Conifers in the Lower Jurassic

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During the early Jurassic period, three conifer genera dominated large areas of the northern hemisphere. The most widespread was *Podozamites distans,* known for its characteristic short and long shoots with tongue-shaped leaves. This species shares similarities with the golden larch (*Pseudolarix*), which can still be found in some areas of eastern and central China. Extensive fossil carpets of leaves indicate that it may have shed its leaves seasonally. Another common conifer genus during this time was *Swedenborgia liaso-keuperianus,* recognised by its five-pointed seed scales, while needle-shaped leaf tufts from this species are rarely preserved. Additionally, conclusions about the ancestor of the umbrella fir (*Sciadopitys verticillata*) found on some Japanese islands can be drawn. The small-needled *Hirmeriella muensteri* was distinguishable from other conifers due to its small rounded pollen cones that occur in mass. Comparisons can be made between these ancient conifers and *Taiwania cryptomerioides*, which today is limited to some relic zones of East Asia. The gymnosperm families present during this period, including the ginkgo, exist today but in a marginal capacity.

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The conifers in the Lower Jurassic of southern Germany. On the left, the ***Swedenborgia liaso-keuperianus*** with its five-pointed seed scales is depicted; in the middle is the most common conifer ***Podozamites distans*** with female and male cones; on the right is ***Hirmeriella muensteri***, with its small round pollen cones and seed scales with two wing seeds.

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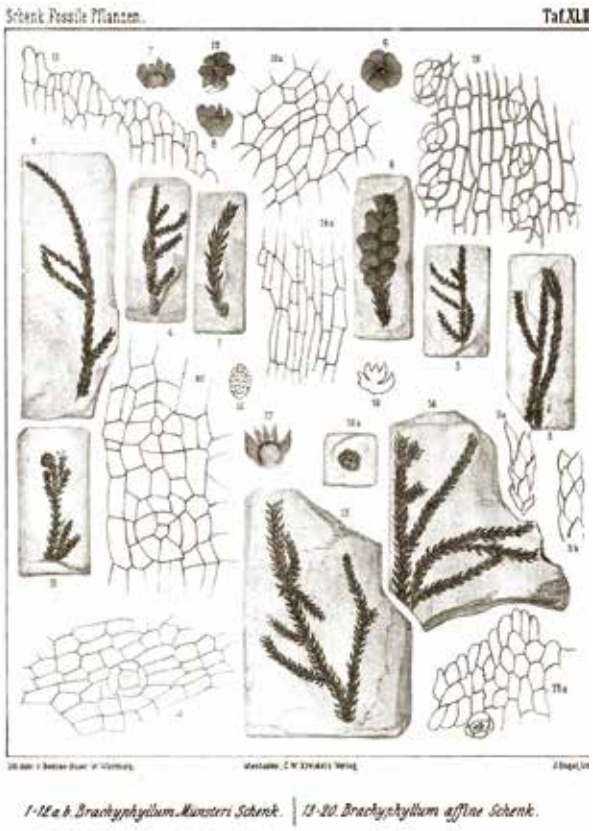
Interestingly, the gymnosperms of the European Lower Jurassic stand out due to their abundance, though limited in species diversity. Notably absent were the ancestors of today's dominant conifer families such as firs, spruces, pines, and junipers. In contrast, relic areas of East Asia featured monotypic descendants like the umbrella firs (*Sciadopitys*), golden larches (*Pseudolarix)*, and *Taiwania,* along with the ginkgo, forming a peculiar gymnosperm vegetation that also contained abundant cycads.
The knowledge of fossil life 200 million years ago is complicated by the fact that although leaves and needles were often found, fertile parts such as pollen cones or seed scales were hardly taken into account during collection. There are further peculiarities, such as the seasonal shedding of leaf needles, which still occurs today and was particularly pronounced in *Podozamites,* which makes precise classification difficult. Another intriguing aspect is the discovery of multi-lobed seed scales or cones in *Swedenborgia*, with delicate needles rarely recovered due to fragmentation during deposition.



Schenk, 1867, Plate 43. *Brachyphyllum muensteri* and *Brachyphyllum affine*, today *Hirmeriella muensteri*

It is important to note that some conifers, such as *Swedenborgia liaso-keuperianus,* had cones that dissolved either on the tree or subsequently on the ground, leading to the prevalence of isolated seed scales. Conversely, species like *Hirmeriella muensteri* predominantly shed whole cones. The detection of potential wing seeds, which rarely remained undamaged, is an overlooked area of research.
Remarkably, many of these conifers, now confined to relic zones, have been traced from the Upper Triassic to the Jurassic throughout the northern hemisphere, spanning regions from Europe to Kyrgyzstan, China, and Mongolia (Wachtler, 2024). Notable examples include *Podozamites* and *Swedenborgia. Hirmeriella muensteri* stands out as a characteristic and easily distinguishable conifer in the Jurassic of Bavaria.

Hirmeriella Hörhammer 1933

Hirmeriella muensteri (Schenk, 1867; Jung, 1968)

1828 *Brachyphyllum mamillare* Brongniart II, p. 335
1867 *Brachyphyllum muensteri* Schenk, Foss. Fl. Keup. Frankens pl. XLIII. Fig. 1-12

1867 *Brachyphyllum affine* Schenk, Foss. Fl. Keup. Frankens pl. XLIII. Fig. 13-20

1870 *Cheirolepis muensteri* (Schenk) Schimper, pp. 247–248, pl. 75, figs. 8–10

1914 *Cheirolepis muensteri* Schenk, Gothan, p. 64, pl 30, figs 5–6; pl. 31/32, fig 5; pl. 39, fig. 3

1933 *Hirmeriella rhaetoliassica* Hörhammer, Bibliotheca Botanica, 107: 29-33, pls. 5-7

1933 *Cheirolepis muensteri* Schenk, Hörhammer, pp. 1–28, pls 1-4

1968 *Hirmerella muensteri* (Schenk) Jung nov. comb., Palaeontographica 55–93, pls 15–19

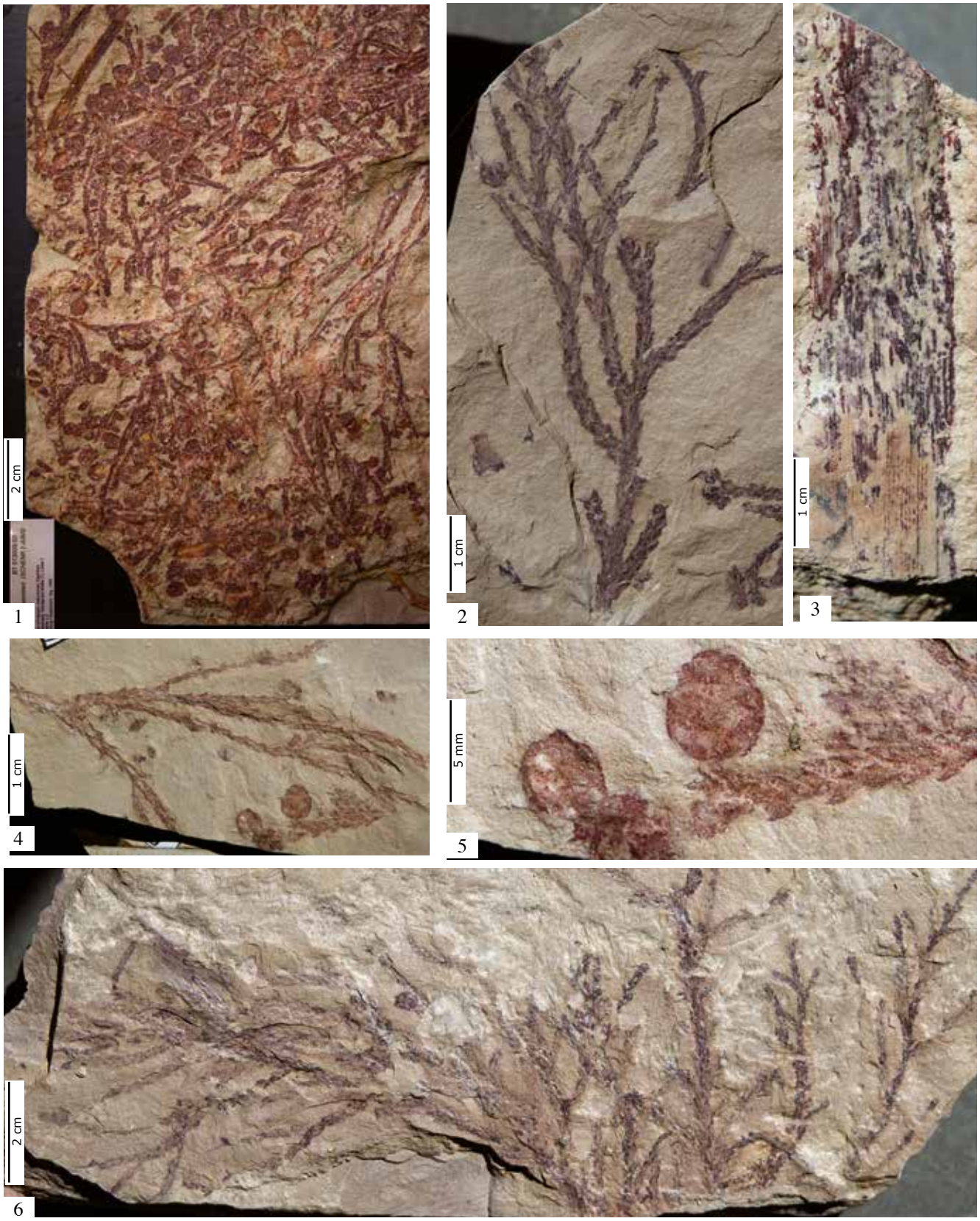
Hirmeriella muensteri is easily distinguishable by its multi-branched branches, short, pointed needle-shaped leaves, small, rounded pollen cones, and female cones consisting of a few seed scales.
As with many plant fossils, the history of research is complex. Schenk (1867) described and illustrated two species of *Brachyphyllum (muensteri* and *affine)* from Eckersdorf near Bayreuth. Since the conifer name *Brachyphyllum (mamillare)* had already been used by Brongniart for a Middle Jurassic conifer foliage, and this allowed a variety of interpretations.

The conifer *Taiwania cryptomerioides*

Today, *Taiwania cryptomerioides* grows primarily in Taiwan, as well as in a contiguous area between southern China, Myanmar, and Vietnam. It was once widespread throughout the northern hemisphere. The findings of its fossils are indistinguishable from *Taiwania cryptomerioides* and are estimated to be up to 110 million years old. The branches, female cone, seed scale, and male cones of *Taiwania* are illustrated here.

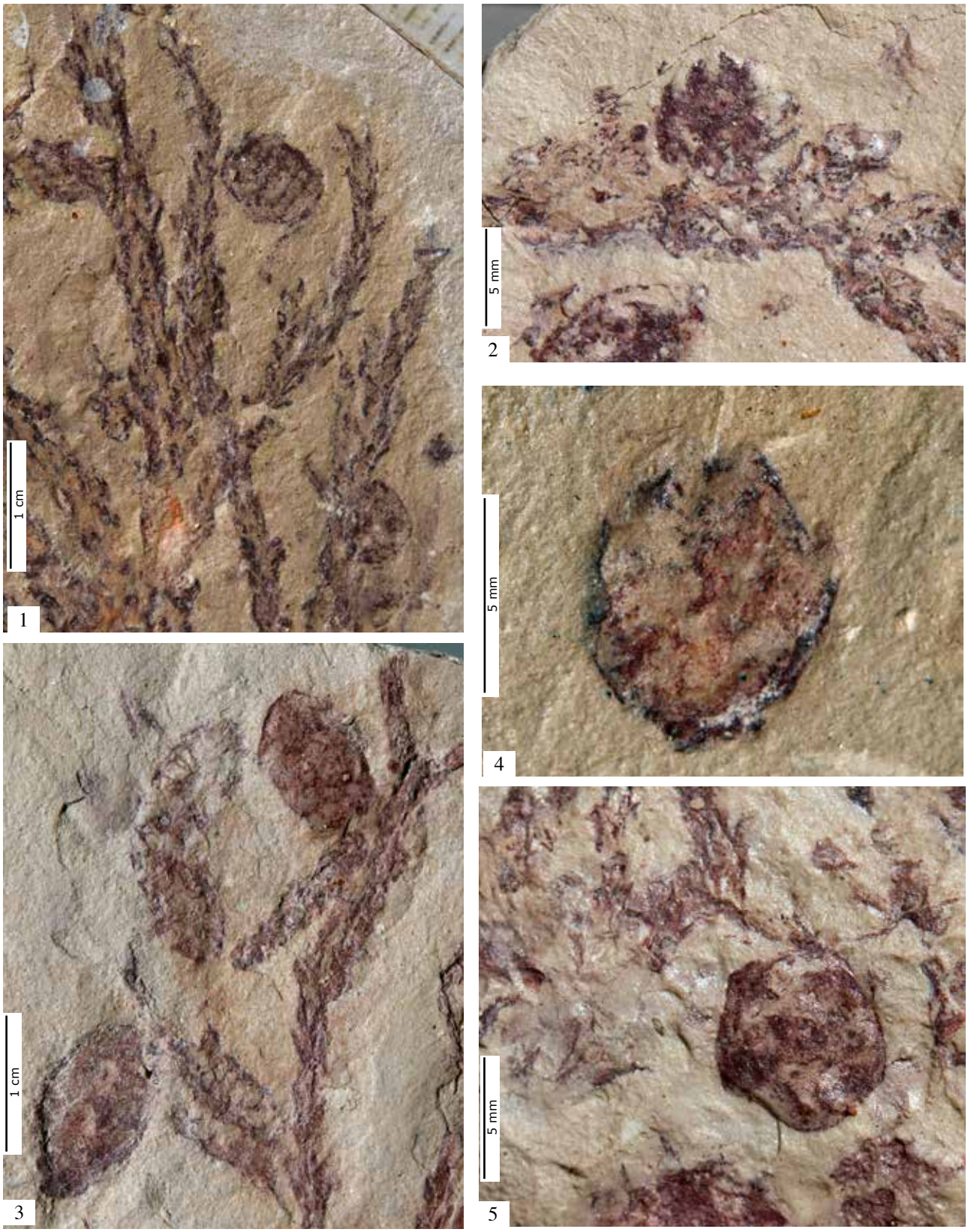
Ludwig Hörhammer (1933) renamed the species *Hirmeriella rhaetoliassica* in honour of his colleague, the German botanist Max Hirmer (1893–1981). However, he devoted a larger part of this work to *Cheirolepis muensteri,* although the genus name created by Wilhelm Philipp Schimper in 1870 was not applicable because it had already been occupied before (1849) by a recent Asteraceae member. It was later discovered that *Hirmeriella rhaetoliassica* and *Cheirolepis muensteri,* both found in Großbellhofen near Nuremberg, represent a single species. Even the depiction of the fertile parts in the publication turned out to be untargeted.

In 1968, the German palaeobotanist Walter Jung correlated the species *Hirmer(i)ella muensteri* with Schenk's original findings (pl 43, Fig. 6) from Eckersdorf based on cone discoveries from the Lower Jurassic of Bavaria. This led to the elimination of other names such as *Cheirolepidium* or *Cheirolepis muenster*i as synonyms (Doweld, 2020).



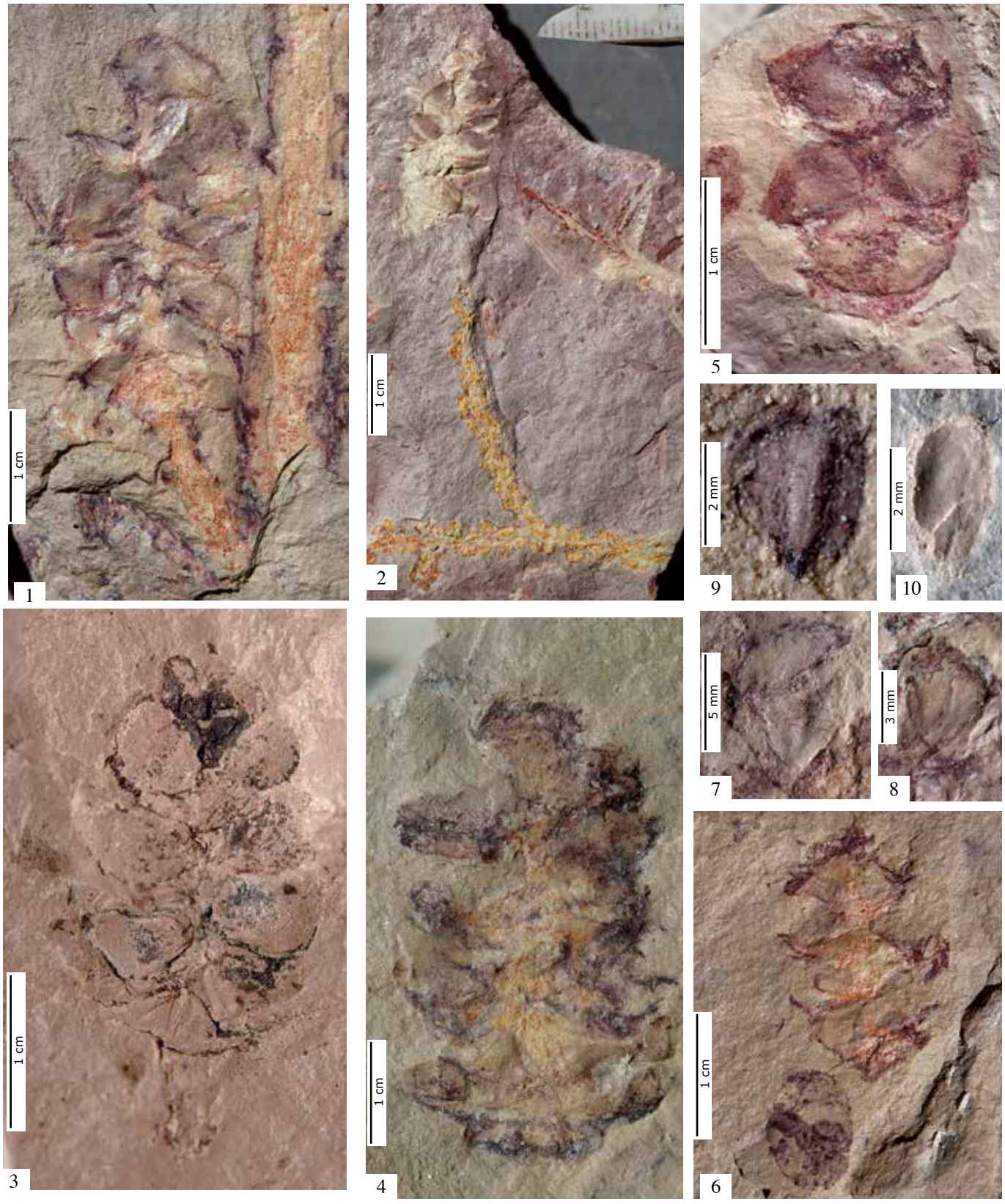
The conifer *Hirmeriella muensteri*. Lower Jurassic. Branchlets

1. Plant bed with branches and male cones (BT 0130009, Urweltmuseum Oberfranken, Bayreuth); 2. Detail of a branchlet (SCHN 06); 3.Twig (SCHN 30); 4-5. Twig and detail of male cones (SCHN 11); 6. Protruding branch (SCHN 03); Schnabelwaid, Ex. Coll. P. Silberhorn; Coll. Wachtler, Dolomythos Museum



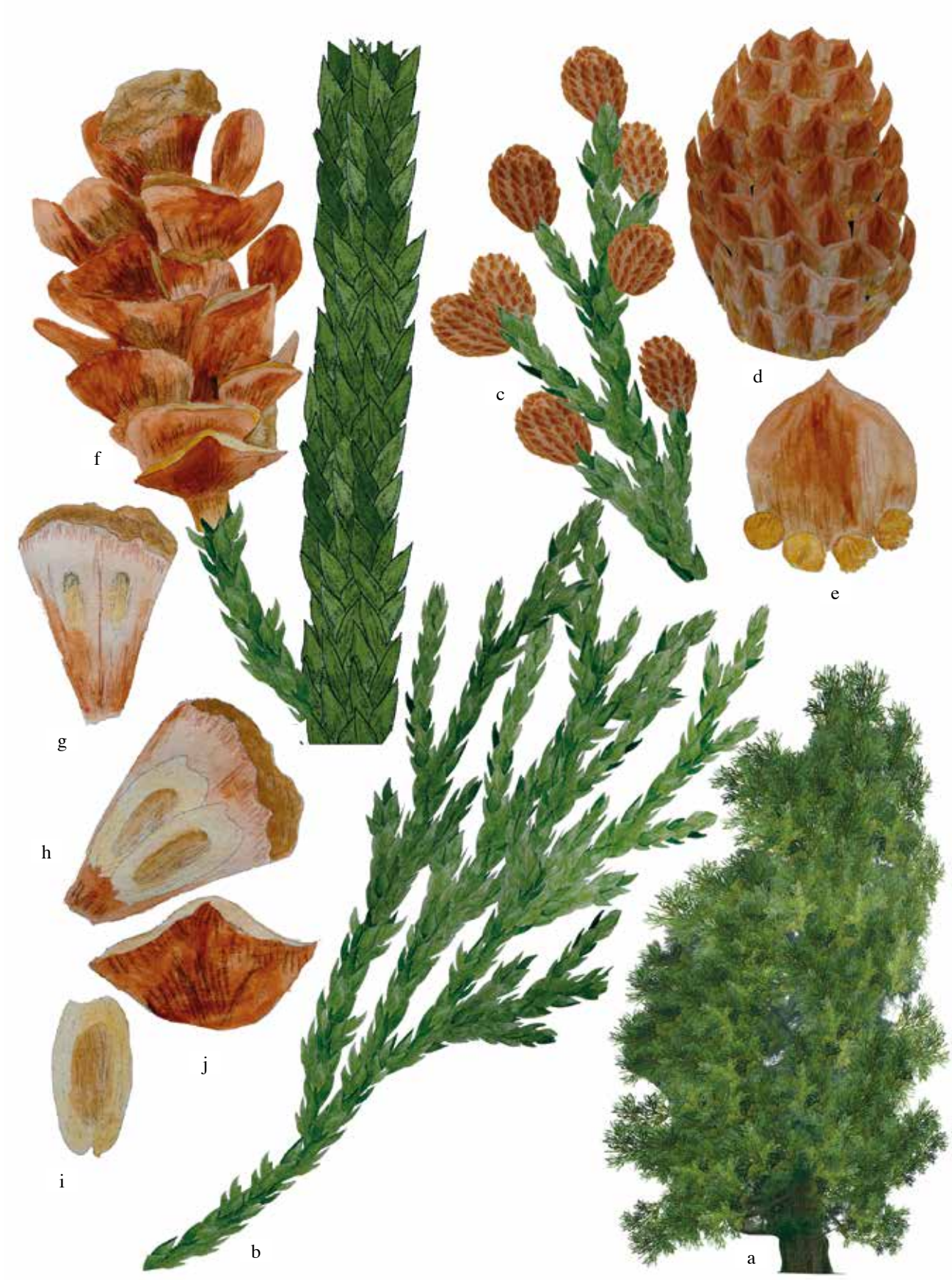
The conifer *Hirmeriella muensteri*. Lower Jurassic. Male cones

1. Branchlet with upper part of the male cone (SCHN 22); 2. Side view of a male cone (SCHN 05); 3. Two pollen cones on a branchlet, as well in the middle a female cone (SCHN 30); 4. Detail of a male cone (SCHN 01); 5. Upper view of a male cone (SCHN 12); Schnabelwaid, Ex. Coll. P. Silberhorn; Coll. Wachtler, Dolomythos Museum



The conifer *Hirmeriella muensteri*. Lower Jurassic. Female cones

1. Female cone on a branchlet (SCHN 04); 2. Seed cone on a twig (SCHN 13); 3. Female cone (Coll. Tischlinger); 4. Female cone (SCHN 39); 5-6. Juvenile female cones (SCHN 23, SCHN 34); 7-8. Seed scale detail (SCHN 56, SCHN 53); 9-10. Winged seed (SCHN 51, SCHN 54); Schnabelwaid, Ex. Coll. P. Silberhorn; Coll. Wachtler, Dolomythos Museum



The conifer *Hirmeriella muensteri*. Lower Jurassic. Reconstructions

a. Tree; b. Sterile twig; c. Branch with pollen cones; d. Male cone; e. Microsporophyll; f. Female cone; g. Seed scale with shed seed; h. Seed scale with two double winged seeds; i. Double winged seed scale; j. Seed scale outside

Description

Plant: *Hirmeriella muensteri* is a multi-branched tree. Its leaves are scaly and contiguous to protruding, typically measuring less than 1 cm in length and less than 0.1 cm in width. The needles are pointed, with younger ones being close-fitting and ovate, while the adult needles are elongated and linear.

Pollen organs: Male cones are found in large numbers on the branches, measuring approximately 1 cm in length and varying in shape from circular to elongated, with a slight stalk. These organs are equipped with a variety of small and close-fitting microsporophylls. The bracts are tapering and slightly toothed, with pollen sacs attached in groups of three or four on the underside.

Seed cones: The seed cones are cylindrical and solitary at the tip of the branches, reaching up to 5 cm in length. The seed scales are fleshy and loosely arranged on top of each other, with entire and bluntly tapered shaped. They are arched on the back and smooth on the top, with seeds in pairs on each scale and wings on both sides, hanging down inversely.

Remarks

The Lower Jurassic conifer *Hirmeriella muensteri* can hardly be related to today's pines (Pinus), firs (Abies), spruces (Picea), larches (Larix), or araucaria. This divergence from the largest coniferous families leaves us with less homogeneous groups, characterised by two or more seed scales, which align more closely with the cypresses (Cupressaceae). Since even the juniper plants and the genus *Cupressus* are hardly comparable here, the circle of possible relationships is further reduced.

In 1967, Schenk drew parallels between the present-day conifer *Athrotaxis*, a typical southern hemisphere gymnosperm with a distribution area mainly in Tasmania, and the African cypress *Widdringtonia*, which is limited to southern Africa, both of which are native to regions that were once part of the former Gondwana continent. Notably, *Hirmeriella muensteri* shows similarities with the monotypic species *Taiwania cryptomerioides,* which was widespread throughout the Northern Hemisphere in the late Jurassic and Eocene periods but is now confined to a few relic zones of East Asia, from China to Japan and Vietnam. Features such as small piercing needles, small pollen cones, and winged seeds formed on both sides allow for comparisons between these species.

Podozamites distans (Braun, 1843; Presl in Münster, 1838)

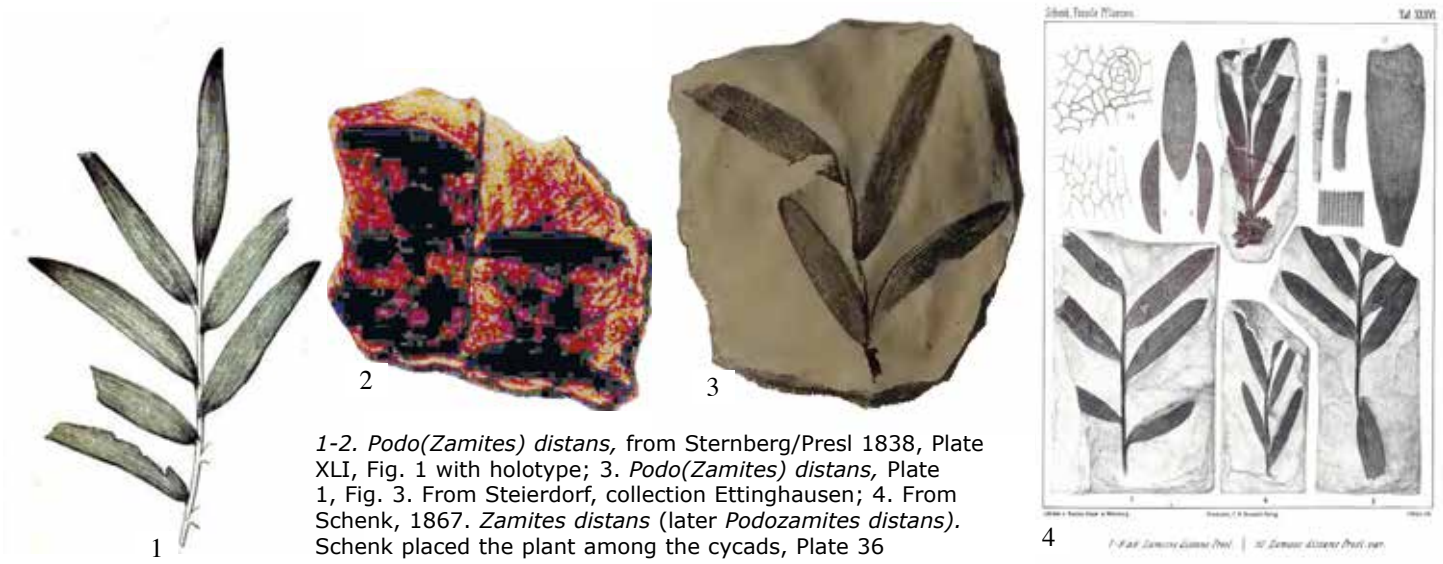
1838 *Zamites distans* Presl in Sternberg, Flora der Vorw. II. p. 196. Pl 41. fig. 1

1838 *Preissleria antiqua* Presl in Sternberg, Flora der Vorw. II. p. 192. Pl Fig. 5. 10

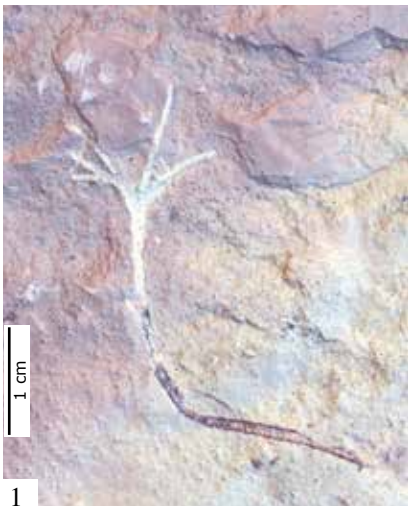
1843 *Podozamites distans* Braun in Münster, Beitr. Heft VI. p 28, 36

1867 *Zamites distans* Schenk, Plate XXXV. Fig. 10, pl XXXVI. Pl XXXVII. Fig. 1

1876 *Podozamites distans* Nathorst, Pl 13, Fig. 6



1-2. Podo(Zamites) distans, from Sternberg/Presl 1838, Plate XLI, Fig. 1 with holotype; 3. *Podo(Zamites) distans,* Plate 1, Fig. 3. From Steierdorf, collection Ettinghausen; 4. From Schenk, 1867. *Zamites distans* (later *Podozamites distans).* Schenk placed the plant among the cycads, Plate 36



Seedlings of *Podozamites distans* (Pechgraben) and for comparison *Pseudolarix amabilis*

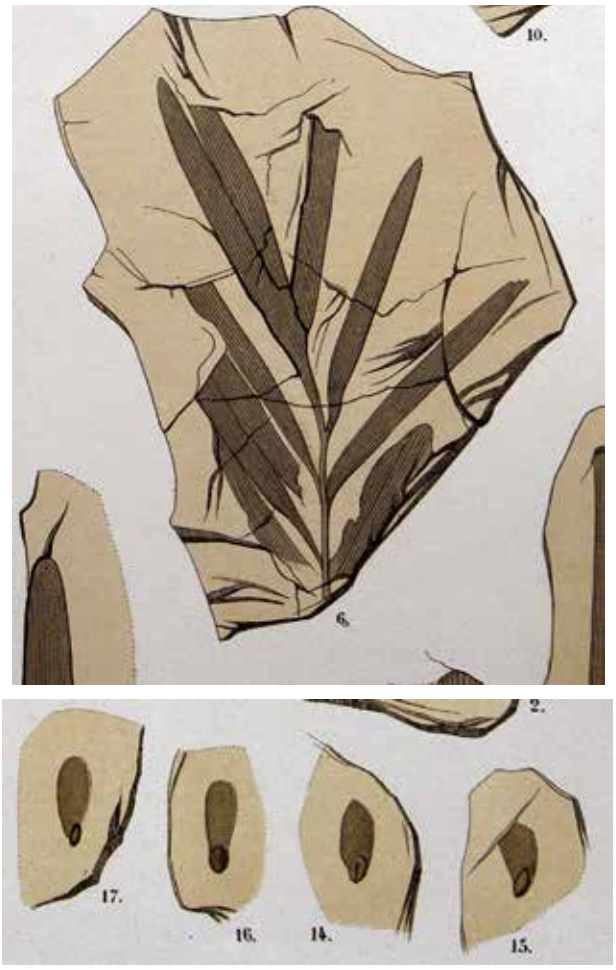
1. Coll. Hauptmann, Urweltmuseum Oberfranken; 2-4. PECH 696, PECH 352, PECH 635 (Coll. Wachtler, Dolomythos-Museum)

5. *Pseudolarix amabilis,* Herbarium of the Arnold-Arboretum, Harvard-University; 6. Seedling.

During the late Triassic and the transition to the Jurassic period, a conifer genus known as *Podozamites* thrived in the northern hemisphere. Despite being discovered in the early 1800s, *Podozamites* remains one of the most enigmatic plants in existence. It dominated large areas in the Early Jurassic (Hettangian) period, particularly in Central Europe.

The history of *Podozamites'* description is complex. In 1838, the Czech naturalist and physician Prešl (1794–1852) described a species called *Zamites distans* in Sternberg's book "*Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt"* (Attempt at a Geognostic-Botanical Representation of the Flora of the Prehistoric World) Vol. 2/September 1838 on page 196, along with a drawing and a poor-quality hand-coloured illustration of the plant on plate XLI, Fig. 1. Jung (1974) had already concluded: "Although there is a handwritten note from Münster on the back of one plate stating that it is the original of the above-mentioned illustration, no greater correspondence can be established between the drawing and the fossil. One must rather

assume that the drawing is a combination of print and counterprint, which Schenk already assumed after studying our Munich material" (1864a, p. 64). Much has been said about this fossil, which originated from Strullendorf near Bamberg and is attested by an original label from the collection of Münster (1776–1844).
Nevertheless, attempts were made (Doweld, 2022) to legitimise another genus name, *Preissleria antiqua* (Vol. 2: 192, pl. XXXIII, Fig. 5, 10, September 1838) from the locality Steindorf near Bramberg. Although, as seen from the pictures, it bore no resemblance to *Podozamites* and was more likely a fern.
The considerations of the botanist Braun (1800–1864), who also came from Bayreuth like Münster, were helpful. In "*Beiträge zur Petrefakten-Kunde*" (Contributions to Palaeontology) published by Münster (1843, sixth issue, page 36), Braun made the decision to rename the plant species from *Zamites distans* suggested by Presl to *Podozamites distans.* This change was necessary since the name *Zamites* was reserved for cycad-like foliage, while *Podozamites* accurately described the coniferous nature of the plant due to its tuft-like short shoots. As a result, various authors (Ettinghausen, 1852; Schenk, 1867; Nathorst, 1876; Gothan, 1914; Langer, 1945; Jung, 1972; Nosova et al., 2017) attempted to shed light on the life cycle, appearance, or structure of the fertile parts and possible evolutionary lines of *Podozamites distans*.



The Swedish palaeobotanist Alfred Gabriel Nathorst (1876) placed *Podozamites distans* (plate 13, Fig. 6) with the cycads, although in central Europe (Braun, 1843), the idea that it was a conifer was accepted. On plate 14, Fig. 13–17, Nathorst depicted winged seeds, which he classified under the new species *Pinites lundgreni*. They probably belong to *Podozamites*, because *Swedenborgia,* which also occurs in the same layers, has different seed scales.

Description

Whole plant: *Podozamites distans* is a tree-shaped plant, estimated to reach heights of 10 to 15 m, with furrowed bark. Its branches exhibit a clear differentiation between short and long shoots, with short shoots growing sideways in a plane and long shoots emerging apically on the branches.
Leaves: The leaf tufts emerge as short shoots in large numbers (containing 10 to 15 leaves) from a woody needle sheath that can measure up to 5 cm long. These slender leaves are elongated and reach about 10 cm in length and 1 cm in width. They taper to a pointed or blunt tip and are characterised by several parallel veins and a concave shape. On long shoots, the leaves are arranged in a spiral pattern and typically taper off towards the end, with variations in width from slender and needle-shaped to broad-leaved.
Pollen cones: The pollen cones are approximately 5 cm in length and 1.5 cm in width, with a slender pedicle about 1 cm long. The microsporophylls arise loosely from the central rhachis, with individual pollen sporophylls measuring about 0.3 cm in length and up to 0.2 cm in width. The bract ends taper and are strongly grooved on the outside, each equipped with two pollen sacs.
Seed cones: The cones grow in tufts together, appearing round to oval and reaching a length of 2 to 3 cm, with a short stem. The seed scales are woody and taper, with seeds emerging together in elongated pairs, with pointed to slightly rounded wings.









The conifer *Pseudolarix amabilis*

1. Tree; 2. Juvenile female cones; 3-4. Young, still green and mature female cones (from Dörken V. M. , Höggmeier A. , 2018); 5. Seed scales outside, inside and seeds; 6. Fallen seeds with broken wings; 7. Pollen cones; 8. Detail of the male cones; 9. Withered pollen cones

Rarely did the classification of a plant cause such problems. The short shoots of *Podozamites distans* were often placed with the Ginkgo and described as *Karkenia hauptmannii,* the woody cuffs as female fructifications with the name *Schmeissneria microstachys* (Kirchner & Cittert, 1994).

Remarks

Although *Podozamites distans* is more common than any other plant, especially in the sand pits at the Pechgraben, and one might assume that all the secrets about reproduction or appearance have been clarified, this is not the case.

Early evidence of this conifer, which exhibits characteristic short and long shoots, can be traced back to the Ladinian/Carnian border in Kyrgyzstan (Madygen Formation) with *Podozamites dobruskinae* (Wachtler, 2024). However, it was completely absent in the Erfurt Formation (Ladin), despite being of a similar age, and was barely present even in the Late Triassic of Europe, possibly due to the Raibl catastrophe during the Carnian period, which brought about numerous changes in the plant world (Wachtler, 2021). From the Lower Jurassic onwards, *Podozamites distans* became widespread in the northern hemisphere, persisting until the Eocene epoch around 50 million years ago. Well-preserved specimens (*Pseudolarix wehrii)* from the Eocene have been discovered, particularly in the Republic/ Washington State (USA).

Due to the peculiarity of the cones and especially the winged seeds, sheaths, and the long and broad leaves that emerge in clusters from them, development lines with the monotypic genus *Pseudolarix,* the golden larch – which today occurs natively in some disjunct areas of eastern and central China –are possible.

Since *Podozamites distans* is by far the most common plant in many lenses of the Lower Jurassic, with carpets of the characteristic tongued leaves in the layers, the assumption of a seasonal shedding arises, as is the case today with some gymnosperms such as ginkgos, larches (Larix), Sequoia trees (Metasequoia), bald cypresses (Taxodium), and golden larches (Pseudolarix). The shedding of leaves is not necessarily limited to a harsh climate, as the distribution area of bald cypresses extends into the subtropical areas of Guatemala and Mexico. A variety of Marattiales ferns and cycads occurring in the same fossil lenses indicate at least a subtropical temperate climate in the Lower Jurassic of Europe.

The rarity of female cones or seed scales found in sediments rich in *Podozamites dis-*

The flattened needles of today's golden larch grow from 2 to 6 cm long, and 1 to 4 mm wide. They turn yellow to reddish in autumn before falling off. They later arise either from a wooded cuff as short shoots or at the end of the branches as long shoots. The flattened needles of the short shoots of *Podozamites* can reach up to 10 cm, with a width up to 1 cm (PECH 377); Sandpit Küfner, Pechgraben, Coll. Wachtler Dolomythos Museum

tans remains unclear. In today's genus Pseudolarix, the cones decay similarly to those of cedars or firs but in contrast to larch trees (Larix), whose cones remain on the tree for years, allowing isolated seed scales to be found on the ground.
One possible explanation is that the leaves of *Podozamites distans* were blown from the hinterland by the wind near the coast, whereas the heavier seed scales remained closer to the source. Consequently, the flying seeds could have been destroyed more easily. This could explain why more flying seeds were found in the Swedish sites (Nathorst, 1856).

Swedenborgia liaso-keuperianus (Braun, 1847; Nathorst, 1876)

1847 *Schizolepis liaso-keuperianus* Braun, p. 86

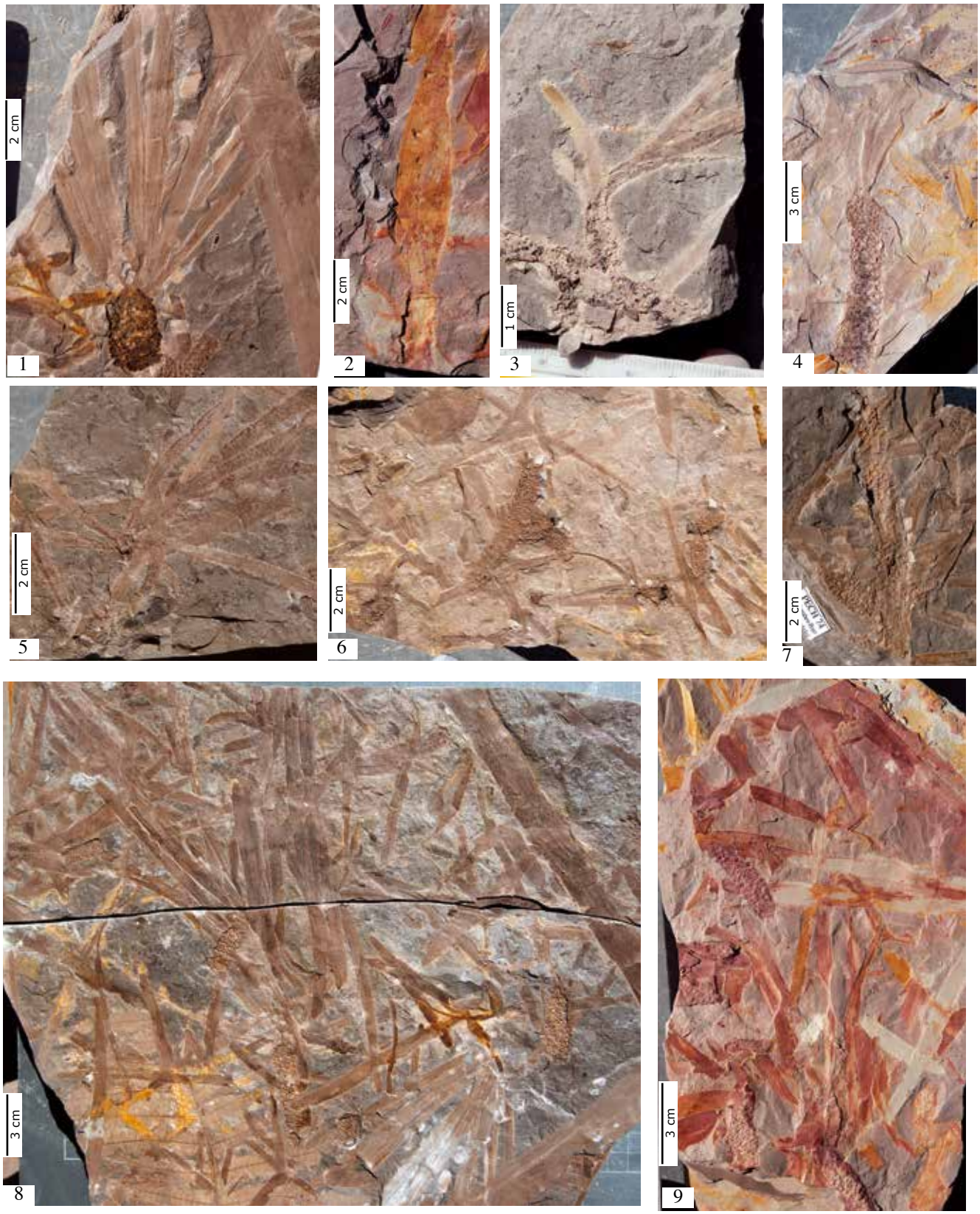
1867 *Schizolepis liasokeuperina* Schenk, p. 179, Plate XLIV. Fig. 1-8

1876 *Swedenborgia cryptomerides* Nathorst, p. 65, pl. XVI fig. 6-12

This conifer, which played an important role in the Lower Jurassic of Northern Bavaria, was initially described in 1847 by Braun under the name *Schizolepis liaso-keuperinus,* where he pointed out: "The seed scales of these conifer are deeply two-lobed, which circumstance certainly justifies the separation of *Voltzia*". The specimen was found in the Veithlahm quarry near Kulmbach (Bayreuth).
However, it was later determined (Doweld, 2001) that the genus name had already been used previously (Nees von Esenbeck, 1842) for a recent sour grass family (Cyperaceae), today known as *Scleria latifolia* Sw. Although attempts were subsequently made to rename it as *Schizolepidopsis* (Doweld, 2001), it was not until 1876 that Swedish Arctic researcher and palaeobotanist Alfred Gabriel Nathorst (1850–1921) named a similar conifer from the Hettangian of Pålsjö (Skåne-southern Sweden) as *Swedenborgia cryptomerides.* Therefore, the valid name for the conifer species found in various locations around Bayreuth in the Lower Jurassic is *Swedenborgia liaso-keuperianus*, regardless of whether *Swedenborgia cryptomerides* from Sweden is a separate species or simply a synonym.
Nathorst chose the genus name to honour the Swedish mystic and theosophist Emanuel (von) Swedenborg (1688–1772), while the species name was based on a supposed

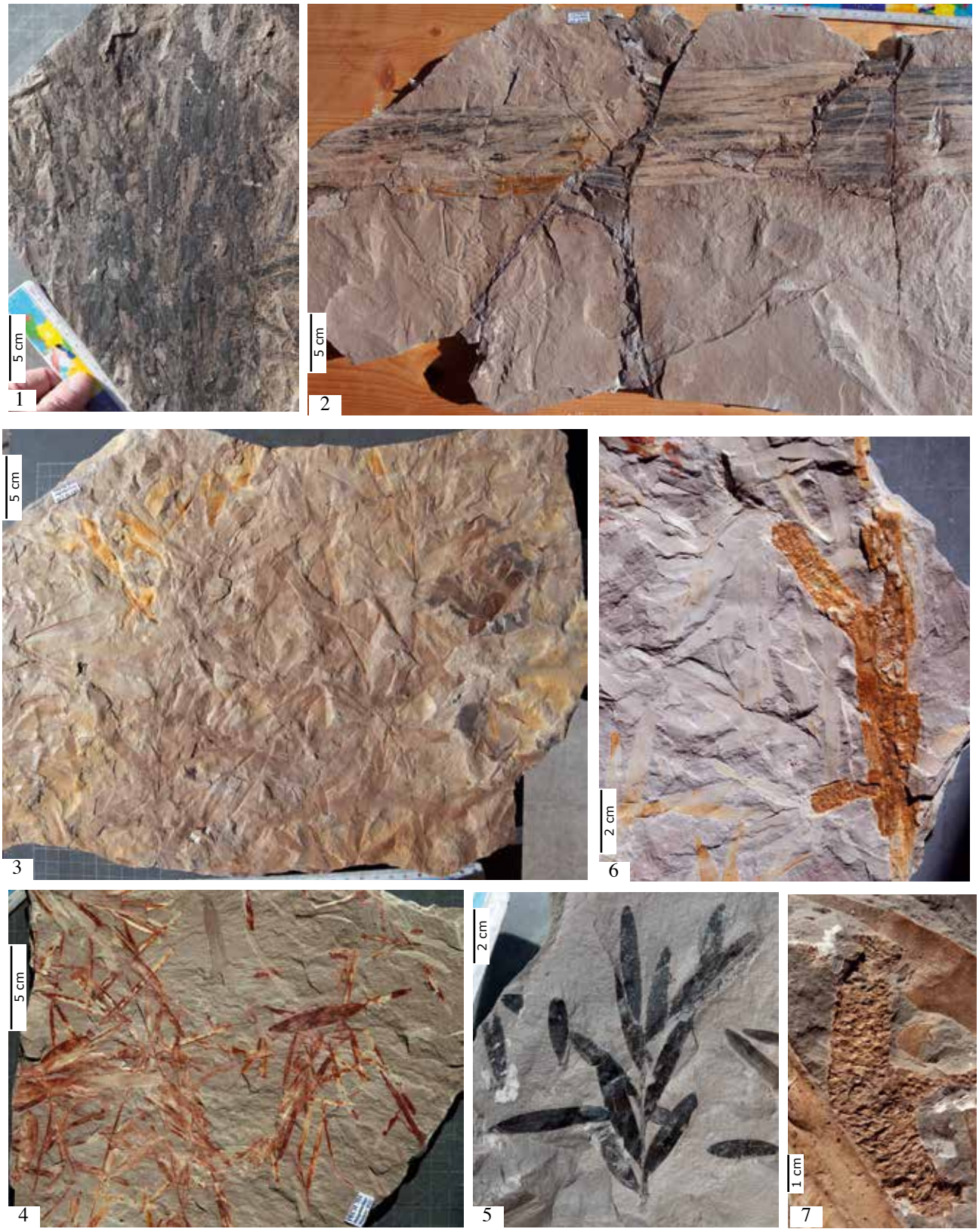
The conifer *Podozamites distans*. Lower Jurassic. Reconstructions

a. Tree; b. Seedling; c. Branch; d. Sheath; e. Short and long shoots; f. Leaves; g. Female cone; h. Seed scale and seeds; i. Pollen cones and microsporophylls



The conifer *Podozamites distans*. Lower Jurassic. Twigs

1. Leaves emerging from a collar (PECH 75); 2. Closed immature leaves (PECH 107); 3. Branch with juvenile short shoots (PECH 378); 4. Longer cuff with leaves (PECH 60); 5. Sheath with short shoots, upper view (PECH 120); 6-7. Various tufts (PECH 103, PECH 74); 7-8. Plates with leaves and various tufts (PECH 123; PECH 116); Sandpit Küfner, Pechgraben, Coll. Wachtler, Dolomythos Museum

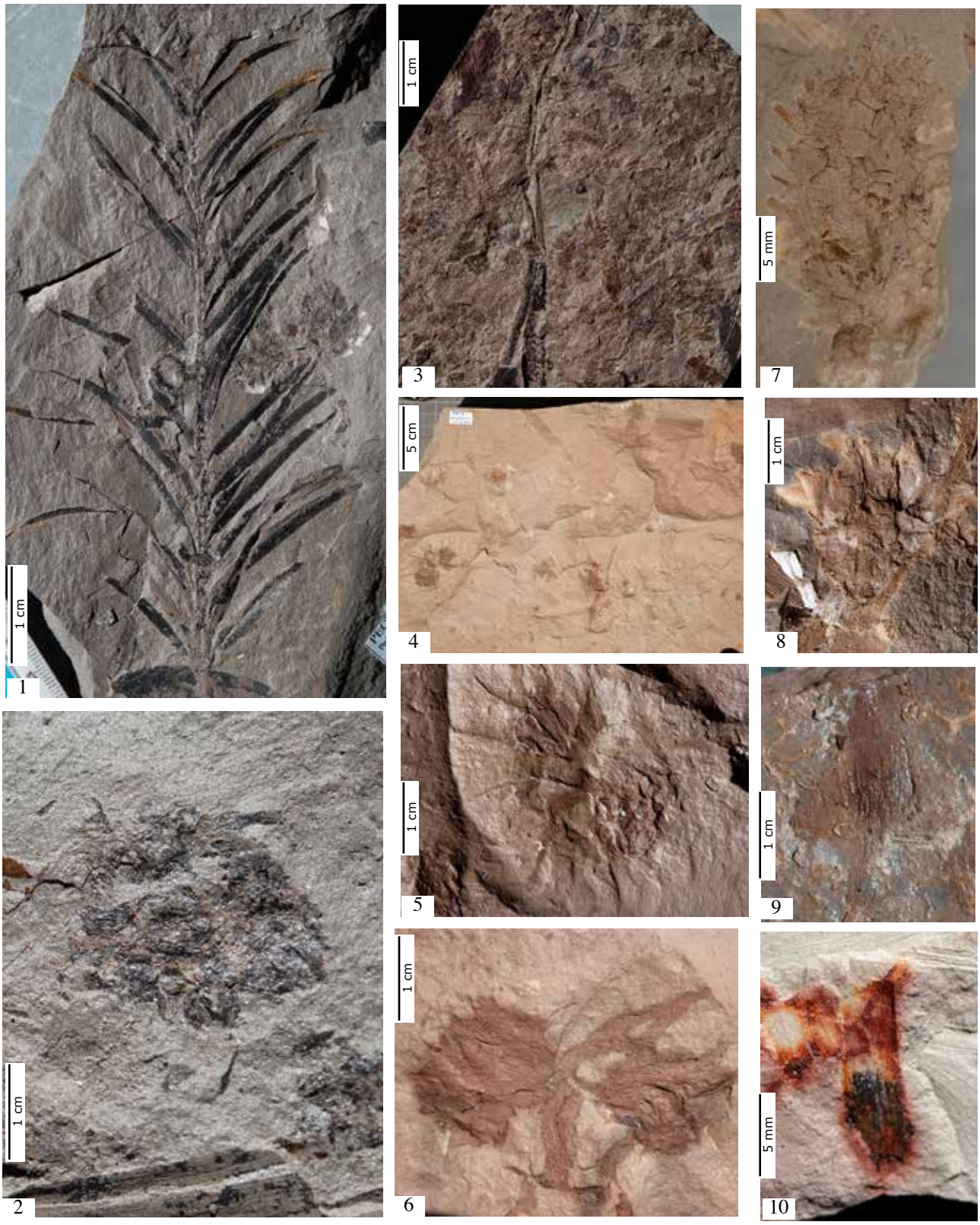


The conifer *Podozamites distans*. Lower Jurassic. Stems and branchlets

1. Stem part (PECH 1023, Coll. thomaseum); stem with attached shark eggs (*Palaeoxyris)* (PECH 369); 3. Large plate with leaves (PECH 129); 4. Plate with short and long shoots (PECH 701); 5. Long shoot (PECH 274); 6. Branch with leaf sheaths and attached leaf tufts (PECH 643); 7. Branching cuff (PECH 07; Sandpit Küfner, Pechgraben, Coll. Wachtler, Dolomythos Museum

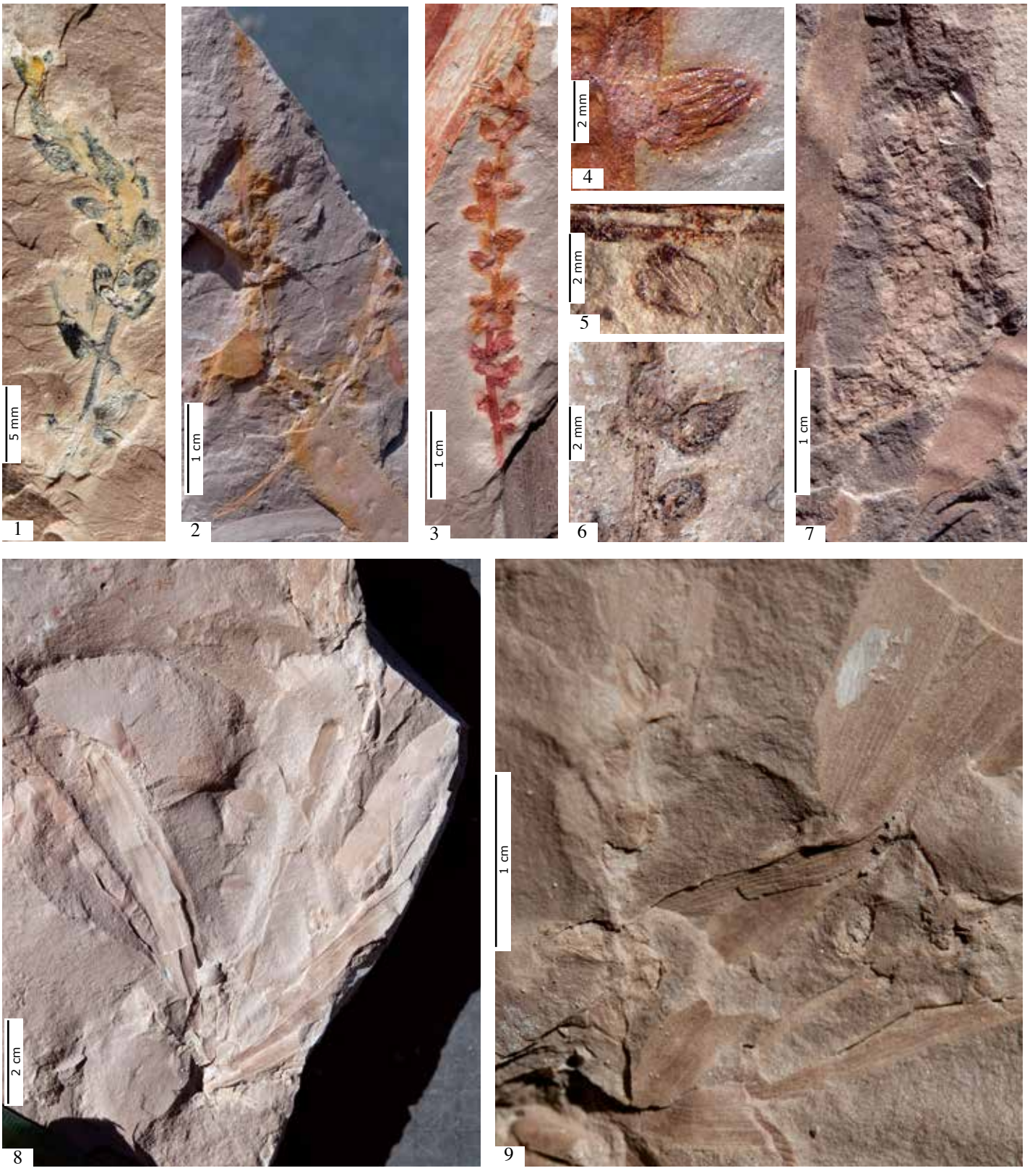
The conifer *Podozamites distans*. Lower Jurassic. Leaves

1-3. Various long shoots (PECH 38, PECH 45, PECH 77); 4. Leaves with female cone (PECH 1014, Coll. thomaseum); 5-6. Single leaves (PECH 310, PECH 308); Sandpit Küfner, Pechgraben, Coll. Wachtler, Dolomythos-Museum



The conifer *Podozamites distans*. Lower Jurassic. Female cones

1-2. Long shoot with female cones (PECH 460); 3. Cone-Compound (PECH 468); 4-5. Several female cones (PECH 17); 6. Two cones (PECH 12); 7. Cone, lateral view (PECH 1014); 8. Juvenile cone (PECH 381); 9. Single seed scale (PECH 270); 10. Winged seed (PECH 692); Sandpit Küfner, Pechgraben, Coll. Wachtler, Dolomythos-Museum



The conifer *Podozamites distans*. Lower Jurassic. Male cones

1. Pollen cone (PECH 53); 2. Two male cones (PECH 524); 3-4. Pollen cones and detail of microsporophylls (PECH 366); 5-6. View and side view of microsporophylls (PECH 34); 7. Pollen cones (PECH 527); 8-9. Short shoot with two pollen cones and detail (PECH 142); Sandpit Küfner, Pechgraben, Coll. Wachtler, Dolomythos Museum

similarity to the modern conifer Cryptomeria.

In addition to *Swedenborgia liaso-keuperianus* from southern Germany and *S. cryptomerides* (Nathorst, 1876) from Sweden, other subspecies such as *S. minor, S. major, and S. benkerti* from various localities in northern Bavaria, *S. megasperma, S. tyttosperma,* and *S. longiloba* from the Russian Donetsk Basin (Stanislavsky, 1971), as well as *Swedenborgia lata, S. rigida, S. coreanica, S. onoyamai*, and *S. attenuata* (Kon'no, 1944) from Greenland, Japan, China, and Korea were introduced, but several of them may be only synonyms.

There is uncertainty surrounding the Lower Jurassic genus *Czekanowskia* from the Amur region in eastern Siberia, as described by Oswald Heer (1876). It could also be a *Swedenborgia* species, unless further examination reveals that the leaf needles exhibit dichotomous bifurcation, in which case it would be classified as Ginkgoales.

One of the most striking features of *Swedenborgia* is its five-lobed (sometimes six) seed scales, with seeds hanging dorsiventrally, usually with a small bilateral wing on each lobe.

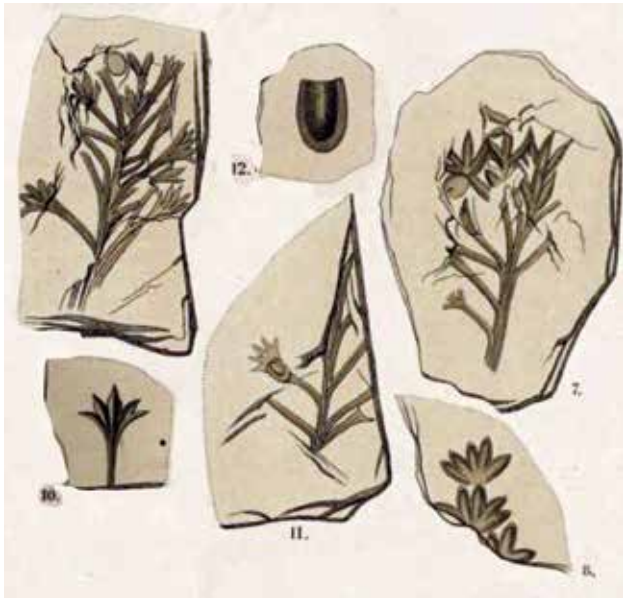
The origins of this conifer can be traced back to the Early Triassic (Olenekian-Anisian) with *Aethophyllum stipulare* (Grauvogel Stamm, 1978), or even further back to the Carboniferous-Permian boundary, with variants such as *Thuringiostrobus* (Wachtler & Perner, 2015). In the Early Triassic period, *Aethophyllum* was considered a characteristic conifer of Central Europe, extending as far as Spain (Juàrez & Wachtler, 2015), while being scarce or absent in the Southern Alps region (Wachtler, 2011). A period of propagation followed in the Ladinian especially in German localities like Ilsfeld with *Swedenborgia nissleri* (Wachtler, 2016).

Challenged arose due to the scarcity of well-preserved branches, with only a few locations in the lenses of the Lower Jurassic Pechgraben near Bayreuth yielding branches that could offer insights into the development of this conifer and its potential present-day representatives. These branches form leaf buds from which the slender, long needles emerge in tufts.

The modern descendants of *Swedenborgia* are primarily represented by the Japanese umbrella fir (*Sciadopitys verticillata)*, which occurs as a monotypic conifer genus on some islands in Japan. This species is characterised by a distinct needle arrangement and fused seed scales, each containing 5 to 9 seeds. Unlike its ancestors from to the large Triassic period, the pollen cones of the Japanese umbrella fir standing in clusters at the ends of the branches are

1-8. Schizolepis Braunii Schenk. | 9-12a. Stachyopitys Preslii Schenk.

From Schenk 1867: *Schizolepis braunii*, Taf. 44, Plate 1–8. Braun described this plant in 1847 as *Schizolepis liaso-keuperianus.* Since the genus name was already occupied by a recent angiosperm (1842), the correct name is *Swedenborgia liaso-keuperianus.*



From Nathorst 1876: *"Bidrag till Sveriges fossila flora".* Plate XVI. Description specimen from *Swedenborgia cryptomerides*

much smaller, measuring only 6 to 12 mm in length today. Interestingly, from the early Triassic to the end of the Ladinian, *Swedenborgia* developed not only extra-long female cones but also pollen cones reaching almost 20 cm, which were reminiscent of male araucaria cones with a large number of pollen tubes hanging from the individual microsporophylls.
However, the *Swedenborgia* conifer must have suffered from the Raibl catastrophe in the Carnian period, as it occured on the Triassic-Jurassic border, resulting in a significant decline in the plant kingdom. This decline was particularly evident in the reduction of female cones and even more so in the male ones. The number of hanging pollen tubes on the microsporophylls was reduced to only two to six in *Swedenborgia liaso-keuperianus*.

Description

Plant: *Swedenborgia liaso-keuperianus* is a tree with spreading branches, characterised by short shoots that are 5 to 15 cm long with thin needles about 0.2 to 0.3 cm wide. These needles emerge in clusters of 10 or more, from small buds, with individual needles showing slight division in the middle or raised segments on each side.
Pollen organs: The pollen organs are about 5 cm long, reaching a width of 2 cm. The individual microsporophylls measure 0.8 to 1.0 cm in length and 0.4 cm in width in the apical area, featuring a short, tapered terminal bract. These microsporophylls are connected to the cone axis with a long, slender petiole, with the number of hanging pollen sacs varying per microsporophyll from two to six.
Seed organs: The adult cones are 7 to 10 cm long and 3 cm wide, connected to the branch by a 1 cm long stalk. These cones composed of spirally arranged macrosporophylls, with seed scales reaching a length of about 1 to 1.5 cm. Each seed scale is provided with a slender petiole from which five (rarely six) apically tapered lobes arise. An elliptical, rounded seed about 0.5 cm long, which develops a small wing, hangs dorsiventrally from each of the lobes in the upper area. The outside of the seed scale is grooved, while the inside is smooth. Juvenile cones are still divided into two to three pairs, only merging in the adult stage.

Remarks

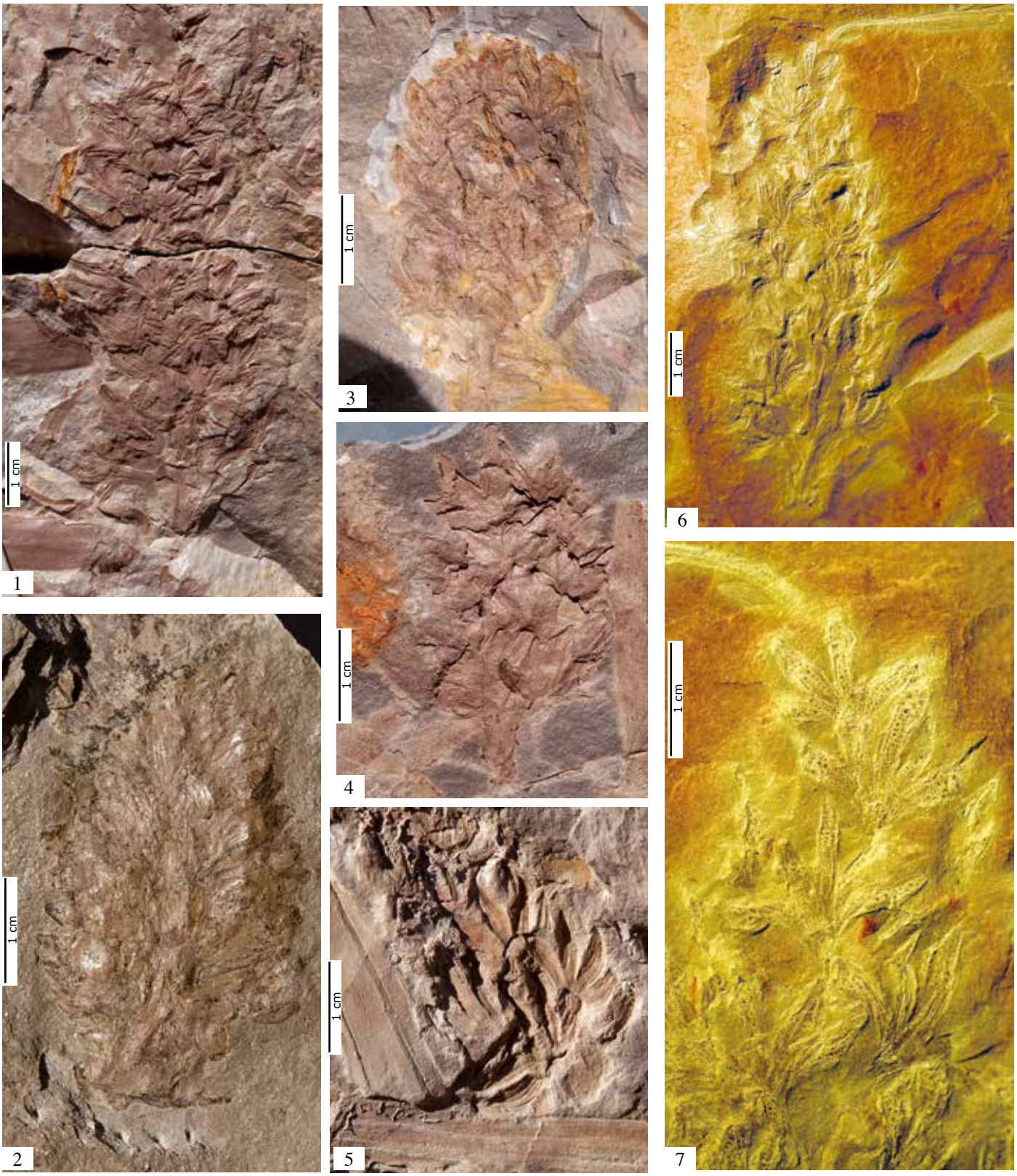
In 2012, Michael Wachtler began his research on the Rhaeto-Liassic floras (Hettangian, upper Lower Jurassic) around Bayreuth and Kulmbach. The Dietz and especially Küfner sand pits in the Pechgraben hamlet (Neudrossenfeld municipality) in the Kulmbach district proved to be particularly fruitful sites in his investigations. Among the several lenses of "*Pflanzensandstein"* (plant sandstone) (Weber, 1968) present at these locations, he found a layer extending over many metres on the south side of the Küfner sand pit that was rich in plant material. Surrounding this layer were more or less consolidated, colourful sandstone layers of varying colours, ranging from grey and violet to yellow, interspersed with shale lenses of differing thicknesses, from 10 cm to 1 m, likely deposited during distinct periods.
These clay lenses are susceptible to rapid deterioration once exposed to the elements. Even the cuticles of the exposed plants quickly fall off. It is a problem particularly with the fossil cycads, which are abundant in the sediments, but also with conifers. In some places, such as the western wedge, the sediments also contain hundreds of shark capsules, *Palaeoxyris muensteri,* concentrated in the lowest layers, suggesting a preference for deposition by hybodontid sharks (*Lissodus*) in close proximity to tree trunks within shallow, sometimes only slightly saline, waters. Such environments protected these capsules from predators, ensuring their survival in the initial dangerous weeks .
Usually, the uppermost – and, therefore, the last – deposited flood layer is rich in the conifer *Swedenborgia liaso-keuperianus*. This is followed by a wide variety of layers, which, along with other plant families, have an overhanging of *Podozamites distans* leaves. Although there is a plentiful supply of conifer cones in various states of preservation, the majority of them belong to *S. liaso-keuperianus*, with well-preserved branches of this genus being rare. A key distinguishing feature of these cones are the five to six-lobed seed scales, with most of the pollen cones also belonging to *Swedenborgia.* The third genus – *Hirmeriella muensteri* – that occurs abundantly in other

The conifer *Swedenborgia liaso-keuperianus*. Lower Jurassic. Branches and leaves

1-2. Complete side branch with leaf buds and detail of the needle tufts (PECH 441); 3-4. Branch and detail of a so-called double needle (PECH 451); 5. Detail of a leaf bud with leaf tuft (PECH 724 Ex Coll. Silberhorn), Sandpit Küfner, Pechgraben, Coll. Wachtler, Dolomythos Museum; 6. Almost complete branch with lateral tufts of needles, (Urweltmuseum Oberfranken, Bayreuth)

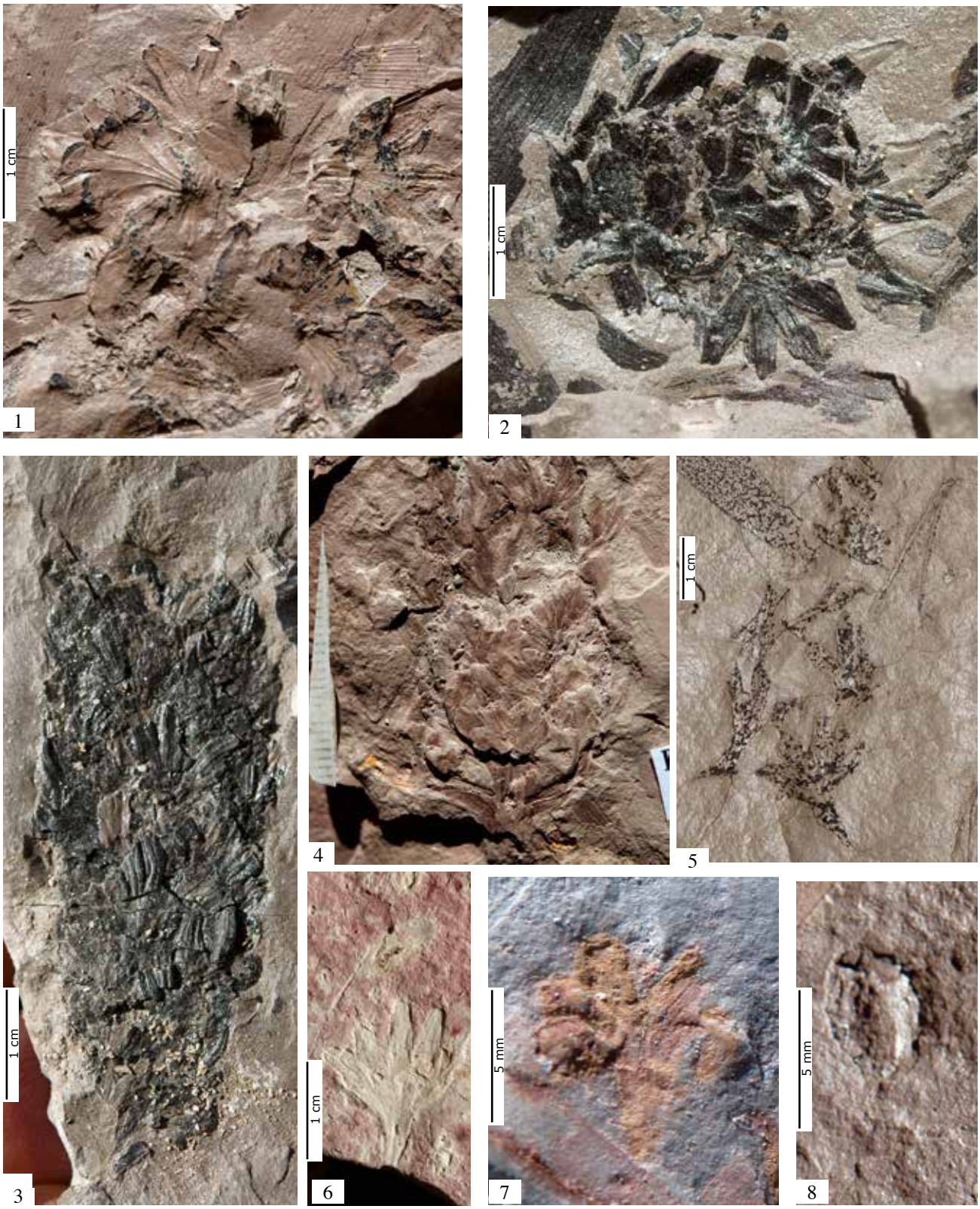
The conifer *Swedenborgia liaso-keuperianus*. Lower Jurassic. Juvenile cones and seed scales

1-5. Slab with lateral branches and various immature female cones (PECH 57); 6-8. Decayed juvenile seed scales with seed imprint (PECH 267, PECH 570); 9. Seed scale, inside view with imprint of the seeds (PECH 503); 10. Five-headed seed scale, outside with imprint of the seed grooves (PECH 412); Sandpit Küfner, Pechgraben, Coll. Wachtler, Dolomythos Museum



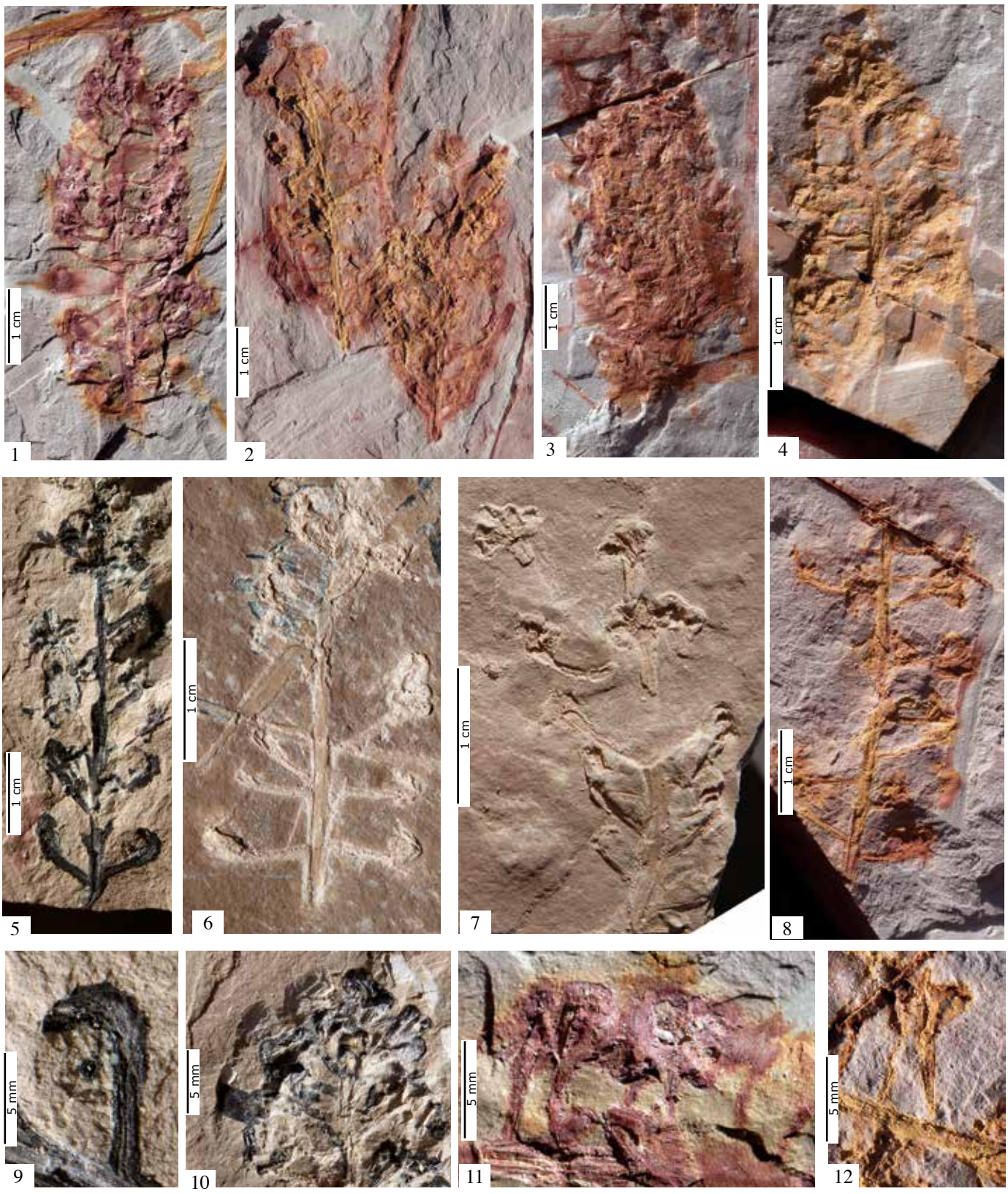
The conifer *Swedenborgia liaso-keuperianus*. Lower Jurassic. Female cones

1-2. Mature cones (PECH 170; PECH 112); 3-5. Juvenile cones and seed scales (PECH 01 PECH 307, PECH 592) Coll. Wachtler, Dolomythos-Museum; 6-7. Beautifully preserved cones and detail of the seed scales (Coll. Jürgen Meyer); All sandpit Küfner, Pechgraben



The conifer *Swedenborgia liaso-keuperianus*. Lower Jurassic. Female cones and seed scales

1-2. Cones upper view (PECH 629, PECH 412); 3. Mature cones (PECH 566); 4. Cone (PECH 606); 5. Isolated decaying seed scales (PECH 387); 6. Seed scales with winged seeds at the upper end (PECH 605); 7. Five-lobed seed scale with seeds (PECH 547); 8. Seeds with imprint of the wing (PECH 629); Sandpit Küfner, Pechgraben, Coll. Wachtler, Dolomythos Museum



The conifer *Swedenborgia liaso-keuperianus*. Lower Jurassic. Male cones

1-2. Various pollen cones (PECH 542, PECH 536, PECH 531, PECH 547); 5-8. Several mainly decayed male cones (PECH 543, PECH 311, PECH 540, PECH 548); 9-12. Detail of the microsporophylls (PECH 543, PECH 555, PECH 542, PECH 548); Sandpit Küfner, Pechgraben, Coll. Wachtler, Dolomythos-Museum

The conifer *Swedenborgia liaso-keuperianus*. Lower Jurassic. Reconstructions

a. Branch with leaf shoots; b. Stem and bark; c. Needles, underside; d. Needles, upper side; e. Female cone; f. Juvenile female cone; g. Female cone, upper view; h. Seed scale, outside; i. Seed scale with five seeds; j. Single slightly winged seed; k. Pollen cone; l. Individual microsporophylls

sand pits (Schnabelwaid) is extremely rare or non-existent. Ginkgo plants are notably absent from the findings.
Historically, this has led to an uncontrolled name convention for many plant parts, such as *Schmeissneria microstachys* (Kirchner & Cittert, 1994), or South American gymnosperms from the Jurassic being combined to form *Karkenia hauptmannii,* which were placed in the ginkgo family. It has become apparent that it is problematic to bring typical Gondwana plants from the southern hemisphere, which have a completely different evolutionary history, into closer connections with Northern Hemisphere plants. In addition, ginkgo leaves were never found in the samples processed by all collectors.
The holotype of the supposed ginkgo plant *Karkenia hauptmannii* is likely a juvenile long shoot of *Swedenborgia liaso-keuperianus.* Similarly, *Schmeissneria microstachys,* first described by Presl in Sternberg (1833) as *Pinites microstachys,* was later reclassified as male cones by other authors (Schenk, 1867; Kirchner, 1992) under *Stachyopitys preslii.* Subsequently, it was once again renamed *Schmeissneria microstachys,* as female organs (Kirchner & Cittert, 1994). These structures do not represent the fertile organs of the ginkgo family. Most of the supposed female cones represent needle sheaths of *Podozamites*, and occasionally of *Swedenborgia.* While ginkgo plants under the name *Baiera* or *Ginkgoites* occur in the Lower Jurassic of Bavaria, they carry berry seeds, as are typical of modern ginkgos.
The *Swedenborgia* species of the Triassic-Jurassic period have a uniform characteristic of at least five-lobed basally fused seed scales. This distinguishes them from the three-lobed seed scales often found in the Permian and Triassic, classified as *Voltzia*, whose descendants are probably to be found in today's Japanese sickle fir (Cryptomeria). It can be assumed that many of the conifers that are prevalent today went their own way from the early Devonian period. The single-seeded berry seeds of the ginkgo or the araucarias, which also only develop one seed, the winged seeds of *Podozamites* and *Hirmeriella,* the three-seeded seed scales of *Voltzia*, or the five-seeded seed scales of *Swedenborgia* with many traceable lines up to the Carboniferous-Permian boundary are too far away from subsequent splitting tendencies.

Since today's largest group of gymnosperms bear needle cuffs, the pines, as well as spruce or fir ancestors, although developed from the Permian onwards, are missing from the Lower Jurassic deposits. Thus, the question remains unanswered as to why gymnosperms now represented only as monotypic genera were so common in the Early Jurassic period and why they were able to spread across the entire northern hemisphere, when today, all of them have been confined to the relict areas of East Asia. This is valid for *Swedenborgia,* believed to be the ancestor of the umbrella fir (Sciadopitys) and *Podozamites* with the golden larch (Pseudolarix) as the most likely descendant. Other gymnosperms, such as *Voltzia* (Cryptomeria), *Hirmeriella (Taiwania*), and the ginkgo family *(Ginkgoites*) also demonstrate similar pattern in distribution over time.

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***Sciadopitys verticillata* (Japanese Umbrella Pine)**

1. Bark; 2. Branches; 3. Lateral branch; 4. Short shoot with tufts of leaves; 5. Single needle, bottom; 6. Pollen cones and detail of the microsporophylls; 7. Juvenile female cone; 8. Mature female cone; 9. Seed scales outside with the grooves of the separated lobes in the Jurassic period; 10. Seed scale inside with the imprints of the seeds; 11–12. Seeds, inside and outside

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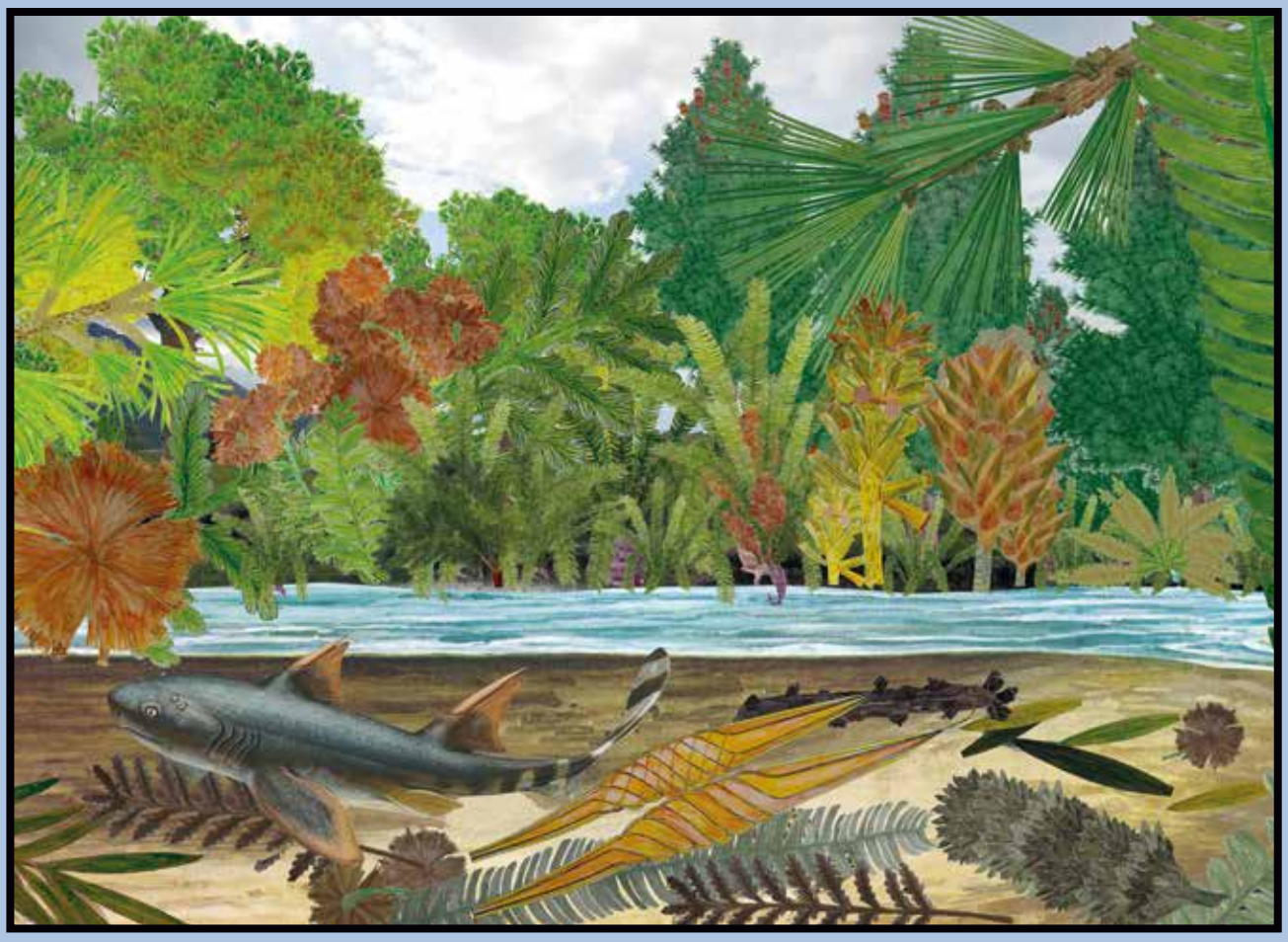

The Fossil Flora of Early Jurassic

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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