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论克拉梭粉外壁的超微结构：西伯利亚侏罗纪的一个孢体

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提要　通过对西西伯利亚西南部某钻孔中侏罗统上部（Callovian, Tyumen 组）所获得的一个 *Classopollis* 的四孢体光学显微镜和切片的透射电镜观察研究后认识到，*Classopollis* 的外壁超微结构与它复杂的外部形态一致。外壁由几层组成：上部均质层，具不平的外、内表面，中间均质层，穴状层和下部均质层。在它们之间的柱状体和穴在赤道区更明显。这种结构与光学显微镜下所见的条纹圈相当。环沟（亚赤道沟）是由柱状区和远极面之间的外壁突然变薄形成的。近极区的穴较之赤道区的要小且形状较不规则。外壁远极面较近极面为薄，远极面隐孔区无穴。比较表明此种花粉与掌鳞杉科花粉形态相似。

关键词　*Classopollis*　外壁超微结构　侏罗纪　西西伯利亚

ON THE ULTRASTRUCTURE OF *CLASSOPOLLIS* EXINE: A TETRAD FROM THE JURASSIC OF SIBERIA

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Abstract A tetrad of *Classopollis* sp. from the southwestern region of Western Siberia (borehole Yarskaya 3, near city Tyumen) in the upper Middle Jurassic (Callovian Tyumen' Formation) was investigated using light microscope and transmission electron microscope. The exine ultrastructure of *Classopollis* corresponds to its complex external morphology. The exine can be defined as regularly alveolate exine (on some regions as columellate exine). It consists of the following layers: the upper homogenous layer, with uneven external and internal surfaces, the intermediate homogenous layer, the alveolate layer, and the lower homogenous one. Columellae and alveolae between them are more distinct at equatorial regions. This structure corresponds to striate ring that is visible through light microscope. A rimula (subequatorial canal) is presented by a sudden narrow thinning of exine between this columellate area and the distal side. Alveolae of the proximal exine are smaller and less regular in form than those at equatorial region. Distal side of exine is thinner than proximal one. In the area of cryptopore the distal exine is deprived of alveolae. The comparison of the present ultrastructural data and the data on fine morphology obtained by other palynologists affirms the similarity between the pollen under investigation and pollen of Cheirolepidiaceae.

Key words *Classopollis,* exine ultrastructure, TEM, Jurassic, Siberia

1 INTRODUCTION

Representatives of the genus *Classopollis* **Pflug have been repeated objects of diverse palynological investigations. The abundance of** *Classopollis* **pollen in Mesozoic deposits has stimulated its application in stratigraphy (Medus and Reyre, 1966; Medus, 1970; Rovnina, 1976). A range of papers is devoted to the nomenclatural and taxonomic problems concerning this genus (Pocock and Jansonius, 1961; Traverse** ***et al,*** **1975). The unique mor-**

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phology with a complex of peculiarities has engaged the attention of morphologists (Pettitt and Chaloner, 1964; Medus, 1977; Courtinat, 1980; Taylor and Alvin, 1984; Rowley and Srivastava, 1986). The systematic assignment of the genus was revealed (Barnard, 1968; Hlustik and Konzalova, 1976a,b). Considerable amount of variation of ultrastructure (Medus, 1977; Rowley and Srivastava, 1986), ultrasculpture (Reyre, 1968, 1970), and elements, attaching pollen grains in tetrads, was demonstrated (Scheuring, 1976; Courtinat, 1980). Some developmental stages in exine ontogeny were proposed (Taylor and Alvin, 1984). Ecology of *Classopollis-producmg*' plants (Vakhrameev, 1981; Rovnina, 1996; Van Konijnenburg-van Cittert and van der Burgh, 1996) and its possible entomophily were discussed (Krassilov *etai,* 1997), and several reviews were published (Srivastava, 1976; Alvin, 1982; Pocock *etaL* 1990; Kedves, 1994).

Thus, *Classopollis* is an example of a quite well studied genus. Nevertheless, we consider the continuation of its electron-microscopic investigation to be very promising. If as much as possible comparable data on the ultrastructure of *Classopollis* from deposits of different regions and different ages are available, it will be possible to reveal the complete morphological variability of the genus and to determine whether it reflects the intraspecific or interspecific variability, or the degree of preservation; and, as a result, to understand the exine evolution of Cheirolepidiaceae pollen.

2 MATERIAL AND METHODS

A tetrad of *Classopollis* sp. Pflug from the southwest region of Western Siberia (borehole Yarskaya 3, near city Tyumen') in the Callovian (the interval 1460.0-1454.2 m, Tyumen' Formation) was investigated (Text-fig. 1). The assemblage contains numerous *Classopollis* (about 49%), rare pollen of Ginkgoaceae, Caytoniales, bisaccate pollen with well distinguishable sacci, and spores of *Leiotriletes, Gleicheniidites* (Rovnina, personal communication). The material was taken from micropaleontological collection of IGIRGI (Institute of Geology and Exploitation of Combustible Fuels, Ministry of Fuel Power Engineering and Russian Academy of Sciences).

The tetrad was studied through light microscope. Photographs were taken with oil immersion. Then the cover glass was taken off the slide. The small piece of glycerin-jelly, which contained the tetrad, was cut with a needle, placed in a capsule and embedded in epon (see Meyer-Melikian and Telnova, 1991 for the detailed description of the method). The block was so oriented that the series of sections were placed in the upper third of the tetrad through the darker pollen grain and the two adjacent ones (Text-fig. 2A). The sections were contracted according to Reynolds method. Ultramicrographs were obtained with a Hitachi H-600 TEM.

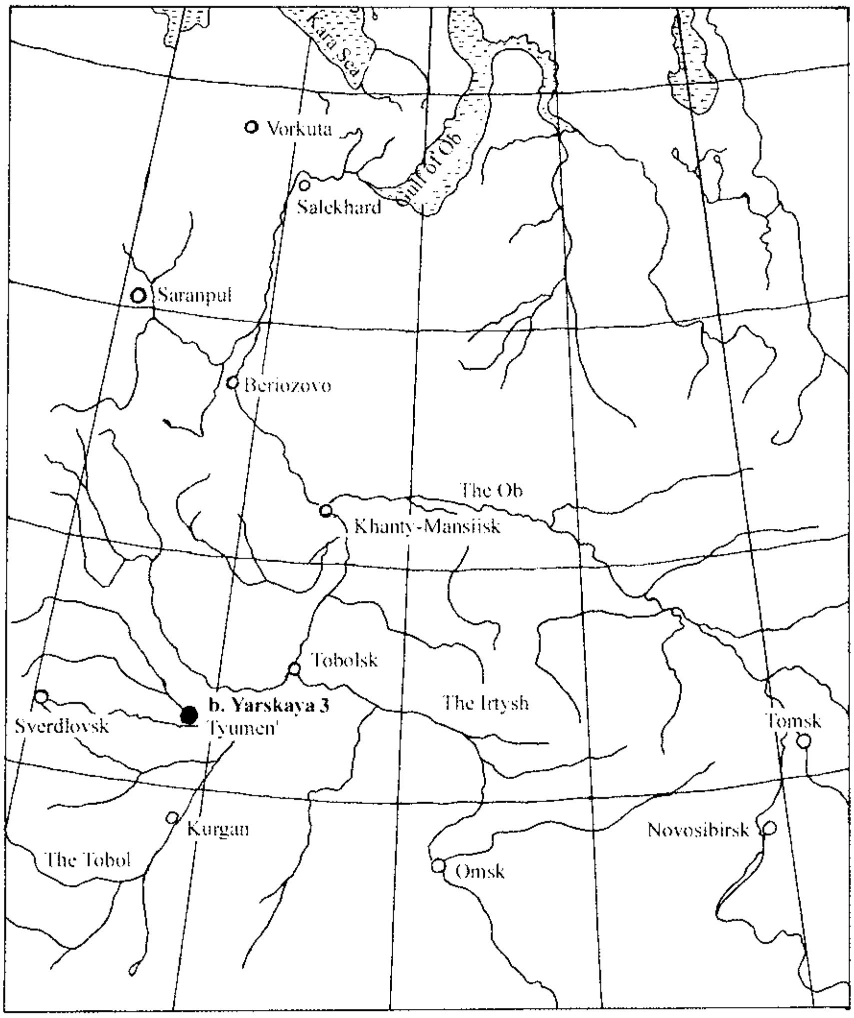
3 MORPHOLOGICAL DESCRIPTION AND INTERPRETATION

The tetrad is tetrahedral (Plate I, 1). Pollen grains of the tetrad were numbered for handy description (Text-fig. 2A). The pollen grain no. 1 lies in distal-polar view. Other pollen grains of the tetrad are flattened in such a way, that we can see the equatorial parts of the pollen grains. The equatorial thickening is well developed on the all four pollen grains. Judging from pollen no. 1 we can hypothesize that striae are narrower than the whole width of equatorial thickening. An optical section of exine in the upper part of pollen no. 1 allows us to distinguish the columellate structure of the equatorial ring. There are rimulae (subequatorial canals) on the pollen nos. 3 and 4 in lateral view. On the pollen no. 1 we can see both rimula and cryptopore. We cannot say anything about proximal trilete mark.

Ultrathin sections show that the exine of pollen is strongly flattened (Plate I, 2-5). Sometimes it is difficult to distinguish the hollow of pollen.

All the obtained sections are placed in the upper third of the tetrad (Text-fig. 2A) and cut the first, second and third pollen. The right section (Plate I, 4; Text-fig. 2C) corresponds to the darker pollen (pollen no. 1); the lower section does to the pollen no. 3 (Plate I, 4; Text-fig. 2C); and the upper section does to the pollen no. 2 (Plate I, 4-5; Textfig. 2C). The montage of section is placed in the central part of pollen grain no. 1, at the level of cryptopore; in the upper part of pollen grain no. 2 (the section is oblique, in the upper part it is superficial, the hollow of the pollen is visible in the lower part of the section); the section of the pollen grain no. 3 is a fragmentary section of the upper part of the pollen.

To reveal the general ultrastructure of exine we have examined a part of the section of the pollen grain no. 2 (Plate I, 3; Text-fig. 2B). The whole exine has equal contrast, but divided into several layers. The most upper layer of exine



Text-fig. 1　Map showing the locality - borehole Yarskaya 3, near the city Tyumen

is tectum. The tectum has equal thickness. Both the upper and inner surfaces of this layer are uneven. There is a narrow space between the tectum and lower layers. The next layer is the inner tectum or tectum of columellae. The columellae represent quite wide and long partitions. There are distinct alveolae between the columellae. The most inner layer is homogenous. This layer may be endexine (considering the poor contrast of sections). Further, the flattened hollow of the pollen grain is visible. The upper layer of the opposite side of the section is homogenous. There are small alveolae, irregular in form. These alveolae differ from the elongated regular alveolae previously discussed. The most inner layer is homogenous. We can see in the left part of the micrograph, that the upper superficial layers connect with columellae not so close as that at the previously described region.

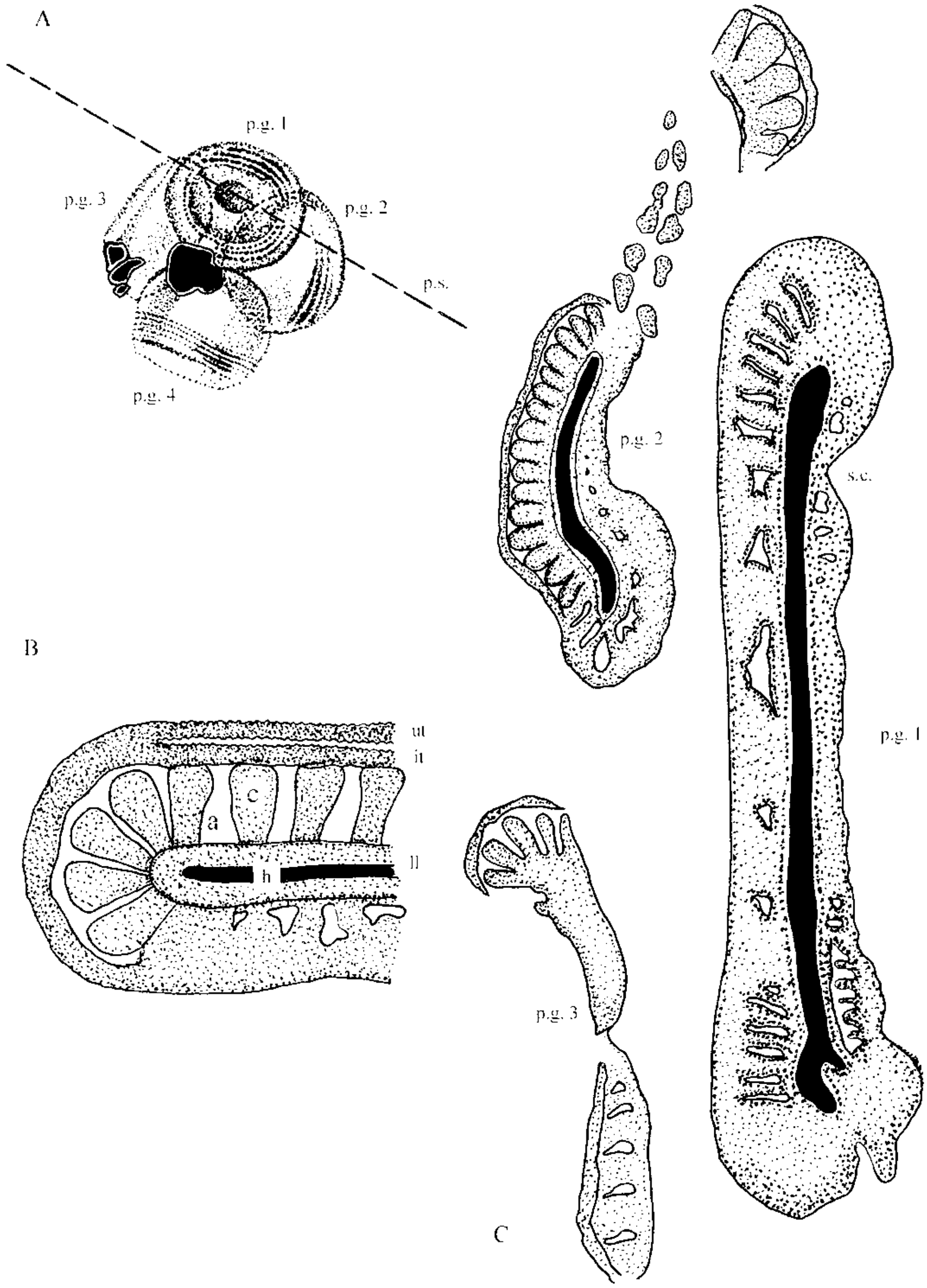
These morphological peculiarities (namely, upper and inner tecta, columellae, and homogenous inner layer) are characteristic of equatorial ring. This type of ultrastructure is visible on all cut pollen grains at the regions, which correspond to equatorial thickenings.

Columellate structure is distinguished at the optical section of the pollen grain no. 1 as well (Plate I, 1). The striae of *Classopollis* are hidden by two solid surface layers of the exine and, thus, are not visible through SEM (according to data of other authors), but are visible in transmitted light. Thus, they are not superficial sculptural elements, but elements of inner structure.

Although this columellate structure is characteristic of the whole equatorial thickening, according to light photos, there are only five to six striae. We consider that the structures, visible in transmitted light as striae, are represented by columellae fused into ridges. These ridges are separated by canals, which are the result of fusion of alveolae. The width of canals may vary, so that ribs have uneven margins and may undulate. Striae discontinuously engird the whole pollen grain at the equator. Columellae do not fuse into ridges at those regions, where there are no

striae in transmitted light. Columellae look in transmitted light as scabrate ornamentation, but do not look as striae. It is very like that the species of the genus *Classopollis* with poorly developed striae (or without striae) but with equatorial ring have this columellate exine that becomes thicker at the equator.

As the sections of pollen grains nos. 2 and 3 are oblique and partly fragmentary, although sections of pollen grain no. 2 demonstrate equatorial morphology sufficiently well, the following description of proximal and distal morphology (including the conclusions on relative thickness of different regions of pollen exine) are mainly based on pollen grain



Text-fig. **2** Showing the tetrad and plane of its sectioning and exine ultrastructure of pollen grains
(A) The tetrad of *Classopollis* under study, p.g. **1** - pollen grain no. **1,** p.g. **2** - pollen grain no. **2,** p.g. **3** - pollen grain no. **3,** p.g. **4** - pollen grain no. **4,** p. s. - plain of sections. (B) The scheme of ultrastructural peculiarities (see also Plate **I, 3).** ut - upper tectum, it - inner tectum, a - alveolae, c - columellae. **11** - lower layer, h - the hollow of the pollen grain. (C) The scheme of the ultrathin section of the tetrad (see also Plate **I, 4-5).** s.c. - subequatorial canal.

no. 1.

The exine of the proximal side morphologically differs from the equatorial exine. The upper layer of the proximal side is homogenous. It is difficult to distinguish sublayers in this layer (two tecta are well distinguished only in the regions of equatorial ring and rimula, at other regions they fuse into a single layer). Middle layer of the proximal side is also homogenous, but contains rare irregular alveolae. The inner homogenous layer is identical with that of equatorial region.

In the rimula (subequatorial canal) region exine suddenly becomes thinner (Plate I, 2). Only two upper homogenous layers and the inner one remain. The columellate layer disappears.

Distal exine is thinner than the proximal one and the equatorial one. There are upper homogenous, middle alveolate, and inner homogenous layers. The middle layer disappears in the region of cryptopore (Plate I, 4, central region of the distal side of pollen grain no. 1 and Text-fig. 2C). Accordingly, cryptopore and rimula are identical in ultrastructure (Plate I, 2 and 4).

4 CONCLUSION

The most important feature, which has been revealed during the present investigation, is the columellate structure of the ectexine. This serves as a distinguishing ultrastructural feature of Cheirolepidiaceae pollen and allows determining dispersed pollen of this family on the basis of TEM even in case of poor preservation. We distinguish two homogeneous layers (named upper tectum and inner tectum), which are situated more superficially than the columellate layer. These homogeneous layers are comparable with upper and inner tecta, visible on the sections, made by Taylor and Alvin (1984) and by Medus (1977). Endexine of different representatives of the genus varies considerably. It may be multilamellate (Taylor and Alvin, 1984; Pettitt and Chaloner, 1964), or be represented by a single lamella (Rowley and Srivastava, 1986) and, probably, be homogenous (present investigation).

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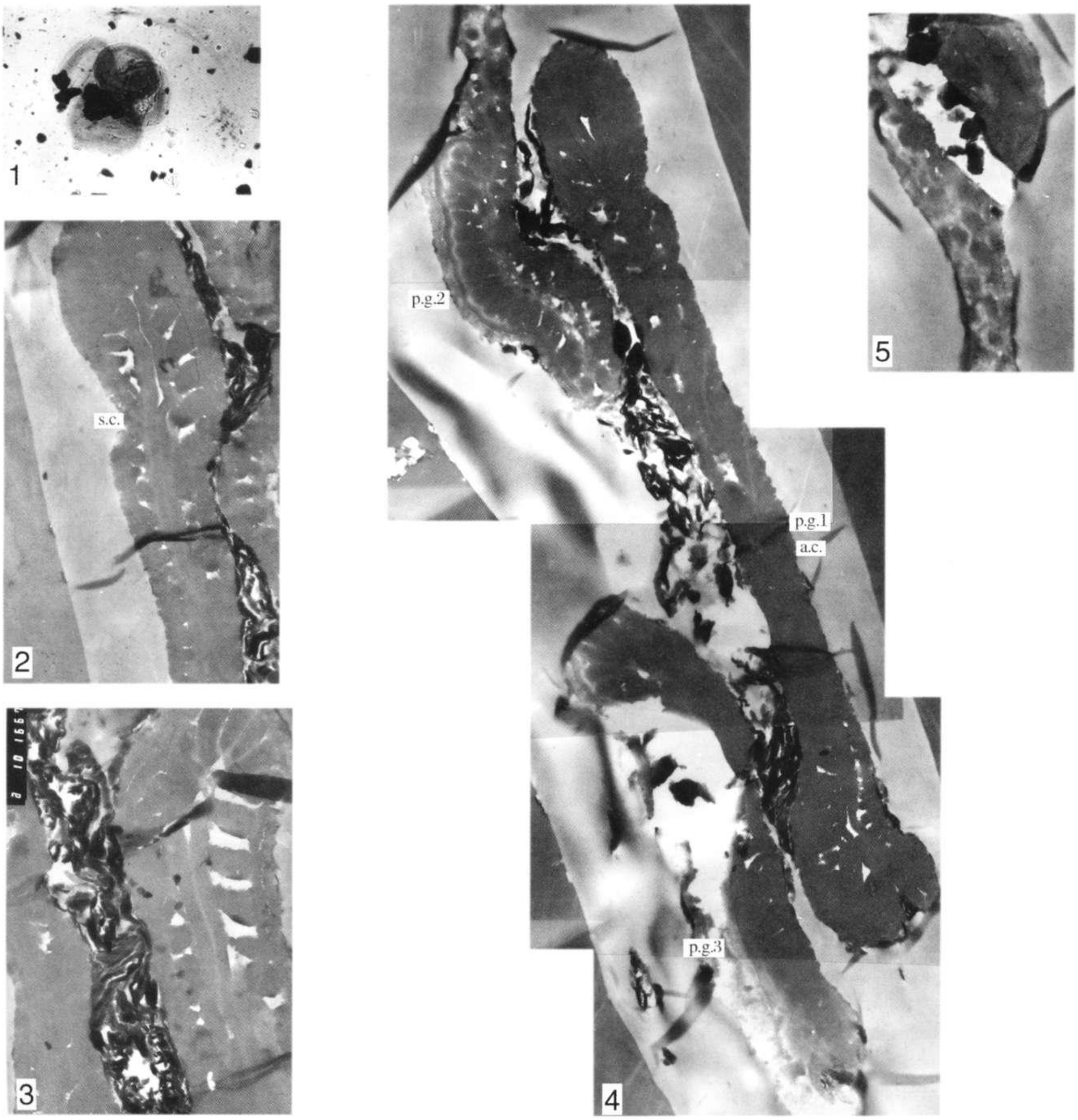

EXPLANATION OF PLATE I

1. Tetrad of *Classopollis.* LM.
2. Pari of the section of the pollen grain no. I. TKM. (\ 8000). s.c. - subequatorial canal.
3. Part of the section of the pollen grain no. 2. equatorial region of the pollen. TKM. (\ 10000).
4. Montage of the ultrathin section of the tetrad under study. TKM. (x 6000). p.g. 1 - pollen grain no. 1. p.g. 2 - pollen grain no. 2. p.g. 3 - pollen grain no. 3.
5. Montage of the ultrathin section of the tetrad under study (continuation). TKM. (\ 6000).