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Piterophyton gen. nov., a new genus of archaic land plants from the Upper Ordovician deposits of the European part of Russia

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Summary: A new genus *Piterophyton* Naug. of psilophytalean (= rhyniophytalean) affinity is established on the basis of a representative collection of plant fossils from the Upper Ordovician deposits of the Leningrad region, north-western area of the European part of Russia. This new genus is represented by the single species *Piterophyton caudatum* Naugolnykh, gen. et sp. nov. The collection studied includes more than twenty stems, some of them are fertile. General questions of early evolutionary phases of the land plant's evolution are discussed in the context of forming of the first soils and appearance of links between soils and various elements of the Early Paleozoic terrestrial paleoecosystems.

Keywords: early plant evolution, psilophytes, new taxa, reproductive organs, paleobotany

North-western regions of the European part of Russia are well-known among broad geologic and paleontological public due to the wide distribution of Lower Paleozoic, mostly Ordovician deposits there. These deposits practically are not metamorphosed and are very weakly changed diagenetically, and therefore they provide perfect subjects for paleoecological observations.

New data from the Ordovician deposits of north-western areas of the European part of Russia (Naugolnykh 2008, 2019) and adjacent regions of Baltica (Cocks & Torsvik 2005) added an extended fact-based basis for reconstructing of the first stages of 'terrestrialisation' of the near-shore Early Paleozoic biotas.

The idea that the terrestrial plants had appeared before Silurian period has a long history (Kozlovski & Greguss 1959; Obrhel 1959, 1968; Richardson 1988; Kenrick & Crane 1997; Crane et al. 2004; Wellman 2004; Retallack 2009; Kenrick & Strullu-Derrien 2014; Raevskaya et al. 2016), although the real fossil records of the pre-Silurian plants, which were adapted for living outside of aquatic conditions/environments, are rather rare. Recent decades have deloped new evidence on the land plants found in the Ordovician deposits around the globe, including well-documented moss-like plants from the Platteville Formation of Wisconsin (Cardona-Correa et al. 2016). Some of the putative higher plants were reported from the Ordovician deposits of Kazakhstan much earlier (Snigirevskaya et al. 1992).

The present paper deals with a new discovery of a higher plant of psilophytalean (= rhyniophytalean) affinity found in the Upper Ordovician deposits of the Leningrad region, Russia. This new finding unequivocally shows that already in the Ordovician time the terrestrial plants colonized dry or seasonally wet areas and littoral low-lands of 'Paleo-Baltica'.

Geological settings, materials and methods

The material studied was collected by the present author during the field season 2021 and originates from the Volgovo section, located in the Leningrad region (geographical coordinates: 59°33'38.7"N 29°36'20.1"E; GPS coordinates: 59.560738, 29.605590).

The Volgovo locality is located 1 km eastwards of the Volgovo village. It is an old quarry wall 7 m high and approximately 10 m long (Fig. 1). General stratigraphic and paleontologic data on the Upper Ordovician (Sandbian) deposits outcropped in the Volgovo section are published in broad paleogeographic context (Terentiev & Gorshenina 2017).

The upper part of the section is represented by the Pleistocene fluvial-glacial deposits consisting of sandy-clay matrix with erratic granite and gneiss stones of different size, varying from one to 20–30 cm in diameter. The observed/visible thickness of the Pleistocene deposits of the Volgovo section is about 4 m.

The Pleistocene deposits are covering/lying above the Upper Ordovician carbonate deposits of mixed heterogenic origin. The Ordovician part of the Volgovo section is described in detail below. The description is made in 'layer-by-layer' style (Fig. 1), from the lower part of the section (layer 1) to the upper part of the section (layer 6).

Layer 1. Massive mudstone of pale-grey to pale-yellowish color, with scarce and badly preserved organic remains, mostly brachiopods and the rare partly disintegrated trilobite carapaces. The observed thickness of layer 1 is 2 m.

Layer 2. Layer 1 is transforming very gradually into layer 2, which is represented by platy marl and mudstone of dark-grey color. The platy mudstone-sand marl of this layer include rare, although well-preserved plant macrofossils described in the present paper as *Piterophyton caudatum* Naugolnykh, gen. et sp. nov. (Figs 2A–G; 3A–F; 4A–G; 5A–F). Thickness of layer 2 is about 20 cm.

Layer 3. Layer 2 is very gradually transforming upwards into layer 3, which is represented by dark-grey, almost black marl and siltstone with a high percentage of organic matter most probably of plant origin. There are numerous plant macro- and mesofossils in layer 3. A sample of the organic-rich siltstone was macerated and processed by means of the 'Three-filters' approach (Naugolnykh 2015; details see below). Various meso- and microfossils were extracted from the matrix. The plant remains obtained as a result of maceration include small fragments of stems conspecific with the stems of *Piterophyton caudatum* (Fig. 6A–H), including the conducting tissues/tracheids (Fig. 6D), isolated cuticles and spores (Fig. 7A–F). A detailed description of these remains is in the taxonomic part of the present paper. Thickness of layer 3 is not equal and varies from 7 cm to 15 cm.

Layer 4. The boundary between layer 3 and layer 4 is not smooth, but distinct. Layer 4 is represented by massive and dense mudstone of pale-rose to grey color. It includes bright dark-red or 'bordo' spots formed by dispersed hematite. Most of the spots are connected by their margins and form a belt-like horizontal zone at the lower part of layer 4. Layer 1 (especially the uppermost part), together with layers 2–4 are dissected by the deep wedge-shaped vertical cracks marked by the bright 'bordo' to dark-red color. According to my opinion, these cracks are ancient and can be interpreted as cracks of desiccation, and these cracks were formed in aerial conditions already in the Late Ordovician time.

Layer 5. The boundary between layers 4 and 5 is smooth and not well-pronounced. Layer 5 is represented by mudstone and dolostone superficially similar to the mudstone of layer 4, but without bright red spots and without well-formed 'aerial' cracks of desiccation. In contrast to layers 1–4, layer 5 contains numerous macrofossils of marine invertebrates, i.e. brachiopods

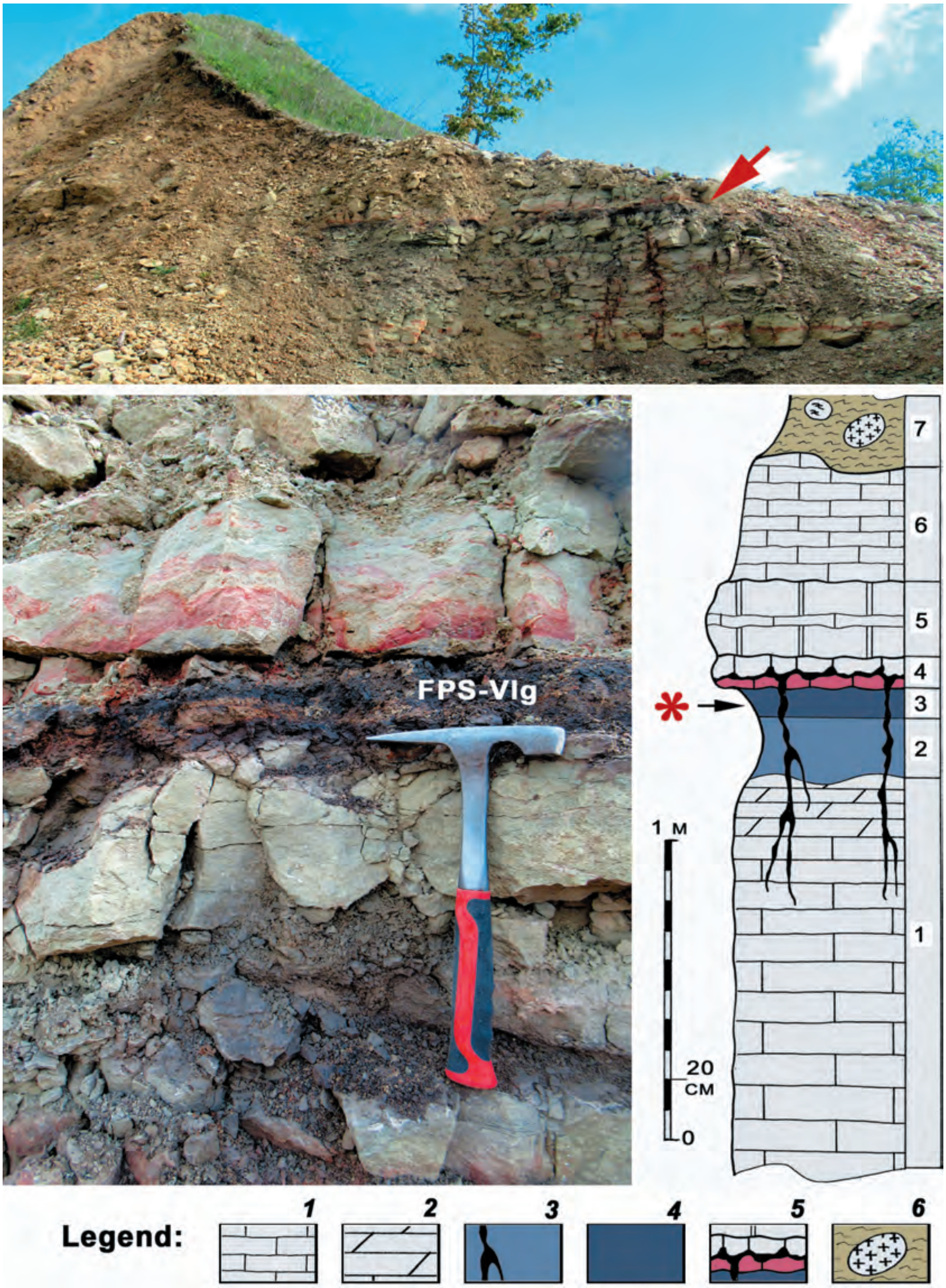

Figure 1. The Volgovo locality; Upper Ordovician, the Sandbian Stage. Left – general view on the fossiliferous bed; right – stratigraphical log of the Volgovo section; FPS-Vlg – the fossil paleosoil profile (the palesol or palaeosole). 1 – mudstone (with double vertical lines: dolostones); 2 – marl; 3 – lower part of the FPS-Vlg profile, dissected by the ancient aerial cracks incrusted by oxides of iron; 4 – upper part of the FPS-Vlg profile; 5 – carbonate crust covering the FPS-Vlg profile and deeply incrusted by oxides of iron; 6 – Pleistocene fluvioglacial deposits. The level with *Piterophyton caudatum* Naugolnykh, sp. nov. is marked by the red asterisk. The scale is in the figure.

and trilobites. The calcified green algae *Cyclocrinites* Eichwald are present in this layer as well. Thickness of layer 5 is 25–30 cm.

Layer 6. Layer 6 is represented by mudstone of pale-grey color. No well-preserved fossils have been found here. The boundary between layers 5 and 6 is not well-defined, smooth and gradual. Upper part of layer 6 is corroded by weathering and split into separate fragments of mudstone. Layer 6 is covered by relatively soft Pleistocene fluvioglacial deposits.

One important sedimentological/lithological feature of the Volgovo locality should be noted in context of further discussion. There are at least two stratigraphical levels or actually the surfaces of bedding, which demonstrate the clear marks of affection in aerial or subaerial conditions. These affections certainly took place in time of the deposit formation. First of all, we detect the presence of numerous cavities formed as a result of dissolving of the consolidated carbonate crust (Fig. 1, layers 2 and 4). This kind of surface weathering was possible in aerial conditions only.

The cuticles and spores described and figured in the present paper were extracted from the matrix by means of the 'Three filters' approach (Naugolnykh 2015) by using three filters (10, 25 and 126 µm grid cell size) for segregation of disintegrated sediment.

The collection studied includes more than twenty plant remains. Twelve of them are of good quality and are figured and described in detail in the present article. The collection studied is kept at the Monographic Department of the Darwin State Museum, Moscow.

Paleobotanical description

Division **Psilophyta (= Rhyniophyta; Psilophytophyta) Zimmermann, 1930**
Classis **Rhyniopsida Krishtofovich, 1925**
Order **Rhyniales Zimmermann, 1959** (= Cooksoniales Doweld, 2001)
Family Incertae Sedis

Genus *Piterophyton* Naugolnykh, gen. nov.

Etymology. After 'Piter', an informal name for the City of Sankt-Petersburg and after Russian tzar Peter I the Great.

Type species. *Piterophyton caudatum* Naugolnykh, sp. nov.

Comparison. The new genus differs from the most similar genus *Volkhoviella* Naugolnykh in a larger size of stems and sporangia and in a completely smooth surface of the stems in contrast to the stems of *Volkhoviella*, which bears spirally arranged flattened thickenings (Naugolnykh 2019, Fig. 2 e–h).

Diagnosis. Same as for the type species.

Composition. Type species.

Distribution. Middle Ordovician of the north-western areas of Russia and adjacent regions.

Piterophyton caudatum Naugolnykh, sp. nov.

Etymology. From *caudatum* (Latin) – tailed, after tail-like ground-surfacing stolons of the plant.

Holotype. No. VLG-1/D1, figured here on Figs 2D and 4D1; the Volgovo locality, Middle Ordovician, European part of Russia [Monographic Dept., Darwin State Museum, Moscow].

Diagnosis. Stems protostelic, simple or dichotomizing up to three times, straight to slightly curved. Stem surface smooth. Sporangia round to ovoid, hemispherical, terminal or rarely lateral. Vertically orientated stems unite both dichotomous and monopodial types of branching. Basal parts of vertical stems with H-type and K-type branching. Lower parts of stems form horizontal stolons. Spores round, large (up to 170–300 μm in diameter), with smooth to finely scabrate sporoderm surface.

Description. The most representative specimen of the collection studied and selected as the holotype (VLG-1) is an almost complete stem with a long and narrow above-ground stem and a branched basal stolon (Figs 2D1; 4D1). General length of the specimen is circa 100 mm, average width of the stem is more or less permanent in the stem (about 2–2.5 mm). Surface of the stem is smooth. Apical portion of the stem is widening and forming an ovoid structure, which can be interpreted as a weakly developed terminal sporangium. Width of the sporangium is 3 mm, length is 4 mm. Basal part of the stem (stolon) is curved and orientated to the possible above-ground portion under an open angle of 115°. The basal part bears three appendages of the same width, possibly once functioning as rhizoids. Mode of the stolon branching is similar to H-type or K-type branching typical of many psilophytes (Schweitzer 1979, 1988, 1990, 2003) and also observed in some other specimens of *Piterophyton caudatum* (see details below). Just near the holotype, one can see isolated slightly curved apical portion 6 mm long and 1.5 mm wide with the ovoid sporangium almost identical to the sporangium preserved in natural connection to the holotype, but slightly shorter. Sporangium is 3 mm long and 3.2 mm wide. Thus, the sporangium is of 'mushroom' shape.

Another representative specimen of *Piterophyton caudatum* (VLG-2) is a stem with one completely preserved above-ground portion and the basal part (stolon) bearing one more above-ground stem in its middle part, but only with its lower part preserved (Figs 2F; 4F). Length of the stem is 74 mm, width is 1.8–2 mm. Apical part of the stem bears a terminal sporangium of ovoid shape, 3 mm long and 2.5 mm wide. Other specimens in hand show practically the same morphological features as the two individuals described above, but less definitely. Some notable specimens are characterized below.

Well-preserved above-ground stem (VLG-3) with apical dichotomy, bearing 'mushroom'-shaped terminal sporangium should be specially noted (Figs 2B; 4B). Length of the observed stem fragment is 30 mm; the width varies from 4 mm at the basal part of the stem to 2 mm just beneath the sporangium, where the stem become narrow and somewhat contracted. Sporangium is 2 mm long and 4 mm wide. There are small round spots inside the place corresponding to the inner cavity of the sporangium. Average diameter of the spots is 200 μm. Thus, the size and shape of the spots fit well the size and the shape of the spores extracted from the matrix containing the remains of *Piterophyton caudatum* (Fig. 7A–F), but the insufficient preservation of the in situ spores hinders their exact and unequivocal interpretation. One more specimen (VLG-6) shows apical dichotomy with two resulting branches, each bears a small undeveloped terminal sporangium (Figs 2E; 4E). Length of this stem fragment is 21 mm, average width of the stem is 1.5 mm. The sporangia are more or less isometric, round, of similar shape and size, reaching 1.9 mm in diameter. The very important specimen (VLG-10) shows the inner structure of the stem (Fig. 3F). One can see three well-defined zones of the stem: central dense zone, most probably formed by conducting tissues (see the description of preparation below), mid-zone of inner bark and outer dense zone corresponding to the periderm or outer bark. The length of this stem fragment is 26 mm. The width of the stem varies from 2 mm at its base to 0.8 mm at its

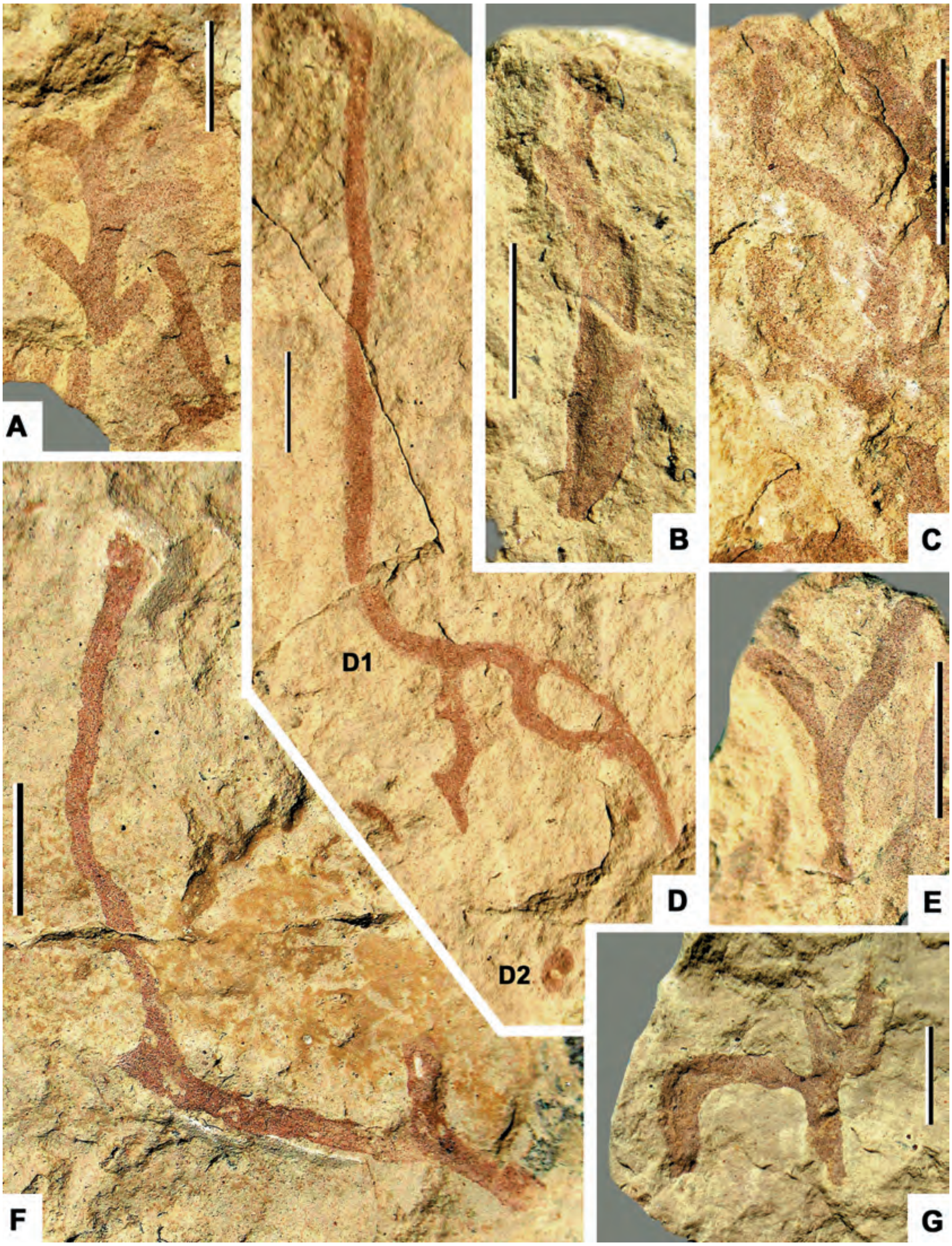

Figure 2. *Piterophyton caudatum* Naugolnykh, gen. et sp. nov. Macromorphology. A – spec. No. VLG-4; B – spec. No. VLG-3; C – spec. No. VLG-5; D – holotype No. VLG-1/D1; E – spec. No. VLG-6; F – spec. No. VLG-2; G – spec. No. VLG-7. The Volgovo locality; Upper Ordovician, Sandbian. Scale bar = 1 cm.

apical part. Macromorphologically more representative counterpart (VLG-8) of the same plant individual bears small a terminal sporangium of ovoid shape (Figs 3A, E; 5A, E). The sporangium is 4 mm long and 2 mm wide.

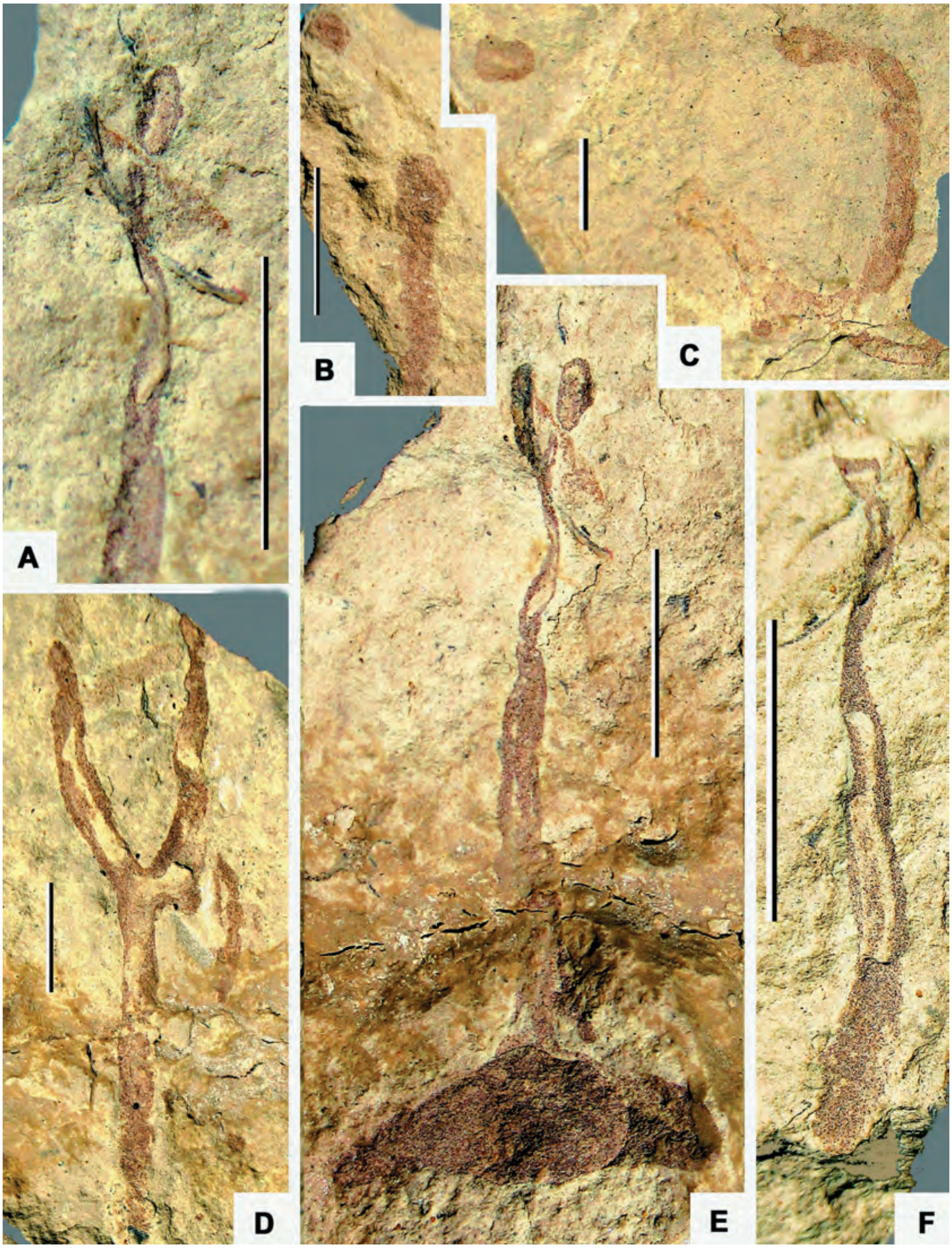

Figure 3. *Piterophyton caudatum* Naugolnykh, gen. et sp. nov. Macromorphology. A, E – spec. No. VLG-8; B – spec. No. VLG-11; C – spec. No. VLG-9; D – spec. No. VLG-12; F – spec. No. VLG-10. The Volgovo locality; Upper Ordovician, Sandbian. Scale bar = 1 cm.

There is a specimen (VLG-5) with two laterally disposed fertile branches (Figs 2C; 4C) showing that the structure of the above-ground stems was more complicated as one can suppose on the basis of the holotype only. The branched stem is 21 mm long and 1 mm wide. Both sporangia

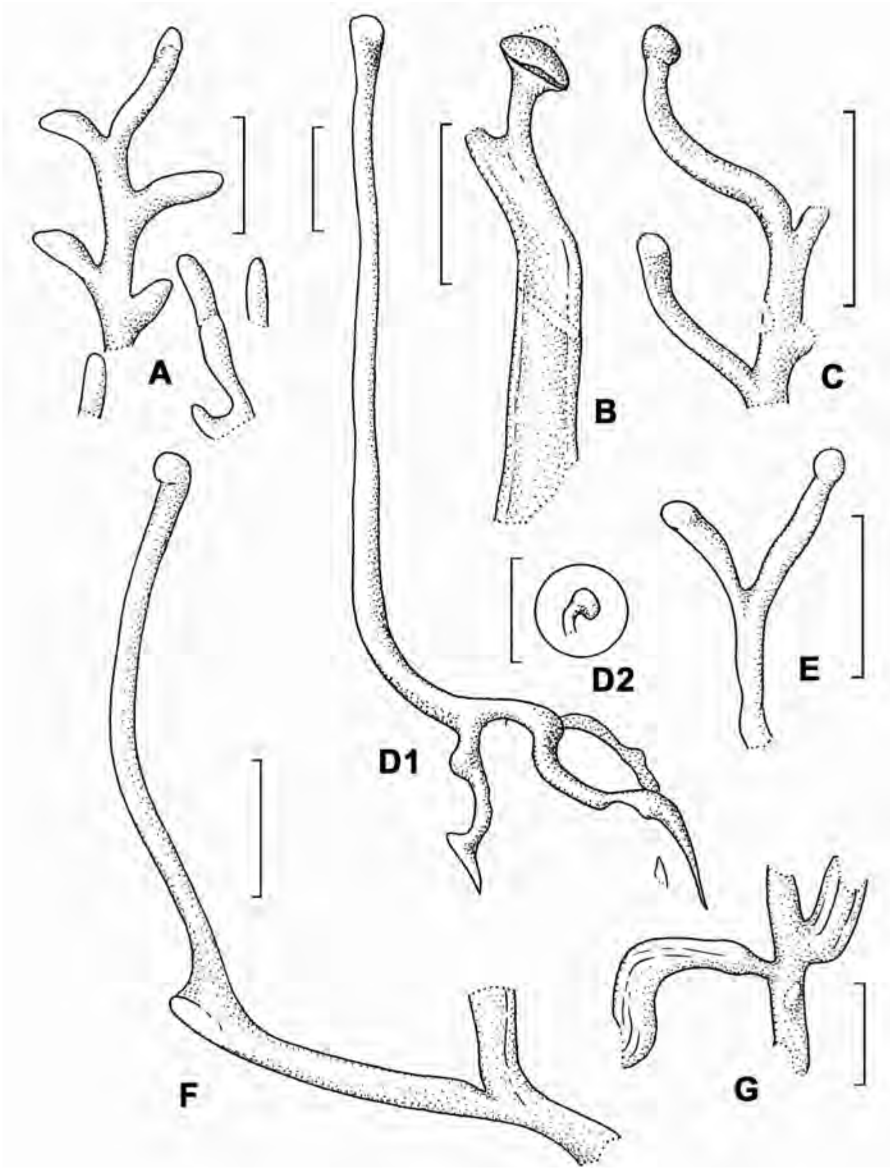

Figure 4. *Piterophyton caudatum* Naugolnykh, gen. et sp. nov. Macromorphology, line tracings. A – spec. No. VLG-4; B – spec. No. VLG-3; C – spec. No. VLG-5; D – holotype No. VLG-1/D1; E – spec. No. VLG-6; F – spec. No. VLG-2; G – spec. No. VLG-7. The Volgovo locality; Upper Ordovician, Sandbian. Scale bar = 1 cm.

are very similar to each other and are of almost one and the same size and ovoid shape. Length of the sporangia is 2 mm, width is 1.5 mm, but the upper sporangium is slightly more definitely pronounced than the lower one. Mode of the stem branching is monopodial. Thus, the species unites both dichotomous and monopodial types of branching. The angle of attachment of both lateral branches to the main stem is one and the same: 50°.

Another specimen (VLG-4) with monopodial branching is shown in Figs 2A and 4A. Observed length of this stem is 22 mm, average width is 1.8 mm. The stem shows five lateral appendages of various length. The appendages disposed on the left (according to position of Figs 2A; 4A) side of the stem are 6 mm long (lower branch) and 4 mm (upper branch). The appendages placed on

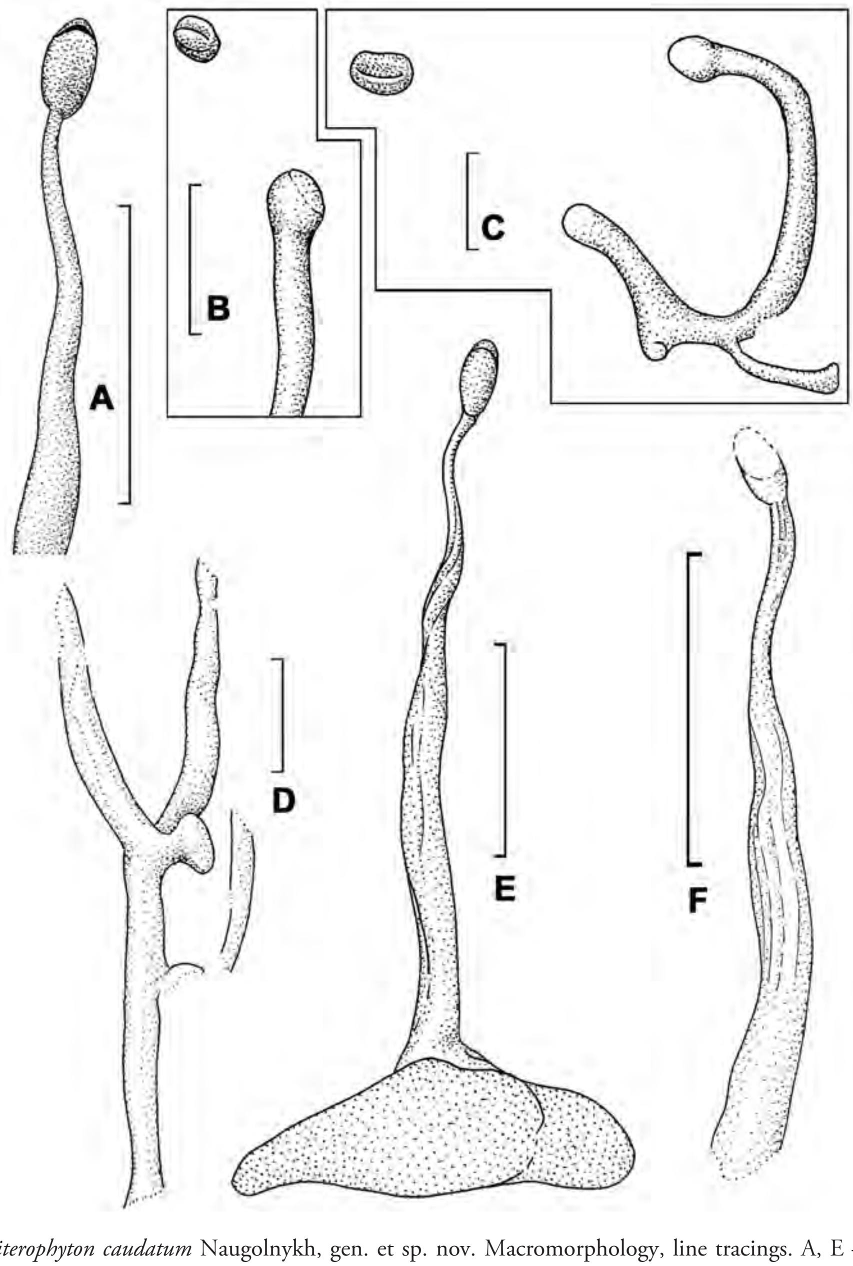

Figure 5. *Piterophyton caudatum* Naugolnykh, gen. et sp. nov. Macromorphology, line tracings. A, E – spec. No. VLG-8; B – spec. No. VLG-11; C – spec. No. VLG-9; D – spec. No. VLG-12; F – spec. No. VLG-10. The Volgovo locality; Upper Ordovician, Sandbian. Scale bar = 1 cm.

the right side of the stem are 4 mm (lower branch), 2 mm (incomplete length; middle branch) and 8 mm (upper branch). The angles of the branch attachments to the main stem are more or less close to each other and vary from 40° to 50°. There is one more specimen (VLG-7) showing monopodial branching, but in contrast to the stems described above it is slightly thicker (width of the lateral appendage reaches 4 mm) and the left lateral appendage strongly curves downwards (Figs 2G; 4G).

There is one fertile specimen (VLG-9) with a distinct H-type or K-type of branching (Figs 3C; 5C). The most well-developed above-ground stem of this specimen is slightly arc-shaped curved and

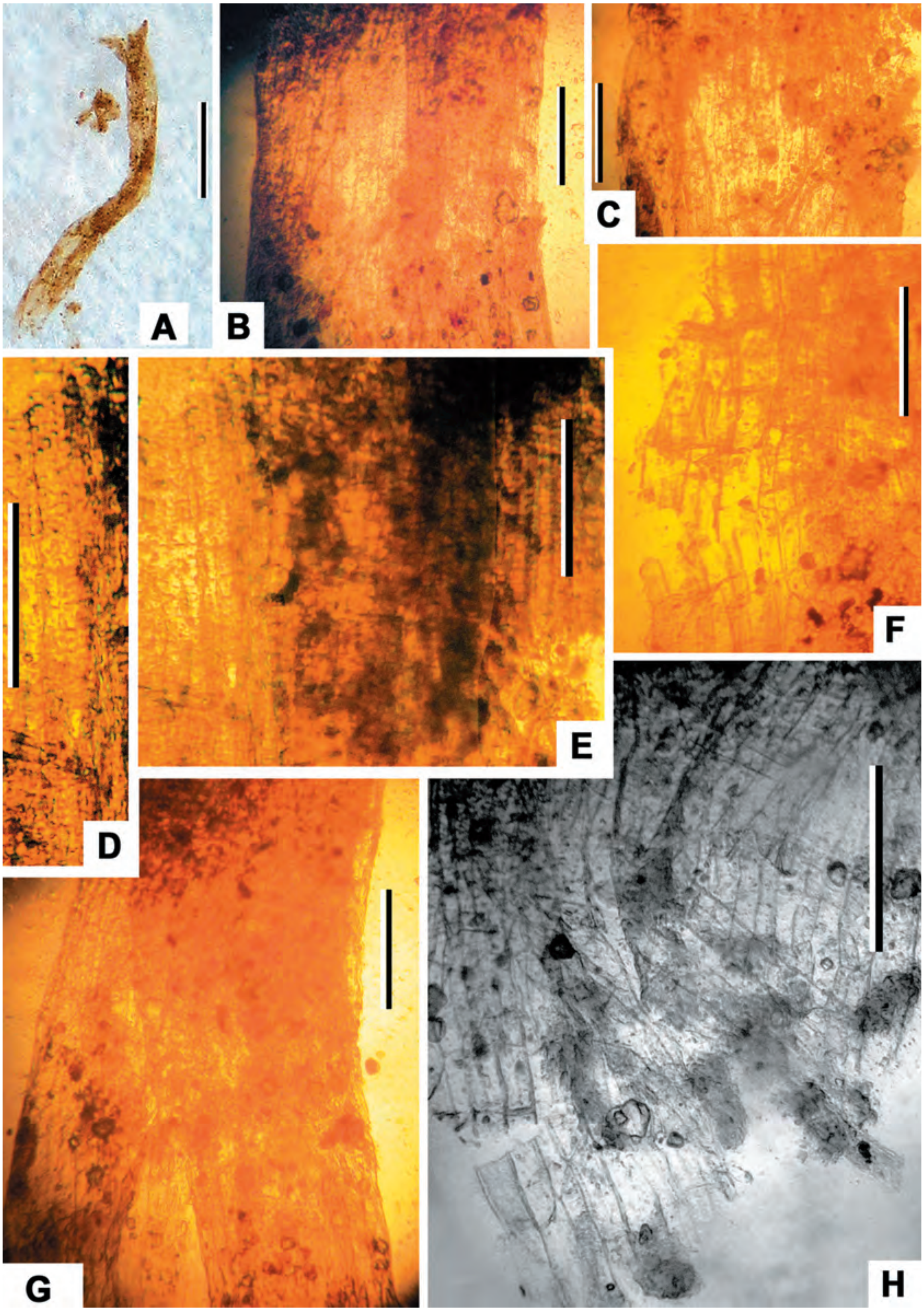

Figure 6. *Piterophyton caudatum* Naugolnykh, gen. et sp. nov. Micromorphology; epidermal – cuticular structure. Spec. No. VLG-Prep 1. A – apical part of a stem; B, C, E, G – cuticles of the middle part of the stem, figured here in Fig. 6A; D – a tracheid with stair-like thickenings; F, H – epidermal cells of rectangular outlines. The Volgovo locality; Upper Ordovician, Sandbian. Scale bar = 1 mm (A); 100 µm (B–H).

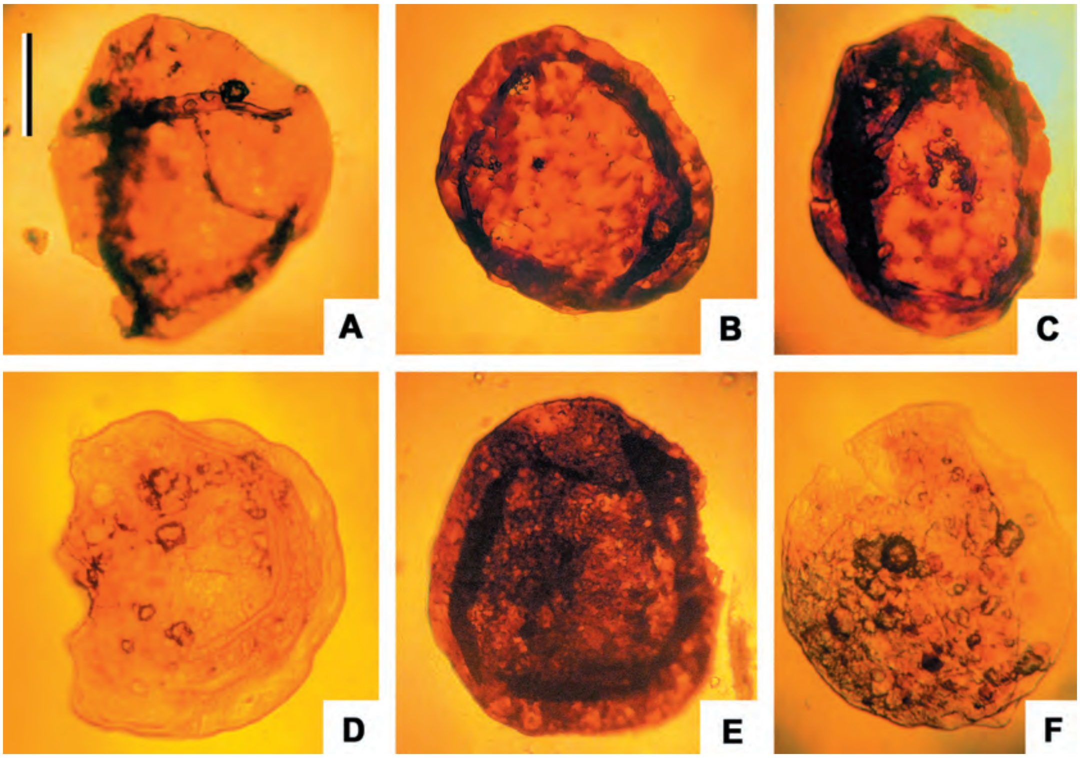

Figure 7. *Piterophyton caudatum* Naugolnykh, gen. et sp. nov., isolated spores extracted from the matrix. The Volgovo locality; Upper Ordovician, Sandbian. Scale bar = 100 μm (A–F).

bears a terminal sporangium of ovoid shape. General length of the specimen is 40 mm, width is 3 mm. The terminal sporangium is 6 mm long and 3.5 mm wide. One more sporangium preserved in isolated state is visible on the same sample near the fertile stem. This sporangium is practically identical to the sporangium preserved in natural connection to the stem, but the isolated sporangium demonstrates a clear narrow split (Figs 3C; 5C, left upper corner), most probably responsible for releasing mature spores. Length of the completely preserved lateral branch (left in Figs 3C; 5C) is 22 mm. The basal part of this branch is somewhat contracted just near its attachment to the main (axial) stem.

Another specimen (VLG-11) combining the fertile stem and isolated sporangium preserved near the stem is shown in Figs 3B and 5B. Length of the observed portion of the stem is 19 mm, the width is 2 mm. The sporangium preserved in natural connection to the stem is 4.5 mm long and 3 mm wide. The isolated sporangium is almost of the same size and shape, but has a well-defined narrow split, which is most likely responsible for the opening of the sporangium, when it was adult. The identical split is visible in the isolated sporangium (described above; Figs 3C; 5C, left upper corner).

One more important specimen (VLG-12) is shown in Figs 3D and 5D. This specimen demonstrates a dichotomous (isotomous) stem with the 'mushroom'-shaped sporangium, which is laterally disposed at the place of dichotomy. General length of this specimen is 55 mm, average width is 3 mm. The angle of dichotomy is 45°. Length of the sporangium is 3 mm, width is 4 mm. Partly detached outer tissues of the left branch (according to position in Figs 3D; 5D) clearly

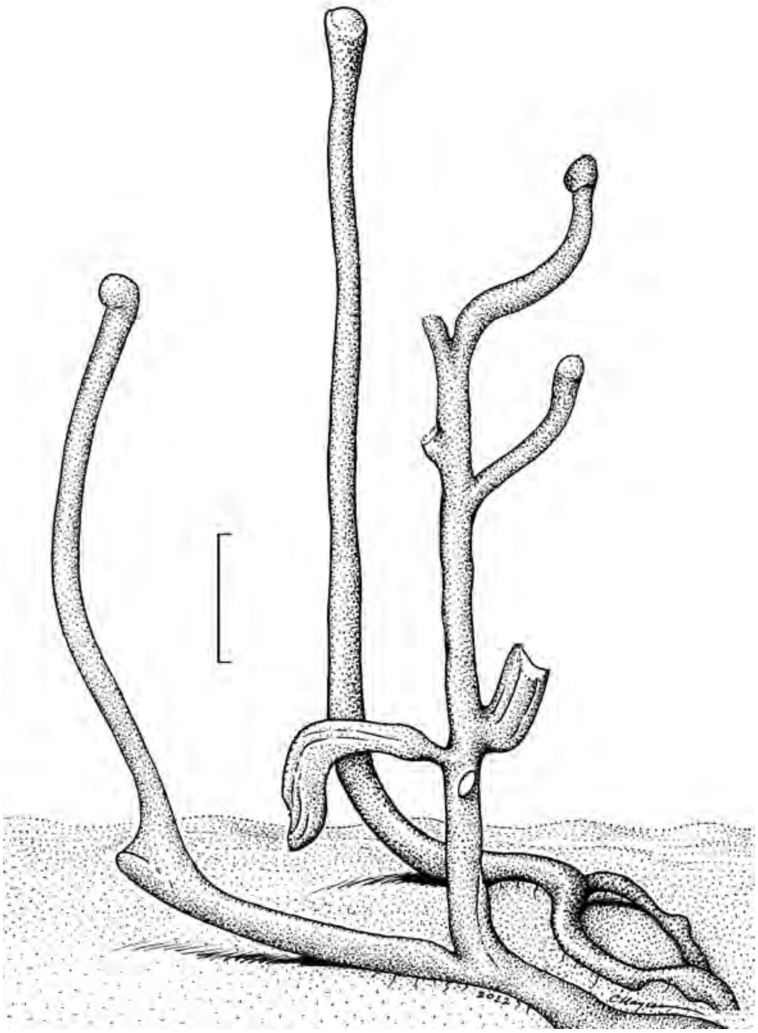

Figure 8. *Piterophyton caudatum* Naugolnykh, gen. et sp. nov.; reconstruction of the plant. Late Ordovician, Sandbian. Scale bar = 1 cm.

show that the stem had dense outer tissues covering soft inner tissues, which are partly replaced by carbonate-clay material. Thickness of the outer tissues is 0.4 mm. Most likely, the outer tissues represent a periderm or bark of the plant.

One young stem was extracted from the matrix almost completely (Fig. 6A). Length of the stem is 3.5 mm, width is 0.5 mm. Apical part of the stem is widening and perhaps corresponds to the damaged and undeveloped sporangium. Although size of this stem is smaller than size of the other available specimens, its general morphology allows attributing this specimen to the same species.

The stem is covered by a well-preserved cuticle (Fig. 6B, C, E–H) with clear cellular structure. The epidermal cells are prolonged by more or less rectangular outlines. Cell sizes vary from 20×60 µm up to 30×120 µm. Both periclinal and centriclinal (radial) cell walls are smooth, straight or slightly curved. Tracheids (Fig. 6D) are observed in this specimen as well. They are 30 µm in diameter, with stair-like thickenings on the tracheid walls. The presence of both cuticles and tracheids leaves no doubt that *Piterophyton caudatum* should be attributed to higher plants.

Numerous spores (Fig. 7) were extracted from the matrix with *Piterophyton caudatum* stems. The spores are round, 170–300 µm in diameter. Sporoderm is smooth (Fig. 7A, D) to weakly scabrate (Fig. 7B, C, E, F). Although no clear well-defined trilete mark is observed on the spores, some of them (Fig. 7A, D) bear unclear suture in the center of the presumably proximal side. Dispersed spores of the same morphological type were reported from the Ordovician deposits of Sweden (Rubinstein & Vajda 2019).

All the specimens studied were used as an integrative basis for preparing a reconstruction of the plant *Piterophyton caudatum* (Fig. 8). According to the author's viewpoint, this plant apparently grew in near-water Late Ordovician paleoenvironments of Paleo-Baltica and surrounding areas.

Comparison and remarks

Piterophyton caudatum Naugolnykh, gen. et sp. nov. described above has many features in common with the fertile stems of *Sporogonites* spp. from the Lower Devonian deposits (the Baviaanskloof Formation of Table Mountain Group, Cape Supergroup) of South Africa (Gess & Prestianni 2021), but the absence of the spore and cuticles of the African plant predicts a detailed comparison of both plants. The new plant is similar to *Volkhoviella primitiva* Naugolnykh, but differs in larger size of the stems and sporangia of *P. caudatum* and also in a completely smooth surface of the stems in contrast to the stems of *Volkhoviella*, which normally bears spirally arranged flattened thickenings (Naugolnykh 2019: Fig. 2e–h). Concerning general morphology of *P. caudatum*, as it was briefly mentioned above, the ground horizontal 'caudal' stolons of *P. caudatum* stems with up-rising vertical fertile stems have many features in common with a large number of other Early and Middle Paleozoic plants of psilophyte or 'rhyniophyte' affinity (Ananiev 1959; Schweitzer 1979, 1987, 1988, 1990; Kenrick & Crane 1997; Taylor & Taylor 1993; Taylor et al. 2009; Hao & Xue 2013; Libertin et al. 2018; Naugolnykh 2021; Oukassou & Naugolnykh 2021). Judging from the presence of other rare plant remains on the same slabs, but of different morphology (flattened and wider stems or thalli), there is at least one more plant of possible psilophytic or algal affinity in the Volgovo locality, but the characterization of this plant is beyond the scope of the present paper.

Discussion

Theoretical basement of appearance of terrestrial adaptations in evolution of intermediate forms between advanced algae and archaic tracheophytes (vascularized/higher plants) certainly needs the undoubted evolutionary links between algae and tracheophytes. But the real fossils of such intermediate forms are very rare. What is more, we do not have any real plant in the modern world, which can be regarded as related to intermediate forms between algae and tracheophytes. But in the same time it is obvious that algae (namely green algae or Chlorophyta) and tracheophytes were linked evolutionary, and the tracheophytes had originated from algae somewhere deep in the geologic history. The exceptions in modern world are lichens with a deeply integrated symbiosis between fungi and algae, but the lichens are too highly specialized for considering them as actual intermediate forms. Nonetheless, there are several plant taxa known from Silurian and Devonian deposits around the world, which demonstrate a mixture of morphological and anatomical features, typical of both algae and tracheophytes. The most well-known plants of this type are so-called 'spongiophytes', represented by several genera, such as possibly synonymous *Shuguria* Tchirkova-Zalesskaya and *Orestovia* Ergolskaya (Krassilov 1981; Krassilov & Polevova 2012).

Early evolutionary phases of the land plants' evolution were closely linked to the formation of the first soils, which appeared due to accumulation of organic matter in terrestrial low-lands and active influence of the organic acids on the clastic substrates on land. Further development of links between soils and various elements of the Early Paleozoic terrestrial paleoecosystems, such as plants and invertebrates (mostly arthropods) lead to the formation of an integrative system with feedback effects between biota and soil.

Paleogeographically the region studied was located near the southern margin of Fennoscandia, located in the Baltica terrain/microcontinent (Cocks & Torsvik 2005: Figs 6, 7). This marginal zone was temporally covered by a shallow-water basin and cyclically exposed in aerial conditions, what created conditions for paleosol (FPS) forming there and the subsequent development of hygrophilous terrestrial biota.

Our knowledge on *Piterophyton caudatum* Naugolnykh, gen. et sp. nov. is enough to attribute this plant to tracheophytes with all confidence, concerning the presence of spores, cuticles and conducting tissues with tracheids. All these data allow to consider *Piterophyton caudatum* as a representative of Psilophyta (= Rhyniophyta), as *Volkhoviella primitiva* Naugolnykh previously described from the Ordovician of the same region. But both *Piterophyton caudatum* and *Volkhoviella primitiva* are still very close to algae and thus can be regarded as possible intermediate forms between algae and typical tracheophytes.

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