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Seedcoat micromorphology and its systematic implications for Gentianaceae of Western China

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Abstract

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Scanning electron microscopy of the seedcoats of 46 species from 7 genera of Gentianaceae from mountainous regions of Western China reveals a high diversity of seed micromorphology. Two main types can be distinguished. The first comprises *Gentiana*, *Gentianopsis* and some species of *Swertia* with sculptured seedcoats. It may further be divided into several sub-types each of which corresponds to either a genus or a section. The second type is characterized by smooth seedcoats and is observed in *Comastoma*, *Gentianella*, *Halenia*, *Lomatogonium* and some species of *Swertia*.

Key words: China, *Gentiana*, Gentianaceae, micromorphology, seed, seedcoat, SEM.

Introduction

The family Gentianaceae has a world-wide distribution and comprises 80 genera with about 700 species. It is of great interest both to botanists and laymen by its large diversity and the beauty of the flowers of some species. Many studies have been devoted to its morphology, palynology, cytology and systematics. Some authors have also used micromorphology of seedcoats to try to improve its classification. Miège & Wüest (1984) studied the European species of *Gentiana* L. and *Gentianella* Moench extensively, using scanning electron microscopy (SEM). They showed that seedcoat micromorphology may be used to subdivide these genera into sections; they also provided a key based on seedcoat characters for these species. The seedcoats of some species of *Gentiana* sect. *Calathianae* (Froelich (=sect. *Cyclostima* Griseb.) have also been studied by Müller (1982) using SEM.

With its high number of gentianaceous species, the Southwestern mountainous region of China including the Gansu, Qinghai, Sichuan, Tibet and Yunnan provinces may represent one of the most important diversification centres of the family. But studies on the seed micromorphology of the family in this region are lacking, except for a few general taxonomic descriptions containing brief mentions of seed characters observed under the light microscope. Seed characters under the light microscope have been used by Ho (1988) to distinguish and genera. In a revision of the classification of the genus,

Ho & Liu (1990) have recently recognized six types of seed micromorphology for the genus *Gentiana*. The study, however, consisted only of a very general description of the main types of seedcoats. Detailed observations on more species and a systematic overall evaluation of the seed micromorphology in the genus *Gentiana* and the other related genera are still necessary.

The present SEM observations on seeds of 46 species of 7 genera from Western China were carried out to elucidate the systematic value of seed micromorphological characters and, furthermore, to detect evolutionary trends among seed microcharacters and their correlation with other characters.

Materials and methods

The species examined are listed in the text. All the seeds examined were collected in the field at various localities, either in the Gansu, Shaanxi and Yunnan Province of Western China. Voucher specimens are deposited in the Herbarium of the Botanical Institute of the University of Neuchâtel (NEU).

Seeds suitable for scanning electron microscopy were selected and soaked in warm water until they reached their full size and were then fixed in 65% ethanol. After dehydration with ethanol and then acetone, the seeds were critical-point dried with CO₂, mounted on stubs and subsequently examined with a Philips PSEM-500 scanning electron microscope after being sputter-coated with ca. 40 nm gold.

Some of the terms defined by Barthlott (1981) were used.

Observations

1. Seedcoat types in the Gentianaceae

The seeds examined may be classified into two groups and several subdivisions, based principally on the shape of the epidermal ornamentations of the seedcoat, particularly the curvature of the outer periclinal wall, or so-called primary sculpture of the seedcoat.

The first is the *Gentiana* group, including species of the genera *Gentiana*, *Gentianopsis* Ma, and some of *Swertia* L. with varied sculpture, from fine reticulations to complicated honeycomb-like or finger-like types. This group may be further divided into the following subdivisions based on the nature of the primary sculpture:

a) fine reticulate type: the curvature of the outer periclinal wall of the seedcoat forms fine reticulate ornamentation with varied shapes and sizes of the meshes. This type is the commonest in *Gentiana* sect. *Cruciata* Gaudin (Fig. 1) and sect. *Chondrophyllae* Bunge (Fig. 9–16).

b) semi-winged type: the seeds have a narrow, oblique wing along one side, as in *G. pudica* Maxim. (Fig. 2).

c) compound lamellar type: the seeds are covered with supercellular membranous lamellae which form spongy and complex hexagonal pits as in *G. apiata* N. E. Br. (Fig. 3–4).

d) honeycomb type: the outer periclinal wall of the seedcoat forms honeycomb-like supercellular pits as in *G. callistantha* Diels et Gilg (Fig. 5–8).

e) undulate type: the epidermal cells rise up into undulation-like sculpture as in *G. expansa* H. Sm. (Fig. 17–19).

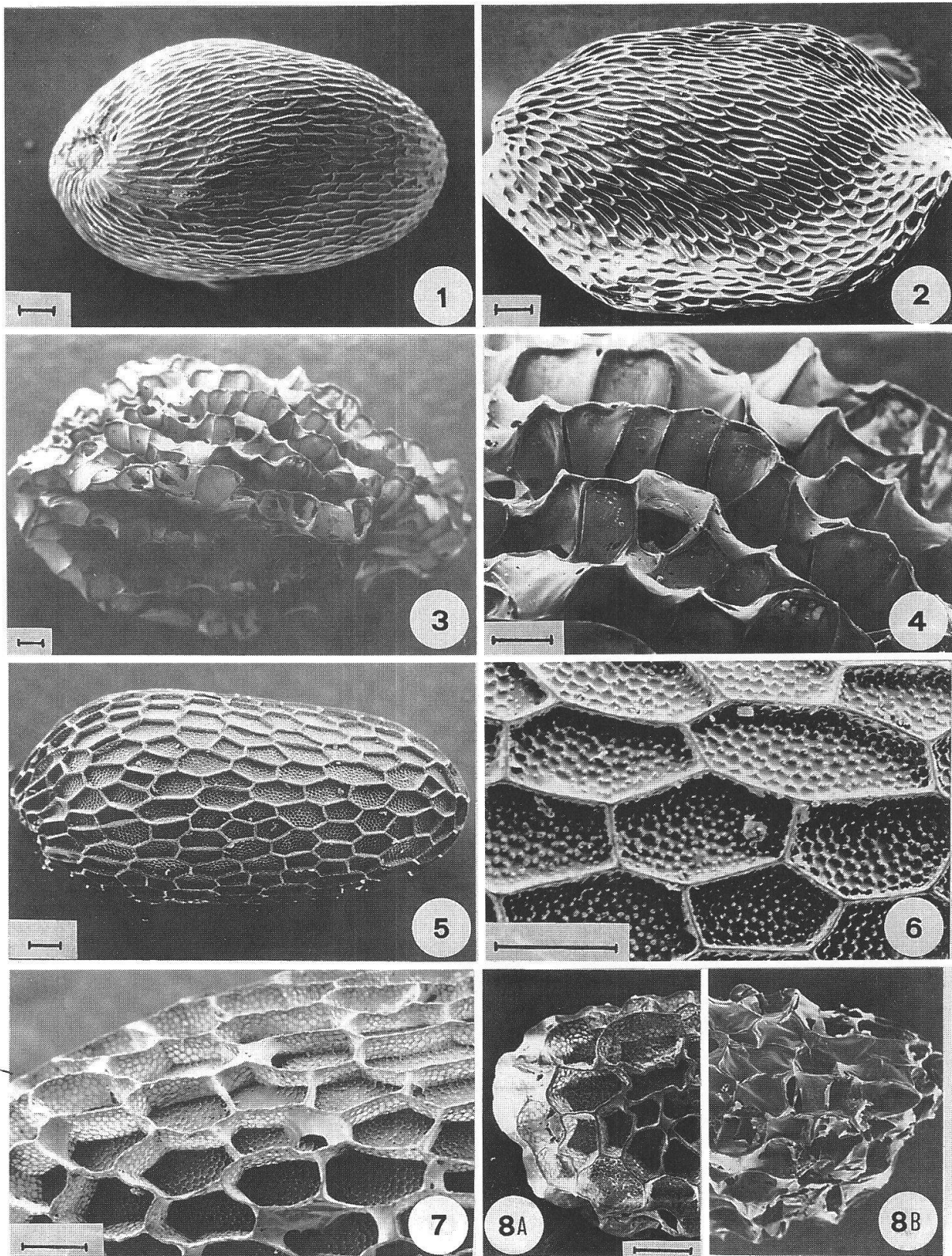


Fig. 1–8. SEM-micrographs of seedcoats of *Gentiana*. – 1: *G. straminea* (sect. *Cruciata*). – 2: *G. pudica* (sect. *Dolichocarpa*). – 3–4: *G. apiata* (sect. *Frigida*). – 5–6: *G. callistantha*; 7: *G. farreri*; 8: *G. regescens* (A. mature seed; B: immature seed with membranaceous cover on its seedcoat) (sect. *Monopodiae*). – Bars = 0.1 mm.

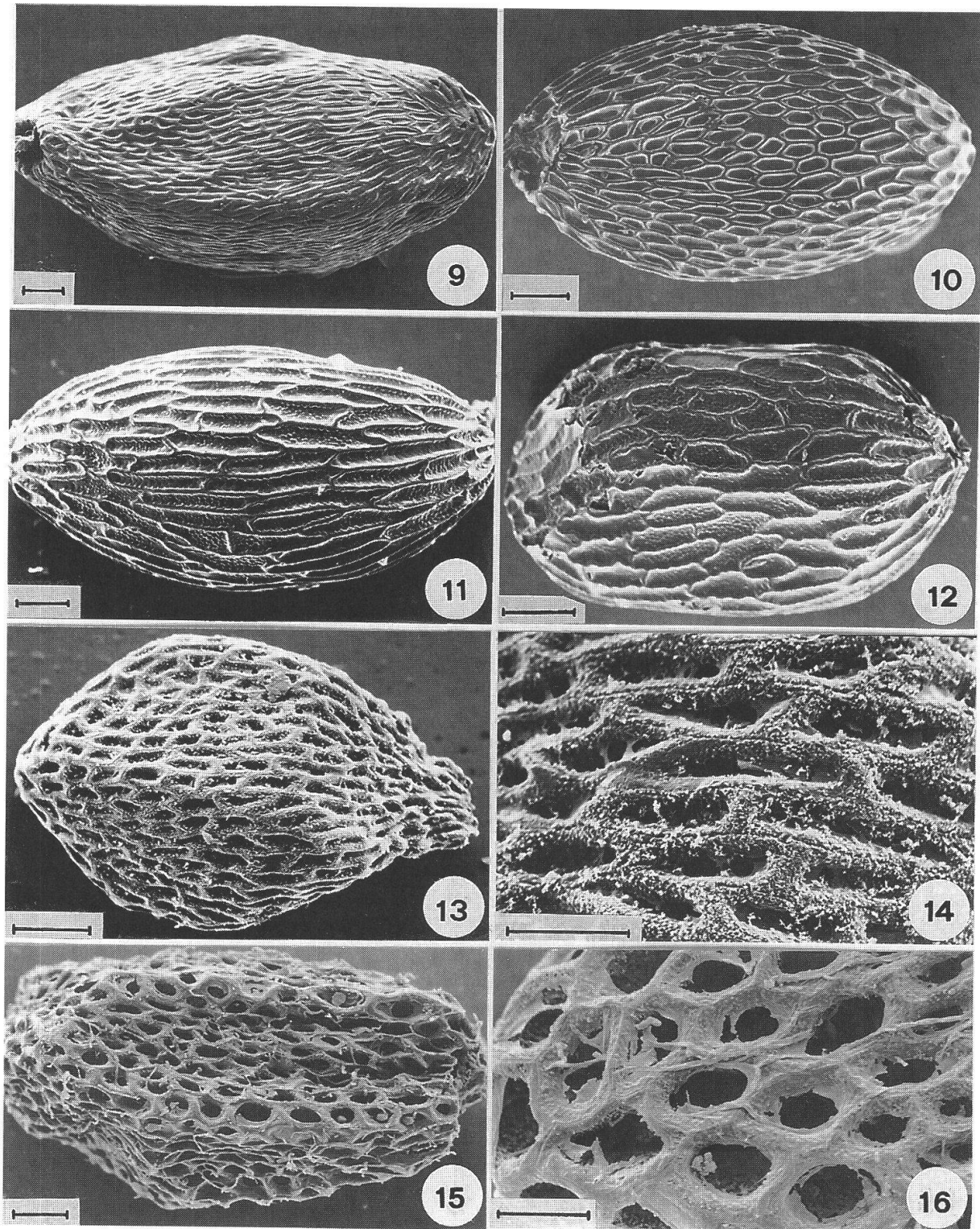


Fig. 9–16. SEM-micrographs of seedcoats of *Gentiana* sect. *Chondrophyllae*. – 9–10: group one: 9: *G. crassuloides*; 10: *G. pseudoaquatica*. – 11–12: group two: 11: *G. leucomelaena*; 12: *G. squarrosa*. – 13–16: group three: 13–14: *G. alsinoides*; 15–16: *G. asterocalyx*. – Bars = 0.05 mm in Fig. 14 and 16; bars = 0.1 mm in others.

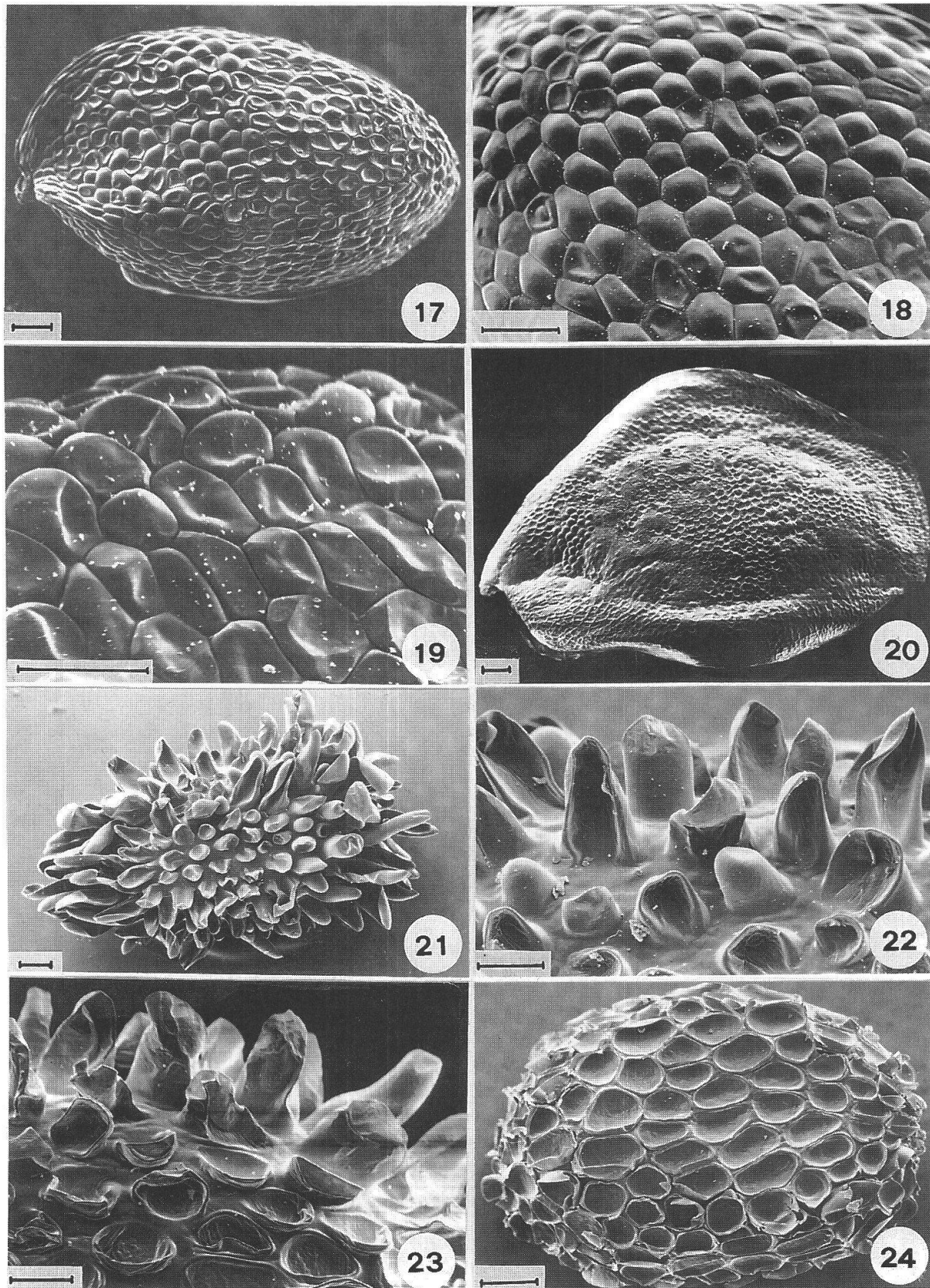


Fig. 17–24. SEM-micrographs of seedcoats of *Gentiana* sect. *Stenogyne*. (17–20) and *Gentianopsis* (21–24). – 17–18: *G. expansa*; 19: *G. primuliflora*; 20: *G. striata*. – 21: *Gentianopsis paludosa* var. *ovato-deltaidea*; 22: *Gentianopsis paludosa* var. *paludosa*; 23–24: *Gentianopsis barbata*. – Bars = 0.05 mm in Fig. 19, 22, 23; bars = 0.1 mm in others.

f) winged type: the seeds have peripheral wings. They are either triquetrous, with wings along three edges as in *G. striata* Maxim. (Fig. 20), or discoid, with wings along the periphery, as in *S. erythrosticta* Maxim. (Fig. 29). The sculpture on the wings and seedcoats is of undulate type.

g) pitted type: the seedcoats have irregular pits on their surface as in *S. diluta* (Turcz.) Benth et Hooker fil. (Fig. 31) and *Gentianopsis barbata* (Froelich) Ma (Fig. 24).

h) finger-like type: the epidermal cells of the seedcoat protrude to form finger-like projections. This type is confined to the genus *Gentianopsis* (Fig. 21–23).

The second group includes the species of *Gentianella*, *Comastoma* (Wettst.) Toyokuni, *Lomatogonium* A. Braun, *Halenia* Borkh. and some of *Swertia*, with smooth or almost smooth seedcoats. The outer periclinal wall never forms projections or any other supercellular appendages (Fig. 25–28 and 30). The only diversity seems to be in the very fine dissimilarities of the epidermal cells and in the cuticle morphology of the cell wall, the so-called tertiary sculpture. It is, therefore, unnecessary to create any subdivision.

2. Seedcoat characters in *Gentian*

Just as the highest diversity of species occurs in the genus *Gentiana*, so does the highest diversity of seedcoat micromorphology. As demonstrated in sections *Calathianae*, *Pneumonanthe* (Gled.) Gaudin, and *Ciminalis* (Adanson) Dumort. by Miège & Wüest (1984) and Müller (1982), the seed micromorphology can provide a taxonomically significant character useful in evaluating intrageneric relationships within the genus. Our present studies on Chinese species mostly confirmed this, but some variations were also noted. The followings are details given section by section.

In sect. *Cruciata* six species were observed: *G. crassicaulis* Duthie ex Burkill, *G. dahurica* Fischer, *G. fetissowii* Regel et Winkler, *G. macrophylla* Pallas, *G. officinalis* H. Smith and *G. straminea* Maxim. The results show a very uniform micromorphology with fine reticulate sculpture on the seedcoat surfaces of all species. The veins forming the reticulations are smooth and much less marked than those of another similar group, sect. *Chondrophyllae*. The meshes are smooth and irregular in shape. No distinct interspecific differences were observed (Fig. 1).

Dolichocarpa T. N. Ho is a new section separated from sect. *Chondrophyllae* by Ho (1875) and based on *G. prostrata* Haenke. Only one of its species, *G. pudica*, was investigated. Each seed has a very narrow, oblique wing along one side, so it was considered a semi-winged type in the present paper. However, the ornamentations on the seedcoat and wing are similar to that of sect. *Chondrophyllae*, i.e. reticulate (Fig. 2).

In section *Frigida* Kusn. only one species, *G. apiata* N. E. Br., endemic to Mt. Taibaishan in Central China, was studied. It has a compound lamellar type of seedcoat with supercellular membranaceous lamellae covering the seeds. The lamellae are formed of a complex, sponge-like structure in which the veins are usually polygonal with a very thin membranous cover (Fig. 3–4). This type seems to be the most complicated in the genus and is confined to this section.

Section *Monopodiae* T. N. Ho is also a new section, segregated from section *Frigida* by Ho (1985). Three species, *G. farreri* Balf. f., *G. callistantha* and *G. regescens* Hemsley, were investigated here. The primary sculpture patterns of the species from honeycombs with membranous cells (Fig. 5–8). The cells are penta-, hexa- and heptagonal, mainly hexagonal. A unique feature of the seeds of all species examined in this section is the special secondary sculpture they possess. These secondary sculpture patterns, such as the hexagonally raised papillae in *G. callistantha* (Fig. 5–6) or the hexagonal nets in *G.*

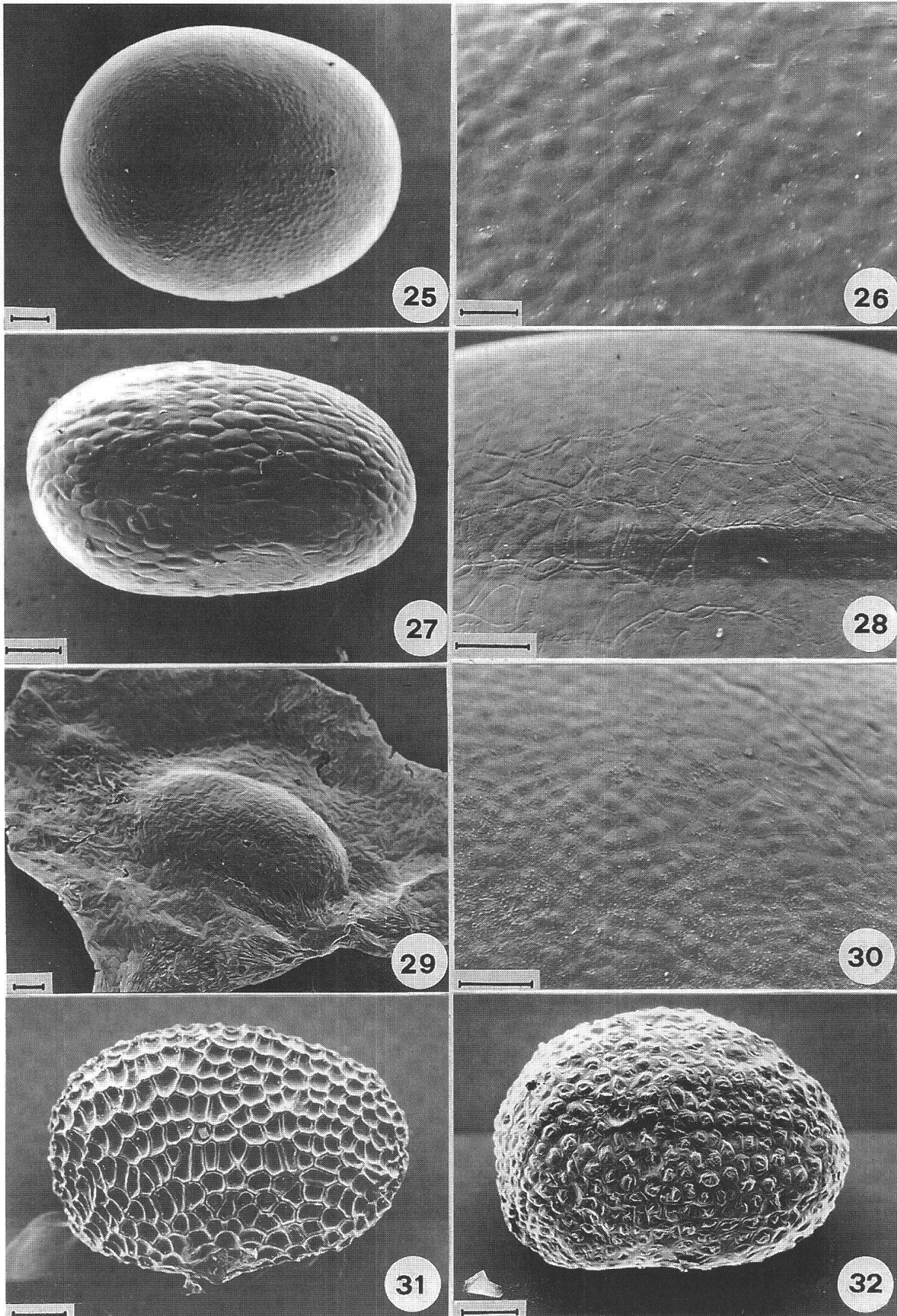


Fig. 25–32. SEM-micrographs of seedcoats. – 25–26: *Comastoma pulmonarium*; 27: *C. polycladum*. – 28: *Gentianella azurea*. – 29: *Swertia erythrosticta*; 30: *S. tetraptera*; 31–32: *S. diluta* (note the membranaceous cover layer in Fig. 32). – Bars = 0.01 mm in Fig. 26, 28 and 30; bar = 0.1 mm in others.

farreri (Fig. 7) and *G. regescens* (Fig. 8 A), are restricted to this section and are, therefore, good diagnostic characteristics. Interspecific differentiation is provided by the shape of the secondary sculpture and the height of the primary sculpture, that is, of the cells. In addition, some immature seeds of *G. regescens* have a membranous cover over their honeycomb sculpture which may represent a developmental variation (Fig. 8 B).

Sect. *Stenogyne* Franchet is heterogeneous in seed micromorphology. Four species, *G. striata*, *G. souliei* Franchet, *G. primuliflora* Franchet and *G. expansa*, were examined. Two different types of seeds were found. The former two species have triquetrous seeds with three winged edges (Fig. 20), but the latter two have more or less elliptical unwinged seeds (Fig. 17–19). The sculpture in all these species is of undulate type, protrusious by the raising of the epidermal cells (Fig. 17–20).

We paid the most attention to section *Chondrophyllae*: 18 species were examined; *G. alsinoides* Franchet, *G. anisostemon* Marquand, *G. aperta* Maxim., *G. aristata* Maxim., *G. asterocalyx* Diels, *G. crassuloides* Bureau et Franchet, *G. exigua* H. Sm., *G. heleonastes* H. Sm. ex Marquand, *G. intricata* Marquand, *G. leucomelaena* Maxim., *G. piaszekii* Maxim., *G. pratii* Kusn., *G. praticola* Franchet, *G. pseudoaquatica* Kusn., *G. spathulifolia* Kusn., *G. squarrosa* Ledeb., *G. tricolor* Diels et Gilg, and *G. vandellioides* Hemsley. The seedcoat sculpture patterns mostly belong to the fine reticulate type. The raised striations of the epidermal cell boundaries interconnect to form the reticulation. The width of the gaps between striations, the size and the shape of the meshes vary from species to species. However, three groups can be recognized. The first, represented by *G. crassuloides* (Fig. 9), has straight and smooth, or almost smooth, rather narrowly spaced striations. Most of the species examined, including *G. aperta*, *G. aristata*, *G. crassuloides*, *G. piaszekii*, *G. pseudoaquatica*, *G. spathulifolia* and *G. tricolor*, belong to this group (Fig. 9–10). The second, represented by *G. squarrosa* (Fig. 12), has more or less pronounced anticlinal undulations and micropapillate secondary sculpture on the periclinal walls and the raised boundaries of the seedcoat cells. *G. leucomelaena*, *G. pratii* and *G. vandellioides* also belong to this group (Fig. 11–12). The third, represented by *G. asterocalyx* and *G. alsinoides*, has rather rough striations with some fine irregular, floccose structures (Fig. 13–16). This group also includes *G. anisostemon*, *G. exigua*, *G. intricata* and *G. praticola*. It is interesting to note that all species of the first and second group were collected from Gansu and Shaanxi, the northernmost part of the area investigated, but the species of the third group were collected from Yunnan, the southernmost part of the area.

3. Seedcoat characters in *Gentianella*, *Comastoma*, *Lomatogonium*, *Halenia*, *Swertia* and *Gentianopsis*

In the genus *Gentianella* the seed of two populations of *Gentianella azurea* (Bunge) Holub were examined. Both have very smooth seedcoats with no obvious sculpture (Fig. 28). This results confirmed the previous, more detailed observations by Miège & Wüest (1984) on the European species of the genus.

In the genus *Comastoma*, *C. pulmonarium* (Turcz.) Toyokuni and *C. polycladum* (Diels et Gilg) T. N. Ho were observed, both showing smooth seedcoats very similar to that of *Gentianella*, but granulate on the surface. A few differences can be found between the above two species: the former has a granulate surface, the latter a somewhat undulate one (Fig. 25–27).

Two species of *Lomatogonium* were examined, namely *L. rotatum* (L.) Fries ex Nyman and *L. macranthum* (Diels et Gilg) Fernald. They also have smooth seedcoats similar to those of *Gentianella* and *Comastoma*. No interspecific difference was found.

Only one species of *Halenia*, *H. elliptica* D. Don, was thoroughly studied. It is also similar to *Gentianella* in having smooth type seedcoats.

Observations on four species of *Swertia*, namely *S. erythrosticta*, *S. diluta*, *S. dichotoma* L., and *S. tetraptera* Maxim., revealed a variable situation in the genus. *S. erythrosticta* has peripherally winged seeds. The seedcoats are usually smooth or irregularly wrinkled (Fig. 29). The seeds of *S. diluta* have irregularly pitted surfaces, a feature unique among the materials examined (Fig. 31). However, some seeds of the species have membranous undulation-like covers over these pits (Fig. 32). This we suppose to represent a developmental variation and the pitted sculpture may be formed from the peeling off of the membranous cover layer. The seeds of *S. dichotoma* and *S. tetraptera* are similar to those of *Comastoma* and *Halenia*, with very finely granulate (or occasionally smooth) surfaces (Fig. 30).

Three taxa of *Gentianopsis*, *G. paludosa* (Hooker fil.) Ma var. *paludosa*, *G. paludosa* var. *ovato-deltaoidea* (Burkill) T. N. Ho, and *G. barbata*, were examined in this genus. Characteristically, all materials show finger-like sculpture on the outer surfaces of the seedcoats. The finger-like projections are usually longer along the periphery and shorter on both the dorsal and ventral surfaces (Fig. 21–23). Some interspecific variations of sculpture were observed. The seeds of *G. paludosa* possess finger-like projections throughout their ripening process (Fig. 21–22), while the seeds of *G. barbata* usually have finger-like projections only along the periphery (Fig. 23), or have only pits instead of this type projections on their whole surface at maturity (Fig. 24). This may represent a developmental variation where the pits were formed from the shedding of the finger-like projections.

Discussion

Seed morphology has been used for a sectional classification of the genus *Gentiana*. The present examinations of more species and genera from China under SEM further confirmed that seeds of the family show considerably diversity but also relative stability in certain taxa. Among the closely related genera in the subtribe *Gentianinae*, two groups have been recognized, based on the position of floral glands: the *Gentiana* group, including *Gentiana*, *Crawfurdia* Wall., *Tripterispermum* Blume and *Megacodon* (Hemsley) H. Sm., and the *Gentianella* group, including *Gentianella*, *Comastoma*, *Gentianopsis*, *Lomatogonium*, *Lomatogoniopsis* T. N. Ho et S. W. Liu, *Swertia* and *Halenia* (Ho & Liu 1990). The present studies on seedcoats confirms this division to a certain extent. Although only the largest genus *Gentiana* was studied here, the former group has sculptured seedcoats, while the latter has mostly more or less smooth seedcoats, except for the genus *Gentianopsis* and some species of *Swertia*. *Gentianopsis* was based on *Gentiana* sect. *Crossopetalum* Froelich ex Griseb. (Ma 1951). Both gross and micromorphology confirm the division. The specific finger-like sculpture on the seedcoats also justify its isolated position in the *Gentianella* group mentioned above. It is also far from the *Gentiana* group from the point of view of seedcoat sculpture.

In the genus *Gentiana*, different patterns of seedcoat sculpture generally distinguish sections and may be diagnostic characters, except that sections *Cruciata* and *Chondrophyllae* have somewhat similar reticulate seedcoat sculpture even though they are quite

different in gross morphology. Section *Monopodiae* was split off from section *Frigida* on the basis of their different branching patterns (Ho 1985). The seedcoat micromorphology confirms this division, since sect. *Frigida* has primary sculpture of the compound lamellar type and no obvious secondary sculpture, while sect. *Monopodiae* has honeycomb-like primary sculpture with special hexagonally raised secondary sculpture. In sect. *Chondrophyllae* three different groups of seedcoat sculpture with subtle differences were distinguished. This seems to be correlated with the geographical distribution as mentioned above. In *Swertia* and *Gentiana* sect. *Stenogyne* seed micromorphology is not always congruent with the gross morphology, especially as regards the presence of wings and the shape of the seeds. Since only limited numbers of species were studied, it is necessary to check more species before any valid conclusion can be drawn.

The developmental variations of seed micromorphology are worthy to be taken into account, not only because they give a better comprehension of sculpture development but also because they supply indications for understanding both the evolution of the sculpture patterns and the relationships between the different types of the sculpture. They also remind us of the importance of avoiding the confusion between developmental and phylogenetic variations of sculpture when we compare different taxa: *Gentianopsis barbata* and *Swertia diluta*, for example, have similar seedcoat sculpture patterns at maturity, but these patterns have very different origins.

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