

## Pollen Morphology of Eight Genera of the Subtribe *Mutisiinae* Less. *sensu* Bremer (Compositae) from Asia

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**Abstract:** The pollen morphology of 28 species and one variety representing eight genera of the subtribe *Mutisiinae* Less. *sensu* Bremer (Compositae) was investigated by scanning electron microscopy (SEM) and light microscopy. The pollen grains are usually radically symmetrical, isopolar, and tricolporate. The shape varies from spheroidal to subprolate in equatorial view and is three-lobed circular in polar view. Based on exine sculpturing observed under SEM, the pollen grains can be divided into three types: (i) type I, with macrogranulate sculpture; (ii) type II, with a finely granulate sculpture; and (iii) type III, with spiny sculpture. The palynological data showed that the *Macroclinidium* Maxim. was remarkably distinguished from those of the other seven genera. The variation of pollen characteristics within the *Mutisiinae* in Asia is little at species level, but it proves some useful information for studying the relationships among genera and it has an important significance in further understanding the evolutionary history of *Mutisiinae*.

**Key words:** Asia; Compositae; *Mutisiinae*; pollen morphology.

The tribe *Mutisieae* Cass. comprises some 76 genera and approximately 970 species with very diverse morphological characters and is considered one of the most important tribes for understanding the systematic relationships within the Compositae because it is a basal lineage in the family (Bremer 1994; Kim *et al.* 2002). *Mutisieae* has been treated as two to five subtribes in different classifications (Bentham 1873; Hoffmann 1890; Carbera 1977). Hoffmann (1890) reduced Bentham's five subtribes to three: *Gochnatiinae* O. Hoffm., *Mutisiinae* (mistakenly printed as *Gerberiinae* O. Hoffm in his key; Bremer 1994), and *Nassauviinae* Less. However, the circumscription and relationships among the subtribes remain ambiguous and controversial. Bremer (1994) made a useful contribution to the cladistic relationships and the classification of the Compositae, and his system is well known

and has been followed by subsequent researchers in palynological, molecular, and other studies (Zavada and de Villiers 2000; Roque and Silvestre-Capelato 2001; Kim *et al.* 2002). In his system of classification, Bremer (1994) divided *Mutisieae* into two subtribes, *Nassauviinae* and *Mutisiinae* (*sensu lato*). *Nassauviinae* was treated to include 24 genera and was mainly distributed in the South and Central Americas, rarely in North America, and with only one genus, *Adenocaulon* Hook, extending to Asia. The subtribe *Mutisiinae*, comprising 52 genera, occurred in the Pan-tropics, among which the largest genus, *Gochnatia* Kunth constituted of 68 recognized species. Other disjunctive genera in this subtribe included *Gerbera* Cass. and *Leibnitzia* Cass. *Gerbera* occurred mainly in Africa, Madagascar, and tropical Asia, with one species distributed in South America. *Leibnitzia* was a small genus distributed in

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Asia and Central America. Five genera of the subtribe were limited to Asia, among which two genera are monotypic and endemic to China, being the shrubby *Nouelia* Franch. and *Myripnois* Bunge. The other three Asian genera were *Pertya* Sch.-Bip., *Ainsliaea* DC, mainly distributed in southeastern and Central Asia, and *Macroclindium*, endemic to Japan.

Following Hoffmann (1890), the account of *Mutisiinae* in the Chinese-language *Flora Reipublicae Popularis Sinicae* (Tseng 1996) recognized six genera in China: *Gochnatia*, *Nouelia*, *Myripnois*, *Pertya*, *Ainsliaea*, and *Gerbera*. *Leibnitzia* was included in a broadly defined *Gerbera* (*sensu lato*). Lin (1997) treated the Chinese *Mutisiinae* in nine genera, including the seven genera as mentioned above and another two genera (*Uechtritzia* Freyn and *Lasiopus* Cass.).

The *Mutisieae* was investigated palynologically by several earlier researchers. Wodehouse (1929a, 1929b) described the pollen morphology of several genera of *Mutisieae*. Crisci (1974) investigated the pollen morphology of the subtribe *Nassauviinae*, recognizing six types of patterns. Skvarla *et al.* (1977) considered that the most diverse pollen occurred in *Mutisieae* within the family of Compositae, both at the exo- and endomorphic levels. The variation of pollen exines examined by transmission electronic microscopy (TEM) in the subtribe *Nassauviinae* was used for delimiting the genera of the subtribe (Crisci 1974). The hitherto most comprehensive general summary was given by Hansen (1991b), based on scanning electron microscopic (SEM) studies of 70 genera of the tribe *Mutisieae sensu* Cabrera plus a few other relevant genera, among which 53 genera of the *Mutisiinae* and *Gochnatiinae* (*sensu* Cabrera) were analyzed. Using pollen data, Roque and Silvestre-Capelato (2001) discussed the delimitations of several genera of *Mutisieae* in South America. While describing the pollen morphology of two south American genera in *Nassauviinae*, namely *Proustia* Lagasca and *Lophopappus* Pusby, Telleria *et al.* (2003) compared them with the exine types found in other genera of *Mutisieae* and concluded that the subtribes *Gochnatiinae* and *Mutisiinae* were artificially

delimited and that tribe *Mutisieae* was better to be treated as two subtribes, namely *Nassauviinae* and *Mutisiinae sensu lato*, as pointed out by earlier authors, such as Robinson (1991), Hansen (1991a), and Bremer (1994). However, the pollen morphology of the subtribe *Mutisiinae* in Asia remained poorly known.

The present study examined the pollen grains of 28 species and one variety representing eight genera of *Mutisiinae* Less. (Compositae) from eastern and south-eastern Asia, of which 22 species were investigated palynologically for the first time. The main aims of the present study were to illustrate the pollen morphology of Asian species in *Mutisiinae*, to determine whether pollen data may provide some useful values for studying the relationships among genera of the subtribe *Mutisiinae*, and to understand further the evolutionary history of the *Mutisiinae*.

## 1 Materials and Methods

The pollen grains of 28 species and one variety of *Mutisiinae* in Asia were obtained in specimens from the herbarium of Kunming Institute of Botany, the Chinese Academy of Sciences (see Appendix I for a list of specimens examined), representing the following eight genera: *Gochnatia*, *Nouelia*, *Myripnois*, *Pertya*, *Ainsliaea*, *Leibnitzia*, *Gerbera*, and *Macroclindium*. In the present study, we followed the generic circumscription of Bremer (1994).

Pollen samples were acetolysed according to the technique of Erdtman (1960) and dehydrated in an ethanol series from 50% to 95%. For light microscopy (LM), pollen slides were prepared by mounting pollen in glycerine jelly directly. Size measurements were based on 20 pollen grains per sample; values of polar axis length (P) and equatorial diameter (E) were measured, and the P/E ratio was calculated to determine pollen size and shape. Pollen aperture was observed directly. For SEM, samples were mounted on glass coverslips and attached to aluminium stubs. After sputter coating, pollen grains were observed and photographed under SEM (KYKY-10000B; Science Instrument Company, Beijing, China) at 15 kV. Descriptive terminology of

the pollen follows Punt *et al.* (1994). A list of voucher specimens for pollen samples is given in Appendix I.

## 2 Results

### 2.1 Description of general pollen morphology in the subtribe *Mutisiinae*

Pollen morphological characters of all 28 species and one variety representing eight genera of *Mutisiinae* under LM and SEM are summarized in Table 1.

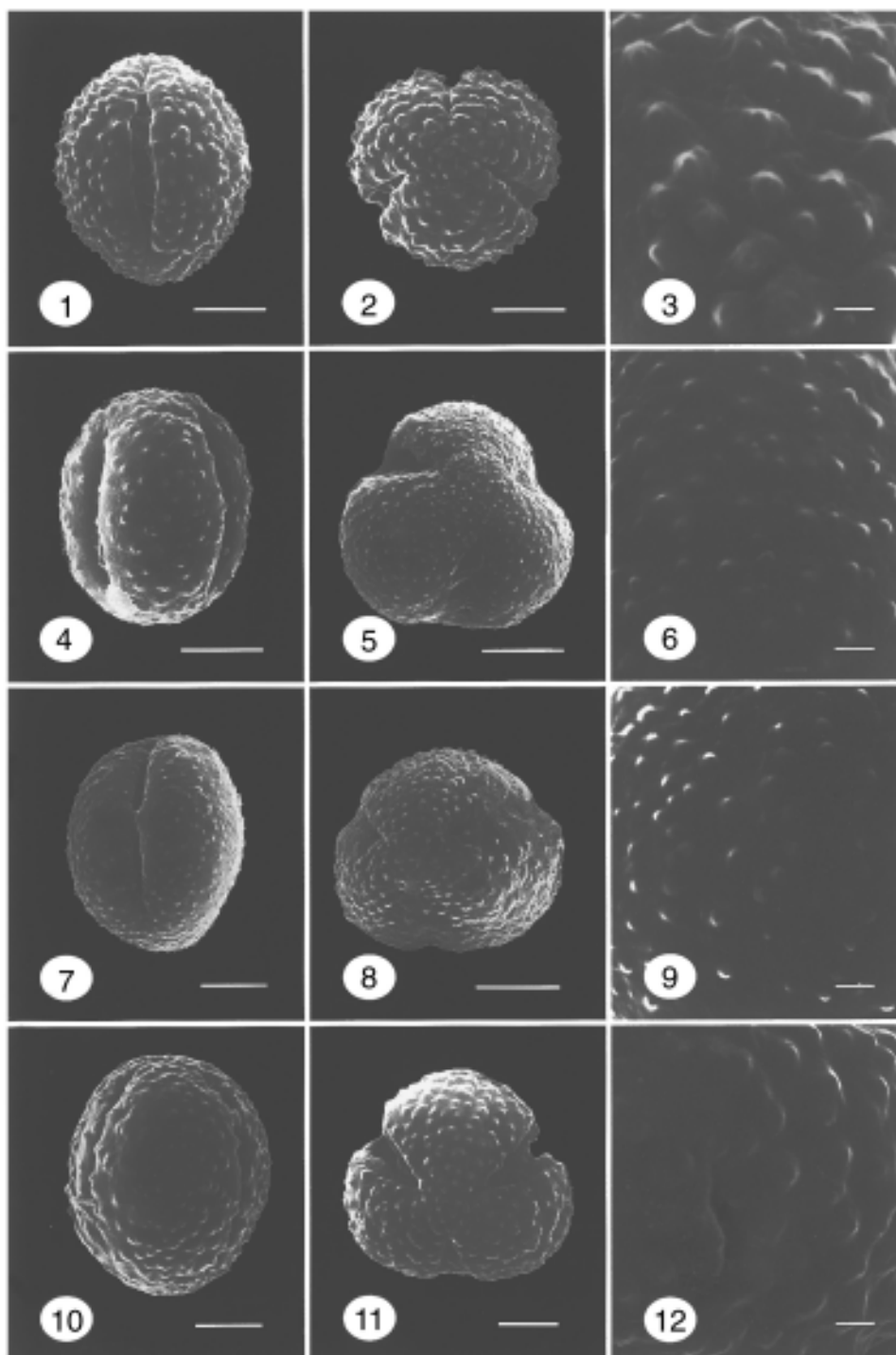
The pollen grains were usually radially symmetrical and isopolar. The size of pollen grains varied from medium to large (P: 36.83–82.33  $\mu\text{m}$   $\times$  E: 29.93–70.63  $\mu\text{m}$ ). Two distinct pollen shape classes were recognized: subprolate (P/E 1.12–1.32) and spheroidal

shaped (P/E 1.02–1.11), elliptic or spheroidal in equatorial view, circular in polar view. The pollen apertures of all species examined were tricolporate (Figs. 1–36). Pollen grains of most species had long colpi extension nearly to two poles (Figs. 10, 16, 23, 31, 36). However, an exception with short colpi was found in three species: *Macroclinidium rigidulum* (Miq.) Makino, *M. robustum* Maxim., and *Ainsliaea acerifolia* Sch.-Bip. (Fig. 27). The colpus membrane in some species was covered with microgranular (Fig. 21), whereas in other species the colpi were sunken and smooth (Fig. 36). The endoaperture was lalongate (Fig. 32), bifurcate (Fig. 20), or had acute equatorial ends (Fig. 23). Three different exine types of pollen grains were found under

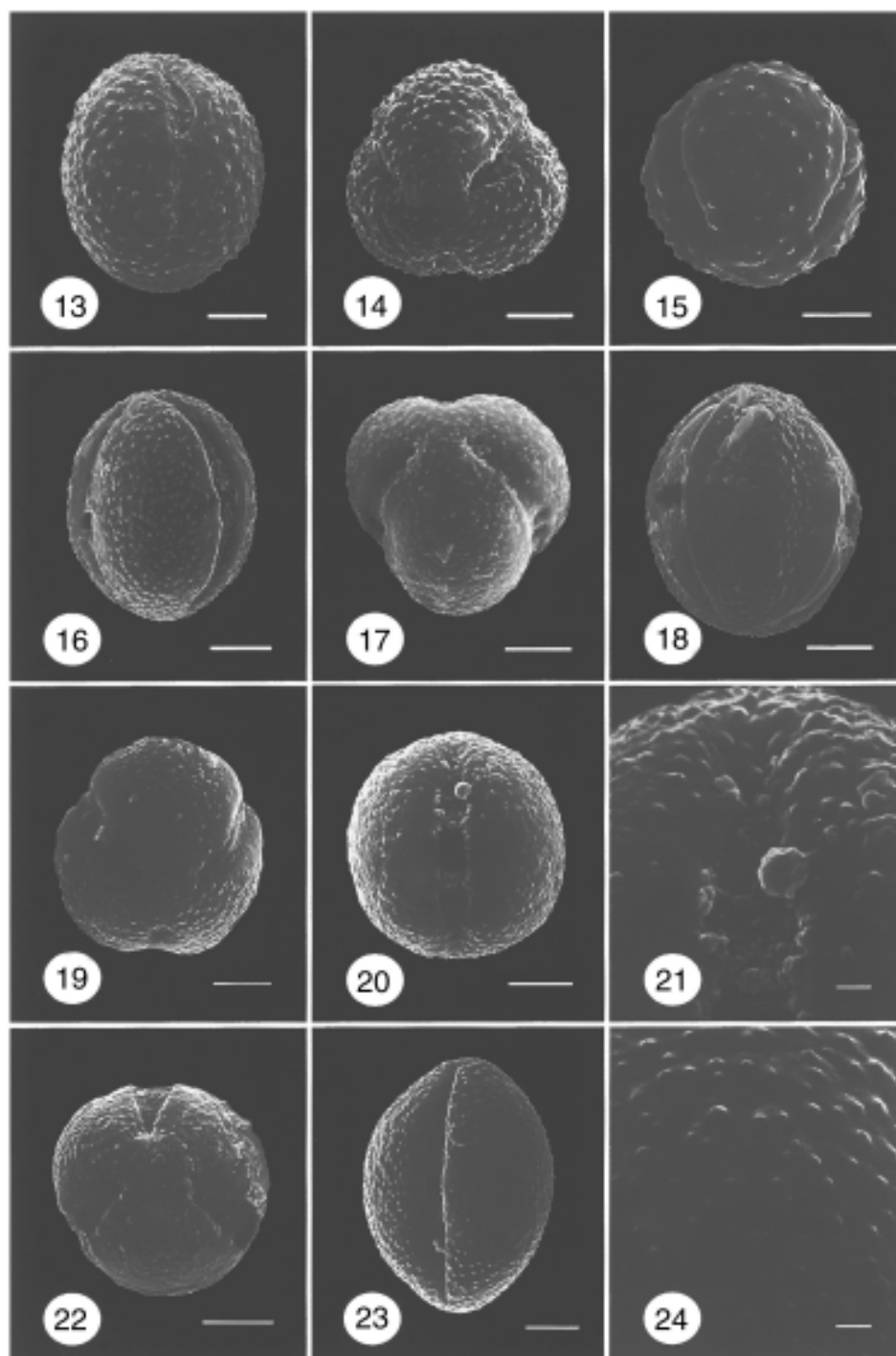
**Table 1** Summary of data on pollen morphology for all species studied (I, with macro-granulate sculpture; II, with a finely granulate sculpture; III, with spiny sculpture)

Taxon	Polar axis ( $\mu\text{m}$ )	Equatorial axis ( $\mu\text{m}$ )	P/E	Pollen shape	Exine sculpturing
<i>Ainsliaea acerifolia</i>	46.08 (42.5–52.5)	41.25 (37.5–45.0)	1.12	Spheroidal	I
<i>A. angustifoliae</i>	55.78 (42.5–55.0)	48.25 (51.25–65.00)	1.20	Subprolate	I
<i>A. aptera</i>	56.75 (50–60)	46.98 (37.5–57.5)	1.21	Subprolate	I
<i>A. latifolia</i>	56.4 (47.5–62.5)	48.75 (42.50–58.75)	1.16	Subprolate	I
<i>A. pertyoides</i>	62.69 (58.75–70.00)	49.68 (37.5–57.5)	1.26	Subprolate	I
<i>Gerbera delavayi</i>	68.98 (62.50–76.25)	62.14 (53.75–68.75)	1.11	Spheroidal	II
<i>G. henryi</i>	67.5 (57.50–78.75)	57.86 (45.00–68.75)	1.17	Subprolate	II
<i>G. macrocephala</i>	82.33 (78.75–86.25)	70.63 (65.75–77.50)	1.17	Subprolate	II
<i>G. nivea</i>	47.50	42.50	1.18	Subprolate	I
<i>G. piloselloides</i>	44.82 (41.10–48.41)	38.12 (33.56–40.95)	1.18	Subprolate	I
<i>G. raphanifolia</i>	63.88 (57.5–72.5)	50.5 (41.25–60.00)	1.27	Subprolate	II
<i>Gochnatia decora</i>	56.75 (50–65)	47.75 (42.5–60.0)	1.19	Subprolate	II
<i>Goch. hypoleuca</i>	48.95 (40.00–51.25)	41.82 (30.0–47.5)	1.17	Subprolate	I
<i>Leibnitzia anandria</i>	46.5 (35.00–53.75)	37.5 (32.5–47.5)	1.24	Subprolate	II
<i>L. nepalensis</i>	43.75 (43.75–50.00)	33.13 (31.25–35.00)	1.32	Spheroidal	II
<i>L. pusilla</i>	49 (45.0–52.5)	47 (38.75–53.75)	1.04	Spheroidal	II
<i>L. ruficoma</i>	37.03 (30.00–41.25)	34.73 (22.5–40.0)	1.07	Spheroidal	II
<i>Macroclinidium rigidulum</i>	73.36 (51.25–81.25)	72.05 (57.5–85.0)	1.02	Spheroidal	III
<i>M. robustum</i>	63.83 (52.5–72.5)	62.5 (53.75–71.25)	1.02	Spheroidal	III
<i>Myriopsis dioica</i>	36.83 (32.5–42.5)	29.93 (27.50–33.75)	1.23	Subprolate	I
<i>Nouelia insignis</i>	75.93 (68.75–85.00)	58.23 (51.25–67.50)	1.30	Subprolate	I
<i>Pertya cordifolia</i>	48.7 (42.5–52.5)	40.05 (32.50–46.25)	1.22	Subprolate	I
<i>P. corymbosa</i>	51.15 (47.5–57.5)	40.13 (36.25–45.00)	1.28	Subprolate	I
<i>P. desmocephala</i>	57 (50.0–62.5)	47.75 (40.0–52.5)	1.19	Subprolate	I
<i>P. discolor</i>	46.85 (40.0–57.5)	38.63 (3.75–43.50)	1.21	Subprolate	I
<i>P. henanensis</i>	50.12 (47.5–52.5)	39.41 (33.75–43.75)	1.27	Subprolate	I
<i>P. phyllicoides</i>	55.78 (45–60)	44 (30.0–47.5)	1.27	Subprolate	I
<i>P. phyllicoides</i> var. <i>berberidoides</i>	60 (52.5–72.5)	51.25 (42.5–60.0)	1.17	Subprolate	I
<i>P. scandens</i>	55.78 (45–60)	44 (35.0–47.5)	1.27	Subprolate	I

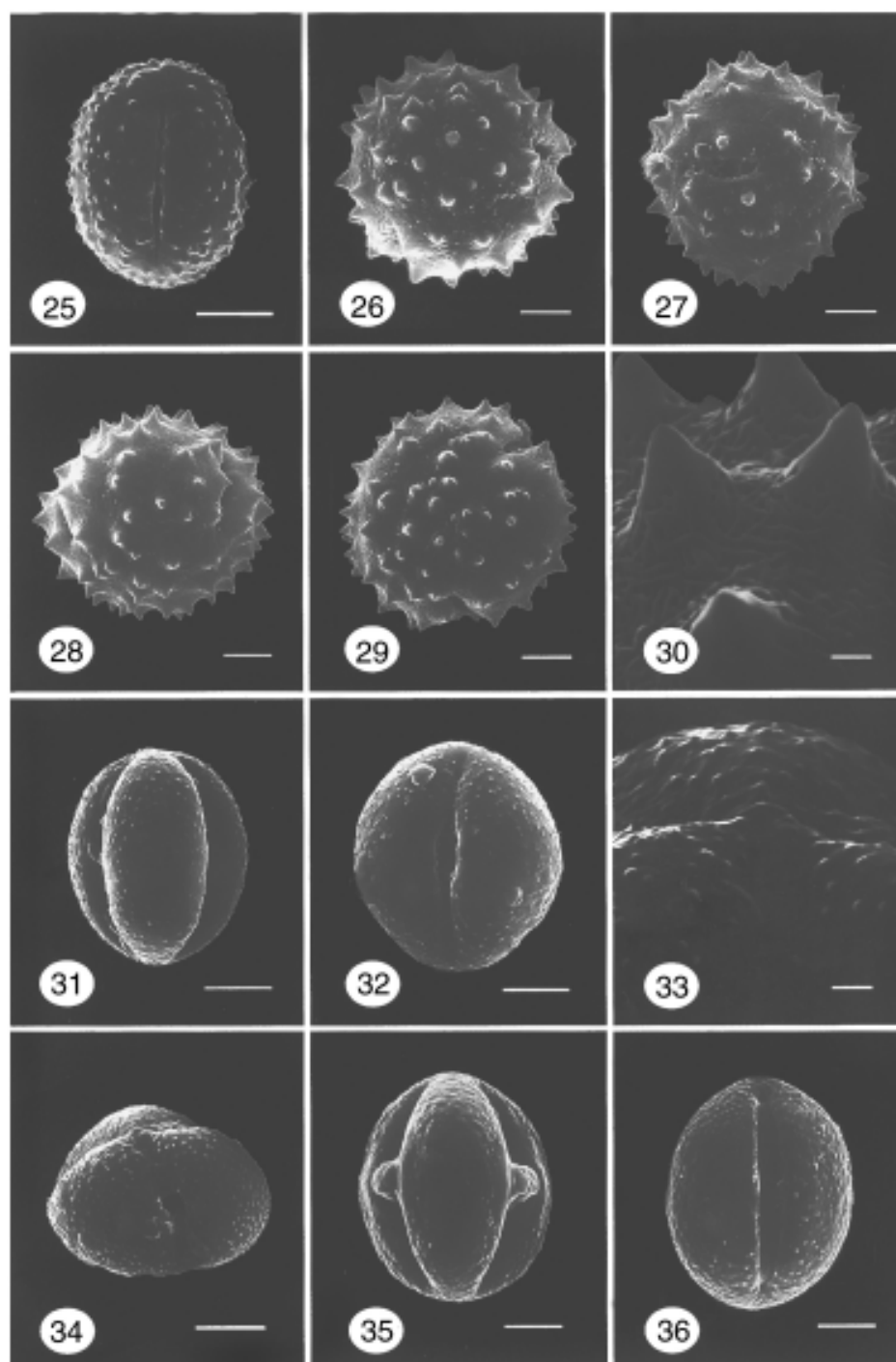
P/E, polar/equatorial axis ratio.



**Figs. 1–12.** Characteristic features of pollen type I; Bars, 10  $\mu\text{m}$  (for whole pollen grains); 2  $\mu\text{m}$  (for details of the exine sculpturing). 1–3. *Gochnatia hypoleuca*, showing an equatorial view (1), polar view (2) and a higher magnification of the exine sculpturing (3). 4–6. *Pertya discolor*, showing an equatorial view (4), polar view (5) and a higher magnification of the exine sculpturing (6). 7–9. *Pertya sinensis*, showing an equatorial view (7), polar view (8) and a higher magnification of the exine sculpturing (9). 10–12. *Ainsliaea pertyoides*, showing an equatorial view (10), polar view (11) and a higher magnification of the exine sculpturing (12).



**Figs. 13–24.** Characteristic features of pollen types I and II. Bars, 10  $\mu\text{m}$  (for whole pollen grains); 2  $\mu\text{m}$  (for details of the exine sculpturing) **13, 14.** *Gerbera nivea*, pollen type I, showing an equatorial view (**13**) and an oblique polar view (**14**). **15.** *Ainsliaea acerifolia*, pollen type I, equatorial view. **16, 17.** *Nouelia insignis*, pollen type I, showing an equatorial view (**16**) and an oblique polar view (**17**). **18, 19.** *Gerbera piloselloides*, pollen type I, showing an equatorial view (**18**) and an oblique polar view (**19**). **20–22.** *Myriopholis dioica*, pollen type I, showing an equatorial view (**20**), a higher magnification of the colpi and colpus membrane (**21**), and a polar view (**22**). **23, 24.** *Gerbera raphanifolia*, pollen type II, showing an equatorial view (**23**) and a higher magnification of the exine sculpturing (**24**).



**Figs. 25–36.** Characteristic features of pollen types I, II, and III. Bars, 10  $\mu\text{m}$  (for whole pollen grains); 2  $\mu\text{m}$  (for details of the exine sculpturing). **25.** *Pertya cordifolia*, pollen type I, equatorial view. **26, 27.** *Macroclinidium rigidulum*, pollen type III, showing a polar view (**26**) and an equatorial view (**27**). **28–30.** *Macroclinidium robustum*, pollen type III, showing an equatorial view (**28**), a polar view (**29**), and a higher magnification of the exine sculpturing (**30**). **31, 32.** *Leibnitzia anandria*, pollen type II, equatorial views. **33, 34.** *Leibnitzia pusilla*, pollen type II, showing a higher magnification of the exine sculpturing (**33**) and an oblique polar view (**34**). **35, 36.** *Gochnatia decora*, pollen type II, equatorial views.

SEM: (i) type I, with macrogranulate sculpture (described as minute supratectal spinuliferous processes by Roque and Silvestre-Capelato (2001) or as microechinate by Telleria *et al.* (2003)); (ii) type II, with a finely granulate sculpture; and (iii) type III, with spiny sculpture (spines were defined if more than 3  $\mu\text{m}$  long).

## 2.2 Description of general pollen morphology in the genera

**2.2.1 *Ainsliaea* DC** This genus occurred mainly in eastern Asia and extended to southeastern Asia. The characters of pollen grains were consistent in the species examined. The pollen grains were medium or large in size, with macrogranulate exine sculpturing. Colpi were long, extending near to the poles, and deeply sunken (Figs. 10–12, 15). Such colpi were present in *A. angustifolia* Hk. f. et. Thoms ex C. B. Clark, *A. aptera* DC, *A. latifolia* (D. Don) Sch.-Bip., and *A. pertyoides* Franch. However, *A. acerifolia*, distributed towards the north extreme corner of the genus in north-eastern China and Korea, was somewhat different in its palynological characters. The exine sculpturing had sparse macrogranules and many small foveolae on the tectum surface (Fig. 15). Colpi were wide, smooth, and always shorter than those of other species, only approximately two-thirds the length of the polar axis.

**2.2.2 *Gerbera* Cass.** The genus *Gerbera* was mainly distributed in tropical Asia and Africa, except for one species in South America. In all species examined from China, the pollen grains were large in size (but medium-sized in *Gerbera nivea* (DC) Sch.-Bip. and *G. piloselloides* (Linn.) Cass.). Two types of exine sculpturing were present in the examined species. *Gerbera nivea* and *G. piloselloides* had a macrogranular tectum. Colpi were wide, with small granules in the species examined, such as *Gerbera nivea* (Figs. 13, 14), but the colpus membrane and margins of the mesocolpium were distinctly smooth in *G. piloselloides* (Figs. 18, 19). Other species had fine granulate exine sculpturing, wide colpi, with a colpus membrane covering with small granular elements (Figs. 23, 24). These characters present in *G. delavayi* Franch., *G. henryi* Dunn,

*G. macrocephala* Y. C. Tseng, *G. piloselloides*, and *G. raphanifolia* Franch.

**2.2.3 *Gochnatia* Kunth.** Two species were studied, namely *Gochnatia hypoleuca* (D. D.) A. Gray in North America and Europe, and *Goch. decora* (Kurz) A. L. Cabrera, distributed in southeastern Asia. Pollen grains of both species were subprolate in shape, but the two species could be distinguished in ornamentation. *Goch. hypoleuca* had a macrogranular exine sculpture, with colpi usually wide at the equator and narrow near the poles, and a colpus membrane often covered by granular elements (Figs. 1–3). *Goch. decora* had fine granular exine sculpture (Fig. 35), with long, sunken, and smooth colpi, pits being present in the two ends (Fig. 36).

**2.2.4 *Leibnitzia* Cass.** This genus was distributed in Asia and America, with extensive geographic disjunctions. In all species examined from China, the pollen characters were basically similar. The pollen grains were medium or large in size. The exine sculpturing of pollen was fine granulate. Colpi were long and deeply sunken (Figs. 31–34). These characters present in *L. anandria* (Linn.) Nakai., *L. nepalensis* (Kunze) Kitam., *L. pusilla* (DC.) S. Gjould ex Kitam. et Gould., and *L. ruficoma* (Franch.) Kitam.

**2.2.5 *Macroclindium* Maxim.** *Macroclindium*, endemic to Japan, had only three species. Two species were studied. Pollen grains of *M. rigidulum* and *M. robustum* were spheroidal and large ( $73.36 \mu\text{m} \times 72.05 \mu\text{m}$ ) in size. Both species had unique spiny tecta. Between the spines, the exine was covered by rugulate-striate ornamentation (Figs. 26–30) and the base of the spines was always perforate. Colpi were very short, only approximately 15–20  $\mu\text{m}$  long.

**2.2.6 *Myripnois* Bunge.** *Myripnois dioica* Bunge. was the only species of the genus and was a shrub endemic to northern China. The pollen grains were subprolate, three-lobed circular in polar view, and medium ( $36.83 \mu\text{m} \times 29.93 \mu\text{m}$ ) in size. The exine sculpturing was macrogranulate, densely covered by macrogranular elements along two poles, and decreasing gradually towards the center of the mesocolpium

and colpi margin. Colpi were long and wide, usually wide at the equatorial region and narrow near the poles. Colpus membranes were covered with granular elements (Figs. 20–22).

**2.2.7 *Nouelia* Franch.** *Neuelia insignis* Franch. was the sole species of the genus and was a shrub endemic to southwestern China. The pollen grains were subprolate in shape and large ( $75.93\ \mu\text{m} \times 58.23\ \mu\text{m}$ ) in size. The exine sculpturing was macrogranulate, with more condensed granules towards each pole. Colpi were very long and deeply sunken (Figs. 16, 17).

**2.2.8 *Pertya* Sch. Bip.** *Pertya* was distributed in Asia, from Japan to Afghanistan. The pollen grains of the genus were medium or large in size and were consistent in the species examined, with macrogranular exine sculpture and long colpi (Figs. 4–9, 25). These characters present in *P. cordifolia* Mattf., *P. corymbosa* Y. C. Tseng, *P. desmocephala* Diels, *P. discolor* Rehd., *P. henanensis* Y. C. Tseng, *P. phyllicoides* J. F. Jeffrey, *P. phyllicoides* var. *berberidoides* J. F. Jeffrey, and *P. scandens* (Thunb.) Sch.-Bip.

### 3 Discussion

The present study revealed that, in the subtribe *Mutisiinae*, the infra-generic pollen morphology was uniform and the species within a genus were fairly similar to each other; the same has already been reported for the subtribe *Nassauviinae* (Crisci 1974). Moreover, we emphasized that exine sculpturing, as an important character, could be used for studying generic relationships in the subtribe *Mutisiinae*.

#### 3.1 Relationships of the *Ainsliaea* group

Mattfeld (1934) indicated the close relationships between *Myriphnois* and *Pertya*, both sharing a similar habit and sessile, few-flowered capitula. Based on a cladistic analysis of morphological data, Hansen (1991a) considered that the Asian genera *Ainsliaea*, *Macroclinidium*, *Myriphnois*, and *Pertya* consisted of a monophyletic group; that is, the *Ainsliaea* group. In their molecular phylogeny inferred from *ndhF* sequences of the *Mutisieae*, Kim *et al.* (2002) reached a similar conclusion and further pointed out that *Myriphnois* and

*Pertya* formed a clade that was sister to *Ainsliaea*. The present study showed that the genera *Ainsliaea*, *Pertya*, and *Myriphnois* share very similar characters in pollen morphology. In all three genera, the exine sculpture was macrogranulate. It backed the morphological and molecular analyses.

Makino (1900 cf. Tseng 1996) divided *Pertya* into two sections: sect. *Macroclinidium* and sect. *Pertya*. The first section, sect. *Macroclinidium* included three species and was endemic to Japan. Bremer (1994) suggested that the section should be placed in its own genus, *Macroclinidium*, on the basis of sect. *Macroclinidium* closer relationships with *Ainsliaea*. For all species examined in the present study, the shape of the pollen grains was mostly subprolate (with the exception of spheroidal pollen grains in five species; Table 1), with long colpi extension nearly to two poles. It is worth mentioning that three species, namely *Macroclinidium rigidulum*, *M. robustum*, and *Ainsliaea acerifolia*, had spheroidal-shaped pollen grains with short colpi. The exine sculpturing of all other species examined in *Pertya* was different from that of both species in Japan (*M. rigidulum* and *M. robustum*), which were placed in sect. *Macroclinidium* by Makino (1900). In addition, the two Japanese species, having typically spiny exines and bearing spines more than  $3\ \mu\text{m}$  long, were remarkably distinct from the other species of *Pertya* and other genera sampled in the present study. As mentioned above, Bremer's (1994) treatment of *Macroclinidium* as a separate genus has been strongly supported by the results of the present study. Interestingly, we noticed that the unique spiny tectum of the two Japanese *Macroclinidium* species was comparable with that of the South American genera *Gongylolepis* R. H. Schomb. and *Wunderlichia* Riedel ex Benth., as well as tropical African genera, such as *Achyrothalamus* O. Hoffm., *Erythrocephalum* Benth., and *Dicoma* Cass., the three genera being placed the *Dicoma* group of *Mutisiinae* by Bremer (1994). However, the relationships between *Macroclinidium* and these spiny American and African genera were not elucidated.



### 3.2 Relationships of the *Gerbera* group

*Gerbera* and *Leibnitzia* were treated in the *Gerbera* group by Bremer (1994). In Hoffmann's (1890) classification, *Leibnitzia* was treated as a section of a broadly defined *Gerbera*. This treatment was followed by *Flora Reipublicae Popularis Sinicae* (Tseng 1996). Tseng (1996) divided the Chinese *Gerbera* into three sections, namely sect. *Anandria* (Siegesb. ex Linn.) O. Hoffm., sect. *Gerbera*, and sect. *Lasiopus* O. Hoffm. Wu and Peng (2002), and Peng (2004) treated *Leibnitzia* and *Lasiopus* as independent genera, based on flora characters with a unique sexual seasonal dimorphism occurring in *Leibnitzia*. Although Hansen (1985), Brummitt (1992), Wielgorskaja and Takhtajan (1995), and Mabberley (1997) did not accept *Lasiopus* as an independent genus, it could be distinguished from *Gerbera* and *Leibnitzia* in having different floral morphological characters (i.e. with female florets in two rows, namely an outer ligulate one and an inner tubular bilabiate one, as well as having stems without bracteal leaves). The pollen morphology of *Gerbera piloselloides*, with macrogranulate exine sculpturing, was different from that of both *Gerbera* and *Leibnitzia*. Therefore, this particular species could be treated with the genus *Lasiopus*. The molecular study of Kim *et al.* (2002) suggested that the *Gerbera* and *Leibnitzia* genera were closely related. This is backed by results of the present study. Of the species of the two genera examined, all (but except for *G. nivea*) had finely granular exine sculpturing.

### 3.3 Relationships of *Gochnatia* and *Nouelia*

*Gochnatia* was a fairly large New World genus with two Asian species (i.e. *Gochnatia decora* and *Goch. spectabilis* Don., with the latter species treated as a synonym of *Goch. decora*; Wu *et al.* 2003) and was a critical taxon for understanding the phylogeny of the *Mutisieae*, as well as the biogeographic relationships of the Asian and American members of the tribe. Roque and Silvestre-Capelato (2001) considered that *Gochnatia* was probably an artificial genus. Bremer (1994) pointed out that the two Asian *Gochnatia* species were related to *Nouelia*, a monotypic Chinese

genus. Kim *et al.* (2002) suggested a basal position of the Chinese monotypic genus *Nouelia* in the *Mustieae* and the polyphyly of the *Gochnatia*, but unfortunately without sampling the two Asian species. A cytological study also showed that both *Goch. decora* and *Nouelia* shared the same chromosome number ( $2n = 54$ ; probably, the chromosome base number  $x = 9$ ; Peng *et al.* 2002), different from those of other genera (e.g. *Ainsliaea*  $x = 12, 13$ ; *Gerbera*  $x = 23, 25$ ; and *Leibnitzia*  $x = 23$ ; Dalington and Wylie 1955). Based on an investigation of 10 different populations of *Nouelia insignis*, the results showed that their chromosome numbers were consistent, suggesting *Nouelia* was a natural group and was an archaic plant. However, our palynological study showed that *Nouelia* had a macrogranulate exine sculpturing, similar to that of some American species of *Gochnatia*, but different from that of *Goch. decora*. The American *Gochnatia*, such as *Goch. hypoleuca* (present study), *Goch. barrosoae* Cabrera, *Goch. hatschbachii* Cabrera, and *Goch. paniculata* Cabrera (Roque and Silvestre-Capelato 2001), had macrogranulate exine, whereas the pollen of *Goch. decora* had a finely granulate exine and can be distinguished from the American species of *Gochnatia*. The present study supports Roque and Silvestre-Capelato (2001), and Kim *et al.* (2002), who suggested that the Asian species of *Gochnatia* could be different from the American members of *Gochnatia* and the genus was polyphyletic.

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**Appendix I** Specimens examined (voucher specimens from which pollen was sampled have been deposited at the herbarium of Kunming Institute of Botany, the Chinese Academy of Sciences)

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- Ainsliaea acerifolia* Sch.-Bip., Liaoning, Shun-Chang Cui 314  
*A. angustata* Chang, Nanchuan, Sichuan, Guo-Feng Li 60245  
*A. angustifolia* Hk. F. et. Thoms ex C. B. Clarke, Gingtong, Yunnan, Quan-An Wu 9083  
*A. aptera* DC, Tibet, Cheng-Yi Wu 75-573  
*A. pertyoides* Franch., Wuding, Yunnan, Jing-San Xin 113  
*Gerbera delavayi* Franch., Gingtong, Yunnan, M. K. Li 3120  
*G. henryi* Dunn, Luquan, Yunnan, Pin-Yi Mao 01722  
*G. macrocephala* Y. C. Tseng, Lijang, Yunnan, K. M. Feng no number  
*G. nivea* (DC.) Sch.-Bip., Zhongdian, Yunnan, K. M. Feng 23335  
*G. piloselloides* (Linn.) Cass., Kunming, Yunnan, Z. H. Yang 101150  
*G. raphanifolia* Franch., Lijang, Yunnan, K. M. Feng 2602  
*Gochnatia decora* (Kurz) A. L. Cabrera, Yangbi, Yunnan, Ren-Chang Qin 22274  
*Goch. hypoleuca* (DD.) A. Gray, Zaragoza, P. Tenorio 2239  
*Leibnitzia anandria* (Linn.) Nakai., Gongcheng, Shanxi, Fen-He River Team 54  
*L. nepalensis* (Kunze) Kitam., Nanmulin Sitsang, Qing-Zang Team 74-2337  
*L. pusilla* (DC) S. Gjould ex Kitam. et Gould., Chaya Sitsang, Qing-Zang Team 13009  
*L. ruficoma* (Franch.) Kitam., Yanyuan, Sichuan, Sichuan Team 77833  
*Macroclinidium rigidulum* (Miq.) Makino, Mt. Nanazugadake, Japan, Tomoyuki Nemoto 3571  
*M. robustum* Maxim., Kannan-yama, Japan, T. Yamazaki 3058  
*Myriopholis dioica* Bunge, Zhulu, Hebei, Chao-Qing Yang 685  
*Nouelia insignis* Franch., Yongsheng, Yunnan, Qing-Zang Team 689  
*Pertya cordifolia* Mattf., Wugang, Hunan, Lin-Han Liu 15926  
*P. corymbosa* Y. C. Tseng., Lingchuan, Guangxi, Zhao-Yu Chen 53707  
*P. desmocephala* Diels, Jiangxi, no corrector 4653  
*P. discolor* Rehd., Lianhuashan, Gansu, Kang He 92-189  
*P. henanensis* Y. C. Tseng, Kuang-Yun Hsien, Sichuan, F. T. Wang 22579  
*P. phylloide* J. F. Jeffrey, Zhongdian, Yunnan, Zhongdian Team 63-2675  
*P. phylloides* var. *berberidoides* J. F. Jeffrey, Jicheng, Sichuan, Sichuan Team 2087  
*P. scandens* (Thunb.) Sch.-Bip. Kochi, Japan, K. Shoma (no number)
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