-3	−
Triainolepideae								
Triainolepis	2.70	SI	N, (M)	−	D, DA	−	2-3	−
Urophylleae								
Leucolophus	1.0	SI	N, M	−	DA	+	4-5	+
Maschalocorymbus	1.25	SI	M, (W)	−	D, P	+	4-5-6	+
Pleiocarpidia	1.45	SI	M, W	−	D, P	+	3-4-5	−
Praravinia	1.20	SI	N, M	−	D, DA	+	1-2, 4-5	−
Urophyllum	1.63	SI	N, (W)	−	D, DA	+	1-2-3	−
Lasianthus group								
Lasianthus	1.23	SI	N, (M)	−	D, DA	+	1-2-(3)	−
Saldinia	1.30	SI, (SC)	N	−	D	−	1	−
Trichostachys	1.30	SC, (SI)	N	−	(D)	+	1	−

solitary, axial parenchyma bands are wide, and the rays are homogeneous and mainly uniseriate.

The presence of styloids in *Morinda morindoides* (Uw 9264) is remarkable, since this crystal type is unusual in wood of Rubiaceae; they are found for instance in *Cosmocalyx*, *Ixora*, *Captaincookia*, and *Versteegia* (Richter and Schmitt 1987, Jansen *et al.* 1999). Among Rubioideae, relatively thin styloids are found in the leaves of some Psychotrieae (Solereder 1893, SJ: pers. obser.).

The secondary xylem of the Prismatomerideae (*Prismatomeris* and *Rennellia*) shows exclusively solitary vessels, fibre-tracheids, heterogeneous bi- or triseriate rays, and diffuse to diffuse-in-aggregates parenchyma cells. The absence of axial parenchyma bands and the occurrence of solitary vessels indicates that *Prismatomeris* and *Rennellia* can be distinguished from the Morindeae s.str., but further data from the remaining genera (*Appunia*, *Caelospermum*, *Pogonolobus*, *Gentingia*, *Motleya*) are desirable.

Although the wood sample of *Damnacanthus indicus* available is juvenile, two features appear to be of taxonomic significance: the absence of axial parenchyma and the presence of septate libriform fibres. Septate fibres with the occasional presence of vesturing on newly deposited thickenings have already been illustrated in detail and much more accurately by Ohtani (1987). This feature appears to be unique in Rubiaceae and as far as we know is not reported in other families. Ohtani (1984) also reported the unusual openings of the perforation plates in this species. In the molecular analysis of Andersson and Rova (1999) the *Mitchella* group was strongly nested in the Morindeae. Wood anatomically, however, *Damnacanthus* differs from the Morindeae and Prismatomerideae.

While *Lasianthus* has traditionally been placed in the Psychotrieae (Hooker 1873, Schumann 1897, Verdcourt 1958, Robbrecht 1993) or the Morindeae (Petit 1964, Robbrecht 1988), *rbc*L and *rps*16 intron sequence data strongly support a basal position of this genus within the Rubioideae, close to the neotropical herbaceous genus *Perama* (Bremer 1996, Andersson and Rova 1999). Wood anatomical features, especially the presence of fibre-tracheids and axial parenchyma which is diffuse to diffuse-in-aggregates, demonstrate that a position of *Lasianthus* within the Psychotrieae is no longer justified.

Helical thickenings in the axial parenchyma are seldom recorded in the secondary xylem of dicotyledons. Sporadic occurrence has been reported in *Lasianthus* by Janssonius (1926) and Ohtani (1986). Other examples are for instance *Trigonia servicea* (Trigoniaceae, Heimsch 1941), few Dipterocarpaceae, Ancistrocladaceae (Gottwald and Parameswaran 1966, 1968), Chrysobalanaceae (ter Welle 1975), and Araliaceae (Oskolski and Lowry 2000). Although the feature is very easily overlooked, we suggest that it characterises the basal most taxa of the Rubioideae, including Pauridiantheae, Urophylleae, and the group of *Lasianthus*. Within one sample the thickenings are of sporadic occurrence and fewer than 1% of axial parenchyma cells have these thickenings. Our observations confirm Ohtani (1986) in that they are more frequent in parenchyma cells which are in contact with or close to the (narrow) vessels. As illustrated by Ohtani (1986) in *Lasianthus japonicus*, it would be interesting to examine by detailed SEM observations whether or not vestures are associated with the thickenings that are found in axial parenchyma cells of other basal Rubioideae. Except for Rubiaceae, the unusual occurrence of vestures in axial parenchyma cells may also be present in Trigoniaceae and Dipterocarpaceae, which both show vestured vessel pits (Jansen *et al.* 2001).

Other genera that have been associated with the Psychotrieae or Morindeae are *Trichostachys* and *Saldinia* (Petit 1963, Robbrecht 1993). The *rps*16 intron analysis in Piesschaert *et al.* (2000a) demonstrated that these genera belong to the *Lasianthus* clade. Support for this position is found in the presence of distinctly bordered pits and the rare occurrence of helical thickenings in the axial parenchyma cells of *Trichostachys*. On the other hand, the presence of at least a few septate fibres in *Saldinia* and *Trichostachys* is not observed in species of *Lasianthus*. The scalariform perforation plates and uniseriate rays probably can be explained by the juvenile wood samples. The specimens of *Trichostachys microcarpa* studied have a monocaul dwarf habit: representatives are low (ca. 1 m), unbranched woody plants with most leaves aggregated towards the tip (Robbrecht 1988).

The tribes Pauridiantheae and Urophylleae, which were previously placed in the subfamily Cinchonoideae *sensu* Robbrecht (1988, 1993), show relatively similar wood features. The genera of these tribes can not be distinguished from each other by wood anatomy only. The wood structure of this group can be interpreted as rather primitive with the presence of fibre-tracheids, diffuse to diffuse-in-aggregate axial parenchyma, and vessel groupings are mostly solitary.

Our major conclusion is that wood anatomy generally corroborates the delimitation and separation of several taxa from the former Coussareeae/Morindeae/Prismatomerideae/Psychotrieae aggregate. In fact, wood anatomy appears to be most applicable to systematics of the Rubiaceae in statements of negation of close relationship rather than positive assertions of close affinity. Moreover, a comparison of the wood structure with independently suggested phylogenies of the Rubioideae suggests that homoplasy (several origins and/or losses) most likely explains the wood anatomical variation. A general treatment of the wood anatomical tendencies in the Rubiaceae will be discussed in a forthcoming paper.

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