The origin of angiosperms

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Researches initiated by Michael Wachtler will attempt to explain the strange angiosperm-genesis with new theories based on surprising new findings.

Today we have about 230,000 angiosperm species, forming about 89% of all plants, only 0.29% gymnosperms; there are about 4% ferns, 3.61% mosses, 2.28% liverworts, but only 0.38% lycopods and 0.05% horsetails. But when we take as indicator the biomass, then the huge conifer trees change the statistics.
From the Middle Devonian – the era of evolution of the first trees and shrubs – about 395 million years ago and the Carboniferous-Permian boundary, in a time interval of only 100 million years, all main tribes existing today such as lycopods, horsetails, ferns or gymnosperms, including conifers, gingkos and cycads, as well as all the insect groups had been present and fully evolved. All the following 300 million years succeeded only in segmentation and breakdown to further genera and species.
Therefore, the question is allowed: Where were in all this time the angiosperms? The evolution of flowering plants represents till now one of the central questions of natural science. The angiosperm fossil record confirmed in the 19th century the rich radiation of flowering plants between the Early and Middle-Late Cretaceous, but not before. Our present knowledge about angiosperms is based on the dogma that first appeared the family of Magnoliaceae than any other flowering plant. We do not usually take into consideration that the genesis of angiosperms could happen in a different way of evolution, maybe a more unexpected step.

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

La nascita delle prime angiosperme

Gli sviluppi del mondo delle piante sono stupefacenti. Se licopodi, equiseti e felci avevano domina-to i boschi europei e americani del Carbonifero, nel Permiano assistiamo a una rarefazione di queste specie, con contestuale diffusione di gimnosperme come conifere, ginkgo o cicadi. Nell'emisfero australe, dove era presente il continente Gondwana, posizionato tra i territori attuali di Australia, Africa meridionale, Sud America e Antartide, si sviluppò tra Carbonifero e Permiano in un clima da fresco a temperato la cosiddetta "flora a Glossopteris". Le piante, che presentavano ovuli e organi polliniferi, si distinguevano per le foglie dalla forma lanceolata, simile a una lingua. Una terza tipologia di vegetazione, ancora più spettacolare, si sviluppò in un continente appar-tato, denominato "Angara" dal ricercatore austriaco Eduard Suess, che comprendeva parte della Russia, degli Urali e della Siberia. Le condizioni di isolamento, protrattesi per diversi milioni di anni, favorirono l'evoluzione di un mondo vegetale del tutto peculiare, i cui esponenti possono essere annoverati in gran parte tra gli antenati delle angiosperme, mentre le gimnosperme erano relegate a un ruolo marginale. È da qui che hanno avuto probabilmente origine molte delle specie di piante da fiore oggi note. Questa teoria venne elaborata per la prima volta d Michael Wachtler nel 2017.A partire dal Permiano inferiore compaiono quindi i precursori delle drupe, quali ad esempio le attuali ciliegie, prugne o albicocche, ma anche gli antenati di querce, aceri, frassini, olmi, con i loro semi alati leggermente differenziati, e persino fiori e piante erbacee a bassa crescita. Sono così simili, per molti aspetti, ai discendenti attuali delle piante da fiore, da esserne quasi indistinguibili, come se in quasi 300 milioni di anni non avessero subito alcuna variazione significativa. Si tratta di una circostanza che mette in dubbio la teoria della magnolia, comunemente accettata, secondo la quale da specie primitive di quest'ultima sarebbero derivate tutte le altre angiosperme. Probabilmente, tutta la teoria evolutiva delle piante da fiore necessita di una revisione, alla luce dei nuovi ritrovamenti avvenuti negli Urali. Una volta sviluppatasi la caratteristica primaria di questi vegetali - i fiori - è relativamente semplice ricondurre tutte le altre circa 370.000 angiosperme a questa linea. Il percorso che ha portato in questa direzione è indubbiamente geniale, come quello seguito dalle conifere e dalle cicadee del Permiano, ancora soprattutto diffuse in Europa e Ameri-ca. Perché mentre nei restanti territori dell'emisfero settentrionale sono stati trovati pochissimi insetti in quel periodo, il continente Angara era l'habitat di un numero tale di grilli, mosche, antenati delle api, ragni, libellule e scarafaggi - molti dei quali potenziali impollinatori -, da rendere ovvia una potenziale simbiosi. Come mai, però, questi antenati delle piante da fiore non si diffusero rapidamente sulla totalità delle terre emerse, soprattutto durante il Triassico, quando tutti i continenti, Angara incluso, si ritrovarono accorpati in un'unica massa continentale per diversi milioni di anni? In realtà, questo può essere spiegato solo in considerazione del fatto che le violente eruzioni vulcaniche della Siberia, fino ad ora additate come le principali responsabili della "madre di tutte le catastrofi", posero fine all'iniziale trionfo delle angiosperme. Furono soprattutto le piante da fiore a subire gli effetti dell'estinzione di massa del Permiano-Triassico; queste specie riuscirono a riprendersi solo all'inizio della prima fase del Cretaceo, quando conobbero un'espansione fulminea su scala planetaria.

Die Geburt der Blütenpflanzen

Eigenartig stellt sich die Entwicklungen der Pflanzenwelt dar. Dominierten die europäisch-amerikanischen Wälder im Karbon die Bärlappe, Schachtelhalme und Farne, erfolgten im Perm deren Niedergang und ein Ausbreiten der Nacktsamer wie der Nadelbäume, Ginkgos oder Palmfarne. Auf der Südhalbkugel, dem ehemaligen Gondwana-Kontinent, welcher sich auf das heutige Australien, das südliche Afrika, Südamerika sowie die Antarktis aufteilte, entwickelte sich zwi-schen Karbon und Perm in einem gemäßigten bis kühlen Klima die sogenannte Glossopteris-Flora, charakterisiert durch Samenanlagen und Pollenorganen, die zungenartigen Blättern entsprangen. Eine dritte, noch spektakulärere Vegetation bildete sich auf einem isolierten Kontinent heraus, der vom österreichischen Forscher Eduard Suess den Namen Angara-Land erhielt und Teile Russlands, des Urals und Sibiriens umfasste. Abgeschottet über viele Millionen Jahre, herrschte dort eine eigenartige Pflanzenwelt, welche zum größten Teil als Vorfahren der Angiospermen einge-ordnet werden kann, während die Gymnospermen im Hintergrund blieben. Viele der heute be-kannten Blütenpflanzen müssen dort ihren Ursprung genommen haben. Diese Theorie erarbeite-te als Erster Michael Wachtler im Jahr 2017 nach intensiven Forschungen in der Ural-Region. So finden sich ab dem Unterperm schon Vorläufer der Steinfrüchte wie der heutigen Kirschen, Pflaumen oder Aprikosen, aber genauso Eichen-Urahnen, Ahorne, Eschen und Ulmen mit ihren leicht variierenden Flügelsamen, ja sogar die Vorläufer niedrig wachsender Blumen und Gräser. Sie erinnern in so vielen Belangen an die heutigen Blütenpflanzen-Nachfahren, dass sie oft kaum von ihnen unterschieden werden können, so als hätte sich in nahezu 300 Millionen Jahren nicht allzu viel verändert. Damit gerät sogar die bisher allgemein anerkannte Magnolien-Theorie ins Wanken, nach der sich aus primitiven Magnolien alle anderen Angiospermen ableiten lassen. Wahrscheinlich muss die gesamte Evolution der Blütenpflanzen aufgrund neuer Funde durch Michael Wachtler aus dem Ural vollkommen umgedacht werden. War einmal die prägendste Eigenschaft aller Blütenpflanzen – die Blüte – entwickelt, lassen sich alle anderen etwa 370.000 Angiospermen relativ leicht ableiten. Und der Weg dahin war genauso genial wie jener der im Perm noch hauptsächlich in Europa und Amerika aufgefundenen Koniferen oder Cycadeen. Denn während sich auf der sonstigen Nordhalbkugel im Perm kaum Insekten finden lassen, fiel der ehemalige Angara-Kontinent durch eine solche Vielzahl an Grillen, Fliegen, Bienenvorläufern, Spinnen, Libellen und Schaben – vielfach unter ihnen potenzielle Pflanzenbestäuber – auf, dass eine Symbiose naheliegend ist. Warum aber konnten sich diese Blütenpflanzenvorfahren in der Folge, besonders in der Trias, als sich alle Kontinente einschließlich Angara für Millionen Jahre vereint hatten, nicht rasant welt-weit ausbreiten? Eigentlich kann dies nur damit erklärt werden, dass die gewaltigen sibirischen Vulkanausbrüche als bisher meistgenannte Ursache dieser „Mutter aller Katastrophen" dem frü-hen Siegeszug der Angiospermen ein Ende setzten. Damit müssen vor allem die Blütenpflanzen als durch die Perm-Trias-Katastrophe in Mitleidenschaft gezogene Lebensgemeinschaft genannt werden. Weltweit erholen konnten sich die Blütenpflanzen dann erst richtig ab Beginn der frühen Kreidezeit, wobei es ihnen dann tatsächlich gelang, sich weltweit rasant auszubreiten.

This study deals with the beginning and propagation of all angiosperms in the Early Permian period from the deciduous trees, over herbaceous flowers and grasses, and will give interpretations on why they could evolve in isolation and why probably the worldwide climate change due to an immense catastrophe in the Permo-Triassic boundary caused a quasi-extinction of the first angiosperms and retarded their spreading all over the world for a long time.

An "abominable mystery"

Charles Darwin's frustrations about the astonishingly late propagating of flowering plants, revealed in his letters to Joseph Hooker, Gaston de Saporta, and Oswald Heer between 1875 and 1881, entered history. After that, researchers all over the world tried to bring light to this question.
Darwin was extremely distressed by the abrupt origin and fast spreading of the flowering plants in the Cretaceous in complete contrast to his theory about the slow evolution of plants and animals through millions of years. Therefore, he speculated a slow and long evolution on an extinct or destroyed landscape or a lost continent.
The absence of angiosperms made it impossible for other animals, especially the insects, to evolve. It was Saporta in 1877 who elaborated on the philosophy of their co-evolution. All these ended then in the famous letter about the "abominable mystery" which Darwin wrote to Joseph Hooker on 22 July 1879. But, another often-thought main preoccupation of his was not that in this time, little was known about the closest relatives of flowering plants or their phylogeny. Darwin's abominable mystery was his abhorrence to the fact that evolution could be rapid and even saltational against his theory that "natura non facit saltum" – nature does not make a leap.
It was not only the "abominable mystery" that Darwin coined in this connection, but in an equal manner, he regarded it as the "most perplexing phenomenon". Especially, Oswald Heer, an acknowledged Swiss naturalist and a proponent of the saltational evolution, wrote in a letter in 1875 that the angiosperms "which forms the bulk of modern vegetation, appears relatively late and that, in geological terms, it underwent a substantial transformation within a brief period of time." All these stand in total contrast to Darwin's slow gradualism. So, according to him, it was effectively a rapid development or surprisingly a long interval of a missing fossil record.
These thoughts preoccupied Darwin nearly till the end of his life in 1882. On 6 August 1881, he wrote again to his friend Hooker, "Nothing is more extraordinary in the history of the Vegetable Kingdom, as it seems to me, than the apparently very sudden or abrupt development of the higher plants. I have sometimes speculated whether there did not exist somewhere during long ages an extremely isolated continent, perhaps near the South Pole." There or in the North between America and Europe, he postulated a much earlier birthplace of all higher plants as well as the pollinating insects. Darwin's thoughts and anxieties can be understood fairly – also, his vision about a lost continent.

A lost continent

If we are able to find flora-elements maybe on a "dark continent" prior to the Cretaceous with many of these properties, we come nearer to the answer of the "abominable mystery."
From the Silurian-Devonian period – when the first plants evolved – Siberia and the Urals occupied a position apart from other landmasses, throughout the Carboniferous till the Permian. This position was between the 30th and 60th north latitude (today's position of Paris is about the 48th latitude; New York is about the 41th latitude. In the Early Permian era, Middle Europe or the Southern States of the United States were near to the equator, about the 15th latitude). Therefore, this northern landmass called Angara – for a long time, till the Triassic period – formed an isolated continent with independent floras and faunas.
Some of the theories about isolated landmasses were evolved by the Austrian geologist Eduard Suess. In his *"Antlitz der Erde"* (The Face of the Earth) in 1885, he hypothesized that in the Paleozoic era, there was one big landmass on the southern hemisphere that he called the Gondwana – from an Indian tribe, the Gonds – comprising Af-

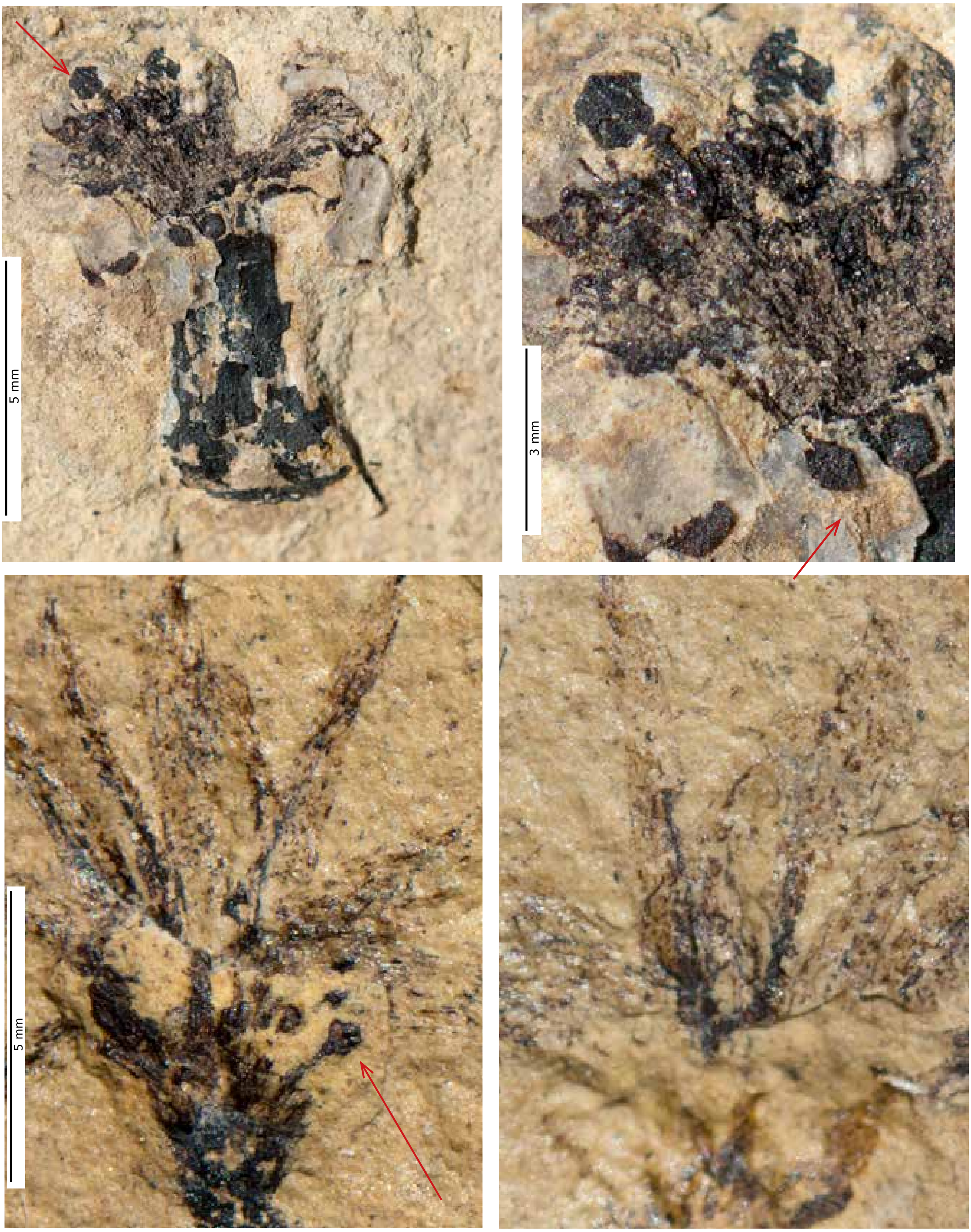
rica, South America, India and Australia. In the north, he located two big paleo-continents: North-America connected to Europe, which he called the Atlantis, and the other, he named Angara after a Siberian river, comprising parts of today's Russia with the Urals and Siberia. He baptized the ocean separating this landmass as the Tethys. It was just a modern opinion based on connected land-bridges, several years before Alfred Wegener elaborated his continental drift theory in 1912.
The Angaran landmass, from the Carboniferous till the Early Cretaceous period, was located north of Europa and North America and therefore, different climatic conditions had prevailed there. Cycads are found today across much of the subtropical and tropical parts of the world, and therefore exist some reasons, that they can not be encountered in raw climate zones. It can be supposed that in wintertime, the landscape in Angara-Land was covered by snow and the trees shed their leaves in autumn. Isolated from the other landmasses, this community remained unique for millions of years.

The "invention" of the flower and the fruit

The extraordinary diversity of angiosperms makes it difficult to elaborate an analogy, but several properties unite them and distinguish them from other seed plants. Especially, the reproductive features classify them as unique in the plant kingdom. These

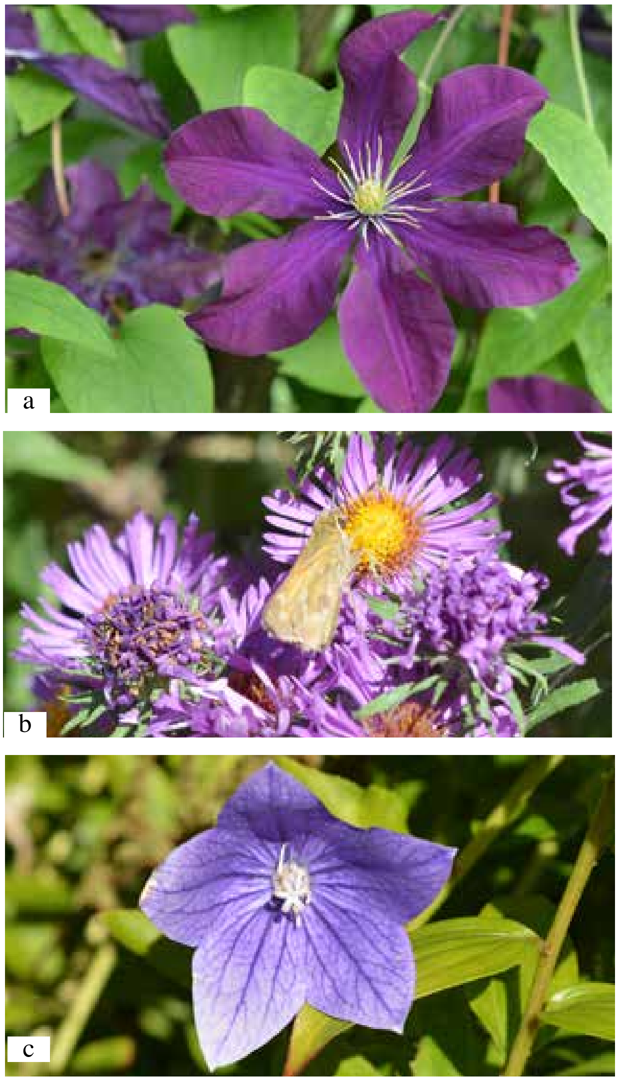
Ann exciting specimen: A flower and an insect were fossilized in the same moment. Coll. Gerasch, Chekarda,Ural, Early Permian.

Reconstruction of Early Permian flowers from Ural.



Hermaphrodite flowers of the Early Permian Angara-Land

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



Today's flowers

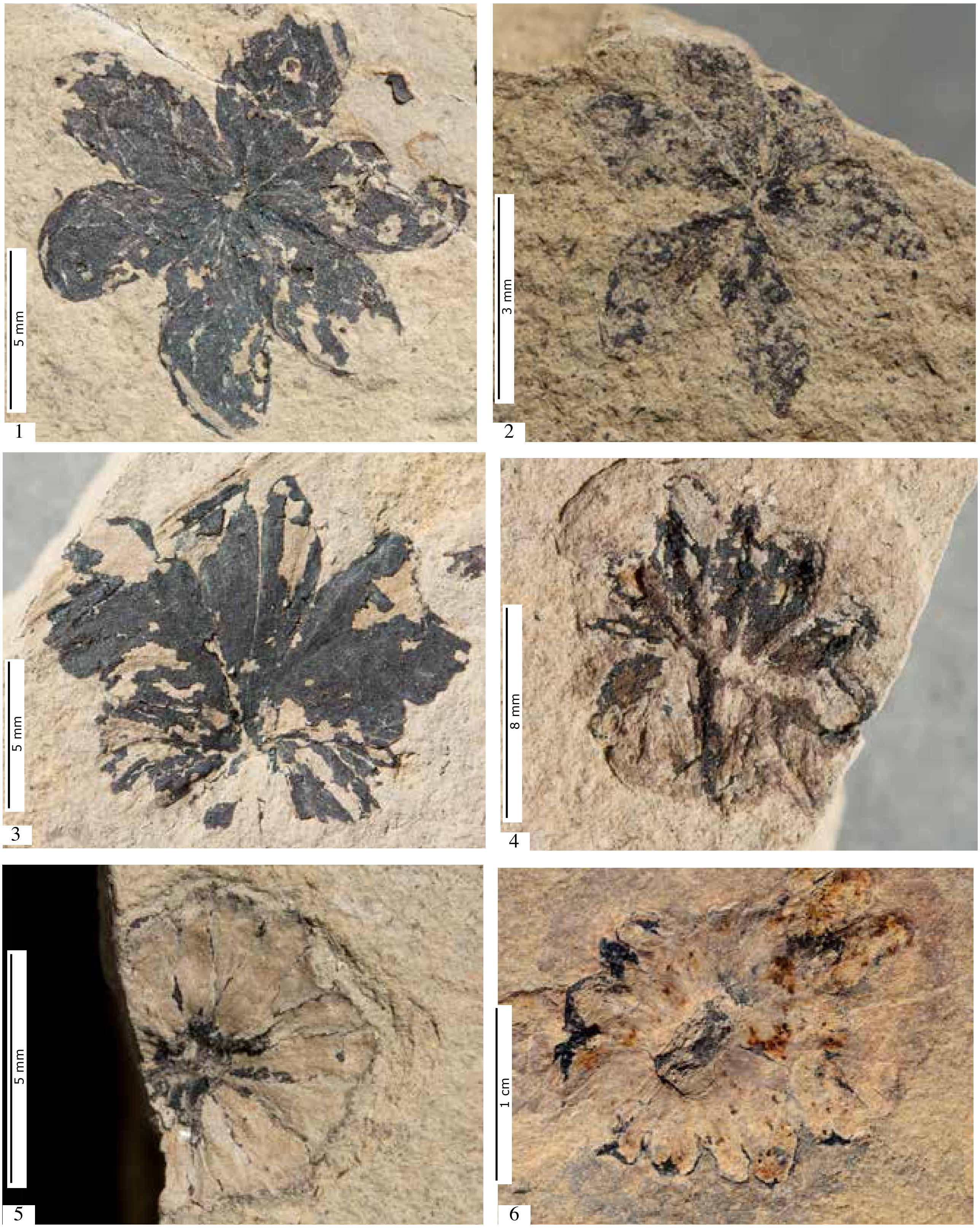
*a. Clematis patens (*Ranunculaceae); *b. Liatris cilindrica* (Blazing star - Asteraceae) visited by an insect; *c. Platycodon grandiflorus* (Balloon flower - Campanulaceae)

Reconstructions of different flowers

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

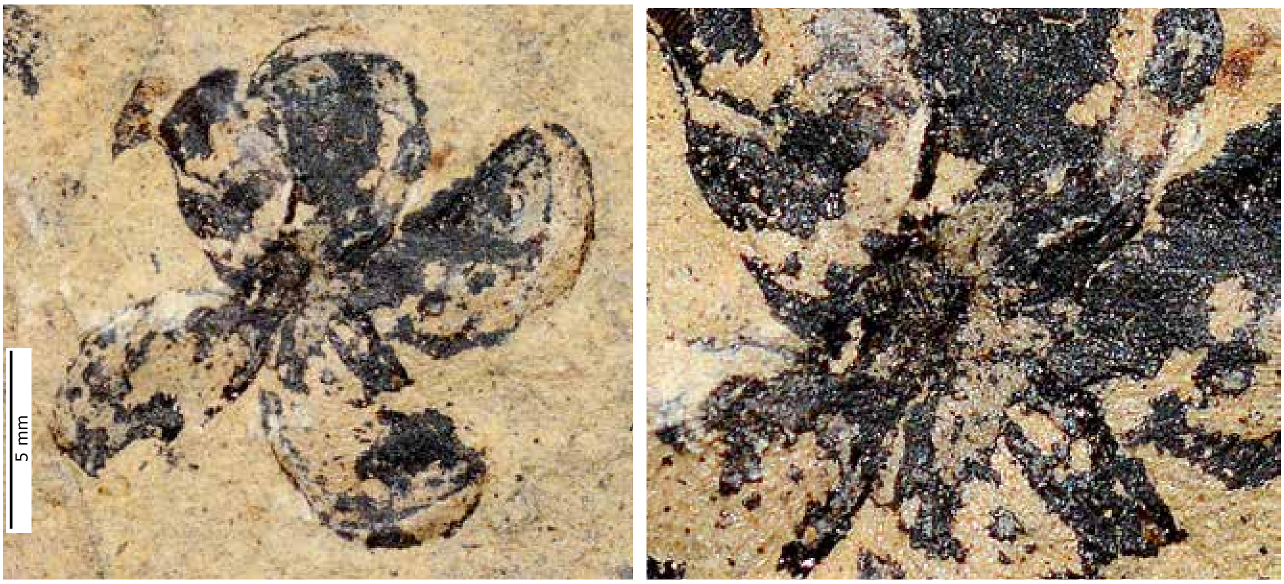
features are the flower formed by female carpels and male stamens, often surrounded by a perianth, consisting of parts that are all of one kind (tepals), or differentiated into an outer circle of sepals and an inner zone of often colourful petals. Most angiosperms are bisexual (hermaphroditic) with both carpels and stamens in the same flower; but some are unisexual with separated androecium and gynoecium. A characteristic of angiosperms is that the stamens are clearly differentiated into a fertile anther and a sterile filament, and the female organ is distinguished by an ovary that encloses the ovules and a stigma that receives the pollen grains.

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



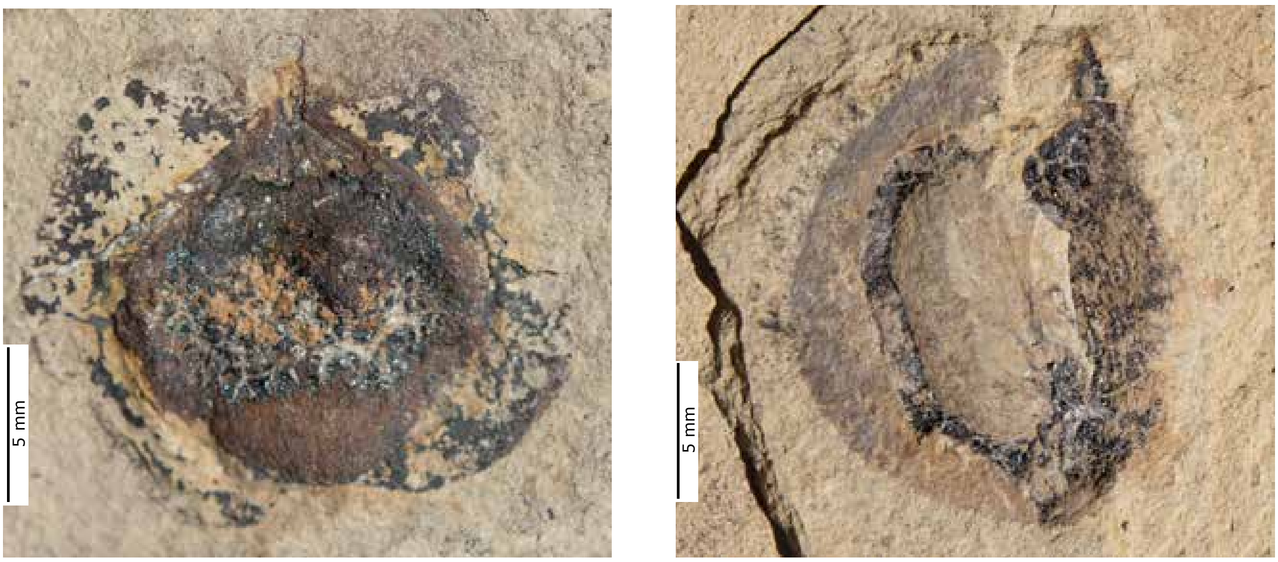
Flowers from six different families

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



Potential stone fruit ancestors - Rosopsida flowers

Flower holding five petals, inside with evidencing the reproductive organs with stamen and anther holding the microsporangia and the pistil (MAT 442, Coll. Gerasch); Matvéevo, Kungurian (Early Permian).

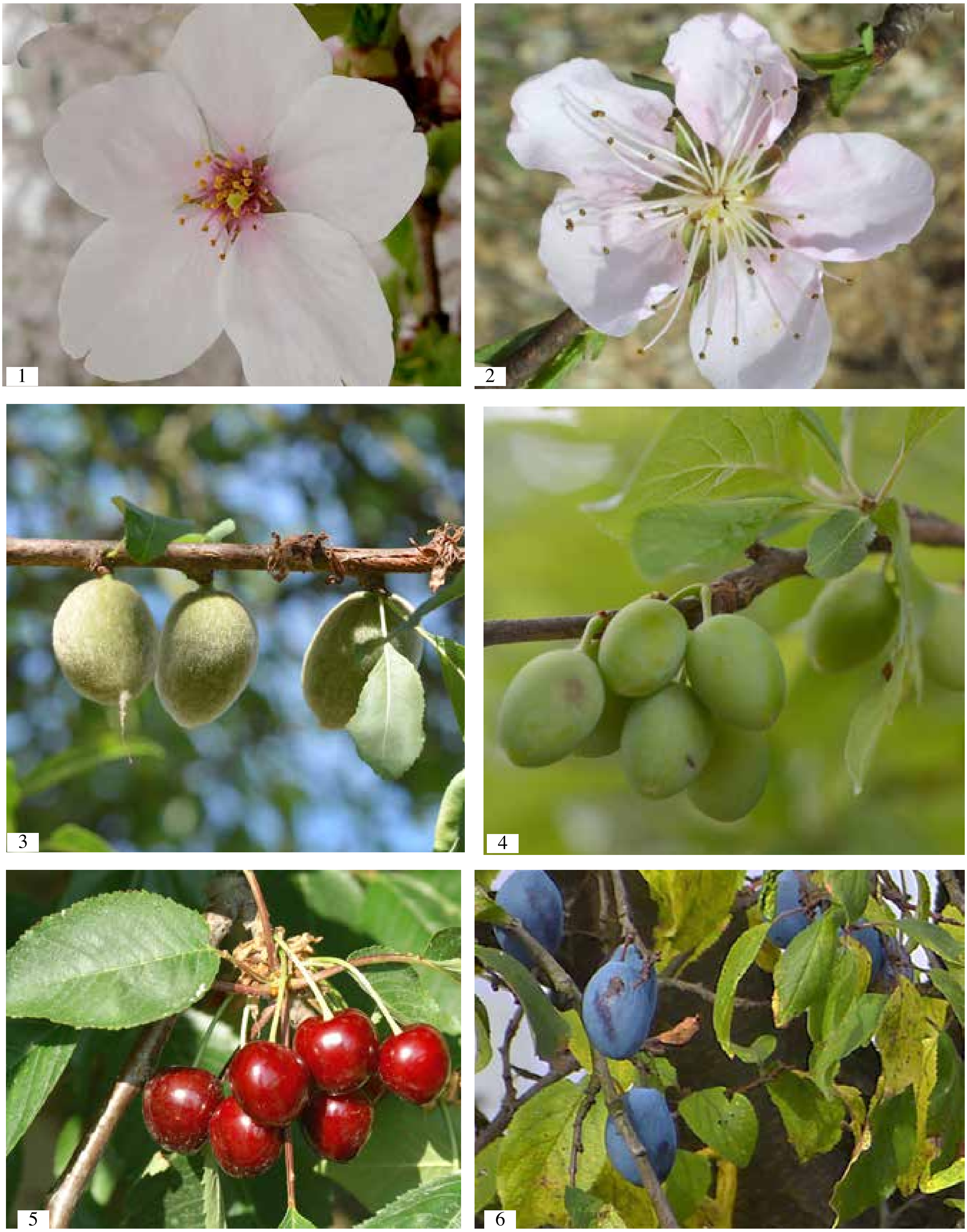


Potential stone fruit ancestor - Stone fruits

Several stone fruits. Note the well conserved fleshly parts outside surrounding a single hard pit of hardened endocarp with a kernel inside; Matvéevo, Kungurian (Early Permian) Coll. Dolomythos

Another feature characterizing the flowering plants is their fruits. They can be very different from one another. The angiosperms produce first an embryo, complete with a constant flow of nutrients from the plant into the developing seed. Therefore, a fruit is a maturing ovary and the diversity is high. They can be fleshy, dry, or the ovary can be fused with other kinds of tissues. They can be dehiscent, when the pericarp splits open to release the seeds, or indehiscent, when the pericarp encloses the whole fruit as the dispersal unit. The fruits of flowering plants protect the enclosed seed and aid in their dispersal.

They can be dispersed by wind, like the samara of an ash or maple, or by water or by animals. Seeds contained in edible fruits must possess the ability to survive the ingestion of animals also.



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

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

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

Two segmented leaves *(Psygmophyllum cuneifolium*, (ARTI 11, Coll. Gerasch), Arti, Artinskian (Early Permian); Samara with attached connecting stipe; Matvéevo, Kungurian (Early Permian) Coll. Dolomythos. Reconstruction

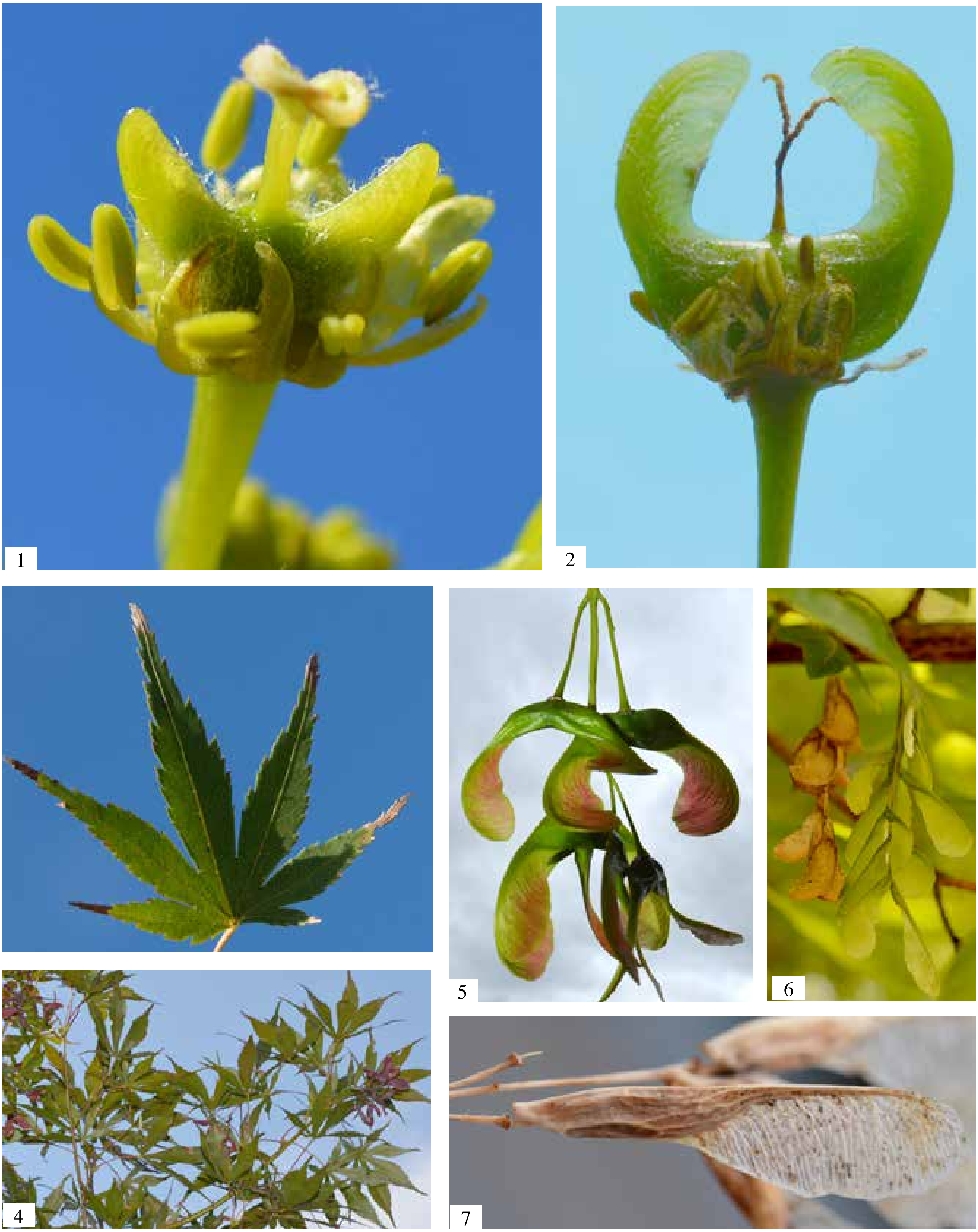
Why are there so many different angiosperms from the beginning?

Strangely the origin of angiosperms based on the fossil record can be dated back in the Angara-landmass to the Carboniferous-Permian era. In the early Permian sediments from Chekarda and Matvéevo in the Ural-region, many different "flowers" could be found. They were inserted as *Asterodiscus, Aspidion, Peltaspermum, Permotheca* without going more into details of which plant they belonged to. Additionally, little attention was given to the inner details of these inflorescences. Considerable differences exist between the plethora of fructifications. Some had five petals as many of today's flowers like the Rosaceae (cherries, apricots, and plums). Others had six petals, or even more more.

Today's flowering plants are divided into monocots and dicots. Usually dicots hold petals in multiples of four or five, reticulated leaf veins, and are both herbaceous and woody. Monocots, the smaller group today, are characterized by parallel leaf veins, petals in multiples of three and are herbaceous. Both were present in the Early Permian Angara.

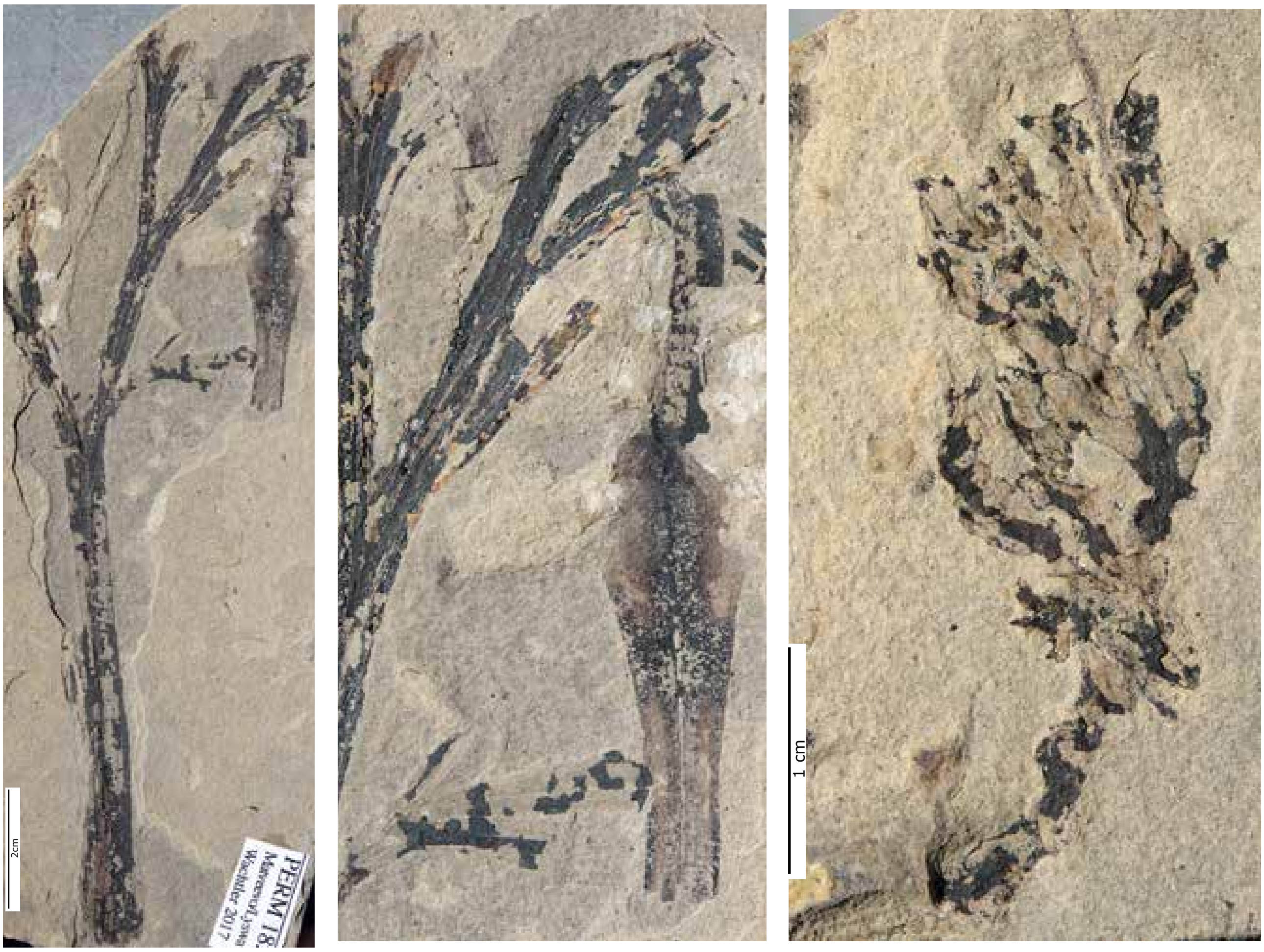
Several "flowers" from Early Permian sediments in the Urals evidences well a diverse stamen with anthers and a gynoecium, also with the impressions of some ovules. It is surprising, and speaks for the extraordinary preservation in these Matvéevo layers, that the slender filament as well the anther with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

The base is a fully developed hermaphroditic flower with ovaries and stamens. Additionally, unisexual fructifications were just as fully evolved. In the Early Permian period, several angiosperm lineages such as deciduous trees comprising maples, oaks, ash trees or stone-fruits as well as herbaceous flowers and grasses, dicots and monocots, were present. Once "invented" the bisexual flow-



Extant Acer: Leaves and seeds (samara)

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



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

Entire twig with attached aliform seed and leaves and detail of the samara (MAT 182); Deciduous flower with male and female infructescences Matvéevo, Kungurian (Early Permian) Coll. Wachtler - Dolomythos Museum

er, composed of stamen and carpel with surrounding petals, sepals or tepals, all further lineages can be deduced. The Magnolia theorem as being the most primitive plant and an evolution of all angiosperms from them cannot be reconstructed. Accompanied with the ascension of flowering plants, we have a coeval rising of all insect groups.

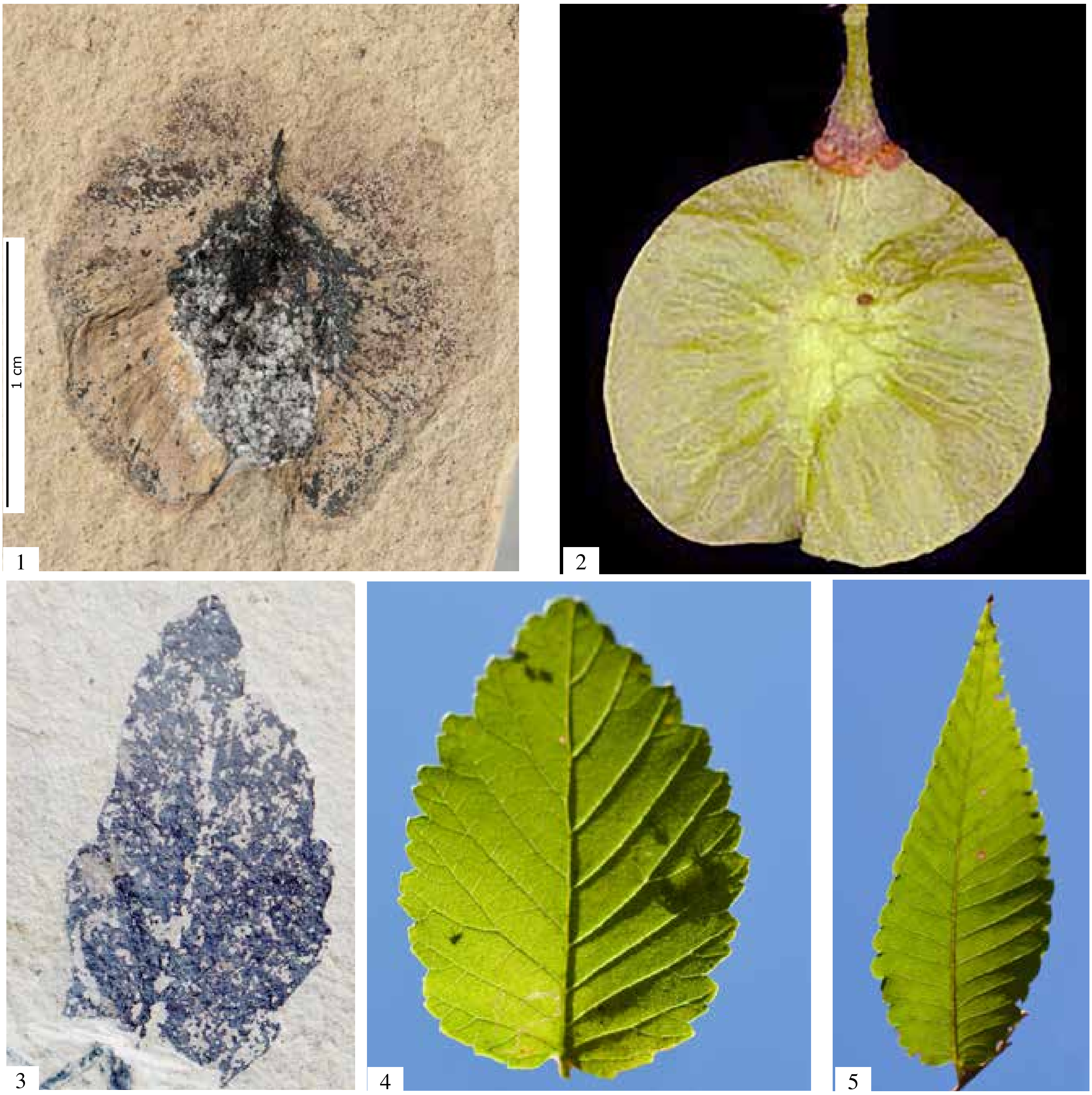
The spreading of diverse lineages of angiosperms in the Early Permian Angara-Land is therefore equally mysterious or not, as the coeval diffusion of gymnosperms in the Euro-American landmass with several subordinated tribes such as conifers, cycads or ginkgos. This coevolution in the Early Permian period simplifies the understanding of angiosperm development considerably, especially when it can be based on solid arguments and facts due to compound findings.

Coeval insect and flowering plant evolution

If somebody is surprised by the richness of Early Permian angiosperm tribes, he must also be astonished at the diversity of insects in Angara. Present were all of today's widespread families such as Mayflies (Ephemerida) Syntonopterida, Odonata Blattinopseida, Caloneurida, Hypoperlida, the Dictyoneurida, the order of Mischopterida, the Psocida, the Thripida, the Psocidea, the Hemiptera, the Palaeomanteida, Coleoptera, the Eoblattida, Blattida and Gryllidae, as well potential progenitors of the Hymenoptera. Some of them can be regarded as potential pollinators. Adherent pollen dust was found on some insects also. Only in this way can we explain there the simultaneous appearance of all main insects-groups and ancestors of angiosperms that exist even today.

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

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



Matvéeva perneri. Potential Ulmus ancestor - samaras

Perfect conserved samara evidencing the seed inside (MAT 346) 2. *Ulmus rubra*. Samara; 3. Leave probably belonging to some Ulmus-ancestor (MAT 434, Coll. Gerasch) 4. *Ulmus pumila.* Leave; 5. *Zelkova serrata* (Ulmaceae);

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

All these big evolution steps on the Carboniferous-Permian border are till now recorded only from old Angara-Land. The concept of slender filaments with pollen-producing anthers was never directly recognized in the European Peltaspermales. It is doubtful that an equal can be found in other fossil sites of the Permian Northern Hemisphere. From France to Germany or the Alps were examined in the last centuries much more than the Siberian Angara, but apart from some Peltaspermales (where this characteristic anthers and filaments were never found) all over the Paleozoic-Mesozoic, such a concept is missing. It is not to exclude that the Peltaspermales with *Autunia-Rachiphyllum-Scytophyllum* leaves had some preangiospermous features. Additionally, all over the European Permian and Triassic, the Peltaspermales play only a marginal existence between the dominant horsetails, ferns and gymnosperms especially. In some well-known and studied locations such as the Middle-Triassic fossil site Ilsfeld, for example, they completely lack such characteristics.

Another point of view

If the hypothesis of the hermaphroditic flowers can be proved by Paleozoic findings the "Magnolia-theory," collapsed like a house of cards. Once the hermaphroditic flower was created, all further developments and segmentations could be deduced easily. Why could this not happen in the Carboniferous-Permian border? The way to the stamen, composed of a sterile filament and the pollen-generating anther, was as difficult and inventory as the pollen-bract-cone of gymnosperms. These are valid also for the ovary of angiosperms, in contrast to the manifold seed- and cone-peculiarities of the gymnosperms.
All depends on the point of view: Assuming that first, the former continent of Angara-Siberia was discovered and for decades, the researchers studied there the evolving of floras and faunas, they would be surprised about the Euro-American completely different vegetation, especially of gymnosperms. We are too much influenced by our Western thinking and we believe only what we have discovered in Europe or America. In Europe, these scientists would wonder about the distinctness of the multitude of gymnosperms. They would note that the juvenile to adult stage would not be so different in the conifers, ginkgos or cycads because of their cone-like structures. They would note with surprise that the typical Angaran flowers or blossoms will be mainly unknown in Euramerica.
But these Angaran researchers would also identify similarities: that the aliform seed from *Sylvella* (Acer ancestor) or *Sadovnikovia* (Fraxinus progenitor) has their counterpart in conifers like *Majonica* or *Wachtlerina* (supposed Abies ancestors); that the microleaves-coated seed of the conifer *Ortiseia* (Araucaria ancestor) has similarities with *Craspedosperma* (Quercus ancestor); that the fleshy stonefruit *Bardocarpus* has an opposite in former Euramerican ginkgo-ancestor *Baiera*. Some of the Angaran scientists would wonder how little insects flew in the Permian Euramerica.
And surprisingly, they would ascertain that the ocean separating the two continents and also their latitude-difference avoided for a long time a common flora-and-fauna exchange.

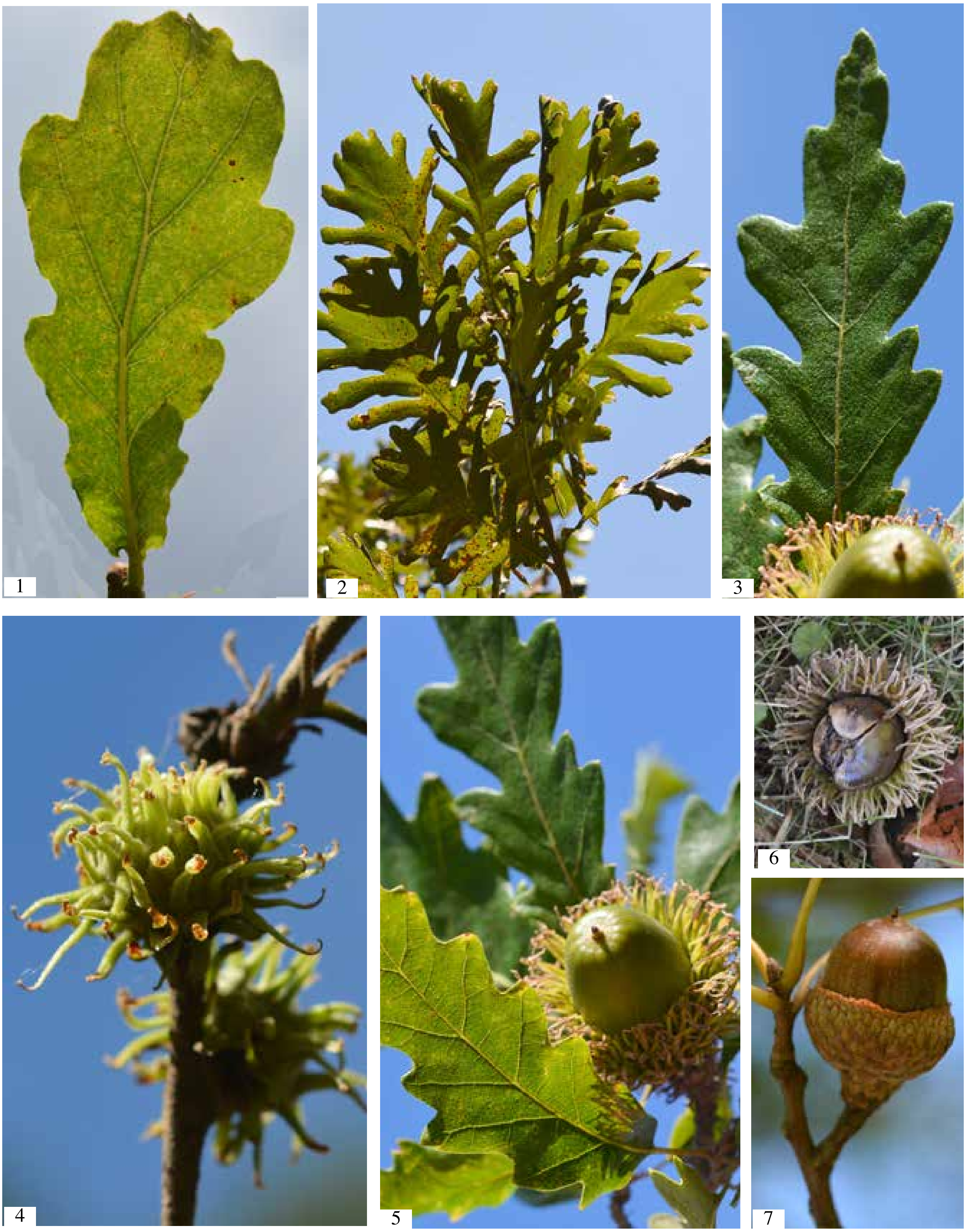
Development of the samara

Aliform seeds are found in many gymnosperms such as the Pinus conifers, the firs and spruces, and in angiosperms such as maples (Acer), ash trees (Fraxinus) or elms (Ulmus). Their genesis must have occurred, therefore, two times independently: around an ovule/seed, various microleaves (called in Devonian times "emergences") aggregated together to form a flying reproductive organ. Early Permian conifers such as Majonica and Wachtlerina evidenced these evolution steps in gymnosperms, while the Early Permian *Sylvella alata* (the potential Acer ancestor) and *Sadovnikovia belemnoides* (thought as Fraxinus progenitor) evolved these in angiosperms in the Angara continent. The same occurred in Araucaria-Quercus. Microleaves (emergences) surrounded the seeds of the Araucaria ancestor *Ortiseia*, that today we recognize only one in the scale-embedded seed, and independently, they coated the single seed of the oak-ancestor *Craspedosperma bardaeanum* partially on the basal side.
The fleshy arils or fruits of the cherry, plum or apricots present in the Angaran Early Permian period as in *Sylvocarpus armatus* find their counter-part in Northern Hemisphere Ginkophyta such as Permian *Baiera,* or in Ullmannia conifers as suggested ancestors of the Taxaceae. Microleaves cling their seeds, forming a compact aril.

2

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

Psygmophyllum expansum. Several well-preserved leaves (ARTI 17, Arti, Artinskian (Early Permian), *Craspedosperma bardaeanum*. Typical oak-acorn, densely covered with mossy bristles Matvéevo Early Permian, Coll. Dolomythos, Reconstruction



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

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

Wind and insect pollination

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

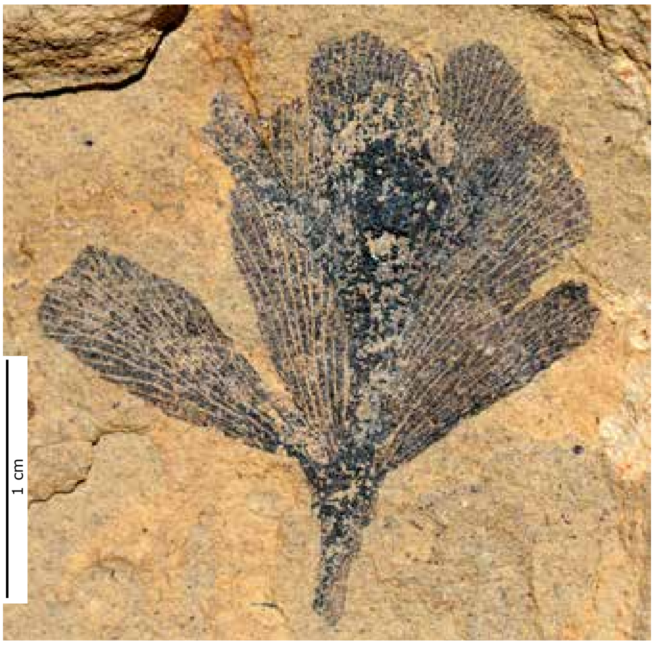
A common origin of the furcating leaves

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

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

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

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

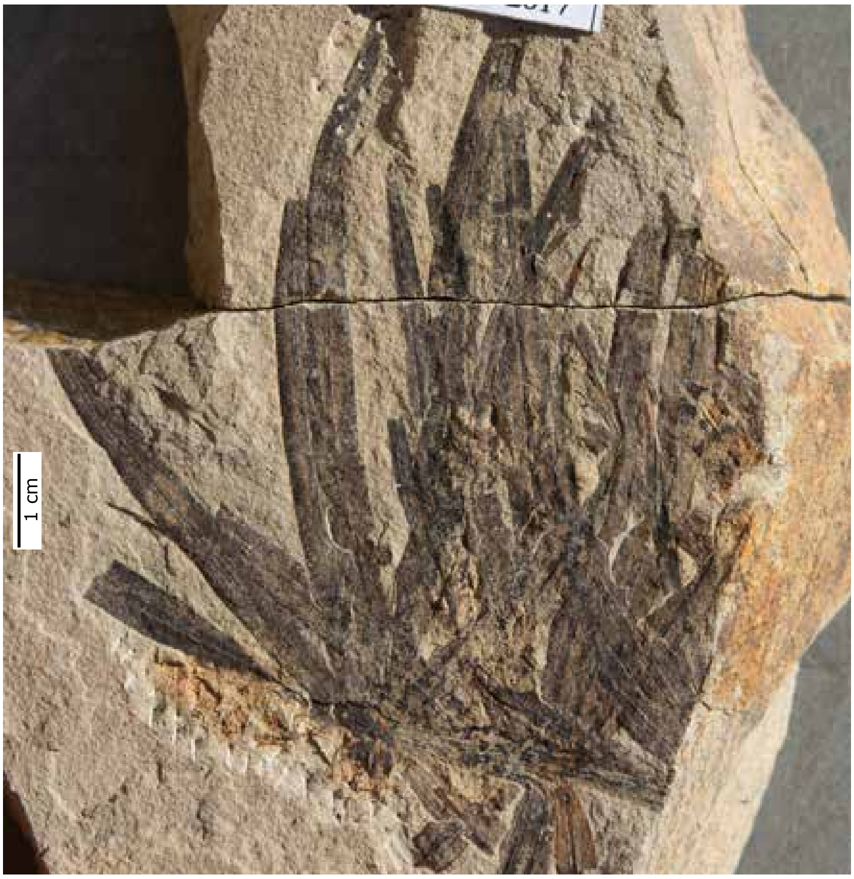


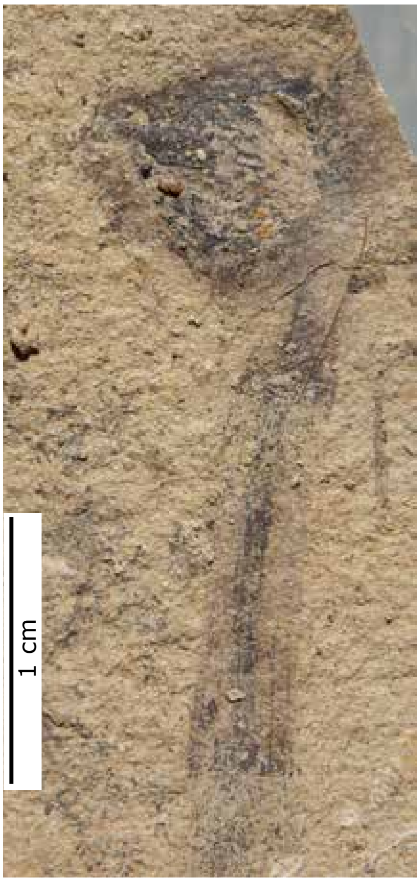
***Peremopteris biarmicum*. Suggested flower**

Exceptionally preserved flower with inside shadow of the carpel with stamen. Interesting are also the reticulate petals (MAT 435), Matvéevo, Kungurian (Early Permian) Coll. Gerasch). *Lavatera maritima.* Flower, stamen and carpel of a Malvaceae.

Heterosporous and hermaphroditic

Hererosporous fertile organs on the same plant are present in angiosperms (a good example is the birch), as well in gymnosperms such as cycads or conifers. Hermaphroditic reproductive system – having both male (micro) and female (mega) parts present on the same flower or cone – is not exclusively a feature of angiosperms. Spores of two types on the same cone are just in the Selaginella clubmosses and especially pronounced in the Carboniferous Sigillaria lycopods or better recognizable in the Tri-





Lyswaia nicolaswachtleri, Campanula-ancestors

Entire plant with detail of a mature and open capsule (MAT 338); Part of a plant with flower (MAT 287); Matvéevo, (Early Permian) Coll. Wachtler, Dolomythos Museum

Campanula alpina (Bell-flower) is widespread in Europe; *Campanula rotundifolia* (Bluebell bellflower) Capsule containing some seeds, with the majority just released. It can be compared with Lyswaia, also eviencing an open capsule.

assic *Sigillcampeia.* They were defined as heterosporous, with microspores and macrospores on the same reproductive organs. Bearing only one megaspore within a multicellular gametophyte as in *Sigillcampeia* can be interpreted as a clear sign indicating the direction of evolution of more complex seed plants.

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

The question of more basal or advanced that does not exist

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

Taezhnoeia geraschi, Poaceae, grass-ancestors

Whole herbaceous plant (MAT 434), Coll. Gerasch. Matvéevo, (Early Permian); recent Poaceae (Panicum virgatum, Switch-grass)

Early Permian insects from Chekarda(Ural)

Sylviodes perloides Reculida - Sylvaphlebiidae

Tcholmanvissia longipes Orthoptera

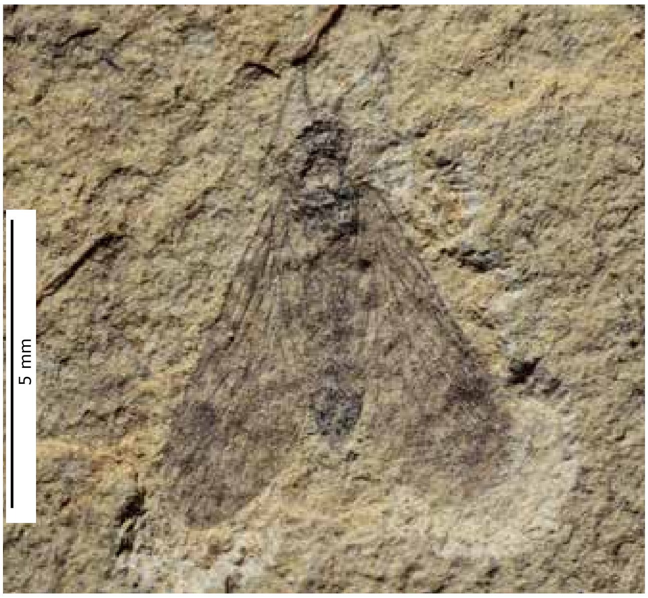
***Paleuthygramma tenuicornis*, Caloneurodea**

Enigmatic relatives of early Orthoptera and Phasmatodea, Chekarda, Early Permian (Coll. Dolomythos).

Culiciforma formosa Reculida - Lemmatophoridae (Grylloblattida)

Uralia maculata Diaphanopterida

Arctotypus sylvaensis Meganisoptera - Meganeuridae



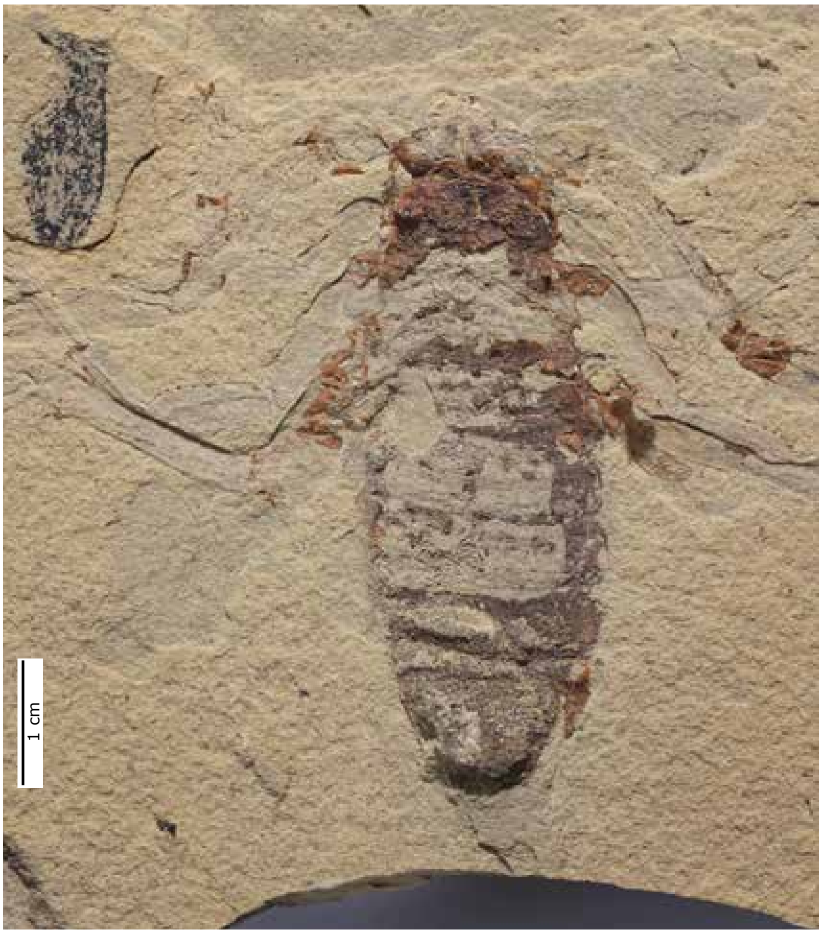
***Maueria pusillus*, Hemiptera, true bugs**

Matvéevo, Early Permian, Kungurian, (Coll. Dammann)

***Uralia maculata*, Diaphanopterida**

Matvéevo, Early Permian, Kungurian, (Coll. Dammann)

Angaroptera nicolaswachtleri Matvéevo, Early Permian, Kungurian, Coll. Wachtler Dolomythos Museum



Permomatveevia perneri, Arachnida, Scorpiones, Matvéevo, Early Permian, Kungurian, (Coll. Martin Dammann)

flowers do not confirm this evolutionary way being just to advanced. The organs were flowers with only one or a few gynoeciums.
So, we arrive at the same phenomenon as in Euro-American gymnosperms. For a long time, it was thought that the genus Cycas was the most primitive and from that evolved all other cycads, or the Araucaria-conifers built the most basal conifer lineage. But in Early Permian, we have fully evolved Cycas ancestors (*Bjuvia, Taeniopteris)* with their multi-seeded covering-blade as well as the Zamia-progenitors (*Nilssonia*) with their two-seeded scale. On the Carboniferous-Permian border, we have winged-seed conifers such as *Majonica*, one-seeded Araucarias (*Ortiseia*), more-seeded seed scales (*Voltzia)* conducting to many known present day Cupressus-conifers. Besides, we have Pinus ancestors (*Fèrovalentinia*) and Ginkgo forefathers (*Baiera*).
The same happened in Angara with their multitude of deciduous trees, low-growing flowers and grasses.

A long isolation

It is more difficult to elaborate a hypothesis about the movement of all gymnosperms and angiosperms in the following million years. Why we have the astonishing worldwide propagation of angiosperms beginning from the Cretaceous and not before? What happened to the angiosperm ancestors of Angara from the Early Permian till the Cretaceous? Why are there only rare insect findings on the European landmass all the time, whereas in the Permian Angara, all main insect families were present abundantly? And what caused great cataclysm like the often cited Permo-Triassic catastrophe?
The more than 242-million-year-old fossil, *Megachirella wachtleri,* is the most ancient ancestor of all modern lizards and snakes, iguanas, chameleons, geckos, known as squamates. *Megachirella* is about 75 million years older than what was thought were the oldest fossil squamata in the world. Some questions can therefore be explained by the poor fossil record.
The others need further hypothesis. Beginning from the Early Triassic all continents were than united into the one supercontinent Pangea, assembled from all earlier continental units. In theory, all plants and animals could spread everywhere, but the questions are: Why certain conifers like the Araucarian-ancestor Ortiseia, abundant in Permian sediments of Europe, vanished Europe after the Triassic and are now distributed especially in the Southern Hemisphere but not in the Northern?

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

If we have mostly all flowering plant tribes in the Early Permian Angara-Land, why could they not radiate all over the landmass when Pangaea assembled to one global continent? An audacious hypothesis can be searched in the largest known volcanic events of the last 500 million years of earth's geological history – the forming of Siberian Traps – spanning one million years between the Permian–Triassic boundary, about 251 to 250 million years ago. Today, basaltic lava covers about two million square kilometres there, but the original extension is estimated at about seven million square kilometres approximately in the region from Siberia over the former Angara-continent.
If this global catastrophe happened really, and this is based on facts and documented by analyses from the extinction of many animal tribes such as the Trilobites or many Nautilids, Angara was the most involved landmass and therefore, it is plausible that this landscape suffered more than all others. It can be suggested that only with difficulties the angiosperms survived on some isolated refuges and that too on a restricted and marginal level. Probably for a long time, till the Cretaceous, they were not able to expand on a large scale. In this case, the most involved victims of these mother of all catastrophes were the angiosperms.

Fundamental theories about Early Permian angiosperm evolution

The origin of Angiosperms can be dated back in the Angara-landmass to the Carboniferous-Permian era. The base is a fully developed hermaphroditic flower with ovaries and stamens. Additionally, unisexual fructifications were just as fully evolved. In the Early Permian period, several angiosperm lineages such as deciduous trees comprising maples, oaks, ash trees or stone-fruits

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

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

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

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

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