

# The Significance of Pollen Morphology in the Taxonomy of *Grewia* and *Microcos* (Tiliaceae) in Peninsular Malaysia and Borneo

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## Abstract

The pollen morphology of 5 species of *Grewia* and 31 species of *Microcos* (including their type species) from Peninsular Malaysia and Borneo were studied using light, scanning and transmission electron microscopy. The pollen of *Grewia* species differs from that of *Microcos* in being larger with a mean polar axis of 53–75 µm and an average equatorial diameter of 39–55 µm, having a coarsely reticulate tectum, a lumina diameter of more than 1.5 µm and a mean exine thickness of 1.55–2.15 µm. *Microcos* pollen is characterised by its smaller size with a mean polar axis of 25–35 µm and an average equatorial diameter of 19–27 µm, a finely reticulate tectum, a lumina diameter of less than 1.5 µm and a mean exine thickness 0.84–0.90 µm. The pollen of all species examined conforms to the previously recognised 'Grewia-type'.

## Introduction

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. *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 and Kubitzki, 2003).

Previous studies on members of the order Malvales showed that pollen morphological characters were useful for segregating the Tiliaceae from the Bombacaceae, Malvaceae and Sterculiaceae (Erdtman, 1952; Nair, 1962; Chaudhuri, 1965; Chaudhuri and Mallik, 1965; Sharma, 1969; Coetzee and Van Der Schijff, 1978; Martínez-Hernández *et al.*, 1978; Zhang and Chen, 1984; Sudhakar and Rao, 1987).

Palynological literature on the family Tiliaceae has been reviewed by Erdtman (1952). He described over 70 species of the family, including some Peninsular Malaysian and Bornean representatives, distributed over 45 genera. Since then there have been a number studies on the pollen of *Grewia* and/or *Microcos* from India (Sharma, 1969; Sudhakar and Rao, 1987), China (Long, 1982; Zhang and Chen, 1984; Wang *et al.*, 1995) and Sudan (El Ghazali, 1993). These studies show the Tiliaceae to be a curypalynous family. Based mainly on aperture type and using tectum ornamentation as subsidiary characters, Sharma (1969) recognised 7 major and 18 minor pollen types, while Zhang and Chen (1984) recognised four pollen types and Erdtman (1952) noted only three pollen types in the Tiliaceae.

Erdtman (1952) classified the pollen of *Grewia* as belonging to a single pollen type, i.e. the 'Grewia-type' characterised by tricolporate grains with reticulate tectum. He, however, did not examine the pollen of *Microcos*. Later, Long (1982), Zhang and Chen (1984) and Wang *et al.* (1995) categorised pollen of *Grewia* and *Microcos* as belonging to the 'Grewia-type'. However, Sharma (1969), using characters of the tectum ornamentation and lumina width, distinguished four pollen types in the Indian species of *Grewia*.

Based on pollen morphological data, Erdtman (1952), Zhang and Chen (1984), Christensen (1986), and Nilsson and Robyns (1986) concluded that the pollen morphology of Tiliaceae closely resembled that of Bombacaceae and Sterculiaceae but differed from that of Malvaceae. Zhang and Chen (1984) supported the separation of *Microcos* from *Grewia* in the Tiliaceae. Sharma (1969) suggested that pollen morphological characters, when combined with other morphological data, can provide useful additional taxonomic characters for delimitating genera and species of the Tiliaceae.

The aim of this study is to investigate the morphological variation in the pollen of *Grewia* and *Microcos*; to assess the taxonomic value of the pollen in the Peninsular Malaysian and Bornean species; and to contribute to a better understanding of the pollen morphology of both genera.

## Materials and methods

Pollen used in the present study was obtained from herbarium specimens listed in Table 1.

The pollen samples were acetolysed following the method of Erdtman (1960). The acetolysed pollen samples were divided for light microscopy (LM) and scanning electron microscopy (SEM) studies. For LM observations, pollen grains were mounted in glycerine jelly stained with safranin and sealed with paraffin wax. Measurements of polar length, equatorial width, colpus length and width were carried out using an Olympus BX41 microscope. For each sample, 20 pollen grains were measured using a calibrated eyepiece micrometer. For SEM observations, the acetolysed pollen grains

**Table 1.** Source of materials studied.

| Species <sup>§</sup>                                                         | Collector                                                                                                                                                                                          | Herbarium                     |
|------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------|
| <b><i>Grewia</i></b>                                                         |                                                                                                                                                                                                    |                               |
| <i>G. occidentalis</i> L. (type species)                                     | Moss 3959 <sup>†</sup> ; Relinhood 483 <sup>†</sup>                                                                                                                                                | BM; L                         |
| <i>G. huluperakensis</i> I.M. Turner                                         | Turner 94-94 <sup>†</sup>                                                                                                                                                                          | SING                          |
| <i>G. laevigata</i> Vahl                                                     | Hashim SAN 33470 <sup>#</sup> ; Kostermans 5234 <sup>#</sup> ; Lee S. 41948 <sup>#</sup> ; Sigin <i>et al.</i> SAN 110601 <sup>#</sup> ; Stone 11856 <sup>#</sup> ; Whitmore FRI 3729 <sup>#</sup> | SAN; SING; KEP; SAN; KLU; KEP |
| <i>G. multiflora</i> Juss.                                                   | Motley 240 <sup>°</sup>                                                                                                                                                                            | K                             |
| <i>G. polygama</i> Roxb.                                                     | Kiah SFN 35286 <sup>#</sup> ; Symington FMS 46716 <sup>#</sup>                                                                                                                                     | KEP; KEP                      |
| <b><i>Microcos</i></b>                                                       |                                                                                                                                                                                                    |                               |
| <i>M. paniculata</i> L. (type species)                                       | Cramer 3405 <sup>#</sup> ; Kanodia 88480 <sup>†</sup>                                                                                                                                              | L; BM                         |
| <i>M. antidesmifolia</i> (King) Burret<br>var. <i>antidesmifolia</i>         | Cockburn FRI 7816 <sup>#</sup> ; King's Collector 4029 <sup>#</sup> ; Whitmore FRI 3417 <sup>#</sup>                                                                                               | KEP; K; KEP                   |
| <i>M. antidesmifolia</i> (King) Burret<br>var. <i>hirsuta</i> (King) Burret  | Creagh <i>s.n.</i> <sup>#</sup> ; Elmer 20911 <sup>#</sup> ; Sibat S. 25179 <sup>#</sup>                                                                                                           | K; SING; KEP                  |
| <i>M. borneensis</i> Burret                                                  | Haviland 2837 <sup>#</sup> ; Tiggi S. 3311 <sup>#</sup>                                                                                                                                            | SAR; SAR                      |
| <i>M. cinnamomifolia</i> Burret                                              | Anderson S. 25147 <sup>#</sup> ; Charington SAN 29852 <sup>#</sup> ; Coode MC 7716 <sup>°</sup>                                                                                                    | SAR; KEP; KEP                 |
| <i>M. dulitensis</i> Airy Shaw                                               | Richards 1767 <sup>#</sup>                                                                                                                                                                         | SING                          |
| <i>M. erythrocarpa</i> (Ridl.) Airy Shaw                                     | Kochummen FRI 16417 <sup>#</sup> ; Mohd. Shah MS 2757 <sup>#</sup>                                                                                                                                 | KEP; SING                     |
| <i>M. fibrocarpa</i> (Mast.) Burret                                          | Kochummen KEP 80640 <sup>#</sup> ; Maingay 1080 <sup>#</sup> ; Mohd. Shah and Sidek MS 1164 <sup>#</sup>                                                                                           | KEP; K; SING                  |
| <i>M. globulifera</i> (Mast.) Burret                                         | Maingay 3064 <sup>#</sup> ; Ogata KEP 105036 <sup>#</sup>                                                                                                                                          | K; KEP                        |
| <i>M. gracilis</i> Stapf <i>ex</i> Ridl.                                     | Chai SAN 26066; Coode <i>et al.</i> MC 6776; Haviland 1683                                                                                                                                         | SAN; KEP; SAR                 |
| <i>M. henrici</i> (Baker <i>f.</i> ) Burret<br><i>ssp. acuta</i> R.C.K.Chung | Ahmad and Termiji SAN 67973 <sup>#</sup> ; Ilias S. 45121 <sup>#</sup> ; Kostermans 10424 <sup>#</sup>                                                                                             | SAN; KEP; L                   |
| <i>M. hirsuta</i> (Korth.) Burret                                            | Clemens 27284 <sup>#</sup> ; Haviland 1471 <sup>#</sup> ; Korthals <i>s.n.</i> (L sheet no. 944.56.122) <sup>#</sup>                                                                               | SING; SING; L                 |
| <i>M. kinabaluensis</i> R.C.K.Chung                                          | Chew and Corner RSNB 4994 <sup>#</sup> ; Sadau SAN 49708 <sup>#</sup>                                                                                                                              | SAN; SAN                      |
| <i>M. lanceolata</i> (Miq.) Burret                                           | Chelliah KEP 104621 <sup>†</sup> ; Mahmud FMS 3717 <sup>#</sup>                                                                                                                                    | KEP; SING                     |
| <i>M. latifolia</i> Burret                                                   | King's Collector 7762 <sup>#</sup> ; Sarawak Museum Series 165 <sup>#</sup> ; Wong WKM 1545 <sup>#</sup>                                                                                           | K; SAR; SING                  |

Table 1 continued

| Species <sup>§</sup>                                                                         | Collector                                                                                                     | Herbarium          |
|----------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------|--------------------|
| <i>M. latistipulata</i> (Ridl.) Burret<br>var. <i>latistipulata</i>                          | Burkill SFN 7826 <sup>#</sup> ; Elmer 20310 <sup>#</sup> ;<br>Teo TP 391 <sup>#</sup>                         | SING; L;<br>SING   |
| <i>M. laurifolia</i> (Hook. ex Mast.) Burret                                                 | Kochummen FRI 16338 <sup>#</sup> ;<br>Zainuddin FRI 17887 <sup>#</sup>                                        | KEP; KEP           |
| <i>M. malayana</i> R.C.K.Chung                                                               | Loh FRI 19249 <sup>#</sup> ; Symington and<br>Kiah SFN 28797 <sup>#</sup>                                     | KEP; SING          |
| <i>M. membranifolia</i> R.C.K.Chung                                                          | Singh SAN 30672 <sup>#</sup> ; Yii S. 61492 <sup>#</sup>                                                      | KEP; KEP           |
| <i>M. opaca</i> (Korth.) Burret                                                              | Korthals s.n. (L sheet no.<br>908.253.752) <sup>#</sup> ; Lee S. 43227 <sup>#</sup>                           | L; SAR             |
| <i>M. ossea</i> Burret                                                                       | Clemens 21071 <sup>#</sup> ; Haviland 42 <sup>#</sup> ;<br>Wong WKM 1290 <sup>#</sup>                         | SAR; SING;<br>BRUN |
| <i>M. pachyphylla</i> Merr.                                                                  | Aban SAN 35880 <sup>#</sup> ; Salleh <i>et al.</i><br>BRUN 15315 <sup>#</sup>                                 | SAN; KEP           |
| <i>M. pearsonii</i> (Merr.) Burret                                                           | Singh and Aban SAN 30135 <sup>#</sup> ;<br>Wright S. 29113 <sup>#</sup>                                       | SAN; SAR           |
| <i>M. phaneroneura</i> Burret                                                                | Hallier 2868 <sup>#</sup> ; Ilias S. 28128 <sup>#</sup>                                                       | BO; SAR            |
| <i>M. reticulata</i> Ridl.                                                                   | Ashton S. 17800 <sup>#</sup> ; Creagh s.n. <sup>#</sup>                                                       | KEP; K             |
| <i>M. riparia</i> (Boerl. & Koord.) Burret                                                   | Hallier 2208 <sup>#</sup> ; Yeob FMS 3190 <sup>#</sup>                                                        | BO; KEP            |
| <i>M. stylocarpoides</i> Burret                                                              | Burley <i>et al.</i> NGS 3243 <sup>#</sup> ; Othman<br>S. 37444 <sup>#</sup>                                  | KEP; SAR           |
| <i>M. subcordifolia</i> R.C.K.Chung                                                          | Kirkup and Thomas DK 727 <sup>#</sup> ;<br>Niga NN 118 <sup>#</sup>                                           | KEP; KEP           |
| <i>M. subpetala</i> Stapf ex Ridl.                                                           | Haviland 1885 <sup>#</sup>                                                                                    | K                  |
| <i>M. sumatrana</i> (Baker f.) Burret                                                        | Fedilis SAN 95781 <sup>#</sup> ; Forbes 2684 <sup>#</sup>                                                     | KEP; L             |
| <i>M. tomentosa</i> Sm.                                                                      | Ang FRI 21599 <sup>#</sup> ; Suppiah FRI<br>28239 <sup>#</sup> ; Zainuddin and Latiff AZ<br>1731 <sup>#</sup> | KEP; KEP;<br>KEP   |
| <i>M. triflora</i> (Blanco) R.C.K.Chung<br>var. <i>triflora</i>                              | Anon. PNH 35319 <sup>#</sup> ; Tai SAN<br>58042 <sup>#</sup>                                                  | KEP; SING          |
| <i>M. triflora</i> (Blanco) R.C.K.Chung<br>var. <i>longipetiolata</i> (Merr.)<br>R.C.K.Chung | Singh SAN 30375 <sup>#</sup> ; Suib S.<br>23458 <sup>#</sup>                                                  | KEP; KEP           |

<sup>#</sup> used for LM and SEM<sup>\*</sup> used for LM, SEM and TEM<sup>§</sup> *Microcos crassifolia* Burret without any flowering material was excluded from this study

were dehydrated through an ethanol series and critical point dried by using liquid CO<sub>2</sub> as the exchange medium. After coating with gold, they were observed with a Jeol JSM-6400 scanning electron microscope. For transmission electron microscopy (TEM) studies, the pollen samples were fixed in 1% OsO<sub>4</sub> for 90 min, dehydrated through an ethanol series, and then embedded in epoxy resin. Ultrathin sections, cut with a glass knife, were stained with 8% uranyl acetate for 5 minutes and then Reynold's lead citrate (Reynolds, 1963) for 10 minutes. Observations were made using a Philips CM12 TEM.

Pollen morphological data for all species are summarised in Table 2. The size classes of pollen following Erdtman (1952) are classified as small (10–25 µm), medium (25–50 µm) or large (50–100 µm). Terminology follows that of Erdtman (1952) and Punt *et al.* (1994).

## Results

### *GREWIA* L.

(Table 2; Plates 1A–C, 2A–C, 3A–D and 4A–B)

#### *Light Microscopy*

The pollen grains of *Grewia* species are single, isopolar, radially symmetric, tricolporate, and rounded-triangular in equatorial outline (ambs). The pollen grains is medium to large (44–80 µm polar length) with an average polar length of 52.9–74.8 µm and an average equatorial axis 38.6–55 µm (Table 2). Pollen grain shape varies from subprolate (P/E = 1.26) to prolate (P/E = 1.36–1.45).

The apertures are tricolporate. The colpi are 1/2–3/4 of polar axis length, narrow (c. 1.5 µm) to wide (3.5–4.5 µm), provided with acute apices and delimited by a clearly defined margin. The endoapertures are lolongate or lalongate, either as wide as, or slightly wider than the colpi.

#### *Scanning Electron Microscopy*

The pollen grains of *Grewia* have a bireticulate-tectate exine. The muri of the primary reticulum are smooth, but somewhat irregular in thickness. The lumina of the primary reticulum are coarsely reticulate and variable in width and shape, and are infilled by a secondary reticulum comprising few to many finer reticulations and/or perforations of varying width and shape. Two types of tectum ornamentation were observed in *Grewia* pollen: type C (coarsely reticulate with a few perforations/microreticulations) and type D (coarsely reticulate with numerous perforations/microreticulations).

#### *Transmission Electron Microscopy*

The exine is 1–2.54 µm thick and consists of an outer ectexine and an inner endexine.

**Table 2.** Pollen morphological characters of *Grewia* and *Microcos* species in Peninsular Malaysia and Borneo.

| Column:<br>Species                               | 1              | 2              | 3    | 4   | 5  | 6    | 7   | 8     | 9 | 10 | 11 | 12 | 13 |
|--------------------------------------------------|----------------|----------------|------|-----|----|------|-----|-------|---|----|----|----|----|
| <b><i>Grewia</i></b>                             |                |                |      |     |    |      |     |       |   |    |    |    |    |
| <i>occidentalis</i> (type species)               | (58–)62.7(–68) | (38–)42(–48)   | 1.49 | l   | p  | 36.7 | 3   | la    | D | co | po | mt | nu |
| <i>huluperakensis</i>                            | (44–)52.9(–60) | (38–)41.9(–46) | 1.26 | l/m | sp | 28.6 | 1.5 | la    | D | co | po | mt | nu |
| <i>laevigata</i>                                 | (70–)74.8(–80) | (48–)55(–62)   | 1.36 | l   | p  | 45.5 | 4.5 | lo    | D | co | rs | mt | nu |
| <i>multiflora</i>                                | (60–)66(–72)   | (38–)45.6(–52) | 1.45 | l   | p  | 35.6 | 4.4 | la    | D | co | po | mt | nu |
| <i>polygama</i>                                  | (50–)55.6(–60) | (32–)38.6(–44) | 1.44 | l   | p  | 34.2 | 3.5 | la    | C | co | po | mt | fe |
| <b><i>Microcos</i></b>                           |                |                |      |     |    |      |     |       |   |    |    |    |    |
| <i>paniculata</i> (type species)                 | (26–)28.9(–32) | (18–)20.2(–22) | 1.43 | m   | p  | 14.5 | 1.9 | la    | A | fi | po | lt | fe |
| <i>antidesmifolia</i> var. <i>antidesmifolia</i> | (20–)25.8(–29) | (19–)21.6(–24) | 1.19 | s/m | sp | 15.5 | 1.4 | ci    | A | fi | po | lt | fe |
| <i>antidesmifolia</i> var. <i>hirsuta</i>        | (23–)27(–31)   | (15–)22.6(–31) | 1.21 | s/m | sp | 14.7 | 1   | ci    | A | fi | po | lt | fe |
| <i>borneensis</i>                                | (23–)25.3(–28) | (16–)18.8(–22) | 1.35 | s/m | p  | 16.7 | 1.7 | ci    | A | fi | po | lt | fe |
| <i>cinnamomifolia</i>                            | (23–)25.1(–26) | (16–)18.6(–22) | 1.35 | s/m | p  | 15   | 1.2 | ci    | A | fi | po | lt | fe |
| <i>dulitensis</i>                                | (26–)31.1(–36) | (19–)23.5(–27) | 1.32 | m   | sp | 16.8 | 1.8 | ci    | A | fi | po | lt | fe |
| <i>erythrocarpa</i>                              | (29–)32.9(–37) | (19–)22.2(–29) | 1.49 | m   | p  | 19.7 | 2.1 | ci    | A | fi | po | lt | fe |
| <i>fibrocarpa</i>                                | (27–)30.4(–34) | (18–)22(–27)   | 1.38 | m   | p  | 18.1 | 1.6 | ci    | B | fi | po | lt | nu |
| <i>globulifera</i>                               | (24–)29.6(–34) | (20–)22.6(–24) | 1.31 | s/m | sp | 18.9 | 1.4 | la    | B | fi | po | lt | nu |
| <i>gracilis</i>                                  | (24–)27(–29)   | (17–)19.1(–22) | 1.41 | s/m | p  | 17.7 | 1.6 | ci    | A | fi | po | lt | fe |
| <i>henrici</i> ssp. <i>acuta</i>                 | (23–)30.4(–39) | (25–)26.9(–30) | 1.13 | s/m | ps | 16.3 | 1.5 | ci    | B | fi | po | lt | nu |
| <i>hirsuta</i>                                   | (29–)33.6(–37) | (19–)22(–24)   | 1.53 | m   | p  | 17.1 | 1.5 | ci    | B | fi | po | lt | nu |
| <i>kinabaluensis</i>                             | (28–)32.4(–37) | (22–)23.1(–27) | 1.40 | m   | p  | 17.7 | 1.2 | ci    | B | fi | po | lt | nu |
| <i>lanceolata</i>                                | (29–)32.3(–34) | (17–)21(–24)   | 1.54 | m   | p  | 19.7 | 3.1 | ci    | B | fi | po | lt | nu |
| <i>latifolia</i>                                 | (32–)33(–34)   | (20–)21.6(–24) | 1.53 | m   | p  | 24.3 | 1.7 | ci    | A | fi | po | lt | fe |
| <i>latistipulata</i> var. <i>latistipulata</i>   | (26–)29.6(–33) | (17–)21.1(–24) | 1.42 | m   | p  | 16.3 | 3.1 | ci    | B | fi | po | lt | nu |
| <i>laurifolia</i>                                | (24–)25.6(–27) | (17–)19(–22)   | 1.35 | s/m | p  | 17.6 | 1.5 | ci    | B | fi | po | lt | nu |
| <i>malayana</i>                                  | (29–)33.7(–39) | (19–)22.2(–27) | 1.52 | m   | p  | 19   | 1   | ci    | B | fi | po | lt | nu |
| <i>membranifolia</i>                             | (30–)32.6(–35) | (23–)27.1(–30) | 1.20 | m   | sp | 20.4 | 1.5 | ci    | B | fi | po | lt | nu |
| <i>opaca</i>                                     | (24–)34.1(–42) | (17–)21.4(–28) | 1.60 | s/m | p  | 16.8 | 1.2 | ci    | A | fi | po | lt | fe |
| <i>ossea</i>                                     | (27–)31.1(–37) | (17–)20.8(–24) | 1.51 | m   | p  | 20   | 1.5 | ci    | A | fi | po | lt | fe |
| <i>pachyphylla</i>                               | (28–)30.1(–33) | (20–)23.1(–28) | 1.30 | m   | sp | 16.7 | 1.3 | ci/la | A | fi | po | lt | fe |
| <i>pearsonii</i>                                 | (31–)35(–38)   | (20–)21.5(–23) | 1.62 | m   | p  | 20   | 1.3 | ci/la | B | fi | po | lt | nu |

**Table 2.** *Continued:-*

| Column:                                    |                |                |      |   |    |      |     |       |   |    |    |    |    |
|--------------------------------------------|----------------|----------------|------|---|----|------|-----|-------|---|----|----|----|----|
| Species                                    | 1              | 2              | 3    | 4 | 5  | 6    | 7   | 8     | 9 | 10 | 11 | 12 | 13 |
| <b><i>Microcos</i></b>                     |                |                |      |   |    |      |     |       |   |    |    |    |    |
| <i>phaneroneura</i>                        | (33-)34.5(-38) | (20-)23.2(-25) | 1.49 | m | p  | 19.6 | 2.3 | ci    | A | fī | po | lt | fe |
| <i>reticulata</i>                          | (28-)28.8(-31) | (19-)21.1(-23) | 1.37 | m | p  | 15   | 1.4 | ci    | B | fī | po | lt | nu |
| <i>riparia</i>                             | (27-)29.7(-32) | (18-)21.6(-24) | 1.38 | m | p  | 16.9 | 3.1 | ci    | A | fī | po | lt | fe |
| <i>stylocarpoides</i>                      | (33-)34.8(-40) | (23-)25.7(-30) | 1.35 | m | p  | 18.2 | 1.5 | ci    | A | fī | po | lt | fe |
| <i>subcordifolia</i>                       | (30-)32.3(-38) | (20-)23.1(-28) | 1.40 | m | p  | 14.7 | 1.7 | ci    | A | fī | po | lt | fe |
| <i>subpetala</i>                           | (28-)30.6(-35) | (20-)21.6(-25) | 1.42 | m | p  | 17.2 | 1.4 | ci    | A | fī | po | lt | fe |
| <i>sumatrana</i>                           | (28-)30.8(-33) | (18-)20.6(-23) | 1.50 | m | p  | 16.8 | 1.2 | ci    | B | fī | po | lt | nu |
| <i>tomentosa</i>                           | (26-)27.2(-28) | (19-)20.9(-23) | 1.30 | m | sp | 16.3 | 3.5 | ci/la | B | fī | po | lt | nu |
| <i>triflora</i> var. <i>triflora</i>       | (28-)29.6(-33) | (19-)20.6(-23) | 1.44 | m | p  | 17.8 | 1.6 | ci/la | B | fī | po | lt | nu |
| <i>triflora</i> var. <i>longipetiolata</i> | (30-)32(-35)   | (23-)24.5(-28) | 1.31 | m | sp | 16.8 | 1.4 | ci/la | B | fī | po | lt | nu |

Legend: / = or

Columns:

1. Length polar axis, P (in  $\mu\text{m}$ )
2. Equatorial diameter, E (in  $\mu\text{m}$ )
3. Ratio between length of the polar axis and equatorial axis (P/E ratio)
4. Size classes (Erdtman, 1952: s = small, 10–25  $\mu\text{m}$ ; m = medium, 25–50  $\mu\text{m}$ ; l = large, 50–100  $\mu\text{m}$ )
5. Shape classes (Erdtman, 1952: p = prolate; ps = prolate spheroidal; sp = subprolate)
6. Average length of colpus (in  $\mu\text{m}$ )
7. Average width of colpus (in  $\mu\text{m}$ )
8. Endoaperture shape (ci = circular; la = lalongate; lo = lolongate)
9. Type of tectum ornamentation (A = finely reticulate with a few perforations/microreticulations; B = finely reticulate with numerous perforations/microreticulations; C = coarsely reticulate with a few perforations/microreticulations; D = coarsely reticulate with numerous perforations/microreticulations)
10. Muri of primary reticulum (co = coarse; fī = fine)
11. Lumina shape (po = polygonal; rs = reticulate subrugulate)
12. Lumina diameter (lt = < 1.5  $\mu\text{m}$ ; mt = > 1.5  $\mu\text{m}$ )
13. Lumina perforations/microreticulations (fe = few; nu = numerous)

The ectexine is thicker than the endexine except at the aperture region. The tectum is 0.23–0.86  $\mu\text{m}$  thick. The columellae are simple, straight, distinctly arranged in single rows in a reticulate pattern, and either support the raised muri of the primary reticulum or support the sunken secondary reticulum. The columellae are 0.46–1.46  $\mu\text{m}$  tall and 0.29–0.77  $\mu\text{m}$  thick. The spaces between columellae range 0.47–1.1  $\mu\text{m}$  in height and 0.18–1  $\mu\text{m}$  in width. The foot layer is 0.24–0.53  $\mu\text{m}$  thick at the mesocolpia, and is often thickened near the aperture.

The endexine appears smooth, thin and is not always discernible except at the aperture region. Below the endexine, at the apertural region, there are generally darkly stained, stout, radial elements towards the intine. The intine is fibrillar and, particularly at the apertures, stratified into a fibrillar layer and enveloping a lens-shaped body with a microtubule layer.

### Remarks

Apart from minor differences, the pollen morphological characters of the Peninsular Malaysian and Bornean species of *Grewia* conform to those of *G. occidentalis* (the type species of the genus), the pollen of *G. occidentalis* compared with *Grewia* species from Peninsular Malaysia and Borneo has a thinner tectum and columellae (0.73–1.23  $\mu\text{m}$ ), and foot layer and endexine (0.06–0.2  $\mu\text{m}$ ).

The pollen of *Grewia laevigata* can be distinguished from pollen of other *Grewia* species by the perforations of the secondary reticulum that encroach into the margins of the primary muri. Pollen of *G. polygama* differs from that of *G. huluperakensis* and *G. multiflora* by having fewer microreticulations/perforations of the lumina.

Sharma (1969) reported that pollen size of *Grewia* species from India was (27.2–) 31(–78.2)  $\mu\text{m}$  in polar length and (18.7–) 21(–57.8)  $\mu\text{m}$  in equatorial diameter. However, among the 17 species he studied, one was a *Microcos* species: *G. microcos* L. is now *Microcos paniculata*. By omitting the pollen size of this species ( $P=(27.2-)$  31(–34)  $\mu\text{m}$ ;  $E=(18.7-)$  21(–22.1)  $\mu\text{m}$ ) from the data, the pollen size of these *Grewia* species in India was (40.8–) 47.4(–78.2)  $\mu\text{m}$  in polar length and (28.9–) 32.6(–57.8)  $\mu\text{m}$  in equatorial diameter. Therefore, in India pollen size of *Grewia* species was larger than that of *Microcos* species (= *G. microcos*).

The exine thickness of *Grewia* species from China was reported by Zhang and Chen (1984) as more than 2.3  $\mu\text{m}$ . This falls within the range of the present study, 0.73–2.54  $\mu\text{m}$  thick.

## MICROCOS L.

(Tables 2 and 3; Plates 1D–F, 2D–F, 3E–H and 4C–D)

### Light Microscopy

The pollen grains in *Microcos* are single, isopolar, radially symmetric, tricolporate, and rounded-triangular in equatorial outline (ambs). Size ranges from small to medium

(20–42  $\mu\text{m}$  polar length) with an average polar length of 25.1–35  $\mu\text{m}$  and an average equatorial diameter of 18.6–26.9  $\mu\text{m}$ . Most *Microcos* species possess medium-sized pollen grains (Table 2). Pollen grain shape varies from prolate spheroidal ( $P/E = 1.13$ ) to subprolate ( $P/E = 1.19$ – $1.32$ ) or prolate ( $P/E = 1.35$ – $1.62$ ).

The colpi are  $1/2$  to  $3/4$  the length of the polar axis, narrow to wide, with acute apices, and delimited by a distinct margin. In most species the endoapertures are circular, but are lalongate in *M. globulifera* and circular to lalongate in *M. pachyphylla*, *M. pearsonii*, *M. tomentosa*, and *M. triflora* (both varieties). In most species, the endoapertures are as wide as or slightly wider than the colpi.

### Scanning Electron Microscopy

The tectum of *Microcos* species are biretulate-ectate. The muri of the primary reticulum are smooth and of somewhat irregular thickness. The lumina of the primary reticulum are finely reticulate and are infilled by secondary reticulum with minute to large microreticulations/perforations of variable number and shape. Two types of tectum ornamentation are found in *Microcos* pollen: type A (finely reticulate with a few perforations/microreticulations) and type B (finely reticulate with numerous perforations/microreticulations).

### Transmission Electron Microscopy

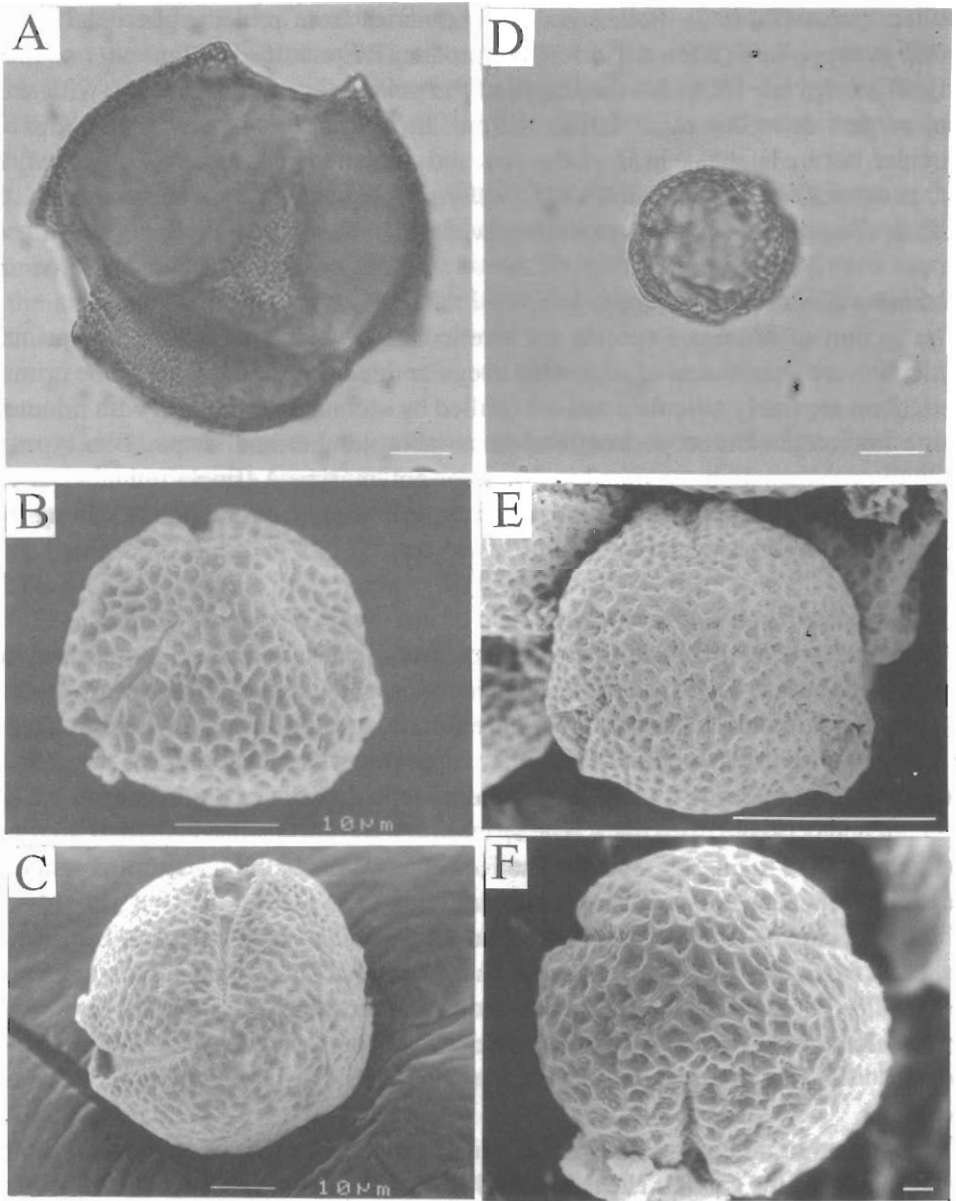
The exine is 0.70–1.05  $\mu\text{m}$  thick and consists of an outer ectexine and an inner endexine. The ectexine is thicker than nexine except at the aperture region. The tectum is 0.18–0.46  $\mu\text{m}$  thick. The columellae are simple, straight, and distinctly arranged in single rows in a reticulate pattern, either supporting the raised muri of the primary reticulum or supporting the sunken secondary reticulum. The columellae are 0.2–0.5  $\mu\text{m}$  tall and 0.14–0.32  $\mu\text{m}$  thick. The spaces between columellae is 0.18–0.45  $\mu\text{m}$  in height and 0.14–0.55  $\mu\text{m}$  in width. The foot layer varies in thickness but is generally markedly thickened at the aperture margin.

The endexine is usually thin and always traceable except towards the apertures, where it may be thicker. The intine often has numerous microtubule layers enveloped by the fibrillar layer. At the apertural region there are relatively stout, darkly stained, radial elements between intine and endexine.

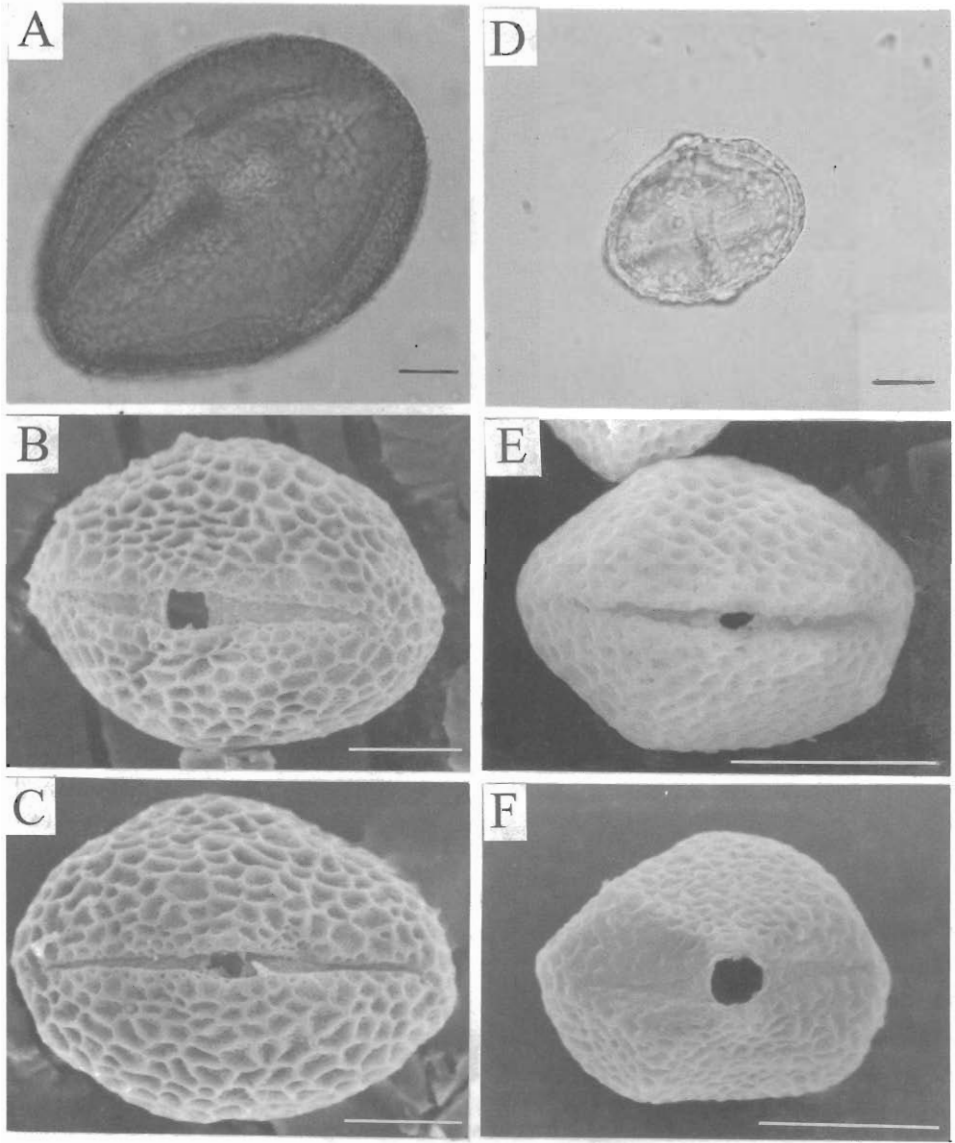
### Remarks

The pollen morphology in the species examined matches that of *M. paniculata* (the type species of the genus). The palynological data in this study conform well with the results reported in China by Long (1982), Zhang and Chen (1984), Wang *et al.* (1995); and in India by Sharma (1969; *G. microcos* = *M. paniculata*).

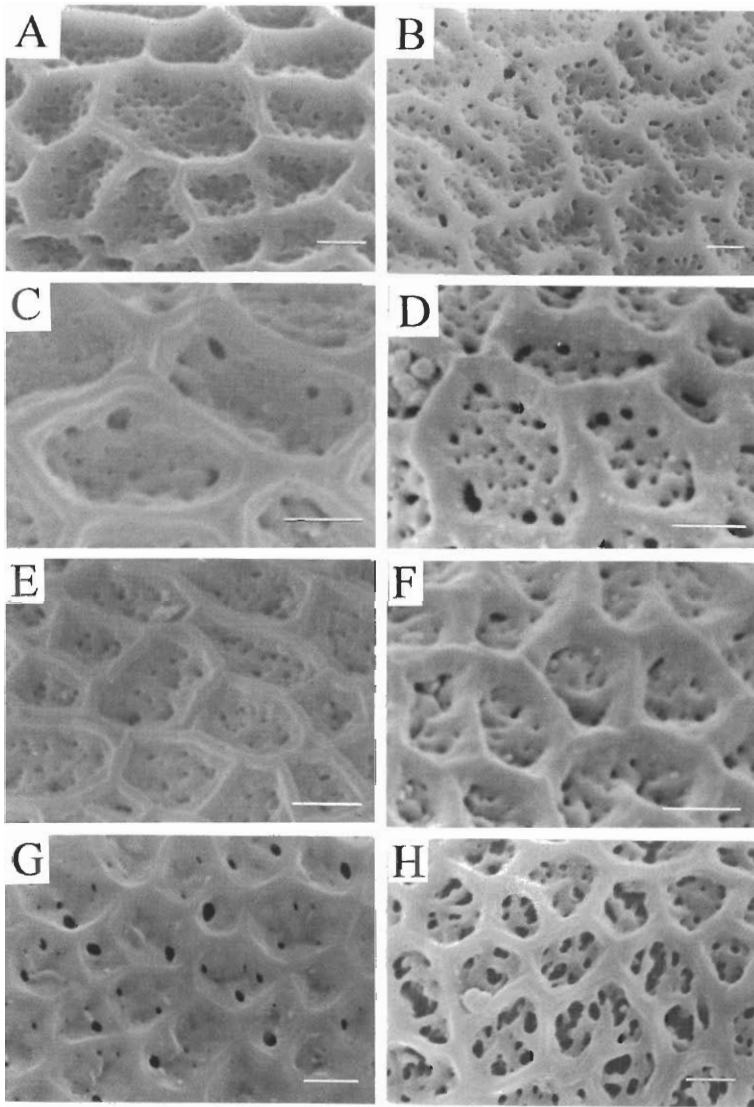
Among the Peninsular Malaysian and Bornean *Microcos* species examined, three main groups can be discerned based on whether the pollen is prolate-spheroidal,



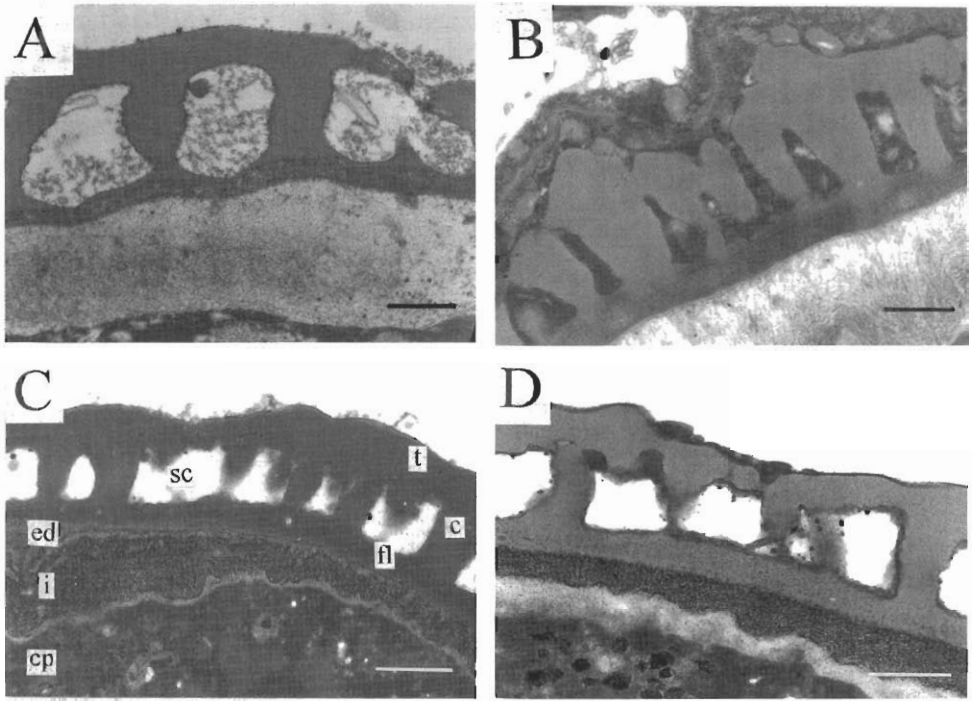
**Plate 1.** LMs and SEMs of selected *Grewia* and *Microcos* species showing tricolporate grains in polar view. **A & C:** *G. laevigata* (A: Whitmore 3729; C: Hashim SAN 33470). **B:** *G. multiflora* (Motley 240). **D:** *M. fibrocarpa* (Kochummen 80640). **E:** *M. paniculata* (Cramer 3405). **F:** *M. malayana* (Loh FRI 19249). Scale bar = 1 µm in F; 10 µm in A–E.



**Plate 2.** LMs and SEMs of selected *Grewia* and *Microcos* species showing tricolporate grains in equatorial view. **A:** *G. laevigata* (Whitmore 3729). **B:** *G. laevigata* (Hashim SAN 33470) with lolongate endoaperture. **C:** *G. multiflora* (Motley 240) with lalongate endoaperture. **D:** *M. fibrocarpa* (Kochummen 80640). **E:** *M. dulitensis* (Richards 1767) with circular endoaperture. **F:** *M. riparia* (Hallier 2208) with circular endoaperture. Scale bar = 1  $\mu$ m in F; 10  $\mu$ m in A–E.



**Plate 3.** SEMs of selected *Grewia* and *Microcos* species showing exine detail of coarsely reticulate pattern (A–D) or finely reticulate pattern (E–H) and lumina detail. **A:** *G. multiflora* (Motley 240), muri variable in width and shape. **B:** *G. laevigata* (Hashim SAN 33470), muri branching inwards toward the lumina forming reticulate subrugulate sculpturing. **C:** *G. polygama* (Kiah SFN 35286), lumina occupied by a few microreticulations/perforations. **D:** *G. huluperakensis* (Turner 94-94), lumina occupied by numerous microreticulations. **E:** *M. henrici* ssp. *acuta* (Ilias S 45121), muri variable in width and shape. **F:** *M. kinabaluensis* (Chew & Corner RSNB 4994). **G:** *M. dulitensis* (Richards 1767), lumina occupied by a few microreticulations. **H:** *M. membranifolia* (Singh SAN 30672), lumina occupied by numerous microreticulations. Scale bar = 1  $\mu$ m in A–H.



**Plate 4.** TEMs micrograph of selected *Grewia* and *Microcos* species showing structure of ectexine and endexine. **A:** *G. occidentalis* (Moss 3959). **B:** *G. multiflora* (Motley 240). **C:** *M. paniculata* (Kanodia 88480). **D:** *M. tomentosa* (Suppiah FRI 28239). Scale bar = 0.36  $\mu\text{m}$  in D; 0.45  $\mu\text{m}$  in A & C; 0.59  $\mu\text{m}$  in B. Abbreviation used: c = columellae; cp = cytoplasm; ed = endexine; fl = foot layer; i = intine; sc = spaces between columellae; t = tectum.

subprolate or prolate. In species with subprolate pollen grains, three subgroups can be distinguished based on whether the endoapertures are circular, lalongate or circular-lalongate. Other pollen morphological characters, e.g. P/E ratio and number of lumina perforations, can be used to further subdivide these subgroups. Likewise, in species with prolate pollen grains, by using palynological characters such as the number of perforations of the lumina, P/E ratios and endoapertures shape, further subdivisions to smaller groups can be made (Table 3).

## Discussion

The pollen morphology of both genera is very similar and adds further confirmation that species of *Grewia* and *Microcos* in Peninsular Malaysia and Borneo have pollen morphological characters belonging to the 'Grewia-type' of Erdtman (1952).

**Table 3.** Grouping of *Microcos* species in Peninsular Malaysia and Borneo based on pollen morphological characters.

| POLLEN SHAPE                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |                                                                                                                                                                                                                    |                               |                                                                                                     |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |                                                                                                                                                                         |                                                                                                                                                                                                                                                                                                                          |                                                                                                                                                                                                                                                                                                                                                                                        |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------|-----------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Prolate-spheroidal                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            | Subprolate                                                                                                                                                                                                         |                               |                                                                                                     | Prolate                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |                                                                                                                                                                         |                                                                                                                                                                                                                                                                                                                          |                                                                                                                                                                                                                                                                                                                                                                                        |
| <i>M. henrici</i><br><i>ssp. acuta</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        | <i>M. antidesmifolia</i> (both varieties), <i>M. dulitensis</i> , <i>M. globulifera</i> , <i>M. membranifolia</i> ,<br><i>M. pachyphylla</i> , <i>M. tomentosa</i> , <i>M. triflora</i> var. <i>longipetiolata</i> |                               |                                                                                                     | <i>M. borneensis</i> , <i>M. cinnamomifolia</i> , <i>M. erythrocarpa</i> , <i>M. fibrocarpa</i> ,<br><i>M. gracilis</i> , <i>M. hirsuta</i> , <i>M. kinabaluensis</i> , <i>M. lanceolata</i> , <i>M. latifolia</i> ,<br><i>M. latistipulata</i> var. <i>latistipulata</i> , <i>M. laurifolia</i> , <i>M. malayana</i> , <i>M. opaca</i> ,<br><i>M. ossea</i> , <i>M. pearsonii</i> , <i>M. phaneroneura</i> , <i>M. reticulata</i> , <i>M. riparia</i> ,<br><i>M. stylocarpoides</i> , <i>M. subcordifolia</i> , <i>M. subepetala</i> , <i>M. sumatrana</i> ,<br><i>M. triflora</i> var. <i>triflora</i> |                                                                                                                                                                         |                                                                                                                                                                                                                                                                                                                          |                                                                                                                                                                                                                                                                                                                                                                                        |
| ENDOAPERTURES                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |                                                                                                                                                                                                                    |                               |                                                                                                     | NUMBER OF LUMINA PERFORATIONS                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |                                                                                                                                                                         |                                                                                                                                                                                                                                                                                                                          |                                                                                                                                                                                                                                                                                                                                                                                        |
| Circular                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |                                                                                                                                                                                                                    | Lalongate                     | Circular-lalongate                                                                                  | A Few                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |                                                                                                                                                                         | Numerous                                                                                                                                                                                                                                                                                                                 |                                                                                                                                                                                                                                                                                                                                                                                        |
| <i>M. antidesmifolia</i> (both varieties),<br><i>M. dulitensis</i> , <i>M. membranifolia</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |                                                                                                                                                                                                                    | <i>M. globulifera</i>         | <i>M. pachyphylla</i> , <i>M. tomentosa</i> ,<br><i>M. triflora</i> var. <i>longipetiolata</i>      | <i>M. borneensis</i> , <i>M. cinnamomifolia</i> ,<br><i>M. erythrocarpa</i> , <i>M. gracilis</i> , <i>M. latifolia</i> ,<br><i>M. opaca</i> , <i>M. ossea</i> , <i>M. phaneroneura</i> ,<br><i>M. riparia</i> , <i>M. stylocarpoides</i> ,<br><i>M. subcordifolia</i> , <i>M. subepetala</i>                                                                                                                                                                                                                                                                                                             |                                                                                                                                                                         | <i>M. fibrocarpa</i> , <i>M. hirsuta</i> ,<br><i>M. kinabaluensis</i> , <i>M. lanceolata</i> ,<br><i>M. latistipulata</i> var. <i>latistipulata</i> ,<br><i>M. laurifolia</i> , <i>M. malayana</i> ,<br><i>M. pearsonii</i> , <i>M. reticulata</i> ,<br><i>M. sumatrana</i> , <i>M. triflora</i> var.<br><i>triflora</i> |                                                                                                                                                                                                                                                                                                                                                                                        |
| NUMBER OF LUMINA PERFORATIONS                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |                                                                                                                                                                                                                    | NUMBER OF LUMINA PERFORATIONS |                                                                                                     | P/E RATIO                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |                                                                                                                                                                         | ENDOAPERTURES                                                                                                                                                                                                                                                                                                            |                                                                                                                                                                                                                                                                                                                                                                                        |
| A Few                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         | Numerous                                                                                                                                                                                                           | A Few                         | Numerous                                                                                            |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |                                                                                                                                                                         |                                                                                                                                                                                                                                                                                                                          |                                                                                                                                                                                                                                                                                                                                                                                        |
| <i>M. antidesmifolia</i><br>(both varieties) <sup>1</sup> ,<br><i>M. dulitensis</i> <sup>1</sup>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              | <i>M. membranifolia</i>                                                                                                                                                                                            | <i>M. pachyphylla</i>         | <i>M. tomentosa</i> <sup>2</sup> ,<br><i>M. triflora</i> var.<br><i>longipetiolata</i> <sup>2</sup> |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |                                                                                                                                                                         |                                                                                                                                                                                                                                                                                                                          |                                                                                                                                                                                                                                                                                                                                                                                        |
| <b>Remarks:</b><br><sup>1</sup> pollen of <i>M. dulitensis</i> differs slightly from that of <i>M. antidesmifolia</i> (both varieties) in being larger, (26–)31.1(–36) x (19–)23.5(–27) µm, with P/E ratio of 1.32.<br><sup>2</sup> pollen of <i>M. tomentosa</i> only slightly differs from that of <i>M. triflora</i> var. <i>longipetiolata</i> in being smaller (26–)27.2(–28) x (19–)20.9(–23) µm.<br><sup>3</sup> pollen of <i>M. pearsonii</i> can be differentiated from that of <i>M. triflora</i> var. <i>triflora</i> by its larger size, (31–)35(–38) x (20–)21.5(–23) µm, and larger P/E ratio, 1.62.<br><sup>4,5</sup> The P/E ratio of pollen is either ≤ 1.40 ( <i>M. fibrocarpa</i> , <i>M. kinabaluensis</i> , <i>M. laurifolia</i> , and <i>M. reticulata</i> ) or > 1.40 ( <i>M. hirsuta</i> , <i>M. lanceolata</i> , <i>M. latistipulata</i> var. <i>latistipulata</i> , <i>M. malayana</i> , and <i>M. sumatrana</i> ). |                                                                                                                                                                                                                    |                               |                                                                                                     | ≤ 1.40                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   | > 1.40                                                                                                                                                                  | Circular-lalongate                                                                                                                                                                                                                                                                                                       | Circular                                                                                                                                                                                                                                                                                                                                                                               |
|                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |                                                                                                                                                                                                                    |                               |                                                                                                     | <i>M. borneensis</i> ,<br><i>M. cinnamomifolia</i> ,<br><i>M. riparia</i> ,<br><i>M. stylocarpoides</i> ,<br><i>M. subcordifolia</i>                                                                                                                                                                                                                                                                                                                                                                                                                                                                     | <i>M. erythrocarpa</i> ,<br><i>M. gracilis</i> ,<br><i>M. latifolia</i> ,<br><i>M. opaca</i> ,<br><i>M. ossea</i> ,<br><i>M. phaneroneura</i> ,<br><i>M. subepetala</i> | <i>M. pearsonii</i> <sup>1</sup> ,<br><i>M. triflora</i><br>var. <i>triflora</i> <sup>3</sup>                                                                                                                                                                                                                            | <i>M. fibrocarpa</i> <sup>4</sup> ,<br><i>M. hirsuta</i> <sup>5</sup> ,<br><i>M. kinabaluensis</i> <sup>1</sup> ,<br><i>M. lanceolata</i> <sup>5</sup> ,<br><i>M. latistipulata</i> var.<br><i>latistipulata</i> <sup>5</sup> ,<br><i>M. laurifolia</i> <sup>4</sup> ,<br><i>M. malayana</i> <sup>5</sup> ,<br><i>M. reticulata</i> <sup>4</sup> ,<br><i>M. sumatrana</i> <sup>5</sup> |

On the basis of palynological characters, the genus *Microcos* in Peninsular Malaysia and Borneo can be distinguished from *Grewia* by a combination of the following characters: pollen size, exine thickness, tectum ornamentation and lumina diameter. The main morphological differences between pollen of *Grewia* and *Microcos* are summarised in Table 4. To some extent, this study supports Burret's view (1926) for segregating *Microcos* from *Grewia*.

**Table 4.** Main differences between pollen of *Grewia* and *Microcos* species in Peninsular Malaysia and Borneo.

| Genus:                      | <i>Grewia</i>       | <i>Microcos</i>     |
|-----------------------------|---------------------|---------------------|
| Characters                  |                     |                     |
| <b>Size</b>                 |                     |                     |
| Length polar axis, P (µm)   | (44–)53–75(–80)     | (20–)25–35(–42)     |
| Equatorial diameter, E (µm) | (32–)39–55(–62)     | (15–)19–27(–31)     |
| <b>Exine</b>                |                     |                     |
| Thickness (µm)              | (1–)1.55–2.15(–2.5) | (0.70)0.84–0.90(–1) |
| <b>Tectum</b>               |                     |                     |
| Ornamentation               | coarsely reticulate | finely reticulate   |
| Lumina diameter (µm)        | > 1.5               | < 1.5               |

Chung (2001, 2002) 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 the morphology of inflorescences, flowers and fruits; by Chattaway (1934) based on wood anatomy; Zhang and Chen (1984) based on pollen morphology; and by Bayer *et al.* (1999) based on combined analyses of plastid *atpB* and *rbcL* DNA sequences.

Conclusions

This study confirms that within the Tiliaceae the pollen of *Grewia* and *Microcos* species occurring in Peninsular Malaysia and Borneo conforms well with the so-called 'Grewia-type' (Erdtman, 1952). Comparison based on results of this study and all available published information indicates that pollen of *Microcos* differs from that of *Grewia* in having smaller size, thinner exine, finer tectum reticulation and smaller lumina, which supports the segregation of *Microcos* from *Grewia*.

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