WOOD ANATOMY OF *GREWIA* AND *MICROCOS* FROM PENINSULAR MALAYSIA AND BORNEO

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Key words: Intervessel pits – tile cells – *Pterospermum*-type – *Durio*-type – Tiliaceae – Malvaceae subfamily Grewioideae

CHUNG, R. C. K., LIM, S. C., LIM, A. L. & SOEPADMO, E. 2005. Anatomi kayu *Grewia* dan *Microcos* dari Semenanjung Malaysia dan Borneo. Kajian telah dijalankan ke atas anatomi kayu *Grewia* (satu spesies) dan sembilan spesies *Microcos* dari Semenanjung Malaysia dan Borneo, dan spesies jenisan kedua-dua genus (*G. occidentalis* dan *M. paniculata*) yang dijumpai di luar kawasan kajian. Pengamatan dalam kajian anatomi kayu ini menyokong pemisahan *Microcos* daripada *Grewia* seperti yang dilaporkan dalam rujukan. Ciri-ciri anatomi yang mengasingkan kedua-dua genus adalah garis kasar salur, susunan, bentuk dan saiz bukaan liang antara salur, corak jenis paksi parenkima dan kepadatan ruji uniseriat. Sel genting *G. polygama* tergolong dalam jenis *Pterospermum*, sementara sel genting *Microcos* dikelaskan sebagai perantaraan jenis sel-sel genting *Durio*.

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Introduction

It has long been apparent to systematists that the delimitation of families within the core Malvales (i.e. Tiliaceae, Sterculiaceae, Bombacaceae, and Malvaceae *s.s.*) is problematic (Hutchinson 1967, Cronquist 1981). Certain genera have been transferred back and forth between these families. The distribution of distinctive characters derived from morphology and palynology is only partly consistent with traditional classifications (Edlin 1935, Erdtman 1952, Takhtajan 1997, Bayer, 1999). Recently these closely related families have been merged into an expanded family Malvaceae *s.l.* with nine subfamilies. The genera formerly included in the family Tiliaceae are now grouped in subfamilies Brownlowioideae, Dombeyoideae, Grewioideae, and Tilioideae of the Malvaceae *s.l.* Morphological and molecular data show that Brownlowioideae and Grewioideae (both *Grewia* L. and *Microcos* L. are classified here) include the vast majority of 'tiliaceous' genera, the rest being Tilioideae (*Tilia* L. and *Craigia* W.W.Sm & W.E.Evans) and Dombeyoideae (*Schoutenia* Korth. and other tiliaceous genera outside the Malesian region) which are more closely related to traditional Sterculiaceae (Judd & Manchester 1997, Bayer *et al.* 1999, Bayer & Kubitzki 2003).

The genus *Grewia* consists of about 280–300 species of trees, shrubs or climbers, distributed from Madagascar, tropical Africa northwards and southeastwards to the Himalayas, China and Taiwan, India, Sri Lanka, Myanmar, Thailand, Indo-China, Malesia, Western Pacific and the northern parts of Australia. In the Malesian region about 30 species are known, of which four occur in Peninsular Malaysia and Borneo. Among the Peninsular Malaysian and Bornean *Grewia*, only *G. polygama* is a tree, while the other species are either woody climbers or treelets. *Microcos* is a genus of about 80 species of trees and shrubs, occurring in tropical Africa (not Madagascar) and Indo-Malesia. In Malesia, some 42 species are known, of which 31 occur in Peninsular Malaysia and Borneo (Chung 2001, Bayer & Kubitzki 2003).

In the past few decades, the delimitation and taxonomic status of *Grewia* and *Microcos* have been the subject of controversy. The disagreement among botanists has arisen since the publication of Burret's monograph of Tiliaceae (Burret 1926; family according to the traditional classification). Chung (2001, 2002, 2003) and Chung *et al.* (2003) identified a total of 42 morphological and micromorphological characters, which in combination can be used to distinguish *Grewia* from *Microcos* species in Peninsular Malaysia and Borneo, and concluded that the two genera are distinct. The findings support previous conclusions reached by Burret (1926) and Bayer and Kubitzki (2003) based on morphology of inflorescences, flowers and fruits; by Chattaway (1934) based on wood anatomy; Zhang and Chen (1984) based on pollen morphology; and Bayer *et al.* (1999) based on combined analyses of plastid *atp*B and *rbc*L DNA sequences.

Wood anatomical literature on the family Tiliaceae has been reviewed by Moll and Janssonius (1906), Pearson and Brown (1932), Kukachka and Rees (1943), Janssonius (1950), Desch (1954), and Sudo (1963, 1988).

Based on wood anatomical evidence, Chattaway (1934), Reyes (1938), Kukachka and Rees (1943), Metcalfe and Chalk (1950), Desch (1954), Phengklai (1998), and Boer and Sosef (1998) supported Burret's (1926) conclusion to recognise

Microcos as a genus of its own, distinct from *Grewia*. The characters used included height of tile cells in the wood-rays and number of tile cells in radial length corresponding to one procumbent cell, distribution pattern of parenchyma in the xylem, presence and shape of solitary vessels, number and size of intervascular pit-pairs, and frequency of uniseriate rays. The differences in wood anatomical structure have also been noted by Moll and Janssonius (1906), Kanehira (1924), Pearson and Brown (1932) and Janssonius (1950), even though these authors did not recognise *Microcos* as a distinct genus.

Moll and Janssonius (1906) examined the wood anatomy of five species of *Grewia* (*G. celtidifolia* Juss., *G. eriocarpa* Turcz., *G. excelsa* Vahl, *G. laevigata* Vahl and *G. microcos* L.) from Java. The first four species belong to *Grewia s.s.*, while *G. microcos* is now recognised as *M. paniculata*. Kanehira (1924) studied the wood anatomy of one species of *Grewia s.l.* (*G. stylocarpa* Warb. which is now recognised as *M. triflora*) from the Philippines, while Pearson and Brown (1932) investigated the wood anatomy of four *Grewia* species (*G. elastica* Royle, *G. laevigata*, *G. oppositifolia* Buch. *ex* DC. and *G. tiliifolia* A.Rich.) from India. In his study of the wood anatomy and identification of Malaysian hardwoods, Menon (1971) included eight species of *Grewia s.l.* (*G. blattaefolia* Corner, *G. elmeri* (Merr.) P.S.Ashton, *G. florida* Gagnep., *G. globulifera* Mast., *G. miqueliana* Kurz, *G. omphacarpa* Miq., *G. paniculata* Roxb. *ex* DC. and *G. stylocarpa*), all belonging to *Microcos*. Wong (1982) briefly described the wood properties of *Grewia antidesmifolia* King, *G. blattaefolia* and *G. laurifolia* Hook. *ex* Mast., all belonging to *Microcos*. More recently, wood anatomical studies were reported by Phengklai (1998) and Boer and Sosef (1998) on two species of *Grewia* (*G. excelsa* and *G. mollis* Juss.) and four species of *Microcos* (*M. antidesmifolia*, *M. grandiflora* Burret, *M. latifolia* and *M. paniculata*) respectively.

The aim of this study was to investigate the variation in the wood anatomy of *Grewia* and *Microcos* species occurring in Peninsular Malaysia and Borneo and to assess their taxonomic value for differentiating the two genera.

Materials and methods

Wood samples used in this study were obtained from institutional wood collections (Kw, KEPw, Lw and SANw; acronyms according to Stern 1988) listed in Table 1 and references are made to their origin and collector's number if known (acronyms following Holmgren *et al.* 1990).

Standard procedures for the study of wood structure were employed to prepare sections and macerations for light microscopic studies (Baas & Zhang 1986, Jansen *et al.* 1998). Descriptive terminology and measurement follow the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989). Wood anatomical data are summarised in Table 2.

Results

Grewia polygama *Roxb.*

Results for *G. polygama* are shown in Table 2 and Plates 1–3.

Growth rings

Growth rings in *G. polygama* are distinct. The following growth ring markers occur in various structural changes in this species: (1) thick-walled of radially flattened fibres in the latewood (always present) and (2) differences in vessel diameter and/or frequency (vessel number) between latewood and subsequent earlywood (semi-ring-porous).

Vessels

The distribution of vessels is typically diffuse, occasionally the wood is semi-ring-porous. This feature was also observed for other species of *Grewia* by Reyes (1938) and Phengklai (1998). In diffuse-porous species, the vessels are solitary, in radial multiples of 2–4(–6), or occasionally in clusters (i.e. laterally adjoining radial multiples) of (2–)4–6. In the semi-ring-porous species, the vessels are mainly solitary in the earlywood, and in multiples and/or in clusters in the latewood.

Solitary vessels are mostly round, but oval vessels are occasionally present. Vessel elements have short tails. Average tangential vessel diameter is 69 μm (range 30–100 μm). Vessel frequency ranges from 41 to 90 (average 62) vessels per mm^2. Average length of the vessel element is 242 μm (range 176–288 μm). Perforation plates simple, usually round, in oblique or slightly oblique, or rarely in horizontal end walls.

Intervessel pits are non-vestured, alternate, loosely arranged and few in number. Pits are characteristically round and rarely oval with a horizontal diameter of 6 to 9 μm. Pit apertures are typically narrowly and transversely elliptic in shape and 1–2 μm in horizontal diameter. However, some pit apertures are coalescent over 2–4 pit chambers. Vessel-ray and vessel-parenchyma pits usually have distinct borders, similar to the intervessel pits in arrangement, shape, size and apertures.

Tracheids and fibres

Vascular tracheids are present. The imperforate cells resemble the narrow vessel elements in size, shape and pitting. Fibres are non-septate and have simple to minutely bordered pits, less than 3 μm in diameter, mainly on the radial walls. Average length of fibres is 884 μm (range 552–1088 μm). Fibre wall thickness varies from medium to thick. The fibre-vessel length ratio is 2.4–5, but mostly ranges from 3.1 to 4.

Table 1 Source of materials studied

Species	Origin and collector's number	Xylarium
Grewia		
G. occidentalis L. (type species)	**South Africa**, *Zeyher s.n.* (Kw 2841; Kw 2843)	Kw; Kw
G. polygama Roxb.	**Peninsular Malaysia**, Kedah, Langkawi, Kuah, *Chung RC 5* (KEP!), Tanjung Rhu, *Chung RC 10* (KEP!)	KEPw; KEPw
Microcos		
M. paniculata L. (type species)	**Pakistan**, Chittagong, Cheoal RF, *Majumder & Islam 64A* (K!), *Majumder & Islam 64B* (K!)	Lw; Lw
M. antidesmifolia (King) Burret var. *antidesmifolia*	**Peninsular Malaysia**, Selangor, Gombak, Genting Sempah, *Mohd. Nur SFN 34308* (K!, KEP!, SING!)	KEPw
M. antidesmifolia (King) Burret var. *hirsuta* (King) Burret	**Borneo**, Sabah, Sandakan, Sepilok Kabili FR, *Kadir SAN A 2893* (K!, KEP!, SING!); Labuk Sugut, Lungmanis FR, *Termiji & Ali SAN 82937* (SAN!)	KEPw; SANw
M. cinnamomifolia Burret	**Borneo**, Sabah, Sandakan, Leila FR, *Hashim SAN 33463* (SAN!)	SANw
M. crassifolia Burret	**Borneo**, Sabah, Sandakan, *Termiji & Bongsu SAN 75820* (K!, SAN!)	SANw
M. globulifera (Mast.) Burret	**Peninsular Malaysia**, Perak, Larut & Matang, Bukit Larut FR, *Piyee FMS 8036* (KEP!)	KEPw
M. latifolia Burret	**Peninsular Malaysia**, Negeri Sembilan, Jelebu, Pasoh FR, *Kuisey FMS 1919* (K!, KEP!, SING!); Pahang, Temerluh, Bukit Langkap, *Pawanche FMS 13759* (KEP!); Perak, Larut & Matang, Pondok Tanjung FR, *Piyee FMS 8049* (KEP!), Kinta, Parit FR, *Symington FMS 11959* (KEP!)	KEPw; KEPw; KEPw; KEPw
M. latistipulata (Ridl.) Burret var. *latistipulata*	**Borneo**, Sabah, Kinabatangan, Segaliud Lokan FR, *Termiji SAN 76378* (K!, KEP!, L!, SAN!, SAR!, SING!), Sandakan *Termiji SAN 81538* (SAN!)	Lw; SANw
M. laurifolia (Hook. *ex* Mast.) Burret	**Peninsular Malaysia**, Selangor, *s.c. KEP 80870* (KEP!)	KEPw
M. reticulata Ridl.	**Borneo**, Brunei, *s.c. FMS 34444* (KEP!). Sabah, Sandakan, *Ahmad & Termiji SAN 68352* (KEP!)	KEPw; SANw
M. triflora (Blanco) R.C.K.Chung var. *triflora*	**Borneo**, S Kalimantan, Djaro Dam, *de Vogel 2141* (BRUN!). Sabah, Sandakan, Gum Gum FR, *Termiji SAN 81296* (SAN!), Sepilok Kabili FR, *Wood & Kadir SAN 17212* (KEP!)	Lw; SANw; KEPw

Table 2 Wood anatomical characters of *Grewia* and *Microcos* species

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Grewia														
occidentalis	r	(200–)242(–280)	(55–)81(–100)	(90–)105(–123)	l	g	b	+	866/1040	e	160/370	589/1620	-	t
polygama	r	(176–)242(–288)	(30–)69(–100)	(41–)62(–90)	l	g	b	+	884/1088	e	145/230	398/880	-	t
Microcos														
paniculata	o	(420–)483(–550)	(60–)94(–120)	(11–)15(–23)	c	p	s	-	1454/1820	u	476/920	786/1580	+	m
antidesmifolia var. *antidesmifolia*	o	(450–)611(–750)	(90–)127(–170)	(9–)14(–32)	c	p	s	-	1272/1700	u	314/470	798/1200	+	m
antidesmifolia var. *hirsuta*	o	(490–)656(–770)	(100–)128(–180)	(4–)5(–7)	c	p	s	-	1370/1600	u	458/720	1472/2525	+	m
cinnamomifolia	o	(500–)657(–770)	(80–)119(–160)	(6–)10(–14)	c	p	s	-	1418/1800	u	443/720	1611/3000	+	m
crassifolia	o	(500–)694(–770)	(100–)150(–200)	(5–)8(–10)	c	p	s	-	1582/1900	u	498/1180	1489/2550	+	m
globulifera	o	(510–)682(–790)	(90–)121(–150)	(5–)9(–17)	c	p	s	-	1512/2200	u	433/780	1125/2650	+	m
latifolia	o	(570–)658(–820)	(80–)116(–150)	(13–)17(–26)	c	p	s	-	1532/1880	u	342/630	887/1670	+	m
latistipulata var. *latistipulata*	o	(600–)669(–750)	(100–)145(–190)	(8–)12(–15)	c	p	s	-	1615/1980	u	626/1600	1362/2630	+	m
laurifolia	o	(470–)707(–870)	(80–)152(–200)	(10–)19(–29)	c	p	s	-	1358/1880	u	554/960	1221/2620	+	m
reticulata	o	(400–)604(–750)	(90–)113(–160)	(7–)13(–20)	c	p	s	-	1166/1480	u	345/620	901/1610	+	m
triflora var. *triflora*	o	(450–)672(–880)	(70–)131(–200)	(5–)14(–30)	c	p	s	-	1526/1900	u	413/790	1530/3630	+	m

Columns:
1. Vessel outline (r = usually round or occasionally oval; o = usually oval or occasionally round)
2. Vessel element length (μm)
3. Tangential vessel diameter (μm)
4. Vessel frequency (per mm²)
5. Intervessel pit arrangement (l = loosely arranged, few; c = compactly arranged, numerous)
6. Intervessel pit shape (g = round, rarely oval; p = polygonal, rarely oval)
7. Intervessel pit aperture (b = large, 1–2 μm in horizontal diameter; s = small, < 1 μm in horizontal diameter)
8. Vascular tracheids (+ = present; - = absent)
9. Length of fibres (average/maximum, μm)
10. Uniseriate rays (e = rare; u = common)
11. Height of uniseriate rays (average/maximum, μm)
12. Height of multiseriate rays (average/maximum, μm)
13. Two distinct sizes (+ = present; - = absent)
14. Tile cells (t = *Pterospermum*-type; m = intermediate to *Durio*-type)

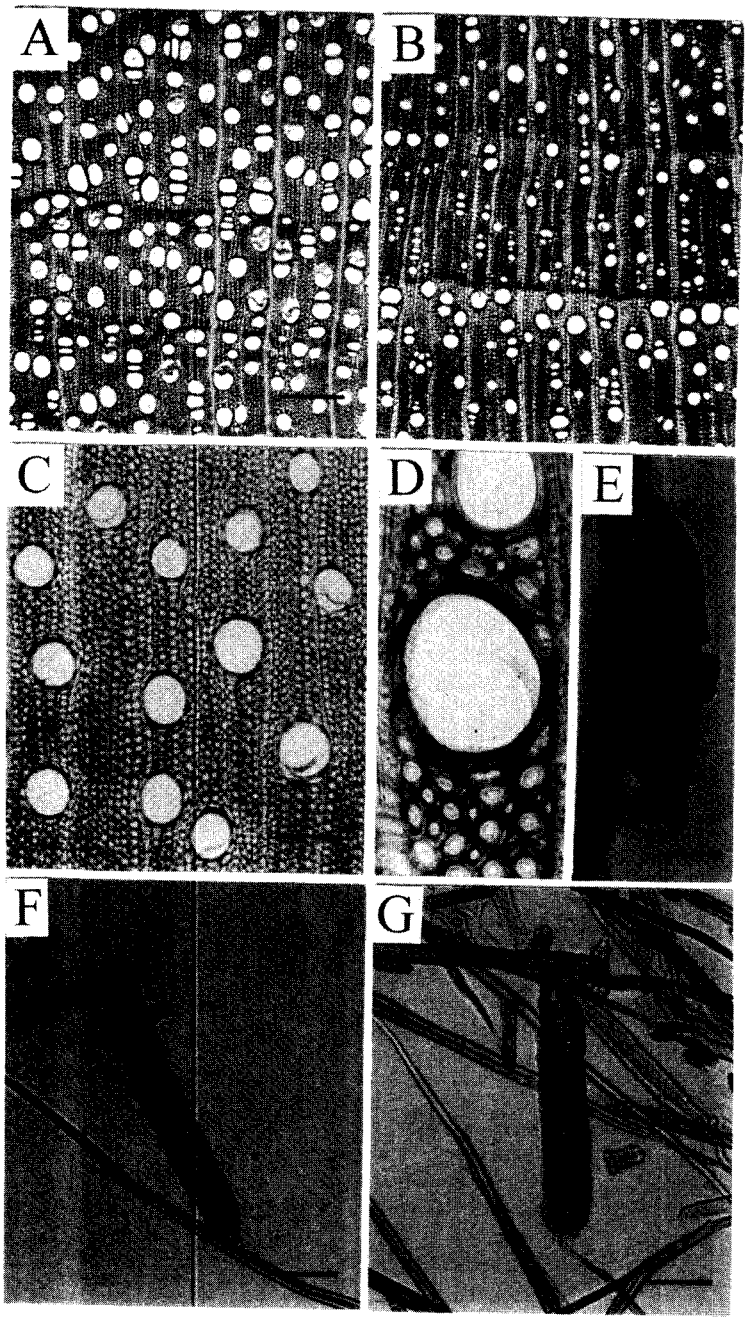

Plate 1 *Grewia.* Transverse sections showing growth rings, vessel distribution, grouping (A–C) and scanty paratracheal parenchyma (D). Vessel elements (E) and vascular tracheids (F–G) in maceration— A & F: *G. occidentalis* (*Zeyher s.n.* = Kw 2843)— B & D–E: *G. polygama* (*Chung RC 5*)— C & G: *G. polygama* (*Chung RC 10*)— Bar equals 2.5 mm in A–B; 10 μm in D; 50 μm in E–G; 100 μm in C.

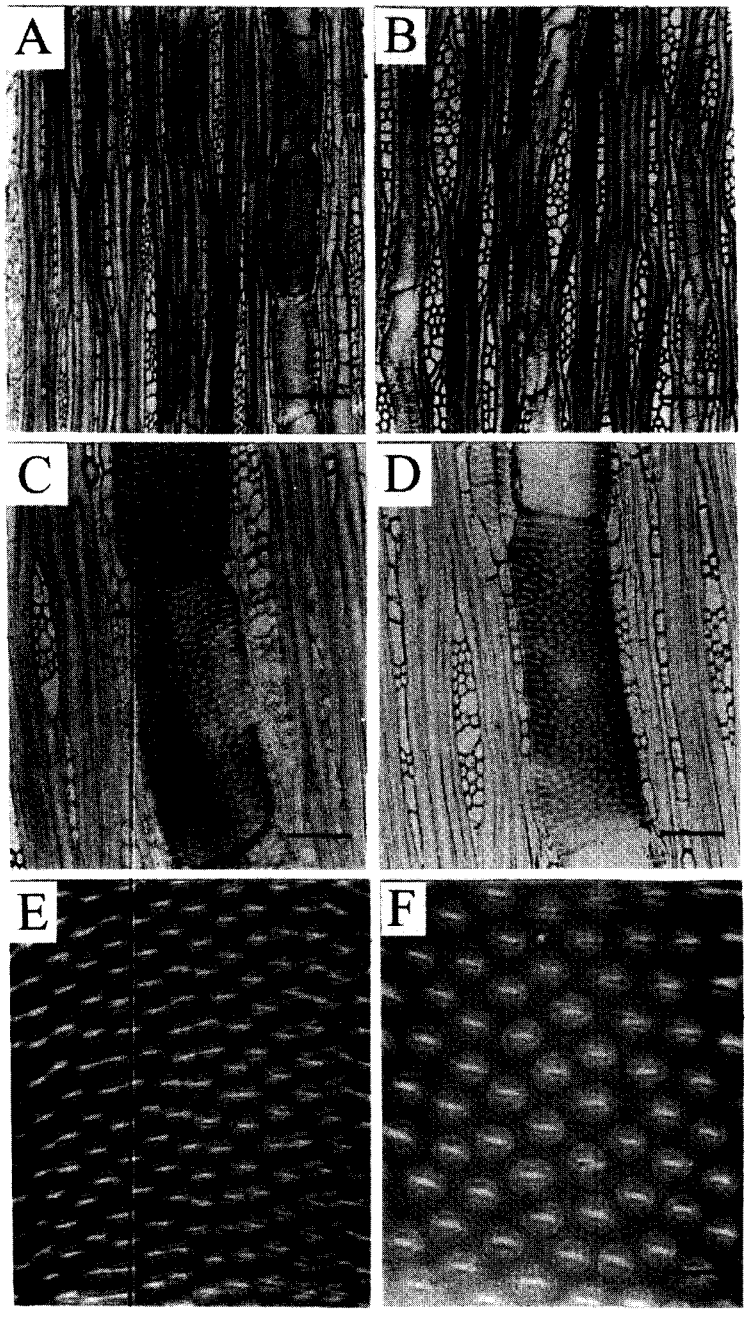

Plate 2 *Grewia*. Tangential longitudinal sections showing rays, axial parenchyma (A–B) and intervessel pits (C–F)— A & E: *G. occidentalis* (*Zeyher s.n.* = Kw 2843)— B: *G. polygama* (*Chung RC 5*)— C–D & F: *G. polygama* (*Chung RC 10*)— Bar equals 10 µm in E–F; 50 µm in C–D; 100 µm in A–B.

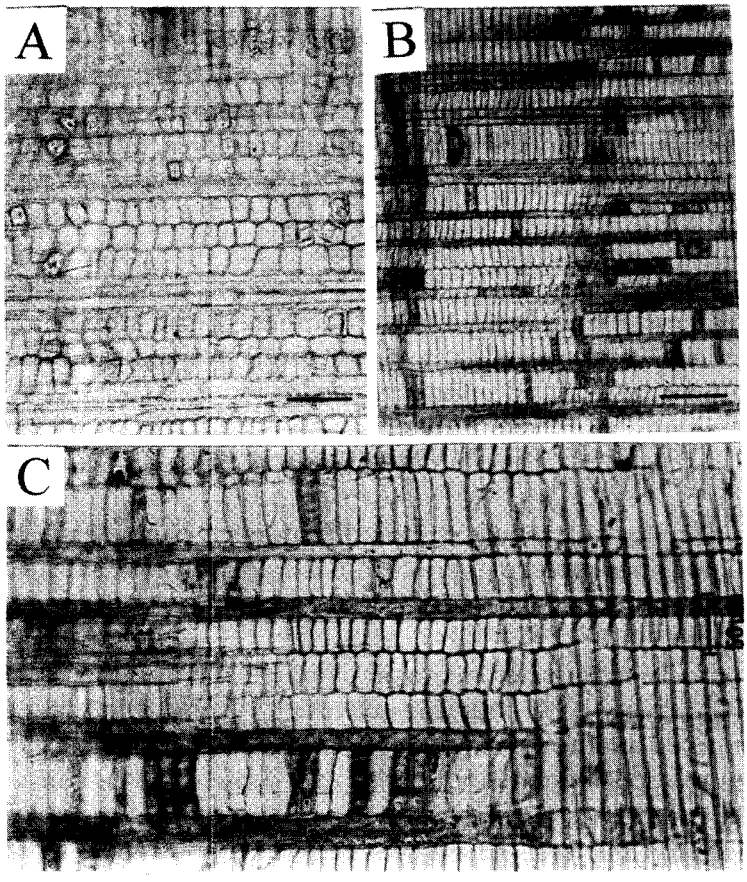

Plate 3 *Grewia.* Radial longitudinal sections showing prismatic crystals (A), cellular composition of rays and tile cells of *Pterospermum*-type (B–C)— A: *G. occidentalis* (*Zeyher s.n.* = Kw 2843)— B–C: *G. polygama* (*Chung RC 5*)— Bar equals 50 µm in A & C; 100 µm in B.

Axial parenchyma

Apotracheal parenchyma is present in the form of marginal or in seemingly marginal bands which form a more or less continuous layer of variable width at the margin of the growth ring or one cell wide irregular short zonate bands. Paratracheal parenchyma is predominantly scanty or occasionally vasicentric with narrow sheath around the vessel. Axial parenchyma strand length varies from 3 to 4 cells.

Rays

Rays are multiseriate (2–3(–4) cells wide) and occasionally uniseriate, with a frequency of 11–17(–18) per mm. The uniseriate rays vary from 80 to 230 µm (average 145 µm) in height, and comprise weakly procumbent and upright cells.

The multiseriate rays vary from 90 to 880 μm (average 398 μm) in height and consist of procumbent cells alternating with (1–)2–4 rows of tile cells.

Tile cells belong to the *Pterospermum*-type, i.e. cells are 2–4 times taller than the procumbent cells and 4–6 cells correspond in height to one procumbent cell. Dark-coloured gum-like contents were occasionally observed in the procumbent and upright or square cells.

Crystals

Prismatic crystals are present in chambered and non-chambered axial parenchyma cells and ray cells (more common). Crystal sand was occasionally observed in procumbent and upright ray cells.

Remarks

Apart from minor differences, the wood anatomical characters of the Peninsular Malaysian *G. polygama* conform to those of *G. occidentalis* (type species of the genus), except that the wood of *G. occidentalis* has higher vessel frequency and taller multiseriate rays.

Crystals have been reported in the procumbent and upright/square cells of the wood rays (Chattaway 1956), but this study found that such crystals also occurred in the chambered and non-chambered axial parenchyma.

Tyloses were reported to be present in *Grewia* species (Pearson & Brown 1932, Metcalfe & Chalk 1950), but were found to be absent in *G. polygama* in this study. Likewise, helical thickening of fibres was reported in *G. asiatica* L. by Nair (1987), but found to be absent in *G. polygama* and *G. occidentalis*.

Microcos *L.*

Results for *Microcos* are given in Table 2 and Plates 4–8.

Growth rings

Growth rings in *Microcos* vary from distinct to indistinct (faint) in most species studied. Growth ring boundaries are marked by slightly thicker walls of radially flattened fibres in the latewood as in *M. latifolia* and *M. latistipulata* var. *latistipulata*, or by a combination of flattened latewood fibres and slight differences in the frequency of vessel number between latewood and earlywood as in *M. antidesmifolia* var. *antidesmifolia*, *M. globulifera* and *M. triflora* var. *triflora*. In *M. antidesmifolia* var. *hirsuta*, *M. cinnamomifolia*, *M. crassifolia*, *M. laurifolia* and *M. reticulata*, on the other hand, the growth rings are indistinct or faint and marked by more or less gradual structural changes at their poorly defined boundaries.

Vessels

Wood diffuse-porous. Vessels are solitary and in radial multiples of 2–4(–6), or rarely in clusters of 2–3(–7). In *M. antidesmifolia* var. *hirsuta, M. cinnamomifolia* and *M. latistipulata* var. *latistipulata,* solitary vessels are dominant, while in *M. antidesmifolia* var. *antidesmifolia, M. crassifolia, M. globulifera, M. latifolia, M. laurifolia, M. reticulata* and *M. triflora* var. *triflora,* solitary or radial multiple pattern may be the dominant type.

Solitary vessels are mainly oval in outline, rarely round in all *Microcos* species. Vessel elements have short to long tails up to 330 μm. Average tangential vessel diameters range 113–152 μm (range 120–159 μm). Vessel frequency ranges from 4 to 32 (average 5–19) vessels per mm^2. There are no significant differences in vessel frequency ranges between species. Average vessel element lengths range from 604 to 707 μm (range 400–880 μm). Perforations are simple, mainly in oblique to slightly oblique, or rarely nearly with horizontal end walls.

Intervessel pits are non-vestured, alternate, compactly arranged, numerous and mainly polygonal to rarely oval. Apertures are mainly transversely elliptic to slit-like and small (less than 1 μm in horizontal diameter). Pit apertures with tendency to coalescent are always present in all species of *Microcos.*

Intervessel pit sizes vary from minute to small (1.5–7 μm in horizontal diameter) in *Microcos. Microcos antidesmifolia* var. *antidesmifolia, M. globulifera, M. latistipulata* var. *latistipulata* and *M. reticulata* have intervessel pits of 1.5–4 μm in horizontal diameter, while *M. antidesmifolia* var. *hirsuta, M. cinnamomifolia, M. crassifolia, M. latifolia, M. laurifolia* and *M. triflora* var. *triflora* have horizontal diameters of 2.5–7 μm.

Vessel-ray and vessel-parenchyma pits usually have distinct borders, and are similar to the intervessel pits in arrangement, shape, size and apertures. Scanty gummy dark red deposits are present in some heartwood vessels of *M. latifolia, M. reticulata* and *M. triflora* var. *triflora.*

Tracheids and fibres

Vascular tracheids are absent. Fibres are non-septate and have simple to minutely and distinctly bordered pits, less than 3 μm in diameter, mainly confined to the radial walls. In other words, the ground tissue in *Microcos* is composed exclusively of libriform fibres as defined by Baas (1986). Fibre walls are very thin to medium in thickness in most *Microcos* species contributing to the relatively low wood density. Like other quantitative features, length of fibres varies greatly (900–2200 μm) with an average length of 1166–1615 μm. The fibre-vessel length ratio ranges 1.1–3.5 with ratio of 1.6–3 being the most frequent.

Axial parenchyma

In *Microcos,* the axial parenchyma cells are predominantly apotracheal diffuse, diffuse-in-aggregates, and in marginal or in seemingly marginal bands. Only scanty paratracheal parenchyma cells were observed around the vessels. Axial parenchyma strands are usually 3–5 cells but sometimes are up to 8 cells long.

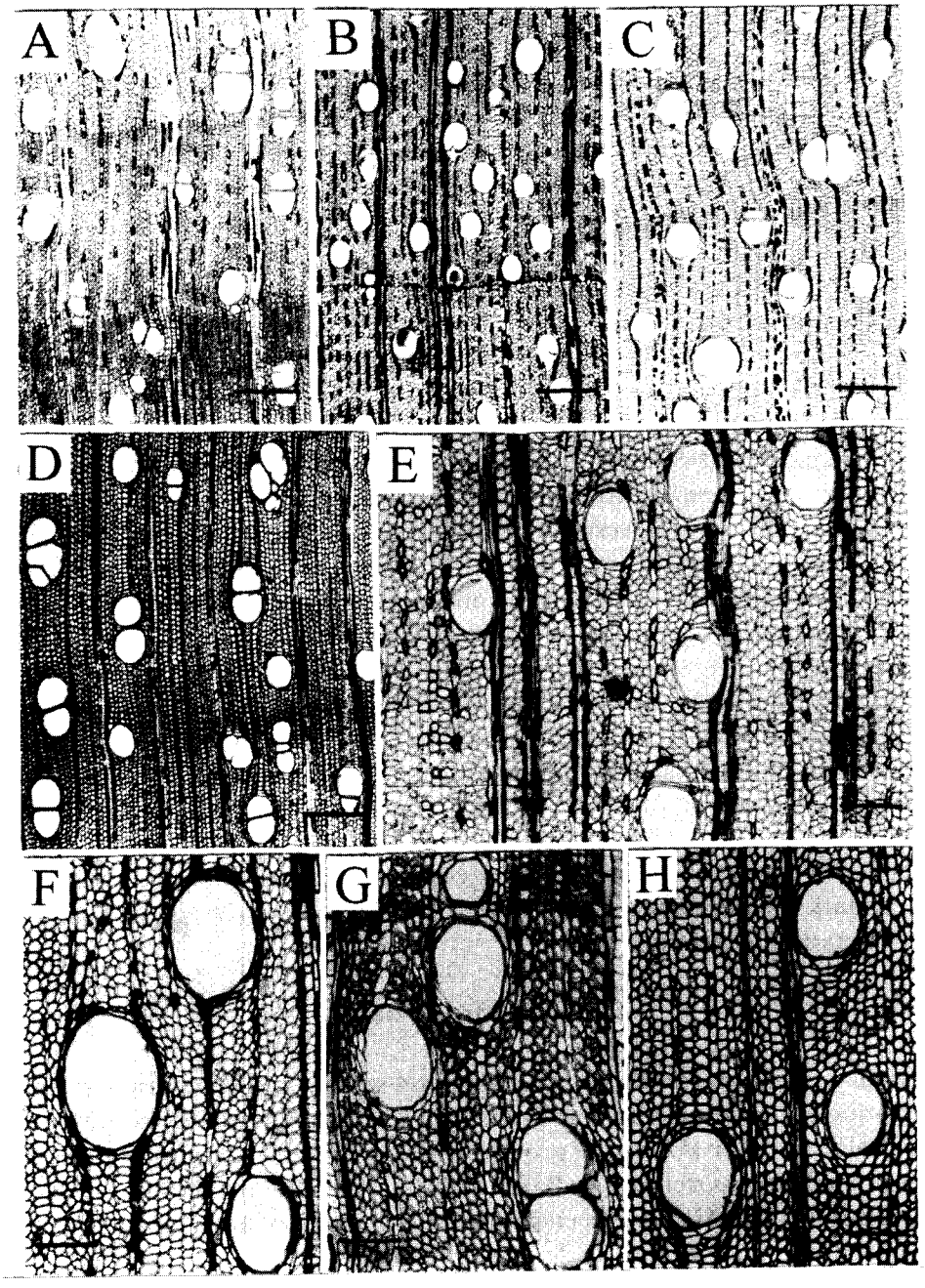

Plate 4 *Microcos.* Transverse sections showing growth rings, vessel distribution, grouping (A–D), and apotracheal diffuse and diffuse-in-aggregates parenchyma (E–H)— A & E: *M. paniculata* (*Majumder & Islam 64A*)— B & G: *M. globulifera* (*Piyee FMS 8036*) — C: *M. latistipulata* var. *latistipulata* (*Termiji SAN 76378*)— D & H: *M. reticulata* (*s.c. FMS 34444*)— F: *M. antidesmifolia* var. *antidesmifolia* (*Mohd. Nur SFN 34308*) Bar equals 2.5 mm in A–D; 100 µm in E–H.

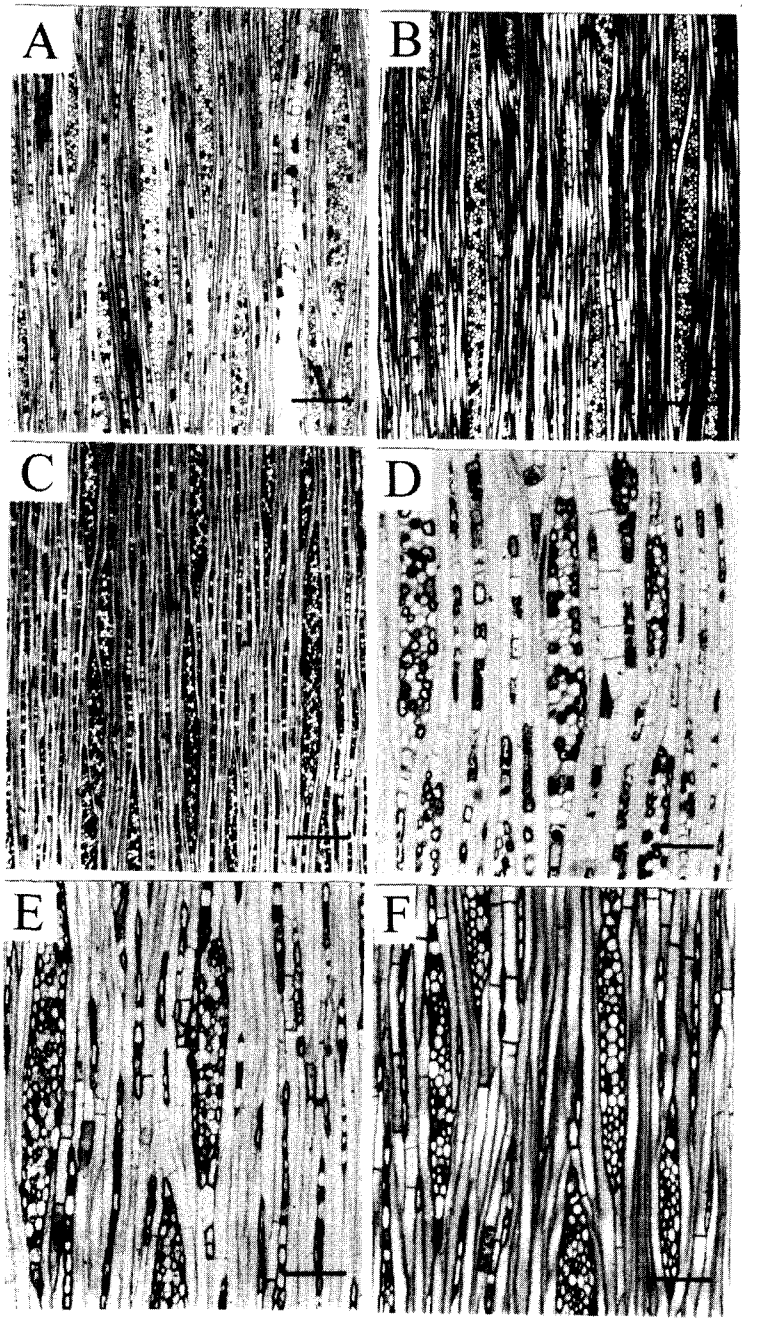

Plate 5 *Microcos.* Tangential longitudinal section showing 1–6(–10)seriate rays and axial parenchyma— A: *M. globulifera* (*Piyee FMS 8036*) — B: *M. latifolia* (*Symington FMS 11959*)— C: *M. laurifolia* (*s.c. KEP 80870*)— D: *M. paniculata* (*Majumder & Islam 64A*)— E: *M. antidesmifolia* var. *antidesmifolia* (*Mohd. Nur SFN 34308*)— F: *M. reticulata* (*s.c. FMS 34444*)— Bar equals 2.5 mm in A–C; 100 μm in D–F.

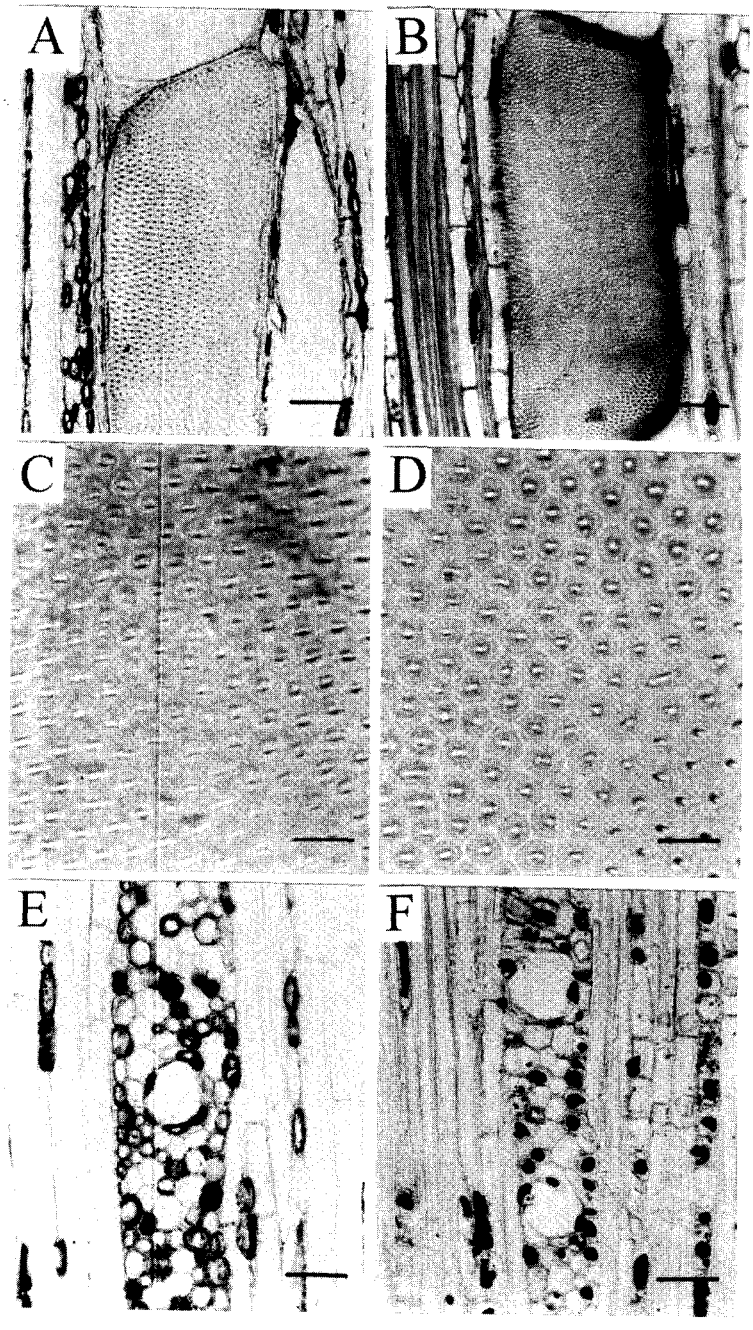

Plate 6 *Microcos*. Tangential longitudinal sections showing intervessel pits (A–D) and intercellular canals with 1–2 radial canals in a ray (E–F)— A & D: *M. crassifolia* (*Termiji & Bungsu SAN 75820*)— B: *M. globulifera* (*Piyee FMS 8036*)— C: *M. paniculata* (*Majumder & Islam 64A*)— E: *M. reticulata* (*Ahmad & Termiji SAN 68352*) — F: *M. triflora* var. *triflora* (*Wood & Kadir SAN 17212*)— Bar equals 10 μm in C–D; 50 μm in A–B and E–F.

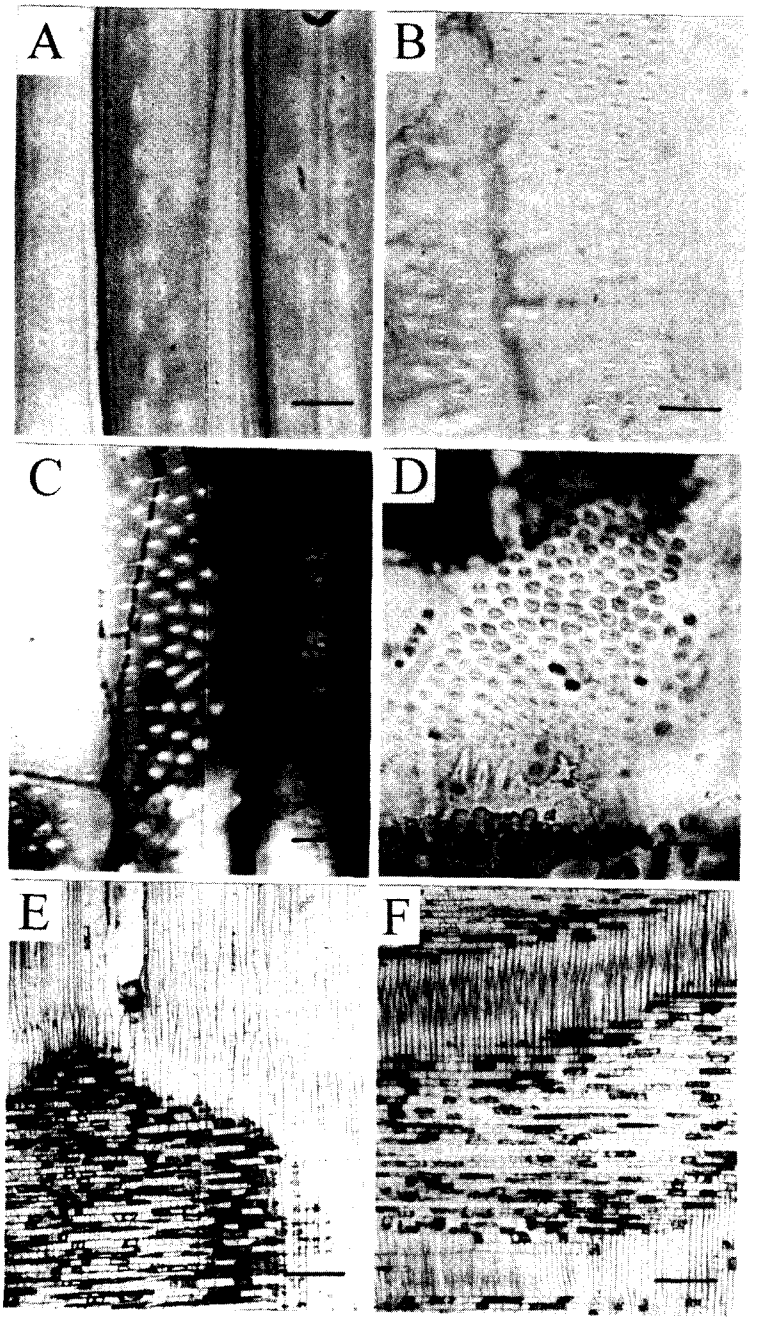

Plate 7 *Microcos*. Radial tangential sections showing fibres with bordered pits with chambers over 3 µm in diameter (A), vessel-ray and vessel parenchyma pits with distinct border (B–D), and cellular composition of rays and axial parenchyma on radial surface (E–F)— A: *M. antidesmifolia* var. *antidesmifolia* (*Mohd. Nur SFN 34308*)— B & F: *M. globulifera* (*Piyee FMS 8036*)—C: *M. latifolia* (*Symington FMS 11959*)—D: *M. reticulata* (*Ahmad & Termiji SAN 68352*)—E: *M. antidesmifolia* var. *hirsuta* (*Kadir SAN A 2893*)— Bar equals 2.5 mm in E–F; 10 µm in A–D.

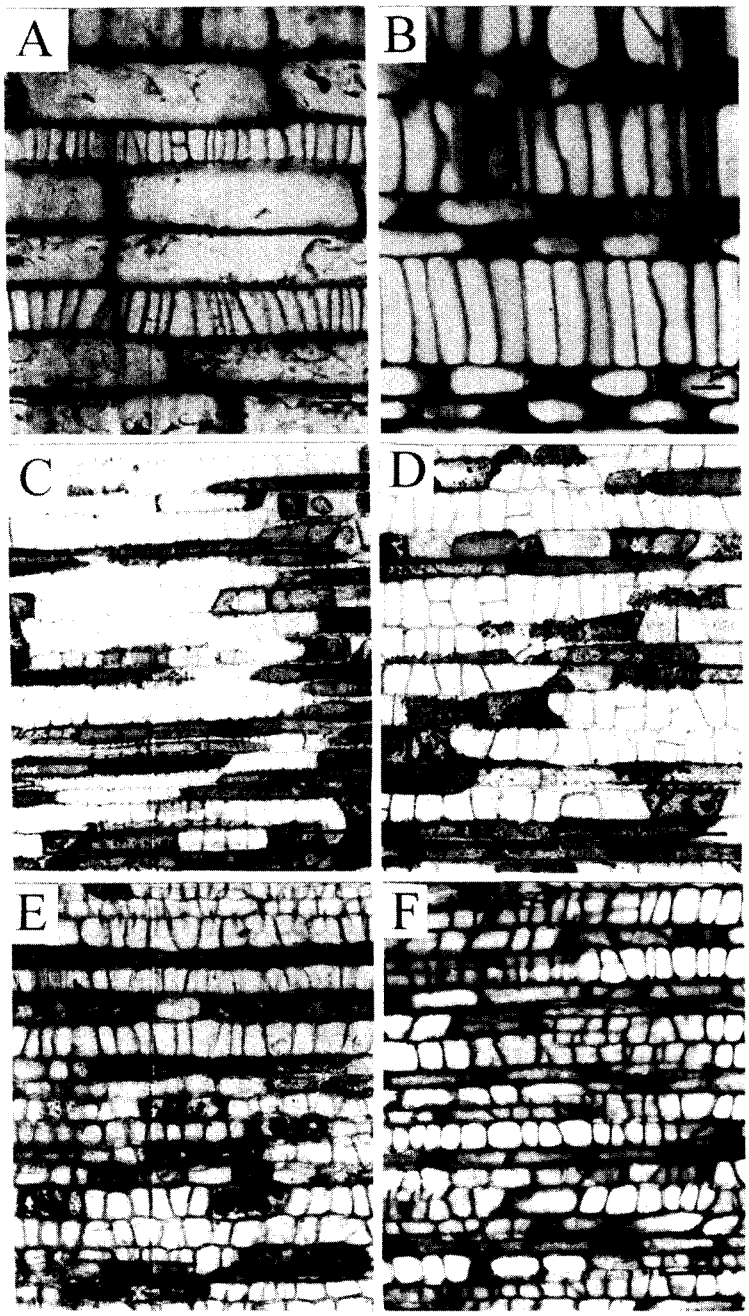

Plate 8 *Coelostegia, Microcos* and *Pterospermum.* Radial tangential sections showing tile cells of *Durio*-type (A), *Pterospermum*-type (B) and intermediate to *Durio*-type (C–F)— A: *C. griffithii* (*Yusof FMS 4222*)— B: *P. javanicum* (*de Zylva FMS 5699*)— C: *M. antidesmifolia* var. *antidesmifolia* (*Mohd. Nur SFN 34308*)— D: *M. antidesmifolia* var. *hirsuta* (*Kadir SAN A 2893*)— E: *M. globulifera* (*Piyee FMS 8036*)— F: *M. latifolia* (*Symington FMS 11959*)— Bar equals 10 μm in A–B; 50 μm in C–F.

Rays

Rays vary tremendously in size and composition. Rays are composed of procumbent cells, alternating with tile cells and (1–)2–4 rows of upright to square marginal cells, usually without well-differentiated sheath cells. Rays of two distinct sizes can be recognised in *Microcos*: uniseriate and multiseriate (2–10-seriate). Uniseriate rays range from 150 to 1180 µm in height with an average of 314–626 µm. The height of multiseriate rays varies from 280 to 3630 µm with an average range 798–1611 µm. Ray frequency varies between 8 and 18 per mm.

In *Microcos*, the tile cells are slightly taller than the procumbent cells but with 3–6 tile cells corresponding to one procumbent cell. The tile cells are neither the *Durio*- nor *Pterospermum*-type, but they belong to the tile cells of intermediate to *Durio*-type as defined by Manchester and Miller (1978).

Dark-coloured gum-like contents are always present in the procumbent and upright cells.

Crystals

Prismatic crystals are absent in *M. cinnamomifolia, M. globulifera, M. laurifolia* and *M. reticulata*, but present in *M. antidesmifolia* (both varieties), *M. crassifolia, M. latifolia, M. latistipulata* var. *latistipulata* and *M. triflora* var. *triflora*. In *M. antidesmifolia* var. *hirsuta, M. crassifolia, M. latifolia* and *M. triflora* var. *triflora*, prismatic crystals are always present in upright and procumbent ray cells. In *M. antidesmifolia* var. *antidesmifolia* and *M. latistipulata* var. *latistipulata*, prismatic crystals are present in the ray cells as well as in the non-chambered axial parenchyma cells.

Remarks

The wood anatomy in the species examined matches that of *M. paniculata* (type species of the genus) from Pakistan and other species from India, Thailand, Java and the Philippines (Moll & Janssonius 1906, Kanehira 1924, Pearson & Brown 1932, Reyes 1938, Boer & Sosef 1998).

Intercellular canals (i.e. radial canals) are present in some of the broad rays of *M. reticulata* (*Ahmad & Termiji SAN 68352*) and *M. triflora* var. *triflora* (*Wood & Kadir SAN 17212*) from Borneo but absent in the rays of *Grewia* (including *G. occidentalis*) and *M. paniculata*. Such canals have not been observed in either the family Tiliaceae or the order Malvales (IAWA Committee 1989; Plates 6E–F).

Discussion

There are significant differences in some wood anatomical features between *Grewia polygama* and *Microcos* in Peninsular Malaysia and Borneo. The main morphological differences are summarised in Table 3. To some extent, this study supports the views by Burret (1926) and Chattaway (1934).

Table 3 Main differences between wood anatomy of *Grewia polygama* and *Microcos* species in Peninsular Malaysia and Borneo

Characters	*Grewia polygama*	*Microcos* spp.
Vessel		
Outline	Usually round, sometimes oval	Usually oval, rarely round
Intervessel pit arrangement	Loosely arranged, few	Compactly arranged, numerous
Intervessel pit shape	Round, rarely oval	Polygonal, rarely oval
Intervessel pit aperture	Large, 1–2 μm in horizontal diameter	Small, < 1 μm in horizontal diameter
Axial parenchyma		
Apotracheal	In marginal or seemingly marginal bands	Predominantly diffuse, diffuse-in-aggregates, and in marginal or in seemingly marginal bands
Paratracheal	Predominantly scanty or rarely vasicentric with narrow sheath around the vessel	Only scanty paratracheal parenchyma cells observed around the vessels
Rays		
Uniseriate	Rare	Common
Tile cells	*Pterospermum*-type	Intermediate to *Durio*-type

Although round and oval solitary vessels are found in both genera, the round ones are predominant in *Grewia* (including *G. occidentalis*), while the oval ones are predominant in *Microcos* (including *M. paniculata*). This observation agrees with reports by previous authors, such as Kanehira (1924), Chattaway (1934), Phengklai (1998), and Boer and Sosef (1998).

Grewia has the lower vessel element length, while in contrast, *Microcos* has the higher vessel element length. For *Grewia*, Pearson and Brown (1932) observed similar values of the vessel element lengths as found in this study. However, Kanehira (1924) reported that *M. triflora* from the Philippines had significantly different higher values of vessel element lengths than observed in this study. This shows that vessel element length varies considerably within any species and even in different parts of the same tree. Vessel element length is seldom used for identifying timbers, but it is much more significant as a measure of phylogenetic status (Chalk 1983).

Vessel diameter is a very useful diagnostic feature and it is best expressed as a mean figure for the tangential diameter. For *Grewia*, however, Pearson and Brown (1932) reported the largest vessel diameter range in four species from India than found in this study. In contrast, Reyes (1938) reported similar vessel diameter range and mean as found in this study. The vessel diameter varies in wood taken from different positions in a tree and also in wood samples of a species of tree grown under different conditions (Chalk 1983). For *Microcos*, the range found in this study is within that recorded for *Microcos* by Metcalfe and Chalk (1950), Kanehira (1924) and Reyes (1938).

The vessel frequency, although useful, is often difficult to determine. For *Grewia*, Pearson and Brown (1932) and Phengklai (1998) observed lower values of the vessel frequency than found in this study. In *Microcos*, however, Reyes (1938),

Metcalfe and Chalk (1950), and Boer and Sosef (1998) reported similar values of the vessel frequency as found in this study.

This study provides additional wood anatomical characters, such as the intervessel pit arrangement, shape, aperture size and types, and vascular tracheids, which were not reported by the previous authors (Moll & Janssonius 1906, Pearson & Brown 1932, Chattaway 1934, Reyes 1938, Metcalfe & Chalk 1950, Desch 1954, Phengklai 1998). In contrast, Pearson and Brown (1932) observed that the intervessel pits were numerous, round or oval to polygonal and occasionally with coalescent apertures in four species of *Grewia* from India.

Based on fibre-vessel length ratio (F/V ratio), Kukachka and Rees (1943) proposed nine generic groupings in the family Tiliaceae. They placed *Microcos* together with *Colona* Cav., *Goethalsia* Pittier and *Luehea* Willd. in 'Group III; F/V ratio = 2.6–4.46', and *Grewia* together with *Vinticena* Steudel in 'Group VI; F/V ratio = 3.06–4.22'. The generic grouping based on the F/V ratio proposed by them was very similar to the taxonomic grouping proposed by Burret (1926) based on gross morphology and Bayer *et al.* (1999) based on molecular data.

Paratracheal vasicentric axial parenchyma reported in *Grewia* by Reyes (1938), Metcalfe and Chalk (1950), Desch (1954), Fahn *et al.* (1986) and Phengklai (1998), was only occasionally observed in this study. Nevertheless, observations of the axial parenchyma features in both genera and their type species (this study) agree with those reported by Pearson and Brown (1932), Chattaway (1934), Reyes (1938), Metcalfe and Chalk (1950), Desch (1954), Menon (1971), Phengklai (1998), and Boer and Sosef (1998). These wood anatomical characters are, therefore, taxonomically useful to distinguish species of *Grewia* from those of *Microcos*.

Rays of two distinct sizes are present in *Microcos* (including *M. paniculata*) but absent in *Grewia* (including *G. occidentalis*). Kanehira (1924), Pearson and Brown (1932), Chattaway (1934), Reyes (1938), Metcalfe and Chalk (1950), Desch (1954), Menon (1971), Phengklai (1998), and Boer and Sosef (1998) reported ray features of *Grewia* and *Microcos* similar to the ones observed in this study. Reyes (1938), on the other hand, observed only the multiseriate rays in *Grewia* species from the Philippines. However, this study confirms the observation of Chattaway (1934) that ray cells in *Grewia* species consist of both uniseriate (uncommon) and multiseriate rays (common). Uniseriate and biseriate as well as multiseriate rays were found in species of *Microcos* from Peninsular Malaysia and Borneo.

Chattaway (1933, 1934) classified tile cells into two groups, i.e. *Durio*-type (in *Coelostegia* Benth. and *Durio* Adans) and *Pterospermum*-type (in *Pterospermum* Schreber.). In *Grewia*, the tile cells belong to the *Pterospermum*-type (Chattaway 1934, Reyes 1938, Metcalfe & Chalk 1950, Desch 1954, Sudo 1963, Phengklai 1998). This type of tile cells observed in *G. polygama* (this study) had been reported by Moll and Janssonius (1906) and Janssonius (1950) in *G. celtidifolia, G. eriocarpa, G. excelsa* and *G. laevigata* from Java, as well as by Chattaway (1934) in *G. elastica, G. multiflora* Juss., *G. oppositifolia, G. rolfei* Merr., *G. rothii* DC., *G. tenax* (Forsk.) Aschers. & Schwf., *G. tiliifolia* and *G. vestita* Wall. from India and tropical Africa.

Previous authors (Chattaway 1934, Reyes 1938, Desch 1954, Ogata 1981, Sudo 1988) reported that tile cells of *Microcos* species belonged to the *Durio*-type. Menon (1971), however, stated that the *Pterospermum*-type of tile cells occurred in eight

species of *Grewia s.l.* (all these species are now recognised as *Microcos*) from Malaysia. Moll and Janssonius (1906) and Janssonius (1950), in their studies of four species of *Grewia* and one species of *Microcos* (*G. microcos* = *M. paniculata*) from Java, did not observe any typical tile cell in *Grewia* or *Microcos*, but considered the wood of *G. microcos* (= *M. paniculata*) sufficiently different from that of the other four species of *Grewia*.

In addition to these two extreme types of tile cells, Chattaway (1933) and Manchester and Miller (1978) recognised at least two intermediate types, i.e. tile cells of intermediate to *Durio*-type (in *Guazuma* Miller) and tile cells of intermediate to *Pterospermum*-type (in *Reevesia* Lindley). Watari (1952), Suzuki (1976), and Manchester and Miller (1978) confirmed that the tile cells of intermediate to *Pterospermum*-type were found in three Malvalean fossil wood samples of *R. miocenica*, *R. oligocenica* and NBW-50 respectively. This study confirmed the occurrence of tile cells of intermediate to *Durio*-type in 10 species of *Microcos* from Peninsular Malaysia, Borneo and Pakistan.

Dark-coloured gum-like contents were frequently observed in the upright and/or procumbent cells of *Microcos* (including *M. paniculata*) but were uncommon in *Grewia* (including *G. occidentalis*). Metcalfe and Chalk (1950) and Kanehira (1924) reported the occurrence of dark gummy contents in the upright or procumbent cells in *Microcos* and *G. stylocarpa* (= now *M. triflora*) respectively.

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