The Evolution of the First Flowers
Early Permian Angiosperms

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In the Northern Hemisphere, from the Devonian till the Triassic period, in addition to the Euramerican landmass, another isolated continent called Angara existed. This area was distinguished by a fasten radiation of plants that have many similarities with today's angiosperms. In the fine-grained sediments, especially from Matvèevo and Chekarda, we encountered a plethora of blossoms. To bring order amongst these fossilised flowers that are more interesting than the leaves in the field of science, several new classifications were introduced: *Tsvetokia nicolaswachtleri* nov. gen. n. sp., *Pasternakia permensis* nov. gen. n. sp. and *Flossia uralensis* nov. gen. n. sp. These represent parts of plants with well-evidenced sexual organs such as pistils or stamina, which are similar to today's blossoms. Four petals with pistil-like organs in the middle characterise *Permotheca colovratica. Claireia pentafolium* nov. gen. n. sp. and *Kunguria perneri* nov. gen. n. sp. are characterised by their five-petaled flowers. *Sextupetalum ottiliethomsonae* nov. gen. n. sp. and *Sextupetalum smirnovi* n. sp. had six-petaled flowers. *Multifolium petaloides* comb. nov. and *Asterodiscus disparis* can be distinguished by their multiple-petaled flowers. *Nanoflos maueri* nov. gen. n. sp. holds multiple-petaled blooms aggregated in panicles. *Aspidion decemnervium* had a corolla with their petals united and *Aspidion campanuliformis* n. sp. had tube-shaped corolla. Flowers getting shed naturally, especially by wind, are not a common event, but it happens. Therefore, finding fossilised blossoms can be regarded as a rare and difficult occurrence.

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

Introduction

In Early Permian (Artinskian-Kungurian), fine-grained sediments of some localities in the Fore-Urals near the city of Perm, especially Chekarda and Matvèevo, angiospermous fossils of many varieties in terms of appearance and structure can be found. Some of them attracted just the attention of older authors (Zalessky, 1927, 1929, 1933, 1934, 1937a, 1937b, 1939) or newer ones (Naugolnykh, 2001a, 2012, 2013, 2014; Naugolnykh & Kerp, 1996; Naugolnykh & Oskolski, 2010) and were partially published with distinct names such as *Permotheca colovratica* (Zalessky, 1929; Naugolnykh, 2013), *Asterodiscus disparis* and *Aspidion decemnervium* (Zalessky, 1937); others remain obscure and nameless till date in the field of palaeobotanical science. This exposes a general problem in palaeobotany; although it is often cumbersome to combine isolated flowers, seeds, fruits or leaves exactly or at least with a high percentage of precision, numerous classifications of individual parts of the same plant are just as confusing (Perner & Wachtler, 2015). This is especially valid for the plethora of flowers and fruits found in many of the Early Permian localities of the Fore-Urals. Mostly, the quality of preservation of plants and insects is superb and unique. However, many of the blossoms are so different from each other that it is appropriate to introduce new genus and species names. If further findings can connect the leaves

Flossia uralensis

Designed holotype CHEK 239, Chekarda

1. Whole flower structure evidencing the seven stamina and the base; 2. Detail of the androecium with stamina and anthers; 3. Magnification of the anther and a burst pollen sac; 4. Other two stamen from the same flower; Coll. Wachtler, Dolomythos, Innichen, Italy.

with the blooms or fruits without doubt, then some of the terms could be cancelled. The introduction of new names was nevertheless reduced to a minimum and only applied when it was scientifically useful. This research gives a short overview about many isolated and often completely different "flowers" found in the Early Permian layers of the Fore-Urals and tries to devise conclusions about the further evolution of the angiosperms.

Genus *Flossia* nov. gen. WACHTLER 2020

Etymology

It is an adaptation from the Latin name "flos", meaning "flower".

Diagnosis

The flower structure consists of long and slender filaments and slightly larger and elongated pollen organs attached to the apex.

Flossia uralensis nov. gen. n. sp. WACHTLER 2020

Type horizon and age

Early Permian, Kungurian, Koshelevka Formation (Irenian substage, uppermost Lower Permian, 275 Mya).

Holotype

CHEK 239, Chekarda, (Coll. Wachtler, Dolomythos-Museum, Innichen, Italy)

Etymology

It is from the Russian-Ural region, where the holotype was found

Diagnosis

It has a compound of stamina with several filaments and anthers grouped into a flower-structure

Description

Flower: Holotype CHEK 239 is 20 mm long and 7 mm wide at the base. The filaments from 10 to 12 mm long, the anther is about 1.5 mm long and 0.2 mm wide and the pol-

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

len-sacs are basifixed. Altogether, seven stamina can be encountered. The basal part probably represents the ovary, but no further details are identifiable.

Discussion

The 20 mm long part of a blossom is one of the most interesting discoveries from the Early Permian localities of the Fore-Urals. *Flossia uralensis* forms a part of several other flowers-like structures, where every single fossilised specimen depicts different, albeit important, details of angiospermy. CHEK 239 shows an inimitable conservation of a long and slender filament on top of which arises the anther with the both immature and mature pollen sacs.
If this specimen could be recovered from an Eocene deposit or compared to today's angiosperms, everybody would recognise the prototype of a perfect flower. Although, today stamens have a remarkable variety, many from the family of Rosaceae (cherries, plums, apricots) and Ranunculaceae, like the Christmas rose (*Helleborus*), depict the same characteristics as *Flossia.*
Effectively, stamen like CHEK 239 from Chekarda, as well as MAT 31 (*Pasternakia permensis)* from the Matvèevo locality were unknown till date as part of Permian sediments and Triassic deposits. One reason behind missing such angiospermous flowers is the not-so-perfect-sedimentation condition of other localities, while the other could be attributed to a totally different way of evolution and vegetation and ecosystem of the Permo-Triassic Euramerican plant kingdom.

Flossia uralensis

Reconstruction

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

It was from the Carboniferous over the Permian and the Triassic dominated by many gymnosperm-families like conifers, cycads or gingkos and between the Devonian, but especially on the Carboniferous-Permian border they split into several subgroups like the ancestors of Abietaceae, Pinoidea, Araucariaceae, or within the cycads in the Cycas and the Zamia-family. All of them were dioecious, with pollen- and seed-organs on different plants and formed different cones.
The only clearly heterosporous plants in the Euramerican Permo-Triassic fossil record were the lycopods, and among them, especially the Sigillariaceae. Early Triassic *Sigillcampeia* (Wachtler, 2016) carried out hermaphrodite fructifications with two kinds of sporophylls: macrosporophylls, bearing one huge sporangia (almost like a seed), and microsporangia. From the Devonian till the Permian in the isolated Angara Land – now forming Siberia – and the destruction on the Permo-Triassic border caused by the biggest catastrophic event in known Earth-history, originated a strange evolution-symbiosis. Insects and flowering plants with mostly heterosporous androecium and gynoecium gave birth to the evolution of the first angiosperms.
It is obvious that *Flossia uralensis* represents only the part of a flower with the petals lost. However, even this incompleteness was good for science, as it was possible to have a rare look inside the flower and their sexual organs. In all other cases, it has passed only as an aggregation of several petals, with no further possibility to obtain more detailed information.

Genus *Tsvetokia* nov. gen. WACHTLER 2020

Etymology

It is an adaptation from the Russian name "цветóк" for "flower".

Diagnosis

The flower has petals, sepals, stamen and one projecting pistil.

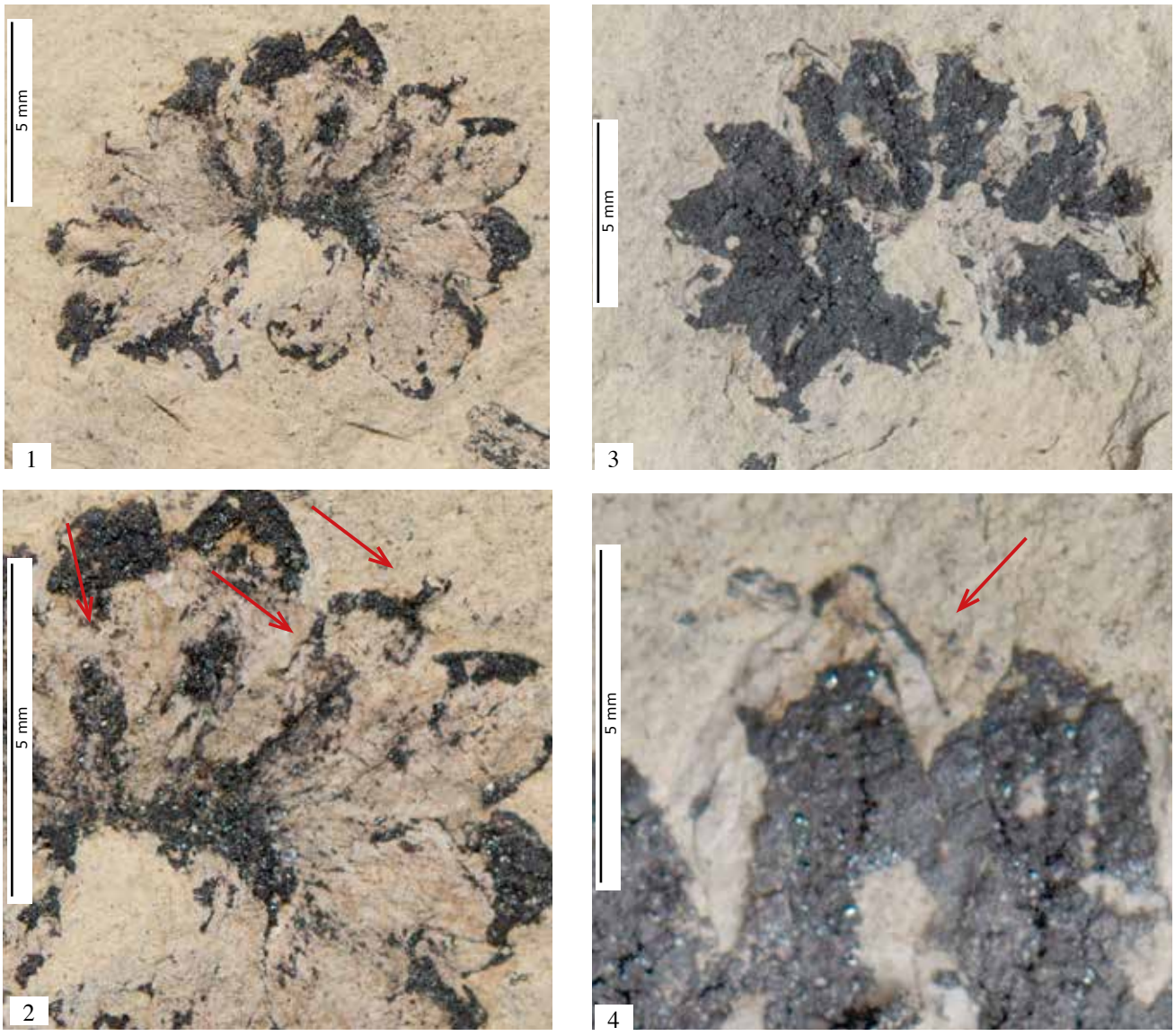
Tsvetokia nicolaswachtleri nov. gen. n. sp. WACHTLER 2020

Type horizon and age

Early Lower Permian, Kungurian, Filippovian substage, Lekskaya-Formation.

Holotype

MAT 509, Matvèevo, (Coll. Wachtler, Dolomythos-Museum, Innichen, Italy)



***Tsvetokia nicolaswachtleri* nov. gen. n. sp. WACHTLER 2020**

1. and 2. Flower evidencing the filaments with pollen anthers and the pistil (designed holotype MAT 509); 3. and 4. Counter-plate with the exposed pistil on the upper side. Flower dimensions 12 x 10 mm, Matvèevo, Coll. Wachtler, Dolomythos, Innichen, Italy.

Etymology

It honours Nicolas Wachtler, who found the holotype and other plants

Diagnosis

The flowers have distinct sepals and petals in addition to several stamina and one single long style with a dish-shaped stigma.

Description

Flower: All blossoms are characterised by one single carpel, with a narrow the petals projecting tubular style. The circular bilobed stigmatic surface expands slightly in a fan-like manner beyond the elongated and cylindrical style. The pistil morphology can be studied well not only in holotype MAT 509 but also in specimen MAT 536 and MAT 709. The style is about 2 mm long. The flowers are approximately 10–12 mm in diameter

***Tsvetokia nicolaswachtleri* - Reconstruction**

and are composed of a number of petals and sepals. MAT 347 and MAT 207, having the same diameter, are good examples of the underside of this flower, with part of the stalk attached.

Genus *Pasternakia* nov. gen. WACHTLER 2020

Etymology

It honours the famous Russian poet and writer, Boris Pasternak, who, in the city of Perm, wrote several poems. Perm was also the base for his main work "Doctor Zhivago".

Diagnosis

The flower has petals, sepals, short stamina and a rounded ovary

Pasternakia permensis nov. gen. n. sp. WACHTLER 2020

Type horizon and age

Early Lower Permian, Kungurian, Filippovian substage, Lekskaya-Formation.

Holotype

MAT 31, Matvèevo, (Coll. Wachtler, Dolomythos-Museum, Innichen, Italy)

Etymology

It is from the easternmost megacity of Europe, Perm. It is also known as the name-giver for the geological period Permian, during which most of the Ural Mountain Range was formed.

Diagnosis

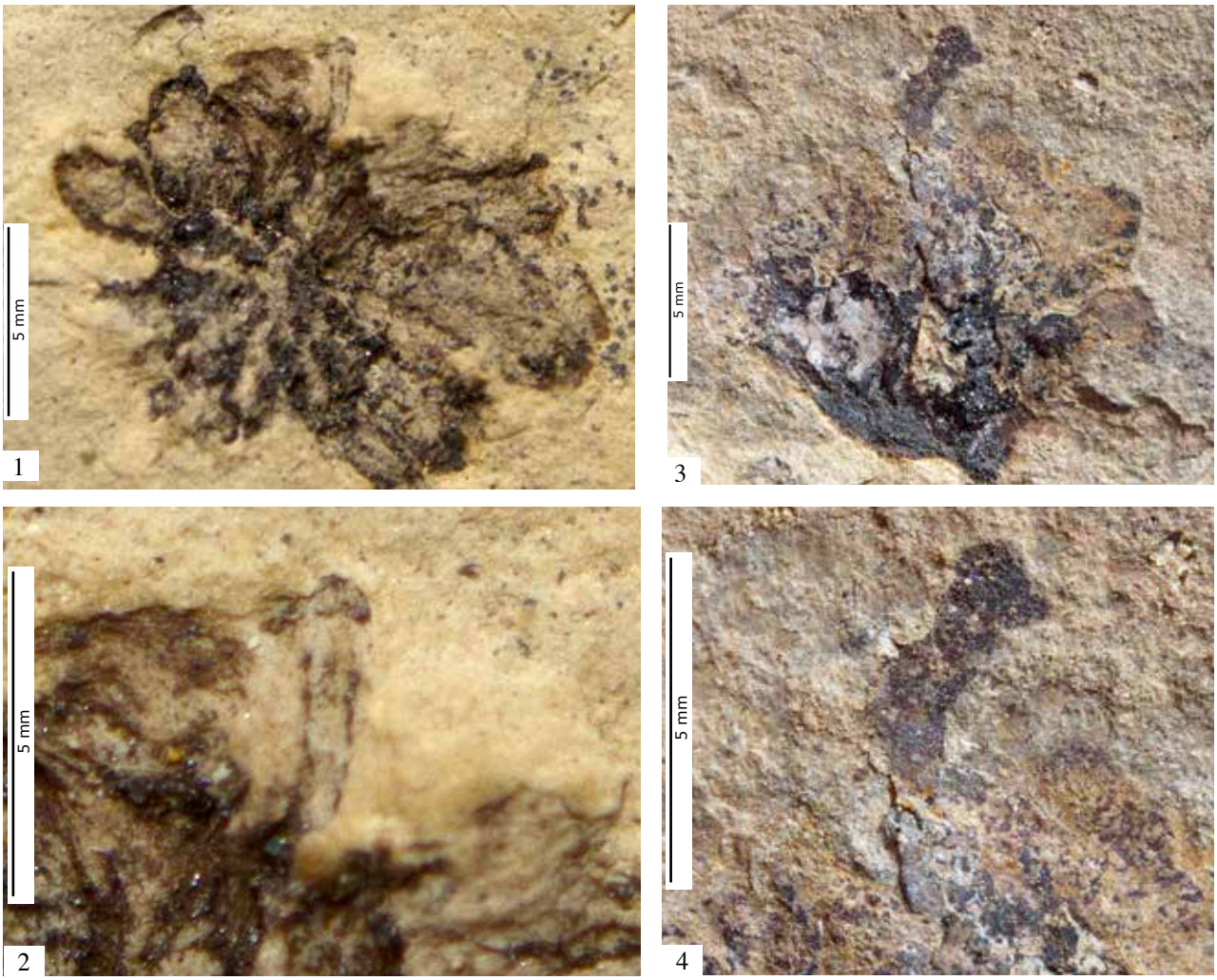
The small-sized flower has anthers on a short filament and an elongated or rounded pistil.

Description

Flower: The holotype MAT 31 is eight mm long (including the ovary and the petals), of which half is the ovary and the remaining comprises seven tapered sepals. Also, one sepal, rounded on the apex, can be observed. Several perfect stamina with one mm long slender filaments and divided anthers are visible and some are hidden by the covering sediment. The pistil is better preserved on the counter-plate and is two mm long and oval. Impressions of two seeds are pressed in the ovary.

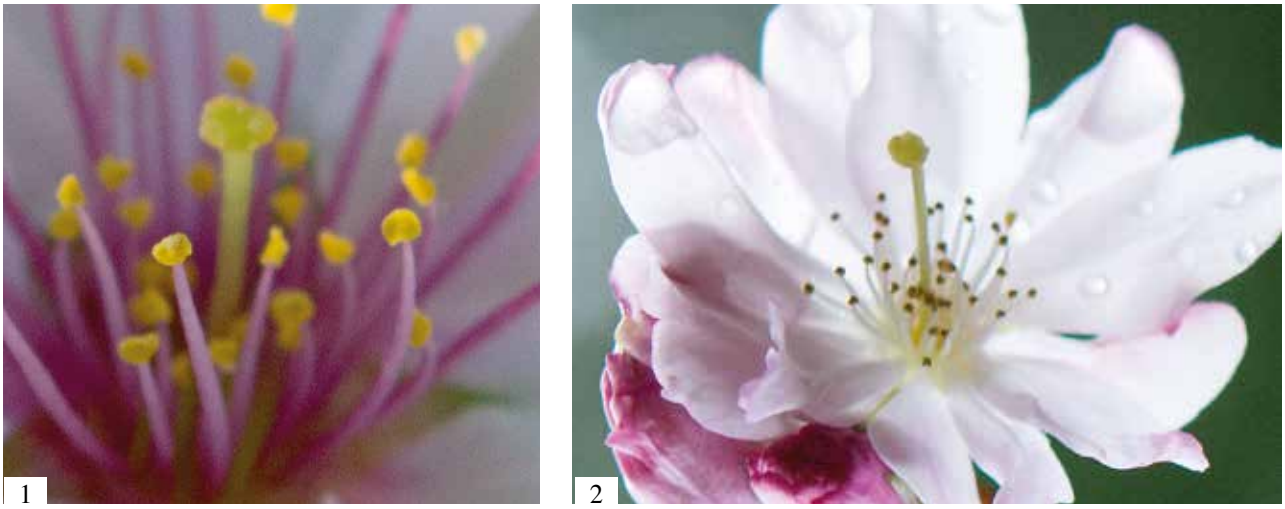
Discussion

Within the three described flower genera, *Tsvetokia nicolaswachtleri, Flossia uralensis* and *Pasternakia permensis* consist many differences to justify different classifications. Naturally, they must also belong to different Proto-angiospermous genera. The stamina of *Flossia uralensis* (CHEK 239) are much longer, especially their filaments, whereas those of *Pasternakia permensis* (MAT 31)

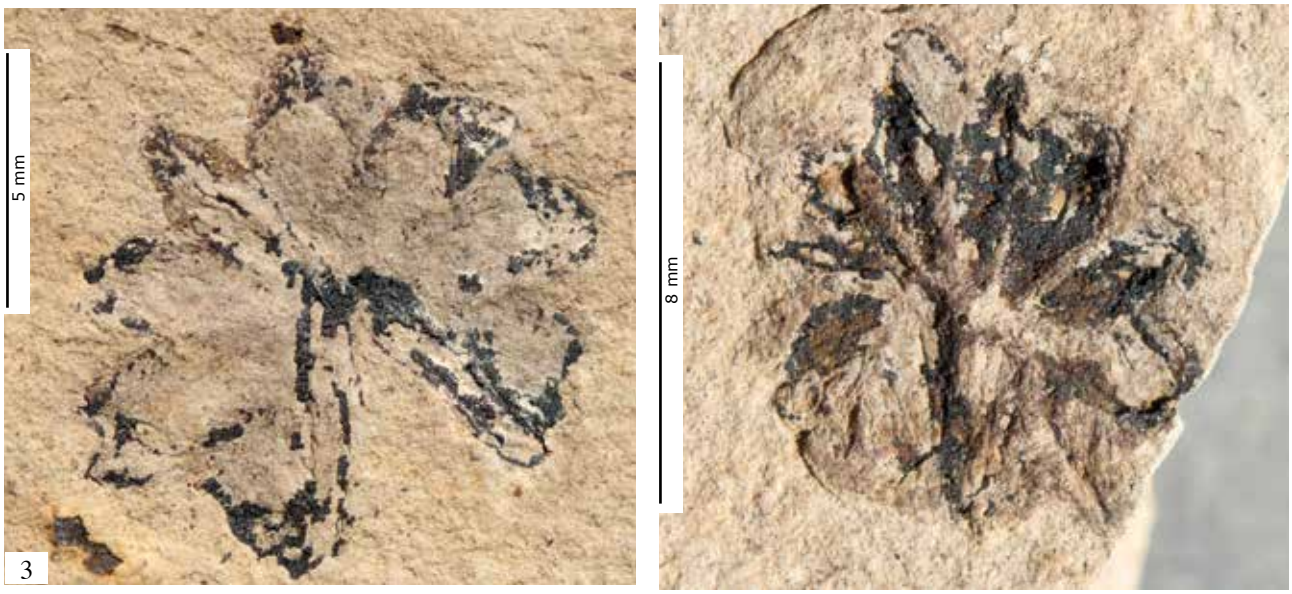


***Tsvetokia nicolaswachtleri* nov. gen. n. sp. WACHTLER 2020. Flowers showing pistil and stamina**

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



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



***Tsvetokia nicolaswachtleri* nov. gen. n. sp. WACHTLER 2020 - Flower's reverse side**

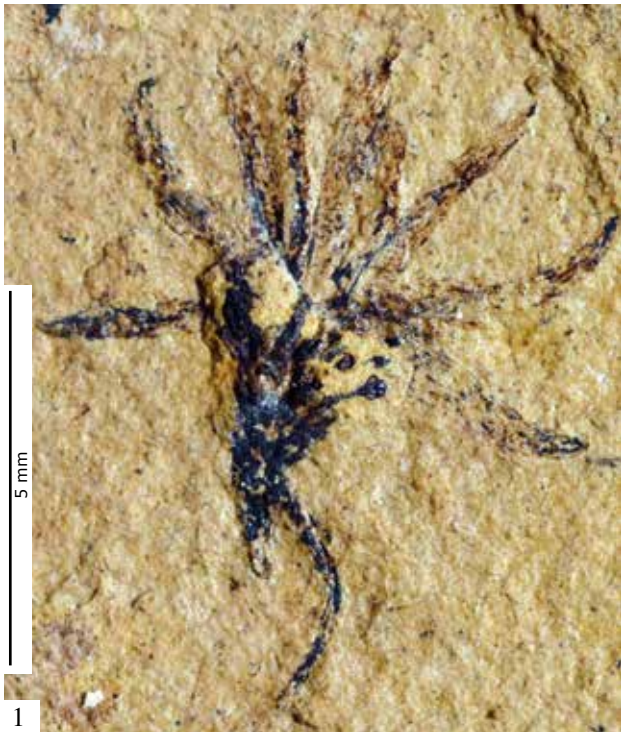
1. Sepals and petals with stalk (MAT 207); 2. Flower reverse side with part of the stalk, sepals and petals (MAT 352), Coll. Wachtler, Dolomythos-Museum, all Matvèevo.

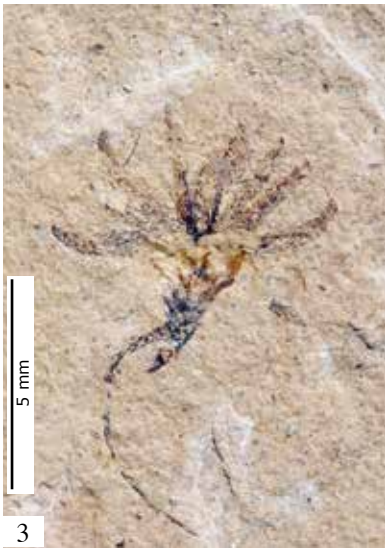
manifest a more stocky and fissured appearance. The rounded gynoecium of *Pasternakia permensis* is different from the ovary of T*svetokia nicolaswachtleri* (MAT 509, MAT 536, MAT 709), having a long style and a dish-shaped stigma, although it can be supposed that both were equipped by a single carpel only. *Flossia uralensis* stands a little apart from the other flowers for having long anthers but lost petals. It is not out of the question that *Tsvetokia nicolaswachtleri* flowers belong to five-petaled flowers such as *Claireia pentafolium* or *Kunguria perneri* or six-petaled plants such as *Sextupetalum ottiliethomsonae* or *Sextupetalum smirnovi.* Due to the complex assemblage of the angiosperm-blossoms consisting of petals, sepals, pistils and stamina that lay over one another in fossilised specimen, no complete insight could be gained. Probably, the four-petaled flower *Permotheca colovratica* is small-sized, whereas *Multifolium (Peltaspermum) petaloides* as well *Asterodiscus disparis* belonged to multiple-petaled flower genera and can therefore be discharged.

During Early Permian, *Tsvetokia nicolaswachtleri, Flossia uralensis* and *Pasternakia permensis* had just developed many novel features of today's angiosperms and the question that follows is: What evolution process occurred in the next 300 million years? That only a few places worldwide have the ideal fine-grained sedimentation conditions is one option. In the Fore Urals, only in a few layers of the Matvèevo and Chekarda quarries did we come across circumstances where even wings of insects or the most subtle parts of plants were conserved.

All over the world, the possibilities of an excellent preservation are recorded only from a few localities such as the Early Cretaceous Crato-Formation in Brazil, with their richness in insects and flowering plants, or some places in West-Northern United States such as Eocene locality Republic or Bridge Creek. Otherwise, many other Permo-Triassic-Jurassic places with good sedimentation conditions have given no angiospermous plants till now.

Pasternakia permensis Reconstruction





***Pasternakia permensis* nov. gen. n. sp.**

Designed holotype MAT 31, from Matvèevo

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

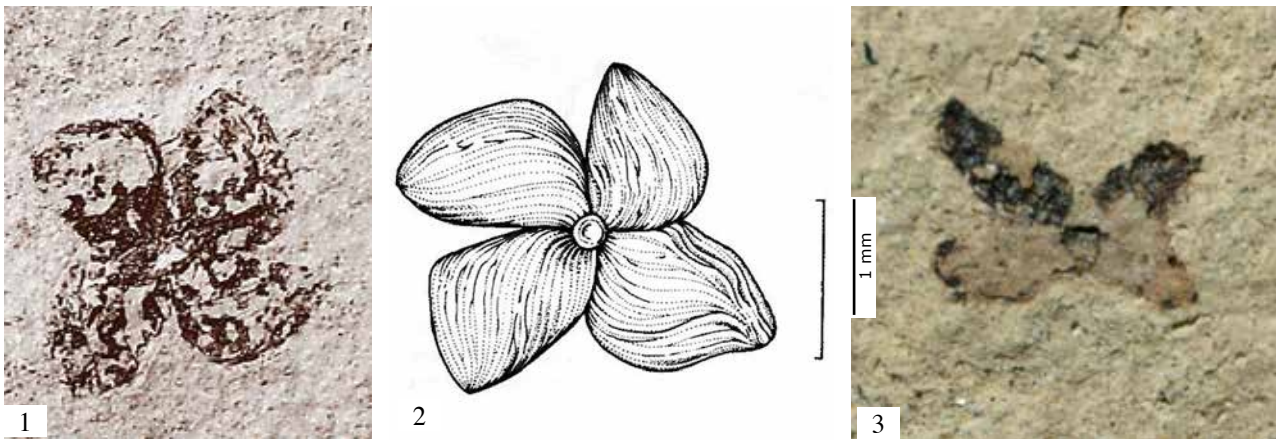
1. Flowers of *Prunus spinosa*, the blackthorn or sloe; 2. Open ovary showing the seeds of *Helleborus niger*

Permotheca colovratica ZALESSKY 1929, NAUGOLNYKH 2013

An interesting flower fossil from the Permian Fore-Urals consists of four petals arranged as a rosette. It was classified as *Permotheca (sardykensis)* by Zalessky (1929) on material from the Upper Kazanian in Kullarovo (Tatarstan, Sardyk River). After that, Naugolnykh (2017, 2013) revised the genus and described another species from Early Permian (Kungurian) deposits in Chekarda as *Permotheca colovratica*. He described it as male reproductive "organ of gymnosperms consisting of four sporangia connected at their bases", with adaptation for dispersal by wind (anemochoria). Additionally, pollen grains have been extracted from this inflorescence.

The ovary-like organ in the middle of the four "petals" can also be interpreted as pistil. To summarise, it can be stated that *Permotheca colovratica,* especially the one found in Chekarda (only 1–2 mm in diameter), is characterised by four-petaloid leaves with the innermost part depicting a circular organ that can be regarded as stigma. Also, today, some plants like *Daphne* or *Cornus* and the dogwood have the same features.

Some flowers are characterised by four petals: 1. *Daphne odora,* native to China and inserted in the family of the Thymelaeaceae; 2. *Brassica napus*, the rapeseed; 3. *Cornus macrophylla,* the large-leafed dogwood, pollinated by a beetle.



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

Genus *Kunguria* nov. gen. WACHTLER 2020

Etymology

It refers to the city of Kungur, which is located near the main Permian fossil sites.

Kunguria perneri nov. gen. n. sp. WACHTLER 2020

Type horizon and age

Early Lower Permian, Kungurian, Filippovian substage, Lekskaya-Formation.

Holotype

MAT 610, Matvèevo, (Coll. Michael Wachtler, Dolomythos Museum)

Etymology

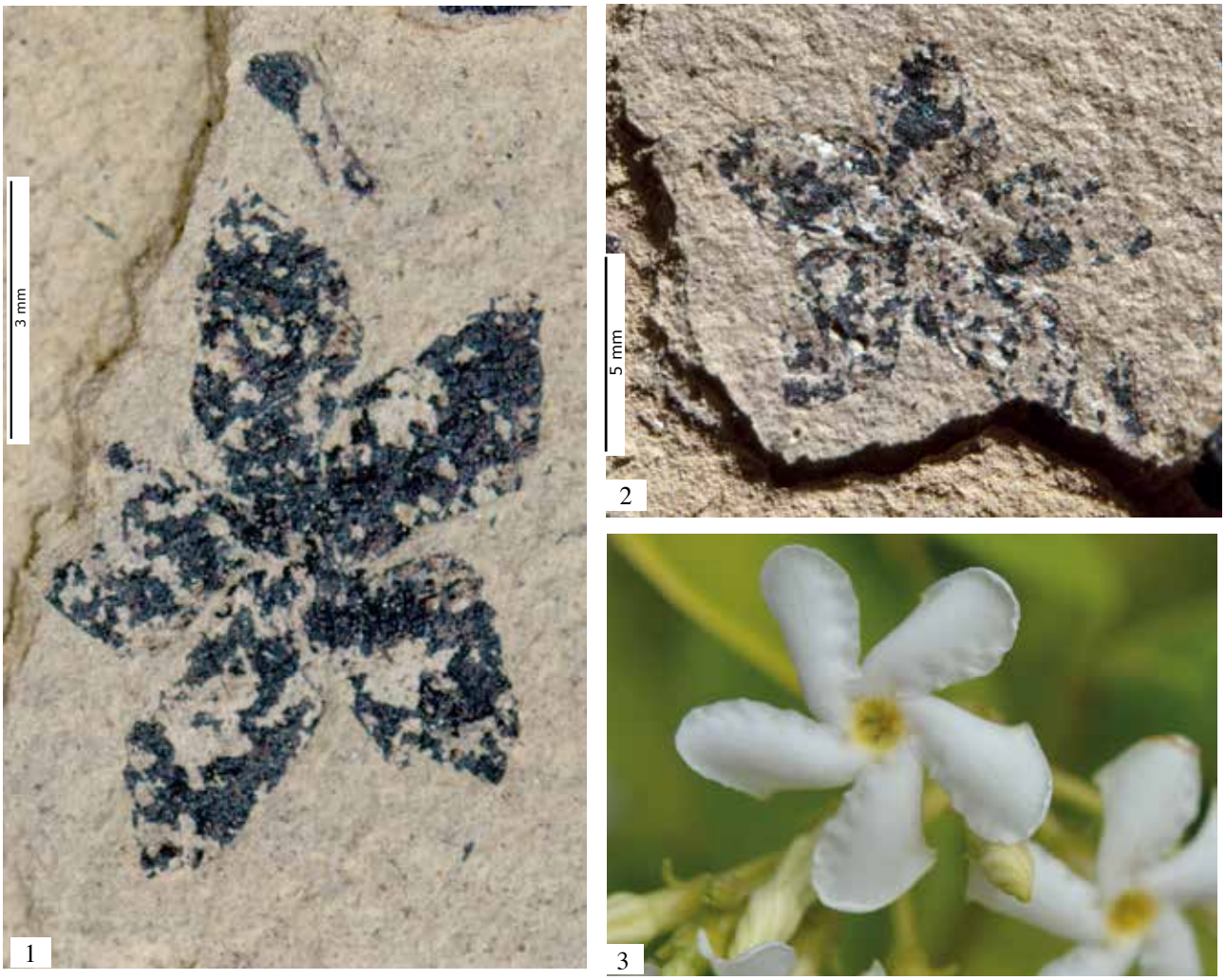
It honours the German researcher, Thomas Perner, for his works in palaeobotany.

Diagnosis

The flower has five slightly pointed petals and sexual organs in the centre.

Description

Flower: Holotype MAT 610 from Matvèevo represents a perfect blossom with five pet-

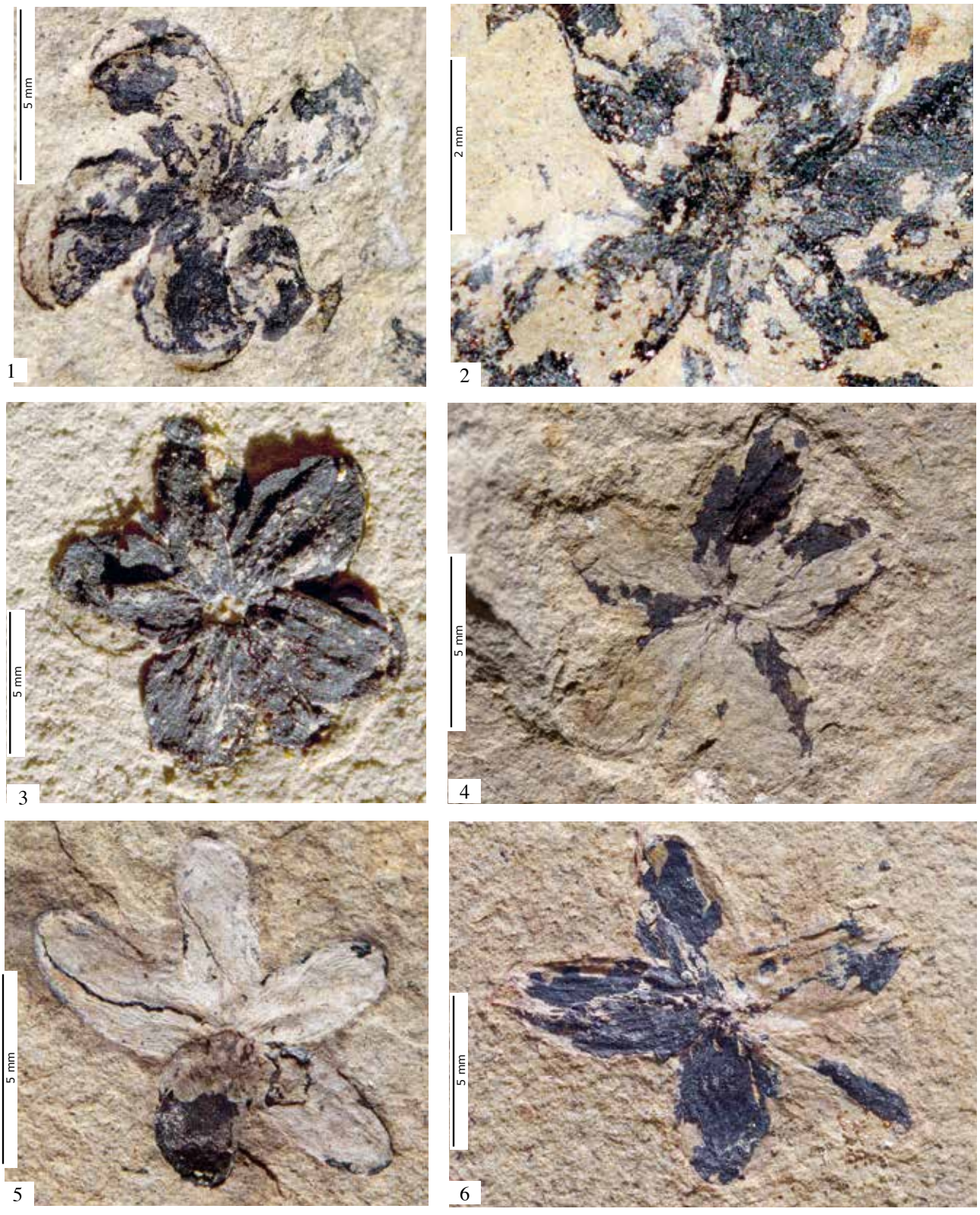


***Kunguria perneri* nov. gen. n. sp. WACHTLER 2020, five-petaled flowers**

1. Five-petaled flower (Designed holotype MAT 610, Coll. Wachtler); 2. Other five-petaled flower (MAT 744, Coll. Perner); all Matvèevo, Early Permian, Dolomythos, Innichen, Italy; 3. *Trachelospermum jasminoides*, known as jasmine (Apocynaceae). The flowers have a tube-like corolla opening out into five petal-like lobes.

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

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



***Claireia pentafolium* nov. gen. n. sp. WACHTLER 2020, five-petaled flowers**

1. and 2. Flower with five petals and detail of the stamina in the centre (Designed holotype MAT 442, Coll. Gerasch, Thomaseum, Langenaltheim); 3. Flower evidencing the stigma of the carpel (Paratype CHEK 321, Coll. Perner, Dolomythos, Innichen), 4. and 6. Flowers with five petals (MAT 210, MAT 348, MAT 201), MAT=Matvèevo, CHEK=Chekarda, Coll. Wachtler, Dolomythos, Innichen, Italy.

als. It is altogether eight mm in diameter. The single petaloid leaves are elongated, largest in the middle and tapered on the apex. Each petal is not longer than three mm.

Genus *Claireia* nov. gen. WACHTLER 2020

Etymology

It is in remembrance of the Russian geologist and palaeontologist, Modeste Onésimowitsch Claire, (1879–1966), (Модест Онисимович Клер), who lived and worked in Ekaterinenburg. He was imprisoned and after his death rehabilitated. He authored or co-authored more than 60 publications and directed the historical geology and palaeontology section of the Ural Society.

Claireia pentafolium nov. gen. n. sp. WACHTLER 2020

Holotype

MAT 442, Matvèevo, (Coll. Gerasch, Thomaseum, Langenaltheim, Germany)

Paratype

CHEK 321, Chekarda, Coll. Perner, Dolomythos-Museum, Innichen, Italy)

Etymology

It is Latin for five, indicating the five petals of each flower.

Diagnosis

The flower has five petals and short pistils, with one central gynoecium.

Description

Flower: All blossoms are characterised by five petalous fruit-leaves forming a radially symmetrical corolla. The petals are elongated, with the smallest part fused basally and rounded apically, forming a cup-like structure. Each flower is about 10 mm in diameter. A good example is holotype MAT 442, where several stamens in the innermost part are visible. A short filament apically holds the anther. Paratype CHEK 321 also shows five petals, and the carpel is visible in the middle. Other five-petaled specimens are CHECK 197 (it is suggested that some sepals are also visible), MAT 348 and MAT 201.

Discussion

Five-petaled "flowers" are relatively common in Early Permian stratas from the Fore-Urals. Some of them suggest having stamina (MAT 442 and MAT 201) or carpels (CHEK 321). Due to different petal leaves (rounded in *Claireia pentafolium* and tapered in *Kunguria perneri)*, it is obvious that they must belong to different genera.

Genus *Sextupetalum* nov. gen. WACHTLER 2020

Etymology

It refers to the six petals that characterizes every blossom.

Diagnosis

The flower has six petals and tubiform till the discoidal stigma in the middle, surrounded by stamen.

Sextupetalum ottiliethomsonae nov. gen. n. sp. WACHTLER 2020

Diagnosis

It is a five-petaled flower with rounded petals and sexual organs in the middle.

Holotype

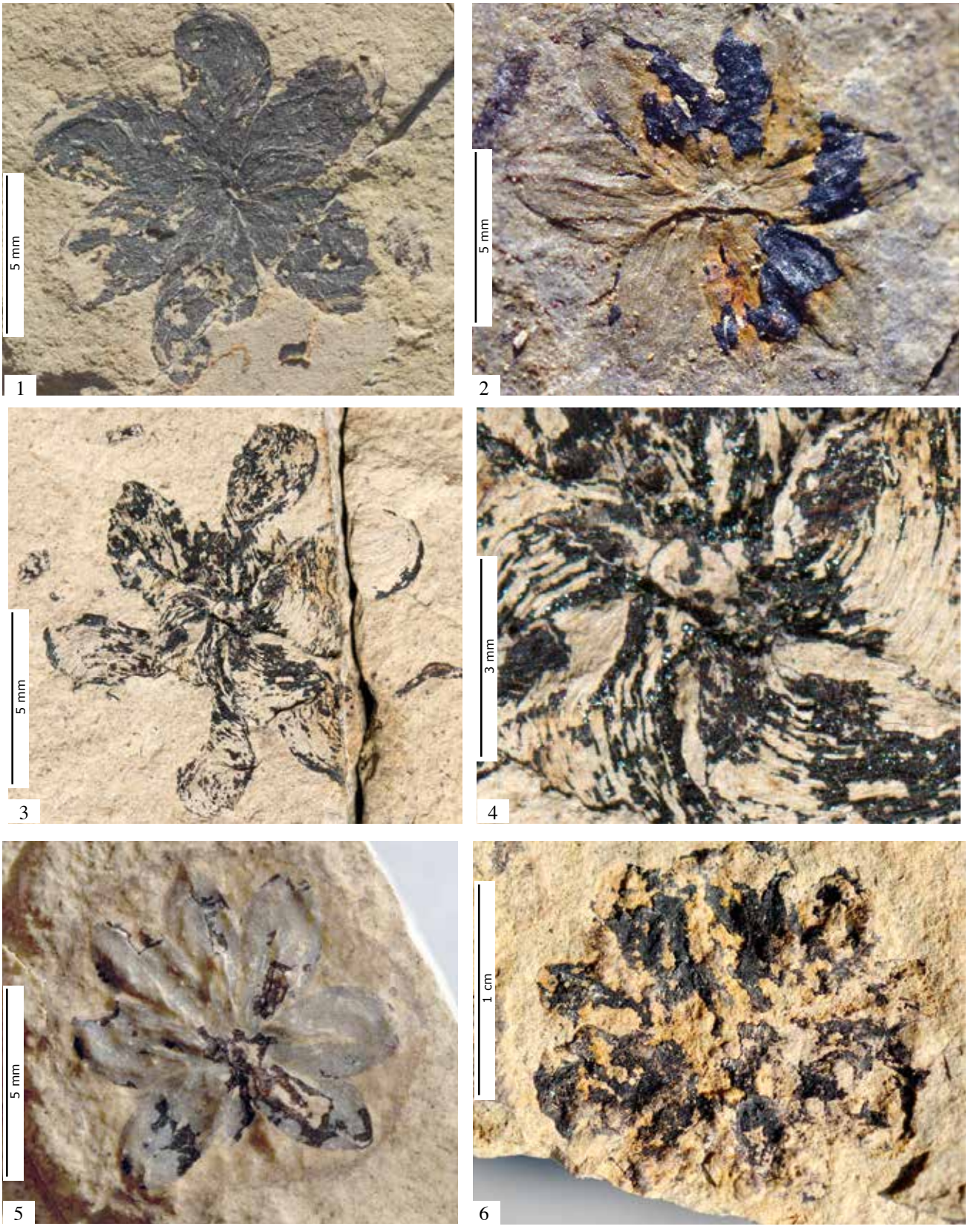
MAT 200, Matvèevo, Paratype MAT 510; (Coll. Michael Wachtler, Dolomythos Museum)

Etymology

It honours Ottilie Nackers-Thomson, the daughter of David Thomson, who dedicated part of life to collecting fossils and sustained palaeontology generously.

Description

Flower: Several flowers from the Fore-Ural area are equipped with six petals. The single



***Sextupetalum ottiliethomsonae* nov. gen. n. sp. WACHTLER 2020, six-petaled flowers**

1. Six-petaled flower (Designed holotype MAT 200); 2. Additional six-petaled flower (MAT 164); 3. and 4. Excellent preserved detail of the stigma of the carpel in the middle (Paratype MAT 510); 5. Six-petaled flower with one sepal (MAT 632); 6. Six-petaled flower with impressions of stamina and pollen (MAT 205). All Matvèevo, Early Permian Coll. Wachtler, Dolomythos, Innichen, Italy.

blossoms are about 10 mm in diameter and the petals are drop-shaped (Holotype MAT 200). The corolla evidence in the innermost part of Paratype MAT 510 a tubiform stigma. The capitate distal stigma is elongated and gives way to a short style. This part of the flower can also be regarded as gynoecium. Other specimens are MAT 164 and especially MAT 204 that is encrusted by pollen dust.

Sextupetalum smirnovi n. sp. WACHTLER 2020

Diagnosis

The flower has six elongated and mostly tapered petals.

Etymology

It honours Sergey Smirnov, head of Department of plant taxonomy, Altai State University – Botanical Garden, Barnaul, Russia.

Holotype

MAT 349, Matvèevo; (Coll. Michael Wachtler, Dolomythos Museum)

Description

Flower: These six-petaled inflorescences are only about six mm in diameter and manifest star-shaped petals. Holotype MAT

***Sextupetalum smirnovi* n. sp. WACHTLER 2019, six-petaled pointed flowers**

1. Six-petaled flower (designed holotype MAT 349, 6 mm diameter); 2. Flower evidencing the anthers and the short filaments in the middle (MAT 634, Coll. Perner), all Matvèevo; 3. CHEK 71 Chekarda; Coll. Dolomythos Museum. 4. *Clematis vitalba,* within the buttercup family; the Ranunculaceae is a compact deciduous climber and characterized by its six petals.

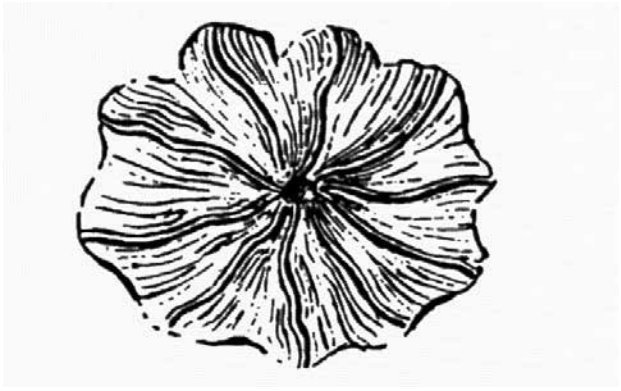
349, as well 634 have the same blueprint: in the innermost part originate subtle filaments and anthers; in CHEK 71, the pistil is visible too.

Discussion

Today we have plants that generate six-petaled flowers, such as *Clematis vitalba* within the buttercup family, Ranunculaceae or *Gardenia jasminoides* and *Sisyrinchium bellum*, the western blue-eyed grass. Interestingly, six-petaled "flowers" were relatively common in Early Permian stratas from the Fore-Urals and therefore, it could not be regarded as one that underwent a long evolution process from maybe many petals to six or a few petals forming a corolla of six. Early Permian five-petaled flowers like *Claireia pentafolium* or *Kunguria perneri* and six-petaled flowers like *Sextupetalum ottiliethomsonae* or *Sextupetalum smirnovi* differ in the number of petals. Pistil and stamen are mainly the same. Especially, the small-sized *Sextupetalum smirnovi* is quite uniform, but it is difficult to establish which Permian plant species it belongs to. All they had just completed their evolution-step in Early Permian. Why no modification occurred in millions of years remains an unresolved mystery.

Aspidion decemnervium, ZALESSKY 1937

Some of the blooms in the Early Permian Fore-Urals hold a calyx with their petals united. They were first described in 1937 by M. D. Zalessky as *Aspidion decemnervium.* They were found in Kroutaia Katouch-



Aspidion decemnervium from Matvèevo after a drawing by M. D. Zalessky, 1937.

1. Aspidion decemnervium, sympetalous flowers (MAT 704, Coll. Gerasch, Thomaseum, Langenaltheim); 2. Under magnification, the united petals as well the ovary and the filaments of the anthers are visible; 3. Other sympetalous flower with small-sized stamina and pistils visible (MAT 752) Matvèevo.

***Aspidion campanuliformis* n. sp. WACHTLER 2020**

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

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

ka near Matvèevo. Because the holotype is lost, comparisons are difficult, but specimen MAT 704 and MAT 752, both from Matvèevo, have many similarities with the Zalessky-drawing. Both show the inner parts of the flower suggesting stamina and pistils. Aspidion is another good example that supports the theory that the process of assembling of the petals occurred just early.

Aspidion campanuliformis n. sp. WACHTLER 2020

Etymology

It is in remembrance of the bell-shaped form of extant Campanulatae.

Holotype

MAT 342 Matvèevo (Coll. Michael Wachtler, Dolomythos Museum)

Diagnosis

It has a tube-shaped corolla with a hole in the middle

Description

Flower: The campanulate bloom is about 12 mm long and 14 mm wide. The flower is shaped like a funnel or cone. An inside view to identify its inner sexual organs is not possible.

Discussion

Today, sympetalous flowers occur in orders like the Convolvulales, Diapensiales, Ericales, Primulales, Plumbaginales, Ebenales, Contortae, Tubiflorae, Plantaginales, Rubiales, Cucurbitales and the Campanulatae. In these families, the flowers have a separate calyx and corolla, with the petals fused sometimes only at the base of the corolla, but often they are united till the apex. They are trumpet-shaped to broadly funnelform or nearly bell-shaped. In the Early Permian Fore-Urals, we can find at least two different types of sympetalous flower: *Aspidion decemnervium* has a flat, wheel-shaped corolla and a small tube in the middle; *Aspidion campanuliformis* is characterised by its tube-shaped corolla forming a cone in the middle.

Fig. 45. *Asterodiscus disparis* Zal. Rive gauche de la rivière Sylva, ravin Kazarinovsky. Étage Bardien. ×2

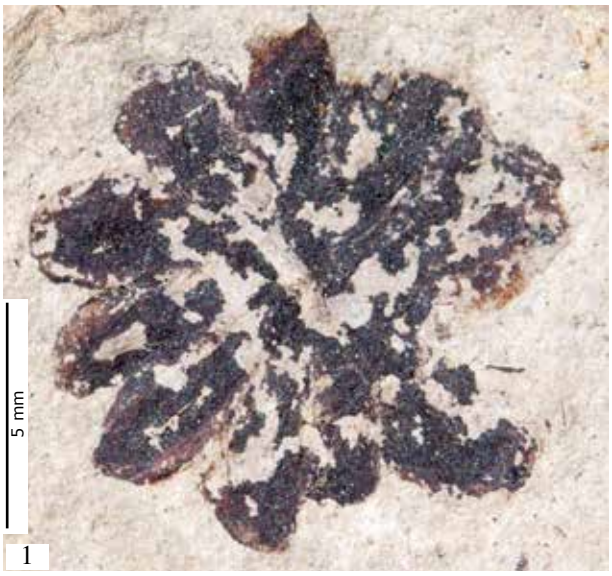
Asterodiscus disparis. Drawing by M. D. Zalessky (1937, p. 80). It represents a multi-petaled flower.

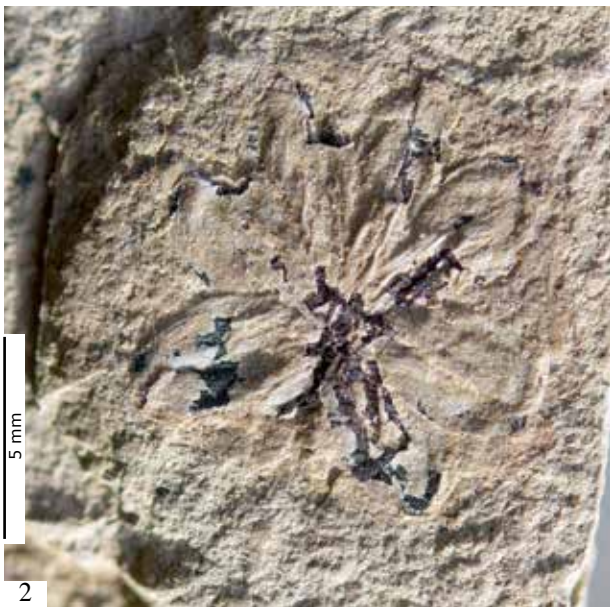
Asterodiscus disparis ZALESSKY 1937

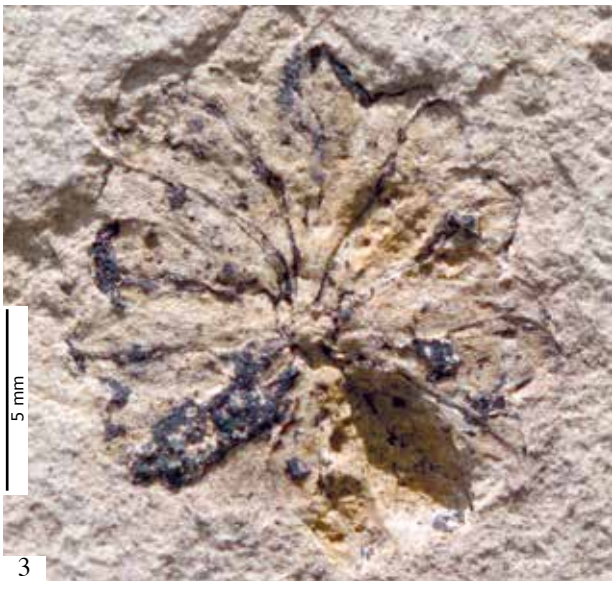
A flower-like structure from the Sylva River described (page 78) and drawn (page 80) by M. D. Zalessky in 1937 represents *Asterodiscus disparis*. According the drawing, it is characterised by nine petals. Naugolnykh (2007) and Zavialova & Karasev (2015) revised the genus and regarded *Asterodiscus* only as a younger synonym of *Permotheca* based on the similarity between the general morphology of the two. But due to the fact that the genus *Permotheca* is occupied only by four-petaled flowers, it is vital to maintain the original name *Asterodiscus disparis* for small multi-petaled flowers.

It is true that in Matvèevo especially, *Asterodiscus disparis* is frequently found, but mostly it can be regarded only as morphogenus. Five-petaled flowers are described as *Claireia pentafolium* or *Kunguria perneri* and six-petaled blossoms as *Sextupetalum ottiliethomsonae* or *Sextupetalum smirnovi,* but this is valid only under best circumstances when the petals are fossilised from the upper side. On the reverse side, in addition to the petals, the sepals must also be visible and be part of the stalk. In this case, sometimes a more petaled blossom will be feigned. Some difficulties arose also with *Tsvetokia nicolaswachtleri* having clearly visible pistils and stamina.

At present, it can only be said that multi-petaled flowers were present not only in the







***Asterodiscus disparis*, Zalessky (1937) flowers**

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

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

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

Genus *Multifolium* nov. gen. WACHTLER 2020

Etymology

It refers to the multi-petaled flower-leaves of their inflorescences.

Diagnosis

The circular flowers have many petaoloid leaves aggregated together.

Multifolium petaloides comb. nov. WACHTLER 2020

Basionym: *Peltaspermum petaloides* Naugolnykh, 2016 (p 85-87)

Naugolnykh (2016) described a petaloid fructification with the name *Peltaspermum petaloides.* Because umbrella-shaped *Peltaspermum* fructifications are typical fruit-organs of many Euro-American Permo-Triassic flora components, it is not useful to apply this term for Angara plants, too; the difference in their features is quite evident. In European Peltaspermales, the seeds are attached to the lower surface of cupulate heads. The single segments are divided into distinctive ribs and between them, the seeds are incorporated.
In Angaran *Multifolium petaloides*, an undefined number of sterile petals surround the fertile parts composed of monoecious male and female organs. They represent a flower and not a fully-grown fruit as in the Peltaspermales. Therefore, it is more appropriate to use the new genus term *Multifolium.*

Genus *Nanoflos* nov. gen. WACHTLER 2020

Etymology

It comes from the Latin name "flos" meaning "flower" and "nano" for dwarfish.

Diagnosis

The short pedicellate flowers have compound panicles.

Nanoflos maueri nov. gen. n. sp. WACHTLER 2020

Holotype

MAT 366, Matvèevo (Coll. Wachtler, Dolomythos Museum, Italy).

Etymology

It honours the local naturalist, Genrich Timofewitsch Mauer (1881–1940), who moved in his free time by boat on the Sylva and Barda River, discovering the world fossil sites – Chekarda and Matvéevo.

Multifolium petaloides, multiple-petaled flowers

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

Diagnosis

The inflorescences bear pedicellate small-sized flowers on short axes, forming racemes or panicles.

Description

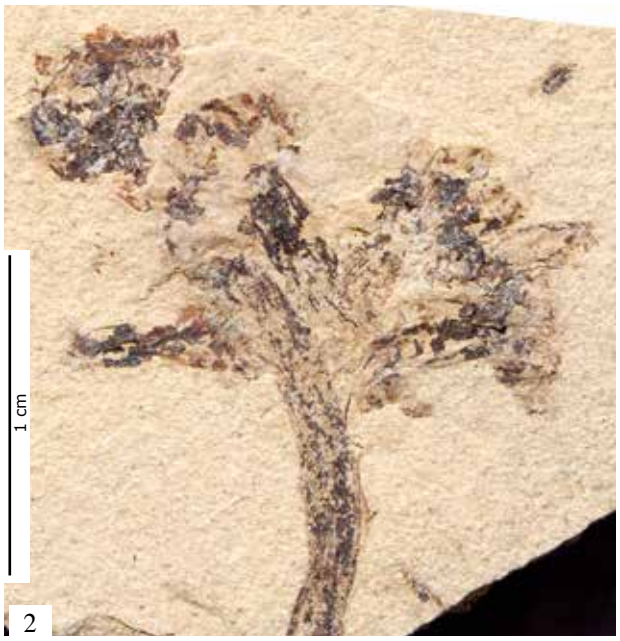
Flower: Holotype MAT 366 has about 20 mm long panicle formed by several (prospectively four) small flower buds. The same is valid for CHEK 73 and MAT 326, representing racemes with lateral branches that end in flower buds.

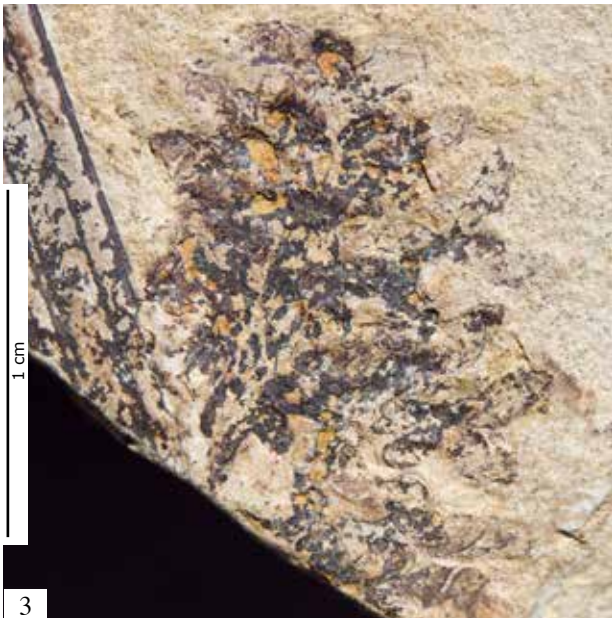
Discussion

Several racemes or panicles holding more flowers were collected. Probably they belong to different plant genera, but till further discoveries expand our knowledge, they have altogether been clubbed as *Nanoflos maueri.* Usually the blossoms of the racemes are small-sized; therefore, they also differ from other isolated four-, five-, six- or multi-petaled flowers.

Conclusion

Flowers being shed naturally, especially by wind, is not a common event, but it occurs. Therefore, finding fossilised blossoms leading to the discovery of fruits or seeds is a rare case; but as seen in here, it is possible. The next difficulty is that if the flowers get dropped into a lake where they sink down to the ground in a short time or get covered on the shore fast by finest mud. All these





***Nanoflos maueri* nov. gen. n. sp. WACHTLER 2020, flowers forming a panicle**

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

*wild cherry, f*orming a panicle of flowers.

constitute today – certainly also in the past, if we go back nearly 300 million years – a rare and fortunate circumstance. Only the rich and best-preserved Early Permian layers in the Russian Fore-Urals, especially of Matvèevo and Chekarda, allow us to have a deep insight into the evolution of plants and, more fortunately, the evolution of the first angiosperms.

The fact that all these fossilised inflorescences represent flowering plants is due to their appearance and blueprint is obvious. Many details distinguish them from the gymnosperms like conifers, ginkgos or cycads. Difficulties arose more due to the fact that

The wonderful mimicry between insects and flowering plants

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

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

many of these flower-like structures differ from each other considerably; therefore, a certain analysis is not easy. To bring order among different flowers having four or more petals in addition to rounded or elongated stigmas, short anthers with a long filament, it was necessary to name at least the most frequently observed flowers and to present their differences. It is obvious that there was no exhausting way to do so. Probably many other classifications must be introduced. It is especially a dilemma in palaeobotany that for every single part of a plant, a new name can be introduced and not as in extant floras for the whole plant.

If somebody walks through an intact springtime meadow, he would wonder about the diversity of the flora, especially the blooming flowers. The same is to the case in Early Permian Fore-Urals, before probably the Permo-Triassic cataclysm destroyed a big part of the ecosystem and pushed the further and faster spreading of the angiosperms by a million years.

The four-petaled *Permotheca colovratica* was one of the first discovered flowers (Zalessky, 1929), and the initial reconstructions help interpret them as ones with a stigma-like organ in the middle. The Russian palaeobotanist, M. D. Zalessky, described in 1937 other flower-like structures such as *Asterodiscus disparis* or *Aspidion campanuliformis*, without going into more in detail about their classification. After that, other "fructification-names" were introduced, such as *Peltaspermum petaloides* (Naugolnykh, 2016), which feverishly tried to connect them with Euroamerican Peltaspermales or other gymnosperms. Effectively, the Permo-Triassic *Peltaspermum* disks constitute an enigmatic frutification even in Europe and America, but they have little in common with the flowers from the Angara continent. Even after intense research inside the European *Peltaspermum,* it was impossible to discover shields stamen or pistils but only seeds. Apart from that, a potential fruit does not represent an evolving bloom.

However, in the Early Permian Fore-Urals, not only can we observe sterile disks, but they also sometimes provide insight into fully formed sexual organs like ovaries or stamina. Therefore, it was useful to introduce the name *Flossia uralensis* for a unique and completely preserved flower, which had never been recorded before, having a wonderful long filament with an apical anther; they represent perfect stamina. *Tsvetokia nicolaswachtleri* was classified as a fructi-

Flowers from the Early Permian Fore Urals

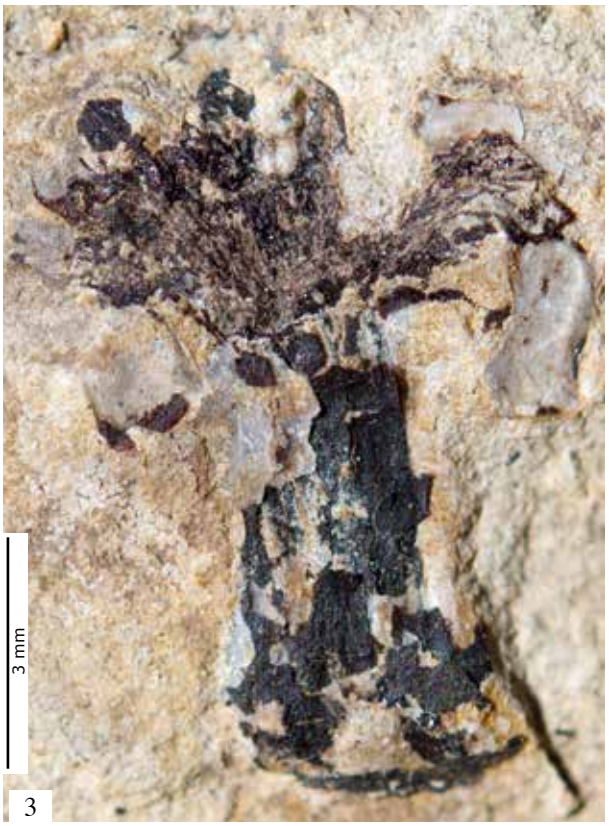
Bottom left: a sympetalous flower of *Aspidion campanuliformis;* **top left:** flower of *Tsvetokia nicolaswachtleri;* **middle:** a Rosaceae, resembling five-petaled flower of *Claireia pentafolium*; **bottom:** a six-petaled blossom of *Sextupetalum smirnovi;* **right:** *Sextupetalum ottiliethomsonae*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

fication, where a monoecious flower incorporating male and female sexual organs on the same blossom could be examined for the first time in Earth history.

In the Permian Fore-Urals, one can observe *Pasternakia permensis* with a perfect pistil including stigma and equipped with a long style like many of today's plants. Members from the group of the Rosaceae, especially the cherry family, could be compared with the flowers of *Pasternakia permensis* or *Tsvetokia nicolaswachtleri* because of their slender single style, as well as the bilobed stigma. This could help in identifying a plethora of five petaled- (*Claireia pentafolium* and *Kunguria perneri*) or six-petaled flowers (*Sextupetalum ottiliethomsonae* and *Sextupetalum smirnovi*) or sympetalous blossoms such as *Aspidion decemnervium* or *Aspidion campanuliformis*, with their tube-shaped corolla. Finally, we encounter multi-petaled flowers like *Multifolium petaloides* (Zhuzhgova et al., 2015) or others going in the direction of Asteraceae, a family of plant thought to appear late in the fossil record due to their highly evolved blossoms and panicles.

All have enough differences to categorise them as different plants with different fruits and leaves. However, what remains unclear is how many more different flowering plants we can encounter in these Early Permian sites; in a black and white world of fossilised plants, a distinction between the green petals and coloured sepals is impossible.

Some fundamental questions cannot be answered satisfactorily even today. In which way did the ovary of these plants evolve? All the angiosperm evolution theories predicted the folded leaf-structure as starting point of the gynoecium. This cannot be unquestionably deduced from the ovary wall of *Pasternakia permensis* or *Tsvetokia nicolaswachtleri.* The protection of the ovule/seed in angiosperms is composed of a micropyle located from where the pollen cell can enter the ovule. The unresolved question is that if the tissue is composed of one single macro-



Several unknown pollen organs or flowers

1. Flower with projecting pollen organs (CHEK 366, 5 mm in length); 2. Isolated stamen with shed pollen (CHEK 341); 3. Flower with stamina (MAT 351, 7 mm in length); 4. Flower with petals and inner circle filled with mud (MAT 416, 5 mm in length; Matvèevo and Chekarda, Coll. Wachtler, Dolomythos Museum)

leaf or its origin lies in the amalgamation of many micro-leaves forming a wallet.
A seed coat with a micropyle can also be seen in fossil gymnosperms and in some Sigillariaceae. The Permian-Triassic Voltziales especially manifest this trend. However, in the gymnosperms like conifers, gingkos and cycads, dioecy is the rule, with distinct female and male cones on the same plant or sometimes even on different ones. Therefore, a bisexual reproductive organ from a hermaphroditic fructification is difficult to deduce. How can unisexual cones come together under homology? This is not so far-fetched; in Permian Euroamerican floras, these occurred in same lycopods, such as heterosporous *Selaginella, Isoetes* and especially in Carboniferous-Permian *Sigillaria* and Triassic *Sigillcampeia*. But the Sigillarias had a totally different evolution system. Microsporangia and macrosporangia originated there on the same fructification, that way resembling the Magnoliaceae. The huge single macrosporangia in *Sigillcampeia* was coated by a protective tissue leaving a narrow open micropyle. In that some primitive clubmosses had more similarities with the Proto-Angiosperms from the Permian than all known gymnosperms.
As theory suggests, during the Devonian, the angiosperms, gymnosperms, clubmosses, horsetails and ferns must have completely developed their essential features. If the Sigillarias can be categorised under the lycophyta – and this is the most accepted theory – then a tribe of clubmosses and primitive angiosperms were originally parented.
Notably, not all angiosperms are hermaphroditic. Many primitive shrubs or trees from the Permian Fore-Urals like maples-ashes or oak-ancestors may have been monoecious, dioecious or polygamodioecious. All these complicate a clear evolution theory. The only certainty is that from the Devonian till the Early Permian, mainly all plant-tribes had just fully evolved; in the following 300 million years, only lateral and marginal developments happened.

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Wachtlerosperma stefanperneri nov. gen. n.: Presumed Early Permian ancestor of the Asteraceae

by
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The Asteraceae or Compositae are one of the most common flowering plants on earth, being of cosmopolitan distribution and reaching all continents except Antarctica. They include over 1900 genera with about 32,000 species. A characteristic feature is their flower composed of a dense head called capitulum or pseudanthium. This is surrounded by a fair amount of involucral coloured leaves. Their fruits, achenes, are often equipped with parachute-like feathery bristles, which enable the seed to be carried by the wind. Here will be described an interesting Early Permian (Kungurian) ancestor of the Asteraceae, *Wachtlerosperma stefanperneri* nov. gen. n., recovered in the Russian Fore-Urals, which was an isolated continent at that time. All the parts are preserved, from leaves to flowers and fruits. Due to its bifurcating leaves, this plant must stand on the frontline of the evolution of the Compositae.

Online: May 2020
Keywords: Angiosperms, Permian, Ural, Angara, Asteraceae

***Wachtlerosperma stefanperneri* nov. gen. n. Reconstruction**

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

Introduction

The Early Permian sediments from the Russian Fore-Urals rarely expose bigger parts of fossilised plants. One of the few examples is represented by an about 30 x 30 cm huge slab with the impressions of an entire interesting plant presenting long and slender forking leaves in connection with a stalk generating a flower/fruit apically.

Wachtlerosperma nov. gen. PERNER 2020

Etymology

It honours the researcher Michael Wachtler for his studies in palaeobotany.

Wachtlerosperma stefanperneri nov. gen. n. sp. PERNER 2020

Holotype

MAT 287, Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

Type horizon and age

Early to uppermost Lower Permian, Kungurian. Matvèevo: Filippovian substage, Lekskaya-Formation.

Diagnosis

Herbaceous plant with bifurcated foliage and fertile leaves having a strong mid-vein ending in an umbel; single inflorescences with many florets, enclosing a fair number of achenes; tepals are long and narrow.

Etymology

It is dedicated to the fossil preparator and palaeontologist, Stefan Perner, who died tragically young.

Description

Plant: Holotype MAT 287, a complete plant, has a length of about 25 cms and a width of 25 cms. The slender leaves end bifurcate and are basally about 6 mm thick; the size gets reduced apically due to their dividing. No mid-veins or other veining are visible.
Fructification: The leaf-like main stalk that holds the inflorescence evidences a strong midrib and is 10 mm thick. The flower-fruit seats on the apical part and is equipped with a fair amount of up to 20 mm long hanging tepals. The umbel is composed of many florets, which are characterised by small-sized petals that surround an inner bed containing the dwarfish seeds or achenes. The individual florets reach a length of 5–10 mm. An isolated and bigger floret (about 10 mm long) is represented by MAT 523. Other suggested fertile stemlets are MAT 322 and MAT 486.

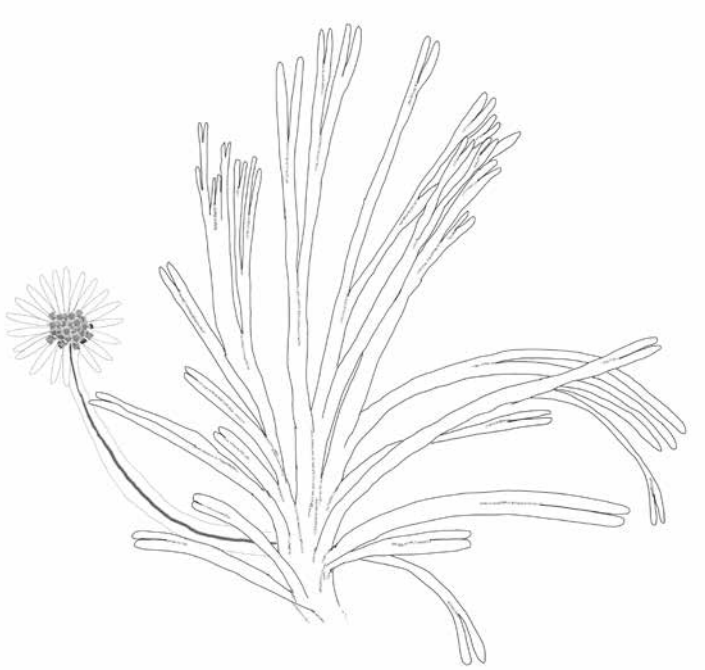
Discussion

Wachtlerosperma stefanperneri is known in mainly all parts although their classification in one of the existing plant-families is not easy. Many of their characteristics hint

***Wachtlerosperma stefanperneri* nov. gen. n. sp.**
1-2. Single floret filled with not fully mature seeds (MAT 523, 10 mm long)

***Wachtlerosperma stefanperneri* nov. gen. n. Plant, leaves and flowers**

1–3. Entire plant with umbel consisting of many inflorescences and bilobed elongated leaves (all MAT 287, designed holotype); 4–5. Detail of the florets from lateral view (4 mm) of the holotype; 6 Isolated stemlet (MAT 322; Matvéevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos Museum

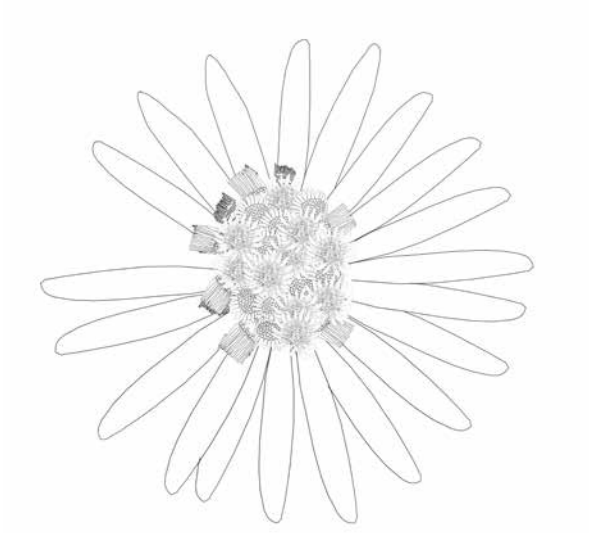


Wachtlerosperma stefanperneri. Reconstruction of the whole plant and the flower

toward Asteraceae, and within them, it can be compared with *Naugolnykhia matvéevoi* (Wachtler, 2017). However, *Wachtlerosperma stefanperneri* has a relatively broad and mid-ribbed flower stalk and forms a basal tuft of many bifurcating leaves. Also, the flower forming an umbel is different. *Asteroforma nicolaswachtleri,* another plant supposed to pertain to the first Asteraceae, evidences a powerful inner head and an outer ray flower composed of petal-like leaves. The fruits of these two genera are represented by parachute-like fructifications described as *Pappusperma*, whereas *Wachtlerosperma stefanperneri* holds single florets with many small-sized seeds inside.

Another solution is to put this Early Permian plant under the category of an evolving line of the Alliaceae, the Allium-family, herbaceous perennials belonging to the monocotyledonous angiosperms and occurring mostly in temperate regions of the Northern Hemisphere. Also, the flowers are born at the top of a leafless stalk in flower clusters that produce seeds within dry capsule fruits, whereas as well as a basal rosette of lance-shaped leaves forms the basis.

Highly interesting is the forking foliage, which, if found isolated, can also be confused with *Psygmohyllum cuneifolium*, a presumed ancestor of Acer. These leaves are so common in the Early Permian layers of the Fore-Urals that they attracted the attention of the



first researchers like Stephan Kutorga from Petersburg in 1838. M. D. Zalessky (1937b) changed the original name *Sphenopteris cuneifolia* (usually a Permian fern), to the term used today, that is, *Psygmophyllum cuneifolium*. But as seen with *Wachtlerosperma stefanperneri,* in addition to some presumed maple progenitor, bilobed leaves built the starting point of almost all plants beginning from the Devonian time. They can belong to different flora elements, from supposed broad-leaved trees to low growing herbaceous plants.

Under which category we can insert *Wachtlerosperma stefanperneri* is therefore speculative, but several interesting facts can be deduced from this: the inflorescences are formed in umbels; they consist of an aggregation of many micro-flowers coating many seeds inside; the stalks that hold the flower bunches can be regarded as reinforced leaves; all features of the Asteraceae family can be observed in this.

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