Cycads from the Lower Jurassic

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Cycads played a crucial role in the Lower Jurassic period of Europe. However, so far there has been little attempt to connect the abundant fronds with the fructifications and cones and to establish relationships with modern cycads. The most widespread species during this time was *Nilssonia acuminata*. As new finds from Pechgraben (Bavaria) have revealed male and female cones, along with two-seeded scales, which bear resemblance to *Encephalartos* cycads. Another species, *Nilssonia polymorpha*, also speaks of a similar connection. Additionally, *Macrotaeniopteris gigantea* and *Taeniopteris tenuinervis* were present but not as common, with their multi-seeded fruit fronds resembling Cycas palm ferns. *Pseudoctenis prossii* and *Ctenis inconstans,* though sporadically found and with unknown fertile organs, may indicate the presence of two-seeded cycad precursors. Other leaf shapes found in the fossils are more likely to be attributed to ferns. The abundance of cycads in the Lower Jurassic period of Europe supports the theory that a subtropical climate prevailed during this time.

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Cycads in the Lower Jurassic. On the left is the most widespread species ***Nilssonia acuminata***, with male and female cones, as well as a two-seeded macrosporophyll; in the middle ***Nilssonia polymorpha*** with female cones; on the right ***Macrotaeniopteris gigantea*** with a female cone and a typical multi-seeded macrosporophyll.

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Although cycads were among the most common flora elements in the Lower Jurassic period of Europe, the actual number of their genera and species remains unclear. This is primarily due to the frequent discovery of partial or complete fronds, while fertile organs are often unrecognised or discarded to their lack of aesthetical appeal. As a result, there is hardly any meaningful information about the overall appearance of the cycads or their classification in older literature.

The cycads first appeared in the Lower Permian, alongside two families that exhibit different characteristics today (Wachtler, 2021; Wachtler, 2015; Perner, 2015): cycads whose sporophylls only have two seeds *(Zamia, Lepidozamia, Macrozamia, Ceratozamia, Encephalartos, Dioon, Microcycas, Bowenia, Stangeria*) and those with a plurality of seeds (*Cycas*). It is believed that the separation between these two tribes took place in the Devonian, after which they went their separate ways. From the Lower Permian onwards, no transitions from two to several seeds or vice versa on macrosporophylls can be detected.

Weylandia, with its tongue-like leaves, tuft of sporophylls, and large number of seeds lined up on both sides, and *Kraeuselia*, with its tongue-shaped leaves and only two seeds anchored per sporophyll, are found in the Middle Devonian of Germany. They are both thought to have played a precursor role in the evolution of cycads. Their pollen cones, on the other hand, displayed similarities from the start (Wachtler, 2023).

Wachtleropteris (Perner, 2015), found in layers of the Lower Permian (Kungurian) of the Dolomites, is one of the most primitive cycad precursors that survived the reign of time, displaying evolutionary features demonstrating transitions into the Devonian. This species developed tongue-shaped leaves that rose up on an axis. Simultaneously, highly developed cycads with two (*Nilssonia*) or more seeds on each macrosporophyll (*Macrotaeniopteris, Taeniopteris*) can be found in the Lower Permian, which can be traced in large numbers throughout the Upper Permian and entire Triassic periods (Wachtler, 2021). The two large families competed from the Lower Permian onwards, in ever-changing amounts, and this up to the present day. Cycads experienced another heyday in the Lower and Middle Triassic, where they were among the dominant plants, especially in the Dolomites (Wachtler, 2016a, b, c). Not only fronds but also female and male cone organs were found in large numbers and boasted excellent quality.

A notable characteristic of the multi-seeded cycads dating back to the Middle Triassic period (*Macrotaeniopteris, Taeniopteris)*, in addition to their leaves that partly resembled banana fronds, was the unique structure of their macrosporophylls. These structures emerged spirally from an elongated axis, standing in contrast to their appearance in the later Triassic or modern times. Each fruit blade can produce up to almost a hundred seeds, such as in *Macrotaeniopteris olangensis* (Wachtler, 2015). In contrast, *Taeniopteris* produced considerably fewer seeds. The first signs of the modern Cycas genus can be traced back to the Middle Ladinian period in Germany (mainly Ilsfeld). *Taeniopteris angustifolia,* a dominant gymnosperm of the time, exhibited macrosporophylls that were always found individually, indicating a decaying tuft, similar to today's *Cycas revoluta* (Wachtler, 2016). However, the tongue-shaped individual leaf fronds remained unchanged. The pollen organs were rounded to slightly elongated cone structures, which were rarely collected because of their disfigured appearance caused by pollen dust.

In the Lower Jurassic period, many sites (Sweden, Germany, Hungary) yielded a variety of cycad species. These included the tongue-shaped, often tattered leaves of *Macrotaeniopteris* and *Taeniopteris,* which were found in smaller numbers, indicating multi-seeded cycads, as well as two-seeded megasporophylls, similar to today's *Encephalartos, Zamia* and *Stangeria* cycads in far greater numbers. These species were classified under genus names such as *Nilssonia, Ctenis, Pseudoctenis*, and *Anomozamites.* In addition, enigmatic plants similar to cycads, which found their way into the nomenclature as Bennettitales, were also described.

The question is entirely justified: how many cycads with two-seeded sporophylls existed in the Lower Jurassic of Central Europe, and how many were multi-seeded ones? One

way to address this question is through the analysis of the sparsely documented megasporophylls.
In the Hettangian of Franconia, *Macrotaeniopteris gigantea* (Schenk, 1867) and *Taenioperis tenuinervis* (Brauns, 1864) from the group of multi-seeded Cycas precursors have been observed, albeit rarely. Determining the number of cycads with two-seeded carpels in the Lower Jurassic lenses poses an equally difficult task. It is plausible that there a dominant species, *Nilssonia acuminata* (Braun, 1843), was prevalent during that time and is now well known. *Nilssonia polymorpha* is also likely to be relatively well researched. In addition, there may have been one or two *Ctenis* species that can be traced back to the Lower Permian, although there is a lack of clearly assignable fertile parts. This exhausts the number of cycad species and genera in the Lower Jurassic of southern Germany.
The characteristics of the various cycads and their role in the evolution of the Lower Jurassic will be discussed in detail in the next section.

Multi-seeded Cycad-Ancestors

Macrotaeniopteris gigantea

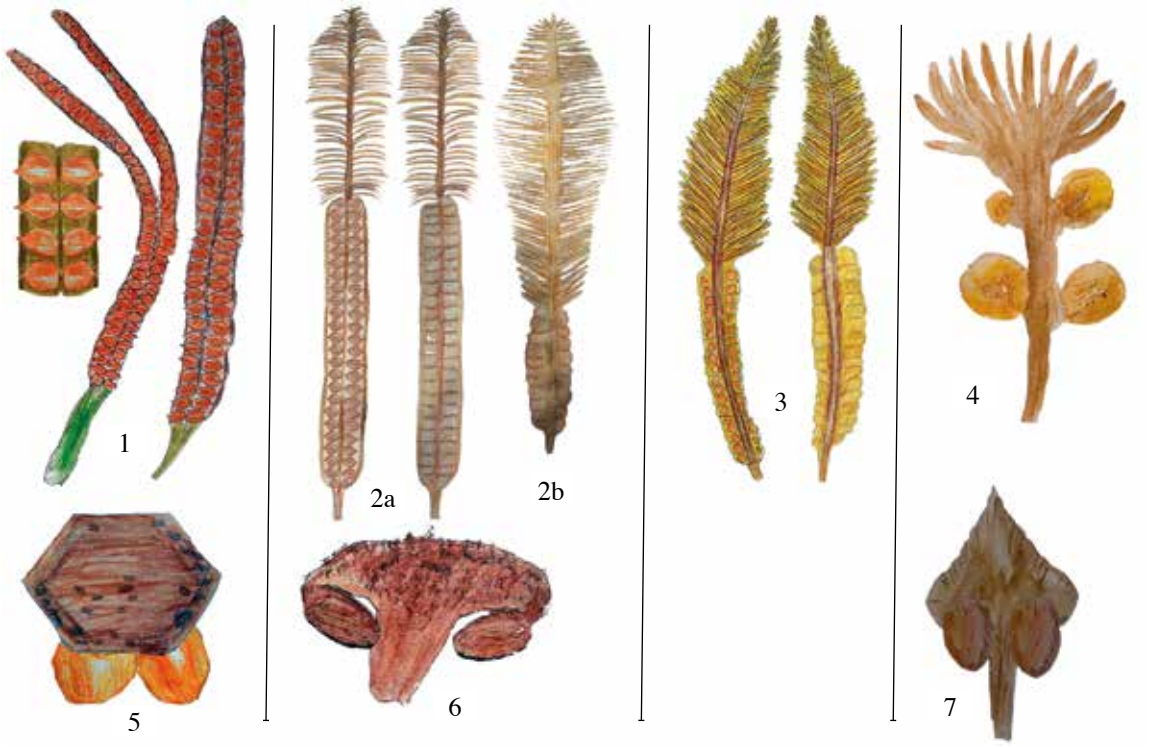
1843 *Taeniopteris magnifolia* Rogers, p. 306, pl Xiv

1867 *Taeniopteris gigantea*, Pl. 28, Fig 12

1869 *Macrotaeniopteris magnifolia* Schimper Traité de Pal. vég, vol 1, page 610

1933 *Bjuvia simplex* Florin, Taf. 1 Fig. 3, plate 2 Fig. 4-7, Taf. 3, Fig. 3-8, Studien über die Cycadales

Whole plant: The plant is characterised by large fronds, similar to today's banana



Macrosporophyll development of cycads from the Permian to the Lower Jurassic

In the Upper Permian, *Macrotaeniopteris wachtleri* (1), an ancestor of multi-seeded cycads, and *Nilssonia brandtii (*5), with two seeds per macrosporophyll, are found. In the rich cycad flora of the Dolomites (Lower Triassic, Anisian, 245 million years ago), there are two representatives of multi-seeded cycads, *Macrotaeniopteris olangensis* (2a) and *Taeniopteris simplex* (2b), aditionally with *Nilssonia primitiva* (6), evolving two-seeded macrosporophylls. In the Middle Triassic, *Taeniopteris angustifolia* (3), a representative of multi-seeded macrosporophylls, predominated. In the Lower Jurassic, the macrosporophylls of the multi-seeded ones become similar to those of today (*Macrotaeniopteris gigantea*) (4). The two-seeded ones (*Nilssonia acuminata*) (7) continue their original development. The split between the multi-seeded and two-seeded palm ferns must have occurred in the Carboniferous and, more likely, in the Devonian.

leaves. These fronds are continuously worn down by the rigours of nature. The apical part of the plant varies in shape from U- to V-shaped. The lateral veins emerge at an angle of 80 to 90° from a central, massive rhachis and run straight, parallel, and un-branched to the edge of the leaf. The leaves can grow to lengths of 30 to 70 cm, with a total width of 20 to 40 cm.

Male cones: These are bulbous to elongated, measuring approximately 6 to 8 cm in length and 4 to 5 cm in width, with a short petiole. The microsporophylls are about 1 cm wide and 1.5 cm long, including the stalk, with pollen sacs located on the underside.

Female cones: These cones resemble tuft-like structures and are composed of individual macrosporophylls with a pyramid-shaped, often segmented bract. At least two till three seeds develop on each side of the basal blade.

Remarks

The genus *Macrotaeniopteris* has a fascinating descriptive history that dates back to 1843 when William Barton Rogers first mentioned it as *Taeniopteris magnifolia* from Virginia (USA). Initially believed to belong to the Carboniferous period, some specimens made their way to Europe, capturing the attention of Alsatian palaeobotanist Schimper (1808–1880). He determined that the specimens were actually from the Lower Jurassic age and bore similarities to plants from the Bayreuth area. Since there were some large-leaved plants among them that could not be reconciled with the genus *Taeniopteris* first described by Brongniart (1828), Schimper renamed the genus to *Macrotaeniopteris magnifolia* in 1869. Austrian palaeontologists Dionýs Štúr (1885) and Fridolin Krasser (1909ab) further expanded the knowledge of *Macrotaeniopteris* based on American findings, introducing a variety of species discovered in the Upper Triassic locality Lunz in Lower Austria (*Macrotaeniopteris haidingeri, Macrotaeniopteris simplex, Macrotaeniopteris angustior, Macrotaeniopteris parvula)*, presented mostly without illustrations. Only *Macrotaeniopteris angustior* exhibited the characteristic whole-leaf structure of this genus. Additionally, these descriptions primarily focused on the leaf, neglecting the fertile organs.

The Swedish naturalist and archaeologist Sven Nilsson (1787-1883). He discovered fossil plants from the Lower Jurassic around Pälsjö in Scania. Adolphe Brongniart honoured him with the genus name of the cycad precursor *Nilssonia*. Photo Wikipedia

In 1867, Schenk described and illustrated *Taeniopteris gigantea* from the Bayreuth area, which fulfilled the criteria for *Macrotaeniopteris.* Schenk also identified macrosporophylls reminiscent of modern Cycas, with at least two seed bodies arising on each side, which he recovered and named *Cycadospadix*. However, in contrast to the Triassic period, the number of seeds had significantly reduced. The potential impact of the Raibl catastrophe in the Carnian on the development of a modified macrosporophyll must be clarified.

In 1933, the Swedish palaeobotanist Florin complicated the overall situation by introducing the new genus *Bjuvia simplex* for large leaf fronds from the Lower Jurassic layers of Bjuv in Scania, Sweden. He associated it with the macrosporophyll already depicted by Nathorst (1902) under the name *Cycadospadix integer,* renaming it *Palaeocycas integer.* However, Florin's decision was met with criticism as his reconstruction drawing was deemed inaccurate, and he disregarded all previous literature by ignoring older names for multi-seeded cycads such as *Dioonites* (Schenk, 1867) and *Dioonitocarpidium (pennaeforme)* (Lilienstern, 1928).



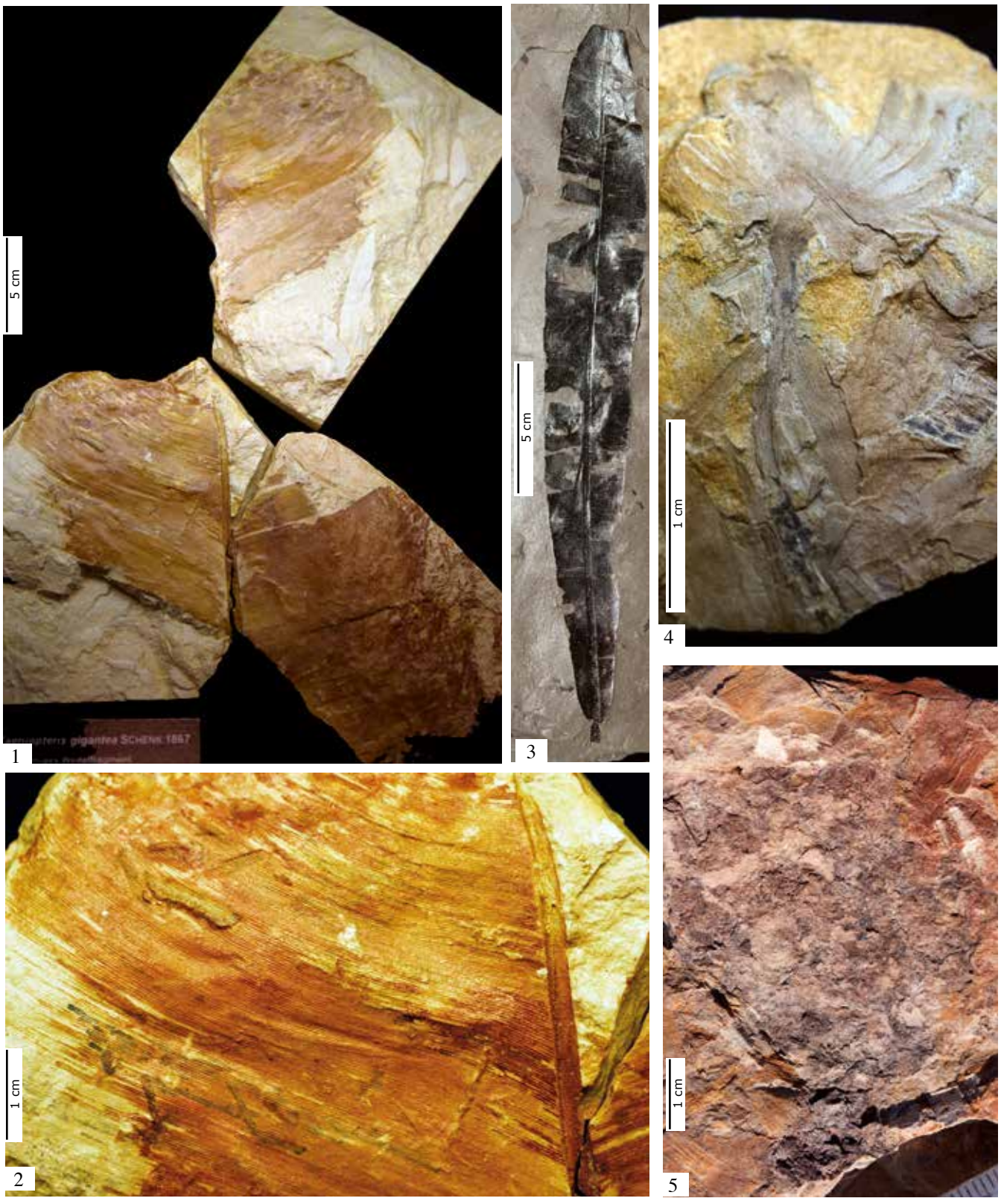







Cycads today

1. *Encephalartos natalensis*, whole plant; 2. *Encephalartos villlosus,* male plant; 3. *Encephalartos leboensis,* female cone; 4. *Encephalartos ferox,* female cone; 5. *Encephalartos lehmannnii,* Detail of a male cone; 6-8. *Encephalartos horridus,* decayed female cone, macrosporophyll, seed; 9. *Encephalartos lehmannnii,* microsporophyll; 10. *Cycas revoluta,* female



The cycad *Macrotaeniopteris gigantea*. Lower Jurassic. Leaves and Macrosporophylls

1-2. Parts of a large frond, Pechgraben, Urwelt-Museum Oberfranken, Bayreuth); 3. Juvenile frond or *Taeniopteris tenuinervis* (PECH 96, Sandpit Küfner, Pechgraben, Coll. Wachtler Dolomythos Museum; 4. Macrosporophyll with attachment cushions for several seeds (*Cycadospadix)*, Pechgraben, Urwelt-Museum Oberfranken, Bayreuth; 5. Pollen cones, possibly belonging to *Macrotaeniopteris* (PECH 113), Sandpit Küfner, Collection Wachtler, Dolomythos Museum

Furthermore, attempts were made to question the validity of the names of the genera *Macrotaeniopteris* (Cittert, 2017) and *Taeniopteris* (Zijlstra et al., 2016). However, their appearance in the Early Permian period and their constant presence until the Jurassic period solidified them as one of the most important and well-researched plant families. Therefore, name changes for these genera do not seem justified. Surprisingly, both genera retained their original compact single leaf form over a period of 100 million years, contrasting with the geometrically segmented fronds of the modern genus Cycas.

Taeniopteris tenuinervis (Brauns, 1864)

1828 *Taeniopteris* Brongn., Prodr. Hist. Vég. Foss. p. 61

1831. Histoire des végétaux fossiles, p. 262, pl. 82, fig. 1-6. Fig. 4. a Typus: Great Britain, Yorkshire, Scarborough; Jurassic (Mus. Natl. d'Hist. Nat., Paris: No. MNHN.F.522); [illustrated in] Brongniart, Hist. Vég. Foss. 1: t. 82, fig. 2. 28 Nov 1831), typ. cons. prop.

1862-1864 T*aeniopteris tenuinervis* Brauns, Palaeontogr. Bd. IX. p. 50. Tab. 13. Fig. 1-3

1867 *Taeniopteris tenuinervis* Schenk, Fossile Flora, Tafel XXV. Fig. 3. 4

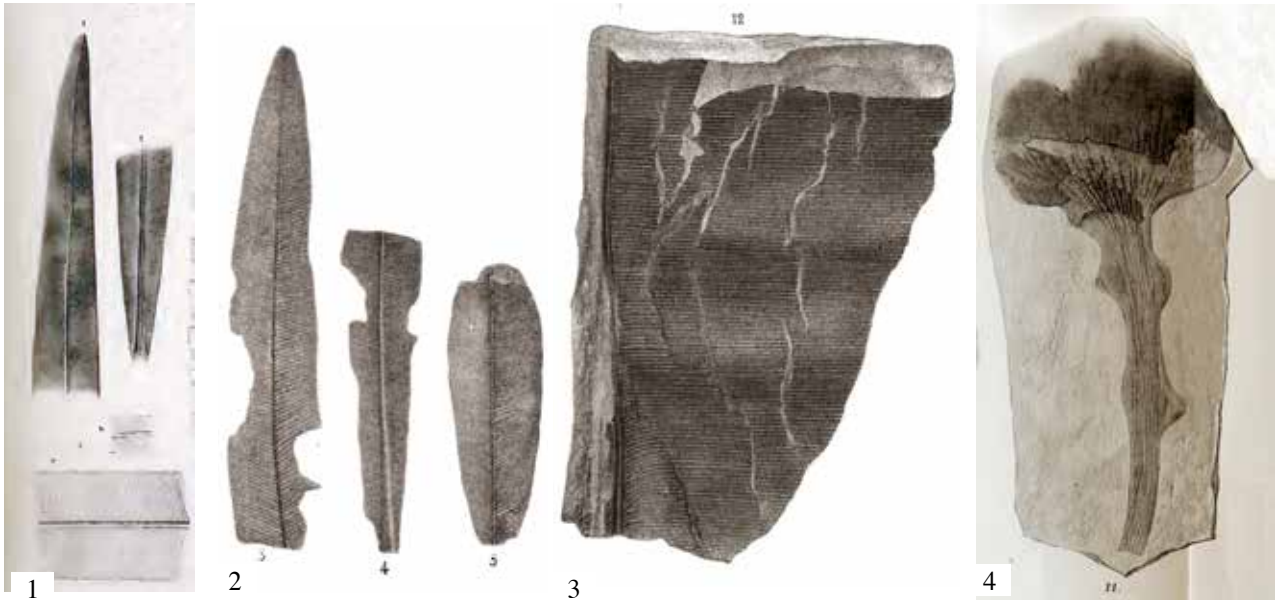
Whole plant: The plant features a cluster-like accumulation of narrow, elongated leaves, reaching up to 30 cm in length and 2 to 3 cm in width. The apical area is rounded with a slight indentation, sometimes tapering to a point. Veins branch off from the rhachis at a slightly offset 90° angle and never dichotomise up to the leaf edge. There is a barely existing petiole, with the lamina immediately widening and continuing almost to the end of the leaf at the same width. The rhachis is broad, traversed by several vascular bundles.

Remarks

The genus *Taeniopteris* was initially introduced in 1828 in apparently insufficient description without illustrations for supposed Triassic ferns by the French palaeobotanist Adolphe Brongniart for elongated, tongue-shaped leaves and branching parallel veins. Brongniart referenced leaves from the English and Swedish Jurassic (*Taeniopteris vittata)*, the locality Stonesfield-Oxford (*Taeniopteris latifolia)* and Northern Italy (*Taeniopteris bertrandi).* In 1831 he added

***Macrotaeniopteris gigantea.* Lower Jurassic. Reconstructions**
a. Female plant; b. Frond c. Macrosporophyll; d. Seeds; e. Male cone

a more accurate description with a plate (Pl. 82).
In 1839, the German botanist Gustav Adolph Kurtze extended its temporal occurrence to the Zechstein (Upper Permian Wuchiapingian) with *Taeniopteris eckardtii,* while Schenk described a T*aeniopteris angustifolia* from the Middle Triassic (Ladin) in 1864. Due to the lack of fertile parts, *Taeniopteri*s was classified in the following decades as a form genus for a variety of different tongue-shaped leaves.
In 2010, Wachtler made significant discoveries from the early Middle Triassic period of the Dolomites (Anisian) with a variety of leaves, as well as male and female cone structures. These findings allowed for the reconstruction of the overall appearance of *Taeniopteris* and confirmed that it must have been a cycadean precursor of the genus Cycas.
Taeniopteris simplex (Wachtler, 2016) was characterised by a number of macrosporophylls, which developed a multitude of chain-like seeds in two rows on the underside. These macrosporophylls feature an apical sterile part with a feather-like end. In the Permian (*Taeniopteris nonensis,* Lower Permian, Kungurian, Wachtler, 2021) and Early Triassic periods, these macrosporophylls emerged at a staggered height from a central rhachis, similar to the leaf fronds in the lower area. However, from the Middle Ladin onwards, there was a shift, and they began to emerge at approximately the same level, resembling the structure seen in today's Cycas. This change resulted in the presence of individual macrosporophylls rather than entire cones in the fossil lenses.
The discovery of typical pollen cones of cycads in the same layers led to the decision to classify *Taeniopteris* as a distinct genus rather than a form genus. It is now considered a precursor to the cycads, with close ties to the present genus Cycas, albeit with small tongue-shaped fronds. Another genus, *Macrotaeniopteris*, emerged in the Lower Permian with similar characteristics but larger fronds reaching up to a metre in length.
After a flowering that lasted almost a 100 million years, *Taeniopteris* only played a marginal role in the Lower Jurassic, approximately 200 million years ago. This decline is surprising, since *Taeniopteris angustifolia* was once a prevalent species in the Middle Ladinian period in Europe and was particularly common at the Ilsfeld fossil quarry (Baden-Württemberg), where numerous well-preserved specimens have been found.



1. From D. Brauns, 1862-1864. *Taeniopteris tenuinervis* (First description specimen); 2. From A. Schenk, 1867. Plate 25, fig. 3-4. *Taeniopteris tenuinervis*; fig. 5. T*aeniopteris stenoneura;* 3: From Schenk, 1867, Plate 28 *Macro(Taeniopteris) gigantea;* 4. From Nathorst, 1902, Plate 1. Fig. 11. *Cycadospadix integer* from Bjuv, Sweden. Macrosporophyll of a cycad with shed seeds (Probably *Macrotaeniopteris*)

The Early Jurassic plant *Taeniopteris tenuinervis* was first described by the German geoscientist David August Brauns (1827–1893) based on tongue-shaped leaves from the Liassic age. Schenk, in 1867, supplemented this description with additional illustrations, although his *Taeniopteris stenoneura* is likely only a synonym of the previously mentioned species. Unfortunately, all findings from the Lower Jurassic sites lack the macrosporophylls associated with them.

Two-seeded cycad ancestors

*Nilssonia (*Brongniart 1825)

1825 *Nilsonia brevis* p. 218 Brongniart, Observations sur les Végétaux fossiles, vol IV

1828 *Nilsonia brevis* Brongn., Prodr. Hist. Vég. Foss. p. 95

The fossil palm fern *Nils(s)onia* was first introduced in the literature by the French palaeobotanist Brongniart (1825 and 1828). This was a tribute to the Swedish natural scientist Sven Nilsson, who discovered the leaves in the Swedish Hör (middle Skåne) and described their geology in the "Svenska Vet. Akad. Handlingar" (1819, 1820, 1823) together with Carl Adolf Agardh and Elias Fries.

Sternberg, K. M. 1838 *„Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt*", Bd. II, H. 7, 8. Carl Presl depicted cycad plants from the Bamberg area: Plate XLIII; Fig. 1+3: *Zamites münsteri*; Fig. 2: *Zamites acuminatus*; Fig. 4-5: *Zamites heterophyllus*

Nilsson joined a number of Swedish natural scientists, including Emanuel Swedenborg (1772), Carl von Linné (1751), and Samuel Gustaf Hermelin (1773), who had previously conducted scientific work in this area. They were succeeded by other outstanding Swedish palaeobotanists like Nathorst (1850–1921), Ernst Antevs (1888–1974), and Florin (1894–1965), who studied the Jurassic plants of Sweden.

The Nilssoniales first appeared in the Lower Permian (Kungurian) of the Dolomites with *Nilssonia perneri* (Wachtler, 2012), and in the Upper Permian with *Nilssonia brandtii* (Wachtler, 2015). *Nilssonia primitiva* (Wachtler, 2016a) and *Nilssonia faustinii* (Wachtler, 2016b) followed in the Lower and Middle Triassic periods of the Dolomites. The male and female cones of these species were elongated to rounded, bearing a resemblance to present-day palm ferns.

Due to the abundance of material, it is assumed that these plants were cycad precursors with two-seeded megasporophylls, such as *Lepidozamia, Encephalartos, Macrozamia, Bowenia, Dioon, Zamia, Microcycas, Ceratozamia* and *Stangeria*, excluding *Cycas.* The initial form of these plants featured a lead that was not yet geometrically segmented but had a pronounced midrib. It was only towards the end of the Triassic period that a frond character similar to today's cycads began to emerge. In the Lower Jurassic of southern Germany, two Nilssoniales were identified: *Nilssonia polymorpha* and *Nilssonia acuminata.* While the former retains characteristics of the Permian and Early Triassic periods, the second already exhibits a clear frond character and could potentially be classified as a separate genus.

*Nilssonia acuminata (*Presl 1838)

1838 *Zamites acuminatus* Presl p. 199, Pl. XLIII, Fig. 2, Loc. Bamberg

1847 *Pterocycadites acuminatus* Braun, *Pt. stenophyllus* Braun, *Pt. rhombiphylus* Braun, Verzeichn. p. 100

1867 *Nilssonia acuminata* Schenk, pag. 131, Pl XXXII Fig. 1-7. Pl XXXIII Fig. 1

Description

Whole plant: The plant is characterised by fronds emerging from a petiole that can reach up to 10 cm in length. The fronds themselves measure between 30 and 50 cm in length and have a relatively wide spread, sometimes appearing V-shaped at the tips. The leaflets have smooth edges, varying in length from 2 to 3 cm but often only 0.5 cm wide on each side. They are covered in a thick cuticle and traversed by a few strong nerves that run parallel to the leaf's end. The individual leaflets can range from pointed to rounded, with some exhibiting a more pronounced sickle-shaped curve. They are broadly connected to the rhachis.
Pollen organs: The cones can grow up to 10 cm in length and 3 to 5 cm in width, featuring a short stalk and numerous octagonal scales. The microsporangia are found in large numbers on the underside of the microsporophylls.
Female organs: They are slightly spherical, emerging from a long and solid petiole. The number of macrosporophylls is lower compared to their male counterparts. The seed scales are short-stalked and end in a pyramid-shaped bract that is serrated on the outer edges. They measure about 2 cm in length, with a width of 1.2 cm and stalk of about 0.5 cm. Each scale bears two seeds that hang downwards, tightly enveloped by the upper part of the seed leaf. The seeds themselves are ovoid and about 1 cm long.

Nilssonia polymorpha Schenk 1867

1825 *Nilssonia brevis* Brongniart Annales des sciences. Tom. IV. p. 218

1825 *Nilssonia? aequalis* — Brongniart, Végétaux fossiles dans le grès de Hoer, p. 219; pl. 12, fig. 6

1867 *Nilssonia polymorpha* Schenk, pag. 127 pl. XXIX, fig. 1-12, XXX, 1-5, XXXI fig 1

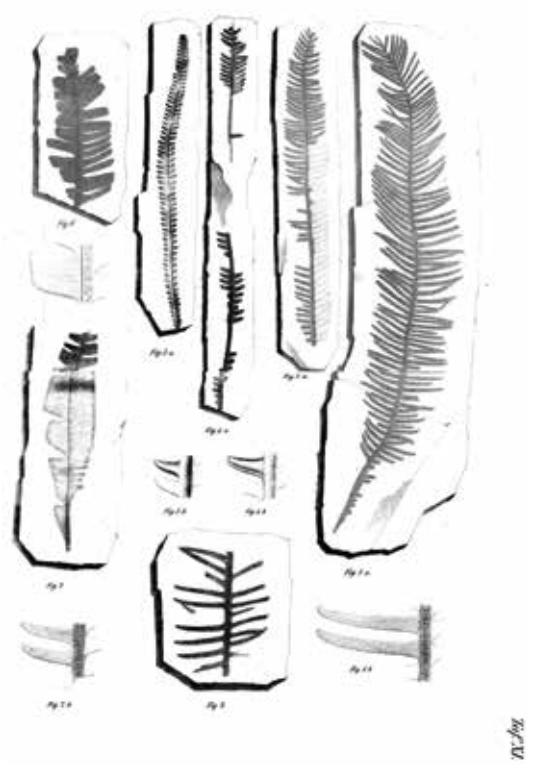
1876 *Nilssonia polymorpha* Nathorst, pl. VIII, fig. 2-15; IX, fig. 1-6; pl. X, fig. 1-3

Description

Whole plant: The plant's leaf fronds exhibit distinct leaf characteristics, spiralling out from a short trunk. The petiole is short, while the fronds can reach lengths of 30 to 50 cm and widths of up to 10 cm. The individual leaflets are broadly attached to the central axis, displaying irregular widths. They are crossed by prominent side veins, which run unbranched to the end of the leaf.
Pollen organs: The cones are slightly spherical, measuring up to 6 cm in length and 5 cm in width. They consist of a large number of geometrically shaped microsporophylls, with the microsporangia found on the underside in large numbers.
Female cones: They are slightly elongated, reaching about 10 cm in length, and composed of deeply segmented macrosporophylls. These macrosporophylls develop two ovoid seeds below the covering bracts.

Remarks

Nilssonia acuminata is the most common cycad species in the Hettangian of Bavaria and is now widely recognised. It is particularly abundant in the Küfner sandpit, where it forms monotypic lenses and stocks. Its relatively small fronds, which stand in contrast to the considerable size of its female cones, poses a special interest. The macrosporophylls of *Nilssonia acuminata* have a tapered, toothed shape, along with a development of two seeds on its underside,

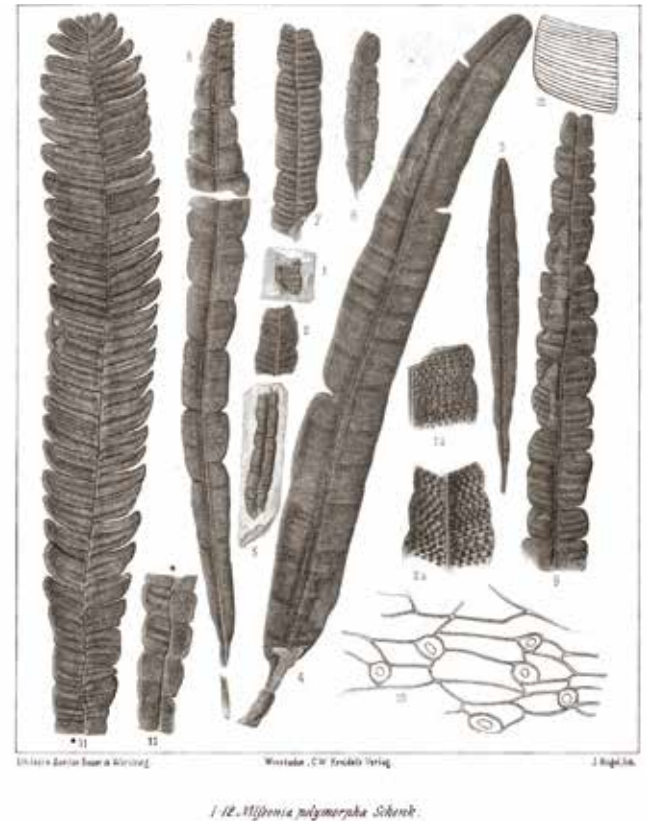


In the by Georg Graf Münster, 1843 published *„Beiträge zur Petrefactenkunde*" Carl Friedrich Wilhelm Braun described various cycad fronds. Plate XI. Fig. 1: *Ctenis angusta; 2: Ctenis, abbreviata,* 3. *Ctenis angusta, varietas*; 4-5. *Ctenis marginata;* 6-7. *Ctenis inconstans*

1-7. Nilssonia acuminata Geppert. | 8-10. Inflorescentia Cycadearum.

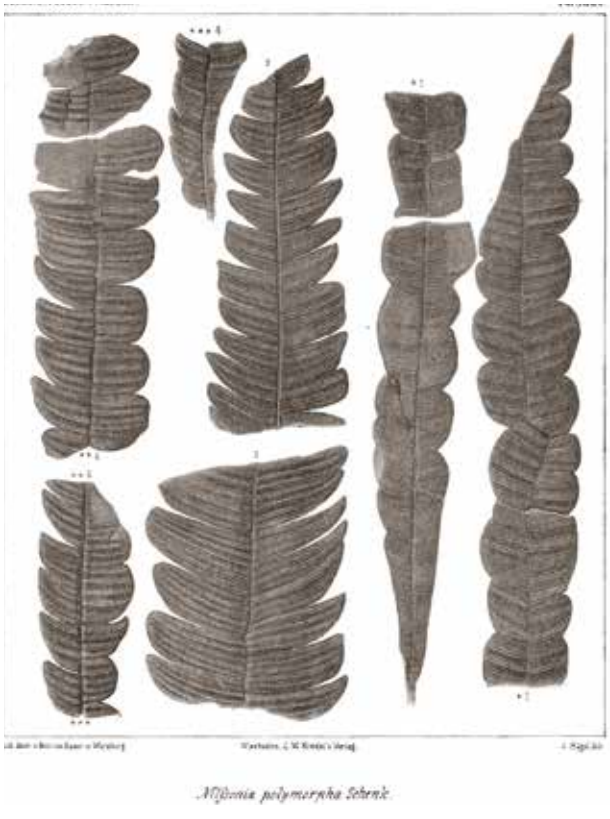
1. Nilssonia acuminata Geppert. | 4. Cycadearum squama.
2,3. Pterophyllum Buchlandi Schenk. | 5-9. Carpolithes.

On the tables XXXII, fig. 1-7 and XXXIII, fig. 1 August Schenk, 1867 depicted the cycad *Nilssonia acuminata*. Fig. 8-10 he defined as *Inflorescentia Cycadearum*, meaning sporophylls belonging to the palm ferns. He also mentioned the seeds on table XXXIII as belonging to the cycads All in all, this theory can be supported.



1-12. Nilssonia polymorpha Schenk.

From August Schenk, 1867, table 29. *Nilssonia polymorpha.* The sori from ferns on the leaves are not correctly interpreted



Nilssonia polymorpha Schenk.

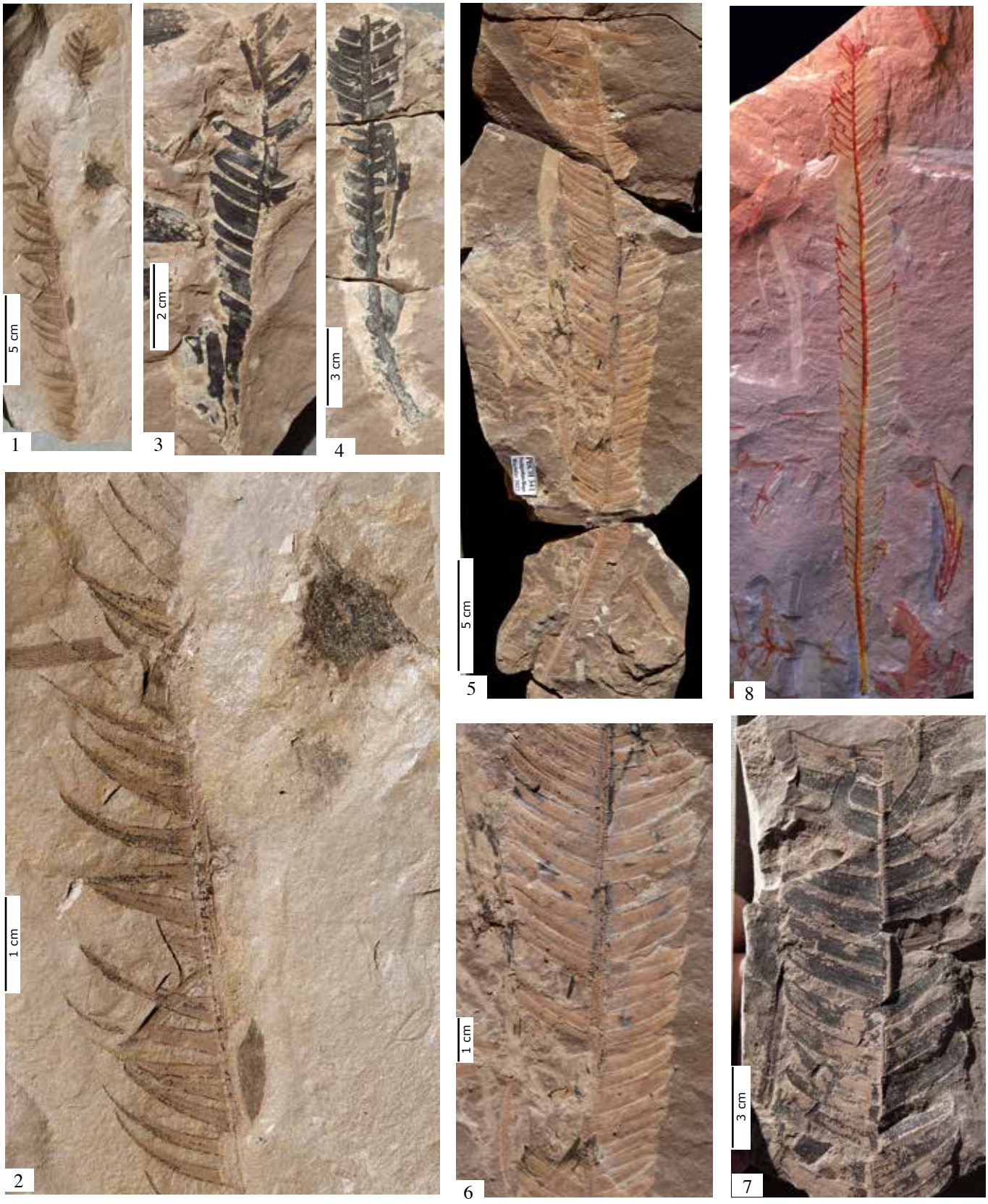
From August Schenk, 1867, table 30. *Nilssonia polymorpha.*

Nilssonia acuminata. **Lower Jurassic. Reconstructions**

a Female plant; b. Seed cone; c. Macrosporophylls, front, back, isolated seed; d. Frond; e. Individual leaflet; f. Male plant; g. Male cone; h. Microsporophyll; i Microsporophyll and sporangia

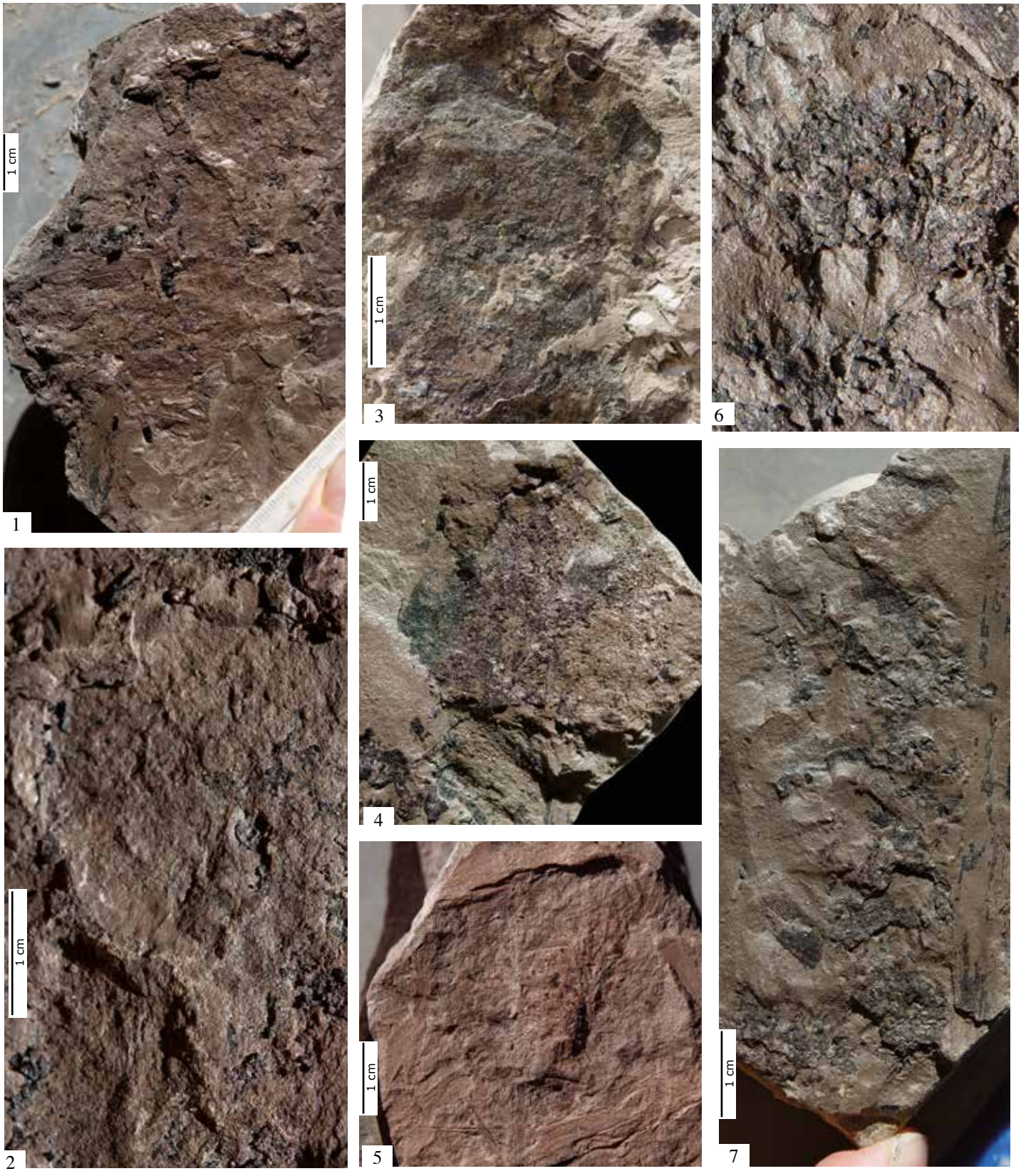
Nilssonia acuminata. **Lower Jurassic. Fronds**

1-3. Frond with cone and detail (PECH 469); 4-5. Several fronds (PECH 465, PECH 445); 6-7. Frond and detail of the leaflets (PECH 362); 8. Complete frond (PECH 645); All Pechgraben, Sandpit Küfner, Coll. Wachtler, Dolomythos-Museum



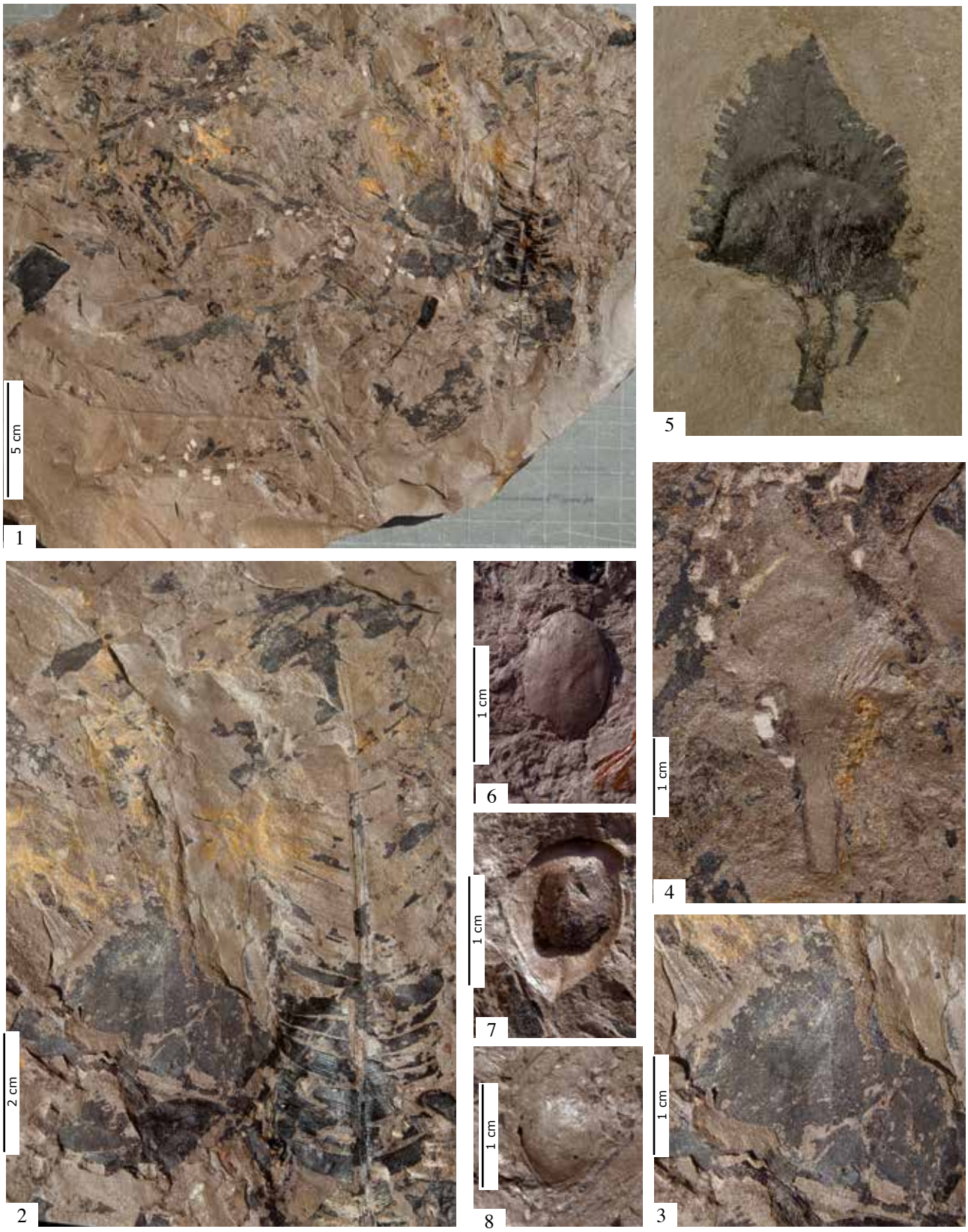
***Nilssonia acuminata*. Lower Jurassic. Fronds**

1-2. Fronds with tapered leaflets, a microsporophyll, and detail (PECH 449); 3-4. Various details of the fronds (PECH 290, PECH 288); 5-7. Fronds and detail of leaves (PECH 341, PECH 597); All Pechgraben, Sandgrube Küfner, Coll. Wachtler, Dolomythos Museum; 8. Complete frond (Nierstein Nature Museum)



***Nilssonia acuminata*. Lower Jurassic. Male cones**

1-2. Pollen cone and detail of the microsporophyll (PECH 602); 3-5. Pollen cones (PECH 26, PECH 262, 565, PECH 534, PECH 520); 6-7. Pollen cone and microsporophyll (PECH 567); All Pechgraben, sandpit Küfner, Coll. Wachtler, Dolomythos Museum



***Nilssonia acuminata*. Lower Jurassic. Female cones and macrosporophylls**

1-4. Decaying female cone with fronds and detail of the megasporophylls (PECH 342); 5. Megasporophyll (PECH 1005, Coll. Gerasch); 6-8. Cycad seeds (PECH 518, PECH 513, PECH 662); Pechgraben, sandpit Küfner, Coll. Wachtler, Dolomythos Museum

1

4

2

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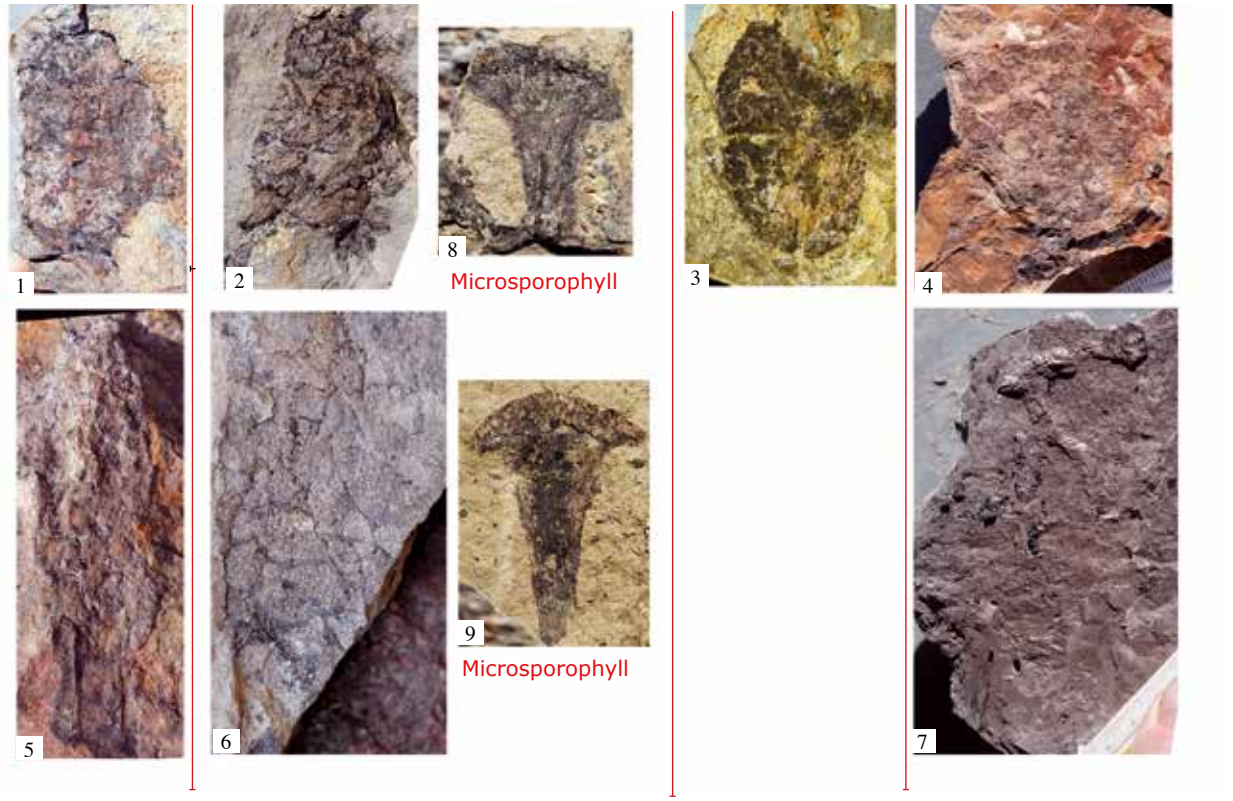
5

***Nilssonia acuminata*. Lower Jurassic. Female cones**

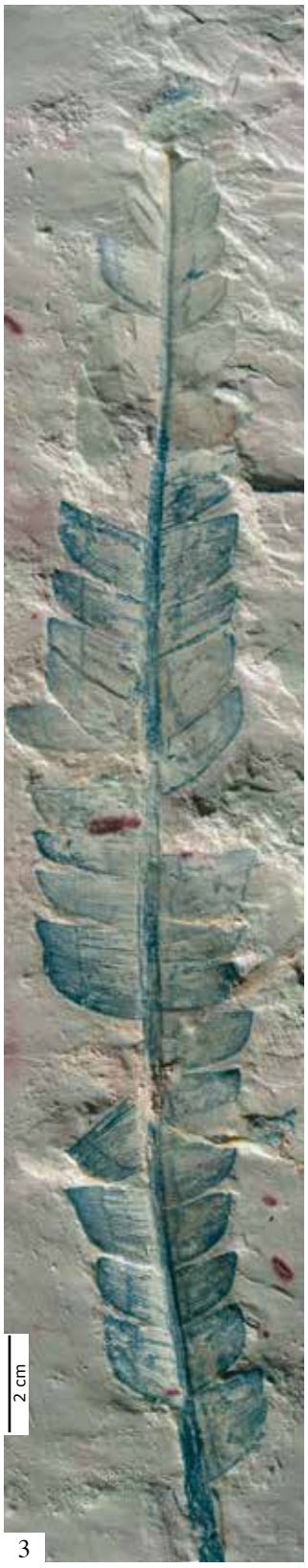
1-5. Juvenile female cone with frond, plate and counterplate, macrosporophyll and detail of the frond (PECH 610); Pechgraben, Sandgrube Küfner, Coll. Wachtler, Dolomythos Museum

making it easy to distinguish the species from T*aeniopteris* cycads.
The male cones of *Nilssonia acuminata* are smaller and composed of a large number of microsporophylls, similar to those found today. The two *Nilssonia* species in the Lower Jurassic of Germany (*N. acuminata* and *N. polymorpha*) differ from each other primarily in their frond structure, despite similarities in their male and female cones.
Nilssonia polymorpha was first described by Schenk in 1867 from the Theta locality near Bayreuth. This has already led to problems in interpretation in the past, which confirms how difficult it is to assign isolated and only partially preserved fronds. Even Schenk, in 1867, arbitrarily mixed the two species without any logic, as evidenced by table XXXIII, Fig. 1., which accurately presents *N. acuminata*. In contrast to *Nilssonia polymorpha*, *N. acuminata* exhibits a geometrically composed structure, which can be compared to today's cycads.

The Nilssoniales during the Permian through the Lower to Middle Triassic periods exhibited a distinct whole-leaf character, with only rare geometrical segmentation and minimal widening along their length. The leaves were terminated in a straight end, giving the appearance of being cleanly cut. The petiole was massive, and the leaves were marked by non-dichotomising parallel nerves stemming from the rhachis. This unique feature sets the Nilssoniales apart from ferns with similar foliage, such as the Triassic *Danaeopsis*, which is a precursor to modern Danaea ferns and *Marattiopsis.*
No reliable evidence of the enigmatic Bennettitales can be found in the Hettangian of Bavaria, since all fossil remains belong to precursors of the cycads due to their fertile organs. There were only sparse findings of other cycads, such as *Ctenis inconstans* and Pseudoctenis prossii, in these layers, but there is no confirmed evidence of fertile organs associated with this species.

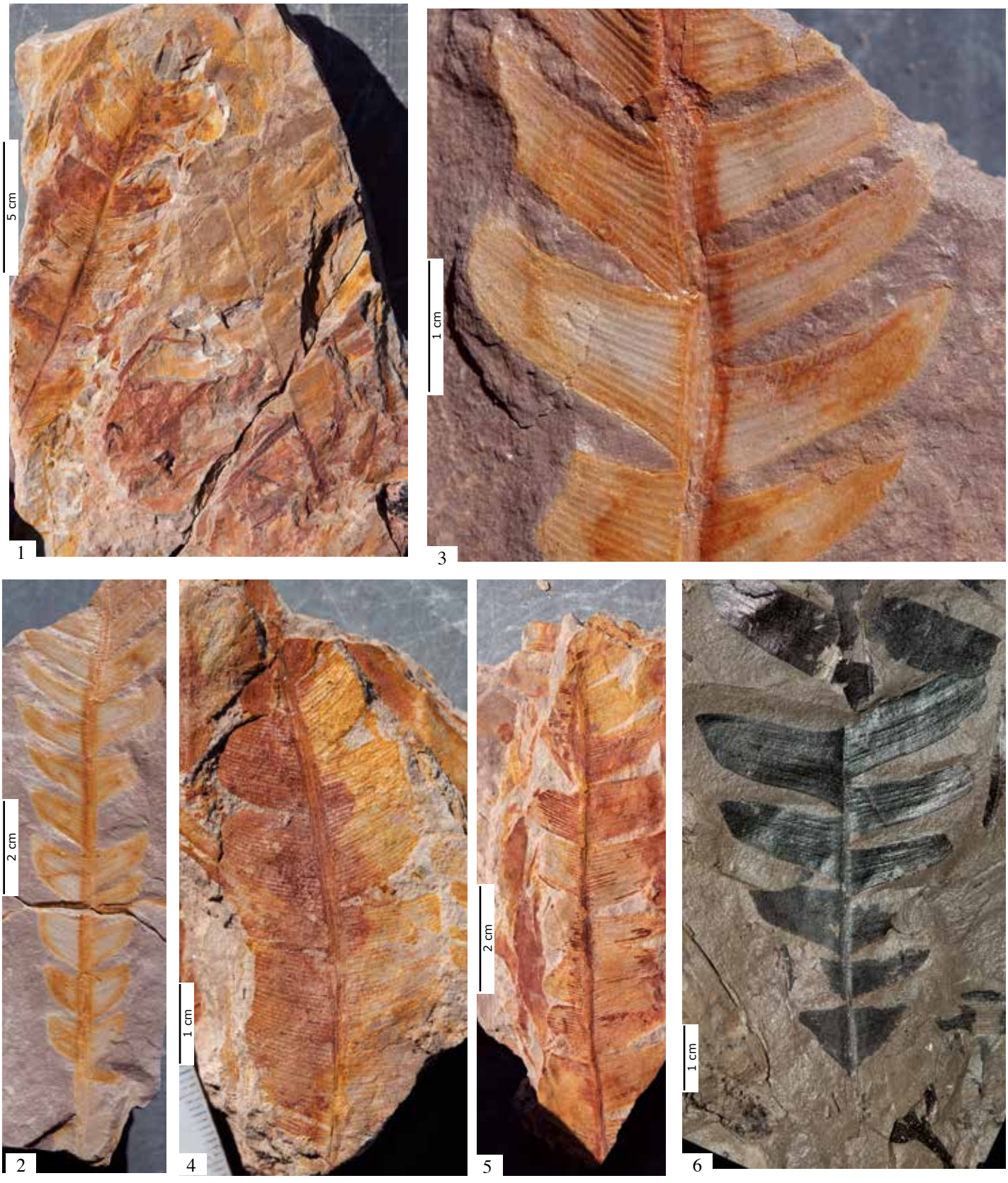


Pollen cones of cycads over millions of years
The characteristics of male cycad cones hardly changed from the Permian to the Jurassic. Most of the multi-seeded cycads (*Taeniopteris, Macrotaeniopteris*) showed rounded shapes (1,2,3,4), while the two-seeded ones (*Nilssonia, Pseudoctenis)* developed elongated ones (5,6,7). Some microsporophylls developed hair-like trichomes (8), others did not (9).



***Nilssonia polymorpha*. Lower Jurassic. Fronds**

1-2. Complete plant with fronds; 3-5. Various fronds (All Pechgraben, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth)



***Nilssonia polymorpha*. Lower Jurassic. Fronds**

1. Cluster of fronds (PECH 47); 2-3. Fronds and detail of leaves (PECH 364); 4-5. Frond (PECH 94, PECH 100, PECH); 6. Basal part of a frond (PECH 443); All Pechgraben, sandpit Küfner, Coll. Wachtler, Dolomythos-Museum

Nilssonia polymorpha. **Lower Jurassic. Male and female cones**

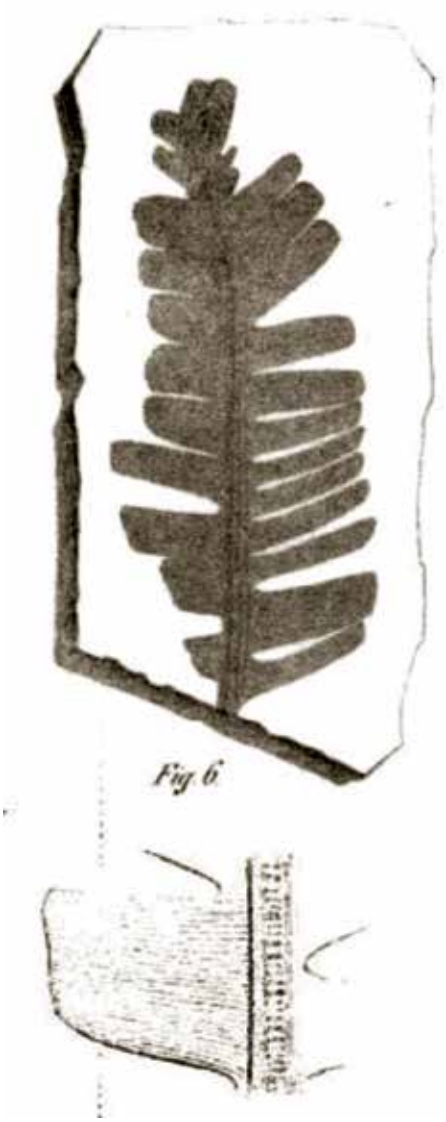
1. Partially decayed female cone (PECH 99); 2. Seed scale (PECH 238); 3-4. Pollen cones (PECH 564, PECH 59); Pechgraben, sandpit Küfner, Coll. Wachtler, Dolomythos Museum

Ctenis inconstans (Braun 1843)

1834 *Ctenis falcata* Lindley & Hutton Fossil Flora Great Britain, p. 63 pl. 103

1843 *Ctenis inconstans*, Braun p. 41 pl. XI Fig. 6-7

The genus *Ctenis* was established in 1834 by the English botanist Lindley (1799–1865) and the geologist and palaeontologist Hutton (1797–1860) for leaf fronds discovered in the Jurassic of Yorkshire (Gristhorpe Bay). Braun, in 1843, further expanded on this publication by describing several new *Ctenis* species (*Ctenis angusta, Ctenis abbreviata, Ctenis marginats,* and *Ctenis inconstans*) from the area around Bayreuth. Among these species, only *Ctenis inconstans* (Plate XI, Figs. 6–7) displayed similarities to the fronds that are sporadically found in the sand pits near the Pechgraben. All other illustrations on Braun's plate XI point in the direction of *Nilssonia acuminata*. However, no definitive fructifications have yet been found.



From Braun in Münster 1843, Tafel. XI,Fig. 6-7 *Ctenis inconstans*

Pseudoctenis prossii (van Konijnenburg-van Cittert, Schmeissner, Hauptmann 1998)

1998 *Pseudoctenis prossii*, van Konijnenburg-van Cittert, Schmeissner, Hauptmann, Tafel 2-6

Pseudoctenis prossii is another rarely occurring genus belonging to the cycad family. The species was initially described in 1998 by Han van Konijnenburg-van Cittert, Stefan Schmeissner, and Sepp and Traute Hauptmann based on findings from Unternschreez, Forkendorf, Schnabelwaid, and the Pechgraben. Notably, the fertile organs associated with the species have yet to be discovered. The frond axis is of this species is broad, with the first leaflets being broadly attached and somewhat shorter than the subsequent ones. The pinnae end in an almost pointed apex, with widths ranging from 1 to 1.4 cm at the base and lengths of up to 20 cm in the middle section. The estimated frond length is between 30 and 40 cm. The leaf veins are arranged closely together, dichotomising only at the base before continuing unbranched to the end.

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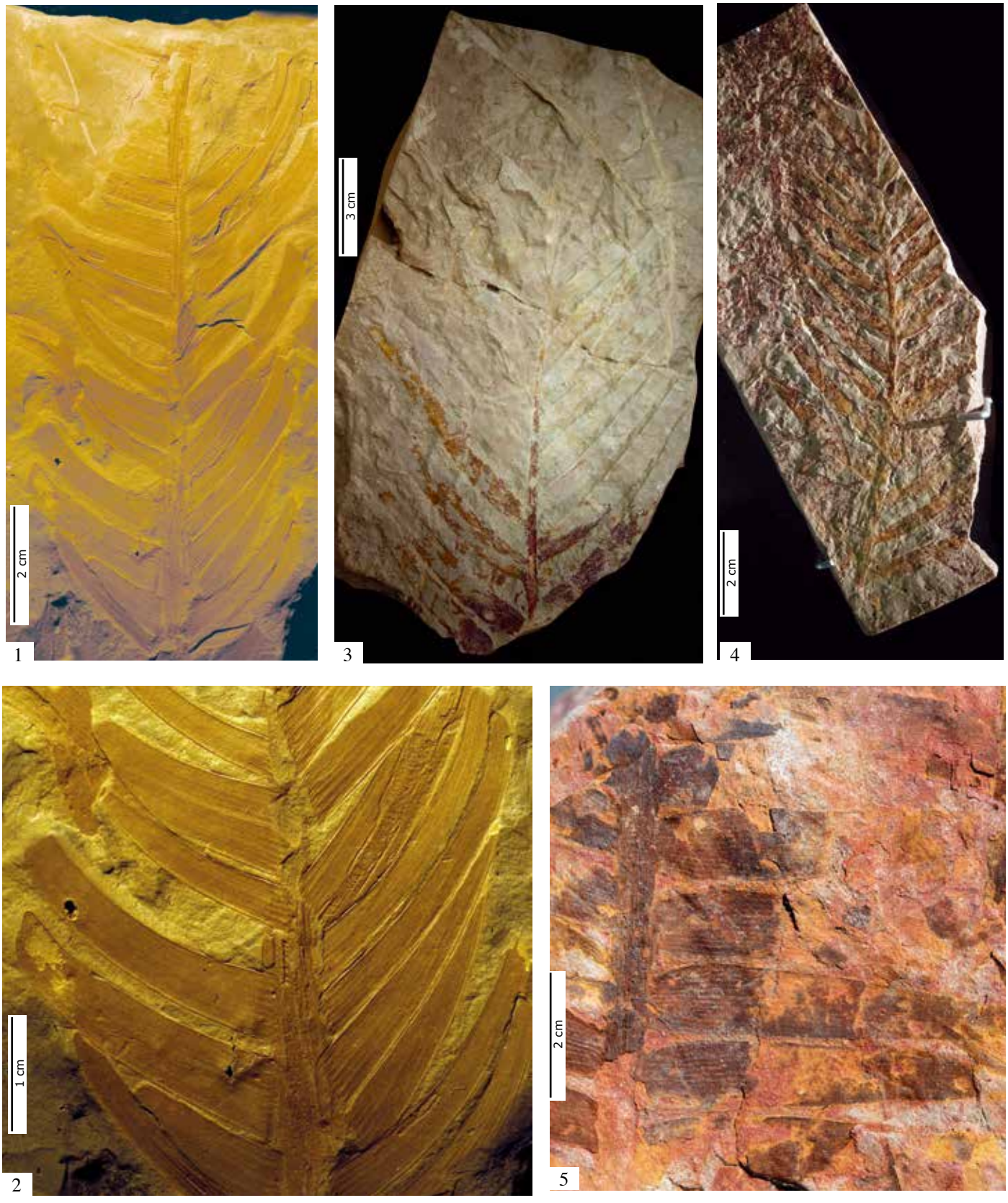
Nilssonia polymorpha. **Lower Jurassic. Reconstructions**

a. Entire plant with two female cones; b. Single frond; c. Single leaflet; d. Macrosporophyll with two seeds; e. Opened seed; f. Male cone g. Microsporophylls, side view and front view; h. Microsporophyll and sporangia with spores, side view; i. Sporangia

***Ctenis inconstans*. Lower Jurassic. Fronds**

1-2. Single frond (PECH 24); 3-5. Various fronds, apical parts (PECH 25); 6-7. Leaflets with details of the lateral veins (PECH 22, PECH 40); All Pechgraben, sandpit Küfner, Coll. Wachtler, Dolomythos Museum



***Pseudoctenis prossii.* Lower Jurassic. Fronds**

1-2. Almost complete frond (Coll. Meyer, Lichtentanne); (PECH 449); 3-4. Frond; (Schnabelwaid, Coll. Hauptmann, Urwelt-Museum Oberfranken, Bayreuth); 5. Part of a frond (PECH 265, Pechgraben, sandpit Küfner, Coll. Wachtler, Dolomythos Museum

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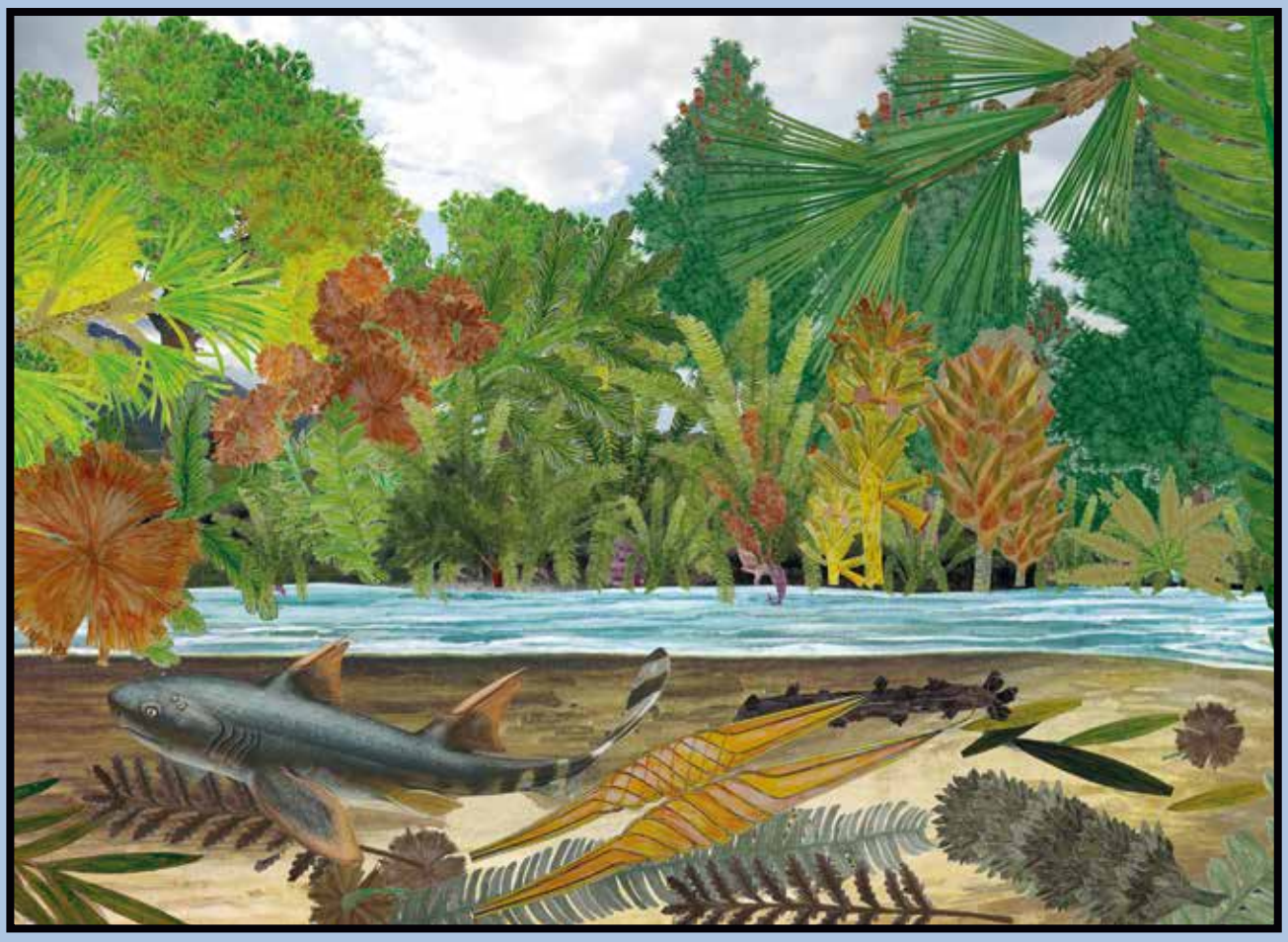

The Fossil Flora of Early Jurassic

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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