

A New Microsporangiate Organ from the Lower Carboniferous of the Novgorod Region, Russia

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Abstract—A new species of the genus *Telangiopsis*, *T. nonnae* O. Orlova et Zavialova, was described on the basis of a microsporangiate organ from the Lower Carboniferous deposits of the Novgorod Region. The morphology of branching fertile axes, synangia, and sporangia was thoroughly studied. The three-dimensional system of fertile axes branches monopodially; ultimate axes bear numerous connivent bunches of synangia, which consist of three to six basally fused elongated ovate sporangia. The morphology and ultrastructure of prepollen grains were studied, which were extracted from the rock matrix surrounding the sporangia. The two-layered exine includes a well-developed endexine and an alveolate ectexine, with one–three rows of large thin-walled alveolae. The new species was compared with other Early Carboniferous microsporangiate organs.

Key words: Early Carboniferous, Novgorod Region, fertile axis, synangia, Lyginopteridales, trilete prepollen, exine ultrastructure.

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INTRODUCTION

During the three last decades, the interest of botanists dealing with fossil and modern plants to Carboniferous synangiate pollen organs has considerably increased: earlier studied materials were revised (Millay and Taylor, 1979; Meyer-Berthaud, 1989), and new taxa were described (Eggert and Taylor, 1971; Stidd et al., 1985; Meyer-Berthaud, 1986; Rowe, 1988; and others). To date, more than 20 genera of microsporangiate organs have been described from the Carboniferous deposits of Europe, Great Britain, and North and South Americas (Erwin et al., 1994). They belong to four orders of Lyginopteridophyta: Calamopytiales, Lyginopteridales, Callistophyllales, and Medullosales. Early Carboniferous deposits only contain members of the first and second orders. The majority of them were found in Scottish and English localities, and the rest was reported from the United States, Germany, and Russia (Orlova, 2002, 2007). The first Russian find of a synangiate organ was preliminary discussed by Orlova (2002); the present paper publishes a detailed study of this fossil.

MATERIAL AND METHODS

The material was collected from the Porog Vittsa 2 locality, situated at the right bank of the Msta River, near the village of Putlino, Borovich district of the Novgorod Region. An imprint of a fertile axis bearing

synangia and numerous casts and imprints of detached synangia were found in yellow ferruginous sandstone. In addition to the fertile axes, sterile remains of Lyginopteridales, Medullosales, and Calamopytiales were found (Orlova and Snigirevskii, 2003, 2004). Fragmentary fronds of *Rhodeopteridium* and *Sphenopteridium* are particularly numerous. The total list of the plant remains found in this locality includes *Archaeosigillaria vanuxemii* (Goepp.) Kidston, *Lepidodendron acuminatum* (Goepp.) Stur, *L. veltheimii* Sternb., *Lepidostrobus* sp. 1, *Lepidostrobus ornatus* Brongn., *Flemingites* sp. 1, *Stigmara* sp., *Archaeocalamites radiatus* (Brongn.) Stur, *Sphenopteridium bifidum* (L. et H.) Benson, *Sphenopteridium* sp. 1, *S. pachyrrhachis* (Goepp.) Pot., *S. jurinae* O. Orl. et S. Snig., *S. gaebleri* Gothan, *Adiantites antiquus* (Ett.) Stur, *A. machanekii* Stur, *Adiantites* sp. 1, *Sphenopteris distans* Sternb., *Sphenopteris* sp. 1, *S. foliolata* Stur., *Rhodeopteridium hochstetteri* (Stur) Purk., *R. goeppertii* (Ett.) O. Orl. et S. Snig., *R. tenue* (Gothan) Kotas., *Lyginodendron* sp., and *Rhynchogonium sulcatum* (L. et H.) Zal. (Orlova and Rasskazova, 2005).

The deposits of the Porog Vittsa 2 locality are characterized by a palynological assemblage with constantly occurring numerous *Lycospora pusilla* (Ibr.) Som. *Lophotriletes grossepunctatus* (Waltz) Isch., *Triquitrites marginatus* H., St. et M., *T. comptus* Will., *Trachytriletes subintortus* Isch., *Schulzospora campyloptera* (Waltz) H., St. et M., *S. magnifica* (Isch.)

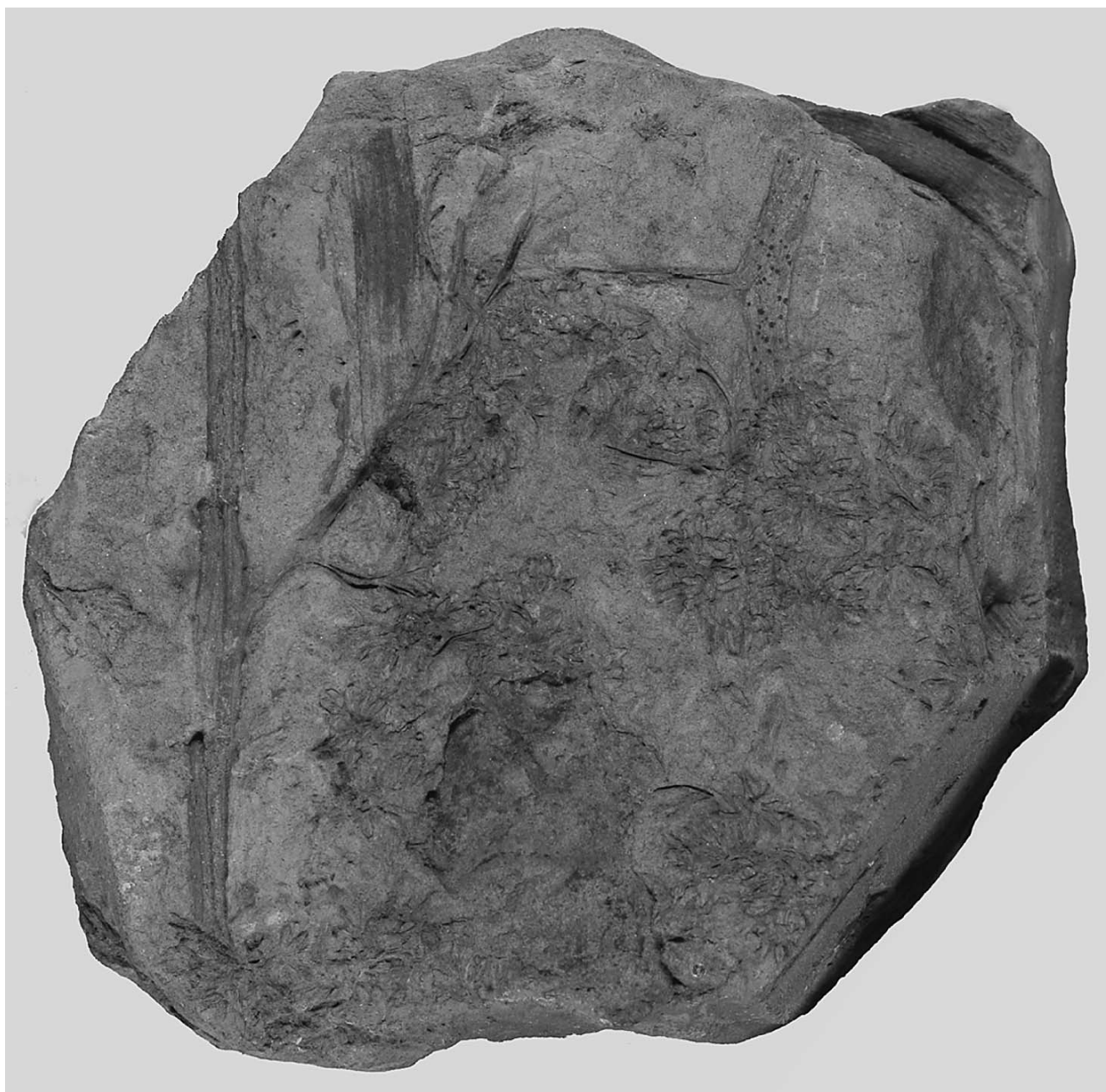


Fig. 1. *Telangiopsis nonnae* sp. nov., holotype MGU, no. 293/47; general view of microsporangiate organ, branching fertile axes and clusters of synangia are shown, $\times 3.5$. Porog Vittsa 2 locality, Borovichi district, Novgorod Region, Russia; Lower Carboniferous, Visean Stage, Upper Visean Substage.

Oshurk., *Tripartites vetustus* Schem., *Punctatisporites glaber* (Naum.) Playf., and some other spores occurring much more rarely (Orlova and Rasskazova, 2005). The palynological assemblage fits the palynological zones *Perotritetes tessellatus*–*Schulzospora campyloptera* (TC), *Raistrickia nigra*–*Triquitrites marginatus* (NM), *Tripartites vetustus*–*Rotaspora fracta* (VF), and *Belisporites nitidus*–*Reticulatisporites carnosus* (NC) of the Upper Visean=Namurian A (Serpukhovian) of West Europe.

Collection, no. 293 is kept at the Department of Paleontology, MGU. Olympus SZ-6045 and Leica MZ16 stereomicroscopes were used during the study and photographing. A rock fragment with detached synangia was macerated after Grishchuk (fluoric acid followed by centrifugation). The organic residue with prepollen grains was mounted on slides and studied in transmitted light, under a Zeiss Axioplan 2 microscope; some prepollen grains were studied under Camscan and Hitachi S-405A scanning electron microscopes



Fig. 2. Reconstruction of pollen organ of *Telangiopsis nonnae* sp. nov. Scale bar 2 mm.

(SEMs). Ultrathin sections were made using an LKB 3 ultramicrotome with a diamond knife and studied under a Hitachi H-600 transmission electron microscope (TEM). In total, 21 prepollen grains were studied in transmitted light; 18, under SEM; and 5, under TEM. Grids with ultrathin sections and films and graphical files documenting the sections are kept at the laboratory of paleobotany, PIN.

SYSTEMATIC PALEOBOTANY

Division Lyginopteridophyta

Class Lyginopteridopsida

Subclass Lyginopterididae

Order Lyginopteridales

Family Lyginopteridaceae Potonie, 1902

Genus *Telangiopsis* Eggert et Taylor, 1971

Telangiopsis nonnae O. Orlova et Zavialova, sp. nov.

Plates 25–29

Etymology. In memory to Nonna Robertovna Meyer-Melikian, our scientific teacher and outstanding botanist, died an early death.

Holotype. MGU, no. 293/47, Geological Faculty; fertile leafless axis bearing terminal synangia; Porog Vittsa 2 locality, right bank of the Msta River, Borovich district, Novgorod Region, Russia; Lower

Carboniferous, Visean Stage, Upper Visean Substage (Fig. 1).

Diagnosis. System of fertile axes branches monopodially, three-dimensional. Main axis with alternating secondary axes. Secondary axes bear alternating tertiary axes terminating with ultimate axes of numerous connivent clusters of synangia gathering in pairs, or, occasionally, single. Synangia 1.2–3.5 mm long and up to 3.5 mm wide in terminal part. Each synangium consists of three–six elongated ovate basally fused sporangia. External surface of sporangia with coarse longitudinal ribs. Prepollen circular to circular-triangular and oval, $27.8 \times 32.0 \mu\text{m}$, trilete, rays reach $3/4$ – $4/5$ of radius. Exine surface verrucate, folded, and equatorially echinate. Exine bilayered, considerably varying in thickness, with alveolate ectexine.

Description (Figs. 1–4). The leafless fertile axis shows a compound architecture. Fertile axes of all orders alternate in three dimensions. The visible length of the main axis (=rachis) is 34 mm, and the width is 2.5 mm. The rachis bears alternating lateral branches (secondary axes), which are situated at a distance of 4–11 mm from each other. The upper axis of the second order is only preserved in the studied specimen (Pl. 25, fig. 2; Pl. 26, fig. 1; Figs. 1, 2). The next secondary axis was situated at a distance of 11 mm below the visible secondary axis. The preserved secondary axis deviates from the main axis at an angle of about 35° and branches three-dimensionally, producing alternating branches. The width of this secondary axis is 0.5–0.6 mm. The tertiary axis deviates from the secondary axis at an angle of 45° at a distance of 5 mm from the point where the secondary axis deviates from the main axis. The terminal fertile axis of the fourth order bearing synangia deviates from the tertiary axis (Pl. 25, fig. 2). All axes are covered with longitudinal ribs (Pl. 26, fig. 1). The distance between adjacent ribs is 0.15–0.2 mm.

The synangia deviate from the ultimate axis in three dimensions. The synangia are attached to the axis with short petioles. Most often, the synangia are in pairs; or, more rarely, they are solitary (Fig. 2). Usually, the clusters of synangia are situated closely to each other and often are partially or completely superimposed (Pl. 25, fig. 1). The synangia consist of three to six sporangia (Fig. 3). Most often, synangia of four or five sporangia occur (Figs. 3c–3e; Pl. 26, figs. 2, 4). Usually, synangia are situated along the bedding plane, and, therefore, in longitudinal section resembling wide cups (Figs. 2, 3; Pl. 26, figs. 2–6). Rarely, they are tear-shaped, small, and consisting of three sporangia (Fig. 3b). Most probably, such synangia were immature. The length of the sporangia preserved along the bedding plane varies from 1.2 to 3.5 mm; and the width in the terminal part reaches 3.5 mm (Table 1). Some synangia are prostrated in shape of a four- or five-pointed star (Fig. 2). Oblique sections of such synangia show that the sporangia are radially situated and have free sides. Therefore, the synangia consist of sporangia fused with each

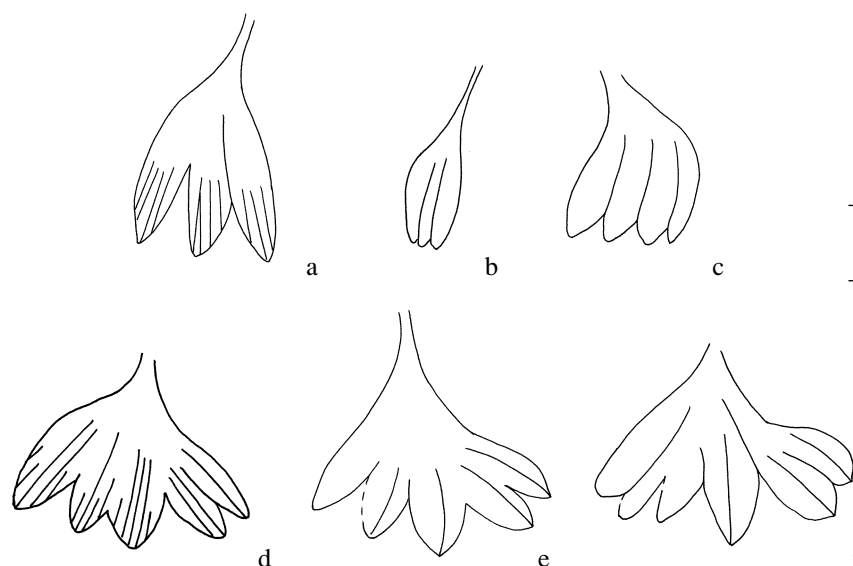


Fig. 3. Morphological diversity of synangia of *Telangiopsis nonnae* sp. nov.: (a, b) synangia composed of three sporangia; (a) mature synangium with longitudinal ribs; (b) immature synangium with smooth surface; (c) synangium composed of four sporangia; (d, e) synangia composed of five sporangia; (d) synangium with longitudinal ribs; (e) synangium with a longitudinal keel; (f) synangium of six sporangia, three of which bear a keel. Scale bar 1 mm.

other in their basal parts and free at the apices. No distinct synangiate cushion was observed. The only region where it is possibly present is shown in Pl. 26, fig. 2 (Fig. 3e). As a rule, the sporangia are elongated ovate with a more acuminate basal part and a less acuminate and occasionally rounded terminal extremity (Figs. 1–3; Pl. 26, figs. 4, 5). Occasionally, the apices of the sporangia are toothed (Pl. 26, fig. 6). Most often, the maximal width of the sporangium is situated in its middle and is equal to 0.4–0.6 mm. The length of the sporangia varies from 1.2 to 2.0 mm. The external surface of the sporangia is covered with coarse longitudinal ribs. There are four to six occasionally dichotomizing ribs on each sporangium (Pl. 25, figs. 2, 3; Pl. 26, figs. 2, 5). In rare cases, a longitudinal keel was observed on sporangia (Pl. 26, fig. 4; Figs. 3e, 3f). Apparently, the sporangia were longitudinally dehiscent. Some sporangia are opened along the bedding plane. Numerous imprints of rounded prepollen grains are visible in longitudinal folds of the walls of such sporangia (Pl. 25, fig. 3). Scattered prepollen grains are also visible in the rock surrounding the synangia.

Numerous sporangiate walls and miospores in monads and tetrads were obtained by the maceration of the rock surrounding the synangia. More than 90% of the palynological assemblage is represented by similar miospores, which were assigned to *Geminospora parvibasilaria* (Naum.) Byvsch on the basis of characters visible in transmitted light (determination was accomplished by M.V. Oshurkova). The prepollen grains are rounded, rounded-triangular, or occasionally, oval. Usually, they are preserved in polar position. The sizes vary from 23.4 to 37.0 μm , $27.8 \times 32.0 \mu\text{m}$ on average (Fig. 4). The proximal scar is trilete, the rays

are closed, up to 3/4–4/5 of the radius of the prepollen grain, and often poorly visible. The exine is thick and bilayered. In some prepollen grains, the exine in the polar region is slightly lighter than in other regions implying that the exine of the proximal and/or distal poles is thinner than the equatorial exine. In transmitted light, the exine appears vermiculate, that, apparently, is resulted from superimposed sculptural elements and inner partitions of the exine. The margin of the prepollen grain is uneven, crenate, and with occasional spinules.

SEM revealed diverse sculpture of the exine (Pl. 27). Numerous small verrucae cover the distal surface, often reaching equatorial regions (Pl. 27, figs. 2, 5, 7), where they occasionally transform into spinules 1.3–1.5 μm long (Pl. 27, fig. 3). The exine is elevated in the equatorial regions, and there are depressions in the polar regions. Although verrucae occur on the proximal face as well, numerous folds are more characteristic of the proximal sculpture. The proximal scar is closed with non-elevated rays and usually is nearly undistinguishable under SEM (Pl. 27, figs. 1, 4). Under SEM, we have only seen a distinct proximal scar in one of the studied specimens (Pl. 27, fig. 6).

TEM revealed two layers in the exine (Pls. 28, 29). The exine thickness varies along the perimeter of the pollen grain: the thickest exine is situated in the equatorial region, reaching 2.3–3.1 μm . The distal exine is 1.3–2.1 μm thick, in places becoming thinner up to 0.7 μm . The proximal exine is 1.1–1.7 μm , becoming sharply thinner up to 0.3 μm under rays of the proximal scar (Pl. 28, figs. 1, 3). Granular elements (cut verrucae) are more numerous on the distal surface of the exine than

Explanation of Plate 25

Figs. 1–3. *Telangiopsis nonnae* sp. nov., holotype MGU, no. 293/47: (1) aggregation of synangia, note numerous synangia constituted of elongated obovate sporangia with rounded apices, $\times 3.2$; (2) ultimate fertile axis bearing pairs of synangia, $\times 7.5$; (3) three sporangia split along the rock matrix, note numerous imprints of prepollen grains, $\times 40$. Porog Vittsa 2 locality, Borovich district, Novgorod Region, Russia; Lower Carboniferous, Viséan Stage, Upper Viséan Substage.

on the proximal surface (Pl. 28, fig. 3; Pl. 29, fig. 4). The external outline of the proximal face is more undulated because of the folds which were visible on the proximal surface under SEM (Pl. 29, fig. 1). The ectexine is alveolate, with relatively thin partitions (0.1–0.15 μm thick), the alveolae are relatively spacious, approximately up to 1.0 μm long and up to 0.8 μm high (Pl. 28, fig. 6). Dependent on the thickness of the ectexine, its alveolae are arranged in one to three tiers: in two or three tiers in the equatorial area; more often in two tiers or, occasionally, in one tier on the distal side; and more often in one tier or, occasionally, in two tiers on the proximal side (Pl. 28, figs. 2, 4).

The endexine is well developed, more electron-dense than the ectexine, 0.1–0.15 μm in average thickness, becoming thinner up to 0.025 μm under the rays (Pl. 28, fig. 5). Its heterogeneous nature is apparent under greater magnifications: the external part is less electron-dense and contains one to three white lines, and the internal part is more electron-dense (Pl. 28, figs. 5, 6; Pl. 29, figs. 3, 5).

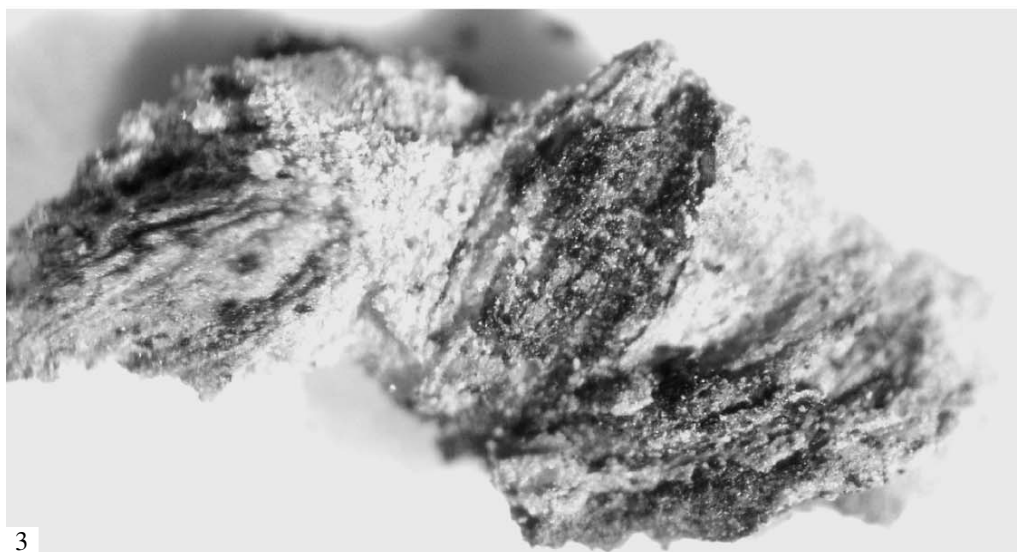
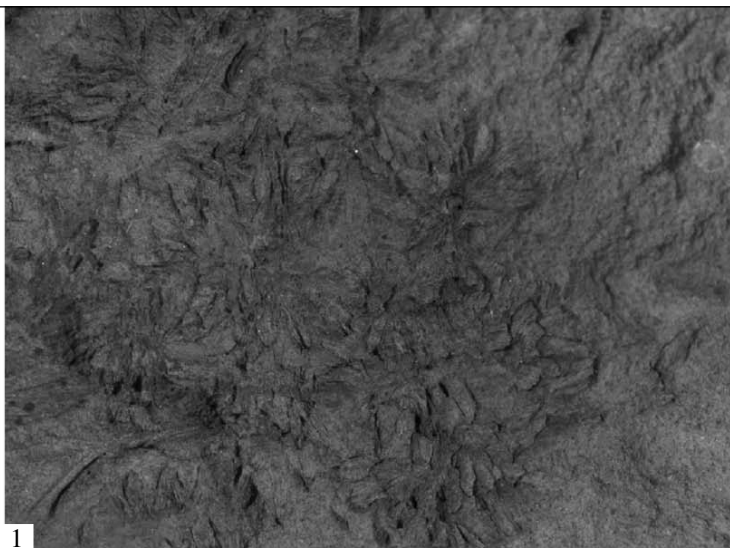
Comparison. The species under description differs from the closest species *T. affine* (Kidst.) Eggert et Taylor (Kidston, 1924) by the mode of branching: *T. nonnae* sp. nov. has a system of axes which branch monopodially, and synangia of *T. affine* are situated on the extremities of terminal axes of equally dichotomizing branches. The differences also concern the outlines of the sporangia: *T. nonnae* sp. nov. has elongated obovate sporangia, and *T. affine* has elongated lanceolate, and nearly linear sporangia. In addition, these two species differ by the external surface of their sporangia: finely longitudinally striate in *T. affine* and coarsely longitudinally striate in *T. nonnae* sp. nov. The prepollen grains are also different: smooth, rounded, and more than 50 μm in diameter in *T. affine*; and sculptured (with verrucae, folds, and equatorial spinules), rounded, rounded-triangular, occasionally oval, and no more than 37 μm in *T. nonnae* sp. nov.

Remarks. As far as the palynological assemblage extracted from the rock matrix surrounding the detached sporangia is nearly completely constituted by miospores of only one species, which general morphology answers that of prepollen grains of the Lyginopteridales, we believe that these miospores represent prepollen grains of the plant under study and we may supply the characteristics of the new taxon with data on their morphology and ultrastructure.

According to the morphological characters visible in transmitted light, the prepollen grains under study are closest to the diagnosis of *Geminospora*. There is a certain discrepancy between the data obtained with help of light and electron microscopes. Although the genus *Geminospora* describes cavate spores, we observed under TEM no distinct cleavage between the exinal layers. Sections of one of the prepollen grains show ectexine and endexine that are loosely mating in the polar area. Unfortunately, this specimen was most probably mechanically damaged (in places the endexine is missing and the same might be true for the adjacent tier of ectexinal alveolae), and we cannot be assured that the observed polar cleavage is not an artifact (Pl. 29). The discrepancy between LM and TEM results can be explained as follows. The species *Geminospora parvibasilaria* was erected on the basis of light microscopical observations, and, therefore, one cannot say with reasonable confidence how the area visible in transmitted light as a cavum looks under TEM. It is a distinct possibility that this area is corresponded by the thickest areas of airy alveolate ectexine, not separating from the endexine. Another conceivable explanation is intraspecific variation: some specimens have a cavum developed to a greater degree, whereas it is developed to a lesser degree or completely lacking in others. An analogous case was described by Zavialova et al. (2004) in Permian pollen grains of *Cordaitina*, varying in the width of their monosaccus. Pollen grains bearing the narrowest saccus show a protosaccus in sections; however, ectexinal partitions slightly do not touch the endexine in specimens with a wider saccus, and the ultrastructure can be defined as intermediate between protosaccus and eusaccus. The wider the saccus is, the wider the distance is between the endexine and ectexinal partitions pending into the saccus cavity. Dealing with TEM, it is difficult to reach statistical amount of studied specimens; therefore, the risk is run that all the sections were obtained from specimens lacking a cavum.

Some sections of four from five specimens studied under TEM show thinned regions on both sides of the exine (Pl. 28, fig. 3; Pl. 29, fig. 1). Since the prepollen grains under study are usually preserved in polar position, and rays of the proximal trilete scar occupy up to 4/5 of the radius, one can suppose that the side showing thinned regions in all sections of the series of sections, and with a thinned endexine in these regions, is the proximal side. However, thinned regions are present on the opposite side as well. Although no shaped distal

Plate 25





Explanation of Plate 26

Figs. 1–6. *Telangiopsis nonnae* sp. nov., holotype MGU, no. 293/47: (1) main axis, $\times 5.5$; (2) two synangia with apices directed to each other, central synangium consists of five prostrate sporangia with slightly pointed apices and longitudinally striate external surface, $\times 11$; (3) cluster of two synangia deviating from an ultimate fertile axis, apices of sporangia are destroyed, $\times 18$; (4) two partially destroyed synangia, synangium to the left consists of five sporangia with a longitudinal keel, $\times 12$; (5) incomplete synangium with distinct longitudinal striation and rounded apices of sporangia, $\times 16.5$; (6) slightly toothed apices of synangia, emerging from the rock matrix at one third of the length of sporangia, $\times 18$. Porog Vittsa 2 locality, Borovichi district, Novgorod Region, Russia; Lower Carboniferous, Visean Stage, Upper Visean Substage.

aperture was observed, the presence of thinned regions also on the distal side is an indirect index that such an aperture is forming. Ultrastructurally, the prepollen grains under study are more advanced than by their general morphology.

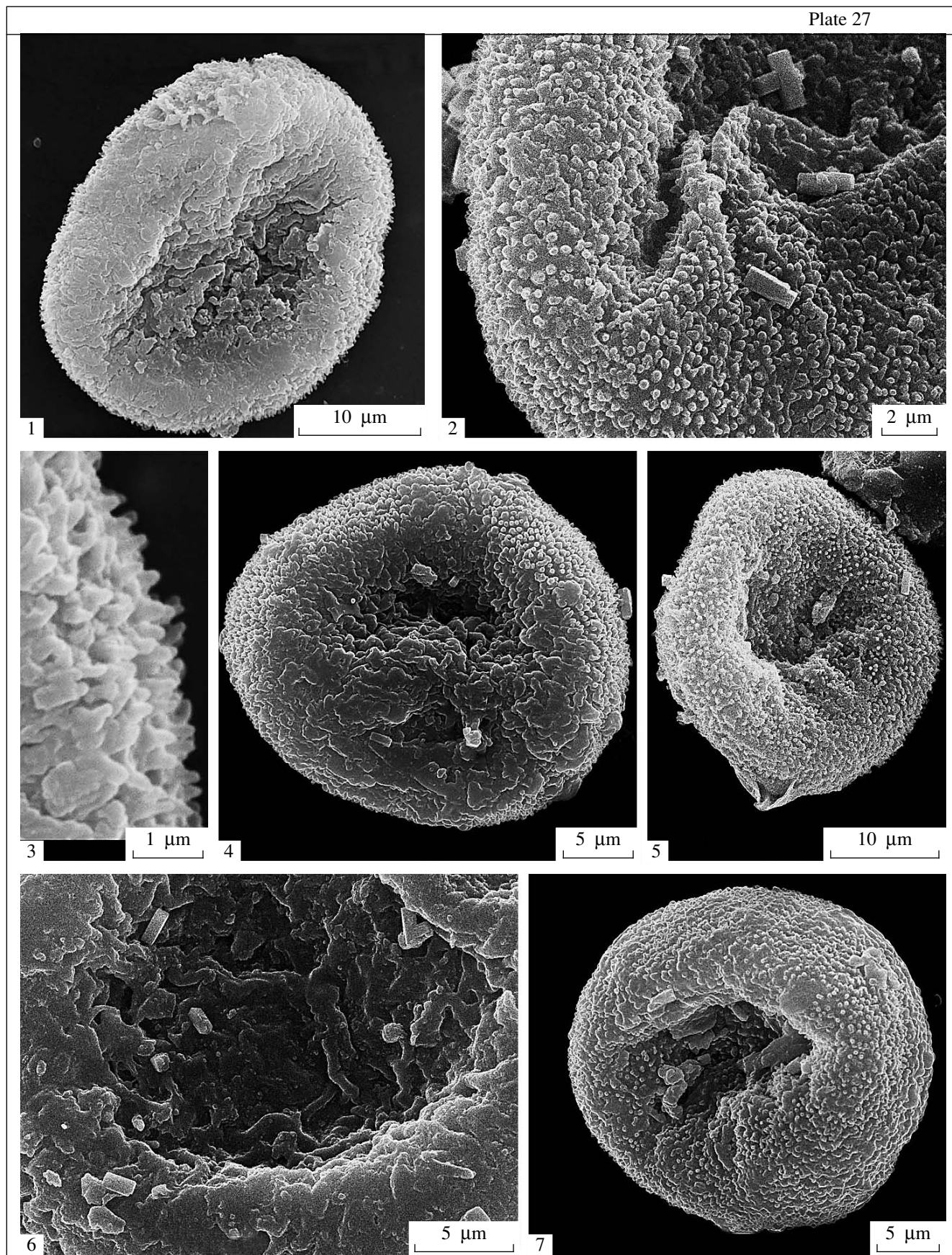
Material. Holotype MGU, no. 293/47.

DISCUSSION

Early Carboniferous synangiate pollen organs of lyginopteridaleans are represented by several genera, occurring as isolated organs or, rarely, associating with sterile structures (Walton, 1931; Jennings, 1976; Rowe, 1988). Remains of *Telangium* Benson and *Telangiopsis*

Table 1. Comparison between the taxon under study and the most similar species of the genus *Telangiopsis*

Species Characters	<i>Telangiopsis arkan- sanum</i> Eggert et Taylor	<i>T. bifidum</i> (Kidst.) Eggert et Taylor	<i>T. affine</i> (Kidst.) Eggert et Taylor	<i>Telangiopsis nonnae</i> sp. nov.
Branching of axes	Monopodial alternating	Equally dichotomizing	Equally dichotomizing	Monopodial alternating
Shape of synangia in lateral view	Cup-shaped	Cyathiform	Cup-shaped	Cup-shaped
Dimensions of sporangia, mm	L 1.0/W 0.8	L 6.3–6.7/W 3.75–4.0	L 2.5–3.5/W 2.78–3.0	L 1.2–3.5/W 2.0–3.5
Number of sporangia per synangium	5–6	12–25	6	3–6
Shape of sporangia	Rounded-triangular	Linear	Elongated lanceolate	Elongated obovate
Dimensions of sporangia, mm	No data	L 2.5–3/W 0.45	L 2.5–3/W 1–1.5	L 1.2–2.0/W 0.4–0.6
Free extremities of sporangia	Pointed	Pointed	Obtuse	Pointed
External surface of sporangia	Smooth	Fine longitudinal striation in the middle part	Fine longitudinal striation	Coarse longitudinal striation
Sporangial cushion	No data	Triangular	Supposedly existed	Not developed
Prepollen grains (corresponding taxon of dispersed miospores)	<i>Punctatisporites</i> , <i>Granulatisporites</i>	<i>Cyclogranisporites</i>	No data	<i>Geminospora parvibasilaria</i> (Naum.) Byvsch.
Morphology of prepollen grains	Rounded, trilete, smooth or punctuate, with folds	Rounded, trilete, smooth	Rounded, trilete, smooth	Rounded, up to rounded-triangular, triangular, sculptured
Dimensions of prepollen grains	47–54	40–50	52	30–35
Geographic region	North America	Great Britain and Ireland	Great Britain and Ireland	Northwestern Russia
Geological age	Early Namurian	Late Visean–Namurian	Late Visean	Late Visean
References	Eggert and Taylor, 1971; Balme, 1995	Kidston, 1924; Balme, 1995	Kidston, 1924	Present paper



Explanation of Plate 27

Figs. 1–7. Surface sculpture of prepollen grains of *Telangiopsis nonnae* sp. nov., SEM: (1, 4, 6) proximal surface of prepollen grains, note folds at the proximal pole, the scar is virtually invisible, with the exception of the specimen shown in Pl. 27, fig. 6; (2, 5, 7) distal surface of prepollen grains, numerous verrucae are visible; (3) spinules on the equatorial surface of the same specimen as shown in Pl. 27, fig. 1. Porog Vittsa 2 locality, Borovichi district, Novgorod Region, Russia; Lower Carboniferous, Visean Stage, Upper Visean Substage.

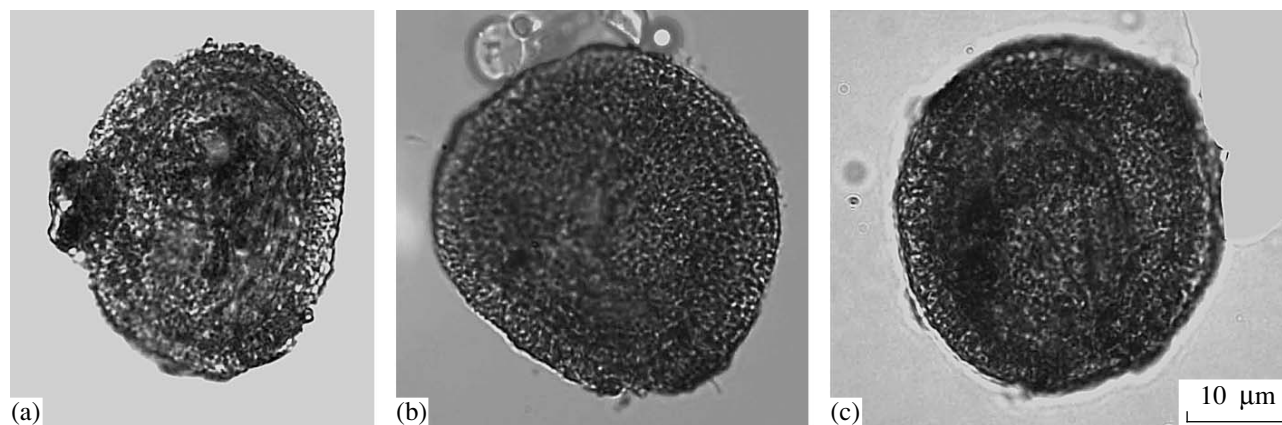
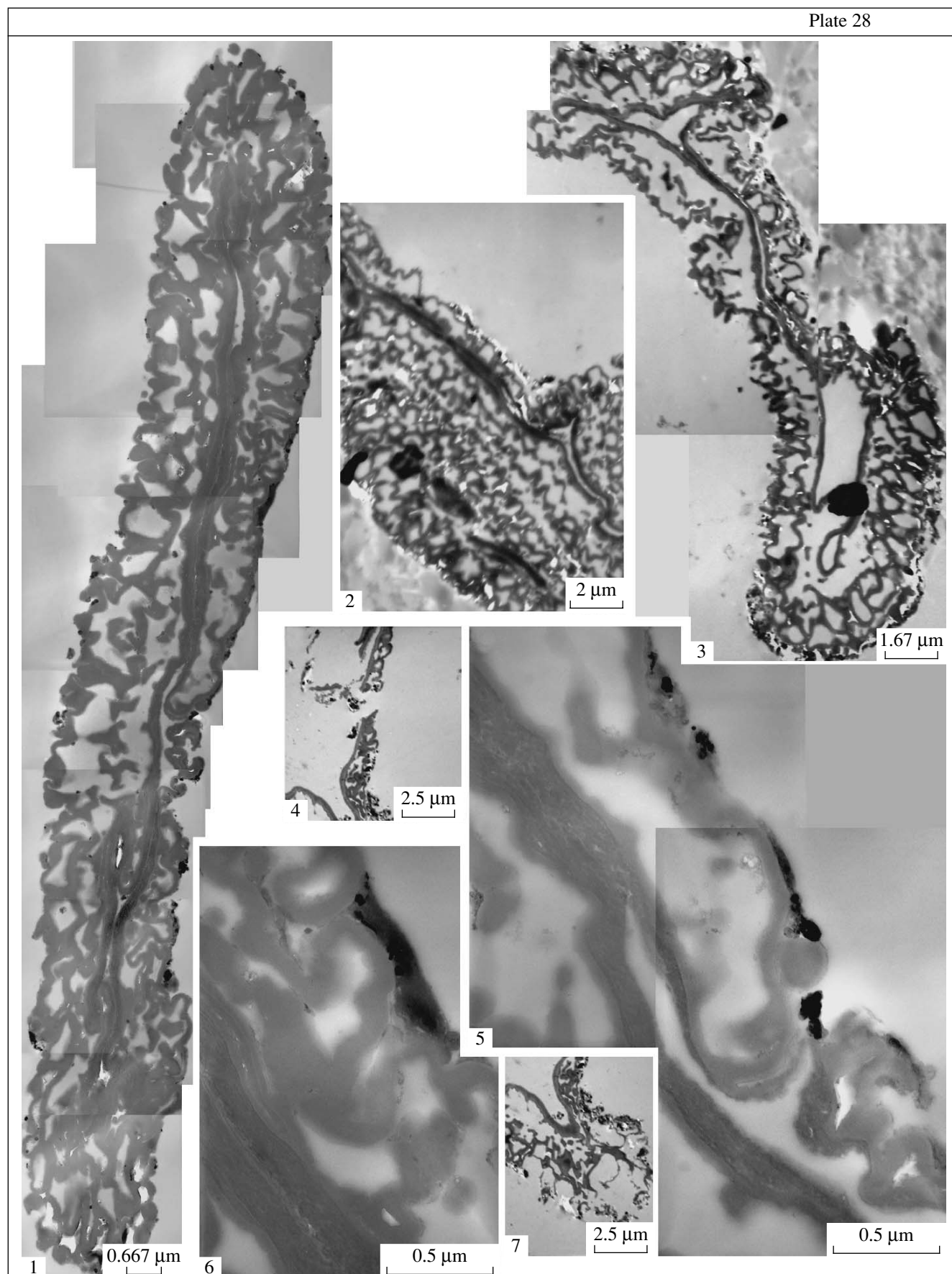


Fig. 4. Prepollen grains of *Telangiopsis nonnae* sp. nov., LM. Porog Vittsa 2 locality, Borovichi district, Novgorod Region, Russia; Lower Carboniferous, Visean Stage, Upper Visean Substage.

are most common. The former genus is known by permineralized remains (Benson, 1904). The latter was separated from *Telangium* on the basis of several characters, the most important of which were the type of preservation and absence of planar leaf structures (Eggert and Taylor, 1971). The diagnosis of the genus *Telangiopsis* was formulated as follows, “Synangiate organs with variable number of sporangia organized into stalked, radial clusters, borne terminally on either dichotomously or monopodially branching axes lacking planated foliar structures. Sporangia fused at base, distally free” (Eggert and Taylor, 1971, p. 31). The taxon under study shows all characters of the above diagnosis and should be assigned to *Telangiopsis*. Unfortunately, the lack of complete information on other species of this genus regarding the morphology and dimensions of the constituting elements of their synangiate organs impedes the comparison between them and *T. nonnae* sp. nov. Because of this, our comparison is restricted to three comprehensively characterized species of *Telangiopsis*: *T. arkansanum* Eggert et Taylor, *T. bifidum* (Kidst.) Eggert et Taylor, and *T. affine* (Table 1). The species under comparison differ in the way how their fertile axes branch. The type species of the genus, *T. arkansanum*, has monopodially branching alternating axes. *T. nonnae* sp. nov. also has monopodially, but three-dimensionally, branching alternating axes. *T. bifidum* and *T. affine* differ from the species under description in having equally dichotomizing axes. The number of sporangia in synangia, a pointed free extremity of the sporangium, and the shape

of the synangia also make *T. nonnae* sp. nov. similar to *T. arkansanum*. However, the latter species has smooth sporangial walls, synangia that are more than two times as small as synangia of *T. nonnae* sp. nov., rounded-triangular sporangia, and larger and morphologically different prepollen (Table 1). *T. nonnae* sp. nov. and *T. bifidum* are only similar in pointed apices of sporangia and different in all other parameters (Table 1). The general morphology of sporangia and synangia of the new species most closely resembles that of *T. affine*. However, sporangia of the latter species usually have an obtuse apex, whereas the apex in *T. nonnae* sp. nov. is rounded (Pl. 26, fig. 5), pointed (Pl. 26, fig. 2), or, occasionally, finely toothed (Pl. 26, fig. 6). Moreover, the two species differ by the external surface of sporangia, which is coarsely striate in *T. nonnae* sp. nov. (Pl. 26, fig. 2) and finely striate in *T. affine*. The shape of sporangia is also different. Rowe (1988) believed that *T. bifidum* and *T. affine* are assignable to synangiate organs of *Dichotangium quadrothecum* Rowe, which were found in association (rather than in organic connection) with fronds of *Diplopteridium holdeni* Lele et Walton. We do not share this opinion and believe that although *T. bifidum* and *T. affine* resemble *Dichotangium quadrothecum* in the morphology of sporangia, several differences allow us to keep these species within the genus *Telangiopsis*.

Let us compare *Telangiopsis nonnae* sp. nov. with pollen organs of some morphologically close members of lyginopteridaleans. The similarity between the species under study and pollen organs of *Dichotangium*



Explanation of Plate 28

Figs. 1–7. Exine ultrastructure of prepollen grains of *Telangiopsis nonnae* sp. nov., TEM, all ultramicrographs are orientated in a way that the distal side of the exine is situated to the left of the figure: (1) ultrathin section of a prepollen grain; (2) area of a section of two prepollen grains, one tier of alveolae on the proximal side and two tiers of alveolae on the distal side are clearly visible in the upper prepollen grain; (3) ultrathin section of a prepollen grain, thinned areas are present on both sides of the exine; (4) area of fragmentary section of the exine in the proximal region; (5) area of an ultrathin section (shown in Pl. 28, fig. 1) in the area of a ray of the proximal scar, endexine of the proximal side becomes thinner, and endexine of the opposite, distal, side is visible; (6) area of an ultrathin section (shown in Pl. 28, fig. 1), note alveolate ectexine of the proximal side and tightly adpressed to each other endexines of the proximal and distal sides; (7) equatorial area of the exine (Pl. 28, fig. 4). Porog Vittsa 2 locality, Borovich district, Novgorod Region, Russia; Lower Carboniferous, Visean Stage, Upper Visean Substage.

quadrothecum from the Upper Visean of Great Britain (Rowe, 1988) is restricted to pointed apices of free extremities of sporangia and longitudinally striate external surface of sporangia. Other parameters, such as the number of sporangia in synangium, general morphology of axes and synangia, etc., are significantly different.

A certain similarity in the prepollen morphology exists between the species under study and the petrified pollen organs of *Melissiotheca longiana* Meyer-Berthaud from the Upper Visean of Scotland (Meyer-Berthaud, 1986). The prepollen grains of *M. longiana* (assigned to *Convolutispora* Hoffmeister, Staplin et Mallow) are also rounded, trilete, with indistinct rays masked by ornamentation. Unlike *T. nonnae* sp. nov., prepollen grains of *M. longiana* are usually preserved in the lateral position rather than polar position. The sculpture is formed by well-developed ridges. As far as the inner morphology of the exine was only studied in thick sections under SEM, it is impossible to judge about the endexine ultrastructure and the ectexine ultrastructure can merely be compared with caution. The ectexine of *M. longiana* is not homogeneous. According to the description of Meyer-Berthaud (1986), it consists of irregularly distributed granulae and rods, occasionally fusing in a more compact alveolate structure. In our opinion, ultrathin sections of this ectexine would very probably resemble those of the alveolate ectexine of *T. nonnae* sp. nov., and granulae and rods are most probably partitions of alveolae cut under various angles. The morphology of synangia of *Melissiotheca longiana* is sharply different from that of *Telangiopsis nonnae* sp. nov. because of the presence of a large synangiate cushion divided into lobes (synangiate cushion is not developed in the species under description) and numerous (50–150) sporangia per synangium.

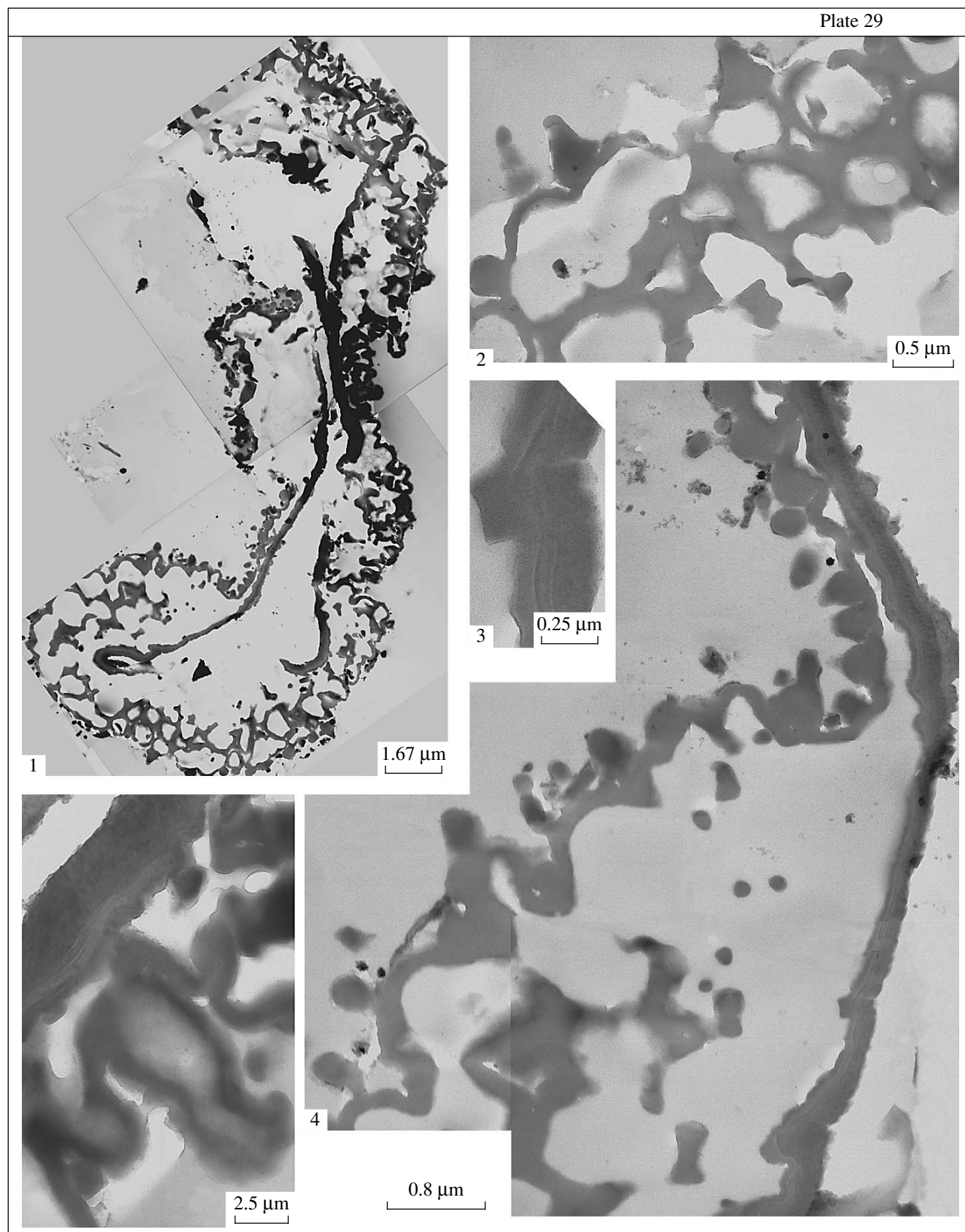
T. nonnae sp. nov. and lyginopteridalean synangiate petrifications of *Schopfiangium varijugatus* Stidd, Rischbieter et Phillips from the Upper Carboniferous of Kentucky (Stidd et al., 1985) have sporangia of the same shape, but the latter species has seven to nine sporangia per synangium in comparison with three to six sporangia in the former. Free extremities of sporangia are also different: apices of sporangia are secondarily pointed in shape of a tooth in *Schopfiangium varijugatus*, which is not the case of the species under descrip-

tion. In addition, *S. varijugatus* has a synangiate cushion, which is not developed in *Telangiopsis nonnae* sp. nov. Prepollen grains of *Schopfiangium varijugatus* (correspond to the dispersed genera *Cyclogranisporites/Verrucosisporites*) and *Telangiopsis nonnae* sp. nov. are similar in several characters (particularly, those of the exine ultrastructure); nonetheless, some differences were also found. Both taxa have rounded prepollen grains with a long-rayed trilete proximal scar. However, the scar in *Schopfiangium varijugatus* is always distinct, whereas it is often poorly visible in *Telangiopsis nonnae* sp. nov., which is apparently related to a better developed various sculpture hiding the closed scar of *T. nonnae* sp. nov. The exine surface is verrucate-folded in both taxa, but spinules are also present in *T. nonnae* sp. nov. Ultrathin sections of the alveolate ectexine of both taxa are extremely similar, in both the orientation of partitions of the alveolae and the ratio between the partitions and cavities of the alveolae. The endexine in *Schopfiangium varijugatus* is thicker than in *Telangiopsis nonnae* sp. nov. and unequivocally multilamellate. In the area of the scar, both the ectexine and endexine become thinner in the two taxa.

To conclude, the peculiar assemblage of morphological and ultrastructural characters of the microsporangiate organ under study has allowed us to describe from the Upper Visean of northeastern Russia a new species of the genus *Telangiopsis*, *T. nonnae* sp. nov. Analysis of the obtained data on the morphology of prepollen grains of *T. nonnae* sp. nov. and published data about other members of lyginopteridaleans shows that the most typical exine ultrastructure of the group is alveolate rather than homogenous. Although the studied prepollen grains are indistinguishable from spores by general morphology, they are more advanced by their inner structure and closer to other groups of seed ferns.

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Explanation of Plate 29

Figs. 1–5. Ultrastructure of prepollen grains of *Telangiopsis nonnae* sp. nov., TEM: (1) fragmentary section of the exine, distal side is to the left of the figure; (2–5) areas of the section shown in Pl. 29, fig. 1; (2) equatorial spinules cut; (3) heterogeneous structure of the endexine; (4) equatorial-distal area, granular elements are sectioned verrucae; (5) area showing one tier of alveolae of the proximal ectexine, note heterogeneous structure of the endexine. Porog Vittsa 2 locality, Borovich district, Novgorod Region, Russia; Lower Carboniferous, Visean Stage, Upper Visean Substage.

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