Rise and Fall of the Sigillaria Seed Clubmoss

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Giant clubmosses, in particular the genus *Sigillaria,* are regarded as the most characteristic plants of the Carboniferous, and the observation of their origin, their rapid development into giants of the forest and their equally rapid decline amounts to one of the most exciting stories in paleobotanical research. If somebody thinks that they are one of the best-known fossil plants due to their large numbers, gigantism and wide distribution, they are subject to misunderstandings. Although it was always thought that clubmosses had died out after a Paleozoic peak at the beginning of the Permian, they survived as dwarfish lycopod *Sigillcampeia* throughout the Triassic, finally fading from the scene at the Jurassic border. However, a mystery remains unsolved: Why did the last catastrophe cause the extinction of this plant family?

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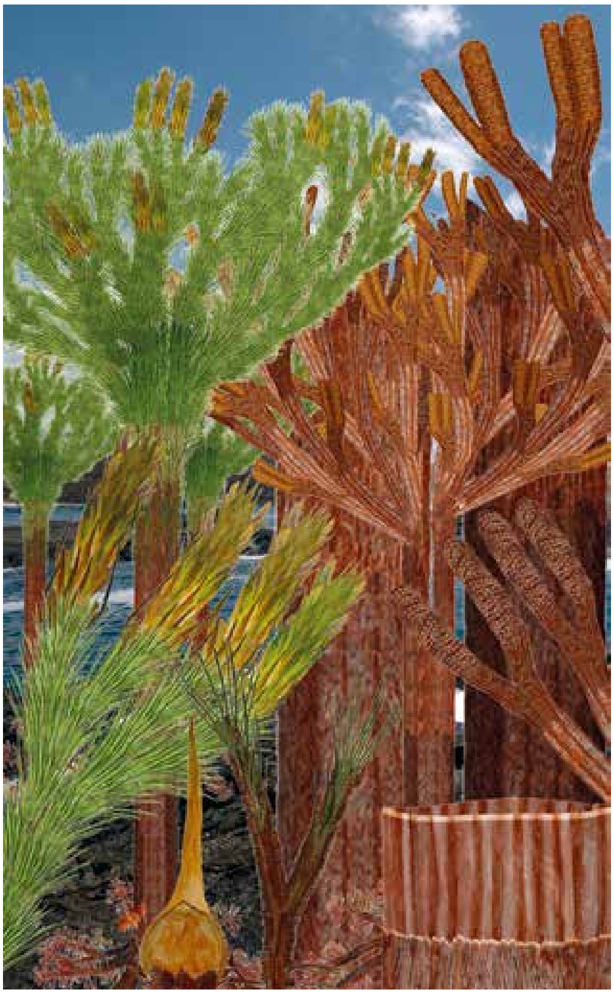


Giant *Sigillaria* in the Upper Carboniferous
A *Sigillaria parallela* primeval forest from the Upper Carboniferous of the Eastern Alps.

Dwarf *Sigillaria* in the Triassic Alps
Bonsai *Sigillcampeia nana* from the Lower Triassic of the Alps.

The beginning of the lycopods (recognisable as such) can be traced back to the Lower Devonian, with the prevalence of *Protolepidodendron wahnbachense* (Pragian-Emsian) (Kräusel & Weyland, 1932; Hartkopf-Fröder & Weber, 2016). *Protolepidodendron leschii* from the Middle Devonian (Eifelian, approx. 390 million years ago), a shrubby lycophyte, shows more recognisable properties, especially characterised by forked-to-unforked leaf needles (Wachtler, 2022) as well as homosporous sporangia.

It remains unclear whether *Protolepidodendron* has more parental affinities with *Lepidodendron,* which developed into giant trees in the Upper Carboniferous, or whether it is more related to today's genus Lycopodium. The low-growth speaks for *Lycopodium,* the basally falling leaves for *Lepidodendron.* Altogether, *Protolepidodendron* represents probably the most archaic stage of development of the two above families, from which both the *Lepidodendron* giant trees and the inconspicuous *Lycopodium* species of the present time could develop. The origin of the heterosporous lycopod families, such as today's Selaginellaceae or the Sigillariaceae, which appeared in the Carboniferous with massive trunks, is still unclear. It can be assumed that they developed also in the Lower Devonian, because possible *Selaginella* ancestors (*Selaginellites devonianus*) from this period (Middle Eifelian) can be found, as from the Lower Carboniferous (Visèum) massive trunks have been recovered and assigned to *Archaeosigillaria* (Wachtler, 2023). An evolutionary theory of a first origin in the Lower Devonian and a slow splitting-off in the course of the following millions of years is therefore invalid: homosporous and heterosporous Lycophyta developed together relatively quickly in the early Devonian. This also applies to many other plant families such as ferns, gymnosperms or horsetails: there was no gradual development but abrupt splits (Wachtler, 2022).

However, one statement remains constant: everything started from dichotomously

***Protolepidodendron leschii*. Branchlets and fertile parts. Middle Devonian, Middle Eifelian**

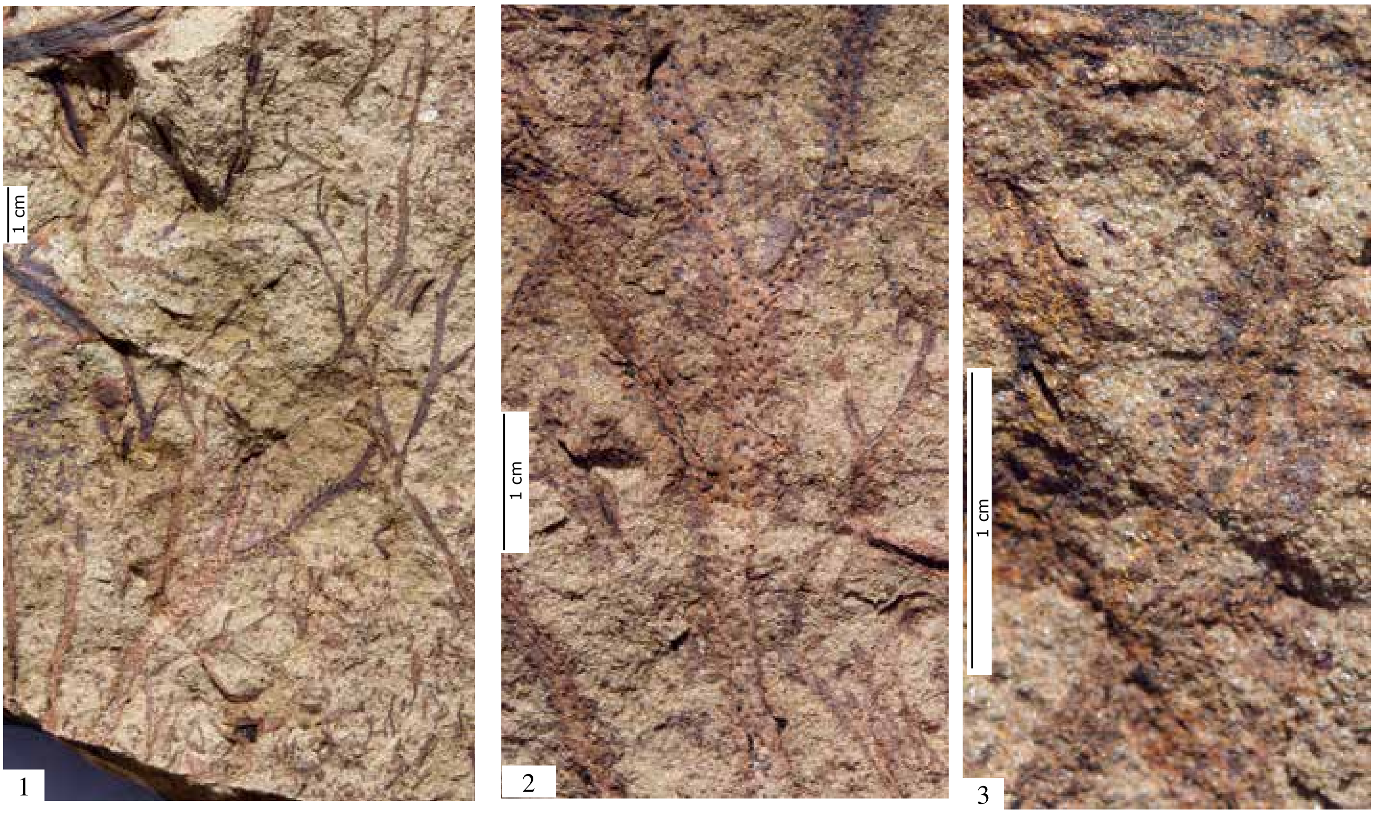
1. Various twigs with unforked and forked leaf needles (LIND 02, Coll. Pohl; 2–3. Branchlet with sporophyll cone in the upper area (holotype LIND 88); Coll. Wachtler, Dolomythos.

divided leaves and fertile scales in the Devonian to undivided and merging leaf needles in the Carboniferous. It remains unclear how the trees were able to develop from the creeping clubmosses in the Devonian to giant trees in the Lower Carboniferous, within a geological period of about 50 million years. Another related question must be answered: how could the multi-layered bark trunks of both *Sigillaria* and *Lepidodendron* develop from dwarfish plants?

A peculiar plant world in the Carboniferous

The tropical climate, which led to the formation of extensive swamps in the Carboniferous, prepared a fertile soil for the development of not only the huge Lycophyta but also giant Calamitaceae horsetails and a variety of treeferns and normal ferns. In turn, the largest coal deposits of all time were created due to conditions similar to the primeval jungles. Mostly, the plants were not transported over long distances by rivers or currents but fell on the spot into the morass/swamp and were petrified there in the fine-grained silt. In some places, the coal formation was too weak to merge and overlay each other, so that the living environment of that time has remained in excellent individual condition to this day; we can thus obtain a robust knowledge of the ancient flora. This is often the case in the Eastern Alps, where there was never any large-scale formation of coal but which sheltered excellently preserved fronds, sporophylls or individual trunks.

Some of the plants with fern-like foliage developed clearly separate seed and pollen systems like gymnosperms (*Cyclopteris)*, while other ferns attracted attention with their own peculiar sporophylls, which are unknown in the species today (*Callipteridium)*; others formed different tropophylls and sporophylls, similar to today's royal ferns (*Osmundites)*. Moreover, tree ferns (*Cyatheites, Dicksonites)* were also present on a large scale, in addition to the precursors of the



***Selaginellites devonianus*. Branchlets and fertile parts. Middle Devonian, Eifelian**

1–3. Slab with various *Selaginellites devonianus* plants, as well as sporophylls with partially shed bracts (3) (holotype LIND 131); Coll. Wachtler, Dolomythos.

Lower Carboniferous Sigillaria (Viséan)

1. *Archaeosigillaria* sp. trunk part (MAR 15, Marinelli hat); 2. *Archaeosigillaria* sp. Macrosporangia (TRÖP 11, Tröpolacher Almweg); Coll. Wachtler, Dolomythos Museum.

Marattiaceae (*Marattiopsis, Danaeites*). The giant horsetails were dominated by the genus *Calamites,* although this expression is somewhat misleading: the sporophyll blueprint had nothing in common with those of today's Equisetum horsetail; only the stem character and, sometimes, the side shoots were similar.

In the Upper Carboniferous, the gymnosperms were largely absent, and they only experienced an explosive development at the Carboniferous-Permian boundary, probably due to long-lasting global cold phases that also affected the regions around the former equator.

Beginning from the Early Permian, the gymnosperms appeared together in a large number of families, such as the conifers with many subgenera like Fir, Araucaria, Pinoidea-ancestors, the cycads with the two groups that still exist today (such as the Cycas-Cycads and the Zamia-Cycads), as well as the Ginkgos; hereby, the assumption arises that their initial development took place at the beginning of the Devonian, with genera like *Calamophyton, Eoconifera, Flabellophyllum Schweitzeria, Weylandia* or *Kraeuselia.* Also, presumably they were pushed back into retreat areas in the course of the Carboniferous, only to thereafter reappear in large numbers right up to the present.

Sigillaria and its way to giant growth

The genus *Sigillaria* can be considered to be, by far, the most common large plant in the Carboniferous of the Alps. Many secrets and a wide variety of names for one and the same plant accompany this clubmoss, but thanks to rich finds from the Carinthian Nockberge, the Carnic Alps and other extremely interesting discoveries from the Triassic of the Dolomites, their appearance, their reproductive properties and even more their development (from giant to dwarf form) can be retraced over 100 million years.

The Sigillariaceae can be called seed lycophyta, a trait not observed in any clubmoss today, with a single large seed and similar (albeit somewhat elongated) microspore vessels. This common characteristic runs throughout all Carboniferous and Triassic Sigillarias, whether they are giant trees or bonsai plants. Other crucial features of both (whether in the Paleozoic or Mesozoic) are the rounded leaf cushions as the remnants of shed leaves, added to elongated narrow leaves with or without a midrib. The elongated wavy pattern in the upper part, as a result of shed sporophylls, runs through all epochs, as does the structure of the sporophyll cones, with the macrosporophylls in the lower area and the microsporophylls in the upper part of the plant.

***Sigillaria parallela*. Various details of the trunks and canopy. Upper Carboniferous**

1. Bark layer from the lower part (Königstuhl, Coll. Kandutsch); 2. Inner layer of a stem (STANG 54); 3. Stem part with details of leaf cushions; 4. Details of the scar cushions of fallen leaves (KOEN 311); 5. Sporophyll cone (STANG 87); Coll. Wachtler, Dolomythos Museum, Innichen.

Various *Sigillaria* leaves, as well as a macrosporangium on the right edge (STANG 47); Coll. Dolomythos.

In addition to many similarities, the biggest differences are found in size. *Sigillaria* of the Carboniferous probably reached growth heights of 20–30 m, with a trunk circumference of 1 m and multiple branches at the crown, while *Sigillcampeia* from the Triassic reached probably only up to 30 cm in height and their stunted trunk forked only once.
The basic structure of the giant *Sigillaria* (seen particularly in the seedling) consisted of a single protostele, with a main vascular bundle, from which many stelae soon branched off and formed plectostelae. Therefore, the giant trunks of the Carboniferous *Sigillaria* were nothing more than a compact series of many thin trunks which formed a main trunk. This could be clearly visible in those parts where the ribbed-to-warty outer layer of the bark fell off and underneath, the closely parallel and connected parts of the trunk came to light. The closer one approached the canopy, the more pronounced the forked side branches appeared, which were geometrically covered with typical roundish, elongated scar cushions formed in the shape of a rhombus. In the upper parts, there were always long, wavy patterns, remnants of the cones from which the sporophylls had fallen off. Had it not been possible to find Bonsai *Sigillcampeia* in the Triassic period, the true shape of all Sigillarias and, especially, their change of generation or the blueprint of the sporophyll cones would still remain a mystery.

Fire Disasters that spread across Continents

In addition to the enormous growth and the appearance of the entire plant, which could be clarified by the abundant finds, layers of ash, many centimetres thick, remain noticeable everywhere the *Sigillaria* occur in huge masses. In them occur a high amount of macrosporangia as well as carpets of microspores. Only above the fire horizons do the fossil remains of Pteridophyta or Calamitaceae appear again, as witnesses to a regenerating vegetation. This phenomenon can only be explained by the fact that after episodic, prolonged periods of drought, which dried out the overripe *Sigillaria* forests, lightning strikes were enough to ignite devastating bush fires, which covered the paleocontinents of that time and destroyed most of the world's vegetation. The hard seed coats of the megasporangia probably also required such catastrophic fires in order to get them to germinate in

1. Exposure of a massive trunk of *Sigillaria parallela* at the Kronalm. A consistent burn horizon is visible above; 2. The Triassic horizons of *Sigillcampeia nana* at Piz da Peres also show layers of ash from wildfires.

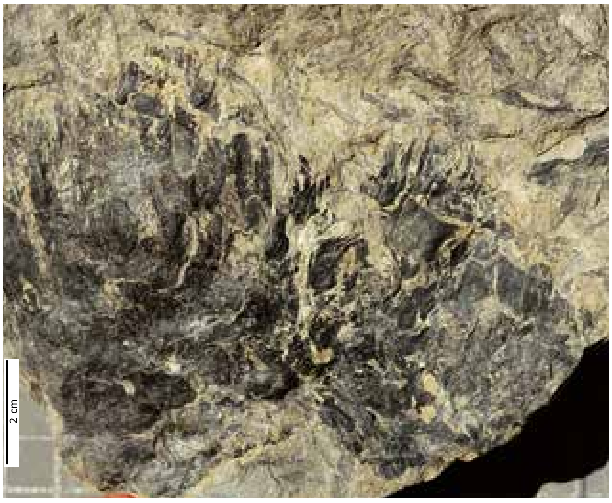
the first place, similar in manner to today's giant Sequoiadendrons.

Surprisingly, there exist extensive fire layers – both between the mighty *Sigillaria* deposits in the Upper Carboniferous of the Carnic Alps or the Nockberge and between the dwarf *Sigillaria* from the Triassic of the Dolomites – which allow the interpretation that the thriving of the giant clubmosses was closely linked to periodically occurring forest fires. We can only guess what effects these fire disasters had on other flora and fauna or on the global climate. In any case, clouds of smoke must have darkened the sky for months, affecting the living world.

The Triassic dwarf *Sigillaria*

Over the Permian, the Sigillariaceae were pushed back further and further, so that in the Lower Permian some remnants of *Sigillaria brardii* in the Germanic Basin or *Sigillaria treneri* in the Dolomites (Kungurian) survived (Wachtler, 2021). Almost doctrinally, they disappeared from the surface of the world toward the Upper Permian. All the more astonishing was the discovery of exhausting layers of the dwarf *Sigillaria, Sigillcampeia nana,* from the Lower Middle Triassic (Anisian) in the Dolomites (Wachtler, 2016), as well as the discovery of another species from the Late Triassic (Carnian) *(Sigillcampeia blauii)*, which documented that the last Sigillariaceae probably existed till the end of the Triassic and finally died out at the Jurassic border.

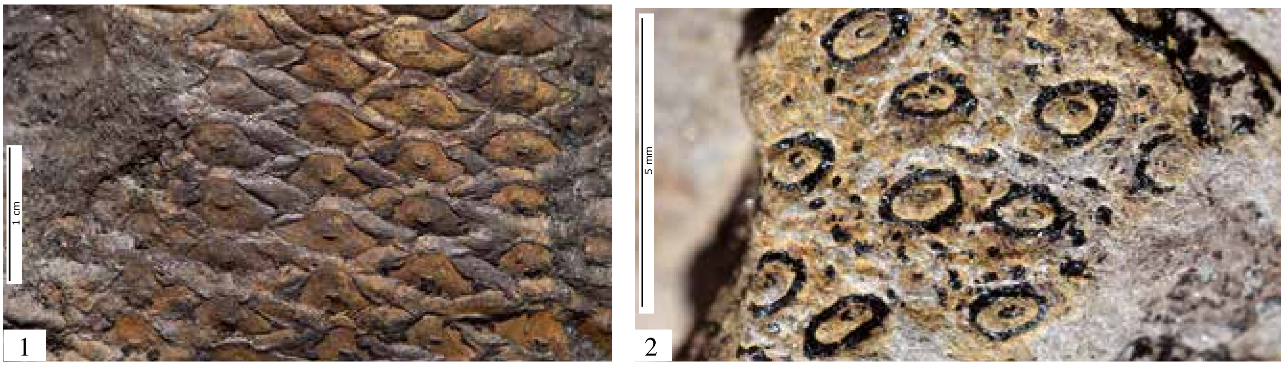
Interestingly, the trunks of *Sigillcampeia* were only 5–12 cm wide and hardly more than 15 cm high, typically forking once in the upper area. The plants were densely covered with grassy leaves up to 25 cm long, developing a midrib in the Early Triassic which disappeared in the course of the Triassic. In the lower parts of the trunk, these leaves usually fell off, so that roundish-to-elongated scars covered the trunks. The two sporophyll clumps in the upper part consisted of elliptical-to-spherical 3–5-cm-long and 2.5–4-cm-wide megasporophylls in the lower part, along with similarly sized but slightly elongated microsporophylls in the upper part. When the sporophylls fell off, elongated, slightly wavy scars remained instead the sporophyll



Sigilcampeia nana. Anisian (Lower Triassic)

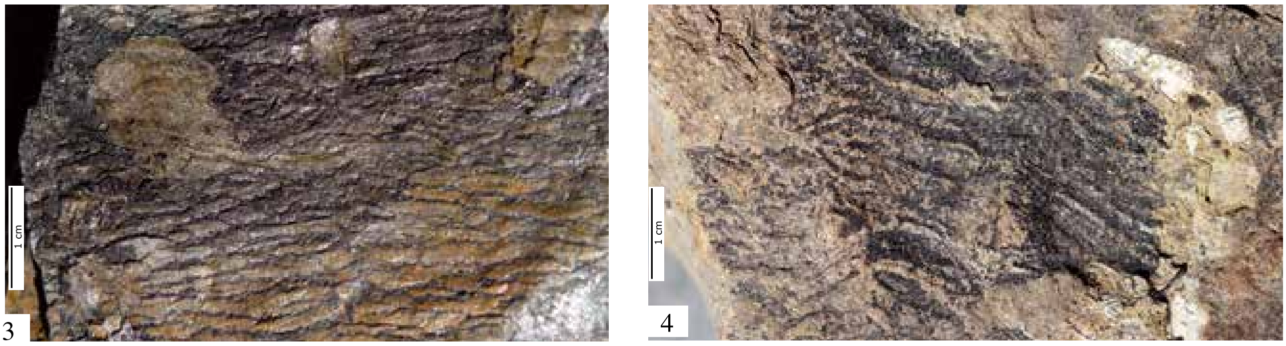
Completely preserved plant with two sporophyll cones (PIZ 741), Piz da Peres, Dolomites; Coll. Wachtler, Dolomythos.

Comparisons between *Sigillaria* (Carboniferous) and *Sigillcampeia* (Triassic)



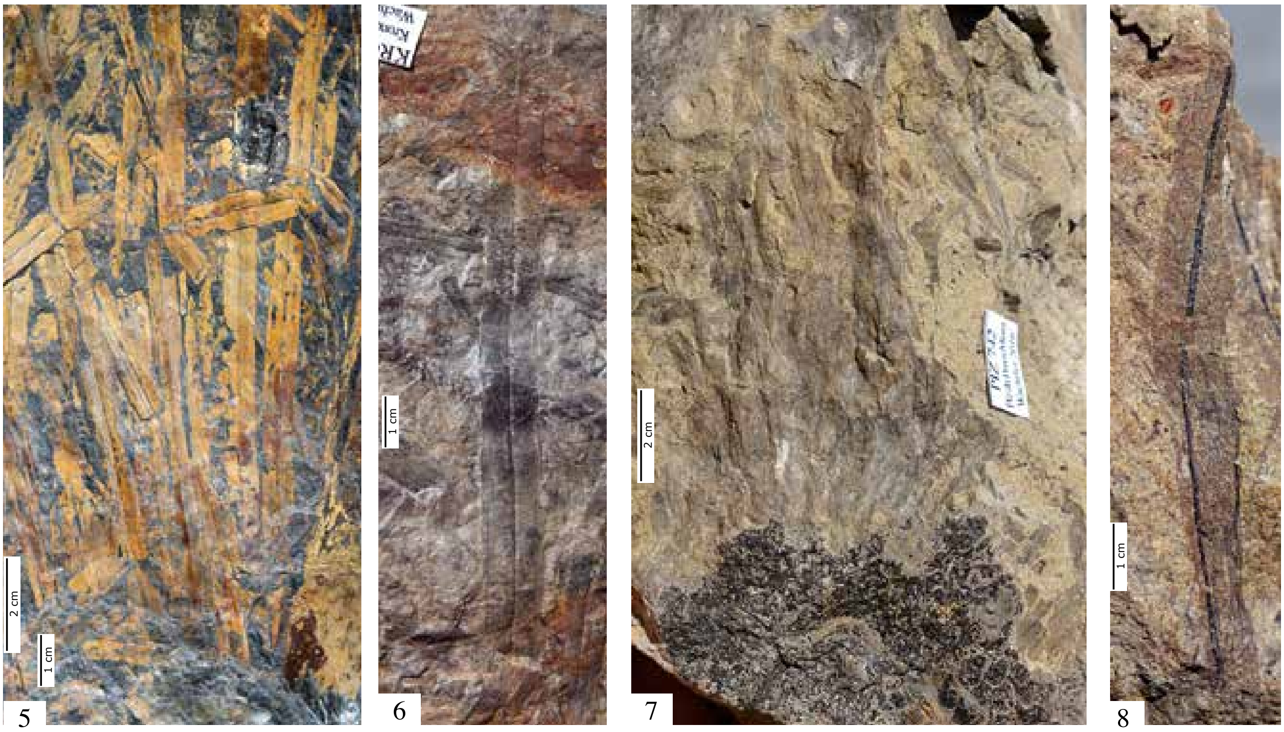
Stems and leaf scars

1. *Sigillaria parallela* (KOEN 268), Carboniferous 2. *Sigillcampeia nana* (PIZ 674, Triassic)



Sporophyll scars

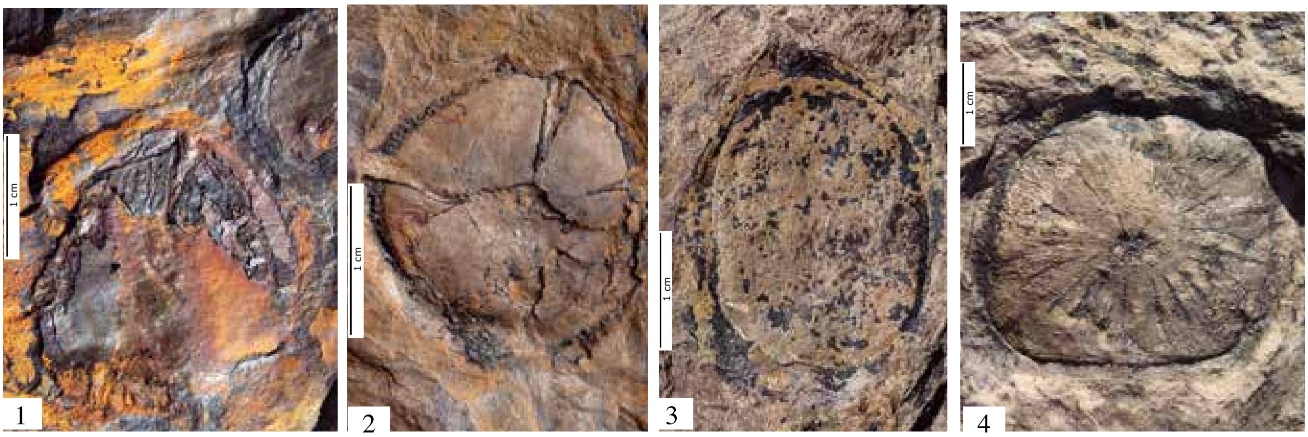
3. *Sigillaria parallela* (KOEN 330, Carboniferous) 4. *Sigillcampeia nana* (PIZ 861, Triassic)



Leaves

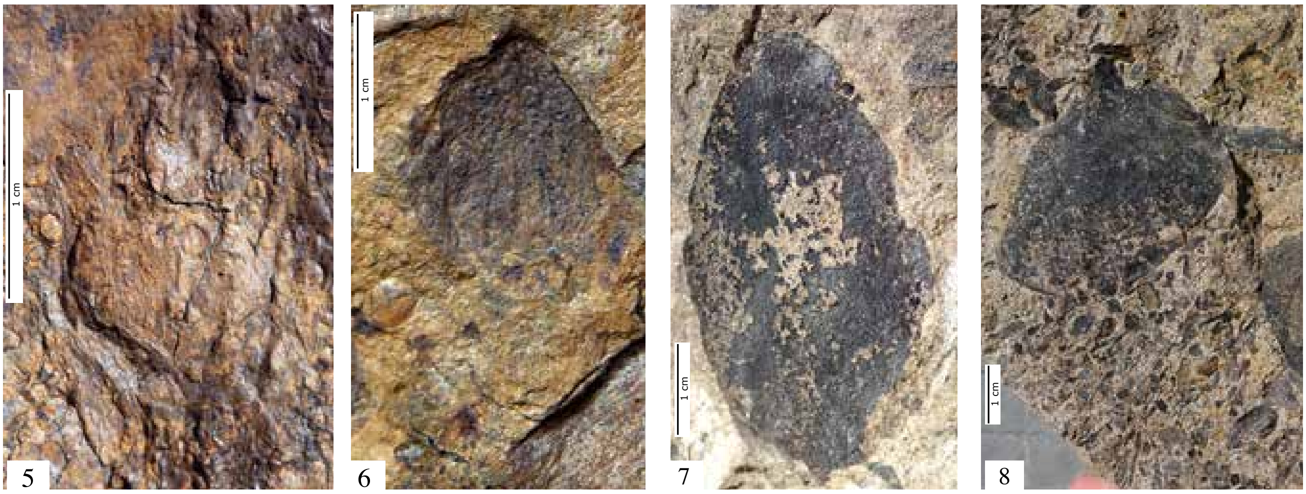
5-6 *Sigillaria parallela* (KOEN 306, KRON 204, Carboniferous) 7-8. *Sigilcampeia nana* (PIZ 742, PIZ 750, Triassic)

Comparisons between *Sigillaria* (Carboniferous) and *Sigillcampeia* (Triassic) sporophylls



Macrosporophylls

1-2. *Sigillaria parallela* (KRON 305, KRON 224, Carboniferous), 3-4. *Sigillcampeia nana* (PIZ 892), *Sigillcampeia blauii* (ZOC 08, Triassic)



Microsporophylls

5-6. *Sigillaria parallela* (KRON 275, KRON 242), Carboniferous 7-8. *Sigillcampeia nana* (PIZ 895, PIZ 929), Triassic

cones. The megasporophylls developed a single large megaspore covered by an integument-like lamina. Only in the upper part did a narrow gap remain open, which had the function of a micropyle and made it possible to let in the microsporangia. The microsporophylls contained a large number of small, roundish microspores, which were released after maturity, either still on the cones or, to a greater extent, after their separation.

Sigillcampeia nana can be found especially in the Early to Middle Triassic of the Dolomites in some layers, especially near the ancient beaches of that time, such as on the Piz da Peres in the Pragser Dolomites (Wachtler, 2016) or, later, in the direction of the Raibl catastrophe in the Late Triassic of the Lienz Dolomites, with regard to *Sigillcampeia blauii* (Wachtler, 2016). Interestingly, similar to those from the Carboniferous, these monocultured are associated with extensive ash layers, which can be regarded as a prerequisite for successful crop rotation, although they are small in stature. Presumably, the *Sigillaria* appeared as swamp plants in the Carboniferous, while in the Triassic they lived in coastal, probably over-salted wetlands, similar to the habitat of today's mangrove swamps.

Extinction of the *Sigillaria* Seed Clubmoss

If the rise of the *Sigillaria* from a giant tree form and their decline to a dwarf plant form is interesting, there are parallels with to-day's plants as well. Recent conifers include

Sigilaria parallela. Reconstructions (Upper Carboniferous). Reconstructions

a. Entire tree with roots and flourishing sporophyll cones; b. Seedling; c. Leaves (abaxial and adaxial); d. Strobilus; e. Microsporophyll (abaxial and adaxial) f. Macrosporangia abaxial and adaxial side, as well as leaf cushions; g. Complete dead tree with roots and bare sporophyll cones; h. Tree with outer bark and a view of the trunk core; i. Side branch with leaf scars; j. Detail of leaf cushions k. Leaf cushions of the sporophylls.

Sigillcampeia nana. (Early Middle Triassic, Anisian). Reconstructions

a. Mature plant with sporophyll stand; b. Single leaf (PIZ 838); c. Leaves with leaf cushions; d. Detail of a sterile leaf scar with typical leaf attachment points (PIZ 933, 957); e. Leaf scars from shed sporophylls (PIZ 902, 909); f. Complete sporophyll crest with basal macrosporophylls and in the upper part the microsporophylls (PIZ 741); g. Macrosporophyll with a megasporangium (PIZ 892, 888); h. Microsporophyll with microsporangium (PIZ 862); Piz da Peres, Dolomites.

Comparisons between *Sigillaria* (Carboniferous) and *Sigillcampeia* (Triassic)

Seedlings und juvenile plants

1. *Sigillaria parallela* (KRON 382, Carboniferous) 2. *Sigillcampeia nana* (PIZ 750, Triassic)

dwarf pines (*Pinus mugo)* and also Scots pines *(Pinus sylvestris)* almost 50 m high. Of course, dwarfism is often related to extreme climatic conditions, which may have taken place in the otherwise-fertile and tropical Lower to Middle Triassic (Anisian), at extremely saline growth sites, as well as in the Upper Triassic (Carnian), which could be explained by the presumably global Raibl Crisis.

Nevertheless, it can be assumed that this form of seed clubmoss disappeared completely from the world between the Triassic and Jurassic, because subsequently, as well as in the present, no remotely plausible descendants of the Sigillariaceae have been found. The only point of certainty is that the Sigillariaceae went their own way as early as the Devonian, never crossing with other homosporous Lycopods or with the Lepidodendrales.

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Carboniferous Fossil Floras from the Eastern Alps

Edited by Michael Wachtler and Nicolas Wachtler

Summary

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

With 600 photos and drawings

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