ULTRASTRUCTURE OF SOME PERMIAN POLLEN GRAINS FROM THE RUSSIAN PLATFORM

N. E. Zavialova, N. R. Meyer-Melikian, and A. V. Gomankov

Abstract

Dispersed pollen grains from the Upper Tatarian of the Russian platform have been studied using LM, SEM and TEM. Saccate pollen grains assigned to *Vesicaspora* and *Protohaploxypinus* (of possible peltaspermous affinity) are characterized by a regular alveolate ectexine in the region of the cappa, by a thin homogeneous ectexine at the apertural area, and by a fine-grained endexine and protosaccus. The protosaccoid appearance of pollen grains may be the result of preservational flattening of the pollen. Protobisaccate pollen assigned to *Piceapollenites,* which could also be produced by peltasperms, is divided into two groups based on ultrastructure: (I) a group with granulous ectexine, and (П) a group with a faint alveolate ectexine. The sporoderm of asaccate monosulcate pollen assigned to *Cycadopites* (possibly Leptostrobales or Ginkgoales) consists of only ectexine which becomes thinner in the apertural region. Asaccate ovoid pollen with four furrows, assigned to *Mulinopollenites* (unknown affinity), has some similarities with *Eucommiites* and *Praecolpatites.* Basic structural elements of the sporoderm (attributed to different representatives of seed ferns) and their possible development within more specialized lines of the seed plants are discussed.

INTRODUCTION

The Upper Tatarian flora of the Russian platform has attracted the attention of palaeobotanists for a long time (Gomankov and Meyen, 1986). Dominated by the peltasperms, it formed an ecotone between tropical Euramevian and boreal Angara floras and was at the same time a phylogenetic source of many typical Mesozoic groups of plants (e.g., Ginkgoales). However, this key evolutionary position of the flora, revealed mostly from plant megafossils, needs to be elucidated in palynological terms. The pollen grains dominating the assemblages of dispersed miospores from the Upper Tatarian of the Russian platform were for a long time morphologically and taxonomically interpreted as the bisaccate pollen of conifers (e.g. Efremova, 1966; Sivertseva, 1966). Other authors attributed them to the pteridosperms (Gomankov and Meyen, 1980, 1986; Gomankov, 1986; Esaulova, 1986), which provoked a set of morphological questions which can be solved by means of electronic microscopy. The principal questions can be formulated as following:

1. Are these pollen grains protosaccate or eusaccate?
2. If they are protosaccate, then how significantly different were they from the asaccate *Vittatina-like* pollen grains, which were also produced by the Upper Tatarian peltasperms (Gomankov and Meyen, 1986; Gomankov, 1986)?
3. Are there any ultrastructural features that can be considered as common for the family Peltaspermaceae, for the order Peltaspermales, or for the class Ginkgoopsida *(sensu* Meyen, 1987)?

The last question focuses attention onto an interesting type of pollen grains from the Upper Tatarian of the Russian platform, i.e. the asaccate and colpate pollen. Usually referred to as "ginkgocycadophytes," it was most probably produced by arising "Mesozoic" taxa such as the Ginkgoales or the Leptostrobales *(sensu* Meyen, 1987) and certainly merits an ultrastructural investigation in comparison with the later representatives of these taxa (Zavialova, 1998).

Five genera were selected for the present study. Three of them *(Vesicaspora, Protohaploxypinus* and *Piceapollenites)* are saccate and belong to different groups of peltasperms (Cardiolepidaceae, Peltaspermaceae, and an uncertain family, respectively). Two other genera *(Cycadopites* and *Mulinopollenites)* possess colpi but are deprived of sacci. The first of these genera could be the initial candidate for being a pollen of "youthful" Ginkgoales or Leptostrobales (Gomankov, 1986), while the natural affinity of the second genus is enigmatic; the external morphology of *Mulinopollenites* resembles pollen grains of *Ephedra* or even the angiosperms (which is quite incredible in the Permian), but the need for the scrupulous investigation of its colpi was stated (Gomankov, 1996) in the first description of the genus.

All the material investigated comes from a single palynological sample collected on the right bank of the Vyatka River near the village of Mulino (Kirovskaya region, Russia). This outcrop is incorporated into the stratotype of the Vyatsky horizon of the Upper Tatarian (Upper Permian) and yields abundant, diverse and well-preserved palynomorphs, as well as plant megafossils and remains of vertebrates (Gomankov, 1997; Gomankov et al., 1998). The assemblages of both plant megafossils and palynomorphs (for which the age could be precisely determined due to the position of the locality in the type section of the Tatarian) were recently described by A. V. Gomankov (1996).

MATERIAL AND METHODS

The pollen grains were macerated by standard methods (Rybakova and Smirnova, 1988). Selected pollen grains were mounted in glycerine jelly for examination with transmitted light. The pollen grains were then mounted onto standard SEM stubs, coated with approximately 200 A of gold-palladium and examined with a Hitachi S-405A SEM. For transmission electron microscopy, individual pollen grains were picked from the SEM stubs with a needle, placed in the capsule and embedded in epon (Meyer-

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Melikian and Telnova, 1991). The pollen grains were sectioned by ultramicrotome with a diamond knife and examined using a Hitachi H-600 transmission electron microscope.

DESCRIPTIONS AND COMPARISONS

Vesicaspora

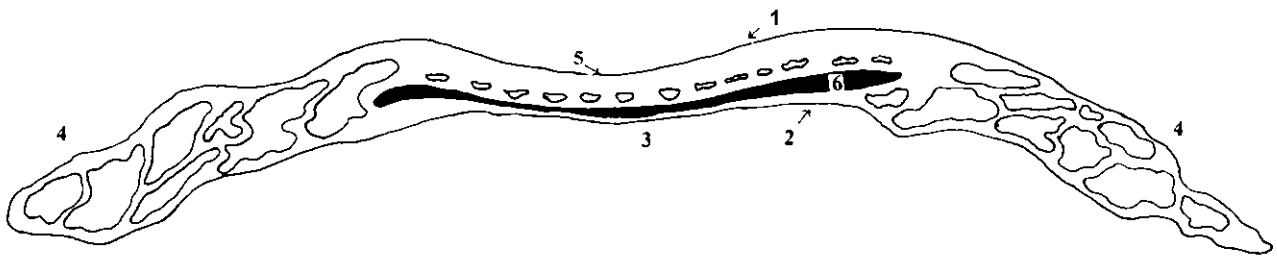
The genus *Vesicaspora* was established by M. P. Schemel (1951) for monosaccate pollen grains from the Pennsylvanian of Iowa. The majority of representatives of the genus found in the Tatarian of the Russian platform are usually identified as *Vesicaspora ex gr. magnalis* (Andreyeva) Hart, which is interpreted as a plexus of three species — *V. magnalis* (Andreyeva) Hart, *V. ovata* (Balme & Hennelly) Hart, and *V. potoniei* (Lakhanpal, Sah & Dube) Hart — with the differences among the three species still remaining rather indefinite (Gomankov and Meyen, 1980). Besides dispersed pollen grains, similar forms were extracted from sporangia of *Permotheca vesicasporoides* S. Meyen, Esaulova & Gomankov, a synangiate organ of peltaspermaceous affinity (Gomankov and Meyen, 1986; Esaulova, 1986).

The dispersed pollen grains identified as *Vesicaspora ex gr. magnalis* are bilaterally symmetrical and monosulcate. In transmitted light they usually appear bisaccate but the examination of a number of specimens (Gomankov and Meyen, 1980) revealed that the grains are monosaccate with a central body surrounded by a bilobed saccus. This observation was confirmed by the present ultrastructural investigations (see below).

The outline of the pollen grain is almost square. In transmitted light the surface appears reticulate or fine-tubercular near the edge of the sulcus; the sulcus membrane appears smooth (Plate 1, fig. 6). The central body, when seen in polar view, is often surrounded by a dark ring which was referred to as "equatorial cingulum" and regarded as a specific character of *V. magnalis* by G. F. Hart (1965).

In SEM, the surface of the pollen grain appears irregularly pitted-tubercular (Plate 2, fig. 5). The sculpture is most obvious on the surface of the saccus. There is a narrow sulcus in the center of the distal side, and the sulcus often has lacerated margins. The ends are acuminate and poorly defined. The sulcus membrane is comparatively smooth and fine-grained. The breadth of the pollen grain measured by SEM is 20 µm, the length is 24 µm.

Ultra-thin transverse sections through the pollen grains reveal that they are strongly compressed (Text-Figure 1). The sporoderm is about 1.5 µm thick (Plate 2, figs. 1-3). Only rare and small fragments of endexine are preserved. These fragments can be observed in exceptional cases as



Text-Figure 1. Scheme of the section of a compressed *Vesicaspora* pollen grain (in the region of the sulcus). 1, Proximal side; 2, Distal side; 3, Area of sulcus; 4, Saccus with irregular-shaped alveolae; 5, Cappas region; 6, Compressed hollow of the pollen grain.

PLATE 1

Figures 1-8,11,12 are light microscope photographs, x500. Figures 9,10,13 are oblique sections of *Protohaploxypinus*, TEM. x10,000.

1 *Mulinopollenites* (see Plate 5, fig. 1. Surface of the pollen grain).

2 *Mulinopollenites* (see Plate 5, figs. 2, 3. Surface of the furrows).

3 *Cycadopites* (see Plate 5, figs. 5, 6. Transverse section of the pollen grain).

4 *Cycadopites* (see Plate 6, figs. 3,5. Longitudinal section of the pollen grain).

5 *Cycadopites* (see Plate 5, fig. 4. Surface of the pollen grain).

6 *Vesicaspora* (see Plate 2, figs. 1-3,6-7. Transverse section of the pollen grain). Polar view. Note the "equatorial cingulum" visible as a dark ring.

7 *Piceapollenites*, group 2 (see Plate 3, fig. 4 - surface of the pollen grain, Plate 4, fig. 6 - section of the pollen grain). Polar view. Note the fold at the region of corpus.

8 *Piceapollenites*, group 1 (see Plate 3, fig. 3 - surface of the pollen grain, Plate 4, figs. 1-5,7 - longitudinal section of the pollen grain). Polar view.

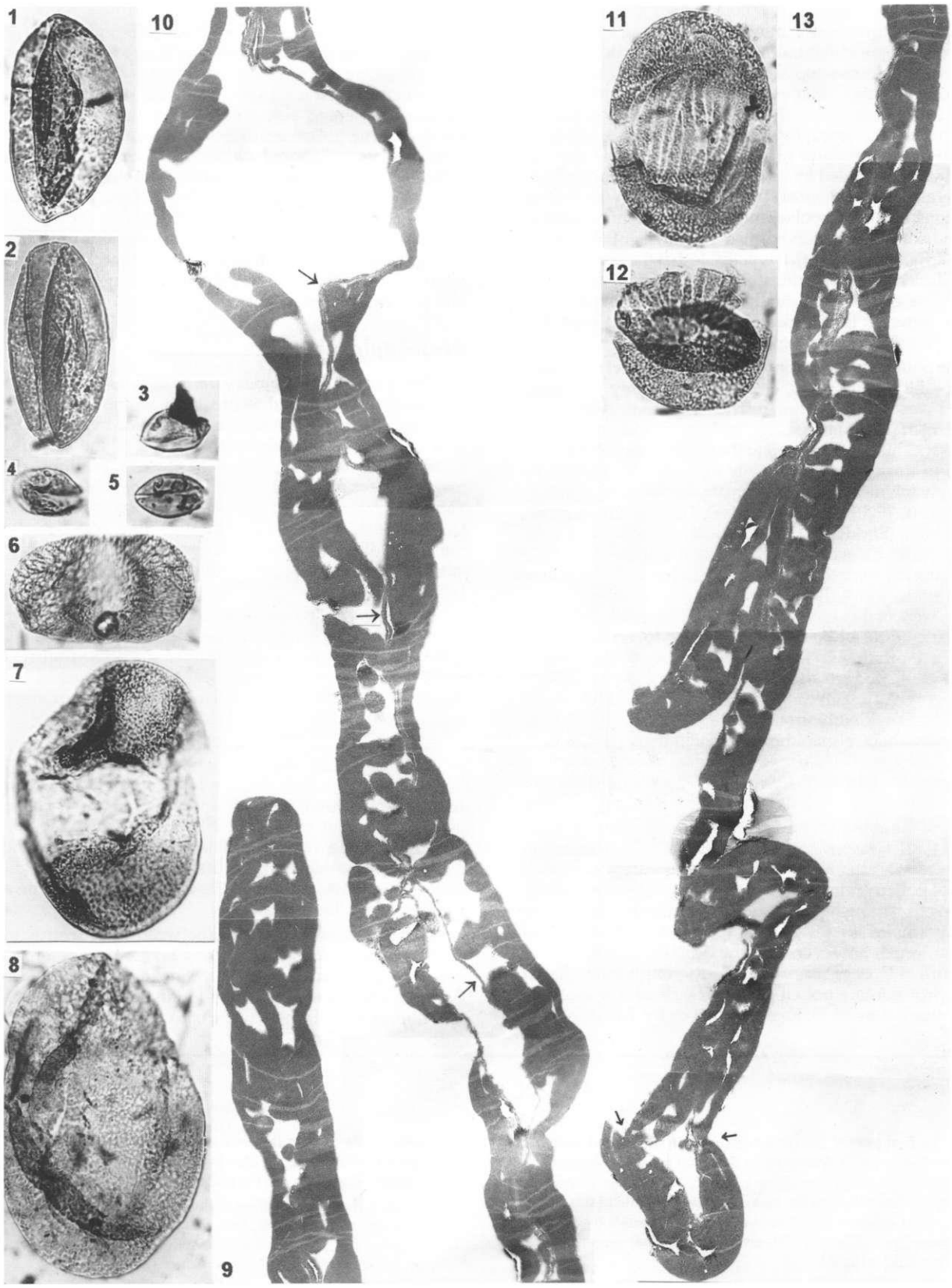
9 The first part of the oblique section of *Protohaploxypin us* (see figs. 10,13). Ultrastructure of the saccus.

10 The middle part of the section (see figs. 9,13). Arrows indicate endexine.

11 Polar view of *Protohaploxypinus* (see Plate 3, fig. 2. Surface of the pollen grain). Note the striate corpus of the pollen grain.

12 Lateral view of *Protohaploxypinus* (see Plate 3, fig. 1. Surface of the pollen grain). Note the striae and reticulations of the saccus.

13 The last part of the section (see figs. 9,10). Proximal side of the pollen grain in the region of cappa. Arrows indicate striae.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pieces of thin granular membrane (Plate 2, fig. 6, at right), while most of the visible patterns are formed by the ectexine. There is a distinctive cappa at the proximal side presented by two homogeneous layers with the intermediate layer of alveolae between them; the length of alveolae is greater than the height (Plate 2, fig. 3, above). The saccus possesses a protosaccate structure with alveolae of variable size and form that are divided by relatively thick partitions whose form is also highly diverse. Two denser areas (with thicker partitions, smaller alveolae, and more abundant remains of the endexine) are observed near the edges of the cappa (Plate 2, figs. 2,6, at right). It is possible that they correspond to the dark ring seen in transmitted light around the central body. The ectexine gradually gets thinner towards the sulcus, where it is represented by a single and very thin layer (Plate 2, fig. 1, above, fig. 7, the arrow).

The pollen of *Vesicaspora* has been the subject of numerous investigations using electron microscopy, although these investigations were restricted by one species, *V. schaubergeri* (Klaus) Jizba from the Pennsylvanian of North America, which is attributed to the Callistophytales. Pollen grains of this type were initially identified in the Middle Pennsylvanian synangiate pollen organ *Idanothekion* (Millay and Eggert, 1970) and in the Upper Pennsylvanian genus *Callandrium* (Stidd and Hall, 1970). M. A. Millay and T. N. Taylor (1970) have examined *Vesicaspora,* using both light and scanning electron microscopy, as well as TEM (Millay and Taylor, 1974). The early ontogenetic stages of *V. schaubergeri* pollen have been detailed by Hall and Stidd (1971) including tetrad configurations and saccus development. G. W. Rothwell (1972,1977) described *V. schaubergeri* pollen grains lodged in the nucellus of a *Callospermarion*-type ovule. A tube-like structure extended from the distal sulcus and divided twice to form three branches. Nothing is known about either the tube content or its function. Millay and Eggert (1974) investigated several developmental stages of *V. schaubergeri* extracted from the reproductive organs *Idanothekion* and *Callandrium.*

All of the above studies revealed a eusaccate organization of *V. schaubergeri* unlike the protosaccate organization of *V. exgr. magnalis,* although the general similarity of both types of pollen grains within the single genus corroborates the close relationship between the Callistophytales and Peltaspermales suggested by S. V. Meyen (1984). It should be mentioned, however, that the described protosaccate structure of *V. ex gr. magnalis* differs strongly from that of other protosaccate pollen grains described, for example those studied by C. B. Foster (1979) or by Taylor and L. Grauvogel-Stamm (1995). The main differences between the two are that the pollen grains of *V. exgr. magnalis* have larger alveolae and a general "single-story" appearance of the structure of the saccus due to the small number of partitions oriented either parallel or subparallel to the surface of the pollen grain. Such a structure may be the result of preservational flattening of the pollen grain, which was a eusaccate one in reality. The close positioning of some partitions to the cappa (Plate 2, figs. 2,6) seems to be an additional argument supporting this assumption. Still, it seems most likely that the pollen grains of *V. exgr. magnalis* did not possess true eusacci, but sacci with somewhat intermediate structure distinguishing itself by few and relatively large alveolae.

Protohaploxypinus

The genus *Protohaploxypinus* was established by Samoilovich (1953) and it has been widely adopted by modern palynologists since the emendation by Hart (1964). It is one of the most abundant genera of the dispersed miospores in the Permian on the Russian platform. The majority of representatives of the genus found in the Upper Tatarian can be assigned to the species *P. dvinensis* (Sedova) Hart (Plate 1, figs. 11, 12), although some authors use a number of different generic and specific names to reflect the variability within this pool of pollen grains (e.g. Molin et al., 1986).

The pollen grains assigned to *P. dvinensis* belong to the Peltaspermaceae using the methodology of Gomankov (1986) including extracting the pollen from the synangia of *Permotheca striatifera* Gomankov & Meyen, as well as from the micropyle of the seeds *Salpingocarpus bicornutus* Meyen and *S. variabilis* Meyen.

Pollen grains of *P. dvinensis* are bilaterally symmetrical in polar view, and they are striate (Plate 1, fig. 11). In transmitted light they appear to be bisaccate, however some SEM photomicrographs indicate that the saccus appears to girdle the entire corpus. There are small tubercles and foveolae irregularly distributed over the surface (Plate 3, figs. 1,2). The sulcus is not clear but according to the TEM data the entire distal part of the corpus appears to be an apertural area (leptoma).

There are several similarities between the ultrastructure of *Protohaploxypinus* and that of *Vesicaspora,* namely the structure of saccus, aperture and endexine. The endexine is similarly preserved as small and indistinct fragments of a thin fibrous membrane. The proximal side of the ectexine

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PLATE 2

1 **The first part of the transverse section of monosaccate pollen grain *Vesicaspora* (see the polar view of the same pollen grain at the Plate 1, fig. 6, LM). Note a thin sporoderm layer at the area of sulcus at the distal side of pollen (a) and a distinctive cappa presented by two homogenous layers with alveolate layer between them (b). TEM. xЮДЮ.**

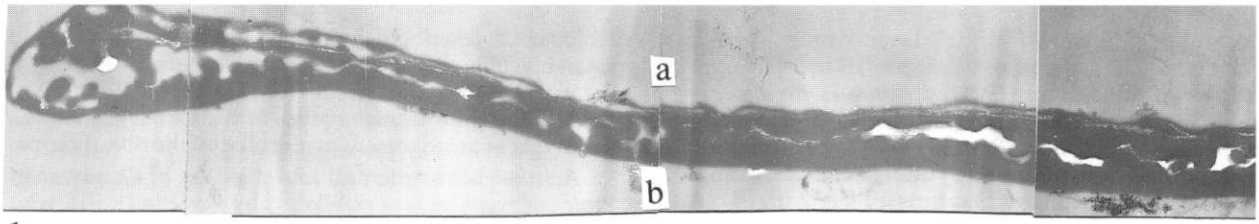
2 **Same transverse section of *Vesicaspora* (continuing) as in fig. 1. Note the alveolate infrastructure of the saccus. TEM. x10,000.**

3 **Area of transverse section of *Vesicaspora.* A region of the cappa (above). Sporoderm becomes thinner at the distal side of the pollen (below), a thin membrane between proximal and distal sides indicates the locality of the compressed cavity of the pollen. TEM. x15,000.**

4 **Area of transverse section of *Protohaploxypinus.* Note the fine-grained endexine, two ribs with a single layer of regular alveolae, a stria between the ribs presented by a thin homogenous layer of ectexine. TEM. xЮДЮ.**

5 **Distal view of *Vesicaspora.* SEM. x1,500.**

6,7 **Area of transverse section of *Vesicaspora.* The arrow indicates the area of sulcus represented by a thin homogenous layer of ectexine. TEM. x15,000. a - distal side of pollen grain; b - proximal side of pollen grain.**



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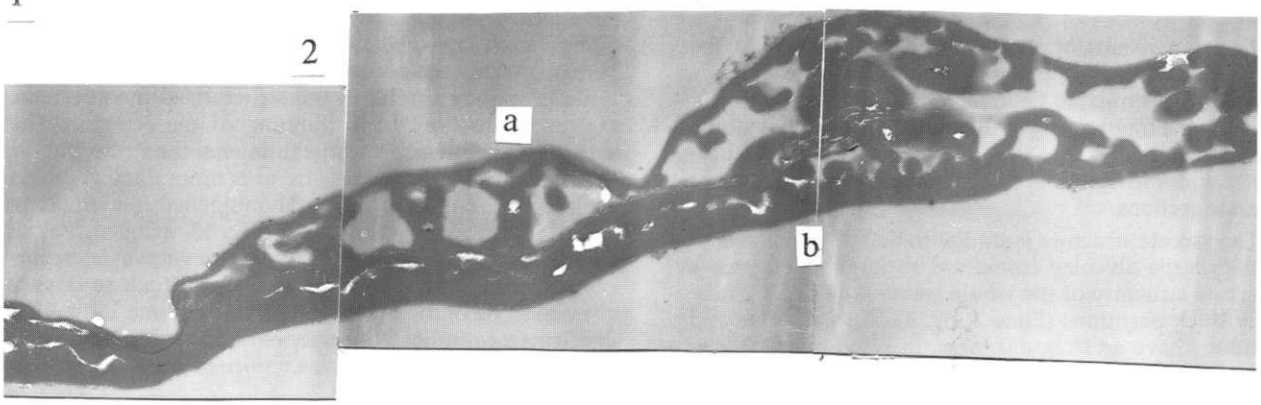

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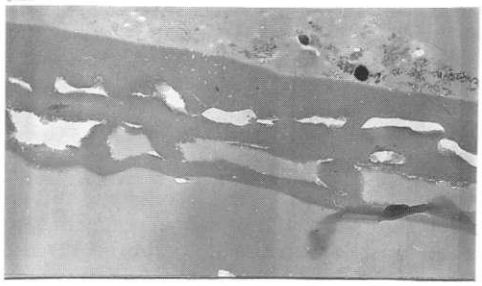

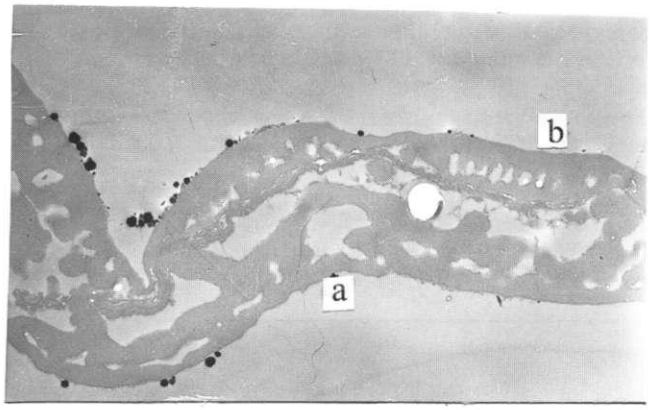

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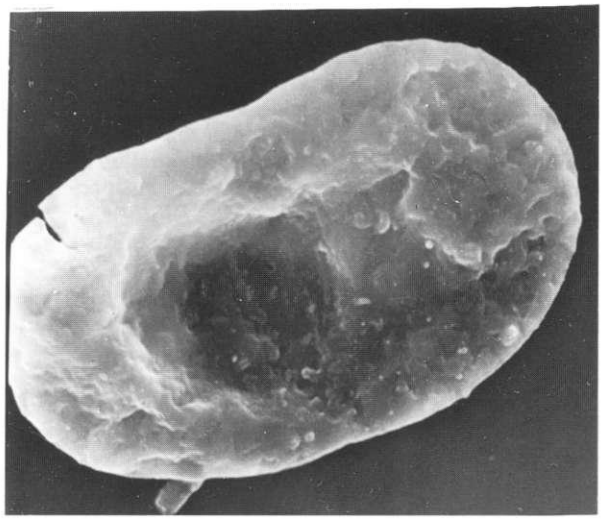

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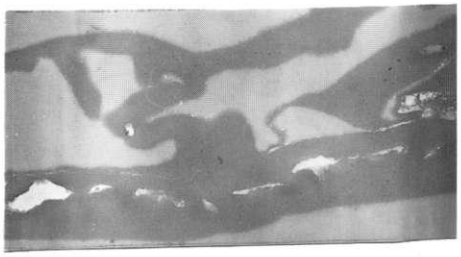

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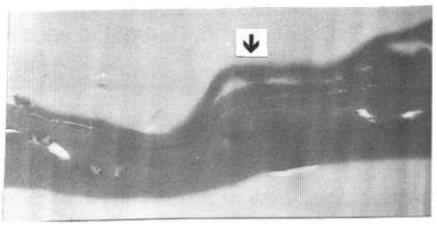
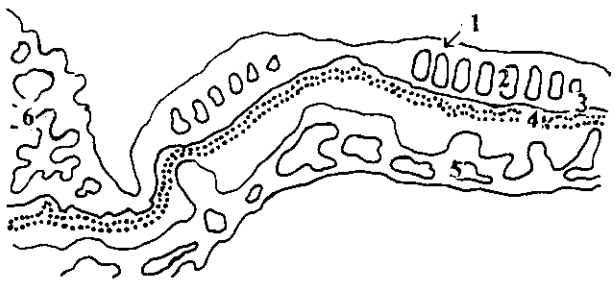


demonstrates a cappa with a single layer of rather regular alveolae whose height (unlike *Vesicaspora)* is usually larger than breadth (Text-Figure 2). The cappa is divided by narrow striae into several longitudinal or oblique ribs, whereas at the sites of striae the alveolae are not present; here the ectexine is represented by a single thin and homogeneous layer (Plate 1, fig. 13, arrows; Plate 2, fig. 4). A circular stria of the same construction surrounds the whole cappa.

The dimensions of the cappa in comparison to the breadth of the whole pollen grain suggest the latter is monosaccate, similar to *Vesicaspora.* Still, the distribution of the endexine fragments and the occurrence of the leptoma on the distal side show that the central body was sufficiently wider than the cappa dividing the saccus into two separate sections.

The saccate structure is similar to that of *Vesicaspora.* It exhibits large alveolae (some are so large to suggest a eusaccate structure of the whole saccus) divided by relatively thick partitions (Plate 2, fig. 4). Both alveolae and partitions have an irregular form. In some cases, a layer formed by more or less uniform small alveolae can be observed on the distal side of the saccus. The structure of this layer resembles that of the cappa, although the outlines of the alveolae are usually less regular. In the apertural area the ectexine is represented by a single thin homogeneous layer.

The pollen grains of the *Protohaploxypinus-type* found in the Gondwana countries are usually attributed to the Glossopteridales because they were repeatedly extracted from male fructifications of this order (Balme, 1995). The ultrastructure of dispersed pollen grains of *P. limpidus* (Balme & Hennely) Balme & Playford from Australia was described by Foster (1979). It differs strongly from that of *P. dvinensis* described above in exhibiting the extremely small alveolae and thick partitions between them both at the cappa and in the saccus (thus undoubtedly demonstrating the protosaccate nature of the saccus) as well as the irregular arrangement of alveolae on the ribs of cappa.



Text-Figure 2. Scheme of the section of a ***Protohaploxypinus*** pollen grain. 1, Homogenous tectum; 2, Alveolate layer; 3, Foot layer; 4, Possible endexines of distal and proximal sides pressed together; 1-3, Proximal side; 5, Distal side; 6, Part of the saccus.

Another ultrastructural investigation of Gondwanan *Protohaploxypinus* was published by Zavada (1991), who extracted pollen grains of this type from the sporangia of *Arberiella.* The main difference between *P. dvinensis* and Gondwanan *Protohaploxypinus* is the well-defined homogeneous (with occasional lamellations) endexine of the latter. They are similar in the structure of the apertural region represented by a thinning of the ectexine. The ectexines of both taxa become thinner at the striae, but for the pollen in this study this trend is more distinct and is interpreted as a single thin and homogeneous layer (Plate 1, fig. 13, arrows; Zavada, 1991, fig. 13, arrows). Pollen assigned to Gondwanan *Protohaploxypinus* is protomonosaccate, however sometimes the structure is very close to those of the pollen in this study (Plate 1, fig. 9). It confirms a complicated influence of flattening of the pollen to possibly reveal the true nature of the saccus.

Piceapollenites

We use the name *Piceapollenites* in the sense proposed by Hart (1965). Most modern palynologists prefer to accommodate the pollen assignable to *Piceapollenites* under the name *Alisporites,* although Jansonius (1971) has clearly shown that the holotype of the type species of *Alisporites* possesses a distinct distal sulcus. We keep the pollen grains described here under the name *Piceapollenites* separately from the mentioned specimen because of this feature.

Pollen grains assignable to *Piceapollenites* are rather diverse in the Upper Tatarian on the Russian platform and may include several species, but a detailed systematic treatment of this group has not been completed to date. Gomankov (1986) has suggested the relationship between the pollen grains *Piceapollenites* and the leaves *Rhaphidopteris,* which could have been produced by peltasperms (Meyen, 1987), but such a connection remains equivocal.

Pollen grains of *Piceapollenites* are bilaterally symmetrical, protobisaccate and elliptical in polar view. They all appear to be of the same type in transmitted light and SEM (Plate 1, figs. 8, 7; Plate 3, figs. 3, 4), but the ultrastructural characteristics revealed by TEM permits separation into two groups which probably correspond to different species.

Group I

Group I is represented by 4 specimens (Plate 1, fig. 8 - LM, Plate 3, fig. 3 - SEM, Plate 4, figs. 1-5, 7). The endexine

PLATE 3

1 **The lateral view of *Protohaploxypinus* showing striate corpus and the surface of the saccus (see this pollen grain in Plate 1, fig. 12, LM). SEM. x1,500.**

2 **Proximal view *of Protohaploxypinus* (see this pollen grain in Plate 1, fig. 11, LM). SEM. x1,000.**

3 **Proximal view of bisaccate pollen grain *Piceapollenites,* group I (see the same pollen grain in Plate 1, fig. 8, LM). Note the granulate surface in the area of central body, SEM. x1,000.**

4 **Proximal view of *Piceapollenites,* group II (see the same pollen grain in Plate 1, fig. 7, and ultrastructure of the corpus in Plate 4, fig. 6, TEM). SEM. x1,000.**

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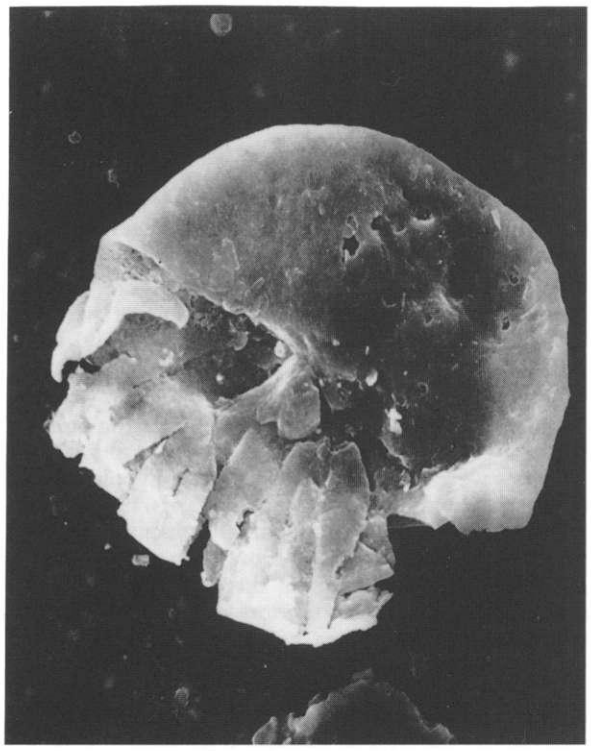

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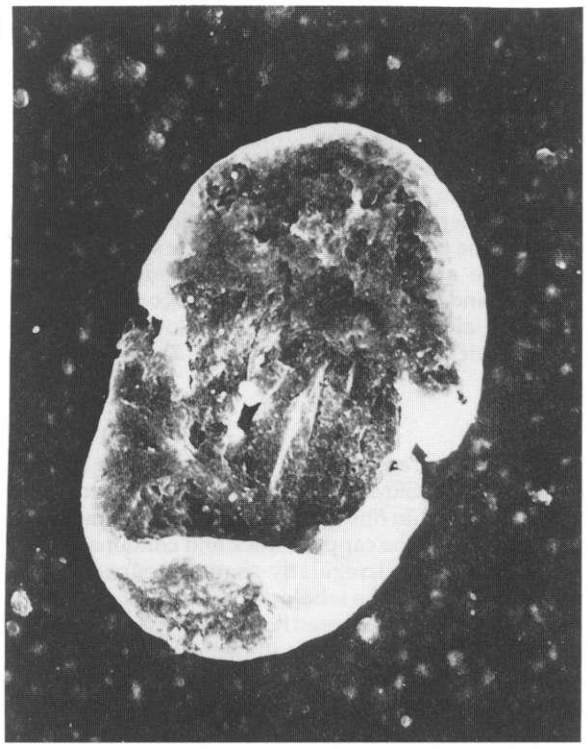

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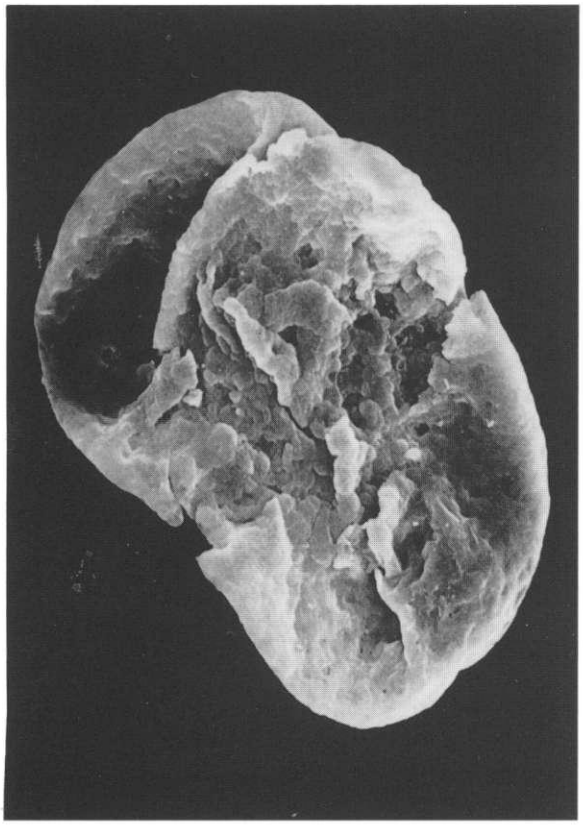

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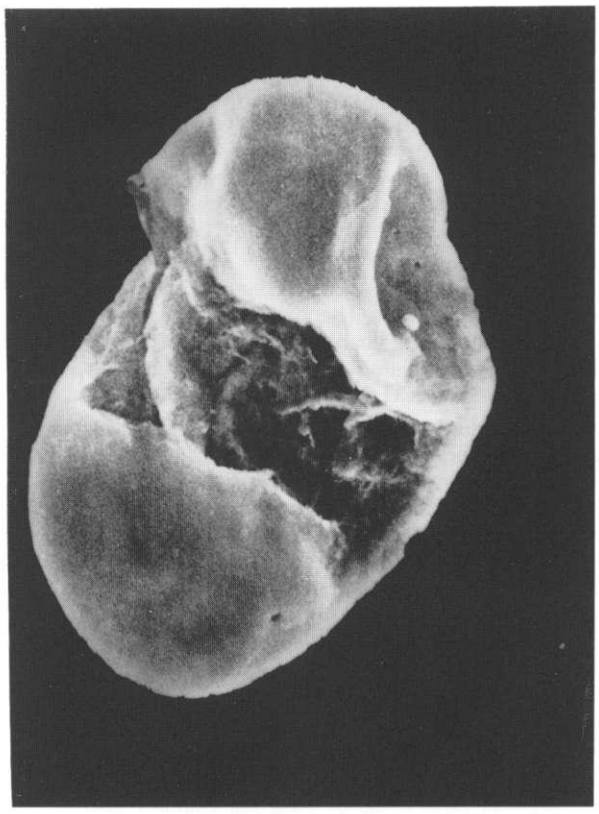


is not preserved. The ectexine in the area of the central body is similar on both the proximal and distal sides and has a "spongy" appearance with a large number of very small cavities (alveolae) (Plate 4, figs. 1-4). On one side (assumed to be distal) the ectexine is very thin and consists mainly of only one layer of alveolae (Plate 4, figs. 3,4), whereas on the other side it can be up to 3 µm thick (Plate 4, figs. 1, 2). Apparently the ectexine on both sides becomes granular in the area of the transition to the sacci. The sacci possess a protosaccate structure similar to that described for *Vesicaspora* and *Protohaploxypinus,* which consists of relatively large alveolae divided by partitions of irregular shape and thickness (Plate 4, figs. 1, 3-5, 7).

Group II

Group II is represented by 3 specimens (Plate 1, fig. 7 - LM, Plate 3, fig. 4 - SEM, Plate 4, fig. 6 - TEM). The endexine is preserved as a thin fine granular membrane (Plate 4, fig. 6). The ectexine at the cappa is thick and contains numerous relatively large, irregularly-shaped lacunae usually located in one layer. The whole distal side of the corpus is covered by thin single-layered homogeneous ectexine and functioned apparently like a leptoma. Available information about the sacci is poor, we suggest that the sacci are of the same structure as the structures described above.

Cycadopites

This genus is usually considered as Mesozoic. A number of species was described from the Permian of Siberia (Hart, 1965), but there is doubt as to whether they represent true monocolpate pollen and are not simply rolled up monosaccate grains (Gomankov and Meyen, 1980; Dyupina, 1986). The pollen of "true" *Cycadopites* is rare in the Permian of the Russian platform. In the Upper Tatarian it is probably represented by a new, undescribed species. Gomankov (1986) has attributed these pollen grains to the Leptostrobales or Ginkgoales, the leaves and female fructifications of which are found in the same deposits.

The pollen grains examined herein (Plate 1, figs. 3-5) are ovoid and monosulcate. The surface of the pollen grains appears smooth using both transmitted and SEM microscopy (Plate 1, fig. 5, Plate 5, fig. 4). The breadth of the pollen measured by SEM is 11.7 µm, and the length is 21 µm.

The sporoderm consists of one layer, apparently representing the ectexine. It is dense and almost entirely homogeneous. In transverse section (Plate 5, figs. 5, 6) there are some morphological differences between the distal and proximal sides. The proximal ectexine contains a single layer of very small alveolae, and this layer divides the proximal ectexine into outer and inner homogeneous parts. The length of alveolae usually exceeds their height; distally they become more distinct, more circular in shape, and are rarely fused.

At the distal side the alveolate layer and inner part of homogeneous ectexine disappear. The outer homogeneous part thins out gradually (in some transverse sections becomes absent). Longitudinal sections show that the inner surface of the distal ectexine (formed by the outer homogeneous part) is uneven, unlike that of the proximal ectexine which is usually smooth (Plate 6, fig. 5).

Thus, the proximal ectexine is distinctly thicker than the distal ectexine (0.65-0.8 Jim and 0.15 µm, respectively), and it has an alveolate layer unlike that at the distal side that is entirely homogeneous.

The ultra-thin sections revealed that all of the pollen grains were compressed (Text-Figure 3); we believe the pollen grains were originally almost circular in polar view (this idea agrees with the conclusions of Harris, 1974, about the initially spherical pollen grains of *Williamsoniella lignieri* Nathorst). Longitudinal sections show close association of the distal and proximal sides of the pollen grains. The hollow of each pollen grain is represented by a narrow space between the sporoderm layers. Transverse sections show not only the compression but a rolling up of the exine. The rolling occurred in the formation of two folds aligned more or less parallel to the sulcus with a narrow chink between them (Plate 5, fig. 5). In transmitted light this chink may be taken for a sulcus. In point of fact the chink usually indicates the position of sulcus, a large part of the thin distal side, which cannot be observed by means of light microscopy or SEM.

During the Mesozoic, the pollen grains assigned to *Cycadopites* were produced by a number of different gymnosperms such as the Peltaspermales, Ginkgoales, Leptostrobales, Pentoxylales, Cycadales, Bennettitales and Gnetales (Balme, 1995). Meyen (1987) noted that pollen grains of at least some of these taxa were not distinguishable by means of light microscopy, whereas the electron microscope investigations were carried out under only one or two representatives of each taxon (Table 1). Information detailing the ultrastructure of the pollen of the Ginkgoales, Leptostrobales and Gnetales (identified as Cycadopites) is still not available.

Cycadopites pollen from the Russian platform, as well as that of the Bennettitales and Pentoxylales, has a smooth surface in SEM, whereas fossil cycad pollen grains are characterized by different species-specific sculpture.

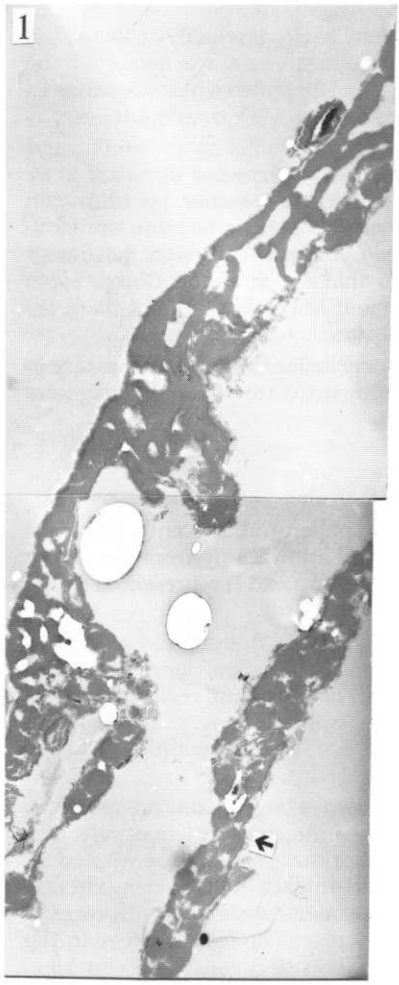
The sulcus is formed by a thinning of the ectexine and encompasses a large part of the distal side of pollen grains in all pollen discussed herein. The exine of all pollen (Table 1), except for one taxon, consists of two layers, the endexine

PLATE 4

1, 2, 4, 5, 7 **Area of one and the same longitudinal section of *Piceapollenites*, group I (see the polar view of this pollen grain in Plate 1, fig. 8). Note the granules (arrow), alveolate structure of the saccus (fig. 5). TEM. x6,000.**

3 **Area of longitudinal section of *Piceapollenites*, group I. TEM. x15,000.**

6 **Area of transverse section of *Piceapollenites*, group II (see the polar view of this pollen grain in Plate 1, fig. 7) at the region of corpus. Note the thin layer of electron-dense endexine. A fold at the upper right part of the photo corresponds to the fold of exine of the corpus (Plate 3, fig. 4). TEM. x15,000.**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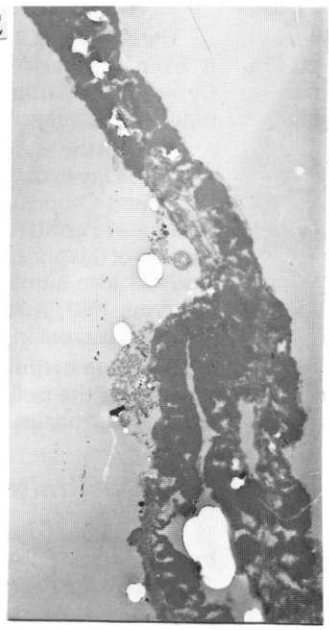
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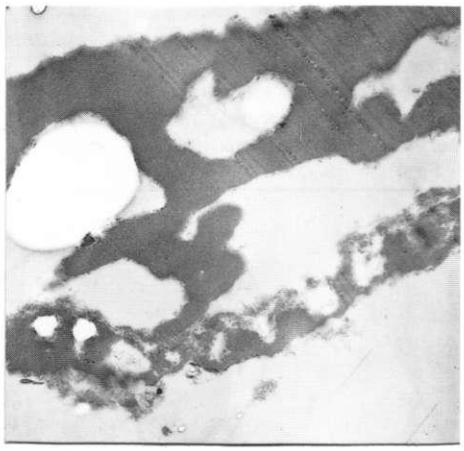
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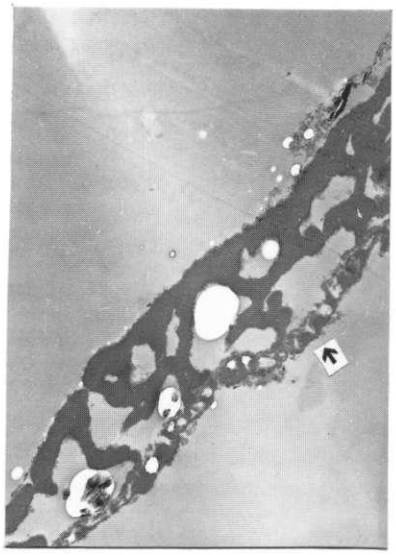
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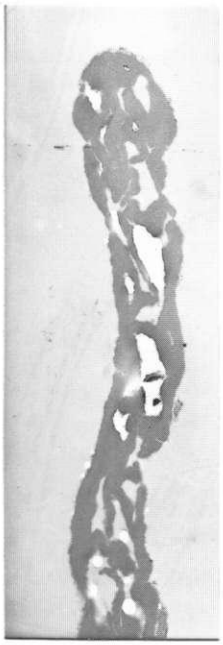
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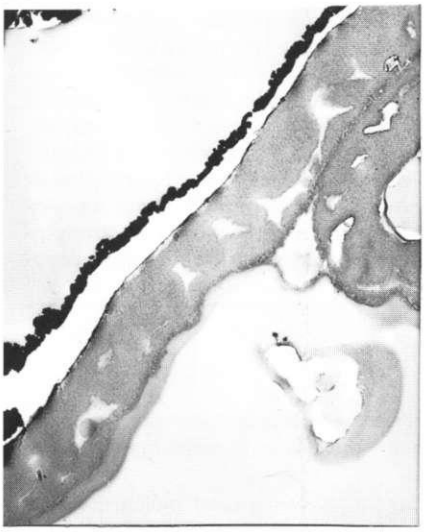
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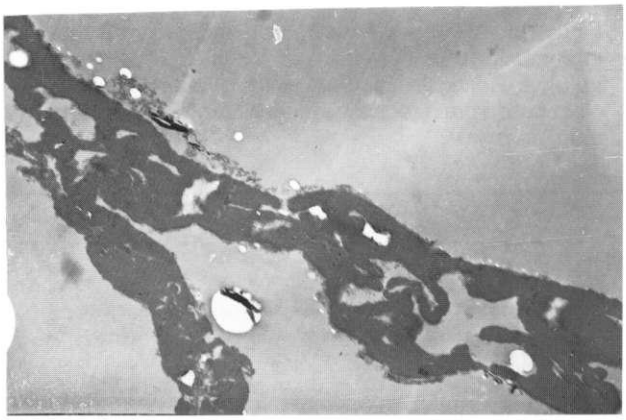
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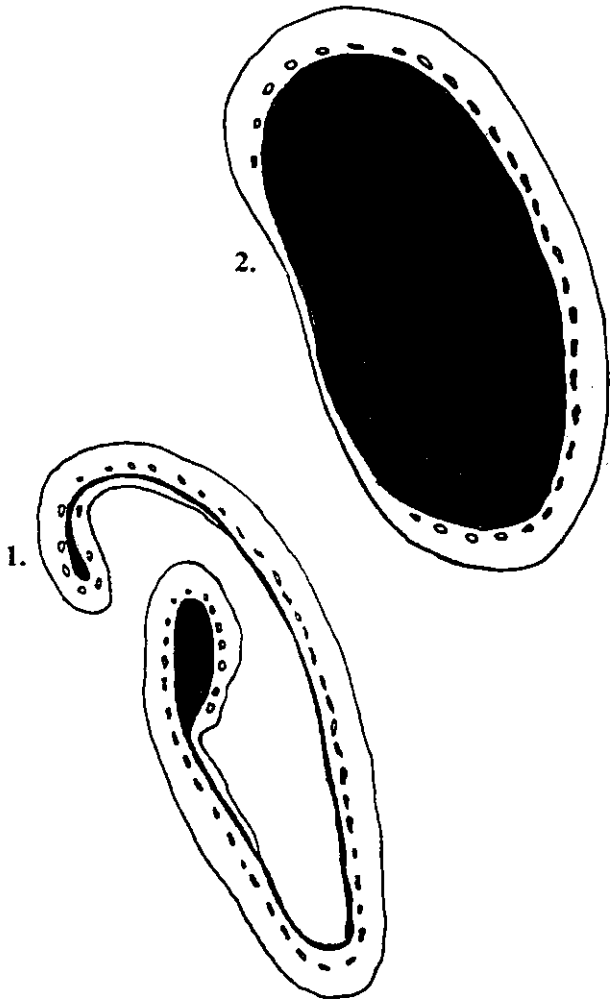
and ectexine. The endexine is homogeneous or faintly lamellate (the lamellae usually are difficult to see), whereas the Permian *Cycadopites* examined herein have no endexine. However, this difference may be caused by variable preservational conditions.



Text-Figure 3. ***Cycadopites.*** 1, Scheme of the transverse section of compressed pollen grains (see Plate 5, fig. 5); 2, Reconstruction of the transverse section of intact pollen grain (ectexine - in white, hollow of pollen grain - in black).

The ectexine of Permian *Cycadopites* clearly distinguishes it from the specific regular-alveolate ectexine of the Cycadales, and from *Cycadeoidea* pollen which possesses an inner ectexine layer consisting of very small granules.

Though the middle ectexine layer of *Leguminanthus* and the inner layer of *Sahnia* was interpreted by Ward et al. (1989) and Osborn et al. (1991) as granular, the ultra-thin sections of Permian *Cycadopites* seem to be more similar to sections of this pollen. The *Cycadopites* ectexine of the present study is also similar to that of the extant *Ginkgo biloba* (Audran, 1987; Audran and Masure, 1978), but there are some differences in sculpture.

For more definitive conclusions it will be necessary to investigate the pollen ultrastructure of fossil Ginkgoales and Leptostrobales.

Mulinopollenites

This genus of dispersed pollen grains recently described by Gomankov (1996) is still known only from the Upper Tatarian of the Russian platform and is represented by the single species *M. bonus* Gomankov.

Pollen grains (Plate 1, figs. 1, 2) are ovoid (40 Jim in length and 23 Jim in breadth), with four long, broad furrows. In SEM the surface of nonapertural regions is almost smooth; the ridges of furrows appear uneven and lacerated; the furrow ends are acute. The furrow membrane is tuberculate with rare pits (Plate 5, figs. 1, 2).

In ultra-thin sections, two layers of exine are revealed. The ectexine is thick, almost homogeneous, especially in its outer part. The inner part of the ectexine is perforated by numerous narrow canals with dark electron dense filling. The inner surface of the ectexine is tuberculate with variable spaces between the tuberculae. The spaces between the tuberculae often contain pieces of fine-grained endexine, which underlies the ectexine as a thin layer. Near the furrows the ectexine gradually becomes thinner. The furrow membrane is 0.1 Jim thick and is composed solely of endexine, which does not become appreciable thinner (Plate 6, figs. 1, 2, 4; Text-Figure 4).

The natural affinity of *Mulinopollenites* pollen remains unknown. In the first description of the pollen (Gomankov, 1996) its morphological similarity with *Praecolpatites* was mentioned, but the ultrastructure of this genus (Foster and Price, 1981) differs from that *of Mulinopollenites* in having lamellate endexine and an "incipient-alveolate" infrastructure of the ectexine (which is not interrupted at the bottom of the furrows). On the contrary, the aforementioned similarity with some ancient angiosperms is strengthened by the fine-grained endexine and tuberculate eleva-

PLATE5

1 **The surface of*Mulinopollenites* (see the pollen grain at the Plate 1, fig. 1). Note the lacerated edge of the furrow. SEM. x4,000.**

2 ***Mulinopollenites* (see this pollen grain at the Plate 1, fig. 2). Note two furrows, the difference between granulate bottom of one of the furrows and smooth sculpture of the pollen at the nonapertural region. SEM. x1,500.**

3 **The region of fig. 2. *Mulinopollenites.* Area of furrow, note granulate sculpture. SEM. x3,800.**

4 **Smooth surface of monosulcate pollen grain *Cycadopites* (see this pollen grain in Plate 1, fig. 5), distal view. SEM. x3ДЮ.**

5 **The transverse section of compressed pollen grain *Cycadopites* (see this pollen grain in Plate 1, fig. 3). TEM. x8,000.**

6 **Area of section 5. Note almost homogenous ectexine contained a single layer of very small alveolae. TEM. x15,000.**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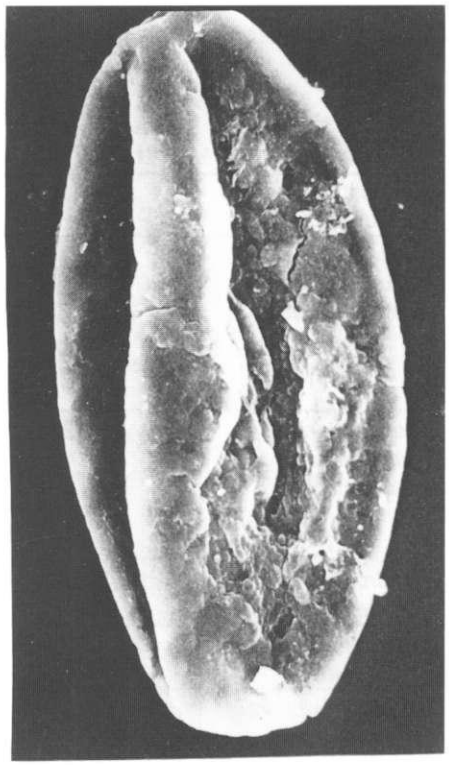
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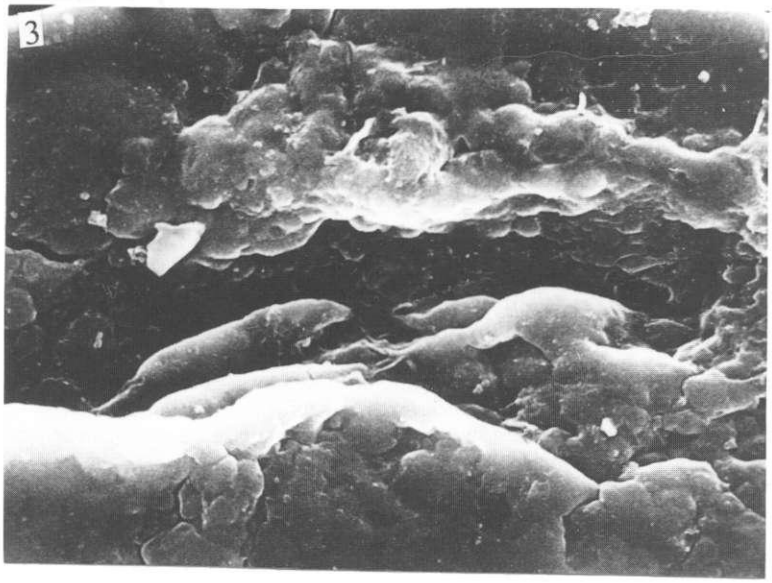
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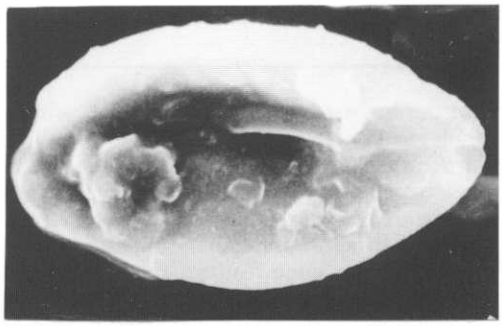
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TABLE 1. Comparative ultrastructure of investigated disperse and in situ *Cycadopites* pollen grains.

Taxon	Size of pollen grain,(pm)	Organization of ectexine/ thickness,(urn)	Organization of endexine/ thickness,(pm)	References
Leptostrobales or Ginkgoales (?)	21x11.7	homogeneous with a single layer of very small alveolas/ 0.15-0.8	absent	present investigation
Cycadeoidea dacotensis/ Bennettitales	25x12	thin, homogeneous outer layer, thicker granular inner layer (sometimes appears homogeneous because of very small granules and little lacunae between them)/ 0.5	homogeneous/ 0.23	Osborn and Taylor, 1995
Legyminanthus siliquosus/ Bennettitales	23x12	thick homogeneous outer layer, intermediate layer of coarse, densely packed granules fuse basally into a thin homogeneous inner layer/ up to 0.6	faintly lamellate/ 0.14-0.3	Ward et al., 1989
Androstrobus balmei/ Cycadales	24.3x17.7	alveolate/ 0.25-0.68	faintly lamellate/ 0.27	Hill, 1990
Androstrobus szei/ Cycadales	24.3-31x 14.5-19.5	alveolate/ 0.55	homogeneous/ 0.1	Hill, 1990
Sahnia laxiphora/ Pentoxylales	26x23	homogeneous outer layer, inner layer presented by large granules separated by irregular lacunae/ 0.69	faintly lamellate/ 0.13	Osborn et al., 1991

tions at the inner surface of the ectexine, which have a morphological potential for developing into the baculate infrastructure typical for the angiosperms. Still the most ancient angiosperms (e .g., *Eupomatia* and *Degeneria)* have a homogeneous ectexine, which is occasionally *(Degeneria)* underlain with sporopollenin granules (Takhtajan and Meyer, 1976). The same features (fine-grained endexine and tuberculate elevations at the inner surface of the ectexine) unite *Mulinopollenites* with *Eucommiidites troedssonii* Erdtman, whose ultrastructure was described by Trevisan (1980). *Eucommiidites* is usually attributed to the Cycadales or Gnetales, although its natural affinity is not absolutely clear.

DISCUSSION

The diversity of pollen observed among the pteridosperms is extremely high (Millay et al., 1978; Millay and Taylor, 1970, 1976; Rothwell, 1972, 1977). While the most primitive representatives of the group, the Lagenostomales, produced prepollen, the more advanced pteridosperms possess a number of features both of gross morphology and exine ultrastructure, which are considered as characteristic for gymnosperms. Many of these features were probably a function of the necessity of regulation of microspore volume associated with the development of the male gametophyte inside the sporoderm. Plants such as *Archaeopteris,* which possessed spores with the elastic sporoderm (Telnova and Meyer-Melikian, 1993), could represent an ancestral stock which developed a variety of pteridosperm pollen. The most important features to develop in connection with the changes in volume are (1) harmomegathy, which later took the function of apertures on themselves, and (2) cavities in the exine which developed into sacci.

Therefore, asaccate pollen grains with one or two sulcae and a monolete suture *(Monoletes* Taylor, 1978), monosaccate *(Vesicaspora)* and bisaccate *(Protohaploxypinus, Piceapollenites)* pollen grains with sacci of varying com-

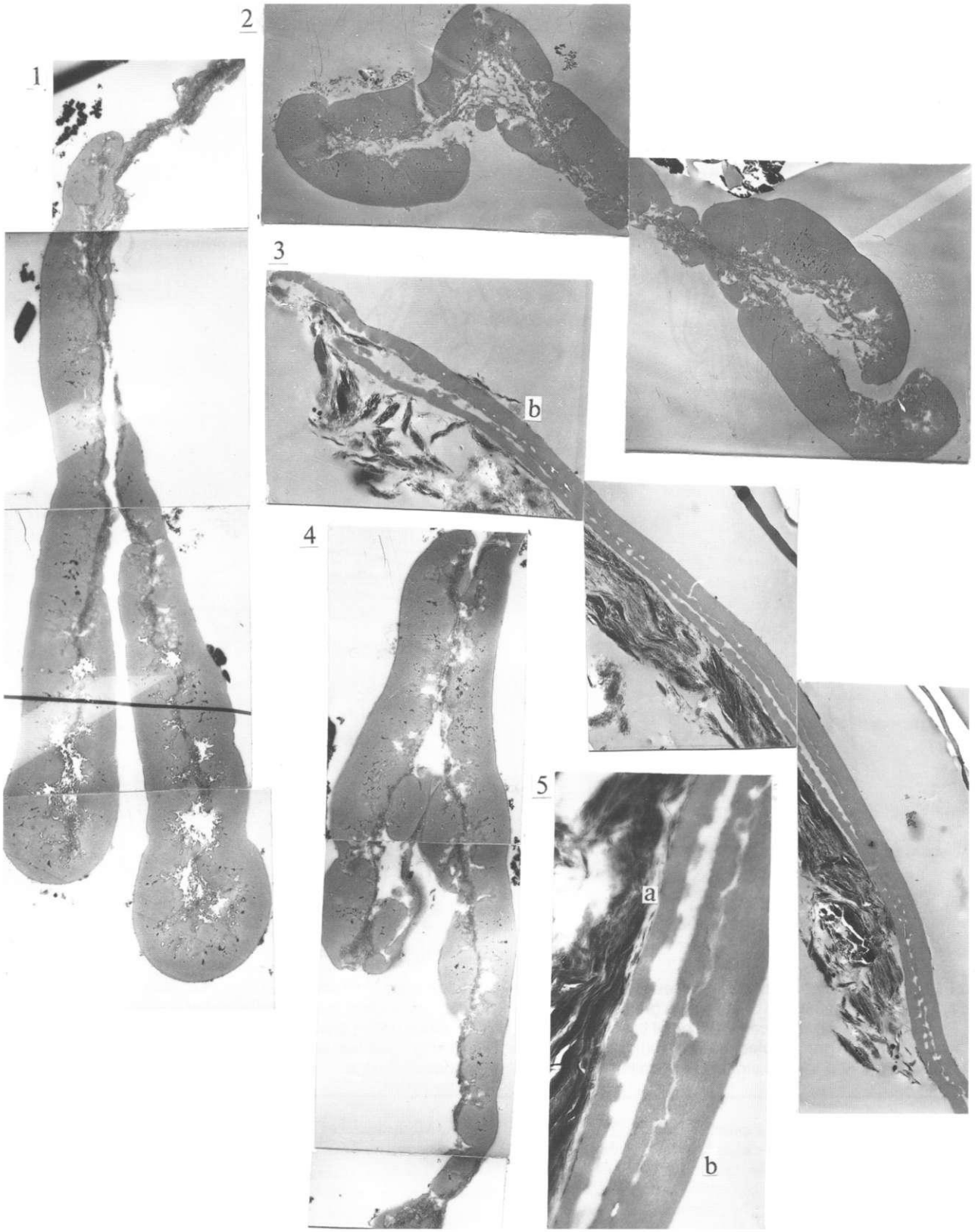
PLATE 6

1, 4 **Montage of transverse section at the middle part of *Mulinopollenites.* The pollen grain is strongly compressed. Note ectexine transpierced by narrow canals, fine-grained endexine. Ectexine gets thinner toward the furrows and disappears at the furrow regions. TEM. x10,000.**

2 **Montage of transverse section of the same pollen grain *Mulinopollenites* (see section in figs. 1,4). Section placed at the end of the grain. Note the thin fine-grained endexine. TEM. x8,000.**

3 **Montage of longitudinal section of *Cycadopites* (see the pollen grain in Plate 1, fig. 4). Endexine is absent. TEM. x8,000.**

5 **Area of section 3. Note thicker proximal side of the grain with narrow canals, thinner distal side represented by homogenous ectexine and compressed cavity between them. TEM. x25,000. a - distal side of pollen grain; b - proximal side of pollen grain.**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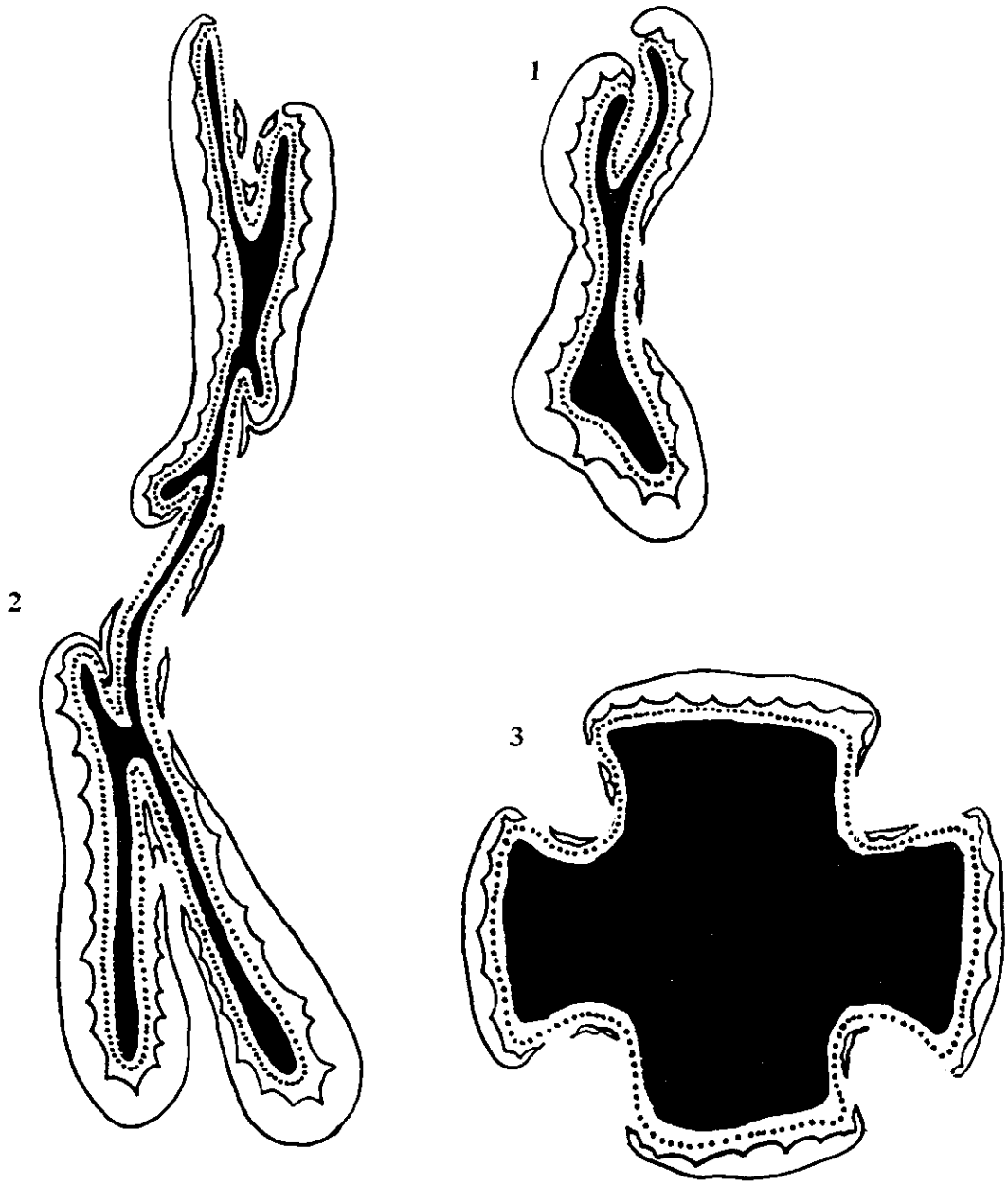

Text-Figure 4. Schemes of the transverse sections of a single pollen grain of ***Mulinopollenites***(see Plate 6, figs. 1, 2, 4). 1, The section in the end of the pollen grain (see Plate 6, fig. 2); 2, The section in the middle part of the pollen grain (see Plate 6, figs. 1, 4); 3, Reconstruction of the transverse section of intact pollen grain (ectexine in white; endexine, points; hollow of pollen grain in black). Abbreviations: a - alveolae; f - furrow; g - granule; sa - saccus; su - sulcus; d.s. - distal side of pollen grain; p.s. - proximal side of pollen grain; f-g - fine-grained endexine.

plexity appeared among the pteridosperms. The infrastructure of the exine may be also highly variable. Some pollen grains possess a single layer of exine, i.e. the ectexine (e.g. pollen of *Crossotheca hughesiana* Taylor and Taylor, 1987). Others have two layers, i.e., ectexine and endexine. The endexine can be lamellate such as in *Potoniea* and *Monoletes* (Taylor, 1978). In other cases it can be granulate or fine-grained. The ectexine can be homogeneous as in the pollen of *Crossotheca hughesiana* (Taylor and Taylor, 1987); alternatively the layer can be almost homogeneous with a single layer of small alveolae, and with definite alveolae as in the Medullosales (Taylor and Taylor, 1987), or it can form a saccus with either proto- or eusaccate structure.

The pollen grains described in the present study belonged to the peltasperms or their nearest descendants. Having been dispersed, they are usually strongly flattened and the endexine is preserved as rare fragments, but the main features of their morphology can be still reconstructed. Although they demonstrate a high diversity in some characters, all fall within the generally accepted concept of the variability of the pteridosperm pollen reviewed above. All of them have a distal aperture and therefore they can be

assigned to the true pollen and not to prepollen (although double germination, as for their modern descendant, *Ginkgo biloba,* cannot be excluded). The construction of the aperture is variable. It may be a simple thinning of the ectexine (leptoma) as in *Piceapollenites* or *Protohaploxypinus,* or it can be represented by a sulcus (as in *Vesicaspora)* or by highly specialized furrows (as in *Mulinopollenites).*

The endexine, when observed, is very thin and fine-grained. It can be considered as a common feature of the peltasperms and allied taxa (Class Ginkgoopsida *sensu* Meyen, 1987), since most of the other gymnospermous pollen grains possess thicker, lamellate endexine. The infrastructure of ectexine outside of the sacci is also similar among the genera examined herein, demonstrating small alveolae disposed usually in a single layer. *Mulinopollenites* represents an exception, but the inner surface of its ectexine is uneven as if bearing "opened" alveolae.

Three of the genera studied which are assigned to the Peltaspermales possess protosacci. However, the structure of these structures is rather peculiar and more "friable" than in other well-known protosaccate genera, possibly suggesting the imitation of the protosaccus by the eusaccus (which is highly flattened due to the preservation). It should be mentioned here that primitive conifers *(Triadispora)* possessed the true protosaccus (Taylor and Grauvogel-Stamm, 1995), and thus the development of eubisaccate pollen proceeded independently in both the Coniferopsida and Ginkgoopsida.

At the same time, the ultrastructure of asaccate *Vittatina*-like pollen, produced by the other representatives of the Peltaspermaceae (to be described in detail elsewhere), differs strongly from that of saccate genera *Vesicaspora, Protohaploxypinus,* and *Piceapollenites.*

This situation enlarges the diversity of pollen ultrastructure among the peltasperms and hampers the elucidation of characters common for all of the Peltaspermales and Peltaspermaceae. In summary, the different features of pollen grains arose once in the pteridosperms, and subsequently developed in parallel and convergent ways, often across phylogenetic lines, as it was initially proposed by Meyen (1984).

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