Lepidodendron clubmoss of the Carboniferous in the Alps

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In addition to the more widespread giant clubmoss *Sigillaria,* the remains of the other huge lycophyta - *Lepidodendron* - are mainly found in the Nockberge. An exact classification is difficult because over the centuries – mainly based on differently shaped leaf cushions of the stems – hundreds of species have been introduced, although other parts of the plant, especially the important fertile organs, have hardly been studied. Since the *Lepidodendron* clubmoss of the Eastern Alps, concerning the fructifications, differ from others or in other places they are not known at all, it is necessary to introduce a new species name: *Lepidodendron fritzii* n. sp., until a systematic review of all Lepidodendrales worldwide may shed more light on this complex family. They likely faced the same fate as that of the Sigillariaceae. The Upper Carboniferous lycopod forests periodically died out due to prolonged periods of drought or due to an increase in the old stock, such that forest fires probably spread across entire continents and destroyed most part of the flora, but also offered space for the recreation of young plants. This is the only way to explain the repeatedly occurring decimetre-thick coal fire layers.

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Keywords: *Lepidodendron*, Upper Carboniferous, Alps, Dolomites, Lycophyta, club moss

***Lepidodendron* forests in the Carboniferous**
Lepidodendron fritzii in the Eastern Alps. In the foreground, a tuft of trees in bloom; more trees grow in the background. A sporophyll cone can be found in the centre right, while a dead tree stands on the right edge.

A classification of the Lepidodendrales, primarily those of the Eastern Alps, turns out to be rather easy. In 1840, the Austrian paleobotanist Franz Unger was the first to describe various *Lepidodendron* species from the Stangalpe in the Nockberge Mountains, always referring to species already described by authors from other areas and mostly comparing the peculiarities of the leaf cushions on the trunks; he included *Lepidodendron ornatissimum, Lepidodphyllum lineare, Lepidodendron rimosum (all Brongniart), Lepidodendron gracile, Lepidodendron undulatum* and again, in 1847, *Lepidodendron lycopodoides* (all Sternberg). Even the name *Lepidodendron* has gone a long way. It was first coined in 1820 by the Czech Count Caspar Maria Sternberg in his *"Flora der Vorwelt",* containing the description of 11 different species, primarily leaf cushions or stem parts. Sternberg thus unified various previously established names such as *Phytolithus, Lithophytus, Typolithi, Phytotypolithi, Palmacites, Lepidotae* or *'scale plant',* because of the scale-like structure of the leaf cushions (Greek 'lepís'/'lepídos' for 'scale').

As early as 1904, the German paleobotanist Franz Fischer was appalled by the *"almost 300 (!) species names"* that had been established in the meantime, for the most part only because of different characteristics of the bark. He prophesied, *'A strong reduction will probably also correspond more to the facts, because based on the observation of our present-day forests, which we always see composed of very few species of the same genus, it can be assumed that these ratios also prevailed in the formation of the Palaeozoic forest swamps'.*

The sporophyll cones of the Lepidodendrales remained unconsidered for a long time, until several subgenera were established here as well, namely *Lepidostrobus* (Brongniart, 1828), *Spencerites,* (Scott, 1897) *Lepidocarpon* (Scott, 1900) or their isolated sporophyll *Lepidophyllum* (Brongniart, 1828). As with the Sigillariaceae, there was soon an overall unsatisfactory starting point, with a myriad of different descriptions of trunk, leaf cushion, leaves or sporophylls, a confusion which even today remains only partially resolved.

Not even among the holotypes kept in the National Museum is there an agreement as


VERSUCH

EINER

GEOGNOSTISCH-BOTANISCHEN DARSTELLUNG

DER

FLORA DER VORWELT.

VON

GRAFEN KASPAR STERNBERG.

1 BAND TEXT.

Cover of the first volume of Sternberg's *"Flora der Vorwelt"* from 1820, in which were described various *Lepidodendron* species. National Museum, Prague.

Bust of Caspar Maria Graf Sternberg (also: Kašpar Maria Šternberk, 1761–1838).

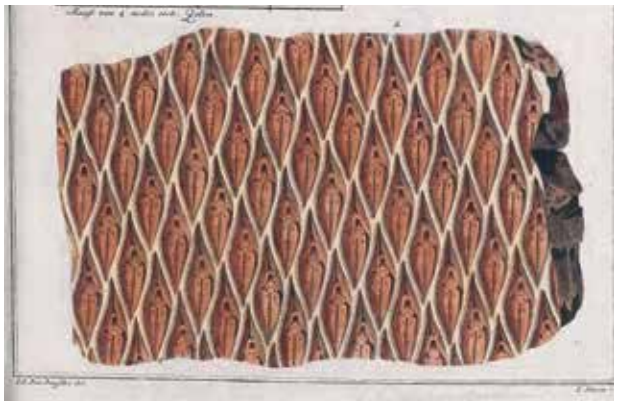
to which species – *Lepidodendron dichotomum, Lepidodendron obovatum* or *Lepidodendron aculeatum* – mentioned simultaneously by Sternberg in 1820 in his *"Flora der Vorwelt"* can be regarded as the original holotype.

Participating in the difficult classification is a phenomenon that also occurs with *Sigillaria:* mostly dead stems, with decorative leaf cushions of shed leaves, are often found in situ, i.e. in those places where they fell to the ground in the moor swamps. Only rarely are the stem parts with attached leaves found. However, they can be found in large numbers, either in loose form or in dense criss-cross fossilised layers. All these parts of the trunk are often found below ash layers, along with sediments of coal several centimetres thick. In addition, the long, slender leaves of the Sigillariaceae are almost indistinguishable from those of the *Lepidodendron*.

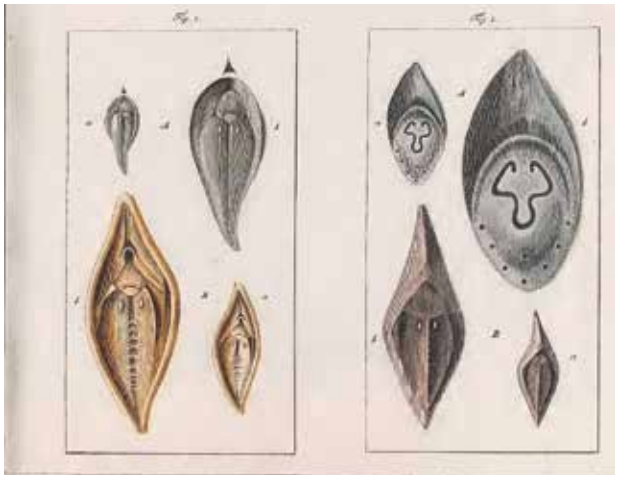
The situation with the Lepidodendronales found in the Nockberge is just as difficult. They all occur in geologically contemporaneous layers, so it can be assumed that they belong to one and the same plant. The species described by Franz Unger from the Stangalpe (*Lepidodendron ornatissimum, Lepidodphyllum lineare, Lepidodendron rimosum, Lepidodendron gracile, Lepidodendron undulatum, Lepidodendron lycopodoides)* hardly offer any help, since he used the names of Sternberg and Brongniart based on their finds from other areas, and thus the meaningful fertile parts were not included by him.

Although those plants from the Nockalm area come relatively close to those of other European localities, such as the Karviná Formation in Knurow, Poland, there are still remarkable distinguishing features. Although all parts of the plant, from the stems to the sporophyll cones, are found in Nockalm in very good quality and even in Knurow, the question of whether they should be classified as *Lepidodendron obovatum* or *Lepidodendron aculeatum* remains unresolved.

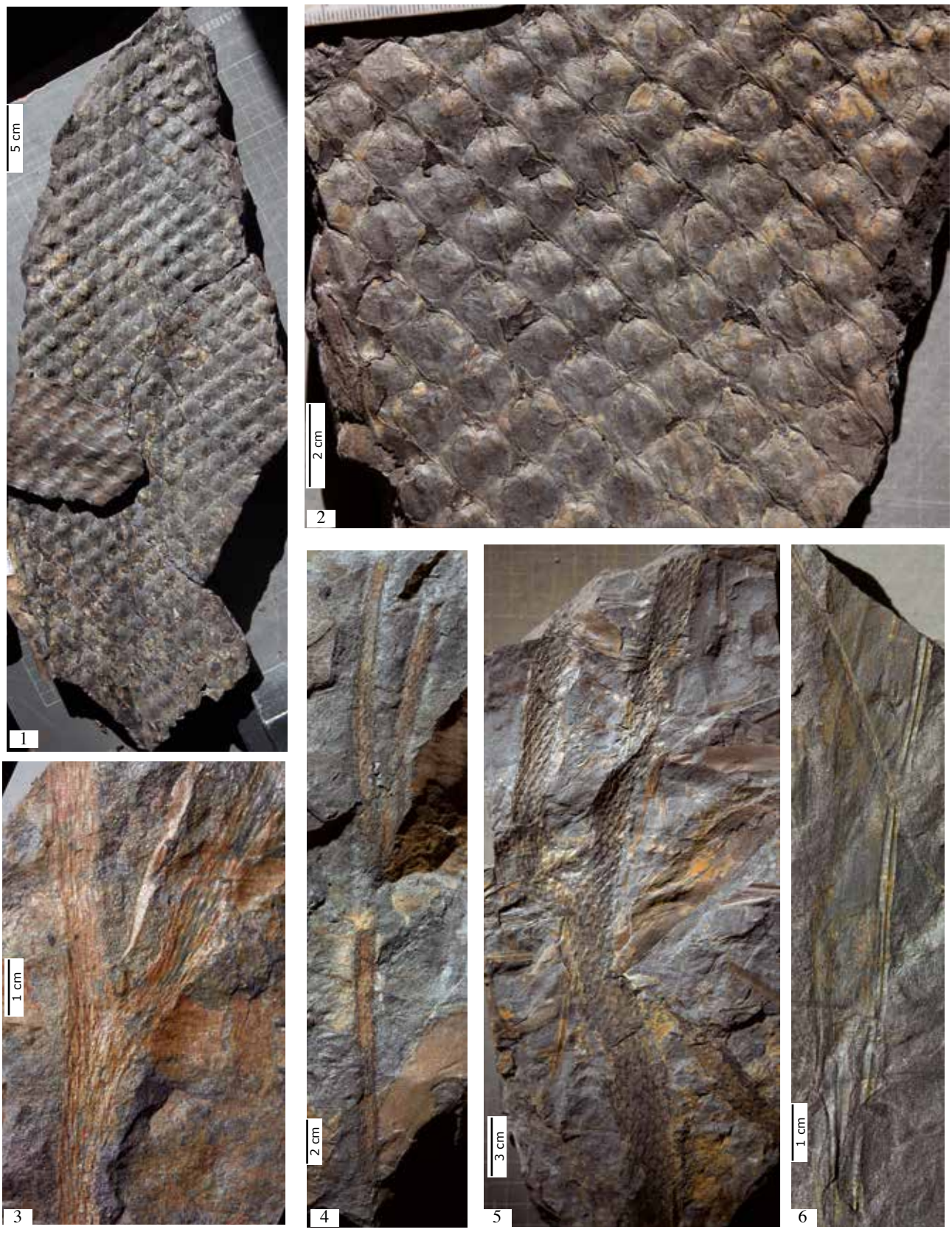
As a matter of fact, the two above plants they are different. Therefore, it might be most appropriate to choose a separate species name for the Lepidodendrons from the Nockberge, perhaps *Lepidodendron fritzii.*



Original from the Sternberg Collection and a hand-coloured illustration from 1820 *(Flora der Vorwelt*, vol. I, 1, pl. 6) with *Lepidodendron obovatum* and *Lepidodendron aculeatum* performed by J. Sturm. Library National Museum, Prague.

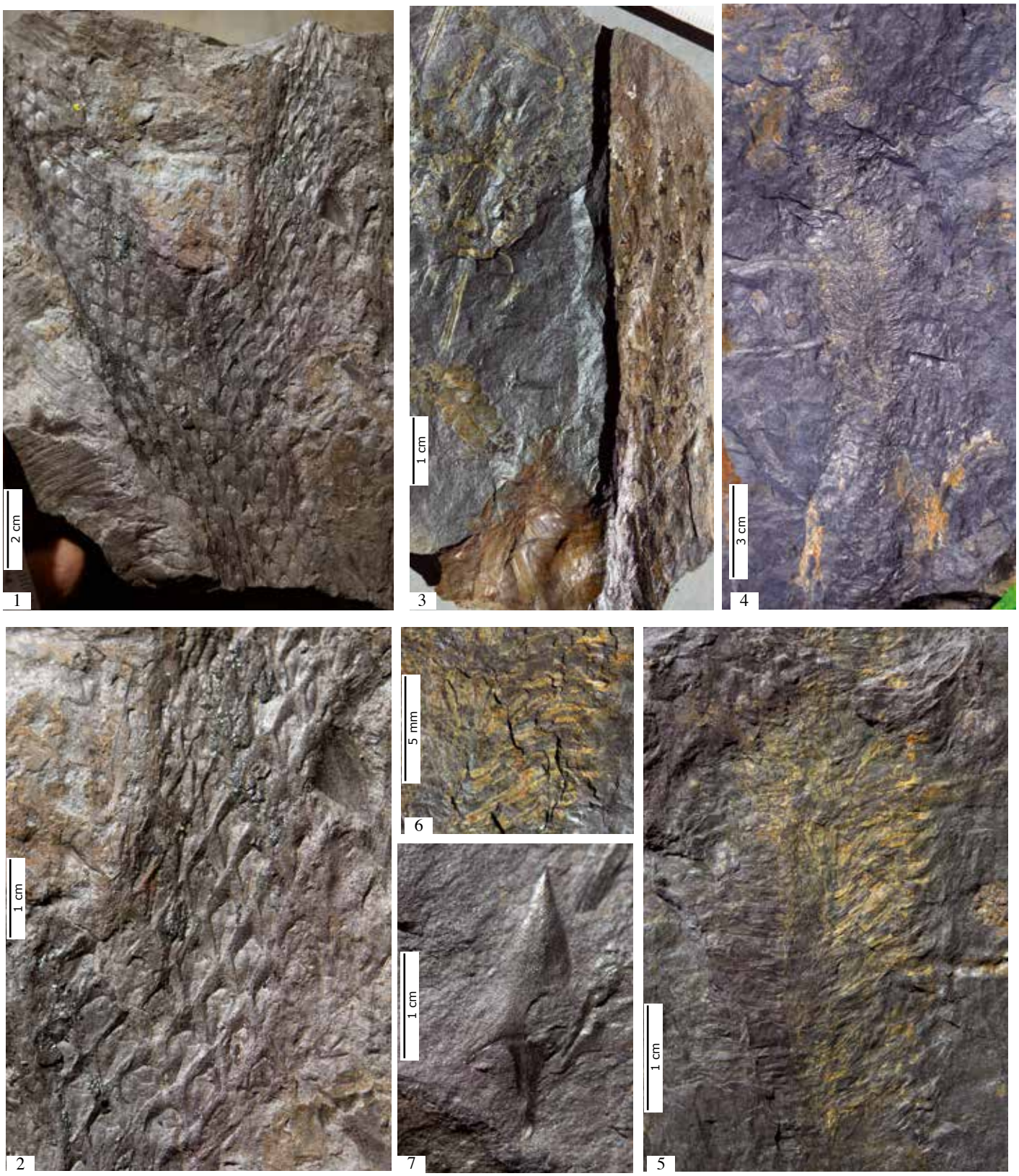


Lepidodendron: Structure of the leaf cushion, from Sternberg, 1820 *(Flora der Vorwelt).*



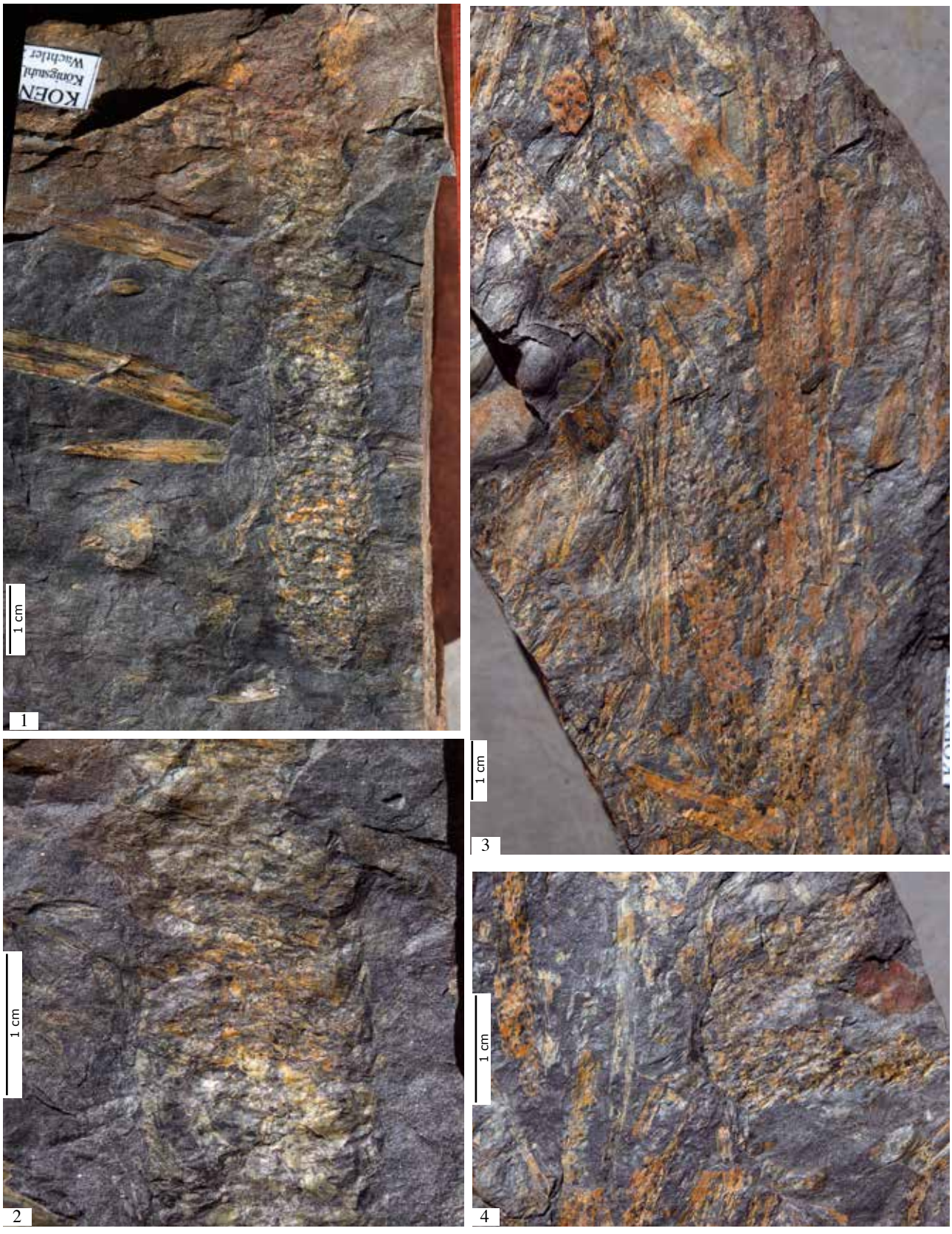
***Lepidodendron fritzii*. Stems and branchlets. Königstuhl (Upper Carboniferous)**

1–2. Part of a stem with detail of leaf cushions (STANG 32); 3. Detail of an apical branch (STANG 41); 4–5. Apical branches (STANG 08); 6. Single leaves (STANG 49); Coll. Kandutsch, Wachtler, all Dolomythos Museum, Innichen.



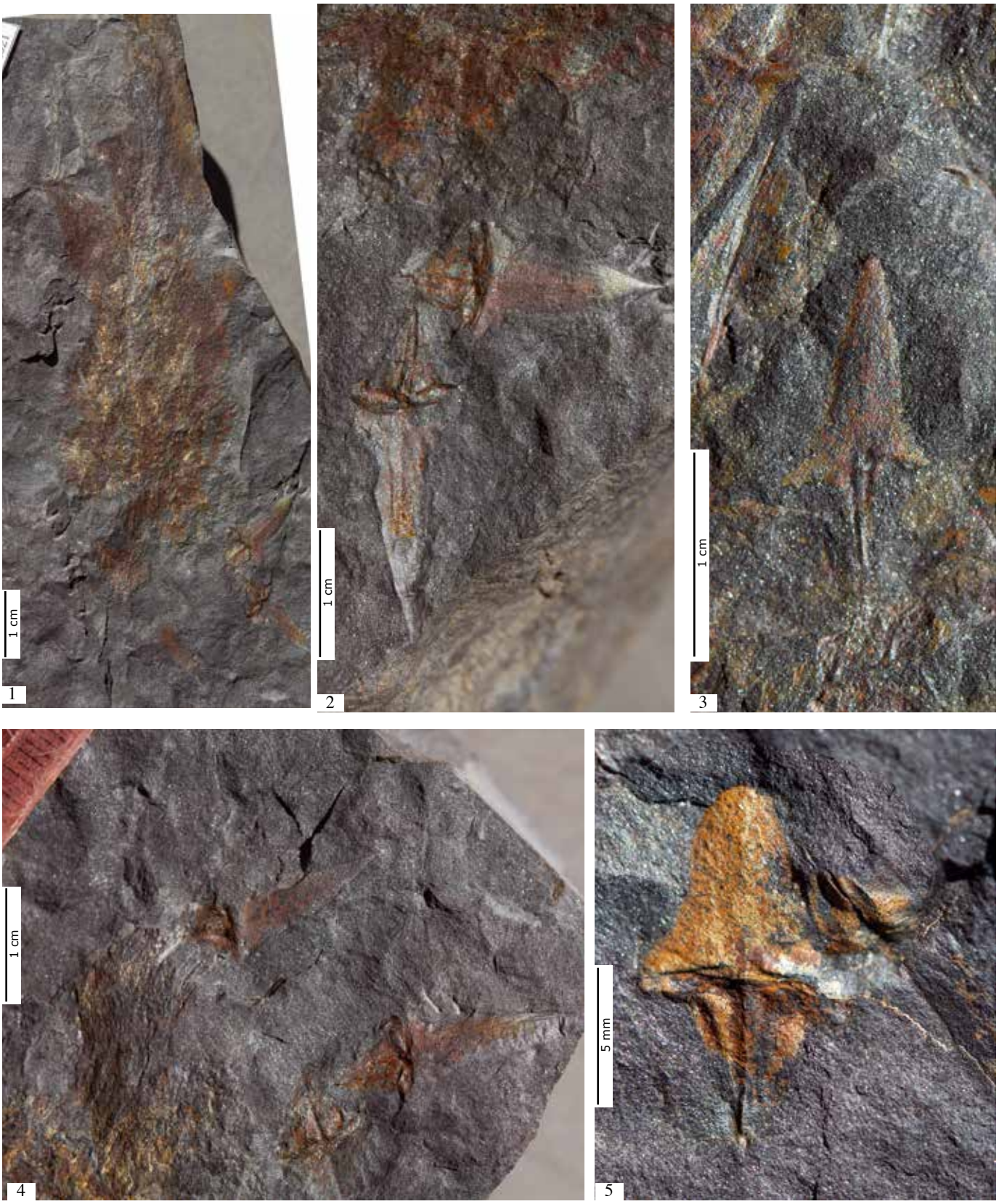
Lepidodendron fritzii. **Stems and Sporophyll cones. Königstuhl (Upper Carboniferous)**

1-2. Apical branching with shed leaves and leaf cushions (STANG 05, paratype); 3. Side branch with leaves (STANG 46); 4-6. Complete cone (STANG 04); 7. Single sporophyll (STANG 03); Coll. Wachtler, Dolomythos Museum, Innichen.



***Lepidodendron fritzii*. Sporophyll cones. Königstuhl (Upper Carboniferous)**

1–2. Complete sporophyll cone with sterile leaves (KOEN 263); 3–4. Side branch with shed leaves (KOEN 219); Coll. Wachtler, Dolomythos Museum, Innichen.



***Lepidodendron fritzii*. Sporophyll cones. Königstuhl (Upper Carboniferous)**

1–4. Decayed cone with sporophylls and detail of the sporangia (KOEN 221, holotype); 5. Single sporophyll (KOEN 180); Coll. Wachtler, Dolomythos Museum, Innichen.

Systematics

LEPIDODENDRON Sternberg, 1820

Lepidodendron fritzii Wachtler, 2022

Locus Typicus
Eastern Alps, Stangalpe and Königstuhl

Geological age
Upper Carboniferous (?Moscovian - Kasimovian-Gzhelian)

Repository
Coll. Wachtler, Museum Dolomythos, Innichen

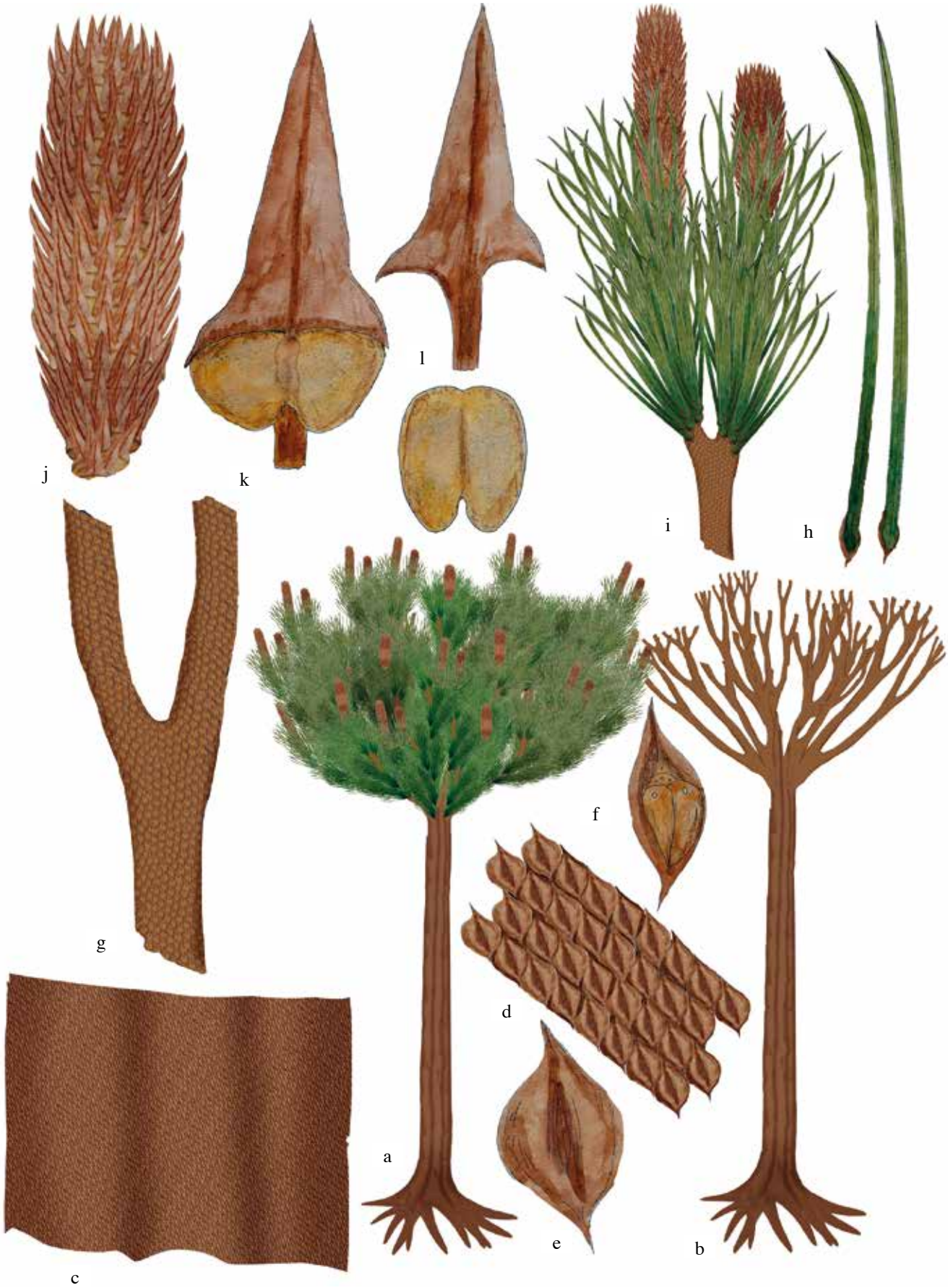
Etymology
Named after the Austrian paleobotanist Adolf Fritz. He primarily researched the Carboniferous flora of Carinthia.

Holotype
KOEN 221 (Decayed cone with shed sporophylls), **Paratype:** STANG 05 (Branchlet)

Diagnosis
Basal trunk and twigs of the first order are covered by leaf cushions of shed branches. Leaves are slender and elongated, with a pronounced central vein. Sporophyll is cone-like with long bracts which fall off at maturity. Sporangia are basally kidney-shaped.

Description
Whole plant: Sturdy trees, probably 1 m in diameter, with a hollow trunk and solid tree bark. The arched leaf pads cover the main trunk in distinct oblique lines. Those on the main trunk are convex due to subsequent growth in thickness or are obliterated as well (STANG 32). Lateral branches have elongated rhombic, sharp-edged pads, up to 1 cm long (STANG 05) and 0.25 cm wide. At the highest elevation of the cushion in the upper area, the break-off point of the sheet is evident from the scars. On branches of the last order or those of the juveniles, the pads are densely packed, touching each other. Leaves are narrow (up to 0.5 cm) and elongated, probably reaching 50 cm in some cases (STANG 49) and being traversed by a prominent midrib.
Fertile parts: Sporophyll cones range from 10–25 cm in length (STANG 46), with a width of 3–5 cm. Individual sporophylls are up to 2 cm long, each ending in a pointed, smooth-edged bract. Sporangia in the lower part are embedded between the sporophyll and the short stalk; they are kidney-shaped and homosporous (STANG 03, KOEN 221 holotype, KOEN 180).

Remarks
The frequency of *Lepidodendron i*s far behind the dominating *Sigillaria* clubmoss in the Upper Carboniferous sediments of the Eastern Alps. Nevertheless, except for the almost similar leaves, they are distinguishable by their leaf cushions on the branches and more easily by their sporophyll cones. Especially, the shed tapering and leathery sporophylls with the kidney-shaped or partially connected sporangia in the lower area make *Lepidodendron* unique. However, questions arise because some sporophyll cones up to 30 cm long are found, along with relatively short ones that reach only 10 cm. Whether these belong to two species or only one cannot be answered with certainty, but they seem to lie within a certain range of variation.
With the introduction of the new species *Lepidodendron fritzii*, a line was drawn under the naming conventions of earlier authors (Unger, 1840; Fritz, Krainer, 1997), who adopted a large number of names from other European localities without regard towards the knowledge of the sporophyll status or even of the entire plant *(Lepidodendron ornatissimum, Lepidodendron gracile, Lepidodendron undulatum, Lepidodphyllum lineare, Lepidodendron rimosum, Lepidodendron lycopodoides, Lepidodendron dissitum, Lepidofloyos laricinus, Lepidostrobophyllum lanceolatum)*. It could be the case that one or the other species corresponds to that obtained from the Nockberge Mountains, but as long as there is no meaningful revision of the Lepidodendrales from other localities, with the recognition of all parts of the plant – from the stems to the leaves and especially the sporophyll cones – such comparisons are impossible.
As an example, an association from the Szczyglowice quarry of the Polish site Knurow is shown here, where all parts are also available in excellent quality. Although this species, sometimes classified as *Lepidodendron aculeatum*, then again as



Lepidodendron fritzii. **Reconstructions**

a. Whole plant with sporophyll cones; b. Dead tree; c. Stem lower half; d. Leaf cushions; e. Leaf cushions lower part; f. Leaf cushions upper part; g. Part of the trunk in the upper part of the tree; h. Leaves; i. Fertile part with leaves and two cones; j. Sporophyll cones; k. Single sporophyll; l. Sporophyll and kidney-shaped sporangia.

Lepidodendron obovatum, resembles those of the Nockberge, its cones nevertheless differ from *Lepidodendron fritzii.* First, this species appears to have a reduced tendency of breaking up the spore cones. While isolated sporophylls are frequently found in the Nockberge, they are rare at the Knurow site. Even the leaf cushions have a different shape – somewhat squat and rounded in the Nockberge mountains, while elongated in Knurow.

It is interesting that in the Austrian Nockberge as well as in the Polish Knurow – in locations of the same age – both smaller and (partly reaching) 25–30 cm cones are found; thus it can be assumed that these are plant-specific peculiarities of one and the same species.

The Lepidodendrales largely disappeared from all the continents towards the end of the Carboniferous. Nevertheless, some must have survived the Permian, since dwarf stands with a probable successor of the Lepidodendrales – *Lycopia dezanchei* – were present in the Anisian (Lower Middle Triassic) of the Dolomites (Wachtler, 2016). These showed similarities with those from the Upper Carboniferous both in the cone structure and in the leaves, even if they reached a growth height of 2–3 m and trunks of 5–10 cm width: a mere imitation of former sizes. They should thereafter have become extinct in the direction of the Middle Triassic.

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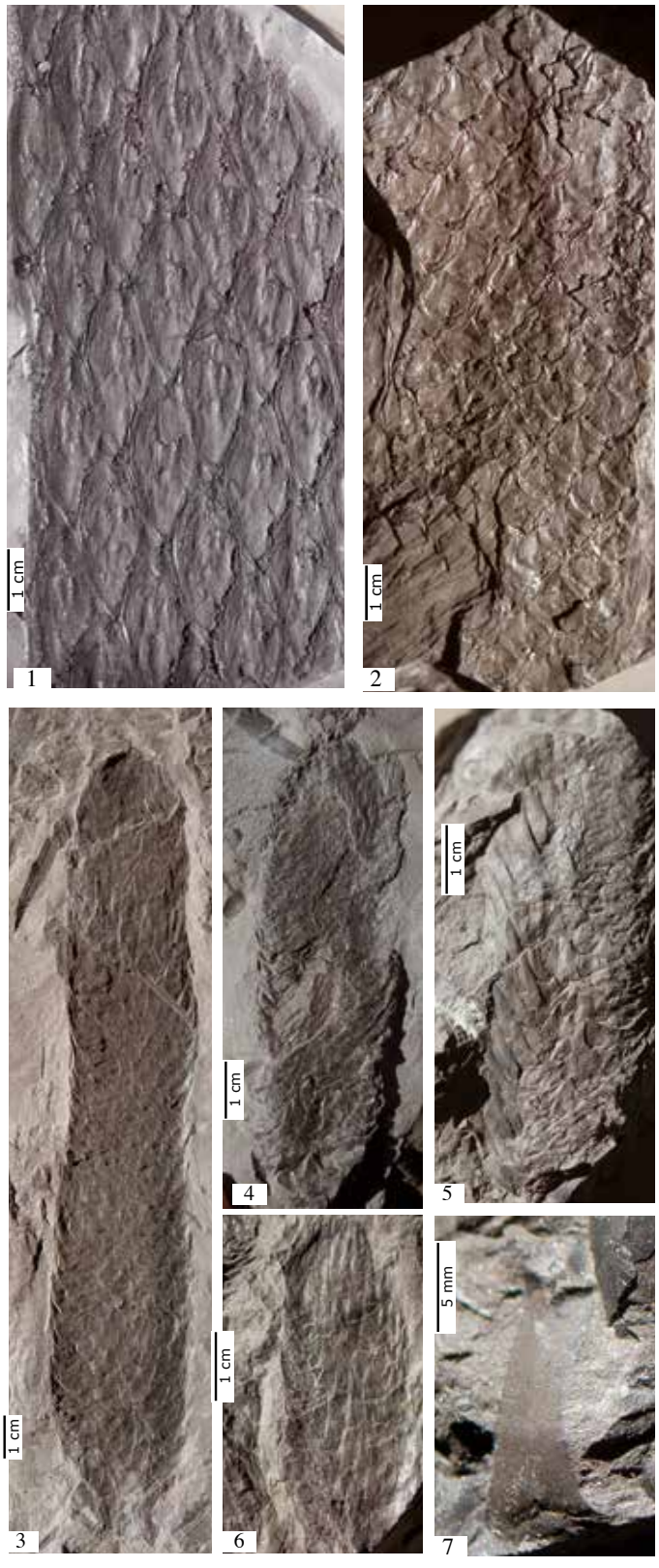

Lepidodendron aculeatum. **Knurow, Poland (Upper Carboniferous)**

1. Stem with leaf scars; 2. Lateral stem with leaves; 3. Large sporophyll cone; 4–5. Smaller sporophyll cones; 6. Juvenile sporophyll cone; 7. Single isolated sporophyll.

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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