Early Permian Origin and Evolution of Angiosperms
The Flowering of Angara-Land

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Our present knowledge about angiosperms is based on the dogma that first appeared the family of Magnoliaceae than any other flowering plant. We do not usually take into consideration that the genesis of angiosperms could happen in a different way of evolution, maybe a more unexpected step. This study will attempt to explain the strange angiosperm-genesis with new theories based on surprising new findings. From the Devonian till the Triassic period – when Euramerica was located near the Equator – we had another continent in the Northern Hemisphere called Angara. On this landmass evolved at the same time a strange symbiosis between insects and flowers, made possible through a peculiar progress: nutrient-rich pollen dust, colourful flowers and sweet fruits on one side, sexuality and reproduction on the other. Isolated from the other landmasses, this community remained unique for millions of years. The knowledge we obtained from two world fossil sites: Chekarda and Matvéevo, in the vast but lost landscapes of the Russian Urals, are due to the conservation of all the particularities and perfection of plants and insects astoundingly. This study deals with the beginning and propagation of all angiosperms in the Early Permian period from the deciduous trees, over herbaceous flowers and grasses, and will give interpretations on why they could evolve in isolation and why probably the worldwide climate change due to an immense catastrophe in the Permo-Triassic boundary caused a quasi-extinction of the first angiosperms and retarded their spreading all over the world for a long time.

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Early Permian broad-leafed trees – Left at the top: Twig with leaves and *Sylvella alata*-samara, a potential progenitor of today's maple (Acer); Middle top and bottom left: Twig, drupes and flowers of *Bardocarpus aliger*, a potential ancestor of the stone-fruits; Right top: Samaras of *Matvéeva perneri,* a potential Ulmus ancestor; Middle right: *Sadovnikovia belemnoides,* an ash (Fraxinus) progenitor; Bottom middle: *Psygmophyllum expansum (Craspedosperma bardaeanum*), a Quercus (oak) ancestor; Bottom: Several unknown blossoms of flowering plants.

Introduction

Russian paleofloras represent for most of the world – also in the 21st century – the terra incognita. Reasons for this isolation are the remoteness of the territories, the Cyrillic language and writing style, and the political inaccessibility for a long time.

When I arrived for the first time in the Urals in 2015, a new continent opened itself to me. I recognized fossil floras that I had never seen in other parts of our world – mainly, all were different. In Europe the Permo-Triassic time is dominated by gymnosperms such as conifers, ginkgos or cycads, while in the old Angara-Land, these play only a subordinate role. The strange new plants I found left me astonished. I noticed insects of all groups such as mayflies, bugs, beetles, crickets, scorpions, spiders, as well as potential progenitors of the Hymenoptera, comprising the bees and wasps, in the Early Permian sediments. Besides, plants looking like today's maples, oaks and ash trees, and stone-fruits were present, and many flowers having the modern-day appearance. I noted surprisingly that in ancient Angara-Land, a totally different plant evolution must have occurred.

I moved from old, known fossil sites – eponym for important geological stages such as the Artinskian (derived from the city of Artinsk; today's Arti) or the Kungurian (derived from the town of Kungur). I visited better-studied localities with their richness in Early Permian (Kungurian) insects and plants such as Chekarda, and I looked for mainly unknown or forgotten hamlets such as Matvéevo. Especially there, I discovered a hidden paradise as testimony of the variegated flowering in the Permian period.

Geology

Although the whole Cisuralian Permian period has been studied for about 200 years, most researches have been done on marine stratigraphy and only in minor cases, on terrigenous sediments.

Therefore, my main attention was directed to lagoonal or near-shore deposits of that time. Our first researches concentrated first on the older Artinskian fossil sites. One was on the new road from the hamlet Panteleykovo to Arti (Sverdlovsk Oblast, GPS: Latitude 56°22'59.47"N, longitude 58°41'41.19"E). There, the Artinskian outcrop consisted of alternating sandstones, siltstones and argillites. Some of the layers held abundant and well-preserved plants, especially of Psygmophyllaceae, and few horsetails and ferns. No conifers were found. The other place was near Arti on the street from Manchazh till Ckekmash, inside a mainly abandoned waste disposal site (GPS: Latitude 56°24'59.34"N, longitude

Huge stems probably from some *Calamites* species. They crop out on the new road Panteleykovo–Arti (Artinskian period).

A slab with the entire *Psygmophyllum expansum* leaves, some ferns and *Paracalamites* from Panteleykovo near Arti (Artinskian period).

The main places visited in the Perm-Kungur-Lyswa area. Source: Thomas Gerasch and Google Earth.

58°14'57.67"E), also of the Artinskian age, which gave the same fossil plants and some conifers additionally. The layers were fragmented; therefore, the recovered specimen was small sized.

From the more recent Kungurian period, the Aleksandrovskoe section between Pridannikova and Achit, near the city of Krasnoufimsk (GPS: Latitude 56°43'10.02"N, longitude 57°49'57.61"E), the Mazuevka site near the Sylva River, about 12 km northeast of Suksun (GPS: Latitude 57°14'38.73"N, longitude 57°27'24.50"E), and the classic fossil site Chekarda, about 20 km east of Klyuchi (GPS: Latitude 57° 1'16.16"N, longitude 57°44'31.80"E), were studied.

Another fossil site was Matvéevo (Lyswa district), about 15 km south-west of Kormovishche (GPS: Latitude 57°47'1.80"N, longitude 57°50'59.60"E), where finest-grained gray to yellow terrigenous siltstones cropped out in diverse beds. The conservation was unique and mainly, all details of the insects and the plants, including their filigree parts, were maintained.

Although all these cited places were visited by us, most attention was given to diverse fossil localities around Matvéevo, being in my opinion the most forgotten place. In Matvéevo, diverse arenaceous and argillaceous outcrops with interesting paleontological material could be recovered. They were identified as Krutaya Katushka 1, Krutaya Katushka 2, Matvéevo, Krasnaya Glinka, and Taezhnoe. Three of them – Krutaya Katushka 1, Krutaya Katushka 2 and Krasnaya Glinka – lay near the Barda River crossing Matvéevo (Naugolnykh, 2014). It is thought that the Matvéevo group is of the Filippovian age, meaning slightly older than the Chekarda beds inserted as Irenian (Naugolnykh, 2014), both pertaining to the Early Permian age.

In contrast to the better-known fossil Lagerstätte Chekarda, the outcrops of Matvéevo were never studied intensely [For more de-

The major fossil site at Matvéevo lies some hundred metres before the village. Local farmers use the main deposit as stone quarry.

tail, see the well-executed and exhausting publication of Serge V. Naugolnykh ”*Fossil flora and stratigraphy of the terrigenous Kungurian beds (Lower Permian) of the basin of the Barda River (Urals, Perm krai). Stratigraphy and Geological Correlation*” (2014)].

There, sometimes also in thinly laminated, gray till white, yellow marls and siltstones, extremely well-preserved plants could be found. Especially in the higher sections, covered above by soil and extant vegetation, the layers also contained a fair amount of fossil insects. The plants were not frequent, but various, including all parts, from leaves to stems, flowers and fruits. Interesting was the huge number of different plant-genera and -species; the same could be said for the richness in different insect families.

Maybe in this region in the Early Permian age, shallow water lakes or lagoons were alternated by temporary streams flowing down. There the plants were deposited not at long transport distances. No marine organisms or shells were found. The percentage of hydrophilic plants such as Equisetales was relatively high, though conifers were rare. But the highest number of plants consisted of Paleoangiosperms, represented by flowers, leaves and fruits, as seen in no other part of the Paleozoic world. Older authors (Zalessky 1937b, 1939, Naugolnykh, 2014) have tried to put all these – from different Euro-American plant-remains to fertile organs – in one of the known classification systems such as Peltaspermales, Callipteridales or Ginkgophyta, but such methods and procedures were not successful. Therefore, this work tries to study the majority of these flora in a totally new, evolving concept.

About the illustrations and interpretations

All the drawings were made by me, as I recognized them on the fossil slabs; therefore, it will be only for the purpose of following scientists: Maybe another could see it in a different way. The coloring is a suggestive interpretation of me. The fascination with the development processes – that happened millions of years ago – is the impossibility of finding out many details, including the true colours or exact aspect. Maybe further findings will help to reach closer to the reality. The examination and survey of Permian Urals are still at the initial stages, and the certainty that surprising discoveries will be made in the next decades enlarges our horizon considerably.

Acknowledgments

I thank Jürgen Meyer and his Russian wife Luzia, with whom the German researcher Silvio Brandt compelled me to visit the Urals in 2015. Together we made the first steps in an unknown territory. The following years together with Thomas Perner, Thomas Gerasch and Martin Dammann, and with my young son Nicolas Wachtler, we tried to explore and study these interesting and undiscovered sites. We worked with passion and respect for nature and for the lovely people that we found everywhere. We felt like timeless passengers in remote geological times. Our interpreter Anastasia Liadova from Perm and our good and experienced driver Alexey Karavaev from Kirov helped us find all the hidden places.

Researchers in Matvéevo – From left: Martin Dammann, Nicolas Wachtler, Thomas Perner, Michael Wachtler, and Thomas Gerasch.

Two important geological times dedicated to the cities in the Perm region: Kungur(ian) and Arti(nskian).

The road to Panteleykovo near Arti (Artinskian period). The fossil sites crop out on both sides of the street.

The Early Permian world fossil site Chekarda

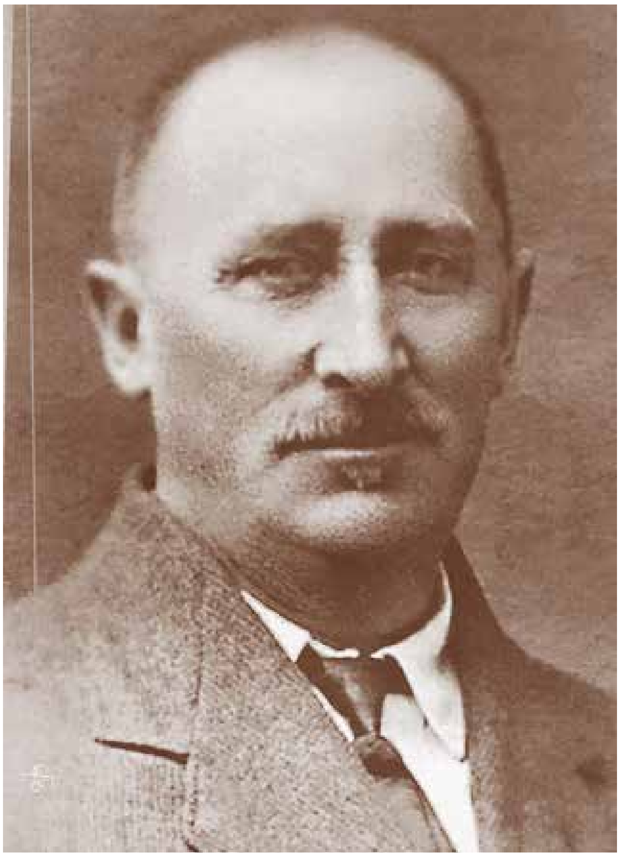
Indications to the way to Matvéevo in May and sightseeing over the lovely hamlet.

One of the fossil sites (Taezhnoe) near Matvéevo is located on the right side of the street, entering to the village.

The Chekarda-river

A short history about the paleobotanical researches in the Western Ural

Leading Russian paleobotanists in 1925 at Petersburg. From left: Afrikan Nikolaevich Krishtofovich (1885–1953), Iván Palibin (1872–1949), the only woman Maria Feodorovna Neuburg (1894–1962), and Mikhail Dmitrievich Zalessky (1885–1953).



Genrich Timofewitsch Mauer (1881–1940), local historian and researcher. His main legacy was to attract the attention to the fossil sites Chekarda and Matvéevo.

The first knowledge about the richness of Uralian fossils of 1838 we have is from Stephan Kutorga, Professor of Natural Sciences at the University of Petersburg, from his "*Beitrag zur Kenntniss der Organischen Ueberreste des Kupfersandsteins am westlichen Abhange des Ural*" (Contribution to the knowledge of organic remains in the Copper Sandstone of the Western Ural), mainly based on the material handled to him kindly by the local collectors. Apart from horsetail-stems (*Calamites*), he described and figured (Plate VI, Fig. 1 and Plate VII, Fig. 1) *Sphenopteris interrupte-pinnata* and *Sphenopteris cuneifolia,* two plants that Wilhelm Philipp Schimper changed to *Psygmophyllum*, later in 1870, due to their fan-shaped form.

For the most complete early studies about Angara-Land's paleobotany, we have to thank Mikhail Dmitrievich Zalessky (Russian: Михаил Дмитриевич Залесский, 15 September 1877 – 22 December 1946) who described in several works the Kungurian floras of the Perm Krai, especially of Chekarda and Matvéevo. Most part of the material was furnished to him by the local naturalist Genrich Timofewitsch Mauer (1881–1940), who moved in his free time by boat on the Sylva and Barda rivers, discovering on that way the world fossil sites, Chekarda and Matvéevo. Mauer had handed over a significant part of the material to the Natural Museums of Kungur and Perm.

Beginning from 1927, Zalessky described these floras, keeping attention also on the little fertile organs, and introducing new genus names such as *Sylvella alata* (a winged seed), *Bardocarpus aliger* (a fleshy stone-fruit) or *Craspedosperma bardaeanum* (an acorn resembling today's oak). Zalessky honoured G. T. Mauer with the genus name *Mauerites (artinensis)* (1933), and *M. gracilis* (1937), which he classified as Ginkgophyta, from the Krutaya Katushka locality near Matvéevo. In the 20th century, Sergei Meyen (Сергей Мейен) (1935–1987) from Moscow studied the Angaran Carboniferous-Permian plants, especially the conifers, intensely. He was one of the leading evolution theoreticians of Russia, bringing new concepts about the nonlinearity of evolution. In his footsteps followed Serge V. Naugolnykh (С.В. Наугольных), born in Perm (1967), one of the most active Russian paleobotanists. His main interest was the Uralian fossil sites of the Permian period.

An isolated continent, Angara, in the Paleozoic-Mesozoic era

From the Silurian-Devonian period – when the first plants evolved – Siberia and the Urals occupied a position apart from other landmasses, throughout the Carboniferous till the Permian. This position was between the 30th and 60th north latitude (today’s position of Paris is about the 48th latitude; New York is about the 41th latitude. In the Early Permian era, Middle Europe or the Southern States of the United States were near to the equator, about the 15th latitude). Therefore, this northern landmass called Angara – for a long time, till the Triassic period – formed an isolated continent with independent floras and faunas. Some of the theories about isolated landmasses were evolved by the Austrian geologist Eduard Suess. In his “*Antlitz der Erde*” (The Face of the Earth) in 1885, he hypothesized that in the Paleozoic era, there was one big landmass on the southern hemisphere that he called the Gondwana – from an Indian tribe, the Gonds – comprising Africa, South America, India and Australia. In the north, he located two big paleo-continents: North-America connected to Europe, which he called the Atlantis, and the other, he named Angara after a Siberian river, comprising parts of today’s Russia with the Urals and Siberia. He baptized the ocean separating this landmass as the Tethys. It was just a modern opinion based on connected land-bridges, several years before Alfred Wegener elaborated his continental drift theory in 1912.

A strange evolving trend

Between the Devonian-Carboniferous-Early Permian, a period of 70 million years, a separate development and symbiosis must have occurred on the Angara continent in contrast to other landmasses. Only in this way can we explain there the simultaneous appearance of all main insects and angiosperms that exist even today.

Not that the remodelling was more than extraordinary! The Euro-American landmass developed a multitude of gymnosperms such as conifers, ginkgos and cycads in the same time. The evolution step was not minor from this point of view. When the characteristic pistil-stamen-complex was “invented” all further steps were predefined. It should than not be surprising that in the Early Permian period in Angara, the angiosperms spread and diversified at the same time. Partially as hermaphroditic flowers, partially as male and female flowers separately on the same tree, we could find all forms like today’s flowering plants have. In that also the angiosperms are not so homogenous as always thought.

Surprisingly, in the Early Permian period, some 100 million years after the first appearance of the first rudimental plants, all main plant- and insect-families existing today worldwide were highly evolved and remained invariable for the next 300 million years. It is more difficult to elaborate a hypothesis about the movement of all gymnosperms and angiosperms in the following million years.

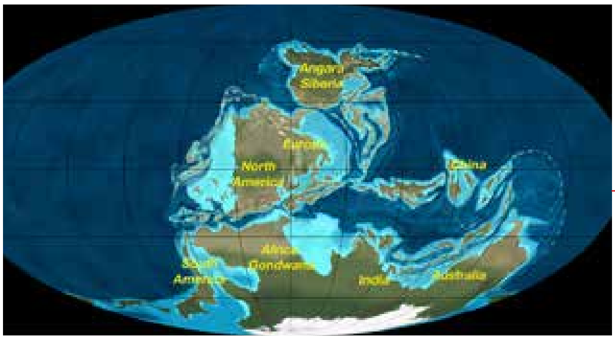
The Angaran landmass, from the Carboniferous till the Early Cretaceous period, was located north of Europa and North America and therefore, different climatic conditions had prevailed there. Cycads are found today across much of the subtropical and tropical parts of the world, and therefore exist some reasons, that they can not be encountered in raw climate zones. It can be supposed that in wintertime, the landscape in Angara-Land was covered by snow and the trees shed their leaves in autumn.

Beginning from the Early Triassic all continents were than united into the one supercontinent Pangea, assembled from all earlier continental units. In theory, all plants and animals could spread everywhere, but the questions are: Why certain conifers like the Araucarian-ancestor *Ortiseia*, abundant in Permian sediments of Europe, vanished in the European Triassic and are now distributed especially in the Southern Hemisphere but not in the Northern? Why we have the astonishing worldwide propagation of angiosperms beginning from the Cretaceous and not before? What happened to the angiosperm ancestors of Angara from the Early Permian till the Cretaceous? Why are there only rare insect findings on the European landmass all the time, whereas in the Permian Angara, all main insect families were present abundantly? And what caused great cataclysm like the often cited Permo-Triassic catastrophe?

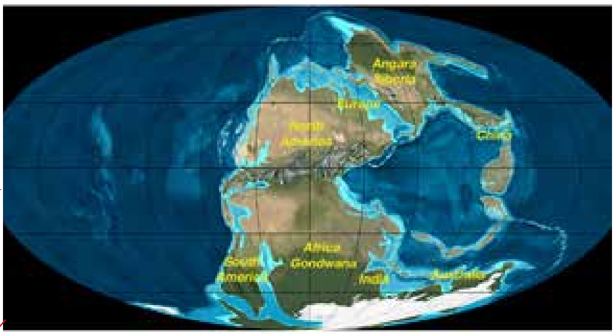
Some questions can be explained by the poor fossil record. The others need further hypothesis. It is true that the sight of evolving of plants changed in the last years enormously.

The drifting of the continent of Angara

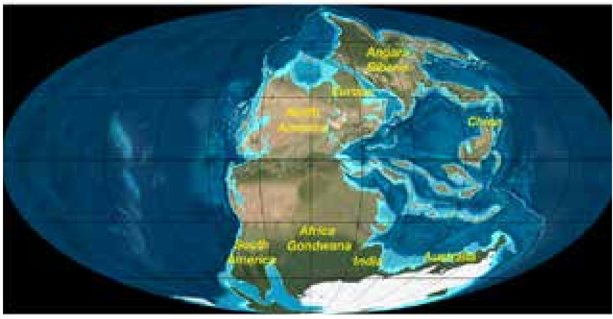
By the drifting of the terrestrian platforms during the last 340 million years, from the Carboniferous till the Early Triassic period, the Siberian-Uralian landmass formed a separate continent with their own fauna and flora. Especially the abundance of many insect families and paleo-angiosperm plants in the Early Permian period is surprising. Note the docking of Angara-Siberia in the Early Triassic with the other continents. After Wikipedia.



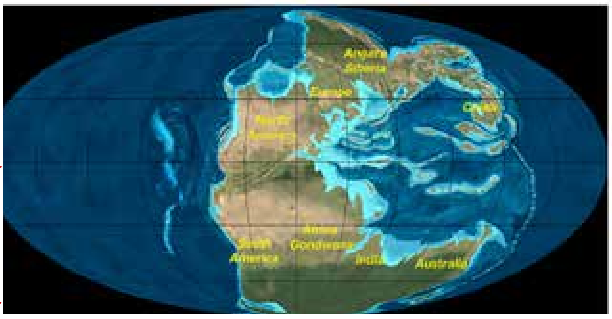
The continents in the Carboniferous, 340 Mio. years ago



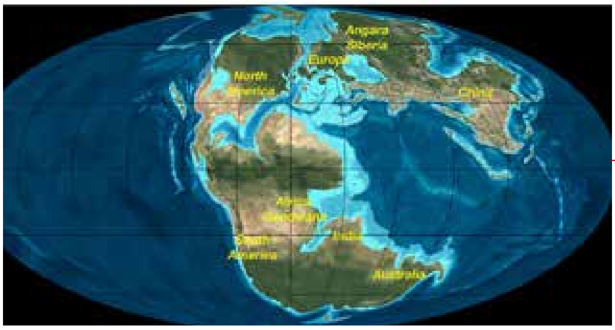
The continents in the Early Permian, 280 Mio. years ago



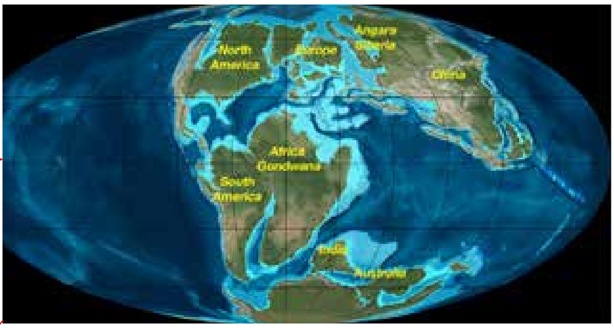
The continents in the Late Permian, 260 Mio. years ago



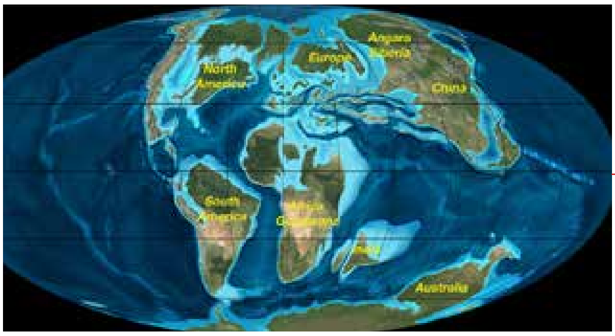
The continents in the Early Triassic, 240 Mio. years ago



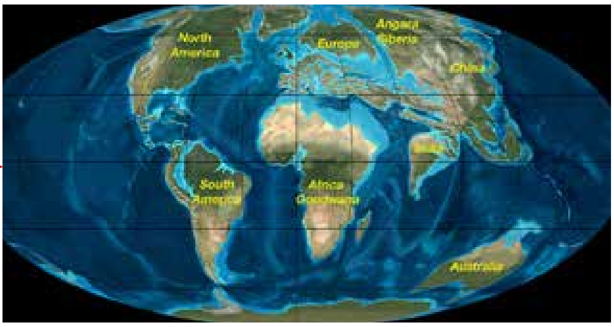
The continents in the Jurassic, 170 Mio. years ago



Continents in the Early Cretaceous, 120 Mio. years ago



Continents in the Middle Cretaceous, 90 Mio. years ago



The continents in the Eocene, 50 Mio. years ago

The characteristics of first angiosperms in the Early Permian period

If somebody walked 280 million years ago on the bank of the Matvéevo Sea, he would recognize a familiar vegetation. Maples, oaks, ash trees, some edible stone-fruits similar to cherries or apricots would surround him. On the meadows, herbaceous flowering plants would bloom in various colours between grasses.

The interested beholder will wonder at some slightly different looking deciduous trees or some strange vegetation. But he will accept this as a result of travelling for the first time to a new continent called by the mystic name Angara. Some of the plants would appear to him well known; for others, he would try to draw comparisons. The interested observer would be astonished by the multitude of flies and bees around him, or by the spiders, scorpions, ants and crickets on the ground. This was the first impression when I arrived first at Chekarda and then, more often at Matvéevo.

Like a keen observer, I collected some of the splendid looking insects and plants, as they were still alive. But all of them were lifeless, each with its own cause of death, such as burying of a cricket in a pit in the ground, a sudden gust of wind pressing a mayfly into the water, or a wave sweeping a careless ant or spider to the sea. I discovered fruits partially coated by their pulp with a drupe inside, hoping to germinate once. I recognized samaras from different trees flutter through the air. Their winged seeds tried to conquer new territories to colonize them. Insects flew from one flower to the next, covered with pollen dust. But, all that I saw happened around 300 million years ago, and I experienced all this only as a contemporary witness of a forgotten fossilised world.

A lost continent and an "abominable mystery"

The evolution of angiosperms represents till now one of the central questions of natural science. Charles Darwin's frustrations about the astonishingly late propagating of flowering plants, revealed in his letters to Joseph Hooker, Gaston de Saporta, and Oswald Heer between 1875 and 1881, entered history (Friedman, 2009). After that, researchers all over the world tried to bring light to this question.

Just in March 1875, the origin of flowering plants caused Darwin considerable concern; therefore, he wrote a letter to the well-accredited Swiss researcher Oswald Heer, saying, "*Plants of this great division must have been largely developed in some isolated area, whence owing to geographical changes, they at last succeeded in escaping, and spread quickly over the world.*"

Darwin was extremely distressed by the abrupt origin and fast spreading of the flowering plants in the Cretaceous in complete contrast to his theory about the slow evolution of plants and animals through million of years. Therefore, he speculated a slow and long evolution on an extinct or destroyed landscape or a lost continent.

The absence of angiosperms made it impossible for other animals, especially the insects, to evolve. It was Saporta in 1877 who elaborated on the philosophy of their co-evolution. All these ended then in the famous letter about the "*abominable mystery*" which Darwin wrote to Joseph Hooker on 22 July 1879. But, another often-thought main preoccupation of his was not that in this time, little was known about the closest relatives of flowering plants or their phylogeny. Darwin's abominable mystery was his abhorrence to the fact that evolution could be rapid and even saltational against his theory that "*natura non facit saltum*" – *nature does not make a leap* (Friedman, 2009).

The angiosperm fossil record confirmed in the 19th century the rich radiation of flowering plants between the Early and Middle-Late Cretaceous, but not before. It was not only the "*abominable mystery*" that Darwin coined in this connection, but in an equal manner, he regarded it as the "*most perplexing phenomenon*". Especially, Oswald Heer, an acknowledged Swiss naturalist and a proponent of the saltational evolution, wrote in a letter in 1875 that the angiosperms "*which forms the bulk of modern vegetation, appears relatively late and that, in geological terms, it underwent a substantial transformation within a brief period of time.*" All these stand in total contrast to Darwin's slow gradualism. So, according to him, it was effectively a rapid development or surprisingly a long interval of a missing fossil record.

These thoughts preoccupied Darwin nearly till the end of his life in 1882. On 6 August 1881, he wrote again to his friend Hooker, "*Nothing is more extraordinary in the history of the Vegetable Kingdom, as it seems to me, than the apparently very sudden or abrupt development of the higher plants. I have sometimes speculated whether there did not exist somewhere during long ages an extremely isolated continent, perhaps near the South Pole."* There or in the North between America and Europe, he postulated a much earlier birthplace of all higher plants as well as the pollinating insects.

The "invention" of the flower

The extraordinary diversity of angiosperms makes it difficult to elaborate an analogy, but several properties unite them and distinguish them from other seed plants. Especially, the reproductive features classify them as unique in the plant kingdom. These features are the flower formed by female carpels and male stamens, often surrounded by a perianth, consisting of parts that are all of one kind (tepals), or differentiated into an outer circle of sepals and an inner zone of often colourful petals (Friis et al., 2011). Most angiosperms are bisexual (hermaphroditic) with both carpels and stamens in the same flower; some are unisexual with separated androecium and gynoecium. A characteristic of angiosperms is that the stamens are clearly differentiated into a fertile anther and a sterile filament, and the female organ is distinguished by an ovary that encloses the ovules and a stigma that receives the pollen grains.

Another point of view

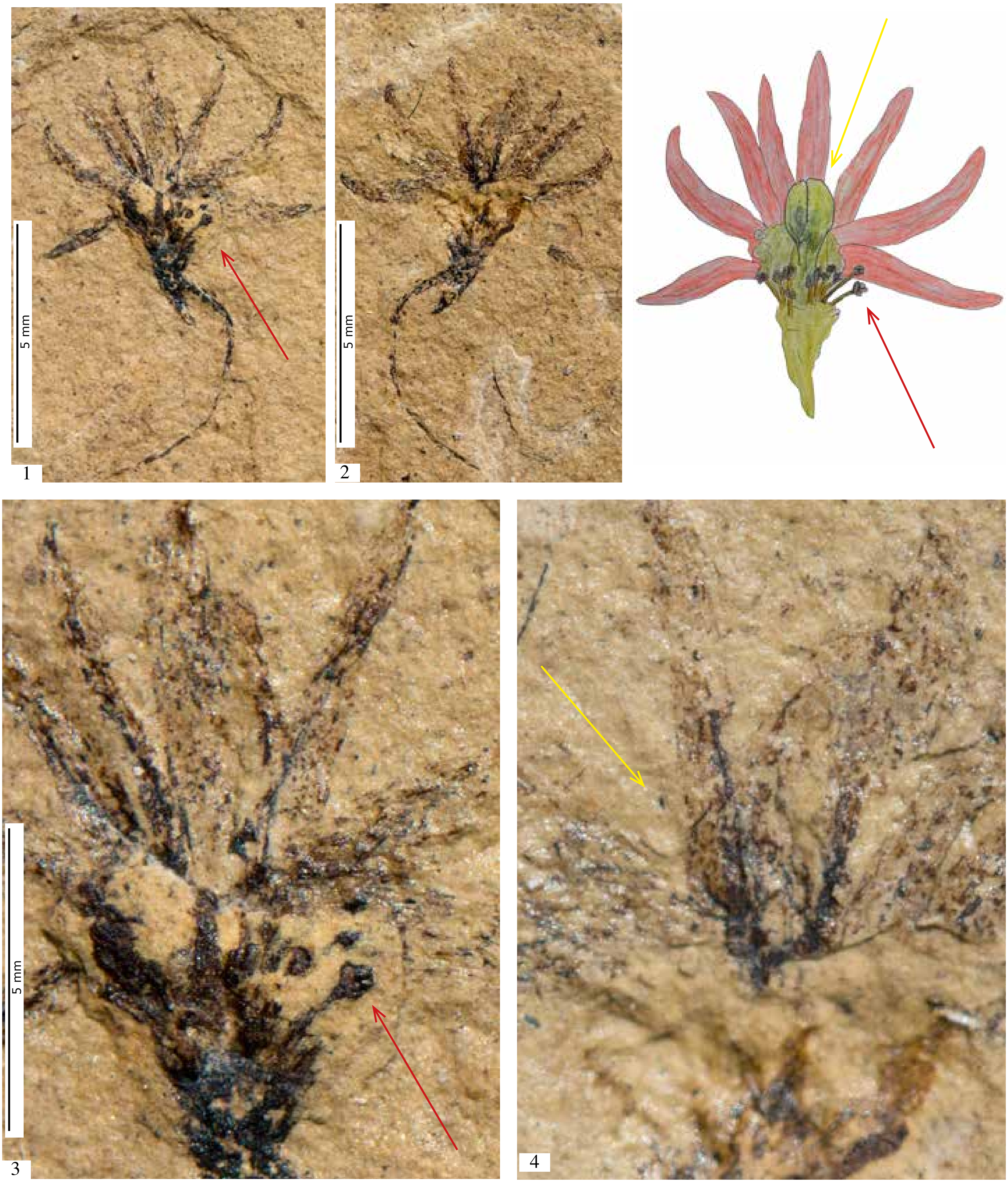
If we are able to find flora prior to the Cretaceous with many of these properties, we come nearer to the answer of the "abominable mystery." From the Devonian to the Carboniferous and Permian periods, all main tribes existing today such as lycopods, horsetails, ferns or gymnosperms, including conifers, gingkos and cycads, had been present and fully evolved. All the following 300 million years succeeded only in segmentation and breakdown to further genera and species. Therefore, the question is allowed: Where were the angiosperms? Darwin's thoughts and anxieties can be understood fairly – also, his vision about a lost continent. It can be supposed that also the angiosperms appear on the world stage in an astonishing simultaneity with other plants in the Permian. If the hypothesis of the hermaphroditic flowers can be proved by Paleozoic findings the "Magnolia-theory," collapsed like a house of cards.

Once the hermaphroditic flower was created, all further developments and segmentations could be deduced easily. Why could this not happen in the Carboniferous-Permian border? The way to the stamen, composed of a sterile filament and the pollen-generating anther, was as difficult and inventory as the pollen-bract-cone of gymnosperms. These are valid also for the ovary of angiosperms, in contrast to the manifold seed- and cone-peculiarities of the gymnosperms.

All depends on the point of view: Assuming that first, the former continent of Angara-Siberia was discovered and for decades, the researchers studied there the evolving of floras and faunas, they would be surprised about the Euro-American completely different vegetation, especially of gymnosperms. We are too much influenced by our Western thinking and we believe only what we have discovered in Europe or America. In Europe, these scientists would wonder about the distinctness of the multitude of gymnosperms. They would note that the juvenile to adult stage would not be so different in the conifers, ginkgos or cycads because of their cone-like structures. They would note with surprise that the typical Angaran flowers or blossoms will be mainly unknown in Euramerica, apart from some *Peltaspermum* discs.

But these Angaran researchers would also identify similarities: that the aliform seed from *Sylvella* (Acer ancestor) or *Sadovnikovia* (Fraxinus progenitor) has their counterpart in conifers like *Majonica* or *Wachtlerina* (Abies ancestors); that the microleaves-coated seed of the conifer *Ortiseia* (Araucaria ancestor) has similarities with *Craspedosperma* (Quercus ancestor); that the fleshy stonefruit *Bardocarpus* has an opposite in former Euramerican ginkgo-ancestor *Baiera.* Some of the Angaran scientists would wonder how little insects flew in the Permian Euramerica.

And surprisingly, they would ascertain that the ocean separating the two continents and also their latitude-difference avoided for a long time a common flora-and-fauna exchange.



Hermaphrodite flowers of the Early Permian Angara-Land

1-4. Flower evidencing androecium and gynoecium. The filaments are topped by an anther with pollen (1+3). The pistil is better visible on the counter plate with the impressions of two ovules (2+4). The flower is surrounded by sepals and petals (MAT 31). Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum

A common origin of the furcating leaves

The evolving of angiosperms and gymnosperms is based on the Ypsilon-furcating leaves of Devonian times. We can observe it all over the world till the Early Permian; then the plants modified just too much to recognize this feature. The most primitive conifer, *Perneria*, had bifurcating leaves, as well the most archaic cycad, *Wachtleropteris* – both recorded from Early European Permian. This is also valid for European Ginkgo-ancestors like *Baiera* or the progenitor of all Pinus conifers *Valentinia* (Wachtler, 2013, Perner, 2013, Wachtler 2015).

On the other side, the most primitive angiosperms from Angara, the maple-ancestor *Sylvella alata, Sadovnikovia belemnoides* (thought as fraxinus progenitor), had furcating leaves, and also, the oak progenitor *Craspedosperma bardaeanum* can be deduced to have lobed leaves. But interestingly, all these gymnosperms and angiosperms – having mainly the same leaf-features –are from the beginning characterized by different fertile organs.

As all gymnosperms derived from the Ypsilon-furcating leaves, we can trace the same in the Angaran-Province, but under totally other circumstances. The original foliage character was a bifurcating leaf, but the juvenile reproduction organ a segmented flower, composed of leaves varying from four to five, and more parts. A similar composition we had in Euroamerican Permian conifers like Pine-ancestor *Valentinia* (Wachtler, 2015), or also in some Euro-American Peltaspermales. But the further evolving stage in Angara was completely different from the Euroamerican gymnosperms.

Heterosporous and hermaphroditic

Hererosporous fertile organs on the same plant are present in angiosperms (a good example is the birch), as well in gymnosperms such as cycads or conifers.

Hermaphroditic reproductive system – having both male (micro) and female (mega) parts present on the same flower or cone – is not exclusively a feature of angiosperms. Spores of two types on the same cone are just in the *Selaginella* clubmosses and especially pronounced in the *Sigillaria* lycopods or better recognizable in the Triassic *Sigillcampeia* (Wachtler, 2016). They were defined as heterosporous, with microspores and macrospores on the same reproductive organs. Bearing only one megaspore within a multicellular gametophyte as in *Sigillcampeia* can be interpreted as a clear sign indicating the direction of evolution of more complex seed plants.

But the pollen organs in angiosperms, usually divided in filament and anther, are much fragile and reduced in size than the pollen scale of gymnosperms. The ovules or seeds were otherwise inserted in the gynoecium – a hollow structure which protected the ovules internally. In gymnosperms, fertilization can, therefore, occur up to a year after pollination, whereas in angiosperms, fertilization begins very soon after pollination.

The question of more basal or advanced that does not exist

Usually our knowledge is based on the doctrine of Magnoliaceae as the most basal angiosperms, often called as the ANITA grade, composed of single species shrub Amborella from New Caledonia, Nymphaeales (water lilies), the Illiciales, Trimeniaceae, Austrobaileya. But these so-called "Basal Angiosperms" cannot be considered a monophyletic group; they are too different among themselves. As "primitive" was considered a flattened and laminar stamen, as we have in *Magnolia, Degeneria* or *Austrobaileya*. But Early Permian Angaran floras manifested just the filament-anther stamen. As rudimentary are regarded numerous tepals or many separate carpels, but the Angaran flowers do not confirm this evolutionary way being just to advanced. The organs were flowers with only one or a few gynoeciums.

So, we arrive at the same phenomenon as in Euro-American gymnosperms. For a long time, it was thought that the genus *Cycas* was the most primitive and from that evolved all other cycads, or the Araucarians built the most basal conifer lineage. But in Early Permian, we have fully evolved Cycas ancestors (*Bjuvia, Taeniopteris*) with their multi-seeded covering-blade as well as the Zamia-progenitors (*Nilssonia*) with their two-seeded scale. On the Carboniferous-Permian border, we have winged-seed conifers such as *Majonica,* one-seeded Araucarias (*Ortiseia*), more-seeded seed scales (*Voltzia*) conducting to all known present

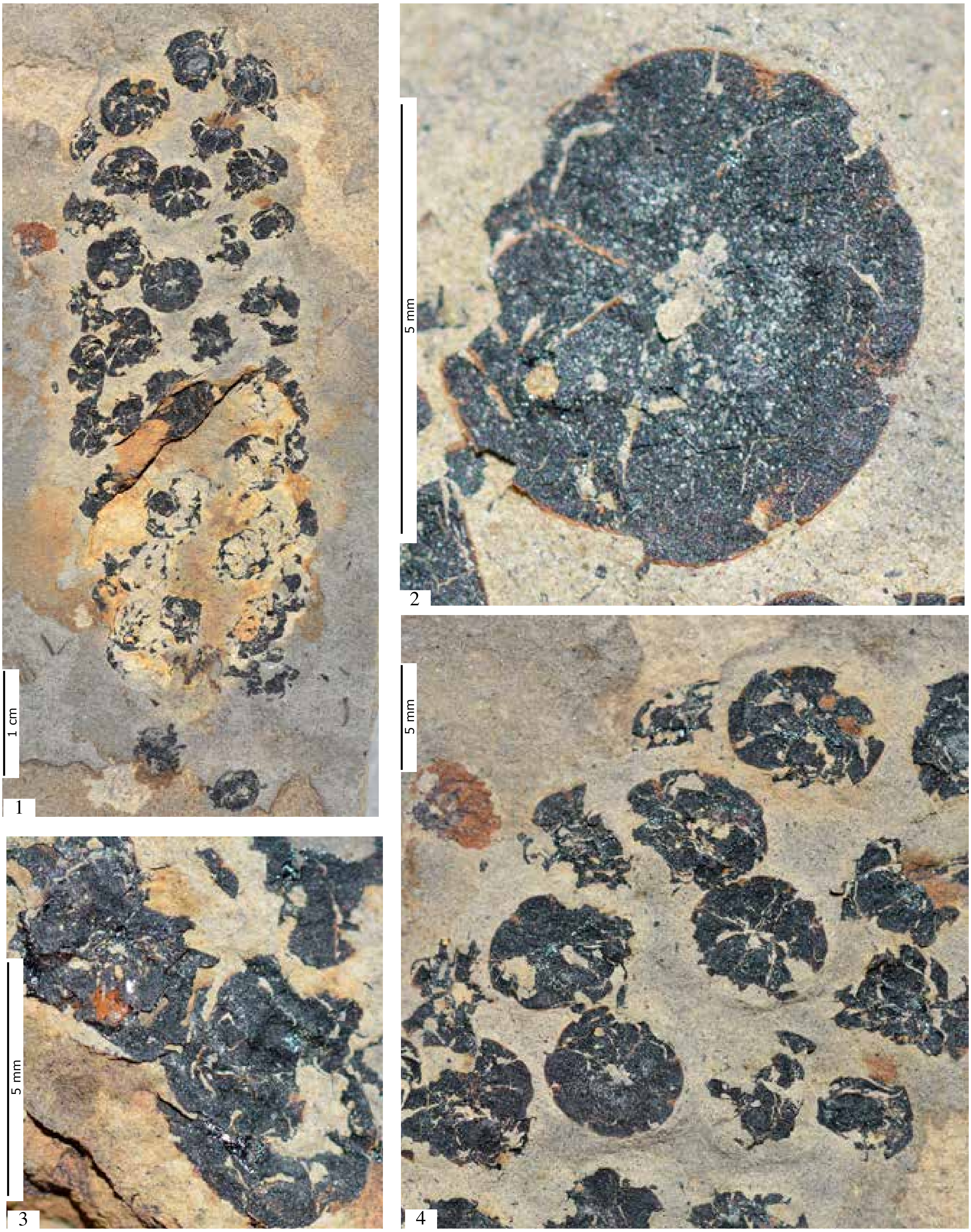
1

2

3

Hermaphrodite flowers of the Early Permian Angara-Land

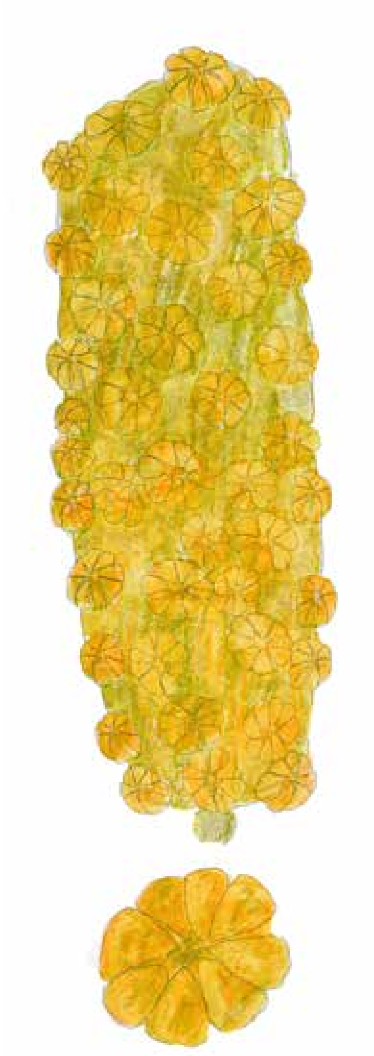
1-4. Flower with whorls of stamen (MAT 351); plate, counter-plate and reconstruction, Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum



Juvenile, mainly-closed flowers probably belonging to maple-ancestor *Sylvella*

1. Whole inflorescence with several mostly-closed flowers; 2. Detail of a closed blossom; 3–4. Some of the flowers are open enough to reveal the free stamen. It is difficult to connect these inflorescence to some of the plants (MAT 104); Matvéevo, Kungurian (Early Permian) Coll. Gerasch.

1. Flower inserted as *Scirostrobus pterocerum* (Naugolnykh) Dowels et Naugolnykh. Reconstruction (MAT 366), Matvéevo, Kungurian (Early Permian) Coll. Wachtler

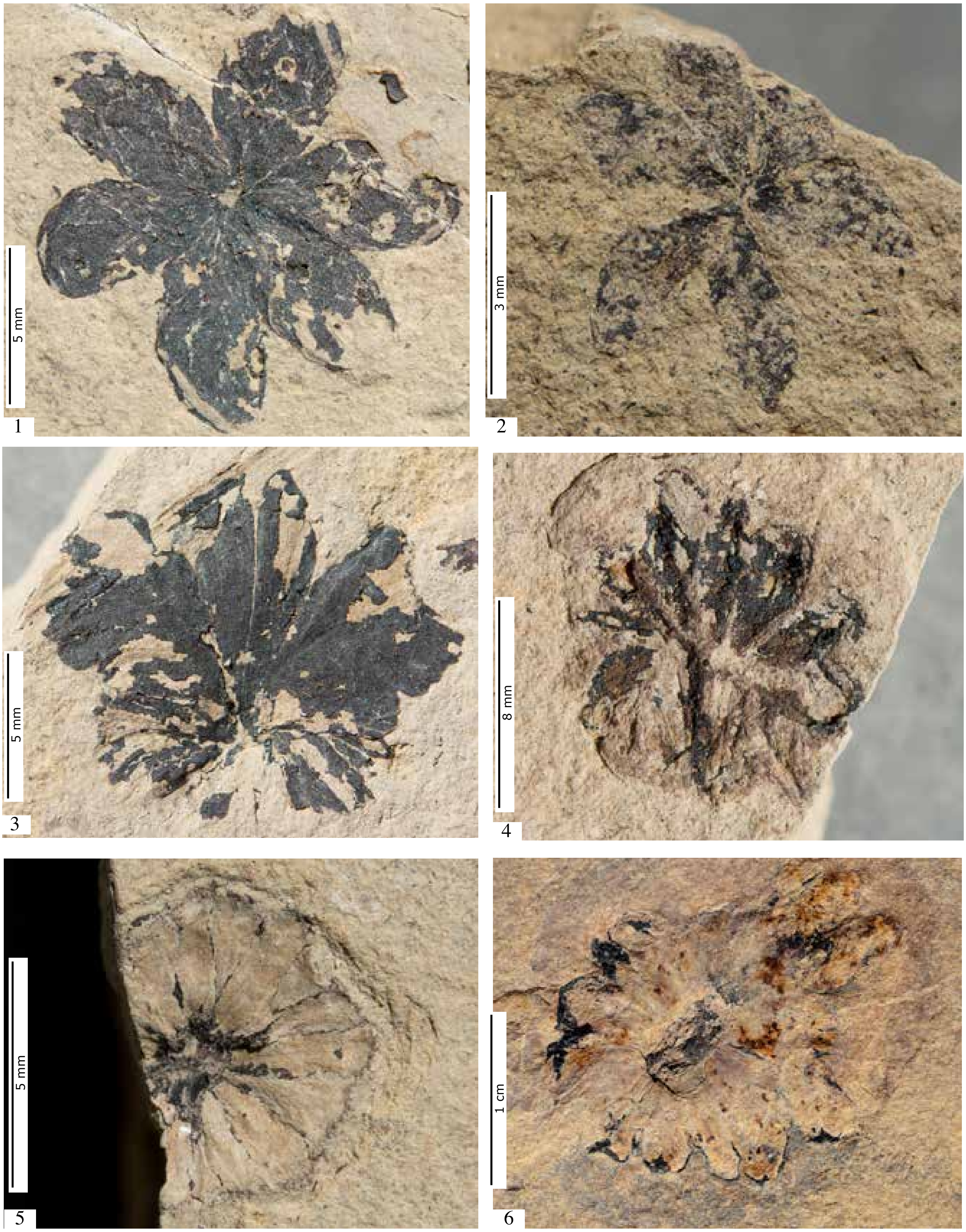


Also, an accurate study of the inflorescences helps not to identify the plant to which they belong. These flowers are characterized by partially visible androecium and gynoecium.

Even if the preservation is excellent, the inner parts cannot always be "read" totally.

Typical flower-compound of a maple

2. Single flower of unknown classification, probably belonging to *Sylvella alata.* Reconstruction, (MAT 44); Matvéevo, Kungurian (Early Permian) Coll. Wachtler



Flowers from six different families

1. Flower with six petals and some sepals (MAT 200); 2. Flower with six petals, with the androecium and gynoecium (MAT 349) inside; 3. Flower resembling today's Convolvulus (MAT 342); 4. Flower with pedicel (MAT 352); 5. Part of a flower with many petals forming the corolla (*Sylvocarpus armatus*, Naugolnykh, 2008) (MAT 357); 6. Flower's reverse side with part of the stipe (MAT 01); Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum

Reconstructions of different flowers

The blossoms in Early Permian Angara-Land were highly specialized and diversified. Reconstructions of the fossilized flowers are on the right side

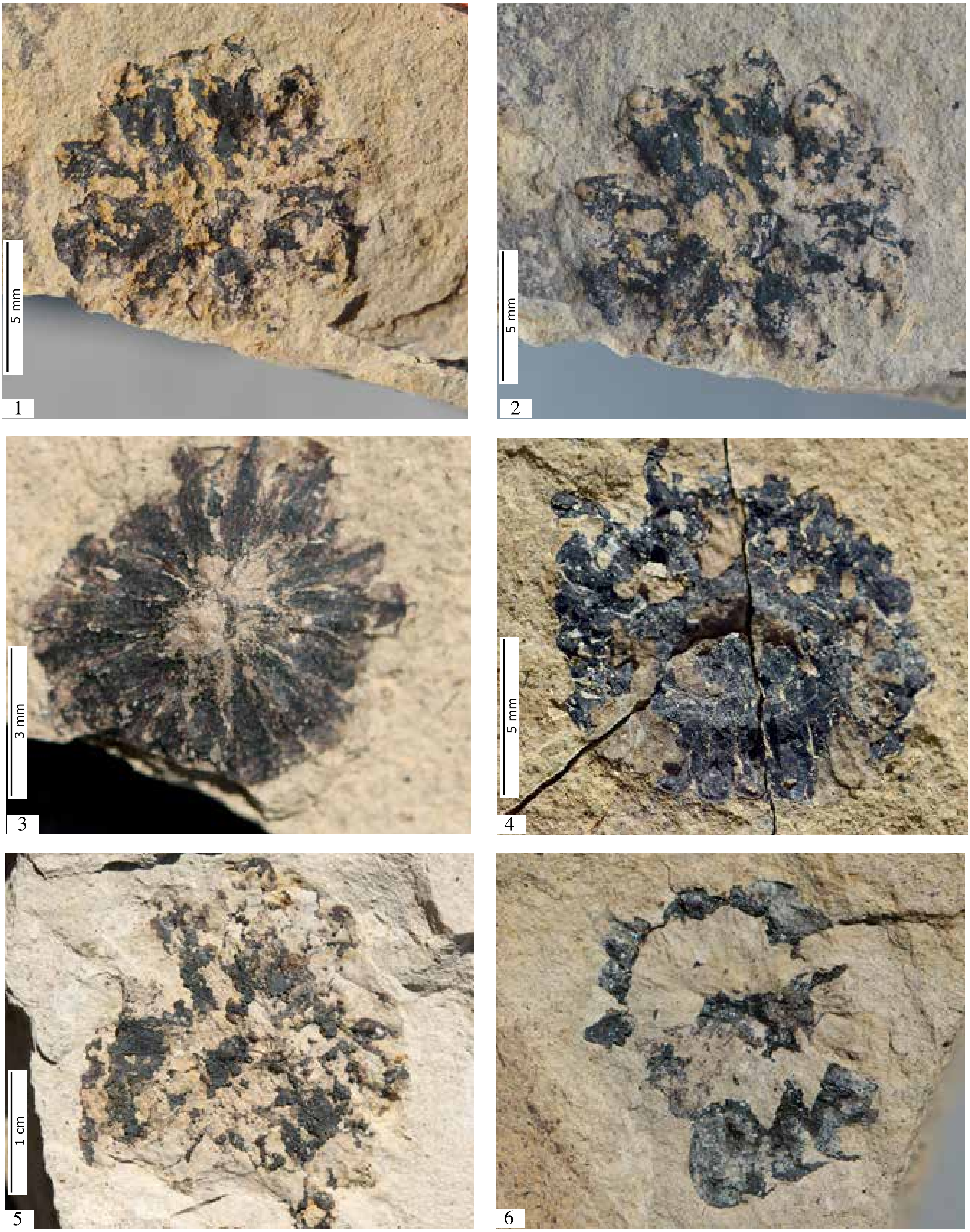
Today's flowers

*a. Clematis patens (*Ranunculaceae); *b. Liatris cilindrica* (Blazing star - Asteraceae) visited by an insect; *c. Platycodon grandiflorus* (Balloon flower - Campanulaceae)

day Cupressus-conifers such as *Cunninghamia, Cryptomeria* or *Juniper.* Besides, we have Pinus ancestors (*Valentinia*) and Ginkgo forefathers (*Baiera*).
The same happened in Angara with their multitude of deciduous trees, low-growing flowers and grasses.

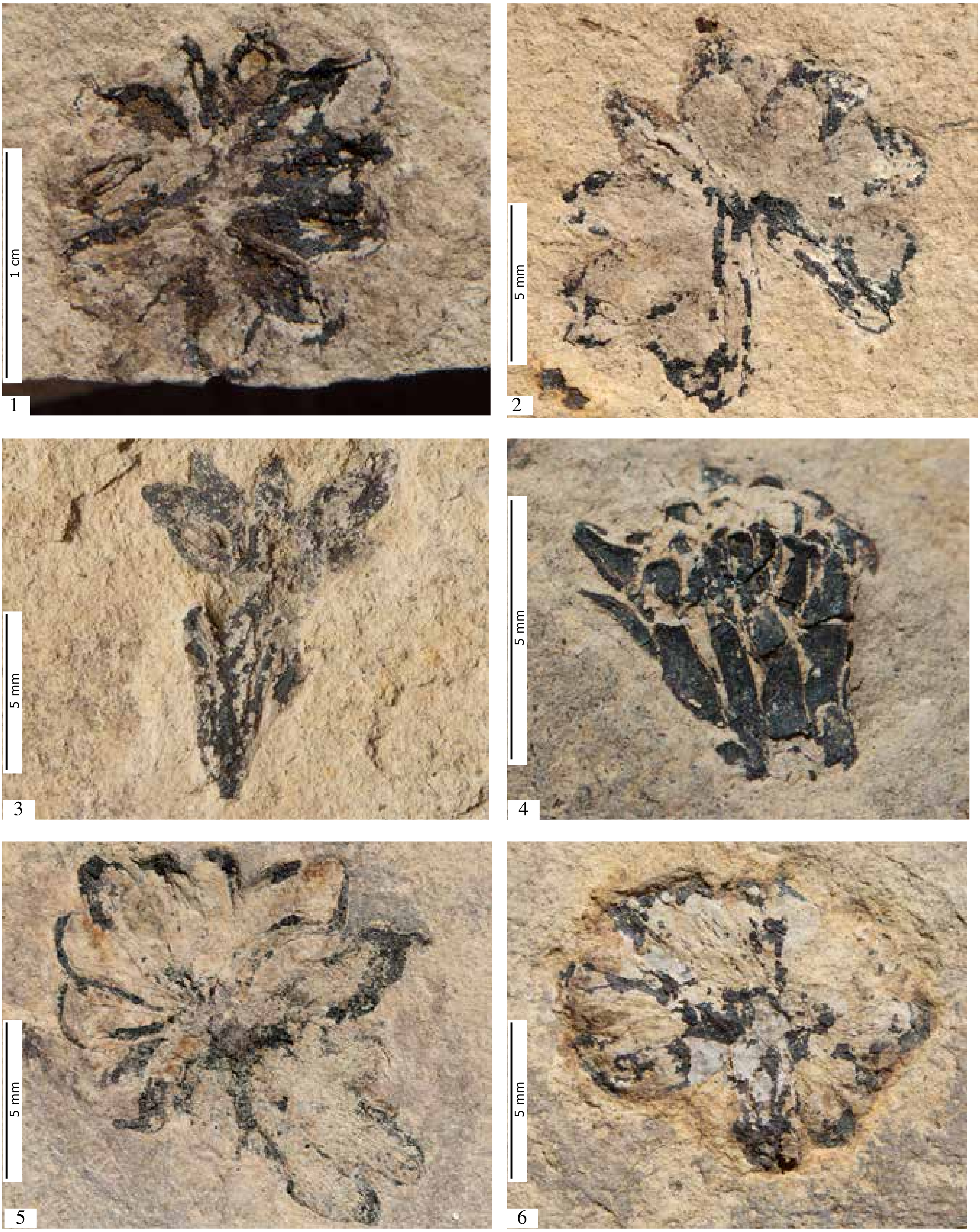
Why are there so many different angiosperms from the beginning?

So, we can analyze the above-mentioned question, which can be enlarged as: "Why are there so many insect groups in these remote times?" Today we have much more angiosperms with about 230,000 species, forming about 89% of all plants, and only 0.29% gymnosperms; there are about 4% ferns, 3.61% mosses, 2.28% liverworts, but only 0.38% lycopods and 0.05% horsetails (Crepet & Niklas, 2009).
But when we take as indicator the biomass, then the huge conifer trees change the statistics. So, till now, we can only establish that between the Middle Devonian – the era of evolution of the first trees and shrubs – about 390 million years ago and the Carboniferous-Permian boundary, in a time interval of only 100 million years, all main today's dominating plant tribes and families evolved, as well as all the insect groups.



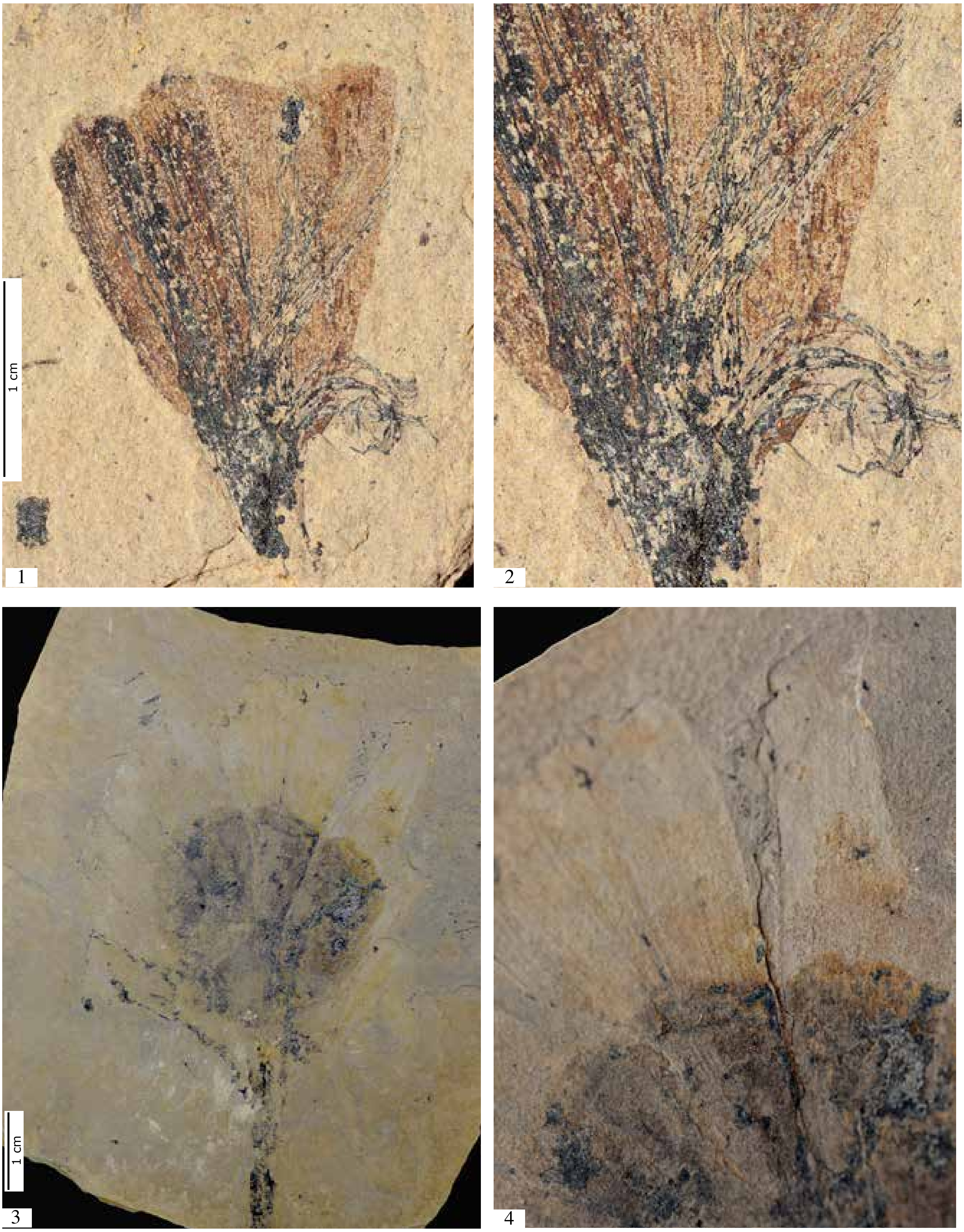
Different flowers from Early Permian Angara-Land

All these flowers differ each from the other. In the past they were often inserted as *Peltaspermum* bringing them near European seed ferns. 1-2. With pollen organ (MAT 203); 3. (MAT 194); 4. (MAT 109); 5. (MAT 363); 6. (MAT 244); Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum



Different flowers from Early Permian Angara-Land

Blossoms with different character 1. (MAT 416); 2. (MAT 207); 3. Lateral view with androecium or gynoecium (MAT 347); 4. Lateral view (MAT 416); 5. (MAT 01); 6. (MAT 341); Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum



1-2. Flower with petals covering the stamens and stigma. The filaments are delicate (2), the probable ovary is collocated on the basal side of the flower (MAT 459). Matvéevo, Kungurian (Early Permian) Coll. Gerasch; 3–4. Another flower with the impressions of the inner fertile organs with androecium or gynoecium (Permian Period Museum, Perm). Reconstructions seen on next side.

Reconstruction of diverse undescribed flowers from Matvéevo. Above, MAT 459, with the delicate filaments and anthers and carpel. Below, reconstruction of a bisexual flower with details of the androecium or gynoecium.

Evolution of the flower

In contrast to the gymnosperms, lycopods, horsetails or ferns, the angiosperms are characterized in the juvenile stage by a characteristic flower, from which originates the fruit in the adult stage. Unfortunately, it is not easy to guess the final fruit from the blossom alone. If it is difficult to work out to which extant fruit a flower belongs to, much more complex it is for fossilised plants. Who can imagine from which flower originated a cherry, an almond, an apricot or a plum, if you have only a blurred black and white photo to examine? So, only the consideration of many facts (in this case, fossils) helps to connect the various and time-staggered parts of a plant.

In the early Permian sediments from Chekarda and Matvéevo, many different flowers could be found. They were inserted as *Asterodiscus, Aspidion* (Zalessky, 1937b), *Peltaspermum, Permotheca* (Naugolnykh, 1991, Naugolnykh & Kerp, 1996, Naugolnykh, 2009) without going more into details of which plant they belonged to. Additionally, little attention was given to the inner details of these inflorescences. Considerable differences exist between the plethora of fructifications. Some had five petals as many of today’s flowers like the Rosaceae (cherries, apricots, and plums). Others had six petals, or even more more.

Specimen MAT 31 – front view of a hermaphrodite flower – evidences well a diverse stamen with anthers and a gynoecium, also with the impressions of some ovules. Another example of well-defined androecium is represented by MAT 351. It is surprising, and speaks for the extraordinary preservation in these Matvéevo layers, that the slender filament as well the anther with the pollen sacs are visible.

All these big evolution steps on the Carboniferous-Permian border are till now recorded only from old Angara-Land. The concept of slender filaments with pollen-producing anthers was never directly recognized in the European Peltaspermales. It is doubtful that an equal can be found in other fossil sites of the Permian Northern Hemisphere. From France to Germany or the Alps were examined in the last centuries much more than the Siberian Angara, but apart from some Peltaspermales (where this charac-

Tettoedischia elongata **- The insect with long proboscis (Early Permian)**

(Alternative combination: *Macroedischia elongata*). In Matvéevo, an insect with an extraordinarily long proboscis was discovered. But which plant needs such a long nectary? It can be the same story happening with Charles Darwin when in 1862, he was sent a star-shaped orchid flower (*Angraecum sesquipedale)*, with an exceptionally long nectary (as long as 30 cm) from Madagascar. In 1907, more than 20 years after Darwin's death, the pollinating insect *Xanthopan morganii praedicta* was discovered fulfilling Darwin's prediction. Courtesy: Perm Museum of Antiquities.

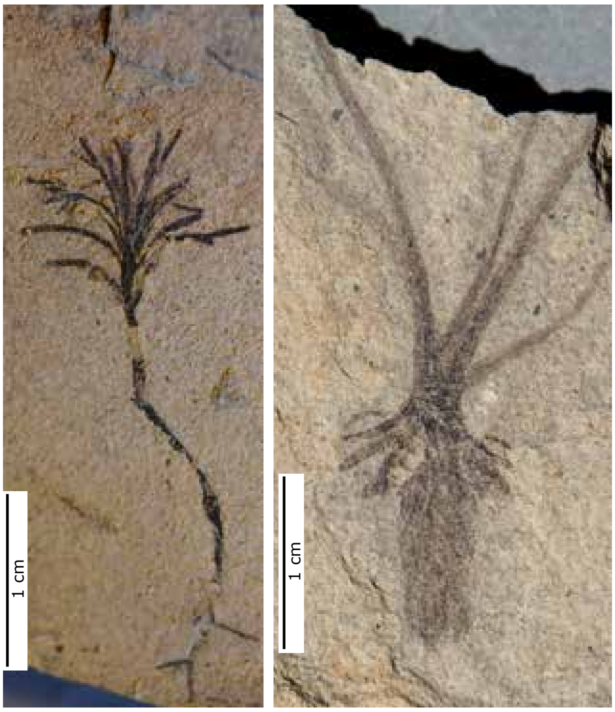
teristic anthers and filaments were never found) all over the Paleozoic-Mesozoic, such a concept is missing. It is not to exclude that the Peltaspermales with A*utunia-Rachiphyllum-Scytophyllum* leaves had some preangiospermous features, but they never incorporated pollen and ovules on the same flower in a hermaphroditic way. Not necessary that they must be equipped with such characteristics, additionally, all over the European Permian and Triassic, the Peltaspermales play only a marginal existence between the dominant horsetails, ferns and gymnosperms especially. In some well-known and studied locations such as the Middle-Triassic fossil site Ilsfeld, for example, they completely lack such characteristics.

Evolution of the fruits

Another feature characterizing the flowering plants is their fruits. They can be very different from one another. The angiosperms produce first an embryo, complete with a constant flow of nutrients from the plant into the developing seed. Therefore, a fruit is a maturing ovary and the diversity is high. They can be fleshy, dry, or the ovary can be fused with other kinds of tissues. They can be dehiscent, when the pericarp splits open to release the seeds, or indehiscent, when the pericarp encloses the whole fruit as the dispersal unit. The fruits of flowering plants protect the enclosed seed and aid in their dispersal. They can be dispersed by wind, like the samara of an ash or maple, or by water or by animals. Seeds contained in edible fruits must possess the ability to survive the ingestion of animals also.

Development of the samara

Aliform seeds are found in many gymnosperms such as the *Pinus* conifers, the firs and spruces, and in angiosperms such as maples (*Acer*), ash trees (*Fraxinus*) or elms (*Ulmus*). Their genesis must have occurred, therefore, two times independently: around an ovule/seed, various microleaves (called in Devonian times "emergences") aggregated together to form a flying reproductive organ (Wachtler, 2016). Early Permian conifers such as *Majonica* and *Wachtlerina* evidenced



Seedlings from Matvéevo

Two undefined seedlings (MAT 329, MAT 383); Matvéevo, Kungurian (Early Permian) Coll. Wachtler

these evolution steps in gymnosperms, while the Early Permian *Sylvella alata* (the potential Acer ancestor) and *Sadovnikovia belemnoides* (thought as *Fraxinus* progenitor) evolved these in angiosperms in the Angara continent. The same occurred in *Araucaria-Quercus*. Microleaves (emergences) surrounded the seeds of the Araucaria ancestor *Ortiseia*, that today we recognize only one in the scale-embedded seed, and independently, they coated the single seed of the oak-ancestor *Craspedosperma bardaeanum* partially on the basal side.

The fleshy arils or fruits of the cherry, plum or apricots present in the Angaran Early Permian period as in *Sylvocarpus armatus* find their counter-part in Northern Hemisphere Ginkophyta such as Permian *Baiera*, or in *Ullmannia* gymnosperms. Also, their emergences cling their seeds, forming a compact aril.

Wind and insect pollination

Although several theories propagate wind pollination (anemophily) of angiosperms as derived from insect pollination (entomophily) in response to pollinator limitation (Culley et al., 2002), an antecedent wind versus a both-wind-and-insect pollination (ambophily) is more plausible to gradual insect pollination. Today, wind pollination is prevalent in about 18% of angiosperm families such as the Ulmaceae, Juglandaceae, Betulaceae, and Fagaceae, and in grasses such as Poaceae and Juncaceae, all being probably present just in the Early Permian era.

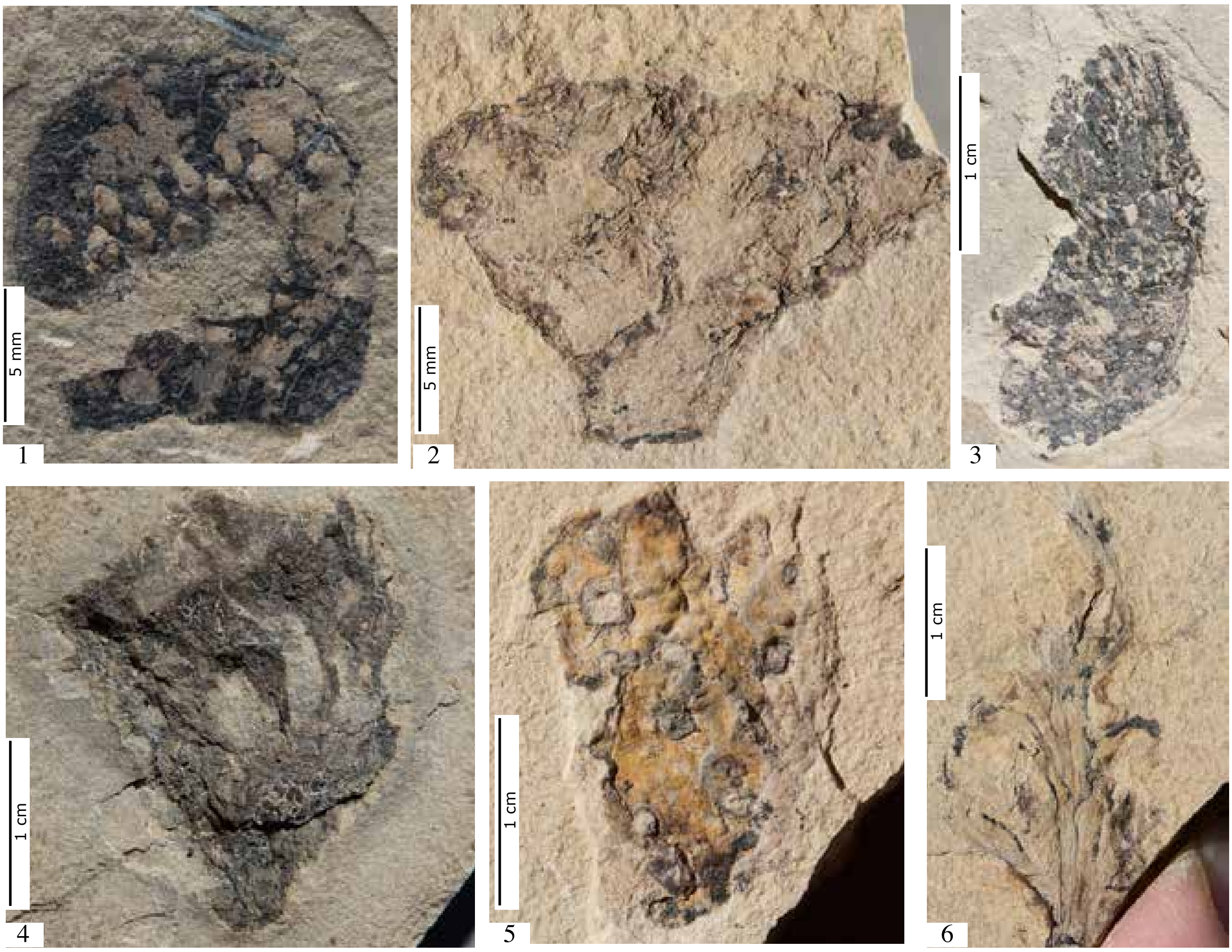
Enigma of the unilateral leaf growth

An interesting feature manifested in Angarian plants is the one-sided growth of the foliage. This is valid not only for preangiospermous flora elements such as *Permocallipteris retensoria* or *Psygmophyllum expansum,* but also for the conifers, especially *Taxodiella bardaeana*. These irregular alternations of branches of different length is till now an unresolved problem, that do not exist in Euro-American floras, characterized by symmetrical and geometrical fern fronds such as *Autunia* or conifers from the *Walchia* group (Wachtler, 2015).

Did the Permo-Triassic catastrophe cause further radiation of the angiosperms?

If we have mostly all flowering plant tribes in the Early Permian Angara-Land, why could they not radiate all over the landmass when Pangaea assembled to one global continent? An audacious hypothesis can be searched in the largest known volcanic events of the last 500 million years of earth's geological history – the forming of Siberian Traps – spanning one million years between the Permian–Triassic boundary, about 251 to 250 million years ago. Today, basaltic lava covers about 2 million square kilometres there, but the original extension is estimated at about 7 million square kilometres approximately in the region from Siberia over the former Angara-continent.

If this global catastrophe happened really, and this is based on facts and documented by analyses from the extinction of many animal tribes such as the Trilobites or many Nautilids, Angara was the most involved landmass and therefore, it is plausible that this landscape suffered more than all others. It can be suggested that only with difficulties the angiosperms survived on some isolated refuges and that too on a restricted and marginal level. Probably for a long time, till the Cretaceous, they were not able



Fruits of unknown affinities

1-6 Early Permian Angara-Land variation of Paleoangiosperms must be higher than what was thought. There are many fruits, cones or seeds, that till now cannot be inserted with satisfaction. (MAT 365, MAT 364, MAT 384, MAT 376, MAT 345, MAT 385), Coll. Wachtler - Dolomythos Museum

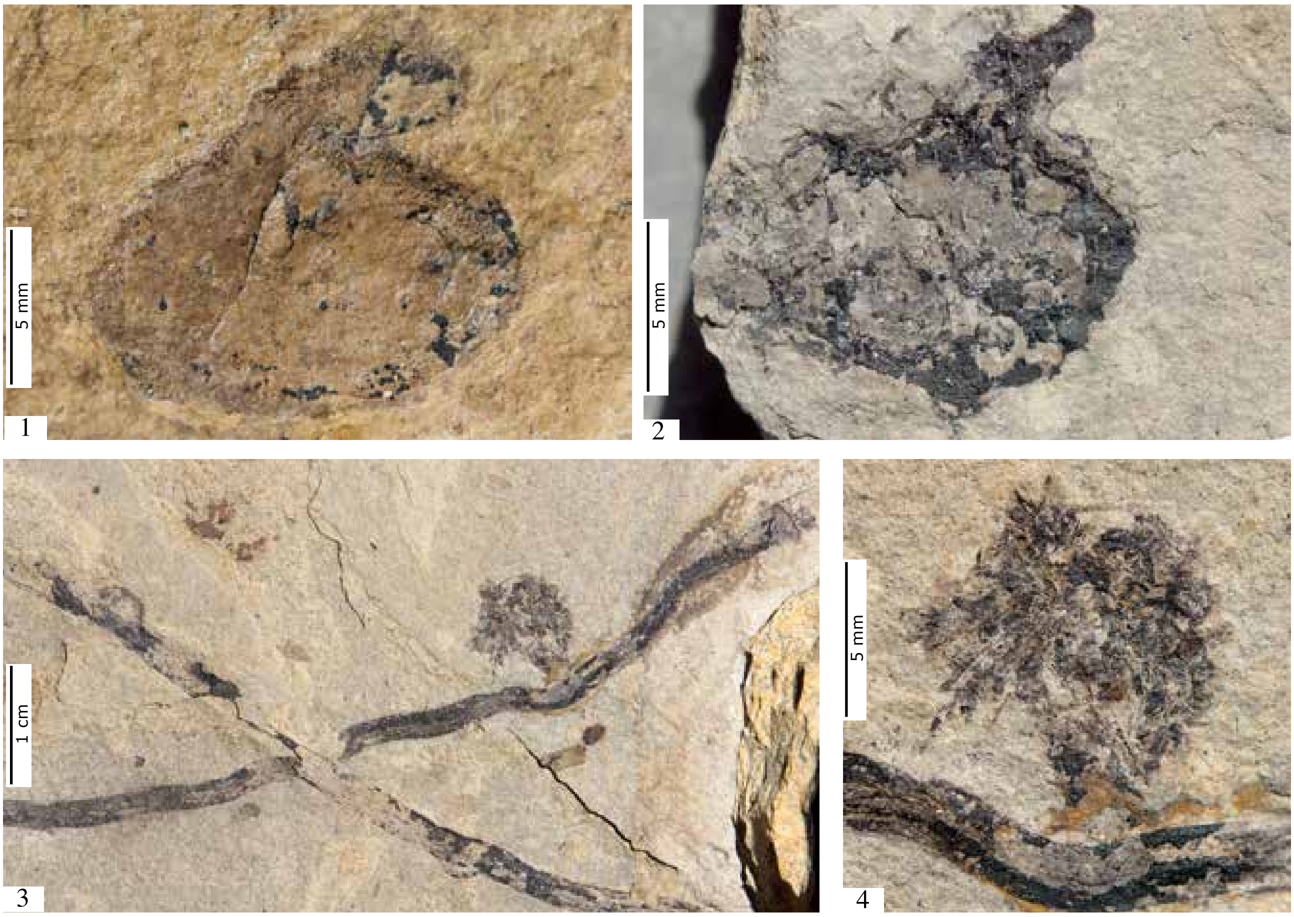
to expand on a large scale. In this case, the most involved victims of these mother of all catastrophes were the angiosperms.

The difficulties in nomenclature

I am convinced that all investigations in the past, especially the evolving of plants, are only tentative due to the fragmentary fossil record. Additionally, in the history of research, numerous taxa were introduced often only based on insignificant features that fitted into their natural variability (Naugolnykh, 2003).

It seems that the European Paleozoic floras were easier to decipher. One is based on the long and intensive researches by many collectors, the other effectively by the lack of Paleoangiosperms – based on different features such as juvenile or adult stages, flowers, fruits, and often mainly, similar leaves and twigs.

The European Paleozoic-Mesozoic flora-world seems to be more restricted in genera, mainly regularly divided into ferns, horsetails, clubmosses, cycads and conifers. Many of them can be correlated easily by their fertile organs. Cones of cycads, lycopods, and conifers can be distinctly identified with a little botanical knowledge. Additionally, they had mainly the same juvenile adult organs. Only future intense researches in these beautiful and surprising fossil sites from Angara-Land, looking especially for fructifications and the small – but interesting and helpful – fertile parts of the plants, hoping for interesting connect-findings in the same time, can help us understand better this magical continent, being till now in big parts a terra incognita.



Fruits of unknown affinities

1-4. Early Permian Angara-Land variation of Paleoangiosperms must be higher than what was thought. There are many fruits, cones or seeds, that till now cannot be inserted with satisfaction. MAT 43, MAT 383, MAT 337, MAT 337)

Fundamental theories about Early Permian angiosperm evolution

Foliage: On the origin of all angiosperm and gymnosperm leaves stands in the Devonian originated multiple furcating leaf needles. It is observable till the Early Permian, then it disappeared mostly.

Reticulate venation: Most, but not all Permian Paleoangiosperms are characterized by net-like furcating veins. This feature we record in the Euro-American floras only in the Triassic Caytonales (*Sagenopteris)*.

Bisexual reproductive organs: Also, Permian lycopods such as *Selaginellites* or *Sigillaria (*especially well-known *Sigillcampeia* from the Triassic) are characterized by homosporous reproductive organs. This evolution process represents, therefore, not an exceptional feature of angiosperms, although the sporangia seed development is different.

Pollination: Probably from the Devonian over the Carboniferous and the Permian periods, anemophily (wind pollination) changed gradually to ambophilly (wind and insect pollination), then to entomophily (insect pollination). Traditional theories supposed an inverse way.

Coeval insect and flowering plant evolution: If somebody is surprised by the richness of Early Permian angiosperm tribes, he must also be astonished at the diversity of insects in Angara. Present were all of today's widespread families such as Mayflies (Ephemerida) Syntonopterida, Odonata Blattinopseida, Caloneurida, Hypoperlida, the Dictyoneurida, the order of Mischopterida, the Psocida, the Thripida, the Psocidea, the Hemiptera, the Palaeomanteida, Coleoptera, the Eoblattida, Blattida and Gryllidae, as well potential progenitors of the Hymenoptera. Some of them can be regarded as potential pollinators. Adherent pollen dust was found on some insects also.

The evolution of stamen: The stamen, understood as a leaf-like filament with apical pollen sacs, has a main identical counterpart in some Early Permian gymnosperms such as the Pinus-ancestor *Valentinia* from Europe, consisting of only a few dwarfish scales with attached pollen sacs.

The evolution of carpel: Paleozoic lycophyta such as *Sigillaria,* as well conifers, have seeds enclosed in an integument with an open micropyle. The ovary wall and an open style could be evolved from an amalgation of many microleaves (as seen in Permian conifer *Ortiseia*) as well from one enclosing macro-leaf (as seen in *Dioonites*-Cycas ancestors).

High diversification in Early Permian era: It is no more surprising about the splitting of gymnosperms at that time. Darwin's theory of slow development of plants and animals must be modified. Saltations occured well. The evolving of an important feature like stamen and carpel make a fast variation and adaptation possible, especially if we had at the same time a high diversification of insects.

The Magnolia dogma as the most primitive flowers: From the Early Permian fossil records, one cannot deduce that the Magnoliids were more primitive than the others. Once evolved, the carpel and stamen forming a geometrical blossom, and this was fully evolved in the Early Permian era – the bisexual flower was born and could modify manyfold its form.

Monocots and Dicots: Today's flowering plants are divided into monocots and dicots. Usually dicots hold petals in multiples of four or five, reticulated leaf veins, and are both herbaceous and woody. Monocots, the smaller group today, are characterized by parallel leaf veins, petals in multiples of three and are herbaceous. Both were present in the Early Permian Angara. On the Euro-American landmass, we have a similar phenomenon with the coeval presence of gymnosperms like the two-seeded (*Zamia*-character) and multiple-seeded cycads (*Cycas*-line). The presence of extremely different lineages, having nevertheless common features, with secessions lineage, probably just in the Devonian, is surprising, but occurs in different plant families.

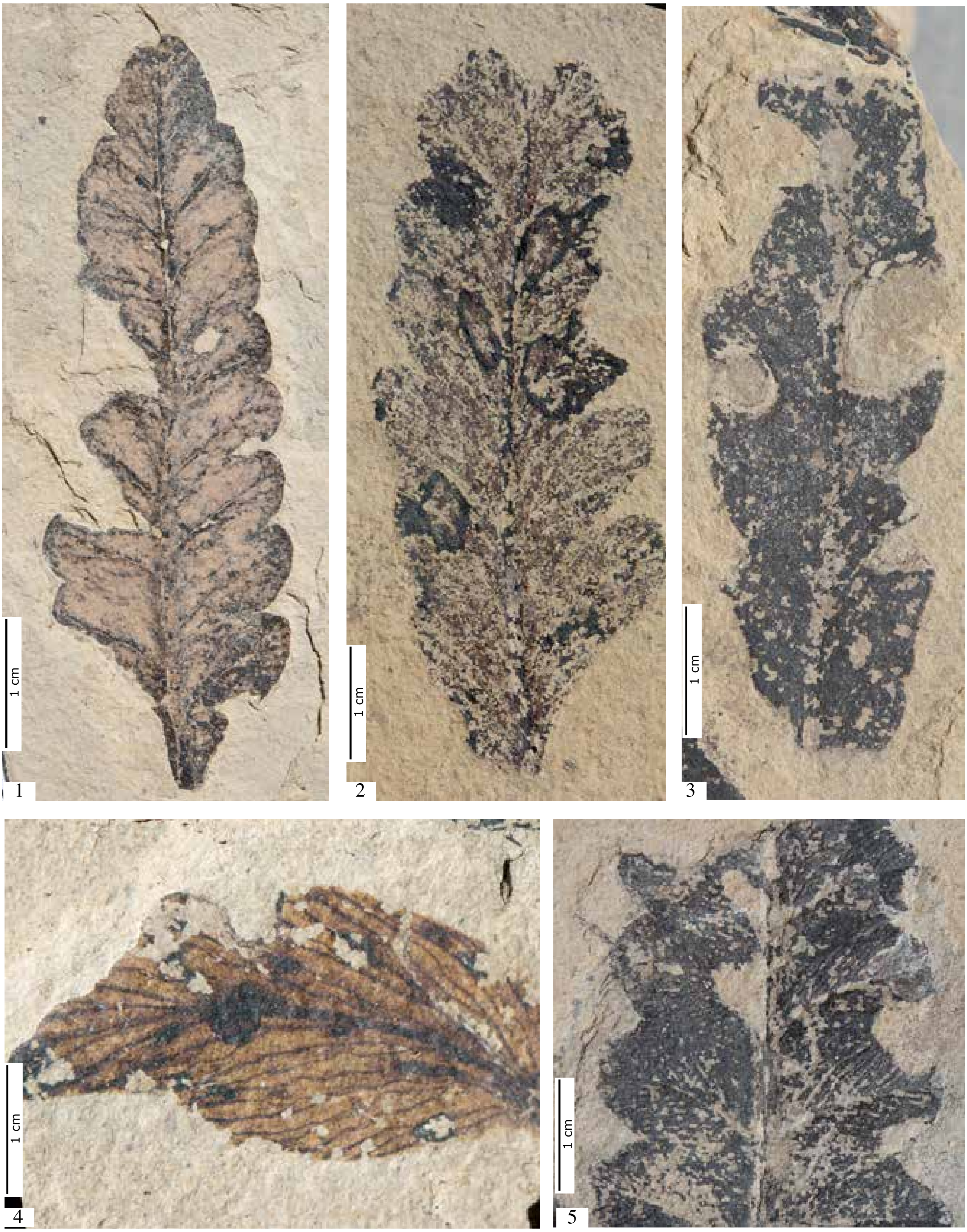
Early cleavage of subgroups: The evolving of the samara, the stone-fruit, the acorn, only taking deciduous trees into consideration, is surprising in the same way, but finds a counterpart in the gymnosperms of the same time. Also, they split during the Early Permian from one-seeded (*Ortiseia)* to wing-seeded (*Majonica*) to more-seeded (*Voltzia*) conifers.

The influence of an immense catastrophe: The Permo-Triassic catastrophe, caused by the largest known volcanic event of recorded earth history and covering approximately the region of the Angara continent, probably pushed back largely the further evolution of angiosperms. Otherwise, the theory of these "mother of all cataclysm" cannot be further sustained.

A long isolation: From the Early Permian till the Cretaceous period, Angara and Euramerica must have been separated by ocean or high mountains. In Angara, we had only a few gymnosperms and in Euramerica, only a few angiosperm progenitors. The same is valid for the insect abundance.

Conclusions

The origin of Angiosperms can be dated back in the Angara-landmass to the Carboniferous-Permian era. The base is a fully developed hermaphroditic flower with ovaries and stamens. Additionally, unisexual fructifications were just as fully evolved. In the Early Permian period, several angiosperm lineages such as deciduous trees comprising maples, oaks, ash trees or stone-fruits as well as herbaceous flowers and grasses, dicots and monocots, were present. Once "invented" the bisexual flower, composed of stamen and carpel with surrounding petals, sepals or tepals, all further lineages can be deduced. The Magnolia theorem as being the most primitive plant and an evolution of all angiosperms from them cannot be reconstructed. Accompanied with the ascension of flowering plants, we have a coeval rising of all insect groups. The spreading of diverse lineages of angiosperms in the Early Permian Angara-Land is therefore equally mysterious or not, as the coeval diffusion of gymnosperms in the Euro-American landmass with several subordinated tribes such as conifers, cycads or ginkgos. This coevolution in the Early Permian period simplifies the understanding of angiosperm development considerably, especially when it can be based on solid arguments and facts due to compound findings.



Interactions between insects and plants

Feeding traces from insects on leaves, cuspate margins, trench marks, holes or egg pouches and irregularly distributed oviposition marks of egg laying (MAT 262, MAT 261, MAT 251, MAT 267, MAT 268) Coll. Wachtler, Perner. Matvéevo, Kungurian (Early Permian).

Early Permian Samara-bearer from Angara

Systematic Paleontology

Division Paleoangiosperms
Order Sapindales
Family Aceraceae

Genus *Sylvella,* ZALESSKY 1937

Taxonomic notes

Sylvella (alata) - Early Permian samaras – was first introduced in 1937 by the Russian paleontologist Mikhail Dmitrievich Zalessky (1877–1946) (pp. 86–87, Fig. 53, 54, and 55), in which he described the flora from Matvéevo in the Perm Krai. Figure 55 evidences an interesting aliform wing with a peduncle.

Sylvella alata, ZALESSKY 1937

Milestones in the description of *Sylvella*

1937 *Sylvella alata* Zalessky, p. 86-87, Fig. 53, 54, 55

1998 *Sylvella alata* Naugolnykh, p. 132, Pl. 87

2007 *Sylvella alata* Naugolnykh, p. 132, Pl. LX Fig 4-9, Pl. LXI Fig. 1-11

2014 *Sylvella alata* Naugolnykh, p. 696, Pl. V Fig. 5

Type horizon and age

Ural, Early Permian, Kungurian (272.3–283.5 Mya)

Description

Fruits: The winged achenes represent typical samaras. A funiculus has a 1 cm long, about 0.5 cm broad, single seeded fruit paired by a wing. The entire samara reaches a length of 3 cm (MAT 202, 192). The flattened wing is fibrous, papery and develops from the ovary wall. The seed is on one side, with the wing extending to the other.

Genus *Psygmophyllum* SCHIMPER, 1870, emend. SAPORTA, 1878

Taxonomic notes

The morphogenus *Psygmophyllum* introduced by Wilhelm Philippe Schimper as fan-shaped foliage (greek Psygmo) was considered for decades in connection with ginkgo leaves, although attached fructifications were never found. Over the course of time, many *Psygmophyllum* species from Angara-Land were described, having had very lacerated forms to compound foliage with dichotomizing main rachis. Due to the fact that Early Permian ginkgophyte leaves (*Baiera*) from European fossil sites are characterized by segmented leaves and were additionally recovered in connection with typical ginkgo seeds, which never occurs with *Psygmophyllum* other solutions must be searched.

Psygmophyllum cuneifolium SCHIMPER 1870 (KUTORGA 1838)

1838 *Sphenopteris cuneifolia*, Kutorga p. 37, Plate VI, Fig, 1, p. 37, Pl. VII, Fig. 1

1937 *Psygmophyllum cuneifolium,* Zalessky: p. 65, Fig. 27

2013 *Psygmophyllum cuneifolium,* Naugolnykh: p. 279, Fig E; p. 280 fig. C-D

2014 *Psygmophyllum cuneifolium,* Naugolnykh: p. 695, Fig 2

Taxonomic notes

The royal professor Stephan Kutorga from Petersburg described first in 1838 plant fossils from the Ural Mountains near Perm, although he had never been in this region. He inserted some flabelliform leaves as *Sphenopteris cuneifolia* and *Sphenopteris interrupte-pinnata*. Zalessky (1937b) changed the name to *Psygmophyllum cuneifolium* to evidence the difference between *Sphenopteris* ferns and these thought ginkgophyte plants.

Type horizon and age

Ural, Early Permian, Artinskian/Kungurian (272.3–290.1 Mya)

Description

Leaves: Psygmophylloid leaves have a wide range of dissection and branching of the leaf lamina. One of them, *Psygmophyllum cuneifolium*, is characterized by deep-

Extant Acer: Leaves and seeds (samara)

1. *Acer platanoides.* Fructification showing the pollen organs and the female infructescence; 2. Aliform samara with decaying pollen organs; 3. Leaf's reverse side; 4. *Acer palmatum* compound leaves and samaras; 5. Seeds hanging in pairs from the tree; 6. *Acer negundo.* Aliform seeds hanging in bunches from a tree; 7. *Acer platanoides.* Old samara.

ly lobed and segmented foliage. In that, it can be confused with the real ginkgophyte ancestor *Baiera* from Middle European fossil sites. Though, attached seeds on these leaves are characterized by a fleshy ovary wall, these cannot be proven by *Psygmophyllum cuneifolium* leaves. Findings from Matvéevo suggest that considerations must be given to extant maple trees (Aceraceae). Some of them (*Acer palmatum*) even today are characterized by their deeply segmented leaf structure. The first appearance they have is in the Artinskian layers, but rare (ARTI 1). At Matvéevo, Mazueeva and Chekarda – localities of the Kungurian age – they reach a large range. Especially well-preserved twigs from Matvéevo (MAT 82, MAT 487, MAT 302) give a deep insight on the structural plan of this plant. Juvenile, incomplete foliage was inserted as *Biarmopteris pulchra.*

Genus *Biarmopteris,* ZALESSKY 1937

Taxonomic notes

The genera *Biarmopteris* (*pulchra*), often interpreted as seed-bearing organs for fossilised planate foliage, was also introduced by Mikhail Dmitrievich Zalessky in 1937 in his findings from Matvéevo.

Biarmopteris pulchra, ZALESSKY 1937

1937 *Biarmopteris pulchra,* Zalessky, p. 47, Fig. 11
1998 *Biarmopteris pulchra,* Naugolnykh, pp. 63, 64
2007 *Biarmopteris pulchra,* Naugolnykh, p. 851 Fig c-e

Description

Leaves: Planate, several times dichotomizing foliage structures (MAT 82, MAT 206) can be found in fair amounts in the Kungurian sediments. Although they feign ovulate structures with seed scars (Naugolnykh, 2007), it seems more likely that they represent juvenile enrolled buds of some *Psygmophyllum* leaves. Still, microscopical analysis never could obtain satisfiable results about seed-bearing systems. Usually the foliar compound branch form four to six times, and the isolated buds are about 1 cm in length. The ultimate segments were formed by the dichotomy of penultimate axes or were pinnately disposed on such axes. The lobes are 0.15–0.3 cm long with an average width of 0.1 cm.

Reconstruction of *Biarmopteris pulchra,* evidencing the enrolled juvenile leaves (MAT 206);

Discussion

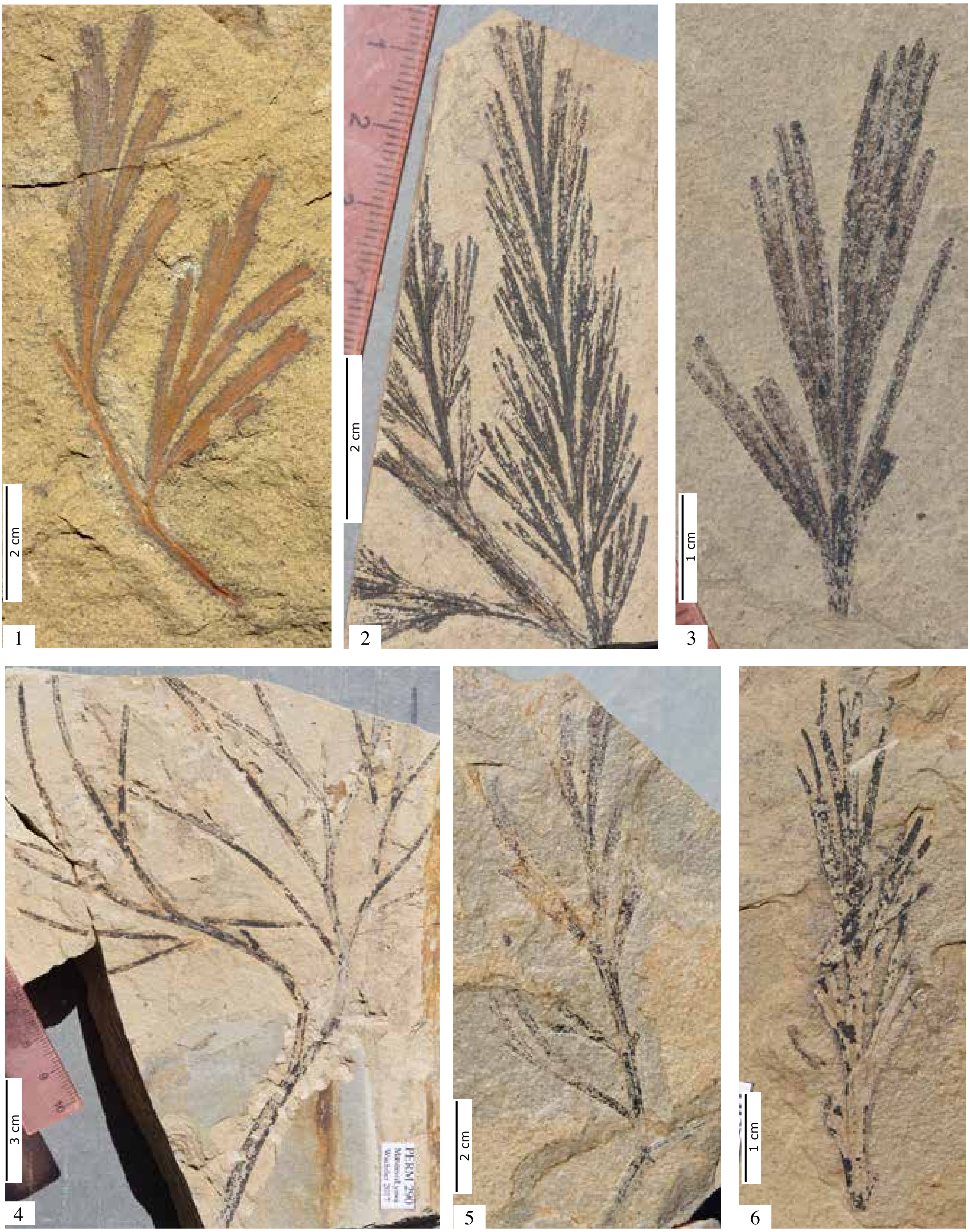
The classification of many flora elements of Permian Angara lacks the attempts to insert them in a schema of knowledge of all parts of the plant.

In the Kungurian layers of the Perm-Krai, *Psygmophyllum cuneifolium* leaves, characterized by their bifurcating foliage, a feature of mainly all primordial Devonian plants are already present globally till the Early Permian period. For all these similarities it is herein difficult to decipher the exact group-belonging only from their foliage type.

Psygmophyllum cuneifolium leaves are just recorded from typical Artinskian strata (Panteleykovo near Arti). Therefore, the evolv-

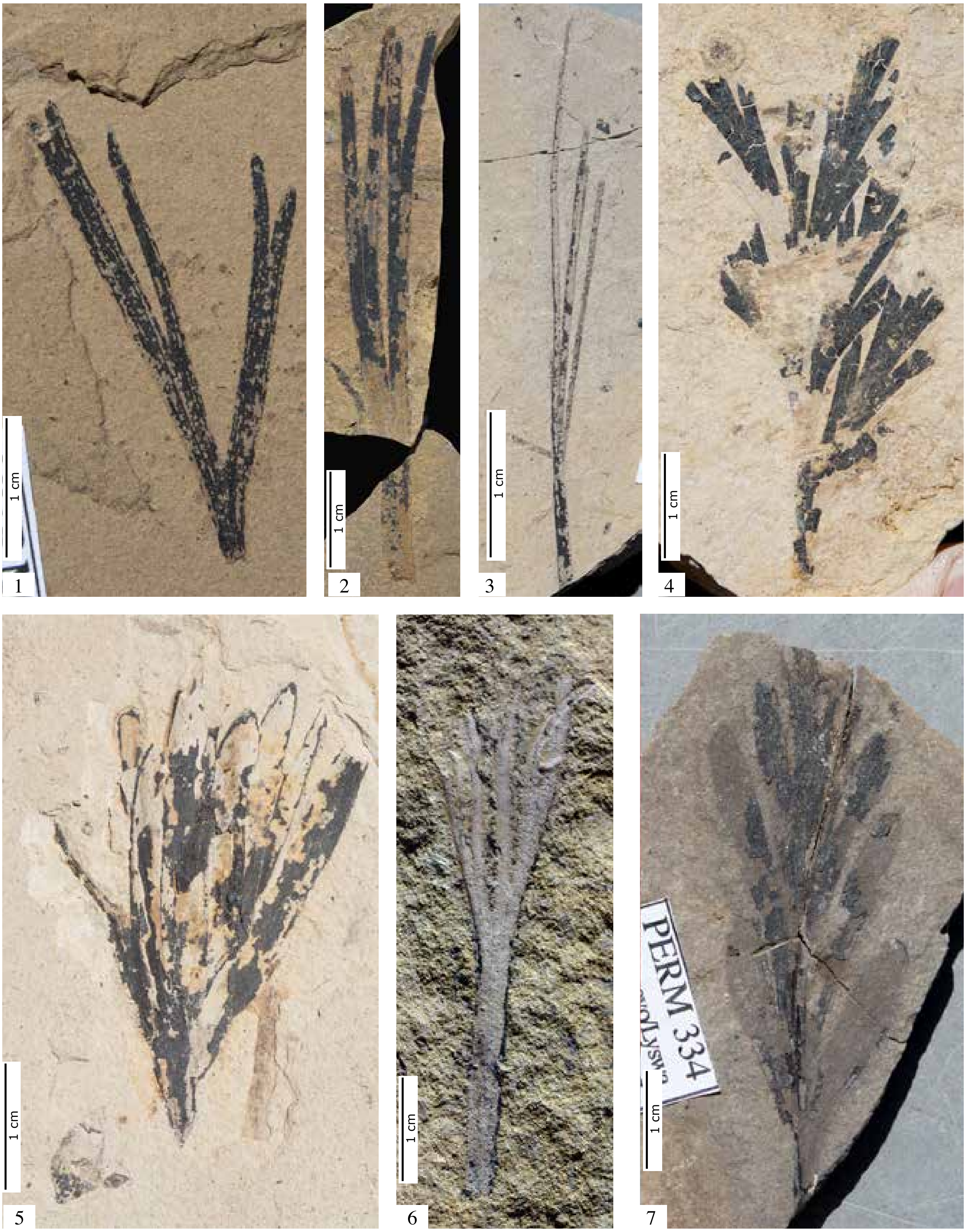
***Sylvella alata*. Potential maple (acer) ancestor (Early-Permian). Reconstructions**

a. Whole twig with leaves and *Sylvella alata*-samara (MAT 82); b. *Biarmopteris pulchra,* juvenile shoots (MAT 206); c. *Psygmophyllum cuneifolium*-twig (MAT 487); d. Detail of an isolated part of a leave (MAT 302); e. *Sylvella alata*-samaras (MAT 191, MAT 202, MAT 186)



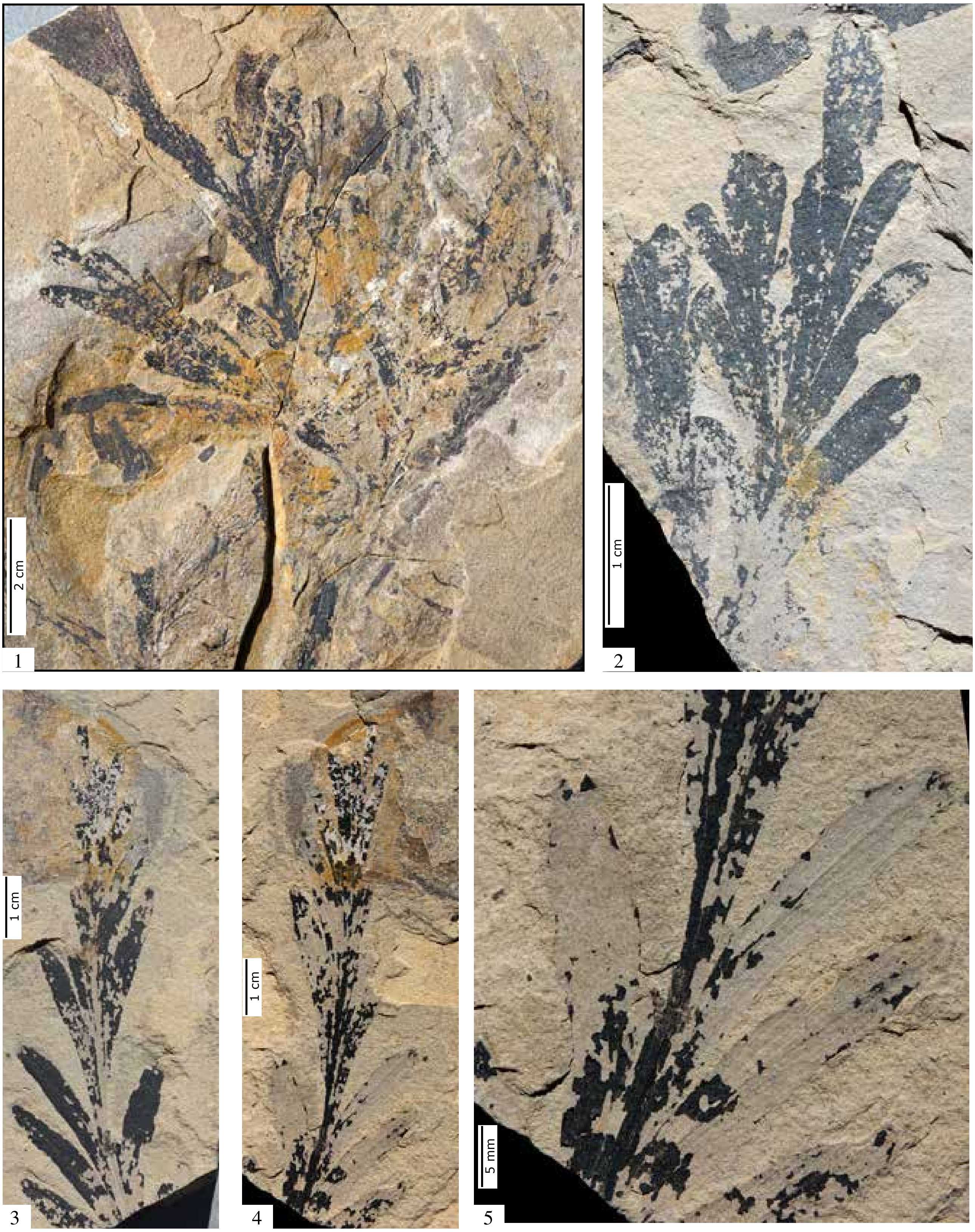
***Psygmophyllum (Sylvella alata)*. Potential Acer (maple) ancestor. Leaves**

1. Two segmented leaves *(Psygmophyllum cuneifolium*, Kutorga), Schimper (ARTI 11, Coll. Gerasch), Arti, Artinskian (Early Permian); 2. Segmented leaves (*Gracilopteris lonchophylloides* (Naugolnykh) (MAT 297); 3. Leaf *(Psygmophyllum intermedium)* (MAT 292); 4-5. Extremely segmented leaves *Psygmophyllum cuneifolium, MAT 290, 286); 6.* Leaf (MAT 283), Matvéevo, Kungurian (Early Permian) Coll. Dolomythos



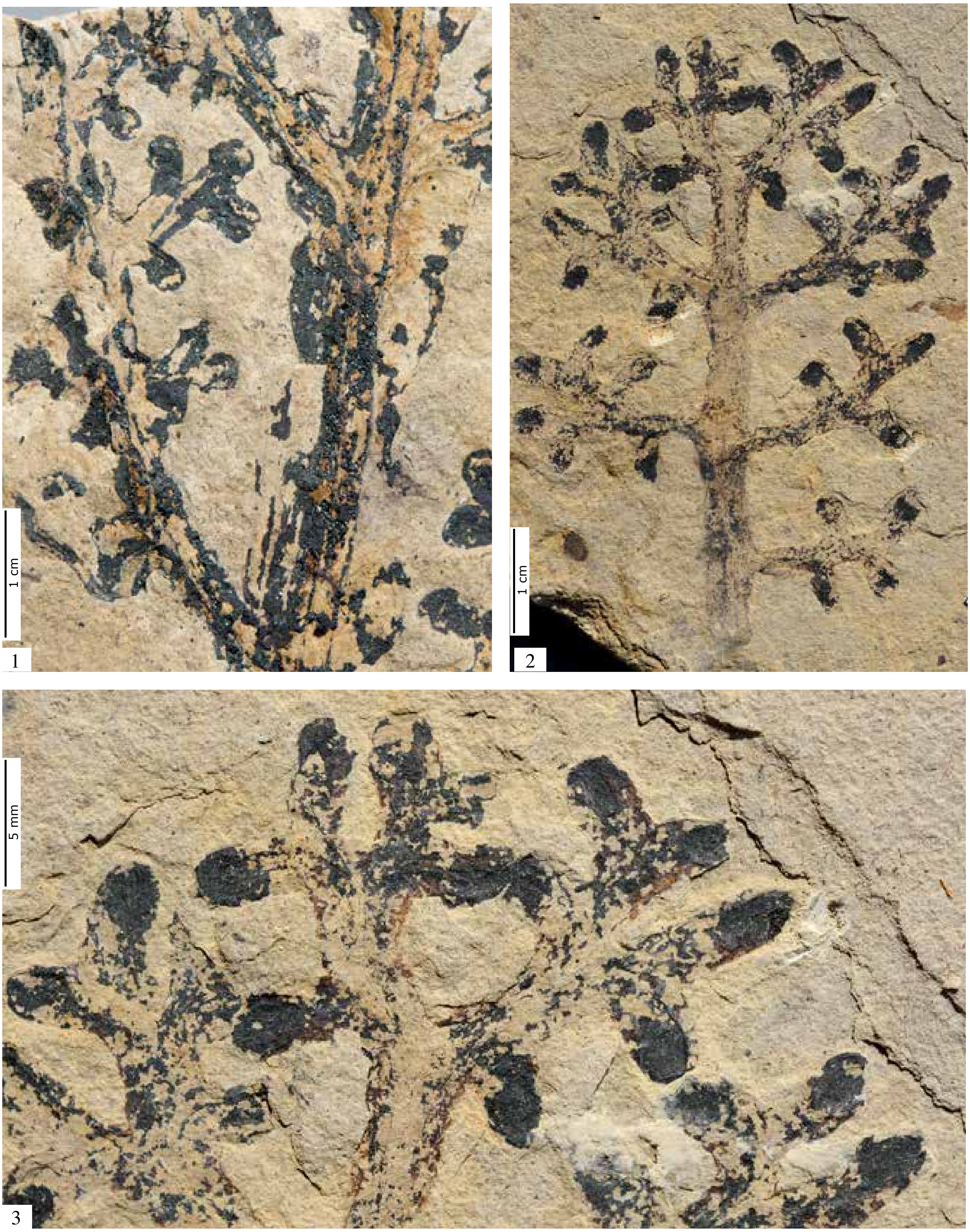
Psygmophyllum (Sylvella alata). Potential Acer (maple) ancestor - leaves

1. Segmented leaves *(Psygmophyllum cuneifolium*, Kutorga)Schimper; 2-3. Segmented leaves (*Psygmophyllum intermedium)* (Naugolnykh) (MAT 166, 293); 4-7. Leaves *(Psygmophyllum cuneifolium)* (MAT 296, 303, 160, 334); Matvéevo, Kungurian (Early Permian) Coll. Dolomythos



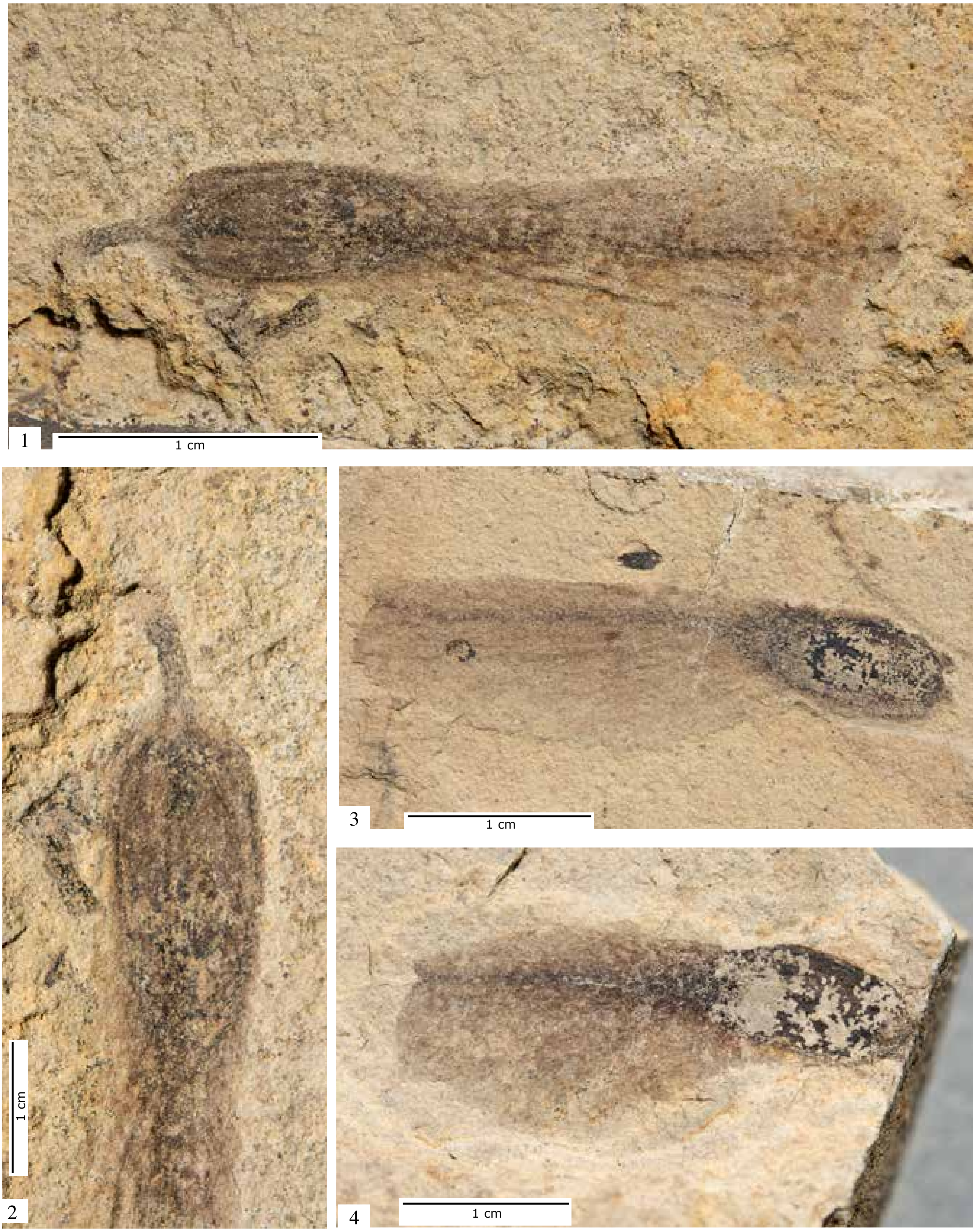
***Psygmophyllum cuneifolium (Sylvella alata)*. Potential acer ancestor. Leaves**

1. Branchlet with several attached leaves (MAT 82, Coll. Perner); 2. Detail of a leaf (MAT 487); 3-5. Branchlet, plate and counterplate and detail of the leaves (MAT 302); Matvéevo, Kungurian (Early Permian) Coll. Perner - Dolomythos



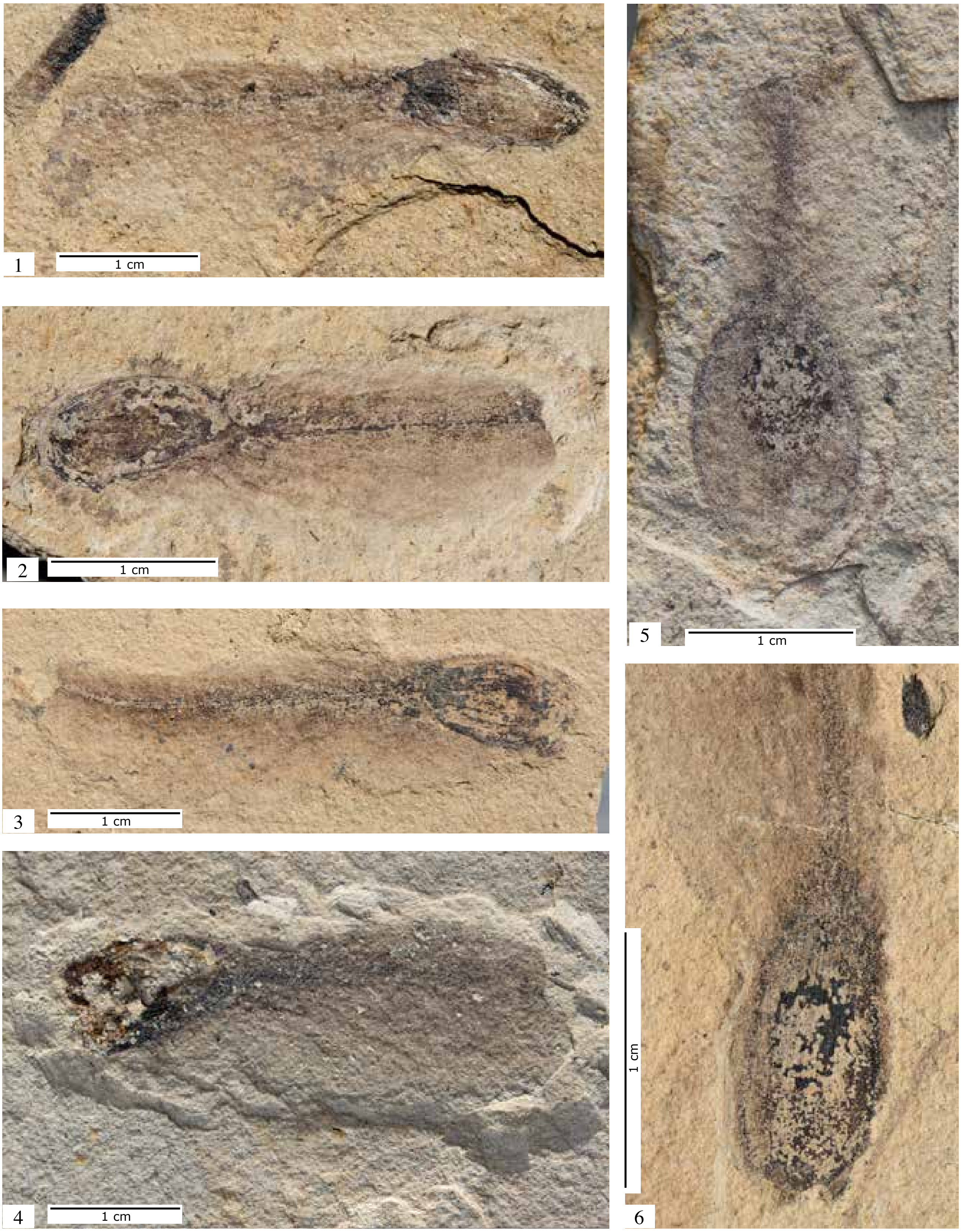
***Biarmopteris pulchra (Sylvella alata)*. Potential acer ancestor. Young leaves**

1. Young growing leaves (MAT 82, Coll. Perner); 2-3. Branchlet with supposed young leaves and detail (MAT 206); Matvéevo, Kungurian (Early Permian) Coll. Dolomythos



***Sylvella alata*. Potential acer ancestor. Winged seeds**

1–2. Samara with attached connecting stipe. Detail of the seed and the stipe (MAT 191); 3–4. Isolated winged seeds. (MAT 202, MAT 186), Matvéevo, Kungurian (Early Permian) Coll. Dolomythos



***Sylvella alata*. Potential acer ancestor. Winged seeds**

1-6. Several examples of seeds enclosed in a "nutlet" attached to a flattened wing of fibrous, papery tissue. (MAT 187, 380, 192, 371 368, 202); Matvéevo, Kungurian (Early Permian) Coll. Dolomythos ing must have occurred on the Carboniferous-Permian border or earlier. They are than frequent in the sediments of Matvéevo, accompanied by *Sylvella alata* samaras. With some caution *Biarmopteris pulchra* shoots, often classified as fertile organs of unknown affinity represent the juvenile foliage of *Psygmophyllum cuneifolium–Sylvella alata*. They were recovered together in Kungurian sediments, especially from Chekarda and Matvéevo (Zalessky, 1937b, Naugolnykh, 1998, Naugolnykh, 2007, Naugolnykh, 2014).

Based on compound findings, it seems that the *Psygmophyllum cuneifolium*-foliage have the most possibilities to belong to *Sylvella alata* aliform fertile organs. If this aliform reproductive organs do not pertain to a conifer and neither to lycopods, ferns or horsetails, the possibilities are restricted, and we have to search for parallels in today's plants. The most similarities we have is with the maples (*Acer*). Their paired fibrous wings are a good pattern for comparing both. In that, they have some similarities with the extant maple leaves, from palmate, veined and lobed, to palmate compound, pinnate compound or pinnate veined. Some species such as *Acer negundo* (Box-elder) or *Acer palmatum* have pinnately compound leaves that may be simply trifoliate or may have five, seven, or sometimes, nine leaflets.

That they do not represent some conifer winged seed – being present in the Euro-American landmasses from Early Permian with the conifer *Majonica,* a potential *Abies* ancestor or *Wachtlerina* – is manifested by their funiculus (MAT 191). In the gymnosperms they are inserted paired on scales forming a distinctive cone.

But which appearance had the bloom belonging to *Sylvella alata*? The question is not easy to resolve, because fruits and flowers in angiosperms differ considerably. Recent maple flowers have four to five sepals, four or five petals (but absent in some species), four to ten stamens, and two pistils or a pistil with two styles. So, in the Kungurian flower diversity, many blossoms can be eliminated. Atmost, similar single blooms we can encounter with some caution in MAT 44. Mat 104 than probably represent a whole inflorescence as a compound of several mostly-closed flowers. The same similarities we have already in today's juvenile maples.

Systematic Paleontology

Division Paleoangiosperms
Order Oleaceae
Family Fraxininae

Genus *Sadovnikovia,* NAUGOLNYKH 1994

Taxonomic notes

The winged reproductive organs of *Sadovnikovia belemnoides* were sometimes thought in connection with the group of Permian lycopods, especially the Pleuromeiaceae or Isoetaceae (Naugolnykh, 1994, 2007, 2012). They were even considered as the ancestor of all Early Triassic *Pleuromeia* species, a widespread clubmoss family in the Early Triassic. Due to fortunate connected findings with attached samaras on twigs can now be stated that this plant has to be classified as Paleoangiosperm, probably as ancestor of the extant Fraxinaceae (Ash).

Sadovnikovia belemnoides, NAUGOLNYKH 1994

Milestones in the description of *Sadovnikovia*

1994 *Sadovnikovia belemnoides* Naugolnykh, p. 172, Fig. 1, Fig. 2

2007 *Sadovnikovia belemnoides* Naugolnykh, pl. 8. Fig. 2-4

2015 *Sadovnikovia belemnoides* Naugolnykh, p. 129

Type horizon and age

Ural, Early Permian, Kungurian (272.3–283.5 Mya)

Description

Fruits: Samaras with seeds in the lower centre of the wing, 3–4 cm long (MAT 182, MAT 283), 1 cm broad on the basal part, reducing the width to the end to 0.5 cm. Wing of the samara is divided sometimes in the middle (MAT 182). Winged achenes are attached with a 1.5 cm long, 0.3 cm broad leafy stalk to the twig, hanging in bunches (MAT 182).

Flowers: Suggested reproductive organs (MAT 219, MAT 374) occurring in a tuft of

Extant ash (Fraxinus). Leaves and seeds (samara)

1. *Fraxinus excelsior.* Male and female infructescences; 2. Aliform seeds hanging in bunches from a tree with old and new aliform samara; 3. Green new samara; 4. Old samara; 5. *Fraxinus tomentosa*. Leaves and twigs.

many-flowered panicles. Some are hermaphroditic with certainty (MAT 374, MAT 219), others not so easy to establish. Panicles 4–5 cm long, 3–4 cm wide. No calyx or corolla observable. Androecium consists of a short stalk, relatively massive stamen, with two pollen sacs (MAT 374).

Leaves: Psygmophylloid leaves, small sized, evidencing a length of about 2 cm, 1.5 cm width (MAT 182, with attached samara), sometimes longer till 5 cm, divided into three to four lobes (MAT 284, 488, 272), flabelliform, ending slightly rounded. Sometimes in literature described as *Psygmophyllum cuneifolium* (Naugolnykh, 2012).

Discussion

The aliform seeds of *Sadovnikovia belemnoides* represent samaras, but in contrast to the thought acer-ancestor *Sylvella alata* from the same Early Permian sediments, the difference to them lies in the seeds, positioned in the lower middle part of the samara and not on the base like *Sylvella alata*.

Therefore *Sadovnikovia* can be regarded as the progenitor of extant fraxinus (ash). Also, the suggested many-flowered panicles indicate in this direction. Only the leaves – being in extant ashes as opposite and pinnately compound – do not correspond to the Early Permian specimens. In *Sadovnikovia belemnoides*, they grow single from the twigs, being slightly incised and two till four times lobed.

How deceptive plant analysis only based on their foliage is can be seen in the case of *Sylvella-Sadovnikovia* leaves. They can be hardly distinguished among themselves. But they pertain nevertheless to different deciduous trees with completely different flowers, although having similar samara, as this is the case today also.

In what way the winged seed or samara evolved requires some discussion. The most plausible answer is a coevolution – like the in European Permian widespread conifer *Majonica* (Wachtler, 2015), having also winged seeds. Probably dwarfish microcleaves, deriving from Devonian emergences overtop the seed, covering them, but in the same manner making it airworthy. Also the samaras of *Matvéeva perneri*, a thought *Ulmus*-ancestor can be brought in connection with this evolving line.

Systematic Paleontology

Division Paleoangiosperms
Order Rosaceae
Family Ulmaceae

Genus *Matvéeva* nov. gen. n. sp. WACHTLER 2017

Etymology

After the lovely hamlet Matvéevo (Perm Krai) where this fossil was found first.

Diagnosis

Elliptic to orbicular samara, with a flat and fibrous wing. Apex with a notch stigma. One seed at the center of the samara.

Matvéeva perneri n. sp. WACHTLER 2017

Type horizon and age

Perm Krai (Russia) Ural, Early Permian, Kungurian (272.3–283.5 Mya)

Holotype

MAT 346 Coll. Wachtler, Dolomythos Museum, Innichen

Etymology

Honouring the paleontologist Thomas Perner who described many European Permian floras.

Diagnosis

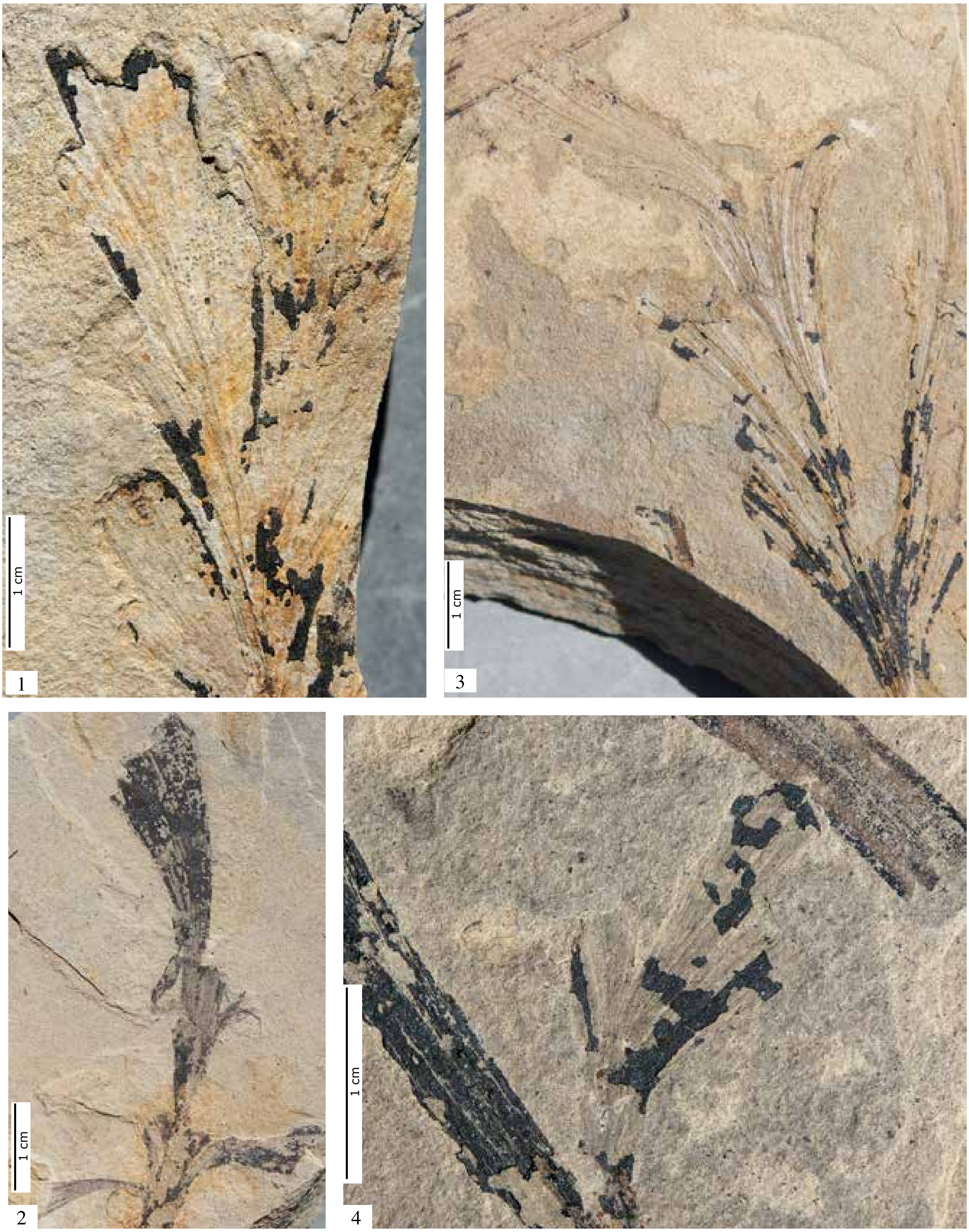
Samara with the seed collocated in the middle of a papery circle. Wing crossed by irregular veins.

Description

Samara: 1.5 cm long, 1.5 cm wide, mainly rounded to slightly elliptical with a persistent 0.3 cm long stigma on the base. Holding peduncle 0.2 cm. Stone-fruit in the middle, 1 cm long, 0.6 cm wide, surrounded by a fibrous tissue, crossed irregularly by thicker and thinner veins, developing from the ovary wall (MAT 346, holotype, but also MAT 435 and 14).

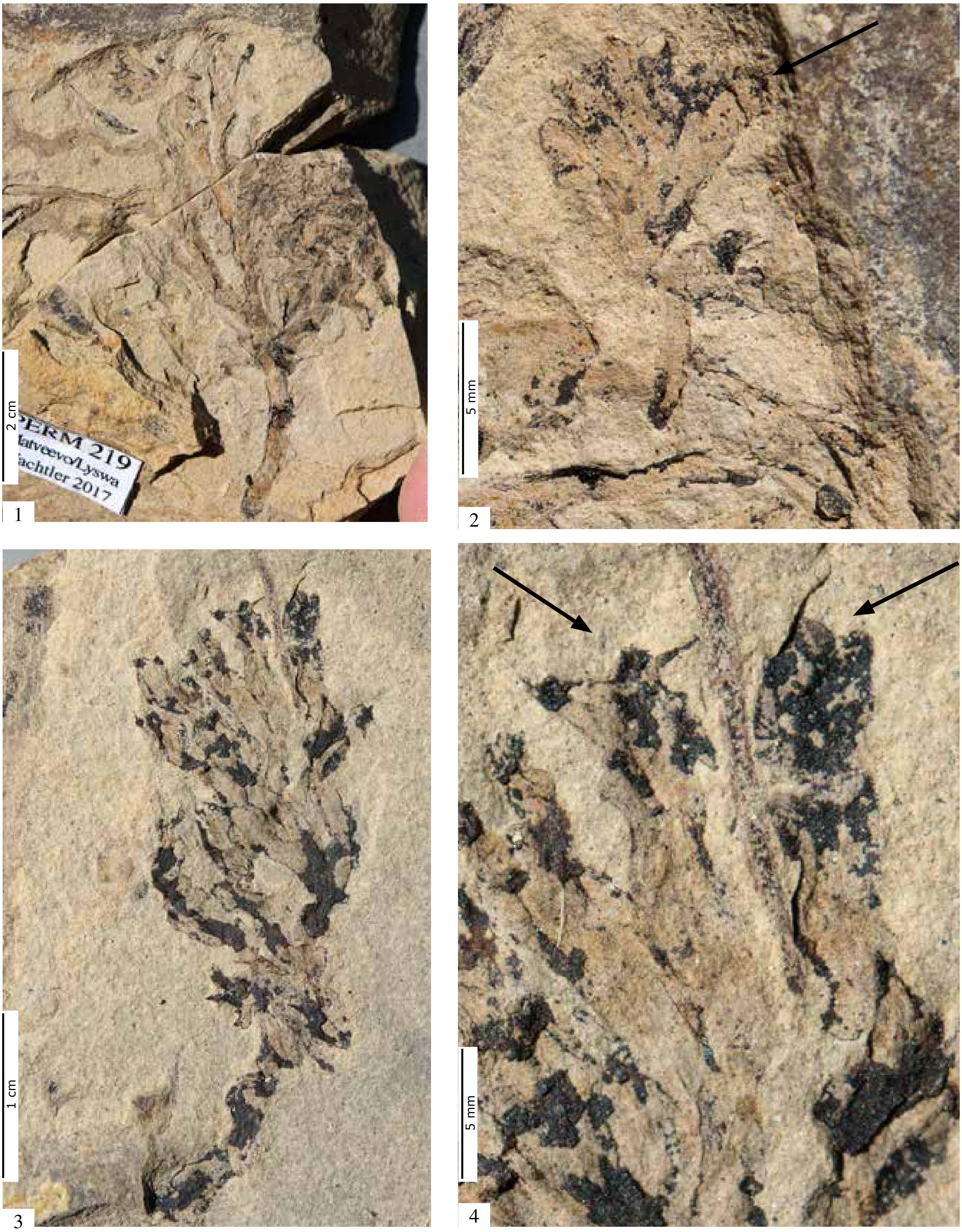
***Sadovnikovia belemnoides*. Potential ash (fraxinus) ancestor (Early-Permian). Reconstructions**

a. Twig with one aliform seed attached (MAT 182); b. Isolated leaf (MAT 182); c. Entire frond (MAT 284); d. Aliform seeds hanging in bunches from a tree with old and new aliform samara; e. Pollen organ (MAT 374); f. Female flower (MAT 374); g. Infructescence with male and female organs (MAT 374, MAT 219); h. Old samara (MAT 182)



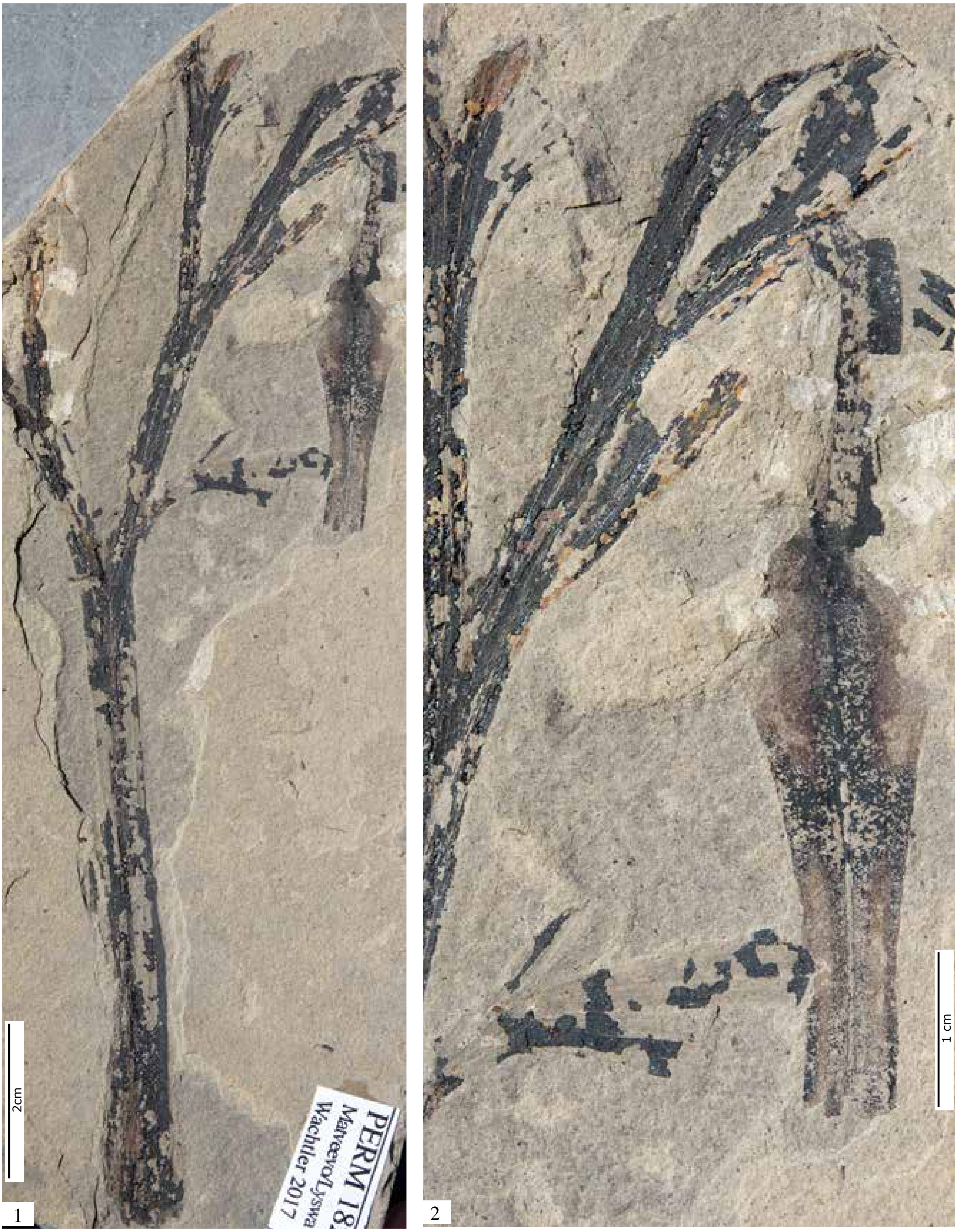
***Sadovnikovia belemnoides*. Potential fraxinus ancestor. Leaves and twigs**

1. Twig with leaves (MAT 488); 4. Twig (MAT 272); 3. Twig with leaves (MAT 284); 4. Detail of a leaf with part of an attached seed (MAT 182); Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum



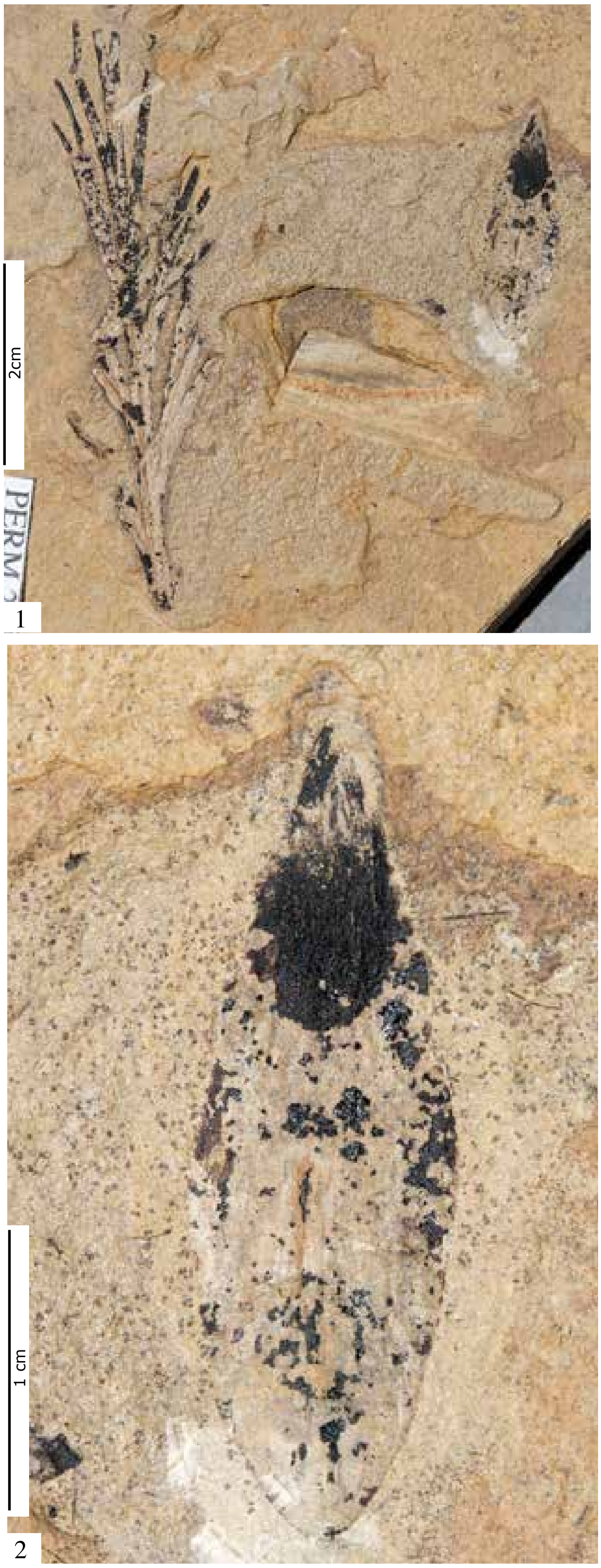
***Sadovnikovia belemnoides*. Potential fraxinus ancestor. Flowers**

1. Flower with male and female organs (MAT 219); Detail of a male pollen organ (MAT 219); 3. Deciduous flower with male and female infructescences; 4. Female flower (left arrow) and male pollen sac (right arrow). Note the carved anther (MAT 374); Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum



***Sadovnikovia belemnoides*. Potential fraxinus ancestor. Winged seeds (samara)**

1. Entire twig with attached aliform seed and leaves. 2. Detail of the seed and the leaves (MAT 182) Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum



***Sadovnikovia belemnoides*. Potential fraxinus ancestor. Winged seeds (samara)**

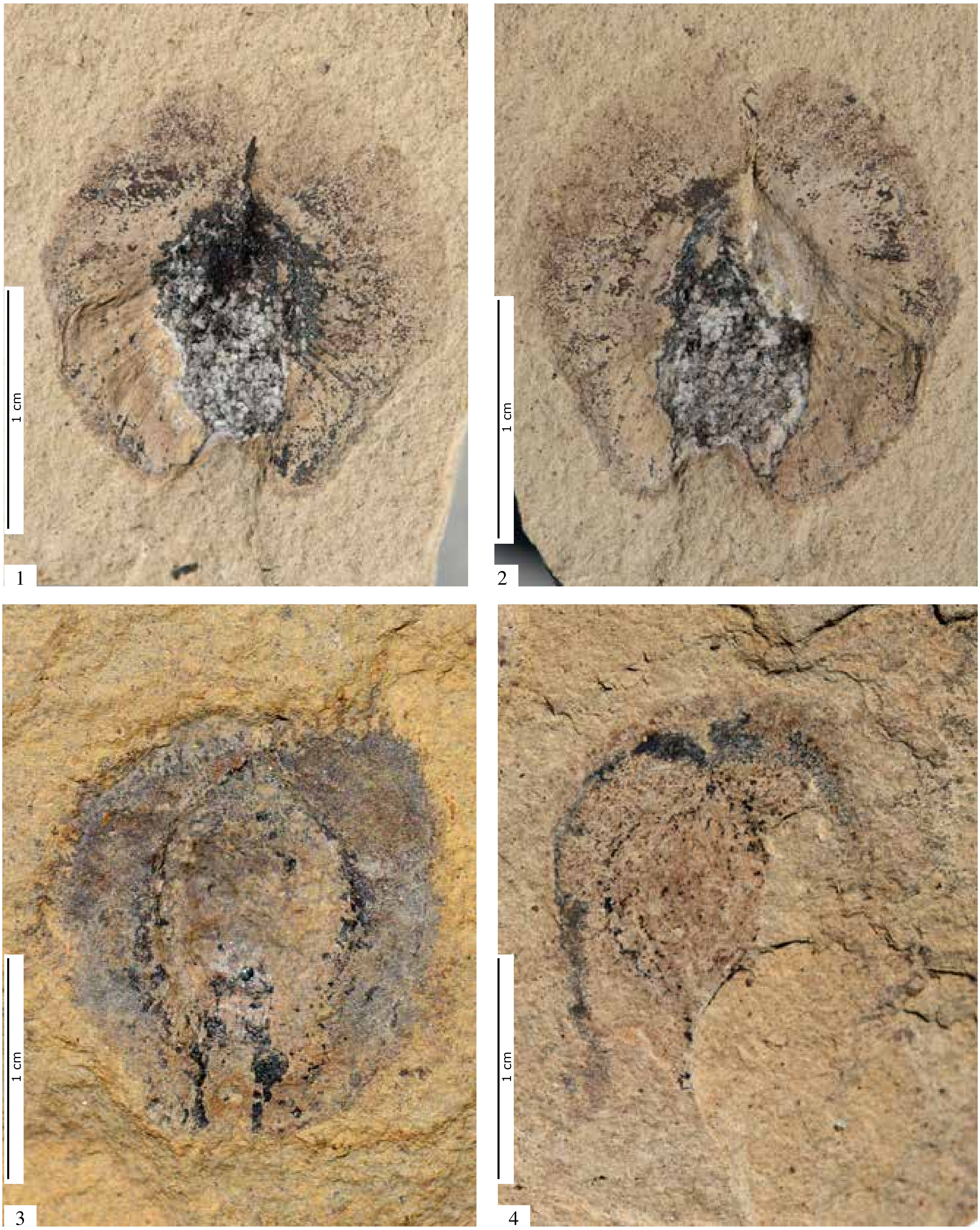
1-2. Twig and detail of the samara (MAT 283) Matvéevo, Kungurian (Early Permian) Coll. Wachtler

Discussion

Some samaras in Matvéevo cannot be inserted in one of the existing classification systems. The seed is in the centre of the rounded wing, like in today's elms (Ulmaceae). The fibrous material is relatively consistent, the strong filigree veins are crisscrossing the wing. Therefore, considerations were taken that the Early Permian (Kungurian) *Matvéeva perneri* represents the ancestor of the elms. Till now, the leaf type belonging to *Matveeva* is not known, probably some multilobed *Psygmophyllum* foliage, or with some possibilities, the strange fronds of *Permocallipteris* can pertain to these samaras. If their blossoms correspond to today's elms, then MAT 31, a hermaphrodite flower, has the most possibilities to belong to *Matvéeva perneri.* Whether this form of samara is common or seldom at Matvéevo is difficult to establish, because the fossilised stonefruits when split on the fossil slab manifest the same features.

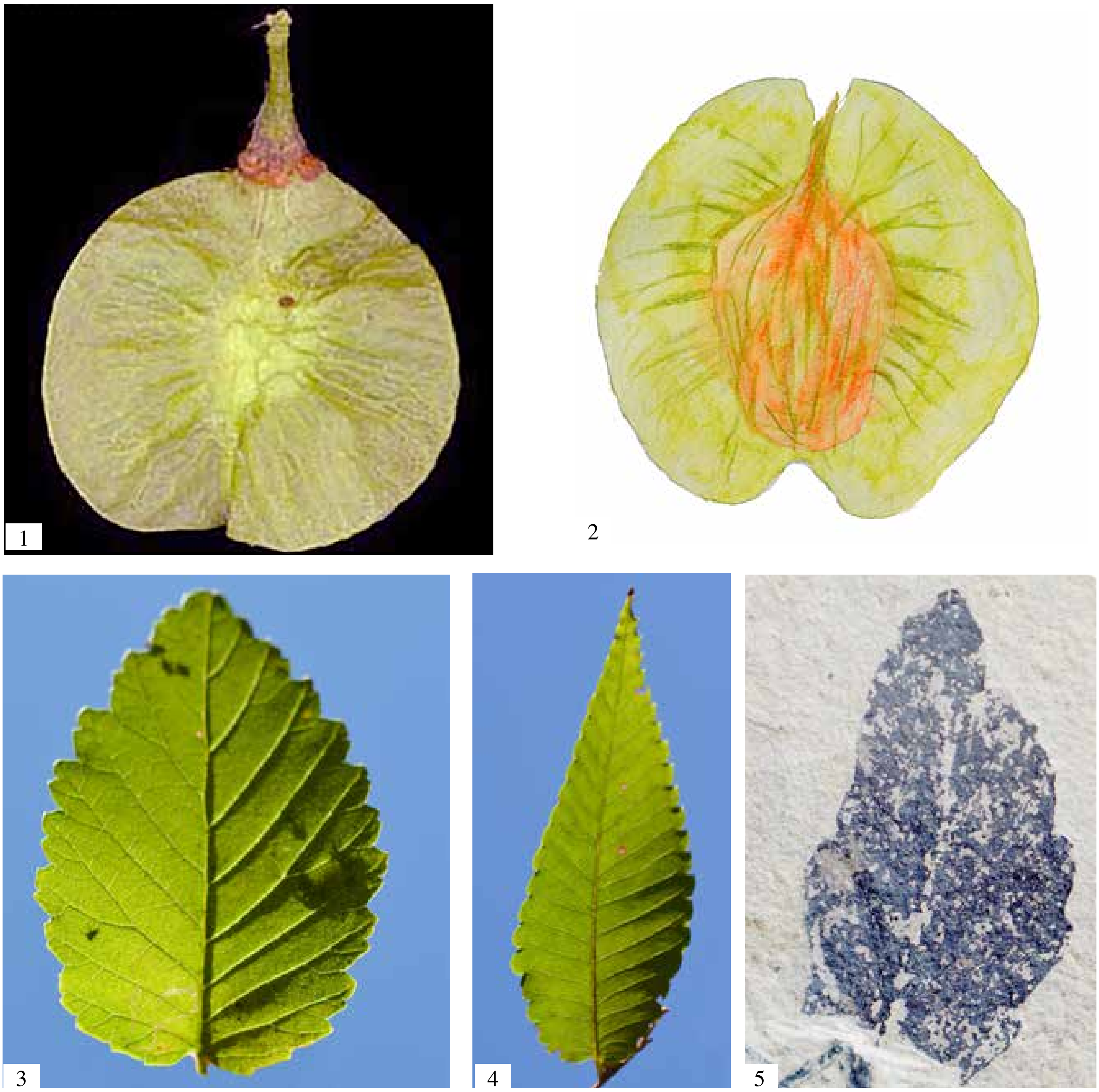
Remarks

Altogether in the Kungurian beds of the Fore-Urals, we encounter three distinct types of Samaras: *Sylvella alata*, having similarities with today's maples, *Matveeva perneri*, thought as the elm ancestor, and *Sadovnikovia belemnoides,* having affinities with the ash. Additionally, we have enough reproductive organs – having resemblances with extant flowers – that can be connected with these Early Permian broad-leaved trees. None of the foliage types has reached the level of today's *Acer, Fraxinus* or *Ulmus* twigs, but all are characterized by a transition stage between Devonian archaic furcate leaves and some modern aspects. Otherwise, none of them can be correlated with the evolution theories based on magnoliid phylogenetic theories. But are these necessary? When on the isolated Angara continent the hermaphrodite flower was "invented" – meaning the anthers had a subtle filament and an pistil enclosing the seeds, in contrast to the Euro-American gymnosperms with cone-like fructifications holding one or more seeds as well as cone-like pollen organs – then the most important step was just done. They do not need the indirect way across large and showy bisexual flowers with many petals, numerous adnate carpels and



***Matvéeva perneri* nov. gen. n. sp. Potential Ulmus ancestor - samaras**

1-2. Perfect conserved samara, plate and counterplate evidencing the seed inside. (MAT 346, designed holotype); Suggested samara (MAT 435, Coll. Gerasch); 4. Another samara. (MAT 14). Coll. Wachtler - Dolomythos Museum



***Matvéeva perneri* nov. gen. n. sp. Potential Ulmus ancestor**

1. *Ulmus rubra*. Samara; 2. *Matveeva perneri.* Reconstruction of a samara (MAT 346); 3. *Ulmus pumila.* Leave; 4. *Zelkova serrata* (Ulmaceae); 5. Leave probably belonging to some Ulmus-ancestor (MAT 434, Coll. Gerasch)

stamens arranged in a spiral fashion on an elongated receptacle. Most of present day angiosperms are characterized by the filament-anther type, the carpel and some surrounding tissues developing into a fruit.

As we believe in the dogma of Carboniferous-Permian origin of mainly all gymnosperms, because we are influenced by our Western way of thinking, we must also accept the other unknown wide landscape of Russia and their unique ways of angiosperm-plant and insect evolution.

The way to a winged seed for the angiosperms was as complicated or easy in the evolution as the winged seed for the conifers. And both angiosperms and gymnosperms – so it seems – reached their purpose independently. More interesting is why for all this time - from Permian till the Cretaceous; 200 million years – this independent evolution stage could remain unmixed. For a long period, the continents were separated effectively; after that, an immense cataclysm or maybe high mountain ranges prevented an exchange.

Early Permian stone-fruits from Angara

Systematic Paleontology

Division Paleoangiosperms
Order Rosaceae
Family Amygdaloideae

Genus *Bardocarpus,* ZALESSKY 1937

Taxonomic notes

In a short notice and a drawing Mikhail Dmitrievich Zalessky (1937b) introduced in science *Bardocarpus aliger*, a consistent seed covered with "épisperme" (episperm = a protective outer layer surrounding the seed) from Matvéevo that was handed to him by H. T. Mauer in 1927.

Bardocarpus aliger, ZALESSKY 1937

1937 *Bardocarpus aliger* Zalessky: p. 88, Fig. 56
1988 *Bardocarpus aliger* Meyen, p. p. 365 Fig. 8.18

Type horizon and age

Ural, Early Permian, Kungurian (272.3–283.5 Mya)

Description

Fruits: From 1.2 x 1.1 cm (MAT 415) to 2.0 x 1.5 cm (MAT 400). Seeds inside are egg-shaped to rounded, covered outside by a fleshy layer (MAT 415, 393,394, 400, 409, 403).
Flowers: Suggested blossoms are hermaphroditic (MAT 442, 40, 348, 201), having five petals, 0.7 cm x 0.8 cm. In the middle are located stamen and anther holding the microsporangia and the ovary (MAT 442). Filament is slender with pollen aggregates on the top (MAT 301, MAT 40).
Leaves: Foliage simple, about 3 cm long, 2 cm wide (MAT 82), aristate and entire with a strong midrib and an acute apex, alternating on the twig.

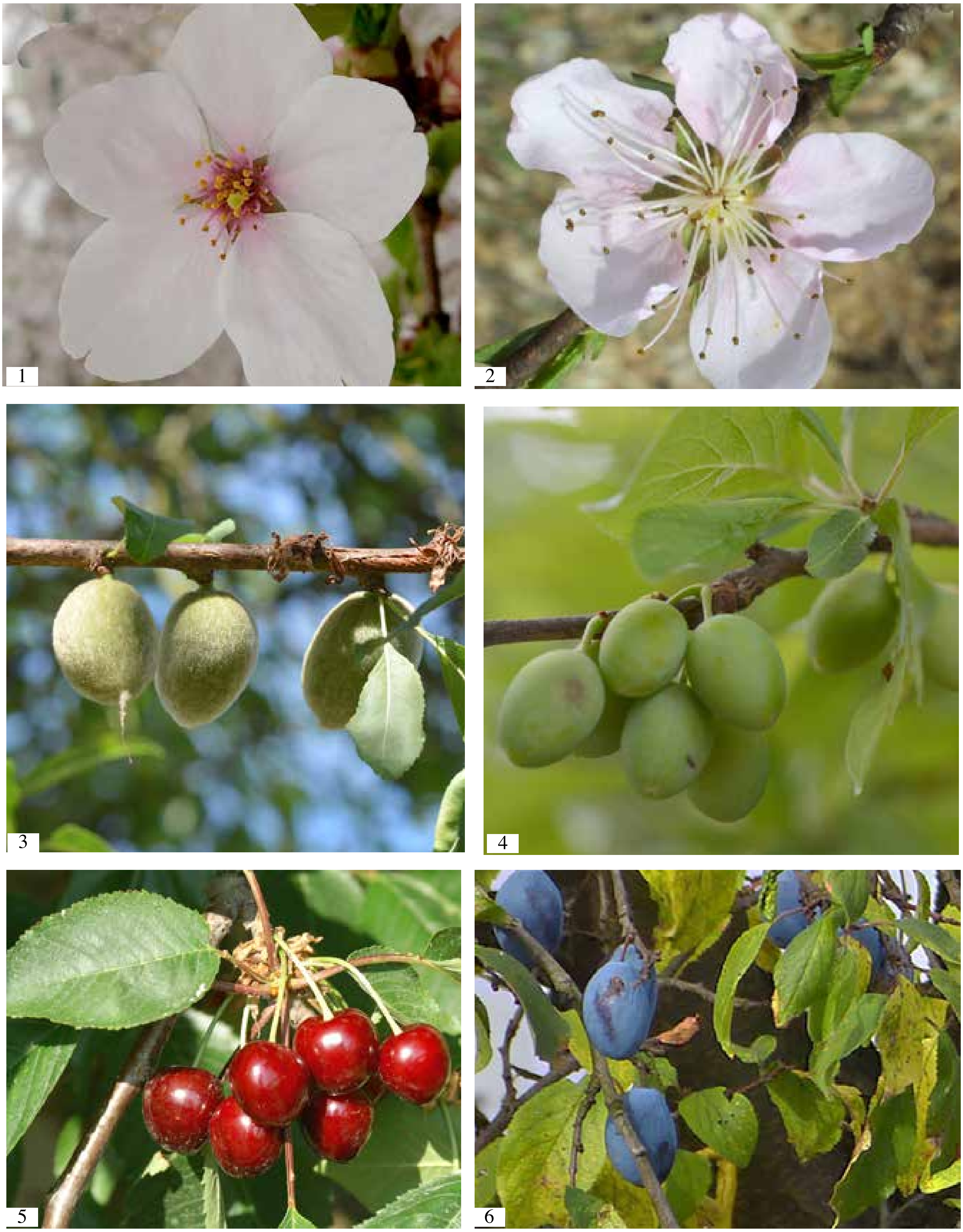
Discussion

Bardocarpus aliger seeds are common in the sediments of Matvéevo. The seed and the fleshy outer drupe covered by a skin attracted Mauer in 1927, who handed the material to M. D. Zalessky for his description in 1937. Also common are fossilised flowers having usually five petals. They differ from the *Permotheca* species like *Permotheca colovratica*, having four sepals (Naugolnykh, 2013) or *Permotheca disparis* (Naugolnykh, 2007) having six. Others such as *Peltaspermum petaloides* (classified sometimes as Angaropeltaceae) had much more segments (Zhuzhgova et al., 2015). Therefore, it seems that five-petal flowers are more abundant in Matvéevo than in other Kungurian sites like Chekarda.

Five petals are interesting, because many of our today's edible stone-fruits like almonds, peach, plums, cherries and apricots, and more distantly, apples, pears and roses are characterized by this feature. Astonishingly, fleshy seeds with these properties, or blossoms holding inside clearly visible filaments with apical anthers are till now never recorded from the Euro-American Permo-Triassic fossil sites. A reason for that could be the bad quality of fossilised impressions, because in Matvéevo, only on perfect conserved specimen the miniature fertile organs can be evidenced well under magnification or what is more probable that they do not exist.

Whether the connected entire and aristate leaves evidencing a strong mid-vein can be brought in connection with the fruit-flowers is not clear till now. It can only be stated that these kind of leaves, seeds and blossoms are relatively abundant in the Matvéevo layers. Because no known Permian gymnosperms can be connected with all these features, the angiosperm way was chosen.

To avoid giving separate names to the flowers and leaves all the complex was classified as *Bardocarpus aliger.* MAT 82 represents a superb conserved twig, MAT 442 a flower with anthers, probably also with an pistil, whereas fossilised stone-fruits are common in the Matvéevo sediments. Therefore, some reasons exist to connect these isolated plant parts. So, we have in addition to the samaras, the acorns – another form of fruit. All of them can be connected by their similar composition of blossoms that helps clear the angiosperm evolution considerably.



Extant genus *Prunus* – Leaves, flowers and stone-fruits

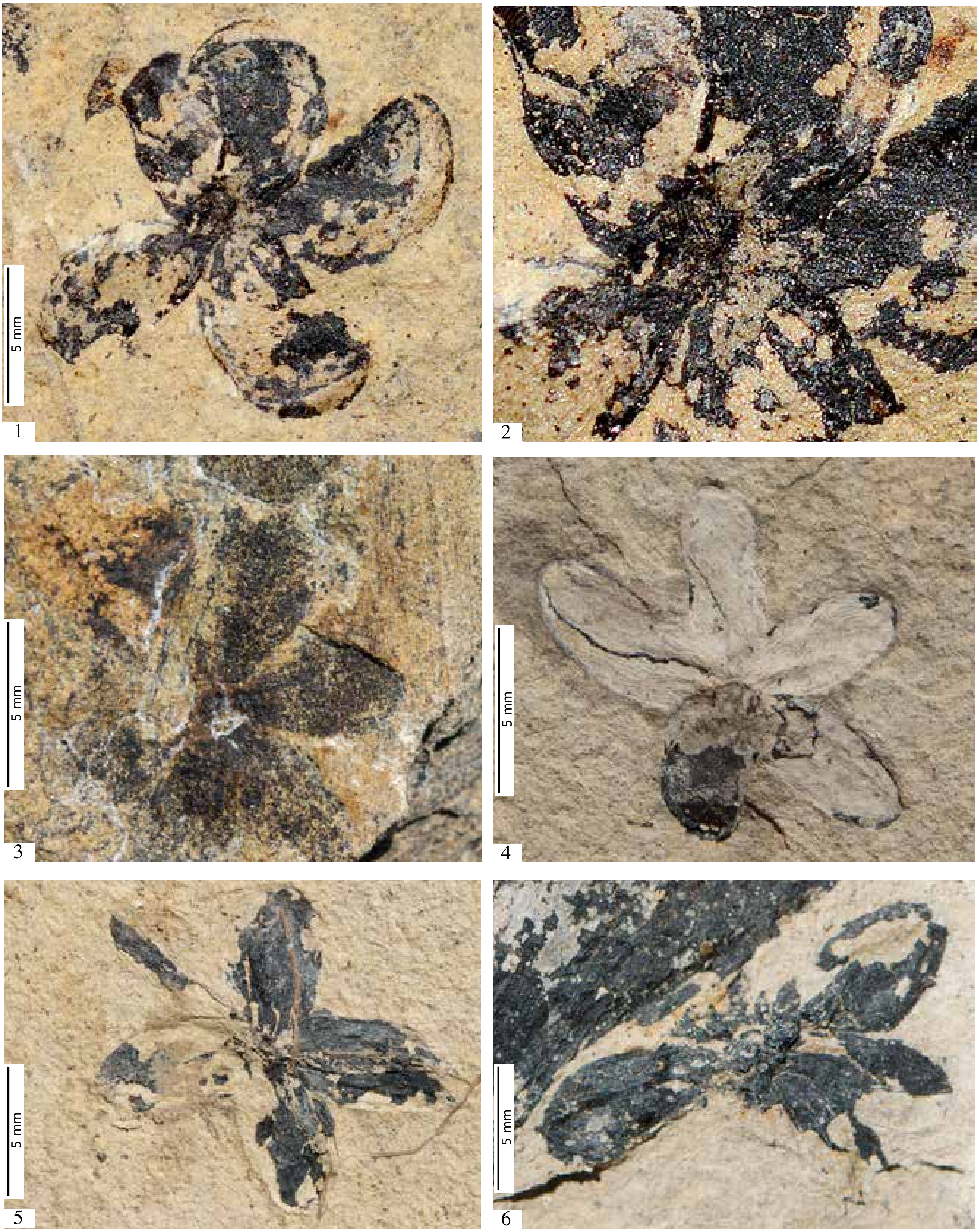
1. *Prunus serrulata* (Japanese cherry). Flower with reproductive organs and female infructescence; 2. *Prunus persica* (peach) flower; 3. *Prunus persica* (peach). Immature fruits and leaves; 4. *Prunus cerasifera* (*cherry plum*). Immature fruits; 5. *Prunus avium* (cherry). Mature fruits; 6. *Prunus domestica* (plum). Mature stone-fruits

Bardocarpus aliger. Potential stone fruit ancestor - Reconstruction

a. Single leaves (MAT 270); b. Flowers holding five petals and evidencing the reproductive structures with androecium and gynoecium (MAT 442, MAT 301, MAT 40); c. Twig (MAT 270); d. Stone fruits with fleshly parts outside and a single kernel inside (MAT 415, 393,394, 400, 409, 403)

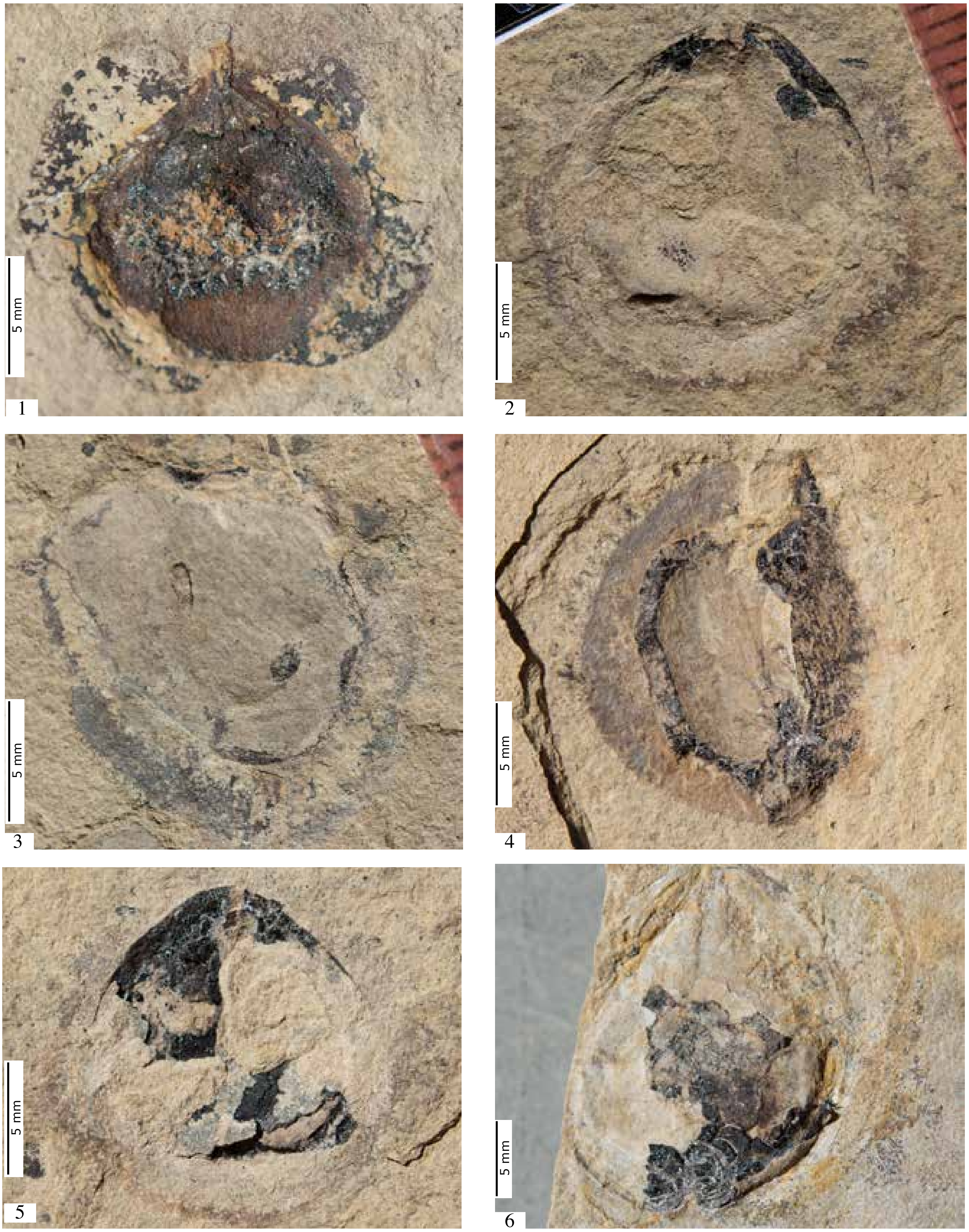
***Bardocarpus aliger*. Potential stone fruit ancestor - Leaves and twigs**

1-3. Twig and leaves thought to belong to *Bardocarpus aliger* (MAT 82); 4. Isolated leave (MAT 270); Matvéevo, Kungurian (Early Permian) Coll. Perner



***Bardocarpus aliger*. Potential stone fruit ancestor - Rosopsida flowers**

1-2. Flower holding five petals, inside with evidencing the reproductive organs with stamen and anther holding the microsporangia and the pistil (MAT 442, Coll. Gerasch); 3. Mature flower with reproductive organs (MAT 40); 4-5. Flowers with five petals (MAT 348, 201); 6. Flower showing the ovary and the anther (MAT 301); Matvéevo, Kungurian (Early Permian) Coll. Dolomythos



***Bardocarpus aliger*. Potential stone fruit ancestor - Stone fruits**

1-6. Several stone fruits. Note the well conserved fleshly parts outside surrounding a single hard pit of hardened endocarp with a kernel inside. (MAT 415, 393, 394, 400, 409, 403); Matvéevo, Kungurian (Early Permian) Coll. Dolomythos

Early Permian oak ancestors from Angara

Systematic Paleontology

Division Paleoangiosperms
Order Fagales
Family Fagaceae

Genus *Craspedosperma,* ZALESSKY 1937

Taxonomic notes

Zalessky (1937b) described and figured two similar specimens from Krasnaia Glinka near Matvéevo, both recorded only by one specimen: *Craspedosperma bardaeanum*, a rounded seed with a tuft of filamentous appendages on the upper side and *Thysanosperma ovatum* with a seed/ ovule surrounded completely by filamentous leaves. Probably, they belong to the same plant and represent only a diverse rear/ front/side view.

Craspedosperma bardaeanum ZALESSKY 1937

1937 C*raspedosperma bardaeanum* Zalessky, p. 87, Fig. 58

2008 *Craspedosperma filiferum* Naugolnykh, p. 546, Fig. 3-5, C*raspedosperma bardaeanum Fig. 6,7,*

Type horizon and age

Ural, Early Permian, Artinskian/Kungurian (272.3–290.1 Mya)

Description

Fruits: Mainly oval to rounded seeds or acorns with a depression on the upper side, tapering on the base, inserted in a cup of distinctly divided filamentous extensions. Seeds about 1 cm long, 0.8 cm wide (MAT 396), but also reaching to 1.4 cm width (MAT 359), tuft of variously developed filamentous appendages, 0.5 high and 2.0 cm wide (MAT 359). In a juvenile stage, divided into two appendixes (MAT 361), altogether 1 cm x 1 cm.

Discussion

Naugolnykh (2008) divided *Craspedosperma,* after findings from Chekarda, into two species: The well-known *Craspedosperma bardaeanum* (Zalessky, 1937b) and a thought new species *Craspedosperma filiferum*, based only on the distinct longitudinally elongated oval outlines of the "core" and the thinner and more numerous filaments. But he admitted that both specimens may belong to the same species (Naugolnykh, 2008). Additionally, Zalessky as well as Naugolnykh figured the specimen with hairy filaments on the upper side and rounded core on the base. I think that the right position will be as in extant oaks (*Quercus)*, with the "hairy" cups surrounding the acorn on the lower side.

Psygmophyllum expansum BRONGNIART 1845 (SCHIMPER 1870)

1845 *Noeggerathia expans*a Brongniart, Pl. B, Fig. 4 a,b,; Pl. E., Fig. I a,b,c,d

1870 *Psygmophyllum expansum* Schimper, Vol. II, p. 192

Taxonomic notes

The genus name *Psygmophyllum expansum* was instituted by Wilhelm Philipp Schimper (1808–1880) in 1870 (Vol II. p. 192, fig. 665–667) for fan-shaped cuneate leaves from Permian rocks of the Ural mountains (Nijni-Troisk), included by Adolphe-Théodore Brongniart (1801–1876) as *Noeggerathia expansa.* Confusion arose when in 1875, Saporta introduced the name *Ginkgophyllum* for the same leaf type.

Description

Leaves: The foliage is characterized by a broad variability on the same layers. Usually, they are compound palmate or flabelliforme, sometimes dissected into two symmetrical parts or with one side more developed than the other. One vein enters into each leaf segment and then may dichotomize.

Discussion

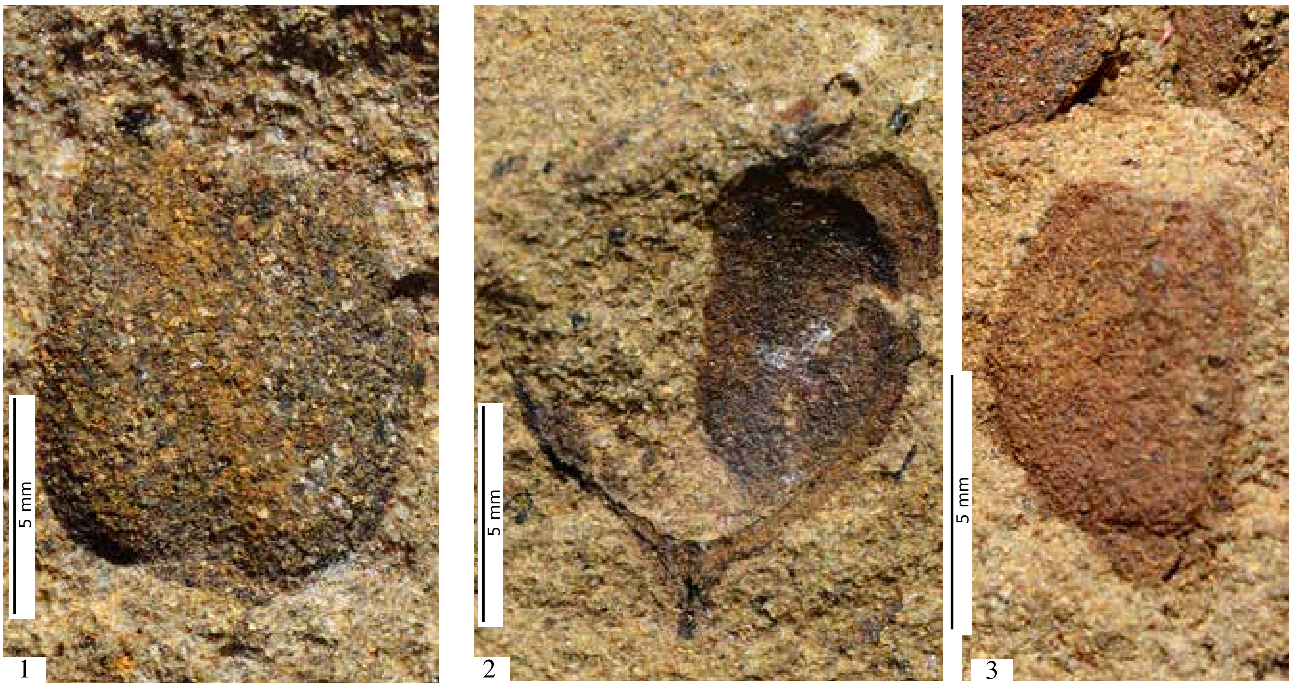
Due to the big variability of the leaves, many sub-species were erected, often based only on one single specimen, and never connecting them with fertile organs [*Psygmo-*

Extant oak (Quercus) – Leaves, flowers and stone-fruits

1. *Quercus rubor.* Isolated leaf; 2. *Quercus frainetto.* Twig with leaves; 3. *Quercus cerris.* Leaves; 4. *Quercus cerris.* Juvenile acorn; 5. *Quercus cerris*. Adult acorn, densely covered with mossy bristles; 6. *Quercus cerris.* Mature shed acorn. 7. *Quercus coccinea*. Adult acorn.

***Psygmophyllum expansum (Craspedosperma bardaeanum)* – Potential quercus (oak) ancestor leaves**

1. *Psygmophyllum expansum* (Brongniart). Several well-preserved leaves – the lower one represents a juvenile form, the other fully grown. (ARTI 17, Arti, Artinskian (Early Permian), Coll. Wachtler-Perner, Dolomythos Museum



***Psygmophyllum expansum (Craspedosperma bardaeanum)* Potential quercus (oak) ancestor-acorn**

1-3. *Craspedosperma bardaeanum* (Zalessky). Seeds thought to belong to *Psygmophyllum expansum* (ARTI 44, 37, 08) All Arti, Artinskian (Early Permian) (Coll. Dolomythos)

phyllum demetrianum, *P. eurinum*, *P. nesterenkoi*, *P. vesnjankianum*, *P. siberianum, P. sibiricum*, and *P. (?) dobrolubovae*. *Psygmophyllum expansum* leaves have similarities with extant oak foliage (*Quercus*) and if we connect *Craspedosperma* acorns, then it can be classified as the most primitive oak ancestor.

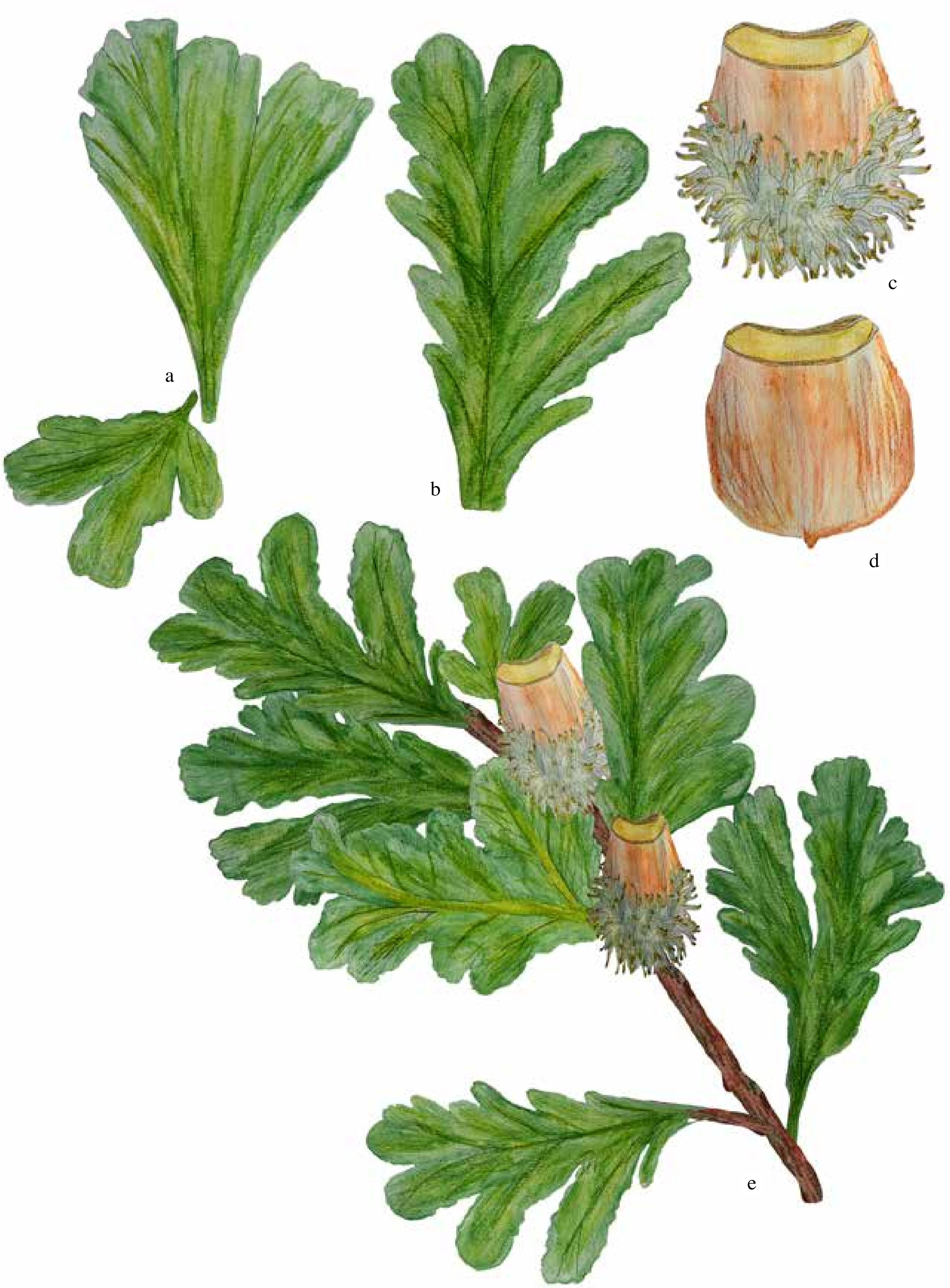
Therefore, the main question is in which evolutionary way can *Psygmophyllum expansum* leaves be connected as the oak progenitor with the other leaves such as *Psygmophyllum cuneifolium* as the potential maple ancestor. Both are just recorded from slightly older Artinskian layers and therefore, their divergence must be occurred before, probably between Carboniferous and Permian periods. Artinskian *Psygmophyllum expansum* leaves, especially juvenile forms (ARTI 17), show a four-lobed foliage type, a character seen also in primitive *Psygmophyllum cuneifolium* leaves (ARTI 11). In that, some parental affinities can be deduced.

But more important is the derivation of their blossoms and seeds – the samara on one side and the acorn on the other. The male flowers of today’s Fagaceae form long drooping catkins; the females have small spikes in the leaf axils. If we regard the samaras of *Sylvella alata* (maple ancestor), *Matveeva perneri* (elm progenitor) and *Sadovnikovia belemnoides* (ash forefather) as single seed coated by many subtle micro-leaves to obtain finally a wing, the typical oak-acorn *(Craspedosperma bardaeanum)* constitute a seed, densely encased on the basal side by dwarfish leaves. In a juvenile stage, it develops as mossy bristles – to repulse animals – and in an adult stage, they will be released from their coat, to be offered as food for dispersing animals. The same connection can be made with the stone-fruits (*Bardocarpus aliger)*, being nothing other than fleshy micro-leaves densely wrapping the seed.

From that point of view, an evolutionary connection can be made with all these astonishingly early, about 300 million years old, diverging Paleoangiosperms. It happened in a similar way to the development of early gymnosperms on completely isolated and different continents. This evolution way seems to be more logical than the difficult deduction of the theorem of Magnoliids as the most primitive flowering plants, that in a short time in the Cretaceous diverged to all other worldwide existing angiosperms, but never documented by evolution facts.

***Psygmophyllum expansum (Craspedosperma bardaeanum*) Potential Quercus (oak) ancestor. Reconstruction of the leave variability**

a. ARTI 11; b. ARTI 14; c. ARTI 12; d. ARTI 19; All Arti, Artinskian, e. MAZ 01 (Matzuevka) Artinskian f. MAT 301 (Matvéevo, Kungurian)

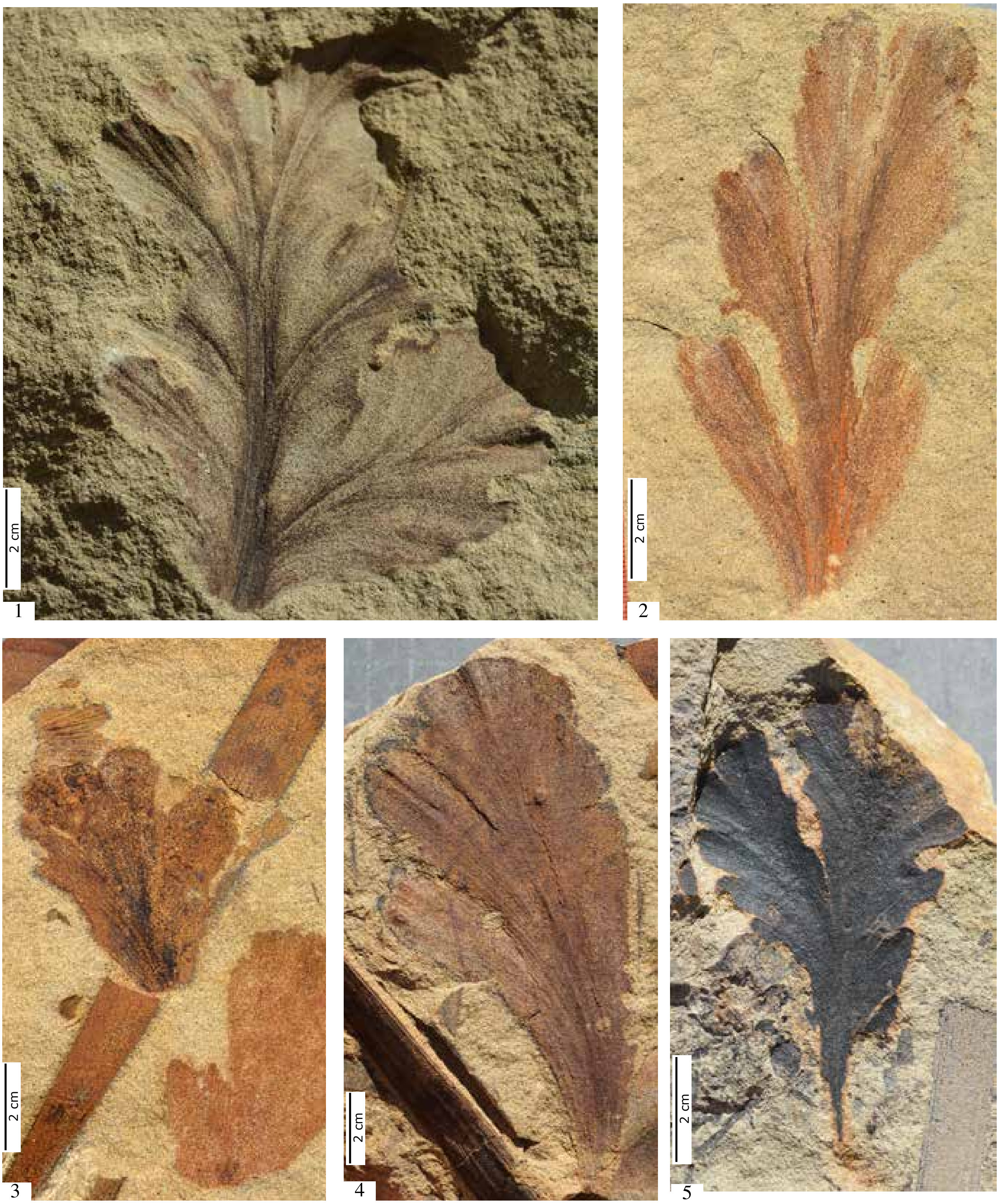


***Psygmophyllum expansum* (*Craspedosperma bardaeanum*) Potential Quercus (oak) ancestor. Reconstruction plant**

a. Juvenile and adult leaves (ARTI 17), Arti, Artinskian; b. Leave (MAT 185, Matvéevo, Kungurian; c. Acorn inserted in a cup of bristles (MAT 361, 428, 496); d. Released seed (MAT 420), e. Suggested twig; All Matvéevo, Kungurian

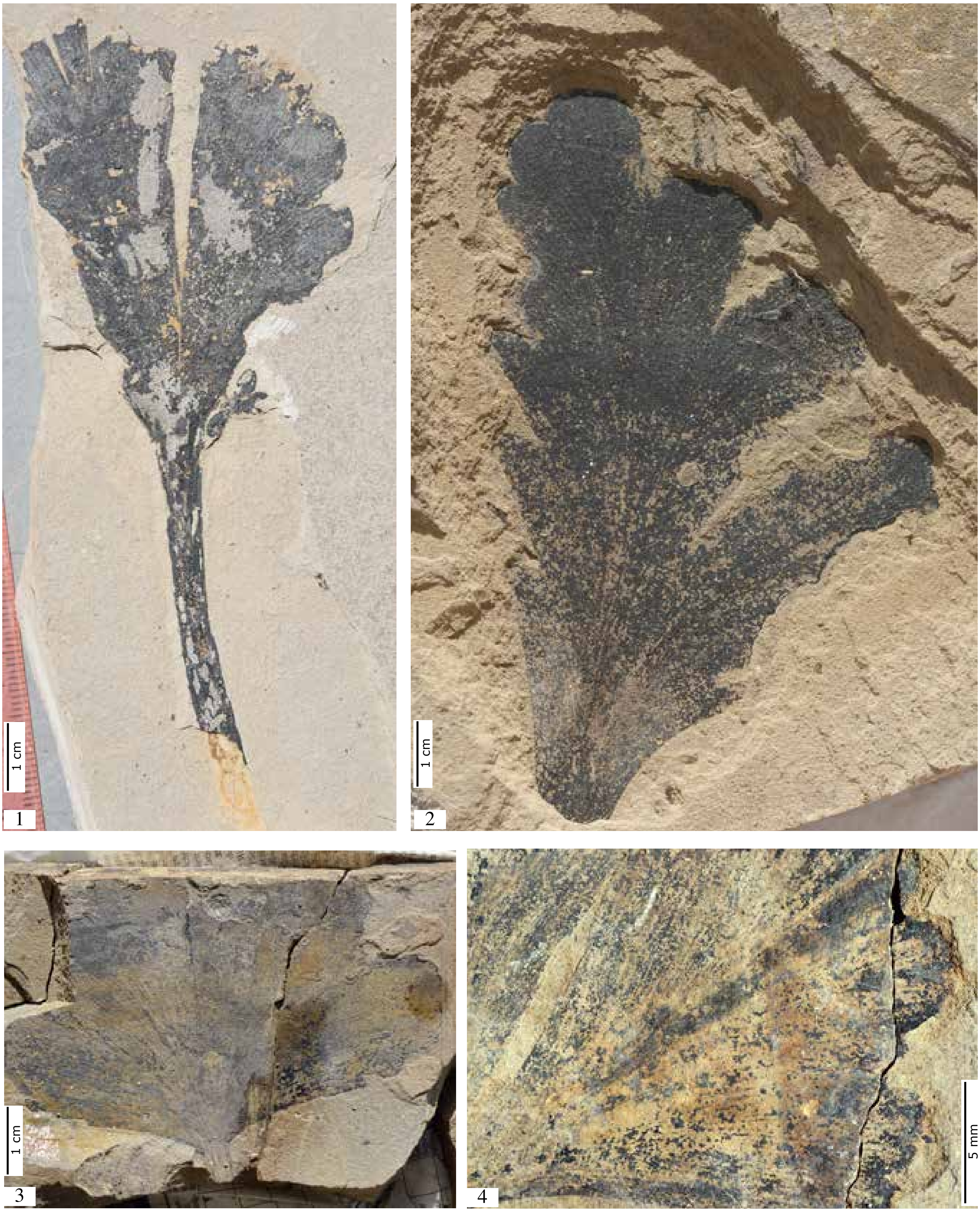
***Psygmophyllum expansum (Craspedosperma bardaeanum)* Potential Quercus (oak) ancestor-leaves**

1-4. *Psygmophyllum expansum* (Brongniart). Several well preserved leaves, evidencing the foliage-variation of these trees (ARTI 11, 14, 23, 50), (Coll. Dolomythos, Arti, Artinskian (Early Permian), Coll. Wachtler-Perner, Dolomythos Museum



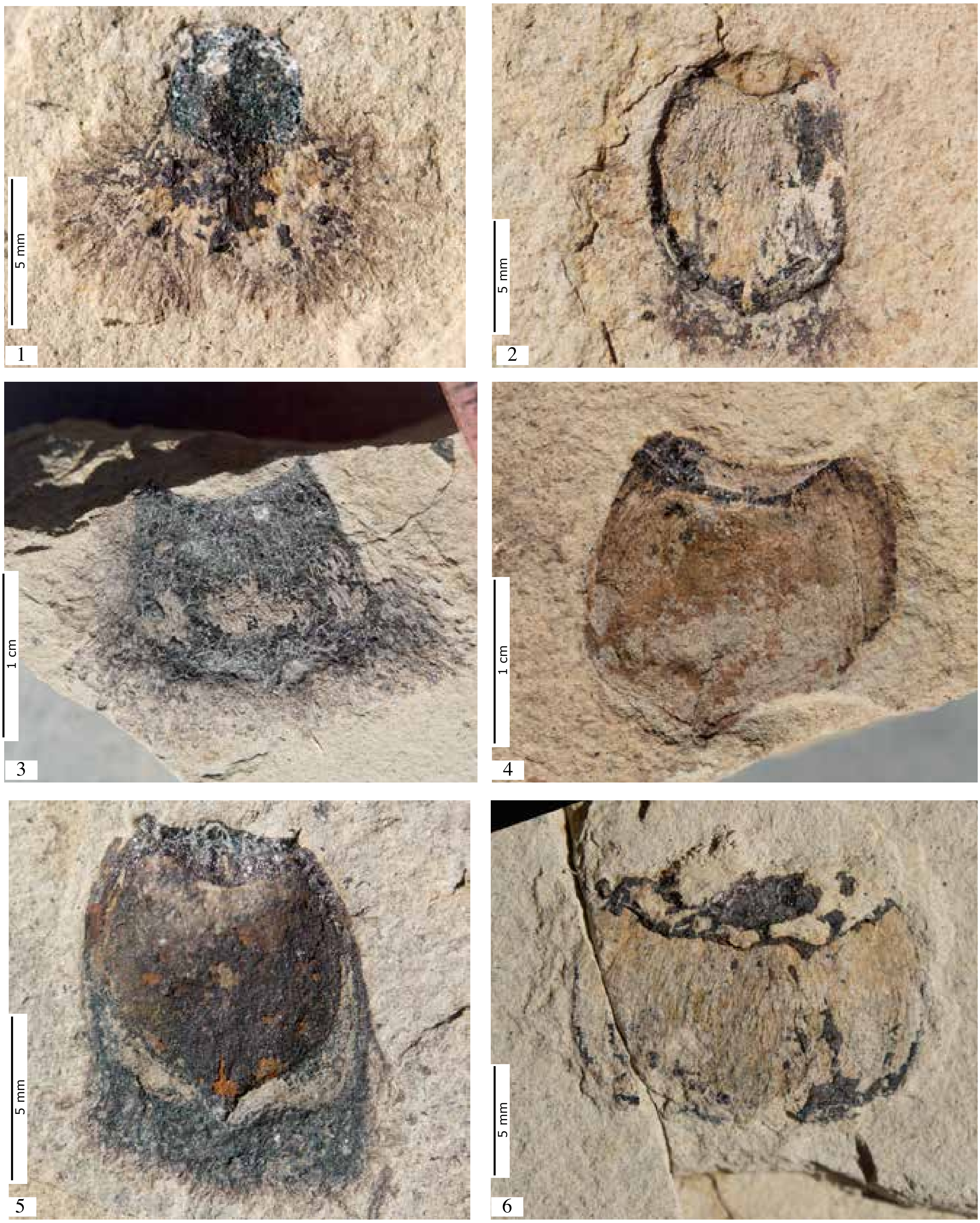
Psygmophyllum expansum (Craspedosperma bardaeanum) **Potential Quercus (oak) ancestor-leaves**

1. *Psygmophyllum expansum* (Brongniart). Leaves from several Artinskian localities, (MAZ 01) Matzuevka, Coll. Dammann, 2. Other leaf (MAZ 02), Matzuevka, Coll. Gerasch; 3. Juvenile leaves (ARTI 10); 4. Adult leave (ARTI 12); 5. Strange segmented leave with seed *Craspedosperma* (ARTI 19); All Arti, Artinskian (Early Permian) Coll. Wachtler-Perner, Dolomythos Museum



***Psygmophyllum expansum (Craspedosperma bardaeanum)* Potential Quercus (oak) ancestor-leaves**

1-4. *Psygmophyllum expansum* (Brongniart). Several well preserved leaves from the slightly younger site Matvéevo, (MAT 301, 185, 133, 129) Kungurian; (Early Permian) Coll. Wachtler-Perner, Dolomythos Museum



***Psygmophyllum expansum (Craspedosperma bardaeanum)* Potential quercus (oak) ancestor-acorn**

1-3. *Craspedosperma bardaeanum* (Zalessky). Seeds thought to belong to *Psygmophyllum expansum.* Typical oak-acorn, densely covered with mossy bristles Matvéevo, (MAT 361, 428, 359, 420, 396, 411) Kungurian (Early Permian), Coll. Dolomythos

Early Permian foliage trees of unknown insertion from Angara

Systematic Paleontology

Division Paleoangiosperms
Order ?

One of the most common plants in the early Permian Russian sediments is *Permocallipteris retensoria.* Its insertion in one of the known families is till now difficult.

Permocallipteris retensoria (ZALESSKY, 1937) NAUGOLNYKH, 2014

Basionym. *Callipteris retensoria* Zalessky 1939: 342, Fig. 16

Selected synonymy.

1939 Callipteris retensoria Zalessky 1939: 342, Fig. 16).

1991 Rhachiphyllum retensorium Zalessky 1937, Naugolnykh 1991: 45–48, Fig. 3; 1992: 31–36, Figs. 11–13

1996 *Peltaspermum retensorium* Zalessky, Naugolnykh & Kerp 1996, Plate I, 1–10; II, 1, 4; III, 1–9; IV, 1–8; V, 1–11; VI, 1–3; Figs 3–5, 6 A–C; Naugolnykh 1998, in part.: 90–97, Plates XI, 2–5, XII, 1, 4–6; XIII, XIV, XVI, 2; Text-Figs 47, 48B, 49A–C, 50–53C–D; Naugolnykh 2007: Plates XVIII, Fig. 1; XIX, Fig. 1–2, 4; XXV, 4; Text-Fig. 57).

Description

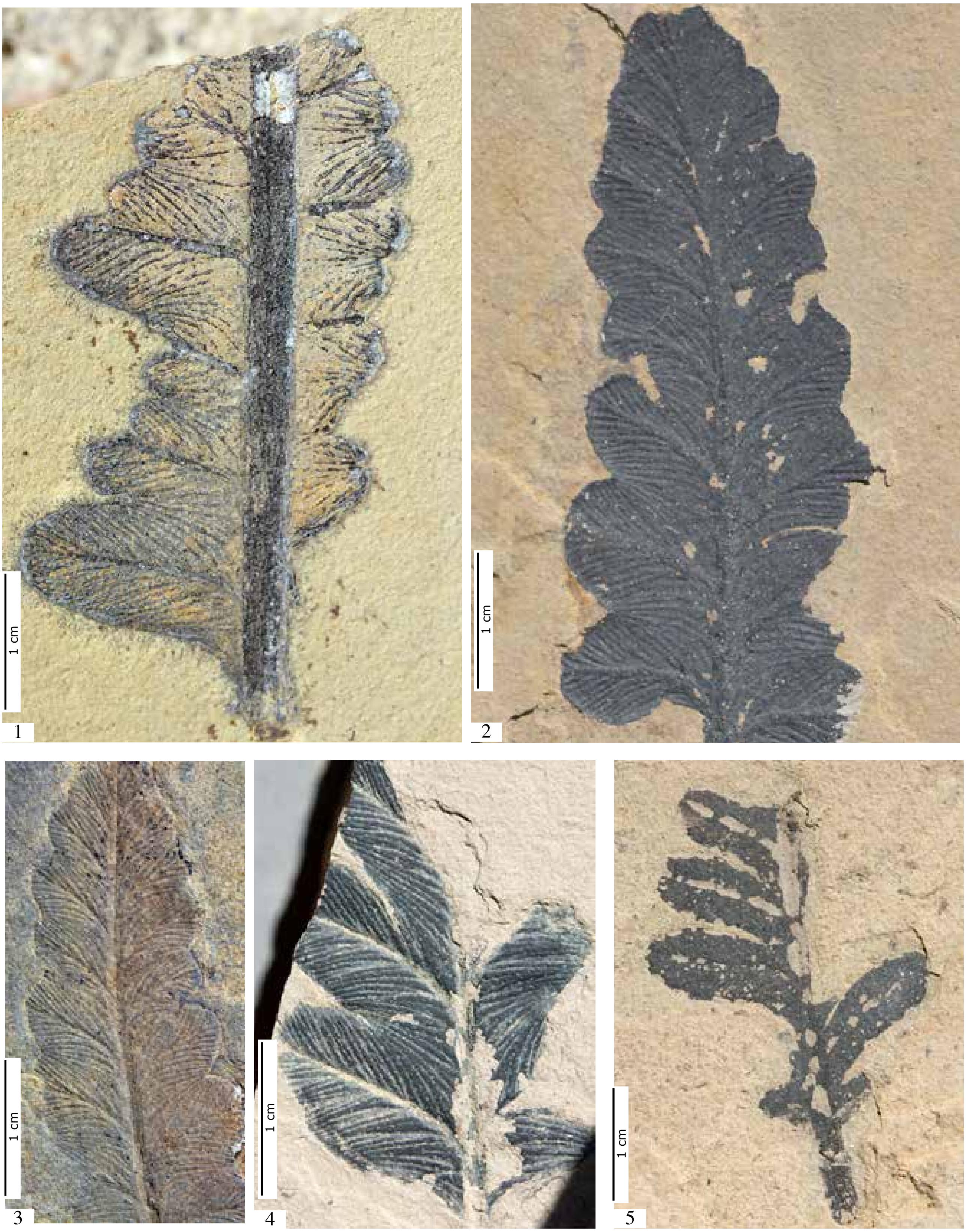
Foliage: Fronds pseudo-bi to tripinnate with leaves densely inserted on the main rachis (MAT 04). Lateral pinnae attached to the frond rachis in an alternate order on one side, usually longer than on the other (MAT 112, MAT 123). Pinnules about 2 cm long, 1 cm wide, basal parts partially or completely coalescently fused. Apex of the pinnules rounded, well-developed mid-vein, lateral veins from simple to twice dichotomizing.
Fertile organs: Probably of *Peltaspermum* type.

Discussion

This flora element lies with its fern-like foliage apart from the normal in some form forking foliage from the Early Permian Floras of Angara-Land. Because it is common beginning from the Artinskian stage over the Kungurian, it was several times described introducing different names all the time. Stephan Kutorga (1838, pl. VII, Fig. 4) figured and described it under the name *Pachypteris latinervia* as a similar foliage type. After them, especially Mikhail D. Zalessky (1927, 1929, 1934, 1937, 1939) established several new species without paying attention to the normal variability of the leaves (Naugolnykh, 2014). So, he introduced names such as *Dicranopteris regia, Sylvopteris conspicua, Callipteris polyneura* (Zalessky, 1937), also *Callipteris cuspidata, Callipteris bardensis, Callipteris patula, Callipteris bella,* and finally *Callipteris retensoria* (Zalessky, 1939).
Also the European seed-fern *Neuropteris (Callipteris conferta*) (Sternberg, 1825) Brongniart, 1849 has in Europe, due to its abundance, a long and varied history behind. It is characterized by pinnate to bipinnate fronds. The individual, sterile, leathery pinnules consisted of a thick, deeply sunken midrib and lateral veins that did not usually branch, although they branched once at the base in rare cases. Soon after that, umbrella-shaped female fructifications known as *Peltaspermum* were associated with these low-growing plants. But since this name was already being used for an extant genus of ferns, the genus name changed to *Autunia conferta* (Kerp, 1988).
Their umbrella-shaped fructifications, named *Peltaspermum,* made them unmistakable. But this group of plants reveals a special problem in palaeobotany: the term *Peltaspermum* pertain to the female fructifications, while the foliage is often referred to using other names such as *Autunia, Rachyphyllum* or *Lepidopteris.* The corresponding pollen organs are even more difficult to recognise and were classified as *Pterispermostrobus (kontheri)* or *Antevsia* in the Triassic. They consist of reduced, flat microfronds with pollen sacs hanging from their undersides. The first appearance of Peltaspermales in Europe we have is on the Carboniferous-Permian border (latest Kasimovian-Gzhelian) with *Wachtlerophyllum schaalii* evidencing y-shaped to several times splitting leaves in net contrast with the tongue-like foliage of *Hurumia (Odontopteris),* neuropterid *Autunia,* or oblong-segmented *Rhachiphyllum* leaves of other Euro-American fossil sites (Perner & Wachtler, 2013). From that point

***Permocallipteris retensoria.* Sterile foliage**

1–2. Frond with deeply incised mid-veins. Plate and counterplate (MAT 04); 3. Apical forked part of a frond (MAT 64); Coll. Perner & Wachtler; 4. Frond evidencing two pseudo-dichotomies. (MAT 05) (Coll. Dammann); Matvéevo, Kungurian (Early Permian)



***Permocallipteris retensoria*. Sterile foliage**

1. Pinnae fragment showing the venation (MAT 112); 2-3. Pinnae fragment showing the venation, plate and counterplate (MAT 123); Coll. Dammann; 4. Pinnae fragment (MAT 263) 5. Basal pinnae-fragment (MAT 271) (Coll. Dolomythos); Matvéevo, Kungurian (Early Permian)

***Permocallipteris retensoria*. Reconstructions**

Several types of leaves. a. Note the strange longer pinnae on the left side (MAT 04); b. Detail of the leaf showing the veins (MAT 04); c. Another frond (MAT 05); d. Detail of a pinna (MAT 112, MAT 123); Detail of a single pinnula (MAT 112)

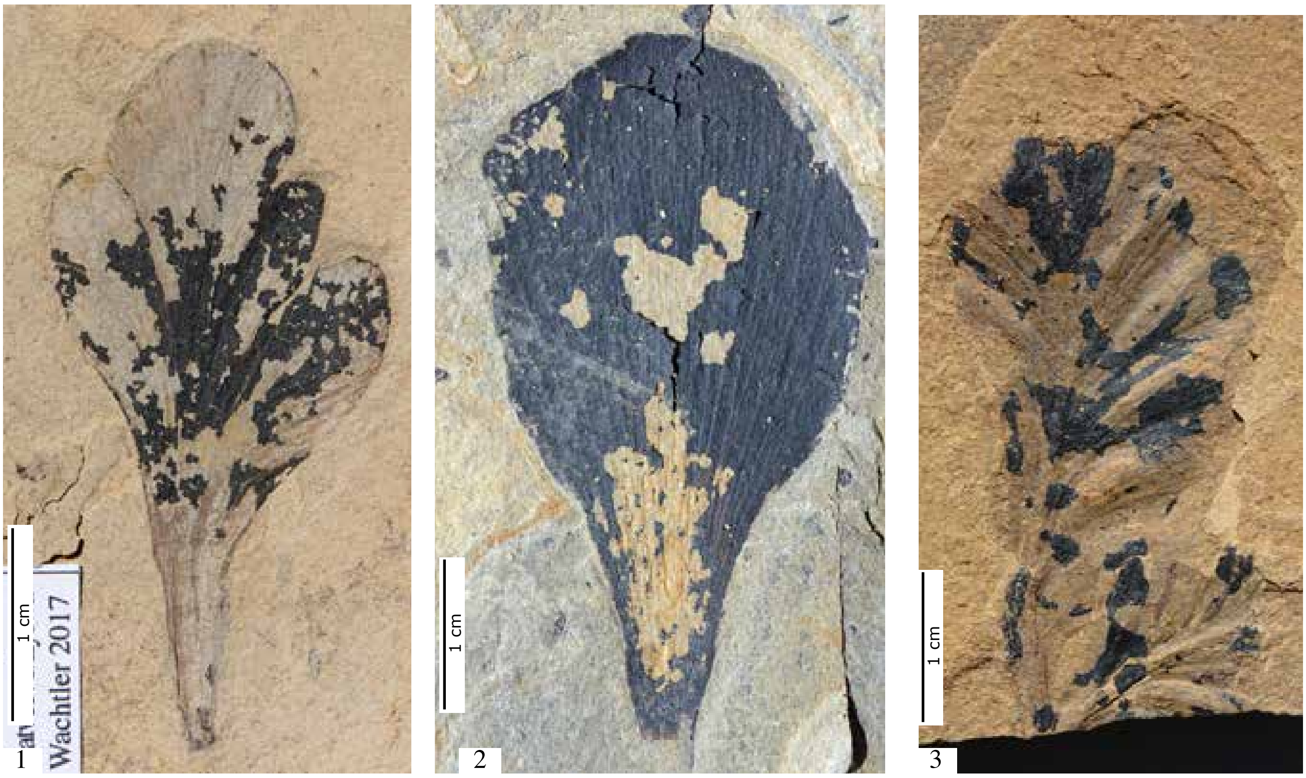
of view, *Wachtlerophyllum schaalii* seems, with its forking and y-shaped leaves having the most primitive appearance, resembling mostly some archaic Devonian foliage type. Similar fronds like the superb European *Autunia* – reaching 50 cm or more – are never recorded from *Permocallipteris*. It seems that they consisted only of 3–5 short and diverging pinna and their blueprint was different from fern-fronds. Also, the exact aspect of the fructifications in the plethora of *Peltaspermum* organs is not clear.

Due to the fact that Angaran floras are conspicuously different from the European ones, the name *Callipteris* has been evidently obsolete and therefore, Serge Naugolnykh (2014) changed the name to *Permocallipteris retensoria*, resolving only partly the problem (Naugolnykh & Kerp, 1996).

Then in which manner Euro-American Peltaspermales differ from the Angaran? Till now, the typical pollen filaments and ovaries or hermadophrite flowers of Angaran plants are not in the same manner recorded in Europe, but only as *Peltaspermum* shields holding inside seeds and pollen aggregations on different parts of the plants. They are, therefore, remarkably different. It is not completely impossible that the Angaran as well the European have some relationships and that effectively in the group of Peltaspermales lies the origin of all angiosperms, but till now, only the Angaran plants can be considered as lying in a direct line to the flowering plants. Interestingly, from Permian to Triassic, the Peltaspermales play only a subordinate role in the Euro-American floras. In Europe, we have in the Triassic with the genus *Scytophyllum* a relative, but overwhelmed by the huge number of conifers and cycads. Another problem is the role of *Permocallipteris* foliage in the Angaran floras or their today's descendants. Some characteristics indicate in direction of the figs (Ficus), the chestnuts (Castanea), or the horse-chestnuts (*Aesculus hippocastanum)*. Especially, the last one evidences some features of *Permocallipteris.*

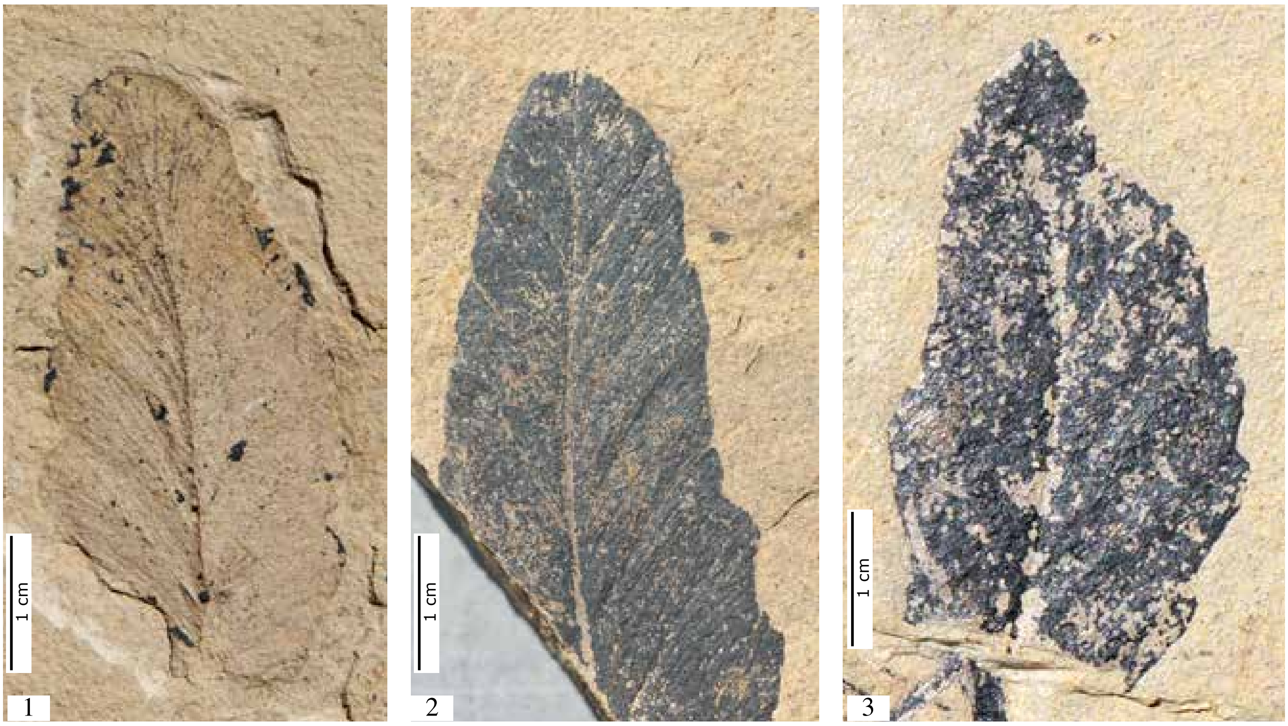
Artinskian leaves of unknown affinities

1-3. Leaves that cannot be connected with other fruits or seeds (ARTI 43, 34, 28), (Coll. Perner & Wachtler), Arti, Artinskian (Early Permian)



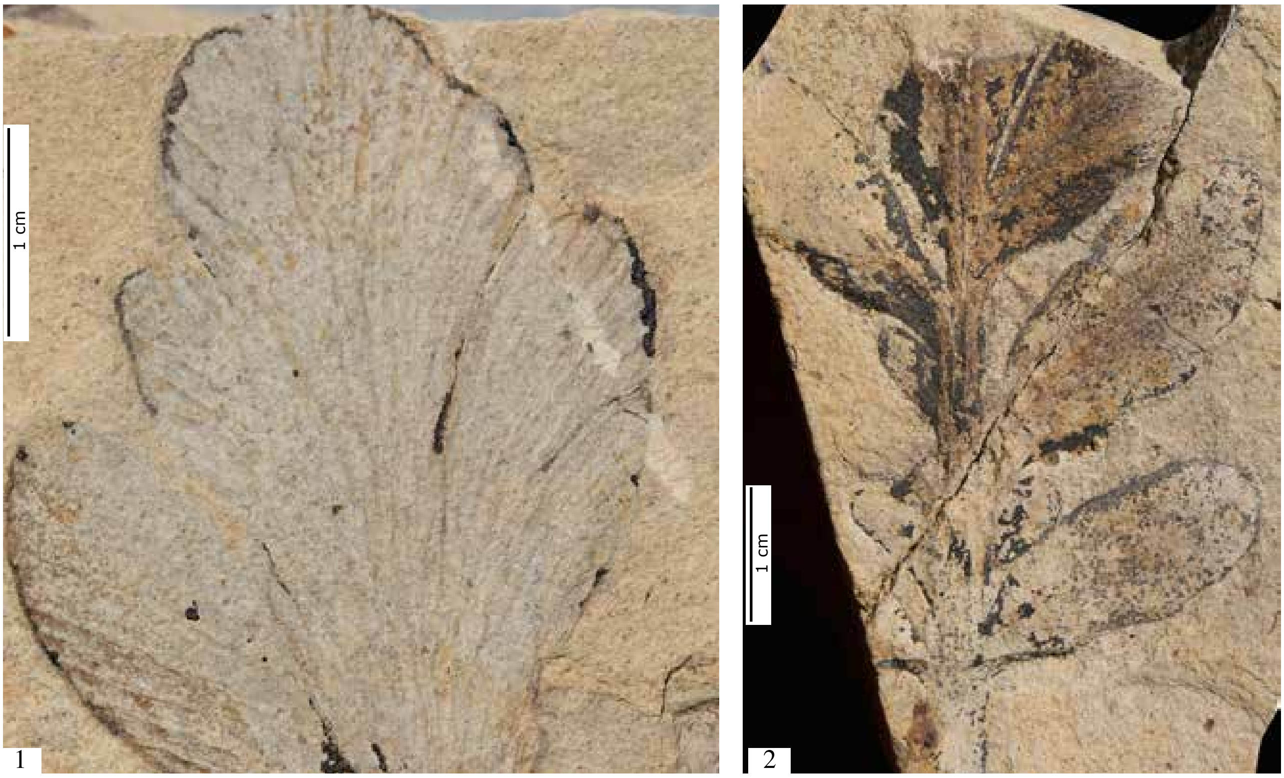
Kungurian leaves of unknown affinities

1-3. Leaves that cannot be connected with other fruits or seeds (MAT 339, MAT 127 (Coll. Dammann, MAT 131); (Coll. Perner & Wachtler); Matvéevo, Kungurian (Early Permian)



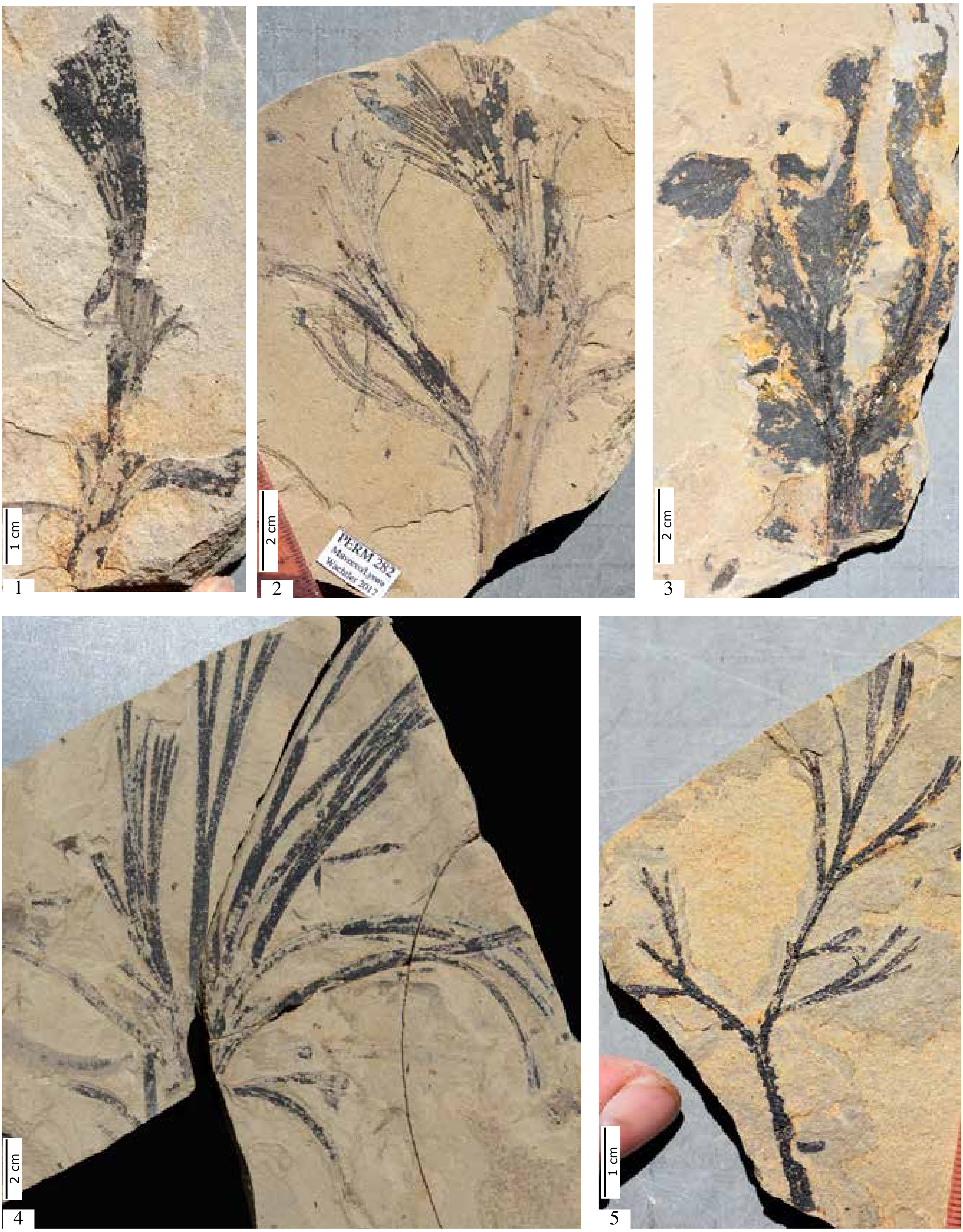
Kungurian leaves of unknown affinities having angiospermous character

1-3. Leaves that cannot be connected with other fruits or seeds, but with reticulate veins (MAT 270, MAT 501, MAT 434, (Coll. Gerasch); (Coll. Perner & Wachtler); Matvéevo, Kungurian (Early Permian)



Kungurian leaves of unknown affinities having angiospermous character

1-2. Leaves that cannot be connected with other fruits or seeds, but with reticulate veins (MAT 339, MAT 269); Matvéevo, Kungurian (Early Permian), Coll. Wachtler-Perner, Dolomythos Museum



Kungurian leaves of unknown affinities

1-3. Leaves that cannot be connected with other fruits or seeds, described also as *Kerpia macroloba* (MAT 272, MAT 282, MAT 451); 4-5. Furcating leaves (MAT 287, MAT 457); Matvéevo, Kungurian (Early Permian); Coll. Wachtler-Perner, Dolomythos Museum

Early Permian herbaceous plant flowers and grasses from Angara

Additional to the broad-leaved trees generating samaras, stone-fruits or acorns, other plants were recovered that have more affinities with today's angiosperms than gymnosperms. Some are well-known such as *Sphenophyllum biarmicum,* inserted formerly as Sphenophyta, but due to new findings of inflorescences, another classification must be carried out. To not bring confusion creating new terms, it was combined with *Peremopteris biarmicum* nov. comb., for a probably synonymous plant introduced by Zalessky in 1937. The same is valid for *Meristophyllum sojanaeanum*, often grouped with the *Cordaites* gymnosperms or Rufloriaceae. At Matvéevo, we record low-growing flowering plants resembling today's Asteraceae. For, these types of plants will be proposed the name *Naugolnykhia matvéevoi* gen. nov. sp. n. Other flowers have similarities with today's Campanulaceae and were described as *Lyswaia nicolaswachtleri* gen. nov. sp. n. Also "grass-like" plants were found: *Taezhnoeia geraschi* gen. nov. sp. n. and *Krasnaia dammannii* gen. nov. sp. n. All these flora elements are characterized by their herbaceous character. Attempt was made to find enough facts to consider these Angaran vegetation as dominated by Paleoangiosperms and that changing our knowledge considerably.

Early Permian insects, flowers and grasses in Angara Land (Matvéevo)

Bottom left: *Naugolnykhia matvéevoi*, a potential daisy-flower ancestor; bottom right: *Peremopteris biarmicum*, a flower of unknown affinities. Top right: *Lyswaia nicolaswachtleri*, probably belonging to the Campanulaceae; middle: The gras *Taezhnoeia geraschi* and the Poaceae ancestor *Krasnaia dammannii.*

Some of the insects: Sitting top left and right: The mayfly (*Misthodotes sharovi)*, left on the flower the true bug (Hemiptera) *Maueria pusillus*, bottom left: the stonefly *Uralonympha varica),* middle right: the Miomoptera *Sellardsiopsis conspicua* searching pollen, middle: the cockroach (Blattodea) *Rachimentomon reticulatum*, the Orthoptera *Angaroptera nicolaswachtleri*; middle bottom: the scorpion *Permomatveevia perneri,* the largest-sized insect of Matvéevo.

***Naugolnykhia matvéevoi* gen. nov. sp. n. Potential daisy-flower ancestor**

1–2. Herbaceous plant with inflorescence and hanging petals (MAT 367, designed holotype); 3. Blossom evidencing hanging petals (MAT 353); 4–5. Inner circle of the floret (MAT 356). Matvéevo, Kungurian (Early Permian) Coll. Wachtler).

Systematic Paleontology

Division: Paleoangiosperms
Family: Asteraceae

Genus *Naugolnykhia* nov. gen. WACHTLER 2017

Etymology

Honouring Serge V. Naugolnykh (C.B. Наугольных), Russian paleobotanist and describer of many plant fossil sites from Permian Ural.

Diagnosis

Herbaceous plants with inflorescences born apically on single, mainly leafless stems. Flowers consisting of ray florets with an inner circular disc.

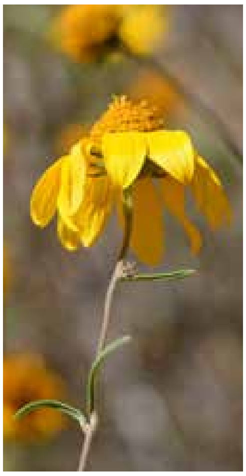
Naugolnykhia matvéevoi nov. gen. n. sp. WACHTLER 2017

Type horizon and age

Perm Krai (Russia) Ural, Early Permian, Kungurian (272.3–283.5 Mya)

Holotype

MAT 367 Coll. Wachtler, Dolomythos Museum, Innichen



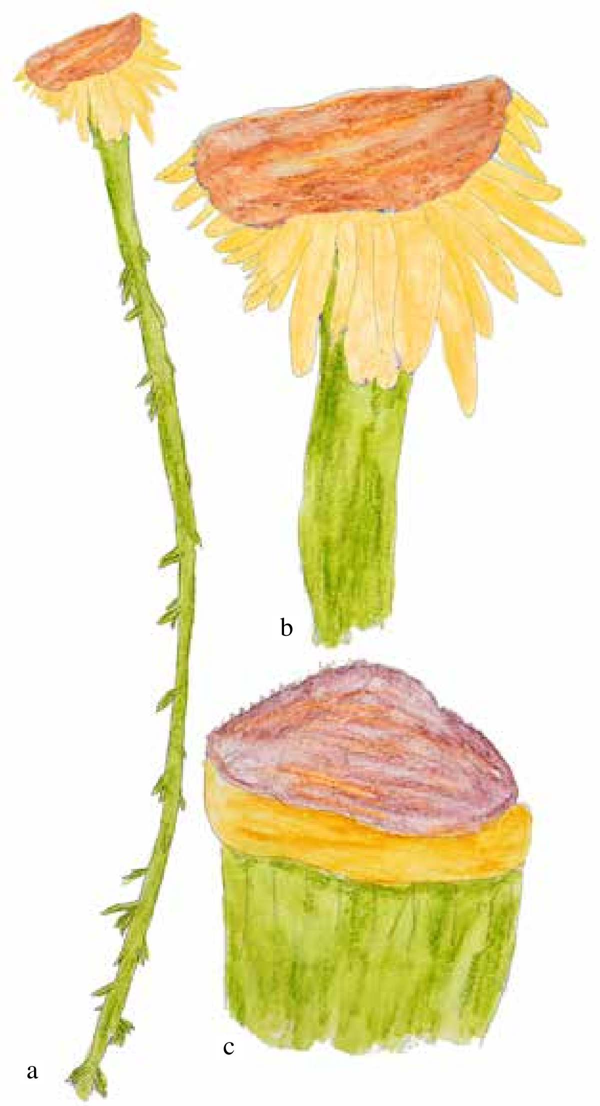
Left: *Encelia farinosa* (brittlebush), from the family of Asteraceae, a native flower from the southwestern United States. Right: *Leucanthemum vulgare*, (Oxeye daisy), a widespread flowering plant native to Europe and temperate regions of Asia.

Etymology

After the village of Matvéevo in the Lyswa district (Perm-Krai) where the plant was found first.

Diagnosis

A slender, long stalk with small-sized leaves held on the apex a blossom, composed of a fair number of petals surrounding a hairy shield.

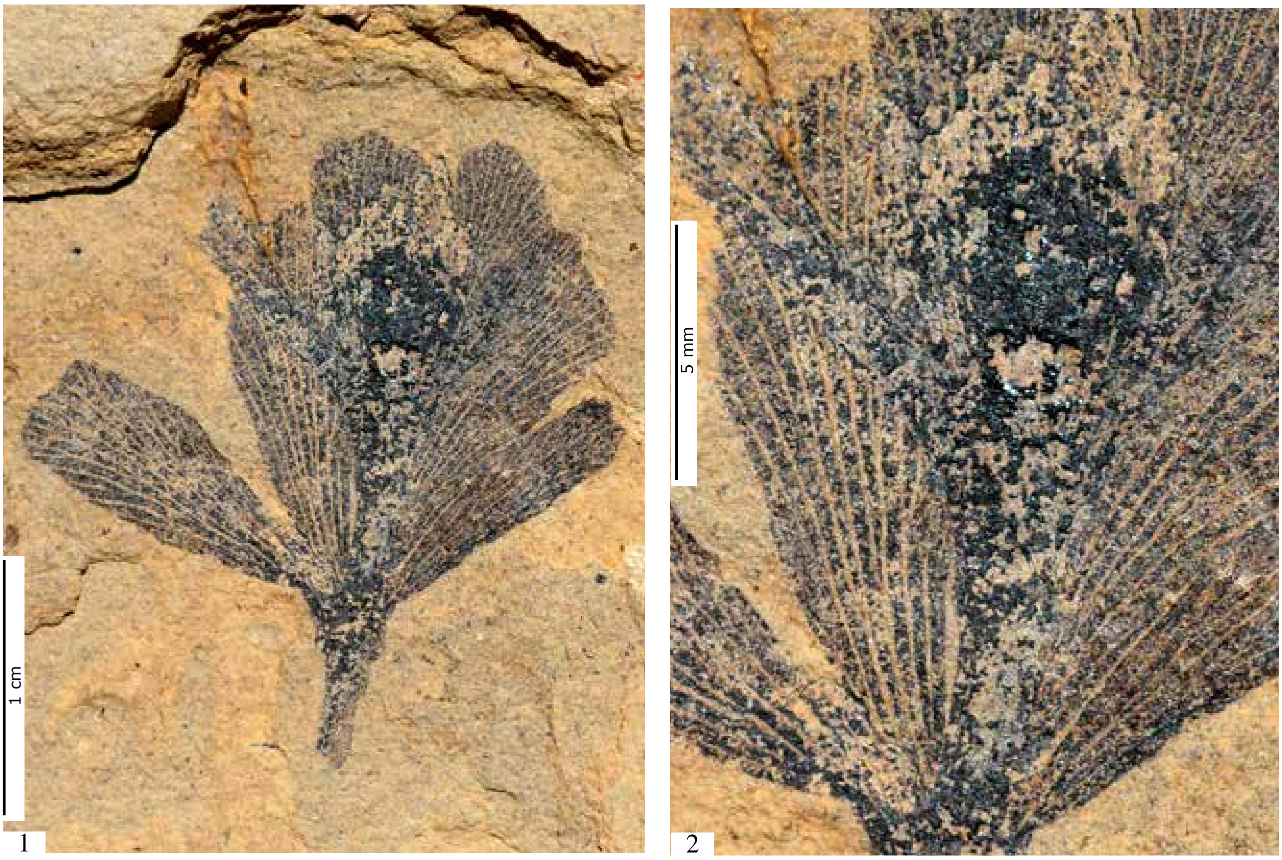


***Naugolnykhia matvéevoi*. Potential daisy-flower ancestor**

a. Flower with dwarfish leaves and the blossom (MAT 367 holotype); b. Blossom with hanging petals and an inner circle disc. c. Inner shield of a withered flower (MAT 353)

Peremopteris biarmicum nov. comb. **Leaves**

1. Plant with probably a flower (arrow), (MAT 328); 2. Juvenile plant (MAT 47); 3. Leaves showing well the dichotomizing veins (MAT 52); 4-6. Twigs with leaves (MAT 332, MAT 58, MAT 95); Matvéevo, Kungurian (Early Permian) Coll. Perner & Wachtler)



Peremopteris biarmicum nov. comb. **Suggested flower**

1-2. Exceptionally preserved flower with inside shadow of the carpel with stamen. Interesting are also the reticulate petals (MAT 435), Matvéevo, Kungurian (Early Permian) Coll. Gerasch).

Description

Herbaceous plant: Slender stipe, mostly naked, 0.2 cm wide, but probably till 15–20 cm long, being equal all over its length. Dwarfish leaves sprouting sometimes, only 0.3 cm in length, spiky and orientated downwards. Preserved length of the stipe is 16 cm. Apical flower 2.0 cm wide, mainly circular (MAT 367 holotype) surrounded by petals. **Flower:** Composed of two circles. An inner disk flower, reaching 1.5 cm in diameter, dome shaped, velvety, covered in a mature stage by finest hairs (MAT 353, MAT 356), and an outer ray flower composed of petal-like leaves. These up to 1 cm long, 0.3 cm wide on the base, tapering to a point (MAT 367, 353). Holotype MAT 367 probably represents a juvenile flower with an intact flower head with their reproductive organs fossilised as undefined agglomeration, whereas MAT 353 and MAT 356 are adult withered blossoms, with only a few isolated and hanging petals.

Discussion

Due to their inconspicuousness, *Naugolnykhia matvéevoi* have never attracted the attention of researchers or collectors, although they are not seldom in the Matvéevo layers. Noticeable is their slender, naked stipe, ending in a flower with a fair number of petals. No search to include *Naugolnykhia matvéevoi* in one of the gymnosperm families satisfy; therefore, attempt was made to insert this plant into the group of Paleoangiosperms. In that, it can be compared well with today's daisy flower (*Bellis perennis*), belonging to the Asteraceae family, with over 1,500 genera and 23,000 species – the largest family of flowering plants. Probably, knowing nothing about the Early Permian age, *Naugolnykhia* could be confused easily with this plant. Both have leafless (daisy flower) or mainly leafless stalks *(Naugolnykhia matvéevoi*); both flowers have a large center and are adorned with delicate petals. Probably the mimicry pistil and the stamen are visible on the juvenile specimen.

Systematic Paleontology

Division Paleoangiosperms
Family Rosaceae

Peremopteris biarmicum nov. comb. ZALESSKY 1937, WACHTLER 2017

Selected synonymy

Sphenophyllum biarmicum, Zalessky 1937b p. 45 Fig. 7, 8

Type horizon and age

Perm Krai (Russia) Ural, Early Permian, Kungurian (272.3–283.5 Mya)

Description:

Leaves: Vegetative foliage with entire margin, ovoid to fan-shaped, dichotomizing several times on the leaf. Leaf size from 1.5 cm x 0.5 cm (MAT 332), till 3 cm x 1.5 cm (MAT 58). Leaves arranged on one level (MAT 328), horsetail like.

Drawing from Zalessky 1937b, p. 45, fig. 7, described as *Sphenophyllum biarmicum* n. sp. from Kroutaia Katouchka near Matvéevo.

Flowers: Whorls of petals, five to six surrounding the ovary, and the anthers, 2 cm x 2 cm. On MAT 435, one carpel and two stamens are visible. Petals resembling vegetative leaves, dichotomizing several times.

Discussion

Mikhail D. Zalessky figured (p. 45, fig. 7 + 8) and described in 1937 a new plant with the name *Sphenophyllum biarmicum* from Matvéevo, inserting it in the Sphenophyta. The most superb specimen figured, but unfortunately lost, represents a bigger twig, 15 cm x 12 cm, evidencing with their often-diverging fronds, an unusual horsetail character. An exceptionally preserved flower from Matvéevo (MAT 435) having the same aspects, but with well-visible carpel and stamen inside and the reticulate venation of the petals/leaves indicate in a direction of Paleoangiosperms, so typical for the Matvéevo flora. To not bring confusion creating new genera and species, this plant fossil was combined with *Peremopteris biarmicum* (Zalessky, 1937b, nov. comb.), due to the fact that Zalessky figured a similar specimen, probably being synonymous on pag. 47, Fig. 10 as *Peremopteris sylvaena*. Difficult is also the classification into one of the today's existing families. The first choices are the Malvaceae with stamens forming a tube around the pistils or from some family belonging to the Potentillas or the Dilleniaceae.

Lavatera maritima. Flower, stamen and carpel of a Malvaceae.

***Peremopteris biarmicum nov. comb.* Reconstruction**

a. Flower evidencing only the petals; b. Carpel with pistil and stamen; c. Complete flower (MAT 435); d. Juvenile twig (MAT 47); e. Sterile leaves (MAT 52); f. Reconstruction of Zalessky's plant from 1937; g. Suggested reconstruction of a twig with flowers.

Systematic Paleontology

Division Paleo-Angiosperms
Family Campanulaceae -Asterales

Genus *Lyswaia* nov. gen. WACHTLER 2017

Etymology

Named after the Lyswa (Russian: Лысьва), in the Perm-Krai, the first big city near Matvéevo.

Diagnosis

Herbaceous plant having leaves with a central midrib, campanulate flowers and as fruits capsule containing the seeds

Lyswaia nicolaswachtleri nov. gen. n. sp. WACHTLER 2017

Type horizon and age

Perm Krai (Russia) Ural, Early Permian, Kungurian (272.3–283.5 Mya)

Holotype

MAT 338 Coll. Wachtler, Dolomythos Museum, Innichen

Etymology

Honouring the researcher Nicolas Wachtler, who made several paleobotanical discoveries in Angaran Permian.

Diagnosis

Herbaceous plant with basal leaves aggregated in tufts. Entire foliage evidencing a central midrib. Flowers solitary in the form of a calyx and seed holding capsules.

Description

Plant: Low-growing plant composed of a bunch of leaves with flowers composing a campanulate corolla and several sepals forming a calyx.
Foliage: Leaves long and slender (about 0.5–0.7 cm wide and 5–10 cm long, tapering at the end with an entire margin and an incised midrib (MAT 338, holotype, MAT 287, MAT 486).

Flowers and fruits: Blossoms solitary on the end of a stipe/leaf, 1 cm long, 0.6 cm wide (MAT 392). Corolla campanulate, with leaf-like sepals surrounding the calyx. Fruits hanging on the corolla, opening the capsule


1

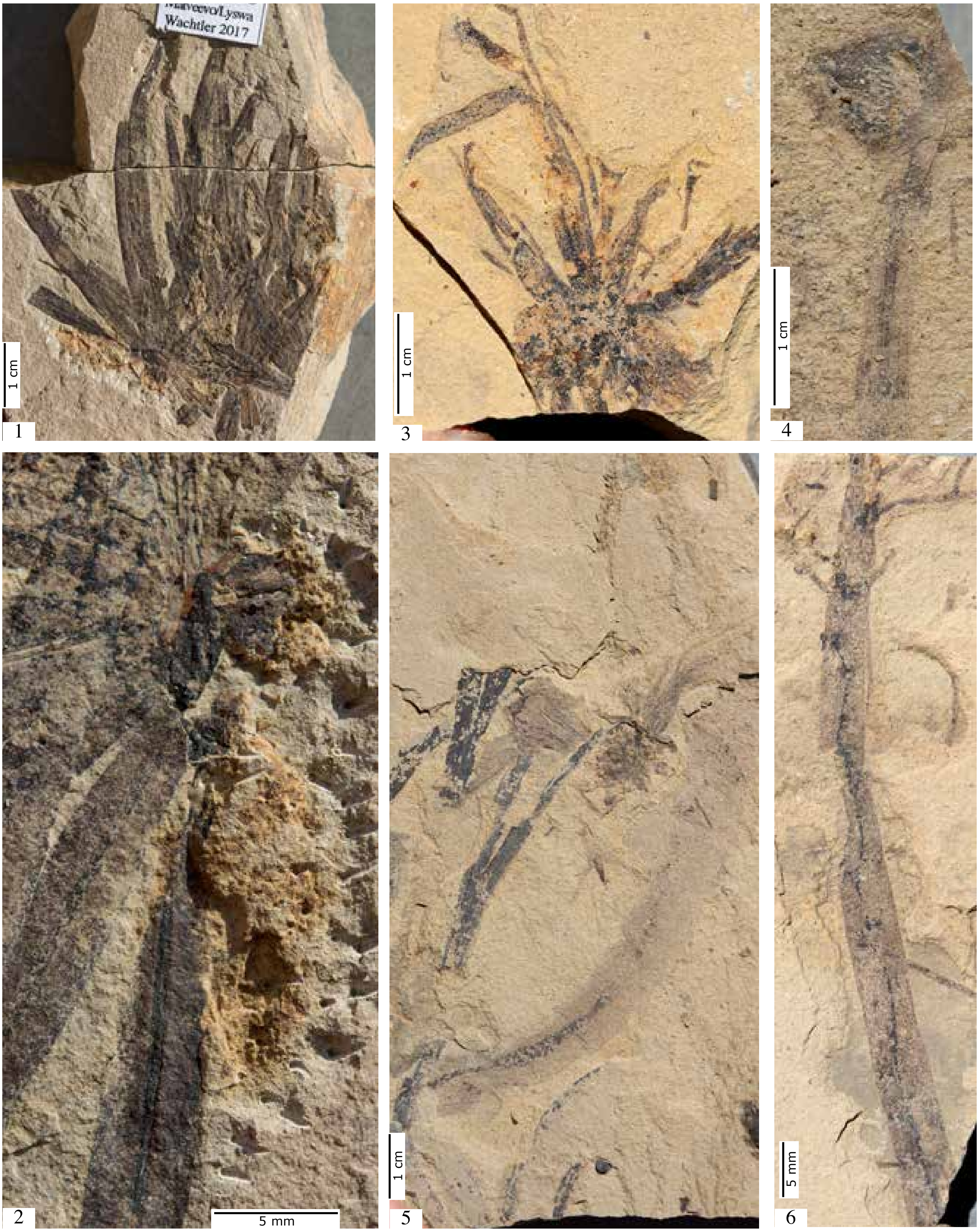

2


3

1. *Platycodon grandiflorus* (balloon flower). A Campanulaceae native to China.

2. *Campanula alpina* (Bell-flower) is widespread in Europe.

3. *Campanula rotundifolia* (Bluebell bellflower) Capsule containing some seeds, with the majority just released. It can be compared with MAT 338, also an open capsule.



***Lyswaia nicolaswachtleri* gen. nov. sp. n. Plant, leaves and flowers**

1–2. Entire plant with detail of a mature and open capsule (MAT 338, designed holotype); 3. Juvenile plant (MAT 458); Coll. Gerasch); 4. Detail of a juvenile campanulate flower, evidencing the sepals (MAT 392) 5. Part of a plant with flower (MAT 287); 6. Detail of an old leave with the central midrib (MAT 486); Matvéevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos Museum just below the calyx to release numerous small-sized seeds (MAT 338). The size of the squashed fruit is 2.0 long, 0.5 cm wide. The fruit is a capsule containing numerous small-sized seeds.

Discussion

From all known herbaceous plants of Early Permian Angara, *Lyswaia nicoalswachtleri* represents the most interpretable flora element due to some lucky findings. With some certainty, we have not only the campanula-like blossom with its composite flower, but also their mature fruit holding dwarfish seeds. Bringing together the complete juvenile plant (MAT 458) with a compound of roots and the adult plant (MAT 338), we can establish that the natural size of these angiosperms did not exceed 10 cm.

In the Matvéevo sediments, herbaceous plants characterized by leaves with a distinctive midrib are encountered in fair amounts. Their blooms and capsule-like fruits cannot be classified in some of the known gymnosperm groups, but this is not new for the Angaran flora.

MAT 458 shows a leaf with a suggested juvenile, but not fully blossoming flower. Visible is the calyx comprising several sepals. The information about this interesting plant will be enlarged by MAT 338, the designed holotype. The leaf character is the same as MAT 458; five sepals can be recognized on the calyx; the fruit is crashed during the fossilisation, the fertile content is visible as a gelatinous mass with seeds not bigger than a few tenth parts of a millimetre.

Searching for a modern representative of *Lyswaia*, we arrive to the extant Campanulaceae (bellflower family), a family in the order Asterales, being almost cosmopolitan, but concentrated in the Northern Hemisphere. The fruits are capsules, the flowers bisexual and bell shaped, consisting of a narrow, tube-like corolla. The leaves are often distinct by a midrib, like *Campanula cespitosa*.

The more difficult questions are why in Early Permian we have just fully developed Campanulaceae and in which evolutionary way can they be connected with the other herbaceous plants. Although a fusion of several petals to one calyx do not represent a big evolution step and can be accepted as obvious evolution way.

Meristophyllum sojanaeanum ZALESSKY, 1937

Basionym. *Meristophyllum sojanaeanum* Zalessky 1937b: p. 100, Fig. 76

Synonym: Meristophyllum indivisum Zalessky 1937b: p. 100, Fig. 77

Noeggerathiopis salamatensis Zalessky, 1937b, p. 67, Fig. 29

Description

Foliage: Leaves 10–15 cm long, cuneiform, at the base 1.2 cm, apical 2.5 cm (MAT 427), diverging sometimes (MAT 439). Veins parallel, diverging one-two times on the basal-middle part (MAT 326). Veins thick-walled adaxially, dense and thin abaxially.

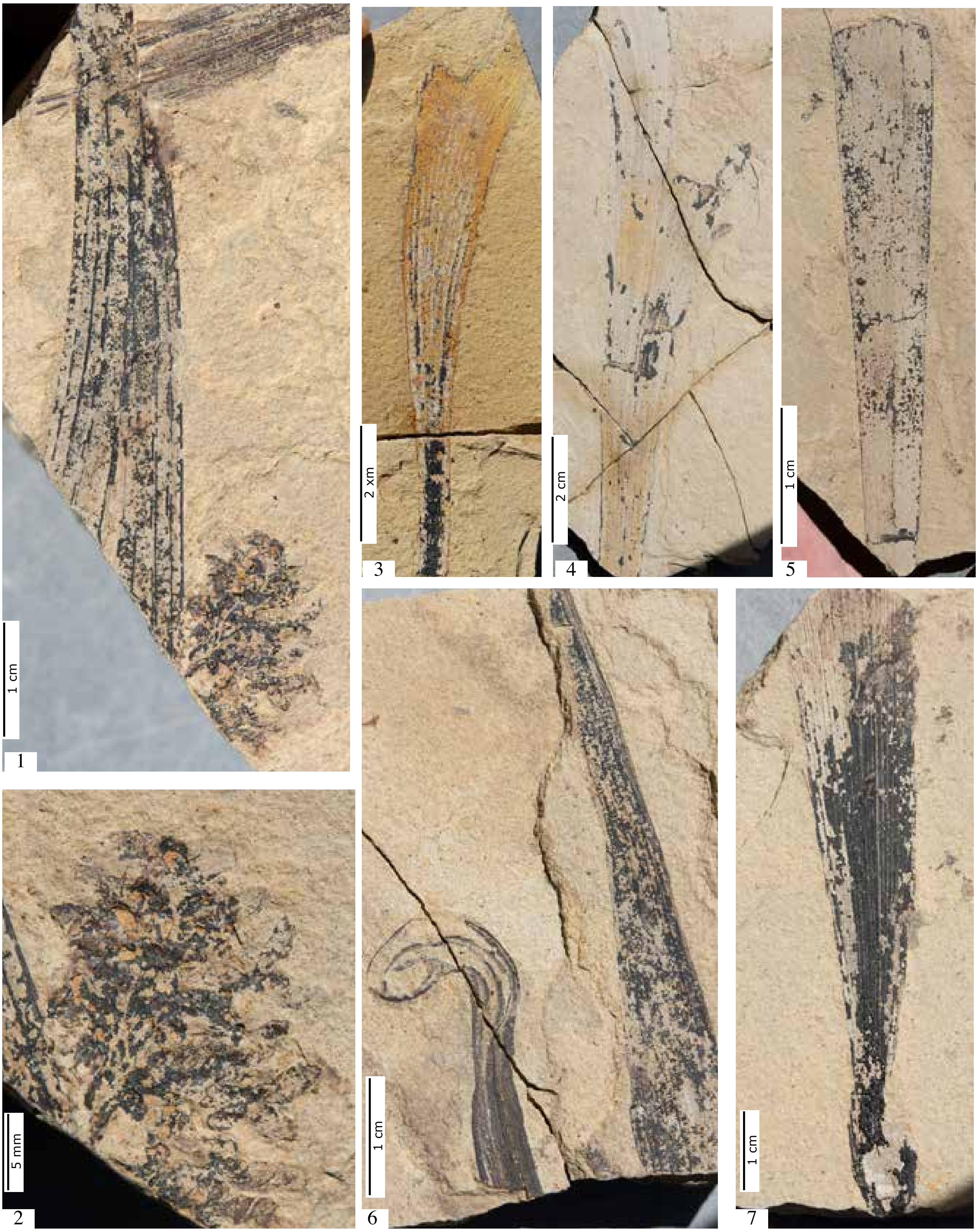
Fertile organs: Specimen MAT 326 evidences a compound flower. Whether it is connected with the leaf or not cannot be established.

Discussion

Zalessky introduced in science *Meristophyllum sojanaeanum* and *Meristophyllum indivisum* (Zalessky 1937b). The first one is characterized by a divided leaf with strong veins, the second by an undivided, dense and thin venation. Both show an obtuse apex. Leaves with this feature are relatively abundant in the Kungurian deposits, but an insertion in one of the known families is not easy. Sometimes, similarities with the Cordaitales were suggested and classified as *Noeggerathiopis salamatensis* (Zalessky, 1937b, Fig. 29), or *Cordaites* (Meyen, 1966). Also, this classification revealed as not satisfying. Therefore, lanceolote parallel-veined leaves were again inserted as new genera with the name *Rufloria derzavinii* (Meyen 1963, 1967, Plate V, fig. 4). 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 where widened apices were attached (Neuburg, 1955). Female head-like aggregations of sterile scales and seed stalks were assigned to the genus *Astrogaussia imbricata* (Naugolnykh, 2014). The female organs consist of slightly asymmetrical rounded and head-

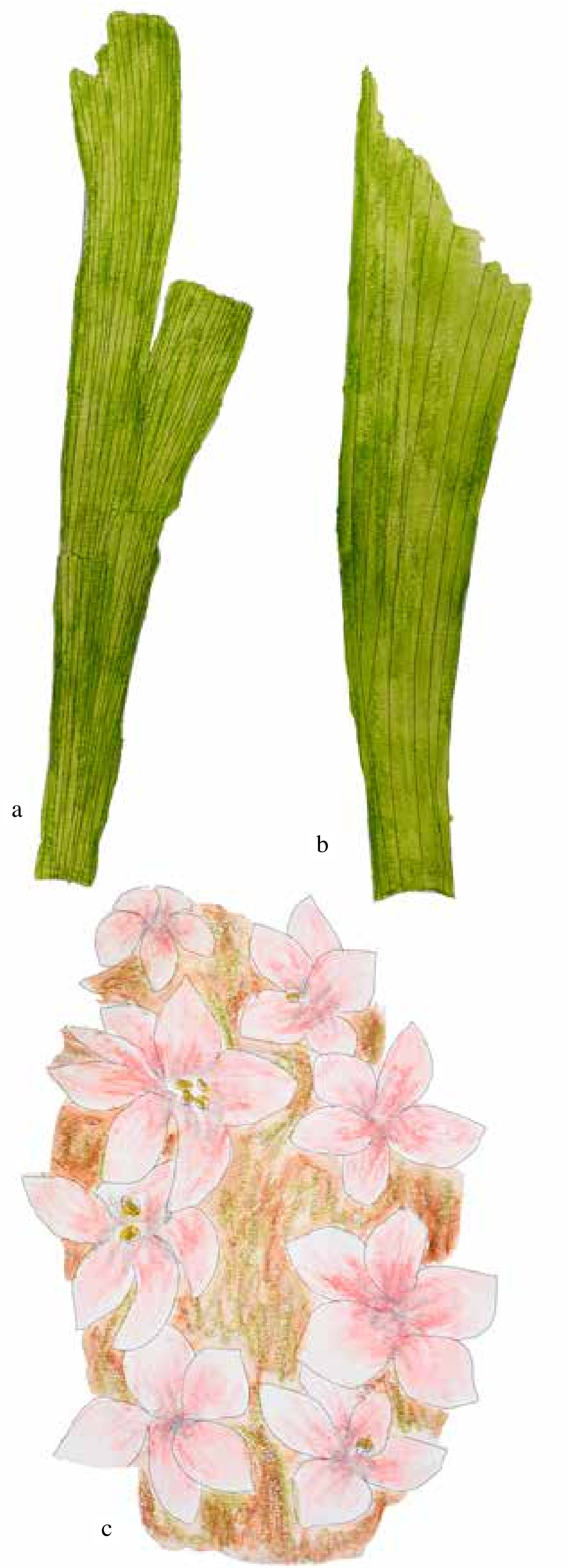
Lyswaia nicolaswachtleri gen. nov. sp. n. Reconstruction

a. Young flower with part of the stipe (MAT 392); b. Suggested reconstruction with blossoms and leaves (MAT 392 and MAT 458); c. Aggregation of leaves (MAT 338, holotype); d. Fruit in form of a capsule releasing seeds (MAT 338, holotype); e. Suggested reconstruction of a mature plant with fruits (MAT 338, holotype)



***Meristophyllum sojanaeanum*. Leaves and fructifications**

1-2 . Leaf with flower and detail (MAT 326); 3. Isolated leaf exhibiting diverging veins (MAT 490, coll. Dammann); 4. Branching leaves with leaf-stomium (MAT 439); 5. Detail of a leaf with a stomium in the upper and lower part (MAT 427); 6. Apical part of a leaf (MAT 426); 7. Basal part of a leaf (MAT 423); Matvéevo, Kungurian (Early Permian); Coll. Wachtler Dolomythos Museum



***Meristophyllum sojanaeanum*. Recosntructions**

a. Branching leaves with leaf-stomium (MAT 439); b. Detail of a leaf (MAT 326); c. Supposed flower (MAT 326)

like aggregations of seed stalks and sterile scales, spirally extending from the common base (Naugolnykh, 2014). If the head-like aggregations of *Astrogaussia imbricata* can be connected with *Meristophyllum sojanaeanum* or the dwarfish flowers from MAT 326 is not so important: the fact is that this plant has no relatives in the Euro-American gymnosperm world. From more interest arises the question in which plant family *Meristophyllum* or also *Rufloria* can be inserted. All the habitus indicate in the direction of the Monocotyledons, angiosperms characterized by long, narrow parallel-veined leaves.

Remarks

There are some plants in Matvéevo that with a certain assumption can be regarded as low-growing or herbaceous; because partly, they were recovered with attached flowers fruits and roots, a classification would be relieved in some aspects. Three of them belonging to different families are till now unknown for Paleozoic-Mesozoic sediments: *Naugolnykhia matvéevoi* nov. gen. n. sp. can be brought in the vicinity of daisy flowers, *Lyswaia nicolaswachtleri* nov. gen. n. sp. has some aspects of today's Campanulaceae, whereas *Peremopteris biarmicum* nov. comb., formerly described as *Sphenophyllum biarmicum* due to its reticulated leaf veins and the form of its androecium and gynoecium, can probably be inserted in some group of the Rosaceae or the Malvaceae. All these can be interpreted as belonging to the dicotyledons.

Systematic Paleontology

Division Paleoangiosperms
Family: Poaceae

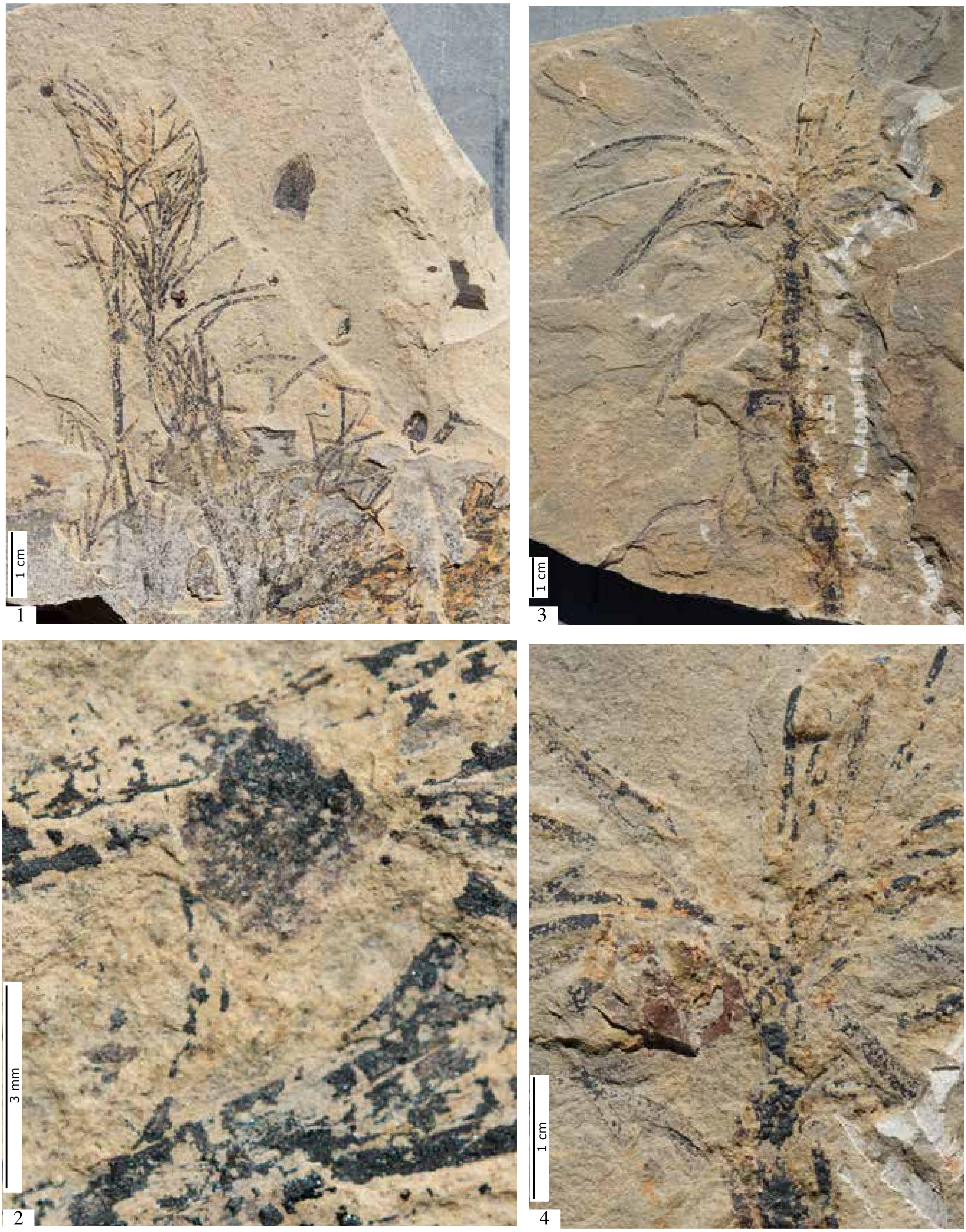
Genus *Krasnaia* nov. gen. WACHTLER 2017

Etymology

Named after Krasnaia Glinka near Matvéevo, were rich fossil layers crop out.

Diagnosis

Herbaceous plants with a slender culm-like stem ending in a tuft of fragile leaves. Fertile organs apically sitting on the stem-leave.



Krasnaia dammannii **gen. nov. sp. n. Plant, leaves and fructifications**

1. Whole plant with roots, leaves and attached fructification (MAT 288 designed holotype); 2. Detail of the fertil organ attached to the leaflets (MAT 288); 3-4. Another mainly complete plant (MAT 285); Matvéevo, Kungurian (Early Permian) Coll. Wachtler Dolomythos Museum

***Krasnaia dammannii* gen. nov. sp. n. and *Taezhnoeia geraschi* gen. nov. sp. n. Reconstructions**

Taezhnoeia geraschi: a. Complete plant; b. Detail of the grass-like leaves (MAT 434, designed holotype); c. *Krasnaia dammannii:* Complete plants with fructification (MAT 288 designed holotype); d. Detail of the fertile part; e. Enlarged detail of the filament and anthers; f. Another similar plant (MAT 285)

Krasnaia dammannii nov. gen. *n. sp.* WACHTLER 2017

Type horizon and age

Perm Krai (Russia) Ural, Early Permian, Kungurian (272.3–283.5 Mya)

Holotype

MAT 288 Coll. Wachtler, Dolomythos Museum, Innichen

Etymology

Honoring the German researcher Martin Dammann who helped study the Permian Angaran flora.

Diagnosis

Grass-like plants with narrow alternating leaves borne in two ranks. Basal part of each leaf enclosing the stem. Small-sized fructifications attached on the apical part of a leave.

Description

Plant: Herbaceous, from 9 cm (MAT 288 holotype) till 14 cm (MAT 285) high, with a slender stem (0.1 cm–0.5 cm width). Alternate diverging leaves ending usually in a tuft compound (MAT 285).
Foliage: Leaves enclosing the stem, till 6 cm long, but only 0.1 cm wide, also in adult plants (MAT 285), with a nearly invisible midrib.
Flowers: Blossoms solitary, on the end of a stipe/leave, 0.2 cm x 0.2 cm. Suggested gynoecium three times segmented, only two stamens recognizable. This on a long slender filament with the anther in apical position (MAT 288 holotype). Other details were difficult to recognize.

Discussion

Krasnaia dammannii nov. gen. n. sp. fits well in a group of herbaceous plants being relatively abundant in the Matvéevo-Fossillagerstätte. In this case the interesting features are their grass-like structure and growth. The Poaceae (Graminaceae) form today probably the most important group of flowering plants based on their cereal and forage crops (Taylor et. al., 2009). Alternating the long, slender leaves in two rows on opposite sides of the stem and the small bisexual flowers organized into inflorescences is one of their characteristics.
The gynoecium present in most of the Poaceae today consist of three fused carpels, a feature recognizable also in *Krasnaia*. The androecium is generally bundled in three stamens, in *Krasnaia*, two are visible, with the doubts about the third one. They are divided into an elongated filament and an apical anther (MAT 288). Amongst the many features of *Krasnaia dammannii* indicates in the direction of today's Poaceae-grasses. Some perplexity exists with a mainly complete plant, MAT 285. Their apical tufts can also indicate in another way, maybe some primitive palm-ancestor.

Hakonechloa macra. A grass from the family of the Poaceae. Taezhnoiea geraschi and Krasnaia perneri evidence some features of today's grasses.

Genus *Taezhnoeia* nov. gen. WACHTLER 2017

Etymology

Named after Taezhnoe, a section in the northern vicinity of Matvéevo.

Diagnosis

Grasslike plant with short rootstocks, growing in tufts. Leaves long and flat evidence of parallel veins.

Taezhnoeia geraschi nov. gen. n. sp. WACHTLER 2017

Type horizon and age

Perm Krai (Russia) Ural, Early Permian, Kungurian (272.3–283.5 Mya)

Holotype

MAT 434 (Gerasch Collection, Senckenberg Forschungsgesellschaft, Frankfurt)

Etymology

Honoring the German researcher Thomas Gerasch, who found and preserved the first specimen.

Diagnosis

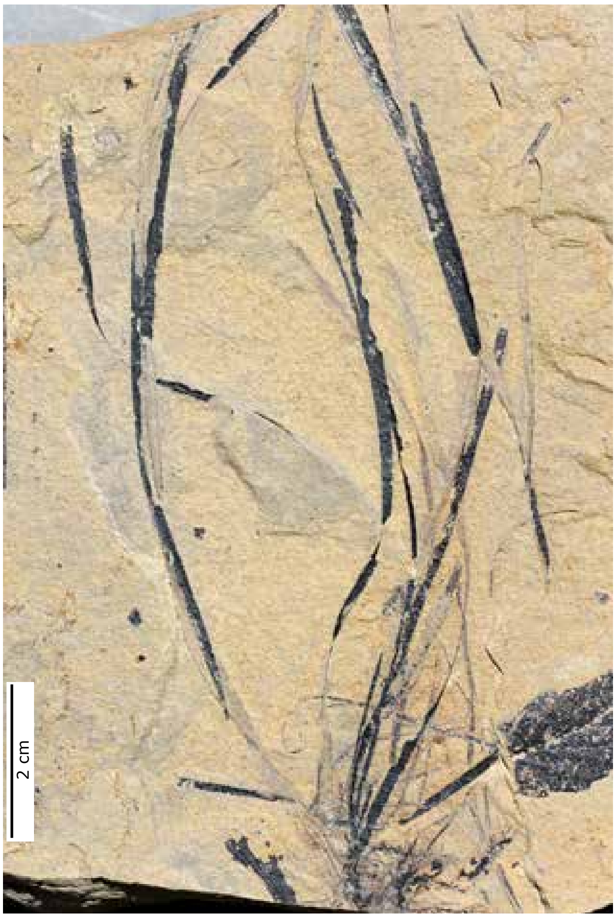
Low-growing, rhizomatous, herbaceous plant. Leaves in a basal aggregation, in the upper parts of the stem a few leaves arising in an alternate manner.

Description

Plant: Grasslike (MAT 434, holotype is 13 cm high) tufted, shortly rhizomatous herb.
Foliage: Till 0.5 width, about 10–15 cm high (MAT 434 is not a complete specimen). Several leaves sprout from a rhizom and are arranged in three vertical rows (tristichous).

Discussion

It is thought that low growing grasses arrive only in Eocene-floras. But in Early Permian Angara-Land we have several plants that surprisingly fulfil just this characteristic. Additionally, to *Taezhnoeia geraschi* gen. nov. sp. n. also *Krasnaia dammannii* gen. n. sp. n. can be regarded as herbaceous grass-like plants. Other herbaceous flora elements till now only represent problematic (MAT 145, MAT 70), although fulfill some aspects of grasses. Whereas *Lyswaia nicolaswachtleri* or *Naugolnykhia matvéevoi* with their blossoms have more affinities with the Dicotyledons, *Taezhnoeia geraschi,* and *Krasnaia dammannii* can be regarded as plants having aspects of the Monocotyledons like all the true grasses today (Poaceae). That *Taezhnoeia geraschi* is effectively herbaceous, is evidenced by holotype MAT 434, also showing part of the root-system. The entire slab, accompanied by a reticulate leave, not pertaining to *Taezhnoeia* but to some deciduous tree, indicate more in some Cretaceous Paleoflora than of Early Permian age. The classification of *Meristophyllum sojanaeanum* is enigmatic—sometimes it was described as *Rufloria derzavinii*. Comparisons with the known fossil record are difficult due to the too many aspects they differ in from the plants till now recorded from the Permian and Triassic. But further researches with more material can certainly enlarge knowledge about its classification in some of the today's ancestor-lines.



Taezhnoeia geraschi gen. nov. sp. n.

1. Whole herbaceous plant the segmented leave pertain to another flora element (MAT 434 designed holotype), Coll. Gerasch. Matvéevo, Kungurian (Early Permian)

Unknown grasslike plants: 1. MAT 145; 2. MAT 70

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