

Leaf Epidermal Micromorphology of *Grewia* L. and *Microcos* L. (Tiliaceae) in Peninsular Malaysia and Borneo

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Abstract

Leaf epidermal morphology of 5 species of *Grewia* L. and 32 species of *Microcos* L. (including their type species) were examined. *Grewia* and *Microcos* both have glandular and non-glandular trichomes. Trichome characters alone cannot be used for delimiting *Grewia* from *Microcos* or for distinguishing species within each genus. Five epidermal characters were useful for distinguishing the two genera in Peninsular Malaysia and Borneo. *Grewia* species differ from *Microcos* species in having radiating cuticular striation of epidermal/subsidiary cells, predominantly anomocytic stomata, stomata elliptic to broadly elliptic in outline with mean length 18.6–22.9 μm and average length-width (L/W) ratios of 1.2–1.4. The *Microcos* species were characterised by the absence of radiating cuticular striation of epidermal/subsidiary cells (except in *M. tomentosa*), predominantly paracytic and anisocytic stomata, stomata broadly elliptic to oblate in outline with mean length 12–16.4 μm and average L/W ratios of 0.9–1.1.

Introduction

The genus *Grewia* consists of about 200 species of small trees and shrubs or rarely scandent shrubs, distributed from tropical Africa northwards to the Himalayas, China and Taiwan, south eastwards to India, Sri Lanka, Myanmar, Thailand, Indo-China, Malesia, Tonga, Samoa and the northern parts of Australia. In Malesian region about 30 species are known, of which 4 occur in Peninsular Malaysia and Borneo. *Microcos* is a genus of about 80 species of trees and shrubs, occurring in tropical Africa, India, Sri Lanka, Myanmar, Indo-China, S China, Hainan, Thailand, and throughout Malesia except for the Lesser Sunda Islands. In Malesia, some 42 species are known, of which 31 occur in Peninsular Malaysia and Borneo (Boer and Sosef, 1998; Phengklai, 1998; Chung, 2001). For species in Peninsular Malaysia and Borneo, a total of 13 macromorphological characters have been identified as diagnostic for distinguishing *Microcos* species from those of *Grewia* (Chung, 2001).

The taxonomic value of leaf epidermal structures is well documented (Wilkinson, 1979; Theobald *et al.*, 1979). In the order Malvales, to which

the Tiliaceae belong, epidermal characters, particularly the type and distribution of trichomes and stomata, are reported useful for delimiting and/or distinguishing taxa at subfamily levels (Metcalf and Chalk, 1950; Inamdar and Chohan, 1969; Rao and Ramayya, 1977; 1983; Inamdar *et al.*, 1983; Salma, 1999).

Work on organography as well as taxonomic significance of leaf epidermal characters in the order Malvales is meagre (Solereder, 1908; Metcalfe and Chalk, 1950). In the Tiliaceae, studies on the taxonomic significance of epidermal characters are very scanty and limited to very few genera from India, i.e. *Berrya* (Inamdar *et al.*, 1983; 1 species), *Corchorus* (Rao and Ramayya, 1981; 1984; 1987; Inamdar *et al.*, 1983; Rao, 1990; Sharma, 1990; Singh and Dube, 1993; 8 species), *Grewia* (Tiwari, 1978; Rao and Ramayya, 1981; 1984; 1987; Inamdar *et al.*, 1983; Sharma, 1990; 32 species), *Microcos* (Inamdar *et al.*, 1983; Sharma, 1990; 1 species), *Triumfetta* (Rao and Ramayya, 1981; 1984; 1987; Inamdar *et al.*, 1983; Rao, 1990; Sharma, 1990; 5 species).

Likewise, the significance of trichomes in plant systematics has long been recognised in the classification of angiosperms (Davis and Heywood, 1963; Edmonds, 1982). Previous studies on the trichome morphology and distribution in the Tiliaceae were conducted by Metcalfe and Chalk (1950), Kostermans (1972), Morawetz (1981), Rao and Ramayya (1987), Rao (1990), and Sharma (1990).

The aim of the present study is to investigate the micromorphological variability of the leaf epidermis and to assess its taxonomic significance in the Peninsular Malaysian and Bornean *Grewia* and *Microcos*.

Materials and methods

Most leaf material investigated was obtained from herbarium specimens available at the Forest Research Institute Malaysia (KEP), unless stated otherwise (herbarium abbreviations as in Holmgren *et al.*, 1990). The species and specimens studied are listed in the Appendix.

Fully developed leaves were selected from dried herbarium specimens. For each leaf, an area from the middle of the lamina, including midrib and leaf margin, was taken. All material was rehydrated in water prior to cuticular maceration in Jeffrey's solution (a mixture of equal volumes of 10% chromic acid and concentrated nitric acid), stained in a solution of Sudan IV in alcohol 70% and mounted in glycerin-jelly. For scanning electron microscopy (SEM), samples of dried leaf specimens (adaxial and abaxial surfaces) were directly mounted on stubs and coated with gold and observed under a JOEL JSM-6400 scanning electron microscope.

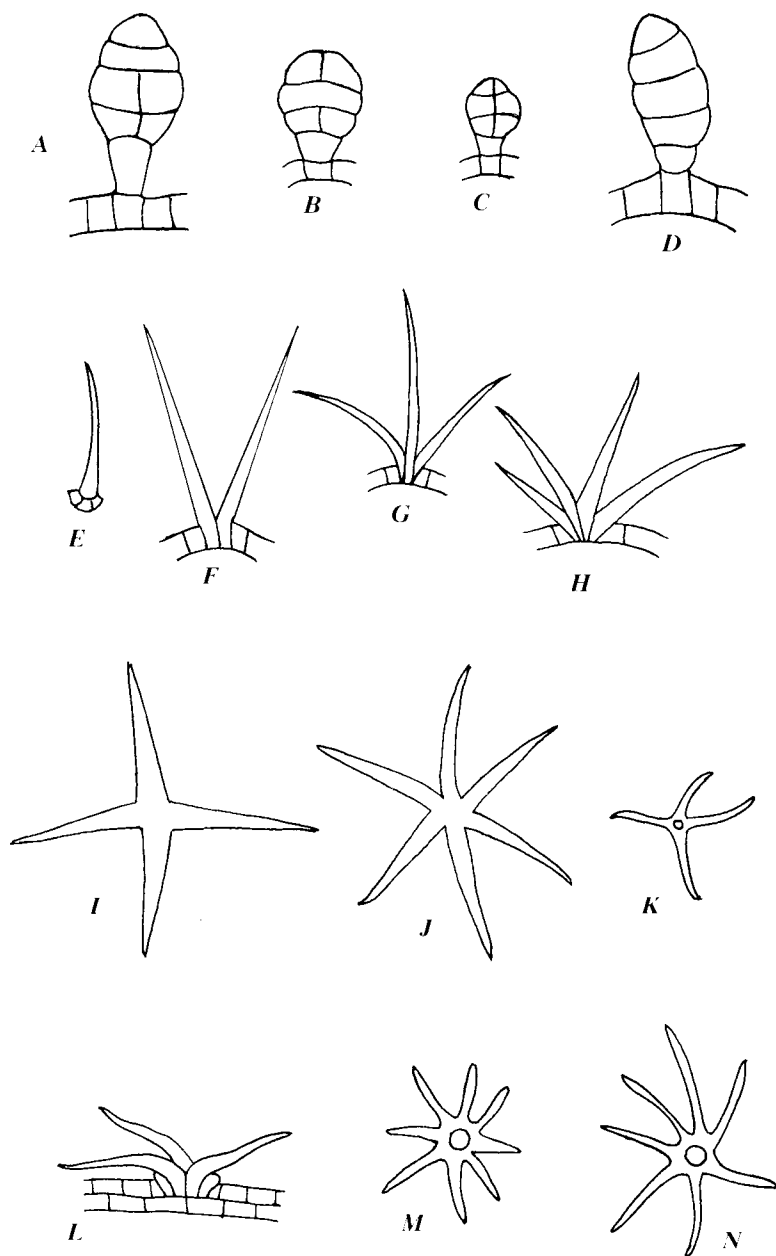


Figure 1. Trichome types in *Grewia* and *Microcos*.

A. short unicellular stalk with multicellular elliptic glandular head; **B.** short unicellular stalk with multicellular broadly elliptic glandular head; **C.** short unicellular stalk with multicellular rounded glandular head; **D.** short unicellular stalk with multicellular oblong glandular head; **E.** simple; **F.** 2-armed tufted; **G.** 3-armed tufted; **H.** 4-armed tufted; **I.** 4-armed stellate; **J.** 6-armed stellate; **K.** 4-armed cushioned stellate; **L.** 4-armed cushioned stellate; **M.** 8-armed cushioned stellate; and **N.** 7-armed cushioned stellate trichomes.

Table 1. Leaf epidermal characters in *Grewia* and *Microcos*

Column:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Species																	
<i>Grewia</i>																	
<i>occidentalis</i> (type species)	se	se	st	a	e/h	s	a	d	-	-	-	-	-	-	+	+	s
<i>luduperakensis</i>	se	se	st	a	e/h	s	h	d	+	++	+	+++	-	-	++	++	s
<i>laevigata</i>	se	se	st	a	e/h	s	h	d	+/-	+/-	-	-	+/-++	++/-+++	+	+	s/l
<i>multiflora</i>	se	se	st	a	h	s	h	d	+/-	++	+++	-	-	-	+	+	s
<i>polygama</i>	se	se	st	a	h	r	a	d	+/-	+/++++	+	-	-	++/-+++	+	++	s
<i>Microcos</i>																	
<i>paniculata</i> (type species)	u	se	st	p/n	b/r/o	r	h	d	-	-/+	-	-	+	+	+	+	l
<i>amidesmifolia</i> var. <i>amidesmifolia</i>	se	se	-	p/n	b/r/o	s	h	d	-	-	-	-	-	-	+	+	l
<i>antidesmifolia</i> var. <i>hirsuta</i>	se	se	-	p/n	b/r/o	s	a	d	-/+	++	+	+/++	-	++	-	+	l
<i>borneensis</i>	se	se	-	p/n	b/r/o	s	h	d	-	-/+	-	-	-	-	-/+	-/+	s
<i>cinnamomifolia</i>	se	se	-	p/n	b/r/o	s	h	d	-	-/+	-	-	-	-	-	+	l
<i>crassifolia</i>	se	u	-	p/n	b/r/o	s	h	d	-	-	-	-	-	-	+	+	l
<i>dulitensis</i>	u	u	-	p/n	b/r/o	r	h	d	-/+	++	+	++	-	-	+	+	l
<i>erythrocarpa</i>	se	se	-	p/n	b/r/o	s	h	d	-/+	-/+	++	+/+++	-	-	++	++	l
<i>fibrocarpa</i>	u	se	-	p/n	b/r/o	s	h	d	+	+/+	+++	++/+++	-	-	+	+	l
<i>globulifera</i>	se	se	-	p/n	b/r/o	s	h	g	+	+/+	+++	++/+++	-	-	+	++	l
<i>gracilis</i>	u	u	-	p/n	b/r/o	s	a	d	+	+/+	-	-	-	++	+	+	l
<i>henrici</i> var. <i>acuta</i>	se	se	-	p/n	b/r/o	s	h	d	-/+	-/+	+	-	-	+++	+	++	l
<i>hirsuta</i>	se	u	-	p/n	b/r/o	s	h	d	-/+	++	+++	-	-	++/+++	+	+	l
<i>kinabaluensis</i>	se	se	-	p/n	b/r/o	s	h	g	-	-	-	-	-	-	-	-	-
<i>lanceolata</i>	se	se	-	p/n	b/r/o	s	h	d	-/+	-/+	-	-	-	+++	+	+	l
<i>laurifolia</i>	se	u	-	p/n	b/r/o	s	a	d	++	-/+	+++	++	-	-	+	+	l
<i>laustipulata</i> var. <i>laustipulata</i>	se	se	-	p/n	b/r/o	s	h	d	-	-	-	-	-	-	+	+	l
<i>laurifolia</i>	se	se	-	p/n	b/r/o	s	h	d	-/+	-/+	-	-	-	+++	-	+	l
<i>malayana</i>	u	u	-	p/n	b/r/o	r	h	d	-/+	++	+++	++	-	-	+	+	l
<i>membranifolia</i>	se	se	-	p/n	b/r/o	s	h	d	-/+	-/+	+	-	-	+++	-/+	-/+	l
<i>opaca</i>	se	u	-	p/n	b/r/o	s	h	d	-/+	-/+	+++	+/++	-	-	+	+	l
<i>ossea</i>	se	se	-	p/n	b/r/o	s	h	d	-	-/+	++	-	+++	-	+	+	s
<i>pachyphylla</i>	se	u	-	p/n	b/r/o	s	h	g	-	-	-	-	-	-	-	+	l
<i>pearsonii</i>	u	u	-	p/n	b/r/o	s	h	d	-/+	-/+	-	-	+++	-	++	+	l
<i>phaneroneura</i>	se	u	-	p/n	b/r/o	r	h	d	++	+++	+++	-	++	++/+++	++	+	l
<i>reticulata</i>	u	u	-	p/n	b/r/o	s	h	d	++	+++	++	+/++	-	++	++	++	l
<i>riparia</i>	se	se	-	p/n	b/r/o	s	h	g	-	-/+	-	-	-	+++	+	+	l
<i>stylocarpoides</i>	se	se	-	p/n	b/r	s	h	d	-/+	-/+	-	-	-	+++	+	+	l
<i>subcordifolia</i>	se	u	-	p/n	b/r/o	s	h	d	+	+	++	-	-	+++	+	+	l
<i>subpetala</i>	se	se	-	p/n	b/r/o	s	a	g	-	-/+	-	-	-	+++	++	++	l
<i>sumatrana</i>	u	u	-	p/n	b/r/o	s	a	d	-	++	-	-	-	+++	++	++	l

Column:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Species																	
<i>Microcos</i>																	
<i>tomentosa</i>	sc	sc	st	p/n	b/r/o	r	a	g	-/+	+++	-	-	-	+++	++	++	1
<i>triflora</i> var. <i>triflora</i>	sc	sc	-	p/n	b/r/o	s	h	d	-	-	-	-	-	-	-	+	s
<i>triflora</i> var. <i>longipetiolata</i>	sc	sc	-	p/n	b/r/o	s	h	d	-	-	-	-	-	-	-	+	1

Legend: / = or; + = present; - = absent; +++ = dense; ++ = moderately dense; + sparse; - = absent.

Columns:

1. Sinuosity of anticlinal cell wall of adaxial epidermis (u = undulate; sc = straight or curved)
2. Sinuosity of anticlinal cell wall of abaxial epidermis
3. Radiating cuticular striation (st = striated)
4. Predominant type of stomata on abaxial epidermis (a = anomocytic; n = anisocytic; p = paracytic)
5. Shape of stomata in outline (e = elliptic; b = broadly elliptic; r = rounded; o = oblate)
6. Elevation of stomata in relation to epidermis (s = same level; r = raised)
7. Stomatal distribution (h = hypostomatous; e = epistomatous; a = amphistomatous)
8. Pattern of stomatal distribution (d = random; g = regular)
9. Occurrence of non-glandular trichome on the adaxial epidermis
10. Occurrence of non-glandular trichome on the abaxial epidermis
11. Frequency of simple trichomes
12. Frequency of tufted trichomes
13. Frequency of stellate trichomes
14. Frequency of cushioned stellate trichomes
15. Occurrence of glandular trichome on the adaxial epidermis
16. Occurrence of glandular trichome on the abaxial epidermis
17. Body/stalk of glandular trichome (s = sessile; 1 = short unicellular).

Micrographs were made of both trichomes and stomata.

The pattern of stomatal distribution was classified as random (i.e., low density of stomata distributed randomly without regular pattern) or regular (i.e., high density of stomata in a regular pattern). Stomatal sizes were measured directly using a calibrated linear eyepiece micrometer. Density mm^{-2} was counted from 25 unit areas on the abaxial surface and stomatal index was determined using the formula adapted from Wilkinson (1979: 114). Trichomes were observed in epidermal peels as well as stereoscopic observations of herbarium specimens. The descriptive terminology of epidermal features is based on Van Cotthem (1970); Radford *et al.* (1974); Wilkinson (1979); Theobald *et al.* (1979) and Baranova (1987). Trichome types are illustrated in Fig. 1 and leaf epidermal characters are summarised in Table 1.

Results

GREWIA L.

(Figure 1; Plates 1 and 2; Table 1)

Stomatal Complex

Epidermal and subsidiary cells

In the species investigated, the anticlinal walls of the epidermal cells on both the leaf adaxial and abaxial surfaces are straight. This particular character, therefore, has no taxonomic value for distinguishing *Grewia* species.

Cuticular striation occurs only on the epidermal cells adjacent to the stomata. The striae radiating from the external edges of guard cells are either long (*G. occidentalis*, *G. huluperakensis* and *G. multiflora*) or, less frequently, short (*G. laevigata* and *G. polygama*).

Stomata

The stomata are mostly surrounded by a limited number of unspecialised cells that are indistinguishable in size and shape from the epidermal cells. However, a few stomata are occasionally accompanied on either side by one or more subsidiary cells parallel to the long axis of the pore and guard cells. Hence, the majority of the stomata are anomocytic or very rarely anisocytic and paracytic types.

The stomatal outline varies from elliptic, broadly elliptic to rarely rounded (*G. huluperakensis* and *G. laevigata*) to exclusively broadly elliptic (*G. multiflora*) or broadly elliptic to rarely rounded (*G. polygama*). The stomata are elevated slightly above the surrounding epidermal cells in *G. polygama*, but positioned at the same level in the other three species.

The stomata are 15–27.2 μm long and 12–22.4 μm wide with a mean length of 18.6 μm in *G. polygama*, 19.5–19.8 μm in *G. huluperakensis* and *G. multiflora*, and 22.9 μm in *G. laevigata*. Mean width ranges from 14.4–15.2 μm in *G. huluperakensis*, *G. multiflora* and *G. polygama* to 17 μm in *G. laevigata*. The range of length-width ratios (L/W) is (1–)1.2–1.4(–1.7).

Stomata distribution

Leaves are either hypostomatous (with stomata restricted to the abaxial surface) in *G. huluperakensis*, *G. laevigata* and *G. multiflora* or amphistomatous (stomata on both sides) in *G. polygama*. In all four species, the stomata are randomly distributed.

The stomatal density ranges from 80 to 180 mm^{-2} , with means ranging from 95 to 157 mm^{-2} . In *G. laevigata*, the stomatal density, (80–)95(–120), is slightly lower than that of *G. huluperakensis*, *G. multiflora* and *G. polygama*, (136–)147–157(–180). Stomatal index ranges between 11.3 and 29, with a mean of 14.1 in *G. laevigata* and 25.9–27.3 in *G. huluperakensis*, *G. multiflora* and *G. polygama*.

Trichomes

Non-glandular trichomes

On the adaxial leaf surface, non-glandular trichomes are sparse in *G. huluperakensis*, and sparse to none in *G. laevigata*, *G. multiflora* and *G. polygama*. On the abaxial surface, dense to moderately dense non-glandular trichomes occur in *G. polygama*, and sparse to none in *G. laevigata*. In *G. huluperakensis* and *G. multiflora*, the abaxial surface is moderately densely covered with non-glandular trichomes.

In *Grewia*, four main types and nine subtypes of non-glandular trichomes are recognised (Fig. 1). These are: (i) simple trichomes, which are long and tapered at the tip; (ii) tufted trichomes, which are either 2-, 3- or 4-armed; (iii) stellate trichomes, which are either 4-, 5- or 6-armed and without a central cushion; and (iv) cushioned stellate trichomes, which are 4–8-armed and with a central cushion. The cushioned stellate trichomes are formed by a multicellular hair base (Figure 1L).

These were observed on either the abaxial, adaxial, or both sides of the leaf (Table 1). Simple trichomes are present in *G. huluperakensis* (sparse), *G. multiflora* (dense) and *G. polygama* (sparse), but absent in *G. laevigata*. The 2–4-tufted non-glandular trichomes are dense in *G. huluperakensis*, but are absent in the other species. Four-armed stellate trichomes are sparsely present in *G. occidentalis* (the type species) but absent in the other species, while the 5–6-armed stellate trichomes are present in *G. laevigata* but absent in the others. The 4–8-armed cushioned stellate non-glandular trichomes occur in *G. laevigata* and *G. polygama*.

but are absent in the other species .

Glandular trichomes

Glandular trichomes are present on both leaf surfaces, varying from sparse to moderately dense. Each glandular trichome consists of a multicellular head which is either sessile or with a short unicellular stalk. The outline of the multicellular head can be elliptic as in *G. huluperakensis* and *G. multiflora*, or broadly elliptic as in *G. huluperakensis*, *G. laevigata* and *G. multiflora*, or rounded as in *G. laevigata*, or oblong as in *G. polygama*. All *Grewia* species examined possess glandular trichomes with short unicellular stalks, except *G. laevigata* which has sessile or short-stalked glandular trichomes.

Remarks

Apart from minor differences, the stomatal characters and trichome micromorphology of these species conform to those of *G. occidentalis* (the type species of the genus *Grewia*).

The leaves of *G. occidentalis* are glabrous on both surfaces except the midrib and secondary veins, which are sparsely covered with 4–6-armed stellate trichomes.

Based on trichome micromorphology, the four species can be segregated into three broad groups as follows:

- Group 1. *G. multiflora*: Simple non-glandular trichomes only
- Group 2. *G. huluperakensis*: Simple and tufted 2–4-armed non-glandular trichomes
- Group 3. *G. laevigata* and *G. polygama*: 4–8-armed stellate and/or cushioned stellate trichomes.

This study mostly confirms earlier investigations (Metcalf and Chalk, 1950; Inamdar *et al.*, 1983; Rao and Ramayya, 1987; Rao, 1990; Sharma, 1990), but with some differences. In *G. polygama* from India, Sharma (1990) observed trichomes with short basal cell, peltate apical cell and 5–10-armed tufted trichomes, but these types were not observed in *G. polygama* from Peninsular Malaysia. This is probably the same as 4–8-armed stellate trichomes as defined by the author. Similarly, Rao also reported simple unicellular and 5–10-armed tufted trichomes in *G. glabra* Blume (now *G. multiflora*). In the present study, only the simple trichomes were observed in Bornean material. The simple unicellular filiform trichomes commonly found by Inamdar *et al.* (1983) in the vegetative and floral parts of *G. asiatica* L. were not observed in the Peninsular Malaysian and Bornean *Grewia* species. Similarly, mucilaginous cells observed by Rao and Ramayya (1984) in the adaxial surface of *G. subinaequalis* DC. and *G. tenax* (Forsk.) Aschers. & Schwf. were not encountered in any

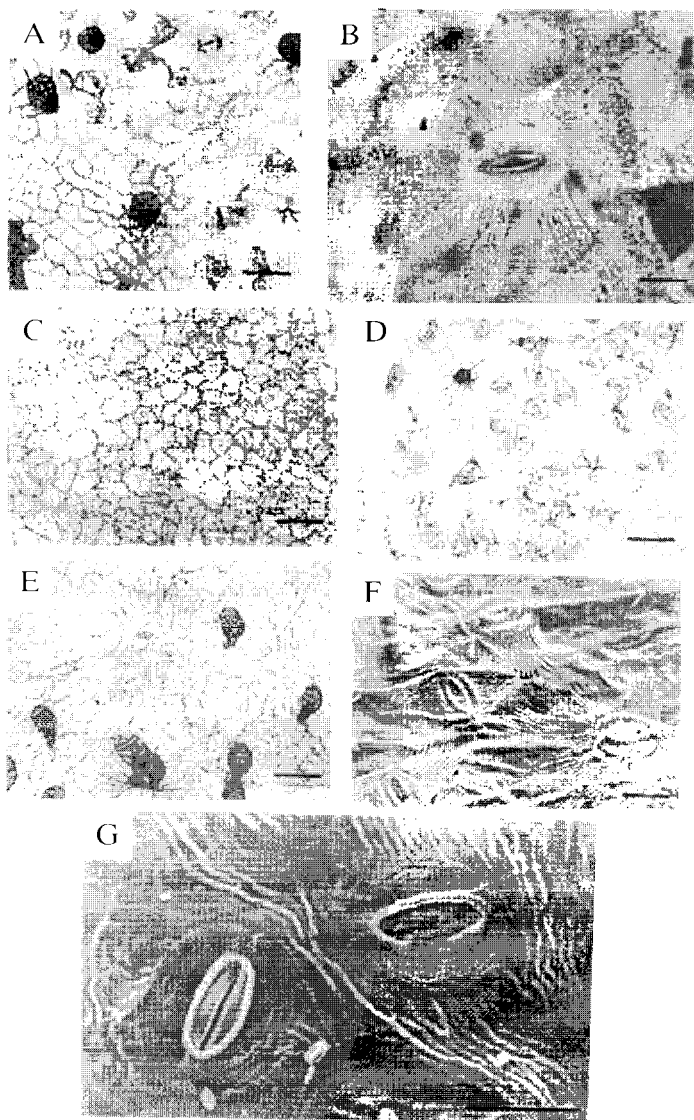


Plate 1. Stomatal complex of *Grewia* species

A: *G. laevigata* (Abdul Samat 265), LMs of abaxial leaf surface showing straight anticlinal wall of epidermal cells. — **B:** *G. occidentalis* (type species, Relinchoonk 483), LMs of abaxial leaf surface with stomata showing stomatal type, stomatal shape in outline, and orientation of striae over epidermal cells. — **C–F:** LMs (C–E) and SEMs (F) of abaxial leaf surface showing stomatal distribution. **C:** *G. occidentalis* (Relinchoonk 483); **D:** *G. laevigata* (Abdul Samat 265); **E:** *G. huluperakensis* (Turner 94–94); **F:** *G. multiflora* (Motley 240). — **G:** *G. huluperakensis* (Burkill & Mohd. Haniff SFN 12410), SEMs of abaxial leaf surface with stomata showing orientation of striae over anomocytic epidermal cells. — Bar equals 10 μm in B, F–G; 50 μm in A, C–E.

Peninsular Malaysian and Bornean material.

MICROCOS L.

(Figure 1; Plates 3 and 4; Table 1)

Stomatal Complex

Epidermal and subsidiary cells

In most species of *Microcos* investigated, the anticlinal walls of the epidermal cells on the adaxial surface of the leaf are straight or curved. In *M. dulitensis*, *M. fibrocarpa*, *M. gracilis*, *M. malayana*, *M. pearsonii*, *M. reticulata*, and *M. sumatrana*, however, these cell walls are usually undulate. On the abaxial surface, the anticlinal epidermal cell walls are straight to curved as in *M. antidesmifolia* (var. *antidesmifolia* and var. *hirsuta*), *M. borneensis*, *M. cinnamomifolia*, *M. erythrocarpa*, *M. fibrocarpa*, *M. globulifera*, *M. henrici* var. *acuta*, *M. kinabaluensis*, *M. lanceolata*, *M. latistipulata* var. *latistipulata*, *M. laurifolia*, *M. membranifolia*, *M. ossea*, *M. riparia*, *M. stylocarpoides*, *M. subepetala*, *M. tomentosa*, and *M. triflora* (var. *triflora* and var. *longipetiolata*), or undulate as in *M. crassifolia*, *M. dulitensis*, *M. gracilis*, *M. hirsuta*, *M. latifolia*, *M. malayana*, *M. opaca*, *M. pachyphylla*, *M. pearsonii*, *M. phaneroneura*, *M. reticulata*, *M. subcordifolia*, and *M. sumatrana*. Cuticular striation of epidermal or subsidiary cells is absent in most species, but short striae are frequently present in *M. tomentosa*.

Stomata

Stomata of *Microcos* species found in Peninsular Malaysia and Borneo are mainly paracytic and anisocytic or occasionally anomocytic. The outline of the stomata varies from broadly elliptic, rounded to oblate in most species of *Microcos* but broadly elliptic to rounded in *M. stylocarpoides*.

Stomatal size varies from 10 x 9 μm to 18 x 18 μm . Mean stomatal length ranges from 12 μm in *M. pearsonii* to 16.4 μm in *M. dulitensis*, and width from 12 μm in *M. subcordifolia* to 16.1 μm in *M. borneensis*. The stomatal length-width ratios (L/W) range from 0.8 to 1.5 with mean length-width ratios of 0.9 in *M. kinabaluensis*, *M. malayana* and *M. tomentosa*, 1.1 in *M. antidesmifolia* var. *hirsuta*, *M. fibrocarpa*, *M. globulifera*, *M. gracilis*, *M. hirsuta*, *M. phaneroneura*, *M. riparia*, *M. stylocarpoides*, *M. subepetala*, and *M. triflora* var. *triflora*, and equal to 1 in the other species.

In *M. dulitensis*, *M. malayana*, *M. phaneroneura*, and *M. tomentosa*, the stomata are raised above the level of the epidermal cells, but in the other species the stomata are at the same level with the epidermal cells.

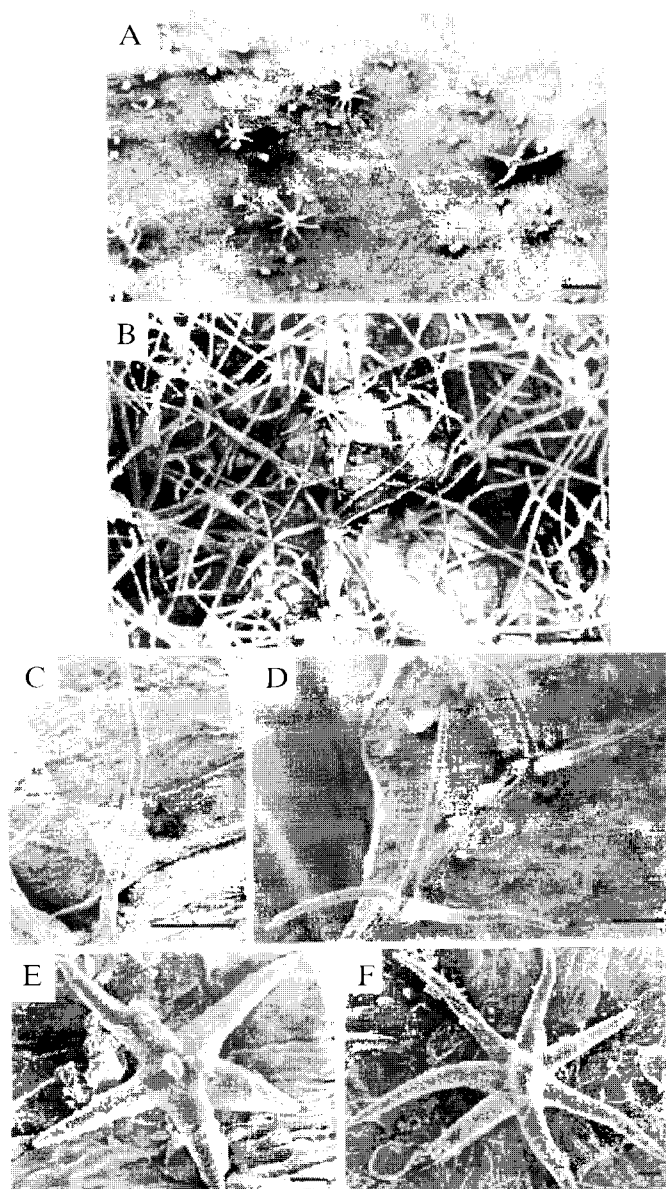


Plate 2. Non-glandular trichomes of *Grewia* species.

A–B: SEMs of abaxial leaf surface showing non-glandular trichomes distribution, **A:** *G. laevigata* (Asik SAN 113171), sparse; **B:** *G. polygama* (Soepadmo & Mahmud ES 1219), dense. — **C–F:** SEMs of abaxial leaf surface showing main types and subtypes of non-glandular trichomes. **C:** *G. multiflora* (Motley 240), simple trichomes; **D:** *G. huluperakensis* (Burkill & Md. Haniff SFN 12410), tufted trichomes of 2- or 3- armed form; **E:** *G. laevigata* (Mohd. Nur SFN 32966), 5-armed stellate trichomes; **F:** *G. laevigata* (Aban SAN 49197), cushioned stellate trichomes of 7-armed form. — Bar equals 10 μ m in E–F; 100 μ m in A–D.

Stomatal distribution

In *M. antidesmifolia* var. *hirsuta*, *M. gracilis*, *M. latifolia*, *M. subpetala*, *M. sumatrana*, and *M. tomentosa*, stomata occur on both surfaces of the leaf, but in the other species they are confined to the abaxial surface. The stomatal distribution pattern in *Microcos* varies from random to regular. The random distribution pattern is predominant in *Microcos* species, while the regular type occurs in only a few species, such as *M. globulifera*, *M. kinabaluensis*, *M. pachyphylla*, *M. riparia*, *M. subpetala*, and *M. tomentosa*.

The stomatal density varies from 84 mm⁻² in *M. malayana* to 316 mm⁻² in *M. riparia*, while the mean stomatal density ranges from 92 mm⁻² in *M. malayana* to 291 mm⁻² in *M. globulifera* and *M. riparia*. The stomatal index ranges from 15.5 in *M. borneensis* to 30.6 in *M. pearsonii*, while the mean stomatal index ranges from 17 in *M. opaca* to 28.4 in *M. globulifera*.

Trichomes

Non-glandular trichomes

Non-glandular trichomes are absent on both the adaxial and abaxial leaf surfaces (including the midrib and veins) of *M. antidesmifolia* var. *antidesmifolia*, *M. crassifolia*, *M. kinabaluensis*, *M. latistipulata* var. *latistipulata*, *M. pachyphylla*, and *M. triflora* (var. *triflora* and var. *longipetiolata*).

On the adaxial leaf surface, non-glandular trichomes are moderately dense in *M. latifolia*, *M. phaneroneura* and *M. reticulata*, sparse in *M. fibrocarpa*, *M. globulifera*, *M. gracilis*, *M. subcordifolia*, and sparse or absent in *M. lanceolata* and *M. tomentosa*. In *M. antidesmifolia* var. *hirsuta*, *M. dulitensis*, *M. erythrocarpa*, *M. henrici* var. *acuta*, *M. hirsuta*, *M. laurifolia*, *M. malayana*, *M. membranifolia*, *M. opaca*, *M. pearsonii*, and *M. stylocarpoides*, the adaxial side of the lamina is glabrous, but the midrib and secondary veins are sparsely to densely covered with non-glandular trichomes.

On the abaxial leaf surface, non-glandular trichomes are dense in *M. fibrocarpa*, *M. phaneroneura*, *M. reticulata*, and *M. tomentosa*, moderately dense in *M. antidesmifolia* var. *hirsuta*, *M. dulitensis*, *M. globulifera*, *M. gracilis*, *M. hirsuta*, *M. malayana*, *M. subcordifolia*, and *M. sumatrana*, and sparse to none in *M. henrici* var. *acuta*, *M. lanceolata*, *M. membranifolia*, *M. riparia*, and *M. stylocarpoides*. In *M. borneensis*, *M. cinnamomifolia*, *M. erythrocarpa*, *M. latifolia*, *M. laurifolia*, *M. ossea*, *M. pearsonii*, and *M. subpetala*, the abaxial surface of the lamina is glabrous, but non-glandular trichomes are present on the midrib and/or secondary veins.

As in *Grewia*, four main types of non-glandular trichomes were observed in *Microcos*, i.e. simple, tufted, stellate, and cushioned stellate trichomes. The leaf surface of *M. dulitensis*, *M. erythrocarpa*, *M. fibrocarpa*,

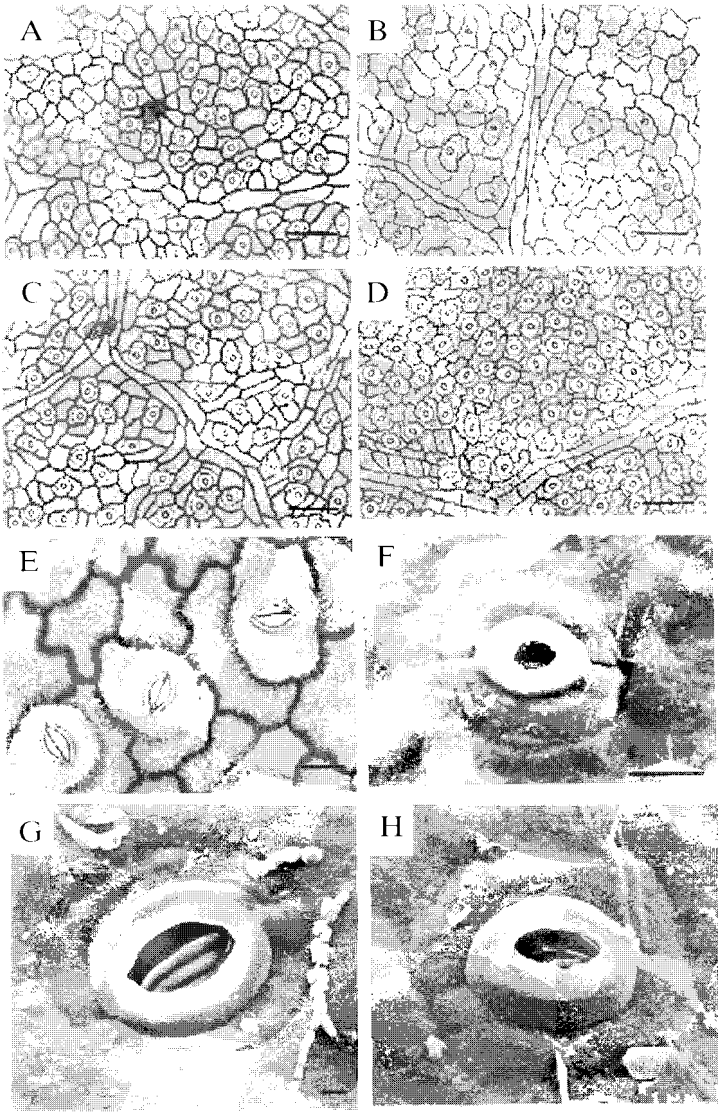


Plate 3. Stomatal complex of *Microcos* species.

A–B: LMs of abaxial leaf surface showing straight or curved (A) and undulate (B) anticlinal wall of epidermal cells. **A:** *M. antidesmifolia* var. *antidesmifolia* (Stone & Chin 13853); **B:** *M. malayana* (Whitmore FRI 15328). — **C–D:** LMs of abaxial leaf surface showing stomatal distribution. **C:** *M. lanceolata* (Kochummen KEP 79086), random; **D:** *M. pachyphylla* (Elmer 21704), regular. — **E:** *M. dulitensis* (Pickles S. 3689). LMs of abaxial leaf surface with stomata showing stomatal type and stomatal shape in outline. — **F–H:** SEMs of abaxial leaf surface with stomata showing variation in elevation of the guard cells relative to epidermal cells (F–G: same level; H: raised). **F:** *M. ossea* (Tong S. 33866); **G:** *M. antidesmifolia* var. *hirsuta* (Scortechini s.n.); **H:** *M. malayana* (Chelliah KEP 104372). — Bar equals 1 μ m in G–H; 5 μ m in F; 10 μ m in E; 50 μ m in A–D.

M. globulifera, *M. latifolia*, *M. malayana*, and *M. opaca* is covered with simple and 2–4-armed tufted trichomes, whereas that of *M. antidesmifolia* var. *hirsuta* and *M. reticulata* is covered with simple, 2–4-armed tufted trichomes and 4–8-armed cushioned stellate trichomes.

A combination of simple and 4–8-armed cushioned stellate trichomes is found in *M. henrici* var. *acuta*, *M. hirsuta*, *M. membranifolia*, and *M. subcordifolia*, while a combination of simple, 4–7-armed cushioned stellate and 4-armed stellate trichomes is observed in *M. phaneroneura*. The midrib and secondary veins of *M. ossea* on the abaxial surface bear simple and 5-armed stellate trichomes, while those of *M. pearsonii* possess dense 5-armed stellate trichomes. *Microcos borneensis*, *M. cinnamomifolia*, *M. gracilis*, *M. lanceolata*, *M. laurifolia*, *M. riparia*, *M. stylocarpoides*, *M. subpetala*, *M. sumatrana*, and *M. tomentosa*, on the other hand, have 4–8-armed cushioned stellate trichomes on the lamina or on the midrib and secondary veins.

Glandular trichomes

In most species (except *M. kinabaluensis*, which has completely glabrous leaves), glandular trichomes of varying density are found on both leaf surfaces. In *M. borneensis* and *M. membranifolia*, glandular trichomes are in clusters of 2–4.

The glandular trichomes of most *Microcos* species investigated possess short unicellular stalks, except in *M. borneensis*, *M. ossea* and *M. triflora* var. *triflora* where the glandular trichomes are sessile. The outline of the multicellular head varies from elliptic (*M. crassifolia*, *M. henrici* var. *acuta*, *M. lanceolata*, *M. pachyphylla*, *M. pearsonii*, *M. riparia*, and *M. tomentosa*) to broadly elliptic (*M. dulitensis*, *M. erythrocarpa*, *M. gracilis*, *M. latistipulata* var. *latistipulata*, *M. laurifolia*, *M. malayana*, *M. opaca*, *M. ossea*, *M. phaneroneura*, *M. stylocarpoides*, and *M. subcordifolia*), rounded (*M. globulifera*, *M. hirsuta*, *M. membranifolia*, and *M. reticulata*), or oblong (*M. latifolia* and *M. triflora* var. *triflora*) or varying from broadly elliptic to rounded in *M. antidesmifolia* var. *antidesmifolia* and var. *hirsuta*, *M. cinnamomifolia*, *M. fibrocarpa*, *M. subpetala*, and *M. triflora* var. *longipetiolata*, or rounded to oblong in *M. borneensis* and *M. sumatrana*.

Remarks

The characters of the stomatal complex in the species examined match those of *M. paniculata* (the type species of the genus *Microcos*), except in the absence of cuticular striation on the epidermal cells in most of the Peninsular Malaysian and Bornean species.

In trichome micromorphology, they also match well with *M. paniculata*. The leaves of *M. paniculata* are glabrous on both surfaces.

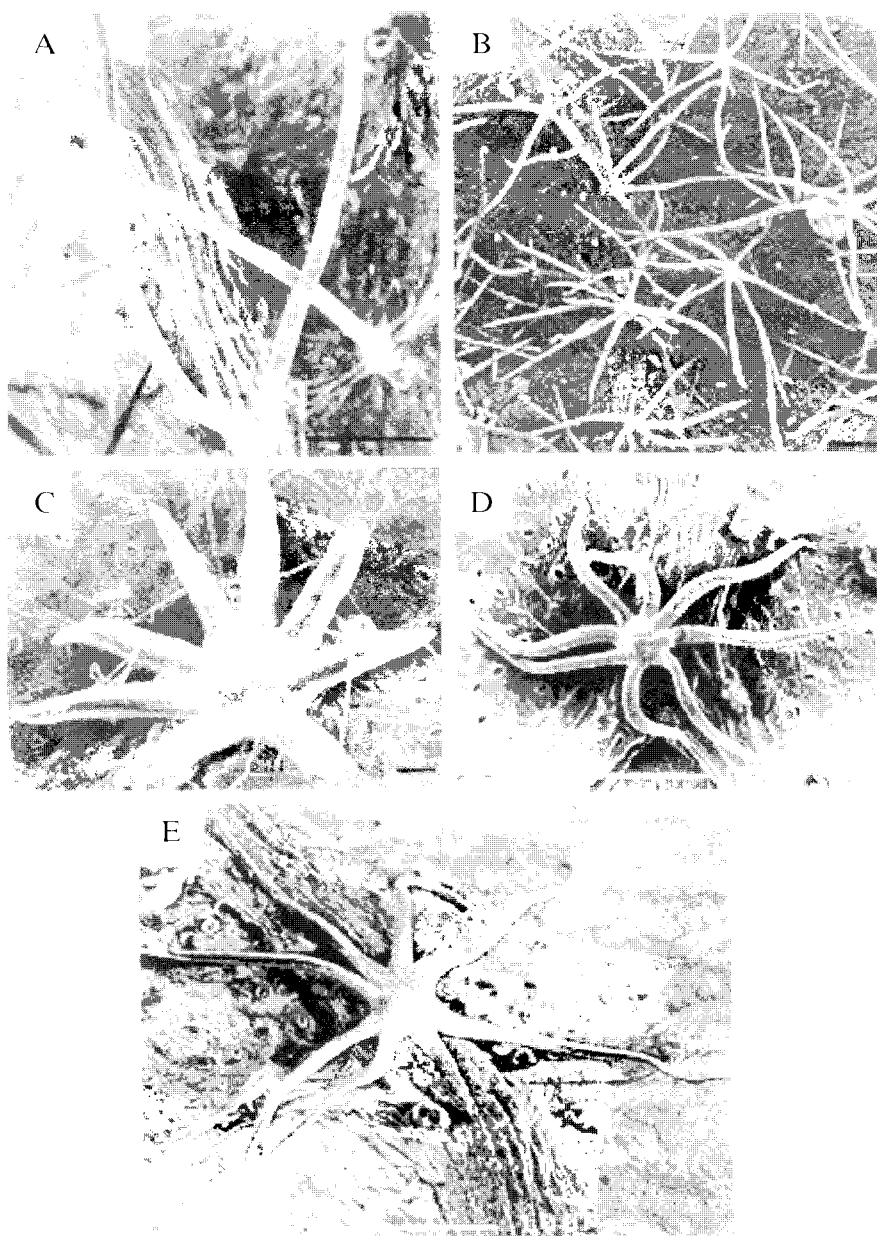


Plate 4. Non-glandular trichomes of *Microcos* species.

A: *M. fibrocarpa* (Lesmy FRI 33964), simple trichomes and 2-armed tufted trichomes. — **B:** *M. tomentosa* (Spare SFN 36245), SEMs of abaxial leaf surface showing dense non-glandular trichomes distribution. — **C:** *M. henrici* var. *acuta* (Ilias S. 36520), 8-armed cushioned stellate trichomes. — **D:** *M. paniculata* (type species, Cramer 3405), 8-armed cushioned stellate trichomes. — **E:** *M. paniculata* (Clemens 4122), 8-armed stellate trichomes. — Bar equals 100 μm in A–E.

except the midrib and secondary veins in the abaxial surface which are sparsely covered with 8-armed stellate and cushioned stellate trichomes.

Based on trichome micromorphology, the Peninsular Malaysian and Bornean species of *Microcos* can be separated into five broad groups:

- Group 1. *M. kinabaluensis*: Glandular and non-glandular trichomes absent.
- Group 2. *M. antidesmifolia* var. *antidesmifolia*, *M. crassifolia*, *M. latistipulata* var. *latistipulata*, *M. pachyphylla*, *M. triflora* (var. *triflora* and var. *longipetiolata*): Glandular trichomes present; non-glandular trichomes absent.
- Group 3. *M. antidesmifolia* var. *hirsuta*, *M. dulitensis*, *M. erythrocarpa*, *M. fibrocarpa*, *M. globulifera*, *M. henrici* var. *acuta*, *M. hirsuta*, *M. latifolia*, *M. malayana*, *M. membranifolia*, *M. opaca*, *M. ossea*, *M. phaneroneura*, *M. reticulata*, and *M. subcordifolia*: Glandular and non-glandular trichomes of simple, tufted, stellate and cushioned stellate hairs present.
- Group 4. *M. pearsonii*: Glandular and non-glandular trichomes of stellate hairs present.
- Group 5. *M. borneensis*, *M. cinnamomifolia*, *M. gracilis*, *M. lanceolata*, *M. laurifolia*, *M. riparia*, *M. stylocarpoides*, *M. subepetala*, *M. sumatrana*, and *M. tomentosa*: Glandular and non-glandular of cushioned stellate trichomes present.

Results of previous studies on the trichomes of *Microcos* (Inamdar *et al.*, 1983; Sharma, 1990) differ slightly from those of the present study. Sharma (1990) reported the occurrence of 5–10-armed tufted stellate trichomes and three-celled unequally 2-armed trichomes with short stalks in *G. microcos* L. (now *M. paniculata*). These two types of trichomes, however, were not observed in any species investigated in the present study.

Discussion

Comparative stomatal complex characters of Grewia and Microcos

The differences between the leaf epidermal characters of *Grewia* and *Microcos* species occurring in Peninsular Malaysia and Borneo are summarised in Table 2. In *Grewia*, the anomocytic stomata are the predominant type, whereas in *Microcos* the paracytic and anisocytic stomata are the prevalent type. Radiating cuticular striation is present on the epidermal cells immediately adjacent to the guard cells in *Grewia* species, but absent on the subsidiary cells or epidermal cells adjacent to the guard cells in *Microcos* species, except in *M. tomentosa*. The stomatal outline in

Grewia species is mainly elliptic to broadly elliptic with average L/W ratios of 1.2–1.4, whereas in *Microcos* species it is mostly broadly elliptic, rounded to oblate with average L/W ratios of 0.9–1.1.

The leaves of *Grewia* species are either amphistomatic, e.g. *G. occidentalis*, *G. polygama*, and *G. subinaequalis* DC. (Rao and Ramayya, 1981), or hypostomatic, e.g. *G. huluperakensis*, *G. laevigata* Vahl, *G. multiflora*, and *G. tenax* (Forsk.) Aschers. & Schwf. (Rao and Ramayya, 1981). Likewise, the leaves of *Microcos* species may be amphistomatic (*M. antidesmifolia* var. *hirsuta*, *M. gracilis*, *M. latifolia*, *M. subpetala*, *M. sumatrana*, and *M. tomentosa*), or hypostomatic (*M. paniculata* and other species from Peninsular Malaysia and Borneo). In the Tiliaceae, amphistomatic leaves have been reported in a few species of *Corchorus* L. and *Triumfetta* L. (Rao and Ramayya, 1981; Singh and Dube, 1993). For related families in the Malvales, Rao and Ramayya (1981) reported exclusively amphistomatic leaves for Malvaceae, exclusively hypostomatic leaves for Elaeocarpaceae, and both amphistomatic and hypostomatic leaves for Bombacaceae and Sterculiaceae.

Table 2. Differences between the epidermal characters of *Grewia* and *Microcos* in Peninsular Malaysia and Borneo.

Genus Characters	<i>Grewia</i>	<i>Microcos</i>
Epidermal/Subsidiary cells		
Radiating cuticular striation	present	absent (except in <i>M. tomentosa</i>)
Stomata		
Type	predominantly anomocytic (occasionally paracytic and anisocytic)	mainly paracytic and anisocytic (occasionally anomocytic)
Outline	elliptic, broadly elliptic (occasionally rounded)	broadly elliptic, rounded. oblate
Average length (µm)	18.6–22.9	12–16.4
Average L/W ratio	1.2–1.4	0.9–1.1

Metcalf and Chalk (1950) stated that in the Tiliaceae, the stomata were exclusively anomocytic (ranunculaceous), but Kundu and Sen (1958), Sen and Paul (1961), and Singh and Dube (1993) demonstrated the presence of anisocytic, paracytic and tetracytic stomata in Indian *Corchorus* species. Likewise, the present study also discovered that the stomata of *Grewia*

species in Peninsular Malaysia and Borneo were predominantly anomocytic and occasionally paracytic, and those of *Microcos* species were mainly paracytic and occasionally anomocytic. For other families in Malvales, Inamdar and Chohan (1969) reported the occurrence of anomocytic, anisocytic and paracytic stomata in the Bombacaceae (*Adansonia digitata* L. and *Bombax ceiba* Burm.f.) and the Malvaceae (*Althaea rosea* Cav.; *Gossypium herbaceum* L.; *Hibiscus rosa-sinensis* L.; *H. schizopetalus* Hook.f.; *H. syriacus* L.; *Malvaviscus arboreus* Cav.; *Sida acuta* Burm.f.; *S. alba* Cav.; and *Thespesia populnea* Sol. ex Corr.Serr.). Hussin and Sani (1998), on the other hand, reported that the stomata of 12 species of *Sterculia* L. (Sterculiaceae) were exclusively anomocytic.

The occurrence of different types of stomatal apparatus in the leaves of a single taxon or in different species of a genus or different genera of a family has been noted by many authors (Metcalf and Chalk, 1950; Kundu and Sen, 1958; Sen and Paul, 1961; Inamdar and Chohan, 1969; Rao and Ramayya, 1983; Singh and Dube, 1993), where usually a few stomata of one type occur along with the predominant stomata of another type. Less often, two or more stomatal types occur together as "codominants" on the same leaf and/or species, as for example in the Convolvulaceae (Pant and Banerji, 1965), and Bombacaceae, Sterculiaceae and Elaeocarpaceae (Rao and Ramayya, 1983).

Taxonomic value of trichome characters in Grewia and Microcos

The present study on the leaf trichomes of Peninsular Malaysian and Bornean *Grewia* and *Microcos* species reaffirms earlier observations on Tiliaceae species (Solereder, 1908; Metcalfe and Chalk, 1950; Tiwari, 1978; Rao and Ramayya, 1987; Sharma, 1990) as well as on related families of the order Malvales (Ramayya and Rao, 1976; Rao and Ramayya, 1977, 1983; Inamdar *et al.*, 1983; Salma, 1999), namely, the existence of several different trichomes types.

Based on the type, distribution and density of non-glandular trichomes, species of *Grewia* can be divided into three broad groups (i.e., non-glandular trichomes exclusively of simple hairs; non-glandular trichomes both simple and 2–4-armed tufted hairs; and 4–8-armed stellate and/or cushioned stellate trichomes). Likewise, five broad groups of species in *Microcos* can be recognised (i.e., glandular and non-glandular trichomes absent; glandular trichomes present but non-glandular trichomes absent; glandular and non-glandular trichomes of simple, tufted, stellate and cushioned stellate hairs present; glandular and non-glandular trichomes of stellate hairs present; and glandular and non-glandular cushioned stellate trichomes present).

The infraspecific variability may be due to genetic variability or ecological factors (Baas, 1975). In *M. triflora*, the two varieties differ in the the body/stalk of glandular trichomes (sessile in var. *triflora*; short unicellular in var. *longipetiolata*) and in *M. antidesmifolia*, the two varieties differ in the occurrence of non-glandular trichomes (absent in var. *antidesmifolia*; simple, tufted and cushioned stellate hairs in var. *hirsuta*). However, this infraspecific variation could not be correlated with ecological data, as information from the herbarium labels was insufficient.

Conclusions

On the basis of leaf epidermal characters, the genus *Microcos* in Peninsular Malaysia and Borneo can be distinguished from *Grewia* by a combination of the following characters: stomatal type, outline, mean length and L/W ratio, and the occurrence of cuticular striation on the epidermal cells immediately surrounding the guard cells. To some extent, this study supports Burret's view (1926) for segregating *Microcos* from *Grewia*. However, trichome micromorphological characters alone cannot be used for distinguishing genera, and species within each genus. According to the ordinal classification defined by APG (1998), stomatal types and trichomes are just minor variations on a pattern common to most Malvaceae, which now includes Tiliaceae.

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Appendix: Source of Materials Studied

The species and specimens studied are given below in alphabetical order:
(1) = maceration only; (2) = trichomes only

Grewia occidentalis L. (type species): *Moss* 3959 (BM); *Relinhood* 483 (L); *Smook* 6553 (BM) — **G. huluperakensis** I.M.Turner: *Burkill & Md. Haniff SFN* 12410 (SING); *Turner* 94–94 (SING) — **G. laevigata** Vahl: *Aban SAN* 49197 (SAN); *Abdul Samat* 265 (KLU); *Amin & Joseph SAN* 60068 (KEP); *Asik SAN* 11317 (KEP, 2); *Mohd. Nur SFN* 32966 (KEP) — **G. multiflora** Juss.: *Blume s.n.* (L sheet no. 908.253.1458; L); *Motley* 240 (K) — **G. polygama** Roxb.: *Chin CSC* 1832 (KEP, 2); *Chung RC* 10 (KEP, 1); *Kamarudin & Mustapa FRI* 42255 (KEP); *Kiah SFN* 35286 (KEP); *Soepadmo & Mahmud ES* 1219 (KEP).

Microcos paniculata L. (type species): *Bhargave* 1787 (L); *Clemens* 4122 (BM); *Cramer* 3405 (L) — **M. antidesmifolia** (King) Burret **var. antidesmifolia**: *Everett FRI* 14442 (KEP); *King's Collector* 4085 (L); *Stone & Chin* 13853 (KLU); **var. hirsuta** (King) Burret: *Creagh s.n.* (K); *Elmer* 20911 (SING); *Enggoh FMS* 48988 (KEP); *Scortechini s.n.* (BO) — **M. borneensis** Burret: *Ashton S.* 17956 (KEP); *Smythies et al. S.* 5877 (KEP) — **M. cinnamomifolia** Burret: *s.c. FMS* 34460 (KEP); *Haviland* 2256 (SAR); *Nicholson & Ping SAN* 17701 (KEP) — **M. crassifolia** Burret: *Amin & Lideh SAN* 70341 (KEP); *Amin et al. SAN* 67317 (KEP, 1); *Ramos* 1704 (K) — **M. dulitensis** Airy Shaw: *Pickles S.* 3689 (SAR); *Richards* 1767 (SING) — **M. erythrocarpa** (Ridl.) Airy Shaw: *Kochummen FRI* 16417 (KEP); *Kochummen FRI* 29363 (KEP) — **M. fibrocarpa** (Mast.) Burret: *Kiah SFN* 35064 (KEP); *Lesmy FRI* 33964 (KEP) — **M. globulifera** (Mast.) Burret: *Chan FRI* 23806 (KEP); *Ogata KEP* 105036 (KEP) — **M. gracilis** Stapf ex Ridl.: *Chai SAN* 26066 (SAN); *Yü et al. S.* 37752 (KEP) — **M. henrici** (Baker f.) Burret **var. acuta** R.C.K.Chung, (ined.): *Ilias S.* 36520 (KEP); *Ilias S.* 45121 (KEP); *Lai et al. S.* 75359 (KEP) — **M. hirsuta** (Korth.) Burret: *Haviland* 1471 (SING); *Korthals s.n.* (L sheet no. 944.56.122; L) — **M. kinabaluensis** R.C.K.Chung, (ined.): *Chew & Corner RSNB* 4216 (SAN); *Chew & Corner RSNB* 4994 (SAN) — **M. lanceolata** (Miq.) Burret: *Chelliah KEP* 104621 (KEP); *Kochummen KEP* 79086 (KEP) — **M. latifolia** Burret: *Whitmore FRI* 8931; *Wong WKM* 1545 (SING) — **M. latistipulata** (Ridl.) Burret **var. latistipulata**: *Burkill SFN* 7826 (SING); *Chai SAN*

29741 (KEP) — **M. laurifolia** (Hook. ex Mast.) Burret: *Kochummen FRI 16338* (KEP); *Razali 2809* (UKMB) — **M. malayana** R.C.K.Chung, (*ined.*): *Loh FRI 19249* (KEP); *Chelliah KEP 104372* (KEP); *Whitmore FRI 15328* (KEP) — **M. membranifolia** R.C.K.Chung, (*ined.*): *Kadir & Jiran SAN A 3367* (KEP); *Singh SAN 30672* (KEP) — **M. opaca** (Korth.) Burret: *Ilias S. 39135* (KEP); *Yü S. 41139* (KEP) — **M. ossea** Burret: *Clemens 21071* (SAR); *Dayang Awa & Ilias S. 45689* (KEP); *Tong S. 33866* (KEP) — **M. pachyphylla** Merr.: *Elmer 21704* (SING); *Salleh et al. BRUN 15315* (KEP) — **M. pearsonii** (Merr.) Burret: *Dewol & Donggop SAN 129474* (KEP); *Meijer & Pereira SAN 47225* (SAN) — **M. phaneroneura** Burret: *Chai S. 36100* (KEP); *Hallier 2868* (BO); *Ong OIIC 716* (KEP, 1) — **M. reticulata** Ridl.: *Ashton S. 17800* (KEP); *Creagh s.n.* (K, 2); *Saikh SAN 69284* (SAN, 2); *Wood SAN A 4788* (KEP) — **M. riparia** (Boerl. & Koord.) Burret: *Hallier 1314* (BO); *Yeob FMS 3190* (KEP) — **M. stylocarpoides** Burret: *Hallier 756* (BO); *Haviland 1685* (SAR) — **M. subcordifolia** R.C.K.Chung, (*ined.*): *Kirkup & Thomas DK 727* (KEP); *Niga NN 118* (KEP) — **M. subepetala** Stapf ex Ridl.: *Haviland 1885* (K) — **M. sumatrana** (Baker f.) Burret: *Forbes 2684* (L) — **M. tomentosa** Sm.: *Carrick 565* (KEP, 1); *Chung RC 9* (KEP); *Everett FRI 13785* (KEP); *Spare SFN 36245* (KEP); *Tachun FMS 23227* (KEP, 1) — **M. triflora** (Blanco) R.C.K.Chung **var. triflora**, (*ined.*): *Forestry Student PNH 35319* (KEP); *Lazo PNII 33406* (KEP); **var. longipetiolata** (Merr.) R.C.K.Chung, (*ined.*): *Aban & Soinin SAN 66898* (SAN); *Haviland 2332* (SAR, 1); *Wong WKM 1244* (KEP).