Insect and Flowering Plant Interactions in the Early Permian

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Strangely, 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) cast a shadow of doubt, but it can be stated that some fossilised insects indicate in this direction. Especially *Karpinskptera pohli* nov. gen. n. sp. will be proposed as belonging to the crown-group of the Diptera.

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Introduction

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 and especially the small hamlets of Chekarda and Matvèevo. 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 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 Eurameri-

Diaries from Genrich Timofewitsch Mauer (1881–1940), the forestman and naturalist, who 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.

can 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 comlete 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 Tsek-*



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).

arda" 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 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 Best Sections – 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 (Sharov, 1999). Other animals have not been found, but the richness of well-preserved insects and plants is unique. Also, the flora is extremely diverse and includes many

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.

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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.

Photos Martin Dammann

The small village of Chekarda and the difficulties crossing the Chekarda brooklet to arrive to the main quarries

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.

The main sections begin 160 metres upstream of the Chekarda River's mouth. This first outcrop is only 50 metres in length, although it is distinct because of its richness in insects and well-preserved big slabs of plants. The second section can be found immediately beyond the Chekarda River's mouth, and it reaches a considerable length of altogether more than a kilometre. The richest layers are at the beginning of the Chekarda River, where finest grained grey till yellow siltstones crop out in diverse lenses (Ponomareva, 1998, Zhuzhgova et al., 2015). There the plants are well-preserved and consist the majority of isolated fern-fronds, small conifer trees or typical Angaran foliage like *Psygmophyllum* varieties and a plethora of well-preserved flowers or fructifications. The majority and best-preserved insects were collected from the marl beds at the beginning of this outcrop. From 5 to 15 well-preserved insects per square meter and a fair number of other partially destroyed or isolated wings can be seen in the better lenses.

After the narrowing of the best layers downstream, they lose most of their finest mud character and change to more sandy lenses, where the possibility to find preserved insects is reduced. Amazing fossilised bigger branches and fronds of plant can be recovered there without any problem but never the finest veins and particularities of flowers, fruits or seeds. Other minor places, mostly for plants, lie in the immediate vicinity of the Chekarda village, inside the stone quarry, on the way arriving from the main road to Chekarda or near the locality of Yulaevo, situated on the left bank of the Sylva River, two kilometres downstream of the Chekarda River mouth; their preservation is good but not enough for fragile insects.

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 (Naugolnykh, 2014). 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 impressions 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 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

Photos Martin Dammann

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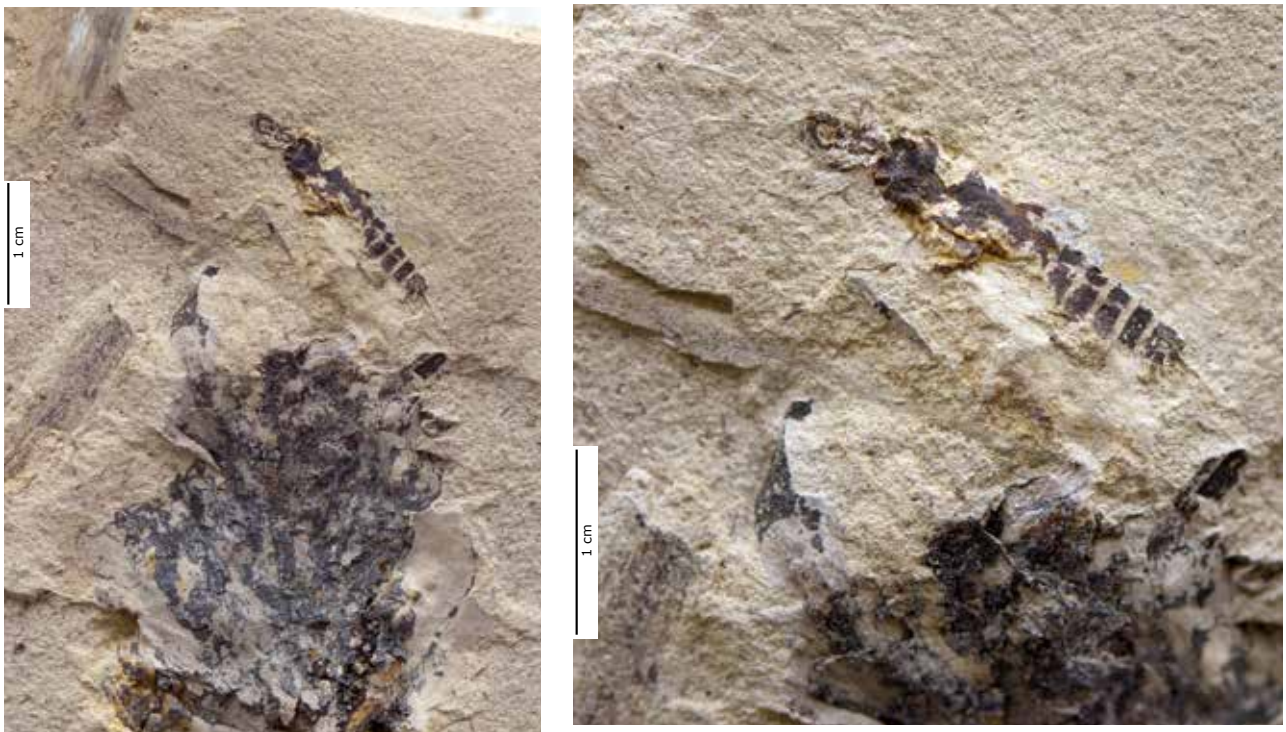
1. The locality of Matvèevo near Lyswa is not well-known but holds excellent preserved plants and insects; 2. A snowstorm cannot interrupt the research; 3. A perfectly preserved new dragonfly larva (*Permomatveevia perneri*) and 4. A mayfly (*Misthodotes sharovi*)

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, remains of fish, brachiopods, large shells of well-preserved nautiloids and ammonoids of good preservation, jaws of cephalopods (Krasnoufimskie Klyuchiki, Sverdlovsk oblast), Divja Mountain, Sobolya, Manchazh (Artinskian) (Naugolnykh, 2018). They were just part of the Cis-Uralian Artinskian sea basin, which was connected to the Boreal Ocean in the north and the Tethys Sea in the south.

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*



***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)

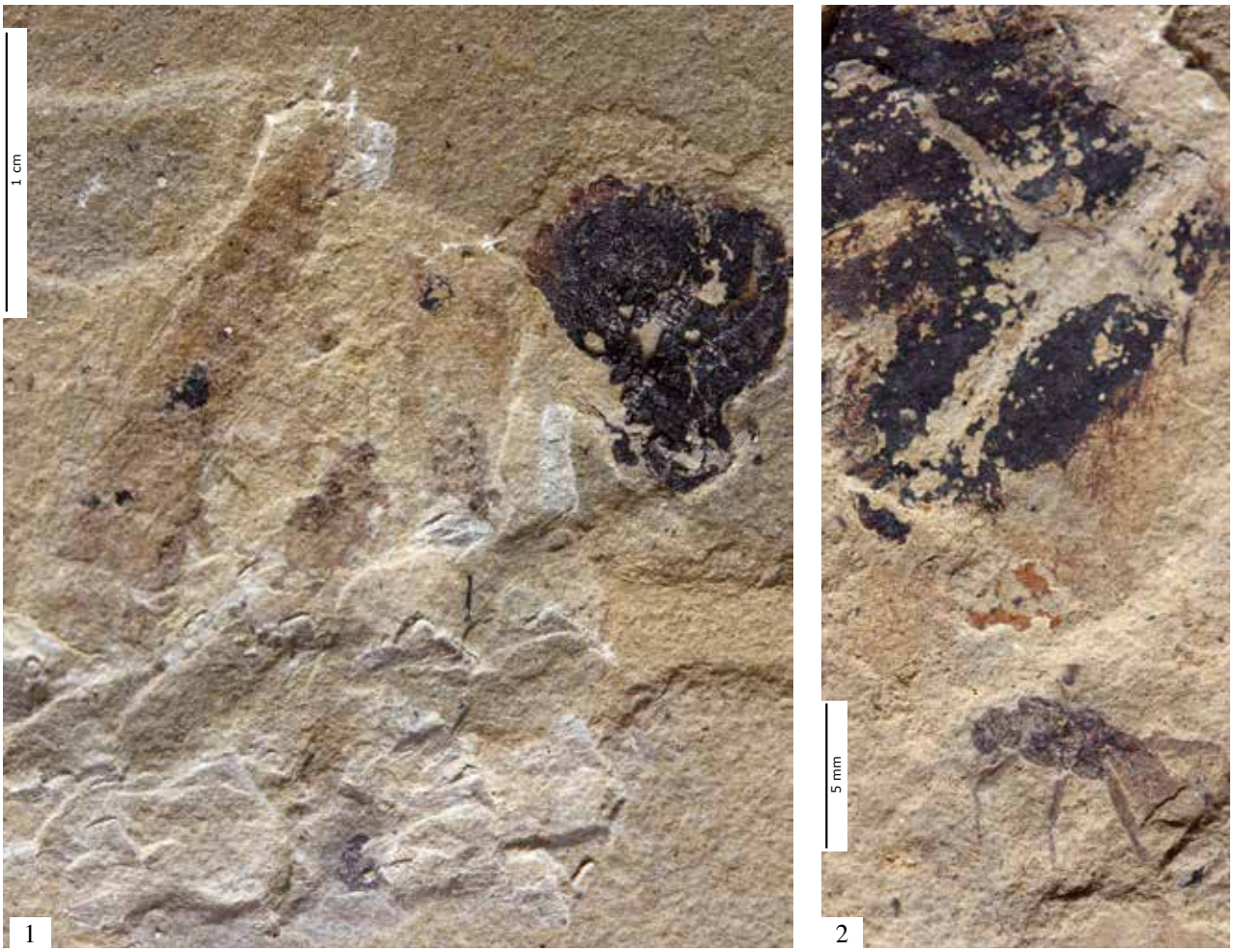
praecursor, Palaecharinus rhyniensis). During this period, Euramerica and the Southern continent of Gondwana moved together, whereas Angara, the Siberian continent stood isolated.

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 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.



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

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 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

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)

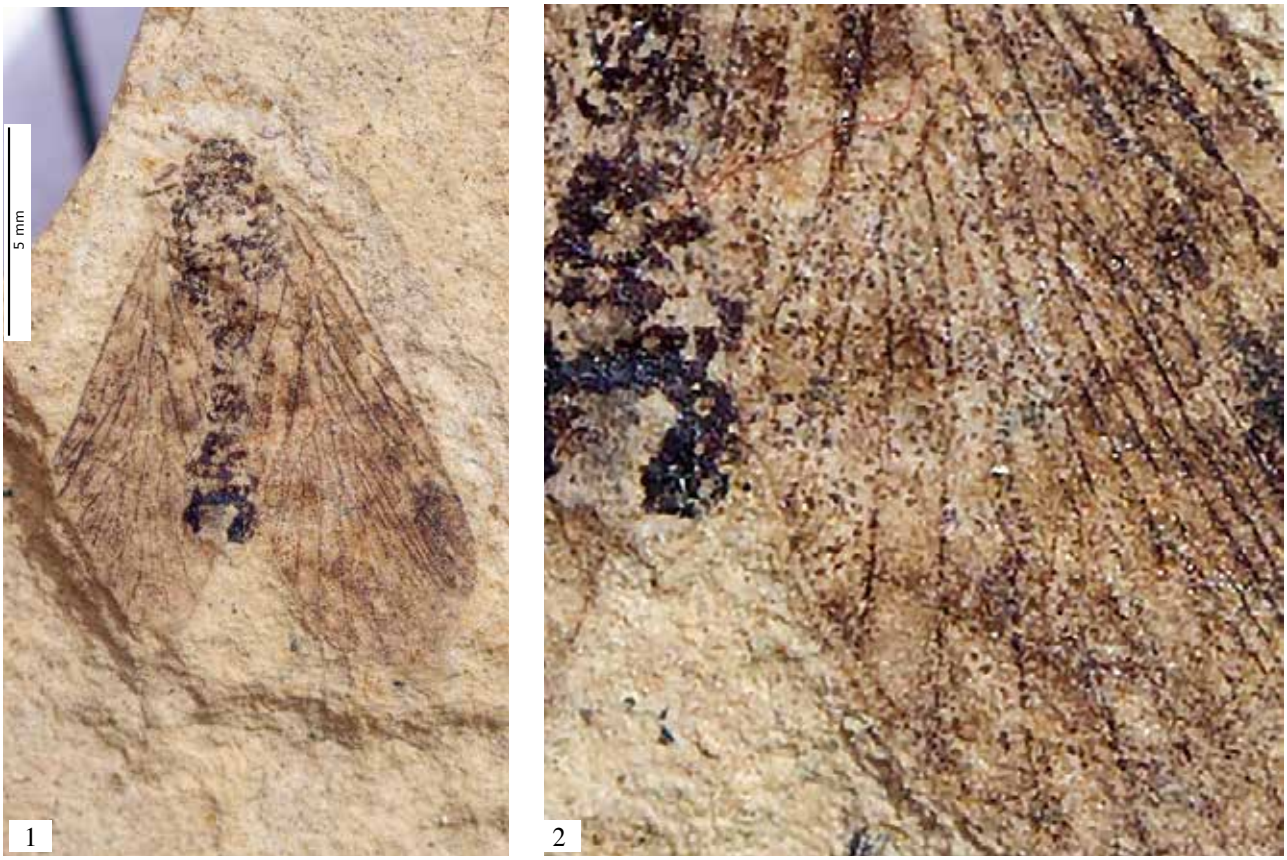
with the plants. Obviously in that case they served as pollinators.

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 (Culley et al., 2002), 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 era.

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 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 descend-



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.

ant 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 line and cannot be compared with the Sibirian Angaraland.

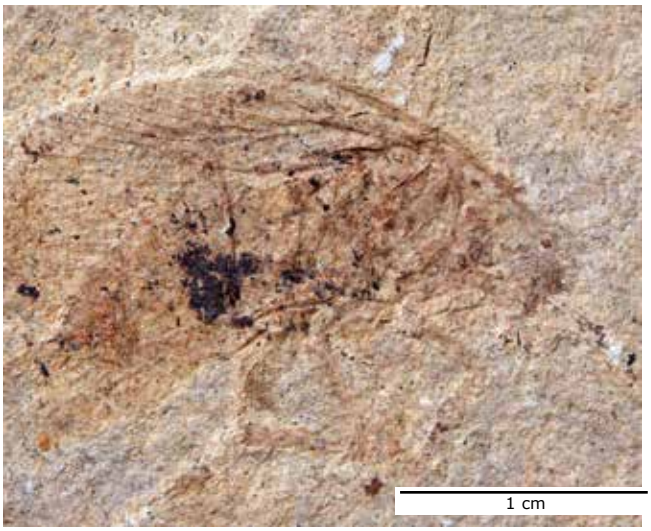
Summarizing can involve the not so far-fetched theory that generously presented nutritious pollen gut brought several advantages and helped a selective pollination. Probably it was more efficient than the accidental fertilisation by wind. If a plant tempted a more favourable insect by adding certain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

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 re-

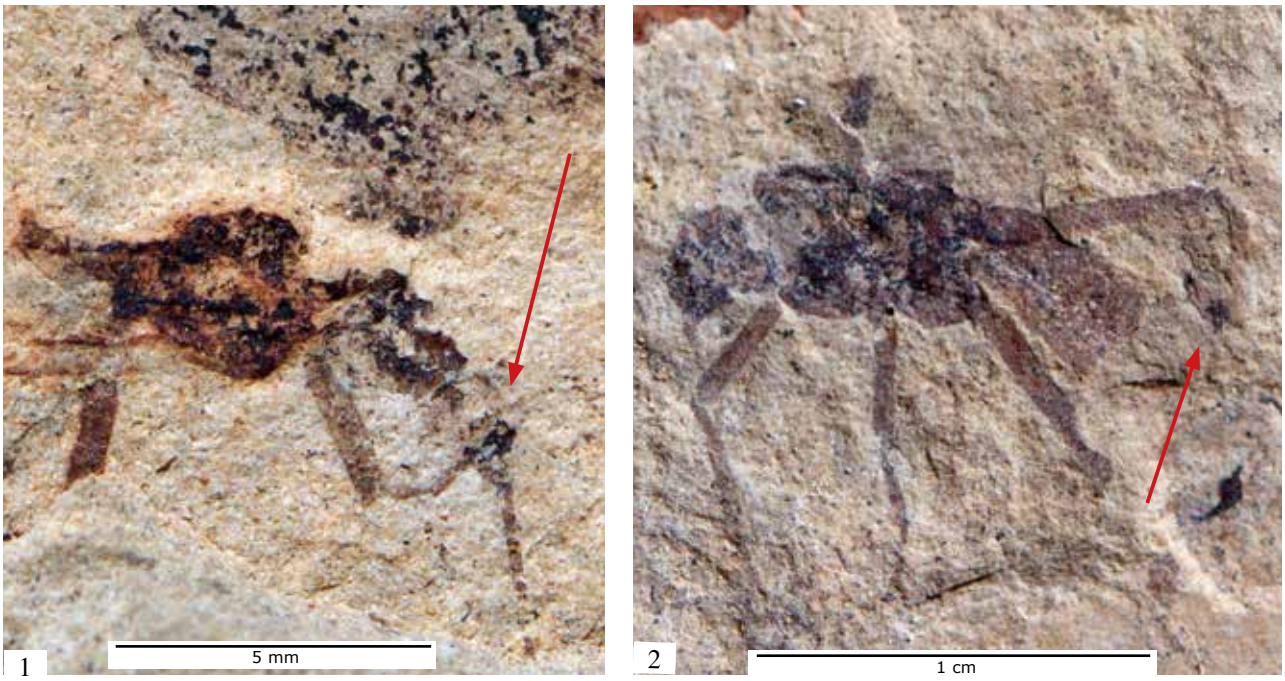
Insects from the Early Permian Fore-Urals with Pollen Gut in the Stomach



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 nmyphs (probably *Uralonympha varica)* with pollen gut on their legs (CEK 93 Coll. Wachtler, CHEK 322, Coll. Perner), Chekarda, Dolomythos-Museum, Italy

stricted dispersion by wind could be enlarged. The cooperation 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 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. From the Triassic till the Cretaceous, the time of worldwide appearance of angiosperms, probably obstacles such as high mountain ranges or a consolidated gymnosperm flora were too high to allow a massive distribution of the insects and flowering plants.

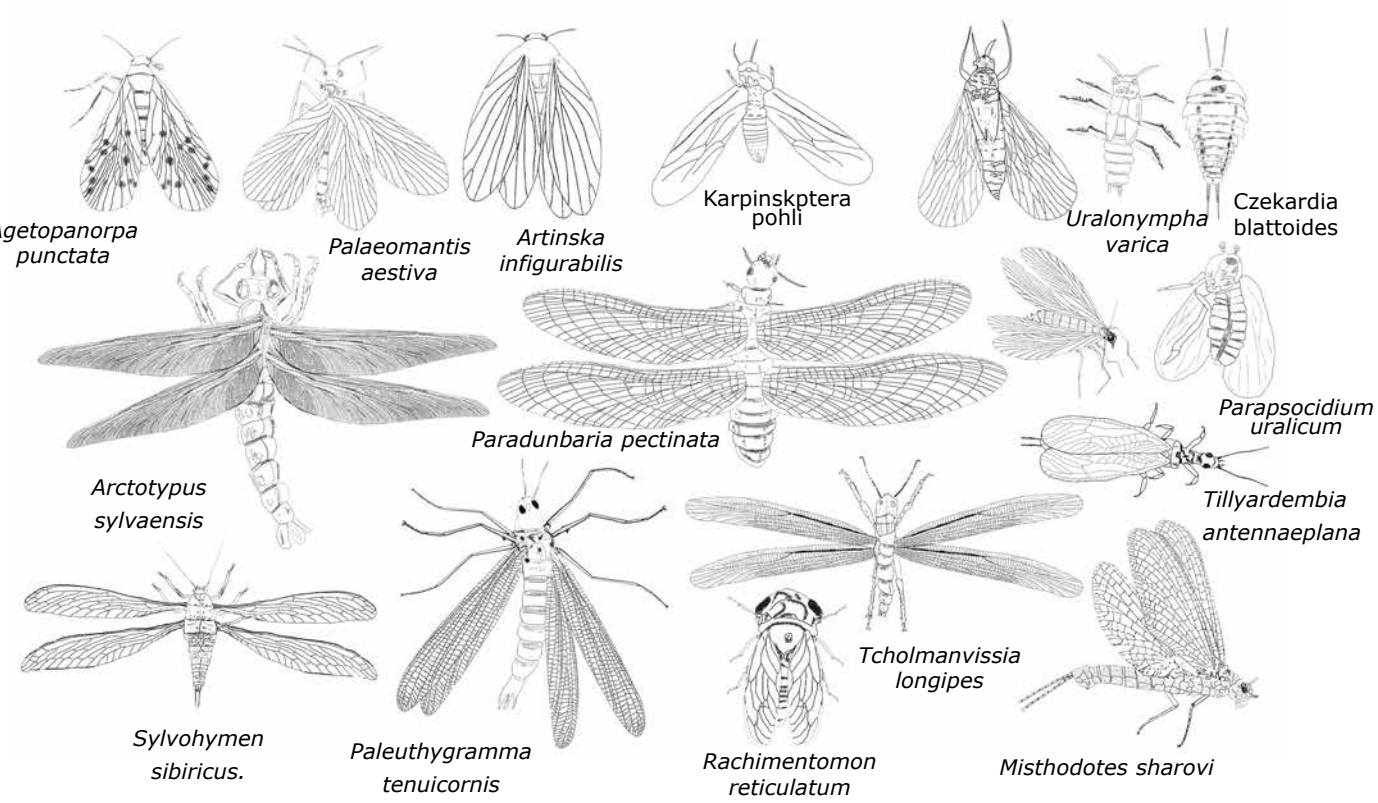
The metamorphosis of insects and angiosperms: Many insects undergo an incomplete or partial change in form and appearance during maturation. Less attention was given to the fact that in flowering plants, a distinctive modification from juvenile blossom to mature fructification stage takes place. This 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 un-

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

known and need further research. Also, the mutual reticulate venation of the leaves and wings requires an interpretation.

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 (Nel et al., 2009).
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 (Nel et al., 2009). 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.



Permian Insects and Angiosperms

Several flowers and insects from the Early Permian Fore-Urals

Moreover, there were no obvious reasons for the usefulness or the background of this dwarfism.

During the Late Carboniferous and especially in the Early Permian, smaller Meganeuridae simultaneously existed, confirming a co-existence of different life habits of these ancient flying predators (Nel et al., 2018). In the Early Permian Fore-Ural, they co-existed with smaller species, reaching only the size of today's dragonflies or Anisoptera. But the huge *Meganeura monyi* (Brongniart, 1884) did not have a large body. Only their wings were proportionally larger than their body when compared with modern dragonflies (Nel et. al., 2009).

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* (Nel et al., 2009; Li et al., 2013).

The forewings of *Arctotypus sylvaensis* were usually slenderer 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 greatly enlarged compound eyes (Nel et al., 2018) 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* (Dammann, 2017) constitutes the largest insect larva found in the Early Permian Kungurian layers. But even *Sylvonympha tshek-*

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

ardensis (Novokshonov & Pankov, 1999) 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.

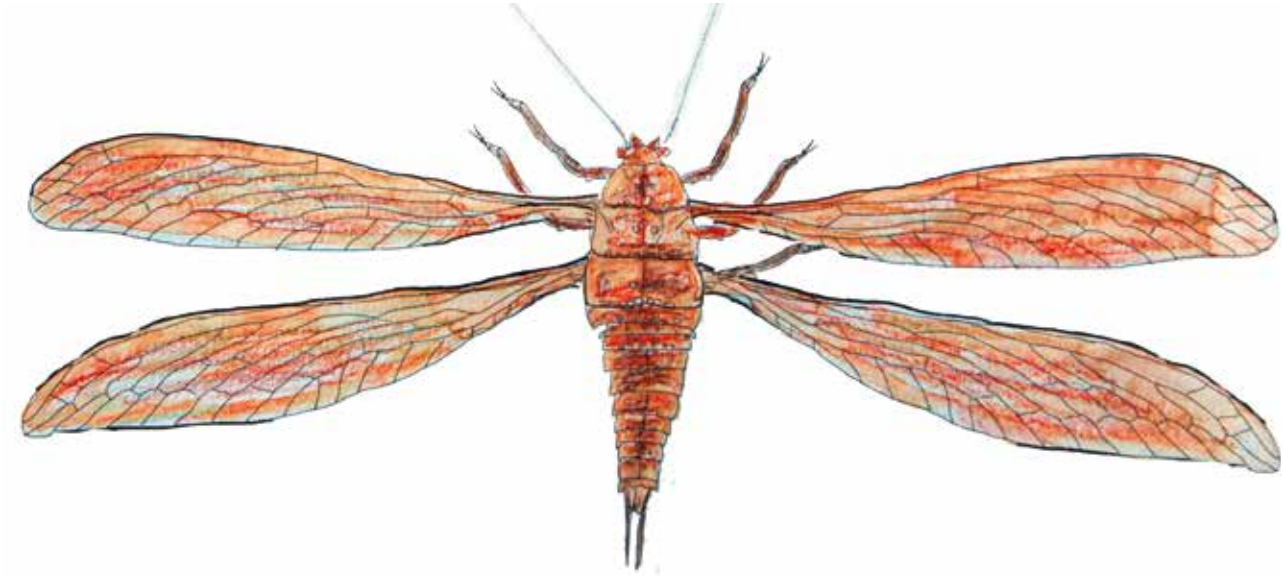
The Spreading of the Megasecoptera and Palaeodictyoptera

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 (Grimaldi & Engel, 2005). 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* (Martynov, 1941) 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 (Kukalová-Peck, 1972). 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 the 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 (Rasnitsyn & Novokshonov, 1997).

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.

The Odonatoptera (Dragonflies)

The first Protoodonata are recorded from the Upper Carboniferous and include 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 hasa 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.

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 Moscov)

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 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 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.

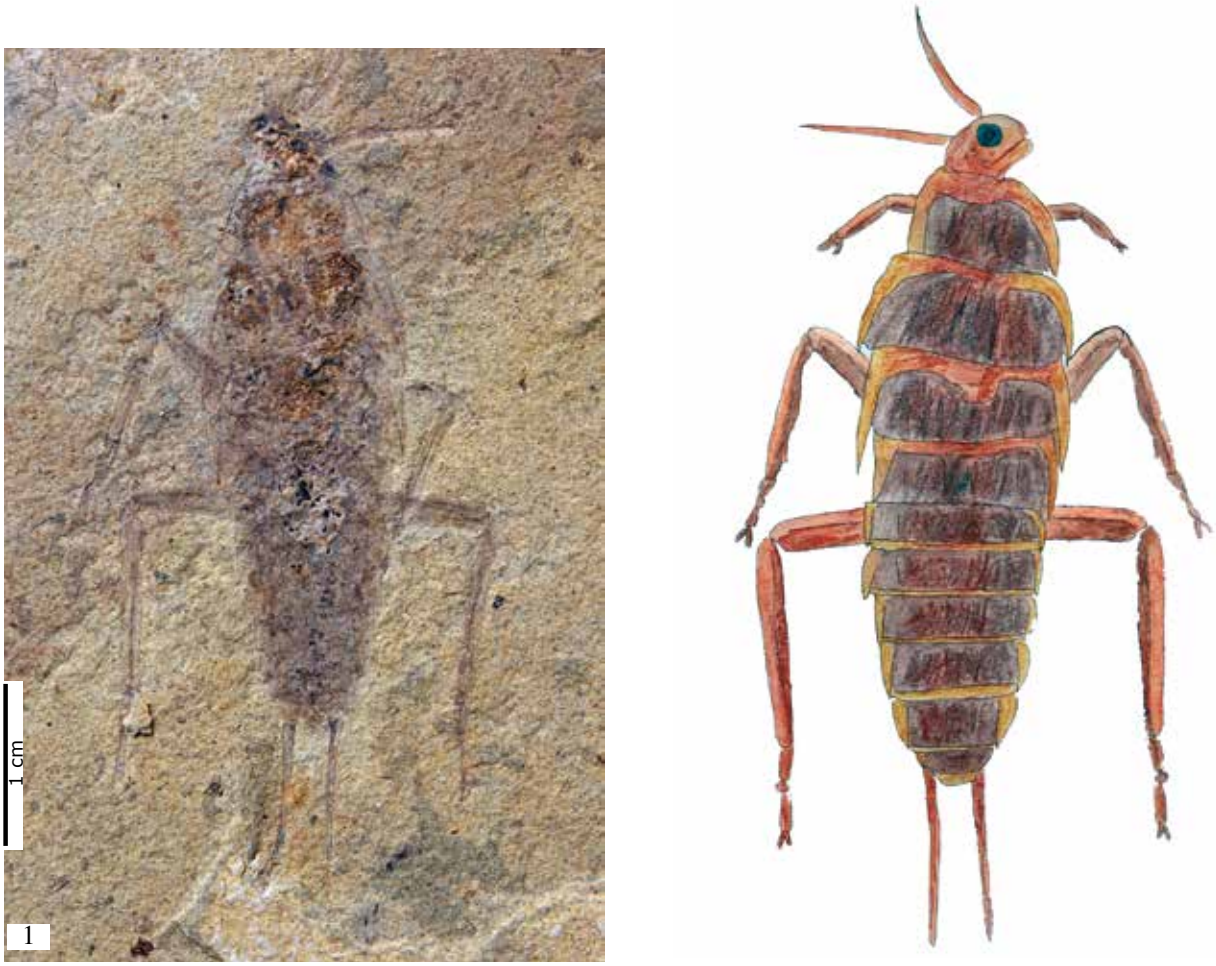
The nymphs of the Misthodotidae are not definitely known. Tschernova (1965) has described a fragment of a nymph from the Chekarda beds and identified it as belonging to *Misthodotes sharovi*. The nymph has nine pairs of gill plates, as in the protereis matid nymphs, but since the entire thoracic region,

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

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 (Gillott, 2013).
In the Neoptera, the sclerites moved away from the tergum and became articulated, making folding of the wings possible. Be-



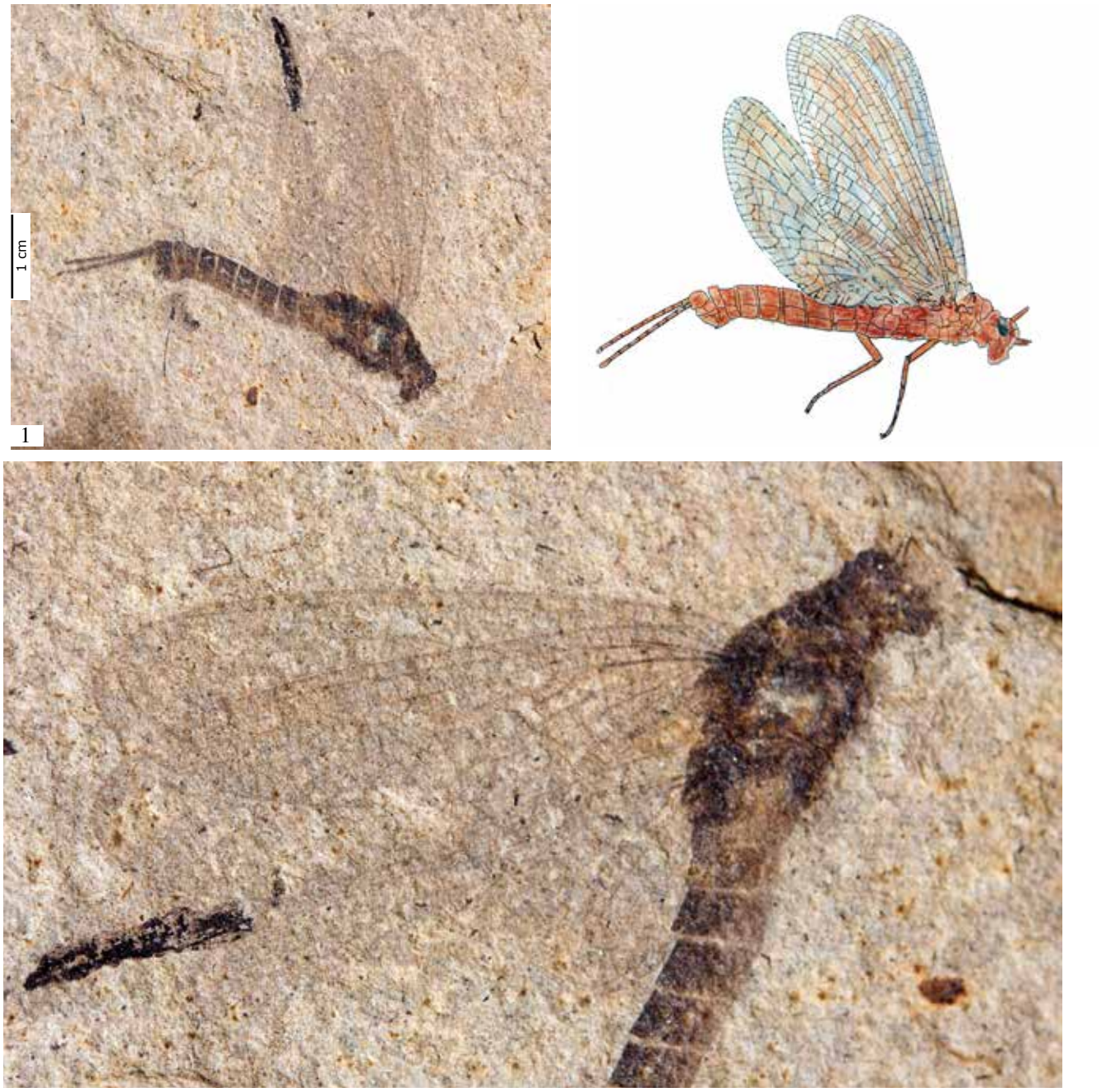
Angaroptera nicolaswachtleri, probably a dragonfly nymph. Otherwise it can be inserted in the Gryllidae or the cicadas. Holotype MAT 190, Matvéevo, Early Permian, Kungurian, Coll. Nicolas Wachtler, Dolomythos Museum

cause 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 20000 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 (Gorochov, 1987), the first Protorthoptera. *Tcholmanvissia longipes* [synonyms: *Metoedischia longipes* (Martynov, 1940) and *Pinegia longipes* (Sharov, 1962)] – the most frequently found species – had jumping legs with broadened femora, whereas all the representatives of this family share



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

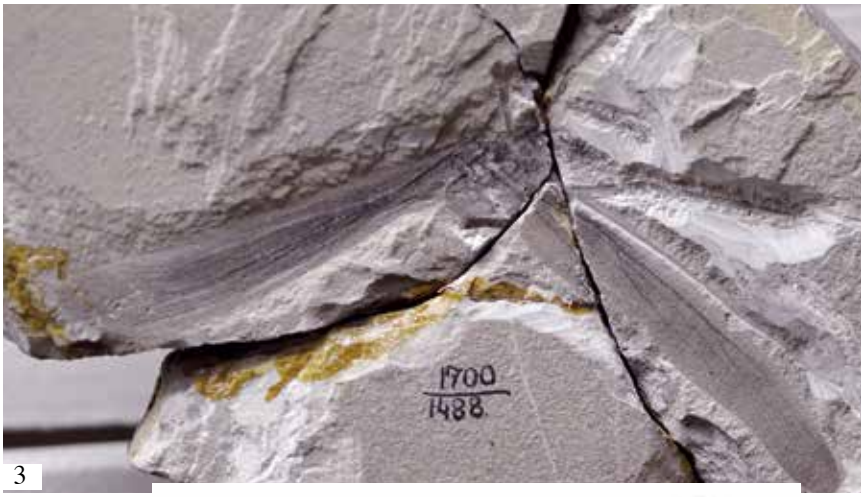
the 'oedischioid' arrangement of the cross-veins in certain areas of the wings (Bèthoux & Nel, 2002b). A close relationship as crown group of the Caelifera will be sustained by analyses (Martynov, 1940; Béthoux & Nel, 2002).

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* (Sharov, 1968) and *Metoedischia* (Martynov, 1928). 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

1

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



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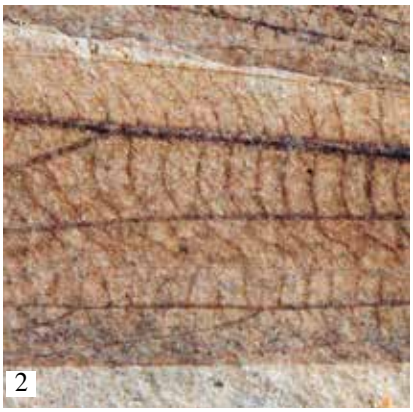

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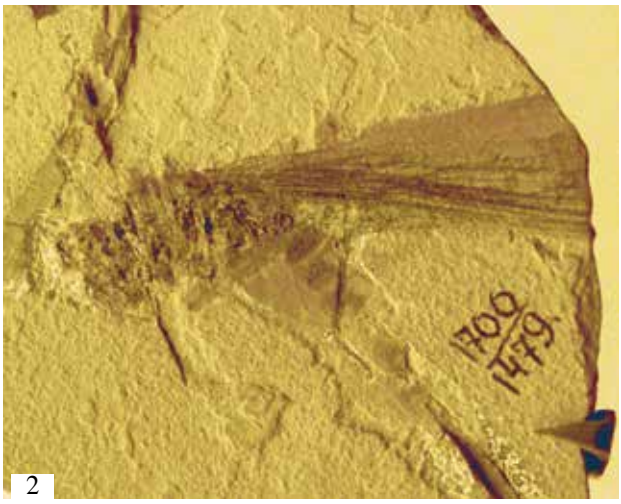
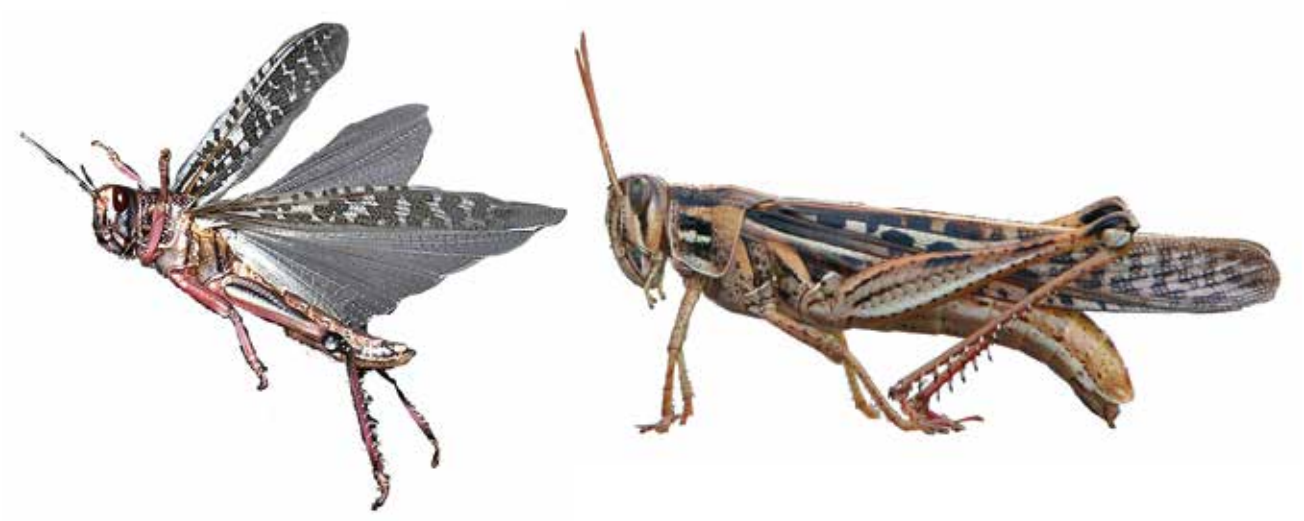


1-2. *Uraloedischia permiensis.* They had elongated hindlimbs making them adapted for jumping as modern grashoppers. Chekarda, Paleontological Institute of the Russian Academy of Sciences, Moscow.



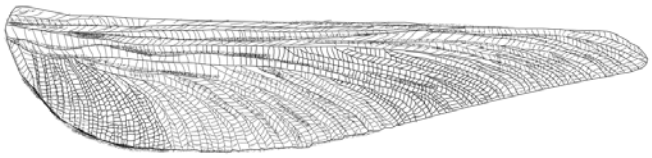
Extant Orthoptera (*Locusta migratoria*) with open wings and in the normal resting position

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 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.

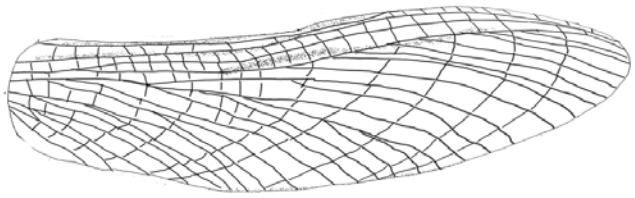
The First Blattodea – Cockroaches

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 (Martynov, 1940; Aristov, 1999), 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 (Aristov, 1999) but also in the Eoblattida (Aristov, 2018).
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* (Martynov, 1940; Aristov, 1999, 2018) 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* (Aristov, 2018).
Adult cockroaches from the Early Permian Fore-Urals were known as *Sylvaprisca focaleata* and *Artinska infigurabilis* (Aristov, 1999). 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.

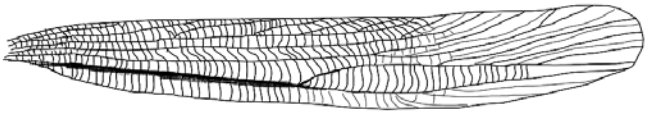


Wing-detail of *Arctotypus sylvaensis*

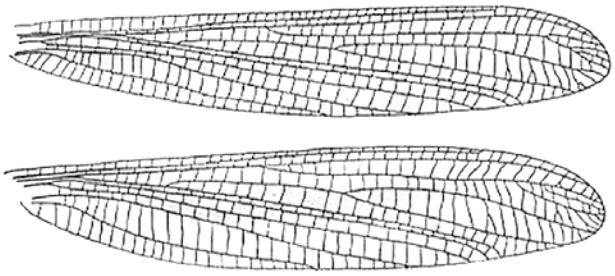


Wing-detail of *Paradunbaria pectinata*

Wing-detail of *Sylvohymen sibiricus*



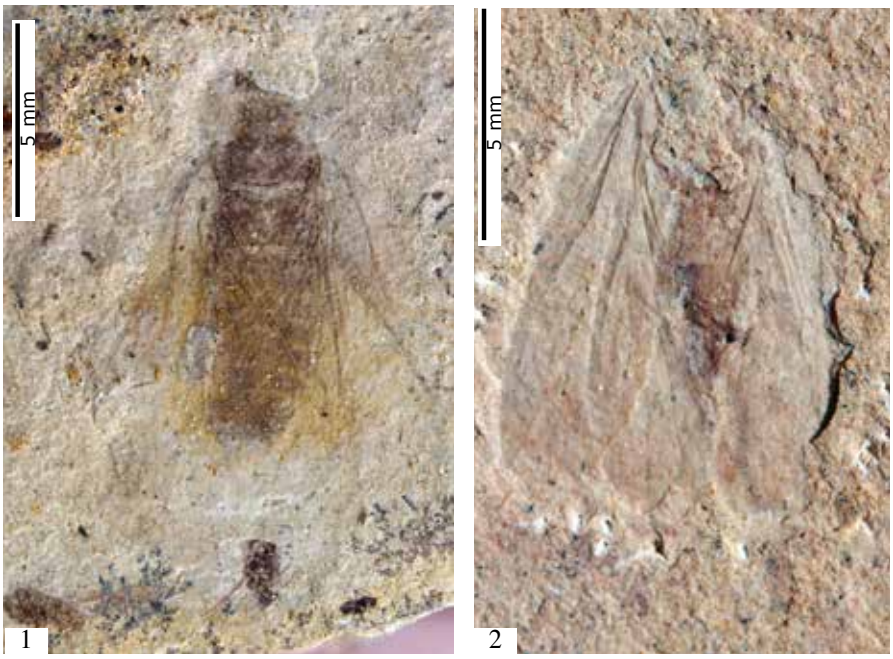
Wing-detail of *Tcholmanvissia longipes*



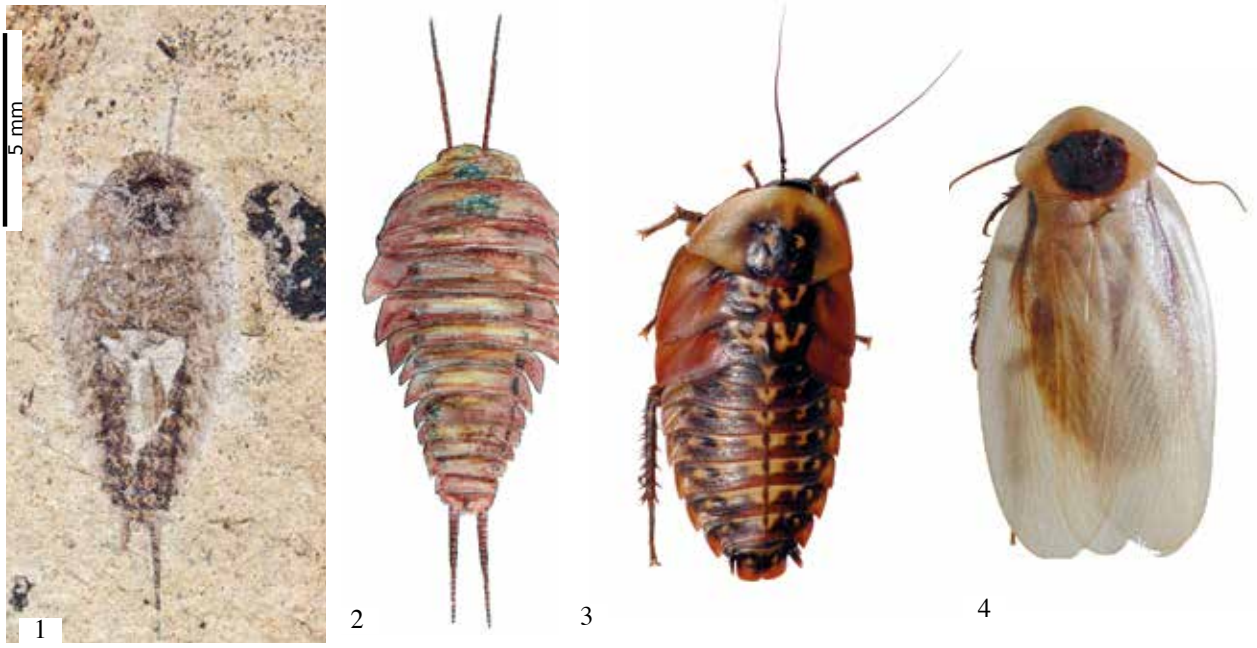
Wing-detail of *Paleuthygramma tenuicornis*

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 superfi-



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).

cially resemble moths (Shcherbakov & Popov, 2002).

The oldest Cicadomorpha, the Archescytinidae, were first recorded in the Artinskian (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 (minor*) and *Sylvacoleus (sharovi* or *richteri*) (Ponomarenko, 2003) 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.

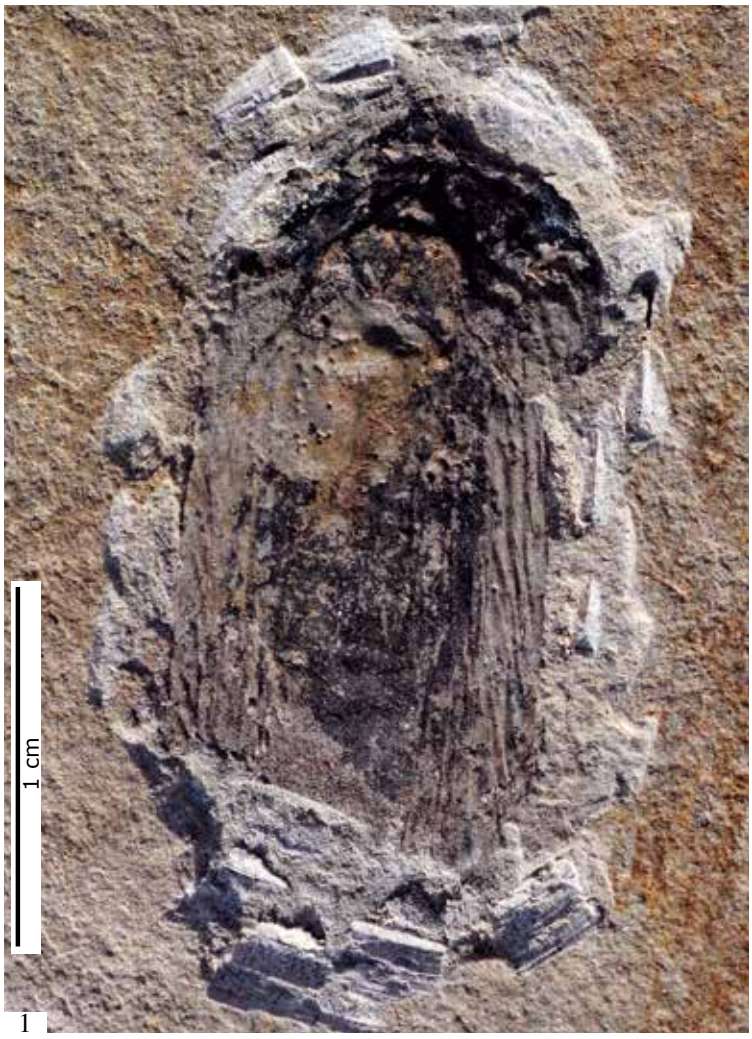
The appearance of beetles was considered to have taken place together with the early diversification of the Holometabola. The Miomoptera and Palaeomanteida were considered as the most archaic group of Holometabola (Rasnitsyn, 1980; Kirejtshuk et al., 2013).

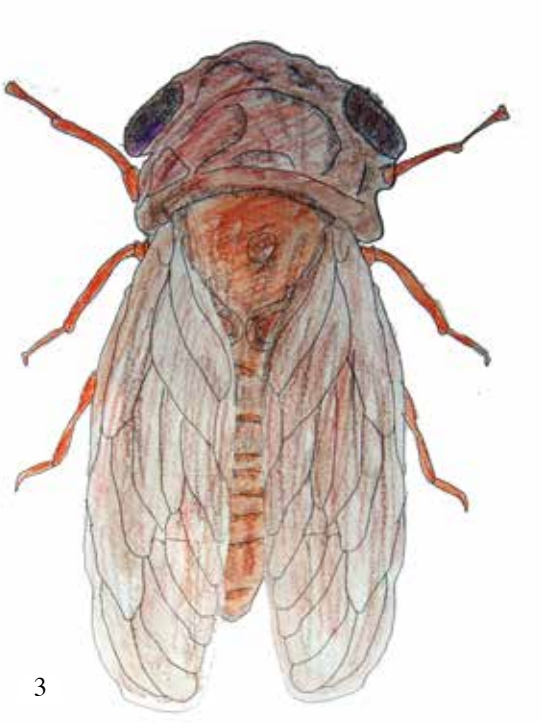
The Ancestors of the Plecoptera (stoneflies) in the Early Permian

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* (Zalessky, 1937) and *Kungurembia* (Zalessky, 1938), 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 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 (Aristov & Rasnitsyn, 2010).

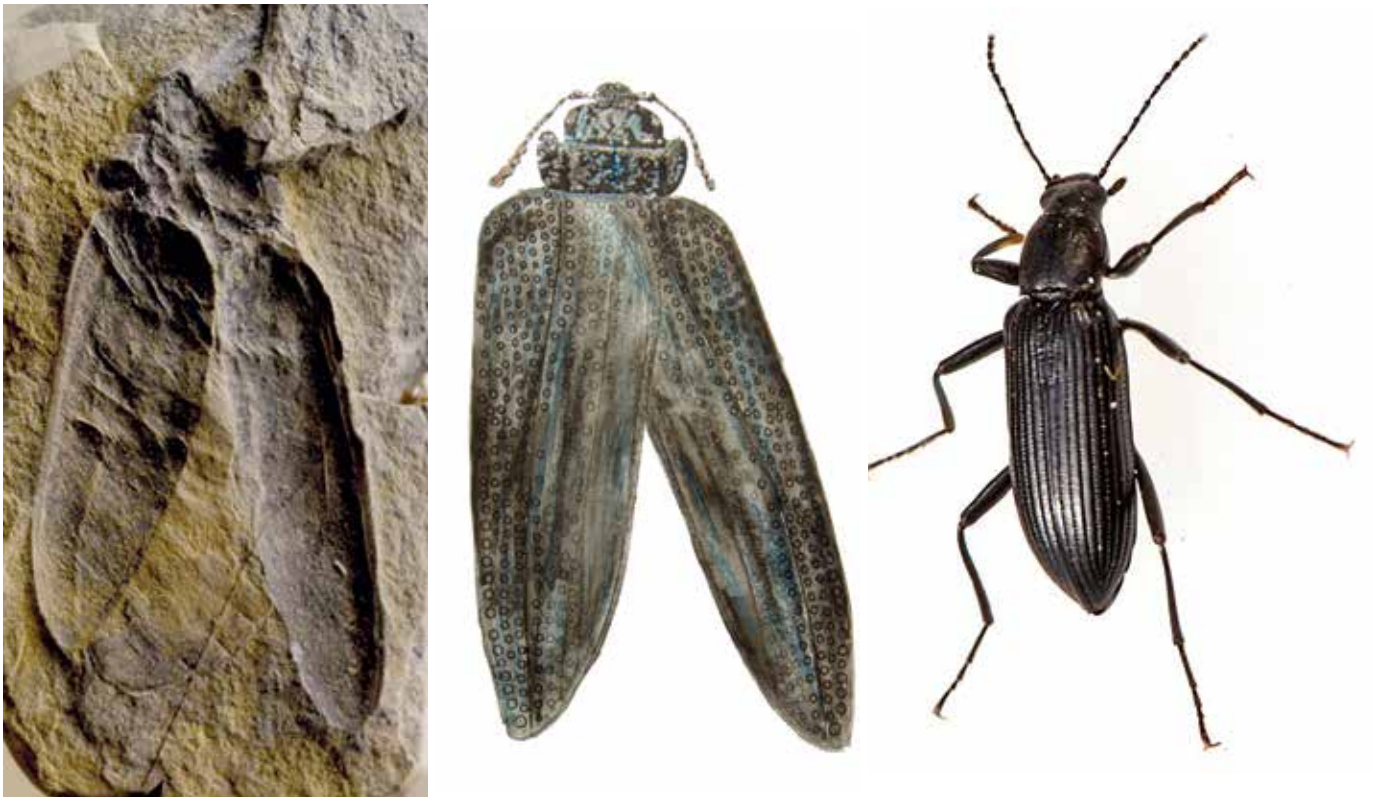
The taxonomic position of some of the genera found in Chekarda and Matvèevo was never unquestionable. Often, they were inserted as Grylloblattida, then they were transferred to the previously strictly Carboniferous order Eoblattida. Especially the classification as progenitors of the Grylloblattida was largely accepted (Zalessky, 1937, 1939; Martynov, 1940; Storozhenko, 1993; Novokshonov, 1995, 1997, 1998, 2000; Aristov, 1999, 2004). Today 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





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).

or perhaps related to the Grylloblattida, and it would be more useful to classify them as Protoplecoptera.

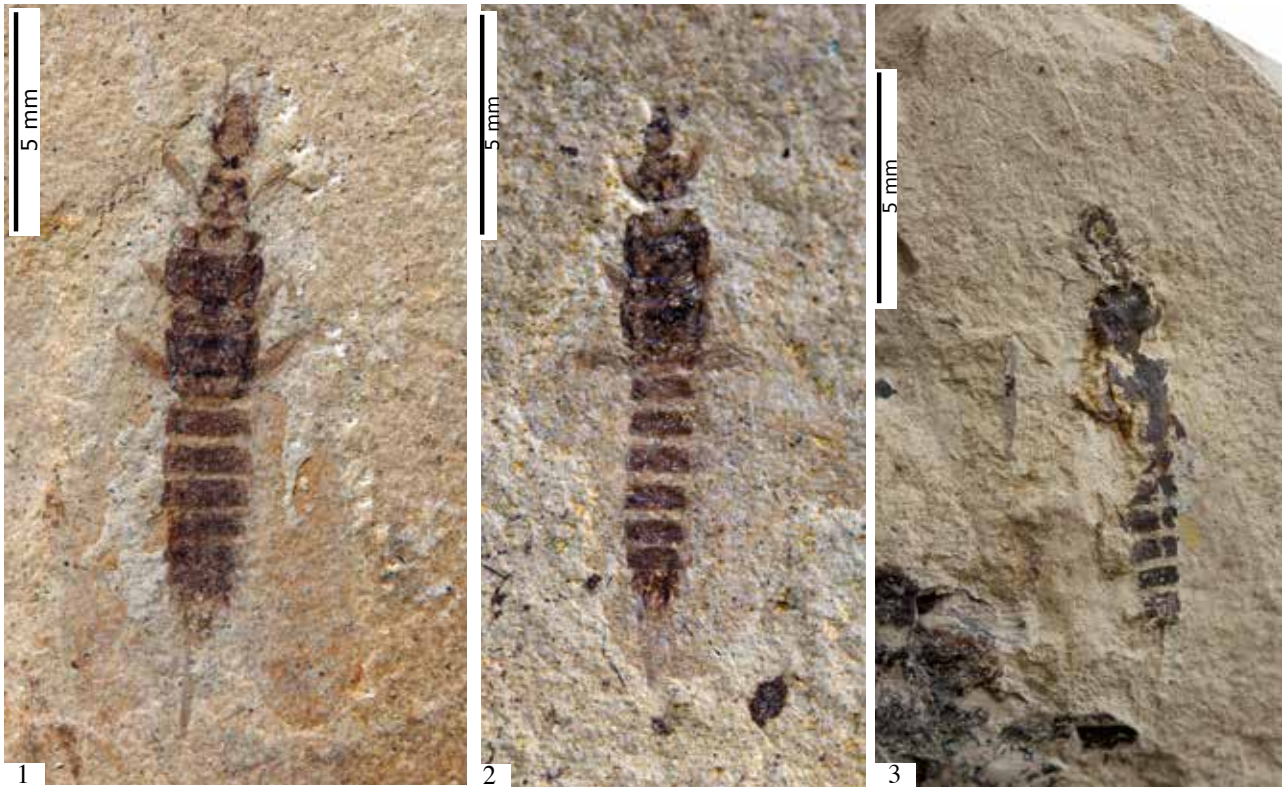
Early Permian Tillyardembiidae notably differed in size and appearance: the dwarfish Permembiidae, with a forewing of only 2.5 mm stands in contrast with the large Atactophlebiidae having a wing-length of 90 mm. Although all the wings were delicate and membranous, a pattern was sometimes difficult to 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 hereas 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 females of *Tillyardembia* were restored (Zalessky, 1938; Vilesov & Novokshonov, 1993). The structure of their wings with weak veins and a convex fore margin let suppose that they were not very good fliers (Aristov, 2004). The fossil evidence indicates that the Permian Plecoptera were pollen eaters, as well as fed on parts of plants or fruits (Afonin, 2000).

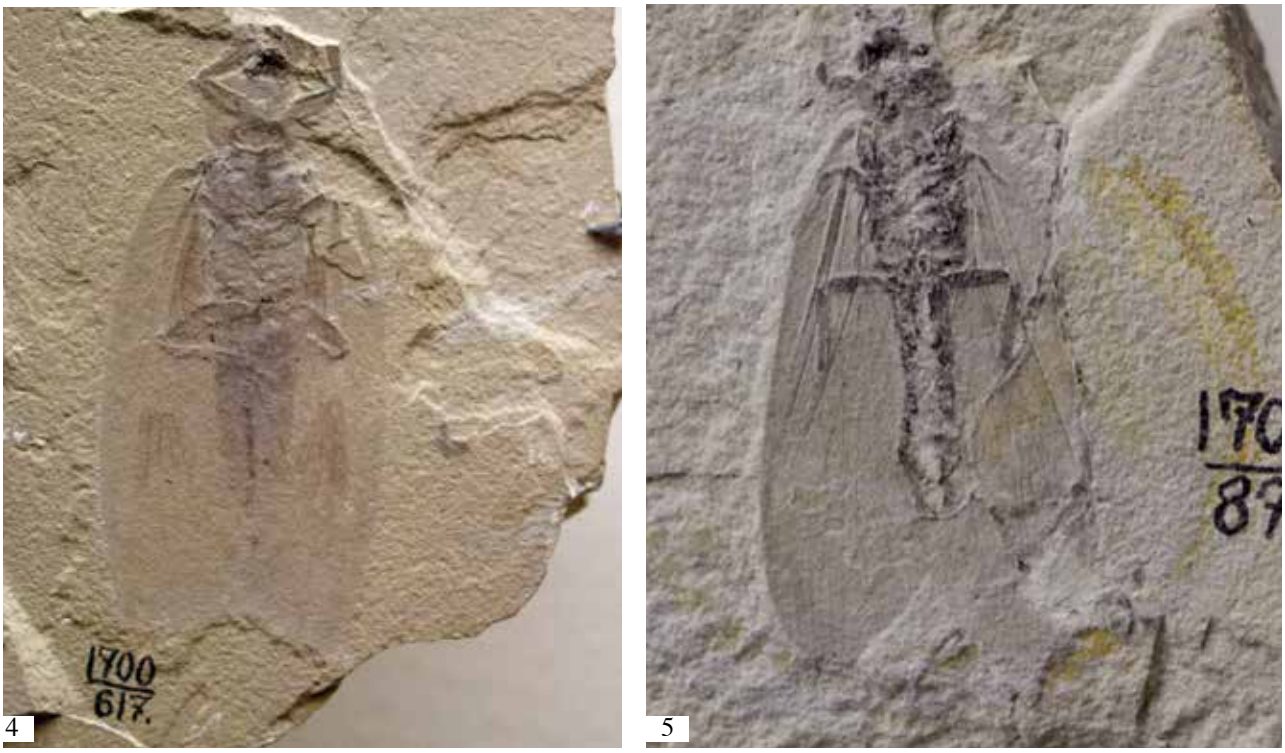
The other dominating family were the Atactophlebiidae (Martynov, 1930) represented by the monotypic genus, *Kirkorella*. The Ideliidae (Zalessky, 1929) were dominated by *Sylviodes perloides* and *Sylvidelia latipennis,* medium-sized insects with a large head and eyes and long antennae. All legs are equally long, whereas the anterior margins of the forewings are convex (Aristov, 2003). 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 (Handlirsch, 1906a) 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" (Prokop et al., 2014).

One of the most common nymphs in the Permian Fore-Urals to be encountered is *Uralonympha varica*. It is strong because of

Early Permian Plecoptera (Stoneflies)

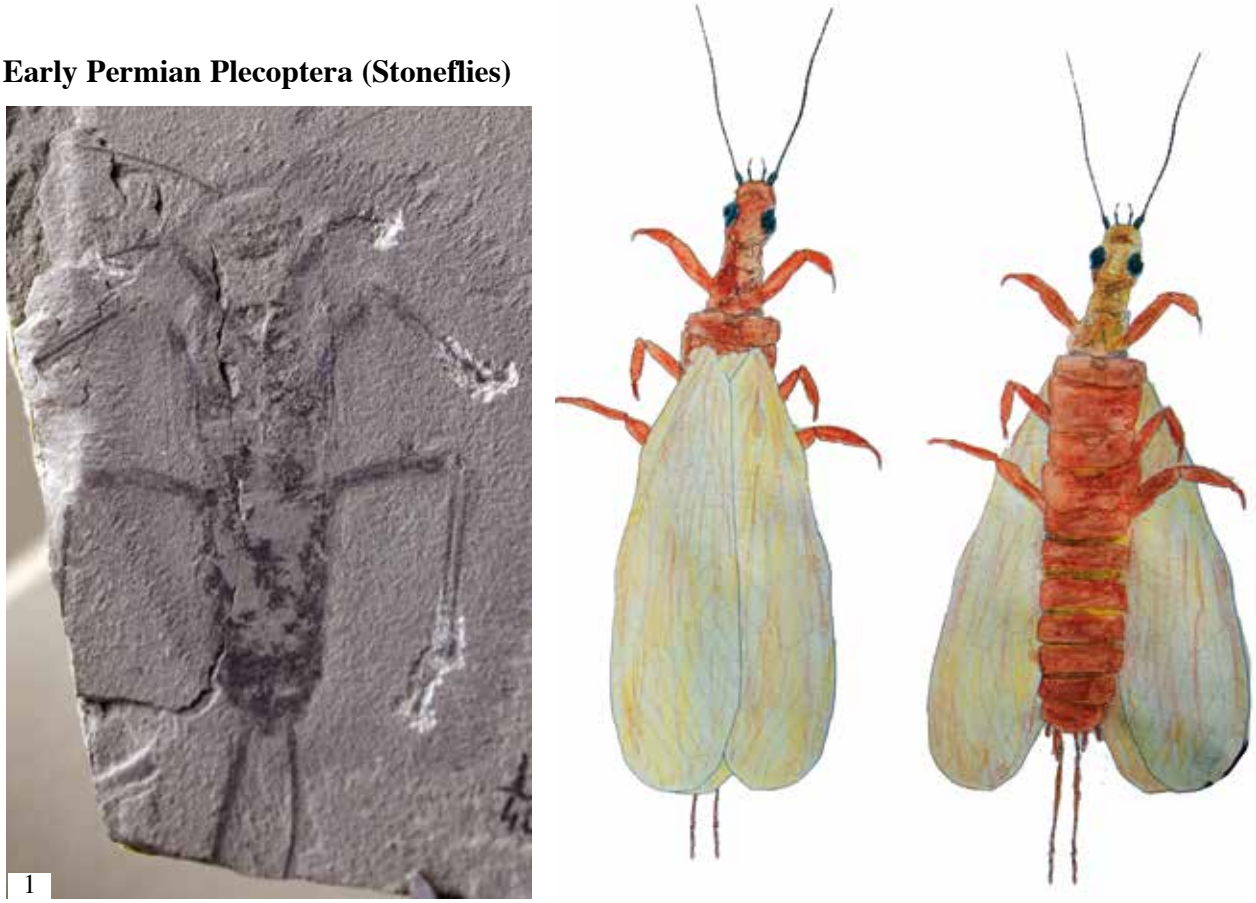


Tillyardembia antennaeplana constitutes the most abundant stone-fly species in the Fore-Urals. 1. A female specimen CHEK 04, Coll Wachtler; 2. CHEK 99 Coll. Dammann; 3. Covered with pollen from a flower in the vicinity (Coll. Gerasch). All Chekarda



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

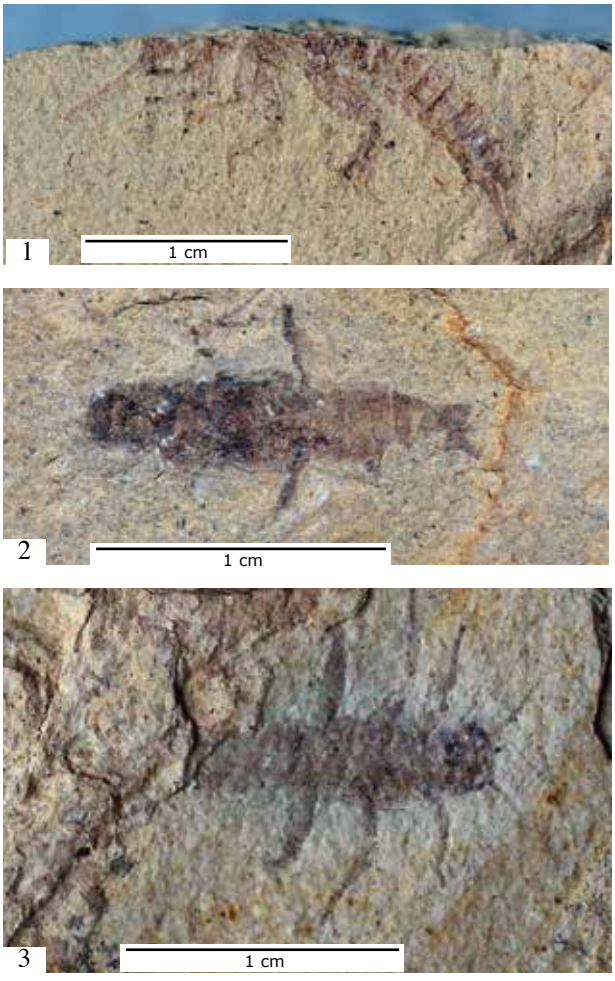
Early Permian Plecoptera (Stoneflies)



The Atactophlebia *Kirkorella mira* is also a very 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)

the prothorax and the legs and has generally been considered an immature form of a stonefly (Zaiessky, 1935; Sharov, 1962).
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 (Carpenter, 1992), others excluded these (Béthoux et al., 2004) and put them in the Hypoperlida, a suggested line of the Plecoptera.



***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 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-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 (Martynov, 1938).

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

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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* (Zalessky, 1939). *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 crossveins. 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 (Grimaldi & Engel, 2005). 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 (Prokop, 2017) or based on other theories as starting point of the Hymenoptera (Rasnitsyn, 1980).
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 (Bashkuev, 2010). The Palaeomanteidae were often inserted in the family of the Miomoptera (Martynov, 1927) and therefore, in the superorder, Acercaria (Prokop, 2017) 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*

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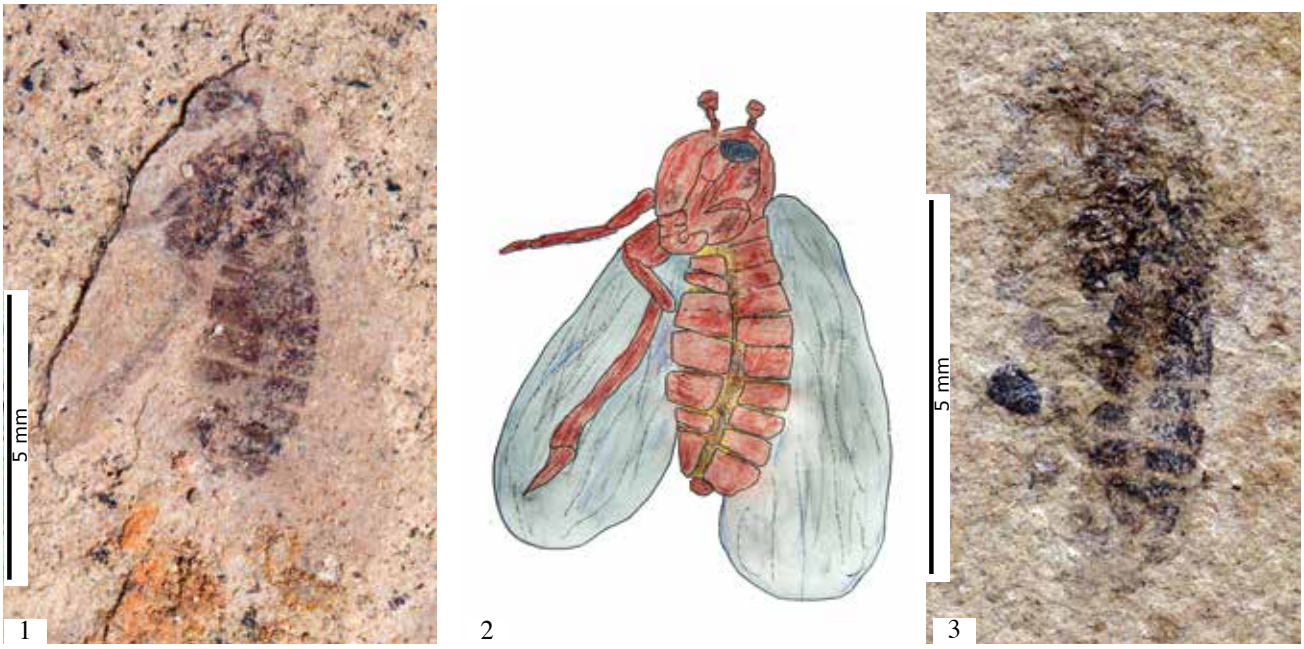
1-2. Paleuthygramma tenuicornis (CHEK 02) Chekarda, Coll. Wachtler. 3-4. Reconstruction of *Paleuthygramma tenuicornis*; 5. Extant antlion *Distoleon annulatus* (Neuroptera, Myrmeleontidae)



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)

tenuicornis, the beetles like *Sylvacoleus sharovi,* or the Cicada *Rachimentomon reticulatum.* Also, *Delopterum rasnitsyni* (Novokshonov, 2000; Prokop, 2017) 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.

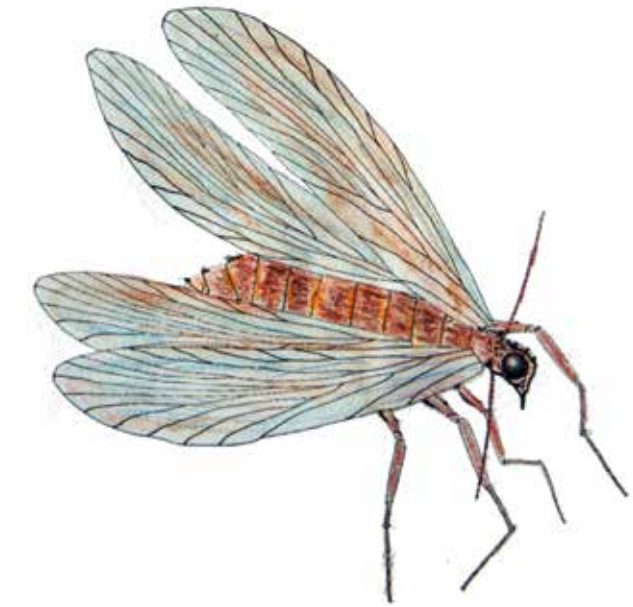
The First Scorpionflies – Mecoptera

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

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

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.



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

In Chekarda and Matvèevo, the most abundant species consist of *Agetopanorpa punctata* (Carpenter, 1930; Novokshonov 1993), 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 (Bashkuev, 2010).

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 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. 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*. The Mecoptera include

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)

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. 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.

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 (Aristov, 2004).

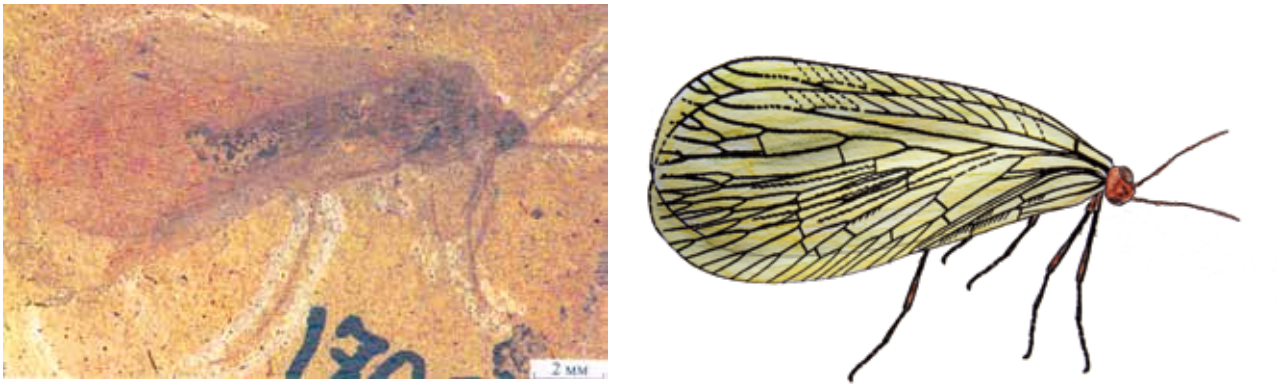
The small size of *Agetopanorpa punctata*, as well as *Palaeomantis aestiva* helped them to extract protein-rich pollen from the dwarfish flowers. Pollen dust was found on the wings or as content in the stomach in both genera. Considering all these slightly different in-

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

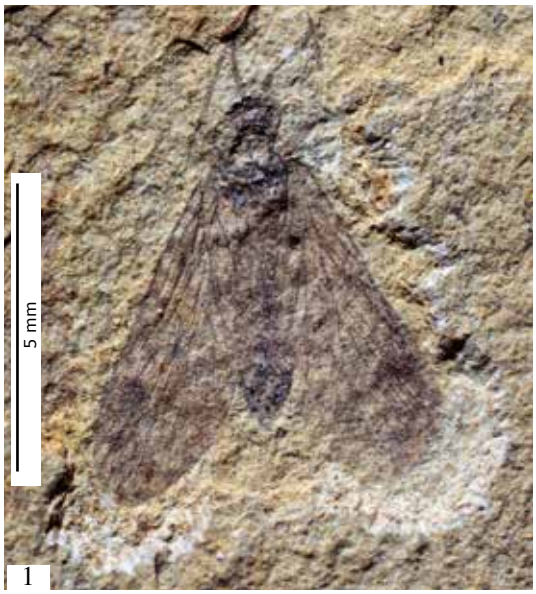
sect tribes in the Early Permian later, evolving trends must be seen sceptically. Mostly all development phases occurred just before the Devonian over the Carboniferous. The often-propagated relationship between Lepidoptera, Trichoptera and Hymenoptera must have originated before because from the Early Permian, all these lines evolved independently.
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.

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 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



The Trichoptera *Marimerobius sukatchevae* (Novokshonov, 1997)



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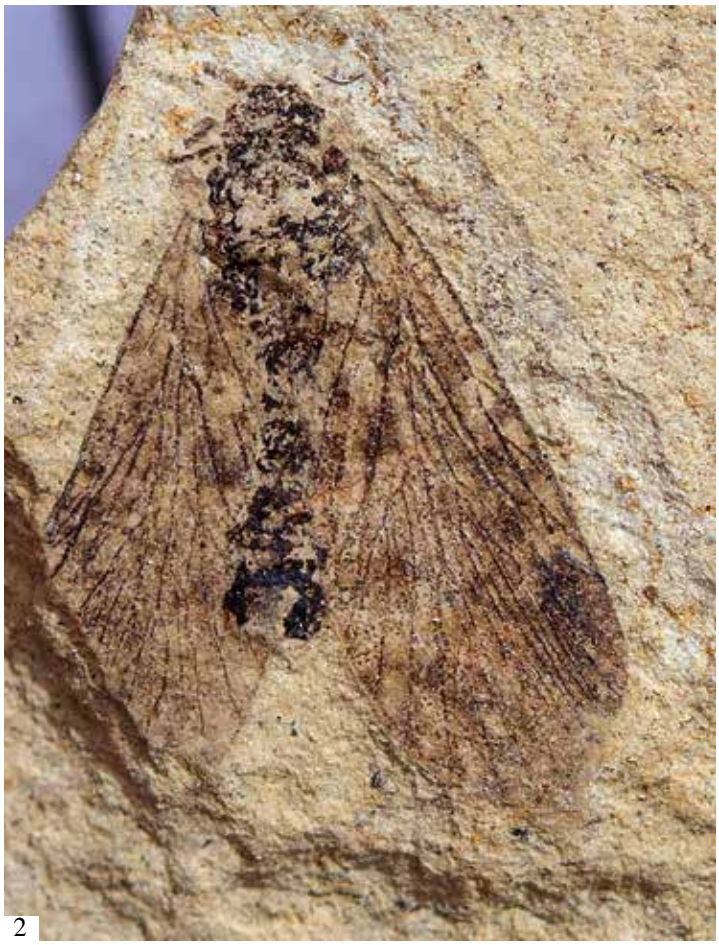

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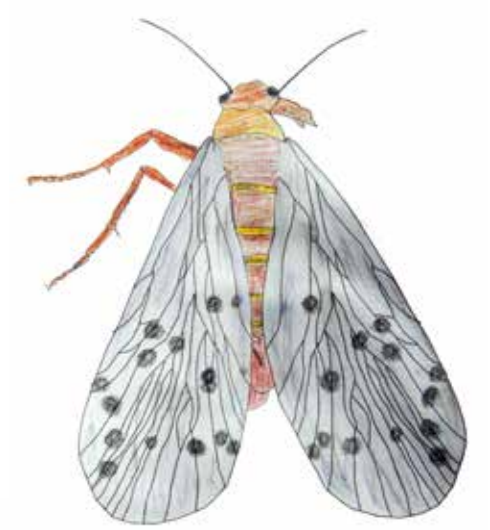
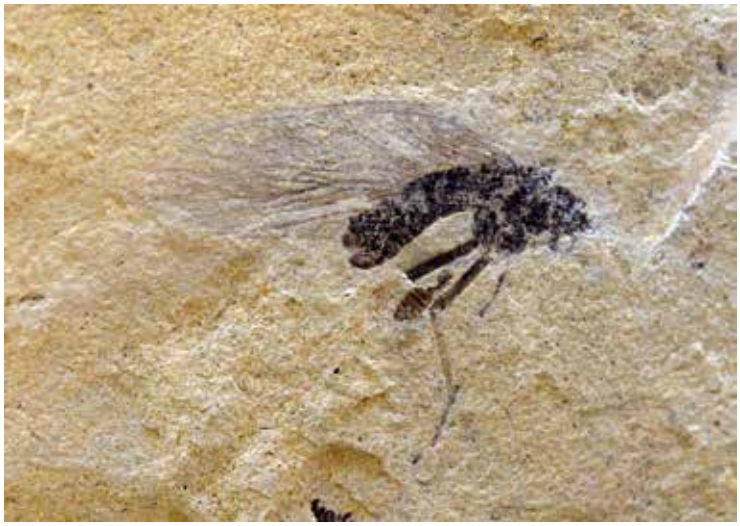
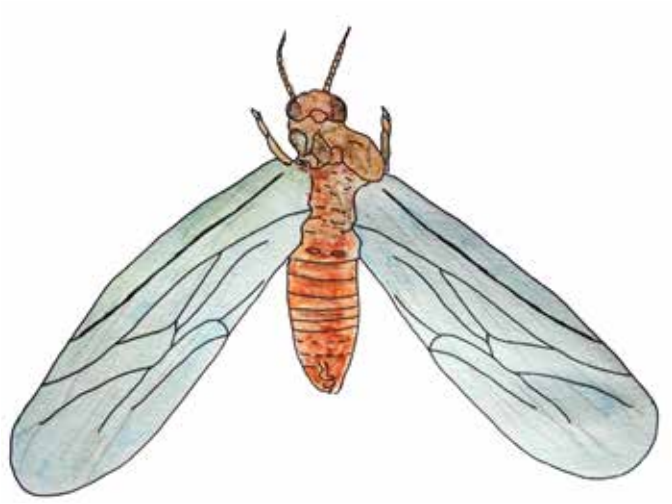


Agetopanorpa punctata, a suggested scorpionfly. 1. Length of wings 5-6 mm, corpus 4 mm, (Coll. Dammann); 2. Detail of *Agetopanorpa punctata, e*videncing details of the rounded patterns and pollen dust covering the wings (Coll. Thomas Gerasch, Thomaseum-Museum, Langenaltheim), Matvéevo, Early Permian,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



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

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



Karpinskptera pohli Reconstruction

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* (Zalessky, 1946), especially *Marimeroblus splendens* (Zalessky, 1946) and *Marimerobius sukatchevae* (Novokshonov, 1997), and then also with *Kamopanorpa uralensis* (Martynov, 1940) and *Uraloptisma maculata* (Ivanov, 1992).

Karpinskptera nov. gen. WACHTLER 2020

Etymology

It honours the palaeontologist, A. P. Karpinski (1847–1936), the father of Russian geology.

Karpinskptera pohli nov. gen. n. sp. WACHTLER 2020

Holotype

CHEK 91, Chekarda (Collection Wachtler, Dolomythos, Innichen, Italy, Kungurian

Etymology

It is dedicated to the German collector, Burkhard Pohl, who helped to develop palaeontology worldwide.

Diagnosis

The insect has two forewings and unrecognisable hindwings.

Description

Minute insects; head rounded; antennae several times segmented and 1 mm long; short antennae, labrum, mandible, maxillary palps not visible. The forewings are 3.5 mm long and 1 mm wide, narrowly rounded; venation present but not well-evidenced. Hindwings not recognisable or probably not present (holotype CHEK 91). The body is slender and about 2 mm long; the abdomen is narrowly segmented (probably 8 parts), without cerci; dorsal parts closed.

Discussion

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

Contributions

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

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

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