The Origin of the Asteraceae
Early Permian evolution

by Michael Wachtler
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Usually, it is believed that the Asteraceae represent one of the most evolved angiosperm families, and as a logical consequence, they evolved late in Earth history. Strangely, we encounter in the Early Permian Fore-Urals flowers, entire plants and single pappus, with many characteristics of extant Asteraceae. They must, therefore, belong to different flowering plants. *Naugolnykhia matvéevoi* consist of a long and slender stalk with a flower composed of two circles. A*steroforma nicolaswachtleri* gen. nov. n. sp. evidence a powerful inner head and an outer ray flower composed of petal-like leaves. *Zalesskya multipla* nov. gen. n. sp. is characterised by their small flowers but has the same features of the former. *Caputosperma geraschi* nov. gen. n. sp. as well as *Caputosperma perneri* n. sp. have blooms with more flower heads clustered together forming panicles. Also, isolated fruit organs resembling extant pappus are found, which are described as *Pappusperma ventilata* nov. gen. n. sp. and represent parachute-like fructifications. All these plants reveal fascinating findings about the evolution of the Asterales, one of the dominating angiosperm families today. A brief insight into the evolution of the Asteraceae is also be given.

Online: May 2020
K*eywords*: Asteraceae, Angiosperms, Permian, Angara, Ural

Early Permian Asteraceae

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

Introduction

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

Till now, the oldest known fossils of the Asteraceae are pollen grains from the Late Cretaceous (Barreda, et al., 2015). Their characteristic flowers arranged to form a capitulum-inflorescence, with hairy or bristle-like pappus equipped with one seed. It can be supposed that plants from the Early Permian Fore-Urals that evidence the same features can probably be inserted in the same schema, which shows that they are potential progenitors of the Asteraceae.

Naugolnykhia matvéevoi WACHTLER 2017

Fortunately, a complete plant resembling mostly the Asteraceae has been preserved. It was described as *Naugolnykhia matvéevoi* (Wachtler, 2017) and consists of a long and slender stalk with dwarfish leaves sprouting sometimes on the stipe. The flower is composed of two circles: an inner disk flower, dome-shaped, velvety, covered by finest hairs during mature stage and an outer ray flower composed of petal-like leaves. No search satisfies the inclusion of *Naugolnykhia matvéevoi* in one of the gymnosperm families; therefore, attempt was made to insert this plant into the group of Paleoangiosperms, especially the ancestors of the Asteraceae. In that, it can be compared well with today's daisy flower (*Bellis perennis*). Probably, if one knew nothing about the Early Permian age, they could confuse *Nau-*

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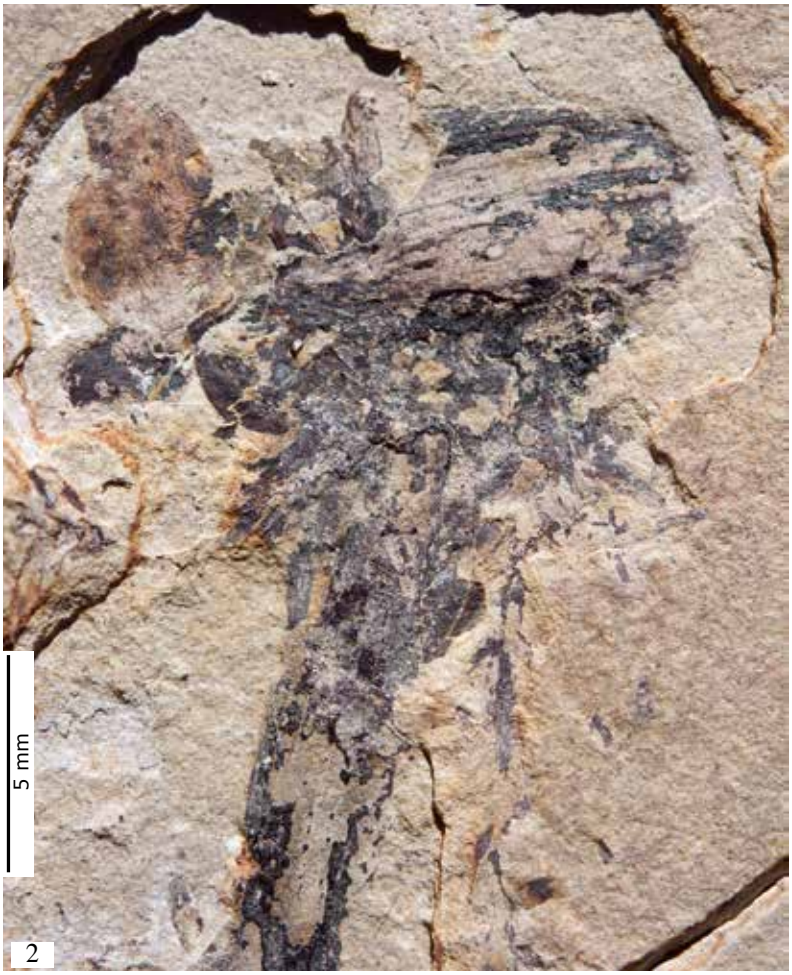
Asteraceae species:

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

Naugolnykhia matvéevoi a potential Asteraceae-ancestor



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

Naugolnykhia matvéevoi. **Reconstruction**

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

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

golnykhia easily with Asteraceae. Both have leafless (daisy flower) or primarily leafless stalks (*Naugolnykhia matvéevoi*); both flowers have a large centre adorned with delicate petals.

Asteroforma nov. gen. WACHTLER 2020

Etymology

It is based on their similarity with the flowers of extant Asteraceae.

Diagnosis

The blossoms have two distinct flower discs; the outer circle holds the petals, and the inner is a compound of fruit-organs.

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

Holotype

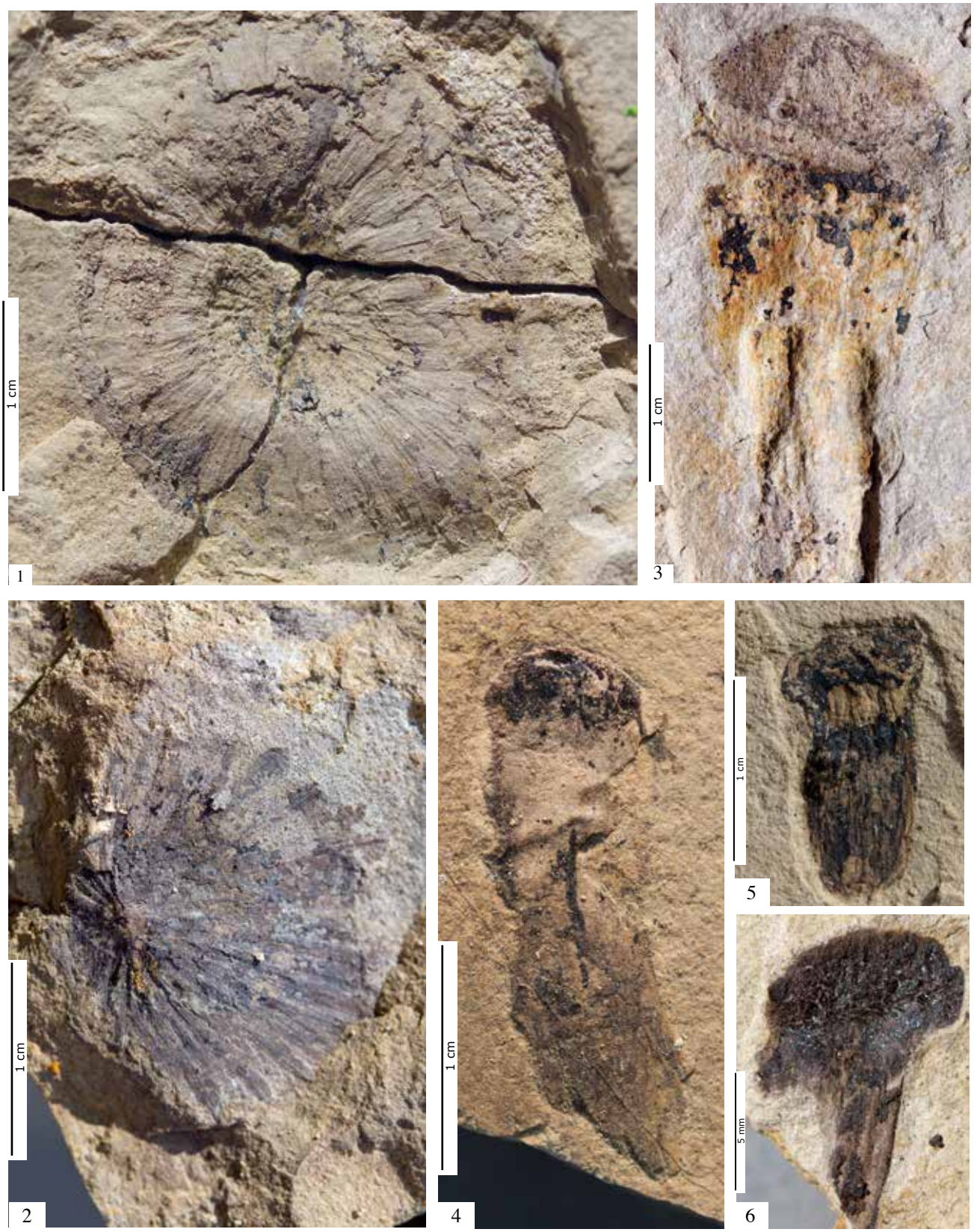
CHEK 65, Chekarda, Paratype MAT 353 is an example of a semi-naked head (Coll. Dolomythos Museum)

Etymology

It honours Nicolas Wachtler, who found the most important specimen and conserved them

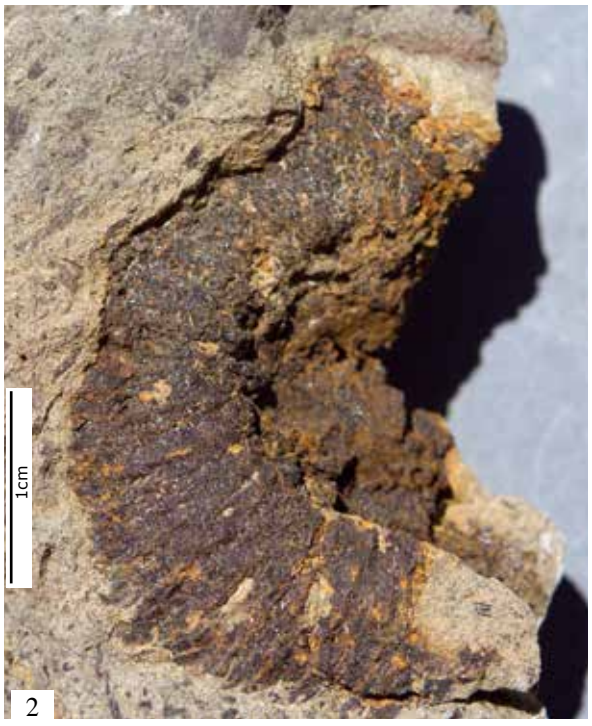
Description

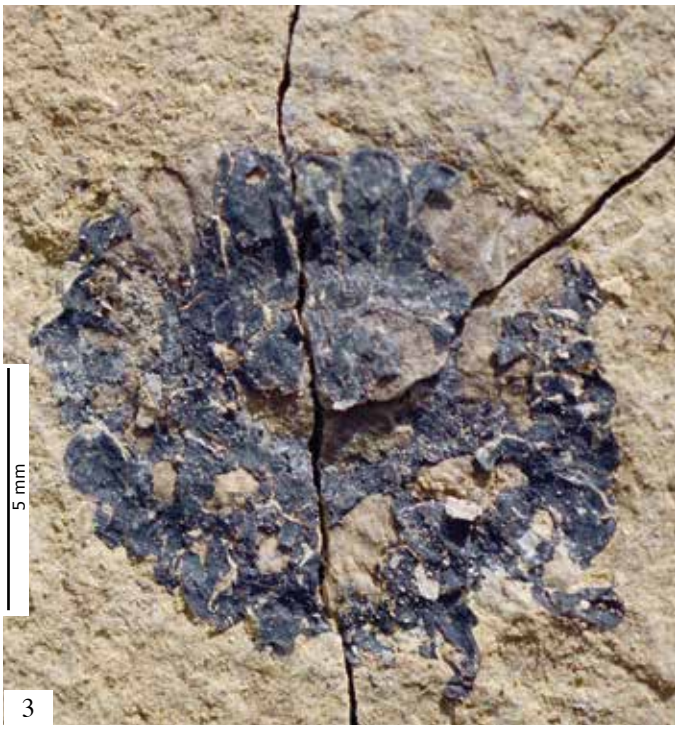
Fruit: The blossoms have a diameter of about 25 mm (designed holotype CHEK 65) and are a compound of two parts: from a ra-



***Asteroforma nicolaswachtleri* (Wachtler, 2020); Asteraceae-progenitor**

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





***Asteroforma nicolaswachtleri* (Wachtler, 2020); Asteraceae-progenitor**

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

Early Permian Asteraceae

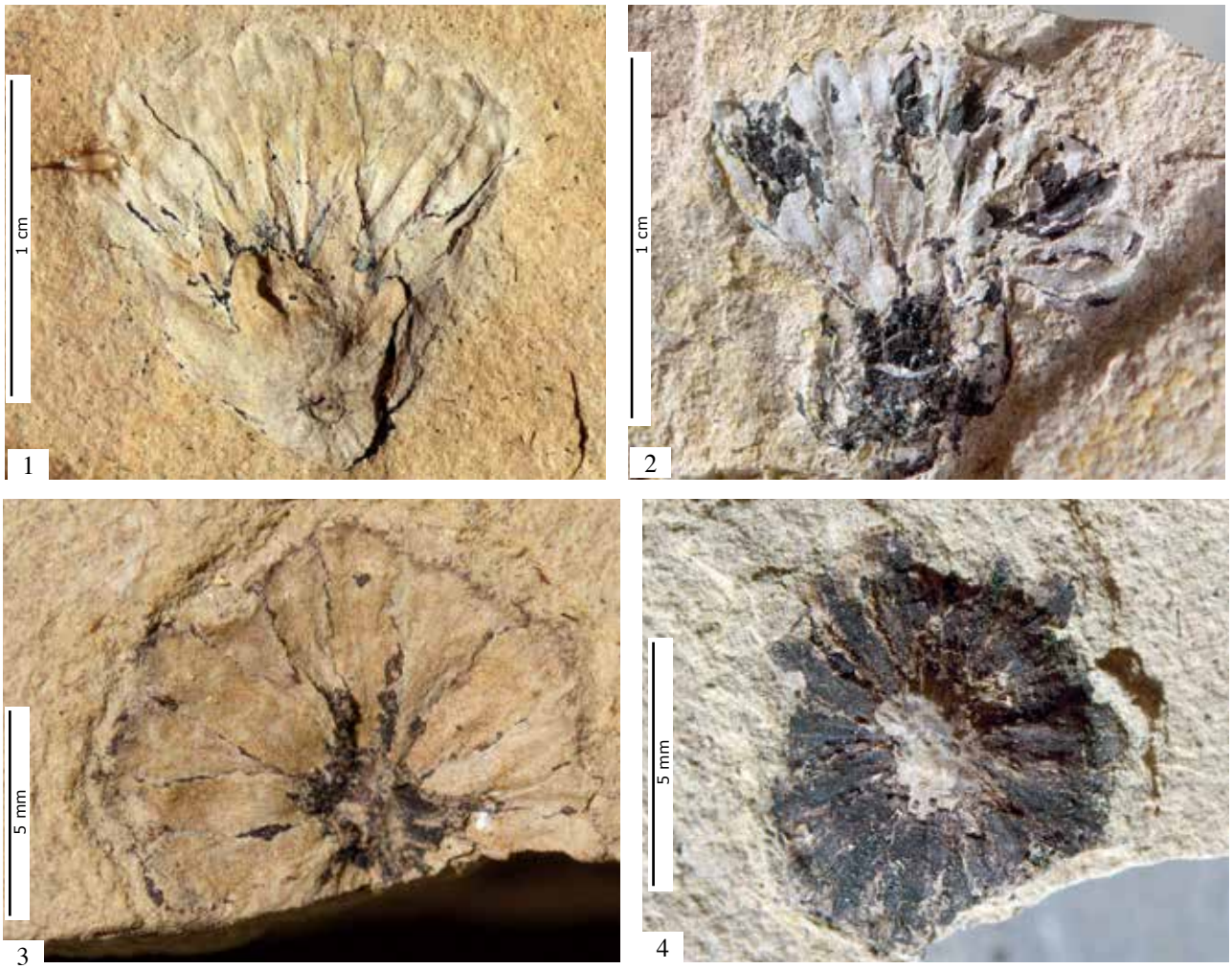
Left: *Asteroforma nicolaswachtleri,* a blossom (holotype CHEK 65) and a naked receptacle with hanging petals (MAT 353); **right:** *Zalesskya multipla,* a multi-petaled flower ((MAT 357) and the lateral view (holotype CHEK 72). The air is filled with several parachutes (holotype CHEK 76, CHEK 356) of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

diate capitula, composed of many inner disk florets sprout a high amount of ray florets. When they are shed, a naked head capitula remains. Paratype MAT 353 is an example of a semi-naked head with a few attached petals; CHEK 221, CHEK 55 and MAT 356 are examples of naked capitula. The head grows to a diameter of 6–7 mm. The stem is stocky and in some cases, it nearly reaches the diameter of the capitula. Probably also CHEK 52 (21 mm width), a lateral view of a flower with intact inner corymbose-paniculiform synflorescences, as well MAT 218 (30 mm in diameter) belong to the same species.

Discussion

In addition to *Naugolnykhia matvéevoi* and *Wachtlerosperma stefanperner*i resembling the extant Asteraceae, another parented blossom was discovered in the Early Permian Fore-Urals – *Asteroforma nicolaswachtleri.* The flower has a diameter of 25 mm and consists of two clearly separated circles. The outer head is composed of many petaloid leaves that surround an inner disc floret. Probably, during the mature stage, this generates the parachute-like structure with the attached seed that was found fossilised in the same sediments as *Pappusperma*.

Due to their inconspicuousness, especially of the heads, *Asteroforma nicolaswachtleri* have never attracted the attention of researchers or collectors, although naked capitulas are seldom found in Chekarda and Matvéevo. In the Early Permian layers, blossoms can be found attached to extremely slender stalks (*Naugolnykhia matvéevoi)*, on stocky stems (*Asteroforma nicolaswachtleri*) or with bilobed leaves on leaf-like stemlets (*Wachtlerosperma stefanperneri*), from which it can be deduced that they all belong to different plant genera. All these small puzzle pieces help to give a better insight into the origins of Asteraceae, particularly because their reproductive organs are found as isolated parachutes.



***Zalesskya multipla* nov. gen. n. sp. WACHTLER 2019, multiple-petaled flowers**

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

Zalesskya nov. gen. WACHTLER 2020

Etymology

It honours Mikhail Dmitrievich Zalessky (Russian: Михаил Дмитриевич Залесский, 1877–1946), who described in several works the Kungurian floras of the Perm Krai, especially of Chekarda and Matvéevo.

Zalesskya multipla nov. gen. n. sp. WACHTLER 2020

Holotype

CHEK 72, Chekarda, Paratype MAT 357, Matvèevo, (Coll. Wachtler, Dolomythos Museum)

Etymology

The word "multipla" is a Latin name referring to their multiple petals.

Diagnosis

The blossoms have a fair amount of partially serrate petals; the inner circle has fruit-organs

Description

Flower: The small flowers hold an undefined number of petals. They are about 7–10 mm in diameter (Paratype MAT 357, MAT 194) and have a length of about 10 mm (Holotype CHEK 72, MAT 503). The capitulum is half-epigynous to epigynous, as suggested in CHEK 72 and MAT 503. Therefore, the disk-flower is buried within the receptacle. The densely aggregated petals of the

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

ray flower usually have a width of 1 mm and a length of 5 mm.

Discussion

Various multi-petaled flowers were recorded from the Early Permian Fore-Urals. Some of them, such as *Multifolium petaloides, Naugolnykhia matvéevoi* or *Asteroforma nicolaswachtleri,* reach considerable sizes of about 20 mm and above. In this range, *Zalesskya multipla* is the most inconspicuousness and small, with the entire flower measuring only 10 mm or less.

In *Naugolnykhia matvéevoi,* the isolated bloom seats on a slender and naked stemlet. *Asteroforma nicolaswachtleri* exhibit two floreal circles: an inner disk flower, covered by finest hairs during the mature stage and an outer ray flower, composed of petal-like leaves. *Zalesskya multipla* has a multi-petaloid ray flower as well but the inner circle is restricted. *Multifolium petaloides* do not hold a significant inner circle either, but the petals have a stronger appearance and are restricted in number.

Zalesskya multipla stands a little apart from this "huge" flower and its clearly epigynous character. Additionally, a sunken ovary has not been recorded so well in other multi-petaloid flowers. Another presumed Asteraceae is represented by *Caputosperma geraschi* and *Wachtlerosperma stefanperneri.* In these flowers, each bloom consists of small clustered spikelet-florets surrounded by "petals" or bracts.

Caputosperma nov. gen. WACHTLER 2020

Etymology

It is from the Latin word "caput" meaning head, referring to the several aggregated little heads forming the blossom.

Caputosperma geraschi nov. gen. n. sp. WACHTLER 2020

Holotype

CHEK 68, Chekarda (Coll. Gerasch Dolomythos-Museum, Italy. Counterplate Coll. Gerasch, Thomaseum, Langenaltheim, Germany)

Diagnosis

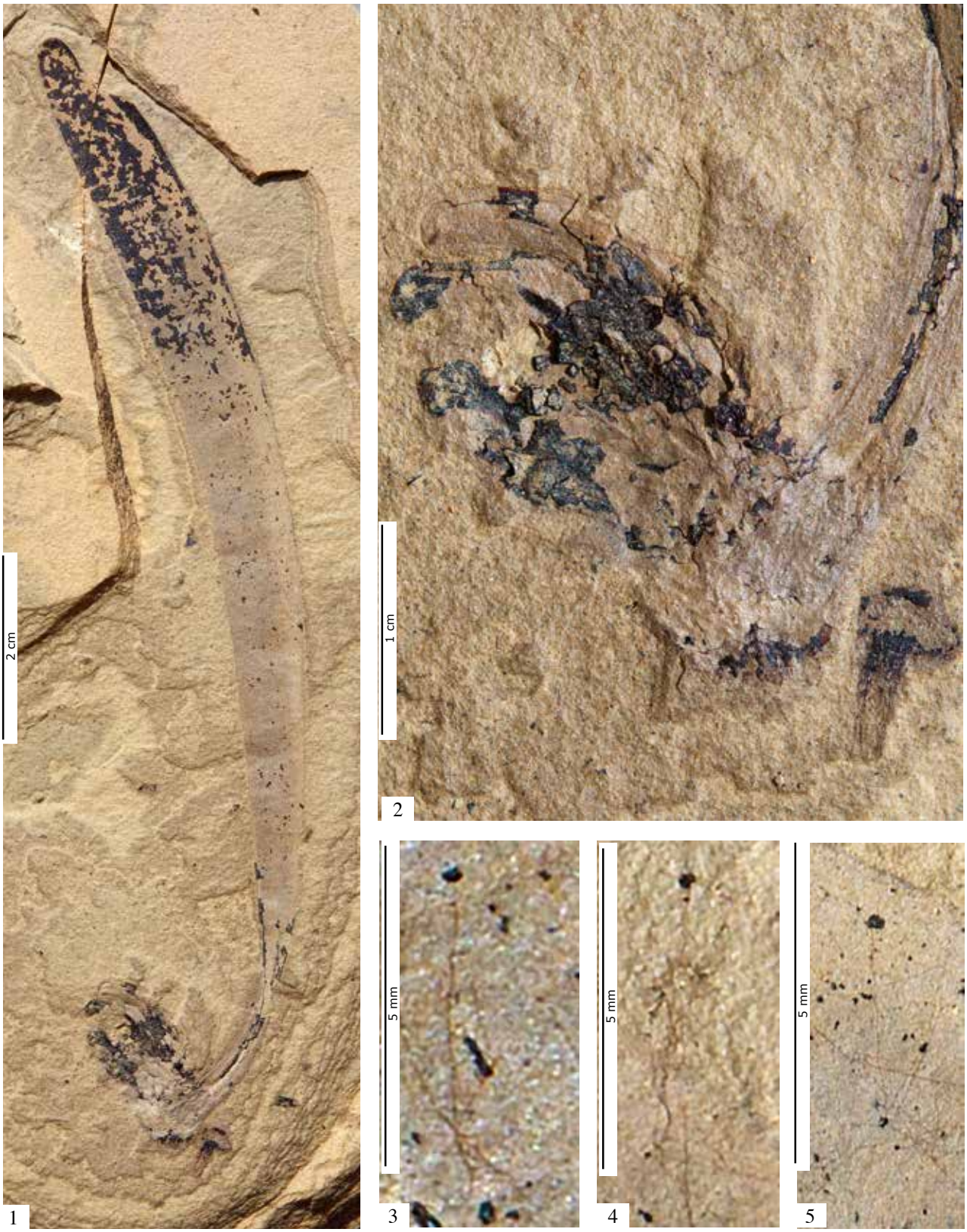
Each bloom consists of many flower heads clustered together.

Etymology

It honours the researcher Thomas Gerasch, who discovered many Permian plants.

Description

Fruit: Holotype CHEK 68 represents a 12 cm long lanceolote linear leaf with smooth edges ending in a rounded apex. Basally attached is a compound synflorescence, consisting of about seven flower heads with



Caputosperma geraschi nov. gen. n. sp. WACHTLER 2020

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

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

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

Leontopodium alpinum var. campestre widespread in Kazakhstan, the Altai Region and Mongolia

shed petals. On several heads, especially on the one shed by sedimentation, several pappus are recognisable. They are scattered on the slab and consist of a about 5 mm long filaments with a pinhead-sized seed on the end.

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

Type horizon and age

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

Holotype

MAT 578, Matvèevo, Paratype MAT 44 (Coll. Perner, Dolomythos-Museum, Italy

Etymology

It honours the German researcher Thomas Perner for his lifelong work in palaeontology.

Description

Flower: From holotype MAT 578 (18 mm in length) originate various distinct and aggregated flower heads, forming synflorescences or panicles. Some small leaves are visible on the lower part and the root complex. It forms a mature specimen with the petals just shed. A juvenile flower is represented by paratype MAT 44 (22 mm in length). It resembles the holotype MAT 578 but evidences well five flower petals. On the base, two small leaves are visible. MAT 360 evidence three separate groups of capitula and a shed petal. Together they have a diameter of 6 mm, which means that each flower head is 1–2 mm or less in diameter. In MAT 638, the outer flower heads evidence some ray flowers. The small flower head can be considered a disk flower, as seen in MAT 578, which is a juvenile plant equipped with roots and various aggregated flower heads. Also, some parachutes are visible, which are about 5 mm long with a pinhead-sized seed.

Discussion

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

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

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

Pappusperma ventilata **nov. gen. n. sp. WACHTLER 2020**

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

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

Asteraceae, *Caputosperma perneri,* with its dwarfish and aggregated synflorescences, could be compared with today's *Leontopodium* (the Edelweiss), *Achyrocline* or *Achillea*, all belonging to the Asterales. Probably five petals are identifiable in the juvenile specimen, and the disk flower produced infinite parachutes during maturity, as can be observed on the fossilised slabs.
Caputosperma is frequently found in Chekarda and Matvèevo, and it also supports the theory of the interesting Early Carboniferous-Permian origin of the angiosperms. However, the enigma surrounding the evolution of the wind-dispersed small parachutes of the various Early Permian Asterales can be connected with other fructifications like the drupes, samaras, acorns or racemes of other fossilised flowering plants in the Permian Fore-Urals.

Pappusperma nov. gen. WACHTLER 2020

Etymology

It is from Greek word "pappos", meaning old man's beard, referring to an appendage or tuft of appendages that crowns the seed and helps the dispersal of the fruit.

Diagnosis

It has the finest impressions of hairy or bristle-like seed organs; They are sometimes umbrelliform or equipped with bristles

Pappusperma ventilata nov. gen. n. sp. WACHTLER 2020

Holotype

CHEK 76, Chekarda (Collection Wachtler, Dolomythos, Innichen, Italy

Etymology

It is from the Latin word "ventulum", meaning blown by the wind.

Description

Fruits: They represent parachute-like achenes equipped with finest hairs. Holotype CHEK 76 is a pappus from which radially sprout several bristly barbs. It is about 5 mm in diameter. CHEK 324 has the same characteristics as the holotype CHEK 76, but it is conserved from the lateral side. CHEK 356 resembles a pappus with a basally attached seed and several outgoing appendices.

Discussion

Some fossilised fructifications, especially from Chekarda, can be found only in finest-grained sediments. They resemble individual parachute or pappus. Each achene has an umbrella-like crown of plumose hairs and must have literally been carried into the atmosphere by strong ascending air currents. That *Pappusperma ventilata* represent an Early Permian pappus is not a far-fetched idea, since in Matvèevo and Chekarda, potential Asteraceae-ancestors like *Naugolnykhia matvéevoi* (Wachtler, 2017), *Asteroforma nicolaswachtleri, Caputosperma geraschi, Wachtlerosperma stefanperneri* or *Zalesskya multipla* can be found. Regarding *Caputosperma geraschi*, it is certain that its pappus is a long, single hair with a pinhead-sized seed attached basically. It is probable that the aforementioned parachutes belong to other genera also, since bristly holotype CHEK 76 seems to be different from CHEK 356, with its long and thin appendages. The evolution purpose of these hair-like, fragile parachutes was to become airborne and be blown with the slightest breeze and cross valleys and slopes. In that, they all resemble extant members of the Asterales. That they were not discovered or described before can be attributed to their inconspicuousness and their need to be preserved only in finest mud.

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The Origin and Evolution of Angiosperms
Early Permian Flowering Plants

Edited by
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Published by Dolomythos Museum, 39038 Innichen, South Tyrol, Italy
First edition May, 2020 ISBN 978-88-944100-4-4

Hardcover Euro 98
Pages 240