# The evolution of horsetails from Permian Angara-Land till Euramerica

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From the Upper Carboniferous over the Permian we have on the Northern hemisphere an arising of the giant horsetails represented especially by the Calamitaceae and the Equisetaceae. The first one disappeared in the Late Permian, whereas the latter constitute today the only one genus of surviving Sphenophyta. A common ancestor of the two groups is difficult to elaborate. This work gives an insight in the evolving of the two families from Russian Angara-Land till Europe and North-America and tries to analyze the differences based mainly on their reproductive organs. A new combination for the Early Permian Angaran character-horsetail was introduced: *Paracalamites campanularis* nov. comb. Also for the American Early Permian Sphenophyta a new species-name to be revealed was necessary: *Calamites kinneyana* n. sp. to delimitate them from the even different European Calamitaceae.

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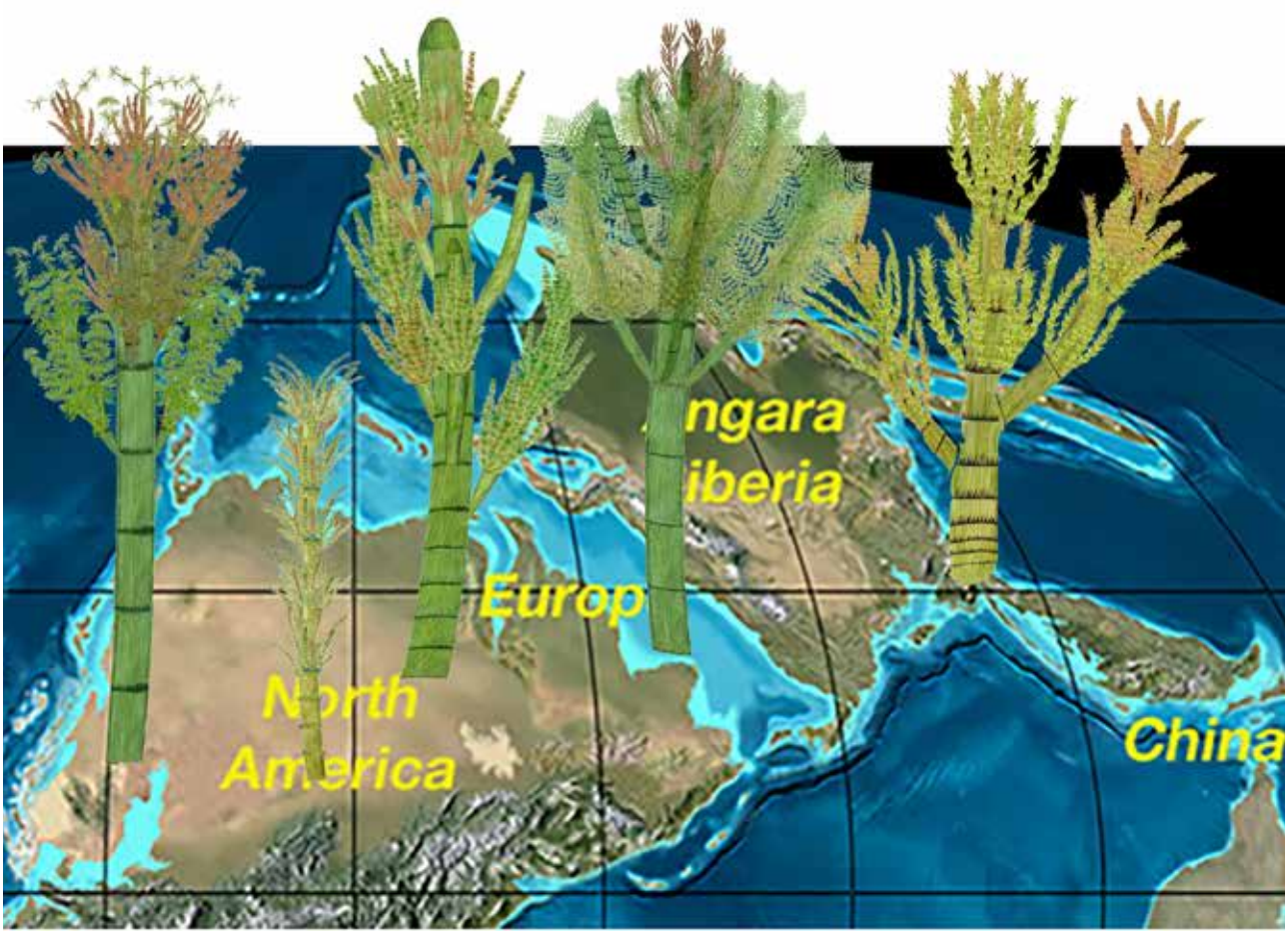
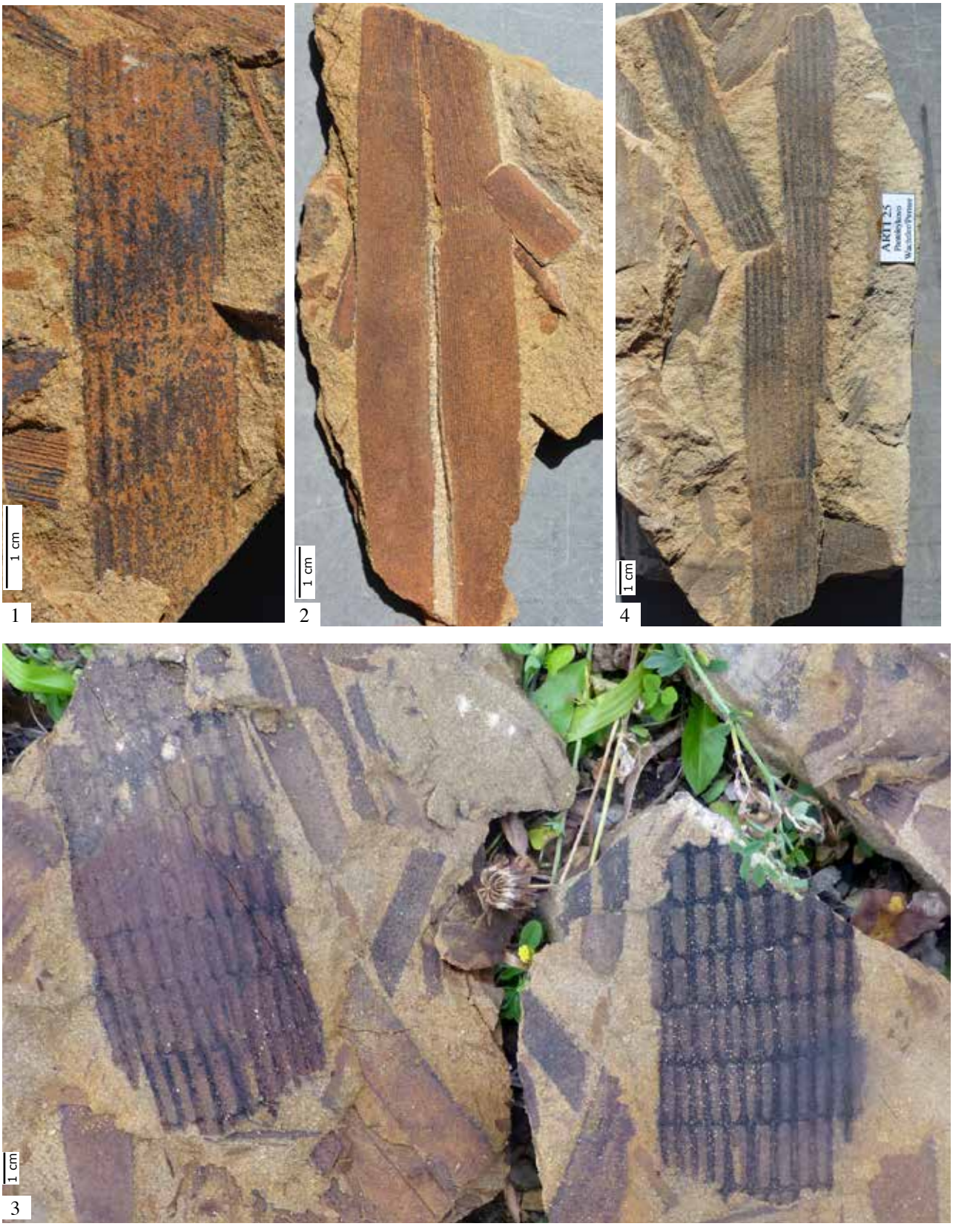



Calamitaceae from the Northern hemisphere on the Carboniferous-Permian border: From left: *Calamites kinneyana* from United States (Earliest Permian); European *Calamites wachtleri* (Earliest Permian); *Calamites tregiovensis* (Early Permian); *Calamites gigas* (Early Permian); *Paracalamites campanularis* (Angara-Land Early Permian)

The origin of Sphenophyta can be traced back to the Devonian, but they reached the Paleozoic-Mesozoic a heyday with huge stems, dominating large parts of the Earth. Over the Paleozoic we can insert the horsetails in two main groups: The Equisetales, with its main Permian-Triassic representative - *Equisetites* - hold mainly ovoid to elongated fertile organs, collected singly or in groups, sitting on a short stem with collar. The infructescences consist of an arrangement of peltate shields with several elongated pending sporangia on the lower surface (Wachtler, 2016). Apart from their impressive stem-size, which today is not equaled 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 therefore as direct relative.
The other group, the Calamitales, are also preserved as voluminous stems with characteristic longitudinal ribs and furrows ornament divided by internodal regions. These fossilised pith casts took the name *Calamites*.
They are accompanied by *Annularia*-leaves and *Calamostachys*-reproductive organs (Taylor et al., 2009). Although the name *Calamites*, introduced by the French paleobotanist Adolphe Brongniart in 1828, was used for the stems or pith casts, in this work it will also use to describe and insert the whole plant composed of secondary whorls, leaves and sporangiophores.
The leaves consisted of verticils surrounding like a collar the branchlet. Some of the species hold decorative circles like *Annularia stellata* or *A. spicata,* other whorls were formed only by needle-like appendixes. The strobili hold sporangia encased by a multiply of sterile bracts, some, especially from Russian Angara are coated by a single scale. Although we have a plethora of different descriptions about parts of the Calamitales the only certain distinguishing feature are their elongated reproductive organs which differ from species to species considerable. The first Calamitaceae appeared in the Lower Carboniferous, although they were seldom, but they spread extensively in the Upper Carboniferous period. They were even widespread in the Lower 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 representative of the Calamitaceae, because the sometimes as Triassic species classified (N*eocalamites merianii*) hold typical *Equisetites*-like cones and were therefore combined as *Schizoneura merianii* (Wachtler, 2016).

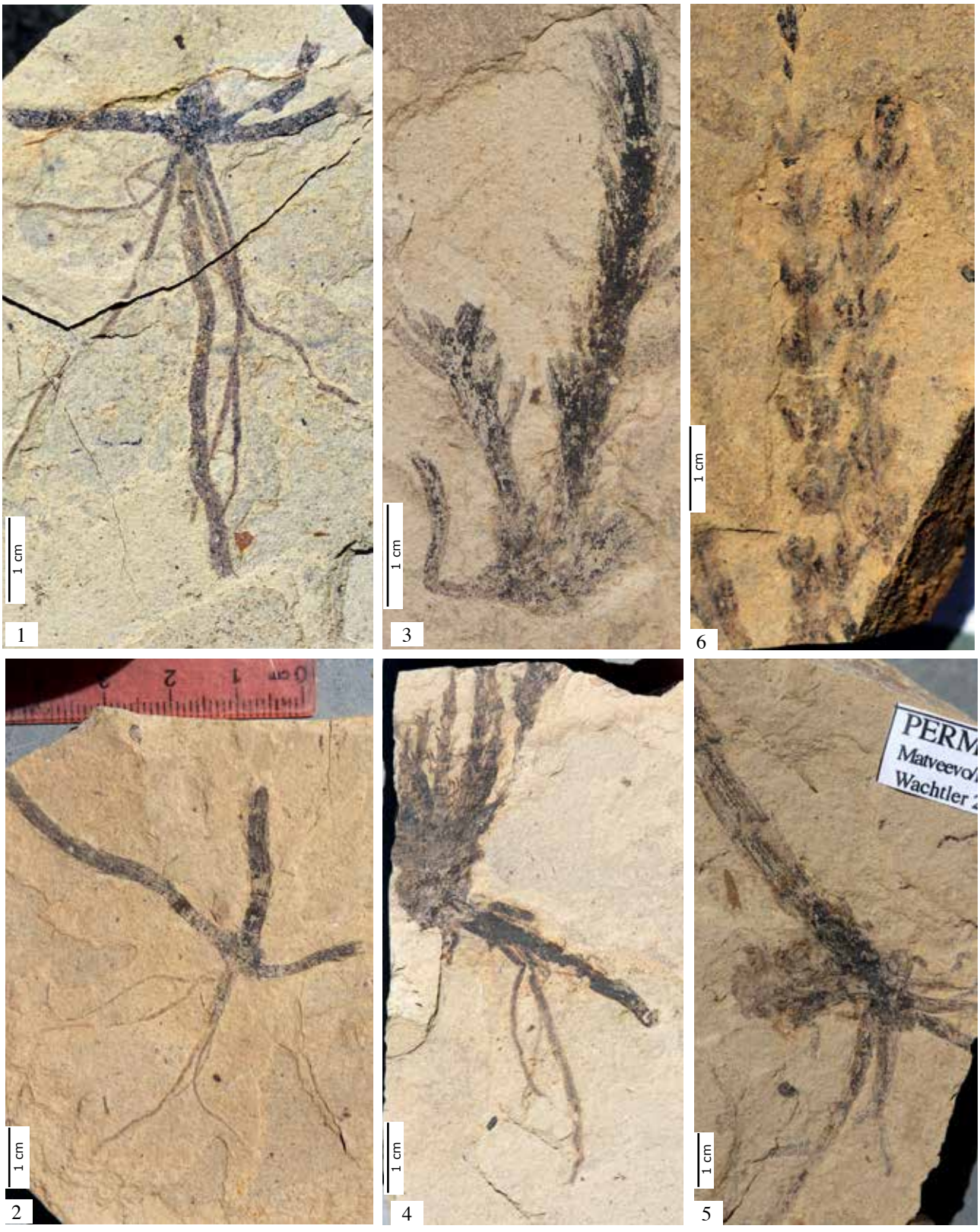
## Can the Calamitaceae and the Equisetaceae be connected?

One of the most interesting questions are if *Calamites* and *Equisetes* where just separated in Devonian, or they have a long lasting common way till a diverging on the Carboniferous-Permian border. One thesis could be that the ancestor of *Equisetites*, a genus being seldom in the Early Permian, branch from the in that time widespread Calamitaceae. In effect we have in the Late Carboniferous especially in the Eastern Alps in the same layers between *Calamites multiramis* and *Calamostachys tuberculata*-strobili another kind of cones, having rhomboid till hexagonal plates classified as *Macrostachya infundibuliformis* (Fritz et al. 1990). In these case *Calamites multiramis* hold two different kind of cones: One with macrosporangia *Calamostachys tuberculata* and the other with elongate tubiform sporangia (*Macrostachya infundibuliformis)* from, which maybe split in these times the Equisetaceae. That this theory is not completely to discharge can be seen in the probably best-known species *Equisetites arenaceus* from the Middle Triassic. Between a majority of obovate strobili there are a minority of elongated slender cones bearing different sporangia (Wachtler, 2016). Otherwise we have to accept that as seen in many other plant tribes the diversification between Equisetaceae and Calamitaceae occurred just on the Devonian-Early Carboniferous boundary. Early Permian *Equisetites*- and *Calamites*-cones in just from the Devonian separated continents Euramerica and Angara support this theory.
Also, the Calamitaceae were not uniform: Some bore lanceolate till spatulate decorative leaf-whorls classified as *Annularia (Annularia stellata, A. carinata* are the most known), other hold only needle-like sheaths like Early Permian C*alamites wachtleri* or in Angara-Land *Paracalamites campanularis*.



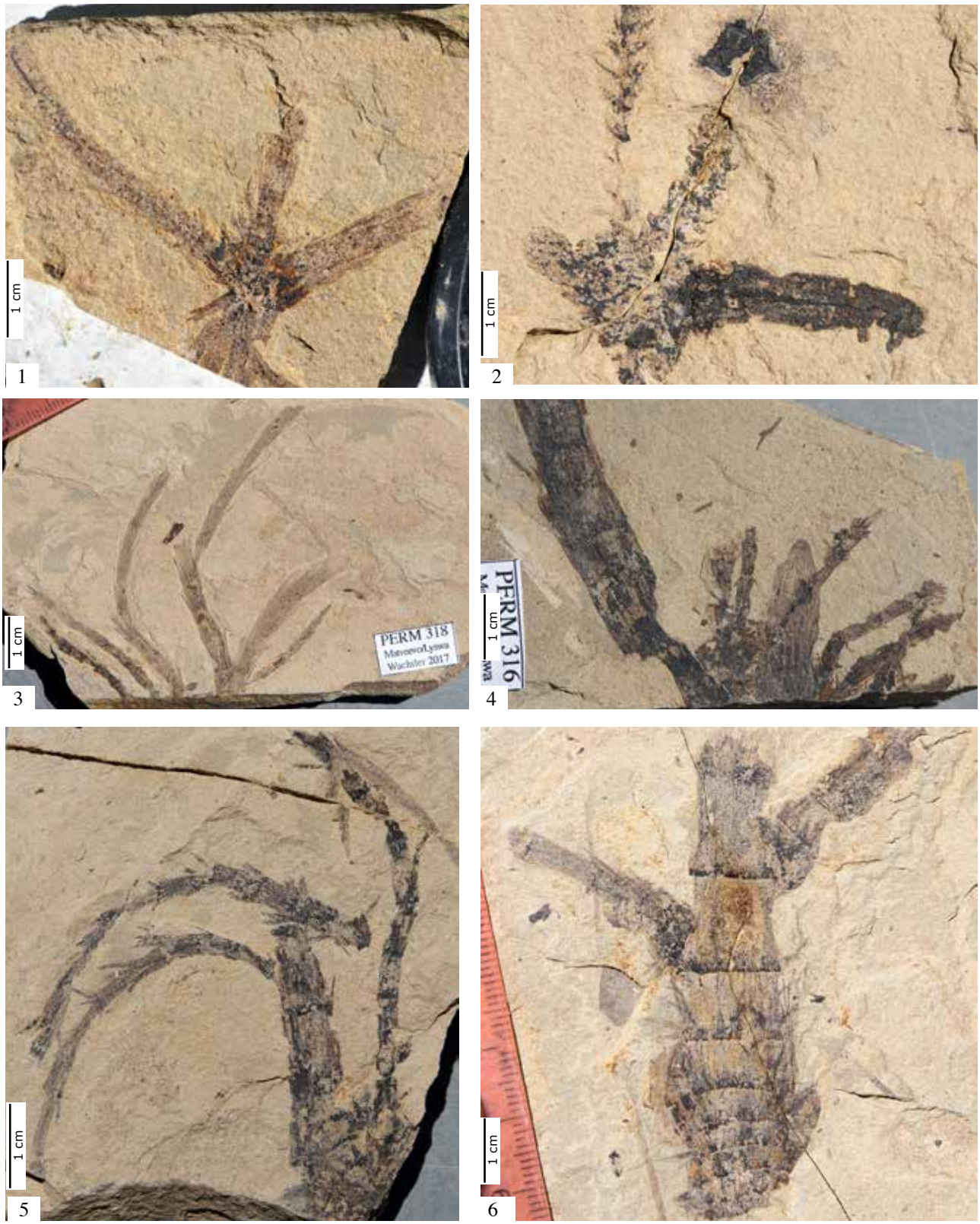

**Equisetaceae and Calamitaceae from Angara-Land. Artinskian**

*Equisetina magnivaginata. 1*-2. Stems (ARTI 22, ARTI 1*); 3.* Apical parts and stems. Plate and counter-plate (ARTI 102) *4. Paracalamites decoratus.* Diverging stem (ARTI 25); Coll. Perner & Wachtler, Arti, Artinskian (Early Permian)




***Paracalamites campanularis*. Early Permian. Fore Urals, Russia**

1-2. Basal stems and roots-system (MAT 111, Coll. Dammann, MAT 300); 3. Plant with leafy lateral shoots (MAT 295); 4-5. Juvenile plants (313, MAT 314); 6. Secondary whorls (MAT 139); Matvéevo, Kungurian (Early Permian) Coll. Wachtler Dolomythos Museum




***Paracalamites campanularis*. Early Permian. Fore Urals, Russia**

1-2. Basal juvenile stems with dwarfish leaves united into leaf sheaths (MAT 117 Coll. Dammann, MAT 312); 3. Several times furcating plant (MAT 318); 4. Plant and apical part (316); 5-6. Adult plants with main stems (MAT 317, 299); Matvéevo, Kungurian (Early Permian) Coll. Wachtler Dolomythos Museum

### Calamitaceae from Russian Angara-Land

Horsetails from the former Paleozoic continent Angara - recovered for the most part in the Fore-Urals - are till now less known. Effectively they stay a little apart from all known Sphenophyta due to the lack of knowledge for the mostly from Western researches influenced works and opinions.
Just in the Artinskian we encounter decorative stems that can be classified as *Paracalamites (decoratus)* and *Equisetina magnivaginata)* (ARTI 22, ARTI 1, ARTI 102, ARTI 25) but due to the rarity of fertile organs an exact insertion is difficult. In the Kungurian beds of the Barda River in the vicinity of Matvéevo and the Sylva River near Chekarda vegetative shoots, leaves and sporangiophores of various Equisetopsida were found. Also in this case a collocation in one of the known Sphenophyta-families is not easy. Just the multitude of names introduced in the past by the scientists confirm that we are only on the begin of a reliable classification. Additionally—as seen in other cases—it is risky, adopting the same genus names from European or Gondwana-sites (like *Phyllotheca*), because the Angara-Flora seems to be especially different from others (Naugolnykh 1998, 2003, 2007).
The stem- or leaf-anatomy cannot be considered convincing enough for a genus-classification, main interest must be given on their reproductive biology. But on this over the centuries was given minor attention and beside them fertile organs are rare to find or to recognize in an enough good quality.

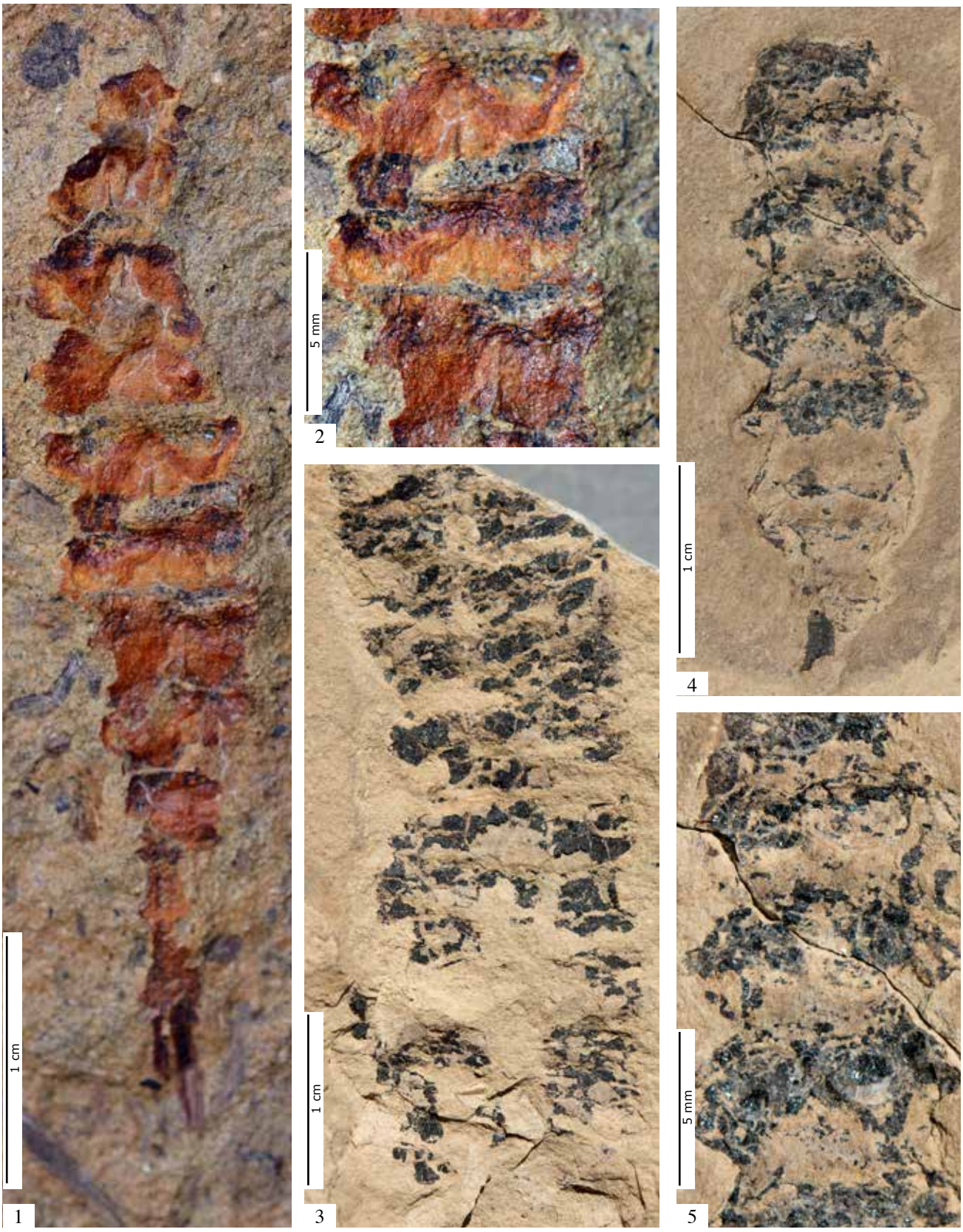
## *Paracalamites campanularis* ZALESSKY, 1937b, comb. nov.

1937b *Phyllotheca campanularis* Zalessky, p. 42, fig. 4
1937b *Phyllotheca scyphulifera* Zalessky, p. 41, fig. 2
1937b *Phyllotheca sylvenis* Zalessky, p. 41, fig. 3
1937b *Phyllotheca biarmica* Zalessky, p. 43, fig. 5
2007 *Phyllotheca campanularis*, Naugolnykh p. VI. Fig. 3
2007 *Phyllotheca biarmica*, Naugolnykh p. X. Fig. 1
2007 *Sachyogyrus multifarius* Naugolnykh p. X. Fig. 2-4
2004 *Phyllotheca campanularis*, Naugolnykh p. 14. Fig. 1, 6, 8
2015 *Phyllotheca campanularis*, Naugolnykh p. 130. fig. 4, p. 131 Fig. 1, 3, 5

**Plant:** Low growing horsetails, diverging several times from a rhizome. Stems with about 3 cm relatively small sized (MAT 299), ending in a telescope-like nested head (MAT 316). Secondary branches, forking from the internodes normally as whorls, sometimes also as consistent twigs. Leaves dwarfish and acuminate, united into leaf sheaths (MAT 295, MAT 117, MAT 318).
**Reproductive organs (***Sachyogyrus multifarius*-type*)*: Cones from 3–6 cm long, 1–3 cm wide, with a short and slender basal stipe (MAT 63, 211, 330). Scales reflexed back on the outside ending with a sharp tip. They coat densely the sporangia on their inner side.

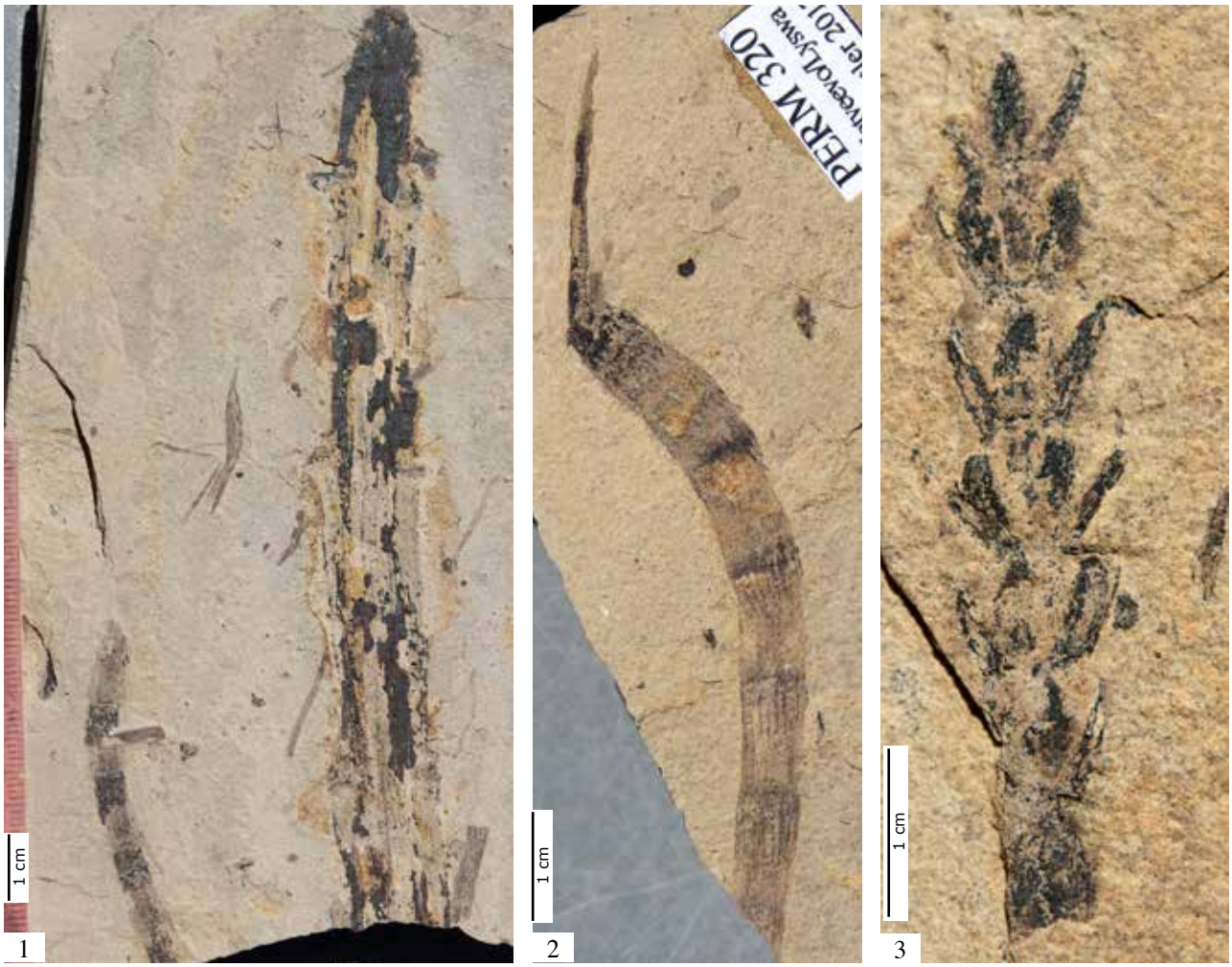
### Remarks

In 1927 M. D. Zalessky introduced in science the name *Paracalamites* for Kungurian stems from Matéevo with tangential striae relatively widely separated, probably to differentiate them from *Equisetina* stems with their narrow longitudinal ribs. Naugolnykh (2002) followed this concept connecting *Equisetinostachys*-cones with *Paracalamites* and changing additionally the name in *Paracalamitina striata.*
Main difference to the Calamitaceae and the Equisetaceae should be their non-strobilar organization of the reproductive organs. Bractless peltate sporangiophores extend from the unbranched primary shoot or from normally developed leafy lateral branches. The sporangiophores occur in regular clusters and form distinct intercalary or terminal fertile one that are internodal (Taylor et al. 2009). Just mixing *Calamites* with *Equisetites* can create problems because in this case both stems, and fertile organs must be regarded as missing link between both, what cannot be accepted due to notable lacunas in the evolutionary concept. Because as Zalessky (1934), as well Naugolnykh (2002) describe with *Paracalamitina* a horsetail from the Upper Permian (Ufimian) Daniko-Shor locality from the Pechora Cis-Urals also the time jump reveals not satisfying for Early Permian Calamitales.
M. D. Zalessky introduced the name *Phylloteca* for one of the most common horsetails, elaborating a plethora of species (*Phyllotheca scyphulifera, Phyllotheca sylvenis, Phyllotheca campanularis, Phyllotheca biarmica*) mainly from Matvéevo but also from the coeval fossil site Chekarda (1937b). But due to the fact that the genus *Phyllotheca* was created




***Sachyogyrus multifarius* horsetail-cone (other indication *Bowmanites biarmensis* (Naug.)**

1-2. Well conserved cone with the reflexed bracts (MAT 63); 3. Sporangiophore (MAT 211); 4-5. Cone hold by a short stipe (MAT 330); Matvéevo, Kungurian (Early Permian) Coll. Wachtler Dolomythos Museum




***Paracalamites campanularis*. Early Permian. Fore Urals, Russia**

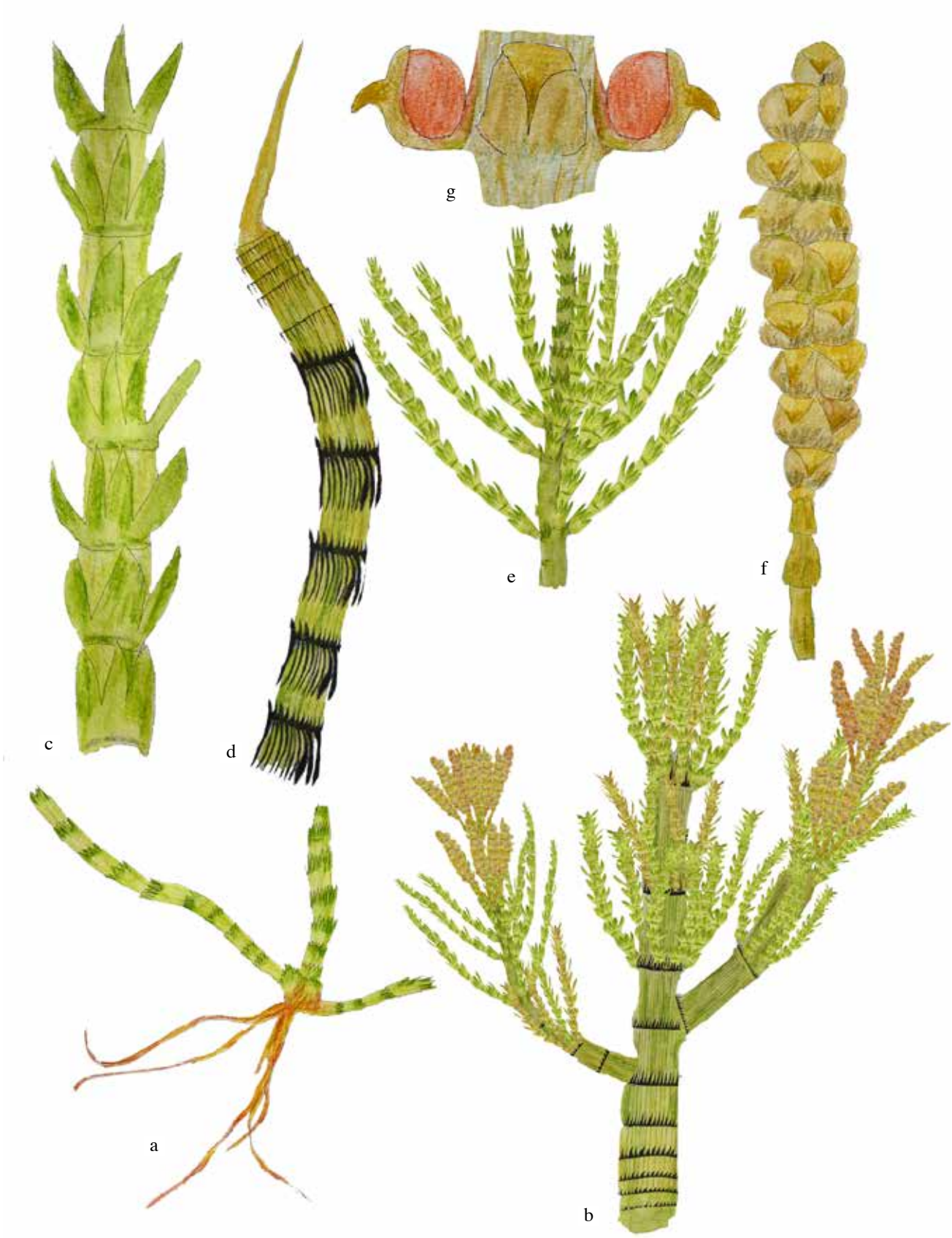
1. Apical part of a plant (MAT 239); 2. Apical part and internodal systems with leaf sheaths (MAT 320); 3. Isolated branchlet and leaves (MAT 321); Matvéevo, Kungurian (Early Permian) Coll. Dolomythos

in 1828, when Brongniart described the type species *Phyllotheca australis* coming from Hawkesbury River, Australia, it is doubtful that these Northern hemisphere Sphenophyta belong really to the Gondwanan family of Phyllothecaceae (Rayner, 1992).

In 1929 M. D. Zalessky described as *Tchernovia (synensis)* a bad conserved leave or reproductive fragment of a plant (Pl XVI, Fig. 4 + 5) inserting it in the Equisetaceae. Till now it is unclear if it not belongs to the Peltaspermales. After that the genus name was widen to a whole family, the Tchernoviaceae (Meyen, & Menshikova, 1983), including other Permian Sphenophyta and sometimes also the genus *Phyllotheca* as well *Paracalamitina* (Naugolnykh, 2002).

In 1939 Zalessky classified other Sphenophyta from the Barda-River. One drawing (pag. 335, fig. 8) evidence a Calamitalean cone, which he named *Sachyogyrus multifarius.* To complicate the situation for Angaran horsetail-strobili was also adopted the genus name *Bowmanites*, 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 creeping Sphenophyta. This inflorescence-genus was than 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*.

This is highly speculative, because it seems that the thought *Sphenophyllum* leaves and twigs indicate more in a seed-plant-direc-




***Paracalamites campanularis.*** **Early Permian. Fore Urals, Russia - Reconstructions**

a. Juvenile plant with roots (MAT 300); b. Adult plant with fertile organs; c. Isolated branchlet and leaves MAT 321); d. Apical part and internodal systems with leaf sheaths (MAT 320; e. Secondary whorls (MAT 139); f. Cone with sporangiophora (MAT 63);g. Detail of the sporangiophora. Matvéevo, Kungurian

tion. Additionally, without going in nomenclature problems can be stated that the original *Bowmanites* cones from Upper Carboniferous of Europe differs to much from Angaran strobili, to left them in this genus.
The not totally satisfying name *Sachyogyrus multifarius* (Zalessky, 1939) can be conserved for Early Permian reproductive organs from Angara-Land. They have affinities with the cones usually belonging to the *Calamites*-horsetails.
Because the Angaran fertile organs of the Sphenophyta differs from all known *Calamites*-strobili, the name *Paracalamites* was maintained and newly interpreted. For the whole plant indeed the genus-name *Paracalamites campanularis,* representing the dominating horsetail in the Kungurian Sylva-River fossil sites in the Fore-Urals is proposed. Additionally, it is thought that *Sachyogyrus multifarius* represent its fertile organs.

### *Calamites* from European Paleozoic

The Calamitaceae dominate the European landmass from the Upper Carboniferous till the Upper Permian. The most known are *Calamites multiramis* in connection with *Annularia stellata* whorls and *Calamostachys tuberculata* reproductive organs in the Late Carboniferous (Moscovian-Kasimovian-Gzhelian, Regional stage Western Europe: Westphalian D, Stephanian). In addition, Early Permian (Asselian-Sakmarian) *Calamites gigas* can be associated with *Annularia carinata* foliage and *Calamostachys dumasii*-fertile organs. Other better known Calamitaceae from the Carboniferous-Permian boundary are *Calamites wachtleri* (Kasimovian-Gzhelian) or *Neocalamites tregiovensis* (Kungurian). It seems that the Calamitaceae disappeared definitely in the Upper Permian with *Neocalamites benckeae* (Wachtler, 2016).
Only sometimes their stems and branching systems hold distinctive features. Some arise from subterran rhizomes other are equipped also with taproots, but both rarely fossilised preserved. On the main stem attached branches were rarely found, but scars of shed branchlets give an insight in the plant-anatomy. The scars are ornamented by a series of wrinkles that extend out from the central scar like the spokes of a wheel. Leaves or *Annularia*-fronds of European Calamitaceae varies also considerably. Some like *Calamites wachtleri* was equipped with subtle needle-like whorls, whereas *Calamites multiramis* or *Calamites gigas* were equipped with aesthetically superb fronds, predominantly appreciated by all collectors, whereas the unimpressive reproductive organs were underestimated.
Their reproductive organs were slightly different each from the other and from that often recognizable. The strobili equipped with a short stipe were aggregated in clusters on specialized branches, born single or as twin-structure. The sporangiophores were inserted on the cone axis in the middle of the internodal restriction. A multiple of sterile bracts coat the normally rounded sporangia densely in a juvenile stage. The bracts open and were partially shed at maturity with the result that only a few or in *Calamostachys dumasii* only one big sustaining bract remain whereas the sporangia desiccate to release their spores.

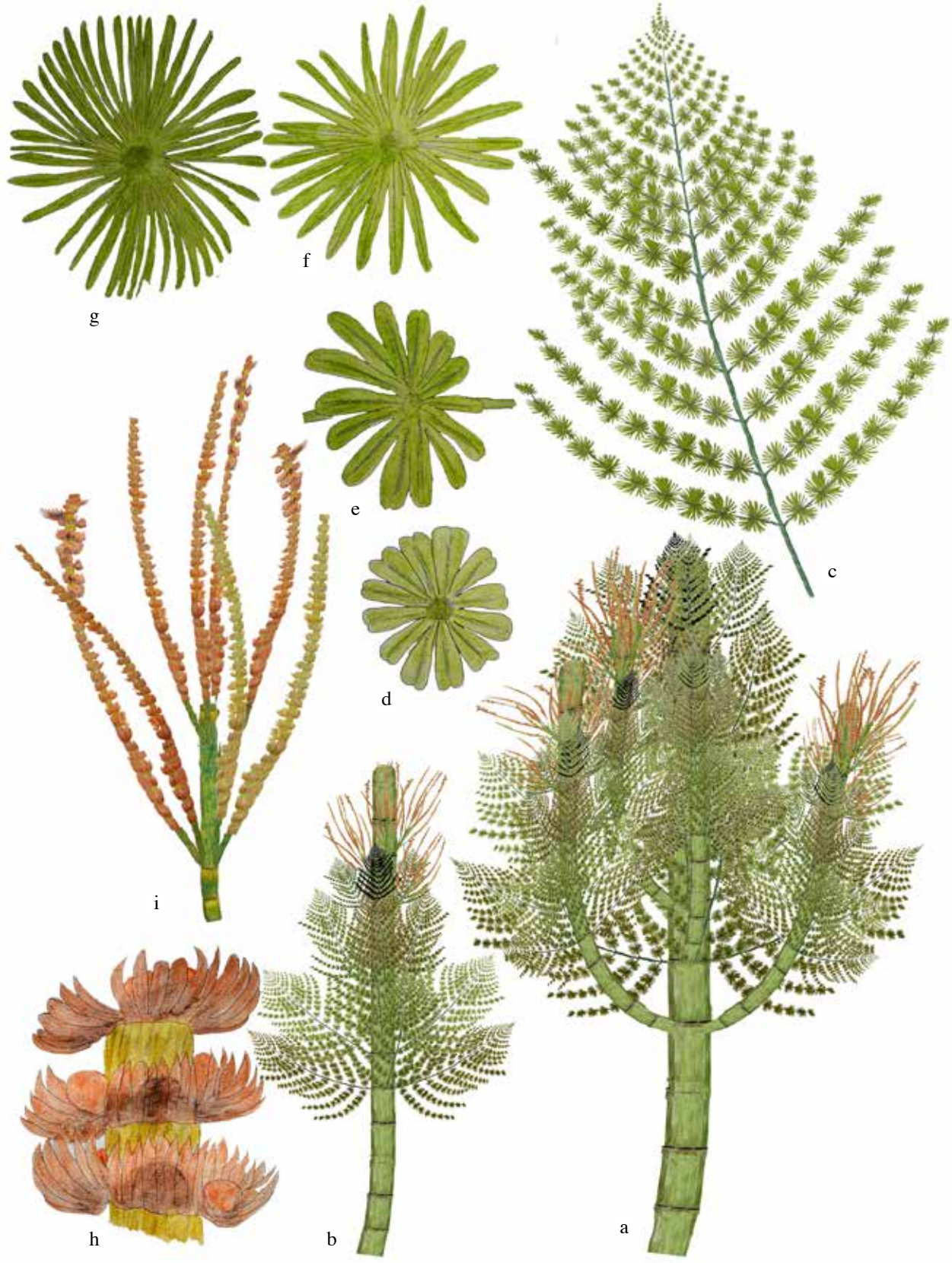
## Calamites multiramis WEISS, 1884

### Type horizon and age

Moscovian-Kasimovian-Gzhelian, Regional stage Europe: Westphalian D, Stephanian

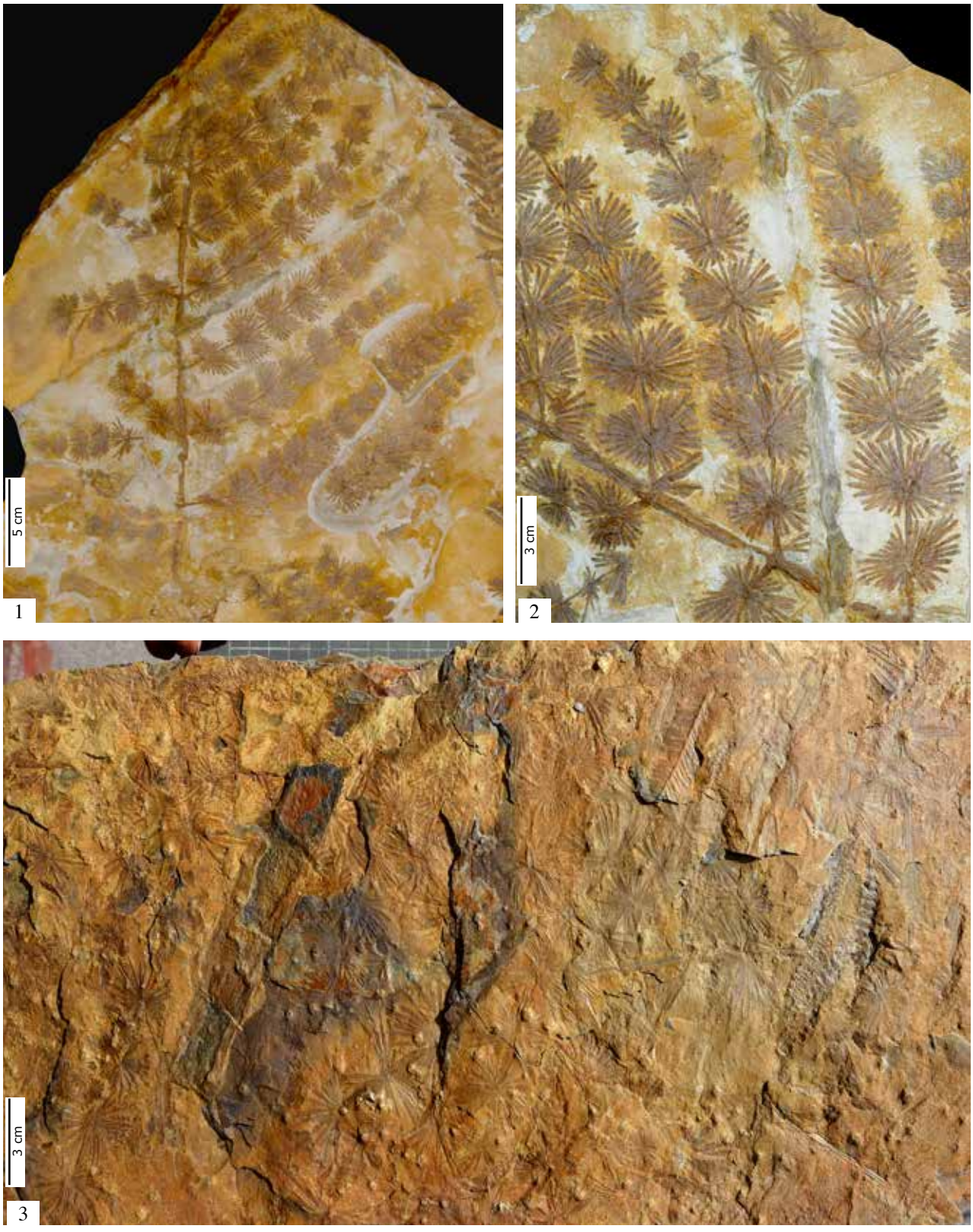
### Description

**Plant:** Probably till 10 m high with a 15–20 cm thick main axis. Pith casts irregularly interrupted by nodes, surface of the stem smooth or furnished with closely spaced transverse furrows and ribs. Nodes producing irregularly lateral branches. Lateral twigs classified as *Annularia stellata*, frond-like with whorls of up to 40 lanceolate to spatulate leaves. In a juvenile stage these leaves are rounded on the apex and characterized by an evident mid-vein, when mature they end acuminate..
**Reproductive organs** *(Calamostachys tuberculata*-type): Complete cones till 10 cm long, but only 1 cm wide, slender, equipped with a 1 cm long basal stipe. Strobili segmented in whorls (sometimes also 30–35) of sporangiophores. These formed by sterile minute and clawing bracts holding on the inner side the rounded sporangia. In an adult stage the bracts open or expand, whereas the sporangia desiccate to release the spores.



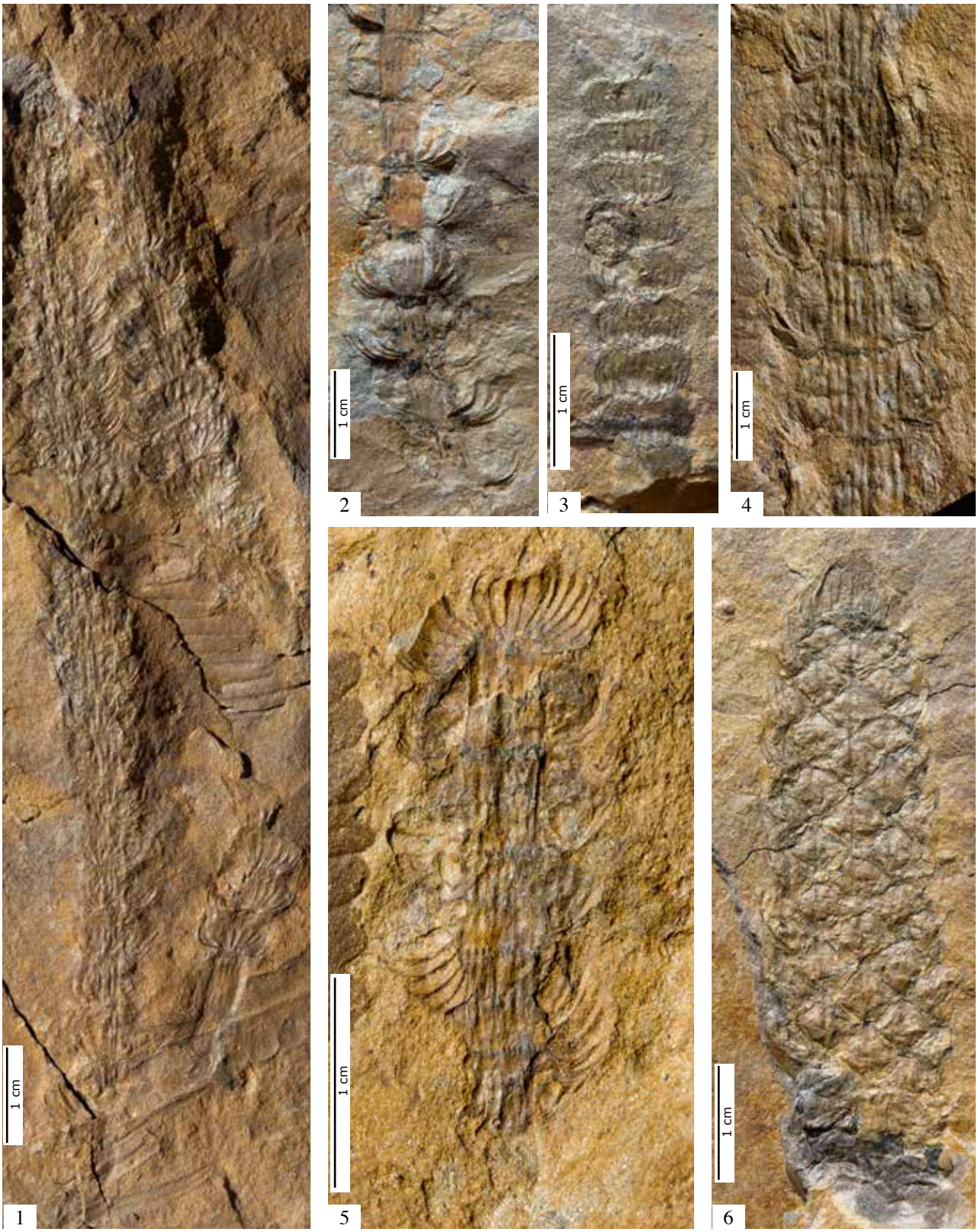

***Calamites multiramis*. *Annularia stellata*-foliage. *Calamostachys tuberculata*-strobili. Reconstructions**

a. Whole plant with strong lateral branches; b. Whole plant with fertile parts; c. *Annularia stellata* Frond; d. Juvenile leaflets (KRON 47); e. Semiadult whorl; f. Adult leaflets (KRON 23); g. Mature whorl with up to 30 leaves (KRON 21); h. Part of a strobilo with bracts and sporangia (KRON 47); i. Entire fertile part with several mature cones (KRON 26); Kasimovian



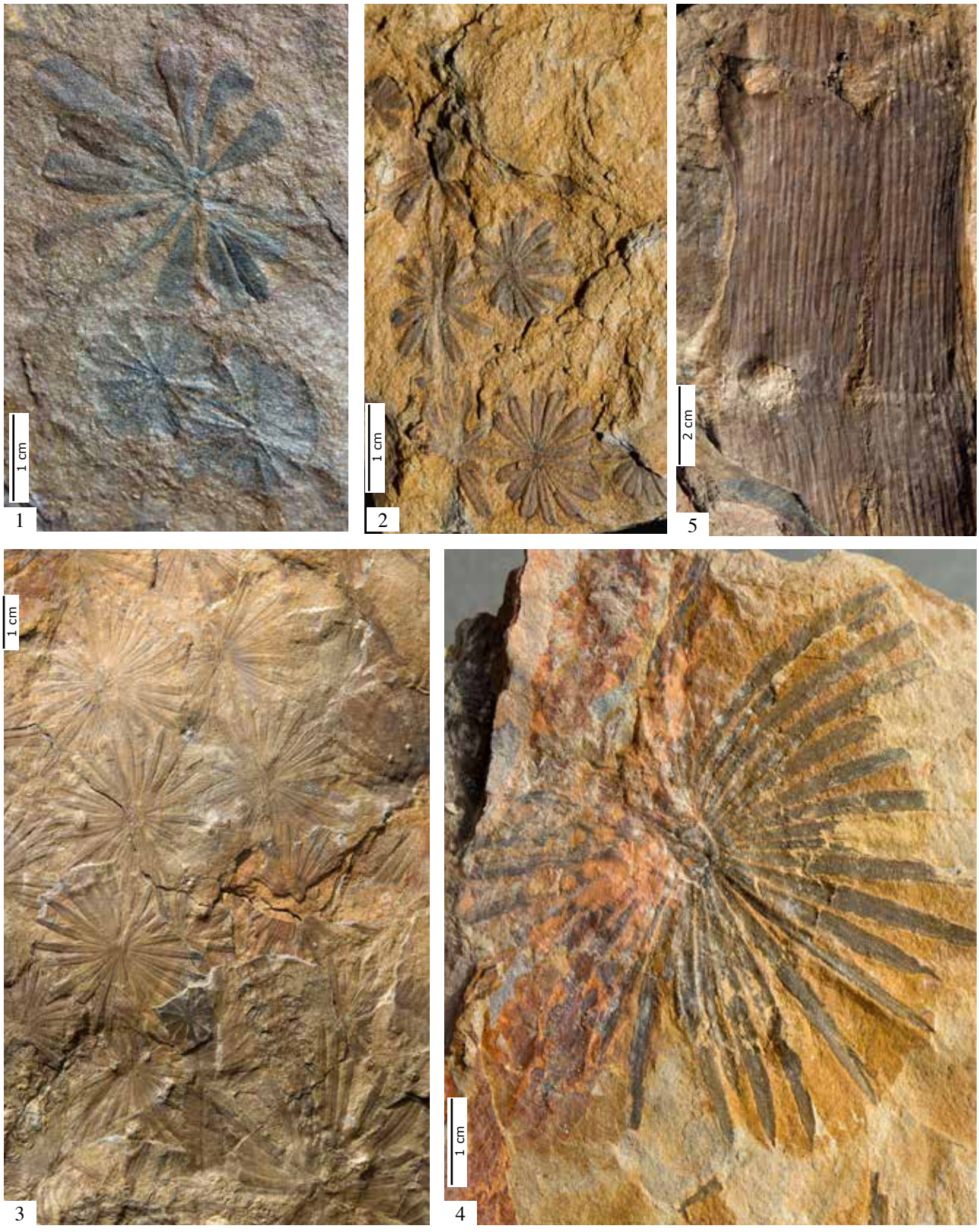

***Calamites multiramis. Annularia stellata*-foliage. Late Carboniferous. Krone. Eastern Alps**

1-2. Exceptionally conserved frond and detail of the single *Annularia* whorls (Museo di Scienze Naturali, Udine); 3. Parts of *Annularia*-fronds in connection with a *Calamites*-stem and several strobili, thought to belong to the same plant (KRON 35), Krone, Carinthia, Kasimovian, Coll. Wachtler, Dolomythos Museum




***Calamites multiramis*. *Calamostachys tuberculata*-strobili. Late Carboniferous. Krone. Eastern Alps**

1. Two entire strobili with basal stipe (KRON 41); 2. Detail of the sporangia clawing bracts (KRON 36); 3. Closed bracts with one open sporangia in the middle (KRON 24); 4. Strobilo with sporangia and encasing bracts (KRON 28); 5. Open bracts (KRON 47); 6. Unusual formed cone (*Macrostachya infundibuliformis*) in connection with Calamites-stems (KRON 29); Krone, Carinthia, Kasimovian, Coll. Wachtler, Dolomythos Museum




***Calamites multiramis. Annularia stellata*-foliage. Late Carboniferous. Krone. Eastern Alps**

1. Juvenile verticils (Sometimes known as *Annularia radiata)* (KRON 04); 2. Several juvenile whorls (Known as *Annularia sphenophylloides)* (KRON 47); 3. Connected adult whorls with a fertile strobilo (KRON 23); 4. Adult whorl with up to 30 leaflets (KRON 21) 5. Stem with internodes (KRON 44) Krone, Carinthia, Kasimovian, Coll. Wachtler, Dolomythos Museum

## *Calamites wachtleri* PERNER, 2013

### Type horizon and age

Latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C

### Description

**Plant:** Horsetail with an erect moderate sized axis. Protruding secondary whorls sprouting or from the internodes or in a tuft from the apex. Leaves delicate, only 2 mm long, acuminate.
**Fertile parts:** Complete cones slender, consisting of alternating whorls (sometimes also 30–35) of sporangia and bracts. These 5–6 cm long and 2–3 mm wide. The pointed bracts claw densely the sporangiophores. The sporangia are rounded to elliptical. Individual cones sprouting between the secondary whorls or on the apex.

## Calamites gigas BRONGNIART, 1828

### Type horizon and age

Gzhelian-Asselian-Sakmarian (Early Permian)

### Description

**Plant:** Horsetail with till 20 cm wide stems and short internodes. Considerable variability in the shape of the ribs can be observed, even within the single specimen. Ribs are not prominent, with a delicate longitudinal striation. Branch scars only rarely recorded. Leaves (*Annularia carinata*) characterized by anisophylly of the verticils. Each verticil possessing 8-18 leaves that are up to 24 mm long distinguished by a prominent mid-vein.
**Reproductive organs** *(Calamostachys dumasii*-type): Strobili in large amount on separate twigs, attached with six to ten strobili on each node. Cones varying in length from 0.5 cm in young and immature specimens till at least 6 cm; the width is from 0.2 till 0.7 cm, including the bracts. Strobilus axes are up to 0.1 cm wide, with a faint longitudinal striation. Sporangiophore-nodes situated at distances of about 0.2 cm. At each node six to eight dwarfish bracts and one longer encase the sporangia. Dwarf-bracts narrow and falcate, 0.15 to 0.4 cm long, inserted at right angles to the strobilus axes. They were shed mostly after maturity, only the main and longest bract remain attached in a mature stage. A basal heel covering a part of the sporangium in the whorl below. Sporangiophores attached to the middle of the internodes and closely sitting on the main bract. Sporangia ovoid, up to 0.2 cm in diameter.

## *Neocalamites tregiovensis* WACHTLER, 2012

### Type horizon and age

Kungurian (Early Permian)

### Description

**Plant:** Sphenophyta, with massive stems characterized by broad longitudinal ribs passing without alternation through the nodes. The nodal diaphragms resemble rounded discs. From the main stems diverges secondary axis, also with relatively wide spaced striae, holding *Annularia* fronds.
**Reproductive organs**: Strobili 5–8 cm long, 1 to 1.5 cm wide. A large number of sterile bracts encasing the sporangia.

## *Neocalamites behnkeae* WACHTLER, 2015

### Type horizon and age

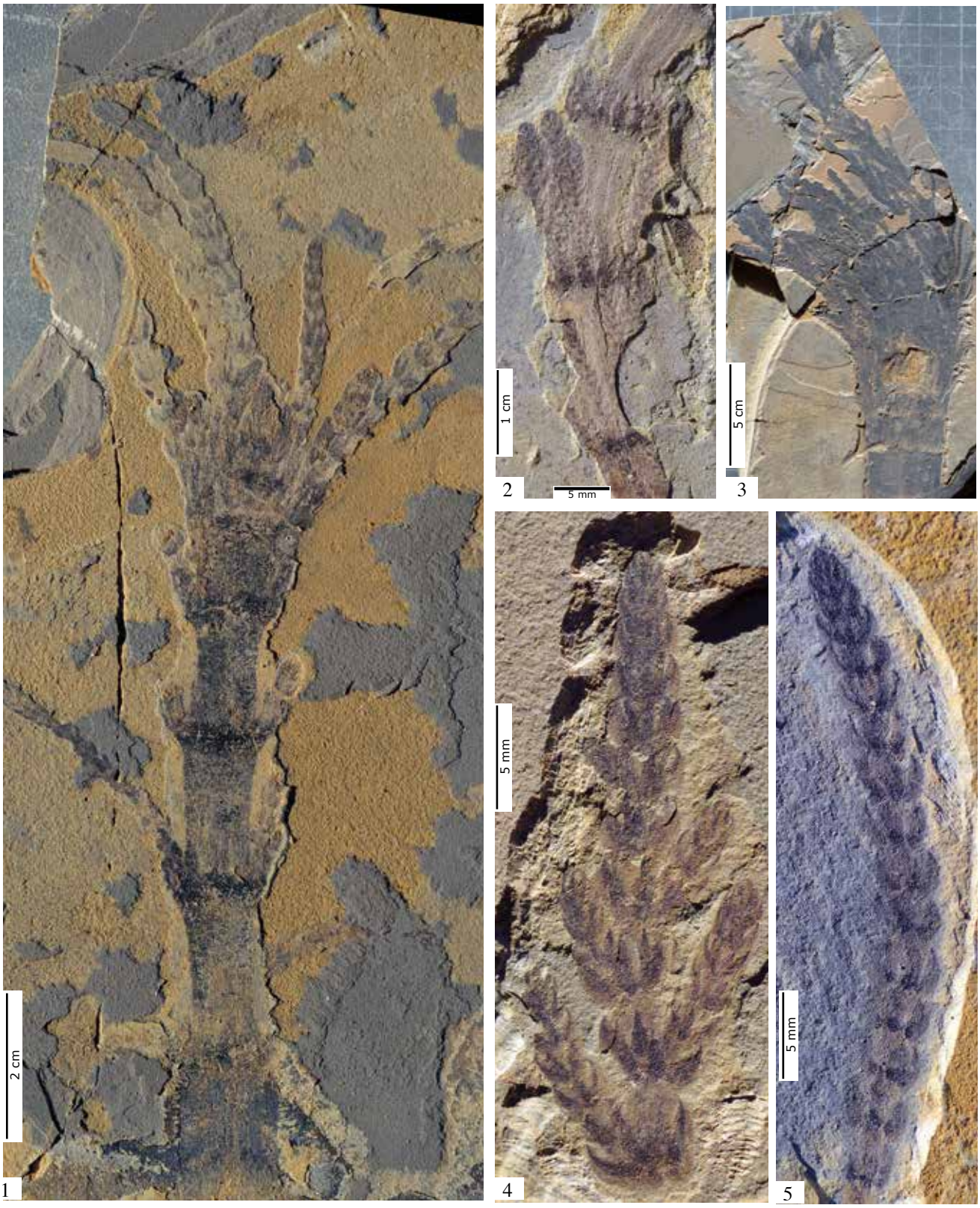
Lopingian (Late Permian)

### Description

**Plant:** Main stems normal sized characterised by broad longitudinal ribs diverging to secondary axes forking at an angle of 45 degrees or less, with narrower tangential striae.
**Reproductive organs**: Strobili 5–8 cm long, 0.5 to 1 cm wide. The elongated and pointed bracts densely and in large amount encase the elliptical to rounded sporangiophores. Sporangia in mature stage desiccated, hold by only a few bracts.

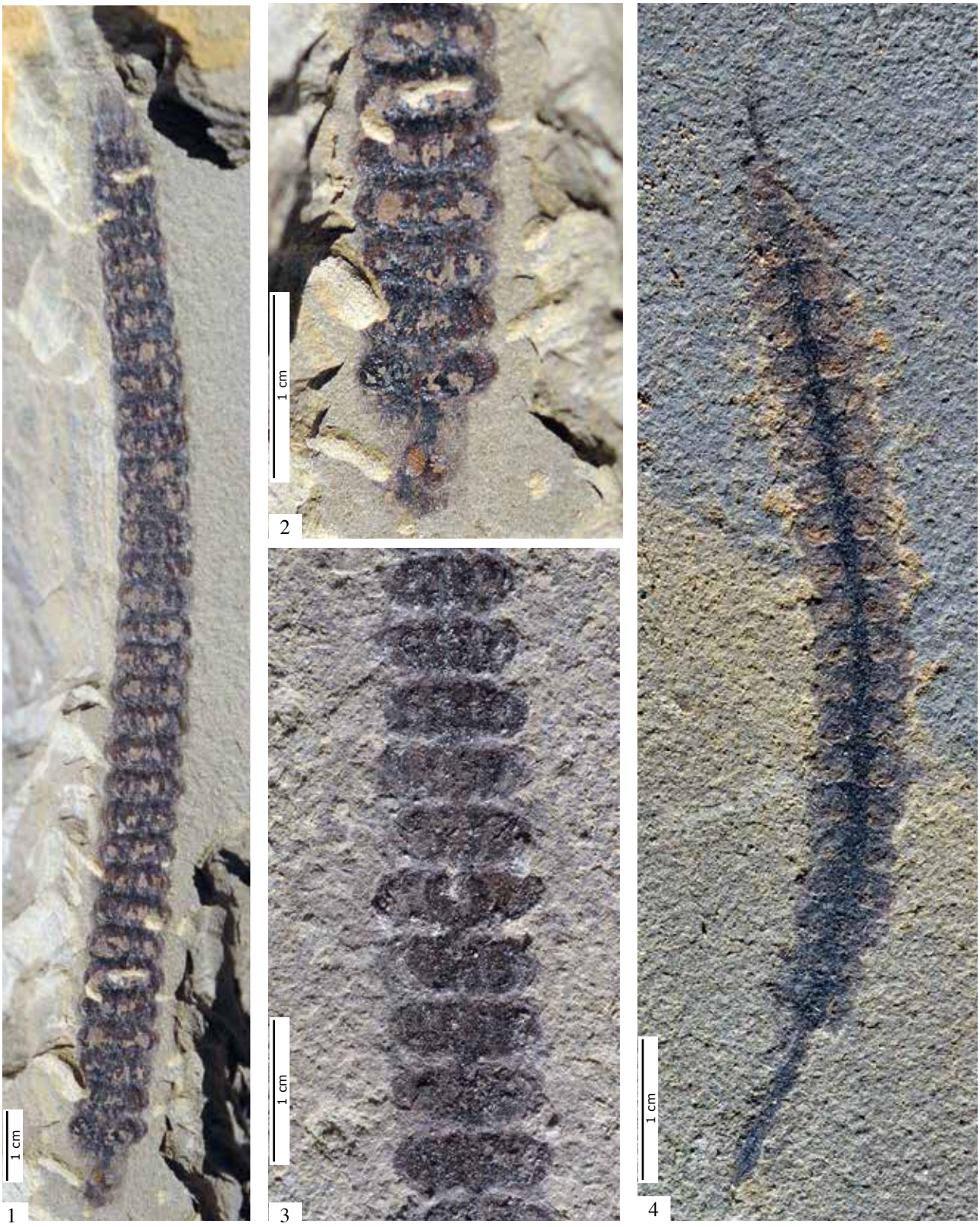
### Remarks

From the Upper Carboniferous till over the whole Permian we have in Europe with the Calamitales a group of horsetails who put




**Understanding Paleozoic Calamitaceae: *Calamites wachtleri* (Kasimovian/Gzhelian)**

1. Apical part of a main stem with secondary whorls (PER 29, holotype); 2. Lateral branches sprouting from a stem (PER 158); 3. Mainly complete stem with sprouting secondary whorls (PER 461); 4. Secondary whorls with leaf sheath(PER 206, Paratype); 5. Part of the secondary whorls and the axis with leaves (PER 189, all Coll. Perner); Niederhausen, Germany




## Understanding Paleozoic Calamitaceae: *Calamites wachtleri* (Kasimovian/Gzhelian)

*Calamostachys:* 1. Immature *Calamites* cone with closely spaced nodes bearing whorls of bracts and sporangia (PER 129); 2. Basal part of the cone (PER 129); 3. Detail of the spaced nodes with the bracts and sporangia (PER 475); 4. Mature cone with detail of the desiccated and open sporangia (PER 471 All Coll. Perner); Niederhausen, Germany


***Calamites wachtleri*. Horsetail. Earliest Permian ((Kasimovian/Gzhelian) - Reconstructions**

a. Whole plant (PER 29); b. Stem-fragment (PER 29B); c. Secondary whorls (PER 206); d. Young cone (PER 129); e) Mature cone with sporangiophora (PER 63, 471).

in the shade the today only existing Sphenophyta, the Equisetaceae. Their stems could have on the surface narrower or larger spaced ribs, massive or only fragile lateral branchlets, hold fronds of beautiful leaf-whorls commonly called *Annularia* or only leaf-sheath with dwarfish foliage, the only distinguishing feature towards all other horsetails where their elongated strobili, with sporangiophores coated by several bracts (*Calamostachys*).
The cones were slender and elongated in Upper Carboniferous *Calamites multiramis (Calamostachys tuberculata*) or more small-sized in Earliest Permian *Calamites gigas (Calamostachys dumasii)*, in this - additionally to all the dwarfish bracts - one all overtopping appendix encase the sporangia (Kerp, 1984). Earliest Permian *Calamites* wachtleri hold no typical *Annularia* whorls, but was equipped with dwarfish leaf-collars. In that it had some resemblances with Angaran *Paracalamites campanularis*, but being distinct from them by the multi-bracted sporangiophores indeed of one scale -bract. *Neocalamites tregiovensis* (Kungurian) was equipped by many filigree bract-leaves, as well also Upper Permian (Lopingian) *Neocalamites benckeae* (Lopingian), thought to be the last representative of the Calamitaceae in the European territories.

## Calamites from American Paleozoic

Over the years in the United States sphenopsids were collected in Carboniferous-Permian deposits especially from New Mexico. Often it was made the attempt to classify the calamitalean horsetails in some of the known - mostly European - floral assemblages like *Annularia stellata, Annularia spinosa* or *Annularia carinata* as foliage-type or *Palaeostachya thuringiaca* and *Calamostachys spicata* as reproductive organs (DiMichele et al., 2013). As encountered in other cases, biocoenosis from distant areas or continents are only of limited suitability for an exact insertion due to the fact that plants change rapidly in time and territory. Because a character-horsetail from the world-famous Kasimovian Kinney Quarry of Central New Mexico differs from the European considerably it is now described as new species *Calamites kinneyana,* trying to insert it in a global concept.

## *Calamites kinneyana* sp. nov. WACHTLER 2017

### Type horizon and age

Kinney Quarry site (Central New Mexico), Middle Missourian (Kasimovian), Wild Cow Formation.

### Holotype

NMMNH P-44727 (New Mexico Museum of Natural History and Science)

### Etymology

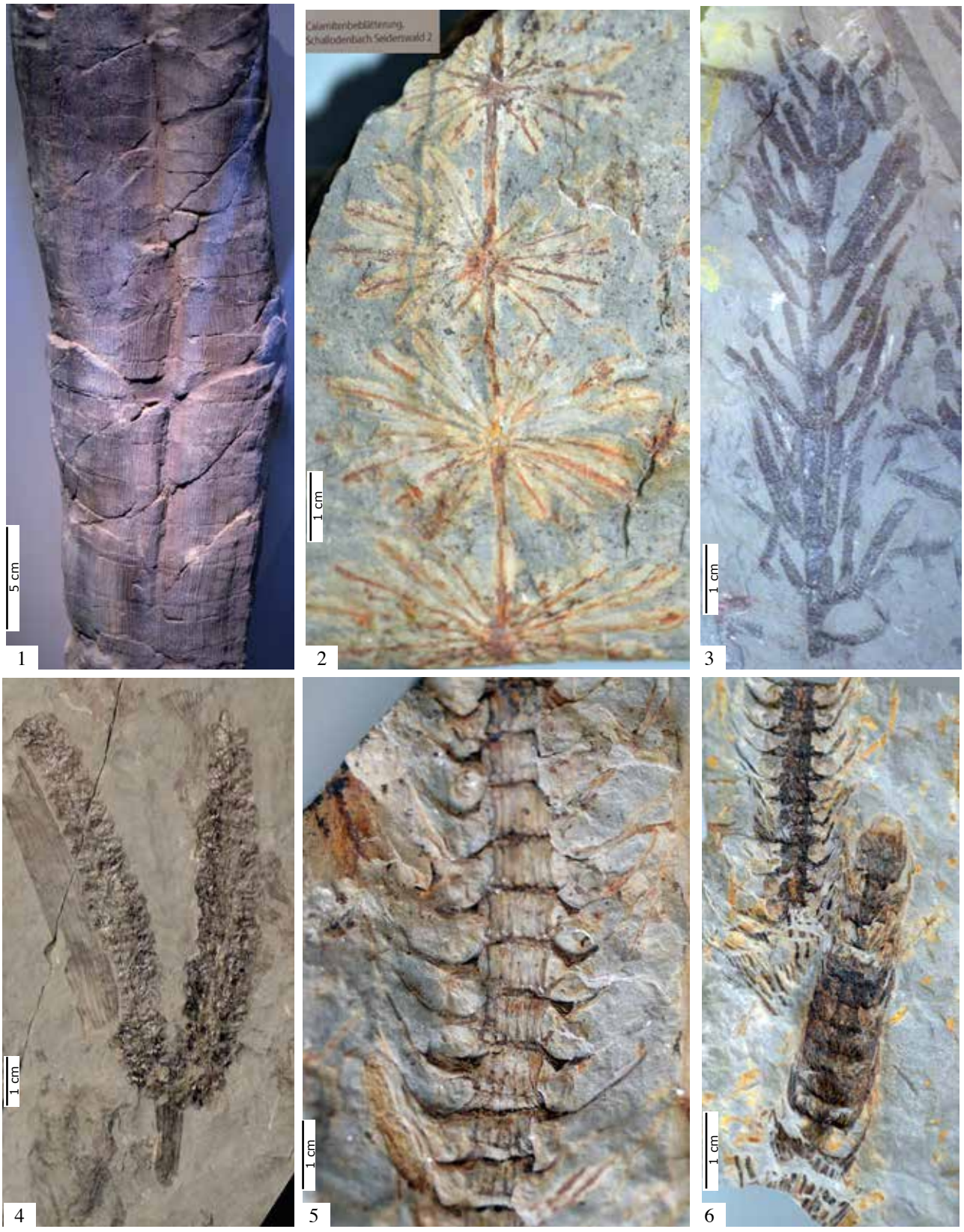
From the locality Kinney Brick Pit, (Central New Mexico)

### Diagnosis

Calamitalean plant characterized by their pending leave-whorls and relatively massive strobili with falcate bracts encasing the single sporangia.

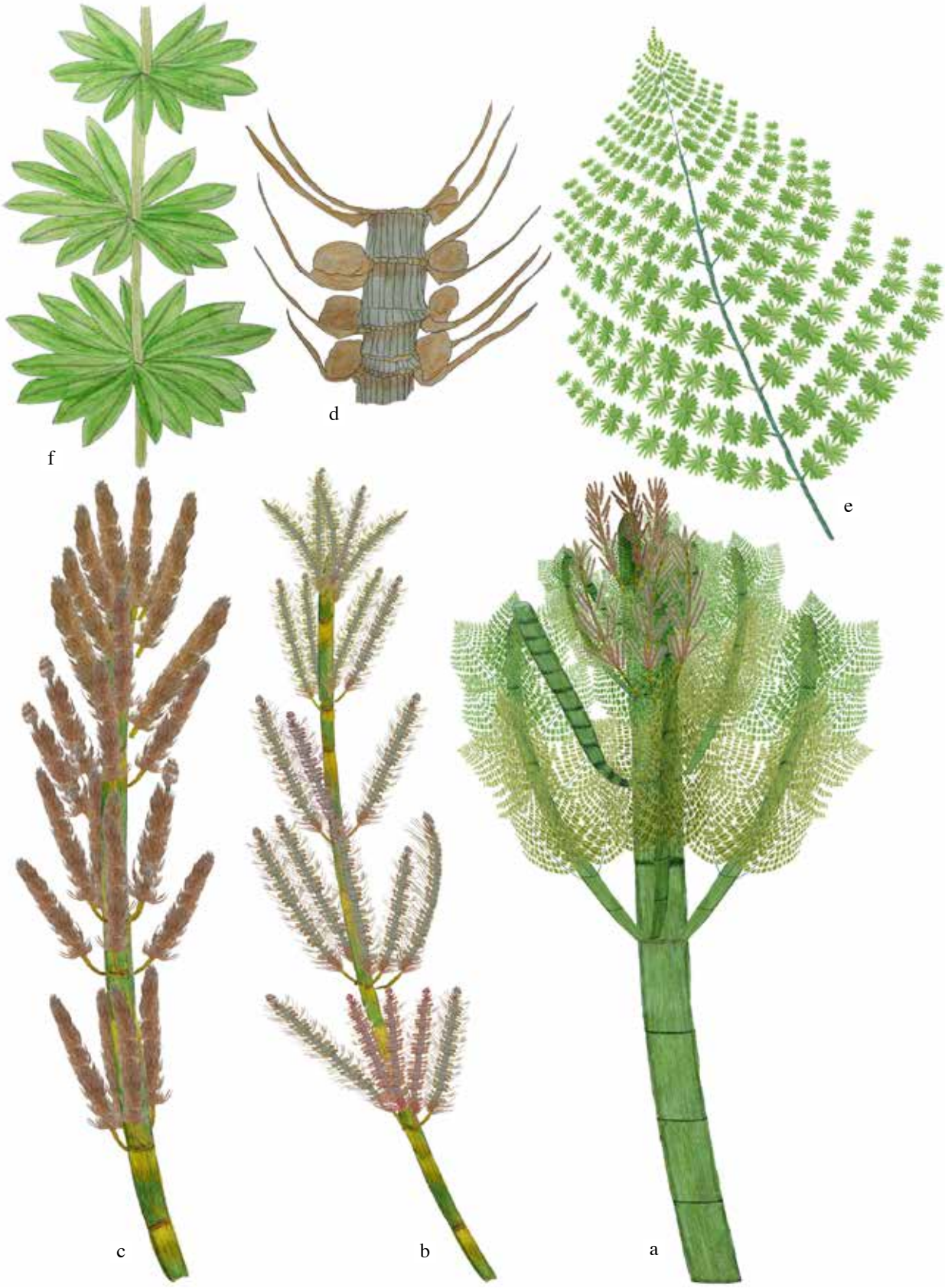
### Description

**Stem:** Holotype NMMNH P-44727 represent a monopodial hollow stem, 7 cm thick with longitudinal striae, interrupted by internodes. Normal stems reached at least 10 cm (USNM 450766).
**Leaves:** On the holotype are deposited secondary whorls that can be brought in connection to the main axis. The foliage is characterized by their acuminate and "hanging" leaflets. The whorls are composed of up to 20 leaves (P-144404), but usually they hold less, reaching in some cases only up to 10 (P-30854).
**Reproductive organs:** Strobili up to 10–12 cm long (P-69245 = conserved part 10 cm), including the bracts 1.5 cm wide, equipped with a 1.5 cm long stipe (0.2 cm thick) that connect the cone with the main or lateral axis. The cones are grouped in clusters on separate branchlets (USNM 450772). Sporangiophore-nodes situated at distances of about 0.5 cm. About six to eight sickel-shaped and pointed bracts claw the sporangia. The bracts are longer than the sporangia and reach till the superposed internode. The sporangia are ovoid, with 0.4 cm in diameter relatively consistent and are attached to the middle of the internodes.



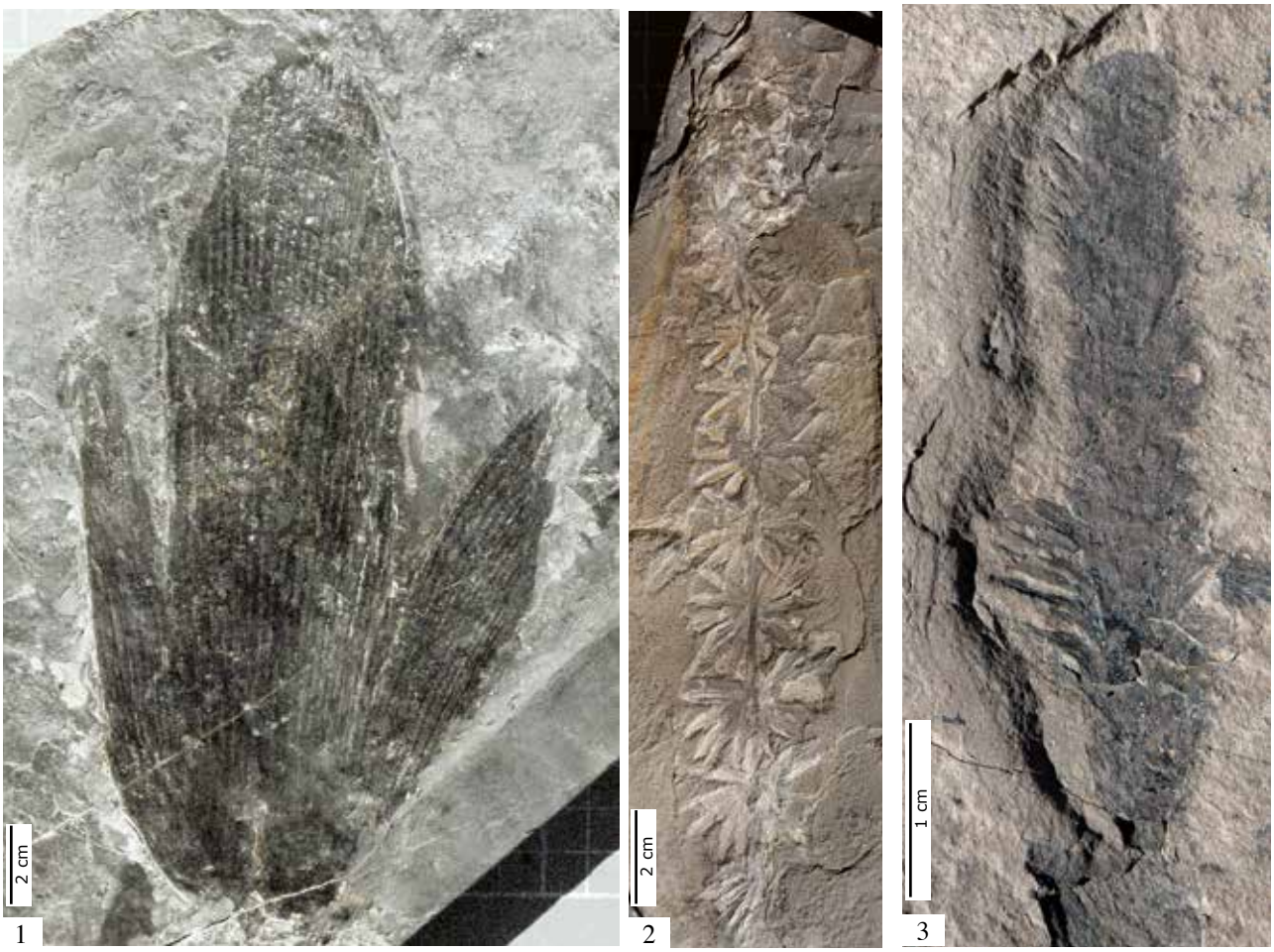

**Understanding Paleozoic Calamitaceae: *Calamites gigas* (Early Permian)**

1. Massive trunk of *Calamites gigas*, Manebach, Thuringia, (Museum of Natural History Chemnitz, 120cm). 2. Foliage of *Annularia carinata*, Oberhausen, (MoP Nierstein); 3. Branchlet holding a fair amount of infructescences of Calamostachys dumasii (St. Wendel, (MoP Nierstein); Two strobili connected together, Sobernheim, (MoP Nierstein); 5. Mature *Calamostachys dumasii* with remaining sterile long bracts; Schalllodenbach (R. Noll); 6. Two strobili, one juvenile another adult with elongated bracts, Schalllodenbach (R. Noll). Asselian-Sakmarian



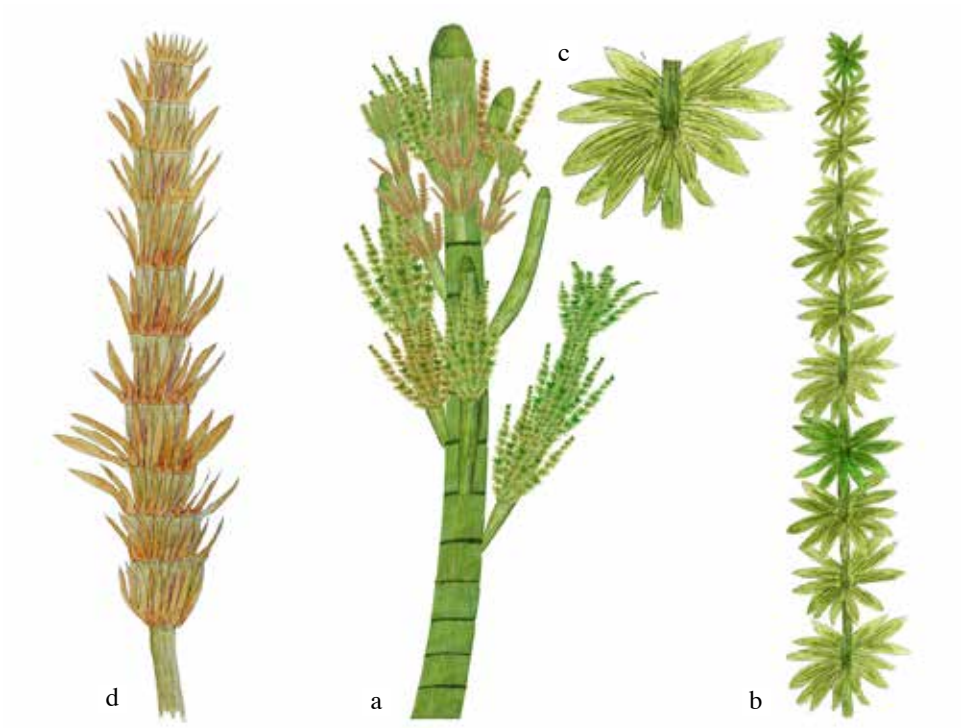

***Calamites gigas*. *Annularia carinata*-foliage. *Calamostachys dumasii*-strobili. Reconstructions**

a. Whole plant with fertile strobili; b. Mature reproductions organs (*Calamostachys dumasii)*; c. Juvenile strobili; d. Mature sporangiophores with partially shed bracts and one remaining holding bract; e. *Annularia carinata;* Entire frond; f. Leaflets; Asselian-Sakmarian




***Neocalamites tregiovensis*. Kungurian, Early Permian, Eastern Alps, Dolomites**

1. Stem with massive lateral branches (TRE 299); 2. Isolated *Annularia*-branchlet (TRE 547); 3. Juvenile cone (TRE 423). Tregiovo, Coll. Wachtler and Valentini, Dolomythos_museum




***Neocalamites tregiovensis*. Kungurian, Early Permian, Reconstructions**

a. Whole plant; b. *Annularia*-branchlet (TRE 547); c. Detail of an *Annularia*-branchlet (TRE 547); d. Juvenile cone (TRE 423) Coll. Wachtler, Museum Dolomythos

### Remarks

The Kinney Brick Pit of Kasimovian age (Lucas et al., 2011) with its character-horsetail *Calamites kinneyana* can be brought in a context from its age with *Calamites multiramis* in connection with *Annularia stellata* whorls and *Calamostachys tuberculata* being widespread all over Kasimovian Europe. Whereas in Early Permian Europe the *Calamitales* are characterized by their slender reproductive organs we encounter on the American continent relatively massive strobili. Additionally, *Annularia stellata* whorls hold more leaflets, which are fleshy, and the cones are more ectomorphic in contrast to the robust reproductive units and the pending delicate leaf-whorls of American *Calamites kinneyana.* Another Early Permian *Annularia* species, *Annularia spinulosa*—the first ever described in 1821 by Kaspar Maria Graf Sternberg from the Döhlen Beds—cannot being connected well because of their different cones. Younger (Gzhelian) European *Calamites wachtleri* is small-sized, also their leaves have not a typical *Annularia*-character, whereas the cones are slim and elongated (Wachtler, 2011, Perner, 2013, Wachtler, 2015). Early Permian European (Asselian-Sakmarian) *Calamites gigas* associated with Annularia carinata foliage and *Calamostachys dumasii*-fertile organs holds in the same way European Calamitalean-features (slender strobilo, more sporangiophores, not pending whorl-leaves). Therefore, are enough reasons to add with *Calamites kinneyana* a new species which can be regarded as a common Paleozoic flora element in America.

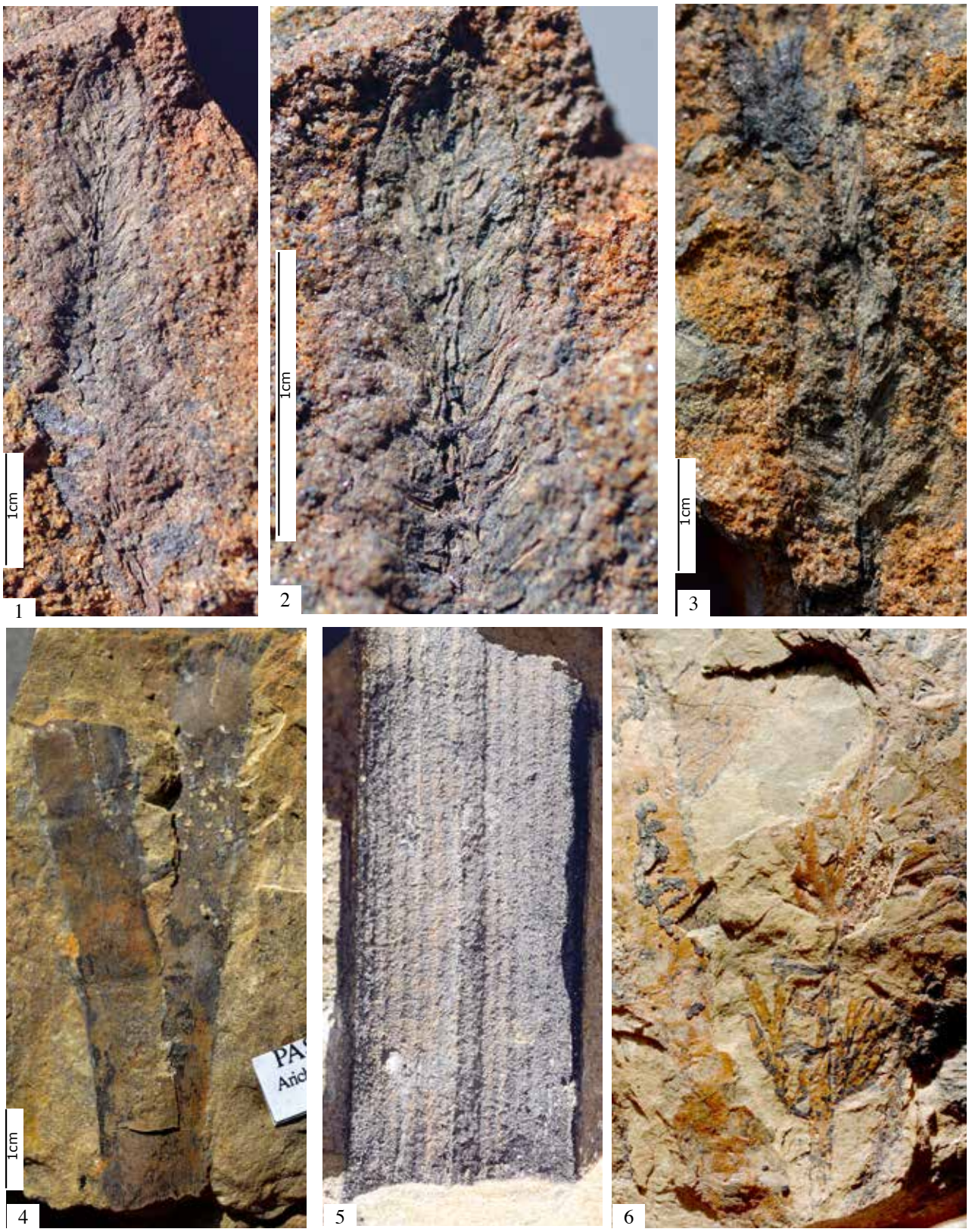
## The Equisetales

Additionally, to the Calamitales, a second group of Sphenophytes, the Equisetales were recorded from the Carboniferous-Permian boundary. They were seldom in Early Permian with *Equisetites hemingwayi, Equisetites vaujolyi* or *Equisetites geraschi* (Perner & Wachtler, 2015), and Upper Permian *Equisetites siberi*, from which are recorded just their characteristic globose cones.

The genus *Equisetites* was introduced in 1833 by Kaspar Maria Graf Sternberg for fossilised species to distinguish them from the only extant genus *Equisetes*.

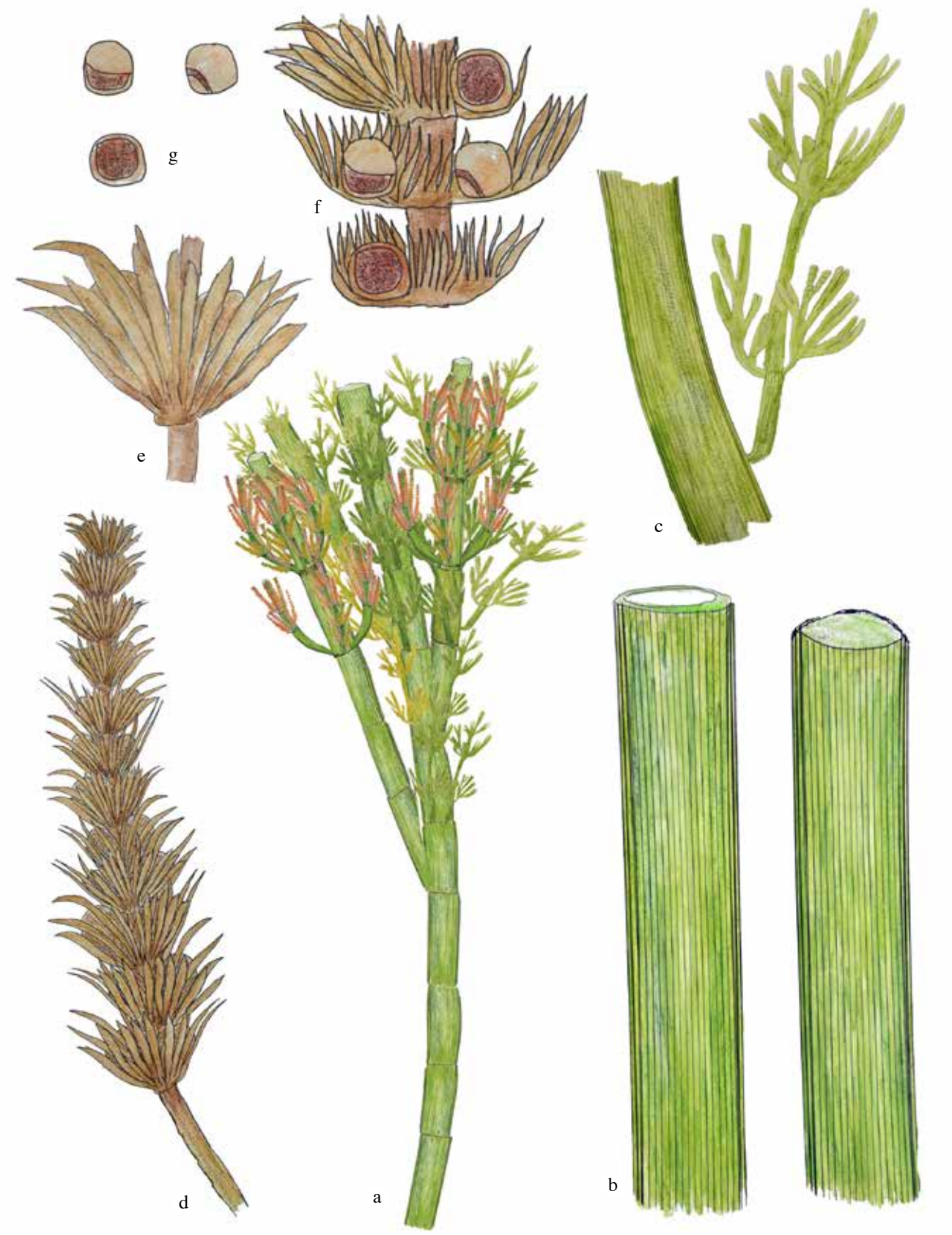
All these horsetail-groups were present in Angara-Land, based on findings of their fertile organs. If all the autochthonous families, summarized in the family of the Tchernoviaceae (Meyen & Menshikova, 1983) like *Phyllotheca* or *Umbellaphyllites* (ex *Annulina*) (Doweld 2002) can be accepted is doubtful because many of the Angaran Sphenophyta hold indeed different reproductive organs, but their elongated strobili can be connected with Northern hemisphere Calamitaceae as well the rounded and nodular Equisetalian cones have similarities with the Sphenophyta *Equisetites*. Because Early Permian (Kungurian) sediments from Matvéevo in the Perm krai spherical cones were recorded, M. D. Zalessky (1939) introduced the name *Equisetina (magnivaginata)* to differentiate them from European *Equisetites* horsetails. This different genus name can be accepted due to some differences between *Equisetites* and *Equisetina*. With the Kungurian E*quisetina magnivaginata*-cones and the *Paracalamites campanularis* strobili from the Fore-Urals Matvéevo it is unquestionable proved that on the Carboniferous-Permian border the Calamitaceae and the Equisetaceae were just largely separated in their reproductive features. Both horsetail reached a main stem-size of about 10 till 20 cm. A third more enigmatic group is composed by the Sphenophyllaceae, usually creeping low growing horsetails. Because the *Calamites*, as well the *Sphenophyllum*-species hold secondary axes with whorls of typical the stem surrounding leaves a distinction is not always easy.

The genus *Equisetites* reached its heyday in the Triassic especially with *Equisetites arenaceus* dominating vast parts of Europe. Strangely in the Middle Triassic (Ladinian) German Hauptsandstein another differently evolved genera, *Schizoneura merianii,* occurred mainly in equal quantities and in the same horizons, together with *Equisetites arenaceus*. Both hold sporangial sacs hanging down on the underside, in *Equisetites* the strobili were mainly rounded, segmented in hexagonal shields, whereas in *Schizoneura* the cones were small-sized and elongated, single sporangiophores were hexagonal but smaller than those of *Equisetites* and equipped with a higher number of sporangial sacs hanging also down on the underside of the protecting shield.



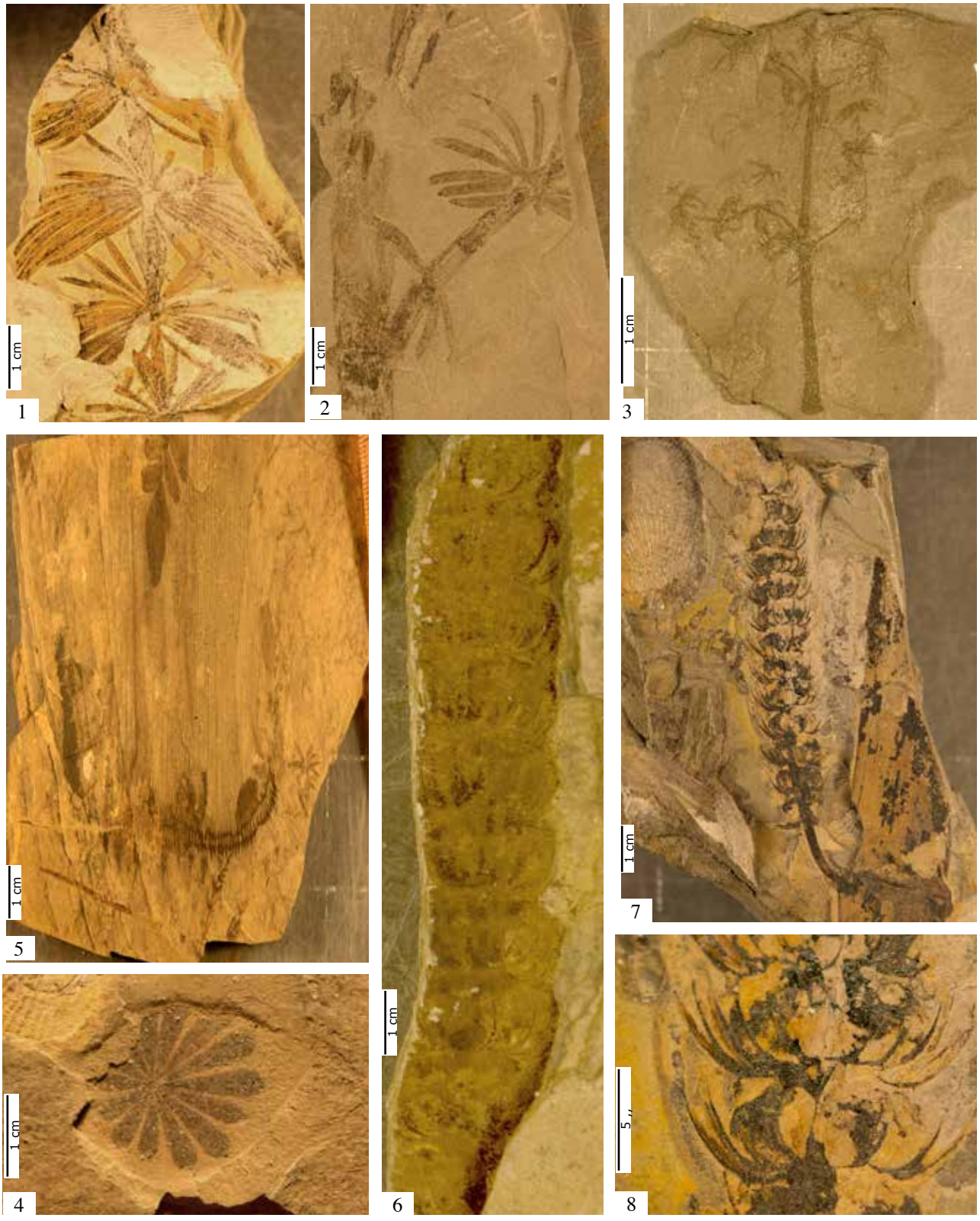

***Neocalamites benckeae*. Lopingian, Late Permian, Eastern Alps, Dolomites**

1-2. Juvenile strobilo and detail of the sporangiophores with a multitude of coating bracts (PAS 210); 3. Adult cone with desiccated sporangia (PAS 727); 4. Main and secondary axis (PAS 421); 5. Stem with distinctive narrow tangential striae (PAS 378); 6. Lateral stem with leave-whorls (PAS 710) Valli del Pasubio, Coll. Wachtler




***Neocalamites benckeae.*** **Lopingian, Late Permian, Eastern Alps, Dolomites. Rconstructions**

1-1. a. Whole fertile plant; b. Stem (PAS 378); c. Lateral stem with leave-whorls (PAS 710); d. Juvenile cone (PAS 210); e. Detail of the sporangiophores with a multitude of coating bracts (PAS 210); f. Part of an adult cone with desiccated sporangia (PAS 727); g. Isolated sporangia (PAS 727)




***Calamites kinneyana* sp. nov. Horsetail. Earliest Permian (Kasimovian)**

1. *Annularia*-whorl (P-14404); 2. Different formed *Annularia*-branchlet (P-71313); 3. Juvenile or apical branchlet (P-30854); 4. Juvenile *Annularia*-leaves (P-37577); 5. Monopodial stem with longitudinal striae, interrupted by internodes and *Annularia* foliage (designed holotype P-44727); 6. Juvenile closed cone (P-71313); 7. Entire cone attached to a stem (P-69245) 8. Detail of the sporangiophores with the coating sterile bracts (P-69245) All Kinney Quarry site (Central New Mexico), Coll. New Mexico Museum of Natural History and Science


***Calamites kinneyana* sp. nov. Horsetail. Earliest Permian (Kasimovian) - Reconstructions**

a. Whole fertile plant; b. Reproductions organs (USNM 450772); c. Single cone (P-69245); d. Sporangiophores with the coating sterile bracts (P-69245); e) Juvenile or apical branchlet (P-30854); f. *Annularia*-whorl (P-71313); g. *Annularia-whorl* (P-14404) All Kinney Quarry site (Central New Mexico).

## Systematic Paleontology

Division Sphenophyta
Order Equisetales DUMORTIER 1829

## *Equisetina ZALESSKY 1939*

### Taxonomic notes

M. D. Zalessky described in 1939 horsetail stem-fragments from Matvéevo (Krasnaia glinka) as *Equisetina*. Although having some similarities with Paleozoic-Mesozoic Equisetites, well known from many European sites, the genus-name *Equisetina* was accepted.

## *Equisetina magnivaginata* ZALESSKY, 1939

1939 *Equisetina magnivaginata* Zalessky, p. 330, Fig. 1, p. 331 Fig. 2, 3

**Vegetative shoots:** Monopodial stems till 10 cm width, characterised by fine internodes (MAT 242, MAT 241) that ends in a telescope-like nested head. There, the internodes are closely spaced (MAT 66). Whorls of shoots are given off from the stem nodes (MAT 250). Each diaphragm is usually surrounded by a leaf sheath, with spine-like teeth.

**Fertile strobili:** Mainly ovoid to round and up to 3 cm long by 2 to 3 cm wide (MAT 75), segmented in many hexagonal bracts. Single sporangiophores 0.3 x 0.3 cm, with hexagonal peltate shields characterized by a slight umbo.

### Discussion

*Equisetina* appears like European *Equisetites*, the stem can be regarded as identical and also the outer appearance of their fertile organs. But till not also the inner life of the sporangiophores of *Equisetina magnivaginata* (MAT 75) are known further speculations cannot be done and therefore the slightly different name *Equisetina* in contrast to Equisetites can be accepted. The first appearance of *Equisetina* we have in Artinskian (ARTI 1, ARTI 22), in the Kungurian of the Sylva-River fossil sites they are than frequent. Similar Sphenophyta, like *Equisetites hemingwayi* (England) or *Equisetites geraschi* (Perner & Wachtler, 2015) from Germany, exist also in the European Early Permian. The main difference between *Equisetites-Equisetina* and the coeval *Calamites* species are the rounded strobili, segmented in several hexagonal scales in comparison to the elongated strobili with the bracts clawing densely the sporangiophores of the Calamitaceae. These splitting in rounded strobili (*Equisetites-Equisetina*) and elongated


***Equisetina magnivaginata* cone**

Strobilus (ARTI 21), Artinskian

***Equisetina magnivaginata* cone**

Detail of the strobilus (MAT 75)

(*Calamites-Paracalamites-Neocalamites*) we can record in the whole Northern Carboniferous-Permian hemisphere.

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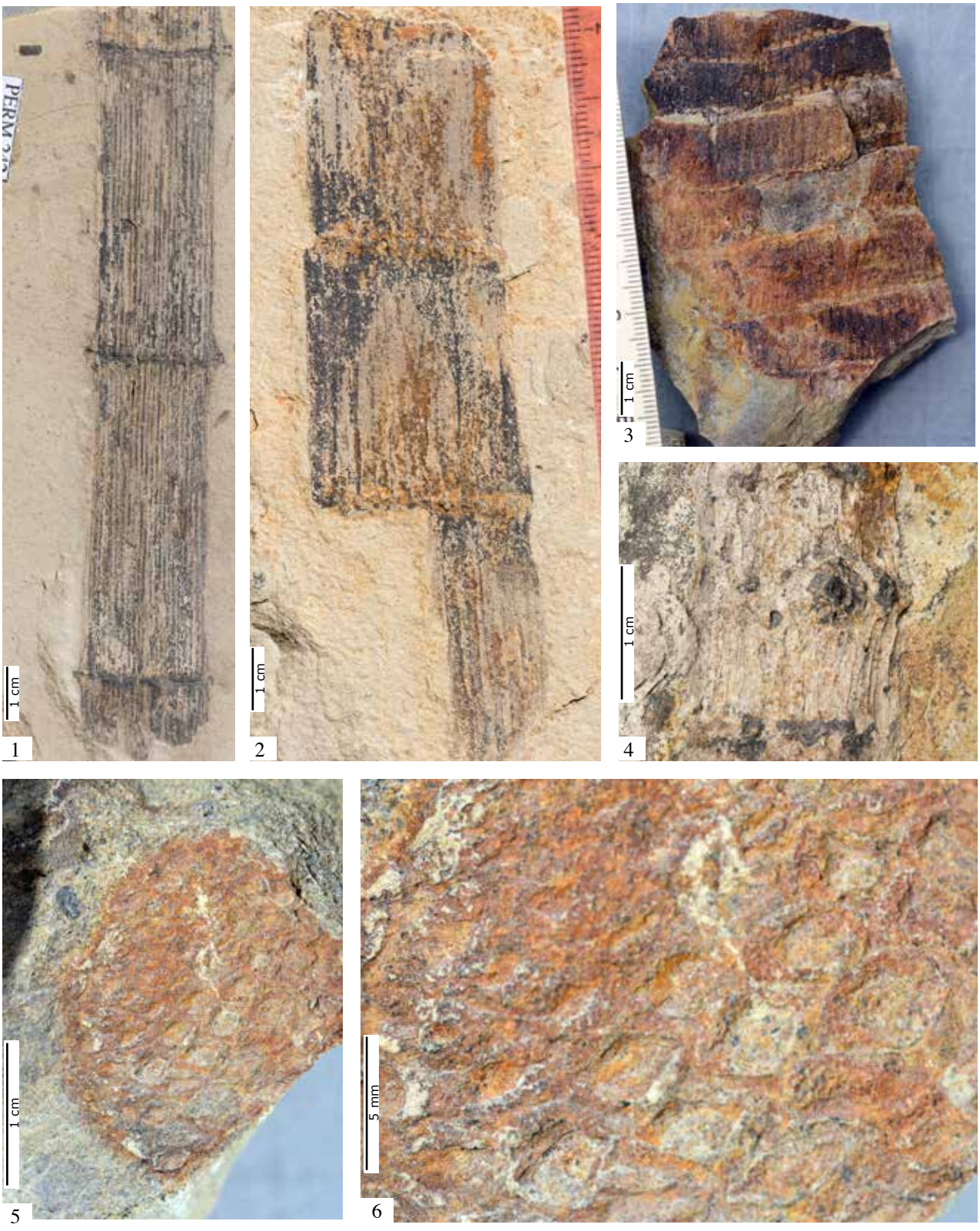
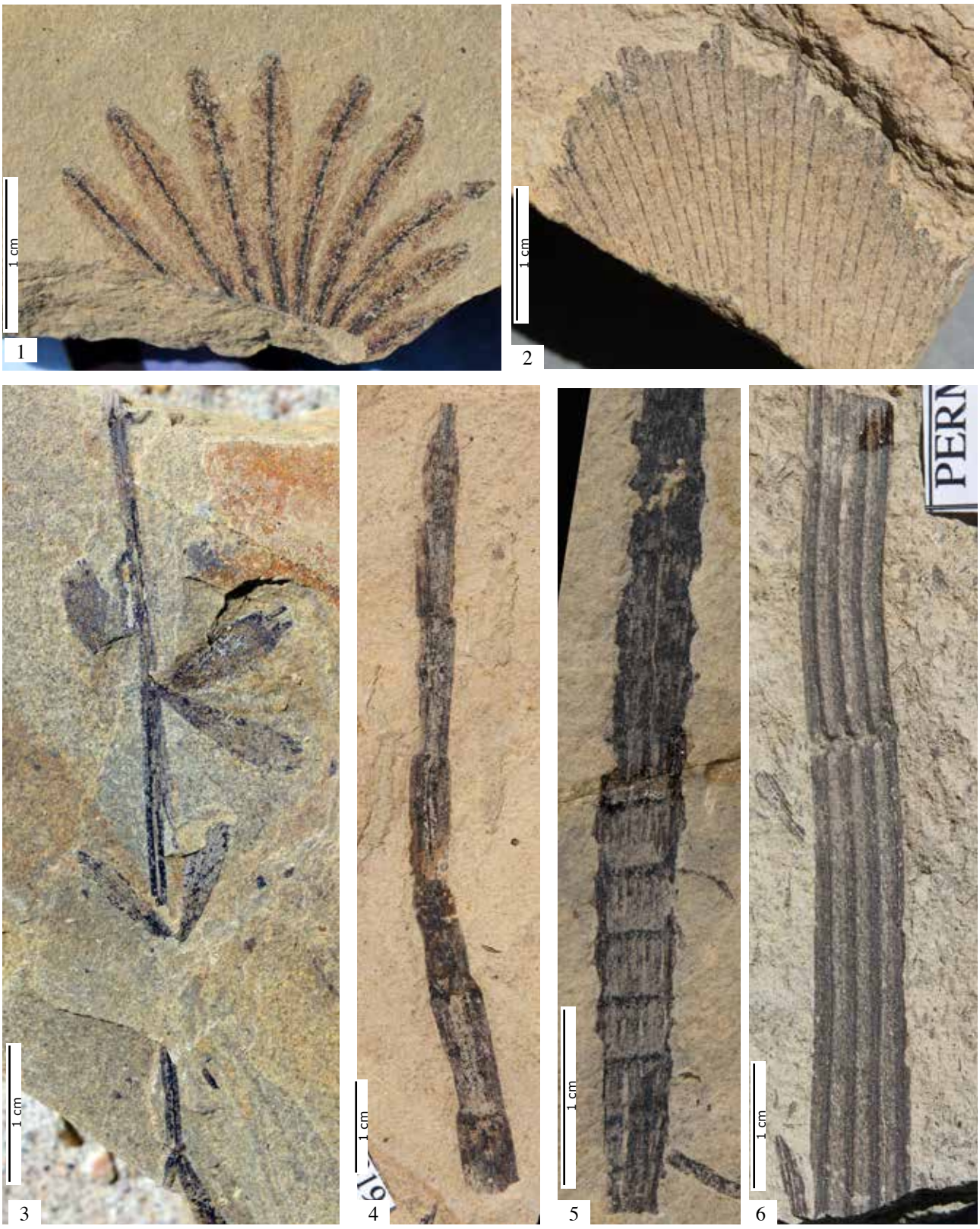



***Equisetina magnivaginata*. Horsetail. Early Permian, Fore Urals, Russia**

1-2. Monopodial stems with internodes (MAT 242, MAT 241); 3. Apical part of a main stem (MAT 66); 4. Shoot axes with lateral branching impressions of the nodes (MAT 250); 5-6. Single strobilus and detail (MAT 75); Matvéevo, Kungurian (Early Permian) Coll. Wachtler, Dolomythos Museum




**Different horsetails from Early Permian of the Fore Urals, Russia**

1. Leaf sheaths, *Calamites-Annularia* (MAT 114, Coll. Dammmann); 2. Leaf sheaths, *Sphenophyllum* (MAT 425); 3. Leaf sheaths, *Sphenophyllum* (MAT 149); 4-5. Apical part (Paracalamites) (MAT 319, MAT 311); 6. Main stem (*Paracalamites)* (MAT 247); Matvéevo, Kungurian (Early Permian) Coll. Dolomythos