

ULTRASTRUCTURE OF THE MOST ANCIENT ANGIOSPERM POLLEN GRAINS FROM THE EARLY CRETACEOUS OF THE UKRAINE

MARGARITA A. VORONOVA and N.N. VORONOV

Institute of Geological Sciences, Laboratory of Palaeobotany, National Academy of Sciences
55-b Olesya Gonchara str., 252054, Kiev, Ukraine; e-mail: ignnanu@geolog.freenet.kiev.ua

ABSTRACT. Eight types of sporoderm structure of pollen grains of the most ancient angiosperms are described. Three types have no equivalents among contemporary angiospermal plants. Seven types were characterized by their homogenous ectexine, although their endexine was diverse: granular, lamellar or fibrous-pseudolamellar. Three types were characterized by features being in ontogenesis columns.

KEY WORDS: Cretaceous, Angiospermae, palynomorphs, Ukraine

INTRODUCTION

Monocolpate pollen of the most ancient angiosperms have been found in the Cretaceous deposits of almost all mainland areas through out the world and have been studied by many researchers: Hughes (1979), Juhasz (1985), Kremp (1968), Walker and Walker (1984), Doyle *et al.* (1977), Doyle (1979) and many others. Special attention has been paid to pollen grains from deposits older than the Aptian. This pollen belongs to the following genera: *Liliacidites* Couper 1953, *Retimonocolpites* Pierce 1961, *Stellatopollis* Doyle 1979 and others. The main purpose of this research was to compare the most ancient angiosperm pollen with that of contemporary taxa. *Clavatipollenites*, whose pollen has been compared with that of ancestors of the Chlorantaceae family, is a good example of this. Ultrastructural analysis of the exine of pollen grains from this family and its comparison were performed by Khlonova (1977).

MATERIALS AND METHOD

Scanning Electron Microscopy was used to study the ultrastructure of the earliest angiospermal pollen grains and to compare it with that of orders of contemporary Angiospermae. In the Ukraine, the pollen of ancient angiosperms has been found in the Barremian and Aptian deposits of the Dnieper-Donets and Prichernomorskaya depressions. These pollen grains were studied at the electron microscopy laboratory of the biological faculty of Moscow M. Lomonosov University under the supervision of Mejer-Melikjan. Mejer-Melikjan's procedures were used for the study of the exine morphology of this early angiospermal pollen. This study permitted comparison of the pollen grains of supposed ancient Angiospermae with those of natural taxa of contemporary ones. It was possible to prove that some of the dispersed pollen

grains had affinities with the families of contemporary taxa. Hence a natural classification system of fossil pollen to the rank of order could be developed and a rather less precise one to families.

SYSTEMATIC PALYNOLOGY

Order Magnoliales

Family Protodegeneriaceae N.N. Voronova 1995
Pl. 1, figs 1–3

Family Protoeupomatiaceae N.N. Voronova 1996
Pl. 1, figs 4–5

Order Laurales

Family Protocalycanthaceae fam. nov.
Pl. 2, figs 4–7

Family Protochlorantaceae fam. nov.
Pl. 2, figs 1–3

Order Nymphaeales

Family Protonymphaeaceae fam. nov.
Pl. 4, figs 1–3

The pollen grains of these families were described from the Barremian deposits of the Ukraine.

Order Piperales

Family Protopiperaceae fam. nov.
Pl. 3, figs 1–4

Order Hamamelidale

Family Protohamamelidaceae fam. nov.
Pl. 4, figs 4–6

Ultrastructural analysis of monocolpate pollen grain exine made it possible to distinguish eight types of exine structure.

DISCUSSION

ORDER MAGNOLIALES

Compared with contemporary taxa of this order the ancient pollen grains have a diverse sporoderma which involves a relatively thick layer of homogeneous exine. Probably the sporoderma surface was originally covered by perine, the remains of which were discovered by SEM and TEM. On separate areas of the homogeneous exine there are electron-dense granules of endexine. This sporoderma type has been described for pollen grains of the contemporary species *Degeneria vitinensis* Bajby et Smith (Takhtajan & Mejer 1979). Many fossil pollen grains have specific protuberances with different internal structures. Differences in sporoderma structure enabled us to describe two families within the order Magnoliales: the Protodegeneriaceae N.N. Voronova and the Protoeupomatiaceae N.N. Voronova. According to the results of our study the Protodegeneriaceae contains five genera and the Protoeupomatiaceae only one.

ORDER LAURALES

The monocolpate or poral pollen grains sometimes have a transitional form of aperture intermediate between colpate and porate. Sometimes too these pollen grains have colpi of varying length and some grains have additional colpi. The fine-grained sporoderma surface is covered by sporopollenin. Around the apertures the structure is reticular and sometimes, pitted. The inner layer of the exine is smooth and the outer one clavate, with fused tips creating a tectate exine. The fossil pollen has been divided into two families, the Protocalycanthaceae N.N. Voronova and the Protochloranthaceae N.N. Voronova. Each family contains one monotypic genus.

ORDER PIPERALES

The pollen grains are distal-monocolpate or distal-triangulate, bilaterally symmetrical, sphaerical or

sphaerical-ellipsoidal. The sporodermal sculpture varies from finely pitted to coarsely verrucose. The separate layers of the sporoderma are clearly distinct; the sporoderma itself is up to 2.5 mm thick. Some parts of the pollen grain surface are covered by the preserved perinium. The colpus is long, up to 3/4 of the equatorial diameter. The aperture zone is wide. The colpus margins are uniform and inturned. In outline the pollen varies from smooth to subundulate. It has been designated as belonging to the Protopiperaceae N.N. Voronova, a family consisting of one monotypic genus.

ORDER RAFFLESIALES

This order contains two types of small more or less ellipsoidal fossil pollen grains, whose surface of which bears slender protuberances. The height, diameter and form of these protuberances can vary; sometimes they merge. On their surfaces there are frequently deposits of sporopollenin. The exine is very thick (up to 1.8 mm) and consists of a homogeneous ectexine (1.2 mm) and the endexine, which is formed by two or three lamellar layers of 0.6 mm. Lamellar endexine is very rare in the pollen sporoderma of contemporary angiosperms. In combination with a homogeneous ectexine it is characteristic only for some of the most primitive members of the Hydroporaceae and Rafflesiaceae. The Protohydroniaceae fam. nov. (Pl. 3, figs 5–7) which was found in the Aptian palynocomplexes, contains the pollen of two genera: *Protohydronore* (two species) and *Protorafflesia* (two species).

ORDER NYMPHAEALES

The fossil pollen grains which have been compared with contemporary ones are assigned to the single family Protonymphaeaceae with two genera: *Stellatopollis* Doyle (one species) and *Protonymphaea* gen. nov. (three species). The sporoderma structure of these pollen grains is very complicated and may be divided into several types. Some have no analogues in contemporary angiospermal pollen grain sporoderma types. It is highly likely that the representatives of ancient plants with such a sporoderma type belong to extinct ancestors of contemporary Nymphaeales.

Stellatopollis pollen exine is double-layered. The ectexine is massive and homogeneous. The endexine is interlaced with small canals and is more massive still. The ridged ectexine bears spines which are irregularly placed, and not contiguous. On the ectexine-endexine boundary columnlike structures are being formed. The exine of *Protonymphaea* gen. nov. is unbroken with the homogeneous ectexine favose-columnar; the endexine is thick, spongy and finely undulate. The exine of some members of its genera consists of a fibrous-favose ectexine

and a granular or finely granulate endexine. The sporoderma of the grains of others consists of a homogeneous ectexine and a friable lamellar endexine.

ORDER HAMAMELIDALES

The pollen grains are meridionally tricolpate, tricolpate-oroid, prolate and some have pororate zones. The type of aperture, their disposition and number, sporoderma sculpture and the pollen grain form are all similar to those of the contemporary Hamamelidaceae and Saxifragaceae. Fossil pollen grains of such type have been assigned to the Protohamamelidaceae fam. nov. which consists of two genera: *Protohamamelis* gen. nov. and *Gunnerapollis* gen. nov.

CONCLUSION

Among the eight types of fossil pollen grain sporoderma sculpture only three are without analogues among the contemporary Angiospermae. This fact can be accounted for by the extreme long-term stability of the sporoderma sculpture. The seven types studied were characterized by a homogeneous ectexine and an endexine represented by various forms. Three types were characterized by features of being in ontogenesis columns.

ACKNOWLEDGEMENTS

We are grateful to Prof. Nonna Mejer-Melikjan for her guidance and invaluable help.

REFERENCES

- KHLONOVA A.F. 1977. Pervye nakhodki pyl'tsy *Clavatipollenites* v melovykh otlozheniyakh Zapadnoy Sibiri. (The first findings of *Clavatipollenites* pollen in Cretaceous deposits of Western Siberia). *Paleontologicheskyy Zhurnal*, 2: 115–121. (in Russian).
- DOYLE J.A. 1979. Potentials and limitations of exine structure in studies of early angiosperm evolution. *Cour. Foesch. Senckenberg*, 30: 54–61.
- DOYLE J.A., BIENS P., DOERENKAMP A. & JARDINS S. 1977. Angiosperm Cent pollen from the Pre-Albian Lower Cretaceous of Equatorial Africa. *Bull. Rech. Explor. Prod. Elf. Aquitaine*, 1(2): 451–473.
- HUGHES N.E., DREWY B.F. & LAING J.E. 1979. Barremian earliest angiosperm pollen. *Palaeontology*, 92(3): 513–535.
- JUHASZ M. & GOCZAN F. 1985. Comparative study of Albian monosulcate angiosperm pollen grains. *Acta biol. Szeged*, 31(1–4): 147–172.
- KREMP F.K. 1968. Probable Angiosperm pollen from the British Barremian to Albian strata. *Paleontology*, 11(3): 79–81.
- PIERCE R.L. 1961. Lower-Upper Cretaceous plant microfossils from Minnesota. *Minnesota Geological Survey Bull.* 42: 1–86.
- TAKHTAJAN A.L. & MEJER-MELIKJAN N.R. 1979. K morfologii pyl'tsevykh zeren semeystva Hydraceae v svyazi s evo sistematicheskimi polozheniem. (To the morphology of pollen from Hydraceae family in connection with its taxonomical state). *Botanicheskyy Zhurnal*, 64(12): 1774–1777. (in Russian).
- VORONOVA M.A. & VORONOVA N.N. 1995. Novye vidy pyl'tsy semeystva Protodegeneriaceae v Barrem-Aptskikh otlozheniyakh Ukrainy. (New species from Protodegeneriaceae family in the Barremian-Aptian deposits of Ukraine). *Geologicheskyy Zhurnal*, 3–4: 106–113. (in Russian).
- VORONOVA M.A. & VORONOVA N.N. 1996. Pyl'tsa pokrytosemennykh semeystva Protoeupomatiaceae N.N. Voronova v porodakh Barrema Ukrainy. (Pollen of angiosperms from the Protoeupomatiaceae fam. N.N. Voronova in the Barremian deposits of Ukraine). *Geologicheskyy Zhurnal*, 1–2: 204–208. (in Russian).
- WALKER J.W. & WALKER A.W. 1984. Ultrastructure of lower Cretaceous angiosperm pollen and their origin and early evolution of flowering plants. *Ann. Missouri Bot. Gard.*, 71: 464–521.

PLATES

Plate 1

All magnifications LM \times 1 000, SEM \times 10 000

Protodegeneriaceae family N.N. Voronova, 1995

1. General features of pollen grain under the light microscope (LM)
2. Fragment of surface of sporoderma in the aperture zone
3. Deformation of favose sporoderma
4. Protoeupomatiaceae family N.N.Voronova 1996
5. Bulges on the sporoderma surface in the aperture zone
6. Structure of sculptural elements in the aperture zone

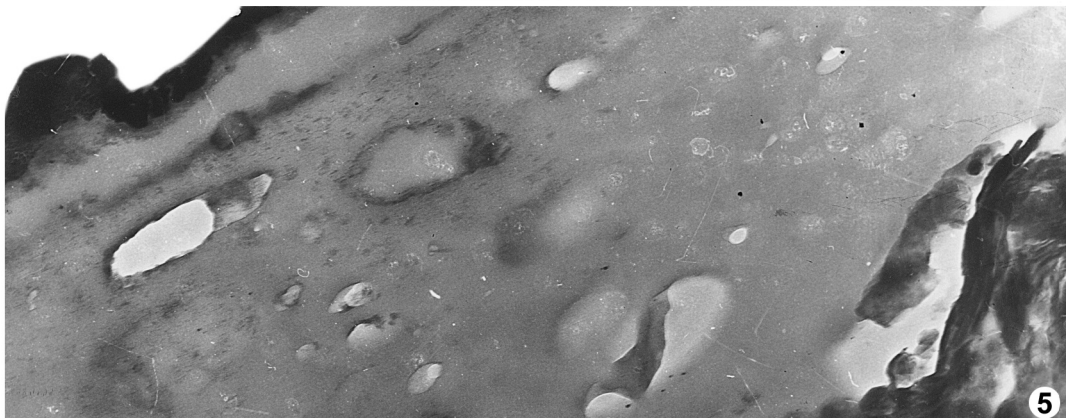
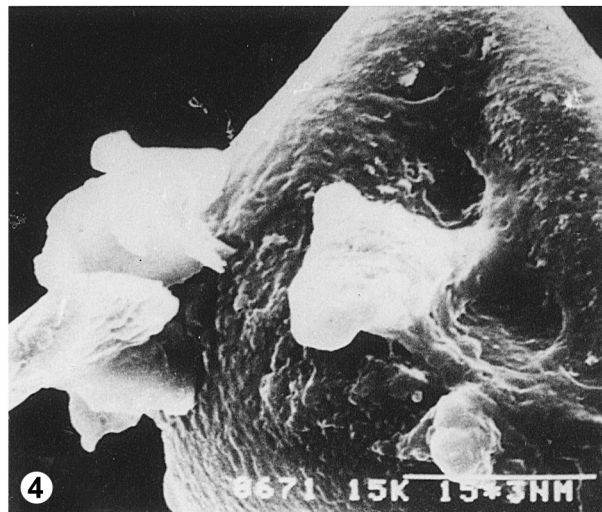


Plate 2

All magnifications LM \times 1 000, SEM \times 10 000

Protochlorantaceae fam. nov.

1. General features of pollen grain under LM
2. General features of pollen grain under SEM
3. Part of sporoderma surface in the aperture zone

Protocalycantaceae fam. nov.

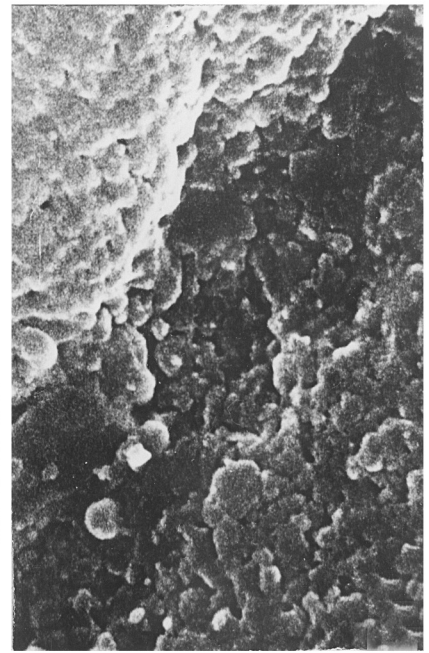
4. General features of pollen grain under LM
5. General features of pollen grain under SEM
- 6–7. Structure of sculptural elements in the aperture zone



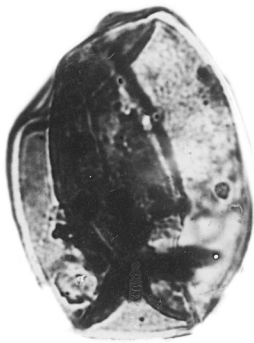
1



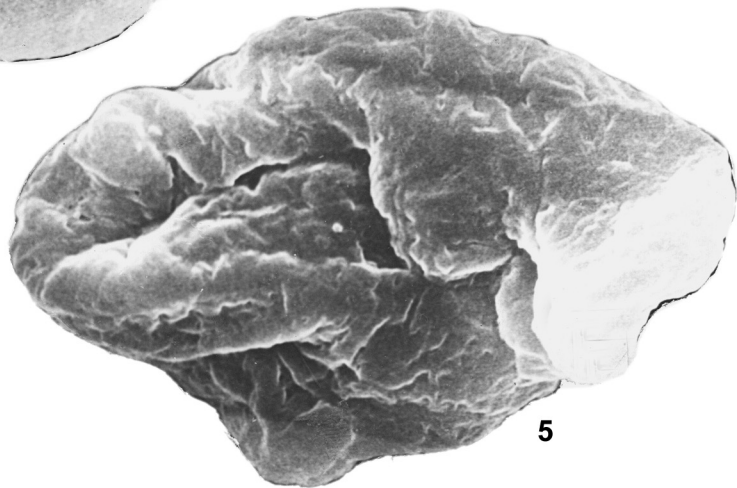
2



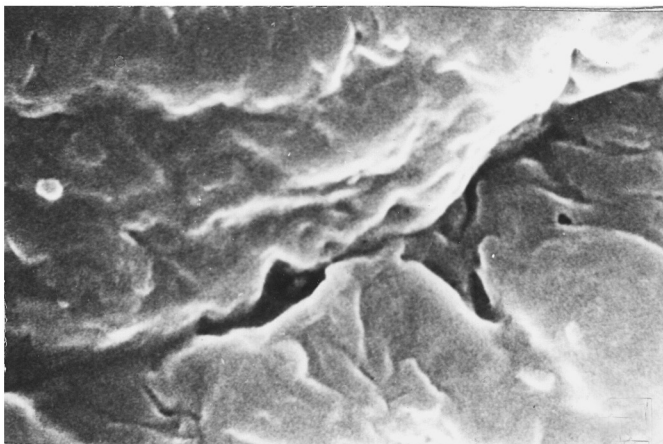
3



4



5



6



7

Plate 3

All magnifications LM \times 1 000, SEM \times 10 000

Protopiperaceae fam. nov.

1. General features of pollen grain under LM
2. General features of pollen grain under SEM
- 3–4. Structure of sculptural elements in the aperture zone

Protohydnoaceae family

5. General features of pollen grain under LM
6. General features of pollen grain under SEM
7. Part of sporoderma surface in the aperture zone

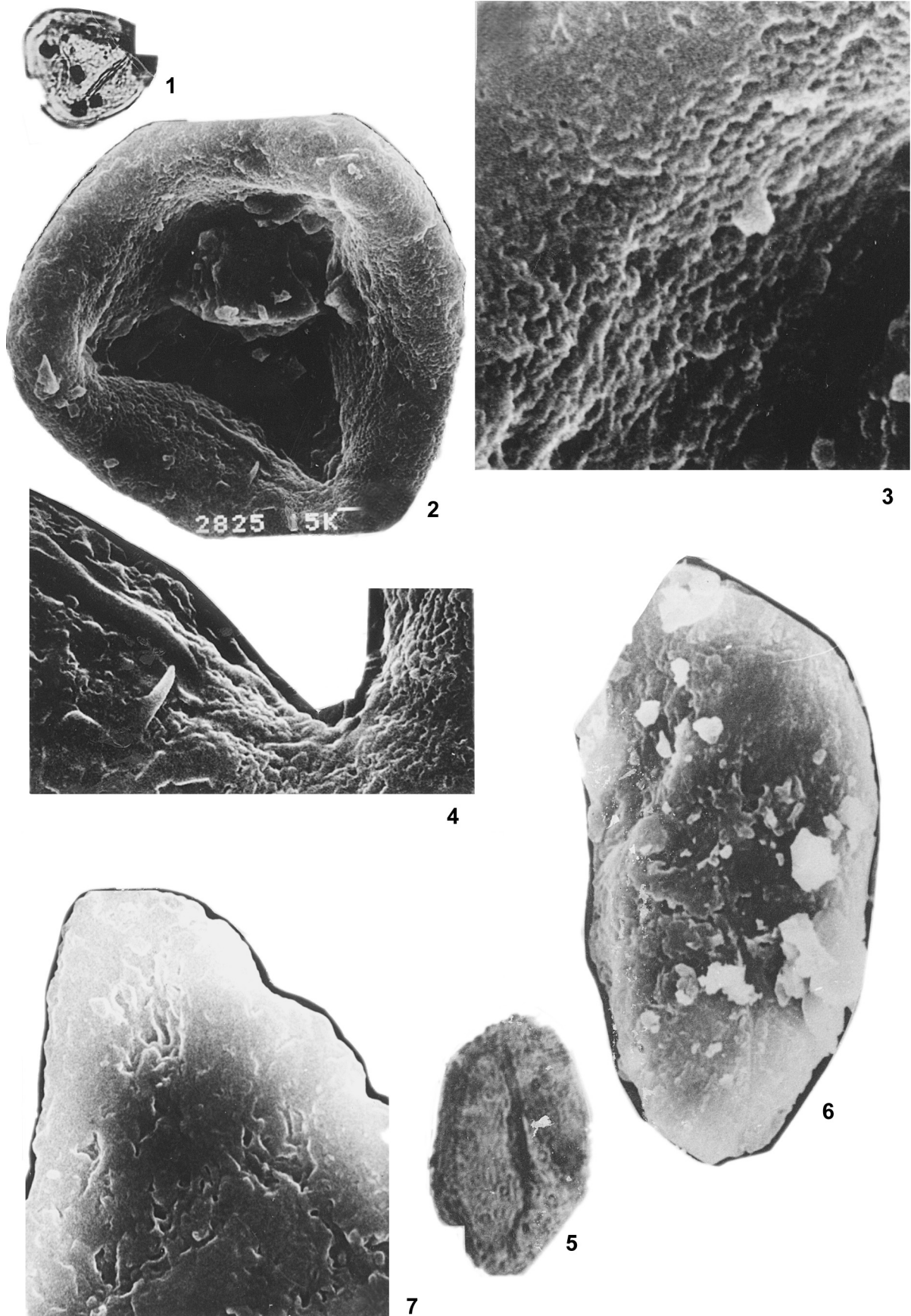


Plate 4

All magnifications LM \times 1 000, SEM \times 10 000

Protonymphaeaceae fam. nov.

1. General features of pollen grain under SEM
- 2–3. Some sculptural elements in the aperture zone. The sporoderma is eroded by canals. On the ectexine-endexine boundary there are being in ontogenesis columns.

Protohamamelidaceae fam. nov.

4. General features of pollen grain under LM
5. Part of pore surface covered by operculum
6. Sculpture of operculum

