

Fossil plants from the Upper Carboniferous of the Eastern Alps

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The many rich sites of fossil plants from the Upper Carboniferous in the Eastern Alps have long aroused the interest of its local population and the attention of researchers. Nevertheless, most of these sites are largely unexplored, first because of their high-altitude alpine location – they are situated far away from roads – and the attendant danger of exposure. Since it is possible to follow the changes in the plant world over the geological ages here, these sites are extremely interesting. Most of them are dominated by *Sigillaria*, along with a minority of *Lepidodendron* lycopods, several *Calamites* horsetails and a variety of ferns, some of which could be defined as seed ferns. In fact, due to the large number of *Sigillarias* found here, it was possible for the first time to obtain detailed information about this enigmatic lycophyte, in addition to data on a variety of highly developed and well-preserved ferns, especially the Osmundaceae, Marattiales and tree ferns, which offered the opportunity to learn more about their evolution. The first conifers, on the other hand, did not appear until the Early Permian.

March 2023

Keywords: Upper Carboniferous Flora, Alps, Clubmoss, *Sigillaria*, *Lepidodendron*, *Calamites*, ferns



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

a. ***Sigillaria parallela***: a giant clubmoss, with a sporophyll cone in the foreground; b. ***Cyatheites alpinus***: a tree fern; c. ***Osmundites polymorphus***: a royal fern; Several different Calamitaceae populated the tropical landscapes at the same time, including: d. ***Calamites carnicus***, e. ***Calamites longifolius***, f. the dwarfish ***Calamites microphyllus*** and g. ***Calamites multiramis***.

The most important sites for Late Carboniferous plants in the Eastern Alps are located in the Nockberge (Stangnock, Königstuhl) and the Carnic Alps (Kronalm and neighbouring areas) and have been known for centuries (Hohenwart, 1783; Unger, 1840; Štúr, 1871). Of global interest is the good state of preservation of these Late Carboniferous plants and the possibility of tracing the sediments in a very small space over the various epochs.

In addition, it is possible to document the plants in these sites, such as the characteristic and widespread clubmoss *Sigillaria parallela*, in vivid detail – from the roots to the bark, trunks, the leaves, the canopy or the peculiar structure of the sporophyll cones, consisting of one single large macrosporangia and associated microsporphylls – and to reconstruct, in that way, the entire tree in question. Even the various Calamitaceae can be correlated with their differing sporangiophores, so that a large number of different species present within the same layers can be studied. It is interesting that several fern families still occurring today – such as the Osmundaceae with their typical separate sporophylls and tropophylls, the tree ferns like *Cyatheites* and *Dicksonites*, as well as ancestors of the Marattiales such as *Marattiopsis* or *Danaeites* – were already fully developed just 300 million years ago and their appearances were similar to what they look like today. Moreover, a seed-bearing fern-like genus *Cyclopteris*, with its different seed and pollen systems, could well be classified into a hitherto-unknown group of gymnosperms, causing major problems. *Callipteridium*, another plant with fern-like foliage, is interesting, with its peculiar sporangia aggregated narrowly; however, because the associated seeds have never been recovered, it is not considered as a seed fern but has to be classified in the category of ferns with completely different sporophylls and tropophylls.

Geological overview

Although the various plant fossil sites in the Eastern Alps all belong to the Upper Carboniferous, this classification is not sufficient for them to achieve added scientific value, as the concomitant timeline spans several million years. The Stangnock Forma-



The Kronalm. The plant fossil sites marked in red.

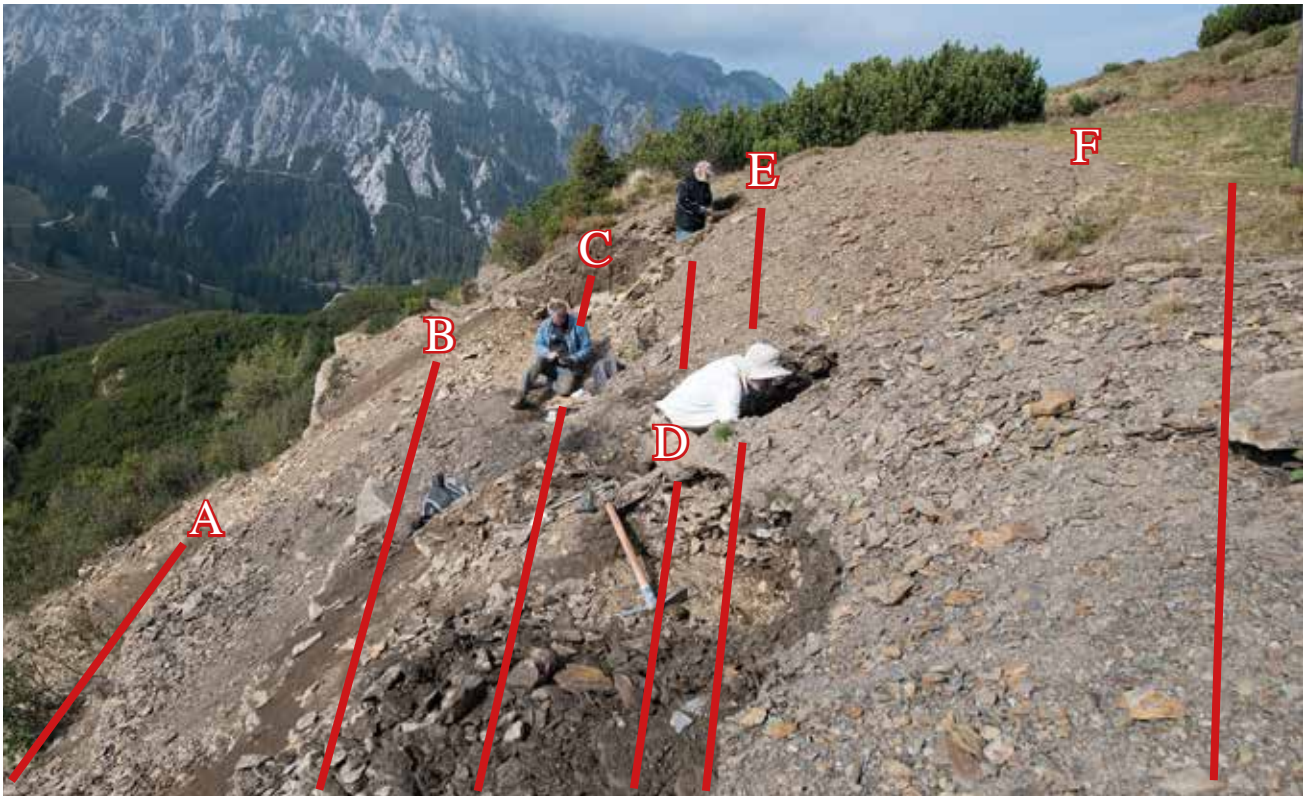


The Königstuhl site in the Nockberge mountains.



The Stangnock site in the Nockberge.

tion (including the Königstuhl and the Tur-racher Karbon) may be somewhat older due to the presence of *Lepidodendron* remains. This assessment should be refined, since a change in the fossil plant world may be observed throughout various strata. To be precise, the lower fossil layers, especially on the Stangnock, are characterised by large *Lepidodendron* trunks and a high proportion of the seed-bearing fern *Cyclopteris alpina* or the enigmatic *Callipteridium ameromii*. This proportion is significantly higher than



The historical fossil site at the Kronalm, at 1730 m above sea level. The lower layer A is dominated by *Calamites multiramis* (*Annularia stellata*-*Calamostachys tuberculata*) and by the Osmunda fern *Osmundites polymorphus*. Other plants such as *Calamites sturii* are present but less common. Layer B is the most variegated. Interestingly, four different *Calamites* species occur within a few square meters (*Calamites multiramis*, *Calamites sphenophylloides*, *Calamites equisetiformis*, as well as the small, creeping *Calamites microphyllus*, all of which are secured by their completely different sporangiophores. There are also various ferns, predominately *Osmundites polymorphus*, *Marattiopsis stopesae*, *Cyatheites unitus* and *Cyatheites alpinus*, as well as the seed fern *Cyclopteris boersmai*. *Sigillaria parallela* occurs only occasionally. Layer C with various smut layers is dominated by *Sigillaria parallela*. Calamitaceae and ferns only occur occasionally. In layer D several ferns, especially *Osmundites polymorphus*, and more rarely *Cyatheites alpinus*, *Marattiopsis stopesae*, *Danaeites perneri* and *Dicksonites pennaeformis*, are common. Sometimes, *Calamites multiramis* is also found. In layer E we experience a temporary sea flooding with brachiopods, crinoids and bivalves. The famous layer F has been studied intensely in the past and is characterised by its abundance of *Calamites multiramis* (*Annularia stellata*) and also *Calamites carnicus* (which only appears here), along with the Osmundaceae *Osmundites polymorphus*.

that in the upper layers, especially on the eastern ridge of the Königstuhl: here, the Sigillariaceae (*Sigillaria parallela*) dominate, mostly accompanied by ferns (*Cyatheites alpinus*, *Osmundites polymorphus*) and *Calamites*, the latter represented here mainly by *Calamites multiramis* and a peculiar species, *Calamites sturii*, which appears almost like a link between the Lepidodendrales and the Calamitaceae, so different from all the others is it, with its monosporangiate sporophylls distinguishable by only one terminal bract. On the other hand, *Lepidodendron fritzii* clubmoss are also represented but rarely found in this area.

On the Kronalm, the layers contain a large number of different *Calamites* species and

ferns (Fritz, Boersma, Krainer, 1990; Fritz, 1990; Kustatscher et al., 2019), along with other lenses in which the Sigillariaceae (*Sigillaria parallela*) dominate. The latter is an extremely interesting plant community in the Upper Carboniferous of the Eastern Alps that provides deep insights into the prevailing and succeeding tropical climate – in the direction of the Early Permian – in light of a devastating cataclysm within a short period of time combined with a cooling of the entire planet, with ice ages subsequently covering large areas of the world and even reaching also its equatorial region. At the beginning of the Permian period, a large number of gymnosperms such as conifers, ginkgoes or cycads arose



The strata on the Krone as well as in the Nockalm area are covered by thick fire horizons, which usually follow deposits rich in *Sigillaria* remains. Only then do lenses occur, which are rich in ferns or sometimes hold shells and brachiopods.

mainly from nothing and began their triumphal march, which continues even now. In the Upper Carboniferous, there were fire catastrophes that spread across continents, in a magnitude never before witnessed in the history of the earth. This suggests that the huge clubmoss vegetation repeatedly pushed the ferns, horsetails or other plants into the background. Periodic dry seasons were probably sufficient to cause the *Sigillaria* forests to wither over long stretches, so that a single lightning strike was enough to trigger catastrophic wildfires that affected large land masses, killing off all vegetation over a long period of time and possibly having a significant impact on the global climate.

Moreover, from a geological point of view, all these above sediments are low-grade altered metamorphic siliciclastic sedimentary rocks (Kabon & Iglseder, 2019). The plants were likely deposited under tropical conditions in flood plains, with short transport routes, even if the fallen trees or low-growing plants were not embedded in situ, as evidenced by their excellent conservation. Whether they were deposited in moors, shallow lakes or swamps (Unger, 1840, 1852, 1870), or meandering/branching river systems (Krainer, 1990) that reached their end point in the basin of the former Variscan mountains, is difficult to interpret, but probably everything mentioned here holds true. The Moscovian – about 310–307 million years ago – should

still be considered as a deposition period for the lower layers, while the Kasimovian-Gzhelian (about 307–303 million years ago) must be the period where the upper deposits became rich in Sigillariaceae (Krainer, 1990; Kabon & Iglseder, 2019).

The plant site on the Kronalm (Corona in Italian), well known for decades, is located at 1730 m above sea level, in the middle part of a plateau-like plain exposed on its eastern side. This approximately 300-meter-thick Corona Formation is composed of flat-lying shales, sandstones, conglomerates and limestones (Forke et al., 2000).

The fossil-bearing layers mostly consist of yellowish fine-grained sandstone and hardened sludge. Again and again, these layers have quartz conglomerate sequences, which likely formed distinctive steps and were stored in the carbon via flooding, with a thickness ranging from a few meters to 30 meters. The horizons bearing plant fossils are often associated with the shale and anthracite seams, which either sit on top of the conglomerates or are situated at their base (Schönlaub & Hubmann, 2002).

New researches

Michael Wachtler began with Georg Kandutsch (Alpdorf, Arriach) initial research on fossil plants from the Upper Carboniferous of the Eastern Alps in 2000, with the team gradually being expanded to include Thomas Perner, curator of Möderndorf's local history



Martin Dammann (Berlin) recovering a fern (*Osmundites polymorphus*) and the same fern after preparation (Dammann Collection).



Michael Wachtler (Dolomythos Museum) studying recovered fossil slabs (2021). Photo: Martin Dammann.



Retrieving a large *Sigillaria* stem (*Sigillaria parallela*) covered by a charcoaled fire horizon.



The two researchers Georg Kandutsch and Werner Hoffmann extracting fossil on the top layer at the Kronalm. This work led to the discovery of a new unknown species of horsetail (*Calamites carnicus*).



Thomas Perner (curator, Museum Möderndorf) discovering a new species of fern (*Danaeites perneri*) in 2022.

museum, Werner Hoffmann (Spital), Thomas Gerasch and Martin Dammann (Berlin). In Möderndorf's local history museum, located next to Hermagor, there is a one-meter *Sigillaria* trunk, about 90 cm thick and weighing 800 kg, gathered from the Kronalm site and dismantled under adventurous conditions.

In terms of geology, the bottom layer A of this site is mainly dominated by *Calamites multiramis*, whose decorative side branches have been classified as *Annularia stellata*. Typical sporangiophores (*Calamostachys tuberculata*) belonging to this plant are often encountered. On the other hand, ferns, which are dominated by *Osmundites polymorphus* (an Osmundaceae) take a back seat, as it were. Rarely are there peculiar sporangiophores that can be assigned to a strange *Calamites* species (*Calamites sturii*). These sporangiophores could even suggest a functional link to the Lepidodendrales.

Moreover, sitting on a quartz conglomerate bench, there is layer B, which can be considered the most variegated of all layers. Interestingly, four different *Calamites* species (*Calamites multiramis*, *Calamites sphenophylloides*, *Calamites longifolius* and *Calamites microphyllus*) occur in a worked area about 30 m long and 1–2 m wide, which are verified by their different fertile organs.

The richness of the different fern families is considerable (*Osmundites*, *polymorphus*, *Cyatheites alpinus*, *Cyatheites unitus*, *Dicksonites pennaeformis*). In particular, seed ferns (*Cyclopteris boersmai*) are rarer. In addition, the club moss *Sigillaria parallela* appears in well-preserved specimen on the right side of the documented horizon. Both layers A and B pertain to a flora that has hardly been destroyed by transport routes. Surprisingly, the lens B is followed by an almost pure *Sigillaria parallela* horizon (C), with large bark trunks of varying conservation statuses. Root residues are present, as also a huge amount of sporangia. All other families such as ferns and horsetails are present but fading into the background. This *Sigillaria parallela* horizon (layer C) is interrupted several times (probably three) by charcoaled horizons, one having a thickness of up to 30 cm, suggesting devastating forest fires. Since these fires also occurred on the Königstuhl

and the Stangnock, it can be assumed that fire disasters periodically devastated large areas of the former continents. In contact with these burn horizons, surprisingly, the largest number of megasporangia and microsporangia of *Sigillaria parallela* are found, indicating parallels with modern-day giant sequoias (*Sequoiadendron*) of North America, where wildfires are thought to be key to the germination of the cones. Also, the sporophylls, often overlooked, are an important way of classifying plants in the past. Sometimes, the sporangia here form extensive fossil carpets. Over these forms a new layer (D) with hardly any *Sigillaria* but a wealth of ferns, including precursors from the Marattiales group (such as *Marattiopsis stopesae* or *Danaeites perneri*, two previously unknown fern species) and treeferns (*Cyatheites alpinus*, *Cyatheites unitus* and *Dicksonites pennaeformis*). They are secured by the appearance of species-typical trunks. Plus, *Osmundites polymorphus* is widespread. The seed fern *Cyclopteris boersmai*, a new species, is present in considerable numbers, whereby *Callipteridium ameromii* must also have occurred, based on the spore organs found. However, due to the similarity of the pinnulae between the individual ferns, a clear determination is not always easy. *Calamites multiramis* is also present, accompanied by particularly decorative *Annularia* fronds. Like nowhere else in the Upper Carboniferous of the Eastern Alps, a slow recovery can be seen in this layer after the devastating forest fires, although the remains of *Sigillaria* are found to be missing. Thereafter, the following layers, poor in plant fossils (starting with layer E), are sporadically interrupted by short-term sea intrusions, in which sea mussels, brachiopods and crinoids were sometimes deposited. The uppermost horizon (layer F) (in the literature stop 10 of the Nassfeld Schönlaub & Hubmann Geotrail, 2002), which was mainly worked on by Italian teams in the 1980s (Kustatscher et al., 2019), is again rich in *Calamites multiramis* (*Annularia stellata*) and the fern *Osmundites polymorphus*. This is no longer a matter of individual, clearly delimited horizons; many clay lenses are sometimes so thin that it is extremely difficult to recover larger, aesthetically beautiful plants that are definitely present therein. In



Flora from the Late Carboniferous of the Eastern Alps (Stangnock)

a. *Callipteridium ameromii*: a seed-like fern; b. *Sigillaria parallela*: a giant clubmoss, in the foreground a shoot, in the background a seedling; c. *Lepidodendron fritzii*: another giant clubmoss; d. *Cyclopteris alpina*: a seed fern with pollen buds below and seeds above.



Flora from the Late Carboniferous of the Eastern Alps (Königstuhl)

a. *Sigillaria parallela*: a giant clubmoss; b. *Marattiopsis stopesae*: Marattiales; c. *Cyatheites alpinus*: a tree fern; d. *Calamites sturii*. In the background: e. *Osmundites polymorphus*: a royal fern; f. *Lepidodendron fritzii*: another giant clubmoss.

addition, a new species of *Calamites* occurs in the uppermost thin-layered lenses, showing similarities to *Calamites multiramis* but being described here as *Calamites carnicus* due to its different leaf whorls and, especially, its sporophyll cones.

On the nearby Rattendorfer Alm, we experience the first appearance of conifers (*Ortiseia*) on the crest of its summit (Grenzlandschichten = Borderland Strata). These were previously classified as belonging to the Asselian-Sakmarian, i.e. to the Early Permian (Krainer, 1990). If the chronological classifications are reliable, there were cataclysmic climate changes within 5 million years – in the vicinity of the equatorial region – from tropical, to Mediterranean, to cool temperate or even cool climates.

Surprisingly again, the conifers occur more in more northerly latitudes (Niederhausen-Flora) (Perner & Wachtler, 2013; Wachtler, 2013; Perner, 2013) in a large number of families such as Araucaria-progenitors (*Ortiseia*) or fir precursors (*Wachtlerina*, *Majonica*), already between the Gzhelian/Upper Kasimovian, i.e. in the Upper Carboniferous, at which time the Alps is still dominated by giant clubmoss trees. In addition, there occurs an archaic conifer – *Perneria* – characterised by dichotomously divided leaf needles, the last indications of Devonian ancestors.

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Carboniferous Fossil Floras from the Eastern Alps

Edited by Michael Wachtler and Nicolas Wachtler

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The many and rich sites of fossil plants from the Upper Carboniferous period in the Eastern Alps have long aroused the interest of the local population and even more of researchers.

Nevertheless, most of the sites are largely unexplored. Most sites are dominated by *Sigillaria*, in minority *Lepidodendron* lycopods, several *Calamites* horsetails and a variety of ferns, some of which could be defined as seedferns. Due to the large number of *Sigillaria*'s, it was possible for the first time to obtain detailed information about this enigmatic lycophyte, and even the variety of highly developed and well-preserved ferns, especially the Osmundaceae, Marattiales and tree ferns, offered the opportunity to learn more about their evolution.

With 600 photos and drawings

Editor: Dolomythos-Museum
 39038 Innichen-San Candido, P. P. Rainerstr. 11 (BZ), Italy
 Registration 36542 from 24/04/2021 - ISSN 2974-7376
 Editor in chief Michael Wachtler
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 www.dolomythos.com

Euro 98,00
Pages 176