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RESEARCH ARTICLE

Structure of the Pollen Exine of *Rhoiptelea chiliantha*

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ABSTRACT: The exine of mature pollen grains of *Rhoiptelea chiliantha* was studied. The size of the pollen grains is about 23 by 27 µm. They are tricolporate with short colpi that are 1-2 µm wide and 10-12 long. The spinules of *Rhoiptelea* are similar in form and size to those of Gentianales. The spinules consist of rods of ca 70 nm in width. These rods are evident throughout the tectum and columellae. The columellae are of two distinct sizes. The smaller ones are ca 70 nm wide and join the tectum and the larger columellae. These larger ones appear to be composed of several 70 nm in width rods. They join the distal surface of the foot layer. The proximal surface of the foot layer is marked by a white line (referred to as a junction plane) where it joins the endexine. The endexine consists of a solid-appearing component adjacent to the foot layer (referred to as endexine-1) and laminar components (endexine-2) that are attached to and apparently become a part of endexine-1. There is no indication of an arcus. In well preserved grains the aperture is covered by an operculum or operculum-like component. In well-rehydrated pollen grains there is an oncus of considerable complexity under the aperture and over the intine. The Ubisch bodies have an exine ornamented with widely-spaced spinules like the spinules on the pollen exine.

KEY WORDS: *Rhoiptelea*, Oncus, Operculum, Columellae, Ubisch bodies (orbicules).

INTRODUCTION

Plants of *Rhoiptelea chiliantha* Diels and Hand., the one extant member of the family Rhoiptelaceae, order Juglandales, were saved from extinction by early cultivation in China, like members of the genera *Ginkgo, Metasequoia, Cercidiphyllum. and Eucommia.*

Muller's (1981) compilation of fossil pollen records related to extant angiospermous families did not include some of the Chinese contributions because these were published after 1980, for example Wang et al. (1995). Song (2000) reported that among them was a second species of the Rhoipteleaceae. The fossil pollen in this family is called *Rhoipteapollis* Zheng 1985 in China (See, Song et al., 1999). The two species, *R. chilianthoides* and *R. triletoides*, were discovered in the Pliocene Santan Formation in continental shelf sediments of the East China Sea, See Wang et al. 1995 and Song, Z. et al. (1999) see also Botanical Review in 2004.

The pollen grains of *Rhoiptelea chiliantha* are very similar to those of the Cretaceous Tertiary extinct Normapolles group (especially the form genus Plicapollis) which comprises pollen with normally three more or less protruding apertures. Batten (1989) points out that the postnormapolles pollen began to appear well before the demise of the Normapolles group and Rhoiptelea like grains have been identified in Maastrichtian and Camparian palynomorph assemblages.

The studies of Skarby (1981) and Friis (1983) showed that pollen of Normapolles type was produced by dicots closely related to the extant order Juglandales, and particularly by *R. chiliantha* Handel-Mazzetti, 1932.

Muller (1984) suggested that the extinct plants producing Normapolles pollen were a group at the family level in the order Juglandales. And Traverse (1988) suggested that "One extant juglandalean genus, *Rhoiptelea*, family Rhoipteleaceae, makes pollen very similar to Normapolles".

As Batten (1989) noted the morphology of 'Normapolles plants' must have been replaced by other species which retained structural characters of their predecessors. The architecture of their pollen, as Batten (1989) reported, is broadly comparable with the pollen grains of Betulaceae, Casuarinaceae, Juglandaceae, Myricaceae and particularly with the Rhoipteleaceae. On the basis of the total list of characters including the structure of the exine, polar and aperture features, Batten (1989) proposed that at least two of these families, the Juglandaceae and Rhoipteleaceae, are probably derived from 'Normapolles ancestors'.

Erdtman (1954, 1971) had suggested that pollen grains of *Rhoiptelea* are to some extent similar to certain pollen types in Betulaceae. A possible relationship between *Rhoiptelea* and the Betulaceae was discussed by Hjelmqvist (1948). Erdtman (1971) noted that the pollen grains in Juglandaceae have several characters also in common with those of Betulaceae, Casuarinaceae, Myricaceae and Rhoipteleaceae. The purpose of this work is to study the exine of mainly mature pollen but also some immature grains of *Rhoiptelea chiliantha.*

MATERIALS AND METHODS

Air-dried anthers of *Rhoiptelea chiliantha* were obtained from herbarium sheets at the Swedish Museum of Natural History, Stockholm. Pollen grains from these anthers were prepared for Scanning Electron Micrography (SEM), see Fig. 1A; and Light Micrographs, see Figs. 1B-E.

For Tranmission Electron Micrography (TEM) the anthers were treated as follows:

1) Anthers were placed in a mixture of 1% lanthanum nitrate in 1 M sodium cacodylate (pH 8, 20℃, 24 h) and then transferred to 2% OsO_4 for 1 h. The material was dehydrated rapidly in an acetone series (total time 10 min). Embedding was in Mollenhauer's (1964) Epon-Araldite mixture No. 3.
2) Anthers were acetolyzed for 4 min (Erdtman, 1960). Water-washed exines were treated in one of two ways.
   a) transferred to 0. 1 M NaOH for 24 h.
   b) transferred to 1% $KMnO_4$ for 24 h.
3) Anthers were left in 0.1 M NaOH for 48h. and then transferred to a mixture of 1 % Alcian blue in 0.1 NaOH for 24 h.
4) Anthers were left in 0.1 M NaOH for 48 h. and then transferred to 1% ruthenium red in 1 M sodium cacodylate (pH 8, 24 h). They were then placed into 2% OsO_4 plus 1% ruthenium red in 0.1 M sodium cacodylate buffer (pH 8, 20℃, 1 h).
5) Anthers were placed in 1% $KMnO_4$ in 0.1 M NaOH for 48 h.

All exines were dehydrated and embedded as per No. 1.

RESULTS AND DISCUSSION

The pollen grains average in size 23 x 27 µm according to Stone and Broome (1971) and 23.5 x 28 µm in Erdtman (1971). These dimensions agree well with our pollen grains taken from herbarium material (Figs. 1A, C-E). The grains are tricolporate, with short colpi (in our dry material colpi are 1-2 µm in width and 10-12 times longer in length than width). Erdtman called them "brevicolpate" (see Fig. 1A).

The tectum is thick, Stone and Broome (1971) cited a thickness of 0.69 µm which is a good average for our material where exines appear to be sectioned transversely. However, many of our illustrations have been sectioned at least somewhat obliquely (Figs. 2A, 2B & 3B). The foot layer is also quite variable in thickness in our sections due to our selection of oblique sections in order to illustrate various aspects of, for example, columellae and spinules (Figs. 2A & 6A).

The apertures

It has often been written that pollen morphology alone may not be credited with information about family relationships. This has been well noted in the case of *Rhoiptelea* by Stone and Broome (1971) and Batten (1989). Stone and Broome and especially Batten have given special attention to the apertures which in *Rhoiptelea* are of the same type as those of Normapolles pollen.

Traverse (1988) noted that the pore structure of Normapolles has been considered to be internally complex. However the photomicrographs of Skarby (1968) clearly show apertural components. In addition our transmission electron micrographs (TEMs) of thin sections of Normapolles pollen have shown apertural structure in considerable detail (Skarby et al., 1990). From these observations it is clear that the Normapolles and *Rhoiptelea* apertures may be regarded as comparatively simple (e.g. Figs. 2B & 6A).

Structure and form of the tectum

As seen in Figs. 4A & B the microchannels in the tecturm are ca 70 nm in width. That is the diameter of the rods of the exine (e.g., the small columellae in Figs. 4A & B). The special features of the tecturn of *Rhoiptelea* pollen are the claw-shaped section of the tectum at the aperture and the shape and size of the spinules. The claw shape of aperture components in sections and the parallel with their equatorial structures are comparable with the other amentiferous orders.

Spinules as a special feature of Rhoipteleaceae

The spinules have a broad base as seen in Figs. 3A & 4A in an oblique section. The tip of sections is ca 70 nm in diameter (see circled site with arrow on Fig. 4A). Based upon the arrangement of spinules (in for example Fig. 1A) and microchannels in (for example Fig. 4A) it may be concluded that the units of the exine rods are hexagonal packing structures in both cross-section and sideview plane are typical for pollen of Normapolles grains (for example *Trudopollis* in: Batten 1986, and Skarby et al., 1990). The spines, and especially those seen on Ubisch Bodies in Fig. 7, are spaced like those of the Gentianales (Vinckier and Smets, 2002). This serves as further evidence for placing the Rhoipteleaceae in Gentianales rather than one of the other amentiferous orders.

The entire surface of the exine is ornamented by spinules that are four to six per μm^2 the spacing of which is dependent upon the convex and concave aspect of the dehydrated grains (Fig. 1A). In the grains Stone and Broome (1971) studied, the spinules were reported to be four to six spinules per μm^2, that is in agreement with our results

Stone and Broome (1971) also gave attention to the similarity of the arrangement of spinules between *Rhoiptelea* and *Engelhardtia*. The arrangement of spinules is entirely different for pollen of Betulaceae and Casuarina, where spinules are located on low ridges in more or less ordered rows (Erdtman et al., 1963; Takeoka, 1965; Barth, 1965; Coetzee and Praglowski, 1984; Zavada and Dilcher, 1986, and Claugher and Rowley, 1987). In Myricaceae spinules are placed separately, as in *Rhoiptelea.*

The columellae

The columellae are of several distinct diameters. As they come distally from the foot layer and endexine many are ca 0.3-0.4. µm in width but where columellar components become a part of the tecturn. they are much smaller, many of them are only ca 0.07 µm (70 nm) wide. That lesser width is the same as or similar to the 70 nm diameter (size) of exine rods (the basic components of exines, see Structure of collumellae). These ca 70 nm columellae are mostly seen associated with the tectum and a part of the large basal portion of columellae as seen in Figs. 3C & 4B. Some of the ca 70 nm columellae are seen to extend from the tectum to the endexine in Fig. 4B.

The structure of the endexine

The endexine is thin between apertures and enlarges to six or more lamellations in the vicinity of the aperture margins (Fig. 2A). The endexine sends out many strands across the aperture during early and middle development (Figs. 5 & 6).

The absence of arcus in pollen of *Rhoiptelea*

Erdtman (1954, 1971) reported that pairs of "arcus" swing from aperture to aperture in pollen of *Rhoiptelea chiliantha.* The partly collapsed exines in Fig. 1A may suggest the presence of arcus but this is not correct as can be seen in our Figs. 1B, 2A & 6A. If there was an arcus it would be seen as a thickened band of exine that extends in a sweeping curve from one aperture to another. The idea that *R. chiliantha* may have arcus that swing from one aperture to another needs to be corrected.

Structure of columellae and the rods of the exine

As stated above columellae have several distinct diameters. As they come distally from the tectum many are ca 0.07 µm (70 nm) in diameter. Columellae attached to the foot layer tend to be 0.3-0.4 µm. Our interpretation is that the large proximal portion of the columellae consist of several of the 70 nm rods. Thus the rods that are the basis for exine construction are ca 70 nm in diameter (for example Fig. 4A) and have a central (core zone) that is ca 40 nm in diameter. In other plants the core zone of the exine rods include protein and carbohydrates that are strongly contrasted by many stains used in TEM preparations. That is the case here in Fig. 4A where each exine unit (microchannel) has a dark core zone and most importantly small columellae (ca 70 nm in diameter) at the base of the tectum show a central dark core (four of these are circled and marked with a arrowhead).

According to the work of Rowley and Prijanto (1977) sporopollenin does not react with any of the stains currently used for TEM work. There is not contrast in pure sporopolleninous material, like the uncontrasted outer part of the rods in Fig. 4A. The contrast seen in sections of exines is due to material within exines along with sporopollenin, most specially within the core zone of exine units.

Ubisch bodies (orbicules)

Ubisch bodies, sometimes called orbicules, are shown for *Rhoiptelea* in Fig. 7. They have been appreciated as similar to exine spinules since Rowley et al. (1959) and Rowley and Prjanto (1977) and with many more well documented examples by Huysmans et al. (1998). The spinules on Ubisch bodies of *Rhoiptelea* are few and have a broad base like the spinules on the exine. These spinules are similar to those illustrated in Gentianales by Vinckier and Smets (2003).

There is some evidence suggesting that Ubisch bodies may be a primitive feature since they are recorded by Taylor and Alvin (1984), Osborn et al. (1991) and others from Mesozoic material.

Wang et al. (2003) found that Ubisch bodies of several monocot species carry a sporophytically produced structural protein (RAFTIN) that is essential for pollen development. As far as we know; comparable studies have not been done with dicotyledonous pollen. The specific nature of Ubisch bodies for some monocotydonous pollen indicate that Ubisch bodies take part in some substantial role in pollen development.

Fossil evidence

Song, et al. (1999) in their paper the "Fossil pollen records of extant anglosperms in China" called the fossil pollen in the Rhoipteleaceae *Rhoipteapollis* (Zheng 1985) in China. Two species, *R. chilianthoides* (pl. 140, Fig. 10) and *R. triletoides* (pl. 140, Fig. 9), were discovered in the Pliocene Santan Formation of the continental shelf of the East China Sea. See The Botanical Review (2004) 70: 425-458.

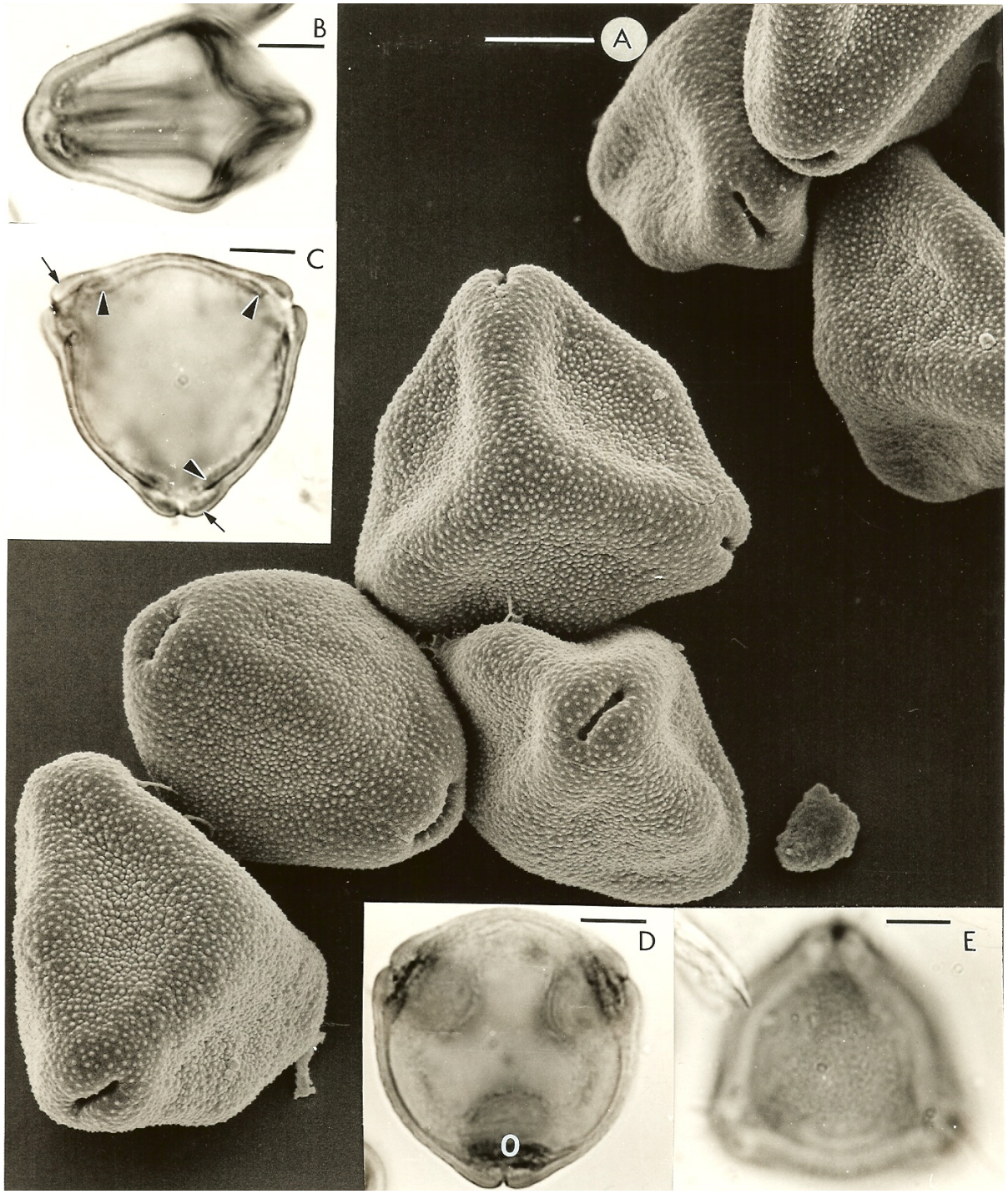

Fig. 1. A Scanning Electron Micrograph (SEM) and four Light Micrographs of *Rhoiptelea chiliantha* pollen grains. A: The SEM illustrates the general shape as seen from different angles of the pollen grains. The spacing and spinule arrangement and the shape of the colpi are shown in dehydrated (dry) pollen grains that are to some extent collapsed. Bar = 5 μm. B: A polar section of a collapsed grain showing that there are no indications of an arcus. Bar = 5 μm. C: A medial section of an expanded pollen grain showing the slight protrusions of the ectoapertures (arrow). The non-protruding endoapertures are marked by arrowheads. Bar = 5 μm. D: An equatorially sectioned grain showing a darkened oncus below each aperture (one is marked by a white O). See the oncus in Fig. 2B. Bar = 5 μm. E: Superficial section of the pollen grain showing the way spinules appear light microscopically. Bar = 5 μm.

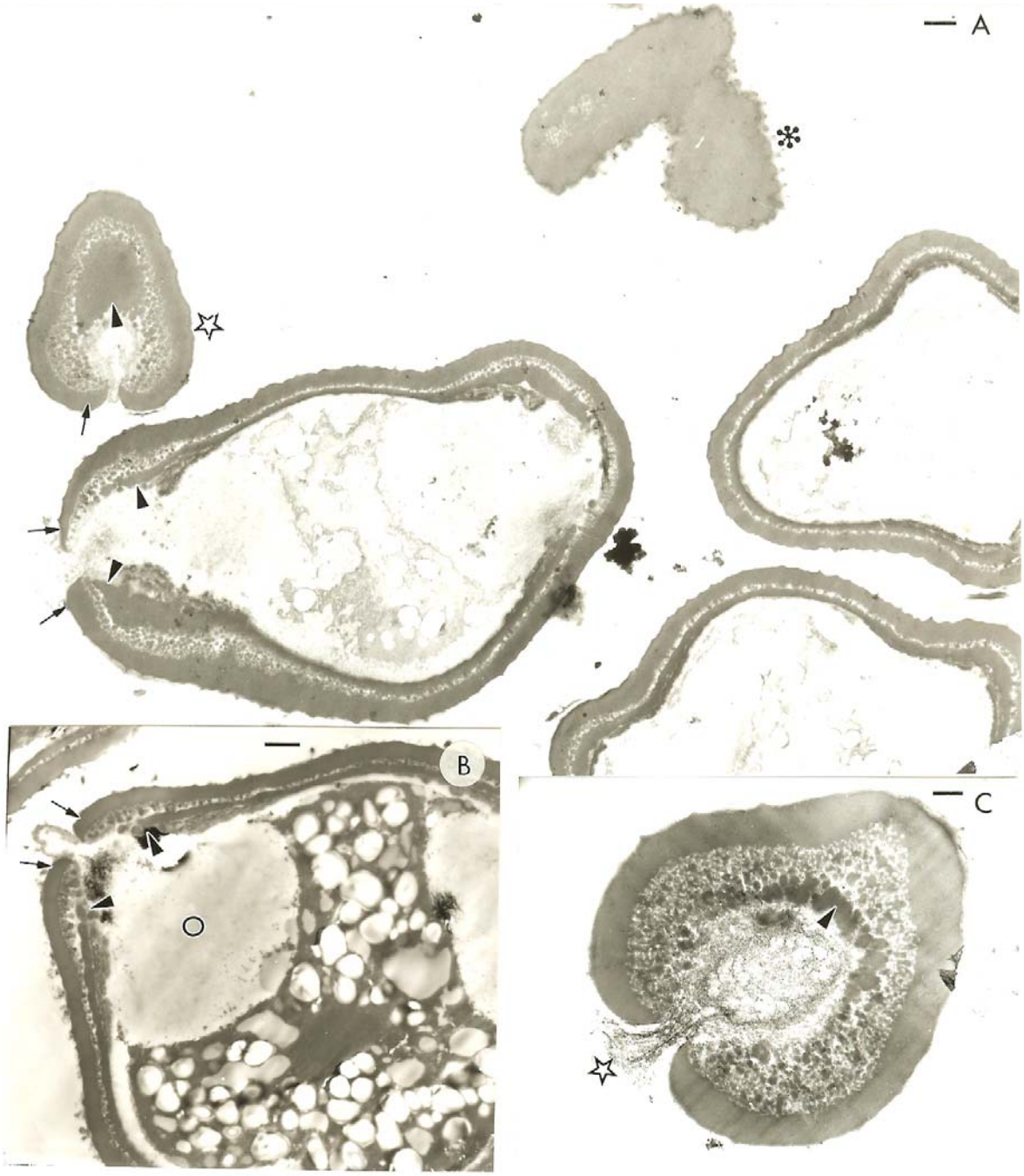

Fig. 2. Transmission electron micrograph (TEM) sections showing apertures, spacing of spinules, presence of onci and opercula in apertural regions. A & B: The apertures in these sections show several of the typical forms of the *Rhoiptelea* pollen ectoapertures (arrows) and endoapertures (arrowheads), depending on planes of sectioning. The surface of the section marked by an Asterisk illustrates the wide and uniform separation of the spinules. The oblique section marked by a star shows the typical "crow foot" arrangement of an *Rhoiptelea* ectoaperture. Also in this very oblique section the endoaperture is seen as a broad sheet (arrowhead). The sections show that the foot layer and endexine are thin except near the apertures. Bars = 1 µm. B: This rehydrated grain shows the large oncus region (O). The ectoaperture is marked by arrows and the endoapertue by arrowheads. The loop over the ectoaperture (between arrows) is part of an operculum. Bar = 1 µm. C: In this oblique section there are components of an operculum (star) between the "crow foot" shaped aperture. Components of the endoaperture and endexine (arrowhead) form a halo some distance from the ectoaperture. Bar = 1 µm.

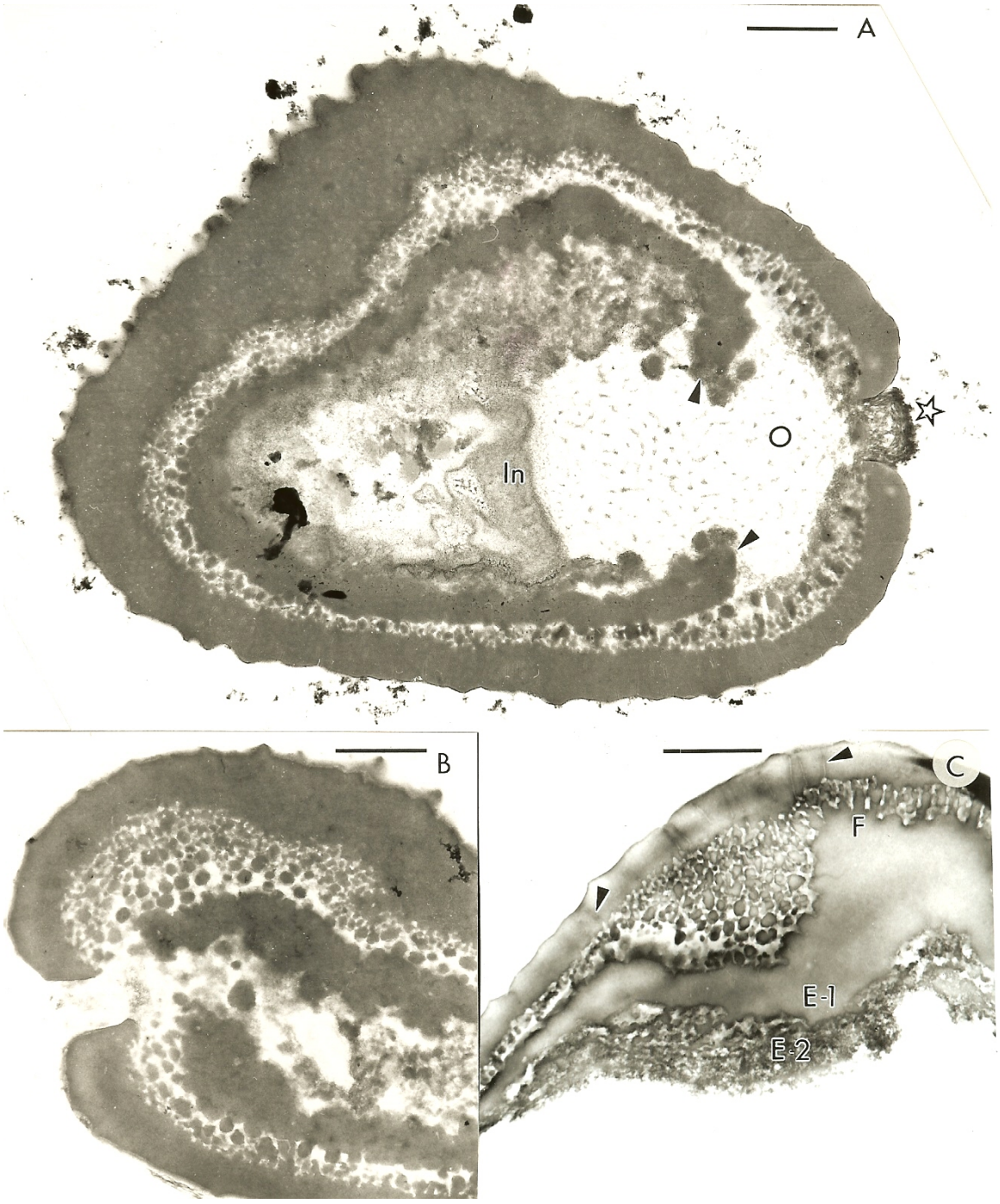

Fig. 3. TEM sections illustrating spinules, micro- channels, oncus and operculum. A: The section is strongly oblique at the left side where the microchannels and columellae are oblong or circular (see enlargment in Fig. 4A). The right side, however, is cut transversly with columellae as radial rods. The operculum (star) covers the ectoaperture. The oncus (O) is associated with columellae, endexine (endoaperture, arrowheads) and intine (In). Bar = 5 μm. B: Oblique section of an aperture showing the extreme hook at the aperture margins. The section shows the circular outline of the small and large columellae (rods). Bar = 5 μm. C: The tectum is sectioned transversally resulting in some micro- channels (arrowheads) running laterally across the tectum. The exine is somewhat infolded resulting in a thickened foot layer (F) and endexine (E-1) to the right and a circular exposure of columellae to the left. The inner portion of the endexine (E-2) appears to have many laminar components. A section such as this one could occur in one of the enfolded grains in Fig. 1A. Bar = 1 μm.

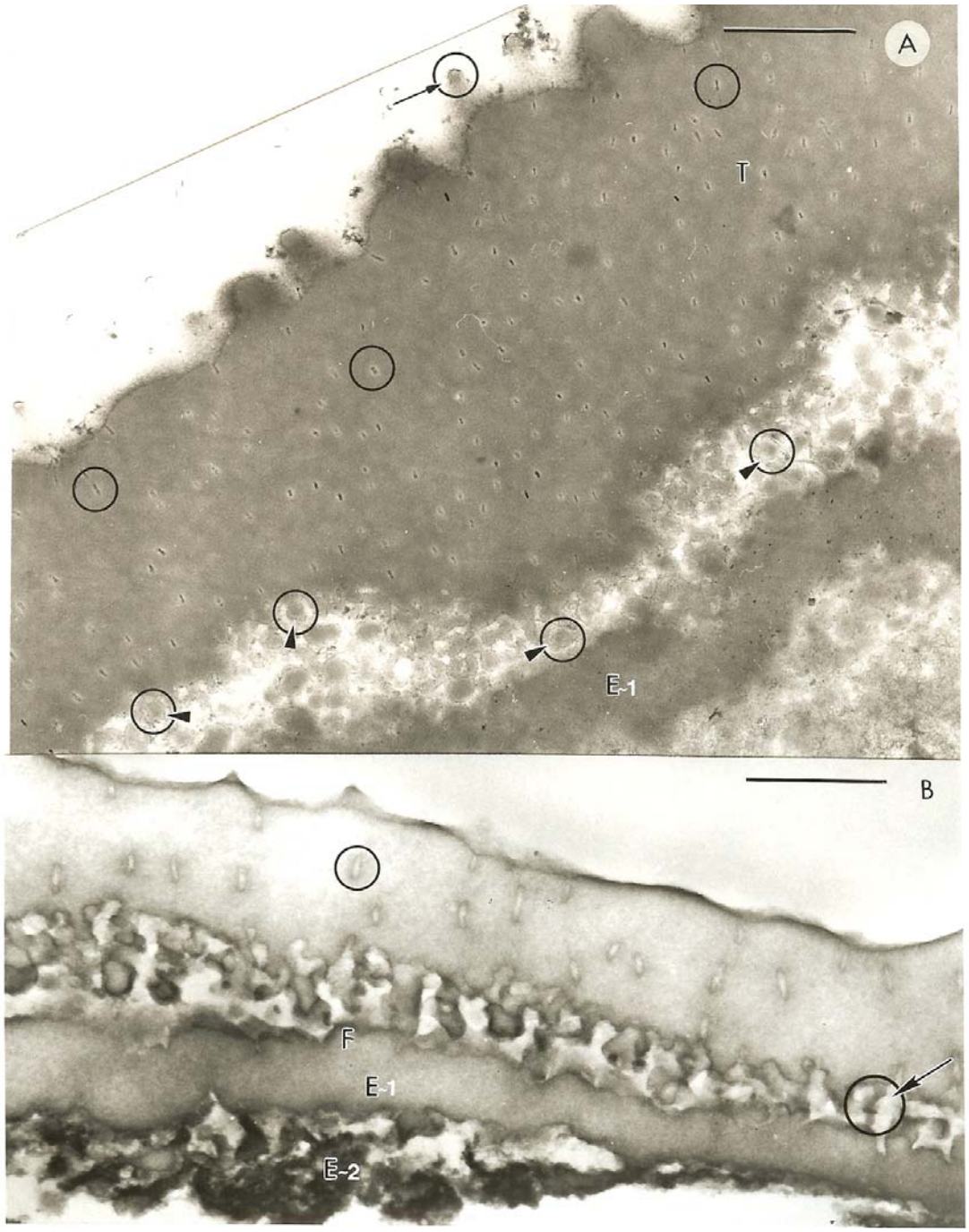

Fig. 4. TEM sections showing spinules, microchannels, columellae and foot layer and endexine. A: The section is an enlargement of Fig. 3A. There are many microchannels in the tectum (T) and each one has a dark core (see No. 4 in Material & Methods) and is surrounded by a clear zone (three are circled). The clear zone is an exine unit (a rod composed of sporopollenin). Both the rod and its core are somewhat elliptical due to the oblique TEM section. One of the spinules shows a summit of a spinule (circled with arrow) with a rod like those in microchannels and in the small columellae. The small columellae have a dark center surrounded by a clear zone (four are circled with an arrowhead). The endexine-1 is marked (E-1). Bar = 0.5 µm. B: The tectum is sectioned somewhat obliquely and as a result microchannels are eliptal (one is circled). These microchannels are similar in width (ca 70 nm) to the diameter of the small columellae connected to the tectum (one is circled with arrow). The microchannels do not have a darkened core, as in Fig. A above, because core subunits were not stained. The foot layer (F) and solid and laminated endexine are marked (E-1 & E-2). Bar = 0.5 µm.

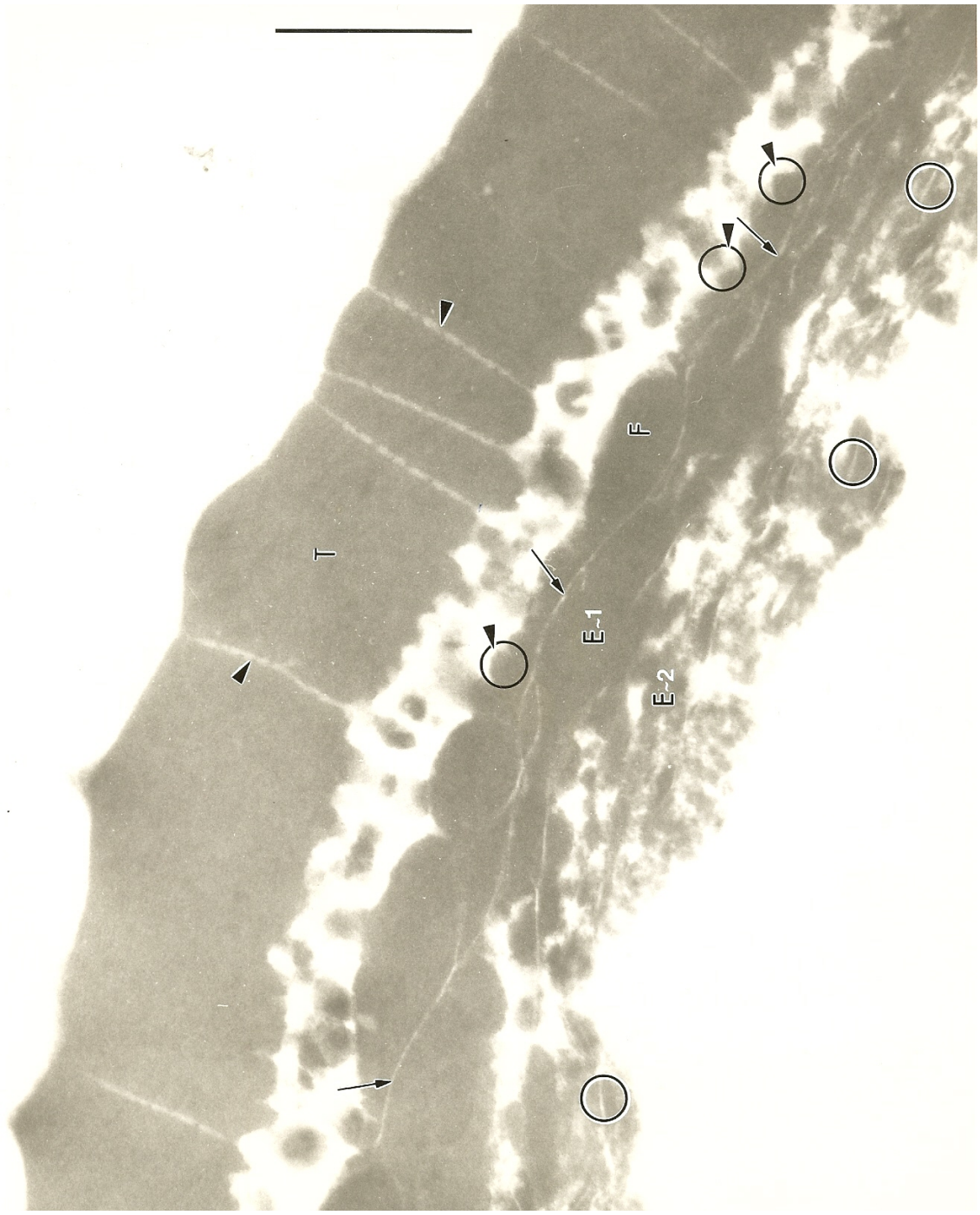

Fig. 5. TEM section with emphasis upon tectum, foot layer and endexine. A: The section is cut transversally showing the radially orientated microchannels (arrowheads) across the tectum (T). The section is thinner than the diameter of most columellae so that many columellae do not appear to be intact and for the same reason only a few microchannels are shown in their whole length in this thin section. An indication of the frequency of microchannels is seen in the section in Fig. 4A. The outer surface of the foot layer (F) has had columellar attachments and is distinctly lobed i.e., the bases of columellae (three lobes are circled with attached arrowheads). The section stain used for this figure (No. 4 in Material and Methods) emphasizes the microchannels in the tectum and white lines in the endexine. The outer white line is at the junction (arrows) between the foot layer (F) and solid endexine (E-1). Other white lines occur within the solid part of the endexine and lamellar parts of the endexine (E-2, three are circled). Bar = 0.1 μm.

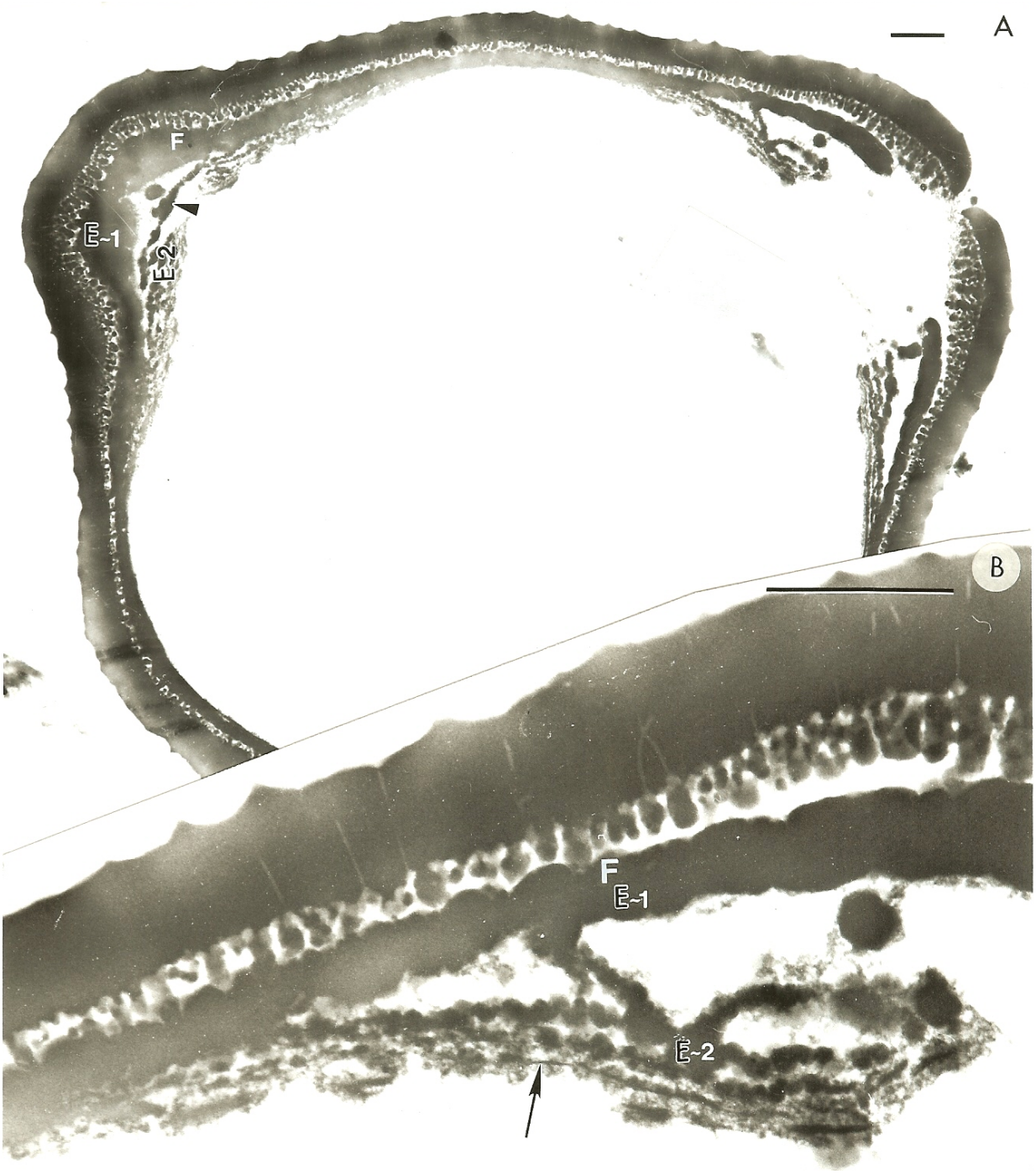

Fig. 6. A-B. TEM sections featuring endexine lamellae in the aperture regions. A: The greatly thickened tectum foot layer (F) and endexine-1 (E-1) is emphasised at the margin of the unopened aperture at the left. One of the endexine-2 (E-2) lamellae is continuous (arrowhead) across the future colpus. A&B: Section B can be seen to be an enlargement of the aperture to the right of fig. A. The lamellar components of endexine-2 can be seen to join the foot layer (F) and the solid endexine-1. The lower lamellae in Fig. B can be seen to have a slender rod.like core (arrow) which we consider to be a major part of the endexine. Bars = 1 μm.

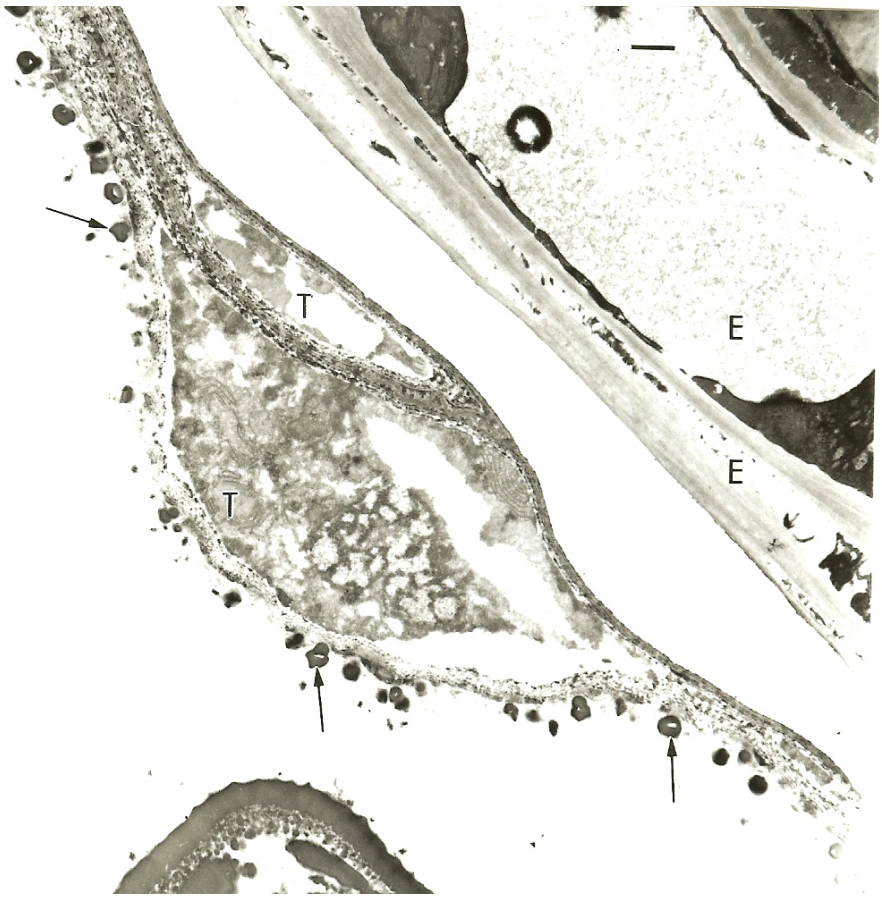

Fig. 7. TEM section of tapetal cells (T) outlined by Ubisch bodies (arrows) adjacent to a small part of a pollen grain. The tapetal cells are separated in this from endothecial cells (E) of the anther wall. The Ubisch bodies show the same wide spaceing between spinules that is evident for the exine of the pollen. Bar = 1 μm.

Speculations about relationship

Since the description by Handel-Mazzetti (1932) of *Rhoiptelea chiliantha* as a species of a new family, the Rhoipteleaceae, there have been speculations about the relationship of this monotypic plant. Krutzsch (1966) and Skarby (1968) have suggested that some representatives of the Normapolles complex, notably *Plicapollis* may be ancestral to *Rhoiptelea.* (Muller, 1981). It has often been written that pollen morphology alone may not be credited with information about family relationships. This has been well noted in the case of *Rhoiptelea* by Stone and Broome (1971) and Batten (1989). Stone and Broome and especially Batten have given special attention to the apertures which in *Rhoiptelea* are similar to those of Normapolles pollen. But as Stone and Broome (1971) have written, the pollen alone does not provide unequivocal evidence for placing the Rhoipteleaceae in one or the other of the amentiferous orders. Shi (1982) provides further information on Rhoipteleaceae in the anglosperm pollen flora of Tropic and Subtropic China.

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LITERATURE CITED

Barth, O. M. 1965. Glossario palynologico. Mem. Inst. Oswaldo Cruz. **63**: 133-161.

Batten, D. J. 1986. Possible functional implications of exine sculpture and architecture in some Late Cretaceous Normapolles pollen. In: Blackmore, S. and I. K. Ferguson (eds.). Pollen and Spores, Form and Function. Published for Linnean Society of London. by Academic Press, London, UK. 443pp.

Batten, D. J. 1989. Systematic relationships between Normapolles pollen and the Hamamelidae. In: Crane, P. R. and S. Blackmore (eds.). Evolution, Systematics, and Fossil History of the Hamamelidae. Volume 2. 'Higher' Hamamelidae. The Systematics Association Special Volume No. 40B. Clarendon Press, Oxford, UK. 591pp.

Claugher, D. and J. R. Rowley. 1087. Betula pollen grain substructure revealed by fast atom etching. Pollen et Spores. **29**: 5-20.

Coetzee, J. A. and J. Praglowski. 1984. Pollen evidence for the occurrence of Casuarina and Myrica in the Tertiary of South Africa. Grana **23**: 23-41.

Erdtman, G. 1943. An introduction to pollen analysis. The Ronald press Co., New York, USA. 239pp.

Erdtman, G. 1960. The acetolysis technique - a revised description. Sven. Bot. Tidskr. **54**: 561-564.

Erdtman, G. 1966. Pollen morphology and plant morphology. Angiosperms. Hafner Publ Co., New York, USA. pp. 553.

Erdtman, G. 1971. Pollen Morphology and Plant Taxonomy - Angiosperms, (Corrected reprint of the 1952 edition). Hafner Publ. Co., New York, USA. 553pp.

Erdtman, G., J. Praglowski and M. Takeoka. 1962. Zur Bedeutung der Pollenmorphologie für die pollenanalytische Vegetationsforschung. Veroff. Geobot. Inst. Rübel, **37**: 57-59.

Friis, E. M. 1983. Upper Cretaceous (Senonian) floral structures of Juglandalean affinity containing Normapolles pollen. Review of Palaeobotany and Palybnology. **39**: 161-188.

Handel-Mazzetti, H. 1932, Rhoipteleaceae, eine neue Familie der Monochlamydeen.Repert. Spec. Nov. Veg. **30**: 75-80.

Hjelmqvist, H. 1948. Studies on the floral morphology and phylogeny of the Amentiferae. Bot. Notiser, Suppl. **2**: 1.

Huysmans, S., G, EI-Ghazaly and E. Smets. 1998. Orbicules in Angiosperms.Morphology, function, distribution, and relation with tapetum types. Bot. Rev. (Lancaster) **64**: 240-272.

Krutzsch, W. 1966. Die sporenstratigraphische Gliederung der Oberkreide im nördlichen Mitteleuropa. Abh. Zentr. Geol. Inst. **8**: 79-111.

Manning, W. E. 1961. Juglandales. In: Ency. Biol. Sci., - Reinhold Pub. Corp., New York, USA. pp. 528-529.

Mollenhauer, H. H. 1964. Plastic embedding mixtures for use in electron microscopy. Stain Technol. **39**: 111-115.

Muller, J. 1970. Palynological evidence on early differentiation of angiosperms. Biological Review of Cambridge Philosophical Society **45**: 417-450.

Muller, J. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. **47**: 1- 142.

Muller, J. 1984. Significance of fossil pollen for angiosperm history, Ann. Missouri Bot.Gard. **71**: 419-443.

Osborn, J. M., T. N. Taylor and P. R. Crane. 1991. The ultrastructure of *Sahnia* pollen (Pentoxylales). Am. J, Bot. **78**: 1560-1569.

Punt, W., S. Blackmore, S. Nilsson and A. Le Thomas. 1994. Glossary of Pollen and Spore Terminology. LPP Foundation, Utrecht, The Netherlands. 71pp.

Rowley, J. R., K. Mohlethaler and A. Frey-Wyssling. 1959. A route for the transfer of materials thrugh the pollen grain wall. J. of Biophy. and Biochem. Cytol. **6**: 537-538.

Rowley, J. R. and B. Prijanto. 1977. Selective destruction of the exine of pollen grains. Geophytol. **7**: 1-23.

Shi, Y.-C. 1982. Rhoipteleaceae. In: Angiosperm pollen flora of tropic and subtropic China. Inst. Bot. South China, Taipei, Taiwan. pp. 352-353.

Skarby, A. 1968. *Extratriporopollenites* (Pflug) emend. from the Upper Cretaceous of Scania. Sweden. Stockholm Contributions in Geology **16**: 1-60, 30 plates.

Skarby, A. 1981. Upper Cretaceous Normapolles anthers, S. Sweden. 13th Int. Bot. Congr. Sydney, Australia, Abstracts, p. 193.

Skarby, A., J. R. Rowley and L. Nilsson. 1990. Exine structure of upper Cretaceous Normapolles grains from anthers (Northeastern Scania, Sweden). Palynol. **14**: 145-173.

Song, Z. 2000. On the first occurrence and flourish of some fossil anglosperm shrub and herb pollen in China and their significance. 138-150. In: Sping. Z (ed.), Palynofloras and palynornorphs of China. Song. Z. (ed.), China Press of University *of* Science and Technology of China, Hefei. In: The Botanical Review (2004) **70**: 425-458.

Song, Z., Y. Zheng, M. Li, Y. Zhang, W. Wang, D. Wang, C. Zhao, S. Zhou, Z. Zhu and Y. Zhao. 1999. Fossil spores and pollen of China. Vol. 1. Late Cretaceous and Tertiary spores and pollen. Science Press, Beijing (in Chinese; English summary). In: The Botanical Review (2004) **70**: 425-458.

Stone, D. E., J. Reich and S. Whitfield. 1964. Fine structure *of* the walls of *Juglans* and *Carya* pollen. Pollen et Spores **6**: 379-392.

Stone, D. E. and C. R. Broome. 1971. Pollen ultrastructure: evidence for relationships of the Jaglandaceae and the Rholpteleaceae. Pollen et Spores **13**: 5-14.

Taylor, T. N. and K. L. Alvin. 1984. Ultrastructure and development of Mesozoic pollen of Classopollis. Amer. Journ. Bot. **71**: 575-587.

Takeoka, H. 1965. Electron microscopic investigations on the surface structure of the pollen membrane of trees. Sci. Reports Kyoto Univ. Agriculture. **17**: 43-69.

Traverse, A. 1988. Paleopalynology. Unwin Hyman, Boston, pp. 600.

Vinckier, S. and E. Smets. 2003. Systematic importance of orbicule diversity in Gentianales. Grana **41**: 158-182.

Wang, A., W. Qun Xia, Xie, R. Datla and G. Selvara. 2003. The classical Ubisch bodies carry a sporophytically produced structural protein (RAFTIN) that is essential for pollen development. Proc. Natl. Acad. Sci. U.S.A. **100**: 14487-14492.

Wang, F., N. Chien, Y. Zhang and H. Yang. 1995. Pollen flora of China. 2nd ed. Science Press, Beijing (in Chinese). In: The Botanical Review (2004) **70**: 425-458.

Zavada, M. S. and D. L. Dilcher. 1986. Comparative pollen morphology and its relationship to phylogeny of pollen in the Hamamelidae. Ann. Missouri Bot. Gard. **73**: 348-381.

馬尾樹花粉外壁構造的研究

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摘要：本文主要描述馬尾樹 (*Rhoiptelea chiliantha*) 成熟花粉粒的外壁構造。成熟花粉粒大小約 23-27 μm、三溝孔、具短溝、寬約 1-2 μm、長約 10-12 μm。馬尾樹花粉粒上的小刺 (spinules) 形狀與大小和一些龍膽目 (Gentianales)植物的花粉粒很相似，小刺是由寬約 70 nm 的棒狀物所組成。這些棒狀物明顯地分佈在蓋頂層 (tectum) 及柱狀層 (columellae) 各處。柱狀層中有兩種大小不同的柱狀體，較小的寬約 70 nm 連接蓋頂層和較大的柱狀體，而較大的柱狀體是由多個寬 70 nm 的棒狀物所組成的，它們會和基層 (foot layer) 末端相連，而基層頂端表面有著明顯分佈的白線 (white line)特徵，就好像是它與外壁內層 (endexine) 的接合面 (junction plane)。外壁內層有兩種組成，鄰近基層的實心組成為 endexine-1，另一則為片狀 endexine-2，它會與外層連接進而成為其 endexine-1 的一部份。沒有觀察到明顯的 arcus 存在。在保存良好的花粉粒上可觀察到花粉孔被孔蓋或似孔蓋物所覆蓋。而水合後的花粉粒會在萌芽孔下方、內壁上方隆起許多複雜的脊狀物 (oncus)。烏氏體 (Ubisch bodies) 上廣泛分佈著類似花粉外壁上的小刺狀裝飾物。

關鍵詞：馬尾樹屬、瘤狀物、孔蓋、柱狀層、烏氏體 (顆粒體)。