Carboniferous floras from the Alpine Tyrol

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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. Due to differences from the somewhat younger plant communities from the Carboniferous of the Eastern Alps, it seemed justified to classify some as new species. Of particular interest is *Lygodites stachei* and the staghorn fern ancestor *Platycerites haeckeli* n. sp., as well as *Callipteridium wachtlerae* n. sp. from the precursor group of Schizaeales. There are also the tree ferns *Cyatheites rummeri* n. sp. and *Dicksonites eggerbergii* n. sp., *Danaeites kerneri* n. sp. is also interesting, as the earliest ancestor of the Danaea ferns. The classification of *Cyclopteris pichleri* n. sp. with their tongue-like leaves is still unclear. 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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Key words: Upper Carboniferous, Moscovian, Bashkirian, Flora, Steinach, *Lepidodendron, Calamites,* Pteridophyta

A flora community from the early Upper Carboniferous of the Alps (315 million years ago). The club moss tree ***Lepidodendron alpinus*** (1) with its massive cones was common. The spore horsetail ***Calamites steinachii*** (2) was also widespread (3). The tree fern ***Cyatheites rummeri*** (3) dominated the fern community. There were also low-growing ferns such as ***Cyclopteris pichleri*** (4), ***Callipteridium wachtlerae*** (5), ***Dicksonites eggerbergii*** (6), the elkhorn precursor ***Platycerites haeckeli*** (7), and the Danaea ancestor ***Danaeites kerneri*** (8).

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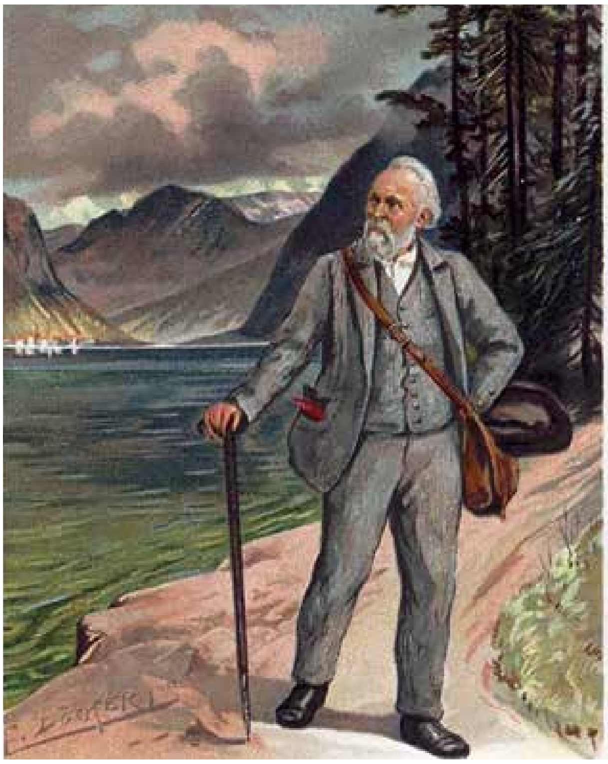
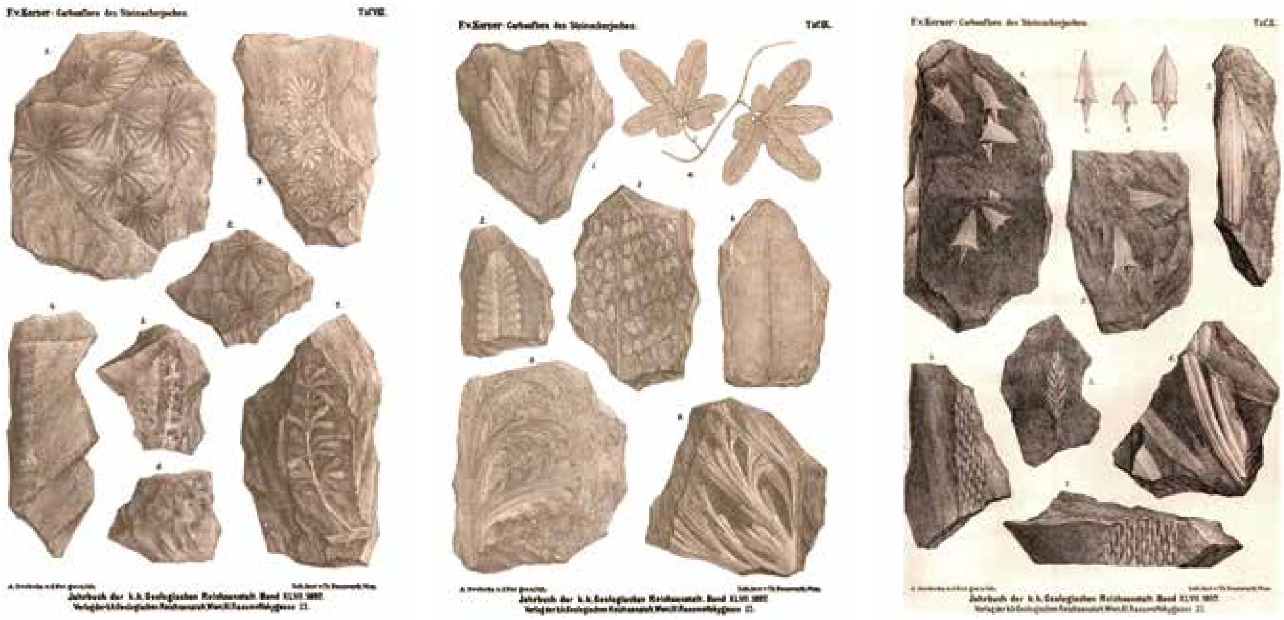
Somewhat in the shadow of the famous Eastern Alpine plant sites from the late Carboniferous of Carinthia and the Carnic Alps are those from the main Alpine ridge on the Brenner (Stubai Alps), which became known as "Steinacher Flora". In some places in the large area - Nößlachjoch (also known as Steinacher Joch) to Eggerjoch, weathered coal outcrops are visible. Traditional mining dates back to the period between 1840 and 1847, when anthracite was mined to a modest extent on the Nösslachjoch and near the Truna-Alm to the southwest (Schulz & Fuchs, 1991). Due to the small thickness of the lentils, this "Nösslacher Erde" (Nösslach Earth) was not mined as fuel coal, but was used as a natural dyeing-component for tobacco or as shoe polish.
From a scientific point of view, the widely interested Tyrolean writer and natural scientist Adolf Pichler (1819-1900) dealt with the plant fossils found there in a short note in 1858, as well as in 1859 and even more in detail in 1869 (*„Aus der Steinkohlenformation des Steinacher Joches"* "*From the coal formation of the Steinacher Joches"*). He let them examine by the German paleobotanist August Schenk, who somewhat superficially recognized various ferns such as C*yclopteris, Cyatheites,* but also other plants such as *Lepidodendron* or *Calamites.*
As far as the history of exploration is concerned, Adolf Pichler (1859) pointed out that in addition to easily crumbling anthracite coal mined "*with shovels and picks,"* poorly preserved plant remains were also found. "*A large amount of plant remains are found in the accompanying slates, although due to the brittleness of the rock it is difficult to preserve anything whole. In addition to several species of bullocks, I think I recognized Anullaria and Sphenophyllum*."
Pichler compared the finds with those known from the Stangalpe in Carinthia, the Valais and the Tarantaise (Savoy).
In 1871, the Slovak geologist Dionys Stur (1827-1893) and a year later (1872) the Austro-Hungarian paleontologist Guido Stache (1833-1921) dealt in more detail with the deposits discovered by Adolf Pichler on the Steinacher Joch, but both only with generic names for the fossil plants and without the use of illustrations. Some of Pichler's plant fossils ended up at the Geologische Bundesanstalt Wien (Federal Geological Institute in Vienna, today



The Tyrolean local historian Adolf Pichler on a hike, around 1899 (postcard by E. Döcker, Verlag Rafael Neuber, Vienna.

Fritz Kerner von Marilaun (1866-1944). In 1897 he published a detailed work on the Carboniferous flora of the Steinacher-Joch (Austrian National Library)



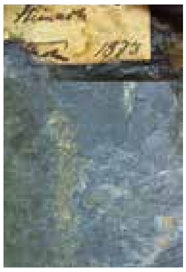
From Fritz von Kerner *„Die Carbonflora des Steinacherjoches“*, 1897. Plate VIII shows several different Calamitaceae described as *Annularia (*1-3) and *Sphenophyllum* (6-7). Also a cone (4) was figured. The second plate IX is dedicated to the ferns with the new described *Lygodium stachei* (1), than *Pecopteris unita* (2), *Neuropteris loschii (*3), *Neuropteris acutifolia* (4), *Rhacophyllum filiciforme* (5-6). Plate X figure clubmosses especially from fig. 1 till 3 fertile scales *(Lepidophyllum pichleri* n. sp), and from 4 till 6 *Lepidodendron (obovatum)* branchlets.

GeoSphere Austria), others were collected by Stache during his excursions in 1870 and 1871 and bequeathed them to the Federal Institute. Stur nevertheless determined a new species of fern, *Lygodium stachei*. Although remarkably similar to modern-day Lygodium ferns, the name *Lygodites stachei* should still be used to indicate that they are fossil ferns. Both compared the fossil remains with those better known from the Stangalpe in the Nockberge in Carinthia, but criticized the lack of *Sigillaria* clubmoss and the rare occurrence of the *Calamites*-horsetails.
In addition to these mostly general descriptions, in 1897 the meteorologist and geologist Fritz Kerner von Marilaun (1866-1944) set a milestone that was unsurpassed for many decades in his publication *„Die Carbonflora des Steinacherjoches“* (*The Carbonflora of the Steinacherjoch)*. On three plates he not only depicted the most striking plant fossils such as horsetails, ferns and clubmosses, but also discussed the geological situation of the various small-sized discovery areas between the Eggerjoch and the Nösslacherjoch. Later, Frech in 1905 and Jongmans in 1938 prospected, all without any specific processing or significant expansion of the findings.
The mining experienced a modest flourishing from 1924 onwards and even more so with the digging of trenches between 1934 and 1937. From 1938 onwards, five tunnels with a total length of 1.3 km were put into operation, so that in the course of the Second World War up to the 1950s, 5,000 tons of hard coal could be mined per year. However, mining stopped again in 1953 (Schulz & Fuchs, 1991). Today only a turistic mining path built in 2006 remembers of this glorious time.

Geological overview

For the geological formation known as the "Steinacher Decke", an age of between 313 and 323 million years was determined using potassium-argon dating (40Ar/39Ar) (Rockenschaub et. al., 2003). Both the Steinacher Nappe I and II fall into this period. This would correspond to an Early Upper Carboniferous, a period between the Bashkirian and the Moscovian (Lower to Middle Pennsylvanian).
The anthracite deposits consist of several embedded lenses with thicknesses of 0.5-2.50 m, which are preserved in a 150-300 m thick sequence with low-grade metamorphic quartz-mica arenites as erosion residue. They do not appear - as in the Nockberge - as bands that can be traced over long distances, but as spatially limited outcrops

The two Alpine geologists Franz von Hauer and Guido Stache (right) working in the field (photo taken around 1860) (Archive of the Federal Geological Institute in Vienna). Guido Stache made researches of the Carboniferous fossils at Brenner, with first publications in 1871.



*Calamites-h*orsetails from the Steinacher Joch, collected between 1871 and 1873. Mainly stems were found, as well as the whorled leaves, which found their way into paleobotanical literature as *Annularia*. Sometimes also fertile part were recovered

Among the clubmosses, *Lepidodendron* predominated, a species characterized by large homosporous cones and root elements known as *Stigmaria.* The leaves were slender and elongated.

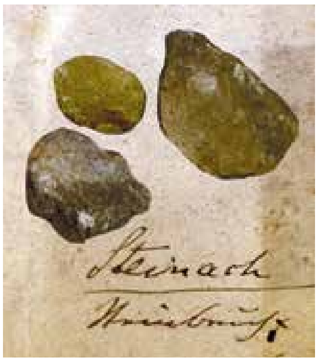
Some of Guido Stache's specimens were found by Adolf Pichler. Stache acknowledges him without envy that these occurrences were first discovered by this Tyrolean naturalist.

With the name *Cyatheites,* he compared some fronds to tree ferns

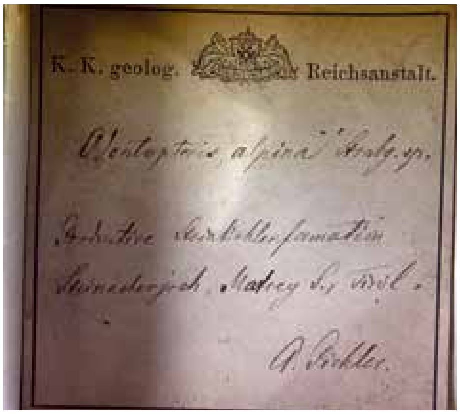
Problems - once as now, are caused by a fern with tongue-like leaves and suggested round seeds. According to Brongniart (1828), it was classified as *Alethopteris*, but more often as *Cyclopteris*

All: Geologische Bundesanstalt Vienna, today GeoSphere Austria

Original specimen from Fritz von Kerner *"The Carbonflora of the Steinacher Joch"*, 1897 in the Federal Geological Institute in Vienna



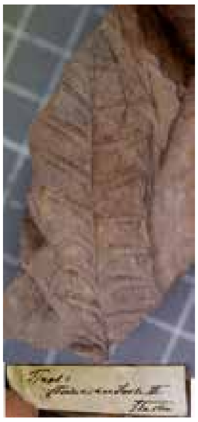
Danaeites



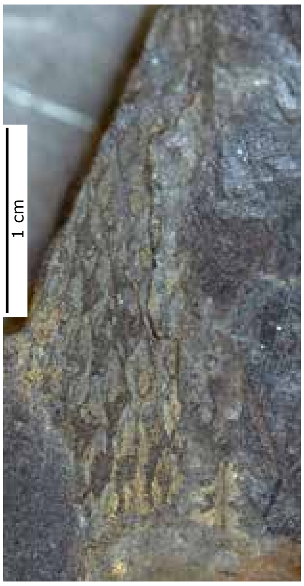
Guido Stache (1833-1921) at an older age

Platycerites (Rhacophyllum)

Callipteridium



The classification of ferns based only on their fronds was never constructive. This applies to *Odontopteris alpina* as well as to *Pteris serlii* (both first described by Brongniart, 1828).



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Club moss collected by Fritz von Kerner (1897), shown on plate X (3.*Lepidophyllum majus,* 4+7. *Lepidodendron obovatum)* as well as the original specimen

In the locality Eggerberg, rocks looking like petrified tree trunks are widespread. A theory is that the ancient clubmoss trees were penetrated by hot hydrothermic solutions during the sedimentation and thus preserved.

(Kerner, 1897; Schulz & Fuchs, 1991; Rockenschaub et. al., 2003). The quality of the plants found also varies.

The oldest evidence of fossil floras in the Eastern Alps can be attributed to the Lower Carboniferous and further narrowed down to the middle Viséum (around 340 million years ago. This so-called "Hochwipfel Formation" sporadically contains plant lenses, with the most interesting recoveries being in the vicinity of the Marinelli Hut (above the Italian locality Forni Avoltri) and the Tröpolacher Almweg above the municipality of Rattendorf (Amerom et al. 1984, Kabon & Schönlaub, 2019). There were found mainly *Calamites* horsetails, clubmosses in the form of *Lepidodendron* and *Sigillaria*, which were able to form considerable trunks, as well as ferns, which, however, still had primitive features similar to those from the Devonian mostly consisting of multiple forking appendices (Wachtler, 2022). Slightly more developed but still primitive floras come from the Nötsch site, which was classified as belonging to the Serpukhovian (Upper Mississippian, 323.2 to 330.9 million years ago) (Krainer & Vachard, 2002).

Since the Steinach Carboniferous flora as well as that from the Tomritsch site near Tröpolach in Carinthia has somewhat more primitive features than the subsequent rich Carboniferous floras of the Carnic Alps and the Nockberge, a deposition period between the Bashkirian and the Moscovian (Middle to Lower Pennsylvanian) is quite plausible.

During this time, the Alps were located slightly south of the equator. In the southern hemisphere, extensive glaciations occurred in the early Upper Carboniferous, which led to cooling even in the northern latitudes of

On the left the Eggerberg (2,280 m), on the right the Nösslachjoch (2,231 m) seen from the Brenner Pass.

The flat mountain ridges of the Eggerberg (2,280 m). Fossil plant deposits are often found in the blackish anthracite sediments.

A rich plant layer towards the Eggerberg contained *Lepidodendron* and ferns.

Another rich plant layer is located east of the Eggerjoch in the direction of Eggerberg. Ferns dominated here, but also clubmoss, especially *Lepidodendron*, and *Calamites* horsetail.

Euramerica, while the tropical climate at the equator remained largely untouched. As a result, attempts were made (Fritz & Krainer 2007; Schönlaub & Forke, 2007; Kustatscher et al. 2019) to chronologically classify the subsequent floras, namely with the name Bombaso Formation (Bashkirian and the Moscovian) as the geologically oldest with the parade sites of Tomritsch and in this case also Steinach; furthermore the Meledis Formation (Kasimovian to Lower Gzehlian) with the localities Straniger Alm, Zollnersee, Cason di Lanza (Rio del Museo), Watschiger Alm, Rudnigsattel, but also Stangnock and Königstuhl; the Pizzul Formation (Gzhelian); the Corona Formation (Gzhelian) with the classic Kronalm fossil deposit, the Auernig Formation (Gzhelian); the Carnizza Formation (Gzhelian); the Lower Pseudoschwaggerinenkalk (Gzhelian, uppermost part of the lowest Asselian); as well as the Grenzland Formation (Asselian) on the Austrian-Italian border ridge of the Rattendorfer Schneide. However, these classifications appear to be chosen in some cases arbitrarily, although they are only poorly supported by the fossil communities and, with a few exceptions, clearly assignable evidence or plant communities are missing.
It seems that the Bombaso Formation coincides with the Tomritsch and Steinach sites, the sites in the Nockberge are somewhat younger and the Kronalpe is located on the border where the first gymnosperms occur. The first remnants of conifers can be found in the Grenzland Formation at the Rattendorfer Schneide or in Kötschach-Mauthen.

The plant communities

Like many other plant sites from the Upper Carboniferous of the Eastern Alps, horizons with ash layers can also be found on the Brenner Pass, probably relics of periodic forest fires. As a result, juvenile populations of ferns and horsetails were able to establish themselves again until the giant club moss regained the upper hand again. Periodic climate changes dried out the club moss forests over large areas, with individual lightning strikes being enough to trigger catastrophic wildfires that affected large land masses, and caused to extinct the vegetation over a long period of time and may have had an impact on the global climate (Wachtler, 2023).

The plants were deposited in floodplains under tropical conditions, whereby transport routes were extremely short, if not even fallen trees or low-growing plants were embedded in place, which is evident from their excellent condition. Whether it was moors, shallow lakes or swamps (Wachtler, 2023), meandering or branching river systems that reached their end point in the basins of the former Variscian Mountains is difficult to interpret, but everything is probably true.

The biggest challenges in the past have been with classification, partly due to the hours-long journey and the associated taking of only a few samples. Only through detailed recoveries by Michael Wachtler from 2023 and with comparisons to other areas in the Eastern Alps satisfactory results were possible. Previous classifications (Kerner, 1897, Schulz & Fuchs, 1991), such as *Neuropterides, Alethopterides, Pecopterides, Schizopterides* in the ferns, or *Calamites* and *Sphenophyllum* in the horsetails or the enigmatic leaves of *Cordaites* are too imprecise without knowledge of their fertile organs. What is interesting about the Steinach Carboniferous flora is the high amount of fern families, with some belonging to the earliest developed and traceable to the present day. There were also giant clubmosses (especially *Lepidodendron*) and *Calamites* horsetail trees.

The ferns

The richest plant family in the Upper Carboniferous at Brenner is the ferns. Some, such as *Cyatheites,* a tree fern precursor, the *Dicksonia* ancestor *Dicksonites* or *Danaeites* from the fern group of neotropical *Danaea* ferns, can be classified relatively easily, possibly also the earliest precursor of the staghorn ferns *Platycerites.*

Callipteridium is probably one of the precursors of the ferns that develop separate sporophylls and tropophylls, such as Schizaea or Anemia today. It is more difficult to classify *Cyclopteris*, which has relatively large spore clusters covered by an indusium, as is partly the case with Polypodiales.

Callipteridium: The new species *Callipteridium wachtlerae* dominated the Carboniferous floras near the Brenner. It was composed of sterile fronds and terminal tropophylls and probably belonged to a precursor group of today's *Schizaea* or *Anemia* ferns. In the Permian, Triassic and Jurassic periods, this family dominated the landscapes in various forms (*Scytophyllum, Thinnfeldia*).

Cyatheites: The new tree fern species *Cyatheites rummeri* was widespread, and both fertile and sterile fronds were recovered. Different arrangements of the sori on the pinnae distinguish it from the well-known and later *Cyatheites alpinus* and *Cyatheites unitus* from the Carboniferous flora of Carinthia.

Platycerites: Today it is known as *Platycerium*, although the name staghorn fern or, even better, leaf fern, anticipates a lot. *Platycerites haeckeli* are the oldest known representatives, and are common at the sites below the Eggerberg.

Danaeites: This precursor group of today's Danaea ferns, widespread in the Neotropics, is also common. *Danaeites kerneri* shows for the first time that the current fronds of this family originated from a fusion of many small pinnae.

Dicksonites: These were also often the ancestors of today's Dicksonia ferns. *Dicksonites steinachii* already had all the characteristics and properties of these plants known as pocket ferns.

Cyclopteris: The decorative and large leaflets of *Cylopteris pichleri* are common. However, direct descendants are difficult to interpret; they are most likely to be found among the Polypodiales such as *Didymochlaena.* Their relatively large sporangia clusters, which are covered by a large indusium, are characteristic.

Lygodites: Although only found once is very interesting and can be regarded to be an ancestor of today's Lygodium ferns.

The clubmoss

Lepidodendron: These massive trees dominated the Carboniferous landscapes more than 300 million years ago. Although the foliage and the bark trunks with their typical leaf scars are similar to other Lepidodendrales, the massive cones differ considerably from others. Isolated scales were often classified as *Lepidostrobophyllum*. For historical continuity, the name *Lepidodendron* was retained with the new species *Lepidodendron alpinus,* although *Lepidostrobophyllum* could well be justified as a subsection. Recent examples can be found in the pine trees of the genus Pinus, as well as the subsections Pinaster or Contortae, which differ mainly in the shape of their cones. Other species such as *Lepidodendron pichleri* or *Lepidodendron fritzii* are rare and mainly dominant in the Carinthian Nockberge-area.

The sporangia horsetails

Calamites: The new species *Calamites steinachii* is common, of which all parts including the spore cones are known. It is a rather small species, with branches that sometimes diverge in clusters.

Comparisons with other Carboniferous flora

The Steinach Carboniferous flora is somewhat isolated among the fossil plants both in the Alps and throughout Europe. Firstly, because it has only been studied to a limited extent scientifically - and this before 1900. But also because the flora community shows considerable differences to other eastern Alpine discovery areas in Carinthia and the Carnic Mountains. These are due to the somewhat older age (Moscovian to Bashkirian), a relatively isolated position away from other fossil sites, and some genera that are still evolving.
However, the plants had already developed sufficiently to distinguish them from those from the Lower or Middle Carboniferous and to clearly classify them as Upper Carboniferous flora.
That the Steinach-plants belong to the typical Carboniferous floras is confirmed by the absence of gymnosperms such as conifers, ginkgos or cycads, which only appeared suddenly and became widespread at the Carboniferous-Permian boundary.
Although all genera occurring in the Steinach Carboniferous flora are known from other areas, particularly from the Carnic Alps and the Nockberge, which are rich in plant fossils, there are differences. These are particularly noticeable in the staghorn fern *Platycerites haeckeli,* which still had small leaves in the Steinach flora, while it developed much larger fronds in the Nockberge and even more so on the Kronalm, probably the latest Carboniferous formation in the Eastern Alps. Differences are also evident in *Danaeites kerneri* with its single leaflets, while in the Carnic Mountains *Danaeites perneri* already had mostly fused leaflets and was similar to today's Danaea ferns. Both *Dicksonites steinachii* and *Cyatheites rummeri* appear to have smaller leaves than their relatives from the Eastern Alps.
While the *Sigillaria*-clubmoss, which were particularly widespread in the Nockberge or on the Kronalm, are largely absent, it is particularly *Lepidodendron alpinus,* which dominated the Tyrolean Upper Carboniferous and showed significant differences in the structure of the cones and stems compared to the *Lepidodendron fritzii* or *Lepidodendron pichleri* species predominant on the Stangnock. The typical large lanceolate sporophyll leaves are no longer known in the following periods, and only occur at the coeval Tomritsch fossil site in Carinthia.

Locus Typicus and geological age

All: Eggerberg, Steinach, Late Carboniferous (Middle to Lower Pennsylvanian (Bashkirian-Moscovian)

Acknowledgments
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Dicksonites Sterzel 1881

In addition to *Cyatheites,* there is another relatively common genus within the tree ferns, which can be considered a Dicksonia precursor due to the arrangement of its sori: *Dicksonites*. The genus name goes back to the German paleobotanist Johann Traugott Sterzel, who described a *Dicksonites pluckeneti* in 1881, 1883 and 1886. Although various attempts have been made (Galtier & Bethoux, 2002) to classify *Dicksonites* as a seed-bearing fern, the first describer, Sterzel, already pointed out unequivocally that it is a fern with affinities to today's Dicksoniaceae due to the sori located at the edge below the leaf lamina. Today's Dicksonia ferns are found in the tropics and subtropics and extend from the American continent to Central America (*Dicksonia navarrensis, Dicksonia sellowiana, Dicksonia karsteniana, Cibotium schiedei)*, but the focus is on the southern hemisphere, with *Dicksonia antarctica*, native to Australia, being the best known. They require a balanced and humid climate all year round, but can also thrive in the Andes up to 4,000 meters above sea level.
As the Dicksonia precursors of the Steinacher flora are older than those from the Carnic Alps and also have other differences with them, it seemed sensible to introduce a new species name.

Dicksonites eggerbergii n. sp. Wachtler 2025

1881 Dicksoniites Pluckeneti Sterzel pag. 223
1883 *Dicksoniites* Pluckeneti Sterzel Pl. VI
1886 *Dicksoniites pluckeneti* Sterzel Pl. XXI, XXII
2022 *Dicksonites pennaeformis* (Sterzel, 1881) comb. nov. Wachtler, fig. 150-151

Etymology

Named after the site where it was found, the Eggerberg, a rocky peak above Trins on the northern side and Obernberg am Brenner on the southern side in the Stubai Alps. The location has been known for its fossil plants since the middle of the 19th century.

Holotype

STEIN 404 (Coll. Wachtler, Dolomythos-Museum, Innichen)

Diagnosis

Leaf blade tripinnate and pinnately lobed, pinnules mostly leathery, venation barely visible. Sori rounded and located submarginally.

Description

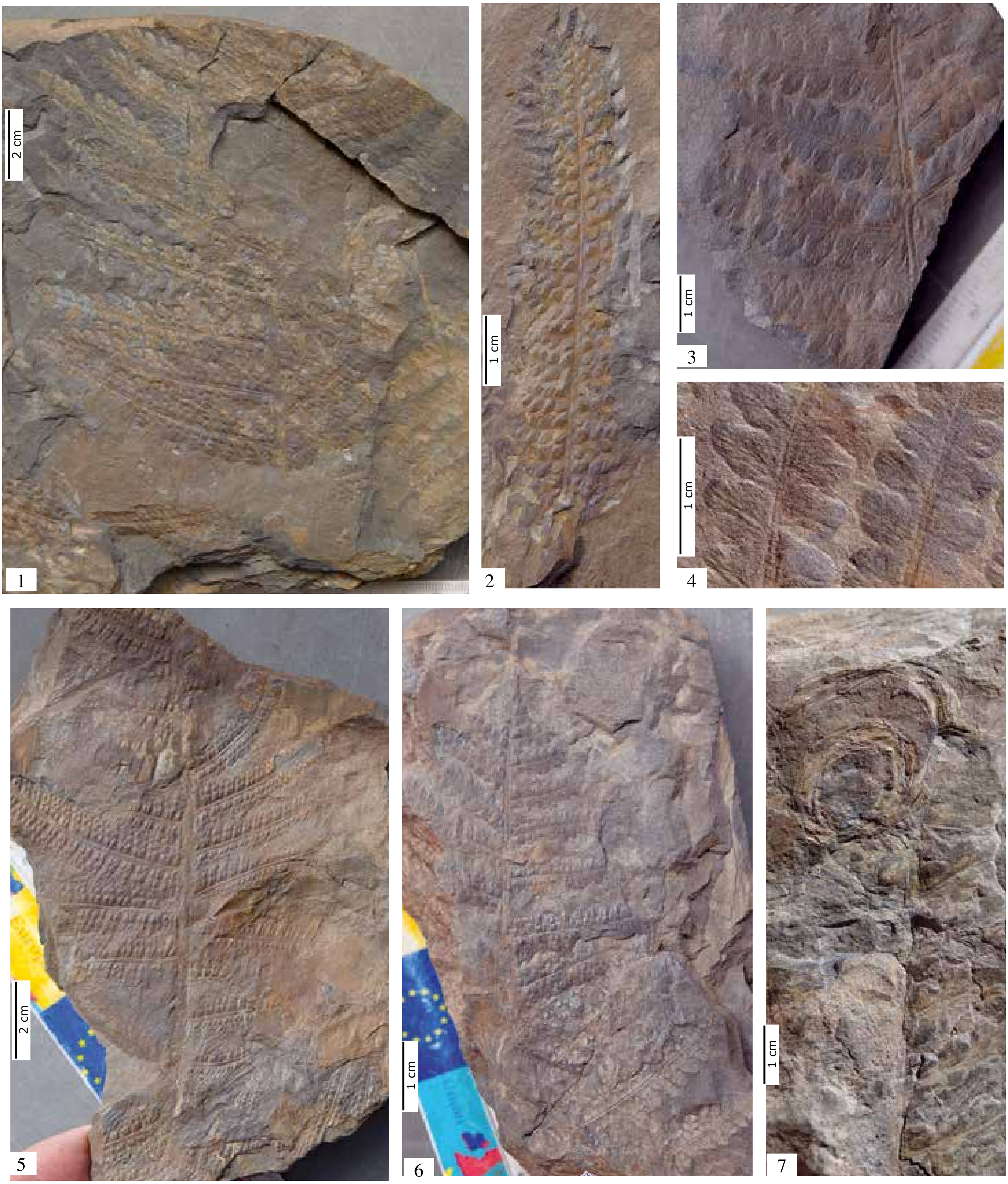
Whole plant: Fronds tripinnate, with gradually decreasing pinnae. Individual pinnae 10-15 cm long and 2 to 3 cm wide, arising from a delicate rachis. Sterile individual pinnae broadly attached, reaching about 5 mm long and 3 mm wide, venation sparse and barely visible (STEIN 404, designated holotype, STEIN 409, STEIN 402). Fertile pinnae somewhat smaller, with leathery lamina, venation not visible (STEIN 408, STEIN 404), STEIN 228, STEIN 227, STEIN 236). Sori sub- to marginal, rounded, developing individually on the lobes, partially protected by the recurved leaf blade.

Remarks

Dicksonites eggerbergii and *Cyatheites rummeri* are among the most common plants in the Steinach Carboniferous flora and are also easily distinguishable from other ferns. The fertile leaflets are small and leathery, the sterile ones somewhat larger but still relatively stocky. This distinguishes them from *Dicksonites pennaeformis* from somewhat younger deposits in the Upper Carboniferous of the Eastern Alps, which in some cases developed almost papery pinnules (Wachtler, 2023). Due to its more massive consistency, *Dicksonites eggerbergii* is consistently found in the form of almost intact fronds, which is less common with the other ferns.
The recent Cyathea and Dicksonia belong to the tree ferns and are so similar to each other in many respects that they were even grouped together into one family in the early days of research. However, this is not justified, as they have gone separate ways at least since the Carboniferous, possibly even since the Devonian. Both are relatively easy to distinguish even in the Carboniferous floras.

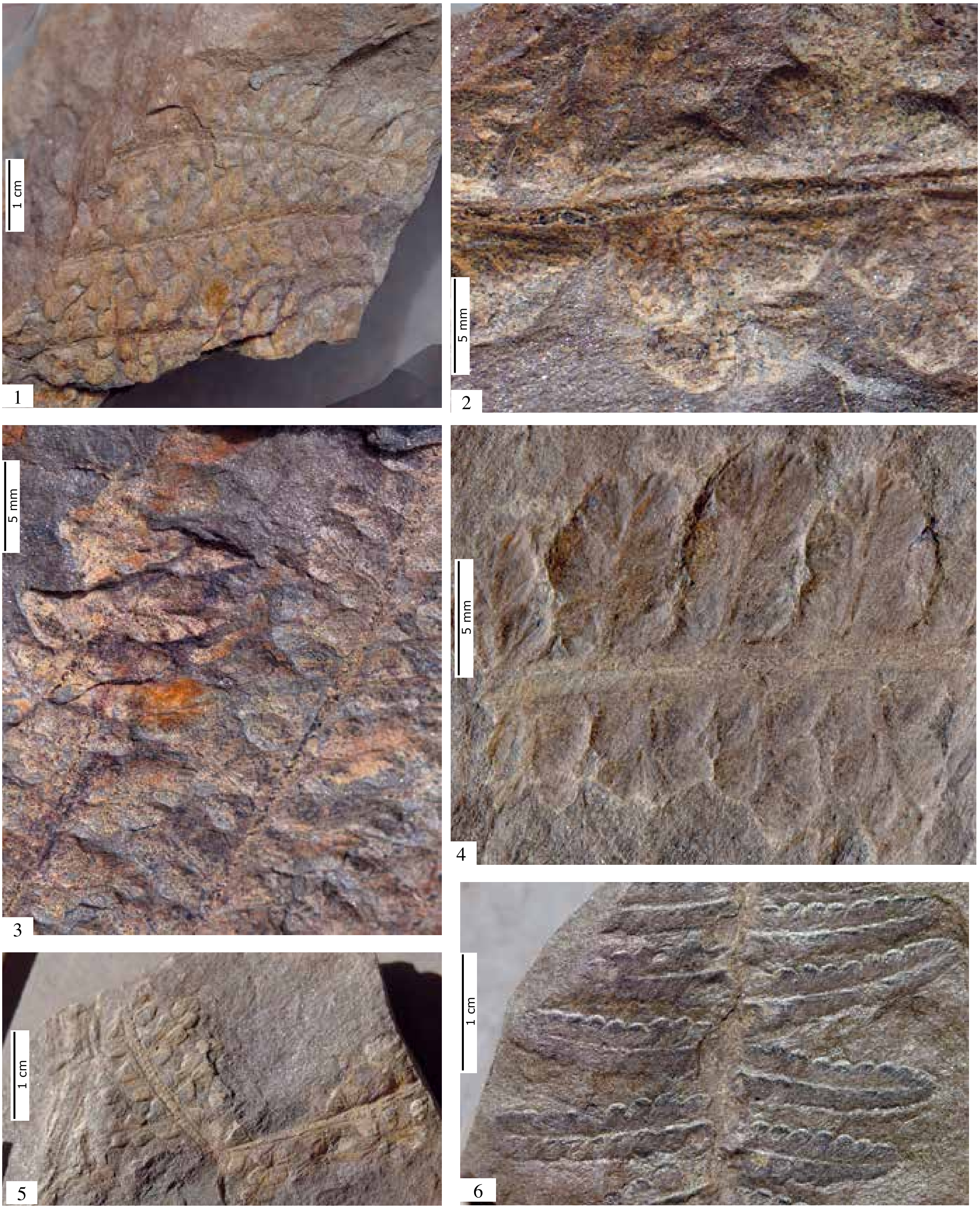
Recent *Dicksonia* ferns

Cibotium schiedei (Mexico): 1. Frond; 2. Part of a frond; 3. Sterile pinnae, upper side; 4. Juvenile sporangia, upper side; 5. Pinnae lower side; 6. Mature fertile sori; ***Cibotium chamissoi*** (Hawai); 7. Mature sporangia; ***Dicksonia navarrensis*** (Mexico-Centralamerica): 8. Whole plant with stem; ***Dicksonia antarctica*** (Australia) 9. Fertile leaflets upper side



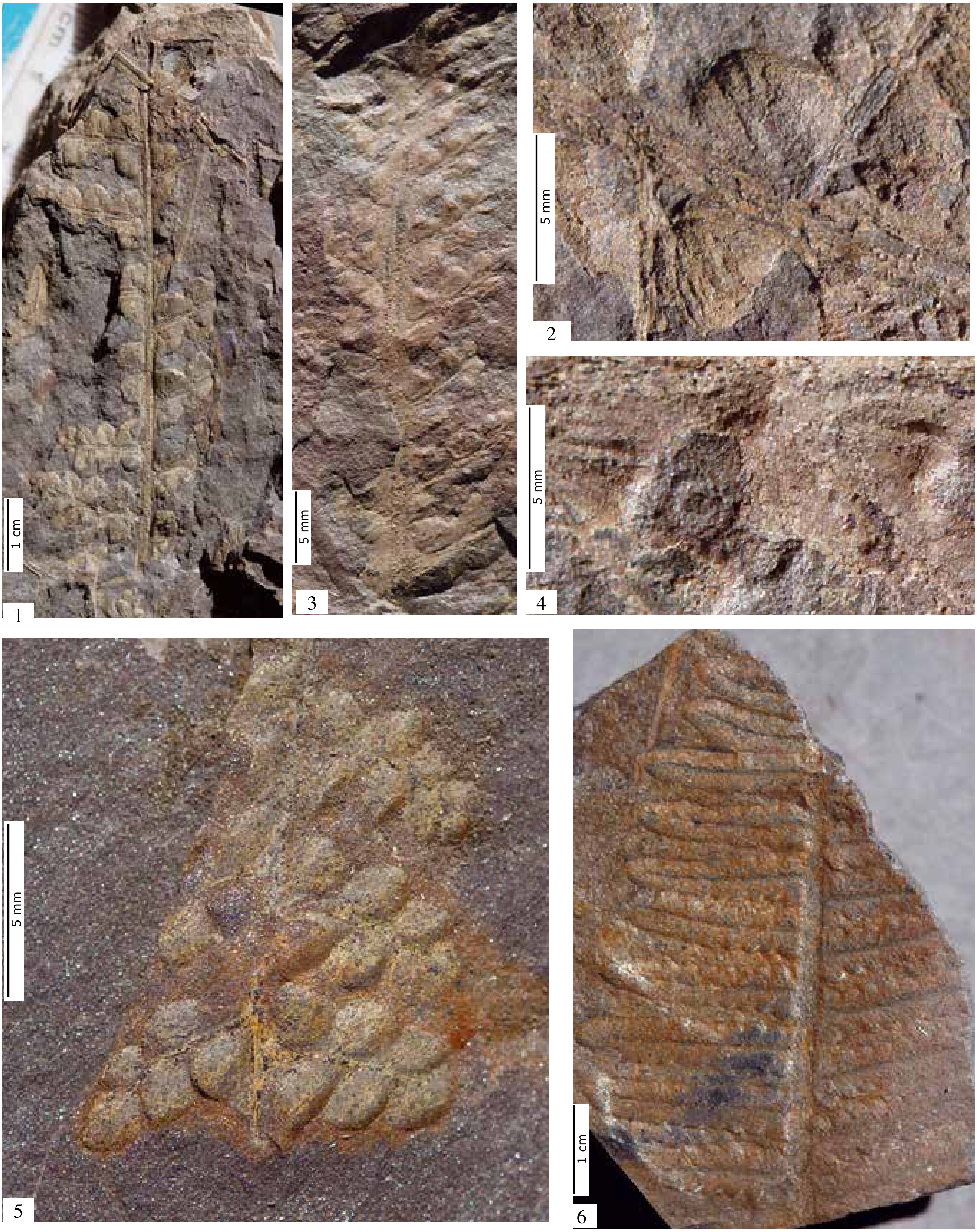
Dicksonites eggerbergii. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)

1. Frond and detail of the leaflets (STEIN 404, designated holotype); 5-6. Various fronds (STEIN 409, STEIN 402); 7. Juvenile enrolled frond (STEIN 265); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



Dicksonites eggerbergii. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)

1-3. Fertile frond and detail of the sori (STEIN 408); 4. Detail of the sterile leaflets (STEIN 404); 5. Frond top view (STEIN 228); 6-7. Sterile pinnae, top view (STEIN 228, STEIN 25); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



***Dicksonites eggerbergii*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1-2. Fertile frond and top view with detail (STEIN 227); 3-4. Fertile leaflets and detail of a mature sorus (STEIN 236); 5. Frond top view (STEIN 228); 5. Fertile pinnulae top view STEIN 318); 6. Sterile pinnulae (STEIN 05); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

***Dicksonites eggerbergii*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

a. Plant; b. Fertile frond; c. Fertile leaflet, upper side; d. Fertile leaflet, lower side; e. Detail of a mature fertile leaflet with sporangia capsules; f. Detail of immature fertile leaflet, upper side; g. Sporangia; h. Spores; i. Sterile leaflet; j. Sterile leaflet, lower side

Cyatheites Goeppert 1836

Another common fern species from the Carboniferous are the ancestors of the Cyatheales. All parts, from the thin trunks with their typical break-off points of the mighty fronds to the fertile and sterile pinnules, are now well known, so that classification as a tree fern precursor can be justified.
The name *Cyatheites* was first introduced by Heinrich Göppert in 1836 in his monograph *"Die fossilen Farrnkräuter" (Fossil ferns)* (p. 319), in which he described 13 species and attributed most of them (10) to the Carboniferous period. He defined this genus as follows: "... *I thought to only include those species in Cyatheites whose fruit clusters are located in the bifurcation of the nerves, which is what makes the genus Cyathea so special..."*.
Since the *Cyatheites* tree ferns of the Steinach Carboniferous flora differ from those from the Carnic Alps and the Nock Mountains such as *Cyatheites alpinus (Sternberg, 1838) and Cyatheites unitus* (Wachtler, 2022) due to their earlier appearance and other characteristics, it seems reasonable to choose a new species name.

Stefan Rummer from Linz working on the site at Eggerberg. It yielded a rich fossil content.

However, towards the end of the Carboniferous, tree ferns largely disappear from the fossil record throughout the Permian, and only re-enter the limelight from the Early Triassic (Anisian), with *Gordonopteris brogliae* from the Dolomites playing an important role (Wachtler, 2016).

Cyatheites rummeri n. sp. Wachtler, 2025

1828 *Pecopteris unita* Brongniart, Pl. 116 Abb. 1-2

1836 *Cyatheites* Göppert, Syst. fil foss. p. 175, 319-329

1855 *Cyatheites unitus* Geinitz, S.25 Pl. 29 Fig.4,5

1870 *Cyatheites unita* Unger, p. 785, Tab 1, Fig. 4, 5

1872 *Cyatheites arborescens,* Stache p. 80

2022 Cyatheites alpinus (Sternberg, 1838) comb. nov. Wachtler, Fig. 138-143

2022 *Cyatheites unitus* (Brongniart, 1828) comb. nov. Wachtler, 2022, pp. 146-147

Etymology

Named after the Austrian Stefan Rummer, who first discovered specimens of excellent quality on the Eggerberg in the Stubai Alps.

Holotype

STEIN 411 (Coll. Wachtler, Dolomythos-Museum, Innichen)

Diagnosis

Fronds tripinnate. Leaflets entire and broadly attached to the base. Sori round, attached close to the leaflet margin on the underside.

Description

Whole plant: Straight and unbranched tree-like stems with distinctive break-off points of shed fronds. Axis of the fronds densely covered with fine leaf hairs. Overall fronds tripinnate. Pinnules entire (STEIN 318, STEIN 126, STEIN 29), opposite to slightly offset and broadly connected to the rachis. Apically rounded to slightly pointed. In the slightly larger, sterile ones, they reached a length of about 1-1.2 cm and a width of 0.5-0.6 cm (STEIN 392). Midvein of the pinnules is clearly defined, the lateral veins are faintly visible and fork once.

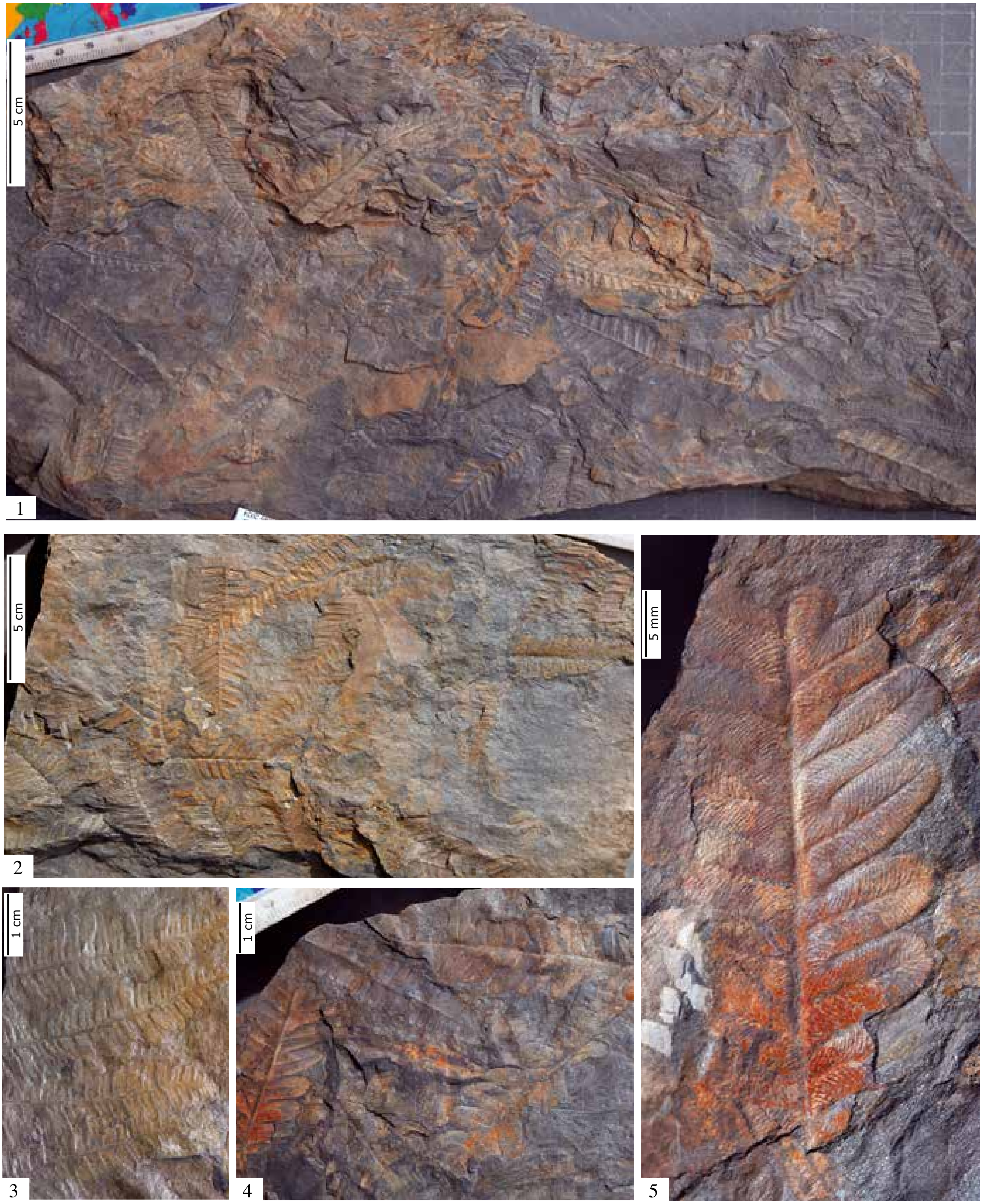
Fertile pinnules, 0.5 to 0.7 cm long and 0.3 cm wide (STEIN 127). Rounded sori on their underside, densely covering the leaf lamina on the outer sides and thus developing a curved outer edge (STEIN 266, STEIN 411, STEIN 129). Veins not visible.

Remarks

Cyatheites is one of the most common ferns in the Upper Carboniferous of the Eastern Alps. Distinctive break-off points of shed fronds on the trunks identify them as tree ferns, as do their rounded sori on the outside of the pinnae. However, in the case of sterile pinnae, it is not always easy to separate them from other pecopterid pinnae such as those of *Osmundites* (Wachtler, 2023f).
Cyatheites rummeri can be distinguished from the slightly later developed Cyatheites unitus by its elongated pinnae and massive occurrence of small leaf hairs. In *Cyatheites alpinus* from the Nockberge in Carinthia and the Carnian Mountains on the Austrian-Italian border, the differences are not so pronounced (Wachtler, 2023f). The pinnae are similarly structured with smaller fertile and larger sterile ones, but they are slightly segmented and leathery on the outside.
The development of the Cyathea tree ferns can be traced seamlessly from the Early Upper Carboniferous (Bashkirian-Moscovian) of Steinach, but also from the other site known from this period in the Carnic Mountains, Tomritsch above Tröpolach (so-called Bombaso Formation), over the somewhat younger localities in the Nockberge (Stangnock and Königstuhl, but also the site near the Cason di Lanza (Rio del Museo), to the most recent Corona Formation (Kasimovian-Gzhelian) with the Kronalpe site. Only in the borderland layers on the Rattendorfer Alm-Cason di Lanza ridge do the fossil communities change in an almost inexplicable way, with gymnosperms, and especially conifers, appearing as if out of nowhere, while a large proportion of the ferns disappear for almost 50 million years until the Middle Triassic (Wachtler, 2016). The reason for this is the massively changing climate conditions.

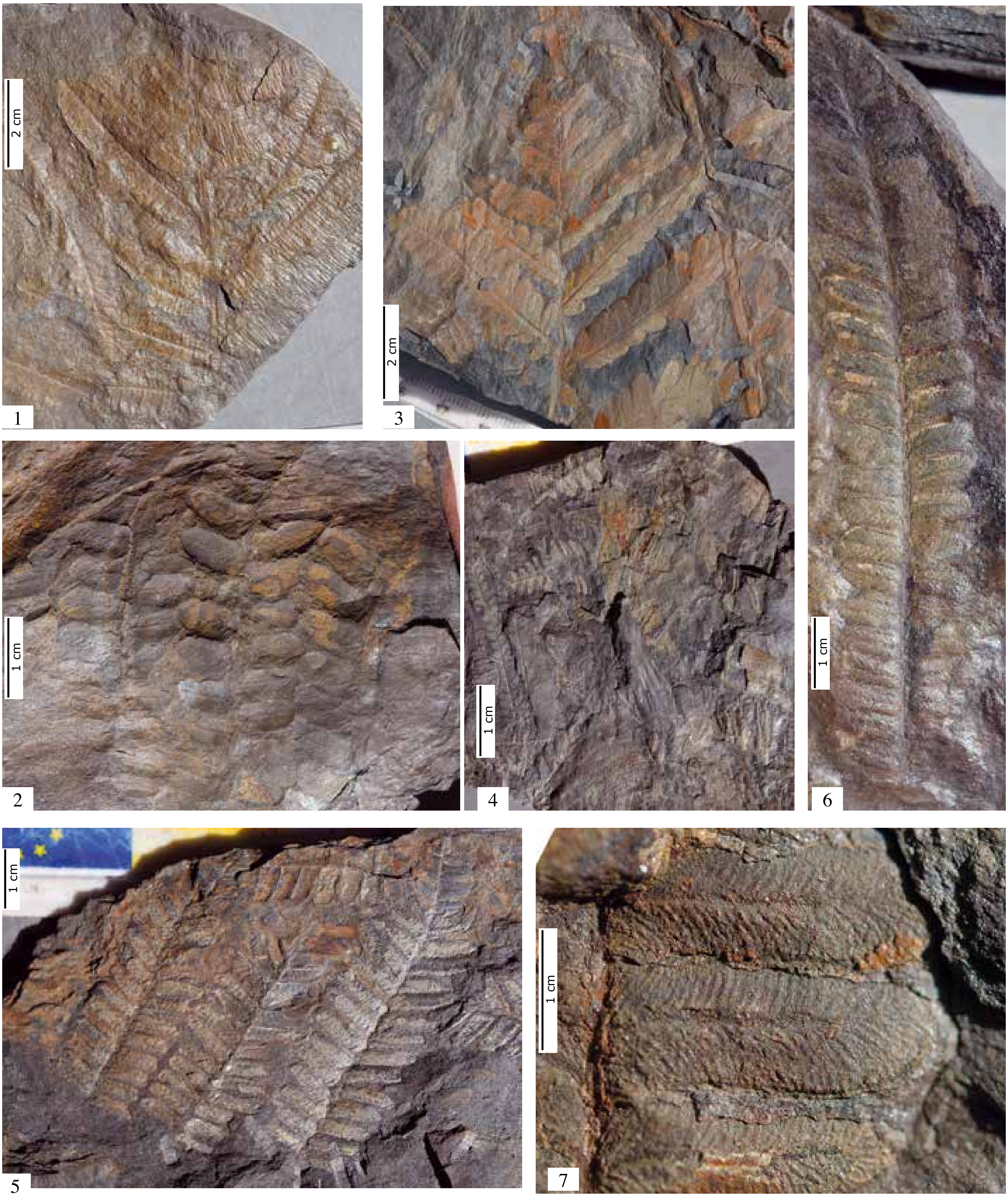
Platycerites Göppert 1854

The name *Platycerites* was first coined in 1852 by the German geologist Heinrich von Dechen (1800-1889) in the "*Geognostis oder auch Geweihfarnchen Beschreibung des Siebengebirges am Rhein*" (Geognostic description of the elhorn ferns from the Siebengebirge near the Rhine). In a list without further explanation, he mentioned *Platycerites wirtgenianus*, referring to a work by the German paleobotanist Heinrich Göppert (1800-1884), which, however, was not published until 1854.
In 1866, the brilliant German illustrator Ernst Haeckel (1834-1919) dealt superficially with the ancestors of this group of ferns, although it was not until 1900 that he depicted today's Platycerium ferns on plate 52 in a partial delivery of his still unsurpassed work "*Kunstformen der Natur*" (Art Forms of Nature), giving them the distinctive name "deciduous ferns" and thus making them popular. His description is also impressive: "*The peculiar shape of Platycerium is based due on the division of labour or the ergonomics of its leaves or "fronds". In most native ferns, these are all of the same structure: delicate, green, usually pinnate or multi-partite leaves, on the underside of which the brown fruit clusters (sori) develop, composed of numerous spore capsules (sporangia); ... In Platycerium, on the other hand, as in some ferns, the plant develops two or even three different types of fronds; one of these, the deciduous leaves, serves only to nourish the plant and does not produce spores; the other, the spore leaves, produce the spores used for reproduction; a third form, the niche leaves or mantle leaves, form a niche at the base of the fern in which dying plant remains accumulate and produce humus. The roots of the fern grow into this fertile humus and obtain their nourishment from it. ... The green deciduous leaves, on the other hand, hang down from these cushions in the form of multi-part fronds that reach several meters in length; they are usually multiply forked, branched like the antlers of a deer or elk.*"
The spore capsules develop on the underside of the fronds in different ways on the different species, sometimes only at the base of individual leaves, sometimes on a



***Cyatheites rummeri*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1. Sterile and fertile fronds on a plate (STEIN 411, designated holotype); 2. Fertile pinnulae top and bottom view (STEIN 127); 3. Frond (STEIN 29); 4-5. Sterile frond parts and detail (STEIN 318); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

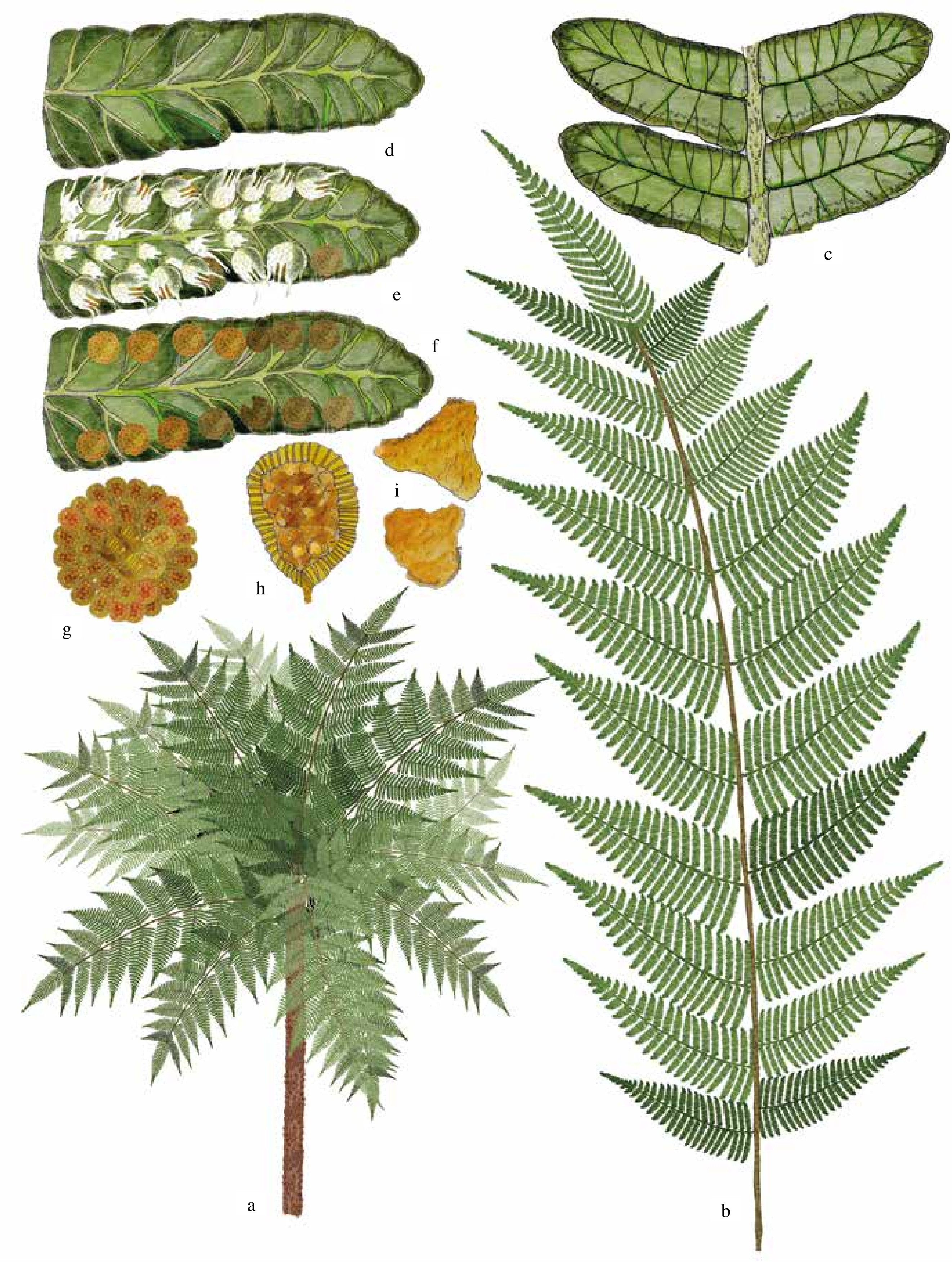


***Cyatheites rummeri*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1-3. Sterile fronds (STEIN 01, STEIN 21, STEIN 314); 4-5. Fertile fronds (STEIN 211, STEIN 126); 6-7. Sterile pinnules and detail (STEIN 29); 4-5. Sterile frond parts and detail (STEIN 15, STEIN 294); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

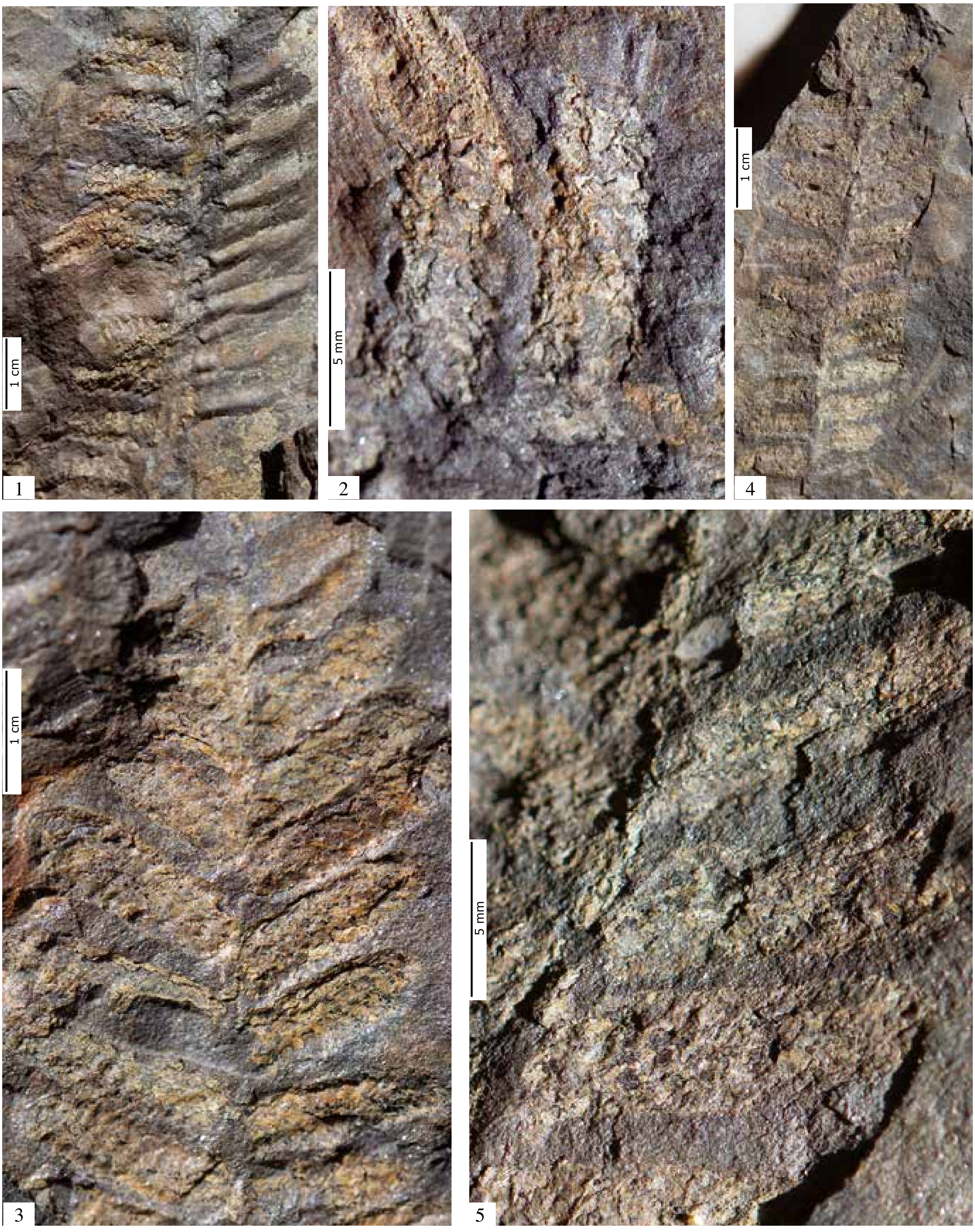
***Cyatheites rummeri*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1-2. Fertile frond and detail of the sori (STEIN 112); 3-4. Fertile frond with sori top and bottom view (STEIN 127); 5-7. Fertile pinnulae (STEIN 266, STEIN 411, STEIN 129); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



***Cyatheites rummeri*. Steinacher-Flora. Fern (Late Carboniferous, Bashkirian-Moskovian)**

a. Plant; b. Frond; c. Sterile leaflet; d. Fertile leaflet, upper side; e. Juvenile fertile leaflet with indusium; f. Fertile leaflet underside with sori; g. Sorus; h. Sporangia with annulus; i. Spores



Cyatheites rummeri. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)

1-2. Fertile pinnae and detail (STEIN 218); 3. Fertile pinnae with sporangia (STEIN 112); 4-5. Fertile pinnae and detail of the sori (STEIN 280); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

Recent *Cyathea*-Ferns

Cyathea salvinii (Central America) 1. Frond; ***Cyathea tuerckheimii*** (Mexico, Nicaragua) 2. Stem; ***Cyathea costaricensis*** Central America) 3-4. Whole plant and juvenile frond; ***Alsophila (Cyathea) firma*** (Mexico) 5. Fertile pinnae, upper side, 6-7. Fertile pinnae underside and detail, 8. Sterile pinnae

From Schimper, 1869, Pl. XLVIII, Fig. 8. *Rhacophyllum flabellatum* (Late Carboniferous Saarbrücken). It represent probably a *Platycerites.*

large part of the lower leaf surface, sometimes at the tips of the forked branches."
However, in 1869/Vol. 3, the Alsatian paleobotanist Wilhelm Philipp Schimper named fern-like ferns with the genus name *Rhacophyllum*, and illustrated five different species in excellent quality, which ranged from the Carboniferous to the Triassic. *Rhacophyllum* as a genus name could survive if *Platycerites* were not ancestors of today's staghorn ferns, which, however, can be ruled out according to the latest state of knowledge.
The approximately eighteen Platycerum ferns of today inhabit the tropical regions of South America (Bolivia, Peru), Africa, Southeast Asia (Indonesia, Malaysia, Singapore, Philippines, Thailand, Myanmar or Vietnam), Australia and New Guinea. They are characterized by extremely diversely shaped leaves, which is in contrast to most ferns, where the shield- to kidney-shaped leaves are sterile and remain on the rhizome even when dead. Fertile leaves are usually elongated and split at the tip to give a multi-segmented appearance, hence their name staghorn fern.
The name Platycerium originally comes from the Greek and stands for "platis" (large) and "keras" (antlers), hence also staghorn fern due to the appearance of the leaves.
Now we need to look into the question of whether the fossil remains found in the Carboniferous period of the Eastern Alps, and especially at the Steinacher Joch, can be seen as the forerunners of the staghorn ferns? Of all the possibilities, this can be a valid theory; in some cases they are strikingly similar to modern *Platycerium* ferns, although their leaves are smaller. Even the spore accumulations on the underside point in this direction. That is why the name *Platycerites* was chosen for this fern-ancestors and, in order to honor the excellent illustrator Ernst Haeckel, this species was named after him.

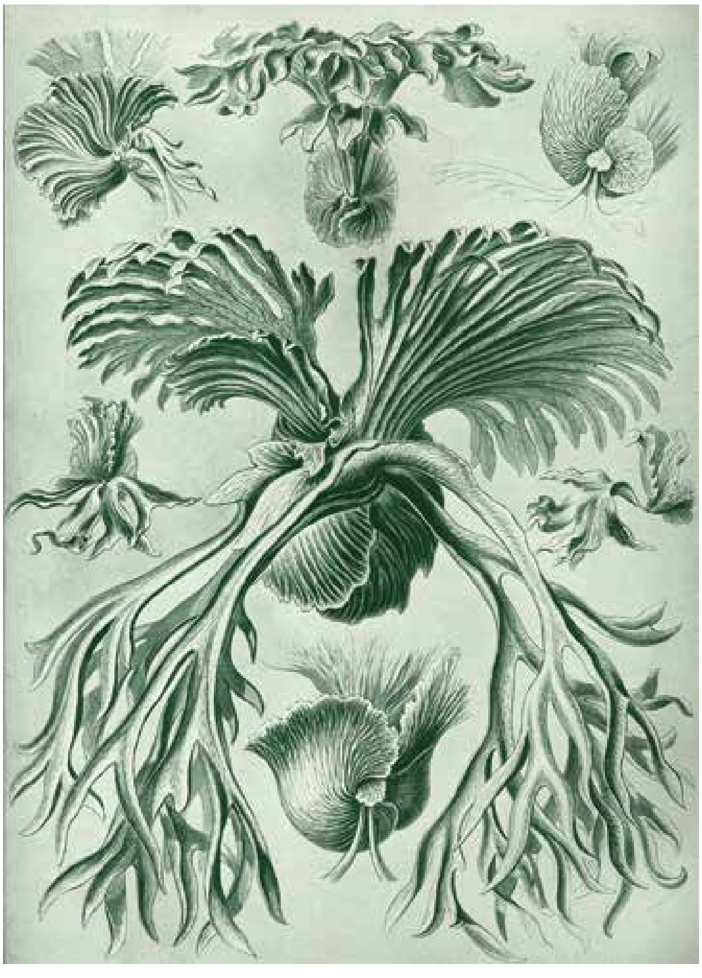
Platycerites haeckeli n. sp. Wachtler 2025

1852 *Platycerites wirtgenianus,* H. v. Dechen, p. 513

1854 *Platycerites wirthgenianus,* Göppert, p. 98

1869 *Rhacophyllum flabelllatum*, Schimper, Traité de Paléontologie Végétale, p. 684, Pl. XLVIII, fig. 8

1897 Rhacophyllum filiciforme Kerner von Marilaun, Pl.



From Ernst Haeckel, 1900 Pl. 52. Fig. 1-4. *Platycerium grande,* Fig. 5, 6. *Platycerium stemmaria,* fig. 7. *Platycerium hilli.* He calls them deciduous ferns.

IX, fig. 5-6
2023 *Cyclopteris boersmai,* Wachtler, pp. 164-167

Etymology

Named after the German physician, zoologist, philosopher, draftsman and freethinker Ernst Haeckel (1834-1919). With his artistic talent, he depicted in his *«Kunstformen der Natur» (Art Forms of Nature)* (1899-1904) the impressive beauty of animals and plants in a manner that had never been achieved before.

Holotype

STEIN 376 (Coll. Wachtler, Dolomythos-Museum, Innichen)

Diagnosis

Fan-shaped, multi-segmented leaves with barely discernible veins. Sporangia completely or partially covering the underside.

Description

Whole plant: Shoots reaching 30 cm (STEIN 87, STEIN 309) or more. Leaf-shaped pinnates arising from a central petiole in large numbers and irregularly, without assuming the typical fern-like character (STEIN 376 holotype, STEIN 337, STEIN 389). Pinnules reaching 2 to 5 cm in length, with almost the same width as height; palmate and irregularly segmented several times (STEIN 77). Veins barely or not visible.
Fertile leaves: Divided at the tip, sometimes shriveled. Sporangia partially covering larger areas of the undersides of the pinnules or only attached to the somewhat more pronounced forks of the leaves. (STEIN 78, STEIN 82, STEIN 87). Sporangia up to 0.1 mm, roundish, with a slightly thickened annulus with radial walls, spores located inside the inner sides.

Remarks

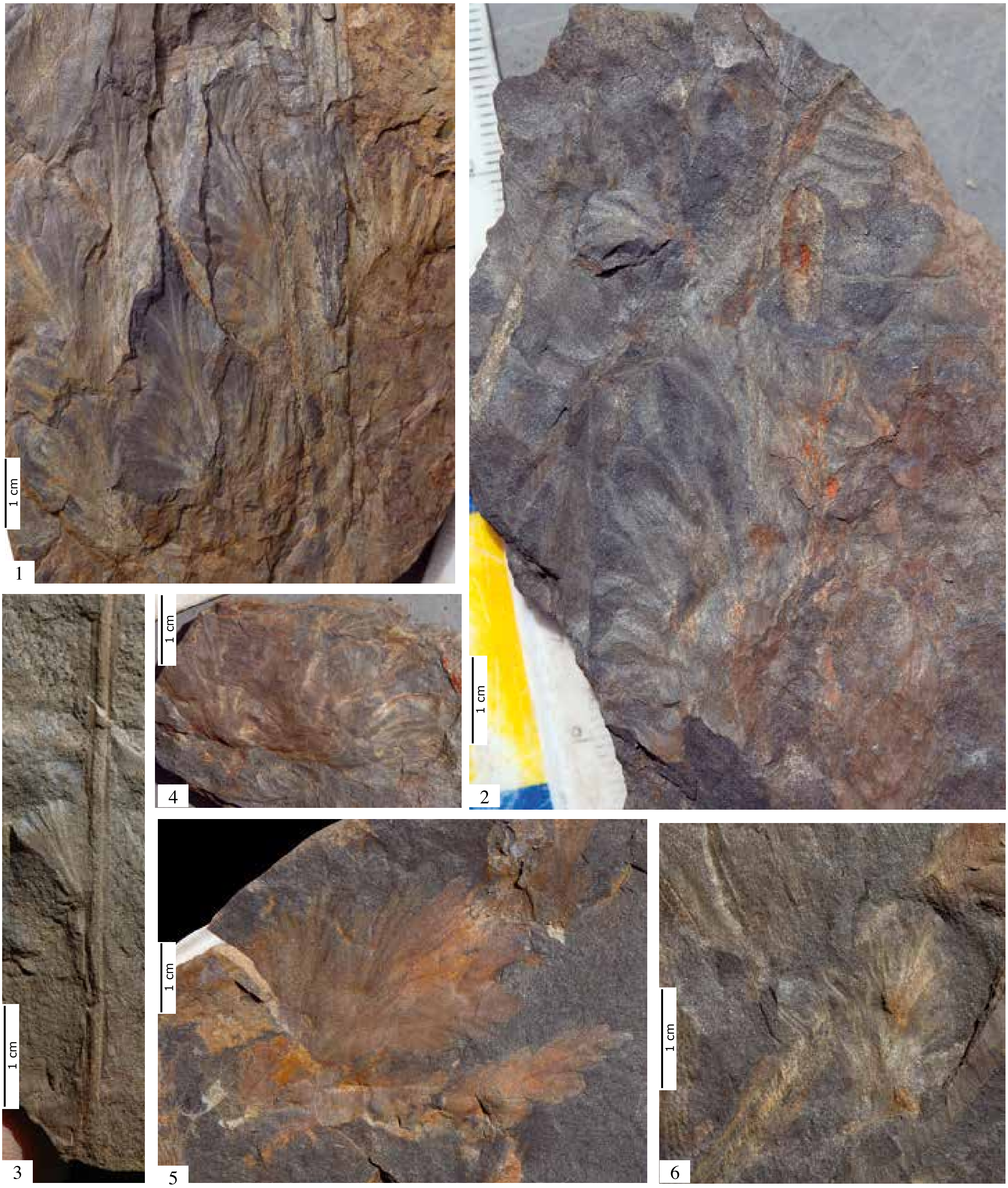
Platycerites haeckeli is a common fern in the Steinach Carboniferous flora, that even complete frond parts can be found. This plant cannot be confused with the other ferns. However, their unaesthetic appearance and their relatively thin leaves tempt collectors to throw them into the rubble.
Most of them are multi-leafed fronds, deposited in a confused manner on top of each other, which arise from a central axis, with the leaves barely exceeding 5 cm in length and width. Veins like those of other ferns are barely or not at all recognizable.
It can therefore be assumed that the evolutionary separation of this family, with its relatively archaic forking branches from the other ferns must have taken place as early as the Devonian, as the pinnae of most other ferns are too different from those of *Platycerites.*
More developed specimens come from slightly younger layers of the Stangnock and the Königstuhl in Carinthia. *Platycerites (Cyclopteris) boersmai* (Wachtler, 2023) is relatively common on the Kronalpe in the Carnic Mountains and can be seen as a further development of *Platycerites haeckeli* from the Steinach flora due to its larger deciduous leaves. In some cases, individual forked leaves have now reached between 8 and 10 centimeters in size. In contrast, there are hardly any differences in the arrangement and structure of the sporangia.
After this heyday of the staghorn ferns in the Upper Carboniferous, however, they disappeared in the Permian.
It was only in the Middle Ladinian of Germany (Erfurt Formation, Ilsfeld, Baden Württemberg) that ferns described as *Rhacophyllum crispatum,* also as *Rhacophyllum phachyrrhachis*, appeared, which show similarities to *Platycerites* ferns (Wachtler, 2016). Further finds can then be found in the Miocene (Göppert 1854).

Callipteridium Weiss 1870

Callipteridium together with the tree fern *Cyatheites,* is the most common fern genus of the "Steinach Carboniferous Flora". However, it has a varied history of research: Due to its peculiar fertile organs, it was classified in the enigmatic group of seed ferns, particularly the Peltaspermales, with pollen and ovules being described using dubious hypotheses.
In various variants, these so-called Peltaspermales have a long range of activity, stretching from the Carboniferous through the Permian, the Triassic and at least up to the Jurassic, with the naming also giving rise

***Platycerites haeckeli*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1-2. Part of a plant with fertile leaves (STEIN 376, designated holotype); 3-4. Fronds and detail of the leaves (STEIN 337, STEIN 389); 5-7. Frond parts (STEIN 306, STEIN 281, STEIN 76); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

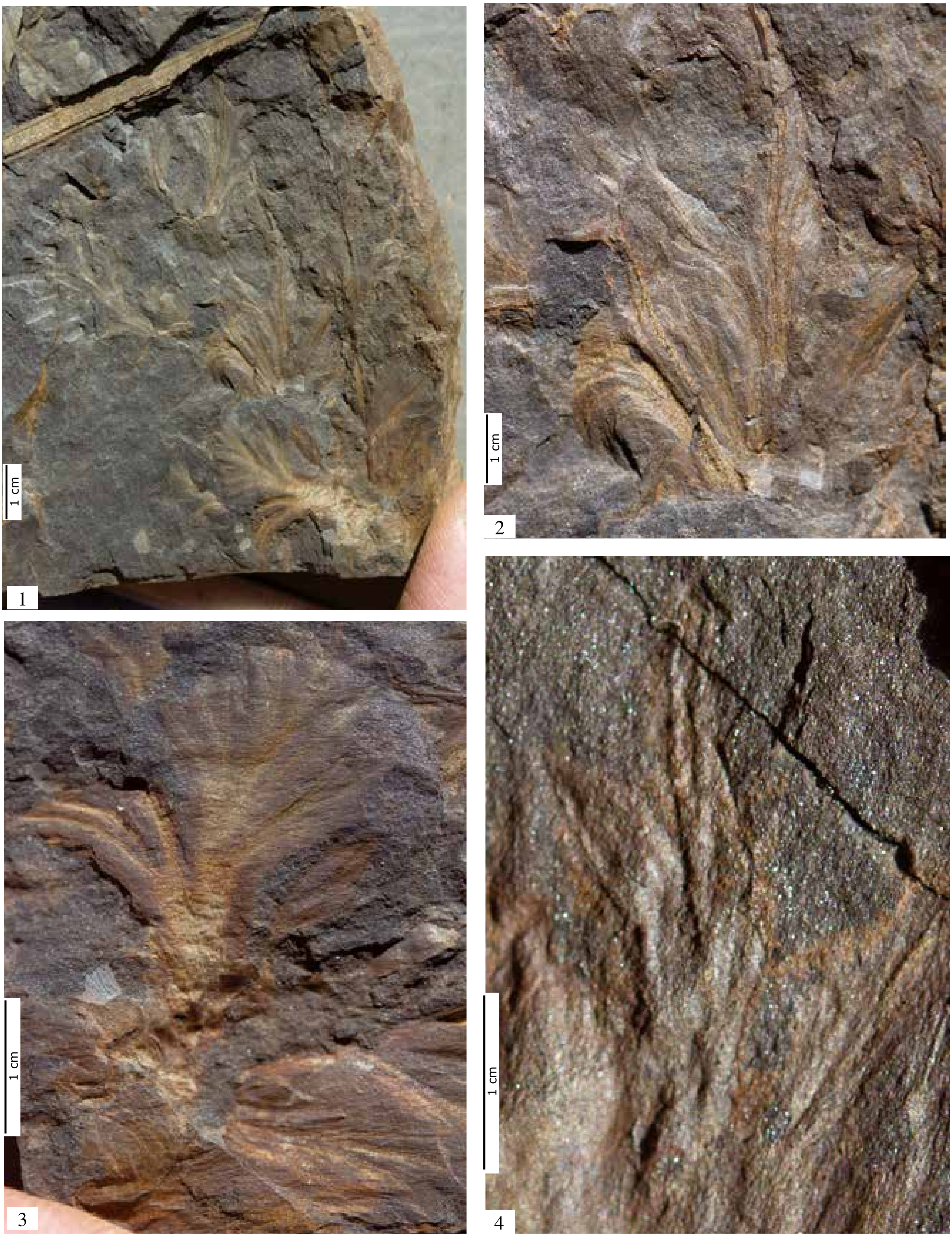


***Platycerites haeckeli*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1-2. Whole frond, partially fertile (STEIN 372, STEIN 309); 3. Juvenile frond leaf (STEIN 260); 4-6. Leaf parts (STEIN 311, STEIN 318, STEIN 301); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

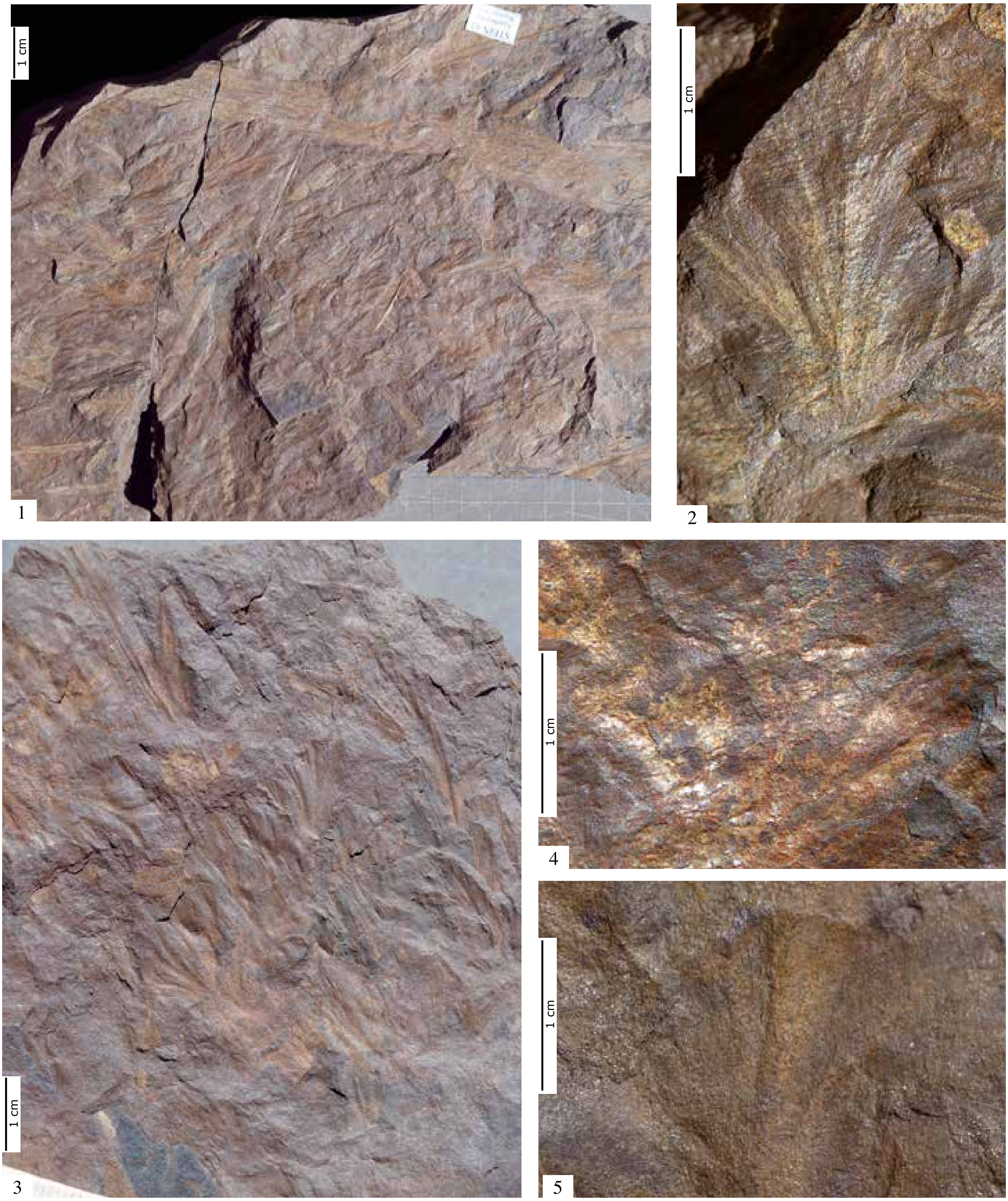
***Platycerites haeckeli*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

a. Plant; b. Fertile frond; c. Fertile leaflets; d. Sporangia; e. Spores; f. Sterile leaflets



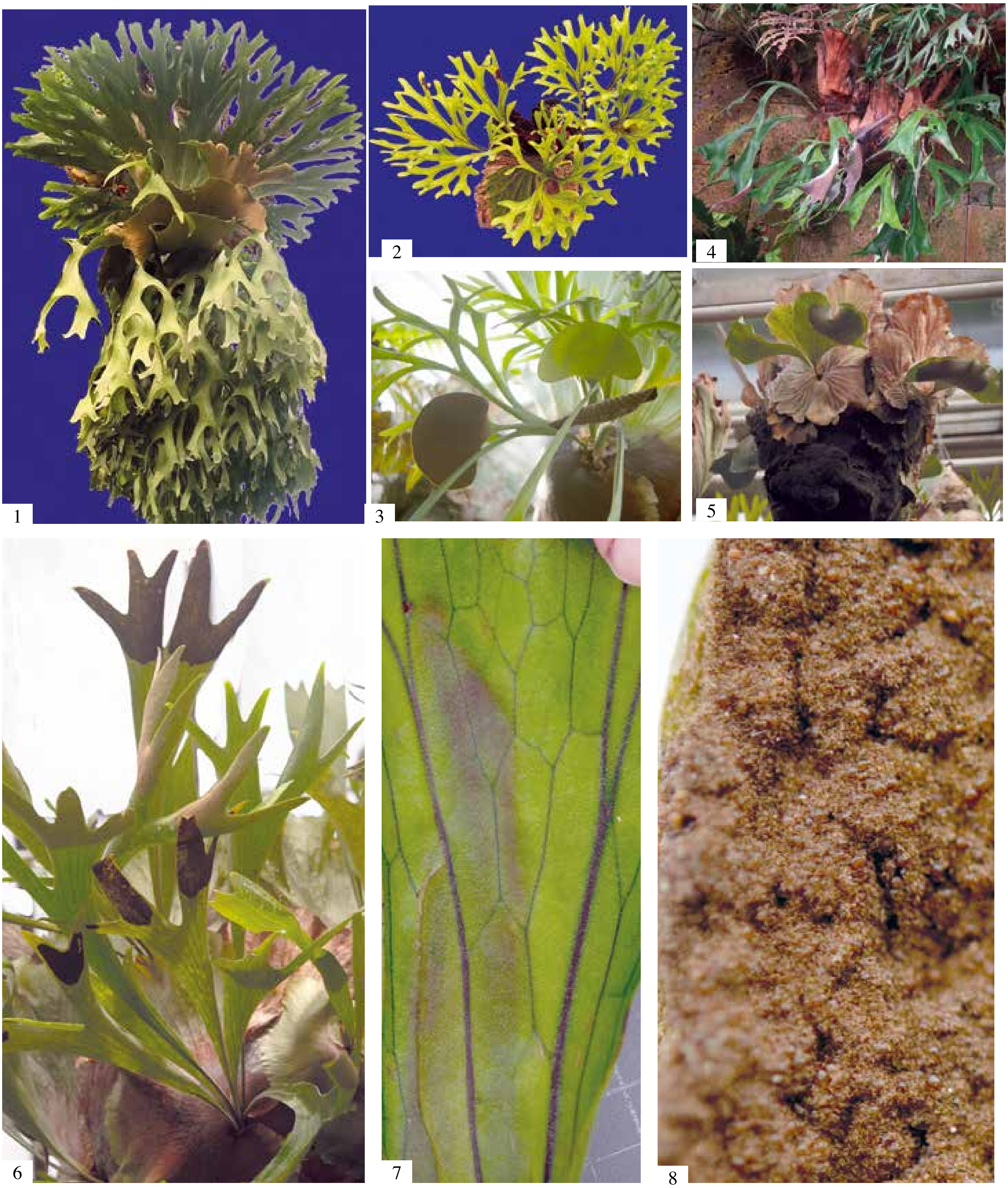
Platycerites haeckeli. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)

1-3. Fertile frond and detail of the pinnae (STEIN 77); 4. Apical part of a fertile frond (STEIN 78); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



***Platycerites haeckeli*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1-2. Almost completely preserved frond and detail of the fertile leaves (STEIN 82); 3-4. Fertile frond and detail (STEIN 87); 5. Fertile frond part (STEIN 382); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



Rezente Geweihfarne (Platycerium)

Platycerium holttumii (Indochina, Thailand) 1. Whole plant; ***Platycerium ridley*** (Malaysia, Sumatra) 2. Whole plant; ***Platycerium coronarium*** (Southeast Asia, Indochina) 3. Whole plant with fertile and steril leaves; ***Platycerium ridleyi*** (Malaysia, Sumatra and Kalimantan) 4. Whole plant; ***Platycerium elephantotis*** (tropic Africa) 5. Whole plant; ***Platycerium superbum*** (Australia) 6. Whole plant with fertile leaves; ***Platycerium bifurcatum*** 7. Frond, upper view fertile; 8. Frond lower side with sporangia

to debate. After the first descriptions as *Callipteris conferta* (Sternberg, 1826, Brongniart, 1849), it was recognized that the name *Callipteris* had already been used in 1804 by the French botanist Jean Baptiste Bory de Saint-Vincent (1780-1846) for a fern found mainly in Australia, which is now classified as Diplazium under the group of Athyriaceae.
It was therefore necessary to reclassify the fossil genus. In the Lower Permian, the name *Autunia* (Krasser, 1919) prevailed, while in the Upper Carboniferous *Callipteridium (sullivanti)*, coined by Christian Ernst Weiss (1833-1890) in 1870, found its way into the literature. Further developed forms were *Lepidopteris* (Schimper, 1869) in the Permian, also *Peltaspermum* (Harris, 1937), Scytophyllum (Bornemann, 1856) in the Triassic and *Thinnfeldia* (Ettingshausen, 1852) in the Jurassic (Wachtler, 2024h). All of them are characterized by separate sterile foliage and completely different sporophyll organs.

Alexa Wachtler prospecting the site in 2024.

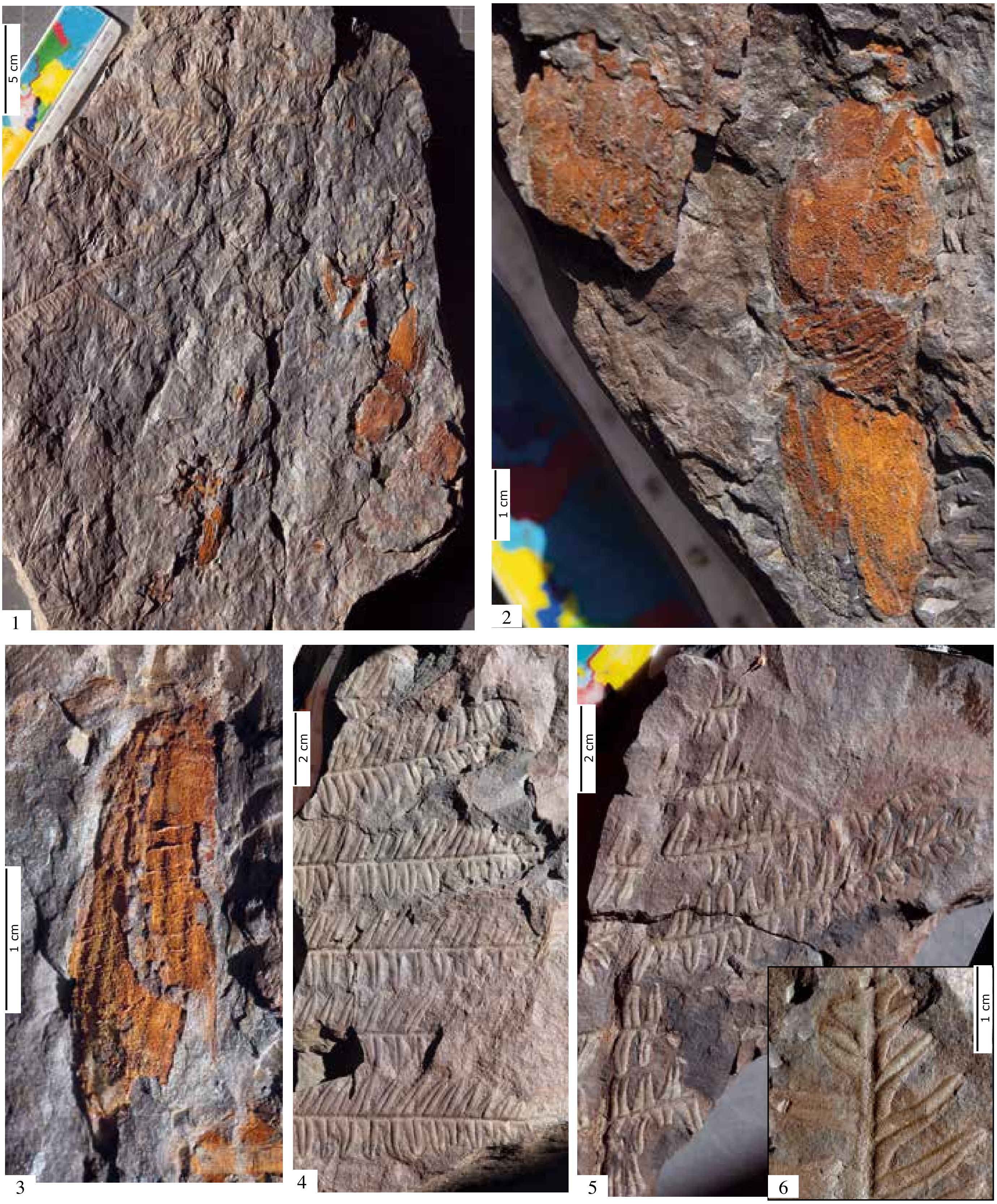
In order not to increase the confusion, the name *Callipteridium* was retained legitimate for those from the Upper Carboniferous.
Problems in classification also arose due to the leaf shapes, which changed many times over the course of millions years and could vary even within the same plant, as well as the peculiar structure of the sporophylls. In the Upper Carboniferous, these were bell-shaped and were mostly found isolated from the fronds (Wachtler, 2024), while in the Permian and Triassic they were shield-shaped and sometimes hung down in large numbers from their sterile trophophylls fronds. A milestone was the thousands of finds from the Upper Jurassic, especially from the Pechgraben fossil site in Upper Bavaria, where all the essential parts were found in context and the appearance of these ferns could thus be identified (Wachtler, 2024h).

Holotype from Weiss, 1870. *Callipteridium sullivanti,* p. 876. pl. XXI Fig. 1

In 1904, the two English paleobotanists Frederick Scott Oliver (1864-1934) and Dukinfield Henry Scott (1854-1934), with significant support from the unnamed Marie Stopes (1880-1958), classified these ferns as Pteridospermae, which means seed fern. Stopes published the popular science book "*Ancient Plants*" under her name, in which she discussed these "pteridosperms" in detail.
These "seed ferns" soon formed a vat and collection of the most diverse fossil plant parts, in which either fertile parts had never been observed up to that point, or isolated ovules that could not be assigned to any known plants.
However, it turned out that they were real ferns with a special annulus for dispersing the spores, which in *Callipteridium, Autunia, Scytophyllum* or especially *Thinnfeldia* developed sporophylls that were decoupled from the trophophylls, similar to today's Schizaeaceae, in which the genera Anemia, Schizaea and Lygodium are grouped

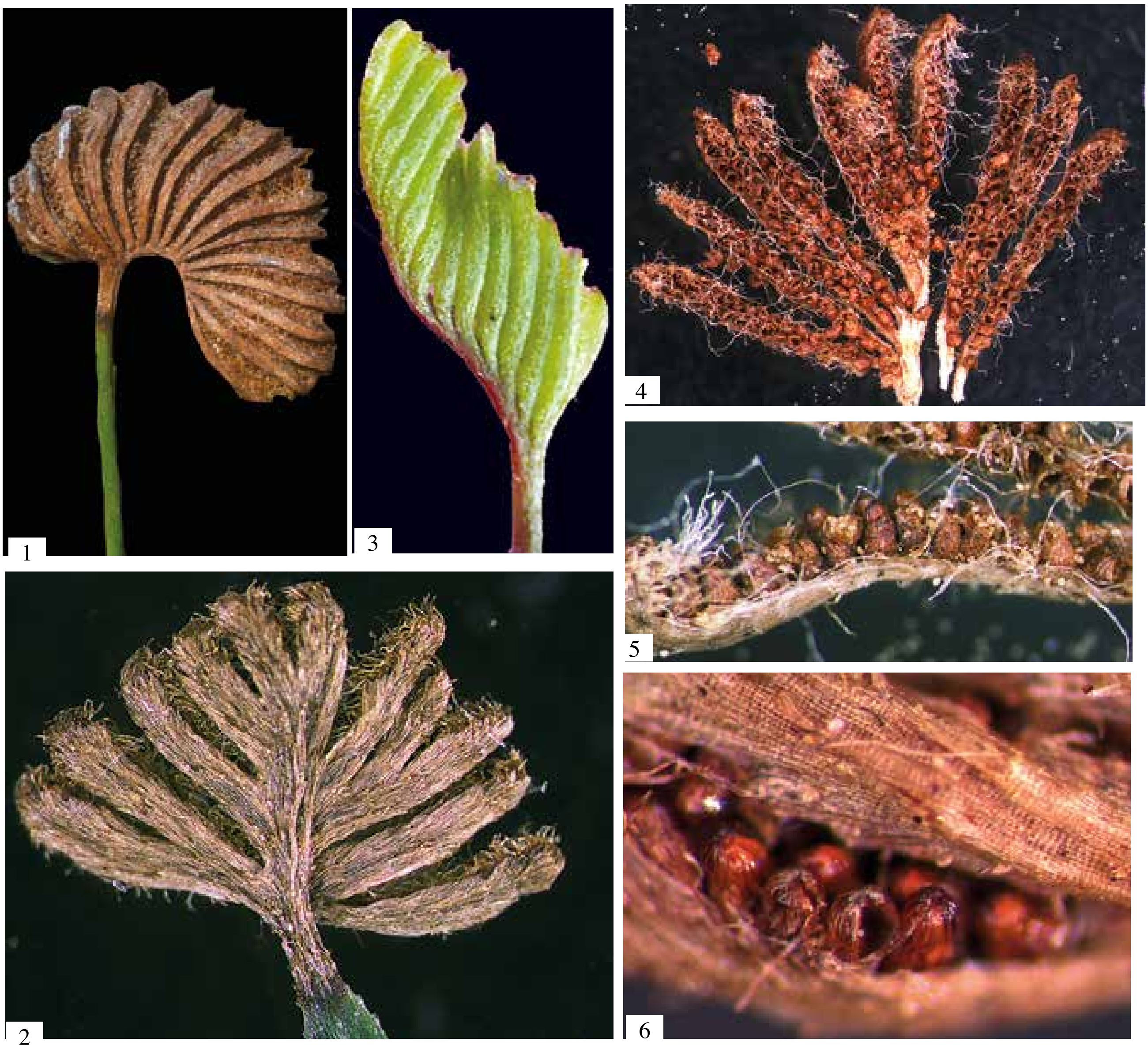
***Callipteridium wachtlerae*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

a. Fertile plant; b. Fertile frond; c. Sterile leaflet; d. Detail of a sterile leaflet; e. Sporophyll, front and back; f. Sporophyll lamina, back and front; g. Sori; h. Spores



***Callipteridium wachtlerae*.Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1-3. Sterile fronds and detail of the sporophylls (STEIN 352, designated holotype); 4. Almost complete fronds (STEIN 225, STEIN 221); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



Recent *Schizaea*-Ferns

Schizaea pectinata (Eastern USA, Chile, Pacific) 1. Fertile frond, outside; ***Schizaea dichotoma*** (Australia, Malaysia) 2. Fertile frond, outside; ***Schizaea bifida*** (Australia) 3. Sterile juvenile frond; 4. Fertile frond lower part with sporangia and sterile hair-like appendices; 5. Sporangia and 6. Detail; Courtesy University of Auckland, New Zeland

together and show similar characteristics. However, a classification as *Schizeites* (Gümbel, 1859) ultimately proves to be inappropriate, since the fossil sporo- and trophophylls differ considerably from today's Schizaeaceae.

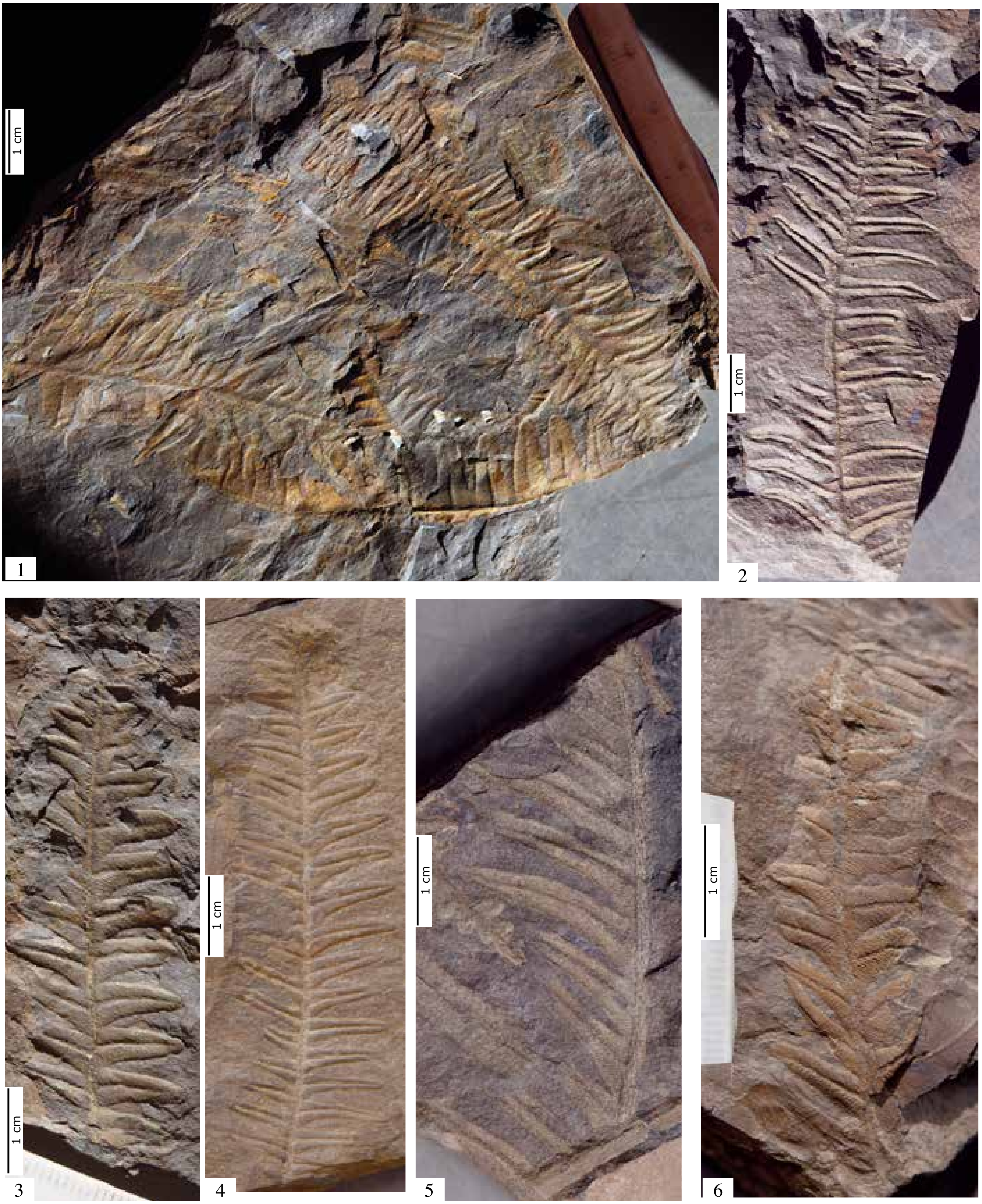
This characteristic fern of the "*Steinach Carboniferous Flora"* spectacularly shows the development from sterile fronds to detached segmented sporophyll leaves in the course of evolution. It is therefore named after its first discoverer, the scientist Alexa Wachtler, as *Callipteridium wachtlerae.*

Callipteridium wachtlerae n. sp. Wachtler 2025

1849 *Pecopteris gigas* Gutbier, p. 14, pl. 6, figs. 1–3
1870 *Callipteridium sullivanti* Weiss, p. 879, pl. XXI, fig. 1
1986d C*allipteridium gigas* Fritz et Boersma, p. 253, fig. 18.
2022 *Callipteridium ameromii* Wachtler, p. 169-174

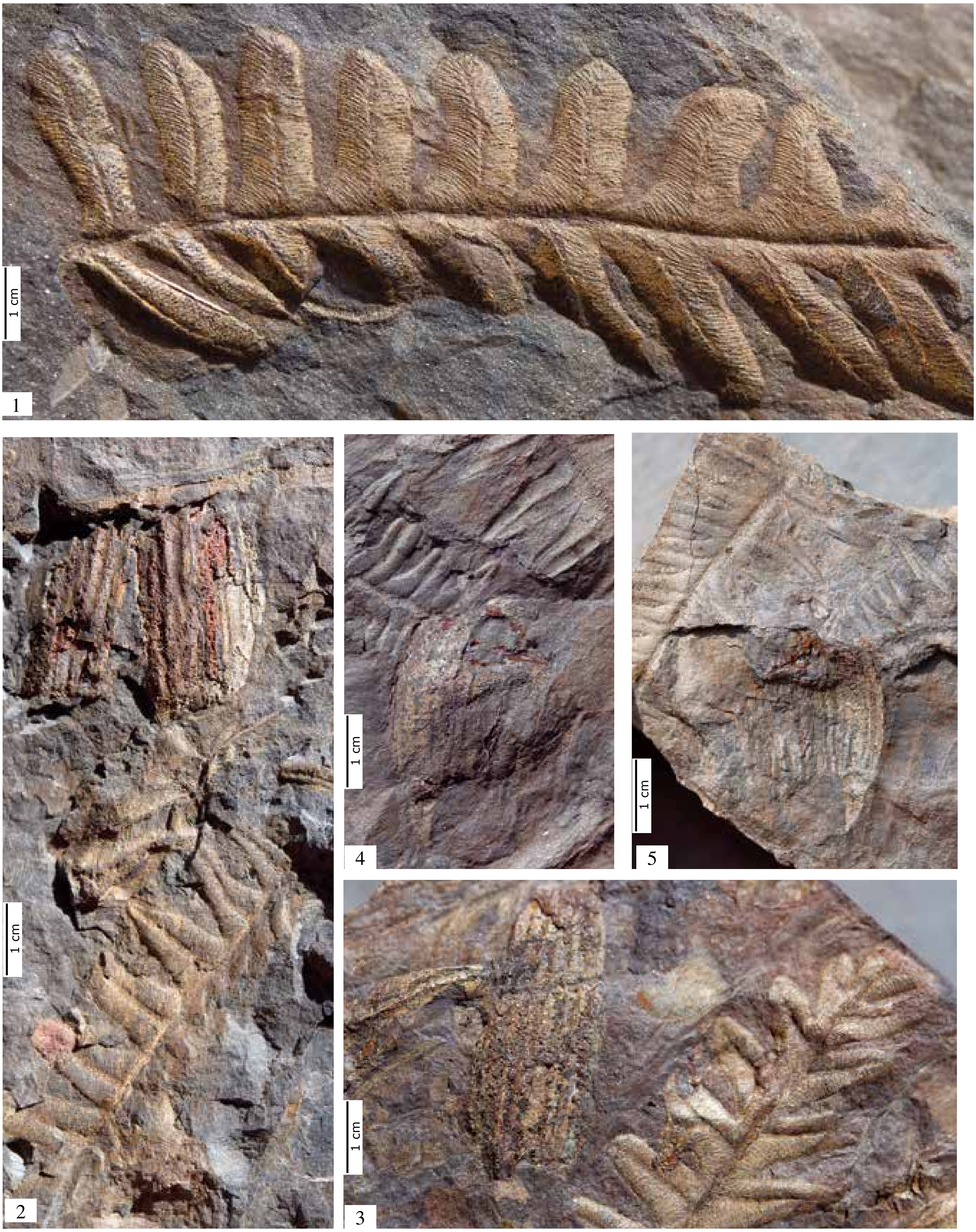
Etymology

Named after the scientist Alexa Wachtler. She discovered this fossil plant on the Eggerberg near Steinach am Brenner and made the first classifications.



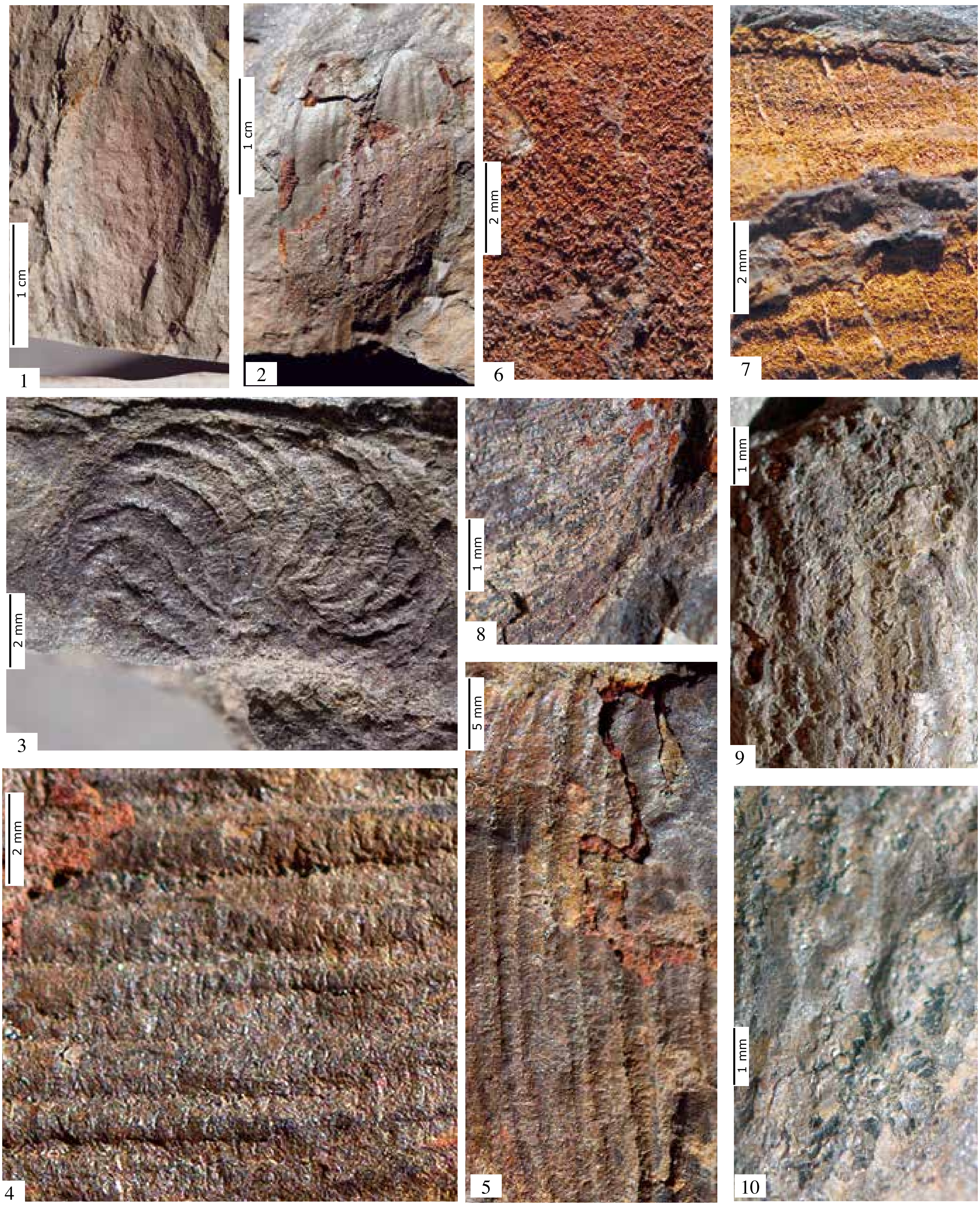
Callipteridium wachtlerae. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)

1. Slab with various isolated fronds (STEIN 229); 2-6. Various forms of tropophylls (STEIN 223, STEIN 263, STEIN 370 STEIN 379, STEIN 198); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



Callipteridium wachtlerae. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)

1. Detail of the pinnae (STEIN 188); 2-3. Various trophophylls and sporophylls (STEIN 207, STEIN 190); 4-5. Isolated sporophylls (STEIN 187, STEIN 184); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



***Callipteridium wachtlerae*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1. Sporophyll, outside (STEIN 359, STEIN 344); 3. Sporophyll, top view (STEIN 331); Sporophyll and detail (STEIN 206); 6-7. Detail of the sporangia (STEIN 352, holotype); 8-9. Detail of the sporangia (STEIN 189, STEIN 210, STEIN 128); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

Holotype

STEIN 352 (Coll. Wachtler, Dolomythos-Museum, Innichen)

Diagnosis

Trophophyll fronds tripinnate. Pinnules of the last order broadly attached to the rachis, elongated, consistently leathery and tapering to a point. Sporophylls bell-shaped segmented with spore primordia developed beneath.

Description

Whole plant: Fronds, tripinnate, reaching about 50 cm in length and 30 cm in width (STEIN 225, STEIN 221).
Sterile fronds: Individual pinnula of the last order opposite to slightly offset, thickened, broadly attached to the base of the rachis. About 2 cm long, 0.5 to 1 cm wide (STEIN 229, STEIN 223, STEIN 263, STEIN 370 STEIN 379, STEIN 198). Pinnules with smooth edges, mostly slightly to extremely pointedly curved upwards, rarely rounded, this only in the lower part of the frond. Small venation in large numbers and close together branching off from the midrib, forking once or at most twice to the middle of the pinnate.
Fertile organs: Sporophylls reaching 2-3 cm in length and 1.5 to 2 cm in width. Lamina consisting of a large number of closely fused sporangia tubes. These are broadly attached to the base of the stem, pointed at the top and tapering with contraction (STEIN 359, STEIN 344, STEIN 331, STEIN 206, STEIN 352 (holotype), STEIN 189, STEIN 210, STEIN 128, STEIN 207, STEIN 190). Sporangia with annulus, releasing spores when mature.

Remarks

Callipteridium wachtlerae is an excellent example of following the evolution of a plant, in this case a fern. The division into sporophylls and trophophylls in particular has confused many generations of researchers and led them to speak of ovules. Now it is possible to understand how the sterile pinnae, which taper to a point in the upper frond area, formed the characteristic fertile capsules with their sporangia collected inside.
In the case of *Callipteridium ameromii* from the Nock Mountains and the Carnic Alps, which came a little later, this process is largely complete and its origin can hardly be determined (Wachtler, 2023g). Now we are dealing with large numbers of spore leaves attached to a spindle, which were bell-shaped when embedded laterally and were pressed apart in a shield-like manner when viewed from above. Due to reduced sporophylls from the Permian (*Peltaspermum, Lepidopteris)*, the Triassic (*Scytophyllum)* to the Jurassic (*Thinnfeldia)*, only shield-shaped aggregates were found and mostly interpreted as ovules.
Callipteridium wachtlerae represent one of the most common plant finds in the Steinach Carboniferous flora, and the details, growth or structure of the plant are well known. However, well-preserved entire fronds are rare. The pinnae are relatively easy to distinguish from other ferns such as *Danaeites, Dicksonites, Platycerites* or *Cyclopteris;* the pinnae are most likely to be confused with *Cyatheites,* but the abundant clusters of sporangia on the rounded pinnae largely rule out confusion.

Danaeites, Goeppert 1836

The name *Danaeites (asplenioides)* was first used by the German paleontologist Heinrich Göppert (1800-1884) in 1836 for a fossil fern genus (pp. 379-380) "*which we still find together ... today in Danaea*". The poor leaf impression of the first description (Plate XIX fig. 4-5) came from the Upper Carboniferous Schatzlar layers, today Žacléř, a small town in the Czech North Bohemia. In 1883, the Slovak geologist and paleontologist Dionýz Štúr studied these finds in more detail by adding further *Danaeites* ferns (*Danaeites sarepontanus, Danaeites villosus, Danaeites marattiaetheca)* from the Carboniferous (pp. 778). The disadvantage in all these finds and descriptions was that they were either not depicted or the pinnae could only be associated with today's Danaea ferns with extreme imagination.
The confusion increased when well-preserved leaves and fronds were subsequent-

ly found from the Triassic (Ladin) of Germany, which were described and combined with constantly changing names such as *Taeniopters marantacea* (Presl in Sternberg, 1820), *Marantoidea arenacea* (Jaeger, 1827), *Danaeopsis marantacea* (Schenk, 1864). The name *Danaeopsis marantacea* (Zijlstra et. al., 2010) was recently officially accepted.

In order not to expand the nomenclature questions, the name *Danaeopsis* continues to be used for the Triassic ferns, while Göppert's *Danaeites* is retained for those from the Carboniferous. In 2016, Michael Wachtler described *Danaeopsis dolomitica* from the early-middle Triassic (Anis) Dolomites, another fully developed Danaea precursor, and subsequently (Wachtler, 2023f) one from the late Upper Carboniferous of the Eastern Alps under the name *Danaeites perneri.* However, it turned out that this fern group extended further back almost to the Middle Carboniferous and it made sense to describe another species.

Danaeites kerneri n. sp. Wachtler 2025

1836 *Danaeites* (Goeppert) Die Fossilen Farrnkräuter, p. 379-380, pl. XIX fig. 4-5

1864 *Danaeopsis marantacea* Schenk, p. 84

1865 *Danaeopsis marantacea* in Schönlein & Schenk, p. 16, pl. 7, fig. 2, 3, 4

1883 *Danaeites sarepontanus* (Stur) p. 780, fig. 29

2023 Danaeites perneri Wachtler, p. 132-134

Etymology

Named after the Austrian paleobotanist, geologist and meteorologist Fritz Kerner von Marilaun (Innsbruck 1866 - Beč, 1944). He worked intensively on "*The Carboniferous Flora of the Steinacherjoch"* (1897).

Holotype

STEIN 394 (Coll. Wachtler, Dolomythos-Museum, Innichen); **Paratype:** STEIN 146, fertile frond

Diagnosis

Fronds pseudo-bipinnate. Pinnules entire, composed of a fusion of many small individual leaflets. On the underside, each individual leaflet develops two rows of partially fused round sori.

Description

Whole plant: Sterile fronds reach a size of 30-50 cm (STEIN 394, holotype; STEIN 243). Individual leaflets about 10 cm long, 1 cm wide, traversed from a midrib to the tip and tapering to a point (STEIN 327). Base barely stalked. Frond leaves composed of a fusion of many small individual leaflets, which are characterized by V-shaped, otherwise undivided venation (STEIN 396).

Fertile fronds similar, consisting of a aggregation of many individual leaflets, each of which is composed on the underside of an accumulation of many round sporangia, arranged in two longitudinal rows (STEIN 146, paratype; STEIN 242, STEIN 89, STEIN 393, STEIN 345, STEIN 245).

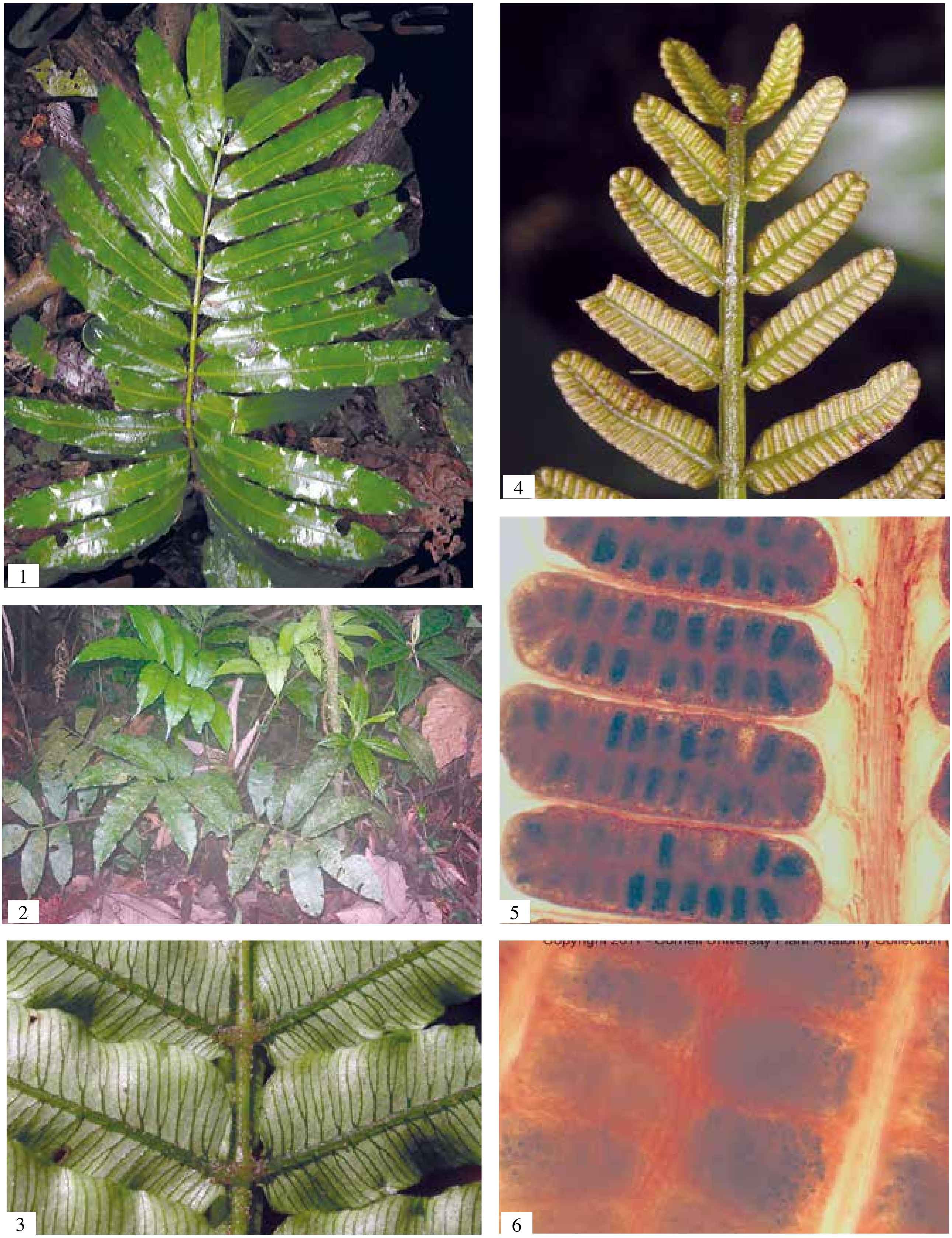
Remarks

Although it appeared in the early Upper Carboniferous (Bashkirian-Moscovian), *Danaeites kerneri* was highly developed, and had a precursor status to *Danaeites perneri,* which appeared later in the Upper Carboniferous (Kasimovian-Gzhelian), especially at the Kronalpe site.

From both Danaea precursors, it can be deduced that they were based on the fusion of many small individual pinnae to form a single pinnae. It also turned out that a common evolution of those Danaea ferns (together with Marattia and Angiopteris), which are mostly classified under the Marattiales, separated at least before the early Upper Carboniferous, which means that any family similarities within this group are probably limited to the Devonian.

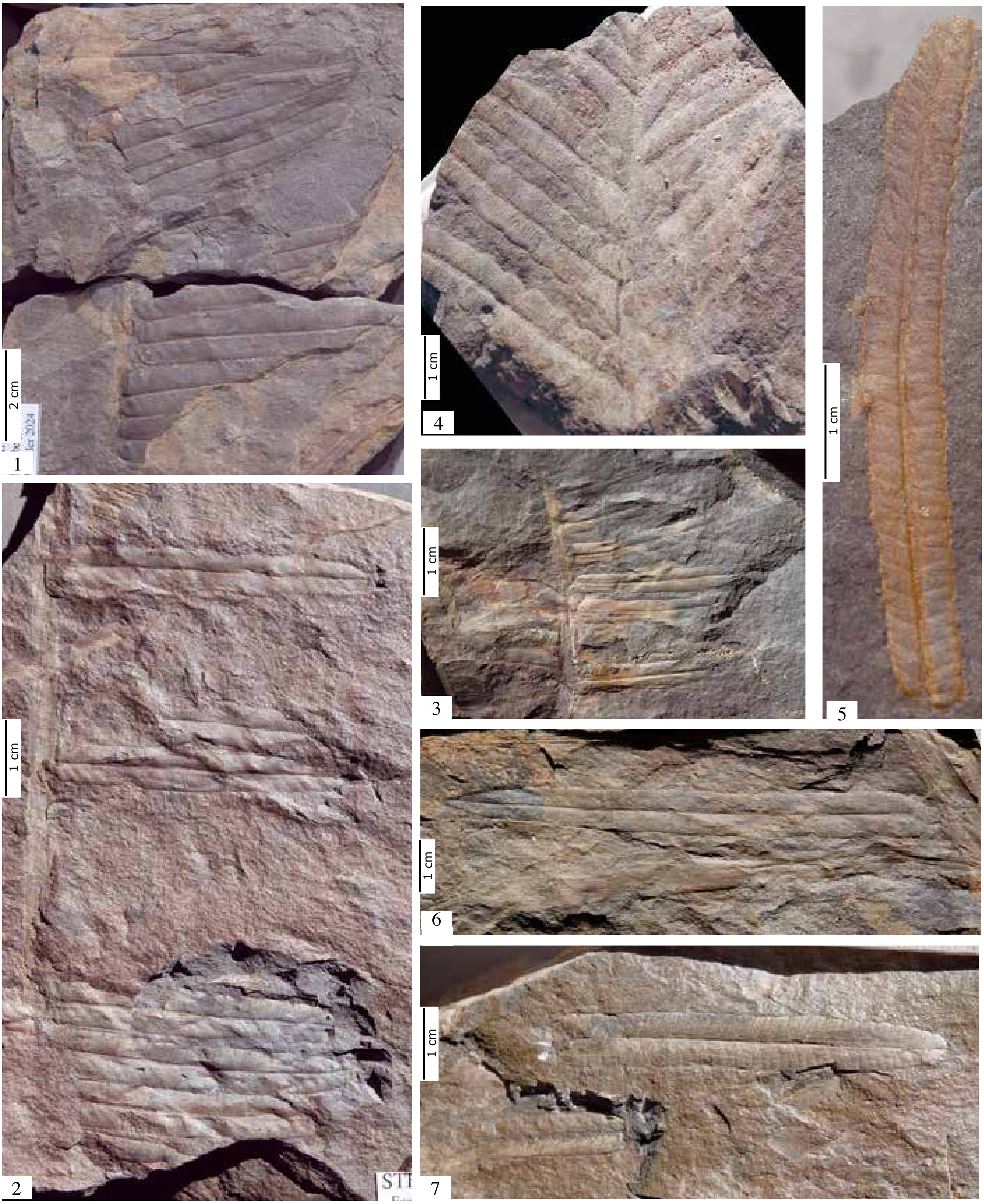
Today's Danaea ferns comprise about 50 species, with their distribution area extending from southern Mexico through Central America, the Caribbean and the northern part of South America to Brazil and northern Argentina.

Their synangia consist of elongated structures that extend from the midrib to the leaf margin, which are embedded in shallow depressions on the underside of the leaf. Danaea is also the only genus of the Marattiales in which sterile and fertile fronds have a different appearance. The latter develop narrower blades and have longer stalks.



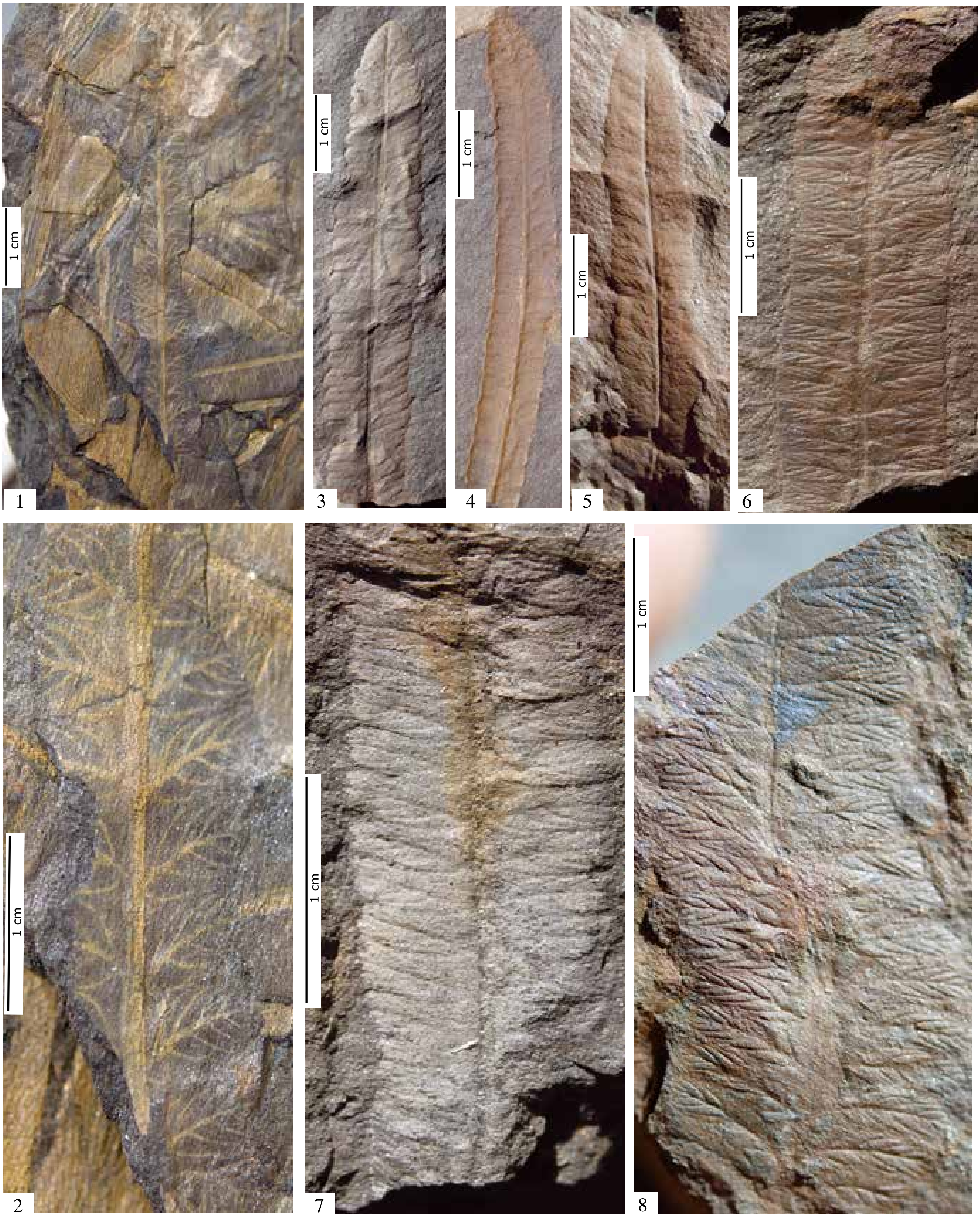
Rezente *Danaea*-Farne

Danaea nodosa 1. Frond; ***Danaea elliptica*** 2. Whole plant; ***Danaea wendlandii*** 3. Lower part of a frond with details of the veins; 4. Fertile frond, lower part; 5-6. Detail of the sproangia (Fotos Cornell University)



Danaeites kerneri. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)

1. Part of a frond (STEIN 394, designated holotype); 2-3. Fronds (STEIN 243, STEIN 145); 4. Apical part of a frond (STEIN 261); 5-7. Sterile individual leaflets (STEIN 322, STEIN 327, STEIN 131); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



***Danaeites kerneri*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1-2. Upper side of pinnae with detail of veins (STEIN 396); 3-6. Isolated sterile pinnae (STEIN 135, STEIN 322, STEIN 295, STEIN 149); 4. Details of veins of sterile pinnae (STEIN 147, STEIN 274); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

***Danaeites kerneri*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

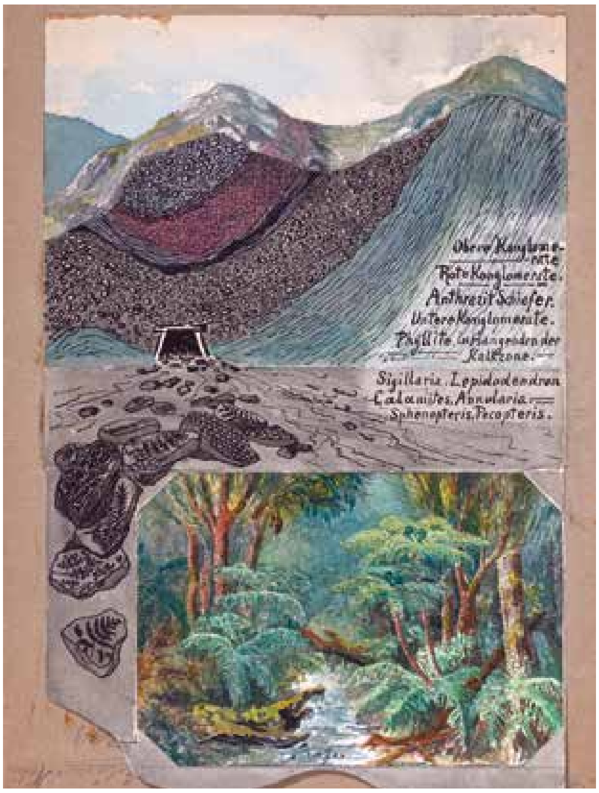
1. Fertile frond (STEIN 146, paratype); 2. Fertile pinnae upper and lower sides (STEIN 242); 3-5. Fertile pinnae and details of the sporangia (STEIN 89, STEIN 393, STEIN 345, STEIN 245); 7-8. Fertile pinnae (STEIN 151, STEIN 278); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

Danaeites kerneri. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)

a. Fertile plant; b. Sterile frond; c. Sterile leaflet; d. Detail of veins; e. Fertile leaflet, underside; f. Fertile leaflet underside with sori; g. Sorus

Cyclopteris Brongniart 1828

An enigmatic fern that is common in the Steinach Carboniferous flora is *Cyclopteris,* although comparisons with today's families or genera are not necessarily useful. One could most likely assume a close relationship with the Dryopteridaceae family, such as the fern Didymochlaena.
The name *Cyclopteris* was first used in 1828 in a short description without illustration by Adolphe Brongiart (p. 51), in which he named three subspecies from the Carboniferous: *Cyclopteris orbicularis, Cyclopteris obliqua* and *Cyclopteris flabellata.* Brongniart made comparisons with today's *Adiantum reniforme* and *Trichomanes reniforme* (today *Hymenophyllum nephrophyllum).* The first illustrations and further descriptions (p. 215-221) were made in the same year 1828 with other species such as *Cyclopteris reniformis, Cyclopteris digitata* (today *Gingkoites digitata,* an ancestor of the ginkgos) and *Cyclopteris trichomanoides.* However, none of the illustrations correspond to the finds from the Eastern Alps.
In 1838, Caspar Graf von Sternberg described a *Cyclopteris alpina* from Stangnock in Carinthia, where he recognized that the pinnae could be attached to long spindles, but could also be connected to the axis without a stalk. A new genus name should therefore actually be chosen for the leaf shapes that often occur in Europe, but in order to maintain continuity, it is proposed to continue using the genus name *Cyclopteris* for tongue-shaped, relatively large leaves with sometimes dichotomous veins.
Of interest are their fertile organs, whose appearance often brought them into contact with seed ferns. However, comprehensive studies of the Alpine Upper Carboniferous deposits from Stangnock, the Cason di Lanza (Rio del Museo), and those from Steinach am Brenner indicate that these are typical fern sporangia with annulus and spores squeezed into them, which were often deposited with a protective leaflet covering them, an indusium.
This is all the more interesting because it means that the structure of the seed ferns, which has been vehemently built up over many decades, collapses like a house of cards: There were never any seed ferns, neither in *Cyclopteris*, nor in *Callipteridium,* nor in *Peltaspermum, Scythophyllum, Sagenopteris* or Thinnfeldia. They are all ferns, because no separate pollen or ovules were formed for them.
Since the *Cyclopteris* ferns, which occur relatively frequently in the Steinach Carboniferous flora, have somewhat different characteristics, a new name is proposed.



From Fritz Kerner von Marilaun: „*Mineralogisches Verwandlungsbilderbuch zur Belehrung für Jung und Alt*" (Mineralogical transformation picture book for instruction for young and old". In short poems, Fritz Kerner describes geological processes, accompanied by watercolors. Among other things, he shows a geological section through the coal deposit of the Nösslach Joch in Tyrol with a picture of life from the Carboniferous period (Volkmar Stingl Archive, now Tyrolean State Museum)

Cyclopteris pichleri n. sp. Wachtler, 2025

1828 *Cyclopteris* Brongniart, Prodr. Hist. Veg. Foss.: 51. Dec 1828 [Foss.], nom. cons. prop.

1828 Cyclopteris orbicularis Brongniart, Hist. Veg. Foss. 1: 220. 6 Jun 1831) Tab. 61. fig. 1-2

1838 Cyclopteris alpina, Sternberg Tab. XXXIX. fig. 3. *Carpolites multistriatus,* Tab. XXXIX fig. 1, 2

1897 Neuropteris acutifolia Kerner, Tab. IX. Fig. 4

2022 Cyclopteris alpina Wachtler, p. 158-162

Etymology

Named after the Tyrolean writer and natural scientist Adolf Pichler (1819-1900). In various publications from 1858 onwards, he first described plant remains from the Nösslacher Joch at the Brenner.

Holotype

STEIN 375, **Paratype:** Stein 377 (Coll. Wachtler, Dolomythos-Museum, Innichen)

Diagnosis

Fronds with tongue-shaped pinnae. Veins densely arranged and delicate, sometimes dichotomizing without ever developing into reticulate venation.

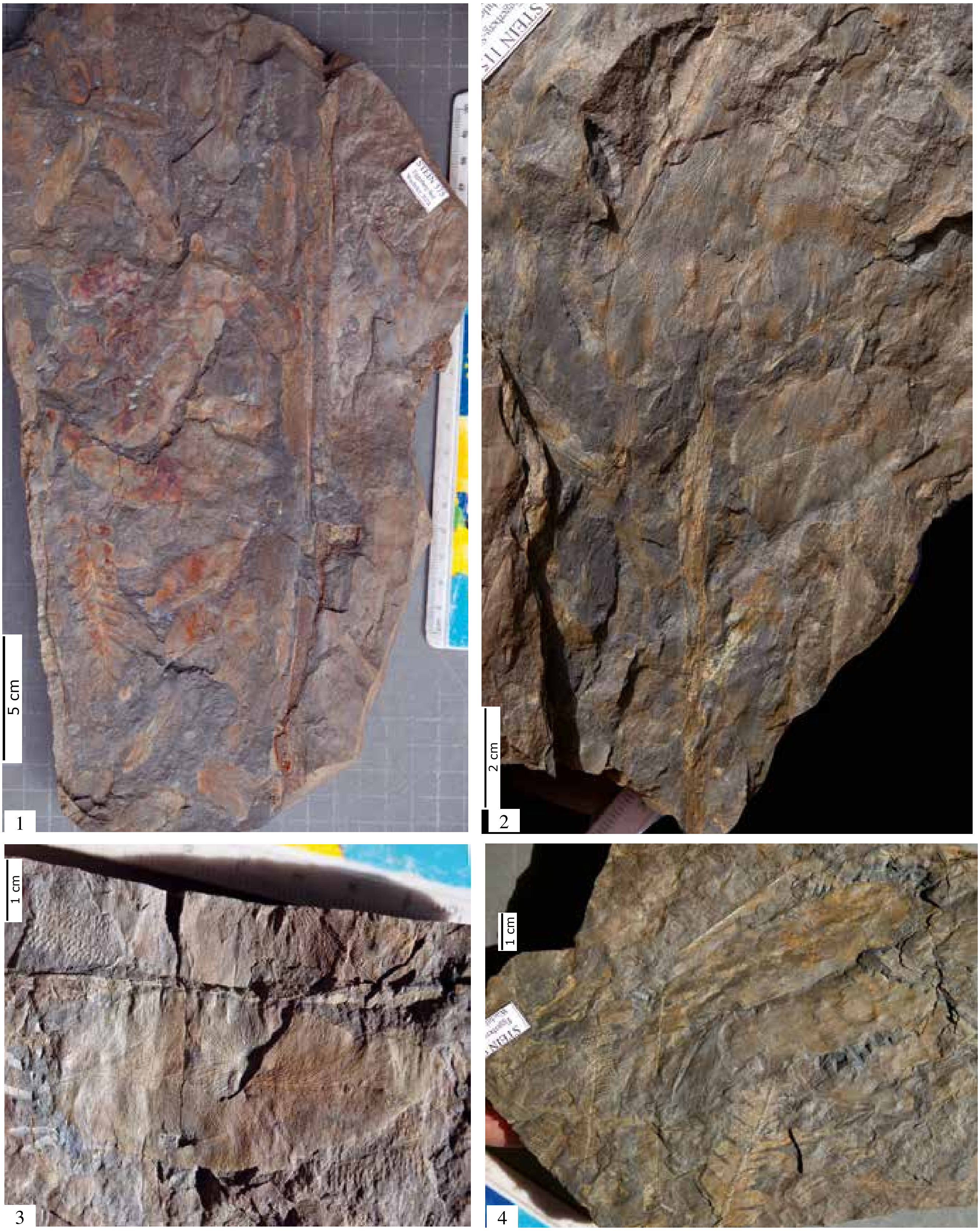
Adolf Pichler in 1854. A few years later (1858) he discovered and described the coal formation of the Steinacher Joch (Archive Michael Wachtler, Dolomythos)

Description

Whole plant: Main stems up to 2 cm thick (STEIN 375, holotype), sometimes forking (STEIN 115). Leaves tongue-shaped, up to 8 cm long, 2 to 2.5 cm wide (STEIN 96, STEIN 99, STEIN 102, STEIN 104, STEIN 105, STEIN 107, STEIN 108, STEIN 268, STEIN 332, STEIN 374, STEIN 413). These are partly leathery, but also paper-thin, sitting on the rachis without a stalk. Leaf veins delicate, arising from the leaf base, forking a few times, but no mesh or net veins forming. All veins equally thick and without a strong midrib.
Fertile organs: Round, flattened (STEIN 377, STEIN 407), about 1 cm tall, 0.8 cm wide. Annulus with spores partially visible within an indusium.

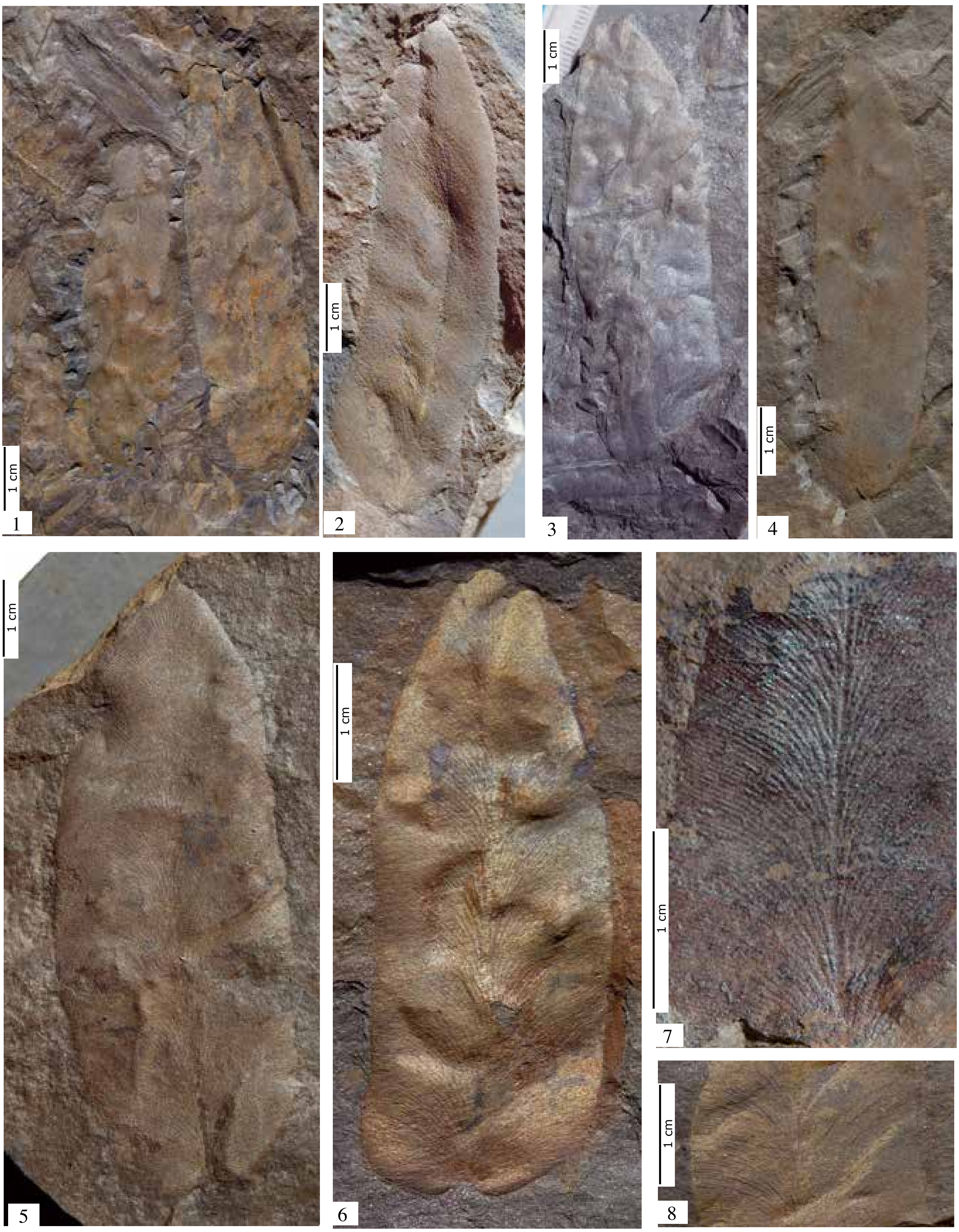
Remarks

Cyclopteris represents a common plant in the European Upper Carboniferous. Franz Unger listed 27 different species from Europe alone in his 1847 book "*Chloris protogæa*", and even finds have been made in the American landmass (Rothwell & Eggert, 1986), so that its distribution area probably extended across the entire northern hemisphere.
The leaves, which were mostly found in isolation, were interpreted as fern aphlebias, although finds prove that it was a plant with short and long shoots. Its earliest appearance, *Cyclopteris pichleri,* dates back to the early Upper Carboniferous, although it later became widespread, particularly on the Stangnock *(Cyclopteris alpinus)* in the Carinthian Nock Mountains, and is found just as abundantly at the Rio del Museo (Cason di Lanza) site in the Carnic Mountains. However, it is completely missing in the Kronalpe fossil site, which belongs to the youngest Carboniferous. *Cyclopteris* is one of the most enigmatic Carboniferous plants: especially at the Stangnock site and at Cason di Lanza, carpets of *Cyclopteris* leaves cover the layers, although complete leaf fronds are rare. At Stangnock, there are also plenty of tongue-like pinnate leaves



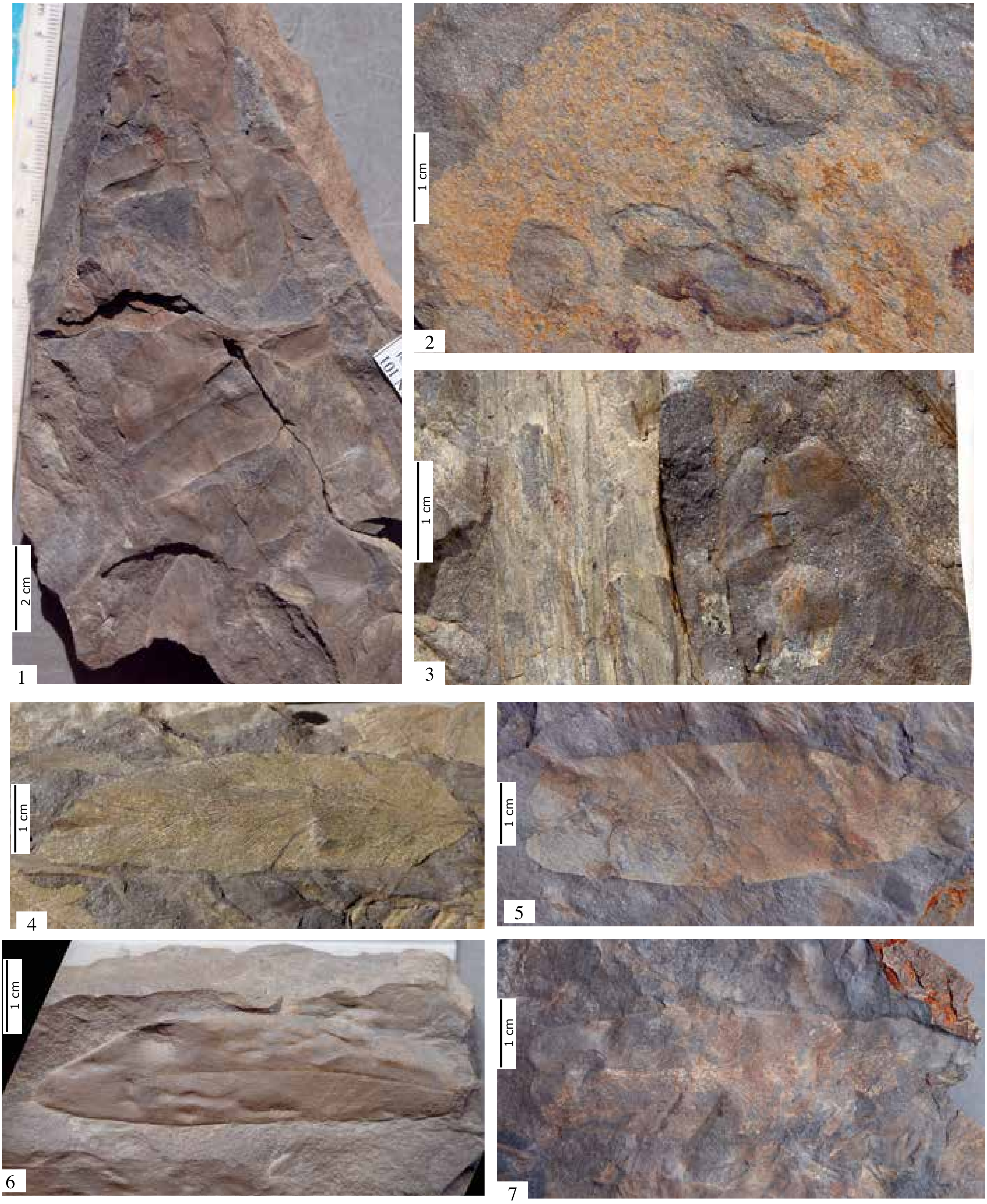
***Cyclopteris pichleri*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1. Branchlet with leaves (STEIN 375, holotype); 2. Various leaves with trunk (STEIN 115); 3-4. Various details of the leaves (STEIN 239, STEIN 96); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



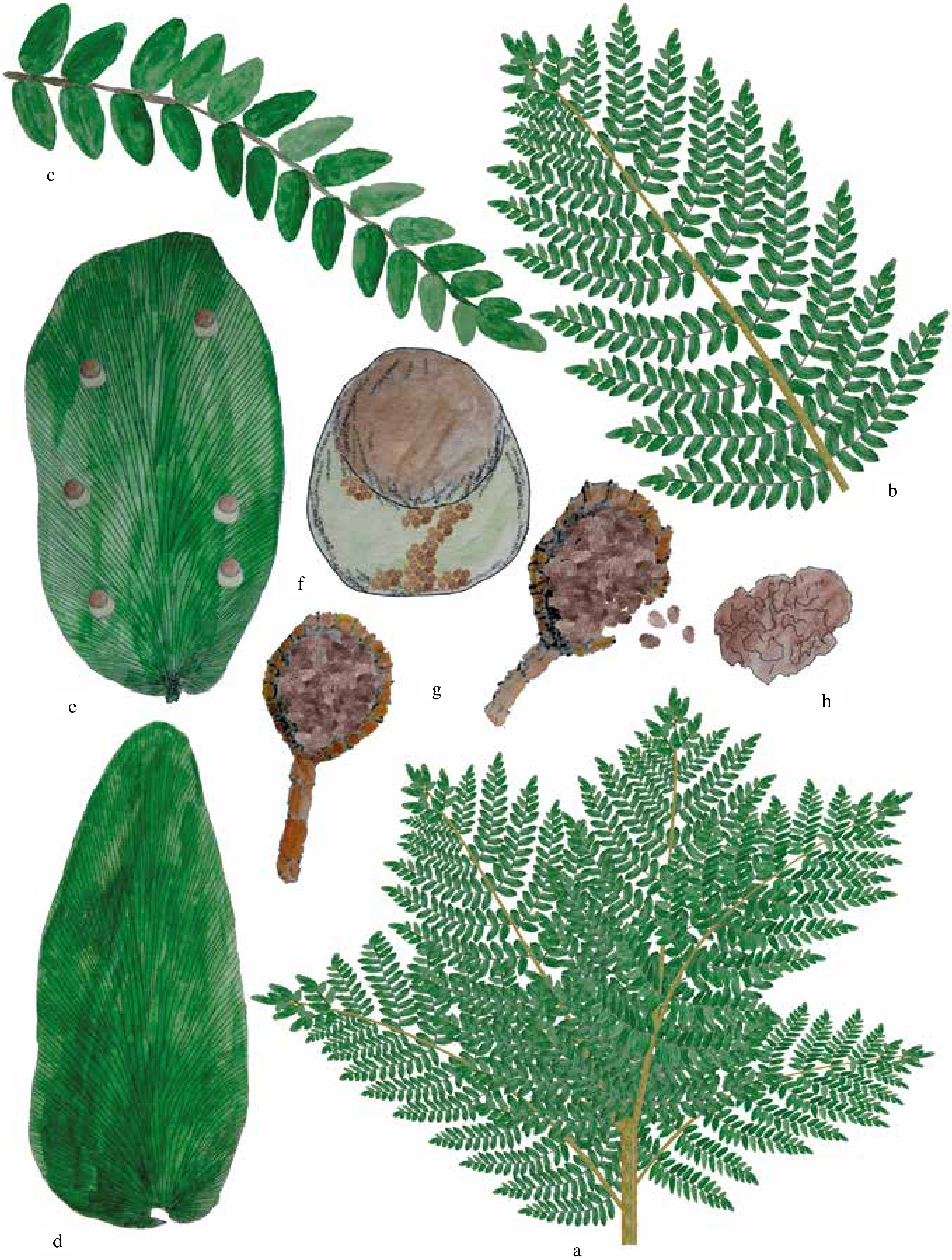
***Cyclopteris pichleri*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1-8. Various details of the leaves (STEIN 96, STEIN 268, STEIN 102, STEIN 104, STEIN 108, STEIN 107 STEIN 105, STEIN 99); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



***Cyclopteris pichleri*. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)**

1. Plate with various leaves (STEIN 101); 2. Fertile parts (STEIN 377, Paratype), 3. Fertile parts (STEIN 407); 4-7. Various leaves (STEIN 332, STEIN 413, STEIN 374, STEIN 375); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



Cyclopteris pichleri. Steinacher-Flora. Ferns (Late Carboniferous, Bashkirian-Moskovian)

a. Whole plant; b. Frond; c. Sterile leaflets; d. Individual leaflets; e. Fertile leaflet underside; f. Sorus; g. Sporangia with annulus closed and opened; h. Spore with thin, long stalks, and also without. The nut-like spore-bearing plants are interesting and have long been the subject of debate. Strangely, after classifying the *Callipteridium* species, which also occur in the Upper Carboniferous and can clearly be classified as ferns with different sporophylls and trophophylls, and *Cyclopteris*, which also has sori that are typical of ferns, there is not a single plant left that could be classified as a seed fern.

Calamites Brongniart 1828

Among the so-called sporangia horsetails, which only have similarities to today's Equisetaceae due to their stem and leaf characteristics, a dominant species can be found in the Carboniferous of Steinach. Although comparisons could be made with the *Calamites multiramis,* which occurs in large numbers especially on the Kronalpe and is characterized by its decorative lateral fronds known as *Annularia stellata*, differences can still be seen. It therefore makes sense to establish a new species and name it *Calamites steinachii* due to its occurrence in the Upper Carboniferous of Steinach.

Calamites steinachii n. sp. Wachtler 2025

1897 *Annularia longifolia,* Kerner von Marilaun,Pl. VIII, Fig. 1

1897 *Annularia fertilis* Kerner von Marilaun Pl. VIII, Fig. 2

1897 *Annularia brevifolia* Kerner von Marilaun Pl. VIII, Fig. 3

1897 *Calamostachys sp.* Kerner von Marilaun Pl. VIII, Fig. 4

1897 *Stachannularia tuberculata* Kerner von Marilaun Pl. VIII, Fig. 5

1897 *Sphenophyllum erosum* Kerner von Marilaun Pl. VIII, Fig. 6

1897 *Sphenophyllum emarginatum* Kerner von Marilaun Pl. VIII, Fig. 7

Etymology

Named after the municipality of Steinach am Brenner, as well as the former name for the discovery area Steinacher Joch in the Stubai Alps (now called Nösslachjoch).

Holotype

STEIN 305 (Fertile organ)

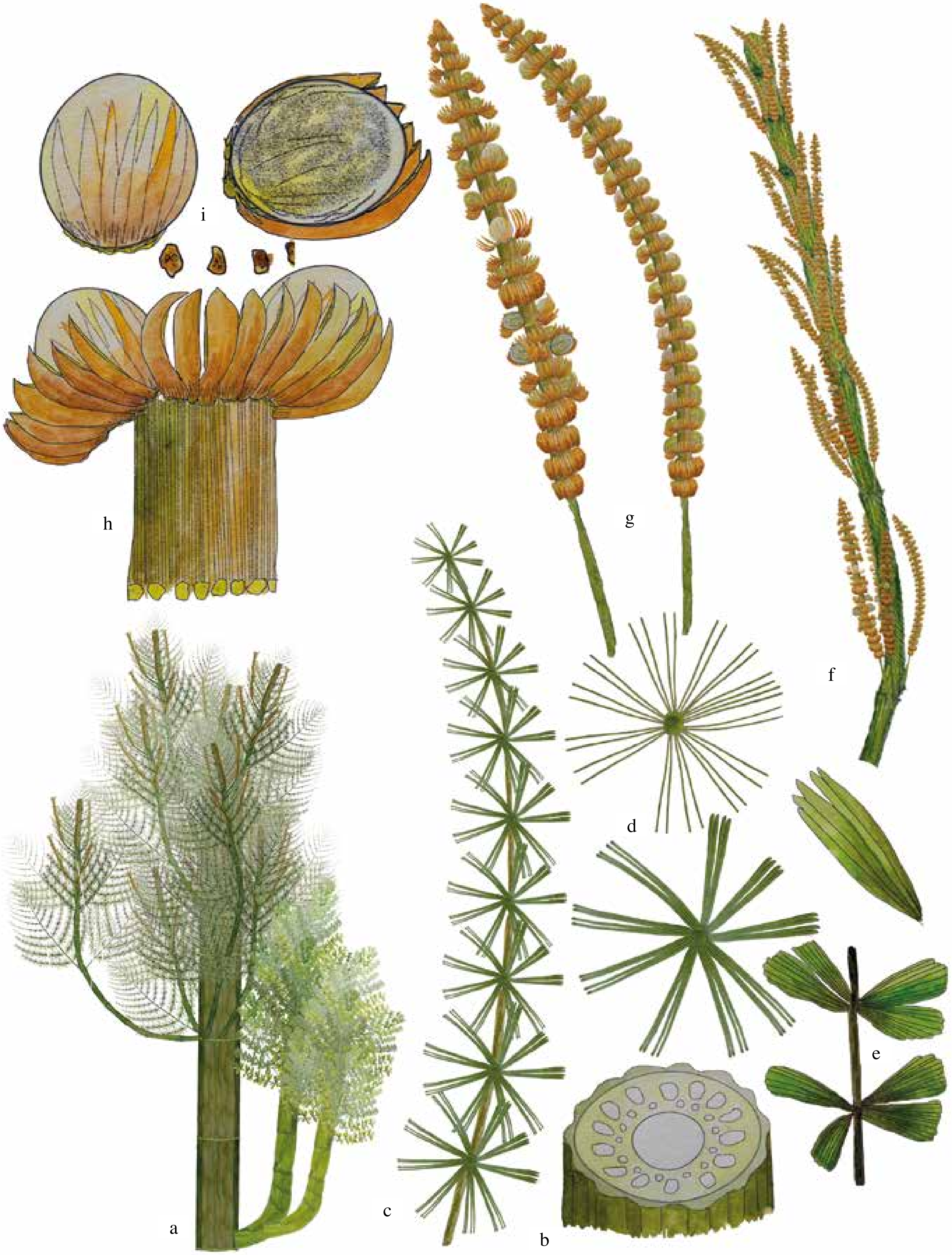
Diagnosis

Stems characterized by internodes, which develop whorls with radial leaflets at regular intervals on the side branches. Sporangiophores with short bracts that tightly clasp the sporangia.

Description

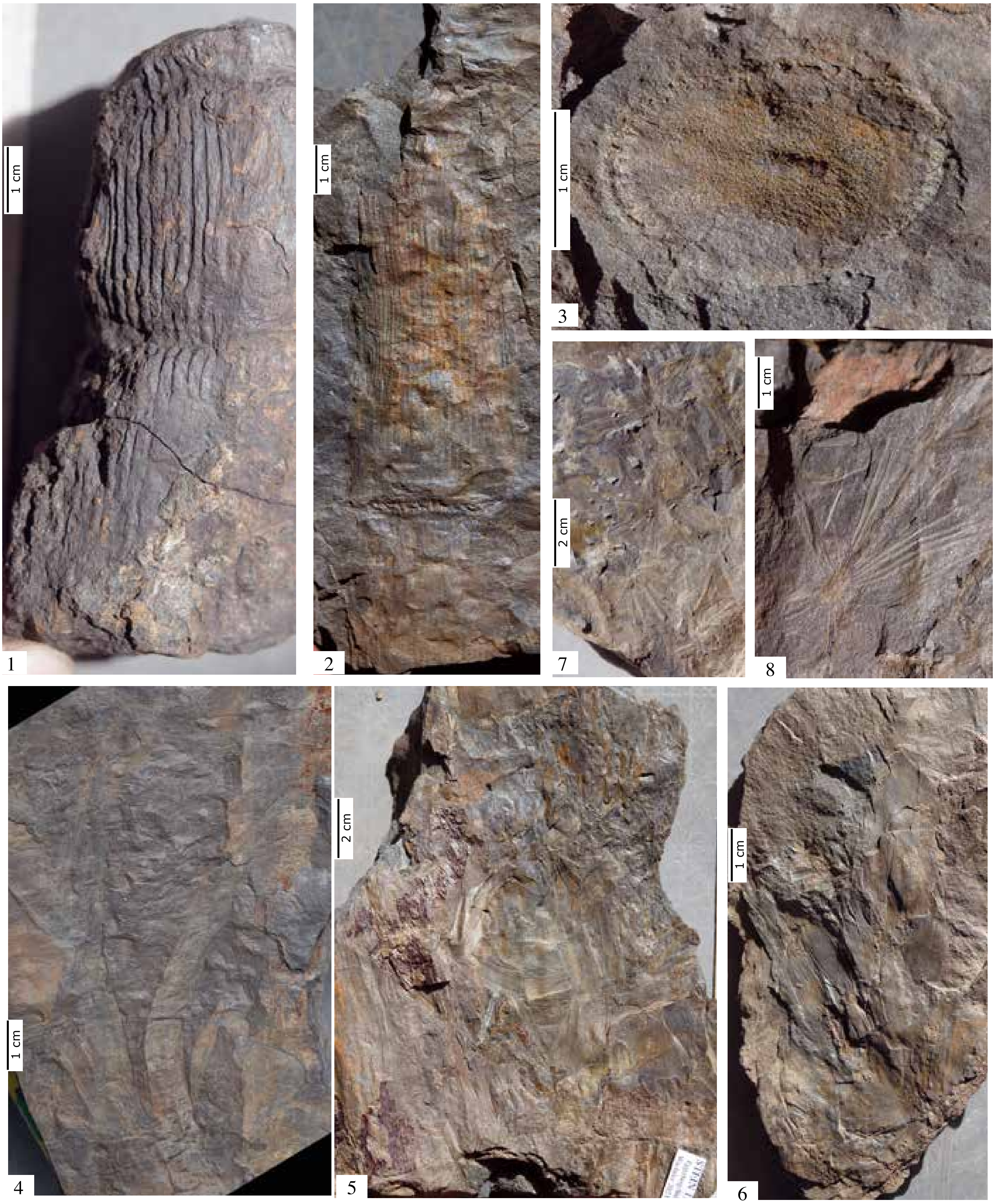
Whole plant: Hollow stems found up to 3 cm in circumference (STEIN 139, STEIN 205) and irregularly interrupted by sheath nodes. Lateral stems branching off in multiple numbers at the same height, some with closely fitting ribs (STEIN 400, STEIN 132, STEIN 190). These frond-like whorls emerge (STEIN 400, STEIN 132, STEIN 190). In the juvenile stage spatula-shaped (so-called

Interesting is *Lygodites stachei* (original by Kerner, 1897), the oldest known precursor of the Lygodium climbing ferns. On the right, recent *Lygodium japonicum* with sterile and fertile fronds.



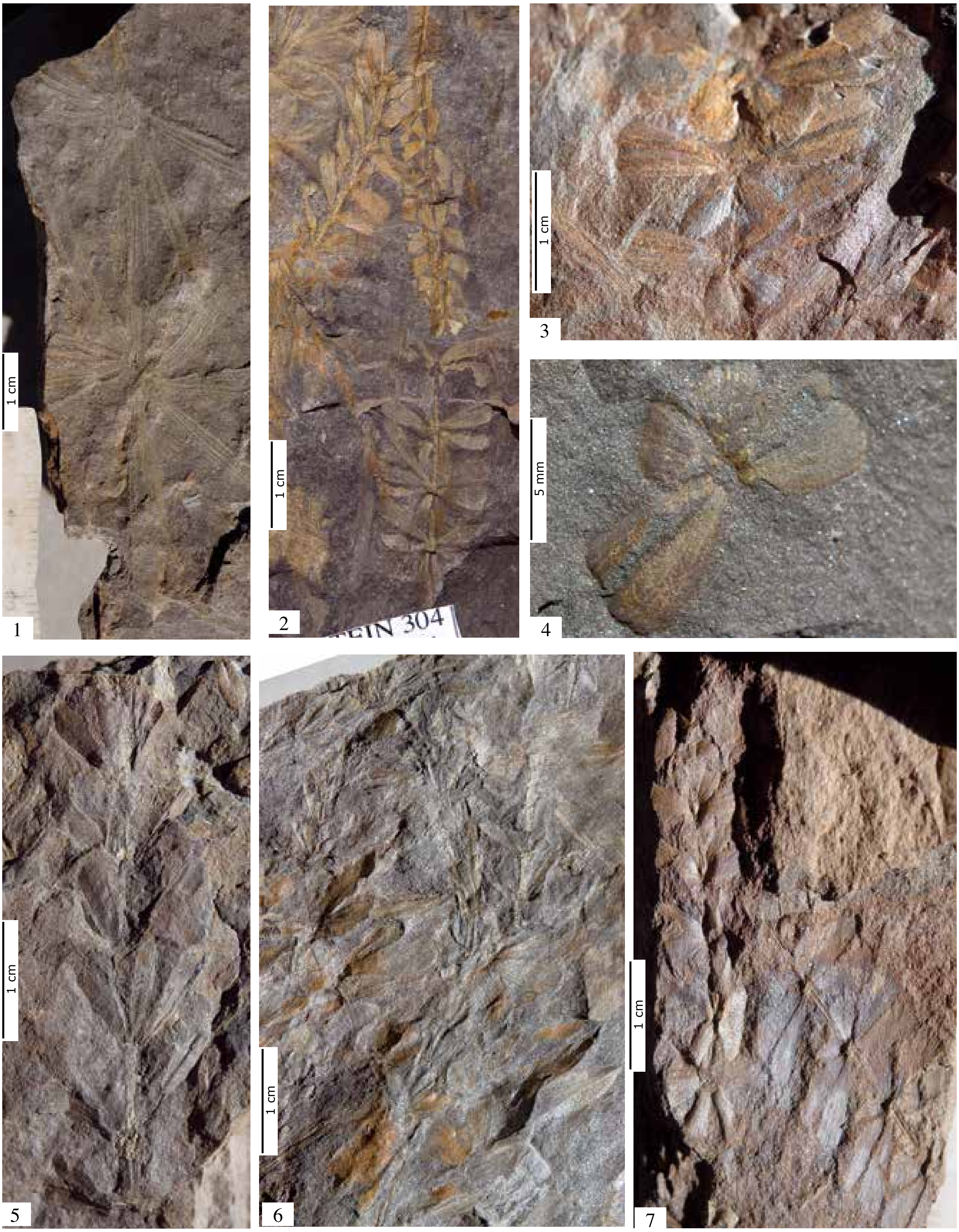
***Calamites steinachii*. Steinacher-Flora. Horsetails (Late Carboniferous, Bashkirian-Moskovian)**

a. Plant with sporangia; b. Stem; c. Sterile frond; d. Detail of leaves; e. Juvenile leaves, f. Fertile sporangia; g. Individual sporophyll cones; h. Detail of a sporangia with holding bracts; i. Sporangia with spores



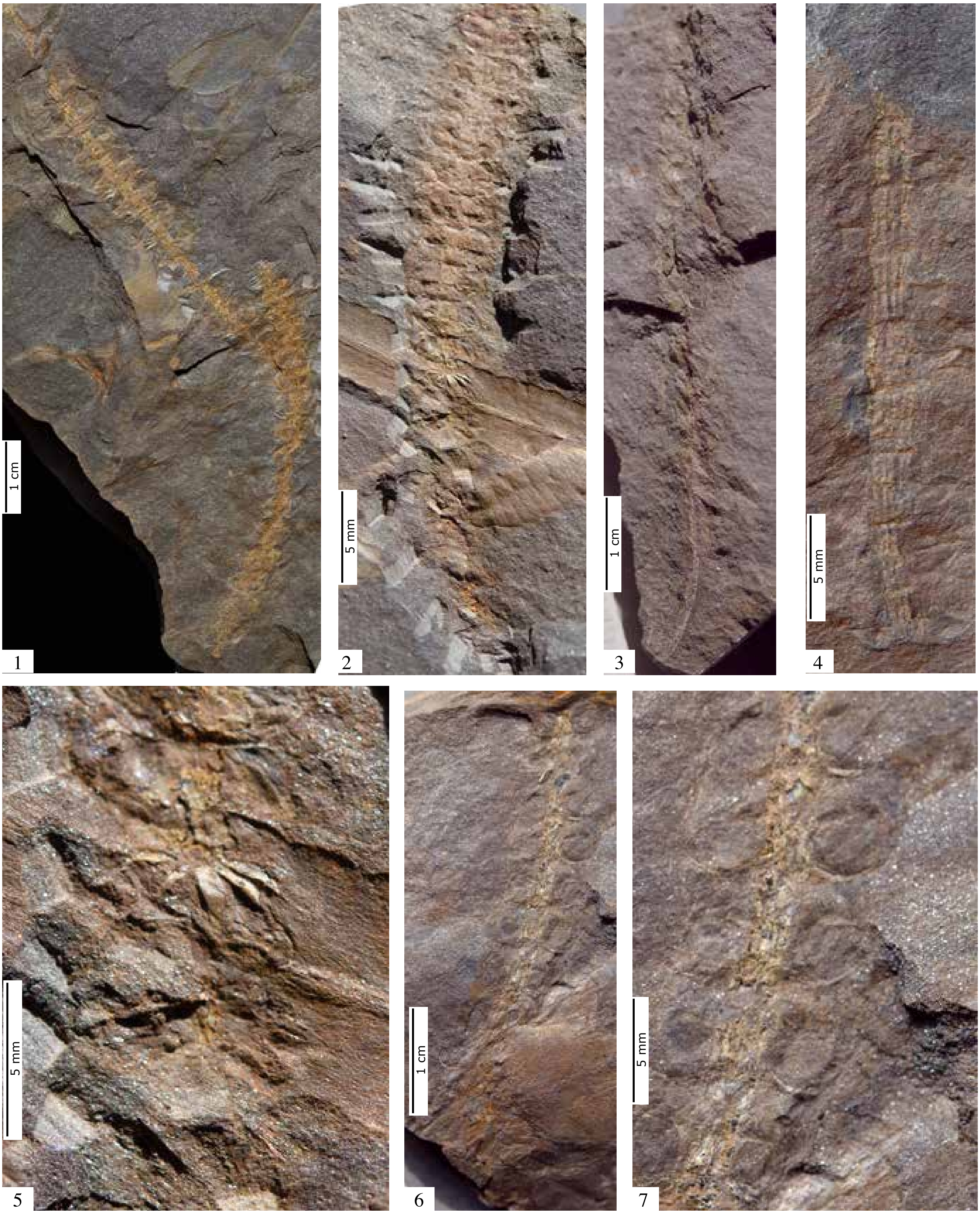
***Calamites steinachii*. Steinacher-Flora. Horsetails (Late Carboniferous, Bashkirian-Moskovian)**

1-2. Parts of stems (STEIN 31, STEIN 139); 3. Internodial sheath top view (STEIN 205); 4-6. Lateral branches (STEIN 400, STEIN 132, STEIN 190); 7-8. Leaves of the lateral branches (so-called *Annularia*) (STEIN 124, STEIN 123); Eggerberg, Steinach, Coll. Wachtler, Dolomythos Museum



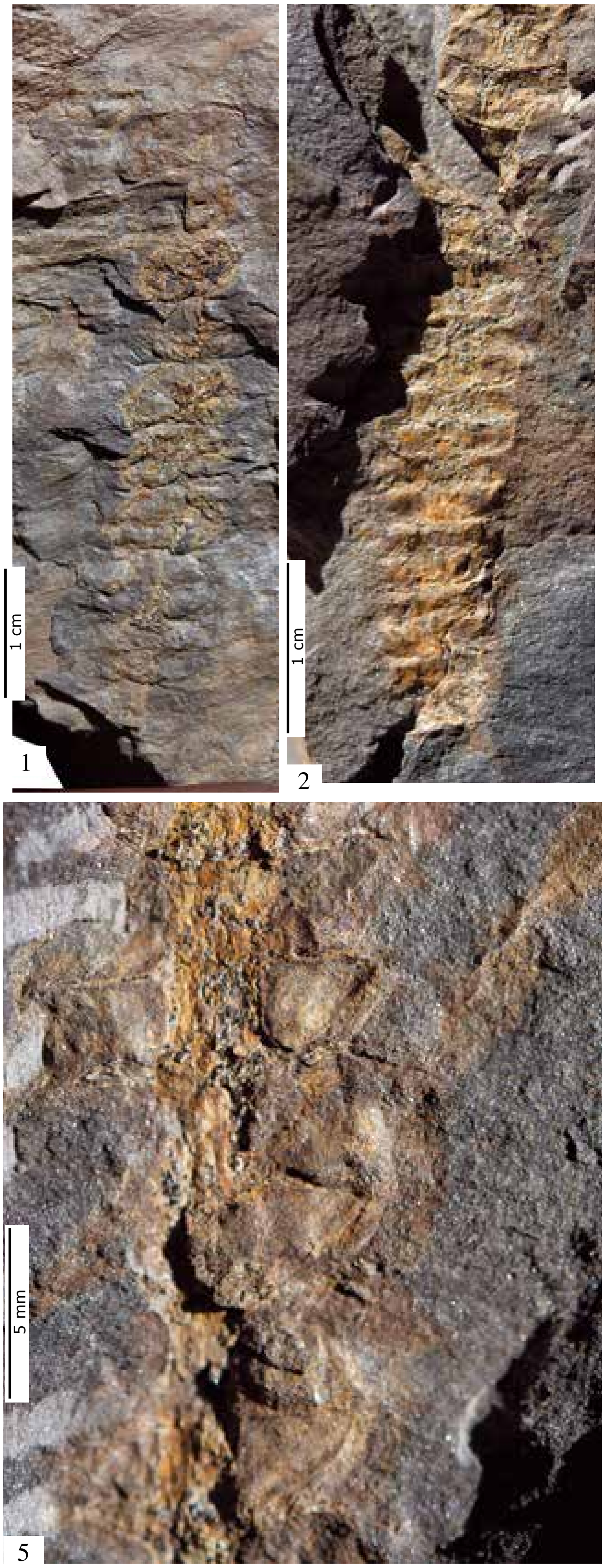
***Calamites steinachii*. Steinacher-Flora. Horsetails (Late Carboniferous, Bashkirian-Moskovian)**

1. Adult leaves of the lateral branches (so-called *Annularia)* (STEIN 343); 2-7. Juvenile leaves of the lateral branches (so-called *Sphenophyllum*) (STEIN 304, STEIN 154, STEIN 140, STEIN 204, STEIN 132, STEIN 333); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



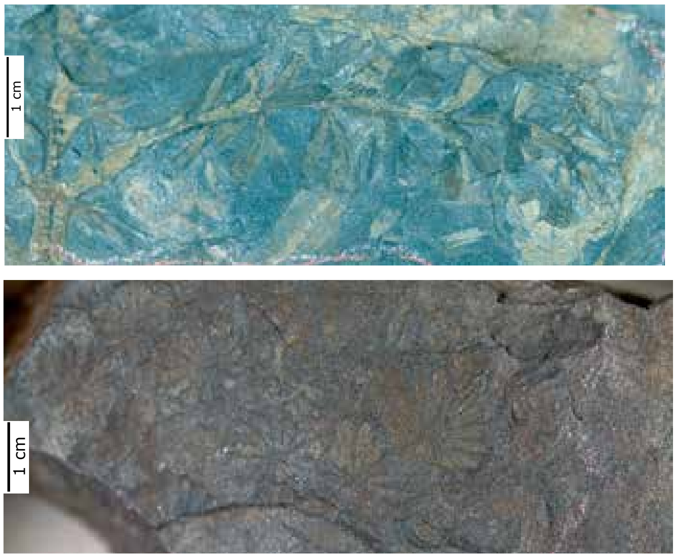
Calamites steinachii. Steinacher-Flora. Horsetails (Late Carboniferous, Bashkirian-Moskovian))

1. Two inflorescences (STEIN 305, designated holotype); 2-4. Various inflorescences (STEIN 203, STEIN 150, STEIN 390); 5. Detail of the bracts of an inflorescence (STEIN 204); 6-7. Inflorescence and detail of the sporangia (STEIN 388); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



***Calamites steinachii*. Steinacher-Flora.**

1-2. Various cones (STEIN 125, STEIN 201); 3. Detail of the sporangia (STEIN 201); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



A primitive species of *Calamites (steinachii)* is also common. All specimens were illustrated by Fritz Kerner on Plate VIII.

Sphenophyllum leaves) (STEIN 304, STEIN 154, STEIN 140, STEIN 204, STEIN 132, STEIN 333), elongated when mature (up to 2-2.5 cm long) doubly needle-shaped, basally connected with a pronounced midrib (STEIN 124, STEIN 123, STEIN 343, so-called Annularia).

Fertile organs: Known as *Calamostachys.* Sporangiophores slender, reaching up to 8 cm in length, rarely more than 1 cm in width, connected to the axes by a 1-2 cm long stalk (STEIN 305, designated holotype, STEIN 203, STEIN 150, STEIN 390, STEIN 204, STEIN 388, STEIN 125, STEIN 201). Sporangiophores consisting of geometrically staggered whorls, with small, pointed bract leaflets clutching the round sporangia. At maturity, the micro-leaflets opened or expanded as the sporangial walls dried to release the spores.

Remarks

Since the beginning of paleobotanical research history, a three-part division of this plants has persisted, divided into stem parts, classified as *Calamites*, the leaf whorls, which are mostly not found in a connected group, which were called *Sphenophyllum* in the juvenile stage and *Annularia* in the adult stage, and the inflorescences called *Calamostachys, Macrostachya, Stachannularia* or *Palaeostachya* (Fritz, Boersma, Krainer, 1990). These nomenclatural peculiarities confused more than they could help to clar-

ify the true appearance or the fertile parts of this entire plant. In this publication, the name of the stem part (*Calamites*) is therefore taken as a synonym for the entire plant (Wachtler, 2023b).
After intensive searches at a site on the Eggerberg, it can be assumed that a single species of Calamitaceae was present in large numbers in this area, which reflects the uniformity of the sporangia cones and the diversity of the leaf whorls refer to different growth stages. Since these differ from those of the Eastern Alps, mainly from the Carnic Mountains or the Nock Alps, it proved to be sensible to give them a new species name: *Calamites steinachii.*
Based on the alpine finds, it can be assumed that the inflorescences of the Calamitaceae of that time were divided into two subgroups: those with many small-leaved bracts, emerging from a plane and firmly clasping the sporangia (*Calamites multiramis, Calamites carnicus, Calamites sphenophylloides,* as well as the small creeping *Calamites microphyllus)*, which can be classified under the subsection *Multibracteata* and to which the new *Calamites steinachii* can also be counted, and the *Monobracteata (Calamites longifolius, Calamites sturii),* which were characterized by a single bract enveloping the sporangia (Wachtler, 2023b).
Since no stems have been found in the Steinach Carboniferous flora that are more than three centimeters thick, it can be assumed that this is a somewhat smaller species, in contrast to *Calamites multiramis* from the Carnic Alps, which has hollow stems up to 15 centimeters thick. Although it is less common than the ubiquitous ferns, *Calamites steinachii* is found in sufficient numbers in the Steinach Carboniferous flora to be able to classify the plant's appearance. Due to the great differences between the sporangia cones and the only genus known today, Equisetum, it is not possible to identify lines of development, so that both genera - *Calamites* and *Equisetites* - probably went their separate ways as early as the Middle Devonian. Confirmed *Equisetites* horsetails only appear in the Permian.

Lepidodendron Sternberg 1820

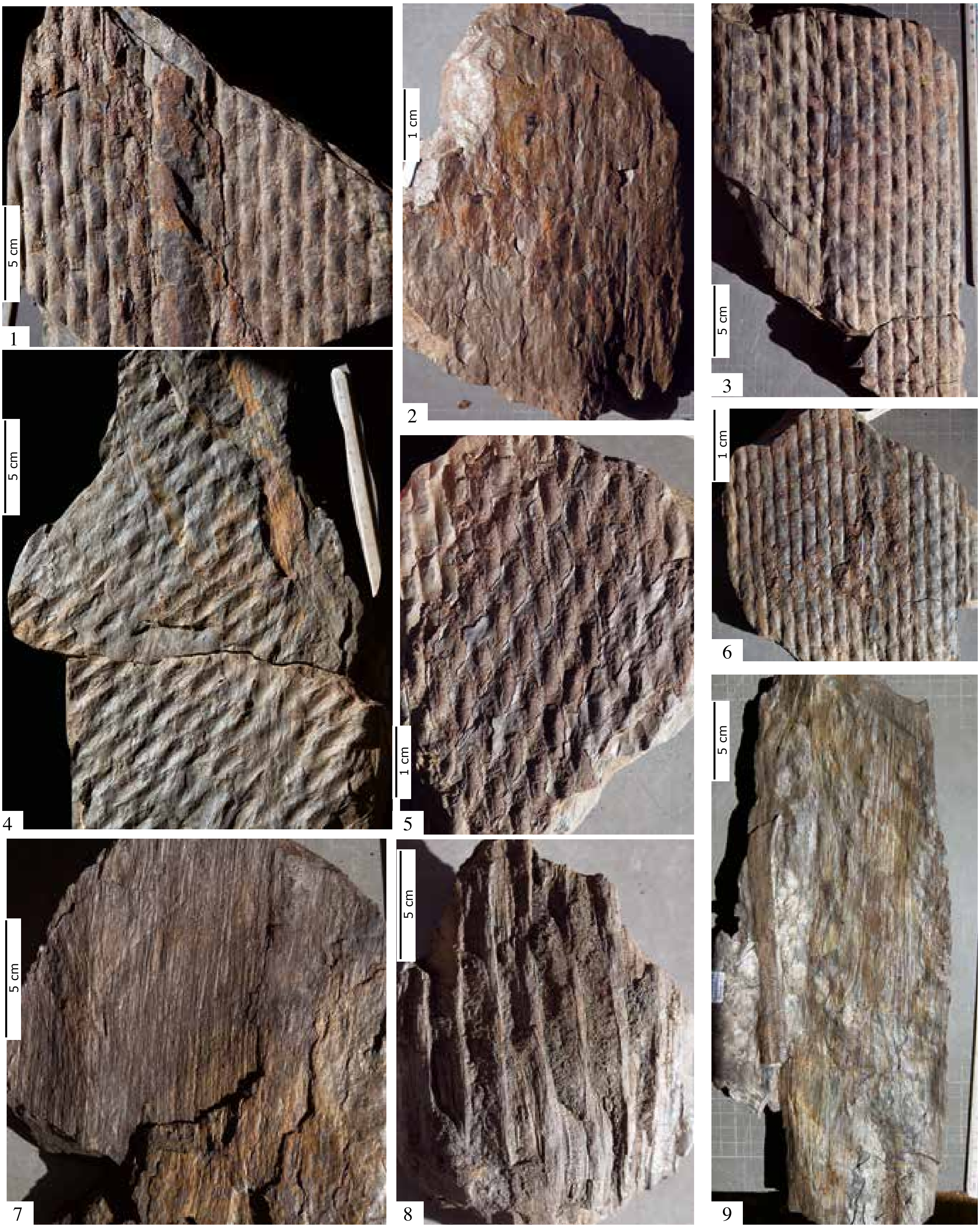
The now extinct giant clubmoss *Lepidodendron* was first described in 1820 by the Czech Count Kaspar Maria Sternberg in his *"Flora der Vorwelt"* (Flora of the Prehistoric World), referring to the scale-like structure of the leaf cushions (Greek lepís, lepídos "scale"). Subsequently, a multitude of species names were coined, probably also because of the different bark structures on the same tree, whereby *Lepidodendron aculeatum*, - mentioned by Sternberg at the same time as others, can be considered the original holotype. It came from the Czech Republic, Kladno Formation, Radnice Member (Late Bashkirian).
The sporophyll structures of the Lepidodendrales were not taken into account for a long time until several subgenera were established there too, such as *Lepidostrobus* (Brongniart, 1828), *Spencerites,* (Scott, 1897) *Lepidocarpon* (Scott, 1900) or their isolated sporophylls *(Lepidophyllum,* (Brongniart, 1828) or *Lepidostrobophyllum* (Lindley & Hutton, 1831). This soon resulted in an overall unsatisfactory starting point, similar to the other giant clubmoss *Sigillaria,* with a multitude of different stem, leaf cushion, leaf or sporophyll descriptions (Fischer, 1904), which even today has only been partially resolved. Another difficulty in distinguishing them arose from the fact that the long, slender leaves of *Lepidodendron* and the other major group *Sigillaria* hardly differed from one another.
However, the leaf cushion markings of the *Sigillaria* were elliptical and round, while those of *Lepidodendron* were higher and wide, roughly rhombic with pointed upper and lower corners. The leaf scar of the discarded leaf blade was located slightly above the middle with small pith cavities, the middle of which was due to the leaf vein of the microphyll, while the two lateral "parichnos" were possibly due to an air-conducting tissue. *Lepidodendron* belongs to the dominant clubmoss genus in the Steinach Carboniferous flora, although surprisingly *Sigillaria,* which is otherwise omnipresent in the Carinthian Nockberge and here especially on the Königstuhl or the Kronalpe, seems to be missing or was at least rare (Fritz, & Krainer, 1997).
Both can be distinguished from the fertile parts: *Sigillaria* was heterosporous with a single large, round macrosporangia and a microsporangia that was just as large, but contained a multitude of microspores

Lepidodendron alpinus. Steinacher-Flora. Clubmoss. Late Carboniferous, Bashkirian-Moskovian

a. Growing tree with sporophyll cones; b. Apical branch; c. Dead tree; d. Apical withered branch; e. Lower bark stem; f. Upper bark stem; g. Apical branch with shed leaves and detail of leaf cushions; h. Leaf needles, inner and outer sides and detail; i. Sporophyll leaf, outer and inner sides; j. Isolated sporangia; k. Sporopyll cone

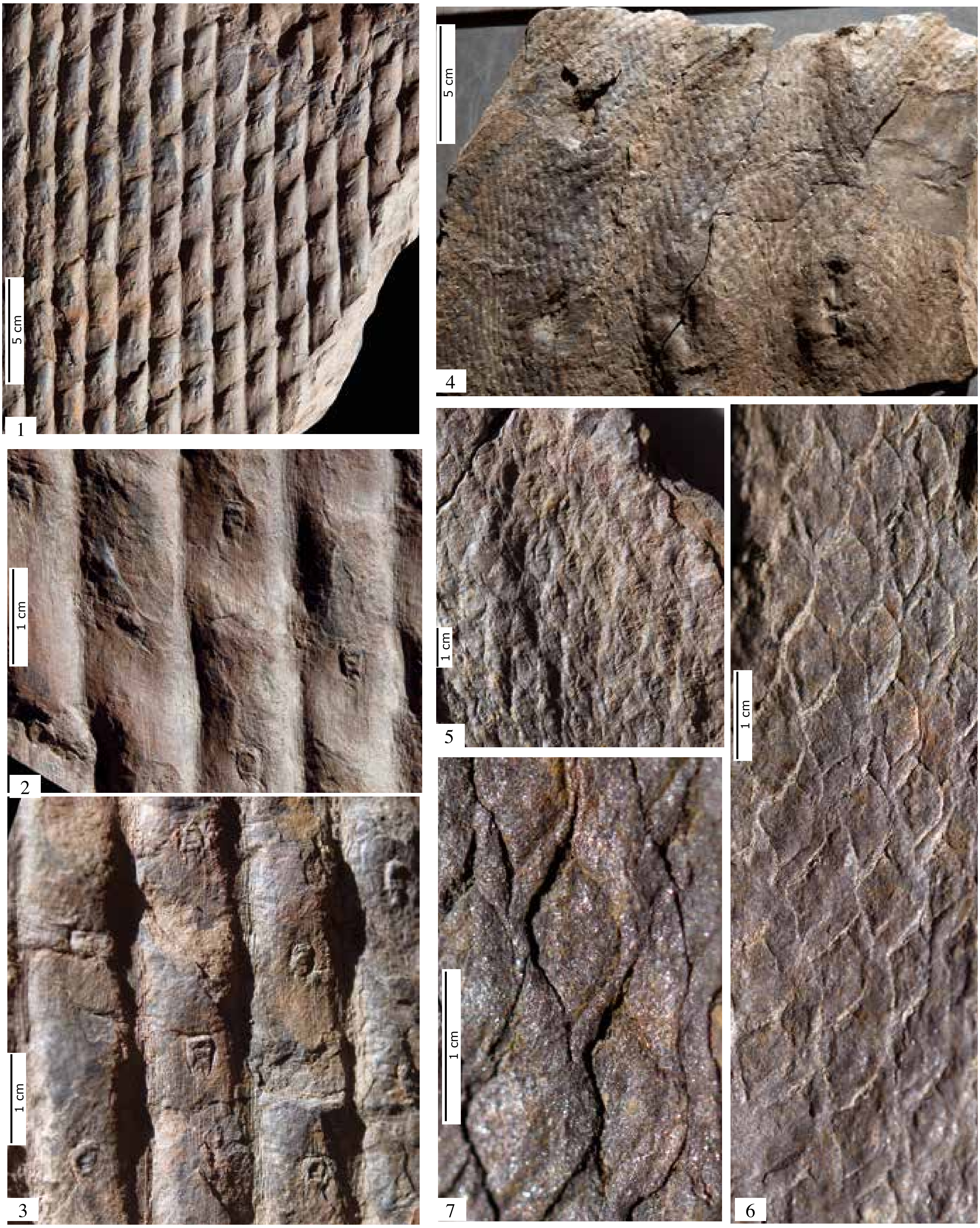
***Lepidodendron alpinus*. Steinacher-Flora. Clubmoss. Late Carboniferous, Bashkirian-Moskovian**

1-6. Bark trunks in the basal area (STONE 64, STONE 286, STONE 65, STONE 69, STONE 70, STONE 70 back); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum



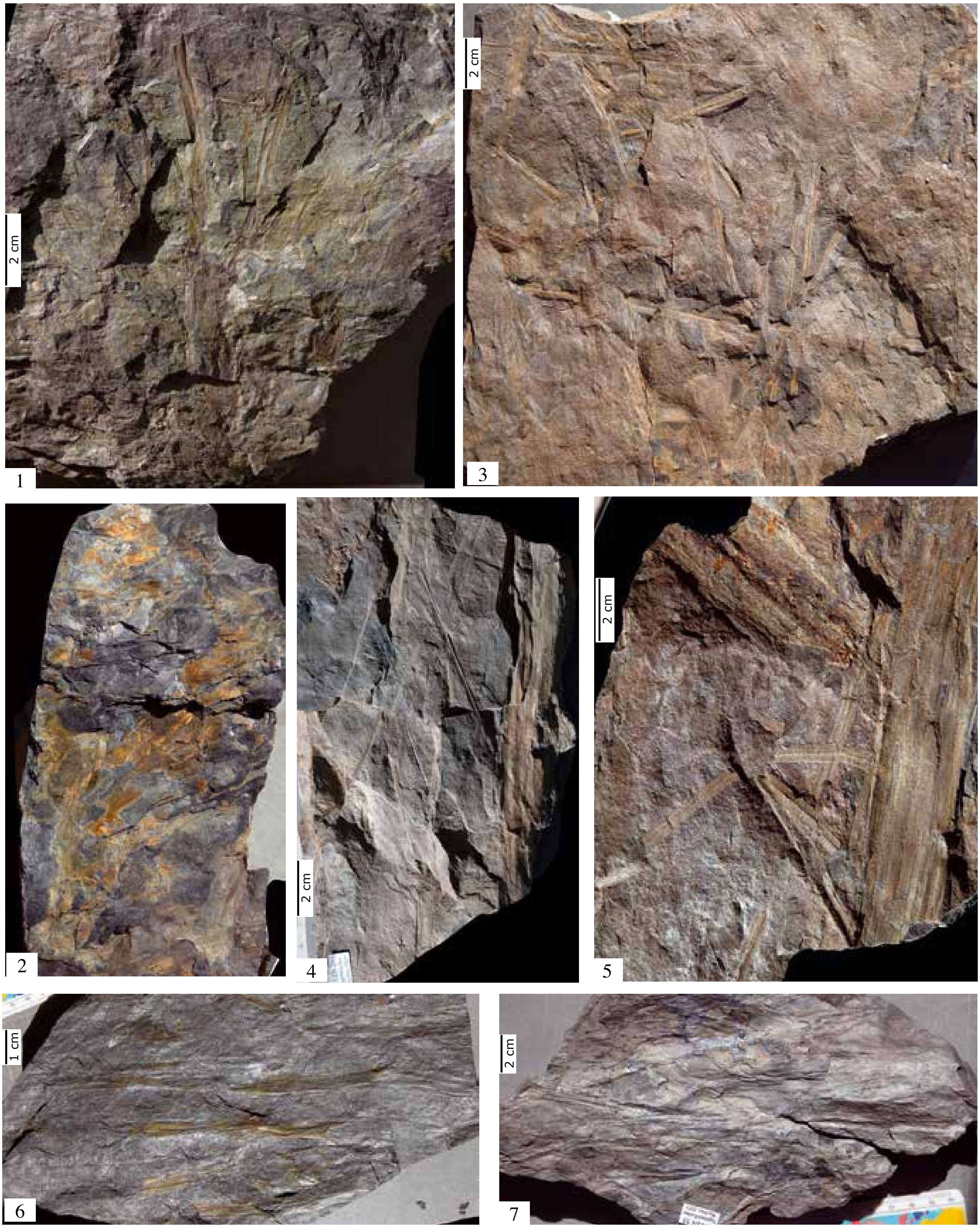
***Lepidodendron alpinus*. Steinacher-Flora. Clubmoss. Late Carboniferous, Bashkirian-Moskovian**

1-9. Bark trunks in the middle to upper range (STEIN 414, STEIN 340, STEIN 414, STEIN 414, STEIN 414, STEIN 414, STEIN 61, STEIN 66, STEIN 44); Eggerberg, Steinach, Coll. Wachtler, Dolomythos Museum



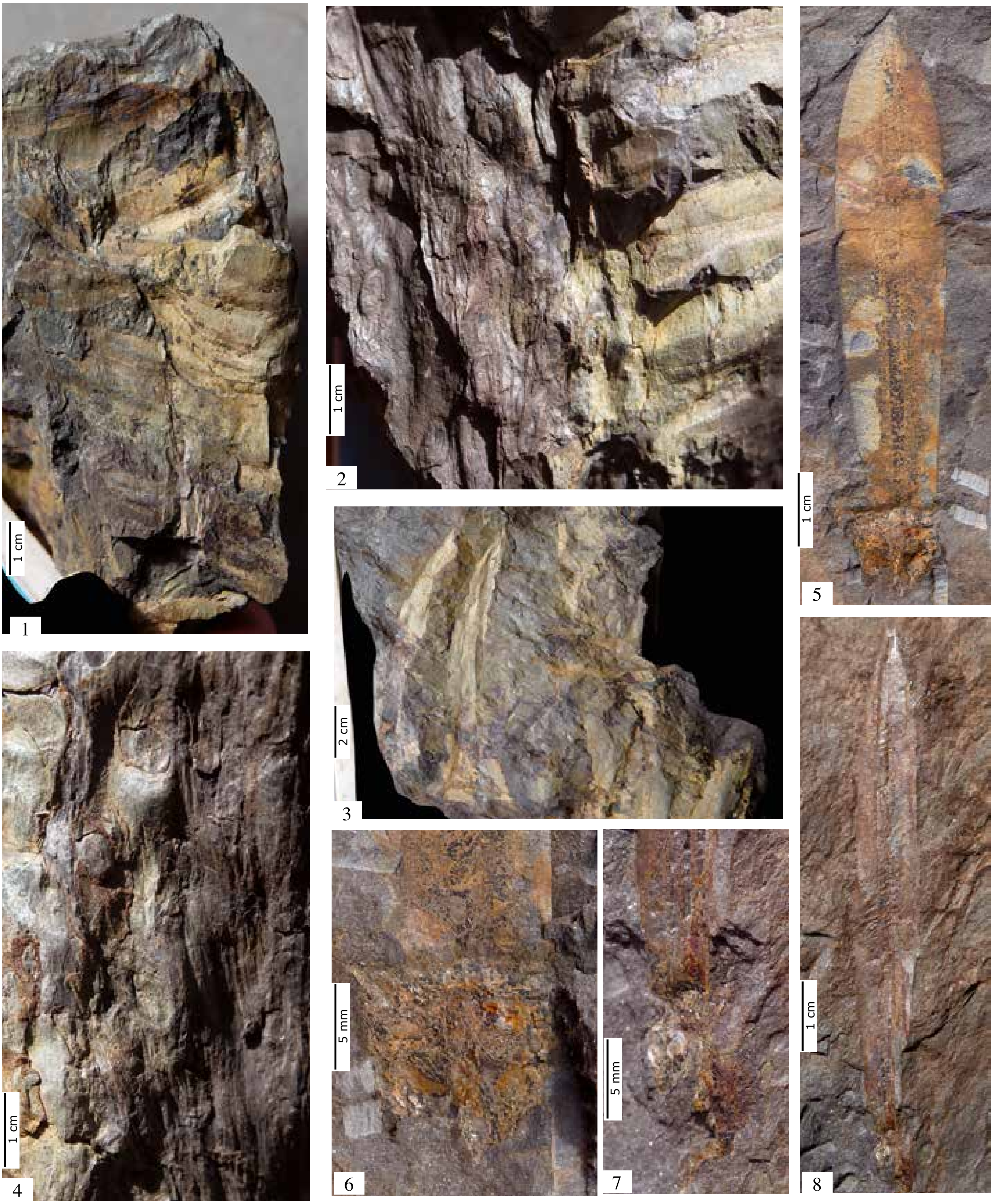
***Lepidodendron alpinus*. Steinacher-Flora. Clubmoss. Late Carboniferous, Bashkirian-Moskovian**

1-3. Bark trunk in the upper area with torn-off areas of the leaves (STEIN 414, paratype); 4. Branches of the trunk in the upper area with torn-off areas of the branches (STEIN 267); 5-7. Leaf cushions in the upper area (STEIN 257); Egg-erberg, Steinach, Coll. Wachtler, Dolomythos Museum



Lepidodendron alpinus. Steinacher-Flora. Clubmoss. Late Carboniferous, Bashkirian-Moskovian

1. Apical branch with leaves (STEIN 33, paratype); 2. Sporangia leaves with sterile leaf needles (STEIN 75); 3-5. Details of the leaf needles (STEIN 410, STEIN 292, STEIN 290); 6-7. Details of the leaf needles, STEIN 51, STEIN 55); Egger-berg, Steinach, Coll. Wachtler, Dolomythos-Museum



Lepidodendron alpinus. Steinacher-Flora. Clubmoss. Late Carboniferous, Bashkirian-Moskovian

1-4. Spore cone and details of the sporangia leaves, as well as the break-off points on the branch (STEIN 39, designated holotype); 5-6. Carpel and detail of the sporangia (STEIN 363 paratype); 7-8. Carpel and detail of the sporangia (STEIN 312); Eggerberg, Steinach, Coll. Wachtler, Dolomythos-Museum

(Wachtler, 2023c). *Lepidodendron* was homosporous, i.e. contained microspores of a single size in the sporangia.
However, several *Lepidodendron* species must have occurred in the Eastern Alps and at Brenner, which can be distinguished by their fruit clusters. Some of them are only about one to two centimeters in size, which Fritz von Kerner (1897) noticed and who made them known with the new species name *Lepidophyllum pichleri*, and also occur in the Nock Mountains, especially at Königstuhl.
This creates a dilemma in paleobotany as to whether the Lepidodendrales should be divided into several genera due to different fruit cones but largely identical tree characteristics. Here, the nomenclature of today's pines is pragmatically applied, which are all in the genus Pinus, although they develop completely different cones, the arrangement and appearance of their leaf needles unite them into a unit. Therefore, the name *Lepidodendron pichleri* is also appropriate here.
Another species developed cones up to 25 cm long and was extremely rare on the Steinacher Joch, but common in the Eastern Alps and was given the name *Lepidodendron fritzii* (Wachtler, 2023e).
In addition, there was a presumably more primitive species with sporophyll leaves up to ten centimeters long, which was dominant both in Carinthia at the Tomritsch fossil point and in the Steinacher Carboniferous flora and is therefore described with the new species name *Lepidodendron alpinus.*

Lepdidodendron alpinus n. sp. Wachtler, 2025

1897 *Lepidodendron obovatum*, Kerner von Marilaun, Pl. X, Fig. 4 + 7

1897 *Lepidodendron majus,* Kerner von Marilaun, Pl. X, Fig. 3

Etymology

For the Alps, since this species occurred both in the Carnic Mountains in Carinthia and the Stubai Mountains in Tyrol.

Holotype

STEIN 39 (Cone with sporophylls), **Paratypes:** STEIN 363 (Isolated sporophyll with sporangia); trunk (STEIN 414); Apical part with leaves (STEIN 33).

Diagnosis

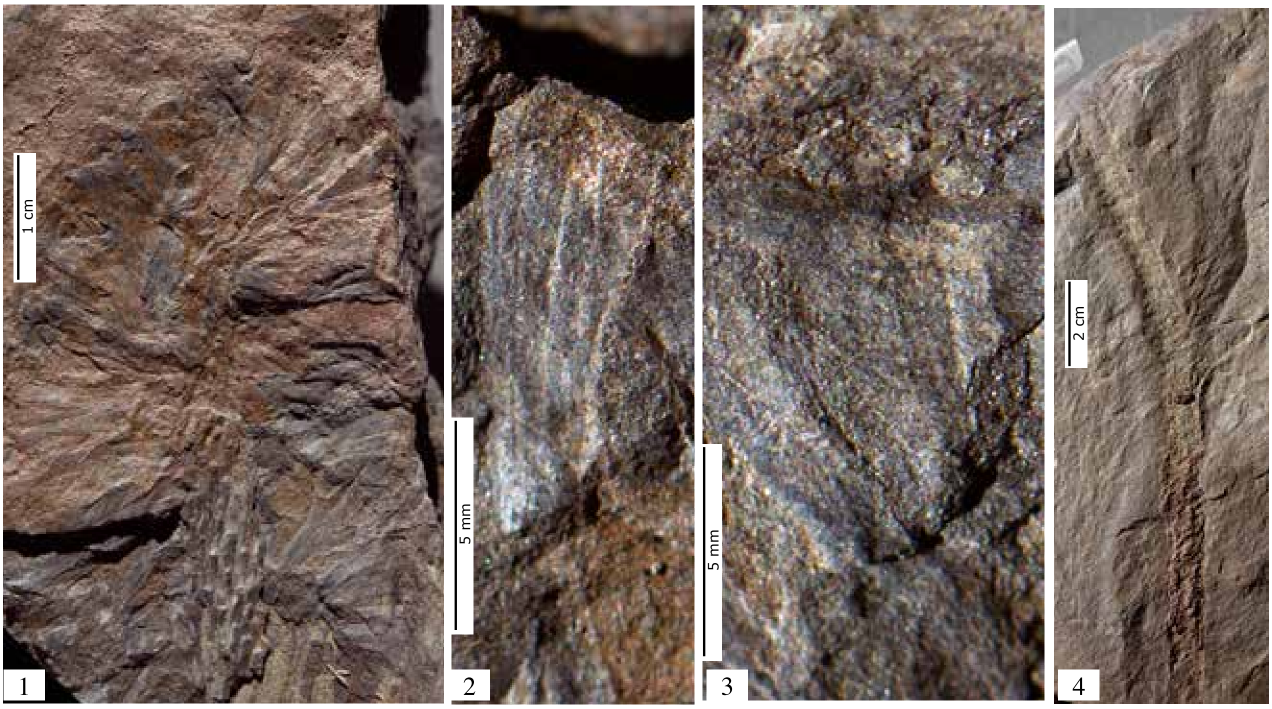
Basal bark of trunk and first order branches covered with leaf pads of shed branches. Leaves slender and elongated, with a pronounced midvein. Sporophyll stands cone-like and homosporous with long bracts.

Description

Whole plant: Massive trees, with hollow trunks and solid bark. Bark furrowed in the lower part (STEIN 69, STEIN 70), with parallel grooves in the middle and upper parts (STEIN 414, paratype). Leaf cushions sometimes visible especially in the uppermost areas with characteristic asymmetrical, rhombic leaf scars, sharp-edged at the top and bottom, rounded at the sides (STEIN 257). Leaves up to 30-50 centimeters long, with a width of 0.5 centimeters, tapering to a point, with a distinctive midrib (STEIN 410, STEIN 292, STEIN 290, STEIN 51, STEIN 55).
Fertile organs: Sporophyll cones reaching a length of about 10 to 15 centimeters (STEIN 39, holotype) consisting of a tuft of sharp-edged fruit leaves, about 8-10 cm long and 1 cm wide (STEIN 363, STEIN 312). These are slightly bulging in the middle area, tapering to a point at the top, crossed by a strong midrib. Homosporous sporangia in the lower area, about 1 cm large, divided into two kidney-shaped parts.

Remarks

Interestingly, in the presumably older deposits of the Upper Carboniferous, in Steinach as well as in the Tomritsch fossil site in Carinthia, *Lepidodendron alpinus* was dominant. It is relatively easy to distinguish from other Lepidodendrales about its long, distinctive sporophyll leaves that fell off individually when ripe. Whereas *Lepidodendron fritzii*, was characterized by slender sporophyll cones that were shed from the tree as a whole. Rather, there are family relationships with a smaller species, *Lepidodendron pichleri,* which was common in the Eastern Alps at various sites (Königstuhl, Zollner See, but also on the Eggerberg) and had a similar structure of the sporophyll cones, although the sporophylls reached lengths of only 1 to 2 centimeters at most and was already described by Kerner von Marilaun in 1897 as



***Lepidodendron fritzii*. Steinacher-Flora. Clubmoss. Late Carboniferous, Bashkirian-Moskovian**

1. Broken cone of a clubmoss (STEIN 216); 2-3. Details of the sporophylls (STEIN 216); 4. Part of a branch (STEIN 272); Eggerberg, Steinach, Coll. Wachtler, Dolomythos Museum

Lepidophyllum pichleri from the sites there. This species was probably also much smaller in size.

Further Lepidodendrales

In addition to the most common *Lepdido-dendron alpinus,* there were at least two other *Lepidodendron* species distinct by their different cone shapes.

Lepidodendron pichleri nov. comb. Kerner 1897, Wachtler 2025

1897 *Lepidophyllum pichleri* Pl. X Fig. 1-2

In 1897, Fritz Kerner from Marilaun on the Steinacher Joch noticed smaller fertile scales with a maximum length of 1.5 cm and a width of 1.2 cm and described them with the new species name *Lepidophyllum pichleri.* Since the stems had typical characteristics of *Lepidodendron*, the name *Lepidoden-dron pichleri* nov. comb. is more appropri-ate. Sporophylls of this type were also wide-spread found on the Königstuhl in the Nock Mountains or on the Rudnigsattel in the Carnic Alps. Stem parts found in the layers point in the direction of *Lepidodendron,* pos-sibly a somewhat smaller species.

Lepidodendron fritzii Wachtler 2023

2023 *Lepidodendron fritzii* Pl. 98-99

Other clubmoss cones resembled the species *Lepidodendron fritzii* (STEIN 216), which is the most common on the Stangalpe. The cones can also reach considerable sizes of up to 20 cm, the sporophylls were small, about 2 cm long and wind densely around the central axis (Wachtler, 2023e).

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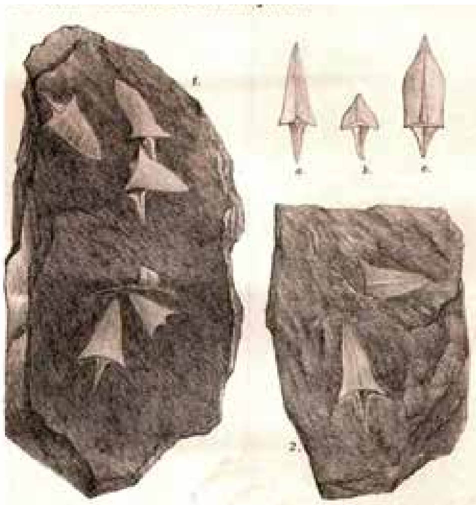

In addition, there must have been another type of *Lepidodendron* cones, which Kerner von Marilaun, 1897, plate 3, noticed. He named it as a new species with *Lepidophyllum pichleri,* although today *Lepidodendron pichleri* would be appropriate. These are common sporophylls, which were also widespread in deposits in the Eastern Alps (Königstuhl, Rudnigsattel).

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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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