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A new species of *Distichophytum* Mägdefrau, 1938 from the Lower Devonian of Siberia (the Torgashino locality, Krasnojarsk krai, Russia)

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Summary: The new species *Distichophytum mogilatii* Naugolnykh, sp. nov. is described from the lower Devonian deposits of the famous Torgashino locality, Krasnojarsk krai, Siberia, Russia. The new plant has fertile organs of long spicate shape, with sporangia biseriately disposed on a thin fertile stem. Sporangia are short-fusiform, with acute apex. Proximally disposed, well-developed sporangia are stalked; apical sporangia and sporangia disposed in the middle part of the fertile organ are sessile. One fertile stem bears up to 50–60 sporangia. Basal parts of opposite sporangia are fused, forming sporangial pairs. Any bracts or bract-like structures are absent. Fertile and sterile stems are curved or almost straight, stem surface is smooth, without any leaves or emergence-like appendages. The salt-extracted ovoid organs (hydathodes) are present just beneath the points of dichotomy of the stems, i.e. in axillary area. In terms of paleoecology and paleoenvironment, the Torgashino locality was formed in a very shallow, pond-like reservoir, most probably weakly saline, lagoon-like, judging from the presence of eurypterids in the same locality. Despite the pond-like reservoirs, where the plants of the Torgashino locality grew, the climatic conditions of this region in early Devonian can be interpreted as semi-arid to arid, because of the red-coloured clastic/terrigenic deposits enriched by oxidized iron, and because of the presence of salt-extracting axil organs, which are present in many taxa of the Torgashino floristic assemblage (for example, *Distichophytum mogilatii* sp. nov. and *Psilophyton goldschmidtii* Halle).

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

The Torgashino locality, disposed in the close vicinity of the city of Krasnojarsk (Krasnojarsk krai, Siberia, Russia), is well-known as an important Lagerstätte, which is characterized by a rich flora of various higher plants (Ananiev 1959; Zakharova 1981; Ananiev & Zakharova 1990, etc.) and a fauna of arthropods (Shpinev 2012, 2015). The Torgashino locality was studied first in the beginning of XX[th] century. But after first studies of the locality, this exclusively important site was considered as completely disappeared because of active anthropogenic/industrial transformation of the local territory. Nonetheless, new studies of this region allowed to find the source strata of the plant megafossils of good or even exceptional preservation located in the same area.

The Torgashino floristic assemblage is a very bright example of early Devonian floras of the world, which is still basically simple in its composition, but already showing several independent lines in higher plant evolution. A taxonomical composition of the Torgashino flora includes *Prototaxites* cf. *forfarensis* (Kidston) Pia, *Jenisseiphyton lebedevii* Ananiev, *Angarolaminariopsis zinovae* Ananiev, *Zosterophyllum myretonianum* Penhallow, *Z. llanoveranum* Croft & Lang, *Taeniocrada decheniana* (Goeppert) Kräusel & Weyland, *T. dubia* Kräusel & Weyland, *Taeniocrada* sp., *Loganiella canadensis* Stolley, *Psilophyton princeps* Dawson, *P. goldschmidtii* Halle, *Psilophytites rectissimum* Hoeg, *Protohyena janovii* Ananiev, *Protobarinophyton obrutchevii* Ananiev, *Distichophytum mucronatum* Mägdefrau, *D. mogilatii* Naugolnykh sp. nov., *Pectinophyton bipectinatum* Ananiev, *Aphyllopteris* sp., *Drepanophycus spinaeformis* Goeppert, *Enigmophyton hoegii* Ananiev, *Platyphyllum fasciculatum* Ananiev, cf. *Protopteridium minutum* Halle, *Bröggeria laxa* Ananiev, *Haspia* cf. *devonica* Kräusel & Weyland (Ananiev 1959; some of the data are reconsidered here). The locality is also characterized by fauna of arthropods, mostly eurypterids *Nanahughmilleria notosibirica* Shpinev (Shpinev 2012) and large undescribed terrestrial scorpionomorphs (personal communication by E.S. Shpinev, 2017).

Materials and methods

The Torgashino locality is a famous Siberian locality of lower Devonian plants. According to the previously published works, the Torgashino locality is disposed in the marginal part of so-called Rybink depression near the City of Krasnojarsk, 1 km westwards of the settlement Torgashino (Ananiev 1959). The locality is represented by a packet of lower Devonian red- or yellow-coloured, fine-grained sandstones and siltstones, covering the Cambrian mudstones with the archaeocyaths (= archaeocyathans; Archaeocyatha). There are two basically contradictive viewpoints on the age of the red-coloured sandstones of Torgashino. The most widespread viewpoint argues for the early Devonian age of this locality (Ananiev 1959, see this work for further citations), but there is at least one more opinion, which summarized the data for considering the Torgashino locality as middle Devonian (Janov 1955). The present author agrees with Ananiev's opinion, that the Torgashino locality is early Devonian.

A considerable part of the collection studied was provided to the present author by Sergey Mogilat, an amateur paleontologist from the City of Krasnojarsk. Additional specimens were collected by the present author himself during a field trip to the Torgashino locality in November 2020.

The recent locality is disposed near the junction of Verkhnjaya and Borisevicha streets, 100 m southwestwards of the junction, in the south-eastern flank of the city-road; in the Leninsky District of the City of Krasnojarsk. The outcrop is approximately 7 m high and 20 m long, represented by red, ochre and yellow-greyish siltstones and fine-grained sandstones. The plant fossils (reproductive organs, leaves, stem fragments and dispersed plant debris) form lens-like bodies disposed in a lower part of the section. There is the fossil, soil-like level (paleosole or FPS-profile) at the basal part of the section.

The collection is temporally kept at the Geological Institute of the Russian Academy of Sciences (Moscow), numbered 4914/34 and 4914/35 (two individual slabs, one is the counterpart of the other). After publishing the research results, the collection will be transferred to monographic department of the State Darwin Museum (Moscow). The collection includes fifteen fertile stems with sporangia and twelve sterile stems belonging to the same species.

Paleobotanical description

Division **Psilophyta (=Rhyniophyta; Psilophytophyta) Zimmermann, 1930**

Classis **Zosterophyllopsida A.S. Foster & Gifford, 1974**

Order **Zosterophyllales Bierhorst, 1971**

Family **Zosterophyllaceae Kräusel, 1938**

***Distichophytum* Mägdefrau, 1938**

***Distichophytum mogilatii* Naugolnykh, sp. nov. (Figs 1A–C; 2A–C; 3A–C; 4A–C)**

Etymology. After Sergey Mogilat, the amateur paleontologist from the City of Krasnojarsk, who collected the early Devonian plants from the Torgashino locality.

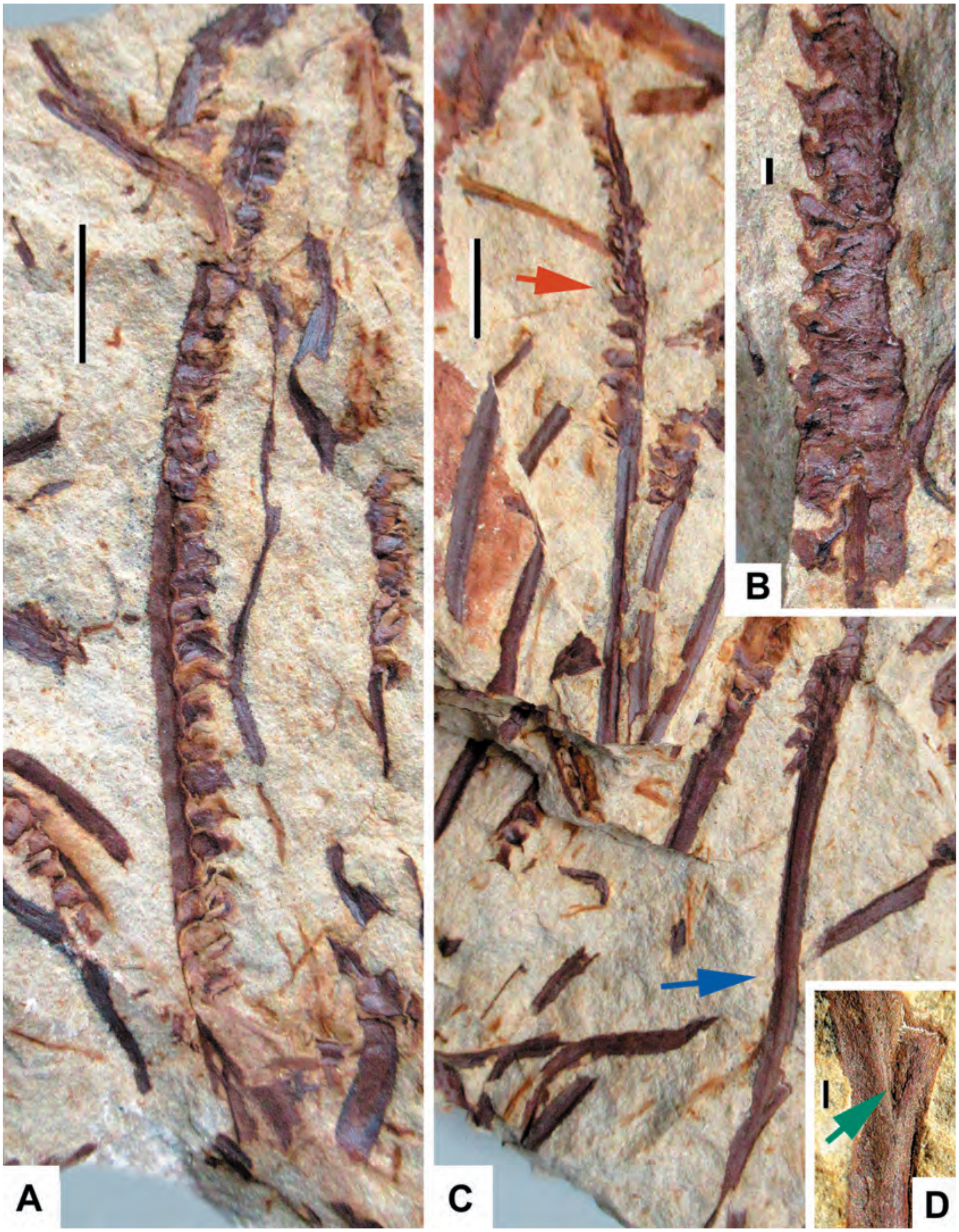

Figure 1. *Distichophytum mogilatii* Naugolnykh, sp. nov. A – spec. GIN 4914/34 A; B – spec. GIN 4914/35 M; C – holotype GIN 4914/35 E (marked by the red arrow), specimen with the bifurcated stem, GIN 4914/35 F (marked by the blue arrow); D – axillary area with the ovoid organ (hydathode) responsible for the salt extracting (marked by green arrow), spec. GIN 4914/35 F. The Torgashino locality; lower Devonian. Scale bars = 1 cm (A, C); 1 mm (B, D).

Holotype. GIN 4914/35 E (figured here on Fig. 1C, marked by the red arrow, Fig. 2B, C, Fig. 3B, C; Lower Devonian, the Torgashino locality, City of Krasnojarsk, Krasnojarsk krai, Siberia, Russia.

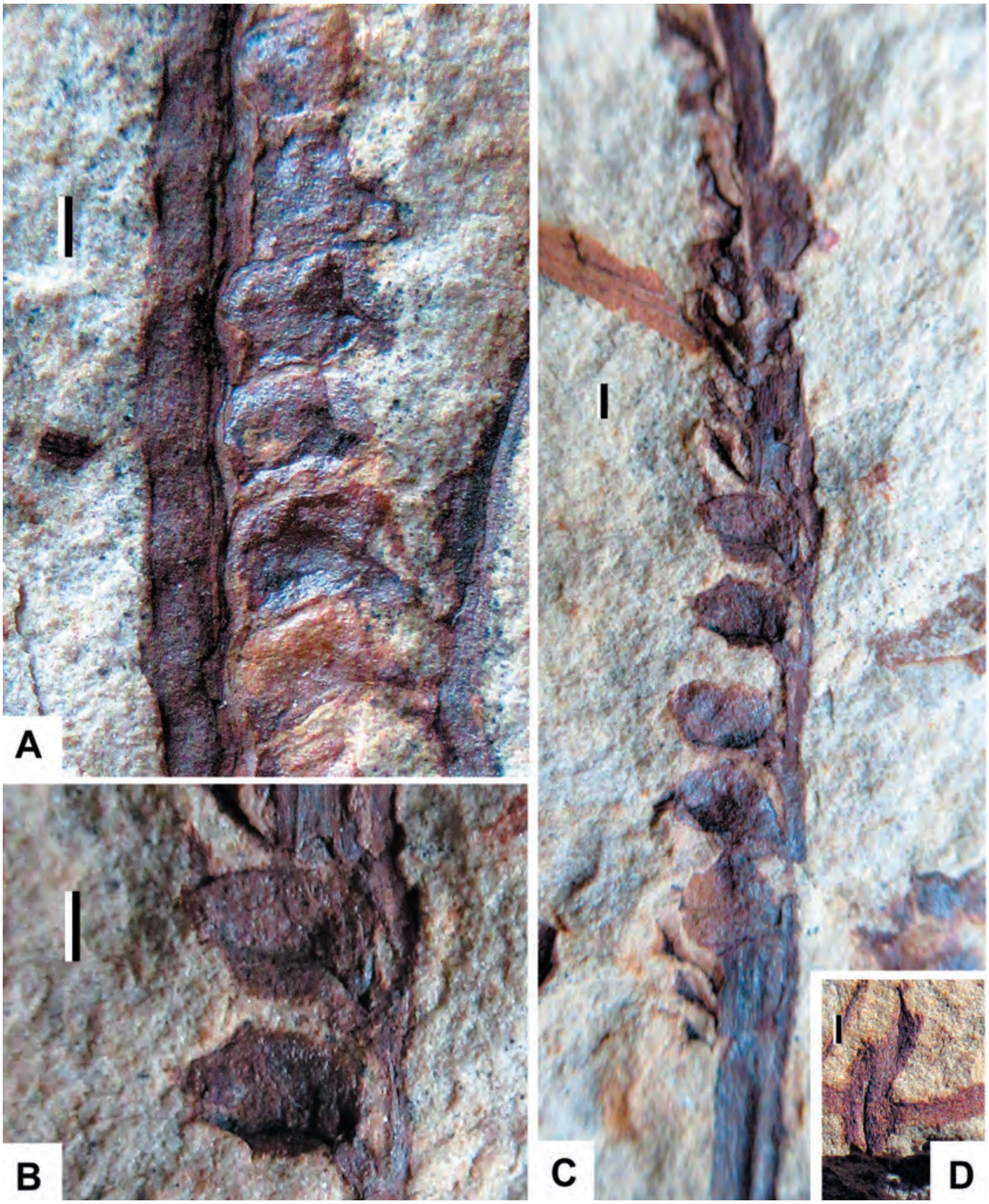

Figure 2. *Distichophytum mogilatii* Naugolnykh, sp. nov. A – spec. GIN 4914/34 A; B, C – holotype GIN 4914/35 E; D – 'K-type' pattern of branching, spec. GIN 4914/34 E. The Torgashino locality; lower Devonian. Scale bars = 1 mm (A–D).

Diagnosis. Fertile organs long spicate, with biseriate sporangia disposed on a thin stem. Sporangia short-fusiform, with acute apex. Proximally disposed, well-developed sporangia are stalked, apical sporangia and sporangia disposed in the middle part of the fertile organ are sessile. One fertile stem bears up to 50–60 sporangia. Basal parts of opposite sporangia fused, forming sporangial pairs. Bracts or bract-like structures are absent. Stem surface smooth. Salt-extracting ovoid organ (hydathode) is present just beneath the point of dichotomy of stems, i.e. in axillary area.

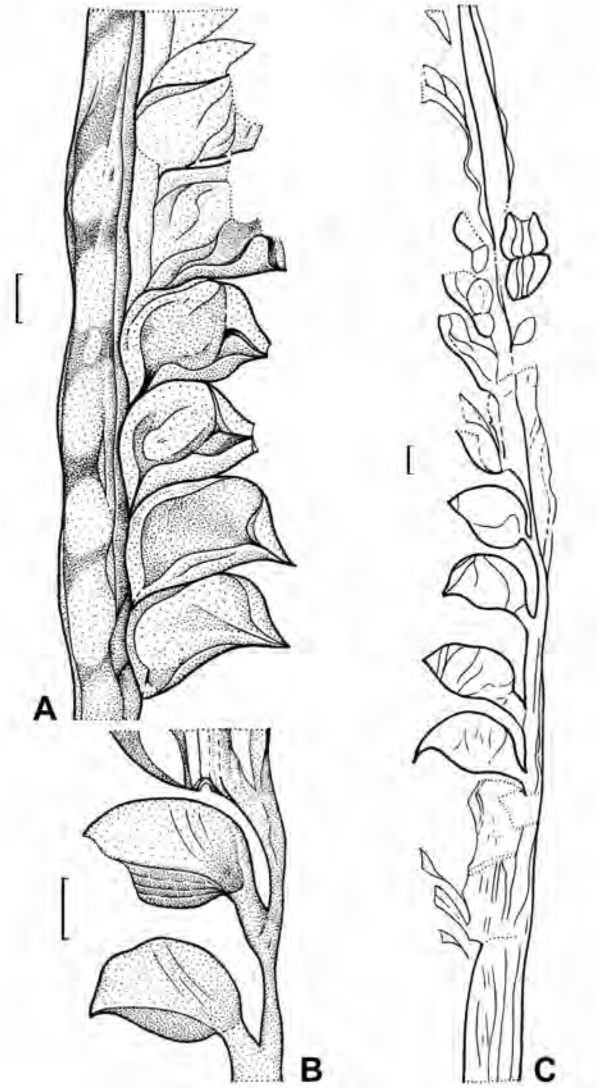

Figure 3. *Distichophytum mogilatii* Naugolnykh, sp. nov. A – spec. GIN 4914/34 A; B, C – holotype GIN 4914/35 E. Line-tracing of the fertile specimens. The Torgashino locality; lower Devonian. Scale bars = 1 mm (A–C).

Description. The collection studied includes fifteen spicate fertile organs, three of them are preserved practically completely. The most well-preserved specimen is selected as a holotype (Figs 1C; 2B, C; 3B, C). Length of the holotype is 75 mm, length of the preserved part of the fertile organ stalk (sterile part of the stem) is 25 mm. Length of the fertile part bearing sporangia is 50 mm. Maximal observed width of the holotype stalk is 1.2 mm.

Since the holotype is visible only from one side of the fertile organ, only one row of sporangia is observed. Sporangia relatively short, of slightly asymmetrical fusiform shape, with narrow stalked basis. The stalk of the sporangium is very short although distinct. Apex of the sporangium is acute, sometimes even spine-like. Length of the well-pronounced sporangial stalk is about 0.5 mm, width varies from 0.3 mm to 0.4 mm. The largest sporangia are disposed on the fertile axis proximally. Size of the sporangia gradually decreases upwards, i.e. distally. Length of the largest sporangia is 3 mm, width is 1.8 mm. The smallest sporangia are 1 mm long and 0.4 mm wide.

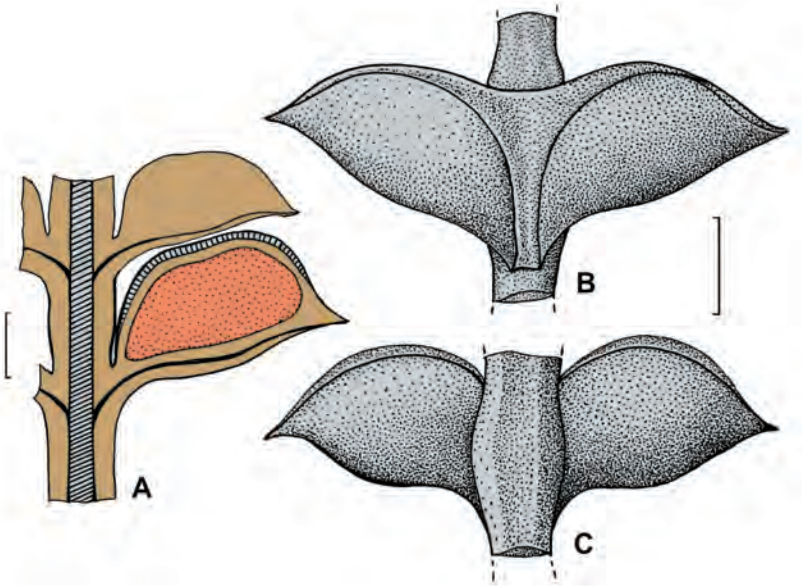

Figure 4. *Distichophytum mogilatii* Naugolnykh, sp. nov. Morphology of the sporangium pairs from the proximal part of the fertile stem (A) and from the middle part of the fertile stem (B, C). A – cross section through the sporangium (an inner cavity of the sporangium is shown in orange colour); B – abaxial (ventral) view; C – adaxial (dorsal) view. The Torgashino locality; lower Devonian. Scale bars = 1 mm (A–C).

The apical sporangia are sessile, without well-developed sporangial stalks. This specimen has more than 20 pairs of sporangia. The most apical (distal) sporangia are small and weakly developed.

One more well-preserved fertile organ (spec. GIN 4914/34 A, Fig. 1A; counter-part GIN 4914/35 A) is larger than the holotype. Length of this specimen is 85 mm, length of preserved part of the basal sterile segment (stalk) of the fertile axis is 10 mm, length of the fertile part bearing sporangia is 75 mm. This specimen is also observed only from its side. The sporangia are sessile. The maximal observed width of the fertile axis is 1.4 mm. Sporangia of this specimen are somewhat larger than the sporangia of the holotype. The largest sporangia are 3.4 mm long and 2 mm wide. Size of the sporangia of this specimen very gradually decreases upwards, in a direction of the fertile organ apex. The apex itself is not preserved. This incomplete specimen bears 28 pairs of sporangia, so the number of the sporangia should be more than 56.

The third well-preserved fertile organ (spec. GIN 4914/F) is 75 mm long, but the apical part of the stem is detached (Fig. 1C, blue arrow). The stem of this specimen is slightly thicker and reaches 2.4 mm width. There is a dichotomy at the base of the stem with the detached right branch, thus it is obvious that the parent plant had branching stems. There are some more once branching (dichotomizing) stems on this slab (at least four), but all of these stems lack sporangia, so it is impossible to prove their belonging to *Distichophytum mogilatii*. Nonetheless, most probably all of the *Distichophytum mogilatii* stems preserved together on one and the same rock slab actually belonged to one and the same parent plant, including sterile stems as well. Fertile axes practically of all studied specimens are slightly curved, although almost straight stems occasionally also occur.

There is an ovoid body disposed just beneath the point of every dichotomy of the stems, i.e. in the axillary area (Fig. 1D). The expression of this body depends on the preservation of the stem.

If we have the positive compressed stem, this body is expressed as a flattened uplifting. If we have negative imprint of the stem, the body is expressed as a shallow depression. Similar organs have been reported before for the putative *Distichophytum mucronatum* from the same locality (Ananiev 1959), but without functional interpretation. According to my opinion, these axillary ovoid structures are organs responsible for salt-extracting in semi-arid climatic conditions. These organs also can be interpreted as a kind of highly specialized hydathodes.

It is important to note that similar organs are known for some other early Devonian plants from the Torgashino locality, for example, *Psilophyton goldschmidtii* Halle (Zakharova 1981). I sincerely think that here we have one and the same adaptation or the evolutionary answer for the same climatic conditions of the paleoenvironment, where the plants grew. Thus, these conditions can be reconstructed as semi-arid to arid, although the shallow-water, pond-like reservoirs were present in this area (details are below).

The fertile part of the stem of this specimen of *Distichophytum mogilatii* is 27 mm long (incomplete length). Most of the sporangia are sessile here, with the exception of the most proximal ones, which have short indistinct stalks. The stem bears a long and flattened medial rib obviously corresponding to the conducting strand of the stem.

One more important specimen of *Distichophytum mogilatii* is 4914/35 M (see here Fig. 1B). This specimen demonstrates a mode of disposition of the sporangia in the middle part of the fertile organ, their fusion in pairs and a sessile position on the fertile axis. The anterior (anadrom, distal or acroscopic) margin of the sporangia bears a thin belt of modified cells, most probably responsible for the opening of the sporangium and for releasing spores. Thus, the dehiscence split of the sporangium was disposed in the anterior (anadrom) margin of the sporangium, as it is shown in the suggested reconstruction (Fig. 4A).

There are some pointed sterile stems found on one and the same bedding plane with the fertile stems of *Distichophytum mogilatii*. Although natural connection of these stems with the fertile stems is not observed, we can suggest that they belonged to the same parent plant because of their close association. Stem surface of both fertile and sterile specimens is smooth, without any emergence-like structures or leaves. We have no data on the basal part of the plant *Distichophytum mogilatii*, but most probably it was organized in the more or less same way as that of other zosterophyllaceans. Branching pattern of the *Distichophytum mogilatii* stems argue for this hypothesis. Since any leaves were absent on this plant, obviously the stems were photosynthetically active.

We don't have good evidence for reconstructing the growth-forms of *Distichophytum mogilatii* yet, but we have a number of reconstructions of its close relatives. *Rebuchia ovata* (= *Distichophyton ovatum*, as it was reconstructed by Taylor & Taylor (1993; reproduced in Taylor et al. 2009, Fig. 8.80), shows a monopodial branching pattern with a relatively dense position of the lateral branches. Such type of growth form certainly was not typical of *Distichophytum mogilatii* with much looser position of the branches and much longer stems. In this respect, the growth form of *Distichophytum mogilatii* should be more similar to the growth form of such zosterophyllacean as *Zosterophyllum rhenanum* Kräusel & Weyland, as it was reconstructed by Schweitzer (1979, 1987: Fig. 17, 1990: Abb. 24). Regarding *Distichophytum mogilatii* and judging from the specimens in hand, the complete length (height) of the plant, was not less than 20 cm when it was alive.

Many zosterophyllaceans have 'H-mode' and 'K-mode' of branching, adapted for forming near-substrate stolon-like subhorizontal basal stems, responsible for mechanical resistance of the proximal part of the plant. Similar 'H-mode' and 'K-mode' of branching was reported for some other early terrestrial plants, for example, *Psilophyton burnotense* (Gilkinet) Kräusel & Weyland (Schweitzer 1988: Abb. 1–3) and for some other psilophyte taxa as well. Judging from the fragmentary preserved parts of stems with similar branching preserved together with the stems of *Distichophytum mogilatii* (Fig. 2D), it is possible to suggest that a similar mode of branching was present in that plant, too.

Distribution. Lower Devonian deposits of Siberia.

Comparison and remarks

Reniform shape of the sporangia of the species *Distichophytum ovatum* (Dorf) Schweitzer (= *Rebuchia ovata* (Dorf) Hueber; nomenclatorial history of this species see in: Dorf 1933; Hueber 1972; Kotyk et al. 2002) is quite different of both the shape of the sporangia in *Distichophytum mucronatum* Mägdefrau (Mägdefrau 1938; see the details below) and the shape of the sporangia of the new species, described in the present paper.

Distichophytum mogilatii has many features in common with the species *Distichophytum mucronatum*, but nonetheless the morphological distance between these two species is too large for considering them being one and the same taxon. The most important difference is that the sporangia of *Distichophytum mogilatii* are distinctly arranged in pairs and thus disposed in opposite order to each other in neighbouring rows. In contrast, the sporangia of *Distichophytum mucronatum* are disposed in alternate order and never form distinct pairs (see, for instance, Schweitzer 1987: Fig. 21; 1990: Abb. 29). Moreover, the sporangia of *Distichophytum mucronatum* are always stalked and never fused at their margins, in contrast to fused sporangia of middle and apical parts of the fertile axes of *Distichophytum mogilatii*.

There is no doubt that *Distichophytum mogilatii* and the genus *Distichophytum* Mägdefrau in general belong to the family Zosterophyllaceae Kräusel, but nevertheless there are some morphological peculiarities, which separate *Distichophytum* from the typical zosterophyllaceans. First of all, sporangia of *Zosterophyllum* are disposed on the stem in spiral order (see for example a large number of publications, i.e. Schweitzer 1987: Figs 18, 19; 2003: Fig. 9; 2004: Text-fig. 5D) in contrast to the sporangia of *Distichophytum*, which form two distinct rows in *Distichophytum mucronatum*, *D. ovatum* and *D. mogilatii*.

Discussion

Early Devonian paleosols, paleoclimate and ecology of *Distichophytum mogilatii* Naugolnykh, sp. nov. In terms of paleoenvironment, we should emphasise that the Torgashino locality was formed in a very shallow, pond-like reservoir, most probably somewhat weakly saline, lagoon-like, judging from the presence of eurypterids in the same locality. The find of the soil-like layer in the basal part of the section is especially important in this respect. Now, general succession of the geological history can be interpreted as step-by-step colonization of the old carbonate substrate formed by lower Cambrian limestones and mudstones with Archaeocyata exposed in terrestrial conditions already in early Devonian. The process of this colonization with permanent adding of the red-coloured terrestrial material from nearest uplifting/mountains was reflected in weakly-developed FPS-profile, i.e. soil microprofile. After the development of a diverse plant community with dominating *Psilophyton goldschmidtii* Halle in lower synusium and larger plants like *Protobarinophyton obrutchevii* Ananiev and *Drepanophycus spinaeformis* Goeppert in upper synusium, this area started to slowly sink, and the water very gradually entered the area. This time was the moment of maximal flourishing of the Torgashino flora, but this episode was not long because of the rapid incoming of terrestrial sediments, which buried the plants practically in the same place, where they lived or with very insignificant transportation. New mass-incomings of sands conserved the 'plant grave' completely and formed the locality, which can be regarded as a typical example of Lagerstätte. Despite the presence of the pond-like reservoirs, where the Torgashino plants grew, the climatic conditions of this region in early Devonian can be interpreted as semi-arid to arid, because of the red-coloured clastic/terrigenic deposits enriched of oxidized iron and the presence of salt-extracting axil organs (hydathodes) present in many taxa of the Torgashino floristic assemblage (for example, *Distichophytum mogilatii* and *Psilophyton goldschmidtii*).

There is no doubt that the earliest history of the terrestrial plants was much longer, than we used to believe before. Now, we know that the higher plants existed on the dry-lands even in Ordovician (Kozlowski & Greguss 1959; Obrhel 1959, 1968; Wellman 2004; Crane et al. 2004; Naugolnykh 2019). This estimation is based on both the new finds of plant micro- and macrofossils and the indirect considerations taking into account a high taxonomic diversity, which proves the long evolutionary history. One of such highly diversified early Devonian plant assemblage is characterizing the Torgashino locality, including morphologically high developed plants like *Distichophytum mogilatii*. Similar highly diversified early Devonian floras have been recently reported from other regions of the world (see, for example, Hao & Xue 2013).

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