Calamites horsetails of the Alps in the Carboniferous

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In the Upper Carboniferous of the Eastern Alps, plants called *Calamites,* resembling horsetails with peculiar fertile organs, reportedly spread. However, many attendant questions remain unanswered; this can be attributed to the large number of different species names coined for one and the same plant, such as individual names for stems or leaf whorls, whereby the structure and appearance of the infructescences are mostly neglected. On the basis of the different fertile organs, one can assume that in the Upper Carboniferous of the Eastern Alps, at least six different subspecies occurred, some within the same layers: *Calamites multiramis*, the most common of all, *Calamites carnicus* sp. n. a species till now recovered only in the Carnic Alps, the small *Calamites microphyllus* nov. comb. and *Calamites sphenophylloides* nov. comb., with wedge-shaped foliage. All of these developed sporophylls coated each sporangium with a multitude of bracts. However, others such as *Calamites longifolius,* nov. comb. – characterised by long needle-like leaves and delicate sporangia – and *Calamites sturii* n. sp., to a greater extent, bore only one single bract covering one sporangium. The latter species remain so removed from the Calamitaceae, and even show relationships with the Lepidodendrales, that one could almost call them *Lepidocalamites.* Since they are all in good preservation conditions, they can be clearly distinguished from one another. Amazingly, their decline occurred at the Carboniferous-Permian boundary, which can only be explained by the drastic changes in climate and the general living conditions.

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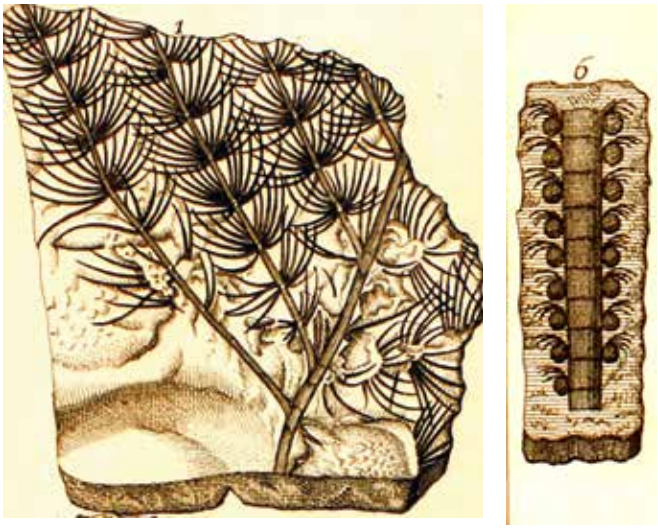
***Calamites* Flora from from the Upper Carboniferous of the Eastern Alps (Kronalm)**

Several different Calamitaceae populated the tropical landscapes at the same time. These include the following, from left to right: a. ***Calamites longifolius***, b. ***Calamites sphenophylloides,*** c. ***Calamites carnicus,*** d. ***Calamites microphyllus*** and e. ***Calamites multiramis.***

In the early days of paleobotanical research – even before the official binary nomenclature was introduced by Linnaeus in 1753 – petrified horsetails attracted attention. Thus, in 1709, the German Gottlieb Friedrich Mylius (1675–1726) depicted a "*completely unknown fruit"*; he recognised *Calamostachys tuberculate,* known as a *Calamites* sporangiophore. In the same year, *Calamostachys tuberculate* was adopted by the Swiss naturalist Johann Jakob Scheuchzer (1672–1733) in his "*Herbarium diluvianum*" together with the illustration of an *Annularia spicata* frond.

Scientific developments

In 1771, the German rhetorician, philologist and geologist Johann Ernst Immanuel Walch (1725–1778) dealt even more closely with coal-age horsetails (*Calamites)* from the mines of Silesia and Saxony. He elaborated that the name for the fossil, "*Calamit*", owed to its resemblance to its reed (Kalamos, from Greek: κάλαμος, pl. κάλαμοι Kalamoi; lat. calamus, pl. calami or Qalam [Arabic]). Notably, throughout antiquity, together with other plants with hollow stems, the sweet flag (*Acorus calamus)* was used as a writing instrument.
However, all the fossil plant names introduced at that time were subsequently considered scientifically obsolete, since the official paleobotanical nomenclature did not commence until December 31, 1820. In a publication by Adolphe Brongniart (1828a: *Calamites (suckowii)*, Histoire des vegetaux fossiles, vol. 1: p. 121), the year 1828 is considered as the first publication date of this highly dominant giant horsetail found in the Carboniferous, although a classification under the Equisetaceae should be treated with caution, since their sporophylls have completely different characteristics.



First drawing of an *Annularia spicata* frond and the sporangia of *Calamostachys.* From Scheuchzer's *"Herbarium diluvianum"* (1709).

The name *Calamites* always refers to parts of stems from the Paleozoic that resembles horsetails. However, since the isolated side branches and whorls that belong to it were often found – having also a decorative appearance – a wealth of other genus and species names were subsequently published, in reality only representing parts of the entire plant.
These names include the term *'Annularia'*, coined in 1822 by Caspar Sternberg (*Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt/Attempt at a Geognostic-Botanical Representation of the Flora of the Prehistoric World* 1 (2) p. 32), or *Asterophyllites* and *Sphenophyllum* introduced by Brongniart (*Prodrome d'une histoire des végétaux fossiles,* 159 [1828 b]), trying to correct some of Sternberg's misleading names (*Schlotheimia, Bornia, Brukmannia, Bechern).* Altogether, the various naming conventions over the decades have led to an almost hopeless situation that is unparalleled in paleobotany (Vogellehner, 1967) and can only be compared to the Babylonian confusion in the case of the giant clubmoss *Sigillaria.*
Nevertheless, towards the end of the 19th century, the scientific 'naming horror' was just beginning. In 1887, Dionýs Štúr recognised more than 170 different species of '*Calamaria*' from the Carboniferous of Schatzlar (today, Žacléř in Czech Northern Bohemia), while the Dutch botanist Wilhelmus Josephus Jongmans (1878–1957), in his Fossilium Catalogus (1913) (since 1914, containing a special volume on horsetails), listed hundreds of different species names of *Calamites, Annularia, Asterophyllites, Sphenophyllum* etc. over dozens of pages.
On the other hand, there were only a few described or illustrated delineations of infructescences. One of them was illustrated by Count Sternberg in 1825 under the name *Brukmannia*, which is no longer valid (*Versuch einer geognostisch-botanischen*

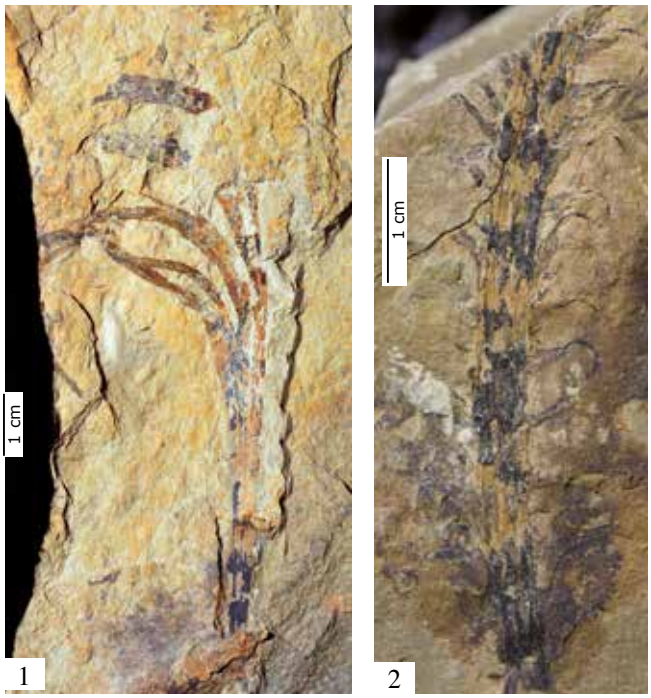
Darstellung der Flora der Vorwelt, I, pl. XXIX). This was followed by *Macrostachya* (Schimper, 1869), *Stachannularia* and *Palaeostachya* (Weiss, 1876) or *Calamostachys* (Weiss, 1884).
Overall, this disproportion between fertile and sterile parts represents an unsatisfactory situation, since it can be assumed that the number of different fructifications most closely corresponds to the number of the species present in a fossil deposit. While it is true that paleobotanical science should not be based on speculation, it is equally important to avoid diluting the overall context through confusing fragmentations when it is highly probable that all the individual parts of a complete plant are known. The appreciation of paleobotany suffers from these fragmentation even today, and this is one reason for the lack of interest in an important branch of research that could explain the development of life and the changes wrought by climate catastrophes.
Future researches must provide meaningful information about the number and appearances of plants by looking for infructescences, instead the leaf shapes that often vary within the same species, depending on whether they are spring shoots or summer leaves, or whether they have basal or apical whorls.

Origin of the Calamitaceae

The Calamitaceae were fully developed in the Lower Carboniferous, with species like *Archaeocalamites radiatus* (Amerom et al., 1984; Kabon & Schönlaub, 2019; Wachtler, 2022), as suggested by fossil findings from the Alps. Precursors that are barely recognisable must therefore be dated back at least to the Devonian. Interestingly enough, the two main so called horsetail lineages were already emerging at that time – the Calamitales and the Equisetales (Wachtler, 2022) – indicating that both lines went their separate ways for almost 400 million years subsequently. It seems that the Calamitaceae originated in the Middle Devonian (*Archaeocalamites antiquus)* within the homosporous lycopod family, while the Equisetaceae (*Archaeoequisetites lindlarensis)* were related to the ferns because of their sporangial parental affinities. A classification of the Calamitaceae as horsetails is questionable, although the name Clubmoss-horsetails may seem more justified.
Between the Devonian and the Lower Carboniferous, the Calamitaceae developed their typical, elongated infructescence, consisting of either one or (usually) a multitude of small-sized bracts originating mostly on the same level, which closely surrounded or clawed at one homosporous sporangia. In the early days, trunks with longitudinal grooves running continuously through the nodes were typical, with somewhat offset ribs (*Mesocalamites*) developing for the first time in the Lower Carboniferous, through the bifurcation of the vascular bundle. The Equisetaceae, which led to the only one modern genus *Equisetum*, were characterised by rounded strobili with elongated spore capsules hanging on the inside, from a hexagonal sporophyll leaf. Especially in the Late Carboniferous, the Calamitaceae spread over all the continents and became the dominant plant, together with the giant clubmoss.

Calamites plants worldwide

Often in their contemporaneous variations, *Calamites* were found in Europe (*Calamites*



Archaeocalamites antiquus. **Middle Devonian**

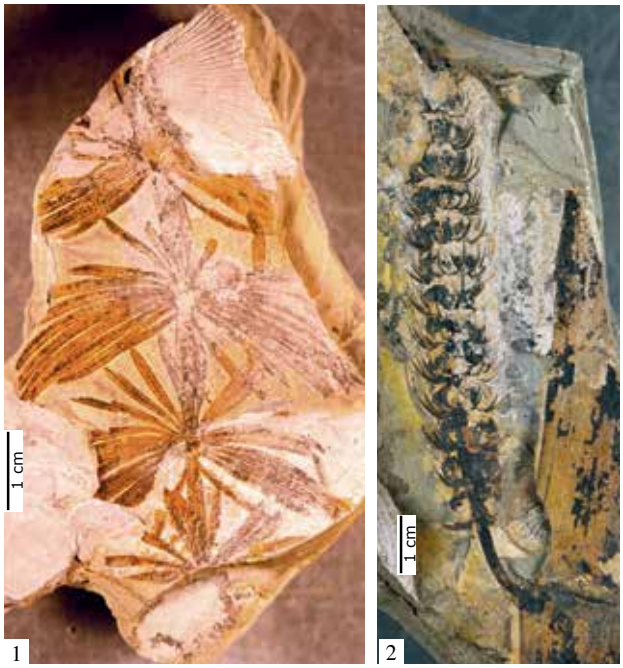
1. Apical part with partially forked side branches (LIND 14, Coll. Pohl, Lindlar); 6. Strobilo with partially dichotomous bracts (LIND 504, Lindlar, Coll. Dolomythos)

Carboniferous-Permian Calamitaceae from Europe

***Calamites wachtleri* (Kasimovium/Gzhelium)**

1. Trunk with side fronds (PER 29); 2. Immature strobilo (PER 129); 3. Mature sporangiophores with desiccated sporangia (PER 471); Coll. Perner; Niederhausen, Senckenberg Museum, Frankfurt

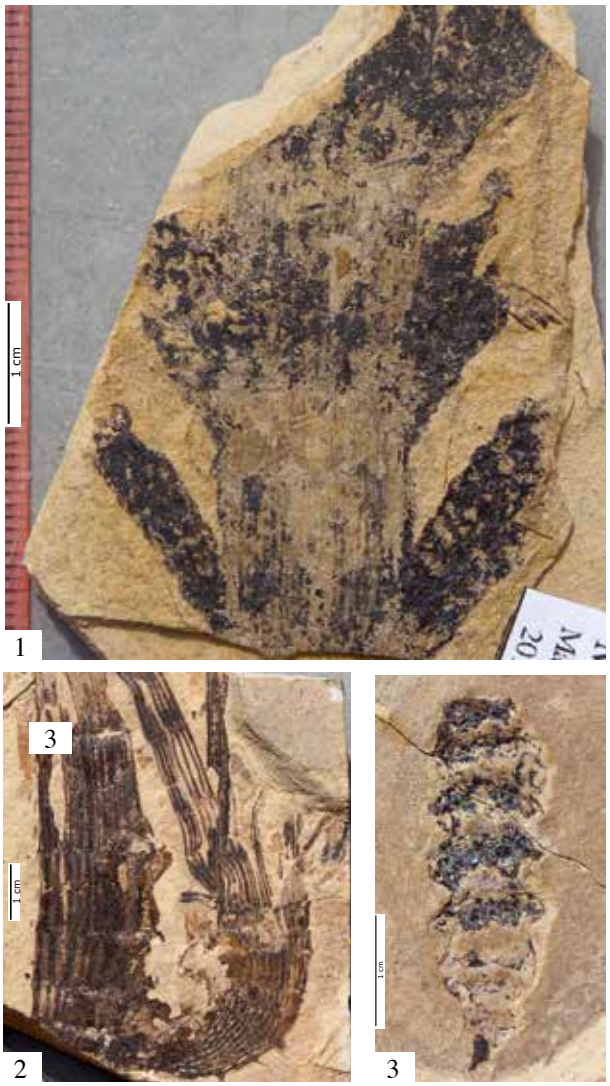
Carboniferous-Permian Calamitaceae from America



***Calamites kinneyana* (Kasimovium)**

1. Frond (P-14404); 2. Strobilo with stem (P-69245), Kinney Quarry (Central New Mexico), Coll. New Mexico Museum of Natural History and Science

Permian Calamitaceae from Angara (Urals)



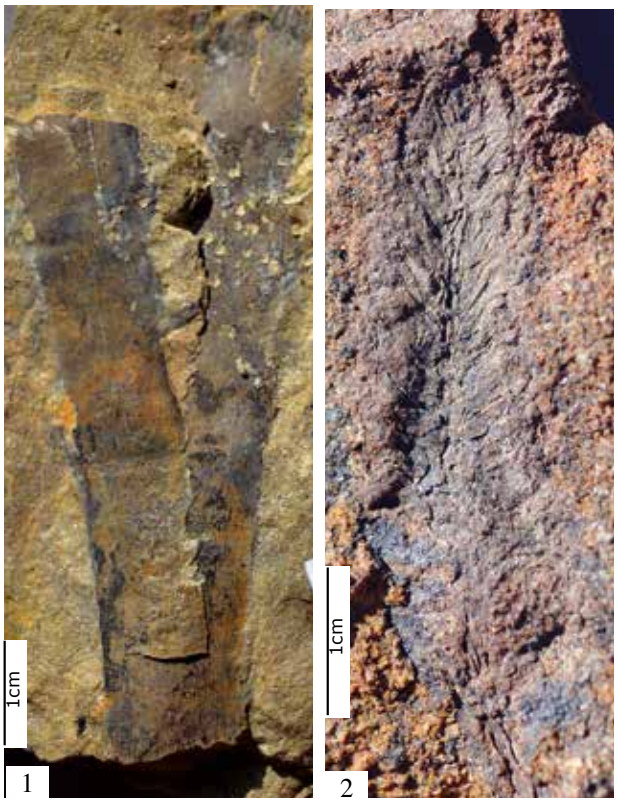
***Paracalamites decoratus* (Kungurium)**

1. Branchlet with strobili (MAT 698); 2. Stem with side branch (CHECK 85); 3. Strobilo (MAT 330), Matveevo, Ural, Coll. Wachtler, Dolomythos

***Paracalamites striatus* (Kungurium)**

1. Multiple side branches (MAT 700); 2. Main stem (CHECK 16); 3. Strobilo (CHECK 89), Urals, Coll. Wachtler, Dolomythos

Late Permian Calamitaceae from the Alps



***Neocalamites benckeae*. Upper Permian**

Last Calamitaceae: 1. Stem (PAS 421); 2. Strobilo (PAS 210), Wuchiapingian, Valli del Pasubio, Coll. Wachtler, Dolomythos

multiramis, Calamites longifolius, Calamites sphenophylloides, Calamites gigas etc.), in America (*Calamites kinneyana*, Wachtler 2018), and they were also widespread in the today's Ural region and Siberia (*Paracalamites decoratus, Paracalamites striatus)* (Perner & Wachtler, 2020), previously the Angara continent.

During the Early Permian, some of them reached shoot diameters of about 10–15 cm and grew up to 10 m in height. Their typical strobili made them easily distinguishable from those of the Equisetales and also from those of other plant families. It was therefore a real cosmopolitan, although there is uncertainty as to whether it developed simultaneously on several land masses, even distant ones, or spread through migration. Its decline occurred towards the end of the Permian, leading to its extinction during the Permian-Triassic catastrophe (Wachtler, 2019). The Upper Permian *Neocalamites benckeae* from the Italian Alps is considered to be the last representative of the Calamitaceae (Wachtler, 2016)

Equisetum horsetails remained overshadowed by the more conspicuous *Calamites* plants throughout the Carboniferous-Permian (Moscovian-Kasimovian) boundary, represented in parallel with the Calamitaceae, with *Equisetites hemingwayi,* or with other Early Permian species such as *Equisetites geraschi* (Perner & Wachtler, 2015), *Equisetites vaujolyi* or the Late Permian *Equisetites siberi* (Wachtler, 2015). The Equisetaceae were even found on the Russian Angara continent, e.g. *Equisetina magnivaginata.*

The heyday of the Equisetales occurred in the Mesozoic, with the Early Triassic *Equisetites mougeotii,* followed by the widespread *Equisetites arenaceus* in the Middle Triassic with the presently-impressive trunk diameter of 20 cm, in some cases. Cone-like sporophyll stands were developed on the main axis or on secondary side branches in aggregations of many strobili. However, in contrast to the those of the Calamitales, the strobili of the Equisetales were encountered very rarely in the sediments. They only occurred frequently in Ilsfeld, a Middle Triassic German site, suggesting that, similar to their present development, they generate their sporangiophores only for a short period of time during spring and then decayed, while the Calamitaceae bore spore cones throughout the whole year.

The Evolution of the Calamitaceae

In 2000, Michael Wachtler began research particularly in the Kronalm areas in the Carnic Alps, as well as in Stangnock and Königstuhl in the Nockberge mountains. Other find areas such as the Rattendorfer Alm, or the Lower Carboniferous fossil sites in the area of Nötsch, the Tröpolacher Alm or the Marinelli hut, were also examined. After years of intensive studies, it was assumed that *Calamites* horsetails were already fully developed in the Lower Carboniferous, about 345 million years ago, and they split up into several different (probably under 10) subspecies in the Upper Carboniferous of the Alps.

Crucially, the innumerable Calamitaceae species names that have been published – which usually only refer to parts of the plants and which provide hardly any noteworthy knowledge about the evolution of

plants – become obsolete. Their main distinguishing feature – the differently shaped infructescence – can be clearly and interestingly delimited in *Calamites.* On the one hand, they show that in some strata in the Upper Carboniferous of the Eastern Alps, there were almost pure horsetail monocultures, but in other lenses within a very small area, about four to five different species competed with each other.

After rigorous research, it was essential to reduce the many Calamitaceae names introduced in the past, in order to create new reconstructions of the entire plant and to find a suitable and meaningful nomenclature. The future should reveal whether this endeavour has been successful. Choosing between the proposal to transfer the name of the main stem of *Calamites* to the entire plant and, thus, pushing into the background or ignoring the terms for the side branches or leaf parts (such as *Annularia, Asterophyllites, Sphenophyllum*) or those for the infructescences (such as *Macrostachya, Palaeostachya* or *Calamostachys)*, is a matter of deliberation for future works.

Alongside the naming conventions, which do not always have much importance attributed to them, the role of these florae in the evolution of the plant world has been brought in the foreground, along with the evidence of the general climate in the Carboniferous and the changes caused by catastrophes that took place. Global apocalypses and the associated temperature fluctuations or completely changed biospheres led to the decline of such florae during the transition from the Carboniferous to the Permian, after a widespread domination of the Calamitaceae in the Carboniferous, which was accompanied by the spectacular emergence (as if out of nowhere) of a completely new plant family – the gymnosperms, consisting of conifers, cycads and ginkgos.

Exploring Alpine Calamitaceae

The Austrian paleobotanist Franz Unger was the first to deal with the horsetails of the Eastern Alps in 1840 and mentioned certain species from the Stangalpe in the Nockalm (*Calamites dubius, Calamites approximatus, Calamites cruciatus, Calamites suckowii, Calamites cistii)* that were already known in other areas of Europe. In addition, he recognised other subdivisions among the Calamitaceae *(Annularia fertilis, Sphenophyllum fimbriatum, Asterophyllites equisetiformis).* In 1870, the year in which Unger died, another publication on the plant fossils of Carinthia appeared, wherein Unger added *Calamites suckowii, Annularia sphenophylloides* and *Annularia longifolia,* all without giving any indication of the appearance of infructescence.

Next came Adolf Fritz and Miente Boersma in 1984: they described a motley mix of stem parts and leaves from the E. Ebersmann collection from Königstuhl, with *Annularia stellata, Calamites cistii, Calamites suckowii, Asterophyllites equisetiformis* and *Sphenophyllum oblongifolium.* In the old Höfer collection from 1869, Fritz and Boersma found *Calamites cistii, Annularia sphenophylloides, Annularia stellata* and *Sphenophyllum oblongifolium* (Fritz & Boersma, 1988). Later, Fritz et al. (1990), in addition to various stem parts (*Calamites cistii, Calamites suckowii, Calamites schuetzeiformis, Calamites cruciatus)* and leaf whorls (*Annularia radiata, Annularia sphenophylloilles, Annularia spicata, Annularia stellata, Asterophyllites equisetiformis),* mentioned for the first time the various inflorescences (*Calamostachys tuberculata, Macrostachya infundibuliformis, Palaeostachya).*

Overall, these were unsatisfactory explanations, but at least they served as significant steps toward decoding the horsetail diversity in the Eastern Alps during the Carboniferous. Kabon and Igsleder (2019) added another *Calamites* fructification (*Calamostachys germanica)* and explained certain leaf whorls (regarding *Sphenophyllum emarginatum* and *Sphenophyllum cuneifolium)*.

Evidently, many attempts were made over decades to maintain the three-part classification between the Calamitaceae stem parts (*Calamites)*, leaf whorls (*Annularia, Sphenophyllum, Asterophyllites)* and infructescences (*Calamostachys, Macrostachya, Palaeostachya).* Altogether, they confused rather than clarifying the true appearance of the horsetail or contributing to detailed information about the crop rotation. It is true that the whorls of the horsetail leaves, especially those of *Annularia stellata* (also known as *Annularia spinulosa*) from the Kronalm, are among the most beautiful plant fossils in the world,

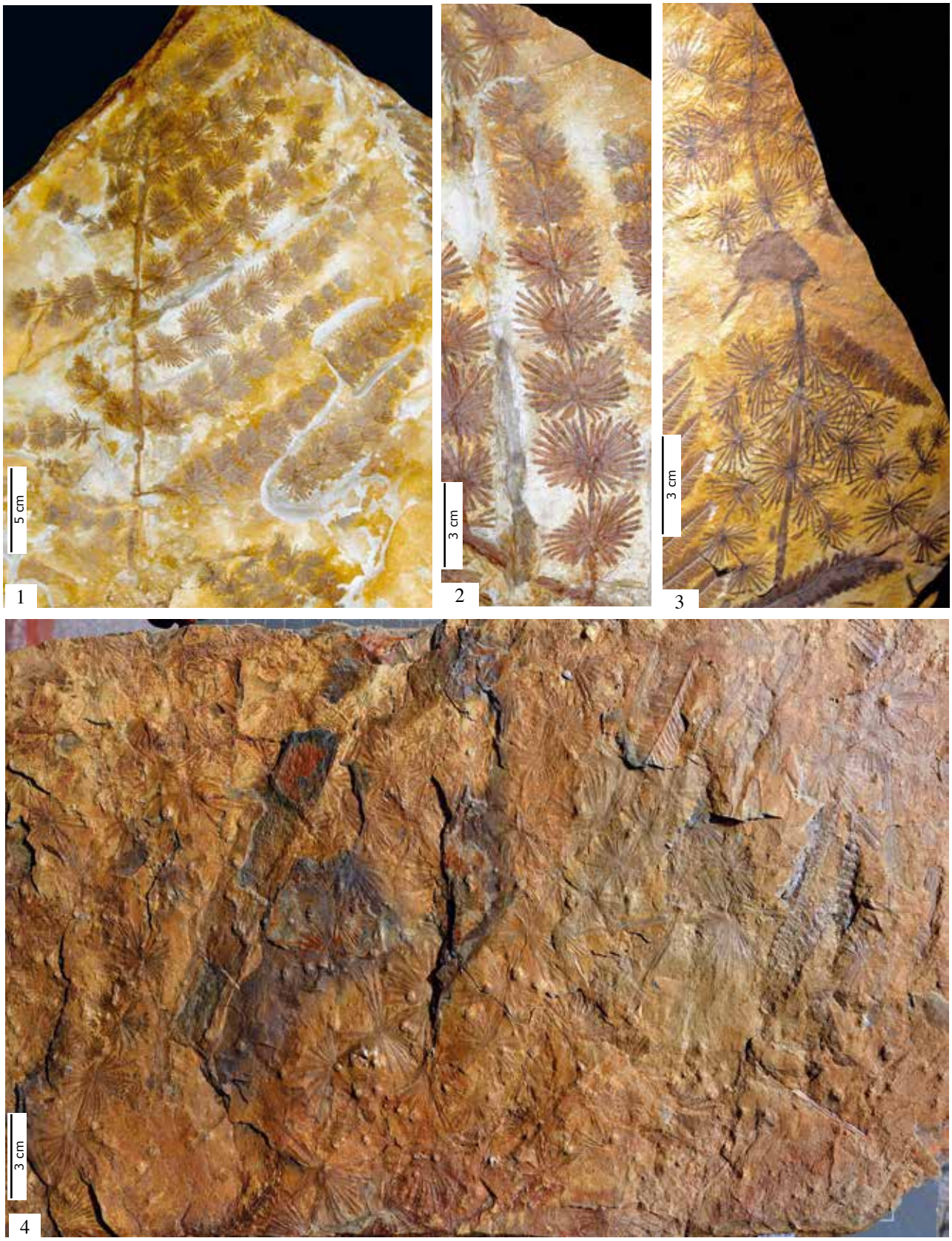
***Calamites multiramis*. Main stems. Upper Carboniferous. Kronalm, Carinthia**

1-2. 10 cm thick trunk with scars from broken fronds (KRON 428); Krone, Carnic Alps, Kasimovian, Coll. Wachtler, Dolomythos Museum

but these represent only side branches of a massive horsetail tree (*Calamites multiramis*) and their infructescence *(Calamostachys tuberculata*).

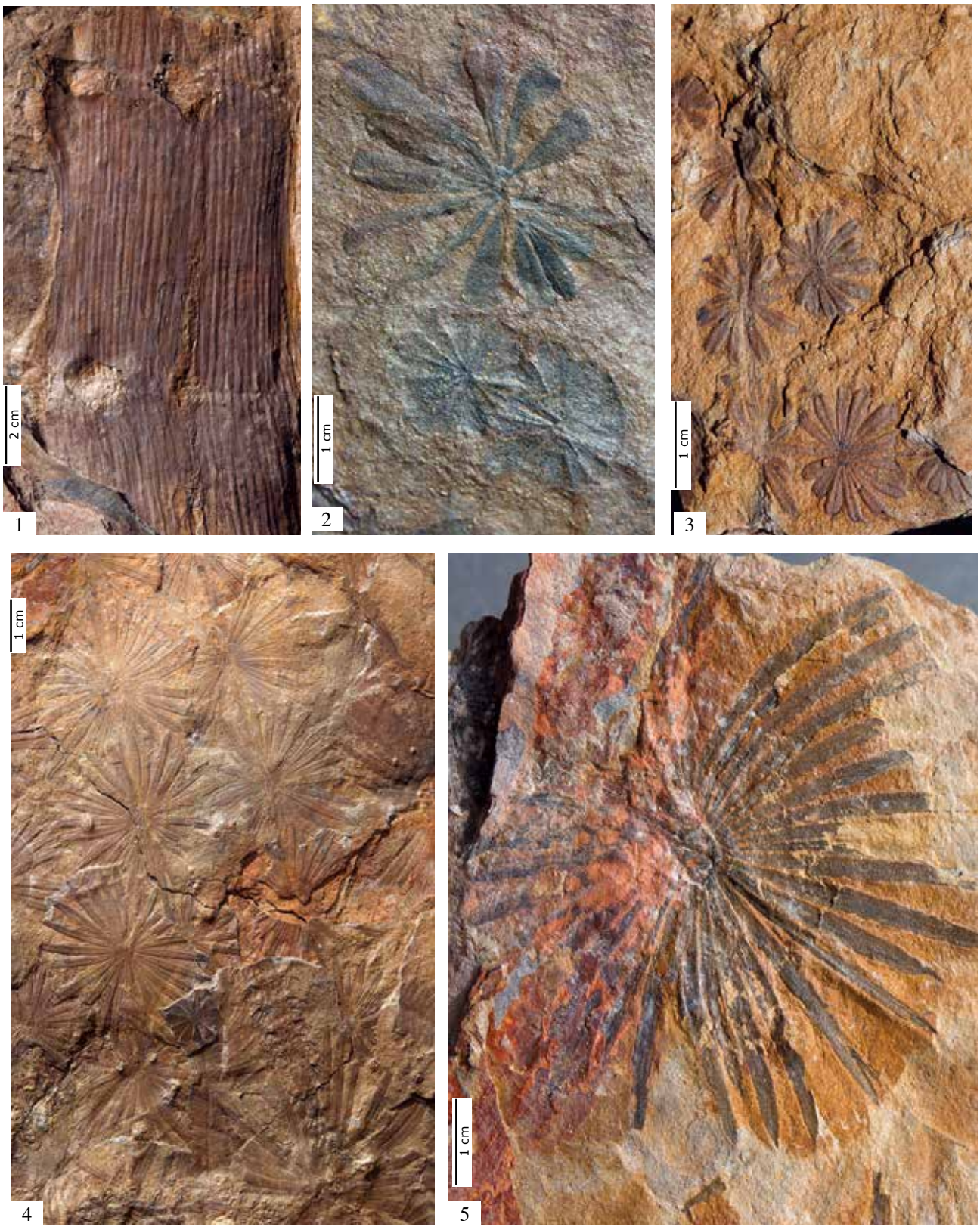
In this publication, therefore, the stem (*Calamites)* is always taken as a synonym for the whole horsetail. Furthermore, an attempt is made to combine the different horsetail parts in order to obtain a complete picture of the plant. Such a meaningful combination is made easier by the fact that some strata on the Kronalm, on the Stangnock or on the Königstuhl are rich in one single species of horsetail, added to the fact that connected parts, such as stems with whorls of leaves or with infructescences, have been found. It is also interesting that the historical site on the Kronalm, at 1730 m above sea level, contained a lens (B) with at least four different *Calamites* species within a few square meters of bedding (*Calamites multiramis, Calamites sphenophylloides, Calamites longifolius*, and the small creeping *Calamites microphyllus)*, while those below (A) featured mainly *Calamites multiramis* with magnificent associated *Annularia stellata* whorls and *Calamostachys tuberculata* infructescences. Moreover, the top layer (F) on the Kronalm produced a modified *Calamites multiramis* species within many thin layers, which was given a new name (*Calamites carnicus)* due to its difference to other Calamitaceae.

The same phenomenon was observed in the Königstuhl in the Nockalm area, which is not so rich in horsetail but contains numerous small *Calamites microphyllus.* However, a very strange species, *Calamites sturii,* was also recovered, especially on the Königstuhl, whose classification engendered difficulties: often, its cones reached up to 10 cm, its sporophylls containing one homosporous sporangium enveloped by a single bract. In this regard, it resembled *Lepidodendron* sporophylls. However, all the Lepidodendrales of the Eastern Alps were character-



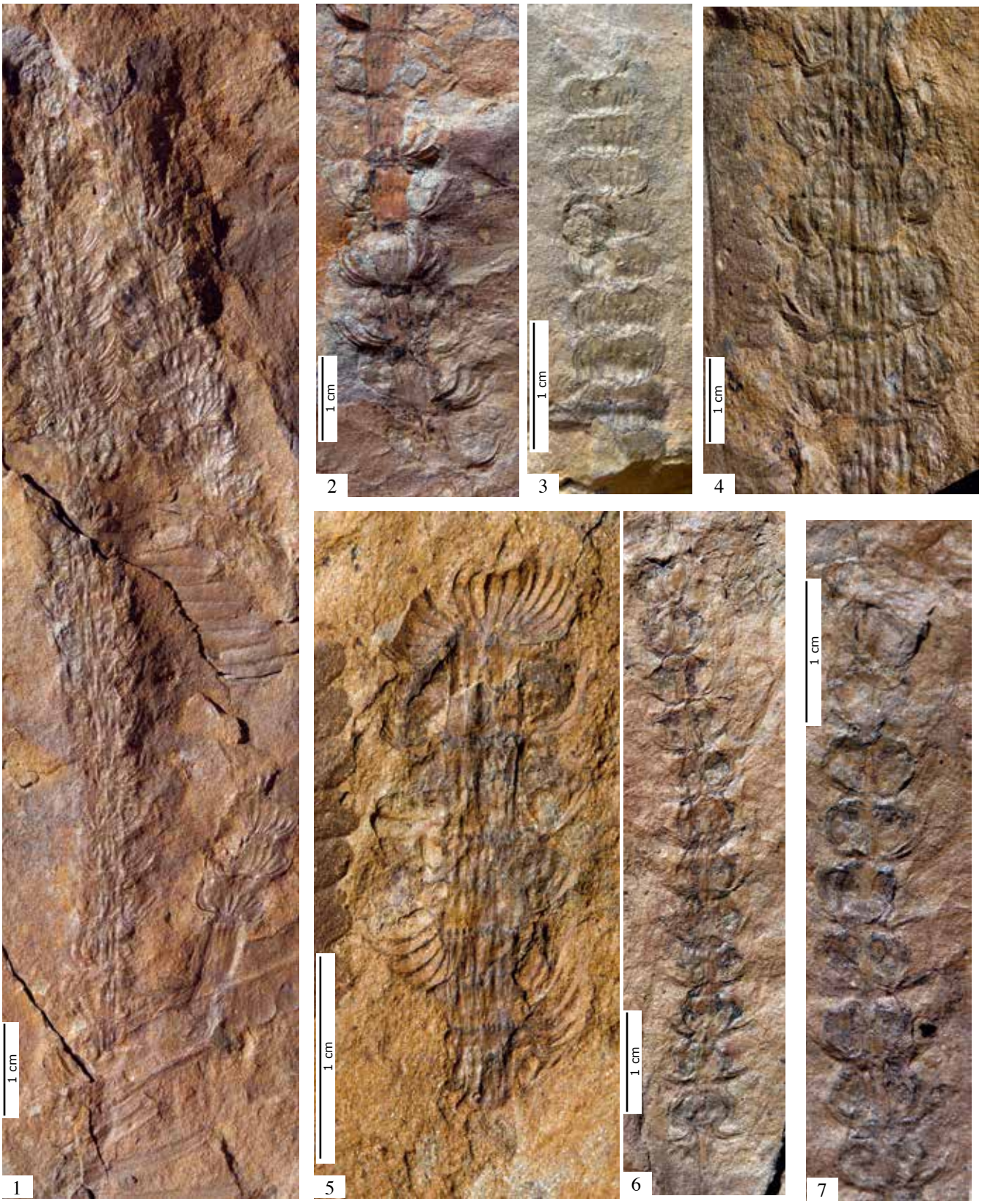
***Calamites multiramis* stems. *Annularia stellata* whorls. Kronalm (Upper Carboniferous)**

1–2. Excellently preserved frond and details of individual *Annularia* whorls (Museo di Scienze Naturali, Udine); 3. Apical part of a frond (Nockalm, Coll. Kandutsch); 4. Parts of an *Annularia* frond in connection with a *Calamites* stem and several strobili (KRON 35); Krone, Carinthia, Coll. Wachtler, Dolomythos Museum.



***Calamites multiramis* stems. *Annularia stellata* fronds. Upper Carboniferous. Kronalm,**

1. Stem with internodes and scars from a shed frond (KRON 44); 2. Immature whorls (sometimes described as *Annularia radiata)* (KRON 04); 3. Various juvenile whorls (KRON 47); 4. Mature whorls associated with a strobilo (KRON 23); 5. Mature whorls with more than 30 side leaves (KRON 21); Krone, Carnic Alps, Coll. Wachtler, Dolomythos Museum.



***Calamites multiramis. Calamostachys tuberculata* Strobili. Kronalpe (Upper Carboniferous)**

1. Two strobili, with details of their characteristic connecting stalk (KRON 41); 2. Detail of the bracts (KRON 36) coating the sporangia; 3. Closed bracts with an opened sporangium (KRON 24); 4. Sporangiophore with sporangia and encasing bract leaflets (KRON 28); 5. Open bracts (KRON 47); 6. Cones with exposed sporangia (KRON 350); 7. Detail of a sporophyll cone with sporangia (KRON 334, Coll Perner); Kronalm, Coll. Wachtler, Dolomythos Museum.

ised by two connected sporangia at each sporophyll stand; perhaps they could be classified as *Lepidocalamites.*
Moreover, the Calamitaceae can be divided into two different subgroups: those with many bracts, which arise from a plane and claw intensely at the sporangia (*Calamites multiramis, Calamites carnicus, Calamites sphenophylloides,* as well as the small, creeping *Calamites microphyllus)* – which can be classified under the subsection Multibracteata – as well as the Monobracteata (*Calamites longifolius, Calamites sturii),* characterised by a single bract enveloping the sporangia. In fact, we observe a similar starting position with today's pines, especially with the two subsections Pinus (Diploxylon or hard-cone pines) and Pinus Strobus (Haploxylon or soft-cone pines).
In the Late Carboniferous, the Carnic Alps or the neighbouring Nockberge lay about ten degrees south of the equator, i.e. in a tropical region. By this time, expansive swampy landscapes, never before seen in the history of the world, had spread far into the northern hemisphere, while the southern globe, especially the Gondwana, was covered by mighty ice sheets. Still, about 90% of the world's coal reserves were created at that time, due to the immense and rapid growth of club moss trees (*Lepidodendron* and *Sigillaria)* and giant horsetails (*Calamites).*
However, the climate changed massively from the Upper Carboniferous onward. The giant trees disappeared within a relatively short period of time, paving the way (on the Carboniferous-Permian border) for the suddenly appearing gymnosperms. Evidence of this argument can be found, above all, on the nearby Rattendorfer Alm, which is still dominated by ferns and horsetails in its lower areas, while conifers appear massively and suddenly on its border ridge.
All Calamites species were mostly accompanied by a dominant fern – *Osmundites polymorphus,* which was a forerunner of today's Osmundaceae (royal ferns) – while others like the tree ferns *Cyatheites alpinus, Cyatheites unitus, Dicksonites pennaeformis, Marattiopsis stopesae* and *Danaeites perner*i (probably forerunners of the Marattia ferns) remained in the background. Plus, there occurred two enigmatic ferns (*Callipteridium ameromii,* from the forerunner group of Peltaspermales) as well as seed ferns like *Cyclopteris alpina* and *Cyclopteris boersmai.*
In some places, consistent layers of lycopod trees were deposited, mainly with *Sigillaria paralella* and to a lesser extent with *Lepidodendron,* whereby their sudden emergence was mostly terminated by thick burn layers, indicating the recurrence of catastrophic forest fires.
It is also interesting that in the Eastern Alps, the development of horsetails from the Lower Carboniferous to the end of the Triassic could be followed over a small area. Possibly, the *Calamites* evolved only slightly before they became extinct in the Alps at the end of the Permian. This would underline that both the *Calamites* family and the family leading to today's *Equisetum* horsetails went their own ways since their origin in the Middle Devonian; there were no more splits between themselves from after this period.

Calamites-species of the Late Carboniferous in the Eastern Alps

Subsection: *Calamites multibracteata*

Calamites multiramis

Synonyms: Side branches: A*nnularia stellata* Synonyms: *Annularia spinulosa, Annularia spicata;* Juvenile fronds: *Annularia radiata* or *Annularia sphenophylloides*); Fertile parts: *Calamostachys tuberculata*

Stems

1884 *Calamites multiramis* Weiss, Beiträge zur fossilen Flora. Steinkohle-Calamarien II, Abh. z. geol. Specialkarte v. Preussen, V, 2, p. 114, t. 10, f. 2; t. 12

Branchlets and whorls

1804 sine nomine Schlotheim: Flora d. Vorwelt, p. 32, t. 1, f. 4.

1820 *Casuarinites stellatus* Schlotheim: Petrefactenk., p.397, nom. inval., Art. 13.1 (f) o. Abb. [nom. illeg.)

1821 *Annularia spinulosa* Sternberg: 32, Taf. 19, Fig. 4 [nov. gen., nov. sp.)

1825 *Bornia stellata* Sternberg: tent. 28, o. Abb. [nov. comb.]

1825 *Annularia spinulosa* Sternberg: tent. 31, o. Abb.

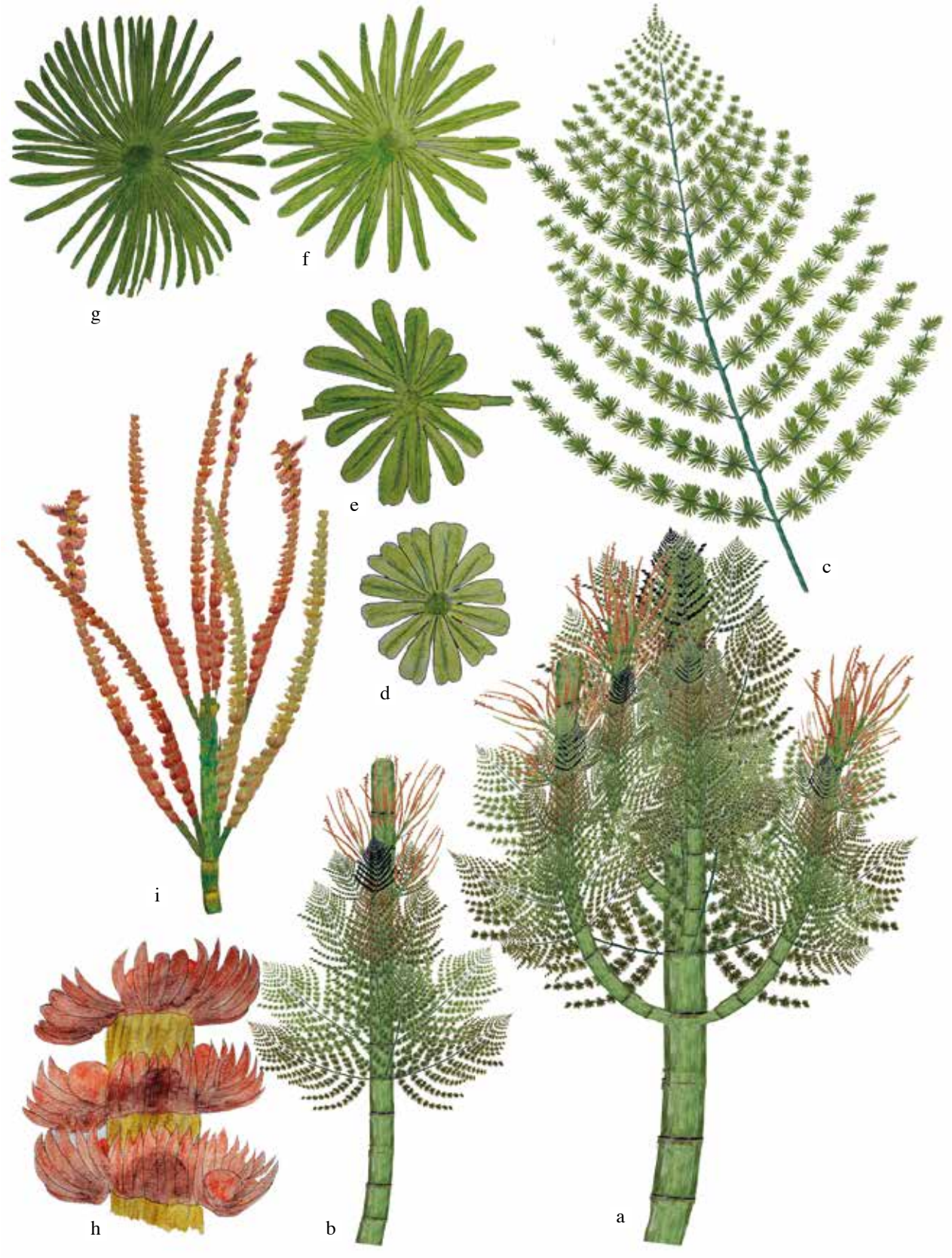
1832 *Casuarinites stellatus* Schlotheim: 5, Taf. 1, Fig. 4

1855 *Annularia longifolia* Brongniart - H . B.GEINITZ: 10, Taf. 19, Fig. 4 ,

Fertile parts:

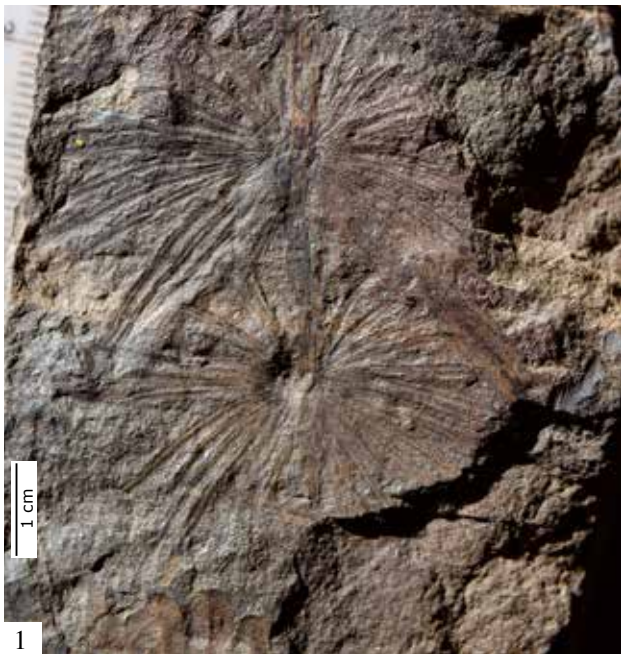
1825 *Brukmannia tuberculata* Sternberg: Vol. I, 4, tent. p. 29, pl. 45 (lectotype), fig. 2 r. (E 42 r.), l. (E 42 l.)

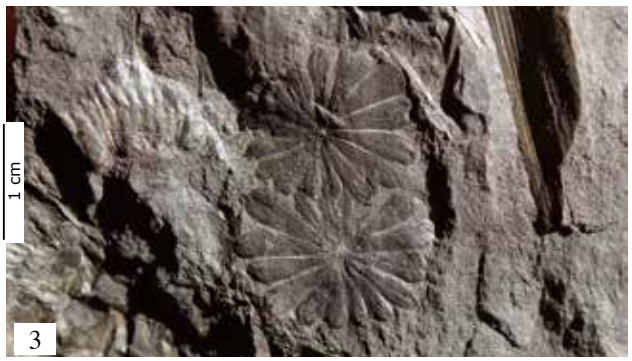
1876 *Stachannularia tuberculata* (Sternberg), Weiss, p. 17, pl. 1, fig 2–4, pl. 2, fig 1–3, 5, pl. 3, fig 3–10, 12



***Calamites multiramis*. *Annularia stellata* whorl. *Calamostachys tuberculata* strobili**

a. Fertile plant with strong side branches; b. Juvenile plant; c. *Annularia stellata* fronds; d. Juvenile whorls (KRON 47); e. Immature whorls; f. Adult whorls (KRON 23); g. Adult whorls with lateral leaflets (KRON 21); h. Part of a sporangiophore with bracts surrounding the sporangia (KRON 47); i. Mature sporophyll cones (KRON 26).





***Calamites multiramis*. Koenigstuhl (Nockalm)**

1. Two *Annularia stellata* whorls (KOEN 33); 2. Stem parts (KOEN 184); 3. Juvenile whorls (KOEN 31); Königstuhl, Carinthia, Upper Carboniferous Coll. Wachtler, Dolomythos Museum.

1884 *Calamostachys tuberculata* (Sternberg) Weiss p. 178

1911 *Calamostachys tuberculata* Jongmans S.293 Abb. 243, 244, 245

1976 *Calamostachys tuberculata* (Sternberg) Barthel, p. 79, pl. 25, figs 3–14

Description

Whole plant: Up to 15 cm thick hollow trunks, probably reaching a height of 7–10 meters. The smooth-to-tightly-ribbed main axes were interrupted at the nodal sheaths by nodes, from which lateral branches arose. These were classified as *Annularia stellata* or *Annularia spicata* and consisted of frond-like whorls developing lanceolate to spatulate leaflets. In a juvenile stage, these leaflets were rounded at the tip and marked by a central vein; in the adult stage, they ended in a pointed shape.

Fructifications: Known as *Calamostachys tuberculata.* Cone-like, slender structures 10–15 cm long but only 1 cm wide were connected to the main branch by a stalk that was about 1 cm long. The sporangiophores consisted of geometrically arranged whorls, with small, pointed bracts clawing around the round sporangia. At maturity, these micro-leaflets opened or expanded while the sporangial walls desiccated to release the spores.

Remarks

Among the horsetails occurring in the Upper Carboniferous, *Calamites multiramis* is the most widespread and best-known, so that the splitting up into side branches (*Annularia stellata, Annularia spinulosa, Annularia spicata)* and the separate names for its infructescences (*Calamostachys tuberculata)* cause more confusion than contribution with regard to expanding the extant knowledge. Importantly, in the Upper Carboniferous, their distribution area covered almost the entire Northern European hemisphere.

In 1709, the Saxon jurist Gottlieb Friedrich Mylius and the Swiss naturalist Johann Jakob Scheuchzer simultaneously published illustrations and descriptions of infructescence, leaf whorls and main stems that could clearly be attributed to *Calamites multiramis.* The philologist Johann Ernst Immanuel Walch (1725–1778), who lived in Thuringia, scientifically dealt with the species in more detail and reproduced a whorl of good quality. In 1820, Ernst von Schlotheim de-

scribed a *Casuarinites stellatus* from the Upper Carboniferous of Thuringia (Cammerberg), focusing on its star-shaped leaf whorls (although the first described specimen was destroyed in the turmoil of World War II). A year later, in 1821, Caspar von Sternberg assigned the name *Annularia spinulosa* to similar leaf whorls from the Döhlen basin in Saxony. Since according to the International Code of Botanical Nomenclature, all names given before 1820 were invalidated (Art.13.f, which was felt by many to be unfair), the official name of this species became *Annularia spinulosa*, (Barthel, 2000), unless one planned to defend the common practice in the paleobotanical literature of continuing to use firmly established names; especially as Sternberg himself later legitimised the name *Bornia stellata* for such leaf whorls. However, since the name *Calamites multiramis* is currently used to refer to the entire plant anyway (in the most absurd case, it would otherwise have to be called *Calamites spinulosus)*, this nomenclature dispute is not discussed any further.
In 1825, Count Sternberg described a fructification with *Brukmannia tuberculata* from the Upper Carboniferous/Lower Permian (Gzhelian/Asselian) in East German Manebach, which was later recognised as belonging to *Calamites multiramis.* The slender strobili consisted of whorled sterile microleaflets, which tightly coated the sporangia. Since these differed from other *Calamites* strobili, they represented the most striking distinguishing feature compared to other species, far ahead of the whorls of leaves or the trunks commonly found in almost all *Calamites* species. The less conspicuous main stems were named *Calamites multiramis* by the German mineralogist, geologist and phytopalaeontologist Christian Ernst Weiß (1833–1890) in 1884. Since trunks with a thickness of up to 15 cm were found on various occasions, a height of around 7–10 m should have been a reality.
Further, in the Kronalm area of the Carnic Mountains, *Calamites multiramis* occurs in some layers (A and F), forming a stand with a multitude of highly decorative and excellently preserved leaf whorls and hundreds of infructescences. Thus, this *Calamites* species should now be well known in terms of all its parts. Although it is rarer in the Nockalm area, many subspecies have nevertheless been named in the past as well as in the present, although some of them have juvenile shoots (known as *Annularia radiata)* or special forms of adult whorls (*Annularia spicata, Annularia spinulosa, Annularia stellata).*

Calamites carnicus n. sp. WACHTLER, 2022

Locus Typicus and geological age
Kronalm, Eastern Alps, Upper Carboniferous (Kasimovian-Gzhelian)

Repository
Coll. Wachtler, Museum Dolomythos, Innichen

Etymology
After the Carnian Alps, where it was found

Holotype
KRON 400 (Frond), **Paratype:** KRON 402

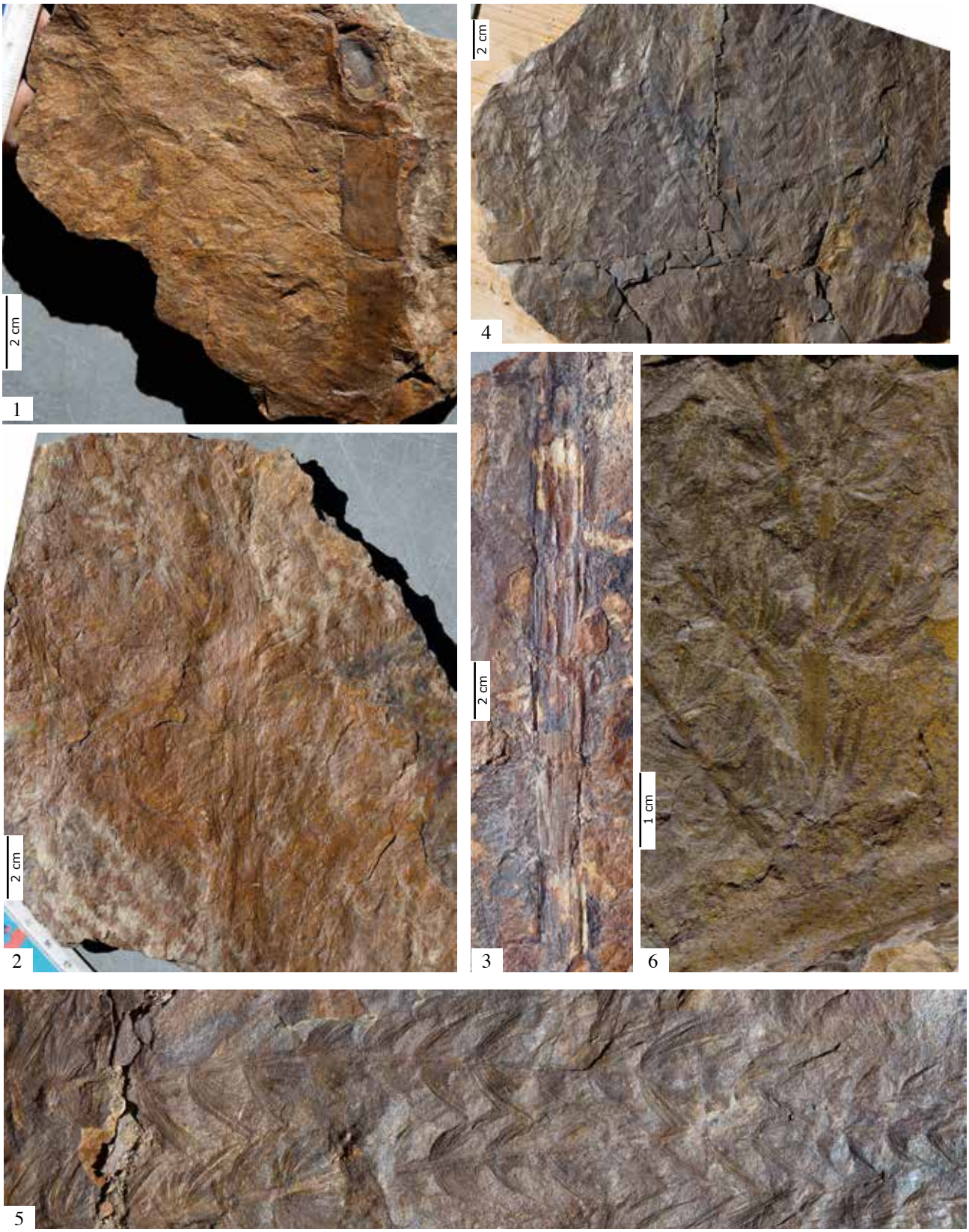
Diagnosis
Stems were interrupted by internodes, which developed whorls at regular intervals on the side branches. Sporangiophores with long bracts clawed at the sporangia.

Description
Whole Plant: Easily 5 m tall, with the main stem reaching a thickness of 4–8 cm. The smooth, partially close-lying ribs of the marrow trunks were irregularly interrupted by nodes, from which lateral branches sprang (KRON 403, KRON 401, KRON 404). These consisted of frond-like whorls which developed lanceolate-to-spatulate leaflets, often pointing upwards (KRON 400, holotype, KRON 326, KRON 68, KRON 88).
Fructifications: The strobili reached up to 10 cm in length and had a width of 1–2 cm, connected to the axes by a short, approximately 1-cm-long peduncle. Especially distinguishable from other species were the characteristically bushy and long-needled bracts that densely enveloped the rounded sporangia (KRON 399, KRON 322, KRON 402, paratype, KRON 398).

Remarks
Although fronds that are confusingly similar to *Calamites multiramis* are found particularly in the upper layers (horizon F) of the Kronalm, the connected sporangiophores indicate that two different, possibly related

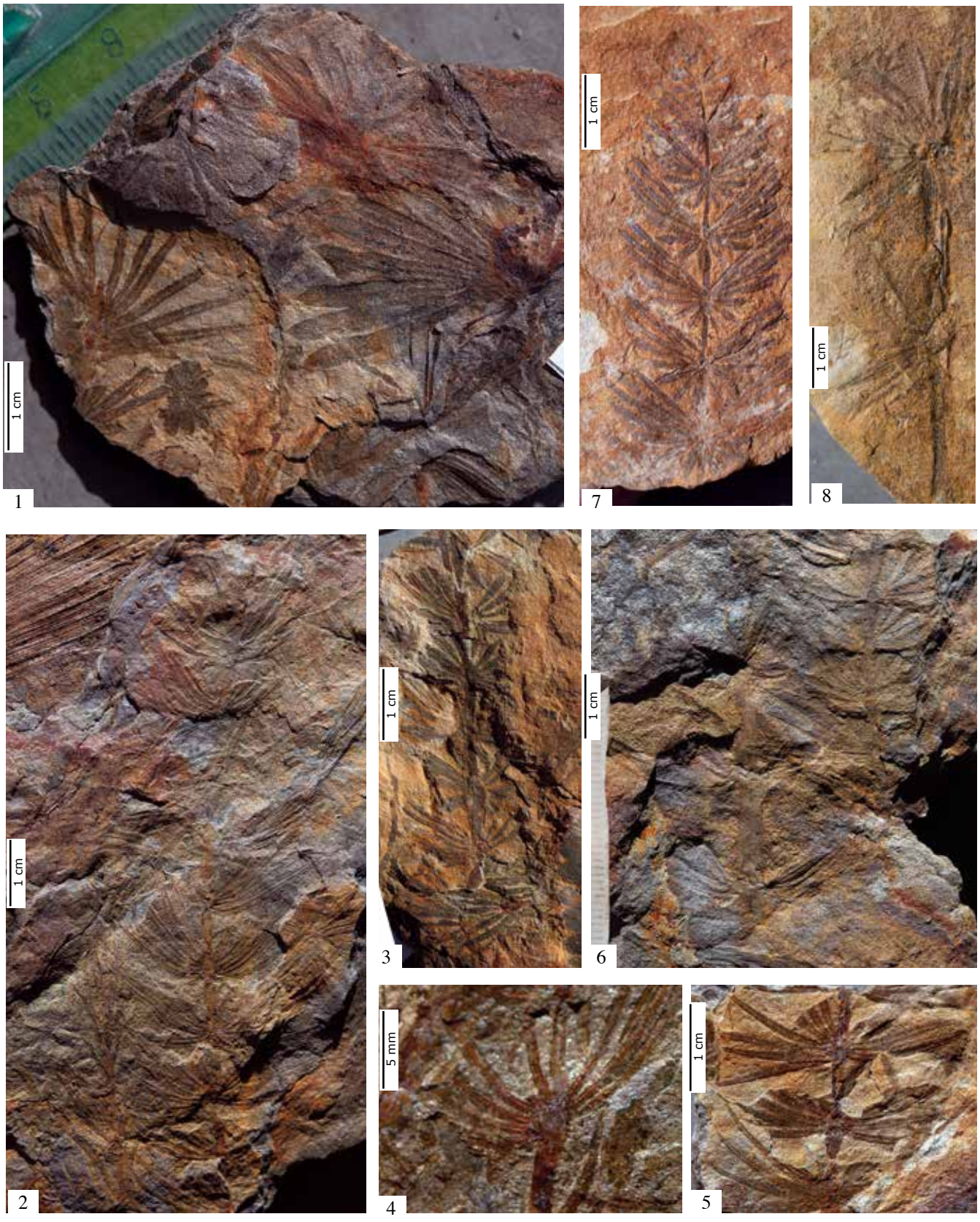
***Calamites carnicus*. Reconstructions**

a. Fertile whole plant; b. Whole frond (KRON 400, holotype); c. Part of a whorl (KRON 403, KRON 401); e. Multiple strobili (KRON 399); e. Strobilo (KRON 402, paratype); f. Part of a sporangiophore with bracts encasing the sporangia (KRON 398); g. Single bracts; h. Single sporangia.



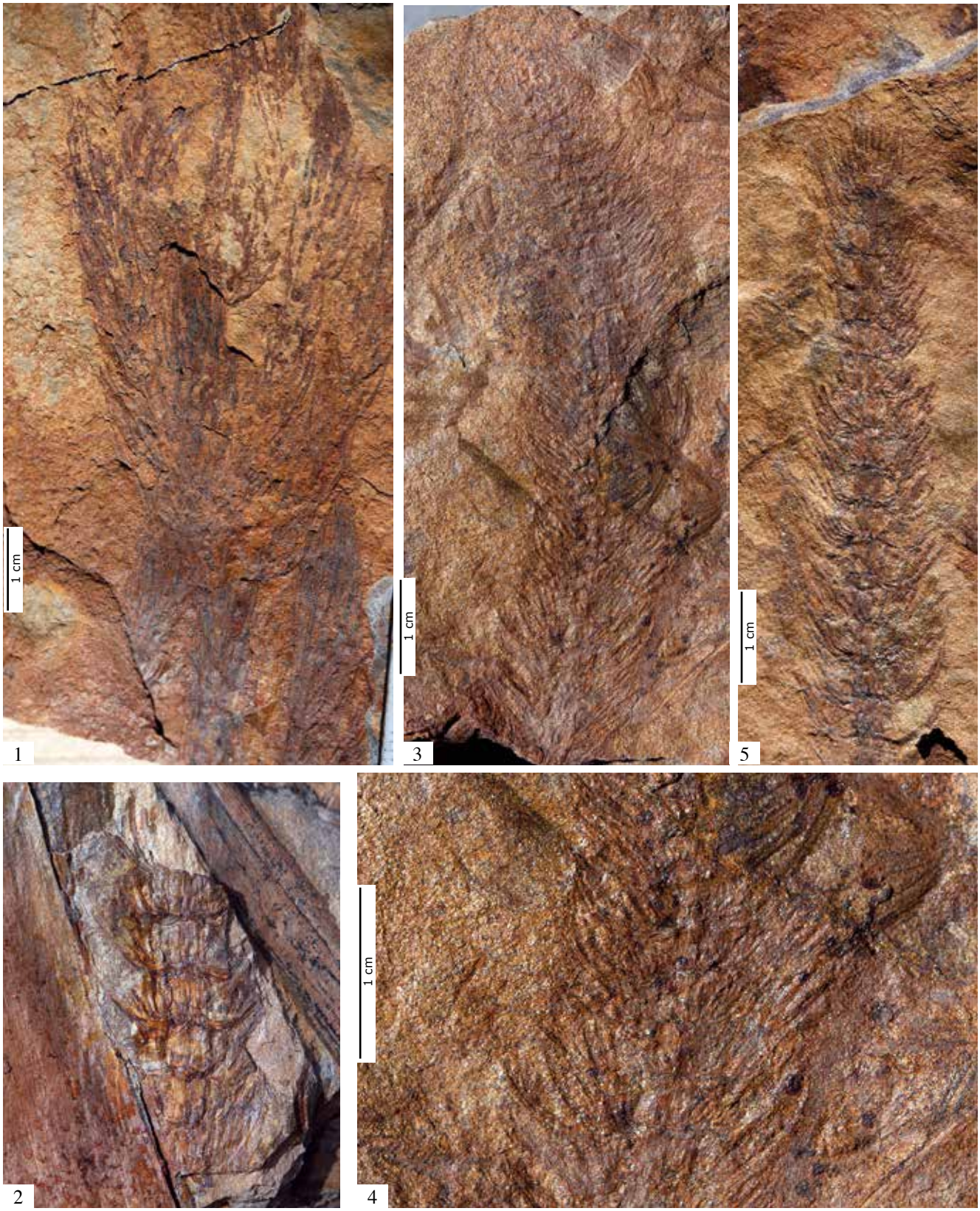
***Calamites carnicus*. Leaves and stems. Upper Carboniferous. Kronalm. Eastern Alps**

1-2. Stem parts with several branching lateral fronds (KRON 403, KRON 401); 3. Juvenile stem (KRON 404); 4-6. Lateral fronds with detail of the leaf whorls (KRON 400, holotype); Coll. Michael Wachtler, Dolomythos Museum, Innichen.



***Calamites carnicus*. Leaves and stems. Upper Carboniferous. Kronalm. Eastern Alps**

1–6. Different stems and lateral fronds of the same plant (KRON 326); 7–8. Whorls (KRON 68, KRON 88); Coll. Michael Wachtler, Dolomythos Museum, Innichen



***Calamites carnicus.* Sporophylls. Upper Carboniferous. Kronalm. Eastern Alps**

1. Cluster of strobili on part of a branch (KRON 399); 2. Detail of a mature strobilo (KRON 322); 3-4. Sporangiophore and detail of sporangia (KRON 402, paratype); 5. Sporangiophores (KRON 398); Coll. Michael Wachtler, Dolomythos Museum.

species occurred at the same time. In contrast to *Calamites multiramis, Calamites carnicus i*s characterised by bushy aggregates with a multitude of slender, long-needled bracts that closely envelop the sporangia. The leaf whorls are also slimmer and mostly directed upward along the axis.
Since *Calamites carnicus* sometimes occurs in the same strata as *Calamites multiramis,* it is not always clearly distinguishable. The multitude of different *Calamites* horsetails, even within contemporaneous depositional spaces, indicate a rapid variation in this genus. *Calamites carnicus* is also relatively easy to distinguish from the small *Calamites microphyllus,* although all the three above species can be classified under the group of Multibracteata Calamitales. Thus, the importance of knowledge regarding the fertile organs, for purposes of classification, becomes clear. Moreover, a precise layer removal of the individual lenses in the field is equally important.

Calamites microphyllus (comb. nov. WACHTLER, 2022)

1848 *Annularia microphylla* Sauveur Veget. foss. d. terr. Houillers de la Belgique. Planches 1848. Taf. LXIX, Fig. 6

1886 *Annularia microphylla* Zeiller, Valenciennes, Atlas,t.60,f.3,4;Text,1888, p. 392.

1887 *Annularia microphylla* Stur, Calamarien, Abh. k.k. Geol. Reichsanst. Wien, XI, 2, p. 211, t. 14, f. 8, 9, t. 15b, f. 2

1913 *Annularia microphylla* Jongmans, Calamariaceen d.Rhein. Westf. Steink. Meded. Ryks Herbarium Leiden, No. 20, p. 49

Description

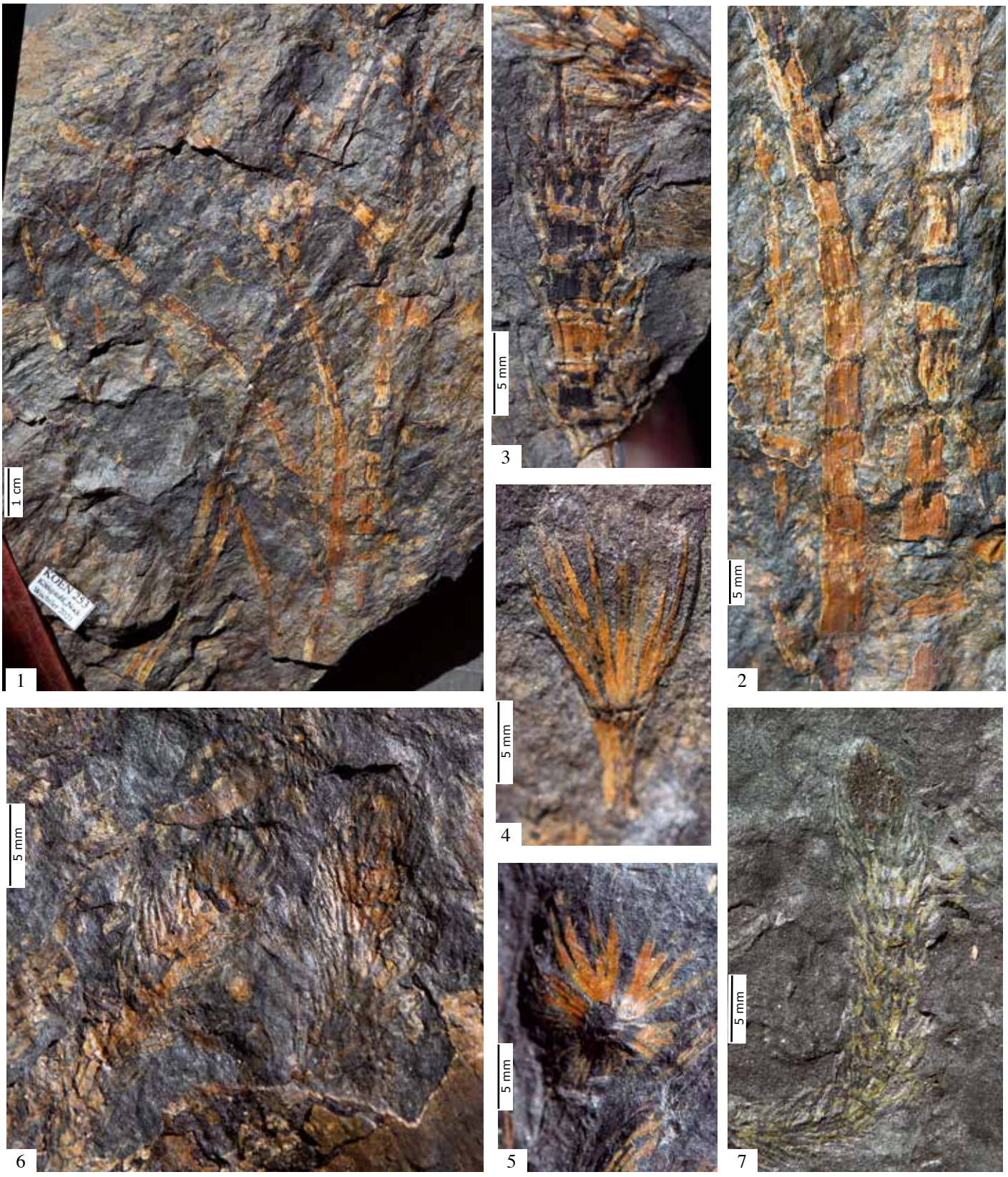
Plant: Low-growing to creeping Calamitaceae, probably reaching a height of only 30 cm. From the root area emerged several narrowly sprouting stems. The main axes of each were about 0.4–0.6 cm thick and broadly ribbed in the longitudinal direction. The internodes were distant by about 0.5–0.8 cm from each other.
The leaf whorls arose closely together, touching at the upper ends or being slightly offset. Individual sheaths were composed of about six main whorl leaves of approximately equal lengths that were fused basally, each of them splitting into four lanceolate microleaves. Each quadruple whorl therein was about 0.6–0.8 cm long and less than 0.1 cm wide and just as basally connected.
Fructifications: The strobili reached a length of up to 5 cm and a width of 1.5 cm. They sprouted in a stemless manner or were shortly stalked directly from the main axis. The sporangiophores developed a multitude of sterile microbracts which protected the sporangia.

Remarks

Especially in the Nockberge area, and more rarely in the Carnic Alps, there was a species among the Calamitaceae that hardly exceeded half a meter in size. Since giant clubmosses, especially Sigillarias, dominated these regions, *Calamites microphyllus* likely settled mainly in the undergrowth and near ponds or marshes. This plant was characterised by its short stature, unique among the Calamitaceae, with the constantly forking side shoots, the internodes barely a centimetre apart, as well as the microscopic, quadruple dichotomous whorls. Since *Calamites microphyllus* was found in large numbers in certain places, it possibly formed isolated populations.
The concomitant infructescence consisted of a large number of small bracts, which closely encased the sporangia (such that it is seldom possible to get an image of their appearance).
In 1848, the Belgian physician Dieudonné Sauveur (1797–1862) revealed an *Annularia microphylla* without a text, only containing a subtitled illustration. However, this name was adopted by the French engineer and paleobotanist René Zeiller (1847–1915) and by the Slovak paleontologist Dionýs Štúr (1827-1893) in 1887, with both descriptions and (more importantly) illustrations. These data roughly indicated the similarity of *Annularia microphylla* to those that frequently occurred in the Nockalm region or the Kronalm, even if no details about the infructescence were given in any previous publications.

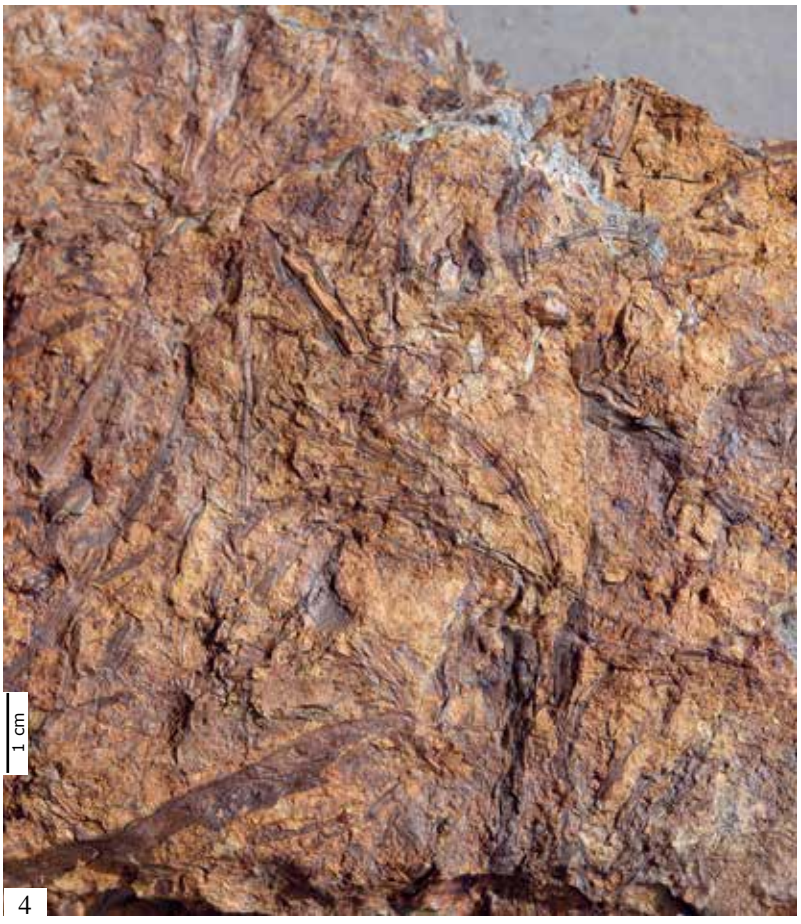
Calamites sphenophylloides (comb. nov. WACHTLER, 2022)

Synonyms: Single Parts. Stems: *Calamites cistii, Calamites schuetzeiformis;* **Whorls:** *Annularia sphenophylloides, Sphenophyllum incisum, Sphenophyllum longifo-*



***Calamites microphyllus*. Upper Carboniferous. Königstuhl. Eastern Alps**

1–2. Various stems with internodes lying close together (KOEN 253); 3. Detail of internodes with branching micro-leaflets (KOEN 257); 4–5 leaf whorls in side and top view (KOEN 257); 6–7. Terminal part of branch with sporophyll stands (KOEN 18, KOEN 149); Coll. Michael Wachtler, Dolomythos Museum.



***Calamites microphyllus*. Upper Carboniferous. Königstuhl. Eastern Alps**

1. Stem with branchlets (KRON 193); 2. Detail of the branches (KRON 193); 3. Detail of a strobilo connected to a frond (KRON 328); 4. Various stems (KRON 262); Coll. Michael Wachtler, Dolomythos Museum.

lium; **Fructifications:** *Macrostachya, Palaeostachya*

1821 *Rotularia cuneifolia* Sternberg, Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt vol. I, 2, p. 33, pl. 26, fig. 4a

1821 *Rotularia marsiliaefolia* Sternberg, 1821, vol. I, 2, pp. 30, 33

1822 Sphenophyllites emarginatus Brongniart, *p. 234, pl.13, fig. 8*

1825 Sphenophyllum emarginatum König, Icones fossilium sectiles, 1. pl. 12, fig. 149.

1828 Sphenophyllum emarginatum Brongniart, Prodrome d'une histoire des végétaux fossiles p. 68

1828 Sphenophyllum fimbriatum Brongniart, Prodrome d'une histoire des végétaux fossiles p. 68

1840 *Sphenophyllum fimbriatum (Rotularia polyphylla)*, UNGER

1869 *Annularia sphenophylloides* Unger, Anthracit-Lager in Kärnthen, Taf. I, Fig. 8

Description

Plant: Growing to about 7–10 m in height, with a main axis that hardly increased in terms of thickness to about 10 cm. The trunk, developing smooth or narrow transverse ribs, was markedly interrupted at varying intervals by internodes from which the lateral branches sprang. These developed delicate whorls of wedge-shaped leaflets (as indicated by the Greek name "sphen" for wedge, and "phyllon" for leaf). The whorls, usually consisting of six individual leaves with one deep incision, reached lengths of up to 2.5 cm (KRON 76, KRON 67). They could be bluntly dentate at the upper end, and sometimes multiple dichotomous veins were visible on the leaflets. Likewise, heterophyll-deviating leaf shapes occurred in the direction of the branch tip.

Fructifications: Thespore cones, massive for a Calamitaceae (KRON 121), could reach a length of 10 cm and a width of 2 cm. They consisted of several bracts which encased the sporangium. The strobili were attached to the main stem by a stalk about 3 cm in length.

Remarks

Slashed wedge-shaped leaf whorls (hence the frequently used name *Sphenophyllum,* for wedge leaf) have been known for a long time. However, the history of their description has turned out to be more tortuous. At the beginning of 1821, the father of paleobotany Caspar Maria Graf Sternberg named a *Rotularia cuneifolia* and a *Rotularia marsiliaefolia* in his "*Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt".* This date is interesting, because in 1957, at the 8th Botanical Congress in Paris, the commencement of paleobotanical nomenclature was decided considering the first edition of Sternberg's "*Flora der Vorwelt" (Flora of the Prehistoric World),* published on December 31, 1820. Thereby, all publications by the German Ernst von Schlotheim before 1820 and the names used therein were rendered obsolete (Kvaček et al., 2021). In 1822, almost simultaneously with the work of Graf, Adolphe Brongniart described a similar plant called *Sphenophyllites emarginatus.* Without any description, however, in 1825 the German-British naturalist Charles Koenig (German Karl Dietrich Eberhard König, 1774–1851) changed the name of this plant to *Sphenophyllum emarginatum.* Interestingly, starting from 1828, even Brongniart used this name in his publications, and in the subsequent decades more than 175 related species and several subspecies and varieties were published (Boersma, 1989). Franz Unger also contributed here, describing in 1840 a *Sphenophyllum fimbriatum* from the Stangalpe that he equated with *Rotularia polyphylla,* without going into details or depictions. Finally, in 1869, it was Unger himself who described and illustrated an *Annularia sphenophylloides* from the Upper Carboniferous of Carinthia.

To put an end to the name haggling, a solution is to use *Annularia sphenophylloides* from the Eastern Alps in a new combination, as *Calamites sphenophylloides.* This does not mean that all wedge-leaf horsetails were tree-shaped; it was partly assumed that the *Sphenophyllum* plants were not only aquatic plants but also climbing, ground-creeping or low-growing (Boersma, 1989). Their distribution area extended between the Upper Carboniferous-Lower Permian over the entire northern hemisphere, from Euramerica to the enigmatic Angara continent (today a part of the Urals and Siberia).

Unfortunately, the fertile parts were neglected in the past. One could see how superficially the related determinations were based, solely on the leaves, for the

***Calamites microphyllus*. Reconstructions**

a. Whole fertile plant (KOEN 253, KRON 262); b. Main stem basal part (KOEN 253); c. Shoot in the upper part with the sheath leaf whorls (KRON 403, KRON 401); d–e. Sheath side-view and top-view with the six side leaves which each divide four times (KOEN 257); f. Sporophyll cone (KOEN 18, KOEN 149, KRON 328); g. Sporangiophore with hidden sporangia; h. Lateral view with leaf bracts and sporangia; i. Single sporophyll obscuring the sporangia; j. Sporangia.

***Calamites sphenophylloides*. Upper Carboniferous. Königstuhl. Eastern Alps**

1. Whorl of leaves with sporophyll stand (KRON 121); 2–3. Twigs with leaf whorls (KRON 76, KRON 67); 4–5. Frond with details of whorls with dichotomously branching veins (KRON 125); 6. Stem (KRON 29); Coll. Michael Wachtler, Dolomythos Museum

***Calamites sphenophylloides*. Upper Carboniferous. Reconstructions**

a. Fertile whole plant with side branches (KRON 69); b. Lateral fronds; c. Leaf whorls (KRON 125); d. Individual leaf whorls (KRON 121, KRON 76, KRON 67); e. Sporangiophore (KRON 121); f. Bracts; g. Sporangia.

plants found on the Kronalm, in terms of trunks, leaves and sporophyll stands. Indeed, these were quite high-growing and massive *Calamites,* with side branches that carried the wedge-shaped whorls of leaves. Their strobili were massive, with the single sporangiophore being encased by several bracts. Regarding this structure, one can assume that this *Calamites* species would also fall under the subsection Multibracteata.

Subsektion: *Calamites monobracteata*

Calamites longifolius (comb. nov. WACHTLER, 2022)

Synonyms: Single parts: Leaves: *Asterophyllites longifolius*, Synonym: *Asterophyllites equisetiformis*

1825 *Brukmannia longifolia* Sternberg, vol. I, 4, p. 45, tent. p. 29, pl. 58, fig. 1

1825 Bornia equisetiformis, Sternberg, Versteinerungen 1; S. 29

1820 *Casuarinites equisetiformis*, Schlotheim, Flora der Vorwelt T. 1, Tafel 2, nom. inval., Art.13.1

1828a *Asterophyllites longifolius* (Sternberg), Brongniart, pp. 159, 176, Plate V, Figs. 5, 6, 8, 9; Plate VI, Fig. 4

1840 A*nnularia longifolia*, Unger, pag. 68

Description

Plant: Growing about 5-10 meters in height, with the main trunk reaching a thickness of about 7–10 cm. Ribs on the stems were variable, being close together in the lower parts of the hollow stems and also forming almost smooth, leaf-like surfaces in the upper parts. The stems were often completely torn. Main trunks were interrupted by strong knots from which irregular lateral branches sprang. Lateral side branches partially showed massive transverse furrows. The foliage on the side branches was characterised by extraordinarily long, needle-like leaves, some reaching a height of 25–40 cm. These leaves were fused together in the basal part (KRON 145, KRON 86, KRON 141, KRON 111, KRON 85, KRON 79, KRON 811, KRON 52, KRON 969, KRON 110, KRON 112, KRON 64, KRON 131).

Fructifications: Complete strobili up to 5 cm long but only 5–8 mm wide, slender, developing at the end of a 5–10-cm-long stalk. The infructescence consisted of whorls of sporangiophores. The rounded sporangia were encased in a single enveloping microbract (KRON 75, KRON 78, KRON 120, KRON 103, KRON 72, KRON 79, KRON 122).

Remarks

Hardly any Calamitaceae species is as difficult to classify as *Calamites longifolius.* This is not because its entire parts, from the trunk and the distinctive long-needled leaves to the delicate sporophyll stands, are unknown or rare, especially in the Eastern Alps! Instead, on the one hand, it is the descriptive history, for the most part based on the naming of the pure stem or, more often, of the leaf whorl. Second, the peculiar tattered end parts of the trunks, as well as a variation from smooth, barely discernible transverse grooves to prominent ribs, which partially suggest the existence of two different related species.

There are two terms which give rise to discussion: the commonly known *Asterophyllites equisetiformis* (Brongniart, 1828), previously described by the German paleobotanist Ernst von Schlotheim (1804, 1820) as *Casuarinites equisetiformis,* and later published by the Czech Scientist Caspar Maria Graf Sternberg as *Bornia equisetiformis.*

Slovak geologist and paleobotanist Dionýs Štúr (1827-1893).

In the same year of 1825, Sternberg classified another species as *Brukmannia longifolia,* which was thereafter transformed into *Asterophyllites longifolius* by Adolphe Brongniart in 1828 and classified by Franz Unger as *Annularia longifolia* in 1840, on the basis of some specimens from the Nockalm area.
All these classifications have been made without ever considering the whole plant, least of all its fertile parts. Especially at the Kronalpe in the Carnic Alps, there is an opportunity to bring all parts of the plant together. Since the primary task of paleobotany is to develop reliable statements, this Upper Carboniferous horsetail species is recombined as *Calamites longifolius*.
The fact that *Calamites longifolius* is part of the Calamitaceae is confirmed by its stem and especially its infructescence. However, its sporangiophores have attracted little interest from collectors or researchers, due to their delicate and inconspicuous appearance compared to other parts. In addition, their long peduncles often break when they are embedded, so that the parts of the stem associated with the fructifications are found rarely.
To sum up, *Calamites longifolius* is particularly common in the find layer B of the Kronalm. Possibly, it is the second-most common variant after *Calamites multiramis,* ahead of *Calamites sphenophylloides* and *Calamites microphyllus,* so that its appearance is relatively easy to understand. Surprisingly, in some strata it occurs simultaneously with three other *Calamites* species over a very small area, while in other lenses it forms a monoculture.
Moreover, its apical, pointed, torn stems, which have often been held as *Cordaites* leaves in the past (KRON 145, KRON 86, KRON 141), also give rise to further discussions. It remains unclear whether these are the terminal stems splintered by the rigours of nature or by secondary enveloping leaves.

Calamites sturii n. sp. WACHTLER, 2022

Locus Typicus and Geological age

Upper Carboniferous of the Eastern Alps, Kasimovian-Gzhelian

Repository

Coll. Wachtler, Museum Dolomythos, Innichen

Etymology

Named after Dionýs Štúr (also Dionys Stur, 1827–1893) was a Slovak geologist, paleobotanist and paleontologist. His main area of focus was the geological exploration of the Alps. He set standards in the description of fossil plants, especially from the Devonian and Carboniferous.

Holotype

KOEN 27 (Strobilo)

Diagnosis

Stems are smooth to tightly ribbed, leaves lanceolate elongated, with sporophyll consisting of individual bracts covering a single sporangium.

Description

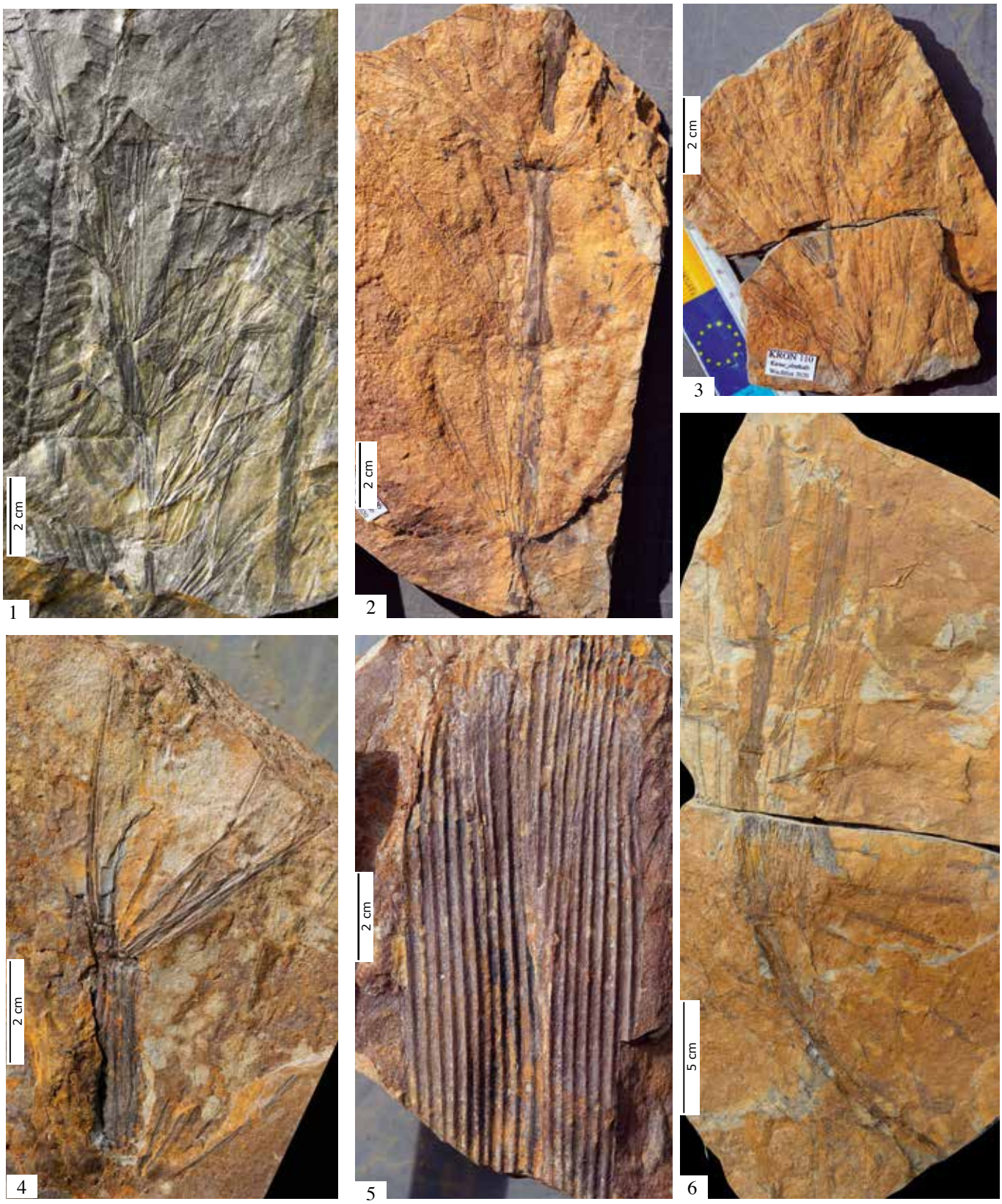
Whole plant: Stems were up to 10 cm thick, with smooth, parallel ribs lying close together (KRON 69, KOEN 266). They were often torn several times, reminiscent of an accumulation of several small stems (KOEN 05). Stem internodes were hardly perceptible (KRON 69) and leaves were lanceolate.
Fructifications: Strobili were up to 15–20 cm long, with a width of 2 cm (KOEN 27, holotype), but mostly smaller (KOEN 10, KOEN 05, KOEN 255, KOEN 20, KOEN 31, KOEN 264, KOEN 43), connected by a short stalk to the main stem or to the lateral branchlets (KRON 69, KRON 17, KRON 29, KRON 66) or bereft of such connections (KOEN 10, KOEN 05). Strobili consisted of a dense arrangement of about 0.5-cm-long sporophylls ending in a single short, pointed bract, whereas basally they enclosed a spherical sporangia. This species was homosporous.

Remarks

This plant, which is difficult to classify, is found in abundance on the Königsstuhl, albeit a little less frequently on the Stangnock or the Kronalm, and is characterised by strobili which, in contrast to those of other *Calamites* species, only evolves a single bract, which in turn develops a homosporous sporangia in the basal area. The stem structure and sporangiophores are in some respects

***Calamites longifolius*. Upper Carboniferous. Kronalm. Eastern Alps**

1–3. Stem parts (KRON 145, KRON 86, KRON 141); 4. Lateral fronds with emerging strobili (KRON 111); 5–6. Stem with branching strobili and detail (KRON 85); 7. Frond part with sporophyll stand (KRON 79); 8. Main stem with branching strobili (KRON 811); Coll. Michael Wachtler, Dolomythos Museum.

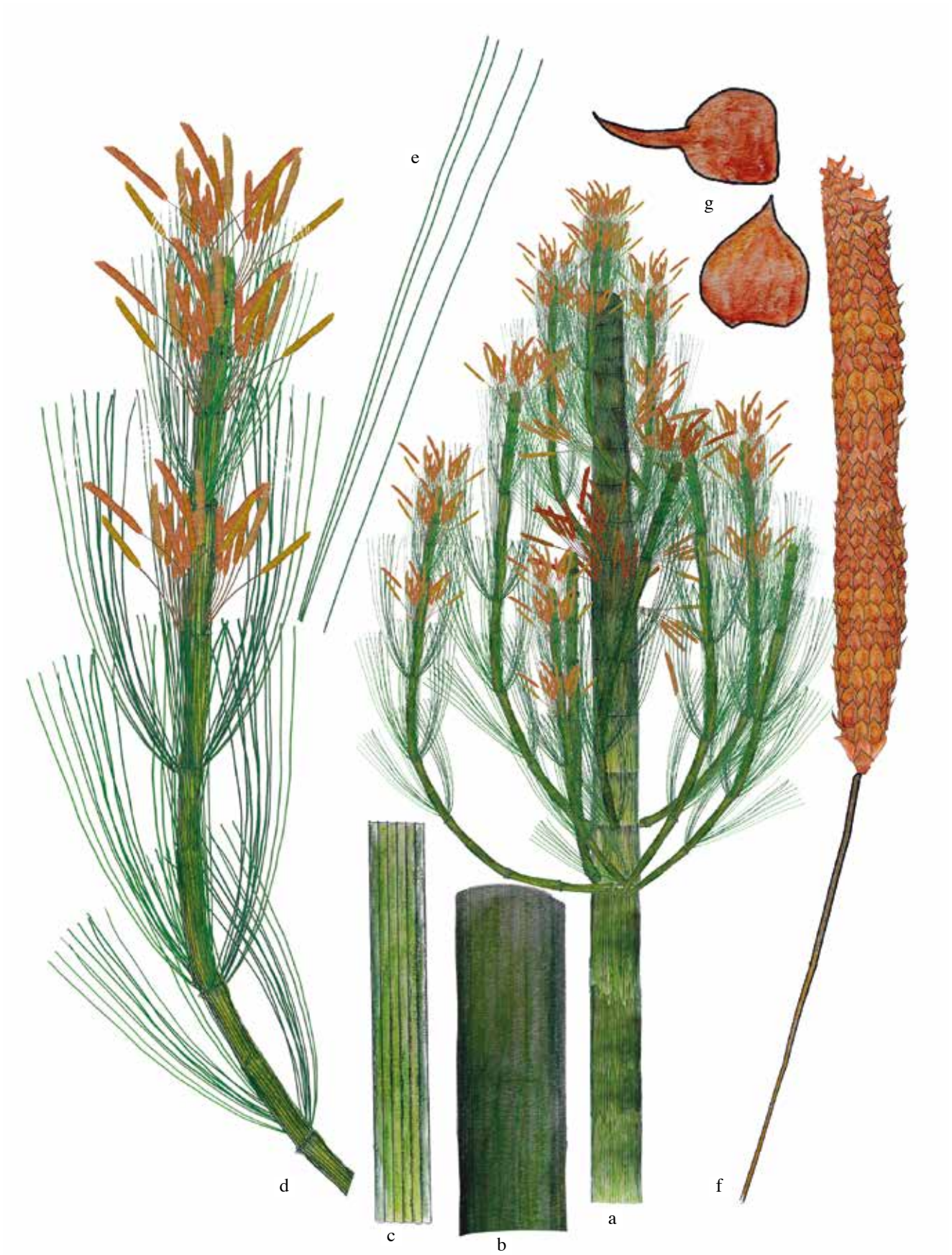


***Calamites longifolius*. Upper Carboniferous. Kronalm. Eastern Alps**

1. Lateral branches with detail of needle-like leaves (KRON 52); 2. Side branchlet (KRON 969); 3. Apical part of a side branch (KRON 110); 4. Side branch with pronounced longitudinal ribs (KRON 112); 5. Main trunk (KRON 64); 6. Branchlet with needle-like leaves (KRON 131); Coll. Michael Wachtler, Dolomythos Museum.

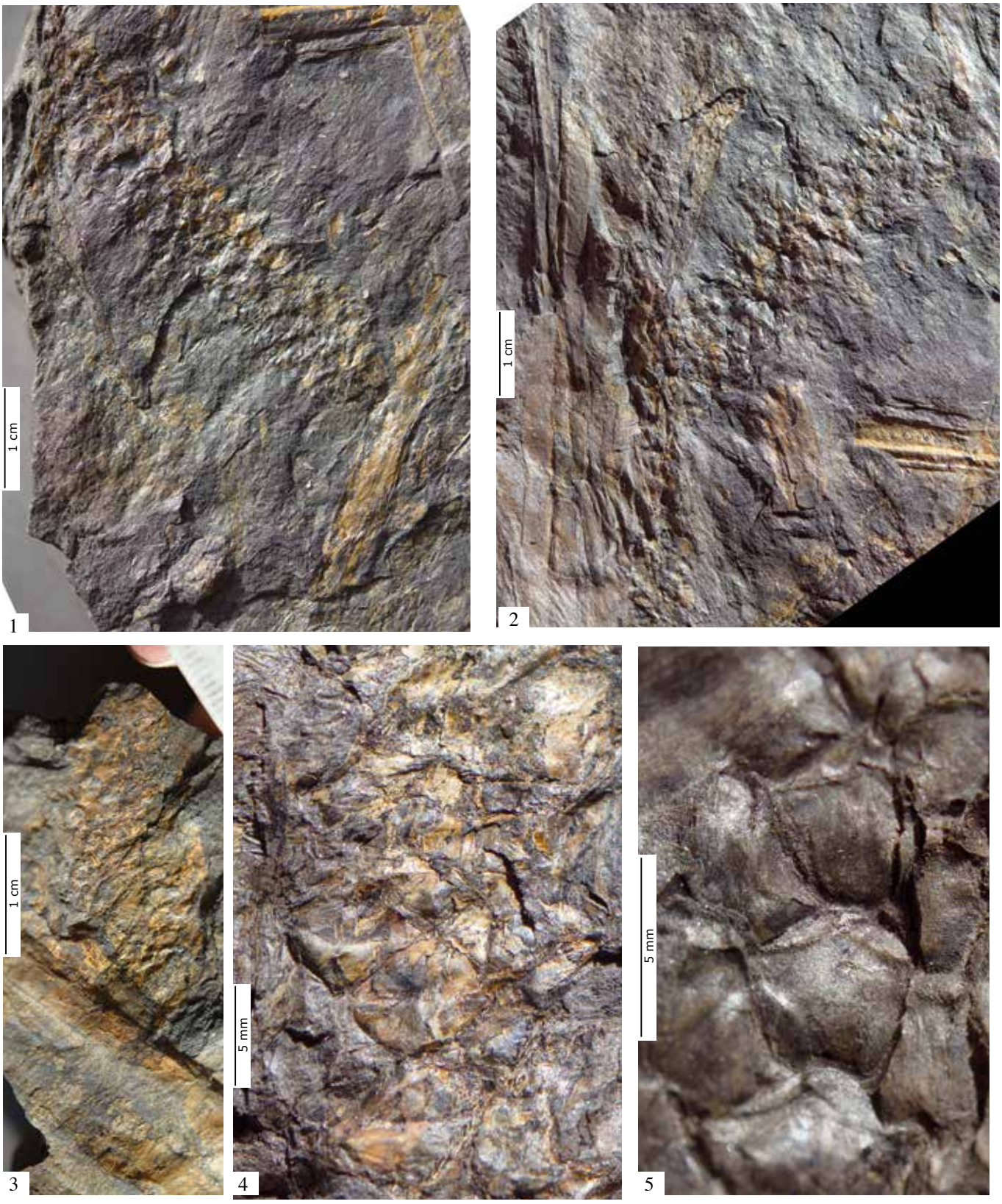
***Calamites longifolius*. Upper Carboniferous. Kronalm. Eastern Alps**

1–2. Frond with strobilo and detail (KRON 75); 3. Different strobili (KRON 78); 4. Two strobili with characteristic overlong connecting stalks (KRON 120); 5. Branch with different strobili (KRON 103); 6–8. Sporophyll stand and detail of bracts (KRON 72, KRON 79, KRON 122); Coll. Michael Wachtler, Dolomythos Museum.



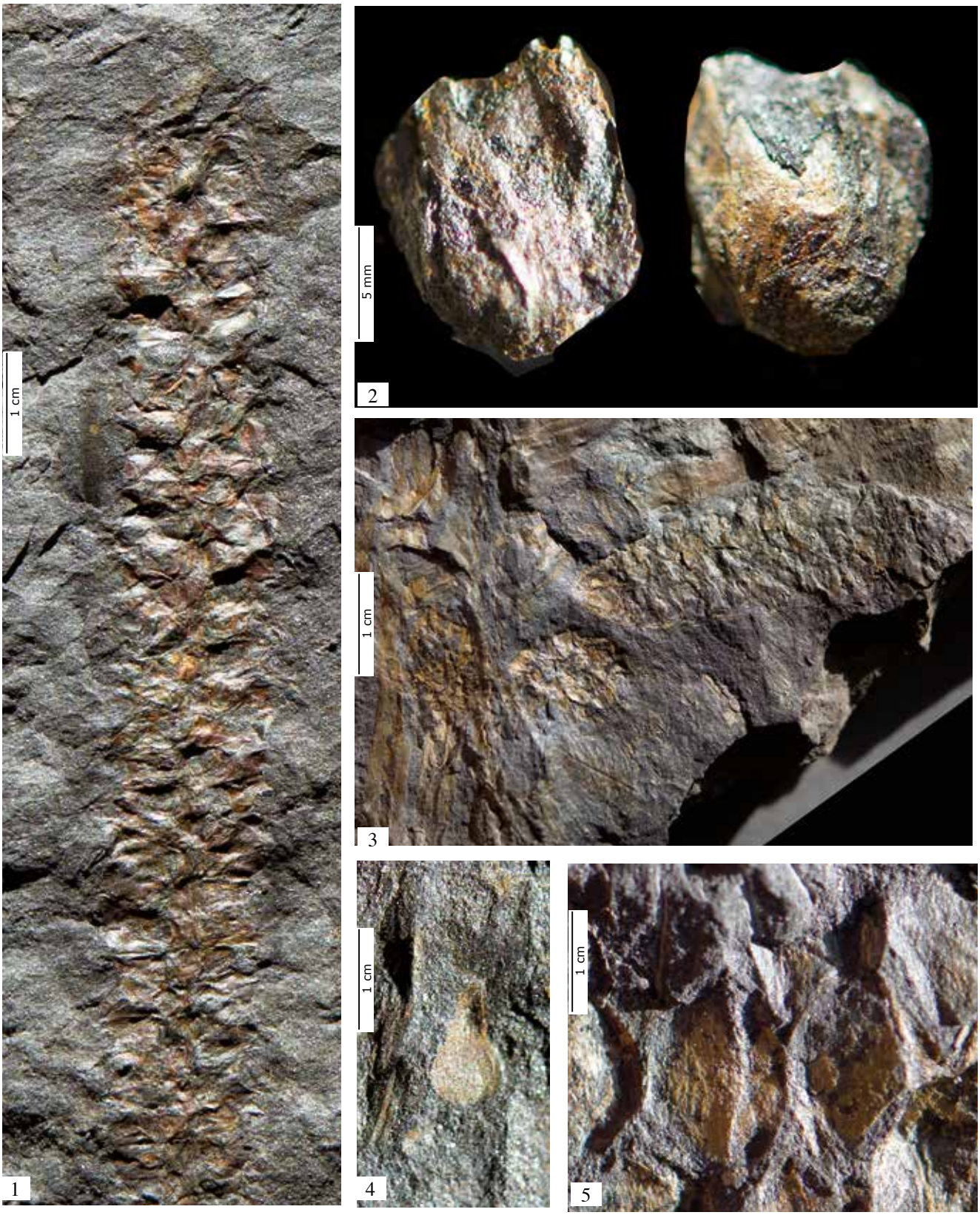
***Calamites longifolius*. Upper Carboniferous. Reconstructions**

a. Fertile whole plant with side branches; b. Main trunk; c. Side stem; d. Side branch with sporophyll stands (KRON 131); e. Needles/leaves (KRON 112, KRON 969); f. Strobilo with a characteristically long connecting stalk (KRON 78); g. Sporangia enveloping bract, lateral and anterior views (KRON 122).



***Calamites sturii*. Upper Carboniferous. Königstuhl. Eastern Alps**

1–2. Sporangial cones on trunk (KOEN 10, KOEN 05); 3. Juvenile strobilo on a trunk (KOEN 255); 4–5. Detail of the bracts (KOEN 20, KOEN 31); Coll. Michael Wachtler, Dolomythos Museum.



Calamites sturii. **Upper Carboniferous. Königstuhl. Eastern Alps**

1–2. Sporophyll cone and details of individual sporophylls (KOEN 27, holotype); 3. Sporophyll cone (KOEN 03); 4–5. Details of individual sporophylls (KOEN 34, KOEN 261); Coll. Michael Wachtler, Dolomythos Museum.

***Calamites sturii*. Upper Carboniferous. Königstuhl. Eastern Alps**

1–2. Sporangial cone (KOEN 10); 3. Juvenile strobilo (KOEN 264, KOEN 43); 4. Detail of a sporophyll stand (KOEN 27); 5. Sporophyll stand with stem (KOEN 266); Coll. Michael Wachtler, Dolomythos Museum.

***Calamites sturii*. Upper Carboniferous. Kronalm. Eastern Alps**

1–2. Main stem with strobilo and detail (KRON 69); 3. Sporophyll cone (KRON 17, Coll. Weiss); 4–5. Excellently preserved cone (KRON 29); 6. Strobilo with basal connecting peduncle (KRON 66); Coll. Michael Wachtler, Dolomythos Museum.

reminiscent of lycophytes, but the laterally arising sporophyll stands have more in common with the overall structure of *Calamites.* The same is valid for the only one sporangium on each sporophyll, in contrast to the Lepidodendrales which are characterised by two closely spaced sporangia. Therefore, this plant is classified as *Calamites sturii,* although it stands relatively isolated under the given genus. It also possibly has a parental affinity with *Calamites* and the Devonian-Carboniferous *Protolepidodendron* clubmoss family. Despite the frequency of the sporophyll cones, the stems or leaves cannot always be clearly assigned due to their similarity with other *Calamites* or Lycophyta, which makes it difficult to find out the exact appearance or structure of the plant.

What we know about the Calamitaceae

Origin in the Devonian and extinction in the Permian: *Archaeocalamites antiquus,* the first precursor of the Calamitaceae, could be found from the Middle Devonian onward. They were fully developed in the Lower Carboniferous (*Calamites radiatus)* and reached their heyday in the Upper Carboniferous, with many species and subspecies spreading worldwide. Their last representatives could be found in the Upper Permian, where they became extinct at the Permian-Triassic boundary.

Differences with the *Equisetes* horsetails: Although the Calamitaceae could be usually classified as giant horsetails, there were (except for their common hollow stem) major differences between them. Their strobili were completely different, which in *Calamites* evolved a slender and elongated strobilo consisting of homosporous sporangia that were clawed by one or more bracts, while in *Equisetites* the rounded cone was formed by a large number of elongated sporangia protected by a mostly hexagonal, table-shaped covering bract. *Calamites* also developed decorative frond-like whorls.

Clubmoss- and fern horsetails: In the case of *Calamites,* the term clubmoss-horsetail would be appropriate, as the only living horsetail genus *Equisetum* probably came from fern developments in the Middle Devonian.

Large number of species in the Upper Carboniferous: In some cases, four to five different Calamitaceae could be found within a few square meters in the Eastern Alps, proving the high variability of these plants.

Multibracteated and Monobracteated Calamitaceae: Some *Calamites* species were characterised by a large number of bracts clawing at a single sporangium, others by only one single bract.

Global distribution: The Calamitaceae were widespread in the Carboniferous and at the beginning of the Permian, especially in the Northern Hemisphere. It is unclear whether they spread through migration in the Devonian or whether they developed autochthonously at different locations.

Extinction at the Permian-Triassic boundary: The Calamitaceae became extinct towards the end of the Permian, without leaving any descendants. Some *Neocalamites* classifications could be described from the Triassic point, due to their fertile organs in the direction of the Equisetaceae.

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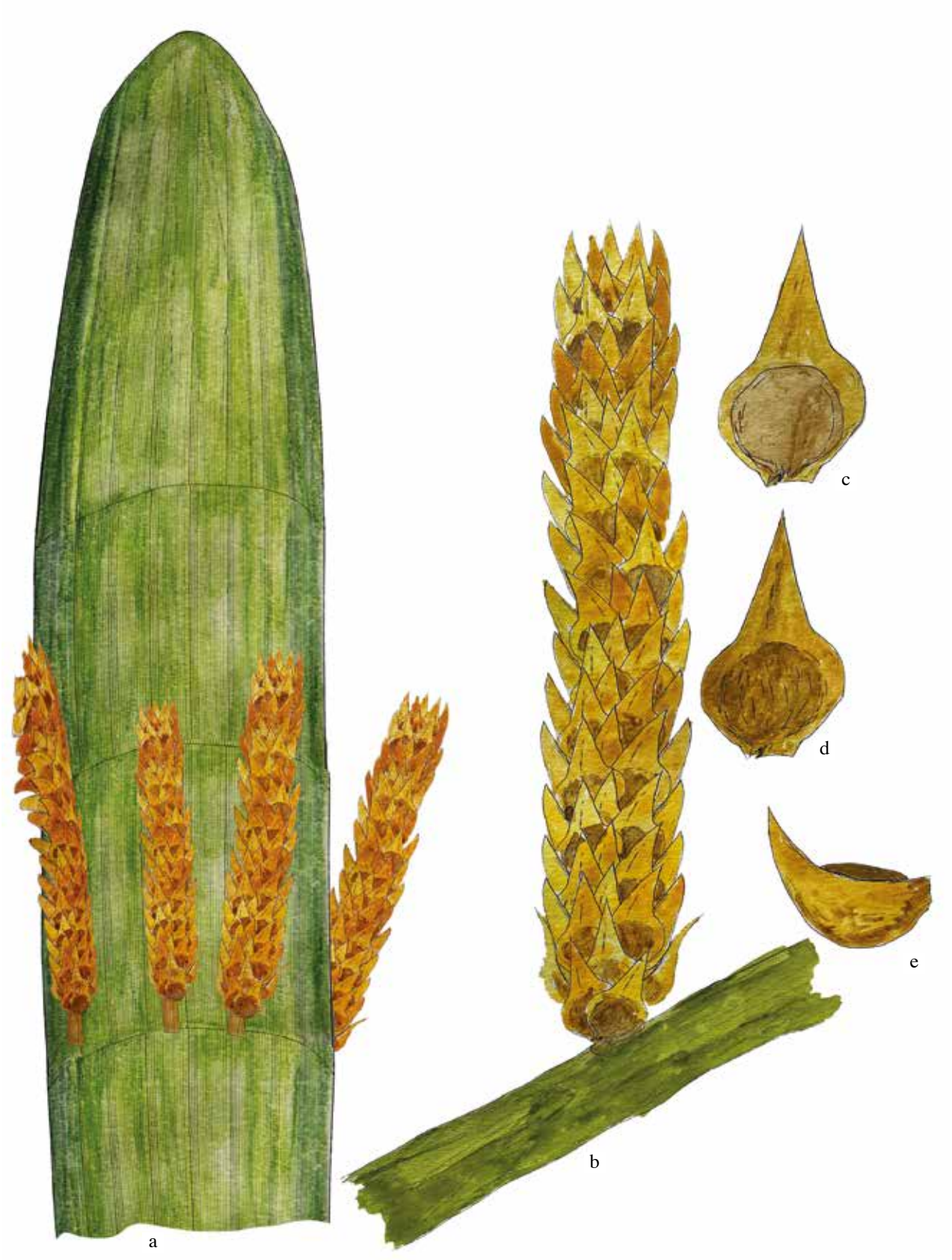

Calamites sturii. **Upper Carboniferous. Reconstructions**

a. Fertile plant on the main stem (KRON 69); b. Fertile side stem (KOEN 10, KOEN 05, KOEN 27); c. Sporophyll inside (KOEN 20, KOEN 34); e. Sporophyll outside; f. Side view (KOEN 20).

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Carboniferous Fossil Floras from the Eastern Alps

Edited by Michael Wachtler and Nicolas Wachtler

Summary

The many and rich sites of fossil plants from the Upper Carboniferous period in the Eastern Alps have long aroused the interest of the local population and even more of researchers. Nevertheless, most of the sites are largely unexplored. Most sites are dominated by *Sigillaria*, in minority *Lepidodendron* lycopods, several *Calamites* horsetails and a variety of ferns, some of which could be defined as seedferns. Due to the large number of Sigillaria's, it was possible for the first time to obtain detailed information about this engimatic lycophyte, and even the variety of highly developed and well-preserved ferns, especially the Osmundaceae, Marattiales and tree ferns, offered the opportunity to learn more about their evolution.

With 600 photos and drawings

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