

Review of the Sporoderm Ultrastructure of Members of the Asterales

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Abstract—Palynomorphological characteristics of the order Asterales are discussed. Particular attention is paid to the pollen morphology of basal families of this group and to that of problematic taxa that are considered as sister groups to the group under study. Ultrastructurally similar sporoderms of several families, including (1) Asteraceae, Calyceraceae, and Goodeniaceae; (2) Campanulaceae, Phellinaceae, and Menyanthaceae; (3) Rouseaceae, Abrophyllaceae, and Columelliaceae, are described. Pollen grains of Alseuosmiaceae and Stylidiaceae show unique ultrastructural features of the exine.

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INTRODUCTION

At different times, concepts of the group of Asteraceae and its relatives has been considered to include different families. These variants concerned a distinct circle of taxa. Thus, the system of Takhtajan (1997) included the subclass Asteridae with 14 families; the system of Thorne (2000) included the suborder Asternae with nine families.

Recently, relationships of Asteraceae have been significantly clarified by extensive genosystematic studies. For example, rbcL sequencing of members of the genera *Carpodetus*, *Abrophyllum*, and *Cuttsia*, which were earlier assigned to the Saxifragaceae sensu lato, has revealed that they compose a separate family, the Rouseaceae, and are close to the clade Asterales (Gustafsson and Bremer, 1997). The genera that currently compose the families Alseuosmiaceae, Phellinaceae, and Argophyllaceae, were earlier assigned to different families of the Hydrangeales. Karehed et al. (1999) place them between the Campanulaceae- and Stydiaceae-relations. The order Asterales is considered in this broad sense on the *Angiosperm Phylogeny Website* (Stevens, 2001). In addition, this study considers some members of the families that occupy the basal position to Euasterids II, which were discussed in relation to the position of the order Asterales in the dicot system (Soltis et al., 2005).

Taxa in the basal part of the systems proposed are of particular interest. As a rule, these genera have repeatedly been moved from order to order in different systems, because they were insufficiently understood. Therefore, more morphological substantiation is needed for the verification of their assignment to one group (clade) or another.

MATERIAL AND METHODS

Pollen grains of 18 members of 12 families were studied. The material was received from the herbarium of Komarov Botanical Institution of the Russian Academy of Sciences, St. Petersburg.

(1) Family Goodeniaceae: *Brunonia australis* R. Brown and *Dampiera eriocephala* Vriese.

(2) Family Columelliaceae: *Columellia sericea* F.A. Humbolt, A.J.A. Bonpland et C.S. Kunth.

(3) Family Calyceraceae: *Calycera eryngioides* Remy, *Gamocarpa caespitosa* R.A. Philippi ex C.M. Hicken, and *Acicarpa pinnatifida* Miers.

(4) Family Campanulaceae: *Platycodon grandiflorum* A. DeCandol.

(5) Family Ixerbaceae: *Ixerba brexioides* A. Cunningham.

(6) Family Vahliaceae: *Vahlia* sp.

(7) Family Phellinaceae: *Phelline erubescens* H. Baillon et F.R.R. Schlechter.

(8) Family Eremosynaceae: *Eremosyne pectinata* S.L. Endlicher.

(9) Family Stylidiaceae: *Stylidium graminifolium* C.L. Willdenow and *Stylidium adpressum* Benth.

(10) Family Argophyllaceae: *Argophyllum nitidum* J.R. Forster et G. Forster and *Corokia buddleioides* A. Cunningham.

(11) Family Rouseaceae: *Abrophyllum ornans* (F. Mueller) Benth. and *Cuttsia viburnea* F. Mueller.

(12) Family Alseuosmiaceae: *Alseuosmia linariifolia* A. Cunningham.

All the samples studied were acetolized, described, and photographed using an Axioplan-2 light micro-

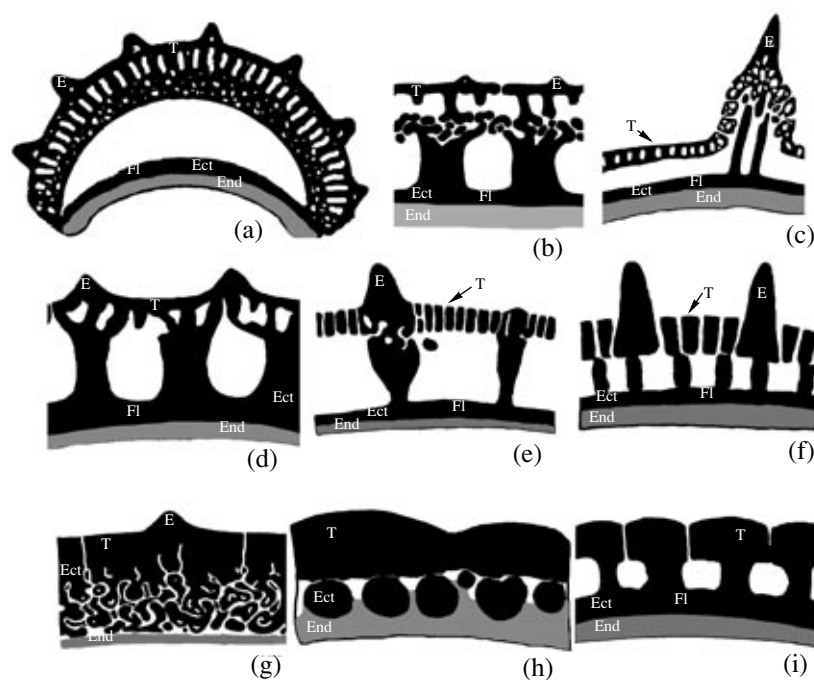


Fig. 1. Sporoderm ultrastructure, schematic: (a) cavate pollen grains; (b) noncavate pollen grains; (c) echinolophate pollen grains; (d) pollen grains with a double columellate layer; (e) Menyanthaceae-type of sporoderm; (f) Campanulaceae-type of sporoderm; (g) noncolumellate medullary sporoderm; (h) columellate-like sporoderm; and (i) simple columellate sporoderm; (a, b, c) sporoderm of the Asteraceae; (e) sporoderm of the Menyanthaceae; (f) sporoderm of the Campanulaceae and Phellinaceae; (g) sporoderm of the Stylidiaceae; (h) sporoderm of the Alseuosmiaceae; and (i) sporoderm of the Columelliaceae, Rousseeaceae, Abrophyllaceae, and Ixerbaceae. Designations: (End) endexine; (Ect) ectexine; (Fl) foot layer; (T) tectum; and (E) echina (spine or spinule).

scope in glycerol-jelly slides. Nonacetolized pollen grains were studied under *Hitachi* and *Camscan* scanning electron microscopes. For transmission electron microscopy, all samples of pollen grains were stained with 2% OsO₄, processed in alcohol, stained with uranyl acetate in 70% alcohol, dehydrated, put in acetone, and embedded in epoxy mixture (Weakley, 1972). Ultrafine sections were made using an ultramicrotome, additionally stained after Reynolds (Geyer, 1973), and studied under a Jeol-100 transmission electron microscope.

RESULTS: THE MAJOR MORPHOLOGICAL CHARACTERISTICS OF POLLEN GRAINS OF THE FAMILIES STUDIED

Asteraceae

Pollen grains of the Asteraceae have long been studied, and a considerable bulk of information about their morphology has been obtained (Skvarla et al., 1977; Meyer-Melikian et al., 2004). Pollen grains of the Asteraceae are three-colporate, medium-sized or large, ellipsoidal or spheroid, more rarely, hexagonal (some members of the tribes Cichorieae, Liabeae, and Vernoniaeae). The colpi are usually long, occasionally shortened (*Ambrosia* and *Xanthium*) or indistinct (some Cichorieae). The sculpture is echinate (spinulose or spinose) or echinolophate. The majority of representatives of the family have cavate pollen grains (Fig. 1a). The

ectexine contains a vast cavity between the columellae and foot layer, so that the ectexine retains its integrity only along the apertural margins. In some members, the foot layer is partially (*Calendula*; Kosenko and Polevova, 2001) or completely (subfamily Barnadesioideae) reduced, and hollow chambers of various sizes and shape occur in the columellae. Noncavate pollen grains (Fig. 1b) have a double columellate layer and occur in different tribes, particularly often in the subfamily Cichorioideae. The morphological diversity of the noncavate ectexine is expressed in various shape and arrangement of inner columellae. Thus, echinolophate pollen grains have slender (high and thin) inner columellae that are only present under spines and ridges (lophae) (Fig. 1c). Spinulose noncavate pollen grains have massive (thick) inner columellae, which are densely positioned and, in the upper part, are transformed into a reticulate infratectum and into outer columellae covered with a tectum. Pollen grains of all Asteraceae have a well-developed endexine, which often becomes thicker and layered in the apertural regions (Polevova, 2004).

Goodeniaceae

In terms of pollen morphology, the majority of genera of the Goodeniaceae are most similar to the Asteraceae (Fig. 1d). Pollen grains of the Goodeniaceae are



three-colporate, ellipsoidal–nearly spherical, medium-sized, or small (in *Dampiera*), and arranged in square tetrads in members of *Leschenaultia*. The colpi are long, the ores are narrowly ellipsoidal, equatorially elongated or with an indistinct outline (*Dampiera*). The surface sculpture (Pl. 9, figs. 5, 10) is verrucate with numerous perforations, striate (*Dampiera* and *Anthodium*), or pitted (*Leschenaultia*). The ectexine has a double columellate layer (Pl. 10, figs. 5, 10), while the endexine is thinner than the foot layer to a varying degree. Members of the genus *Dampiera* have a simple columellate ectexine and an extremely thin endexine.

Calyceraceae

The Calyceraceae are very similar in pollen morphology to the Asteraceae and Goodeniaceae (Fig. 1d). Pollen grains of the Calyceraceae are three-colporate, spheroidal or rhomboidal, and medium-sized. The colpi are long, bordered in *Calycera*; ores have indistinct outlines. The surface sculpture is finely verrucate, with depressions in mesocolpia in members of *Acicarpha* (Pl. 9, figs. 2, 3). The ectexine is with a double columellate layer (Pl. 10, figs. 2, 6); in members of *Acicarpha*, columellae in depressions are simple (Pl. 10, fig. 2). The endexine is only slightly thinner than the foot layer.

Menyanthaceae

Pollen grains of the family Menyanthaceae have little in common with the three above-described families (Fig. 1e). They are three-colporate, spheroidal, and large or medium-sized. The surface sculpture is spinose and pitted or reticulate between the spines. The ectexine is formed by a double columellate layer, which differs from the analogous layer of the Asteraceae. Well-developed inner columellae always support solid spines. There is a composite tectum between the spines, which represents either a net or a layer pierced with numerous, densely spaced vertical channels.

Campanulaceae

Members of the family Campanulaceae show generally similar pollen morphology to the Menyanthaceae (Fig. 1f). Pollen grains of the Campanulaceae sensu lato are very diverse in the apertural types. They may be 3–4–5–6–8–12-porate (either equatorial or global), 3–5–6–9-colpate, or three-colporate. The pollen grains are usually medium-sized or large. The shape ranges from ellipsoidal-spherical to flattened-spherical. The

surface is spinose or spinulose (Campanuloideae; Pl. 9, fig. 11), striate or reticulate (Lobelioideae), or smooth (Cyphioideae and Sphenocleioideae; Pl. 9, fig. 17). The general structural pattern of the ectexine resembles that of the Menyanthaceae (Pl. 10, fig. 14); two rows of columellae of identical height and width are seen in sections. The inner columellae are more loosely arranged, they may be rooted in the endexine rather than in the foot layer (foot layer is absent) (*Parishella*, *Codonopsis*, *Platycodon*, and *Ostrowskia*). The outer row is constituted by columellae that are separated by densely spaced narrow channels. The endexine is usually well developed (Dunbar, 1984; Shrestka and Tarasevich, 1992; Tarasevich and Shrestka, 1992).

Phellinaceae

The family Phellinaceae is virtually indistinguishable from the Campanulaceae in exine morphology (Fig. 1f). Pollen grains of the Phellinaceae are three-colpate, spheroidal, and medium-sized. The colpi are long. The surface sculpture is spinose, pitted between the spines (Pl. 9, fig. 13). The exine ultrastructure of *Phelline* (Pl. 10, fig. 13) is extremely similar to that of the Campanulaceae: there are two rows of straight columellae of identical height and width, inner columellae are arranged more loosely, rooted into a thick foot layer, while the endexine is thin.

Stylidiaceae

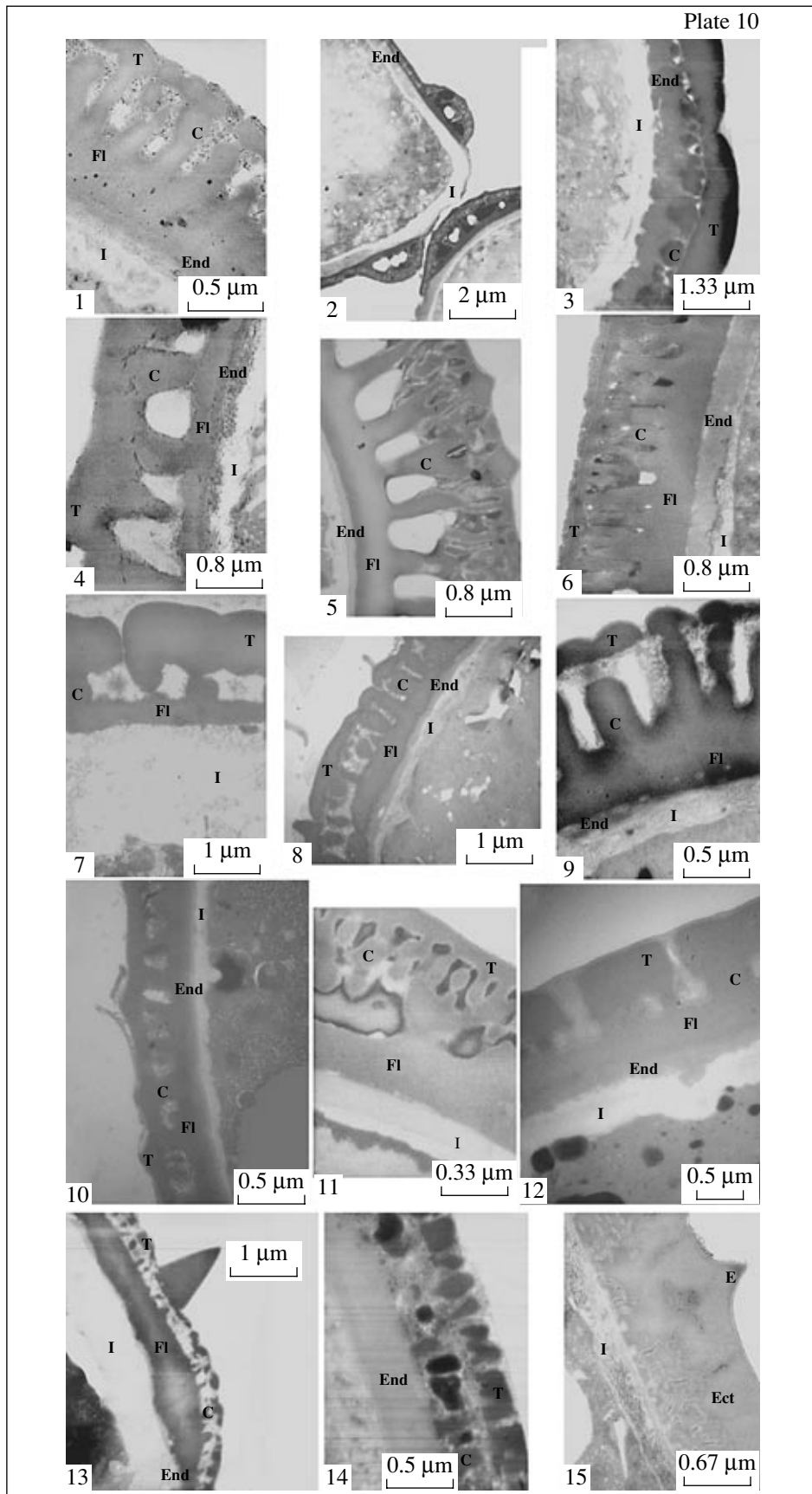
The family Stylidiaceae stands significantly apart with reference to the exine ultrastructure (Fig. 1g). Pollen grains of the Stylidiaceae are three-colpate (*Donatia*) or six-colpate (*Stylidium*), nearly flattened-spheroidal or spheroidal, medium-sized. The colpi are long. The surface is smooth, pitted (*Donatia*), or spinulose (*Stylidium*), the spinules are also present on the apertural membrane (Pl. 9, fig. 16). The ectexine is devoid of columellae; in the inner part, it is transpierced by numerous sinuous channels, which appear in sections as a medullar structure (Pl. 10, fig. 15). Neither foot layer nor endexine were revealed.

Alseuosmiaceae

The ectexine of Alseuosmiaceae is difficult to interpret as columellate ectexine (Fig. 1h). Pollen grains of this family are three-colpate, rounded or rhomboidal, and medium-sized. The colpi are long. The exine is thick and irregularly tubercular. The sculpture is

Explanation of Plate 9

Figs. 1–17. Pollen grains, SEM: (1) *Alseuosmia linariifolia* A. Cunningham; (2) *Acicarpha pinnatifida* Miers; (3) *Calycera eryngioides* Remy; (4) *Argophyllum nitidum* J. R. Forster et G. Forster; (5) *Brunonia australis* R. Brown; (6) *Abrophyllum ornans* (F. Mueller) Benth; (7) *Columellia sericea* Humboldt, Bonpland et Kunth; (8) *Corokia buddleioides* A. Cunningham; (9) *Cuttsia viburnea* F. Mueller; (10) *Dampiera eriocephala* Vriese; (11) *Platycodon grandiflorum* A. DeCandolle; (12) *Eremosyne pectinata* Endlicher; (13) *Phelline erubescens* H. Baillon et F.R.R. Schlechter; (14) *Vahlia* sp.; (15) *Ixerba brexioides* A. Cunningham; (16) *Stylidium adpressum* Benth; and (17) *Cyphia dentata* E. Wimmer.



coarsely wrinkled (Pl. 9, fig. 1). The ectexine includes a thick tubercular tectum and thick granular-like columellae. The foot layer is absent. The endexine is well developed (Pl. 10, fig. 3).

Columelliaceae

In contrast to all the above-described families, the Columelliaceae have a sporoderm with typical simple columellae (Fig. 1i). Pollen grains of this family are three-colporate, nearly flattened-spheroidal, and medium-sized. The colpi are long. The ores have unclear outlines. The sculpture of the surface ranges from finely reticulate to wrinkled-pitted (Pl. 9, fig. 7). The ectexine has simple columellae (Pl. 10, fig. 7). The endexine is only present near the apertural margins.

Rousseaceae

As the Columelliaceae, the family Rousseaceae is characterized by a simple (typical) columellate ectexine (Fig. 1i). Pollen grains of the Rousseaceae (including the Carpodetaceae and Argophyllaceae) are three-colporate, nearly spheroidal, and medium-sized. The genus *Carpodetus* has pollen grains arranged in tetrahedral tetrads. The colpi are long, the ores are small (*Corokia*), or apertures have unclear borders (*Argophyllum*). The exine surface is smooth (*Argophyllum*, Pl. 9, fig. 4), pitted with numerous perforations (*Carpodetus*), or finely verrucate (*Corokia*; Pl. 9, fig. 8). The ectexine (Pl. 10, figs. 4, 8) has simple columellae, which are very short in *Carpodetus* (Praglowksi and Grafstrom, 1984). The endexine is slightly thinner than the ectexine.

Abrophyllaceae

Members of the family Abrophyllaceae also have a simple columellate exine (Fig. 1i). Pollen grains are three-colporate, usually spheroidal, and small. The colpi are long, ores are narrowly ellipsoidal, equatorially elongate, rarely, hardly discernible (some species of *Abrophyllum*). The surface sculpture is finely verrucate (*Abrophyllum*; Pl. 9, fig. 6) or shortly striate (*Cuttsia*; Pl. 9, fig. 9). The ectexine is of the usual angiospermous columellate type (Pl. 10, fig. 9). The endexine is very thin.

Ixerbaceae

The relatively distant family Ixerbaceae also shows a simple exine structure (Fig. 1i). Pollen grains of *Ixerba* are 5–6-colporate, flattened-spheroidal, and medium-sized. The colpi are long; the ores are small and have indistinct margins. The exine surface is smooth, with numerous perforations, or very finely reticulate (Pl. 9, fig. 15). The ectexine has simple columellae; the endexine is less developed than the thick foot layer (Pl. 10, fig. 12).

DISCUSSION

The sporoderm ultrastructure of the Asteraceae has been studied rather thoroughly. Within the family, two main structural patterns are distinguished, i.e., a cavate and noncavate sporoderm. Noncavate pollen grains prevail among the Cichorioideae, whereas only one tribe of the Asteroideae, Anthemideae, has noncavate pollen grains. Cavate pollen grains are present in many tribes. The pollen grains of the tribes Cichorieae, Liabeae, and Vernonieae, and the subtribe Nassauviinae are distinguishable from typical noncavate pollen grains only by the quantitative ratios between the structural elements of the exine. Pollen grains of the Cichorieae, Liabeae, and Vernonieae have a double columellate layer only under the spines; a large ectexinal cavity is situated near the lacune floor and between spines. Pollen grains of the subtribe Nassauviinae only differ from typical noncavate pollen grains in a bifurcating inner columellae of the ectexine. The basal subfamily Barnadesioideae stands apart from the other subfamilies of the Asteraceae. On the one hand, pollen grains of this subfamily may have depressions on mesocolpia similarly to members of the tribe Cichorieae; on the other hand, all members of the subfamily that have been studied lack a foot layer in the mesocolpia, similarly to some cavate pollen grains with a discontinuous foot layer (*Calendula*).

However, with reference to the search for taxonomic relationships, noncavate pollen grains of the typical structure, which were described as early as 1977 by Skvarla et al., are most significant. This type of sporoderm morphology analogous to the noncavate type of the Asteraceae is known in the Goodeniaceae and Calyceraceae. On the other hand, pollen grains with the exine differentiated along the surface also occur in these families. Thus, the sporoderm of *Acicarpha* shows simple columellate morphology in the mesocolpia, but is virtually indistinguishable in the apertural regions from typical noncavate Asteraceae. The only differences are discernable in the transitional region

Explanation of Plate 10

Figs. 1–15. Exine ultrastructure, TEM: (1) *Abrophyllum ornans* (F. Mueller) G. Bentham; (2) *Acicarpha pinnatifida* Miers; (3) *Alseuosmia linariifolia* A. Cunningham; (4) *Argophyllum nitidum* J.R. Forster et G. Forster; (5) *Brunonia australis* R. Brown; (6) *Calycera eryngioides* Remy; (7) *Columellia sericea* Humboldt, Bonpland et Kunth; (8) *Corokia buddleioides* A. Cunningham; (9) *Cuttsia viburnea* F. Mueller; (10) *Dampiera eriocephala* Vriese; (11) *Gamocarpha caespitosa* R.A. Philippi ex C.M. Hicken; (12) *Ixerba brexioides* A. Cunningham; (13) *Phellina erubescens* H. Baillon et F.R.R. Schlechter; (14) *Platycodon grandiflorum* A. DeCandolle; and (15) *Stylidium adpressum* Bentham. The arrow indicates simple columellae.

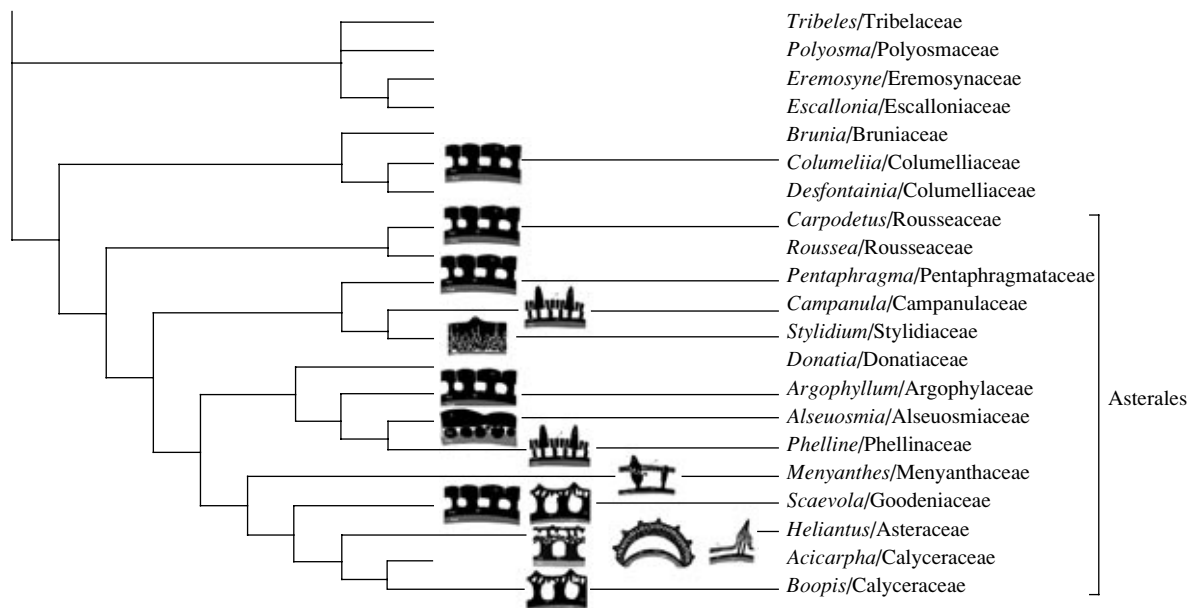


Fig. 2. The distribution of types of sporoderm ultrastructure mapped onto the molecular cladogram (modified from Bremer et al., 2002).

between the inner and outer columellae. In the Asteraceae, the two rows of columellae are connected by a certain reticulate layer (infratectum), whereas an analogous layer is not found in the Goodeniaceae and Calyceraceae. The inner columellae are large in their basal part and branch in the apical part to transform into thinner branches of the outer columellae. It is of interest that, in pollen grains of *Acicarpa*, the noncavate ectexine is located at the margins of the apertures, while the centers of the mesocolpia contain depressions with a simple columellate ectexine. By contrast, many members of the Goodeniaceae have a noncavate ectexine in the centers of mesocolpia and apocolpia, while towards the apertures, the ectexine becomes thinner and transforms into simple columellae. In some members, the apertural border includes only the tectum and foot layer without columellae; thus, the aperture is completely bordered in the ectexine.

The ectexine of the Menyanthaceae and Campanulaceae is characterized by a peculiar architecture. Large columellae in the upper part are covered with a thick tectum that is transpierced with numerous perforations and crowned with supracteal spines. The sporoderm of the Menyanthaceae is supplied with reticulate or labyrinth areas in the upper part of the columellae. Such areas are particularly distinct near spines. Members of the Menyanthaceae have many ultrastructural variants within the frame of this structural pattern. By contrast, all numerous members of the Campanulaceae sensu lato are uniform in sporoderm structure. The only varying character is the extent to which the foot layer is developed, ranging from very thick (the majority of taxa) to discontinuous (Lobelioideae) or nearly lacking. Nonetheless, members of the family Campanulaceae

demonstrate a wide diversity of apertural types (Dunbar, 1975a, 1975b; Avetisyan, 1986). Pollen grains of the Phellinaceae also belong to this ultrastructural type. They differ from the Campanulaceae only in the smaller elements (both columellae and perforations) of the ectexine. Consequently, the sporoderm of the Phellinaceae is more similar to the ordinary columellate sporoderm of angiosperms than that of the Campanulaceae.

Pollen grains of the Stylidiaceae are extraordinary in exine ultrastructure. The sporoderm of the Stylidiaceae is thick and complex (as in other members of the group studied); however, there are no analogues in other plant groups to its acolumellate and medullar (labyrinth-like) morphology.

Similarly to the Stylidiaceae, the Alseuosmiaceae is also characterized by a thick tectum and the absence of a foot layer. However, the infratectum in this family resembles short and wide granular-like columellae that support the tectum only with a narrow bridge. In addition, unlike the Stylidiaceae, the Alseuosmiaceae have a well-developed endexine.

The other taxa under study (Columelliaceae, Rousseaceae, Abrophyllaceae, and Ixerbaceae) have pollen grains with a columellate ectexine that is typical for angiosperms. Thus, the simple columellate ectexine characterizes the families Columelliaceae and Pentaphragmataceae, which occupy a basal position in the Asterid clade (Dunbar, 1978). Among more specialized groups, these are members of the Rousseaceae and Abrophyllaceae (families that are close to the Campanulaceae) and, in addition, some representatives (*Dampiera*) of the Goodeniaceae, a family that is close to the Asteraceae. This conclusion is supported by the analy-

sis of other morphological characteristics (Hansen, 1997). Thus, morphological data (including palynological) and molecular data suggest that *Dampiera* along with the related genera *Anthotium* and *Lechenaultia* are the least complex and most closely related to the ancestral group of the Asteraceae.

Pollen grains of *Eremosyne* (Eremosynaceae) and *Vahlia* (Vahliaceae) have a genuine reticulate sculpture and short colpi (Pl. 9, figs. 12, 14). They have nothing in common with pollen grains of taxa related to Euasterid II, which agrees with molecular data on these groups (Bremer et al., 2002).

CONCLUSIONS

The distribution of palynomorphological characters mapped onto the cladogram of Euasterids shows that the basal groups have a sporoderm structure typical of angiosperms (Fig. 2). Later in the course of evolution, the exine ultrastructure became more complex in two independent ways. In the families Campanulaceae, Phellinaceae, and Menyanthaceae it changes toward the Campanulaceae type. Menyanthaceae, having an ectexine of the Campanulaceae type, are comparable to the Asteraceae in the degree of ultrastructure complexity. In the families Asteraceae, Calyceraceae, and Goodeniaceae, the complexity of the ectexine is derived independently (from the taxa discussed above), and reaches the greatest diversity in the Asteraceae.

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REFERENCES

1. E. M. Avetisyan, "Pollen Morphology of the families Campanulaceae, Sphenocleaceae, and Pentaphragmataceae," *Botan. Zh.* **70** (8), 1003–1009 (1986).
2. B. Bremer, K. Bremer, N. Heidari, et al., "Phylogenetics of Asterids Based on 3 Coding and 3 Non-coding Chloroplast DNA Markers and the Utility of Non-coding DNA at Higher Taxonomic Levels," *Mol. Phylog. Evol.* **24**, 274–301 (2002).
3. A. Dunbar, "On Pollen of Campanulaceae and Related Families with Special Reference to the Surface Ultrastructure: 1. Campanulaceae subfam. Campanuloidae," *Bot. Notiser.* **128**, 73–101 (1975a).
4. A. Dunbar, "On Pollen of Campanulaceae and Related Families with Special Reference to the Surface Ultrastructure: 2. Campanulaceae subfam. Cyphioideae and subfam. Lobelioidae; Goodeniaceae; Sphenocleaceae," *Bot. Notiser.* **128**, 103–118 (1975b).
5. A. Dunbar, "Pollen Morphology and the Systematic Position of the Genus *Pentaphragma* Wall. (Pentaphragmataceae): The Use of Compound Fixatives," *Grana* **17**, 141–147 (1978).
6. G. Geyer, *Ultrahistochemie Histochemische Arbeitsvorschriften für die Elektronenmikroskopie* (Fischer, Jena, 1973).
7. M. H. G. Gustafsson and K. Bremer, "The Circumscription and Systematic Position of Carpodetaceae," *Austral. Syst. Bot.* **10**, 855–862 (1997).
8. H. V. Hansen, "Studies in the Goodeniaceae and the Brunoniaceae with a Discussion of Their Relationship to Asteraceae and Calyceraceae," *Nord. J. Bot.* **17**, 495–510 (1997).
9. J. Karehed, J. Lundberg, B. Bremer, and K. Bremer, "Evolution of the Australian Families Alseuosmiaceae, Argophyllaceae and Phellinaceae," *Syst. Bot.* **24**, 660–682 (1999).
10. Ya. V. Kosenko, "Developmental Patterns of Sporoderm in Members of the Family Asteraceae," *Byull. Mosk. O–va Ispyt. Prir., Otd. Biol.* **109** (1), 31–37.
11. Ya. V. Kosenko and S. V. Polevova, "The Structure of Pollen Grains in Representatives of the tribe Calenduleae (Compositae) and the Possibility of Their Identification," in *1 International Seminar of Pollen As an Indicator of the State of Environment and Paleoecological Reconstructions* (VNIGRI, St. Petersburg, 2001), pp. 101–107 [in Russian].
12. N. R. Meyer-Melikian, I. Yu. Bovina, Ya. V. Kosenko, et al., *Atlas of Pollen Grains of Asteraceae: Pollen Morphology and Development of Sporoderm in Certain Representatives of the Family Asteraceae* (KMK, Moscow, 2004) [in Russian].
13. S. V. Polevova, "Ultrastructural Features of Spiniferous Pollen Grains of Asteraceae and Some Other Families," *Byull. Mosk. O–va Ispyt. Prir., Otd. Biol.* **109** (1), 22–30 (2004).
14. J. Praglowski and E. Grafstrom, "The Genus *Carpodetus* (Escalloniaceae): A Pollenmorphological Enigma," *Grana* **24**, 11–21 (1984).
15. K. K. Shrestkha and V. F. Tarasevich, "Comparative Morphological Study of Pollen of the Genus *Cyananthus*, with Special Reference to Its Systematics and Position within the Family Campanulaceae," *Botan. Zh.* **77** (10), 1–13 (1992).
16. J. J. Skvarla, B. L. Turner, V. C. Potel, and A. S. Tomb, "Pollen Morphology in the Compositae and Morphologically Related Families," in *The Biology and Chemistry of the Compositae* (London, 1977), Vol. 1, pp. 141–248.
17. D. Soltis, P. Soltis, P. Endress, and M. Chase, "Phylogeny and Evolution of Angiosperms" (Washington, 2005).
18. P. F. Stevens, "Angiosperm Phylogeny Website, Version 6, May 2005," <http://www.mobot.org/MOBOT/Research/APweb/orders/asteralesweb.htm>.
19. A. L. Takhtajan, *Diversity and Classification of Flowering Plants* (Columbia Univ. Press, New York, 1997).
20. V. F. Tarasevich and K. K. Shrestkha, "Palynological Data on the Position of the Genus *Ostrowskia* in the Family Campanulaceae," *Botan. Zh.* **77** (9), 27–35 (1992).
21. R. F. Thorne, "The Classification and Geography of the Flowering Plants: Dicotyledons of the Class Angiospermae (Subclasses Magnoliidae, Ranunculidae, Caryophyllidae, Dilleniidae, Rosidae, Asteridae, and Lamiidae)," *Bot. Rev.*, No. 4, 441–647 (2000).
22. B. S. Weakley, *A Beginner's Handbook in Biological Electron Microscopy* (Churchill Livingstone, Edinburgh, 1972).