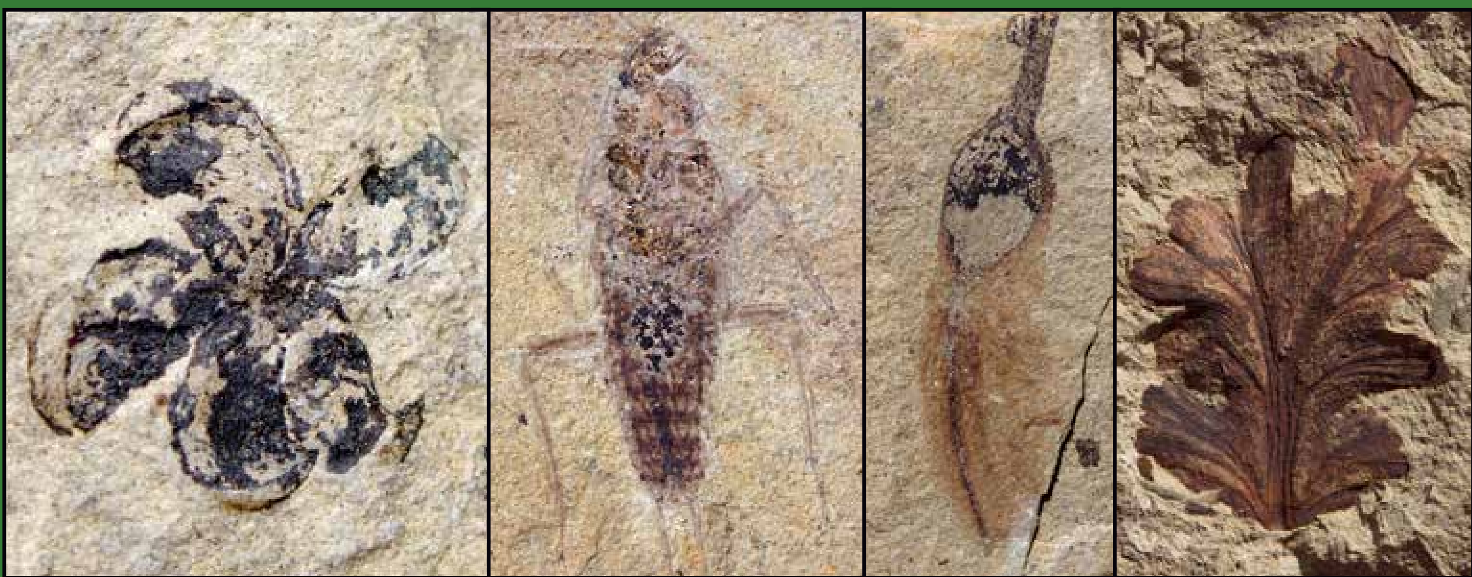
Michael Wachtler

The Origin of Flowering Plants
The First Angiosperms



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In the Northern Hemisphere, from the Devonian till the Triassic period, in addition to the Euramerican landmass, another isolated continent, called Angara (today's Siberia) existed. This area was distinguished by a fasten radiation of plants that have many similarities with extant angiosperms. We encounter also many different insect families. Why could the flowering plants and the insects not spread across the entire world? On the Permian-Triassic border, the biggest catastrophe in Earth's history occurred. It originated in Siberia due to an immense vulcanism. Additionally we need to investigate another phenomenon. When was it possible that especially birds were able to transport seeds over long distances? Probably not before the Jurassic-Cretaceous. Remarkably, in this time, the sudden worldwide appearance of flowering plants falls.

Published by Dolomythos Museum, 39038 Innichen, South Tyrol, Italy

Printed in Italy by Dialog GmbH Brixen (BZ), June, 2022

mail: info@dolomythos.com, www.dolomythos.com

Printed copy: Euro 49,00

Origin and evolution of angiosperms

Today we have about 230,000 angiosperm species, forming about 89% of all plants, only 0.29% gymnosperms; there are about 4% ferns, 3.61% mosses, 2.28% liverworts, but only 0.38% lycopods and 0.05% horsetails. But when we take as indicator the biomass, then the huge conifer trees change the statistics. From the Middle Devonian – the era of evolution of the first trees and shrubs – about 395 million years ago and the Carboniferous-Permian boundary, in a time interval of only 100 million years, all main tribes existing today such as lycopods, horsetails, ferns or gymnosperms, including conifers, gingkos and cycads, as well as all the insect groups had been present and fully evolved.

All the following 300 million years succeeded only in segmentation and break- down to further genera and species. Therefore, the question is allowed: Where were in all this time the angiosperms? The evolution of flowering plants represents till now one of the central questions of natural science. 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.

Our present knowledge about angiosperms is based on the dogma that first appeared 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 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.

A landscape in the Early Permian Ural-region, the former Angara-continent

An "abominable mystery"

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. 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, "*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 mil-lions of years. Therefore, he speculated a slow 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 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.

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. Darwin's thoughts and anxieties can be understood fairly – also, his vision about a lost continent.

A lost continent

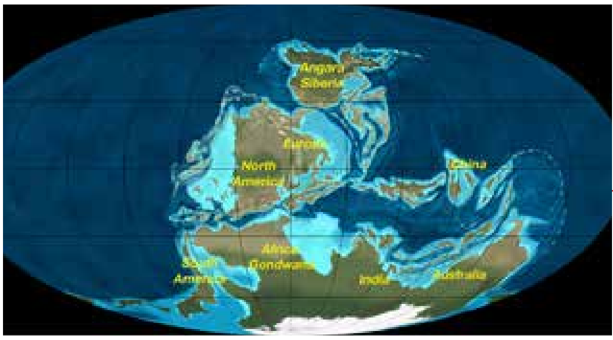
If we are able to find flora-elements maybe on a "dark continent" prior to the Cretaceous with many of these properties, we come nearer to the answer of the "abominable mystery."

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.

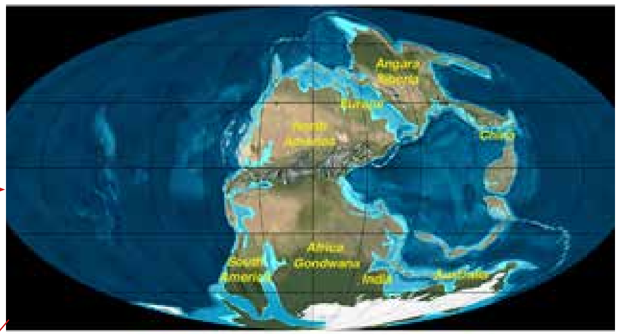
Some of the theories about isolated landmasses were evolved by the Austrian geologist Eduard Suess. In his "Antlitz der Erde" (The Face of the Earth) in 1885, he hypothesized that in the Paleozoic era, there was one big landmass on the southern hemisphere that he called the Gondwana – from an Indian 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 Atlantis, and the

The drifting of the continent of Angara

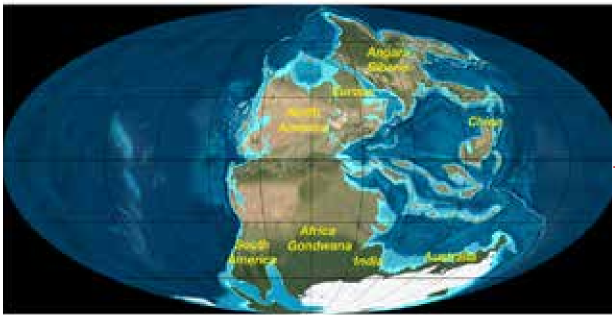
By the drifting of the terrestrian platforms during the last 340 million years, from the Carboniferous till the Early Triassic period, the Siberian-Uralian landmass formed a separate continent with their own fauna and flora. Especially the abundance of many insect families and paleo-angiosperm plants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



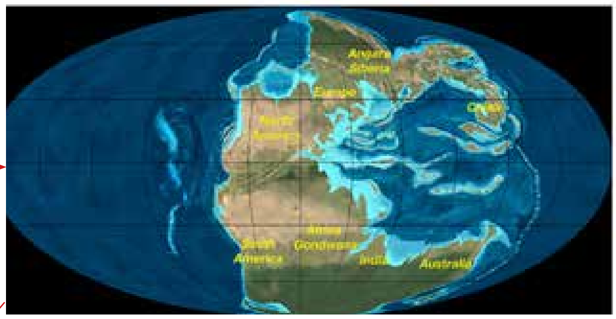
The continents in the Carboniferous, 340 Mio. years ago



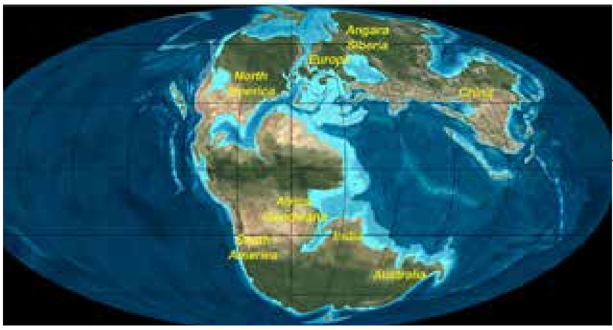
The continents in the Early Permian, 280 Mio. years ago



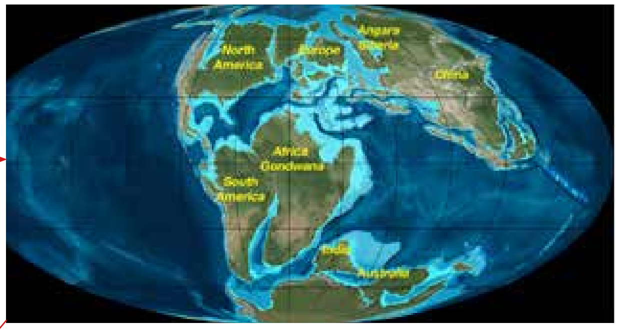
The continents in the Late Permian, 260 Mio. years ago



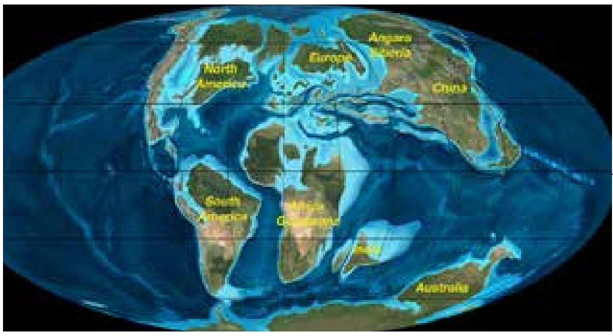
The continents in the Early Triassic, 240 Mio. years ago



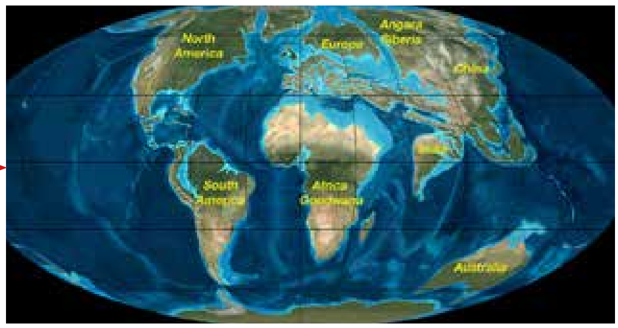
The continents in the Jurassic, 170 Mio. years ago



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

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.
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. Isolated from the other landmasses, this community remained unique for millions of years.

Characteristics of first angiosperms in the Early Permian

If somebody walked 280 million years ago on the bank of the Matvéevo Sea in today's Ural-region, 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. 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.

The "invention" of the flower and the fruit

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. Most angiosperms are bisexual (hermaphroditic) with both carpels and stamens in the same flower; but 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.
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 fossilized 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.
Another feature characterizing the flowering plants is their fruits. They can be very dif-

ferent 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. But why are there so many different angiosperms from the beginning?

Early Permian origin of the flowering plants

Strangely the origin of angiosperms based on the fossil record can be dated back in the Angara-landmass to the Carboniferous-Permian era. In the early Permian sediments from Chekarda and Matvéevo in the Ural-region, many different "flowers" could be found. 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.

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. Both were present in the Early Permian Angara.

Several "flowers" from Early Permian sediments in the Urals evidences well a diverse stamen with anthers and a gynoecium, also with the impressions of some ovules. It is surprising, and speaks for the extraordinary preservation especially at Matvéevo and Chekarda, that the slender filament as well the anther with the pollen sacs are visible.

The base is a fully developed hermaphroditic flower with ovaries and stamens. Once "invented" the bisexual flower, composed of stamen and ovary with surrounding petals, sepals or tepals, all further lineages can be easily 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. This coevolution in the Early Permian period simplifies the under- standing of angiosperm development considerably, especially when it can be based on solid arguments and facts due to compound findings.

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.

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 wide- spread families: The Meganisoptera, like *Arctotypus sylvaensis,* survivors from the huge Meganeura griffinflies, the Megasecoptera (*Sylvohymen, Asthenohymen* or *Bardohymen*), as well as modern looking mayflies (Ephemerida with *Misthodotes sharovi*), the Orthoptera (*Tcholmanvissia longipes*), the Blattodea (*Sylvaprisca focaleata* and *Artinska infigurabilis*), the Plecoptera (stoneflies) like *Tillyardembia*, ancient book-lices (*Parapsocidium uralicum*) the Neuroptera *Paleuthygramma tenuicornis*, the beetles like *Sylvacoleus sharovi*, or the Cicada *Rachimentomon reticulatum* were recorded. We also encounter many well-preserved scorpionflies (Mecoptera) like *Agetopanorpa punctata* or the crown-group of the Acercaria with *Palaeomantis aestiva* or *Delopterum rasnitsyni*, caddisflies like *Marimerobius* and perfectly preserved Arachnida like *Permarachne.* About the presence of the Lepidoptera (butterflies) and the Hymenoptera, the sawflies, wasps, bees, ants, as well as the true flies (Diptera) cast a shadow of doubt, but it can be stated that some fossilised insects indicate in this direction.

Many of them can be regarded as potential pollinators. Adherent pollen dust was found on many insects also. Only in this way can we explain there the simultaneous appearance of all main insects-groups and ancestors of angiosperms that exist even today.
Although several theories propagate wind pollination (anemophily) of angiosperms as derived from insect pollination (entomophily) in response to pollinator limitation, 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.
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.
All these big angiosperm-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 Permo-Triassic fossilised plants. It is doubtful that an equal can be found in other fossil sites of the Permian Northern Hemisphere. Localities in France, Germany or the Alps were examined in the last centuries more than the Siberian Angara, but apart from some Peltaspermales (where this characteristic 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 *Autunia-Rachiphyllum-Scytophyllum* leaves had some preangiospermous features. But they never reached the level of the angiosperms. All over the European Permian and Triassic, the Peltaspermales play only a marginal existence between the dominant horsetails, lycopods, 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.

Another point of view

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.
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 "enations" or "emergences") aggregated together to form a flying reproductive organ. Early Permian

The evolution of the samara (winged seed) in the plant kingdom must be occurred twice. In the angiosperms and the gymnosperms

Permian, Matveevo, Ural (280 millions years ago) Acer-Ancestor, Samara *Sylvella alata*

Eocene Republic, Washington, USA (50 millions years ago) Aceraceae Samara *Acer manchesteri*

Permian, Seceda, Dolomites (260 millions years ago) Abiesa ancestor. Winged seed *Majonica alpina*

Eocene Republic, Washington, USA (50 millions years ago) Abiesa ancestor. Winged seed *Abies milleri*

conifers such as *Majonica* and *Wachtlerina* evidenced 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 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 Per-

Micro-leavescoating the seed

Permian *Craspedosperma bardaeanum* (Quercus ancestor) from the Fore-Urals

Permian *Ortiseia leonardii* (Araucaria ancestor)

The coating of the seeds with microleaves as basis to form an aril occurred indipendentely also at least two times - in the angiosperms as well the gymnosperms - in the Early fossil record.

mian period as in *Bardocarpus aliger* find their counterpart in Northern Hemisphere Ginkophyta such as Permian *Ginkgoites* or *Baiera,* and also in *Ullmannia* conifers as suggested ancestors of the Taxaceae. In every case microleaves cling their seeds, forming a compact aril.

And surprisingly, they would ascertain that the ocean separating the two continents, maybe high mountain-ranges and also their latitude-difference avoided for a long time a common flora-and-fauna exchange. Till the evolution of the birds.

The 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 *Fèrovalentinia*.

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. Interestingly primitive Asteraceae from Angara-continent like *Wachtlerosperma stefanperneri* evidence also these feature.

All these gymnosperms and angiosperms – having mainly the same leaf-features – were 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. Their reproduction organs were a segmented flower, composed of leaves varying from four, five, six and more parts today called petals. Therefore the further evolving stage in Angara was completely different from the Euroamerican gymnosperms.

Most, but not all Permian Paleoangiosperms from Ural are characterized by net-like furcating veins. This feature we record in the Euro-American floras only in the Ginkgophyta (*Ginkgoites*) but with an other evolving concept and the Triassic Caytonales (*Sagenopteris*).

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 many, but not all conifers. Dioecious, plants also being either male or female are also known from the angiosperms (*Salix caprea* commonly called pussy willow) but also the gymnosperms (Gingkos, Cycads, Araucaria-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 common in the *Selaginella* clubmosses and especially pronounced in the Carboniferous *Sigillaria* lycopods or in Triassic *Sigillcampeia.* 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 Araucaria-conifers built the most basal conifer lineage. But in Early Permian, we have fully evolved Cycas ancestors (*Macrotaeniopteris, 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 scales (*Voltzia*) conducting to many known present day Cupressus-conifers. Besides, we have Pinus ancestors (*Fèrovalentinia*) and Ginkgo forefathers (*Ginkgoites, Baiera*).
The same happened in Angara with their multitude of deciduous trees, low-growing flowers and grasses.

A long isolation

It is more difficult to elaborate a hypothesis about the movement of all gymnosperms and angiosperms in the following million years. 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?
The more than 242-million-year-old fossil, *Megachirella wachtleri,* is the most ancient ancestor of all modern lizards and snakes, iguanas, chameleons, geckos, known as squamates. *Megachirella* is about 75 million years older than what was thought were the oldest fossil squamata in the world. Some

questions can therefore be explained by the poor fossil record.
The others need further hypothesis. Beginning from the Early Triassic all continents were than united into the one supercontinent Pangea, assembled from all earlier continental units.

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 his- tory – the forming of Siberian Traps – spanning one million years between the Permian– Triassic boundary, about 252 to 251 million years ago. Today, basaltic lava covers about two million square kilometres there, but the original extension is estimated at about seven 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 to expand on a large scale. In this case, the most involved victims of these mother of all catastrophes were the angiosperms.
Another interesting observation might be: When was it possible that especially birds were able to transport seeds over long distances? Probably not before the Jurassic-Cretaceous. Remarkably, in this time, the sudden worldwide appearance of flowering plants falls.

Fundamental theories about Early Permian angiosperm evolution

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, dioecious as well monoecious angiospermous fructifications were present. 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 re-constructed. 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 land- mass with several subordinated tribes such as conifers, cycads or ginkgos.

Nicolas and Michael Wachtler in Mazuevka

Historical overview about the researches in the Permian landscape

When the English scientist Roderick Impey Murchison travelled through Russia and the Ural-region near Perm in 1841, he never expected to discover one of the most important gaps in the Earth's history. Between the Carboniferous, characterized by its huge lycopod and horsetail trees, and the Triassic, there existed another overlooked, fifty million-year-long period, the "Permian system", as Murchinson indicated in a letter. During this time, a revolution that we can observe everywhere today took place. Insects and a special family of plants – the angiosperms or flowering plants – began their fruitful symbiosis to conquer the world. In a short period during the Paleozoic era, they generated all the features to adapt well and fit better than other plants and animals. And in no place can we experience this evolution better than in the Early Permian Fore-Urals. In two slightly time-different stages, the Artinskian and Kungurian, and two localities, Chekarda and Matvèevo we can follow the creation of a magical world as it occurs today.

In 1841, Roderick Impey Murchison (1792–1871) travelled with the French palaeontologist, Edouard de Verneuil, Estonian-Russian mining expert Alexander von Keyserling, and the Russian officer and mineralogist, Nikolai Koksharov, from Moscow to Perm. Near the small town of Vyazniki and in several other places during their exploration of the western flanks of the Ural Mountains and near the city of Perm, Murchison noticed that based on rocks and fossils, the layers must be regarded as intermediate between Carboniferous and Triassic.

In the first letter presented to the Geological Society of London in April 1842, Murchison and Verneuil gave further details about marine fossils from Kazan, Vyatka and Perm. In 1845, Murchison wrote an interesting analysis, "*On the whole, however, we confess we are disposed to view these variegated sands and marls like those of Orenbourg as a part of the Permian system.*"
From that moment on, other geologists too began to write about the "Permian System", so that one of the last remaining gaps in the geological time scale could be

Kungur in a photo from 1900 (Kungur Museum). The Kungurian geological stage remembers this city.

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

filled. After that also other scientists realised that this "Permian system" or Permian was widespread across the world. Just before Murchinson gained scientific fame for describing the Silurian system in England and Wales, he also participated in understanding the Devonian time.
Due to long-lasting political circumstances and the remoteness of the locations, we have unsatisfactory information about the different stages and fossil record from these areas. Although, the Permo-Triassic beds cover about 1.4 million square kilometres of European Russia, reaching the Ural mountain range and providing an important record of changes in terrestrial environments to marine ecosystems before, during and after the end-Permian mass extinction.

The paleobotanical researches in the Western Ural

The first knowledge about the richness of Uralian fossils we have from Stephan Kutorga, Professor of Natural Sciences at the University of Petersburg, from his 1838 published "*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 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 the palaeobotanist 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. 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, Ekaterinenburg and Perm.
Beginning from 1927, Zalessky described these floras, keeping attention 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-

The small town Arti in the Sverdlovsk Oblast, Russia, about 200 kilometres southwest of Ekaterinenburg.
In 1874, the Russian geologist, Alexander Karpinsky, named the Artinskian age of the Permian Period due to many outcrops in this area.

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.

The World Fossil Lagerstätten Chekarda and Matvèevo

One of the most important outcrops is situated along the Sylva River in vicinity of the confluence with the small Chekarda brooklet behind the hamlet of Chekarda (Suksun district in the Perm krai). The layers are composed of fine clastic sediments named Koshelevka Formation (Irenian horizon) being part of the Early Permian Kungurian. The sediments were deposited by shallow and not marine rivers or are remnants of small lakes. Only isolated impressions of fishes and Diplopoda and Symphyla have been recorded. Other animals have not been found, but the richness of well-preserved insects and plants is unique. The flora is extremely diverse and includes many species and genera of plants. More difficult is determining the connection and relationship of the diverse parts of the plants, from the flowers, seeds, fruits, leaves and branches. A reduction in many species and genera described till date would be reasonable in the future. Also, the cooperation and complementarity between insects and plants is only partly explored.
In the background stood all the time the other Early Permian high yield location, Matvèevo (Lysvinsky district near Lysva), on the Barda River. Matvèevo is regarded as slightly older than Chekarda, pertaining mostly to the Filippovian (Kungurian) horizon. Different outcrops classified as Krutaya Katushka 1, Krutaya Katushka 2, Krasnaya Glinka, Matvèevo, Taezhnoe and Barda were found. The richest place is a quarry used by the local people as filling material before passing the bridge over the Barda River. Different small lenses hold interesting and well-preserved plants and insects.
The richness in insects is not as much as in Chekarda (Suksun District), but superb im-

A stone-fruit from the collection of Mauer, 1938 (Museum Ekaterinenburg)

pressions that are variegated and preserved in the finest mud-siltstone are found. For both places, Matvèevo and Chekarda, it cannot be established with certainty if one is dominated by flowers or seeds and fruits, also, an autumn-based sedimentation or, due to a special richness in flowers, spring-based floods are suggested. It seems that these vary from layer to layer. Other locations around Kungur, Krasmoufinsk and Arti are sometimes rich in plant remains, but due to their rougher sandstones, insects were not or seldom preserved. This is valid for Artinskian-aged Yugush (with nice seeds), Pantelekovo, Manchazh, near Arti, and Kungurian-aged Mazuevka (with well-preserved plants), Aleksandrovskoe (Sverdlovsk region, Krasnoufimsk district) and Rakhmangulovo (Krasnoufimsk district.
Other full marine Early Permian localities released some isolated plant fragments in association with a higher quantity of whole carapaces of trilobites, conularians, re-

A box of fossils with specimen from the Mauer-collection (Museum Perm) mains of fish, brachiopods, large shells of well-preserved nautiloids and ammonoids of good preservation, jaws of sharks (Krasnoufimskie Klyuchiki, Sverdlovsk Oblast), Divja Mountain, Sobolya, Manchazh (Artinskian). They were just part of the Cis-Uralian Artin-

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).

The outstanding Russian palaeobotanist Mikhail Dmitrievich Zalessky (1877-1946) described the first plants from Chekarda and Matveevo.

Mazuevka Site Near the Sylva River, Northeast of Suksun: The long outcrop yields not only huge and perfectly preserved *Psygmophyllum* foliage but also *Rufloria* leaves and ferns.

skian sea basin, which was connected to the Boreal Ocean in the north and the Tethys Sea in the south.

The Global Importance of the Early Permian Angiosperms from the Fore Urals

One of the greatest problems in palaeobotany that can be resolved here is the angiospermy. Cycads, which are dominant in the European Permo-Triassic floras, were never found in the layers of the former Angara-Land and also no gingkos. From the gymnosperms, only some conifers are found, but nothing in comparison with their dominance in Euramerican floras. However, in the Fore Urals, we encounter many hermaphroditic flowers with stamen and carpel, Asteraceae-like umbels consisting of many inflorescences and frequent florets, a multitude of samaras, that looks like those of maples, and acorns from oaks. Additionally, aggregated fruits,

The hamlet Matvéevo in spring

Photos Martin Dammann

The small village of Chekarda

umbrella-like parachutes resembling pappus, racemes, berry fruits and flowers looking like Magnolias can be found.
The problem of classifying the extraordinary multitude of plants from the Early Permian Angara-continent can only be resolved by the intense studying of their fructifications. Seeds and fruits have a greater possibility of preservation due to their hardened character and are very specific in many plant groups. The foliage has only limited meaningfulness due to their variety even within the same plant or tree and similarity concerning many families.
Only in Chekarda and Matvèevo, we recorded at least six aggregated fruits, including Magnolia-like, and, surprisingly, their flowers. There were four different kind of spikes, typically to grasses, and fruits resembling the Campanulaceae and Phytolaccaceae. Pappus, florets and capitula from probably five different Asteraceae were present. Extensive presence of samaras from five different broad-leaved trees like maples, elms or ashes can be found. Moreover, we encountered four acorns or nuts, typically from oaks or hazelnuts, and two different drupes from stone fruits.
Although the flowers today, just like in the past, are small-sized, more than ten different development stages were discovered. Mostly, they have clearly defined carpels and stamen incorporated in the same plant.
Without counting the cones of the conifers, the various strobili of the horsetails and the ferns, we encountered almost 25–30 different fruits that cannot be inserted in the European Permian’s usually known gymnosperm-concepts. Also, it will be impossible to find solutions in former theories, if we do not accept that the angiosperms evolved just on the Carboniferous-Permian border.
Older authors (Zalessky, 1937b, 1939; Naugolnykh, 2014) have tried to put all the remains of plants from the Fore Urals in one of the known Euramerican classification systems, such as Peltaspermales, Callipteridales, Coniferales or Ginkgophyta, but such methods and procedures were not successful. The Angaran vegetation was quite different from all other known floras worldwide to be obliged to elaborate a totally new, evolving concept.

The difficulties crossing the Chekarda brooklet to arrive to the main quarries

The Chekarda - fossil site

Photos Martin Dammann

Chekarda 2016-2019

1. The river Sylva (immediately downwards after the confluence with the Chekarda brooklet); in these siltitic lenses, best-preserved insects and plants can be recovered.

2. A sudden rise in the level water after melting of snow can block the return.

3. A short break where the expedition team of Sharov and Novokshonov set their basecamp (Michael Wachtler, Thomas Perner, Nicolas Wachtler, Thomas Gerasch. Photo courtesy by Martin Dammann).

4–5. The small quarry upstream of the confluence is rich on bigger plant remains and well-preserved insects.

The Matvèevo - fossil site

Matvèevo - Taezhnoe, the most rich sediments

Krutaya Katushka on the Barda-River upstream of Matvèevo

Matvèevo - Krasnaya Glinka

An original specimen (*Psygmophyllum cuneifolium)* from Matvèevo (Krutaya Katushka Barda-River) collected in 1933 by Genrich Timofewitsch Mauer (1881–1940), the local historian and researcher. He moved in his free time by boat on the Sylva and Barda rivers, discovering the world fossil sites Chekarda and Matvéevo (Ural Geological Museum, Ekaterinenburg).

The Mazuevka - fossil site

Mazuevka site near the Sylva River, northeast of Suksun

The Panteleykovo - fossil site

On the road from Panteleykovo towards Arti, a rich Artinskian plant-deposit discovered by Michael Wachtler crops out.

The Evolution of the First Flowers

In the fine-grained sediments, especially from Matvèevo and Chekarda, we encountered a plethora of blossoms. These represent parts of plants with well-evidenced sexual organs such as pistils or stamina, which are similar to today's blossoms. Four petals with pistil-like organs in the middle characterise *Permotheca colovratica. Claireia pentafolium* and *Kunguria perneri* are characterised by their five-petaled flowers. *Sextupetalum ottiliethomsonae* and *Sextupetalum smirnovi* had six-petaled flowers. *Multifolium petaloides* and *Asterodiscus disparis* can be distinguished by their multiple-petaled flowers. *Nanoflos maueri* holds multiple-petaled blooms aggregated in panicles. *Aspidion decemnervium* had a corolla with their petals united and *Aspidion campanuliformis* had tube-shaped corolla. Flowers getting shed naturally, especially by wind, are not a common event, but it happens. Therefore, finding fossilised blossoms can be regarded as a rare and difficult occurrence.

If somebody walks through an intact springtime meadow, he would wonder about the diversity of the flora, especially the blooming flowers. The same is to the case in Early Permian Fore-Urals, before probably the Permo-Triassic cataclysm destroyed a big part of the ecosystem and pushed the further and faster spreading of the angiosperms by a million years.
Especially in vicinity of the hamlets Chekarda and Matvèevo located near the city of Perm, angiospermous fossils of many varieties in terms of appearance and structure can be found. The fact that all these fossilised inflorescences represent flowering plants is due to their appearance and blueprint obvious. Many details distinguish them from the gymnosperms like conifers, ginkgos or cycads. Difficulties arose more due to the fact that many of these flower-like structures differ from each other considerably. Therefore an analysis is not always easy. To

Early Permian flowers. **Left:** P*asternakia permensis* (upper part), *Clareia pentafolium* and *Aspidion campanuliformis.* **Middle:** *Tsvetokia nicolaswachtleri*, upper part *Sextupetalum ottiliethomsonae* and *Sextupetalum smirnovi.* **Right:** *Flossia uralensis*

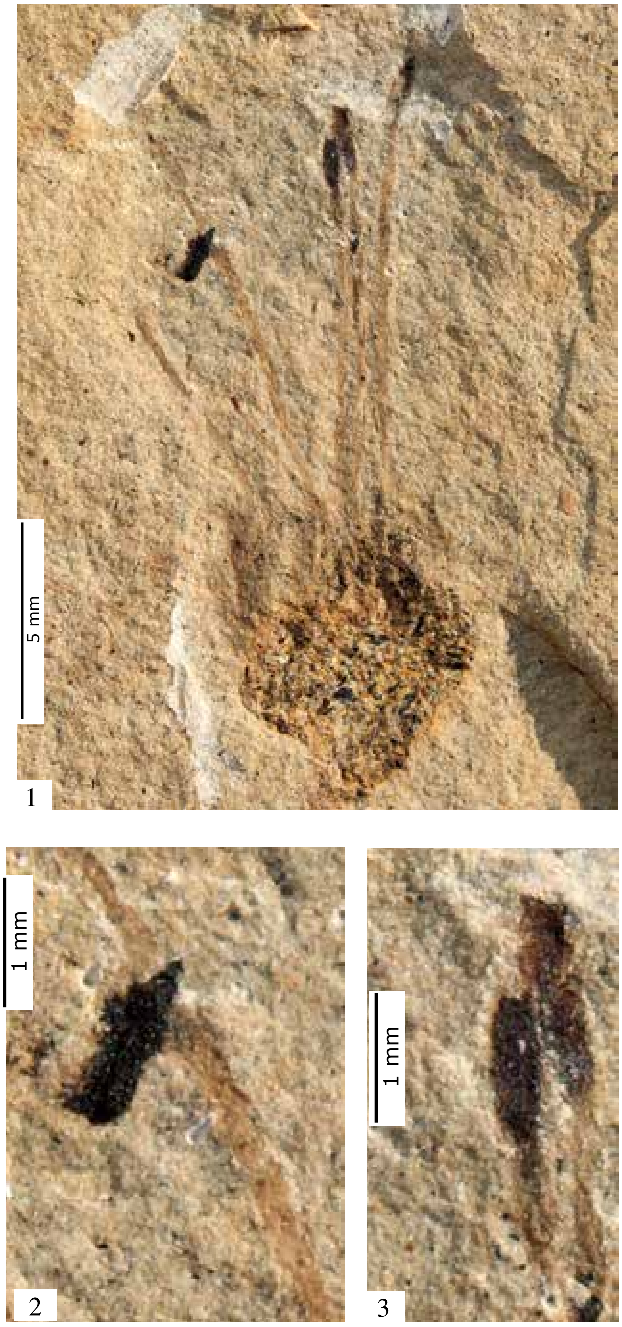
bring order among different flowers having four or more petals in addition to rounded or elongated stigmas, short anthers with a long filament, it was necessary to name at least the most frequently observed flowers and to present their differences.
This exposes a general problem in palaeobotany. Although it is often cumbersome to combine isolated flowers, seeds, fruits or leaves exactly or at least with a high percentage of precision, numerous classifications of individual parts of the same plant are just as confusing. This is especially valid for the plethora of flowers and fruits recovered in many of the Early Permian localities of the Fore-Urals.
The only certainty is that from the Devonian till the Early Permian, mainly all plant-tribes had just fully evolved; in the following 300 million years, only lateral and marginal developments happened.

Different flower-types

In the isolated Permian Angara Land originated a strange evolution-symbiosis. Insects and flowering plants with mostly heterosporous androecium and gynoecium gave birth to the evolution of the first angiosperms.
Mostly, the quality of preservation of plants and insects is superb and unique. However, not only can we observe sterile disks, but they also sometimes provide insight into fully formed sexual organs like ovaries or stamina.
Some fundamental questions cannot be answered satisfactorily even today. In which way did the ovary of these plants evolve? All the angiosperm evolution theories predicted the folded leaf-structure as starting point of the gynoecium. The protection of the ovule/seed in angiosperms is composed of a micropyle located from where the pollen

Flowers from the Early Permian Fore Urals

Bottom left: a sympetalous flower of *Aspidion campanuliformis;* **top left:** flower of *Tsvetokia nicolaswachtleri;* **middle:** a Rosaceae, resembling five-petaled flower of *Claireia pentafolium*; **bottom:** a six-petaled blossom of *Sextupetalum smirnovi;* **right:** *Sextupetalum ottiliethomsonae* with its sepals and petals.



***Flossia uralensis.* Stamen**

1. Whole flower structure evidencing the seven stamina and the base; 2. Magnification of the anther and a burst pollen sac; 3. Other two stamen from the same flower; Coll. Wachtler, Dolomythos, Innichen, Italy.

Flower of *Helleborus niger,* commonly called Christmas rose, an evergreen perennial angiosperm from the buttercup family, Ranunculaceae. The stamina resembles Early Permian *Flossia uralensis.*

Wilt flower of cherry plum (*Prunus cerasifera*). The petals are naturally shed; only the androecium with stamina and anthers is visible.

cell can enter the ovule. The unresolved question is that if the tissue is composed of one single macro-leaf or its origin lies in the amalgamation of many micro-leaves forming a wallet.

Therefore, it was useful to introduce the name *Flossia uralensis* for a unique and completely preserved flower, which had never been recorded before, having a wonderful long filament with an apical anther; they represent perfect stamina. *Tsvetokia nicolaswachtleri* was classified as a fructification, where a monoecious flower incorporating male and female sexual organs on the same blossom could be examined for the first time in Earth history.

One can observe the flower of *Pasternakia permensis* with a perfect pistil including stigma and equipped with a long style like many of today's plants. Members from the group of the Rosaceae, especially the cherry family, could be compared with the flowers of *Pasternakia permensis* or *Tsvetokia nicolaswachtleri* because of their slender single style, as well as the bilobed stigma. This could help in identifying a plethora of five petaled- (*Claireia pentafolium* and *Kunguria perneri*) or six-petaled flowers (*Sextupetalum ottiliethomsonae* and *Sextupetalum smirnovi*) or sympetalous blossoms such as *Aspidion decemnervium* or *Aspidion campanuliformis*, with their tube-

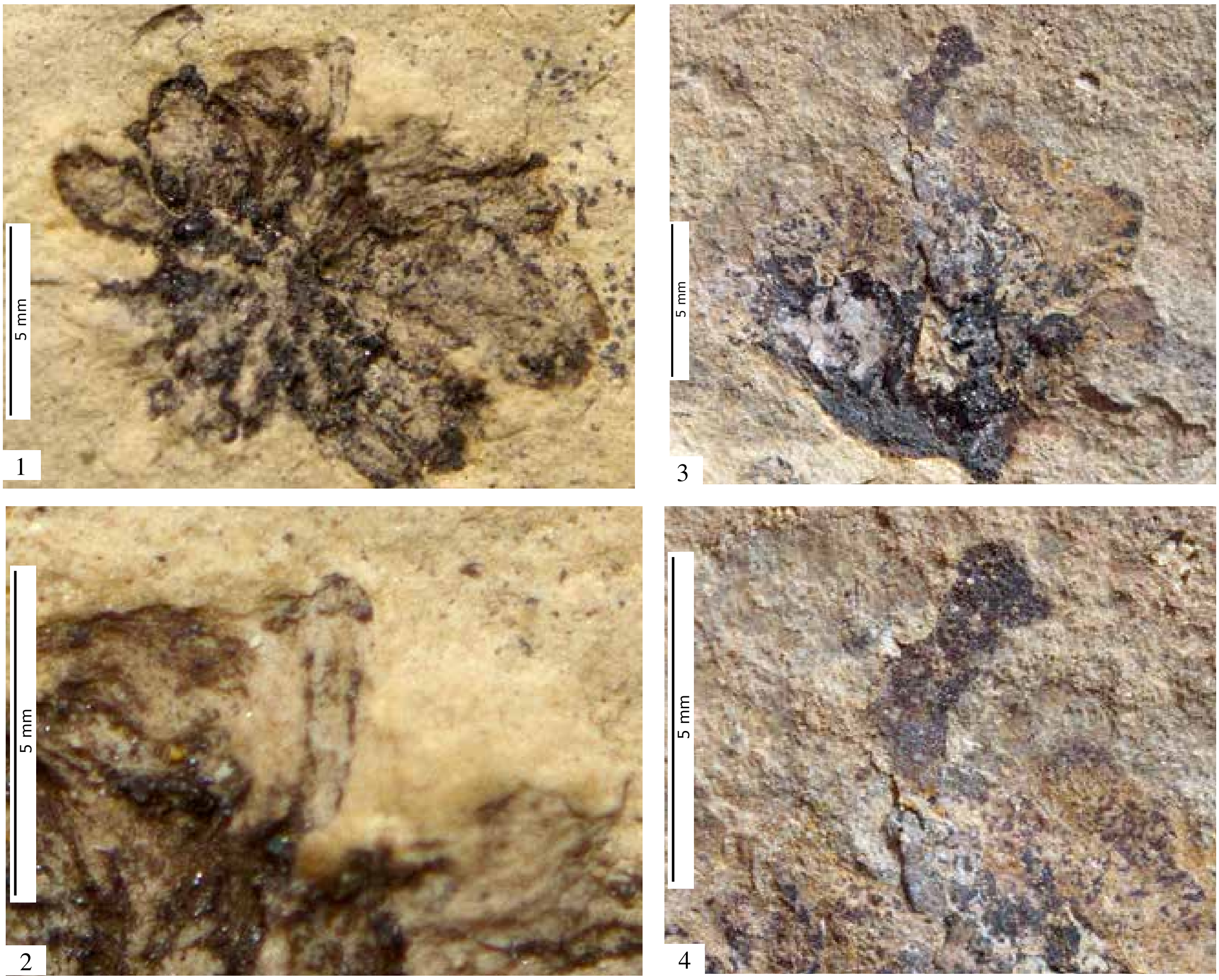
***Tsvetokia nicolaswachtleri* - Reconstruction**

***Tsvetokia nicolaswachtleri.* Flower with pistil**

1. Flower evidencing the filaments with pollen anthers and the pistil 2. Counter-plate with the exposed pistil on the upper side. Flower dimensions 12 x 10 mm, (MAT 509) Matvèevo, Coll. Wachtler, Dolomythos, Innichen, Italy

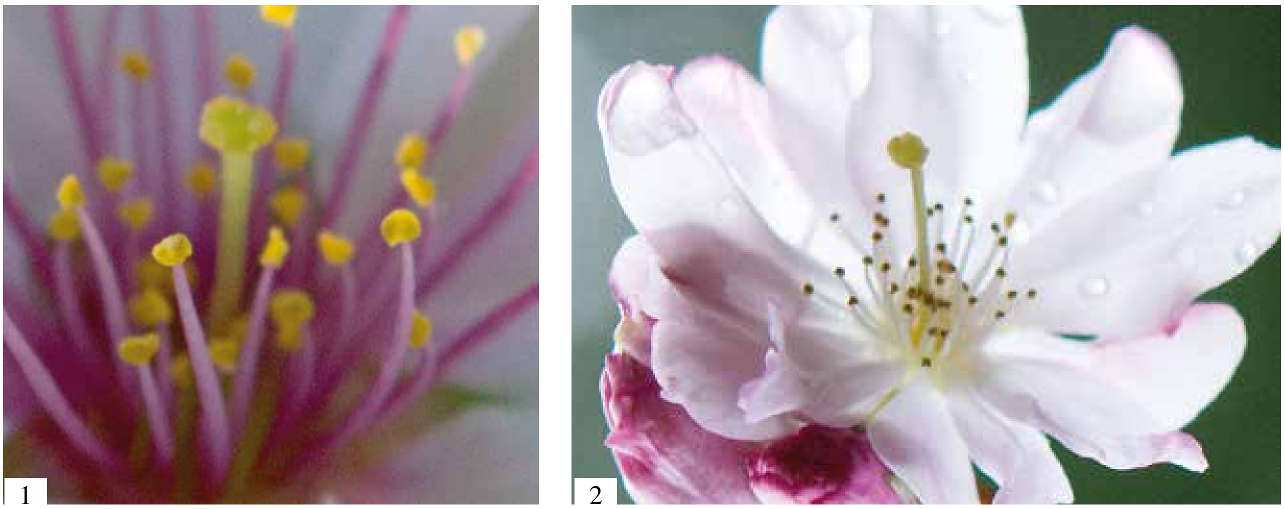
***Tsvetokia nicolaswachtleri.* Flower reverse side**

Flower reverse side with part of the stalk, sepals and petals (MAT 352), Coll. Wachtler, Dolomythos-Museum, all Matvèevo.



Tsvetokia nicolaswachtleri. **Flowers showing pistil and stamina**

1. Flower with the pistil in the middle; 2. Detail of the stigma and the stylar canal (MAT 536, Coll. Wachtler); 3–4. Flower with the projecting gynoecium and detail of the style and stigma (MAT 709, Coll. Gerasch); Matvèevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos, Innichen, Italy.



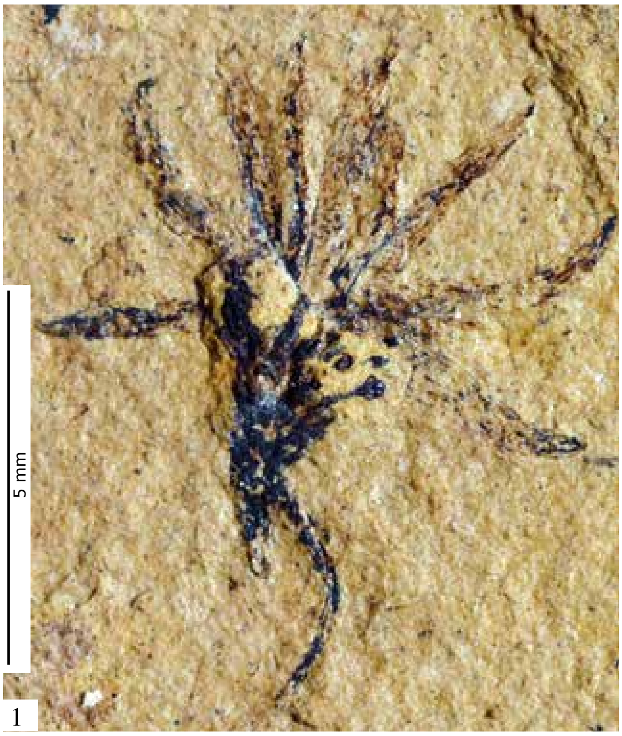
1. Stamina and pistil of *Prunus serrulata,* the Japanese flowering cherry
2. Projecting pistil with the stigma of *Prunus subhirtella*, the winter-flowering cherry.

shaped corolla. Finally, we encounter multi-petaled flowers like *Multifolium petaloides* or others going in the direction of Asteraceae, a family of plant thought to appear late in the fossil record due to their highly evolved blossoms and panicles.
All have enough differences to categorise them as different plants with different fruits and leaves. However, what remains unclear is how many different flowering plants we can encounter in the Early Permian sites of Angara-Land; in a black and white world of fossilised plants, a distinction between the green petals and coloured sepals is impossible.
Effectively, stamen like *Flossia* from Chekarda, as well as *Pasternakia permensis* from the Matvèevo locality were unknown till date

Naturally shed flowers of *Prunus cerasifera* (Cherry Plum). Wind and weather are sometimes able to pull the flowers off the tree, but finding intact fossil flowers is a rare event.

as part of Permian sediments and Triassic deposits on the Euramerican landmass.
One reason behind missing such angiospermous flowers is the not-so-perfect-sedimentation condition of other localities, while the other could be attributed to a totally different way of evolution and vegetation and ecosystem of the Permo-Triassic Euramerican plant kingdom. The only clearly heterosporous plants in the Euramerican Permo-Triassic fossil record were the lycopods such as heterosporous *Selaginella, Isoetes* and especially in Carboniferous-Permian *Sigillaria* and Triassic *Sigillcampeia*. The Sigillarias carried out hermaphrodite fructifications with two kinds of sporophylls: macrosporophylls, bearing one huge sporangia (almost like a seed), and also microsporangia.
But the Sigillarias had a totally different evolution system. Microsporangia and macrosporangia originated there on the same fructification, that way resembling the Magnoliaceae. The huge single macrosporangia in *Sigillcampeia* was coated by a protective tissue leaving a narrow open micropyle. In that some primitive clubmosses had more similarities with the Proto-Angiosperms from the Permian than all known gymnosperms.
Notably, not all angiosperms are hermaphroditic. Many primitive shrubs or trees from the Permian Fore-Urals like maples-ashes or oak-ancestors may have been monoecious, dioecious or polygamodioecious. All these complicate a clear evolution theory.
During Early Permian, *Tsvetokia nicolaswachtleri, Flossia uralensis* and *Pasternakia permensis* had just developed

Pasternakia permensis Reconstruction



Pasternakia permensis

Holotype MAT 31, from Matvèevo

1. Flower evidencing androecium and gynoecium; the flower is surrounded by sepals and petals; 2. Filaments are topped by an anther with pollen; 3. The gGynoecium is better visible on the counter plate; 4. Ovary with impressions of two ovules. Kungurian (Early Permian) Coll. Wachtler, Dolomythos, Innichen, Italy.

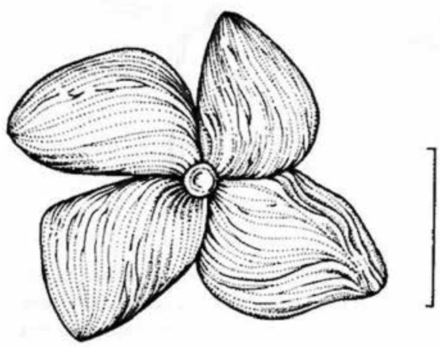
1. Flowers of *Prunus spinosa*, the blackthorn or sloe; 2. Open ovary showing the seeds of *Helleborus niger*

many novel features of today’s angiosperms and the question that follows is: What evolution process occurred in the next 300 million years? That only a few places worldwide have the ideal fine-grained sedimentation conditions is one option. In the Fore Urals, only in a few layers of the Matvèevo and Chekarda quarries did we come across circumstances where even wings of insects or the most subtle parts of plants were conserved.
All over the world, the possibilities of an excellent preservation are recorded only from a few localities such as the Early Cretaceous Crato-Formation in Brazil, with their richness in insects and flowering plants, or some places in West-Northern United States such as Eocene locality Republic or Bridge Creek. Otherwise, many other Permo-Triassic-Jurassic places with good sedimentation conditions have given no angiospermous plants till now.

Interesting flowers from the Early Permian Fore-Urals

Flowers being shed naturally, especially by wind, is not a common event, but it occurs. Therefore, finding fossilised blossoms leading to the discovery of fruits or seeds is a rare case; but as seen in here, it is possible. The next difficulty is that if the flowers get dropped into a lake where they sink down to the ground in a short time or get covered on the shore fast by finest mud. All these constitute today – certainly also in the past, if we go back nearly 300 million years – a rare and fortunate circumstance.
Only the rich and best-preserved Early Permian layers in the Russian Fore-Urals, especially of Matvèevo and Chekarda, allow us to have a deep insight into the evolution of plants and, more fortunately, the evolution of the first angiosperms.

Some flowers are characterised by four petals: 1. *Daphne odora,* native to China and inserted in the family of the Thymelaeaceae; 2. *Cornus macrophylla,* the large-leafed dogwood, pollinated by a beetle.



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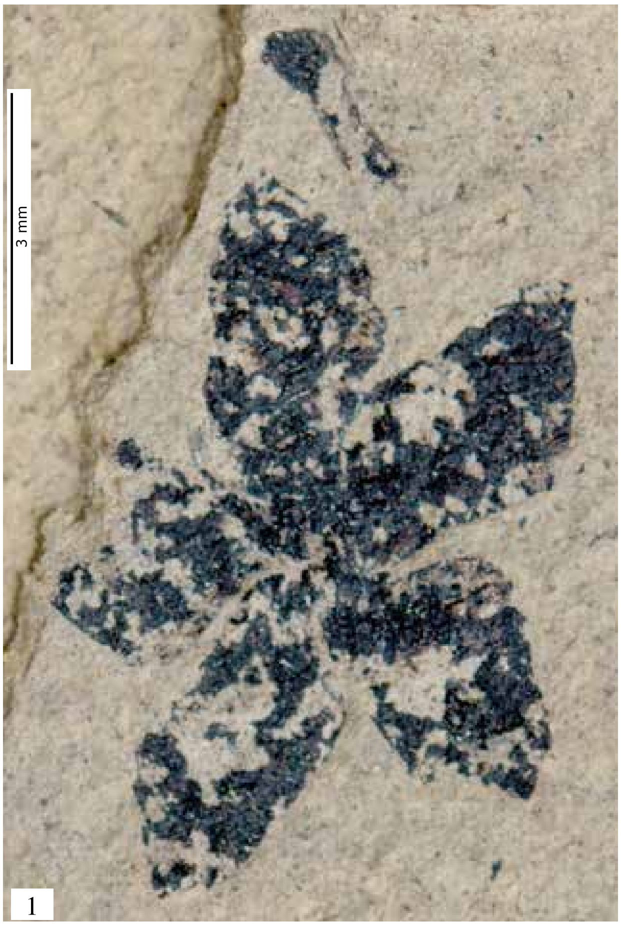
Permotheca colovratica

3. Flower with 4 petals (CHEK 362, Chekarda), Coll. Perner, Dolomythos Museum; 4. Holotype 4856/243 from Chekarda; Drawing made by Naugolnykh, 2013 (scale bar: 2 mm); Interesting is the pistil-like organ in the middle of the four “petals”

Flossia uralensis shows an inimitable conservation of a long and slender filament on top of which arises the anther with the both immature and mature pollen sacs.
If this specimen could be recovered from an Eocene deposit or compared to today's angiosperms, everybody would recognise the prototype of a perfect flower. Although, today stamens have a remarkable variety, many from the family of Rosaceae (cherries, plums, apricots) and Ranunculaceae, like the Christmas rose (*Helleborus*), depict the same characteristics as *Flossia.*
The flowers of ***Tsvetokia nicolaswachtleri*** ave distinct sepals and petals in addition to several stamina and one single long style with a dish-shaped stigma. The blossoms are characterised by one single carpel, with a narrow the petals projecting tubular style. The circular bilobed stigmatic surface expands slightly in a fan-like manner beyond the elongated and cylindrical style. The flowers are approximately 10–12 mm in diameter and are composed of a number of petals and sepals.

The small-sized flower of ***Pasternakia permensis*** has anthers on a short filament and an elongated or rounded pistil. Also, one sepal, rounded on the apex, can be observed. Several perfect stamina with slender filaments and divided anthers are visible.
Within the three described flower genera, *Tsvetokia nicolaswachtleri, Flossia uralensis* and *Pasternakia permensis* consist many differences to justify different classifications. Naturally, they must also belong to different Proto-angiospermous genera. The stamina of *Flossia uralensis* are much longer, especially their filaments, whereas those of *Pasternakia permensis* manifest a more stocky and fissured appearance. The rounded gynoecium of *Pasternakia permensis* is different from the ovary of T*svetokia nicolaswachtleri*, having a long style and a dish-shaped stigma, although it can be supposed that both were equipped by a single carpel only. *Flossia uralensis* stands a little apart from the other flowers for having long anthers but lost petals.
Due to the complex assemblage of the angiosperm-blossoms consisting of petals, se-



***Kunguria perneri,* five-petaled flowers**

1. Five-petaled flower (Designed holotype MAT 610, Coll. Wachtler); Matvèevo, Early Permian, Dolomythos, Innichen, Italy; 2. *Trachelospermum jasminoides*, known as jasmine (Apocynaceae). The flowers have a tube-like corolla opening out into five petal-like lobes.


1


2

1. The green sepals from *Prunus avium*, commonly called wild cherry. They form a green calyx, the outermost whorl of parts from a flower. The petals were just shed; 2. The white-coloured five petals of the Rosaceae (*Malus sylvestris,* the apple) represent the corolla. The green underlying sepals (calyx) and the corolla together make the perianth.

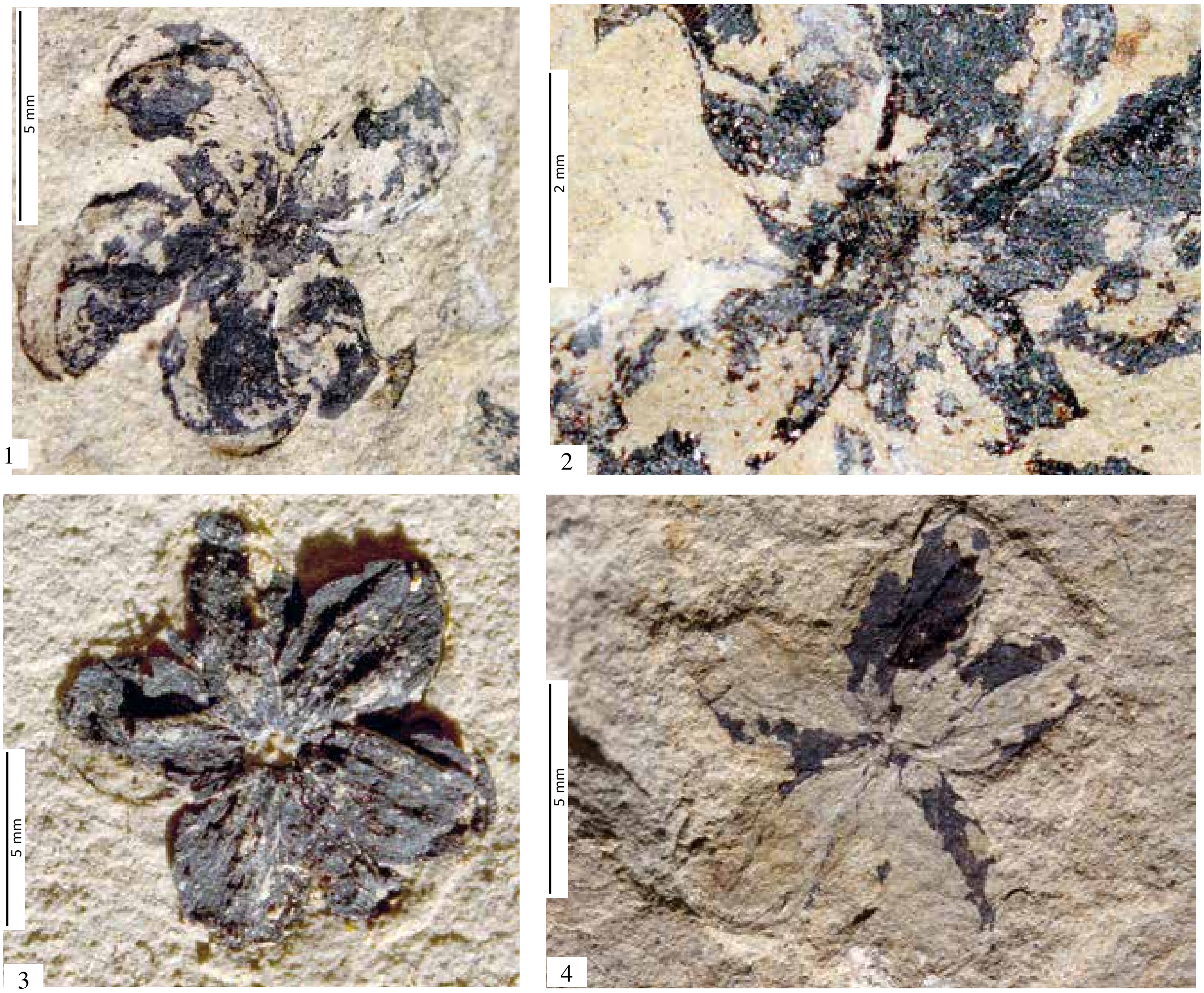

1


2


3


3

Today's flowers with five petals: 1. *Prunus cerasifera* (cherry plum); 2. *Prunus armeniaca* (apricot), 3. *Saxifraga hirculus,* commonly called marsh saxifraga; 4. *Geranium subcaulescens* (grey cranesbill)



Claireia pentafolium. **Five-petaled flowers**

1. and 2. Flower with five petals and detail of the stamina in the centre (Holotype MAT 442, Coll. Gerasch, Thomaseum, Langenaltheim); 3. Flower evidencing the stigma of the carpel (CHEK 321, Coll. Perner, Dolomythos, Innichen), 4. Flower with five petals (MAT 210); MAT=Matvèevo, CHEK=Chekarda, Coll. Wachtler, Dolomythos, Innichen, Italy.

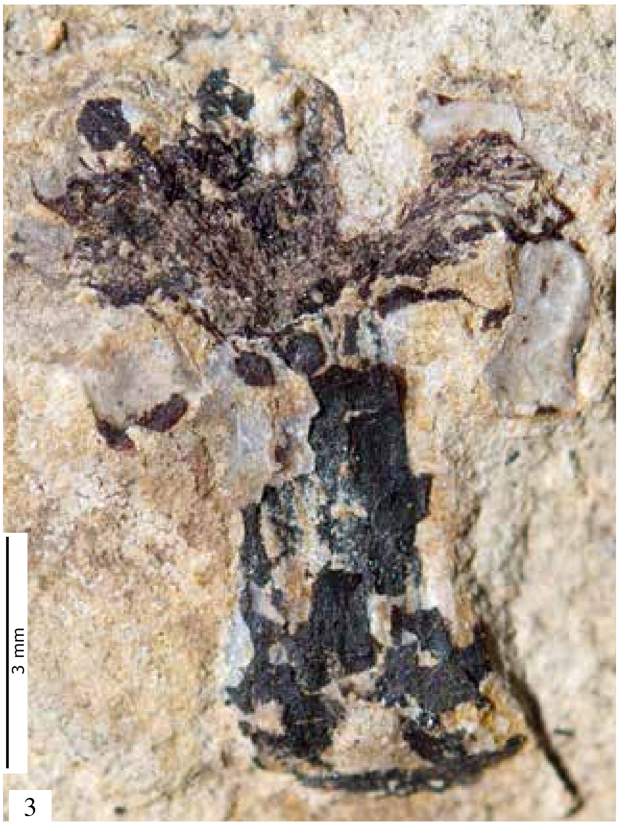
pals, pistils and stamina that lay over one another in fossilised specimen, no complete insight could be gained.

An interesting flower fossil from the Permian Fore-Urals consists of four petals arranged as a rosette. ***Permotheca colovratica,*** is characterised by four-petaloid leaves with the innermost part depicting a circular organ that can be regarded as stigma. Also, today, some plants like *Daphne* or *Cornus* and the dogwood have the same features.

Five-petaled “flowers” are relatively common in Early Permian stratas from the Fore-Urals. The flowers are equipped with short pistils, and one central gynoecium. Due to different petal leaves (rounded in ***Claireia pentafolium*** and tapered in ***Kunguria perneri***), it is obvious that they must belong to different genera.

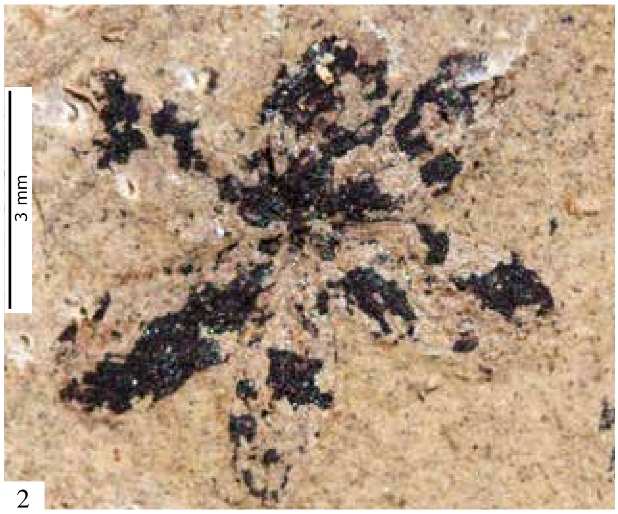
Interestingly, six-petaled “flowers” were relatively common in Early Permian stratas from the Fore-Urals and therefore, it could not be regarded as one that underwent a long evolution process from maybe many petals to six or a few petals forming a corolla of six. Six-petaled flowers like ***Sextupetalum ottiliethomsonae*** with its rounded petals or the small-sized flower of ***Sextupetalum smirnovi,*** with mostly tapered petals differ only little. Pistil and stamen are mainly the same.

Today we have plants that generate six-petaled flowers, such as *Clematis vitalba* within



Several unknown pollen organs and flowers

1. Isolated stamen with shed pollen (CHEK 341); 2. Flower with stamina (MAT 351, 7 mm in length); Matvèevo and Chekarda, Coll. Wachtler, Dolomythos Museum)

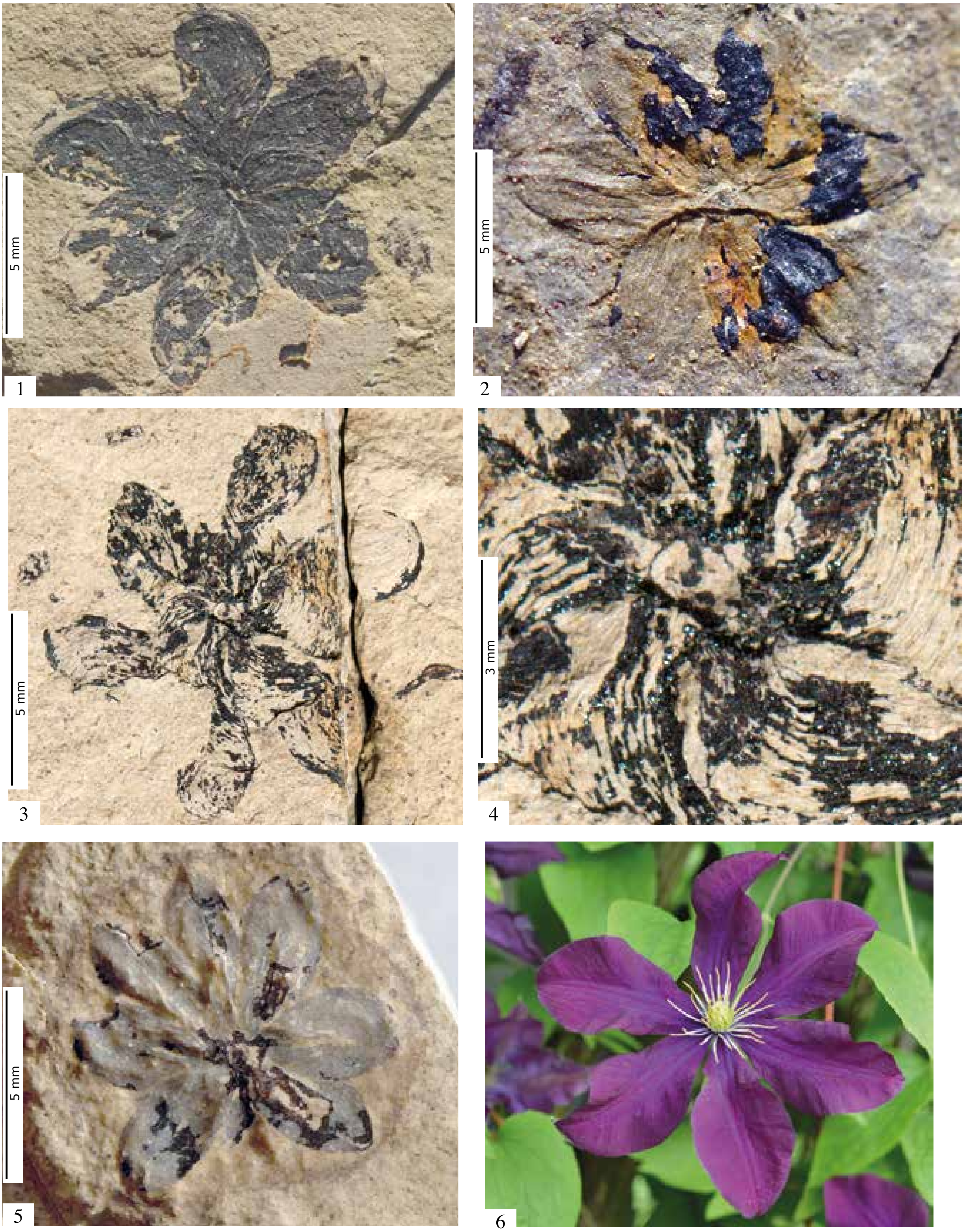


***Sextupetalum smirnovi*, six-petaled pointed flowers**

1. Six-petaled flower (designed holotype MAT 349, 6 mm diameter); 2. Flower evidencing the anthers and the short filaments in the middle (MAT 634, Coll. Perner), all Matvèevo

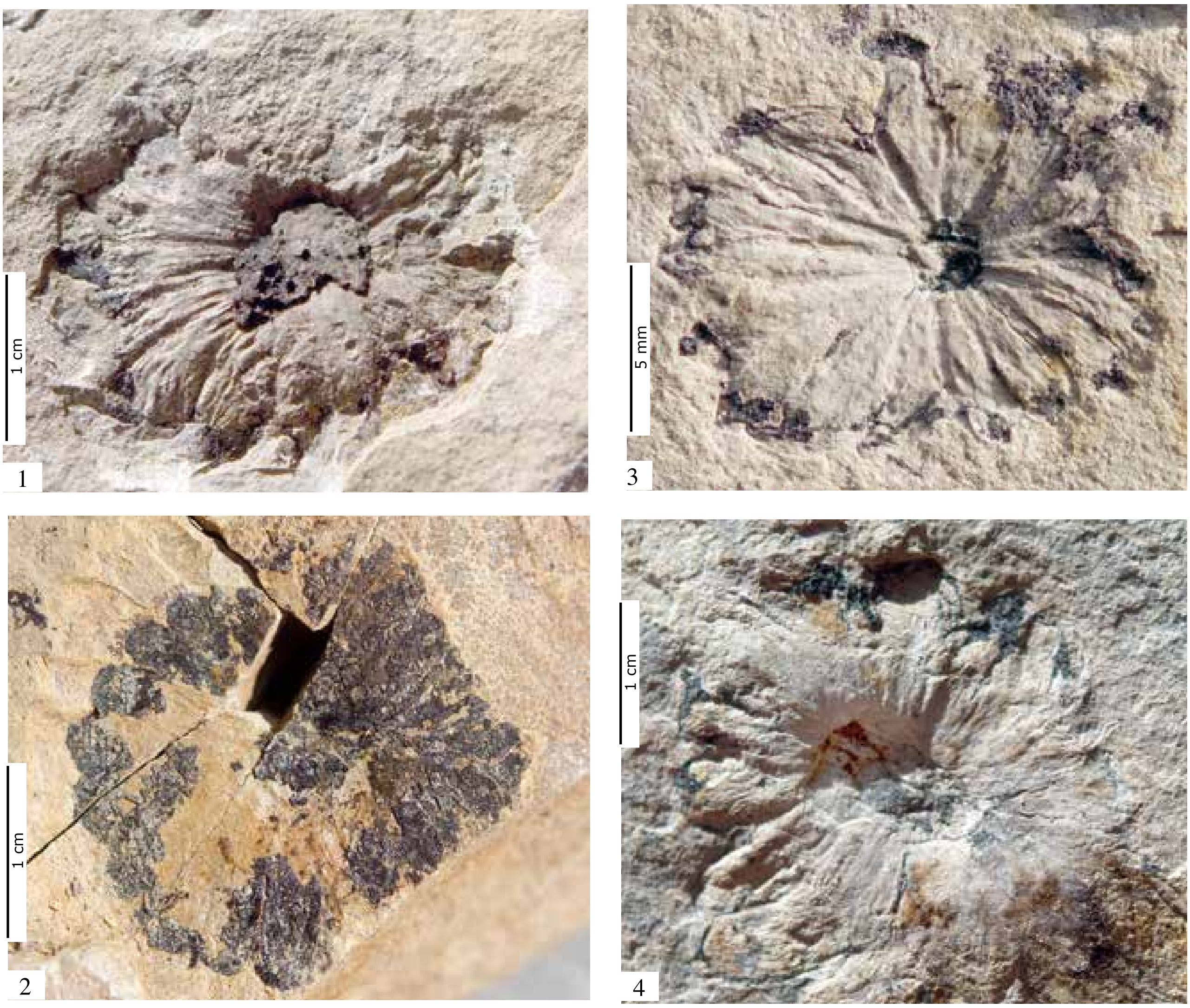
the buttercup family, Ranunculaceae or *Gardenia jasminoides* and *Sisyrinchium bellum*, the western blue-eyed grass.

In the Early Permian Fore-Urals, we can find two different types of sympetalous flower, meaning a calyx with their petals united. ***Aspidion decemnervium*** has a flat, wheel-shaped corolla and a small tube in the middle; ***Aspidion campanuliformis*** is characterised by its tube-shaped corolla forming a cone in the middle. Both show the inner parts of the flower suggesting stamina and pistils. Today, sympetalous flowers occur in



Sextupetalum ottiliethomsonae. **Flower with six petals**

1. Six-petaled flower (Holotype MAT 200); 2. Additional six-petaled flower (MAT 164); 3. and 4. Excellent preserved detail of the stigma of the carpel in the middle (Paratype MAT 510); 5. Six-petaled flower with one sepal (MAT 632); All Matvèevo, Early Permian Coll. Wachtler, Dolomythos, Innichen, Italy; 6. *Clematis vitalba*, within the buttercup family; the Ranunculaceae is a compact deciduous climber and characterized by its six petals.



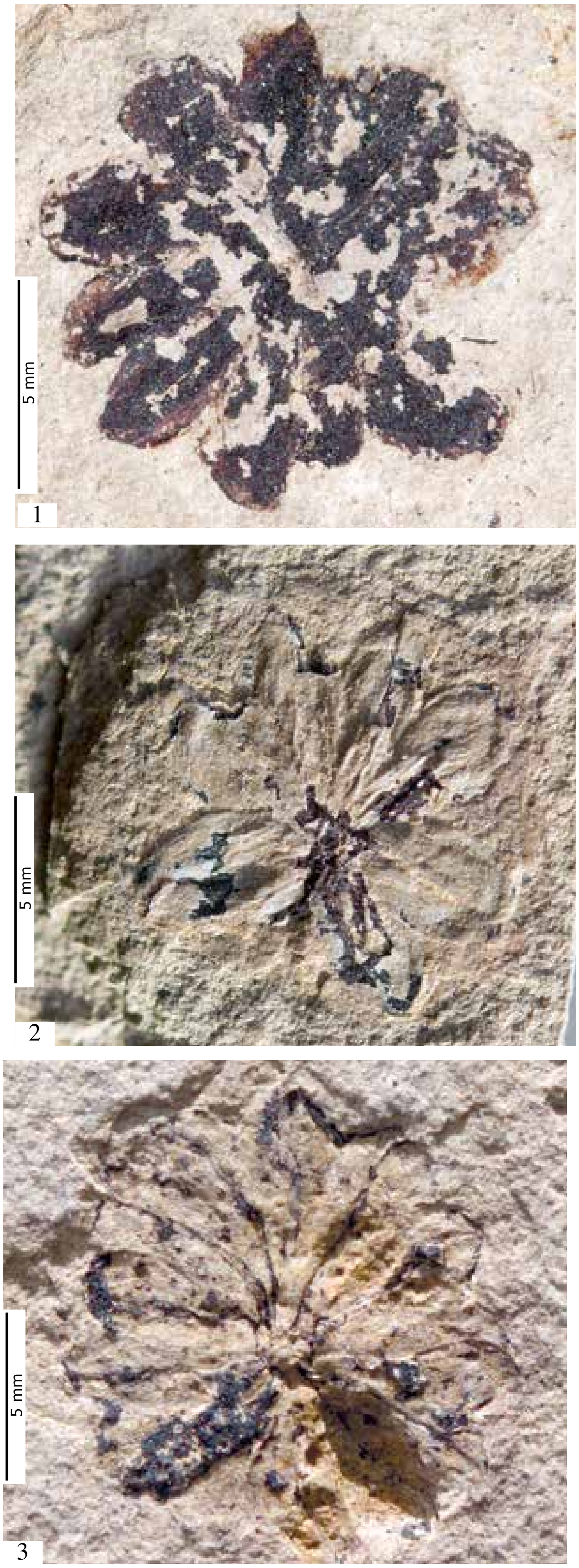
***Multifolium petaloides*, multiple-petaled flowers**

1. Multi-petaled flower with probable pollen dust in the middle (CHEK 67, 21 mm diameter); 2. Multi-petaled flower (CHEK 78); 3–4. Corolla with small tube (MAT 522, MAT 01); MAT = Matvèevo, CHEK = Chekarda, Coll. Wachtler, Dolomythos-Museum, Italy.

orders like the Convolvulales, Diapensiales, Ericales, Primulales, Plumbaginales, Ebenales, Contortae, Tubiflorae, Plantaginales, Rubiales, Cucurbitales and the Campanulatae. In these families, the flowers have a separate calyx and corolla, with the petals fused sometimes only at the base of the corolla, but often they are united till the apex. They are trumpet-shaped to broadly funnelform or nearly bell-shaped. ***Aspidion*** is therefore another good example that supports the theory that the process of assembling of the petals occurred just early.

In the same layers herbaceous plants having leaves with a central midrib and fruits capsule containing the seeds were found. Probably campanulate flowers like those of *Aspidion decemnervium* or *Aspidion campanuliformis* belong to them. The basal leaves are aggregated in tufts. The fruits hang on the corolla and open the capsule to release numerous seeds. The size of the squashed fruit is 20 mm long and about 5 mm wide.

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



Asterodiscus disparis. **Flowers**

1–3. Multi-petaled flowers (MAT 505, MAT 632, MAT 707); they all are about 10 mm in diameter. All Matvèevo, Coll. Wachtler, Dolomythos, Innichen, Italy

angiosperms did not exceed 10 cms. In the Early Permian sediments, herbaceous plants characterised by leaves with a distinctive midrib are encountered in fair numbers.

Searching for a modern representative of *Lyswaia*, we come to the extant Campanulaceae (bellflower family), a cosmopolitan but concentrated in the Northern Hemisphere. The fruits are encapsulated, the flowers are bisexual and bell-shaped, consisting of a narrow, tube-like corolla. The leaves are often characterised by a midrib, such as in *Campanula cespitosa.*

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

Multi-petaled flowers were present not only in the form of single blossoms but also as racemes or panicles in the Early Permian of the Fore-Urals. It is still not resolved as to which family they belong to, and all the classifications are only tentative. Therefore, a lot of work expects the future generation to correlate flowers, fruits and leaves.

In ***Multifolium petaloides,*** an undefined number of sterile petals surround the fertile parts composed of monoecious male and female organs.

Several racemes or panicles holding more flowers were collected. Probably they belong to different plant genera, but till further discoveries expand our knowledge, they have altogether been clubbed as ***Nanoflos maueri.*** Usually the blossoms of the

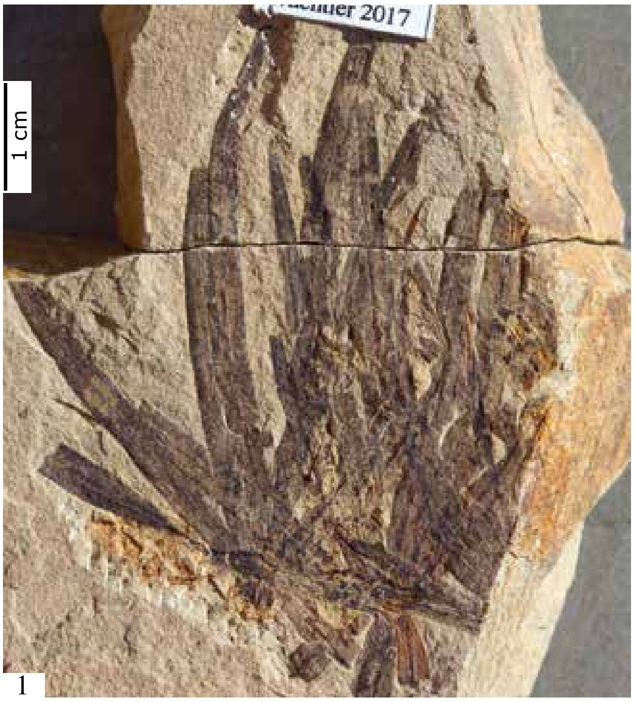
Fig. 145. *Asterodiscus disparis* Z a l.
Rive gauche de la rivière Sylva, ravin Kazarinovsky. Étage Bardien. ×2

Asterodiscus disparis. Drawing by M. D. Zalessky (1937, p. 80). It represents a multi-petaled flower.

1. Aspidion decemnervium, sympetalous flowers (MAT 704, Coll. Gerasch, Thomaseum, Langenaltheim). The united petals as well the ovary and the filaments of the anthers are visible; 2. Other sympetalous flower with small-sized stamina and pistils visible (MAT 752) Matvèevo. 3. *Aspidion decemnervium* from Matvèevo after a drawing by M. D. Zalessky, 1937.

Aspidion campanuliformis. 1. and 2. Plate and counterplate of the holotype MAT 342; Matvèevo Coll. Wachtler, Dolomythos Museum, Italy.

Sympetalous flowers with united petals can be observed, especially in the Convolvulaceae (*Convolvulus chinensis).*



***Lyswaia nicolaswachtleri.* An ancestor of the Campanulaceae**

1–2. Entire plant with detail of a mature and open capsule (MAT 338, Coll. Wachtler)

racemes are small-sized; therefore, they also differ from other isolated four-, five-, six- or multi-petaled flowers. Deciphering all these flowers is not easy and most is valid only under best circumstances when the petals are fossilised from the upper side. On the reverse side, in addition to the petals, the sepals must also be visible and be part of the stalk. In this case, sometimes a more petaled blossom will be feigned.

Another low-growing plant with multi-petaled flowers is ***Uraloflos campeiae.*** The plant reaches a lenght of 10-12 cms. The leaves sprout from the main rachis and are about 4-5 cms in length. A strong midrib is present in each leaf. The flowers are aggregated in the umbels growing on a short but stout peduncle. Each single flower/fruit is 5–7 mm long, seems to be composed of five petals and seats on a short pedicel.

Uraloflos campeiae did not form a capitulum, typical of the Asteraceae in the Early Permian layers, such as *Naugolnykhia matvéevoi, Asteroforma nicolaswachtleri* or *Wachtlerosperma stefanperneri.* While the leaves in the three genera mentioned did not exist or are only slightly distinctive, in *Uraloflos campeiae,* they are quite

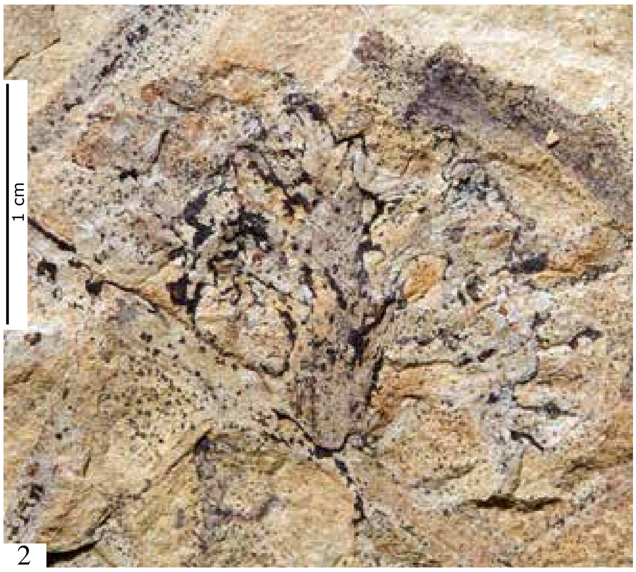
1. The flower of *Campanula sibirica;* 2. *Campanula rotundifolia* (Bluebell bellflower) capsule containing some seeds, most of them released. It can be compared with MAT 338, which is also an open capsule.

***Nanoflos maueri* Flowers forming a panicle**

1. Flower bud with diverse small-sized blooms (Holotype MAT 366); 2. Panicle with lateral branches supporting several flowers, (CHEK 73); 3. A panicle with several five-petaled flowers (MAT 326); MAT = Matvèevo, CHEK = Chekarda, Coll. Wachtler, Dolomythos-Museum, Italy.

Wild cherry *(Prunus avium), f*orming a panicle of flowers.

pronounced. The only one feature that is common among all these herbaceous and low growing plants are their aggregation of many small flowers to form one unit. While gymnosperms never form umbels, it is a common feature in the angiosperms, including the extant ones. It is difficult to establish which plant of today's can be compared with *Uraloflos campeiae,* but many of the monocots or dicots can be worthy of consideration.
It is interesting beyond doubt that aggregated flowers in the form of corymbs, umbels or capitula were frequent in the Early Permian layers of the Fore-Urals, and they debunked the common theory about the relatively late appearance of these kind of flowering plants.



Uraloflos campeiae

1. Entire plant with long narrow leaves and aggregated flowers in the upper part (Holotype CHEK 75, Chekarda); 2. Detail of the compound corymb from the holotype CHEK 75 (Chekarda, Coll. Wachtler. Dolomythos); 3. Reconstruction of CHEK 75.

The Early Permian Origin of the Asteraceae

The Asteraceae or Compositae are one of the most common flowering plants on earth, being of cosmopolitan distribution and reaching all continents except Antarctica. They include over 1900 genera with about 32,000 species. A characteristic feature is their flower composed of a dense head called capitulum or pseudanthium. This is surrounded by a fair amount of involucral coloured leaves. Their fruits, achenes, are often equipped with parachute-like feathery bristles, which enable the seed to be carried by the wind. Usually, it is believed that the Asteraceae represent one of the most evolved angiosperm families, and as a logical consequence, they evolved late in Earth history. Strangely, we encounter in the Early Permian Fore-Urals flowers, entire plants and single pappus, with many characteristics of extant Asteraceae. They must, therefore, belong to different flowering plants. *Naugolnykhia matvéevoi* consist of a long and slender stalk with a flower composed of two circles. A*steroforma nicolaswachtleri* evidence a powerful inner head and an outer ray flower composed of petal-like leaves. *Zalesskya multipla* is characterised by their small flowers but has the same features of the former. *Caputosperma geraschi* as well as *Caputosperma perneri* have blooms with more flower heads clustered together forming panicles. *Wachtlerosperma stefanperneri* due to its bifurcating leaves, must stand on the frontline of the evolution of the Compositae.

Also, isolated fruit organs resembling extant pappus are found, which are described as *Pappusperma ventilata* and represent parachute-like fructifications. All these plants reveal fascinating findings about the evolution of the Asterales, one of the dominating angiosperm families today.

The Greek name Aster is used to refer to the star-like form of their inflorescences. Many Asteraceae are herbaceous plants, although some also have shrub-like features, or are climbers, and a few are trees (*Olearia*). The leaves are often inconspicuous, mostly arranged in an alternating pattern, and rare-

Early Permian Asteraceae

Left: *Caputosperma perneri,* blossoms (MAT 44); **middle:** a mature pappus (Holotype MAT 578); **right:** *Caputosperma geraschi* (holotype CHEK 68) releasing its parachutes. On the left side is visible the scorpionfly *Agetopanorpa punctata* and in the middle, the Meganeuridae *Arctotypus sylvaensis.*

ly opposite to each other. However, some Asterales have lanceolate-linear leaves that have some affinities toward the monocotyledons, a feature that became interesting in the Early Permian fossil record of the Fore-Urals. They can be distinguished easily from other plants due to their characteristic inflorescence. What appears to be a single flower is, in reality, a "compositae" (therefore the other name) of many small flowers. This interior cluster of single flowers is commonly called a "head" or capitula. The head is surrounded by sepal-like bracts (phyllaries), which enclose the flower till the time it opens. Each mini-flower is composed of five fused petals, which generate hairy or bristle-like organs called pappus. Every pappus holds a small seed on the tip, which is connected with the hairy organ that functions like a parachute. This can be easily blown by the wind and dispersed elsewhere. The radially symmetrical disk flower has identical petals arranged in one or many rows in a circle around the middle. Therefore, they are largely pollinated by insects due to their showy capitulum.

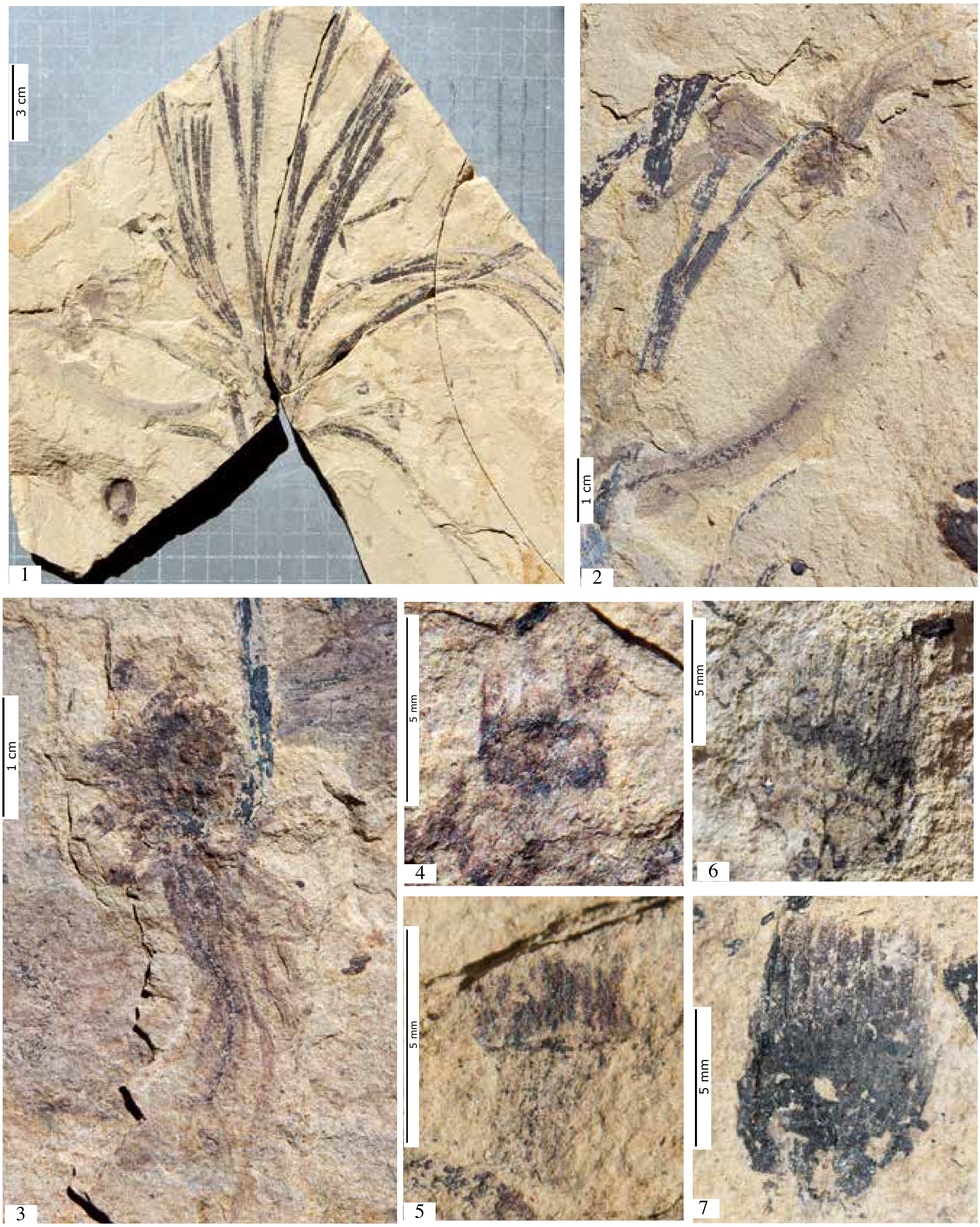
Till now, the oldest known fossils of the Asteraceae are pollen grains from the Late Cretaceous. Their characteristic flowers arranged to form a capitulum-inflorescence, with hairy or bristle-like pappus equipped with one seed. It can be supposed that plants from the Early Permian Fore-Urals that evidence the same features can probably be inserted in the same schema, which shows that they are potential progenitors of the Asteraceae.

Different Asteraceae-ancestors

Interestingly several thought Asteraceae-ancestors were just present in the Kungurian deposits of the Fore Ural. The most rudimental seems to be ***Wachtlerosperma stefanperneri*** a herbaceous plant with bifurcated foliage and fertile leaves having a strong mid-vein ending in an umbel. It was equipped with single inflorescences

Wachtlerosperma stefanperneri. **Reconstruction**

Left the entire plant with the flower is visible; on the right side, a detail of the umbel and an isolated floret with the shadows of not fully mature seeds (MAT 523)



***Wachtlerosperma stefanperneri*. Plant, leaves and flowers**

1–3. Entire plant with umbel consisting of many inflorescences and bilobed elongated leaves (all MAT 287, designed holotype); 4–5. Detail of the florets from lateral view (4 mm) of the holotype; 6-7. Single floret filled with not fully mature seeds (MAT 523, 10 mm long); Matvéevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos Museum

evidencing many florets and enclosing within a fair number of achenes. The tepals were long and narrow. One of the examples is represented by an about 30 x 30 cm huge slab with the impressions of an entire plant presenting long and slender forking leaves in connection with a stalk generating a flower/fruit apically. *Wachtlerosperma stefanperneri* is known in mainly all parts although their classification in one of the existing Compositae plant-families is not easy.
Highly interesting is the forking foliage, which, if found isolated, can also be confused with other Protoangiosperms like *Psygmophyllum cuneifolium*, a presumed ancestor of the Aceraceae. These leaves are so common in the Early Permian layers of the Fore-Urals that they attracted the attention of the first researchers like Stephan Kutorga from Petersburg in 1838 or M. D. Zalessky.
Bilobed leaves built the starting point of almost all plants beginning from the Devonian time. They can belong to different flora elements, from supposed broad-leaved trees to low growing herbaceous plants and on the Euramerican landmass to all gymnosperms like conifers, cycads or ginkgos.
Several interesting facts about the origin and evolution of Asteraceae can be deduced from *Wachtlerosperma*: the inflorescences are formed in umbels; they consist of an aggregation of many micro-flowers coating many seeds inside; the stalks that hold the flower bunches can be regarded as reinforced leaves; all features of the Asteraceae family can be observed in this.
Another mainly complete recovered Early Permian Asteraceae is represented by ***Naugolnykhia matvéevoi**.* It consists of a long and slender stalk with dwarfish leaves sprouting sometimes on the stipe. The flower is composed of two circles: an inner disk flower, dome-shaped, velvety, covered by finest hairs during mature stage and an outer ray flower composed of petal-like leaves.
In that, it can be compared well with today's marguerites. Probably, if one knew nothing about the Early Permian age, they could confuse *Naugolnykhia* easily with Asteraceae. Both have leafless (daisy flower) or primarily leafless stalks (*Naugolnykhia matvéevoi*); both flowers have a large centre adorned with delicate petals.
In addition to *Naugolnykhia matvéevoi* and *Wachtlerosperma stefanperner*i resembling the extant Asteraceae, another parented blossom was discovered in the Early Permian Fore-Urals – ***Asteroforma nicolaswachtleri.*** The flower has a diameter of 25 mm and consists of two clearly separated circles. The outer head is composed of many petaloid leaves that surround an inner disc floret. Probably, during the mature stage, this generates the parachute-like structure with the attached seed that was found fossilised in the same sediments as *Pappusperma*. Due to their inconspicuousness, especially of the heads, *Asteroforma nicolaswachtleri* have never attracted the attention of researchers or collectors, although naked capitulas are seldom found in Chekarda and Matvéevo. In the Early Permian layers, blossoms can be found attached to extremely slender stalks (*Naugolnykhia matvéevoi)*, on stocky stems (*Asteroforma nicolaswachtleri*) or with bilobed leaves on leaf-like stemlets (*Wachtlerosperma stefanperneri*), from which it can be deduced that they all belong to different

Asteraceae species:
1. *Encelia farinosa* (brittlebush), a native flower from the Southwestern United States; 2. *Arnica montana*, widespread in the Alps. There are many resemblances with Early Permian *Naugolnykhia matvéevoi,* beginning from the leaves till the head and the hanging petals.


1


2

Naugolnykhia matvéevoi a potential Asteraceae-ancestor

1–2. Holotype of *Naugolnykhia matvéevoi* (MAT 367, Matvèevo, Coll. Wachtler, Dolomythos-Museum), an herbaceous plant with inflorescence and hanging petals

***Naugolnykhia matvéevoi.* Reconstruction**

Flower with dwarfish leaves and the blossom with hanging petals and an inner disk (MAT 367 holotype); also the withered flowers are visible.

1

2

*1. Leucanthemum vulgare (*Oxeye daisy), a flowering plant native to Europe and temperate regions of Asia; 2. *Aster altaicus*, an Asteraceae widespread across Eastern Asia and Siberia. From a radiate yellowish brown capitula sprout about 20 bluish to purple petals. Some Asters have wilted revealing the hairy pappus. *Asteroforma nicolaswachtleri* had probably the same feature. The inner disk florets are different from the outer ray florets.

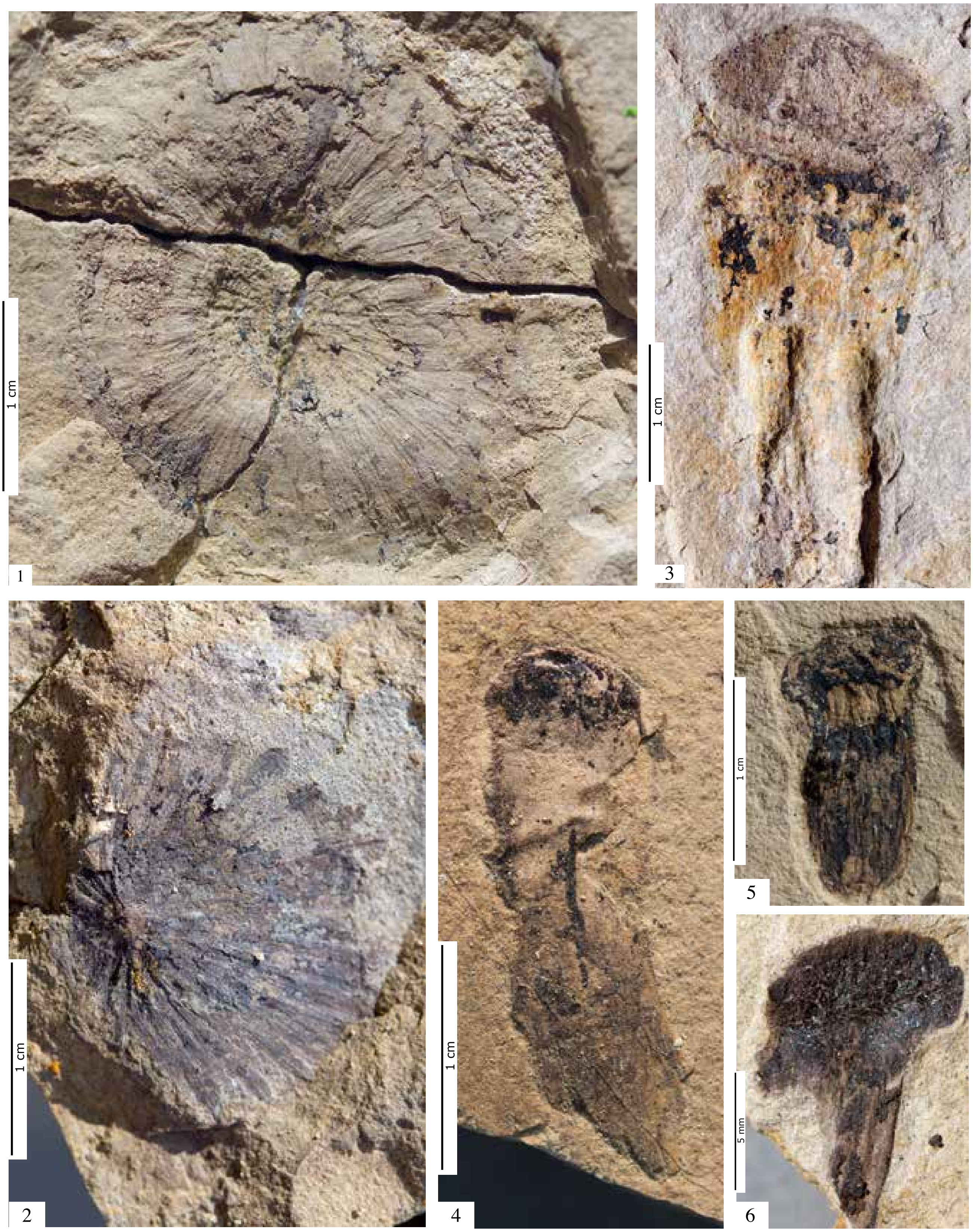
plant genera. All these small puzzle pieces help to give a better insight into the origins of Asteraceae, particularly because their reproductive organs are found as isolated parachutes.

Various multi-petaled flowers were recorded from the Early Permian Fore-Urals. Some of them, such as *Multifolium petaloides, Naugolnykhia matvéevoi* or *Asteroforma nicolaswachtleri,* reach considerable sizes of about 20 mm and above. In this range, ***Zalesskya multipla*** is the most inconspicuousness and small, with the entire flower measuring only 10 mm or less. *Zalesskya multipla* stands a little apart from this "huge" flower and its clearly epigynous character. Additionally, a sunken ovary has not been recorded so well in other multi-petaloid flowers.

In the same layers, along with big flower heads (like *Naugolnykhia matvéevoi, Asteroforma nicolaswachtleri* or *Zalesskya multipla*), we encounter panicles with dwarfish and aggregated flower heads that were classified as *Caputosperma.* Two distinct species are observable: ***Caputosperma perneri*** was a small plant, reaching probably only a few centimetres, whereas ***Caputosperma geraschi*** had leaves reaching a length of about–12 cms. Both species had parental affinities towards their small and aggregated flowerheads and pappus that resembled dwarfish pins equipped with a basal head, what represented the seed. They are not rare but inconspicuous; therefore, they could have been overlooked easily.

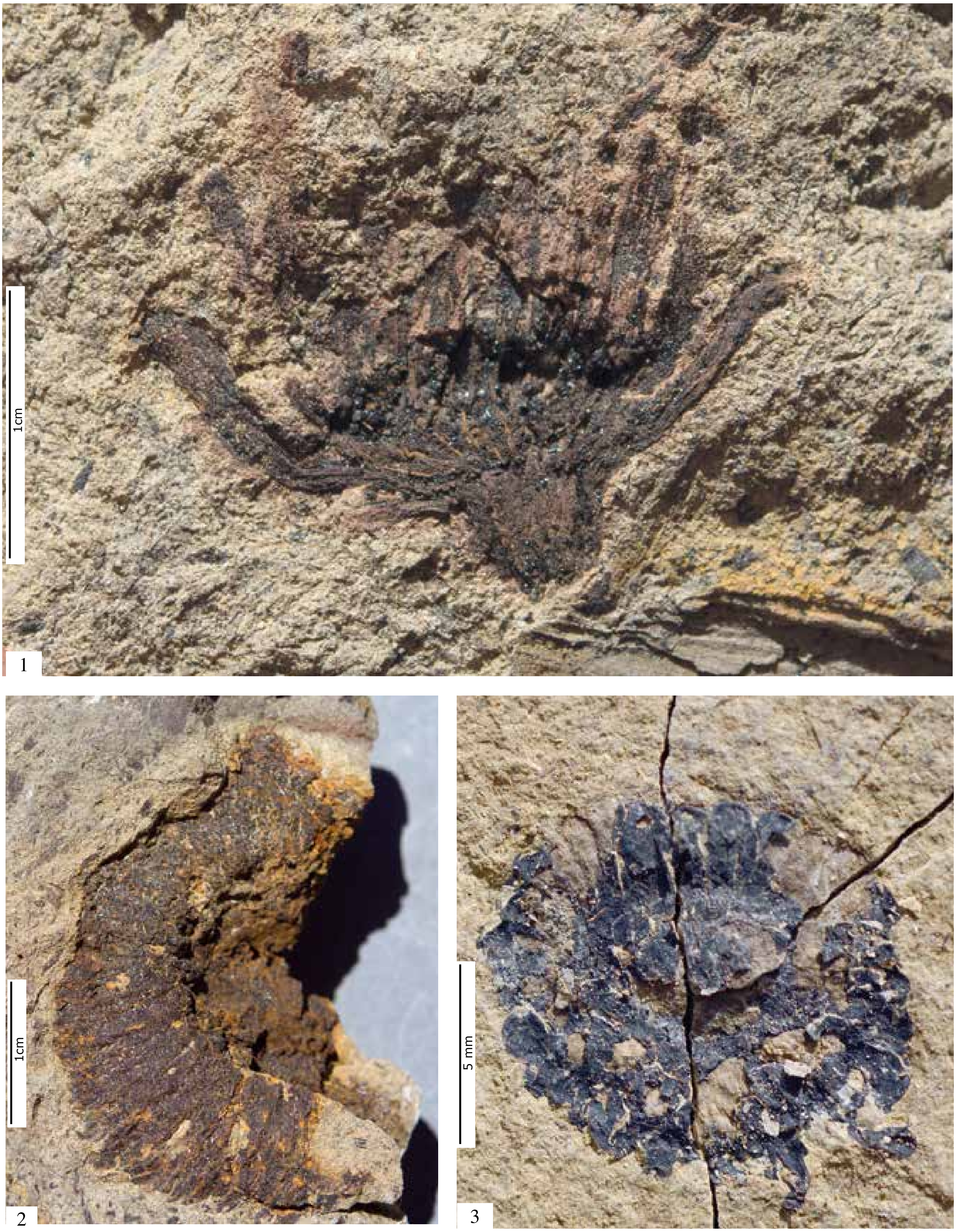
Within dicotyledons – to which the Asteraceae belong – some genera like *Tragopogon (pratensis)*, the goat's-beard have lanceolate-linear leaves, although their flower head is completely different from the synflorescences of *Caputosperma geraschi*. Notably, the lanceolate-linear leaves of *Caputosperma geraschi* resemble that of monocotyledons more than dicotyledons.

The smaller one – *Caputosperma perneri* – evidence only tapered smooth leaves. Due to the fact that parts of the roots were also found preserved, it is supposed that it formed lawns in the understory of the broadleaved trees. Among the various plants of the Early Permian Fore-Urals resembling Asteraceae, *Caputosperma perneri,* with its dwarfish and aggregated synflorescences,



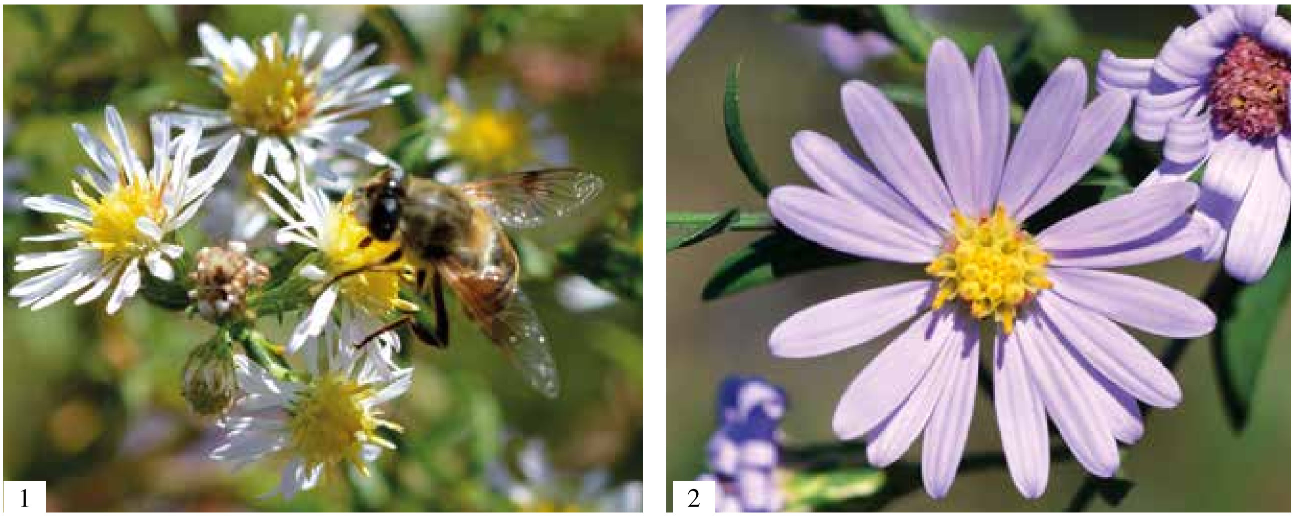
***Asteroforma nicolaswachtleri*. Asteraceae-progenitor**

1. Blossom, upper view (holotype CHEK 65, Chekarda); 2. Other blossom, underside (MAT 746); 3. Receptacle evidencing hanging petals (MAT 353, paratype); 4–6. Naked heads of the flower with the parachutes released (CHEK 221, CHEK 55, Chekarda; MAT 356, Matvéevo) Kungurian (Early Permian) Coll. Wachtler, Dolomythos-Museum

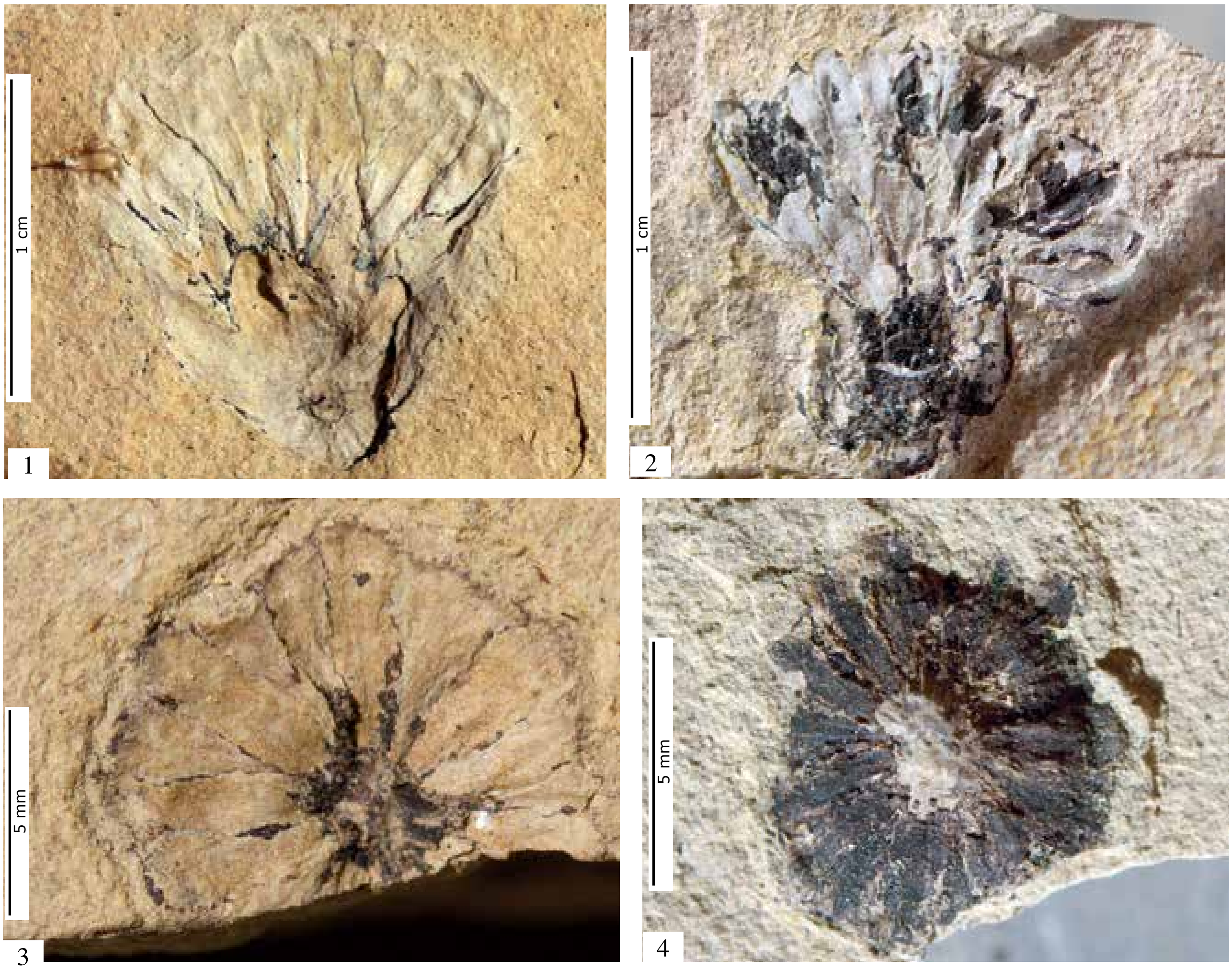


***Asteroforma nicolaswachtleri.* Asteraceae-progenitor**

1. Blossom, lateral view (CHEK 52, Chekarda); 2. Blossom, upper view (MAT 218, Matvèevo); 3. Flower with many petals and an inner head (MAT 109, Matvéevo) Kungurian (Early Permian) Coll. Wachtler, Dolomythos-Museum

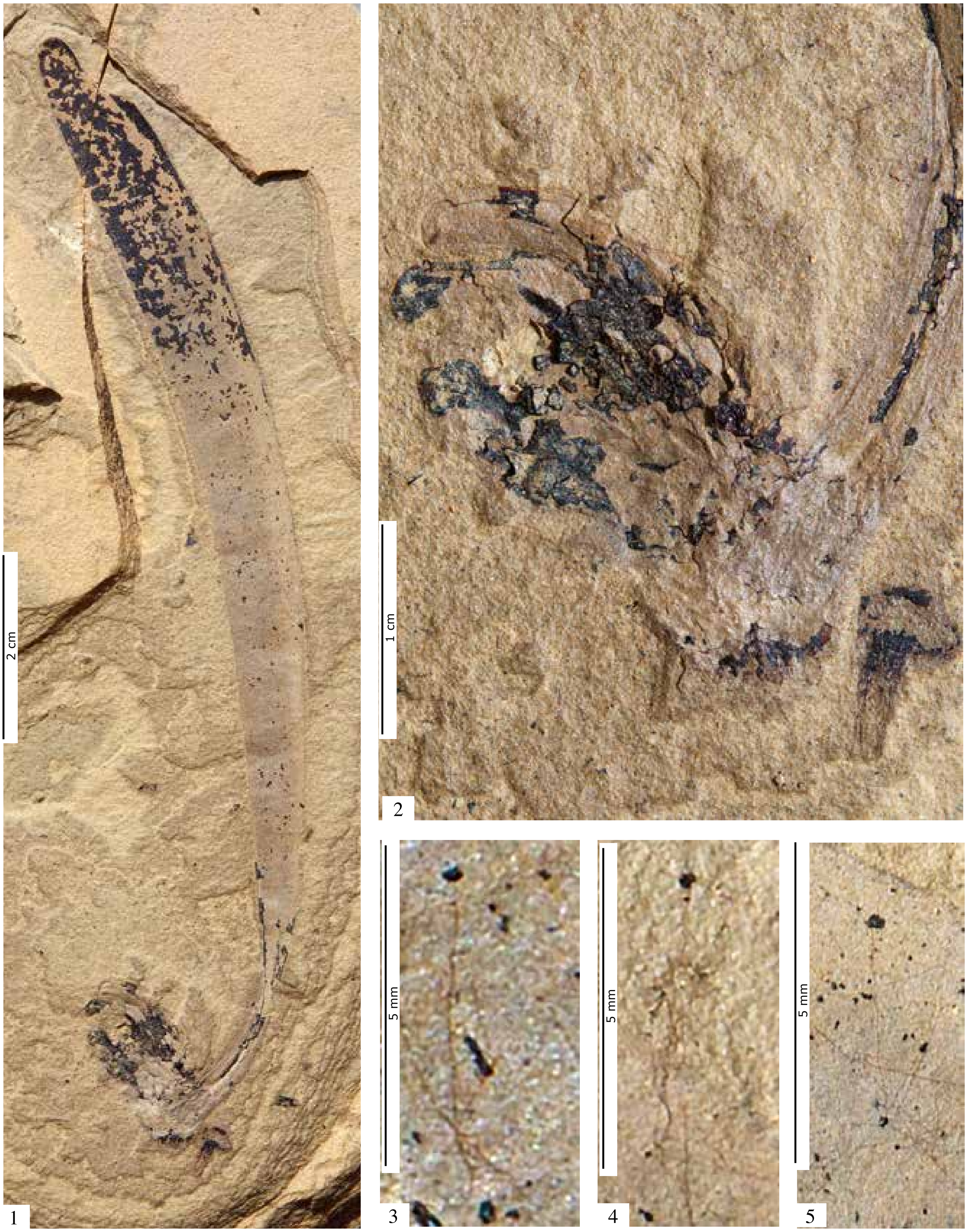


Asteraceae flowers: 1. *Euthamia caroliniana,* an American Compositae pollinated by a bee; 2. *Symphyotrichum laeve* (smooth blue aster)



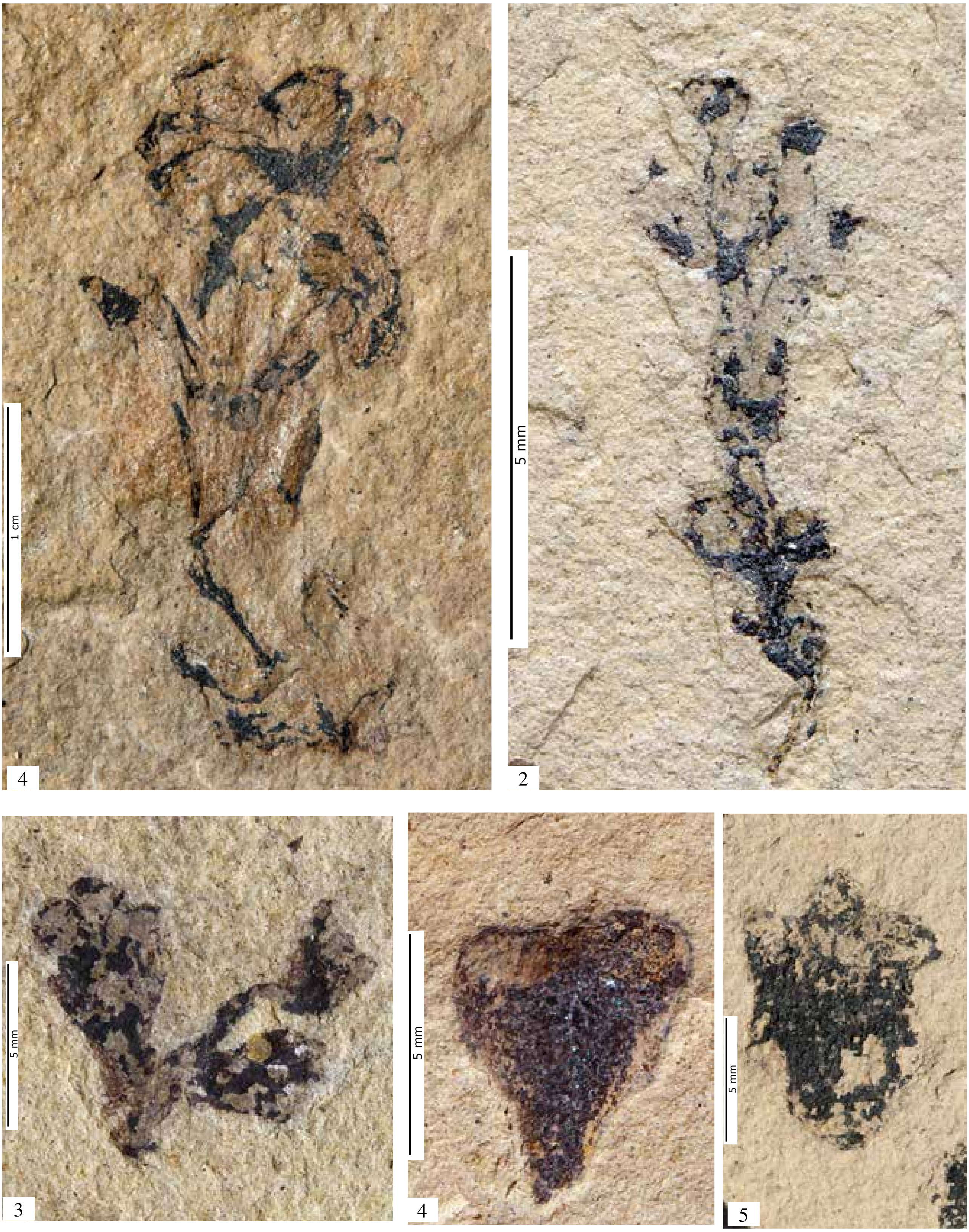
Zalesskya multipla. **Multiple-petaled flowers**

1. Multi-petaled flower, lateral view (Holotype CHEK 72, Chekarda); 2. Other specimen, lateral view (MAT 503); 3. Flower with an outer and inner circle (MAT 357, Paratype); 4. Fossilised flower, bottom view (MAT 194). All Matvèevo, Coll. Michael Wachtler, Dolomythos-Museum, Innichen, Italy



Caputosperma geraschi

1. Plant with attached blossom and lanceolate-linear leaves with smooth edges and rounded tip (CHEK 68, holotype); 2. Detail of fructification, with one spikelet-floret shed; 3–5. Different parachutes from the holotype, about 5 mm long and hold a pinhead-sized seed (Chekarda, Coll. Gerasch, Dolomythos-Museum, Italy. Counterplate Coll. Gerasch, Thomaseum, Langenaltheim, Germany)



Caputosperma perneri

1. Flower bud (Paratype MAT 44, 22 mm long); 2. Juvenile plant with roots and aggregated flower heads (holotype MAT 578, 18 mm length); 3. Aggregated flower heads (MAT 531, 8 mm length); 4. Flower head. Note the small-sized parachutes on the left side (MAT 638, 7 mm length); 5. Single clustered flower head, (MAT 360, 7 mm length). All Matvèevo, Coll. Wachtler, Dolomythos-Museum, Innichen, Italy

Early Permian Asteraceae

Left: *Asteroforma nicolaswachtleri,* a blossom (holotype CHEK 65) and a naked receptacle with hanging petals (MAT 353); **right:** *Zalesskya multipla,* a multi-petaled flower ((MAT 357) and the lateral view (holotype CHEK 72). The air is filled with several parachutes (holotype CHEK 76, CHEK 356) of *Pappusperma ventilata,* belonging to some Asteraceae ancestor. On the left is visible the stonefly *Palaeomantis aestiva.*

could be compared with today's *Leontopodium* (the Edelweiss), *Achyrocline* or *Achillea*, all belonging to the Asterales. Probably five petals are identifiable in the juvenile specimen, and the disk flower produced infinite parachutes during maturity, as can be observed on the fossilised slabs.

Caputosperma is frequently found in Chekarda and Matvèevo, and it also supports the theory of the interesting Early Carboniferous-Permian origin of the angiosperms. However, the enigma surrounding the evolution of the wind-dispersed small parachutes of the various Early Permian Asterales can be connected with other fructifications like the drupes, samaras, acorns or racemes of other fossilised flowering plants in the Permian Fore-Urals.

Some fossilised fructifications, especially from Chekarda, can be found only in finest-grained sediments. They resemble individual parachute or pappus. Each achene has an umbrella-like crown of plumose hairs and must have literally been carried into the atmosphere by strong ascending air currents. That ***Pappusperma ventilata*** represent an Early Permian pappus is not a far-fetched idea, since in Matvèevo and Chekarda, potential Asteraceae-ancestors like *Naugolnykhia matvéevoi, Asteroforma nicolaswachtleri, Caputosperma geraschi, Wachtlerosperma stefanperneri* or *Zalesskya multipla* can be found. Regarding *Caputosperma geraschi*, it is certain that its pappus is a long, single hair with a pinhead-sized seed attached basically. It is probable that the aforementioned parachutes belong to different Asteraceae genera or species.

The evolution purpose of these hair-like, fragile parachutes was to become airborne and be blown with the slightest breeze and cross valleys and slopes. In that, they all resemble extant members of the Asterales. That they were not discovered or described before can be attributed to their inconspicuousness and their need to be preserved only in finest mud.

Pappusperma ventilata

1. Individual parachute with umbrella-like plumose crown, apically ending in a barb (holotype CHEK 76); 2. Lateral view of a pappus with long hairs (CHEK 324); 3. Parachute with finest hairs, spreading from every side, (CHEK 356); All Chekarda, Coll. Wachtler, Dolomythos Museum.

Parachutes of *Taraxacum officinale* and a pappus of *Saussurea alpina*; one single achene is fixed with a peduncle on the apical part of a barb-like parachute.

The Evolution of Magnoliaceae in the Early Permian

The Magnoliaceae played an important role in the evolution of angiosperms. New recoveries from the Russian Fore-Urals in the Early Permian (Kungurian) forming an isolated continent called Angara evidence that we have to search the origin of the Magnolias and other tribes of angiosperms on the Carboniferous-Permian border. Among all the proposed ancestors, *Geraschia wachtleri* matches the concept of a real Magnolia from the flower till the floral buds or cone-like aggregates more than the others. Also, supposed flower buds and multiple fruits were recovered in association. The fact that they were found together with a plethora of insect families emphasizes a symbiosis between animals and plants, regarded commonly as prerequisite for the evolution of flowering plants.

Along with *Geraschia*, we find not only the ancestors of samara-, acorn- and drupe-bearing plants but also presumed members of the Rosaceae and the Asteraceae family.

In that, these early Magnoliaceae cannot be regarded as more primitive than other angiosperms, but it can be established that almost all of today's plant tribes, including

Geraschia wachtleri. Magnolia-ancestor

Complete flower with he well-preserved insect, *Tillyardembia antennaeplana*, a plecoptera (stonefly), Dolomythos-specimen; (Holotype CHEK 05, Chekarda, Coll. Gerasch, Dolomythos-Museum); Reconstruction

***Geraschia wachtleri.* Early-Middle Permian Magnolia**

Left: a juvenile flower bud (MAT 406); **middle**: a whole flower with open stamens (CHEK 05); **right:** two cones (MAT 355 and CHEK 214); some *Tillyardembia antennaeplana* insects are seen flying above the flowers.

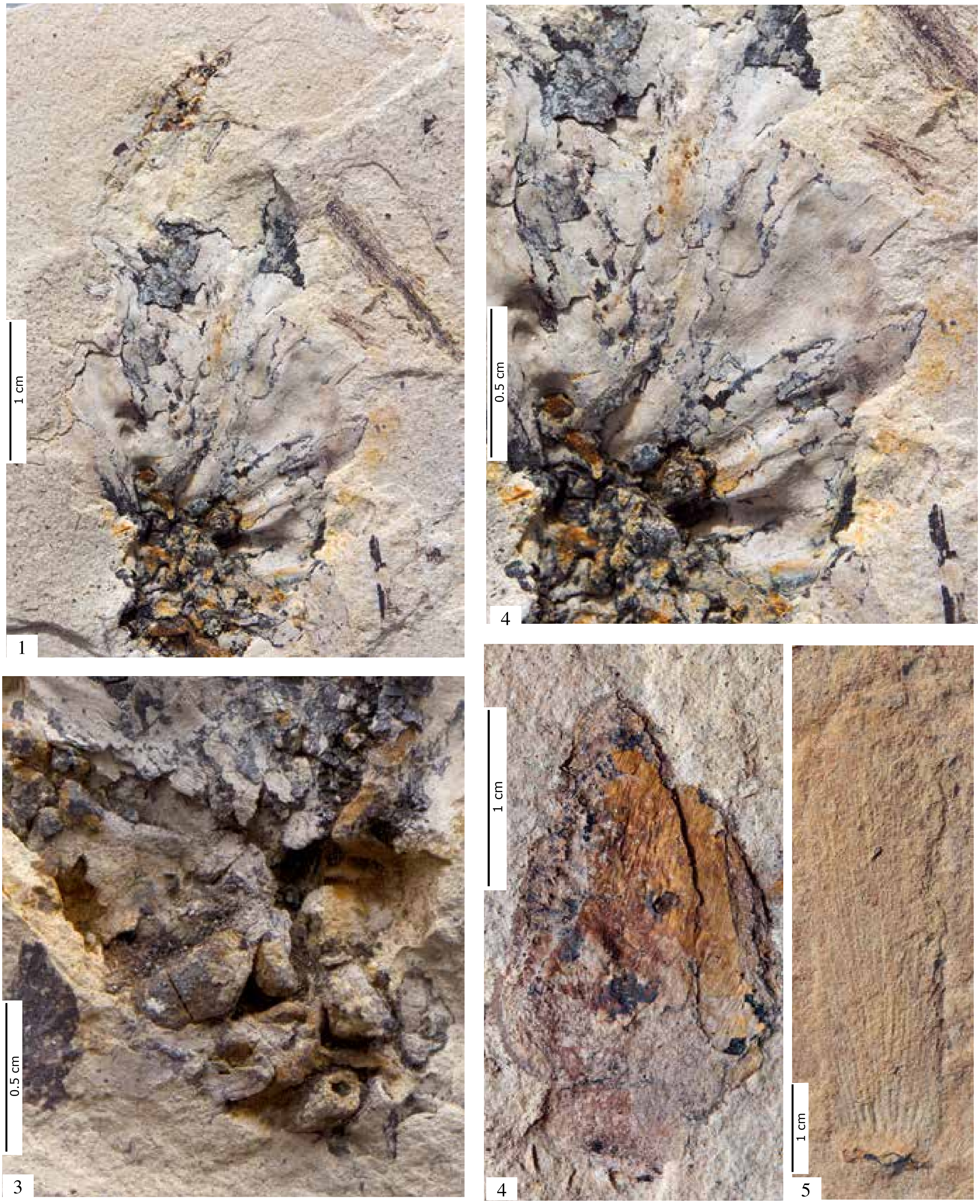
the angiosperms had their evolution stage just between Devonian and Early Permian. The Artinskian-Kungurian localities from the Fore-Urals are rich in flower-like fossils and multiple-fruit-fructifications, and they are additionally distinguished from other Euramerican Permian localities by their richness in insects. The reason behind this abundance of Proto-Angiosperms are not entirely resolved yet, but it can be attributed to the simple fact that we cannot accept millions of years' gap between the Early Permian and the presumed origin of the angiosperms in the Cretaceous.

The first Magnoliaceae

The discovery of Early Permian *Geraschia wachtleri*, a flower with an accompanying insect on the same slab, from Chekarda by Thomas Gerasch can be regarded as the "century's finding". Connected fossil plant-insect interactions are rare; beautiful preservations are even more so. So, if fortunate fossilisation conditions allow a broken part of the flower to provide an insight into the blueprint of the carpels and stamens, then this can be regarded as a "lucky punch". The fossilised flower is interesting not only because of the enveloping tepals but also for the basal opening or damage by sedimentation when some of the fertile inner parts were exposed. The tubiform channels have resemblances with the stamens, sprouting from the lower part of today's Magnolias.

The flower consists of distinct whorls of fruit-leaves and surrounds an inner part of reproductive organs that can be interpreted as stamens and carpels. The cone-like fruits originate from a short stem and contain multiple seeds. The complete flower of the holotype is 37 mm long and 30 mm wide, with a fair amount of tepals in whorls that are spirally attached to the main base. The single obovate tepals are 15–20 mm long and 5–10 mm wide. Numerous tubiform spirally arranged stamens at the base of a cone-like structure are visible due to a broken opening by the fossilisation.

Although mutual plant-insect sedimentation can mean all or nothing, it is nevertheless a valuable source of a symbiosis, as it happens today in many angiosperm families. So why was it different nearly 300 million years ago?



***Geraschia wachtleri.* Magnolia-flower Kungurian, Early-Middle Permian**

1–2. Flower with the broken basal part evidencing the interior blueprint of the plant and detail of the various tepals (CHEK 05, holotype, Thomaseum-specimen); 3. Detail of the exposed numerous adnate carpels on the basal part (CHEK 05, Coll. Gerasch, Dolomythos-Museum); 4. More evolved flower bud (MAT 406); 5. Suggested flower leaf (CHEK 129, 5 cm); MAT = Matvèevo, CHEK = Chekarda; Kungurian.

Geraschia wachtleri. **Magnolia-flower Kungurian, Early-Middle Permian. Cones and leaves**

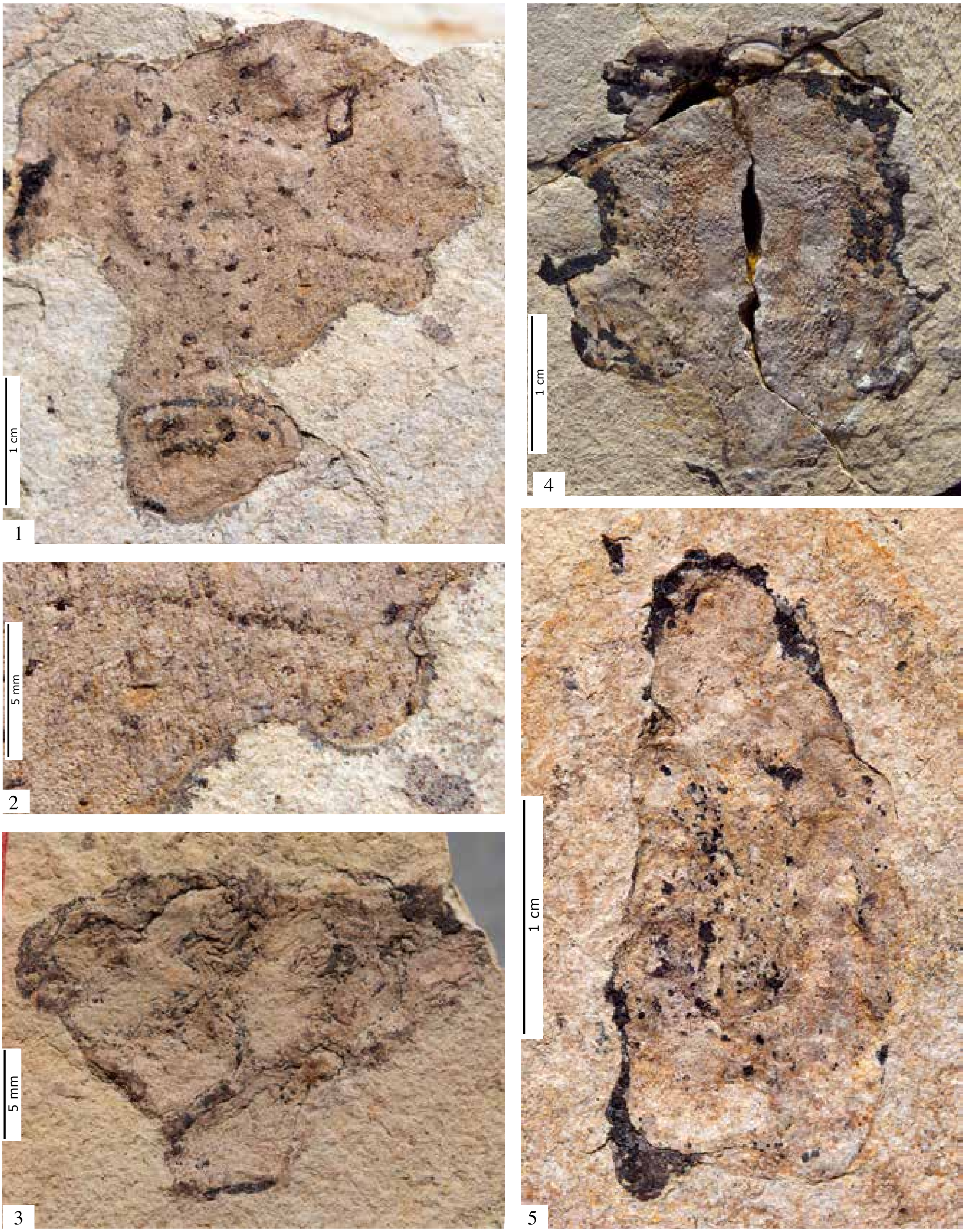
1. Multiple fruits in an early stage of growth, (CHEK 311, Coll. Perner); 2. Flower bud (CHEK 205); 3. Twig (CHEK 105, Chekarda); 4. Leaves (MAT 648, Matvèevo); Kungurian, Coll. Wachtler, Dolomythos-Museum, Italy

Magnolias today

1. Flower bud of *Magnolia liliiflora*; 2–3. *Magnolia grandiflora,* cone with the tepals detached and detail of the stamens (below) and the carpels (upper part)

Today Magnoliaceae - Foliage and flowers

1–2. Single leaf and wilted flowers of *Magnolia grandiflora*; 3. Leaves of *Magnolia virginiana*



Uralofructa magnoliformae. **(Kungurian) cones**

1–2. Multiple fruit with detail of one single seed (Holotyp MAT 355); 3–4. Cones with several seeds (MAT 364 and CHEK 214); 5. Mature cone with some isolated seeds (MAT 679). Kungurian (Coll. Wachtler, Dolomythos-Museum)

The wonderful mimicry between insects and flowering plants

The symbiosis between flowering plants and insects was one of the biggest evolution steps in Earth.

Who is able to distinct on a *Matveeva perneri* leaf the insect *Marimerobius sukatchevae*? On the panicle of *Wachtlerosperma stefanperneri* the true fly *Karpinskptera pohli?* On *Peremopteris biarmicum* a *Palaeomantis aestiva*? On a flower of *Tsvetokia* the scorpionfly *Agetopanorpa punctata?* On *Geraschia wachtleri* the stonefly *Tillyardembia antennaeplana?*

One of the most complex problems in palaeobotany is a fait accompli that the various parts of a plant can only seldom be found in direct connection, such as leaves with the fruits or cones, or even flowers with their fruits. Therefore, it is important to accurately search through stratigraphically coherent lenses or layers till enough material for fairly reliable statistics is gained. In this case, we tried to combine all the parts of the thought Early Permian Magnoliaceae *Geraschia wachtleri*, with the risk of possible misinterpretation. Science must find solutions and not create confusion!

Also, the immature, as well as the mature cones have many resemblances with today's Magnolias.

Suggested reproductive organs are cone-like, sitting on a stout peduncle. They consist of densely settled multiple fruits and are elongated or ovoid. They were described as *Uralofructa magnoliformae* representing multiple partially-decomposed fruits. On some bracts, rounded or elongated seeds of about 5 mm diameter are found attached. The outside from the follicles hanging rounded seeds have no differences with the extant ones. Suggested leaves are shortly petiolate, broadly ovate; margins are unlobed or slightly lobed and apices are acute or rounded.

The further evolution of the Magnoliaceae

Today the family of the Magnoliaceae includes about 210 species divided between the genera, *Magnolia* and *Yuvalia*. They have a classic disjunct distribution with the centre in east and southeast Asia and a secondary agglomeration in Eastern North America, Central America, the West Indies and some species in South America. Although having a global distribution extending into the temperate zones of both hemispheres, most of their diversity flourishes in tropic to subtropic areas.

Magnolia flowers do not have true petals and sepals but are composed of petal-like tepals. The flowers grow at the end of the tree's branches. They are composed of numerous spirally arranged stamens at the base of a cone-like receptacle where they do not produce true nectar, rather a large quantity of pollen grains. On the upper part, they give rise to a fair amount of spirally arranged carpels. At maturity, the carpels develop into a

Magnolia cones

1–4. Diverse growth stages and seed development of *Magnolia virginiana;* 5–6. Adult cones of *Magnolia grandiflora* (the last one has been cut in the middle)

Early Permian aggregated fruits

A landscape of the former Angara continent with some aggregated fruits; on the **upper side** from **left to right** – *Sylvafructa aggregata,* a red *Permofructa multipla* and *Matvèevofructa bardaensis.* On the **lower side** sprout some *Uralofructa magnoliformae*, supposed cones of a Magnoliaceae progenitor.

woody, cone-like aggregate containing the seeds. The fruit flesh then splits open, exposing the individual seeds covered by a fleshy aril.

Another resembling plant family is *Liriodendron.* The flower is similar, the fruit is also cone-like, but it produces winged samaras.

As known till date, the Magnoliaceae appear in the macrofossil record about 100 million years ago. Often, therefore, they are regarded as the most primitive angiosperms that give valuable indications regarding the origin and evolution of flowering plants.

Another multifollicular angiosperm fruit from the Middle Cretaceous (Albian-Cenomanian) of Kansas is represented by *Archaeanthus*. Clusters of samaras (other interpretation) follicles were borne terminally at the apex of a stout branch. *Archaeanthus linnenbergeri* was connected with *Liriophyllum kansense* leaves. Hence, it can be stated that Middle Cretaceous *Archaeanthus*-samaras and *Liriophyllum*-leaves have striking resemblances with today's *Liriodendron tulipifera*, and a gap of about 100 million years in the fossil record of angiosperms can be filled. One unresolved question is how closely are samara-bearing *Liliodendron* and follicle-holding *Magnolia* parented?

From the Cretaceous till the Permian, we have effectively filled a gap in the angiospermian and magnolian fossil record of about 160 million years. Causes for the above can be the Permo-Triassic crisis, a continental drift causing a change from temperate forests to a tropical vegetation or even difficulty for plants to migrate over long distances due to huge mountain ranges, uniform climates over long periods and the missing of good seed-disperses like the birds.

Multiple angiospermous fruits

In today's plant kingdom, most fruits are simple and develop from a single carpel or a compound ovary. However, some fruits with robust seed coats and kept together by a peel or by forming a follicetum are recorded.

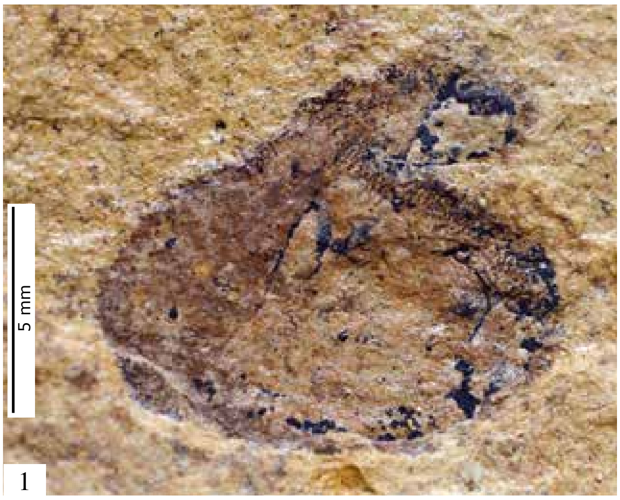
***Permofructa multipla*. Early-Middle Permian**

1. Fruit with an apical depression, evidencing many seeds on the basal part (Holotype MAT 365); 2-3 Aggregated fruits (MAT 573, CHEK 189); Coll. Wachtler, Dolomythos Museum, Italy.

We encounter multiple or aggregated inflorescences that have all the conditions to coalesce together, forming an aggregate fruit after maturation. These types of fruits today are classified as clusters of several separate carpels of one single, apocarpous gynoecium like the raspberries, where each unit is a single carpel.
However, they can also represent multiple fruits originating from separate flowers and representing inflorescence. These two multi-ovary fruit types can appear nearly identical in form; raspberry (*Rubus idaeus*) is an example of an aggregate of drupes where the single fruitlets are crowded pressing against one another on a raised thalamus. It resembles mostly the multiple fruit mulberry, but the differences between the two are considerable. Compound fruits are found today, especially in the Annonaceae (Soursop family), which are heart-shaped, holding many round protuberances. In the strawberries (*Fragaria*), the minute achenes are buried as small specks on a fleshy edible thalamus.

Other examples of aggregate follicles are the Magnoliaceae. When the flower matures, the thalamus elongates so that the aggregate fruit looks like a bunch of fruits.
In the Early Permian (Kungurian) regions of the Fore-Urals (Russia), a fair amount of different and novel multiple angiospermous fruits were recovered: *Matvèevofructa bardaensis, Permofructa multipla, Sylvafructa aggregata* or *Uralofructa magnoliformae*. All of them can be considered aggregate fruits or follicetum enveloping several hardened seeds. Some of them can be correlated with today's composite fruitlets that show a clustered character, some others have many similarities with extant Magnolias, and for the remaining, comparisons are difficult.

Matvèevofructa bardaensis is characterized by mainly rounded fruits connected with a short stalk to the tree. From the outer appearance, it is not clear if it can considered a mature syconium that contains numerous one-seeded druplets as in today's figs (ficus) or *Cornus kousa,* or it is a seed covered by an aril, similar to the recent cherries, almonds or plums.
Permofructa multipla represents a fructification with a hollow depression on the upper part. The fruit contains many seeds. It seems that the fruitlets separate from the central core when dropped off, leaving the hollow depression at the base.
Sylvafructa aggregata has a thin but tough skin that covers the fruit, allowing it to shine through quite a number of hard, smooth and rounded seeds. The individual seeds are circular and reach a size of 0.2 cms.
Difficult is the interpretation for *Sylvafructa aggregata* and *Permofructa multipla*. Although some are tempted to think, upon superficial examination of a strawberry fruit, this is probably to exclude due to delicateness of their pulp. The source of these fruits must be a robust seed and a preservation capable involucrum, such as the chambered seed head of extant lotus, loculicidal capsules from the Celastraceae (*Euonymus*) or the capsule from *Silene latifolia* resembling in some aspects *Sylvafructa aggregata*.
Uralofructa magnoliformae are multiple fruits that originate from a stout peduncle. The rounded seeds are distributed on the outer side of the bracts. The name comes due to their similarity with the cones of Magnolia. The reproductive organs are cone-like, sitting on a stout peduncle, consisting of densely settled multiple fruits and are elongated or ovoid. Some cones can also be a result of aborted floral shoots released into the soil after or during the blooming period. Other fossilised cones probably represent partially decomposed multiple fruits. Also, they usually have a stout peduncle. Each segmented bract is rectangular to polygonal. On some bracts, several rounded till elongated seeds of about 5 mm diameter are attached.



Matvèevofructa bardaensis. **Kungurian**

1. Fruit attached on a stipe (Designed holotype MAT 43);
2. Fruit (MAT 383); All Matvèevo, Coll. Wachtler

***Sylvafructa aggregata.* Kungurian, Early-Middle Permian**

1. Fruit evidencing the seeds (Holotype MAT 345, Matvèevo); 2. Fruit (CHEK 26) Chekarda, Coll. Wachtler; 3. Oval fruit composed of many seeds (MAT 577); 4. Fruit (MAT 589); Matvèevo and Chekarda, Coll. Wachtler, Dolomythos-Museum, Innichen, Italy.

Early Permian ancestors of the Phytolaccaceae

One of the common flora elements of the Early Permian (Kungurian) Fore-Urals (Russia), especially the localities of Cherkarda and Matvèevo, consist of flowers, inflorescences, racemes, fruits and seeds that can be distinguished in most cases due to some of their characteristic features. The fossilised parts of the plant have many similarities with extant Phytolaccaceae, known as pokeweeds, an herbaceous perennial shrub. Probably *Sylvocarpus armatus* can be accepted as their crown ancestor.

In 2008, the Russian palaeobotanist, Serge V. Naugolnykh, described new "peltate seed-bearing capsules" consisting of umbrella-shaped shields with absent radial ribs on the capsule surface, naming the fruits *Sylvocarpus armatus*. Effectively these circular flowers/fruits represent a common flora element of the Kungurian sediments from Matvèevo and Chekarda and therefore, flowers, racemes and berry fruits through different growing stages have been recorded. In Matvèevo especially, springtime inflorescences predominate racemes and flowers of *Sylvocarpus armatus*; in Chekarda, more mature berries, fruits or seeds can be found. Although the leaves are not known with certainty, and therefore, the appearance of the whole plant is speculative, just their fertile parts can be regarded as sensational for its different growing stages. Also, sometimes the recovered stamina and ovaries give valuable clues about the flora evolution in the Early Permian.

Sylvocarpus armatus can be regarded as one of the most interesting plants of the Early Permian Fore-Urals. That *Sylvocarpus*

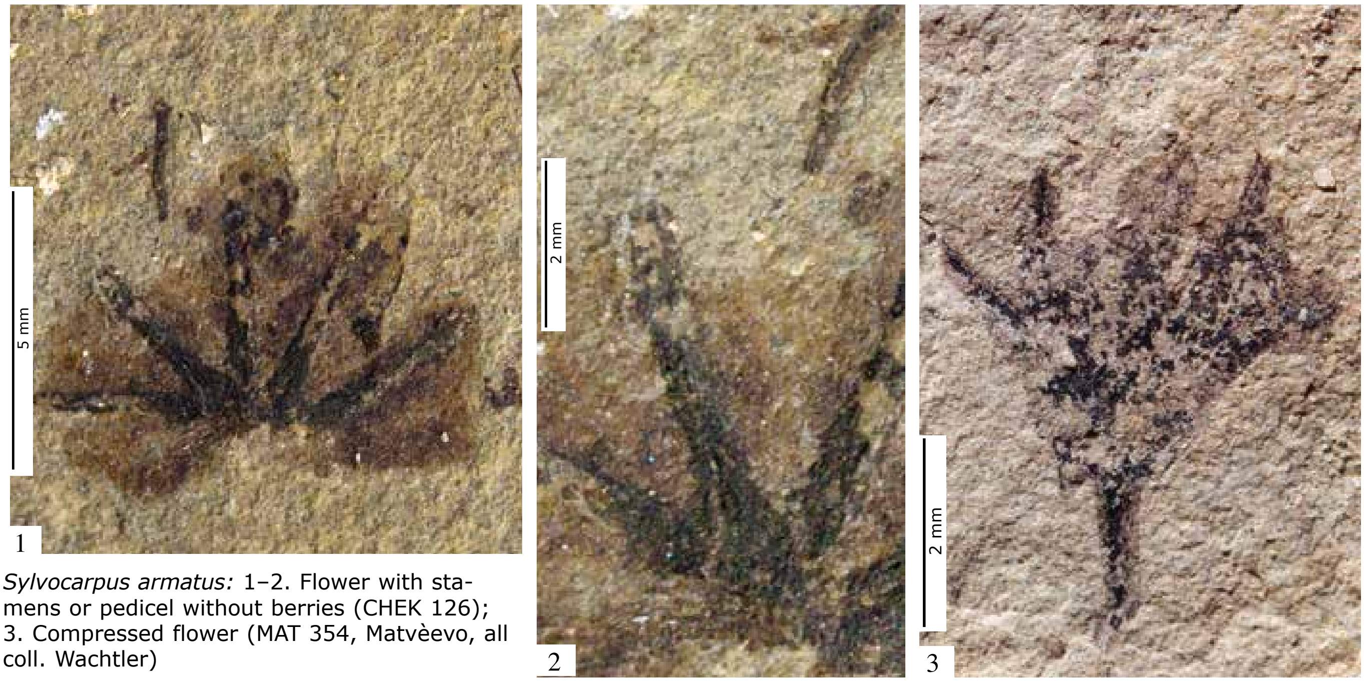
Early Permian landscape with flowers, berries and racemes of *Sylvocarpus armatus*

Left: a complete raceme; **middle and right** are visible isolated berries with the shadows of the seeds inside; **middle**: an insect, *Delopterum rasnitsyni*, searching for food; **right:** the insect, *Agetopanorpa punctata*, can be seen.

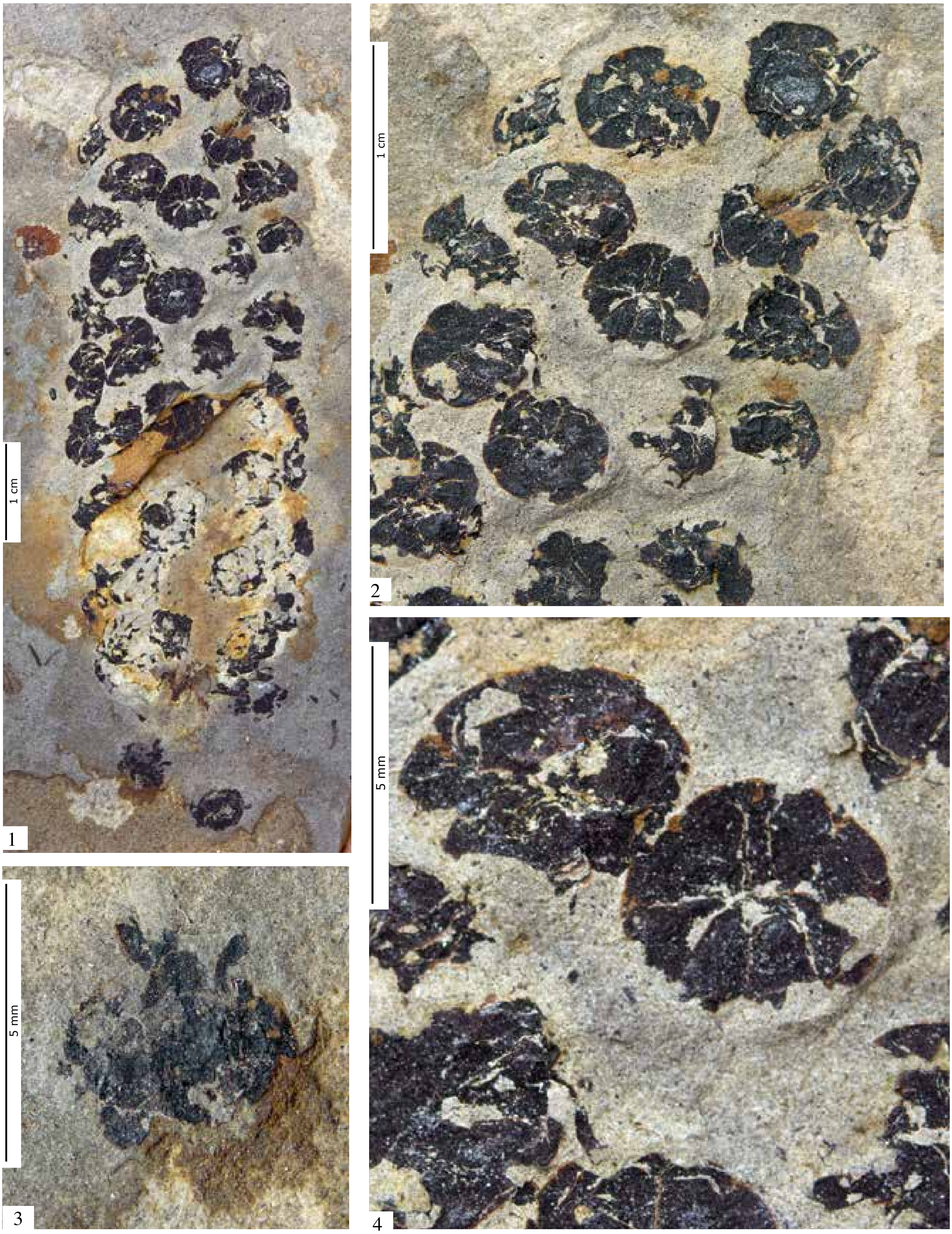
armatus forms a raceme, meaning an unbranched inflorescence holding pedicellate flowers and does not correspond to a spike bearing sessile flowers or a panicle with its multi-branched inflorescences is obvious. From the outer appearance, racemes of *Sylvocarpus armatus* have many similarities with extant *Phytolacca*.

The crown-group of the Phytolaccaceae

Sylvocarpus armatus represents an agglomeration of individual circular flowers/ fruits to form an inflorescence which changes to a raceme after maturation. The developing berries covered by a fleshy aril hold a fair amount of small elongated seeds inside.
A completely preserved raceme is about 70 mm long and 35 mm wide and consists of an aggregation of about 70–100 individual flowers/fruits. Each one is circular and slightly segmented and has a diameter of about 5 mm. Stamen and pistil are preserved on some flowers. The seeds or berries – usually 7–8 in number – are circular and have a diameter between 6 mm and 8 mm. A smooth berry peel coats the inner fleshy pulp, and the elliptic to elongated seeds of about 1 mm diameter are inserted on the outer margin. The foliage definitely remains unknown till date, but probably short petiolate leaves can belong to *Sylvocarpus armatus*. They are oblong, entire on the margin, tapering slightly apically and have a reticulate venation, typically for the Early-Permian locations of the Fore-Urals.
Among the existing angiosperms, the family of *Phytolacca*, also known as pokeweed – herbaceous perennial and robust, non-woody shrubs – have major similarities with Early Permian *Sylvocarpus armatus*.
Pokeweeds are native to Eastern North America, the Midwest and the Gulf Coast, but they are also naturalised in parts of Europe and Asia, comprising about 65 species in 18 genera. The entire leaves alternate on the stem and are elongated. The flowers develop in racemose clusters. Each blossom is radially symmetric, equipped with usually five sepals and no petals. The number of stamens fluctuate between five and 30 and are inserted in one or several whorls. Also, the number of carpels vary from five to 16. They are united on the base (or free) and inserted in a ring. Each encloses a single anatropous ovule. The flowers are self-fertile.
In autumn, the racemes hang from the plant showing soft berries that are round and equipped with a flat indented top and bottom. Pedicels with the berries released have a distinctive and rounded five-part calyx.
Pokeweeds reproduce only by their glossy and lens-shaped seeds, contained in a

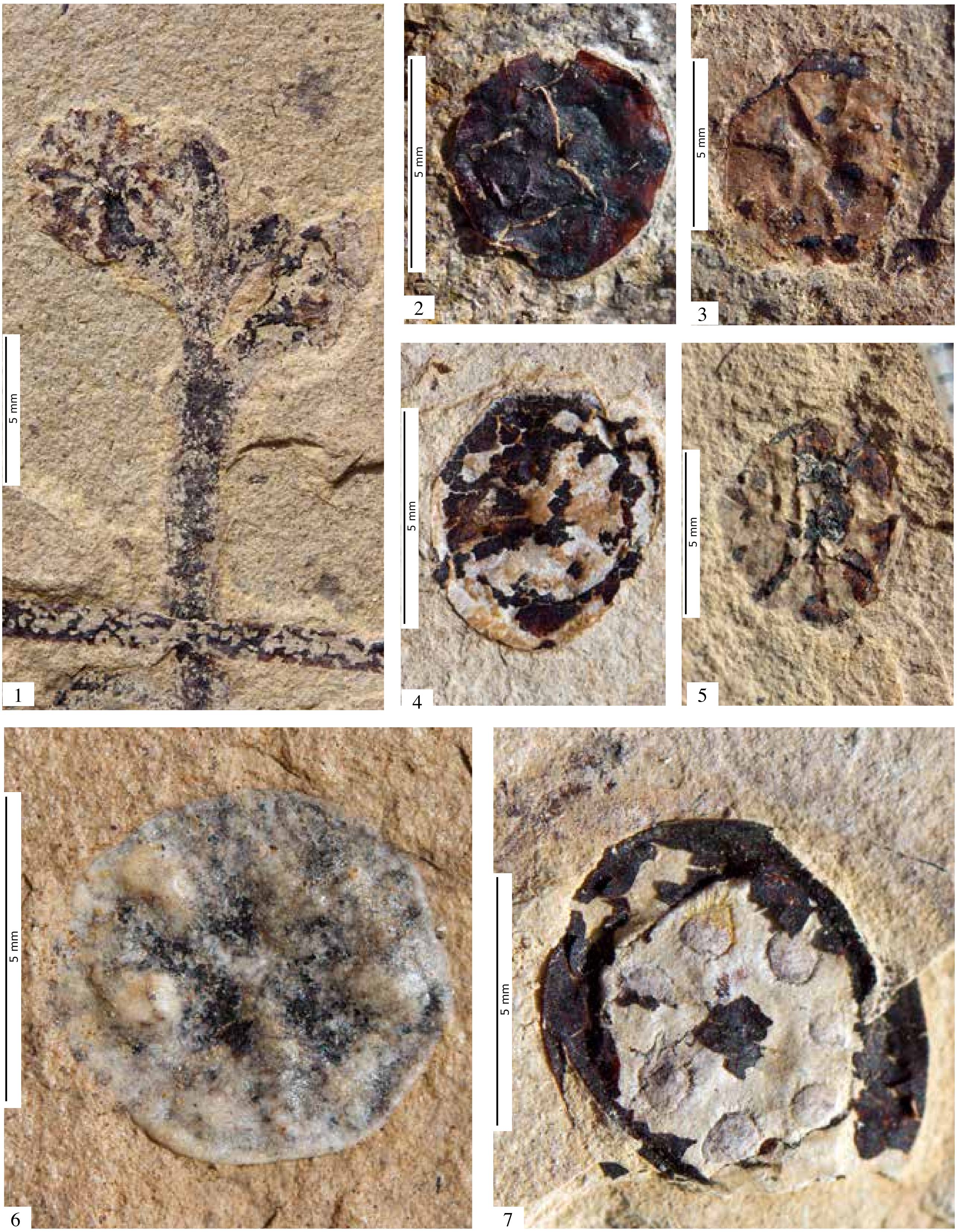


Sylvocarpus armatus: 1–2. Flower with stamens or pedicel without berries (CHEK 126); 3. Compressed flower (MAT 354, Matvèevo, all coll. Wachtler)



***Sylvocarpus armatus,* (Kungurian, Early-Middle Permian)**

1. Complete raceme; 2. Upper part of the inflorescence; 3. Isolated flower from the basal part with pollen anthers and supposed stigma; 4. Detail of closed berries; MAT 104 (Matvèevo, Lyswa, Coll. Gerasch, Thomaseum, Langenaltheim)



Sylvocarpus armatus, (Kungurian, Early-Middle Permian)

1. Part of a raceme/inflorescence (MAT 719, Coll. Gerasch); 2. Isolated berry (MAT 590); 3–5. Developing fruits (MAT 663, MAT 670 and MAT 532); 6. Fruit berry coating some seeds (MAT 635); All Matvèevo, Lyswa, 7. Fruit berry with seven exposed seeds; CHEK 334, (Chekarda; All Coll. Wachtler, Museum Dolomythos, Innichen, Italy)

***Sylvocarpus armatus.* Suggested leaves**
1. Twig (CHEK 81); 2. Single leaf (CHEK 121); (Chekarda; All Coll. Wachtler, Museum Dolomythos, Innichen, Italy)

fleshy, celled berry. A plant can, in that way, produce 1,500 to 7,000 seeds annually. The seeds have an extraordinary long viability and can remain fertile in the soil for up to 50 years. After the germination follows a rapid growth.
Phytolacca-like fossil has been described from the Upper Cretaceous Cerro del Pueblo Formation, Coahuila, Mexico as *Coahuilacarpon phytolaccoides.* Multiple infructescences composed of berries with six locules, each containing a single seed, were recorded. The embryo developed in a curved ovule with pendulous placentation, a berry anatomy that is similar to that of the genus *Phytolacca*. Other Phytolaccaceae are also known from the Pleistocene.
Though plants with multiple-flowers and fruits forming racemes are common in the extant flora kingdom, such as the *Sorbus* (rowan berry), *Hippocastanus* (chestnut), also the Piperales, among all of them, the Phytolaccaceae are most similar to *Sylvocarpus armatus.* These also due the fact that similar berries are mostly known from the Phytolaccaceae.

Interesting but unresolved is the question whether other plants from Early Permian are parented with *Sylvocarpus armatus*, although certainly not samara evolving plants and not those forming parachutes either. Also, the development of the stone fruits must have occurred in another way. As of now, it can be stated that in the Early Permian Russia/Siberia, racemes with multiple flowers had fully evolved, and these concern not only *Sylvocarpus armatus* but also other Protoangiospermous plants. They were hermaphroditic and developed berries containing multiple seeds. Therefore, *Sylvocarpus armatus* has its origin just between the Devonian till the Carboniferous, as many other plants in the former Angaraland.

Sylvocarpus armatus. **Kungurian, Early-Middle Permian) reconstructions**

a. Part of a raceme/inflorescence (MAT 104, holotype); b. Flower with anthers (MAT 104); c. Single anther; d. Maturing berry (MAT 719); e. Raceme with berry partially lost (CHEK 126); f. Fruit berry with seven exposed seeds (CHEK 334) g. Single leaf; h. Twig (CHEK 81)

Phytolacca recent

1. *Phytolacca acinosa*, (Indian Poke) flowers; 2. Raceme and fruits; 3. Mature flower with fused carpels and wilted anthers; 4. Detailed view of a mature berry.

5. Pedicels without berries have a distinctive and rounded five-part calyx; 6. Squeezed berry; 7. Dried berry showing 7–8 seeds; 8. Leaf

The ancestors of the Apiaceae

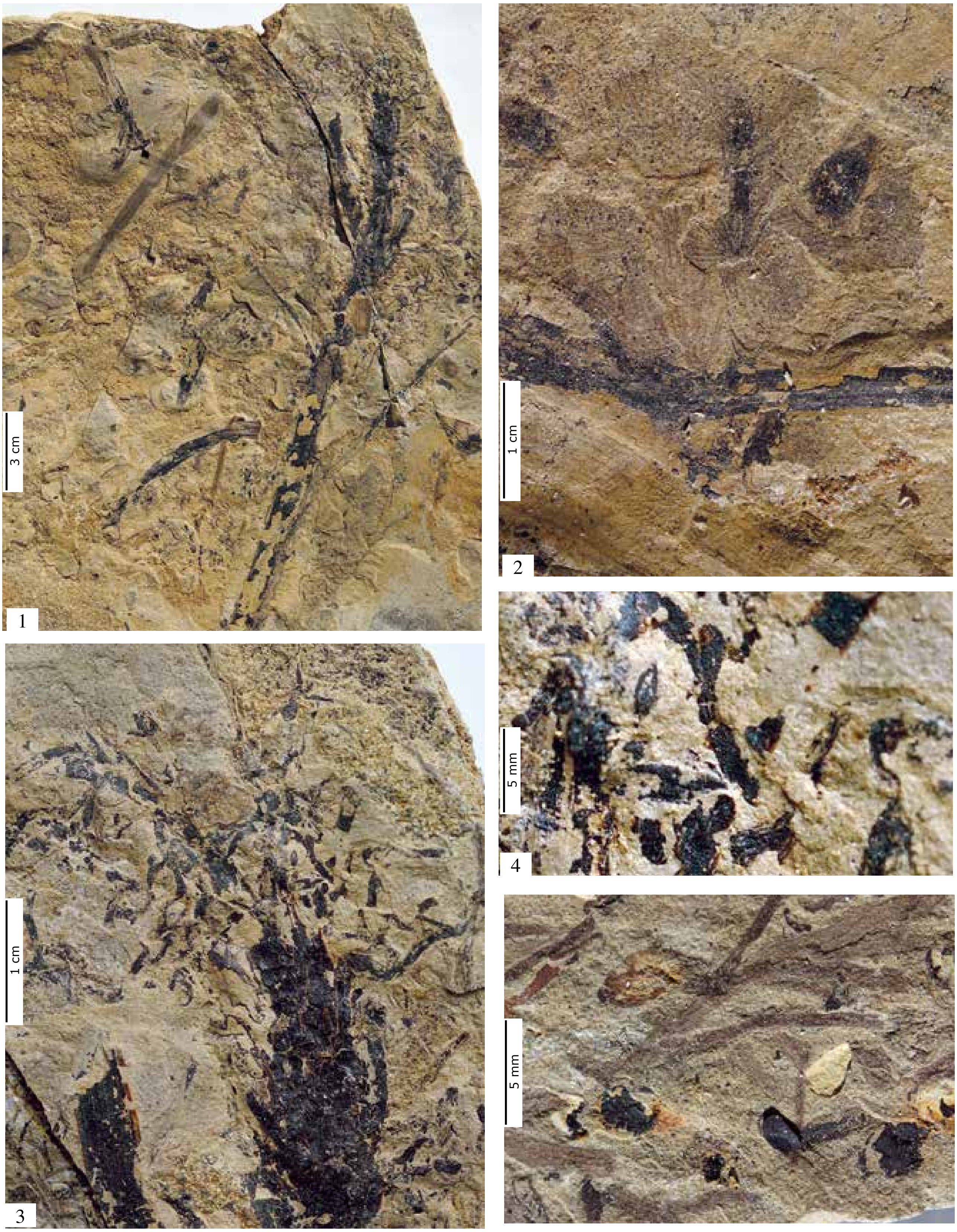
The Early Permian (Kungurian) localities of the Russian Fore-Urals, especially the area around Cherkarda and Matvèevo, are characterised by their richness in broad-leaved plants. In the background, the undergrowth is found covered by low-growing shrubs, creepers and grasses. From one side, they might not have been attractive enough to capture the attention of the fossil-collectors and, therefore, they were overlooked for decades.

Dammannia scaratiae represents probably the oldest known ancestor of the angiosperm family of Apiaceae. Fortunately, they can – due to their small size – be recovered in a complete form. The plant, a low-growing shrub, has an erect stalk and apically forking branchlets with small seeds and the pedicels. The leaves are attached to the basal part of the forking secondary branchlets. The apical part of the plant consists of several umbels that hold small seeds. The leaves are pinnately dissected or lobed, entire to serrate, with pinnate to palmate venation. Numerous pedicel sprout from the apical parts of the erect stalks. They can be interpreted as main umbels, further divided into several secondary umbelets. The fruits/seeds are small, sometimes slightly winged and elongated and 1 mm long.

Among all the existing families, especially the Apiaceae (Umbelliferae), herbaceous plants appearing usually as creepers or tree-like shrubs have some characteristics with this plant. In today's Apiaceae, numerous flowers are grouped together in an umbrella-shaped flower head known as a compound umbel.

About 3000 members of this family found all over the world, mainly in the temperate regions and rarely in tropical areas, include

Early Permian landscape from Angaraland with *Dammannia scaratiae,* probably the oldest known representative of the angiosperm family Apiaceae.



***Dammannia scaratiae*.(Kungurian, Early-Middle Permian)**

1. Mostly entire plant; 2. Attached leaf; 3. Apical part of the plant evidencing several secondary umbelets with seeds; 4. Detail of the small and elongated seeds (All CHEK 252); 5. Seeds (CHEK 218), Chekarda, Kungurian, Coll. Dammann.

5

some well-known vegetables and herbs, such as the carrots, celery, fennel, coriander and angelica. Some are weeds of hedgerows and woodland (cow parsley and hogweed), and some are grown as ornamental garden plants (*Eryngium, Astrantia* and *Aciphylla*). The Apiaceae are characterised by hollow stems, alternate leaves, often deeply dissected or lobed, entire to serrate, with pinnate to palmate venation. The flowers are small and simple, with five petals aggregated in umbels. The fruits and seeds vary considerably within the group, having small schizocarps connected by an artition, sometimes elongated or spiny seeds. They remain paired until maturity and then fall up apart.

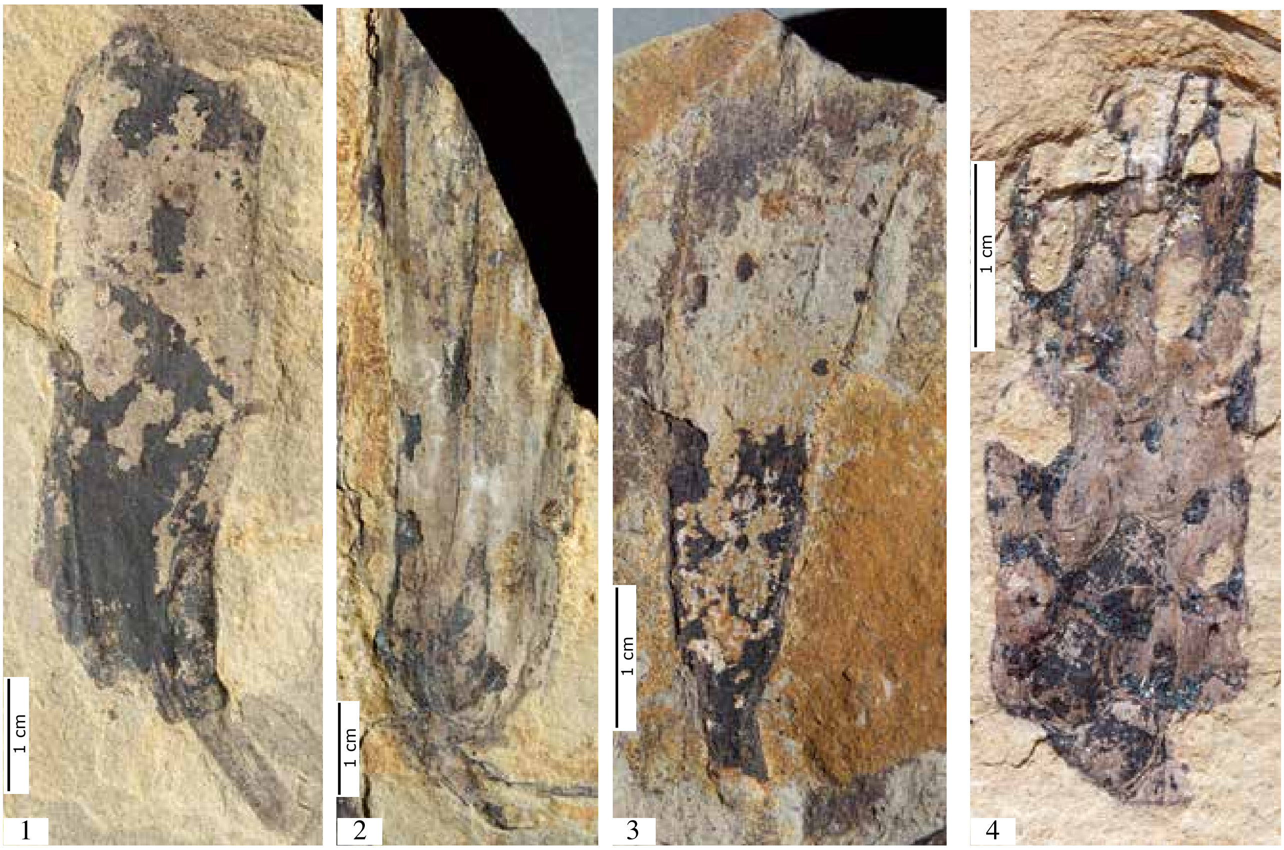
Extant *Ferula songorica* belonging to the Apiaceae

Early Permian begin of the Leguminaceae

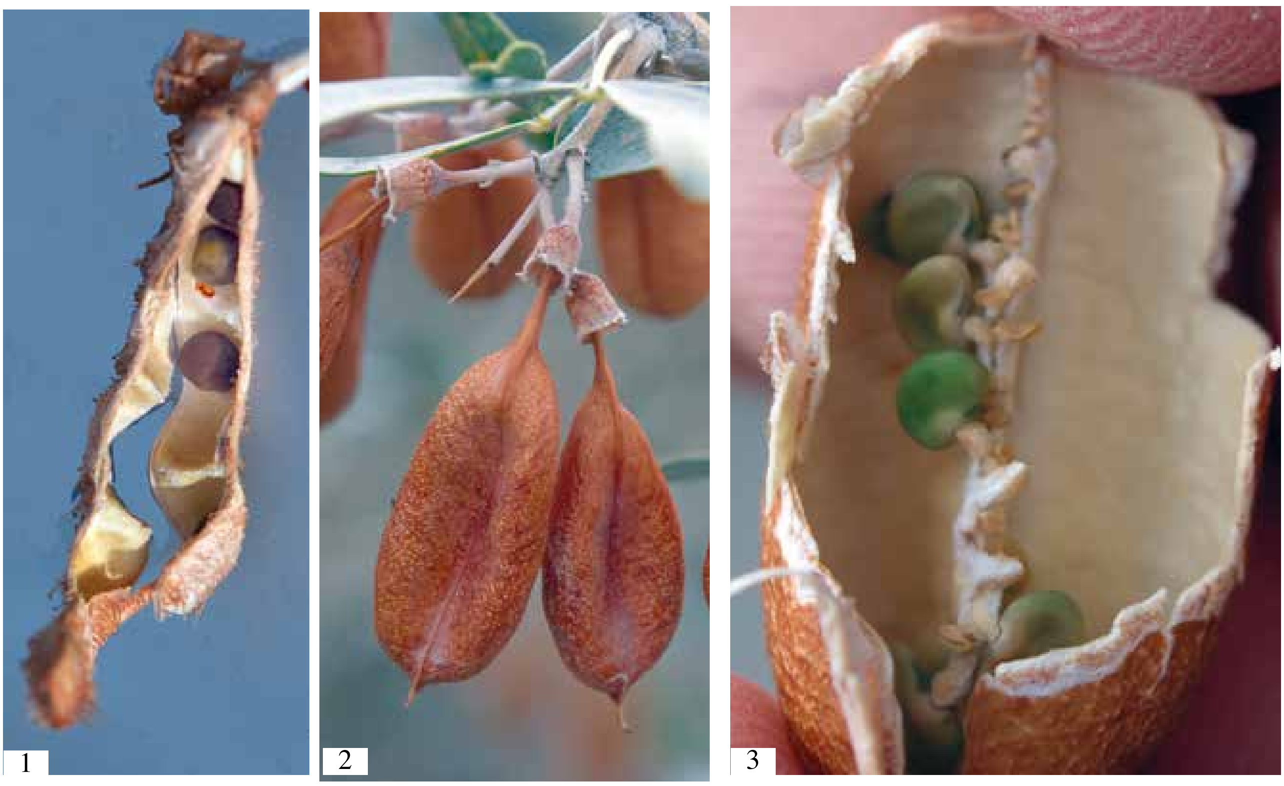
Some plants from the former Early Permian Angaraland have so many similarities with today's angiosperms that it is easy to find connections and solutions to study further evolution of flowering plants. Highly interesting are the fruit capsules resembling extant Leguminosae (Fabaceae) of *Pernerocarpus leguminosa*. The fruits have the character of pods, are 5-6 cms long (or even longer arriving till 10 cms) these fruit capsules are elongated and robust, with seeds hidden inside. They are connected to the main plant by a peduncle.

Pernerocarpus leguminosa fruit capsules resemble mostly extant Leguminosae (Fabaceae), with over 19,000 species and 730 genera of trees, shrubs and herbs and a worldwide geographical distribution, the third largest family of angiosperms, only surpassed by the Orchidaceae and the Asteraceae. Although the pods of *Pernerocarpus* were never found in connection with the leaves, some of the many enigmatic fern-fronds were never found fertile. Although the first known legumes appeared during the Late Paleocene, about 56 million years ago, it can be supposed that just like them, many other paleoangiosperms appeared on the Carboniferous-Permian border of the Fore-Urals, belonging during that time to an isolated continent called Angara. To state the obvious, all properties of *Pernerocarpus* speak for a classification as the earliest known Leguminosae. However, it is not resolved if they contain the seeds within their pods in one row or like specimen record shows – in two rows.

Pernerocarpus leguminosa with fruit pods



Pernerocarpus leguminosa 1. Fruit pod with peduncle (holotype MAT 756); 2–3. Other fruit capsules (MAT 758 and MAT 757); 4. Probable inside view of a pod with the seeds (MAT 672), Matvèevo, Coll. Wachtler, Dolomythos Museum.



Today's Fabacee (Leguminosae)

1. *Glycyrrhiza uralensis,* also known as Chinese liquorice, is used as a sweetener and in traditional Chinese medicine; an open pod with seeds; 2–3. *Halimodendron halodendron*, also known as Russian salt tree, belongs to the Fabaceae; an open legume with seeds.

The Arising of the Monocots

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

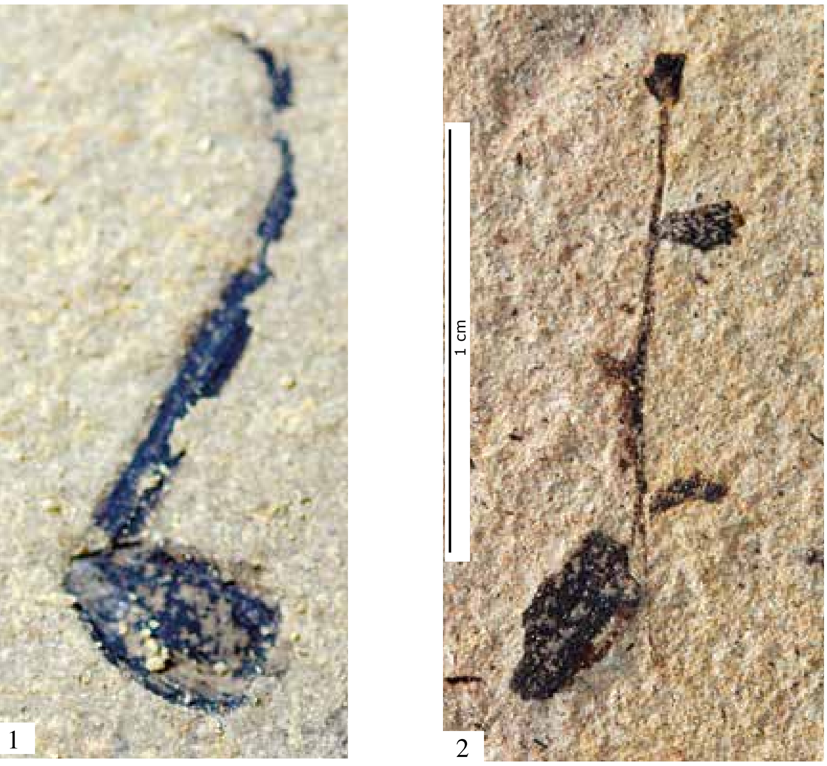
The differences between monocots and dicots are interesting: when a monocot seed germinates, it produces only one single usually long and narrow leaf, which has the exact features of the adult one. Notably, dicots otherwise germinate with two seed-leaves. Monocot leaves are often long and narrow, with straight parallel veins. The stems are mostly unbranched. The foliage of the dicots varies in shape and size. The veins go from the central midrib to the edge of the leaf, crossing and joining to form a netted pattern all over the leaf. The stems of dicots are usually tough and can grow wider each year, and they are often branched. The parts of the flowers of monocots exist in threes, whereas the flower parts of the dicots originate in fours, mostly in five or

Angaran Grass Landscape

Several Early Permian monocots; **from left:** *Krasnoufimskia graminaeformis, Krasnaia dammannii,* the low-growing *Ufaherbaria gaiae;* **right:** *Taezhnoeia geraschi* six petals. The calyx is a separate ring of sepals under the corolla. The seed pods or fruits of monocots usually have three parts, whereas the fruits and seeds of dicots are quite variable in shape, size and texture. There are mostly more seeds in a seedpod of dicots than in monocots.

Early Permian Monocots and Dicots

When and in which way did both the lineages originate? In the Early Permian Angaraland, seedlings belonging to the monocots were present, as well as those having all the features of dicotyledons. We also observe various parallel-veined foliage in the leaves of both groups, such as *Meristophyllum sojanaeanum, Meristophyllum indivisum* and *Rufloria derzavinii* or *Rufloria recta*. Even grass-like *Taezhnoeia geraschi* evidences dense parallel veins.
Other plants can be regarded as typical dicots with their reticulate veins. Parallel veins are not an exclusive feature of the Permian Angara flora. The variation in parallel-veined leaves in the former Angaraland is extensive. We encounter many different foliage types that must belong of course to different plants also. Effectively, a classification into primitive monocots is not so bizarre. Inconspicuous fructifications, which are appropriate to many grasses (Poaceae), are not so rare in the Permian Fore-Urals, but they were often overlooked in the past. *Krasnoufimskia graminaeformis, Taezhnoeia geraschi* or *Krasnaia dammannii* have unambiguous properties of today's grasses. Also, parallel-veined foliage like *Meristophyllum sojanaeanum, Meristophyllum indivisum* and *Rufloria derzavinii* have more in common with some monocots than with the Permian floras of Euramerica. Some leaves reach extraordinary lengths of more than 40 cms, some others have their veins spread wide apart, and a group split their leaves forming pairs. Some are perfect linguiform, resembling *Glossopteris* plants from the southern hemisphere Gondwanaland. Nevertheless, it can be stated that in no other region do these parallel-veined leaves reach such a propagation as in the Permian Angara region. Therefore, the axiomatic assumption is: Why do we have such as diversity? Where lies the origin of this variety? In which context stand these supposed monocots with the dicots?
Upon superficial examination, we encounter two kinds of leaves: parallel-veined with bilobed axes (*Meristophyllum*) and parallel-veined single leaves (*Rufloria*). Probably they belong to different genera, but till the time connected fruits are not found, every classification is doubtful.



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

Meristophyllum Leaves

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

Rufloria Leaves

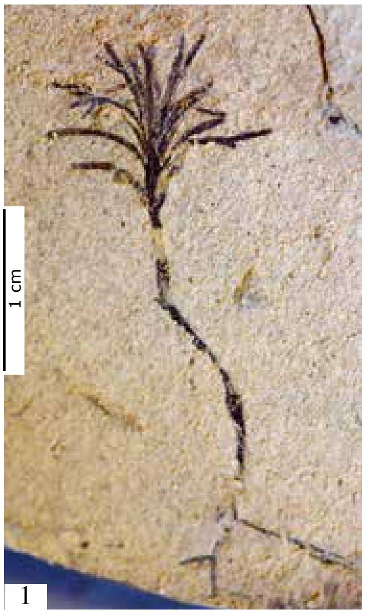
Rufloria-leaves are inhomogeneous, varying in length from 10–15 cms, sometimes even reaching up to 50 cms. In comparison with *Meristophyllum*, they are fossilised individually. All are parallel-veined but there exist differences in terms of being densely to largely veined. The apex can be tapered or obtuse rounded. Often, they are equipped with an abscission mark. The most commonly known is *Rufloria derzavinii* (Meyen, 1992), while other species are known as *Rufloria recta*, *Rufloria salamatensis* (Meyen, 1963; Zalessky, 1937). Female head-like aggregations of sterile scales and seed stalks were assigned to the genus *Astrogaussia imbricata* (Naugolnykh, 2014). Based on this, it can be supposed that *Meristophyllum* and *Rufloria* can be inserted in the category of monocotyledons with unknown fructifications till date.

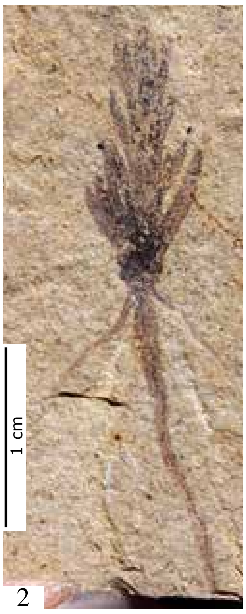
Other Plants Resembling Monocots

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

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

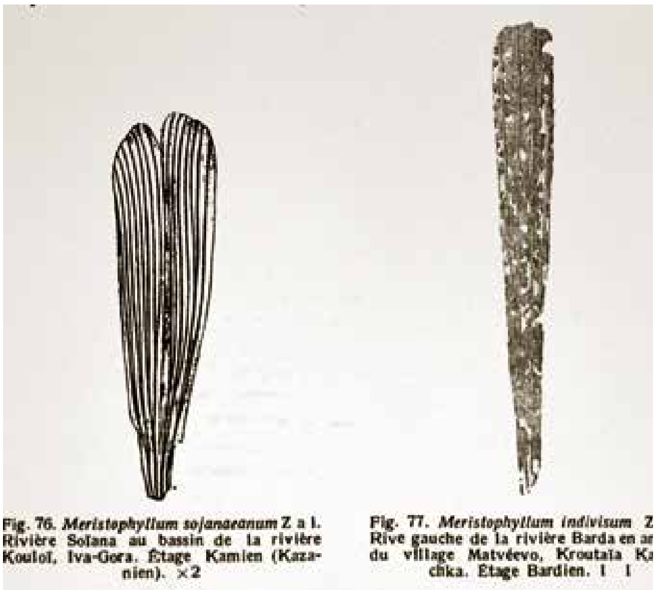
A complete preserved leaf of *Rufloria derzavinii* (44 cm long and 3–5 cm wide, CHEK 388, Chekarda, Coll. Nicolas Wachtler) and the parallel-veined monocot grass *Acorus calamus* with lateral fructifications





Seedlings

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



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

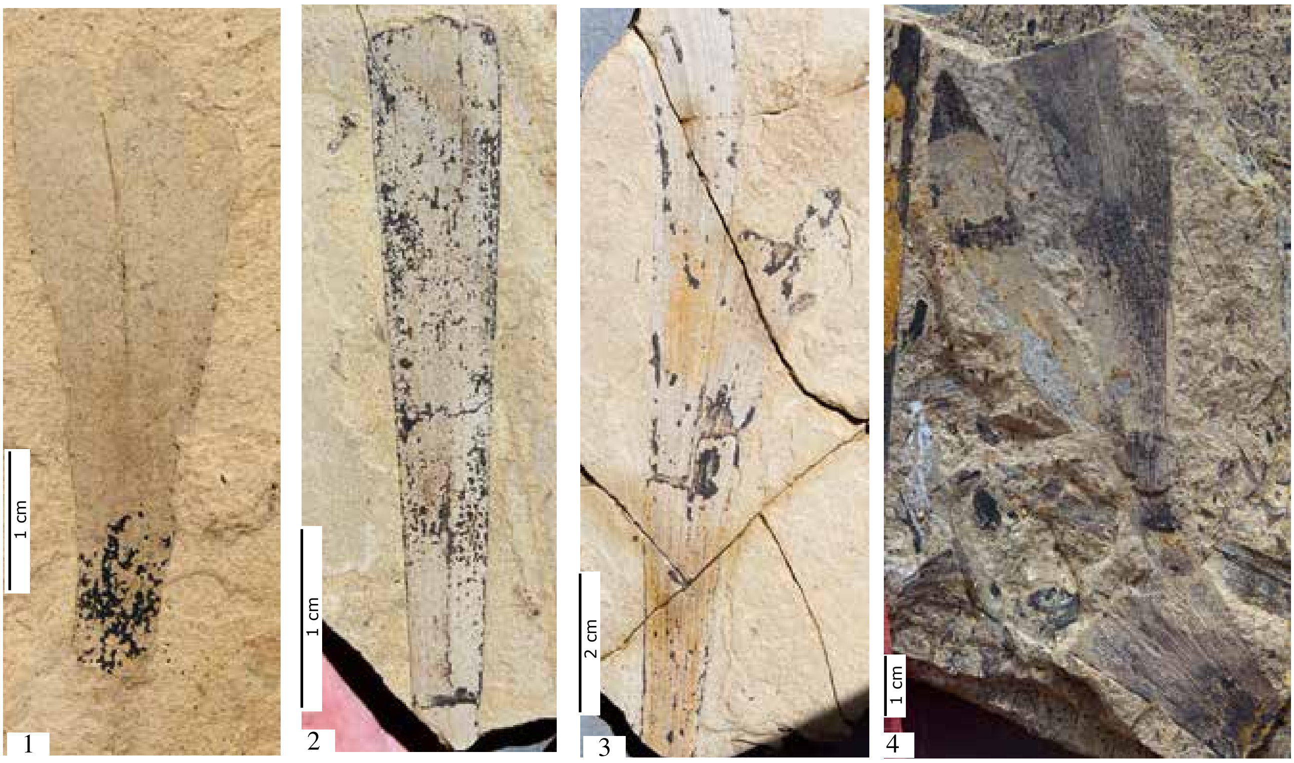
Poaceae grasses

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

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

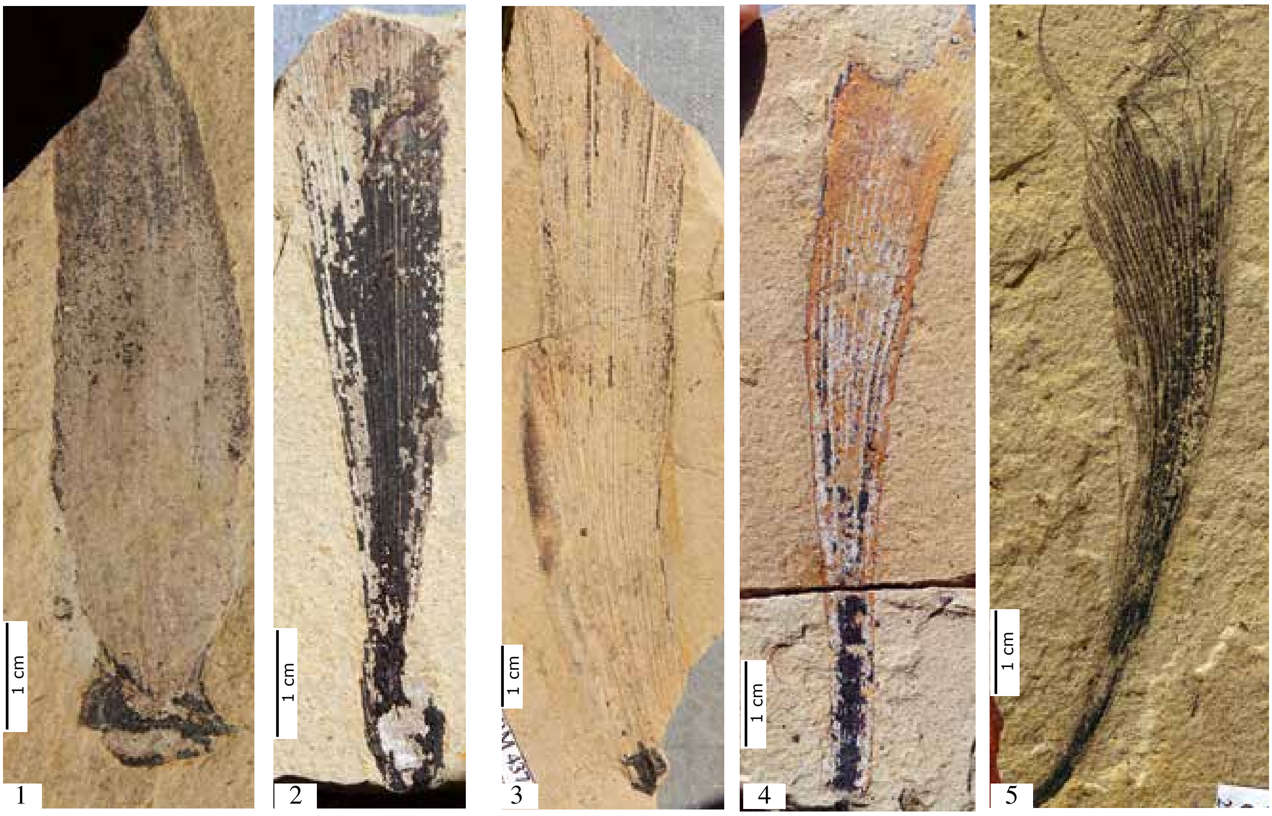
Deschampsia cespitosa known as tufted hairgrass, a perennial widespread Poaceae

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



***Meristophyllum*-Leaves**

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



***Rufloria*-Leaves**

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

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

An interesting Early Permian grasslike plant is represented by ***Taezhnoeia geraschi.*** Several leaves sprout from a rhizome and are arranged in three vertical rows (tristichous). The single leaves taper apically and are parallel-veined. In that they have all the aspects of monocotyledons like the true grasses of today (Poaceae). Several fertile parts can be regarded as spikelets belonging to *Taezhnoeia* and consisting of two bracts that are fused with the fruit wall; all are closed. Although often overlooked, *Ufaherbaria gaiae, Krasnoufimskia graminaeformis* and even *Taezhnoeia geraschi* are characterised by the same assemblage of their fertile parts. The fact that some can be classified as spikelets (*Taezhnoeia geraschi*), while other as caryopsis (*Krasnoufimskia graminaeformis*) justifies the classification in other genera too. Also, their leaves notably differ amongst themselves.

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

these localities can certainly enlarge the knowledge about its classification that would relate it with some of today's ancestor lines. Also ***Krasnaia dammannii*** fits well in a group of herbaceous graminoceous plants being relatively abundant in the Matvéevo-Fossillagerstätte. In this case, the interesting features are their grass-like structure and growth. The plant is characterised by a slender culm-like stem ending in a tuft compound of fragile narrow leaves. The foliage evidence a nearly invisible midrib. The fertile organs are sitting apically and solitary on the stem-leaves, forming a strange cluster of pollen sacs and seeds. Because of many features such as their low-growing appearance, *Krasnaia dammannii* also clearly resemble today's grasses, but a detailed indication towards which monocot-group they belong to is still not identifiable.
Also ***Krasnoufimskia graminaeformis*** is fairly common in Matvèevo as well as in Chekarda, but only whole plants can be classified without doubt. This is especially valid in case of their panicles or isolated spikelets that can be analysed, due to their inconspicuous character, only if attached to the plant. Additionally, in the Early Permian sediments, we encounter other plants that have mainly the same panicles or spikelets as *Ufaherbaria gaiae* but generate different small elongated leaves or evidencing the same stems and stalks but different caryopsis.
The entire plant, about 15 cm in size consists of two basal leaves that are from 4 to 5 cm long and are equipped with a strong midrib. The leaves have an entire margin and end is tapered. The main 0.5 cm thick stemlet forks several times after the middle. Two entire panicles are attached in additional to another mostly decayed one. The isolated spikelets are about 1 cm long and are composed of many caryopses consisting of elongated seeds fused with the fruit wall. The spikelets sit on a slender, 10 mm long petiole. The single corn grain is 10 mm long and 1 mm wide and ends in a spike projecting 10 mm from the tapering fruit wall. The single seeds are slightly furrowed.
The interest in these grass-like plants was never extraordinary. Probably they were thrown away with the trash many times and regarded only as decomposed parts of plants. Also, the panicles of *Krasnoufimskia*

Taezhnoeia geraschi **Reconstruction**

Krasnaia dammannii **Reconstruction**

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

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

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

Ufaherbaria gaiae

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

***Ufaherbaria gaiae* – reconstruction**

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

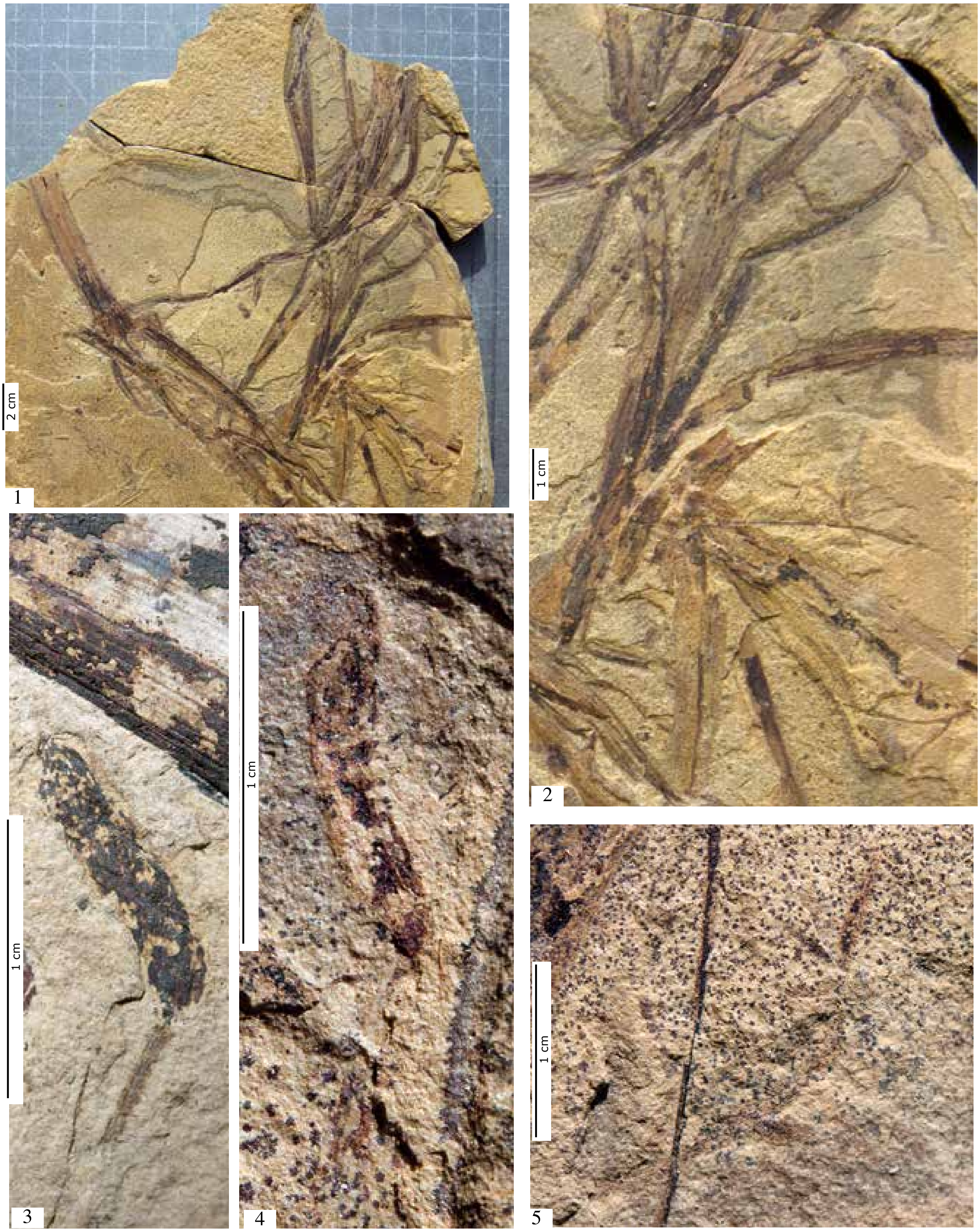
graminaeformis could be discovered only after an intensive, albeit extremely interesting, study of the whole plant, which tells a lot about the evolution of grasses, one of the most extensive plant families on Earth. The Poaceae (Graminaceae) form the most important group of flowering plants for human beings because of their cereal and forage crops. Alternating long, slender leaves in two rows on opposite sides of the stem and small bisexual flowers organised into inflorescences are two of their characteristic features.

Ufaherbaria gaia*e* can also be inserted into the group of Early Permian herbaceous plants collected from the Fore-Urals. It is probably more common than it seems. However, since only entire plants can be classified without doubt, partially preserved specimen or those without connecting fertile parts are often let go. Basal tufts of leaves can be seen in many of today's angiosperm families, including the Poaceae, Alliaceae, Gentianaceae and many others.

This herbaceous plant, about 10 cm in size, is composed of a basal rosette forming clumps. The leaves are about 4–5 cm long and 1 cm wide, lanceolate and tapering apically. A midrib is seen. The inflorescences are small panicles equipped with unbranched fertile stalks and hold several hanging seeds on the apex. They reach a length of about 5 mm and a width of 1 mm. Because of their corn grains, an insertion into the category of Graminaceae ancestors is possible. This is not so unfounded because as seen in the Early Permian sediments from Chekarda and Matvèevo, other plants like *Krasnoufimskia graminaeformis* or *Taezhnoeia geraschi* formed panicles with spikelets. Otherwise their basal leaves resemble dicots more.

***Krasnoufimskia graminaeformis*. Plant, leaves and fructifications**

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



***Krasnoufimskia graminaeformis*. Plant, leaves and fructifications**

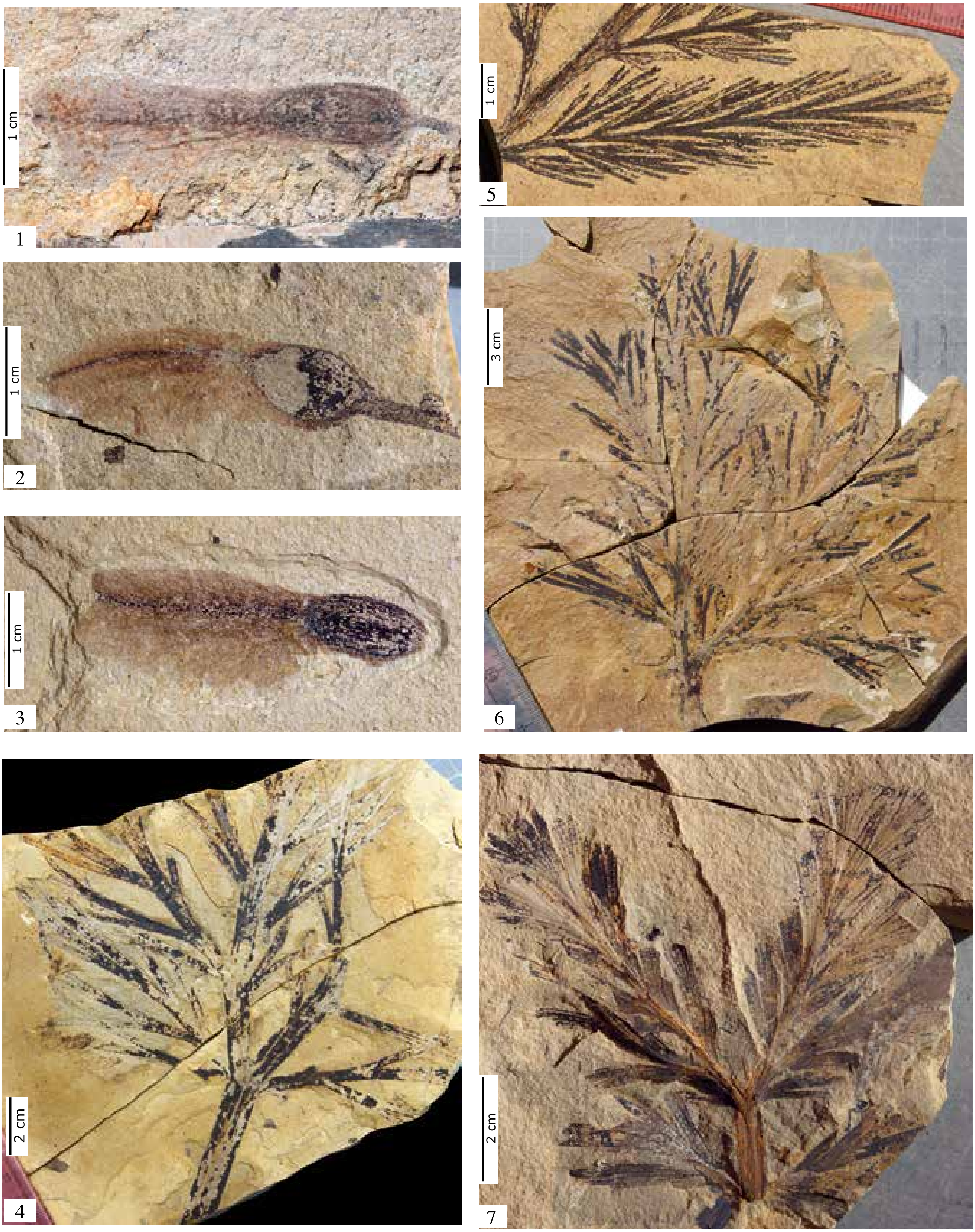
1. Several plants deposited together (CHEK 200); 2. Detail of a single plant 3. A fruit forming a caryopsis, with the seed coat fused to the fruit wall (MAT 753, Matvèevo, Coll. Wachtler); 4–5. Several seeds with the fused seed coat (CHEK 200); Chekarda Kungurian (Early Permian) Coll. Gerasch, Dolomythos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

A Short History of the Evolution of Broad-leaved Angiosperms in the Early Permian

The Fore-Urals (Russia) are extremely rich in fossilised Early Permian deciduous tree leaves and fructifications. They resemble the extant in mainly all aspects. Why we have millions of years of gap after a heyday in Permian till the Cretaceous can only be explained by a Permo-Triassic cataclysm that mostly influenced the isolated Paleozoic continent, Angara and the lack of potential seed propagators such as birds. The samaras of maple ancestor *Sylvella alata* with associated *Psygmophyllum cuneifolium* leaves, as well as those of ash progenitor *Sadovnikovia belemnoides*, elms like *Matvéeva perneri, Uralosamara palaeozoica* having affinities with today's *Ulmus alata* and birch-samaras described as *Samzalesskya triquetra* with their pollen organ, *Kungurosperma elongata* and female catkins of *Kungurosperma russica* were common. Also, nuts held in leafy involucres like hazelnut-resembling *Nucifructa primaeva* or oak-acorn *Craspedosperma bardaeanum* with the common leaves of *Psygmophyllum expansum* were widespread. Rare are the fruits in capsiconum form of extant Liquidambar-resembling *Neuburgosperma radiata.* Primitive stone fruits like *Bardocarpus aliger* are omnipresent in these Early Permian sediments, whereas interesting Hesperideæ like *Parvunucleus dammannii* with one big seed surrounded by smaller seeds, probably an evolution connecting link to extant Citrus fruits, are seldom found. It can be supposed that gymnosperms and angiosperms had a different evolution-line since the Devonian.

Early Permian broad-leaved fruits

Left: samaras from ash ancestor *Sadovnikovia belemnoides,* maples (*Sylvella alata*) and elms (*Matvéeva perneri*); **middle:** birches (*Samzalesskya triquetra*), oak-acorns (*Craspedosperma bardaeanum);* **right:** stonefruits (*Bardocarpus aliger, Parvunucleus dammannii*) and nuts (*Nucifructa primaeva)*. Several Early Permian insects are flying in the background and document a mutual symbiosis.



***Sylvella alata* (samara), *Psygmophyllum cuneifolium* (leaves). 280 millions years ago Acer-ancestors**

1–3. **Samaras:** note that the strongest vein in Early Permian Aceraceae is arranged in the middle and not on the upper border as in the extant ones (MAT 191, CHEK 64, MAT 721); 4-7. **Leaves:** note a continuous evolution from needle-like to palmate, (MAT 608, MAT 297, CHEK 63, CHEK 25) (All Chekarda and Matvèevo).

Early Permian maples and ashes

Left: a twig *Psygmophyllum cuneifolium*, (CHEK 63) and a samara *Sylvella alata* (CHEK 64), of potential *Acer* ancestors; **right:** a twig with attached samara and male flower-panicles of *Sadovnikovia belemnoides* (MAT 182 and MAT 366) a potential *Fraxinus* ancestor; **middle:** Early Permian cicada *Rachimentomon reticulatum.*

The Evolution of Macro- and Micro-leaves

The most plausible answer is a coevolution originating in the Devonian with two kind of leaves. Macro-leaves that gave origin to the needles of conifers, the fronds of cycads, the broad leaves of ginkgos and deciduous trees and the angiosperms. The other development was dwarfish micro-leaves, called emergences or ennations. These microleaves originally were not true leaves because they did not contain vascular tissue. These micro-leaves began to develop many important features: they protected the seeds from environmental impact, coated till overtopped the seed, making them airworthy in the form of samaras, as seen in gymnosperms like the Abietaceae or in angiosperms like maples, ashes, elms and many others. They developed, also other characteristics like covering the seed completely to generate a fleshly aril, such as that which we have in ginkgo or yew seeds or in the angiosperms to form a tasty drupe like today's apricots or cherries. Other micro-leaves coated the seeds or fruits only partially as we encounter in Araucaria seeds or in the oaks. All these essential features in the plant kingdom and widespread reproduction instruments were developed over a surprisingly short period of time, and most probably, their final blueprint was finished between the Carboniferous-Permian border about 300 million years ago.

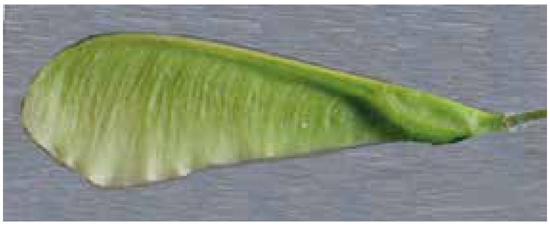
If one focuses on the key question, that is, if the angiosperms are monophyletic, which means that they originated from one common ancestor, so the answer could only be positive. However, these happened in the Devonian about 400 million years ago! From this moment onwards, they began to separate from each other. Moreover, the answer to the counterquestion about the monophyly in gymnosperms is also positive; but even that happened in Devonian times.

Early Permian Samara Bearer

It is proven that winged seeds called samaras appeared early in the fossil record. Beginning from the Carboniferous-Permian border, aliform seeds are recorded from the conifers like *Wachtlerina* and *Majonica* and from angiosperms like *Sylvella, Matvéeva, Sadovnikovia* or *Samzalesskya* The development of a winged seed in the angiosperms was as complicated or easy in the coevolution as the winged seed for the conifers, and both angiosperms and gymnosperms – or so it seems – reached their purpose independently. None of the foliage types has reached the level of today's *Acer, Fraxinus* or *Ulmus* twigs, but all of them were characterised by a transition stage between Devonian archaic furcate leaves and extant broad-leaved features.

The Progenitors of the Maples – Aceraceae

The first samaras resembling Aceraceae are recorded from *Sylvella alata*, a name first introduced in 1937 by the Russian palaeontologist, Mikhail Dmitrievich Zalessky (1877–1946), in which he described the Early Permian flora from Matvéevo in the Perm Krai, reproducing an interesting aliform wing with a peduncle. The seed was connected to a flattened and fibrous wing.

Extant Aceraceae
Samaras (*Acer turcestanicum, Acer negundo*); **Leaves:** *Acer saccharinum; Acer platanoides*


Aceraceae with deeply segmented leaves: *Acer japonicum* and *Acer palmatum* remember mostly the Permian foliage.

1. Leaves of *Acer negundo.* The leaves do not resemble maples, but ashes. 2. The samaras are typical of the Aceraceae; 3. Extant *Fraxinus profunda* (Pumpkin-ash). The compound frond is an evolution of the amalgation of diverse single needle-like leaves.

The associated leaves of the samara *Sylvella alata* were probably those described first in 1838 by the royal professor, Stephan Kutorga, from Petersburg. He inserted some flabelliform leaves as *Sphenopteris cuneifolia* and *Sphenopteris interrupte-pinnata*, which Zalessky (1937b) later changed to *Psygmophyllum cuneifolium* to depict the difference between *Sphenopteris* ferns and the presumed ginkgophyte plants.

The leaves are characterised by deep-lobed and segmented foliage, a feature that survived mostly till *Acer palmatum*. A bifurcating foliage represents a distinguishing mark of almost all primordial Devonian plants and can be encountered in many other Permian flora elements. Nevertheless, because of all these similarities, it is thus difficult to decipher their exact family only from their foliage type. *Psygmophyllum cuneifolium* leaves were poorly present in typical Artinskian layers (Panteleykovo, near Arti). They are more than frequently available in the slightly younger Kungurian sediments of Matvéevo and Chekarda, accompanied by *Sylvella alata* samaras.

Because these aliform reproductive organs do not pertain either to a conifer or to lycopods, ferns or horsetails, the possibilities are restricted, and we have to search for parallels in today's angiospermous plants. The most similarities we have to extant maple leaves that comprise today's palmates, veined and lobed to palmate compound, pinnate compound or pinnate veined leaves. 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. Their paired fibrous wings can also be compared well.

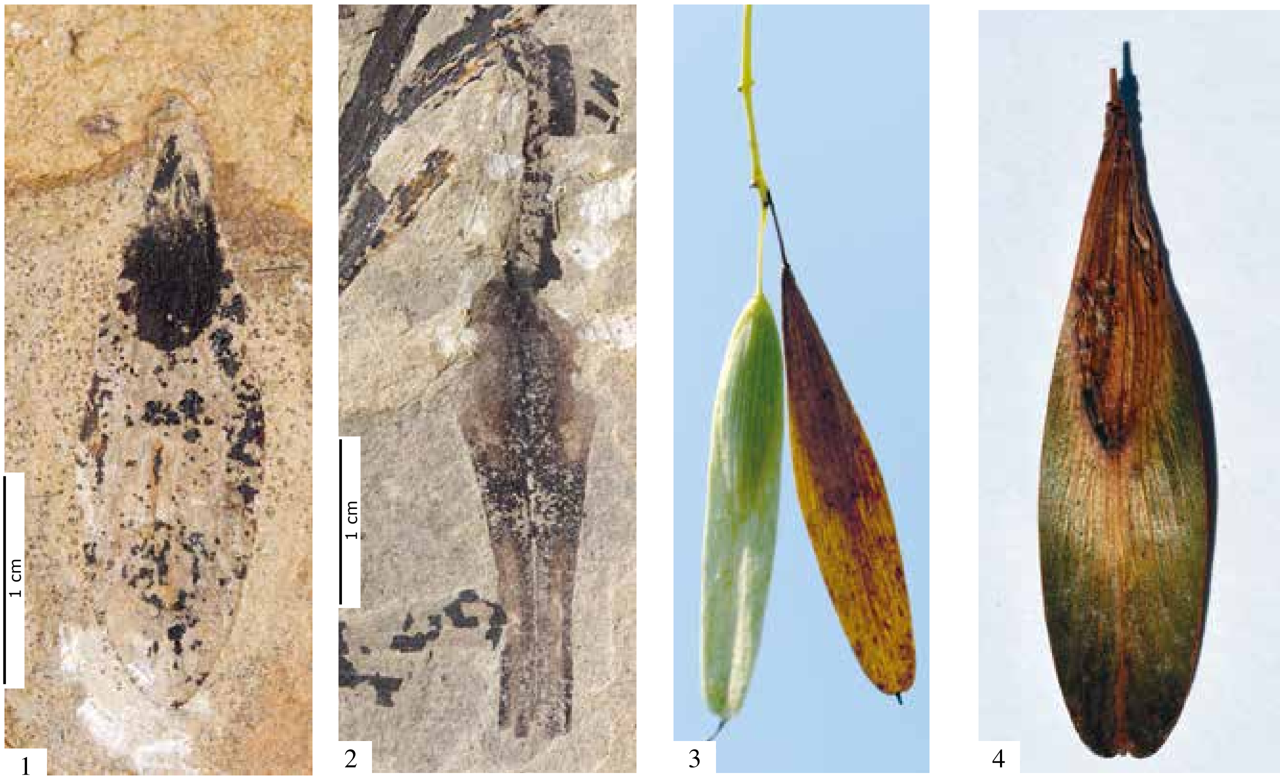
Today the Aceraceae are distributed with about 120 species throughout the Northern Hemisphere. Acer fossils recorded till date begin from the Eocene. The most reliable indicators are the leaves, but their characteristic features are the samaras, which changed little to nothing from Early Permian till the Eocene and the present. However, the big gap of nearly 250 million years from their first appearance till rebirth in the Paleogen still remains unresolved, which is also valid for other angiosperms.

The Birth of the Ashes (Fraxinaceae)

Other samaras in the Early Permian of the Fore-Urals were classified as *Sadovnikovia belemnoides*. Their winged reproductive organs were sometimes thought to be in connection with Permian lycopods, especially the Pleuromeiaceae or Isoetaceae Due to fortunate connected findings with attached samaras on twigs, it can be stated that this plant must be classified as Paleoangiosperm, and in this case, as the ancestor of the extant Fraxinaceae (ashes). This will additionally be supported by suggested reproductive organs resembling most of today's ashes occurring in a tuft of many flowered panicles. Some are hermaphroditic. Because the seeds are not positioned on the base like *Sylvella alata*, rather in the basal middle part of the samara, they can

Sadovnikovia belemnoides **– potential fraxinus (ash) ancestor; winged seeds (samara) and leaves**

1. Entire twig with attached aliform seed and leaves; 2. Another complete twig (MAT 556); 3. Detail of a twig evidencing well the blueprint of single leaves (MAT 555); 4-5. Leaves (MAT 732, MAT 556). All Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum, Italy



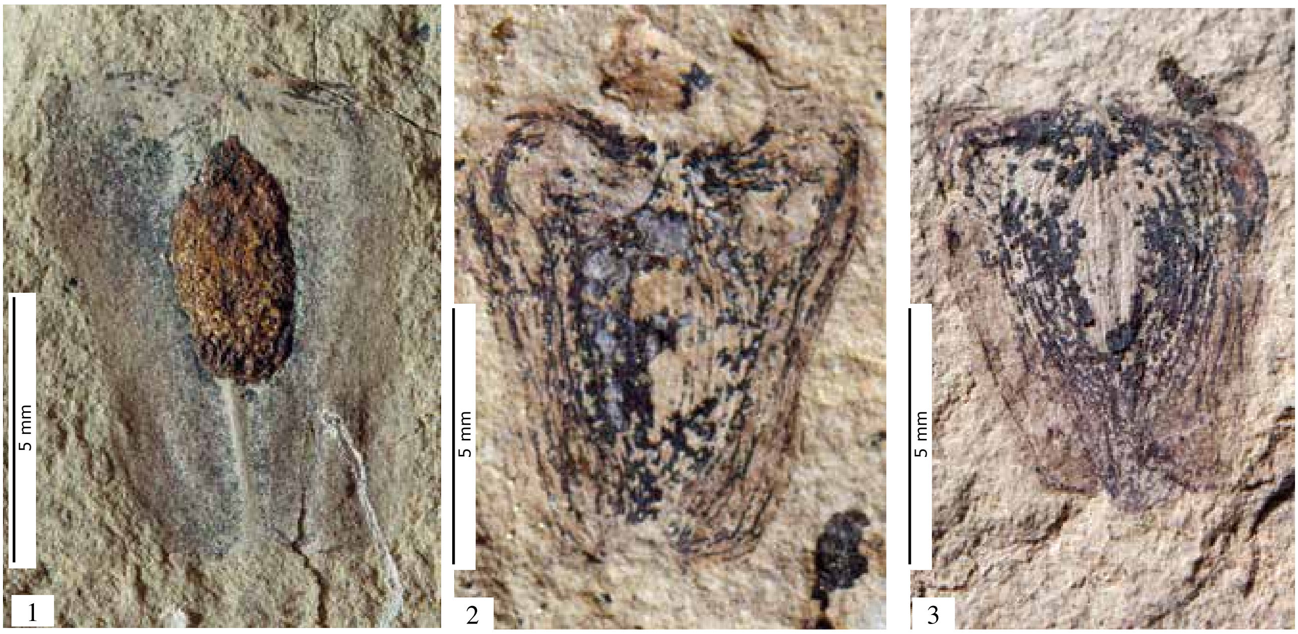
1-2. Samaras of Early Permian *Sadovnikovia belemnoides* (MAT 283, MAT 182, Coll. Wachtler, Dolomythos-Museum); 3-4. Comparison with extant ash-samaras: *Fraxinus excelsior*

5–6. Panicles of Early Permian *Sadovnikovia belemnoides* (MAT 366, MAT 219); 7. Comparison with extant ash panicle F*raxinus excelsior*; 8. Detail of a male flower from *Sadovnikovia belemnoides* (MAT 374) and 9. Extant male flower of *Fraxinus excelsior*; panicles and samaras from the ashes did not change in a 300 million years interval.

also easily be distinguished from Aceraceae ancestors.
The connected leaves are divided into three to four lobes and are flabelliform, with slightly rounded ends. Interestingly, the leaves of *Sadovnikovia belemnoides* resemble the pinnately compound leaves of *Acer negundo* (boxelder maple or ash-leaved maple)*,* whereas the samaras correspond those of extant *Fraxinus.* In that it can be documented how closely related ashes and maples are. Unlike other maples which have palmately lobed leaves, *Acer negundo* generates pinnately compound leaves that usually have three to seven leaflets or simple leaves, whereas their reproductive organs can be similar to maple-like samaras.

Winged seed of B*etula papyrifera and Betula occidentalis,* the water birch.

Members of the genus *Fraxinus*, known as ash trees, include today about 40–50 species, divided into six sections (Dipetaleae, *Fraxinus, Melioides, Ornus, Pauciflorae* and *Sciadanthus*). They are widely distributed in the northern temperate zone from Eurasia to North America, comprising shrubs and trees with simple to compound leaves. They are found in diverse habitats, from semi-deserts to subtropical or temperate environments, and from sea level to subalpine altitudes.
The ashes are represented by wind- as well as insect-pollinated species, in which the wind-pollinated dominate two-third of it. The breeding systems range from hermaphrodites to androdioecious and polygamous to dioecious species. This supports the theory that in the Early Permian, the plants had characters suitable for the transport of the pollen by wind as well by insects. Comparing Early Permian *Sadovnikovia belemnoides* with today's Fraxinaceae, the sexual organs formed in panicles, as well as their samaras were almost the same. Although it was hypothesised that the ashes evolved in the Eocene about 50 mililon years ago with species like *Fraxinus flexifolia*, nothing speaks against an earlier evolution during the Permian. Too similar are extant and fossilised Early Permian species. In future, therefore, attention must be to the phylogeny, maybe even encountering some ash-fossils during the Jurassic.



Samzalesskya triquetra. 1. Well evidenced nutlet surrounded by wings (CHEK 313); 2. Winged seed enclosing a nutlet, CHEK 330; Chekarda; 3. Specimen from Matvèevo, MAT 747; coll. Wachtler, Dolomythos-Museum

***Kungurosperma elongata* Birch pollen organ**

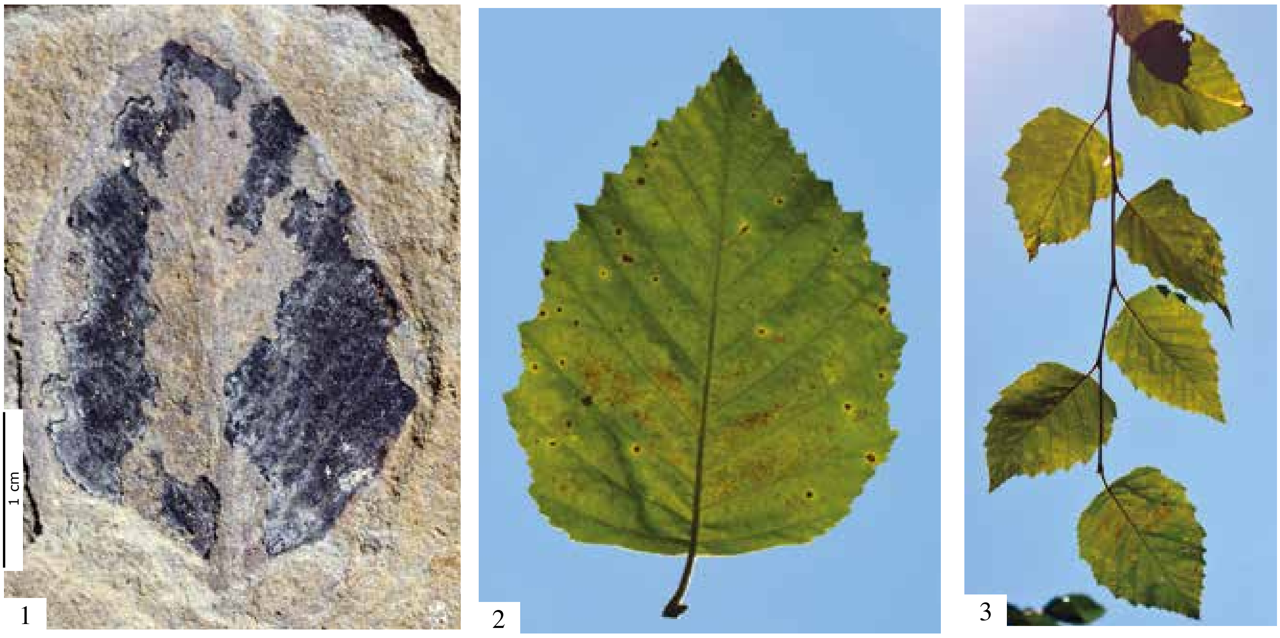
1-2. Pollen organ (Holotype MAT 725, Coll. Gerasch; 15 mm long, 5 mm wide) and detail of a bract; 3. Male catkin of *Betula pendula*; 4. Detail of the male bracts of *Betula costata*

***Kungurosperma russica.* Birch female organ**

4. Female catkin (Holotype MAT 387; 25 mm long, 10 mm wide); 2. Female catkin (CHEK 121; 30 mm long, 10 mm wide, Chekarda); 4. Adult cone of the Dwarf birch (*Betula glandulosa);* 5. Female juvenile and mature cone of *Betula utilis.* 6. Female cones of *Betula utilis*

***Samzalesskya triquetra*. Early Permian birches**

Left: A pollen cone (*Kungurosperma elongata,* MAT 725*)* and a samara (*Samzalesskya triquetra,* CHEK 313, CHEK 330;*)* right: a female catkin (*Kungurosperma russica,* MAT 381, CHEK 121*)* of a potential Early Permian birch ancestor, middle: over the twig a mayfly (*Misthodotes sharovii*), relatively common in these sediments.



1. Suggested leaf of an Early Permian birch-ancestor (MAT 126, Matvèevo, Coll. Dammann, Dolomythos-Museum;
2-3. Leaves of extant *Betula nigra*

The Beginning of the Birches – Betulaceae

Today the six extant genera of the Betulaceae are usually divided into two tribes: the Betuleae, including *Alnus* and *Betula* and the Coryleae, including *Carpinus, Corylus, Ostrya* and *Ostryopsis.* This can be regarded as an arbitrary classification because their fruits differ considerably from the other samaras, nuts or drupes.

In the context of fossil history, it can be established that extant birches (Betula) are more related with the elms or maples, and that they were just clearly differentiated and recognisable from the Carboniferous-Permian border onwards. From the Early Permian regions of the Fore-Urals, leaves, small-sized samaras, male and female catkins that resemble birches in many ways are known. After bringing *Samzalesskya triquetra* in connection with other parts of the plants or the leaves, it is thought that it probably can be regarded as ancestor of the Betulaceae.

Samzalesskya triquetra represents a nutlet with distinct wings on each side, just like today's birch, whereas *Samaropsis* is a seed totally covered by microleaves like extant Aracauria conifers or represents an aril.

Additionally, elongated male catkins (*Kungurosperma elongata*), as well as female fructifications (*Kungurosperma russica)* were found. The morphological details of all these associated infructescences, fruits, staminate inflorescences are similar to those of extant Betula and allows a classification in this group as reasonable.

The pollen organs, about 3 cm long, are composed of a fair number of coarsely ridged bracts that are helically arranged. The base of the bract is slightly cupped. The female catkins were solitary, elongated infructescences equipped with relatively long persistent bracts. They are between 2.5 cm and 3.0 cm long and 1.0 cm wide.

In angiosperms, elongated catkins are encountered in several broad-leaved trees like the hazel (*Corylus*), alder (*Alnus*), willow (*Salix*), birch (*Betula*), poplar (*Populus*) and walnut (*Juglans*). Establishing to which Early Permian ancestor the catkins of *Kungurosperma* belong is difficult, but similar fruits, seeds or leaves related to birch progenitor *Samzalesskya triquetra*, as well as the hazel progenitor *Nucifructa* indicate an association. The leaves of extant birches differ in size, shape and morphology of the teeth. Therefore, it is suggested that they also existed in the Early Permian.

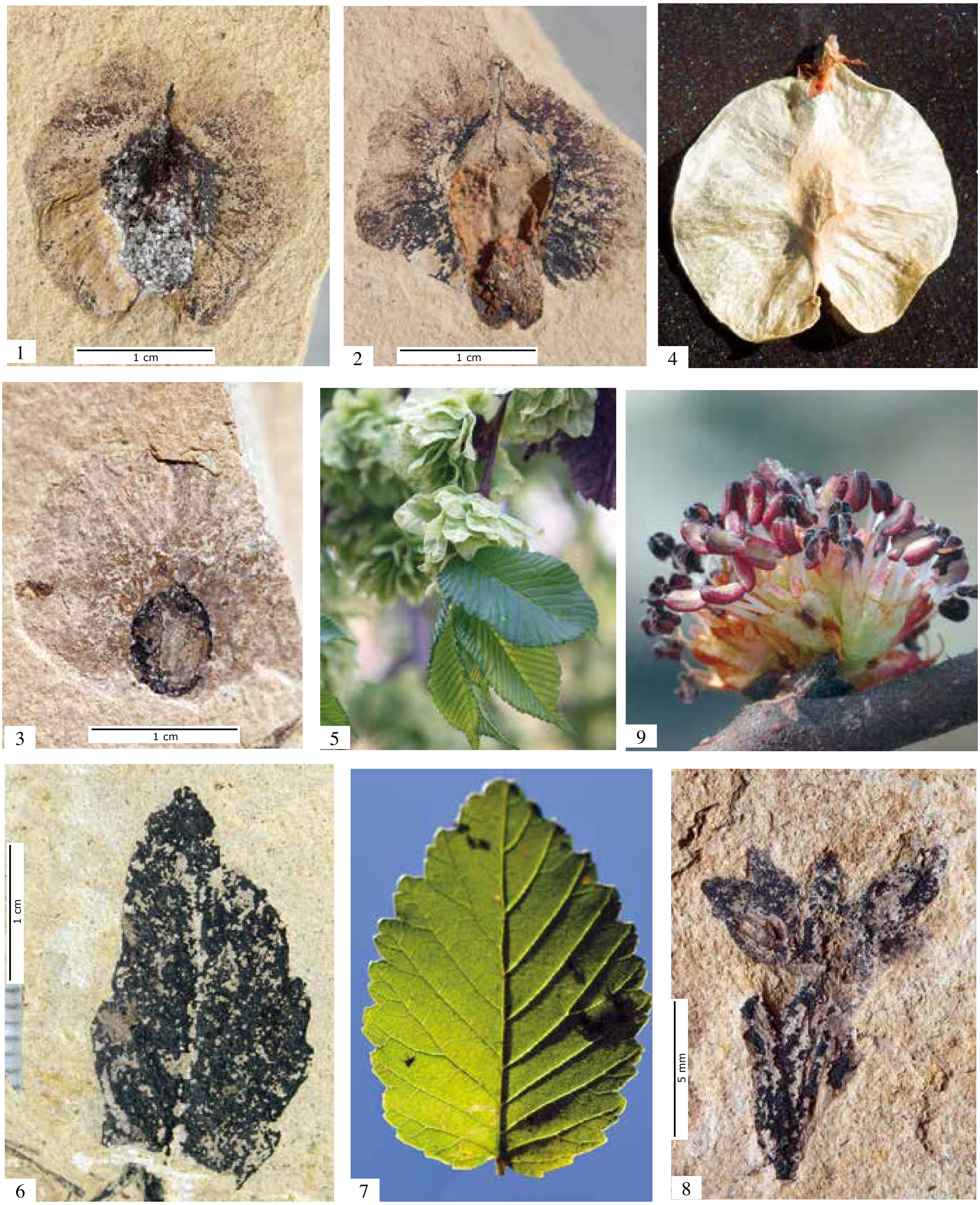
The Origin of the Elms – Ulmaceae

Some samaras classified as *Matvéeva perneri* have their seeds inserted in the centre of a rounded wing, such as in today's elms (Ulmaceae) or China genus *Dipteronia*. The fibrous material of these samaras is relatively consistent and the strong filigree veins crisscross the wing. Also, in comparison to extant, the seeds are clearly distinct, being more nutlike. They are relatively common in the Kungurian deposits Chekarda and Matvèevo and can be distinguished easily by their rounded samaras, although the leaves present some doubts. Therefore, considerations were taken that Early Permian (Kungurian) *Matvéeva perneri* represents the oldest known ancestor of the elms.

Today there are about 40 species of *Ulmus* (elm) distributed across North America, Europe and Asia and crossing the Equator to reach Indonesia. The flowers were wind-pollinated. Elm leaves are alternate, with serrate margins. The samaras of the elms are flat, light and papery, surrounding the seed laterally.

From the outer aspect, closely related is *Dipteronia* with only two living species, *Dipteronia sinensis* and *Dipteronia dyeriana* – both endemic to China. The inflorescences are paniculate, terminal or axillary. The leaf arrangement is opposite and pinnate, the leaf margin is serrate. The fruits are distinctive winged schizocarps, composed typically of two subelliptical mericarps. The mericarps are joined to each other at their proximal edges along an axis continuous with the pedicel.

The fossil record of *Dipteronia*, that is mainly not to distinguish from extant ones, goes back till the Paleocene Fort Union Formation of Hell's Half Acre, Central Wyoming, which are about 60–63 million years old. In the Eocene, they were with *Dipteronia brownii* (recorded from Western Canada and USA, especially from the intensively collected locality of Republic, Washington) just widespread. Leaves and fruits of *Ulmus* ancestors are also recorded



***Matvéeva perneri*. Ulmaceae from the Early Permian**

1-3. Samara (MAT 346, MAT 629, MAT 14), Coll. Wachtler, Dolomythos-Museum); 4-5. Samaras of extant elms (*Ulmus minor, Ulmus glabra* with leaves); 6. Supposed leaf of *Matvéeva perneri* (MAT 434, Coll. Gerasch). 7. Leaf of extant *Ulmus pumila*; 8. Suggested flower from *Matvéeva perneri, 9. Ulmus glabra,* extant flower

Early Permian elms (*Matvéeva perneri* and *Uralosamara palaeozoica*

Left: a fruit organ of *Uralosamara palaeozoica* (MAT 641) resembling today's *Ulmus alata.* **Middle:** Twig (MAT 434) and samara of *Matvéeva perneri* (MAT 346, MAT 629, MAT 14, MAT 684); **right:** the Megasecoptera *Sylvohymen sibiricus,* an insect belonging probably to the earliest dragonflies

from the Early–Middle Eocene of British Columbia and Washington (especially Republic) and were assigned to two species: *Ulmus okanaganensis* is based on leaves attached to flowering and fruiting twigs and isolated leaves and samaras with extremely reduced or absent wings. In *Ulmus okanaganensis,* the flowers appear to have occurred together with the leaves in spring, based upon a twig displaying young inflorescences and unfolding leaves. A second type of foliage is assigned to *Ulmus chuchuanus*. Similar Ulmus leaves were recorded from the Paleocene from Russian Far East, described as *Ulmus furcinervis*, and from Paleocene–Eocene sediments from Svalbard classified as *Planera ulmifolia*.

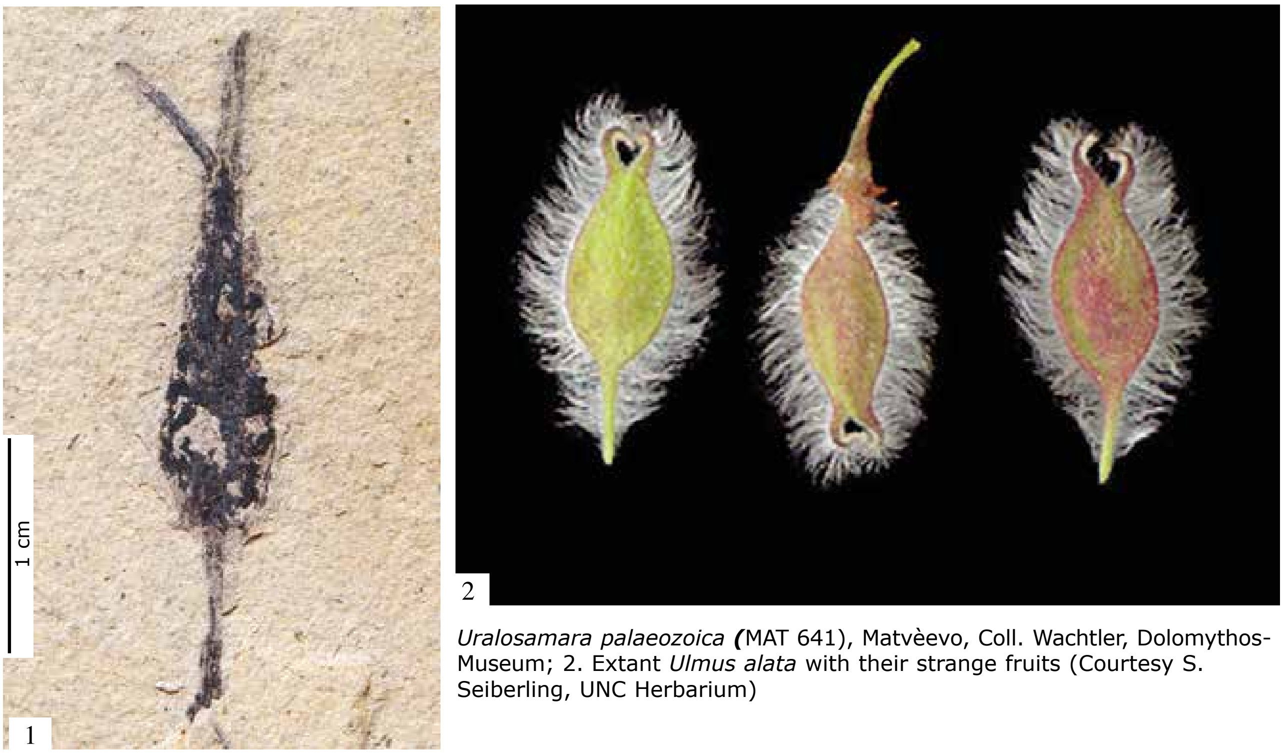
It is difficult to establish if *Matvéeva perneri* has more in common with *Ulmus* or *Dipteronia,* but typical schizocarp samaras, being a characteristic feature of *Dipteronia*, were never recorded from the Early Permian Fore-Urals.

Extant *Ulmus minor* samaras have short pedicels, whereas *Ulmus laevis* samaras have long, articulated pedicels and ciliated margins. Therefore, *Matvéeva perneri* samaras can be compared with *Ulmus minor* or *Ulmus glabra.* Interestingly, Early Permian *Matvéeva* samaras cannot be distinguished from Eocene or extant ones.

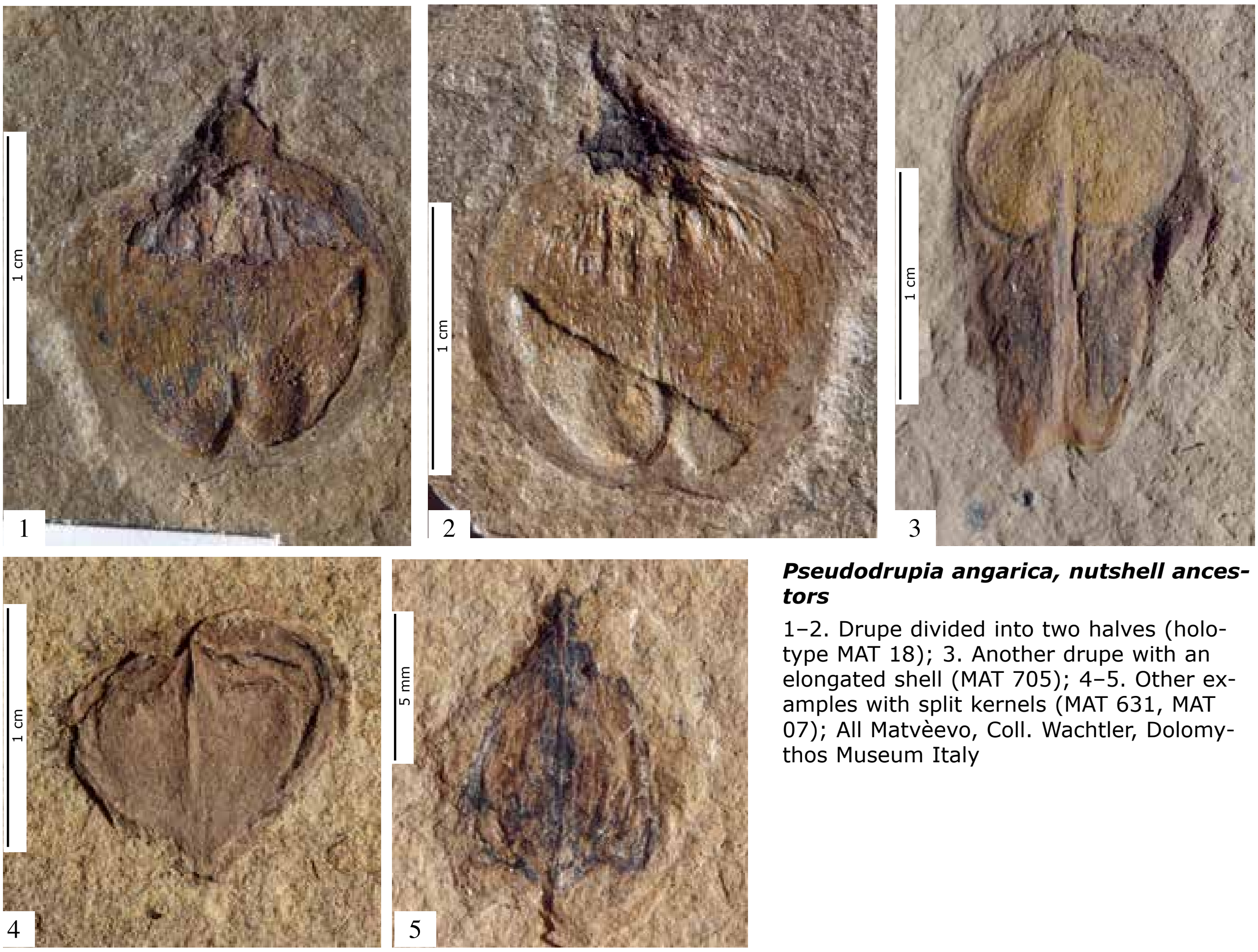
Although a close relationship between Aceraceae and Ulmaceae was suggested, just their undoubtable distinct presence in Early Permian layers manifest that they are separate families since the Carboniferous-Permian border, and we can only accept them in the sense of co-evolution. The most notable difference between today's elm samaras and the Early Permian is the well-evidenced stout seed that suggests some relationships with stone fruits.

Till now, the leaf type belonging to *Matveeva* is not exactly known, because in the Early Permian layers of Chekarda and Matvèevo, a plethora of identical leaf-types existed. If their blossoms correspond to today's elms, then *Tsvetokia nicolaswachtleri,* a hermaphrodite flower, has the maximum possibility of belonging to *Matvéeva perneri.*

Another interesting supposed Ulmus-ancestor is represented by ***Uralosamara palaeozoica.*** To encounter resembling fruits, we have to go till the Eocene of Western North America and after that to extant *Ulmus alata,* restricted to southeastern and southcentral part of the USA. *Ulmus alata* today forms a small- to medium-sized deciduous tree with comparatively small leaves for elms. The flowers are apetalous and wind-pollinated and are born on a long pedicel. Afterwards, these flowers are replaced by flattened and elliptical samaras that hold a single small nutlet in the centre. Characteristic features are the graceful hairs covering the samara and a pair of curved claws on the tip. In that, samaras of *Ulmus alata* mostly resembles Permian *Uralosamara palaeozoica.* The flattened and elongated



Uralosamara palaeozoica **(**MAT 641), Matvèevo, Coll. Wachtler, Dolomythos-Museum; 2. Extant *Ulmus alata* with their strange fruits (Courtesy S. Seiberling, UNC Herbarium)



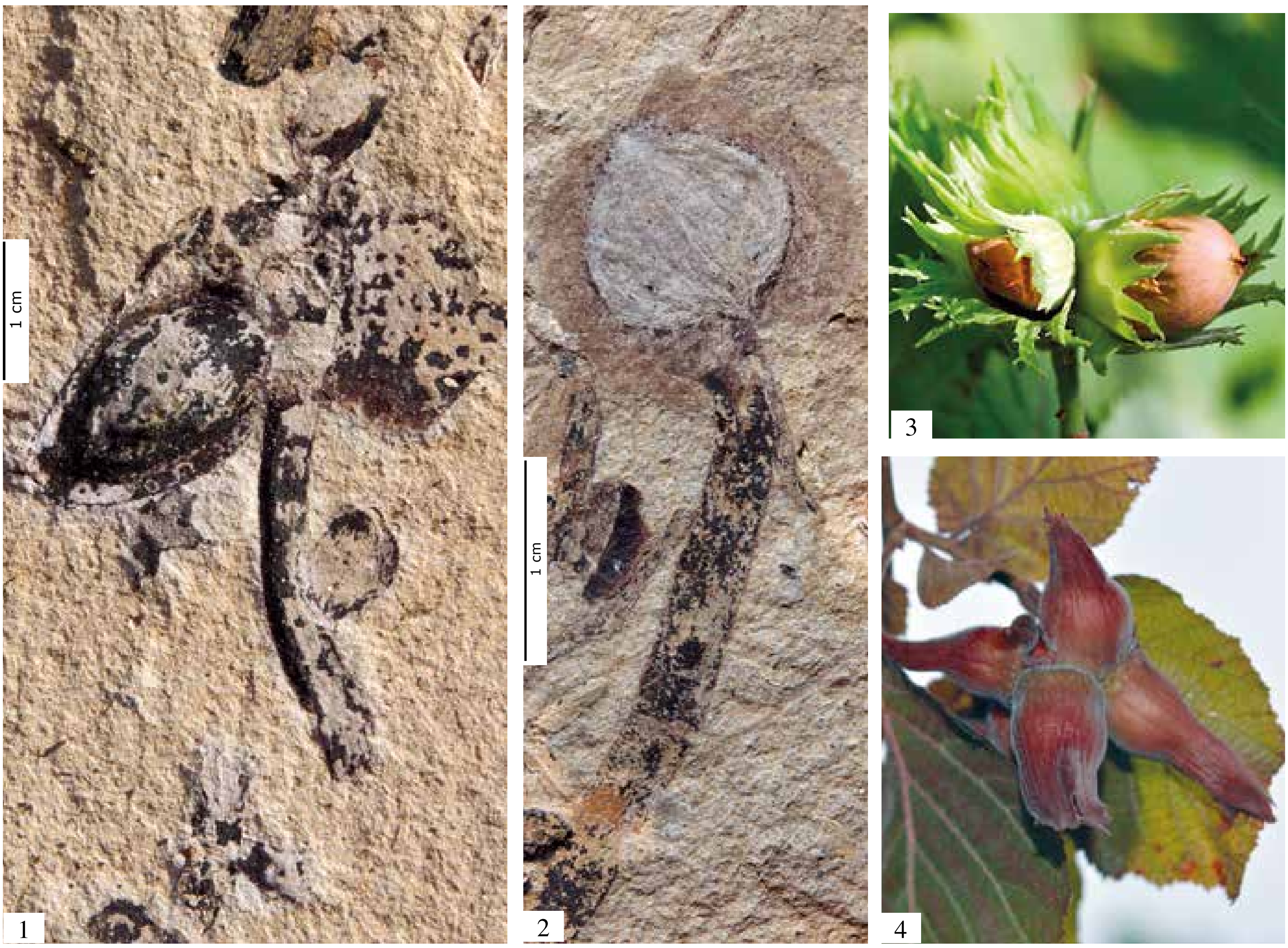
***Pseudodrupia angarica*, nutshell ancestors**

1–2. Drupe divided into two halves (holotype MAT 18); 3. Another drupe with an elongated shell (MAT 705); 4–5. Other examples with split kernels (MAT 631, MAT 07); All Matvèevo, Coll. Wachtler, Dolomythos Museum Italy samara have a pair of stigmas on the tip. It is characterised by a long, delicate pedicel. Furthermore, the samara is covered densely by filigree hairs. *Uralosamara palaeozoica* is relatively rare in the Early Permian sediments of the Fore-Urals.

Pseudodrupia angarica, characterized by one split kernel coated by an outer hard pericarp, can be regarded as a good example of a missing link between paired samaras like Early Permian *Sylvella alata,* stone fruits like *Bardocarpus aliger* and *Craspedosperma* acorns. It is therefore different from the Early Permian Fore-Urals' elm samaras like *Matvéeva perneri* having their seeds inserted in the centre of the rounded wing. Today we encounter split kernels in one nutshell like *Carya* (pecan nuts), *Juglans* (walnut) or those with winged seeds like *Pterocarya* (wingnuts). The smooth shell coated the inner divided kernel totally. Unfortunately, *Pseudodrupia angarica* is relatively rare in Matvèevo or Chekarda and thus the connecting leaves are not known.

First acorns or oak ancestors

One of the most common fruits from the Early Permian Fore-Urals are represented by acorns generating a cup-like structure. This cupula is characterised by a tuft of filamentous appendages that enclose half a seed or ovule. They were described and drawn first by Mikhail Dmitrievich Zalessky (1937b) from Matvéevo as *Craspedosperma bardaeanum.* Additionally, we encounter, widespread in all Permian sediments of this region, leaves with a broad deviance that varies from compound palmate to flabelli-



***Nucifructa primaeva* and extant hazelnuts**

1. Holotype CHEK 225; one nut is visible, the other probably was just released; 2. Juvenile nut-like infructescence, with a nut mostly covered by protecting leaves (CHEK 181); Chekarda; Kungurian, Early Permian, Coll. Dolomythos-Museum, Innichen, Italy; 3-4. Extant *Corylus avellana*, the common hazelnut. Adult and juvenile specimen.

Early Permian hazelnuts and sweetgums (***Nucifructa primaeva*** and ***Neuburgosperma radiata***)

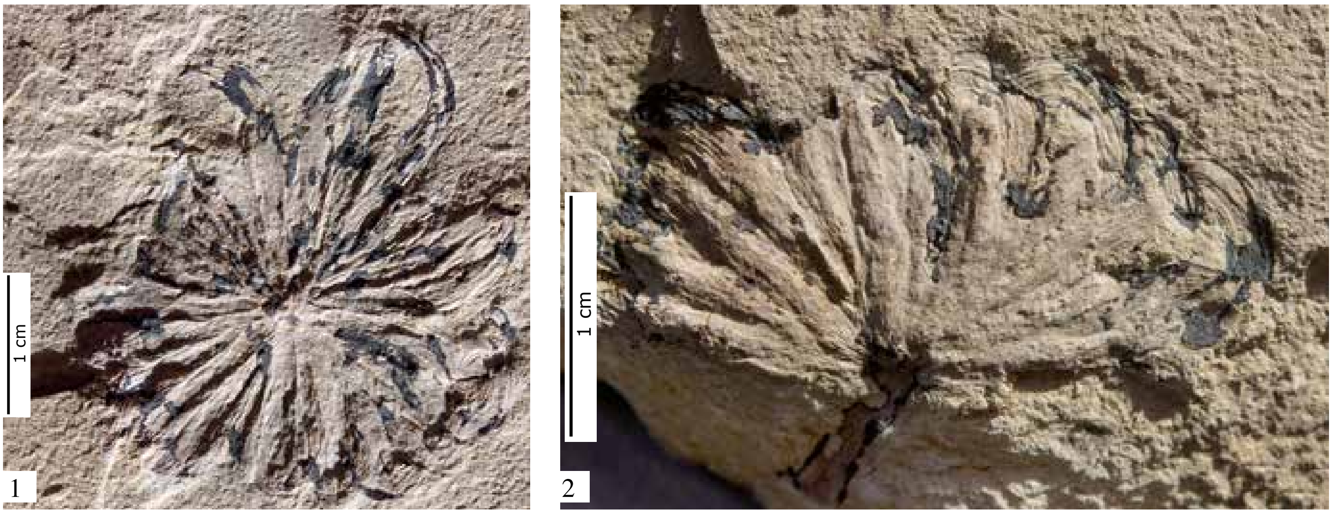
Left: the hazelnut ancestor *Nucifructa primaeva* (holotype CHEK 225, CHEK 181); **right:** the multicapsular fruit organs from the *Liquidambar* progenitor *Neuburgosperma radiata* (MAT 500); **middle:** the cockroach nymph *Czekardia blattoides;* **bottom left:** the Permian grasshopper *Uraloedischia permiensis*

forme, with usually one side more developed than the other. Sometimes they are also dissected into two symmetrical parts. One vein enters each leaf segment and then dichotomizes. These attractive leaves classified as *Psygmophyllum expansum* can be regarded, due to their conspicuous form, as most typical leaf-type of Russian Permian.

The morphogenus *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). These 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 the former Angaraland were described as having lacerated forms to compound foliage with dichotomizing main rachis. Since Early Permian Ginkgophyte leaves (*Baiera*) from European fossil sites are characterised by segmented leaves and were additionally recovered in connection with typical ginkgo seeds, which never occur with *Psygmophyllum*, other solutions must be searched for. *Psygmophyllum expansum* leaves have many similarities with extant oak foliage (*Quercus*), and if we connect *Craspedosperma* acorns, then it can be classified as the most primitive oak ancestor. *Craspedosperma bardaeanum* cupulas are densely encased on the basal side by dwarfish leaves. In a juvenile stage, they develop as mossy bristles – probably to repulse animals – and when mature, they are released from their coat, to be offered as food for dispersing animals. In that, they resemble extant oak acorns.

The Oldest Hazelnuts

Nuts found attached to stalks are not frequent in the Early Permian layers of Matvèevo or Chekarda. However, when they lack the surrounding involucre that is needed to confirm placement as coryloid genus, it is almost impossible to deduce which family they belong to. So as certain ancestor of the Corylaceae – in strictu sensu the hazelnuts – only those with a stalk and the involucrum attached can be considered.



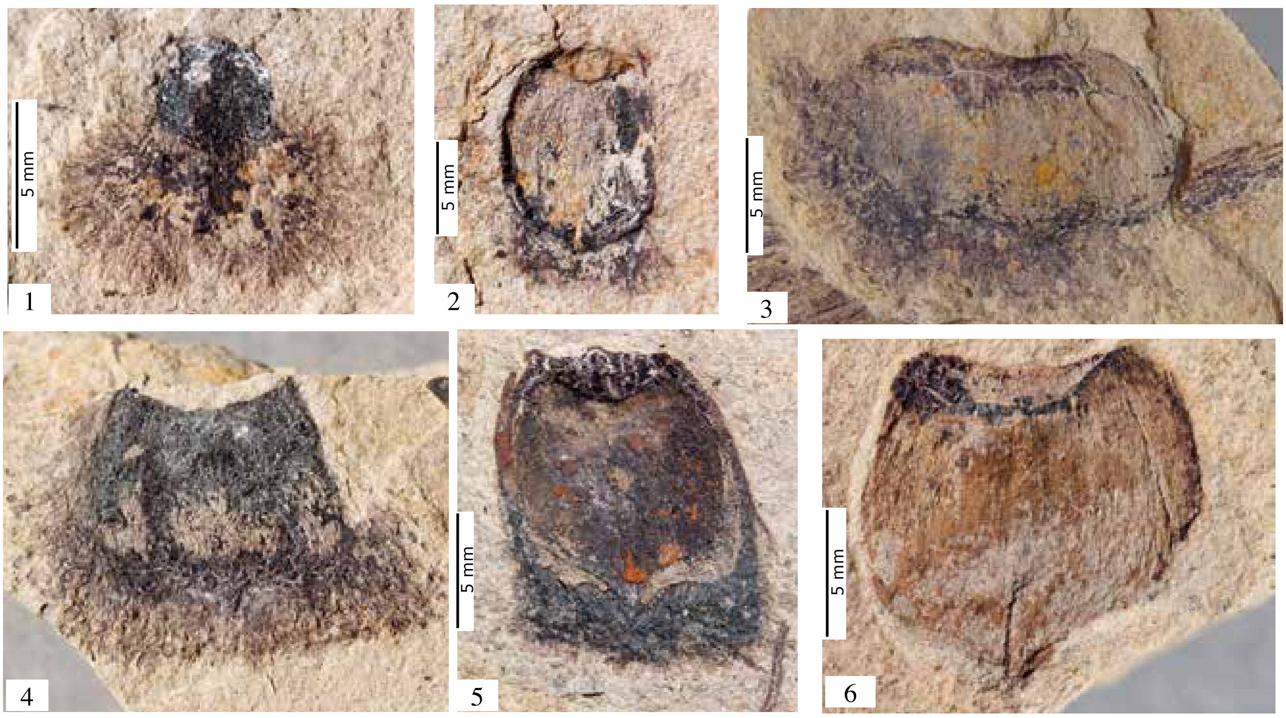
Neuburgosperma radiata. Liquidambar-ancestor
1-2. (MAT 500, Matvèevo, Coll. Wachtler, Dolomythos-Museum

Liquidambar styraciflua, the sweetgum: the globose and spiked fruits are composed of numerous capsules. The spikes are slightly incurved on the apical side, such as in *Neuburgosperma radiata* and hang from a short stalk.

The involcrum of *Nucifructa primaeva* recovered in the Early Permian Fore-Urals is composed of one dissected leaf or maybe it can be regarded as undefined amount of protecting bracts. The involucre covers, like the acorn of the oaks, only the basal part of the nuts. It is suggested that *Nucifructa primaeva i*s in some way parented with *Craspedosperma bardaeanum*, a potential *Quercus* progenitor.

The ancestors of Liquidambar

This highly interesting fruit ***Neuburgosperma radiata*** is not very common in the Early Permian Fore-Urals, but due to its characteristic globose and spiked fructification, it is easily recognisable. The spikes must have been hollow inwards and therefore, it can be assumed that *Neuburgosperma radiata* represents a multicapsular fruit organ. The nearest parental affinities we have is extant *Liquidambar* (sweetgum), a deciduous tree native to temperate areas of North America and tropical montane regions of Mexico. They are recognised by their five-pointed leaves, whereas the fruit balls are globose and spiked, composed of numerous (40–60) capsules, with one or two seeds in each. When they open



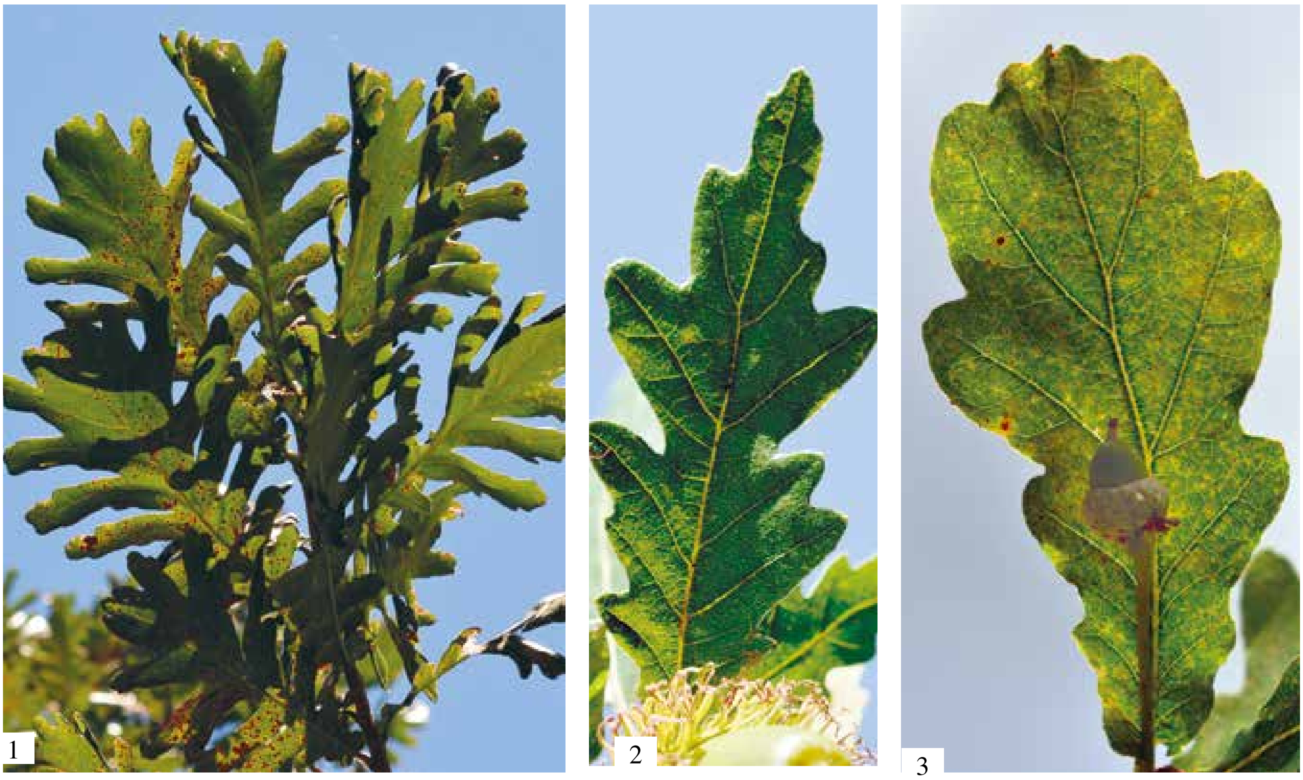
Early Permian oak-acorn *Craspedosperma bardaeanum*

1-2. Juvenile acorns (MAT 361; MAT 428); 3-5. Adult acorns with attached cupula (MAT 540; MAT 359; MAT 396) 6. Acorns released from the cupula (MAT 420); Chekarda; Kungurian, Early Permian, Coll. Dolomythos-Museum, Innichen, Italy;

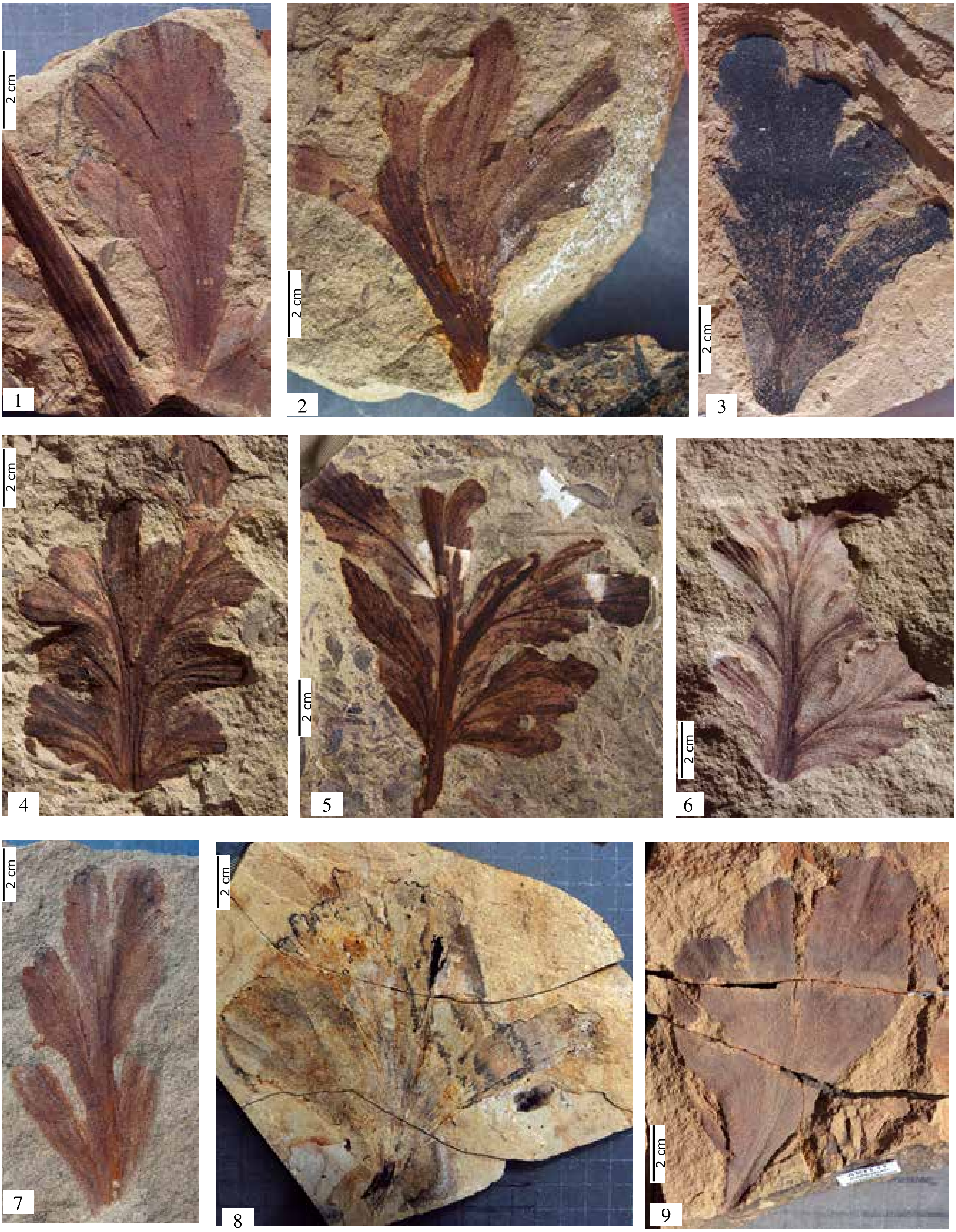
Early Permian oaks (***Psygmophyllum expansum***-leaves and ***Craspedosperma bardaeanum***-acorns)

Twig with leaves and acorns of the Quercus-ancestor *Craspedosperma bardaeanum.* In the middle is recognizable the beetle *Sylvacoleus sharovi,* in the upper left side the scorpionfly *Palaeomantis aestiva.*

Different extant oak-acorns
1–3. *Quercus cerris* juvenile, adult and mature acorn released from the tree; 4. *Quercus alba* acorns on the soil



Various extant oak leaves
1. *Quercus frainetto*; 2. *Quercus cerris*; 3. *Quercus rubor*; The leaves vary considerable within the same genera



Various Early Permian oak-ancestor leaves (***Psygmophyllum expansum***)

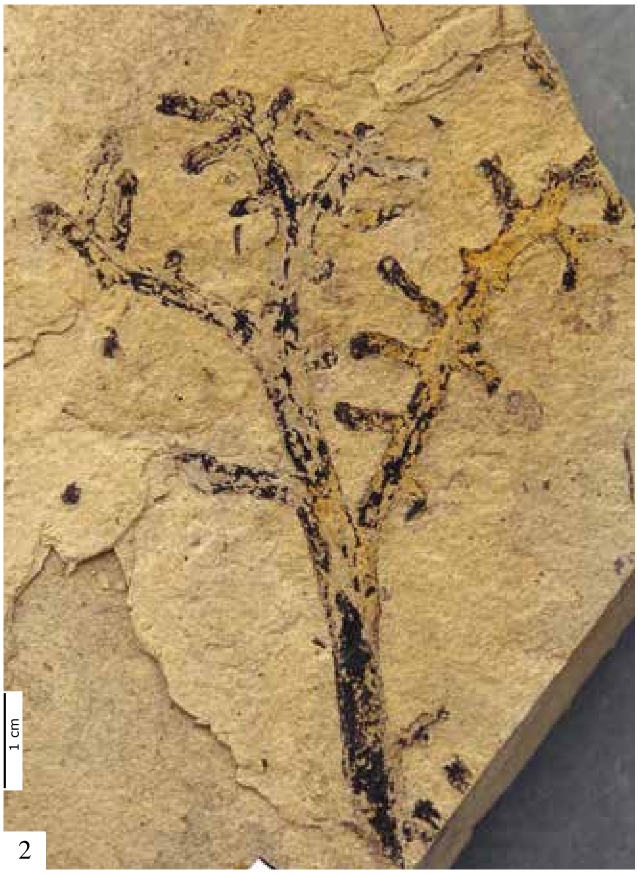
1. ARTI 19; 2. CHEK 29; 3. MAT 185; 4. MAZ 18; 5. MAZ 03; 6. MAZ 36; 7. MAZ 37; 8. MAT 506; 9. ARTI 11; (MAT = Matvèevo; CHEK = Chekarda; MAZ = Mazuevka; ARTI = Panteleykovo); All Coll. Dolomythos-Museum; Italy

Buds of a cherry tree, *Prunus domestica.*

and the winged seeds are released, a small hole is left behind. They are spiny and remain intact after their seeds are dispersed. In autumn, the entire globose fruits fall because of which they can be encountered abundantly beneath the trees. *Liquidambar* has a long fossil record, reaching back with fruits till the Eocene Republic Flora.

The Oldest Stone Fruits

In a short notice and through a drawing, Mikhail Dmitrievich Zalessky (1937b) introduced *Bardocarpus aliger,* a consistent seed covered with "épisperme", a protective outer layer surrounding the seed, from Matvéevo that was handed to him by the forestman H. T. Mauer in 1927. In the stone fruit or drupes, an outer fleshy part (mesocarp or flesh) covered by a skin (exocarp) surrounds a hardened endocarp with a seed inside. The drupe is therefore the hard, "lignified" ker-



Early Permian stone-fruit ancestor *Bardocarpus aliger*-leaves: 1. Juvenile buds from big slab MAT 82 with accompanying leaves, Coll. Perner, Dolomythos-Museum; 2. Twig with incompletely evolved leaves

Parvunucleus dammannii

This highly interesting fruit from Early Permian Chekarda (designed holotype CHEK 216, 22mm in diameter) shows a big seed in the middle and many small-sized seeds surrounding them. In that it forms a intermediate fruit with small-sized seeds like apples, pears, oranges, grapes, pomegranates (*Punica granatum*) etc.

nel that derives the wall of the flower from the ovary. There exist also aggregate fruits, which are composed of small, individual drupes (such as a raspberry). Each one is termed a drupelet that together form an aggregate fruit. Other fruits from the Rosaceae such as apples or pears have a polypyrenous drupe called a core. Drupes are common in the Early Permian sediments of the Fore-Urals. Normally, the hard part or seed of the drupes are egg-shaped or rounded, evidencing the shadow of an outer ring that coats a fleshy layer. Sometimes they are connected to a short stalk. The distance from the seed till the skin-like border can only be interpreted as a fleshy outer drupe covered by a peel.

Common in Chekarda as well as Matvèevo are fossilised flowers having five petals described as *Claireia pentafolium*. They differ notably from others like *Permotheca colovratica* having four sepals or *Sextupetalum ottiliethomsonae* and *Sextupetalum smirnovi* holding six-petaled flowers, and *Multifolium petaloides* with their multi-petaled flowers.

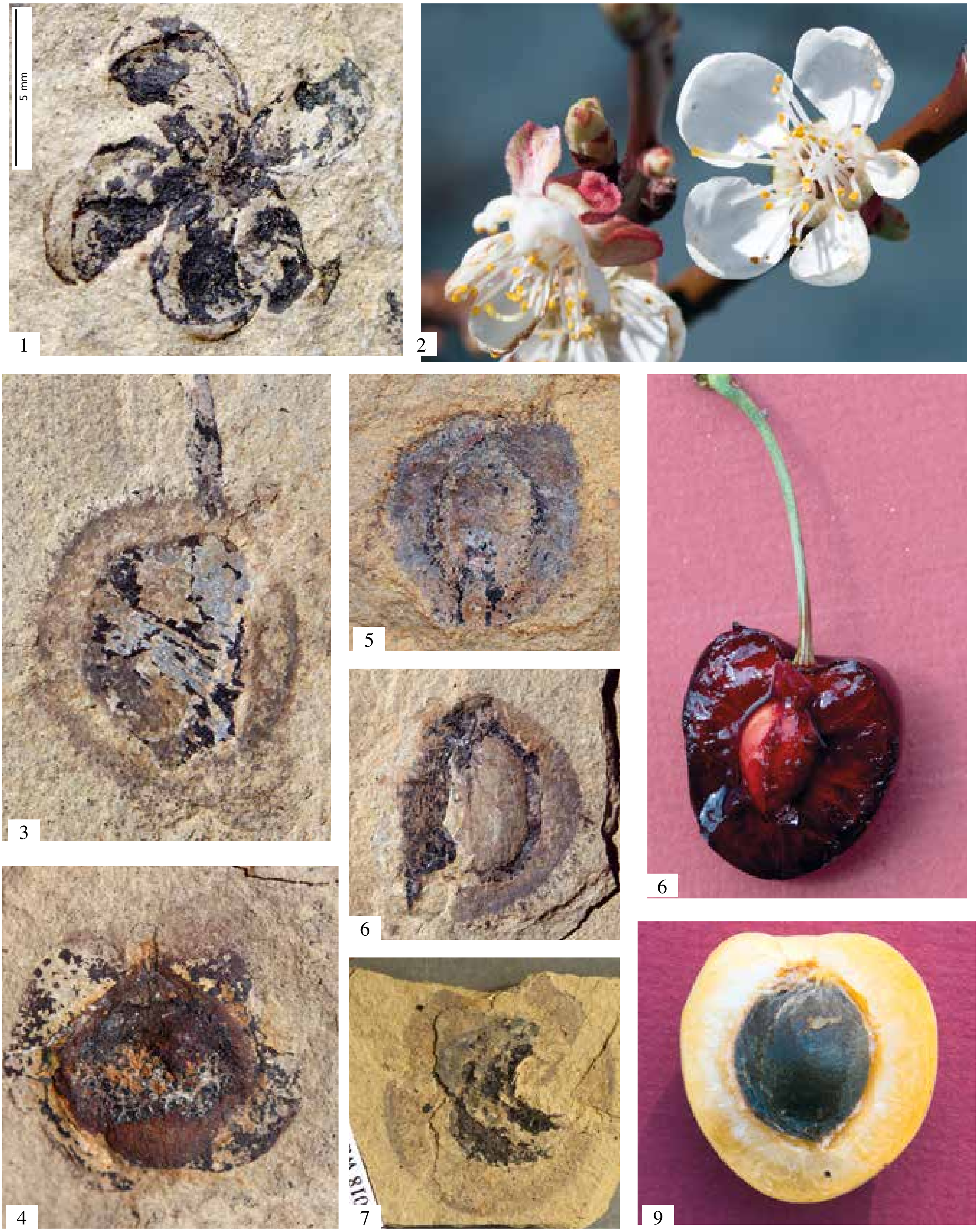
Five petals are interesting because many of today’s edible stone fruits like almonds, peach, plums, cherries and apricots and more distantly related ones, such as apples, pears and roses, are characterized by this feature. Whether the connected entire and aristate leaves evidencing a strong mid-vein can be brought in connection with the fruit-flowers is not clear till now. These kind of leaves, seeds and blossoms are relatively abundant in the Early Permian layers of the Fore-Urals.

Astonishingly, fleshy seeds with these properties or blossoms holding inside clearly visible filaments with apical anthers were till now never recorded from the Euro-American Permo-Triassic fossil sites.

A reason could be the bad quality of fossilised impressions because in Matvéevo and Chekarda, the miniature fertile organs can be evidenced well under magnification only in perfectly conserved specimen. Or probably they did not exist in Paleozoic-Mesozoic Europe. Because no known Permian gymnosperms with all these features can be connected, the angiospermic way was therefore chosen. Stone fruits, meaning those of the Rosids family date till now back to the Eocene of Western North

Early Permian stone fruit ancestor *Bardocarpus aliger* leaves

1. Whole twig and juvenile buds; 2. Detail of a leaf (MAT 82) Coll. Perner, Dolomythos-Museum; 3. Leaf of *Prunus avium*



Early Permian stone-fruit ancestor *Bardocarpus aliger*-flowers and drupes: 1. *Claireia pentafolium* a flower with five petals and detail of the stamina in the center (MAT 442, Coll. Gerasch, Thomaseum, Langenaltheim), 2. Flower of *Prunus armeniaca,* the apricot; 3-7. Drupes belonging to a stone-fruit (MAT 654 with attached stalk); MAT 415, MAT 435; MAT 400, MAT 549 all Matvèevo); Coll. Wachtler, Dolomythos-Museum; 6. Cherry(*Prunus cerasifera)* cut in the middle; 9. Apricot fruit with seed (*Prunus armeniaca*)

America or Messel in Germany. Mostly they were classified under the walnut family.

The first hesperidae

Parvunucleus dammannii can be regarded as a rare drupe in the Early Permian sediments of the Fore-Urals, and its classification or parental affinities with existing plant kingdom are difficult to correlate.

The fossilised drupe has a diameter of about 2 cm, out of which the main kernel measures 1.0 cm. Around them about 20 smaller elongated seeds having a size of only 2–3 mm can be counted. A skinny protective peel covers the whole fruit. The main seed is extremely charcoaled and very consistent. Additional conclusions can be made: the evolution from the stone fruit to the hesperidia like oranges or apples occurred through the stone fruits like apricots or cherries by reducing their main big nucleus to many small drupelets. It constitutes, therefore, one of the few samples where a real missing link could be studied. Most of the other flora elements from the Fore-Urals had their ancestors just before, between the Devonian-Carboniferous border. The differences from *Bardocarpus aliger* are obvious – *Bardocarpus* represents a freestone in form of a lignified drupe coated by a fleshy outer layer, composed of endocarp, mesocarp and exocarp. *Parvunucleus dammannii* can additionally be regarded as other missing links between aggregate accessory fruits like *Chekardofructa permica* or *Permofructa multipla*. Within an evolution context, this makes sense and explains, in some way, the development of stone-fruits, hesperida and aggregate fruits including today's raspberries or strawberries.

Early Permian stonefruits (***Bardocarpus aliger*** and ***Parvunucleus dammannii***)

On the left side sprouts stonefruit ancestor *Bardocarpus aliger* (MAT 442, MAT 654, MAT 82). On the right side hangs a fruit of *Parvunucleus enigmatica,* a strange aggregated drupelet (CHEK 216). On the left side sits the antlion *Paleuthygramma tenuicornis*, whereas in the middle is flying the Paleodictyoptera *Paradunbaria pectinata*.

Insect and Flowering Plant Interactions in the Early Permian

The Ural region on the border between Europe and Siberia represents one of the richest Early Permian places worldwide for almost all insect tribes that we know of today. Two outstanding localities can be mentioned, although they are not largely known to the public: Chekarda and Matvèevo, small villages between the cities of Perm and Ekaterinenburg. Not only 300 million years old outstanding insect variety is seen, but also a completely different flora makes this region unique worldwide because an almost unbelievable interaction between flowers and insects has been preserved there till today. All of this occurred especially in the Paleozoic on a continent called Angara, which remained isolated for many million years. Interestingly, almost all dominating insect families were present on the Carboniferous-Permian border and inside them were many potential pollinators. The Meganisoptera, survivors from the huge Meganeura griffinflies especially *Arctotypus sylvaensis,* the Megasecoptera (*Sylvohymen, Asthenohymen* or *Bardohymen*), as well as modern looking mayflies (Ephemerida with *Misthodotes sharovi*), the Orthoptera (*Tcholmanvissia longipes*), the Blattodea (*Sylvaprisca focaleata* and *Artinska infigurabilis*), the Plecoptera (stoneflies) like *Tillyardembia*, ancient book-lices (*Parapsocidium uralicum*), the Neuroptera *Paleuthygramma tenuicornis*, the beetles like *Sylvacoleus sharovi*, or the Cicada *Rachimentomon reticulatum* were recorded. We also encounter many well-preserved scorpionflies (Mecoptera) like *Agetopanorpa punctata* or the crown-group of the Acercaria with *Palaeomantis aestiva* or *Delopterum rasnitsyni*, caddisflies like *Marimerobius* and perfectly preserved Arachnida like *Permarachne.* About the presence of the Lepidoptera (butterflies) and the Hymenoptera, the sawflies, wasps, bees, ants, as well as the true flies (Diptera) *Karpinskptera pohli* cast a shadow of doubt, but it can be stated that some fossilised insects indicate in this direction.

No other place yields not only so rich and highly preserved Permian insect fossils but also such a strange fossil flora as the Fore-Urals. But no world heritage at present announce from this miracle, now cordons forbid the entering. Moreover, the difficulties to arrive in one of the remotest regions of this planet are enormous. You cannot find bars

An Early Permian landscape in the Fore-Urals with flowerings plants and insects

and restaurants and even the accommodations are far, so that the best way to survive there would be by using the old-fashioned tent. Huge streams like the Barda and the Sylva River block the entry but open new and mysterious rock-layers by eroding with their river currents every year.
If you love silence, the gliding flow of the streams without noise presents a striking contrast between itself and the rapidly growing Russian metropoles, with its routine circulating helicopters, moving trains and honking cars. Looking inside millions of years of the past sitting beside the quiet river allows you a timeless meditation, sometimes interrupted by tremendous amount of happiness when on a fine stone slab, well-defined outlines of a complete insect or a flower appear in front of your eyes. Till today, more than 8.000 insect fossils ascribed to 25 orders, 99 families, 200 genera and 257 species in total have been recovered and described (Aristov & Rasnitsyn, 2015). Others like the Wellington Formation (Artinskian Stage of Elmo and Midco in USA) yield considerably less and only partly preserved or fragmented insects. Looking at today's existing families, the theory of a slow evolution of insects evolution must be seen in a different light. The transformation occurred faster between Devonian and Carboniferous-Permian border, and this is also a valid reason for the arising of the flowering plants.
The Carboniferous-Permian border was a period of change and the background why mainly the complete plant- and animal-kingdom modified is till now unresolved. As in the plant kingdom we have a surprising simultaneous arising of mainly all insect-tribes that made doubtful the evolution-theory of a slow and gradual development of plants and animals. But whereas on the Euramerican Permian landmass the gymnosperms spread, in the other northern continent Angara evolved and diversified in a short time the angiosperms. Although the Paleozoic is labelled by the giant insects and especially the Meganeuridae, it can be stated that in the same time we encounter many smaller insect-families. Although the Early Permian Fore-Ural are one of the richest and probably most complete areas worldwide for insects and protoangiospermous plants, a long lasting political and traffic-wise isolation prevented extended studies. With this paper will be tried to synthesize the most important insights about the insect-evolution and their further developing.

The History of Insect Research in the Permian Fore-Urals

In 1925, Genrich Timofewitsch Mauer (1881–1940), a modest forestman and amateur naturalist from the small town Kungur arrived by boat and horse in the isolated villages of Chekarda and Matvèevo near the Barda and Sylva River. His collections, which are now mainly stored in Moscow, Ekaterinburg and Perm, were first described by the palaeobotanist, Mikhail Dmitrievich Zalessky, beginning from 1929, and the palaeoentomologist Georges Zalessky in 1937 and 1939, followed by the outstanding entomologist, Andreas Vassilievitch Martynov (Андрей Василиевич Мартинов). Georges Zalessky described and classified many insects from the Fore-Uralian localities in his main work "*Etudes des insectes Permiens du basin de la Sylva et problémes de l'évolution dans la classe des insectes*" (Zalessky, 1939).
Around the same time, Andreas V. Martynov, collected important data about the Polyneoptera and Palaeoptera, and he was also the first to compare the Chekarda fauna with the coeval insects from Elmo, Kansas in the United States. He was convinced that insect fossils should be studied and compared on modern insect orders and therefore, he drew attention for using the insects as stratigraphical indicators.
His wife, Olga Martynova, published in 1940, two years after his death, with the help of the Russian entomologist, Boris B. Rohdendorf (1904–1977), a voluminous synthesis about the "*Permian fossil insects from Tsekarda*" with a broad selection of drawings and plates. After the first heyday between 1930 and 1940, other researches and expeditions followed through the years. From 1959 till 1961, the acknowledged palaeoentomologist, Aleksandr Grigorevich Sharov (А.Г. Шаров), and from 1989 till 2000, Viktor Grigoryevich Novokshonov (1966-2003) with his students, gathered large insect collections from the Fore-Urals (Wachtler, 2017).
They were followed in recent times by Alexandr Pavlovich Rasnitsyn (Александр Павлович Расницын, born in 1936) and

Photos Martin Dammann

1. The locality of Matvèevo near Lyswa is not well-known but holds excellent preserved plants and insects; 2. A snowstorm cannot interrupt the research; 3. A perfectly preserved new dragonfly larva (*Permomatveevia perneri*) and 4. A mayfly (*Misthodotes sharovi*)

The river Sylva on the confluence with the Chekarda River. The fine-grained sandstone near the water is the location of the best-preserved insects and plants.

Daniil Sergeevich Aristov. Most of the oldest collections by T. G. Mauer, E. V. Permyakova, M. D. Zalessky or G.M. Zalessky are stored in Moscow, in the Vernadskii State Geological Museum (SGM) or the Palaeontological Institute of the Russian Academy of Sciences, especially those collected by V.G. Novokshonov between 1989–2000.
All the collections give a stupendous insight into the richness and variety of insects from the Early Permian in the Cisurals especially from the two outstanding locations, Chekarda and Matvèevo. Over the course of time, a multitude of insect genera and species were described based partially on wing fragments or poorly preserved specimen, which now need an urgent revision. Nevertheless, it can be established that the area around the rivers Sylva and Barda in the Fore-Urals hold one of the best keys worldwide to the knowledge about the evolution of insects after the Carboniferous-Permian border, a period during which almost all families appeared in an extremely short time.

The First Arising of the Insects

The first rudimental insects appeared in the Early Devonian about 400 million years ago. Fossil hexapods of springtails as well as bi-articulated mandibles, features known only from true insects like Zygentoma (silverfishes) and winged Pterygota, were found in the Rhynie Chert of Scotland (*Rhyniella praecursor, Palaecharinus rhyniensis*). During this period, Euramerica and the Southern continent of Gondwana moved together, whereas Angara, the Siberian continent stood isolated. In the Carboniferous, we encounter just the appearance of many diverse insect families. Orthoperoid and palaepterous groups, apterygotes, primitive hemipteroids and holometabolous hexapoda could be encountered and surprisingly, the largest insects of all time, *Meganeura*, large griffinflies with wing-sizes of more than 70 cms.
The Carboniferous-Permian border was a break in the fauna as well the flora. The reasons are still unclear. The giant lycopods on the Northern globe disappeared and made

Diaries from Genrich Timofewitsch Mauer (1881–1940), the forestman and naturalist discovered the fossil sites, Chekarda and Matvèevo. He donated his collections to Russian Museums in Moscow, Perm or Ekaterinenburg (Courtesy Perm Museum).

Married entomologists: Olga Mikhailnova Martynova (1900–1997) and Andreas Vassilievitch Martynov (1879–1938) (Courtesy V. D. Ivanov). Olga, more than 20 years younger than Andreas, was his student when they got married. Together, they studied the Permian insects.

place for a huge number of gymnosperms, such as conifers, cycads and ginkgos. The southern globe was affected during that time by extensive glaciations. On the often ignored Angaraland – today's Russia and Siberia – flourished a strange vegetation based on broad-leaves and a plethora of plants that can only be classified as having mostly all characters of the angiosperms. With them spread an infinite number of different insect groups.

Plant and Insect Interactions in the Permian

Till now it is not clear in which way began the interactions and what activated the interesting symbiosis between plants and insects. That it was obvious just in the Early Permian can be seen on diverse slabs found in Matvèevo and especially in Chekarda. On several specimen, flowers and insects were fossilised in an immediate vicinity. One extremely interesting fossil (CHEK 05) evidences a well-preserved Magnolia-like flower (*Geraschia wachtleri*) on which was deposited nearby an insect from the group of Eoblattida (*Tillyardembia antennaeplana)*. Numerous suggested adnate carpels on the basal part are covered by tepal-like leaves.

Other slabs with insect, plant or flower sedimentation are CHEK 323, where three insects belonging mostly to the Plecoptera and Mecoptera were deposited near the flower of a probable Asteraceae progenitor. On specimen CHEK 322, a stonefly nymph was fossilised near a berry (*Sylvocarpus armatus*), probably an ancestor of the Phytloaccaceae.

An almost entire plant of *Dammannia scaratiae,* a probable ancestor of the Apiaceae (Umbelliferae) evidence an embedded wing of some Permochorista (CHEK 98). Although sedimentation in the vicinity is not automatically an indication of an executed pollination, all parameters point to a solid interaction between insects and Protoangiosperms.

Pollen Content on Early Permian Insects

This will be supported by additional specimen with pollen content in the stomach of the fossilised insects or attached to the legs or wings. This was noted by Krassilov et al. (1999) and Afonin (2000). From the gut of *Tillyardembia antennaeplana,* they extracted pollen grains of the formal genus *Cladaitina* and revealed the significance of pollen for the Early Permian insects. Pollen



Left: Insect belonging to the group of Plecoptera (*Sylvardembia matura*) from Chekarda collected by Genrich Timofewitsch Mauer (1881–1940). (Foto in the **middle**: Courtesy Ural Geological Museum, Yekaterinburg). **Right:** From 1959 till 1961, entomologist Alexandr Grigoryevich Sharov (1922–1973) organised expeditions to Chekarda, collecting abundant material, especially insects (Courtesy: Perm Museum).

Tillyardembia antennaeplana, Grylloblattida

Flower of *Geraschia wachtleri* (probably belonging to the Magnoliaceae) and the impression of an accompanying insect (*Tillyardembia antennaeplana*) from the stonefly family (CHEK 05, Chekarda, Detail of the holotype, Coll. Gerasch, Dolomythos-Museum, Italy)

content was also found in the stomach of the Miomoptera *Sellardsiopsis conspicua* (MAT 181, Matvéevo), Gryllidae like *Angaroptera nicolaswachtleri* (MAT 190, Matvéevo) (Wachtler, 2017) and *Tillyardembia* (CHECK 323). Therefore, it can be stated that most of the insects in the Early Permian Fore-Urals had, in various ways, contact or interactions with the plants. Obviously in that case they served as pollinators.

It can be assumed that the first Proto-angiosperms were wind- as well as insect-pollinated. Although several theories propagate wind pollination (anemophily) of angiosperms as derived from insect pollination (entomophily) in response to pollinator limitation, an antecedent wind versus a both-wind-and-insect pollination (ambophily) to a gradual predominantly insect pollination is more plausible. 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.

The way to the interaction between insects and plants is not based on an evolution-miracle but is a logical consequence of certain developments especially in the former Angaraland and, only in a minor case, in the Euro-American region. The hard and most of the season closed pollen cones in addition to the piercing needles or fronds of conifers of the gymnosperms were only of limited suitability for a faster radiation of the insects. In the former Siberian Angaraland, from the Devonian evolved mostly hermaphroditic plants with a richness of open pollen-plugs.

The evolution of angiosperms and insects is mainly based on the dogma that the flowering plants need a pollinator. But the fecundation requires only a short time in the plant life every year. With what were the insects then occupied or what did they eat for the rest of the year? Here come in action another and more important factor of

1. Three insects, the one on the left probably belongs to the Blattodea *Sylvaprisca focaleata,* the one in the middle could be the caddisfly *Palaeomantis aestiva* (CHEK 323, Coll. Perner); right: lateral view of the multi-petaled flower, *Zalesskya multipla*, probably an ancestor of extant Asteraceae; 2. The stonefly larva *Uralonympha varica* (6 mm) was deposited near a berry of *Sylvocarpus armatus*, a potential ancestor of the Phytolaccaceae, known as pokeweeds (CHEK 322, Chekarda). Coll. Perner, Dolomythos Museum, Italy

the Permian Angara-continent – juicy fruits, lush leaves and tasty nuts. A plethora of multiple or aggregate fruits can be found in Matvèevo or Chekarda: They were known as *Matvèevofructa bardaensis, Permofructa multipla, Sylvafructa aggregata* or *Uralofructa magnoliformae*.

Some of them can be correlated with today's composite fruitlets that show a clustered character, while for others, comparisons are difficult. Then we encounter delicious small berries like those of *Sylvocarpus armatus*, a presumed progenitor of the Phytolaccaceae or one of the most common stone fruits *Bardocarpus aliger,* probably an early descendant of drupe-bearing broad-leaves like today's apricots or cherries.

Also, another question is not easy to answer: Why do we need so many different insects and why so many paleoangiosperms? This obvious problem is not unsolvable. Different flowers from huge to small-sized required the development of new insects, from dwarfish till voluminous. Within the evolution context, it is more understandable that this happened just in the Permian hundred million years earlier than presumed Early Cretaceous or the Jurassic.

The suggestion is that on the Euramerican continent in the Permian, we had a richness of gymnosperm tribes like two-seeded till many seeded cycads, gingkos like *Baiera* with its coated seeds, wing-seeded *Majonica* conifers, one-seeded Araucarian ancestors like *Ortiseia*, hard and small pine-tree cones from *Férovalentinia*. Many lycopods partially reached mostly the level of a hermaphroditic plant. However, this was the other evolving

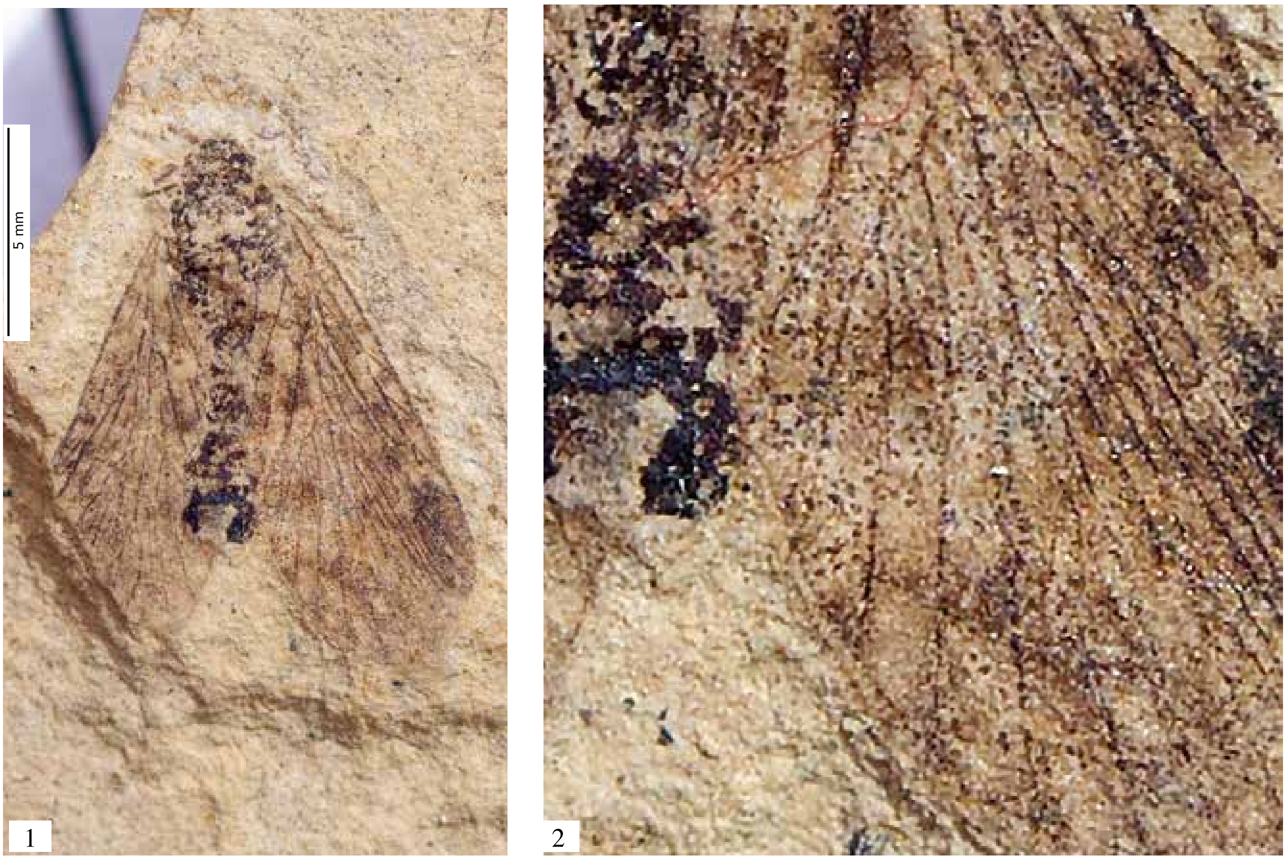
An almost entire plant of Dammannia scaratiae, a probable ancestor of the Apiaceae (Umbelliferae) and an embedded wing of a *Permochorista* (CHEK 98, Chekarda, Kungurian, Coll. Dammann)

line and cannot be compared with the Sibirian Angaraland.
Summarizing can involve the not so far-fetched theory that generously presented nutritious pollen gut brought several advantages and helped a selective pollination. Probably it was more efficient than the accidental fertilisation by wind. If a plant tempted a more favourable insect by adding certain aromatic ingredients or substances, then the flower could count every year on a productive symbiosis.

The Giant Meganeuridae in the Permian Ural

The Meganisoptera represents a Late Carboniferous-Permian order of huge to gigantic insects, occasionally called griffinflies. The former name, Protodonata, given for their similarities with extant Odonata (damselflies and dragonflies) indeed, is no more in use. Interestingly, the first described Late Carboniferous *Meganeura monyi* (found in France) as well as Early Permian *Meganeura permiana* (from Kansas, USA) reached wingspans of up to 70 centimetres, making them the largest insects that ever lived.

During that time, the Meganisoptera and especially the Meganeuridae were widespread across a large area covering Euroamerica, Siberia and Northern China. The Carboniferous Meganeuridae were also well-adapted to live in humid and warm palaeoenvironments, and after successfully being able to adapt, the climate in the following drier Permian time. Therefore, the question as to why in the Late Carboniferous, where the atmosphere contained more oxygen than in the Permian, with an oxygen concentration comparable with the present, only the Meganeuridae could reach never recorded gigantism remains unanswered till date. Maybe it was due to the lack of other competitors, or that open spaces allowed to move better. Probably the species did not move inside the dense swamp forests filled with giant lycopods and horsetails but preferred open habitats, patrolling above large rivers, ancient lakes, open forests or even above the canopy.
Notably, we encounter an identical phenomenon in the flora with the lycopods and horsetails that reduced their size from the Carboniferous till the Permian considerably. Moreover, there were no obvious reasons



1–2) Pollen dust covers the wings of *Agetopanorpa punctata*, a suggested scorpionfly (MAT 495), Coll. Thomas Gerasch, Thomaseum-Museum, Langenaltheim), Matvéevo, Early Permian, Kungurian.

for the usefulness or the background of this dwarfism.

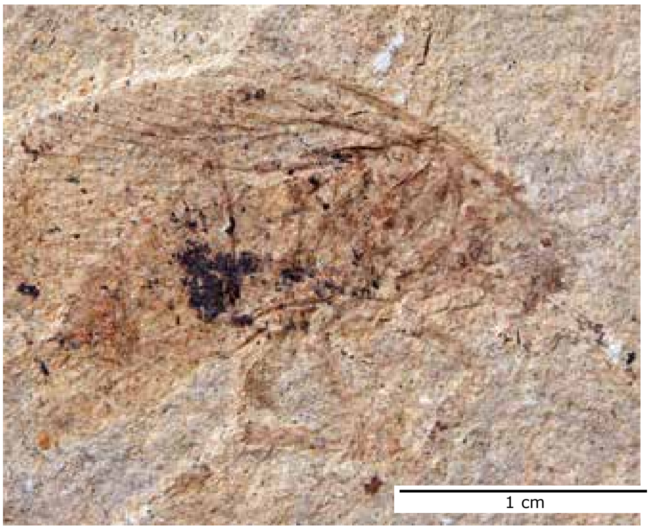
During the Late Carboniferous and especially in the Early Permian, bigger and smaller Meganeuridae simultaneously existed, reaching only the size of today's dragonflies or Anisoptera and confirming a co-existence of different life habits of these ancient flying predators. But the huge *Meganeura monyi* did not have a large body. Only their wings were proportionally larger when compared with modern dragonflies.

In the Permian Angaraland, the most well-known Meganisoptera was *Arctotypus sylvaensis*, described for the first time in 1940 by Martynov. From the slightly younger (Middle Permian, Roadian) lagoonal sandstone of the Iva-Gora Beds Formation previously in 1932, he had just described another Meganisoptera genus, *Arctotypus sinuatus*.

The forewings of *Arctotypus sylvaensis* were usually slender and slightly longer than the hindwings, but both evidenced a similar venation. Unlike the true dragonflies, the Odonata, the Meganeuridae were presumably active predators. The few complete specimen suggest that they possessed enlarged compound eyes that were specialized for long-distance vision above the animal in flight, a trait convergent with modern hawker dragonflies or the perchers.

The Meganisoptera, *Arctotypus sylvaensis*, thus represents together with the Orthoptera *Tcholmanvissia longipes*, the form and size of most impressive insects of the Early Permian Ural region, giving an insight into the evolution of Odonata and Orthoptera in the next millions of years. Some nymphs from the early Permian Fore-Urals can be regarded as belonging to the Meganisoptera. *Permomatveevia perneri* constitutes the largest insect larva found in the Early Permian Kungurian layers. But even *Sylvonympha tshekardensis* reached a considerable size. The larvae display an averagely broad, robust body with very long extremities. Especially, the posterior legs appear enormous in relation to the (visible) body length. The three pairs of legs hold robust pedipalpal claws straight and modestly. *Permomatveevia* was characterised by a strong pair of chelicera and two median eyes close to the central anterior margin.

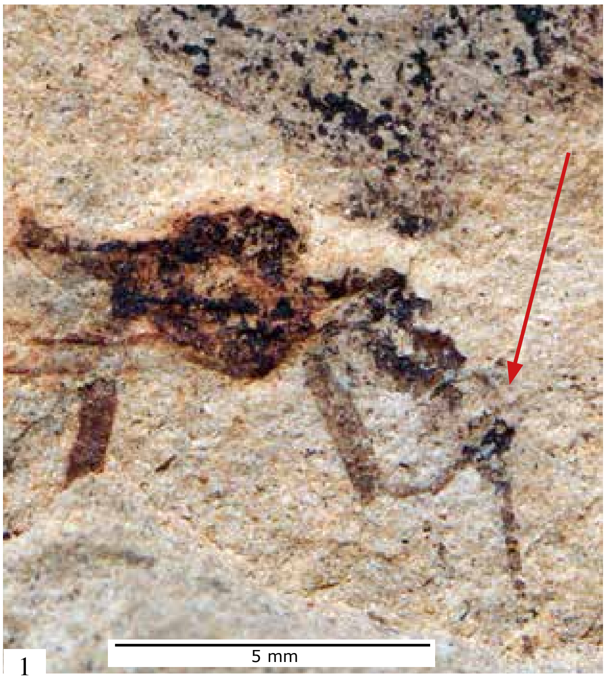
Insects from the Early Permian Fore-Urals with Pollen Gut in the Stomach

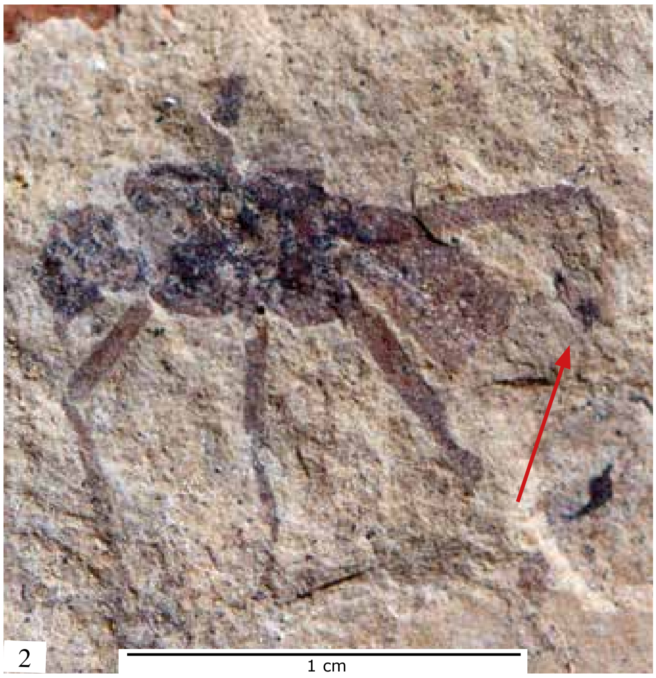


Sellardsiopsis conspicua

Body length is 20 mm (MAT 181); lateral view showing pollen content in the stomach and attached to the wings; right: magnification of the pollen gut content. Coll. Wachtler, Matvèevo.

Angaroptera nicolaswachtleri, probably a dragonfly nymph; otherwise, it can be inserted in the Gryllidae or the cicadas. The stomach is filled with pollen grains (holotype MAT 190, Matvéevo, Early Permian, Kungurian, Coll. Nicolas Wachtler, Dolomythos Museum)





1–2. Two stonefly nymphs (probably *Uralonympha varica)* with pollen gut on their legs (CHEK 93) Coll. Wachtler, CHEK 322, Coll. Perner), Chekarda, Dolomythos-Museum, Italy

1. Two insects, *Tillyardembia antennaeplana* (bigger one) and the Miomoptera *Delopterum rasnitsyni,* on the same slab (CHEK 359, Coll. Perner) 2. The cicada *Ra-chimentomon reticulatum* hanging on a blade of grass (MAT 189, Coll. Wachtler)

The Spreading of the Megasecoptera and Palaeodictyoptera

A big but obscure group of insects from the Early Permian Fore-Urals is included in the Megasecoptera and in the closely related Paleodictyoptera. Probably they must be segregated into other natural groups. The Megasecoptera are recorded from the Upper Carboniferous over the Permian, and it is suggested that they are related to the mayflies and dragonflies. Terms given especially by Zalessky (1937), such as *Sylvohymen, Asthenohymen* or *Bardohymen*, indicating towards extant Hymenoptera (sawflies, wasps, bees and ants) are confusing because they cannot be regarded as directly parented. The Megasecoptera, especially the most abundant *Sylvohymen sibiricus* from the Early Permian Fore-Urals, hold two pairs of long, slender and slightly subequal wings. The wings evidence a poor venation pattern, and they were palaeopterous, meaning that they were unable to fold them over the abdomen like the dragonflies (Odonata).

Like the Paleodictyoptera, the Megasecoptera often had sucking mouthparts. They were probably used to pierce plant casings and extract plant materials, such as spores and pollen. The head was small, short and broad, with large projecting eyes, holding long antennae. The Early Permian Palaeodictyoptera, usually bigger than the Megasecoptera, were represented especially by medium to very large *Paradunbaria pectinata,* a monotypic genus that was found in fair amounts in Chekarda. They were characterised by beak-like elongated mouthparts, including sharp piercing stylets and a sucking pump-like organ. The fore and hindwings were almost equal. Unlike modern sucking insects, such as the Hemipterans, the mouthparts were either held vertically below the head or projected forwards. They probably used these organs to suck juices from plants, although some may have been ectoparasites or predators.

Another genus belonging to the Palaeodictyoptera was *Uralia maculata.* It was inserted within the clade Cimiciformes or Scarabaeiformes. The Diaphanopterida most strikingly differ from Dictyneurida and other related orders in folding back the wings roof-like over the abdomen at rest, instead of keeping them permanently outstretched. Another difference is the apparently identical venation of both pairs of wings.

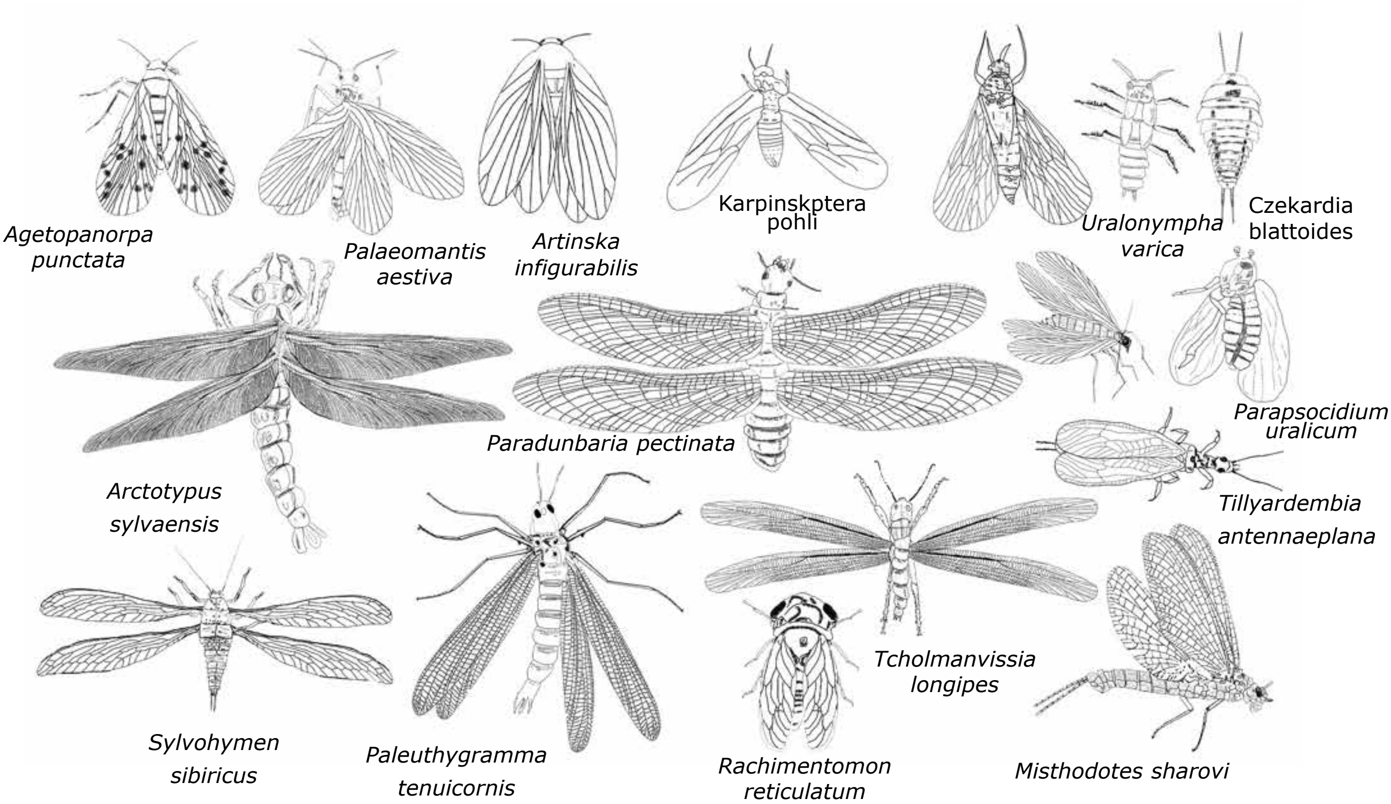
The Odonatoptera (Dragonflies)

The first Protoodonata are recorded from the Upper Carboniferous and include now about 3,000 known species. Most live in the tropics, but a fair amount can also be encountered in the temperate regions all around the world. They are characterised by large, multifaceted eyes, two pairs of strong, transparent wings that are held flat and away from the body that make them agile fliers. Dragonflies undergo incomplete metamorphosis. Their life cycle includes three stages – egg, nymph and adult. All dragonfly nymphs are predators. They can be encountered in still waters but can be found in slow flowing parts of rivers and streams as well. Odonate nymphs generally have long bodies, large heads with large eyes and long, slender legs.

An insect nymph from Matvèevo – *Angaroptera nicolaswachtleri* – has strong resemblance with modern dragonfly nymphs. It has a body length of 3.5 cms, a moderate-sized insect larva, with strong body and slender limbs. The antennae and cerci are delicate. Some affinities indicate in the direction of Gryllidae or Cicadoidea, and that *Angaroptera nicolaswachtleri* represent an Orthoptera to which the grasshoppers, locusts, crickets or the cicadas belong.

The Mayflies (Ephemeroptera)

The Mayflies are known from the Early Permian. In the Permian, they were abundantly found along with specimen recovered from North America till Western Europe and the Russian Fore-Ural region, mostly belonging to the genus *Misthodotes*. They evidence a strong larval fidelity to freshwaters (standing or running) and a short adult stage devoted solely to reproduction. Mayflies are also unique among other insects because of an intermediate winged stage between the aquatic nymph and the reproductive imaginal stage called the subimago. In contrast to other insects they evidence some strange features: the Ephemeroptera and Odonata cannot fold their wings back over the abdomen. This adaptation of other insects increased their



Permian Insects and Angiosperms
Several flowers and insects from the Early Permian Fore-Urals

ability to move freely over a substrate and to penetrate small spaces. The hindwings of insects like the Dermaptera, Coleoptera, or the cockroach Diploptera, fold up transversely, as well as longitudinally in some cases, with extraordinary complexity.

Therefore, the Ephemeroptera and the Odonata, sometimes were inserted together in the family of the Paleoptera, which was considered the sister group of all other extant primarily winged orders. As seen in the Early Permian, a plethora of many totally different insect groups simultaneously appeared, so that the evolution and diversification of many insect tribes is prejudiced by many unresolved questions. Another theory suggested that Ephemeroptera are only a sister group of Odonata and Neoptera. This concept is based on several features unique to mayflies, such as the presence of a subimaginal stage, the nonfunctionality of adult mouthparts and the presence of only one axillary plate in the wing articulation.

Misthodotes sharovi from the Permian Fore-Urals is characterised by its bigger forewings and reduced hindwings, evidencing a dense venation. The wings typically did not fold flat over the abdomen. They were equipped with two filamentous cerci reaching considerable length. The antennae otherwise were short and fine.The nymphs of the Misthodotidae are not definitely known. Tschernova (1965) has described a fragment of a nymph from the Chekarda beds and identified it as belonging to *Misthodotes sharovi*. The nymph has nine pairs of gill plates, as in the protereis matid nymphs, but since the entire thoracic region, including the wing pads, is not preserved, there is really no evidence for associating the specimen with *Misthodotes* or even with its family.

The Rise of Many Neoptera Tribes in the Early Permian

The Neoptera (from New Latin words "neo", meaning new and "ptera", meaning wing) include today a plethora of families, such as the beetles, flies, wasps, butterflies, true bugs, lice, bees, fleas, ants, stoneflies, grasshoppers, mantids and cockroaches. All of them had reached a milestone in insect evolution using the ability to flex their wings over the abdomen. In the Paleoptera, either fossil or extant like the mayflies and dragonflies, the fusion of sclerites occurred to form additional plates that became united with some veins. In that, it strengthened the attachment of the wings but made it impossible to fold the wings.

In the Neoptera, the sclerites moved away from the tergum and became articulated,

A Meganeuridae probably *Arctotypus giganteus,* Chekarda, Courtesy: Perm Museum of local lore. The difference between other *Arctotypus*-species is notable. It could belong to a new genera.

A wing of the Meganeuridae *Arctotypus sylvaensis* from Chekarda. Paleontological Institute of the Russian Academy of Sciences, Moscow. Reconstruction

making folding of the wings possible. Because of that the flight efficiency was also increased. Another advantage was that the Paleoptera probably needed open spaces, whereas the Neoptera could easily move between the leaves and flowers, increasing the interaction between plants and insects.

The Origins of the Orthoptera

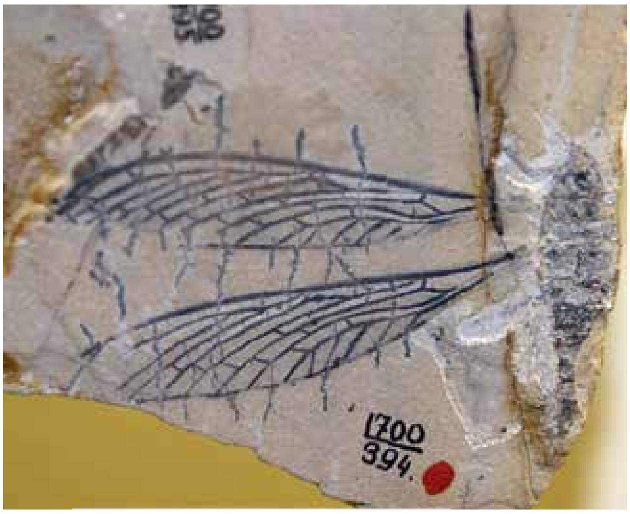
The Orthoptera appeared first in the Upper Carboniferous and comprise today about 20,000 species, which are distributed worldwide, with the biggest variety in the tropics. They are subdivided into two suborders, although this is based on superficial differences: the Caelifera, including the grasshoppers and the locusts; the Ensifera, including the crickets and other closely related insects such as the katydids and wetas. The body length of the Orthoptera can reach considerable sizes of 12 cms, with wingspans of over 22 cms. Their characteristic features include an incomplete metamorphosis, a strange sound-producing stridulation by rubbing their wings against each other or their legs and the wings or legs containing rows of corrugated bumps. The tympanum or ear is located in front of the tibia in crickets, mole crickets and katydids and on the first abdominal segment in grasshoppers and locusts. All these organisms use vibrations to locate other individuals. Grasshoppers and other orthopterans are also able to fold their wings.

In the Early Permian of the Fore-Urals, we encounter the Tcholmanvissiidae, including two closely related subfamilies, the Tcholmanvissiinae (described first by G. Zalessky, 1929) and the Tettoedischiinae, the first Protorthoptera.

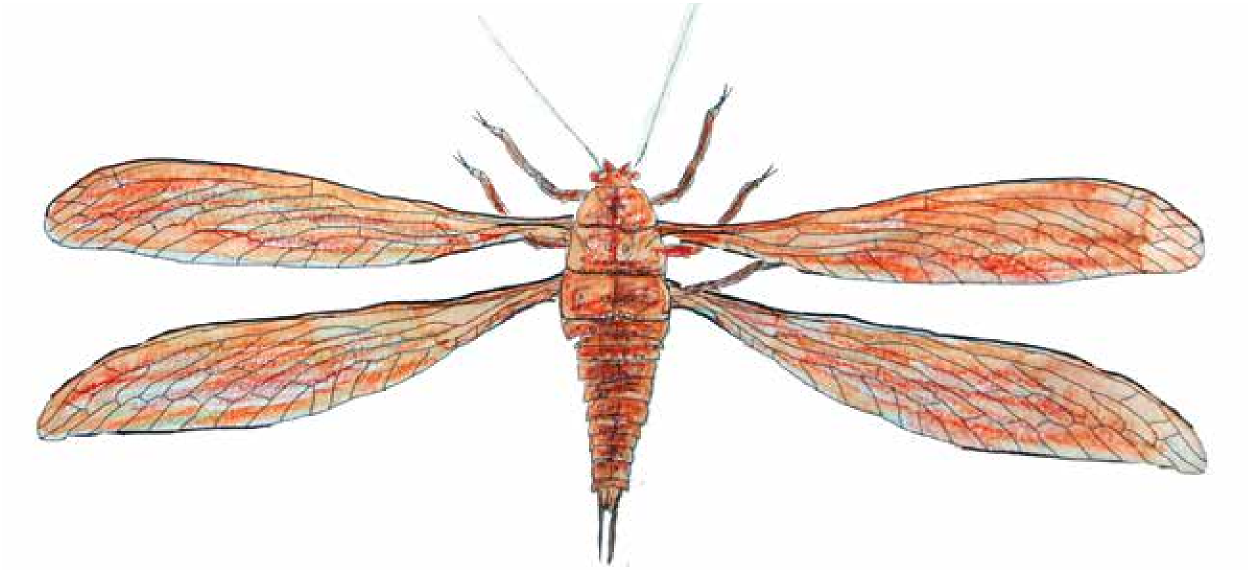
Tcholmanvissia longipes (synonyms: *Metoedischia longipes* and *Pinegia longipes)* – the most frequently found species – had jumping legs with broadened femora, whereas all the representatives of this family share the 'oedischioid' arrangement of the cross-veins in certain areas of the wings. A close relationship as crown group of the Caelifera will be sustained by analyses.

Another group of Orthopterans in the Early Permian Fore-Urals are represented by the Oedischiidae. Although they appeared in the Late Carboniferous, they experienced a heyday in the Permian with genera like *Uraloedischia* and *Metoedischia*. They had a cylindrical body with elongated hindlegs and musculature adapted for jumping. The mandibulate mouthparts were adapted for biting and chewing. The hindwings were held folded fan-like under the forewings. The forewings were narrower than the hindwings and hardened at the base, while the hindwings were membranous, with straight veins and numerous cross-veins. From the Permian Urals, *Uraloedischia permiensis* and *Metoedischia longipes* are especially known.

Although the Tcholmanvissiidae as well the Oedischiidae have about the same wing features, it is possible that *Tcholmanvissia*



The Megasecoptera *Sylvohymen sibiricus.* Female specimen. Fore wing length 50 mm, maximum width 9 mm. The veins are secondarily coloured by manganese. Chekarda, (Paleontological Institute of the Russian Academy of Sciences, Moscow). Right: Detail of an isolated wing within a plant (Coll. Gerasch).



The Megasecoptera *Sylvohymen sibiricus.* Reconstruction.

longipes, as well as *Uraloedischia permiensis* may also belong to the same insect, and we have to study them only under different fossilisation conditions. *Paleuthygramma tenuicorne* has some affinities with the Protothoptera, although it was also inserted in the Caloneurodea. Altogether, it can be stated that the Protorthoptera played an important role in the Early Permian Fore-Urals. They had resemblance with today's grasshoppers, but evidence still shows difficulties to flex their wings on the abdomen. Nevertheless, they were just good jumpers. The arrangement of the mouthparts made them well-adapted for chewing fruits, seeds, flowers or other parts of plants.

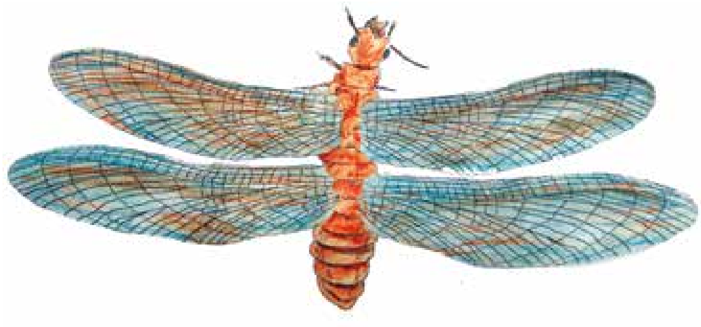
The First Blattodea – Cockroaches

The cockroaches, being members of the order Blattodea along with the termites and mantises, include currently 460 genera and about 4,600 species. They are widespread across cold areas till the tropics. Some cockroaches are connected with human habitats, associated as pests.

The existence of the Blattodea in the Paleozoic, especially in the Early Permian Fore-Urals was often suggested, but substantial evidence was never easy to obtain. In particular, adult fossilised specimen were inserted not only in other insect orders like the Grylloblattida, Orthoptera or the Hypoperlida, but also in the Eoblattida.

Paradunbaria pectinata, pertaining to the Palaeodictyoptera - Spilapteridae. Body length 25.0, forewing 22.0 x 7.0, hindwing 23.0 x 9.0, (Paleontological Institute of the Russian Academy of Sciences Moscow.

Uralia maculata belonging to the Diaphanopterida is a first representative of the Cimiciformis (Chekarda, Paleontological Institute of the Russian Academy of Sciences, Moscow)



The Paleodictyoptera *Paradunbaria pectinata*

The difficulties in the classification are due to the fact that only a simultaneous recovering of adult and juvenile insects and their comparison with extant specimen allows making reasonable hypothesis about their ranking. It also seems that the locality of Matvèevo is somewhat richer in Blattodea than Chekarda. The nymphs of *Czekardia blattoides* can well be connected with the Blattodea, especially the extant genus of *Blaberus*. The larvae evidence a slightly elongated body (about 15 mm length and 6 mm wide), the head is transversal, with normal eyes, and the antennae are short. All segments of the body are transversal and longer than wide. The tarsus is three-segmented, and the cerci are well-developed and long. Like current Blattodea, the nymph's have a different appearance, lacking wings and being segmented as the adults. Other larva described and thought to belong to Permian cockroaches in this area are *Iblatta attrepida* and *Tshekardushka artenatis*. Adult cockroaches from the Early Permian Fore-Urals were known as *Sylvaprisca focaleata* and *Artinska infigurabilis*. They were medium-sized insects. The antennae and legs were thin and long, the thorax was broad, and the wings were membranous, evidencing no strong veins.

Permian Cicadas

The Cicadas form a small part of the order, Hemiptera, a diverse group of insects whose mouthparts comprise a jointed rostrum for piercing and sucking up liquid food. They have prominent eyes set wide apart, short antennae and membranous front wings. The Cicadoidea are divided into two families, the majority falling within the Cicadidae and just two extant species plus some fossil species in the order Tettigarctidae. There are almost 2,000 named species, with perhaps as many again awaiting description. Extant Cicadinea are found all around the world in temperate to tropical climates. The cicadas spend most of their lives as underground nymphs, emerging once in 13–17 years.

The earliest known fossil, Cicadomorpha, appeared in the Early Permian along with the families, Aphidinea and Auchenorrhyncha. Others like Palaeontinidae, commonly known as giant cicadas, can also be regarded as cicadomorphs with large bodies, small heads and four broad wings. They superficially resemble moths.

The oldest Cicadomorpha, the Archescytinidae, were first recorded in the Artinskian

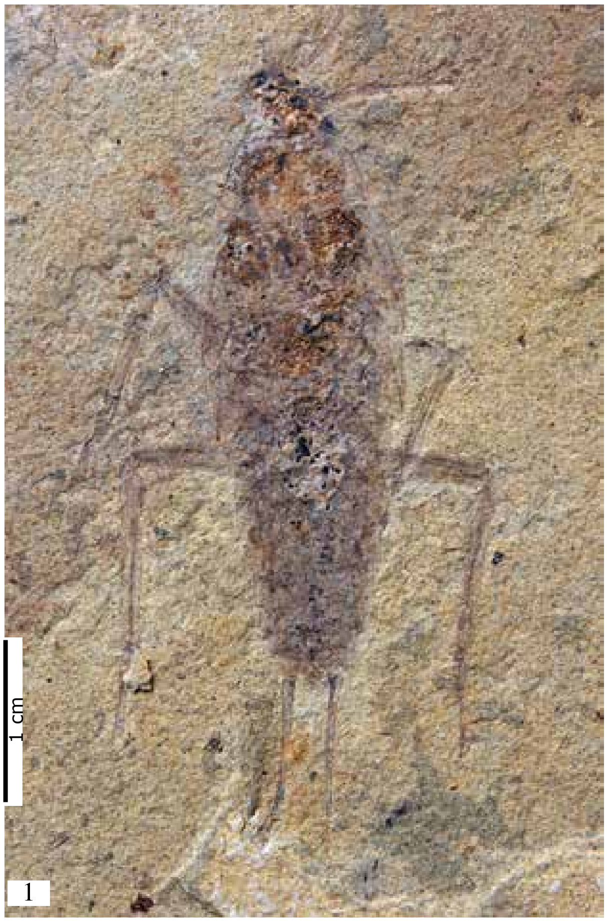
Permomatveevia perneri, a probable Meganeura-nymph. The six massive legs indicate in this direction (MAT 122), Matvéevo, Early Permian, Kungurian, (Collection Martin Dammann). The overall (visible) body length is 50 mm, its overall width 16mm.

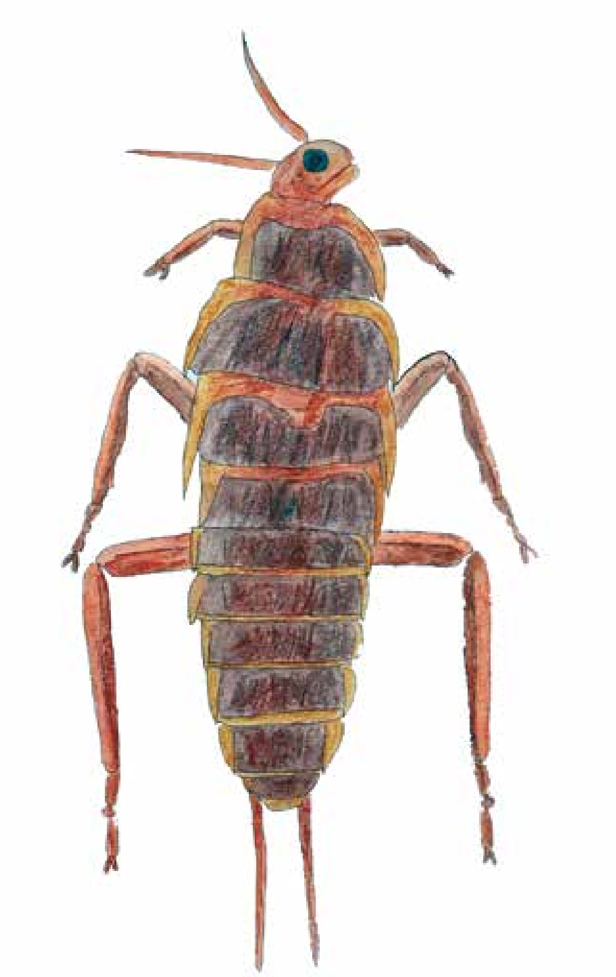
(Early Permian) becoming abundant already in the Kungurian faunas of the Urals (Chekarda and neighbour localities). Also, the earliest members of Aphidina appeared in the same Kungurian beds as minor components of the fauna. Especially, Early Permian cicada *Rachimentomon reticulatum* from the Fore-Urals manifest just as many properties of extant cicadas, such as a broad body and prominent compound eyes set wide apart on the sides of the head. The mouthparts form a long rostrum. Two pairs of powerful membranous wings are also characteristic features of this insect.

Permian Beetles – Coleoptera

The Coleoptera or beetles are one of the most diverse insect orders in taxonomy and ecology and comprise today a large order of insects, with about 400,000 species, forming about 40% of all the described insects. They were found in almost every ecosystem except for the arctic regions or the oceans and are distinct because of their two pairs of wings, with the forewings hardened into elytra, whereas the hindwings are membranous and folded into the protective forewings. They become adults after a relatively immobile pupal stage. Some beetles are characterised by a marked sexual dimorphism, with the males having enormously enlarged mandibles.

The origin of the Coleoptera must be searched between the Carboniferous-Permian border. Early Permian Tshekardocoleidae, comprising genera like *Tshekardocoleus*



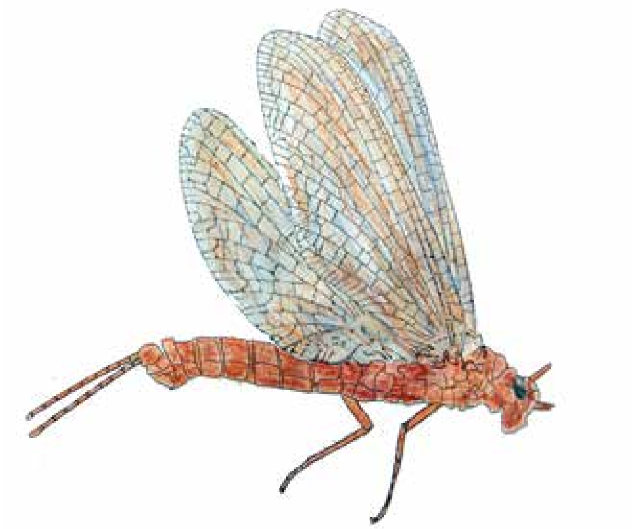


Angaroptera nicolaswachtleri, probably a dragonfly nymph. Holotype MAT 190, Matvéevo, Early Permian, Kungurian, Coll. Nicolas Wachtler, Dolomythos Museum

(minor) and *Sylvacoleus (sharovi* or *richteri*) manifest all the features of today's beetles. The Tshekardocoleidae were medium-sized insects (around 1 cm) with elongated body and well-developed eyes. The elongated wings were characterised by a reticulate pointed venation, with the forewings hardened. These distinguish them from other insects. The appearance of beetles was considered to have taken place together with the early diversification of the Holometabola. The Miomoptera and Palaeomanteida were considered as the most archaic group of Holometabola.

The Ancestors of the Plecoptera (stoneflies) in the Early Permian

The Plecoptera (from Greek braided wings) comprise about 3,500 species and are found in both the Southern and Northern Hemispheres. The name Plecoptera was attributed due to the complex venation of their two pairs of wings, which are membranous and fold flat over their backs, although some species are wingless too. Stoneflies undergo little or no metamorphosis. They are characterised by simple mouthparts with chewing mandibles, long, multiple-segmented antennae, large compound eyes and two or three ocelli. The legs are robust, with each ending in two claws. The abdomen is relatively soft and may include remnants of the nymphal gills even in the adults. Both nymphs and adults have long, paired cerci projecting from the tip of their abdomens. The nymphs resemble wingless adults and are herbivorous.
In the Kungurian sediments from Matvèevo and Chekarda, stonefly remains are common. Especially, the Tillyardembiidae composed mainly of *Tillyardembia* (and *Kungurembia*, constitute about 24% of the most abundant families in Chekarda. In minor cases, we encounter the Atactophlebiidae, represented by *Kirkorella mira*, where nymphs and subimagoes are known, with



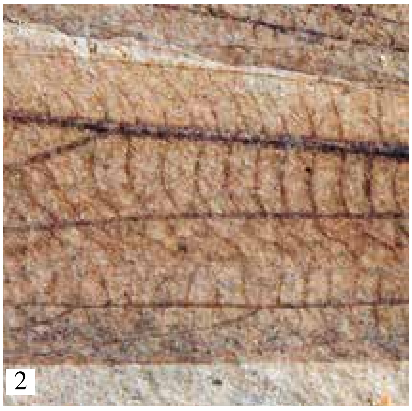
A mayfly (*Misthodotes sharovi*) from Matvéevo (MAT 183), Early Permian, Kungurian, (Coll. Wachtler).

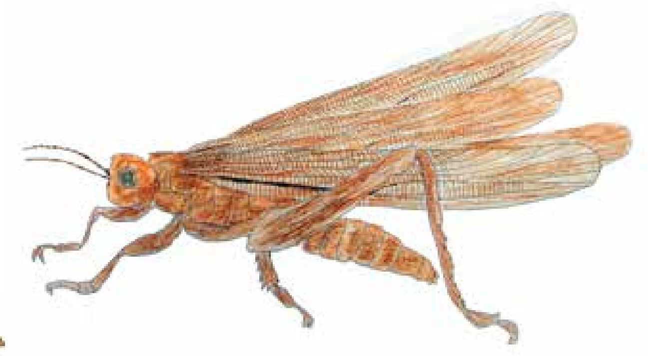
Lemmatophoridae (about 14%), Ideliidae (about 11%), and Liomopteridae (about 10%). Sylvaphlebiidae (about 5%), Euryptilonidae (about 3%) and Sheimiidae (about 1.5%) are recovered only in small amounts. The families, Sylvardembiidae, Sojanoraphidiidae, Sylvabestiidae, Euremiscidae, Probnidae, Visheriferidae, Permembiidae, Aliculidae, Megakhosaridae, Idelinellidae and Kortshakoliidae constitute less than 2% each (Aristov, 2003). Whether all of them can be accepted as belonging to the Plecoptera is doubtful but many depict their features. Especially, the forewing venation between the Tillyardembiidae and the stoneflies is very similar.

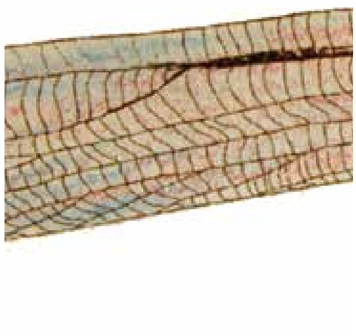
The taxonomic position of some of the genera found in Chekarda and Matvèevo was never unquestionable. Often, they were inserted as Grylloblattida, then they were transferred to the previously strictly Carboniferous order Eoblattida. Especially the classification as progenitors of the Grylloblattida was largely accepted.Today

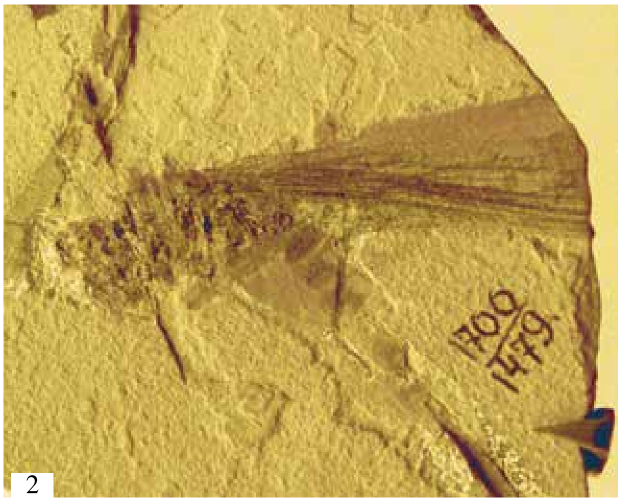
Tcholmanvissia longipes
Orthoptera ancestors

1. Isolated wings, the upper one folded. CHEK 01, Chekarda, Coll. Wachtler; 2. Detail of the venation; 3. *Tcholmanvissia longipes* , Palaeontological Institute, Russian Academy of Sciences (Moscow). 4. Reconstruction upper view and lateral









1-2. *Uraloedischia permiensis.* They had elongated hindlimbs making them adapted for jumping as modern grashoppers. Chekarda, Paleontological Institute of the Russian Academy of Sciences, Moscow.

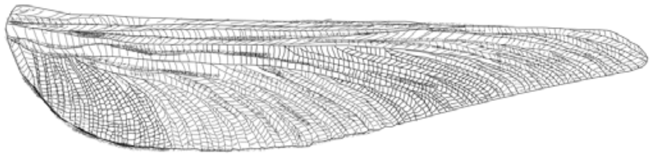
Extant Orthoptera (*Locusta migratoria*) with open wings and in the normal resting position

the Notoptera, known as icebugs or ice crawlers, comprise a small group of tiny, wingless insects with a head resembling that of a cockroach and long antennae and having elongated cerci. Most are nocturnal and therefore, their eyes are either missing or reduced. They cannot tolerate warmth – most species die at 10 °C. The 26 living species inserted in four genera have a small distribution range. All these features make it doubtful that the Tillyardembiidae can be regarded as ancestors or perhaps related to the Grylloblattida, and it would be more useful to classify them as Protoplecoptera.

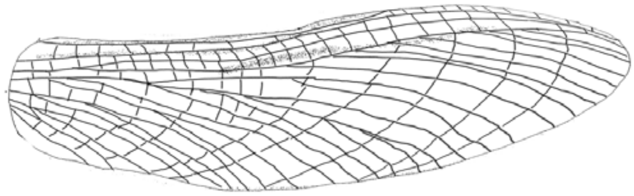
Early Permian Tillyardembiidae notably differed in size and appearance: the dwarfish Permembiidae, with a forewing of only 2.5 mm stands in contrast with the large Atactophlebiidae having a wing-length of 90 mm. Because all the wings were delicate and membranous, a pattern was sometimes difficult to establish. The mouthparts had a chewing tendency. The pronotum varied from heavily elongated and narrow in Tshekardominidae to transverse in Sylvaphlebiidae. The legs were cursorial, usually medium-long; the forelegs were the shortest whereas and the hindlegs the longest.

The Tillyardembiidae constitute especially of the species *Tillyardembia antennaeplana,* the most frequent genus in the Permian Kungurian deposits, and their abundance made them one of the best studied insects of the Fore-Urals (Chekarda and Matvèevo). At least the body structure of males and fe-

males of *Tillyardembia* were restored. The structure of their wings with weak veins and a convex fore margin let suppose that they were not very good fliers. The fossil evidence indicates that the Permian Plecoptera were pollen eaters, as well as fed on parts of plants or fruits.
The other dominating family were the Atactophlebiidae represented by the monotypic genus, *Kirkorella*. The Ideliidae were dominated by *Sylviodes perloides* and *Sylvidelia latipennis,* medium-sized insects with a large head and eyes and long antennae. All legs are equally long, whereas the anterior margins of the forewings are convex. Some of the Ideliidae from Chekarda were transferred to the interesting family of the Paoliidae, a neopteran clade and potential sister group of the Dictyoptera. The Paoliida are considered to be of crucial interest for the phylogeny of Pterygota or also as an ancestor group of a part of the Hemiptera – "paoliid line".
One of the most common nymphs in the Permian Fore-Urals to be encountered is *Uralonympha varica*. It is strong because of the prothorax and the legs and has generally been considered an immature form of a stonefly. Today the presence of Plecoptera in a stream or still water is usually an indicator of good water quality. The insects remain in the nymphal form for one to four years and undergo 12 to 36 molts before emerging and becoming terrestrial as adults. Therefore, in these Early Permian deposits, the number of fossilised nymphs are generally higher than other insects. Before becoming adults, the nymphs leave the water, attach to a fixed surface and molt one last time. Adult stoneflies only survive for a few weeks.
The classification of *Synomaloptila longipennis* characterised by an elongated, flattened body and four membranous wings is also doubtful even today. Although they were inserted sometimes in the Caloneurodea, others excluded these and put them in the Hypoperlida, a suggested line of the Plecoptera.

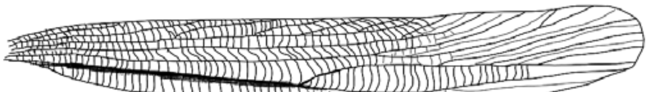


Wing-detail of *Arctotypus sylvaensis*

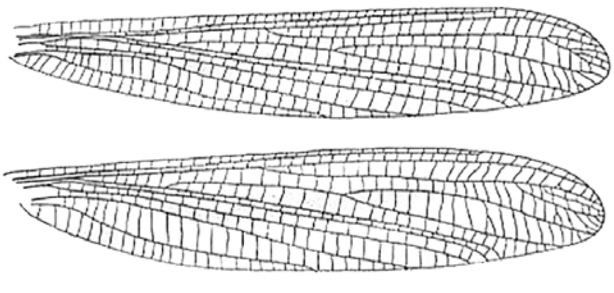


Wing-detail of *Paradunbaria pectinata*

Wing-detail of *Sylvohymen sibiricus*



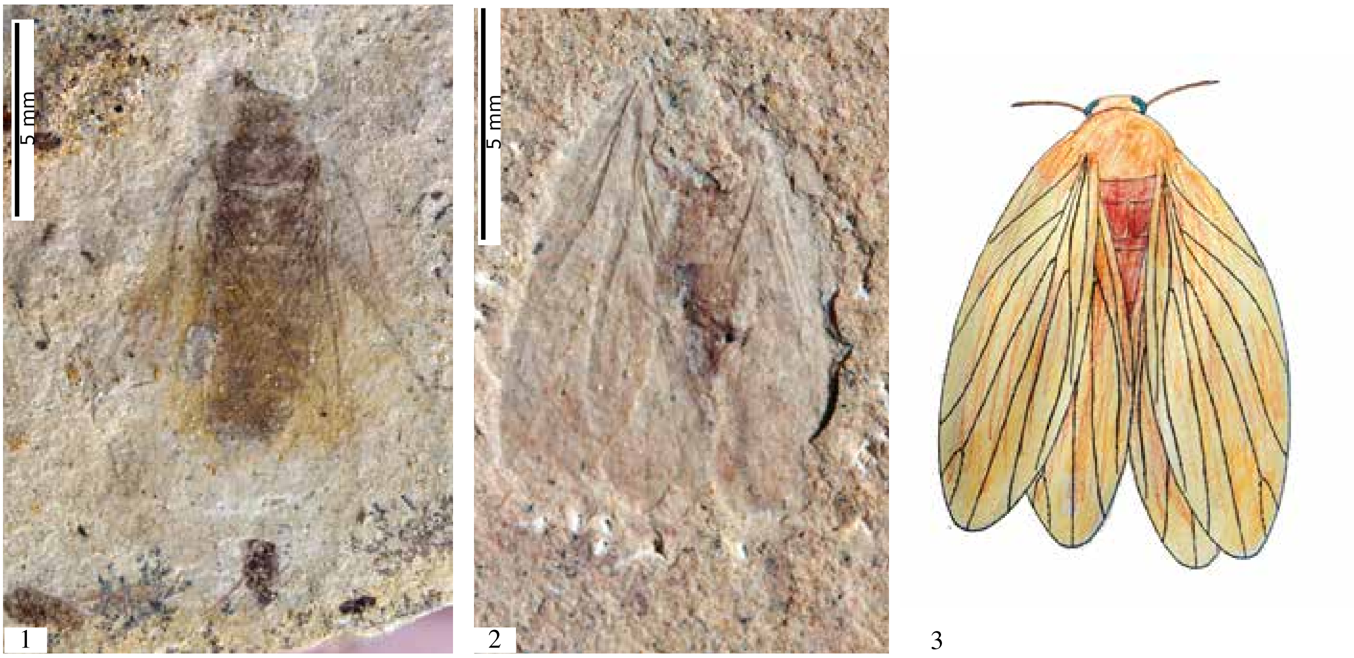
Wing-detail of *Tcholmanvissia longipes*



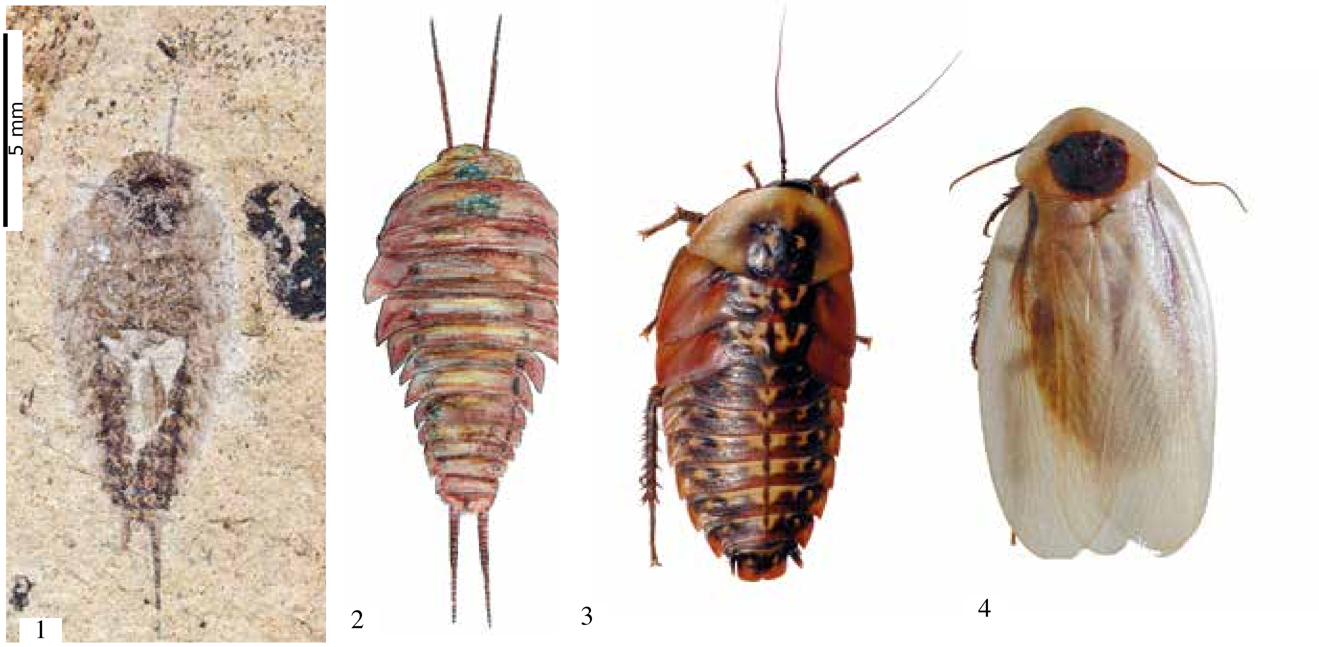
Wing-detail of *Paleuthygramma tenuicornis*

The Progenitors of the Neuroptera

The order Neuroptera or net-winged insects today comprises about 6,000 species, including the lacewings, mantidflies, antlions and their relatives. Almost all Neuropterans have four membranous wings, all about the same size, with many veins. They have chewing mouthparts and undergo complete metamorphosis. The antlions have a worldwide distribution, but the greatest diversity occurs in the tropics, and a few species are also found in cold-temperate locations. The Neuropterans first appeared during the Permian period and continued to diversify through the Mesozoic era.
In the Early Permian Fore-Urals, the most common Neuropteran insect was medium-



Two fossil insects belonging probably to the Blattodea: 1. *Sylvaprisca focaleata,* (CHEK 10, Coll. Dammann); 2. *Artinska infigurabilis,* CHEK 92 10 mm, Chekarda Coll. Wachtler; 3. Reconstruction of *Artinska*



1. The cockroach-nymph *Czekardia blattoides*, (MAT 493 Matvéevo, Coll. Wachtler); 2. Reconstruction; 3-4. The extant cockroach larva *Blaberus* and right an adult specimen of *Blaberus discoidalies* (Wikicommons).

sized *Paleuthygramma tenuicornis*, bearing a short head and mouth parts equipped with long and segmented antennae. The four wings, about 20 mm long but only 5 mm wide, were membranous and probably translucent and multiveined. The abdomen was somewhat more corporeal as known from extant antlions.

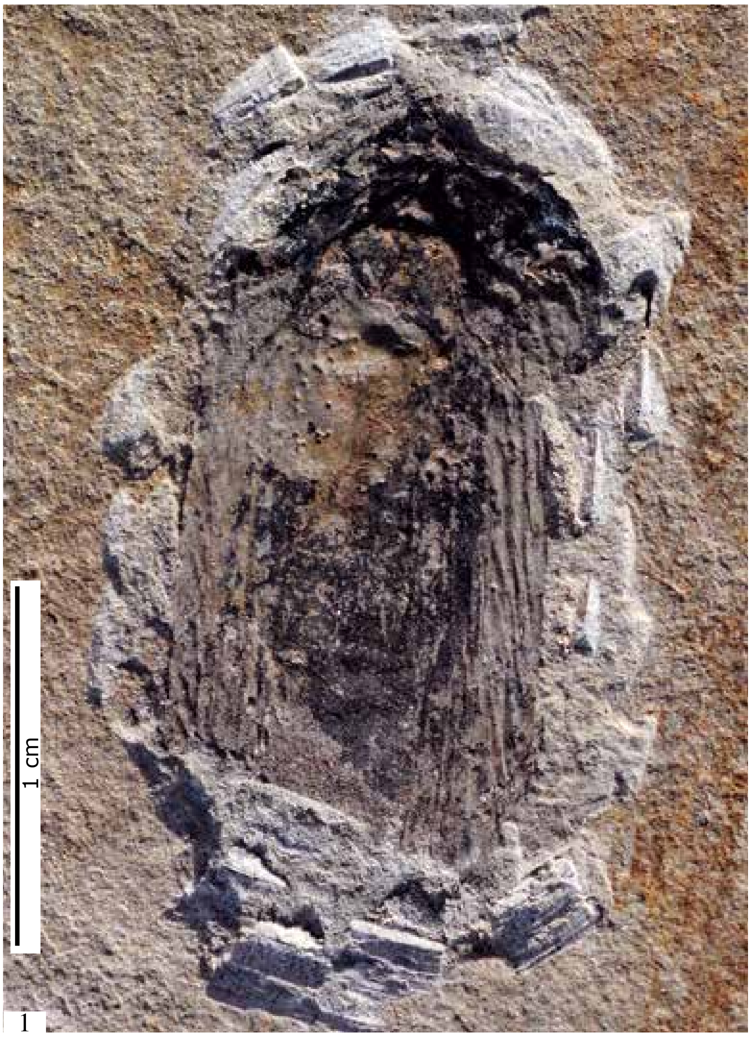
Sometimes *Paleuthygramma* was also inserted in the group of the Caloneurodea and then considered to be primitive Cimiciformes, Scarabaeiformes. Also, they were inserted as Archaeothoptera (Bethoux & Nel, 2002). Others suggested the classification as Paraneoptera (Rasnitzyn, 1980), but probably the most useful classification would be to insert them as Neuroptera and, in this group, connecting them with primitive antlions.

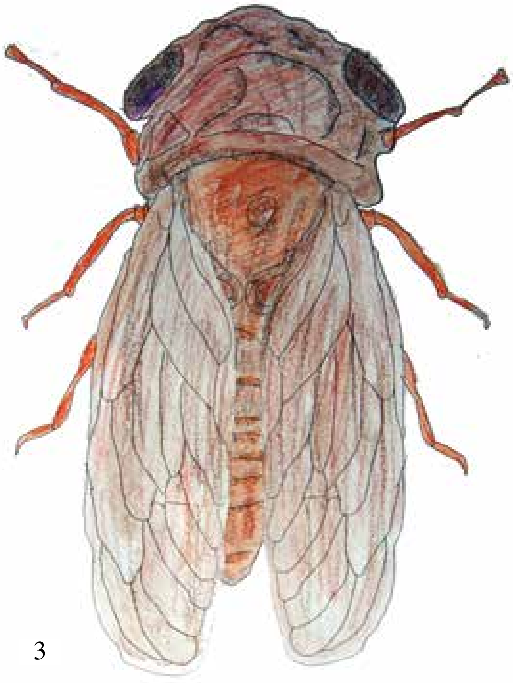
Ancient Pscodoea or Book Lices

The Psocodeans include the bark lice, book lice and true lice. They are represented by minute insects with large heads and protruding eyes, holding two pairs of wings, the forewing being larger than the hindwing. Both wings evidence a reduced venation. Immature lice and adults look similar. It is thought that they are closely related to Hemiptera and Phthiraptera and represent the most primitive hemipteroids in this group due to their primitive mouthparts.
In the Permian Fore-Urals, we encounter the Psocida *Parapsocidium*, especially *Parapsocidium uralicum*. *Parapsocidium*, less than 10 mm in size, was a minute insect characterized by a strong furrow into a dorsal and ventral lobe, unlike today's book-lices. The dorsal lobe was posteriorly adjacent to the antennal insertion, and the ventral lobe was not fused with the maxilla bearing no cerci. The mandibles were elongated and adapted for chewing. The wings were membranous, evidencing a relatively simple venation pattern, with few cross-veins. Interestingly, *Parapsocidium uralicum* was equipped with short corporeal antennae, whereas the abdomen had just nine segments and no cerci like extant book-lices. Aristov and Rasnitsyn (2015) described a complete moulting case of insect larva with a body length of 9 mm as *Cavalarva caudata*. Probably even they belong to the Psocodeans. The insect larva is campodeiform, with distinct hypognathous head bearing antennae with short and thick scape and pedicel and thin, elongate flagellum and, possibly, with compound eyes. Thoracic segments were distinctly wider than the head and the abdomen.

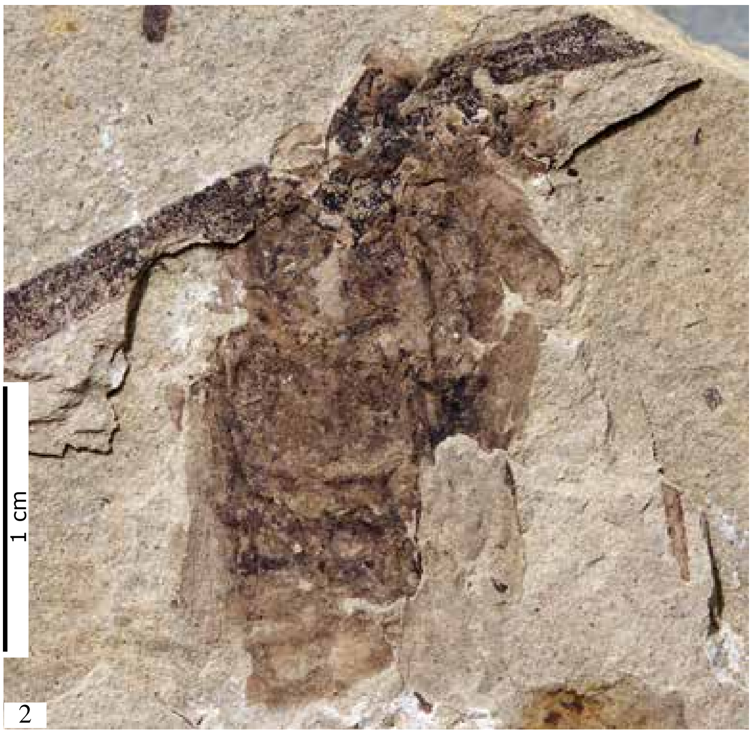
The Difficult Way of the Holometabola

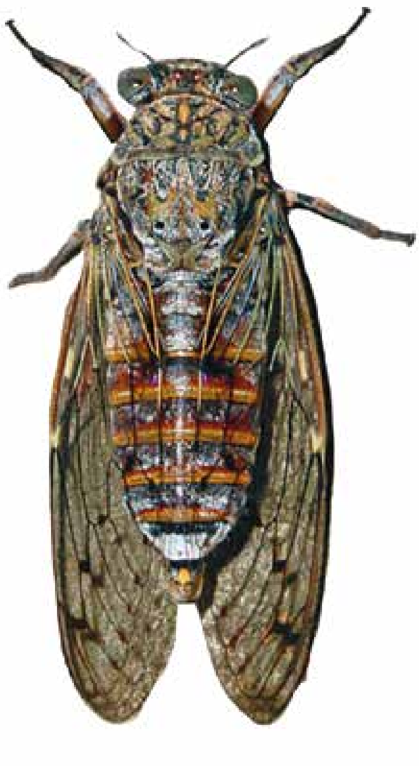
The Holometabola include those insects that undergo a complete metamorphosis as opposed to hemimetabolous insects that have an incomplete metamorphosis or another group that virtually has no change from immature to adult stage (ametabolous). The Holometabola are the biggest group, including about 85% of all insects. On the Carboniferous-Permian border, almost all important pollinating insects such as Plecoptera, Mecoptera and Hymenoptera like the ants, bees, wasps, Lepidoptera and Trichoptera and probably also the Diptera were almost or fully evolved. The evolution of the single families is poorly understood. These regard the in the Fore Urals frequent Miomoptera or Hypoperlida, thought to be a stem group of the Acercaria or based on other theories as starting point of the Hymenoptera.
One suggested Miomoptera family recovered in the Early Permian sediments of the Fore-Urals is represented by the Palaeomanteidae. They were small insects, with unspecialised chewing mandibles and short abdominal cerci. The four wings were of equal size, with a relatively simple venation. Especially *Palaeomantis aestiva* and *Palaeomantis laeta* can be regarded as fairly common in the best Early Permian Ural locations of Chekarda and Matvèevo. The small cerci are the first distinctive feature with the other similar insect genus *Agetopanorpa punctata*, bearing additionally beautiful coloured circles on their wings. The Palaeomanteidae were often inserted in the family of the Miomoptera (and therefore, in the superorder, Acercaria or sometimes also thought to be related to the lacewings (Neuroptera). *Palaeomantis aestiva* and *Agetopanorpa punctata* can be classified in the Early Permian as those insects that differ most from other insect-lines like the Meganeuridae (*Arctotypus sylvaensis*) the Megasecoptera (*Sylvohymen, Asthenohymen* or *Bardohymen*), the Mayflies (Ephemeroptera) like *Misthodotes sharovi*, the Orthoptera (*Tcholmanvissia longipes*), the Blattodea (*Sylvaprisca focaleata* and *Artinska infigurabilis*), the Plecoptera (stoneflies) like Tillyardembia, ancient book-lices (*Parapsocidium uralicum*), the Neuroptera *Paleuthygramma tenuicornis*, the beetles like *Sylvacoleus sharovi,* or the Cicada *Rachimentomon reticulatum.* Also, *Delopterum rasnitsyni* was inserted in this interesting Acercaria crown group. It has short cerci but surprisingly long gonostyli.
Another group of presumed Acercaria ancestors comprise the Hypoperlida, established by Martynov in 1928. They differ from the Palaeomanteidae because of their short and barely perceptibly cerci. In the Early Permian Fore-Urals, we encounter the genera Hypoperla and Idelopsocus particularly.



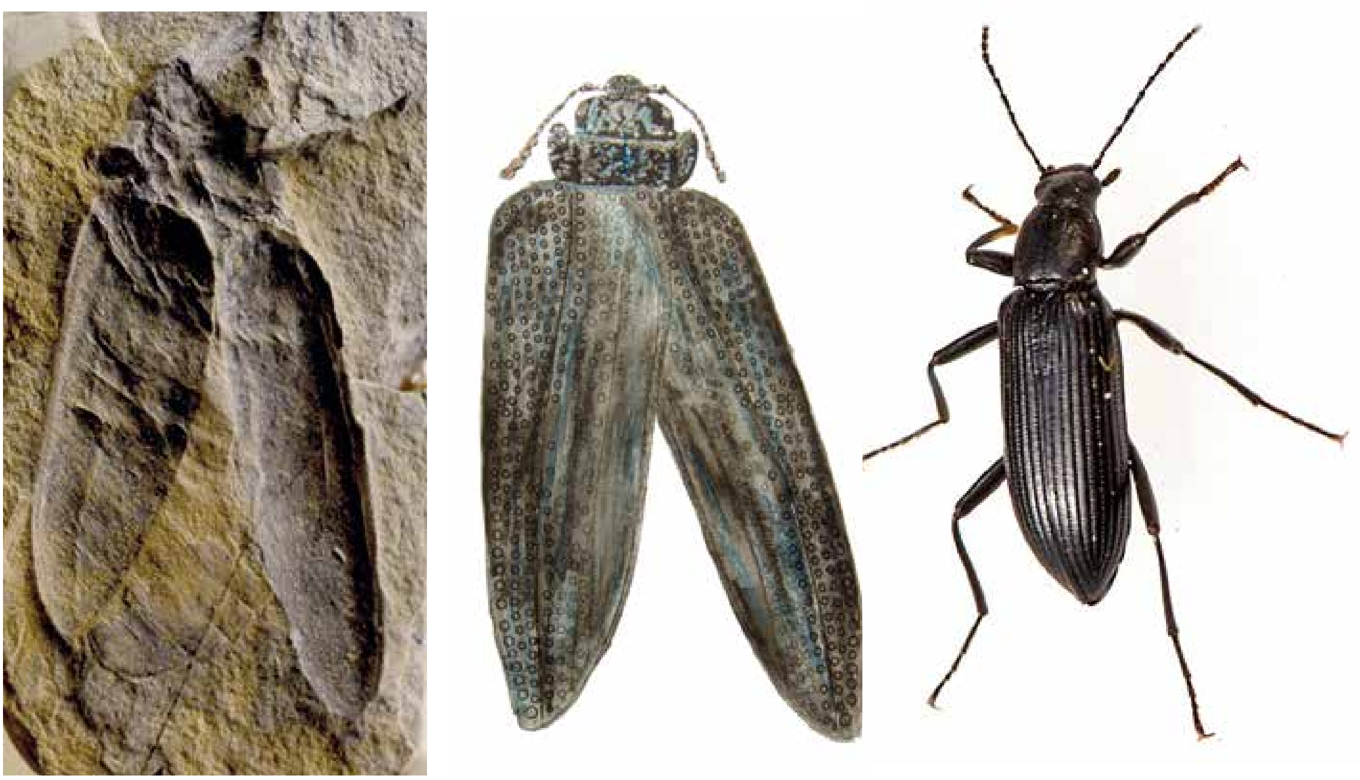


1-2. Early Permian cicada *Rachimentomon reticulatum.* Complete length 18 mm, (MAT 184); Matvéevo, Early Permian, Kungurian, (Coll. Wachtler)





The European cicada *Cicada orni*



The beetle *Sylvacoleus sharovi,* Chekarda, (Paleontological Institute of the Russian Academy of Sciences, Moscow). Reconstruction. Right the extant Coleoptera *Strongylium tenuicolle* (Wikicommons).

The First Scorpionflies – Mecoptera

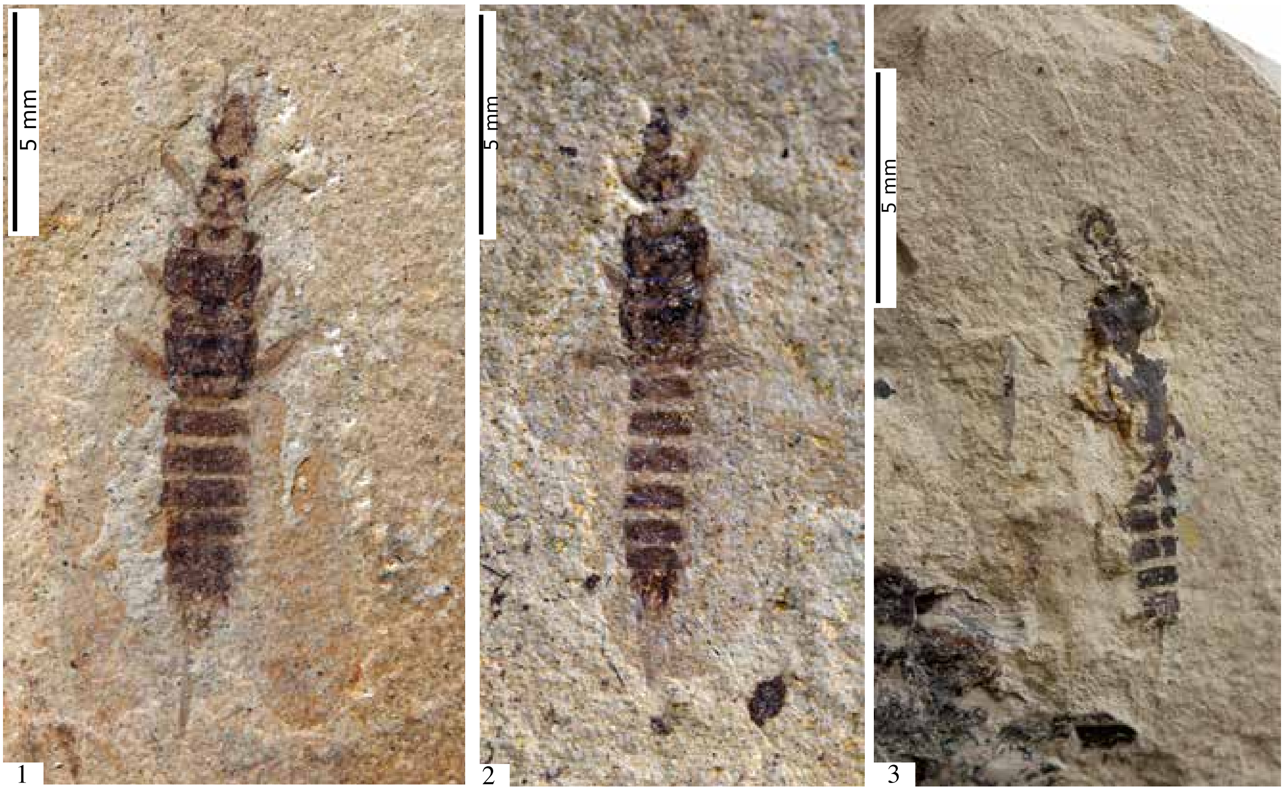
Today the Mecopterida comprise only a relict group with less than 400 species, the greater number of which belong to the genera *Panorpa* (scorpion flies) and *Bittacus* (hanging flies). Their ancestors probably constitute a highly interesting insect group because it is thought that significant pollinators like the Hymenoptera (sawflies, wasps, ants, bees), the Trichoptera (caddisflies), the Lepidoptera (butterflies and moths) and single pair of wings equipped Diptera (flies) can be deduced from the crown group.

The oldest undoubted Mecopterans are recorded from the Carboniferous–Permian boundary. They reached a first heyday in the Permian and continued to be one of the most abundant groups till the Cretaceous. After that they declined an continue to do so even today. Permian scorpionflies are known from almost all continents, with the richest and most numerous localities in Eurasia, especially in the Fore-Urals. Russia has yielded the most complete sequence of scorpion flies from the Early Permian till the Triassic.

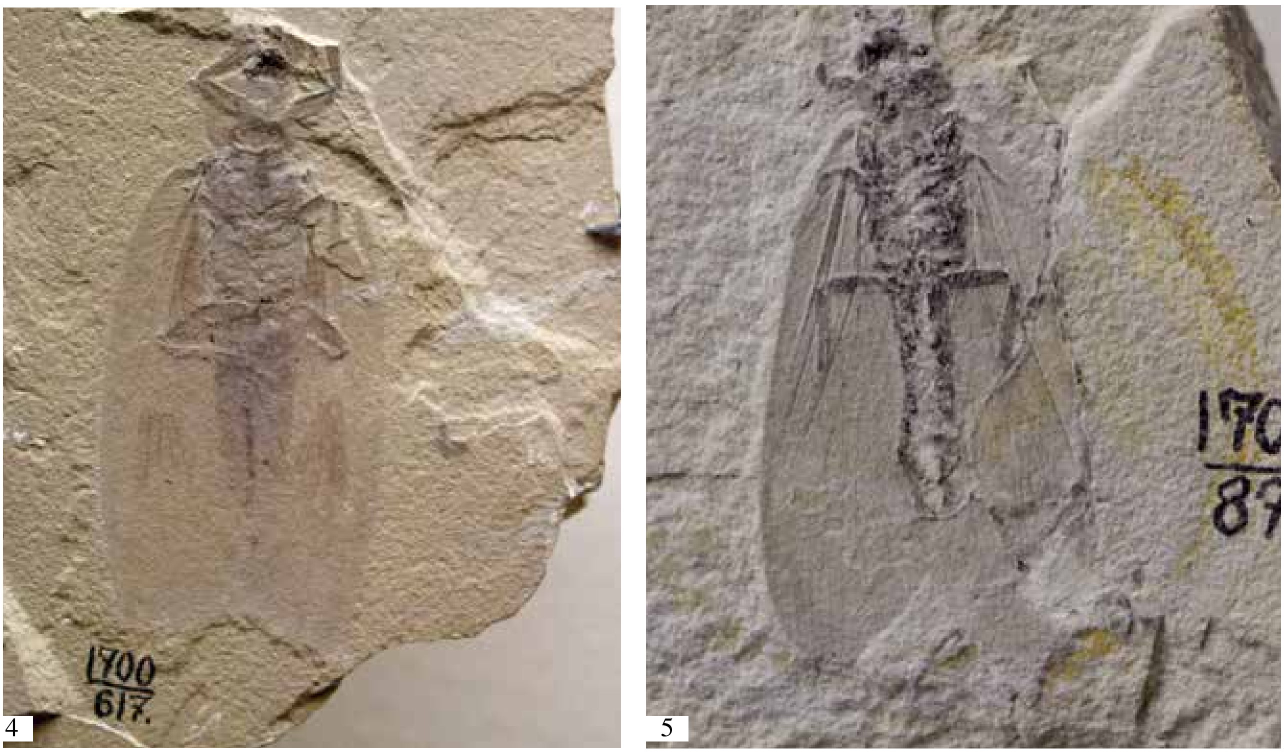
The Mecoptera include the Diptera, Hymenoptera (bees, wasps, ants), Lepidoptera (butterflies and moths), Coleoptera (beetles), holometabolous insects, meaning that the larva and adult of the same individual are totally different from each other structurally as well as in their way of life. Between these phases there is a resting phase, the pupa. The Mecoptera are essentially terrestrial insects undergoing their transformations in the soil. In Chekarda and Matvèevo, the most abundant species consist of *Agetopanorpa punctata*, sometimes also described as *Agetochorista punctata,* with more than half of the recorded Mecoptera specimens, followed by *Protopanorpa* constituting 12%. Both genera belong to the subfamily Agetopanorpinae, constituting more than 80% of Mecoptera in Chekarda; remaining 20% fall in the subfamilies of Permochoristidae.

All extant Mecoptera, and supposedly also the fossil representatives (except some Paratrichoptera), possess two pairs of more or less homonomous wings. These wings generally are provided with a rich venation, often with many cross-veins. The wings are elongated, often carrying

Early Permian Plecoptera (Stoneflies)

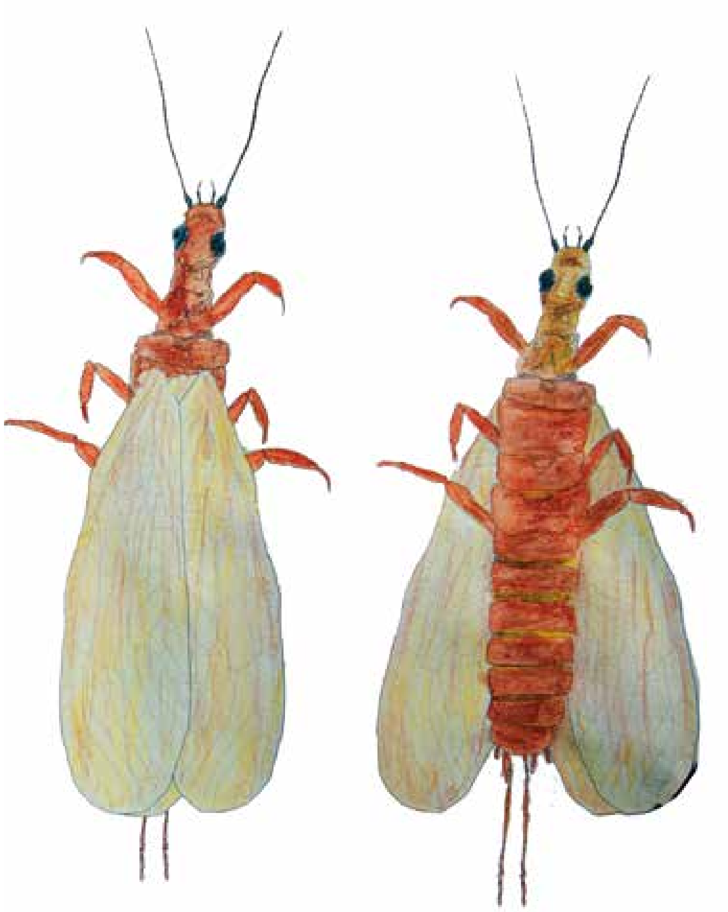


Tillyardembia antennaeplana constitutes the most abundant stone-fly species in the Fore-Urals. 1. A female specimen CHEK 04, Coll Wachtler; 2. CHEK 99 Coll. Dammann; 3. Covered with pollen from a flower in the vicinity (Coll. Gerasch). All Chekarda



4. The Ideliidae *Sylvidelia latipennis* and 5. *Sylviodes perloides*; both Chekarda, (Paleontological Institute of the Russian Academy of Sciences, Moscow)

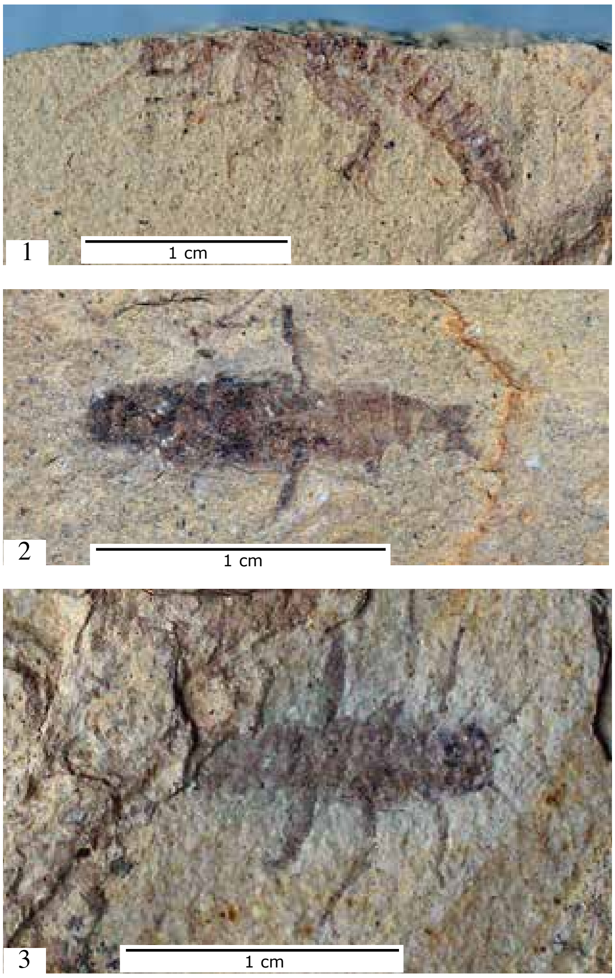
Early Permian Plecoptera (Stoneflies)



The Atactophlebia *Kirkorella mira* is also a common Plecoptera (Chekarda, Paleontological Institute of the Russian Academy of Sciences, Moscow). 2. Reconstruction of the stonefly *Tillyardembia antennaeplana* upper side and below.

Plecoptera: 1. Stonefly-nymph A*croneura abnormis;* 2. Adult specimen *Isoperla grammatica* seen from below and from upper side (Wikicommons)

coloured spots. This is also one of the most distinctive features to insert early Permian *Agetopanorpa punctata* in the family of scorpion flies bearing well-evidenced coloured circles on their wings.
Permian *Agetopanorpa punctata* is represented by small, about 10 mm, insects with long beak-like rostra, membranous wings and slender, elongated bodies. They evidence no cerci and have relatively simple mouthparts, with a long labium, long mandibles and fleshy palps. The antennae are composed of multiple segments. Extant Mecoptera are considered important pollinators, and effectively in the stomach as well as on parts of the body or the wings, pollen gut can be recorded in Permian *Agetopanorpa*.



Uralonympha varica, stonefly larva

1. Lateral view, body length 20 mm, (MAT 454); 2. Overview, body length 14 mm, (MAT 453); (both Coll. Gerasch); 3. Overview, body length 12 mm,); All Matvéevo, Early Permian, Kungurian, (Coll. Dammann)

The small size of *Agetopanorpa punctata*, as well as *Palaeomantis aestiva* helped them to extract protein-rich pollen from the dwarfish flowers. Pollen dust was found on the wings or as content in the stomach in both genera. Considering all these slightly different insect tribes in the Early Permian later, evolving trends must be seen sceptically. Mostly all development phases occurred just before the Devonian over the Carboniferous. The often-propagated relationship between Lepidoptera, Trichoptera and Hymenoptera must have originated before because from the Early Permian, all these lines evolved independently. Another suggested Mecoptera is represented by *Culiciforma formosa*, a medium-sized insect. The antennae were long, filiform, and the eyes were large. The elongated front- and hindwings were similar in size, and the crossveins were numerous. The body was slender, evidencing and reaching about 15 mm.
The special features of the mouthparts from the Palaeomanteidae contribute to a faster transformation. The elongation of the mouthpart into a rudimentary “cone” (elongation of the labrum, mandibles and maxilla) allowed a suction feeding of the nectar accompanied by their long laciniae and easy chewing of plant tissue owing to their acute mandibles with strong molar plates.

Synomaloptilia longipennis (Hypoperlida). Chekarda (Paleontological Institute of the Russian Academy of Sciences, Moscow)

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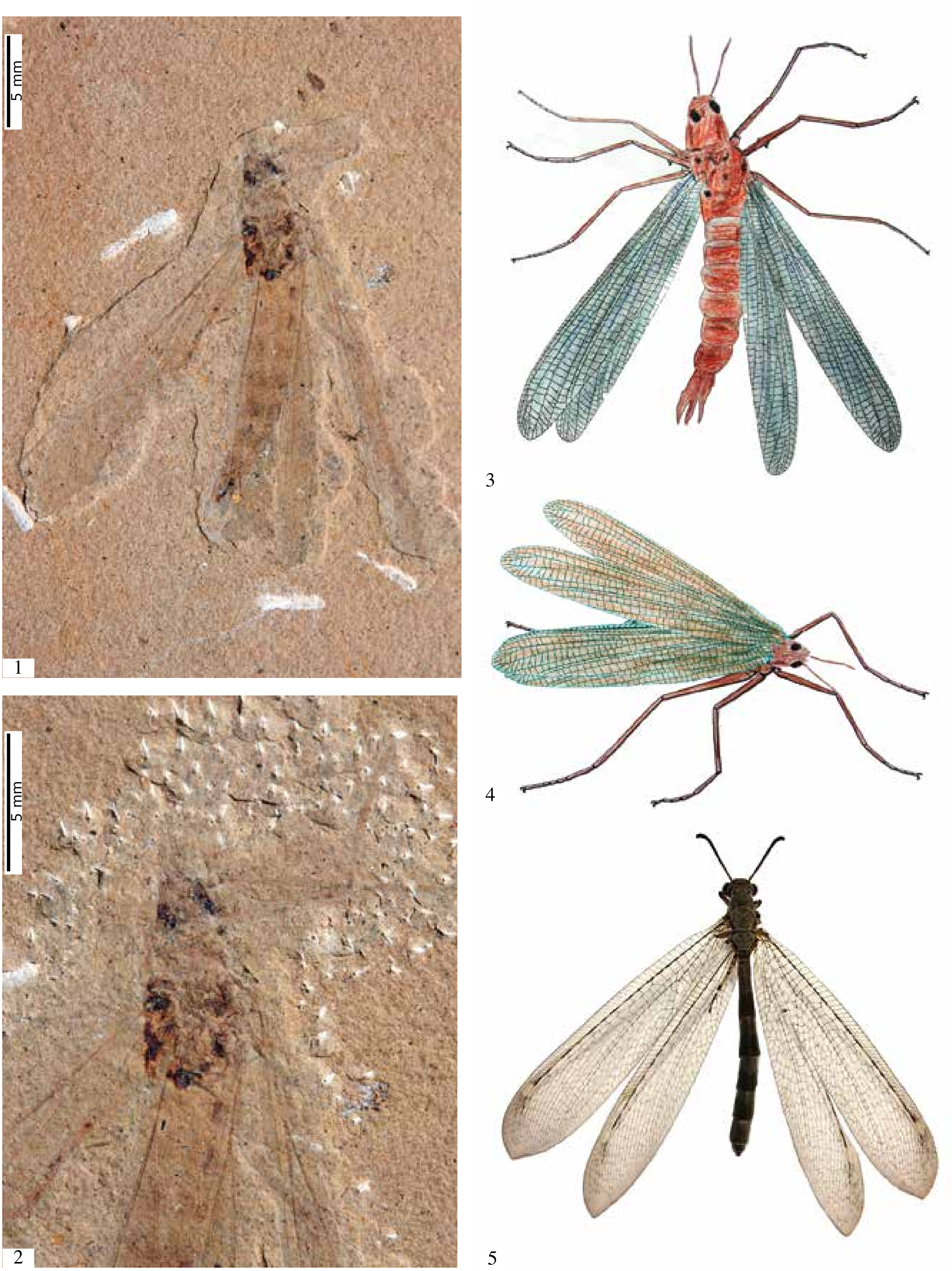
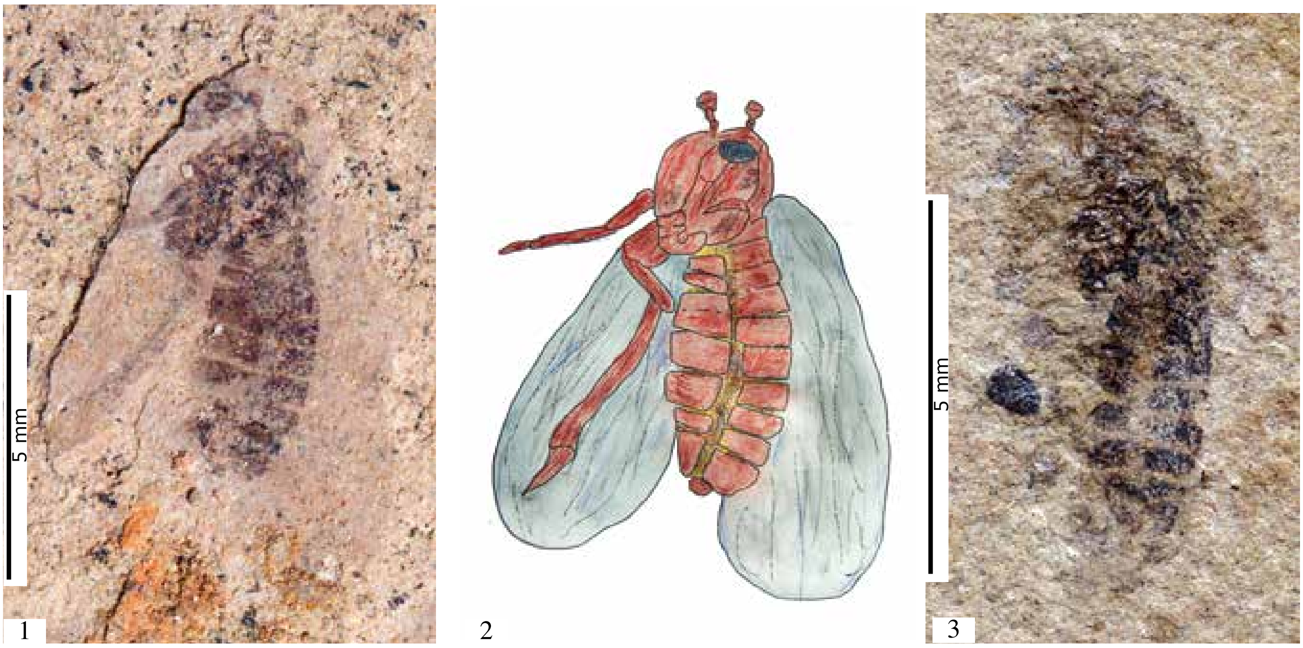
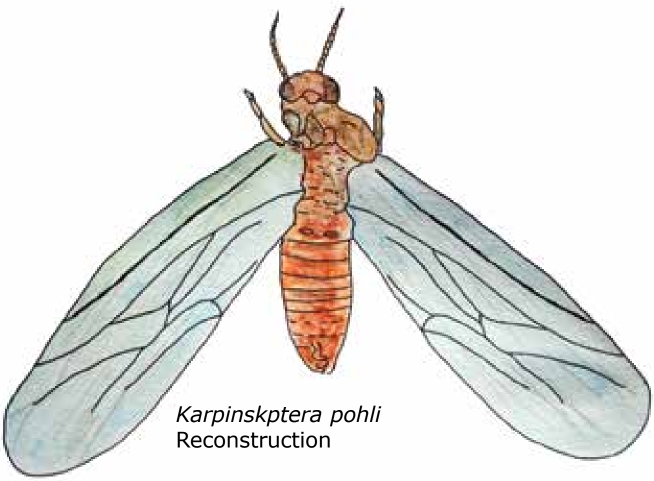


*1-2. Paleuthygramma tenuicorni*s (CHEK 02) Chekarda, Coll. Wachtler. 3-4. Reconstruction of *Paleuthygramma tenuicorni*s; 5. Extant antlion *Distoleon annulatus* (Neuroptera, Myrmeleontidae)



1. Early Permian book-lice *Parapsocidium uralicum (*CHEK 03), Chekarda; 2. Reconstruction; 3. Juvenile specimen of the Psocodea *Cavalarva caudata;* complete length 8 mm (MAT 33); Matvéevo, Early Permian, Kungurian, (All Coll. Wachtler, Dolomythos Museum)

Karpinskptera pohli with two fore-wings and not recognizable hindwings. In that it has many resemblances with extant Diptera or true flies (Holoytpe CHEK 91, Chekarda, Coll. Wachtler, Dolomythos Museum)

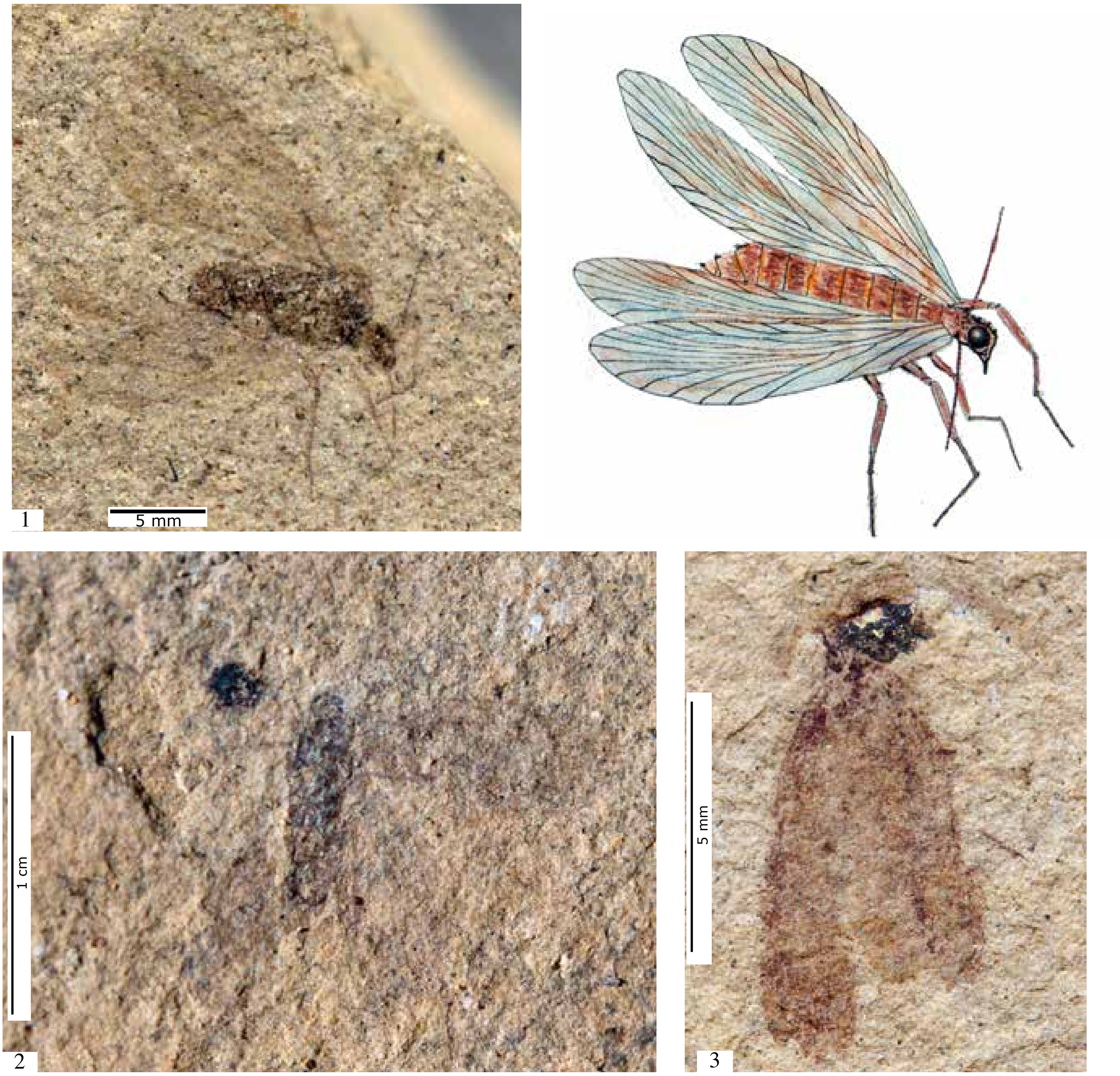


Karpinskptera pohli
Reconstruction

Juvenile specimen of the book-lice *Liposcelis corrodens.* Adult exemplar of the bark louse *Ectopsocus meridionalis* (Wikicommons)

Early Trichoptera – Caddisflies

Trichoptera or caddisflies are classified in about 45 extant families containing some 14,500 species and occur in almost every type of freshwater habitat and on every continent except Antarctica, making them one of the most abundant insect orders in streams and lakes. All members have a hemimetabolous life cycle: egg, multiple immatures and a different adult stage. The moth-like adults have reduced mouthparts lacking proboscis, the antennae are



Delopterum rasnitsyni in several fossilisation positions (MAT 452 Col. Gerasch; MAT 496, Coll. Perner; MAT 188 Coll. Wachtler) Matvéevo, Early Permian, Kungurian.

multisegmented and filiform and often as long as the wings, and the compound eyes are large. They are characterised by haired or often scaled wings. Fore and hindwings are almost equal in size and relatively poor veined. They date back worldwide to the Permian, being particularly numerous and diverse during the Triassic, Jurassic and Cretaceous. Due to their similarity, caddisflies (Trichoptera) and Lepidoptera (moths and butterflies) were often correlated and thought to have a common ancestor. Therefore, more knowledge about Permian Trichoptera or even Lepidoptera would be interesting for studying the further evolution of insects. The Trichoptera were present in the Early Permian with the genus *Marimerobius*, especially *Marimeroblus splendens* and *Marimerobius sukatchevae* and then also with *Kamopanorpa uralensis* and *Uraloptisma maculata*.

Early Diptera

Karpinskptera pohli represents a highly interesting insect because no hindwings are evidenced. It is improbable that they were destroyed or tattered. In that, Karpinskptera has more similarities with the two-winged

Early Permian Acercaria-progenitors

Palaeomantis aestiva (CHEK 88) from the stem group of Acercaria, included in the family of Miomoptera. Right a magnification of the short cerci. Coll. Wachtler, Chekarda

*Sellardsiopsis conspicua***.** Miomoptera or Mecoptera. Body length 20 mm, Interesting is the pollen-content in the stomach (MAT 181; Matvéevo, Early Permian, Kungurian, (Coll. Wachtler)

Diptera, especially the Brachycera. It is probable that further studies can find out more details about its classification.

Conclusions

Backdating of angiosperm origin to the Carboniferous-Permian border: If the most accepted theories manifested as prerequisite for the arising of angiosperms and the reciprocal dawn of insects, then the beginning of flowering plants must be moved from the Cretaceous to the Permian.

Permian interaction between insects and plants: There are enough proofs that just in the Early Permian, insects and plants had mutual connections. They were sources of nutrition and provided support through the exchange of pollen. The insecure and restricted dispersion by wind could be enlarged. The co-operation was extended additionally through good seed dispersal, and delicious fruits made long lasting alliances possible.

Faster evolution of various insect- and plant-families: Between the Carboniferous and the Permian, almost all of today's known insect and plant families evolved rapidly. The reason behind this can only be mutual advantages. A more nutritious or more tasty pollen accumulation attracted more insects, and small blossoms prevented the entrance of bigger insects. Higher-growing flowering plants required an improvement in the ability

Reconstruction of *Palaeomantis aestiva* (CHEK 88) seen from top and below. Right the extant Trichoptera *Brachycentrus appalachia.*

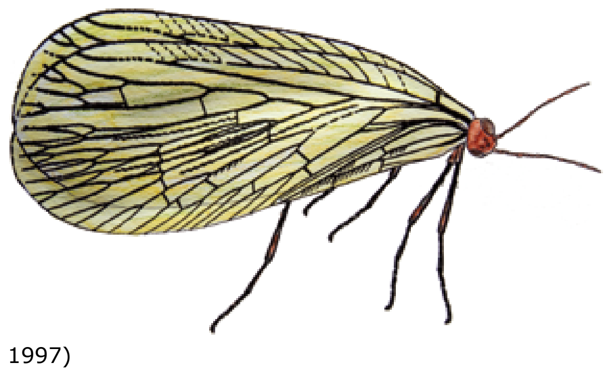
to fly. Bigger calyxes offered hiding places for small insects against predators.

Origin of angiosperms in Angara-Siberia: Such a rich Early Permian flowering plant flora can be encountered only in the Fore-Urals. What could be the reason? From the Carboniferous on the Euramerican continent, a multitude of gymnosperms such as conifers, ginkgos and cycads evolved. They can be regarded as good pollinators to a limited extent. Therefore, only a few fossilised insects were recovered from the Permian over the Triassic. In Angara-Siberia, the same niche was filled from the Devonian with mostly hermaphroditic plants, whereas the gymnosperms occupied only a marginal existence. The reason for that was probably only an evolutionary coincidence.

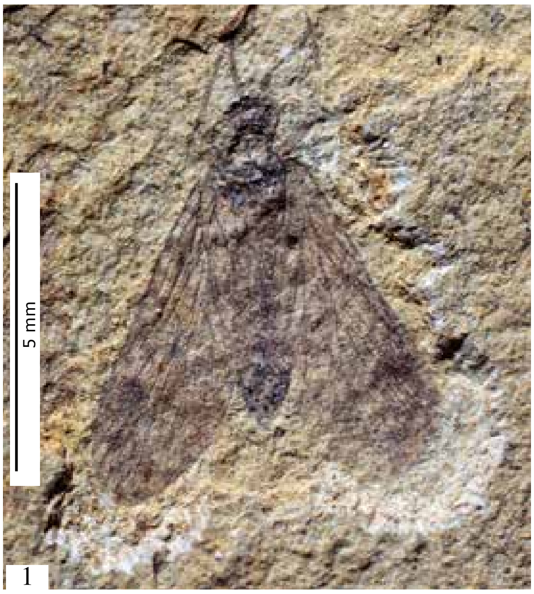
A delayed propagation of angiosperms and insects all over the world: Why could the angiosperms and the insects not spread across the entire world? From the Silurian till the Permian, Angara was an isolated continent. On the Permian-Triassic border, the biggest catastrophe in Earth's history occurred, and if science is to be believed, it originated in Siberia due to an immense vulcanism.

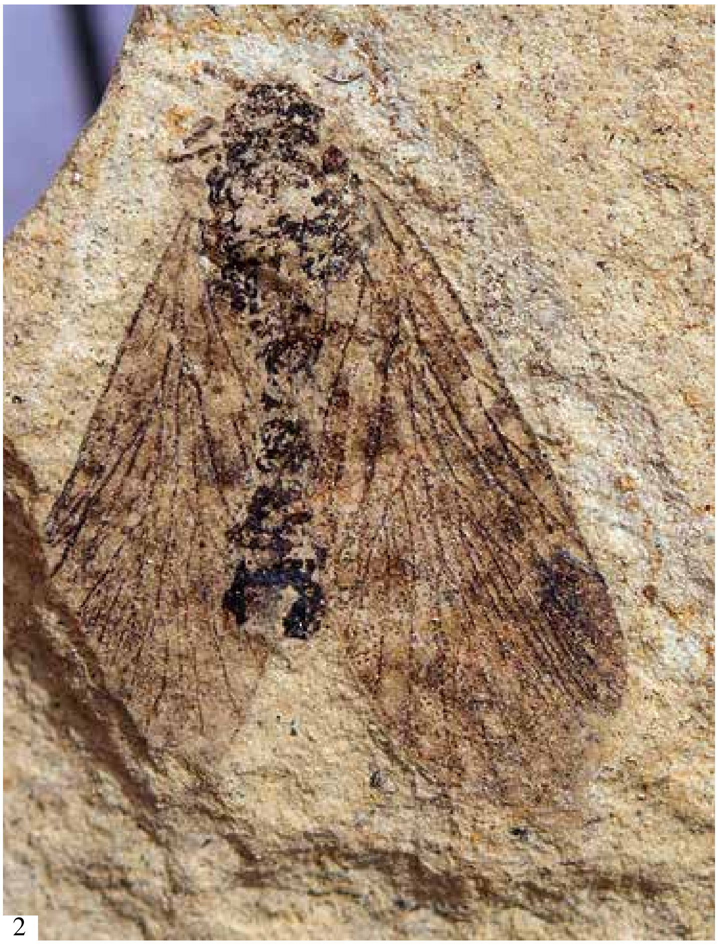
Additionally we need to investigate another phenomenon. When was it possible that especially birds were able to transport seeds over long distances? Probably not before the Jurassic-Cretaceous. Remarkably, in this time, the sudden worldwide appearance of flowering plants falls.

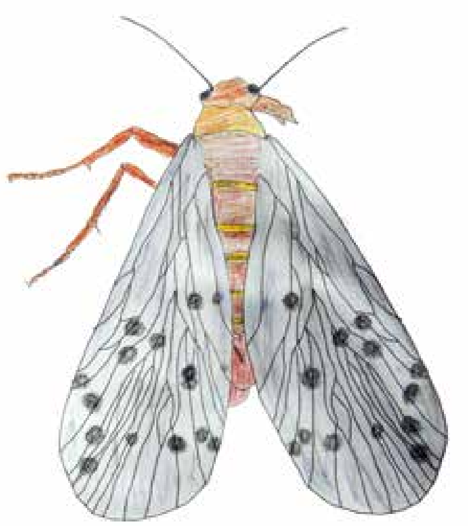
The metamorphosis of insects and angiosperms: Many insects undergo an incomplete or partial change in form and appearance during maturation. Less attention was given to the fact that in flowering plants, a distinctive modification from juvenile blossom to mature fructification stage takes place. This is not the case in gymnosperms, where the cones remain almost the same throughout maturation. The reason for connections in Permian between insects and angiosperms and this transformation is unknown and need further research. Also, the mutual reticulate venation of the leaves and wings requires an interpretation.



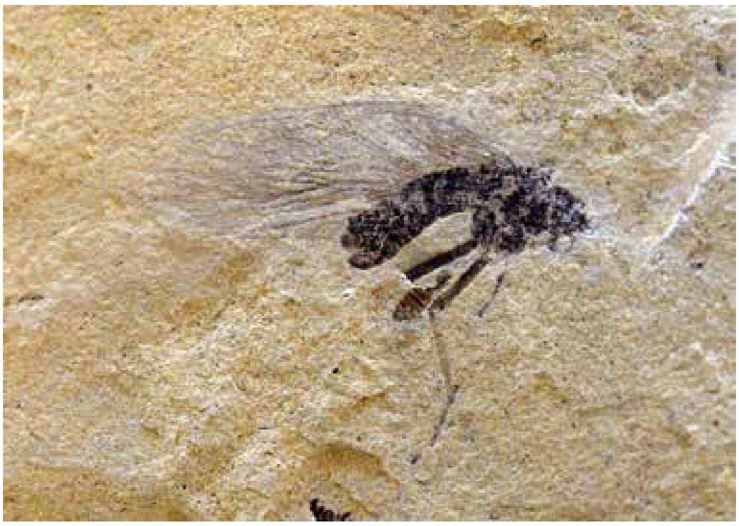
The Trichoptera *Marimerobius sukatchevae* (Novokshonov, 1997)







Agetopanorpa punctata, a suggested scorpionfly. 1. Length of wings 5-6 mm, corpus 4 mm, (Coll. Dammann); 2. Detail of *Agetopanorpa punctata, e*videncing details of the rounded patterns and pollen dust covering the wings (Coll. Thomas Gerasch, Thomaseum-Museum, Langenaltheim), Matvéevo, Early Permian, Kungurian; 3. Reconstruction. Extant Mecoptera (scorpionfly) *Panorpa communis*



Another Mecoptera is represented by *Culiciforma formosa* (Courtesy: Permian Period Museum)

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