The Arising of the Monocots

by
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The angiosperms are divided into two main groups: the monocots (monocotyledons) and the dicots (dicotyledons). About 20% belong to the monocots, including not only the most economically important plant families, the Poaceae (true grasses) but also the largest of all plant families, the orchids. Other prominent monocot groups include the lilies, irises and palms. Inconspicuous fructifications, which are appropriate to many grasses (Poaceae), were not rare in the Early Permian Fore-Urals, but they were often overlooked in the past. *Krasnoufimskia graminaeformis* nov. gen. n. sp., *Taezhnoeia geraschi* and *Krasnaia dammannii* have unambiguous properties of today's grasses. Parallel-veined foliage like *Meristophyllum sojanaeanum, Meristophyllum indivisum* and *Rufloria derzavinii* have more in common with the monocots than other plant families. Herbaceous plants like *Ufaherbaria gaiae* nov. gen. n. sp. constitute an interesting new genus, but their classification under one of the existing systems is difficult even today.

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Angaran Grass Landscape

Several Early Permian monocots; **from left:** *Krasnoufimskia graminaeformis, Krasnaia dammannii,* the low-growing *Ufaherbaria gaiae;* **right:** *Taezhnoeia geraschi*

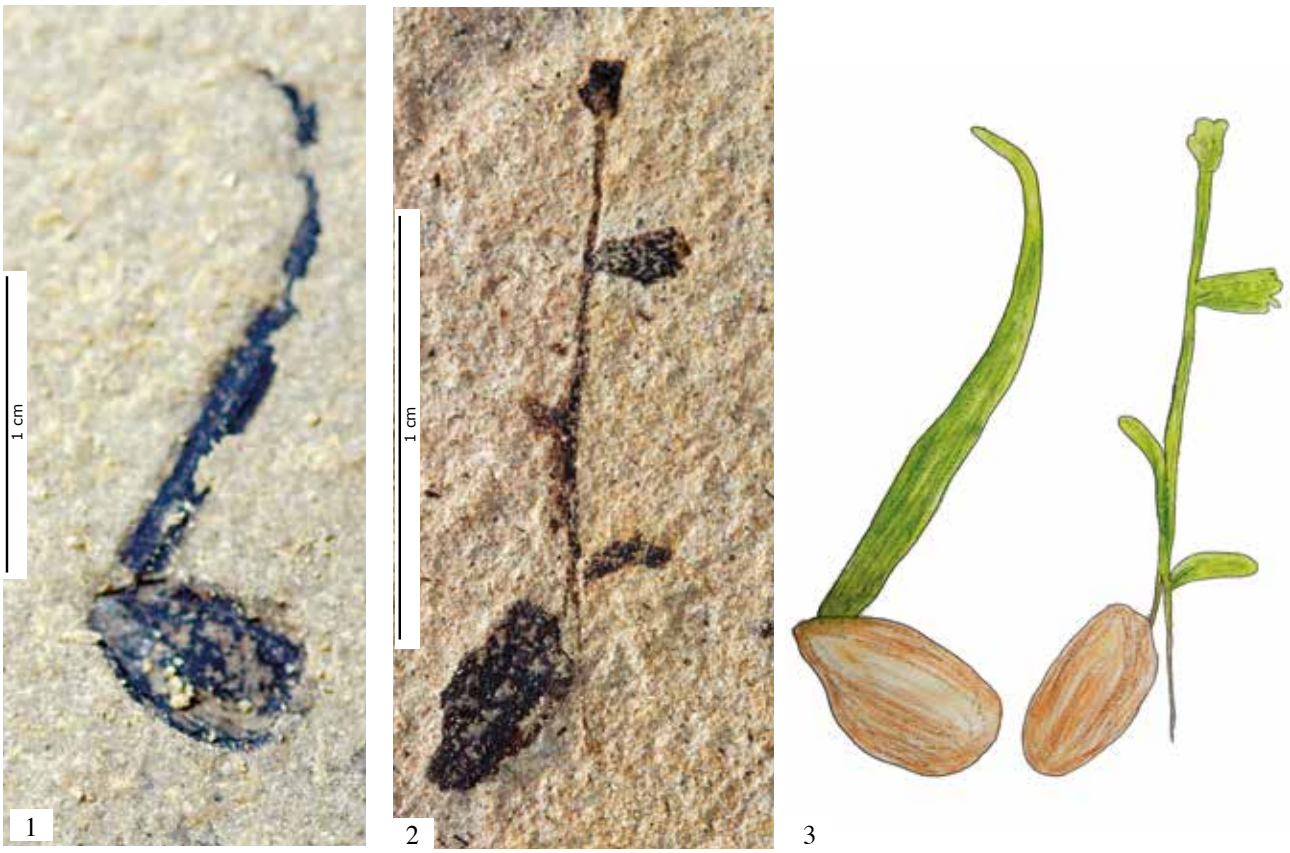
Introduction

The differences between monocots and dicots are interesting: when a monocot seed germinates, it produces only one single and usually long and narrow leaf, which has the exact features of the adult one. Notably, dicots otherwise germinate with two seed-leaves. Monocot leaves are often long and narrow, with straight parallel veins. The stems are mostly unbranched. The foliage of the dicots varies in shape and size. The veins go from the central midrib to the edge of the leaf, crossing and joining to form a netted pattern all over the leaf. The stems of dicots are usually tough and can grow wider each year, and they are often branched. The parts of the flowers of monocots exist in threes, whereas the flower parts of the dicots originate in fours, mostly in five or six petals. The calyx is a separate ring of sepals under the corolla. The seed pods or fruits of monocots usually have three parts, whereas the fruits and seeds of dicots are quite variable in shape, size and texture. There are mostly more seeds in a seedpod of dicots than in monocots.

Early Permian Monocots and Dicots

When and in which way did both the lineages originate? In the Early Permian Angaraland, only seedlings belonging to the monocots were present (MAT 751), as well as those having all the features of dicotyledons (CHEK 336). We also observe various parallel-veined foliage in the leaves of both groups, such as *Meristophyllum sojanaeanum, Meristophyllum indivisum* (Zalessky, 1937) and *Rufloria derzavinii* or *Rufloria recta* (Meyen, 1992). Even grass-like *Taezhnoeia geraschi* evidences dense parallel veins.

Other plants can be regarded as typical dicots with their reticulate veins. Parallel veins are not an exclusive feature of the Permian Angara flora. In the Euramerican vegetation, they are recorded among the Carboniferous-Permian *Cordaites*, an enigmatic tree with long foliage tufts and a doubtful classifica-



1. A typical monocot seedling displaying only one embryonic cotyledon inside the seed to resorb the endosperm (12 mm length, MAT 751, Matvèevo, Coll. Wachtler); 2. Seedling showing a pair of opposite cotyledons, typical of the dicots (14 mm length, CHEK 336, Chekarda, Coll. Perner); 3. Reconstruction

tion. Sometimes, they were regarded as ancestors of all conifers, but both had just fully evolved at the same time, while other theories regarded them as lycopods. Till now only hermaphroditic cones have been discovered, which is a feature of the Lycophyta. The Permo-Triassic *Sigillaria* especially had the same kind of foliage, and it is known that they also hold hermaphrodite fructifications.

The Euramerican variation in the parallel-veined feature of the leaves is nothing in comparison to those in the former Angaraland. There, we encounter many different foliage types that must belong of course to different plants also. Effectively, a classification into primitive monocots is not so bizarre. Inconspicuous fructifications, which are appropriate to many grasses (Poaceae), are not so rare in the Permian Fore-Urals, but they were often overlooked in the past. *Krasnoufimskia graminaeformis, Taezhnoeia geraschi* or *Krasnaia dammannii* have unambiguous properties of today's grasses. Also, parallel-veined foliage like *Meristophyllum sojanaeanum, Meristophyllum indivisum* and *Rufloria derzavinii* have more in common with some monocots than with the Permian floras of Euramerica. Some leaves reach extraordinary lengths of more than 40 cms (CHEK 388), some others have their veins spread wide apart (MAT 326 and MAT 490),

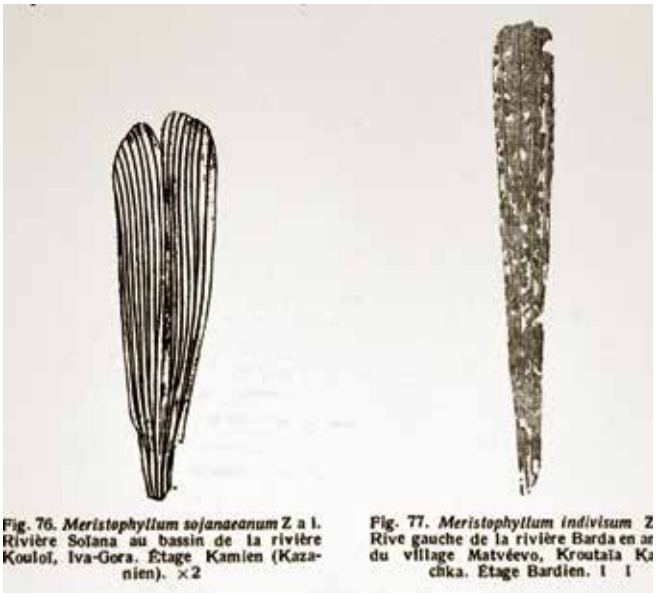
Elymus goloskokovii, belonging to the Graminaceae with long leaves and spikes, native to Kazakhistan

A complete preserved leaf of *Rufloria derzavinii* (44 cm long and 3–5 cm wide, CHEK 388, Chekarda, Coll. Nicolas Wachtler) and the parallel-veined monocot grass *Acorus calamus* with lateral fructifications

and a group split their leaves forming pairs (MAT 439, MAT 427 and MAZ 16). Some are perfect linguiform (MAZ 24), resembling *Glossopteris* plants from the southern hemisphere Gondwanaland. Nevertheless, it can be stated that in no other region do these parallel-veined leaves reach such a propagation as in the Permian Angara region. Therefore, the axiomatic assumption is: Why do we have such as diversity? Where lies the origin of this variety? In which context stand these supposed monocots with the dicots? An answer can be that astonishingly the primitive lycopods are more closely related to the angiosperms than the gymnosperms. Some Sigillariaceae like Permo-Triassic *Sigillcampeia* had almost reached the hermaphroditic angiospermous stage of development.
Upon superficial examination, we encounter two kinds of leaves: parallel-veined with bilobed axes (*Meristophyllum*) and parallel-veined single leaves (*Rufloria*). Probably they belong to different species and genera, but till the time connected fruits are not found, every classification is doubtful.

Meristophyllum Leaves

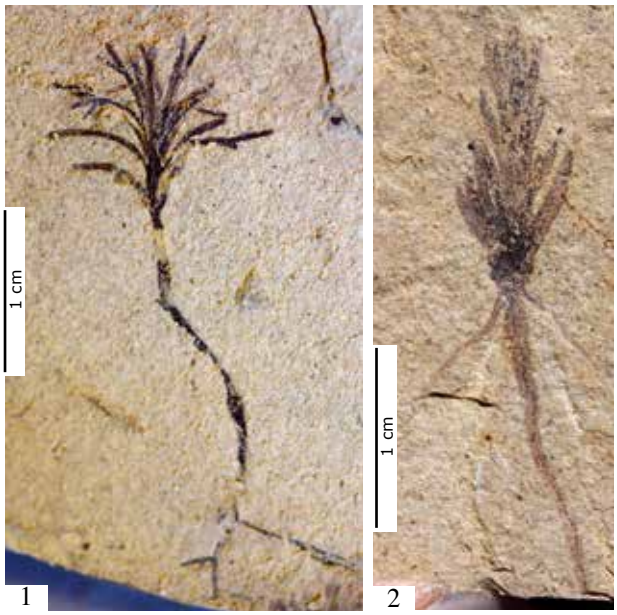
Zalessky (1937) introduced two species: *Meristophyllum sojanaeanum* and *Meristophyllum indivisum,* in which he noted that leaves of one kind split into two and the other do not. The leaves are usually 10–15 cm long and cuneiform. The veins are parallel and dense. They diverge one or two times on the basal-middle part. Leaves with this feature are relatively abundant in the Kungurian deposits like Mazuevka, Chekarda and Matvèevo, but an insertion into one of the known families is not easy.



Meristophyllum sojanaeanum (left) and Meristophyllum indivisum after a drawing by Zalessky, 1937.

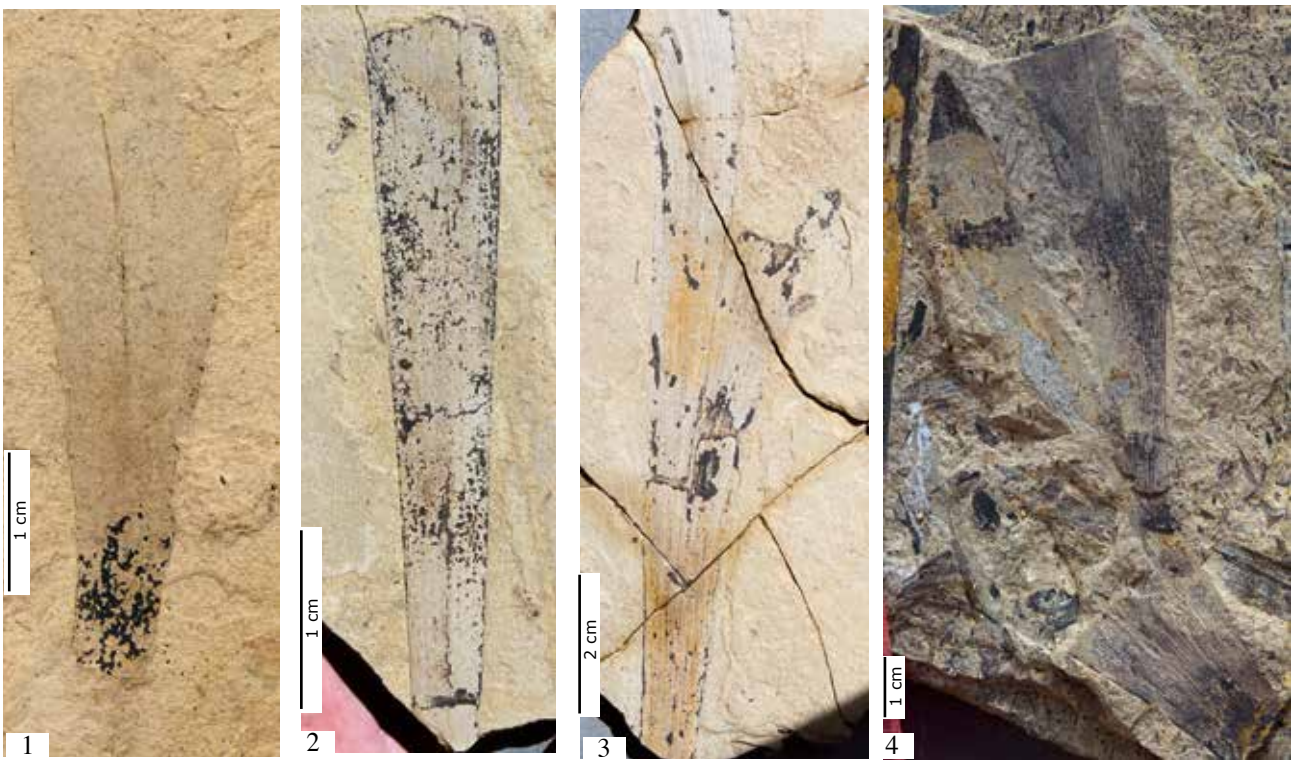
Rufloria Leaves

Rufloria-leaves are inhomogeneous, varying in length from 10–15 cms, sometimes even reaching up to 50 cms. In comparison with *Meristophyllum*, they are fossilised individually. All are parallel-veined but there exist differences in terms of being densely to largely veined. The apex can be tapered or obtuse rounded. Often, they are equipped with an abscission mark (MAT 429, MAT 423 and MAT 437). The most commonly known is *Rufloria derzavinii* (Meyen, 1992), while other species are known as *Rufloria recta* (Meyen, 1966), *Rufloria salamatensis* (Meyen, 1963; Zalessky, 1937), *Noeggerathiopsis* (Naugolnykh, comb. nov., 2016). Some authors connected the genus *Rufloria* with the family of Vojnovskyaceae (Neuburg, 1955), an enigmatic and intriguing family of fossil gymnosperms from Angara (Naugolnykh, 2010). Originally, *Vojnovskya paradoxa* exhibiting parallel-veined leaves was connected with cone-like reproductive organs, consisting of an axis on which reflexed seed stalks with widened apices were attached (Neu-



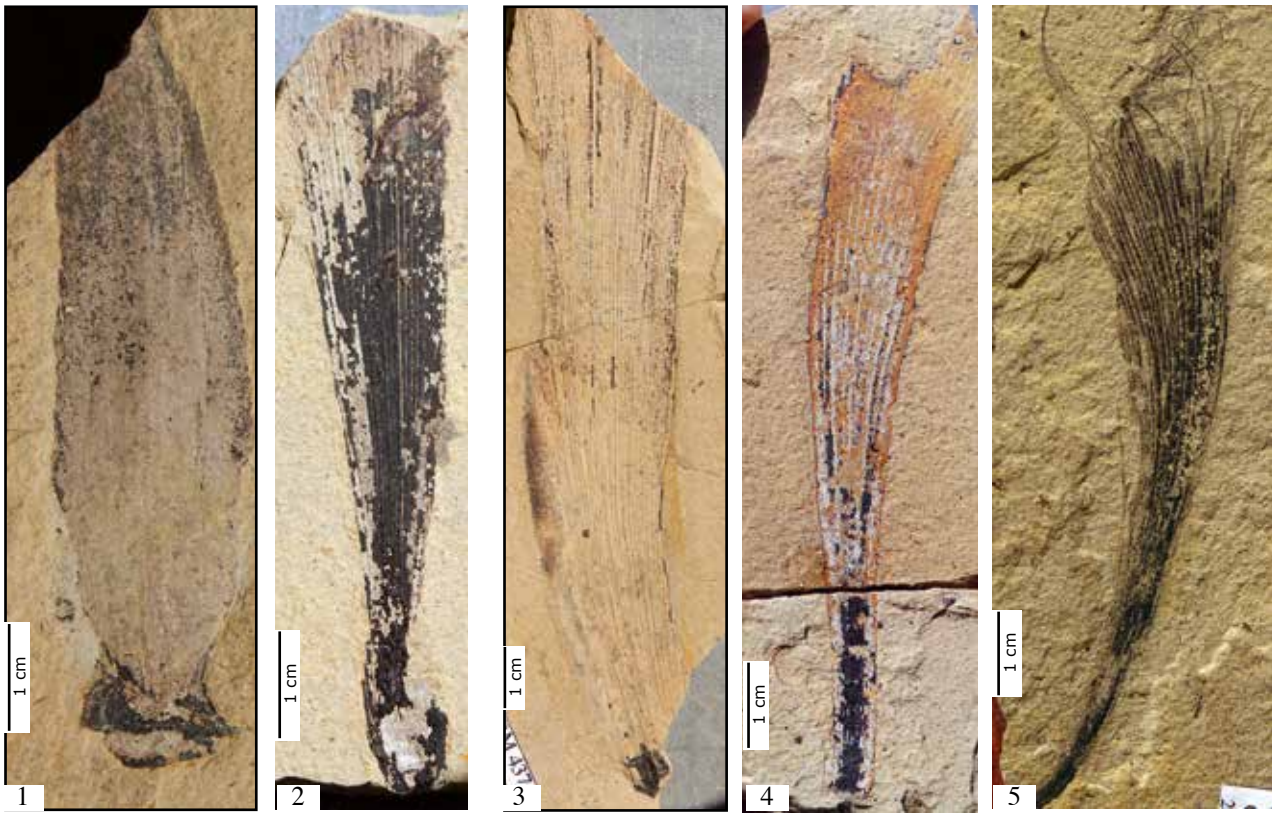
Seedlings

Seedlings with insecure classification: 1. MAT 329; 2. MAT 324; Matvèevo



***Meristophyllum*-Leaves**

1. Juvenile bilobed leaf (MAT 653, Coll. Perner, Matvèevo); 2–3. Forking leaves (MAT 427 and MAT 439); 4. Several forking leaves with dense parallel veins (MAZ 16, Mazuevka) Dolomythos Museum, Italy.



Rufloria-Leaves

1–3. Leaves with abscission marks (MAT 429, MAT 423 and MAT 437, Matvèevo, Coll. Wachtler); 4–5. Parallel veined leaves (MAT 490, Coll. Dammann, CHEK 46, Chekarda)

Taezhnoeia geraschi (MAT 434 holotype, 13 cm high), a low-growing, herbaceous plant with foliage in basal aggregation, whereas in the upper parts of the stalk, only a few leaves arise in an alternate manner. The attached closed spikelets represent their fertile parts and can be found on the same slab.

burg, 1955). Female head-like aggregations of sterile scales and seed stalks were assigned to the genus *Astrogaussia imbricata* (Naugolnykh, 2014). Based on this, it can be supposed that *Meristophyllum* and *Rufloria* can be inserted in the category of monocotyledons with unknown fructifications till date.

Other Plants Resembling Monocots

There are other plants in Matvéevo that, with a certain assumption, can be regarded as low-growing or herbaceous. Partially, they have clearly evidenced parallel veins or hold spikes or forms caryopsis, with the seed coat fused to the fruit wall, such as in *Taezhnoeia geraschi, Krasnaia dammannii* and *Krasnoufimskia graminaeformis.* Some monocot-resembling plants still cannot be classified well under one of the existing systems.

Taezhnoeia geraschi WACHTLER 2017

Another Early Permian grasslike plant is represented by *Taezhnoeia geraschi*. Several leaves sprout from a rhizome and are arranged in three vertical rows (tristichous). The single leaves taper apically and are parallel-veined. In that they have all the aspects of monocotyledons like the true grasses of today (Poaceae). Several fertile parts on the holotype MAT 434 can be regarded as spikelets belonging to *Taezhnoeia* and consisting of two bracts that are fused with the fruit wall; all are closed. Although often overlooked, *Ufaherbaria gaiae, Krasnoufimskia graminaeformis* and even *Taezhnoeia geraschi* are characterised by the same assemblage of their fertile

Phragmites australis (Poaceae) represents a cosmopolitan reed grass.

parts. The fact that some can be classified as spikelets (*Taezhnoeia geraschi*), while other as caryopsis (*Krasnoufimskia graminaeformis*) justifies the classification in other genera too. Also, their leaves notably differ amongst themselves.

Even now it is thought that low-growing grasses arrived only in Cretaceous till Eocene floras. However, more indications fulfilling the characteristics required for the Graminaceae like we have in Early Permian Angaraland cannot be found. Searching alternatives with Permian gymnosperms are not exhausting and therefore, more attention has to be given to why we have a gap between their supposed first appearance on the Carboniferous-Permian border and their second resurrection in the Cretaceous. Future studies have the task to focus more attention on these often ignored details. Also, more material that can be recovered from these localities can certainly enlarge the knowledge about its classification that would relate it with some of today's ancestor lines.

***Taezhnoeia geraschi* Reconstruction**

***Krasnaia dammannii* Reconstruction**

Poaceae grasses

Today's grasses with the inconspicuous spikes, *Panicum virgatum* and Switch grass

Hakonechloa macra, a grass from the family of the Poaceae. *Taezhnoiea geraschi* and *Krasnaia dammannii* evidence some features of today's grasses.

Deschampsia cespitosa known as tufted hairgrass, a perennial widespread Poaceae

Stipa capillata, a perennial bunchgrass species from the family of Poaceae, from the steppe of Kazakhstan

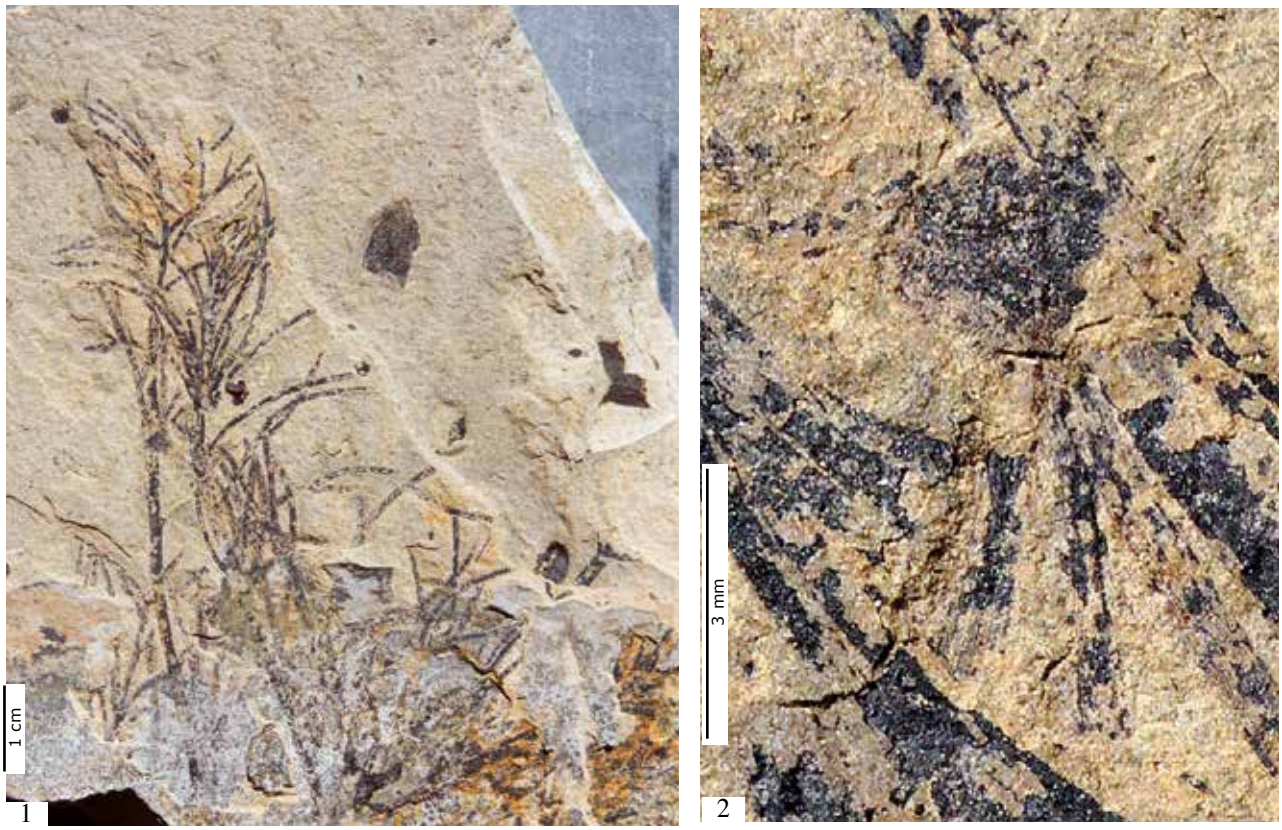
Krasnaia dammannii WACHTLER 2017

Also *Krasnaia dammannii* fits well in a group of herbaceous graminoceous plants being relatively abundant in the Matvéevo-Fossillagerstätte. In this case, the interesting features are their grass-like structure and growth. The plant is characterised by a slender culm-like stem ending in a tuft compound of fragile narrow leaves. The foliage is characterised by a nearly invisible midrib. The fertile organs are sitting apically and solitary on the stem-leaves, forming a strange cluster of pollen sacs and seeds. Because of many features such as their low-growing appearance, *Krasnaia dammannii* also clearly resemble today's grasses, but a detailed indication towards which monocot-group they belong to is still not identifiable.

Krasnoufimskia nov. gen. PERNER & WACHTLER 2020

Etymology

It is based on Krasnoufimsk (Russian: Красноуфи́мск), a town in Sverdlovsk Oblast, Russia, located on the banks of Ufa



***Krasnaia dammannii* – Plant, leaves and fructifications**

1. Whole plant with roots, leaves and attached fructification (MAT 288 holotype); 2. Detail of the fertile organ attached to the leaflets; some stamens with anthers sitting on slender filaments are visible; Matvéevo, Kungurian (Early Permian) Coll. Wachtler Dolomythos Museum

River; many of the Early Permian fossil sites such as Chekarda lie in the vicinity.

Krasnoufimskia graminaeformis nov. gen. n. sp. PERNER & WACHTLER 2020

Holotype

MAT 200, Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

Diagnosis

The plant has large triangular basal leaves with long and fleshy leaf-like petioles; fruits forming a caryopsis, with the seed coat fused to the fruit wall seen.

Etymology

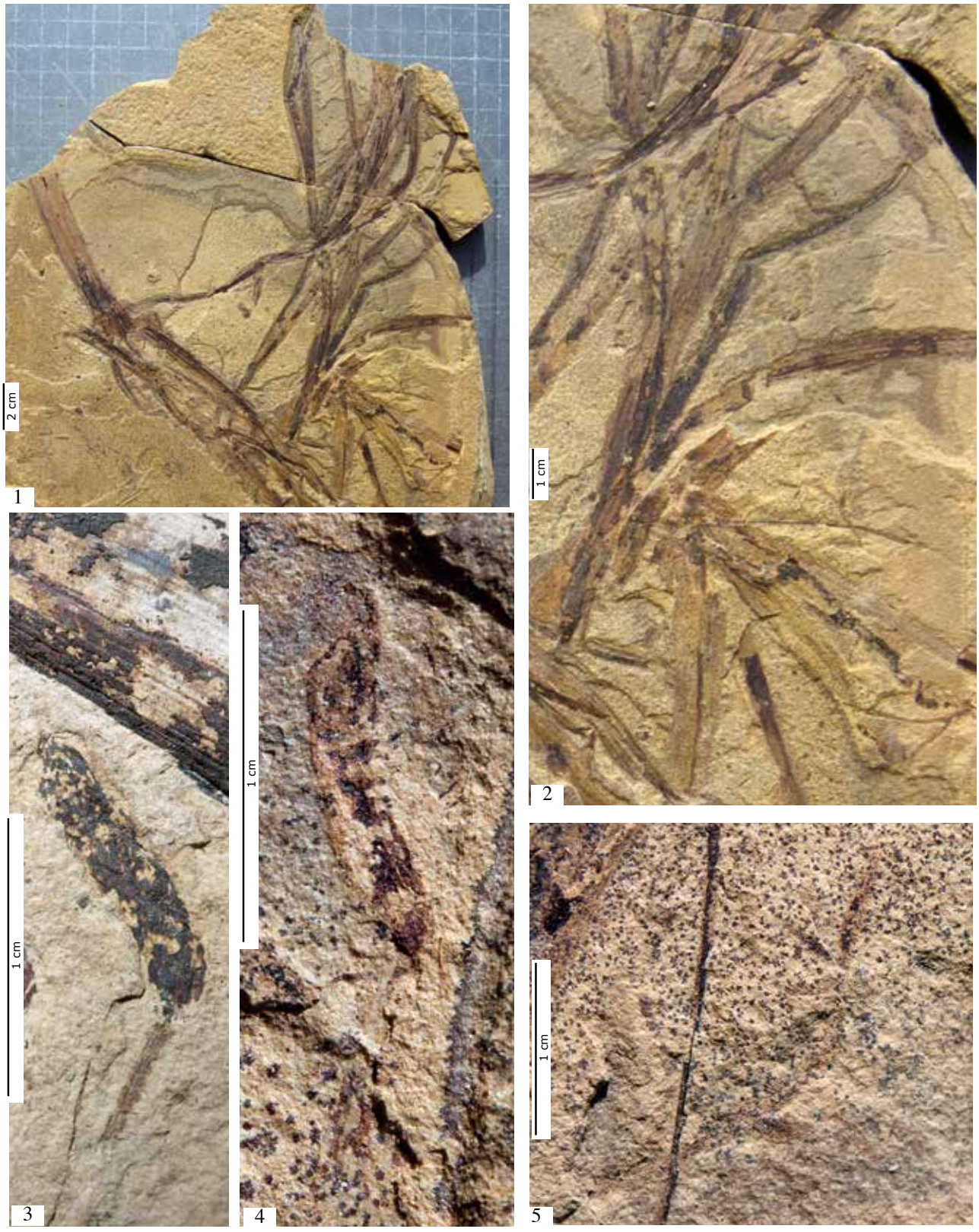
It is named after their resemblance with the Gramineae, known as grasses, a large family of monocotyledonous flowering plants

Description

Plant: The most complete plant, holotype MAT 516, is 15 cm long and consists of two basal leaves that are from 4 to 5 cm long and are equipped with a strong midrib. The leaves have an entire margin and end is tapered. The main 0.5 cm thick stemlet forks several times after the middle. Two entire panicles are attached in additional to another mostly decayed one. The isolated spikelets are about 1 cm long and are composed of many caryopses consisting of elongated seeds fused with the fruit wall. Isolated grains are better evidenced in CHEK 200, a 20 x 20 cms slab with several *Krasnoufimskia graminaeformis* plants deposited. Also, several stems (1–2 cm thick) fork in the upper part. The most complete spikelets (CHEK 200 and MAT 753) sit on a slender, 10 mm long petiole. The single corn grain is 10 mm long and 1 mm wide and ends in a spike projecting 10 mm from the tapering fruit wall. The single seeds are slightly furrowed.

***Krasnoufimskia graminaeformis* gen. nov. sp. n. – plant, leaves and fructifications**

1. Entire plant of the designed holotype MAT 516; 2. The seed-bearing parts sprout as terminal panicles from the stemlets; 3. After their seeds are released, empty spikelets remain; 4. Two basal leaves of the holotype; Matvéevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos Museum



***Krasnoufimskia graminaeformis* gen. nov. sp. n. – plant, leaves and fructifications**

1. Several plants deposited together (CHEK 200); 2. Detail of a single plant 3. A fruit forming a caryopsis, with the seed coat fused to the fruit wall (MAT 753, Matvèevo, Coll. Wachtler); 4–5. Several seeds with the fused seed coat (CHEK 200); Chekarda Kungurian (Early Permian) Coll. Gerasch, Dolomythos Museum

Reconstruction of the grass-like *Krasnoufimskia graminaeformis* showing the whole plant and panicles with spikelets

Discussion

Krasnoufimskia graminaeformis is fairly common in Matvèevo as well as in Chekarda, but only whole plants can be classified without doubt. This is especially valid in case of their panicles or isolated spikelets that can be analysed, due to their inconspicuous character, only if attached to the plant. Additionally, in the Early Permian sediments, we encounter other plants that have mainly the same panicles or spikelets as *Ufaherbaria gaiae* but generate different small elongated leaves or evidencing the same stems and stalks but different caryopsis.

The interest in these grass-like plants was never extraordinary. Probably they were thrown away with the trash many times and regarded only as decomposed parts of plants. Also, the panicles of *Krasnoufimskia graminaeformis* could be discovered only after an intensive, albeit extremely interesting, study of the whole plant, which tells a lot about the evolution of grasses, one of the most extensive plant families on Earth. The Poaceae (Graminaceae) form the most important group of flowering plants for human beings because of their cereal and forage crops (Taylor et al., 2009). Alternating long, slender leaves in two rows on opposite sides of the stem and small bisexual flowers organised into inflorescences are two of their characteristic features.

Ufaherbaria nov. gen. PERNER & WACHTLER 2020

Etymology

The name is from the Ufa River in Sverdlovsk Oblast, Russia, which crosses the main Early Permian fossil sites, and "herba", meaning grass in Latin.

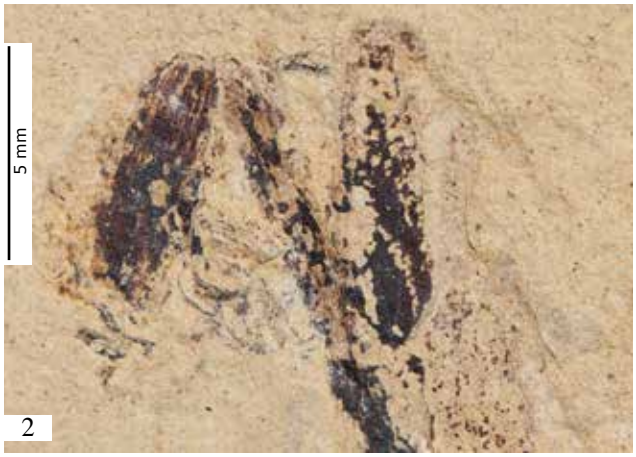
Ufaherbaria gaiae nov. gen. n. sp. PERNER & WACHTLER 2020

Holotype

MAT 515, Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

Etymology

It is named after the Greek name "gaia" meaning "Mother Earth".



Ufaherbaria gaiae

1. Complete plant (designed holotype MAT 515, 9 cm high); 2. Detail of the fructification and hanging seeds; Matvéevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos Museum.

Diagnosis

This herbaceous plant has a basal tuft of lanceolate tapering leaves; the inflorescences are small panicles forming aggregated elongated corn grains.

Description

Plant: The complete holotype MAT 515 is 9 cm high and is composed of a basal rosette forming clumps. The leaves are about 4–5 cm long and 1 cm wide, lanceolate and tapering apically. A midrib is seen. The fertile stalks are unbranched and hold several

Ufaherbaria gaiae – reconstruction

This herbaceous plant is characterised by strong basal leaves and a compound of hanging seeds on a leaf-like stem.

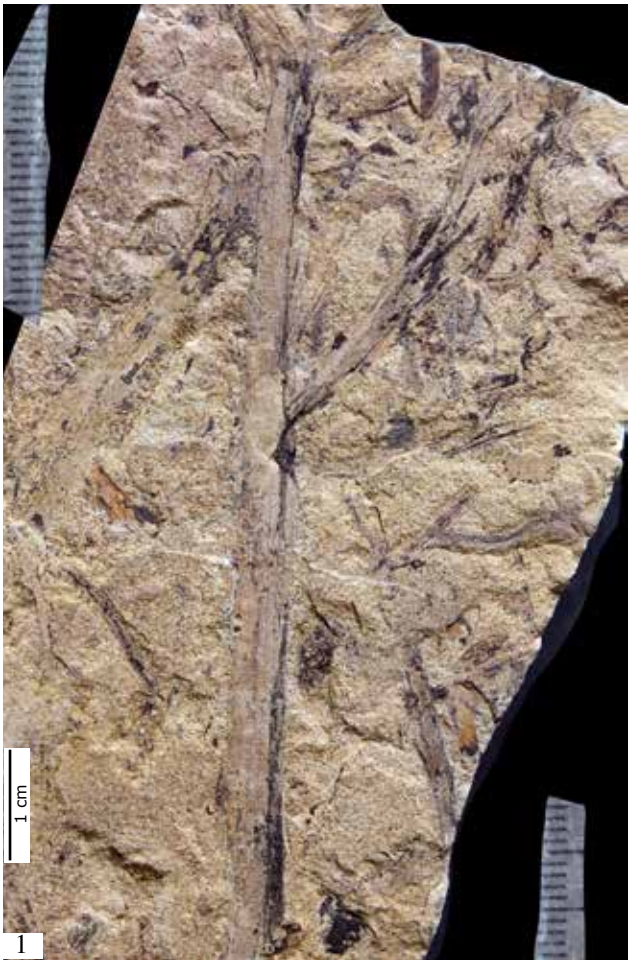
hanging seeds on the apex during the maturation stage. They reach a length of about 5 mm and a width of 1 mm.

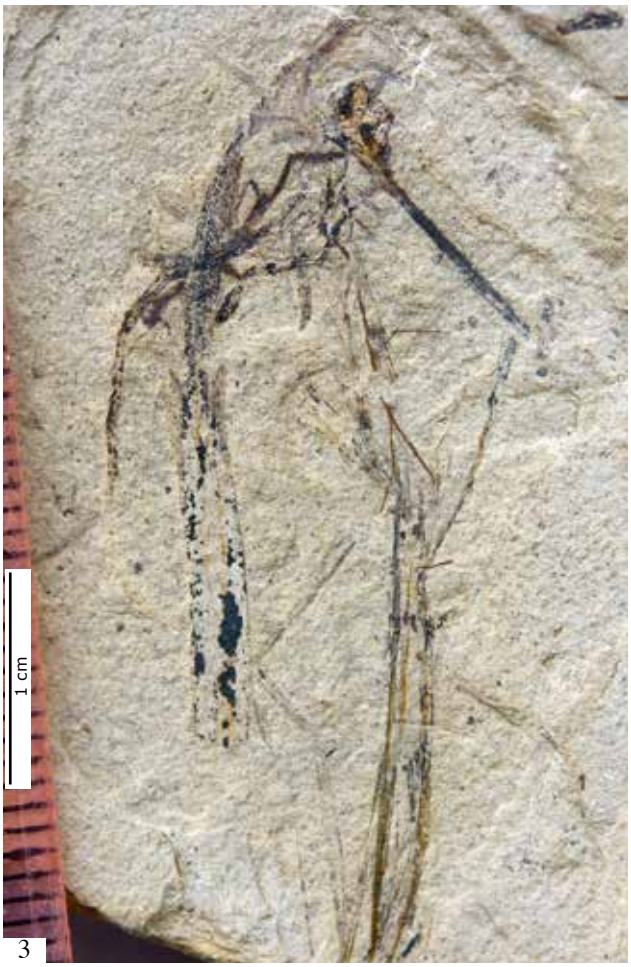
Discussion

Ufaherbaria gaiae can also be inserted into the group of Early Permian herbaceous plants collected from the Fore-Urals. It is probably more common than it seems. However, since only entire plants can be classified without doubt, partially preserved specimen or those without connecting fertile parts are often let go. Basal tufts of leaves can be seen in many of today's angiosperm families, including the Poaceae, Alliaceae, Gentianaceae and many others.
Because of their corn grains, an insertion into the category of Graminaceae ancestors is possible. This is not so unfounded because as seen in the Early Permian sediments from Chekarda and Matvèevo, other plants like *Krasnoufimskia graminaeformis* or *Taezhnoeia geraschi* formed panicles with spikelets. Otherwise their basal leaves resemble dicots more.

Contributions

Thomas Gerasch, Martin Dammann, Thomas Perner, Nicolas Wachtler and Michael Wachtler made fossil specimens available. Michael Wachtler analysed the data, made





Grasses with unknown fruit organs

1–2. Plant with hanging seeds, maybe belonging to *Krasnoufimskia graminaeformis* (CHEK 207); 3–4. Plant with segmented spikes, maybe belonging to K*rasnaia dammannii* (MAT 612)

the drawings, photos and wrote the paper. Thomas Perner supported the work financially.

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