Lower Carboniferous Floras from the Eastern Alps

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The Eastern Alpine floras from the Lower Carboniferous (Viséum) are generally poorly preserved and fragmented. But they are interesting because the giant clubmosses such as *Lepidodendron* and *Sigillaria,* as well as the *Calamites* horsetails (*Archaeocalamites radiatus)* were already fully developed in this early geological period. In addition, fern communities were widespread. Some showed relationships with primitive Devonian plants such as *Praecallipteridium* or *Rhodeopteridium* with its bifurcated leaf emergences, but other had just developed modern characteristics. One of the most interesting ferns required a new description as, *Adiantites flabellifolium* n. sp. Although in the Lower Carboniferous the following development lines are still difficult to recognize a wealth of plants that determine the earth today were formed due to the widespread humid and tropical climate. These concern the tree fern precursors *Cyatheites* or *Dicksonites,* but also the Danaea ancestors (*Danaeites)*. Like hardly anywhere else in the world, in this small-sized area, which includes the extended Dolomites World Heritage, a period of more than 100 million years of seamless plant development and the associated climatic catastrophes can be seen, documented in many layer sequences from the Carboniferous, the Permian over the Triassic, which was crucial for the evolution of ferns, horsetails, clubmosses and gymnosperms such as conifers, ginkgoes and cycads.

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A flora community from the Lower Carboniferous of the Alps (around 330 million years ago). Common was a primitive *Calamites* horsetail, ***Archaeocalamites radiatus*** (1), with multiply forked leaf needles. The ferns were dominated by ***Adiantites flabellifolium*** (2), ***Rhodeopteridium leptofoliatum*** (3), and ***Praecallipteridium parvifolium*** (4). In the meantime, various club moss trees (***Lepdidodendron*** (5,6), ***Sigillaria*** (7)) also reached gigantic growth that only lasted a few million years and was never reached again later.

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The oldest occurrences of fossil plants in the Eastern Alps can be traced back to the Lower Carboniferous and, more specifically, to the middle Viséan (around 340 million years ago) (van Amerom et al 1984). Here it is a sequence of layers that sometimes reach a thickness of thousand meters - the Hochwipfel-Formation - in which different flora communities can be found from time to time. However, precise classifications are difficult, not only because of their rarity and often poor state of preservation. The nomenclature, especially the large number of described plant species, also needs to be revised.
Another, somewhat younger location was classified as *"Noetsch Carboniferous"* and probably belongs to the upper Viséan to the older Serpukhovian (Amerom & Schönlaub, 1992). Both floras show plant fossils, which allow us to draw conclusions about their ancestors in the Devonian, but some of which were also surprisingly highly developed.

Lower Carboniferous (Viséan) floras

The Hochwipfel-Formation, named after the 2,195 m high Hochwipfel above the Rattendorfer Alm, extends in the Carnic Alps on the Austrian side - from Lake Wolajer to Thörl-Maglern - and on the Italian side from Forni Avoltri to Paularo. The most interesting fossil plant finds occur near the Rifugio Marinelli, above Forni Avoltri (van Amerom et al 1984), and the Tröpolacher Almweg above the municipality of Rattendorf (Kabon & Schönlaub, 2019). It can be assumed that the plants were often destroyed by long transport routes, so that meaningful details were rarely preserved. *Calamites* horsetails, clubmosses in the form of *Lepidodendron* and *Sigillaria* are particularly common. Only in the rarest cases reasonably recognizable fern fronds can be located.
From the late 19th century onwards, these oldest floras in the Eastern Alps attracted the interest of researchers such as Stur, 1868, Frech 1894, Gortani, 1905 and 1906, and Vinassa de Regny, 1905 and 1906. The two Italian geologists Michele Gortani (1883-1966) and Paolo Emilio Vinassa de Regny (1871-1957) we owe the knowledge of the first plant finds near the Marinellihütte

The Rifugio Marinelli in the Italian region of Friuli Venezia Giulia is located at 2120 m above sea level. The Lower Carboniferous plant horizons are located on the hilltop behind the hut in the direction of Monte Coglians.

The Tröpolacher Almweg is located above the hamlet Rattendorf near the Nassfeld. The plant layers from the Lower Carboniferous emerge on the path or near the ski slopes.

(*Calamites* sp. or the fern *Neurodontopteris auriculata)*, which they alternately assigned to the Lower or Upper Carboniferous (Vinassa de Regny & Gortani, 1905, 1906). After some intense debates between Vinassa de Regny, Gortani, Frech and Geyer, it was the Austrian geologist Franz Heritsch (1943) who coined the term Hochwipfel facies and assigned it to the Lower Carboniferous (Kabon & Schönlaub, 2019).
It was only after the Second World War that further research began, especially by Dutch paleobotanists under the direction of Hendrick W. J. van Amerom (1933-2018), who examined the sites around the Rifugio Marinelli above Collina (Amerom et al. 1984).
They discovered *Archaeocalamites radiatus* at various sites and newly described suspected fern precursors

such as *Rhodeopteridium aphlebiotum* and *Rhodeopteridium leptofoliatum,* as well as *Cardiopteridium dijkstrae.* They also recognized *Sphenopteridium* ferns and correlated clubmosses such as *Lepidodendron lossenii* with other sites from East Germany.
The next paleobotanical milestone occurred in 2019 by Herbert Kabon and Hans Peter Schönlaub with a publication about the flora of the Hochwipfel Formation around the Carinthian Tröpolacher Alm. The fossil plants in this area were probably slightly younger than those in the Marinellihütte, but earlier than the Nötsch Formation and have been deposited probably in the Late Viséan (Kabon & Schönlaub, 2019).
What all localities have in common is that the conservation status of the plants is sometimes fragmented and poor. Only coastal and transport-resistant Calamitaceae stems are reasonably well conserved and common. The plants were probably carried into nearby waters, where centimeter-thick layers of flotsam in the form of larger horsetails or club moss stems accumulated, and were only rarely embedded in finer mud, where also delicate ferns, seeds or fructifications sometimes survived in relatively good conservation.

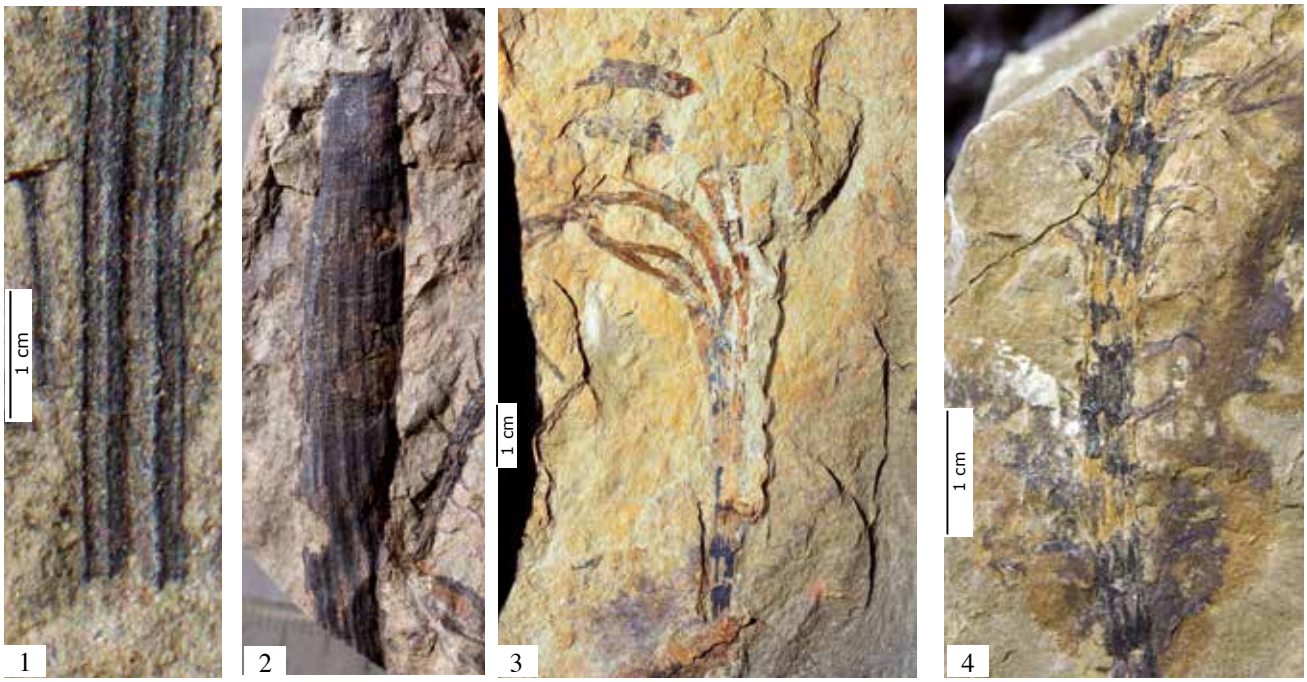
Lower Carboniferous (Serpukhovian) Floras

The plant fossils from the various sites in the Nötsch area in Carinthia are probably somewhat younger, probably deposited between the Upper Viséan and the older Serpukhovian (Upper Mississippian) (Amerom & Schönlaub 1992). In the sediments can be found more highly developed club moss plants, especially *Lepidodendron*, more rarely *Sigillaria,* widespread were also *Archaeocalamite*s horsetails, and various ferns, some of which had just relatively modern features, similar to those from the Upper Carboniferous, while others can be almost equated with ancestors from the Devonian time. Here too, as in the Hochwipfel formation, the presence of gymnosperms can be ruled out, even if only as Protogymnosperms.
The Slovak geologist and paleontologist Dionýs Štúr was the first to study the Nötsch Carboniferous (1871), where

The Oberhöher (Fischerhube) fossil site near Nötsch. There are found mainly brachiopods, trilobites and crinoids. From Koninck L. G. 1873. Fragment of *Calamites* (*Bornia radiata* = *Archeocalamites radiatus*). Oberhöher, Nötsch

he concluded that the age was Lower Carboniferous based on the presence of *Archaeo(calamites*) transitionis and *Lepidodendron veltheimianum.* In 1873, the Belgian paleontologist and chemist Laurent-Guillaume de Koninck was the first to depict the trunk of *Calamites* described as *Bornia radiata* from Nötsch.
F. Frech (1894) and P. G. Krause also suspected a Lower Carboniferous deposition due to the primitiveness of the plants

An extraordinarily well-preserved fern frond with the location name Nötsch (Pb/02/6/13). Old find in the Federal Geological Institute Vienna (Geosphere Austria). The *Lepidodendron* branch also comes from the same fossil site.



Archaeocalamites antiquus. Middle Devonian, Middle Eifelian. 1-2. Part of stems (LIND 153, LIND 252, Coll. Wachtler, Dolomythos); 3. Lateral branchlets (LIND 14); 4. Branchlets (LIND 504, both Coll. Pohl). Lindlar, North Rhine-Westphalia

and pointed out similarities with well known finds from the "Culm Fora" in the Rheinisches Schiefergebirge (Rhenish Slate Mountains) (Amerom & Schönlaub 1992). Shortly beforehand, first in 1875 with the processing of the "Mährisch-Schlesischen Dachschiefer" (Moravian-Silesian roofing slate) and two years later, in 1877, with the Culm flora of the Ostrava and Waldenburg layers, Dionýs Štúr (1827-1893) worked on these Lower Carboniferous floras, in an exemplary manner and until hardly surpassed in the present. It turned out that many plants, such as the Calamitaceae, which appeared in many subspecies later in the Upper Carboniferous, were particularly noticeable because of their rich foliage on the side branches with multiple splitting into slender leaf needles (Stur, 1875). Ferns such as the primitive multi-forked *Rhodea* (later changed to *Rhodeopteridium* by Zimmermann, 1959 because retained a synonym of a flowering plant), or the variety of delicate *Adiantites* ferns (Stur, 1877) can also be found in both - the Culm flora and the Eastern Alps.

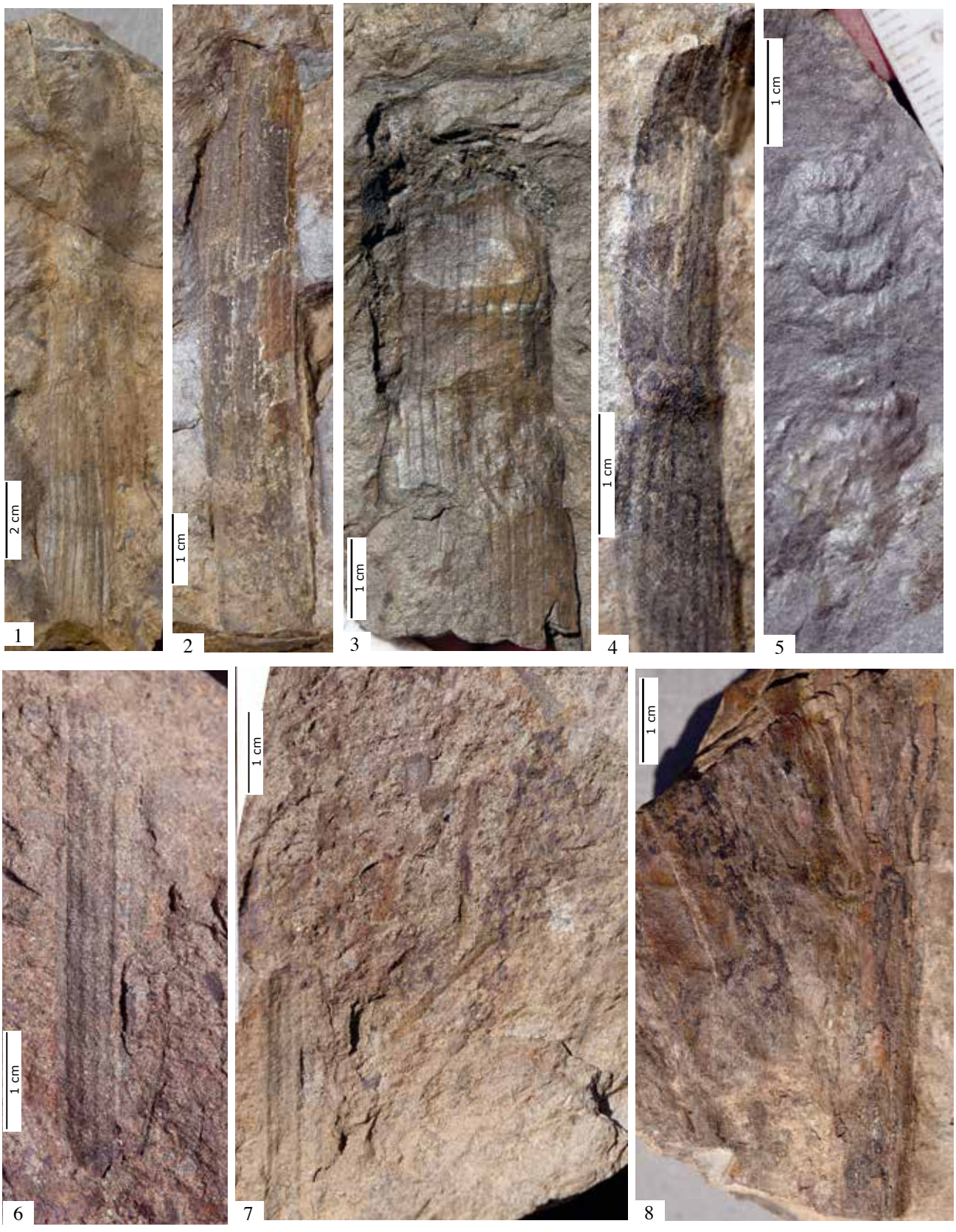
The Dutch paleobotanist Hendrick W. J. van Amerom, together with the Austrian private researcher Herbert Kabon (1999, 2000, 2003), dealt most intensively with the plant fossils around Nötsch, with their specimen finding their way into the Kärntner Botanikzentrum (Botanischer Garten), Klagenfurt (Paleobotanical collection of the Carinthian State Herbarium in Klagenfurt).

Calamitaceae

Most commonly found are the remains of precursors of the Calamitaceae, which later appeared in many subspecies in the Upper Carboniferous of the Eastern Alps. This group of plants, which only have distant similarities with today's horsetail genus *Equisetum,* developed from the Middle Devonian (Eifelian, approx. 390 million years ago) with *Archaeocalamites antiquus* (Wachtler 2023b). It appears that the most ancestral lineage of *Calamites* is found in the homosporous lycophytes, while the Equisetes species known today diverged probably from ancestral ferns.

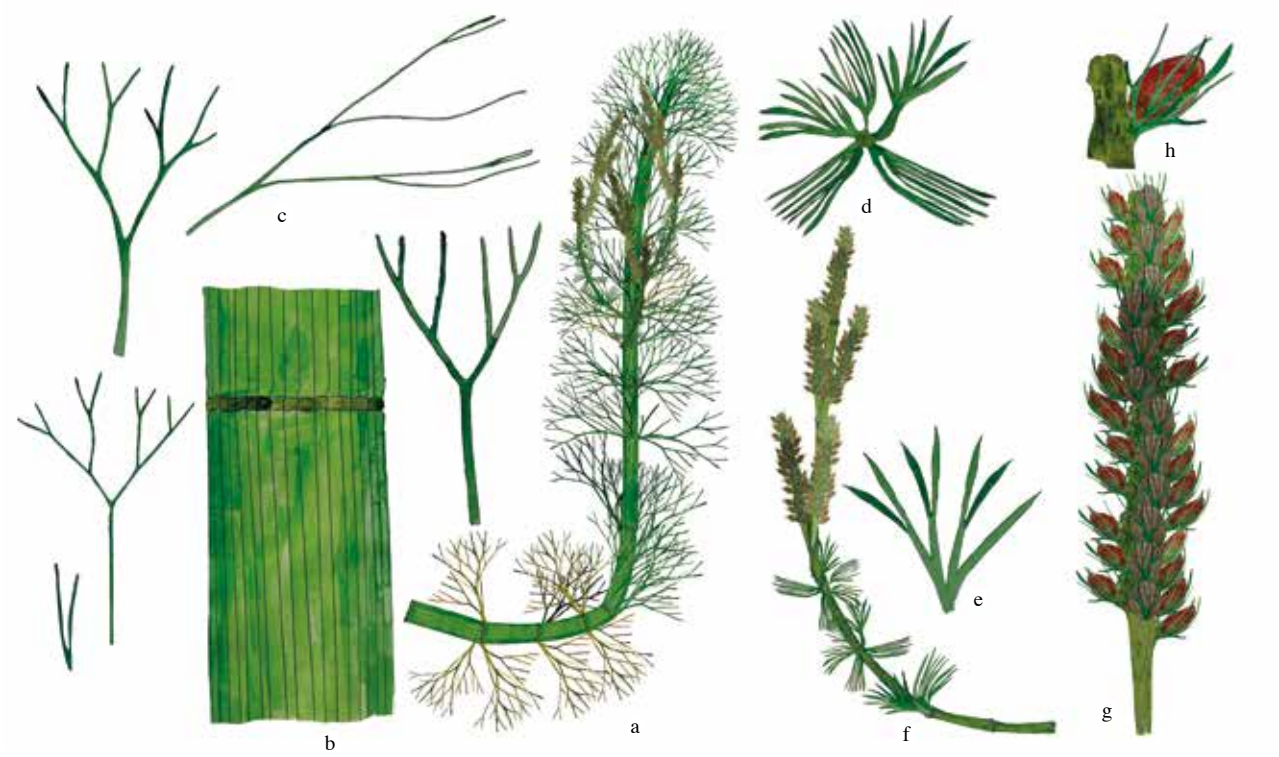
In the Lower Carboniferous, especially in the Hochwipfel Formation, the Calamitaceae were among the dominant recovered fossil plants due to their hard stems. However, today exist a nomenclatural confusion, based on different descriptions for trunk parts, side branches and spore cones (Taylor et al 2009).

This will not be discussed here, although the name *Archaeocalamites* will be confirmed



Early Carboniferous horsetails from the Eastern Alps (Viséan), ***Archaeocalamites radiatus***

1-2. Stems (MAR 10, MAR 16); 3. Part of a stem with internodes (MAR 12); 4. Stem with scars of the lateral branchlets (MAR 32); 5. Sporangiophore (MAR 09); All Marinelli-Hat); 6. Part of a stem (TRÖP 08); 7. Stem with fertile cone (TRÖP 06); 8. Stem (TRÖP 24) Tröpolacher Almweg; Coll. Wachtler, Dolomythos-Museum



Early Carboniferous horsetails (Viséan-Serpukhovian), *Archaeocalamites radiatus*

a. Plant with sporangia; b. Trunk part; c. Detail of the leaves; d. Leaf whorl on a lateral branchlet; e. Detail of a side branch leaflets; f. Branchlet with cones; g. Cone; h. Detail of a sporophyll

for fossil plants resembling horsetails from the Devonian to the Lower Carboniferous, while *Calamites* is used for those from the Upper Carboniferous to the Upper Permian. The Calamitaceae were later among the big losers of the Permian-Triassic crisis and died out without leaving any descendants. From this point onwards, the triumph of today's horsetails began with the fossil genus *Equisetites* and today's *Equisetum*.

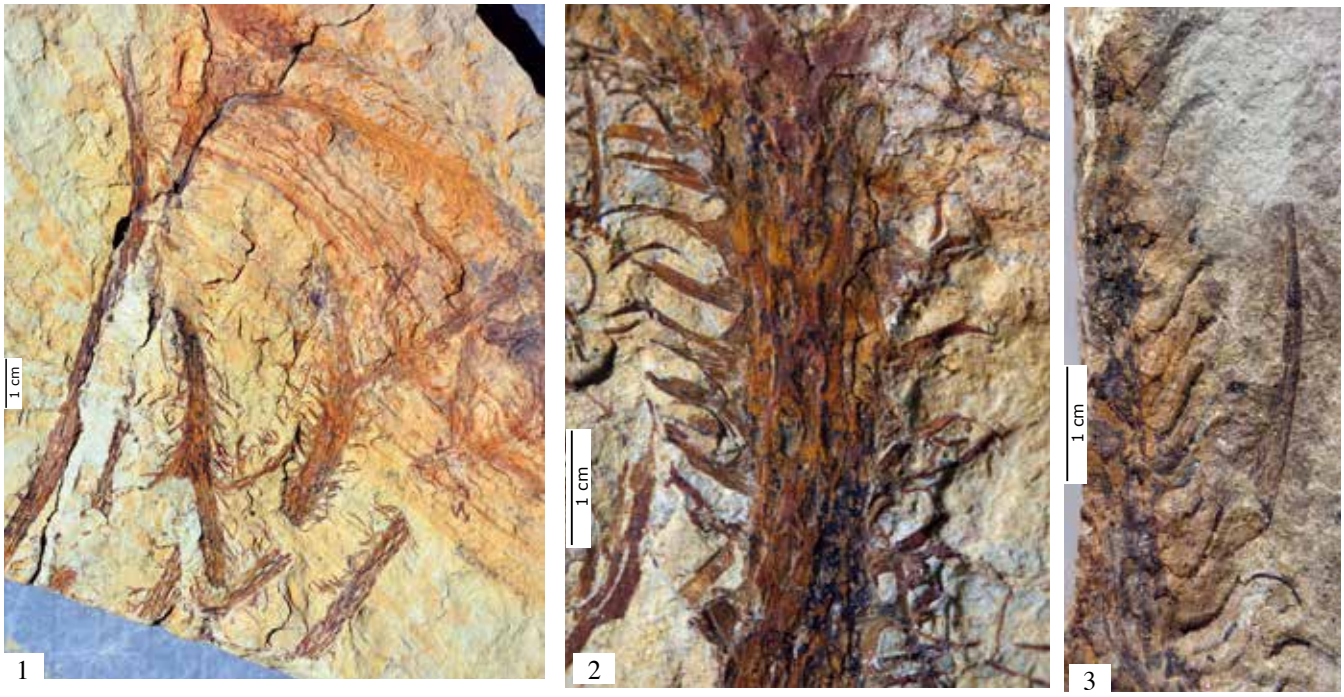
Their classification as a separate genus *Archaeocalamites* is justified by their longitudinal grooves running straight through the nodes and their multi-forked leaf needles. In the later ones, the grooves on the internodes continued slightly displaced and therefore forked manner, while the laminas on the side branches became leaf-shaped and were classified as *Annularia* (Amerom & Schönlaub, 1992; Amerom & Kabon 1999, Amerom & Kabon, 2003, Kabon & Schönlaub 2019). The predominant species in the Viséan was *Archaeocalamites radiatus*. Originally described by Adolphe Brongniart in 1828 as *Calamites radiatus,* the Slovak paleontologist Dionýz Štúr recognized, based on finds in the also Lower Carboniferous Culmflora (Moravian-Silesian region) that the differences to *Calamites* made it sensible to establish a separate genus (1877).

Whether the evidence from the Culm flora is conspecific with that from the Eastern Alps is uncertain due to its fragmentary nature. Meanwhile the name *Archaeocalamites radiatus i*s used both for those from the Hochwipfel formation and by Nötsch for trunks reminiscent of horsetails and forked long leaf needles of the secondary branches, although it would be appropriate in future to classify the slightly younger ones as a separate species. There appear to be differences in the fertile organs, with most having a sporangia surrounded by forked leaf needles. It appears that some have two interconnected and inversely hanging sporangiophores, where the name *Archaeocalamites transitionis* might probably be useful here.

All other names used for individual plant parts only cause confusion and do not lead to any useful results. The forked leaf whorls are most likely to be recognized in the somewhat younger Steinach flora (Bashkirian-Moskovian) in *Calamites steinachii* (Wachtler, 2025a). They then

Early Carboniferous horsetails from Eastern Alps (Viséan-Serpukhovian), ***Archaeocalamites radiatus***

1. Part of a stem (Nöt 12B); 2. Part of a stem (Nö 6/1-BPB 2003); 3. Stem (Nö 6/2); 4-5. Stem with lateral branches (P8-1B-BPB 38, NöP 18/A-BPB 1932); 6-7. Secondary branchlet whorls (Nöp97A, Nöp 28A-BPB 1947); 8. Lateral branchlet (HeG 42A-BPB 1989); 9. Suggested cone with bipartite sporangia (NöP 15A-BPB 1923); Ex. Coll. H. Kabon, Kärntner Botanikzentrum (Botanischer Garten), Klagenfurt



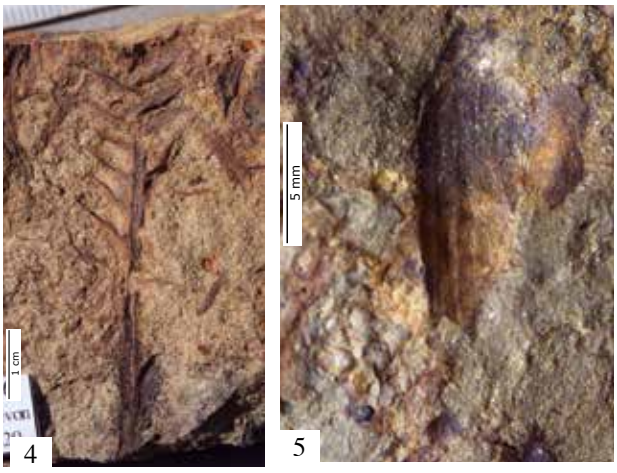
Protolepidodendron leschii. Middle Devonian, Middle Eifelian, 1.-2. Branchlets with partially furcating or not leaf needles (LIND 02,LIND 510, both Coll. Pohl); 3. Cone (Holotype LIND 88, Coll. Wachtler, Dolomythos-Museum); Lindlar, North Rhine-Westphalia

disappear towards the Upper Carboniferous and are no longer noticeable in the most known plant from the Kronalpe in Carinthia, *Calamites multiramis* (*Annularia stellata*), as well as others from these areas (*Calamites carnicus, Calamites microphyllus*) (Wachtler, 2023b).

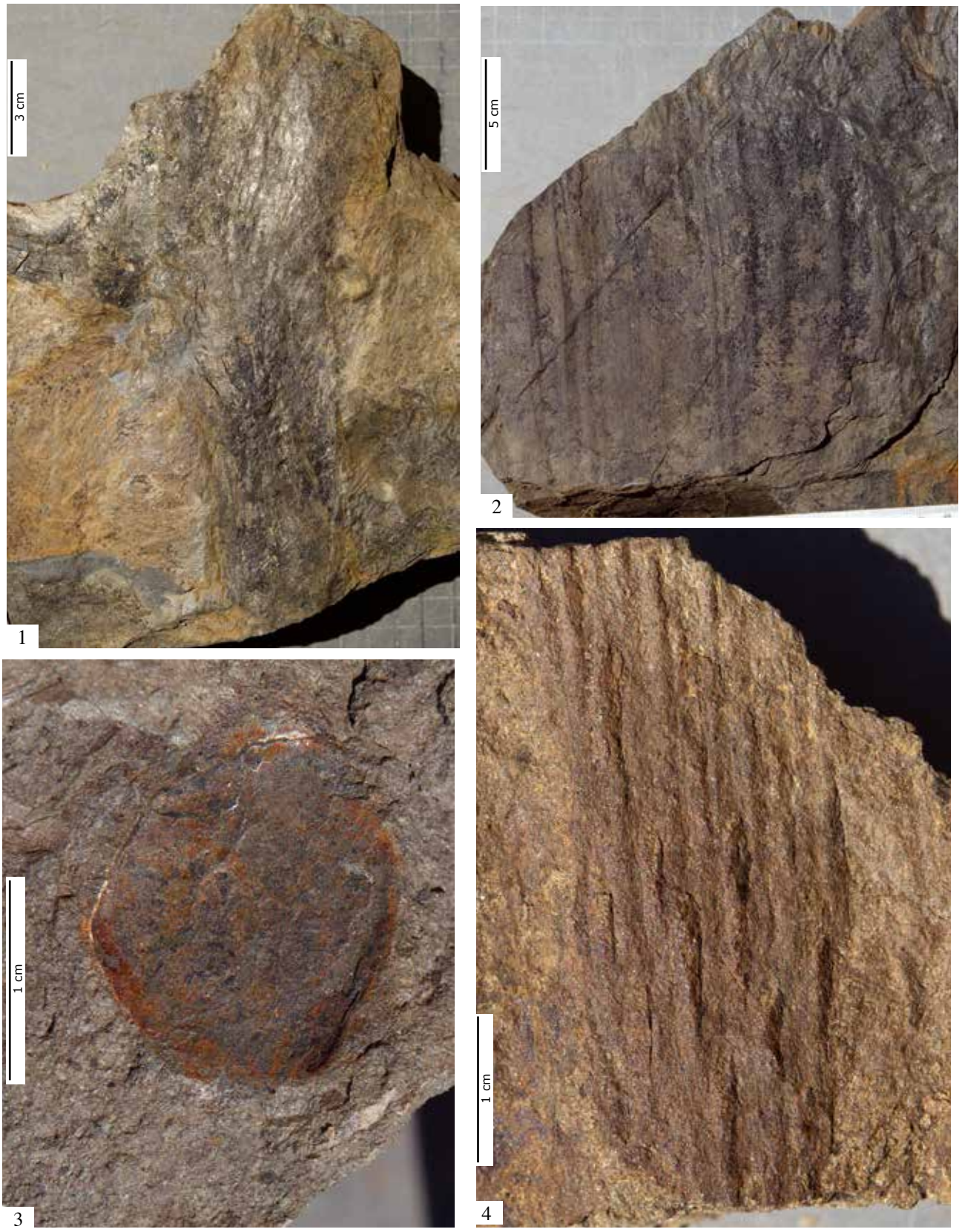
Lycophytes

At least two *Lepidodendron* species and one Sigillaria were probably present within in the club moss trees in the Lower Carboniferous. This can be deduced from the distinctive and meaningful leaf cushions on the trunks of *Lepidodendron* and *Sigillaria*, and even more due to two different *Lepidodendron* cones and the megasporangia of *Sigillaria.* One, *Lepidodendron jostenii,* first described from Hermsberg near Bad Bleiberg, is characterized by bifurcated leaf cushions and was recombined instead of *Eleutherophyllum jostenii* (Amerom & Kabon, 2003). The fertile cones consist of bracts attached almost vertically to the axis, which bend sharply upwards halfway through. The fertile scales are firmly attached to the axis and are pressed together close to the cone. Similar cones are known from the Upper Carboniferous as *Lepidodendron fritzii* (Wachtler 2023).

Another species *Lepidodendron lossenii* developed bracts about 6 cm long and over 1 cm wide with a prominent central vein. The sporangia were kidney-shaped at the lower end. Descendants are *Lepidodendron alpinus*, which occurred in the early Upper Carboniferous and is particularly well known from the fossil sites Steinacher Joch in North Tyrol and Tomritsch in Carinthia (Wachtler 2025).



Archaeosigillaria lindlarensis. Fertile and sterile parts. Middle Devonian, Middle Eifelian. 4. Mature strobilo with a shed sporophyll (LIND 146); 5. Sporophyll with squeezed spores (LIND 69); All Coll. Wachtler, Dolomythos



Early Carboniferous clubmoss from the Eastern Alps (Viséan)

1. Lepidodendron lossenii. Apical part of a stem (MAR 13; 2. *Archaeosigillaria* or *Lepidodendron* sp. Big part of a stem (MAR 15) both Rifugio Marinelli; 3. *Archaeosigillaria* sp., macrosporangia(TRÖP 11); 4. *Archaeosigillaria* sp., Apical part of a stem (TRÖP 20); Both Tröpolacher Almweg; Coll. Wachtler, Dolomythos-Museum

Early Carboniferous clubmoss (Viséan-Serpukhovian). ***Lepidodendron, Sigillaria***

1. Trunk of Lepidodendron or *Sigillaria* (He D 14); 2. Stem of *Lepidodendron* (Nöt 12A); 3-4. *Lepidodendron jostenii* (Synonyms: *L. lycopodioides, L. veltheimianus*). Lateral branchlets (Nöt 16A); 5-6. Stem of *Lepidodendron jostenii* with furcating leaflets (He G 40); 7. Trunk of *Sigillaria* (Ep 7-1); Ex. Coll. H. Kabon, Kärntner Botanikzentrum (Botanischer Garten), Klagenfurt

Lepidodendron, cones

1-2. Cone belonging possibly to *Lepidodendron jostenii* (Nöt 6A-BPB 60); 3. Sporophyll of an other *Lepidodendron* species (Nöt 11A-BPB 59), Coll. H. Kabon, Kärntner Botanikzentrum (Botanischer Garten), Klagenfurt

Giant club moss trees in the Lower Carboniferous

Even if it seems difficult to understand, there were considerable differences in the lycophytes of the Eastern Alps throughout the Carboniferous period. ***Sigillaria parallela:*** a. Whole tree; b. Cone; c. Sporophylls with micro- und macrosporangia; ***Lepidodendron alpinus:*** d. Tree; e. Cone f. Homospore sporophyll; ***Lepidodendron josteni:*** e. Tree; Cone, g. Homospore sporophylls

Early Carboniferous ferns (Viséan) *Rhodeopteridium leptofoliatum*

1. Frond with sporangia and detail (MAR 18); 3. Apical sporangia (MAR 33); 4. Branchlet with sporangia (MAR 20); 5-6. Various sporangia (MAR 06); 7-9. Various branchlets (MAR 18, MAR 17, MAR 03); All Rifugio Marinelli, Coll. Wachtler, Dolomythos

***Rhodeopteridium sp*. (Viséan-Serpukhovian). Nötsch**

1. Frond (Nöp 6), 2. Frond (Nöp 10); 2. Frond (Nöp 41), 3. Frond (nöp 41) Ex. Coll. H. Kabon, Kärntner Botanikzentrum (Botanischer Garten), Klagenfurt

Of today's ferns, J*amesonia* offers the greatest comparison possibilities.

Jamesonia flexuosa. 4. Frond. 5. Single pinnula with clusters of sporangia

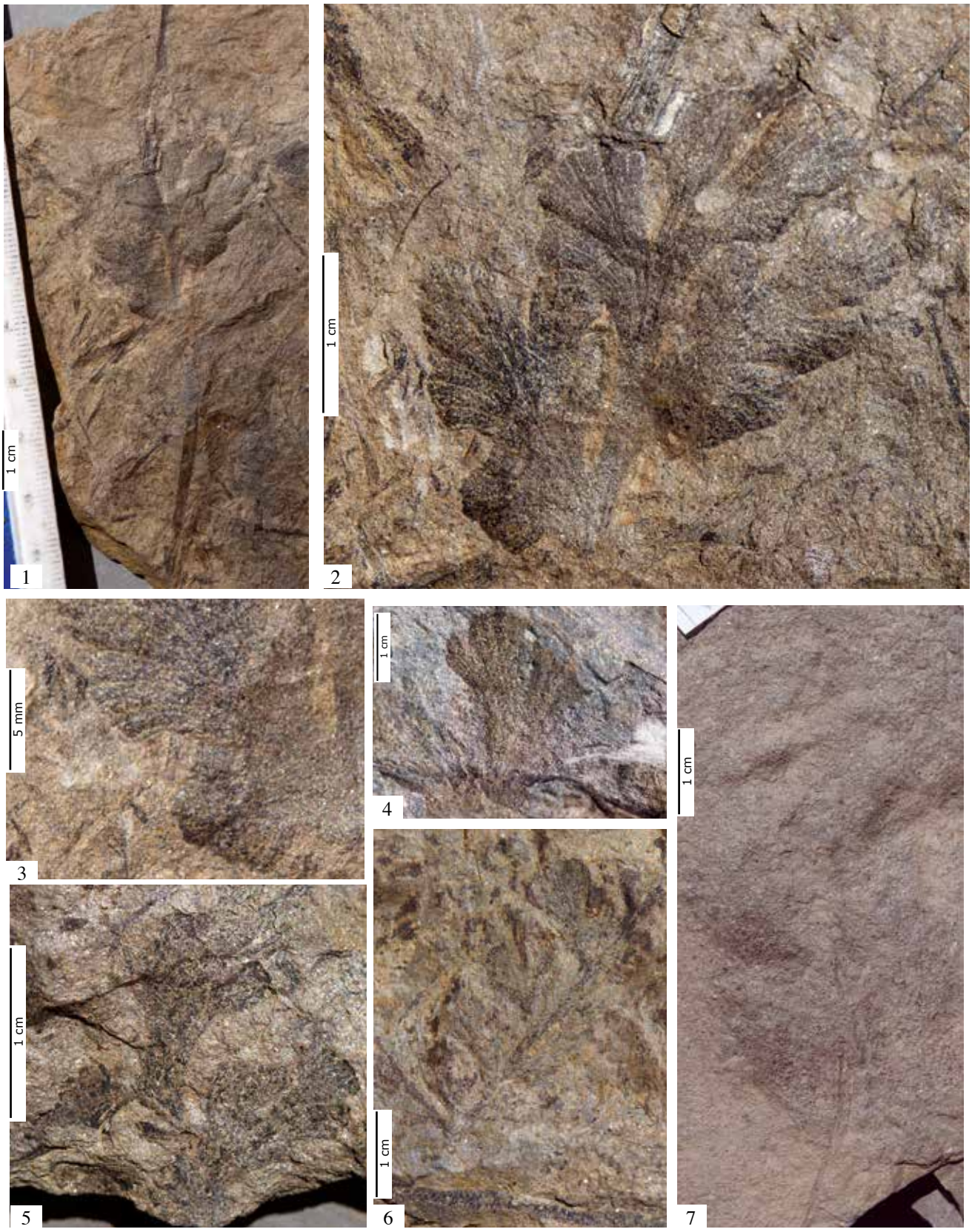
At least one *Archaeosigillaria* species was also developed, which is documented by rounded leaf scars on the trunks and the typical rounded sporophylls. It is likely to point in the direction of *Sigillaria parallela,* which occurred in large numbers in these areas in the Upper Carboniferous.

Since in the oldest deposits in the Eastern Alps, near the Rifugio Marinelli, there are trunks with a diameter of 20 cm, these are likely to have developed into giant club moss trees within a geologically short period of time from the Upper Devonian to the oldest Lower Carboniferous. They achieved in the Upper Carboniferous a massive growth habit that was never thought possible and dominated the landscapes of the northern hemisphere for several million years.

Based on the finds obtained so far, especially the fertile organs, it is certain that at least three giant clubmosses were developed in the Lower Carboniferous of the Eastern Alps, but there are considerable gaps in their appearance or their ecological niche, which should be closed by increased finds.

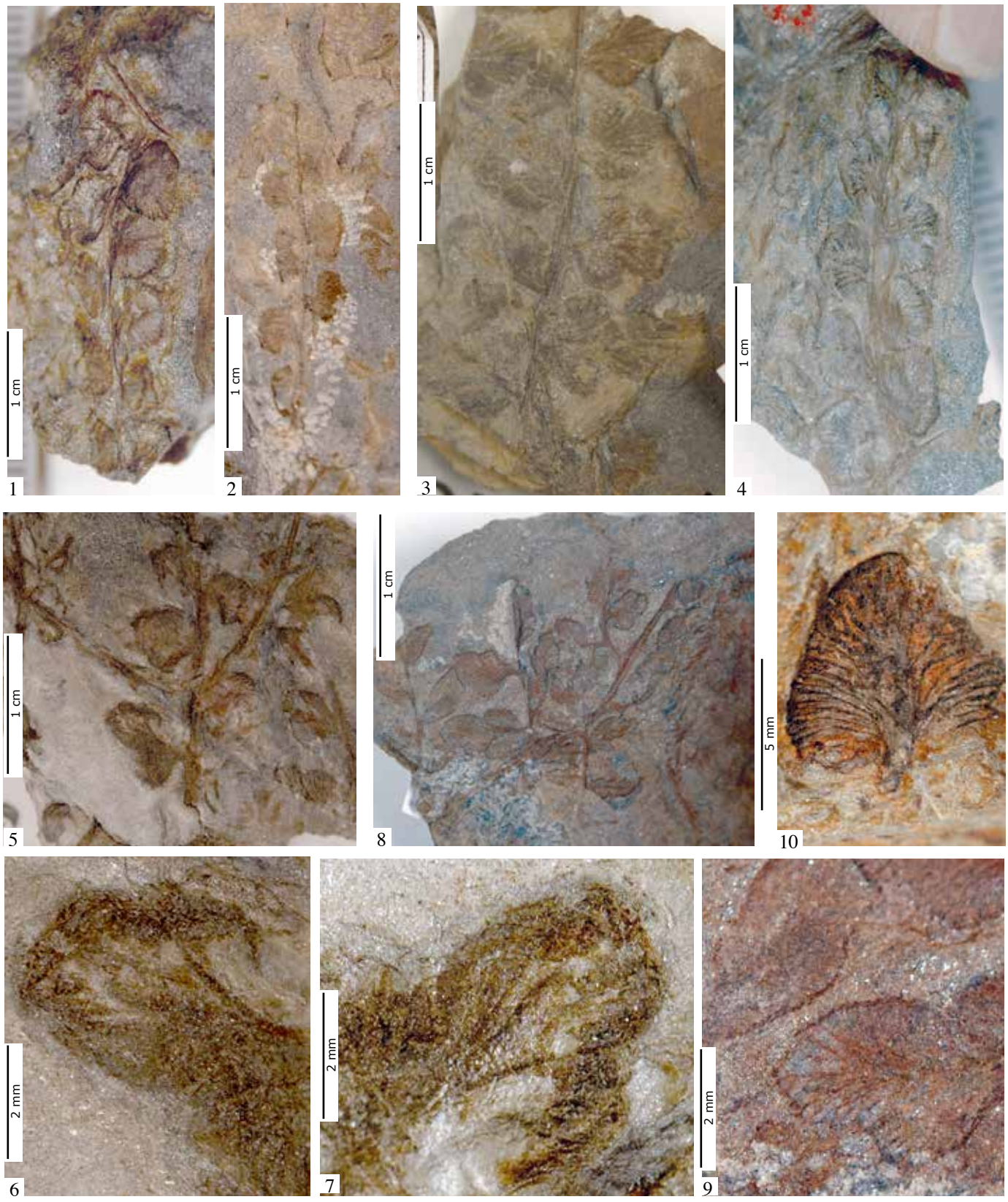
Ferns

In addition to the horsetails and clubmosses, ferns played an important role in the Lower Carboniferous of the Alps. In the Upper Carboniferous, there were already recognizable ancestors of now widespread groups such as *Osmundites, Cyatheites, Dicksonites, Platycerites, Danaeites*, endings for fossil plants introduced in paleobotany, with presumed evolutionary lines to modern ferns such as Cyathea, Osmunda, Dicksonia, Platycerum or Danaea. The *Callipteridium* ferns are somewhat out of place in the Carboniferous, although family relationships with the modern Schizaeales can be assumed, and Cyclopteris with possible close relationships to the Dryopteridaceae.



Early Carboniferous ferns (Viséan). ***Adiantites dijkstrae***

1-3. Frond and detail, as well part of a fertile pinnula (MAR 01); 4-6. Several fronds with partially segmented with pinnules (MAR 18, MAR 27, MAR 16);7. Fertile frond (MAR 11); all Coll. Wachtler, Dolomythos-Museum



Early Carboniferous ferns (Viséan-Serpukhovian). ***Adiantites flabellifolium***

1-4. Frond and leaflets (Nöp 37, Nöp 17, BPB 19474, Nöp 38); 5-7. Fertile frond and details of the sporangia (Nöp 35, designed holotype); 8-9. Fertile frond, upper view (Nöp 52); 10. Single pinnula (Nöt 24) Ex. Coll. H. Kabon, Kärntner Botanikzentrum (Botanischer Garten), Klagenfurt

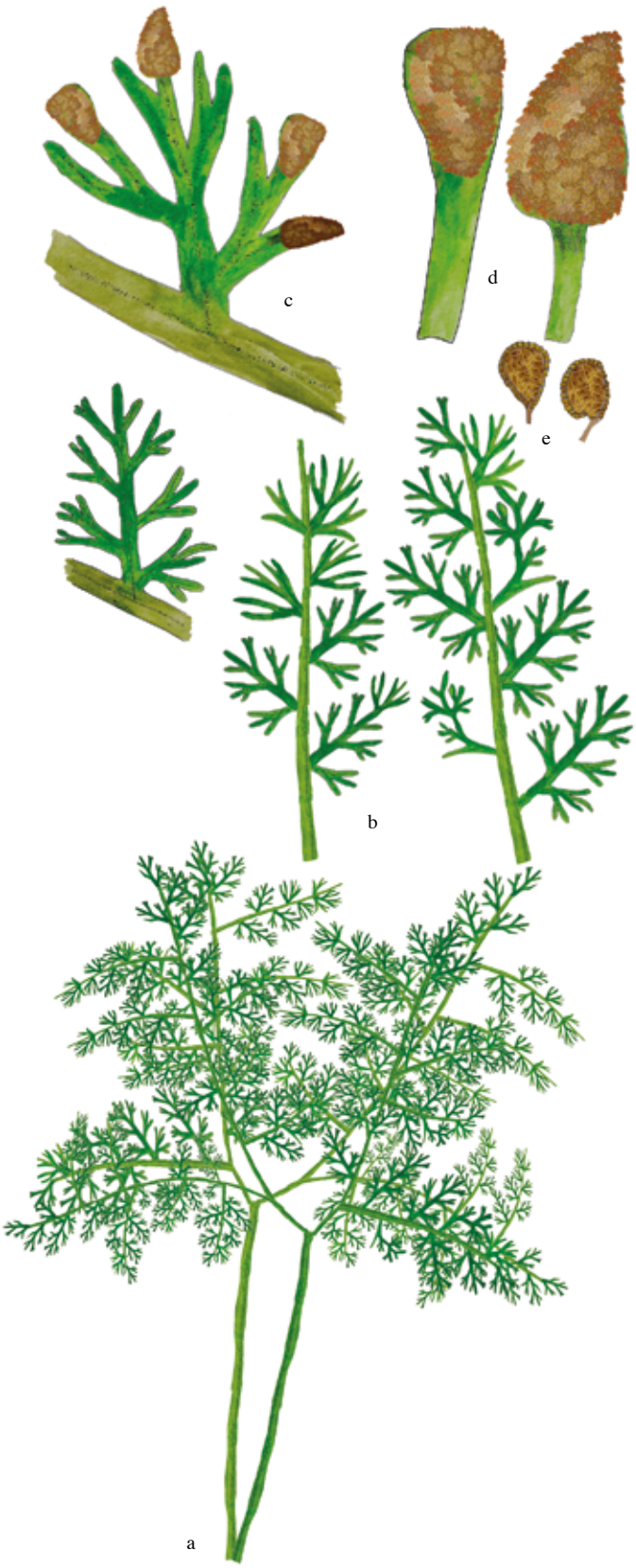
One would have to assume that the geologically relatively short period of time from the earliest Upper Carboniferous (Bashkirian-Moskovian) with its diversity of ferns in the Alps and the plants deposited between the Serpukhovian and the Viséan, a time difference of approximately 20 million years, would allow interpretations about family relationships. While this is easily possible with *Calamites* and the clubmosses *Lepidodendron* and *Sigillaria*, even though they are now extinct, the classification of ferns is more difficult.
Since it can be assumed that the fern precursors from the Upper Carboniferous did not appear out of nowhere or migrated from distant areas, but rather developed from precursors from the Lower Carboniferous, the evolutionary lines should be searched for through mimicry work and precise research. Remaining on artificial terms introduced over the decades such as *Pecopteris, Neuropteris, Sphenopteris, Alethopteris, Mariopteris, Alloiopteris, Corynepteris* and many others would be counterproductive.
The fundamental task of paleobotany should be to trace evolutionary lines based on milestones up to the present day, which is possible in many cases. Future research will then have a relatively easy opportunity to revise and complete these classifications.
It should be noted that in the Lower Carboniferous there are still some transitional floras between the Middle Devonian and Carboniferous, and although interpretations are possible, in some cases they cause difficulties.

Rhodeopteridium Zimmermann 1959

The most primitive features of all fern-like species are exhibited by a plant that is relatively common both in the Viséan of the Marinelli-Hat and in the somewhat younger deposits of the Nötsch Carboniferous, which found its way into science as *Rhodeopteridium.* It was originally described by Walter Zimmermann (1892-1980) in his 1959 work *"Phylogenie der Pflanzen"* (Phylogeny of Plants) as a paradigm of his *"Übergipfelungstheorie"* known also as theory of telomes. This explains that originally equivalent shoots are divided into main axes and lateral minor axes, with the former overgrowing the latter due to larger growth impulses. In the next phase, called pinnation, the side axes align themselves in a plane using connecting leaf material.
Stur (1877) described a wealth of *Rhodea* species from the Culm flora of Germany, all of which were characterized by their dichotomous leaf needles. Walter Zimmermann changed the original name for the fossil plant *Rhodea* (p. 274-28, p. 727, Fig. 139 B) to *Rhodeopteridium* because in 1806 the German botanist Albrecht Wilhelm Roth had first described a recent flowering plant as *Rohdea* and the similarities in pronunciation seemed too confusing. Out of respect for the great German paleobotanist, this should be accepted.
Although the genus *Sphenopteris* from the Carboniferous-Permian has some similarities, it can only be considered a vat of many fern-like species without knowledge of their fertile organs.
Three species have been described from the Lower Carboniferous of the Rifugio Marinelli (Amerom et al, 1984), of which two (*Rhodeopteridium aphlebiotum, Rhodeopteridium leptofoliatum)* were classified as new. Here the somewhat more common species *Rhodeopteridium leptofoliatum* (leptus = thin, foliatus with leaves, i.e. *Rhodeopteridium* species with thin leaves is preferred), and the second is considered a synonym.
Its simple axis system is characteristic, with the narrow, long leaf needles either forking in the summit area or simply ending undivided. Interestingly, sporangia cover the apical area. These appear, where visible, as ring-shaped structures with thickened radial and basal walls, an annulus, that contains the spores inside, which indicates modern features within the ferns.
One could argue that in the early Upper Carboniferous, *Platycerites haeckeli,* a small-growing fern (Wachtler, 2025), particularly widespread on the Steinacher Joch near the Brenner, can be accepted as the oldest ancestor of today's staghorn ferns (Platycerium). It was followed by *Platycerites boersmai* (Wachtler, 2023) in the Upper Carboniferous with larger and flat leaves. All of them have widespread sporangia encrustations, preferably on the upper section of the lamina. In the Middle Triassic (Erfurt Formation, Ilsfeld, Baden Württemberg) there are more developed forms with *Platycerites*

***Adiantites flabellifolium*. Early Carboniferous**

a. Whole plant; b. Frond part; c. Single pinnula; d. Fertile frond part; e. Fertile pinnule with sporangia; f. Sporangia



***Rhodeopteridium leptofoliatum*. Early Carboniferous**

a. Whole plant; b. Various individual pinnae; c. Fertile pinnules; d. Apical part of a pinnula with sporangia encrustations; e. Sporangia

(Rhacophyllum) crispatum, or *Platycerites (Rhacophyllum) phachyrrhachis* (Wachtler, 2016), which all can be regarded as being precursors of the Platycerium fern genus.
However, intensive analysis reveals considerable differences that exclude a lineage of *Rhodeopteridium* ferns from the staghorn ferns. These are their sprawling fronds and their relatively delicate leaf blades. However, there are extensive similarities among today's ferns with *Jamesonia,* a fern widespread in the Neotropics of America in around 50 subspecies. Their dichotomous primitive leaflets and sporangia would suggest this.

Adiantites Göppert 1836

Research history

1836 Adiantites oblongifolius Göppert p. 227, Pl. XXI Fig. 4-5

1865 Adiantum antiquum Ettinghausen p. 22, Fig. 1, Taf. VII Fig. 1

1877 *Cycadlopteris antiqua* Stur Pl. XIII fig. 2-4

1877 *Adiantides antiquus* Stur Pl.VI, fig. 4-6; Taf XVII, Fig. 3-4

A common and modern-looking fern from the Lower Carboniferous is represented by Adiantites. It was first mentioned and illustrated by one of the great paleobotanists of the 19th century, Heinrich Robert Göppert (1800-1884) in his monograph (1836) *„Fossile Farnkräuter*" (Fossil Ferns) (p. 172, p. 216, *Adiantites oblongifolius* Pl. XXI Fig 4-5). Göppert named more than 20 different species, which ranged from the Carboniferous to the Jurassic, and originally also included fossil ginkgoes from the Jurassic. However, classification often proved problematic due to the extensive lack of images of the fertile leaflets. In 1865, Carl von Ettinghausen published ferns from the Moravian-Silesian Dachschiefer as *Adiantidum antiquum,* while D. Stur again set a milestone (1877) by publishing a large number of well-preserved *Adiantites* fronds from the same layers. Stur named another genus, *Cycadopteris antiqua,* pointing out on plate XIII, Fig. 3, pointed out *"the impression of the folded edge of the leaf"*, a characteristic feature of today's Adiantum ferns.
Another similar genus was described by the Swedish botanist Alfred Gabriel Nathorst (1850-1921) in 1914 from the Spitsbergen Carboniferous as *Cardiopteridium spetsbergense*, and mentioned in the same treatise other *Adiantites* ferns. Amerom et al, 1984, based themselves on this genus when they published the Lower Carboniferous flora of the Marinelli-Hat in the Italian Eastern Alps. They added additionally a new species *Cardiopteridium dijkstrae.*
Since today's Adiantum ferns have peripheral sori and sporangia under a bent edge, just like those found in the Lower Carboniferous of the Alps, and even the circular to fan-shaped leaflets have similarities, the name *Adiantites*, coined by Göppert in 1836, is preferable. Therefore, those from the Rifugio Marinelli are recombined as *Adiantites dijkstrae.* On the other hand, the relatively numerous ferns found in the somewhat younger Nötscher Carboniferous are now renamed as A*diantites flabellifolium*.

Order FILICALES Bower, 1899

Adiantites dijkstrae (van Amerom, Flajs, Hunger 1984) comb. nov.

Research history

1984 *Cardiopteridium dijkstrae,* van Amerom, Flajs, Hunger, p. 19, Fig. 17. pl. VIII, Fig. 1-9, 13, 14, 17

Last order fronds up to two centimeters long, segmented several times and thus appear to be smaller leaflets. Rounded to slightly elongated, venation of the lamina visible, dichotomizing once or twice. Fertile pinnae folded over at the edges. Sporangia located at the edge with annulus.

Adiantites flabellifolium n. sp. Wachtler 2025

Research history

2003 *Cardiopteridium dijkstrae*, van Amerom & Kabon p. 545. pl. VI, Fig. 3, 3a

Etymology

From the Latin "*flabellum*" for fan and "folium" for "leaf". Fan-shaped leaflets.

Holotype

Nöp 35 (fertile part of a frond; Ex. Coll. Herbert Kabon, Coll. Kärntner Botanikzentrum (Botanischer Garten), Klagenfurt


1


2


3

Today's ***Adiantum***-Maidenhair fern. ***Adiantum raddianum*** (Central America, Caribbean) 1. Frond; ***Adiantum polypyllum,*** (Guatemala, Columbia, Venezuela, Trinidad and Tobago), 2. Fertile frond 3. Detail of pinnula sori located on the edge

Diagnosis

Fronds with pinnate leaflets. Sori sitting on the edge of the folded pinnae.

Description

Whole plant: Fronds tri-pinnate, petioles of the last order notched in the middle and dividing several times (NÖP 52). Pinnules, about 5 mm long, slightly less wide, rounded to ovoid, partly conically bulbous (Nöp 37, Nöp 17, BPB 19474, Nöp 38). Veinlets arising from a pseudo-midrib and dividing once or twice.
Fertile pinnae: Like the sterile ones, sporangia are located on the bent edge of the blade (Nöp 35). Spores are located within a closed annulus, which opens when ripe.

Remarks

Adiantites flabellifolium represent one of the most interesting plants of the entire Alpine Carboniferous, although surprisingly its occurrence is limited to the Lower Carboniferous, while it has never been found in the plant rich Upper Carboniferous sites of the Eastern Alps. It is astonishing that their delicate pinnules and fronds have been preserved in greater numbers (Amerom & Kabon 2000, 2003), while far more robust ferns occur in smaller quantities. Already Amerom et al. (1984) noted that they are the most common at the Marinelli-Hat after *Calamites,* although it should be noted that *Sphenopteridium cf. silesiacum* is probably a synonym due to its similarity. This can also be confirmed for the sites around Nötsch.
In other occurrences (Nathorst, 1914, Zhao & Wu, 1982), which have been described under a wide variety of names such as *Cardiopteridium, Cardiopteris, Sphenopteridium*, it is important to determine whether the fertile pinnules have sporangia located at the edges or whether they have to be classified elsewhere. Similarities with *Adiantites* can be found in the early Middle Triassic with *Wachtleria nobilis* (Kandutsch, 2011), which also developed marginal spores, but may be placed in the direction of the Lindsaea ferns.

Praecallipteridium Wagner 1963

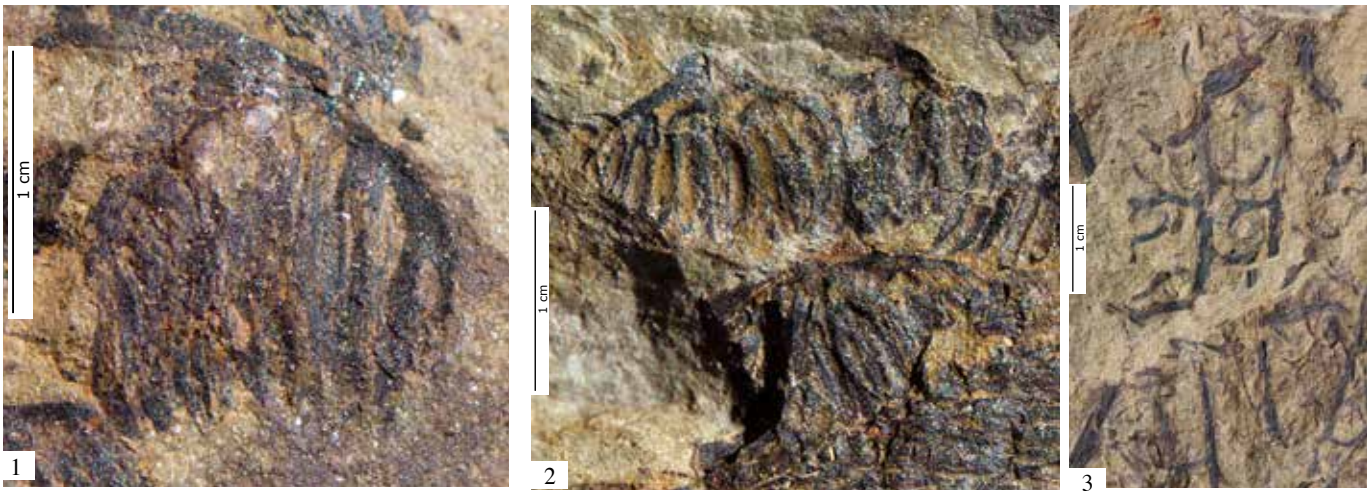
Research history

1963 *Callipteridium (Praecallipteridium) armasi* (Zeiller) Wagner p. 721

1966 *Callipteridium (Praecallipteridium) armasi* (Zeiller) Wagner p. 7103-106, pl. 17, fig. 37, pl. 18 figs. 38-39, pl 21 fig. 46

1999 P*raepecopteridium parvifolium* Van Amerom & Kabon, p. 656-661, pl. 8, f. 1, la; p. 12

2000 *Praepecopteridium parvifolium* Van Amerom & Kabon Pl. 11, Fig. 1, la; Pl. E 1



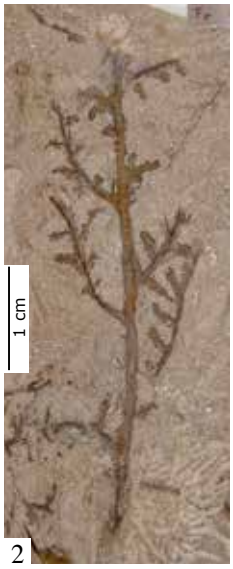
Protopteridium philippae. Middle Devonian, Middle Eifelian. 1-2. Aggregation of various sporangia (LIND 115, LIND 111); Typical bifurcate leaf telomes of the first fern like plants (LIND 153); All Coll. Wachtler, Dolomythos); Former Collection of Manfred Fuchs and Alice Philipp in the BGS-quarry, Lindlar

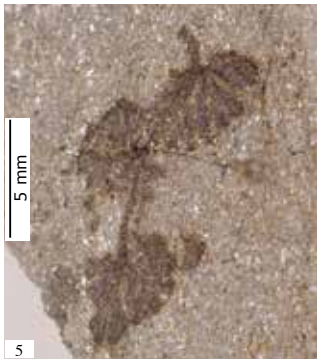
Another interesting fern species is *Praecallipteridium parvifolium,* although here too the history of research needs to be discussed. Their family represents one of the most peculiar and long-lived fern genera, which dominated the landscape from the Carboniferous through the Permian, the Triassic and the Jurassic and was often classified among the so-called seed ferns. The best known name is Peltaspermales. They represent bell-shaped to umbrella-like fertile aggregates, with separate sterile fronds which over the course of millions of years and even within the same plant could vary from tongue-like to smallsized pinnulas. Finally the name *Callipteridium* (Weiss, 1870) was used for species from the Upper Carboniferous, for Permian representatives *Lepidopteris* (Schimper, 1869) and also *Peltaspermum* (Harris, 1937), in the Triassic prevailed the name *Scytophyllum* (Bornemann, 1856) and in the Jurassic *Thinnfeldia* (Ettingshausen, 1852) (Wachtler, 2024h). All of them were characterized by separate, sterile foliage and completely different sporophyll fronds.

The thousands of finds from the Upper Jurassic, especially from the Pechgraben fossil site in Upper Bavaria, were a milestone, because all essential parts were found in connection and so the appearance of these ferns could be reconstructed and demystified (Wachtler, 2024h).

In the Eastern Alps, this fern occurs abundantly in the early Upper Carboniferous (Bashkirian-Moskovian) (Steinach flora on the Brenner) as *Callipteridium wachtlerae* (Wachtler, 2025) and in the late Upper Carboniferous (Kasimovian-Gzhelian) as *Callipteridium ameromi* in the Nockberge and on the Kronalpe. Therefore it can be supposed to find earlier development lines from the Lower Carboniferous. A species first described in the Nötsch Carboniferous as *Praepectopteridium parvifolium* (van Amerom & Kabon, 1999) is ideal here. However, since the Carboniferous fern genus *Pecopteris* is a repository for a multitude of small, dichotomizing pinnules without any information about their fertile organs, it would be more appropriate to prefer the genus *Praecallipteridium* introduced by R. H. Wagner (1963) and thus change the name to *Praecallipteridium parvifolium.* In the Culm Flora, leaves and even fronds of similar characteristics occur as *Neuropteris antecedens* (Stur, 1877). All of them show somewhat smaller but still similar fronds compared to those from the Upper Carboniferous.

The main feature is their smooth-edged, elongated pinnules, which are usually slightly to extremely pointed upwards. Their delicate nerves branch off in large numbers and close together from the center of the pinnae, only to fork once or at most twice to the middle. Their sporophyll carriers consist of a large number of tightly fused, pointed sporangia tubes. The sporangia formed therein are composed of an annulus, with the spores inside being thrown out when ripe. Here there are interesting connections to similar bell-like sporangia structures from

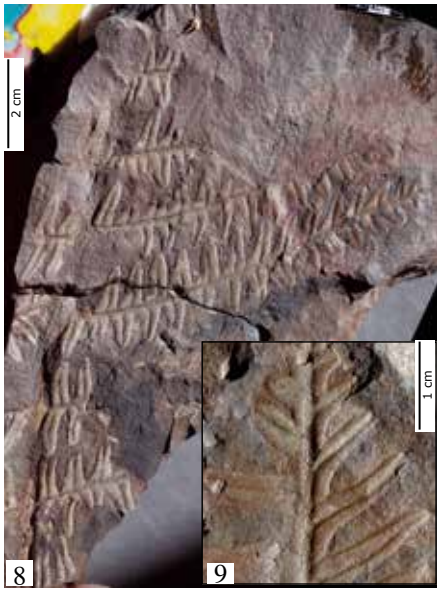




***Praecallipteridium parvifolium* (Viséan-Serpukhovian)**

1. Frond (He G7, Holotyp, Amerom & Kabon, 1999), 2. Frond (He G 18), 3. Part of a frond (Nöp 10); 4-5. Sporangia (HeG 35, He G3); Ex. Coll. H. Kabon, Kärntner Botanikzentrum (Botanischer Garten)

Today's ***Schizaea***-ferns. ***Schizaea pectinata*** (Eastern USA, Chile, Pacific) 6. Fertile frond upper view; ***Anemia mexicana*** 7. Sporo- and tropophylls



Callipteridium wachtlerae.(Bashkirian-Moscovian) 8. Frond (STEIN 221); 9. Apical part of a pinnula (STEIN 217); 10. Sporophylls and tropophylls (STEIN 207, Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

Callipteridium ameromii (Kasimovian-Gzhelian). 11. Sporophyll (STANG 20); 12. Sterile pinnae (STANG 22); Stangnock, Coll. Wachtler, Dolomythos-Museum

***Praecallipteridium parvifolium* (Early Carboniferous. Viséan-Serpukhovian)**

1. Sterile frond; b. Fertile frond; c. Sterile pinnae; d. Isolated leaflet; e. Fertile Aggregation; f. Adulte sporophyll; g. Juvenile sporophyll

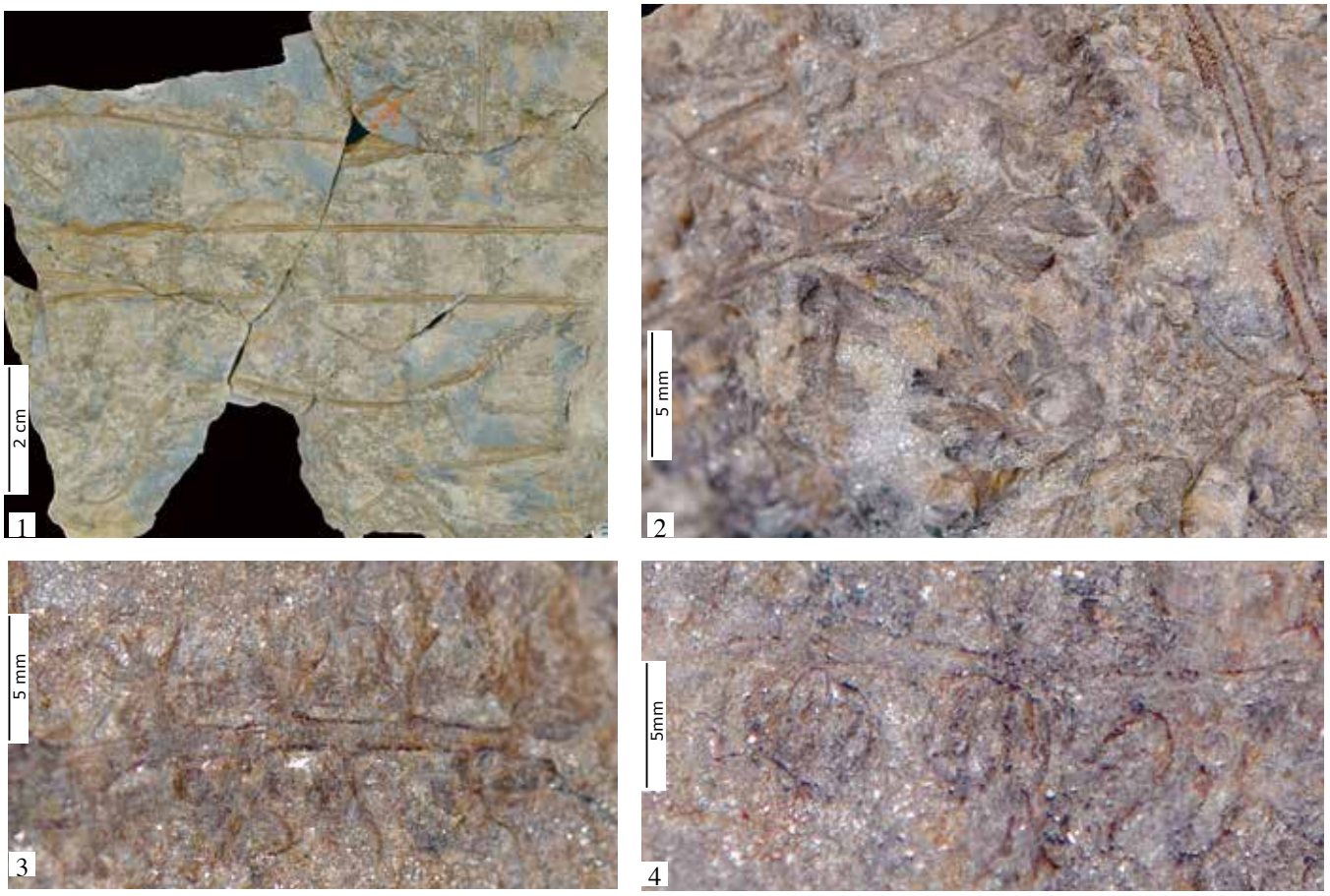
the Middle Devonian, called *Protopteridium philippae* (Wachtler, 2023), whereby those from the Lower Carboniferous can be more closely associated with those from the Devonian than with those from the Upper Carboniferous. This makes *Praecallipteridium parvifolium* one of the extremely interesting connecting plants between the Devonian-Lower Carboniferous and Upper Carboniferous to the Jurassic.
Similar ferns with different sporophylls and sterile tropophylls can be found in today's Osmundaceae (royal ferns) and especially in the Schizaeaceae, which includes the genera Anemia and Schizaea and which can probably be considered descendants of the callipterids.

Corynepteris Bailey 1860

Another primitive fern from the late Lower Carboniferous is *Corynepteris (similis)*, manifested on a relatively large slab from the Nötsch (Nöp) site. The majority of the pinnules are fertile with sporangia grouped into synangia. The leaflets are only partially connected to each other with a leaf lamina and appear toothed (Amerom & Kabon, 2003). The relatively strong veins dichotomize once or twice. The sterile fern species *Alloiopteris* should probably also be associated. Immediate descendants are unknown; no similar fern was found even in the Upper Carboniferous; the Triassic fern *Anomopteris* may fulfill some related requirements (Wachtler, 2016). The classification as Zygopteridales also hardly adds any knowledge (Taylor et al., 2009).

Other ferns

Since highly developed ferns such as the precursors of the tree ferns (*Cyatheites*), Dicksonia (*Dicksonites)*, Danaea (*Danaeites)* were already present in large numbers and fully developed in the early Upper Carboniferous some of these must be evolved at least in simple forms in the Lower to Middle Carboniferous.
Dicksonites: Some pinnae from the Hermsberg (He) site, described as *Mariopteris (mosana)* (van Amerom & Kabon, 2000), can probably be classified as



Early Carboniferous ferns (Viséan-Serpukhovian)

Corynepteris similis. 1-4. Frond and detail of the pinnae an the sporangia (Nöp 90); Ex. Coll. H. Kabon, Kärntner Botanikzentrum (Botanischer Garten), Klagenfurt

Dicksonites, although the poor recoveries makes a more precise classification difficult. *Dicksonites steinachii* from the Early Upper Carboniferous, numerous and with large fronds found on the Eggerberg fossil site (Wachtler, 2025), already had characteristics and properties today known as soft tree ferns. Other well-preserved fronds come from younger layers of the Upper Carboniferous, especially from the Kronalpe (*Dicksonites pennaeformis)* site (Wachtler, 2023).

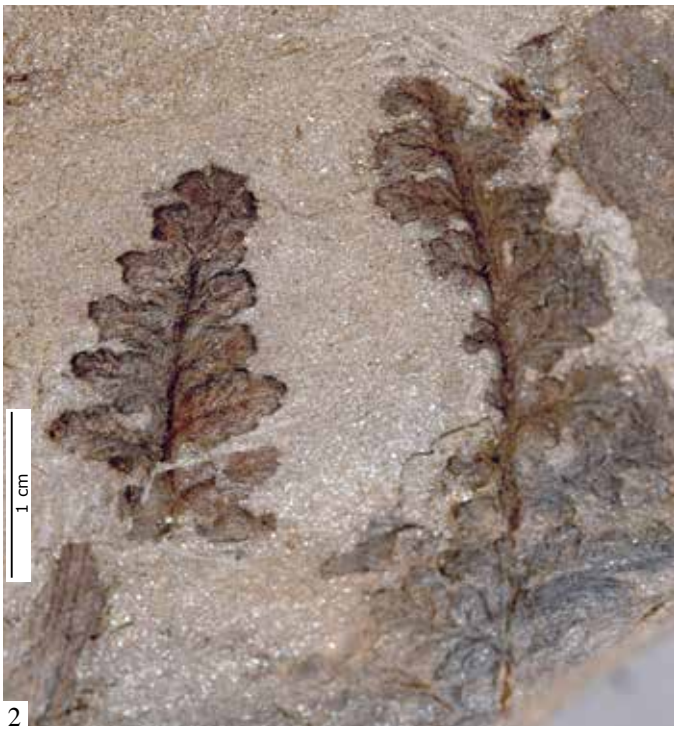
Cyatheites: Pinnules and frond parts described as *Pecopteris aspera* and *Neuropteris obliqua* (van Amerom & Kabon, 1999, 2000, 2003) are likely to represent fertile and sterile fronds of the tree fern *Cyatheites.* They are than frequent in the early Upper Carboniferous from Steinach in North Tyrol or in the Tomritsch fossil site in Carinthia with *Cyatheites rummeri.* In the early days of paleobotanical research (Sternberg 1828), *Cyatheites alpinus* and *Cyatheites unitus* were described from the Nockberge and the Kronalpe. However, the evidence from the Nötsch Lower Carboniferous is not sufficient to make further classifications.

Danaeites: Isolated fronds from the Lower Carboniferous of Nötsch are reminiscent of *Danaeites.* This suspected precursor of the Danaea ferns occurs frequently in the Upper Carboniferous with *Danaeites kerneri* in the Steinacher flora and with *Danaeites perneri* on the Kronalpe (Wachtler, 2025, Wachtler, 2023). In the Lower Triassic of the Dolomites, this fern is known as *Danaeopis dolomitica*, and in the Middle Triassic with *Danaeopis marantacea* in magnificent fronds from Middle German fossil sites (Wachtler, 2016).

Summary

Although the Lower Carboniferous floras of the Eastern Alps are incomplete, which characterizes many flora in this period, valuable conclusions can still be drawn,

1



2

Dicksonites sp. **Early Carboniferous**

1-2. (He G 16,(He G 22) Ex. Coll. H. Kabon, Kärntner Botanikzentrum (Botanischer Garten), Klagenfurt)

some of which are surprising. Ancestors of the gymnosperms are completely missing. They only appear in abundance at the Carboniferous-Permian border, seemingly out of nowhere, and simultaneously with all of today's important groups such as conifers, cycads and ginkgoes.

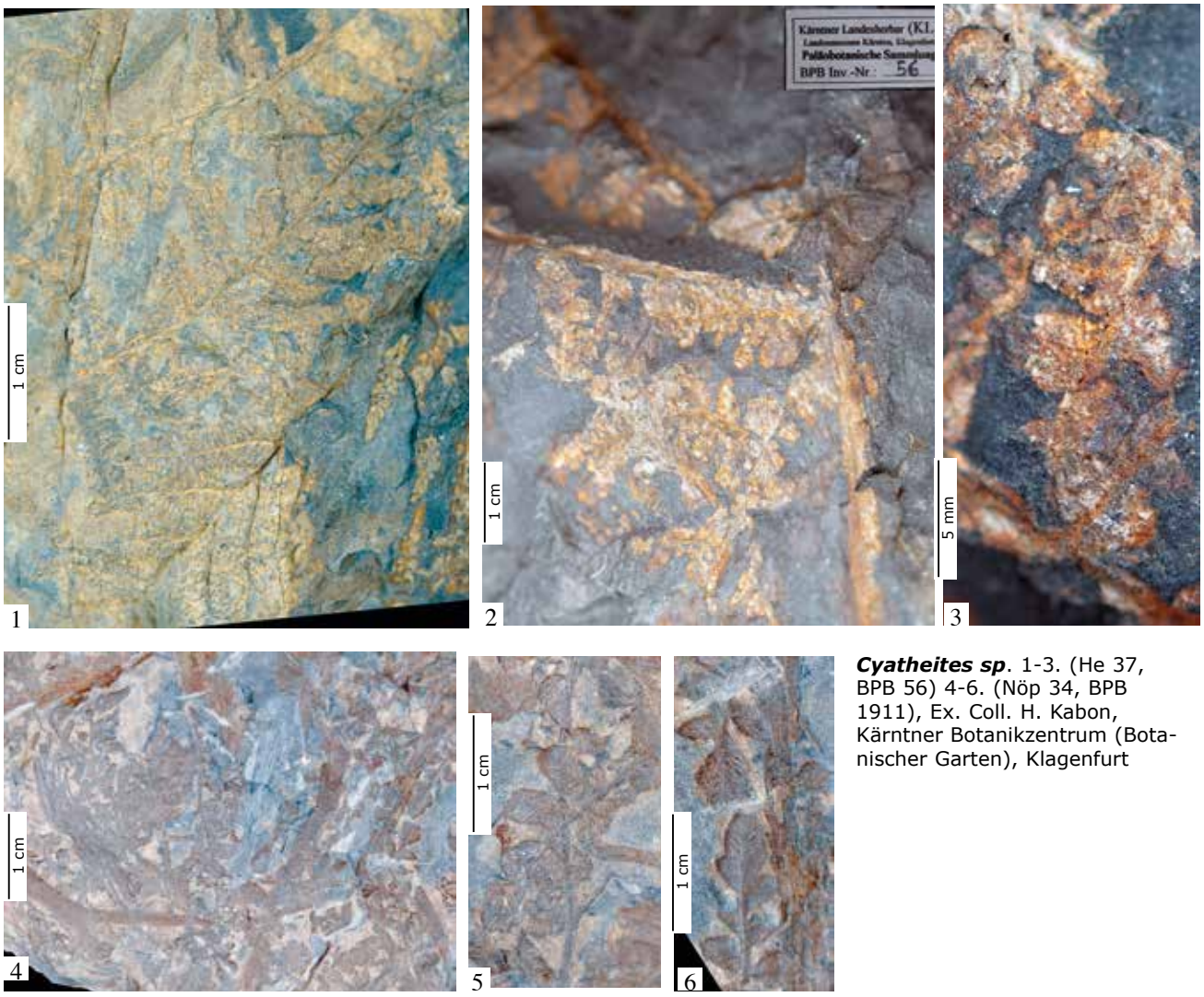
Whereas the clubmosses were small plants in the Devonian, from the Lower Carboniferous onwards they appeared with *Lepidodendron* and *Sigillaria* with gigantic growth and were divided into species with different sporophyll cones. The same is valid for the *Calamites* horsetails. Surprisingly, *Archaeocalamites radiatus* from the Lower Carboniferous, with its irregularly dichotomized leaf needles, still shows a level of development that can be more closely associated with Devonian plants and no longer occurs in the Upper Carboniferous floras. The flat whorls called *Annularia* dominate there.

However, we experience the greatest diversification and splitting up with the ferns, with some, like *Rhodeopteridium,* having strong similarities with predecessors from the Devonian, while others, like *Adiantites,* developed highly modern features that are reminiscent of today's ferns.

There are also ferns with different sporophylls and tropophylls such as *Praecallipteridium,* while others are likely to be precursors of today's ferns such as *Cyatheites, Dicksonites* or *Danaeites.* They reached their full development and expression a few million years later in the Upper Carboniferous.

Acknowledgments

First of all, thanks should be given to the tireless private researcher Herbert Kabon from Villach. He dedicated his life to paleobotany in Carinthia, making extraordinary discoveries, partially with the Dutch paleobotanist Hendrik Willem Josef van Van Amerom (1933-2018), as well as with the former director Hans Peter Schönlaub of the Geologische Bundesanstalt, Vienna (GABA) (Federal Geological Institute in Vienna, today Geosphere Austria).Thanks I owe to the head of the botany department at the State Museum for Carinthia in Klagenfurt, Roland K. Eberwein. He helpfully made all of the collections accessible and did not skimp on valuable information. A special thank you goes to Daniela Festi and Davide Di Franco from Geosphere Austria, Vienna



Cyatheites sp. 1-3. (He 37, BPB 56) 4-6. (Nöp 34, BPB 1911), Ex. Coll. H. Kabon, Kärntner Botanikzentrum (Botanischer Garten), Klagenfurt

for providing the material from old holdings of the Federal Geological Institute (GBA).

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Early Carboniferous ferns (Viséan-Serpukhovian).

1. *Mariopteris acuta* (VöB 6A, BPB 55);
2. *Alloiopteris similis* (Nöp 54B, BPB 47);
3-5. *Archaeopteridium tschermakii (*E1-6B, BPB 1998; E 1-9A, BPB 1991; Ev 1, BPB 34)
4. *Mariopteris mosana* (NöP 23A, BPB 1941);

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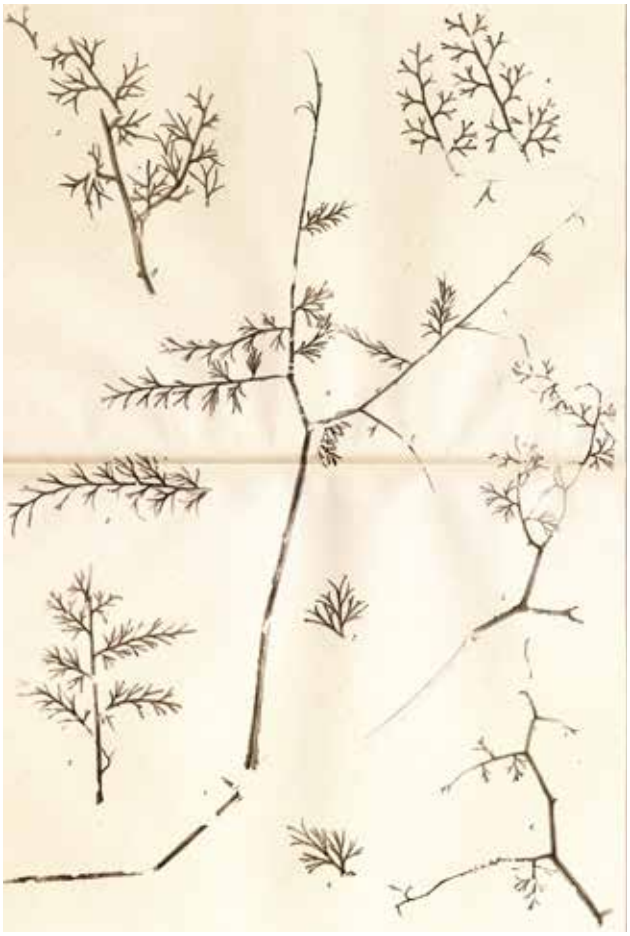
Plants from the Culm Flora of the same age in Germany for comparison (From Stur 1875-1877)

Archaeocalamites radiatus. Plate IV + V



Rhodea (Rhodeopteridum) patentissima. Plate IX

Adiantides antiquus. Plate XVI

Neuropteris (Praecallipteridium) antecedens. Plate XV

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Michael Wachtler

The oldest flora in the Alps

More than 315 million year old living worlds

The Eastern Alpine floras from the Lower Carboniferous (Viséum) are generally poorly preserved and fragmented. But they are interesting because the giant clubmosses such as Lepidodendron and Sigillaria, as well as the Calamites horsetails (Archaeocalamites radiatus) were already fully developed in this early geological period. In addition, fern communities were widespread.

Within the rich Carboniferous flora of the Alps, the "Steinacher Flora" (Stubai Alps) deposited around 315 million years ago (Middle Moscovian to Lower Bashkirian) on the border ridge between North and South Tyrol plays a special role, although it has rarely attracted the attention of scientists. Above all, the abundance of fossil ferns stands out, although some of them have been preserved in such good quality that it is possible to become clarity about their structure and their fertile characteristics. The club moss trees were dominated by Lepidodendron alpinus n. sp. with large homosporous cones and Lepidodendron pichleri, while in the horsetails Calamites steinachii n. sp. is common. It is also interesting that the primitive flora from the Devonian and Lower Carboniferous with difficult to recognize evolutionary lines has now come to an end, which enables interpretations of the development of a wide variety of families and genera up to the present day.

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