

Fungi on the Devonian thalloid plant *Schuguria* (Orestoviaceae)

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ABSTRACT

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Schuguria, an alga-like thalloid form from the Middle Devonian (Givetian) of the Pavlovsk Quarry, Voronezh Region, European Russia is heavily infested with spore-bearing and conidial structures that occur in the cortex cavities forming pseudothecia and acervuli. The fungal remains are assigned to new teleomorph and anamorph morphotaxa *Speirascoma schuguriae* gen. et sp. nov. and *Setacervula schuguriae* gen. et sp. nov., respectively. They supposedly represent an archaic group of ascomycete with a relatively massive helical structure (ascogonium?) in the centrum of the fruiting body. Symbiotic relationships of the *Ascophyllum-Mycosphaerella* type is suggested for the cutinized thalloids and their associated fungi.

Key-words—Fossil fungi, Early land plants, Symbiosis, Devonian.

डिवोनी थैलसाभ वनस्पति *सुगुरिया* (ओरेस्टोविएसी) पर कवक

वैलेंटिन क्रॉसीलॉव

सारांश

पाव्लोव्स्क क्वैरी, वोरॉनिज़ अंचल, यूरोपीय रुस के मध्य डिवोनी (जिवेटी) से प्राप्त *सुगुरिया* शैवाल-सदृश थैलसाभ प्ररुप बीजाणु-धारी एवं कोनिडियम संबंधी संरचना से बहुत ग्रस्त है जो स्यूडोथीसिया और एसरवुलि गठित करती हुई वल्कुट गुहिकाओं में मिलती है। कवक अवशेष क्रमशः नवीन पूर्णरुप एवं जटिलकायांतरी आकृतितैक्सो *स्पीरास्कोमा सुगुरिए* वंश प्रकाशन जाति नवम और सेटासर्वुला *सुगुरिए* वंश प्रकाशन जाति नवम को नियत हैं। वे कल्पित रूप से फलन काय की कशेरुकाय में सापेक्षतया विराट कुंडलिनी संरचना (ऐस्कोथानी ?) के साथ ऐस्कोसीकवक के एक पुरातन समूह को रूपायित करती हैं। *ऐस्कोफायल्लम-मायकोस्फ़ीरेल्ला* की सहजीवी संबंधता क्यूटिनमय थैलसाथ एवं उनकी सहयोगी कवक हेतु सुझावित है।

संकेत-शब्द—जीवाश्म कवक, प्रारंभिक स्थलीय वनस्पति, सहजीवन, डिवोनी ।

INTRODUCTION

MICROSCOPIC fungi constantly associate with cutinized thalloid plants forming cuticular mats and coals in the Devonian of Siberia, European Russia and Canada. They are assigned to higher plants of the family Orestoviaceae that vary in development of conducting tissues, some of the feebly vascularized, as *Schuguria*, probably representing the gametophytic form of an isomorphic reproductive cycle (Krassilov & Polevova, 2012). Fungal remains were recognized

on the typical *Orestovia* from Kuznetsk Basin (Krassilov, 1981), but they were poorly understood at the time. The Middle Devonian material from Pavlovsk, European Russia constantly exhibits fruiting bodies with spores and conidia assigned to new morphotaxa of Devonian fungi described below.

MATERIAL AND METHODS

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

exposing the Late Givetian sandstones and shales with plant impressions and cuticular mats of bilaterally compressed thalloid plants. *Schuguria*, is preserved as mineralized compressions of tubular thalli with a thick cortex speckled with hemispherical pustules interpreted as gametangial conceptacles (Istchenko & Istchenko, 1981; Krassilov & Polevova, 2012) and their crater-like scars, some emptied of their cellular content, appearing as perforations through the cortex. The pustules are commonly infested with fungi, their original structure being to a different extent distorted. Fungal remains also occur on spore tetrads found in association with cutinized thalloids (Krassilov & Polevova, 2012).

The maceration methods are described in Krassilov & Polevova (2012). The material was studied with the stereomicroscope Leica 300, dissecting light microscope Nikon Eclipse and scanning electron microscope FEI Quanta 200. 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).

SYSTEMATICS

Fungal remains constantly associate with the thalli appearing as an obligate component of a symbiotic system. Both teleomorph and anamorph stages are found. Here they are given different names as is the established practice in mycology.

Genus—*SPEIRASCOMA* Krassilov gen. nov.

Type species—*Speirascoma schuguriae* Krassilov sp. nov.

Etymology—Gr. *speira*, coil and *ascoma*, ascospore fruiting body.

Diagnosis—Ascoma pseudothecial in the corticle cavities (conceptacles) of cutinized thalloid plants, hyphae septate, centrum of helically coiled hyphae, asci borne in fascicles, conical, apically thickened, paraphyses lacking, ascospores rounded-elliptical aseptate striate, sporocarpia cleistocarpic or with irregular opening, bearing stout myceloid appendages.

Speirascoma schuguriae Krassilov, sp. nov.

(Pl. 1.1-3; Pl. 2.1-3; Pl. 3.1-3; Pl. 4.1; Pl. 6.1-2; Pl. 7.1-3)

Etymology—from genus *Schuguria* Tchirkova-Zalasskaya 1957.

Holotype—Pl. 1.3, SEM mount no. RPS-34S, Institute of Evolution, Haifa.

Locality—Pavlovsk Quarry, Voronezh Region, European Russia.

Horizon—Yastrebovsk Formation, Middle Devonian (Late Givetian).

Diagnosis—As for the genus.

Description—On *Schuguria*, a cutinized thalloid plant from the mid-Devonian of Pavlovsk Quarry, the fruiting bodies are developed in the cortical cavities interpreted as gametangial conceptacles (Istchenko & Istchenko, 1981; Krassilov & Polevova, 2012). The cavity is approached by a solitary hypha that penetrates the neck canal cell. The ascoma is central or somewhat eccentric (occasionally there are two twin ascomata per locule), rounded elliptical, about 150-250 μm wide, filling the locule, but shrunk off the walls and cleft at maturity, leaving a slightly raised cushion when detached. The outer wall is formed by tabloid cells of the conceptacles, that are partly destroyed revealing a compact hyphal structure (Pl. 3.1). The centrum is well defined, initiated by a coiled indistinctly septate hypha here interpreted as ascogonial. In the incipient ascomata the ascogonial hypha enters the neck canal cell and coils in the canal (Pl. 2.2) acquiring a flattened cylindrical form of 2-3 coils (Pl. 1.1). The ascogenous hyphae depart from the central helix, conferring a whirling structure to the whole ascoma.

Thick ascogenous hyphae arise as short protuberances of the central helix (Pl. 2.3; Pl. 6.1), penetrating the locule as irregularly twisted tentacles (Pl. 6.2) and coiling over the periphery. Their propagation is intercellular, extending over anticlinal walls of the locule that shows hyperplasia of cells divisions by a series of thin transverse walls. Asci occur in dense fascicles on the upturned branches of ascogenous hyphae (Pl. 1.3; Pl. 7.1, 3). They are conical, with a prominently thickened apical cap that is occasionally detached, but scarcely forming a regular operculum. Ascospores are seen as spherical or elliptic bodies transpiring through the walls. No evidence of paraphyses or pseudoparaphyses is obtained.

The sporocarps developed from the pseudothecial ascomata either show an irregular hole in the centre or are cleistocarpic, covered with a patchily preserved peridium exposing a coarse reticulate network when peeled off (Pl. 4.1). The cleistocarps bear long irregularly branched appendages that appear as thick mycelial hyphae (Pl. 4.1). A few appendages taper, but the rest are digitate on ends. Shed appendages leave stumps that are supported with 3-4 radial cells of the surface network.

The non-released spores occasionally preserved in the pits of the surface network are globose, about 10 μm in diameter, slightly depressed at the poles, striate parallel to the equator (Pl. 3.2, 3).

Comparison and interpretation—The fruiting bodies are here described as pseudothecial because they develop in preformed cavities and involve the surrounding tissue in the wall formation. However, the sporocarps are essentially cleistocarpic, occasionally with irregular opening. The asci are thick-walled and probably bitunicate, but this feature, as well as the thickened apices, remain obscure.

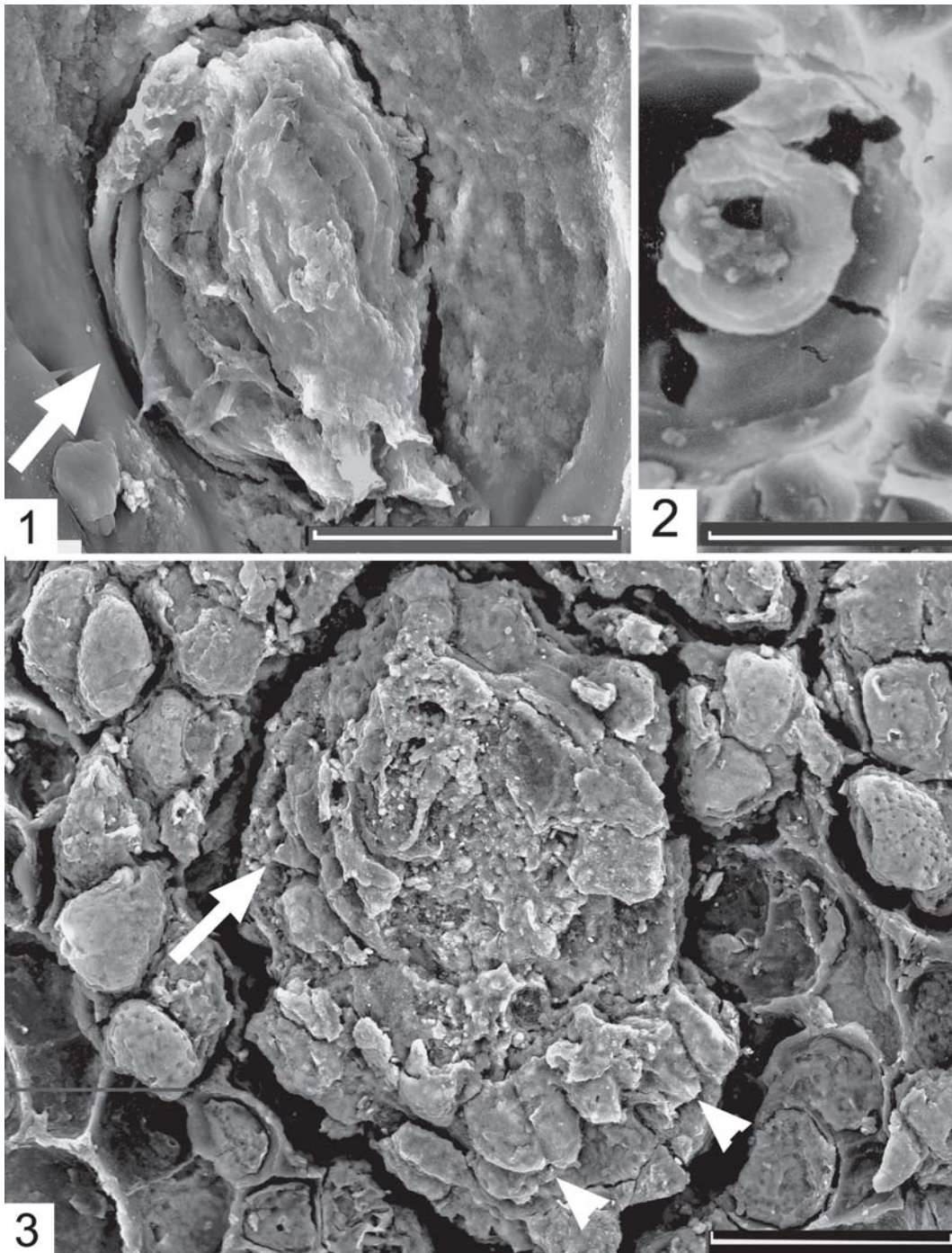


PLATE 1

Speirascoma schuguriae gen. et sp. nov. on *Schuguria ornata* Tchirkova-Zaleskaya from the Devonian of Voronezh Region, SEM, scale bars 100 μ m.

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| <p>1. Loosely coiled ascogonial hypha (arrow), no. RPS-32S.</p> <p>2. Penetration of ascogonial hyphae in the neck canal cell, no. RPS-3S.</p> | <p>3. Ascoma showing a loosely coiled ascogonial hyphae (arrow) and asci (arrowheads), RPS-34S, holotype.</p> |
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The Palaeozoic fungi with spiny sporocarps endowed with dense partly forked appendages like in *Dubiocarpon* (Stubblefield *et al.*, 1983; Stubblefield & Taylor, 1988) are presently assigned to zygomycetes, although having no close analogues among the extant representatives of the phylum. In contrast, *Speirascoma* is comparable to a number of fossil and extant ascomycetes.

In the Devonian ascomycete *Palaeopyrenomycites devonicus* Taylor *et al.*, 2005, the globose perithecia develop in substromatal chambers or under spines on aerial stems and rhizomes of *Asteroxylon*. They are similar to *Speirascoma* in shape and dimensions, but are ostiolate and lack appendages. They also lack a definite centrum in early development starting with proliferation of somatic hyphae. The asci are borne in hymenium with paraphyses, yet are similar in having apical thickenings.

The most intriguing feature of *Speirascoma* is the conspicuous coiled structure in the centre of ascoma. It is here interpreted as ascogonium of the type known in the present day ascomycetes, such as *Spherotheca*, *Sordaria*, *Myxotrichum*, *Mycosphaerella*, etc. (reviewed in Luttrell, 1951; Moore-Landecker, 1996). In *Mycosphaerella* (Dothideales), the ascogonium is coiled in the central part of the globose pseudothecium, giving off the copiously branched ascogenous hyphae. Like in *Speirascoma*, asci are produced in fascicles lacking paraphyses or pseudoparaphyses. However, in *Mycosphaerella* the ascogonium enters a preformed pseudothecial tissue, while fertilization is mediated by a long trichogyna emerging from the ostiole.

Coiling of ascogonium around antheridium is a characteristic feature of fertilization in the Eurothiales (*Myxotrichum*, *Neosarthorya*, *Petalosporus*), in which cleistothecium is formed by somatic hyphae swarming around the ascogonial coil (Benjamin, 1955; Wong & Chien, 1986). Similar configuration of initial cells is illustrated in *Petalosorus* having rudimentary peridium (Ghosh *et al.*, 1963). Though separated by the formal distinctions between pseudothecial and cleistothecial fruiting bodies, the Devonian ascomycetes and extant representatives of the order have similar globose sporocarps with continuous or net-like cover and with long appendages.

In *Micosphaera* (Erysiphales), the ascoma is initiated by the jointly coiled ascogonium and antheridium. Their subtending somatic hyphae produce small spherical cleistothecium endowed with dichotomously branched terminally digitate appendages (Braun, 1987).

Genus—*SETACERVULA* Krassilov, gen. nov.

Type species—*Setacervula schuguriae* Krassilov sp. nov.

Etymology—L. *seta*, bristle and *acervare*, to heap.

Diagnosis—Conidioma of amassed interwoven conidiophores, blister-like at maturity, setose. Setae of two types, long recoiled and short spinulate. Conidiophores septate terminated with elongate conidiogenous cells marked by parallel scars (annelidic). Conidia produced in chains or clusters, ovoid, minutely warted.

Setacervula schuguriae Krassilov, sp. nov.

(Pl. 4.2; Pl. 5.1-3; Pl. 8.1-3)

Etymology—from *Schuguria* Tchirkova-Zalesskaya 1957.

Holotype—Pl. 5.1, SEM mount no. RPS-45S, Institute of Evolution, Haifa.

Locality—Pavlovsk Quarry, Voronezh Region, European Russia.

Horizon—Yastrebovsk Formation, Middle Devonian (Late Givetian).

Diagnosis—As for the genus.

Description—As in *Speirascoma schuguriae* (above), these fungal remains occur on *Schuguria*, a cutinized thalloid plant from the mid-Devonian of Pavlovsk Quarry. The fruiting bodies are developed in the cortical cavities interpreted as gametangial conceptacles (Istchenko & Istchenko, 1981; Krassilov & Polevova, 2012). A single or a few relatively thick septate hyphae enter the cavities (Pl. 8.3), subtending the central body of interwoven conidiophores and spreading setae that are occasionally preserved, but mostly broken leaving prominent stumps (Pl. 4.2). The conidiomas are rounded-ovate, about 250 x 200 - 400 x 300 µm, detachable as dense conidiocarps, but sometimes disintegrated *in situ*. The conidiocarps show a reticulate pattern of basal hyphae, their upright ends protruding as setae. The larger setae in the central part are about 100 µm long without broken tips, 20-25 µm thick at the base, indistinctly septate, leaving polygonal detachment scars. A shorter seta of the central group is 70 µm long, recoiled, slightly flattened and minutely serrate at the tip. Slender spine-like setae more regularly occur along the margin (Pl. 4.2)

Under dissecting light microscope, the conidiomas appear opaque with elongate ampuliform protuberances over the margin representing conidiogenous cells that are occasionally preserved with clusters of small ovoid conidia (Pl. 8.1, 2). A series of transverse scars (annellations) are discernible suggesting an annellidic conidiogenous cell (that keeps growing after production of consecutive conidia). Under SEM, the conidiophores are seen as tightly interlaced, septate hyphae with elongate terminal conidiogenous cells showing a series of oblique scars (at arrowhead in Pl. 5.2) that confirm LM evidence of annellidic conidiogenesis. The conidia are ovoid, minutely warted (arrow in Pl. 5.2). Chains of similar conidia are occasionally preserved on ascostromata of

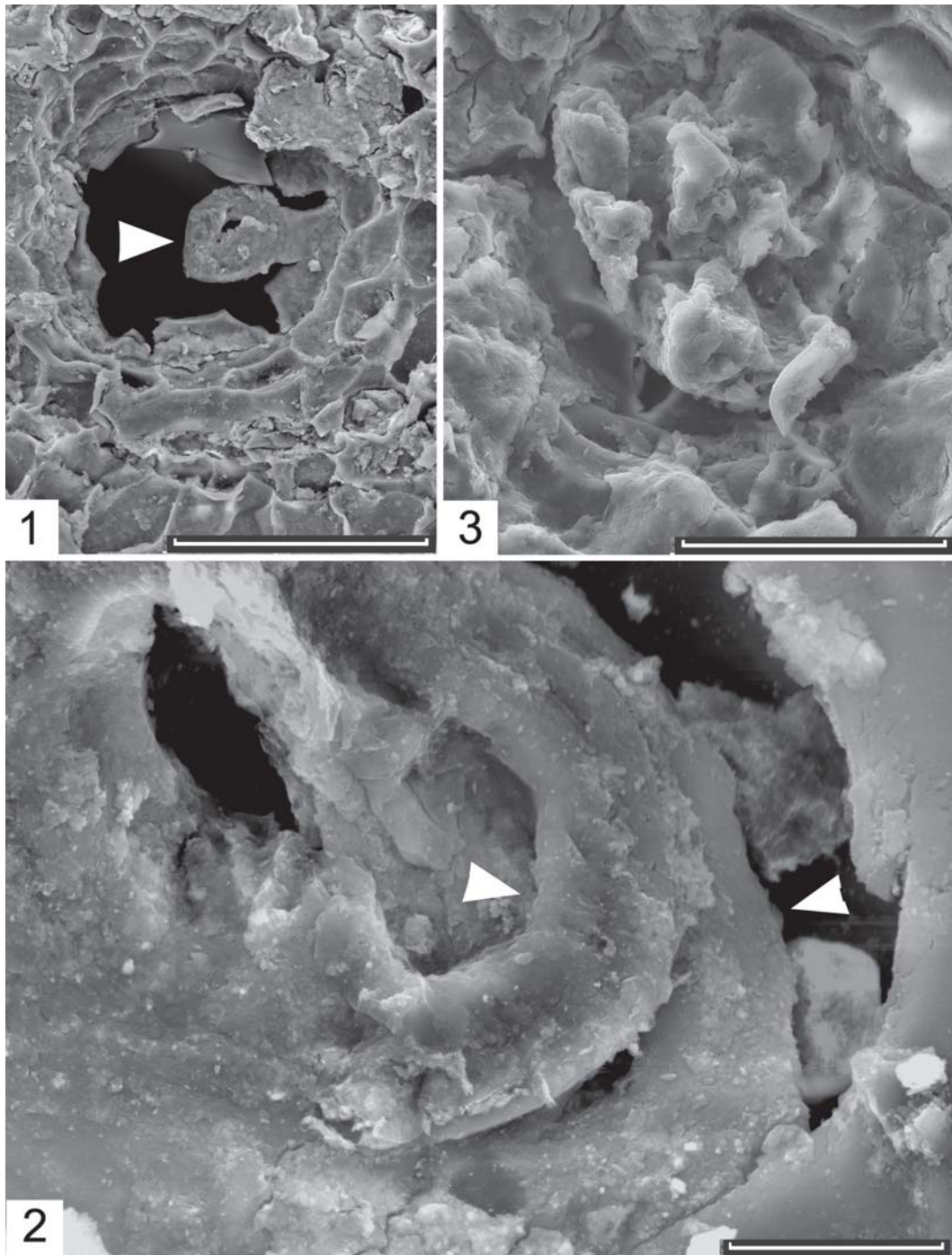


PLATE 2

Speirascoma schuguriae gen. et sp. nov. on *Schuguria ornata* Tchirkova-Zaleskaya from the Devonian of Voronezh Region, SEM,

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| <p>1. Conceptacle neck with hypha coiled around the neck canal cell, no. RPS-112S, scale bars 200 μm.</p> <p>2. Coiled ascogonial hypha (arrowheads on the coils) penetrating</p> | <p>the neck canal cell, and note septation of the hypha, no. RPS-115S, scale bars 20 μm.</p> <p>3. Ascogenous hyphae entering the locule, no. RPS-113S, scale bar 100 μm.</p> |
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Speirascoma schuguriae accompanied by the boat-shaped corrugate bodies that can be ripe conidia of the same species.

Comparison and interpretation—The conidiomata co-occur with *Speirascoma schuguriae* perhaps representing anamorph of the same ascomycete. At low magnifications, ripe conidiomata are recognizable as relatively massive black coaly bodies. They do not form a thick-walled stromata and appear opaque under LM, but show a small-celled surface network under SEM.

Anamorphs of fossil fungi are rarely recognized and insufficiently studied. In *Palaeopyrenomycites devonicus* Taylor *et al.* 2005, the acervuli (assigned to the same species as the teleomorph) are tufts of septate conidiophores developing in small depressions on stems of *Asteroxylon*. The conidiogenesis is thought to be thallic with arthroconidia developing from segments of disarticulated conidiophores, although phialidic type is also a possibility. No setae are mentioned.

Under formal classification, the conidial structures on *Schuguria* are comparable with acervuli of Coelomycetes or sporodochii of Hyphomycetes, the latter formed of interwoven conidiophores, yet not developing compact fruiting bodies. Among the anamorphs of modern Ascomycota, *Colletotrichum* (Glomerellaceae, Sordariomycetes) has small setose acervuli of branched septate conidiophores. The ampuliform conidiogenous cells are cylindrical showing periclinal thickenings. The conidia are crescent-shaped, smooth or verruculose (Damm *et al.*, 2009).

DISCUSSION

The ascomata *Speirascoma* and conidiomata *Setacervula* although most probably belonging to one and the same biological species of ascomycetes, represent different levels of evolutionary development. Sparing a few features that need clarification, the conidiomata appear quite modern and classifiable under the existing formal system. On the other hand, the ascomata, although showing similarities with respective structures of present day ascomycetes, seem peculiar in the early representatives of the group. My interpretation of the helical centrum as derived from a coiled initial hypha implies a more robust and persistent ascogonium than in modern ascomycetes, probably betraying an archaic developmental feature.

In fungi infesting algal conceptacles, such as *Mycosphaerella*, the ascogenous and conidiogenous generations may alternate at the same site, which might have been the case in *Setacervula schuguriae* as well, although occasional conidia on sporocarps indicate that anamorph and teleomorph stages overlapped in time. The mycelial hyphae on tetrads found with *Schuguria ornata* (Krassilov & Polevova, 2012) suggest that fungus propagated with spore dispersal.

The relationships between the fungi and cutinized thalloid forms remain problematic. The cutinized thalloid Orestoviaceae are the alga-like semiaquatic plants probably representing an incipient land plant morphology persisting in wetland habitats until the mid-Devonian when such habitats became widespread. This suggestion is supported by their associated spore tetrads that are comparable to pre-Devonian tetrads of cryptic progenitorial land plants. 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.

On *Schuguria*, the fungal remains are found in the cortical cavities interpreted as gametangial conceptacles, while in *Orestovia* they seem to infest stomatal pits, but are insufficiently studied for a detailed comparison. In the Devonian ascomycete *Palaeopyrenomycites devonicus* (Taylor *et al.*, 2005), perithecia occur in substomatal chambers of a sporophytic plant. Homology between stomata and gametangial initials is a possibility worth considering.

The constant association of cutinized thalloids with fungi implies symbiotic relationships widespread at the early land colonization stage. In particular, a green alga - chitrid symbiosis is described from the Lower Devonian Rhynie peat assemblage (Taylor *et al.*, 1992).

The constant occurrence of fungal remains in the cortical cavities of *Schuguria* implies symbiotic relationships of the type represented by the obligate associations of brown algae *Ascophyllum nodosum* and *Pelvetia canaliculata* with ascomycetes *Mycosphaerella ascophylli* and *M. pelvetiae*, respectively (Church, 1893; Cotton, 1908; David, 1943; Weber, 1967). *Ascophyllum* fails to reproduce unless infected with *Mycosphaerella* (Weber, 1967). Such symbiotic systems are like lichens, but with structural relationships between algal and fungal components reversed, resulting in “antilichen” of a kind.

CONCLUSION

This study of fungal remains occurring in the cortex cavities of cutinized thalloid plants (the Orestoviaceae) revealed some microscopic features for which no modern analogues were found associated with the features that appear quite modern. The fungi represented by both teleomorph and anamorph stages are scarcely assignable to any order of modern Ascomycota, although comparable to extant representatives of Erysiphales and Eurothiales, from which they differ in the morphology of initial cells and organization of ascoma, conceivably archaic.

Taxonomic affinities of thalloid compressions forming cuticular mats in the mid-Devonian wetland deposits remain poorly understood. There are many unexplored possibilities,

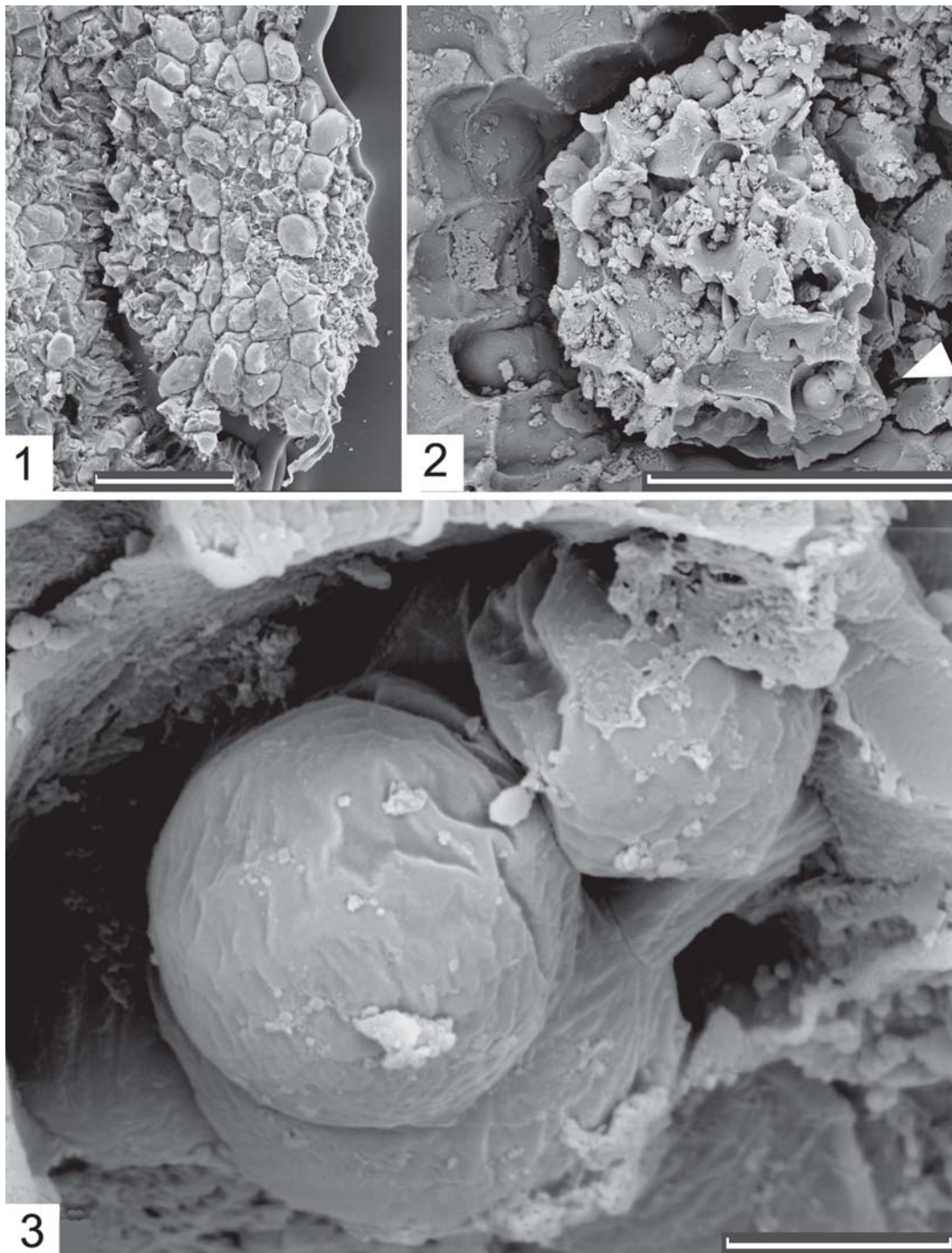


PLATE 3

Speirascoma schuguriae gen. et sp. nov. on *Schuguria ornata* Tchirkova-Zalesskaya from the Devonian of Voronezh Region, SEM.

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| 1. | Pseudothecium with remnants of conceptacle wall over the peridium, no. RPS-114S, scale bar 200 μ m. | 3. | Ascospores magnified, scale bar 10 μ m. |
| 2. | Ascocarp with ascospores preserved in the pit of the surface | | reticulum (arrow), no. RPS-45S, scale bar 50 μ m. |

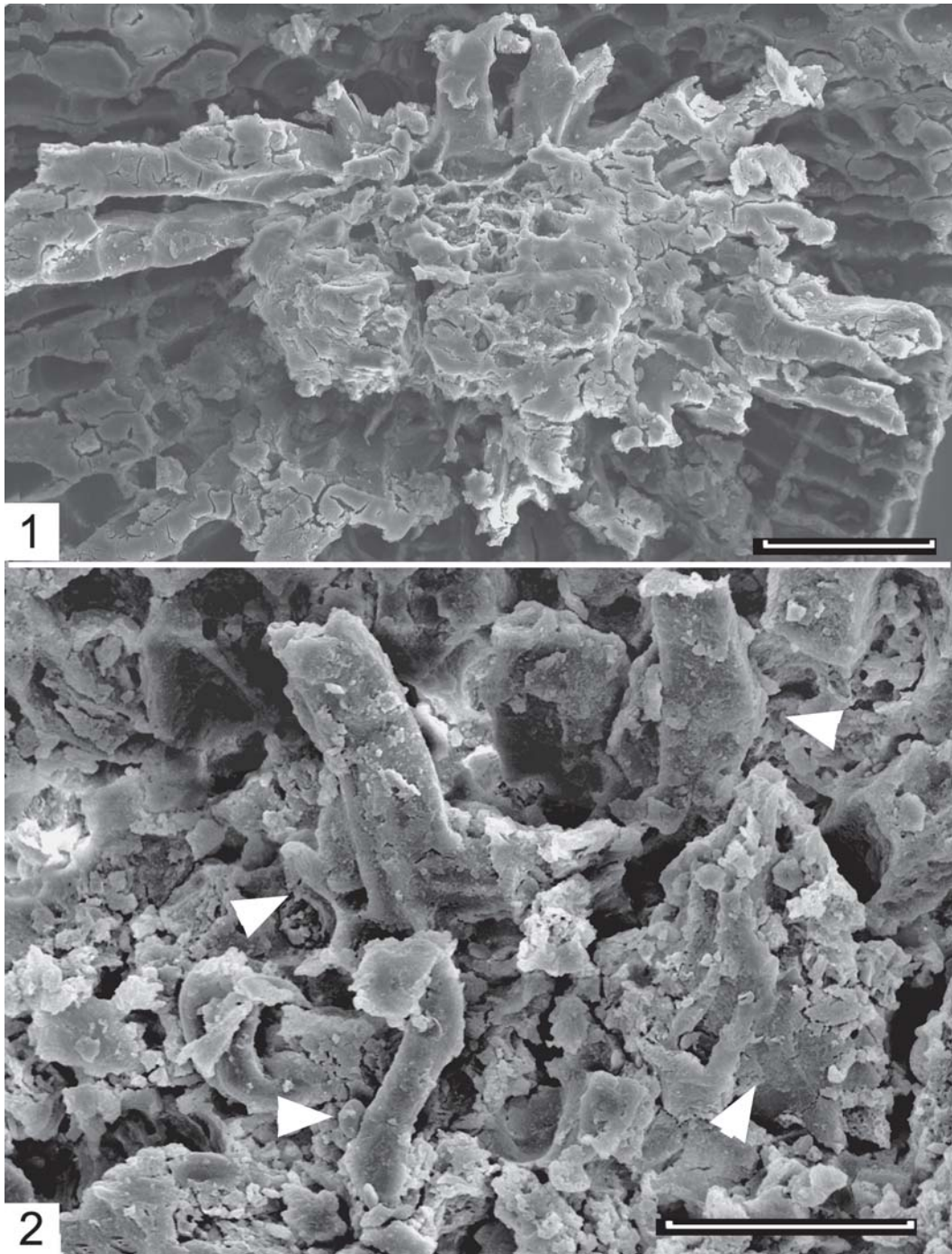


PLATE 4

Speirascoma schuguriae gen. et sp. nov. (1) and *Setacervula schuguriae* gen. et sp. nov. (2) on *Schuguria ornata* Tchirkova-Zalesskaya from the Devonian of Voronezh Region, SEM, scale bars 100 μ m.

1. Cleistothecium with myceloid appendages, showing coarse surface network between smooth patches of peridium, no. RPS 40S.
2. Conidioma with stumps of two thick setae and a shorter recurved seta in front view, arrowheads on setae and their stumps, no. RPS-46 S.

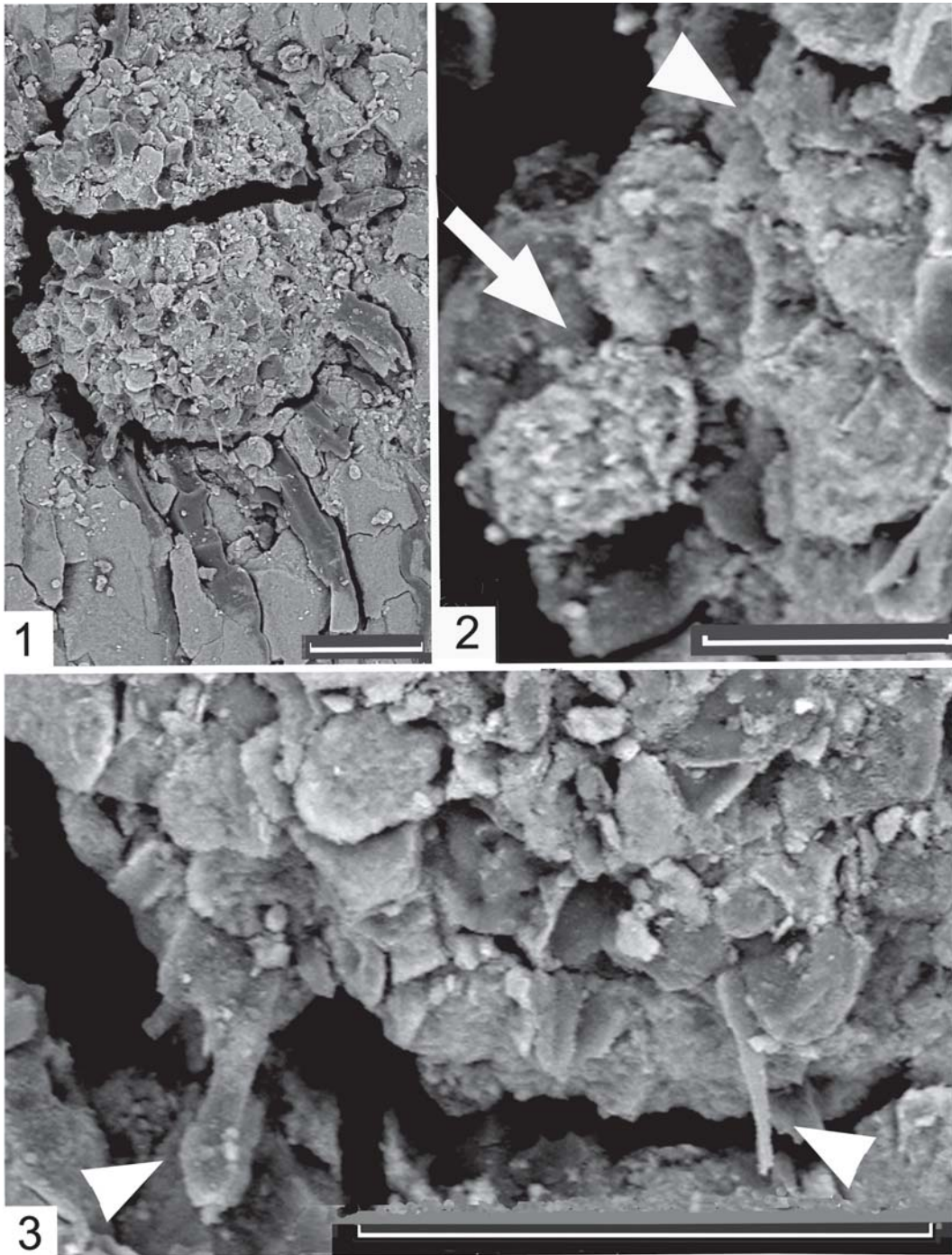


PLATE 5

Setacervula schuguriae gen. et sp. nov. on *Schuguria ornata* Tchirkova-Zaleskaya from the Devonian of Voronezh Region, SEM.

1. Conidioma at the plexus of thick haustorial hyphae, no. RPS-45S, holotype, scale bar 100 μ m.
2. Part of conidioma magnified to show the obliquely striate conidiogenous cells (arrowhead) and conidia (arrow), scale bar 20 μ m.
3. Part of conidioma magnified to show slender setae, scale bar 100 μ m.

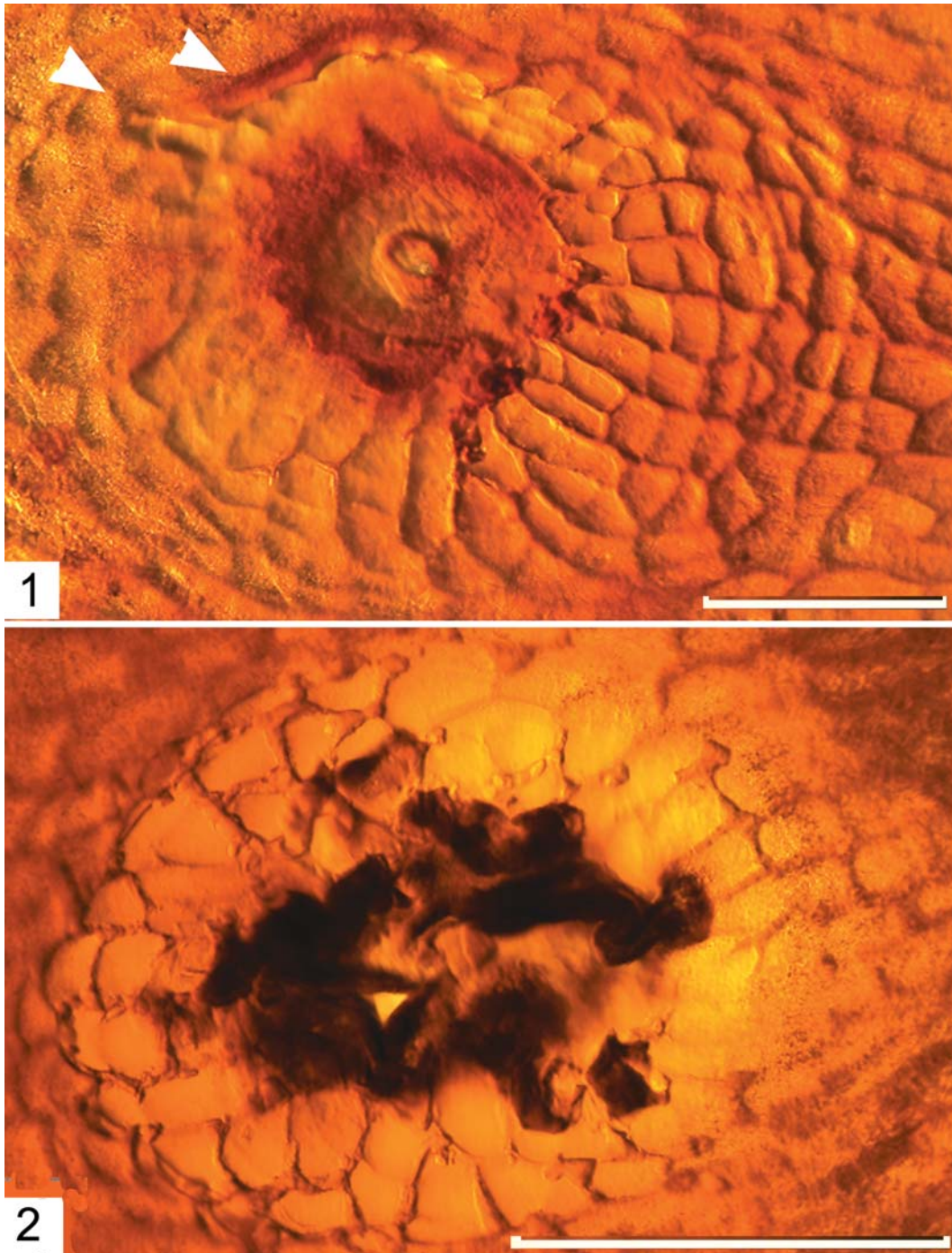


PLATE 6

Speirascoma schuguriae gen. et sp. nov. on *Schuguria ornata* Tchirkova-Zalesskaya from the Devonian of Voronezh Region, LM.

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| 1. | Incipient ascoma in the centre of conceptacle, with ascogenous hyphae seen as short protuberances radiating from the centrum, arrow on hyphae approaching the conceptacle, no. RPS- | 16L, scale bar 100 μ m. |
| 2. | Branching ascogenous hyphae spreading over the locule, no. RPS-81L, scale bar 200 μ m. | |

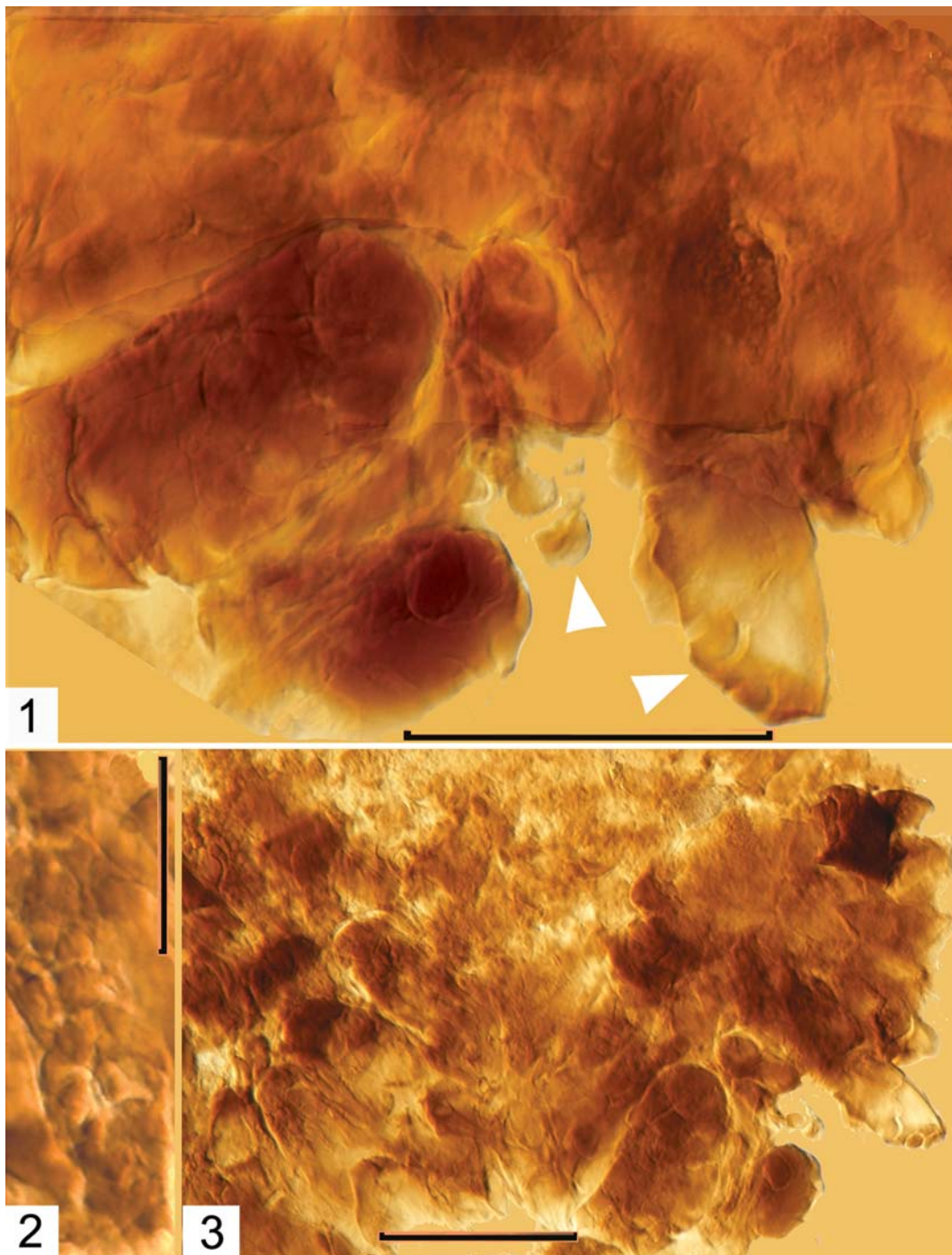


PLATE 7

Speirascoma schuguriae gen. et sp. nov. on *Schuguria ornata* Tchirkova-Zalesskaya from the Devonian of Voronezh Region, LM, scale bar 50 μ m.

- 1, 3. Clusters of asci, arrowheads on ascospores, no. RPS-43L. 2. Asci showing filled ascospores, no. RPS-44L.

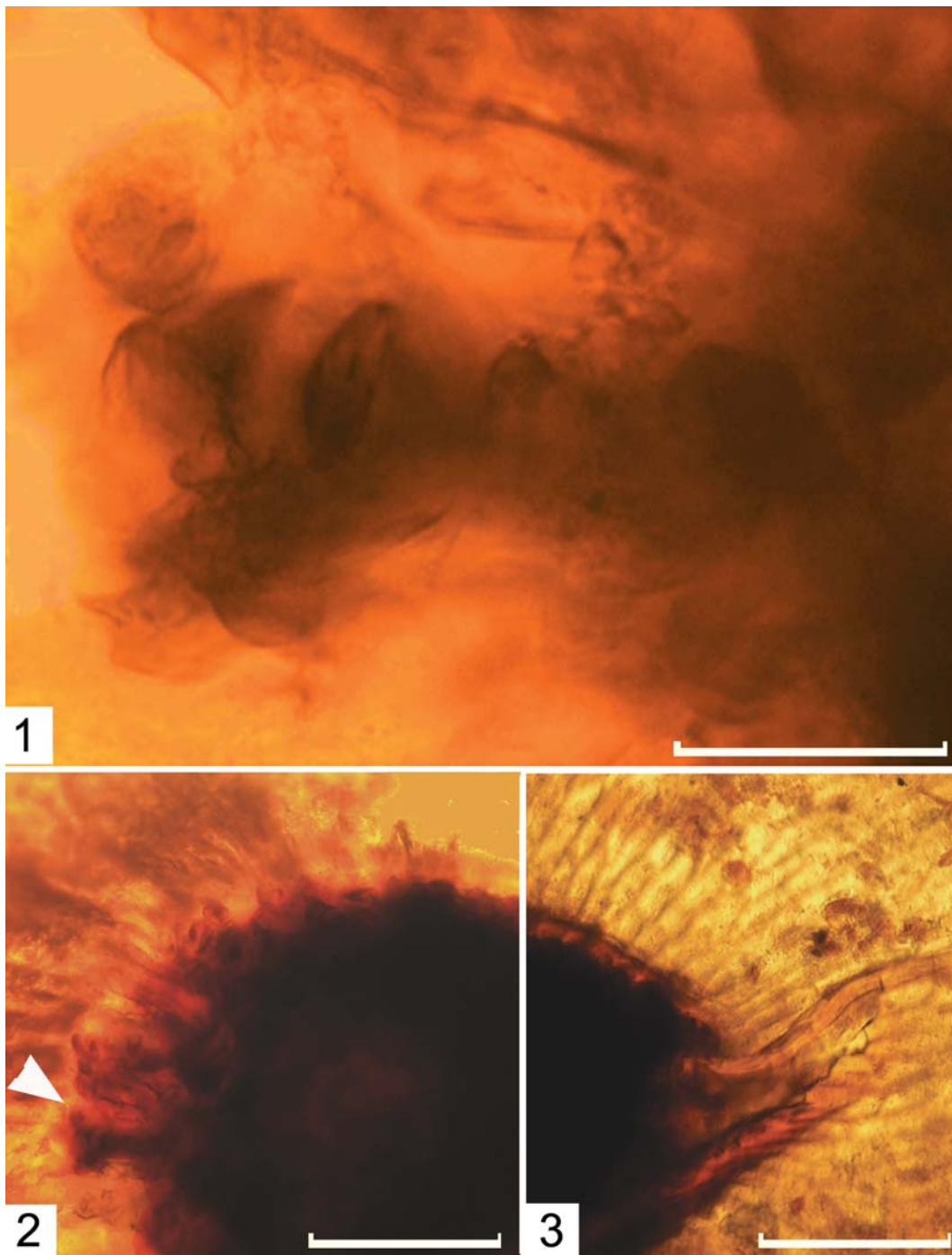


PLATE 8

Setacervula schuguriae gen. et sp. nov. on *Schuguria ornata* Tchirkova-Zalesskaya from the Devonian of Voronezh Region, LM.

1. Conidiogenous cell with conidia released, showing oblique constrictions (annellations), no. RPS-25L, scale bar 50 μ m.
2. Opaque conidioma with conidiophores protruding over the margin (arrow on conidiogenous cell shown in Fig. 1), no. RPS-25L, scale bar 100 μ m.
3. The same conidioma, opposite end with initiating hyphae preserved, scale bar 100 μ m.

including ecological differentiation of sexual and asexual stages represented by the alga-like *Schuguria* and the better adapted to terrestrial life *Orestovia*. Their associated fungi might have been different, but so far inadequately studied for comparison.

It is suggested that Orestoviaceae and accompanied spore tetrads represent conservative forms retaining incipient land plant morphology. If so, then their association with fungi may be an evidence in favour of symbiotic land plant origin. Constant occurrence of fungal fruiting bodies on cutinized thalloid forms finds their modern analogy in symbiotic relationships between brown algae and pseudothecial ascomycetes of the family Mycosphaerellaceae.

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