The Ferns in the Lower Jurassic

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Ferns played a substantial role in the Lower Jurassic period in the northern hemisphere. Interestingly, it is the ancestors of the Matoniaceae (*Phlebopteris angustifolia, Laccopteris goepperti),* which are now limited to a few relict zones, as well as the Dipteridaceae (*Thaumatopteris schenkii, Chlathropteris muensteriana, Dicytophyllum acutilobum, Sagenopteris nilssoniana*) occurring in the same areas in large numbers. *Otozamites brevifolius* and *Acrostichites princeps*, which are leptosporangiate ferns, are more difficult to classify. Another fern, *Thinnfeldia rhomboidales,* was often found alongside them in the landscapes. While usually associated with seed ferns due to the lack of convincing evidence of ovules, *Thinnfeldia rhomboidales* is likely to be placed in the large Schizaeales group owing to its distinct tropophyll and sporophyll fronds. Similarly, *Phialopteris heterophylla,* a small climbing fern, falls into this category as well. A precursor to Marattiales *Marattiopsis intermedia*, was widespread, whereas the tree ferns (*Cyatheites asterocarpoides)* were less common. The abundance of ferns found during this period allowed for the identification of fertile and sterile fronds. The primary objective is to expand our knowledge of the development of the Filicopsida at the Triassic-Jurassic boundary and address climate developments.

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The ferns in the Lower Jurassic, about 200 mio. years ago, of Southern Germany. The Matoniaceae were present with ***Phlebopteris angustifolia (***1) and ***Laccopteris goepperti*** (2). More numerous, however, were the Dipteridaceae with ***Dictyophyllum acutilobum*** (3), ***Clathropteris muensteriana*** (4), ***Sagenopteris nilssoniana*** (5). There were also other leptosporangiate fern groups such as ***Otozamites brevifolius*** (6) and ***Acrostichites princeps*** (7). Additionally, tree ferns like ***Cyatheites asterocarpoides*** (8) grew in this region. The Marattiales with ***Marattiopsis intermedia*** (9) and precursors of the Schizaeales like ***Thinnfeldia rhomboidales*** (10) were prevalent.

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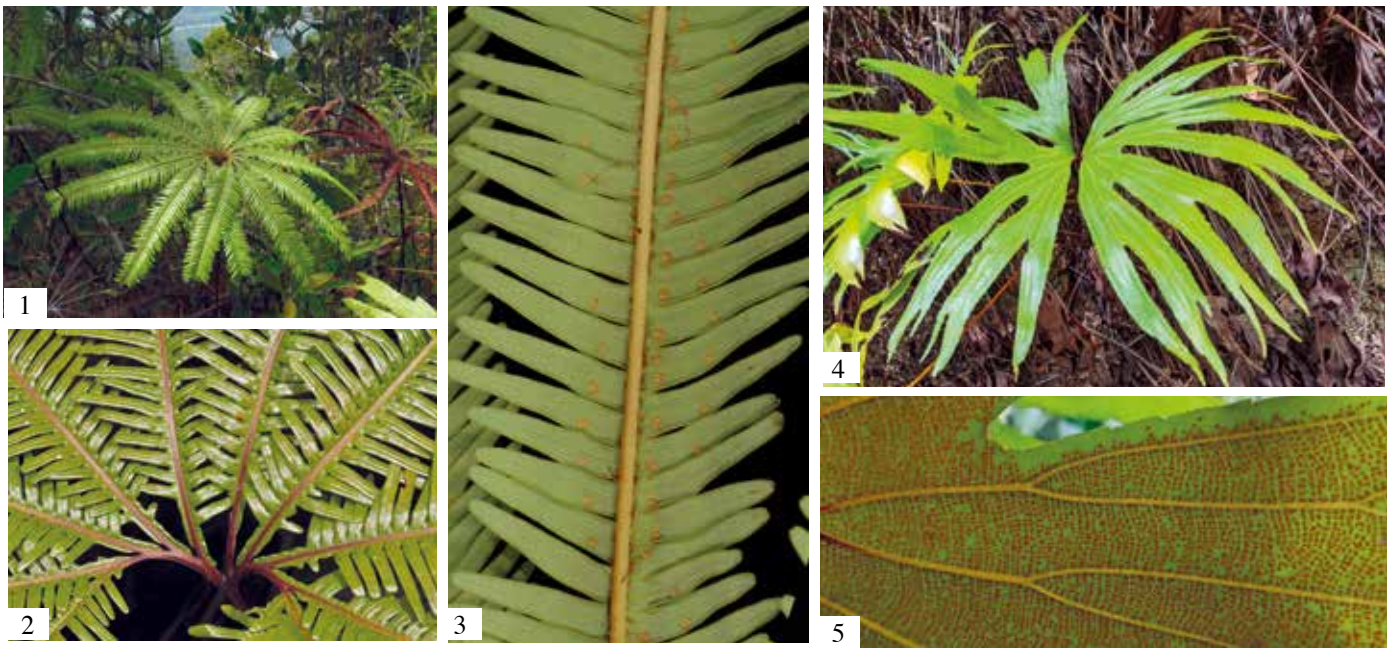
The ancestors of Matoniaceae and Dipteridaceae were present in the Triassic period, although they were rare. However, during the Lower Jurassic, there was a flowering period leading to the emergence of many new genera. As time progressed into the later Jurassic, these plants were gradually replaced by other species and began to fade into the background.

Today, Matoniaceae and Dipteridaceae play a minor role within the fern family and are primarily found in warm tropical and subtropical relict zones in Asia, Australia, and Polynesia, as well as in mountainous regions with sparse vegetation. Despite their limited distribution, these families are not commonly found. One distinguishing feature is their creeping rhizomes, from which fronds emerge either on a long petiole or in close succession without stems. Additionally, they often display a mesh-like pattern of side veins on their leaflets. The small sporangia of the Dipteridaceae are found scattered or densely covering the underside of the leaf, with spores housed within a ring-shaped annulus that catapults them when ripe. On the other hand, the genus *Matonia* features a few larger, semicircularly grouped sori on the underside of the leaves.

As with many fossil plants, the evolutionary history of the various fern families have only recently been extensively studied. The European Lower Jurassic sites play an outstanding role here. On the one hand, it was possible to clarify, based on findings from the Bayreuth area, that the fern *Sagenopteris,* which first appeared in the early Middle Triassic (*Sagenopteris keilmannii,* Wachtler, 2016; *Sagenopteris nadali,* Juárez & Wachtler, 2015), belong not to the seed ferns – as previously reported (Cittert & Morgans, 1999) – but to a genus close to the Dipteridaceae. The arrangement of the sporangia on the underside of the mesh-like fronds and the absence of ovules supports this reclassification.

Beginning in the Middle Triassic (Ladin) period, a precursor of the Dipteridaceae known as *Chiropteris* emerged. As we enter the Lower Jurassic, there were multiple divergences and a worldwide spread of this family. Through comparisons of the fertile fronds, it is evident that Matoniaceae (*Phlebopteris, Laccopteris)* and Dipteridaceae *(Thaumatopteris, Chlathropteris, Dicytophyllum, Sagenopteris*) coexisted, and they continue to thrive in the vegetation of tropical and subtropical landscapes in East Asia and around the Australian landmass.

This does not necessarily mean that all families are present in the fossil sites of the same age. Some lentils are richer in certain



1-3. *Matonia pectinata.* Plant and fronds with sori; 4-5: *Dipteris conjugata.* Fronds and base with sporangia (Source: Ferns and Lycophytes of the World).

Precursors of the Matonia and Dipteris ferns from the Triassic

1

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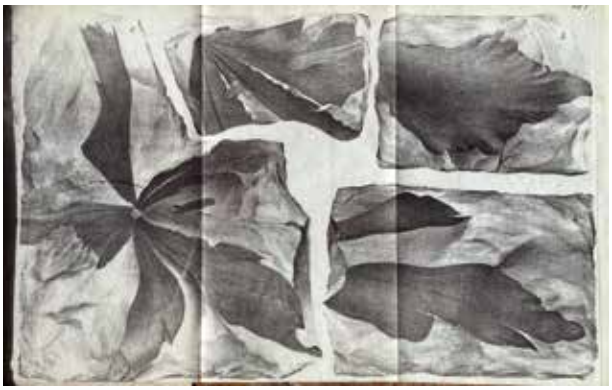
1-2. Sagenopteris keilmannii. Lower Middle Triassic (Anisian), Piz da Peres, Dolomites, Coll. Wachtler, Naturmuseum Südtirol

Chiropteris lacerata from the Erfurt-Formation, Middle Triassic (Illingen, Coll. Donà)

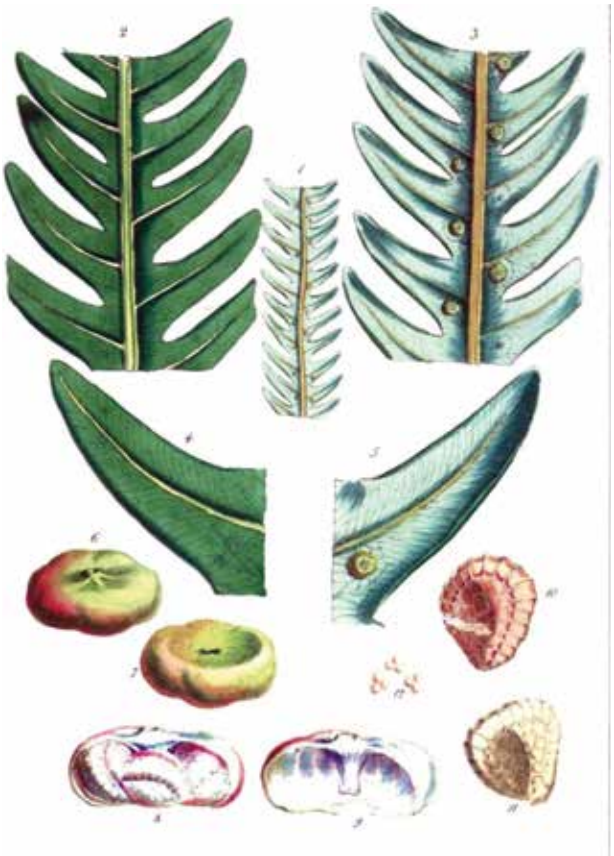


From Bronn, 1858: *Chiropteris digitata*, Middle Triassic, Lettenkeuper. First illustration of a Dipteridaceae, Archive Wachtler-Dolomythos-Museum

genera, while others are characterised by monocultures, influenced by varying sediments in different regions.
During the Lower Jurassic period, prominent genera included *Phlebopteris* (Brongiart, 1836), *Laccopteris* (Presl, 1838), *Dictyophyllum* (Lindley & Hutton, 1834), *Clathropteris* (Brongniart, 1828), *Thaumatopteris* (Goeppert, 1841), *Goeppertella* (Oishi & Yamasita, 1936), and *Hausmannia* (Dunker, 1846). The classification of *Camptopteris* (Presl, 1838) remains uncertain, potentially serving as a synonym of *Clathropteris* or *Dictyophyllum*. These ferns reached their peak in the Lower Jurassic but declined in significance towards the end of the Jurassic and into the Cretaceous period (Choo et al., 2016). The exact categorisation of all fern genera into Matoniaceae or Dipteridaceae is ambiguous, as many modern fern families share similar fertile properties. Notably, *Otozamites* (Braun, 1843) and *Achrostichites* (Göppert 1841) stand out due to their lack of mesh veins and typical pecopterid leaflets.

Progenitors of the Matoniaceae

Today, Matonia ferns consist of only two species (*Matonia pectinata, Matonia foxworthyi),* which are primarily native to Malacca, Borneo, and Sumatra. They are large terrestrial ferns with long petioles – some measuring a metre long. At the ends of these stems, there are hand-shaped fronds, sometimes resembling a broken wheel or a funnel, with a diameter of up to half a meter. The unique shape of the strikingly leathery, coarse leaflets is the result of a basal dichotomous bifurcation, where only the outer branch divides, while the inner branch becomes a one-sided leaflet, displaying similarities to the modern Dipteridaceae.
On the underside of the fronds are sori, covered by a shield-like indusium consisting of thick-walled cells, containing around 6 to 10 sessile or short-stalked sporangia. These sporangia have a strong annulus, which runs



Characteristics of the current species *Matonia pectinata.* The sporangia are united in sori on the underside of the fronds. After Franz Bauer, 1842: Genera Filicum, Coll. Wachtler, Dolomythos

Characteristics of the current species *Dipteris conjugata.* The sporangia are located on the underside of the fronds. Sometimes hair structures, so-called paraphysis, form from the stalk of the sporangia or between them from the receptacle (Reconstruction M. Wachtler).

Juvenile enrolled ferns

1-5. It is difficult to draw any conclusions about their genus from the curled-up juvenile ferns (1-3. Coll. Hauptmann, 4-5. (PECH 32, Coll. Wachtler, BOCK 35 Ex Coll. Friess, Coll Dolomythos).

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***Phlebopteris angustifolia*. Fronds. Lower Jurassic (Hettangian)**

1. Completely preserved plant with fertile fronds (BOCK 01); 2-3. Detail of the pinnules and veins (BOCK 05, BOCK 08, BOCK 10, Unternschreez, Sandpit Bocksrück, Ex-Coll. Silberhorn, Coll. Wachtler-Dolomythos); 5. Sterile frond (PECH 212, Pechgraben, Coll. Wachtler, Dolomythos)

Phlebopteris angustifolia. **Fronds. Lower Jurassic (Hettangian)**

1. Fertile frond (Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 2. Detail of the basal frond branches (BOCK 18, Unternschreez, sandpit Bocksrück, Ex-Coll. Silberhorn, Coll. Wachtler-Dolomythos); 3. Juvenile enrolled fern (PECH 471); 4. Fertile frond (PECH 69); 5-6. Fertile pinnule and detail of the sporangia (PECH 10); 7-8. Fertile leaflets, upper side (PECH 02, PECH 13, Pechgraben, Coll. Wachtler, Dolomythos)

in an oblique ring shape over a large part of the sporangium, enclosing the spores (Fukarek, 1992).
Two Matonia ancestors, *Phlebopteris angustifolia* and *Laccopteris goepperti,* are found relatively frequently in the Hettangian of Upper Franconia due to the different forms of their sori.

Phlebopteris Brongniart 1836

1836 *Phlebopteris polypodioides* Brongiart Hist. veget. foss. Tab. 83. Fig. 1

Phlebopteris angustifolia

1823 *Gutbiera angustiloba* Presl in von Sternberg: p. 116, pl. 33, figs. 13 a–e

1843 *Andriana baruthina* Braun p. 42, pl. 3–4, 6, 12, pl. 10, figs. 1–3

1867 *Gutbiera angustiloba* Presl-Schenk p. 64, pl. 18, figs. 5–10

1867 *Andriana baruthina* Braun Schenk p. 87–89, pl. 21, figs. 1–7, pl. 22, fig. 1

1867 *Andriana baruthina* Braun var. *remota;* Schenk, p. 87, pl. 24, fig. 1

Historically, Presl (1823) and Braun (1840) separated this relatively common fern into the genera *Andriana (A. baruthina,* Braun 1840) for sterile fronds and *Gutbiera (G. angustiloba,* Presl in Sternberg, 1838) for fertile fronds. Schenk also maintained this distinction. In the end, the name *Phlebopteris angustifolia* prevailed for this characteristic fern from the precursor group of the Matoniaceae in the European Lower Jurassic.

Description

Whole plant. The plant features around 8 to 12 fronds, measuring approximately 25 cm in length. It is relatively slender and narrows towards the tip, emerging from a strong petiole. The fronds are only weakly fused to each other basally. The individual pinnules, which reach a size of barely 1 cm, exhibit weak dichotomising veining due to their leathery nature.
Fertile fronds: They are similar to the sterile ones, with a distinguishing feature being the grouped sori with a pronounced depression in the middle only on the underside. There are usually 6 to 10 fertile fronds, with around 8 sporangia in the respective inner courtyards. These sporangia

From Schenk, 1867. *Andriana baruthina (Phlebopteris angustifolia)* Taf. XXI, Fig. 1-8

From Schenk, 1867. Pl. XXIV, Fig. 1. *Andriana baruthina*; Fig. *Laccopteris goepperti,* fig. 2-5. *Laccopteris goepperti; Fig. 6-10. Laccopteris muensteri.*

It can be assumed that both *Andriana baruthina* and *Laccopteris muensteri* belong to the same species *(Laccopteris goepperti)*. The representation of the sori and sporangia indicate this. It is probably a precursor group of the Matonia ferns.

The fern *Phlebopteris angustifolia*. Lower Jurassic (Hettangian) Reconstructions

a. Whole plant; b. Sterile frond; c. Detail of the leaflets; d. Fertile frond; e. Fertile leaflet, underside; f. Fertile leaflet, upper side; g. Closed and open sorus with sporangia

consist of a strong, almost circular annulus with a predetermined breaking point that releases the spores in the catapult mechanism when ripe.

Laccopteris Presl 1838

The example of *Laccopteris* confirms the significance of understanding the sori and sporangia in the classification of ferns. The original description of this genus is based on poorly preserved sterile remains of fern pinnules, as documented by Presl in Sternberg in 1838 (*Laccopteris elegans)*, which are currently housed in the Palaeontological Museum in Munich. There has been some uncertainty regarding the exact location of the specimen's discovery, with indications pointing towards Reundorf near Bamberg, rather than Steindorf as initially stated by Presl. Despite subsequent attempts to reclassify it as *Thaumatopteris brauniana* (Popp, 1863), the arrangement of the sori disproves this hypothesis.
This genus was legitimised through extensive descriptions by Schenk (1867), whereby he correctly differentiated between *Laccopteris elegans* and introduced the new species *Laccopteris goepperti* (Plate XXIII + Plate XXIV, Figs. 2–5) and *Laccopteris muensteri* (Plate XXIV, Figs. 6–10) described and illustrated.
Schenk's excellent illustrations showcased a distinct sori structure, resembling that of *Phlebopteris* from the precursor group of Matonia ferns rather than Dipteridaceae. Additionally, he depicted an *Andriana baruthina* on Plate XXIV, which was first described by Braun in 1843. Amidst the confusion, *Laccopteris goepperti* (Presl, 1838; Schenk, 1867) emerges as the most appropriate designation, with *Laccopteris muensteri* likely serving as a synonym for the former.

Laccopteris goepperti Popp 1863

1838 *Laccopteris elegans* Presl in Sternberg, Flora der Vorw. II. pag. 115. Tab. 32. Fig. 8. a. 1-3. b. c

1841 *Laccopteris braunii* Göppert, Gatt. foss. Pfl. Lief. 1-2. p. 7. Pl. 5. Fig. 1-7

1841 *Laccopteris germinans* Göppert, Gatt. foss. Pfl. Lief. 1-2. p. 9. Tab. 6. Fig. 1-12

1843 *Andriana baruthina* Braun in Münster, Pl. X Fig.1-4

1863 *Thaumatopteris brauniana,* Popp. Neues Jahrb. Mineral. Geol.

1867 *Thaumatopteris brauniana* Schenk Pl. XVIII, Fig. 1-3. Tafel. XIX, Fig. 1

1867 *Laccopteris goepperti* Taf. XXIII. Fig. 1-12. Pl. XXIV. Fig. 2-5

1867 *Laccopteris muensteri* Taf. XXIV. Fig. 6-11. Pl. XXV. Fig. 1-2

Laccopteris goepperti. Pécs-Fünfkirchen, Hungary, Ex-Coll. Perner, Coll. Wachtler, Dolomythos Innichen

Description

Plant: It features 5 to 9 fronds about 30 to 50 cm in length, sprouting from a strong stemlet. The individual lateral leaflets can reach lengths of up to 15 cm, with widths ranging from 1 to 2 cm, and possess entire edges. These leaflets are arranged broadly along the axis, ending in a rounded shape, with a prominent central vein. Delicate mesh-like nerves branch off from this central vein, often barely visible.

The fern *Laccopteris goepperti* . Lower Jurassic. Reconstructions
a. Whole plant; b. Fronds; c. Fertile frond part; d. Sterile pinna; e. Fertile pinna

Fertile parts: The pinnulas that bear sporangia are stockier compared to the sterile ones due to the lateral curling of the leaflets. The median vein stands pronounced in these pinnulas, while the lateral nerve is less visible than in the sterile ones. The sori are located on the underside of the pinnula segments, arranged in two rows from loose to densely packed. Each of the approximately 8 to 10 sporangia consist of a multi-membered, ring-shaped annulus that does not completely close, containing circular spores.

Remarks

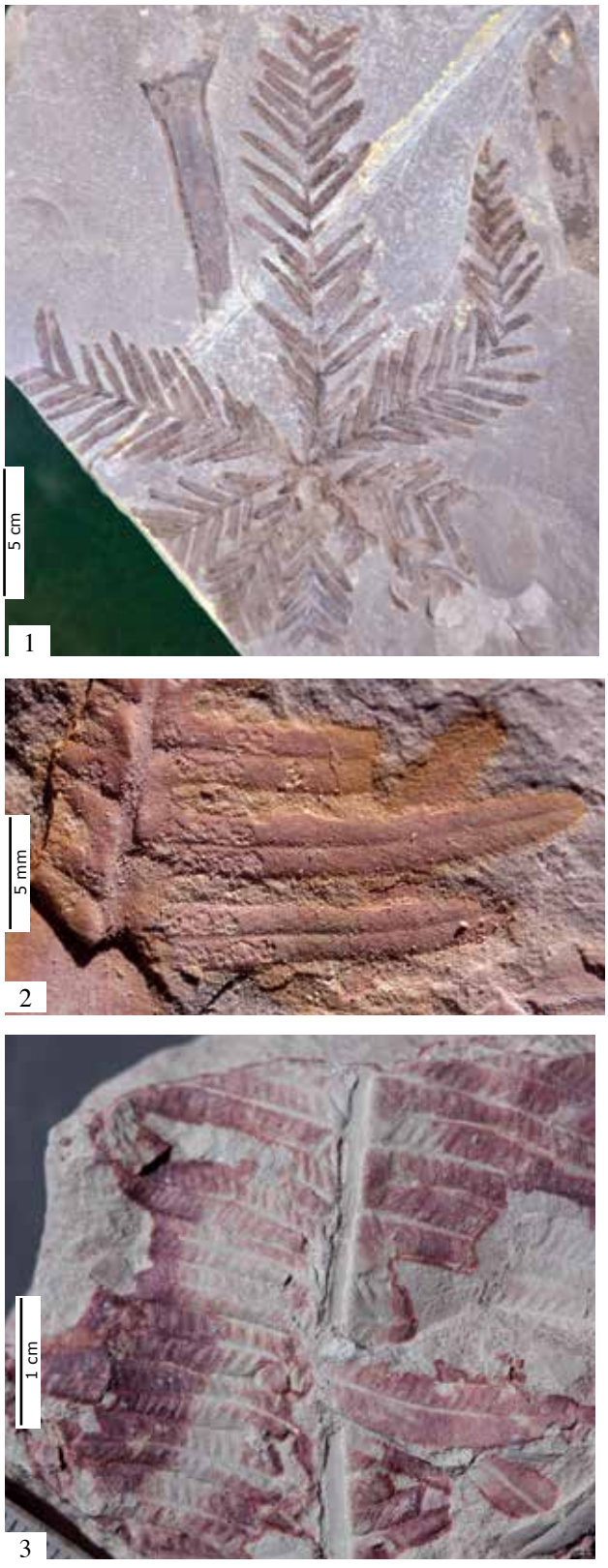
Phlebopteris and *Laccopteris* are considered to be the ancestors of Matonia, not Dipteridacea, based on the arrangement and structure of their sori. *Phlebopteris* is more commonly found, with *Phlebopteris angustifolia* standing out for its leathery pinnules and prominent clusters of sori. Another species, *Phlebopteris muensteri*, has been described (Schenk, 1867), but due to its sporangia arrangement, it is classified under the Dipteridacea and requires a different genus name. *Laccopteris* is rarely found in Upper Bavaria, appearing to be more characteristic of plants from Pécs in Hungary.

Precursors of the Dipteridaceae

The fern genus Dipteris, which is prevalent in tropical to subtropical regions spanning from East Asia to Australia, Samoa, and New Guinea, consist of seven species. Among these, *Dipteris conjugata, Dipteris chinensis,* and *Dipteris novoguineensis* are the most well-known. These species are characterised by their creeping, bristle-like rhizomes.

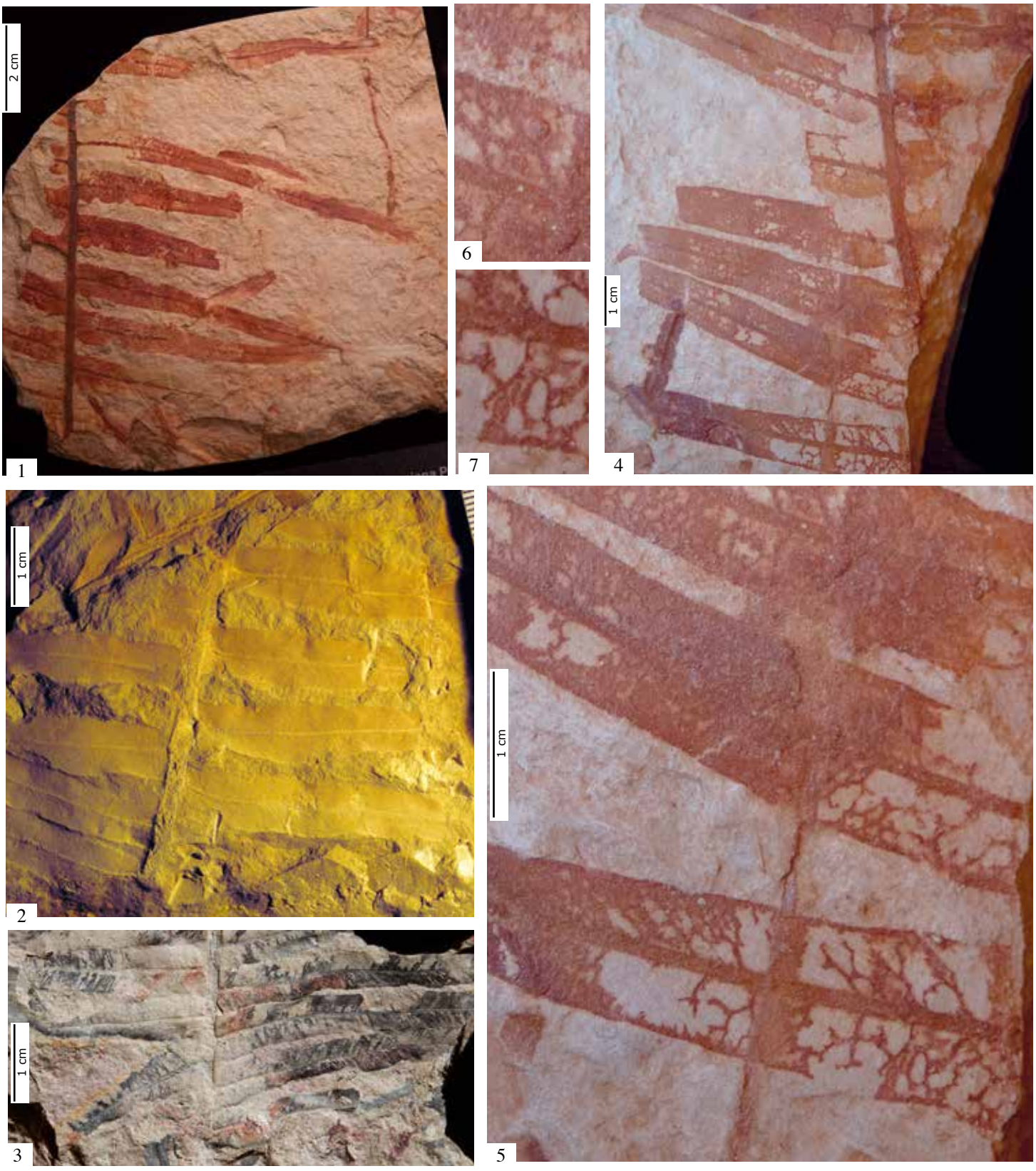
The leaves or fronds of Dipteris are similar to those of Matonia, being divided dichotomously with the central section reaching the deepest point. The small, isolated sporangia of Dipteris, in contrast to the distinctive sori of the Matonia ferns, are found scattered on the underside of the leaves. The mesh-like venation of the veins is a unique characteristic of Dipteris.

The separation of Matoniaceae and Dipteridaceae into distinct families during the Lower Jurassic period suggests an earlier split between the two. However, there is a



***Laccopteris goepperti.* Frond**

1. Juvenile plant (Pechgraben, Coll. Stapf, Nierstein); 2. Pinna (PECH 148, Pechgraben, Coll. Wachtler; 3. Fertile pinnules (BOCK 33, Unternschreez, Ex.Coll. Silberhorn, Coll. Wachtler)



***Laccopteris goepperti.* Lower Jurassic. Hettangian. Fronds**

1. Frond (Unternschreez, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 2. Frond (Unternschreez, Coll. Meyer, Lichtentanne; 3. Frond Ex. Coll. Silberhorn, Dolomytos-Museum (PECH 711); 4-7. Frond and detail of the sporangia (Unternschreez, sandpit Bocksrück, Ex-Coll. Hauptmann, Coll. Tischlinger)

lack of evidence linking the Carboniferous and Permian periods.
The relevant genera *Dictyophyllum, Clathropteris, Thaumatopteris*, and the enigmatic *Sagenopteris* found in the Lower Jurassic of Europe can be distinguished from one another.

Dictyophyllum Lindley & Hutton 1834

1834 Dictyophyllum rugosum Lindley et Hutton, Mitteljura Yorkshire

Dictyophyllum was originally described by Braun in 1843 and 1847 as *Diplodictyon (acutilobum* and *D. obtusilobum)* before Schenk adopted the name *Dictyophyllum,* which was coined in 1834 by Lindley and Hutton.

Dictyophyllum acutilobum

1843 *Diplodictyon obtusilobum* Braun in Münster, Beitr. VI. p. 14. Tab. 13. Fig. 11-12

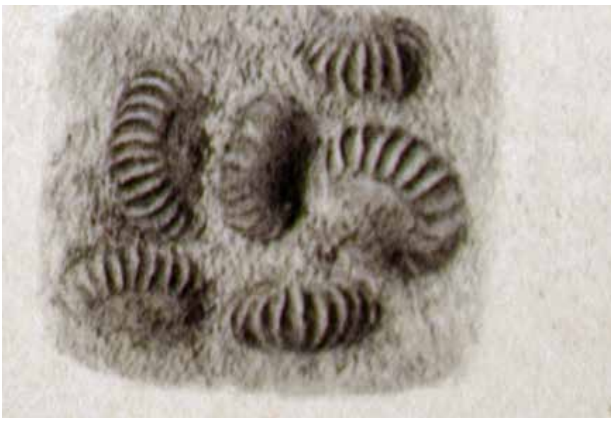
1847 *Diplodictyon acutilobum* Braun, Flora, p. 83

1867 *Dictyophyllum obtusilobum* Schenk Pl XVI. Fig. 1, a. b

1867 *Dictyophyllum acutilobum* Schenk Pl IX. Fig. 2-5. Tafel. XX. Fig. 1

The fern genus *Dictyophyllum*, considered a precursor group of the Dipteridacea, existed from the Upper Triassic to the Lower Cretaceous in various tropical and subtropical regions. Notably, *Dictyophyllum nilssoni* from Palsjö in Scania, Sweden (Nathorst 1876, 1906) and *Dictyophyllum exile* are extensively studied species; they are well-known for their prevalence in discoveries and being

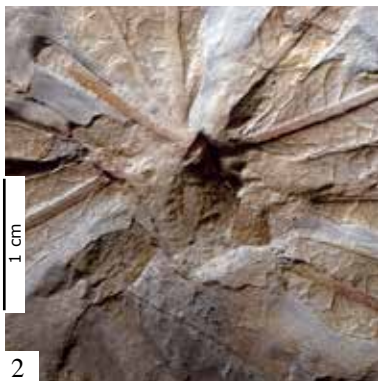
From August Schenk, 1867, Pl. 16. *Dictyophyllum obtusilobum* and Pl. 20 *Dictyophyllum acutilobum*



From Alfred Gabriel Nathorst 1867, 1906: Pl. 2-3 *Dictyophyllum nilssoni;* Pl. 4 *Dictyophyllum exile,* Pl. 6, Fig. 24, *Dictyophyllum acutilobum,* sporangia, Lower Jurassic Hör, Schweden

The fern *Dictyophyllum acutilobum*. Lower Jurassic. Reconstructions

a. Whole plant; b. Sterile frond; c. Fertile frond; d. Sterile pinna; e. Fertile pinna f. Sporangia with spores, annulus and paraphysis appendages

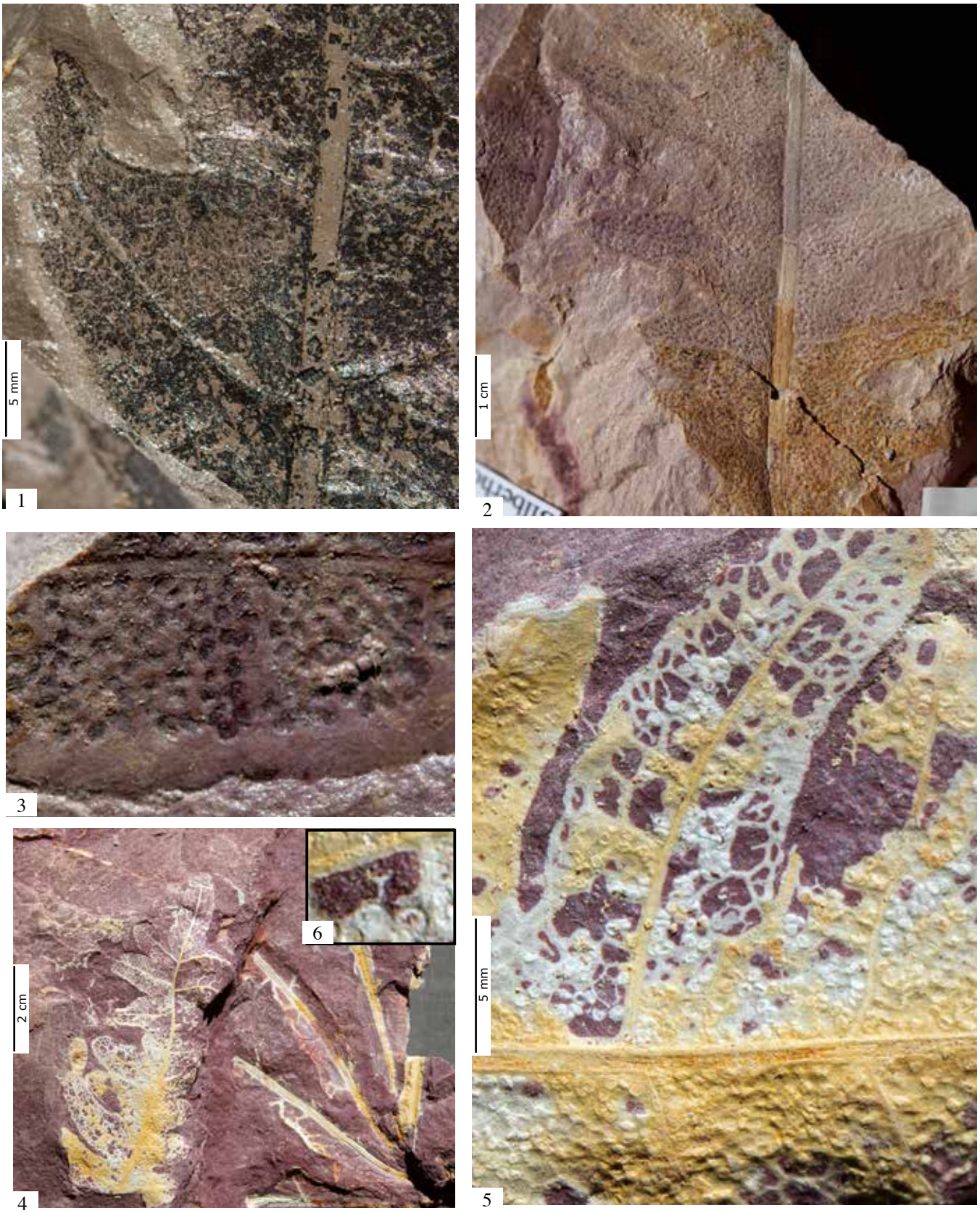


***Dictyophyllum acutilobum*. Lower Jurassic. Hettangian. Fronds**

1-3. Complete plant and detail of the fronds (Pechgraben, sandpit Dietz, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 4. Part of a frond (PECH 93, Coll. Wachtler, Dolomythos Innichen

Dictyophyllum acutilobum. **Lower Jurassic. Hettangian. Fronds**

1. Juvenile plant with root area; 2. Complete, juvenile plant; 3-4. Fronds with long pinnules; 5-6. Side view of the plant (Pechgraben, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth)



***Dictyophyllum acutilobum*. Lower Jurassic. Hettangian. Fronds**

1. Fertile pinna (PECH 40, Pechgraben, Coll. Dolomythos); 2-3. Fertile pinnules (BOCK 11); 4-6. Basal frond part with individual leaflets and detail of the sporangia and the (6) paraphysis (BOCK 19, Unternschreez, Sandgrube Bocksrück, Ex-Coll. P. Silberhorn, Coll. Wachtler, Dolomythos Innichen)

Juvenile plant of *Dictyophyllum acutilobum* (Pechgraben, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth)

found in almost complete fronds (Nathorst, 1906; Cittert et al., 2020). These species have existed in Sweden as early as the late Triassic (Rhaetian) period. *Dictyophyllum acutilobum,* in particular was widespread in Central Europe.

Description

Plant: The root system of this plant exhibits poor development, giving rise to up to 20 individual fronds that display a striking peacock wheel-like appearance emerging from a nearly stemless base. When fully grown, these individual fronds can reach lengths of 30 to 50 cm. They are connected at the axis to the full leaflet side and irregularly fused with the other leaflets. The individual pinnules taper to a point and have slightly wavy edges. The median nerve of the individual pinnules is well-developed, with resulting secondary nerves that fan our irregularly, with sometimes stronger and weaker veins, creating a mesh-like pattern. Most pinnules have a maximum width of 5 cm, although some exceptions exist where slender side feathers can reach lengths of up to 20 cm. These variations fall within the expected range for this plant species.

Fertile parts: The small sporangia are irregularly distributed on the underside of the blade, extending up to the tip of the pinnula. Due to their dense clustering, the circular ribbed annulus ring – which is not completely closed – within which the individual spores are located, is rarely visible. Unique hair structures, known as paraphyses, grow from the stalk of the sporangia or between them from the receptacle. The exact function of these structures remains unclear.

Remarks

Dictyophyllum is a unique species that stands out among Dipteris precursors due to its almost completely stemless nature. Unlike other species, *Dictyophyllum* typically lacks strong and long petioles from which individual fronds emerge. One key distinguishing feature of *Dictyophyllum* from *Clathropteris meniscioides* is the absence of rectangular segments on the fronds, as well as the presence of pointed individual pinnules. Additionally, the rounded sporangia with paraphyseal appendages, some of which are well-preserved as fossils, are characteristic of *Dictyophyllum.*

The extent to which the Middle European species *Dictyophyllum acutilobum* differs from the Swedish *Dictyophyllum nilssoni* and *Dictyophyllum exile* is currently unclear. Further clarification can only be achieved as more information on spore details become available. It is worth noting that of the two species described around Bayreuth, *Dictyophyllum acutilobum* is expected to remain distinct while *D. obtusifolium* will likely be considered a synonym due to their similarities.

Clathropteris Brongniart 1828

The fern genus *Clathropteris,* named by Brongniart (1825), has a rich history. Brongniart first described *Filicites meniscioides* from the Rhaetian of Hoer in Sweden, which he depicted in 1828, and later in 1849, he merged the genera *Camptopteris platyphylla* to create *Clathropteris meniscioides.*

It is assumed that a slightly different species of *Clathropteris* exists in Bavaria, as evidenced by *Camptopteris muensteriana*,

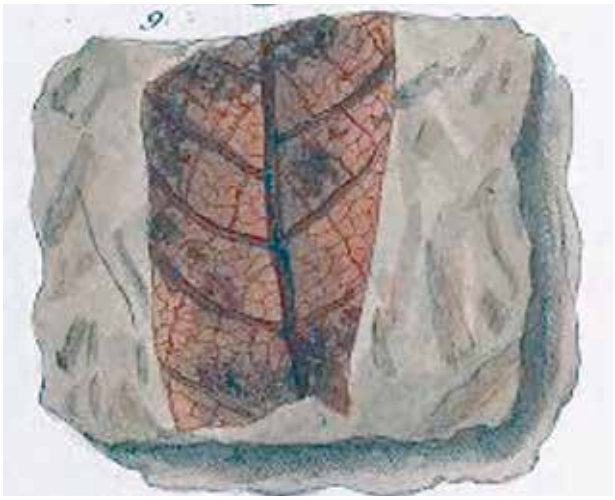
illustrated by Presl in Sternberg in 1838, which may now be referred to as *Clathropteris muensteriana* (Pag. 168, Pl. XXXIII, Fig. 9). Even Schenk, in 1867, used this name.
Clathropteris was probably a cosmopolitan species from the Late Triassic to Jurassic periods. Specimens have been found not only at the original description site of Hör in Sweden and the sites known since the early 19th century in Bavaria but also in Pécs in Hungary, Cerro Bayo in Argentina, and even Antarctica (Bomfleur & Kerp, 2010b). The fern has also been found in North America (New Mexico, Arizona) (Ash, 1970), Svalbard, Japan, Malaysia, and China (Choo et al., 2016). The fern's frequency, appearance, and fertile parts are well documented due to its abundant occurrence in various locations around the world.

Clathropteris muensteriana Presl in Sternberg 1838

1825 *Filicites meniscioides* Brongn., p. 218; pl. 11
1828 *Clathropteris meniscioides* Brongn., p. 62
1838 *Camptopteris muensteriana* Presl in Sternberg, Flora der Vorw. II. p. 168. Tab. XXXIII. Fig. 9.
1867 *Clathropteris muensteriana* Schenk Taf. 17; Taf. 16

Description

Plant: The sturdy stalk of this plant produces a plurality (8–12) of single, fan-shaped fronds that are interconnected at the base. The leaves are characterised by strong lateral nerves that regularly branch off from the central rhachis. These nerves divide the leaves into rectangular fields, which are then interconnected like a mesh by delicate veins. As the fronds narrow towards the tip, the rectangular segments become smaller, giving the leaves a slightly toothed appearance along the edges. The individual side fronds can reach lengths of 30 to 45 cm and a width of 10 cm.
Fertile fronds: The small sporangia (about 0.2 to 0.5 mm in diameter) are distributed unevenly on the underside of the pinnules, with no apparent connection to the rectangular main veins, showing a tendency to be arranged towards the edge of the frond. The spores are enclosed within a ring-like annulus that is not completely closed and released in large numbers when mature.

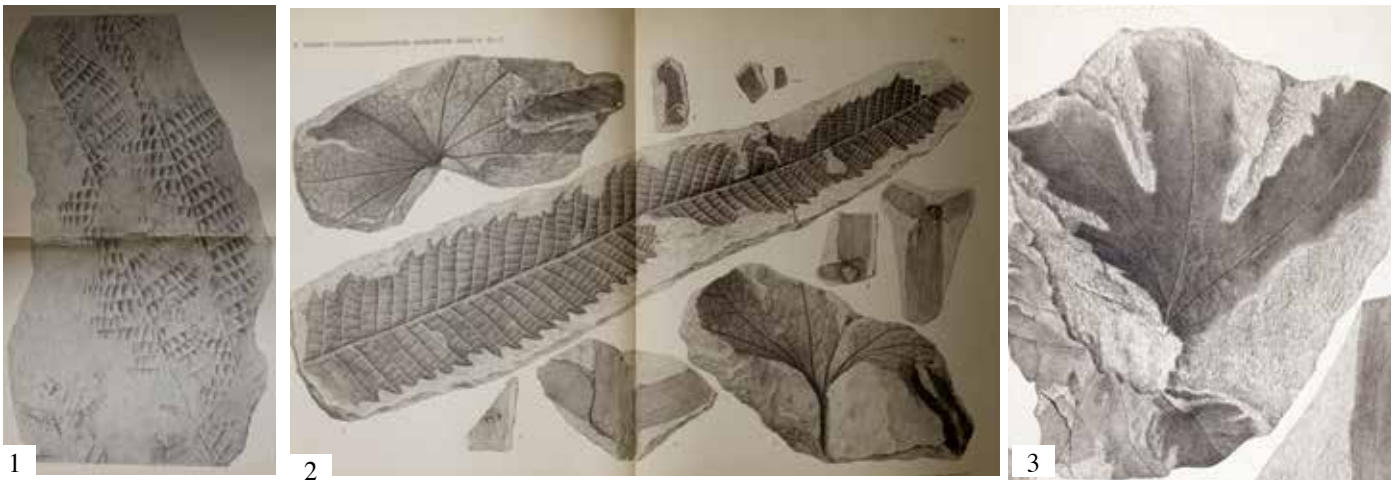


From Presl in Sternberg, 1838 *Camptopteris muensteriana,* Taf. XXXIII, fig. 9. The fossil comes from Strullendorf near Bamberg. The correct name should be *Clathropteris muensteriana.*

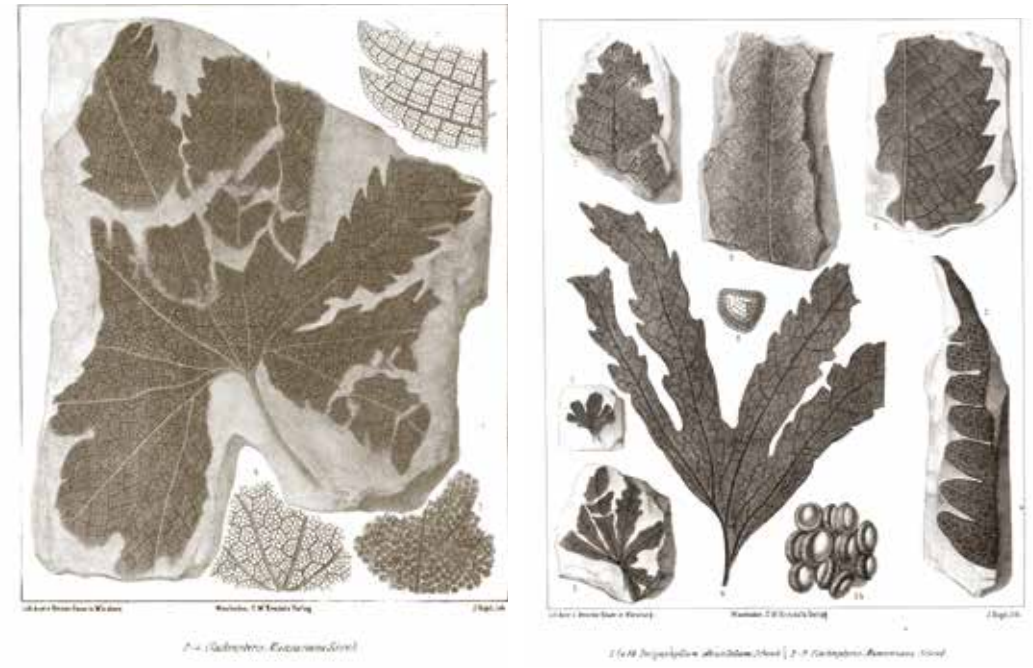
Clathropteris muensteriana, juvenile frond, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth

Remarks

In 1906, Nathorst extensively studied the plant's structure, including detailed descriptions of its root system. The horizontal and repeatedly forked roots of this plant are noteworthy.
It is astonishing that plant families began to spread globally from the Upper Triassic period onwards, despite their absence in previous eras. The reasons for this phenomenon remain unclarified. The fern spores were



Clathropteris meniscioides. 1. After Nathorst, 1906, the holotype of Brongniart from Hoer (Bossagrafven) in Scania (Sweden); 2. Adult and juvenile specimens; 3. Juvenile frond (Hoer)



From Schenk 1867: Left Pl. 17, *Clathropteris muensteriana* with detail of the small sized sporangia; Right Pl. 16. *Clathropteris muensteriana* with enlarged sporangia

likely able to travel long distances through water and wind more easily than the relatively heavier seeds of gymnosperms. Similar distribution patterns can be observed in the northern hemisphere.

The distribution range of conifers such as *Swedenborgia* and *Podozamites* extends from Europe to China, although they did not manage to reach the southern hemisphere. On the other hand, the Dipteridaceae and Matoniaceae families are prominently located in the southern hemisphere, along with araucarias, which were abundant in the Permian and Triassic periods in the northern landmasses.

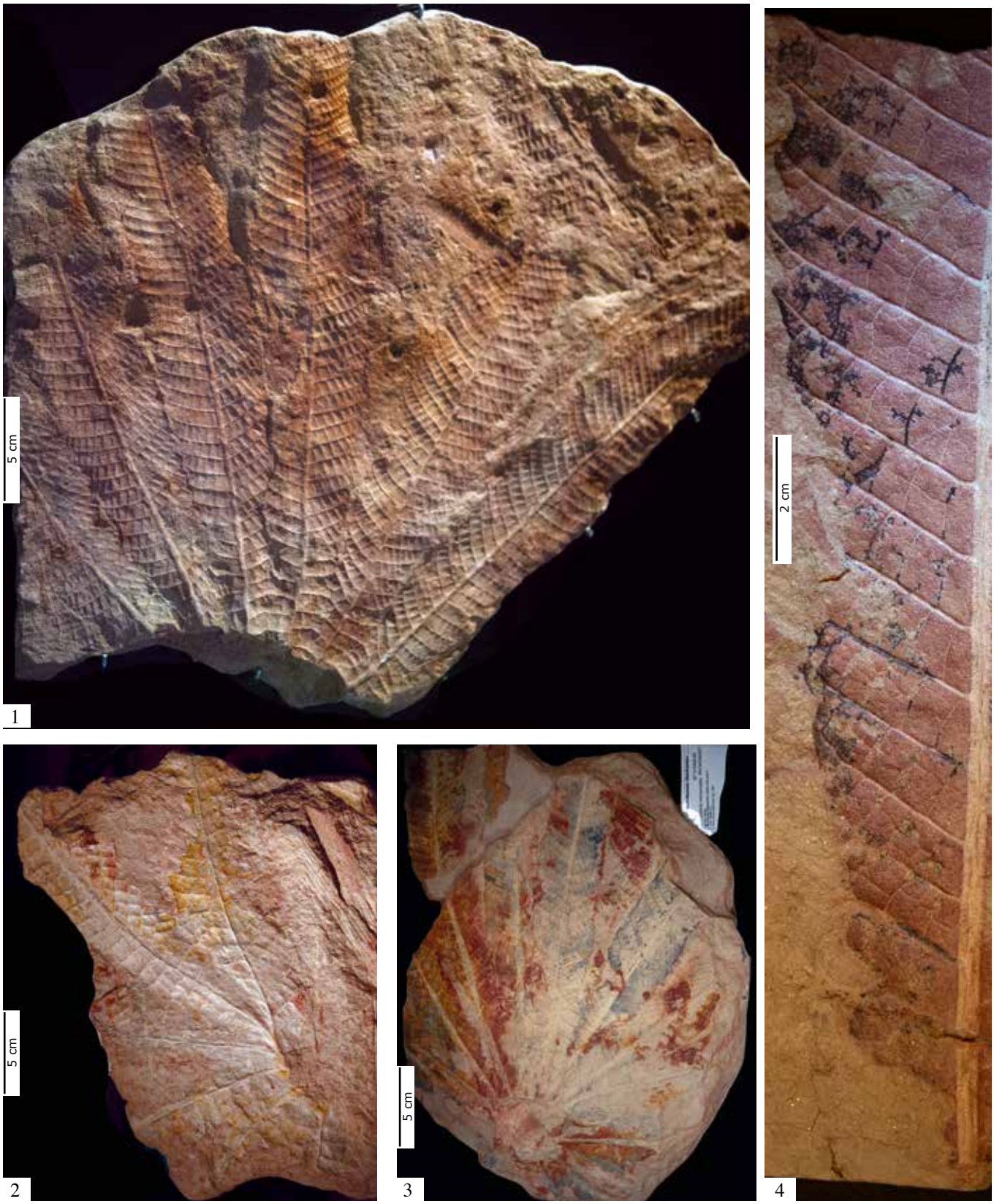
Thaumatopteris Göppert 1841

Within the diverse Lower Jurassic fern community of the Dipteridacea progenitors, a notable genus emerges: *Thaumatopteris.* It was first described superficially as *Thaumatopteris muensteri* by Göppert in 1841. Subsequently, this genus gained further recognition through the work of Swedish palaeobotanist A. G. Nathorst in 1907. Nathorst's discoveries, especially from Stabbarp, led to the introduction of the new species *Thaumatopteris schenkii.*

Upon closer examination, it became evident that *Thaumatopteris schenkii* exhibited

The fern *Clathropteris muensteriana*. Lower Jurassic. Hettangian. Reconstructions

a. Juvenile and adult whole plant; b. Single frond; c. Part of a sterile frond; d. Fertile frond part; e. Detail of the sori



Clathropteris muensteriana. **Lower Jurassic. Hettangian. Fronds**

1-3. Whole plant (Pechgraben, sandpit Dietz, all Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 4. Detail of a frond (Pechgraben, sandpit Dietz, Ex-Coll. Hauptmann, Coll.Tischlinger, Stammham)

***Clathropteris muensteriana*. Lower Jurassic. Hettangian. Fronds**

1-2. Complete frond (BT 014981.00, Sandpit Dietz, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 3. Detail of a fertile frond (Pechgraben, SandpitDietz, Ex-Coll. Hauptmann, Coll. Tischlinger, Stammham)

***Clathropteris muensteriana.* Lower Jurassic. Hettangian. Fertile Fronds**

1-2. 1-2. Fertile frond with the rectangular fields littered with small sporangia (Pécs, Hungary, Ex-Coll. Perner, Coll. Wachtler, Dolomythos)

significant differences in the structure and arrangement of sori and sporangia. Some characteristics aligned more closely with Matonian precursors (*Phlebopteris* and *Laccopteris)*, while others bore resemblance to modern Diptericadacea.

Nathorst's interpretation (1907) positioned *Thaumatopteris* as a genus akin to Dipteris ferns, characterised by numerous small sporangia irregularly distributed on the underside of fronds. *Thaumatopteris brauniana* (Popp, 1863; Schenk, 1867) was consequently reclassified as the fern *Laccopteris goepperti. Thaumatopteris schenkii*, on the other hand, retained its classification due to distinctive mesh veining of small pinnules and species-typical sporangia. However, it remains a rarity in the sand pits of Upper Bavaria.

Thaumatopteris schenkii Nathorst 1907

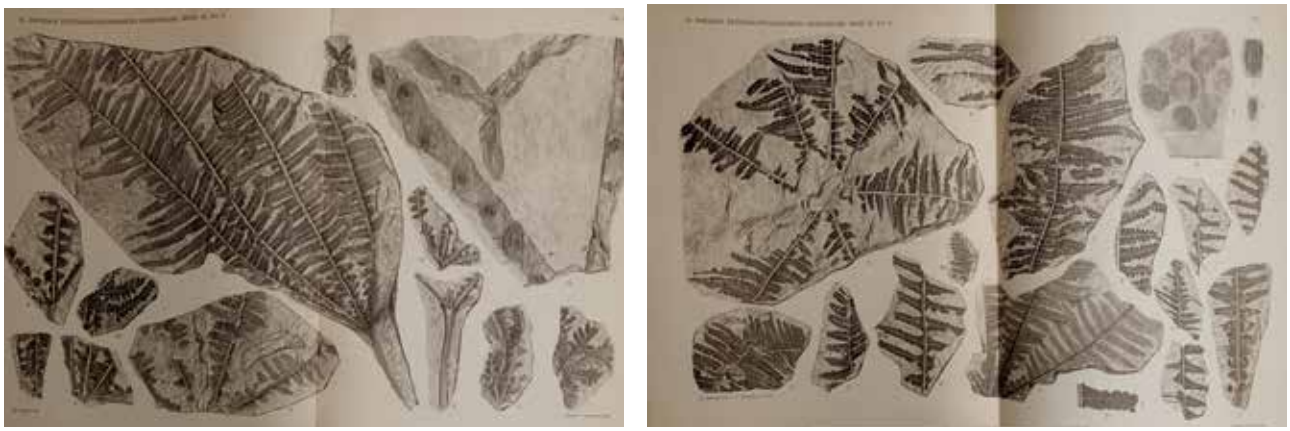
1841 *Thaumatopteris muensteri* Göppert, Gattungen fossile Pflanzen. Taf. I. fig. 1, Taf. II. Fig. 1-6.

1876 *Thaumatopteris brauniana,* Nathorst, p. 30, Taf. 8 fig. 1

1907 *Thaumatopteris schenki* Nathorst, Taf. 1 fig. 1-11, Taf. 2, fig. 1-18

Description

Plant: The fern has a long-stalked base, giving rise to seven to 10 individual branches at the same height. The pinnately segmented leaves, though occasionally fused, exhibit a gradual size progression from base to tip. The pronounced midrib contrasts with the subtle main vein of pinnules, barely noticeable and irregularly adorned with a faint mesh vein.



From Nathorst, 1907. *Thaumatopteris schenkii* Tafel 1 + 2. Helsingborg, Palsjö, Sweden

Fertile parts: The pinnules appear the same as the sterile ones, with sori located on the underside of the leaflet segments from loose to densely packed. The multi-membered, ring-shaped annulus encloses sporangia within its inner courtyard.

Remarks

The fern genus *Thaumatopteris* is relatively rare in Bavaria compared to its frequency in Swedish localities, particularly *Thaumatopteris schenkii* (Nathorst, 1907). The mesh veining of the pinnules is weak and far less pronounced than in *Dictyophyllum* or *Chlathropteris*. A specimen described by Schenk (1867) as *Laccopteris (Thaumatopteris) muensteri* is now considered a synonym of *Dictyophyllum* (Nathorst, 1875). Nathorst (1907) noted that *Thaumatopteris* fronds are more upright and less connected at the base, whereas in *Dictyophyllum*, they are more spreading. The outer edges of the fronds appeared to be rolled downwards in *Thaumatopteris.* This is particularly true for the fertile fronds.

Sagenopteris Presl in Sternberg, 1938

Sagenopteris is a genus within the Dipteridaceae precursors with an eventful history of exploration. It was first described in 1824 by Brongniart as *Filicites nilsonianus* and illustrated a year later. In 1838, the Czech palaeobotanist Presl introduced the name *Sagenopteris* in Sternberg's monograph *"Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt"* (Attempt at a geognostic-botanical representation of the flora of the prehistoric world) and described several species, mainly from the Strahldorf (Strullendorf) locality near Bayreuth. However, the names *Sagenopteris rhoifolia* and *Sagenopteris acuminata* were already in use by Brongniart for *Filicites nils(s)onianus* from Sweden in 1824, leading to the establishment of the name *Sagenopteris nilssoniana* for those ferns found in the Lower Jurassic of Upper Bavaria.
The Swedish naturalist Nilsson (1787–1883) was the first to systematically search for plant fossils in the sediments near Hör. He sent these specimens to Brongniart and Sternberg and deserves to be honoured for his work. However, Brongniart made a transcription error in *"nilsonianus"*, which was later correctly corrected to *Sagenopteris nilssoniana,* similar to the name *Nils(s)onia* for a cycad genus widespread in these sediment layers.

Sagenopteris nilssoniana

1825 *Filicites nilsonianus* Brongniart, pl. 12. fig. 1

1838 *Sagenopteris rhoifolia* Presl in Sternberg, vol. II, 7/8, p. 164, vol. II, 7/8: 165, pl. 35, fig. 1

1838 Sagenopteris nilsoniana (Brongniart) Ward = *Sagenopteris rhoifolia* Presl in Sternberg

1838 *Sagenopteris acuminata* Presl in Sternberg, vol. II, 7/8: 165, pl. 35, fig. 3

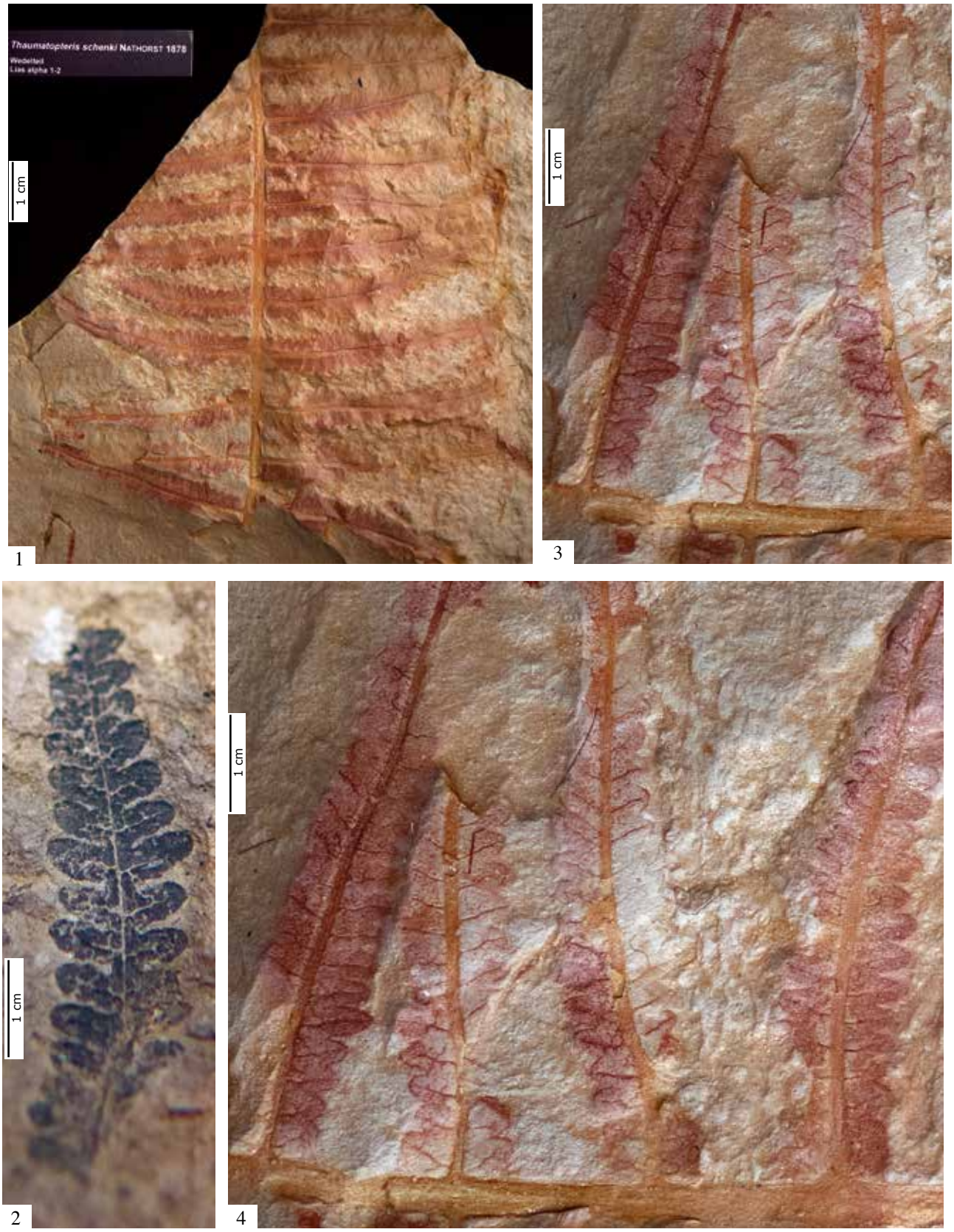
=1838 *Sagenopteris diphylla* Presl in Sternberg, vol. II, 7/8: 165, pl. 35, fig. 4

=1838 *Sagenopteris semicordata* Presl in Sternberg. vol. II, 7/8: 165, pl. 35, fig. 2

1841 *Sagenopteris elongata* Göpp., Gatt. foss. Pf. p. 114. Tab. 15. 16. Fig. 1-7

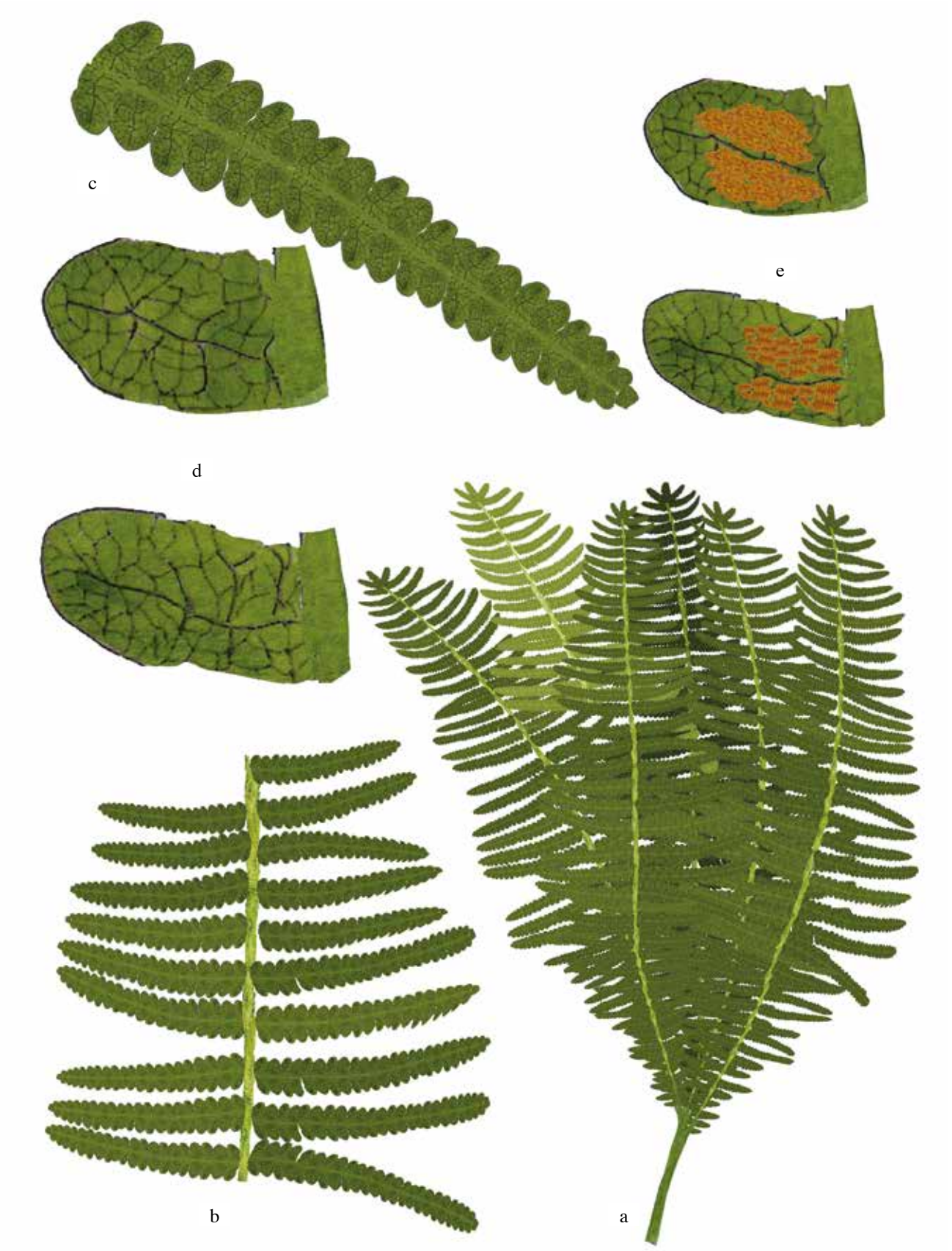
1867 *Sagenopteris rhoifolia* Schenk Pl. XII. Fig.1-6, Pl XIII. Fig. 4—10

1900 *Sagenopteris nilssoniana* (Brongniart) Ward, 352



Thaumatopteris schenkii. **Lower Jurassic. Hettangian. Fronds**

1. Part of a frond; 2. Pinnules; 3. Fertile fronds and detail of the pinnules (Forkendorf, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth)



The fern *Thaumatopteris schenkii.* Lower Jurassic. Hettangian. Reconstructions
a. Whole plant; b. Part of a frond; c. Pinnules; d. Individual pinna; e. Fertile little pinnae

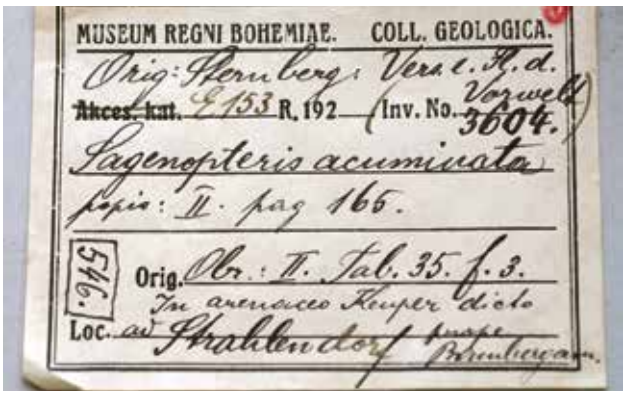
Description

Plant: The fern is characterised by its pointed to rounded, entire-edged leaves with distinctive mesh veining. The foliage emerges in 4 leaves from a long, central spindle. The plant can grow up to 20 cm in length, with the stem and leaves occupying about half of that length. The pinnules are slightly contracted at the base and the median nerve of the segments is prominent, gradually fading towards the tip. The lateral veins branch off from the median nerve at an acute angle, ascending obliquely to the edge, repeatedly forking and reconnecting to form an elongated mesh network. The middle segments of the leaves are typically longer than the two lateral ones.

Fertile parts: The sporangia are unevenly distributed on the underside of the leaves, sometimes sparsely, without any apparent connection to the main veins. The spores are enclosed within a half to three-quarters closed ring-like annulus. The total size of the sorus is less than 1 mm.

Remarks

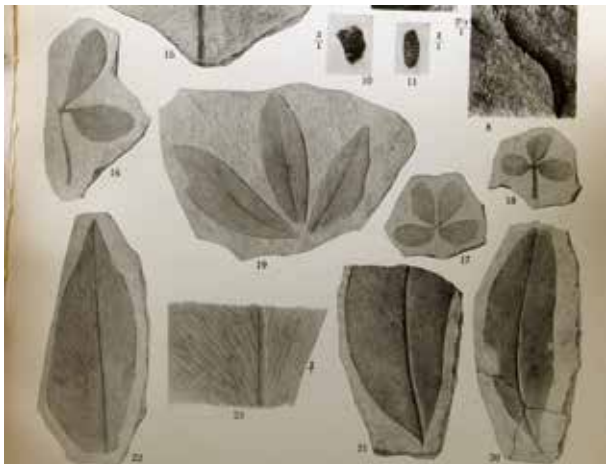
Sagenopteris has historically been classified under the Caytonales family and grouped with the seed ferns based on the discovery of pollen organs (*Caytonanthus*, Harris, 1941) and ovules (*Caytonia*, Thomas, 1925) in Middle Jurassic deposits at Cayton Bay in Yorkshire, northern England. It was initially believed that these findings were found in the same layers and, therefore, could be attributed to *Sagenopteris.* However, further research suggests these structures likely belonged to the enigmatic and ubiquitous fern *Thinnfeldia (Pachypteris).* The supposed pollen organs were likely juvenile stages of development of this plant,



Right: Illustration of *Sagenopteris rhoifolia* from C. Presl in Sternberg's "Attempt at a geognostic-botanical representation of the flora of the prehistoric world" (1838). The specimen was lost duringf the Second World War.

Left: *Sagenopteris acuminata* from Strahlendorf (properly Strullendorf), a municipality in the Upper Franconian district of Bamberg, has been preserved. It is probably a synonym of Brongniart's *Filicites nilsonanius.*

From Schenk, 1867 Pl. XII, *Sagenopteris rhoifolia.* They mainly come from the Strullendorf site near Bamberg, which was particularly productive at the time



From Halle, 1910. *Sagenopteris nilssoniana* from the Swedish Hör

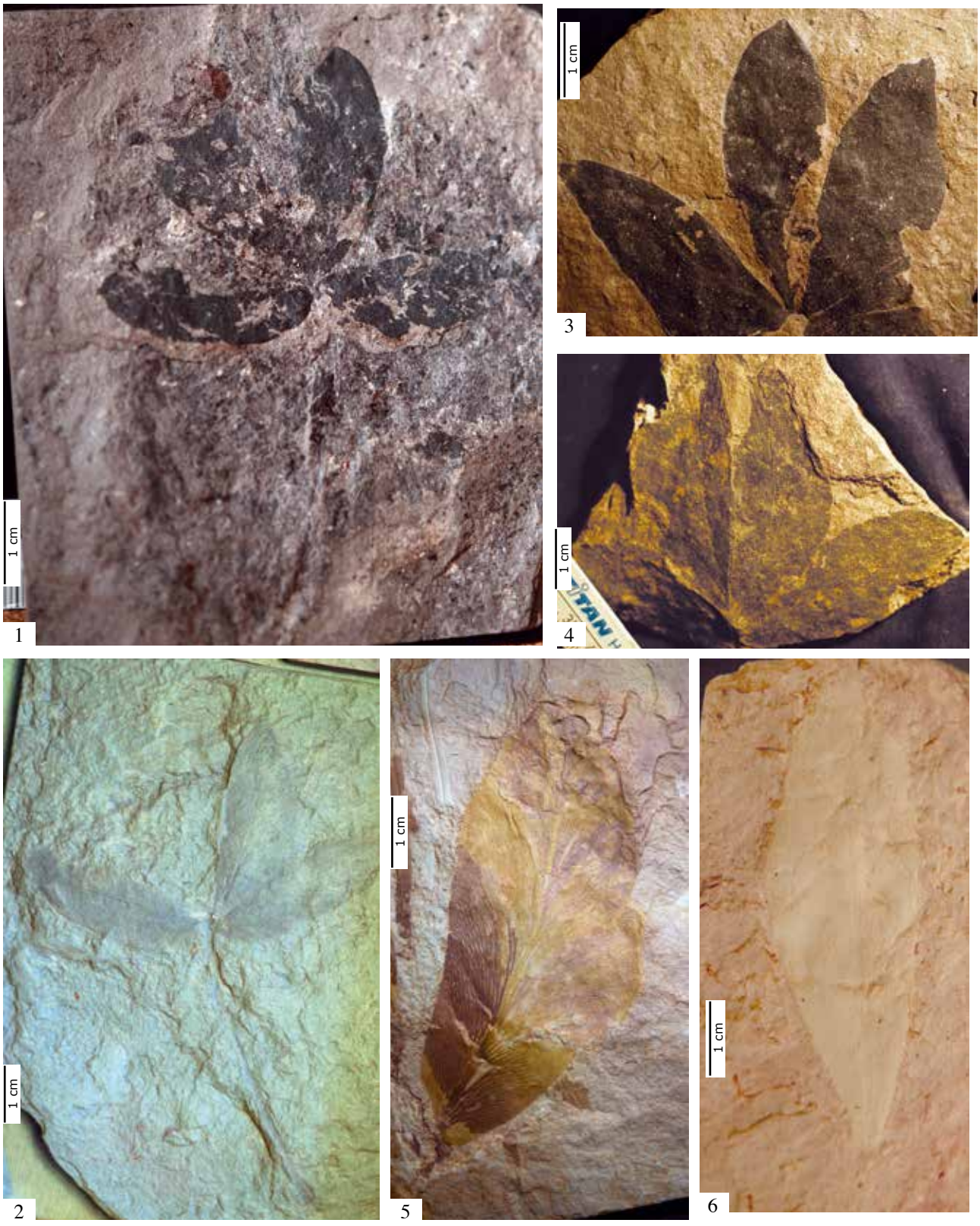
while the so-called ovules were probably adult sporophylls. *Sagenopteris* was a fern belonging to the group of Dipteridaceae precursors, indicated by the small and irregularly distributed sori scattered on the underside of the leaves. Specimens of this species were found in the Lower Middle Triassic deposits in the Dolomites (*Sagenopteris keilmannii*, Wachtler, 2016) and in deposits of approximately the same age in the Balearic Islands (*Sagenopteris nadali,* Juárez & Wachtler, 2015). Some specimens reached heights of up to half a meter, with fronds consisting of four leaf segments measuring up to 15 cm in size without the petiole. *Sagenopteris* largely disappeared during the Middle Triassic to the Upper Triassic periods, possibly due to the Raibl catastrophe, which led to a general thinning of the fern vegetation. However, *Sagenopteris* reappeared in the Lower Jurassic on a pan-European level, with evidence found in Sweden, Germany, and Hungary.
Despite its resurgence, *Sagenopteris* remained a rare plant element, with some locations, such as the otherwise fern-rich Pechgraben near Neudrossenfeld, lacking any traces of the fern. Although *Sagenopteris* is particularly common in the Pross sand pit at Unternschreez, completely preserved fronds with four leaf segments are rarely found. The species shares similarities with today's *Dipteris conjugata* with its four-leaved fronds on a stem.

Ferns not belonging to *Dipteris* or *Matonia* precursors

Furthermore, other ferns were found in the Bavarian locations, which are less common than the ones mentioned previously and do not necessarily belong to the Dipteris or Matonia ancestors. They are characterised by small sporangia located on the underside of the pinnules.

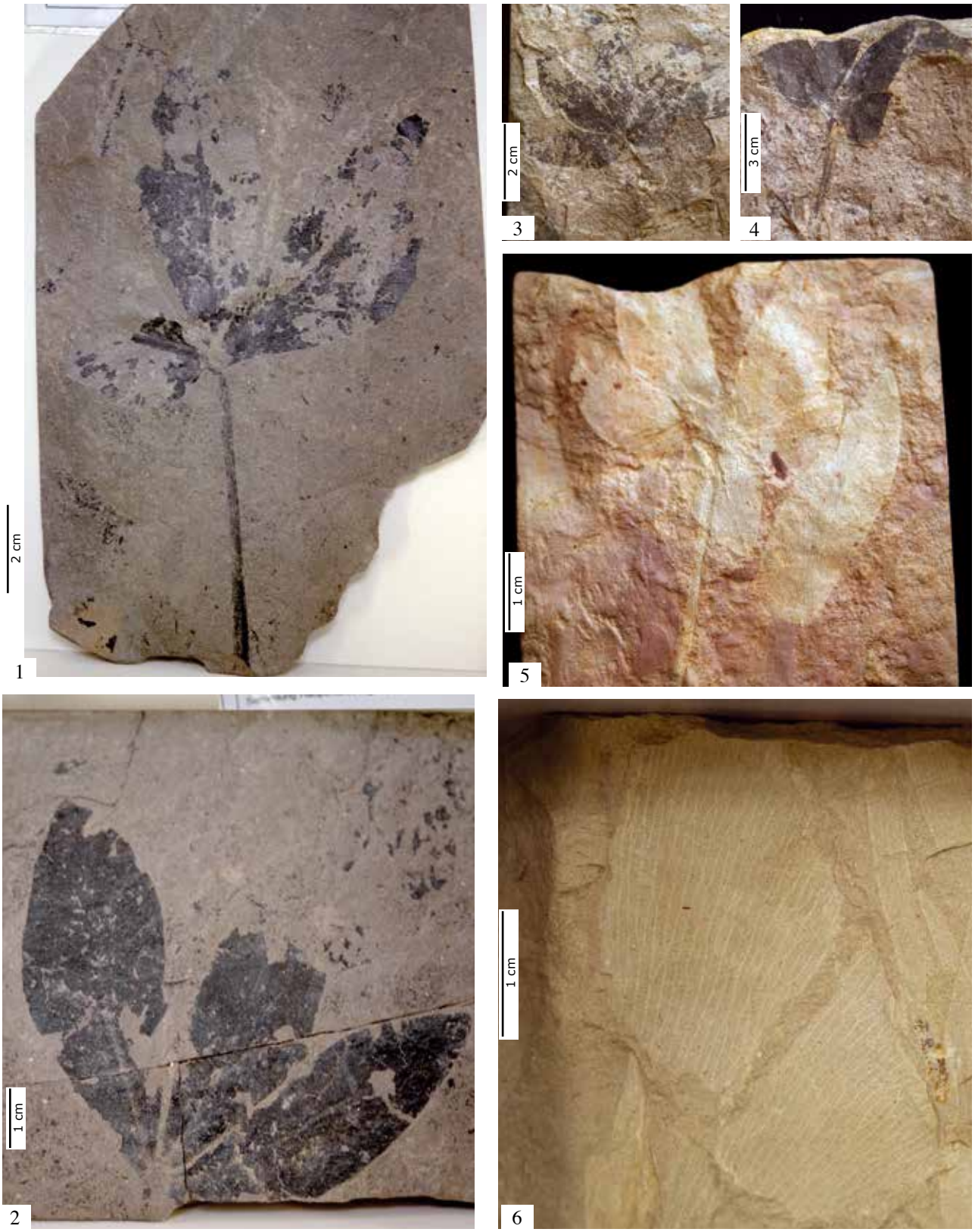
Otozamites Braun 1843

Otozamites is a fern that is difficult to classify. The genus was named in 1843 by the Bayreuth pharmacist and palaeobotanist Braun. He described them as having "Fronds pinnate; pinnules alternate and crowded, eared and only attached to part of the base; Veins radiate from the point of attachment to the edge of the leaf."
Braun identified several species within the *Zamites* species, including a *Zamites brevi-*



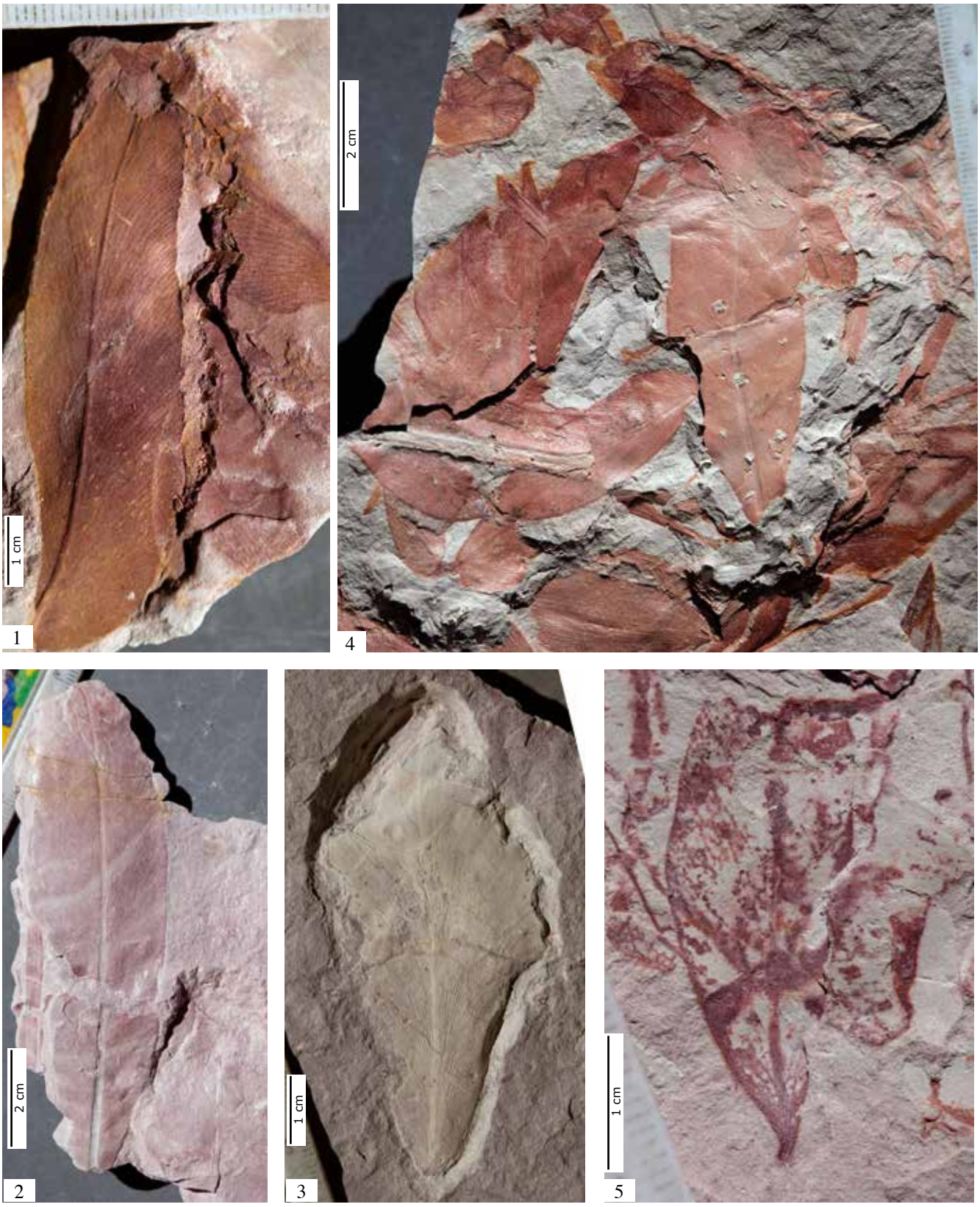
***Sagenopteris nilssoniana*. Lower Jurassic. Hettangian. Fronds**

1-2. Four lobed fronds 1.(Forkendorf, Sandpit Schmidt, Ex-Coll. Hauptmann, Coll. Tischlinger; 2. Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 3-4. Mainly complete frond (Forkendorf, Coll. Meyer, Lichtentanne; 5-6. Single leaves (Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth; Ex-Coll. Hauptmann, Sammlung Tischlinger)



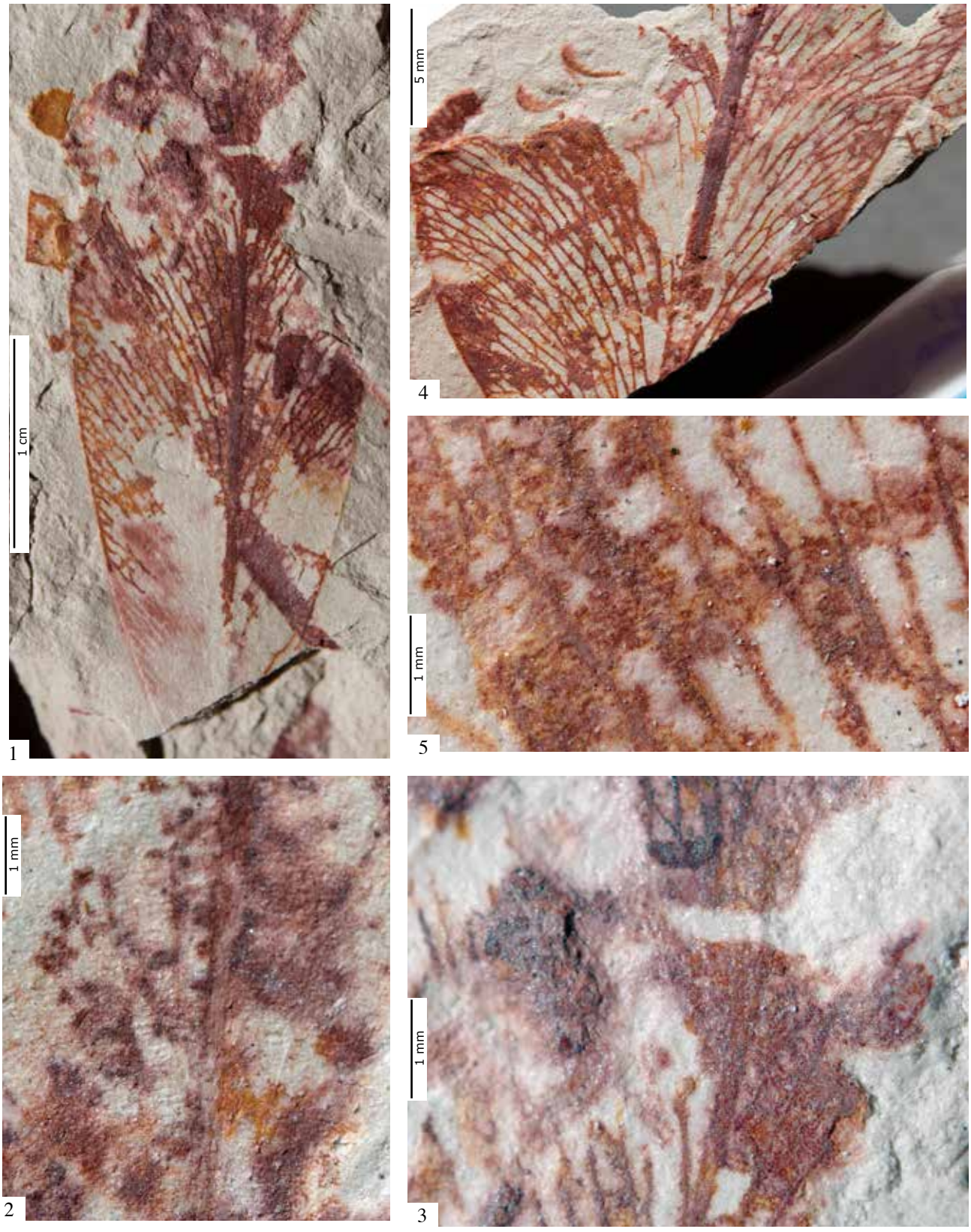
Sagenopteris nilssoniana. **Lower Jurassic. Hettangian. Fronds**

1-2. Frond (FORK_BT_015513.00; FORK_BT_015511.00, Forkendorf, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 3-4. Juvenile fronds (Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth; 5-6. Detail of the fronds and the mesh veining (BOCK_BT_014338.00, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth)



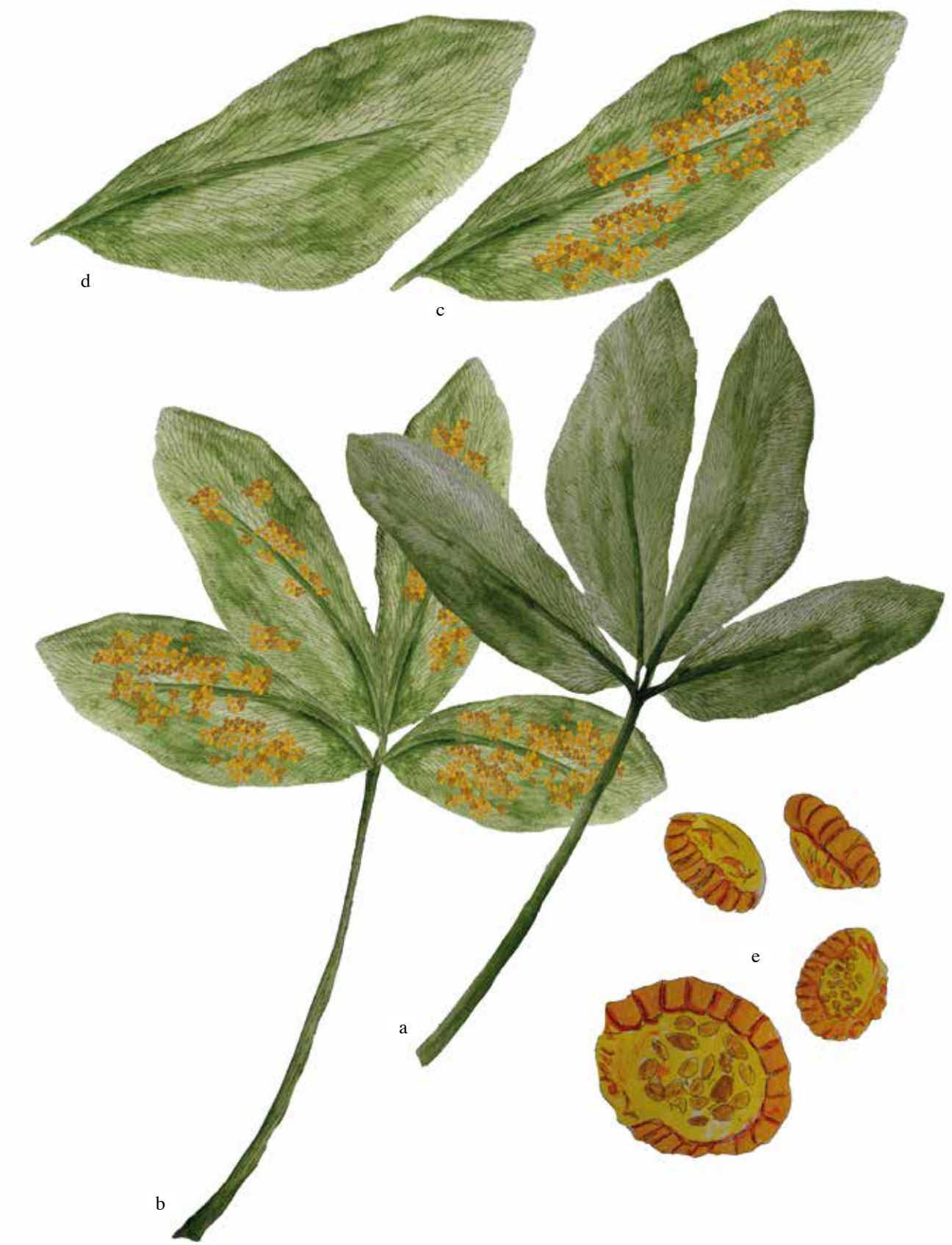
Sagenopteris nilssoniana. **Lower Jurassic. Hettangian. Fronds**

1-3. Single leaves (SCHR 05, BOCK 32, BOCK 22, Unternschreez, Sandpit Bocksrück, Ex-Coll. Silberhorn, Coll. Wachtler-Dolomythos); 4-5. Accumulation of leaves and fertile single leaf (Unternschreez, Sandpit Bocksrück, Ex-Coll. Friess, Coll. Wachtler-Dolomythos)



***Sagenopteris nilssoniana*. Lower Jurassic. Hettangian. Fertile fronds**

1-3. Fertile individual leaves and detail of the sporangia (SCHR 03, SCHR 09 Unternschreez, Sandpit Bocksrück, Ex-Coll. Friess, Coll. Wachtler-Dolomythos); 4-5. Fertile single leaf with excellently preserved mesh veining and detail of adult sporangia (Unternschreez, Sandpit Bocksrück, Ex-Coll. Friess, Coll. Wachtler-Dolomythos)



The fern *Sagenopteris nilssoniana.* Lower Jurassic. Hettangian. Reconstructions

a. Sterile frond; b. Fertile frond; c. Fertile leaflet; d. Sterile single leaflet; e. Sporangia and spores

folius, which he also reproduced. Schenk, in 1867, attempted to rename the genus to *Otopteris* in order to disassociate it from cycads due to its peculiarities. In the end, the name chosen by Braun, *Otozamites brevifolius,* prevailed.
Schenk illustrated what he believed to be a fertile frond on plate 29, sections under 8 and 8a, and compared the structure and arrangement of the sporangia to modern fern genus *Lindsaea* and *Adiantum*. However, it was observed that the sporangia covered the underside of the pinnules and were not arranged at the edges.
Although the appearance of the leaflets may resemble those of the modern Anemiaceae genus, primarily found in the Neotropics with concentrations in North America extending to the northern part of South America, the lack of separate sporophylls and tropophylls contradicts this classification. The sporangia, sparsely distributed on the underside of the pinnules, exhibit a nearly circular annulus and spores within the inner circle, characteristics that align with other leptosporangiate fern genera present today.

Otozamites brevifolius Braun 1843

1843 *Otozamites brevifolius* Braun in Münster, Beitr. p. 36

1843 *Zamites brevifolius* Braun in Münster, Beitr. Heft VI. p. 29, Pl. 13. Fig. 13-14

1867 *Otopteris bucklandii* Schenk, Fossile Flora, Pl. XXXI Fig. 2-3; Taf. XXXIII, fig. 2-3; Pl. XXXIV, Fig. 1-8

Description

Plant: The fronds are densely covered with elongated, pointed to bluntly tapered leaflets that sometimes overlap. These leaflets can sometimes reach up to 10 cm in length and 1 cm in width. The pinnules stand opposite and are only partially connected to the rhachis. The leaf veins radiate basally without forming a pronounced median vein. Sometimes, the nerves branch dichotomously and run freely at the edge of the pinnule.
Fertile fronds: Small sporangia are located on the underside of the pinnulae, ranging in size from 0.1 to 0.3 mm. These sporangia are circular with an almost closing annulus on the outside, while the spores are found in the inner courtyard.

Remarks

Otozamites brevifolius is commonly found in sufficient numbers in the Hettangian of Franconia, but it is more common in the Upper Triassic of northern Italy. Both Braun and Schenk classified this genus of plants as ferns, likely due to their dichotomously bifurcated nerves, which distinguish them from cycads.

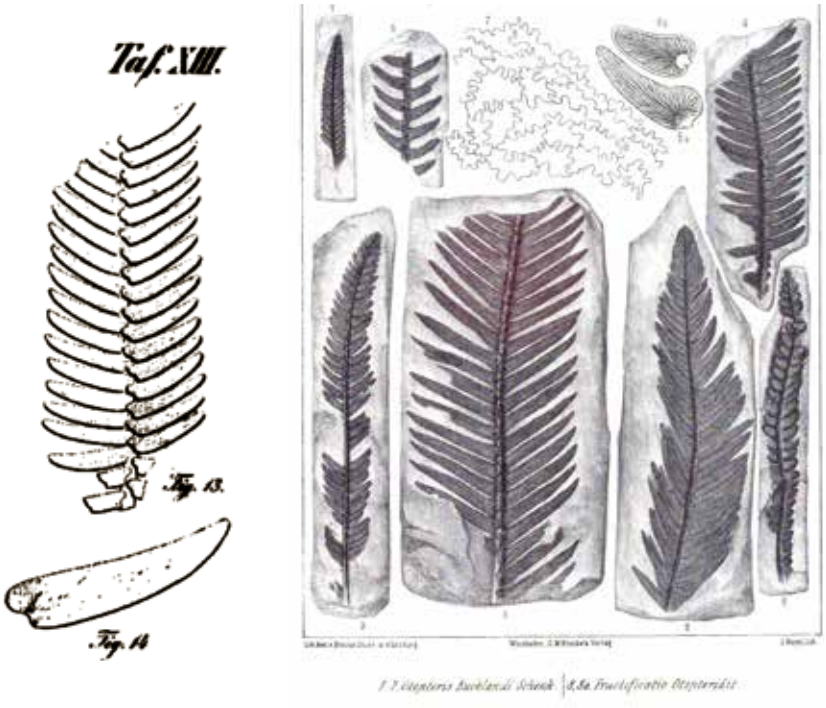
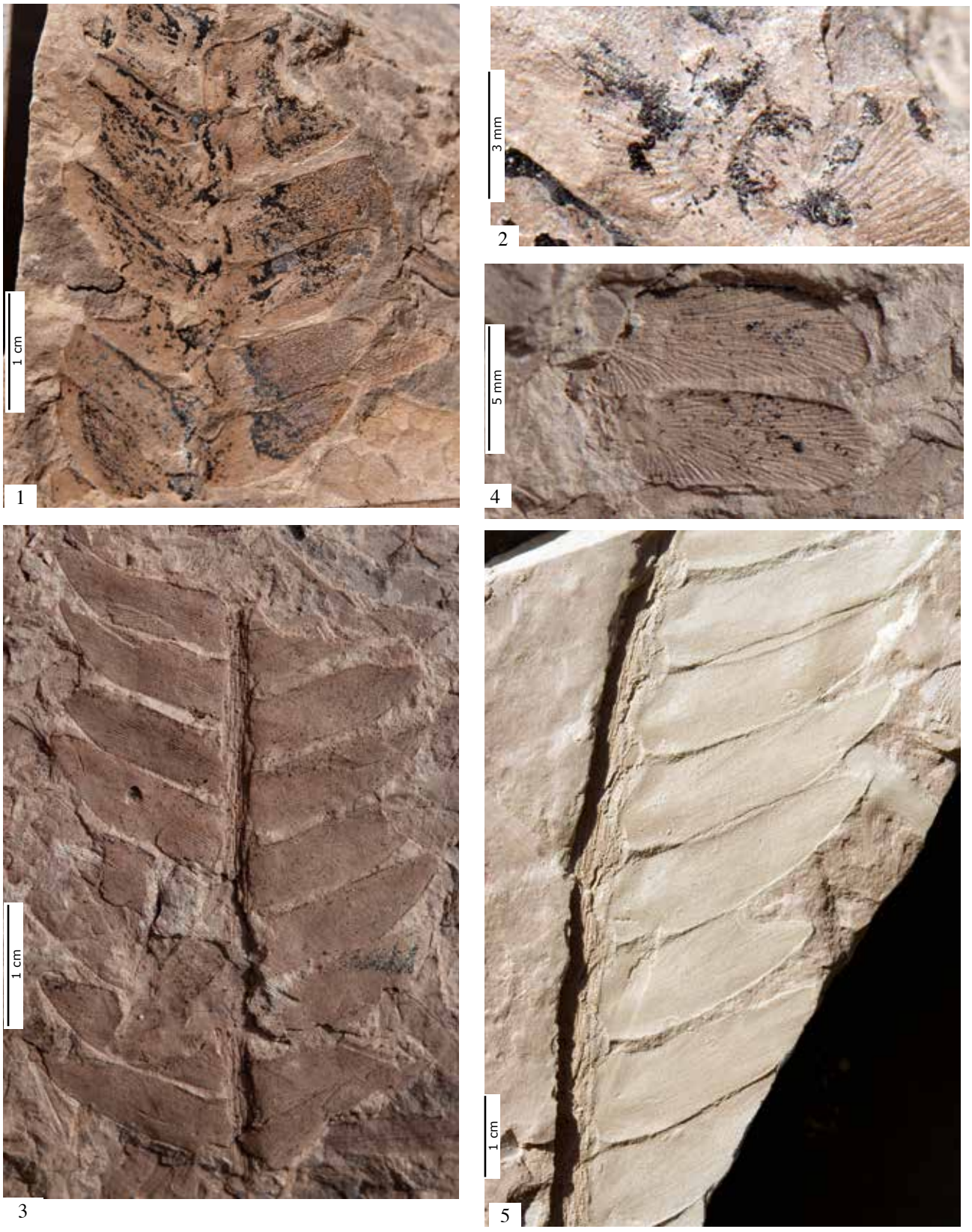


Plate XIII. From Braun 1843, *Zamites brevifolius,* Tafel XXXIV. From Schenk, 1867 *Otopteris bucklandi.*

Schenk depicted supposed fertile pinnules (8 und 8a).

***Otozamites brevifolius*. Lower Jurassic. Hettangian. Fronds**

1. Several fronds (Coll. Hauptmann, Urweltmuseum Oberfranken, Bayreuth); 2-8. Several fronds (PECH 261, PECH 50, PECH 237, PECH 56, PECH 207, PECH 23, PECH 61); All Pechgraben, sandpit Küfner, Coll. Wachtler, Dolomythos-Museum



***Otozamites brevifolius*. Lower Jurassic. Hettangian. Fronds**

1-2. Fertile pinnae with detail of the sporangia (PECH 254); 3-4. Fertile part of a frond (PECH 203); 5. Frond with detail of veining (PECH 594) All Pechgraben, sandpit Küfner, Coll. Wachtler, Dolomythos-Museum

Acrostichites princeps Göppert 1841

Classifying another rare fern genus is even more challenging. It is known in its entirety, including the sporangia on the underside of the pinnules, which are similar to those of many Dipteris species, but further conclusions are difficult to draw.
Although it is unsatisfactorily classified here as *Acrostichites princeps* (Göppert, 1841), it was first named and illustrated in 1838 as *Sphenopteris princeps* by Presl in Sternberg and later changed by Göppert. However, the earlier illustrations do not provide a clear direction, leaving room for various interpretations and questions.

1838 *Sphenopteris princeps* Presl in Sternberg, vol. II, 7/8, p. 126, pl. 59, figs 12, 13,

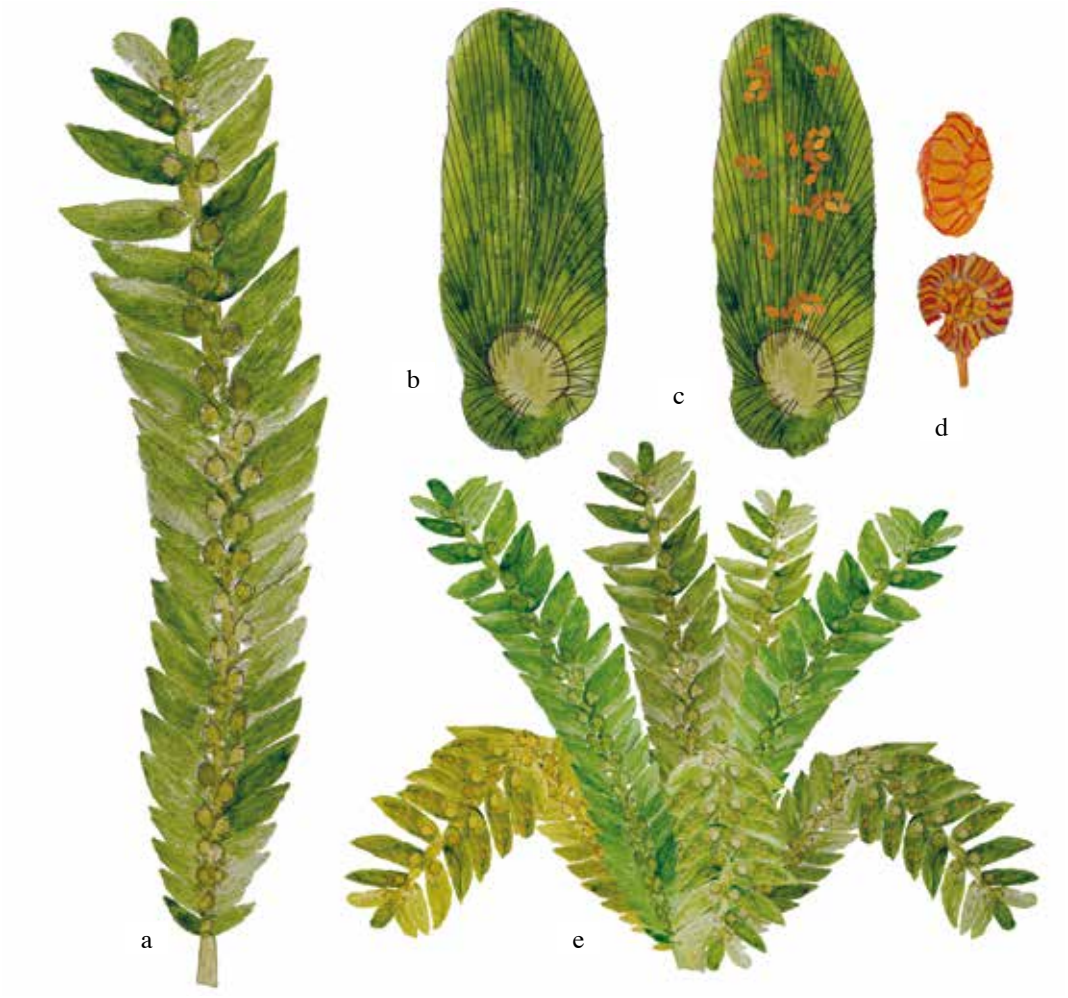
1867 *Acrostichites princeps* Schenk Tafel VII. Fig.3 —5. Tafel VIII. Fig.1a.

Description

Whole plant. Fronds that arise about eight from a base and can grow up to 25 cm long, narrowing towards the tip. Individual pinnules can reach up to 5 cm in length, with a central median nerve from which the lateral veins divide twice dichotomously to the end of the leaf.
Fertile fronds: Similar to the sterile ones, with fertile parts arranged in two rows along the midrib and are not sunken. The sporangia are irregularly scattered on the underside of the fronds, with a multi-membered annulus ring with the spores in the middle.

Marattiopsis Schimper 1869

Marrattiopsis is a formative fern from the Lower Jurassic period. Initially, Schimper (1869) mistakenly classified a fern from the Lower Miocene of the Czech Republic



The fern *Otozamites brevifolius*

a. Single frond; b. Sterile pinna; c. Fertile pinna; d. Sporangia; e. Whole plant

as *Marattiopsis dentata,* which was later determined to actually belong to the Blechnaceae family (Bomfleur et al., 2013). However, Schimper (1869) also described and depicted *Angiopteridium muensteri* from the Early Jurassic layers of Bayreuth.
There has been some debate regarding whether this genus, which is closely related to the Marattiales, should be called *Marattiopsis* or *Angiopteridium*. While the characteristics of the fern suggest similarities with today's Angiopteris ferns, there are also Marattia ferns with similar characteristics. As a result, the name *Marattiopsis (intermedia)* has been widely accepted.

Marattiopsis intermedia Münster 1836

1836 *Taeniopteris intermedia* Münster in Bronn and Leonhard, Jahrb. für Mineralogie. p. 510-511

1867 *Taeniopteris intermedia,* Schenk, pl XX, Fig. 2-8

1869 *Marattiopsis dentata* Schimper

1874 *Angiopteridium muensteri* Schimper, Traité de paléontologie végétale, pl XXXVIII, fig. 1-6

1874 *Angiopteridium hoerense* Schimper, Traité de paléontologie végétale, pl XXXVIII, fig. 7

1919 *Marattiopsis hoerensis A*ntevs, pl. 2, Fig. 2-13; Taf. 6 Fig. 40

In the Bayreuth area, Münster (1836, pp. 510–511) first observed this fern and referred to it as *Taeniopteris intermedia,* highlighting the fragmentary nature of the findings and the marginal elongated fructifications. Schenk (1867, plate XX) depicted it as *Taeniopteris intermedia,* while Schimper (1874) classified it as *Angiopteridium muensteri.* In addition, another species, *Marattiopsis (Angiopteridium) hoerense,* was identified from the Swedish Hettangian (Schimper, 1874; Antevs, 1919).

Description

Plant: The sporotropophylls feature protruding bipinnate fronds, with individual pinnules reaching up to 30 cm in length and 2 to 3 cm in width. The pinnules taper, have a rounded concave base, and a pronounced midrib. Side veins bifurcate once in the lower part and then continue undivided to the edge.
Fertile fronds: The sporangia grow together to form synangia about 2 to 3 mm long and a maximum of 1 mm wide, which

Acrostichites princeps. Fronds

1-2. Whole plant (Pechgraben, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 3.Whole plant with mainly complete fronds (Forkendorf, Coll. Meyer, Lichtentanne

1

2

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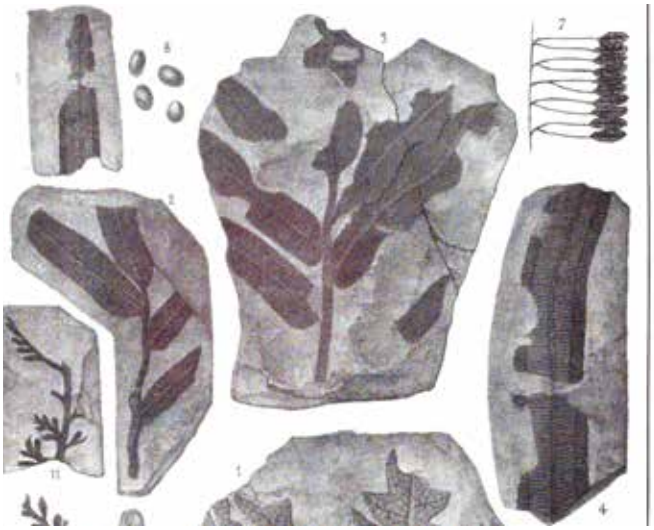
Acrostichites princeps. **Lower Jurassic. Hettangian. Fronds**

1-2. Whole plant with sporangia (Forkendorf, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 3. Frond (Forkendorf, Coll. Meyer, Lichtentanne

The fern *Acrostichites princeps*. Lower Jurassic. Hettangian. Reconstructions

a. Fertile entire plant; b. Sterile entire plant; c. Sterile frond; d. Sterile pinna; e. Fertile frond; f. Detail of the fertile pinnules



From August Schenk, 1867, Taf. XX, *Taeniopteris (Marattiopsis) intermedia*

From Wilhelm Schimper, 1874, Traité de paléontologie végétale, *Angiopteridium muensteri* pl XXXVIII, fig. 1-6. Theta near Bayreuth, and *Angiopteridium hoerense*, pl. XXXVIII, fig. 7

are located on the underside of the pinnae. These capsule-like sporangia are divided into segments and burst open when ripe to release the spores.

Remarks

Today, Marattiales are found primarily in subtropical and tropical rainforests worldwide. These plants are made up of leaf fronds that can reach up to 5 to 6 m in length, making them the largest in the plant kingdom. The fronds are typically single or multi-pinnate in structure. Marattiales are divided into the main groups *Marattia* and *Angiopteris,* as well as the more distant groups including *Danaea, Christensia, Ptisana* and *Eupodium*.

Fossil evidence of Marattiales date back to at least the Upper Carboniferous period, with species like *Marattiopsis stopesae* and *Danaeites perneri* (Wachtler, 2023f). Additionally, specimens from the Permian period, such as *Angiopterites murchinsonii* (Wachtler, 2021), have been discovered, indicating the early diversification of these plants into different families. Interestingly, in the Upper Carboniferous period, individual pinnae of Marattia and Danaea precursors were formed by the merging of closely growing pinnae.

Marattiopsis intermedia is found relatively frequently in the Hettangian of Upper Franconia, particularly in the Pechgraben area, although complete fronds are rare. However, it is easy to distinguish this species from other ferns due to its characteristic synangia structures.

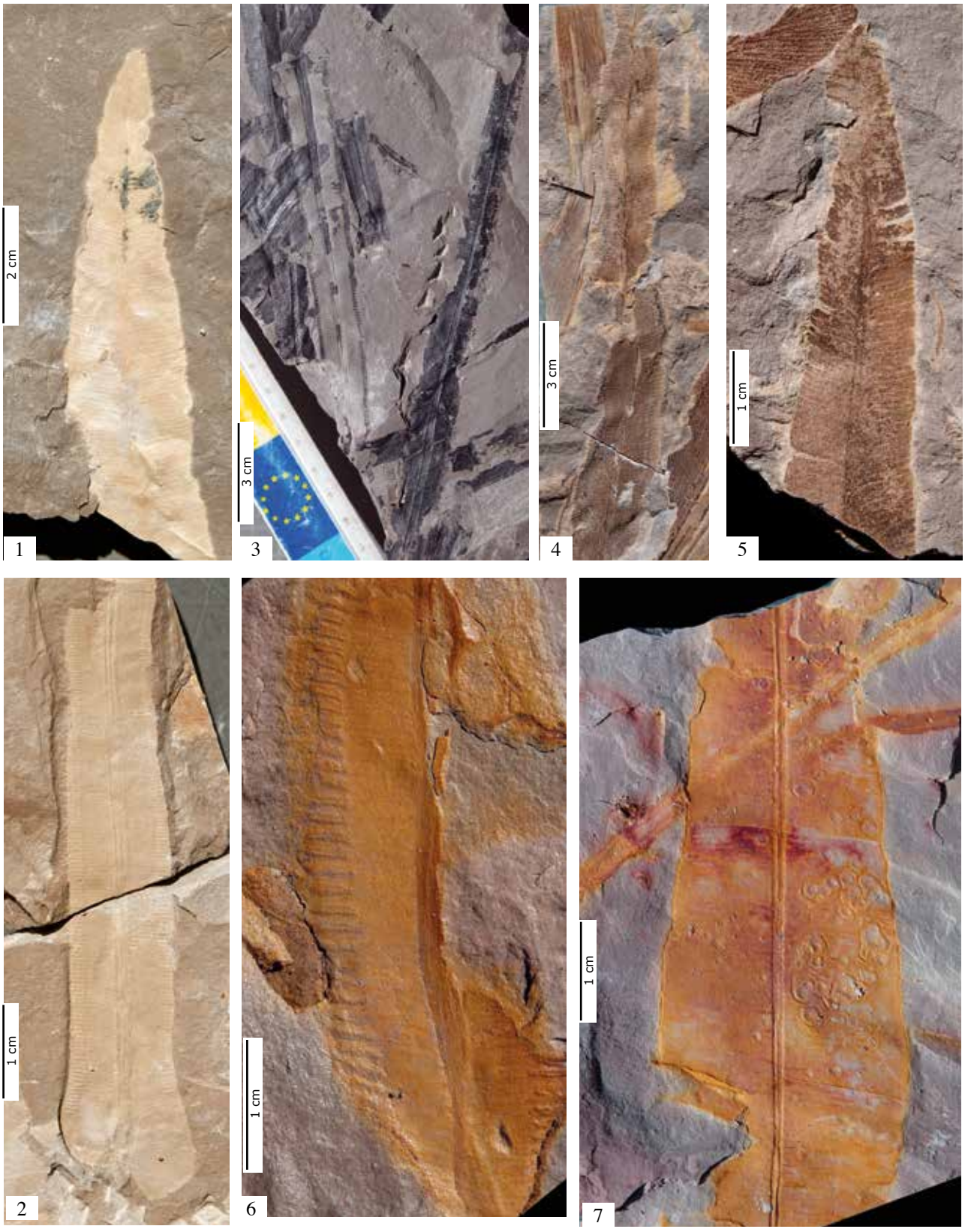
Cyatheites Goeppert 1836

While Dipteris and Matonia ancestors, along with the Marattiales and especially the enigmatic *Thinnfeldia*, dominated the fern landscapes of the Lower Jurassic period, tree ferns fell somewhat into the background, possibly due to their preference for more distant habitats, away from the banks.

The German botanist and palaeontologist Göppert (1800–1884) was the first to recognise the similarity of fossil ferns to the tree fern Cyathea, naming them *Cyatheites* in 1836. Among the specimens he examined, ferns dating back to the Carboniferous (*Cyatheites schlotheimii*) period up to the Jurassic period were ranked. Notably, a *Cyatheites asterocarpoides* from the renowned Upper Bavarian locality Strullendorf near Bamberg caught his attention. This particular specimen had been shown to him in advance by Sternberg and given the name *Gutbieria angustiloba* by Presl (in Sternberg, 1838). The original specimen was lost in the turmoil of the Second World War, but the pictures suggest a resemblance to *Phlebopteris.* Nevertheless,

The fern *Marattiopsis intermedia*. Lower Jurassic. Hettangian. Reconstructions

a. Whole plant; b. Complete frond; c. Fertile pinnules; d. Sterile pinnules; e. Fertile pinnae; f. Detail of fertile pinnae g. Synangia; h. Spores



***Marattiopsis intermedia*. Lower Jurassic. Hettangian. Fronds**

1. Apical part of a frond (PECH 286); 2. Basal part (PECH 284); 3-5. Various frond parts (PECH 394, PECH 198, PECH 250); 6. Fertile pinnules (PECH 360); 7. Frond with traces of insect feeding (PECH 350); All Pechgraben, sandpit Küfner), Coll. Wachtler, Dolomythos-Museum

Marattiopsis intermedia. **Lower Jurassic. Hettangian. Fertile fronds**

1-3. Details of the synangia (PECH 249, PECH 50, PECH 394); 4. Almost complete fertile pinnule (PECH 526); 5-6. Basal fertile pinna (PECH 525, PECH 626); All Pechgraben, sandpit Küfner, Coll. Wachtler, Dolomythos Museum

Marattiaceae

1-3. *Marattia fraxinea.* Plant, frond and detail of the synangia; 4-8. *Angiopteris evecta:* Frond, juvenile and mature synangia

fronds and fertile organs from the Lower Jurassic of Upper Franconia indicate that at least one tree fern was present. Therefore, the name *Cyatheites asterocarpoides* is upheld for this species and included in the long list of Cyatheaceae spanning from the Carboniferous era to the present day.

Cyatheites asterocarpoides, Goeppert 1836

1836 *Cyatheites asterocarpoides* Göppert, Syst. fil foss. p. 327

1838 *Gutbieria angustiloba* Presl in Sternberg

Description

Whole plant: It features multiple branching fronds with leaflets arranged in an opposite to staggered pattern. The individual smooth-edged pinnules are concavely positioned on the rhachis and grow in an opposite to slightly offset manner. At the apex, they culminate in a rounded to slightly pointed shape and reach lengths of about 0.5 cm and widths of 0.2 to 0.3 cm. The central vein of the pinnules is distinct, while the side nerves are less developed and irregularly fork one to three times. The unbranched, tree-shaped trunks are notable for their slender nature and the absence of fronds.
Fertile fronds: Resembling the sterile fronds, the fertile fronds bear rounded sori on their underside in two rows to the left and right of the central vein. The pinnae exhibit a slightly downward curve along the outer edges.

Remarks

The Cyatheaceae of today are notable for their tall, slender trunks, and typical scar cushions from fallen fronds, a characteristic that may have been present in the past as well. These tree ferns are found in tropical and subtropical areas around the world, reflecting the prevailing climate of the Lower Jurassic period. In contrast to the Carboniferous era, where magnificent fronds and well-preserved trunks were found in large numbers due to their allochthonous embedding in the extensive swamp areas, fossil tree ferns with well-preserved fronds from the Triassic and Jurassic periods are less common and often found in relatively small fragments.
The transportation of these fossils over long distances suggest that they may have


1


1

Marattia kaulfussii. Marattiaceae

1. Pinnae with synangia; 2. Fronds

The fern *Cyatheites asterocarpoides*. Lower Jurassic. Hettangian. Reconstructions

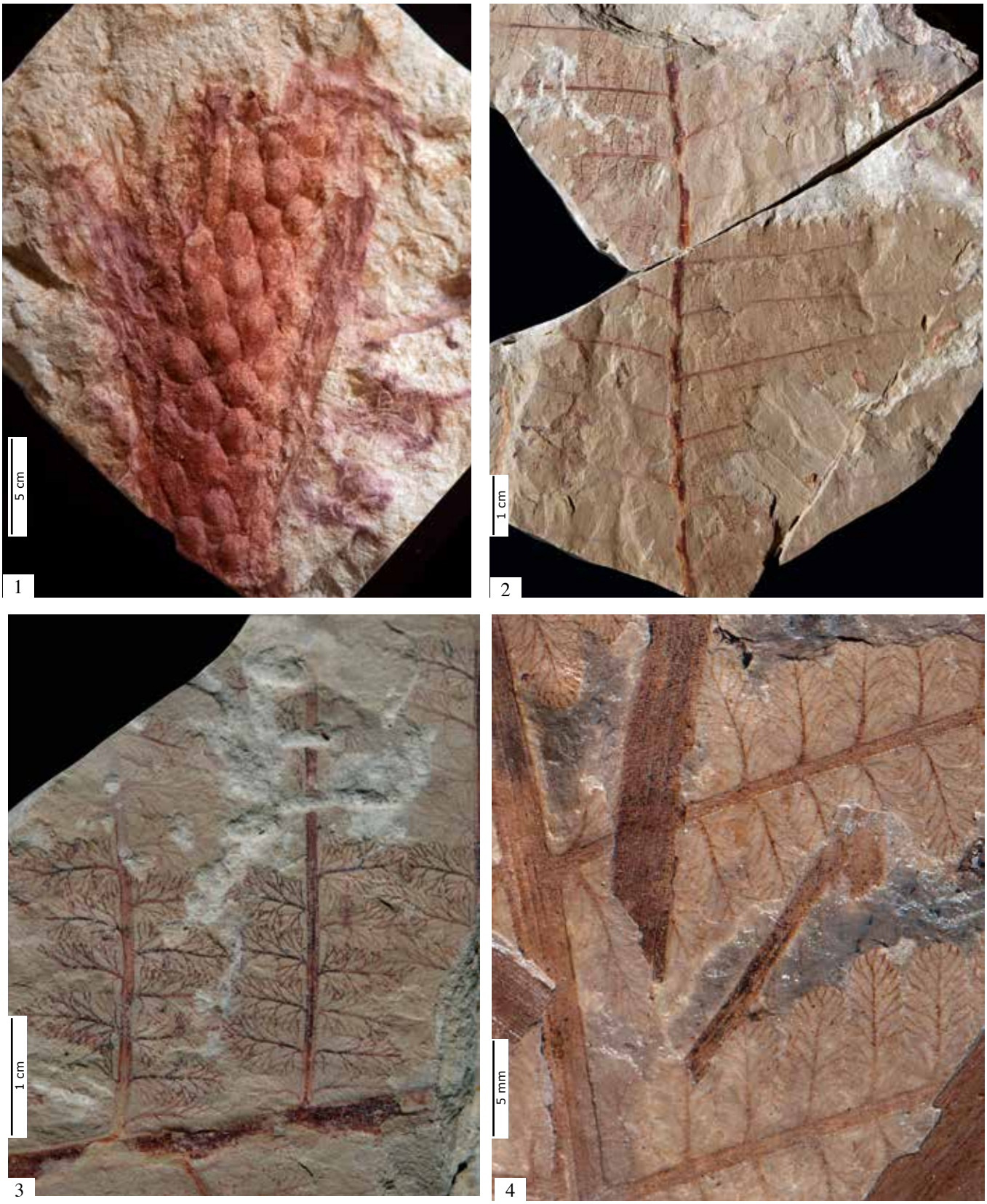
a. Whole plant; b. Fertile frond underside; c. Fertile frond upper view; d. Fertile pinnules, top and underside; e. Fertile individual pinna, top view and underside; f. Sori; g. Sterile pinnules and individual pinna





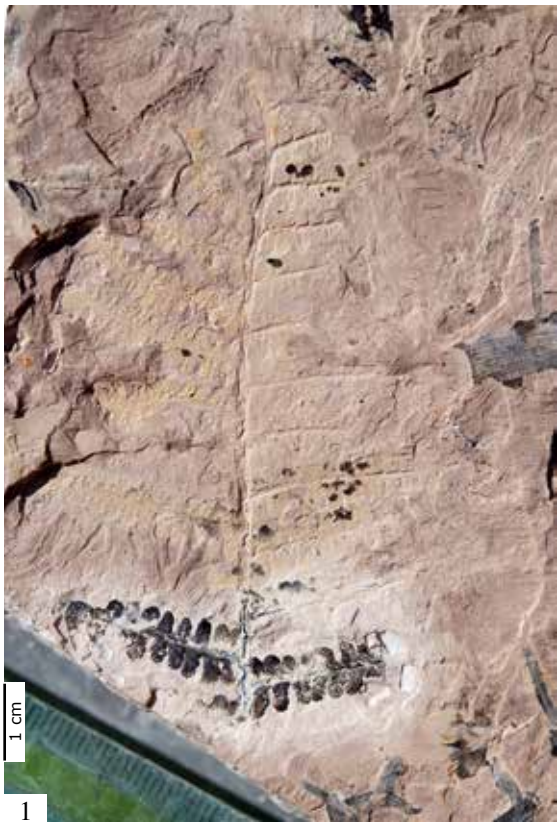
Cyatheaceae

1. *Cyathea fortunei.* Whole plant; 2. *Cyathea australis.* Part of a stem; 3. *Cyathea medullaris.* Sterile frond; 4-5. *Cyathea browni.* Fertile frond, upper view and underside



***Cyatheites asterocarpoides*. Lower Jurassic. Hettangian. Fronds**

1. Part of a stem (Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 2-3. Part of a frond (SCHN 07, Schnabelwaid, Ex-Coll. Silberhorn, Coll. Wachtler, Innichen); 4. Detail of the pinnules (PECH 123, Pechgraben, Coll. Wachtler, Dolomythos)



***Cyatheites asterocarpoides*. Lower Jurassic. Hettangian. Fertile fronds**

1. Part of a fertile frond upper side (PECH 150, Pechgraben, Coll. Wachtler, Dolomythos) 3-4. Fertile pinnules (Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth)

originated in the hinterland. Their two-row, rounded and pronounced sori arranged along the middle vein, as well as their unique trunks with visible break-off points of the fronds make them relatively easy to distinguish from the Dipteridaceae or the Marattiaceae found in the same sediments.

Thinnfeldia Ettinghausen 1852

One of the most common and yet most enigmatic ferns in the Lower Jurassic is *Thinnfeldia (rhomboidales)*. As with many other plants, classifying this species in the realm of palaeobotany presents a challenging task. The variability in leaf shapes and the difficulty in connecting fertile parts have made it a complex subject of study. *Thinnfeldia* has often been classified under the group of Peltaspermales, alongside seed ferns (Taylor et al., 2006). However, a consistent differentiation between pollen and ovules has not been established. In addition, over time, the Peltaspermales formed a vat of ferns with a wide variety of fertile systems. From *Callipteridium* in the Carboniferous, *Autunia* and *Callipteris* in the Permian, to *Scytophyllum* in the Triassic and *Thinnfeldia* in the Lower Jurassic, the group has shown substantial variation.
The name *Thinnfeldia* itself has been subject to doubt. In 1828, the founder of French palaeobotany Adolphe Brongniart introduced *Pachypteris lanceolata* and *Pachypteris ovata* from the Middle Jurassic of England (Pag. 49) without illustration.
A year later, in 1829 he described them again, with a plate (45) figuring both. It, therefore, deserved priority unless the leaf shapes and plant structure differed considerably from those found during the Triassic-Jurassic transition. This nomenclature was thereby limited to the Middle Jurassic and never caught on in the main central German discovery areas.
In 1852, the Austrian palaeobotanist Ettingshausen (1826–1897) coined the term *Thinnfeldia.* Ettingshausen identified small differences in the shapes of the fronds and named them *Thinnfeldia rhomboidales, Th. speciosa, Th. Münsteriana* and *Th. parvifolia.* This nomenclature preceded Braun's (1800–1864) description of similar foliage in 1854 in Bayreuth by two years with *Kirchneria (decurrens, ovata* and *polymorpha*).

Thinnfeldia rhomboidales Ettinghausen 1852

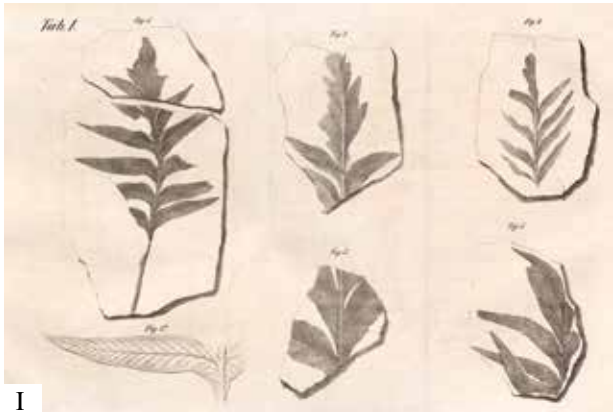
1852 *Thinnfeldia rhomboidales* Ettingshausen Pl I. Fig. 4-7
1854 *Kirchneria* Braun in Münster, p. 87
1867 *Thinnfeldia rhomboidalis* Schenk Pl XVII. Fig. 1-8
= *Thinnfeldia decurrens* Schenk Pl XXVI Fig. 1-5
= *Thinnfeldia obtusa* Schenk Pl XXVI Fig. 6-8
= *Thinnfeldia saligna* Schenk Pl XXVII Fig. 9-12
=*Thinnfeldia laciniata* Schenk Pl XXVIII Fig. 1-4

The palaeobotanist and geologist Walter Gothan (1879–1954, Berlin) made significant contributions to the study of the genus *Thinnfeldia* in 1912. In his monothematic work titled "*Über die Gattung Thinnfeldia Ettingshausen"* (On the genus *Thinnfeldia*), he organised and analysed findings from his own collection and those left to him. By adopting the proposal put forward by Ettinghausen, Gothan solidified the classification of the species *Thinnfeldia rhomboidales,* which was commonly found in the Lower Jurassic around Bayreuth.
Despite these advancements, the descriptions of *Thinnfeldia* have been lacking in detail, particularly regarding connections with the fertile organs. Kirchner and Müller (1992) attempted to address this gap by studying specimens from Middle Franconia in Bavaria (Großbellhofen). They attributed a supposed ovule (*Umkomasia franconica)* and the pollen organ *Pteruchus septentrionalis* to the genus *Thinnfeldia*. While the supposed seed organ *Umkomasia* belongs to the conifer *Hirmeriella* due to the presence of leaf needles and cones (whose co-occurrence in the same layers is confirmed by the two authors), *Pteruchus septentrionalis* can be assumed to be an adult sporophyll part of *Thinnfeldia.*
Kirchner and Müller (1992) described *Pteruchus* as a "male fructification, consisting of a 5–7 cm long, almost 1 cm wide main axis, from which 1–2 cm long stems extend all around, where oval to circular, up to 1.5 cm x 0.7 cm measuring heads seated, dorsally with pustular surface, ventrally covered by numerous pollen sacs 3.00 to 6.3 mm long and 0.5–2.2 mm wide, which protrude marginally above the heads, forming an entire sporophyll head 2.3 cm x 1.5 cm." The associated spores were called *Alisporites thomasii.*
The illustrations on plate 3, fig. 1–6, depict sporophyll heads that are found rela-

tively frequently in the Küfner sandpit in Pechgraben. However, Kirchner and Müller (1992) assigned *Thinnfeldia* to the group of Corystospermaceae (Umkomasiaceae), which seems questionable since the first description of *Umkomasia*, but also of *Pteruchus,* was made by Harris in 1933 for Triassic-Jurassic fossils from South Africa, formerly part of the Gondwana continent. These fossils have also been identified in Australia (Anderson et al., 2019). The connections between these regions pose challenges, as Gondwana, Euramerica, and the Siberian Angara landmass have evolved into separate continents since the Devonian-Carboniferous period. Nevertheless, the genus name *Thinnfeldia* is also used for the fertile organs.

In addition, additional fructifications known as *Stachyopitys preslii* were discovered in Upper Franconia and described as pollen organs of the Ginkgoales (Cittert, 2010). The segmented, partially open, almost circular annulus with spores within the individual sporangia suggests a classification as male ginkgo organs is obsolete, as they are more likely to be ferns. These structures are believed to be juvenile, developing sporophylls of *Thinnfeldia*. Another milestone was achieved by the collector Sepp Hauptmann, when he was able to recover a complete *Thinnfeldia* plant, with fronds and fertile elements intact (today Coll. Jürgen Meyer). Fuchs and Wachtler made further discoveries of shield-shaped sporophylls in 2022.

All specimens are characterised by segmented, shield-shaped aggregates that are nearly completely covered in hair-like trichomes. Beneath these aggregates, leptosporangiate spore sacs span almost the entire length of the lamina. It is important to note that these structures do not represent ovules. In this regard, the appearance of the fertile organs in both juvenile and adult stages of *Thinnfeldia* clarifies their classification within the group of ferns that develop separate sporophyll and tropophyll, resembling the Osmundacea or Schizaeales families. These families include genera such as *Anemia, Schizaea* and *Lygodium.* While no extant genus can be definitively identified as a direct descendant of *Thinnfeldia*, a combination of the foliage and sporophyll fronds of *Anemia phyllitidis* and the sporophylls of *Schizaea bifida* provides a comprehensive representation of the Lower Jurassic fern *Thinnfeldia.*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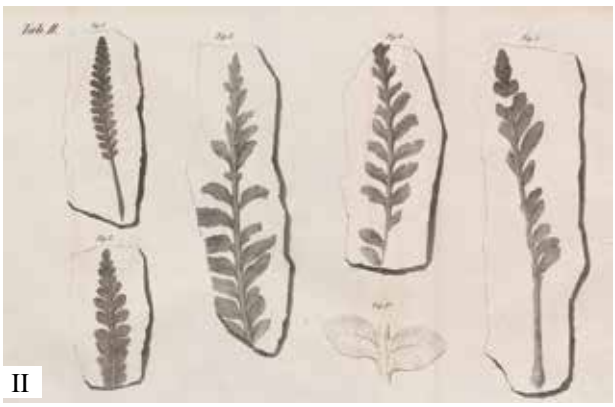
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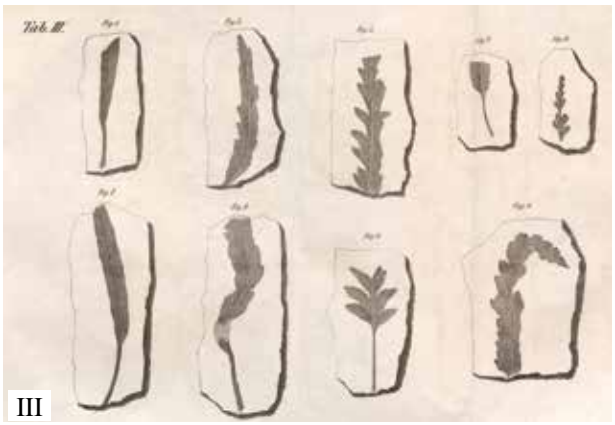

III

From Braun, 1854. „*Beiträge zur Urgeschichte der Pflanzen*". All plants described as *Kirchneria* correspond to *Thinnfeldia*, therefore Ettinghausen, 1852, takes precedence. Plate I: *Kirchneria decurrens*. Lias-Sandstein Eckersdorf bei Schloss Fantasie near Bayreuth

Tafel II: *Kirchneria ovata*. Lias-Sandstein Teufelsloch near Bayreuth

Tafel III. *Kirchneria polymorpha.* Lias-Sandstein Teufelsloch near Bayreuth

From Schenk 1867: Tafel XXVI. *Thinnfeldia decurrens* (Fig. 1-5); *Thinnfeldia obtusa* (Fig. 6-8); Plate XXVII *Thinnfeldia rhomboidales* (Fig. 1-8); *Thinnfeldia saligna* (Fig. 9-12). All from several sandpits around Bayreuth.There are no reasons to split the leaf shapes in so many species.

Description

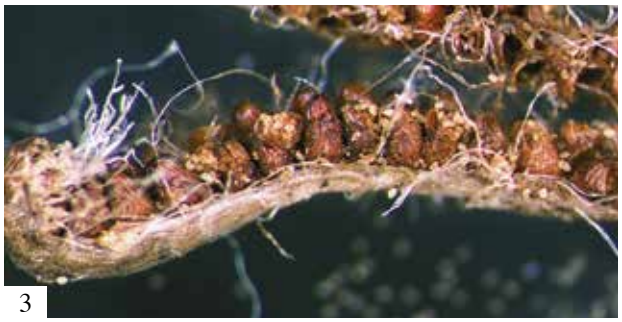
Plant: This low-growing fern is characterised by its striking division into fertile and sterile fronds. The leaf shape varies, with alternately to oppositely arranged pinnules that can range from short-stemmed to almost sessile. The foliage can be leathery to rigid or paper-thin. The rhachis can range from massively woody to thin, the appearance of the pinnules can vary from entire, elongated, blunted, sometimes tapering to segmented, bulbous, elliptical, or bluntly tapered edges. The veins are thin, mostly barely noticeable, coming together at the base, then branching off and either remaining single or usually dividing once towards the edge of the leaf.

Fertile Organs: The highly modified separate sporophyll fronds of this plant form in large numbers, arising from their own axis and connected to the main rhachis by a stalk. In the juvenile stage, fertile structures are composed of loose paired sori. As they mature, they form many shield-shaped, round sporophylls, sometimes stacked on top of each other, which reach a size of 1 to 2 cm. These sporophylls are divided into several segments, about six to eight, that spread out in a star shape from a central axis. The leaf lamina is densely covered with hair-like leaflets on the sterile side. On the fertile side, which may be partially covered with an indusium before maturity, a large number of sporangia develop, carrying spores within a ring-shaped annulus. In the adult stage, these spores are released through a catapult mechanism.

Remarks

The true character of the common genus *Thinnfeldia* remained a mystery for decades due to the rarity of finding entire plants with a combination of sterile and fertile fronds. However, recent research has confirmed that *Thinnfeldia* is a type of fern with distinct sporophylls and trophophylls. Structurally, *Thinnfeldia* bears a resemblance to today's Schizaeaceae, specifically in terms of the foliage of the genus Anemia, also known as the flowering fern, with sporophyll fronds similar to Schizaea. Some ferns, such as *Schizaea bifida*, are almost completely covered by hair-like trichomes on the sporangia-free surface of the lamina, which

Foliage of *Anemia phyllitidis* and *Thinnfeldia rhomboidales* from the Lower Jurassic, Pechgraben collected by Sepp Hauptmann, (Urweltmuseum, Bayreuth (above) and Jürgen Meyer Collection, Lichtentanne, Saxony). From a leafy frond a large number of shield-shaped sporophylls arise, one on top of the other

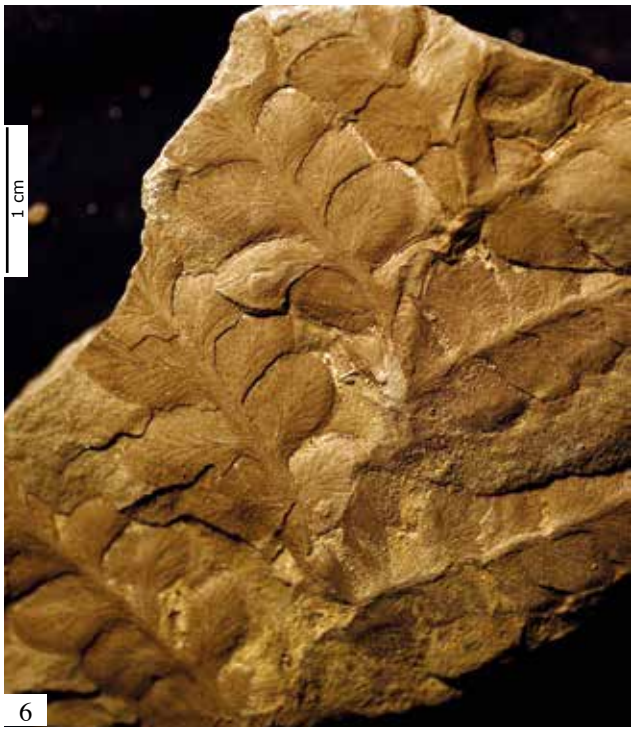


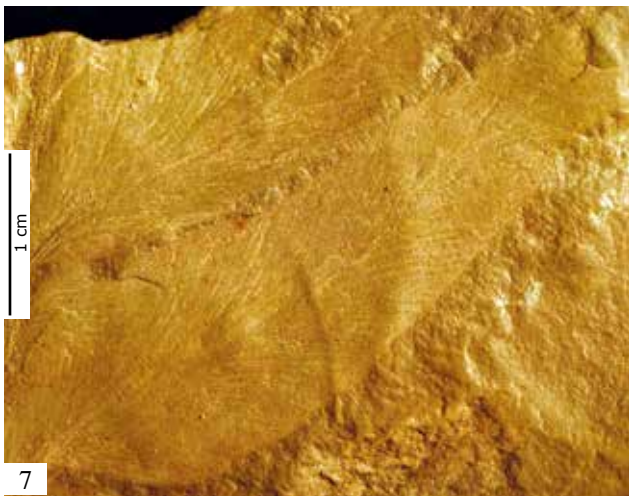
Schizaea bifida, 1. Fertile fronds, outside, 2. Fertile fronds, inside with sporangia and trichomes; 3. Sporangia and 4. Detail; Courtesy University of Auckland, New Zeland

Thinnfeldia rhomboidales, 1. Sporophyll (PECH 657); 2. Sporophyll (PECH 675); 3. Detail of individual sporophylls with surrounding hairlike leaves (PECH 661), Pechgraben, Küfner, Coll. Wachtler, Dolomythos-Museum

***Thinnfeldia rhomboidales*. Lower Jurassic. Hettangian. Fronds**

1-7. Several fronds (PECH 393, PECH 27; PECH 260; 4-5. PECH 1021, PECH 1007, Coll. Gerasch, thomaseum; 6-7. PECH 368; PECH 257; all except 4-5: Coll. Wachtler, Dolomythos-Museum



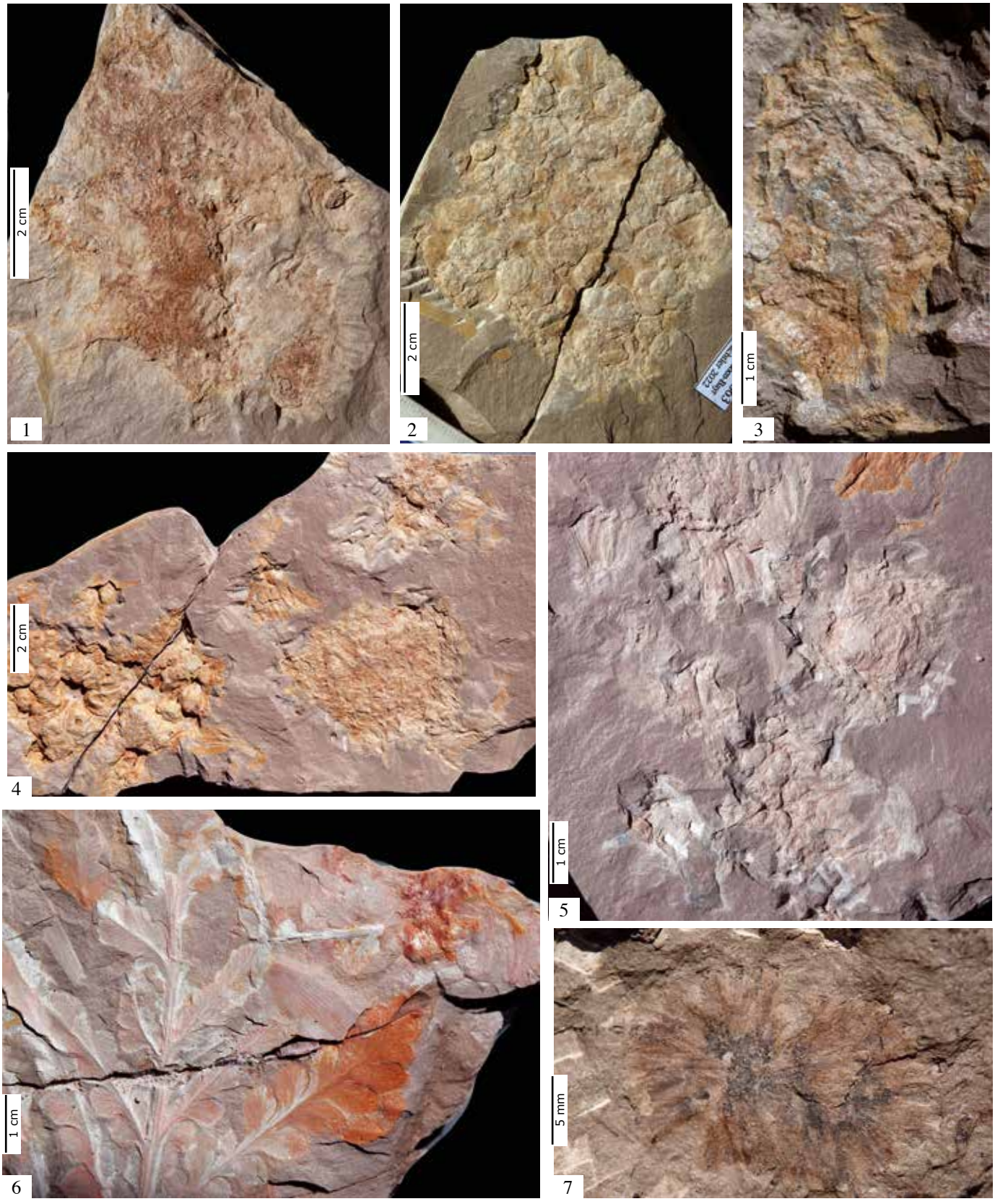


***Thinnfeldia rhomboidales*. Lower Jurassic. Hettangian. Fronds**

1-2. Isolated cuticle (Coll. Sepp Hauptmann, Urwelt-Museum Oberfranken); 3. Isolated cuticle-leaves (PECH 395); 4-5. Detail of the pinnae (PECH 299, PECH 390, Coll. Wachtler, Dolomythos-Museum); 6-7. Frond and detail of the pinnules (Both: Ex. Coll. Sepp Hauptmann; Coll. Jürgen Meyer Lichtentanne)

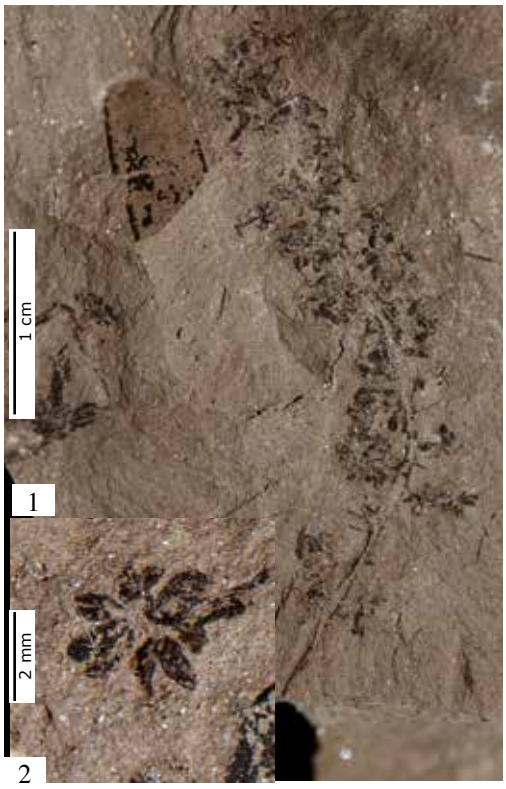
***Thinnfeldia rhomboidales*. Lower Jurassic. Hettangian. Feeding traces**

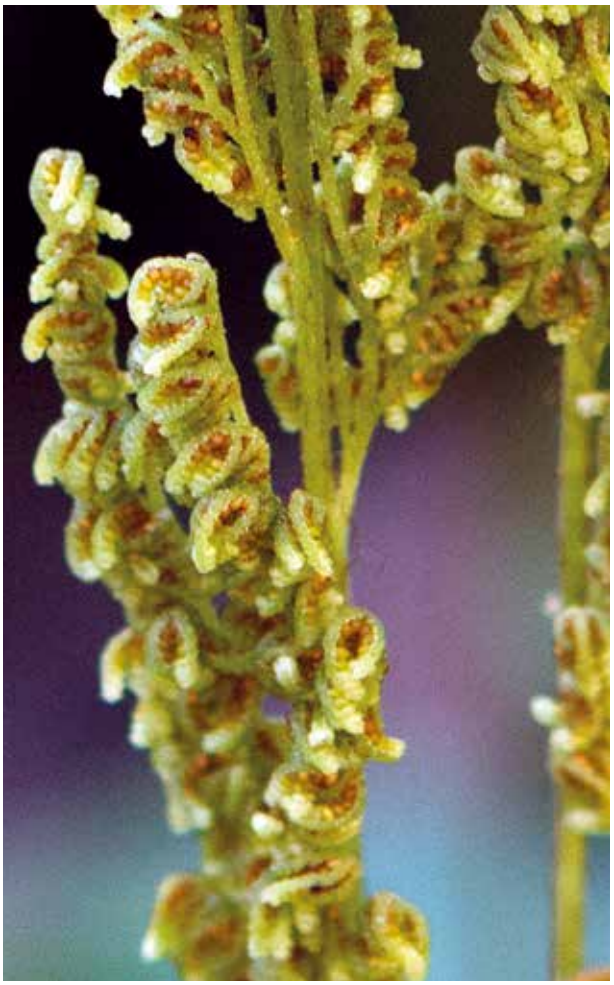
1-5. Leaflets with feeding traces (PECH 293, PECH 110, PECH 346, PECH 359, PECH 106, Coll. Wachtler, Dolomythos-Museum)

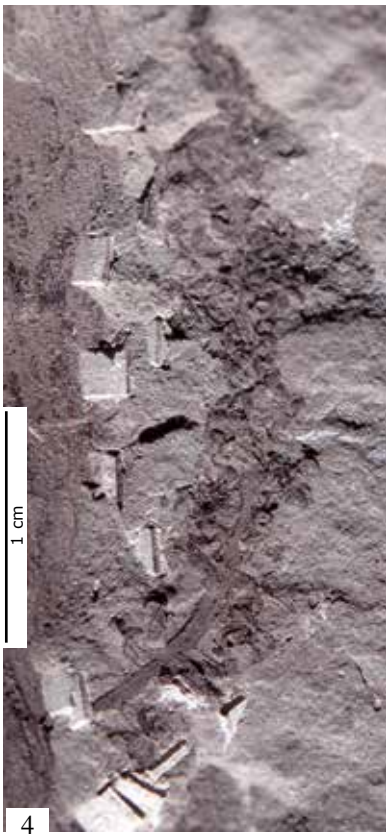


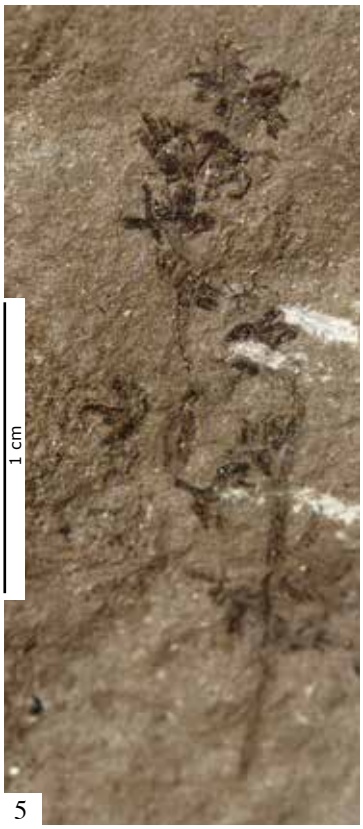
***Thinnfeldia rhomboidales*. Lower Jurassic. Hettangian. Sporophylls**

1. Sporophyll tuft (PECH 669); 2-3. Dissolving sporophylls (PECH 663, PECH 680); 4-5. Isolated sporophylls (PECH 665, PECH 666); 6. Frond with sporophylls (PECH 664); Several aggregated sporophylls (PECH 652); Coll. Wachtler, Dolomythos-Museum)





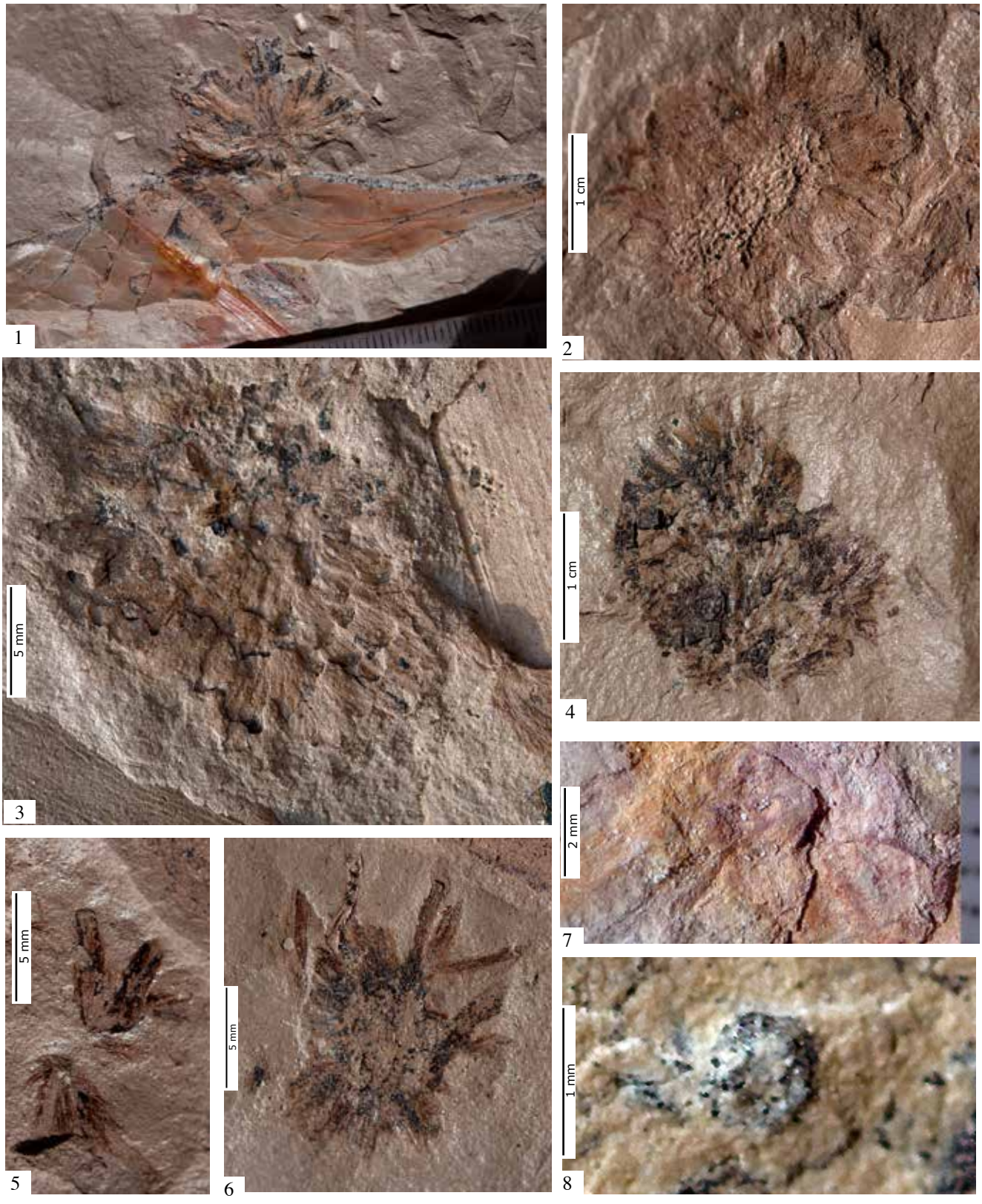




***Thinnfeldia rhomboidale*. Juvenile sporophylls**

Stachyoptys preslii. 1-2. Juvenile sporophylls and detail (PECH 131); 3. Juvenile sporophyll tuft (Coll. Meyer, Lichtentanne); 4-5. Juvenile sporophylls (PECH 631, PECH 10); All Pechgraben, Coll. Wachtler, Dolomythos,

Thinnfeldia rhomboidales has some similarities with the modern fern *Anemia phyllitidis* from the Schizaeales group. Juvenile and adult sporophylls are similar.



***Thinnfeldia rhomboidales*. Lower Jurassic. Hettangian. Adult sporophylls**

1. Frond with isolated sporophyll and shark capsule (*Palaeoxyris muensteri)* (PECH 675); 2-4. Several sporophylls (PECH 367a, PECH 367b, PECH 659); 5-6. Bifid sporophyll parts (PECH 367); 7-8. Sporangia (PECH 676, PECH 684); All Pechgraben, sandpit Küfner, Coll. Wachtler, Dolomythos-Museum

partially extend to the underside of the sporangia-bearing surface. Today, there are around 140 to 160 known species, divided into four to five genera, in the tropics and subtropics.

Phialopteris Presl in Sternberg, 1838

Phialopteris heterophylla (Sternberg & Göppert) (Cittert, Pott, Kustatscher, Schmeissner, Dütsch et Van der Burgh, comb. nov., 2018)

1836 *Asterocarpus heterophyllus* Göppert, p. 382

1838 *Phialopteris tenera* C.Presl in Sternberg, p. 114, pl. 31, figs 1a–6

1841 *Sphenopteris braunii* Göppert, p. 69, pl. 10, figs. 1, 2

1867 *Coniopteris braunii* (Göppert) Schenk, p. 36, pl. 6, figs 6–8

1958 *Phialopteris tenera* C.Presl in Sternberg; Kräusel, p. 70, pl. 3, fig. 8

1968 *Phialopteris tenera* Presl in Sternberg; Weber, p. 45, pl. 4, figs 43–45, pl. 5, figs 46–49

2018 *Phialopteris tenera* Presl in Sternberg; Weber, p. 45, pl. 4, figs 43–45, pl. 5, figs 46–49

2018 *Phialopteris heterophylla* Sternberg ex Göppert) Van Konijnenburg-Van Cittert, Pott, Kustatscher, Schmeissner, Dütsch et Van der Burgh, comb. nov. pl. 1-3

Phialopteris heterophylla is an inconspicuous and particularly rare climbing fern, which possesses both fertile and sterile fronds. The structure of its sporangia places it within the Schizaeaceae family (Cittert et al., 2018), closely resembling the modern *Lygodium*.

Description

Whole plant: It features multiple branching, liana-like appearance with delicate pinnules. Single pinnula can grow up to 2.5 cm long with a thin rhachis and multiple serrated edges.

Fertile parts: The plant has individual rounded sporangia arranged in two rows on a thin lamina, giving them a spike-shaped appearance. These range from lengths of 0.5 to 0.7 cm.

Remarks

Despite its unique characteristics, *Phialopteris heterophylla* is seldom collected, likely due to its inconspicuous appearance. Its closest modern counterpart is the *Lygodium* fern from the Schizaeales group, found in tropical Afro-Asian regions and some subtropical areas. Like *Lygodium, Phialopteris heterophylla* is a climbing fern that relies on neighbouring plants for support. This behaviour is observed in Lower Jurassic finds around Bayreuth, where these ferns exhibit unlimited peak growth rather than limited rhachis growth seen in other fern species.

The fern *Lygodium* is similar to *Phialopteris heterophylla* from the Lower Jurassic. *Lygodium japonicum:* Fertile parts above, sterile fronds below, (Wikipedia)

***Thinnfeldia rhomboidales*. Lower Jurassic. Hettangian. Reconstructions**

a. Plant with sporophyll crest; b. Different types of fronds; c. Juvenile sporophyll aggregate; d. Detail of a juvenile sporophyll; e. Sporophyll aggregate from outside; f. Sporophyll aggregate with sporangia; g. Bifid spore leaf from the inside and (h) outside with detail of the sporangia.

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From Schenk, 1867, Pl. 6, Fig. 7-8, *Coniopteris braunii* (*Phialopteris heterophylla)*

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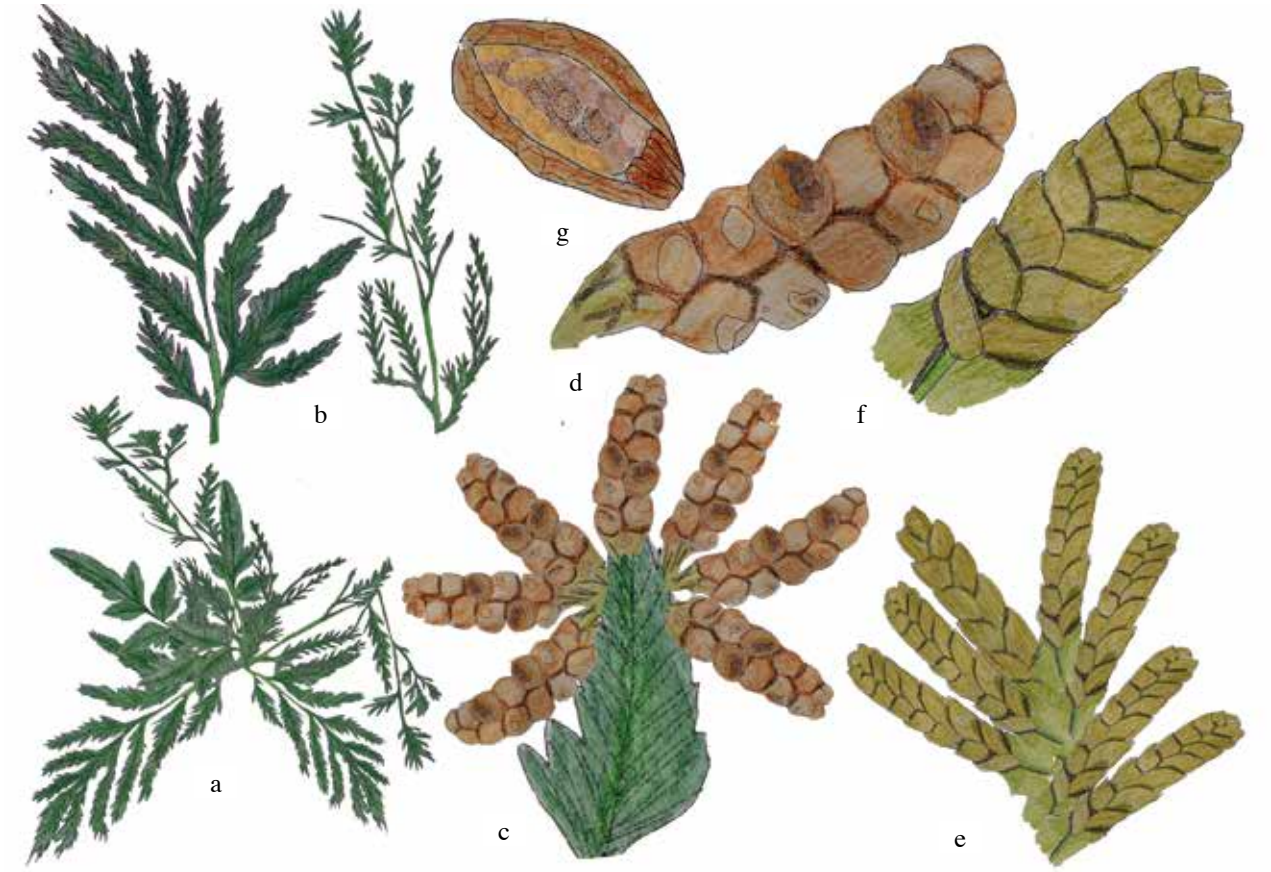

The fern *Phialopteris heterophylla*. Lower Jurassic. Hettangian. Reconstructions

a. Whole plant; b. Different types of foliage; c. Adult sporophyll spike; d. Adult sporophyll spike; e. Juvenile sporophyll spike; f. Juvenile sporophyll spike; g. Spore capsule

***Phialopteris heterophylla* Lower Jurassic. Hettangian. Fronds**

1. Original from Schenk, 1867, *Coniopteris braunii,* Taf. 6, Fig. 8, Eckersdorf, Inv. 759); 2. Original from Sternberg, 1838, Pl. 32, Fig. 1, Reindorf/Bamberg; Both Urweltmuseum, Oberfranken); 3. Juvenile plant (PECH 589), 4-5. Detail of a frond (PECH 708); 6. Frond (PECH 590); Sandpit Küfner, Coll. Wachtler, Dolomythos-Museum)

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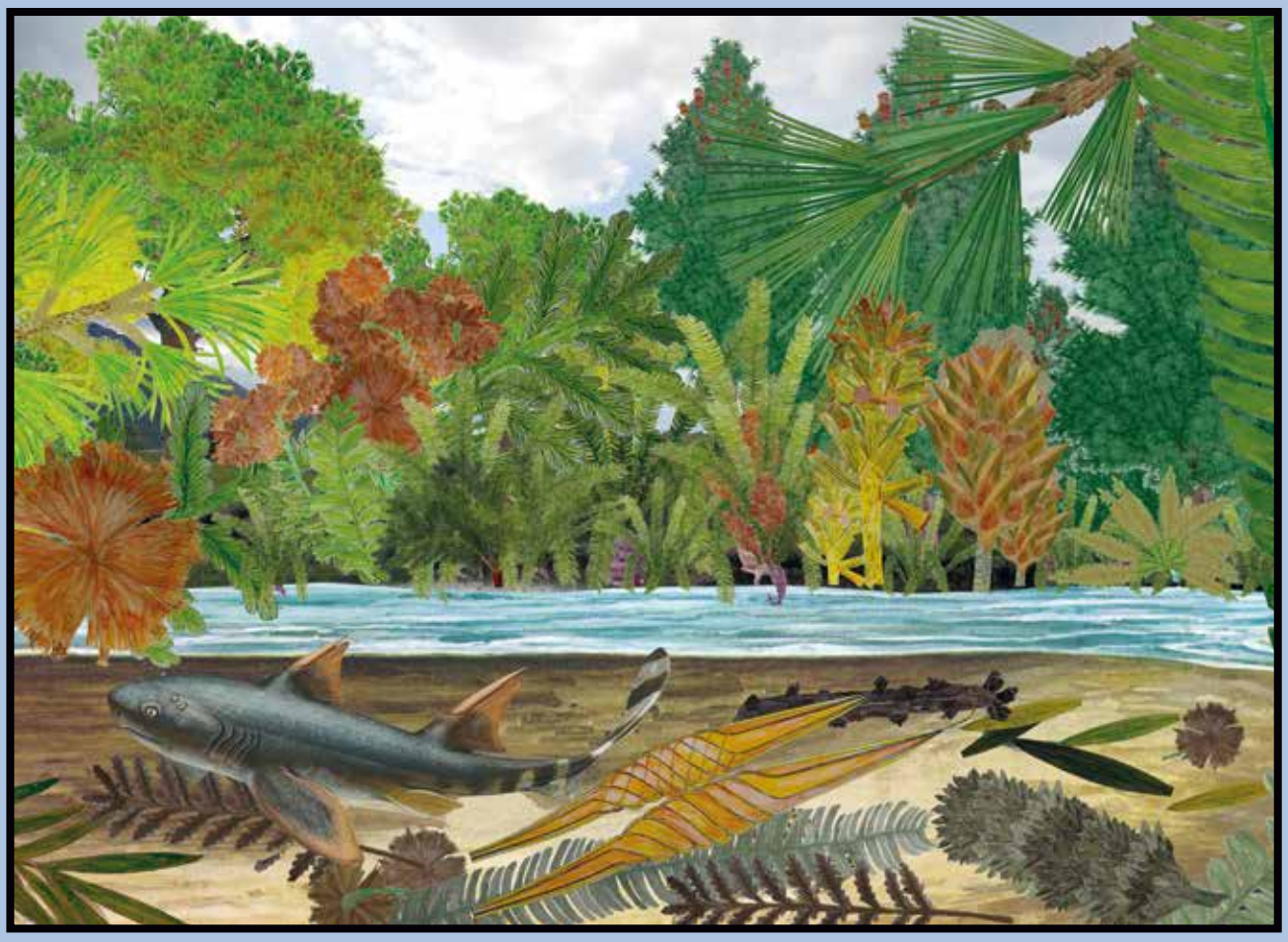
The founder of French paleobotany Adolphe Théodore Brongniart (1801-1876) Copper engraving (L'Illustrazione Italiana, March 1876, n. 22). Archive Dolomythos



The Fossil Flora of Early Jurassic

A catastrophic decline in vegetation during the Upper Triassic period was followed by a remarkable resurgence of flora in the Lower Jurassic era. However, the family of flowering plants, which is prevalent today, was clearly absent during this time. Even potential ancestors of these plants remain unidentified. During the Lower Jurassic period, conifers such as Podozamites, Swedenborgia, and Hirmeriella dominated, although they are now only found in limited areas in East Asia, represented by species like the golden larch (Pseudolarix), umbrella fir (Sciadopitys), Taiwania, and precursors of ginkgo (Ginkgoites). Cycads, including the two-seeded Nilssonia and Ctenis, as well as the multi-seeded Macrotaeniopteris, were also quite common. Interestingly, ferns that are now rare, such as Matonia (Phlebopteris, Laccopteris) and ancestors of Dipteris (Thaumatopteris, Chlathropteris, Dicytophyllum, Sagenopteris, Otozamites), played an important role during this period. Another notable fern, Thinnfeldia, which can be classified within the large Schizaeales group due to its distinct trophophyll and sporophyll fronds, was abundant. Precursors of Marattiales (Marattiopsis) were numerous. Horsetails were represented by Equisetites and Schizoneura, while strange clubmosses such as Bernettia, Bavarostrobus and Lepacyclotes also had a notable presence, with no clear descendants identified.

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