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Densoisporites polaznaensis sp. nov. : with comments on its relation to *Viatcheslavia vorcutensis* Zalessky

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ABSTRACT

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A new species of lycopsid microspores, *Densoisporites polaznaensis*., is described. The spores were extracted from clayey matrix containing stems and phylloids of *Viatcheslavia vorcutensis* Zalessky, a characteristic lepidophyte of the lowermost Upper Permian (Solikamskian) of the Ural Mountains and Russian Platform. The fossils studied came from the Polazna Locality of the Ufimian (Roadian) age, situated near Perm City, Russia. The spores of *D. polaznaensis* are 30-69 μm, round to subtriangular, having almost smooth proximal side with clearly visible trilete scar with rays extended to the spore equator. Distal side of the spores has a fine granulate relief, formed by widely spaced distinct granulae. The sporoderm is two-layered; the outer layer consists of numerous interlaced lamellae and the inner layer includes a single lamella. At some sections, in the central region of spores, "laminated zones" were detected in the inner layer. There is a weakly developed cavity in the sporoderm. *Viatcheslavia vorcutensis* is represented by wide stem fragments (up to 30 cm in diameter). Leaf cushions are present on old lowermost stem parts, but any attached phylloids/sporophylls were not found, the phylloids/sporophylls obviously were shed. Leaf cushions usually are round, with clear scar of leaf attachment and ligular depression on the upper margin of the cushion. Two small areas of parenchymatous tissues (possible parichnos) are occasionally seen. On the basis of co-occurrences and typological extrapolation with related taxa of lycophytes belonging to the family Pleuromeiaceae, it is suggested that microspores of *Densoisporites polaznaensis* were produced by *Viatcheslavia vorcutensis*. The palaeoecology of *Viatcheslavia vorcutensis* interpreted as a halophytic plant is discussed.

Key-words—Permian, Russian Platform, Lycophytes, *Viatcheslavia*, Palaeoecology, *Densoisporites*.

डेन्सोईस्पोराइटीज़ पोलेज़नाएन्सिस नवप्रजाति : *वियातचेसलाविया वोरक्यूटेन्सिस* ज़ेलस्सकी के इसके सम्बन्ध पर टिप्पणियाँ

सरगी वी. नोगोलनिख एवं नेटालिया ई. जेवियालोवा

सारांश

लोइकोप्सिड सूक्ष्मबीजाणुओं की एक नयी प्रजाति *डेन्सोईस्पोराइटीज़ पोलेज़नाएन्सिस* वर्णित की गई है। यूराल पर्वत श्रेणियों तथा रशियन प्लेटफार्म के निम्नतम उपरि परमियन (सोलीकामस्कियन) से लक्षणित लेपिडोफाइट *वियातचेसलाविया*

वोरक्यूटेन्सिस ज़ेलस्सकी के तने एवं पर्णाभों से युक्त मृण्मय आधारी से बीजाणुओं को निकाला गया। रूस के पर्म शहर के निकट स्थापित यूफीमियन (रोडियन) आयु की पोलेज़ना संस्थिति से प्राप्त जीवाश्मों का अध्ययन किया गया। *डी. पोलेज़नाएन्सिस* के बीजाणु 30-69 µm, गोल से अधः त्रिभुजीय हैं जिसमें बीजाणु के मध्य तक विस्तृत रेज़ के साथ स्पष्ट रूप से दिखाई पड़ते त्रिअरीय धब्बों की लगभग मसृण निकटस्थ भुजा है। बीजाणुओं का निचला भाग सूक्ष्म दानेदार उच्चावच है जो कि दूर-दूर अलग-अलग दानों से बना है। बीजाणुचर्म दो परतों का बना है जिसकी बाहरी परत में असंख्य अंतर्ग्रंथित पटलिकाएँ हैं तथा अन्तः परत में एक पटलिका है। कुछ भागों में, बीजाणुओं के केन्द्रीय क्षेत्र में, अन्तः परत में "स्तरित मंडल" खोजा गया है। बीजाणु चर्म में अल्परूप से विकसित गुहिका है। *वियातचेसलाविया वोरक्यूटेन्सिस* को चौड़े तने तन्तुओं (30 सेमी. तक व्यास में) द्वारा निरूपित किया गया है। पर्ण गद्दियाँ तने के पुराने निम्नतम भागों पर उपस्थित होती हैं परन्तु कोई भी उससे जुड़े पर्णाभ/बीजाणुपर्ण नहीं पाए गए, पर्णाभ/बीजाणुपर्ण स्पष्ट रूप से झड़ गए थे। पर्ण गद्दियाँ प्राय : गोल होती हैं और उस पर पत्ती के जुड़ाव के स्पष्ट निशान होते हैं तथा गद्दी के ऊपरी किनारे पर जीभिकायुक्त धसकन होती है। मृदुतक युक्त ऊतकों (संभवतः पैरिक्नोस) के दो छोटे क्षेत्र कभी-कभी दिखाई देते हैं। प्लियूरोमीएसी कुल के लाइकोफाइटीज़ से संबंधित वर्गकों की सहउपस्थिति तथा प्ररूपविज्ञानीय बहिर्वेशन के आधार पर यह प्रस्तावित किया जाता है कि *डेन्सोइस्पोराइटीज़ पोलेज़नाएन्सिस* के सूक्ष्म बीजाणु *वियातचेसलाविया वोरक्यूटेन्सिस* द्वारा निर्मित हुए थे। लवणमृदोद्भिद् पादप के रूप में निर्वचनित *वियातचेसलाविया वोरक्यूटेन्सिस* की पुरापारिस्थितिकी की चर्चा की गई है।

संकेत शब्द—परागाणुविज्ञान, त्रिकॉल्पसी परागकण, टर्शियरी, भारत.

INTRODUCTION

ONE of the most important aspects of palynological and palaeobotanical investigations is attributing dispersed spores and pollen to specific parent plant. This problem is quite complicated, especially in respect to Palaeozoic higher plants, because many of them have no extant relatives, and evidence on spores and pollen preserved *in situ* in sporangia is rather poor (for review see: Balme, 1995). Nonetheless, sometimes new information concerning the precise systematic position of isolated dispersed spores could be obtained from monodominant plant assemblages, where most abundant spores or pollen can be safely correlated with predominant plant megafossils.

The locality studied shows exactly this case of a monodominant assemblage with the only species of plant megafossils and only species of spores that could be assigned to one and the same parent plant. The significance of the evident correlation between microspores, which should be described as a new formal species, and stems of *Viatcheslavia vorcutensis* is additionally emphasized by stratigraphic value of the latter species, a typical index-fossil, specific of the lowermost Upper Permian (Ufimian; Solikamskian Horizon or regional stage) and widely distributed over the western slope of the Ural Mountains.

The present paper includes new evidence on macromorphology of *Viatcheslavia vorcutensis*, its sporophylls, phylloids, growth habit and ecological strategy, as well as detailed description of *Densoisporites polaznaensis* sp. nov., considered as microspores of *Viatcheslavia vorcutensis*.

MATERIAL

The collection studied originated from several localities belonging to the lowermost Upper Permian, i.e., Ufimian according to Russian stratigraphic nomenclature. Recently this stratigraphic interval is also indicated as the Middle Permian (Roadian).

The localities are disposed near Perm City and are represented by the type sections of Solikamskian Horizon (Fig. 1). Plant remains are preserved as compressions/impressions in clayey mudstones of light grey or brownish colour. Collections 3773(11) and 4859 are housed at the Geological Institute of Russian Academy of Sciences. The quantitative relationship between taxa, recognized in macro-and microfossil assemblages is shown in Fig. 2.

PLATE 1 ⟶

Macromorphology of *Viatcheslavia vorcutensis* Zalessky and its predecessor *Sadovnikovia belemnoides* Naugolnykh.

1. *Sadovnikovia belemnoides* Naugolnykh, sporophyll; dark stomatiferous band pointed by the arrow.
2, 4, 5, 8. Cortex of *Viatcheslavia vorcutensis* Zalessky.
3, 6. Phylloids *Viatscheslaviophyllum* sp.
7 Sporophyll and phylloids of *Viatcheslavia vorcutensis* Zalessky localitites.

1, 6. Chekarda-1, layer 10, Upper Kungurian.
3. Krasnaya Glinka, Lower Kungurian (see Naugolnykh, 1998 for exact geographical and stratigraphical position of these localities).
2, 4, 5, 7, 8. Polazna, Lower Ufimian.

Magnification: x 1(6), x 1.5 (2, 4, 5, 7), x 1.7 (3), x 2 (1, 8).

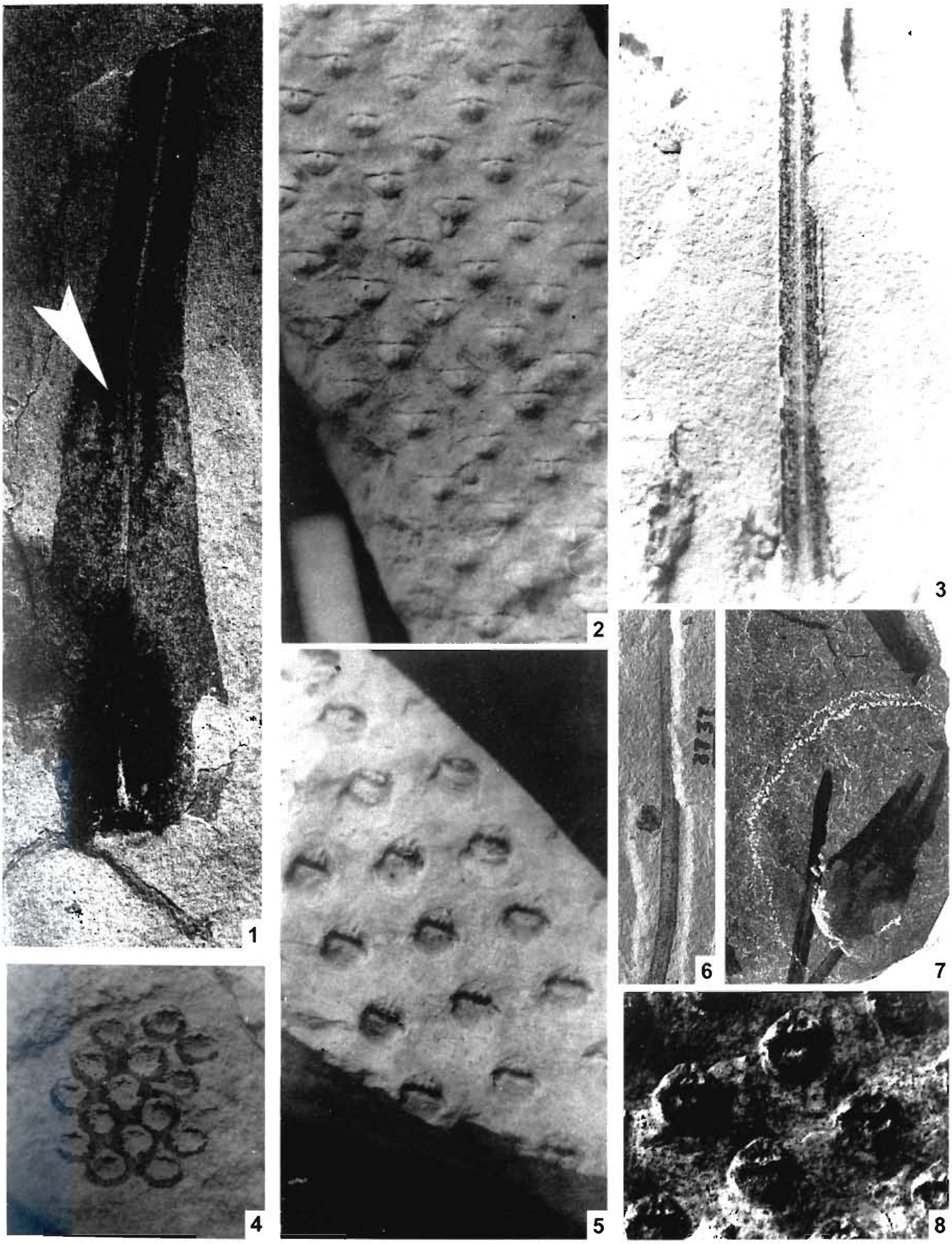

PLATE 1

METHODS

Spores were extracted after dissolution of mudstone matrix in concentrated HNO_3. Then, after washing in distilled water and drying, the spores to be studied with SEM were mounted on standard stubs and coated with gold-palladium (approximately 200 Å). For TEM the spores were removed from SEM stubs with a needle, embedded in epon (technique in Meyer-Melikian & Telnova, 1991; Telnova & Mayer-Melikian, 2002) and sectioned in an ultramicrotome with a diamond knife.

SYSTEMATICS

Family—PLEUROMEIACEAE Potonie, 1904

Genus—VIATCHESLAVIA Zalessky, 1936

VIATCHESLAVIA VORCUTENSIS Zalessky, 1936

(Pl. 1, Fig. 3. a-c)

Initially only cortex fragments with relatively well preserved leaf cushions were assigned to this species (Zalessky, 1936; Zalessky & Tschirkova, 1937). Original material of *Viatcheslavia vorcutensis* came from the Lower Ufimian coal-bearing deposits of the Pechora Basin (Northern Urals, Russia). However, the study of some additional specimens collected from the type area by Neuburg (1960a) clearly proved the assignment of the isolated phylloids described as *Viatscheslaviophyllum vorcutense* Neuburg 1960 to the same parent plant. Recently, several sporophylls of *Viatcheslavia vorcutensis* and additional specimens of cortex and phylloids have been studied from the Perm City Region (Naugolnykh, 1998, 2001).

Since quite wide fragments of stems have been found (up to 30 cm in diameter), we believe that the parent plant of *Viatcheslavia vorcutensis* certainly was arborescent. Old lowermost stem parts bear leaf cushions, but there are no preserved phylloids or sporophylls in attachment. This clearly indicates that the phylloids/sporophylls were shed. Judging from the smooth surface of the cushions and the semi-lunar scar of the phylloid base, it is assumed that the phylloids and sporophylls were separated from the cushions by an abscission layer. Leaf cushions usually are round, with clear scar of leaf attachment located at the central part of the cushion, and ligular depression on the upper margin of the cushion. Two small areas of parenchymatous tissues are occasionally present. These areas can be interpreted as parichnos.

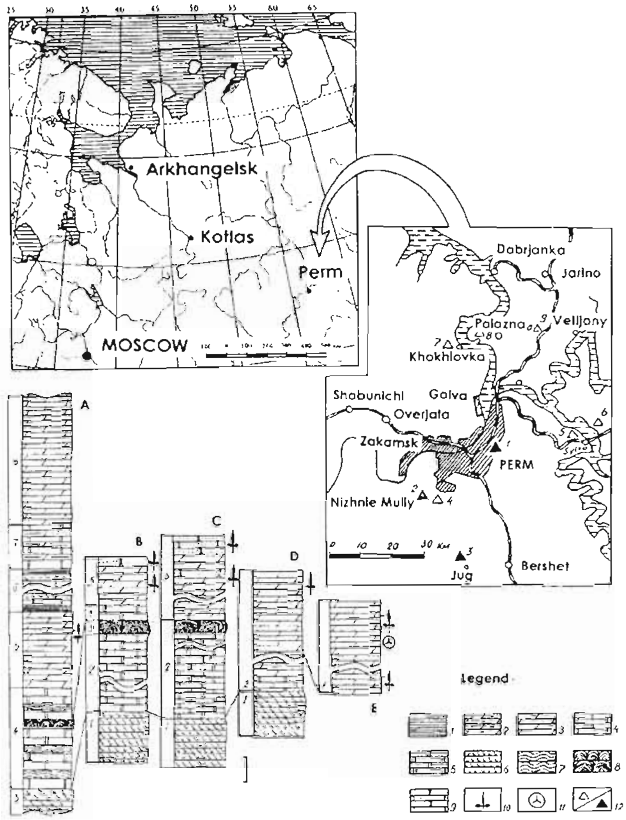

Fig. 1—Geographic and stratigraphic position of the localities studied. Stratigraphical columns: A. Chumkassky quarry. B. Sylva. C. Alebastrovo. D. Khokhlovo. E. Polazna. Legend: 1 argillite (siltstone). 2. clayey marl. 3. marl with remarkable part of carbonate material. 4. mudstone. 5. dolomite. 6. gypsum and anhydrite. 7 stromatolites with undulated surface. 8. semispherical stromatolites. 9. sandstones. 10. plant megafossil assemblages. 11. palynological assemblage. 12. localities of plant remains (white triangular-recently studied. black triangular-ancient copper mines: 1 Motovilikha. 2. Mullinsky Mine. 3. Jugovsky Mine. 4. Lysaya Gora. 5. Sylva. 6. Alebastrovo. 7 Khokhlovka. 8. Chumkassky quarry. 9. Polazna). Scale for A-E-1m.

Phylloids of *Viatcheslavia vorcutensis* are straight, linear, with a single median rib (vein). The phylloids apex is pointed and acute; its base is slightly expanded. Margins of the phylloids bear a denser cuticle, and, therefore, they look darker than the rest of the surface of the phylloid. The best developed

PLATE 2 ⟶

Densoisporites polaznaensis sp. nov., SEM.

1-3. Proximal faces of the spores.
2. The close proximal scar is elevated. note uneven equatorial margin formed by sculptural elements.
4. Lateral view of the spore.
5. Distal view, note the sculptural differences between the distal and proximal faces.
6-10. Distal sculptural.
9. Note small pits distributed among verrucate sculptural elements.
Locality: Polazna, Lower Ufimian.
Magnification: x 1300 (1-6), x 3250 (7-10).

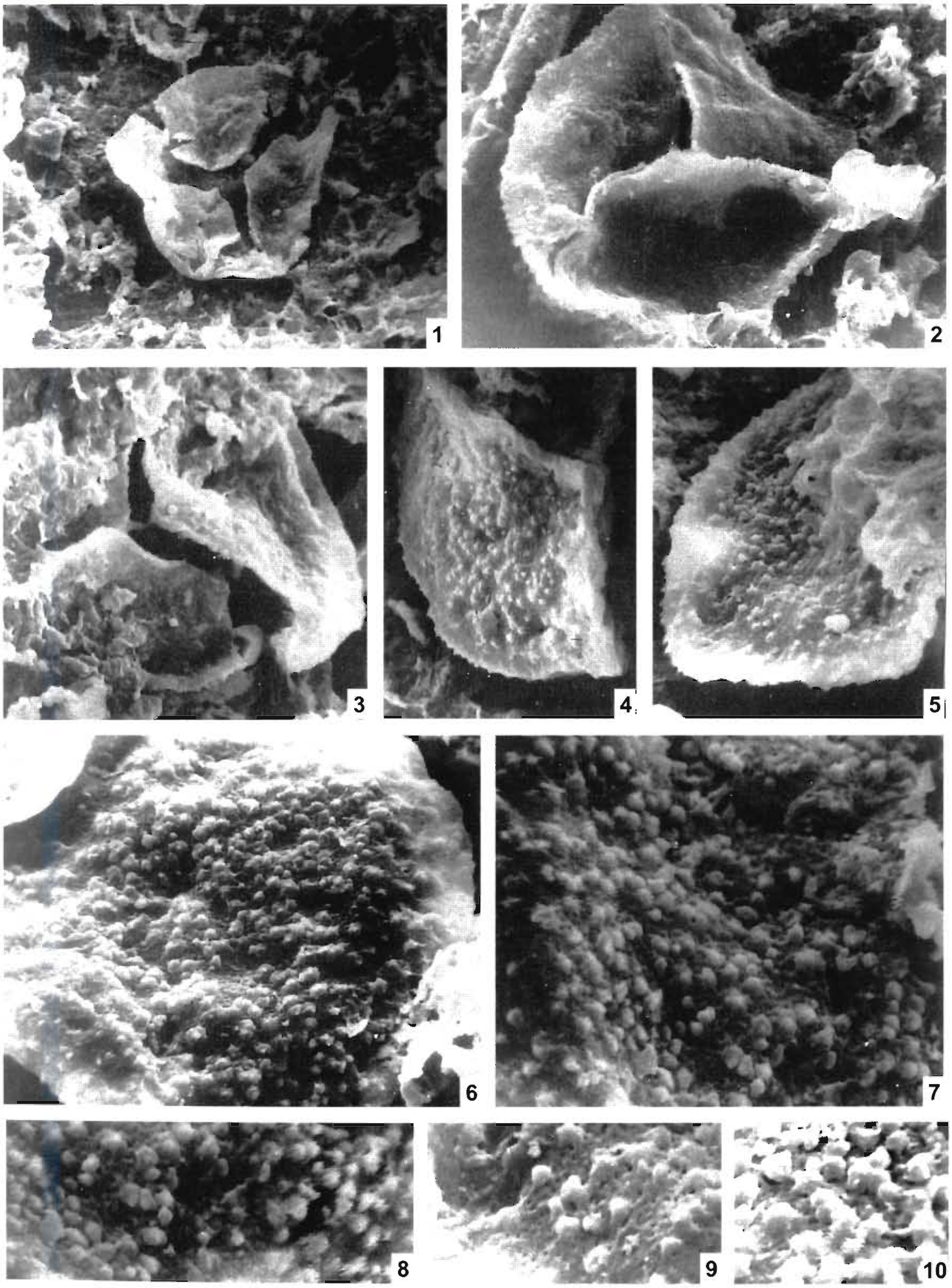

PLATE 2

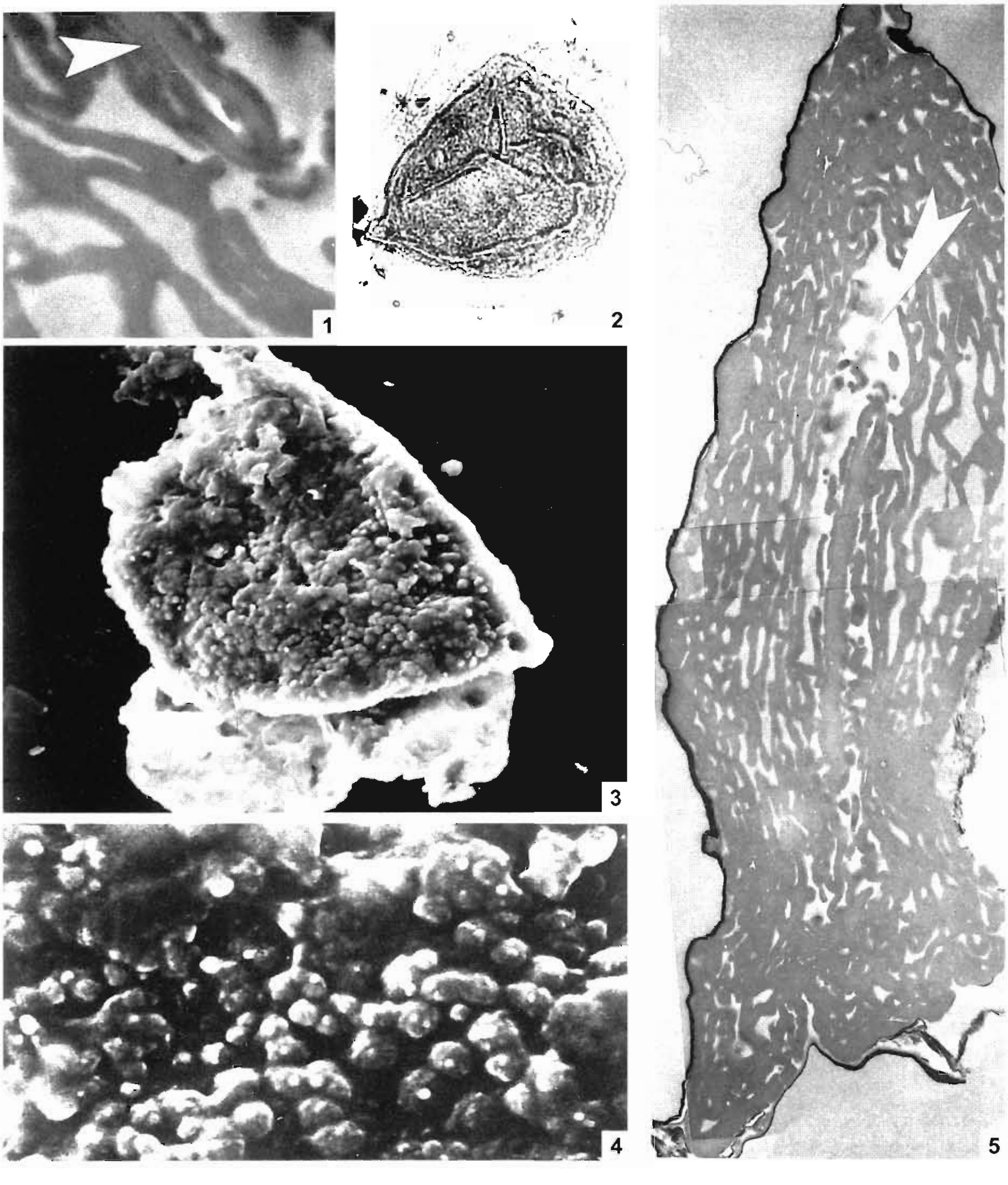

PLATE 3

Morphology and ultrastructure of one and the same spore of *Densoisporites polaznaensis* sp. nov. Holotype

1. Detail of sporoderm ultrastructure, the arrow shows the inner sporoderm layer, enlargement of fig 5, TEM
2. Proximal face of the spore, LM.
3. Distal side, SEM.
4. Granulate surface of the spore distal side, SEM
5. Cross section through the periphery of the spore; cavity is clearly visible (arrow), TEM Locality: Polazna, Lower Ufimian. Magnification x 20000 (1), x 700 (2), x 1000 (3), x 4000 (4), x 8000 (5).

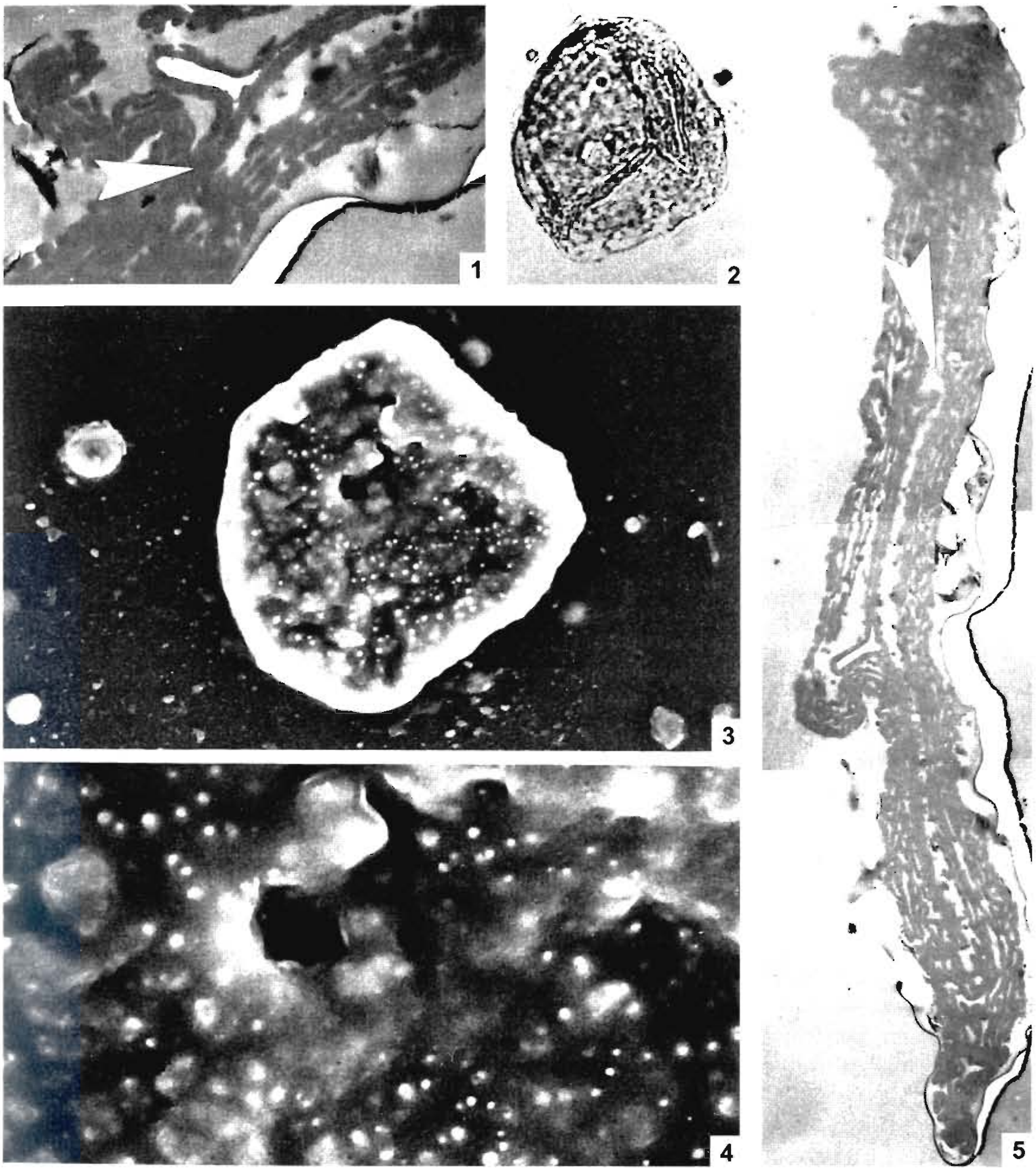

PLATE 4

Morphology and ultrastructure of one and the same spore of *Densoisporites polaznaensis* sp. nov.

1 A detail of the scar ultrastructure, the arrow points the inner sporoderm layer, TEM.

2 Proximal face of the spore, LM.

3 Distal face, SEM.

4 Granulate surface of the spore distal side, SEM.

5 Cross section through the spore peripheral part; note the cavity (arrow) between inner and outer layers, TEM. Locality: Polazna, Lower Ufimian

Magnification. x 10000 (1), x 600 (2), x 1000 (3), x 3000 (4), x 5000 (5).

phylloids show two long dark stripes located along the median vein. These stripes are stomatiferous, typical of some other Upper Palaeozoic lepidophytes.

The sporophylls are subtriangular or rhomboidal, apex is pointed, sporophyll base bears scar of attachment. A single thin median vein runs from the sporophyll base up to the apex. The sporangium was attached to the proximal part of the sporophylls on its adaxial surface. Each sporophyll of *Viatcheslavia vorcutensis* also has two dark longitudinal stripes (stomatiferous bands?) located along the median vein. The normal size of the sporophyll is 3 x 1 cm.

Viatcheslavia vorcutensis stems show a peculiarity, not typical of arborescent Carboniferous lycophytes of the equatorial realm, being reported, however, in *Subsigillaria brardii* Weiss from the Lower Permian of Germany (Barthel, 1983), *Cyclodendron leslii* (Seward) Kräusel from the Lower Permian of Gondwana (Anderson & Anderson, 1985), and *Angarodendron obrutschevii* Zalessky from the Carboniferous of Angaraland (Meyen, 1976). This character is a periodical development of uncommon cyclic zones of dense or, in contrast, very loose arrangements of the leaf cushions. The zones certainly reflect different rates of plant growth in seasonal climate of Upper Palaeozoic moderate climatic zone. Large leaf cushions disposed in dense arrangement most probably were bearing sporophylls, small leaf cushions disposed in normal and relatively loose arrangements were bearing phylloids.

The deposits containing remains of *Viatcheslavia vorcutensis* show numerous signals of climate aridity, i.e., rock-salt, gypsum, ancient desiccation surface cracks, etc. The xeromorphic habit of *Viatcheslavia vorcutensis* supports its interpretation as a halophytic plant.

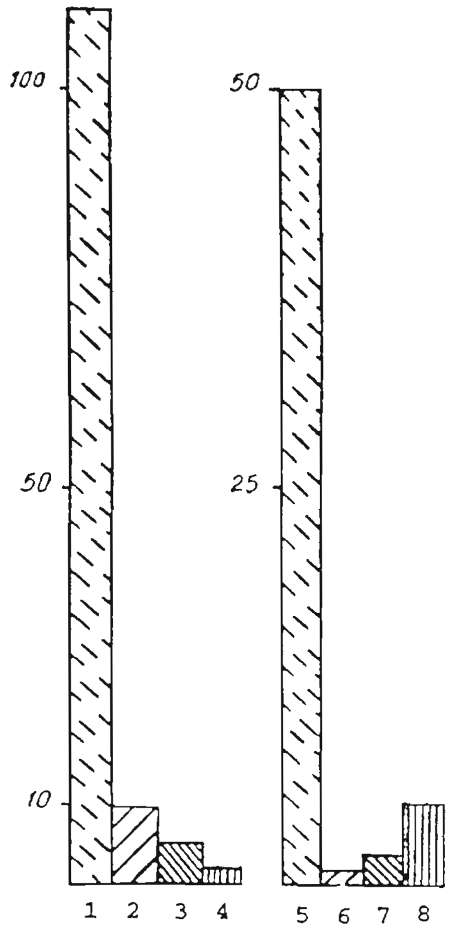

Fig. 2—Quantitative relationship between taxa identified in the micro- and macro-fossil assemblage of Polazna Locality. Spores and pollen grains: 1. *Densoisporites polaznaensis* sp. nov., 2. *Vittatina*, 3. *Cladaitina*, 4. *Calamospora*; plant megafossils: 5. *Viatcheslavia vorcutensis*, 6. peltasperms, 7. *Rufloria*, 8. sphenophytes (mostly *Paracalamites*). Vertical scale shows the number of identified specimens.

Genus—DENSOISPORITES Weyland & Krieger, 1953

Type species—DENSOISPORITES VELATUS Weyland & Krieger, 1953

DENSOISPORITES POLAZNAENSIS sp. nov.

(Pl. 2-6, Fig. 3 d, e)

Diagnosis—Spores trilete, cavate, rounded to subtriangular, finely granulate in transmitted light, 30.0-69.0 µm in size. Proximal face (SEM data) scabrate, with distinct trilete scar nearly reaching the equator. Distal surface sculptured by numerous distinct granules, occasionally perforated. Sporoderm two-layered, lamellate, with a weakly developed cavity (TEM data).

Description—The spores are trilete, cavate, rounded to subtriangular (some crushed spores have irregular outlines), 30.0-(49.5)-69.0 µm (12 specimens of sufficient preservation were measured). The proximal scar is distinct, trilete, with rays nearly reaching the equator. Under LM, the spores appear finely granulate, with a distinctly two-layered sporoderm. The proximal surface as seen under SEM is uneven with occasional

PLATE 5 ⟶

Morphology and ultrastructure of the spore of *Densoisporites polaznaensis* sp. nov.

1-8. General view, LM.

9, 10. The same spores as in (6 and 3 subsequently), proximal side, SEM.

11 Cross section through the spore (the same spore as shown in Plate (3) peripheral part; the numerous interlaced lamellae of the outer layer pointed out by arrow, TEM.

Magnification: x 600 (1-8), x 1000 (9,10), x 5000 (11).

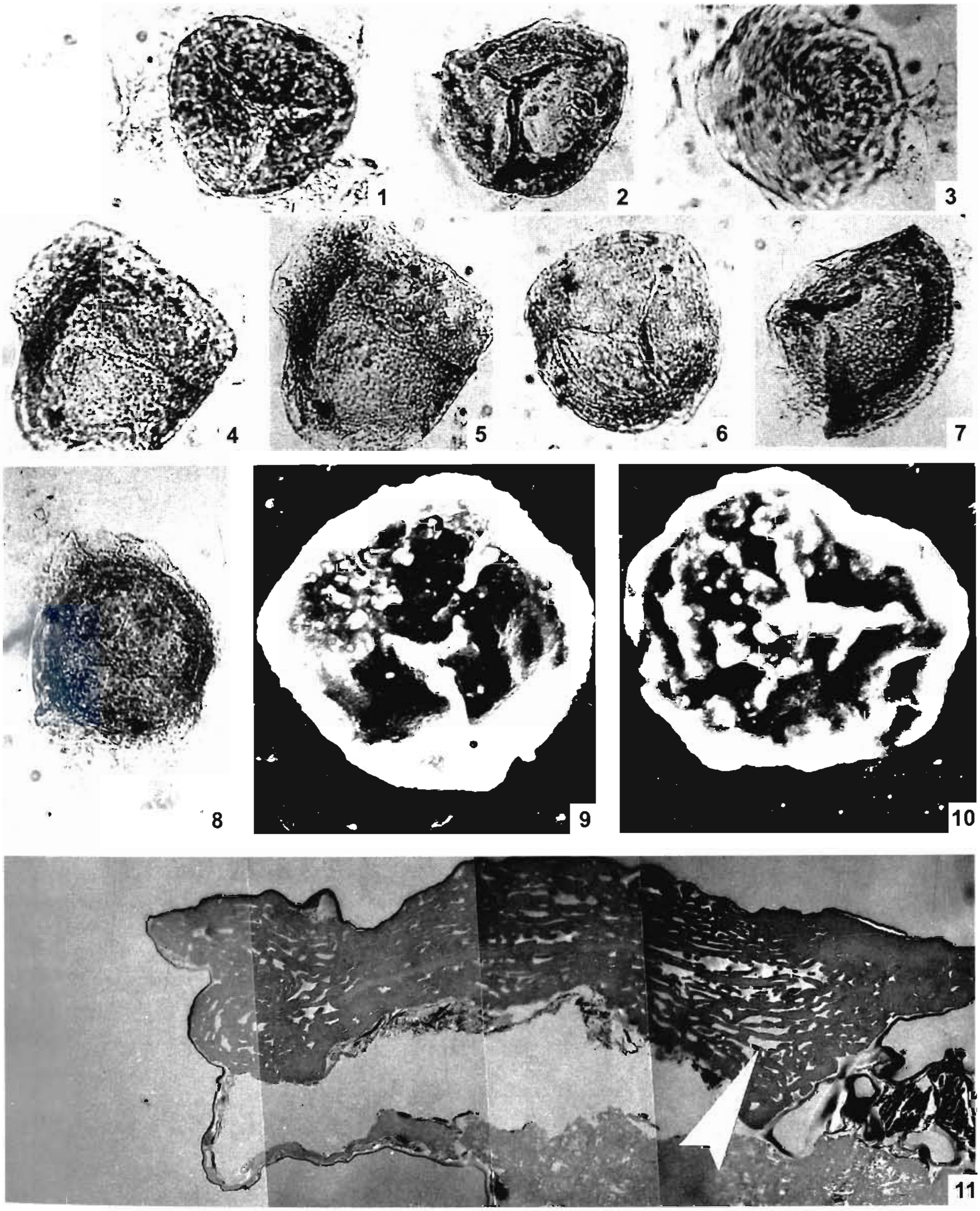

PLATE 5

granules 0.25-0.88 µm in diameter. The proximal scar when closed is elevated (Pl. 2.2). The uneven equatorial margin clearly demonstrates the presence of sculptural elements (Pl. 2. 2, 4, 5). Distally the surface is covered by numerous granules varying in size from 0.33 to 1.5 (0.3 in average) µm (Pl. 2. 4-10) and in shape (some sculptural elements resemble cones, Pl. 2.5).

TEM data confirm two-layered structure of the sporoderm. The outer layer consists of numerous (up to 10) lamellae, which interlace and join, forming an irregular network. Between lamellae there are 0.05-0.25 µm wide and 0.13-1.63 µm long lacunae. As a rule, the lamellae are 0.05-0.25 µm thick, except for the uppermost lamella, which at places reaches 0.75 µm in thickness. It is also pierced by 0.06-0.38 µm wide perforations. Evidently, the repeatedly thickened and thinned and perforated structure of the uppermost lamella corresponds to the granulate and occasionally pitted morphology of the spore surface as seen with SEM (Pl. 6. 7, 8). The inner layer of the sporoderm consists of a single lamella 0.1-0.15 µm thick, surrounding the spore hollow, which looks as a narrow slit due to a strong flattening of the spore during fossilisation. In some sections, the inner layer appears to spilt in the region of the proximal pole (Pl. 6. 1, 5, 7) forming a structure comparable with "laminated zones" described by Lugardon *et al.* (1999). In these zones the inner sporoderm layer is thickened up to 0.62 µm (each lamella is about 0.06 µm). A narrow cavity exists in the bottom of the outer sporoderm layer (Pl. 3. 5; Pl. 4. 1, 5). Some elements of the outer sporoderm layer occur between the cavity and inner sporoderm layer. The cavity, as a rule, is 0.2-0.5 µm wide, at places reaches 0.67-0.73 µm, better developed distally, but also present proximally, in particular, near the laesura. In the laesura region, the spore hollow is less flattened, the lamellae of the outer sporoderm layer are interrupted (Pl. 6. 6, 7).

Holotype—Specimen lost, Figured here on Plate 3, 1-5.

Repository—Geological Institute of Russian Academy of Sciences, coll. 4859.

Type Locality—Polazna Locality.

Stratigraphic Horizon—Upper Permian, Ufimian, Solikamskian Horizon.

Comparison & Remarks—The newly established species differs from the type species *D. velatus* Weyland & Krieger, as well as from other related forms by a very weak development of the cavity between the sporoderm layers. Because of this some immature spores of *D. polaznaensis* also can be assigned to *Lycospora* Schopf according to its formal diagnosis. In addition, more distinct sculptural elements and only rare

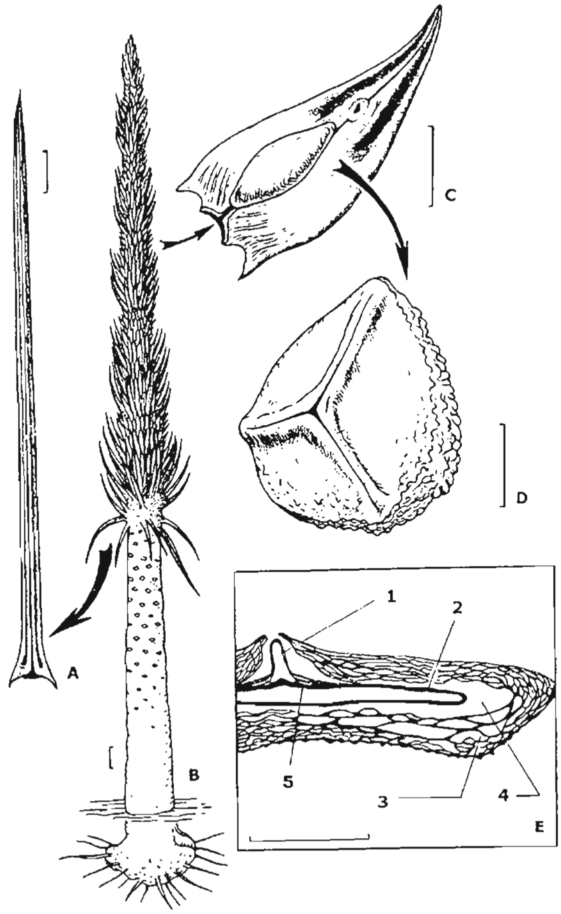

Fig. 3—*Viatcheslavia vorcutensis* Zalessky: morphology of phylloid (A), general habit (B), structure of microsporophyll (C), microspore (D) and sporoderm ultrastructure (E). Scale: 1 cm (A, C), 10 cm (B), 15 µm (D, E). 1 proximal scar; 2. inner layer represented by the single lamella; 3. outer layer represented by numerous interlaced lamellae; 4. cavate area between inner and outer sporoderm layers; 5. laminated zones.

PLATE 6 ⟶

Morphology and ultrastructure of the spore of *Densoisporites polaznaensis* sp. nov.

1-2. Montage of a cross section through the central region of the spore shown also in figs 3, 5, 6, 7, the proximal scar is open, TEM.

3 General view of the spore shown in figs 1, 2, 5, 6, 7, LM.

4. General view of the spore shown in fig. 8, LM.

5. Laminated zone of the inner sporoderm layer, enlargement of fig. 7, TEM.

6. Cross section the proximal scar, TEM.

7. Enlargement of the montage (figs 1, 2), note two rays of the proximal scar, laminated zone of the inner sporoderm layer, strongly compressed hollow of the spore, and distal sculptural elements, TEM.

8. The most developed distal sculptural elements, TEM.

Magnification: x 5000 (1, 2), x 600 (3, 4), x 33000 (5), x 10000 (6, 8), x 13000 (7).

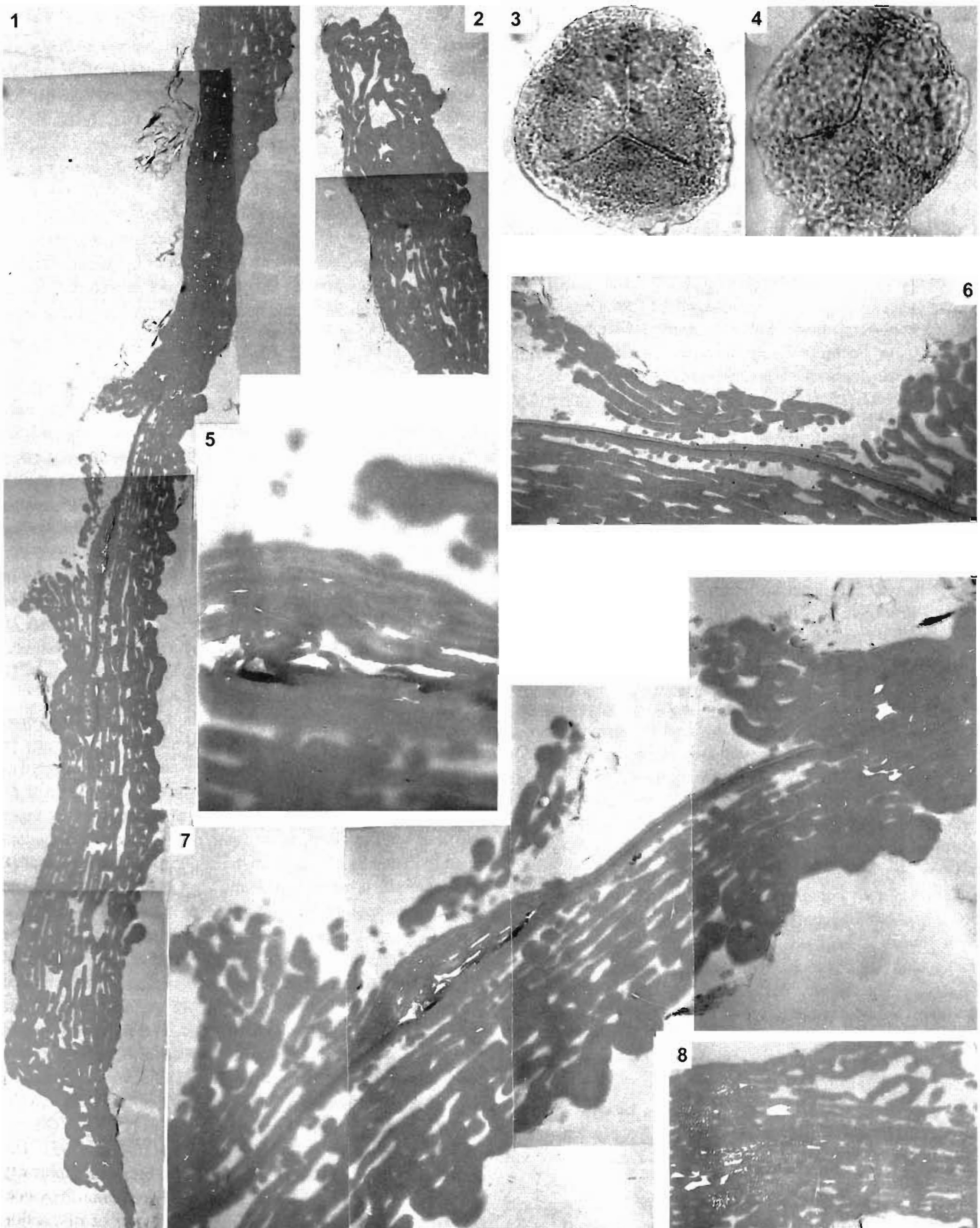

PLATE 6

surficial perforations differentiate the new species from *D. nejburgii*.

Discussion—General similarity between sporophylls of the Kungurian lycophyte *Sadovnikovia belemnoides* Naugolnykh, Ufimian (Roadian) *Viatcheslavia vorcutensis* Zalessky and Triassic lycophytes commonly united in one genus *Pleuromeia* Corda (Dobruskina, 1985; Fuchs *et al.*, 1991; Krassilov & Zakharov, 1975; Magdefrau, 1931; Meng, 1996; Neuburg, 1960b; Snigirevskaya, 1989; Wang, 1996, etc.) together with the related genus *Tomiostrobus* Neuburg emend. Sadovnikov (Sadovnikov, 1982; Dobruskina, 1985; Yaroshenko, 1988) gives an idea that all the forms listed above are linked phylogenetically (Naugolnykh, 1994). In the same case, Lower Permian Sadovnikovia shows intermediate Pleuromeiaceae/Isoetaceae characters. The most ancient *Isoetes* has been reported from the Middle Triassic of northern China (Wang, 1991). According to authors opinion, the Isoetaceae had separated from the Pleuromeiaceae at least during Early Permian, and then, in the Triassic time, both families developed independently.

Several published electron-microscopical studies of fossil cavate spores allow us to compare their fine morphology with that of the spores under description. Yaroshenko (1975, 1985, 1988) has studied Triassic spores of possible lycophyte affinity with LM and SEM. She substantiated the relationship between dispersed spores of *Densoisporites nejburgii* and the lycophyte *Pleuromeia rossica* based, in particular, on the similarity in the ornament (LM data) and sculpture (SEM data) of the spores. She considered the two-layered cavate spongious appearance of the sporoderm in transmitted light to be characteristic of lycophyte spores. Recently Lugardon *et al.* (1999, 2000) have continued the study of *P. rossica* spores using both SEM and TEM. Therefore, having a considerably complete information on the morphology of *P. rossica* spores and their dispersed analogues assigned to *D. nejburgii*, we have recognised several common features between them and the spores of *D. polaznaensis*. Thus, the dimensions of *D. polaznaensis* (30-69 µm) are comparable with those of dispersed *D. nejburgii* (33-71 µm) and *P. rossica* (35-48 µm, after Yaroshenko 1975, or 32.6-39.1 µm, measured in figs 1-3, Lugardon *et al.*, 1999). The greater size variability shown by the dispersed spores might have been related to the different maturation of the spores.

Another common feature is the trilete scar nearly reaching the equator and well distinguishable both in transmitted light (Yaroshenko, 1975, pl. XIII, fig. 8, XIV, fig. 10; Lugardon *et al.*, 1999, fig. 1) and with SEM (Pl. 2.2 of the present paper; Yaroshenko, 1975, pl. XIII, fig. 1, XIV, fig. 1; Lugardon *et al.*, 1999, fig. 3).

Surficial perforations similar to those of *D. nejburgii* and *P. rossica* are also occasionally visible in our material (Pl. 2. 9). Both LM and TEM data confirm the two-layered and cavate structure of the sporoderm. The upper sporoderm layer described here as lamellate with interlaced lamellae looks very similar to the outer wall of *P. rossica*, determined by Lugardon *et al.*, 1999 as a spongy layer formed of cylindrical or tangentially expanded elements, irregularly fused together and roughly arranged parallel to the spore surface. The similarity of these layers includes also the proximal scar region, where the elements of the layers are ruptured leaving a free space over the proximal scar region.

In the non-apertural regions, the morphology of the inner sporoderm layer of *D. polaznaensis* corresponds to that of *P. rossica*. In some sections, in the region of the proximal pole, we have also observed a change in the inner layer morphology, comparable with the "laminated zones", described by Lugardon *et al.* (1999) in microspores of *Pleuromeia rossica* between the apertural rays, near the proximal pole. In *P. rossica* the inner layer is markedly thickened and tangentially cleft in ten or so laminae irregularly segmented and linked. The presence of 'laminated zones' in *P. rossica*, *P. sternbergii*, and the modern *Isoetes* as well as other their ultrastructural similarities allow to suggest (Lugardon *et al.*, 1999; Grauvogel-Stamm & Lugardon, 2001) very close relationships between *Pleuromeia* and the modern *Isoetes* and to assign them to a distinct group among heterosporous lycopsids.

The last thing to be noted is the presence of a cavity in both species better developed distally but also discernible proximally (including proximal scar region). We consider *D. polaznaensis* and *P. rossica* spores to have enough in common for the assignment of *V. vorcutensis*, as a parent plant of *D. polaznaensis*, to the family Pleuromeiaceae.

The differences between the spores of *D. polaznaensis* and *P. rossica* are mostly related to the surface morphology. In particular, *P. rossica* spores have uneven pitted (perforated as TEM images demonstrate) surface, while the sporoderm of *D. polaznaensis*, though occasionally perforated, bears more distinct sculptural elements (granulae), especially abundant distally. The ultrastructure of the upper sporoderm layer of *D. polaznaensis* is more regular allowing us to name it lamellate rather than spongy.

D. polaznaensis also shows a certain similarity in the ultrastructure of the upper sporoderm layer to the spores of *Lycospora perforata* Bharadwaj and Venkatachala extracted from the Carboniferous lepidophyte cone *Lepidostrobus binneyanus* Arber (Thomas, 1988, pl. 1, figs 2-6), spores of *Retispora* species from the Devonian/Carboniferous transboundary deposits of the Timano-Pechora Province of Russia (Telnova & Meyer-Melikian, 1993, p. 45-47, pls. XXVI-XXVII), and spores of *Archaeoperisaccus* Naumova (Meyer & Raskatova, 1984; Telnova & Meyer-Melikian, 1993). The latter genus is a widely dispersed and biostratigraphically important in the Upper Devonian of the Euramerian Province, its systematic assignment remains a matter of discussion (Meyer & Raskatova, 1984; Balme, 1995). The similarity with the lycophyte *D. polaznaensis* provides an additional indirect evidence of its lycopsid affinity.

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