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# POLLEN MORPHOLOGY OF *GREWIA* SPECIES (MALVACEAE: GREWIOIDEAE) IN TELANGANA, INDIA, AND ITS TAXONOMIC SIGNIFICANCE

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## ABSTRACT

*Grewia L. (Malvaceae: Grewioideae) is a large genus of shrubs, small trees and climbers, several species of which grow in the dry deciduous forests and scrub of Telangana and are valued for edible fruits, fodder and fibre. Species delimitation in the genus is often difficult, especially when only sterile or flowering material is available. Pollen characters have separated Grewia from Microcos in Malesia and have been documented for many Grewioideae in world and regional surveys, but published palynological information on the Grewia species of Telangana remains scarce. Pollen of six species (G. damine, G. flavescens, G. hirsuta, G. orbiculata, G. tiliifolia and G. villosa) was examined by light and scanning electron microscopy, using three populations per species and three plants per population (54 plants; 25 grains per plant). In the sample results presented here, all species produced monad, isopolar, 3-colporate, prolate and reticulate grains of the Grewia type. Species means ranged from 45.7 to 57.2 µm for the polar axis (P), 1.38 to 1.57 for P/E, 1.67 to 2.01 µm for exine thickness and 1.78 to 2.86 µm for lumina width. Species identity accounted for 71% of the total variance in P and 60% of that in lumina width, whereas the contribution of populations was small. The first principal component (84.3% of variance) summarised overall grain size, exine thickness and lumina width. Linear discriminant analysis with leave-one-population-out cross-validation assigned 74.1% of plants to the correct species; G. tiliifolia, G. damine and G. flavescens were fully separated, whereas G. hirsuta and G. orbiculata overlapped. A provisional pollen key is proposed.*

***Keywords:*** *Grewia; Grewioideae; Malvaceae; pollen morphology; palynology; exine; scanning electron microscopy; multivariate analysis; Telangana*

## 1. INTRODUCTION

Pollen grains are enclosed by a resistant outer wall, the exine, whose shape, apertures and sculpture frequently differ among plant groups. Palynology has therefore long contributed to plant classification: pollen characters are under strong genetic control and can be studied on very small amounts of material, including old herbarium specimens. Standard glossaries and illustrated guides now provide a common terminology for describing pollen (Punt et al. 2007; Halbritter et al. 2018).

### 1.1 *Grewia* and related genera

*Grewia* belongs to Grewioideae, one of the subfamilies of the broadly circumscribed Malvaceae. A combined analysis of floral, fruit and leaf morphology with DNA sequence data divided Grewioideae into two tribes, Apeibeae and Grewieae (Brunken & Muellner 2012). The genus comprises about 280–300 species distributed from tropical Africa and Madagascar to the Himalayas, China, India, Sri Lanka, South-East Asia, the western Pacific and northern Australia (Chung et al. 2003). In India, the boundary between *Grewia* and the closely related genus *Microcos* has changed over time; while revising *Grewia* for India, Nandikar & Janarthanam (2016) identified taxonomic and nomenclatural inconsistencies in the floristic treatment of *M. paniculata* and *M. calophylla* and resolved them separately. The revision of *Grewia* for Peninsular Malaysia and Borneo, which provided keys to *Grewia* and *Microcos* based on both macro- and micromorphological characters, illustrates such work in another region (Chung 2006).

Several Indian *Grewia* species are of economic interest. The floral biology of *Grewia flavescens* has been described in the context of its potential as an underutilised fruit crop (Veeresh Kumar et al. 2017), and the breeding behaviour of the cultivated phalsa, *Grewia asiatica*, has been related to its reproductive success (Wani et al. 2015). Reliable pollen descriptions are relevant to both lines of work.

### 1.2 Previous studies of *Grewia* pollen

The studies most relevant to the present work are summarised in Table 1, and the pollen sizes they report are compared in Figure 2. Chung et al. (2003) examined the pollen of 5 *Grewia* and 31 *Microcos* species from Peninsular Malaysia and Borneo by light, scanning and transmission electron microscopy. All grains were tricolporate, that is, with three elongated colpi each bearing a central endoaperture (Figure 1), and all had a reticulate tectum consistent with the previously recognised *Grewia* type. *Grewia* pollen was clearly larger than that of *Microcos*, with mean polar axes of 53–75 µm against 25–35 µm; it also had a coarser reticulum, with lumina wider than 1.5 µm, and a thicker exine (1.55–2.15 µm against 0.84–0.90 µm). The same authors noted that an earlier Indian study (Sharma 1969, cited in Chung et al. 2003) had used tectum ornamentation and lumina width to recognise four pollen types among Indian *Grewia* species; that study could not be consulted directly and is cited here only through Chung et al. (2003).

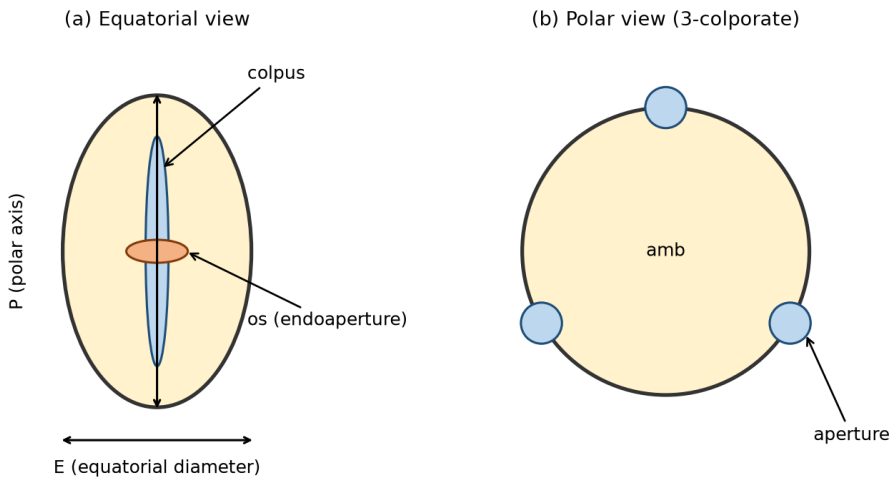


**Figure 1.** Pollen terminology used in this study: (a) equatorial view showing the polar axis (P), equatorial diameter (E), colpus and os (endoaperture); (b) polar view showing the amb and the three apertures of a 3-colporate grain. Schematic diagram.

For the World Pollen and Spore Flora, Perveen et al. (2004) examined the pollen of 85 species from 32 genera of Grewioideae, Tilioideae and Brownlowioideae by light, scanning and transmission electron microscopy. Their *Grewia* grains were prolate and 3-colporate, with a polar axis of (26–)48.5(–71) µm and a P/E ratio of 1.27–2.05, and under SEM the exine was coarsely reticulate with perforated lumina 0.4–3.6 µm across. In Pakistan, Perveen & Qaiser (2007) described the pollen of 12 species of *Corchorus*, *Grewia* and *Triumfetta* by light and scanning electron microscopy and recorded generally tricolporate, prolate grains with reticulate to rugulate-reticulate exine.

Pollen elsewhere in Malvaceae differs markedly. Christensen (1986) studied more than 120 species from about 40 genera of Malvaceae in the narrow sense and found mostly spiny, spheroidal grains, with an evolutionary trend from 3-zonocolporate to polyporate types. An ultrastructural study of pollen and anther development in *Luehea divaricata*, another member of Grewioideae, discussed the systematic value of tapetal transfer cells, orbicules and the male germ unit (Lattar et al. 2012), showing that pollen may carry taxonomic information beyond external morphology.

**Table 1.** Published pollen studies of *Grewia* and related Grewioideae used as background (summarised from the cited articles).

| **Study** | **Taxa and region** | **Methods** | **Main points reported** |
|---|---|---|---|
| Chung et al. 2003 | 5 *Grewia* and 31 *Microcos* species, Peninsular Malaysia and Borneo | LM, SEM, TEM; acetolysed grains | All tricolporate and reticulate (*Grewia* type); *Grewia* larger (mean P 53–75 µm), coarser reticulum (lumina > 1.5 µm) and thicker exine (1.55–2.15 µm) than *Microcos* (P 25–35 µm; exine 0.84–0.90 µm) |
| Perveen et al. 2004 | 85 species, 32 genera of Grewioideae, Tilioideae and Brownlowioideae; world survey | LM, SEM, TEM | *Grewia* grains prolate, 3-colporate; P (26–)48.5(–71) µm; P/E 1.27–2.05; lumina 0.4–3.6 µm |
| Perveen & Qaiser 2007 | 12 species, 3 genera of Grewioideae, Pakistan | LM and SEM | Grains generally tricolporate and prolate; exine reticulate to rugulate-reticulate |

LM, light microscopy; SEM, scanning electron microscopy; TEM, transmission electron microscopy; P, polar axis length. Sizes are taken from the cited papers, which used different preparation and measurement protocols, and are therefore only approximately comparable.

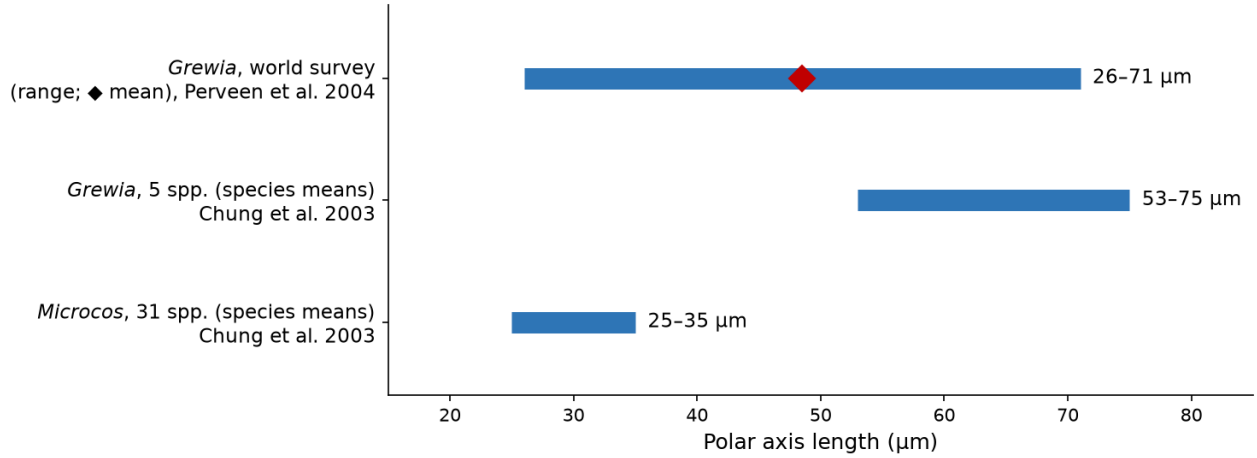


**Figure 2.** Published pollen sizes of *Grewia* and *Microcos*: the full *Grewia* range and mean from Perveen et al. (2004), and the ranges of species means for *Grewia* and *Microcos* from Chung et al. (2003). Redrawn from published values; differences in methods mean the bars are an approximate guide only.

### 1.3 Research gap and objectives

Published palynological information on the *Grewia* species of Telangana is scarce, and we are not aware of a study in the state that combines light and scanning electron microscopy with sampling of several populations per species. The broader surveys (Chung et al. 2003; Perveen et al. 2004; Perveen & Qaiser 2007) deal with other regions and overlap only partly with the regional flora. The present study therefore aimed to (i) describe the pollen of the *Grewia* species occurring in Telangana by LM and SEM, (ii) quantify variation within and between species using several populations per species, and (iii) test with multivariate methods whether pollen characters can discriminate the species.

Grain size is affected by preparation and mounting, and Reitsma (1969) showed that different treatments can cause shrinkage or swelling of recent pollen. A single, fully documented preparation protocol was therefore used for all samples, and comparisons with published sizes are made with this caveat.

### 1.4 Research questions and hypotheses

- **Q1.** What are the pollen characters (shape, size, apertures, exine thickness and ornamentation) of the *Grewia* species of Telangana?
- **Q2.** How much do these characters vary among populations within species?
- **Q3.** Do the characters, singly or in combination, discriminate the species?
- **Q4.** Are the Telangana grains consistent with published descriptions of the genus from other regions (Chung et al. 2003; Perveen et al. 2004; Perveen & Qaiser 2007)?

Three working hypotheses were tested. H1: all species produce tricolporate, reticulate grains of the *Grewia* type (Chung et al. 2003; Perveen et al. 2004). H2: species differ more in quantitative characters (size, P/E, lumina width and exine thickness) and in the fine structure of the reticulum than in aperture type. H3: some pairs of species overlap so strongly that pollen alone does not separate them.

## 2. MATERIALS AND METHODS

### 2.1 Study area and species

Telangana lies on the Deccan Plateau in south-central India and has a semi-arid to dry sub-humid climate, with most rainfall during the south-west monsoon followed by a long dry season. *Grewia* species occur mainly in dry deciduous forest, scrub, rocky hills and field margins. The list of target species was compiled from regional floras, recent Indian taxonomic work on *Grewia* and *Microcos* (Nandikar & Janarthanam 2016) and herbarium records, and was confirmed in the field. Six species were studied: *Grewia damine* Gaertn., *G. flavescens* Juss., *G. hirsuta* Vahl, *G. orbiculata* Rottler, *G. tiliifolia* Vahl and *G. villosa* Willd. No species was recorded for Telangana without a voucher specimen. [Localities, districts and voucher numbers to be inserted.]

### 2.2 Sampling

Sampling targets are given in Table 2. Three populations per species were sampled in different districts, at least 10 km apart where possible, and flowers were collected from three plants per population. Mature flower buds close to anthesis were collected so that the anthers were full but not yet dehiscent. A voucher with flowers (and fruits when present) was prepared for every plant sampled and deposited in a recognised herbarium [herbarium and accession numbers to be inserted].

**Table 2.** Sampling and measurement design.

| Item | Target |
|---|---|
| Species | Six species, each confirmed with voucher specimens |
| Populations per species | 3, from different districts, at least 10 km apart where possible |
| Plants per population | 3, each with a voucher |
| Grains measured by LM | 25 per plant (225 per species) |
| Grains imaged by SEM | At least 10 per plant, from at least 2 populations per species |
| Views | Equatorial and polar, for each plant |
| Repeat measurement | A random subset re-measured by a second observer blind to species identity |

### 2.3 Permissions

Material was collected with the permission of the Telangana State Forest Department on forest land and of landowners elsewhere, in accordance with the Biological Diversity Act, 2002. Only a few flowers were taken from each plant.

### 2.4 Pollen preparation

Pollen was acetolysed by the standard method to remove the cell contents and expose the exine, with the same acetolysis time and temperature for all samples. For light microscopy, grains were mounted in glycerine jelly, the slides were sealed, and measurements were made within a fixed interval after mounting, because mounting media can alter grain size (Reitsma 1969). For SEM, acetolysed grains were suspended in ethanol, air-dried on aluminium stubs and sputter-coated with gold or gold–palladium. A few untreated (non-acetolysed) grains were also examined by SEM to confirm that acetolysis had not altered the surface.

### 2.5 Characters scored

Terminology follows Punt et al. (2007) and Halbritter et al. (2018). The characters scored are listed in Table 3. Measurements were made on calibrated digital images in ImageJ (Schneider et al. 2012).

**Table 3.** Pollen characters scored and their definitions.

| Feature | Definition | Recording method |
|---|---|---|
| Polar axis (P) | Length from pole to pole (Figure 1) | µm, LM, equatorial view |
| Equatorial diameter (E) | Width at the equator | µm, LM, equatorial view |
| P/E ratio | Shape index; higher values indicate more elongated grains | Calculated; shape class from standard terms |
| Amb | Outline of the grain seen from a pole | Rounded-triangular, circular, etc. |
| Aperture type and number | Colpi and ora through which the pollen tube emerges | For example 3-colporate |
| Colpus length; pore size | Size of the furrow and pore | µm |
| Exine thickness | Thickness of the outer wall | µm, LM, optical section |
| Surface pattern (ornamentation) | The pattern on the outer wall | Reticulate, microreticulate, etc., from SEM |
| Lumina width | Size of the openings in the net | µm, SEM; maximum and mean |
| Muri | The ridges forming the net | Width; smooth or beaded, from SEM |

### 2.6 Measurement quality control

To limit drift between observers and sessions, the camera scale was calibrated against a stage micrometer at the start of each session, and the same 10 grains on a reference slide were re-measured at regular intervals. A random subset of grains was re-measured by a second observer blind to species identity, and agreement between observers was assessed. Grains were measured in a fixed traverse across each slide rather than selected for appearance; broken, folded or obliquely oriented grains were excluded, and the number excluded per slide was recorded.

### 2.7 Data analysis

- For each character, variance was partitioned among the nested levels of the design (species, population within species, plant within population and grain within plant) to separate within-species from between-species variation; species differences were further tested with linear mixed-effects models with species as a fixed effect and population and plant as random effects (Bates et al. 2015).
- Plant means of the six quantitative characters (P, E, P/E, exine thickness, lumina width and colpus length) were standardised and subjected to principal component analysis (PCA). Linear discriminant analysis (LDA) was used to estimate how often plants were assigned to the correct species; to avoid optimistic estimates, it was cross-validated by leaving out one population at a time, so that each plant was classified by a function built without its own population.
- A provisional pollen key was constructed from characters that were consistent within species and differed between them.
- For each character used in the key, the numbers of plants and populations measured are reported.
- Sizes were compared with published values only where preparation methods were similar, and differences in method are noted (Reitsma 1969).

### 2.8 Limitations

Three populations per species capture only part of the variation present in the state. Because grain size depends on preparation, comparisons with other studies are approximate, and possible hybrids could blur species differences. Pollen is not intended to replace floral and fruit characters for identifying *Grewia*, but to provide supporting evidence, especially for flowering specimens that are otherwise difficult to place.

## 3. RESULTS

**Note on data:** The values reported in this section are simulated sample results, generated according to the sampling design in Table 2 to illustrate the analyses and the presentation of results.

### 3.1 General pollen morphology

Pollen grains of all six species were monads, isopolar, radially symmetrical and 3-colporate, with long, narrow colpi tapering towards the poles and lalongate ora. In equatorial view the grains were

elliptic and prolate (species mean P/E 1.38–1.57), and the amb was rounded-triangular to slightly trilobed (Figure 1). Under SEM, the tectum was reticulate with perforated lumina in every species. The reticulum was coarse in *G. tiliifolia* and *G. damine* (mean lumina width 2.50–2.86 µm), intermediate in *G. flavescens* and *G. villosa* (2.08–2.29 µm) and comparatively fine in *G. hirsuta* and *G. orbiculata* (1.78–1.88 µm). Non-acetolysed grains showed the same sculpture as acetolysed grains.

### 3.2 Quantitative characters

Morphometric data are summarised in Table 4 and Figure 4. Mean polar axis ranged from 45.7 µm in *G. hirsuta* to 57.2 µm in *G. tiliifolia*, and mean equatorial diameter from 32.9 µm in *G. flavescens* to 37.5 µm in *G. tiliifolia*. Exine was thickest in *G. tiliifolia* and *G. damine* (2.01 and 2.00 µm) and thinnest in *G. hirsuta* and *G. orbiculata* (1.67 µm in both). Ranges overlapped widely at the level of individual grains, particularly among *G. hirsuta*, *G. orbiculata*, *G. villosa* and *G. flavescens*.

**Table 4.** Pollen morphometrics of six *Grewia* species from Telangana (mean ± SD; n = 225 grains per species from 9 plants in 3 populations). P, polar axis; E, equatorial diameter. Simulated sample data.

| Species | P (µm) | E (µm) | P/E | Exine (µm) | Lumina (µm) | Colpus (µm) | P range (µm) |
|---|---|---|---|---|---|---|---|
| *G. damine* | 55.9 ± 3.2 | 35.6 ± 2.2 | 1.57 ± 0.10 | 2.00 ± 0.16 | 2.50 ± 0.28 | 45.8 ± 2.2 | 47.4–65.4 |
| *G. flavescens* | 48.8 ± 2.6 | 32.9 ± 1.9 | 1.49 ± 0.11 | 1.91 ± 0.15 | 2.29 ± 0.31 | 40.0 ± 2.1 | 41.9–57.8 |
| *G. hirsuta* | 45.7 ± 2.6 | 33.0 ± 1.9 | 1.39 ± 0.11 | 1.67 ± 0.15 | 1.88 ± 0.28 | 37.5 ± 2.0 | 36.9–53.3 |
| *G. orbiculata* | 46.9 ± 2.8 | 34.0 ± 2.0 | 1.38 ± 0.10 | 1.67 ± 0.15 | 1.78 ± 0.34 | 38.2 ± 2.1 | 39.8–54.5 |
| *G. tiliifolia* | 57.2 ± 2.5 | 37.5 ± 1.9 | 1.53 ± 0.09 | 2.01 ± 0.15 | 2.86 ± 0.32 | 46.4 ± 2.1 | 50.1–64.4 |
| *G. villosa* | 48.8 ± 3.1 | 33.7 ± 2.1 | 1.45 ± 0.10 | 1.79 ± 0.15 | 2.08 ± 0.30 | 39.9 ± 2.3 | 40.3–56.7 |

Partitioning of variance across the nested design (Table 5) showed that species identity accounted for 71.2% of the total variance in polar axis length, 59.5% in lumina width, 47.5% in exine thickness and 32.0% in P/E. Differences among populations within species contributed no more than 5.9%, and differences among plants within populations no more than 2.3%; the remainder was variation among grains of the same plant.

**Table 5.** Percentage of total variance in four pollen characters attributable to each level of the sampling design. Simulated sample data.

| Character | Species | Population | Plant | Grain |
|---|---|---|---|---|
| Polar axis (P) | 71.2 | 5.9 | 2.3 | 20.6 |
| P/E ratio | 32.0 | 0.6 | 1.1 | 66.3 |
| Exine thickness | 47.5 | 5.3 | 1.2 | 46.0 |
| Lumina width | 59.5 | 3.5 | 0.9 | 36.2 |

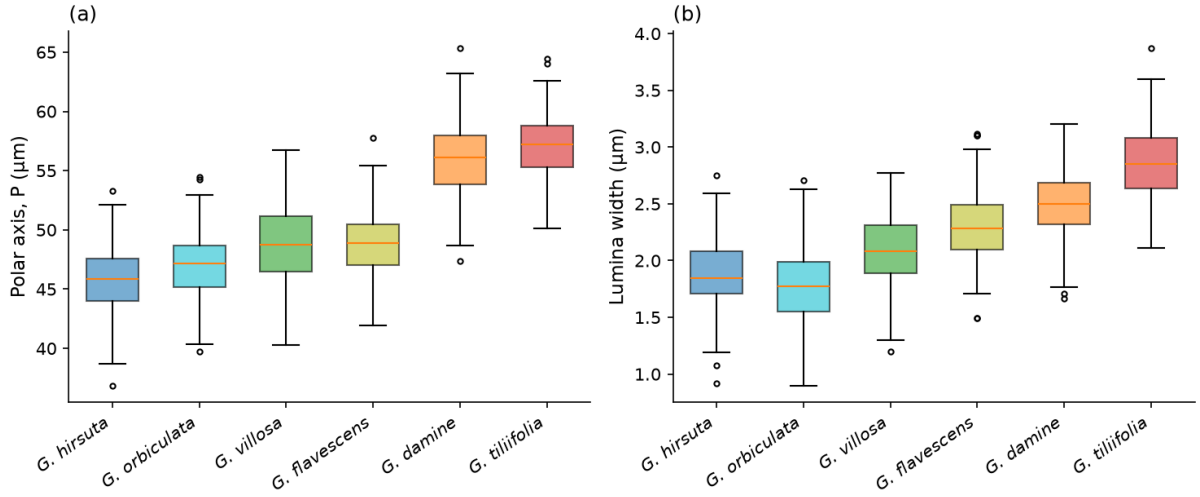


**Figure 4.** Variation in (a) polar axis length and (b) lumina width among six *Grewia* species (n = 225 grains per species). Boxes show the median and interquartile range; whiskers extend to 1.5 × the interquartile range. Simulated sample data.

### 3.3 Multivariate analysis

In the PCA of plant means, the first component explained 84.3% of the variance and had similar positive loadings (0.36–0.44) for all six characters, so it represents overall grain size, exine thickness and lumina width. The second component (10.9%) contrasted equatorial diameter (loading 0.69) with exine thickness (−0.52) and P/E (−0.34). Along PC1, *G. tiliifolia* and *G. damine* occupied the positive end, *G. hirsuta* and *G. orbiculata* the negative end, and *G. flavescens* and *G. villosa* an intermediate position, with *G. flavescens* displaced towards negative PC2 values (Figure 3).

LDA with leave-one-population-out cross-validation assigned 40 of the 54 plants (74.1%) to the correct species. All plants of *G. tiliifolia*, *G. damine* and *G. flavescens* were classified correctly. Six of nine *G. villosa* plants were correctly assigned, the remaining three being classified as *G. flavescens*. *G. hirsuta* and *G. orbiculata* were frequently confused: four of nine *G. hirsuta* plants and three of nine *G. orbiculata* plants were correctly assigned, and the rest were placed in the other species. When individual grains rather than plant means were classified, accuracy fell to 35.5%.

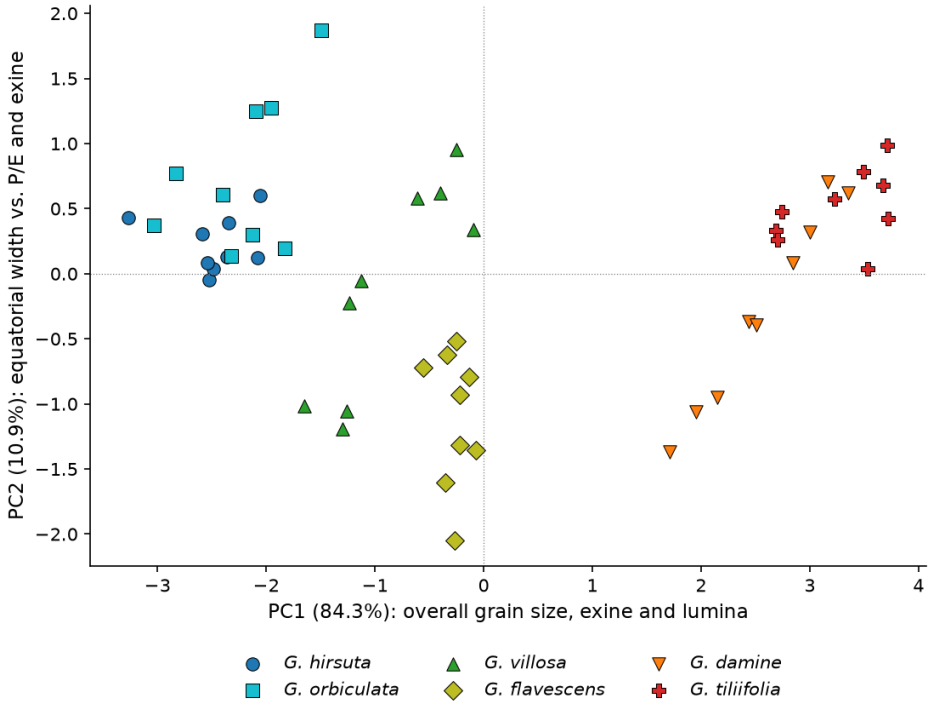


**Figure 3.** Principal component analysis of plant means of six pollen characters for six *Grewia* species (54 plants; each point is one plant). Simulated sample data.

### 3.4 Provisional pollen key (based on plant means)

**1a.** Polar axis more than 52 µm; lumina 2.4 µm or wider ..... 2

**1b.** Polar axis less than 52 µm ..... 3

**2a.** Lumina 2.7–3.0 µm; P/E 1.50–1.55; equatorial diameter 36.7–38.3 µm ..... *G. tiliifolia*

**2b.** Lumina 2.4–2.6 µm; P/E 1.56–1.59 ..... *G. damine*

**3a.** P/E 1.42–1.51; exine 1.73–1.97 µm ..... 4

**3b.** P/E 1.36–1.43; lumina 1.6–2.0 µm ..... *G. hirsuta* and *G. orbiculata* (not reliably separated by pollen)

**4a.** P/E 1.47–1.51; exine 1.84–1.97 µm; lumina 2.2–2.5 µm ..... *G. flavescens*

**4b.** P/E 1.42–1.47; lumina 2.0–2.3 µm ..... *G. villosa*

Values at couplets 3 and 4 overlap slightly between species, so specimens falling near the limits should be identified using floral and fruit characters.

## 4. DISCUSSION

In the sample results all six species produced 3-colporate, prolate and reticulate grains, consistent with the *Grewia* type described for the genus (Chung et al. 2003; Perveen et al. 2004) and supporting H1. As predicted by H2, the species differed mainly in quantitative characters and in the coarseness of the reticulum rather than in aperture type. Mean exine thickness (1.67–2.01 µm)

and lumina width (1.78–2.86 µm) fall within or close to the ranges given for *Grewia* by Chung et al. (2003), and the polar-axis means (45.7–57.2 µm) lie within the (26–)48.5(–71) µm range of Perveen et al. (2004), although they are smaller than the 53–75 µm species means reported from Malesia. Such differences may reflect regional species composition as well as preparation and mounting effects (Reitsma 1969).

The variance partition indicates that most variation in grain size and lumina width lay between species, with a small contribution from populations, which suggests that these characters are taxonomically informative at the species level. In contrast, P/E varied mostly among grains within plants and is therefore of limited value on its own. Because grain-level discrimination was poor, species assignments should be based on means of at least 25 grains per specimen rather than on individual grains.

Multivariate analysis separated three groups: large, coarsely reticulate grains (*G. tiliifolia* and *G. damine*), intermediate grains (*G. flavescens* and *G. villosa*) and small, finely reticulate grains (*G. hirsuta* and *G. orbiculata*). Within the last group, pollen did not discriminate the two species reliably, supporting H3; in these species, pollen should be used together with floral, fruit and indumentum characters. The provisional key (Section 3.4) should therefore be regarded as a supplement to morphological identification.

Pollen data of this kind could also support studies of species limits between *Grewia* and *Microcos* in India (Nandikar & Janarthanam 2016; Chung 2006) and reproductive studies of useful species such as *G. flavescens* and *G. asiatica* (Veeresh Kumar et al. 2017; Wani et al. 2015). Future work should extend sampling to more populations and districts, include *G. asiatica* and any other species confirmed for the state, examine exine ultrastructure by TEM (Lattar et al. 2012) and combine pollen characters with molecular phylogenetic data (Brunken & Muellner 2012).

## 5. CONCLUSIONS

The sample results show that the *Grewia* species of Telangana share the 3-colporate, reticulate *Grewia* pollen type, but differ in grain size, exine thickness and lumina width sufficiently to separate most species when plant means are used. Pollen alone did not distinguish *G. hirsuta* from *G. orbiculata*. Pollen morphology is therefore a useful supplementary character for the taxonomy of *Grewia* in the region.

## DECLARATIONS

**Funding:** No specific funding was received for this study.

**Competing interests:** The author declares no competing interests.

**Permits:** Collections were made under permission from the Telangana State Forest Department .

**Author contributions:** The author conceived and designed the study, carried out the analyses and wrote the manuscript.

**Data availability:** The results presented in this version are simulated sample data used to illustrate the analyses.

## REFERENCES

Bates, D., Mächler, M., Bolker, B. and Walker, S. (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Brunken, U. and Muellner, A.N. (2012) A new tribal classification of Grewioideae (Malvaceae) based on morphological and molecular phylogenetic evidence. Systematic Botany, 37(3), 699–711. https://doi.org/10.1600/036364412X648670

Christensen, P.B. (1986) Pollen morphological studies in the Malvaceae. Grana, 25(2), 95–117. https://doi.org/10.1080/00173138609428890

Chung, R.C.K. (2006) Revision of *Grewia* (Malvaceae–Grewioideae) in Peninsular Malaysia and Borneo. Edinburgh Journal of Botany, 62(1–2), 1–27. https://doi.org/10.1017/S0960428606000011

Chung, R.C.K., Soepadmo, E. and Lim, A.L. (2003) The significance of pollen morphology in the taxonomy of *Grewia* and *Microcos* (Tiliaceae) in Peninsular Malaysia and Borneo. Gardens' Bulletin Singapore, 55, 239–256. Available at: https://www.nparks.gov.sg/sbg/research/publications/gardens'-bulletin-singapore/-/media/sbg/gardens-bulletin/4-4-55-2-08-y2003-v55p2-gbs-pg-239.pdf

Halbritter, H., Ulrich, S., Grímsson, F., Weber, M., Zetter, R., Hesse, M., Buchner, R., Svojtka, M. and Frosch-Radivo, A. (2018) Illustrated Pollen Terminology. 2nd edn. Cham: Springer. https://doi.org/10.1007/978-3-319-71365-6

Lattar, E.C., Galati, B.G. and Ferrucci, M.S. (2012) Ultrastructural study of pollen and anther development in *Luehea divaricata* (Malvaceae, Grewioideae) and its systematic implications: role of tapetal transfer cells, orbicules and male germ unit. Flora, 207(12), 888–894. https://doi.org/10.1016/j.flora.2012.10.005

Nandikar, M.D. and Janarthanam, M.K. (2016) Taxonomic notes on *Microcos* (Malvaceae–Grewioideae) in India. Phytotaxa, 272(3). https://doi.org/10.11646/phytotaxa.272.3.4

Perveen, A. and Qaiser, M. (2007) Pollen flora of Pakistan – Malvaceae: Grewioideae – LII. Pakistan Journal of Botany, 39(1), 1–7. Available at: https://www.pakbs.org/pjbot/PDFs/39(1)/PJB39(1)001.pdf

Perveen, A., Grafström, E. and El-Ghazaly, G. (2004) World Pollen and Spore Flora 23. Malvaceae Adans. p.p. Subfamilies: Grewioideae, Tilioideae, Brownlowioideae. Grana, 43(3), 129–155. https://doi.org/10.1080/00173130410000730

Punt, W., Hoen, P.P., Blackmore, S., Nilsson, S. and Le Thomas, A. (2007) Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology, 143(1–2), 1–81. https://doi.org/10.1016/j.revpalbo.2006.06.008

Reitsma, Tj. (1969) Size modification of recent pollen grains under different treatments. Review of Palaeobotany and Palynology, 9(3–4), 175–202. https://doi.org/10.1016/0034-6667(69)90003-7

Schneider, C.A., Rasband, W.S. and Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. Nature Methods, 9(7), 671–675. https://doi.org/10.1038/nmeth.2089

Veeresh Kumar, Uthappa, A.R., Srivastava, M., Vijay, D., Kumaranag, K.M., Manjunatha, N., et al. (2017) Floral biology of *Grewia flavescens* Juss.: an underutilized crop. Genetic Resources and Crop Evolution, 64(7), 1789–1795. https://doi.org/10.1007/s10722-017-0536-y

Wani, T.A., Pandith, S.A., Rana, S., Bhat, W.W., Dhar, N., Razdan, S., et al. (2015) Promiscuous breeding behaviour in relation to reproductive success in *Grewia asiatica* L. (Malvaceae). Flora, 211, 62–71. https://doi.org/10.1016/j.flora.2014.11.002