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Comparative pollen morphology and ultrastructure of *Platanus*: Implications for phylogeny and evaluation of the fossil record

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Abstract

Pollen of *Platanus* was studied using light (LM) and electron microscopy (SEM and TEM). Overall, pollen is uniform in modern *Platanus* (small, tricolpate, prolate to spheroidal, reticulate, semitectate). A number of characters, however, display remarkable variability within a taxon and even a single anther (size; foveo-reticulate, fine to coarse reticulate ornamentation). *Platanus kerrii* (subgenus *Castaneophyllum*) differs from the remaining species by its high and "folded" reticulum and possibly the smooth colpus membrane. Moreover, to our knowledge, pollen of the *P. kerrii* – type is not known from the fossil record. The exine in modern and fossil Platanaceae shows great structural similarity, but the thickness of the foot layer within the ectexine is less variable and normally smaller in modern taxa. Furthermore, in Early Cretaceous to Early Cainozoic Platanaceae a number of distinct pollen types occurred that are not known within the modern *Platanus*. Considering pollen of Platanaceae from the Early Cretaceous to today, a dynamic picture of the evolution of the family emerges. In the first phase (Early Cretaceous) pollen of extinct genera such as *Aquia* differed considerably from modern *Platanus* and shows strong similarity to basal eudicot taxa such as Ranunculales (e.g. Lardizabalaceae). The Late Cretaceous *Platananthus hueberi* displays a distinct coarse reticulum that is unknown from modern *Platanus* but similar to some taxa of Hamamelidaceae (e.g. *Exbucklandia*). After the first phase of eudicot radiation that appears to have been characterized by strongly reticulate evolution, platanaceous diversity decreased in the course of the Cainozoic. Despite this, the pollen type of the modern subgenus *Castaneophyllum* (*P. kerrii* type) seems to be an innovation that originated after the initial radiation of the family.

Keywords: *Eudicots, evolution, intraspecific variability, subgenus* Castaneophyllum, *subgenus* Platanus

Platanus (Sycamore, Plane tree) is a small tree genus in the Northern Hemisphere consisting of about seven species in Europe and Asia Minor, south-eastern Asia, and North America (Nixon & Poole, 2003; Table I). Two modern subgenera are recognized on the basis of leaf morphology and the number of heads in the inflorescences among other characters. Although previously placed within the Hamamelidales (cf. Cronquist, 1981; Takhtajan, 1987; Schwarzwalder & Dilcher, 1991), recent molecular phylogenetic studies suggest that *Platanus* is rather basal within eudicots and sister group to the Southern Hemisphere Proteaceae (e.g. Chase et al., 1993; Drinnan et al., 1994; Qiu et al., 1999, 2005; Angiosperm Phylogeny Group II, 2003; Hilu et al., 2003), forming the order Proteales together with Nelumbonaceae. In contrast, Hamamelidaceae (and Altingiaceae) are now placed within the Saxifragales that belong to the core eudicots (Fishbein et al., 2001; Angiosperm Phylogeny Group II, 2003; Fishbein & Soltis, 2004).

The sister group relationship between Platanaceae and Proteaceae is surprising from the morphological perspective. Morphological cladistic analyses (cf. Doyle & Endress, 2000) could not resolve a monophyletic [Nelumbonaceae - (Proteaceae+Platanaceae)] Proteales but suggested that Platanaceae and Proteaceae belong to a basal grade of eudicots together with *Nelumbo*, *Euptelea*, Buxaceae, and Trochodendraceae. Comparative morphological studies (Igersheim & Endress, 1998; Endress & Igersheim, 1999) corroborated a possible sister group relationship of Platanaceae and Proteaceae instead of a Platanaceae-Hamamelidaceae sister

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Table I. Subgenera and species of *Platanus* recognized in Nixon & Poole (2003).

Taxon (Nixon & Poole, 2003)	Variety	Distribution
Platanus kerrii Gagnep.[a] (1)		Vietnam
P. orientalis L.[b] (4)		South-eastern Europe, south-western Asia
P. racemosa Nutt.[b] (3)	var. *racemosa*	California, Baja California
P. racemosa Nutt. (2)	var. *wrightii* (S. Wats.) Benson	Arizona, New Mexico, Chihuaha
P. gentryi Nixon & Poole[b] (1)		Sonora, Sinaloa, Chihuaha
P. occidentalis L.[b] (2)	var. *occidentalis*	Eastern Canada, eastern USA
P. occidentalis (1)	var. *palmeri* (Kuntze) Nixon & Poole ex Geerinck	Texas, Coahuila
P. rzedowskii Nixon & Poole[b]		Nuevo Leon, Tamaulipas
P. mexicana Moric.[b] (7)	var. *mexicana*	Veracruz, Puebla, Oaxaca, Chiapas
P. mexicana Moric. (2)	var. *interior* Nixon & Poole	San Luis Potosi, Queretaro

[a]subgenus *Castaneophyllum*, [b]subgenus *Platanus*, numbers in brackets indicate number of accessions for each taxon (see Specimens Investigated).

group relationship. The possible relation between Platanaceae and Proteaceae may be old and the apparent distinctiveness between the two families may be due to a substantial amount of extinction of closely related lineages (Magallón & Sanderson, 2001, 2005; Judd & Olmstead, 2004).

Although Platanaceae has an excellent fossil record that extends back to the Early Cretaceous (Friis et al., 1988; Crane et al., 1993; Pedersen et al., 1994), its present morphological diversity has not been adequately documented. Pollen is the most abundant source of palaeobotanical information and can be used to establish presence or absence of certain taxa at a certain time period. It has previously been noted that pollen of modern Platanaceae is rather uniform (Pacltová, 1982; Zavada & Dilcher, 1986) and pollen development of *P.* × *acerifolia* (Aiton) Willd. was studied in detail by Suarez-Cervera et al. (1995), although a thorough comparative study of pollen of all species of *Platanus* using modern methods has not been carried out to date. Nevertheless, knowledge of modern *Platanus* pollen is crucial when assessing possible relationships between fossil and modern pollen of Platanaceae and between Platanaceae and other eudicots.

In the present paper we studied pollen of all modern species and varieties of *Platanus* recognized in Nixon and Poole (2003) except for *P. rzedowskii* Nixon & Poole (figured in Zavada & Dilcher, 1986). We used light (LM) and electron microscopy (both SEM and TEM) to document morphological plasticity of modern species of *Platanus*. Based on this, we compare modern pollen to previously published pollen data from the fossil record and discuss character evolution in Platanaceae. We tested whether pollen characters can be used for distinguishing subgeneric groups and to infer evolutionary pathways.

Material and methods

Pollen for this study was obtained from herbarium specimens of the herbaria National Autonomous University of Mexico (MEXU) and Swedish Museum of Natural History (S), and collected from planted trees in the case of *P.* × *acerifolia* (see Appendix for a list of voucher specimens). All herbarium material was checked prior to pollen sampling to confirm the specific identity of the specimen. The nomenclature used in a recent morphological revision of *Platanus* by Nixon and Poole (2003) was followed (Table I). For pollen terminology Erdtman (1969) and Punt et al. (1994) were followed.

For light microscopy (LM) pollen was acetolyzed using the standard procedure of Erdtman (1969). Anthers were placed in a drop of the acetolysis mixture on a microscope slide and macerated for some hours until the cell content became transparent. The slide was then heated over the candle flame of a tea light until the cell content was removed and the pollen had obtained a brown colour. Pollen grains were then moved to another slide into a drop of glycerine.

For scanning electron microscopy (SEM) untreated anthers were mounted on a stub with adhesive carbon tape and sputter coated with gold for 60 s using an Agar High Resolution sputter coater (20 mA). Pollen was observed using a Hitachi 4300 scanning electron microscope. The specimens (individual anthers) for transmission electron microscopy (TEM) were fixed with 1% OsO_4, dehydrated in an ethanol series, stained with uranyl acetate, dehydrated in acetone, and embedded in epoxy resin. Pollen grains were sectioned with an ultramicrotome LKB-3 and ultra-thin sections were then post-stained with lead citrate for 15–20 minutes, and examined using a Jeol 100 B transmission electron microscope.

Results

Light and scanning electron microscopy (Figures 1, 3, 4, 8, 10, 11, 14, 15)

Pollen of *Platanus* is relatively small (Table II). For the polar axis, values obtained from SEM and LM measurements differed considerably in most cases except for *P. mexicana* var. *mexicana* and *P. orientalis*. No overall trends such as SEM measurements being smaller than LM measurements were observed. Instead, in some taxa (e.g., *P. kerrii*) SEM measurements yielded significantly lower values than LM, while in others (e.g., *P. racemosa*) SEM values were much higher than LM values. For the equatorial axis, in all samples lower values for pollen size were obtained from SEM measurements than from LM. Largest pollen (polar axis) was encountered in *P. occidentalis* var. *occidentalis* (33.1 μm in LM). The smallest pollen (polar axis) was found in *P. mexicana* var. *mexicana* (12.4 μm in LM, Table II). In *P. occidentalis* pollen size (polar axis) decreases along a north-south gradient from Canadian specimens to the specimen from Texas (*P. occidentalis* var. *palmeri*).

Pollen is tricolpate (occasionally 4-colpate) and prolate, subprolate, subspheroidal, or spheroidal in shape. In polar view the outline ranges from circular to trilobate, to rarely triangular. In equatorial view the outline is circular to elliptical, often slightly rectangular, sometimes with one polar side longer than the other (Figure 10 K), or twisted and then 'pear-like' (Figures 1 H, 3 D). The colpus varies from long and narrow in prolate grains, with the colpi more or less parallel to the polar axis (Figure 3 E), to short elliptic to almost circular in prolate, subprolate, and subspheroidal pollen (Figure 3 C). The ratio of colpus length to polar axis was smallest for *P. gentryi* and *P. kerrii* and largest for *P. occidentalis* var. *occidentalis*. In some pollen grains the colpi converge towards the poles at their apices, or their long axis is conspicuously oblique to the polar axis of the pollen grain (Figures 3 L & 10 K).

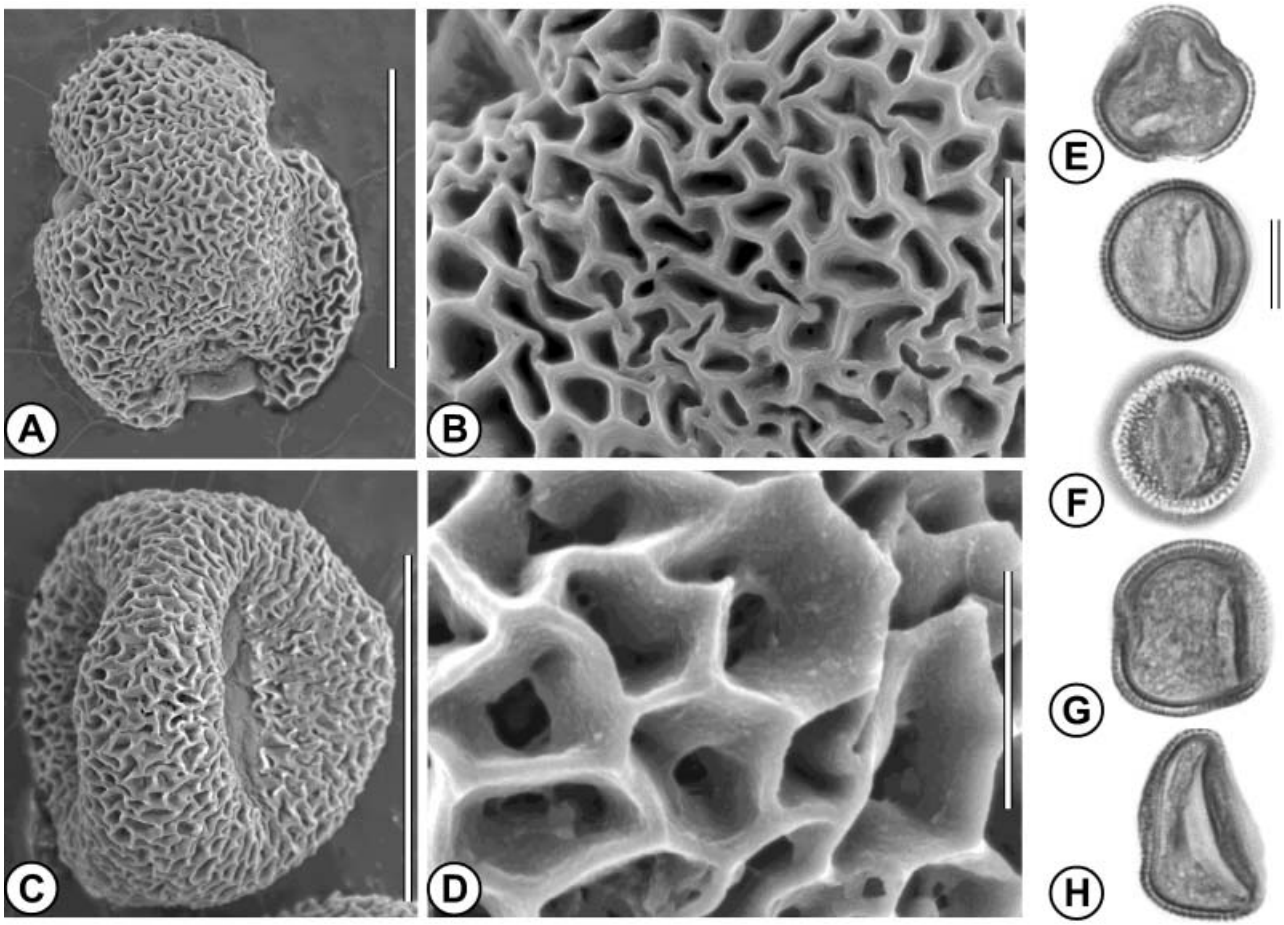


Figure 1. *Platanus kerrii* Takhtajan 8745. SEM, LM. **A–D**. SEM micrographs. **A.** Polar view. **B.** Detail of reticulum, polar view. **C.** Equatorial view, note smooth colpus membrane. **D.** Detail of reticulum, equatorial view, showing high muri. **E–H.** LM. **E.** Polar view, optical section showing nexine, columellae, and tectum. **F.** Equatorial view, above: focus on pollen wall, below: focus on reticulum. **G.** Equatorial view showing rectangular outline of pollen grain. **H.** 'Pear-like' equatorial view. Scale bar – 12 μm (A, D); 10 μm (E–H); 1.5 μm (B); and 1.2 μm (C).

Table II. Comparative pollen morphology of modern *Platanus*.

Taxon	Measurements in LM (μm)			Size SEM (μm)		Reticulum	Endexine pattern[a]	Foot layer/ ectexine	Tectum/ ectexine	Columella/ sexine
	Polar axis mean (min-max)	Equatorial diameter (from equatorial view)	Colpus Length/polar axis	Polar axis mean (min-max)	Equatorial diameter (from equatorial view)					
P. kerrii	18.35 (16.5–21.6)	18 (16.0–20.1)	0.62 (0.52–0.74)	15.4 (14–20)	13.7 (10.4–15.3)	Folded pattern	2	0.3	0.45	0.33
P. racemosa var. *racemosa*	17.85 (14.8–20.3)	19.8 (15.7–23.1)	0.67 (0.51–0.8)	20 (18.2–23.8)	15.3 (14.5–16.2)	Fine, coarse, intermediate	1, 2	0.25–0.3	0.4–0.45	0.39–0.42
P.racemosa var. *wrightii*	19.4 (17.5–22.8)	22.2 (19.1–26.5)	0.65 (0.52–0.77)	22.3 (18–25.5)	16.2 (14.3–17.6)	Fine	2	0.25	0.5	0.3
P. gentryi	22.2 (20.1–24.7)	20.7 (17.9–23.9)	0.6 (0.46–0.71)	20.1 (18.4–22.3)	15.5 (13.4–18.6)	Intermediate	–	–	–	–
P. orientalis	20.4 (15.6–24.1)	20.35 (16.3–23.8)	0.64 (0.48–0.81)	19.8 (14.5–24)	15.8 (12.8–18.6)	Fine, coarse, intermediate	1, 1*, 2	0.2–0.34	0.38–0.54	0.3–0.4
P. mexicana var. *mexicana*	19.1 (12.4–23.4)	20.4 (17.8–24.6)	0.71 (0.49–0.84)	20 (15.9–24)	15.9 (12.4–19)	Fine, coarse, intermediate	1, 1*, 2	0.27–0.33	0.44–0.45	0.33–0.4
P. mexicana var. *mexicana* [Chiapas]	17.7 (15.7–19.1)	15.5 (12.5–18.7)	0.7 (0.56–0.82)	17.3 (16–18)	12.75 (11.5–14)	Fine	1*	0.42	0.4	0.31
P. mexicana var. *interior*	18.7 (14.7–21.5)	18.8 (16.2–21.9)	0.67 (0.5–0.82)	20 (17.6–22.75)	15.45 (11.6–19)	Fine	1*	0.3	0.5	0.32
P. occidentalis var. *palmeri*	17.6 (15.4–22.9)	18.7 (15.6–22.6)	0.71 (0.53–0.83)	16.5 (15.9–17)	13.85 (11–17.6)	Fine	2	0.22	0.47	0.39
P. occidentalis var. *occidentalis*	26.9 (21.8–33.1)	25.1 (19.7–29.5)	0.77 (0.63–0.86)	22 (19–27.4)	17 (15.2–21.5)	Fine to intermediate	1	0.3	0.42	0.4
P. × *acerifolia*	21.4 (19.1–27.0)	21.4 (18.7–25.7)	0.68 (0.55–0.88)	16.2–17.6	14.3–17.6	Fine	2			

[a]Numbers refer to morphologically distinct 'Group 1' and 'Group 2' endexine types, 1* to a modified Group 1 endexine. See text for explanation.

All species show a clearly layered exine, with nexine, columellae, and tectum in LM. The thickness of the exine is around 1 to 1.5 μm, with the nexine normally being slightly thinner than the sexine.

The colpus membrane is typically covered with globular structures representing non-continuous elements of the ectexine that may be singular or merge to form groups. This was observed in all specimens except for *P. kerrii*, where the membrane lacks any globular structures in the grains examined. In a few cases the margin of the colpus forms conspicuous bulges (*P. gentryi*, not shown).

Pollen is reticulate, semitectate and columellate. The reticulum consists of polygonal or rounded elements that tend to assume a more rounded appearance when the reticulum is coarser. The muri are acute to bluntly acute and on their crests have small tips at the conjunctions of individual elements (''crown-like''; Figure 3 K); the lumina are rounded to rectangular. In grains with a conspicuously coarse reticulum the muri may be broken so that the reticulum is interrupted having freely ending sections (Figure 3 M). In general, the appearance of the reticulum may vary considerably within a species. Some species show a distinctly coarse reticulum in one specimen and a fine reticulum in another specimen, or may combine different patterns on the same pollen grain (cf. *P. racemosa*, *P. orientalis*; Figure 8 B–H). In addition, *P. kerrii* differs from the remaining species in having relatively high muri that show a folded pattern (Figure 1 A–D).

Ultrastructure (Figures 2, 5–7, 9, 12–14)

In general, the ultrastructure is markedly similar between the different taxa of *Platanus*. In all species studied Ubisch bodies are found attached to the anther wall corresponding to those reported for *P.* × *acerifolia* by Suarez-Cervera et al. (1986). Measurements for the thickness of different exine layers for each species are provided in Table III. Highest values for foot layer, columellae, and tectum thickness were encountered in *P. kerrii* and *P. mexicana* var. *mexicana*, the latter displaying a large variability in all layers of the ectexine. The ratio of foot layer to ectexine ranges from 0.2 to 0.4 (Table II).

Based on differences in the structure and electron density of the endexine the material studied can be divided into two groups, which we consider to represent two slightly different ontogenetic stages of the pollen wall.

Group 1. Typically, samples falling within this group are characterized by an endexine that is homogeneous in the non-apertural region and more electron dense than the ectexine (Figure 13 A, C, F, G). The endexine becomes fragmented towards the aperture with elements of differing size (Figure 13 C–E). This condition was observed in specimens of *P. mexicana* (specimens R. Ortega O. 01270; G. Suárez 16; F. Ventura A. 16805), *P. occidentalis* (E. Wall s.n.), *P. orientalis* (Anderberg & Anderberg 90-20), and *P. racemosa* (Wiggins & Thomas 22).

Additional distinctive features were observed in three specimens. In *P. mexicana* var. *interior* (E. Arguelles s.n.; Figure 13 A) lamellations appearing as 'white lines' (cf. Suarez-Cervera et al., 1995, Figure 33) or membranous remnants of the degraded tapetum were found in the aperture region. One specimen (*P.* '*orientalis*', N. Stojanoff 201/677) does not show the fragmented endexine in the aperture region but exhibits elongated elements in the outer part of the endexine giving it a layered appearance (Figure 9 E). One specimen of *P. mexicana* var. *mexicana* (E. Matuda 5124) appears to fall within Group 1 based on its electron dense endexine (Figures 12 G, 13 G). The endexine, however, is less fragmented in the aperture region, and instead has fine lamellae represented by 'white lines' (Figure 13 I).

Group 2. The endexine is homogeneous and less electron dense than the ectexine (Figure 9 F). It becomes conspicuously thicker towards the aperture, where it is structured and ''interrupted plaques'' sensu Suarez-Cervera et al. (1995) can be observed (Figure 2 C, D, Figure 9 A).

This condition was found in *P. mexicana* var. *mexicana* (specimen S. Avendana R. 137), *P. occidentalis* var. *palmeri* (J. M. Poole et al. 2521), *P. orientalis* (T. Å. Tengwall s.n., G. Erdtman 140), *P. racemosa* (E. K. Balls 9126, C. Epling s.n.), *P. wrightii* (Nelson & Nelson 1408), and *P. kerrii* (A. Takhtajan 8745).

It is important to note that in some specimens features typical of one or another of the two groups occur in combination, thereby linking the two groups (e.g., *P. orientalis*, G. Erdtman 140, *P. mexicana* var. *interior*, E. Arguelles s.n., where the endexine is more electron dense than the ectexine but consists partly of plate-like structures; Figures 9 G & 13 A).

In the specimens of Group 1 the cells of the anther wall are still present, but have lost most of their living cell content (protoplast). Also, we sometimes observed that the anther has endothecial cells with irregularly thickened walls characteristic for anthers at the latest stage before dehiscence. The latter condition is typical of pollen referred to Group 2.

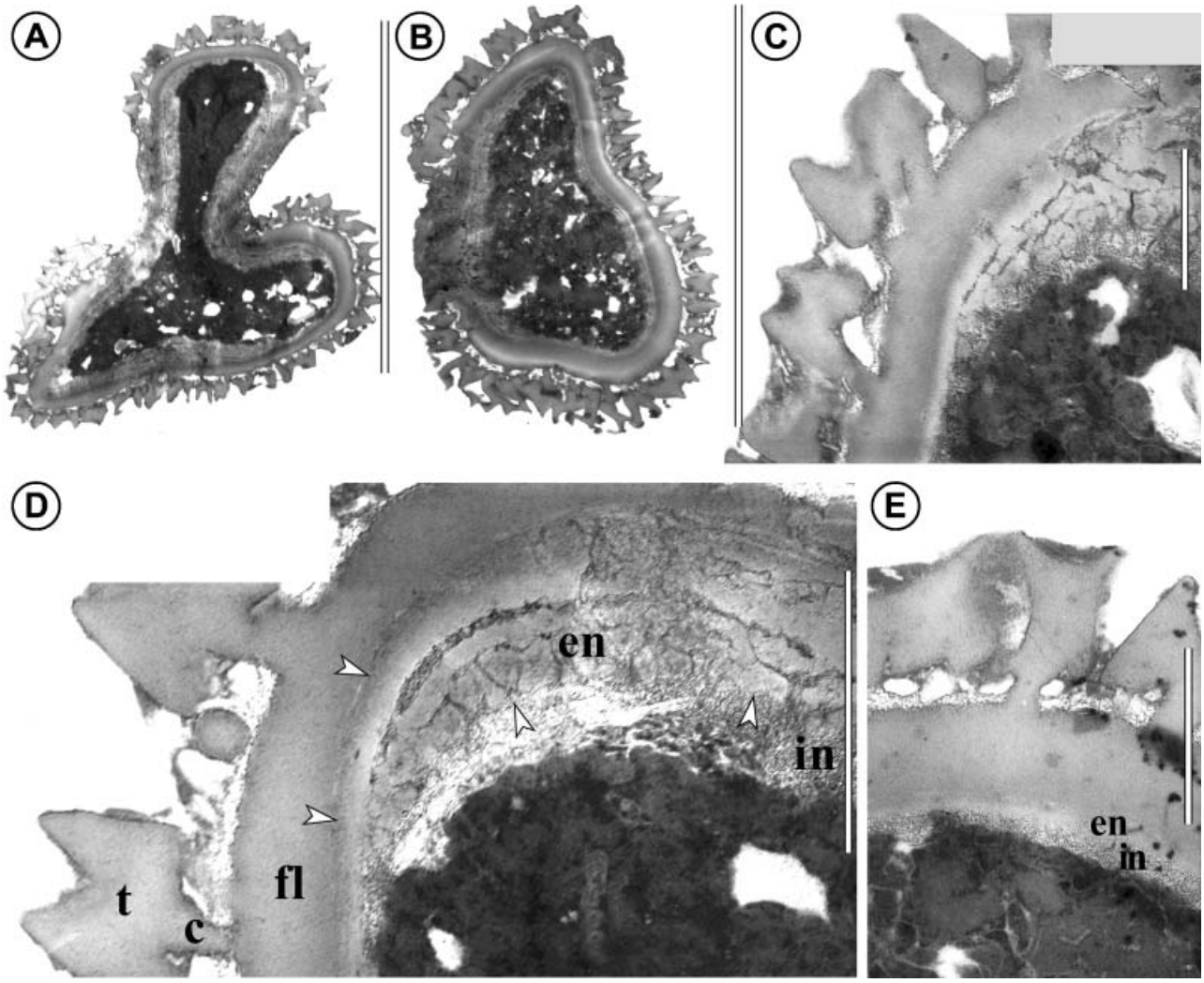


Figure 2. *Platanus kerrii* Takhtajan 8745. TEM. **A.** Equatorial section through whole grain showing high muri. **B.** Oblique section through a pollen grain showing one colpus. **C, D.** Details of pollen wall towards aperture region. Endexine forms plate-like structures in aperture region. Arrowheads indicate borders of endexine. **E.** Detail of pollen wall in non-apertural region. Endexine is thin and less electron dense than ectexine. t=tectum, c=columellae, fl=foot layer, en=endexine, in=intine. Scale bar – 10 μm (A, B) and 1 μm (C–E).

Discussion

LM and SEM observations

The combined LM and SEM study of *Platanus* pollen essentially shows a high degree of uniformity among different taxa and overlapping patterns of variability between them. This is true for nearly all pollen characters observed including pollen size, reticulum pattern, and shape and size of colpi (cf. Tables II, III). One exception appears to be *P. kerrii*, the only member of the subgenus *Castaneophyllum*. The pollen of this species (Figure 1) displays a relatively high reticulum that is conspicuously folded. Also the thickness of the tectum measured in TEM was found to be greatest in *P. kerrii*. This, along with the smooth colpus membrane, would appear to support the distinctiveness of this pollen types and be in accordance with the isolated systematic placement of *P. kerrii* in the subgenus *Castaneophyllum*. However, only one sample of this species was included in our study, which comes from the same plant studied by Zavada and Dilcher (1986). There is clearly a need to collect new material for *P. kerrii*.

For the specimens of *P. occidentalis* a clear north-south gradient in polar axis length was found. This is likely to reflect a climatic gradient but more data are needed to confirm this. Apart from *P. occidentalis* the largest range of pollen size was observed for *P. orientalis*, where size differences occurred randomly between specimens from various Mediterranean areas.

Pacltová (1982) examined a number of modern and fossil species of *Platanus* using LM and, for one living taxon: *P.* × *acerifolia*, SEM. Based on morphological features she was able to assign dispersed fossil

pollen to *Platanus*. She considered three pollen characters, observable with LM, informative for the distinction of species; namely the marginal area of the colpus ('exogerminal') irregular, the surface of the colpus membrane ('endogerminal') with structural elements, and the ratio of the thickness of endexine plus foot layer (nexine) to columellae and tectum (sexine). While the first character may be characteristic for *Platanus* it is not found in all members of Platanaceae (see Table IV for taxa having an ectexine rim associated with a smooth exogerminal). The surface of the colpus membrane is highly variable in members of the subgenus *Platanus* and all fossil Platanaceae, and patterns of the endogerminal are unlikely to be of diagnostic value. In addition, the structural elements on the colpus membrane typically found in Platanaceae (excepting *P. kerrii*) are a common feature in the pollen of many flowering plants. In contrast, the ratio between nexine and sexine is a useful character. However, it is very difficult to assess reliably using only LM. For a more thorough evaluation optical sections should be complemented by ultrathin sections from TEM.

TEM observations

A previous ontogenetic study of *P.* × *acerifolia* by Suarez-Cervera et al. (1995) documented various stages of pollen development towards the mature pollen grain. The deposition of the intine starts at a stage referred to as "young pollen grains" and is finished at the stage called "ripe pollen" (Suarez-Cervera et al., 1995). Based on the absence of pro-Ubisch bodies in the tapetum cells and structural characteristics, we observed most of the similarities in our material to the two latest stages described by Suarez-Cervera et al. (1995).

We have referred our material to two morphological groups without implying any ontogenetic sequence, and the combination of conditions characteristic for Group 1 and Group 2 pollen present in some specimens, suggest that these groups merely reflect slightly different endexine states of almost or fully mature pollen. Nevertheless, we do not know how and to what extent pollen collected from herbarium specimens may have undergone structural changes.

Comparability of modern and fossil pollen acetolyzed, non-acetolyzed

Zavada and Dilcher (1986) used acetolyzed pollen for TEM observations and stated that a thin endexine may be present in pollen of *Platanus* but that this might well be a staining artefact. It has previously been shown that the endexine and possibly the whole exine are sensitive to acetolysis, and that features such as white lines and lamellate structures of the endexine may not be observable

Table III. Pollen wall dimonsions for extant *Platanus* and fossil platanoids (below line).

Taxon	Endexine thickness [a] (μm)	Foot layer thickness (μm)	Columella thickness; width (μm)	Tectum thickness; width (μm)	Ectexine thickness (μm)
P. kerrii	0.12 > 0.6–1.2	0.4	0.29; 0.18	0.57; 0.43	1.26
P. racemosa var. *racemosa*	0.08–0.09 > 0.25–1.1	0.20–0.35	0.27–0.33; 0.17–0.2	0.38–0.5; 0.31–0.42	0.85–1.1
P. racemosa var. *wrightii*	0.19 > 0.5	0.22	0.2; 0.19	0.48; 0.28	0.91
P. gentryi	–	–	–	–	–
P. orientalis	0.05–0.13 > 0.3–1.0	0.14–0.28	0.18–0.22; 0.15–0.18	0.28–0.47; 0.3–0.34	0.69–0.9
P. mexicana var. *mexicana*	0.05–0.2 > 0.3–0.8	0.19–0.4	0.19–0.27; 0.15–0.18	0.32–0.55; 0.33–0.36	0.72–1.22
P. mexicana var. *mexicana*[Chiapas]	0.14 > 1.05	0.35	0.15; 0.23	0.33; 0.31	0.83
P. mexicana var. *interior*	0.1 > 0.9	0.29	0.23; 0.18	0.49; 0.38	1.0
P. occidentalis var. *palmeri*	0.12 > 1.0	0.17	0.24; 0.22	0.37; 0.36	0.78
P. occidentalis var. *occidentalis*	0.17 > 0.6	0.2	0.2; 0.27	0.29; 0.3	0.68
Aquia brookensis	0.1 > 1.0	0.5	0.3	0.3	1.1
Platananthus potomacensis	0.2 > 0.7	0.3	0.1	0.2	1.2
Hamatia elkneckensis	0.1 > 0.7	0.5	0.5	0.2	1.2
Platananthus hueberi	0.03 > 0.6	0.3	0.3	0.5	1.1
Platananthus scanicus	0.1 > 0.7	0.8	0.2	0.5	1.5
Dispersed stamen (Friis et al., 1988)	0.15 > 0.75	0.4	0.1	0.35	0.85
Archaranthus	–	0.47	0.23	0.34	1.04
Platananthus speirsae	–	0.3–0.4	0.2–0.3	0.2–0.3	0.7–1.0
Chemurnautia staminosa	–	0.53	0.53	0.4	1.23
Platananthus synandrus	–	0.3–0.4		0.2–0.3	

[a]non-aperture region > aperture region.

Table IV. Comparative pollen morphology of Cretaceous and Early Cainozoic Platanaceae.

Taxon	Age and origin	Size (μm)	Ectexine rim	Reticulum	Muri tips	Endexine pattern	Endexine apertural v. non-apertural	Foot layer: ectexine	Tectum/ectexine; Columella/sexine
Aquia brookensis Crane et al., 1993	Early-Middle Albian; Am	10–11 × 12	?	Fine; "foveo-reticulate"	Absent?	Granular; layered below aperture	Very thick-very thin	0.45	0.27; 0.5
Platananthus potomacensis Friis et al., 1988	Late Albian; Am	5–8 × 8.5–12	–	Fine	Weak or absent	Finely granular below aperture	Thick-thin	0.5	0.33; 0.33
Hamatia elkneckensis Pedersen et al., 1994[a]	Latest Albian; Am	10 × 12	–	Intermediary to coarsely	Weak or absent	Granular; layered below aperture	Thick- very thin	0.42	0.17; 0.71
Sarbaya radiata Krassilov & Shilin, 1995[a]	Cenomanian-Turonian; EuA	13.5–16.5 × 17.5	–	Fine	Present	Unknown	Unknown	Unknown	Unknown
Quadriplatanus georgianus Magallón et al., 1997	Coniacian-Santonian; Am	7.7–16.5 × 11–16.9	–	Uniformly, fine	Present	Unknown	Unknown	Unknown	Unknown
Platananthus hueberi Friis et al., 1988	Santonian or Campanian; Am	9–12 × 13–15	–	Very coarse	Absent	Laminate to granular below aperture	Thick- very thin	0.27	0.45; 0.37
Platananthus scanicus Friis et al., 1988	Santonian-Campanian; EuA	13.5–15 × 15–16.5; 15–16.5 × 16–18 [b]	+	Fine	Possibly weak	Laminate to granular	Thick- very thin	0.53	0.33; 0.28
Unassigned stamens Friis et al., 1988	Santonian-Campanian; EuA	9–12 × 12–15	–	Fine, atypical	Absent	Laminate	Very thick-thin	0.47	0.41; 0.22
Archaranthus krassilovii Maslova & Kodrul, 2003[c]	Maastrichtian-Danian; EuA	13.3–15.3 × 16–16.8	+	Fine	Possibly present	Granular, layered, ? white lines below aperture	Very thick-thick	0.45	0.33; 0.39
Platananthus speirsae Pigg & Stockey, 1991	Paleocene; Am	18 × 18–22	+	Fine; "modern type"	Present	Preserved in aperture region	Unknown	?0.4–0.43	?0.28–0.30; 0.5
Associated with *Platanites hebridicus* Forbes	Probably Early Paleocene[d]; EuA	16–20	?	Fine	Present	Unknown	Unknown	Unknown	Unknown
Chemurnautia staminosa Maslova, 2002[c]	Paleocene-Eocene, EuA	11–13 × 13–16	–	Fine	Possibly present	Granular, layered, ?white lines below aperture	Very thick-thick	0.43	0.32; 0.43
Platananthus synandrus Manchester, 1986	Eocene; Am	10–14 × 12–16	+	Fine	Present	Not preserved	Unknown	0.35/xx	0.25/xx; 0.4
Platanus neptunii (Ettingsh.) Bůžek, Holy & Kvaček, 1967	Miocene to Oligocene; EuA	13–19 × 15–25[e]; 14–18 × 16–20[f]	–	Fine	Present	Unknown	Unknown	Unknown	Unknown

[a] tricolporate pollen, [b]after different chemical treatments, [c]for TEM measurements see Tekleva & Maslova 2004, [d] Crane, Manchester & Dilcher 1988, [e]Pacltová 1982, based on LM measurements from two localities; [f]Kvaček & Manchester 2004, A=America, EU=Eurasia.

after acetolysis (Rowley, 1995). Suarez-Cervera et al. (1995) documented the structure of the endexine of *P.* × *acerifolia* during various stages of pollen development. In the present study using non-acetolyzed material we encountered endexine conditions very similar to those documented in the ontogenetic study by Suarez-Cervera et al. (1995). Similar ultrastructural details can also be observed in a number of published accounts on Cretaceous and Tertiary platanaceous pollen (Friis et al., 1988, 1991; Pigg & Stockey, 1991; Crane et al., 1993; Friis & Pedersen, 1996). Specifically, in species such as *Platananthus potomacensis* Friis, Crane & Pedersen and *P. scanicus* Friis, Crane & Pedersen the endexine in the aperture region forms granular structures similar to our Group 1-pollen, whereas in an unassigned dispersed platanaceous stamen from the Santonian/Campanian of southern Sweden (Friis et al., 1988) the endexine forms plate-like structures comparable to our Group 2 pollen. Pollen grains of *Archaranthus krassilovii* Maslova & Kodrul and *Chemurnautia staminosa* Maslova (Tekleva & Maslova, 2004) show fine lamellae in the aperture region that are similar to those found in one specimen of *P. mexicana* var. *mexicana* (E. Matuda 5124).

The endexine may show different resistance to acetolysis in different taxa and therefore may display structural differences between acetolyzed and non-acetolyzed pollen (Erdtman, 1969; Zavada & Dilcher, 1986; versus present study). This implies that utilizing non-acetolyzed modern pollen for TEM observations may provide valuable additional information for understanding endexine structures of fossil platanaceous pollen.

Modern and fossil pollen of Platanaceae

Size of pollen. It has previously been noticed that Early Cretaceous pollen of Platanaceae is comparatively small (Friis et al., 1988) and, along with the more developed perianth in the staminate flowers bearing this pollen and the valvate anther dehiscence, it has been claimed that this may be due to different pollination mechanisms in these early forms (insect dispersal versus wind dispersal in extant *Platanus*, compare also Hesse, 1978). Although there is an overall trend towards larger pollen from the Early Cretaceous to the present (Tables II, IV), modern *Platanus* has retained relatively small pollen. Smaller pollen than in modern species still occurs in some Early Cainozoic taxa (e.g. *Platananthus synandrus* – Manchester, 1986), whereas dispersed pollen from Miocene deposits fall well within the range of modern species of *Platanus* (see for example, Hoffmann et al., 2002; Kvaček & Manchester, 2004). Also, some authors (Friis et al., 1988) have noticed differences in pollen size depending on the chemical treatment of the material. In general, size comparisons may be complicated due to measuring pollen with different methods. SEM measurements of modern pollen in some cases differ substantially from LM measurements (Table II). The same might be true for measurements of fossil pollen given in the literature (see Kvaček & Manchester, 2004).

Pollen grains measured in LM for this study were measured twice; firstly just after mounting them in glycerine and, secondly, a few months later. In both cases the same values were obtained. We consistently obtained larger equatorial diameters for pollen grains measured in LM. In contrast, measurements of the polar axis were either the same in LM and SEM, or they were larger in LM or SEM. This suggests that harmomegathic changes of *Platanus* pollen grains affect the equatorial axis more than the polar axis.

Reticulum. In modern and fossil Platanaceae a number of different reticulum types occur. Pollen of some Early to Late Cretaceous taxa displays a highly distinct reticulum, such as the very fine foveo-reticulate type seen in *Aquia brookensis* (Crane et al., 1993), and the conspicuously regular and coarse reticulum in *Platananthus hueberi* (Friis et al., 1988). The reticulum of the extant *Platanus kerrii* (subgenus *Castaneophyllum*) also appears to be distinct. Apart from these exceptions, most of the fossil and modern Platanaceous taxa show a common, intermediary types of reticulum as found in modern members of the subgenus *Platanus*. Within species the reticulum pattern appears to be fairly stable in most Cretaceous and Early Cainozoic Platanaceae. This is in contrast to modern pollen where some taxa exhibit a remarkable variety of patterns (cf. Figure 8).

The markedly coarse and regular reticulum in *Platananthus hueberi* has not been observed in any other Platanaceae, modern or fossil. In modern *Platanus*, a similarly coarse reticulate sculpture apparently develops from a fine reticulum by loss of some muri bridging the space between adjacent columellae (Figures 3 M, 10 L).

Muri are more or less triangular in cross-section in pollen of modern taxa. At the conjunctions of three (sometimes two) sides of a polygon characteristic tips can be seen especially clearly in TEM ultrathin sections (e.g. Figure 5 G) and under SEM (Figures 3 K, 10 I). In Early Cretaceous fossils muri tend to be rounded-triangular and, therefore, the tips are less apparent. Since muri tips are observable

in other families such as Gunneraceae (Wanntorp et al., 2004*b*) we do not consider them a diagnostic feature for *Platanus*. Basically, any pollen with a reticulum consisting of muri with triangular cross-section has the potential to form muri tips.

Aperture margin. In modern species of *Platanus* the transition between non-apertural and apertural regions is defined by a zone, where the reticulum breaks up and some of the lumina open towards the colpus membrane. Freely ending muri and isolated columellae typically intermingle with the sculptural elements of the colpus membrane. While in some fossil pollen the transition between apertural and non-apertural regions is more distinct. In *Platananthus hueberi* the coarse reticulum abruptly changes into a narrow margin consisting of smaller lumina (cf. Friis et al., 1988, pl. 4, Figures 1, 2; Friis & Pedersen, 1996, pl. 3, Figures 4, 5). In *Hamatia* the lumina of the reticulum gradually decrease in size towards the border with the colpus membrane (cf. Pedersen et al., 1994, pl. 6, Figures 1–3).

Another type of transition is found in a number of Late Cretaceous to Early Cainozoic taxa. Here, the reticulum forms a distinct rim made up of fused elements of the ectexine (Figure 16 C, D). This was first mentioned by Maslova and Kodrul (2003; 'sporopollenin thread') for specimens from the Amur region (Russian Far East). When reviewing the literature we found that this type also occurs in specimens from Europe and North America, but is most prominent in pollen from the Paleocene and Eocene of North America (cf. Manchester, 1986, Figures 61–63; Pigg & Stockey, 1991, pl. 5, Figures 1, 3), and also in specimens from Europe (cf. Friis et al., 1988, pl. 6, Figure 4; Friis & Pedersen, 1996, pl. 3, Figure 3).

These characteristics, with the exception of the *Hamatia* pattern (see above), appear to be constant and may be useful for distinguishing taxa. However, our observations hinge solely on published illustrations and descriptions and therefore may not reflect the entire variability.

Ectexine. Although the ectexine in modern and fossil Platanaceae shows high structural similarity, the thickness of the foot layer within the ectexine is less variable and normally thinner in modern taxa. The ratio of columellae to columellae plus tectum (sexine) is about 0.3–0.4 in modern species, whereas it differs considerably among fossil taxa (0.2–0.7; Tables II, III, IV) and no trend can be seen from the Early Cretaceous to the Eocene.

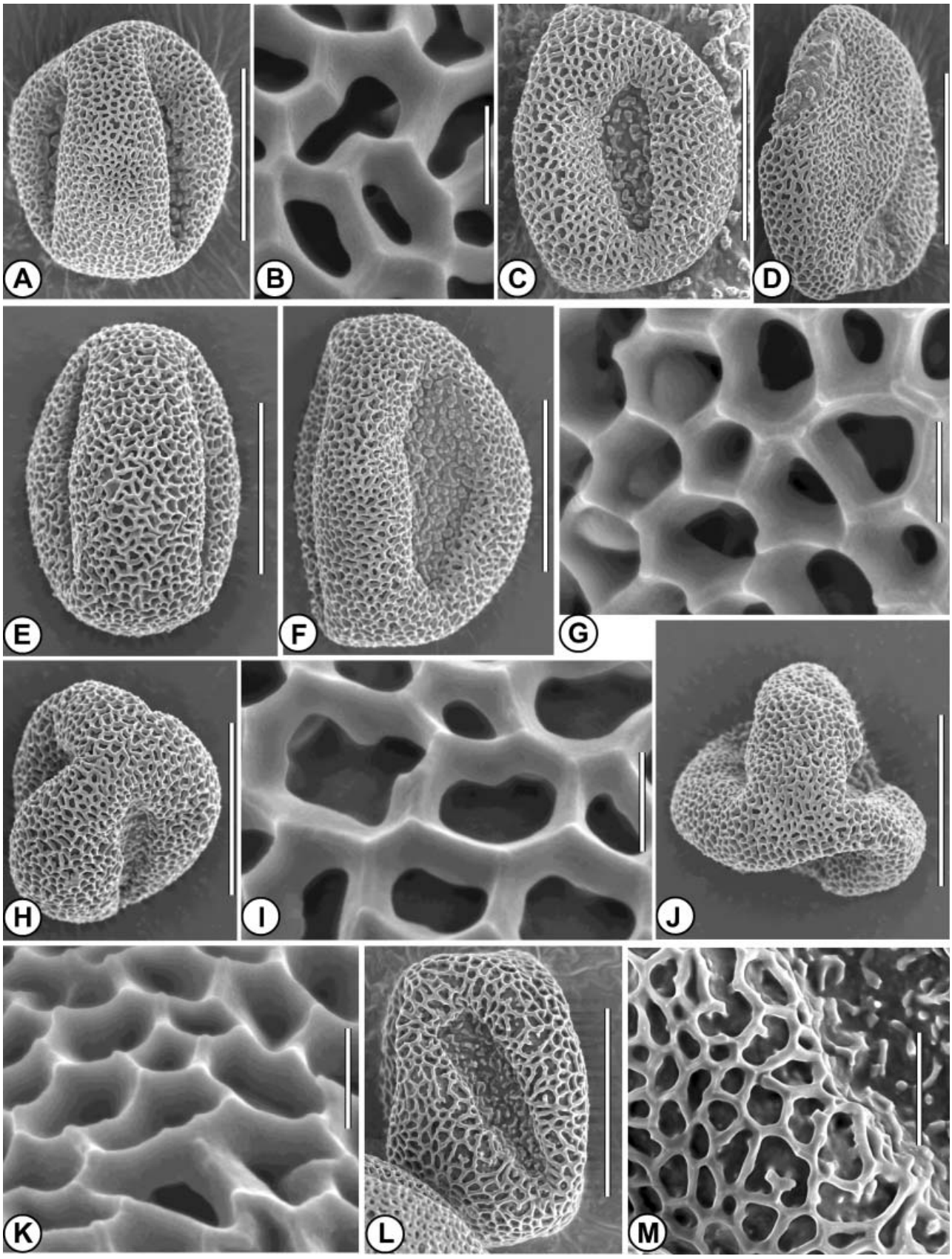
Endexine. Both modern and fossil pollen of Platanaceae is characterized by a rather uniform structure of the endexine, which differs in electron density from the ectexine, homogeneous and thin in the non-apertural region and layered or laminate to granular and thick below the aperture. We found two conditions of endexine structure in modern species, which are comparable essentially to the latest ontogenetic stages described by Suarez-Cervera et al. (1995) for *P.* × *.acerifolia*.

In general, most of the fossil pollen with known ultrastructure shows a coarse granulation of the endexine below the aperture region, which is similar to the condition in modern pollen referred to Group 1. Only a few fossil specimens (cf. pollen of an unassigned dispersed stamen from the Late Cretaceous of Sweden, Friis et al., 1988, pl. 8, Figures 4–7) show a more compact laminate endexine structure, comparable to our Group 2 pollen. Although the general type of endexine can be considered the same for fossil and modern taxa, marked differences are seen mainly in endexine thickness in the aperture region (cf. Table III).

Significance of pollen characters for the systematic placement of equivocal fossil taxa

In a number of accounts on Cretaceous plants with platanaceous aspects, information from pollen (LM, SEM, and TEM) is not sufficient to determine the systematic position of the staminate flowers that produced the pollen. This is particularly true in cases where male and female reproductive structures display a mosaic of features found in different modern families. Examples are infructescences of *Kasicarpa* N. Maslova, Golovneva & Tekleva with adhering pollen that show features of Hamamelidaceae, Altingiaceae, and Platanaceae (Maslova et al., 2005), and flowers with a combination of floral and pollen characters found in Platanaceae and Hamamelidaceae described by Crepet et al. (1992), both from Turonian deposits. Discussion as to whether such fossils belong to Hamamelidaceae or to Platanaceae,

Figure 3. *Platanus racemosa*, *P. gentryi*. SEM. **A–D.** *Platanus racemosa* var. *racemosa*, **A, B, D.** Wiggins & Thomas 22, **C.** E. K. Balls 9126. **A.** Equatorial view showing long colpi. **B.** Detail of A, reticulum. **C.** Equatorial view showing short and broad colpi. **D.** 'Twisted' pollen. **E.** *P. gentryi*, Gentry 5807, equatorial view. **F, G.** *P. racemosa* var. *wrightii*, Daniel & Wagner 3428. **F.** Equatorial view showing long and broad colpus. **G.** Detail of reticulum. **H, I.** *P. gentryi*, Gentry 5807. **H.** Polar view. **I.** Detail of coarse reticulum. **J, K.** *P. racemosa* var. *wrightii*, Daniel & Wagner 3428. **J.** Polar view, twisted pollen grain. **K.** Detail of reticulum, note 'crown-like' appearance of muri. **L, M.** *Platanus racemosa* var. *racemosa*, E. K. Balls 9126. **L.** Equatorial view, note oblique course of colpus and coarse reticulum. **M.** Detail of reticulum showing incomplete muri. Scale bar – 15 μm (L); 12 μm (A, C–F, H, J); 3 μm (M), and 600 nm (B, G, I, and K).



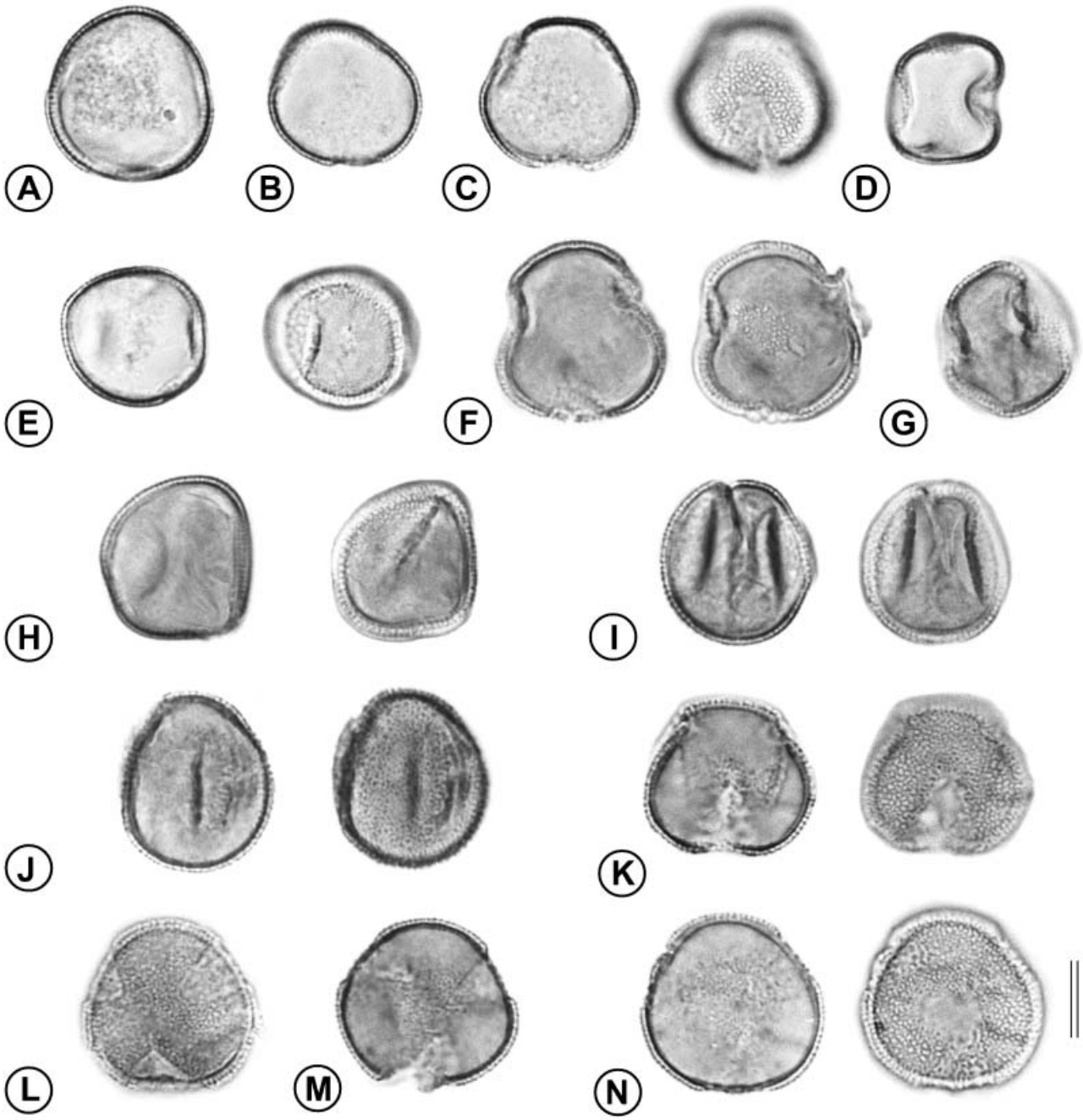
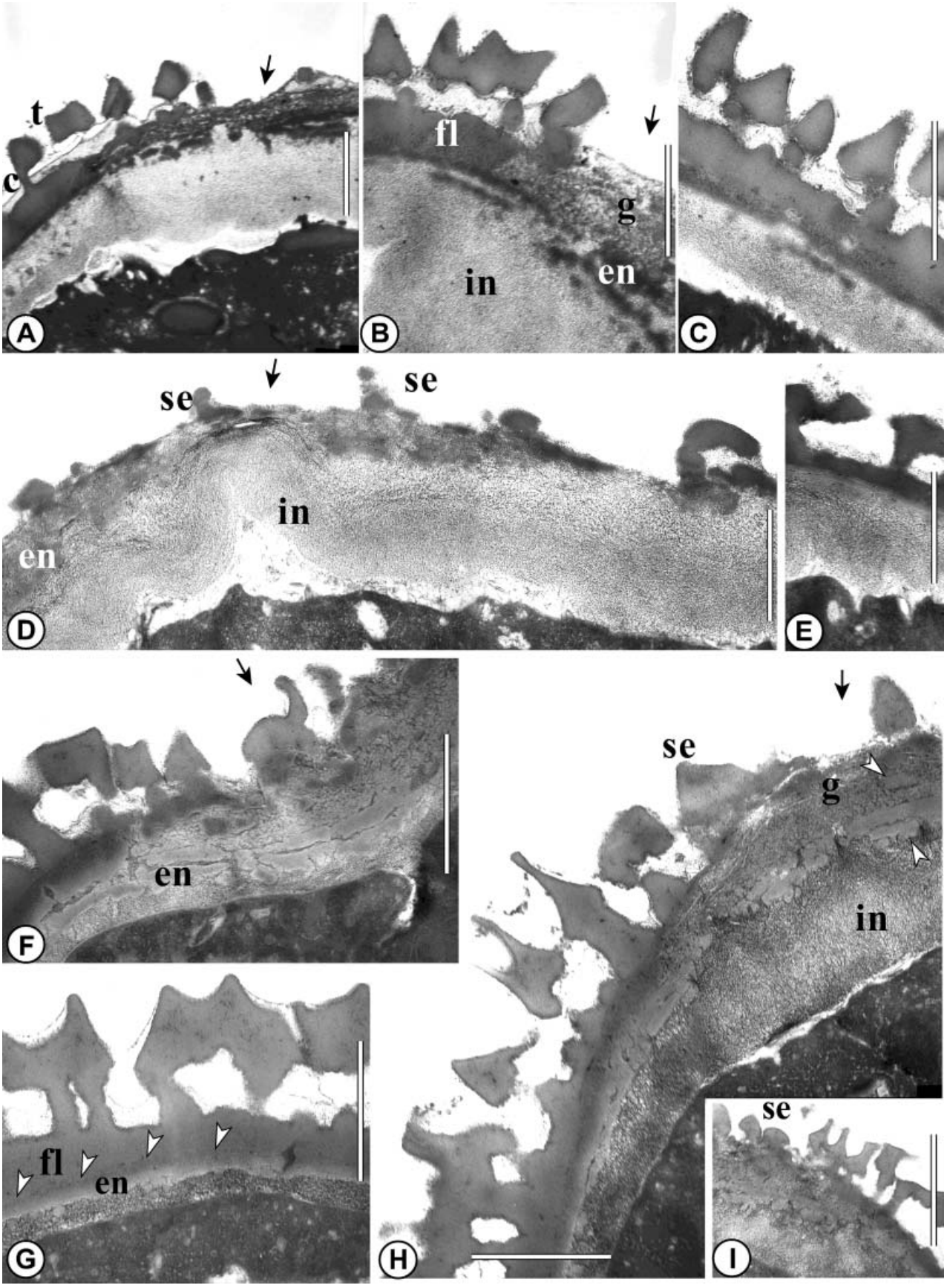


Figure 4. *Platanus racemosa, P. gentryi*. LM. **A–E.** *Platanus racemosa* var. *racemosa*, E. K. Balls 9126. **A, B.** Polar view, showing layered pollen wall. **C.** Polar view, focus on pollen wall (left), and on reticulum (right). **D.** Polar view, possibly 4-colpate pollen. **E.** Equatorial view, focus on pollen wall (left), and on reticulum (right). **F–I.** *P. racemosa* var. *wrightii*, Daniel & Wagner 3428. **F.** Polar view, two foci. **G.** "Twisted" pollen grain. **H.** Equatorial view, two foci, note oblique colpus. **I.** Equatorial view, two foci. **J–N.** *Platanus gentryi*, Gentry 5807. **J.** Equatorial view, two foci. **K.** Polar view, two foci. **L, M.** Polar view, two foci. Note clearly visible nexine, columellae, and reticulum. **N.** Polar view, two foci. Scale bar – 10 μm.

Figure 5. *Platanus racemosa* var. *racemosa*. TEM. **A–C.** Wiggins & Thomas 22. **A.** Transition non-apertural to aperture region. Endexine is more electron dense than ectexine, homogeneous in non-apertural region, and forming dark granular structures in aperture region. **B.** Detail of aperture region showing endexine as dark granular structures embedded in intine and glycocalyx. **C.** Detail of non-apertural region. **D–E.** E. K. Balls 9126. **D.** Aperture region; endexine consists of plate-like structures; aperture membrane is beset with structural elements. **E.** Non-apertural region showing laminated endexine. **F–I.** C. Epling 8533. **F.** Transition non-apertural region to aperture region, endexine is less electron dense than ectexine, and forms plate-like structures. **G.** Non-apertural region showing thin intine, thin endexine, and foot layer, columellae, and tectum. **H.** Aperture region showing endexine possibly embedded in remnants of glycocalyx, and intine thickening towards aperture. **I.** Transition non-apertural region to aperture region. t=tectum, c=columellae, fl=foot layer, en=endexine, in=intine, se=structural element on colpus membrane, g=glycocalyx, black arrows indicate colpus, white arrowheads indicate border of endexine. Scale bar – 1 μm.



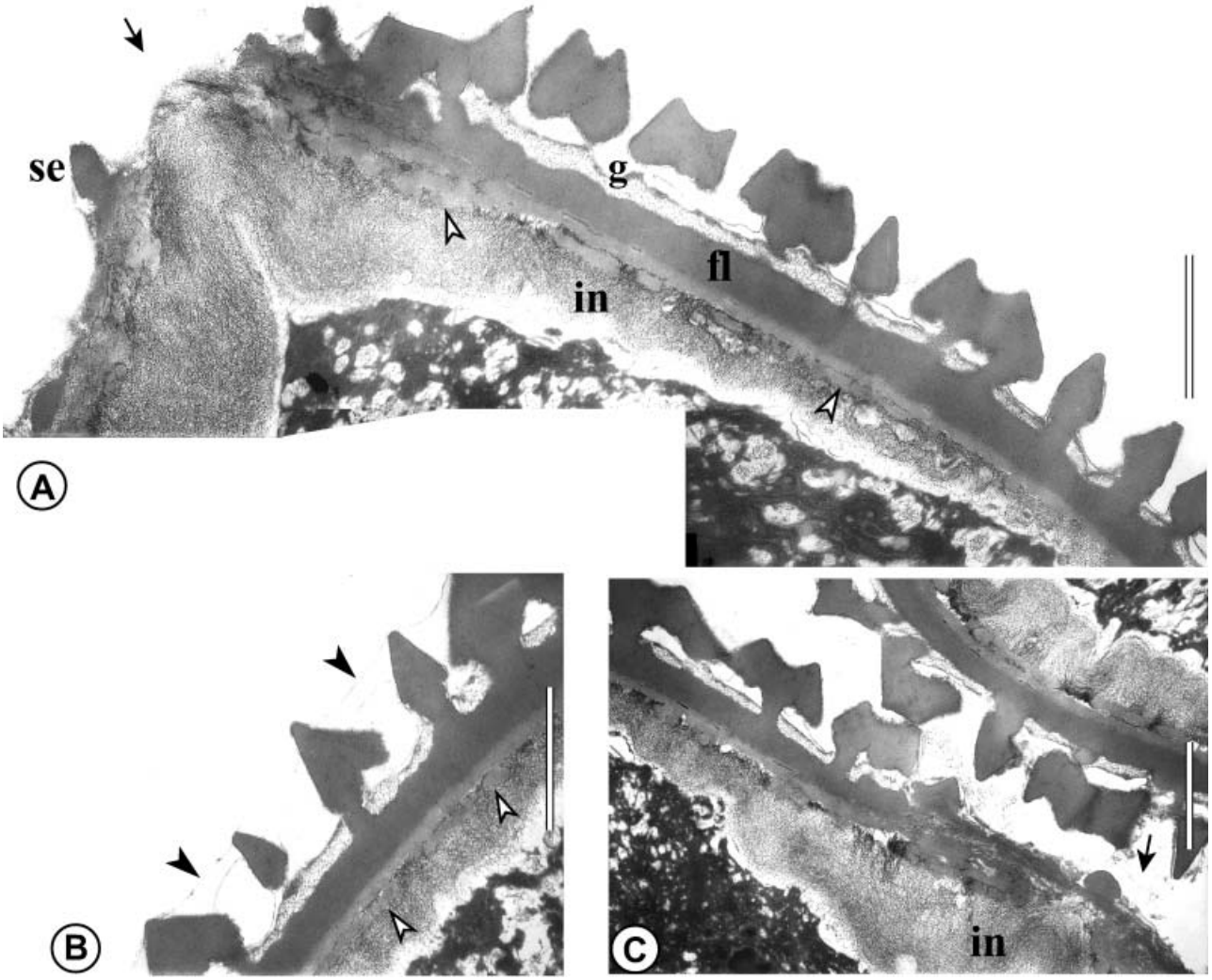


Figure 6. *Platanus racemosa* var. *wrightii*. TEM. **A–C.** Nelson & Nelson 1408. **A.** Transition non-apertural to aperture region. The laminated plate-like endexine and the intine become thicker towards aperture. Colpus membrane is beset with structural elements. Between columellae remnants of glycocalyx are seen. **B.** Non-apertural region showing laminated endexine, less electron dense than ectexine, and possibly pollenkitt between muri. **C.** Pollen wall of two adjacent pollen grains. fl=foot layer, en=endexine, in=intine, se=structural element on colpus membrane, g=glycocalyx, black arrows indicate colpus, white arrowheads indicate border of endexine, black arrowheads indicate possibly electron-translucent pollenkitt. Scale bar – 1 μm.

for instance, appears to be pointless. Viewed in a phylogenetic context, these fossils are likely to belong to extinct families that are perhaps not closely related to either Hamamelidaceae or Platanaceae.

In contrast, a number of features that superficially appear to be 'untypical' of Platanaceae, such as the well-defined filaments of anthers in *Aquia*, are not in conflict with the placement of this genus in the Platanaceae. All basal eudicots and some of the core eudicots (e.g. Hamamelidaceae) have both short and long filaments (von Balthazar et al., 2005; Doyle & Endress, 2000).

Platanaceous pollen and evolutionary trends within basal eudicots and Platanaceae

Based on the fossil record the initial radiation of members of basal eudicots and perhaps also basal core eudicots happened within a restricted period of time in the Early Cretaceous (Ranunculales, Early Albian, von Balthazar et al., 2005; Buxales, Late Albian; Nelumbonaceae, Late Albian; Platanaceae, Early Albian; Trochodendrales, Albian; cf. Magallón & Sanderson, 2001). A fairly rapid diversification of basal eudicots appears also to be indicated by a great number of molecular studies that recovered the same lineages of basal eudicots but inferred conflicting relationships among them (e.g., Hilu et al., 2003; Kim et al., 2004; Soltis et al., 2005, and references cited therein). Also Platanaceae may have had a phase of rapid radiation during the Early to mid-Cretaceous, with a number of features evolving in parallel (e.g. tricolporate pollen in *Hamatia* and *Sarbaya*; Pedersen et al., 1994; Krassilov & Shilin, 1995). Nevertheless, both fossil and modern pollen

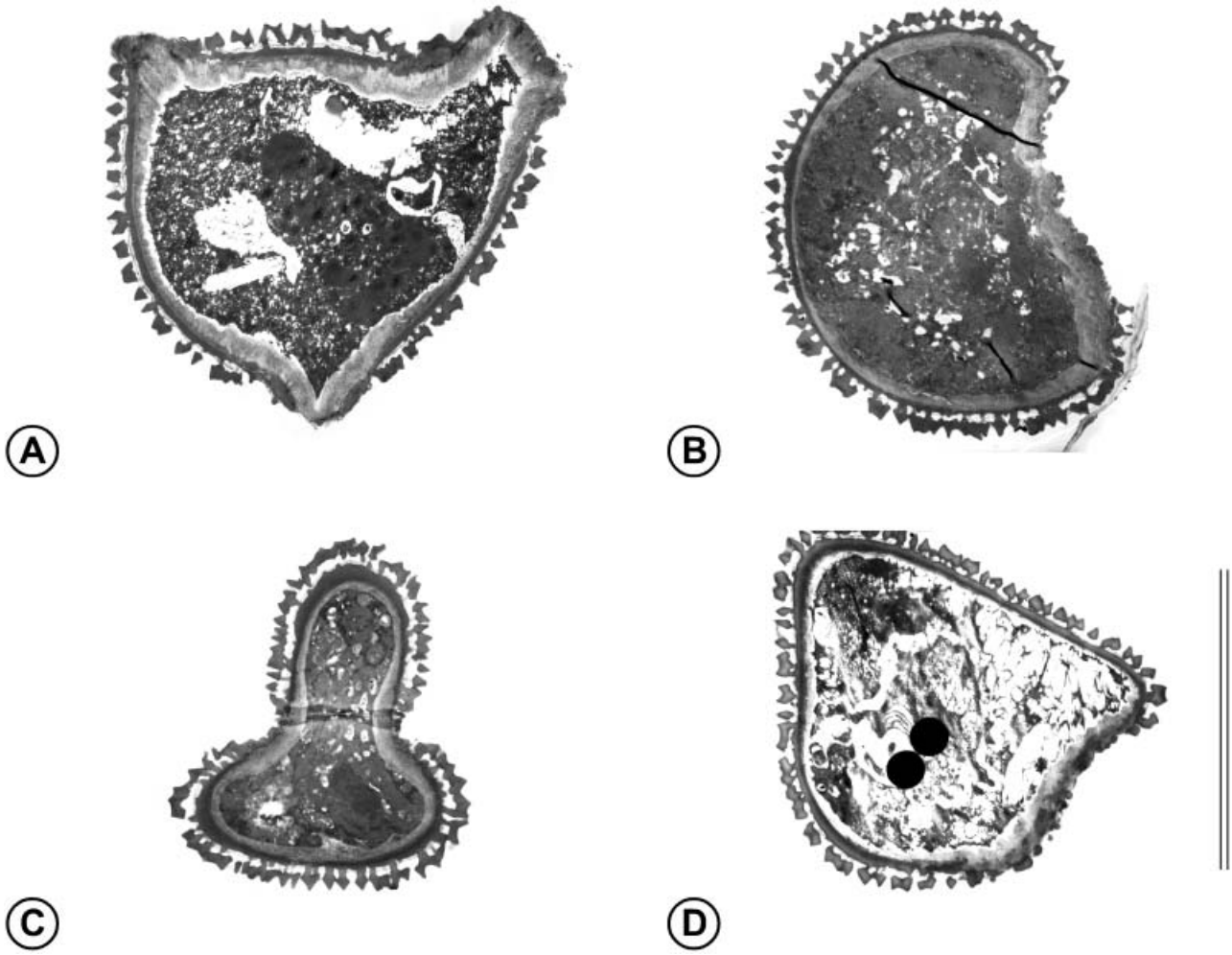
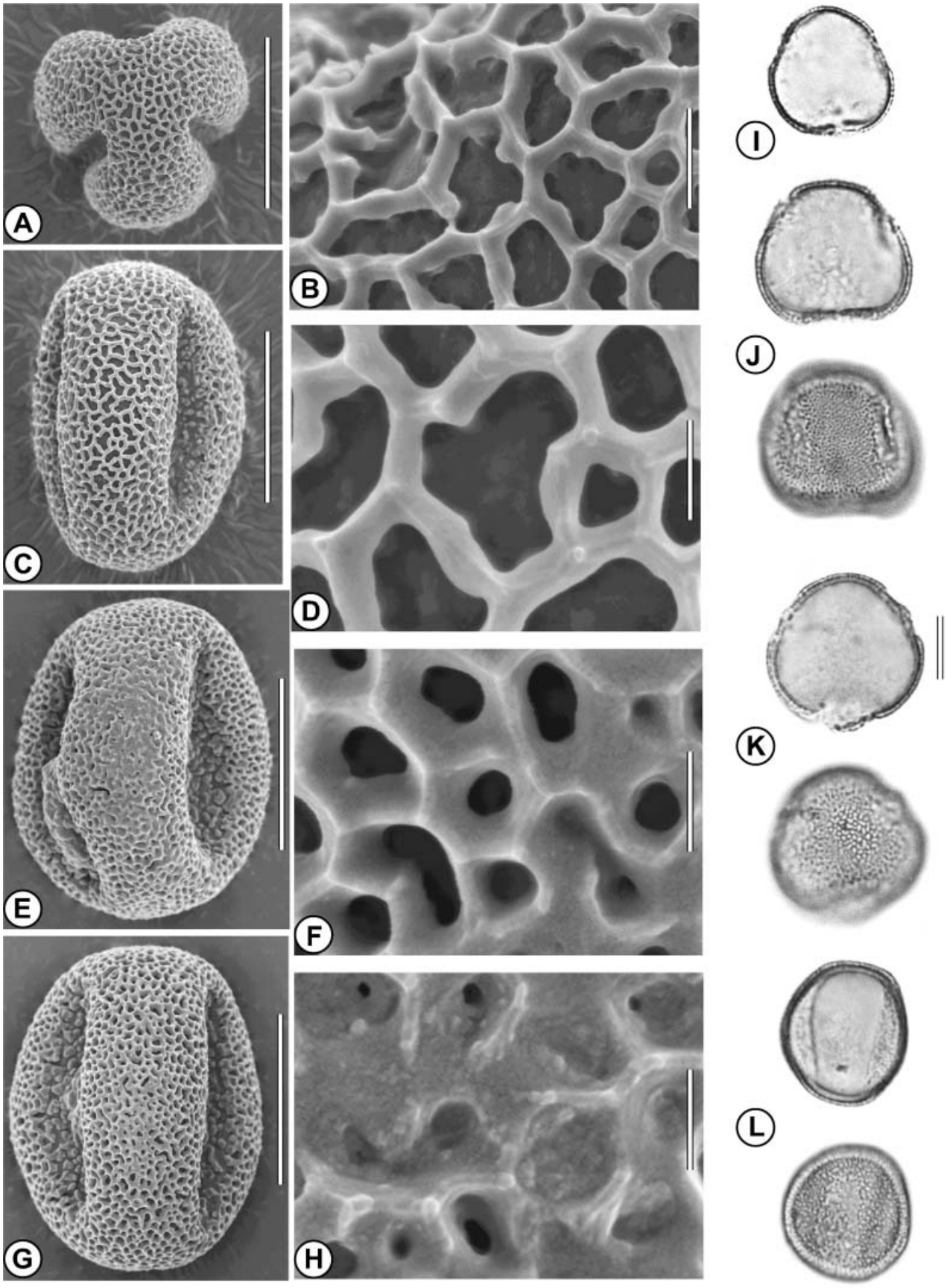


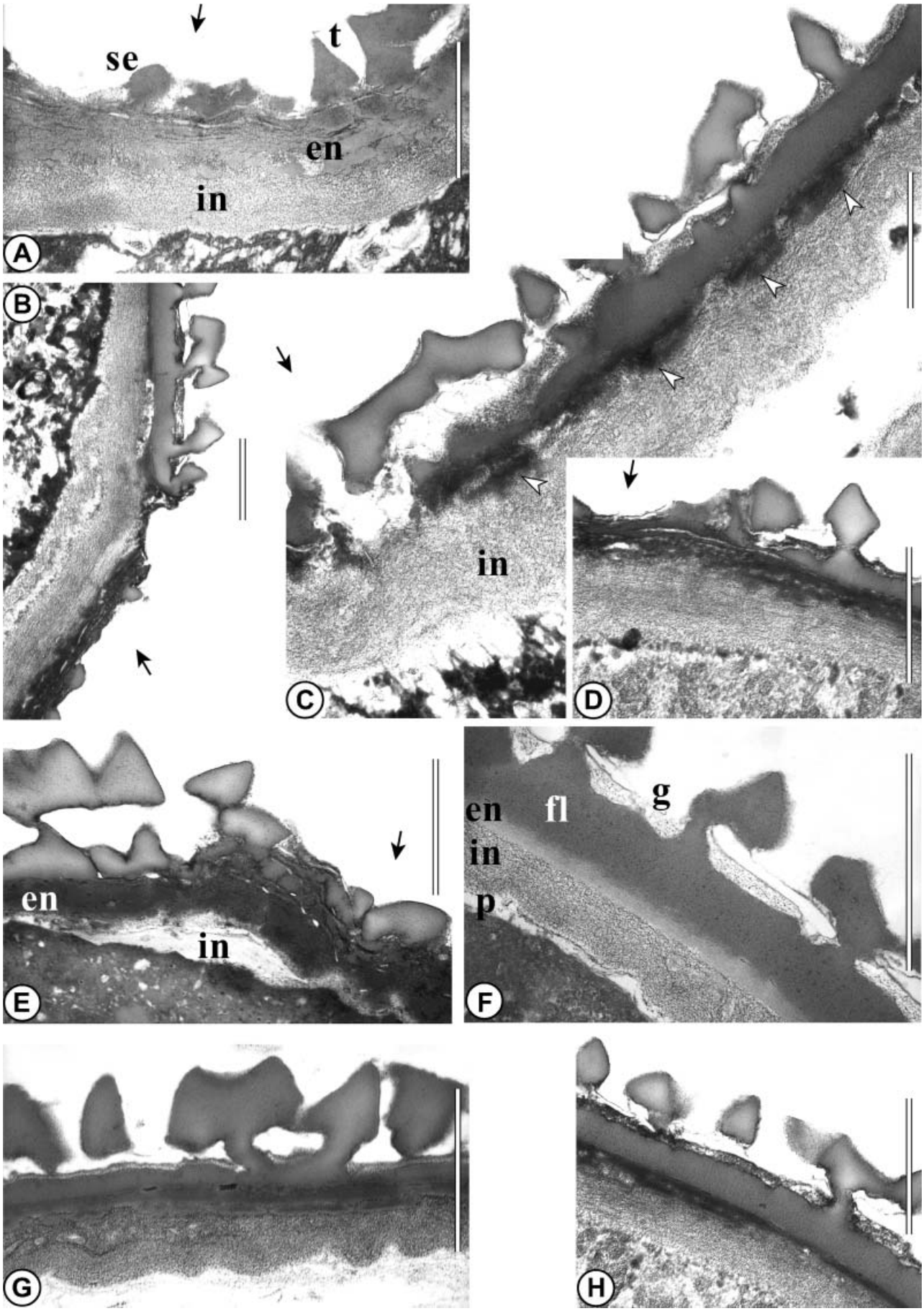
Figure 7. *Platanus racemosa, P. orientalis*. TEM. **A.** *Platanus racemosa* var. *wrightii*, Nelson & Nelson 1408. Equatorial section through whole grain. **B, C.** *P. racemosa* var. *racemosa*, **C.** Epling 8510. Oblique section through pollen grain. **D.** *P. orientalis*, T. Å. Tengwall s.n. Oblique section through pollen grain showing one colpus. Scale bar – 10 μm.

of Platanaceae fall well within a common type of tricolpate (semi)tectate (reticulate) pollen as found in many basal eudicots and basal core eudicots (cf. Walker, 1976, *Euptelea*; Bogle & Philbrick, 1980, Exbucklandioideae, Disanthoideae, Hamamelidoideae within the Hamamelidaceae; Blackmore et al., 1995, Menispermaceae; Wanntorp et al., 2004*a*, *b*, Gunneraceae). Because this type of pollen comprises a large number of features that can be considered plesiomorphic in eudicots (Donoghue & Doyle, 1989), it is not surprising that Zavada and Dilcher (1986), in utilizing pollen characters for a cladistic study, found that Platanaceae clustered with taxa as distantly related as Salicaceae (rosids).

Figure 8. *Platanus orientalis*. SEM, LM. **A–D, I.** Anderberg & Anderberg 99-20. **E–H, J–L.** Erdtman 140. **A–H.** SEM micrographs. **I–L.** LM. **A.** Polar view. **B.** Detail of coarse reticulum, polar view. **C.** Equatorial view. **D.** Detail of coarse reticulum, equatorial view. **E.** Equatorial view. **F.** Detail of fine reticulum. **G.** Equatorial view. **H.** Detail of almost closed reticulum probably clogged with residual pollenkitt. **I.** Small pollen grain, polar view. **J.** Polar view, two foci. **K.** Polar view, two foci. **L.** Equatorial view, two foci. Scale bar – 12 μm (A, C, E, and G); 10 μm (I, J, K, L); 1.2 μm (B); and 600 nm (D, F, and H).

Figure 9. *Platanus orientalis*. TEM. **A, F**. T. Å. Tengwall s.n. **B–D, H.** Anderberg & Anderberg 90-20. **E.** Stojanoff 201/677. **G.** G. Erdtman 140. **A.** Aperture region, endexine consists of plate-like structures and is embedded in intine. **B.** Transition non-apertural to aperture region, endexine consists of dark granular structures below aperture and is covered with less electron dense structural elements. **C.** Transition non-apertural to aperture region. **D.** Aperture region. **E.** Aperture region, endexine is more electron dense than ectexine, forming elongated compact elements. Variant of Group 1 pollen. **F.** Non-apertural region, endexine is less electron dense than ectexine. Group 2 pollen. **G.** Non-apertural region, endexine slightly more electron dense than ectexine, its outer part homogeneous and its inner part fragmented and embedded in intine. **H.** Non-apertural region. Thin endexine more electron dense than ectexine. t=tectum, fl=foot layer, en=endexine, in=intine, se=structural element on colpus membrane, g=glycocalyx, p=protoplast, black arrows indicating colpus, white arrowheads indicating border of endexine. Scale bar – 1 μm.





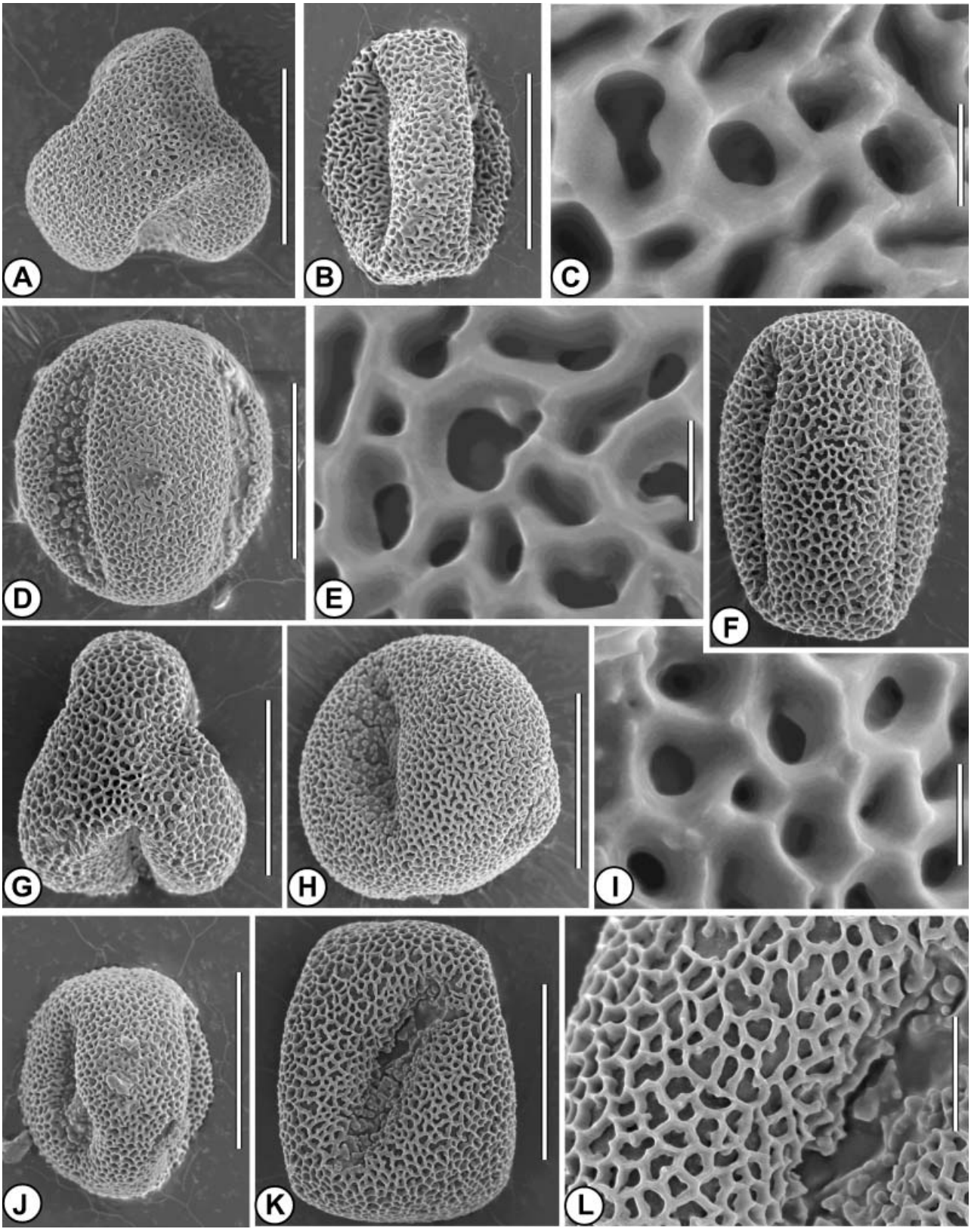


Figure 10. *Platanus mexicana*. SEM. **A–E.** *Platanaus mexicana* var. *interior*. **F–L.** *P. mexicana* var. *mexicana*. **A, D, E.** May AM 70. **B, C.** Arguelles s.n. **F, G, K, L.** G. Suarez 16. **H.** Ventura 16805. **I, J.** Tenorio 12515. **A.** Polar view. **B.** Equatorial view. **C.** Detail of reticulum, equatorial view. **D.** Equatorial view showing structural elements on colpus membrane. **E.** Detail of reticulum. **F.** Equatorial view, large pollen grain with rectangular outline. **G.** Polar view. **H.** Equatorial view. **I.** Detail of reticulum of grain shown in J. **J.** Equatorial view. **K.** Equatorial view showing oblique colpus. **L.** Detail of K showing coarse reticulum. Scale bar – 12 μm (A, B, D, F, G, H, J, K); 3 μm (L); and 600 nm (C, E, I).

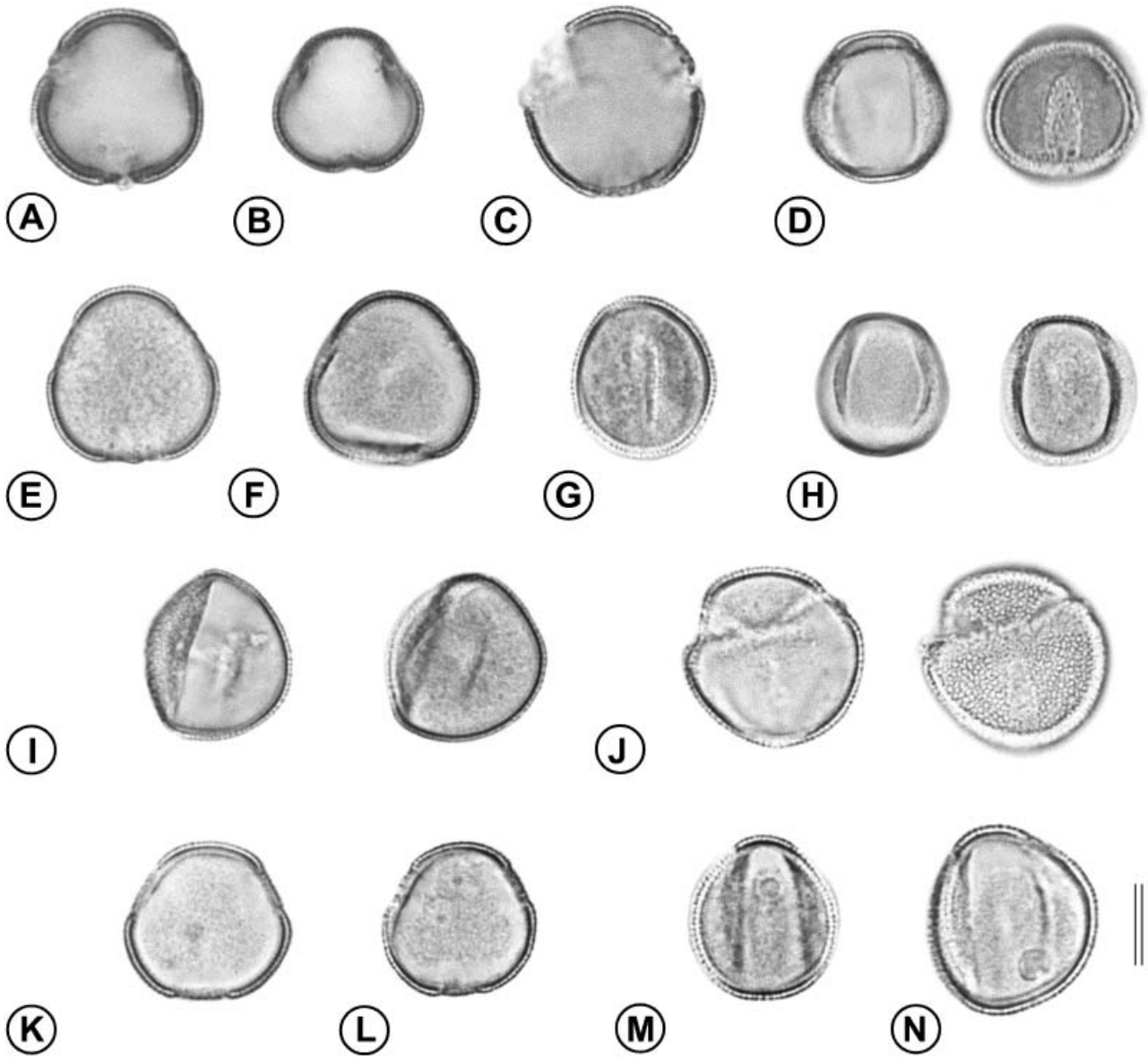


Figure 11. *Platanus mexicana*. LM. **A–I.** *Platanus mexicana* var. *mexicana*. **J–N.** *Platanus mexicana* var. *interior*. **A, B.** G. Suarez 16. **C–I.** Munn-Estrada et al. 2039. **J–N.** Arguelles s.n. **A, B.** Polar view. **C.** Polar view. **D, E.** Equatorial view, two foci. **E, F.** Polar view. **G–I.** Equatorial view, different foci. **J.** Polar view, two foci. **K, L.** Polar view. **M, N.** Equatorial view. Scale bar – 10 μm.

In contrast, pollen of Proteaceae, which has been suggested to be the modern sister group of Platanaceae, is markedly different from platanaceous pollen (Blackmore & Barnes, 1995). Unlike the pollen apertures in most other eudicots, the apertures in the pollen of Proteaceae are arranged according to Garside's rule (apertures are formed in threes at four points of the tetrad; Garside, 1946). This feature, which is extremely rare in flowering plants, has also been reported in the Illiciales, which are among the basal-most angiosperms, as well as Arecaceae and Iridaceae in the monocots, and Proteaceae, *Myrothamnus*, and Olacaceae in the eudicots (see for example, Harley & Dransfield, 2003; Harley, 2004; Furness & Rudall, 2004). By contrast, trilete apertures of fern spores are typically formed following Garside's rule. Another unusual feature of Proteaceae is the occurrence of both simultaneous and successive microsporogenesis (Blackmore & Barnes, 1995). While simultaneous microsporogenesis is found in almost all eudicots, successive microsporogenesis occurs frequently among basal angiosperms and monocots (Harley & Dransfield, 2003). Kreunen and Osborn (1999) reported partly successive microsporogenesis for Nelumbonaceae that are suggested sister group to Platanaceae+Proteaceae.

A rich Cretaceous record of platanaceous reproductive structures with *in situ* pollen in the Northern Hemisphere (for example, Friis et al., 1988; Crane

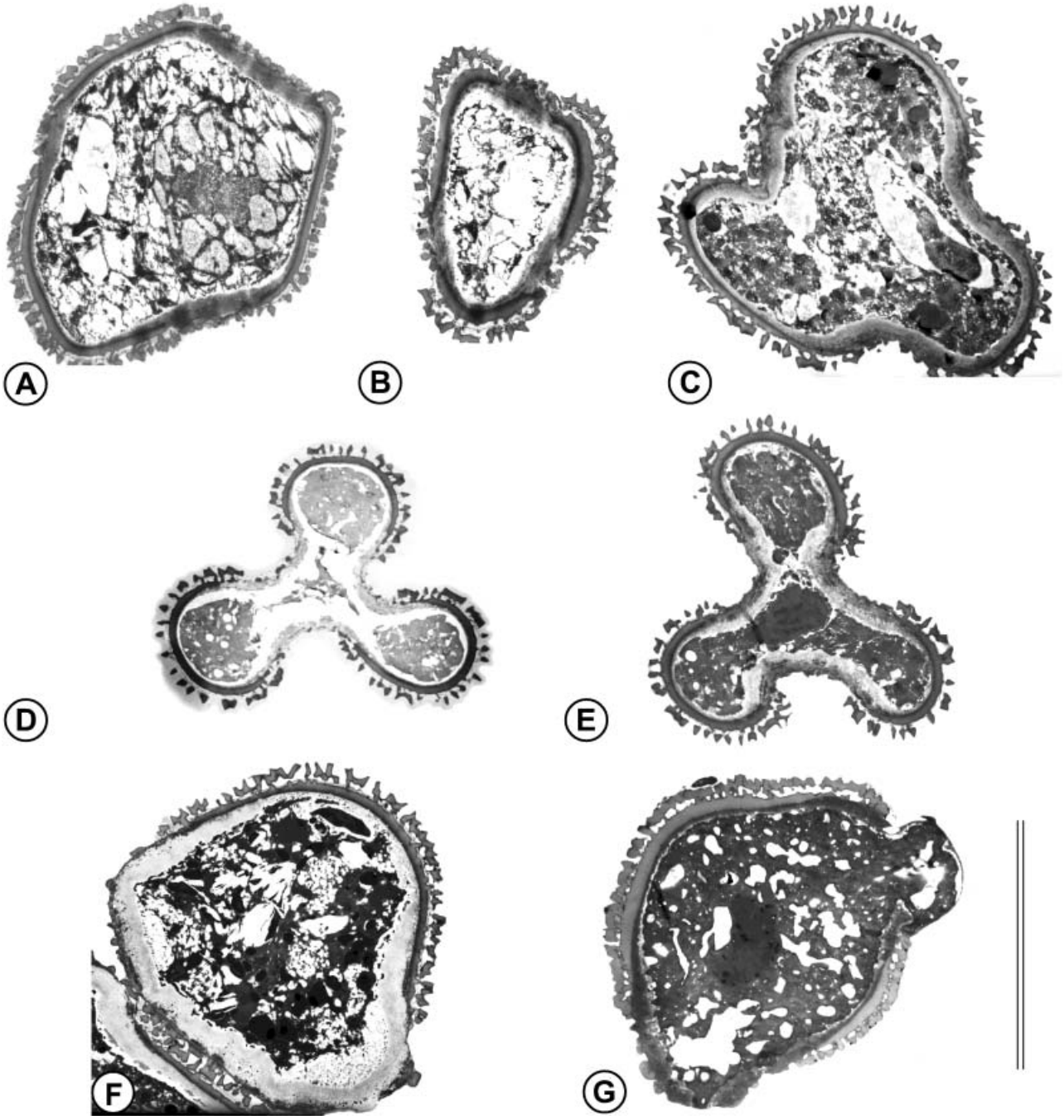
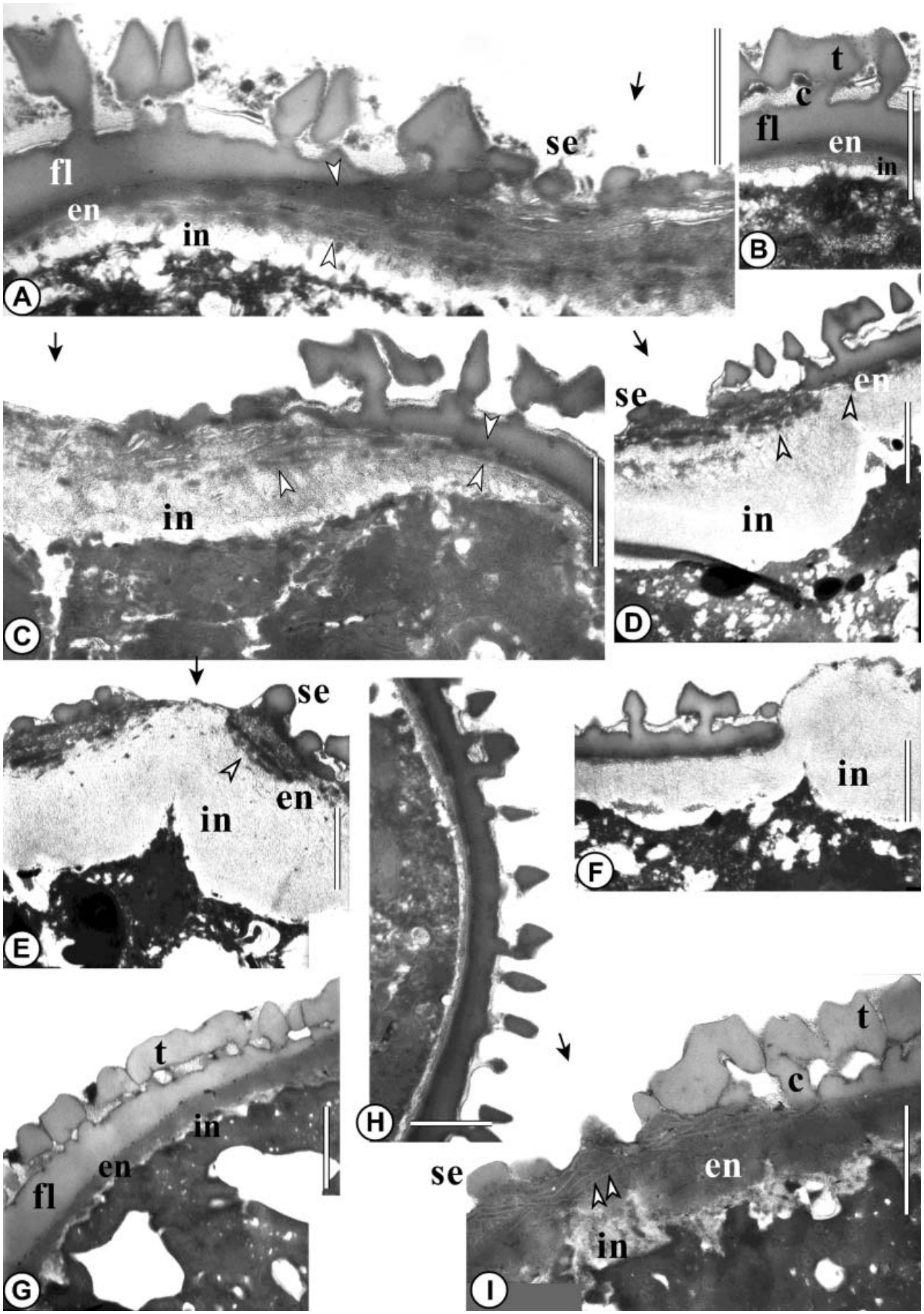


Figure 12. *Platanus mexicana*. TEM. **A, B.** *Platanus mexicana* var. *interior*. E. Arguelles s.n., equatorial section through whole grain. **C–G.** *P. mexicana* var. *mexicana*. **C.** G. Suarez 16, equatorial section through whole grain. **D, E.** R. Ortega 01270, equatorial section through whole grain showing transition from non-apertural to aperture region, Group 1 pollen. **F.** F. Ventura A. 16804, oblique section through pollen grain. **G.** E. Matuda 5124, oblique section through pollen grain; note thick foot layer in non-apertural region and thick endexine in aperture region. Scale bar – 10 μm.

Figure 13. *Platanus mexicana*. TEM. **A, B.** *Platanus mexicana* var. *interior.* E. Arguelles s.n. **C–I.** *P. mexicana* var. *mexicana*. **C, H.** R. Ortega 01270, **D–F.** F. Ventura 16804, **G, I.** E. Matuda 5124. **A.** Transition non-apertural to aperture region. Note "white lines" in outer aperture region between endexine and colpus membrane. **B.** Non-apertural region showing compact endexine more electron dense than ectexine. **C.** Transition non-apertural to aperture region. **D.** Aperture region with distinct dark granular structures of the endexine. **E, F.** Aperture showing protruding intine and thin colpus membrane. **G.** Non-apertural region showing compact endexine. **H.** Non-apertural region. **I.** Aperture region, showing conspicuous lamellation of endexine, probably white lines. t=tectum, c=columellae, fl=foot layer, en=endexine, in=intine, se=structural element on colpus membrane, g=glycocalyx, black arrows indicating colpus, white arrowheads indicating border of endexine. Scale bar – 1 μm.



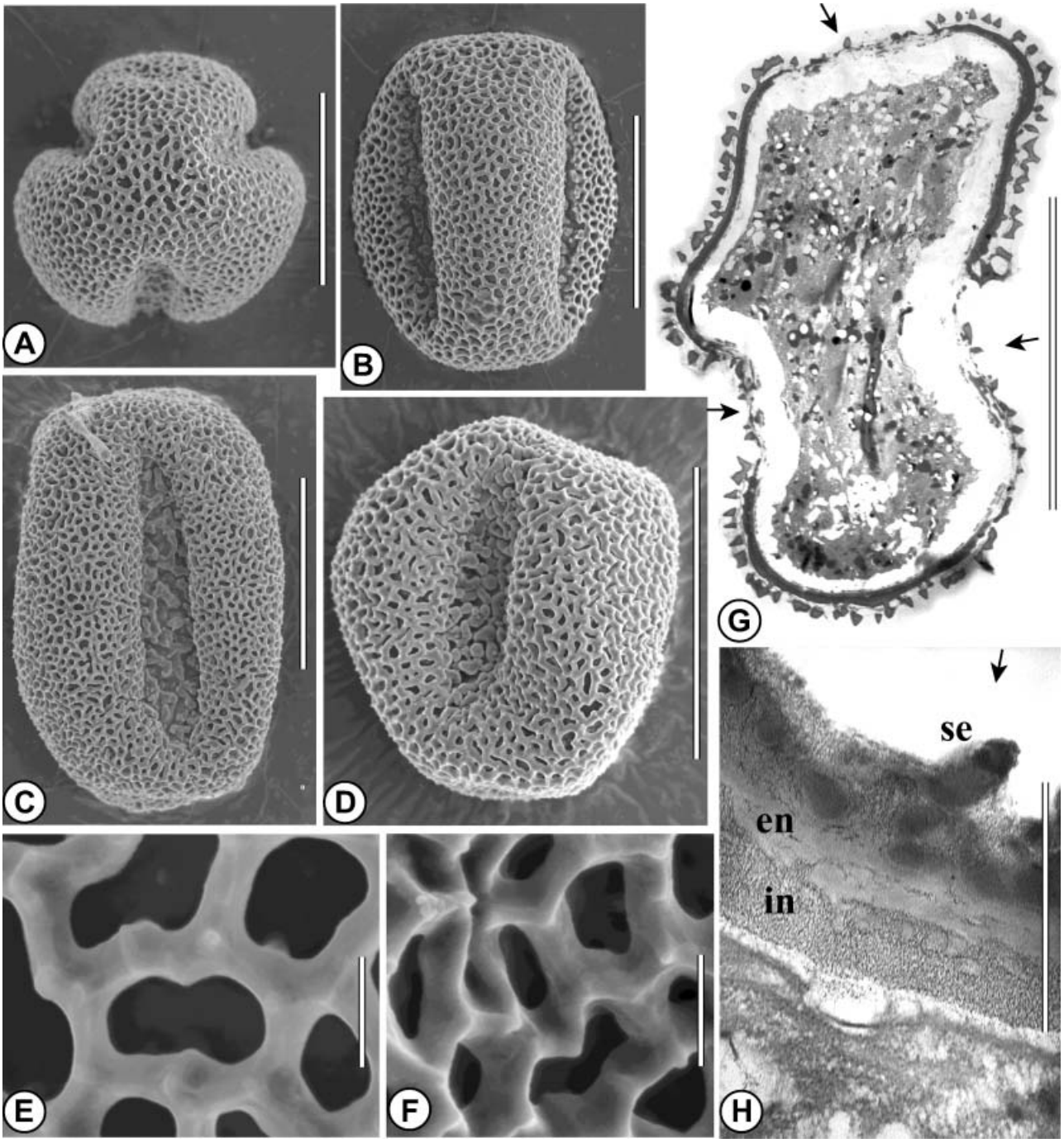


Figure 14. *Platanus occidentalis*. SEM, TEM. **A–C, E, G.** *Platanus occidentalis* var. *occidentalis*, **D, F, H.** *P. occidentalis* var. *palmeri*. **A, B, E.** D. C. Bossert 28. **C, G.** E. Wall s.n. **D, F, H.** J. M. Poole et al. 2521. **A.** Polar view. **B.** Equatorial view. **C.** Equatorial view, large pollen grain. **D.** Equatorial view showing short colpus. **E, F.** Details of reticulum. **G.** Equatorial section through whole grain showing non-apertural and aperture regions. **H.** Detail of aperture region showing plate-like endexine and structural elements on colpus membrane. en=endexine, in=intine, se=structural element on colpus membrane, black arrows indicating colpus. Scale bar – 12 μm (A–D); 10 μm (G); 1 μm (H); and 600 nm (E, F).

et al., 1993; Magallón et al., 1997; Maslova, 2003) indicates that by the late Early Cretaceous pollen of Platanaceae was essentially similar to modern *Platanus* pollen. At the same time, the distinctive pollen of Proteaceae – mostly oblate, triporate, tricolpoidate, or biporate with simple apertures (see for example, Erdtman, 1969; Blackmore & Barnes, 1995; Dettmann & Jarzen, 1998) is known from Late Cretaceous sediments of the Southern Hemisphere (Hill et al., 1995; Dettmann & Jarzen, 1998). These two pollen types are considerably different. Unlike the plesiomorphic Platanaceae

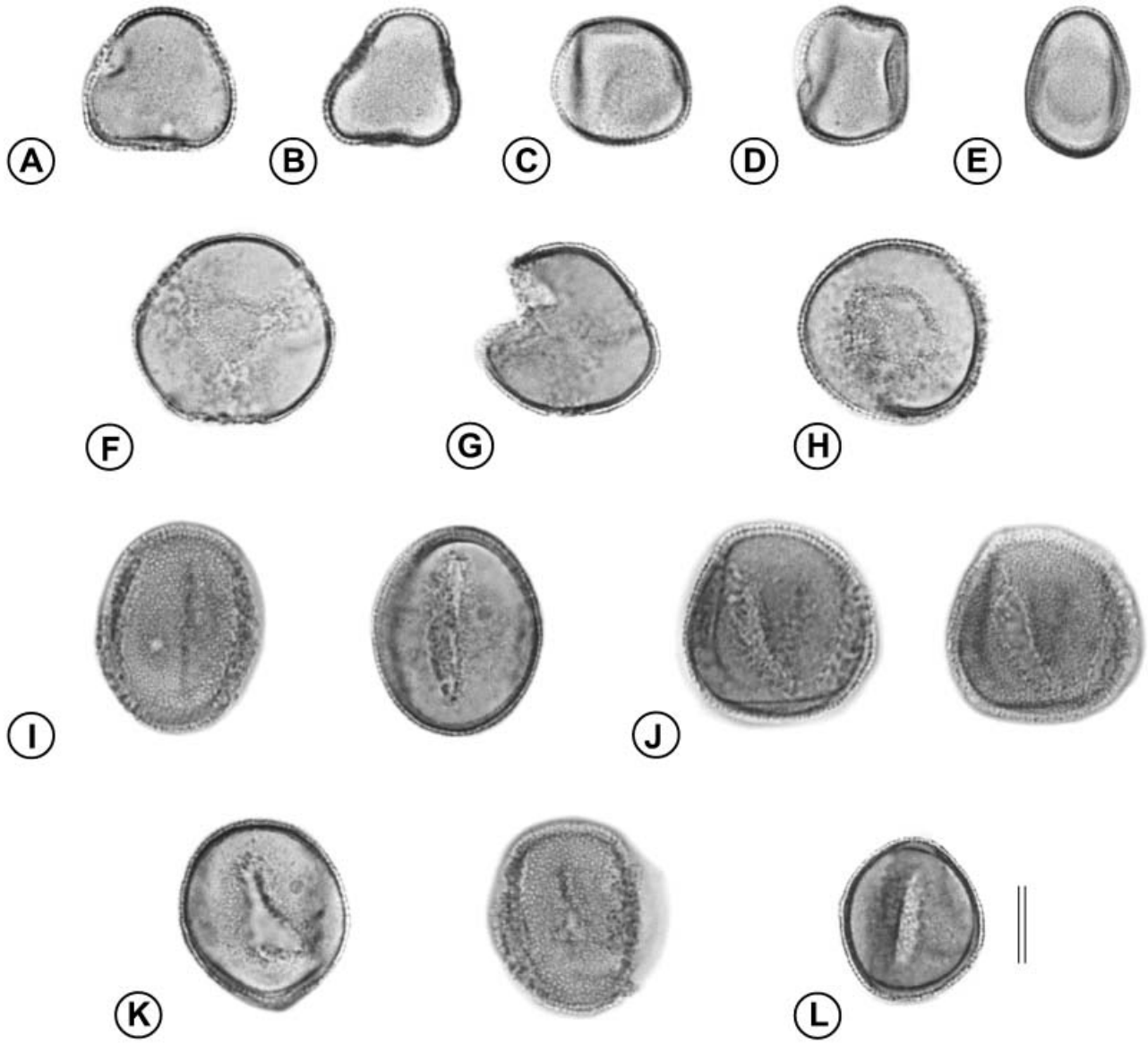


Figure 15. *Platanus occidentalis*. LM. **A–E.** *Platanus occidentalis* var. *palmeri*, J. M. Poole et al., 2521. **F–L.** *P. occidentalis* var. *occidentalis*, E. Wall s. n. **A, B.** Polar view. **C–E.** Equatorial view. **F.** Polar view. **G.** Polar view, showing thick nexine. **H.** Polar view. **I.** Equatorial view, two foci. **J.** Equatorial view, two foci, oblique colpus. **K.** Equatorial view, two foci. **L.** Equatorial view. Scale bar – 10 μm.

pollen type, pollen of Proteaceae appears to be derived. A hypothetical pollen type ancestral to Platanaceae+Proteaceae (or even leading to Proteaceae) would be expected to be of a common tricolpate tectate or semi-tectate, reticulate eudicot pollen type, and would give no clue to later Protealean evolutionary developments; it would be difficult to detect in the fossil record.

Nelumbonaceae, which is suggested to be sister to Platanaceae+Proteaceae within the Proteales (Chase et al., 1993; Soltis & Soltis, 1997; Qiu et al., 1999 etc.), shows similar tricolpate pollen to Platanaceae but differs from Platanaceae by the late formation of apertures in the free spore stage (Kreunen & Osborn, 1999). Earliest fossils attributable to Platanaceae and Nelumbonaceae are of Early and Late Albian age, respectively (summarized in Magallón & Sanderson, 2001). Already by the Late Cretaceous, Nelumbonaceae fruit-receptacles were strikingly similar to the highly derived modern *Nelumbo* (Gandolfo & Cuneo, 2005) suggesting a split of the three families Nelumbonaceae, Platananceae, and Proteaceae prior to the Late Cretaceous.

Considering pollen of Platanaceae from the Early Cretaceous till today, a dynamic picture of the evolution of the family emerges. In the first phase (Early Cretaceous) pollen of extinct genera such as *Aquia* differed considerably from modern *Platanus* and shows strong similarity to basal eudicot taxa such as Ranunculales (e.g. Lardizabalaceae; see

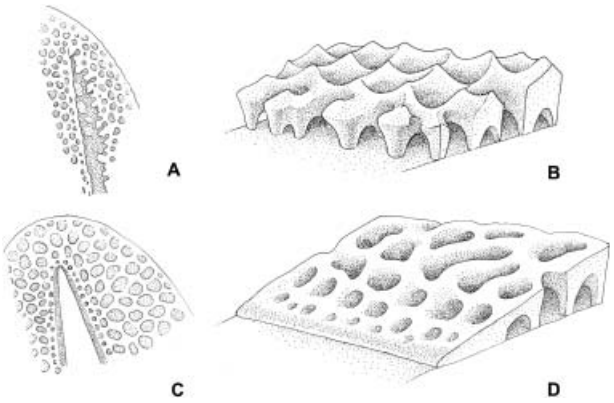


Figure 16. Line drawings, aperture margin and reticulum in extant and some fossil Platanaceae. **A, B.** *Platanus* subgenus *Platanus*. **A.** Overview of pollen grain, equatorial view. The reticulum breaks up; lumina open towards the aperture. **B.** Detail of A, note crown-like tips of muri. **C, D.** Maastrichtian-Paleocene *Platanaceae*. **C.** Overview of pollen grain. Lumina fuse to form an ectexine rim. **D.** Detail of C, note the rounded muri. Both types of aperture margins may have either crown-like or rounded muri.

Crane et al., 1993, Blackmore et al., 1995). The Late Cretaceous *Platananthus hueberi* displays a distinct coarse reticulum that is unknown from modern *Platanus* but similar to some taxa of Hamamelidaceae (e.g. *Exbucklandia*; see Friis et al., 1988; Bogle & Philbrick, 1980). At the same time the earliest true *Platanus* appears to be infructescences from the Santonian of Central Europe (Knobloch & Mai, 1986). The infructescences of *Platanus laevis* (Velenovský) Velenovský have pistillate heads that are around 20 mm in diameter, and carpels with elongated styles. It is unknown whether or not the carpels had dispersal hairs. These infructescences co-occur with leaves that are identical to modern *Platanus* (leaf architecture and epidermal features; *Platanus intermedia* Knappe & Rüffle; Knappe & Rüffle, 1975). From the same locality platanaceous pollen, *Platanus quedlinburgensis* Pacltová (Pacltová, 1982) and leaves belonging to extinct groups of Platanaceae have been reported; see for example, *Credneria* spp., *Dewalquea westerhausiana* (Lesqu.) Rüffle & Knappe, Richter (1905); Kvaček et al. (2001). Platanaceous plants with distinct pollen – types continue to emerge until at least the (mid) Eocene (*Platananthus speirsae, P. synandrus*; Pigg & Stockey, 1991; Manchester, 1986; staminate inflorescences). At the transition Palaeocene/Eocene *Platanus* [*P. stenocarpa* N. Maslova (Maslova, 2002); *P. hirticarpa* Manchester (Manchester, 1994) – infructescences] typically co-occurs with extinct lineages of Platanaceae (for instance *Macginicarpa*, *Tanyoplatanus* in western North America, Manchester, 1994). This was probably the time when the family was most diverse. Only in the Neogene did platanaceous diversity decrease. Despite this, the pollen type of the modern subgenus *Castaneophyllum* (*P. kerrii* – type) seems to be a modern innovation that originated after the initial radiation of the family. A number of Palaeogene to Neogene Platanaceae [*P. neptunii* (Ettingshausen) Bůžek, Holý, & Z. Kvaček, *P. bella* (Heer) Z. Kvaček, Manchester, & Guo] traditionally ascribed to the subgenus *Castaneophyllum* have recently been suggested to belong to their own subgenus (Kvaček et al., 2001; Kvaček & Manchester, 2004) based on flower and fruit characters. This is in accordance with the dissimilarity of pollen of *P. neptunii* with pollen of *P. kerrii*. To our knowledge, pollen of the *P. kerrii* – type has not been reported in the fossil record.

Conclusions

Both SEM and TEM observations of modern *Platanus* pollen provide important morphological characters supporting the concept of two extant subgenera in *Platanus*. A number of ultrastructural features of the pollen wall in modern species appear to characterize late stages in pollen development. These characteristics are also encountered in Late Cretaceous and Early Cainozoic platanaceous pollen. Furthermore, SEM observations show great intraspecific variability of the reticulum (narrow to wide) in modern species. Due to the absence of large sample sizes (for male flowers with pollen *in situ*), intraspecific pollen variability is difficult to assess for early platanaceous plants. Investigations of dispersed pollen using LM, SEM, and TEM are needed to complement studies of pollen *in situ*. Despite this, Cretaceous and Early Cainozoic platanaceous plants produced a number of pollen morphotypes that are not known from modern members of the family.

Within the basal eudicots, the pollen characters described for Platanaceae are not sufficient to resolve phylogenetic relationships. A number of Late Cretaceous mesofossils containing platanaceous pollen have been compared to either Platanaceae or Hamamelidaceae (for example, Crepet et al., 1992; Maslova et al., 2005). These fossils comprise a mosaic of morphological characters found in both families, but also autapomorphic features, and thus may represent extinct families related to basal eudicots. To better understand relationships within basal eudicots, such fossils would have to be analysed in a phylogenetic context.

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Specimens Investigated

Voucher information for the material studied.

Platanus kerrii Gagnep., Vietnam. Takhtajan 8745, 9-2-1974. S

Platanus orientalis L., Iraq: Kurdistan. Rovanduz G. Erdtman no. 140, 4/1957. S

Platanus orientalis L., Crete: between Ierapetra and Sitia. A.-L. Anderberg & A. Anderberg no. 99–20, 10-4-1999. S

Platanus orientalis L., Turkey: Antalya. T. Å. Tengwall s.n., 6-3-1936. S

Platanus "*orientalis*" L. (perhaps *P.* × *acerifolia*), Bulgaria. N. Stojanoff 201/677, 4-5-1929. S

Platanus gentryi Nixon & Poole (as *P.* cf. *racemosa* Nutt.), Mexico: Sinaloa, Los Alisos, Dto. de Badiraguato, 3000 ft. H. S. Gentry no 5807, 4-3-1940. MEXU

Platanus racemosa Nutt. var. *racemosa*, Mexico: Baja California, between San Quintin and El Rosario, arroyo Socorro. I. L. Wiggins & J. H. Thomas no. 22. MEXU

Platanus racemosa Nutt. var. *racemosa*, USA: California. E. K. Balls 9126, 18-2-1953. S

Platanus racemosa Nutt. var. *racemosa*, USA: California. C. Epling s.n., 10-4-1930. S

Platanus racemosa var. *wrightii* (S. Wats.) Benson. USA: Arizona, along Forest Service Road 112 from Pioneer Pass to creek crossing ca. 6 miles NE of pass. T. F. Daniel & W. H. Wagner jr no. 3428, 12-4-1984 MEXU

Platanus racemosa var. *wrightii*. USA: Arizona. A. Nelson & R. A: Nelson 1408, 6-4-1935. S

Platanus mexicana Moric. var. *mexicana* (as *P. chiapensis* Standley). Mexico: Puebla, munic. Zacoapoaxtla, KM 12 de la carretera Zacoapoaxtla-Cuetzalán, Cañada Apulco, 1390 m a.s.l. G. Suárez no 16, 3-3-1980. MEXU

Platanus mexicana var. *mexicana* (as *P. lindeniana*). Mexico: Veracruz, cerca de rancho viejo, Coatepec, 1340 m a.s.l. R. Ortega O. no 01270, 26-2-1979. MEXU

Platanus mexicana var. *mexicana* (as *P. lindeniana*). Mexico: Veracruz, munic. Naolinco, San Pablo, 1300 m a.s.l. F. Ventura A. no. 16805, 30-1-1980. MEXU

Platanus mexicana var. *mexicana* (as *P. lindeniana*). Mexico: Oaxaca, Sierra Mazateca, Eloxochitlan de Flores Magón, ca. 2 KM de Puente de Fierro, 1412 m a.s.l. X. Munn-Estrada et al. No. 2039, 4-3-2002. MEXU

Platanus mexicana var. *mexicana* (as *P. lindeniana*). Mexico: Chiapas, Siltepec, Cascada, 1600 m a.s.l. E. Matuda no. 5124, 4-3-1945. MEXU

Platanus mexicana var. *mexicana* (as *P. lindeniana*). Mexico: Veracruz, Consolapa, munic. Coatepec, 1250 m a.s.l. S. Avendano R. no. 137, 26-2-1976. MEXU

Platanus mexicana var. *mexicana* (as *P. lindeniana*). Mexico: Puebla, Chila, munic. Honey, 1650 m a.s.l. P. Tenorio L. et al. No. 12515, 23-2-1987. MEXU

Platanus mexicana var. *interior* Nixon & Poole (=*P. mexicana* sensu Moricand?), Mexico: Hidalgo, Xochicoatlán Molango, abundant along the river Chinameca, 1072 m a.s.l. A. May Nah no. AM70, 20-11-1963. MEXU

Platanus mexicana var. *interior* (as *P. lindeniana*). Mexico: Querétaro, Ajuchitlan, 2100 m a.s.l. E. Arguelles s.n. MEXU

Platanus occidentalis L. var. *occidentalis*. Canada: Ontario. E. Wall s.n., 25-5-1902. S

Platanus occidentalis var. *occidentalis*, USA: Lousiana. D. C. Bossert no. 28. MEXU

Platanus occidentalis var. *palmeri* (Kuntze) Nixon & Poole ex Geerinck, USA: Texas. J. M. Poole no. 2521. MEXU

Platanus × *acerifolia* (Ait.) Wild., Bot. Garden. Adler, GUS

Platanus × *acerifolia*. Kungliga Bibliotek, Stockholm, T. Denk, May 2005.

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