Early Permian Conifers from Angaraland and Their Role in the Gymnosperm Evolution

by
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The conifers in Early Permian Angaraland—that time being a separate continent—play only a subordinate role in dominating all the vegetation of the Paleoangiosperms. Two conifers are frequent: *Kungurondendron sharovii,* with its bracted scales tightly fitting the seeds, with two small winged seeds like today's spruces and T*axodiella bardaeana*, branching irregularly with incurved small foliage and additionally characterised by their small female cones, holding on each scale several seeds. Another extremely interesting conifer is *Stukenbergia kungurica* nov. gen. n. sp. due to its winged seeds, resembling extant cedars. Maybe the long-needled leaves classified as *Bardella splendida* can be regarded as belonging to this conifer. The classification of *Meyenophyllum conifera* nov. gen. n. sp. in one of the existing conifer families otherwise is problematic.

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Early Permian Angaran conifers. **Left:** trees, twigs and cones from *Taxodiella bardeana,* a conifer belonging to the Voltziales and a suggested ancestor of Cupressaceae trees. The cones are equipped with multi-seeded scales. Right: *Kungurodendron sharovii*, a conifer widespread in the Kungurian landscapes of former Angaraland, probably an ancestor of the spruces

Introduction

Deciphering the secrets of the Early Permian conifers from the Fore-Urals is not easy because they play a subordinate role in the dominating Paleoangiosperm-flora. Probably they occupied more the hinterland of the lakesides and the transport way for sedimentation was longer, which is what makes a classification more difficult. In the past, often people tried to examine the gymnosperms on the basis of their needles and twigs, but this is even less effective. Only studying the fertile parts of the conifers, their seeds and cones can give a chance to obtain significant results.

Especially in the European Permo-Triassic fossil sites the conifers are largely the dominating plant-group and therefore, thousands of specimen comprising all parts of the trees are available; all this is known based on researches that can be traced back to two hundred years. All these are not available in the Ural region. Hence, we stand only at the beginning of an intense scientific collection.

The first Permian conifers of the Siberian Angaraland were described in the middle of the last century together with other plant remains under generic names like *Araucarites, Pinus, Steirophyllum, Ullmannia, Voltzia* and *Walchia* (Eichwald, 1854, 1854–1861, Goeppert, 1864–1865). Several other species were later classified by Mikhail Dmitrievich Zalessky (1937, 1939) from the Kungurian period of the Middle Fore-Urals. These were *Walchia uralica W. appressa, W. bardaeana, Walchia peremiana, Ullmannia bardaeana, Bardella splendida Ammatopsis mira, Voltzia principalis, V. prisca, Taxodiella recticaulis Uralodendron verticillatum* and *Biarmodendron foliosum.*

The research was intensified in the 1970s by Sergey Meyen (Meyen, 1988) culminating in his work "*Permian conifers of Western Angaraland"* (1997), in which he tried to put order in the multitude of different collected conifer remains. Zalessky often gave only superficial and short descriptions and figured the specimen only by drawings made by himself. Additionally, many of the old findings, including Zalessky's material, got lost over the decades.

We encounter relatively indisputable slender cones generating two small seeds from a conifer known as *Kungurondendron sharovii.* Additionally, we have sparse scales with two relatively huge winged seeds that can belong to some extant *Abies* or *Cedrus* ancestor, as well cones that generate three seeds and more. The question is: How many conifers did we have in total in the Kungurian period in Chekarda or Matvèevo? Because it seems that the number was not exorbitant.

Kungurodendron sharovii MEYEN 1997

Kungurodendron represents one of the most frequently found conifers in the Early Permian (Kungurian) sediments of Chekarda and Matvéevo. The vegetative shoots are less numerous as the fertile parts or isolated found scales. The majority of the cones recovered are slender – upto 10 cms long – with tapered bracts densely coating the fructification (CHEK 21, CHEK 95, CHEK, 138 CHEK 186, MAT 223, MAT 602). Sometimes cones with open or shed scales can be recovered. Their scales evidence, as opposed to earlier authors' view (Naugolnykh, 2014, 2016), only two shortly winged, relatively small seeds (CHEK 397 and CHEK 158).

Usually the individual scales had a length of 9–10 mm, the seeds were composed of seeds about 2 mm in size and a 1 mm long winged appendix (CHEK 158, CHEK 327). The two-winged seeds were inserted basally on the scales, and sometimes their impression were left on the scale. For the pollen cones, it is not clear if they are similar to the female because it seems that MAT 71 and MAT 124 represent male cones. The question of which extant conifer can be connected with *Kungurodendron sharovii* is worth exploring. The two-winged seeds exclude single seeded *Araucaria* ancestors like *Ortiseia* from Europe or multi-seeded conifers like the Voltziales. From the two-seeded conifers, Abies progenitors like *Majonica* or *Wachtlerina* (Wachtler, 2015) – widespread in Europe on the Carboniferous-Permian border and throughout the Permian – held the seed scale projecting bract, and the entire scales were shed at maturity – all of these features that we find in today's Abietaceae. This bract does not exist in *Kungurodendron*. The isolated scales are different because they only disaggregate on the soil and not on the tree, typical of the

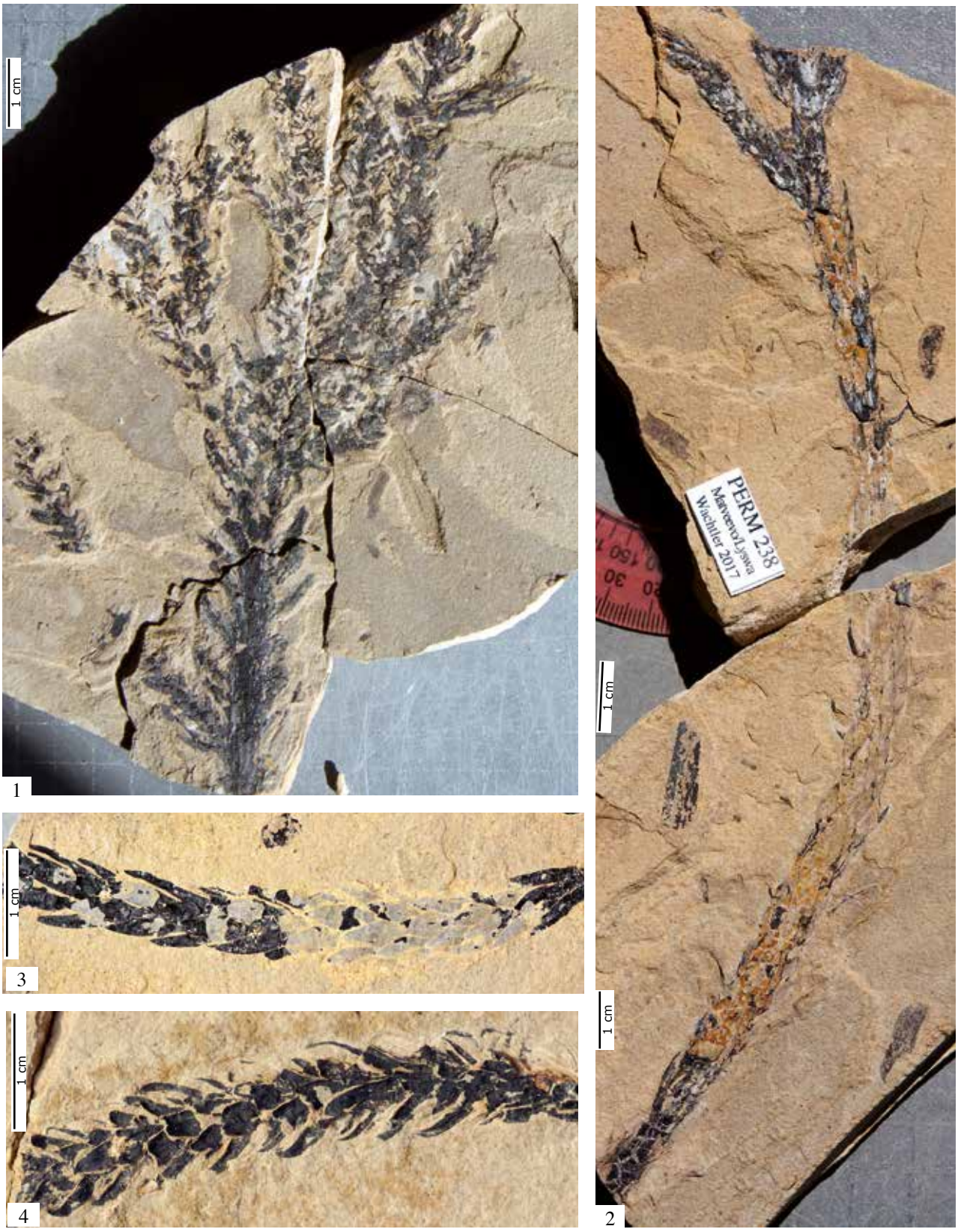
Picea pungens a spruce species. The cones can be compared with *Kungurodendron.* They were shed entirely after maturity and disintegrated slowly on the soil.

Abietaceae. The most convincing similarities we encounter in today's Piceaeceae are to the spruces. *Picea pungens*, the blue spruce, for example is, with its slender cones, not so far in appearance from *Kungurodendron*. They lose, as many other spruces, their cones entirely where they break down on the soil.

Taxodiella bardaeana ZALESSKY 1937b, MEYEN 1997

The genus name, *Taxodiella*, was introduced by M. D. Zalessky (1939) as basionym to *Taxodiella recticaulis* (Zalessky, 1939, p. 367) from Chekarda. Additionally, he described, from the other Kungurian locality Matvéevo, a conifer as *Walchia bardaeana* (Zalessky, 1937b, p. 74 Fig. 39). The Russian palaeontologist, Sergey Meyen (1997), noted that the specimen *Taxodiella recticaulis*, being published in 1939, has to be treated as a younger synonym, and therefore, he proposed the combination *Taxodiella bardaeana*, for coniferalean shoots with small incurved leaves found especially in Chekarda and Matvéevo. He noted that the generic name *Walchia* is unsuitable for these Angaran conifers, and they must belong to a separate natural genus. Meyen unified other names introduced by Zalessky like *Walchia uralica* or *Walchia peremiana* to *Taxodiella bardaeana*, noting that they must belong to the same conifer.

Taxodiella bardaeana is an interesting conifer with branchlets of three successive orders, evidencing an irregular alternation of different foliage length on one side of the main axis (MAT 205, MAT 115, MAT 228). *Taxodiella bardaeana* holds two kind of shoots: the needles of the main branch are needle-shaped, lanceolate, flattened, with slightly convex margins, up to 0.6–1.0 cm long (MAT 123, MAT 205, MAT 230, MAT 229). The other leaves represent typical false whorls lying in a reduction and com-



***Kungurodendron sharovii*. Conifer - branchlets and leaves**

1. Complete branch (MAT 601); 2. Twig (MAT 238) 2-5. Twigs and details of the needles. Sometimes they are extremely pressed to the branchlet, other are incurved or only slightly pointed (MAT 444, MAT 72); Matvéevo, Kungurian (Early Permian) Coll. Wachtler

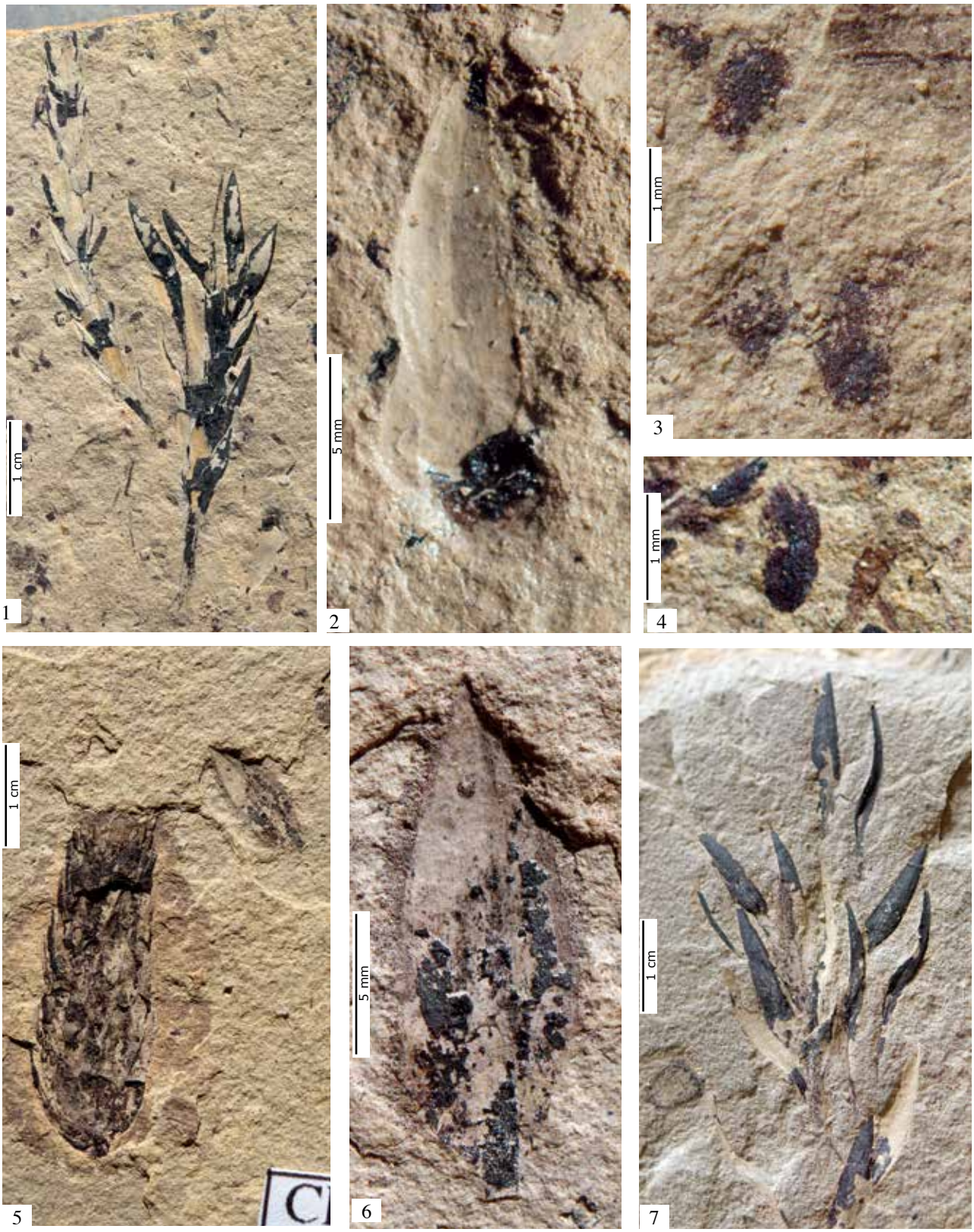
***Kungurodendron sharovii*. Conifer - cones**

1–6. Complete female cones with pressed scales (CHEK 95, CHEK 186, CHEK 138, MAT 223, MAT 602, CHEK 21, Coll. Wachtler); 7–8. Supposed male cones (MAT 71 Coll. Wachtler, MAT 124, Coll. Dammann) Chekarda, Matvéevo, Kungurian (Early Permian)

pression to a bundle (MAT 204) and can also be considered short shoots forming a tuft of many leaves (Naugolnykh, 2014). They are equipped basally with a long single bract. The leaves/needles are produced sometimes, but not always, in dense clusters (MAT 204, MAT 601).
The pollen cones are only upto 1 cm long and 0.7 cm wide, equipped with dwarfish scales (MAT 230). Suggested female cones are small, 3–4 cm long and 2–3 cm wide. One bract covers the seed scale in the middle (MAT 221). The seed scales are segmented, with apices hooked backwards and crowned by many (probably about eight) ovules or scars from released seeds in the upper part (MAT 461).
Considerations can be made about the relationship of *Taxodiella bardaeana*. Cones with three or more seeds were inserted in the artificial group of the Voltziaceae, the latter being widespread in the European Permian till the Triassic. They appeared in Earliest Permian (Kasimovian-Gzhelian) sediments (Wachtler, 2015), sometimes with up to 25 cm long female inflorescences collocated terminally on branchlets and equipped with a large number of loose, spirally arranged, multi-lobed seed scales (*Seymourina niederhauseni*). It is not always easy to distinguish the sterile bracts from fertile seed scales, but it is suggested that they hold depending on species from three to eight fertile scales. We encounter them in the Kungurian in the Alps (*Seymourina vialli*) and especially in the German Upper Permian Zechstein as *Pseudovoltzia liebeana*. The size of their seed cones and pollen cones decreased or increased sometimes. The Voltziaceae were especially widespread in the Triassic (Wachtler 2016), being equipped with three naked seeds hanging dorsiventrally from the upper side of the scale (all *Voltzia* species) till five seeds (*Aethophyllum stipulare, Swendenborgia nissleri* from the Middle Triassic of Europe). Interestingly, today we do not have similar conifers because the only one resembling *Cryptomeria japonica* or *Cunninghamia lanceolata* bear, in fact, three seeds on each seed scale, but the cones are dwarfish in comparison with those of the Voltziales.
A little different seems to be the evolution way of *Taxodiella bardaeana*. This conifer can probably be regarded as an interesting

***Kungurodendron sharovii*. Seed scales**

1. Seed scale outer side (CHEK 397); 2. Decomposing cone with scales from the inner side (CHEK 188) Chekarda, Kungurian (Early Permian) Coll. Wachtler



***Kungurodendron sharovii*. Conifer - cones**

1-3. Two disintegrating cones (or one broken in the middle) with an isolated scale on the left side evidencing the shadows of two winged seeds. Around the cone many short-winged seeds are scattered (CHEK 158); 4. Other seed (CHEK 327); 5-6. Decomposing cone and isolated scale showing two shortly winged seeds (CHEK 400); 7. Disintegrating cone (CHEK 15); Chekarda, (Early Permian-Kungurian) Coll. Wachtler, Dolomythos-Museum

Kungurodendron sharovii

Early Permian conifer from Angara-continent with twigs, cones and seed scales

Taxodiella bardaeana

Early Permian conifer from Angara-continent with twigs, cones and seed scales holding more seeds

Stukenbergia kungurica

Early Permian conifer from Angara-continent with twigs (*Bardella splendida* type), cones and two winged seed scales
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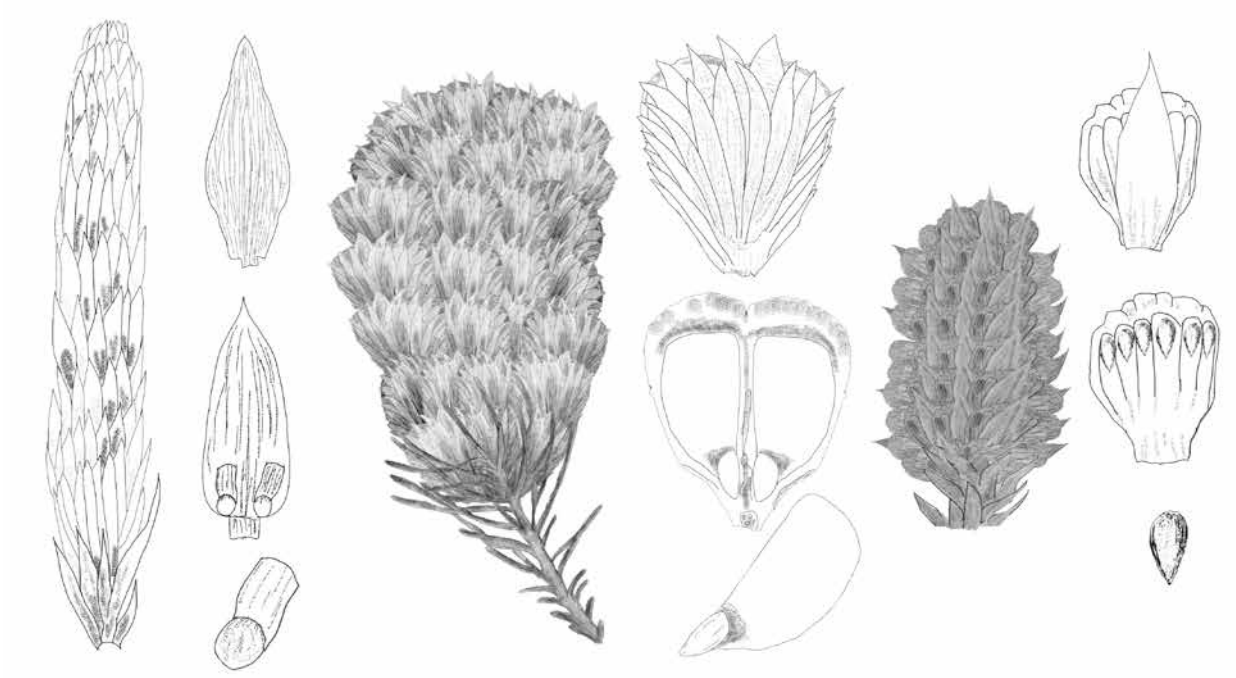
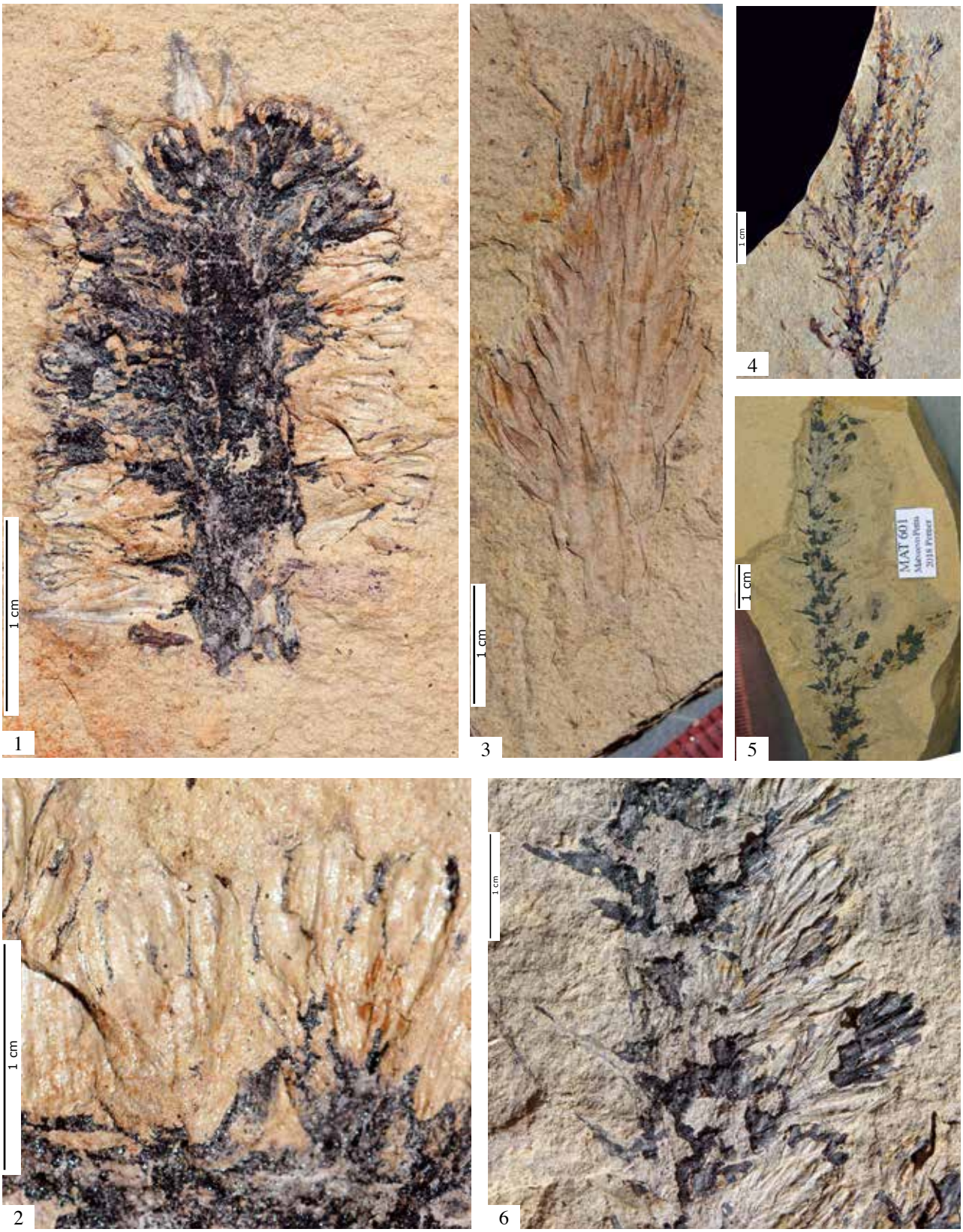
Conifer cones and seed scales from Angara-continent



Kungurodendron sharovii **Stukenbergia kungurica** ***Taxodiella bardaeana***

***Taxodiella bardaeana*. Voltzialean conifer**

1-3. Part of a twig with juvenile female cones and dwarfish pollen organs. The branchlets are diverging in three orders (MAT 205); 4-5. Branchlet with buds. Note the different length of the lateral twigs (MAT 204); 6-7. Branchlet with a pollen cone (MAT 230); Matvéevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos Museum



***Taxodiella bardaeana*. Voltzialean conifer - female cones**

1-2. Mature and open female cone (MAT 461, Coll. Gerasch); 3. Closed female cone, evidencing the bracts (MAT 221); 4. Twig (MAT 123, Coll. Dammann); 5-6. Twig with secondary shoots (MAT 601); Matvéevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos, Italy

Metasequoia glyptostroboides native to China; seed cone and leaves in their typical growing form; *Taxodiella bardaeana* could be an ancestor of this conifer.

missing link between some "tuft"-bearing conifers like *Metasequoia, Gyptostrobus* or *Sequoia*. Because *Glyptostrobus* has very different seed cones, it seems that *Metasequoia* and *Sequoia* evidence the most resemblances, especially when we look at the high amount of seeds for each scale that are almost equal in *Taxodiella* or both *Sequoia* genera. It is not to exclude that *Taxodiella bardaeana* can therefore be considered a relative of *Metasequoia*.

Stukenbergia nov. gen. WACHTLER & PERNER 2020

Etymology

It is named after the Russian geologist and palaeontologist, Alexandr Antonovich Stukenberg (1844–1905), who introduced the Kungurian stage in 1890.

Diagnosis

The conifer scale holds two relatively large winged seeds; The petiole base of the scale is narrowed.

Type horizon and age

It is from the Early to upper Lower Permian, Kungurian.

Stukenbergia kungurica nov. gen. n. sp. WACHTLER & PERNER 2020

Holotype

MAT 646, Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

Etymology

It is named after the Kungurian stage and the city of Kungur in the vicinity of the metropolis Perm.

Description

Seed scales: Holotype MAT 646 is 17 mm long and 15 mm wide and incorporates two

***Stukenbergia kungurica* nov. gen. n. sp. Conifer seed scale**

1. Seed scale with two winged seeds (designed holotype MAT 646); 2–3. Female cone composed of seed scales and covered by micro-leaves (MAT 502); 4. Other female cone (MAT 580); Matvéevo, Kungurian (Early Permian), Coll. Wachtler, Dolomythos Museum

***Stukenbergia kungurica* nov. gen. n. sp. (Kungurian, Early-Middle Permian)**

1-2. Suggested naked stipe with the seed scale shed (MAT 390, MAT 664); 3. Suggested male cone (MAT 214); Matvèevo, Kungurian, Coll. Wachtler, Dolomythos-Museum)

distinct large winged seeds that are 13 mm long. Each seed is elongated and tapering basally, and the wing is broadest apically. Like in the extant genus *Cedrus,* the scale is attached to the rachis with a petiolate base and dismembers from it by abscission at maturity.

Cones: Suggested fructifications are about seven cm long, 3–3.5 cm wide (MAT 502 and MAT 580), bulbous and composed of scales that evidence many micro-leaves on the outer side. When the seed scales are released, a naked stipe with typical abscission patterns remain (Mat 390, MAT 664).

The suggested male cones are about seven cms long and evidence many short bracted pollen tubes (MAT 214).

Foliage: It may be of the *Bardella splendida*-type with its long needles.

Discussion

The knowledge of Paleozoic-Mesozoic conifers was, in the past, mainly based on the arrangement of needles or leaves, whereas less attention was given to the structure of their fertile parts like cones, especially seed scales. The first researcher who noted the importance of the individual composition of fossilised conifer seed scales was the Dutch palaeontologist, Johanna Clement-Westerhof (1984, 1987) on material from the Dolomite-mountains in Italy.

The conifer name *Majonica alpina* (1987) was therefore given only for an isolated seed scale and not for the foliage or the twig. It was a right decision because some conifers today, such as the genera *Abies, Cedrus, Araucaria*, dissolve their cones either when they are still on the


1


2


3

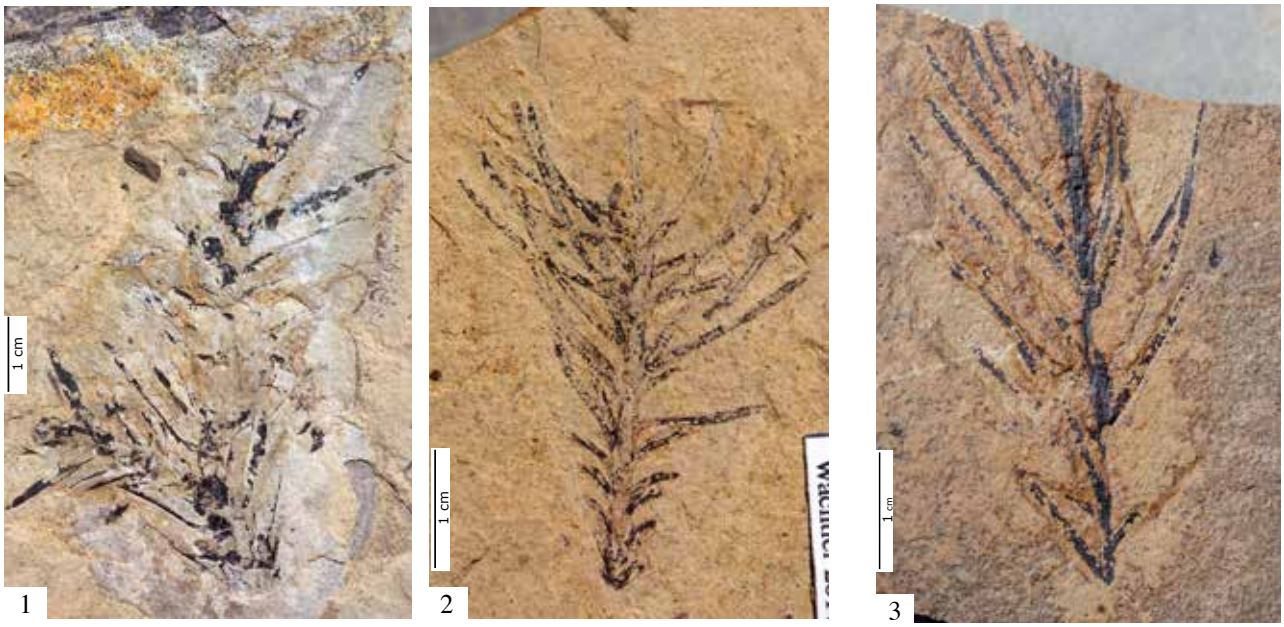

4


5


6

Extant Cedrus conifers (*Cedrus libani - Cedrus deodara*)

1. Cone of *Cedrus libani;* 2. Naked stipe of *Cedrus deodara* with the seed scales shed naturally; 3. Pollen cone; 4. Dissolving cone on the soil; 5. Isolated seed scale outer side; 6. Seed scale with one seed; the other was just released (all *Cedrus deodara*).



***Bardella splendida.* Branchlets and leaves**

1-3. Isolated twigs, showing the heterophylly of the leaves (MAT 236, MAT 235, MAT 61); Matvéevo, Kungurian (Early Permian) Coll. Wachtler

tree or on the soil. Therefore, it is almost impossible to find entire cones, or only in rare cases, when strong storms tear entire twigs from the tree. This must be taken into consideration for fossilised conifers. Therefore, *Stukenbergia kungurica*'s name was chosen this way – naming first the seed scale – and afterwards, if all doubts are cleared and a connected cone, seed scale and twig is found, then the oldest name can be accepted.

The next question is in which direction do seed scales of *Stukenbergia kungurica* indicate? It is true that in some way they are similar to Permian Majonicaceae conifers and they represent an ancestor of the Abietaceae. But the Majonicaceae from the Permian of Europe were all equipped (Wachtler, 2015) with one seed scale projecting bract, like in today's Abietaceae, which cannot be seen in *Stukenbergia*. So, the Abies lineage probably can be discharged, as well as the Araucarian lineage that is characterised by only one wingless seed coated by many micro-leaves. But we have another family that seems to be the most acceptable for *Stukenbergia* – the cedars.

The cedars are widespread from the Himalayas till the Mediterranean region and hold cones that disintegrate on the tree or at least on the soil. Their decomposed seed scales have many similarities with those of *Stukenbergia kungurica.* The typical feature of almost all Paleozoic conifers – the many micro-leaves on their seed scales – amalgamated in the following million years as seen also in Araucaria ancestor *Ortiseia* (Wachtler, 2015). Also, the supposed naked stipes (MAT 390, MAT 664) probably belonging to *Stukenbergia* indicate that they can be connected with rudimentary, narrow bract scales. Therefore, regarding *Stukenbergia kungurica* as an ancestor of the cedars is not so bizarre.

Another question is which foliage type can be connected with *Stukenbergia*. Most likely *Bardella splendida* is a good candidate. As seen with *Majonica* from Europe to a plethora of seed scales recovered, only some sparse twigs were found, which suggested that they were shed only in rare cases, as noted in today's Abietaceae also. *Bardella* twigs have something in common with extant cedar foliage. But to be certain, we would have to wait for further research.

Bardella splendida ZALESSKY 1937b

Fairly common are, especially in Matvèevo, some long needled foliage. They can reach a length of three cms or more (till 6–7 cms),

***Meyenophyllum conifera* gen. nov. sp. n. Plant, leaves and inflorescence**

1–2. Plant with two inflorescences. 3. Detail of an inflorescence (All MAT 504, designed holotype); Matvéevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos Museum

are slightly to not incurved, and they taper at the apex. They were described and drawn by Mikhail Dmitrievich Zalessky (p. 76, fig. 43). One solution can be that they can be connected with the seed scales and cones of *Stukenbergia kungurica,* a presumed Early Permian cedar ancestor.

Meyenophyllum nov. gen. WACHTLER & PERNER 2020

Etymology

It honours Sergei Meyen (Сергей Мейен) (1935–1987) from Moscow, who extensively studied the Angaran Carboniferous-Permian flora, especially the conifers. He was one of the leading evolution theoreticians of Russia, bringing new concepts about the nonlinearity of evolution.

Meyenophyllum conifera nov. gen. n. sp. WACHTLER & PERNER 2020

Holotype

CHEK 504, Chekarda (Collection Wachtler, Dolomythos, Innichen, Italy

Etymology

It is named after its resemblance to the conifers.

Type horizon and age

It is from the Early to upper Lower Permian, Kungurian.

Diagnosis

The plant has long needle-like leaves and single apical cones.

Description

Plant: Holotype MAT 504 has a length of 17 cms, whereas the longest leaves are four cms long and have a width of one cm. The plant bears terminal cones. The foliage is smooth, rounded till slightly tapered on the apical part and has no mid-vein. The fruc-

Reconstruction of *Meyenophyllum conifera* with the insect *Agetopanorpa punctata*, a scorpionfly and *Paleuthygramma tenuicornis* (Caloneurodea).

tifications are four to five–5 cms long and about 1.5 cms broad and consist of an arrangement of leaves that are similar to the sterile one.

Discussion

The classification or insertion of *Meyenophyllum conifera* into one of the existing families is not easy. From the first appearance, it can be regarded as belonging to some conifer genus, but some details suggest that its appearance is not gymnospermous. It is true that in the Early Permian of the Fore-Urals we encounter conifer genera like *Taxodiella bardaeana* (Zalessky, 1837b; Meyen, 1997), holding small incurved leaves or *Kungurondendron sharovii* (Meyen, 1997) with its vegetative shoots branching seldom and irregularly. The only conifer with relatively long needles is represented by *Bardella splendida* (Zalessky, 1937b), but it has no similarities with *Meyenophyllum conifera.*
The strange branching is also not like those from the lycopods. Unfortunately, in today's angiosperms, we encounter plants that look like lycopods as *Hippuris* or like conifers (*Erica* or *Phylica*) because of their foliage. Even some of the extant Liliaceae like *Lilium bulbiferum* with their erect stem and lanceolate leaves, terminal inflorescences have similarities with Early Permian *Meyenophyllum conifera*. Therefore, we must wait for further findings to classify this plant well.

Contributions

Thomas Gerasch, Martin Dammann, Thomas Perner, Nicolas Wachtler and Michael Wachtler made fossil specimens available. Michael Wachtler analysed the data, made the drawings, photos and wrote the paper. Thomas Perner supported the work financially.

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