

New Fossil Plant from the Late Devonian Strata of Northern Timan (Russia)

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Abstract—Remains of a new fossil plant *Petrosjania salarina* gen. et sp. nov. were found in the Upper Devonian deposits of the Northern Timan (eastern coast of the Chosha Bay of the Barents Sea). This plant has a number of features characteristic of different groups of higher plants: Barrandeinoid stems (characteristic of the Barrandeinales), flabelloid leaves on stems (Devonian groups *incertae sedis*) and perfoliate leaves (characteristic of many plants, including horsetails), fibrous root system (typical for Pteridophyta, Monocotyledones). The systematic position of the new fossil plant, its morphology and possible relationships are discussed.

Keywords: Late Devonian, Barrandeinales, *Petrosjania* gen. nov., flabelliform leaves, fibrous root system, Northern Timan

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INTRODUCTION

Northern Timan with its diverse complex of deposits formed in the conditions of a vast delta of a large river under the strong influence of tidal processes: multidirectional currents and rhythmic fluctuations in sea level (Beznosov et al., 2018, 2021) is one of the classic localities of Late Devonian floras of global significance (Snigirevsky, 1997b). Localities of plant fossils are known almost everywhere along the eastern shore of the Chosha Bay of the Barents Sea and the Volonga, Velikaya, Peschanka, Sula, and Pesha rivers and their tributaries, as well as smaller streams (Fig. 1).

The preservation of the remains is in most cases very good. Many of the fossil plants are new and are considered endemic. Snigirevsky (1997a) described the history of paleobotanical research in Northern Timan.

MATERIAL AND METHODS

The vast majority of large fragments of the new plant were found in pinkish-gray siltstones overlying the ridges of the coastal sandbar of the Late Devonian basin. These sandbars stretch in relatively narrow stripes in the direction from north to south (in the current orientation) and are indicators of the coastal environment in the paleobasin. The presence of overlying siltstones indicates shallowing of the landward parts of the basin and the formation of shallow-water or sub-

aerial environments (Snigirevsky et al., 2020; Beznosov et al., 2021).

Numerous smooth, monopodially branching axes of the new plant were found in the siltstones. When splitting, carbonaceous crusts were separated from several axes of these plants, which were studied using a Hitachi-3000 scanning electron microscope (Figs. 2a, 2b).

The plant remains described in the work come from deposits of the Upper Devonian Ust'e Bezmoshitsa Formation, exposed along the coast of the Chosha Bay (2.5–3 km north of Cape Vostochny Ludovatyj Nos), as well as in the upper reaches of the Sula River (Fig. 1) (collections by L.S. Kossovoj, 1956–1964, N.B. Kosykh, 1993 and the present authors, 1993, 2019). Based on the miospore and vertebrate assemblages, these deposits are correlated with the Sirachoy Horizon of the Upper Frasnian Substage (Beznosov et al., 2021).

Unfortunately, due to the extreme size of the fragments of the described plant, only a few were collected: a rounded base, several fragments of the main stem with second-order lateral axes, a flabelloid leaf attached to the axis, as well as several fragments of lateral axes and large isolated leaves. The studied samples are housed in the Paleontological Museum of St. Petersburg State University (coll. PM St. Petersburg State University-21) and in V.L. Komarov Botan-

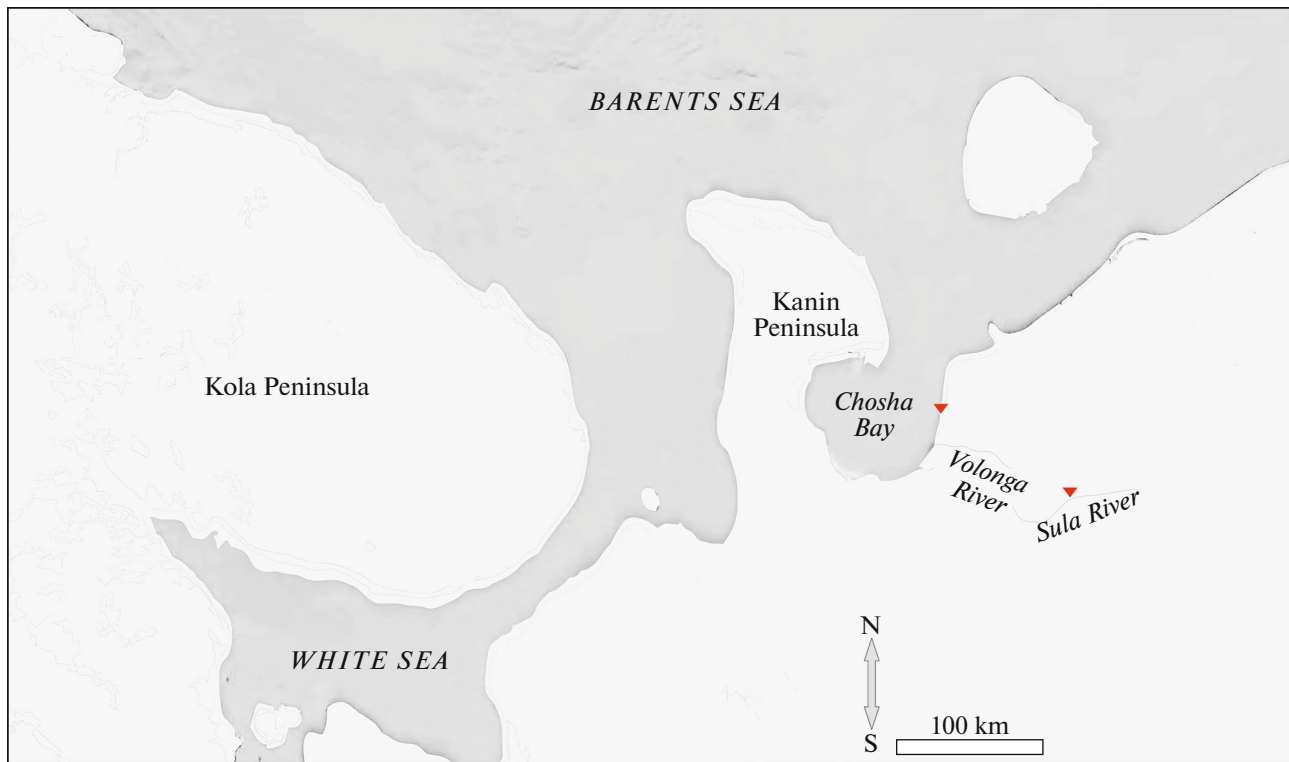


Fig. 1. Map showing localities.

ical Institute, Russian Academy of Sciences (coll. BIN 3212).

TAPHONOMIC OBSERVATIONS

Root systems arranged in wide circles (Pl. 11, figs. 1, 2) are observed on the siltstone bedding surfaces. There are about a dozen such root formations, which are the basal parts of the new plant. It is interesting that at a relatively high density (10 “circles” of the root systems of these plants over an area of about 60 m²), we did not find signs of paleosol reworking anywhere in the siltstones.

The expanded base during the life of the plant, most likely, was half immersed in sediment. The shoots were buried autochthonously, some of them subvertically, at the site of plant growth; other fragments were buried after having fallen to the surface of the sediment. At one of the sites, it was noticed that before burial the stem was slightly withered and bent, as evidenced by the longitudinal wrinkles on the stem and its bend, which are interpreted as postmortem. Also, a section of a horizontally located stem with very large branch scars was found in the autochthonous position. Its length is more than one meter. Its convex part has been preserved, filled with rock after the death of the plant and the decay of its tissues. This site, in addition to siltstone of the same composition as the host rock, contained numerous ribbon-like roots that

belonged to the same plant. Very often isolated leaves are found in the locality, which is why in some cases they can be confused with the large foliage of *Archaeopteris archetypus* Schmalhausen (see also the “Discussion” section), but their difference is a smooth rounded edge with an edge curved into the rock in *Petrosjania* gen. nov. (Pl. 12, fig. 3), and all the leaves of *Archaeopteris* are flat and their upper edge is sometimes weakly dissected, undulating, or not very prominent. This may indicate that the leaves of the new plant were tougher during life than the leaves of *Archaeopteris*. When burying the leaf margins of *Petrosjania* gen. nov. sometimes the leaf blades were bent and broken, which in some cases gave the impression of a thick, fleshy leaf.

TERMINOLOGY

The lower part of a large plant, reaching a height of three meters or more, was discovered in the fossil state; the root system and the lower part of the stem with second-order axes extending from it have been preserved; on the latter there are leaves of two types. Whorled leaves (Fig. 3; Pl. 12, figs. 1–3) with leaves forming a bell-shaped sheath (Osnoy..., 1963, p. 486). They were arranged in a fan-shape around the axes. It is easier to understand their appearance in the fossil state by imagining their lifetime form: it was a continuous bell-like sheath, first sheathing the stem, and then diverging upward and in different directions; in

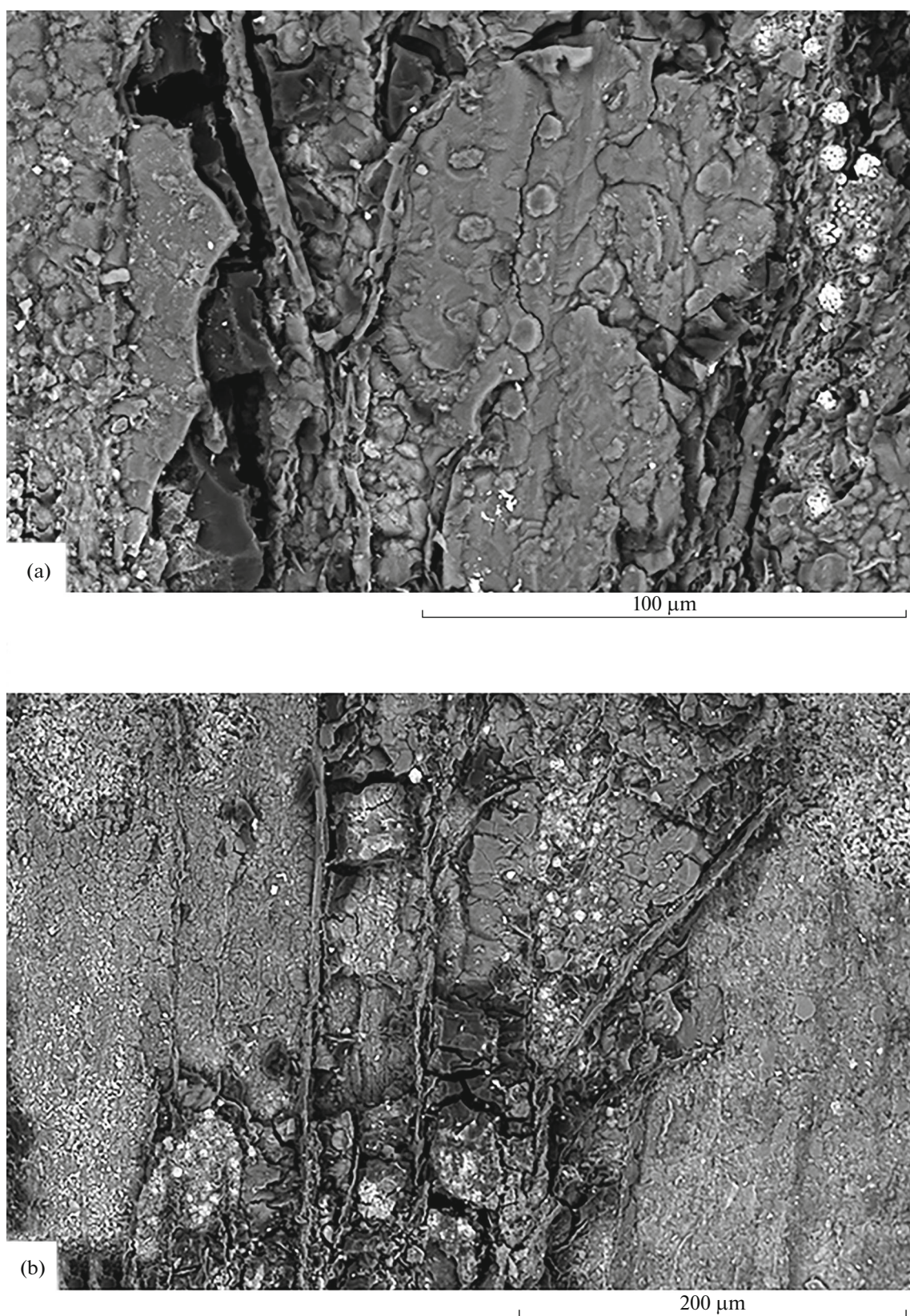


Fig. 2. *Petosjania salarina* gen. et sp. nov., specimen BIN 3212/49: (a) anatomical structure of vascular tissues of second-order axes, tracheid with simple pits; (b) outlines of tracheids from a carbonaceous pyritized crust in the area of the vascular root bundle; Russia, Nenets Autonomous Okrug, eastern coast of the Chosha Bay of the Barents Sea, approximately 2.5–3 km north of Cape Vostochny Ludovatyj Nos; Upper Devonian, Frasnian, Sirachoy Horizon, Ust'e Bezmoshitsa formation.

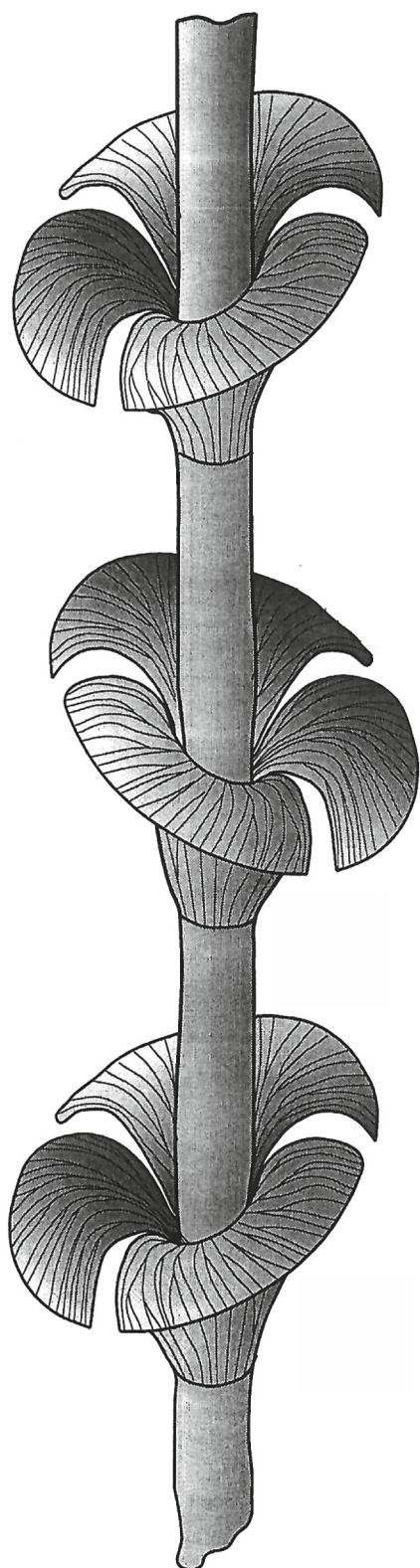


Fig. 3. *Petrosjania salarina* gen. et sp. nov., reconstruction of part of the axis with three perfoliate leaves (see Pl. 12, figs. 1, 2).

places, apparently due to growth, splitting into unequal segments (Fig. 3; Pl. 12, figs. 1–3). Another type of leaves of the new plant were flabelloid, sitting on long petioles at the bases of oppositely and monopodially branching axes. The term “flabelloid” or “flabelliform” leaves is used to describe the broadly fanned leaves of plants, the most typical example of which is the genus *Ginkgo* L.

When characterizing large isolated leaves of unclear taxonomy occurring from the Lower Devonian up to Permian and possibly Triassic deposits (Jurina and Putyatina, 1997, 2000), the generic name *Platyphyllum* (Dawson) White was widely used, which was replaced by Stone (1973) with *Flabellofolium* Stone. Previously, they were called “*Ginkgo*-like megaphylls”, “psymgophylloid foliage”, “platyphylls”, etc. After Høeg (1967) proposed the group Palaeophyllales Høeg of unclear systematic position, most of the isolated large leaves of the genera *Platyphyllum* (*Flabellofolium*), *Psymgophyllum* Schimper, *Ginkgophyton* Matthew, *Ginkgophytopsis* Høeg, *Ginkgophyllum* Saporta, *Enigmophyton* Høeg and others were assigned to it. Some of the flabelloid leaves were found in natural association with plant fragments, which, however, remained unclear. These are *Enigmophyton* and *Germanophyton* Høeg (Høeg, 1942). The nature of their attachment to the axes was usually not established anywhere, although it was implied in reconstructions (Høeg, 1942, text-fig. 25; Gothan and Weyland, 1954, text-figs. 61, 62).

At the site of drying or falling off (breaking off during the process of fossilization or during rock splitting) the perfoliate leaves formed transverse sinuous lines on the axes of the second order, similar to the nodal lines of sphenopsids. In this case, these are “false nodal lines”, corresponding to the place of attachment of leaves to the axes of the second or third order. The passage of thin ribs through these lines is not a taxonomic character: below the false nodal line they correspond to veins extending from the axis into the leaf, and above it they have a different nature (for example, they correspond to vascular bundles of the arthrostele in the stem). When describing the vegetative system of a plant, we denote the main above-ground shoot (first-order axis) by the term “stem”; lateral branches are, respectively, “axes” of the second and third orders.

SYSTEMATIC PALEONTOLOGY

CLADE EUPHYLLOPHYTA

CLASS INCERTAE SEDIS

Order Barrandeinales Novák, 1961

Genus *Petrosjania* Snigirevsky et Lyubarova, gen. nov.

Etymology. in honor of Nina Mikhailovna Petrosjan (1930–2001), a famous Russian paleobotanist.

Type species. *Petrosjania salarina* sp. nov.

Diagnosis. Lower part of a plant reaching a height of at least 3 meters. Basal part of the stem expanded. Root system of fibrous type. From the main stem in a spiral arrangement, numerous straight axes of the second order depart; large branch scars correspond to the places of their falling off. Axis smooth, semicircular in cross section; their branching monopodial. Leaves large, of two types: (a) in nodes of monopodia, rarely flabelloid with a narrow long petiole; (b) on some axis of the second and/or third order forming a bell-shaped sheath. Leaves dissected into unequal lobes or entire. Venation fan-shaped, veins many times dichotomizing within leaves; their margins smooth, slightly undulating.

Species composition. Type species.

Comparison. The morphology of the lower part of the stems of the new plant has features characteristic of both pteridophytes (including propteridophytes) and lycophytes. The branch scars located along the parastichs resemble representatives of the genus *Barrandeina* Stur, widespread in the Middle and Late Devonian. It was in the *Barrandeina* from the Middle Devonian of Bohemia that leafy shoots were discovered (Kräusel and Weyland, 1933), which were the basis for the widely known reconstruction (Gothan and Weyland, 1954). In representatives of the genus *Barrandeina*, the leaves are linear in shape and arranged spirally on the stems; sometimes the leaves are dichotomous, sometimes they slightly widen in the upper part (Jurina, 1981). Thus, the scars on the surface of *Barrandeina* stems (leaf attachment points) are of a completely different shape and nature than those of a new plant (branch scars).

Høeg (1942) placed representatives of the genus *Enigmophyton* Høeg from the upper Givetian/lower Frasnian of Spitsbergen, which had rare wide fan-shaped leaves attached to the stems at the places of their bifurcation, in close relationship with the *Barrandeina* (Jurina, 1981). The arrangement of fan-shaped leaves (at the nodes) is similar to what we observed on the new plant, however, the axes of *Enigmophyton* were thin and dichotomous, in our case they are wide and monopodially branched.

Pseudobornia ursina Nathorst from the Upper Devonian of Bear Island has complex, spine-like leaves collected in whorls (Schweitzer, 2006).

In the leaf shape, *Petrosjania* is most similar to *Xiphophyllum* Chen. However, the nature of the shoots indicates that *Xiphophyllum* belongs to Sphenophyllales.

The set of morphological characters of *Petrosjania* could well serve as the basis for identifying a new family, but the lack of data on the reproductive organs of the new plant does not yet allow this.

Remarks. Plant remains from Ellesmere Land (Nathorst, 1904) are worth discussing in more detail. Described as *Archaeopteris archetypus* from the mate-

rials of the “Fram” Norwegian polar expedition, the specimens show in some cases an extreme resemblance to the leaves of a new plant. Moreover, identification of some specimens considered by A. Nathorst as “aphlebia of the cyclopteroid type”, is in most cases, doubtful.

Having a wide base, embracing the stem with a conducting system smoothly passing from it into the leaf, these leaves correspond to cyclopteroids to a much lesser extent than the specimens described.

However, Nathorst (1904, p. 17) himself noted that “keine Exemplare vorliegen, die Aphlebien-tragenden Spindelreste noch mit *Archaeopteris archetypus* verbunden zeigen” (no specimens are available that show the aphlebia-bearing rhachises remains connected with *Archaeopteris archetypus*) and even “der Umstand, das sie zusammen vorkommen, diese Zusammengehörigkeit nicht sicher beweist”... (the fact that they occur together does not prove this connection). Among the North Timan specimens, such co-occurrence also occurs; moreover, on the reverse side of one slab with *P. salarina*, a branch undoubtedly belonging to *A. archetypus* is clearly visible. In addition, the leaf-bearing stems are less distinctly ornamented than those that are clearly *A. archetypus*. Based on the above, we place these specimens from Ellesmere Land within the synonymy of the new species.

It is also possible that some of the “unidentifiable parts of the stems” illustrated by Nathorst (Nathorst, 1904, pls. 4 and 5) could belong to the genera *Pseudobornia* or *Petrosjania*, due to the relative smoothness of their surface, large size and the presence of branch scars and nodal (or “false nodal”) lines.

Petrosjania salarina Snigirevsky et Lyubarova, sp. nov.

Plate 11, figs. 1–4; Plate 12, figs. 1–7

Archaeopteris archetypes (part.): Nathorst, 1904, p. 17, pl. 2, fig. 3; pl. 6, figs. 1–2, 4–6.

Taenioocrada timanica: Tschirkova-Zalesskaya, 1957, p. 73–75; text-figs. 51–53, pl. 1, fig. 6, pl. 2, figs. 7, 9; Snigirevsky, 1995, p. 10; 1996, p. 93; Orlova et al., 2016, pp. 97, 98, 99, 101.

Petrosjania salarina (nom. nud.): Snigirevsky, 1997c, p. 37.

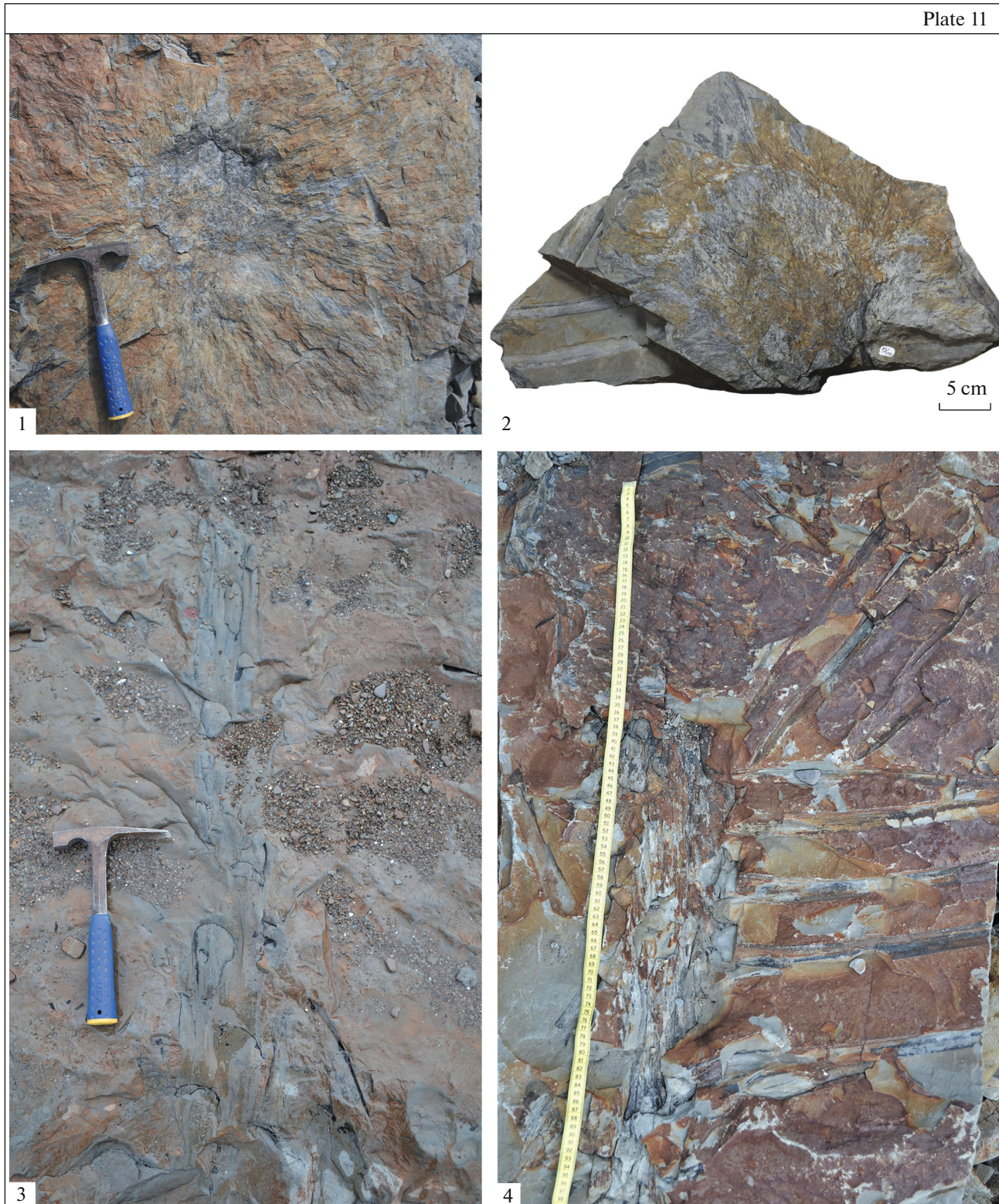
Pseudobornia sp. 1: Orlova et al. 2016, pp. 98, 99, 101, pl. 1, fig. 4.

Etymology. From the species name of Atlantic salmon *Salmo salar* L., 1758, common in the rivers of Northern Timan.

Holotype. PM SPbSU–21/351; Russia, Nenets Autonomous Okrug, eastern coast of the Chosha Bay of the Barents Sea, 2.5–3 km north of Cape Vostochny Ludovatyj Nos; Upper Devonian, Frasnian Stage, Sirachoy Horizon, Ust’e Bezmoshitsa formation; designated herein, Pl. 12, figs. 1, 2, 5.

Diagnosis. The same as for the genus.

Description (Figs. 2, 3). The root system is fibrous. Numerous ribbon-like imprints of simple roots extend radially from the expanded base of the



Explanation of Plate 11

Figs. 1–4. *Petrosjania salarina* gen. et sp. nov.: (1) root system forming a wide circle, top view (imprint of specimen BIN 3212/48, shown in fig. 2); (2) root system forming a wide circle, bottom view, the specimen is the base of a stem with root appendages, specimen BIN 3212/48; (3) basal part of stem with branch scars; (4) the largest fragment of a plant with second-order axes and branch scars on the surface; Russia, Nenets Autonomous Okrug, eastern coast of the Chosha Bay of the Barents Sea; Upper Devonian, Frasnian, Sirachoy Horizon, Ust'e Bezmoshitsa Formation. (1, 3, 4) Field photographs. Hammer length 30 cm.

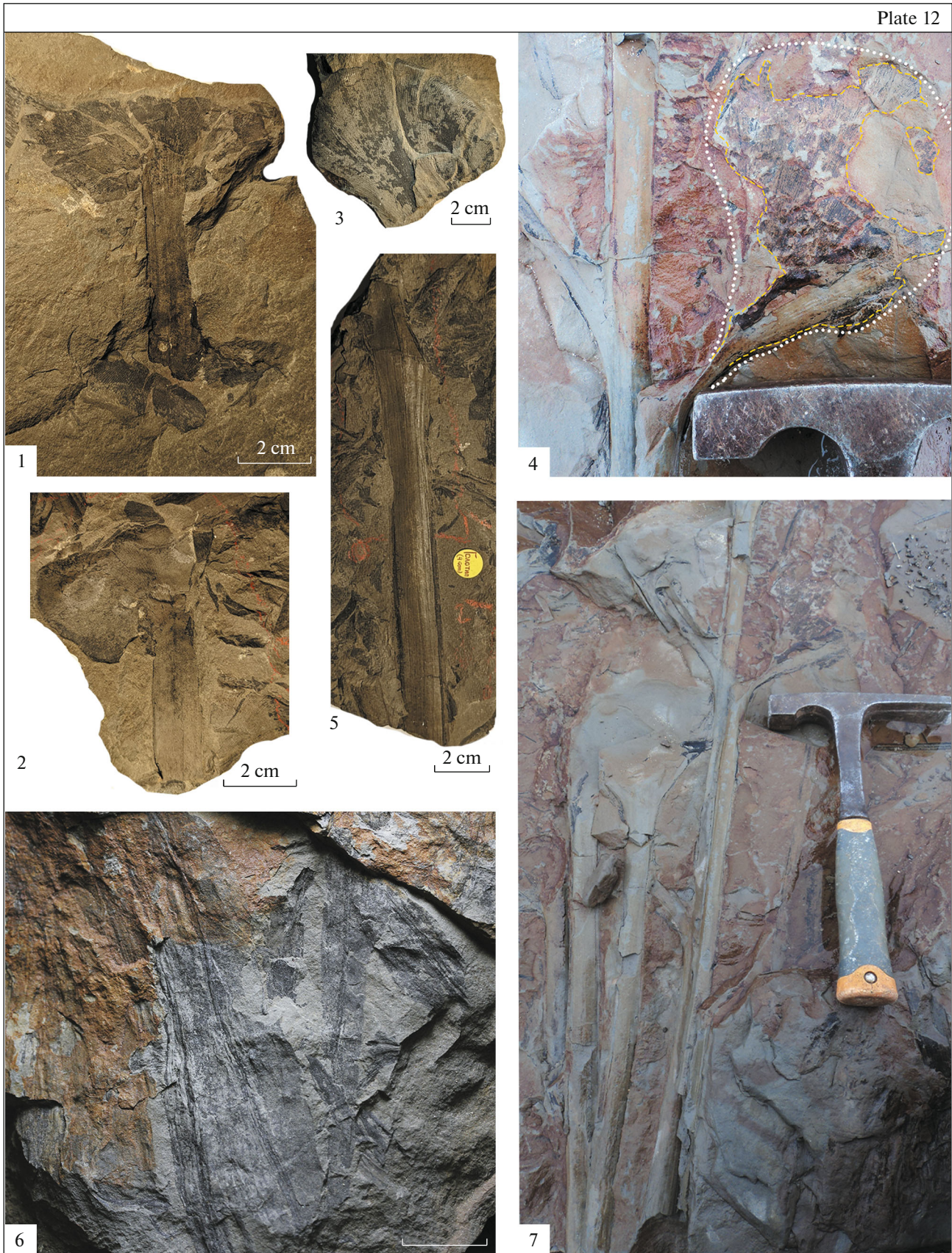
stem (Pl. 11, figs. 1, 2), in the center of which the imprint of a vascular bundle is visible (Pl. 12, fig. 6). The width of ribbon-shaped roots is up to 1 cm; their length reaches 10–15 cm; vascular bundle width is 2–3 mm. The bases of the stems have been preserved in the fossil state in the form of wide circles with a gently indented middle part. The diameter of the most fully preserved of them is about 30 cm (the depressed part corresponding to the base of the stem), with a total diameter (taking into account the radial ribbon-like imprints of the roots) of about 1 m. The carbonized and pyritized material made it possible to obtain images of poorly preserved vascular tissues using a scanning electron microscope. In Fig. 2b, the outlines of at least two tracheids (from the central part of the ribbon-like imprint of the root) are clearly visible, and in Fig. 2a—surface of a tracheid with chaotically arranged simple pores (a fragment of carbonized material of the second-order axis).

The lower parts of the stems were preserved in the form of large fragments up to 3 m long. Second-order axes were attached to them; large branch scars, corresponding to the attachment points of the lateral branches, reach a length of 10 cm and a width of 6 cm. The width of the stems is from 20 to 25 cm on the widest fragments. The scars on the imprints of the stems, including two or three, are located along fairly clearly visible parastichies, forming an angle with the axis of the stem of approximately 45° (Pl. 11, fig. 3).

Second-order axes branch monopodially; branching from opposite to alternating. The length of the internodes in this case is not constant; in particularly large preserved areas it is 70 cm. On one of the most complete fragments (Pl. 11, fig. 4) there are at least six second-order axes, in turn branching monopodially at various distances. On one of the axes (Pl. 12, fig. 7) the branching is located 47 cm from its base; on this branch there is a large flabelloid leaf with a long petiole (Pl. 12, fig. 4). The second axis, lying under the first (Pl. 12, fig. 7) has four branches: the first—25 cm from the lower part; the second—20 cm from the first; the third—3 cm from the second; the fourth is 20 cm from the third. The third axis (Pl. 12, fig. 7) is shorter (40 cm) and ends in an opposite branch. The fourth axis (Pl. 12, fig. 7) also ends 40 cm from the base, but instead of branches, the base of a flabelloid leaf is visible, but not petiolate, but forming an axil. The remaining axes are preserved incompletely. It is important to note that after branching, the width of the axes does not change. The width of these axes is usually 2.0–2.5 cm, but there are wider ones (up to a maximum of 4 cm). The axes are flattened, semicircular in cross section, convexly facing upward. The third order axes depart from the second order axes at an angle from 45° to 90° . Even though branching of the second-order axes is frequent and ubiquitous, only the basal parts of the third-order axes have been preserved (Pl. 12, fig. 7). Their width, as a rule, is half the width of the second-order axes (1.0–1.5, maximum 2 cm). The

surface of the axes of both the second and third orders is smooth, but in some places a thin longitudinal striation is noticeable: there are, on average, six ribs and grooves separating them per 1 mm. Sometimes larger, delimited by unevenly wide intervals, poorly distinguishable longitudinal grooves are visible; in the middle of these intervals, barely perceptible riblike elevations run parallel to the grooves (Pl. 12, fig. 5). Transverse constrictions of the axes can be considered as nodes of sphenopsid plants; in this case, all ornamentation elements, reaching such a node, cross it without visible changes, moving into the next internode (Pl. 12, fig. 5). Within internodes, ribs and grooves can approach each other and become dichotomous. Sometimes on the surface of the second-order axes, tiny, irregularly located scars are noticeable, the central parts of which are, as it were, “impressed” into the rock; radial wrinkles diverge along the periphery from the depression (most likely marking the boundaries of narrow epidermal cells), continuing on the surface of the axes. The nature of these scars is unclear (the presence of stomata has not been established). Nodal lines are uneven, usually arched; the bend is usually directed upward. Such internodes are either equal in length and amount to 6.5 cm (Pl. 12, figs. 1, 2; Fig. 3); or their length is not the same; however, they are absent on most samples. All of the mentioned elements, except for the prominent nodal lines, are very weak. The leaf arrangement is different: both whorled perfoliate and petiolate. We have not established the pattern of arrangement of leaves on the shoots. On one of the fragments there are three whorls of perfoliate leaves in a row (Pl. 12, fig. 1, 2; fig. 3); at the base of only one branch a very large flabelloid leaf was found in natural connection with the plant (Pl. 12, fig. 4). The leaves are large, dissected to varying degrees. The veins pass into the leaf directly from the surface of the axis (Pl. 12, fig. 2), following the finest ribs and grooves (obviously, traces of vascular bundles and spaces between them). The venation is fan-shaped. The veins within the leaf sometimes dichotomize at least twice, slightly widening and becoming thinner towards the margin. The veins in the leaf approach at right angles to the tangent drawn to the edge of the leaf at each point where the vein enters the edge (Pl. 12, figs. 1–3). There are fragments of leaves in the form of sectors of a wide arc with veins directed strictly along the radii (Pl. 12, fig. 3). The maximum length of the leaves is 5 cm, usually about 3 cm. It is difficult to say anything about the width of the leaves, since the segments into which they are split are unequal in width.

Petiolate flabelloid leaves are large, located at the base of second-order monopodial branches. The length of the best-preserved leaf from the place of attachment of the petiole is 17 cm, the width at the widest part is at least 10 cm (Pl. 12, figs. 4, 7). The leaf shape is broadly fan-shaped. The venation is fan-shaped.



M a t e r i a l. 15 specimens of varying state of preservation and completeness from the type locality.

BARRANDEINOID-LIKE PLANTS AND ITS PLACE IN NATURAL CLASSIFICATION

The base of *Petrosjania* stems (they lack secondary wood) is an extension generally characteristic of plants of many taxonomic groups. The same basal expansion is found in many Devonian large plants: *Barrandeina* Stur, *Duisbergia* Kräusel et Weyland, *Pseudosporochnus* Potonié et Bernard, *Calamophyton* Kräusel et Weyland, *Wattieza* Stockmans, *Eospermatopteris* Goldring, etc. Naugolnykh (2015) compared them with the fibrous root systems of modern tropical plants *Roystonea regia* (Kunth) O.F. Cook. Numerous ribbon-like roots diverged from the basal swelling, in the middle of each of which a thin vascular bundle is preserved. In many cases, isolated fragments of root formations of this appearance can easily be confused with remains attributed to the genus *Taeniocrada* White. They also branch dichotomously at sharp angles, and also have a relatively constant width with a large length of flat “shoots”. Some of the forms recorded in these sections by Snigirevsky (Snigirevsky, 1995, 1996; Orlova et al., 2016) and identified as *Taeniocrada timanica* Tschirkova-Zaleskaya and *Taeniocrada* sp. are, in fact, most likely root formations of *Petrosjania*. The peculiar type of rhizoid structure—long, ribbon-like, rarely dichotomous appendages—is characteristic not only of the plants listed above with basal widening of stems and fibrous root systems. *Stigmaria* rhizophores also had ribbon-like appendages (rootlets), or rhizoids (DiMichele et al., 2022), that penetrated uncompact sediment in wet tropical coal-forming forest habitats of the late Paleozoic. It is possible that the wide ribbons, which acted as roots, increased the plane of contact with the soil and contributed to the surface diffusion of solutions into the plant. The width of sediment coverage by root formations was very small. The entire rhizosphere of *Petrosjania* most likely extended no more than 1 meter laterally from the base of the stem and was 10–15 cm deep.

Obviously, due to the weakness and not very high development of the root systems under discussion, these plants could not actively carry out pedoturbation

(Algeo and Scheckler, 1998), which may partly explain the lack of visible paleosol reworking of the sediment (now siltstone) in the places where these plants grow.

The structure of the surface of the stems and axes of the plant is interesting: it is different on different organs and parts. The bases of the stems with basal swellings have an uneven, tuberous-pitted surface with a chaotic distribution of tubercles and dimples of uneven size. Such a surface was formed by breaking off numerous rootlets (appendages) — rhizomes. The surface of the lower parts of the stems, at a distance of at least two to three meters from the base, bears distinct branch scars arranged in distinct parastichies.

A stem surface of this kind can be a strong argument for classifying this plant as a lycophyte (?) plant close to *Barrandeina*. The axes of the plant, extending from the lower part of the stem, have an obvious resemblance to some ancient arthropods. Their smooth surface often bears thin longitudinal striation; occasionally there are formations very close to the nodes observed, for example, in *Pseudobornia ursina* (Schweitzer, 2006, pl. 23, fig. 1; pl. 25, fig. 3). However, the branch scars of *Pseudobornia* are in no way similar to the twig scars of *Petrosjania*. Regarding the morphology of the surface of the axes of the second and third orders of the new plant, the question arises of the justification of identifying such fragments as *Pseudobornia* sp. and *P. ursina*. Often in the paleobotanical literature, especially in works of a stratigraphic nature, in view of the need to identify the samples delivered to specialists in order to determine the age of host rocks, lists of forms were compiled in the conclusions, in which *Pseudobornia* “fit” very well: the Ursa-Stufe, upper Devonian. Smooth stems of this appearance were found in many places besides Bear Island. It is quite possible that some of these finds may belong to different genera, and their identification as *Pseudobornia* may be erroneous. The considerations mentioned above convince us that it is inappropriate to consider synonymously some similar smooth shoots from various regions of Eurasia. We will mention only a few works that provide “new localities” of remains belonging to similar plants: Thuringia (Mägdefrau, 1936, p. 217, pl. 10, fig. 5, 6); the eastern slope of the Urals (Zalesky, 1937, p. 7, pl. 7, figs. 4, 4a); Minusa Basin (Ananiev, 1955, p. 290, pl. 63, fig. 3, pl. 65, fig. 1; Polevoy..., 1955, pp. 54, 55, pl. 35, figs. 7, 8); Western

Explanation of Plate 12

Figs. 1–7. *Petrosjania salarina* gen. et sp. nov.: (1, 2) axis with leaves forming a bell-shaped sheath; three whorls of leaves are visible. The upper (with two whorls) and lower (with one whorl) parts of the axis were uncovered on different sides of one specimen—holotype PM SPbSU-21/351; (3) isolated axilar leaf, specimen PM SPbSU-21/353; (4) ginkgo-like megaphyll attached to the base of the lateral tertiary axis; dots outline the supposed outline, dotted lines indicate the preserved part of the megaphyll; (5) an axis with a clearly visible nodal line and longitudinal sculpture—holotype PM SPbSU-21/351; (6) ribbon-like imprints of roots extending from the base of the stem; traces of a vascular bundle are clearly visible in the center, specimen BIN 3212/48; (7) the longest fragments of the lateral axes of the second order with a clearly visible monopodial branching pattern and a ginkgo-like megaphyll attached to the node of the third order axis (see fig. 4); Russia, Nenets Autonomous Okrug, eastern coast of the Chosha Bay of the Barents Sea; Upper Devonian, Frasnian, Sirachoy Horizon, Ust’e Bezmoshitsa Formation; (4, 7) field photographs. Hammer length 30 cm.

Mongolia (Osnovy..., 1963, p. 504); Donets Basin (Ishchenko, 1965, pp. 47, 48, pl. 14, fig. 5, pl. 15, figs. 1–3). Some fragments of isolated *Petrosjania* leaves may also be confused with either large leaves of *Archaeopteris* plants or other flabelloid leaves (see “Comparison” and “Remarks” sections).

On the new plant, flabelloid leaves were found in direct attachment to the axes. It is important that they have a fundamentally different appearance and, based on previous general ideas, it can be argued that they could not be on the same mother plant. A similar type of leaves (petiolate and sessile) was found in the Chinese plant *Xihuphyllum megalofolium* (Wu, Zhao et Deng) Chen emend. Huang, Liu, Deng, Basinger et Xue (Huang et al., 2017) from the Upper Devonian Wutung Formation (Zhejiang Province). However, some of the materials illustrated in the cited work show an obvious resemblance to *Enigmophyton* (Høeg, 1942, fig. 25; pl. 36, fig. 1; pl. 37, figs. 1, 2; pl. 38, fig. 4; pl. 39, figs. 1, 3; and Huang et al., 2017, fig. 4C; appendix 2F). This does not confirm the synonymy of the discussed taxa, but only supports the homology of leaf organs in rather primitive Devonian plants, which formed leaf blades of various shapes to increase the assimilation surface and photosynthetic activity. Unfortunately, the generative organs of the plant are unknown. However, it has been preserved in relatively large fragments, and most of it can be reconstructed. Therefore, comparison with other ancient plants is made primarily based on the similarity of habit and set of characteristics. The new genus should be assigned to the order Barrandeinales Novák, but significant differences in the morphology of the vegetative system do not allow its inclusion in the family Barrandeinaceae Kräusel et Weyland.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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