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Morphology and ultrastructure of some monosaccate pollen grains of *Cordaitina* Samoilovich 1953 from the Permian of Russia[*]

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ABSTRACT. *Cordaitina* pollen grains from three localities of the Perm Region (Kungurian Stage) of Cis-Urals and Tunguska Basin (Kazanian? Stage) of Siberia were studied under LM, SEM, and TEM. The pollen grains are monosaccate, circular-elliptical, with a small trilete or monolete scar, which is occasionally lacking. The saccus appears smooth under SEM, finely reticulate under LM, reflecting in transmitted light the interior partitions occasionally superimposed by the surface folds. The saccus is filled with rather loose alveolate structure with mostly radial ectexinal partitions that reach the endexine in the protosaccate type of pollen grains. Alternatively, the partitions, or some of them, are unrooted forming an intermediate protosaccate/eusaccate infrastructure. This variation is gradational rather than discrete and is correlated with the thickness of the saccus ectexine: the thicker sacci tend to be more definitely eusaccate. A finely punctate LM view of the corpus reflects a peculiar crochet-like sculpture formed of interlaced threads or rugae (under SEM), which are confacered here as a diagnostic feature of the Permian *Cordaitina*. In TEM micrographs, the ectexine attenuates confacerably towards the polar regions, while its outermost layer, the tectum, becomes finely undulate forming the crochet-like pattern. The innermost layer, or endexine, is relatively thin over the distal face and at the saccus/corpus border increasing proximally and attaining the maximal thickness towards the proximal scar. It is interrupted at the borders of the proximal laesurae. Distally the endexine appears dense and homogeneous, although proximally, and especially over the proximal scar, it becomes loose, layered, formed either of vaguely defined lamellae or of fine granules. This differentiation suggests an ontogenetic layering of the endexine. The ultrastructural data indicate proximal rather than distal germination placing the Permian *Cordaitina* in the prepollen grade. The potential palynotaxonomic significance of the type of sculpture, saccus infrastructure and apertural morphology is discussed.

KEYWORDS: pollen grains, pollen ultrastructure, gymnosperms, cordaites, Permian, Russia

INTRODUCTION

The Late Palaeozoic floras of the northern temperate realm (the Angara realm of the palaeophytogeographical classification of Vakhrameev et al. 1978) are dominated by the ribbon-shaped parallelinerved leaf morphotypes (*Cordaites*, *Rufloria*) in association with reproductive organs (*Vojnovskya*, *Gaussia*, *Krylovia*, etc.) that are assigned to the endemic families Vojnovskyaceae and Rufloriaceae, treated here after Meyen (1982, 1987) as cordaites. They are constantly accompanied by the *Cordaitina*-type

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saccate pollen morphotypes apparently produced by these cordaitalean plants. The natural affinity of *Cordaitina* pollen grains of Permian age was also confirmed by Meyen (1982, 1987) who had extracted them from the male fructifications *Kuznetskia* (Vojnovskyaceae) and *Pechorostrobus* (Rufloriaceae).

After a long period of abundant occurrences in the majority of the Late Carboniferous and Permian fossil plant localities of Siberia and the Urals, the Angaran cordaites declined during the Tatarian lacking in the latest Tatarian (Vyatkian). However, *Cordaitina* extends far beyond the level of cordaite extinction as documented by macrofossils. It is not uncommon in the Early Triassic (Yaroshenko & Gomankov 1998), suggesting its heterogeneity and leaving an open question the systematic affinity of this long-living pollen genus as an entity.

With this controversy in mind we undertook ultrastructural study of the Permian and Triassic monosaccate pollen grains. This paper deals with the ultrastructure of the Permian members of the genus *Cordaitina* focusing on interpretation and palynotaxonomic significance of the sculptural characters, the types of sacci and the inner layer (endexine). This will be followed by a description of the Triassic forms and implications for palynomorphological evolution and systematic affinity.

MATERIAL

The material comes from the samples collected by A. G. Sharov (sample no. 3737), N. I. Emelyanov and G. N. Sadovnikov (sample no. 3761), and V. S. Skundin (sample no. 47(2)). Samples nos 3737 and 3761 are deposited in the Komarov Botanical Institute of the Russian Academy of Sciences (St.-Petersburg), and sample no. 47(2) in the Geological Institute of the Russian Academy of Sciences (Moscow).

Sample no. 3737 (Fig. 1) comes from the Irenian Horizon of the upper Kungurian Stage, cropping out on the left bank of the Sylva River, Perm Region, the stratotypic area for the Kungurian (Permyakov 1938). The locality is rich in various plant megafossils (Meyen 1997, Naugolnykh 1998).

The palynological assemblage is dominated by monosaccate pollen grains: *Cladaitina* (about 23%), *Cordaitina* (4%), *Reticulatina* (4%), *Iunctella* (4%), *Gemmites* (2.5%), and *Florinites* (0.5%). The bisaccate genus *Protohaploxypinus* is also abundant (21%) represented by several species of which *P. perfectus* (Naumova) Samoilovich is the most common (10.5%). Other members of the assemblage are *Piceapollenites* and *Platysaccus* (infraturma Disacciatrileti 13.5%) and the asaccate striate *Vittatina subsaccata* Samoilovich (9%), *V. connectivalis* (Zauer) Utting (1.5%), and *Weylandites tataricus* Gomankov (1.5%). The *Vesicaspora* morphotype accounts for 3.5% of the assemblage. The genera *Striatoabieites*, *Hamiapollenites*, *Limitisporites*, and *Yugasporites* are represented by solitary pollen grains. Spores of *Apiculatisporites* and *Kraeuselisporites* are extremely rare in the assemblage making up less than 0.3% of the total amount of the miospores.

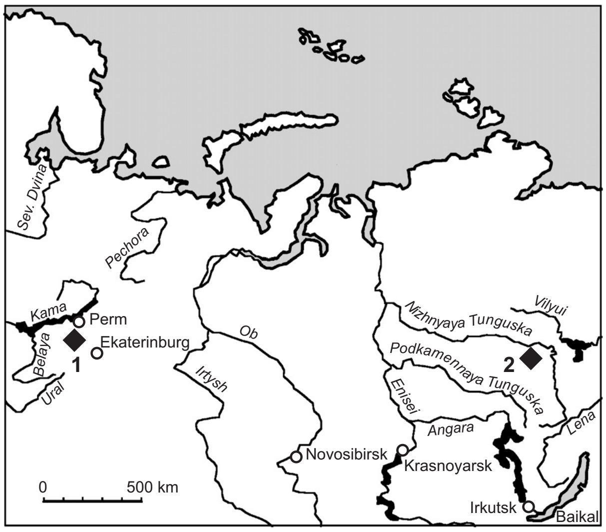

Fig. 1. The map of the localities studied. **1** – Locality of sample no. 3737, **2** – Locality of samples nos 3761 and 47(2)

Sample no. 3761 (Fig. 1) comes from the upper part of the Pelyatka Formation of the Kazanian (?) Stage, Middle Permian, cropping out on the right bank of the Ilimpeya River, 3 km below the mouth of its tributary Bol'shaya Khovorikta River, the Tunguska Basin (Gomankov & Meyen 1980). The succession of cordaitalean assemblages of the Tunguska Basin has been subdivided by Meyen (1982) into a number of stages, of which the fourth ruflorialean-cordaitalean stage, RC-4, occurs at the level of the Pelyatka Formation. The megafossil assemblage (numbers of specimen in brackets) consists of *Phyllotheca* (2), *Pecopteris* (1), *Cordaites* (30), *Rufloria* (124), *Crassinervia* (2), *Lepeophyllum* (1), *Cladostrobus* (3), and *Tungussocarpus* (16). Sporangiate strobiles *Cladostrobus lutuginii* Zalessky contained pollen grains of the *Cladaitina* type studied by Maheshwari and Meyen (1975).

Cladaitina dibneri Maheshwari & Meyen, originally described from this locality, constitutes about 55% of the palynological assemblage. Other components are pollen grains of *Cordaitina*, *Samoilovichisaccites*, and *Crucisaccites* (summarily ca. 2%). Spores (mostly *Acanthotriletes* and *Neoraistrickia*) account for 41.5% of the assemblage.

Sample no. 47(2) also comes from the upper part of the Pelyatka Formation (Fig. 1), the Kazanian (?) of the Ilimpeya River 1.5 km upstream of the Yangurakta Island, the Tunguska Basin. Yaroshenko preliminary studied the palynological assemblage (Yaroshenko 1967) and revised the palynotaxonomy for the present paper. The assemblage is dominated by monosaccate pollen (over 60%). Pollen taxa include *Cordaitina* spp.

(16%), *Cladaitina* spp.: *Cladaitina dibnerae* Maheshwari & Meyen and *Cladaitina* sp. (44%), *Circulisporites* (1.0%), and *Vitreisporites* (0.5%). Among spores, *Raistrickia obtusosetosus* Luber, *R. rectispinus* (Luber) Virbitskas, *Neoraistrickia* spp. and *Horriditriletes* sp. constitute about 32% of the assemblage. Less prominent are *Retusotriletes nigritellus* (Luber) Foster (2.0%), *Nigrisporites marginatus* (Portn.) Drjagina (3.0%). *Calamospora* sp., *Punctatisporites* sp., *Verrucosisporites* spp., *Apiculatisporis* sp., *Turrisporites* sp., and *Remysporites psilopterus* (Luber) Luber are occasionally present.

The assemblage is tentatively assigned to the Kazanian based on correlation with the *Cladaitina*-dominated *Cladaitina dibnerae – Turrisporites sibiricus* assemblage of the Tutonchana Formation, the Nizhnyaya Tunguska River near Gagarii Island (Yaroshenko 1990). Both the locality 47(2) and the Gagarii Island assemblages share their dominant *Cladaitina* elements with our sample no. 3761.

METHODS

To extract miospores, the rock samples were crushed and treated consecutively with concentrated HCl, HNO_3, and 5% solution of KOH in order to remove the carbonates and to clarify the organic matter. The sediment was centrifuged in the heavy liquid (CdJ_2). The organic particles come to the surface were gathered and then kept in distilled water.

Individual pollen grains found under dissecting microscope were picked up with fine wooden needle or extracted with Carl Zeiss Micrurgie equipment and placed in glycerin for LM. For scanning electron microscopy the pollen grains were mounted on standard stubs, coated with gold-palladium and examined under Hitachi S-405A SEM. For transmission electron microscopy individual pollen grains were removed from slides or SEM stubs with a needle and embedded in epon (technique in Meyer-Melikyan & Telnova 1991). The pollen grains were sectioned by LKB 3 ultramicrotome with diamond knife and examined under Hitachi H-600 TEM.

NOTES ON MORPHOLOGY AND TAXONOMY

After the genus *Cordaitina* was established by Samoilovich in 1953, various pollen forms were assigned to it. As Dibner (1971) has mentioned, palynologists (especially in the former USSR) tended to assign nearly all monosaccate pollen grains, and even some spores, to this genus, in effect enormously extending its limits. Some authors (e. g. Medvedeva 1960, Hart 1965) recognized about twenty species of *Cordaitina* with rather indistinct morphological boundaries making the intrageneric taxonomy intricate and difficult for practical application.

Dibner (1971) in the course of her revision of Angaraland cordaitalean pollen has restricted *Cordaitina* to monosaccate pollen grains with paraconditional saccus attachment. According to Dibner (op. cit.), both proximal and distal saccus roots of *Cordaitina* are circular and are located so close to the corpus equator that they merge with it into a single contour in the polar view under LM. At the same time the pollen grains were confacered as eusaccate warranting such terms as “saccus root” and “paraconditional attachment”.

However, our recent studies of ultrastructure in Permian saccate pollen of Angarian realm revealed a wide occurrence of protosaccus-like structures with a gradual transition from corpus to saccus exine (Zavialova et al. 2001). In many cases, the endexine delimiting the corpus is not preserved and any definite line of “saccus attachment” cannot be recognized at all. In this connection, the following questions arise concerning the morphology of *Cordaitina*:

– do these pollen grains have any saccus at all?

– is it possible to speak of any “attachment” of saccus to corpus as a character delimiting genera of monosaccate pollen grains?

– what is the nature (and taxonomic significance) of closed lines (single or several) discernible under LM on *Cordaitina* pollen grains as concentric with their outlines?

The results of the ultrastructural observations for *Cordaitina* pollen grains are described below. On the whole, the archetype of *Cordaitina* proposed by Dibner (1971) has been retained in our work as well. All examined pollen grains demonstrate an equatorial thickening of ectexine visible also under SEM (Pl. 5, fig. 2, Pl. 6, fig. 2, Pl. 7, fig. 2, Pl. 9, fig. 2). Its inner boundaries (usually both proximal and distal ones) are rather prominent due to the sharp increase of infratectal ectexinal elements (Pl. 3, fig. 1, Pl. 4, fig. 4, Pl. 5, fig. 3, Pl. 6, fig. 3, Pl. 8, figs 1, 5, Pl. 10, figs 1, 4). Moreover, the ectexinal sculpture changes at these boundaries (Pl. 6, fig.4). So we can reasonably define this feature as a saccus with quite distinct roots and confacer it as being attached to the corpus in paraconditional manner (Bharadwaj & Tiwari 1964, Maheshwari 1967).

A discrepancy with Dibner’s interpretation of *Cordaitina* morphology (preventing us to accept completely Dibner's emendation and to use the name *Cordaitina* Samoilovich emend. Dibner 1971 in the title of our paper) consists in that proximal and distal roots of the saccus do not merge with the corpus equator in polar view being located rather far from it. The corpus equator of our specimens is usually visible in LM polar view as a clear and flat dark line running between the saccus root and the outer contour of the pollen grain. The absence of such line distinct from the saccus roots in most of the specimens figured by Dibner (1971) may be preservational – the endexine delimiting the corpus was not preserved in such specimens. Thus, in all species of *Cordaitina* the actual distance between the corpus equator and the saccus equator would be much less than that given by Dibner.

Dibner (1971) has reduced the number of species of *Cordaitina* to five, viz. *C. uralensis* (Luber) Samoilovich (type species), *C. rotata* (Luber) Medvedeva, *C. punctata* (Luber) Hart, *C. abutiloides* (Andrejeva) Dibner and *C. schopfii* (Madvedeva) Dibner. Although the distinctions between these species remain not very clear and need confirmation by ultrastructural study of topotypic material we can adopt this classification for the time being. According to it, all our specimens can be identified as *Cordaitina rotata*. Many "forms" (intraspecific taxa) were described within this species by previous authors, but only one, *C. rotata* f. *arctica* (Kara-Murza) Dibner, which is characterized by the diameter of more than 100 μm, pertains to our specimens to accommodate the largest of them (No. 3737/204-9(E)).

MORPHOLOGICAL DESCRIPTIONS

POLLEN GRAINS FROM LOWER PERMIAN

Genus **Cordaitina** Samoilovich 1953

Species ***Cordaitina rotata*** (Luber) Medvedeva 1960

Specimen No. 3737/204-7(E)

Pl. 1, figs 1–4, Pl. 2, figs 1–4, Pl. 3, figs 1–5, Pl. 4, figs 1–6

Description. The pollen grain is elliptical, 66 × 78 μm, monosaccate, with an annular equatorial saccus about 9 μm wide. The corpus equator is visible through the ectexine as a thin dark contour. The saccus is finely reticulate and the reticulum spreads some distance over the corpus equator as if the saccus were marginally clasping the corpus (paracondition). The rest of the corpus is nearly smooth. A well-defined trilete scar of the proximal face appears as an open triangle with the faces about 12 μm long (Pl. 1, fig. 1).

The pollen grain has been sectioned over three lines, I – III in Fig. 2. Section I (Pl. 1) cuts the saccus not reaching the corpus. The saccus exine is about 3.6 μm thick showing two layers, the tectum and infratectum, enclosing a central cavity (Pl. 1, fig 2). The tectum is relatively thin, of nearly uniform thickness about 0.30–0.45 μm, gently undulate, perforated with widely scattered pores 0.15–0.3 μm. The infratectum is much thicker, asymmetrical, with the distal (recognized by the sections cutting across the haptotypic mark, section III, Pl. 3) partitions straight or slightly arched, widely spaced, unbranched or rarely branched. The proximal infrastructure is more chaotic, consisting of curved or punctuate irregular ectexinal elements, conceivably oblique to the plane of the section (Pl. 1, figs 2, 4). The central part devoid of infrastructure is elliptical, 13.6 × 3 μm. Owing to the presence of a central hollow, which is quite narrow in comparison with the infratectal structure, the saccus can be defined as intermediate between eusaccate and protosaccate architectures.

The subsequent section (II) cuts across the periphery of the corpus revealing the inner

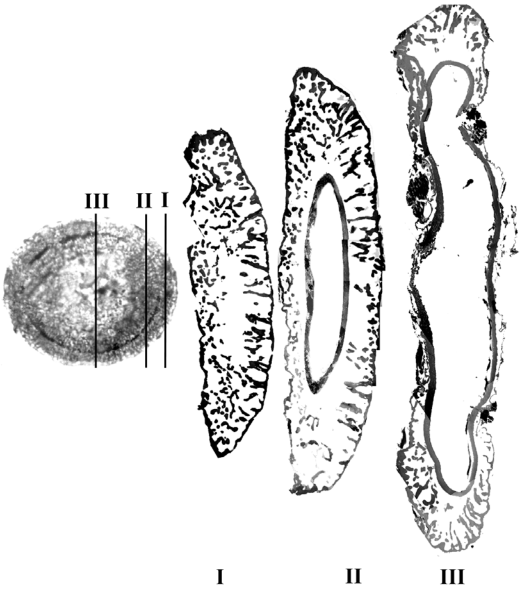

Fig. 2. Pollen grain of *Cordaitina rotata*: position of sections, I–III over specimen No. 3737/204-7(E)

exinal layer (endexine; Pl. 2). This section also confirms an intermediate character of the saccus ultrastructure: the majority of the partitions are not rooted in the inner layer although occasional partitions approach it rather closely. The distal ectexine is thicker than the proximal one (4.08–4.23 and 1.81–3.47 μm respectively). Different orientation of the proximal and distal partitions, though evident, is not as conspicuous as in the previous section through the saccus (compare Pl. 1, fig. 2). The endexine is likewise asymmetrical, but of reverse proportions, 0.91–1.12 μm proximally, 0.6–0.68 μm distally. Moreover, on the distal face it is denser and almost homogeneous at magnifications below 6 000, with narrow, widely scattered slits faintly visible at higher magnifications only, while proximally it is strewn under numerous distinct elongate slit-like alveolae 0.06–0.38 μm long, 0.05–0.11 μm wide (Pl. 2, fig. 3). We refrain from describing such ultrastructure as lamellate because actually it appears as narrowly alveolate (under cleft-like alveolae) on the proximal face and almost homogeneous on the distal face (Pl. 2, figs 1, 2).

The last section (III) cuts through the polar (central) regions of the pollen grain showing the saccus and both sides of the corpus, including the haptotypic mark of the proximal face (Pl. 3). The saccus ultrastructure does not differ from the described above (compare Pls 1, 2). The distal tectum of the corpus appears as a thin undulate homogeneous layer about 0.07 μm thick resting directly on the inner layer or locally separated from it by a narrow space, which fluctuates from 0.25 to 1.38 μm (Pl. 3, fig. 5). Undulations of the tectum apparently correspond to the surface features observed under SEM in the specimen No. 47(2) and elsewhere (Pl. 5, fig. 1, Pl. 6, fig. 4, Pl. 7, fig. 4, Pl. 9, fig. 4).

In the peripheral region, the inner layer is of uniform thickness in both faces of the grain, increasing in thickness towards the median plane, whereas in the central region it acquires an asymmetry being 0.53–0.80 μm distally, 0.90 μm proximally and is conspicuously inflated up to 1.3 μm in the area of haptotypic mark (Pl. 3, fig. 1). Moreover, the ultrastructure of the inner layer in this area is considerably less dense and the lamination is obvious, with numerous irregularly intersecting lamellae, separated by slits ca. 0.6 μm long (Pl. 3, figs 3, 4). Close to the triangular scar, the inner layer becomes thinner (0.33 μm) owing to wedging out of the lamellae while spaces between the lamellae become wider (Pl. 3, fig. 3).

Specimen No. 3737/204-5(E)

Pl. 4, figs 1–6

Description.The pollen grain is subcircular, 88 × 92 μm in diameter, with a narrow equatorial saccus about 2–4 μm wide. Under LM, the saccus/corpus boundary appears as a thin dark slightly uneven contour. The radial partitions of the saccus transpire through the tectum resembling a columellate infrastructure in optical section of the saccus. The polar area is lighter and faintly punctate. The proximal scar is trilete, with asymmetrical arms 6–9 μm long (Pl. 4, fig. 1).

The ultrastructure of this pollen grain has been studied along two lines over the peripheral area (section I, Pl. 4, fig. 1, arrow) and in the region of the proximal scar (section II, Pl. 4, fig. 1, two arrows). Over the periphery of the pollen grain, the tectum is 0.2 μm thick, slightly undulate, perforated by minute pores about 0.08 μm. The infratectal layer is formed of unbranched or seldom branched partitions rooted in the inner layer. The inner layer (endexine) appears dense, homogeneous and of uniform thickness of 0.4 μm in the peripheral regions (Pl. 4, figs 3, 4). This section clearly demonstrates that the exine of one face (the distal one as will be shown on the basis of sectioned polar region, Pl. 4, figs 2, 5) is thicker than the opposite, mainly on account of asymmetrically developed ectexine, which is 1.41–2.32 μm thick distally and 0.66–1.41 μm thick proximally. The distal ectexine is formed by radial partitions. On the proximal face the partitions are gradually reduced towards the central region where the ectexine appears granulate (Pl. 4, fig. 2).

Section II (Fig. 2) shows the saccus in the median plane, where it is slightly more expanded (4.51 μm maximum) and more clearly differentiated from the corpus, over which the ectexine is considerably reduced (Pl. 4, fig. 6). Most of the saccus partitions reach the inner layer. Thus, this saccus type differs from that described above (specimen No. 3737/204-7(E)) and is more definitely protosaccate.

Towards the corpus the ectexine is gradually attenuated on both sides. The tectum is undulate, forming the same type of sculpture as described under SEM below (e.g., specimen No. 47(2), Pl. 7, fig. 4). On account of undulations of the tectum the thickness of corpus ectexine varies from 0.37 to 0.77 μm distally and from 0.19 to 1.1 μm proximally. The distal infratectum is formed of short widely spaced unbranched partitions; the proximal ones are reduced to a few granules (Pl. 4, fig. 6).

The inner layer of the distal face remains homogeneous though slightly thicker than in the peripheral section (0.53 μm against 0.4 μm over the periphery). The proximal endexine expands up to 0.67 μm towards the polar region and up to 0.93 μm at the immediate vicinity of the scar. This is accompanied by the appearance of irregular slits that divide the inner layer into a number of vaguely defined lamellae. Thus, a distinction between the apertural and non-apertural inner layer ultrastructures is much like in the specimen No. 3737/204-7(E) above: the non-apertural inner layer is nearly homogeneous or inconsistently subdivided by widely spaced slits (alveolae), while the expanded and finely split apertural region of it appears more like a lamellate endexine.

Specimen No. 3737/204-6(E)

Pl. 5, figs 1–8

Description. The pollen grain is circular, about 54 μm in diameter, monosaccate; the width of the saccus as seen under LM is 6–9 μm. The saccus appears microreticulate with radial folds (the SEM and TEM observations show these folds to correspond to the inner partitions of the saccus). The corpus is punctate; nearly smooth in the polar regions. The proximal scar is a minute trilete with thin closed laesurae about 6 μm long (Pl. 5, fig. 4).

Under SEM, the distal face of the corpus is sculptured with interlaced threads that form a crochet pattern (Pl. 5, fig. 1) that is typical of the Permian *Cordaitina* readily distinguishing it from other contemporaneous saccate pollen grains. The threads are about 0.66 μm wide, 1.84 μm long, connected by two or three knee-like joints. The apparently smooth regions of the corpus (Pl. 5, fig. 2) are preservational features. At the distal pole the sculptural elements are smaller than over the corpus/saccus junction.

The surface of the saccus is more or less smooth. The corpus/saccus boundary is not as sharply defined on the surface as it appears under LM. However, only the distal surface was studied in this pollen grain under SEM, while the boundary might have been more distinct on the proximal face as in specimen No. 3737/204-9(E) described below. In addition, TEM of the specimen No. 3737/204-6(E) shows a sharper proximal saccus/corpus transition.

Under TEM, the tectum of the saccus is 0.2–0.33 μm thick, occasionally perforated by pores 0.1 μm wide (Pl. 5, fig. 3). Partitions of the saccus are 0.3 μm thick, somewhat irregular, occasionally branched. Most of partitions reach to the endexine, occasionally leaving a narrow space up to 2.5 μm wide. Therefore, this structure is of the same type (intermediate between protosaccus and eusaccus) as in specimen No. 3737/204-7(E), where a peripheral section through the saccus showed an inner space lacking infrastructural elements.

Both distally and proximally the ectexine attenuates towards the corpus region. The ectexine partitions are becoming progressively shorter, unbranched, and the tectum comes to nearly resting on the inner layer in the polar areas. The tectum is finely undulate in the polar regions and is more coarsely folded in the regions adjacent to the saccus. This pattern corresponds to the fine/coarse differentiation of the sculptural features as seen under SEM (Pl. 5, fig. 1). The transition between the areas of fine and coarse undulations is slightly sharper proximally than distally.

The pollen grain is peculiar on account of its thick endexine, which is about 1.17 μm on the distal face, slightly thicker (1.34 μm) at the periphery of the proximal face, and up to 1.84 μm over the region of proximal scar (Pl. 5, figs 5, 7, 8). The endexine of all non-polar regions except that of the proximal pole appears almost homogeneous (Pl. 5, fig. 6). In the region of the proximal scar it becomes considerably thicker and looser. The most striking feature of the endexine of the proximal pole is that it is granular (Pl. 5, fig. 7, arrow) rather than lamellate as in other pollen grains.

Specimen No. 3737/204-9(E)

Pl. 6, figs 1–7

Description. The pollen grain is rounded-elliptical, considerably larger (125.0 × 102.4 μm) than the other pollen grains of *Cordaitina*, with a faintly marked monolete scar.

Under LM, the exine is lighter (thinner) in the corpus region than over the saccus (Pl. 6, fig. 1).

The proximal face of the pollen grain was studied under SEM (Pl. 6, figs 2, 4, 6). The saccus/corpus boundary is fairly distinct, situated at a distance of 20.5–21.3 μm from the margin of the pollen grain (Pl. 6, fig. 4, arrows). The saccus surface is almost smooth, except occasional radial folds. The corpus shows a crochet sculpture (Pl. 4, fig. 6) identical to that described in specimen No. 3737/204-6(E). The threads are up to 1.33 μm long, 0.33–0.67 μm wide. The sculpture is finer in the polar region (Pl. 6, fig. 2). The proximal scar is monolete, smooth, 13.3 μm long, somewhat curved, probably a transformed trilete with one arm reduced (Pl. 6, fig. 2, arrow).

TEM micrographs show a tectum 0.2–0.4 μm thick, with perforations 0.15 μm wide (Pl. 6, figs 3, 5, 7). Most of inner partitions of the saccus cavity are radially aligned, scarcely branching (Pl. 6, fig. 3, above). They reach the endexine, which enables us to define this structure as protosaccate. Judging by the TEM images, the real thickness of the saccus approximately agrees with that measured under LM. The sharp saccus/corpus boundary seen under SEM corresponds to a reduction of ectexine at this border in sectioned material. On the proximal face this transition is slightly sharper. The ectexine partitions become shorter towards, and eventually disappear at both poles (Pl. 6, fig. 5).

The endexine outside the proximal pole region appears homogeneous (Pl. 6, fig. 3), 0.6–0.7 μm thick over the distal face, approximately 0.4 μm thick at the saccus/corpus border, and up to 1.14 μm thick near the proximal scar. In the latter region the endexine becomes looser showing a finely granulate ultrastructure (Pl. 6, fig. 7, arrows).

POLLEN GRAINS FROM
THE MIDDLE PERMIAN

Genus ***Cordaitina*** Samoilovich 1953

Species ***Cordaitina rotata*** (Luber) Medvedeva 1960

Specimen No. 47(2)

Pl. 7, figs 1–6, Pl. 8, figs 1–6

Description. The pollen grain is rounded-elliptical, monosaccate (Pl. 7, fig. 1). Under LM, the saccus is reticulate. Towards the equator the elements of the reticulum are radially aligned. The corpus exine is thin, almost smooth, with occasional short preservational folds. Yet it appears punctate under a greater magnification (Pl. 7, fig. 3). We failed to recognize either a distal aperture or a proximal scar.

Unlike other studied specimens this one possesses irregularly pentagonal central area delimited by saccus root on one of the sides. Although this feature was ascribed a taxonomic significance at specific or generic level, we tend to consider it as preservational. The fold at this saccus root seen at the upper part of Pl. 8, fig. 1 confirms such interpretation. Several species of monosaccate pollen grains described by Dibner (1971), e. g. *Libumella rugulifera* (Luber) Dibner, *Luberisaccites stipticus* (Luber) Dibner and *L. geminus* (Luber) Dibner, include forms with irregularly pentagonal saccus roots along with “normal” pollen grains with round or oval saccus roots. However, in *Cordaitina* pentagonal roots have been never mentioned before.

The dimensions of the pollen grain measured under SEM are 121.9 × 101.87 μm, width of saccus varies from 15.03 to 26.72 μm. It is evident judging from SEM images that both the saccus and corpus ornaments seen under LM result from superposition of sculptural and structural elements of the exine (Pl. 7, fig. 2). As in other pollen grains described above, the crochet-like sculpture covers the corpus (Pl. 7, fig. 4). The sculpture is formed of interlaced threads 1.5–2.0 μm long, 0.5–1.2 μm wide, joined by two or three. The crochet is coarser towards the saccus with larger threads 2.0 μm long, 1.2 μm wide (Pl. 7, fig. 2). At places the crochet pattern is partly or entirely obliterated (Pl. 7, fig. 2, white arrow) or formed of smaller elements less than 1.5 μm long, 0.5 μm wide. The elements decrease gradually towards the pole. Locally at the corpus/saccus boundary, the tectum is destroyed exposing tips of infratectal elements about 0.5 μm in diameter (Pl. 7, fig. 6, arrow). The saccus surface is irregularly folded.

The pollen grain was damaged during preparation for TEM, and the sections were ruptured at several points, yet the main features of the exine are distinguishable (Pl. 8). The ectexine is different over the corpus and saccus regions, whereas the endexine is uniform throughout (Pl. 8, figs 1, 5). The latter is distinct, rather thick, 0.6–0.77 μm, apparently homogeneous (Pl. 8, figs 2, 3). Under magnifications over 15000, it shows bead-like punctuations (Pl. 8, fig. 4).

The tectum is 0.2–0.33 μm thick over the saccus (Pl. 8, fig. 6). The cavity of the saccus is filled by widely spaced, unbranched or seldom branched radial partitions, 0.27–0.47 μm thick (Pl. 8). Most partitions are rooted in the endexine. The saccus ectexine is up to 3.1 μm, attenuating gradually towards the corpus. The ectexine of the corpus is a single undulate layer 0.13–0.2 μm thick, resting directly or with a gap of 0.87 μm on the endexine (Pl. 8, figs 2, 3). The undulations appear as a crochet pattern under SEM. Both faces of the corpus are ultrastructurally similar.

We conclude that the punctate ornament of the corpus visible under LM (Pl. 7, fig. 3) is formed of crochet threads. The reticulate pattern of the saccus as seen under LM is formed of a superposition of irregularly folded surface over the infratectal partitions. Since the pollen grain is somewhat obliquely compressed, the reticulate ornament at the saccus/corpus border results from superposition of peripheral sculptural elements of the corpus over the infratectum of the saccus. The TEM data show that both sides of the pollen grain are morphologically similar, lacking either apertural or haptotypic features.

Specimen No. 3761/392 4(E)

Pl. 9, figs 1–4, Pl. 10, figs 1–4

Description. The pollen grain is 97.1 × 83.8 μm, rounded-elliptical, monosaccate, with a small trilete scar. Under LM, the reticulate saccus appears considerably darker than the punctate corpus (Pl. 9, fig. 1).

Under SEM, the surface of the saccus is radially folded (Pl. 9, fig. 2). The saccus is 12.0–22.6 μm wide, rather sharply delineated from the corpus. The crochet sculpture of the corpus is not so prominent as in the pollen grains described above, yet the interlaced threads 1.0 μm long, 0.38 μm wide are occasionally present (Pl. 9, fig. 4). The proximal trilete scar is rather large, with laesures gaping at ends, 11.5–16.0 μm long (Pl. 9, fig. 3).

The TEM image shows the tectum of the saccus 0.37 μm thick, occasionally perforated by pores 0.1 μm wide. This pollen grain differs from others by asymmetrical development of the saccus, which is much thicker and more prominently onlaps the corpus distally (Pl. 10, figs 1, 4). Proximally, the saccus partitions are irregular, filling the entire cavity of the saccus. Distally, the partitions are radially aligned, mostly not reaching the endexine, with a gap 1.25–1.75 μm. Thus, this saccus structure can be assigned to the intermediate type (above). The saccus/corpus boundary is sharp proximally and even more so distally. The outermost layer of the corpus exine is steeply undulate, considerably thinner (0.13 μm thick) than the tectum of the saccus (Pl. 10, fig. 2). Undulations correspond to the crochet pattern (SEM).

The endexine is thick, cleaved by several rows of narrow tangentially aligned slits 0.07–0.33 μm (Pl. 10, fig. 2, arrow). In the saccus region the endexine is thinner than over the corpus, 0.88–1.07 μm and 1.27 μm respectively (compare Pl. 10, fig. 2). Near the proximal scar, the endexine is up to 2 μm thick, interrupted at the rays (Pl. 10, fig. 3).

DISCUSSION

The *Cordaitina* pollen grains from three localities of the Kungurian to Kazanian ages show a range of common features as well as a considerable variability in both general morphology and ultrastructure. Their outline is circular, subcircular or elliptical; the dimensions (diameters in circular grains, long axes in elliptical grains) vary from 54 to 125 μm. In optical section, equator of the corpus appears as a thin dark contour transpiring through the ectexinal layers at a distance of 2–9 μm from the margin of the pollen grain. Ectexine of the saccus extends some distance over this line onlapping the corpus. It appears under LM as a darker peripheral part of the pollen grain much thicker than the central part of the corpus.

Under LM, the saccus is finely reticulate, while under SEM it appears smooth, uneven, occasionally with radial folds. The surface features correspond to undulations of the tectum. Yet the fine reticulum seen under LM in forms with smooth saccus reflects the interior ectexine partitions rather than surface features. The radial folds are infrastructural as in the Early Permian pollen grain No. 3737/204-6(E) or superficial as in the Middle Permian pollen grain No. 3761/392 4(E). In the latter case, the reticulate LM pattern is formed of superposition of surface folds and inner partitions. In some pollen grains (specimen No. 3737/204-5(E)) the infrastructure appears collumellate (in optical section) over the saccus margin owing to the widely spaced almost unbranched ectexinal partitions, compressed in equatorial plane. Under SEM, the saccus/corpus boundary is sharp in specimen No. 3737/204-9(E)) or gradual in specimen No. 47(2). Measured under SEM, the width of the saccus varies from 12.0 to 26.76 μm.

The corpus is much lighter (thinner) than the saccus, featureless or finely punctate. The latter pattern corresponds to a peculiar type of crochet-like sculpture formed of interlaced threads or rugulae discernible in all pollen grains studied under SEM. The crochet is constantly present over the corpus getting coarser towards the periphery but never extending over the saccus. In ultrastructural sections the threads correspond to undulations of the tectum. Insofar as such undulations are observed in all pollen grains, including those not studied under SEM, we consider this type of sculpture as a constant feature of the Permian *Cordaitina* readily distinguishing it from many Permian saccate pollen genera that are commonly smooth or irregularly sculptured or else preservationally pitted (Zavialova et al. 2001).

The tectum of the saccus is 0.2–0.45 μm thick, occasionally perforated by pores 0.08–0.3 μm wide. The saccus cavity is filled by the loose, rather thick (0.2–0.3 μm), weakly branched partitions. The partitions reach to the endexine forming an infrastructure that is defined as protosaccate. Otherwise they may be not rooted or mostly so forming an intermediate protosaccate/eusaccate infrastructure. The variation is gradational rather than discrete, correlated with the thickness of the saccus ectexine: the thicker sacci tend to be more definitely eusaccate (Tab. 1).

Table 1. Correlation between the thickness of saccus ectexine and of saccus cavity

Specimen number	Maximum thickness of saccus ectexine (μm)	Maximum thickness of saccus cavity devoid of partitions (μm)
3737/204-6(E)	8.2	2.50
3737/204-7(E)	7.1	3.00
3761/392-4(E)	4.4	1.75
47(2)	3.3	0.87
3737/204-5(E)	3.2	–
3737/204-9(E)	2.3	–

Certainly, this conclusion is valid only for the pollen grains under investigation. Yet it accords with the repeatedly expressed doubts concerning phylogenetic significance of eusaccate versus protosaccate structures (Osborn & Taylor 1993, 1994). Anyway, a loose saccus infrastructure with weakly branched radial partitions is characteristic of the Permian *Cordaitina*, whereas variation over the protosaccus – eusaccus continuum can be used, if not in a broad phylogenetic context, then for a delineation of species over a particular lineage of pollen morphotypes. Phylogenetic relationships of protosaccate and eusaccate forms might have varied in different groups of saccate pollen grains.

In its saccus structure *Cordaitina* is fairly isolated among monosaccate pollen morphotypes. The geologically older ultrastructurally studied cordaitalean pollen grains from the Pennsylvanian of North America are definitely eusaccate (Millay & Taylor 1976). Among the protosaccate forms, the saccus infrastructure of *Nuskoisporites dulhuntyi* Potonié & Klaus (Utrechtiaceae, Late Permian, Europe) is formed of numerous, thin, densely packed, irregularly oriented ectexine partitions. The saccus completely envelops the corpus and is of a uniform thickness over the distal and proximal faces (Poort et al. 1997). In *Potonieisporites* (the Late Carboniferous – Early Permian Utrechtiaceae), the saccus is of the same general morphology, but of a looser infrastructure (Poort et al. 1996). In the dispersed pollen grains *Cannanoropollis* and *Plicatipollenites* (the Permian of Australia), the saccus does not cover the corpus (Foster 1979). The Permian species of *Cordaitina* appear quite different from all these protosaccate forms in the radially arranged, widely spaced ectexine partitions, as well as in the intermediate protosaccate/eusaccate condition. They are also unlike the Early Triassic *Cordaitina* pollen grains (preliminary described in Zavialova et al. 2002), which are closer to *Cannanoropollis* and *Plicatipollenites* as far as their saccus structures are concerned.

In the Permian members of *Cordaitina*, the ectexine gently (or occasionally abruptly) attenuates towards the polar areas. The tectum decreases from 0.2–0.45 μm over the saccus regions to 0.07–0.2 μm over the corpus. The infratectal partitions become wider spaced, shorter, disappearing at the poles, where the finely undulate tectum rests directly on the endexine gapping at the tips of undulations only. The proximal and distal ectexines of the corpus are morphologically similar.

Cordaitina is characterized by a rather small proximal scar. In the pollen grains studied it appears as an open triangle or a closed trilete, with arms 6–12 μm long. In some pollen grains the arms are asymmetrical; one of them may be reduced. In specimen No. 3737/204-9(E) the scar appears monolete, and in specimen No. 47(2) it is not distinguishable either under LM, or SEM, or TEM. We could not recognize in our material any distinctive structure that might have been interpreted as a short distal furrow indicated in the Dibner's diagnosis of the genus (Dibner 1971).

The most intriguing structure revealed by TEM studies is the endexine. This innermost layer of the exine varies in thickness (from 0.33 μm up to 2.0 μm) and the ultrastructural details both from specimen to specimen and in different regions of one and the same pollen grain. Thus, it is relatively thin over the distal face and at the equator increasing proximally and attaining a maximum thickness towards the proximal scar. These variations are accompanied by structural changes. In the regions adjacent to the saccus and over the distal face, where the endexine is the thinnest, it appears homogeneous or almost so (occasionally with small slit-like alveolae), while proximally it is strewn with numerous slit-like alveolae that are considerably larger and denser than the distal ones. These tangentially aligned slits cleave the endexine into the vaguely defined lamellae. The alveolae are most numerous in the thickest part of endexine, in the vicinity of the proximal scar. The endexine is interrupted directly on the borders of the arms. In pollen grains Nos 3737/204-6(E) and 3737/204-9(E) the innermost layer is granulate rather than lamellate in the thickest endexine areas. Specimen No. 47(2) is exceptional in lacking proximal scar and showing a uniformly thick (0.6–0.77 μm) homogeneous endexine all over the pollen grain.

The proximal scar of Carboniferous and Permian monosaccate pollen grains is often considered as residual, unrelated to germination. Such pollen grains are supposed to germinate distally. However, although *Cordaitina* pollen grains studied have a thin distal exine, they lack any distinct distal aperture. At the same time, a regular increase of thickness of the inner layer, accompanied by ultrastructural changes in the region of the proximal scar may indicate an apertural function of the latter. If so, germination in most Permian members of *Cordaitina* might have been proximal placing them in the prepollen grade (Gomankov 2000). Notably, in the single specimen No. 47(2) lacking a proximal scar the inner layer is uniform and homogeneous (in such inaperturate grains germination might have been irregular and not confined to any definite location on the corpus).

Sections through the proximal scar contribute significantly to our understanding of the endexine morphology. A differentiation of nonapertural endexine and that of the proximal scar region seems to comply with an assumption that this structure might have been ontogenetically layered, with the lamellae tightly compressed and indistinct except in the proximal scar region. At least such conditions are met in a few examples of fossil and living gymnosperms. According to Osborn and Taylor (1994), in *Gothania* and *Caytonanthus* the inner layer of immature pollen grains is more distinctly lamellate than in the mature ones. A similar situation arises during the ontogeny of saccate pollen in several extant conifers: at the free-spore phase, the lamellae are stretched, tightly adpressed and virtually indistinguishable as separate units (Kurmann 1990).

The unexpected joint occurrence of weakly lamellate and finely granulate endexine in a single pollen morphotype pose a problem to be elucidated with a more comprehensive material. Whatever its evolutionary significance, the proximal scar ultrastructure can be used as a distinguishing feature of the Permian *Cordaitina* when compared to other monosaccate prepollen. Irrespective of the lamellate/finely granulate variation, the general architecture of proximal scars is identical in all the specimens studied. Both in the trilete and monolete varieties, the endexine becomes thicker and looser towards the scar until it is interrupted by the laesures. Incidentally, such ultrastructure differs from the proximal scar ultrastructure in the Early Pennsylvanian *Gothania* (Taylor & Daghlian 1980) where the inner layer thickness hardly increases in the proximal scar region, while the outer layer is raised dome-like gaping over the laesures lined only by the delicate outer and inner membranes. An optical section through laesures of another cordaitalean pollen grain of the same age (Millay & Taylor 1976, pl. 1, fig. 3) shows a considerable decrease of the inner exine layer in this region.

These examples confirm the significance of ultrathin sections cut through polar areas. Such sections are not only the most informative in respect to apertural structures but they also reveal a number of ultrastructural characters of potential palynotaxonomic significance. Our data on *Cordaitina* shows that superficially similar pollen grains may differ substantially in their polar ultrastructures. In particular, such differences pertain to the inner layer structure and the polarity of germination. In the Permian representatives of *Cordaitina* the ultrastructural complexity of the proximal scar area as compared to the distal exine makes proximal germination more plausible. Accordingly, a prepollen rather than pollen condition can be inferred for this pollen morphotype.

The position of *Cordaitina* in the general picture of diversity of pollen morphotypes among Cordaitales (= Cordaitanthales after Meyen 1987) and early Coniferales is of interest. Traditionally *Cordaitina* was regarded as the pollen of Angaran cordaites, what besides its geographical distribution was substantiated by the finds of such pollen grains in situ (Meyen 1982, Balme 1995). However, among pollen morphotypes bound with cordaites and primitive conifers, *Cordaitina* is more similar to the Euramerian genera than to the other Angaran genera. For example, pollen grains of *Cladaitina* type were extracted from the rufloriaceous male fructifications *Cladostrobus* and described to have a weakly developed saccus attached to the corpus only on the proximal face (Maheshwari & Meyen 1975). Similar organization presumably have pollen grains of *Acusporidatina* and *Reticulatina* (Koloda 1996) extracted from sporangia of *Timanostrobus* (conifer-like representative of Vojnovskyaceae) and *Kungurodendron* (primitive Angaran conifer), respectively (Gomankov 1995, 1997, 2000, Meyen 1997, Meyer-Melikyan et al. 1998). Meanwhile many pollen morphotypes (*Felixipollenites*, *Sulisaccites*, *Florinites*, *Potoniesporites*, *Nuskoisporites*) assignable to the ancient Euramerian pinopsids (Balme 1995) demonstrate a torus-like saccus attached to the corpus along its equator and, in terms of general morphology, similar to that of *Cordaitina*. However, to clearly elucidate trends in pollen morphology of cordaites and early conifers, much more ultrastructural data are necessary. Information on more ancient (Carboniferous) representatives of *Cordaitina* would be appropriate. Triassic members of this complicated genus is an aim of our nearest studies.

CONCLUSION

We have studied the ultrastructure of several Permian representatives of *Cordaitina* under LM, SEM and TEM and found them sharing such features as the protosaccate to intermediate proto/eusaccate structure, the peculiar crochet corpus surface sculpture, the conspicuous inner layer (endexine), and its differentiation in apertural (proximal scar) and non-apertural regions. Another implication of the inner layer differentiation is that germination might have been proximal rather than distal as typical of the cordaitalean pollen grains. However, this conclusion is only tentative at this stage awaiting further studies.

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PLATES

Plate 1

Cordaitina rotata (Luber) Medvedeva

Specimen No. 3737/204-7(E), Kungurian. Scale bar (1) – 30 μm, (2–4) – 1 μm

1. Proximal face showing open trilete scar, LM
2. Section I (Fig. 2), showing the intermediate protosaccate – eusaccate structure. The tectum of the saccus is perforated by widely scattered pores (arrows), the distal ectexine (**d**) partitions are mostly unbranched, radially oriented, the proximal (**p**) ones are more chaotic. Note the hollow (**s.h.**) in the center, TEM
3. Detail of the distal face showing the tectum with a pore (arrow) and the radial ectexine partitions, TEM
4. Detail of the proximal face with the irregularly oriented ectexine partitions, TEM

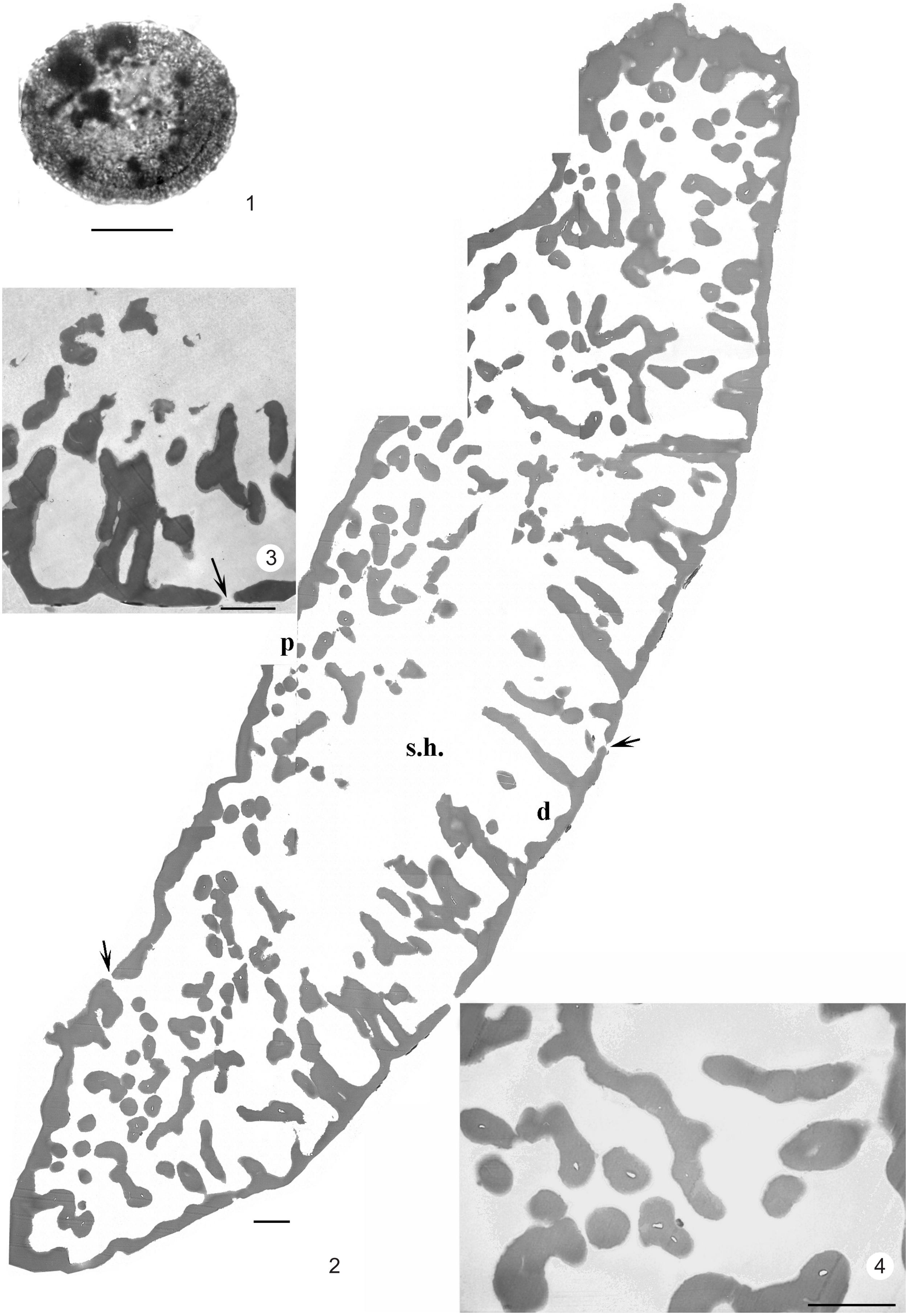

1
3
p
s.h.
d
2
4

Plate 2

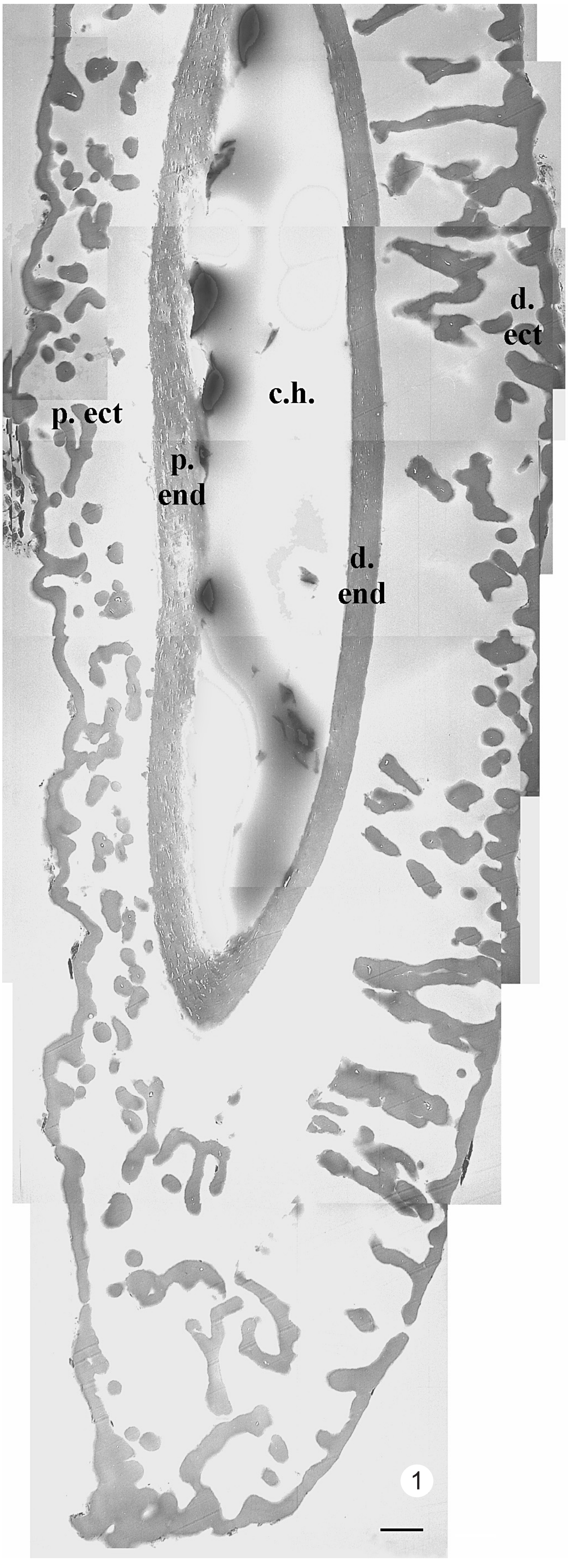
Cordaitina rotata (Luber) Medvedeva

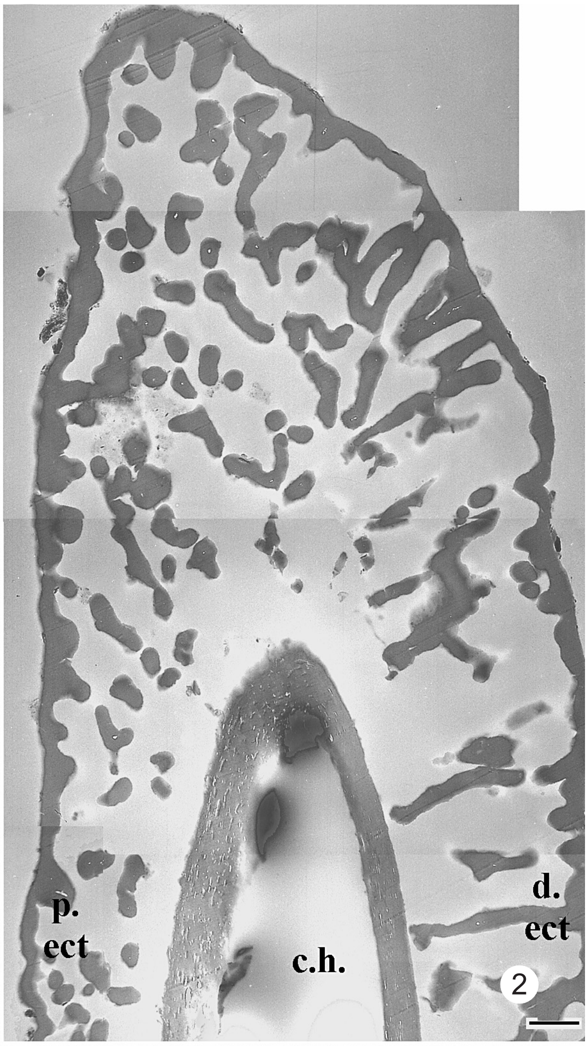
Specimen No. 3737/204-7(E), Kungurian. Scale bar 1 μm

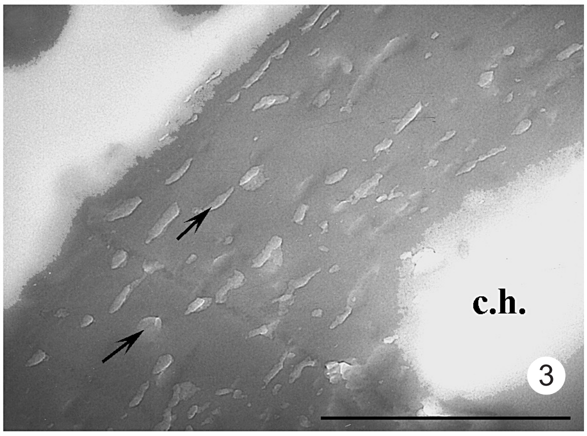
1, 2. Section II (Fig. 2) across the periphery of the corpus. The central hollow (**c.h.**) is bordered by endexine (**end**) that is dense and almost homogeneous distally (**d**), with a few small alveolae, and much thicker and looser proximally (**p**). Most ectexinal (**ect**) partitions are not rooted in the endexine, TEM

3. Proximal endexine with numerous slit-like alveolae (arrows), TEM

4. Detail of the proximal exine showing tectum (**t**), ectexine (**ect**) and endexine (**end**), TEM


p. ect
p. end
c.h.
d. ect
d. end
1


p. ect
c.h.
d. ect
2


c.h.
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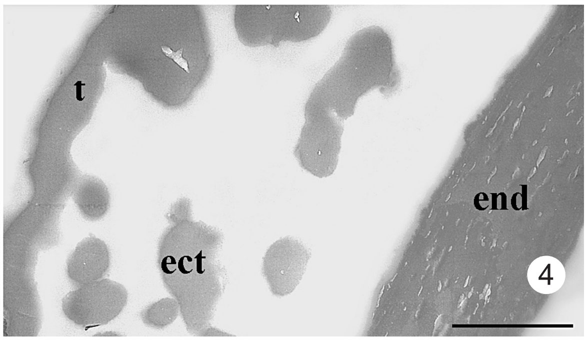

t
ect
end
4

Plate 3

Cordaitina rotata (Luber) Medvedeva

Specimen No. 3737/204-7(E), Kungurian. Scale bar 1 µm

1. Section III (Fig. 2) through the pole regions showing undulate tectum (**t**) over the corpus. The endexine attains the maximum thickness in the proximal scar region, interrupted over the border of the laesure (arrows), **p** – proximal face, **d** – distal face, **c.h.** – central hollow, TEM
2. Part of saccus (**s.h.** – hollow of the saccus) with a nearly homogeneous endexine (**end**), TEM
3. Detail of the proximal scar region. Section cuts through two arms (arrows) of the scar, TEM
4. Proximal scar region, TEM
5. Distal face of the corpus with undulate tectum (**t**) resting directly on endexine (**end**), TEM

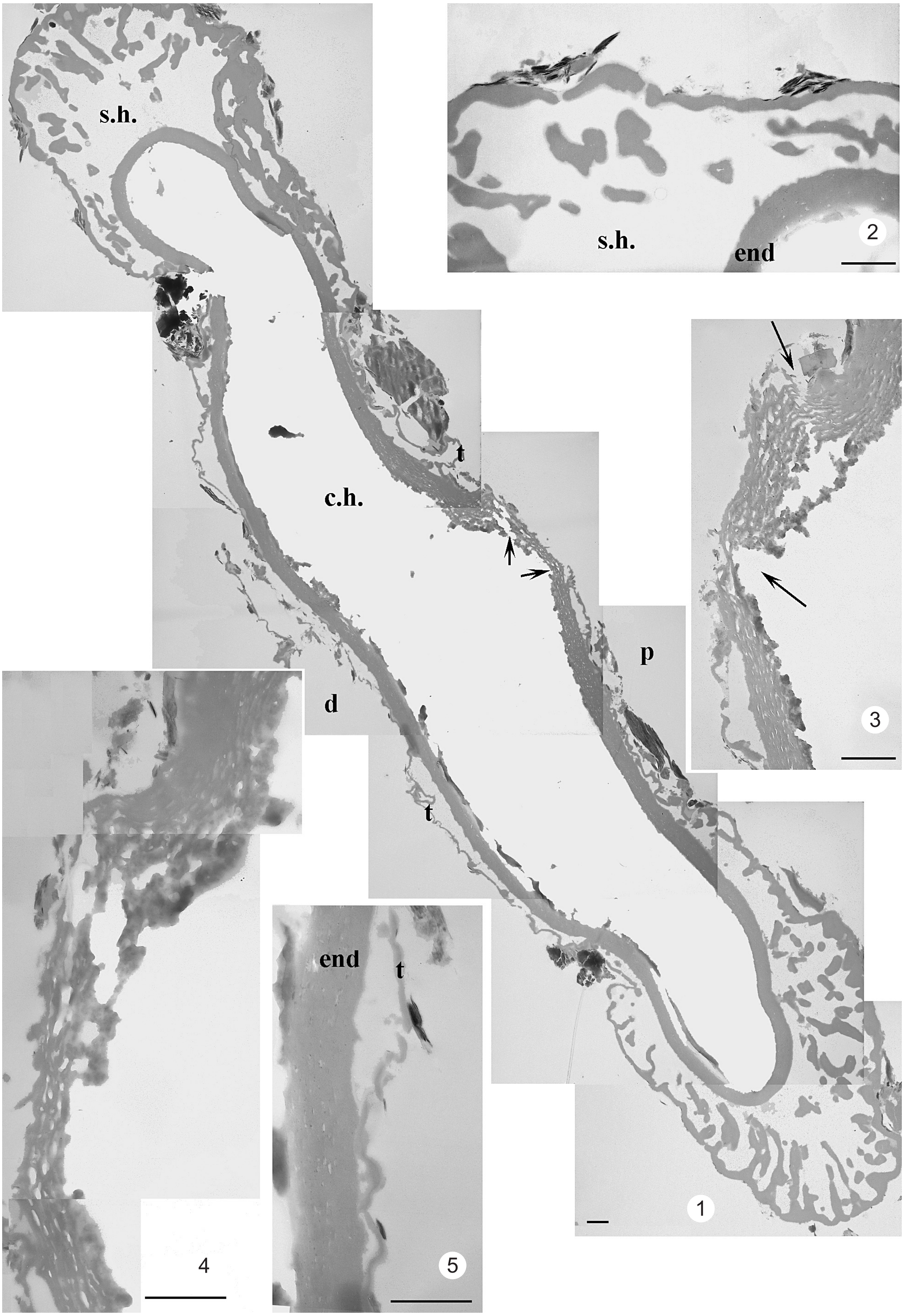

s.h.
c.h.
t
p
d
t
1
s.h.
end
2
3
4
end
t
5

Plate 4

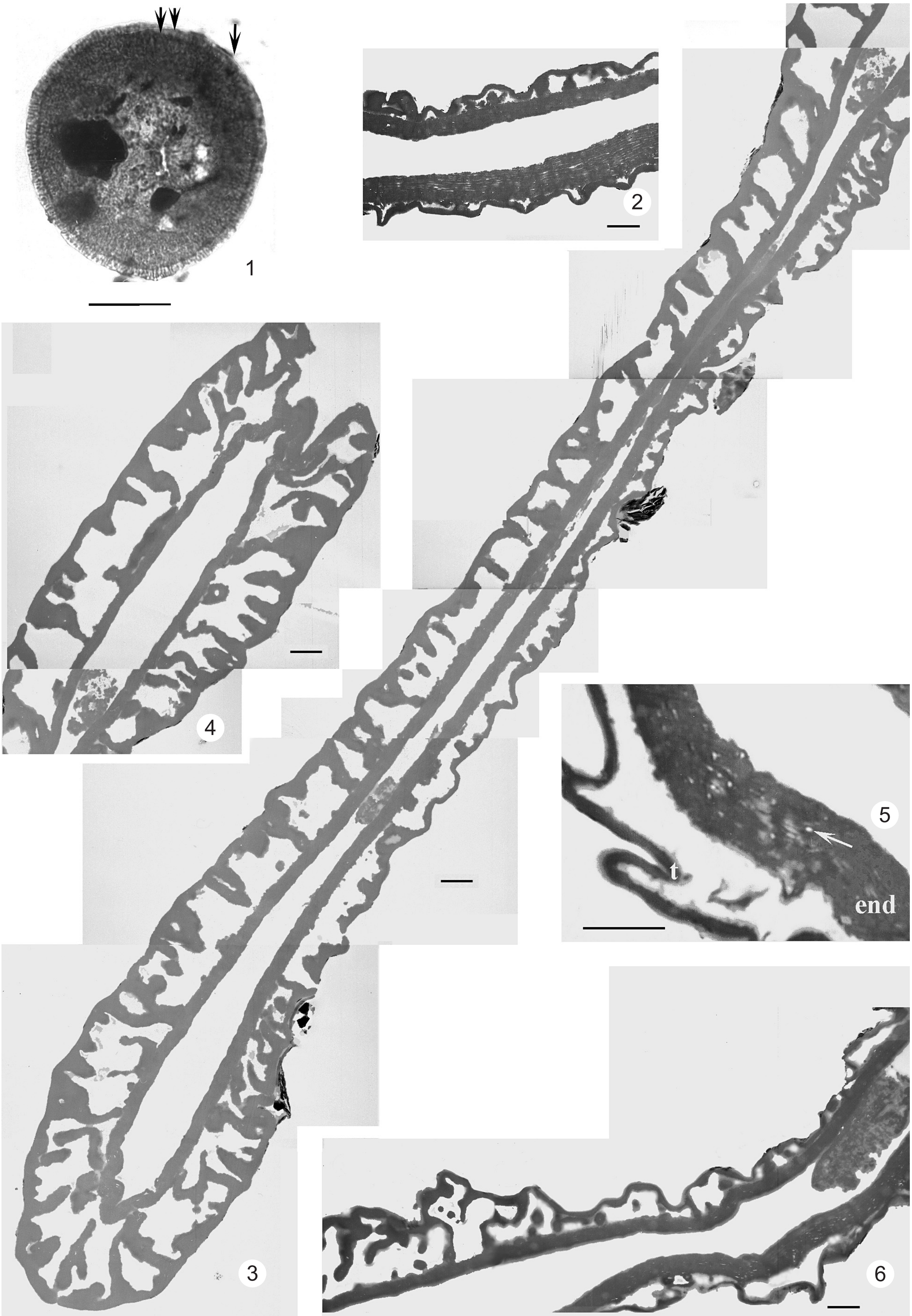
Cordaitina rotata (Luber) Medvedeva

Specimen No. 3737/204-5(E). Scale bar 1 μm

1. Proximal view showing closed trilete scar with slightly asymmetrical arms. Radial partitions of the saccus appear columellae-like in optical section, one arrow indicates the position of section I (over the peripheral area, figs 3, 4), two arrows mark the position of section II (in the region of the proximal scar, figs 2, 5, 6), LM
2. Detail of the section through the central region showing undulate tectum over the remnants of infratectum. Proximally, the endexine is thickened and vaguely lamellate, TEM

3, 4. A section through the peripheral region; the radial ectexinal partitions of the narrow saccus reach the endexine. The proximal ectexine is thinner than the distal one. The endexine is uniform throughout, TEM

5. Detail of section through the proximal pole showing undulate tectum (**t**) and thickened endexine (**end**) with indistinct alveolae (arrow), TEM
6. Details of saccus ultrastructure in the central region of the pollen grain. The ectexinal partitions are more frequently branched than in the peripheral regions and they reach to the endexine, TEM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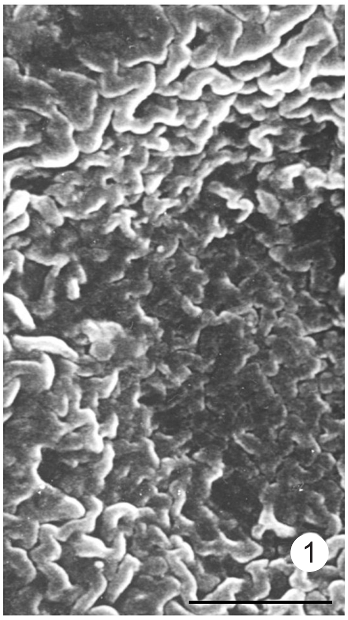
t
end
3
6

Plate 5

Cordaitina rotata (Luber) Medvedeva

Specimen No. 3737/204-6(E), Kungurian, **c.h.** – central hollow, **p** – proximal face, **d** – distal face

1. Detail of the distal surface, with crochet sculpture of threads joined by two or three at the nods, SEM. Scale bar 5 µm
2. Distal surface of the pollen grain. The corpus is sculptured with interlaced threads or rugae. The smooth areas are preservational feature, SEM. Scale bar 10 µm
3. Section through the central region of pollen grain showing undulate tectum (arrows) over the corpus regions, the intermediate protosaccate/eusaccate ultrastructure, and thick endexine that expands and becomes looser proximally, TEM. Scale bar 1 µm
4. Proximal view of pollen grain with minute proximal scar. Endexine transpires through the upper exinal layers as a distinct dark line. The saccus appears finely reticulate; the corpus is punctate, nearly smooth towards the scar, LM. Scale bar 20 µm
5. Detail of section through the polar region showing slightly expanded proximal endexine, TEM. Scale bar 1 µm
6. Median section showing thin tectum (**t**) resting on endexine, TEM. Scale bar 1 µm
7. Detail of section cut still nearer to the proximal scar. Note finely granulate endexine (arrow) over the proximal scar area, TEM. Scale bar 1 µm
8. Detail of section through the proximal scar. The expanded endexine is interrupted by laesura (arrow), TEM. Scale bar 1 µm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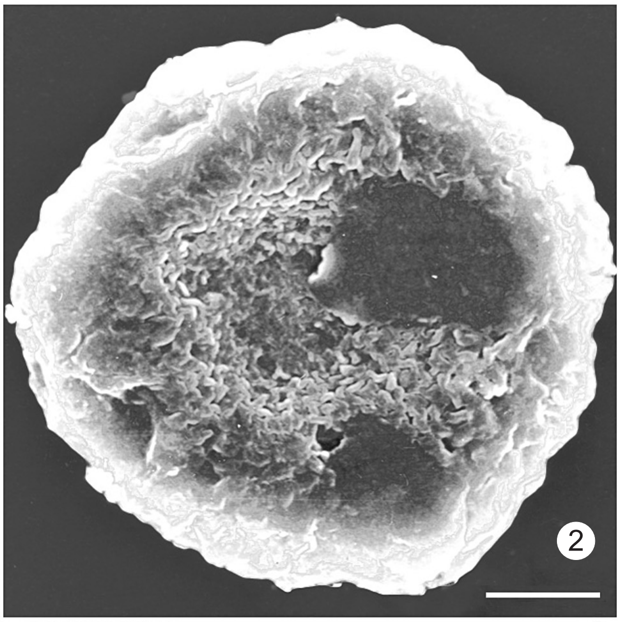
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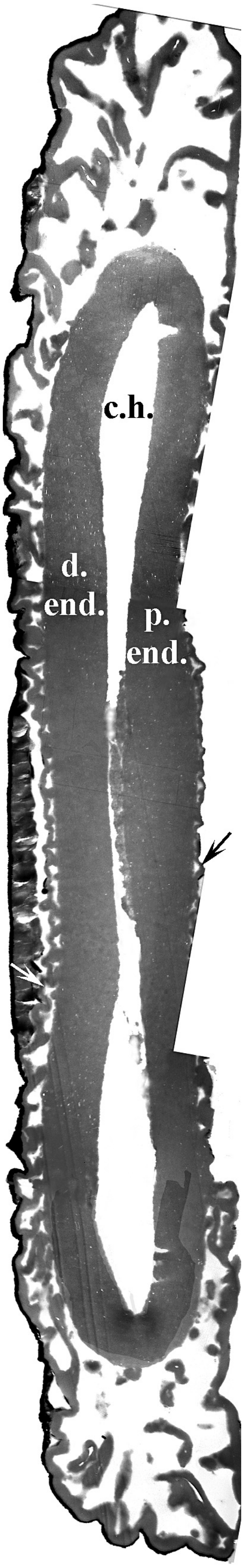

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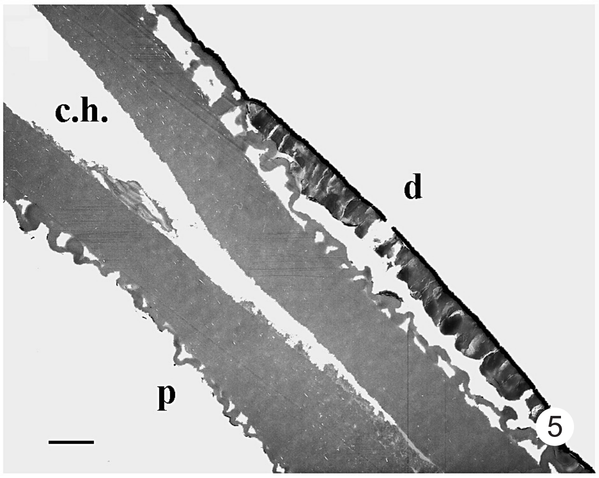

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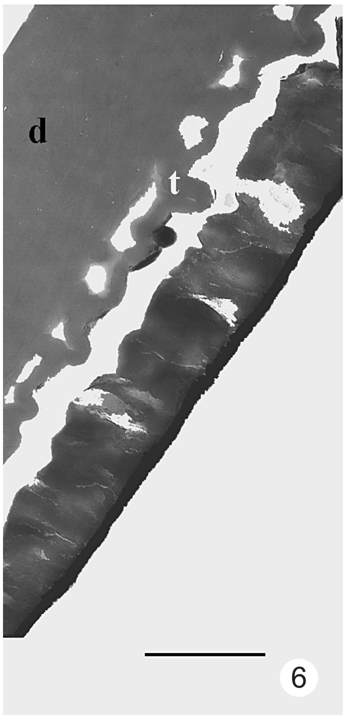

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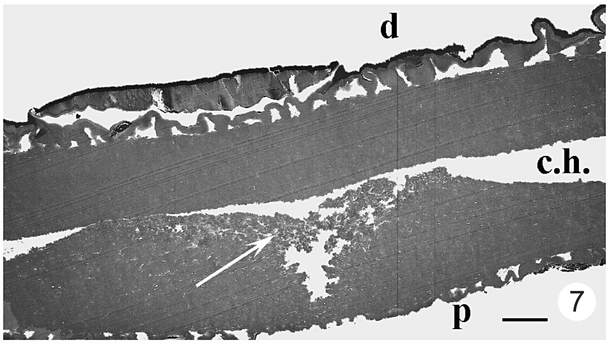

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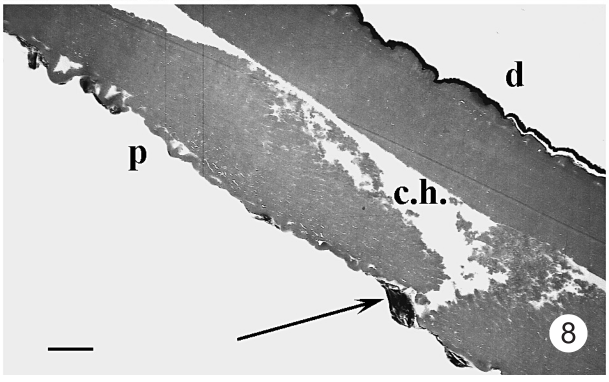

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Plate 6

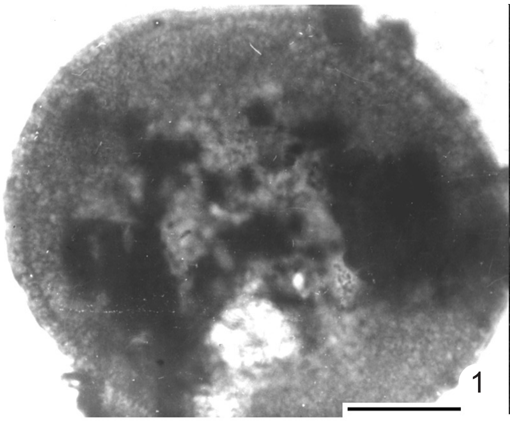
Cordaitina rotata (Luber) Medvedeva

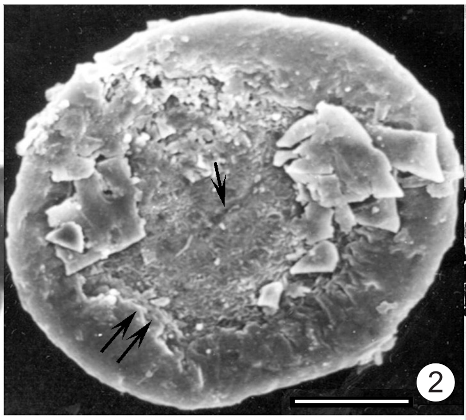
Specimen No. 3737/204-9(E), Kungurian, **p** – proximal face, **d** – distal face

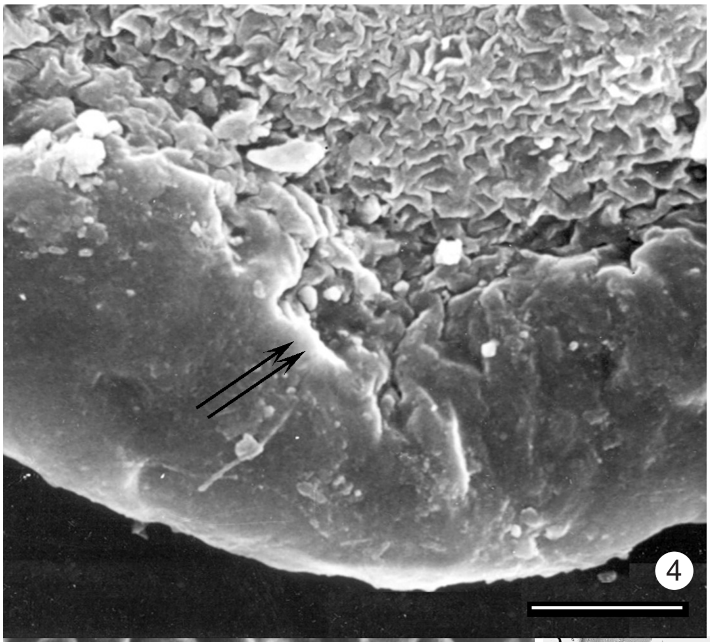
1. Pollen grain with a faintly marked monolete scar, LM. Scale bar 30 µm
2. Proximal surface of the pollen grain. Note slightly curved monolete scar (arrow) and sharp saccus/corpus boundary (two arrows), SEM. Scale bar 30 µm

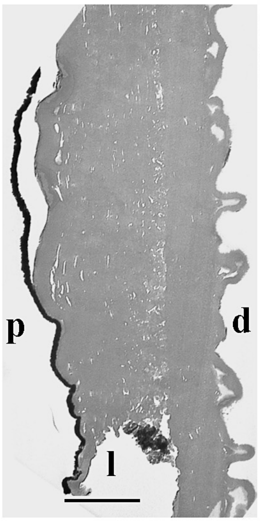
3, 7. Part of section through the central region of flattened pollen grain, its central hollow (**c.h.**) being compressed as a thin interrupted line slightly gapping towards the protosaccus (**s**). The endexine is granulate (two arrows) in the proximal scar area and homogeneous (arrow) outside it, TEM. Scale bar 2 µm

4. Blow up of the saccus/corpus boundary (arrows) showing differentiation of the surface sculpture, SEM. Scale bar 10 µm
5. Detail of section through the central region (same as in fig. 3) showing granulate ultrastructure of proximal endexine interrupted by the laesures (**l**) and much thinner almost homogeneous distal endexine, TEM. Scale bar 1 µm
6. Detail of corpus showing the crochet-type sculpture, SEM. Scale bar 3 µm









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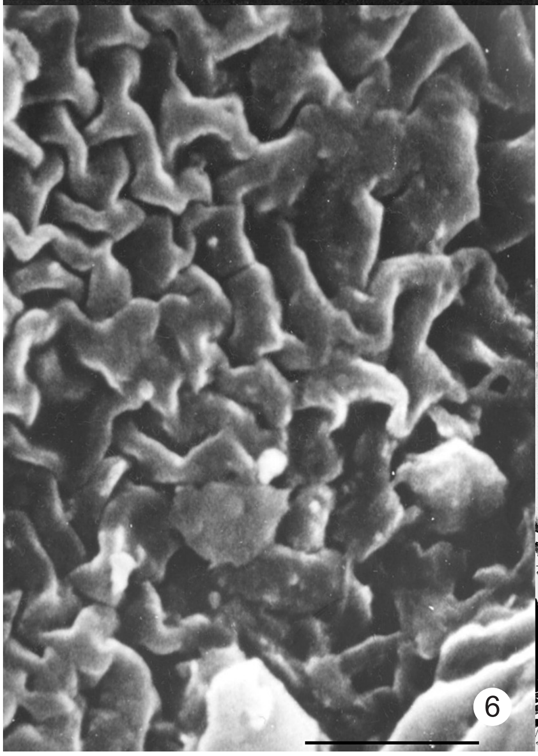
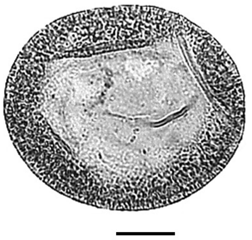


Plate 7

Cordaitina rotata (Luber) Medvedeva

Specimen No. 47(2), Kazanian

1. Pollen grain showing a reticulate infrastructure of the saccus and nearly smooth corpus, LM. Scale bar 30 µm
2. Surface of obliquely compressed pollen grain mechanically ruptured (black arrows) at several points, at places the crochet pattern is partly or entirely obliterated (white arrow), SEM. Scale bar 20 µm
3. Enlargement of reticulate saccus infrastructure, LM. Scale bar 20 µm
4. The crochet-type sculpture of the corpus, SEM. Scale bar 5 µm
5. Enlargement of the same pollen grain showing a differentiation of sculptural elements over the saccus (**s**) and corpus areas (**c**), SEM. Scale bar 20 µm
6. Saccus/corpus transition. The tectum is locally ruptured exposing the ectexinal partitions (arrow) of the saccus, SEM. Scale bar 5 µm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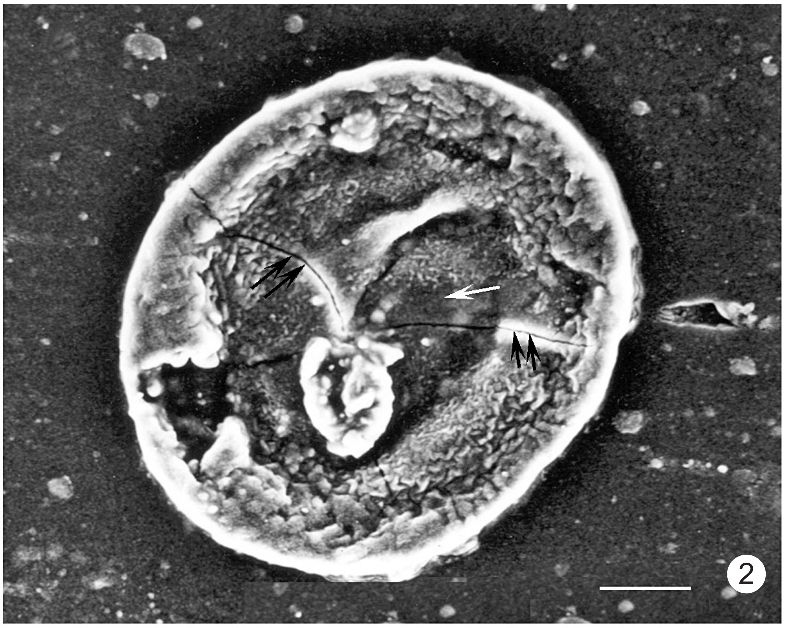
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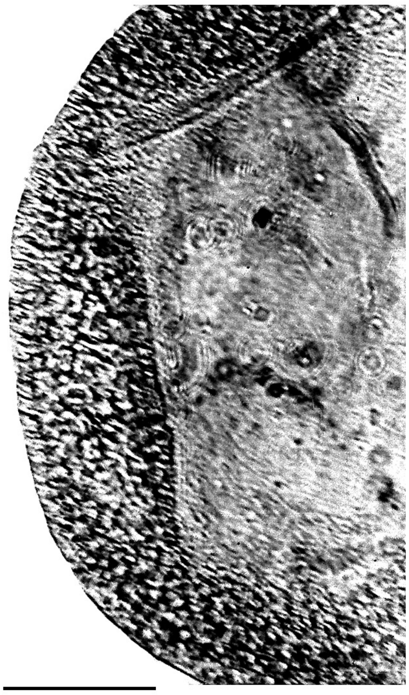
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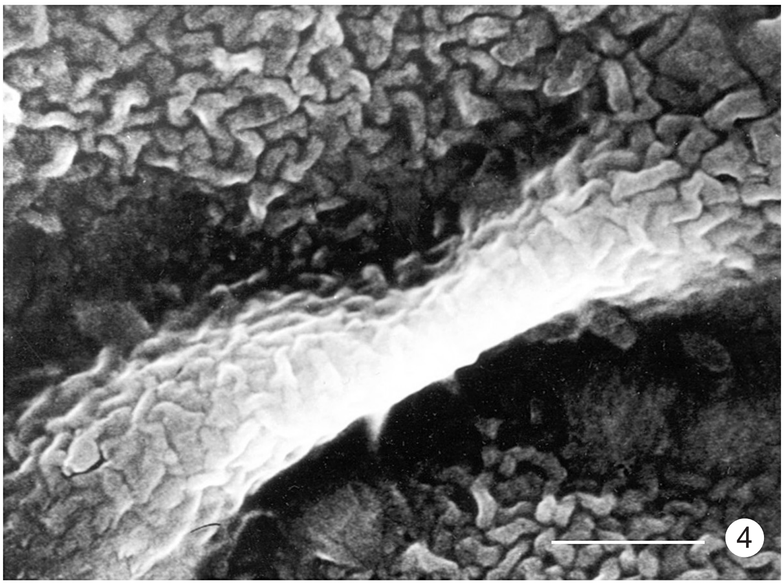
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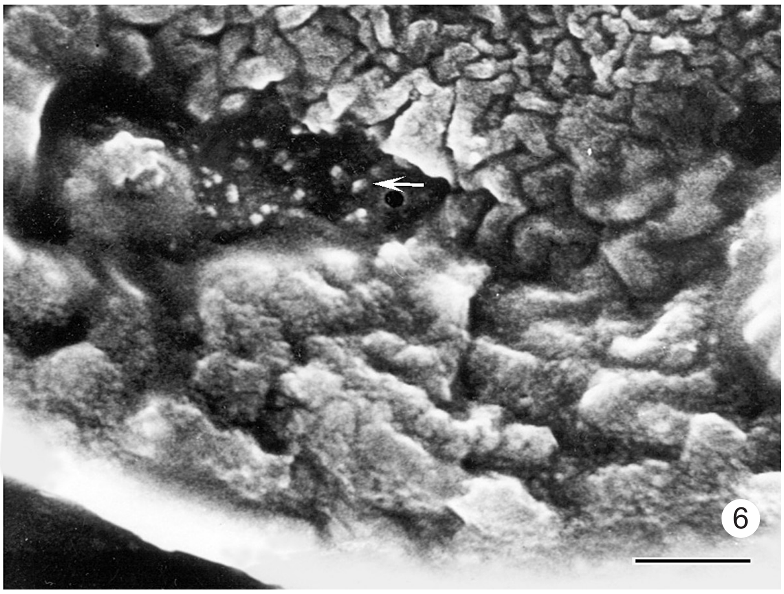
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Plate 8

Cordaitina rotata (Luber) Medvedeva

Specimen No. 47(2), Kazanian, **c.h.** – central hollow, **s** – saccus, **end** – endexine, **t** – tectum

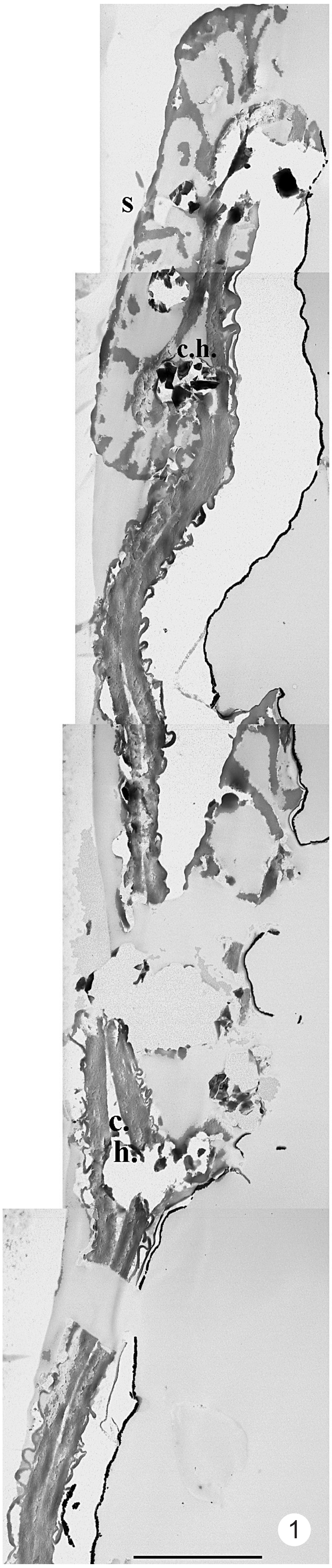
1, 5. Section through central region of inaperturate pollen grain. The exine is uniform over both faces (the ruptures are preservational), TEM. Scale bar – 5 μm

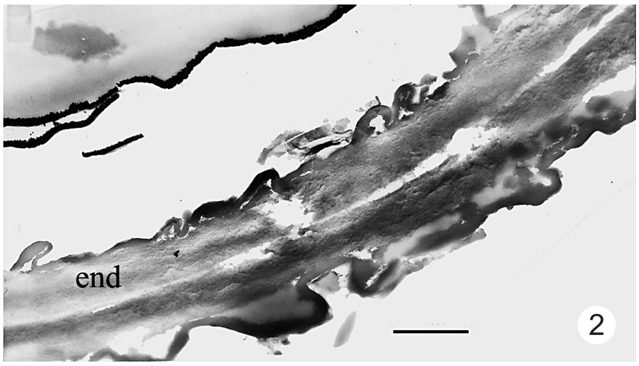
2. Corpus region with a single-layer ectexine (tectum) resting directly on the endexine, TEM. Scale bar 1 μm

3. Enlargement of Fig. 2, TEM. Scale bar – 1 μm

4. Endexine ultrastructure over the region adjacent to the saccus, TEM. Scale bar 1 μm

6. Saccus region showing a tectum, the unbranched ectexine partitions and a dense endexine, TEM. Scale bar 1 μm


s
c.h.
c.
h.
1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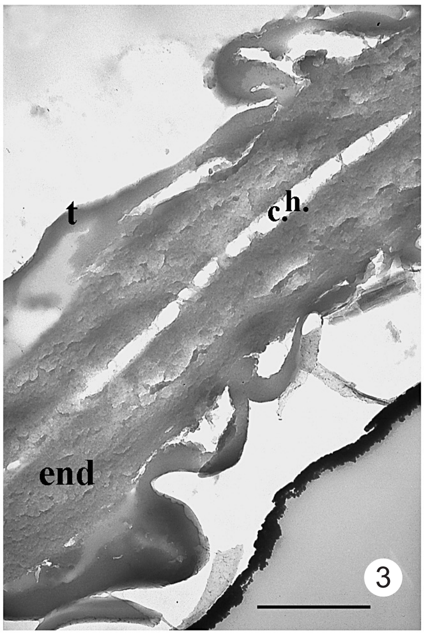
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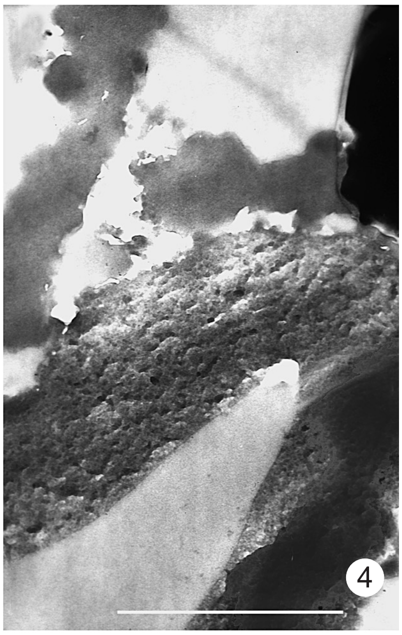
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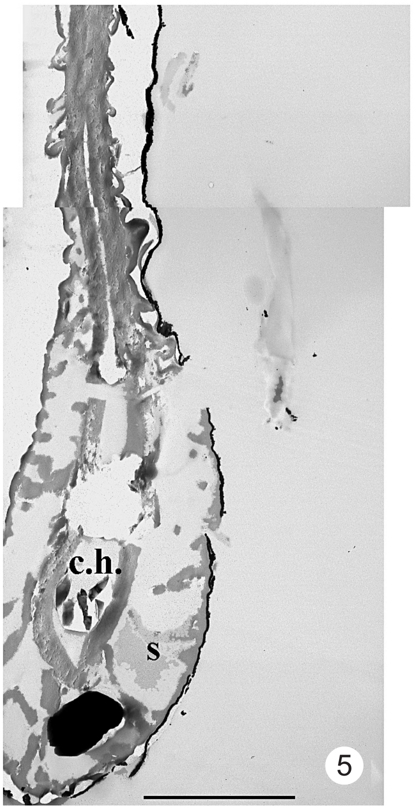
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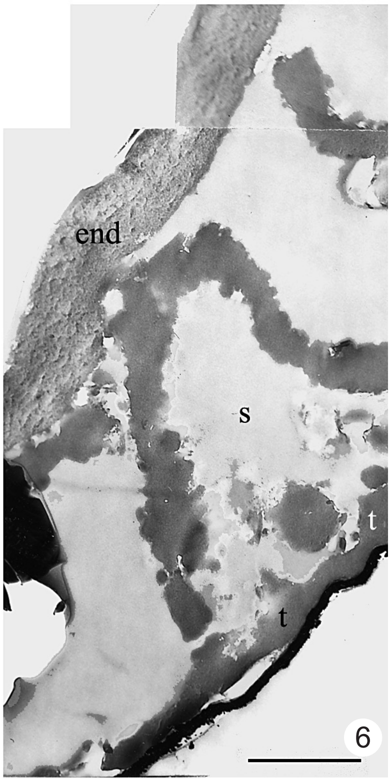
end
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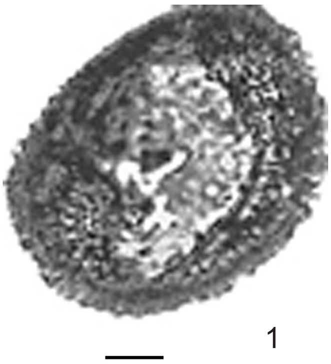
Plate 9

Cordaitina rotata (Luber) Medvedeva

Specimen No. 3761/392 4(E), Kazanian

1. Pollen grain showing a reticulate saccus, punctate corpus and small trilete scar, LM. Scale bar 30 µm
2. Proximal face, the saccus is radially folded (black arrow), the scar (white arrow) is scarcely visible, SEM. Scale bar 20 µm
3. Enlargement in the scar (arrow) area, part of the saccus (**s**) is also seen, SEM. Scale bar 10 µm
4. Crochet-type corpus sculpture, SEM. Scale bar 5 µm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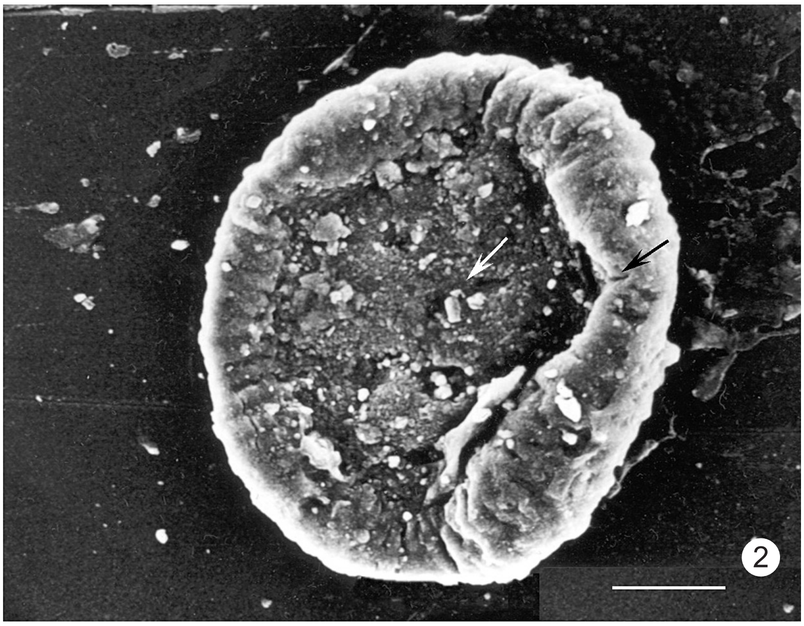
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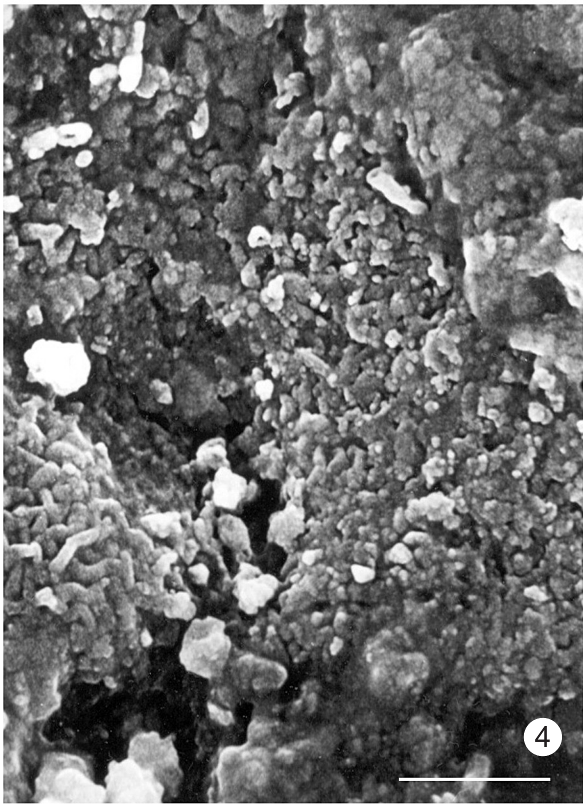
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Plate 10

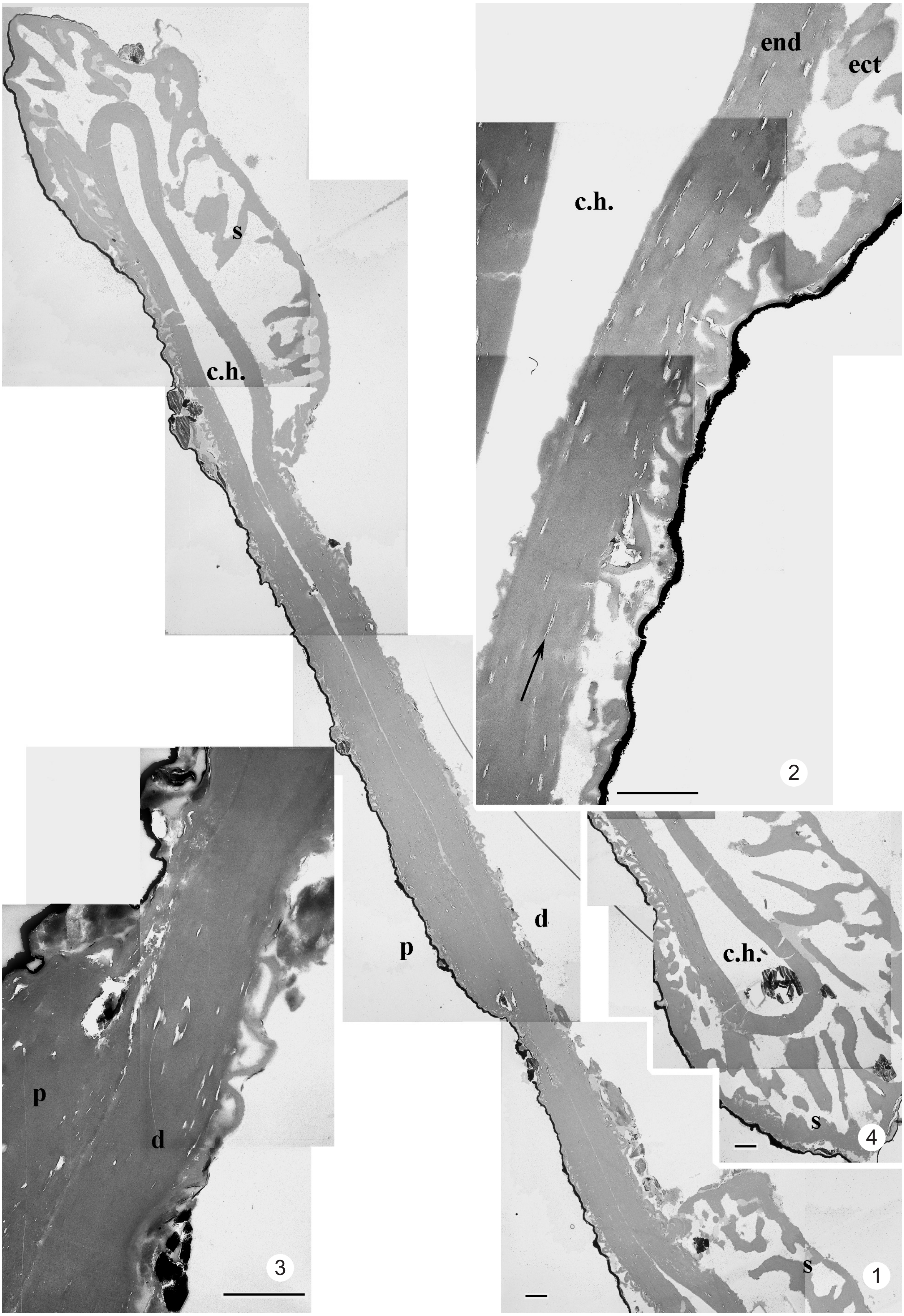
Cordaitina rotata (Luber) Medvedeva

Specimen No. 3761/392 4(E), Kazanian, **s** – saccus, **p** – proximal face, **d** – distal face, **ect** – ectexine, **end** – endexine, **c.h**. – central hollow. Scale bar 1 μm.

1, 4. Median section of pollen grain with asymmetrical distally pendant saccus. The saccus/corpus transition is rather sharp. The endexine is prominent, proximally thickened, TEM

2. Proximal nonapertural exine. Note attenuation of ectexine towards the corpus and the distinctly layered endexine, the arrow indicates one of narrow slits, TEM

3. Adpressed exines of distal and proximal faces, the proximal one is considerably thicker, TEM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