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

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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. 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* nov. gen. n. sp. having affinities with today's *Ulmus alata* and birch-samaras described as *Samzalesskya triquetra* comb. nov. with their pollen organ, *Kungurosperma elongata* nov. gen. n. sp. and female catkins of *Kungurosperma russica* nov. gen. n. sp. were common. Also, nuts held in leafy involucres like hazelnut-resembling *Nucifructa primaeva* nov. gen. n. sp. 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* nov. gen. n. sp. Primitive stone fruits like *Bardocarpus aliger* are omnipresent in these Early Permian sediments, whereas interesting Hesperideæ like *Parvunucleus dammannii* nov. gen. n. sp. with one big seed surrounded by smaller seeds, probably an evolution connecting link to extant Citrus fruits, are seldom found.

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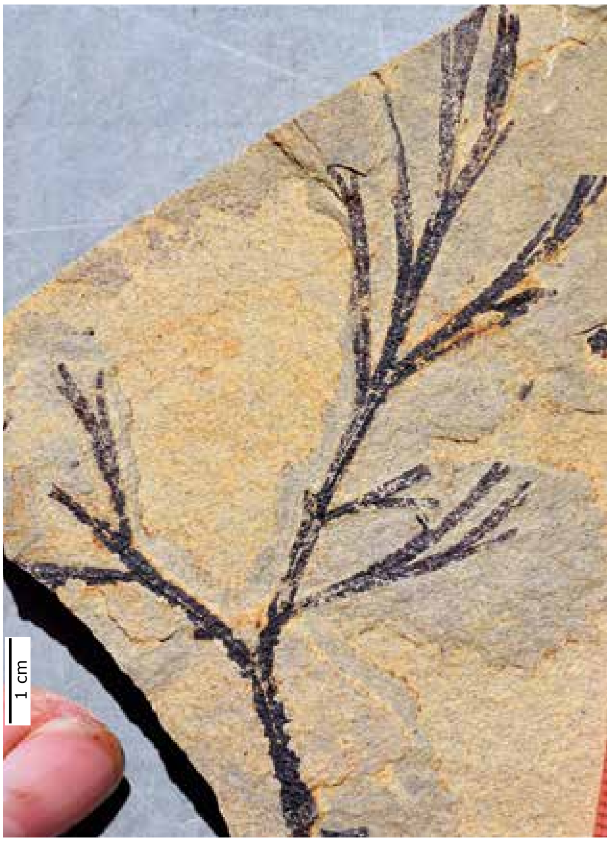
Early Permian broad-leaved fruits

Left: samaras from ash ancestor *Sadovnikovia belemnoides,* maples (*Sylvella alata*) and ashes (*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.

It can be supposed that gymnosperms and angiosperms had a different evolution-line since the Devonian.

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, from subtle emergences or small leaf-like ennations that were projected from the stems. These ennations 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, over a short period of time, 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.



Psygmophyllum cuneifolium – probably the most primitive leaf-type (MAT 457, Mateevo, Coll. Gerasch

The Strange Continent of Angara

As we believe in the dogma of Carboniferous-Permian origin of almost all gymnosperms because we are influenced by our Western way of thinking, we must also accept that there existed an extended and largely unknown continent called Angara during Permo-Triassic times, which forms today's Russia and Siberia.

Some of the theories about isolated landmasses were proposed by the Austrian geologist, Eduard Suess. In his "Antlitz der Erde" (The Face of the Earth) in 1885, he hypothesised that in the Paleozoic era, there was one big landmass in the southern hemisphere that he called the Gondwana – comprising Africa, South America, India and Australia. In the north, he located two big paleo-continents: North-America connected to Europe, which he called the Atlantis, and the other one 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 (Wachtler 2016).

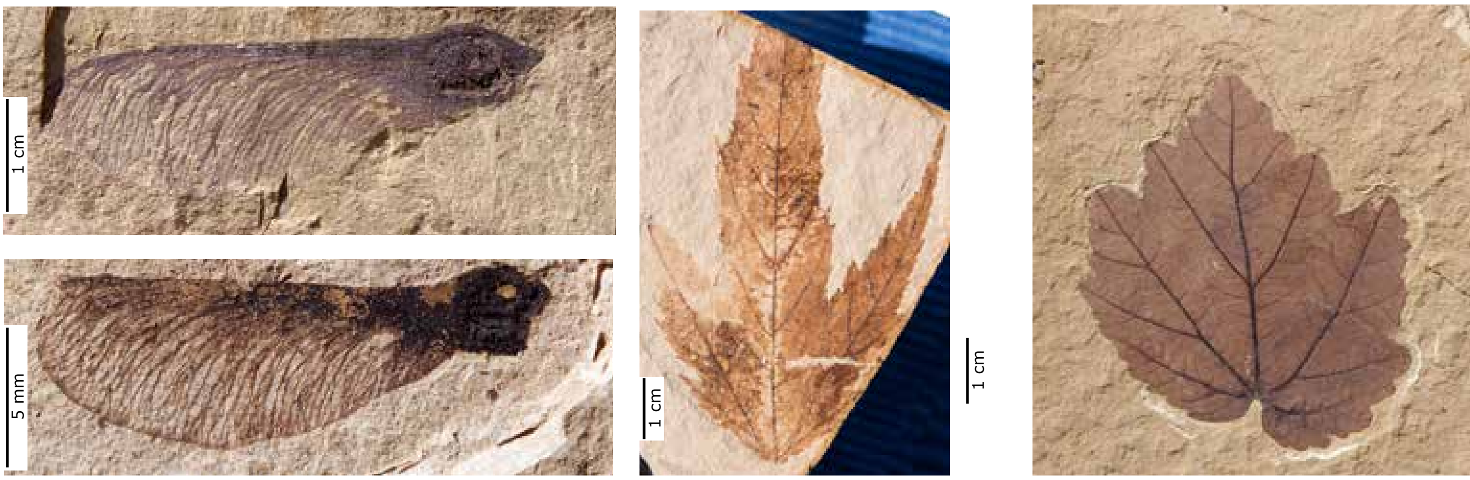
From the Silurian-Devonian period – when the first plants evolved – Siberia and the Urals occupied a position apart from other landmasses, throughout the Carboniferous till the Permian. This position was between the 30th and 60th north latitude (today's position of Paris is about the 48th latitude; New York's is about the 41st latitude. In the Early Permian era, Middle Europe or the Southern States of the United States were near to the equator (about the 15th

Early Permian Fore Urals (Artinskian-Kungurian) 290-280 millions years ago) Acer-ancestors

Samara: *Sylvella alata* (MAT 721 Coll. Gerasch, Matvèevo, CHEK 64, Chekarda); **Leaves:** *Psygmophyllum cuneifolium* (MAT 651, MAT 608, Matvèevo)

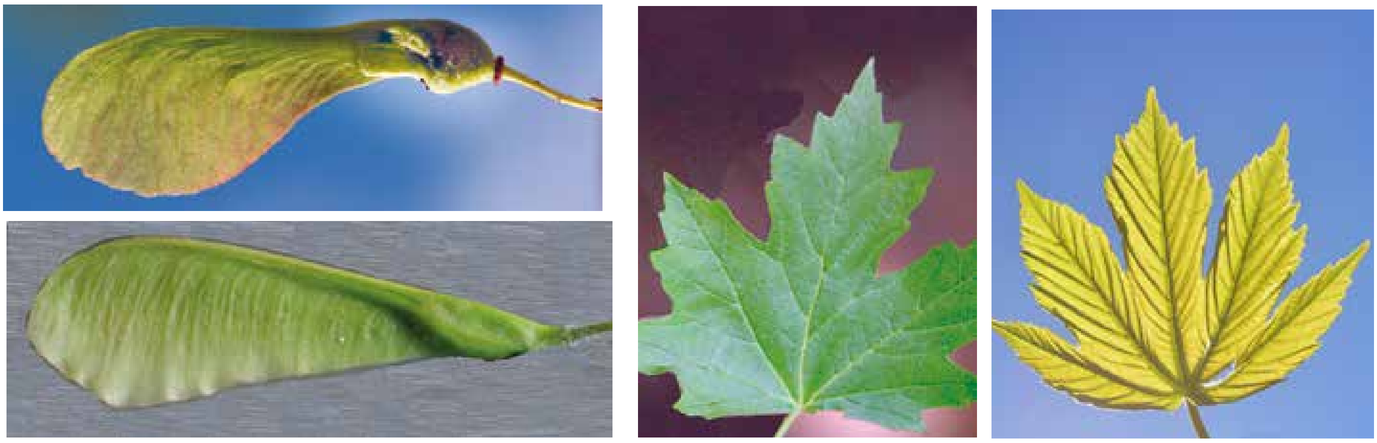
Eocene Republic, Washington, USA (50 millions years ago) Aceraceae

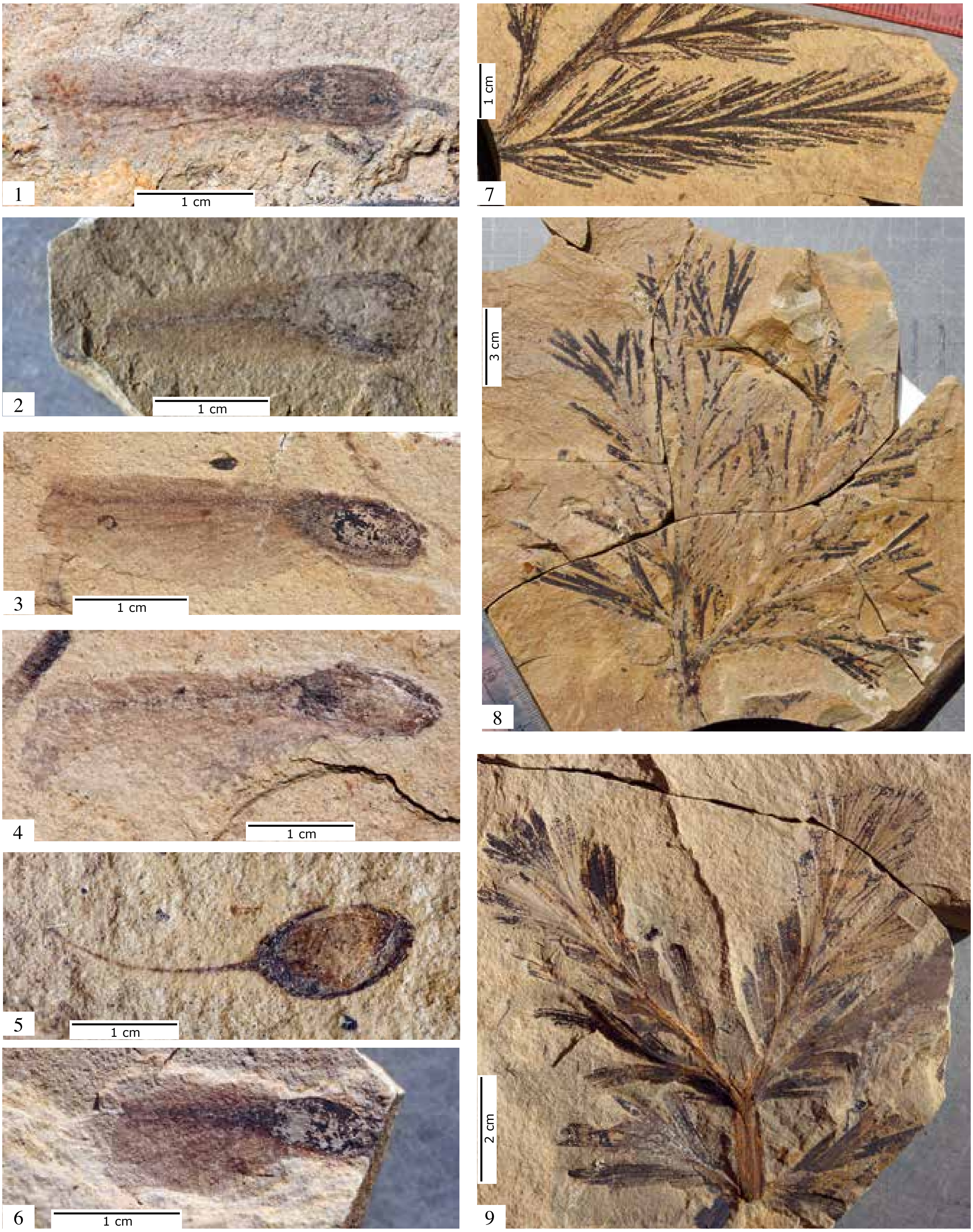
Samaras, leaves from: *Acer manchesteri and Acer arcticum*



Extant Aceraceae

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





Acer ancestor *Sylvella alata* (samara) and *Psygmophyllum cuneifolium* (leaves)

1–6. **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, MAT 721, MAT 202, MAT 187, MAT 17, MAT 186 All Matvèevo); 7–9. **Leaves:** note a continuous evolution from needle-like to palmate, CHEK 25, CHEK 63, MAT 297 (Chekarda and Matvèevo).

latitude. Therefore, this northern landmass of Angara – for a long time, till the Triassic period – formed an isolated continent with independent floras and faunas.

On the Angaraland, a unique development of angiospermic plants and insects occurred during the Early Permian. This strange concept cannot be correlated with the evolution theories based on Magnoliid phylogeny, meaning that the Magnoliaceae represent the oldest and most primitive angiosperms on Earth. But why are the Magnolias regarded as the most primitive flowering plants?

An evolution process beginning in the Permian could be regarded as more logical than the faster Cretaceous radiation based on the Magnolias. Another question is how the concept of Magnoliaceae fit in Permian times. An agglomeration of many pollen pistils and stigmas constitutes not an insoluble wonder for nature. Due to fortunate circumstances, perfectly formed Magnolia flowers, with all the features from an extant one, were recovered in Early Permian layers, which suggests that this step in evolution was made early.

In Early Permian Euramerican biocenosis, we encounter cycads with many seeds for each fruit-blade like today’s genus Cycas, as well as with only two seeds like the extant Zamia, and they get together the long way from Permian till today over 300 million years. The same is the case with Araucaria and Abietaceae progenitors. In both the cases, we cannot encounter a more primitive or progressive way of evolution.

When on the isolated Angara the hermaphrodite flower was "invented", – meaning anthers having a subtle filament and an carpel enclosing the seeds in comparison with the Euro-American gymnosperms with cone-like fructifications holding one or more seeds as well as cone-like pollen organs – then the most important step was just done. Apart from that, not all angiosperms choose to show bisexual flowers with many petals, adnate carpels and stamens arranged in a spiral fashion on an elongated receptacle. Many flowering plants from the Carboniferous-Permian border, but with first evolution steps towards the Devonian, searched an independent solution. We encounter, even today, wind-pollinated plants. Others were probably phlegmatic and opened their propagation in two ways: the insects and the wind. But all this occurred just during the beginning of angiospermy between the Carboniferous-Permian border.

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

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

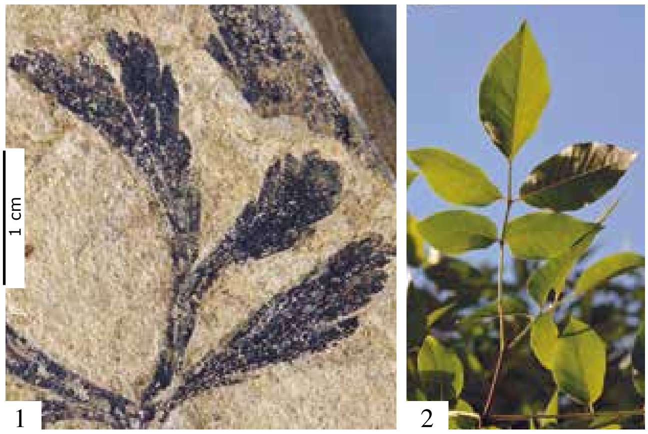
1. Entire twig with attached aliform seed and leaves; 2. Another complete twig (MAT 556); 3. Detail of a twig evidencing well the blueprint of single leaves (MAT 555); All Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum, Italy

1. Leaf of *Sadovnikovia belemnoides* (MAT 732) a potential ash-progenitor and 2. Leaves of *Acer negundo.* The leaves do not resemble maples, but ashes. 3. The samaras are typical of the Aceraceae

Also, in the fruit and seed evolution, many plants were open to many possibilities. Some found that a wing, originally composed of many micro-leaves, was a good solution, such as the maples, elms, ashes or birches. Others discovered that a partial embracing of these micro-leaves was enough to shed their seeds at maturity like the oaks or hazelnuts. Others again decided that many micro-leaves coating a seed gave the advantage that animals would eat them, especially when net-like arranged micro-leaves were filled with aromatic juices. We know them as drupes or stone fruits and we enjoy them as cherries, apricots or plums. Some plants found that micro-leaves could also give a good parachute, such as the dandelions.

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.

All these are dangerous theories in modern times because then the question that follows is: Made a strange God really all our life in a short time?

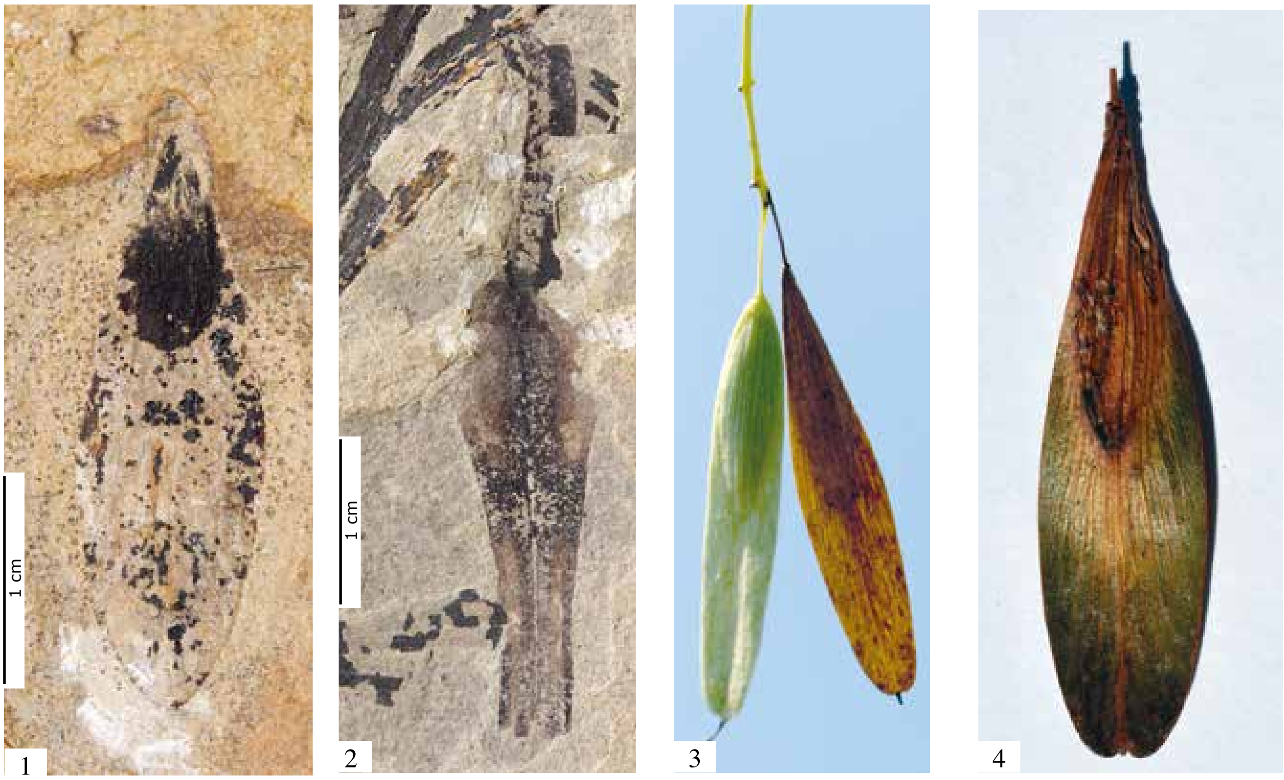


1. Other leaf-type of *Sadovnikovia belemnoides* (MAT 556) and 2. Extant *Fraxinus tomentosa.* The compound frond is an evolution of the amalgation of diverse single needle-like leaves.

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* (Wachtler, 2017). 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.

Why all this time – from Permian till the Cretaceous, over 200 million years – this independent evolution stage remained unmixed, since in Europe and America, we could not record angiosperms in Permian and Triassic. For a long period – from the Silurian till the Permian – Angara was separated from the Euramerican landmass. After that, an immense cataclysm on the Permo-Triassic border brought it to a fatal standstill. Later on, maybe factors such as high mountain ranges, different climatic zones, well-adapted ecosystems prevented a spreading.



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.

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.

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. In the gymnosperms from the Euroamerican continent, ginkgo ancestors like *Baiera* and *Pinus* progenitors like *Ferovalentinia* or one of the most primordial conifers, *Perneria,* spreading in the latest Carboniferous are rather similar to angiospermous *Psygmophyllum cuneifolium* or psygmophylloid leaves belonging to *Sadovnikovia*. 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 (Zalessky, 1937b; Naugolnykh, 1998; Naugolnykh, 2007; Naugolnykh, 2014).

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 (Naugolnykh, 1994, 2007, 2012). They were even considered to be the ancestors of all *Pleuromeia* species, a widespread clubmoss family appearing abruptly in the Early Triassic and vanishing right in the Middle Triassic. 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 certainly hermaphroditic. Because the seeds are not positioned on the base like *Sylvella alata*, rather in the basal middle part of the samara, they can also easily be distinguished from Aceraceae ancestors.

Early Permian maples and ashes

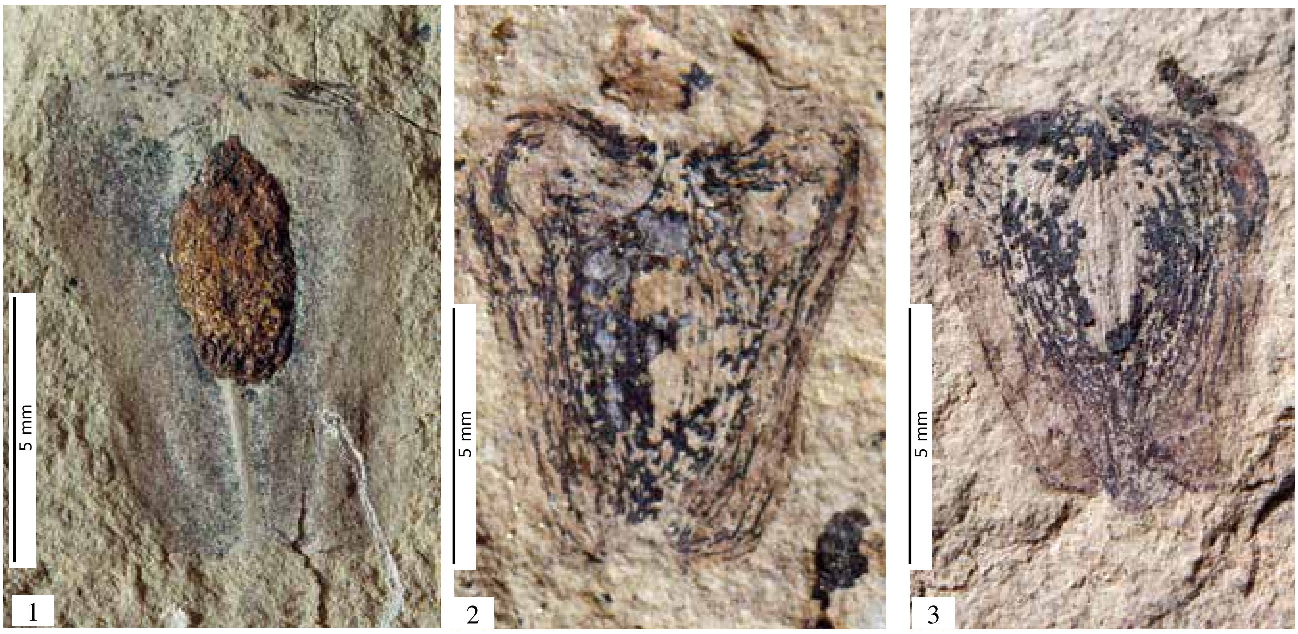
Left: a twig (*Psygmophyllum cuneifolium*, CHEK 63) and a samara (*Sylvella alata*, CHEK 64) of potential *Acer* ancestors; **right:** a twig with attached samara and male flower-panicles of *Sadovnikovia belemnoides* (MAT 182 and MAT 366) a potential *Fraxinus* ancestor; **middle:** Early Permian cicada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

The 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.

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 (Wallander, 2013).

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 (Hinsinger et al., 2013) with species like *Fraxinus flexifolia*, nothing speaks against an earlier evolution during the Permian. Too similar are extant and fossilised Early Permian species.



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

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

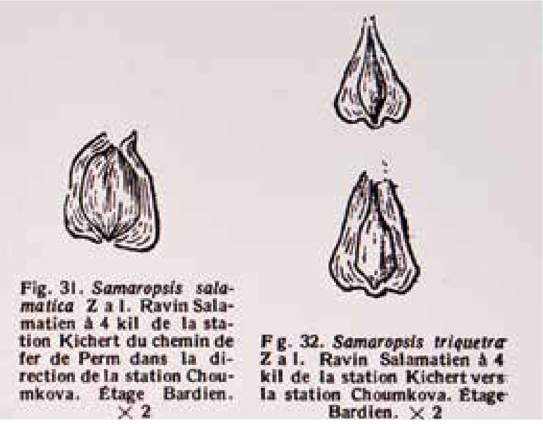


Fig. 31. *Samaropsis salamatica* Z a l. Ravin Salamatien à 4 kil de la station Kichert du chemin de fer de Perm dans la direction de la station Choumkova. Étage Bardien. × 2

F g. 32. *Samaropsis triquetra* Z a l. Ravin Salamatien à 4 kil de la station Kichert vers la station Choumkova. Étage Bardien. × 2

Samaropsis salamatica and *Samaropsis triquetra* described and drawed by M. D. Zalessky in 1937. One can be regarded as synonymous.

In future, therefore, attention must be to the phylogeny, maybe even encountering some ash-fossils during the Jurassic.

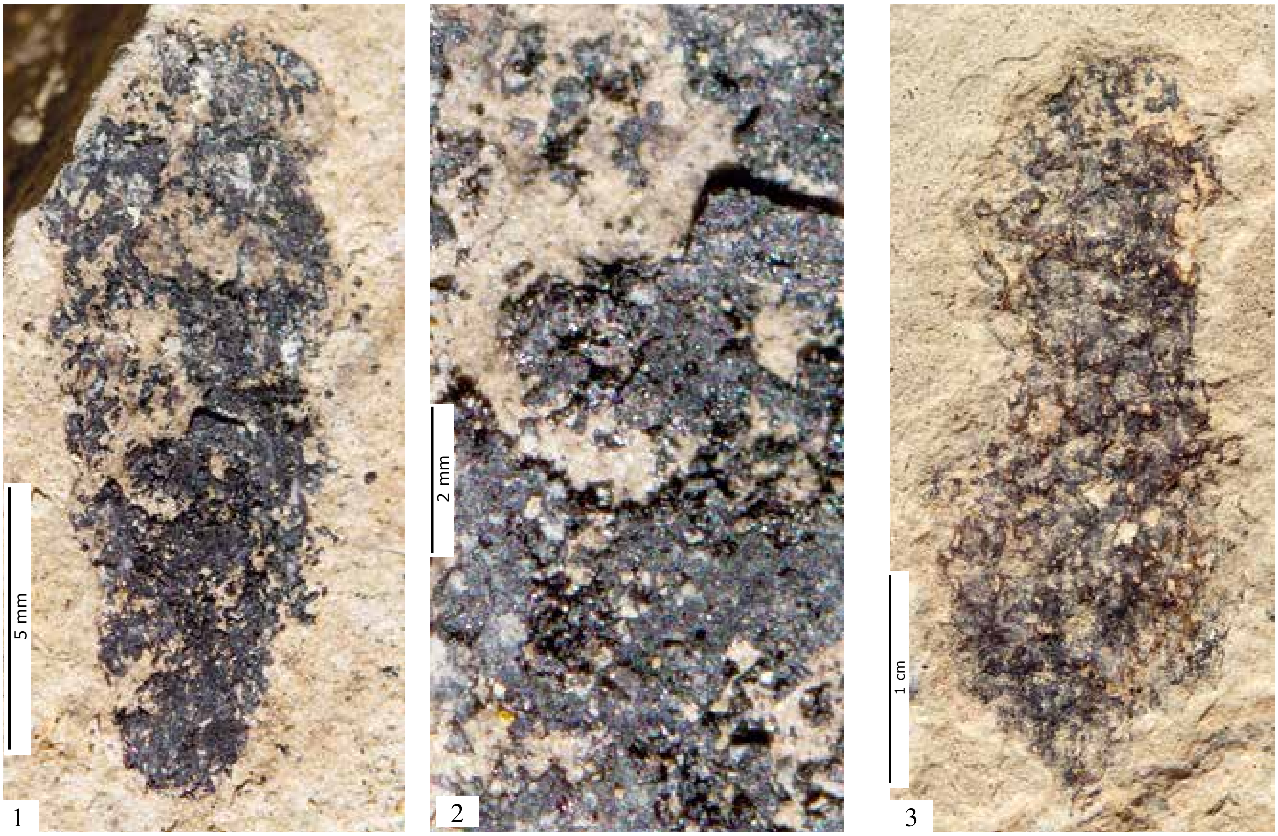
The Beginning of the Birches – Betulaceae

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.
The latest fossil record of the birches go back till the Early Eocene of Western North America. *Betula leopoldae* leaves have many similarities with the extant *Betula alleghaniensis,* and their suggested catkins and flowering bodies (Crane & Stockey, 1986b) resemble mostly those known from today's birches.

Samzalesskya nov. gen. WACHTLER 2020

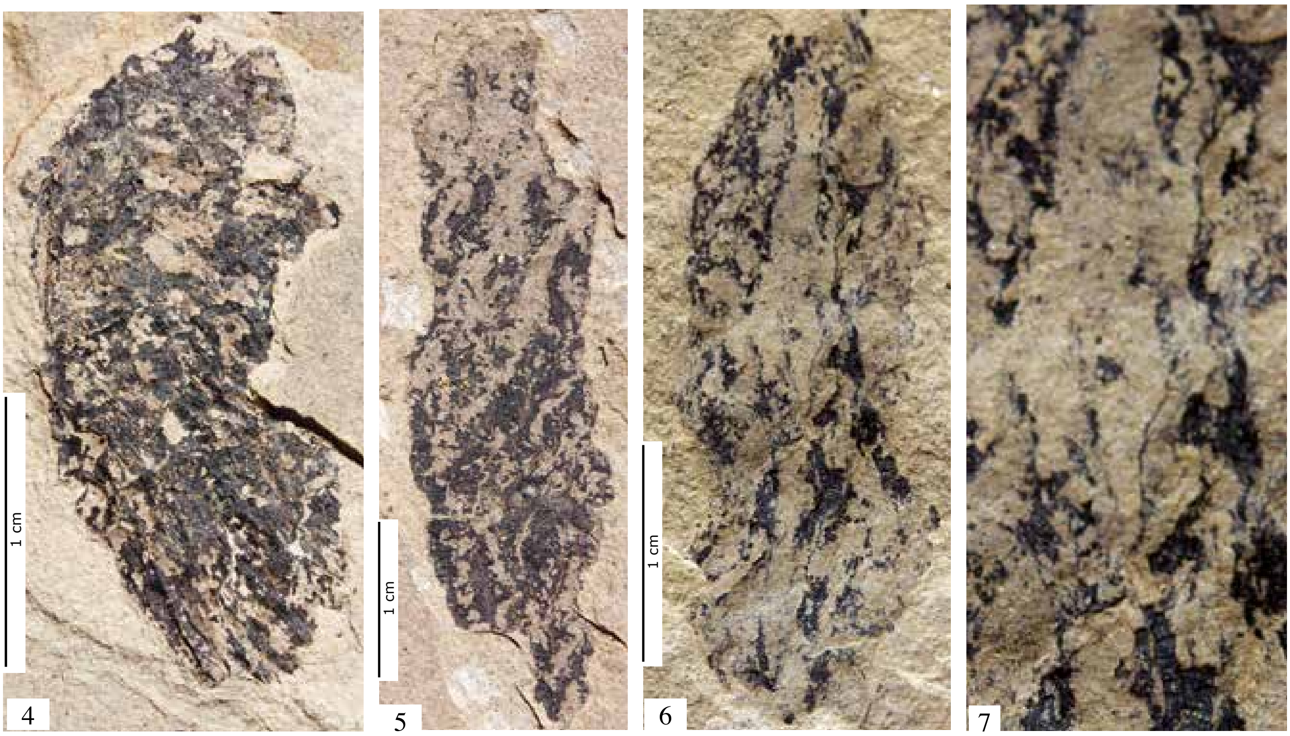
Etymology

The name refers to "semen", the Latin word for seed and honouring Mikhail Dmitrievich



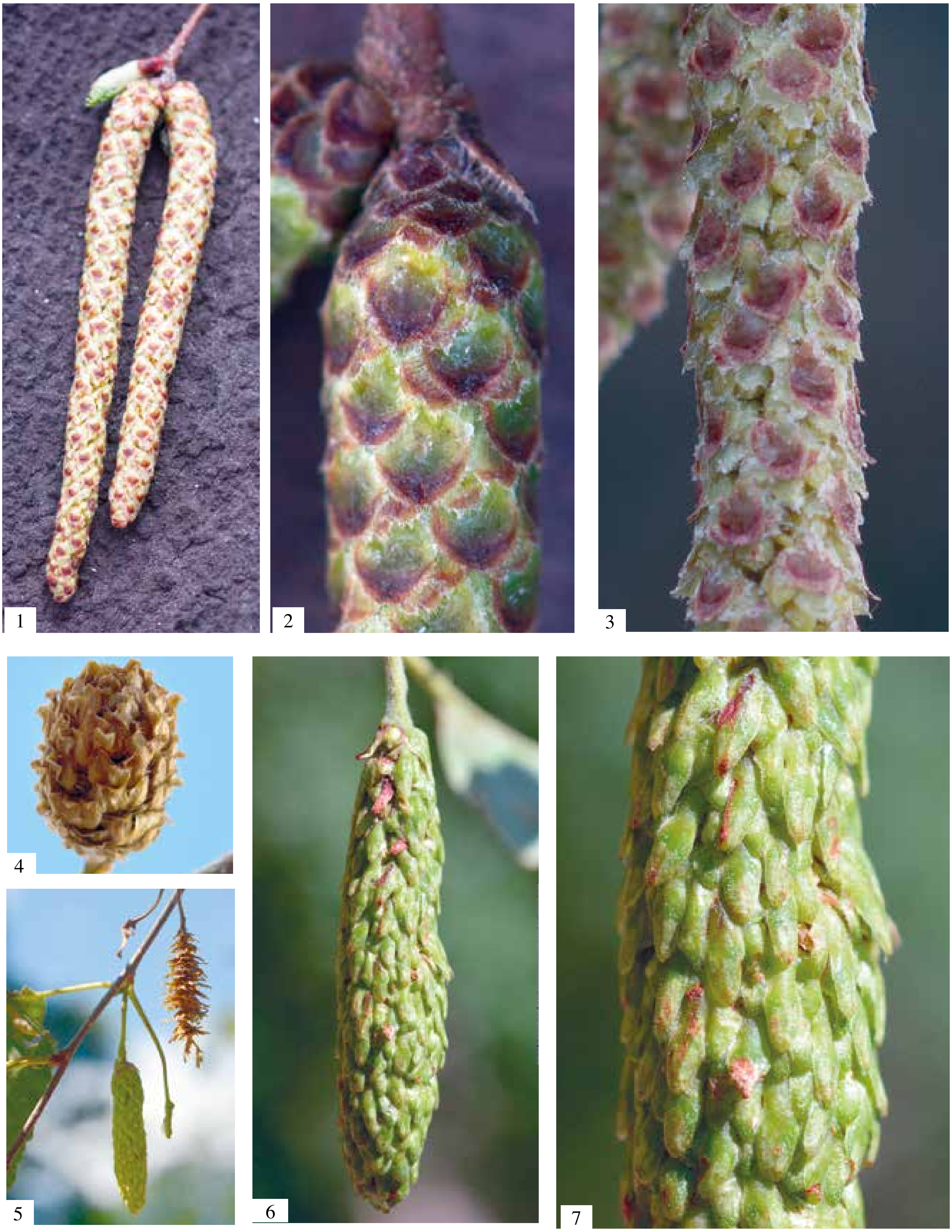
Kungurosperma elongata **nov. gen. n. sp. WACHTLER 2020**

1-2. Pollen organ (Holotype MAT 725, Coll. Gerasch; 15 mm long, 5 mm wide) and detail of a bract; 3. Pollen organ CHEK 209 (32 mm long, 10 mm wide).



Kungurosperma russica **n. sp. WACHTLER 2020, suggest birch-ancestors**

4. Female catkin (Holotype MAT 387; 25 mm long, 10 mm wide); 5. MAT 381 (30 mm long, 10 mm wide); Matvèevo, Coll. Wachtler, Dolomythos-Museum; 6-7. Female catkin and detail (CHEK 121; 30 mm long, 10 mm wide, Chekarda)



Birches today

1. Male catkin of *Betula pendula*; 2. Detail of male bracts of *Betula pubescens*; 3. Detail of the male bracts of *Betula costata*; 4. Adult cone of *Betula rotundifolia;* 5. Female juvenile and mature cone of *Betula utilis.* 6-7. Female cones of *Betula utilis*

Early Permian birches (*Samzalesskya triquetra*

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.

Zalessky (Russian: Михаил Дмитриевич Залесский) (1877–1946), who described small winged seeds for the first time.

Diagnosis

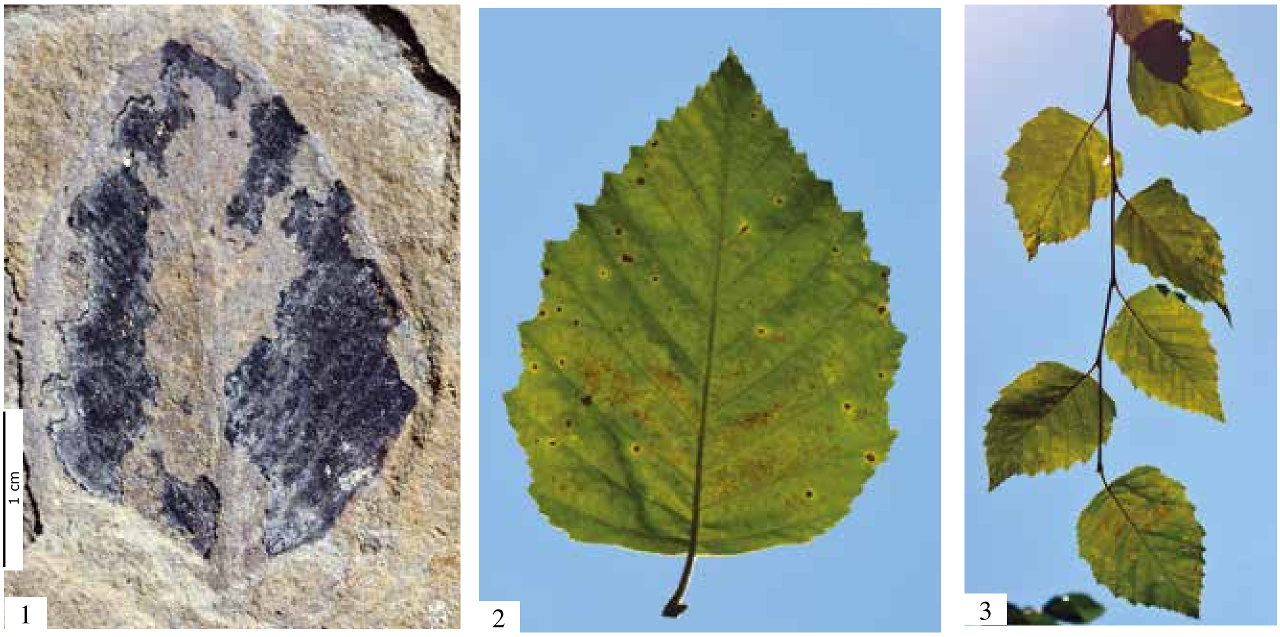
The oval nutlets have two wings that are wider than the body of the seed; the mature nuts are well-evidenced to be elongated and tapering on one side.

Samzalesskya triquetra comb. nov. WACHTLER 2020

Basionym: *Samaropsis salamatica* ZALESKY, 1937 (p 68-69)

After bringing *Samzalesskya triquetra* in connection with other parts of the plants or the leaves, it is thought that it probably represents an ancestor of the Betulaceae.

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. 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. In 1864, the German palaeontologist and botanist, Johann Heinrich Robert Göppert, (1800–1884) in Breslau described and figured from the Permian layers of Braunau (Bohemia, Czech Republic) a "winged fruit", classifying it as *Samaropsis ulmiformis* (pp. 177–178, plate XXVIII, 10 and 11). Due to



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

the completely encasing aril, it can be suggested that this fruit belongs to a gymnosperm, probably a conifer like *Ortiseia* (Wachtler, 2015).

In 1937, M. D. Zalessky classified two new winged seeds from the Early Permian Fore-Urals as *Samaropsis salamatica* and *Samaropsis triquetra*. In the description, both the drawings seem to be similar and can be regarded as synonymous, and therefore, it is suggested to accept only the name *Samaropsis triquetra.* Also, the classification as *Samaropsis* belonging to a gymnosperm seed is questionable. Therefore, a proposal will be put forth to introduce the new genus-name *Samzalesskya salamatica*, honouring M. D. Zalessky.

The differences between the aforementioned species and *Samaropsis* are obvious: *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 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. Leaves like MAT 126 can especially be regarded as similar to extant Betulaceae.

Kungurosperma nov. gen. WACHTLER 2020

Etymology

The name is from the city of Kungur (Russian: Кунгу́р), located on the western ridges of the Ural Mountains and from Latin and Greek "sperma", meaning reproductive organ.

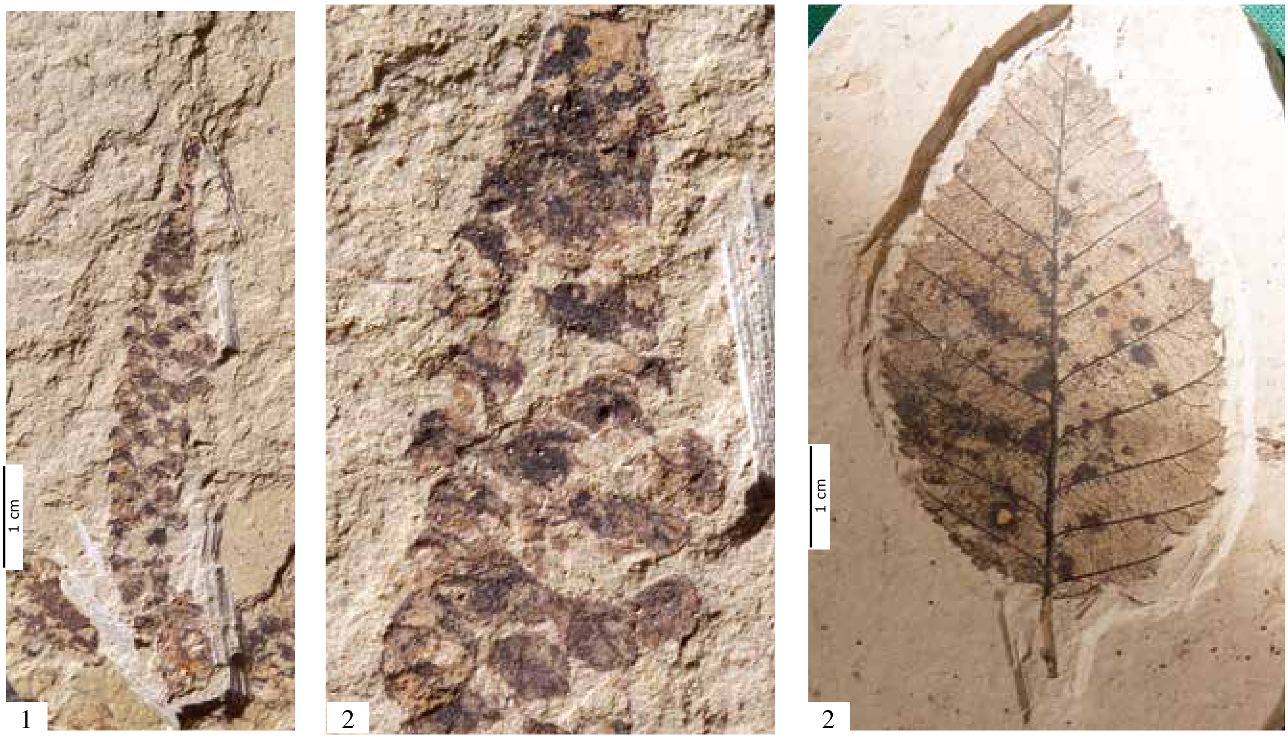
Kungurosperma elongata nov. gen. n. sp. WACHTLER 2020

Holotype

MAT 725, Matvèevo (Collection Gerasch, Thomaseum, Langenaltheim, Germany

Etymology

It is from the Latin word "elongatus", meaning elongated.



1-3. Fruits and leaf of *Betula leopoldae* from the Eocene deposit Republic (Washington State, USA, Stonerose-Center)

Diagnosis

The elongated fruits contain a fair number of bracts.

Description

Pollen organ: Infructescence holotype MAT 725 is 15 mm long and has a width of about 5 mm. It is composed of a fair number of coarsely ridged bracts that are helically arranged and approximately 1.5 mm wide. The base of the bract is slightly cupped. Pollen grains are visible on each bract. It probably does not represent a mature pollen organ. CHEK 209 is larger than an adult specimen, measuring 32 mm long and 10 mm wide.

Kungurosperma russica **n. sp. WACHTLER 2020**

Etymology

It is from the country, Russia, to which the Ural-region belongs.

Holotype

MAT 387, Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

Description

Fruit: Solitary, elongated infructescence equipped with relatively long persistent bracts. They are between 25 mm (holotype MAT 387) and 30 mm (MAT 381 and CHEK 121) long and 10 mm wide. No peduncle of the fruit organs is visible.

Discussion

Although elongated infructescences are not so abundant in Chekarda and Matvèevo, they represent common reproductive structures. Due to their consistent differences, they must belong to different plants, and the classification as *Kungurosperma elongata* (a presumed pollen organ) and *Kungurosperma russica* (a seed organ) are only tentative till further analyses identify with certainty the plant to which they belong. The infructescences of *Kungurosperma* can be regarded as catkins more than cones. Gymnosperms cones like those of cycads or conifers differ notably due to their bigger size and their composition. In angiosperms, elongated catkins are encountered in a fair number of 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. Further findings can help to resolve this enigma.

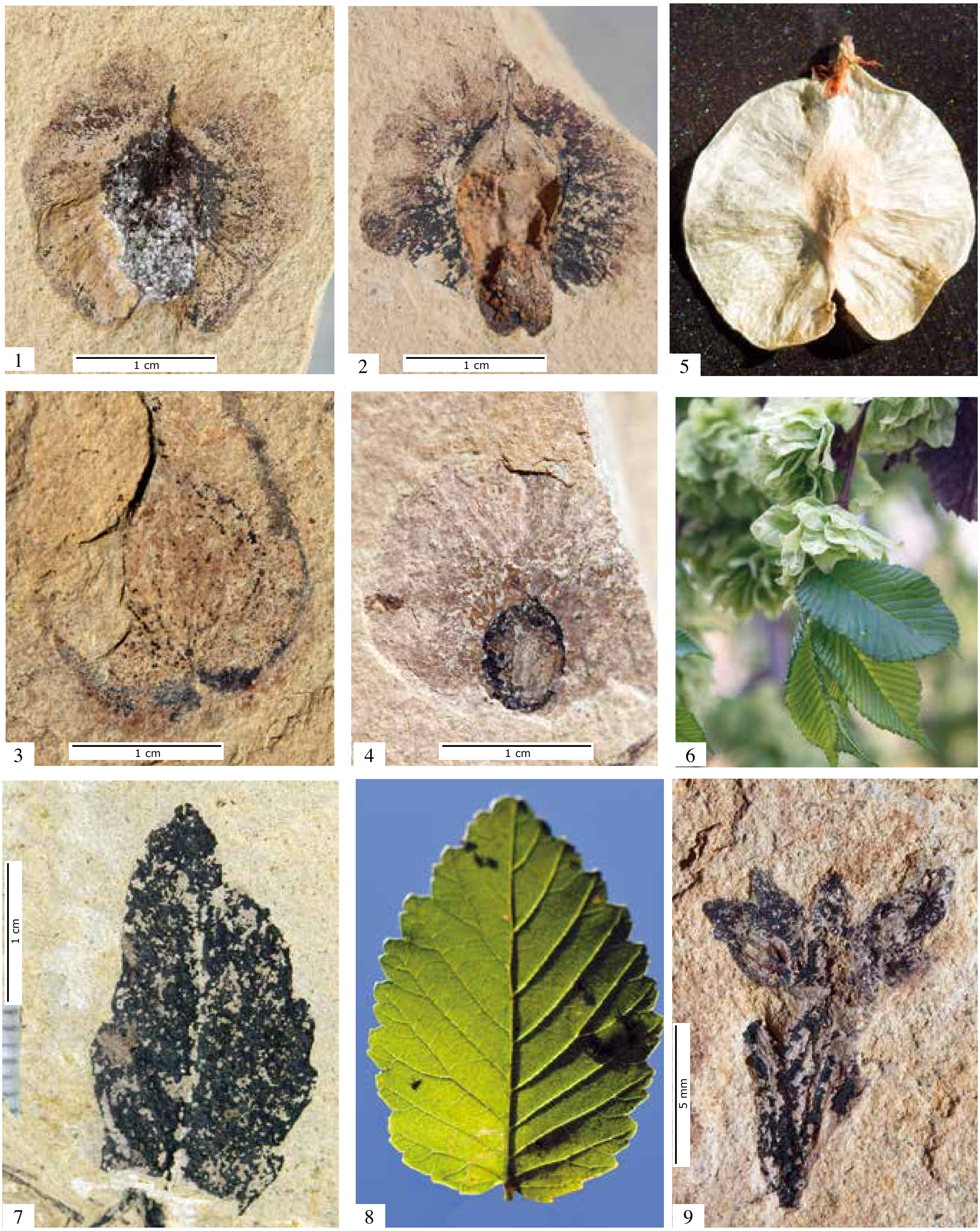
The Origin of the Elms – Ulmaceae

Some samaras classified as *Matvéeva perneri* (Wachtler, 2017) 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

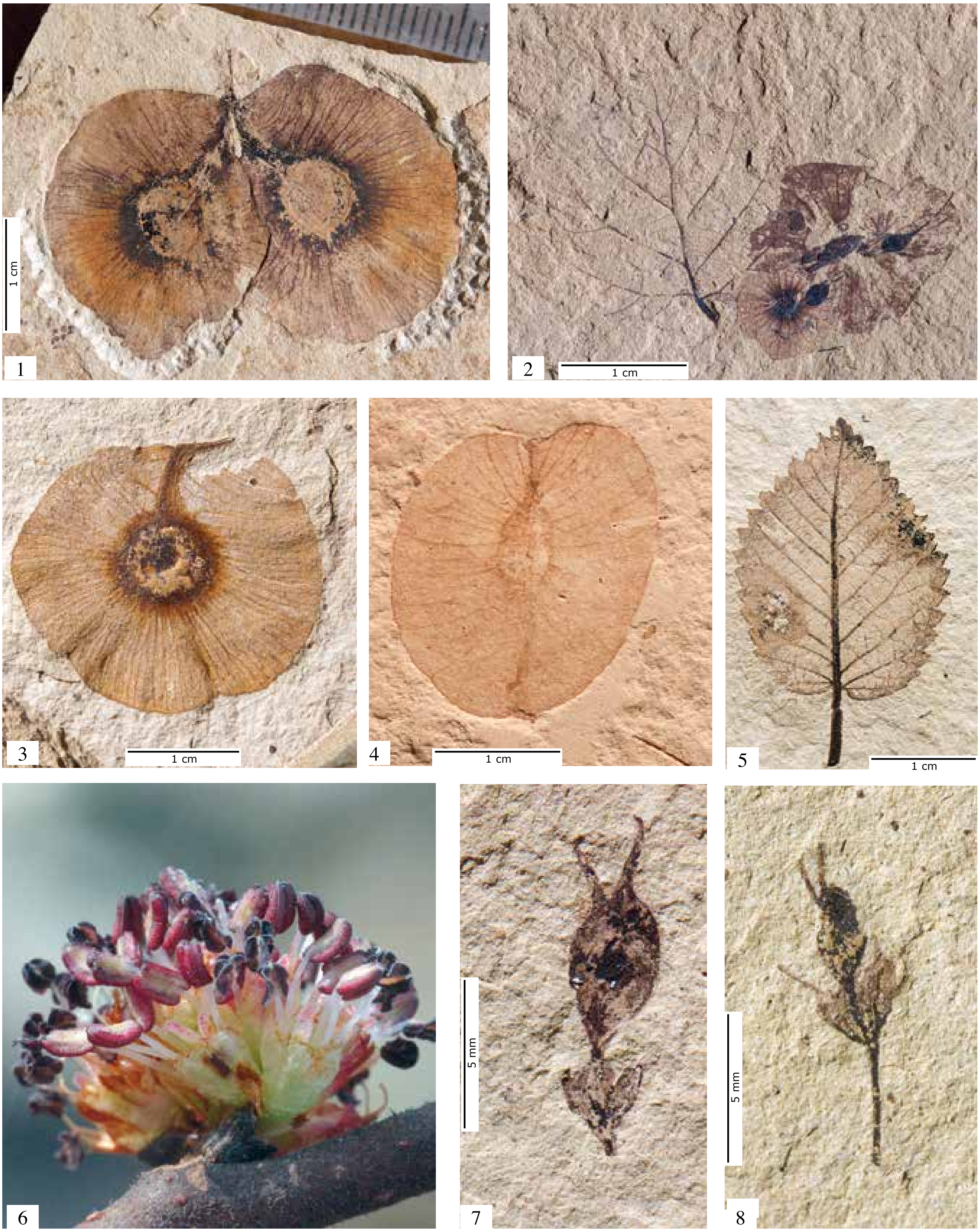
Early Permian elms (*Matvéeva perneri* and *Uralosamara palaeozoica*)

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



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

1-4. Samaras classified as *Matvéeva perneri* (MAT 346, MAT 629, MAT 14, MAT 684, Coll. Wachtler, Dolomythos-Museum); 5-6. Samaras of extant elms (*Ulmus minor, Ulmus glabra* with leaves); 7. Supposed leaf of *Matvéeva perneri* (MAT 434, Coll. Gerasch). 8. Leaf of extant *Ulmus pumila*; 9. Suggested flower from *Matvéeva perneri.*



Ulmaceae from the Eocene

1–3. Schizocarps and mericarps of *Dipteronia brownii,* with attached leaves (Stonerose Museum, Republic, Washington-State, USA); 4. *Craigia oregonensis*, samara from a presumed Eocene elm (Basswood, Oregon); 5. Leaf of *Ulmus okanaganensis,* Eocene, (Republic); 6) *Ulmus glabra,* extant flower; 7–8. Fruits of *Ulmus alata,* another elm species, Eocene (Republic, Stonerose Museum)

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

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 (McClain & Manchester, 2001). Leaves and fruits of *Ulmus* ancestors are also recorded 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* (Denk & Dillhoff, 2005). 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 Carboniferus-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 one 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.*

Uralosamara nov. gen. WACHTLER 2020

Etymology

It is based on the Ural region, from where it was recovered in Early Permian sediments. The winged fruit are called samara.

Diagnosis

The flattened and elongated samara have a pair of stigmas on the tip.

Uralosamara palaeozoica nov. gen. n. sp. WACHTLER 2020

Holotype

MAT 641, Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

Etymology

It is from the Greek word "Palaeozoic", meaning "old life", the earliest of the three geologic eras; it is the longest of the Phanerozoic eras, lasting from 541 to 251.902 million years ago.

Description

Fruit: Holotype MAT 641 is 30 mm long from the stalk till the end of the elongated stigmas. Maximum width of the bulbous seed corpus is 4 mm. The basal pedicel is 7 mm long. Finest hairs cover the outside of the samara.

Discussion

Uralosamara palaeozoica is relatively rare in the Early Permian sediments of the Fore-Urals and was sometimes classified as *Gomphostrobus* (Naugolnykh, 2012) due to resemblances with the bifurcate bracts of some Euramerican Permian conifers. But the difference is obvious: *Gomphostrobus* never has a basal peduncle because it forms part of a conifer cone. *Uralosamara palaeozoica* indeed is characterised by a long, delicate pedicel. Furthermore, the samara is covered densely by filigree hairs. 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.*

Pseudodrupia nov. gen. WACHTLER 2020

Etymology

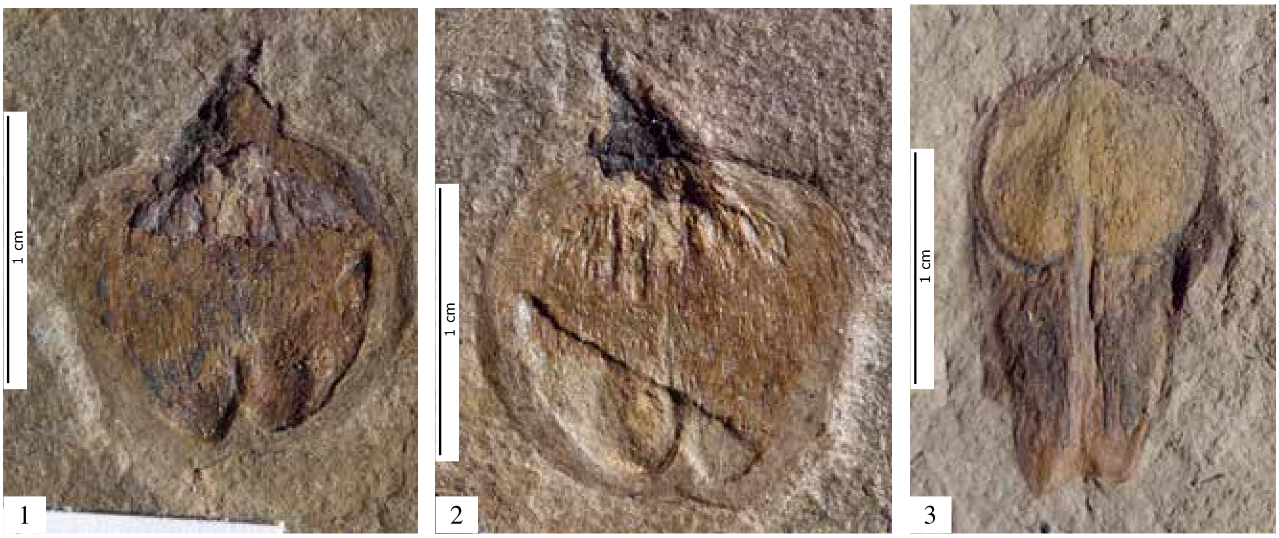
It is from the word "drupe" for stone fruit and the Greek ψευδής, pseudes, "false" meaning something that superficially appears to be.

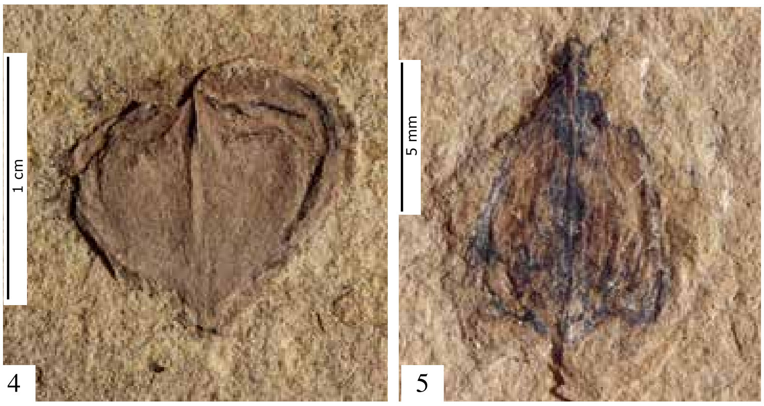
Pseudodrupia angarica nov. gen. n. sp. WACHTLER 2020

Type horizon and age

Early to uppermost Lower Permian, Kungurian: **Matvèevo:** Filippovian substage, Lekskaya-Formation; **Chekarda:** Irenian substage, Koshelevka Formation

Kungurian leaf-variation in Matveevo and Chekarda





***Pseudodrupia angarica* nov. gen. n. sp. WACHTLER 2020**

1–2. Drupe divided into two halves (designed 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

Holotype

MAT 18, Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

Etymology

The Austrian geologist, Eduard Suess, hypothesised in 1885 that in the Paleozoic era, another big landmass in the northern hemisphere was located in addition to the Euroamerican continent, which he named Angara after a Siberian river.

Diagnosis

It has one split kernel coated by an outer hard pericarp.

Description

Fruit: Some drupes vary considerably from the simple kernels known from the Early Permian Fore-Urals. They are divided into two segments. Holotype MAT 18 is 14 mm long, in which the subtle stalk is only of 2 mm. The width is 13 mm, in which the bony nutshell occupies 1.5 mm on each side. The fruit is globose and surface is smooth. The interior of the nut is divided into two connected segments of equal size. Another specimen, MAT 705, is a little different because of its elongated hardened and split appendix. The short stalk, which connects the fruit with the main stem is visible in all drawn specimen (also MAT 631 and MAT 07). All are typically divided into two connected chambers.

Discussion

Pseudodrupia angarica 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. Today we encounter split kernels in one nutshell like *Carya* (pecan nuts), *Juglans* (walnut) or those with winged seeds like *Pterocarya* (wingnuts). As effectively noted in holotype MAT 18, the smooth shell coated the inner divided kernel totally. It is therefore different from the Early Permian Fore-Urals' elm samaras

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.*

like *Matvéeva perneri* having their seeds inserted in the centre of the rounded wing. 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 flabelliforme, 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* 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.

Nucifructa nov. gen. WACHTLER 2020

Etymology

It is from the Latin word "nucis" for nuts and fruits.

Nucifructa primaeva nov. gen. n. sp. WACHTLER 2020

Holotype

MAT 725, Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

Etymology

It is from the Latin word "primaeva", meaning the oldest.

Diagnosis

The infructescence has attached involucres containing nuts at the end of a stout stalk.

Description

Fruit: Two paired nuts, each 10 mm long and 6 mm broad, hold basally attached involucres. The nuts are ovoid, tapering on the apical side. The stalk is stout. On holotype CHEK 225, one nut is attached, whereas the other was just released and only an empty involucre is visible. CHEK 181 represents probably not a completely evolved infructescence, where the protecting leaves cover almost the whole nut.

Discussion

The involcrum of *Nucifructa primaeva* 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.

Supposed coryloid fossilised specimen are known from the Paleocene in Greenland, England and the USA (Montana), but all of them lack the coating leaves. In the Eocene, we encounter with *Corylus johnsonii* infructescences with attached involucres containing nuts or nut casts or isolated paired or single nuts (Pigg et al., 2003).

Neuburgosperma nov. gen. WACHTLER 2020

Etymology

It is in remembrance of Maria Feodorovna Neuburg (1894–1962), one of the first Russian palaeobotanists studying Permian floras.

Diagnosis

The elongated hanging fruits are composed of many radially spreading fruit-leaves containing the seeds.

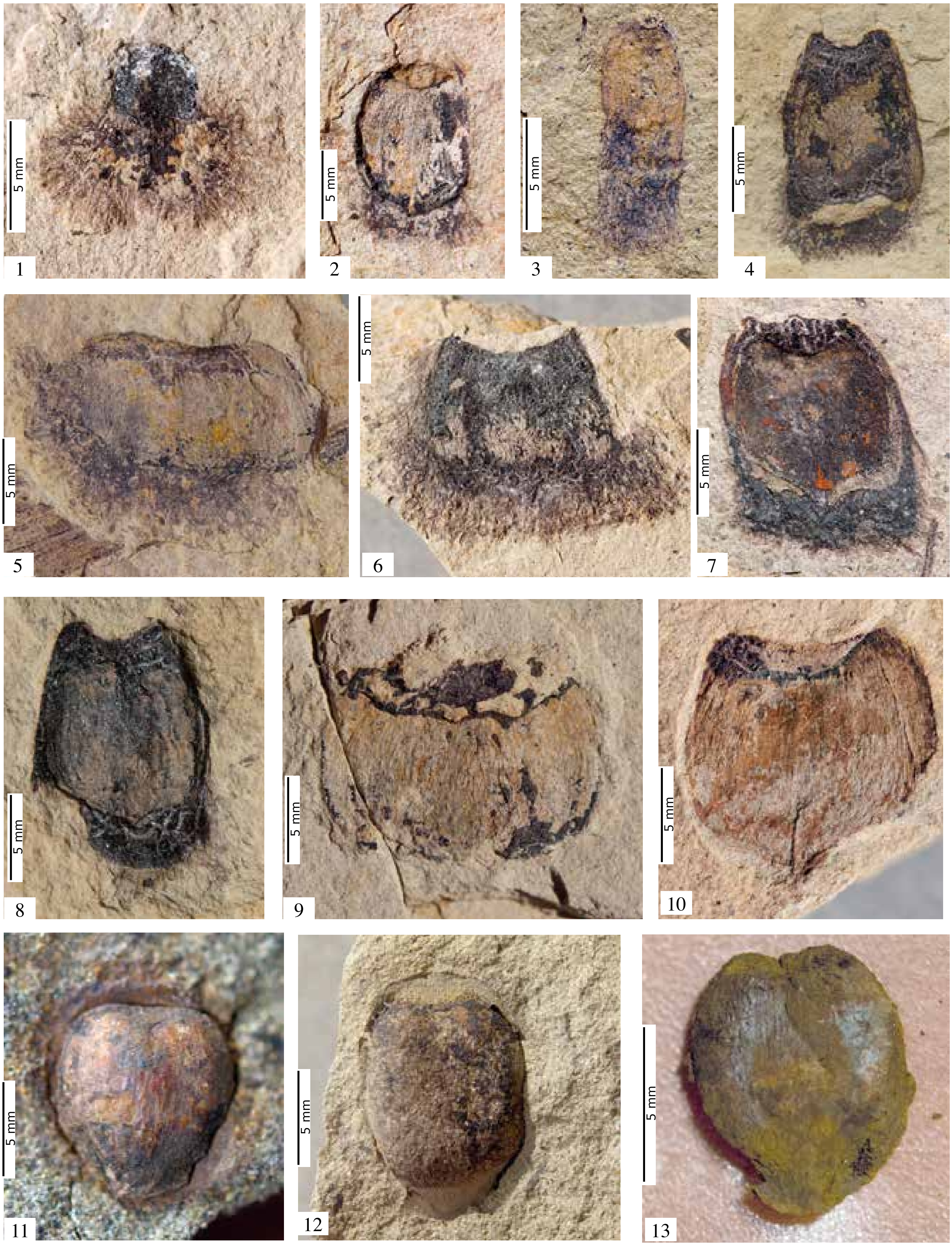
Neuburgosperma radiata nov. gen. n. sp. WACHTLER 2020

Holotype

MAT 500, Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

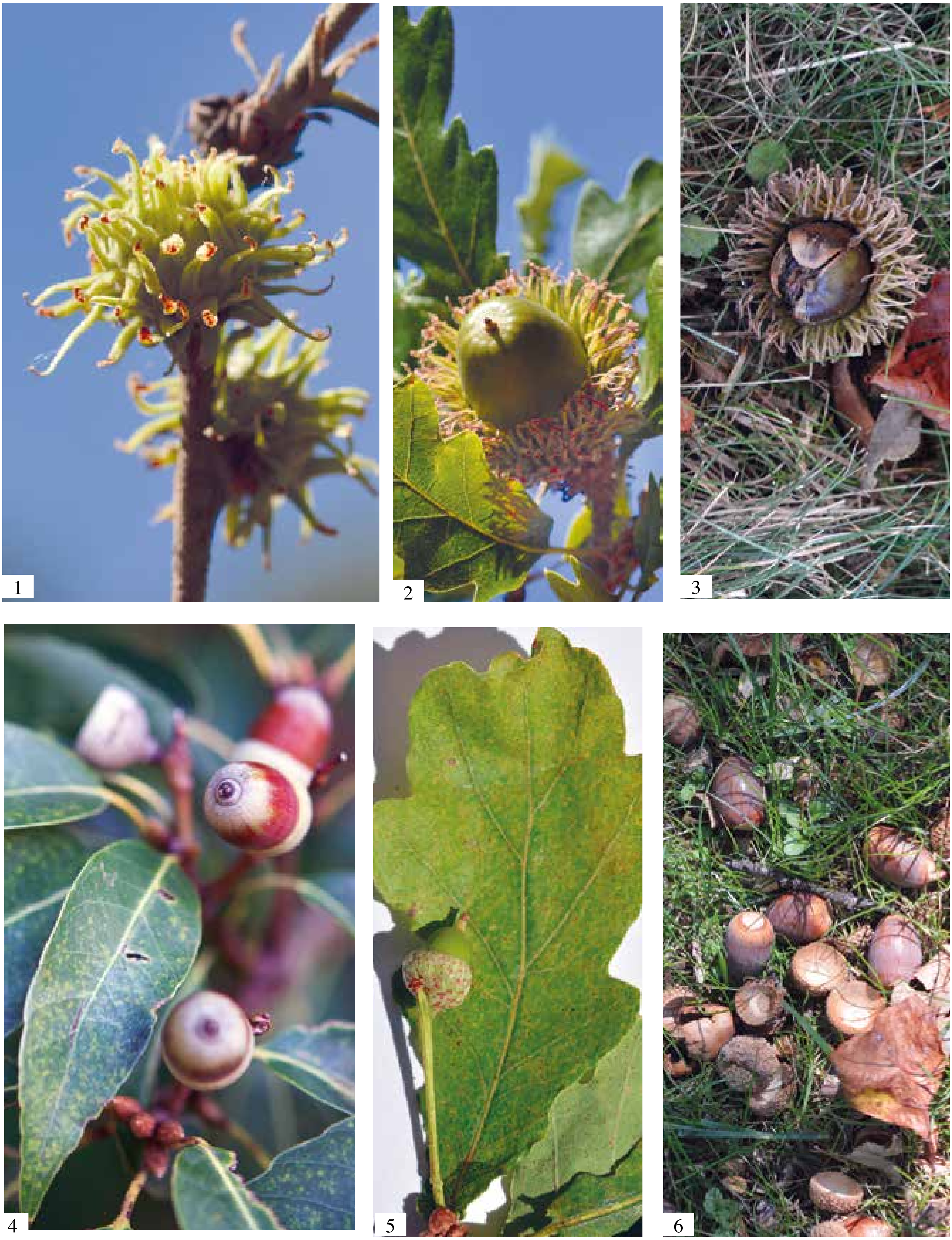
Etymology

It is from the Latin word "radiatus", meaning the radially spreading leaves.



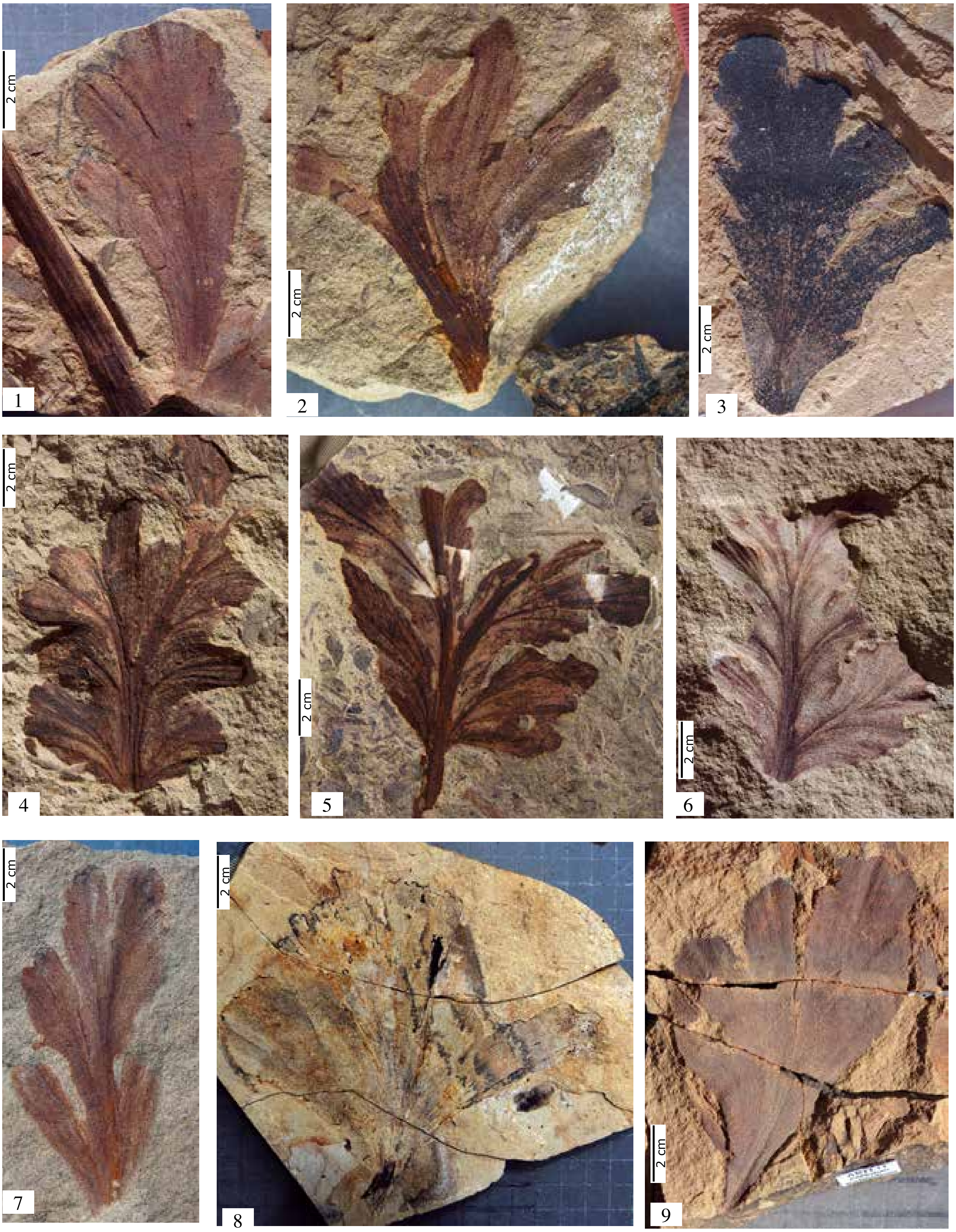
Early Permian oak-acorn *Craspedosperma bardaeanum*

1-4. Juvenile acorns (MAT 361; MAT 428; MAT 22; MAT 539); 5-8. Adult acorns with attached cupula (MAT 540; MAT 359; MAT 396; MAT 587) 9-13. Acorns released from the cupula (MAT 411; MAT 420; ARTI 16; CHEK 61; ARTI 21)



Different extant oak-acorns

1–3. *Quercus cerris* juvenile, adult and mature acorn released from the tree; 4. *Quercus myrsinaefolia;* 5. *Quercus rubor;* 6. *Quercus alba* acorns on the soil



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

Various extant oak leaves

1. *Quercus alba;* 2. *Quercus frainetto*; 3. *Quercus cerris*; 4. *Quercus rubor*; 5. *Quercus glabrescens.* The leaves vary considerable within the same genera

***Nucifructa primaeva* nov. gen. n. sp. WACHTLER 2020**

1. Designed holotype CHEK 225; one nut 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

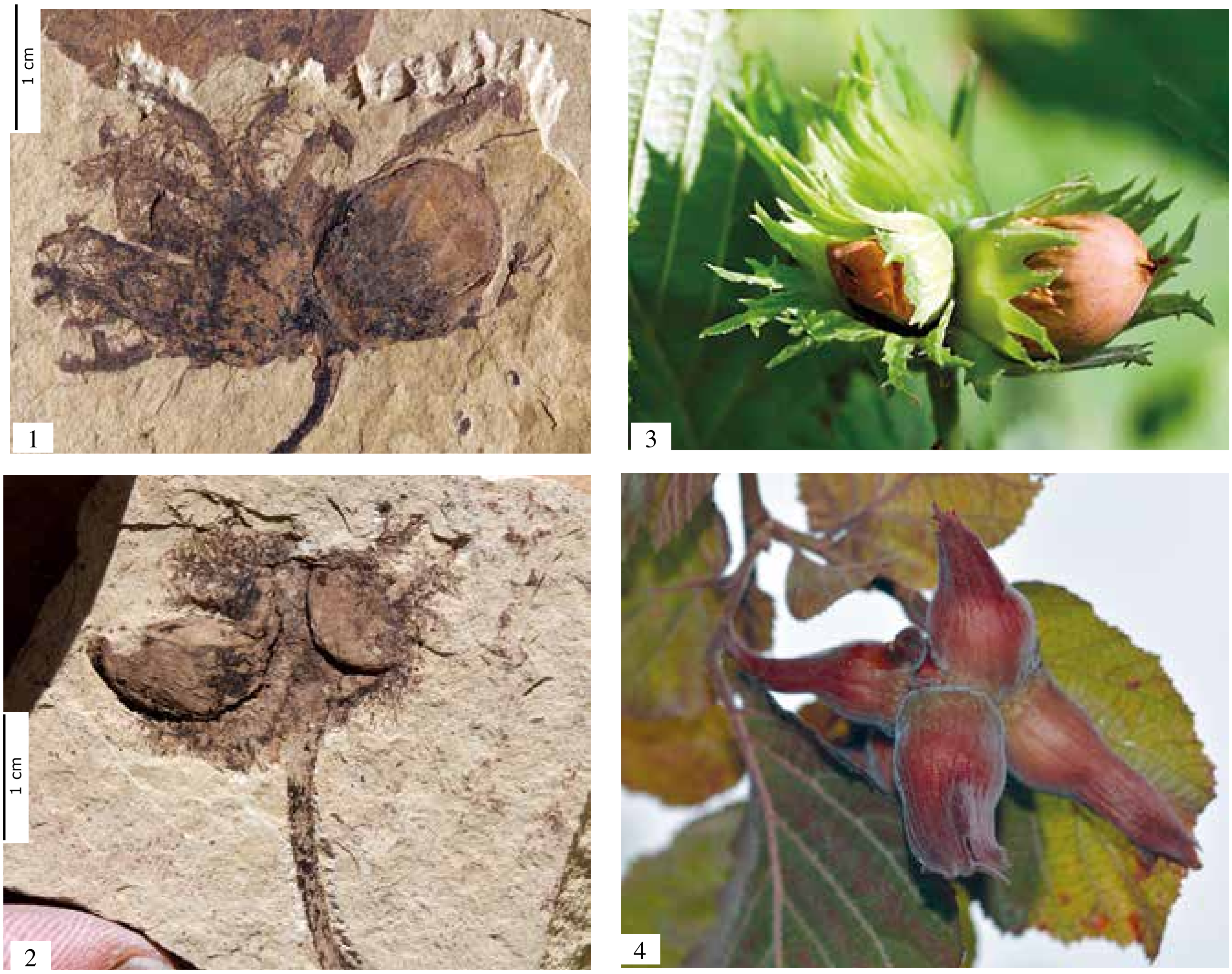
Description

Fruit: The holotype MAT 500 has a circumference of about 20 mm and is composed of many radially spreading fruit-leaves. Apically, they are often slightly incurved. They hang on a short, 15 mm long stalk. The hollow fruit-leaves probably hold the seeds inside, but unfortunately none in the holotype is open to confirm this.

Discussion

This highly interesting fruit 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 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 (Middle Eocene Republic Flora).



Eocene and extant hazelnuts

1-2. Corylus johnsonii (Corylaceae) from the Eocene of Western America (Republic, Stonerose-Center); 3-4. Extant *Corylus avellana*, the common hazelnut. Adult and juvenile specimen.

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" kernel 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 also 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*

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*

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 back to the Eocene of Western North America or Messel in Germany (Collinson et al., 2012). Mostly they were classified under the walnut family.

Parvunucleus nov. gen. WACHTLER 2020

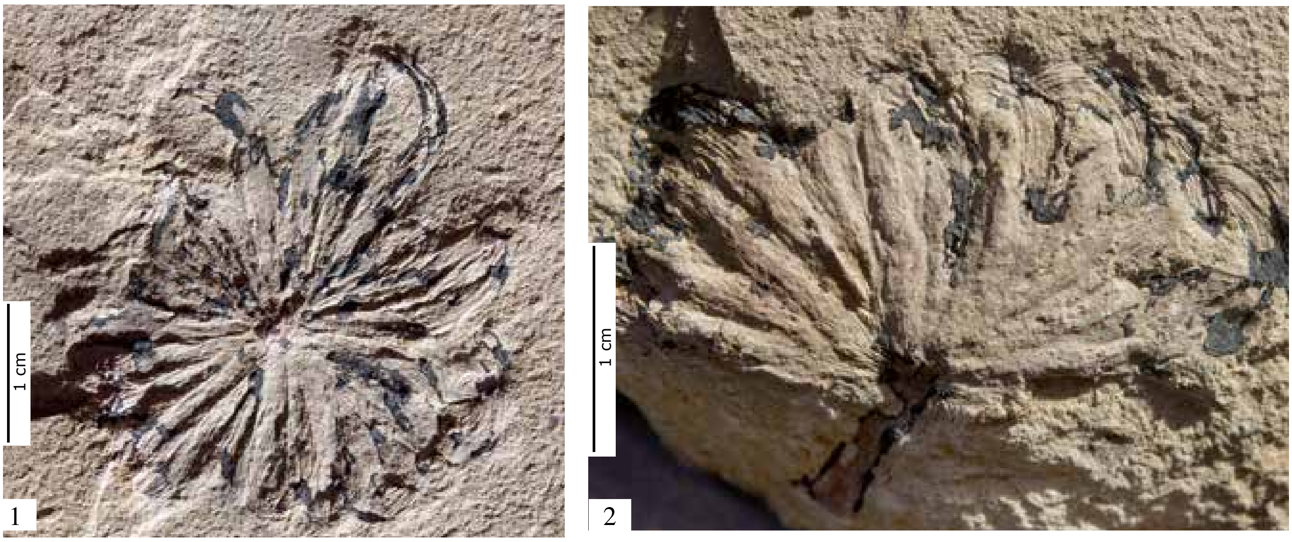
Etymology

It is from the Latin name "parvum", meaning small and "nucleus" for kernels and fruit with small seeds.

Parvunucleus dammannii nov. gen. n. sp. WACHTLER 2020

Holotype

CHEK 216, Chekarda (Collection Wachtler, Dolomythos, Innichen, Italy



Neuburgosperma radiata **nov. gen. n. sp. WACHTLER 2020**

1-2. Designed holotype and counterplate 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.

Etymology

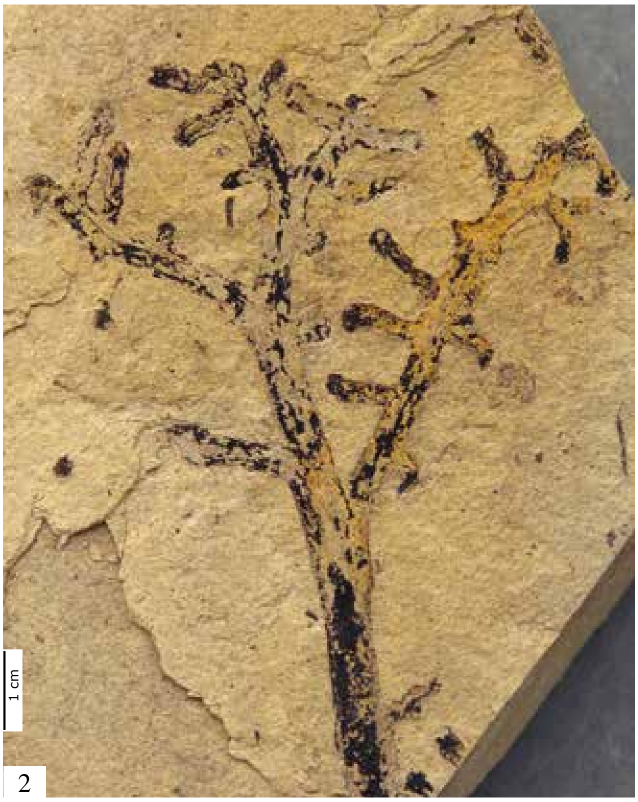
It honours the German researcher Martin Dammann, for his researches in palaeobotany and palaeontology.

Diagnosis

The berry fruit have big seeds in the middle and a fair amount of small kernels surrounding them.

Description

Fruit: The drupe CHEK 216 has a diameter of 22 mm, out of which the main kernel measures 10 mm. 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.



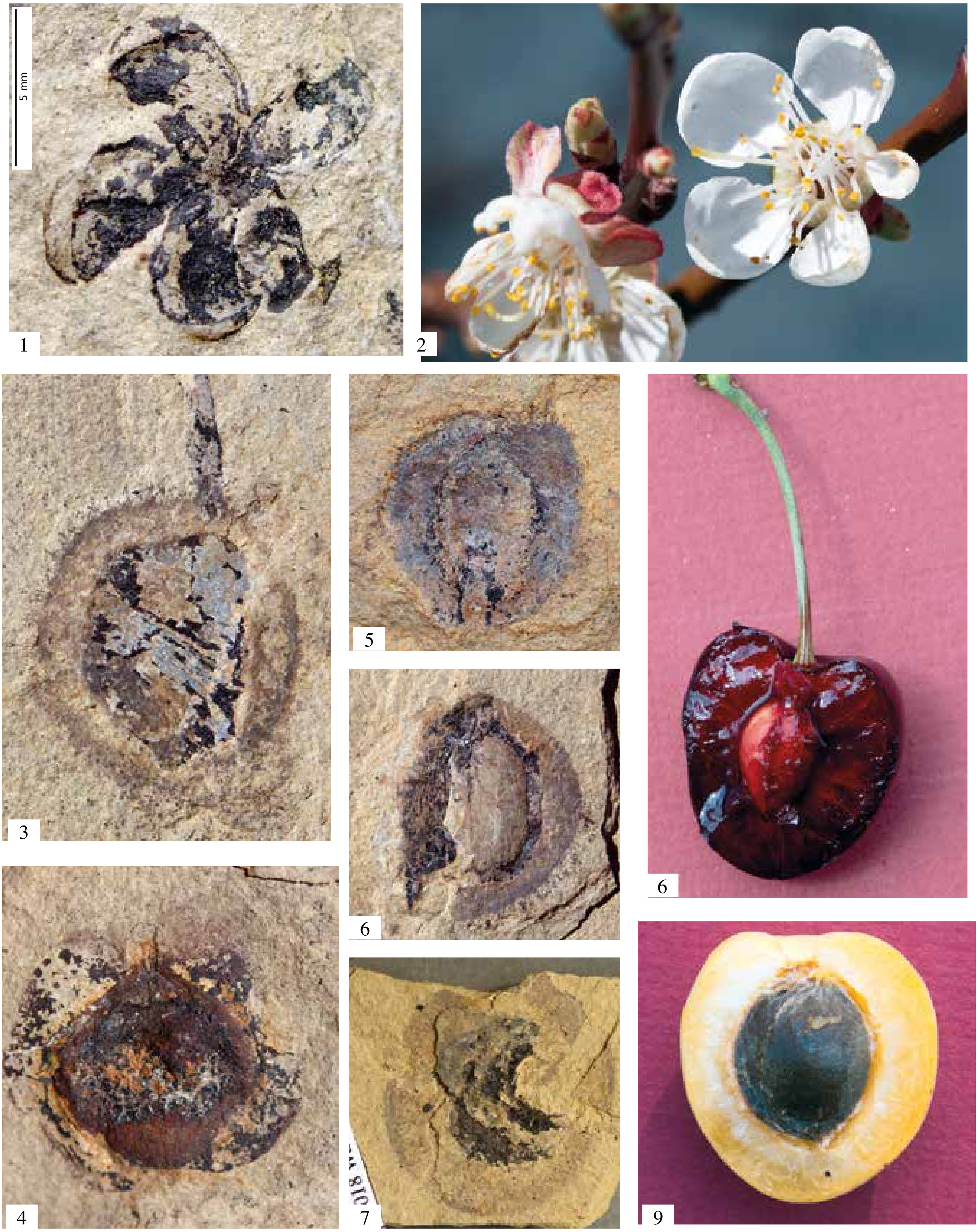
Early Permian stone-fruit ancestor *Bardocarpus aliger*-leaves: 1. Juvenile buds from big slab MAT 82 with accompanying leaves, Coll. Perner, Dolomythos-Museum; 2. Twig with incompletely evolved leaves; 3. Buds of a cherry tree, *Prunus domestica.*

Discussion

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. Only same 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* (Wachtler, 2017) are obvious – *Bardocarpus* represents a freestone in form of a lignified drupe coated by a fleshy outer

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 avium)* cut in the middle; 9. Apricot fruit with seed (*Prunus armeniaca*)

***Parvunucleus enigmatica* nov. gen. n. sp. WACHTLER 2020**

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.

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

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*.

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* (Wachtler, 2020). 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.

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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