

Devonian thalloid plants (Orestoviaceae) and associated spore tetrads

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ABSTRACT

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Schuguria Tehirkova-Zaleskaya, 1957 is a cutinized mat-forming thalloid plant similar to *Orestovia* Ergolskaya, 1936, but differs in the crater-like surface structures interpreted as gamentangial conceptacles. Typical stomata is lacking in *Schuguria*, while the conducting tissue is relatively feebly developed. It is suggested that *Schuguria* and *Orestovia* represent sexual and asexual generations of a nearly isomorphic reproductive cycle. Persistent spore tetrads are abundantly preserved in maceration residue of the mats and adhering to cutinized thalloids. On evidence of association and similar ultrastructure of the cuticle and sporoderm, the tetrads might have been produced by a sporophytic member of the Orestoviaceae. At the same time, they are comparable to the Early Palaeozoic tetrads of putative incipient land plants.

Key-words—Early land plants, Orestoviaceae, Reproductive cycle, Spore tetrads, Devonian.

डिवोनी थैलसाभ पादप (ओरेस्टोविएसी) एवं सहयोगी बीजाणु चतुष्क

वैलेंटिन क्रॉसीलोव एवं स्वेतलाना पोलीवोवा

सारांश

सुगुरिया ट्चिरकोवा-ज़लेस्काया, 1957 ओरेस्टोविया इर्गोल्सकाया, 1936 के सदृश क्यूटिनमय लता-रचित थैलसाभ पादप है, परंतु युग्मक-धानीय धानी के रूप में व्याख्यायित ज्वालामुखी-विवर पृष्ठीय संरचनाओं से भिन्न है। विशिष्ट रंभ *सुगुरिया* में न्यून है, जबकि संचारित कोशिका सापेक्षतया स्वल्पी विकसित है। सुझावित किया जाता है कि *सुगुरिया* एवं ओरेस्टोविया तकरीबन समजीवी पुनर्उत्पादी चक्र के लैंगिक एवं अलैंगिक पीढ़ियों को निरूपित करती हैं। लताओं के द्रव सम्मर्दन अवशेष में स्थायी बीजाणु चतुष्क प्रचुरता से परिरक्षित हैं तथा क्यूटिनमय थैलसाभों से चिपके हैं। साहचर्य और उपचर्म एवं बीजाणुचर्म की सदृश परासंरचना के प्रमाण के आधार पर, चतुष्क ओरेस्टोविएसी के बीजाणुउद्भिदी सदस्य से उत्पन्न हुए होंगे। उसी समय, वे तथाकल्पित प्रारंभी स्थल पादपों के प्रारंभिक पुराजीवी चतुष्कों के तुल्य हैं।

संकेत-शब्द—प्रारंभिक स्थल पादप, ओरेस्टोविएसी, पुनर्उत्पादी चक्र, बीजाणु चतुष्क, डिवोनी।

INTRODUCTION

Orestovia and allied thalloid thickly cutinized plants are widespread in the mid-Devonian of Laurasia forming extensive cuticular mats and coal seams. Originally described as probable higher plants (Ergolskaya, 1936), *Orestovia* was then assigned to higher algae (Kräusel & Venkatachala, 1966;

Niklas & Chaloner, 1976). Krassilov (1981) described stoma-like structures and tracheid-like conducting cells in the type species *Orestovia devonica* Ergolskaya from the Devonian of Kuznetsk Basin arguing for an incipient higher plant. Similar structures have been also recognized in *Orestovia petzi* (Gensel & Johnson, 1994) and in *Orestovia*-like forms from European Russia (Snigirevskaya, 1993).

At the same time, Istchenko and Istchenko (1981) have reported *Orestovia* and allied plants supposedly representing an extinct group of higher algae from the Pavlovsk Quarry, Voronezh Region, European Russia. They based their opinion on the crater-like cavities and dome-like pustules scattered over the thalli and interpreted as conceptacles and nemathecium, respectively.

Further study of thalloid plants from the Pavlovsk Quarry (Krassilov *et al.*, 1987a) has shown that at least some of them had conducting strands, although feebly developed in comparison with the typical *Orestovia*. Whether the differences were of taxonomic or ecological nature remained uncertain. In *Bitelaria*, supposedly representing a distinct order Bitelariales (Istchenko & Istchenko, 1981; Krassilov *et al.*, 1987a), testifies to a considerable disparity of cutinized thalloid forms representing more than one type of cortex histology. Permanent spore tetrads are reported for the first time in association with cutinized thalloids.

The thalloids are heavily infested with fungi that will be described in our forthcoming publication.

MATERIAL AND METHODS

The material came from the Pavlovsk Quarry in the upper reaches of the Don River, Voronezh Region, European Russia

(Fig. 1). The quarry cuts a sequence of Late Givetian sandstones and shales (on their palynological age assignment see Rzhonsnitskaya, 2000; Raskatova, 2004) containing scattered shoot remains of an archaeopterid *Tanaitis* (Krassilov *et al.*, 1987b) and cuticular mats of bilaterally compressed thalloid plants (Fig. 2).

The compressions can be separated by needle, but immersion in hydrofluoric acid is necessary for removing mineral film with small organic debris deposited on the surface and infiltrated in the flattened interior hollow. Fragments about 2-3 cm long were cleared in Schultze's mixture of nitric acid and potassium chlorate for several hours. The compressions are bilateral with sharp edges along which they can be split and spread with needle. Alkali treatment makes the cuticles more transparent, but destroys non-cutinized interior tissues and fungal remains, hence avoided for material set out for this purpose. SEM mounts were made from both intact and split fragments, the latter glued their exterior or interior side up or both sides were in turn exposed. The maceration residues were surveyed under stereomicroscope for structurally preserved fungal remains and spores. Photographs were obtained with the stereomicroscope Leica 300, dissecting light microscope Nikon Eclipse and scanning electron microscope FEI Quanta 200.

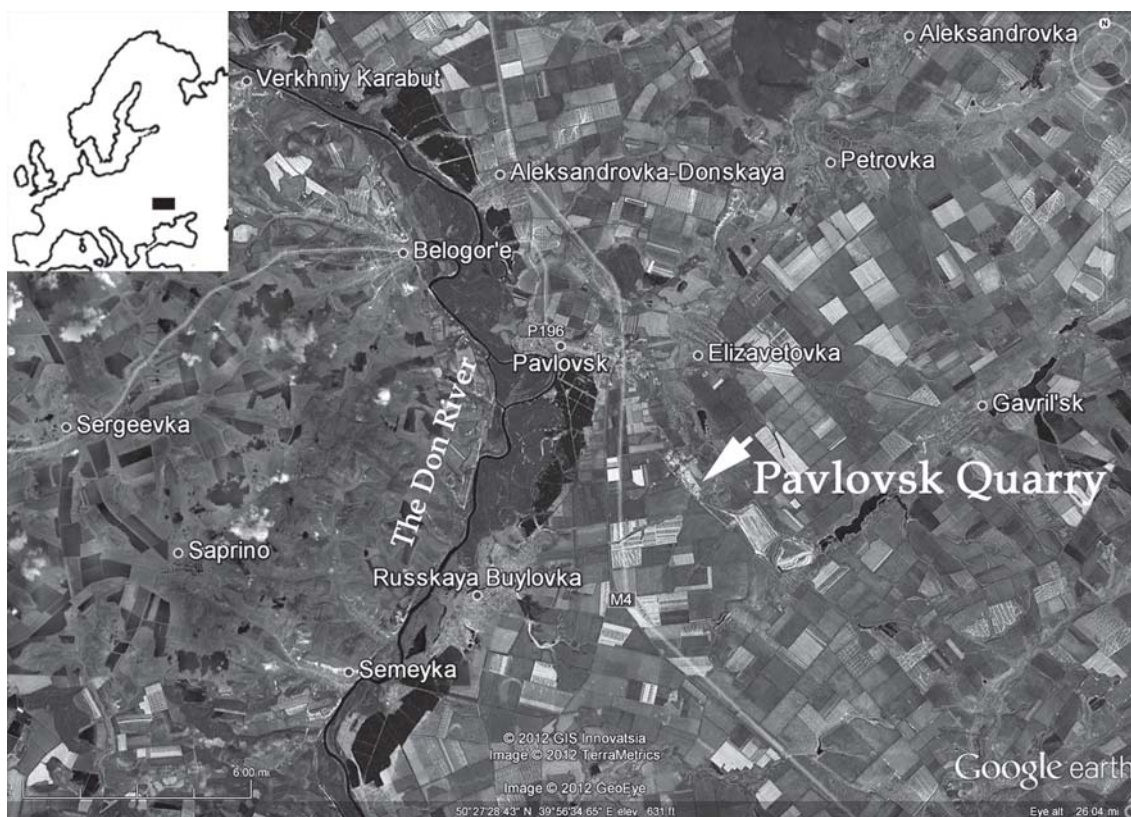


Fig. 1—Locality Pavlovsk Quarry (arrow) on Google earth map; study area (rectangle) on insertion.

For TEM, the tetrads were fixed with OsO₄, dehydrated, placed in the mixture of epons (Epon-812, DDSA and MNA), sectioned with Ultracut-R of the Leica-5 microsystem, and studied under TEM JEM-1011.

The collection is presently deposited in the Paleontological Institute, Moscow, no. 4821 and in the Institute of Evolution, University of Haifa, no. RPS-L (for glass slides) and RPS-S (for SEM mounts).

Valentin Krassilov made preparations of the thalli and spores for LM and SEM and is responsible for their morphological interpretation. Svetlana Polevova conducted TEM study of cuticle and sporoderm.

SYSTEMATICS

Genus—SCHUGURIA Tchirkova-Zalesskaya 1957 emend.

Schuguria ornata Tchirkova-Zalesskaya 1957 emend.

(Pl. 1.1-6; Pl. 2.1-3; Pl. 3.1-5; Pl. 6.5, 6)

1957—Tchirkova-Zalesskaya, 1957, p. 92, Pl. 11, figs 58, 59; Pl. 18, figs 101-106.

Name—Istchenko and Istchenko (1981) have recognized several species of cutinized thalloid plants assigned to *Orestovia* and the newly erected genera *Orestovites* and *Rhytidophyton*. However the distinctions between these morphotaxa are for the most part preservational (smooth, folded, furrowed or fissured thalli) and they are here considered as representing a single taxon conspecific with *Schuguria ornata* Tchirkova-Zalesskaya 1957 from the Shugurovo Locality on the Volga River, for which a new combination *Orestovia ornata* has been proposed by Istchenko and Istchenko (1981). It will be shown later in the paper that thalloid plants from Pavlovsk differ from typical *Orestovia* from Kuznetsk Basin, western Siberia, representing either a distinct growth form or a distinct developmental stage

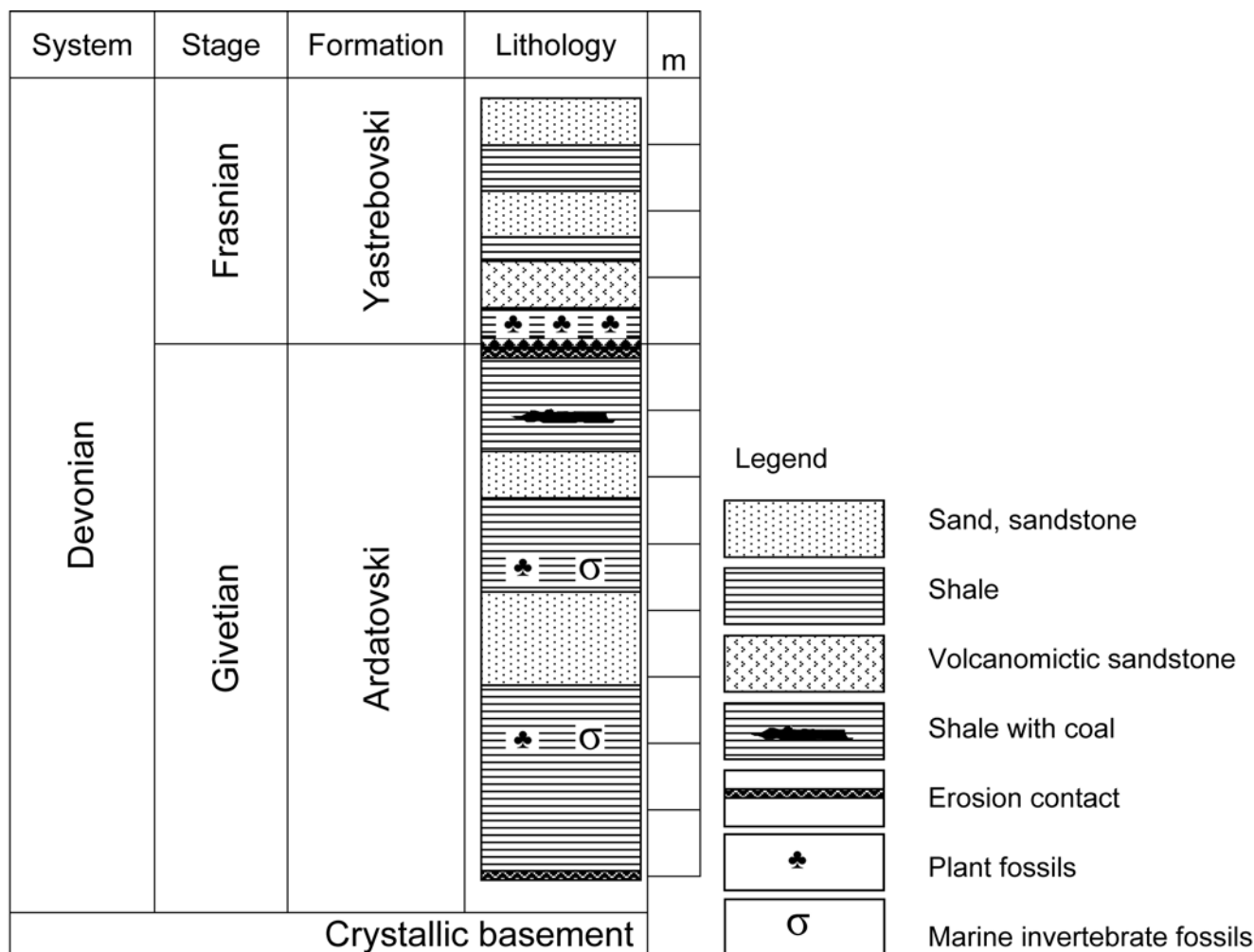


Fig. 2—Stratigraphic column of Devonian deposits, Pavlovsk Quarry (after Raskatova, 2004).

of reproductive cycle. Whatever biological interpretation may be, the morphological differences impel separate morphotaxon. The generic name *Schuguria* (spelled *Shuguria* Antropov, 1950) has been used for microfossils from the same locality assigned to foraminifera till 1965 and therefore holding no priority over *Schuguria* Tchirkova-Zalesskaya 1957 as a botanical taxon.

Description—The thalli are flat compressions, but their surface prominences are uniformly developed on both surfaces and protrude on the edges, indicating an originally tubular shape. Most fragments are about 10-15 cm long, parallel-sided or gradually attenuated to one end, unbranched (Pl. 1.1). Dichotomy was observed in a few fragments that branch at acute angle, with the arms apparently extending in one plane.

A mineral film with spores and other small organic debris abundantly sticking to the cortex suggests a slime cover. The cortex is heavily cutinized, externally smooth or irregularly folded and fissured. The cortex transparencies reveal two superimposed layers of elongate cells (Pl. 1.6). The cell walls are strongly marked on the cortex interior, with dense ridges flanked by irregular spongy stripes (Pl. 1.2) invading the lumina at the cell joints (in brown algae a similar spongy fabric appears with hydrolysis of pectin in the two-layered – the internal cellulose, the external pectin-cell walls).

The medullar tissues comprise a subcortical parenchymatous layer and a central strand about 1 mm wide consisting of narrow tubular cells (Pl. 1.3). Their transverse walls are oblique to the tube length, poorly defined. The side walls show indistinct annular thickenings and small circular or irregular pits 6-8 μm wide, with slightly raised borders that appear as transverse bars when contiguous (Pl. 1.4).

At low magnification, the cortex appears speckled with crater-like pits that are stretched with elongation of the thallus and some are emptied of their content, appearing as perforations through the cortex. Their density varies from a few to about 30 per 1 sq. mm and they are irregularly scattered or, in the areas of relatively uniform distribution, irregularly filed (Pl. 1.5; Pl. 2.1). They are more uniformly distributed over the cortex interior, but are not evident on the surface before developing radial structure with a central opening (Pl. 2.1, 2).

Various developmental stages are preserved, starting with a protruding elliptic basal cell about 50 μm wide, conspicuously darker and thicker than the surrounding undifferentiated cells of subcortical parenchyma, producing a hemispherical mass of radially disposed polygonal cells cut off at anticlinal and periclinal divisions (Pl. 2.3). The mature structures are circular or rounded-elliptic in outline, 300-600 μm in diameter, formed of about 30-40 radial files of isometric cells cut off by tangential divisions, with a circular opening in the middle (Pl. 2.2). The radial cells increase toward the periphery where they meet the surrounding cortical cells that tend to deflect from longitudinal to concentric disposition forming a transitional zone. The locule apparently develops by decay of central cells and is crowned

with a neck of thin-walled cells forming a membranous fringe of a thick pack-like neck canal cell (Pl. 3.1, 3, 4). The neck cells may appear stomata-like partly owing to the coiled initial hyphae of fungal fruiting bodies that invade the canal (to be described with fungal remains). The membranous fringe is partly or completely destroyed at maturity and the neck canal cell drops out, and contributes to the stoma-like aspect of the neck cell. The locule is lined with small bulging cells some of which are conspicuous in transmitted light being filled with a dark content, while the others are ruptured and hollow. With collapse of the central tissue, the pustules are destroyed leaving the crater-like depressions encircled by the raised borders of thick-walled cells (Pl. 2.1).

Interpretation—In general aspect, *Schuguria* is similar to brown algae, in particular the Scytosiphonales, in which gametophytes grow as tabular thalli bearing plurilocular gametangia, and the Laminariales, in which the cortex of the outer parenchymatic and inner prosenchymatic cells is covered with alginic cuticle (Sze, 1993). A layer of conducting cells with large pores on end walls is developed between the cortex and medulla. In the Fucales, small cavities, cryptostomates, scattered over the surface are homologous to conceptacles. Typically, the conceptacles are spherical cavities opening to the exterior.

As recognized by Istchenko and Istchenko (1981) and confirmed by our study, the multicellular concentric structures of *Schuguria* (*Orestovia*) *ornata* are similar to gametangial conceptacles of the Fucales and Ascoseirales, in which gametophytes develop on free-living sporophytes from an initial cell, or prospore, that differentiates in the meristoderm and is developmentally shifted to subcortex. The initial stages in *Ascoseira*, as illustrated in (Moe & Henry, 1982), are fairly similar to those of *Schuguria*. In both the conceptacle initials appear as an enlarged thick-walled cell of the inner cortical layer producing by successive anticlinal divisions a basal chamber with gametangial or sporangial sori and with a neck reaching to the surface. In the extant alga, the surrounding cortical cells undergo rapid divisions forming radial files. Similarly, the arrangement of surrounding cells in *Schuguria* suggests their derivation by a rapid division of adjacent cortical cells induced by the developing conceptacle.

Using the morphologically and developmentally similar conceptacles of *Ascoseira* as a model for interpretation of reproductive structures of *Schuguria*, we suggest, that the hollow bulging cells protruding from the the lining of the locule correspond to the similarly produced gametangia of *Ascoseira* that are likewise detachable and are released through the neck. In the extant alga they contain small pyriform reproductive cells (swarmers) that are homologous to the fuclean eggs, but develop parthenogenetically without conjugation and are thereby defined as spores; a distinction between gametes and spores (and, respectively, between gametangia and sporangia) being developmental rather than morphological in this case.

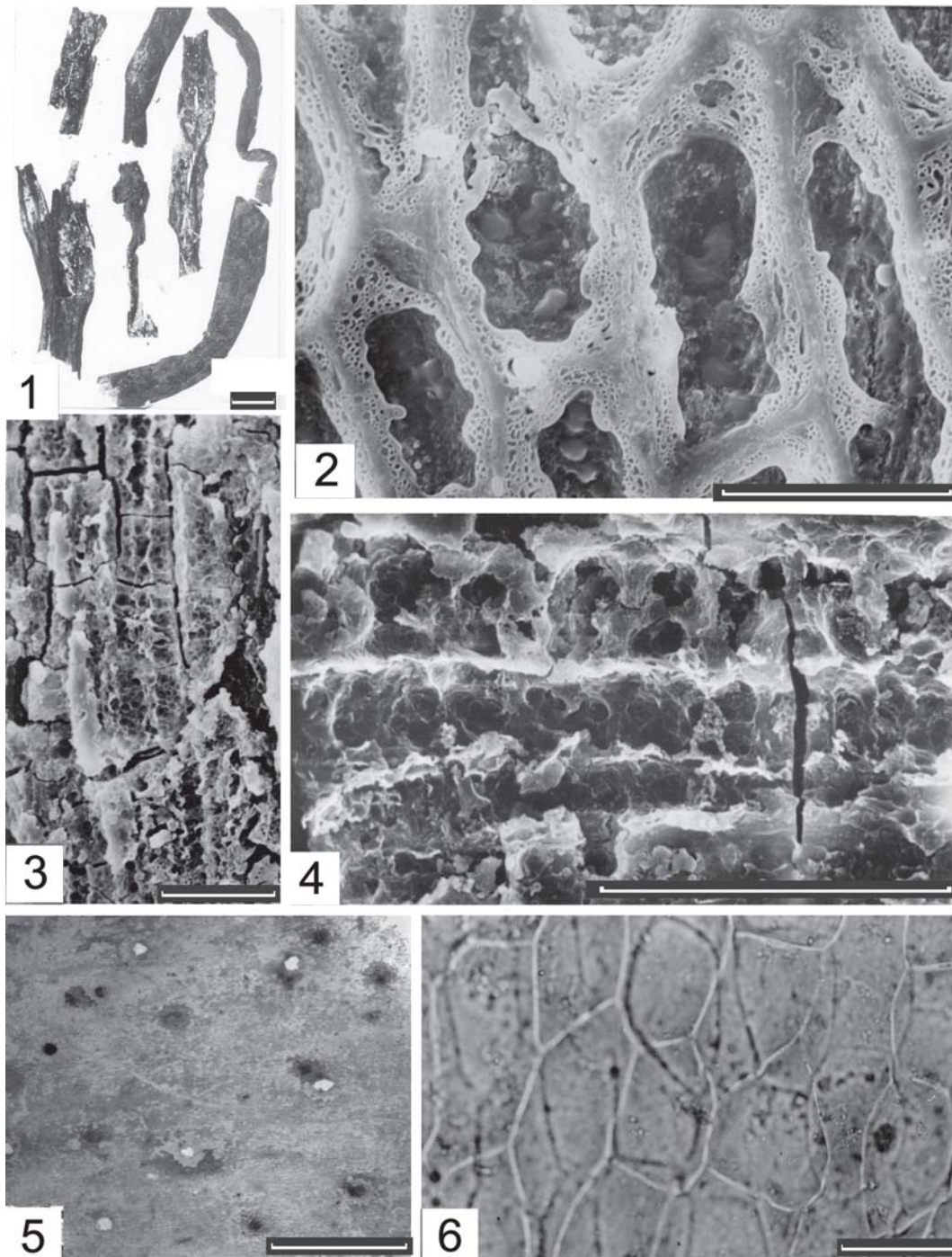


PLATE 1

Schuguria ornata Tchirkova-Zalesskaya, emend. from the Middle Devonian of Voronezh Region.

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| <p>1. Compressions of thalli, LM, scale bar 10 mm.</p> <p>2. Epidermal cells of the cortex, SEM, scale bar 100 μm.</p> <p>3. Central strand of tubular conducting cells (tubes), scale bar 100 μm.</p> | <p>4. Tubular cells, scale bar 100 μm.</p> <p>5. Surface pitting, LM, scale bar 5 mm.</p> <p>6. Cortex transparency showing two superimposed cell layers, LM, scale bar 100 μm.</p> |
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ASSOCIATED SPORE TETRADS

(Pl. 4.1-7; Pl. 5.1-6; Pl. 6.1-4)

Several types of spores were found in maceration residues, but the most frequently associated with *Schuguria* and commonly attached to the thalli are permanent tetrads of the type shown in Pl. 3.1-5. Masses of tetrads representing sporangial contents stuck to the thalli, but none is organically connected in the material at hand.

Several dozens tetrads were studied with LM and SEM showing either distinct cruciate (Pl. 4.1, 5; Pl. 5.3-5), or apparently tetrahedral (Pl. 3.1, 5) configuration (Pl. 4.2-4; Pl. 5.2, 6), the former with cell divisions in the opposite pairs at 90° to each other, most distinct in Pl. 2.1 and Pl. 2.5. However the dimension ranges and surface ornamentation are alike for both types. The tetrads are rounded-elliptic, ranging from 104.5 x 94.5 µm to 172.5 x 165.7 µm, average of 10 counts 114.2 x 108.3 µm. The spores are trilete with laesurae unequally developed, one arm being shorter than the other two in the cruciate tetrads. The equatorial outline is elliptic to rounded-triangular. The lateral aspect is lens-shaped, biconvex, with a distinct curvature. The contact facets are minutely scabrate (Pl. 6.1, 2), the distal face and the broad curvatures are sculptured with minute spinules or conical smoothed down to low verrucae in effaced tetrads.

In optical section, the sporoderm is about 5.5-7.5 µm thick, two layered, with the outer layer (exospore) about twice thicker than the inner layer (Pl. 4.6). In TEM sections, the exospore consists of external homogeneous and internal lacunal zones (Pl. 6.3, 4). On the distal side and over the curvatures, the homogeneous zone is fairly thick, but vanishes over the contact areas. The lacunae are widely spaced and of irregular shapes in the distal sporoderm, but denser and smaller proximally. A slender lamellate layer is discernible under the exospore in the trilete scar region.

A tetrad bearing slender mycelium of branched anastomosing hyphae is shown in Pl. 5.1.

Remarks—Spore tetrads found with *Schuguria* resemble the Silurian-Early Devonian permanent tetrads that are commonly considered to be evidence of early land plants (selected references from numerous publications: Gray & Boucot, 1971; Gray *et al.*, 1974; Burgess & Richardson, 1991; Steemans *et al.*, 1996; Edwards *et al.*, 1999). The most similar are the “cross tetrads” with spores about 30 µm in equatorial diameters, distally sculptured with rounded verrucae (a condition met in the effaced tetrads of *Schuguria*, above) and with distinct curvatures (Steemans *et al.*, 1996).

Cuticle of *Schuguria* was sectioned and compared with tetrad sporoderm on assumption that, if of the same plant, the ultrastructure should be similar because deposition of waxes is controlled by the same genes. The cuticle shows a thick homogeneous and a thinner lacunal zones. The lacunae are

irregularly spaced, somewhat stretched parallel to the margins, decreasing toward the inner margin (Pl. 6.5, 6).

DISCUSSION

The cutinized thalloid forms are assigned to the Orestoviaceae or affiliated with the likewise controversial Spongiophytaceae (compare interpretations in Gensel *et al.*, 1991 with that of Stein *et al.*, 1993). Their mid-Devonian age seemingly precludes the possibility of them being an ancestral group of terrestrial higher plants, but their associated spore tetrads are of the type widely spread in the Silurian and occasionally found in the geologically older deposits, probably representing an early group of plants with terrestrial adaptations, commonly linked to liverworts on evidence of permanent tetrads in this group. However, the mid-Devonian plant assemblages are a mixture of advanced and archaic morphologies. The cutinized thalloids and associated tetrads, despite their relatively late appearance in the fossil record, still may represent an incipient land plant morphology, attesting to remarkable evolutionary conservatism of an ancestral group.

In *Schuguria*, conducting tissue is feebly developed in comparison with *Orestovia*, in which the vascular elements show regular helical thickenings and intercellular pitting of lateral walls (Krassilov, 1981). In *Orestovia*, the two-celled epidermal structures with subsurface chambers are interpreted as stomata (Krassilov, 1981), whereas the multicellular concentric structures of *Schuguria* lacking discernible guard cells and initiated in subcortex are interpreted as gametangial conceptacles. However, since stomata might have derived from sex organs (Pant, 1960), homology between stomatal structures of *Orestovia* and conceptacle neck cells of *Schuguria* is a possibility worth considering.

Certainly, *Schuguria* is more alga-like of the two, but the differences are much the same as between sporophytes and gametophytes of higher plants. Conducting cells occur as hydroids with pitted and irregularly thickened walls in gametophytes of some bryophytes (e.g., *Symphyogyna*: Schuster, 1984), as well as in the Psilotaceae (Manton, 1942). The feebly vascularized *Schuguria* and the more conspicuously vascular *Orestovia* may represent sexual and asexual generations of a nearly isomorphic developmental cycle. Conceivably, sporophytes have developed on *Schuguria* mats when raised above water. Both stomata and tracheid-like cells are developed in sporophytes of hornworts, but lack in their gametophytes. At the same time, the antheridial cavities of hornworts appear similar to the crater-like depressions of *Schuguria* and *Bitelaria* (Pl. 7.4, 5).

Johnson and Gensel (1992) erroneously stated that *Bitelaria* was assigned to higher algae by Krassilov *et al.* (1987a). In fact this plant revealed some bryophytic features supposedly derived in the group of the mid-Devonian cutinized thalloids. The cortical cylinder of *Bitelaria* consists of

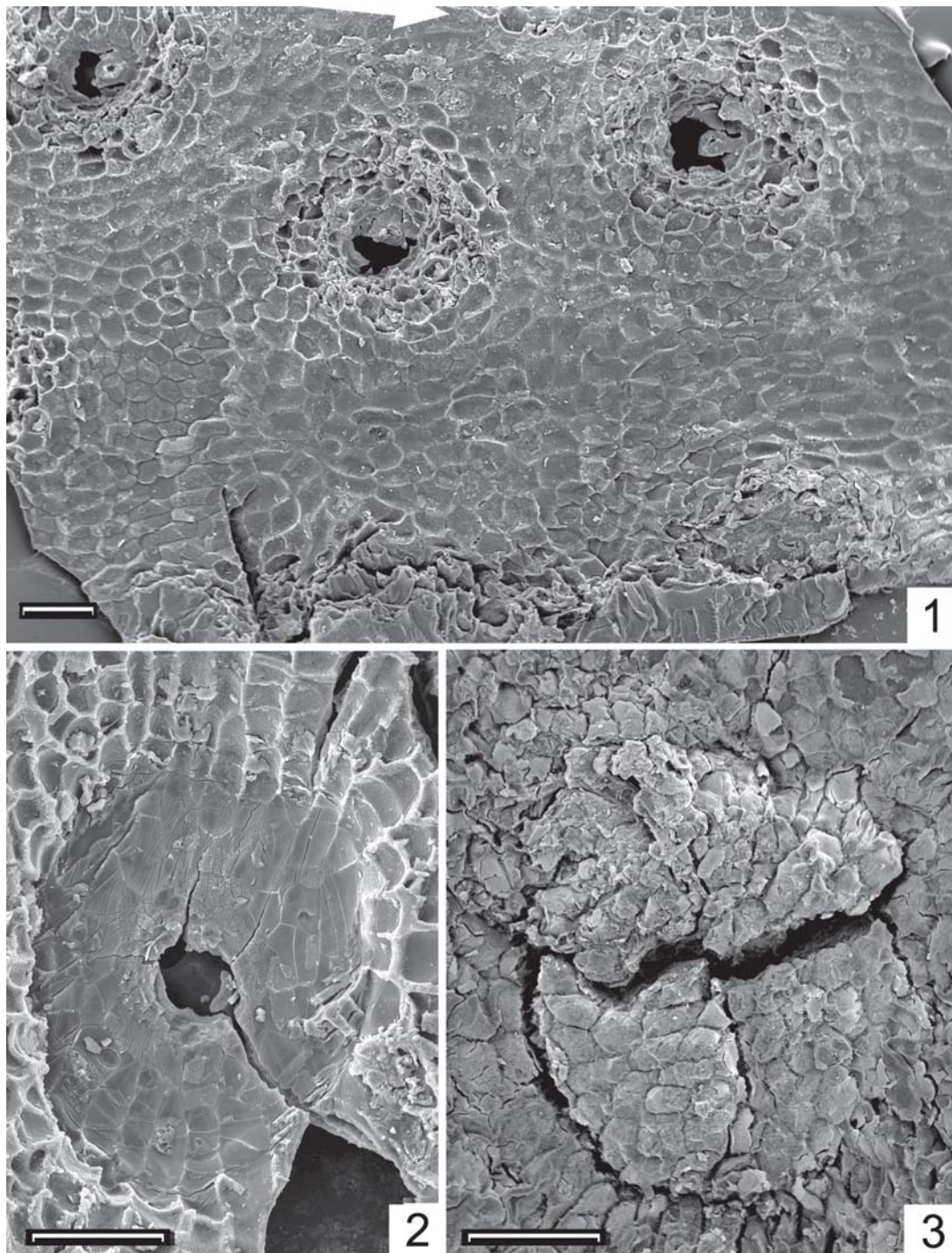


PLATE 2

Schuguria ornata Tchirkova-Zalesskaya, emend. from the Middle Devonian of Voronezh Region, conceptacles, SEM.

1. Cortex interior with several conceptacles.
2. Conceptacle, cover cells with a central opening.

3. Conceptacle, infilling cell mass cut by compression cracks.

Scale bar 200 μm for Figs 1-3.

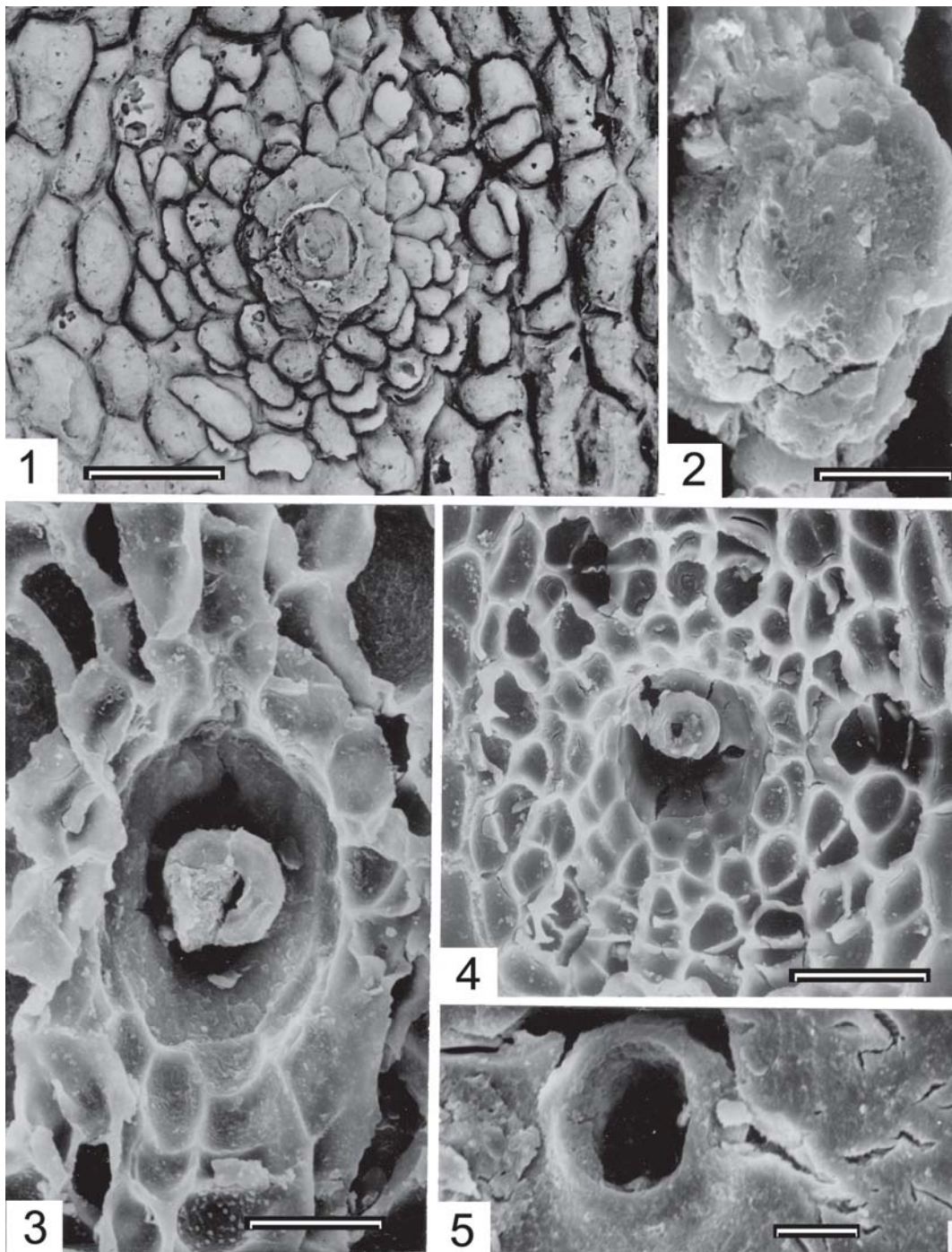


PLATE 3

Schuguria ornata Tchirkova-Zalesskaya, emend. from the Middle Devonian of Voronezh Region, conceptacle cells.

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| <p>1. Interior view of conceptacle with the neck cell and the bulging radial cells (gametangial sorus?), scale bar 30 μm.</p> <p>2. Conceptacle initial forming cell column by periclinal divisions, scale bar 50 μm.</p> | <p>3. Interior view of conceptacle with the neck canal cell detached, scale bar 25 μm.</p> <p>4. Interior view of conceptacle with the neck canal cell displaced and invaded by the coiled fungal hyphae, scale bar 100 μm.</p> <p>5. Surface opening of neck canal, bar 20 μm.</p> |
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PLATE 4

Spore tetrads found with *Schuguria ornata* Tchirkova-Zalesskaya, emend. from the Middle Devonian of Voronezh Region, LM.

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| <p>1, 5. Cruciate type tetrad with partitions between spore pairs at 90° to each other.</p> <p>2-4. Tetrads of apparently tetrahedral configuration, size variation.</p> <p>6. Spore magnified showing two sporoderm layers (arrow).</p> | <p>7. Spore from disintegrate tetrad.</p> <p>Scale bar 50 μm for Figs 1-6, 10 μm for Fig. 7.</p> |
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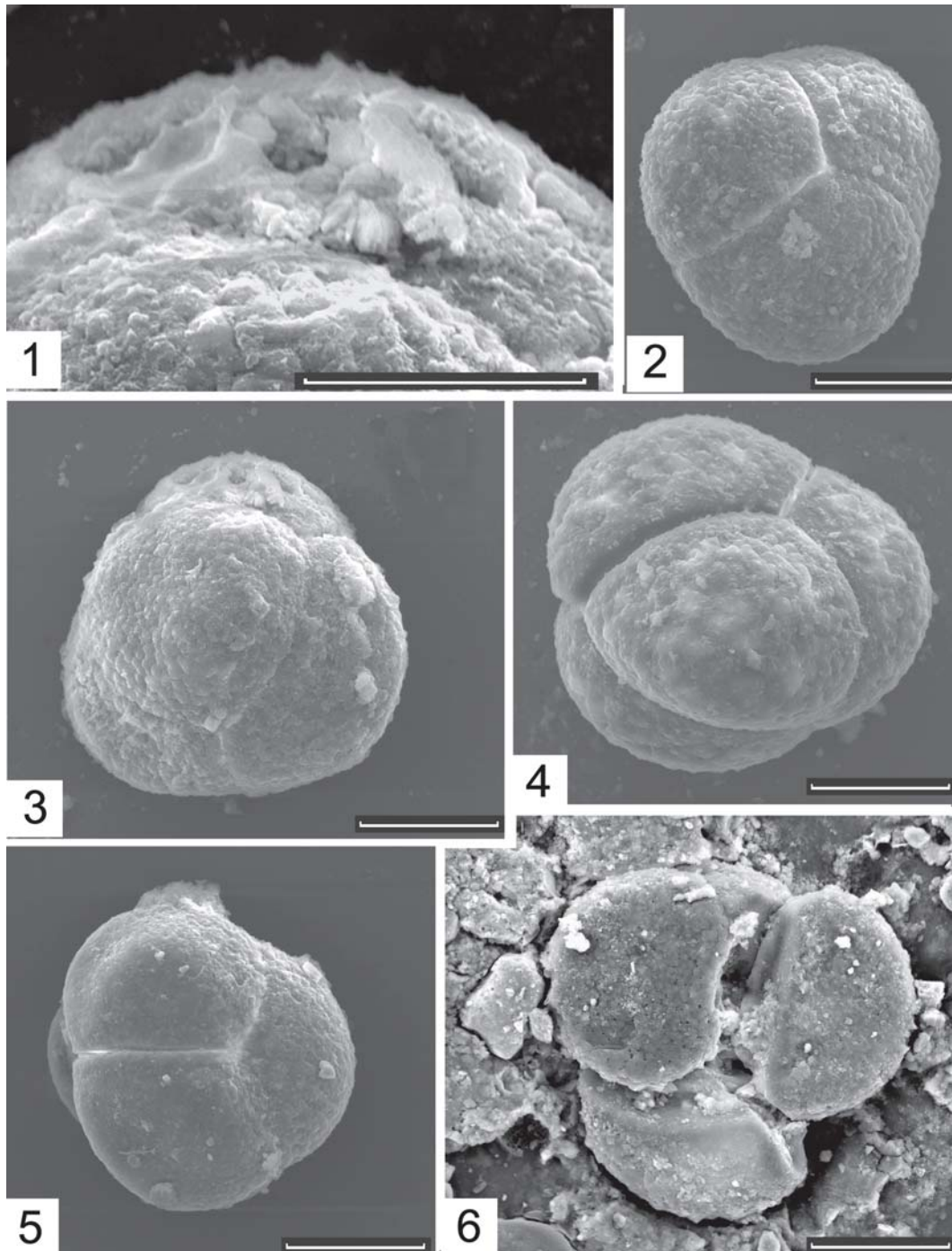


PLATE 5

Spore tetrads found with *Schuguria ornata* Tchirkova-Zalesskaya, emend. from the Middle Devonian of Voronezh Region, SEM.

1. Slender mycelium on tetrad shown in Fig. 2.
- 2, 3. Spore tetrads of tetrahedral configuration.
- 4, 5. Spore tetrads of cruciate configuration.

6. Spore tetrad attached to the thallus of *Schuguria ornata*.

Scale bars 20 μm for Fig. 1, 50 μm for Figs 2-6.

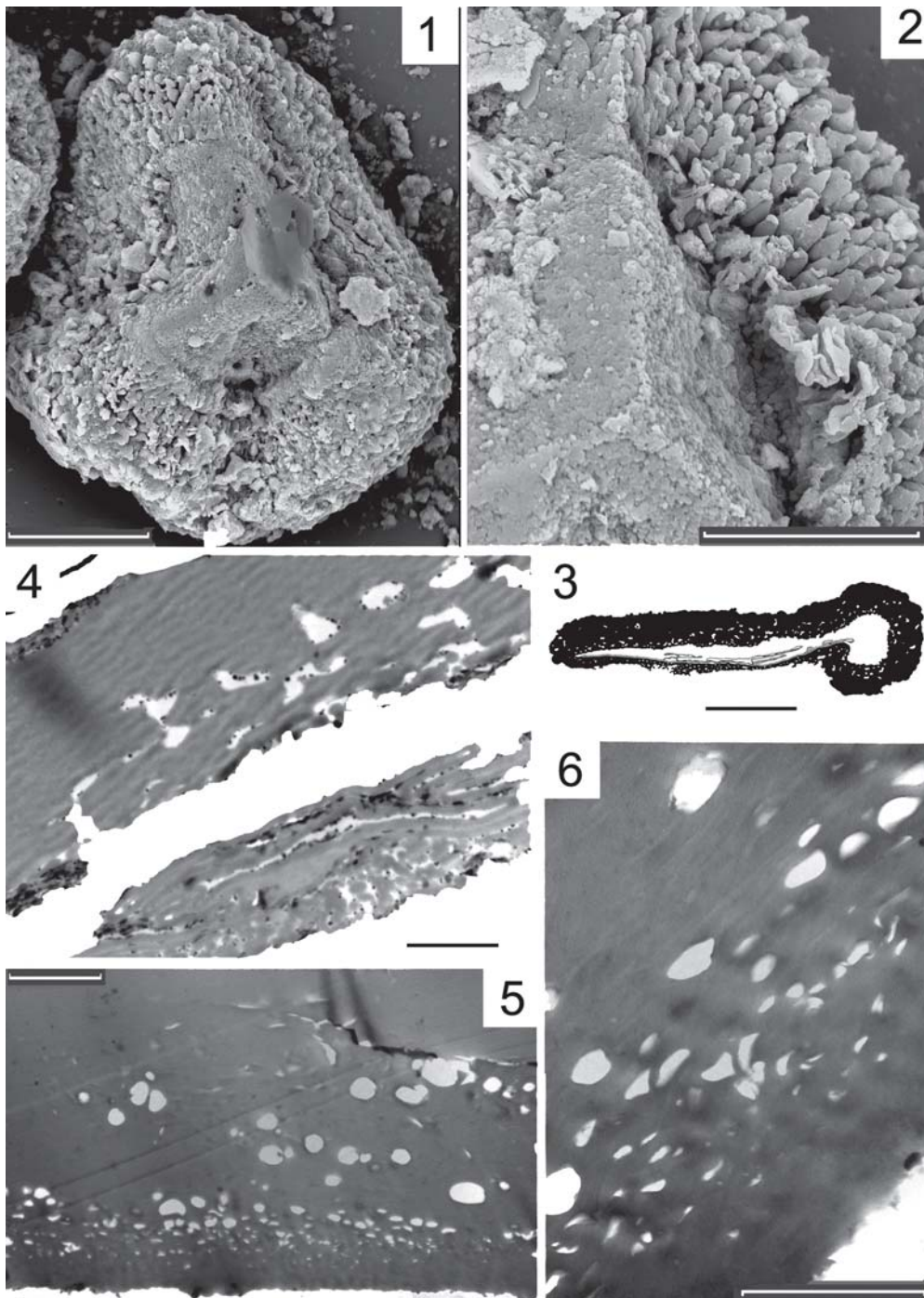


PLATE 6

Spores of tetrads found with *Schuguria ornata* Tchirkova-Zalesskaya, emend. from the Middle Devonian of Voronezh Region compared with cuticle of this plant.

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| <p>1. Spore, proximal face, SEM.
 2. Sculptural elements of proximal face, SEM.
 3. Schematic sporoderm section.</p> | <p>4. Sporoderm ultrastructure, TEM.
 5, 6. Cuticle ultrastructure, TEM.</p> |
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Scale bars 20 μm for Figs 1-3; 2 μm for Figs 4-6.

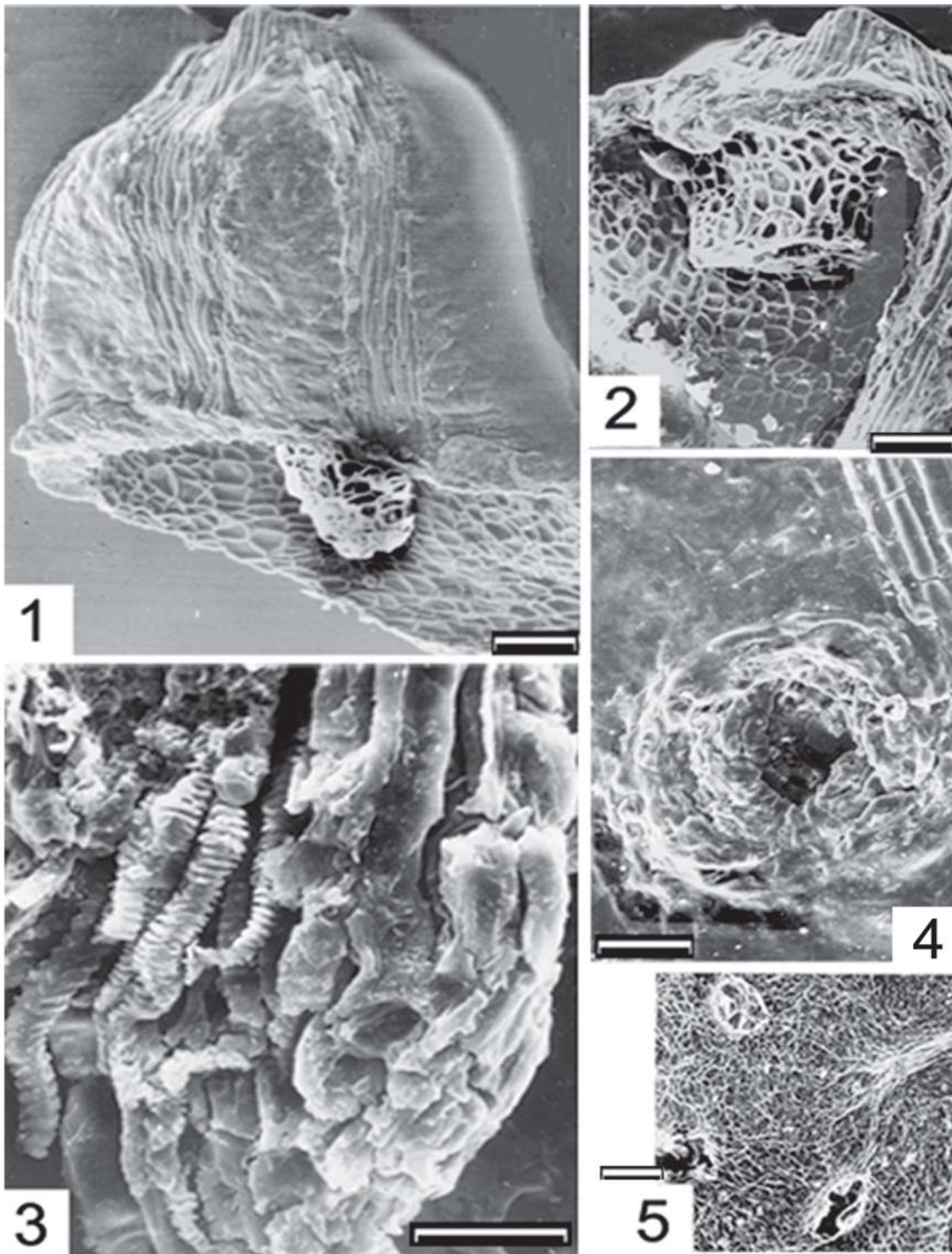


PLATE 7

Bitelaria dubjanskii T. Istchenko et A. Istchenko from the Middle Devonian of Voronezh Region, SEM (after Krassilov *et al.*, 1987a).

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| <p>1. Clavate structure (sporophyte) with involucre ruptured at the apex and the central column protruding from the base, scale bar 100 μm.</p> <p>2. Clavate structure split to show distal end of the central column, scale bar 100 μm.</p> | <p>3. Tracheid-like cells over the central column, x 2000, scale bar 10 μm.</p> <p>4. Crater-like structures, scale bar 100 μm.</p> <p>5. <i>Anthoceros</i> sp., extant, thallus with antheridial cavities, scale bar 100 μm.</p> |
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parenchymatous layer of broad polygonal cells traversed by the veins of elongate hydroid-like cells with thin pores and indistinct transverse thickenings (Pl. 7.1). Prominent structures of the outer cortex are the crater-like pits and clavate protuberances, the latter occurring singly on thicker veins of the outer cortex. Their inner cavity is lined with parenchymatous cells that also form a central column (Pl. 7.1, 2) that is enveloped by a layer of tracheid-like cells with distinct helical thickening (Pl. 7.3). The crater-like depressions were compared to reproductive structures of extant hornworts, in which antheridia develop in hypodermal cavities with a membranous cover that open crater-like at maturity (Schuster, 1984). The clavate structures are closely comparable with hornwort sporophytes in which tracheid-like cells occur in peripheral tissue of the central column (Proskauer, 1960).

Notwithstanding these bryophytic features in the relatively advanced member of the group, the typical Orestoviaceae and their associated spore tetrads lend no support to the recent theory of land plant origin from bryophytic ancestors, rather implying an isomorphic alternation of generations in primitive semiaquatic (amphibious) forms.

CONCLUSION

Our revision of *Schuguria*, a cutinized thalloid plant form the mid-Devonian of European Russia and comparison with *Orestovia* as interpreted in Krassilov (1981) led us to suggest that these two members of the Orestoviaceae might have been related as gametophytic and sporophytic generations of an amphibian form probably reintroducing incipient higher plant morphologies into the mid-Devonian helophytic plant communities. This suggestion is supported by the find of permanent tetrads in close association with the cutinized thalloids and comparable in sporoderm ultrastructure with the cuticle of the latter. Similar cruciate tetrads from pre-Devonian deposits are thought to be produced by bryophytic ancestors of land plants. However, if the Orestoviaceae were a "Lazarus" group of pre-Devonian plant world, then alternation of generations in incipient land plants might have been isomorphic rather than characterized by preponderance of haploid phase as in bryophytes. At the same time, a remote affinity to hornworts is suggested by *Bitelaria*, an advanced group of the mid-Devonian thalloids.

There are many possibilities that remain unexplored, including ecological differentiation of sexual and asexual generations represented by the alga-like *Schuguria* and the better adapted to terrestrial life *Orestovia* that seem to occur in different cuticular mat facies. The amazing uniformity of reproductive cycle in higher plants with haploid gametophytes and diploid sporophytes is a sharp contrast to the diversity of alternation modes in higher algae, implying an adaptive significance of the basic differentiation probably related to amphibian life style in incipient higher plants, with sexual and

asexual generations playing different roles in colonization of terrestrial habitats.

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