The Middle Devonian Flora Explosion

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The Middle Devonian (Eifelian) flora of Lindlar (North Rhine-Westphalia, Germany) occupies a prominent position in the development of the plant world. For the first time, we experience in this period tree-shaped Protoconifers like *Calamophyton primaevum*, with two-seeded bracts, and sparsely settled microsporangia on cone-like structures, similar to modern-day firs or pines. In addition, we come across *Eoconifera fuchsii* n. gen. n. sp., with a symmetrical arrangement of branches, as well as one macrosporangia, which show clear tendencies in the direction of the Araucaria family This observation also applies to typical araucaroid microsporophylls. Another group of Protoconifers, *Schweitzeria enigmatica* n. gen. n. sp., with spreading branches are also found to have developed. Their many-seeded sporophylls, observed in the Voltziaceae throughout the Permian and the Triassic, are also found today in *Cryptomeria, Sciadopitys* or *Sequoia*. In addition, the first Ginkgos (*Flabellophyllum divisium* n. gen. n. sp.) are probably found, indicated by their leaf shape. Two families from the crown group of cycads are also possibly present: *Kraeuselia pohlii* n. gen. n. sp., with a two-seeded habit corresponding to today's Zamiaceae, as well as the Cycas-cycad *Weylandia rhenana*, with a large number of seeds developing in parallel along one axis on both sides. All these flora are characterised by clearly separated seeds and pollen organs, having cone-like shapes. The development of ferns begin with *Protopteridium philippae* n. sp., and likewise those of horsetails begin with the ancestors of today's Equisetum line (*Archaeoequisetites lindlarensis* n. gen. n. sp.) and *Archaeocalamites antiquus* n. sp. Moreover, the club moss family (*Protolepidodendron leschii* n. sp.; *Selaginellites devonianus* n. sp.) can be compared to later genera. Interestingly enough, in the flora of Lindlar we observe the crown groups of many of today's plant families.

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A Middle Devonian plant community (Lindlar 390 million years ago)

1. ***Calamophyton primaevum:*** An ancestor of the Abietaceae or Pinoidea with pollen cones and seed cones; 2. ***Protolepidodendron leschii:*** A progenitor of the lycopod; 2. ***Protopteridium philippae:*** An ancestor of the ferns; 4. ***Kraeuselia pohlii:*** A cycad precursor (Zamia, two-seeded) with a pollen cone; 5. ***Weylandia rhenana:*** (Cycas – multi-seeded sporophylls); and 6. ***Eoconifera fuchsii:*** a precursor of the araucarias.

The characteristic plant of the Middle Devonian of Germany, *Calamophyton primaevum,* a progymnosperm, has been known for a long time. Additionally, we can observe other similar-looking but nevertheless different plants in this region during the above period.

Calamophyton primaevum

The history of exploration of *Calamophyton primaevum* is spectacular. In 1914, the Swedish paleobotanist Alfred Gabriel Nathorst (1850–1921) described a Middle Devonian plant from western Norway, naming it *Hyenia sphenophylloides.* Kräusel and Weyland published a paper in 1926 introducing the new species *Hyenia elegans* from the Kirberg locality in the Rhineland (1926, p. 126, Contributions to the knowledge of Devonflora II); on page 137 of the same publication, they described another new genus, *Calamophyton primaevum*. This naming was based on suspected relationships with the horsetail *Calamites*. To increase the associated confusion, the authors established another genus, *Duisbergia mirabilis,* in their next paper in 1929 (Contributions to the knowledge of Devonflora III). Over time, various other authors (Fairon-Demaret & Berry, 2000, Giesen & Berry, 2013) suggested that all three genera represented only different parts of the same plant. In that case, the name *Hyenia elegans* would take precedence. However, since it was not clear whether the name from the Central Devonian Hyenfjords used by Nathorst (1914) really corresponded to the Central European findings, *Calamophyton primaevum* (Kräusel & Weyland, 1926) was nevertheless considered to be appropriate. Hence, a script written by Hermann Weyland in 1925, containing the naming of *Calamophyton primaevum,* should not be recognised, due to the lack of adequate description requirements.

However, it was only over the following decades that the true appearance of this plant was felt. Kräusel and Weyland (1934) reconstructed *Duisbergia mirabilis* with a tub-shaped stem and hardly any branches in the upper half, while Schweitzer (1990) defended the two genera *Hyenia* and *Calamophyton* as different; only Giesen and Berry (2013) achieved a good reconstruction of *Calamophyton primaevum*, based on excellent finds from Lindlar. Still, they failed to obtain detailed knowledge of their fertile plant parts. This was probably because these parts can hardly be found in the mostly coarse sandy deposits. Although *Calamophyton* has been found in the Middle Devonian sediments from the Eifelian to the Givetian, across present-day Germany, Belgium, Norway, Bohemia, the United States of America and Argentina (Beck, 1960), its relationships to other plants have so far remained unclear. A more detailed description of its fertile parts is given here, along with an attempt to unravel the secrets of this important Protoconifera and its role in the further development of progymnosperms.

Geology

Middle Devonian, Middle Eifelian, Mühlenberg Formation

Systematic

Class: PROGYMNOSPERMAE Beck, 1960

Order: PROTOCONIFERA Chlonova, 1960

Genus: *CALAMOPHYTON* Kräusel & Weyland, 1926

Calamophyton primaevum Kräusel & Weyland, 1926

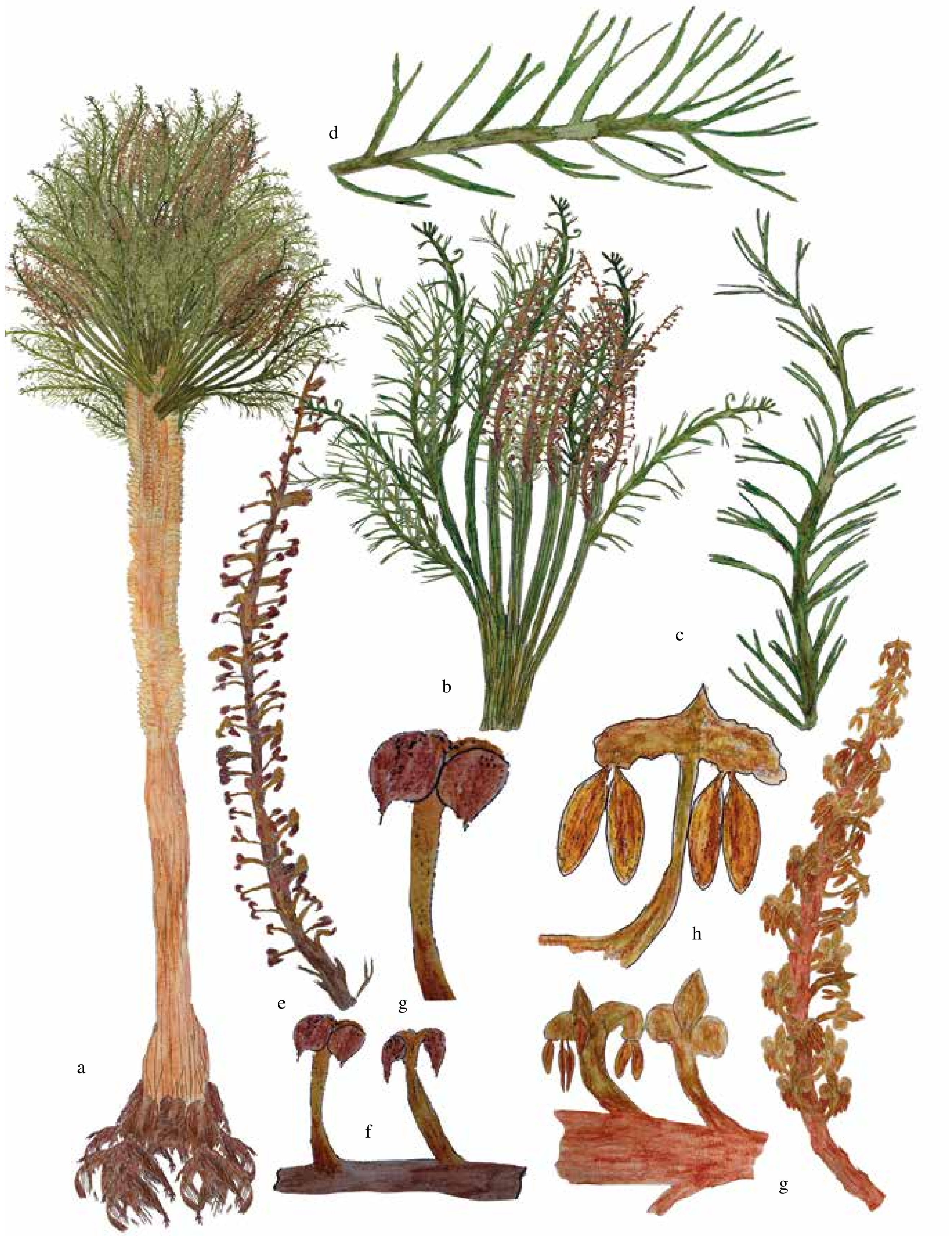
1926 *Calamophyton primaevum* Kräusel & Weyland, pl. 10 Fig. 2-11, Pl. 11, Pl. 12 Fig. 1-3, Pl 15 Fig. 2; Pl.fig. 23-29

1926 *Hyenia elegans* Kräusel & Weyland, Pl. 9 Fig. 2 Textfig., 16a. Pl. 9 Fig. 3-4. Pl. 9 Fig. 6, Pl. 9 Fig. 8-9, Pl. 10 Fig. 1

2013 *Calamophyton primaevum* Giesen & Berry p. 670, Fig. 4 ab, p. 672 Fig. 6, a-h, p. 674, Fig. 7 a-h, p. 676, Fig. 9, p. 677, Fig. 10, p. 678, fig. 11 a-e, p. 680, fig. 13 a-h

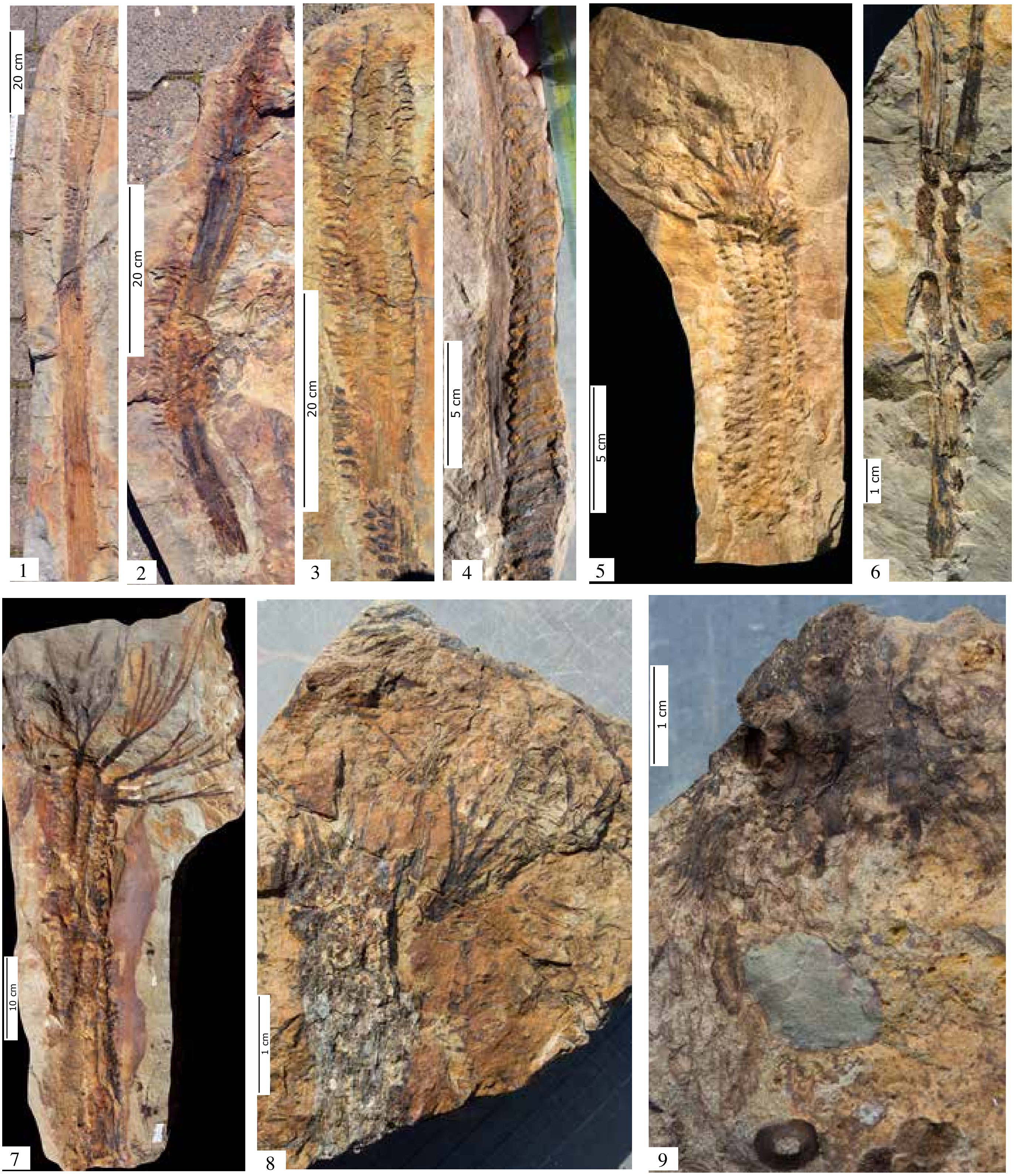
Description

Whole plant: This was probably a small tree growing about 160–200 cm in height, with a slender trunk reaching a width of about 10–15 cm at the base and about 5–7 cm in diameter from the middle. Its roots consisted of tightly packed, branching, small side roots that extended downward and outward (LIND 67). The lowest part of its trunk ran without side branches; even leaf scars could not found there (LIND 06). With increasing height, the first leaf scars could be found, relics of fallen side branches, arranged in geometric rows. They formed strands reaching



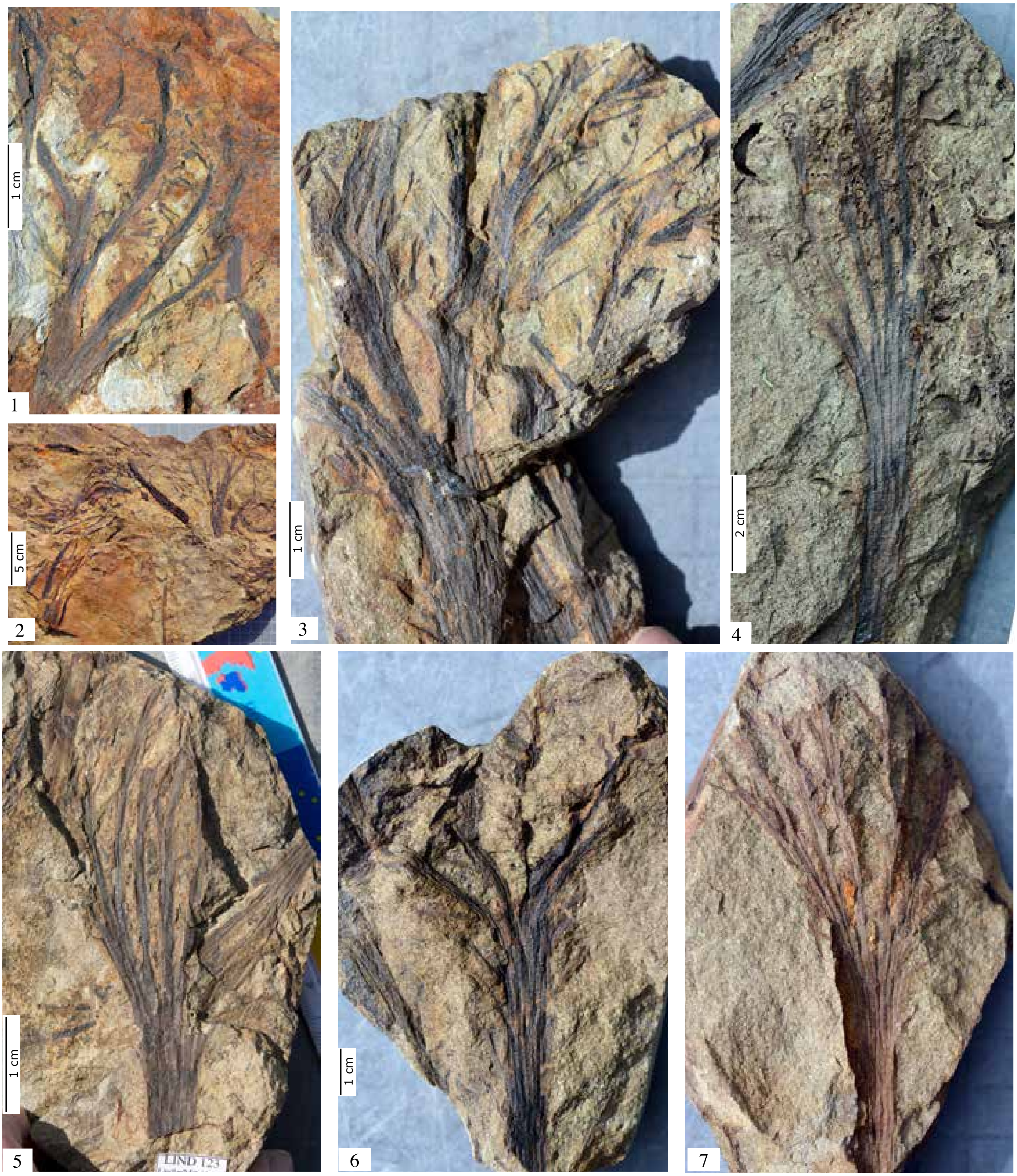
***Calamophyton primaevum*. Reconstructions**

a. Whole plant with female cones (LIND 06, LIND 208, LIND 183, LIND 180, LIND 67); b. Branchlets with female fructifications (LIND 123, LIND 03, LIND 23, LIND 48, LIND 30, LIND 35, LIND 32); c-d. twigs; e. Female sporophylls (LIND 01, LIND 225, LIND 185); f-g. Ovules; g. Pollen cones (LIND 16); h. Detail of the microsporophylls



***Calamophyton primaevum*. Stems and Roots**

1. Part of a stem, about 120 cm long (LIND 06, Coll. Pohl); 2-3 Parts of the trunk with scars from the lateral branches (Coll. Pohl, total length, about 60 cm; 4. Part of a stem with lateral branchlets (LIND 208, Coll. Wachtler); 5. Apical part of a trunk with leaf scars and a tuft of twigs (LIND 183, Coll. Wachtler) ; 6. Juvenile plant (LIND 64); 7. Perfectly preserved tree trunk with partially fertile tuft (LIND 250); 8. Apical tuft (LIND 180); 9. Root system (LIND 67, Coll. Wachtler, Dolomythos

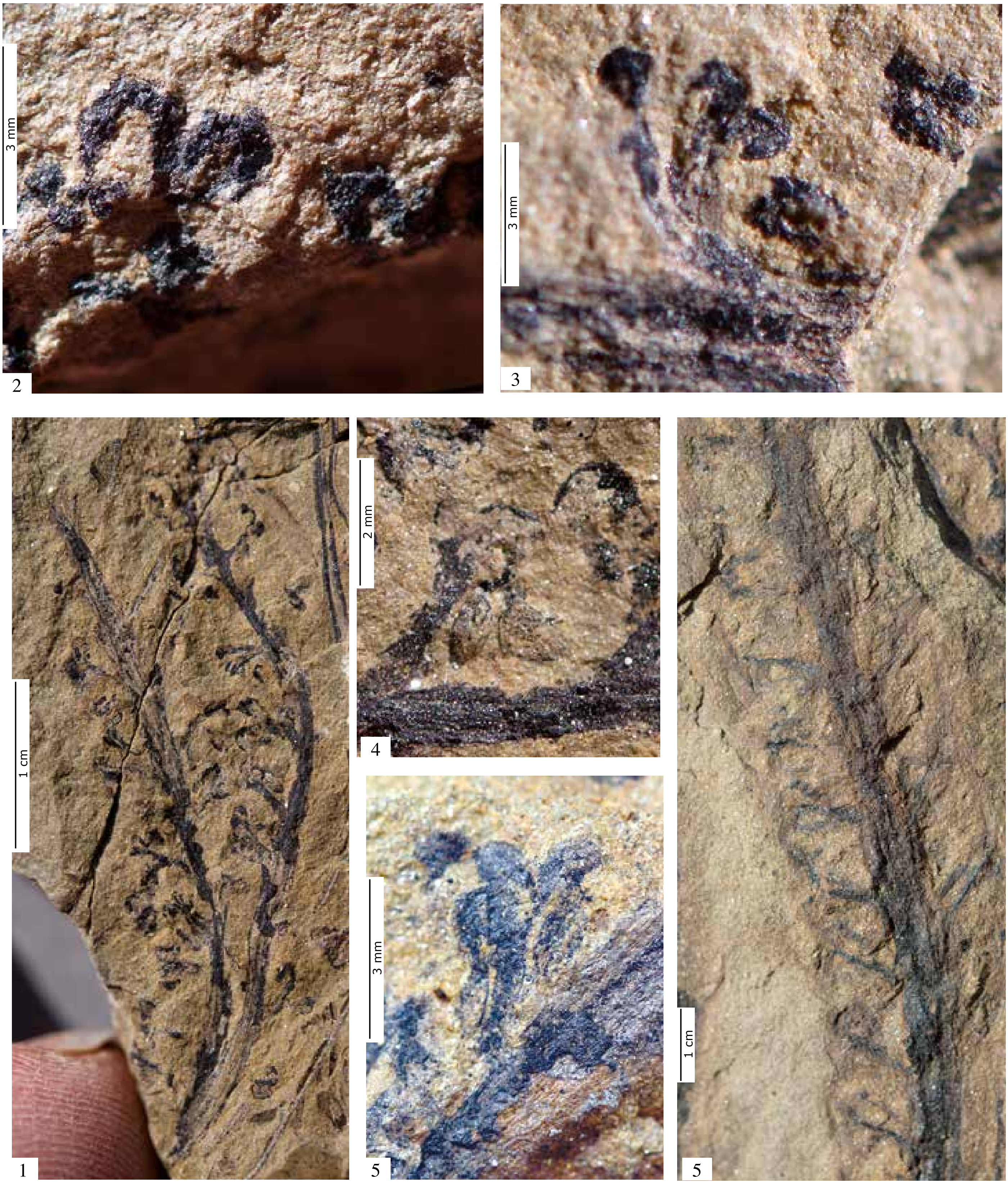


Calamophyton primaevum. Branchlets

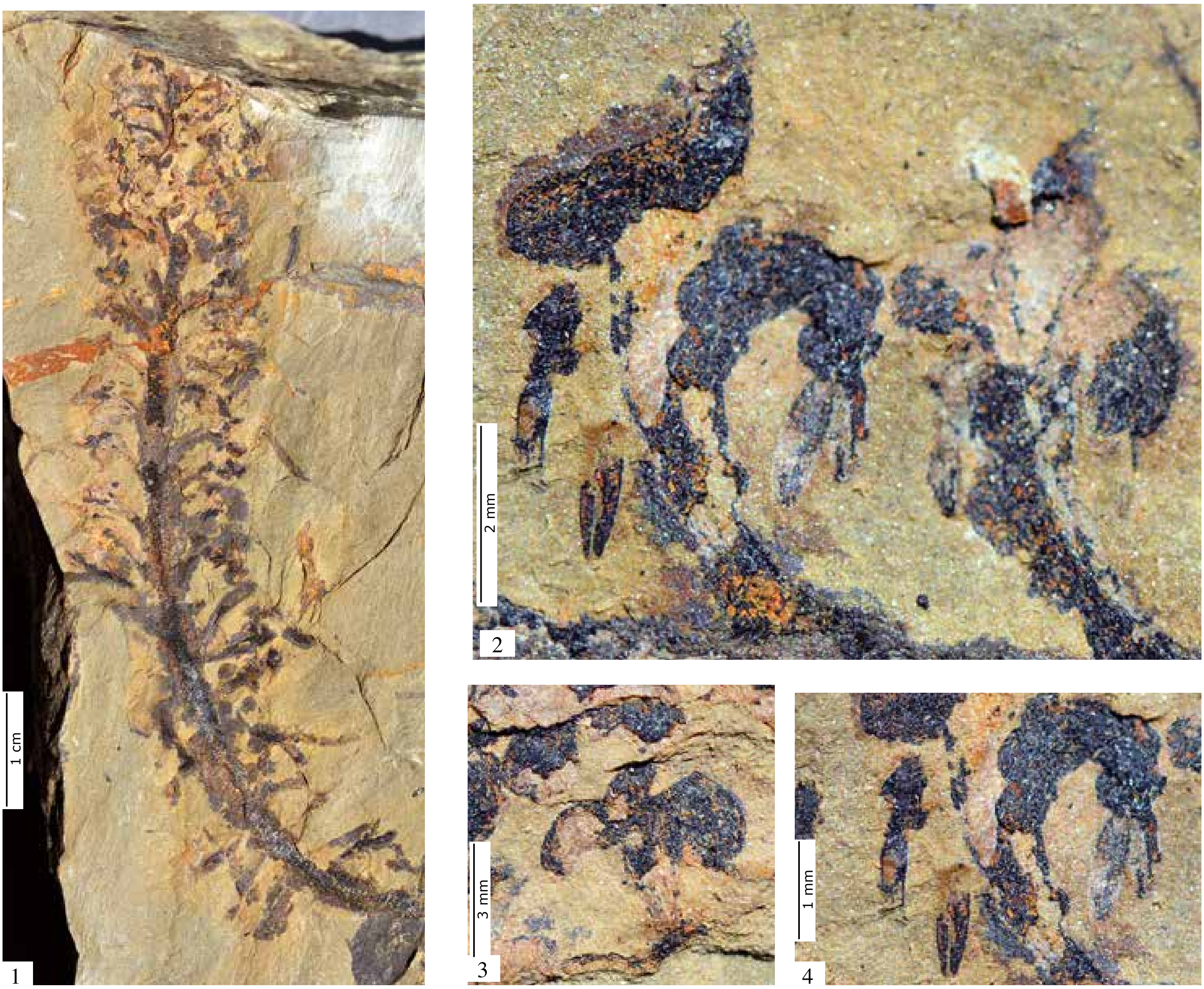
1. Trunk part with lateral branchlets (LIND 03); 2. Isolated branches (LIND 23; 3. Branch with leaf needles (LIND 48); 4-7. Typical branch structure of *Calamophyton primaevum* (LIND 30, LIND 123, LIND 35, LIND 32) Coll. Dolomythos

***Calamophyton primaevum*. Twigs and leaf needles, Macrosporangia**

1-4. Branchlets, and detail of the Macrosporangia (LIND 01, Coll. Pohl); 5-6 Detail of individual sporangia (LIND 225), Coll. Wachtler, Dolomythos



Transitional form *Calamophyton primaevum* to *Schweitzeria enigmatica*. Macrosporangia
1-4 “Seed cones” and detail of Macrosporangia aggregated in twos or threes (LIND 185); Macrosporangia aggregated in threes (LIND 33); 5. Macrosporophylls (LIND 121); Coll. Wachtler, Dolomythos



***Calamophyton primaevum*. Microsporangia**
1-4 Branch with Microsporangia (LIND 16, Coll Pohl)

a depth of 2 cm into the trunk (LIND 208); the trunk in the upper part was densely covered with it. Only in its crown, a large number of side branches spread out in all directions (LIND 183, LIND 180).

Branchlets: The multi-fingered (from five to ten fingers) side branches (LIND 30, LIND 123, LIND 35) of this tree diverged from a main axis. Sometimes they furcated, again dichotomously (LIND 23, LIND 37).

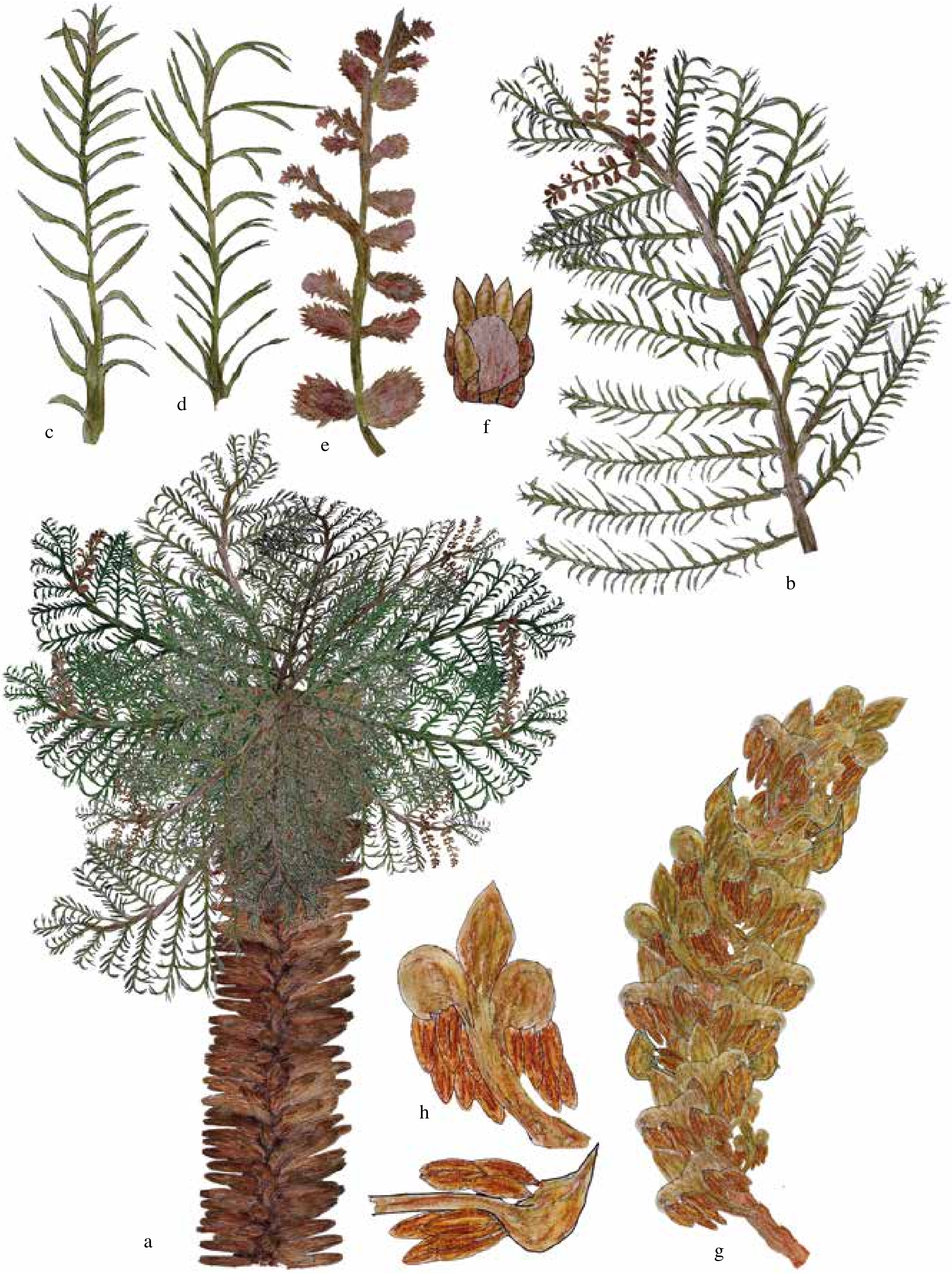
Leaves: They were either needle-like or ended apically in a Y-shape (LIND 10, LIND 127) and reached about 1 cm in length.

Cones and Megasporangia: The macrosporophylls aggregated into loose cones and consisted of a long, thin bract stalk of approximately 0.5 cm, which branched at the upper end (LIND 01). Usually, there were two seeds hanging there, while sometimes there were only one or three of them.

Pollen cones and Microsporophylls: They consisted of a loose cone structure, similar to the female tree, with a developed bract from which, at the lower end, the pollen sacs hung in pairs (LIND 16). They were oblong in shape and about 1 mm long.

Remarks

While the external appearance of a *Calamophyton primaevum* is largely known through the work of Giesen and Berry (2013), its fertile parts require more detailed explanations.



***Eoconifera fuchsii.* Reconstructions**
a. Whole plant; b. Twig with female cone (holotype LIND 238), c-d. Side branches basally and apically with dichotomous leaves; e-f. Female fructification with detail of the Macrosporangia (LIND 238), LIND 31); g-h. Pollen cone with detail of Microsporangia (LIND 230)

Their structure could only be better clarified by the collections by Manfred Fuchs, using some few-millimetres thick, finely muddy lenses. Surprisingly, in the Middle Devonian this tree must have developed toward comprising macrosporangia groups with one, two or more seeds. Although the evolution was still somewhat chaotic, since macrosporangia with one, two, three or more seeds could develop at the same sporophyll, it nevertheless represented an important step in the development of many conifer ancestors.

It could be assumed that *Calamophyton primaevum* was mainly characterised by paired ovules, which paved the way for today's Pinoidea or Abietaceae. A trend towards the late-Carboniferous-early-Permian *Gomphostrobus, Wachtlerina* or *Majonica*, the oldest known and verified Abies ancestor, could therefore be affirmed. As mentioned, the microsporangia of this tree were arranged in pairs, with two pairs of pollen sacs hanging down from a bract attached to the main axis. In addition to its different branch formations – symmetrical in *Eoconifera*, tufted plagiotropic in *Calamophyton*, widespreading in *Schweitzeria enigmatica* – the different male and female cone structures can also be used as a distinguishing feature.

Other Protoconifera

In the Middle Devonian, further progymnosperms must have developed. These conclusions could be drawn from their different ovules, pollen counts and branch formations. Indeed, one of them was distinguished by symmetrically arranged branches. Loose cone structures found in connection with only one macrosporangia on each seed scale, in addition to pollen cones with microsporophylls, which could be compared with today's Araucaria, completed the classification. Thus, sufficient material gathered from Lindlar made it possible to set up a new genus.

Class: PROGYMNOSPERMAE Beck, 1960

Order: PROTOCONIFERA Chlonova, 1960

Genus: *EOCONIFERA* Wachtler, 2022

Diagnosis

Conifer ancestor with symmetrically arranged branches and rudimentary cone forms. One single seed coated by small-sized microleaflets.

Etymology

Derived from the Greek word 'Eos' which means 'early'.

Eoconifera fuchsii Wachtler, 2022

Etymology

Named after Manfred Fuchs, who collected in Lindlar for more than 25 years. His findings can mainly be accessed from the collections of Burkhard Pohl (Groß-Bieberau, Hessen, Germany), and Michael Wachtler, (Dolomythos Museum, Innichen, Italy).

Holotype

LIND 238 (Branchlets with Macrosporophylls)

Paratype

LIND 230 (pollen cones)

Diagnosis

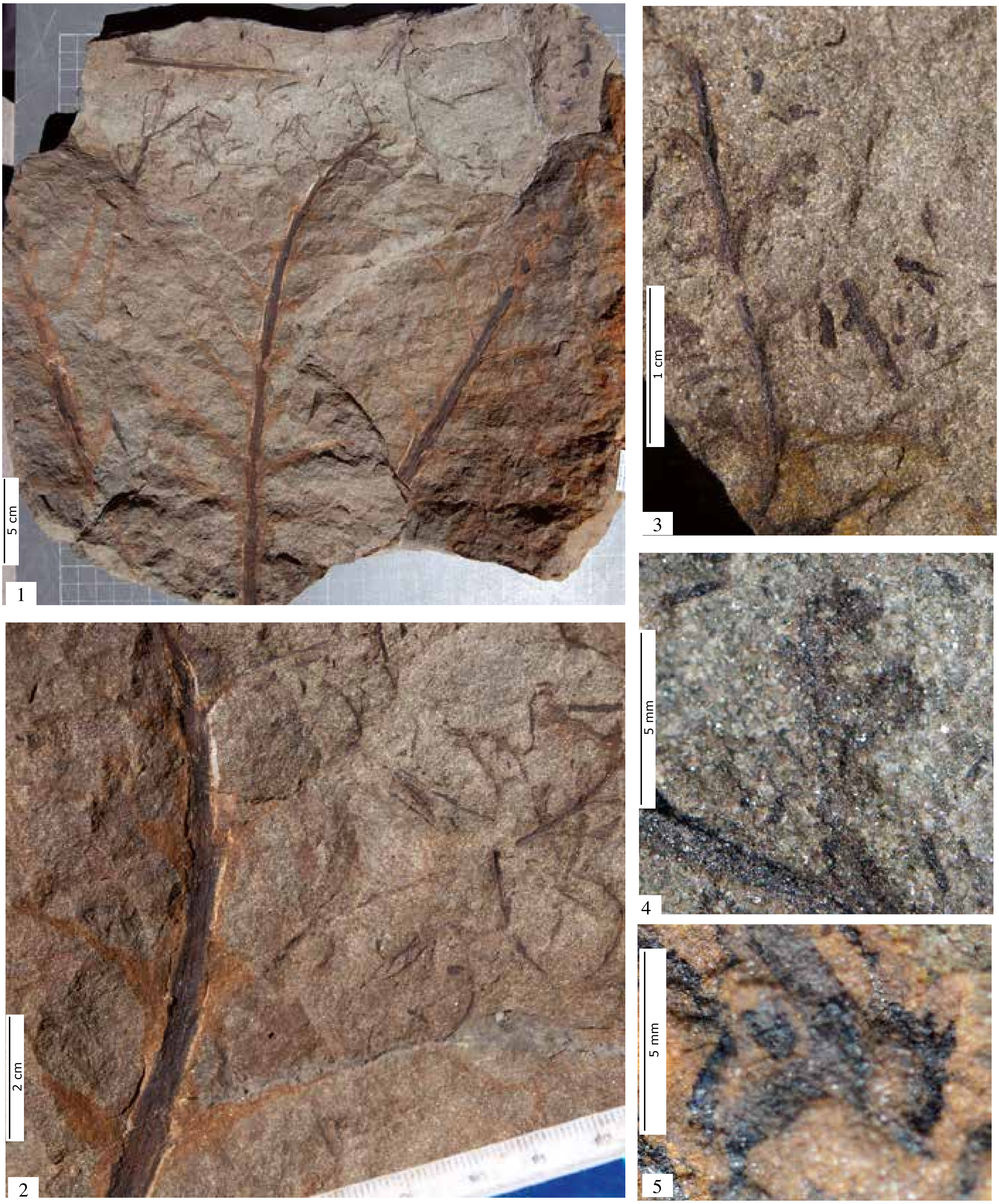
Branch arrangement in the manner of *Araucaria heterophylla.* Female cones with loosely developed megasporophylls covered by tiny leaflets. Microsporangia in a loose cone form consisting of pollen sacs hanging dorsiventrally from the end of the bracts.

Description

Whole plant and branchlets: Branches had an equilateral symmetrical structure (Holotype LIND 238). The leaves were awl-shaped and became needle-like in the lower part of the branch and forked apically in the upper part of the branchlets.

Female cones and Megasporangia: Cones were 3–4 cm long with sparse, loose macrosporophylls, developing singly or sometimes in pairs. In the lower part of the seed scale, dwarfish leaflets densely coated the seeds (LIND 238, LIND 31). The single seeds were roundish, about 3–4 mm in diameter.

Pollen cones and Microsporangia: Male organs were 3–5 cm long and 1.5 cm wide, grouped around a main axis (LIND 230, paratype). For each bract, a majority (10–15) of pollen sacs hung in the direction of the cone axis. Individual pollen sacs were about 1 cm long and 0.1 cm wide (LIND 230, paratype).



***Eoconifera fuchsii*. Branchlets and Cones**

1. Several branchlets; 2. Detail of a branch; 3. Fertile branch; 4. Detail of a macrosporangia with dwarfish coating leaves (All holotype LIND 238); 5. Detail of macrosporangia with coating sterile microleaves (LIND 31); Coll. Wachtler, Dolomythos

***Eoconifera fuchsii*. Branches and Cones**

1. Several pollen cones on a branchlet (LIND 230, Paratype); 2-3 Detail of two pollen cones; 4-5 Individual microsporophylls; 6. Detail of microsporangia (all Paratype LIND 23); Coll. Wachtler, Dolomythos

Remarks

Although *Calamophyton primaevum* is the most common progymnosperm from Lindlar and is relatively easy to recognise with its tufted branches, there must still have existed other trees that could be assigned to the protoconifers category on the basis of their characteristics. This is understandable, as there were already a large number of fully developed gymnosperms at the Carboniferous-Permian boundary, such as the two cycad tribes that still exist today (*Cycas, Zamia*), the Ginkgo, and various conifer precursors (Wachtler, 2021). It should not go unnoticed that other gymnosperm families also developed on other paleocontinents of the time, such as Angara, today's Siberia and the Urals.

In summary, *Eoconifera fuchsii* could be distinguished from *Calamophyton* by the former's symmetrically arranged branches and its cones, formed by loosely arranged macrosporophylls, with only a single macrosporangia encased by tiny leaflets. Even their microsporangia showed different structures: in *Calamophyton* there were mostly two microsporangia on each side of a bract, while in *Eoconifera* a large number of them could be observed hanging dorsiventrally from the upper side of the scale. The tree-like *Eoconifera* may therefore have assumed a ancestral role in the direction of the Araucaria conifers. Large parts of its leaves consisted of slightly awl-shaped undivided needles, but sometimes the leaves forked in a Y-shape, especially in the apical area. Notably, no other plant in the Middle Devonian has branchlets pointing as far in the direction of the typical extant conifers as *Eoconifera.* Its pollen cones, in particular, reached a high level of development and could be compared with just with the cones from the Permian.

Class: PROGYMNOSPERMAE Beck, 1960

Order: PROTOCONIFERA Chlonova, 1960

On the basis of branchlets, parts of stems and fructifications that cannot otherwise be classified, another protoconifer may have developed in Lindlar. This is described in more detail.

Genus: *SCHWEITZERIA* Wachtler, 2022

Diagnosis

Protoconifer with spreading branches and sometimes dichotomously forked needles.

Etymology

Named after the German pharmacist and paleobotanist Hans-Joachim Schweitzer (1928–2007), who researched many Devonian flora.

Schweitzeria enigmatica Wachtler, 2022

Etymology

Derived from the Latin 'aenigmaticus', meaning 'enigmatic' or 'difficult to solve'.

Holotype

LIND 128 (branch with stem part)

Diagnosis

A multitude of branchlets arising from the apical part of the trunk, sometimes dichotomized. Needles are subtle, forked or unforked.

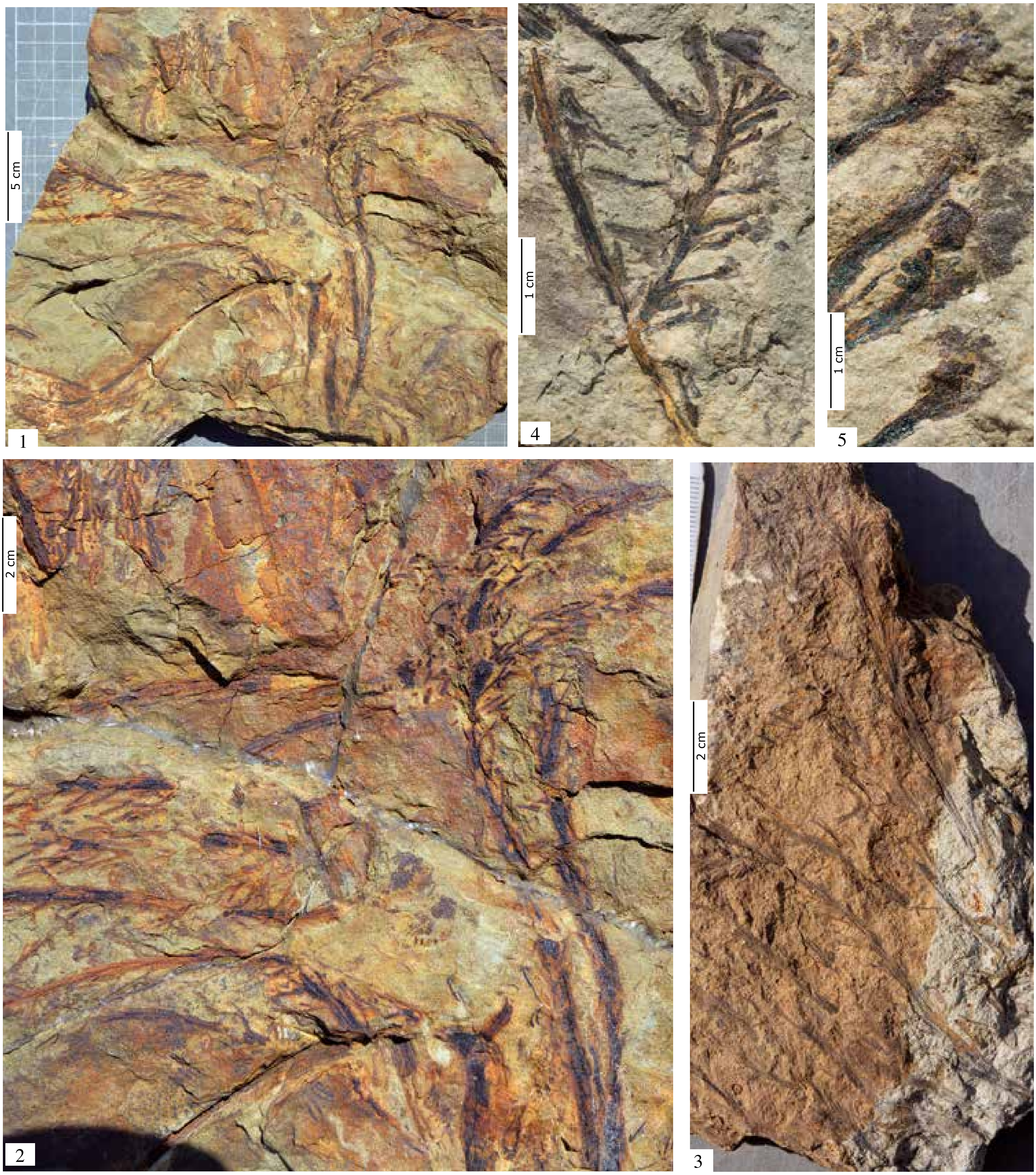
Description

Whole plant and branchlets: Stem reached a diameter of 6–8 cm at the apex (LIND 226), riddled with scars from fallen branches (LIND 113). A large number of side branches (holotype LIND 128, LIND 223) arose upright or laterally from the bluntly tapering tree crown. The slender twigs spread out unequally long and sometimes bifurcated into a second to third order (LIND 127, LIND 128). The leaves were needle-like, delicate, at best 1 cm long and about 0.1 cm wide, with some (but not all) forking in a Y-shape (LIND 10). Main branches were sometimes leafy.

Fructifications: Not fully known, but LIND 74 could probably belong to this plant. It had macrosporophylls that developed from short needles and formed triply segmented bracts.

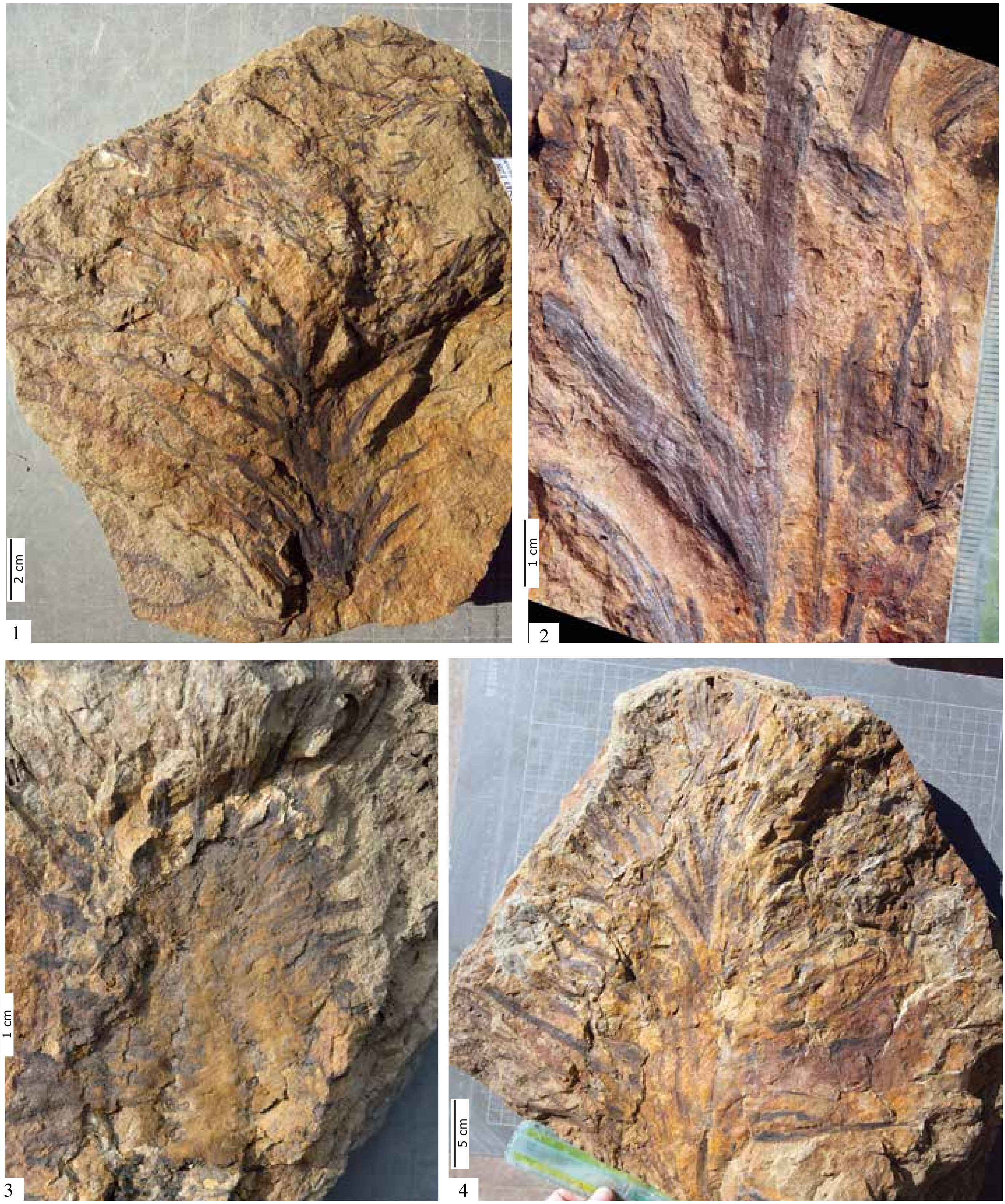
Remarks

If the frequently occurring protoconifer *Calamophyton primaevum* can be classified relatively accurately by its small branches, which arise from a central axis and branch off like fingers at the same level, and *Eoconifera fuchsii* can also be classified relatively accurately due to its symmetrical branch arrangement, then *Schweitzeria enigmatica* stands out due to its wide, oscillating branches furcating from the main trunk onward. Its individual leaf needles are similar to those of the aforementioned plants, due to their Y-shaped forks, but



***Schweitzeria enigmatica*. Twigs and leaf needles**

1-2 Branchlets (LIND 10, Coll. Pohl); 3. Diverging branchlets (LIND 127); 4-5. Macrosporophylls and detail (LIND 74); Coll. Wachtler, Dolomythos); Collected by Manfred Fuchs, BGS Quarry, Lindlar



***Schweitzeria enigmatica*. Trunks and sterile branches**

1-2 Apical part of the stem with diverging branchlets (holotype LIND 128); 3. Apical stem part (LIND 113); 4. Apical part with branch-tuft (LIND 223); All Coll. Wachtler, Dolomythos

Schweitzeria enigmatica. **Reconstructions**
a. Upper part of plant (LIND 128 Holotype), b. Branchlet (LIND 10), c. Basal part of a branch, d. Apical part

the needles are more delicate. Overall, the three different genera of protoconifers found in Lindlar do not differ significantly, and yet they constitute the starting point of many conifers known today. Since at the Carboniferous-Permian border single-seeded Araucaria ancestors *(Ortiseia)*, two-seeded Abietaceae ancestors (*Gomphostrobus, Wachtlerina, Majonica*) as well as the ancestors of the pines (*Férovalentinia*) and three- to multi-seeded conifers (Voltzia) were already fully developed, their basic evolutionary plans must have their origins during the 100 million years from the Middle Devonian to the Late Carboniferous. The only conifer with recognisable Devonian traits seems to be *Perneria thomsonii* from the Carboniferous-Permian transition, which developed forked leaves in its upper part and unforked needles in its lower part (Wachtler, 2021). Another interesting feature of *Schweitzeria* is that it sometimes formed leaves instead of branches, which could also be interpreted as indicating a merging line to the cycads. The relative gaps between the progymnosperms, especially in the Upper Carboniferous, between lycopod trees (*Lepidodendron, Sigillaria), Calamites* horsetails and various ferns, were probably due to the then-prevailing tropical and rainy climate, which the protoconifers, ginkgos and protocycads urged in the background.

Protocycads

In addition to the protoconifers, the first development of cycads must have also occurred in the Devonian. Fully developed cycad precursors can be found from the Early Permian, being divided just into the two families that still exist today: the multi-seeded Cycas cycads (in the Permian: *Macrotaeniopteris, Taeniopteris)* and the two-seeded Zamia cycads (in the Permian: *Nilssonia, Pseudoctenis).*

Wachtleropteris valentinii can be regarded as the most archaic cycad in the Early Permian and is characterised by its leaves – originating from a central axis – having entire edges and tongue-shaped forking. This dichotomous bifurcation of its leaves may have originated in the Middle Devonian, although it can be assumed that this represents the most primitive form of development. Tongue-shaped leaves with a strongly developed rhachis are also found in Lindlar, which – recovered in the Permian or the Triassic – are

***Kraeuselia pohlii*. Macrosporangia**

1. Shield-shaped seed scale with two macrosporangia on each underside (LIND 76, paratype); 2-3. Megasporophyll (LIND 76); Coll. Wachtler, Dolomythos

immediately recognisable as cycad ancestors (*Taeniopteris, Wachtleropteris)*. Even the similar Permian-Triassic seed scales are found in the Middle Devonian.

Interestingly, in Lindlar we find another protogymnosperm with a tuft-like infructescence, which is characterised by a large number of seeds branching off on both sides of a central rhachis on one level. This was first described in 1974 by H J Schweitzer as *Weylandia rhenana*. If this may seem hypothetical, the associated entire-margined, forked lower leaves, as well as the apical aggregation of many-seeded sporophyll stands, point towards Permian Cycas-cycads such as *Taeniopteris.*

However, the situation is different with the two-seeded protocycads (Zamia line). Here, we find fully developed seed scales even in the Middle Devonian. An early split in the Devonian must therefore be assumed for the two large cycad families. Despite intensive research, no splitting lines between the Cycas-Cycads and the Zamiaceae have subsequently been identified, especially after the Carboniferous-Permian transition.

It is not only the macrospophylls that reached a high level of development in the Middle Devonian. The pollen cones, which are relatively uniform in all cycads, may have been formed as early as the Middle Devonian. Pollen organs are frequently found in Lindlar, a situation which can neither be attributed to the fern ancestors *Protopteridium* nor to other protogymnosperms, so that the assumption that they could be developing microsporophylls and pollen cones of cycads seems plausible. In this evolutionary mix, the crown-plant between gymnosperms and ferns must be found under difficult circumstances of classification. Since the two-seeded, tongue-shaped leaves mentioned above have so far attracted scant attention, it has been necessary to introduce a new genus by name.

Class: PROGYMNOSPERMAE Beck, 1960

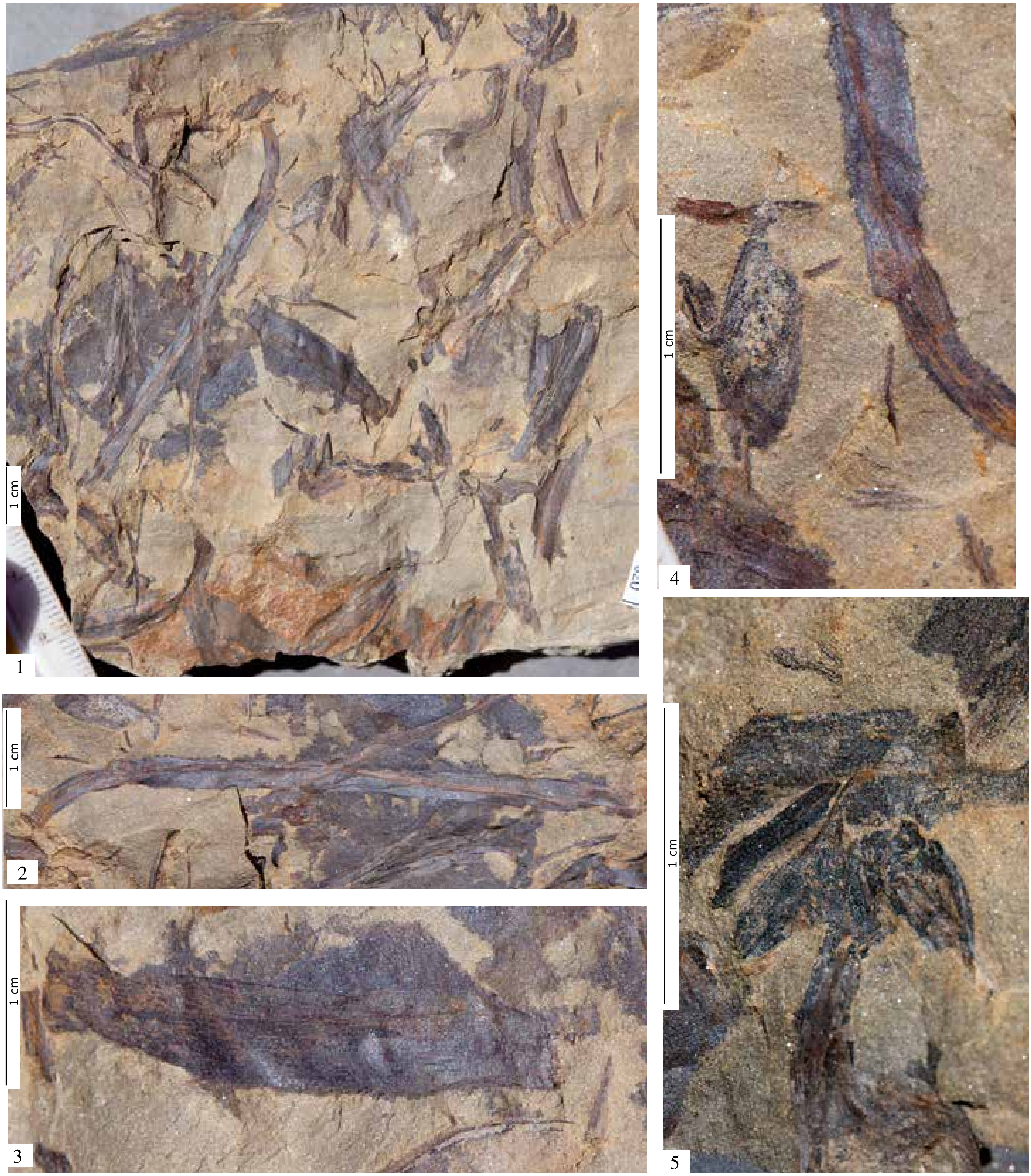
Genus: *KRAEUSELIA* Wachtler, 2022

Etymology

Named after the German paleobotanist Richard Kräusel (1890–1966) who, together with Hermann Weyland, researched the Devonian flora of the Rhineland.

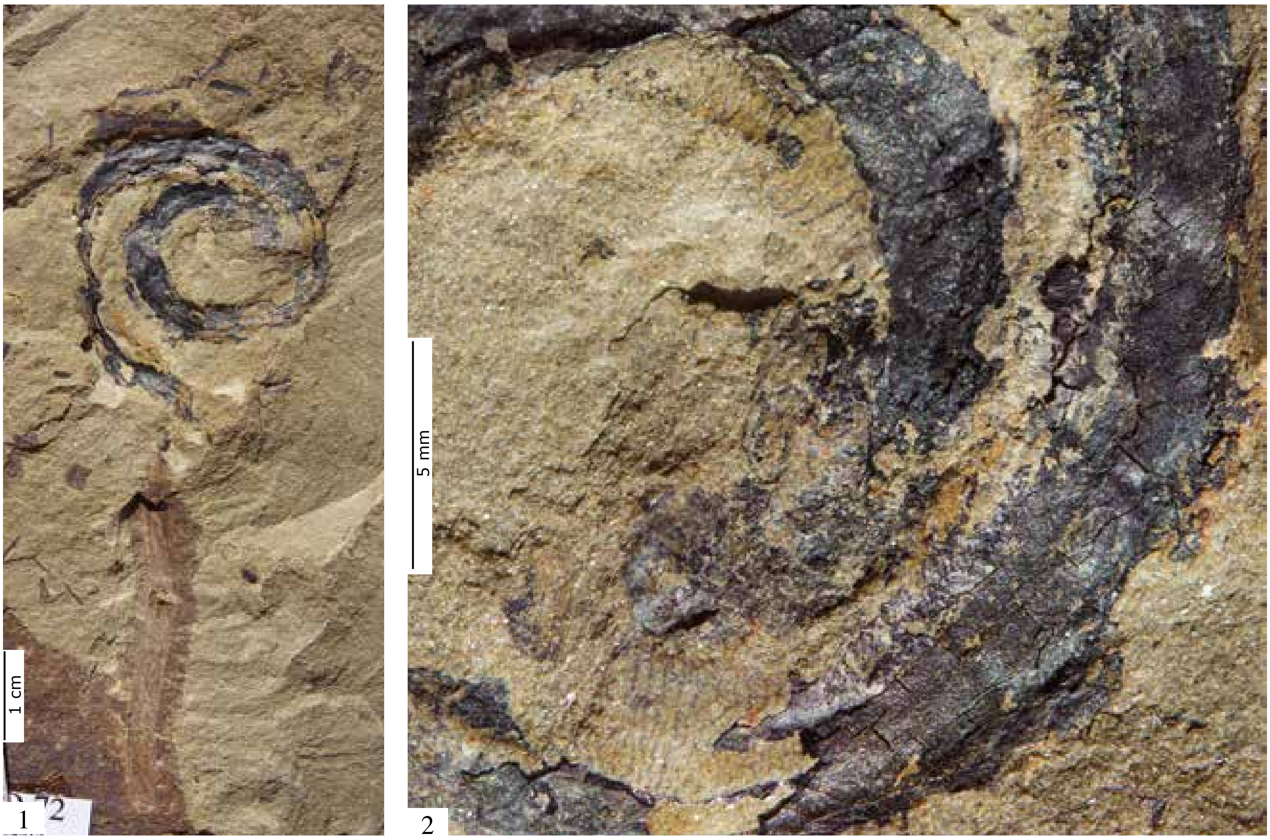
Diagnosis

Dichotomously dividing tongue-shaped leaves, which are crossed by a strong central rhachis.



***Kraeuselia pohlii*. Leaves and Macrosporangia**

1. Plate with tongue-shaped leaves and Macrosporangia; 2-3 Leaves with pronounced rachis; 4-5 Macrosporangia (all LIND 242, holotype); coll. Wachtler, Dolomythos); Collected by Manfred Fuchs, BGS Quarry, Lindlar



Kraeuselia pohlii* or *Protopteridium philippae

1-2 Curled cycad or fern leaf (LIND 72); Coll. Wachtler, Dolomythos; BGS Quarry, Lindlar

The macrosporophylls are characterised by seeds hanging downwards from a scale. The pollen cones, consisting of several Microsporophylls, have an arrangement of small microsporangia on their undersides.

Kraeuselia pohlii Wachtler, 2022

Etymology

Named in honour of Burkhard Pohl from Großbieberau, the collector and supporter of scientific research.

Holotype

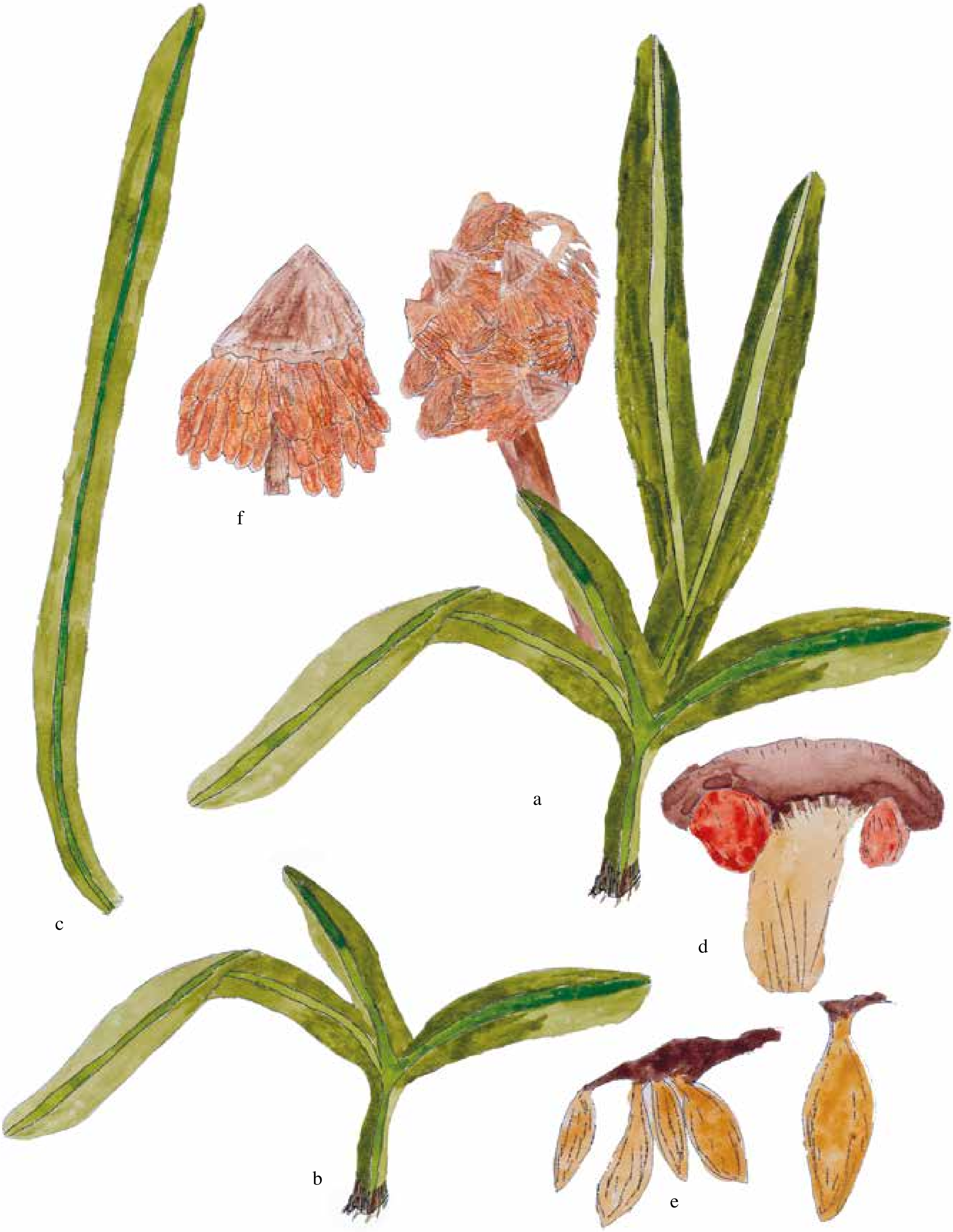
LIND 242 (leaves and megasporophylls)
Paratype: LIND 75 seed scale; LIND 76 pollen organ

Description

Whole plant: It has tongue-like, apically rounded leaves, with a pronounced midrib and a short stalk. They are up to 6 cm long and 0.5–0.8 cm wide (LIND 242 holotype).
Female fructifications: Megasporophylls are up to about 0.6 × 0.6 cm in size (paratype LIND 76). The seed scales develop a consistent stalk about 0.3 cm wide, terminating in a rounded, hammer-like head which encloses two elliptical seeds, about 0.1–0.3 cm long, on its underside.
Pollen organs: These are cone-shaped, arising from a stalk about 1.0 cm long that develops a fair number of microsporophylls, which in turn have a size of 1.0–2.0 cm. The individual microsporophylls generate a large number of small, hanging microsporangia. Tiny hairs are visible on the pyramidal upper part of the microsporophylls (LIND 75, paratype, LIND 239, LIND 243, LIND 66).

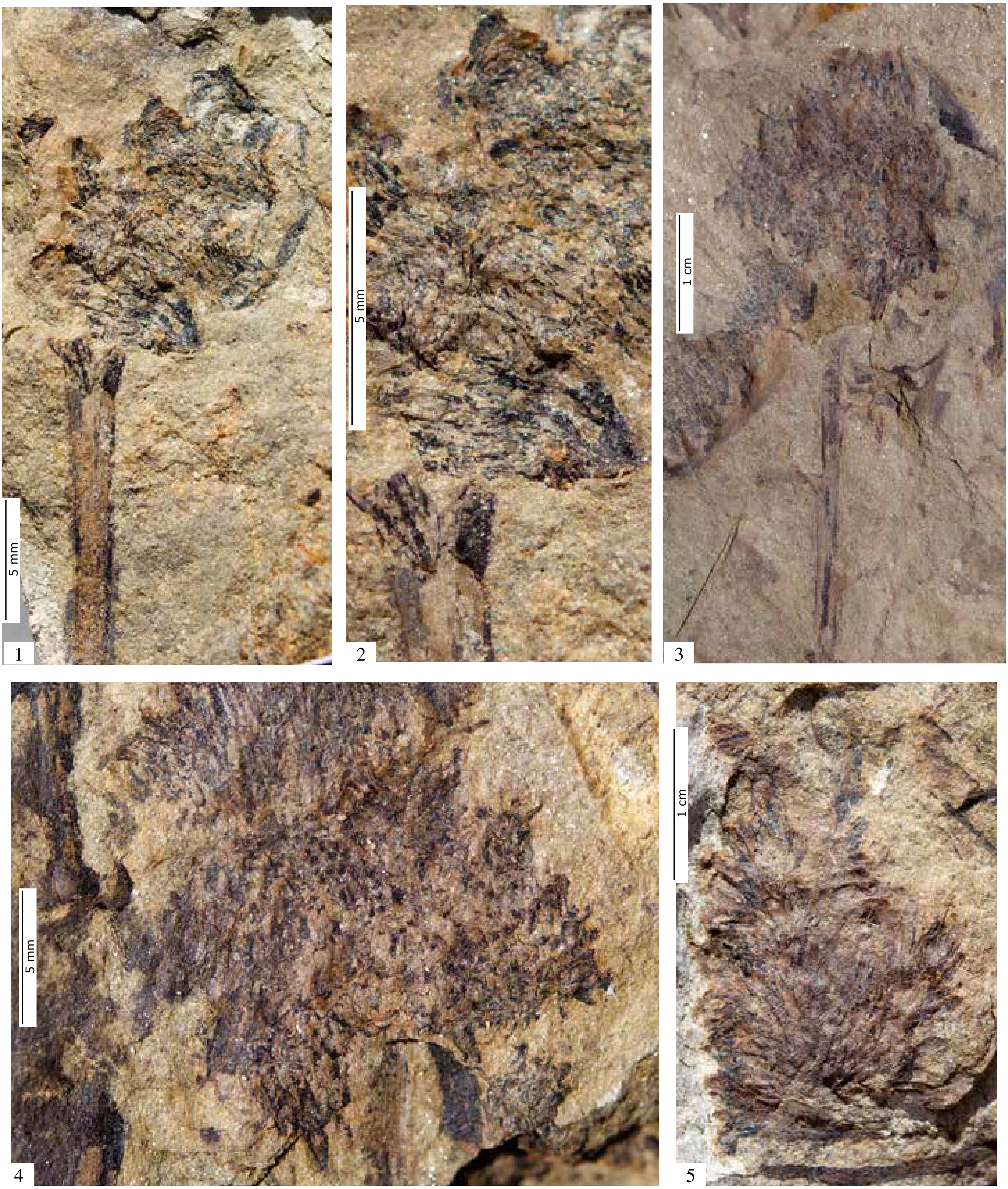
Remarks

Forked parts of this plant’s leaves, with an unusually strong middle rhachis, can be found again and again in Lindlar. In addition, the plant contains shield-like seed organs and cone-shaped united microsporophylls, which cannot be assigned to other plants. Surprisingly, rolled-up leaves, typical of ferns and cycads, are observed in this plant as well. If a proximity to the fern precursor *Protopteridium philippae* is also considered alongside the above data, the separating



Kraeuselia pohlii. Reconstructions

a. Whole plant with male cone (LIND 75); b. Part of a plant (LIND 242), c. Single sheet (LIND 242); d. Megasporophyll (LIND 76); e. Single macrosporangia (LIND 242); f. Microsporophyll (LIND 75)



Kraeuselia pohlii. Microsporophylls

1-2 Cone-like aggregated microsporophylls with detail of individual microsporangia (LIND 75 Paratype); 3-4. Cones with hanging Microsporophylls (LIND 239); 5. Aggregation of microsporophylls (LIND 66); Coll. Wachtler, Dolomythos factor must also be pondered. Since relations with lycophytes, horsetails, protoconifers and ferns (due to seed formation) can be ruled out in this case, other solutions must be considered. In many respects, *Kraeuselia pohlii* can therefore be considered as an ancestor of Permo-Triassic cycads.

These cycads include forked, tongue-shaped leaves like those found in the Early Permian genus *Wachtleropteris valentinii* (Wachtler, 2021), but also consist of shield-shaped megasporophylls with two seeds hidden underneath. In fact, the aggregation of several microsporophylls to form a cone structure, typical of all earlier and present-day cycads, may have developed as early as the Middle Devonian. The high level of development of the cycads in the early Permian cannot be explained otherwise. Interestingly, the evolution of the multi-seeded Cycas ancestors and the two-seeded Zamiaceae (*Zamia, Encephalartos, Stangeria, Bowenia)* took separate paths from the Devonian onward, and it is understandable that no connecting or splitting lines were ever found over the following 390 million years or more.

Here, the same paradox that one finds with the horsetails comes to light. Although the families *Equisetum* and *Calamites* are overtly similar, both must have gone through completely different lines of evolution and their kinship points must have been reduced to a minimum. This holds true for the cycads as well. *Weylandia,* as a potential ancestor of multi-seeded Cycas ancestors, struck its own line of development from the Middle Devonian, as did *Kraeuselia*, as a potential ancestor of the Zamia cycads, which means that both large cycad families are as separate from one another as ferns are from conifers. It is therefore important to examine the organ structures of the enigmatic *Weylandia rhenana* more closely.

Class: PROGYMNOSPERMAE Beck, 1960

Genus: *WEYLANDIA* Schweitzer, 1974

Weylandia rhenana Schweitzer, 1974

1974 *Weylandia rhenana* Schweitzer, p. 5-8; Figures 5-8
1990 *Weylandia rhenana* Schweitzer, p. 52 Fig. 61

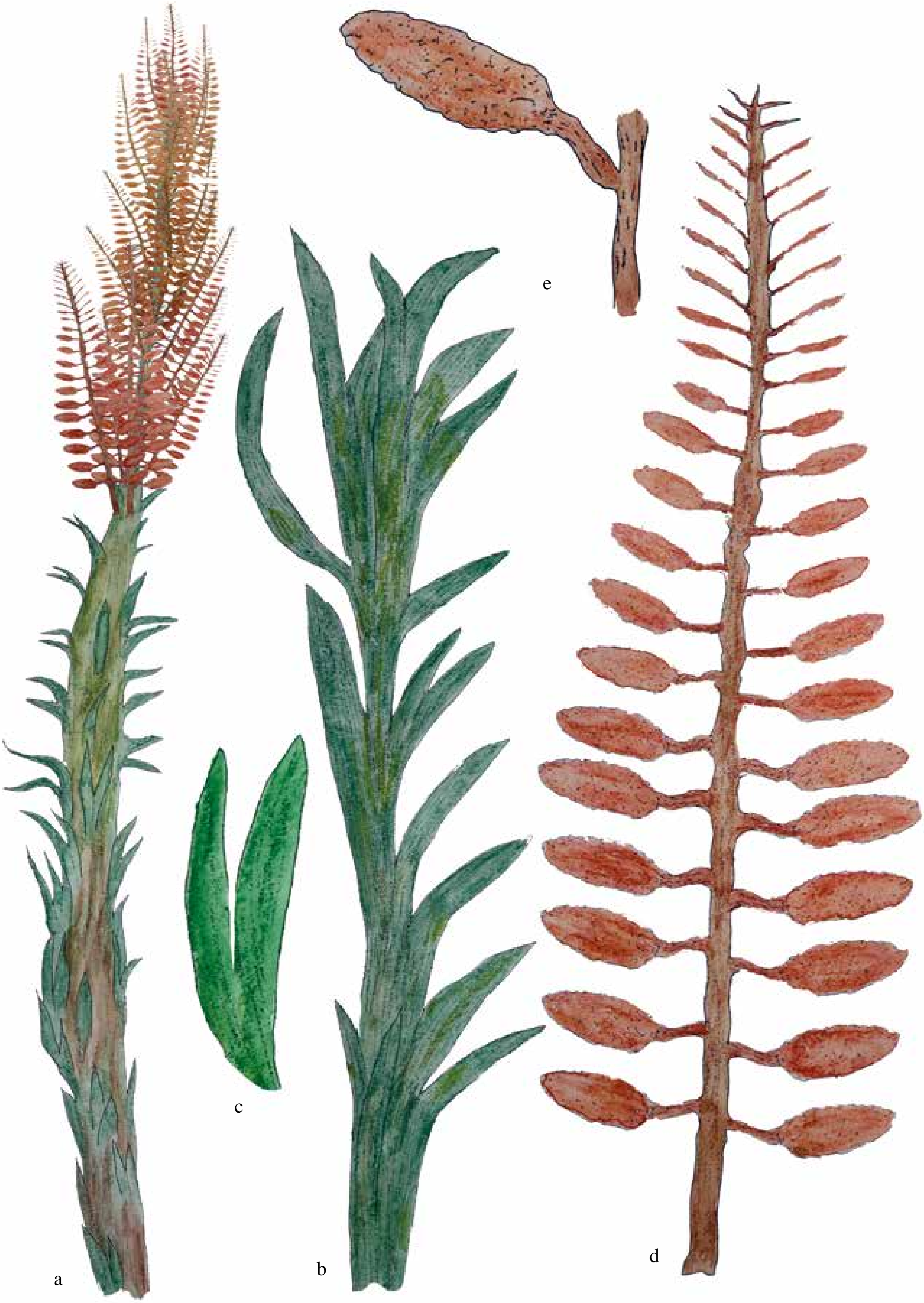
Etymology

Weylandia was named by the pharmacist Hans-Joachim Schweitzer after the German chemist and botanist Hermann Gerhard Weyland (1888–1974), who, together with Richard Kräusel (1890–1966), explored the Devonian floras of Germany. Owing to its occurrence in the Rhine region, the word *"rhenana"* was added to it.

Remarks

H. J. Schweitzer (1974) characterised Weylandia rhenana as follows: '*Monopodial, about 1 m high plants of Picea-like habit. The max. 3 cm wide trunk probably emerges from a pale-shaped base, in the lower area loosely with spirally arranged, bent back (sterile) branches, in the upper area with closely following, also spirally arranged, but shorter and straight, fertile branches. Branching or unbranched short shoots with numerous narrow ellipsoidal sporangia arise from these.' (Monopodiale, etwa 1 m hohe Pflanzen von Picea-ähnlichem Habitus. Der max. 3 cm breite Stamm wahrscheinlich aus einer pfahlförmigen Basis hervorgehend, im unteren Bereich locker mit schraubig angeordneten, zurückgebogenen (sterilen) Ästen, im oberen Bereich mit dicht aufeinander folgenden, ebenfalls schraubig angeordneten, aber kürzeren und geraden, fertilen Ästen bestanden. An diesen verzweigte oder unverzweigte Kurztriebe mit zahlreichen schmal-ellipsoidischen Sporangien entspringend.)*

Schweitzer named the Schiffahrt quarry near Lindlar, within the Mühlenberg strata (Middle Eifelium), as the location of findings. In his species diagnosis, Schweitzer also stated the following: *'The upper area of the trunk, on the other hand, is densely covered with spirally arranged branches that branch off at very acute angles (20 to 30 degrees) and run in a straight line. The lower ones are about 6 cm long. They have a diameter of approx. 0.6 cm. The branches become shorter and thinner towards the top, so that the plant ends in a point. Short shoots, up to a maximum of 2 cm long, arise on all branches in a very dense, screw-like arrangement, which are branched on stronger branches and unbranched on weaker ones and carry numerous, approx. 5 mm long ellipsoidal sporangia. There are so many sporangia that the branches are almost veiled by them.' (Der obere Bereich des Stammes ist dagegen dicht mit schraubig angeordneten, unter sehr spitzen*



Weylandia rhenana. Reconstructions

a. Whole plant with seed sporophyll stand (LIND 182); b. Juvenile plant (LIND 154), c. Detail of dichotomous foliage (LIND 154); d. Female single sporophyll strobilo (LIND 125, LIND 182); e. Single macrosporangium (LIND 182, LIND 203)

Winkeln (20 bis 30 Grad) abgehenden und geradlinig verlaufenden Ästen besetzt. Die unteren sind etwa 6 cm lang. Sie haben einen Durchmesser von ca. 0.6 cm Nach oben werden die Äste immer kürzer und dünner, so daß die Pflanze in einer Spitze endet. An allen Ästen entspringen in sehr dichter, schraubiger Anordnung bis zu höchstens 2 cm lange Kurztriebe, die bei stärkeren Ästen verzweigt, bei schwächeren unverzweigt sind und zahlreiche, ca 5 mm lange ellipsoidische Sporangien tragen. Es sind so viele Sporangien vorhanden, daß die Äste geradezu von ihnen verhüllt werden.)

On the whole, this diagnosis can be recognised as correct. However, there are some ambiguities: the sterile leaves fork from time to time and no branches are visible in the fertile ones. The leaves are smooth-edged, tapered and can reach lengths of about 10 cm.

The big difference, however, lies in the structure of the *Weylandia* megasporophylls. The megasporangia settle in parallel on both sides of the fertile rhachis. They sit on a short stalk, are elongated elliptical and reach a length of about 0.5 cm, including the stalk (0.1 cm) (LIND 182, LIND 130, LIND 203).

But under which extended family can *Weylandia* be classified? A classification under the progymnosperms is obvious. However, the Protoconifers *Calamophyton, Schweitzeria* or *Eoconifera* have leaf shapes that are different to those of *Weylandia.* The greatest differences are in the apical area: in *Weylandia* we find a tuft of fertile macrosporophylls, instead of sterile branchlets and fertile cones.

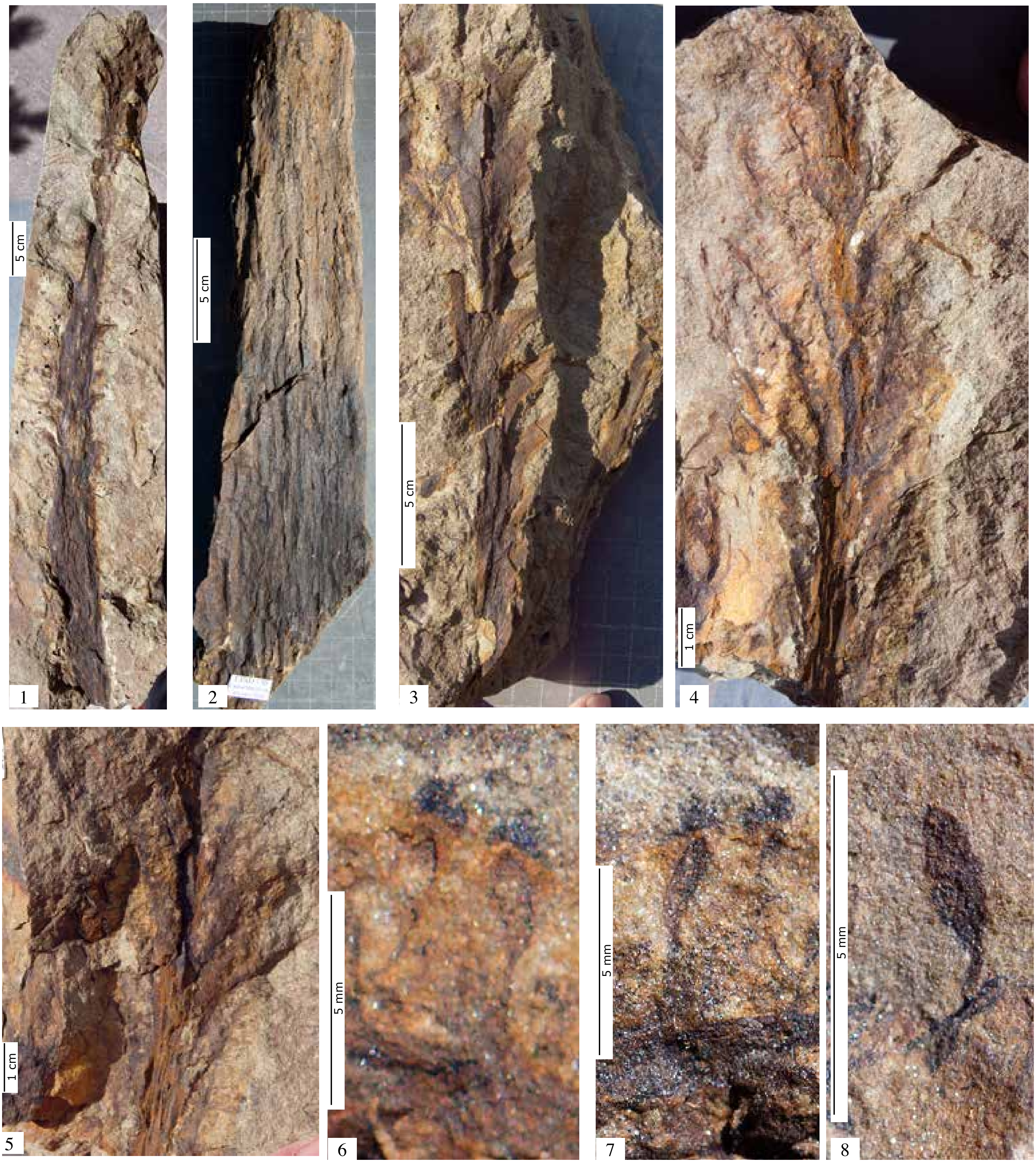
A classification among the protoconifers is therefore unlikely for *Weylandia.* Individual seeds lined up in parallel to one another on an axis are atypical for conifers, but they do resemble a plant family among the gymnosperms, namely the Cycas-cycads. As strange as it may sound, due to the fertile crest formed by a large number of megasporophylls of *Weylandia*, a classification belonging to the crown group of cycads cannot be far-fetched. In fact, *Taeniopteris* cycads occurring in the Permian and especially in the Triassic are characterised by tongue-like leaves emerging from a central axis, while their associated infructescences are also similar to *Weylandia.*

Detail of leaf ramifications of *Weylandia rhenana* (LIND 154)

Only beginning from the Middle to Late Triassic, the megasporophylls of the *Taeniopteris* Cycas-cycads arose from one level, such that no combined sporophyll tufts could be subsequently found; only individual megasporophylls consisting of an aggregation of seeds could be noted, similar to the case of today's Cycas-cycads.

The latter's tongue-shaped leaf structure – in contrast to the divided fronds occurring today – was normal over the whole Permian, up till the Triassic-Jurassic boundary.

Thus, *Weylandia* represents one of the most interesting and enigmatic plants of the Middle Devonian and can be considered as a crown group of the Cycas-cycads.



Weylandia rhenana. Plant with megasporophylls. Middle Devonian, Middle Eifelian

1. Almost completely preserved plant with a tuft of megasporophylls in the upper part, length 70 cm, stem width 5 cm (LIND 182); 2. Lowest part of a trunk (LIND 130); 3. Leaves (LIND 154); 4. Part of a seed-bearing tuft (LIND 125); 5-6 Detail of megasporophylls with enlargement of two megasporangia (LIND 125); 7-8. Detail of other megasporangia (LIND 182, LIND 203); Coll. Wachtler, Dolomythos

Class: PROGYMNOSPERMAE Beck, 1960

Genus: FLABELLOPHYLLUM Wachtler, 2022

Etymology

Derived from the Latin "flabellum" for "fan-shaped".

Diagnosis

Long, narrow leaves that divide several times.

Flabellophyllum divisum Wachtler, 2022

Etymology

Derived from the Latin "dividere" which means "shared".

Holotype

LIND 202

Description

Foliage: Various deeply dissected leaves dividing several times, merging basally. The individual leaf needles reach a length of 6 cm and a width of 0.3 cm, ending in a pointed to slightly rounded apex (holotype LIND 202, LIND 195).

Remarks

Flabellophyllum divisum is relatively rare in the Lindlar sediments, but is interesting because of its similarity to the Permian-Triassic ginkgo family. Since no related fruit organs have been found so far, an exact classification into a particular plant family is doubtful; therefore the, question of whether it forms a part of the ginkgo crown group cannot be confirmed. As a ginkgo precursor, if it had reached an astonishingly high level of development. Both the Permian finds (*Ginkgoites pohlii,* Wachtler, 2021) – that can be classified with relative certainty as Ginkgo ancestors due to the seed berries found in connection with them – and the late Permian finds (*Ginkgoites gasseri, Baiera digitata,* Wachtler, 2021) have many features of today's Ginkgos but, at times, have archaic appearances. Furthermore, *Flabellophyllum divisum* shows more resemblance to the Late Carboniferous *Baiera perneri*, although this cannot be proven with certainty due to the lack of concomitant infructescences.

Flabellophyllum divisum. Probable ginkgo ancestor. Reconstruction

However, the individual seeds hanging from a stalk, which have been found repeatedly in Lindlar, could belong to *Flabellophyllum divisum,* in which case it could well be the first ginkgo ancestor. So, it is to be hoped that further studies will shed light on these interesting leaf shapes in order to enable a clearer classification.

Order FILICALES Bower, 1899

Genus: *PROTOPTERIDIUM* Krejčí, 1880

1880 *Protopteridium hostinense* Krejčí, p. 203

1881 H*ostinella hostinensis* Stur pp. 352-361 Taf III, Fig. 1, 2; Taf. IV, Fig. 1-8.

1904 *Pseudosporochnus* Potonie & Bernard, FI. Dev. de l'etage H de BARRANDE, S. 14, Fig. 11-41.

1923 *Hostinella hostinensis* Kräusel & Weyland, pp. 158-171,- Taf. 6, .Fig. Taf. 7, Fig. 1-3; Taf. 8, Fig. 1-5; Taf. 9, Fig. 1-13.

Historical overview

The genus name *Protopterium (hostinense)* was used in 1880 by the Czech geologist Jan

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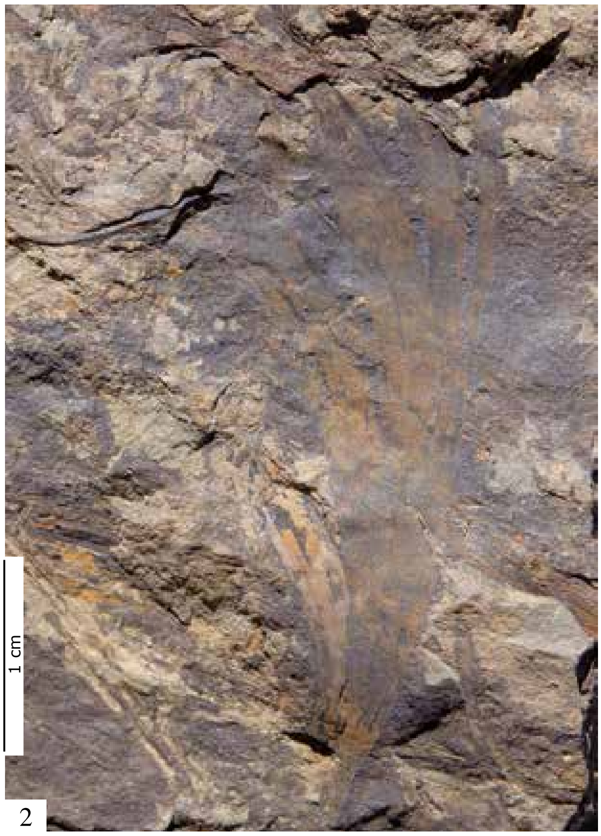

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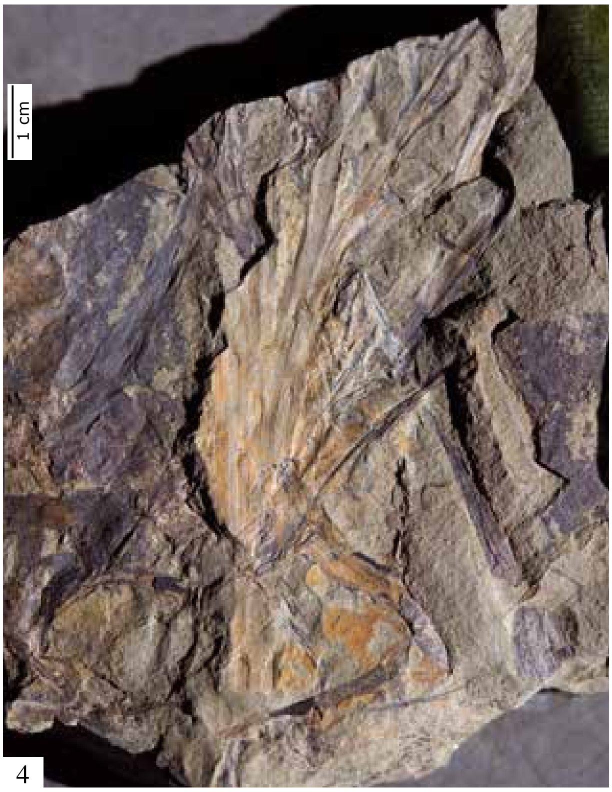

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Flabellophyllum divisum. Plant and lLaves. Middle Devonian, Middle Eifelian

1-2 Tuft of leaves (LIND 202, holotype); 3. Various leaves (LIND 195); 4. Aggregated Leaves (LIND 206); Coll. Wachtler, Dolomythos

Krejčí for a Middle-Upper Devonian (Givetium) '*fern frond with a serpentine, slightly curved stem and one-sided branches, on which the leaflets are unilaterally turned upwards and how half curled up on young fern shoots...Oval pinnulae with a strong central nerve can be seen on the side branches, which makes them similar to Pecopteris leaflets' (Farrenwedelzweig...mit schlangenförmig leicht gekrümmtem Stengel und einseitigen Ästchen, auf denen die Fiederblättchen einseitig gegen oben gekehrt und wie an jungen Farrenstrieben halb eingerollt sind...Man erkennt an den Seitenästchen ovale Fiederblättchen mit einem starken Mittelnerv, wodurch sie eben den Pecopterisblättchen ähneln)* (Krejčí, 1880, p. 203).

Thereafter, Štúr (1881) changed the plant's name to *Hostinella hostinensis,* illustrated it in detail and classified it among the algae *('a very handsome alga, with a stem about 20 cm high, long twigs branching sympodial-dichotomically above, with dichotomously branched sterile, and dichotomously pinnate fertile twigs and twigs"; "eine sehr ansehnliche Alge, mit einem circa 20 ctm. hohen Stamme, langen, oberwärts sympodial-dichotomisch verzweigten Ästen, mit dichotomisch verzweigten sterilen, und dichotomisch-fiedertheiligen fertilen Zweigen und Zweigchen').*

Although attempts have been made to discredit the generic name *Protopterium (hostinense)* as invalid and to shift it in the direction of *Rellimia* (Bonamo, 1977), it can ultimately be assumed that *Protopteridium* takes precedence over all other names that follow later (Matten & Schweitzer, 1982).

In 1923, Kräusel and Weyland used the name *Hostinella hostinensis* for a species from the Honseler Formation of the Hardtberg (lower Givetian) (Hartkopf-Fröder & Weber, 2016). They considered *Protopterium (hostinense)* to be a 'still entirely obscure object' which was to be related to *Psilophyton* and not to the ancestral ferns.

Subsequent research, especially from the Upper Devonian, confirmed that *Protopterium*, although characterised by rudimentary sparse leaves branching and arched spore heads directed upwards, was situated at the origin of the barely classifiable and recognisable ancestral ferns. In the Upper Devonian, the genus then became *Rhacophyton* (Crépin, 1875), which seems justified given the major differences in the structure of the plant that had meanwhile occurred, with many relevant characteristics, such as the beginning of pinnae formation, effectively pointing more in the direction of fern ancestors. Because of their diversity as early as the Devonian, *Protopterium/Rhacophyton* could be considered as the starting point for many fern families, especially in the Carboniferous.

Protopteridium philippae n. sp. Wachtler, 2022

Etymology

Named after the German Alice Philipp, who collected many plant fossils and generously made them available to science.

Holotype

LIND 240. Plate with sterile and fertile parts. Coll. Wachtler, Dolomythos Museum, Innichen.

Diagnosis

A low-growing plant composed of fronds from which rudimental leaves/needles branch, varying from monopodial to dichotomous branching. Fertile pinnae are sparsely distributed along the rhachis, having a recurved structure. They hold, on their inner side, short branches from which the sporangia hang densely.

Description:

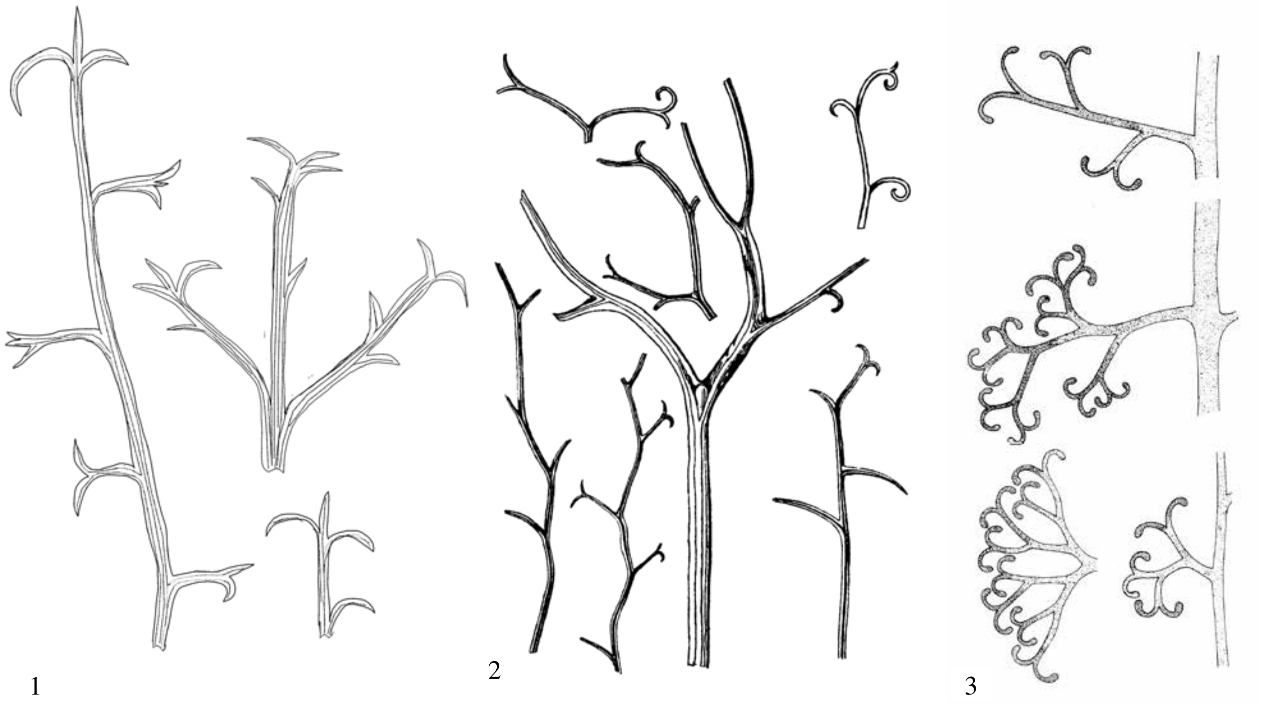
Sterile fronds: Fronds are about 30–50 cm long (LIND 253 = 30 × 27 cm; holotype LIND 240 = 22 cm), with only sparse secondary axes branching off. Main stem circumference no thicker than 0.3 cm. Roots short (preserved part of seedling, LIND 213 = 1 cm), pinnulae (or enations) either monopodial (LIND 106) or dichotomizing (LIND 246, LIND 95), sometimes also tridactylous (LIND 95), especially in the upper part, about 1 cm long.

Fertile fronds: Fertile aggregates are about 1.5 cm long, beginning with a short sterile stalk (holotype LIND 240) that curves upward towards the major axis. Sometimes (but not always) they have a dense system of three-dimensional ramifications. The upper part of each individual frond is smooth; five to eight branches arise from the lower part, from which the ovoid or elongated sporangia hang in dense clusters (LIND 240, LIND 111, LIND 115, LIND 197, LIND 119,

***Protopteridium philippae*. Reconstructions**

a. Juvenile plant with roots (LIND 213); b. Entire plant with sporangia; c. Complete individual frond (LIND 253); d-e. Model-like side shoots (LIND 246, (LIND 95, LIND 158, LIND 157); f. Fronds with sporangia (LIND 240, Holotype); g. Aggregation of sporophylls (*Osmunda* habitus) (LIND 200); h. Detail of spore accumulations (LIND 186, LIND 114, LIND 79, LIND 106, LIND 82) i. Detail of spores (LIND 111, LIND 115)

The first Evolution of the ferns



Pinnulae of Ferns: Development from the Middle Devonian to the Upper Devonian

1. *Protopteridium philippae* (Lindlar, Middle Eifelian, (Early Middle Devonian) Mühlenberg Formation); 2. *Protopteridium hostinense* (Hostinella) (From Käusel & Weyland, 1923; Gräfrath, Lower Givetian, (Late Middle Devonian), Honseler strata); 3. *Rhacophyton condrusorum*, Famennian (Upper Devonian), Walheim-Aachen, Condroz sandstone). From Schultka 1978

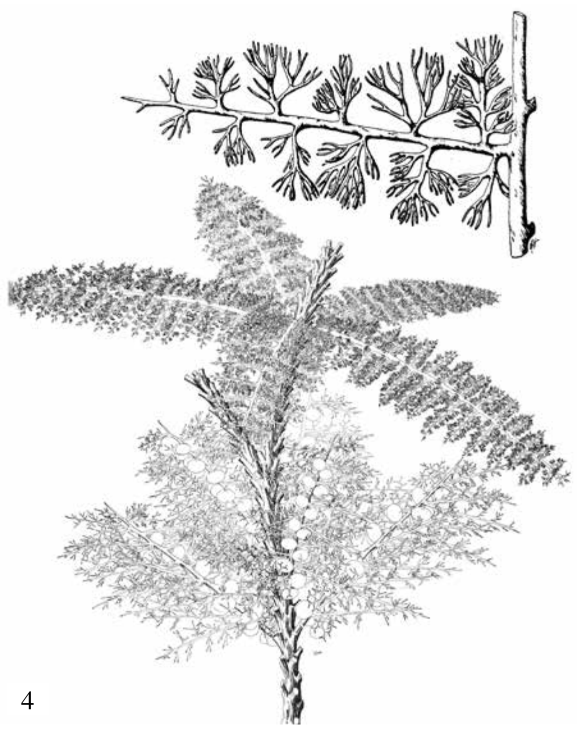
LIND 186, LIND 114 , LIND 79, LIND 106, LIND 82). The single sporangia found do not exceed 0.4 cm in length and have a width of 0.1 cm, sometimes but not always ending in a distal, pointed and delicate appendix. Moreover, the sporangia are aggregated in two but again form clusters in four, being aggregated in a further agglomeration of about 16 sporangia. Altogether, one single fertile frond can hold about one hundred or more single sporangia, but the latter can furthermore be aggregated in many other fertile blades (LIND 111). Finally, the sporangia are homosporous.

Remarks

Protopterium philippae is one of the most common flora elements in the Lindlar quarry, even if cases of a reasonably complete plant are extremely rare. In most cases, there are either sterile branches only a few centimeters long or the characteristic semicircular sporophyll fronds. The low-growing plant probably reaches around 30–50 cm in size.

Probably, *Protopterium philippae* represents the crown group of ferns that can still be recognised today, because the possible precursors in the direction of the Lower Devonian are so archaic that useful derivations are hardly possible. On the other hand, from the next developments – up to the Upper Devonian – especially in its presumed successor R*hacophyton,* one can already recognise clear indications of the pronounced little pinnulae and fronds of today’s ferns.

However, the sporophylls in the Lindlar of the Middle Devonian are so different each other that one could just easily describe several different *Protopteridium* species. Although the differences with the 5–10 million years younger *Protopteridium hostinense* (belonging to the Givetian) are not great, the even more primitive character of both the fertile fronds and the foliage of *Protopterium philippae* from the Eifelian is evident. On a related note, it was a stroke of luck for Jan Krejčí (1880) to assume this plant’s assignment to the Pteridophyta with the name *"Proto"* (for original) and *"pteridium"* (for fern), i.e. "original fern", as rarely do paleobotanical findings contribute to nomenclature elsewhere.



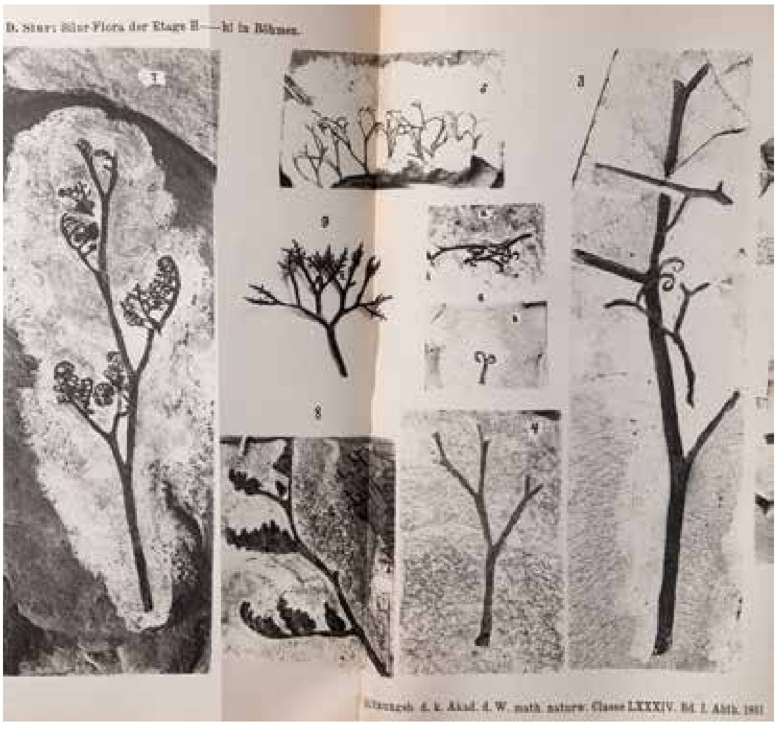
4. *Rhacophyton ceratangium,* Hampshire Formation, Famennian, Upper Devonian. From: Andrews & Phillips

In fact, attempts were made to discredit the name given by Krejčí, for example by Štúr (1881) naming the plant *Hostinella hostinensis,* and also by Kräusel and Weyland (1923) naming it as *Hostimella hostimensis,* or by Lang (1926) naming it *Milleria thomsonii* (invalid, as it is reserved for a modern-day Asteraceae), or by Bonamo (1977) naming it *Rellimia thomsonii* with regard to similar plant parts from the Givetian of New York (Gilboa). However, overall the theory of the usually thoughtful Devonian plant scientist H J Schweitzer can be augmented (Matten & Schweitzer, 1982) into this matter: despite some substantive flaws (understandable considering the time), the name chosen by Krejčí (1880) endures, especially with regard to the illustrations of his first described specimen by Štúr (1881).

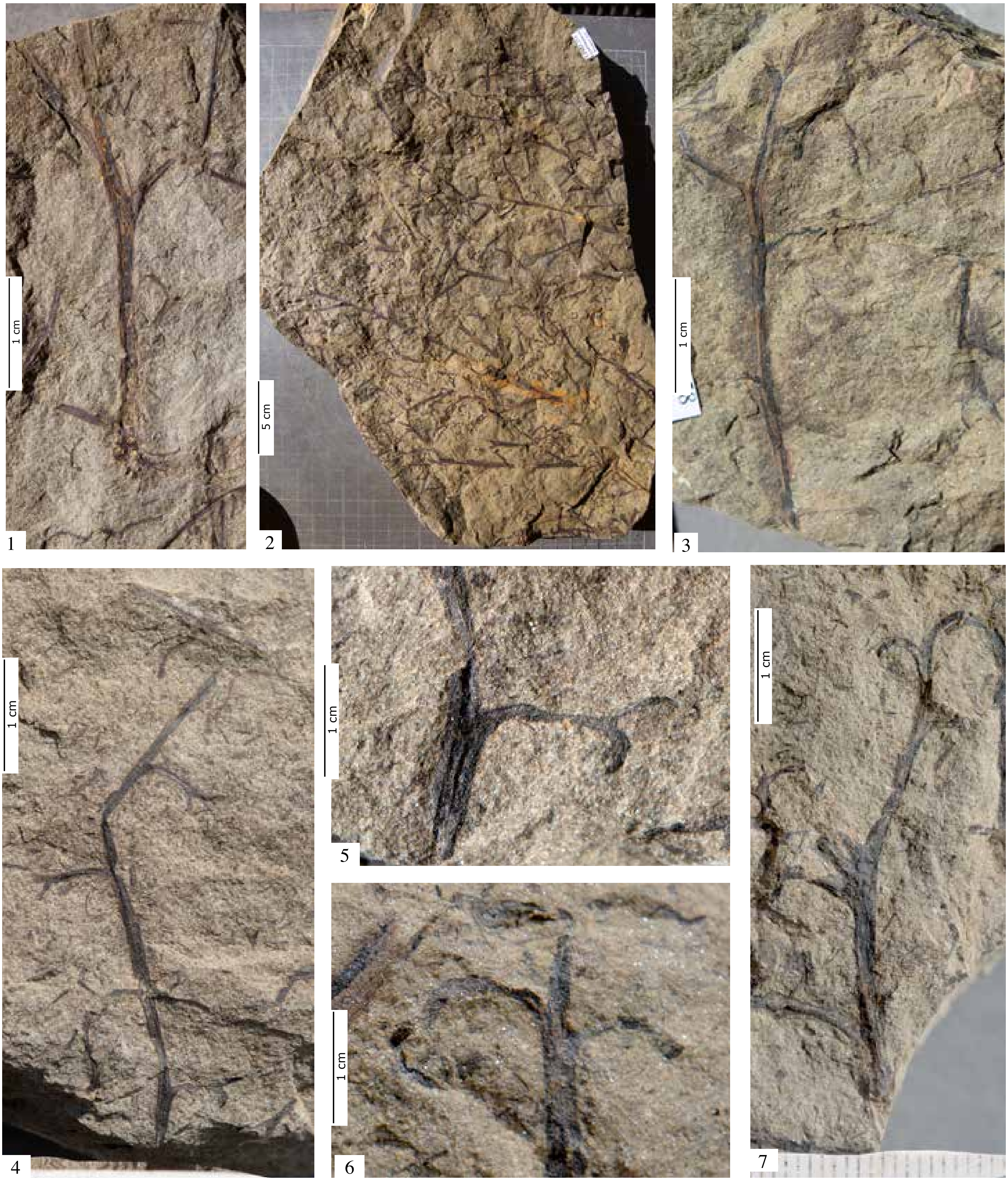
Discrediting older names so that later-born authors can credit themselves with new names is not justified, out of respect for previous researchers who struggled with many difficulties in their lives. However, the name *Rhacophyton* can be accepted for Upper Devonian ferns similar to *Protopterium,* since the development gap or time difference of over 30 million years allows the same.

On the other hand, it seems strange that from a simple Y-shaped dichotomous *Protopterium* leaf needle, through further bifurcations within about 30 million years via *Rhacophyton*, the typical pinnate leaf of ferns should have arisen; this can be considered an excellent example of evolutionary lines that were hitherto hardly considered possible.

As a result, the typical tissue (epidermis) forms around the leaf veins and develops the classic pinnate shape of today's ferns. The high level of development of the *Protopteridium* sporophylls as early as the Lower Middle Devonian is an interesting observation. In principle, many of the following fern families can be derived from this basic building plan: the Osmundaceae, with their separate tropophyll and sporophyll fronds (holotype LIND 240 is a good example) and the *Cyathea* or *Dicksonia* progenitors (LIND 249), all of which achieved worldwide distribution in the Carboniferous. In this vein, Štúr (1881) already pointed out

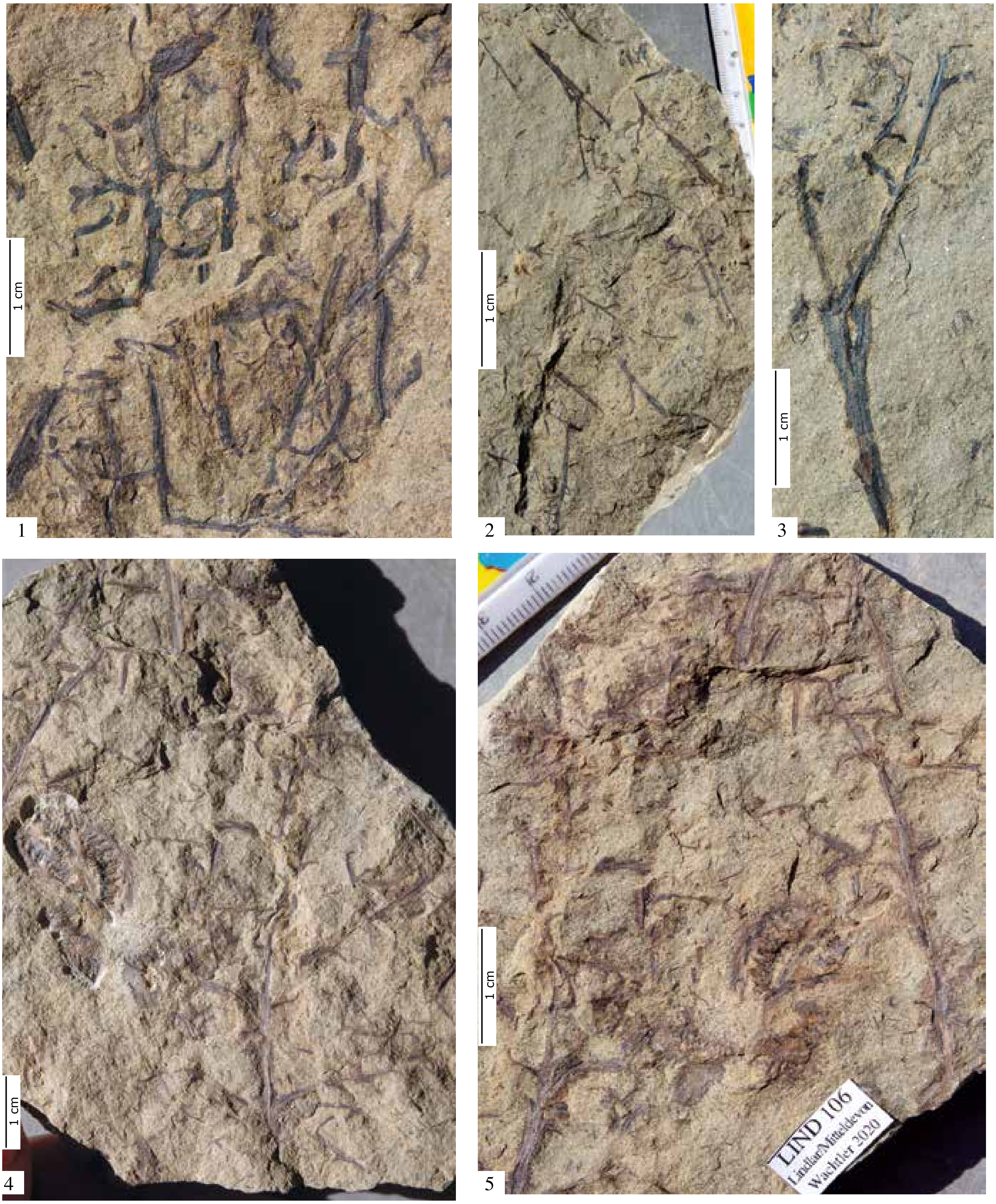


In 1881 D. Stur (plate IV) illustrated various plants described by J. Krejčí in 1880 as *Protopteridium hostinense* and named them *Hostinella hostinensis*, assigning the plants to fossil algae. Among them no. 8 represents a specimen described by Krejčí. It is obvious that the valid name *Protopteridium hostinense* KREJČÍ, 1880, has to be maintained.



***Protopteridium philippae*. Sterile fronds. Middle Devonian, Middle Eifelian**

1. Plant with roots - seedling (LIND 213), 2. Biggest frond found (LIND 253); 3. Frond with primitive leaf branches (LIND 158); 4-5 Detail of leaves dividing two to three times (LIND 246); 6-7. Fronds with two to three times dichotomous leaves (LIND 95); All Coll. Wachtler, Dolomythos, Collected by Manfred Fuchs and Alice Philipp in the BGS-Quarry, Lindlar



***Protopteridium philippae*. Sterile and Fertile Fronds, Middle Devonian, Middle Eifelian**

1. Fronds with juvenile leaves (LIND 153), 2-3. Fronds (LIND 159); 4. Beautiful frond with sterile and fertile areas (LIND 249); 5. Frond with fertile parts (LIND 106); All Coll. Wachtler, Dolomythos); Collected by Manfred Fuchs and Alice Philipp in the BGS quarry, Lindlar

***Protopteridium philippae*. Fertile and Sterile Fronds. Middle Devonian, Middle Eifelian**

1-3 Sterile and fertile frond. Detail of sporophylls (Holotype LIND 240); 4-5. Holotype counterplate with detail of mature sporangia; All Coll. Wachtler, Dolomythos); Collected by Manfred Fuchs and Alice Philipp in the BGS quarry, Lindlar

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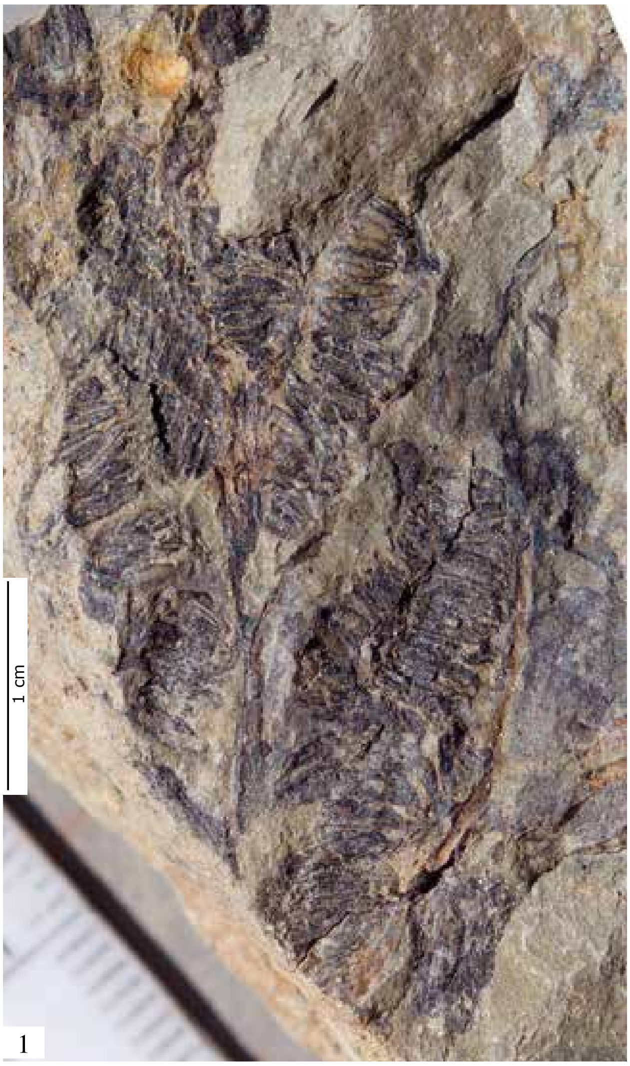
***Protopteridium philippae*. Fertile parts Middle Devonian, Middle Eifelian**

1-5 detail of sporophylls (LIND 186, LIND 114, LIND 79, LIND 106, LIND 82); All Coll. Wachtler, Dolomythos; Collected by Manfred Fuchs and Alice Philipp in the BGS quarry, Lindlar



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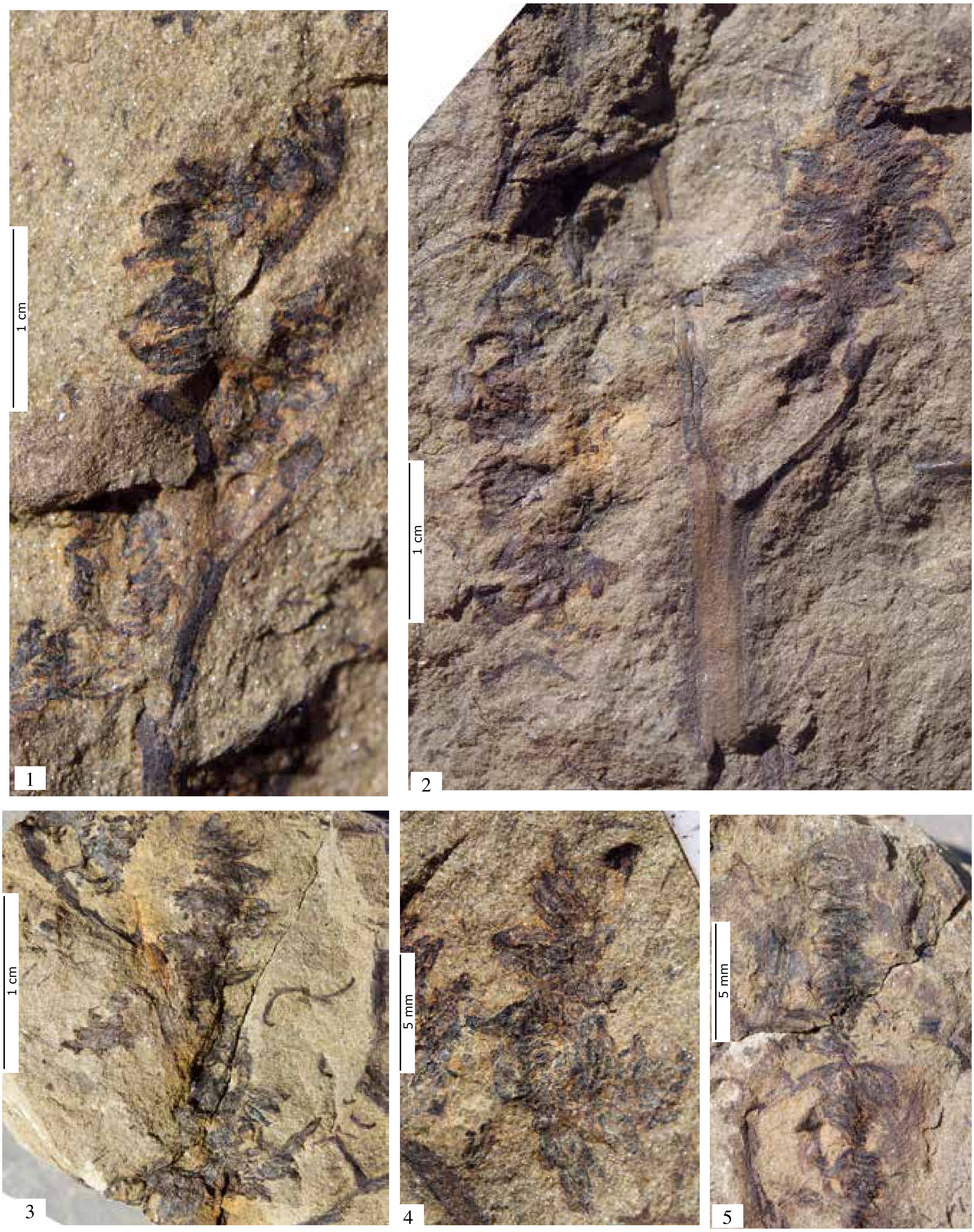
***Protopteridium philippae*. Fertile parts. Middle Devonian, Middle Eifelian**

1-2. Tuft of sporophylls and detail (LIND 111), 3-4. Aggregation of individual sporangia (LIND 115, LIND 197) 5. Fertile frond with an isolated sporangium on the right LIND 119); All Coll. Wachtler, Dolomythos); Collected by Manfred Fuchs and Alice Philipp in the BGS quarry, Lindlar



***Protopteridium philippae*. Fertile parts. Middle Devonian, Middle Eifelian**

1-5 Accumulation of sporangia (LIND 107, LIND 248, LIND 120, LIND 80, LIND 115); All Coll. Wachtler, Dolomythos); Collected by Manfred Fuchs and Alice Philipp in the BGS quarry, Lindlar

Protopteridium philippae.
Arrangement of sporophylls towards the Osmundaceae (LIND 200).

the similarity of *Protopteridium* with regard to *Pecopteris (Cyatheites).*

Protopterium and later *Rhacophyton* seem to have been real cosmopolitans that, in addition to Europe *(Protopterium philippae, Protopterium hostinensis)*, were also able to spread in North America (*Protopterium thomsonii),* Siberia and Morocco (Gerriene et. al, 2010). This also holds true for *Rhacophyton* from the Late Devonian, such as *Rhacophyton condrusorum* (Crepin, 1875, Schultka, 1978) from Europe or *Rhacophyton ceratangium* from Virginia, North America, (Andrews & Phillips, 1968).

However, the various classifications of *Protopterium* or *Rhacophyton* as Aneurophytales, Zygopteridales, Coenopteridales or Trimerophytophyta (Taylor et al., 2009) hardly herald any gains in knowledge, since they do not provide any solutions as to the evolutionary direction in which *Protopterium* moved.

Another crucial question is, to which other Middle Devonian flora elements is Protopteridium most likely related? It is least related to the Lycophyta (*Protolepidodendron, Selaginellites)*, which had already separated from the other families at that time. In this regard, if one compares the male sporophyll levels of progymnosperms such as *Calamophyton primaevum, Eoconifera fuchsii* and also the suggested cycad ancestors (*Weylandia rhenana, Kraeuselia pohlii),* one can notice similarities. The same applies to found, rolled-up fronds, which must be placed either with the cycads or the ferns. Plus, even with the *Equisetum* horsetail ancestors *(Archaeoequisetites lindlarensis),* family relationships open up. Notably, some specimens from Lindlar show aggregated sporophyll stands, with spore receptacles united on the underside of a shield-like sporangiophore (LIND 17).

If we probably arrive at the crown group of many plant families in the Middle Devonian, a question remains: under what circumstances did some plants become seed-carriers (i.e. the gymnosperms) while others, such as ferns or horsetails, found another way, with the formation of homosporous sporophylls. Here, the middle way seems to be more effective: if we find homosporous Protopterium ferns at one end of the evolution scale, this is followed by heterospore clubmoss *Selaginellites devonianus* (i.e. with megaspores and microspores within the same cone formation) and, finally, by the gymnosperms, with different megaspores (seeds) and microspores (pollen sacs) on the same or different plants. Such changes must have taken place in the Middle Devonian, within an amazingly short period of time, subsequently determining the entire flora of the world up to the present time.

Horsetails

Family SPHENOPHYTA
Class CALAMITACEAE Unger, 1840

Genus *ARCHAEOCALAMITES* Stur, 1875

Archaeocalamites antiquus sp. nov. Wachtler 2023

Etymology

Derived from the Latin *"Antiquus"* meaning "old"; progenitor of the Calamitaceae.

Holotype

LIND 201, Coll. Wachtler, Dolomythos Museum, Innichen.

Diagnosis

Stems similar to *Calamites,* with straight longitudinal ridges (also present across the internodes). Sporophyll-strobili are elongated and slender, consisting of a geometrical series of whorls fused into nodal sheaths. Sporangia are sessile basally, enveloped by needle-like bracts.

Description

Plant: Stems have characteristic horizontal ridges or furrows interrupted by irregular nodes but running through in a straight line (holotype LIND 201, LIND 153). Side branches sprout laterally from the nodes.
Fertile organs: Strobili are slender, about 5–6 cm long and 2–3 mm wide. They consist of a plurality of needle-shaped sterile bracts fused with whorls arising at the same level. They sometimes fork in the upper half. The sporangia arise adaxially in the basal part and are enveloped by the bracts.

Equisetaceae

Genus *ARCHAEOEQUISETITES* nov. gen. n. sp. WACHTLER 2022

Etymology

Derived from the Greek "archaïos" which means "old"; also, a reference to the horsetail lineage *Equisetites* (today's *Equisetum).*

Diagnosis

Horsetail with elongated ribs, repeatedly interrupted by internodes. Cone-shaped strobili with sporangiophores which carry sporophylls hanging onto the axis under a shield-shaped bract.

Etymology

Derived from *"ancient horsetail".*

Archaeoequisetites lindlarensis n. sp. Wachtler 2022

Etymology

Derived from the Lindlar site, BGS Vitar Quarry, GPS: N 051°01.740, E 007°22.420, North Rhine-Westphalia.

Holotype

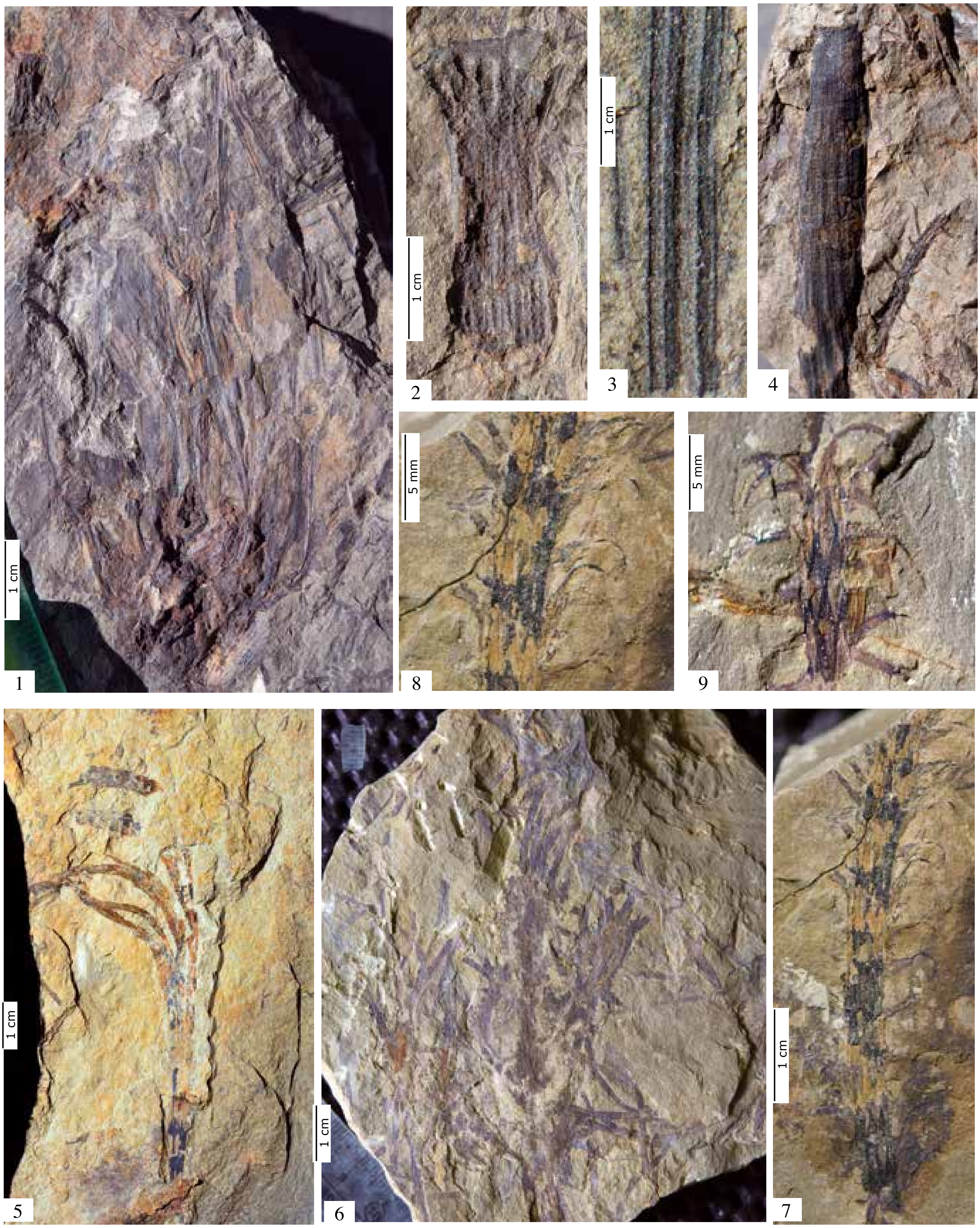
LIND 514, Coll. Burkhard Pohl, Grossbieberau.

Description

Plant: Main axes are repeatedly interrupted by internodes. These give rise to delicate secondary branches, only 0.2 cm thick but up to 10–15 cm long, which form composite whorls (LIND 11).
Fertile organs: Cone-shaped strobili are composed of several sporangiophores from which a large number of elongated spore sacs, about 0.5 cm long, hang on the underside (holotype LIND 514).

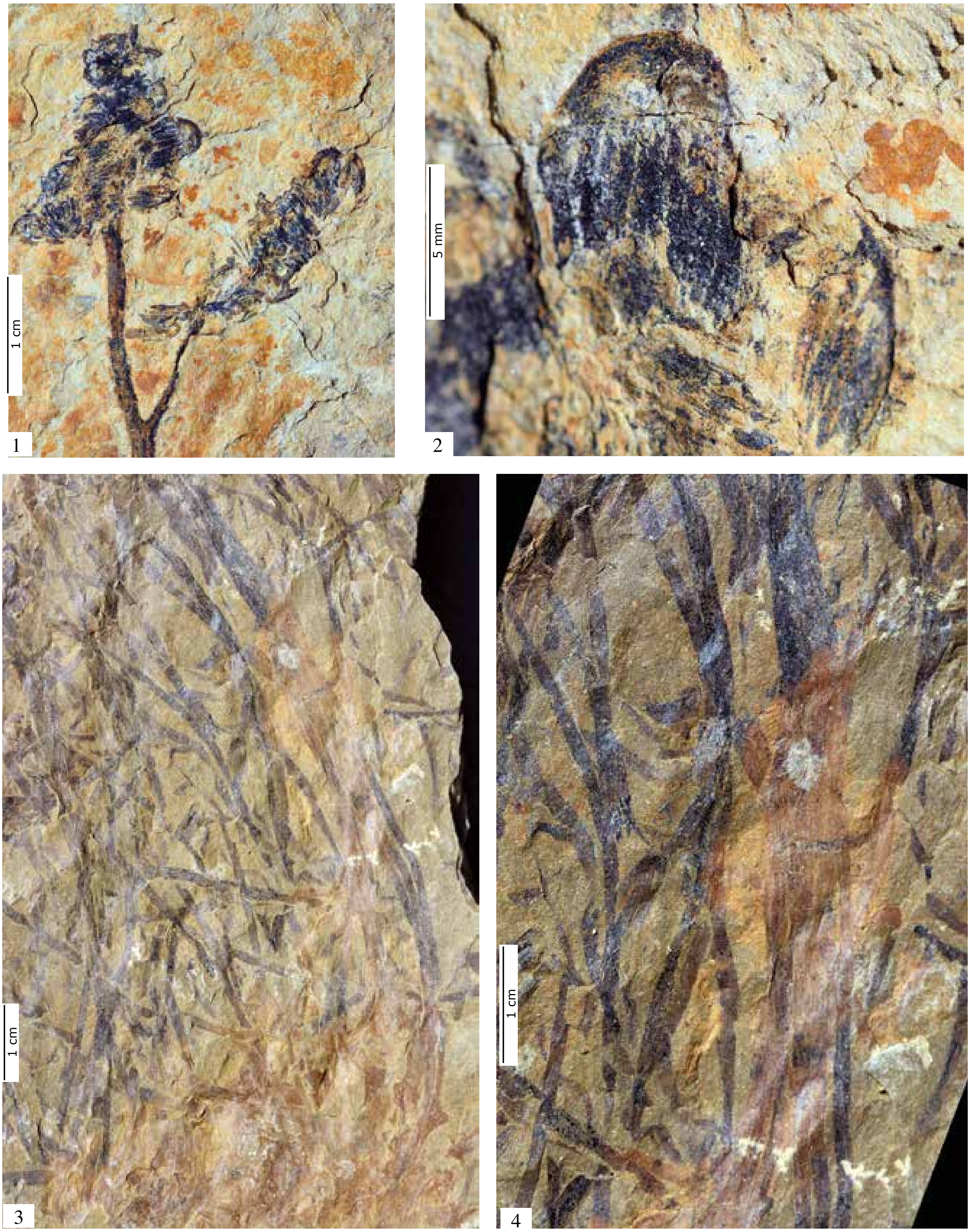
Remarks

Based on the Lindlar findings, the origin of the Sphenophyta could be dated back to the Middle Devonian. Interestingly, the two main suggested horsetail lineages were formed during this period: the Calamitales and the Equisetales. Moreover, in the Late Devonian, we encounter *Pseudobornia ursina* (Nathorst, 1902; collected by Johan Gunnar Andersson in the 1890s on Bear Island). Hans-Joachim Schweitzer (1967) interpreted such fossils as belonging to a large, 15–20 m high tree, whereby the apparent connections with horsetails, especially with the Calamitaceae, were worked out. From the Lower to the Middle Carboniferous (Tournaisian to Viséum), fully developed Calamitaceae *(Archaeocalamites*) with their characteristic, elongated infructescence were reportedly present. They consisted of a large number of sheaths with bracts arising on the same level, which closely coated the sporangia. Longitudinal grooves running continuously through the nodes were characteristically



***Archaeocalamites antiquus*. Stems. Middle Devonian, Middle Eifelian**

1-2. Apical part of a plant with partially forked side branches (holotype LIND 201, Coll. Dolomythos); 3. Stem (LIND 153); 4. Stem part belonging to either *Archaeocolamites* or *Protolepidodendron;* (LIND 252); 5-6. Stem with forked side branches (LIND 14, LIND 501, Coll. Pohl); 7-9. Strobilo with partially dichotomous bracts (LIND 504, LIND 503)



***Archaeoequisetites lindlarensis*. Sporophyll-cones and Stems. Middle Devonian**
1-2 Detail of a sporangiophore with laterally hanging spore vessels (holotype LIND 514); 3-4. Various stems with internodes and lateral branches (LIND 11); Coll. Pohl, Grossbieberau

present, with somewhat offset ribs appearing first around this time, due to the forking of the vascular bundle *(Mesocalamites).*

Especially in the Late Carboniferous, the Calamitaceae spread in many, often simultaneous, variations such as *Calamites multiramis, Calamites equisetiformis, Calamites incisum, Calamites gigas* etc. Some species of the related genus *Neocalamites* managed to survive into the late Permian only to become extinct during the Permian-Triassic catastrophe (Wachtler, 2019). The Upper Permian *Neocalamites benckeae* from the Italian Alps is considered to be the last representative of the Calamitaceae.

Additionally, *Calamites* horsetails (*Paracalamites decoratus, Paracalamites striatus)* (Perner & Wachtler, 2020) were also widespread, in the Early Permian, on the Angara continent (currently part of the Ural region and Siberia) as well as on the American landmass (*Calamites kinneyana,* Wachtler, 2017). Their typical strobili made them easily distinguishable from those of the Equisetales as well as those of all other plant families. They were therefore cosmopolitan, although it is unclear whether they arose simultaneously in the Devonian on several landmasses (some of which were far away) or whether they spread through migration.

The first development of the Calamitaceae must therefore have taken place between the Lower and Middle Devonian, so that *Archaeocalamites antiquus* can be regarded as the first correctly recognisable Calamitaceae. Interestingly, their strobili and bracts gripping the sporangia indicate closer family relationships to the Lycophyta (*Protolepidodendron*) than to the other horsetail group that survives today, i.e. the Equisetales.

The development of the Equisetum horsetails had a similar trajectory. Having an early Middle Devonian origin with *Archaeoequisetites lindlarensis,* they remained overshadowed by the more widespread *Calamites* family throughout the Carboniferous, but they spread on a larger scale throughout the Carboniferous-Permian (Moskovian-Kasimovian) boundary with *Equisetites hemingwayi,* similar to their spread via other Early Permian species such as *Equisetites geraschii* (Perner & Wachtler, 2015), Equisetites vaujolyi or the late Permian *Equisetites siberi* (Wachtler, 2015). Some of them reached shoot diameters of about 10 cm and grew up to 2–3 m in height. With *Equisetina magnivaginata,* the Equisetaceae became even more widespread on the Russian Angara continent.

The heyday of the Equisetales was observed in the Mesozoic, with the Early Middle Triassic Equisetites mougeotii, followed by *Equisetites arenaceus* in the Middle Triassic. They were present on a large scale especially on the European landmass and developed impressive trunks, some having a diameter of 20 cm. Moreover, cone-like sporophyll stands were developed on the main axis or on secondary side branches in the aggregations of many Equisetales strobili (Wachtler, 2016).

However, in contrast to the Calamitales, the strobili of the Equisetales are very rarely found in the sediments everywhere. They only occur frequently in Ilsfeld, a Middle Triassic German site, suggesting that like today's Equisetales, they flourished only for a short period of time in the spring season and then disintegrated.

Archaeoequisetites lindlarensis can thus be counted among the crown group of Equisetales. During the Middle Devonian, even the differences between the progymnosperms (protoconifera, protocycads), the ferns (*Protopteridum)* as well as *Archaeoequisetites* became blurred, especially in their microsporangiate forms. However, by this time the gymnosperms had already reached the level of evolution that led to seed formation, while the ferns and horsetails avoided this step and nevertheless remained successful in their way of evolution.

Where their classification as "horsetail" is not appropriate, the Calamitaceae may have evolved in close association with the clubmoss family but may have remained monosporangic in formation, just like the Lyopodium family, while other Lycophyta such as the Selaginellaceae became heterosporous, or even almost achieved seed formation (e.g. the *Sigilaria)*.

All of the above data can be taken as indication that the Calamitaceae and Equisetaceae went their separate ways and showed little parental affinities even in the Middle Devonian. Characteristically, the stems of both *Archaeoequisetites* and *Archaeocalamites* initially comprised an aggregation of connecting individual branches, which later formed a reinforced main axis.

***Archaeocalamites antiquus*. Reconstructions**

a-b. Part of a stem (LIND 201, holotype, LIND 153, LIND 14); c-d. Sporophyll-cone with sporangia (LIND 504, LIND 503)

***Archaeoequisetites lindlarensis*. Reconstruction**

a. Part of a stem (LIND 11); b. Sporophyll cone (LIND 514, holotype); c-d. Detail of a sporangia (LIND 514)

Lycophyta from the Middle Devonian

At least two different Lycophytes can be distinguished in Lindlar: *Protolepidodendron* and *Selaginellites*. In contrast, the process of their nomenclature is more complex. *Protolepidodendron scharyanum* was introduced in the scientific literature by the Czech geologist Jan Krejčí, first in 1879 and 1880, from Central Bohemia (Hostin, near Srbsko), with this name deeming it a progeny of *Lepidodendron,* a giant clubmoss that had reached its heyday in the Carboniferous. This species name also honours the master brewer Jan Michael Schary (1824–1881) from Smichov, who was a great collector of fossils. Krejčí (1879) highlighted the main feature of the plant as follows: *'The twig is covered with fine, at the end partially dissected, elongated lanceolate leaves' ('Der Zweig ist mit feinen, am Ende theilweise zerschlitzten, länglich lanzettförmigen Blättchen bedeckt').*

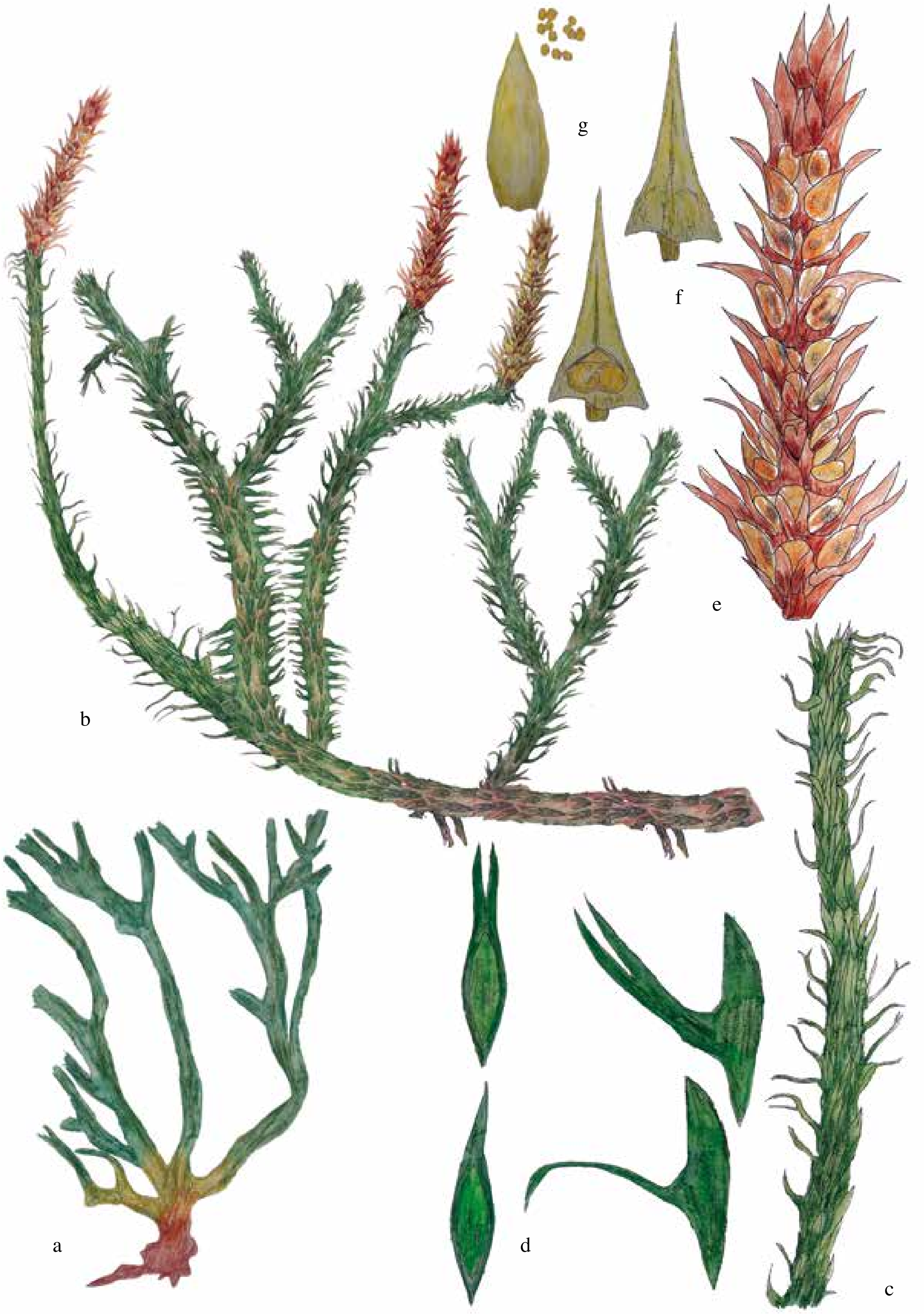
Protolepidodendron scharyanum from the Czech locality Hostin (Krejčí collection). He noticed the forked leaves. They are atypical for today‘s lycophytes or the Carboniferous genus *Lepidodendron.*

Just one year later, Dionýs Štúr (1881) changed the *Protolepidodendron* name to *Chauvinia scharyana*, although the latter was already occupied by a recent genus of algae. He also reproduced the main specimen from Krejčí for the first time (plate 1, fig. 1). Both these authors regarded this plant as belonging to the Late Silurian. In this vein, although there have been attempts (Yurina & Orlova, 2008) to discredit this name, the descriptive diagnosis cited by Krejčí should be sufficient and endure.

The German paleobotanist Henry Potonié and Bernard Renault (1904) used the original name *Protolepidodendron* again, but without further descriptive diagnoses. That is what Walter Gothan (1921) did after the death of Potonié (1857–1913) on his behalf and with the following classification: *"They are simple or forked small branches with lepidodendroid sculpture, but apparently without particular leaf scars and stigmata; small leaflets were attached to them, which in one species were forked at the tip." ("Es sind einfache oder gegabelte kleine Zweige mit lepidodendroider Skulptur, aber anscheinend ohne besondere Blattnarben und Närbchen; an ihnen sassen kleine Blättchen an, die bei einer Art an der Spitze gegabelt waren").*

All the above authors emphasized one characteristic of this club moss plant: it had both forked and unforked leaves. In 1932, Kräusel and Weyland described another similar plant – *Protolepidodendron wahnbachense* – from the German Wahnbachtal. These were Lower Devonian deposits from the Emsian, while the Bohemian *Protolepidodendron scharyanum* belonged to the Middle-Upper Devonian Givetian. As a result, the name *Protolepidodendron wahnbachense* was changed to *Estinnophyton wahnbachense* (Fairon-Demaret, 1979), owing to the multiple branching of its individual fertile leaf needles; moreover, another generic name, *Leclercqia* (Banks, Bonamo & Grierson, 1972), was introduced. The deeper meaning of these reclassifications cannot be fathomed or can at most be traced to human vanity, since there were hardly any significant deviations of this plant at the genus level over the 20-million-year development path from the Lower to the Middle Devonian.

Here, a question that arises, particularly regarding the Mühlenberg Formation of the BGS quarry in Lindlar, which belongs to the Middle Eifelian: to which species of Lycophyta do these frequently found above specimens belong? They have sometimes been described as *Protolepidodendron scharyanum* (Schweitzer, 1990), although some characteristics suggest that these specimens differ from those of the Givetian and also (even more) from the older *Protolepidodendron wahnbachense.* The following new species name for this lycopod plant (which is situated in a middle position) – *Protolepidodendron leschii* – seems to be the most expedient. This assumption also applies to the second genus found at Lindlar. In fact, their similarities to today's moss ferns make it credible to classify them as *Selaginellites devonianus*, as the oldest ancestor of this family (only after it became widespread, especially from the Carboniferous till the Triassic).



***Protolepidodendron leschii*. Reconstructions**

a. Root and basal part of the plant (LIND 241); b. Branchlet with sporophyll-cone (LIND 88, holotype); c-d. Isolated branch with two types of foliage: dichotomous and needle-like LIND 71, LIND 219, LIND 230, LIND 216); e. Sporophyll cone (LIND 88, Holotype); f. Sporophyll adaxial and abaxial (LIND 146, LIND 119); g. Microsporangia (LIND 69)

Protolepidodendron leschii

Class Lycopodiopsida

Order Lycopodiales

Familiy: Lycopodiaceae

Genus: *PROTOLEPIDODENDRON* (Krejčí, 1880)

1879 *Protolepidodendron scharyanum* Krejčí

1881 *Chauvinia scharyana* Stur p. 333, Taf. 1, Fig. 1-2 nom. illeg., Art. 52.1

1921 *Protolepidodendron scharyanum,* Gothan ex Potoniè

1932 *Protolepidodendron wahnbachense,* Kräusel & Weyland

Protolepidodendron leschii n. sp. Wachtler, 2022

Holotype

LIND 88 (Branchlet with Sporophyll-cone), Coll. Wachtler, Dolomythos-Museum, Innichen

Etymology

Named after the German astrophysicist, natural philosopher, science journalist, TV presenter and audiobook speaker Harald Lesch, Professor of Physics at the Ludwig-Maximilian-University in Munich and Lecturer in Natural Philosophy at the Munich School of Philosophy.

Diagnosis

Herbaceous club moss with undivided-to-forking leaf needles. Strobili are terminal and spike-like, with elongated bracts. Sporangia are located basally on the sporophylls.

Description

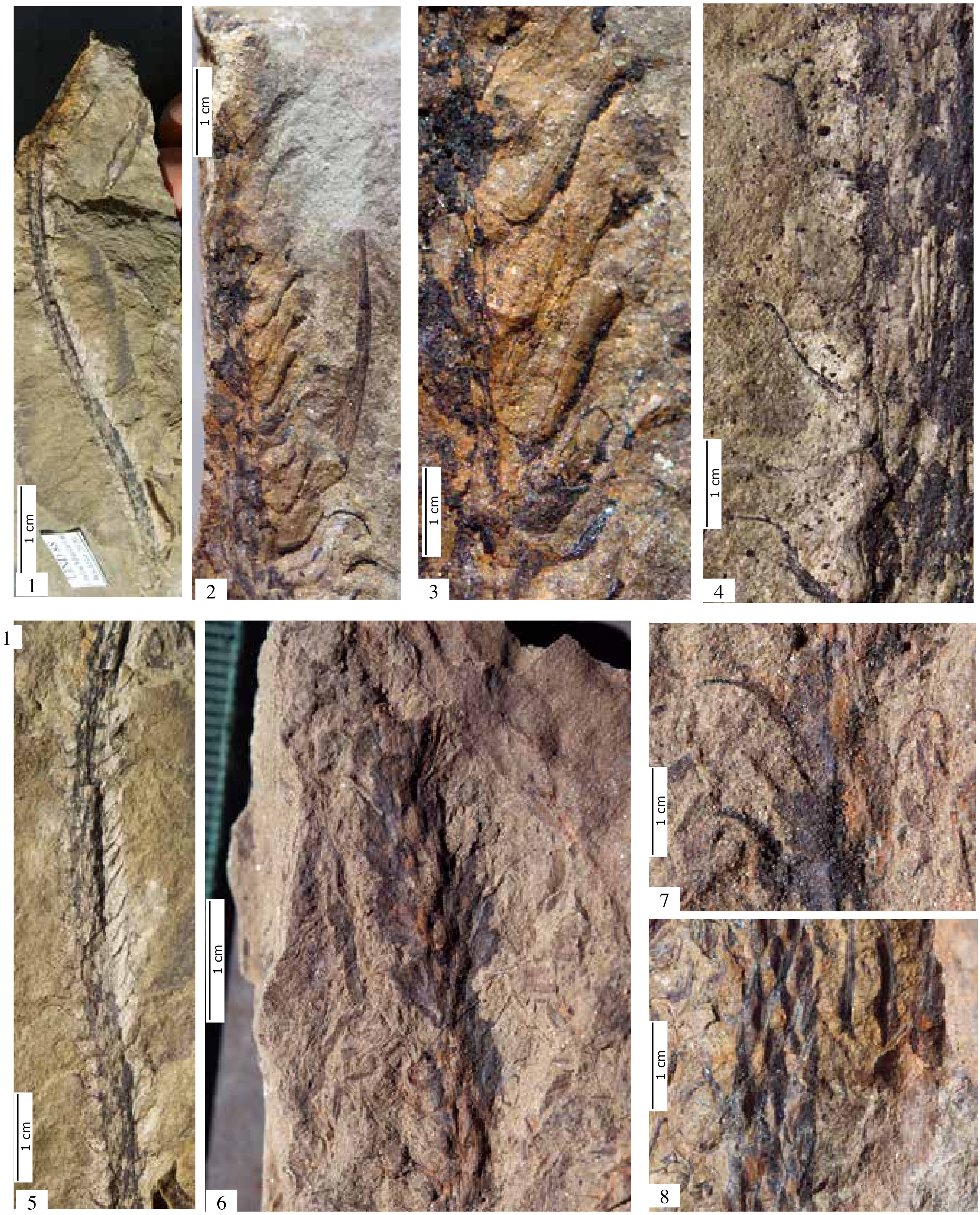
Plant: Shrubby, low-growing plant (LIND 241), probably no taller than 50 cm, with widely branched, upright-to-creeping stems (LIND 216). The individual leaf needles envelop the branches at loose intervals but can also be shed after maturity. They have a single, unbranched, barely recognisable vascular strand (LIND 02) and are usually no longer than 1 cm. They fork apically (LIND 217), although undivided leaf needles (LIND 207) are also found.

Strobili: The spike-like sporophyll is usually no longer than 5 cm (holotype 88) and is located at the end of the upright stem. The bracts are undivided and up to 1–2 cm long, with two sporangia located on the upper side of the leaf base (LIND 146, LIND 119, LIND 69) and protected by a thin, enveloping velum. Sporangia are probably homosporous (LIND 69).

Remarks

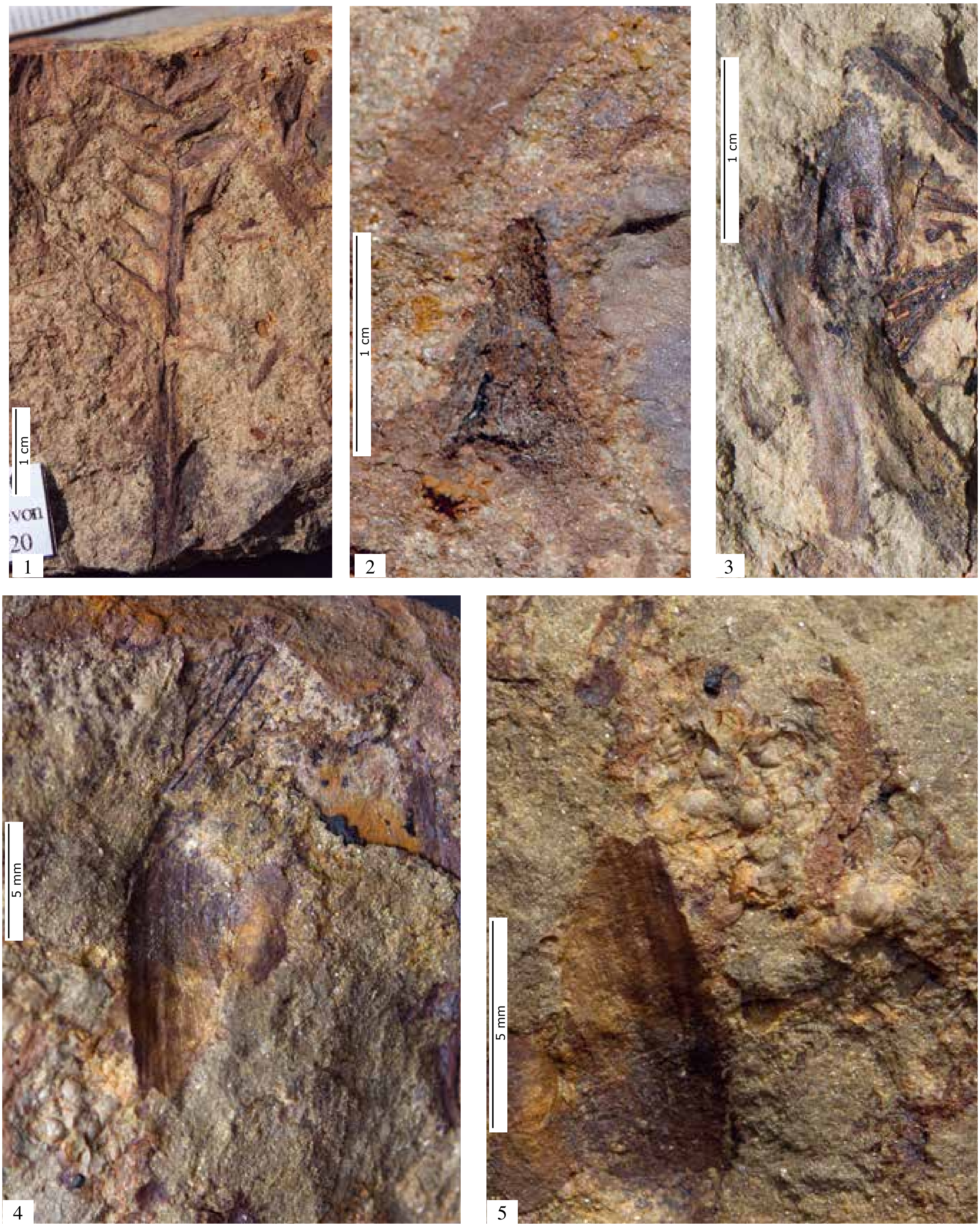
Protolepidodendron leschii is one of the most common plants in the Lindlar BGS quarry and is relatively easy to classify due to its shrubby character, with its forked-to-unforked leaf needles. In 1974, Schweitzer described *Lycopodites lindlarensis* as a new species, which, however, probably only represented the mature, open sporophyll stands of *Protolepidodendron leschii* (see LIND 146). In general, the genus *Lycopodites* – first described by Brongniart in 1822 for Carboniferous low-growing clubmoss – is difficult to interpret, since it ranges from the Devonian to the Eocene and, thus, contains a vat of undefinable lycopods.

Another similar lycophyte, *Protolepidodendron wahnbachense* (Kräusel & Weyland, 1932), belongs to the Lower Devonian Wahnbach Formation (Siegenian-Pragian) (Hartkopf-Fröder & Weber, 2016). However, it is characterised by more primitive, apical, doubly-forked, sterile and, above all, fertile leaves that clearly differ from *Protolepidodendron leschii.* Its sporangia also seem to have a different character. Indeed, its genus name was later changed to *Estinnophyton wahnbachense* (Fairon-Demaret, 1979). Furthermore, in 1972 the term Leclercqia (complexa) (Banks, Bonamo & Grierson, 1972) was introduced for similar fertile and sterile multi-forked leaf needles; they were described from the west flank of the North American Brown Mountains (Gilboa, NY) and were restricted to the Middle Givetian. Probably, this club moss could be better classified as *Protolepidodendron complexa.* Further, the Bohemian *Protolepidodendron scharyanum,* first described by Krejčí (1879), also belongs to the Middle Upper Devonian. It resembles *Protolepidodendron leschii* in some parts but has a higher developmental stage. However, there are ambiguities here, since both Krejčí (1879) and



Protolepidodendron leschii. **Fertile and Sterile Parts. Middle Devonian, Middle Eifelian**

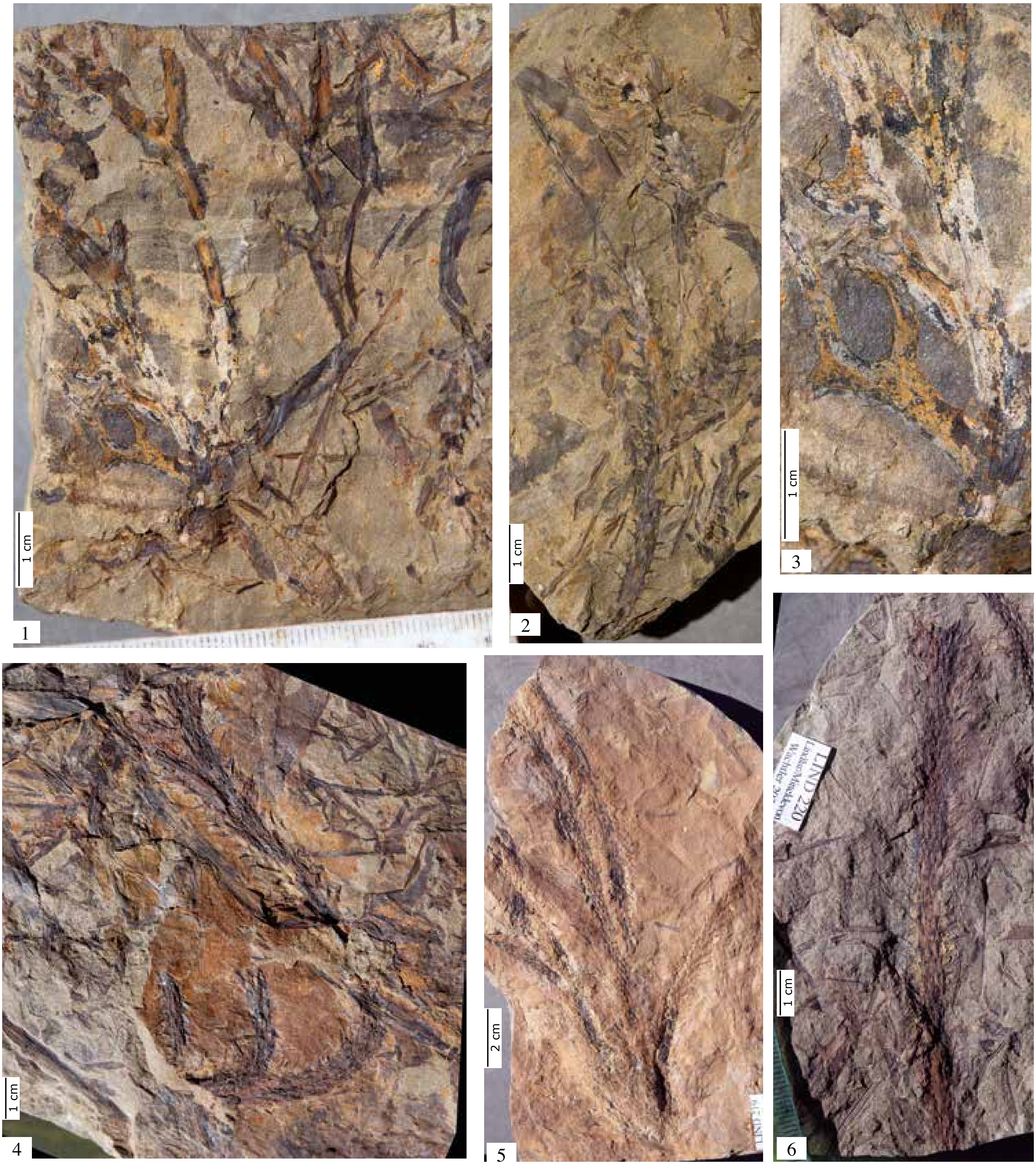
1-5. Twig with sporophyll-cone in the upper part. Details of bracts and partially dichotomous leaves (holotype LIND 88); 6. branch with unforked leaf-needles (LIND 205); 7-8 branch with forked leaves (LIND 217, LIND 97); All Coll. Wachtler, Dolomythos



***Protolepidodendron leschii*. Fertile and Sterile Parts. Middle Devonian, Middle Eifelian**
1-2. Mature strobilo with a shed sporophyll and detail (LIND 146); 3. Sporophyll with two sporangia (LIND 119); 4-5. Sporophyll with shed spores (LIND 69); All Coll. Wachtler, Dolomythos

***Protolepidodendron leschii*. Twigs. Middle Devonian, Middle Eifelian**

1-6. Various branches with partly unforked and forked leaf needles (LIND 02, Coll. Pohl; (LIND 71, LIND 219, LIND 230; Coll. Wachtler, Dolomythos



***Protolepidodendron leschii*. Twigs. Middle Devonian, Middle Eifelian**

1-3. Lower part of a plant with roots partially encasing stones (LIND 241); 4. Apical part of a branch (LIND 216); 5-6. Branchlets (LIND 219, LIND 220); All Coll. Wachtler, Dolomythos (to a greater extent) Štúr (1881) did not depict any fertile organs of this plant. However, if the following pictures (2–10), described as *Lessonia bohemica* and *Fucus nováki* on plate 1. by Štúr (1881), in addition to *Protolepidodendron scharyanum (*Fig. 1), belong to the same plant – which seems quite plausible – then it could well amount to a transitional stage between *Protolepidodendron* and *Lepidodendron.* To be precise, we find true Lepidodendrales beginning with the Lower Carboniferous.

Therefore, we can see a quite comprehensible evolutionary trend, starting from repeated division of sterile and fertile leaves in the Lower Devonian *Protolepidodendron wahnbachense*, via the Middle Devonian *Protolepidodendron leschii* and *Protolepidodendron scharyanum* (which developed both dichotomous and unforked foliage), to the no-longer-dividing leaf needles of the Carboniferous or to the unforked leaves of modern Lycopodiales.

The question of whether *Protolepidodendron* evolved only one type of sporangia, like today's *Lycopodium* clubmoss, or was heterosporous like today's *Selaginella* or like the Sigillarias in the Carboniferous (Wachtler 2022) – i.e. whether it developed both megasporangia and microsporangia – begs a clear answer: it was homosporous. The only opened *Protolepidodendron* specimen from Lindlar (LIND 69) shows an abundance of pressed-out, relatively large microsporangia. Even from the Carboniferous Lepidodendrales, there is no clear evidence of a heterospore orientation. Another relevant question is, does *Protolepidodendron* have more basic features of *Lepidodendron,* or is it more closely related to today's genus *Lycopodium*? The low growing indicates *Lycopodium,* whereas the basally falling leaves signify *Lepidodendron.* Altogether, we probably observe the most basic stage of development of both the above families, from which both the *Lepidodendron* giant trees and the inconspicuous Lycopodium species of the present could develop. However, the middle position of the medium-sized *Lycopia* (Wachtler, 2016) occurring in the Triassic must first be clarified. Otherwise, *Protolepidodendron* hardly shows any relationship to the other plants of Lindlar, such that it can be assumed that the latter went their own ways as early as the Lower Devonian.

Genus: *SELAGINELLITES Zeiller, 1906*

Taxonomic overview

In 1906, Renè Zeiller introduced the genus *Selaginellites* for fossilised heterosporous clubmosses resembling today's Selaginellas.

Selaginellites devonianus sp. nov. Wachtler 2022

Holotype

LIND 131 (Complete plant with sporophylls), Coll. Wachtler, Dolomythos-Museum, Innichen.

Etymology

Named after the Devonian period.

Diagnosis

Low-growing clubmoss with spreading branches that fork several times. Basal trunk is partially bare, densely covered in the upper part with tiny-small leaf-needles that sometimes bifurcate dichotomously. Small sporophyll clusters with heterosporous sporangia are observed.

Description

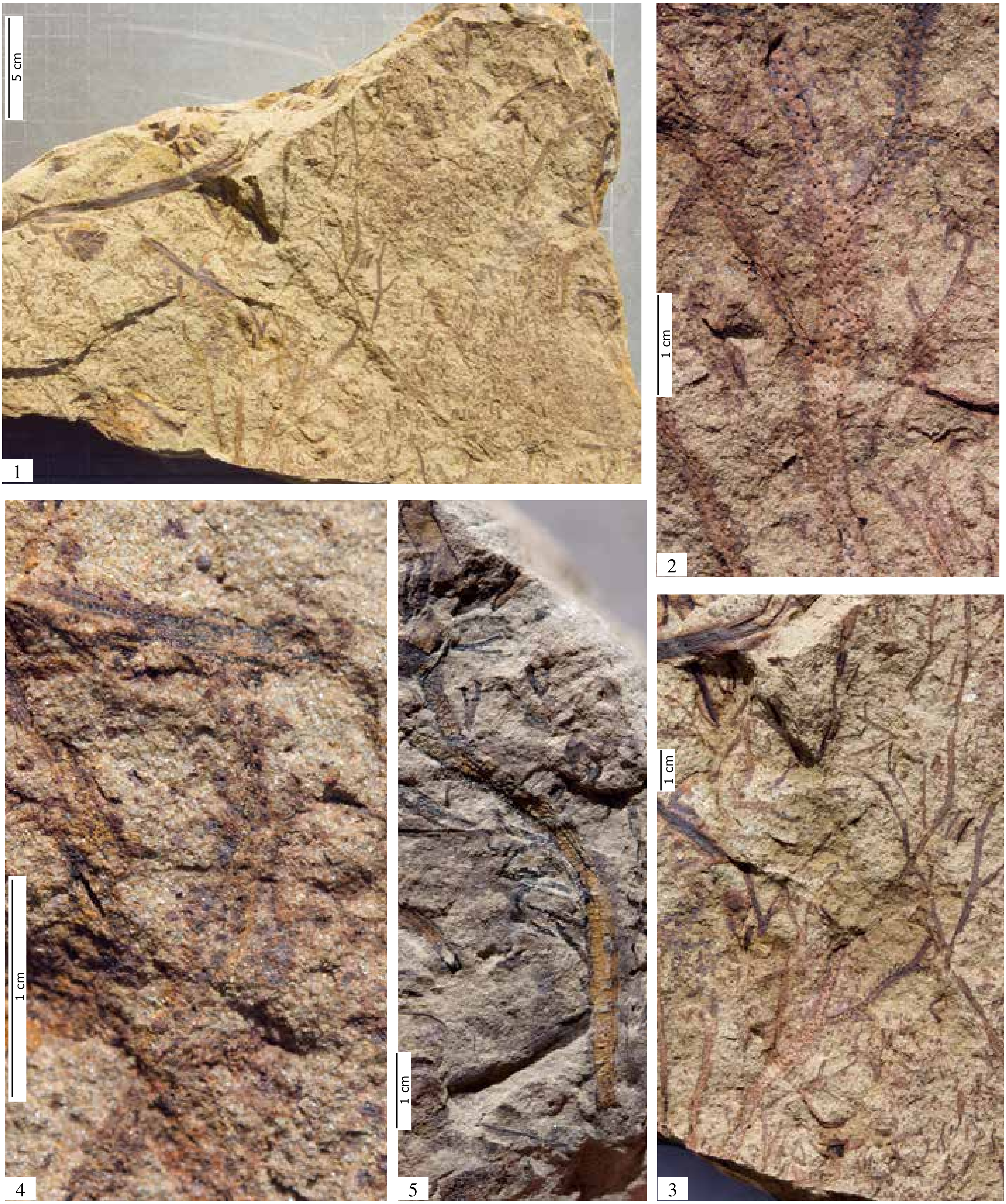
Plant: Twigs spread bushy, branch and diverge several times (holotype 131), probably reaching up to 30 cm. Several side branchlets diverge from the main axis, bifurcating regularly to irregularly. In the lower part, the plant is covered with small leaf scars from shed leaves (LIND 192).

Leaves: Leaf-needles are tiny, less than a millimetre long, sometimes close together and tightly coating the axes. In the apical area, they fork sporadically.

Fertile Parts: The strobili develop at the end of sterile shoots. They are elongated and reach a length of 2–3 cm (Holotype 131), with a width of only 0.2 cm. The small megasporangia and microsporangia end in an elongated tip; they fall off at maturity.

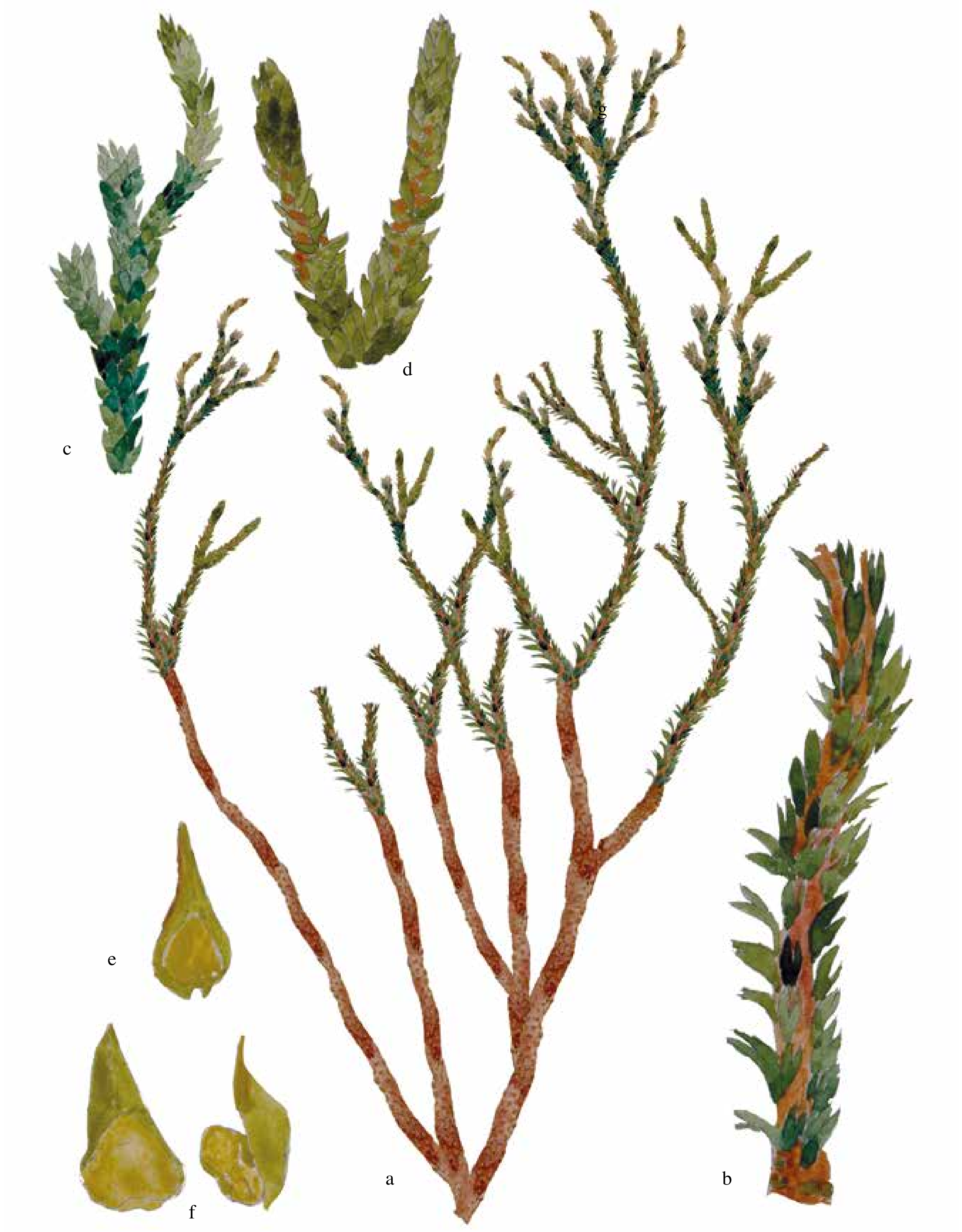
Remarks

Due to its inconspicuousness, *Selaginellites devonianus* is more difficult to recognise than the other clubmoss plant *Protolepidodendron leschii,* the latter being widespread in Lindlar. Only the whole plants and branches of the former can be classified reasonably well. It can therefore be considered a stroke of luck that at least one plate with some almost



***Selaginellites devonianus*. Branchlets and Fructations. Middle Devonian, Middle Eifelian**

1-3. Plate with several plants (Holotype LIND 131); 4. Sporophyll cone with shed bracts (holotype LIND 131); 5. Branchlet (LIND 192) All Coll. Wachtler, Dolomythos



***Selaginellites devonianus*. Reconstructions**

a. Whole plant with sterile and fertile parts (LIND 131, holotype); b. Basal branch with forked leaflets (LIND 131); c. Branch with unforked leaflets (LIND 131); d. Two sporophyll cones (LIND 131); e. Miicrosporophyll (LIND 131); f. Macrosporophyll, internal and lateral views (LIND 131) complete specimens (LIND 131) could be recovered, which has all the characteristics of the *Selaginellites* species occurring later in the Permian Triassic and also those of today's Selaginellas.

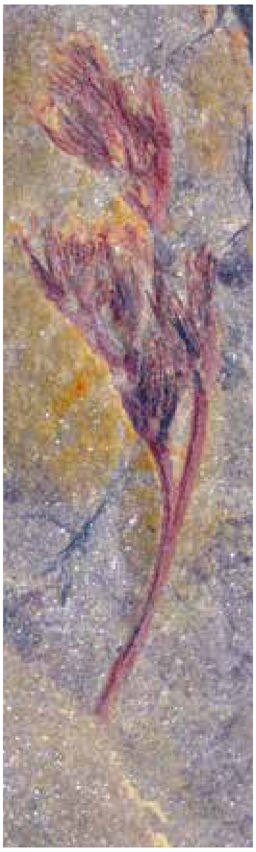
While the fossil finds of the Selaginellaceae now extend back to the Devonian, plants of this genus were widespread from the Early to Middle Carboniferous (Visean). In fact, they were assigned to different species such as *Selaginellites fraipontii, S. denticulata, S. leptostachys, S. macrophylla, S. primaeva* (Thomas, 1997), *S. zeilleri* (Halle, 1907) and *Selaginellites suessei* (Zeiller, 1906).

In particular, the Upper Carboniferous *Selaginellites gutbieri,* with branched trunks and tiny leaves, was common in the coal flora. Surprisingly, both isophyllous and anisophyllous species (with two different leaves) already coexisted at this time. Especially in the Triassic, these species occupied many niches, from tropical areas like the Early Middle Triassic Dolomites *(Selaginellites leonardii)* to the time of the Raibl cataclysm in the late Triassic (Carnic) *(Selaginellites perneri)* (Wachtler, 2016; Wachtler, 2021). In summary, this plant, which occurs in large numbers in the Raibl Formation, mainly in the Lienz Dolomites, gives us a robust insight into its growth, structure and fertile organs (Wachtler, 2021). In particular, its tiny, fertile and sterile leaves give the appearance of a bare plant, and only in the rarest of cases do the micro-leaves protrude so far that we can get a good overall picture of their development.

Sometimes, especially in *Selaginellites perneri,* the carpets of fallen sporophylls are found; this can also apply to *Selaginellites devonianus* where, in some locations of the holotype LIND 131, typical isolated sporophylls are clearly visible.

Notably, although fossilised Selaginellas have long been known, their remains have rarely been noticed or collected due to their inconspicuousness and fragility.

Today's Selaginellaceae belong to a widespread family of herbaceous lycopods that have adapted to different climate conditions and soil types and which today include about 750 subspecies (Wachtler, 2011). They can be distinguished from Lycopodium, which is also herbaceous, by their heterosporous sporangia, i.e. their different microsporophylls and



Moresnetia zalesskyi, an enigmatic seed-bearing plant from the Upper Famennian (Late Devonian), (Bocq Valley, near Dorinne (Namur, Belgium). Coll. Reinhard Gaipl, Senckenberg-Museum, Frankfurt.

It is till now difficult to establish the family to which Moresnetia belong. It could be one of the seed ferns widespread in the Carboniferous.

megasporophylls are found on the same strobilo, in contrast to the homosporous Lycopodium. Usually, they produce only small, barely perceptible leaves and also have bare branches, a characteristic that can also be observed in *Selaginellites devonianus.* It could even be the case that *Mosellophyton hefteri* (Schaarschmidt, 1974) from the Lower Devonian (Upper Lower Emsian) in the Olkenbacher Mulde (SE-Eifel, Rhineland-Palatinate, SW-Germany) – occurring sporadically in this location – is a precursor to the *Selaginellites.* It appears that this plant genus has changed little over nearly 400 million years, since its first appearance in the early Devonian to the present day.

Finally, even with the findings in Lindlar, the evolution of another large group of clubmoss plants, namely the *Sigillaria,* which were so dominant in the Carboniferous, remains unexplained. Their distinctive large sporangia should be easily recognisable, but their origin must likely have been somewhere else.

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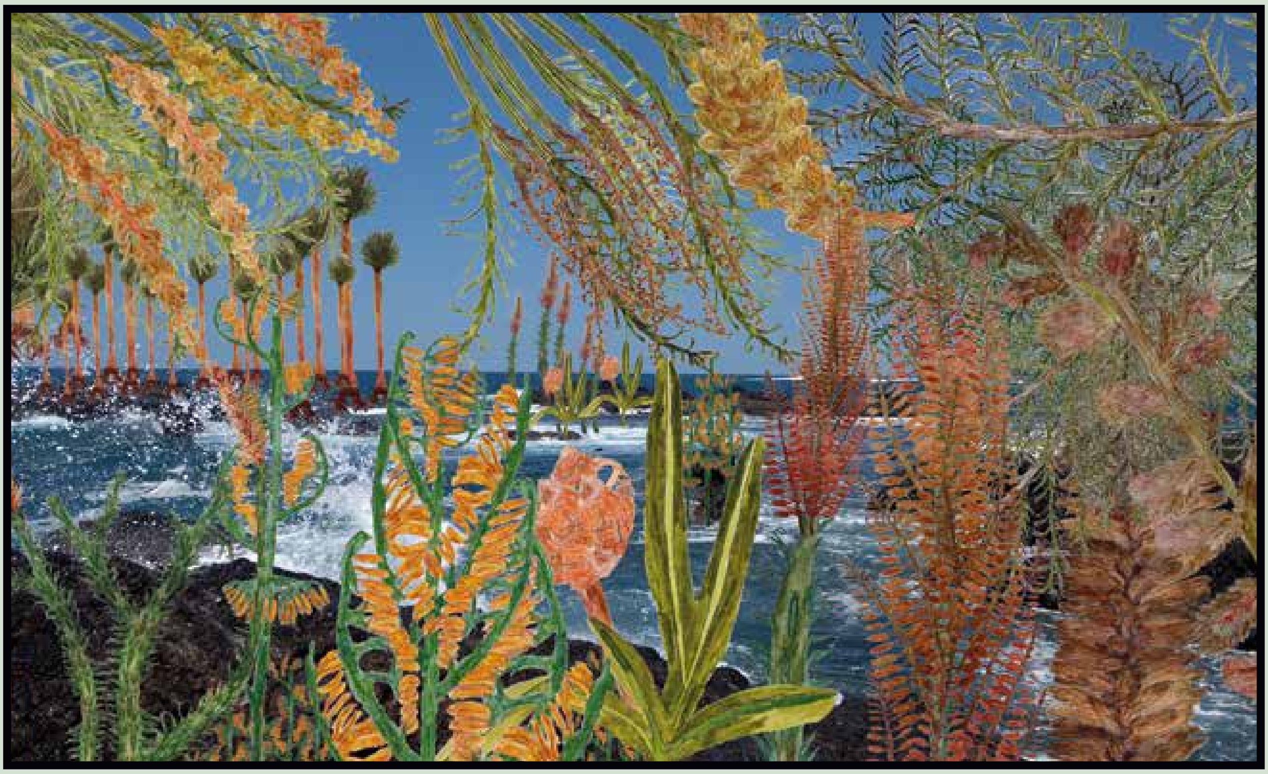

The Middle Devonian Flora Explosion

The Origins of Higher Plants

Edited by
Michael Wachtler and Nicolas Wachtler

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A fundamental task of paleobotany is to find theories about the origin and evolution of the crown groups of different plant stems. In the Carboniferous, we find fern families, lycopods and horsetails that still exist today; fully developed and recognisable gymnosperms can be seen from the Carboniferous-Permian transition onwards. Astonishingly, these gymnosperms reached an incredible level of development more than 300 million years ago, which makes it plausible that the splitting lines are to be found in the Devonian period. In fact, in the Middle Devonian, we encounter barely recognisable ancestors of these gymnosperms, such as conifers, gingkos or cycads, as well as archaic progenitors of the ferns, clubmosses and horsetails. Further back in the Lower Devonian, the boundaries become blurry, such that references to plant families existing today are hardly imaginable.

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