Horsetails from Early Permian Fore-Urals

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Horsetails from the former Paleozoic continent, Angara, were one of the first described plants along with *Psygmophyllum* leaves from Russia. However, it was a long and rocky road, which till now is only partially trodden, that had to be covered to enlarge our knowledge about these highly interesting plants. One of them – *Equisetina magnivaginata* – a low-growing Sphenophyta with rounded strobili resembles in many parts today's *Equisetum*. Other two found in the same Artinskian-Kungurian layers can be inserted due to their characteristic cones in the Calamitaceae. *Paracalamites striatus* with its fertile organs *Sachyogyrus multifarius* resemble the European *Calamostachys* type. The pointed bracts on the slender strobili claw densely the sporangiophores. *Paracalamites decoratus*, otherwise with its fertile organs *Kutorgastachys eichwaldii* nov. gen. sp. n., was equipped with only one bract coating the entire sporangia. This feature was never encountered in other parts of the world before.

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Horsetails from Early Permian Sibirian Angara-continent

Left: the Calamitaceae *Paracalamites decoratus* with attached *Kutorgastachys eichwaldii*-strobili; in the **middle**: the Equisetaceae *Equisetina magnivaginata* with cones; **right:** another Calamitaceae *Paracalamites striatus* with *Sachyogyrus multifarius* strobili.

Introduction

The origin of Sphenophyta can be traced back to the Devonian, but they reached a heyday in the Paleozoic-Mesozoic, with huge stems dominating large parts of the Earth. The horsetails were also a common flora element in the Early Permian Angara-continent, being present in several genera and species. The most important features to classify fossilised horsetails are their different stems, side leaves and the strobili. Additionally, different growth-stages must be taken into consideration. In the Permian Angaraland, we encounter about three to four different trunks with parallel ridges that are aggregated more distantly or narrowly. We record four or more possibilities of lateral stemlets with different appearance of the leaves or leaf-sheaths, and we encounter the most important recognition feature - till now three different strobili. One of them - Equisetina magnivaginata - a low-growing horsetail with rounded strobili resembles in many parts today's Equisetum. Two others - Paracalamites decoratus and Paracalamites striata - can be classified as belonging to the Calamitaceae.

The Origin of the Horsetails

Through the Paleozoic, we can insert the horsetails in two main groups: the Equisetales, with its main Permo-Triassic representative *Equisetites*, which holds ovoid fertile organs, collected singly or in groups, sitting on a short stem with collar (Wachtler, 2016). Apart from their impressive stemsize of about 10–20 cms, which today is not equalled by any other species of horsetail and their richness in fertile strobili for any single plant, only the extant horsetail genus *Equisetes* is similar and can be regarded as relative.

The genus *Equisetites* was introduced in 1833 by Kaspar Maria Graf Sternberg for fossilised species till the Tertiary period, to distinguish them from the extant genus *Equisetes*. The Equisetaceae can be distinguished from other Sphenophyta by their usually bulbous or elongated reproductive organs segmented in many hexagonal bracts. These peltate shields hold their sporangial sacs hanging down on the underside. The main stems and lateral stemlets evidence narrow parallel veins. A whorl of ta-

pering leaves forms a collar around the leafsheaths.

The other group, the Calamitales, are also preserved as voluminous stems with characteristic longitudinal ribs and furrow ornament divided by internodal regions. These fossilised pith casts took the name Calamites. They are accompanied by the art-form names Annularia leaves and Calamostachys reproductive organs (Taylor et al., 2009). Although the name Calamites, introduced by the French palaeobotanist, Adolphe Brongniart in 1828, was used for the stems or pith casts, in this work, it will be used for the whole plant, including secondary whorls, leaves, strobili and sporangiophores.

The leaves of the Calamitaceae consisted usually of verticils surrounding the secondary branchlets like a collar. Some of the species, especially on the Euramerican continent, hold decorative circles like *Annularia stellata* or *Annularia spicata*, while other whorls were formed only by needle-like appendices like *Calamites wachtleri* (Perner, 2013; Wachtler 2012, 2013). The strobili hold sporangia encased usually by several sterile bracts.

The first Calamitaceae appeared in the Lower Carboniferous, although they were rare, and spread extensively in the Upper Carboniferous period. They became common in the Permian, only to decline suddenly after that. Some species in the related genus Neocalamites managed to survive into the Late Permian, only to disappear after that from the face of the Earth. Upper Permian Neocalamites benckeae from the Italian Alps can be regarded till now as last known representative of the Calamitaceae, because sometimes Triassic species classified merianii) (Neocalamites held Equisetites-like cones and were combined as Schizoneura merianii (Wachtler, 2016).

One of the most interesting question is: Where did the most dominant Paleozoic horsetail families, *Calamites* and *Equisetes*, separate in Devonian, or did they have a long-lasting common way till before diverging on the Carboniferous-Permian border? What were the differences between the Sphenophyta on Angara and the Euramerican landmass? Can Permo-Triassic Equisetites or Angaran genus *Equisetina* considered parented with today's *Equisetum*?









Primary and secondary branching of today's horsetails

1. Equisetum telmateia, biggest European horsetail with lateral branchlets; 2. Equisetum bogotense, stem axis and detail of lateral branching; 3–4 Closed and open sporangiophores of the field horsetail (Equisetum arvense).

The Research History of Permian Horsetails from the Russian Angara Continent

Horsetails from the former Paleozoic continent Angara arouse the interest of the first scientists. Unfortunately, the research was never intense, and above all, only a few local people were able to reach the intellectual horizon to collect fossils systematically. Additionally, the Permian Russian Sphenophyta every time remained out of light from an exchange of knowledge due to mostly Western researches influencing works, doctrines and opinions.

The first mention we have is in 1838 from Stephan Kutorga, Professor of Natural Sciences at the University of Petersburg, who described several horsetails from the Kama-Belaja river confluence (Calamites articulatus, Calamites columella, Calamites trigonus, Calamites irregularis, Calamites cellulosus) but without mentioning the exact localities. That some were found in the Fore Urals can be taken into consideration because in his work, he described two

characteristic plants from this area (Sphenopteris interrupte-pinnata and Sphenopteris cuneifolia), which Wilhelm Philipp Schimper changed to Psygmophyllum later in 1870.

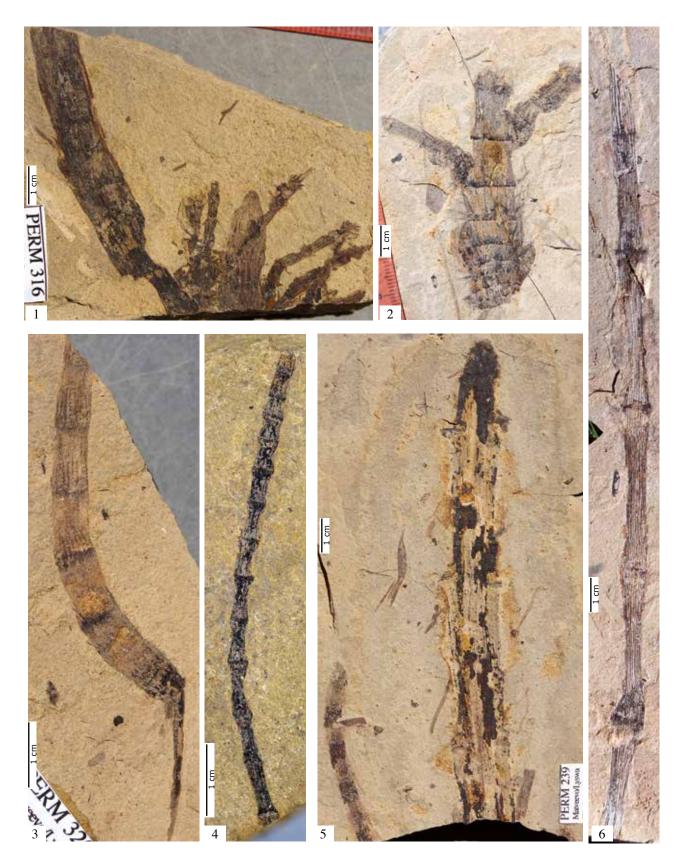
Some years later, in 1846, the German-Russian geologist, physician and naturalist, Karl Eduard von Eichwald (1795–1876) (Russian: Эдуард Иванович Эйхвальд) described several plants like Calamites that he collected near Artinsk in the Ural region besides some Goniatites and brachiopods (Bei Artinsk im Ural, wo eine Menge Goniatiten, aber alles neue Arten wie G. d'Orbignianus Hossae, Kingianus, mit dem Nautilus tuberculatus und bicarinatus, Orthoceratites ovalis, Calamites Suckowii, Stigmatodendron Ledebourii, Haidingera pyriformis, Knorria imbricata u. dergl. vorkommen).

Based on the collections of Eichwald and Kutorga, the Russian palaeobotanist, M. D. Zalessky (1927) changed the genera name *Calamites* to *Paracalamites*, adapting it for various species (*Paracalamites kutorgae*,



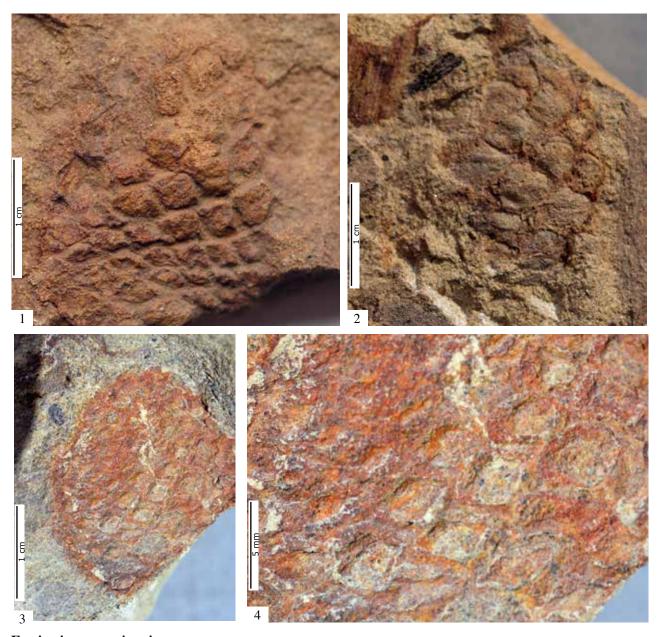
Equisetina magnivaginata. Early Permian Equisetaceae

1–3. Juvenile plants or seedlings with attached creeping rhizomes (MAT 699, MAT 300, MAT 295); 4. Part of a stemlet with detail of the leaf-sheaths (MAT 883); 5. Almost complete stem with leaf-sheaths (CHEK 18); 6–7. Juvenile plants with basal stemlets (MAT 318, MAT 317), Chekarda, Matvéevo, Kungurian (Early Permian)



Equisetina magnivaginata. Early Permian Equisetaceae

1. Several stemlets and an apical part (MAT 316); 2. Stem with lateral branches (MAT 299); 3. Lateral stemlet (MAT 320); 4. Stemlet with internodes (MAT 340); 5. Apical part of a stem with lateral branchlet (MAT 239); 6. Monopodial stem (MAT 723); Matvéevo, Kungurian (Early Permian) Coll. Wachtler Dolomythos Museum



Equisetina magnivaginata cone

1. Strobilus (ARTI 21 Artinskian, Panteleykovo); 2. Strobilus (MAZ 20, Mazuevka); 3-4. Single strobilus and detail (MAT 75); Matvéevo, Kungurian; (Early Permian Coll. Wachtler, Dolomythos Museum

Paracalamites decoratus, Paracalamites striatus), drawing them but without going more into detail about their scientific importance. Probably the reason was to differentiate European Calamites species from those of Russia and to distinguish Paracalamites species usually having relatively widely separated tangential striae from Equisetales with narrow longitudinal ribs. This concept was intuitive but nevertheless not absurd because differences do exist between Euramerican Calamitaceae and those from the Siberian Angaraland.

To encrease the confusion, M. D. Zalessky, in 1937, applied the name *Phylloteca*, – created in 1828, when Brongniart described the species *Phyllotheca australis* coming from Hawkesbury River in Australia (Rayner, 1992) – for other most common horsetails in the Fore-Urals, elaborating a plethora of species (*Phyllotheca scyphulifera* (p. 41, Fig. 2), *Phyllotheca sylvenis* (p. 41, Fig. 3), *Phyllotheca campanularis* (p. 42, Fig. 4), *Phyllotheca biarmica* (p. 43, Fig. 5).

It is doubtful that Northern hemisphere Sphenophyta can belong to a Gondwanan



Equisetina magnivaginata Reconstruction

A landscape with the small *Equisetina magnivaginata* horsetail. In the foreground, some creeping rhizomes are visible. **Right:** some horsetails generate strobili that look like extant *Equisetum*.

family like the Phyllothecaceae. Additionally, in 1939, he added more species like *Phyllotheca aperta* (p. 335, Fig. 6) and mixed fertile strobili with sterile foliage establishing the name *Sachyogyrus multifarius* (p. 335, fig. 7 and 8), all from Chekarda and Matvèevo. As if we can find today on a normal lake on a few square metres so many different horsetail-species and genera!

Unfortunately, in 1934, M. D. Zalessky changed the name *Paracalamites striatus* again to *Paracalamitina striata* for two specimens from the Petchora basin, justifying by saying that they have resemblances with *Phylloteca striata*. All in all, an untraceable process.

Naugolnykh (2002) followed this concept of adopting the name *Paracalamitina striata* and connecting *Equisetinostachys* cones to them. But *Equisetites* strobili differ largely from *Calamites* fructifications! In *Equisetites*, like in all of today's horsetails, peltate sporangiophores are aggregated in strobili, while in *Calamites* the reproductive organs (*Calamostachys* type) are

composed of pointed bracts that claw the sporangiophores densely.

In 1929, M. D. Zalessky had described Tchernovia (synensis) as a poorly preserved leaf or reproductive fragment of a plant (PI XVI, Fig. 4 & 5), inserting it in the Equisetaceae. It is still unclear if it belongs to some paleo-angiospermous fruit organ. After that, the genus name was expanded to a whole family, the Tchernoviaceae (Meyen & Menshikova, 1983), including other Permian Sphenophyta and sometimes the genus Phyllotheca, as well as Paracalamitina (Naugolnykh, 2002). Whether all the autochthonous families summarized in the family of the Tchernoviaceae (Meyen & Menshikova, 1983) like Phyllotheca or Annulina (Neuburg, 1954) can be accepted is doubtful because just the name Annulina for secondary branching horsetail leaves was declared invalid and changed to Umbellaphyllites (Doweld, 2002).

To complicate the no-go situation for Angaran horsetail strobili the genus name *Bowmanites* was also adopted, introduced by E. W. Binney (1871, p. 59, pl. XII, Fig.

1-3) (Bowmanites cambrensis) for Upper Carboniferous cones from South Wales thought to belong to Sphenophyllum horsetails, usually referred to as creeping Sphenophyta. This inflorescencegenus was then accepted by Naugolnykh for Angaran Sphenophyllum plants (1998, Bowmanites biarmensis p. 32, Fig. 12D, or 2007 Bowmanites biarmensis p. 112, Fig. 42, Pl XI, fig. 1,5, Pl. XII Fig. 3) bringing the fertile parts in connection to Sphenophyllum biarmicum (Naugolnykh, 2002, 2004, 2005, 2007, 2016). This is highly speculative because it seems that the thought Sphenophyllum leaves and twigs indicate more in a seed-plant direction. Additionally, without going into nomenclature, problems can be stated that the original *Bowmanites* cones from Upper Carboniferous of Europe differ a lot from Angaran strobili. The multitude of names introduced in the past by the scientists confirm that we are only at the begin of a creating a reliable classification.

We have the same problem with Euramerican Calamitaceae: many names for the same plant. The most widespread Upper Carboniferous European horsetail stem is classified as *Calamites multiramis*, the sometimes beautiful preserved lateral twigs took the name *Annularia stellata*, the reproductive organs *Calamostachys tuberculata* and so on.

Using the name Annularia carinata for Angaran Calamitaceae is not justified either because it is reserved for Early Permian Gzhelian-Asselian-Sakmarian Calamites gigas in connection with Calamostachys dumasii reproductive organs and Annularia carinata whorls characterised by anisophylly of the verticils and distinguished by a prominent mid-vein (Wachtler, 2017).

To avoid the Babylonian language confusion of naming genera and species that probably nobody is able to understand, a simplified system will be proposed based on their reproductive organs because the stem- or leaf anatomy of the horsetails cannot be considered convincing enough for a genus classification. To make it short, we encounter in the Early Permian Fore-Urals at least two strobili unquestionably belonging to the Calamitaceae and, till now, one pertaining to the Equisetaceae. The question is therefore, which fructification belongs to which stem and leave-whorl?

Equisetaceae from the Early Permian Angara Continent

All horsetails today included in the genera Equisetum are herbaceous plants with a branched root system that creeps underground. The shoots above the ground grow from this rhizome. The stems are long, grooved, bearing hollow shoots (internodes) that are separated from each other by cross walls (diaphragms). The whorled leaves, which are arranged in rings like a collar, grow from the nodes. Leaf nodes encompass the lower parts of the internodes, creating the pattern typical of horsetails. The reproductive organs consist of apical, egg-shaped structures comprised of shield-like sporangiophores, where the sporangia are located on the underside.

Equisetina magnivaginata ZALESSKY, 1939

In 1939, M. D. Zalessky (Zalessky, 1939, pp. 329–331, Fig. 1–3) introduced the name *Equisetina magnivaginata* for naked stems collected in Chekarda and Matvèevo to differentiate them from European *Equisetites* horsetails. This different genus name can be accepted due to some differences between *Equisetites* and *Equisetina*. Although Zalessky never found strobili – bulbous fructifications with peltate shields from these localities – these can be regarded as belonging to *Equisetina*.

Plant: Low-growing horsetail with creeping rhizomes (MAT 699, MAT 300, MAT 295). The main stems did not exceed a thickness of 2 cms and a length of 50–70 cms (MAT 340, MAT 239, MAT 723). Lateral branches sprouted, but they were not frequently seen. The stems were segmented with sheaths formed of minute leaves, coating the internodes (MAT 883, CHEK 18).

Inflorescences: Equisetina magnivaginata generate just one apically sitting, about 2–3 cms in size, strobilo [ARTI 21 (Artinskian, Panteleykovo), (Kungurian MAZ 20, Mazuevka), (MAT 75)], probably on the main stem or on the few lateral branches. The sporangiophores were equipped with hexagonal covering bracts.

Remarks:

Equisetina magnivaginata constitutes the most common horsetail, especially in Matvèevo and less in Chekarda. This horsetail is interesting due to several facts: it was a



Kutorgastachys eichwaldii - Calamitaceae strobili

1–2. Several elongated strobili attached to the main stem; a bract pattern is visible (MAT 698); Matvéevo, Kungurian; Early Permian Coll. Wachtler, Dolomythos Museum

low-growing Sphenophyta and therefore the whole plant is known. Main feature was its reduced number of strobili. This constitutes a big difference to the till 20 cm in diameter reaching and up to twenty infructescences on each lateral branchlet generating *Equisetites arenaceus* from the European Triassic.

In that, Equisetina magnivaginata was more similar to extant Equisetum species than all Equisetites species of the Euramerican Permo-Triassic. Astonishingly, it is easier to trace an evolution line from Equisetina magnivaginata to today's Equisetum horsetails than from the huge stems with hundreds of strobili of Equisetites.

The first appearance of *Equisetina* we have in Artinskian sediments near Arti in several places (Yugush_01, Panteleykovo 06, 28), also with cones (Panteleykovo 21). The distinction on the basis of the stems is not easy because even *Rufloria* (a presumed monocot angiosperm) and some Calamitaceae sometimes show narrow veins. But *Ruflo-*

ria has a distinguishing feature, that is, no leaf-sheaths; Paracalamites decoratus has a mosaic-ornament on their main and lateral stems, whereas Paracalamites striata and other horsetails have broader parallel ridges. Equisetina is widespread in Kungurian sediments from Matvèevo and less from Chekarda and Mazuevka.

Equisetina magnivaginata from the Angara can therefore mostly be distinguished by their long segmented stems with minute tapering leaves on the leaf-sheaths and the narrow parallel veins.

On the Euramerican continent, the Equise-tales were recorded from the Carboniferous-Permian boundary. They were rare in Early Permian with Equisetites hemingwayi, Equisetites vaujolyi or Equisetites geraschi (Perner & Wachtler, 2015) and Upper Permian Equisetites siberi, of which just their characteristic globose cones are recorded. The genus Equisetites, bridged the Permian-Triassic transition without bigger restrictions

or changing, to form one of the dominant plant families over the Triassic (Wachtler, 2016).

Especially the species *Equisetites arenaceus* dominated in the Early-Middle Triassic vast parts of Europe. This giant horsetail arrived with its monopodial hollow stem, segmented at symmetrical distances, till a diameter of 20 cms. Many lateral branches sprout in whorls from beneath the collar. The small leaves were fused with the stem. The strobili were mainly ovoid to round and up to five cm long and 2-3 cm wide, collected singly or in groups on the lateral branches. The sporangiophores were equipped with hexagonal covering on leaves and a slight umbo. On the underside, numerous hanging spore sacs were arranged around a tablelike attachment connected to the central axis. The big difference - and unknown in living horsetail plants - is the up to 20 infructescences on each lateral branchlet, while today the plants tend to have just one single sporophyll cone. Another parented horsetail was Schizoneura with smaller strobili and bracts.

Calamitaceae from Russian Angaraland

Additionally, we encounter in the Early Permian Fore-Urals, at least two different genera of Calamitaceae. They can be distinguished mostly because of their different infructescences. Also, their stems vary considerably between each other. More difficulties arose about the leaf-structure of their lateral branchlets that need further examination.

Kutorgastachys nov. gen. PERNER & WACHTLER 2020

Etymology

It honours Stephan Semenowitsch Kutorga (1805–1861), Professor of Natural Sciences at the University of Petersburg. In 1838, he edited "Beitrag zur Kenntniss der Organischen Ueberreste des Kupfersandsteins am westlichen Abhange des Ural" (Contribution to the knowledge of organic remains in the Copper Sandstone of the Western Ural) that was the first publication about the richness of Uralian fossils.

Diagnosis

The reproductive organs from Calamitaceae horsetails are coated by one single bract scale.

Kutorgastachys eichwaldii nov. gen. n. sp. PERNER & WACHTLER 2020

Type horizon and age

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

Holotype

MAT 63, Matvèevo (Collection Wachtler, Dolomythos, Innichen, Italy

Etymology

It is named after the German-Russian geologist, physician and naturalist, Karl Eduard von Eichwald (1795–1876) (Russian: Эдуард Иванович Эйхвальд), who, in 1846, first described plants collected near Artinsk in the Ural region.

Description

Reproductive organs: The strobili are about five cm long, 1–3 cm wide, with a short and slender basal stipe (designed holotype MAT 63; also MAT 211, 330, MAT 718). One single scale coats each sporangium densely. This scale is often reflexed back on the outside, especially after maturity.

Stems: Of Paracalamites decoratus-type. Monopodial stems up to 10 cms thick characterised by a mosaic pattern of elongated and deeply incised segmented chambers (ARTI 25, MAT 66). Lateral branches with the same features, beginning basally incurved and restricted with telescopic jointed internodes and finishing apically in the same way (MAZ 31, MAT 731, MAT 696 CHEK 379). That both the main stem and also the lateral have the same mosaic-form pattern is clearly evidenced in CHEK 55. Stemlets of the third order: Probably of Annulina neuburgiana type (Neuburg, 1954, Radczenko, 1966). These broad-ridged with internodes coated by leaf rosettes; leaves varying from only a few cm till up to 10-15 cm and a width of 0.5 cm.



Paracalamites decoratus with Kutorgastachys-strobili. Reconstruction

Paracalamites decoratus was a Calamitaceae endemic to the Permian Angaraland. The characteristic mosaic-like pattern of the main and lateral stems renders them different from other known Calamites species. Also, their strobili were formed by entirely fertile bract-leaves that coat the sporangiophores.

Discussion

Kutorgastachys eichwaldii-fructifications, as well as Paracalamites decoratus stems and Annulina neuburgiana strobili are frequently seen and can be distinguished from other plants apart from the Sphenophyta without doubt. Also, their cones can be differentiated well from other more typical Calamitesresembling infructescences from Sachyogyrus multifarius-type. The main problem is deciding as to which stem and leaf-whorls do they belong? That the main stem is connected in a strange way with the stemlets of the second order could be identified due to lucky findings (CHEK 55). That the stemlets of the second order hold branchlets of third order can be seen in CHEK 379. They were characterised by deeply incised ridges which on the segments were coated by short but also very long leaves of the Annulina neuburgiana type. In that, they have many resemblances with the horsetail genus Schizoneura (paradoxa and S. merianii) from the European Triassic. The difference is that Schizoneura hold strobili with shields and sporangiopores like Equisetites, whereas Early Permian Kutorgastachys resembled the Calamitaceae more.

Sachyogyrus multifarius, Calamitaceae

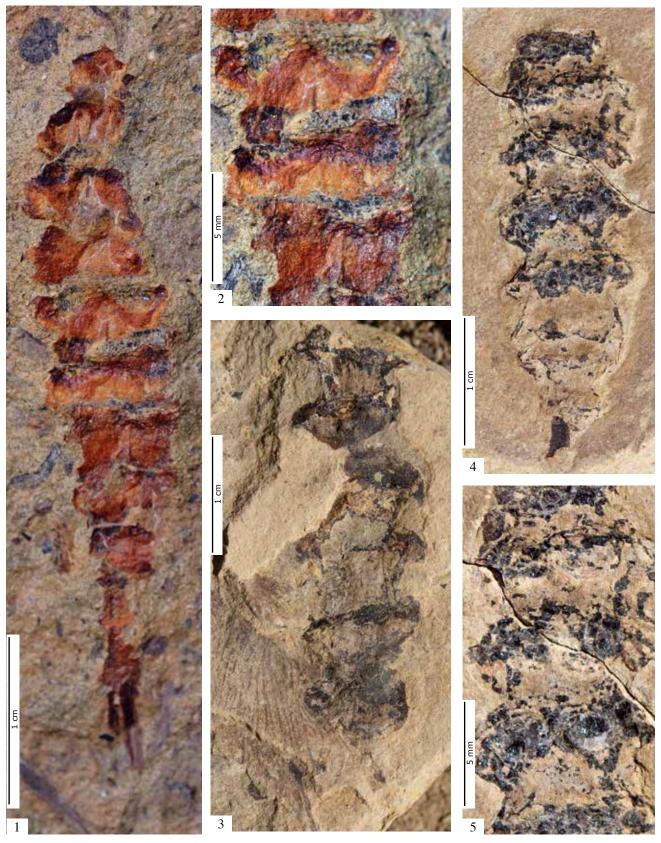
In 1939, Zalessky described and named the fertile organ of a horsetail with the name Sachyogyrus multifarius (Zalessky, 1939, p. 335, Fig. 8), connecting it with sterile Equisetina branchlets. Bringing order in the different schema can be stated as Sachyogyrus multifarius represents a reproductive organ of a Calamitaceae resembling mostly the Calamostachys type from the Euramerican continent and belonging to Kungurian Paracalamites horsetails. The connecting branchlets can be searched in some Annularia-whorls frequent in these layers.

Plant: Horsetail with main stems (of *Paracalamites striatus*-type) reaching a size till 10 cm in diameter (MAT 244). Longitudinal ribs relatively broad spaced



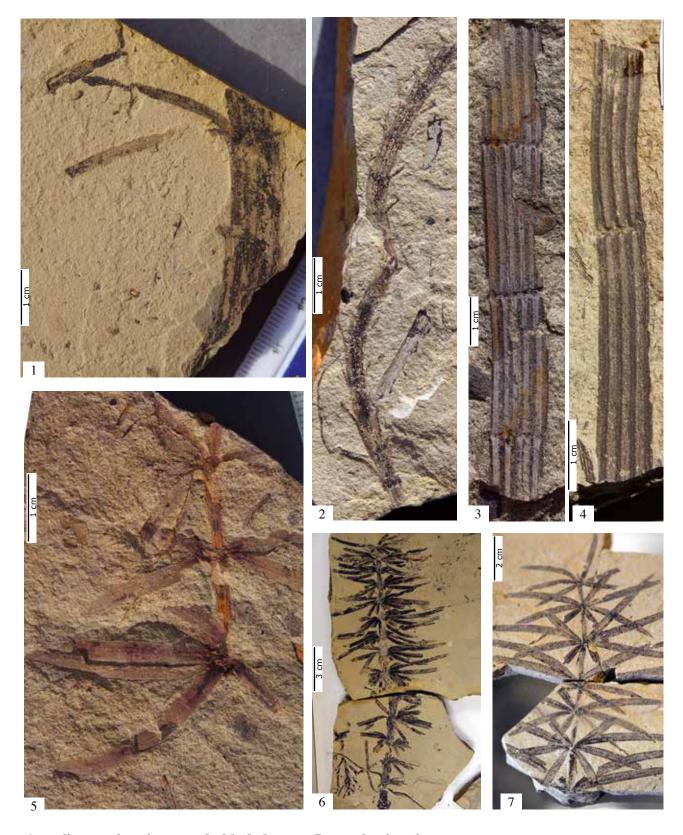
Calamitaceae from Angara-Land. Paracalamites decoratus

1. Monopodial main stem from the Artinskian locality Panteleykovo (ARTI 25); 2. Lateral branchlet with basally telescopic-jointed internodes (CHEK 312, Chekarda, Coll. Perner); 3. Lateral branchlet with densely arranged leaf-sheath (MAZ 31, Mazuevka); 4–5. Lateral branchlets with details of the mosaic-ornament (MAT 731, MAT 696, Matvèevo); 6. Huge lateral branchlet CHEK 379, Chekarda, Coll. Dammann) 7. Apical part of a main stem (MAT 66, Matvèevo); 8. Interesting main stem in connection with a lateral branchlet (CHEK 85, Chekarda, Coll. Wachtler).



Kutorgastachys eichwaldii strobili belonging to Paracalamites decoratus

1-2. Well conserved cone with reflexed bracts (Designed holotype MAT 63); 3. Sporangiophore (MAT 718, Coll. Gerasch); 4-5. Additional cone (MAT 330); Matvéevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos Museum



Annulina neuburgiana, probably belong to Paracalamites decoratus

1. Stemlet with long lateral leaves on the leaf-sheaths (MAT 708); 2. Small lateral stem with leaf-whorls. 3–4. Lateral stems with deeply incised ribs (CHEK 20, MAT 247); 5. Whorl of leaves (MAZ 41, Mazuevka); 6–7. Branches of the third order (Perm Museum)



Paracalamites striatus with Sachyogyrus multifarius-strobili

The Calamitaceae Paracalamites striatus from Early Permian Angaraland with Sachyogyrus multifarius cones

with periodic nodes. Lateral branchlets ending with a tuft of many secondary shoots. Secondary whorls 5 mm wide, from five to seven cm long characterised by closely spaced internodes surrounded by a leaf sheath. Leaves delicate, 2 mm long acuminate (CHEK 83, MAT 139, MAT 321, MAT 700). Mainly, about three leaves on each side form a whorl. Therefore, it can be suggested that altogether ten to twelve leaves form the collar.

Reproductive organs: Of Sachyogyrus multifarius type. Complete cones 5-6 cm long and 2-3 mm wide. CHEK 89 represents a young immature cone, MAT 734 is a mature cone with many empty sporangia. The sporangiophores are rounded to elliptical and 1-2 mm in size. Both consist of alternating whorls (about 25-30) of sporangia and bracts. The pointed bracts claw the sporangiophores densely. The cones are distinguished by a short basal stipe.

Remarks: It is obvious that *Sachyogyrus* multifarius as well as Kutorgastachys

eichwaldii represent two distinct Calamites horsetail strobili. But Sachyogyrus multifarius is similar to European Calamitaceae like Calamostachys, where a common feature is their microleaves clawing the sporangia in Kutorgastachys eichwaldii with only one protecting leaf envelop the sporangia.

Conclusion

It can be stated that the horsetails dominate the riverbanks or lakes of the early Permian Angara, and their most favourable growing places were brackish water areas (Wachtler, 2017). With the Kungurian Equisetina magnivaginata cones and Sachyogyrus multifarius as well as Kutorgastachys eichwaldii fructifications, it is proved that on the Carboniferous-Permian border, the Calamitaceae and the Equisetaceae were largely different in their reproductive features. But the questions are not answered completely. In the sediments from Chekarda and Mat-

vèevo different leaf-whorls of the Annular-



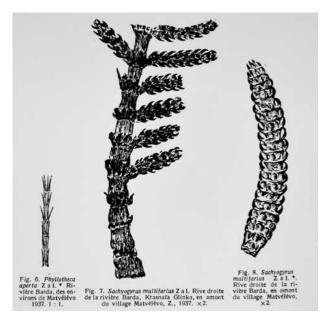
Calamitaceae from Angara-Land. Paracalamites striatus

1. Monopodial main stem from the Artinskian locality Panteleykovo (ARTI 22); 2. Main stem, 8 cm wide (MAT 244, Matvèevo); 3–5. Stems with diverging leaves or branchlets (CHEK 343 Coll. Gerasch, MAT 241, CHEK 16); 5) Lateral branchlet (CHEK 83); 6. Detail of a lateral branchlet (MAT 101, Coll. Dammann).



Sachyogyrus multifarius - Paracalamites striatus cones and sterile branchlets

1–2. A complete Calamitalean cone and detail of the clawed seeds (CHEK 89); 3–4) Another cone (MAT 734); 5) Agglomeration of diverse secondary branchlets (MAT 700); 6–7) Isolated lateral branchlets with coating leaves (MAT 139, MAT 321); Kungurian (Early Permian) Coll. Dolomythos Museum



Sachyogyrus multifarius. Original drawing from Zalessky 1939; branchlets and cones. Also *Phyllotheca aperta* described by Zalessky can be regarded as a sterile leaf-synonym of *Sachyogyrus multifarius*.

ia type as well as *Peremopteris biarmicum* were encountered additionally. Therefore, other horsetail strobili can also be expected.

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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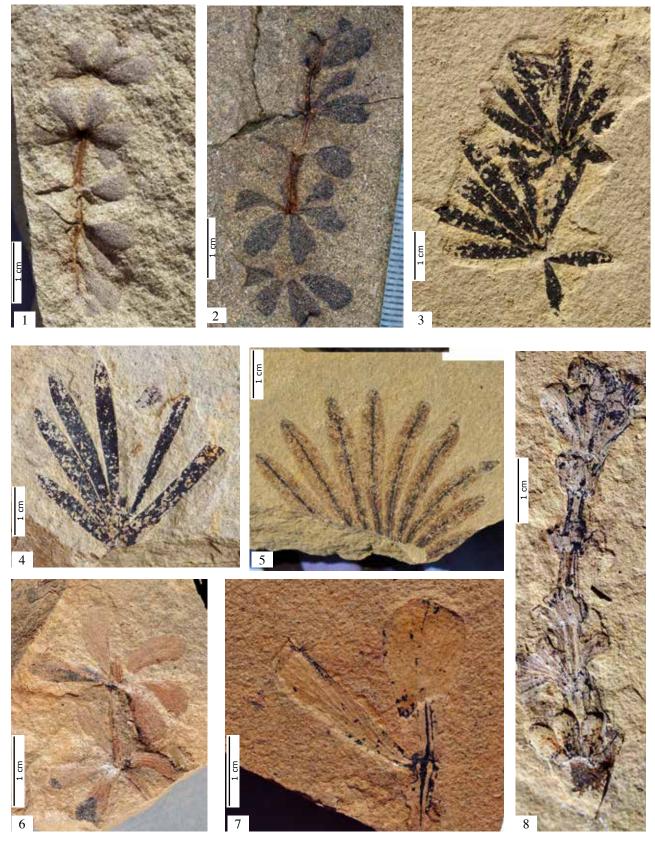
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Horsetail leaves of not completely resolved classification

1-2. Sphenophyllum-type branchlets (CHEK 20, coll. Wachtler, CHEK 347 Coll. Gerasch); 3-5. Annularia-type whorls (MCHEK 57, Coll. Wachtler, CHEK 693, Coll. Perner, MAT 114 Coll. Dammann); 6-8. *Sphenophyllum biarmicum*-type whorls (CHEK 368, MAT 52, MAT 47, Coll. Wachtler); Kungurian (Early Permian) Coll. Dolomythos Museum

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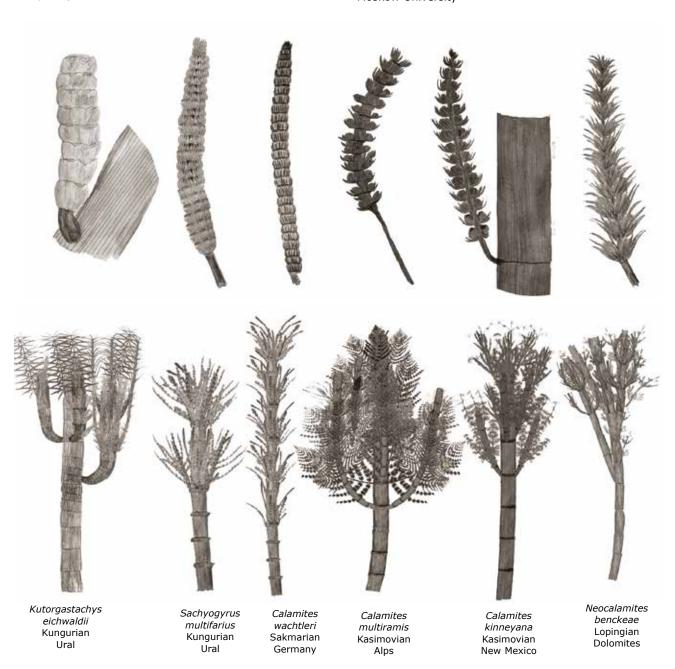
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Various Calamitaceae from all over the world

Kungurian Kutorgastachys from the Fore Urals differs probably most



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