

## *Palaeobotrychium* gen. nov., the first discovery of an ophioglossalean fern from the Middle Carboniferous deposits of Russia

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**Summary:** The paper is devoted to the description of the most ancient fertile ophioglossalean fern attributed to a new genus and species *Palaeobotrychium carbonicus* Naugolnykh, gen. et sp. nov. This new taxon is based on a single although well-preserved monopinnate fertile frond (the holotype) with fan-shaped pinnules dissected into linear segments or lobes. The material originates from the lowermost Middle Carboniferous (Bashkirian) deposits of the Moscow syncline in Russia. The floristic assemblage containing *Palaeobotrychium carbonicus* also includes other typically Carboniferous higher plants, i.e. sphenophytes *Calamites suckowi* Brongniart, *C. cistii* Brongniart and trigonocarpalean (= medullosalean) pteridosperms *Neuropteris* sp., *Odontopteris* sp. and *Mixoneura obliqua* (Brongniart) Zalessky.

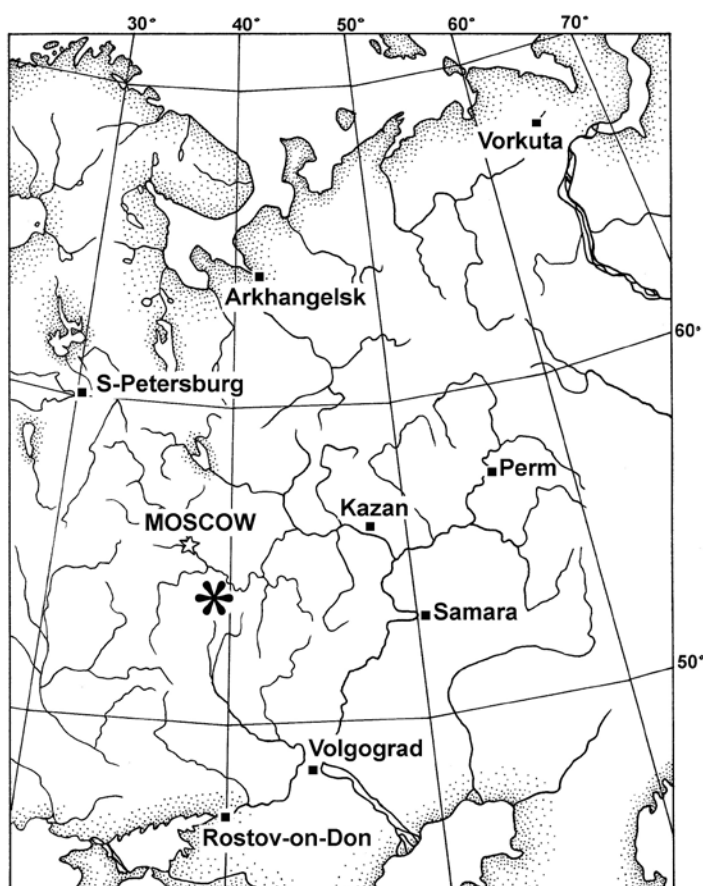
**Keywords:** Ophioglossales, new taxa, Carboniferous, *Palaeobotrychium*, fertile fronds, evolution, Russia, gen. nov., sp. nov.

Geological history of the different fern orders and families has been studied in very different extent. Phylogenetical predecessors of some fern groups, such as the orders Marattiales and Osmundales, are known very well now and can be traced back to the Late Palaeozoic (KIDSTON & Gwynne-Vaughan 1907; Millay 1977, 1997; Hill et al. 1985; Lesnikowska & Millay 1985; Lesnikowska & Galtier 1992; Lesnikowska & Willard 1997; Barthel & Rössler 1995; Barthel 2005; Naugolnykh 2013; etc.). But origin and first evolutionary stages of some other fern orders and families remain unclear and even mysterious.

One of such fern groups is the order Ophioglossales (taxonomical review see in: Sun et al. 2001). The most ancient true ophioglossalean ferns are reported from the Cenozoic deposits (Rothwell & Stockey 1989; Taylor et al. 2009). These Cenozoic ophioglossalean finds show that this fern order certainly has older evolutionary predecessors (Rothwell 1996).

In 2014, the author was invited by A. Ippolitov, a researcher from the Geological Institute of Russian Academy of Sciences (Moscow), to take a part in visiting the Serebrjansky quarry (Rjazan region, the City of Mikhailov, Russia; Figs 1; 2) for collecting Carboniferous fossil plants. During this field excursion, a large collection of fossil plants was obtained.

The floristic assemblage (Fig. 3 A–D) of the Serebrjansky quarry includes the sphenophytes s.l. *Calamites suckowi* Brongniart (Fig. 3 C), *C. cistii* Brongniart (Fig. 3 D) and the trigonocarpalean (= medullosalean) pteridosperms *Neuropteris* sp., *Odontopteris* sp. and *Mixoneura obliqua* (Brongniart) Zalessky (Fig. 3 A, B). Large arborescent lycopodiopsids like *Lepidodendron* or *Sigillaria* were not found. Most probably, the initial Carboniferous vegetation of that area was generally represented by shrubby plants, which grew in near-shore maritime lowland. The general taxonomic composition of the Serebrjansky floristic assemblage, especially the presence of *Mixoneura obliqua*, is very similar to some of the Middle Carboniferous floras of Donetsk Basin (Zalessky & Tchirkova 1938).



**Figure 1.** Geographical position of the studied locality (the Serebrjansky quarry; marked by an asterisk).

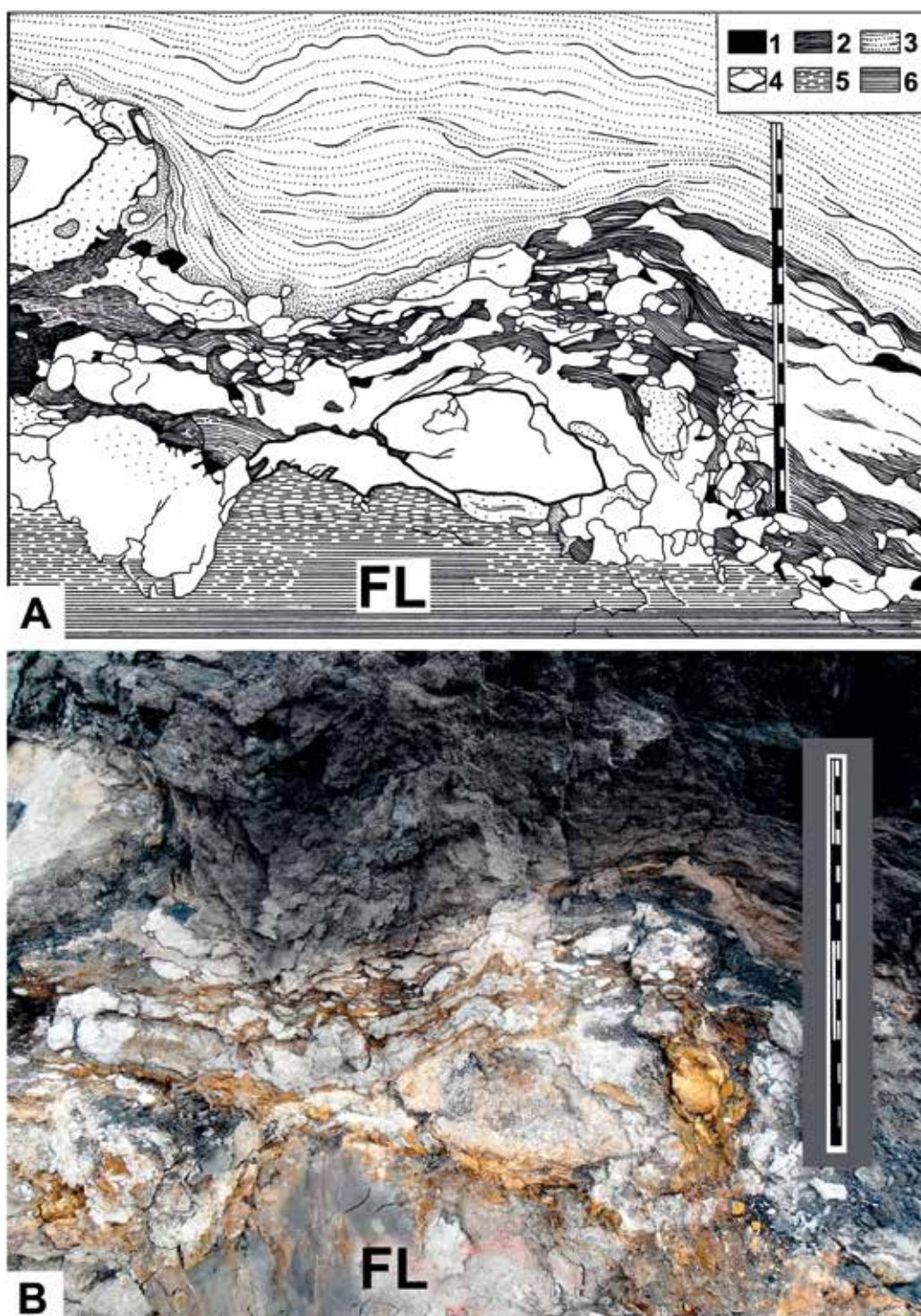
One very interesting and uncommon fern fossil was found together with the Carboniferous sphenophytes and pteridosperms of the Serebrjansky quarry. After a careful study of this fossil, it was discovered that this remain should be attributed to a new genus and species of ophioglossalean ferns. The present paper is focused on the description of this new taxon.

## Materials and methods

The Serebrjansky quarry (Fig. 1) is disposed on the left bank of the Pronya River (the right income of the Oka River).

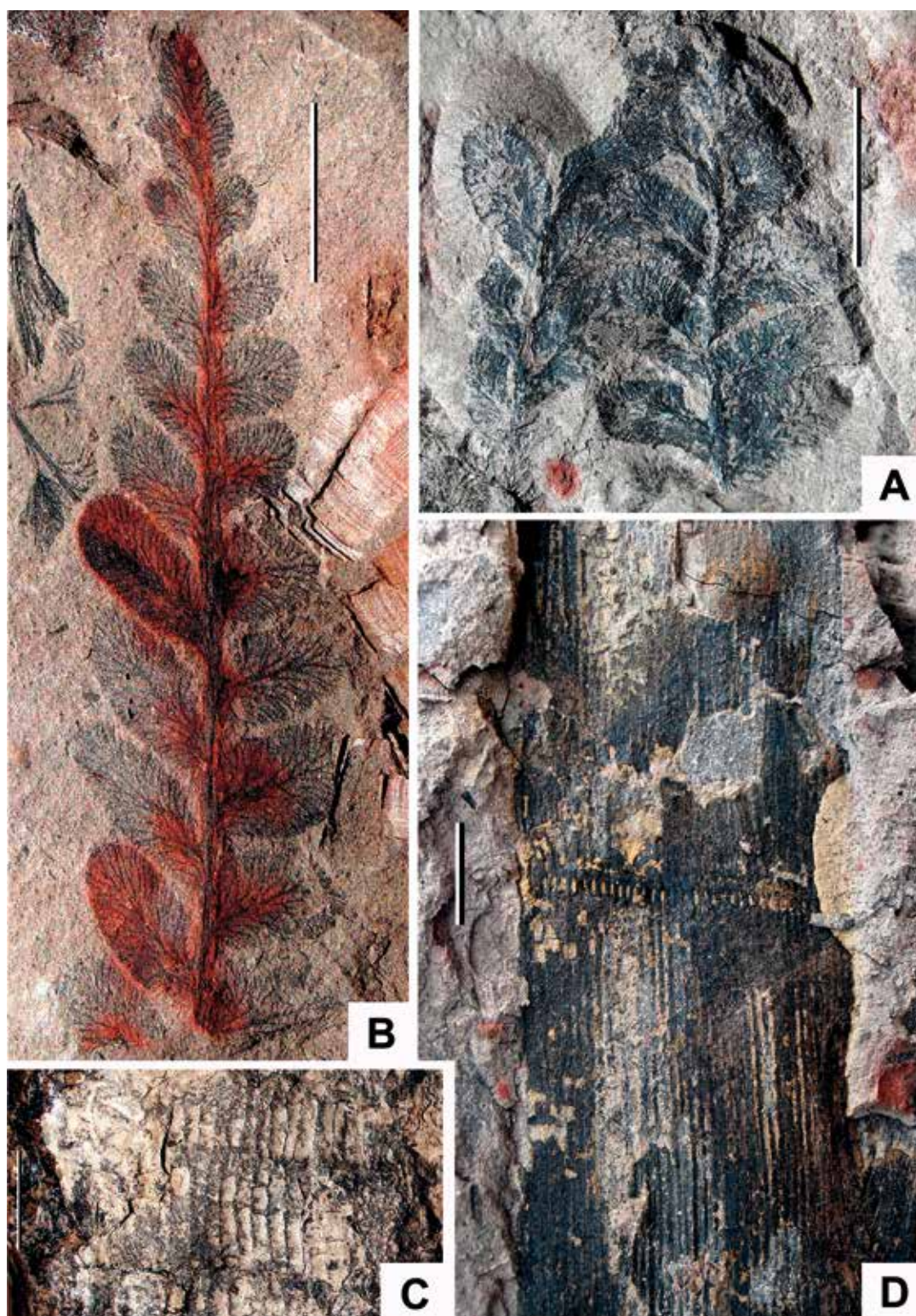
Geologically, the general succession of the deposits outcropping in the Serebrjansky quarry includes four main units (bottom-up): (1) the Lower Carboniferous limestones and mudstones, which are explored for preparing cement and other building materials; (2) dense gray clays with the small red spots and the numerous plant megafossils of Carboniferous age, probably of the lowermost Bashkirian stage; (3) well-defined hydromorphic fossil paleosoil (FPS-profile), probably of the Late Carboniferous or Permian age; similar hydromorphic FPS-profiles were reported from the uppermost Lower Carboniferous deposits of South China (NAUGOLNYKH & JIN 2014); (4) the Middle and Upper Jurassic dark-gray relatively soft clays with numerous marine invertebrates, mostly ammonites and belemnites and rare finds of marine reptiles. The plant-bearing Carboniferous layer lies just below the FPS-profile (Fig. 2).

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**Figure 2.** Stratigraphical relationship between the Middle Carboniferous (Bashkirian) plant bearing-layer (FL), the Upper Carboniferous or Permian paleosol (paleosol or the FPS-profile) and the marine Jurassic clays and shales. 1 – soil clay enriched by organic carbon; 2 – dense dark-colored soil clay; 3 – clay and shales of marine origin, Middle Jurassic, Callovian; 4 – limestones and secondary carbonates influenced by action of the pedogenic processes, the FPS profile; 5 – Carboniferous clays and alevrolites changed by influence of action of the pedogenic processes; 6 – Carboniferous plant-bearing clays and siltstones.

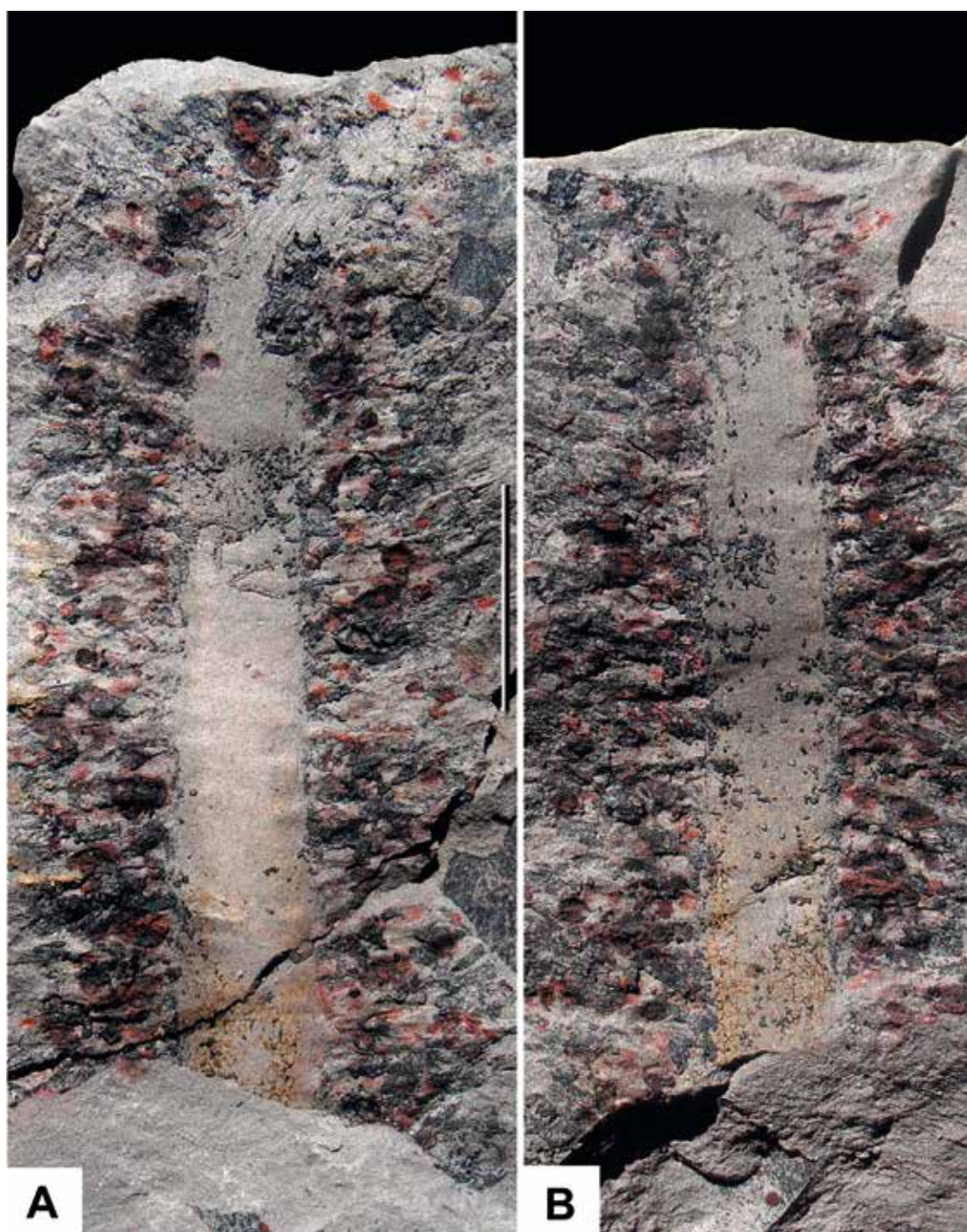




**Figure 3.** The Carboniferous floristic assemblage of the Serebrjansky quarry. A, B – medullolean pteridosperm *Mixoneura obliqua* (Brongniart) Zalessky, pinnae of the last order (penultimate segments); C – sphenophyte (calamostachyan) *Calamites suckowi* Brongniart; D – sphenophyte (calamostachyan) *Calamites cistii* Brongniart. Scale bars = 1 cm.



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**Figure 4.** *Palaeobotrychium carbonicus* Naugolnykh, gen. et sp. nov. The holotype (A – GIN 4914/27; B – counterpart GIN 4914/28). Scale bar = 1 cm.

The layer with the Carboniferous plant megafossils of the Serebrjansky quarry is very similar to the deposits of the Vereiskian Horizon of the Bashkirian Stage (the lowermost Middle Carboniferous) of the Opran (= Apran; the other broad-spread spelling of this river name) River Basin in the Tula region, which also include plant megafossils, such as *Calamites* sp., *Sigillaria* (*Rhytidolepis*) sp. and *Neuropteris heterophylla* Brongniart (KHVOROVA 1953). I think that here we have one and the

same stratigraphical level or 'datum plane' corresponding to the short-time uplift of this area and contemporary development of the swamp-forest vegetation of the typically Euramerian habit.

The fossil plants studied are preserved as compressions and impressions. The compressions are coalified and somewhat stained by hydroxides of iron. All the details of venation and macro- and mesomorphology of the plants are well-seen. The new species (and genus) is represented by a single well-preserved specimen (holotype).

A small piece of the fertile pinnule of the holotype, possessing sporangia, was macerated in concentrated nitric acid. The spores preserved in the sporangia *in situ* were obtained as a result of the maceration. The *in situ* spores were studied by means of optic microscopy and by Vega Tescan MV 2300 scanning electron microscope at the Geological Institute of the Russian Academy of Sciences, Moscow. The collection studied is kept in the Geological Institute of the Russian Academy of Sciences (GIN).

## Description

Division Pteridophyta Schimper, 1879

Classis Ophioglossopsida Thomé, 1874

Order Ophioglossales Newman, 1840

Family Ophioglossaceae C. Agardh, 1822

**Genus** *Palaeobotrychium* Naugolnykh, gen. nov.

**Type species.** *Palaeobotrychium carbonicus* Naugolnykh, sp. nov.

**Etymology.** From latinized Greek 'palaeo' (ancient) and *Botrychium* – generic name of the modern ophioglossalean fern.

**Diagnosis.** Monopinnate fertile fronds with thick straight or slightly curved rachis and cuneate flabelliform pinnules. Rachis surface smooth. Pinnules of subtriangular shape, with wedge-shaped basis and lobed apex. Venation fan-shaped. Veins from simple to twice dichotomizing. Pinnules bear ovoid sporangia 1.5 mm long and 1 mm wide in average. Sporangia are split by prolonged furrow into two valves. Sporangia isosporous. Spores round to ovoid, with monolete or trilete mark and granulate sporoderm.

**Comparison.** *Palaeobotrychium* is different from the genus *Botrychium* in presence of well-developed leaf lamina of fertile pinnules, which is a characteristic feature of the new genus.

**Distribution.** Carboniferous of the Russian platform.

*Palaeobotrychium carbonicus* Naugolnykh, sp. nov. (Figs 4 A–B; 5; 6 A–G; 7 A–D; 8 A–D; 9 A–D; 10 A–C)

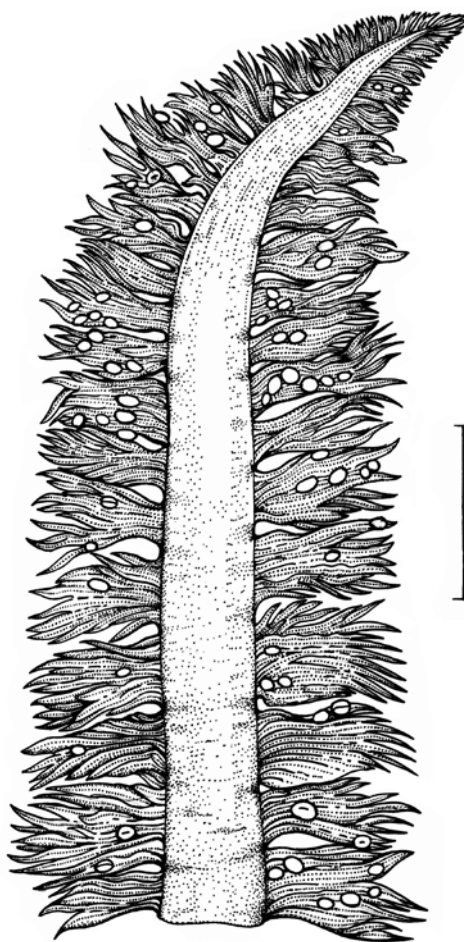
**Etymology.** After the Carboniferous period.

**Holotype.** Geological Institute of the Russian Academy of Sciences GIN, No 4914/27; 4914/28.

**Diagnosis.** Same as for the genus.

**Description.** Our understanding of this plant is based on a single specimen (Fig. 4 A, B). This specimen (holotype) is the presumably almost completely preserved, fertile monopinnate frond

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**Figure 5.** *Palaeobotrychium carbonicus* Naugolnykh, gen. et sp. nov. Reconstruction of the fertile frond, based on the holotype GIN 4914/27. Scale bar = 1 cm.

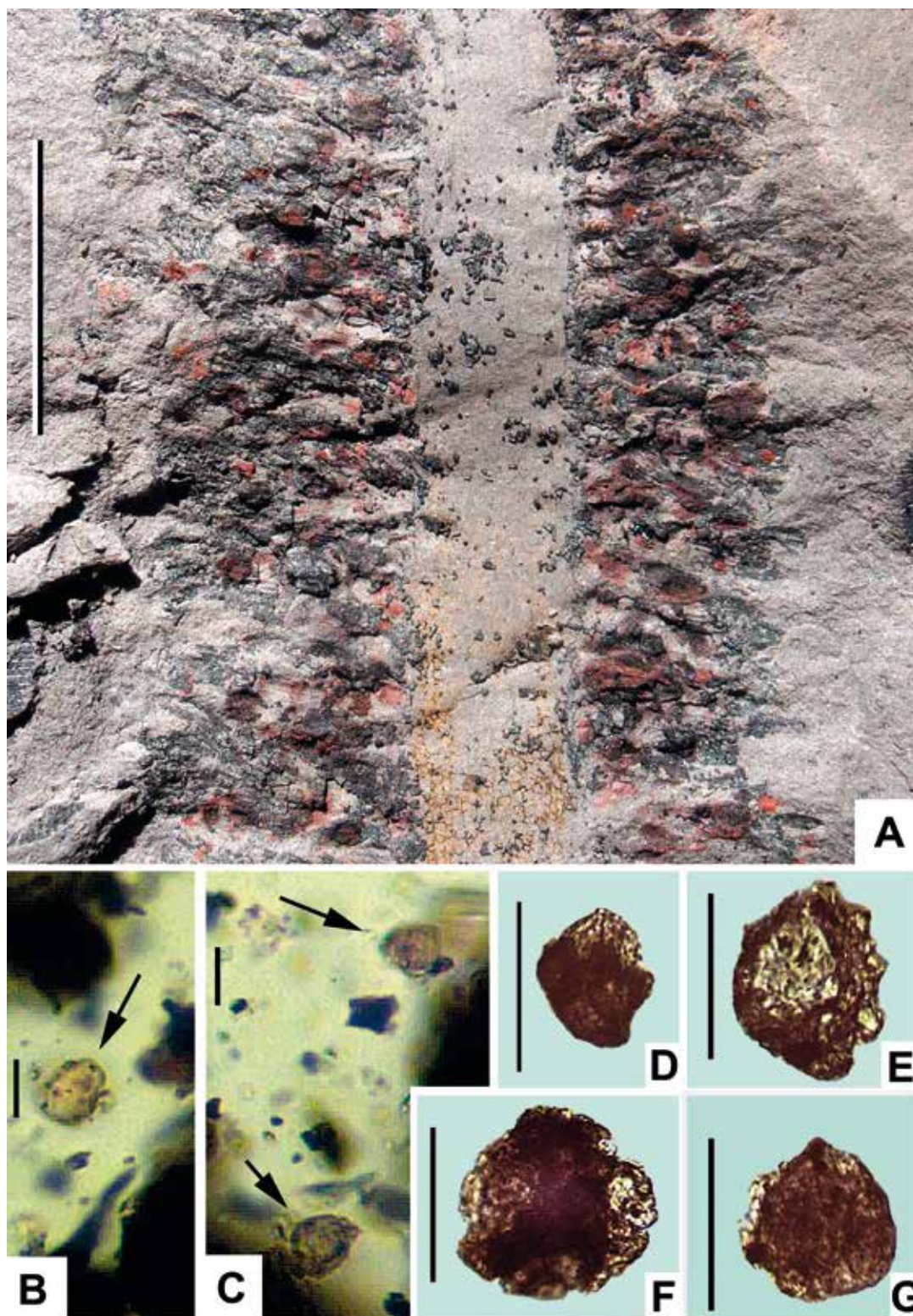
with a thick robust rachis and pinnately arranged pinnules (ultimate segments = segments of last order).

The rachis is straight in its basal and middle parts, but slightly curved in its apical part (Figs 4 A, B; 5). Apical curving according to my viewpoint is formed by initial coiling of the frond apex, what is typical of many recent and fossil ferns. Length of the frond is 6 cm, width is 2.2 cm. Width of the basal part of the rachis is 0.8 cm. Rachis width is gradually decreasing towards the frond apex. Surface of the rachis is relatively smooth, but it has very faint transverse folds in its marginal areas and very fine longitudinal striation in its apical part.

Each side of the frond rachis bears twenty pinnules. It is difficult to estimate the exact number of the pinnules, because they are connected to each other by their margins and even almost fused at the apical part of the frond.

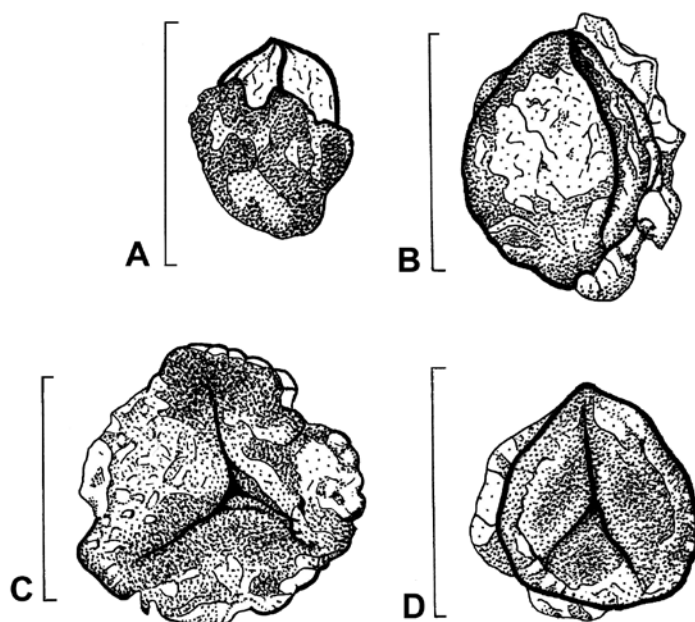
Pinnules of subtriangular shape, generally cuneate, with a wide lobed apical part (Figs 5; 6 A; 8 B, C). Although the general shape of the pinnules is cuneiform, the pinnule base is still relatively wide. Because of this, the pinnules cannot be classified as sphenopteroid in the strict sense of this term. Maximal observed length of the pinnules is 8 mm, width is 4.5 mm. Size of the pinnules





**Figure 6.** *Palaeobotrychium carbonicus* Naugolnykh, gen. et sp. nov. Morphology of the holotype GIN 4914/28 (A) and the spores, preserved *in situ* (B–G). In figures B and C the spores are marked by arrows. Scale bars = 1 cm (A); 50  $\mu$ m (B–G).



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**Figure 7.** *Palaeobotrychium carbonicus* Naugolnykh, gen. et sp. nov. Morphology of the spores, preserved *in situ* (A–D); line-tracing after Fig. 6D–G. Scale bars = 50  $\mu$ m.

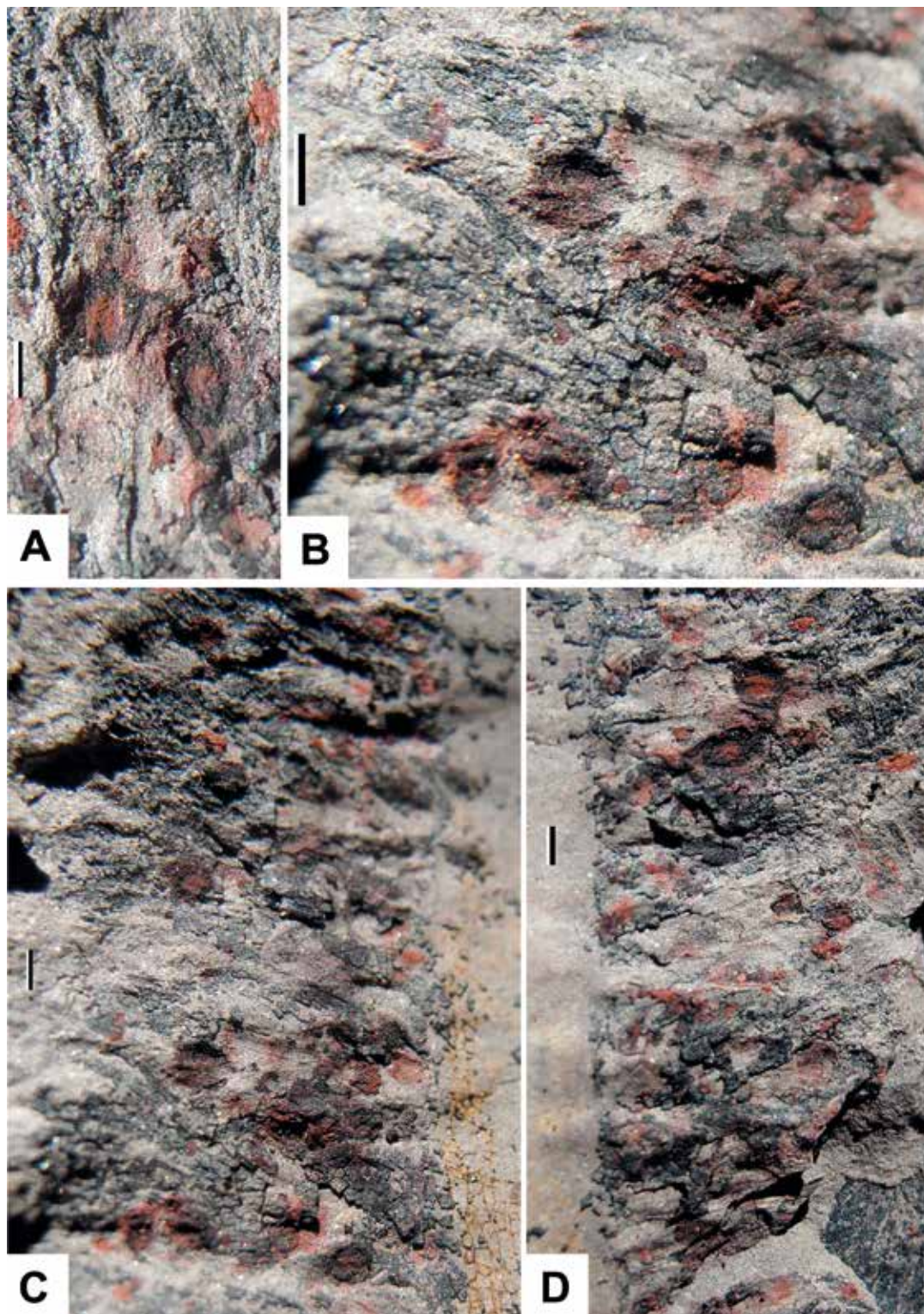
gradually decreases towards the frond apex. Apical part of the pinnule is dissected into 8–10 acute lobes. The lobes are narrow and long, 3 mm long and 0.5 mm wide. In average, the longest lobes are disposed in the middle part of the pinnule apex, and the shortest lobes are in lateral parts of the pinnule apex. But this arrangement of the apical lobes is not absolutely regular, because in some cases the shorter lobes could be disposed closer to the middle part of the pinnule. Apical lobes are disposed not in one and the same plane, but situated more or less three-dimensionally.

Venation of the pinnule is fan-shaped and conditionally can be classified as odontopteroid. Veins are very fine, mostly simple, but sometimes once to twice dichotomizing. Each well-developed pinnule has 8–10 veins. Each vein reaches into the apical lobe of the pinnule.

It is very difficult to state which surface of the leaf blade we can see on the holotype. Judging from the general topology of the rachis and pinnules, we can suggest that the abaxial surface of the leaf blade is observed.

The abaxial surface of the pinnules bears numerous sporangia (Figs 5; 6A; 8A–D). The sporangia are disposed irregularly in respect to each other, but always orientated by their long axes along the pinnule length (Fig. 8B). The sporangia are ovoid, 0.5–1 mm long and 0.3–0.8 mm wide. The sporangium is split by a prolonged furrow into two symmetrical valves. The furrow can be interpreted as a split for opening of the sporangium for spore release.

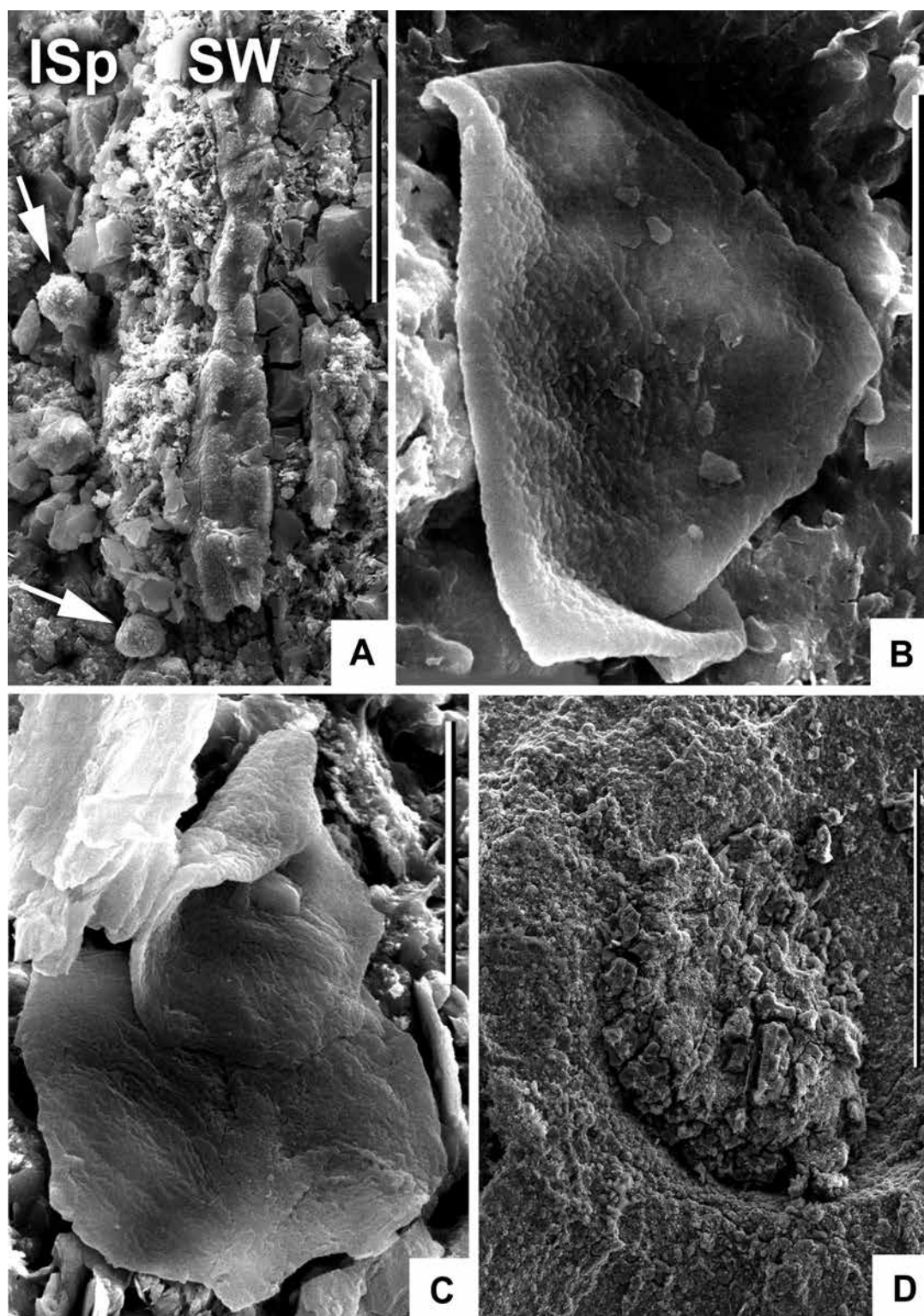
During the maceration of sporangia, numerous spores preserved *in situ* were extracted (Figs 6B–G; 7A–D; 9A–C; 10A–C). The spores are mostly round (Figs 6E–G; 7B–D; 10C), but sometimes the spores of subtriangular shape also occur (Fig. 9B). Average diameter of the spores is 30  $\mu$ m, the smallest spores are 19  $\mu$ m in diameter, the largest spores are 38  $\mu$ m in diameter. Spore scar from monolete to trilete. The spores are united in diads and tetrads. Spores possess very thin outer layer (the so-called perine), which can be easily detached from the spore and often is not



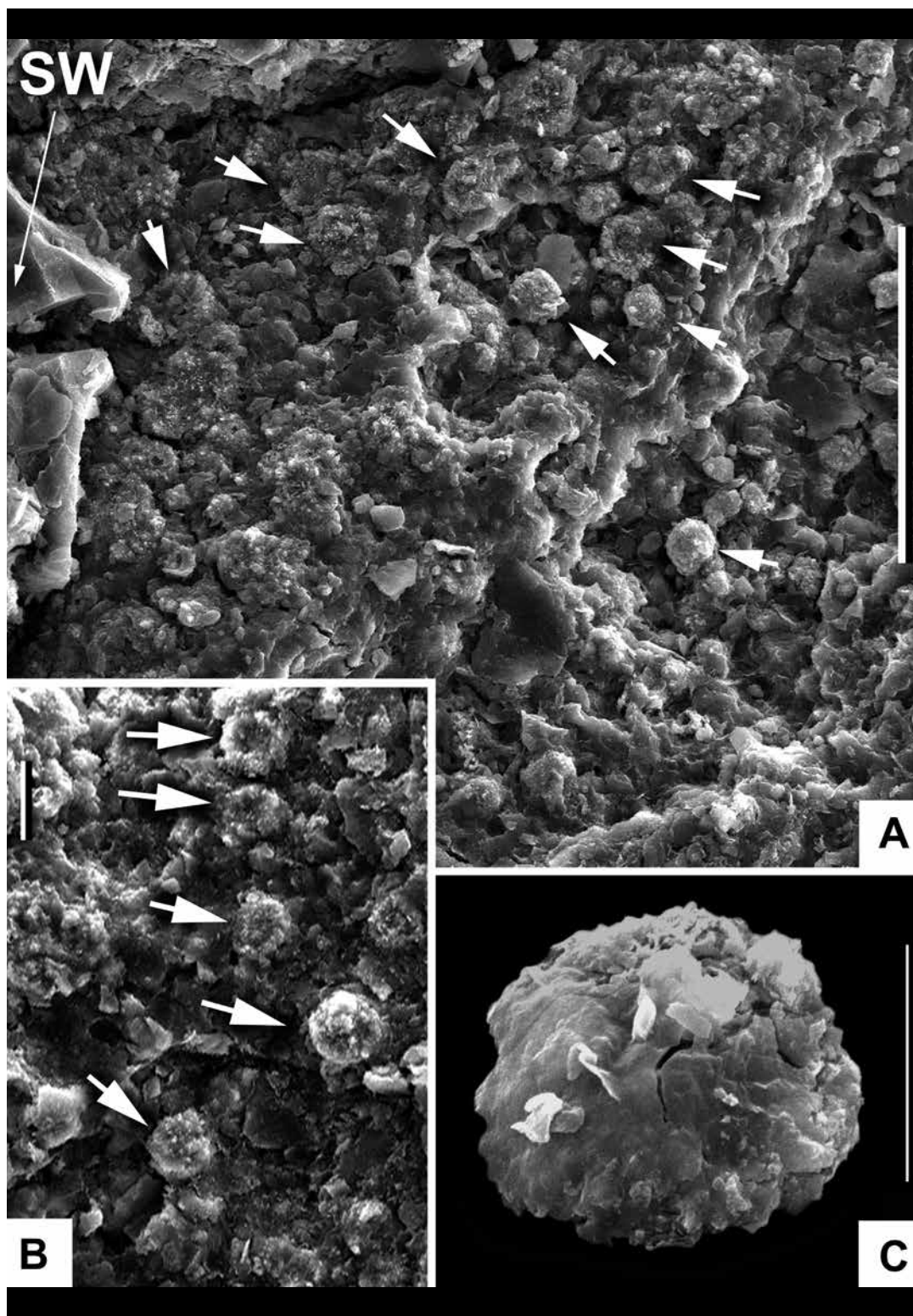
**Figure 8.** *Palaeobotrychium carbonicus* Naugolnykh, gen. et sp. nov., detailed structure of the holotype GIN 4914/28. A – apical part of the pinnule with two sporangia attached to the lamina of the fertile pinnule; B – two neighboring pinnules with the lobed apices (left) and two well-seen bivalve sporangia; C – the pinnules attached to the left margin of the pinna (the viewpoint on the abaxial side of the frond), several ovoid sporangia are clearly visible; D – pinnules attached to the right margin of the fertile pinna (view on the abaxial side of the frond). Scale bar = 1 mm.



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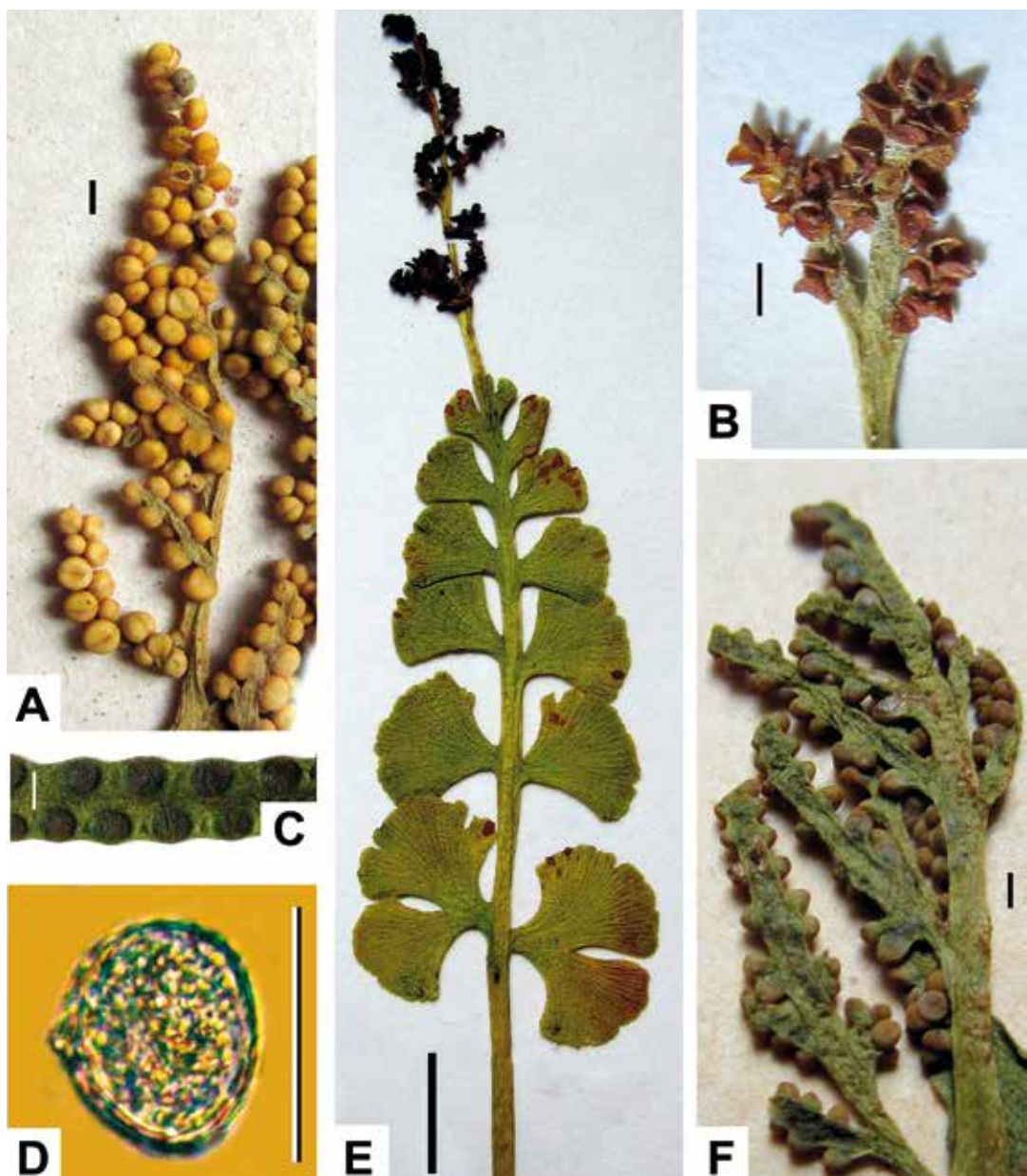
**Figure 9.** *Palaeobotrychium carbonicus* Naugolnykh, gen. et sp. nov., holotype GIN 4914/27. A – spores, preserved *in situ* in the sporangium (ISp – *in situ* spores, SW – sporangial wall, two spores are marked by arrows); B – *in situ* spores with the granulate sporoderm, the distal side of the spore; C – two *in situ* spores with the granulate sporoderm with small granulae; D – scar of the sporangium attachment. Scale bars = 20  $\mu$ m (B, C); 50  $\mu$ m (A); 500  $\mu$ m (D).



**Figure 10.** *Palaeobotrychium carbonicus* Naugolnykh, gen. et sp. nov. A, B – the spores, preserved *in situ*, disposed inside the partly destroyed sporangium (SW – the wall of the sporangium); some spores are marked by arrows; C – *in situ* spore with granulae on the proximal surface. Scale bars = 100 µm (A); 20 µm (B); 10 µm (C).



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**Figure 11.** Recent ophioglossalean ferns *Botrychium lunaria* (L.) Sw. (A, B, D–F) and *Ophioglossum vulgatum* L. (C). A, B, D–F – Vladimir region, Kovrov district, Ivano-Esin Forest Reserve; collected by I. Krylov, June 1973, the Herbarium of the Main Botanical Garden, No. 012, Moscow. C – Pskov region, Losnjansky district, Polistovskiy Reserve; collected by N.M. Reshetnikova & E.O. Korolkova, 22 June 2005, the Herbarium of the Main Botanical Garden, No. 016, Moscow. A, B, F – fertile pinnae; C – part of the sporophyll; D – the spore; E – sterile and fertile leaves of one individual plant. Scale bars = 1 cm (E); 1 mm (A, B, C, F); 50 µm (D).

preserved completely (Fig. 6 D; 7 A). The sporoderm is fine-granulated (Fig. 9 B). Sometimes larger granulae can also be observed (Fig. 10 C).

**Remarks and comparison.** The species *Palaeobotrychium carbonicus* has many features in common with the modern representatives of the order Ophioglossales, especially with the genus *Botrychium* Sw. The new genus *Palaeobotrychium* is very similar to *Botrychium* in the

thick and relatively smooth rachis of the fertile frond (Fig. 11 E, B), in shape and size of the sporangia (Fig. 11 A, B, F), longitudinal position of the sporangial split and morphology of the spores (Fig. 11 D). One more important character, which can be used as a basis for certain phylogenetical conclusions, is the shape of the fertile pinnules of *Palaeobotrychium*, which is very similar to the fan-shaped pinnules (ultimate segments) of the sterile frond of the recent *Botrychium* (Fig. 11 E). This similarity can be explained by the presence of such fan-shaped fertile pinnules of the hypothetical ancestral ‘pre-*Botrychium*’ fern, which then was reduced into the fertile leaf of the recent species of *Botrychium* practically lacking the leaf blade of the fertile pinnules (Fig. 11 A, B, F). The genus *Palaeobotrychium* gen. nov. can be interpreted as such ‘pre-*Botrychium*’ ancestor. As a matter of fact, some parts of the leaf blade are preserved in modern *Ophioglossum* L. (Fig. 11 C).

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