The development of horsetails in the Mesozoic

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The horsetail *Equisetum* has remained almost unchanged for over three hundred million years. Findings over recent decades have shown that their direct ancestor must have developed to its final form by at least between the Carboniferous and Permian. To differentiate the fossilised specimens from the modern versions of today, the latter are referred to as *Equisetum*, and started in the Tertiary period, the older ones as *Equisetites*. *Equisetites mougeotii* in the Early Triassic followed by *Equisetites arenaceus* in the Middle Triassic reached its heyday based not only on their widespread occurrence but also due to their impressive size of partially 20 cm thick stems. Another slightly different line also characterised the Triassic: the horsetail genus *Schizoneura paradoxa* in the Early Triassic and *Schizoneura merianii* in the Middle Triassic. They all colonised the swamps and flood areas of this period and have therefore been recovered in large quantities as plant fossils. A new deep insight based on recent findings is planned by the author.

Key words: *Equisetum, Equisetites*, *Schizoneura,* Triassic
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A horsetail-association in the Middle Triassic: Left the Sphenophyta *Equisetites arenaceus* with several sporophylls, on the right side *Schizoneura merianii*. They occupied the same habitat in the German Hauptsandstein.

All horsetails today are herbaceous plants with a more or less branched root system that creeps underground. The shoots above ground grow from this rhizome. They 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.

Horsetail transition from Carboniferous to the Permian

The origin of Sphenophyta can be traced back to the Devonian, but in the Carboniferous they reached an extraordinary heyday. They were inserted into four main groups: the Pseudoborniales, the Sphenophyllales, the Calamitales and the Equisetales. *Pseudobornia ursiana* from the Late Devonian comprises trees up to 20 m high with split sporangiophores holding the sporangia inside tapered dwarfish leaves. The Calamitales were trees with strongly undulate stems, and the infructescences were elongated with bract-like leaves which tightly hold the sporangia (Perner & Wachtler, 2015). The Sphenophyllales were mostly creeping to climbing plants with whorled, wedge-shaped leaves. The cones resembled those of the Calamitales.

The only Sphenophyta group from which today's horsetails can be deduced is represented by the Equisetales. Although the forerunner, the Paleozoic–Mesozoic genus *Equisetites* can be regarded as lying in a direction-line to today's *Equisetum*, their massive up to 20 cm thick tree-like stems do not correspond to extant Sphenophyta. Otherwise their fertile organs can be connected well.

Plants in the genus *Sphenophyllum* usually have slender trunks with ribs like those of *Calamites*. There were usually 6 to 12 wedge-shaped leaves on the nodes that together formed a whorl around the branches. The genus is recorded from the Upper Devonian and was prevalent all over the entire northern hemisphere. The best-known Lower Permian species were *Sphenophyllum oblongifolium, S. longifolium, S. angustifolium* and *S. thonii.* The fertile cones, growing out from the nodes of the trunks could be up to 5 cm long, and up to ten bracts would grow together on their lower edges. The sporangiophores each bore two sporangia.

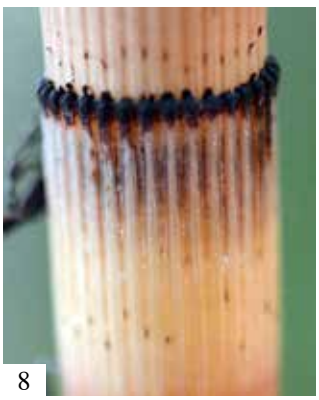
The *Calamites* sporophylls also appeared to be uniform overall, but were still different from the subsequent *Equisetites* species or the genus *Equisetum* of today. The biggest differences can be seen in the verticillate sporangiophores with a shield-like character in *Equisetum* and *Equisetites*, in contrast to the *Calamites* with their multiple bracts, each of which contained a sporangium, that sprouted out at the same height. In spite of this, its original design and organisation with longitudinally ribbed internodes, knot-like nodes between each internode, and whorled foliage extending from the nodes, barely changed. The first species of *Calamites* appeared in the Lower Carboniferous, although they were uncommon, but they spread extensively all over the world in the Upper Carboniferous. The horsetails in the *Calamites* genus, however, achieved considerable heights in the Lower Permian. Around Chemnitz in Germany, for example, trunks with diameters of up to 60 cm were found, which means heights of up to 20 m can be assumed. From the Carboniferous to the Permian most of the ancient horsetail tribes vanished. The *Calamites* survived for some time in the Permian. This also applies to the creeping, wedge-leaved *Sphenophyllum* species recorded till the Early–Middle Permian.

Neocalamites can be regarded as a transitional species all over the Permian. The grooves on the trunks, which could be up to 10 cm thick, were usually arranged like those on *Equisetites,* and they did not form clearly visible rings on the nodes. The striae between each other were also much larger than those of *Equisetites*. Instead, relatively thick lateral branches, which were divided into nodes and internodes, would split up, also in total contrast with the fragile *Equisetites* branchlets. They were even widespread in the Lower Permian as *Neocalamites (N. tregiovensis*), only to decline suddenly after that (Wachtler, 2012). *Neocalamites behnkeae* have been found in the Upper Permian, but they are uncommon (Wachtler, 2013). Some species are thought







Primary and secondary branching of today‘s horsetails

1. *Equisetum giganteum*. Main stem and branching of first order; 2-3. *Equisetum bogotense*. Stem axis and detail of lateral branching; 4. *Equisetum telmateia*, biggest European horsetail with lateral branchlets; 5-8. *Equisetum hyemale.* Shoots with telescope-like inserted internodes, detail of a node with lateral branches.

Structure of extant horsetails and fertile parts

1. *Equisetum schaffneri*, basal shoot. 2. *Equisetum giganteum.* Unbranched shoots. 3. *Equisetum hyemale*. Apical part with telescope-like internodes. 4-6. Closed and opened sporangiophores of the field horsetail (*Equisetum arvense*). The fertile parts flourish slightly earlier than the sterile and wilt after the pollination.

to have survived into the Triassic period, but there are many doubts because the blueprint of the *Neocalamites* or *Calamites* species, their fertile leaves clawing the seeds, are not furthermore recognisable.

The triumphal march of *Equisetites*

So, in the end, there remained just one big genus of horsetails, probably originating in the Late Carboniferous, becoming more and more important. These were Early Permian *Equisetites (Equisetites hemingwayi),* but also *Equisetites vaujolyi* and *Equisetites geraschi* (Perner & Wachtler, 2015). Due to the different structure of the vegetative shoots, it can be assumed that they must have become separate genera sometime between the Carboniferous and Permian periods. Equally important was *Equisetites siberi* from the Dolomites of the Upper Permian. Its shoots, which were as thick as an arm, and the whorl of leaves that grew to form a collar surrounding the shoots, bear an amazing resemblance to those of Triassic horsetails. They would have grown shoots 10 cm thick and reaching heights between 2 and 5 m, from a rhizome.
Throughout the entire Permian period, the horsetails played an essential role. The specimens from a wet climate demonstrated that the scientists who envisioned a dry and arid climate were wrong. They also, especially the genus *Equisetites,* bridged the Permian–Triassic transition without bigger restrictions or changing, to form one of the dominant plant families over the Triassic. In particular *Equisetites mougeotii* in the Early Triassic followed by *Equisetites arenaceus* in the Middle Triassic began, with their powerful hollow stems, to represent a characteristic element of flora extending through practically the entire Triassic (Wachtler, 2011). Apart from their impressive size, which today is not equalled by any other species of horsetail, both these *Equisetites* species are a little similar in structure to the swamp horsetail (*Equisetum palustre*), although the maximum size of the latter is only 1 m. Its lateral branches are also vigorous and numerous and divided into fertile and sterile side shoots. 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.

***Equisetites mougeotii* (Anisian)**

1. Stem fragment with one internodium (PIZ 279); 2. Stem apex with telescope-like nested internodes (PIZ 582). All Coll. Wachtler, Piz da Peres, Anisian, Dolomites.

Equisetites sp. Seekofel, Carnian, Dolomites, Coll. Wachtler

The *Schizoneura* complex

It was thought that the genus *Neocalamites* also survived the Permian–Triassic transitional period unscathed. But new research has established that most of the Triassic *Neocalamites* species (like *N. merianii* and *N. hoerensis*) must be inserted in the genus *Schizoneura,* having more affinities with *Equisetites.* Especially in the German Middle Triassic we encounter relatively often slender, sometimes slightly rounded to elongated horsetail sporophylls that do not pertain to *Equisetites arenaceus,* but are also different from the *Calamites* fertile parts. A first important step was taken by Lea Grauvogel-Stamm (1978), who undertook research on the Sphenophyta *Schizoneura paradoxa* from the Early Triassic. She established that two slightly different strobili sprout on the same plant. Those called *Echinostachys oblonga* are small-sized and rounded, while those called *Echinostachys cylindrica* are more elongated. The single sporangiophores were distinctly smaller, as in E*quisetites arenaceus*, the spore-tubes were grouped around the holding axis and not hanging from the underside of the covering shields as in *Equisetites* or in all today's *Equisetum* species (Grauvogel, 1978, Pl. 11, Fig. 4–6). Otherwise in the Middle Triassic *Schizoneura merianii* (Wachtler, 2016) this phenomenon is not recorded: the dwarfish spore cases are attached on the small-sized peltate shields. Therefore, also *Schizoneura* has more affinities with *Equisetites* than with *Neocalamites*. Adding to the confusion, in the plant-rich German Middle Triassic, is the high amount of described leaf species to which only a few to no fertile organs are attached. But in most cases aesthetic branchlets find more acceptance in the collector-scene than some unsightly infructescences.

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Systematic Paleontology

Division Sphenophyta
Order Equisetales DUMORTIER 1829
Family Equisetaceae MICHAUX, ex DC 1804

Equisetites STERNBERG 1833

Taxonomic notes

Equisetites was first described in 1833 by Baron Sternberg to differentiate today's Equisetum from the Mesozoic species. *Equisetites mougeotii* was named after the french paleobotanist Joseph Antoine Mougeot (1815-1889)

Equisetites mougeotii BRONGNIART 1828
Early Triassic character - horsetail

Description

Vegetative shoots: Monopodial stems arising from a creeping rhizome, characterised by fine internodes that have longer distances (10 to 15 cm) in the middle and ends in a telescope-like nested head. There, the internodes are closely spaced. Whorls of shoots are given off from the stem nodes. Each diaphragm is usually surrounded by a leaf sheath, with spine-like teeth. Fertile organs on the end of the main stem often or on the lateral branches often more than one aggregated together.
Fertile strobili: Fertile organs on lateral branchlets, usually more than one aggregated together. They consist of an arrangement of peltate shields with several elongated fertile appendices on the lower surface directed towards the main axis. The spherical slightly elongated strobili, sitting on a short, slender peduncle are from 4 cm to 6 cm long, 2.5 to 3 cm wide and consist of several whorls of hexagonal sporangiophores. The peltate shields evidence about 8 to 12 elongated sporangia on the lower surface. Sporangia are at most 2 mm long and 0.5 mm wide. The strobili are globose and densely packed when immature, and cylindrical when mature with open shields to release the spores.

Equisetites arenaceus JAEGER 1827
Middle Triassic character-horsetail

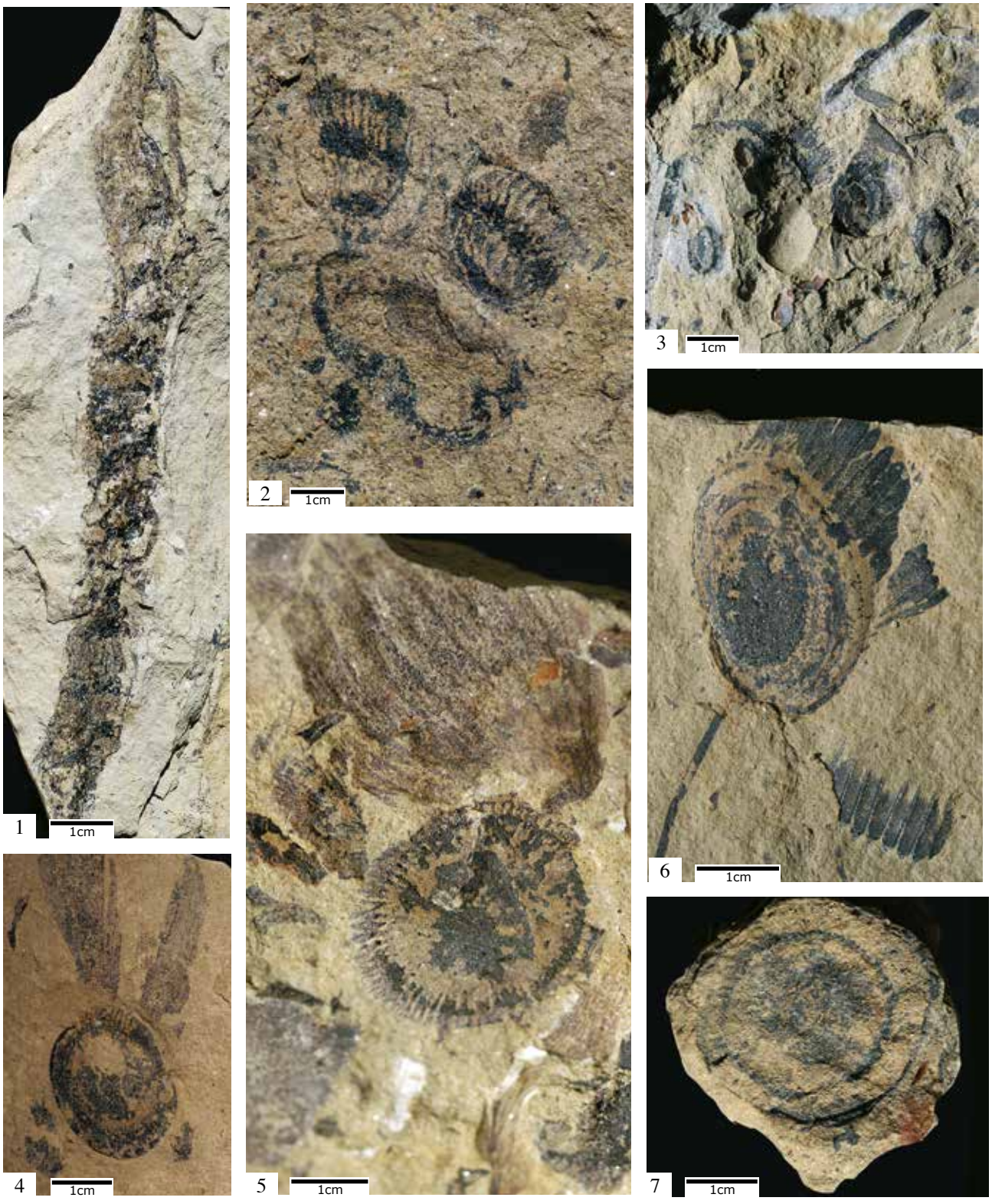
Whole plant: Giant horsetail with monopodial hollow stems up to 20 cm thick, segmented at symmetrical distances. In the upper section a series of delicate secondary stems branching off the telescopic-jointed internodes.
Leaf structure: At the mature node intersections a collar of tapering fused leaves. Lateral branches sprouting in whorls from beneath the collar, divided into sterile and fertile shoots.
Strobili (*Equisetostachys*): Mainly ovoid to round and up to 5 cm long by 2 to 3 cm wide, collected singly or in groups on the verticillate lateral branches of the penultimate or ultimate order, sitting on a short stem with collar. Single elongated infructescences also reaching a length of up to 10 cm. Sporangiophores with hexagonal covering leaves and slight umbo. On the underside numerous (10–14) hanging spore sacs arranged around a table-like attachment connected to the central axis.

Remarks

There are only marginal differences between Early Triassic (Olenekian-Anisian) *Equisetites mougeotii* and Middle Triassic (Ladinina-Carnian) *Equisetites arenaceus*, Both can be considered a "giant horsetail", although it seems that the older one was a little smaller. Dispersed strobili have been attributed to the organ genus *Equisetostachys*, sometimes also to *Equicalastrobus*.
Two main facies are distinguished in the Triassic deposits of Europe: the Middle-European - (mainly France, Switzerland and Germany) and the Alpine facies (mainly Italy, Austria and the Balkan). Olenekian-Anisian floras with a richness of sphenophyta are mainly known from the Vosges (Grauvogel-Stamm, 1978) and from the Dolomites (Wachtler, 2012). Sphenophyta from the Ladinian come from the German Hauptsandstein (Kelber, 1999, Kelber & Van Konijnenburg-Van Cittert, 1998) and the Dolomites (Wachtler & Van Konijnenburg-Van Cittert, 2000). In some sediments, especially in the German Keuper they dominate the flora, whereas in coeval Southern Alps layers they stand largely behind the conifers and the cycads. Strangely in the German Hauptsandstein the two slightly different horsetails *Equisetites arenaceus* and *Schizoneura merianii* occur mainly in equal quantities together in the same horizons.

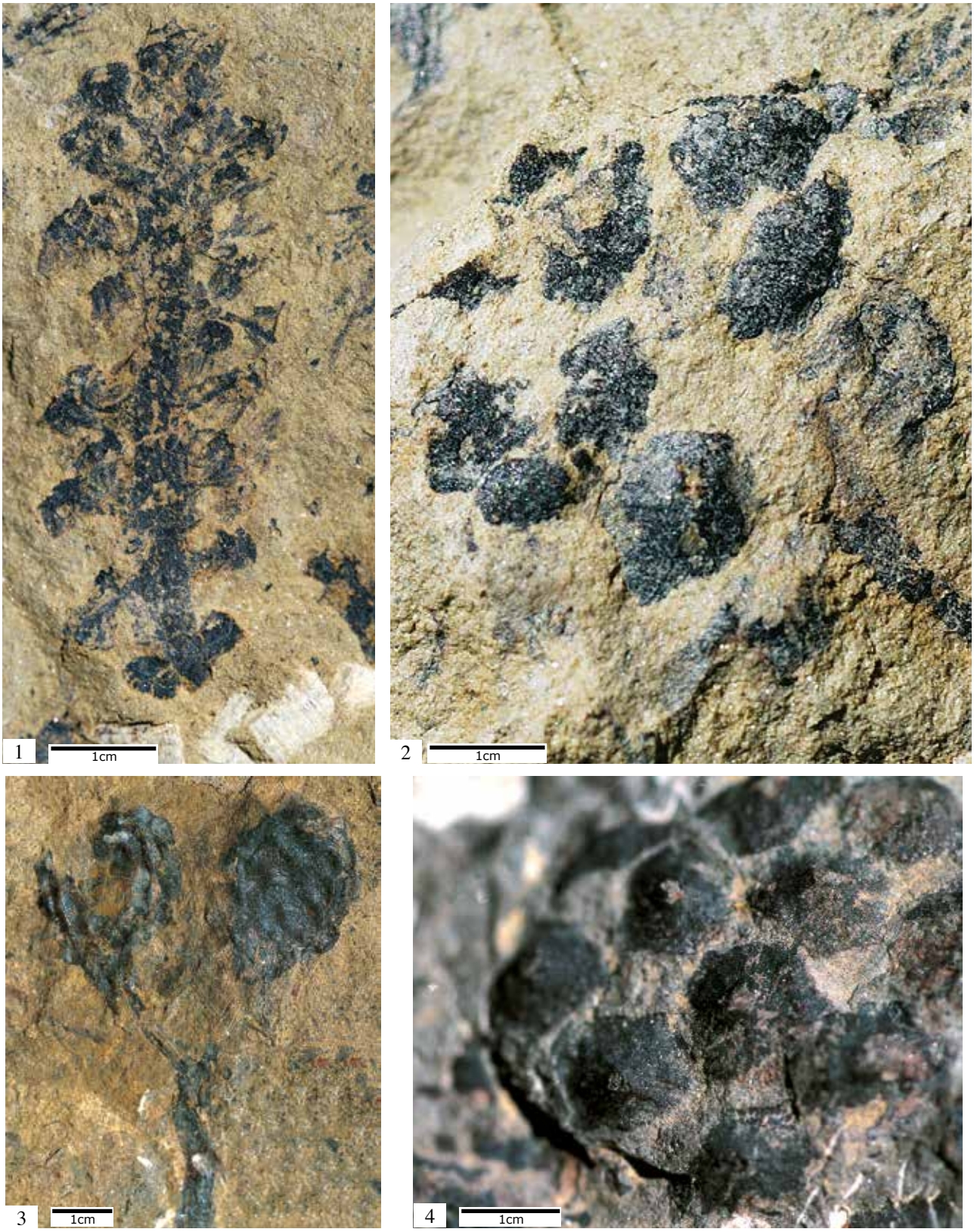
The Sphenophyta *Equisetites mougeotii* in the Anisian of the Dolomites. Reconstructions

a. Entire plant; b. Branching shoots (PIZ 634); c. Apical part (PIZ 582); d. Diaphragm with proximal leaf sheaths (PIZ 636); e. *Equisetostachys richthofeni.* Fertile strobilus showing open sporangiophores (PIZ 633); f. Lateral view of sporangiophore; g. Two attached and closed strobilus (KÜH 676).



The Sphenophyta *Equisetites mougeotii* (Early-Middle Triassic of the Alps) Stems

1. Apical stem fragment with several nodes (PIZ 600); 2. Stem with two lateral branchlets. Probably the main axis was destroyed and so, small shoots grow out on the last nodium (PIZ 634); 3. Several nodes with the brackish water-loving shells *Neoschizodus laevigatus elongates* (PIZ 204); 4. Diaphragm with attached lateral branchlets (PIZ 189); 5. Diaphragm (PIZ 131); 6. Diaphragm with proximal leaf sheaths (PIZ 636); 7. Three-dimensionally preserved stem (PIZ 635), all Coll. Wachtler, Piz da Peres, Dolomites, Anisian)

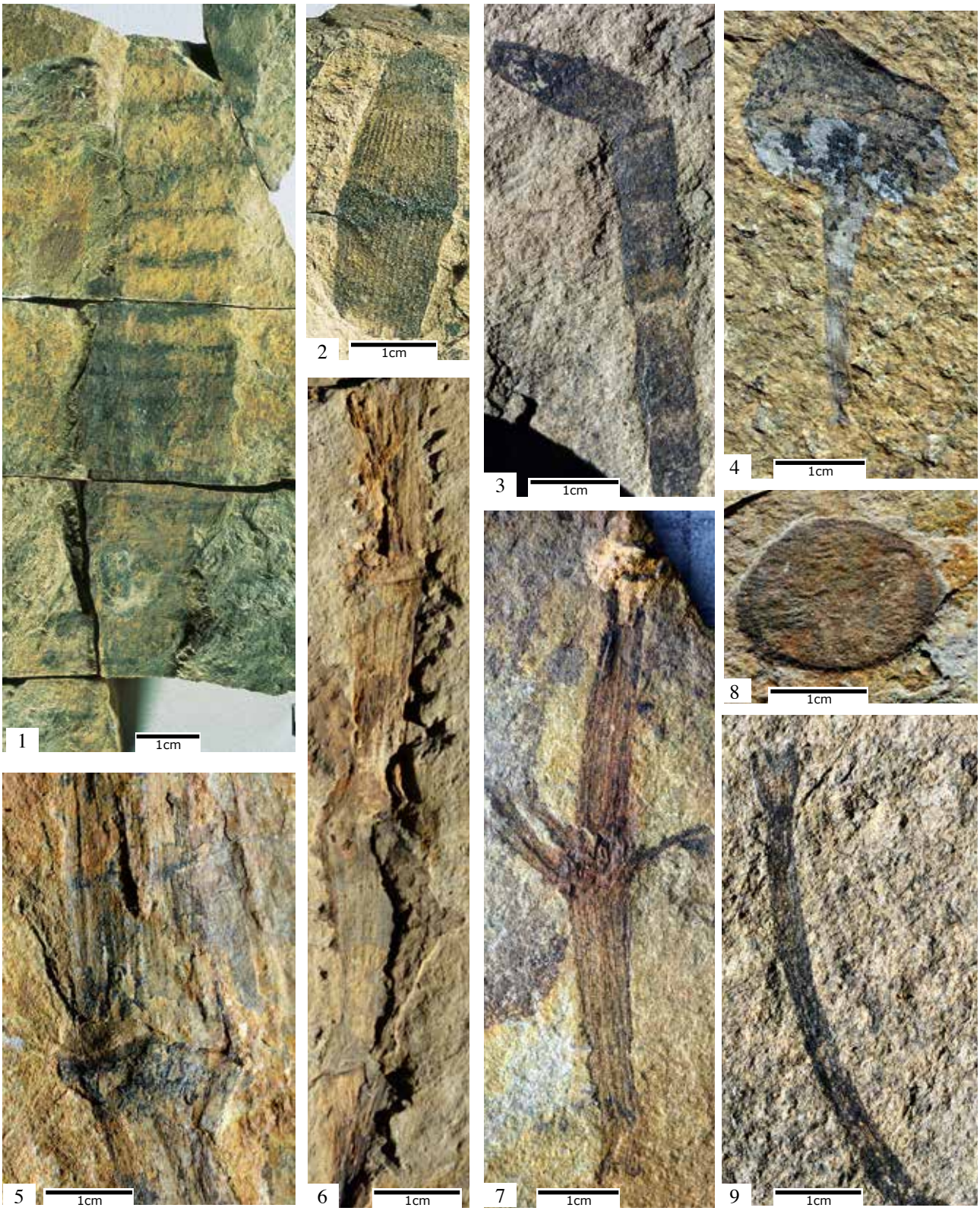


The Sphenophyta *Equisetites mougeotii* (Early-Middle Triassic of the Alps) Fertile organs

1. Fertile open strobilus showing open sporangiophores (PIZ 633, *Equisetostachys richthofeni*, Holotype); 2. Fertile strobilus with some open sporangiophores (PIZ 173); 3. Two closed strobili on a slender shoot (KÜH 676, *Equisetostachys richthofeni).* 4. Mainly closed sporangiophores (KÜH 714), all Coll. Wachtler, Dolomites, Anisian)

The Sphenophyta *Equisetites arenaceus* (Middle Triassic) Reconstructions

a. Whole plant (ILS 556); b. Main stem with leave-sheath (ILS 202, 453, 305); c. Apical part, lateral view of the telescope-like inserted internodes (ILS 113, 47); d. Sterile secondary branch (ILS 486); e. Last order shoot with strobili (ILS 118); f. *Equisetostachys-cone* rounded (ILS 568); g. Elongated *Equisetostachys oblongus*-cone *(ILS 116, 461);* h. Mature strobilus with inner view on the sporangia (ILS 277); i. Detail of the sporangiophores lateral and seen from below (ILS 265, 414).

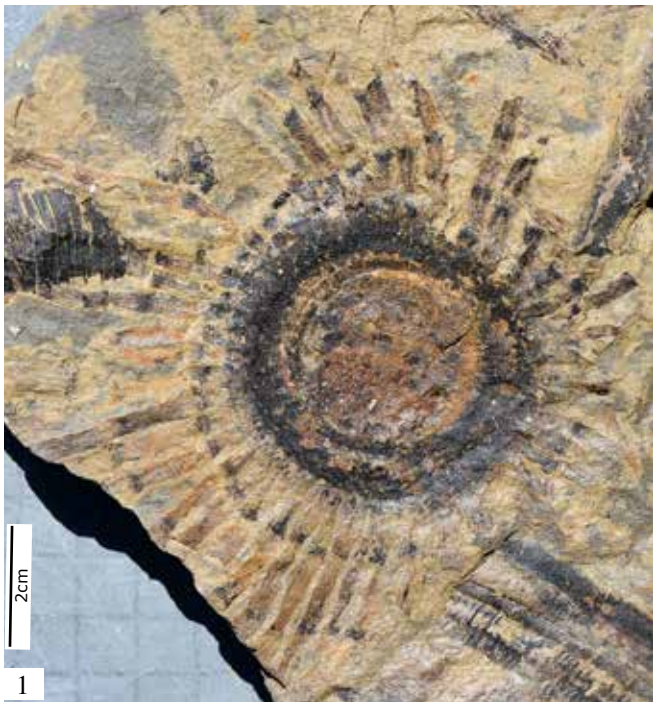


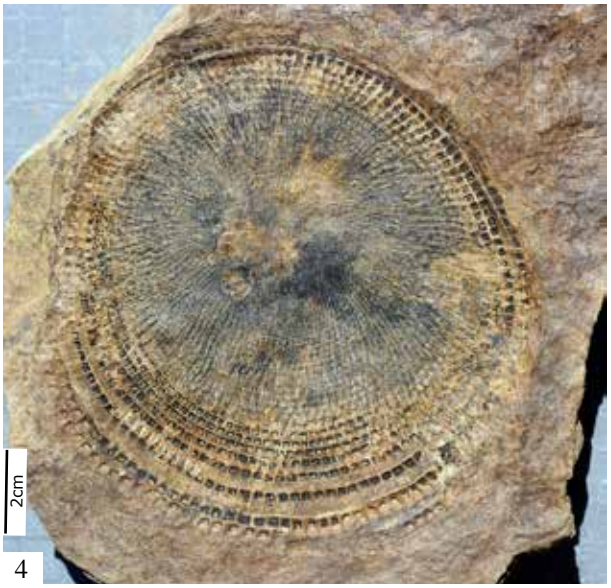
The Sphenophyta *Equisetites arenaceus* (Middle Triassic of the Alps) Sterile and fertile organs

1. Main stem (WRI 044); 2. Apical part of a secondary branchlet (WRI 04) 3. Apical part of a branchlet (PER 03, Coll. Faustini) 4. Cone on a stem (PRE 37) 5-6. Stem with detail of the telescope-like inserted internodes (PRE 04); 7. Lateral branching on a stem (PRE 12, Coll. Faustini) 8. Sheath (PRE 02); 9. Broken branchlet with leaf-sheath, Ladinian - Langobardian, Southern Alps, Coll. Wachtler

The Sphenophyta *Equisetites arenaceus* (Middle Triassic, Germany) Main stems

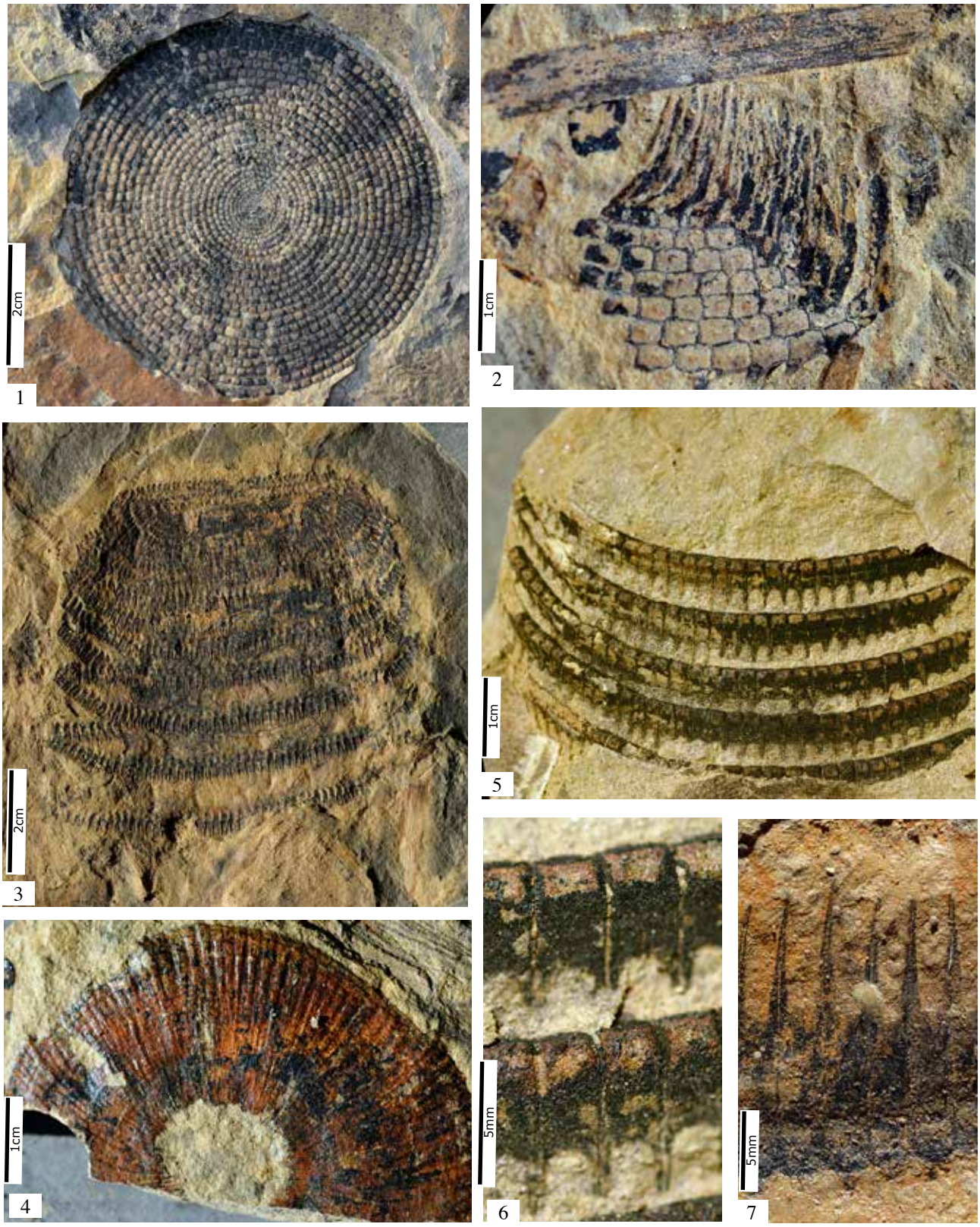
1. Basal part of a main stem, maximal wide 20 cm (ILS 530, Coll. Nißler); 2. Main stem with several internodes, 50 cm length, (ILS 893 Coll. Pohl); ; 3. Apical part with internodes growing within one another (ILS 531, all Coll. Nißler); 4. Several massive stems deposited together. 5. Shoot axes with lateral branching impressions of the nodes (ILS 763, Coll. Frieß), Ladinian





***Equisetites arenaceus* (Middle Triassic, Germany) Lateral shoots**

1. Main stem with first order branching, overview (ILS 894, Coll. Pohl); 2. Main stem with first order branching, lateral view (ILS 787 Coll. Frieß); 3. Main stem with lateral branchlets (ILS 827, Coll. Silberhorn); 4. Apical part of a main stem (ILS 895, Coll. Pohl), Ladinian

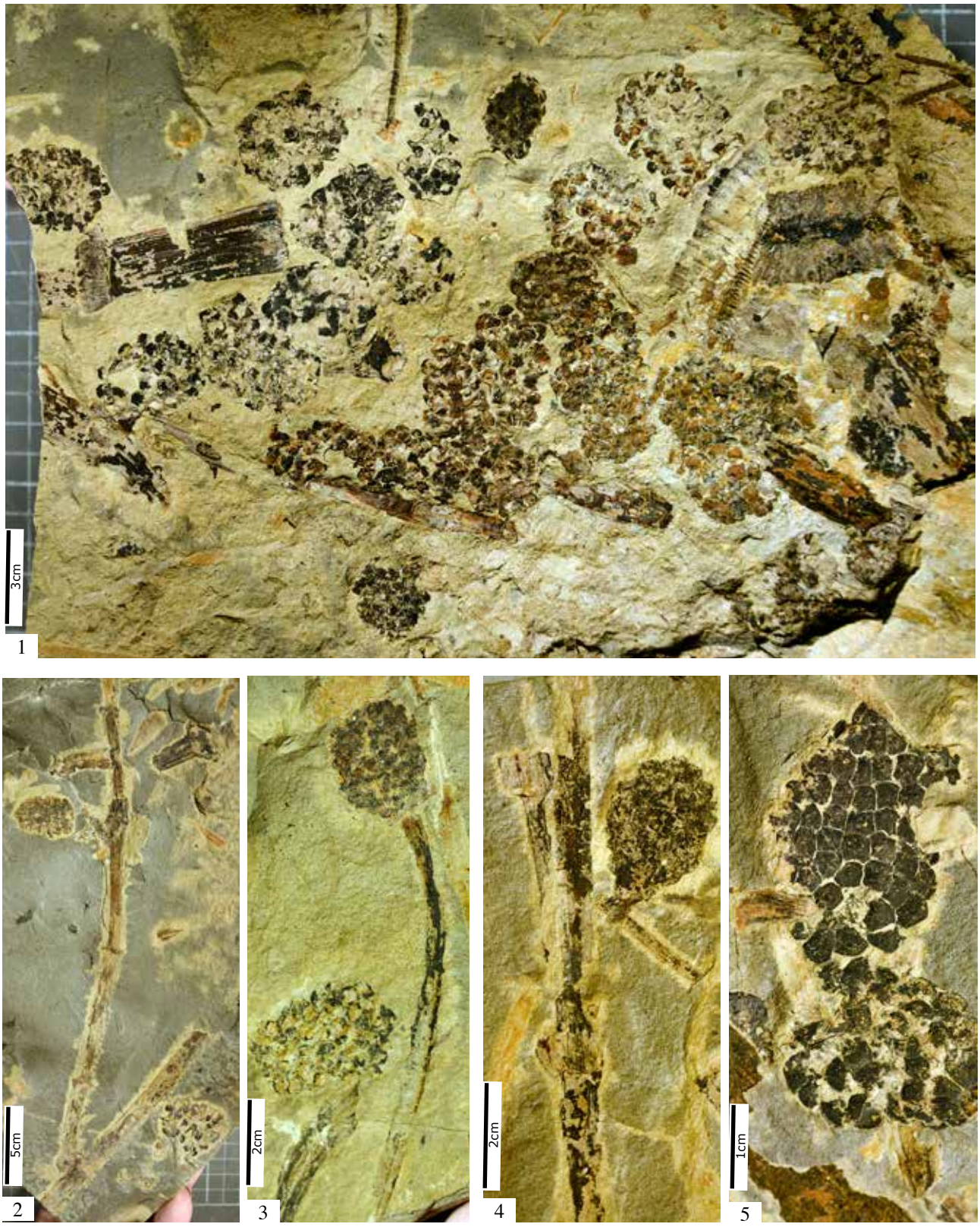


***Equisetites arenaceus* (Middle Triassic, Germany) Stem and apical parts**

1. Apical part of the main stem seen from the upper side (ILS 47) and 2. Detail of the leave-segments (ILS 434); 3. Stem end with the circle-internodes nested each inside other (ILS 113); 4. Diaphragma with the sediment filled hollow core (ILS 125); 5. Impression of the diaphragma and 6-7. Detail of the leave-tips (ILS 516, 133 all Coll. Nißler), Ladinian

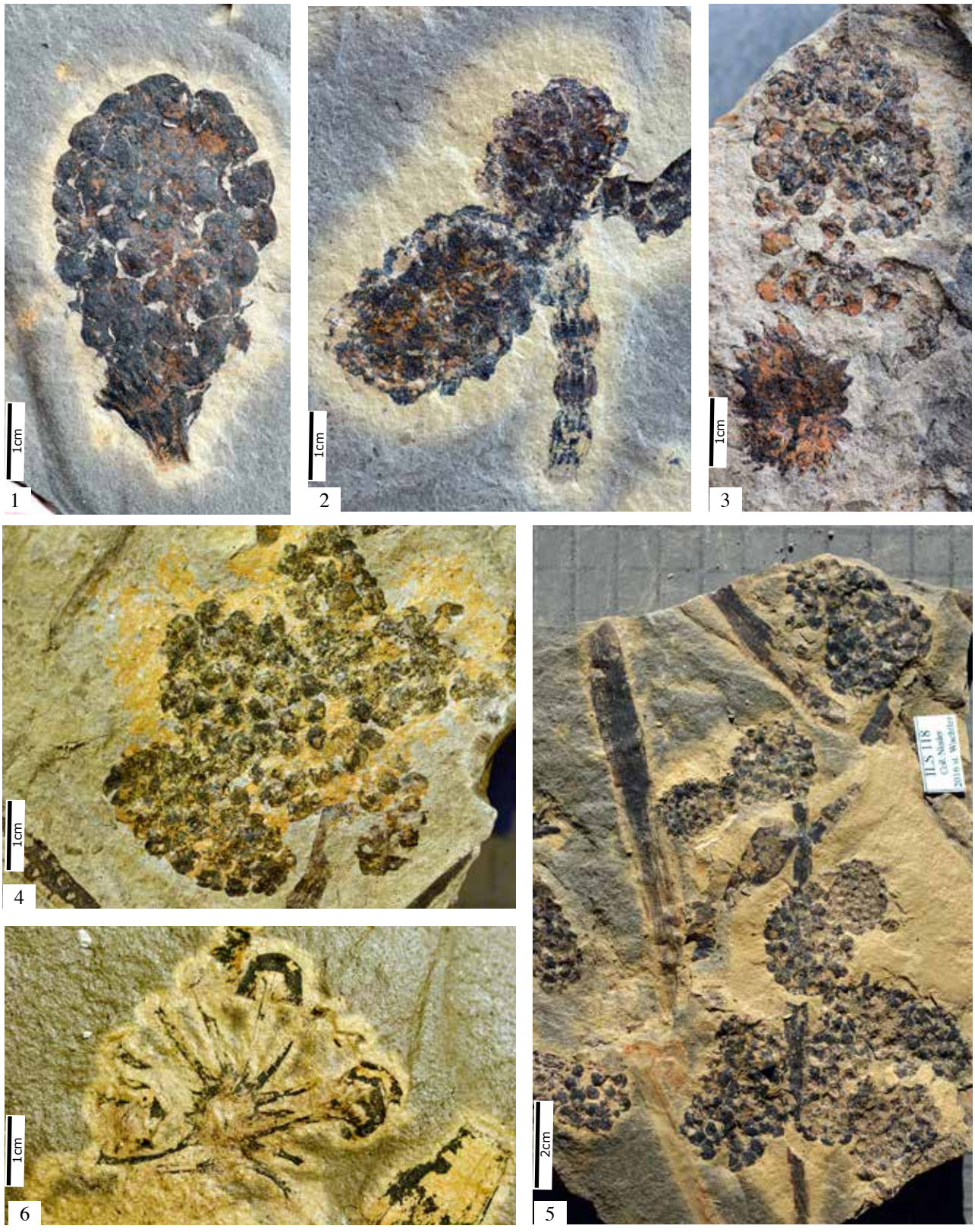
***Equisetites arenaceus* (Middle Triassic, Germany) Lateral shoots**

1. Apical part of a shoot (ILS 777); 2. Leave-collar with lateral shoots (ILS 811 both Coll. Frieß); 3. Forking branches with sheath (ILS 106); 4-5. Branchlets of the first order with internodes (ILS 486, 611); 6-7. Forking shoots (ILS 616, 621, all Coll. Nißler), Ladinian



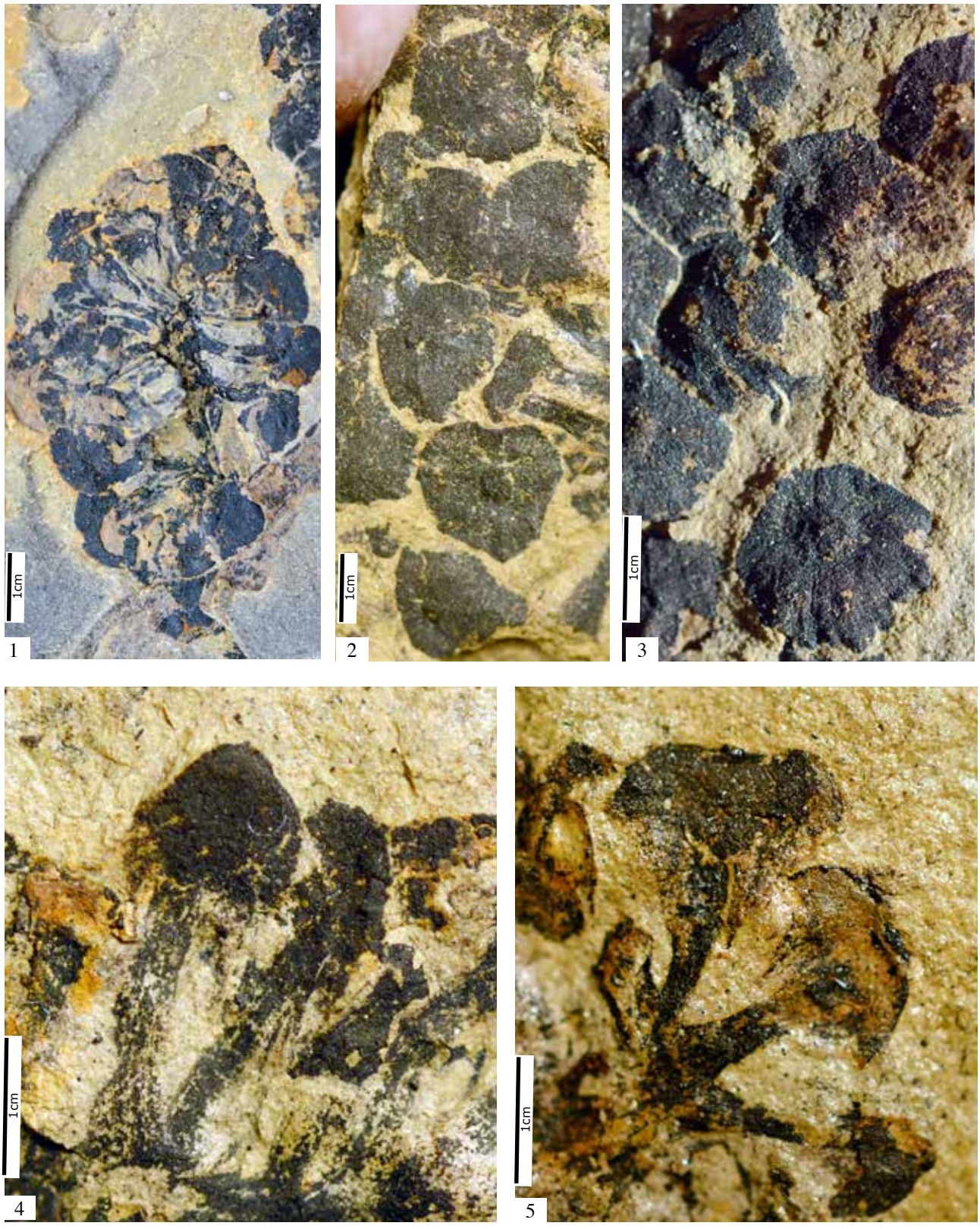
***Equisetites arenaceus* (Middle Triassic, Germany) Strobili**

1. A fair amount of strobili deposited on a slab (ILS 31); 2. Lateral branching with strobili (ILS 32); 3. Apical strobilus (ILS 308); 4. Intermediate strobilus (ILS 397); 5. Exterior view on mosaic-like sporangiophores (ILS 442, all Coll. Nißler), Ladinian



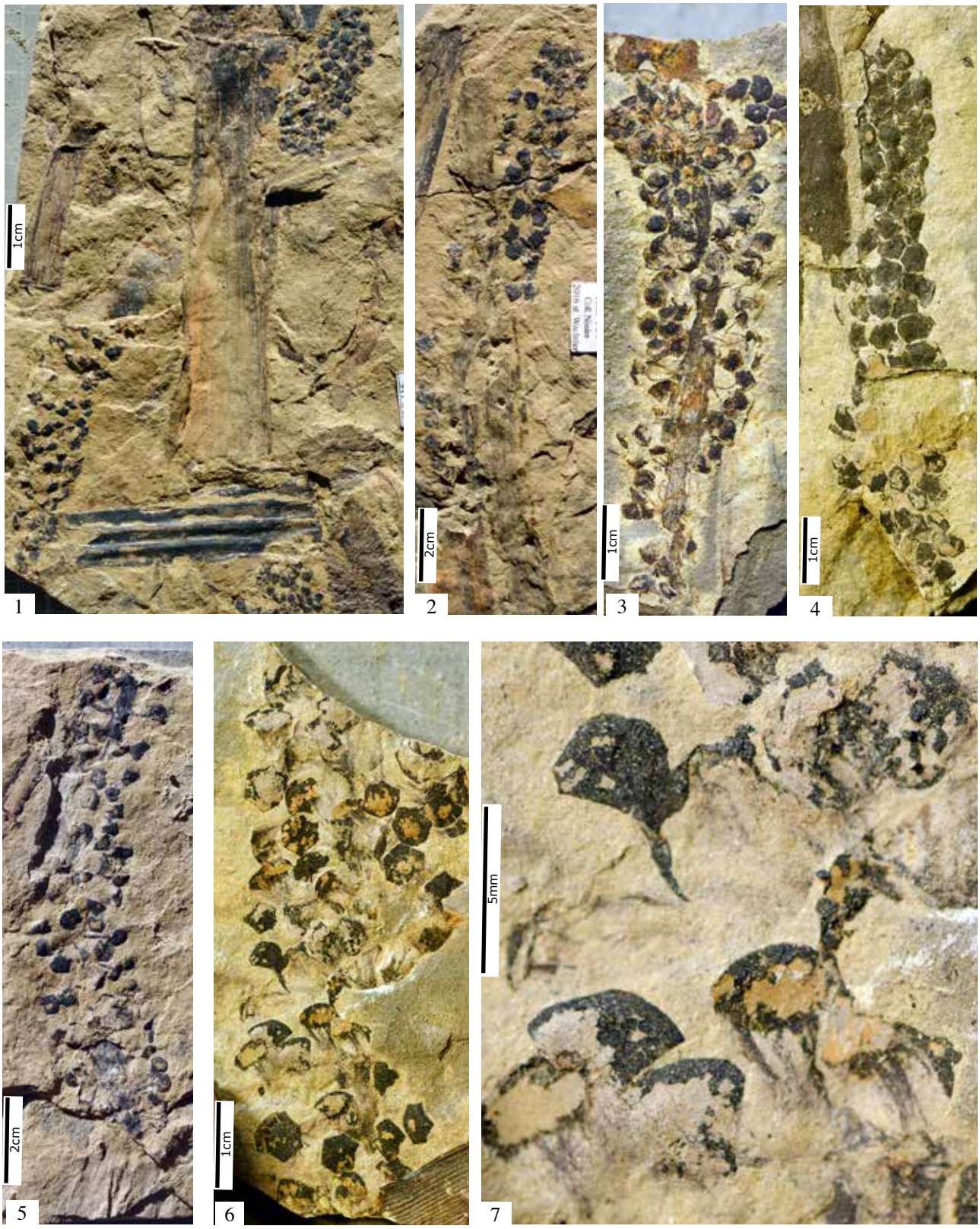
***Equisetites arenaceus* (Middle Triassic, Germany) Strobili**

1. Single strobilus with basal collar (ILS 801); 2. Two connected cones (ILS 809); 3. Detail of a "horsetail cone" with top view of the basal collar (ILS 769, all Coll. Frieß); 4. At least five strobili aggregated on a branchlet (ILS 452); 5. Lateral shoots with several connected strobili (ILS 118); 6. Top view on a cone (ILS 396, all Coll. Nißler), Ladinian



Equisetites arenaceus (Middle Triassic, Germany) Sporangiophores

1.Inside view on an open cone (ILS 606); *2-3.* Detail of the sporangiophores from the outside with the umbo in the middle and lateral hanging spore-sacs (ILS 414, 107); 4-5. Lateral-view of the sporophylls with hanging sporangia-tubes (ILS 277, 568 all Coll. Nißler)



***Equisetostachys oblongus* (Middle Triassic, Germany) Details of the sporangiophores**

1-4. Several elongated strobili (ILS 116, 109, 461, 290); 5. Elongated semi-decayed strobilus (ILS 193); 6-7. Cone with detail of the sporangiophores and the hanging spore-sacs (ILS 265, all Coll. Nißler).

Systematic Paleontology

Division Sphenophyta
Order Equisetales DUMORTIER, 1829
Family Equisetaceae MICHAUX, ex DC, 1804
Genus *Schizoneura* SCHIMPER & MOUGEOT 1844

The *Neocalamites-Schizoneura* issue

Throughout the Triassic further horsetail plants emerge, the classification of which is difficult and associated with much speculation. One of these involves the issue of the *Neocalamites-Schizoneura*. Due to several lucky related finds from Ilsfeld, in particular a basal stem with three cones attached (ILS 750) by Gerald Frieß, it has now been possible to establish without doubt that many of the horsetail elements found in the German Hauptsandstein (Middle Triassic) which could not be classified under *Equisetites* can be unified under a new combination *Schizoneura merianii* thus rendering many other names like *Neocalamites* obsolete.

Schizoneura merianii nov. comb. WACHTLER 2016

In the Keuper there were frequent findings of narrow to rounded horsetail cones with small covering shields which did not belong to *Equisetites arenaceus*, but which also could not be related to *Calamites* infructescences which surrounded the sporangia like claws.

Diagnosis

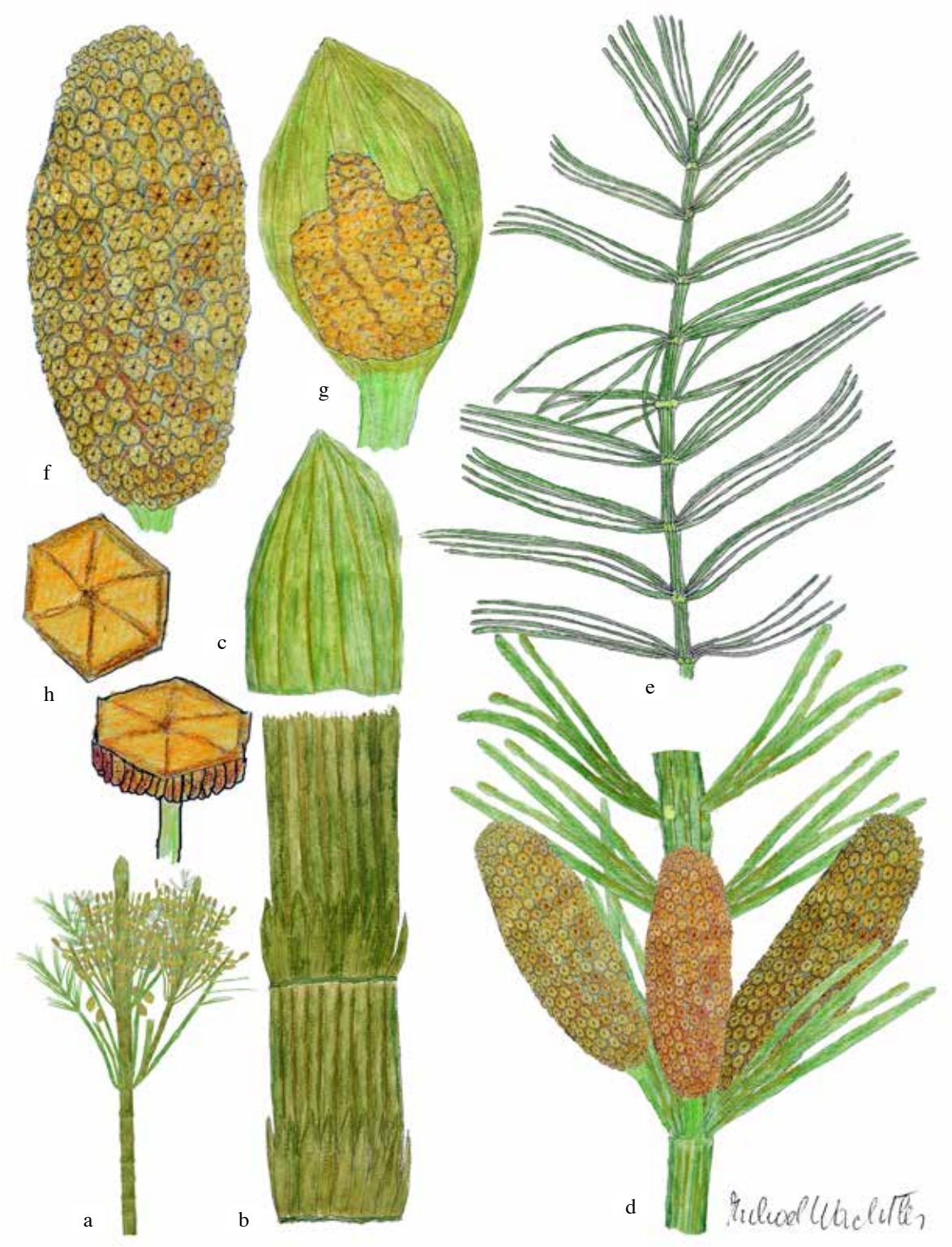
Horsetail with monopodial stem surrounded by wide leaf sheaths. Sterile narrow elongated leaves in groups of four branching from the lateral shoots twice per nodule. Cone-like sporangial clusters, sporangiophores small, hexagonal with spore sacs hanging on the underside of the covering shields.

Description of *Schizoneura merianii*

Whole plant: Stems up to 12 cm thick covered with wide smooth leaf sheaths of up to 1 cm thickness (ILS 104, 484). Stem discrete to the nodal attachment point and not fused together with the sheath. Tip of the main shoot not with telescopic sections like *Equisetites arenaceus* but instead covered with tapered sheathing leaves (ILS 360). Secondary stem with similarly broad-edged serrated pattern as the main axis (ILS 325, 222, 105),
Leaf structure: Below the sheaths two leaf rosettes branching off in groups of four. These up to 30 cm long, 0.5 cm wide (ILS 292, 279). In the juvenile stage closed, only opening in the growth phase to show their quadruple leaf groups (ILS 35).
Strobili (*Echinostachys*): Cone-like strobili, either elliptically rounded or elongated (ILS 750). In the juvenile stage surrounded by sheathing bracts which are shed as the plant matures (ILS 152). Sporangiophores hexagonal but smaller (0.3 cm) than those of *Equisetites arenaceus* and with a higher number of 0.1 cm sporangial sacs hanging down on the underside (ILS 609, 615, 543, 550).

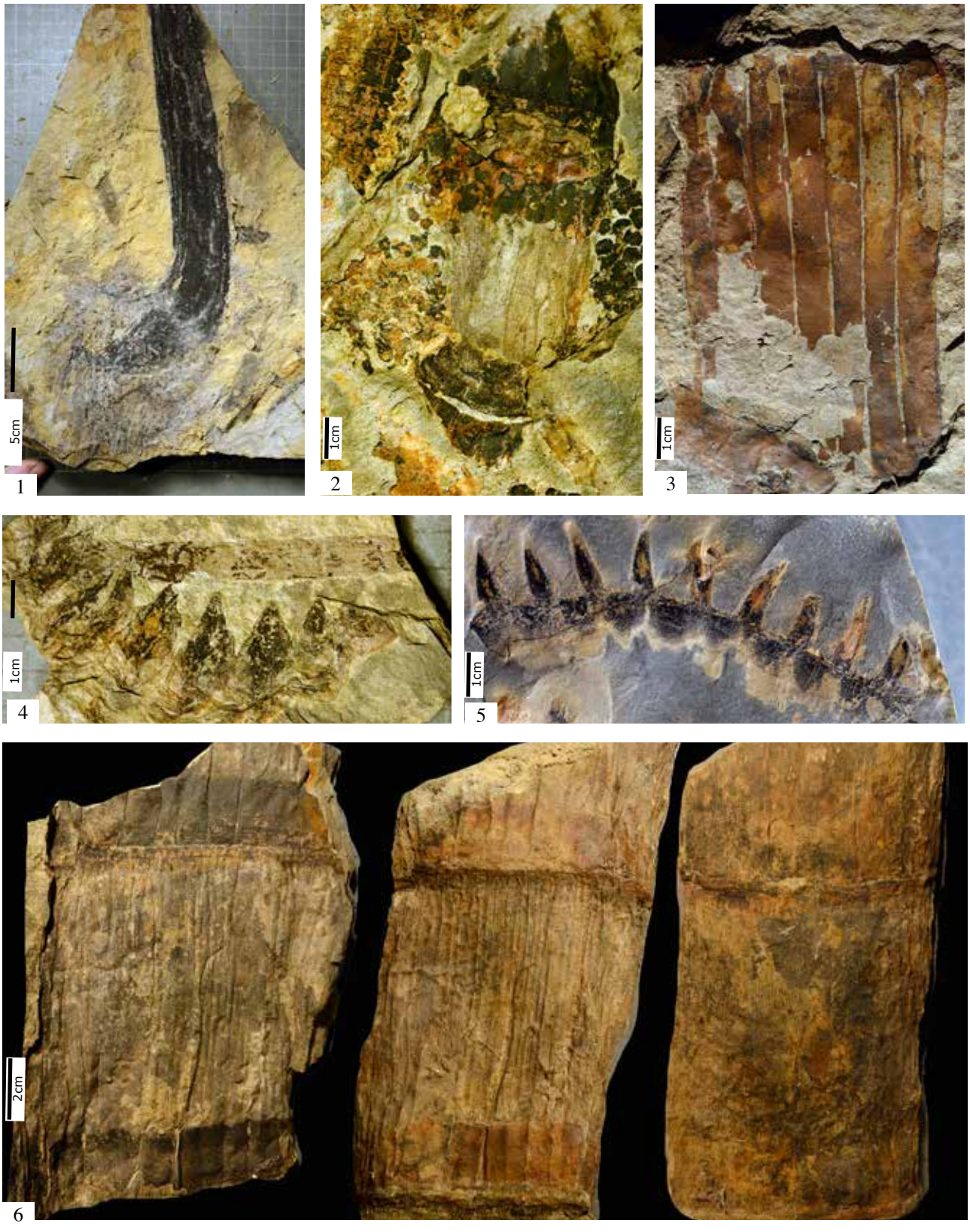
Remarks and ecology

Since the infructescences of *Schizoneura* from the Keuper shows no parallels with the genus *Neocalamites*, the distinctions from or similarities to the Early Triassic *Schizoneura paradoxa* (Buntsandstein) should be explored. The juvenile shoots of this latter are often shown as bound together, representing an early growth stage which in the course of development produces a four-leaf arrangement and can therefore be considered the same as *Schizoneura* from the Middle Triassic Hauptsandstein. The structure of the vegetative elements, particularly the monopodial main stem with the secondary branching, also shows no major differences. Even the different hexagonal table-like arrangement of sporangial clusters are equivalent in both *Schizoneura*-species. What is undeniably different however is the arrangement of the spore cases, which in *Schizoneura paradoxa* are organised in several circles around the sporangiophore stem (Grauvogel, 1978) whilst in *Schizoneura merianii* from the Hauptsandstein they hang from the underside of the sporangiophores covering shields in a similar arrangement to extant horsetails. However no convincing reason for this difference can be found even under the aspect of evolutionary considerations. For both *Schizoneura* species however classification as Equisetaceae can be considered sensible.



The Sphenophyta *Schizoneura merianii* (Middle Triassic) Reconstructions

a. Whole plant; b. Main shoot with leave-sheath (ILS 405 484); c. Apical shoot with cover-leaves (ILS 360, 47); d. Fertile shoot with strobili (ILS 750); e. Apical part of a branchlet with typical tuft-like leaves aggregated to four (ILS 35, 292); f. Terminal strobilus *Echinostachys oblonga* (ILS 124, 121); g. juvenile cone partially hidden by cover-leaves (*Echinostachys* - *Bernettia*-Typ) (ILS 152, 349), h. Sporangiophore upper side and laterally.

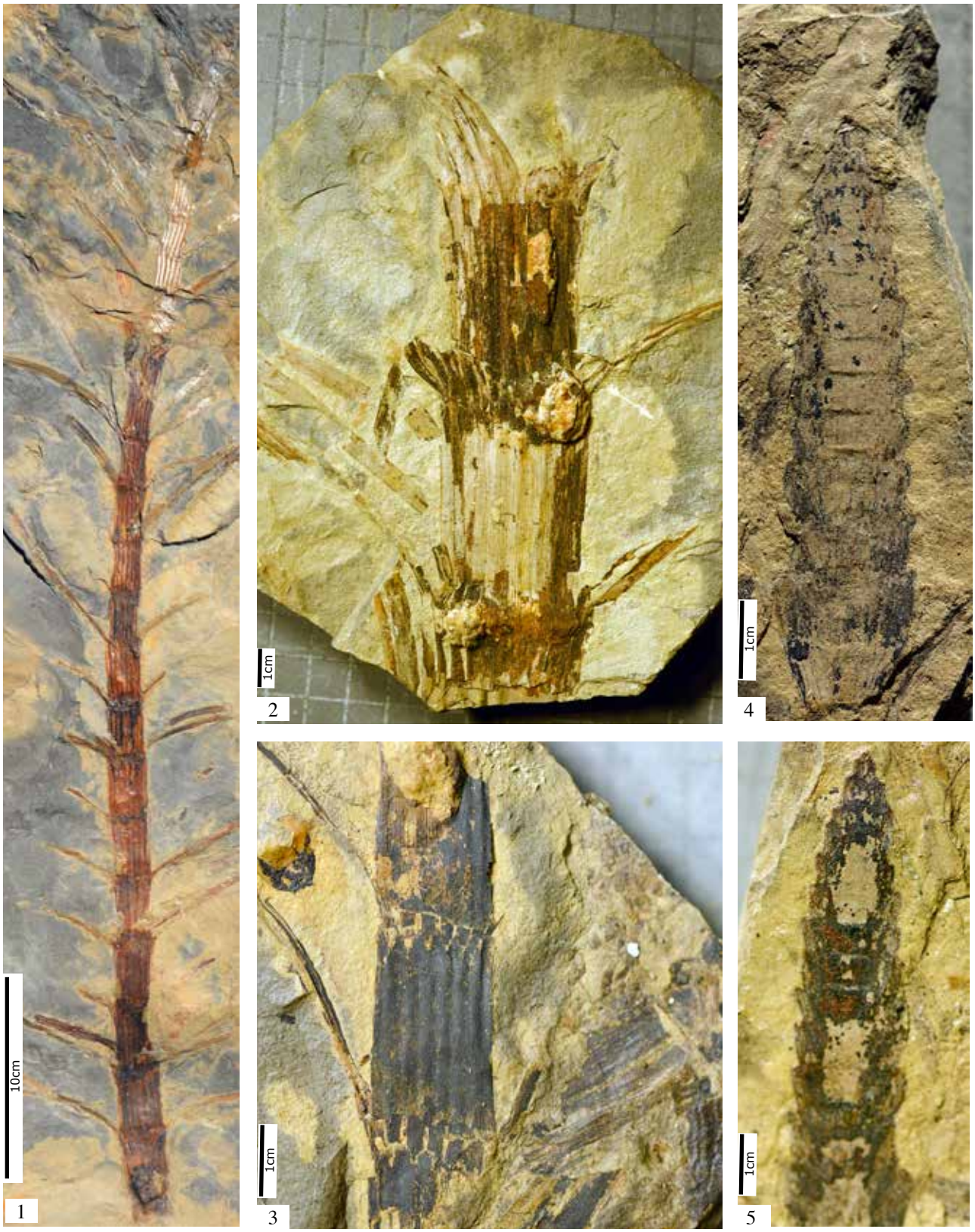


Schizoneura merianii (Ladinian-Middle European basin) Stems

1. Suggested root and basal stem (ILS 477); 2. Main stem (ILS 484) 3. Stem with leave-sheath (ILS 104); 4. Detail of the sheath (ILS 362, all Coll. Nißler); 5. Leave-sheath (ILS 807, Coll. Frieß); 6. The range of variation of the stems. All parts came from the same plant. Inner and exterior view. Some parts resemble *Equisetites* (ILS 682, Coll. Nißler)

Schizoneura merianii (Ladinian-Middle European basin) Stems

1. Basal part of a stem (ILS 872); 2. Apical part with cover leaves (ILS 873, both Coll. Pohl); 3. Apical cover leaves (ILS 360); 4. Main stem with internodes (ILS 405); 5. Lateral branchlets from the main stem (ILS 376); 6. Stem with diverging branchlets (ILS 494, all Coll. Nißler).



***Schizoneura merianii* (Ladinian-Middle European basin) Branches**

1. 60 cm long part of a stem with lateral branchlets (ILS 865, Coll. Pohl); 2. Impressions of the lateral diverging branchlets (ILS 375); 3. Main and lateral branchlets (ILS 222); 4-5. Apical parts of branchlets of the last order (ILS 123, 561, all Coll. Nißler)

***Schizoneura merianii* (Ladinian-Middle European basin) Strobili**

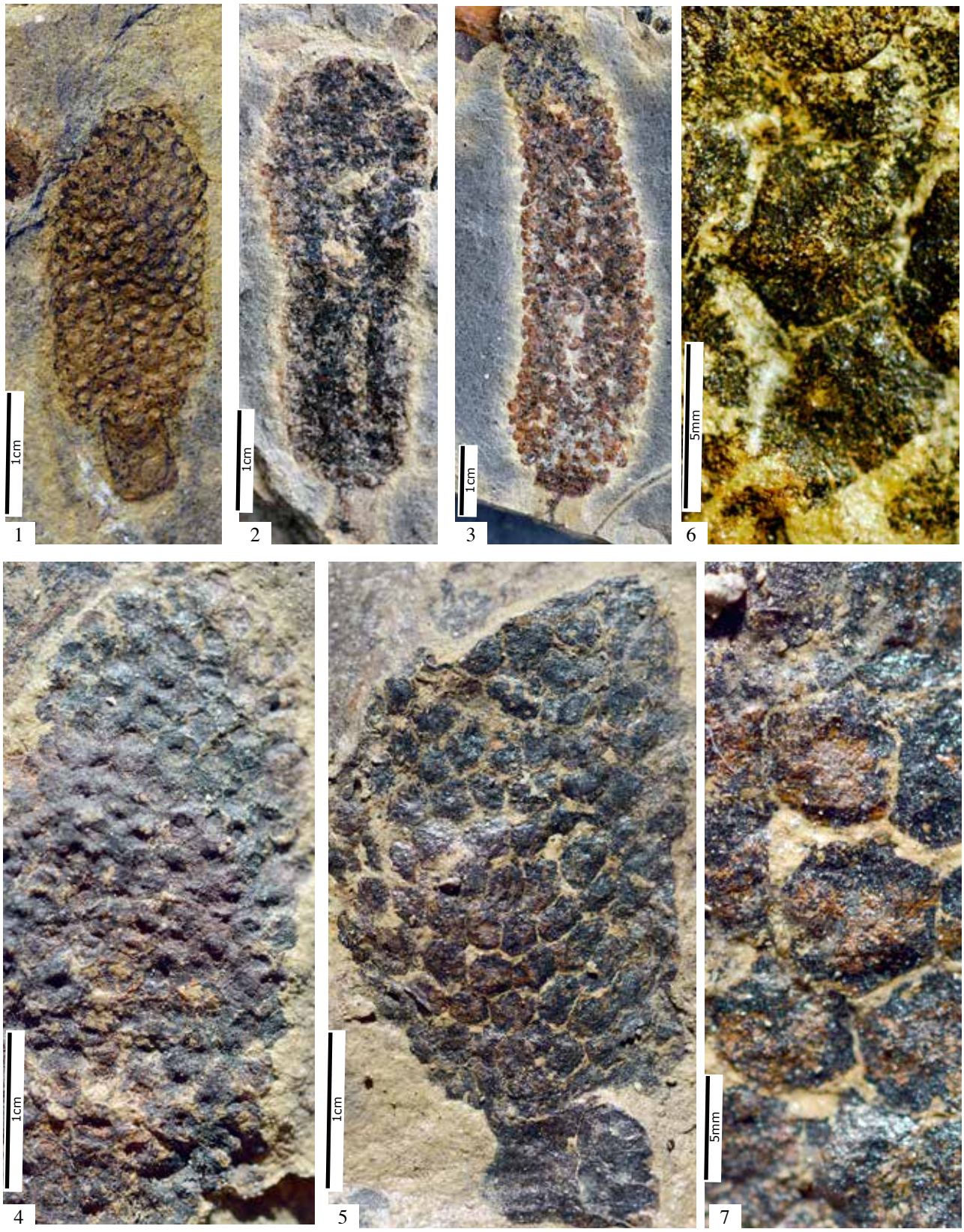
1. Several strobili connected grow directly from the branchlet (ILS 874, Coll. Pohl); 2-4. Three strobili connected on a shoot. This impressive discovery resolves a paleobotanical enigma (ILS 750, Coll. Frieß);

***Schizoneura merianii* (Ladinian-Middle European basin) Strobili**

1. Detail of the connected strobili (ILS 874); 2-3. Partially attached strobili (ILS 875); 4. Two connected strobili (ILS 864, all Coll. Pohl); 5-6. Variegated fertile organs from elongated till stocky bulbous deposited on the same slab (ILS 788, Coll. Frieß)

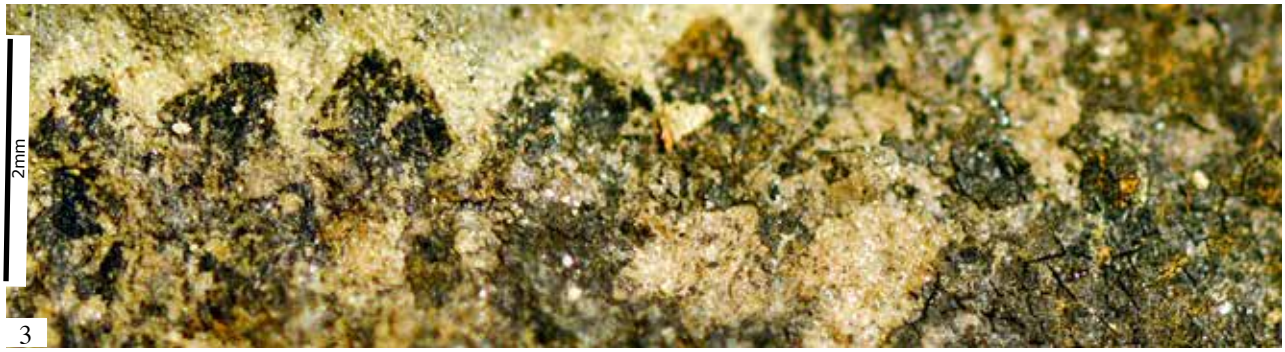
Schizoneura merianii (Ladinian-Middle European basin) Strobili

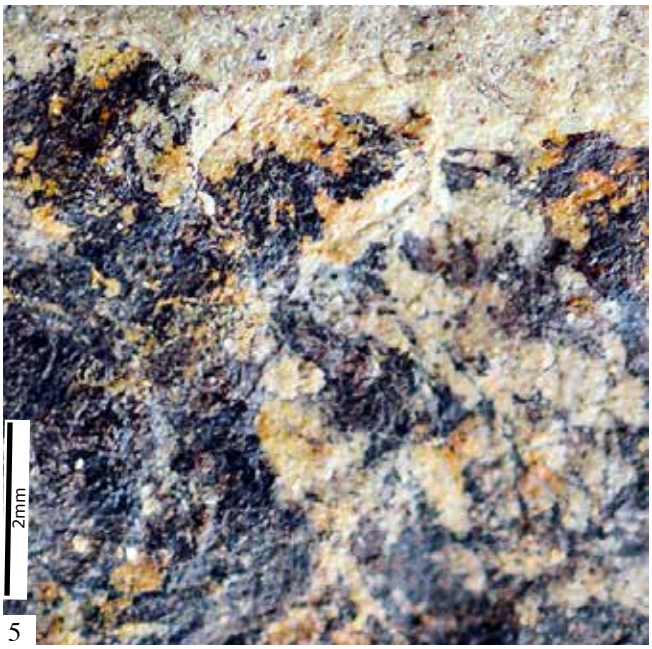
1. Two strobili, one hidden by cover-leaves, the second just free (ILS 152); 2. Strobilus from *Schizoneura* and on the lower part *Equisetites* (ILS 257); 3. Detail of a hanging cone (ILS 551), 4-6. Shoots with attached strobili (ILS 122, 428, 121, all Coll. Nißler)



***Schizoneura merianii* (Ladinian-Middle European basin) Strobili and sporangiophores**

1-3. The diversity of the strobili (ILS 828 Coll. Silberhorn, ILS 759, 810 Coll. Frieß); 4-5. Cones a (ILS 121, 274); 6-8. Detail of the hexagonal terminal shields, which hold the sporangia on the lower side (ILS 274, 543, all Coll. Nißler)





***Schizoneura merianii* (Ladinian-Middle European basin) Strobili and sporangiophores**

1-2. Lateral view of the sporangiophores with hanging pollen sacs, 0.4 mm long (ILS 609, 615); 3. Lateral view of the sporangiophores with hanging spore sacs (ILS 550); 4. Totally from pollen tubes covered sporangiophore-shields (ILS 604, all Coll. Nißler); 5. Cover shields with hanging pollen tubes (ILS 788, Coll. Frieß)