The Lower Cretaceous Flora of Central Europe

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The sediments from the Lower Cretaceous (Berrasian), known as German Wealden, mainly from the clay pits around Duingen, have fascinated researchers since the early 19th century due to their abundance of fossils. Sparsely occurring horsetails (*Equisetites* sp.), and ferns (*Dennstaedtites geinitzii* nov. comb., as well as *Wiedenrothia klipsteini,* nov. gen.), but a large number of well-preserved gymnosperms such as ginkgos (*Ginkgoites pluripartitus*), conifers (especially *Sphenolepis sternbergiana*, but also T*sugites garbermannii* n. sp., and *Tsugites linkii* nov. comb.), as well as numerous genera of cycads, formed a floral community that was relatively poor in species but abundant in quantity. The highlight is the large number of plant remains from a family, which has been classified under a variety of names, but above all as Bennettitales. Although these were sometimes associated with the beginning of the angiosperms, well-preserved new finds show that they belong to the cycads and are related to today‘s genus Dioon (*Dioonites dunkerianum, Dioonites lyellanum* nov. comb.). There are also Zamia cycads (*Zamites aequalis, Ctenis humboldtianum, Nilssonia schaumburgense, Ceratozamites kurwius* nov. gen.) and sparse ancestors of the genus Cycas (*Taeniopteris beyrichii*). A club moss, *Seppeltia bockii* gen. n. sp. stands somewhat isolated there. Although we are on the arising of flowering plants appearing a little later everywhere, there is no evidence of their appearance or at least possible lines of development in the Lower Cretaceous of Europe. Their rapid appearance must therefore have other reasons, as happened at the Carboniferous-Permian boundary with the equally sudden spread of gymnosperms (conifers, cycads, ginkgos): climate change and, in the case of angiosperms, the emergence of birds as ideal seed dispersers.

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A flora community from the Lower Cretaceous of Central Europe (140 million years ago). The cycad ***Dioonites lyellanum (*1)** with its peculiar female and massive male cones was common. ***Gingkoites pluripartitus* (2)** was also widespread. The conifers were dominated by ***Sphenolepis sternbergiana* (3).** The club moss family was represented by ***Seppeltia bockii* (4).** The ferns included ***Dennstaedtites geinitzii* (5)** and ***Wiedenrothia klipsteini* (6).**

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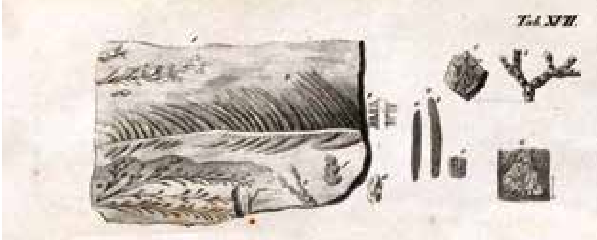
One of the first pioneers in the research of the northwest German Lower Cretaceous floras was the German geologist, botanist and lawyer Friedrich Adolph Roemer (1809-1869), who published two works in 1836 "*Die Versteinerungen des Norddeutschen Oolithen-Gebirges*" (The Fossilizations of the North German Oolith Mountains) and an Addendum with the same name in 1839, where he described some plant fossils, but the majority of his work was dedicated to vertebrate fossils.

The geologist, paleontologist and zoologist Wilhelm Dunker (1809-1885, who was the same age), also did this in 1843 and especially 1846 „*Monographie der norddeutschen Wealdenbildung*" (Monograph of the North German Wealden Formation). The term Wealden derived from the southern English landscape of Weald or the district of Wealden. This meant sediments deposited in the (Early) Lower Cretaceous (around 140-145 million years ago), attributed to fresh and brackish water currents (Schneider & Wiedenroth, 2009).

Although Dunker's area of interest was the macological identification of gastropods and molluscs, he nevertheless devoted nine plates with detailed engravings to plant fossils, in which he also classified the abundant ginkgos with the name *Cyclopteris digitata*, among the Adiantum ferns. In addition, he described and named six new cycadophytes, while taking four more from previous authors such as Brongniart, Göppert or Roemer. The large number of these cycads, classified primarily as *Pterophyllum*, but also as *Cycadites* and *Zamites*, gave rise to nomenclatural difficulties in the following decades.

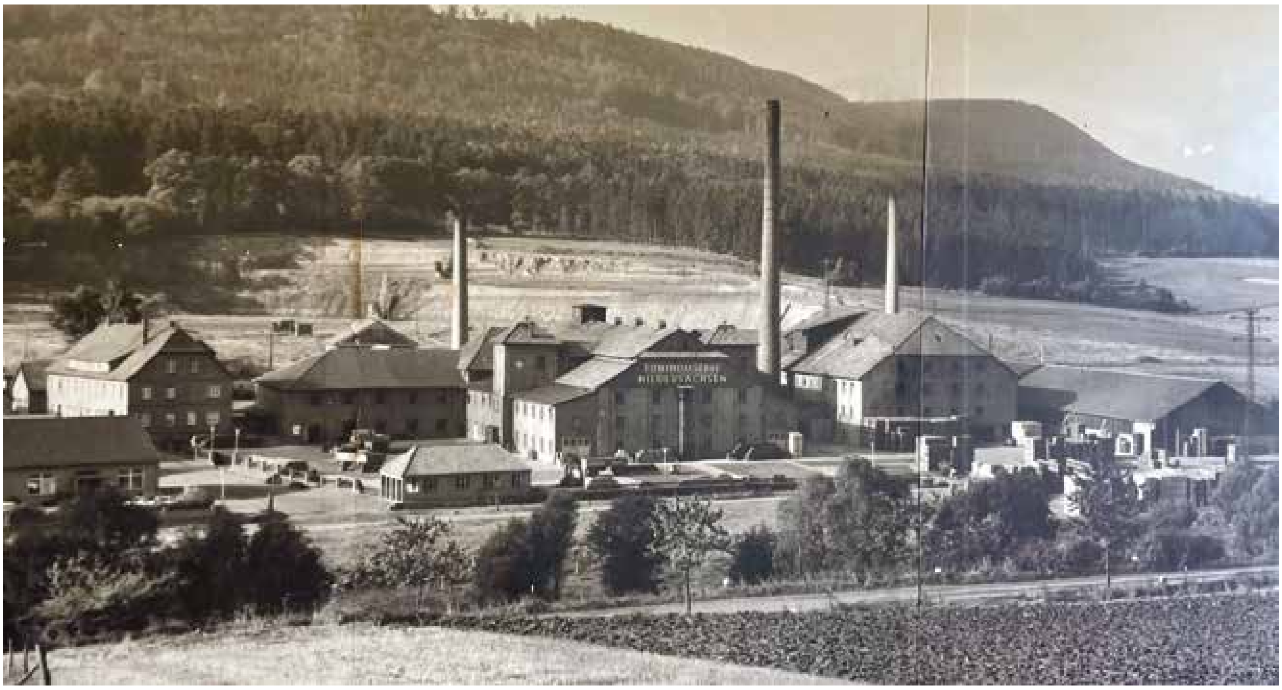


The only plants figured by Roemer (1839) from the Wealden, Germany: They were classified by him as mosses (*Muscites imbricatus* and *M. falcifolius)*. There were also *Cheilanthites denticulatus,* a fern, *Cycadites* (4) and *Abies linkii* (2), a conifer, now *Tsugites linkii.*

In 1846, the German geologist and paleontologist Wilhelm Dunker reproduced plant fossils from the Duingen area on nine plates (Wikipedia).

Dunker was followed by one of the most productive German paleobotanists, August Schenk (1815-1891), who published and depicted (1871) in the fourth part of his „*Beiträge zur Flora der Vorwelt. Die Flora der nordwestdeutschen Wealdenformation*" (Contributions to the Flora of the Ancient World. The Flora of the Northwest German Wealden Formation) a variety of plants on 22 plates. Previously he had already studied the flora of the Middle Triassic Keuper (1864) and the Lower Jurassic (1867) in an exemplary manner.

A clay pit near Duingen (around 1900-1910). The mining of the sought-after pottery clay dates back to the Middle Ages (Dolomythos-archive)

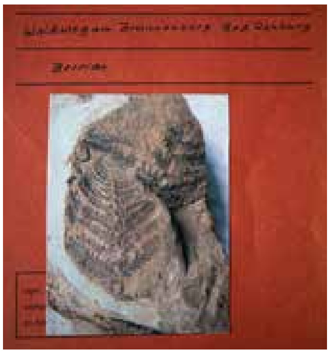


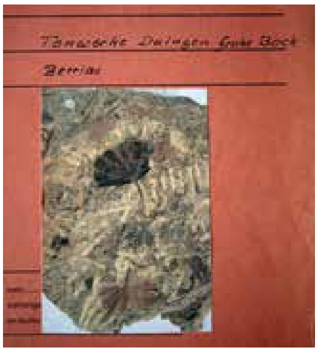
Coppengrave clay processing near Duingen around 1960. In the background was located the clay pit, which hold a considerable number of plant fossils (Garbermann archive).

The fossil flora of the English Wealden was examined and described even earlier beginning from 1801 onwards, with the English father of biostratigraphy William Smith (1769–1839). The work of the English paleontologist Gideon Mantell (1833) should also be highlighted.
Both Dunker (1846) and Schenk (1871) named sites that are no longer or only partially accessible today: These include Obernkirchen, Harrel near Bückeburg, Hohenbostel, Barsinghausen, Osterwald, Duingen, Koppengraben, Weidenbrücker Berg and Deister.
This heyday in the 19th century was followed by a decades-long inactivity which was only ended in 2013 by Christian Pott, Michael Guhl and Jens Lehmann with a specific work on the fossil plants around Duingen.
Over the decades, however, local collectors were active in the clay pits that were still being worked on, and were sometimes soon closed, and brought to light an enormous amount of well-preserved fossil plants,

Animal remains were only found sporadically. Parts of a fish (*Lepidotus roemeri)* (Coll. Seppelt)

The bivalves were dominated by *Margaritifera (Unio) menkei* (Dunker, 1837, 1846), (Coll. Wachtler, Dolomythos)





The private researcher Kurt Wiedenroth (born 1938) from Garbsen near Hanover. He explored the Lower Cretaceous sites around Hanover with great commitment and meticulousness.

which were also excellently prepared. These include Kurt Wiedenroth, who dedicated himself over decades to the intensive search of plant fossils in the various quarries south of Hannover from Alfeld to the Rehburg Mountains.
His collections found their way into, among others, the Geoscientific Collection of the University of Bremen (2007), the Museum für Naturkunde Berlin, the Dolomythos Museum (Italy) and private collections.
Dieter Garbermann's career is particularly astonishing. Born in 1940, living in Brunkensen for all the time, he found work in the neighboring Coppengrave brickworks until the business closed in 1986. For more than forty years after he dedicated his life in finding plant fossils and even when he was over eighty, he went to the sites around Duingen, so that he became one of the greatest experts.
Over the years, he bequeathed a large part of his collection to Stephan Seppelt from Sibbesse, a preparator highly specialised in fossils, who himself collected the outcrops, resulting in a wealth of plant fossils that had probably never been achieved before. All of these collections and the large number of fructifications found made it possible for this publication to come about and thus also improved knowledge of a flora that is

84-year-old Dieter Garbermann has been working on the sites for more than forty years. And this still with-heavy hand tools. The so-called "flowers" particularly captivate collectors. They represent cycad fructifications.

The Bock clay pit in Duingen (coordinates: Lat: 52.00035129° N, Long: 9.67578607° E). Like other areas of the German Wealden, it is characterized by a wealth of well-preserved plant fossils.

more than 140 million years old and is on the verge of the appearance of the first flowering plants.

Massive trunks of gymnosperms are found again and again

Geology

Depending on the various researches, the Early Cretaceous Wealden Floren, mainly from the Hildesheim district in Lower Saxony, belong to the Bückeberg Formation (Pott, Guhl, Lehmann, 2013), i.e. the upper part of the Berriasian to the early Valanginian, which is approximately 140 million years old or corresponds to the Deister Formation (Krakow & Schunke, 2016), classified as early Berriasian, which would date back two to three million years. However, precise zircon analyzes or dating using radium-argon methods are missing.

The sediment was deposited by fresh water supplies, with periodic flooding from the nearby sea. Eggs of hybodont sharks (*Palaeoxyris jugleri)* found correspond to the depositional conditions of many Triassic-Jurassic sites in Central Europe such as Ilsfeld (Ladin) (Wachtler, 2016) or Pechgraben (Hettangian) (Wachtler, 2024). The climate was humid subtropical, although the poverty of ferns and horsetails, as well as the abundance of cypress-like conifers and small-leaved ginkgoes, indicate a deterioration in living conditions.

The climatic conditions and plant communities correspond roughly to coastal regions of

A lens in the southern part of the Bock clay pit was rich in fertile organs of *Dioonites.*

Photos by Kurt Wiedenroth with the most fossil-rich layers in the Bock clay pit

today's Mexico, characterized by longer dry and rainy seasons.

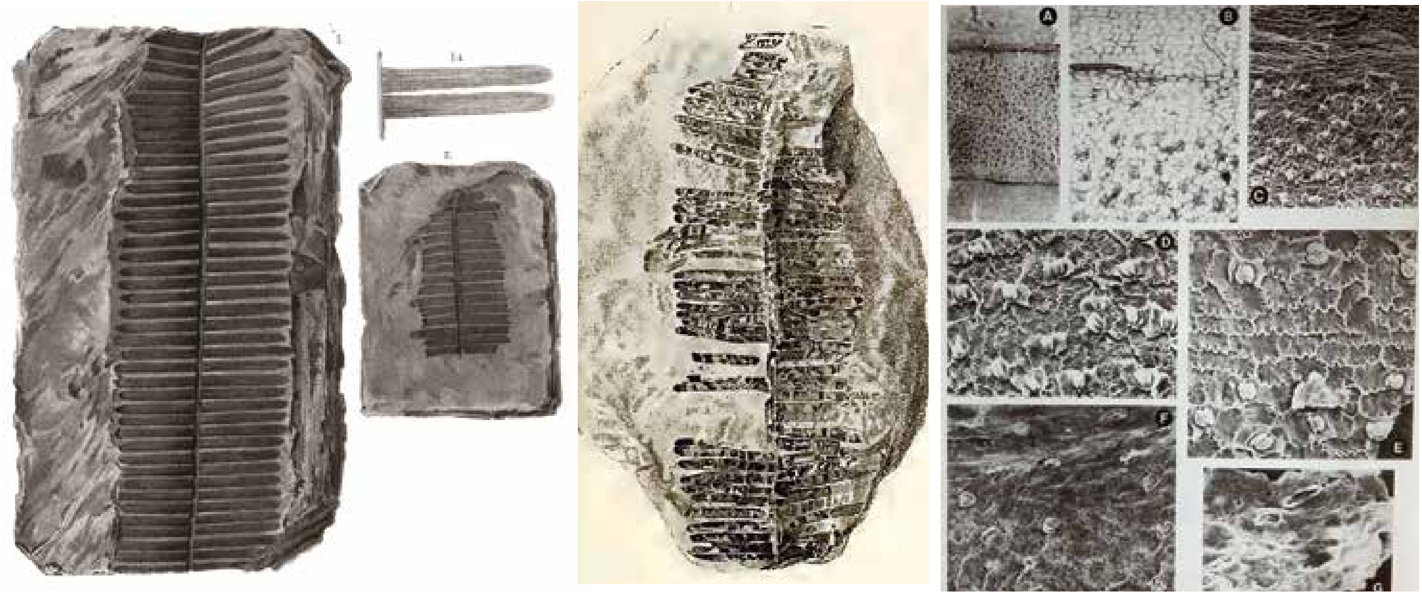
In the clay pits, which have been exploited for centuries, meter-thick layers of clay alternate with hard, compressed carbonate beds that are a maximum of one meter thick and contain numerous plant fossils. Above all, the fossil-free clays were mined, which were characterized by pronounced plasticity and high raw breaking strength even when small amounts of water were added. Until the end of the 19th century, sought-after pottery was made from it, which was waterproof and acid-proof without glaze. They were suitable for making bottles and storage containers. Later, stoneware, clay tubes, as well as floor tiles and facade clinker bricks were produced. Today they are used primarily as binding clays in the production of roof tiles (Krakow & Schunke, 2016).

It should be noted that the plant fossils do not always come from lenses of the same age. They can usually be followed for a few meters, tapering at their ends or beginning again slightly offset in height, due to changes in flooding conditions. Then again, no plant preservation took place for indefinite periods of time until conditions arose again that could lead to slightly changed plant compositions.

The plant communities

The striking thing about the German Wealden is the wealth of a wide variety of cycads, which are very interesting among the ancestors of the recent genus Dioon (*Dioonites dunkerianum, Dioonites lyellanum*), Zamia (*Nilssonia schaumburgense, Zamites aequalis, Ctenis humboldtianum*), Ceratozamia (*Ceratozamites kurwius*) and Cycas *(Taeniopteris beyrichii*) can be classified. Other gymnosperms are represented by the dominant conifer (*Sphenolepis sternbergiana*), less commonly are ancestors of today's Tsuga conifers (*Tsugites garbermannii* and *Tsugites linkii*), as well as rich accumulations of fossil ginkgoes (*Ginkgoites pluripartitus*).

Ferns, mainly *Dennstaedtites geinitzii* and *Wiedenrothia klipsteini*, and horsetails play a minor role. Lycopods, as dominant as they were especially in the Carboniferous but also in the Triassic and Lower Jurassic, are only represented by the low-growing *Seppeltia bockii.*



From Dunker, 1846. Holotype of *Dioonites (Pterophyllum) lyellanum,* Plate VI, Fig. 1 + 2; Middle: From Schenk, 1871. Other illustration of the holotype (Plate XXXIV, Fig. 1), kept in the Humboldt University of Berlin (HUM 3555), as well as cuticle analyzes of it (from Watson & Sincock, 1992, p. 113+114).

Cycads of the Lower Cretaceous

With their wealth of species and also in terms of quantity, the cycads are among the most distinctive features in the Lower Cretaceous quarries of Central Europe. Nevertheless, there are considerable differences in assessment of the number of genera and species. Based on fronds and cones, three species from the group of Zamia precursors were present, namely *Nilssonia schaumburgense* (Dunker 1846), *Zamites aequalis* (Dunker, 1846), and *Ctenis humboldtianum* (Dunker, 1846). *Ceratozamites kurwius* (Pott, Guhl & Lehmann, 2014) with its two-horned sporophylls can be considered a precursor of today's Ceratozamia cycads, being now native to the Neotropics of Central America. In addition, the most common cycad family in terms of quantity was one or two species of the enigmatic Dioon ancestors: *Dioonites lyellianum* (Dunker, 1846), and *Dioonites dunkerianum* (Göppert, 1836), which, however, where classified with a variety of names for the same species such as *Pterophyllum* or *Ptilophyllum* for sterile fronds or descriptions only for fructifications such as *Williamsonia* or *Bennettites*.

A particularly beautiful "flower", a partially decayed cone of *Dioonites lyellanum*, found in 2024 by Dieter Garbermann.

Based on their appearance, especially that of the abundant female cones, they are likely to have a precursor status to the Central American cycad genus Dioon. Rarely, a species from the group of multi-seeded cycas ancestors with *Taeniopteris beyrichii (*Schenk, 1871) occurs, although the related genus *Macrotaeniopteris*, which dominated the floras in the Permian, Triassic and Jurassic periods for almost 150 million years, could be present, but was never found.

All other genera and species, which have so far been described primarily on the basis of frond fragments, are questionable, as additional fructifications are missing. A list of species based solely on sterile fronds is hardly effective, as they are similar to one another in many respects.

However, the cycads, as abundant as they were in the German Wealden, have often given rise to discussions. A dilemma lies in the fact that cones or seed scales were collected extremely rarely. In addition to the female cones, the male cones cause problems even more, they are usually covered in thick pollen crusts and are so unattractive that they usually end up in the rubble. In addition, male cycad cones are similar to each other, both now and then, so that classification is difficult.
Particularly abundant are fructifications, which collectors called "flowers" and oft they were connect as ancestors of angiosperms. Only surprisingly wide-ranging finds by Dieter Garbermann and Stephan Seppelt, and earlier by Kurt Wiedenroth, have contributed to shedding light on the fossil finds from Wealden in northwest Germany, which are characterized by too many names and misconceptions, and at the same time provide a solution to one of the biggest enigmas of paleobotany, the solution of a plant group called the Bennettitales.

Dioonites Miquel 1861

One of the most common plants in Duingen is a cycad, which is now well known thanks to a large number of finds, but its classification has always been problematic. This should therefore be comprehensively reviewed.

Dioonites lyellanum Dunker 1846

Research history

Classifications for the different parts of the plant:

Pterophyllum

1828 *Pterophyllum* Brongniart Prodrome d'une histoire des Végétaux fossiles, p.95

1828 *Zamia mantelli* Brongniart, p. 94

1828 *Pterophyllum Williamsonis* Brongniart Prodrome d'une histoire des Végétaux fossiles, p.95

1820 *Algacites filicoides* Schlotheim

1846 *Pterophyllum lyellianum* Dunker, pl VI Fig 1-2, Duingen

1846 *Pterophyllum lyellianum* Pott, Guhl, Lehmann pl. V, Fig. 2-5, pl. VI 1-4

1861 *Dioonites lyellianus*, Miquel p. 30

1871 *Pterophyllum lyellianum* Schenk p. 230, Pl. XXXIV. fig. 1. 2 a. b.

Williamsonia

1870 *Williamsonia* Carruthers p. 680, p. 692

1870 *Williamsonia gigas* Carruthers p. 693

2013 *Williamsonia joanwatsoniae* Pott, Guhl, Lehmann pl. VII, Fig. 1-4, pl. VIII 1-4

Bennettites

1870 *Bennettites* Carruthers p. 694

1870 *Bennettites gibsonianus* Carruthers p. 694, pl. 57 fig. 1-8, pl. 58 fig. 1-5, pl. 59 Fig. 1-8

The year 1828 can be considered the birth of scientific research into fossil cycads: At the same time, the English theologian and paleontologist William Buckland (1784-1856) described fossilized cycad stems and named them *Cycadeoidea megalophylla* and *Cycadeoidea microphylla*, depicting them in detailed drawings and with recent ones Cycas and Zamia cycads compared. The French paleobotanist Adolphe Théodore Brongniart (1801-1876), on the other hand, listed fossil cycad fronds from England, Sweden and Germany in his book *"Prodrome d'une histoire des Végétaux fossiles",* published in December 1828, without illustrations and with makeshift genus and species descriptions like *Cycadites, Zamites, Pterophyllum, Mantellia* and *Nils(s)sonia*.
Decades later (1870), the English botanist and geologist William Carruthers (1830-1922) noticed further differences in the appearance of fossil cycads, so he

Various magnificent fronds from the former Kurt Wiedenroth collection, now either in Bremen or the Berlin Natural History Museum. Precise classifications based on the shape of the fronds are not always helpful.

A cycad community from the Lower Cretaceous of Central Europe. The cycad ***Dioonites lyellanum*** (1) with its peculiar male and female cones dominated the landscape. The Cycas ancestor ***Taeniopteris beyrichii*** was found less frequently (2). ***Ctenis humboldtianum*** (3) stood out because of its massive fronds. ***Ceratozamites kurwius*** (4) enriched the landscape, as did the frequently found ***Zamites aequalis*** (5).

divided them into four divisions: Cycadea, Zamieae and two newly created groups, the Williamsonieae and the Bennettiteae, which were subsequently united to form the enigmatic family of Bennettitales. However, it triggered a controversy that continues to this day, as flower-like impressions on the trunks were sometimes interpreted as the beginning of the angiosperms. As a result, it was recognized that such silicified trunks, often preserved in three dimensions, were found in sediments that ranged from the Upper Triassic through the Jurassic and into the Cretaceous.

In 1933, the Swedish paleobotanist Rudolf Florin discovered that the leaves of cycads differ from each other in the structure of the stomata cells. Thus, fronds that were similar in appearance represented different families and lineages. Building on this, he characterized leaves of fossil genera such as *Pterophyllum* (Brongniart, 1828), *Ptilophyllum* (Morris, 1840) but also *Nilssonia, Zamites, Ctenis*, as well as *Macrotaeniopteris* and *Taeniopteris*.

This treatise will not go into the many attempts to classify the enigmatic group of Bennettitales (Wieland, 1906, Lundblad, 1950, Harris, 1932, 1969), but rather will examine the rich finds from the Lower Cretaceous of Central Europe, as it is precisely these that provide improved insights in the classification and appearance of this group of plants.

Since a large number of sterile fronds, as well as fertile organs, have been described since the beginning of paleobotanical research, it is important to identify description priorities and sort out any duplicate names for one and the same plant.

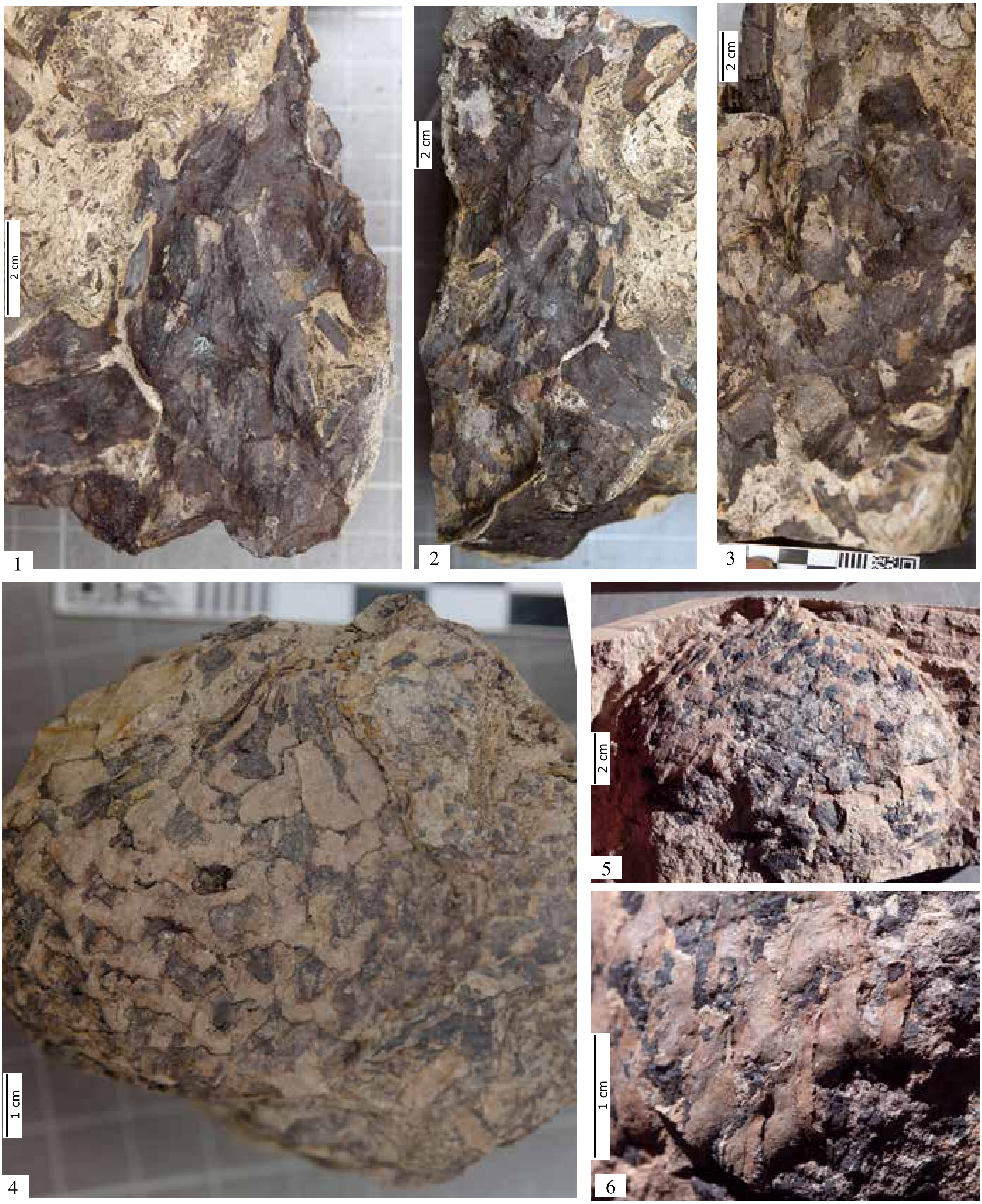
In 1846, the German natural scientist Rudolf Wilhelm Dunker published a comprehensive work on the fossil plants from the Wealden of northwest Germany. He classified a particularly common species in the Lower Cretaceous, with a holotype from Duingen, as *Pterophyllum lyellianum* and depicted it (Plate VI, Fig. 1+2). Dunker was referring to a generic name by Adolphe Brongniart from 1828, in which he established various sterile cycad fronds such as *Pterophyllum longifolium* from the Lower Jurassic of Germany, but also *Pterophyllum williamsonis, Pterophyllum majus* or P*terophyllum minus* from the Lower Jurassic of Sweden. Previously, in 1843, the German paleontologist

Dioonites lyellanum. Early Cretaceous. Leaf fronds

1. Completely preserved frond (DUING 295, Coll. Seppelt); 2. Apical part of a frond (DUING 14); 3. Frond broken in the middle (DUING 09, both Coll. Wachtler); 4. Frond (DUING 255, Coll. Seppelt); 5-6. Two almost completely preserved fronds (Coll. Wiedenroth); 7. Juvenile frond (DUING 297, Coll. Seppelt); 8-9. Fronds and detail of the leaflets (DUING 17); 10. Detail of a pinnula (DUING 14, both Coll. Wachtler); all Tongrube Bock, Duingen

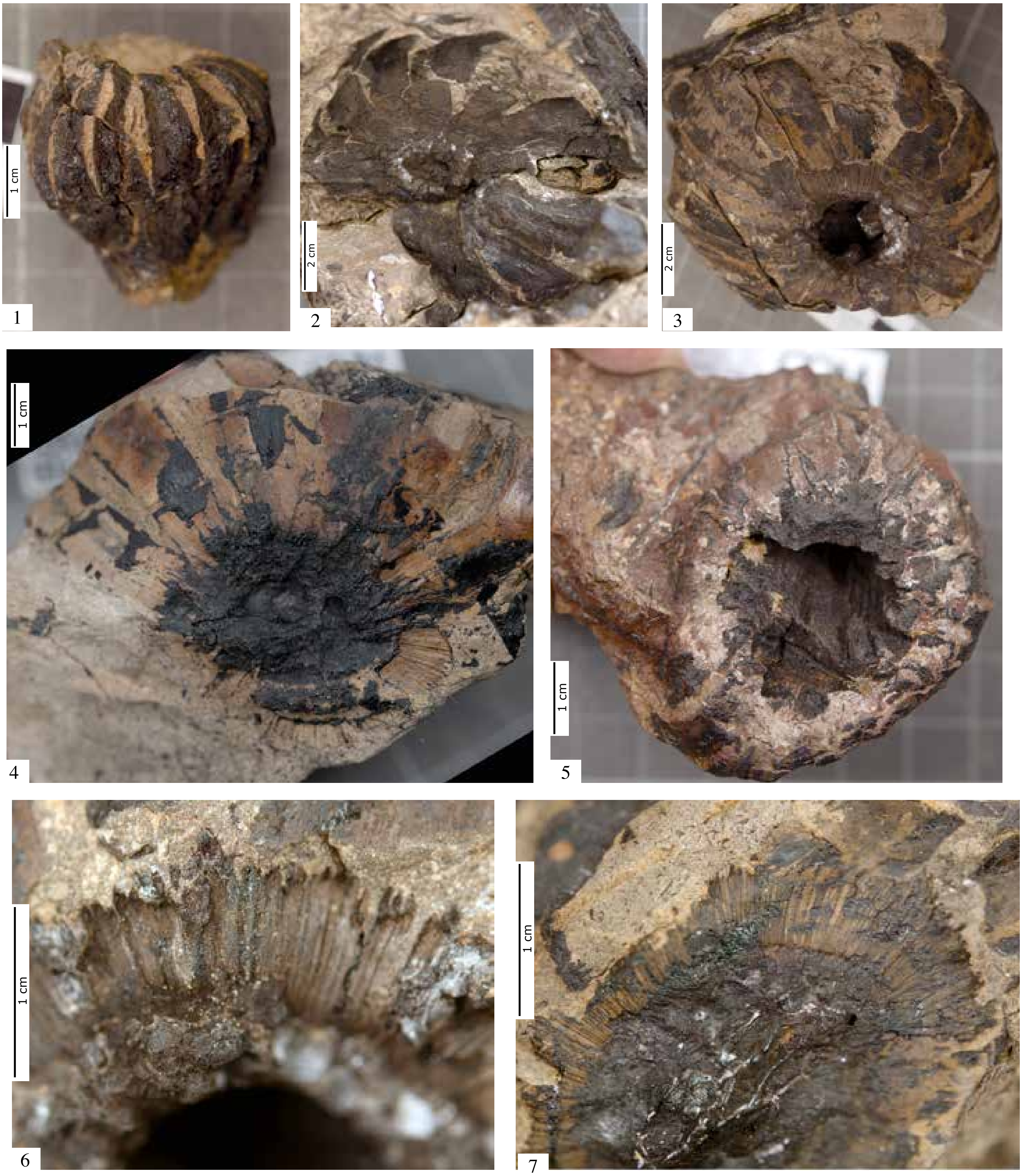
***Dioonites lyellanum*. Early Cretaceous. Male cones**

1-2. Partially preserved large pollen cones and detail of the microsporophylls (DUING 384, Coll. Garbermann); 3. Pollen cone; 4. Outside of a microsporophyll (Both Coll. Wiedenroth); 5-6. Isolated microsporophylls (DUING 62, DUING 61, both Coll. Wachtler); all Duingen



***Dioonites lyellanum*. Early Cretaceous. Stems and female cones**

1-3. Various details of the trunk base with separated frond scars (DUING 227, DUING 228, DUING 229); 4. Completely-preserved juvenile female cone (DUING 202, all Coll. Stefan Seppelt); 5-6. Juvenile cone and detail of seed scales (DUING 137, Coll. Wachtler, Dolomythos); all Duingen, Tongrube Bock

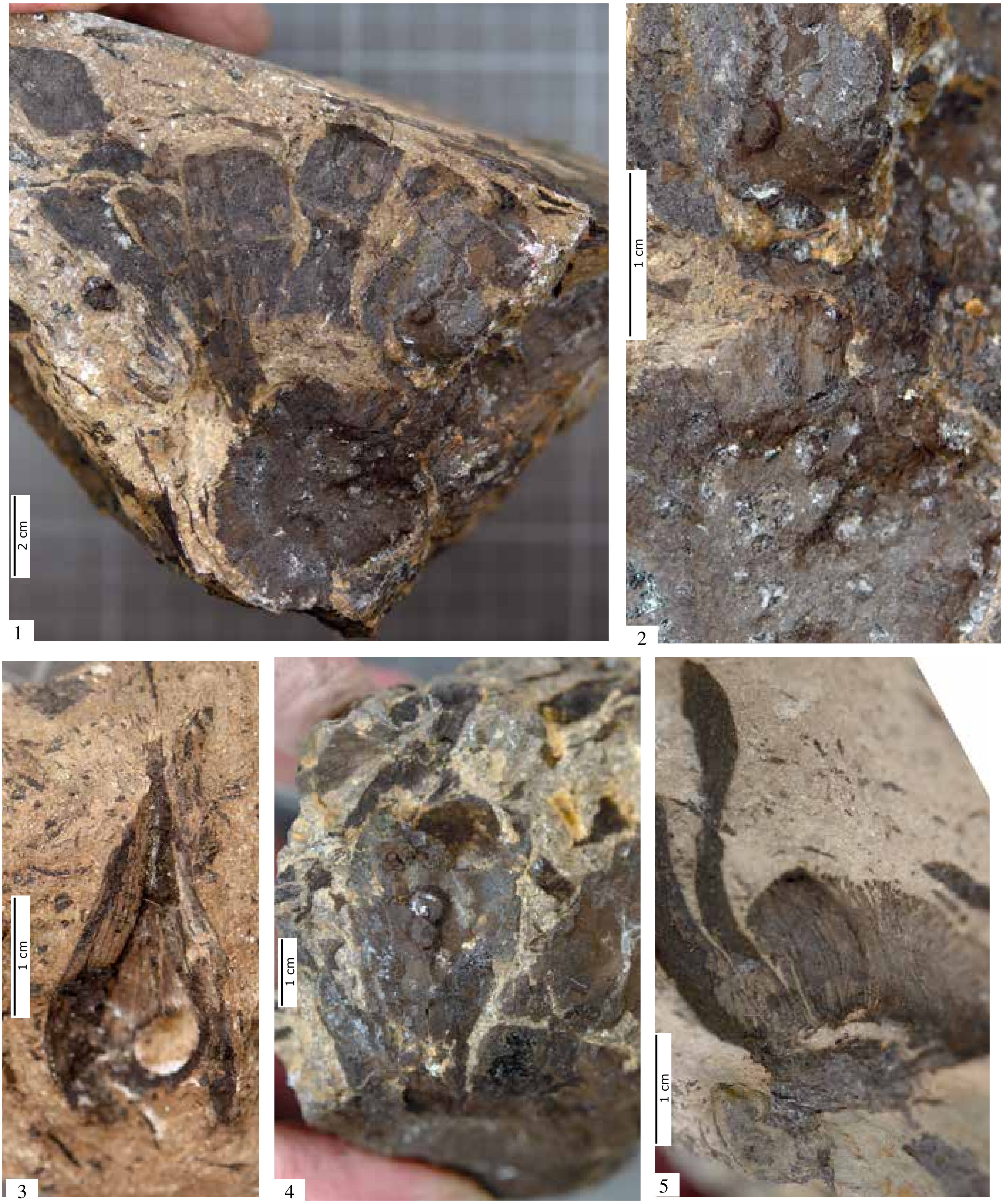


Dioonites lyellanum. Early Cretaceous. Female cones

1. Three-dimensionally preserved basal part of a seed cone (DUING 247); 2-3. Basal view of cones with seed scales (DUING 245, DUING 246); 4. Basal view of a cone with seed scales and partially recognizable seeds (DUING 249); 5. Hollow view of a cone with dissolved rhachis (DUING 209); 6-7. Detailed view of the outgoing radial sterile leaf basis (DUING 238, DUING 218, all Coll. Stefan Seppelt); Duingen, Tongrube Bock

***Dioonites lyellanum*. Early Cretaceous. Female cones and seeds**

1. Inner part of a female cone with isolated seed (DUING 347); 2. Inner part of a female cone without macrosporophylls (DUING 342); 3. Female cone with beautifully preserved seed scales (DUING 391, all Coll. Garbermann) 4. Cone with isolated macrosporophylls and partially visible seeds (DUING 85, Coll. Wachtler); 5. Isolated scale with one seed (DUING 429, Coll. Garbermann); 6. Part of a decayed seed cone, as well as detail of the inner part (DUING 344) 7-10. Isolated seeds (DUING 376 DUING 377, DUING 383, DUING 375, Coll. Garbermann); all Duingen



***Dioonites lyellanum*. Early Cretaceous. Female cones**

1-2. Basal cone part with seed scales and detail of the seeds (DUING 216); 3. Isolated seed scale with seeds (DUING 208); 4. Basal part of a cone with isolated seeds (DUING 223); 6. Detail of stem base (DUING 213); 5. Lateral view of a seed scale and part of the sterile palisade ring (DUING 212, all Stefan Seppelt collection); Duingen, Tongrube Bock

1. Today's root of a cycad and 2.Cycad root complex from Duingen (DUING 301, Coll. Garbermann)

3. *Dioon edule.* Recent trunk base with frond abscission point. 4. *Dioonites lyellanum.* Stem base of a shed frond (DUING 229, Coll. Seppelt)

Heinrich Robert Göppert (1800-1884) had first described a *Pterophyllum dunkerianum* from Wealden, Germany, in honor of Dunker. However, the German-Dutch botanist Friedrich Anton Wilhelm Miquel (1811-1871) suspected that both *Pterophyllum lyellianum,* first described by Dunker, 1846, and *Pterophyllum dunkerianum* (Göppert, 1843), were ancestors of the modern cycad genus Dioon, native to Central America. He therefore changed these names in his "*Prodromus systematis Cycadearum"* (1861) to the new generic names *Dioonites lyellanum* and *Dioonites dunkerianum.* The holotype of *Pterophyllum (Dioonites) lyellianum*, which is still stored at the Humboldt University in Berlin, was subsequently depicted in a more faithful lithographic print by August Schenk (1871). Based on later cuticle analyses, as well as the stomatal apparatus by Joan Watson and

***Dioonites lyellianum.* Male plant**

h. Male plant; i. Pollen cones; j. Microsporophyll upper surface; k. Microsporophyll, underside with pollen sacs; l. Isolated pollen sacs

***Dioonites lyellianum*. Early Cretaceous. Female plant. Reconstructions**

a. Female plant; b. Detail with three seed cones, partially disintegrated; c. Juvenile female cone; d. Ripe, partially decayed cone; e. Macrosporophylls, front, back; f. Isolated seeds; G. Leaf fronds

Dioon. Cycad

Dioon edule. 1. Several generations of female cones, partially cauliflower decayed; 2. Decaying female cone; 3. Macrosporophyll, exterior; 4. Macrosporophyll, inside; 5. Macrosporophyll with two seeds; 6. Macrosporophyll with two dried seeds; 7-8. Male cones in different stages of growth

Dioon. Cycadeen

Dioon spinulosum. 1-2. Male plant and detail of leaves; ***Dioon holmgreni***; 3. Fronds; ***Dioon edule.*** 4. Stem with decayed cauliflower female cone; 5. Decayed female cone with seeds between the macrosporophylls

Caroline A. Sincock (1992, p. 113-114), these fronds were later classified in the enigmatic group of Bennettitales.
However, there were also names for the fructifications such as *Williamsonia joanwatsoniae* (Pott, Guhl, Lehmann, 2013), *Weltrichia, Bennettistemon valdensis* (Pott, Guhl, Lehmann, 2013), *Cycadolepis* (Pott, Guhl, Lehmann, 2013), which increased the confusion.
Ostensibly, it is now important to find a uniform name for the entire plant, although the name *Dioonites lyellianum* coined by Miquel (1861) still proves to be the most effective. The species name therefore includes those flower-like structures with seeds that are often found in Duingen (*Williamsonia joanwatsoniae, Weltrichia, Bennettistemon valdensis, Cycadolepis* (Pott, Guhl, Lehmann, 2013), as they are considered to belong to the sterile *Dioonites* fronds, as well as pollen cones or isolated microsporophylls. Over time, other species names were added for sterile leaf fragments from the Wealden of northern Germany such as *Ptilophyllum aequale* (Göpppert ex Dunker, 1846; Pott, Guhl, Lehmann 2014 nov. comb. *Pterophyllum goeppertianum, P. humboldtianum* (Dunker, 1846), but these do not belong to the precursors of Dioon, but are Zamia ancestors.

Description

Whole plant: Trunks with cycad character (DUING 227, DUING 228, DUING 229; in DUING 229 the breakage of the fronds on the trunk are clearly visible). Leaf fronds are stalked and slender, probably reaching 50 cm or more (DUING 295). Individual leaflets a maximum of one centimeter wide, reaching 10 cm in length (DUING 295), alternating or opposed, entire margins, crossed by four to five equally strong, delicate or barely visible veins that run parallel to the edge (DUING 14, DUING 17). Apex of the leaves blunt to extended upwards on one side (DUING 17).
Female fructifications: Juvenile cone-like, with the fruit scales fitting tightly around a central spindle (DUING 202). Seed scales fall off from the double-circled inner part after maturity, leaving resinous secretion ducts at the break-off points (DUING 347, DUING 342). Macrosporophylls more leaf-like than other cycads, curved up at the tip and tapering to a point (DUING 391, DUING 429, DUING 212). Seed leaves furrowed in the basal part, with two seeds hanging on the axis-facing side of the thickened scales towards the central rhachis (DUING 85, DUING 429). Seeds slightly elongated, to egg-shaped, about 0.8 to 1.2 cm long and 0.5 to 0.8 cm wide (DUING 376 DUING 377, DUING 383, DUING 375). The basal seed scales remained fused to the circular stem body, similar to a sunflower blossom (DUING 238, DUING 218, DUING 249, DUING 347, DUING 342). Basal part deeply furrowed, connected to another circular inner part of the trunk.
Pollen cones: Large, reaching 15 to 25 cm in length and 5 cm wide, sometimes buckling under its own weight (DUING 384). Microsporophylls about 1-1.2 cm wide, 1 cm high, tapering. Bearing pollen sacs on the underside (DUING 62, DUING 61).

Remarks

Due to the rich finds within a lens on the southern part of the Bock clay pit, consisting of trunks, leaf parts and so-called "flower" fructifications, the overall picture can be looked at in more detail, evolutionary lines can be shown to the present and, above all, this plant can be demystified.
What is certain is that it was a bisexual plant, with separate male pollen and female ovules, with the flower-like structures forming the final state of decayed female cones with partially detached seed scales. The dark areas lying between the lamellae of the circular bodies are likely to represent clumped secretory ducts and not pollen capsules, as they were sometimes referred to in the past to indicate hermaphroditism, similar to flowering plants.
Although we are at the limit of the global appearance of flowering plants in the Lower Cretaceous, developments in this regard must be ruled out. The general desire for true hermaphroditism, as often occurs in angiosperms, has not been confirmed (Pott, 2014). Of today's gymnosperms, the cycads come into question because of the fronds that are very common in the clay pits of Duingen. One genus in particular stands out here, due to its trunk character, shoots branching off next to or

on the mother plant, and decaying female cones: the cycad genus Dioon, which is subdivided in eleven to fourteen species, mainly in Mexico, but also in Honduras and Nicaragua. It occupies a special position within the cycads due to its leaf-like macrosporophylls. These disintegrate when ripe, and at the same time several flower-like wreaths with macrosporophylls remain on the mother plant in the apical area, but also on the side areas, for years. The seed scales are flattened at the tip, broadened and curved up and develop two seeds at the bottom.
The pollen cones are elongated, the microsporophylls are arranged spirally around a cone axis, with the pollen sacs on their underside.
Particularly in the Eocene, dating back to the beginning of the Cenozoic 65 million years ago, Dioon populated a large part of North America, although expansion to South America was made impossible due to the continental separations that existed at the time. With the cycas genus Dioon it is possible to have an approximate overview of the most common cycad genus in the Lower Cretaceous of Duingen. This also solves the mystery surrounding the *Bennettites*. These are probably nothing other than precursors of today's cycad genus Dioon.

Dioonites dunkerianum Göppert 1843

Another cycad species found relatively frequently in the clay pits of Duingen is *Dioonites dunkerianum*, although it can be assumed that this also belongs to the progenitor family of the genus Dioon.

Research history

1843 *Pterophyllum dunkerianum* Göppert fossile Cycadeen, p. 134

1846 *Pterophyllum dunkerianum* Dunker, p. 14 Pl. II, fig. 3, Pl. VI, Fig. 4

1861 *Dioonites dunkerianum,* Miquel, p. 30

1871 *Pterophyllum dunkerianum* Schenk p. 233, Pl.XXXVI, Fig. 1-5

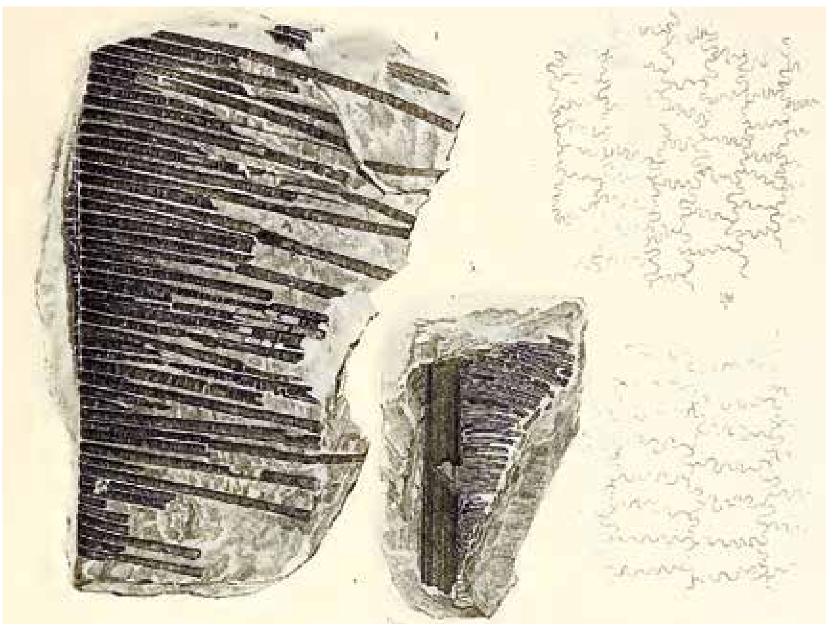
1933 *Pseudocycas dunkerianum* Florin, p. 13, Fig. 2

1992 *Pseudocycas lesleyae* Watson & Sincock p. 30, pl 3, figs 1-4, text Fig. 15-20
2013 *Pseudocycas lesleyae* Pott, Guhl, Lehmann p. 30, Pl. IX, Fig 1-4, Pl. X, fig. 1-7

Description

Leaf fronds: Alternating narrow linear leaf segments arise from an extremely strong, sometimes 2 cm thick rhachis (DUING 210). These have pointed ends, entire edges and are only 0.2 to 0.3 cm wide and 10 to 15 cm long. They stand crookedly upright on the upper part of the fronds and hang down on

From Dunker 1846, Plate VI, Fig. 4, *Pterophyllum dunkerianum* (Göppert, 1843)



After Schenk 1871, Plate XXXVI, Fig. 1-5 *(Pterophyllum) Dioonites dunkerianum*

***Dioonites dunkerianum*. Early Cretaceous. Fronds**

1-2. Completely preserved fronds (Coll. Wiedenroth); 3-4. Fronds and detail of the veins (DUING 210 Coll. Seppelt); 5. Basal part of a frond with massive rhachis (DUING 210 Coll. Seppelt); 6. Apical part of a frond (DUING 18, Coll. Wachtler, Dolomythos Museum); all Duingen the lower part. Five to six parallel, delicate nerves branch off from the rhachis and run the entire length to the apex.

Remarks

With its narrow-leaved, almost needle-like fronds, *Dioonites dunkerianum* resembles some Zamiaceae such as *Zamia soconuscensis* or *Encephalartos* species such as *Encephalartos cycadifolius*. After the first vague classifications as *Pterophyllum dunkerianum* (Göppert, 1843, Dunker, 1846), and *Dioonites dunkerianus* (Miquel, 1861), it was the Swedish paleobotanist Rudolf Florin in 1933 who, based on cuticle analyzes and studies of the stomata, assigned this plant to the Bennettitales and the name was somewhat unfortunate changed to *Pseudocycas dunkeriana.*
Not enough, the two Englishwomen Joan Watson and Caroline Sincock (1992) changed the nomenclature again to *Pseudocycas lesleyae* and honored the prima ballerina Lesley Collier from the Royal Ballet in London. Pott, Guhl and Lehmann (2013) also followed this nomenclature. However, it is not explained why a fossil plant that was studied and depicted just as intensively by Göppert in 1843, then again in 1846 by Dunker and also by Schenk in 1871, should suddenly be given the name of an English dancer in 1992. It is correct that, based on the analyzes of the stomata, it is a Bennettite and therefore a predecessor of the Dioon cycads. Furthermore, if it is proven that the specimens from English Wealden are conspecific with those from German Wealden, then international nomenclature rules would still have to retain *Dioonites dunkerianum* as the legitimate name. Therefore, in the future, the main focus should be on finding cones that definitely belong to it.

***Dioonites dunkerianum*. Reconstruktion**
Whole frond and single pinnula

Nilssonia Brongniart 1828

The Nilssoniales are an old group of cycads that are already known from the early Permian (*Nilssonia perneri,* Wachtler, 2013, experienced a peak in the Triassic (*Nilssonia primitiva,* Wachtler 2016) and even characterized the Lower Jurassic of Upper Bavaria *(Nilssonia polymorpha*, Wachtler, 2024). Today's representatives of these so-called two-seeded, single-leaf cycads are unknown. *Nilssonia* was first described by Adolphe Brongniart in the early days of paleobotanical research (1828) from Lower Jurassic layers in Sweden and, based on related findings, can be assigned to the two-seeded Zamiaceae precursors. Their fronds, which appear almost as single leaves, or poorly lacerated in the Permian. In they Triassic they were characterized by an irregular segmentation (Wachtler, 2021, Wachtler, 2016), although the leaves took on more geometrically segmented shapes, which became more pronounced in the Lower Jurassic (Wachtler, 2024).
A *Nilssonia* species that retained its whole-leaf character from the Permian and Triassic can be found in the Lower Cretaceous of Central Europe: *Nilssonia schaumburgense* (Dunker, 1846).

Nilssonia schaumburgense (Dunker 1846), Wachtler 2024 comb. nov.

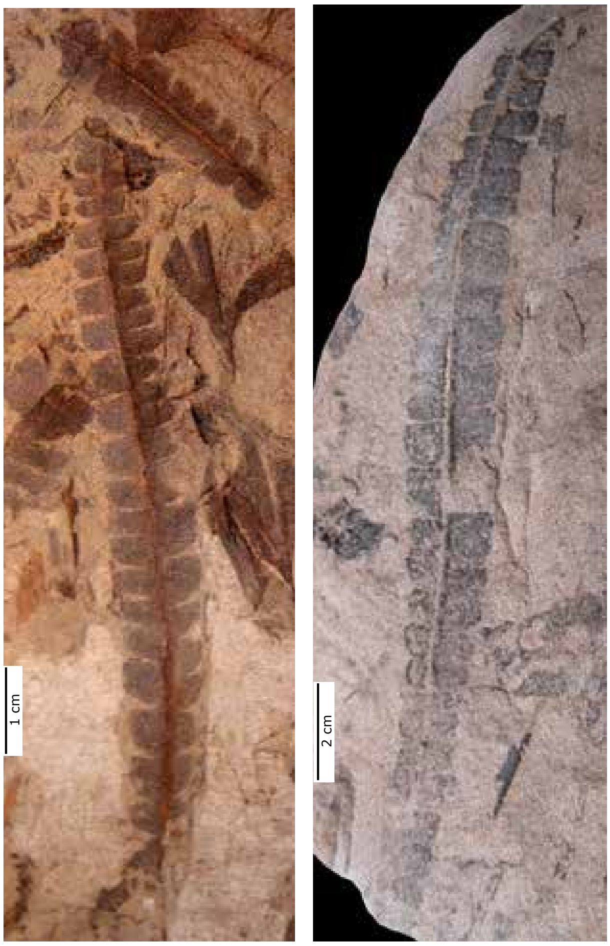
Research history

1846 *Pterophyllum schaumburgense* Dunker, p. 15 Pl. 1, Fig. 7, Pl. II, Fig. 1, Pl. 6, Fig. 5-10
1846 *Anomozamites schaumburgensis* Schimper, traite II. p. 141
1871 *Anomozamites schaumburgensis,* Schenk, p. 231, Pl. XXXIII. fig. 1-9
2005 *Nilssonia bluebirdii* Watson & Cusack, p. 65, text. fig. 49BC
2013 *Nilssonia bluebirdii* Pott, Guhl, Lehmann, Pl .II, Fig. 7-10

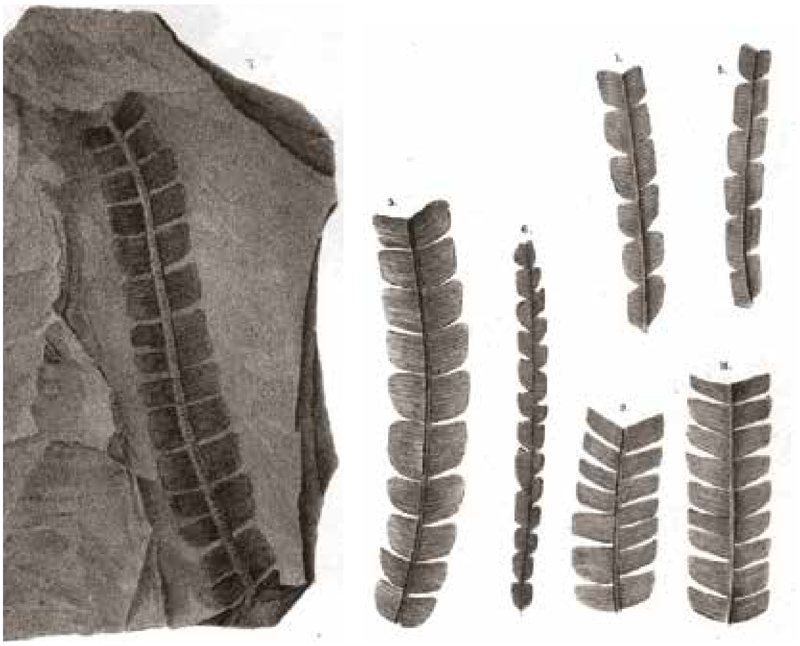
Both Dunker (1846) and Schenk (1871) described cycad precursors with the name *Nilssonia schaumburgense* from various Lower Cretaceous sites (Harrel near Bückeburg, Oesede near Osnabrück, Obernkirchen, am Deister, Kehburg) with partially segmented fronds, but with clearly visible whole-leaf character. However, these appear to be largely missing in the most known Duingen fossil deposit.

Description

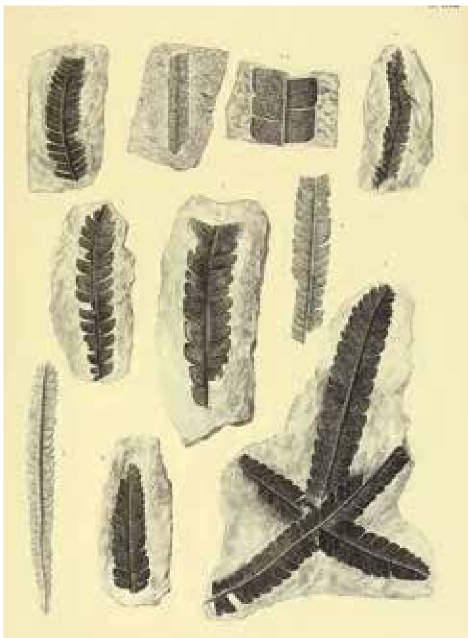
Whole plant. Leaf fronds with more or less recognizable individual leaf character. Most of them arise spirally from a short trunk. Petiole short, reaching fronds 30 to 50 cm long, with a total width of up to 10 cm. Individual leaflets attached broadly to the



Nilssonia schaumburgense, Forest path on Brunnenberg, Bad Rehburg. Coll. Wiedenroth



Pterophyllum schaumburgense. Froms Dunker, 1846, Plate 1, Fig. 7, Plate 6, Fig. 5-10



From Schenk, 1871, Plate XXXIII, fig. 1-9. *Anomozamites schaumburgensis*

***Nilssonia schaumburgensis*. Early Cretaceous. Reconstructions**

a. Plant; b. Single frond; c. Male cone; d. Microsporophyll below and laterally

***Ceratozamites kurwius*. Early Cretaceous. Reconstructions**

a. Plant with pollen cones; b. Single frond; c. Detail of pinnules; d. Microsporophyll below and top view

central axis, with irregular width. These are crossed by strong lateral veins, which run unbranched to the end of the leaf.
Pollen organs: Probably corresponding to those from the Triassic and Jurassic. Slightly spherical, up to 6 cm long and 5 cm wide. Consisting of a large number of geometrically shaped microsporophylls. Microsporangia on the underside in large numbers.
Seed cones: Slightly elongated, reaching about 10 cm in length, composed of deeply segmented macrosporophylls. These develop two ovoid seeds below the covering bracts.

Remarks

The seed cones consisted of a spindle with spiral-shaped macrosporophylls. These developed two seeds hanging inverted under the apical shield. In this they were similar to today's Zamiaceae. The pollen cones of all these cycad genera, like today's ones, are difficult to tell apart.

Ceratozamites Wachtler, 2025

In the Duingen quarries there was another not so rare species of cycad, which could actually also be assigned to the Nilssoniales if its fruit scales did not form two horned terminal bracts. Today, such seed and pollen cones are only found in *Ceratozamia*, which is widespread in the Neotropics, mainly in Mexico, but also in other areas of Central America such as Belize, Guatemala and Honduras with around 30 species. Their preferred habitat is moist to wet coastal mountains, although some species can even penetrate into desert areas. The recent genus was first described in 1846 by Adolphe Brongniart (Annales des Sciences Naturelles; Botanique. 3rd Series, Volume 5, 1846, page 7). Its two bract horns (Cerato in Greek: the horn) at the end of the macro- and microsporophylls are characteristic.

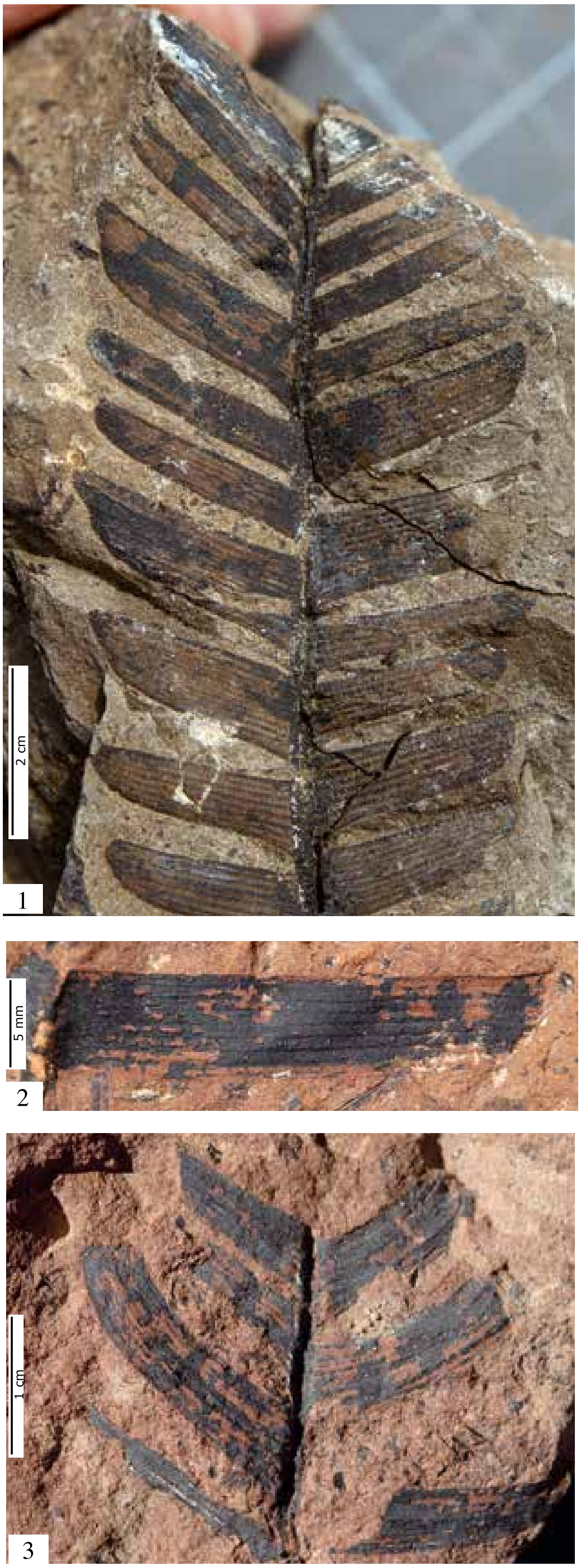
Diagnosis

Cycad precursors with irregularly wide frond leaves. Sporophylls characterized by their two horns.

Ceratozamites kurwius Pott, Guhl, Lehmann, 2014, Wachtler 2024 nov. comb.

Research history

2014 *Nilssonia kurwia* Pott, Guhl, Lehmann, Pl. II, Fig. 2-6, Pl .III fig. 1-10



Ceratozamites kurwius

1-3. Various frond parts (DUING 364, DUING 361, (Coll. Garbermann), DUING 16, Coll. Wachtler), Duingen

***Ceratozamites kurwius*. Early Cretaceous. Fronds, macro- und microsporophylls**

4. Basal frond part with stem (DUING 09); 5. Frond part (DUING 93, both Coll. Wachtler); 6-7. Fronds with seeds (DUING 362); 8-9. Basal fronds with cones (probably seed cones (DUING 369, Coll. Garbermann); 10-11. Almost completely preserved pollen cones and detail of the doubly horned sporophylls (DUING 211, Coll. Seppelt); all Duingen

From Dunker, 1846. *Zamites aequalis*. Pl. VI, Fig. 3, The specimen comes from Duingen

From Schenk, 1871. *Zamites aequalis* Pl. XXXVII. fig. 2.

From Dunker, 1846. *Pterophyllum humboldtianum,* Pl. 4

Description

Whole plant: Petiole short (about 4-5 cm long), reaching fronds 30 to 50 cm long. Apical with V-shaped termination. Individual leaflets attached broadly to the central axis, with slightly irregular segment widths. About three to cm long, up to 1 cm wide. Leaflets traversed by strongly developed lateral veins, which extend unbranched to the end of the leaf (DUING 09, DUING 16, DUING 93).
Pollen cones: Elongated, tapering apically (DUING 211) usually massively encrusted with pollen dust. Microsporophylls with double umbo (DUING 211), otherwise hexagonal.
Seed cones: Elongated, tapering apically. Macrosporophylls larger than those in the pollen organs. Hexagonal with bi-horned appendix. Seeds up to about 1 cm long and rounded (DUING 362).

Remarks

Ceratozamites kurwius could be included in the list of Zamia ancestors if the sporophylls of the fruit cones were not equipped with bihorned bracts, which, although rare, could still be found. This cycad precursor was first described as *Nilssonia kurwia* (Pott, Guhl, Lehmann, 2014); whereby "kurwia" is a transmogrify of the collector's name Kurt Wiedenroth. This brings us to a full circle: all cycad families still found in the northern hemisphere, namely the precursors of Cycas, Zamia, Ceratozamia and Dioon, were already present in the Wealden of Europe. A special role is played by Encephalartos, which occurs in southern Africa as far as Sudan and may also be included. Other explanations must therefore be sought for the evolution of southern hemisphere cycads such as Stangeria, Bowenia and Lepidozamia.
How important the fructifications and not the fronds are for the classification of these plants can be seen from the fossil remains of these cycads.

Zamites aequalis Dunker 1846

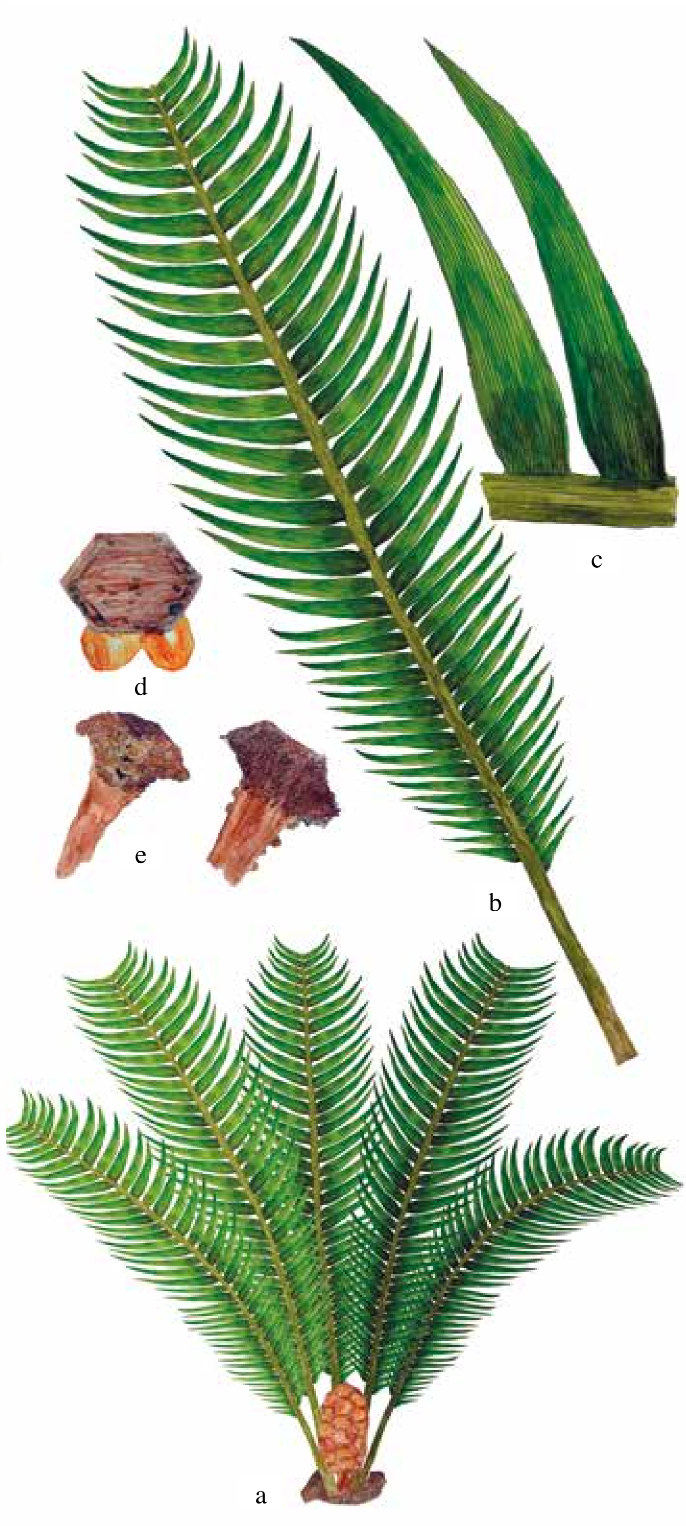
In addition to *Ceratozamites, Dioonites*, the Cycas ancestors (*Taeniopteris*), there was another relatively common genus with two-seeded seed scales within the Zamiaceae (*Nilssonia, Ctenis)* in the Lower Cretaceous: *Zamites aequalis.*

Research history

1846 *Zamites aequalis* Dunker p. 17, Pl. VI, Fig. 3, Duingen
1861 Podozamites aequalis Miquel, prodr. Cycad. p. 30. Duingen

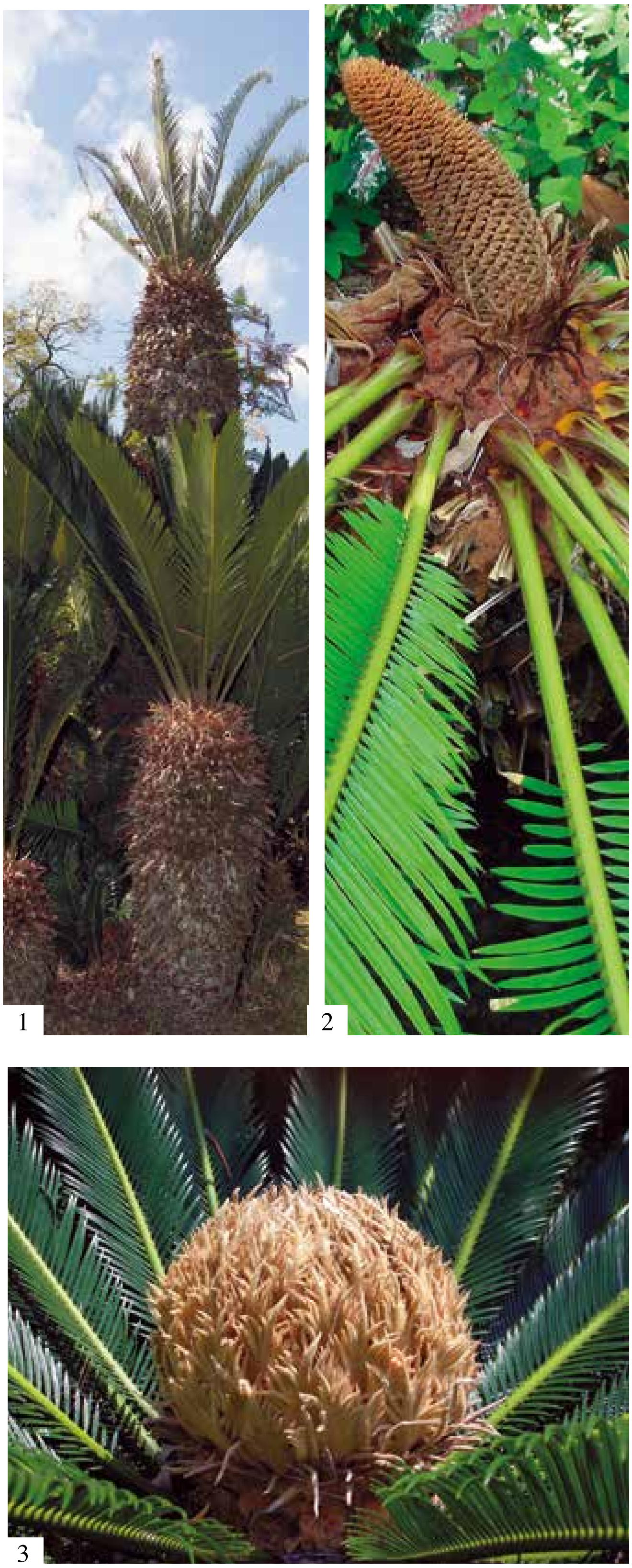
***Zamites aequalis*. Early Cretaceous. Reconstructions**

a. Whole plant; b. Single frond; c. Pinnula; d. Female cone; e. Seed scale; f. Microsporophyll, underside and lateral view



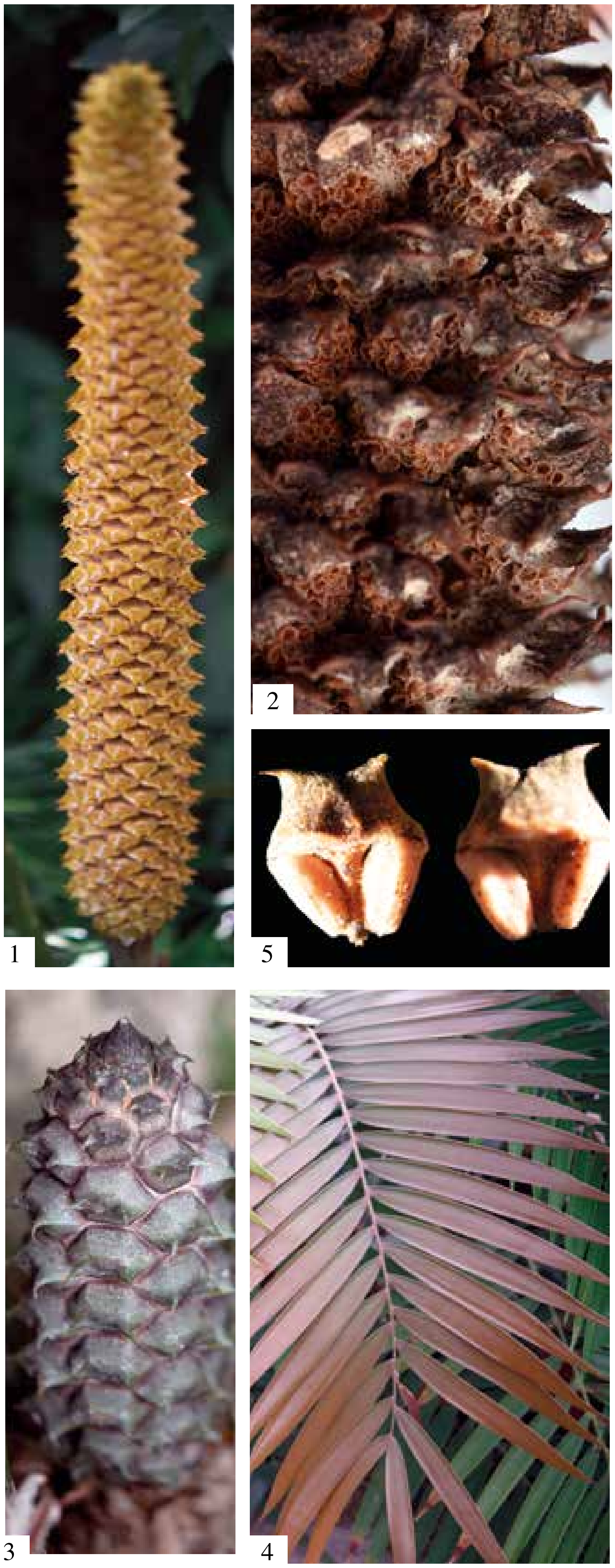
***Ctenis humboldtianum*. Early Cretaceous. Reconstructions**

a. Whole plant; b. Single frond; c. Pinnules; d. Seed scale; f. Microsporophyll, top and bottom



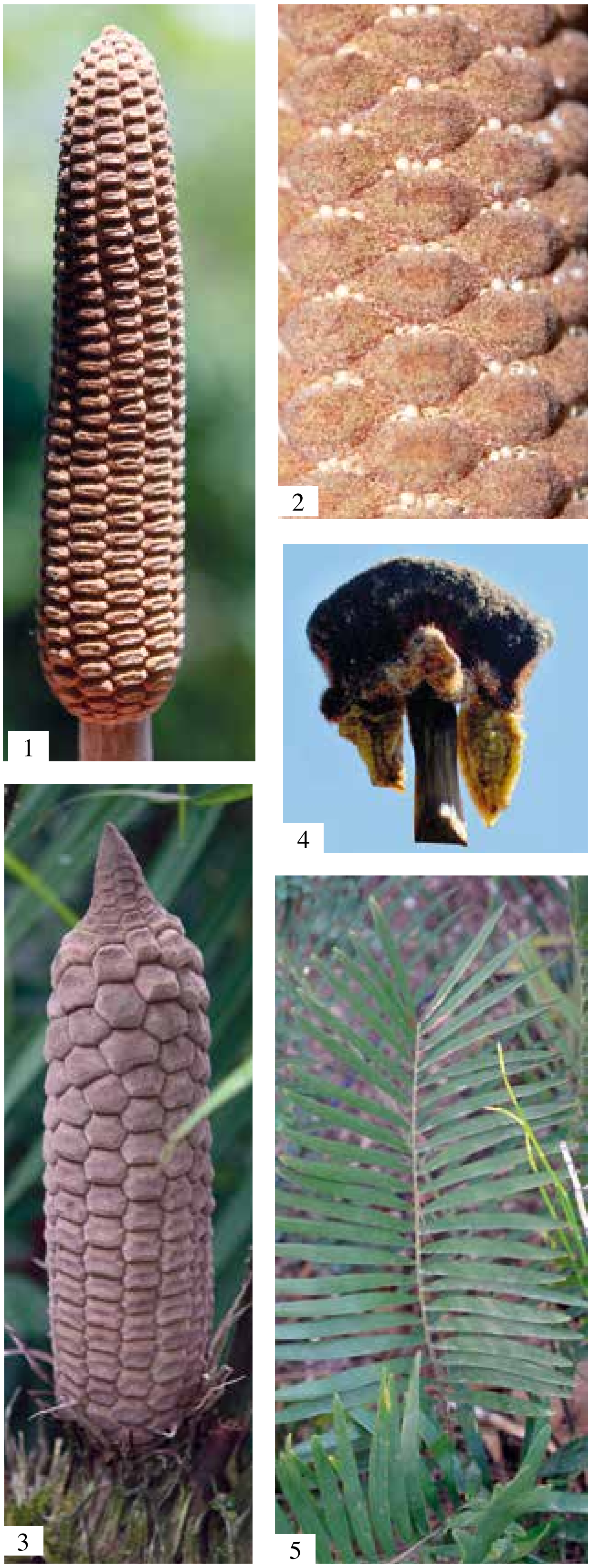
Cycas (Tropics and subtropics, old and new world)

Cycas revoluta. 1. Whole plant; 2. Male plant; 3. Female plant



Ceratozamia (Central America)

Ceratozamia robusta. 1. Pollen cone; 2. Detail of microsporophylls; ***Ceratozamia fuscoviridis.*** 3. Seed cone; 4. Frond; ***Ceratozamia hildae.*** 5. Seed scales (Bot. Garden, Munich, XX-0-M-2004/2662)

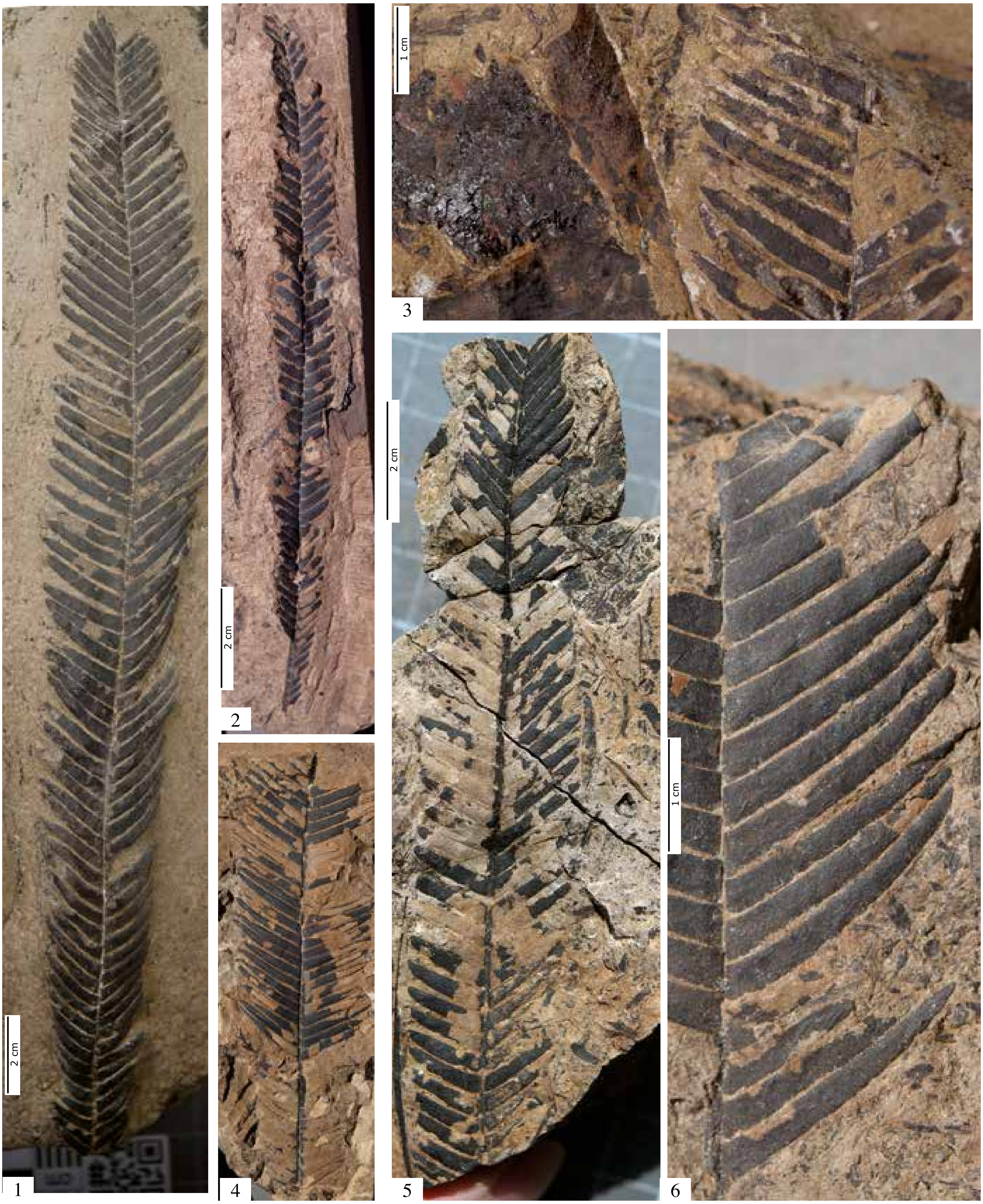


Zamia (Central America, Northern South America)

Zamia furfuracea. 1. Male cone; 2. Detail of the mckrosporophylls; *Zamia fairchildiana.* 3. Seed cone; ***Zamia floridana.*** 4. Seed scale 5. Frond

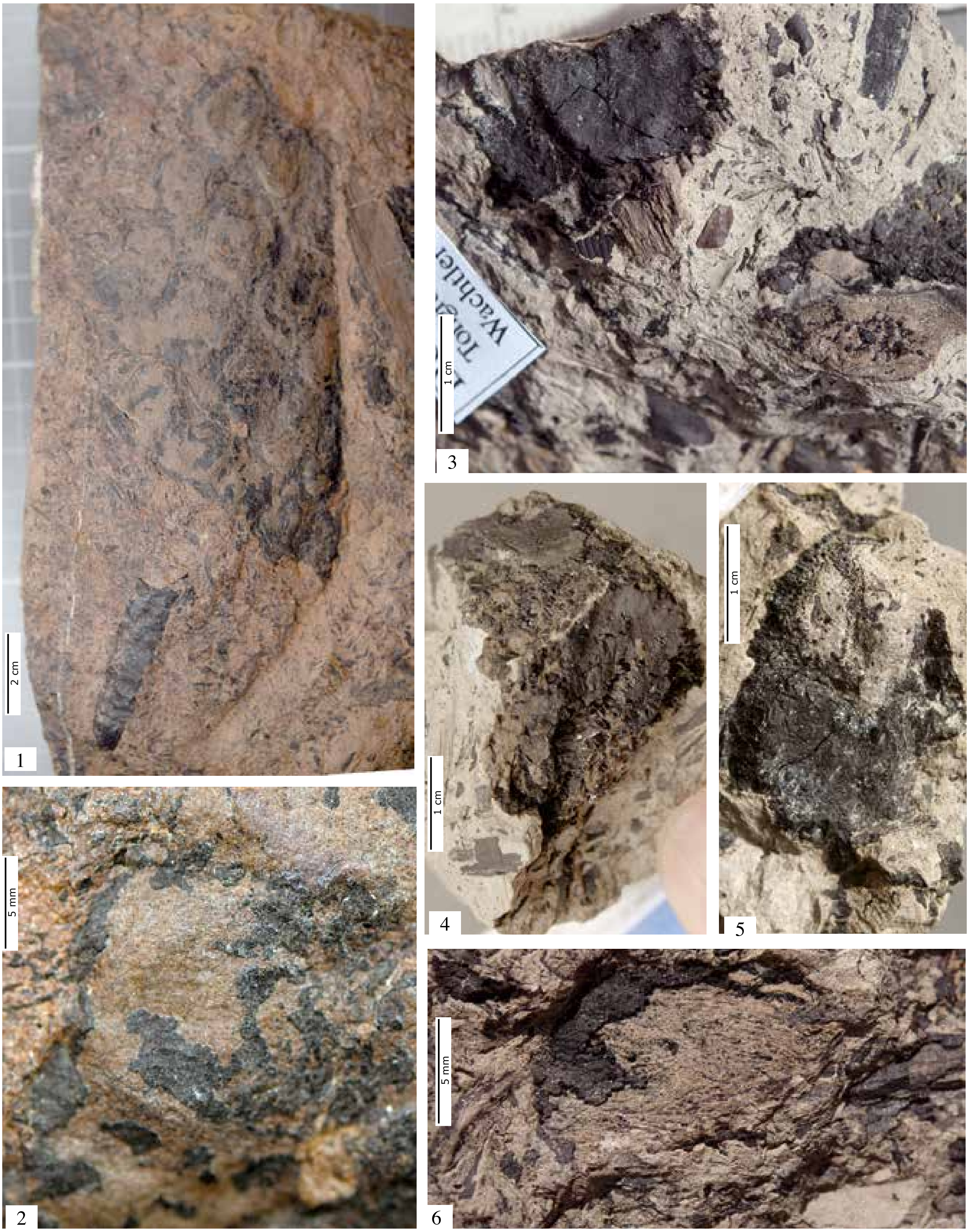
Encephalartos (Southern to Central Africa)

Encephalartos hildebrandtii. 1. Female plant; ***Encephalartos lebomboensis.*** 2. Male cone and 3. Microsporophyll; ***Encephalartos horridus.*** 4. Empty seed scale; 5. Seed; 6. Female cone; ***Encephalartos sclavoi***. Female cone



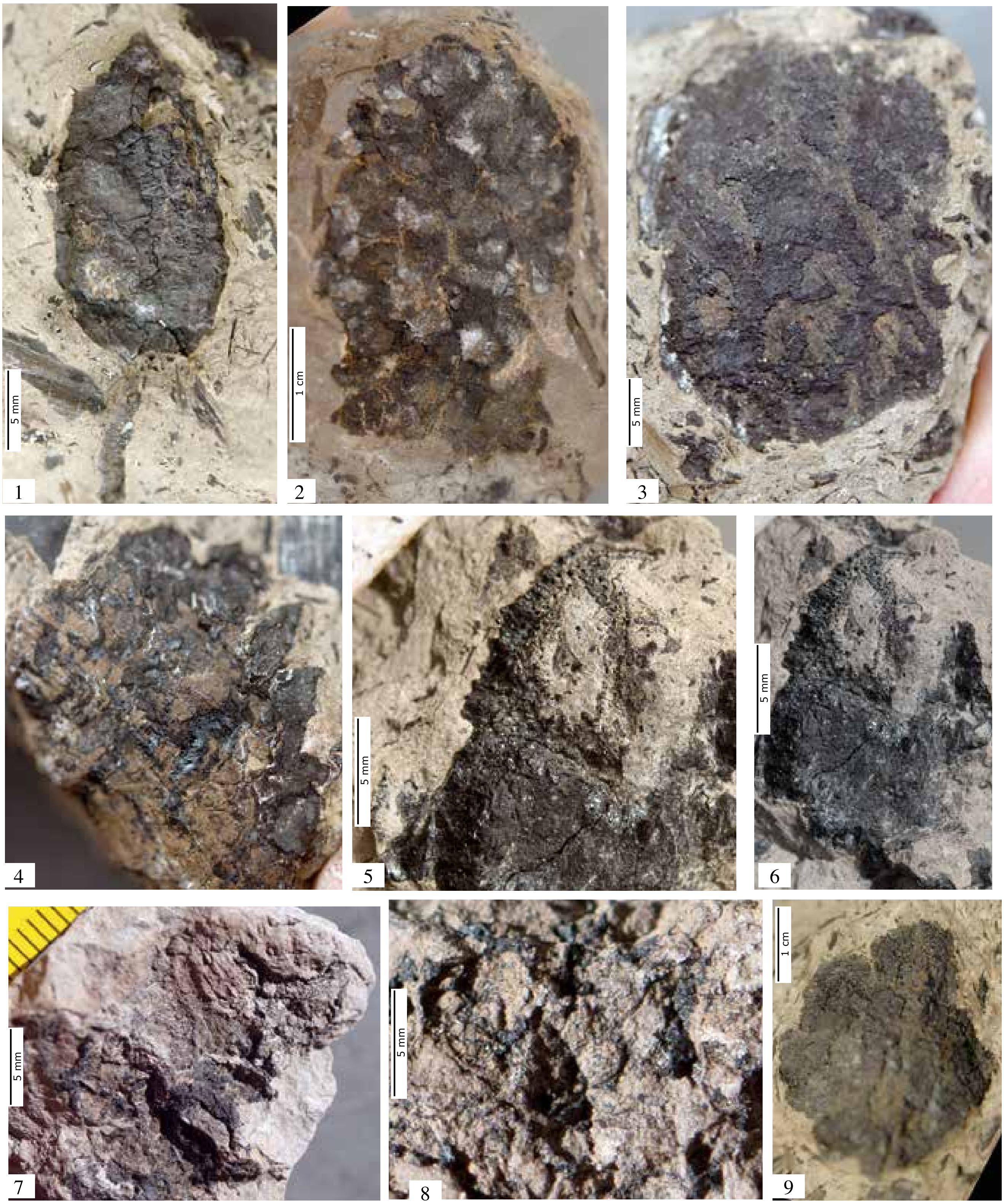
***Zamites aequalis*. Early Cretaceous. Fronds and seeds**

1. Whole frond (DUING 250, Coll Seppelt); 2. Juvenile fronds (DUING 98) 3. Frond with microsporophyll (DUING 81); 4. Frond (DUING 99, both Coll. Wachtler); 5. Frond and detail of a seed deposited next to the frond (DUING 368, Coll. Garbermann); 6. Detail of a frond (DUING 101, Coll. Wachtler); Duingen



Cycads. Early Cretaceous. Female and Male cones

1-2. Female cone from *Zamites aequalis*, *Nilssonia schaumburgense* or *Ctenis humboldtianum*, and detail of a macrosporophyll (DUING 204, Coll. Seppelt); 3-5. Male cones, partially dissolved (DUING 51); 6. Detail of a microsporophyll (DUING 69, Coll. Wachtler - Dolomythos Museum); all Duingen



Cycads Early Cretaceous. Female and male cones

Globose cycad pollen cones probably belonging to *Zamites, Nilssonia* possibly also to *Taeniopteris,* elongated from *Ctenis* or *Dioonites.* 1-2. Juvenile pollen cones (DUING 417, DUING 415, Coll. Garbermann); 3-5. Rounded pollen cones (DUING 419, DUING 418 Coll. Garbermann); 6. Outside of a microsporophyll (DUNG 51); 7-8. Decayed male cycad cone and detail of the microsporangia (DUING 128, both Coll. Wachtler); 9. Top view of a decayed male cycad cone (DUING 421, Coll. Garbermann); all Duingen, Tongrube Bock

Cycads. Early Cretaceous. Female and male cones

Globose cycad pollen cones probably belonging to *Zamites, Nilssonia* possibly also to *Taeniopteris,* elongated from *Ctenis* or *Dioonites.* 1. Pollen cones (DUING 385, Coll. Garbermann); 2-4. Partially dissolved pollen cones (DUNG 52, DUING 53, DUING 10); 5-7. Isolated microsporophylls (DUING 64, DUING 41, DUING 66, Alle Coll. Wachtler, Dolomythos Museum); 8-10. Seeds (DUING 368, DUING 65, DUING 379, Coll. Garbermann); 11. Isolated macrosporophyll (DUING 68, Coll. Wachtler-Dolomythos-Museum); Duingen

1. Almost completely preserved frond of *Ctenis inconstans* from the Early Jurassic of Bayreuth (Coll. Fuchs, Coll. Pohl)

2. *Ctenis* from the Segelhorst limestone works, Late Jurassic, Kimmeridgian, Coll. Wiedenroth

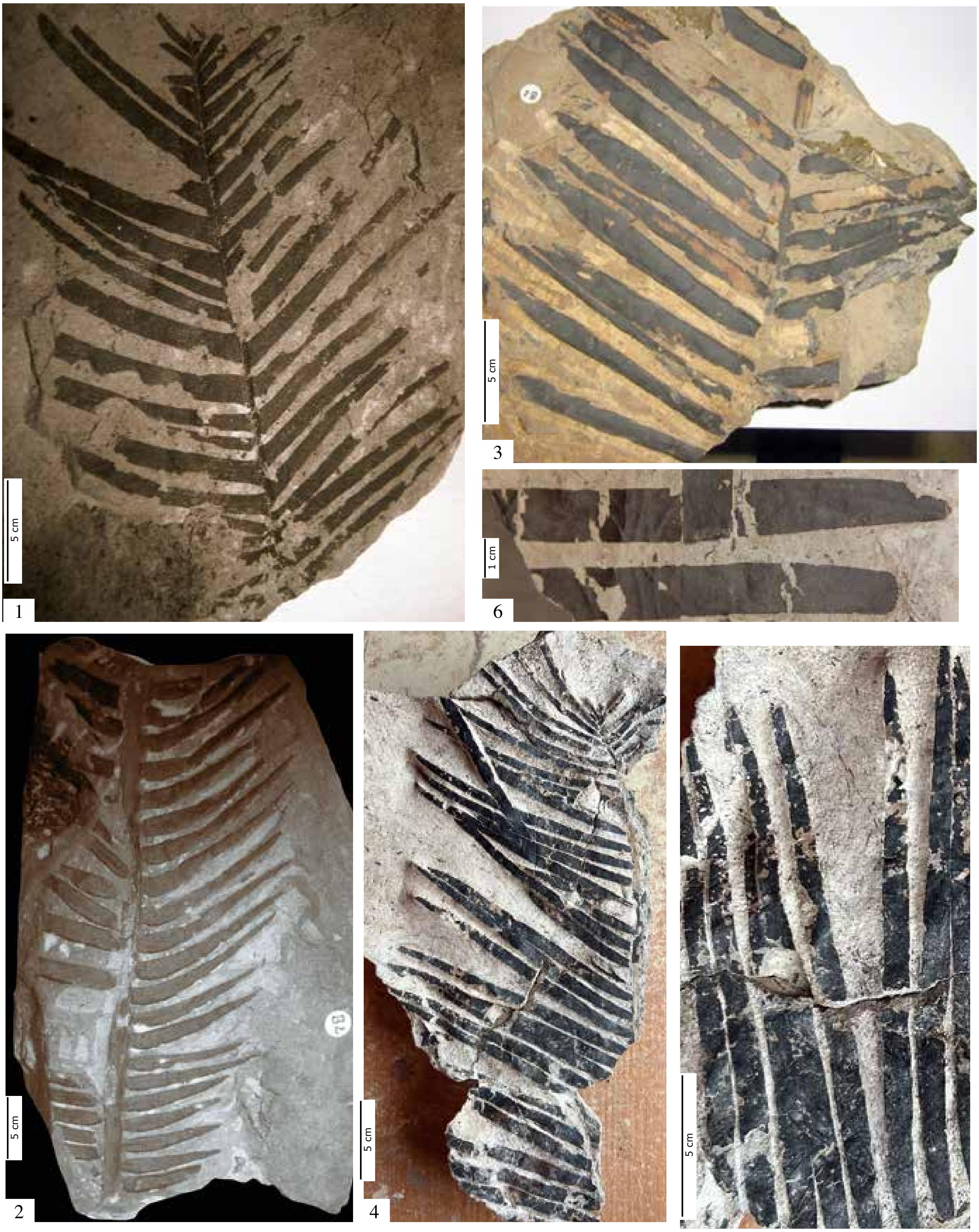
1871 *Zamites aequalis* Schenk, p. 238, Pl.XXXVII. fig. 2.
2013 *Ptilophyllum aequale,* Pott, Guhl, Lehmann, Pl. II, Fig. 11-14, Pl IV, fig. 1-9, Pl. V Fig. 1

Description

Whole plant: Fronds arising from a short petiole. A total of 30 to 50 cm long, reaching a width of 5-7 cm (DUING 250, DUING 368) and partially tapering off into a V-shape at the end. Pinnules in two rows starting from the midrib. Leaf leaflets, broadly attached to the rhachis, with entire margins, up to 2-3 cm long but often only 0.5 cm wide, with a thick cuticle, crossed by barely visible nerves that run parallel and unbranched to the end of the leaf. These are tapered to a point to slightly flattened, weaker or more crescent-shaped.
Pollen cones: Roundish (DUING 385, DUING 52), massively encrusted with pollen dust (DUING 53, DUING 10). Cones disintegrate into individual microsporophylls. Overall difficult to tell apart from the other cycad cones.
Seed cones: Long and slender, about 12 cm long, 5 cm wide (DUING 204). Macrosporophylls umbrella-like, bearing one seed underneath on each side (DUING 68). Seeds rounded to elongated, about 1 cm large (DUING 65, DUING 368).

Remarks

The fronds of *Zamites aequalis* from the Wealden were similar to those of *Zamites acuminatus f*rom the Lower Jurassic of Central Europe (Wachtler, 2024). They can be separated relatively easily from the simultaneously occurring *Nilssonia schaumburgense* (Dunker, 1846) with its pronounced whole-leaf character, from *Ceratozamites kurwius* (Pott, Guhl, Lehmann, 2014) with its variable width fronds and clearly visible side veins, from *Ctenis humboldtianum* (Dunker, 1846) with its large fronds, as well as elongated and with pointed lateral leaflets and *Taeniopteris beyrichii* (Schenk, 1871) with a pronounced whole-leaf character.



***Ctenis humboldtianum*. Early Cretaceous. Fronds and pinnules**

1-3. Mostly preserved fronds (Coll. Wiedenroth); 4-5. Large frond (35 cm high) and detail of the pinnules (16 cm long) (DUING 399, Coll. Seppelt); 6. Detail of individual leaves (DUING 267, Coll. Seppelt); Duingen

However, there are greater difficulties in distinguishing between *Dioonites lyellanum* (Dunker, 1846), which developed somewhat longer, narrow side leaflets, but can only be analyzed by examining the different stomata.
Pollen and seed cones, on the other hand, are relatively difficult to tell apart from *Ctenis humboldtianum* and *Nilssonia schaumburgense,* as they were all two-seeded macrosporophylls, somewhat easier from those of *Ceratozamites kurwius* and clearly from the macrosporophylls of *Dioonites lyeallanum.*

Ctenis Lindley & Hutton 1834

The genus *Ctenis* was established in 1834 by John Lindley (1799-1865) and William Hutton (1797-1860) for leaf fronds from the Jurassic of Yorkshire (Gristhorpe Bay). Referring to this publication, Karl Friedrich Wilhelm Braun, (1843) described several *Ctenis* species from the Lower Jurassic of Bayreuth (*Ctenis angusta, Ctenis abbreviata, Ctenis marginats* and *Ctenis inconstans)*. Even if in the end only *Ctenis inconstans* could be legitimized (Wachtler, 2024). The fronds of Ctenis are distinguishable from others to their bigger size. Similar frond shapes can be found today within the Zamiaceae, so that *Ctenis* can be placed in this large group.
The genus *Ctenis* was established in 1834 by John Lindley (1799-1865) and William Hutton (1797-1860) for leaf fronds from the Jurassic of Yorkshire (Gristhorpe Bay). Referring to this publication, Karl Friedrich Wilhelm Braun, (1843) described several *Ctenis* species from the Lower Jurassic of Bayreuth (*Ctenis angusta, Ctenis abbreviata, Ctenis marginats* and *Ctenis inconstans),* although in the end only *Ctenis inconstans* can be legitimized (Wachtler, 2024). Their fronds are distinguishable from the others by their size and spreading pinnules. Similar frond shapes can be found today within the Zamiaceae, so that *Ctenis* can be placed in this large ancestor-group.

Ctenis humboldtianum Dunker 1846, Wachtler 2024 comb. nov.

Research history

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

1843 *Ctenis inconstans*, Braun p. 41 pl. XI Fig. 6-7
1846 *Pterophyllum humboldtianum* Dunker, Monogr. p.13.tab.4.

1861 *Dioonites humboldtianus* Miquel, p. 30
1871 *Dioonites humboldtianus* Schenk, Pl. XXXV. fig. 3-5

Description

Whole plant. Fronds, up to 50 cm or more long, arising from a petiole up to 10 cm long and about 1 cm wide at the base. Leaflets broadly attached to the rhachis, about 10 cm long, 1 to 1.5 cm wide at the basal level, then gradually decreasing in size to become apically pointed and curved upwards (DUING 399, DUING 267). The closely spaced leaf veins may or may not ever dichotomize at the base and then continue unbranched to the end.
Seed and pollen cones: Cannot be determined with absolute certainty, but belongs to the two-seeded cycad precursors. Cones probably elongated and slender, about 12 cm high and 3-5 cm wide.

Remarks

Ctenis cycads occur with *Ctenis inconstans* in the Lower Jurassic, but can also be found in Central Europe in the Upper Jurassic, and as *Ctenis humboldtianum* in the Lower Cretaceous of Central Europe. However, the earliest representatives probably date back to the Permian (as *Pseudoctenis*), but exact classifications have not yet been completely clarified. They become somewhat more common from the Lower Triassic (Anisian: *Pseudoctenis braiesensis*), especially in the Dolomites (Wachtler, 2016). They can be distinguished from all other cycad precursors by their massive, 60 cm, probably up to a meter long fronds, with wide, tapering, relatively long side leaflets.
Previous classifications as *Pterophyllum humboldtianum* (Dunker, 1846) or *Dioonites humboldtianus* (Miquel, 1861, Schenk, 1871) do not seem to be justified. In addition to the Zamia precursors with their two-seeded fruit scales, which were also strongly present from the Lower Jurassic (*Zamites acuminatus)* and also in the Lower Cretaceous (*Zamites aequale)*, this would mean that the evolution of this cycad group took place in two separate lateral lines from the Permian onwards.

Taeniopteris Brongniart 1828

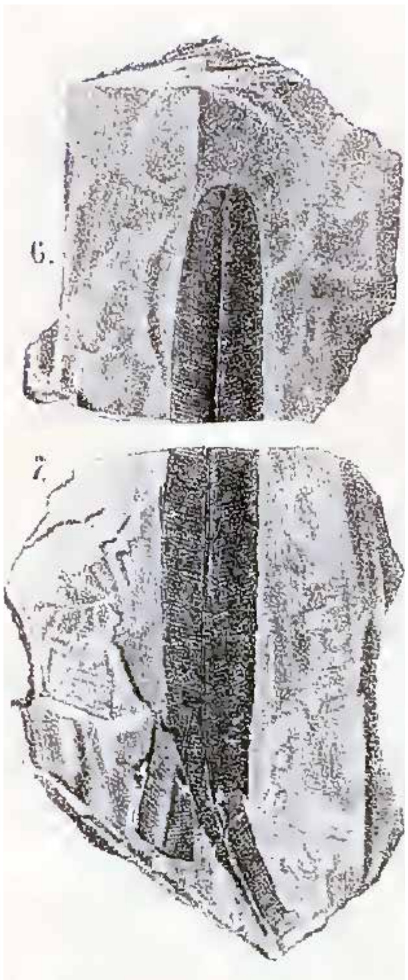
Although rare, tongue-like leaves can be found under the name *Taeniopteris* from the Permian (Lower Permian: *Taeniopteris nonensis,* Wachtler 2021, Upper Permian: *Taeniopteris eckardtii* (Kurtze, 1839), and then especially in the Triassic (Lower Middle Triassic: *Taeniopteris simplex* (Wachtler, 2016); Middle Triassic: *Taeniopteris angustifolia,* Schenk, 1864) through the Lower Jurassic *(Taeniopteris tenuinervis,* Brauns, 1864) to the Cretaceous and can be counted among the at least four- or more-seeded Cycas precursors (Wachtler, 2016).
The genus *Taeniopteris* was first introduced into the literature in 1828 by the French paleobotanist Adolphe Brongniart, poorly and without illustration, for elongated, tongue-shaped leaves with a broad blade and parallel veins branching off from it. He referred to leaves from the English Jurassic such as the first described species *Taeniopteris vittata,* but also *Taeniopteris latifolia* and *Taeniopteris bertrandi,* which he supplemented with a more detailed description in 1831 (Pl. 82).
Their structure is well known through excellent finds, which contain all parts including the fructifications - especially from the Triassic of the Dolomites (Anise) and the Middle Ladin of Germany (Ilsfeld) (Wachtler, 2016).

Taeniopteris beyrichii Schenk 1871, Wachtler 2024 comb. nov.

Research history

1869-1874 *Oleandra neriifolia*, Schimper Pl. XXVII, fig. 13
1871 *Oleandridium beyrichii,* Schenk p. 221, Tab. XXIX, fig. 6-7

Taeniopteris beyrichii. Early Cretaceous. Fronds
1-2. Fronds (DUING 373, DUING 374, Coll. Garbermann); 3. Frond (DUING 117, Coll. Wachtler) Duingen



Schenk, 1871. *Oleandridium beyrichii,* Tab. XXIX, fig. 6-7, today *Taeniopteirs beyrichii*

***Taeniopteris beyrichii*. Early Cretaceous. Reconstructions**

a. Plant; b. Single frond; c. Female plant; d. Pollen cone

2013 *Nilssonia bluebirdii* Pott, Guhl, Lehmann, p. 18 Pl. II, Fig. 7-10

In his descriptions and illustrations of *Oleandridium beyrichii,* August Schenk referred to a work by Schimper published in 1869 in which he named an *Oleandra neriifolia* from the Wealden. However, various reasons led Schenk to point out the question of this plant by defining "*the secondary nerves numerous, delicate, emerging at an almost right angle, dichotomous or simple".*
The Cycas ancestor *Taeniopteris* constantly developed undivided lateral nerves, in contrast to the Triassic widespread fern genus *Danaeopsis* with its once or twice dividing veins (Wachtler, 2016, Wachtler, 2024). Due to the poor condition of the specimens in the German Wealden and their rarity, a clear answer is fraught with questions, but they are probably *Taeniopteris* leaves. The name *Nilssonia bluebirdii* (Pott, Guhl, Lehmann) is therefore inappropriate, as the Nilssoniales had a different leaf character and generated even more different seed cones.

Description

Whole plant: Tuft-accumulation of narrow, elongated tongue-like leaves. (DUING 373, DUING 374, DUING 117). Rounded in the apical area with a slight indentation to a point. Fronds up to 30 cm long, reaching 2 to 3 cm wide. Veins branch off from the blade at a slightly offset 90 degree angle and never dichotomize until the edge of the leaf.
Seed cones: Isolated macrosporophylls, having four or more seeds on the left and right of a leaf blade with a more or less pinnate apex.
Pollen cones: Slightly rounded, developing a large number of microsporophylls on a spindle.

Remarks

Both - *Taeniopteris* and *Nilssonia* - show a simultaneous presence over an extremely long period of time, ranging from the early Permian (Wachtler, 2021) to the Lower Cretaceous, i.e. more than 150 million years. They were characterized by - from the clear single-leaf character to the irregular, sometimes randomly torn frond leaves. Surprisingly, both representatives

disappeared from the world stage in this form from the Lower Cretaceous onwards, as today's representatives are unknown.
However, *Taeniopteris* (developing 8-16 seeds on both sides of a crest-like leaf blade), as well as *Macrotaeniopteris* (sometimes up to 60 seeds on each blade) on one side, and on the other side the two-seeded *Nilssonia*, together with *Ctenis* and *Zamites,* confirm that both cycad families Cycas and Zamia, which still exist today, probably split up in the Lower Devonian (Wachtler, 2023), since later separations can no longer be traced back to evolution, even if they disappeared from the fossil record throughout the Carboniferous period. This makes considerations of Cycas as the most original form of cycads obsolete.
A little later, the genus Dioon (as Jurassic-Cretaceous *Dioonites)* and Ceratozamia (in the form of *Ceratozamites)* appeared in the fossil record, while the Encephalartos ancestors probably also go back to the Lower Jurassic. Unless older representatives are still found, probably on the former American continent. Today, as then, cycads are considered good indicators of a humid, tropical to subtropical climate, regardless of the equatorial position of the continents at the time.

Ginkgoes from the Lower Cretaceous

Ginkgos are one of the most common plants in the clay pits around Duingen. Interesting are their mostly small leaves, which still reveal the fan-like character of today's ginkgoes. The slightly larger leaves that sometimes occur, as well as the segmented ones, are probably within the range of variation of this species or represent short shoots.
Although the German world traveller Engelbert Kaempfer described and depicted ginkgo trees imported from Japan in 1712 and Carl Linnaeus adopted the name with the species name G*inkgo biloba* in 1771, only a few trees were planted in Europe until 1800, so that a broader knowledge about this enigmatic plant inserted in the gymnosperms only slowly took a larger interest.

Research history

1836 *Adiantites cyclopteris* Göppert, pl. XXXIV fig. 8a

1836 *Adiantites digitatus* Göppert, p. 217

1846 *Cyclopteris digitata* Dunker p 9-10, pl. I, fig 8+10, pl. V, fig. 5+6, pl. VI, Fig. 11

1869-1874 *Baiera pluripartita,* Schimper p. 423, pl. XXXI, fig. 12

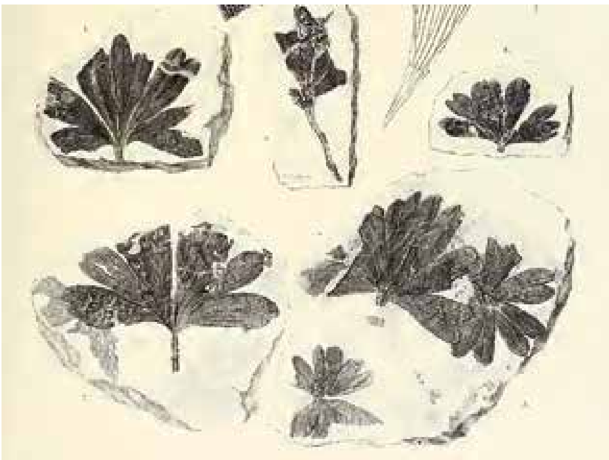
1871 *Baiera pluripartita*, Schenk,p. 212, pl. XXIV, fig. 1-4

1881 *Ginkgoites pluripartita* Heer, p. 6

2013 *Ginkgoites pluripartitus* Pott, Guhl, Lehmann, p. 34, Pl. XI Fig. 2-7

In the early days of paleobotanical research, it was difficult to classify segmented leaves that came from different geological epochs beginning from the Permian to the Cretaceous. They were therefore classified as algae (*Fucoides*, Brongniart, 1828, *Zonarites,* Sternberg 1833) or ferns (*Cyclopteris*, Brongniart, 1828, (*Adiantites,* Göppert, 1836).
In 1843, the German botanist C. F. Wilhelm Braun described two deeply segmented leaves from the Lower Jurassic of Bavaria as *Baiera dichotoma* and *Baiera taeniata.* He mentioned two others, *Baiera huttoni* and *Baiera digitata* from the Middle Jurassic site Gristhorpe Bay (North Yorkshire, England), and a *Baiera furcata* from Hayburn Wyke, not far away.
Braun placed all these plants from the Jurassic under the hydropterids, the water ferns, today consisting of the families Salviniales and Marsileales. Not even Dunker (1846) was able to recognize a connection between the fan-like leaves found in the Lower Cretaceous of northern Germany, typical of today's ginkgoes, and assigned them to the enigmatic fern genus *Cyclopteris digitata*, depicting and describing the specimens in his possession in excellent quality. Most of the illustrations probably concern specimens from the clay pits around Duingen, as well as other localities such as Osterwald, Bückeburg and Rodenberg.
The name *Baiera* was subsequently adopted by authors such as Wilhelm Schimper (1869-1874) and Schenk (1871), which also applied to the finds from the North German Wealden Formation depicted by Dunker (1846) as *Cyclopteris digitata.* Since Wilhelm Schimper noticed differences between the name *Cyclopteris digitata* from the North German Wealden Formation coined by Dunker (1846) and that from the Lower Jurassic, he changed the name to *Baiera pluripartita* (1869). However, Schimper also

From Rudolf Wilhelm Dunker (1846). *Cyclopteris digitata (Ginkgoites pluripartitus*) Pl. V, fig. 5 + 6). Suggested locality Duingen



From A. Schenk, 1871, *Baiera (multi)pluripartita*, pl XXIV Fig. 1-4.1-4. Specimen from collections in Munich, Göttingen, Berlin

From W. Schimper (1869-1874). *Baiera pluripartita*, pl XXXI, Fig. 12. Schimper takes over the specimen drawn and described in Dunker in 1846, but reversed (Archive Wachtler-Dolomythos)

left these fossil plant impressions within the ferns. Schenk now also adopted the name *Baiera pluripartita* and in 1871 reproduced new specimens from various collections.

In 1876, the Swiss paleobotanist Oswald Heer was the first to notice a similarity to the only species *Ginkgo biloba* that still exists today, based on recoveries spanning several eras on Lake Baikal and eastern Siberia, as well as from Pécs (Fünfkirchen) in Hungary. In various publications (until 1880) he succeeded in refining the connections by finding typical ginkgo seed berries and pollen cones. However, he also failed due to the dilemma of drawing a dividing line between the deeply lacerated conifer-like Ginkgo precursors and the fan-shaped leaves similar to the modern *Ginkgo biloba.* He switched between the names *Baiera* and *Ginkgo* several times, all without clear explanations or conclusions.

Interestingly, after a peak bloom over the entire Permian period in the Triassic period, the ginkgos almost completely disappeared and only resurrected again in the Lower Jurassic (Wachtler, 2024), this time occurring almost across the entire northern hemisphere as far as Asia and Siberia. Most of them were small leaves, which were barely half the size of today. It was not until the Eocene that the fan-shaped leaf shapes that reached their present size emerged.

In 1919, the American paleobotanist Charles Seward tried a new interpretation by introducing the name *Ginkgoites* for fossil ginkgo plants. Although many ginkgo leaves, especially in the Permian and also in the Jurassic, are characterized by a needle-like leaf character, but not all of them. *Ginkgoites murchisonae* (Wachtler, 2021) from the Upper Permian of the Dolomites developed fan-like leaves. In the course of the research, such a large number of names were coined for supposed ginkgos from all parts of the world, such as *Baiera, Jeanpaulia, Sphenobaiera, Karkenia, Ginkgophyllum* or *Psygmophyllum* (Wachtler, 2024), that even experts had little insight. Since the ginkgoes were already characterized by typical seed

Ginkgoites pluripartitus, Duingen. One of the best specimen (40 x 30 cm); Ex-Wiedenroth; Now Collection and photo: Uwe Starke

berries and catkin-like pollen systems in the early Permian period and this character trait is typical even for today's ginkgo plants, *Ginkgoites* and, in the case of the Lower Cretaceous finds from the greater Duingen area, the species name *Ginkgoites pluripartitus* are likely to turn out to be the most suitable. This is in view of the fact that Ginkgo-typical fleshy seeds and pollen cones are found in large numbers in these layers.

Description

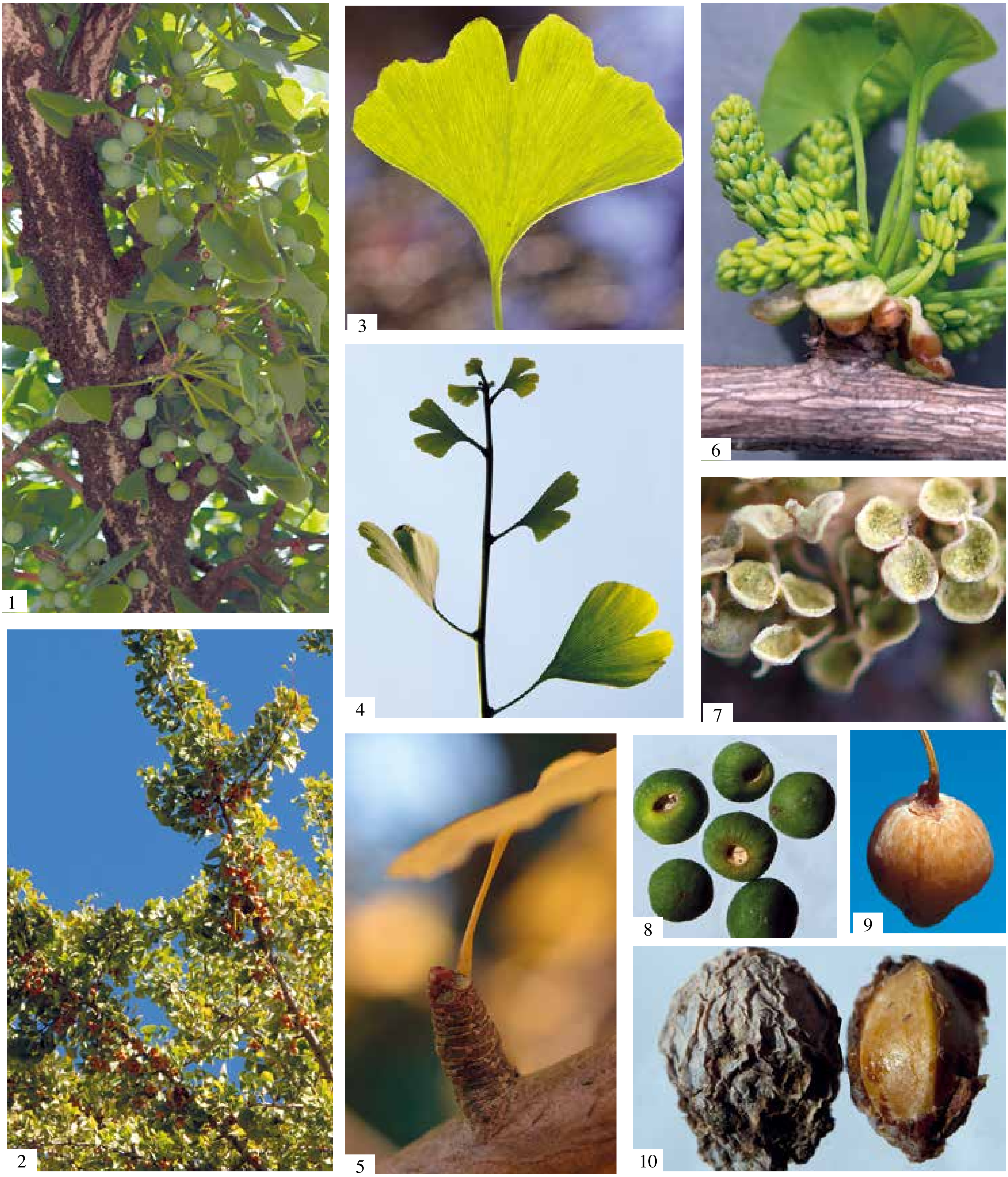
Whole plant: Tree-like with fan-like leaves. These are generally only 4-5 cm long, with a width of about 6 cm, additionally to an about 3 cm long petiole. Branchlets divided into short and long shoots. Leaves deeply notched several times. Veins from the petiole enter into the leaves and branch sometimes without ever connecting again (DUING 253, DUING 251, DUING 83). Seedlings found relatively often in Duingen (DUING 338, DUING 330, DUING 353, DUING 261 DUING 118).

Seeds: Consisting of an internal embryo, a woody sclerotesta and a fruit-like seed coat (sarcotesta). Ginkgo seeds up to 2 cm long and 1-1.5 cm wide (DUING 33), seed coat also sometimes preserved (DUING 70, DUING 112).

Pollen cones: About 3-4 cm long, plus a 1 cm long petiole. Consisting of an elongated axis with screw-shaped microsporophylls. Pollen sacs (about two to four) hanging inverted on a delicate connecting stalk (DUING 351). Capsules burst when ripe to release pollen (DUING 358).

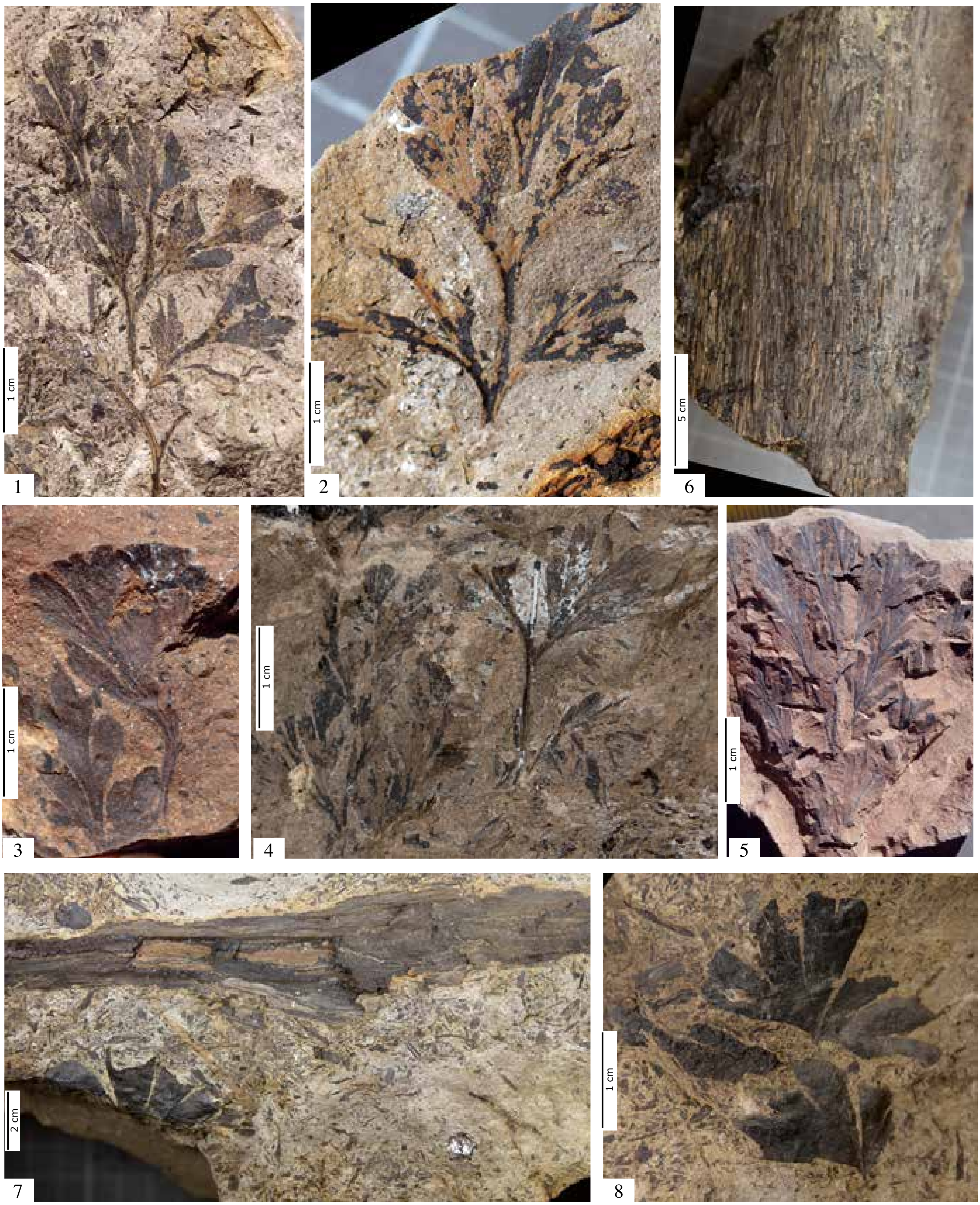
Remarks

While the most archaic ginkgos were characterized by their needle-shaped foliage in the early Permian period (Wachtler, 2013), but also in the Lower Jurassic (Wachtler 2021a), especially from the Middle Jurassic onwards, we experience the gradual merging into fan-like leaves similar to today's. This process is already well advanced in the Lower Cretaceous finds. *Ginkgoites* was one of the most common plants in the German Wealden and is well documented by seeds, pollen systems and leaves.



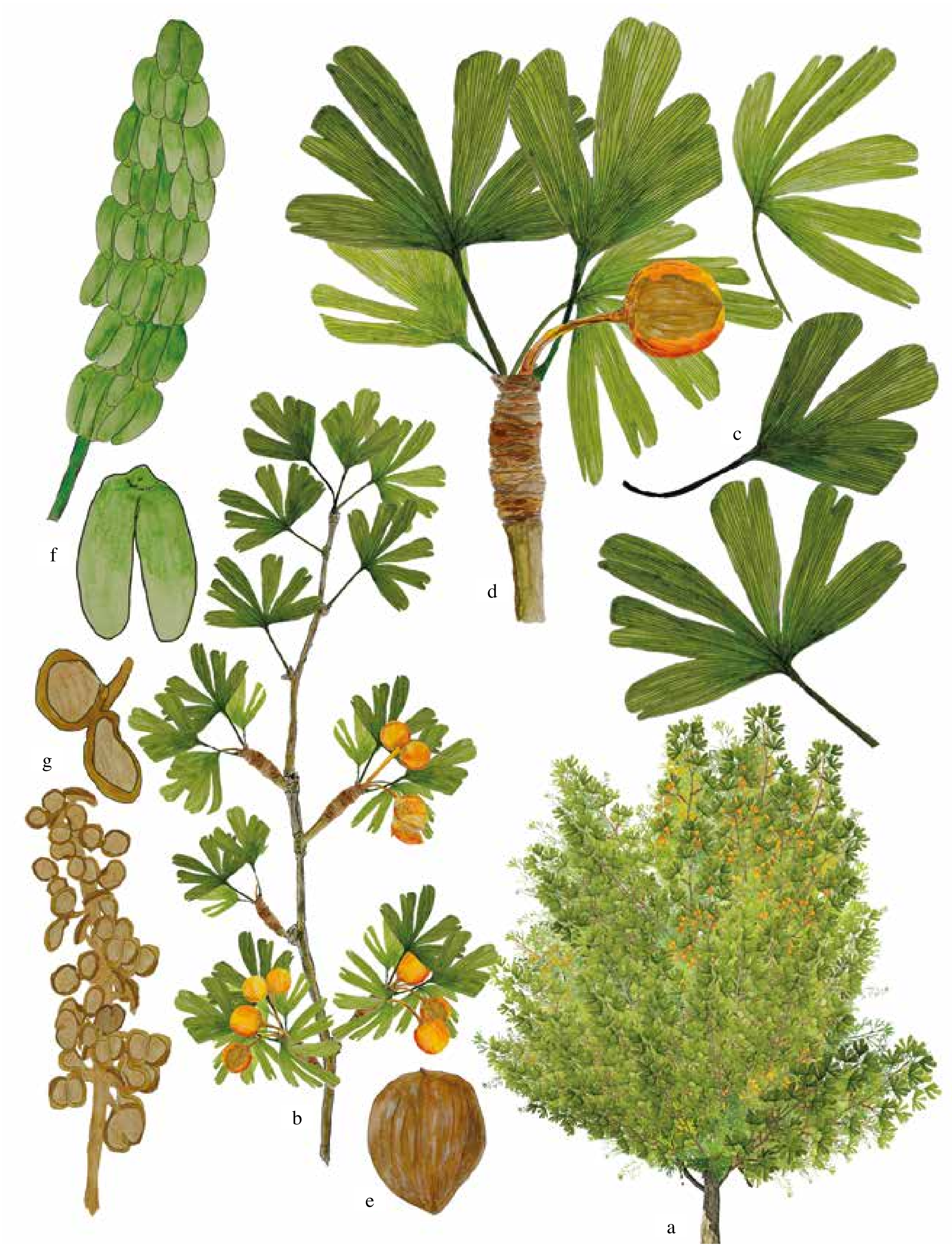
***Ginkgo biloba*. Leaves, seed berries, pollen cones**

1. Tree with seeds in spring; 2. Autumnal tree with ripe seeds; 3-4. Different leaves; 5. Characteristic leaf cuff; 6. Immature pollen cones; 7. Mature microsporophylls; 8. Green, unripe seeds in spring; 9. Ripe ginkgo seed; 10. Dropped seeds with dried out pulp and protruding core



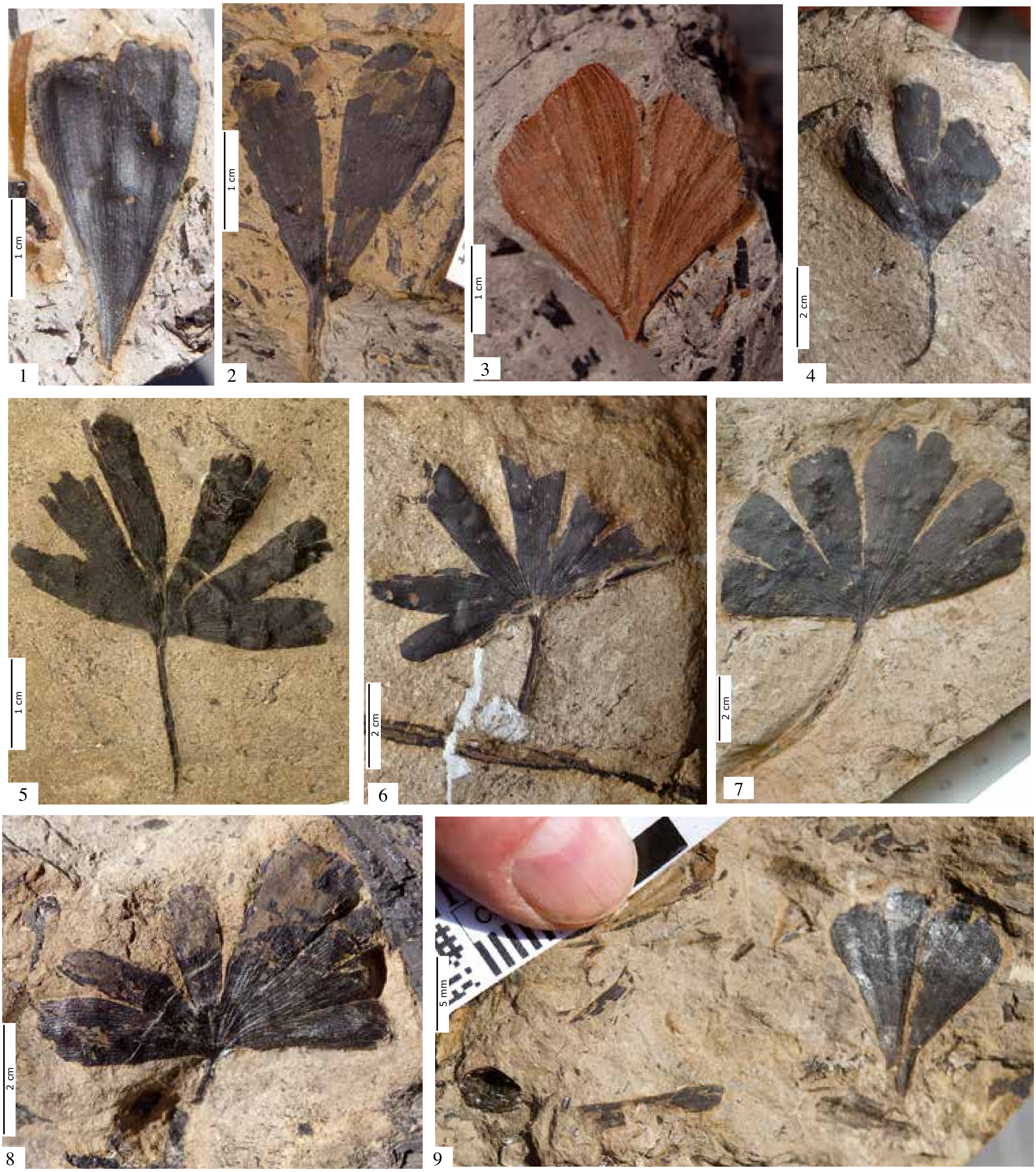
Ginkgoites plurpartitus. Early Cretaceous. Seedlings

1-3. Various seedlings (DUING 338, DUING 330, DUING 353, Coll. Garbermann), 4-5. Seedlings (DUING 261 Coll. Seppelt, DUING 118, Coll. Wachtler); 6-7. Presumable stems (DUING 226, DUING 243, Coll. Seppelt); 8. Aggregation of leaves from a short shoot (DUING 262, Coll. Seppelt); Duingen



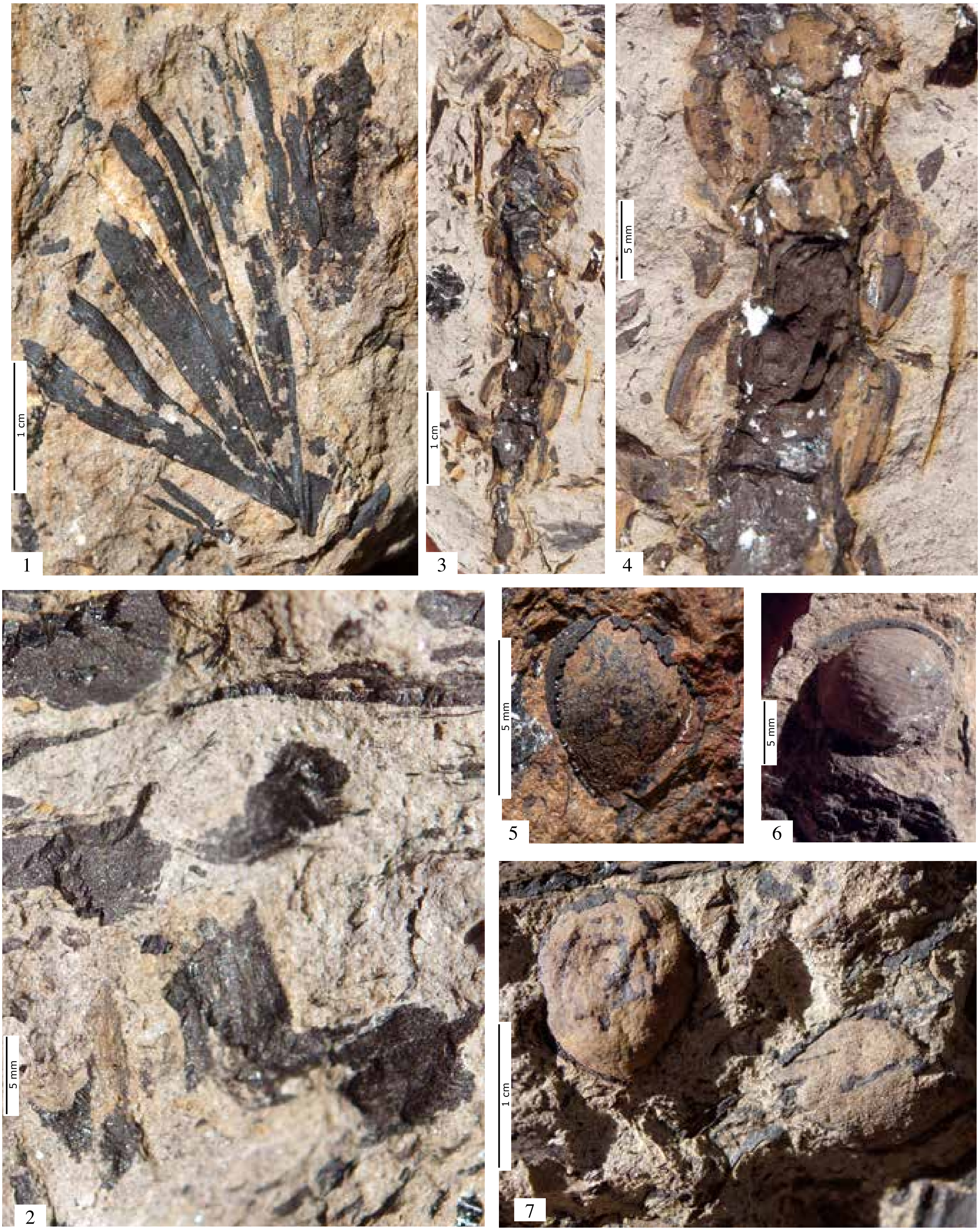
***Ginkgoites pluripartitus*. Early Cretaceous. Reconstruktions**

a. Female tree; b. Branch with short and long shoots and seeds; c. Leaves; d. Short shoot with overripe seeds; e. Mature seed without sarcotesta; f. Juvenile pollen cone and microsporophyll;g. Mature pollen cone and microsporophyll



***Ginkgoites plurpartitus*. Early Cretaceous. Leaves and seeds**

1-4. Various juvenile leaf forms (DUING 326, Coll. Garbermann; DUING 76, DUING 73 both Coll. Wachtler; DUING 252, Coll. Seppelt); 5-6. Adult leaf forms, short shoots (DUING 253, DUING 251, both Coll. Seppelt); 7. Perfectly preserved leaf (Coll. Wiedenroth); 8. Leaf (DUING 83; Coll. Wachtler); 8. Leaf and seeds (DUING 337, Coll. Garbermann); All Duingen



***Ginkgoites plurpartitus*. Early Cretaceous. Seeds and pollen cones**

1. Leaf and adult pollen cone (DUING 358); 2. Adult pollen capsules (DUING 351); 3-4. Juvenile pollen cone and detail (DUING 349, all Coll. Garbermann); 5-7. Isolated seeds, some with shell remains (DUING 70, DUING 112, DUING 33, all Coll. Wachtler); Duingen

Seedlings of *Ginkgo biloba*

Today ginkgos are widely cultivated due to its resistance to environmental influences in temperate zones around the world. The ginkgo avoids excessive cold and heat with low rainfall, so it is believed that it flourished during the Permian and Cretaceous periods, thriving in similar temperatures.

Conifers in the Early Cretaceous

In terms of quantity, the conifers in the German Wealden are somewhat in the background behind the numerous cycads and even the ginkgos. Nevertheless, based on the foliage and even more the various cones, it can be assumed that at least three species were present. In addition to the ubiquitous *Sphenolepis sternbergiana*, of which all parts, branches, seed- and pollen cones are well known due to their quantity, there were other conifers that are rare and therefore less easy to classify.
Possible descendants today can only be narrowed down using an exclusion process. No family relationships can be established with today's conifers such as pines (Pinus), firs (Abies), spruces (Picea), larches (Larix) or even with the Araucarias, nor with the Cupressaceae such as *Thuja* or *Juniper* because they are too large differences in their cones or seed scales (Wachtler, 2024).
Therefore, the genus name *Abietites (linkii)* described and illustrated by Roemer (1839), Dunker (1846) and also by Schenk (1871) must be questioned. Although this conifer is documented by rarely occurring branch parts, a peculiarity of the Abietaceae (firs) - their cones breaking down into individual seed scales on the tree - has never been found. Therefore a different classification must be made. Similarities with southern hemisphere conifers (*Athrotaxis, Widdringtonia*) have also to be discharged.
At least there remains a large group that has recently been fragmented into individual genera, but overall has the most similarities with the conifers from the Wealden: the conifer family *Tsuga,* which is now native to the northern hemisphere, especially if one takes into account *Tsuga, Pseudotsuga* and *Nothotsuga*, as well as the monotypic genus *Cathaya* added.
Although they all have different leaf needles, they all show similarities in their seed and pollen cones. Their ranges lie in the temperate but relatively humid areas of North America and East Asia. Excluding the dominant conifer species *Sphenolepis sternbergiana*, classification as *Tsugites* (Lakow, 1895) could be a possibility for the other conifers occurring in the Wealden.

Sphenolepis sternbergiana Schenk, 1871

Research history

1846 *Muscites sternbergianus* Dunker p. 20, pl. VII, Fig 10 (aus Duingen)

1846 *Thuites kurrianus* Dunker p. 20, pl. VII, Fig 8

1871 *Sphenolepis sternbergiana*, Schenk p. 243, Pl. XXXVII, Fig. 3-4, Pl. XXXVIII 3-13

1871 *Sphenolepis kurriana*, Schenk p. 243-245, Pl. XXXVII, Fig. 5-8, Pl. XXXVIII 1-2

2013 *Sphenolepis sternbergiana*, Pott, Guhl, Lehmann, p. 38, Pl. XII, 1-7

Sphenolepis sternbergiana is the most common conifer, so both branches and male and female cones are relatively well known. After extremely vague descriptions by Friedrich Adolph Roemer (1836) and an illustration addendum in 1839, it was Rudolf Wilhelm Dunker, 1846, who depicted further conifers from Wealden in northern Germany and gave them the names *Thuites kurrianus* and *Muscites sternbergianus,* being the second classified under the mosses. However, since both occur together and are very similar, they only represent one and the same species.

The name *Thuites* coined by Sternberg (1825) could actually have stuck if it had really been a forerunner of today's conifer genus Thuja, the tree of life, but this can be ruled out based on the different cones and foliage, that already August Schenk (1871) noticed. Schenk went into detail about this conifer, coined the new genus name *Sphenolepis* and renamed the species described by Dunker (1846) as *Thuites kurrianus* to *Sphenolepis kurrianus.* Since they were both a single species, the species name *Sphenolepis sternbergiana* ultimately prevailed for this widespread conifer.

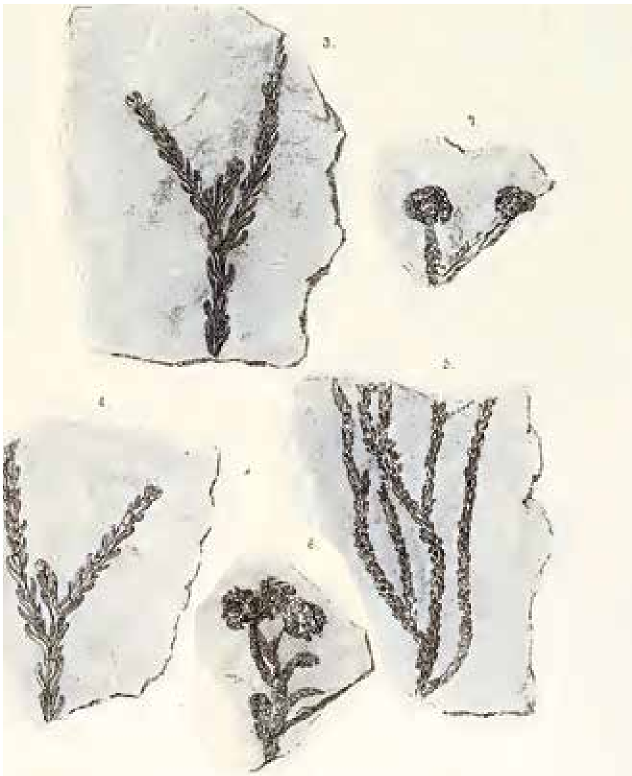
From Dunker, 1846, Plate VII, Fig. 8. *Thuites kurrianus;* Fig. 9. *Abietites linkii*, Fig. 10 *Muscites sternbergianus*

Description

Whole plant: Tree with multiple diverging side branchlets (DUING 20). Leaves needle-like, adjacent to protruding, usually barely 1 cm long, reaching less than 0.1 cm wide. Needles with entire edges pointed, the younger ones close-fitting, the adults elongated linear and sometimes crescent-shaped (DUING 330, DUING 289, DUING 293, DUING 20, DUING 31).

Pollen cones: In large numbers on terminal branches (DUING 106, DUING 13, DUING 333). Reaching about 1 cm in length and width, from circular to slightly elongated and slightly stalked. Provided with a large number of small and tightly fitting microsporophylls. Bracts tapering and slightly toothed, pollen sacs in twos (DUING 139) to four on the underside (DUING 295, DUING 294, DUING 361, DUING 339, DUING 87, DUING 339, DUING 43, DUING 42).

Seed cones: Female organs cylindrical, solitary at the tip of the branches, reaching up to 5 cm in length and width (DUING 283). Seed scales fleshy, loosely lying on top of each



From Schenk, 1871, Plate XXXVII: 3-4. *Sphenolepis sternbergiana*, 5-8. *Sphenolepis kurriana*

From Schenk, 1871, Plate XXXVIII: 1-2. *Sphenolepis kurriana*, 3-13. *Sphenolepis sternbergiana*

***Sphenolepis sternbergiana*. Early Cretaceous. Reconstruktions**

a. Tree with seed cones; b. Twig; c. Seed cone; d. Seed cone, upper view; e. Seed scale outside and inside; f. Seeds; g. Pollen cone; h. Microsporophylls in different views

It is often a long way from the discovery to the fully prepared fossil. Stephan Seppelt split this plate with the conifer *Sphenolepis sternbergiana* and three pollen cones (1) in the Bock quarry in Duingen. He assembled the plates and worked out the whole male cones (2) with the branchlet in great detail (3) (DUING 295, Coll. Seppelt).

other (DUING 270, DUING 287, DUING 289, DUING 282, DUING 24, DUING 281, DUING 241, DUING 248). With entire margins but bluntly tapered; arched on the back, with delicate grooves on the surface. Elongated wing seeds, two on each scale.

Remarks

Already in the Lower Jurassic of northern Bavaria, a genus of conifers, which was described as *Hirmeriella muensteri* (Schenk 1867, Jung 1968) (Wachtler, 2024), is often found in the sand pits there (especially the locality Schnabelwaid) (Wachtler, 2024. It shows striking similarities to those from the Early Cretaceous. The pollen cones resembles, just like the multi-branched branches with their tightly fitting small needle leaves. The female cones also show analogies to *Sphenolepis.* But each individual seed scale was twice short-winged, typical of today's monotypic conifer genus *Taiwania cryptomerioides,* which was widespread throughout the northern hemisphere in the later Jurassic and Eocene, and is now only found in a few Relict zones of East Asia, limited from Taiwan to southern China, Myanmar, Japan and Vietnam.

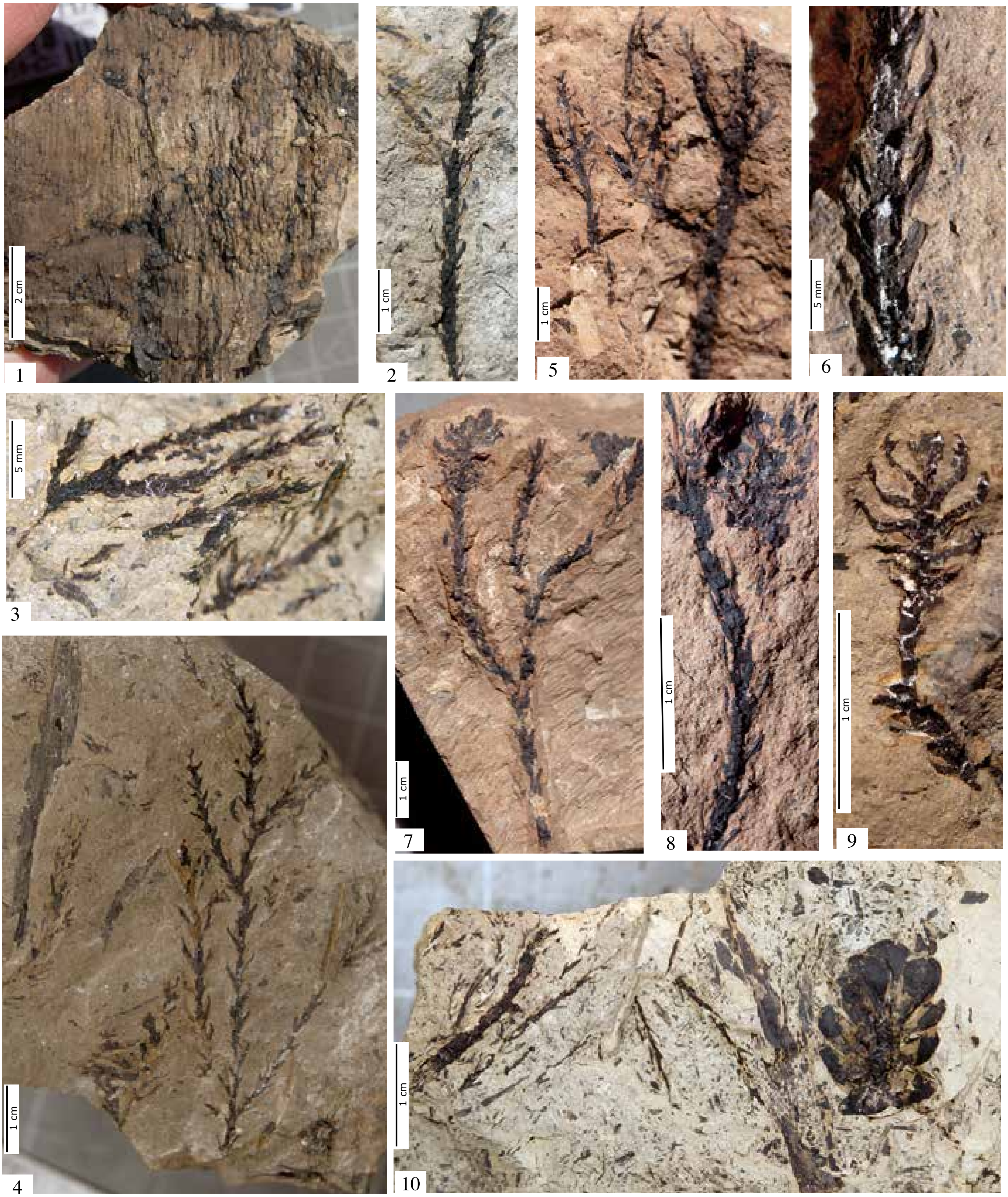
Therefore another solution must be found. In *Sphenolepis,* however, the seeds were simple and long winged, which is clearly visible on the impression of the female cone scales and is also proven by rarely found winged seeds (Coll. Wiedenroth). A closer relationship with *Hirmeriella* can therefore be ruled out and *Sphenolepis sternbergiana* can be attributed to the *Tsuga* ancestor.

Tsugites Lakowitz 1895

There are some doubts as to whether other conifers, which are known from their seed cones and isolated branches, can be classified as precursors of the large Tsuga family, perhaps also Cathaya. The name *Tsugites (brunnstattensis)* was coined in 1895 by the German botanist Conrad Lakowitz (1859-1945) for sterile branches from the Early Oligocene from Brunnstatt in Alsace Lorraine and was subsequently largely forgotten.

Cathaya and Tsuga

Tsuga canadensis. Twigs (1), Juvenile pollen cones (2), adult pollen cones (3), juvenile seed cone (4), adult seed cone (5), two winged seeds (6); **Tsuga chinensis.** Seed scales outside and inner view (7-8); ***Tsuga heterophylla.*** Tree with seed cones (9), female cone (10); ***Tsuga diversifolia***. Female cone (11); ***Nothotsuga longibracteata,*** Branchlet (12) and female cone (13); ***Cathaya argyrophylla.*** Twig from a herbarium (New York, Botanical Garden) (14); Seed cone (15).

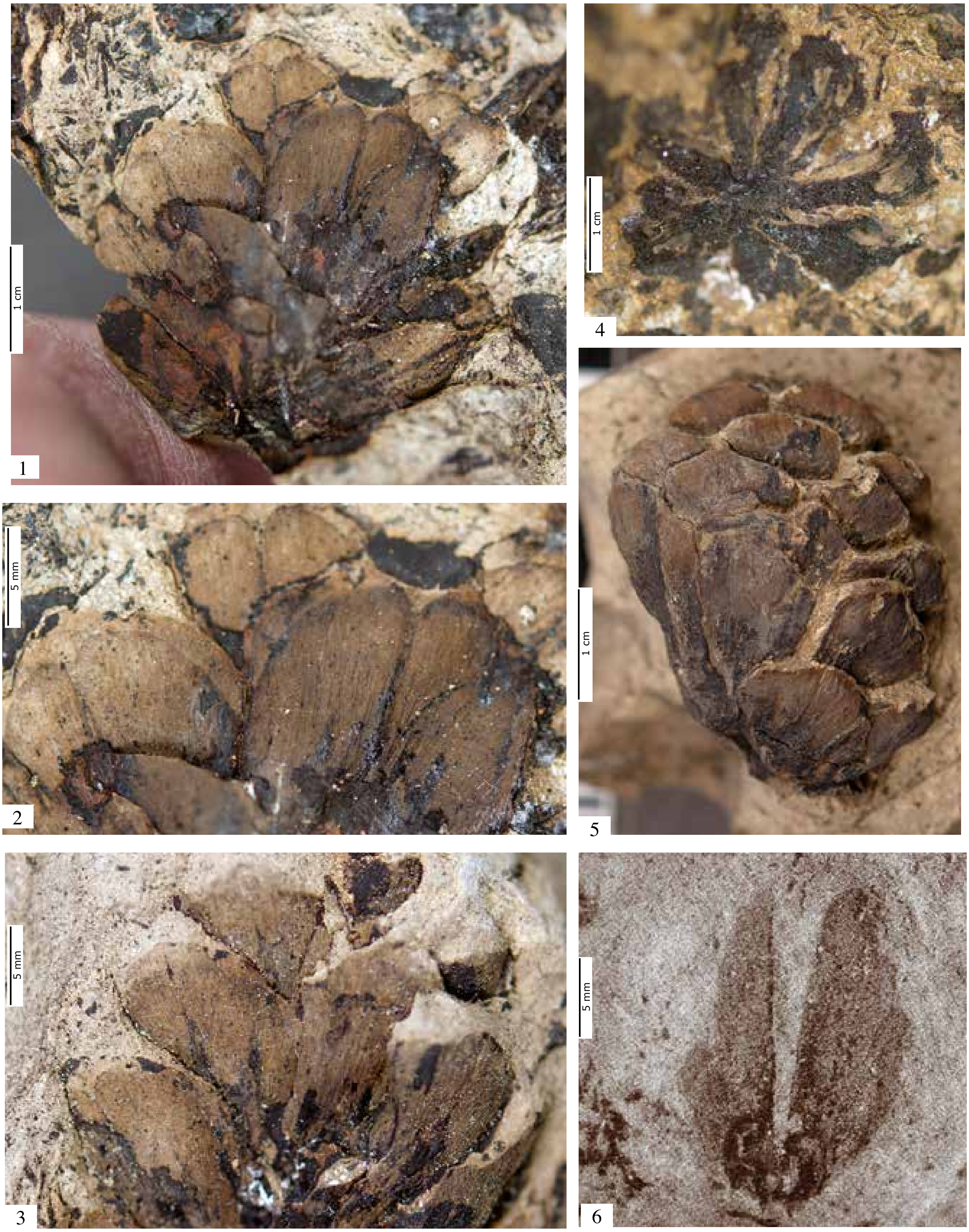


***Sphenolepis sternbergiana*. Early Cretaceous. Branchlets**

1. Part of a stem (DUING 316, Coll. Garbermann); 2-6. Various branchlets (DUING 330 Coll. Garbermann; DUING 289, DUING 293, Coll. Seppelt; DUING 20, DUING 31, Coll. Wachtler); 7-8. Branchlets with pollen cones (DUING 106, DUING 13, Coll. Wachtler); 9. Branchlet with decayed pollen cone (DUING 333, Coll. Garbermann); 10. Seed cone with branchlets (DUING 283, Coll. Seppelt)

***Sphenolepis sternbergiana*. Early Cretaceous. Seed cones**

1-2. Seed cones and isolated seeds (DUING 270); 3. Several seed cones (DUING 287); 4. Juvenile seed cones (DUING 289); 5-6. Various seed cones (DUING 282, DUING 24, all Coll. Seppelt); Duingen



***Sphenolepis sternbergiana*. Early Cretaceous. Seed cones**

1-2. Seed cones and detail of seed imprints (DUING 267); 3. Seed cone detail (DUING 281); 4. Juvenile seed cone, top view (DUING 241) 5. Three-dimensionally prepared seed cone (DUING 248, all Coll. Seppelt); 6. Winged seed scales (Coll. Wiedenroth); All Tongrube Bock, Duingen

***Sphenolepis sternbergiana*. Early Cretaceous. Seed cones**

1. Juvenile seed cone (DUING 335); 2-3. Seed cones with shadow of the winged seeds (DUING 301, DUING 317); 4. Seed cones, bottom view (DUING 325) 5. Seed cones, lateral view (DUING 324); 6. Three cones (DUING 306, all Coll. Seppelt); 7. Cones with seeds (DUING 319, Coll. Garbermann); Duingen

***Sphenolepis sternbergiana*. Early Cretaceous. Pollen cones**

1-2. Pollen cones on a branchlet (DUING 100, DUING 106, Coll. Wachtler); 3. Ripe pollen cones (DUING 294, Coll. Seppelt); 4-6. Various details of pollen cones (DUING 243, DUING 339, DUING 287, Coll. Seppelt); 7. Seed cones and pollen cones (DUING 237, Coll. Seppelt); 8. Juvenile cone (DUING 361, Coll. Garbermann), 9. Broken pollen cone (DUING 42, Coll. Wachtler); 10-12. Various pollen cones (DUING 129, DUING 35, DUING 48, all Coll. Wachtler); 13-14. Detail of the two pollen sacs (DUING 139, Coll. Garbermann); Duingen

Tsugites linkii nov. comb. (Roemer, 1839), Wachtler 2024

Research history

1839 *Abietites linkii* Roemer Nachträge p. 10, Pl. XVII, Fig. 2

1846 *Abietites linkii* Dunker, Monographie Wealden, p. 18, Pl. VII, Fig. 10

1847 *Pinites linkii* Endlicher, Synopsis Coniferarum p. 283

1850 *Abietites linkii* Göppert, p. 207

1871 A*bietites linkii* Schenk, Beiträge Flora Vorwelt, p. 241, XL Fig. 1-7

Description

Leaves: Needle-shaped, 1-2 cm long, slightly crescent-shaped (DUING 310, DUING 135).
Pollen cones: Slightly elongated, up to two cm long, barely 1 cm wide (DUING 138).
Seed cones: Cone-shaped, elongated, rounded, up to 4-5 cm long, 3-4 cm wide (DUING 311). Macrosporophylls grooved on the outside, rounded apically (DUING 95, DUING 307, DUING 311), about 1 cm wide, 1.5 cm long.

Tsugites garbermannii sp. n. Wachtler 2024

Holotype

DUING 393 (Coll. Garbermann) **Paratype:** DUING 392 (Seed cone)

Etymology

Named after Dieter Garbermann (Brunkensen, Alfeld, Lower Saxony). For more than forty years he collected in the clay pits around Duingen and compiled a rich paleobotanical collection. Even when he was over eighty, he worked on the lenses with heavy equipment and made scientifically valuable discoveries. He bequeathed a large part of his collection to the preparator and geologist Stephan Seppelt from Sibbesse.

Diagnosis

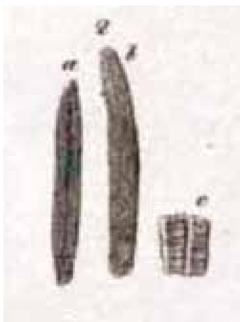
Conifer with long, slender, grooved leaf needles. Seed cones elongated, developing scales with a long bract and two winged seeds.

Description

Leaves: Needle-shaped, 3 to 5 cm long, 0.1 to 0.2 cm wide. Longitudinally furrowed, apex obtuse (DUING 393, holotype, DUING 120). Tuft-like to loosely connected to the main branch.
Pollen cones: Not yet assigned.
Seed cones: Slender, up to 5 cm long, 2-3 cm wide (DUING 393, DUING 309, DUING 50, DUING 84). Macrosporophylls arranged spirally around an axis (DUING 02, DUING 303). Seed scales furrowed on the outside, with elongated bracts, seeds winged (DUING 310).

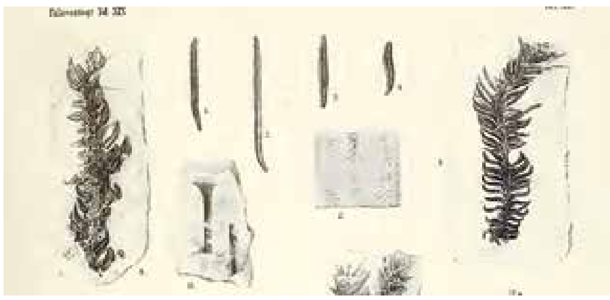
Remarks

In addition to the ubiquitous conifer *Sphenolepis sternbergiana,* characterized by short, tapering and sometimes tightly fitting needles, rounded seed cones with loose, fleshy seed scales, and small rounded pollen cones, there were other, less common conifers, which in *Tsugites garbermannii* have long-needle leaves with elongated seed cones, in *Abietites (Tsugites) linkii* sickle-shaped protruding, pointed needles and rounded seed cones. Both had elongated seed scales, which is what distinguishes them from *Sphenolepis*, as well as the different leaf foliage.
A dilemma of the Early Cretaceous finds around Duingen, however, is that although



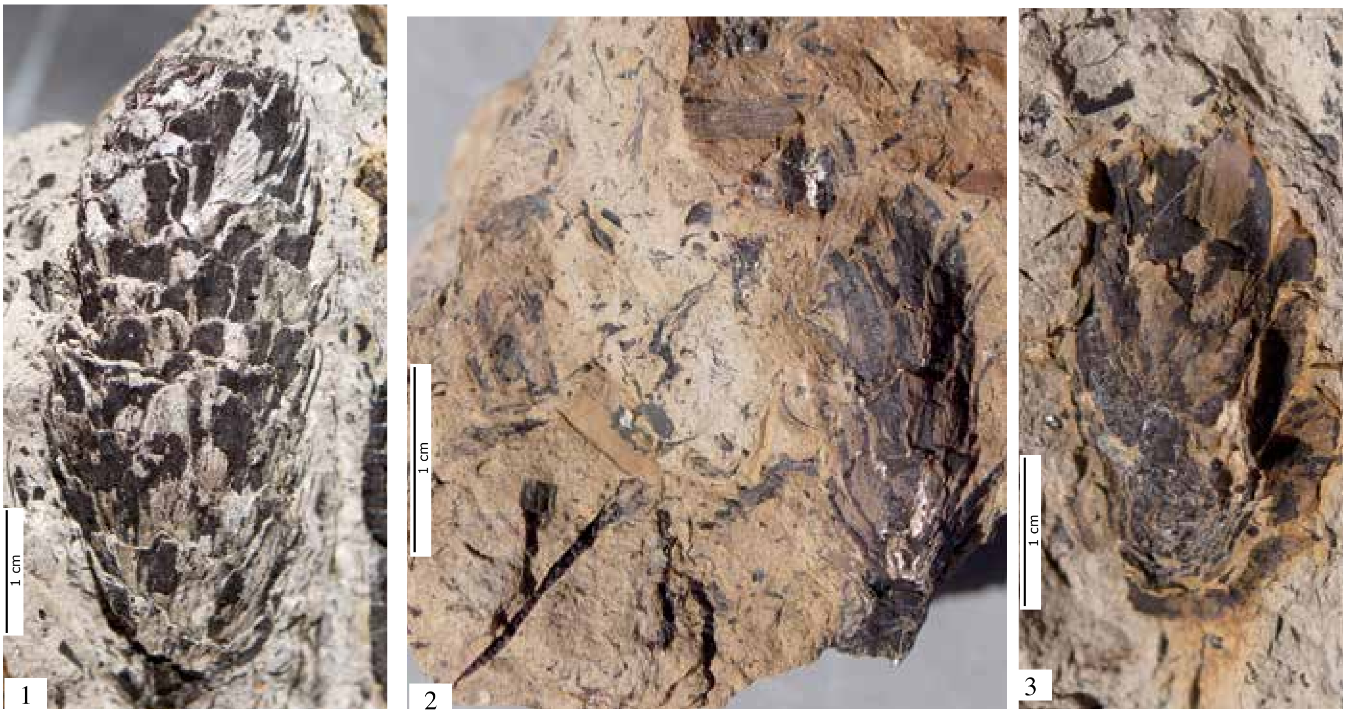
Left: From Roemer, 1839 *Abietites linkii,* pl. XVII Fig 2.

Below: From Schenk, 1871, *Abietites linkii,* pl. XL, fig. 1-7



Tsugites linkii **nov. comb. Early Cretaceous. Seed cones**

1. Seed cone (DUING 95; Coll. Wachtler) 2. Seed cone (DUING 310); 3-4. Various seed cones (DUING 311, DUING 307, all Coll. Garbermann); 5. Branchlet with pollen cone (DUING 138, Coll. Wachtler); 6. Part of a branchlet (DUING 215, Coll. Seppelt); Duingen



Tsugites garbermannii **n. sp. Early Cretaceous. Seed cones and leaves**

1. Seed cone (DUING 392, Paratype, Coll. Garbermann); 2-3. Seed cone, accompanied by leaves (DUING 84, DUING 50, Coll. Wachtler); Tongrube Bock, Duingen

seed cones are found in sufficient numbers, the associated foliage and twigs are relatively rare. We experience a similar peculiarity in the Middle Triassic of Ilsfeld, where male and female cones of the conifer *Swedenborgia nissleri* are in excellent condition, although branches are largely missing (Wachtler, 2016). It was only in the Lower Jurassic of northern Bavaria that large deposits of twigs were found alongside a large number of cones from *Swedenborgia liasokeuperianus,* so that this genus of conifers with their five-seeded macrosporophylls became well known (Wachtler, 2024).

Both, *Swedenborgia nissleri* in the Middle Triassic of Ilsfeld and Tsugites in the Wealden of Duingen, stands further away from the banks probably meant that the more destruction-resistant cones survived the transport, but branches were often chopped up. However, existing findings confirm that *Tsugites garbermannii* bore long pine-shaped leaf needles, while *Tsugites linkii* developed shorter, protruding, sickle-shaped leaves.

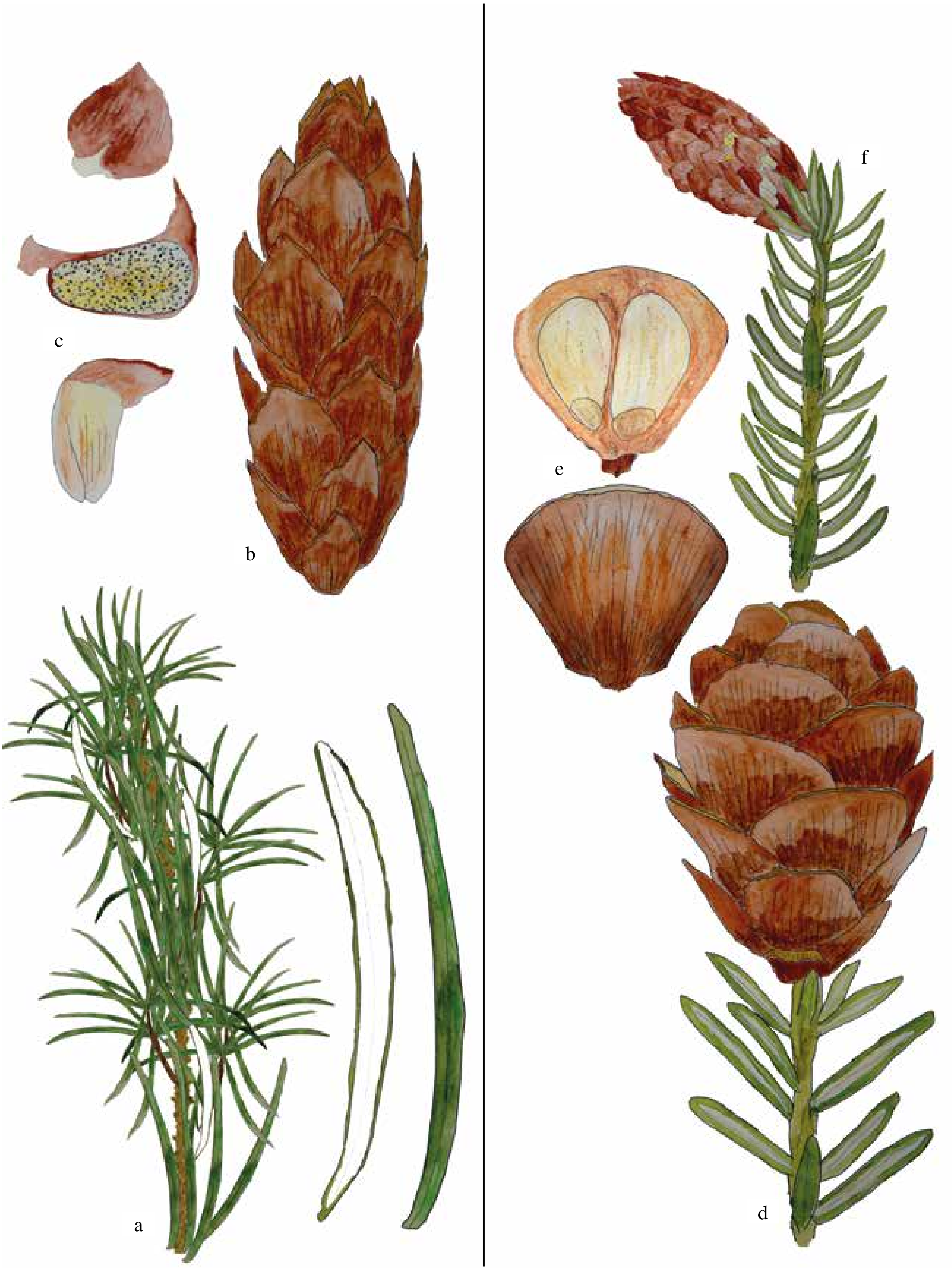
Since the name *Abietites* does not prove to be useful, as there are large differences to the fir ancestors, which were fully developed and spread from the Lower Permian onwards, other solutions have to be sought, the most likely being ancestors of today's *Tsuga* conifers. These are partly large conifers that only occur in relict zones in China (*Cathaya, Nothotsuga*), and then again in both North America and East Asia (*Tsuga, Pseudotsuga*). They were native to Europe until the Tertiary and were only displaced there by the ice ages. *Tsugites garbermannii* probably points more towards *Cathaya argyrophylla,* the pigeon tree or *Nothotsuga longibracteata, Tsugites linkii* towards that of *Tsuga heterophylla* or *Tsuga diversifolia.*

Clubmosses

After the Lycopodiaceae dominated the landscapes in the Carboniferous, with giant trees such as *Lepidodendron* or *Sigillaria,* in the Triassic period with smaller representatives such as *Lycopia dezanchei, Eocyclotes alexawachtleri* or *Sigillcampeia nana* (Wachtler, 2016, Wachtler, 2021), they continued to be abundantly present also in the Early Jurassic with today unknown genera such as *Bernettia inopinata* and *Bavarostrobus friessi* (Wachtler, 2024a,e)

Tsugites garbermannii **n. sp. Early Cretaceous. Seed cones and leaves**

1-2. Seed cone and leaf needles (DUING 393, holotype finder Manfred Fuchs, Coll. Garbermann); 3. Branchlet with long leaf needles (DUING 120, Coll. Wachtler); 4. Leaf needles and winged seeds (DUING 310); 5-7. seed cones in different growth stages (DUING 309, DUING 302, DUING 303, all Coll. Garbermann); 8. Seed cones (Coll. Wiedenroth); Duingen



Tsugites garbermannii und Tsugites linkii. Early Cretaceous. Reconstructions

Tsugites garbermannii. Branchlet, with single needle front and back; b. Female cone; c. Microsporophylls; ***Tsugites linkii.*** d. Female cone on a branchlet; e. Seed scale and seeds, front and back, f. Pollen cone with branchlet

where they colonized areas near the rivers and banks, the question arises to what extent this trend continued in the Lower Cretaceous.
In the German Wealden, an enigmatic plant caused problems in the classification in the past and which, for various reasons, should be classified as club moss: *Seppeltia bockii.*

Class Lycopodiopsida

Order Lycopodiales

Family: Lycopodiaceae

Seppeltia nov. gen. Wachtler 2024

Diagnosis
Plant with a short trunk and broad-leaved sporophylls growing around an axis.

Etymology

Honoring the geologist and preparator Stephan Seppelt from Sibbesse (Hildesheim district). Together with Dieter Garbermann (Brunkensen, Alfeld, Lower Saxony) they collected and researched the clay pits around Duingen for decades.

Seppeltia bockii sp. n. Wachtler 2024

Research history

2014 *Cycadolepis sp.*, Pott, Guhl, Lehmann Pl VII, Fig. 8

Holotype
DUING 122, Dolomythos-Museum

Etymology

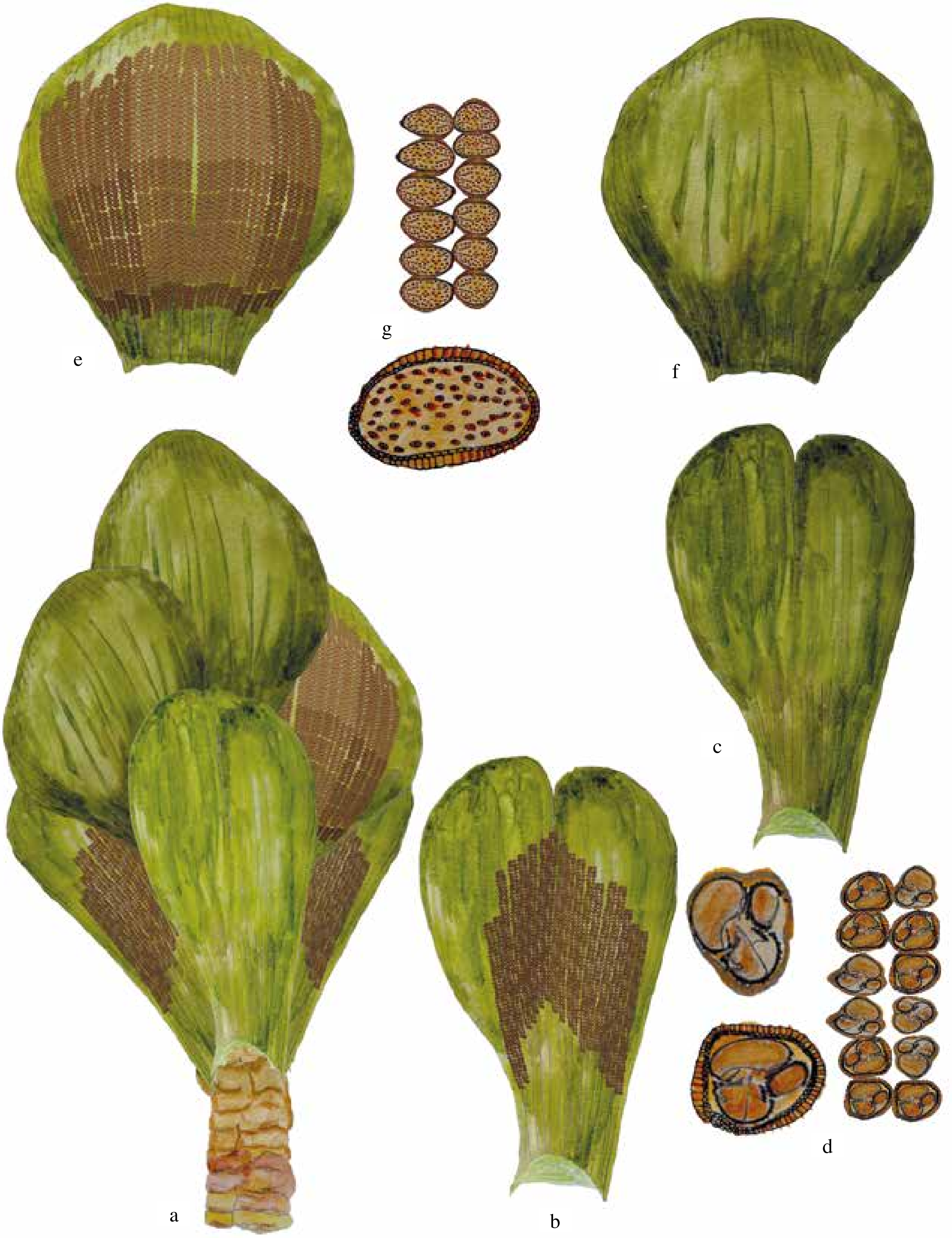
After the Bock clay pit in Duingen, from which the majority of the plant fossils come.

Description

Whole plant: Short-stemmed, up to 5 cm high (DUING 340), with broad-leaf-shaped, partially fertile scales, which were arranged helically around an axis. Macrosporophylls located in the lower or outer areas of the sporophyll crest (DUING 122, designated holotype), bracts up to 10 cm long, with a concave break in the lower part, about 3 cm wide at the base, then diverging in a belly shape and reaching a width of about 6 cm (DUING 131). Apically rounded (DUING 122, DUING 124, DUING 131, DUING 132). Microsporophyll leaves wider, sometimes 12 cm, reaching a height of 6 cm (DUING 123). These are densely populated with rows of microsporophylls (DUING 123, DUING 121, DUING 11, DUING 59).

Remarks

Seppeltia bockii is one of the not rare plants in the Wealden around Duingen, but the classification caused description problems due to the sterile and fertile remains that were found in fragments. In this it is reminiscent of other clubmosses such as *Bernettia inopinata* from the Lower Jurassic of Central Europe, which has also been given different classifications. Its long, lanceolate leaves were described as *Desmiophyllum gothani,* the sterile spore leaves were classified under the name *Chlamydolepis lautneri,* the microsporophylls as *Piroconites kuespertii,* and the macrosporophylls as *Bernettia inopinata.* It was only after discoveries associated with heterosporous parts that a classification as club moss was considered sensible (Wachtler, 2024).
The same may apply to *Seppeltia bockii*, as there are remarkable similarities to *Bernettia,* which developed around 50 million years earlier. *Lepacyclotes,* which occurs from the Early Triassic to the Lower Jurassic, also belongs to the low-growing enigmatic club moss plants (Wachtler, 2016). However, today's representatives are unknown because the few existing lycophytes such as *Selaginella, Lycopodium* or *Isoetes* have other lines of origin.
The most likely possibility of confusion with other fossil plants from the Early Cretaceous is the enigmatic fern *Wiedenrothia klipsteini.* Their tongue-like leaves, mostly found in a consistent leathery type, show some similarities. Nevertheless, their typical frond character, typical of ferns, their elongated leaves, and their sporangia with an annulus indicate in direction to the Polypodiopsida. *Seppeltia* probably preferred brackish water areas near the banks, where it probably occurred in pure populations.



Seppeltia bockii. Early Cretaceous. Reconstructions

a. Whole plant; b. Leaf with macrosporangia, inside; c. Leaf with macrosporangia, outside; d. Macrosporangia; e. Fertile leaf with microsporangia, inside; f. Fertile leaf with microsporangia, outside; g. Microsporangia

Seppeltia bockii **nov. gen. sp. n. Early Cretaceous. Fertile leaves**

1-2. Leaf with macrosporophylls and detail (DUING 122, designated holotype, ex. Coll. Wiedenroth, Coll. Wachtler, Dolomythos-Museum); 3-6. Various leaves with microsporangia (DUING 124, DUING 131, DUING 132, DUING 133, all Ex. Coll. Wiedenroth, Coll. Wachtler, Dolomythos-Museum); 7. Microsporophyll leaf with short stem base (DUING 340, Coll. Garbermann); all Duingen

Seppeltia bockii nov. gen. sp. n. Early Cretaceous. Fertile leaves

1-3. Leaf with microsporangia (DUING 123, DUING 121, DUING 11, ex. Coll. Wiedenroth, Coll. Wachtler, Dolomythos-Museum) 4-5. Leaf and detail of sporangia (DUING 59); 6-8. Details of the sporangia (DUING 123, DUING 11, DUING 124, ex. Coll. Wiedenroth, Coll. Wachtler, Dolomythos Museum); Bock Duingen clay pit

Ferns

The ferns stay in the background among the ubiquitous cycads, but also the conifers and gingkos. Relatively common is a species that was already described by Dunker (1846) and Schenk (1871) as *Pecopteris geinitzii.* The first describer, Dunker (1846), called this a "*beautiful species"* and figured the holotype with velvety pinnules in good quality. Schenk also opted to the genus *Pecopteris geinitzii* and criticized that a precise classification "*can only be made when well-preserved fertile parts are known".*

He compared the pinnae found with tree ferns such as *Alsophila loddigesii,* a synonym of the modern *Cyathea australis.* However, these remains and especially the fertile fronds that are now present have little similarity to Cyathea ferns, but are in today's extended family Dennstaedtiaceae, a subgroup of the globally distributed Polypodiales. The bracken fern *(Pteridium aquilinum)* in particular is considered a frugal pioneer plant, as well as a weed that is difficult to eradicate.

Since the first name *Pecopteris (geinitzii)* is a collection of a wide variety of similar leaf shapes, which included all sorts of fern families from the Carboniferous to the Cretaceous, most of which were not even related to each other, the genus name should be replaced by a more appropriate one.

Referring to Brongniart (1849), who proposed the genus name *Cladophlebis*, Schenk (1871) classified a fern from the German Wealden as *Cladophlebis.* Since the illustrations of Schenk's *Cladophlebis (albertsii)* (Pl. XXVII, Fig. 4) differed considerably from those of Dunker (1846), the species name *Cladophlebis geinitzii* was most likely to be used for the characteristic fern of the German forest. Provided that *Cladophlebis* includes fern ancestors from the Dennstaedtiaceae group. That's not the case.

Doweld (2013) already stated in a nomenclatural work on this fern genus: "*Cladophlebis in its original 1849 circumscription was a curious mixture of various unrelated species of fossil plants, which have been later reclassified not only into distinct genera, but different orders and even phyla of vascular plants".* Doweld therefore suggested using the name *Cladophlebis* only for sterile fern foliage of supposed Osmundaceae, especially from the Triassic.

He also discussed the specimens from Dunker (1846), where he pointed out the poor state of preservation of the sterile pinnules of *Neuropteris albertsii* and considered them to be atypical for a *Cladophlebis* species. They also belonged

Left: Dunker, 1846, *Pecopteris geinitzii,* Pl. 8, fig 3abc

Middle: Schenk 1871, *Pecopteris geinitzii,* Pl. XXIX fig 2, 2a

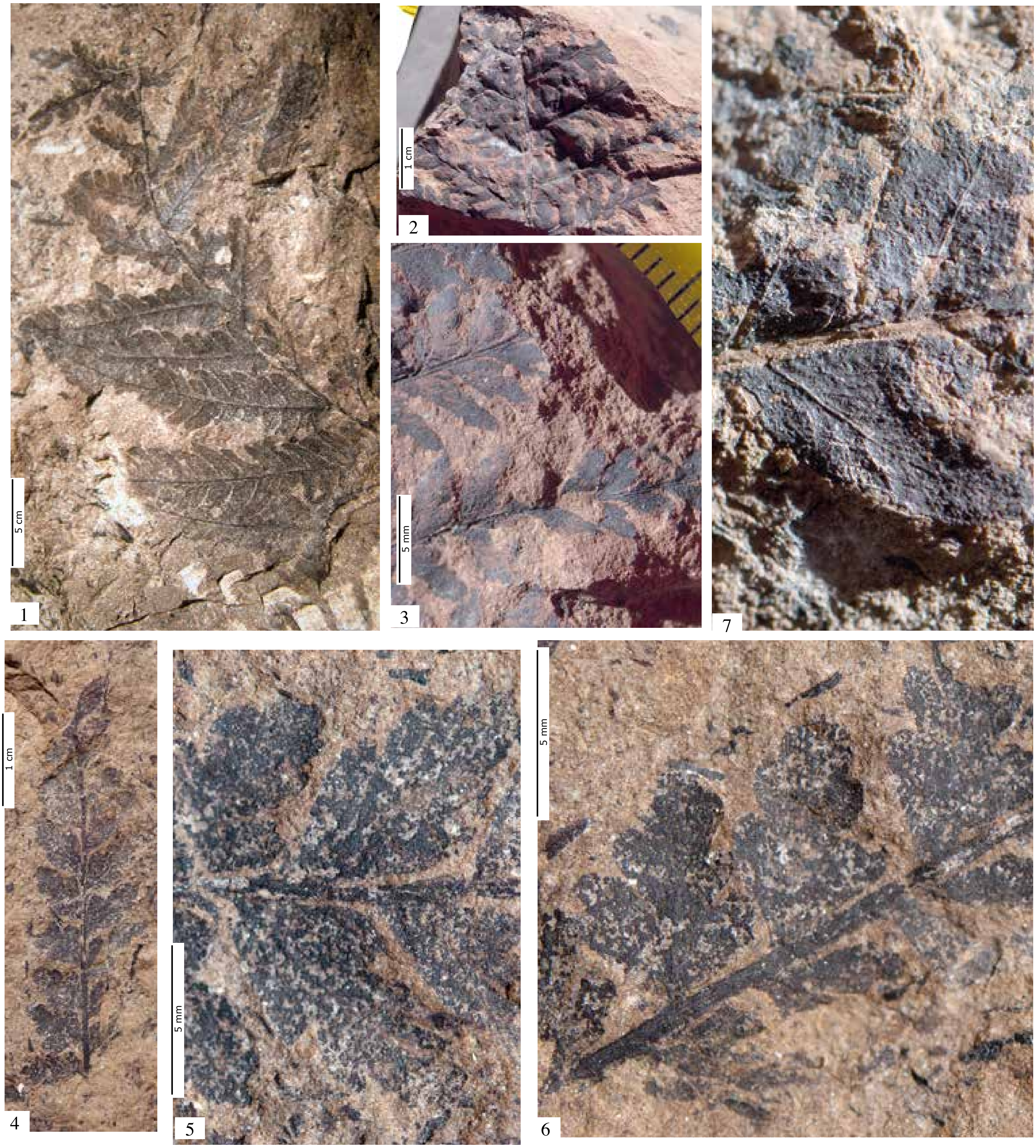
Right: Schimper 1869, *Sphenopteris mantelli (*Pl. XXXI, Fig. 3); *Pecopteris cordai (*fig. 4). It is the same specimen from Dunker, *(Pecopteris geinitzii),* only drawn reversed.

Dennstaedtiaceae. Ferns

Pteridium aquilinum, bracken, plant (1) and fertile pinnules (2); ***Hypolepis tenuifolia,*** Frond (3), fertile frond, upper view (4), mature fertile pinnules (5); ***Dennstaedtia bipinnata,*** Fertile juvenile pinnules and detail (6-7); ***Dennstaedtia producta***, fertile pinnula with juvenile sori (8); ***Dennstaedtia cornuta,*** mature sporangia (9)

Dennstaedtites geinitzii **Early Cretaceous. Fronds**

1-2. Frond with isolated juvenile pinnula on the left (DUING 28); 3-4. Isolated sterile pinnula (DUING 60, DUING 91); 5-6. fronds and detail of pinnulae (DUING 136, all Coll. Wachtler); 7. Parts of fronds (DUING 260, DUING 291, both Coll. Seppelt); 8. Leaflets (DUING 291, Coll. Seppelt); 9. Pinnulae (DUING 70, Coll. Wachtler); all Duingen



***Dennstaedtites geinitzii*. Early Cretaceous. Fronds**

1. Almost complete frond (Coll. Wiedenroth); 2-3. Frond and detail of the pinnae (DUING 111); 4-6. Fertile frond part with detail of the sori and sporangia (DUING 02); 7. Detail of a fertile pinnae with sporangia (DUING 135, all Coll. Wachtler, Dolomythos Museum); Duingen

to Cretaceous finds (Doweld, 2013). This further limits the legitimacy of the genus *Cladophlebis,* as using this name from the Cenozoic era, starting 66 million years ago, was not considered useful. These considerations can be supported due to the discovery of well-preserved sterile and fertile frond remains in the Wealden around Duingen.

Since even the name *Cladophlebis* had degenerated into a confusion for a large number of different sterile fern leaves, which were considered to be ancestors of the Osmundaceae, Dicksoniaceae or Schizaeaceae and thus degenerated into a formal genus, this name also turns out to be unhelpful.

The difficulty now is to find a genus name that does justice to its role as a precursor to the Dennstaedtiaceae. A *Dennstaedtites confragosus* from the chalk was described in 1953 by the Russian botanist Natalia Andreevna Bolkhovitina (Bolkh.) (Наталья Андреевна Болховитина 1915 -1997). Even if the naming cannot fulfil today's nomenclature requirements, respect should still be given to researchers in those countries that conduct science under the most difficult circumstances.

Therefore, the genus name *Dennstaedtites* is suggested, which is most appropriate primarily for the Early Cretaceous finds from the German Wealden due to the many similarities. This fern is thus recombined as *Dennstaedtites geinitzii.*

Class Polypodiopsida

Family Leptosporangiate Ferns (Polypodiidae)

Dennstaedtites Bolkhovitina, 1953

Dennstaedtites geinitzii Dunker 1846, Wachtler 2024 comb. nov.

Research history

1846 *Pecopteris geinitzii* Dunker, Monogr. p. 6., tab. VIII. fig. 3. ab

1846 *Neuropteris albertsii* Dunker, Monogr. p. 8., tab. VII. fig. 6

1869 Sphenopteris mantelli Schimper Pl. XXXI, Fig. 2-3

1869 Pecopteris cordai Schimper Pl. XXXI, fig. 4

1871 *Pecopteris geinitzii* Schenk, p. 215, Pl. XXIX, 2. 2 a.

2013 *Cladophlebis albertsii* Pott, Guhl, Lehmann Pl I, Fig. 3

Description

Whole plant: Low-growing fern with 3- to 4-pinnate fronds. Sporangia united to form sori, mostly located at the edges of the leaflets. Fronds sometimes reach 30-40 cm in size. Pinnulae opposite, short-stalked to sessile, almost trapezoidal in juvenile development, partially segmented like a comb in the adult stage and slightly toothed (DUING 291). Veining delicate, only faintly visible. Individual pinnulae between 0.5 and 1 cm long and 0.3 to 0.5 cm wide (DUING 91, DUING 136, DUING 329)

Fertile fronds: Same as the sterile, tender, sori marginally located on the underside of the pinnae (DUING 02, DUING 135). Partly heavily crusted.

Remarks

Dennstaedtites geinitzii, together with *Wiedenrothia klipsteini*, is considered the only relatively common fern in the German Wealden around Duingen, although well-preserved larger remains are extremely rare. This could be explained by the fact that ferns did not grow near the banks and populated more the hinterland, although the widespread absence of horsetails in these layers is just as striking. However, *Dennstaedtites* also occurs in neighboring Upper Cretaceous layers (Kimmeridgian) (Coll. Wiedenroth).

Ferns from the family Dennstaedtiaceae (*Blotiella, Dennstaedtia, Histiopteris, Hypolepis, Leptolepia, Microlepia, Monachosorum, Paesia, Pteridium, Sitobolium* are widespread worldwide and are only missing in the polar regions and deserts.

Class Polypodiopsida

Family Leptosporangiate Ferns (Polypodiidae)

Wiedenrothia Wachtler, 2024 nov. gen.

Another fern from the Lower Cretaceous has been the subject of discussion since the beginning of research. In 1846, Wilhelm Dunker described and figured two species of ferns under the names *Cyclopteris klipsteini* and *Cyclopteris mantelli.* The same speci-

Dennstaedtites geinitzii. Early Cretaceous. Reconstructions

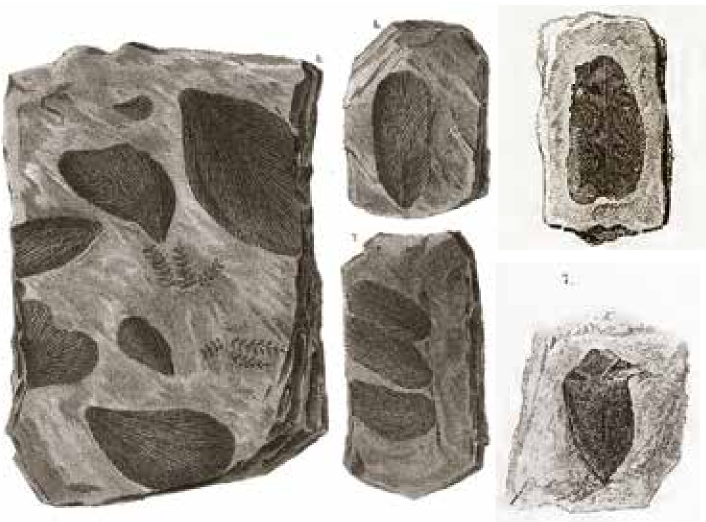
a. Whole plant; b. Fertile lealfets, outside; c. Fertile pinnulae, inside with sori; d. Sporangia in calyx; e. Lateral view sporangia, top view and single sporangium; f. Sterile pinnulaeinside and outside; g. Juvenile leaflet

Dennstaedtites is also known in good specimens from the Upper Cretaceous (Kimmeridgian). Location Segelhorst, Coll. Wiedenroth.

mens were published by C. Ettinghausen (1852), and then again by P. W. Schimper in a magnificent work published in several editions from 1869 to 1874, in which he renamed the same finds, now kept in Berlin, as *Aneimidium mantelli* and illustrated them accurately, but reversed (Schimper, 1869, Fig. 13). Schenk (1871) described the same *Cyclopteris klipsteini* mentioned by Dunker (1846) "f*rom the iron-shot clay sandstones of Duingen"* now changing the name in *Aneimidium klipsteini* as "*leaves pinnate (?), segments elongated, obovate, entire, rounded at the tip, with sitting on a contracted base, 2.5 centim. long, 1 centim. wide"* and further "*The nerves of this species are very delicate and only reveal the dichotomy in individual places. That it must be generally present is evident from its large number in the upper part of the segment compared to the smaller number in the lower part.*" All authors, however, emphasized the veins of the leaves too much in their illustrations.

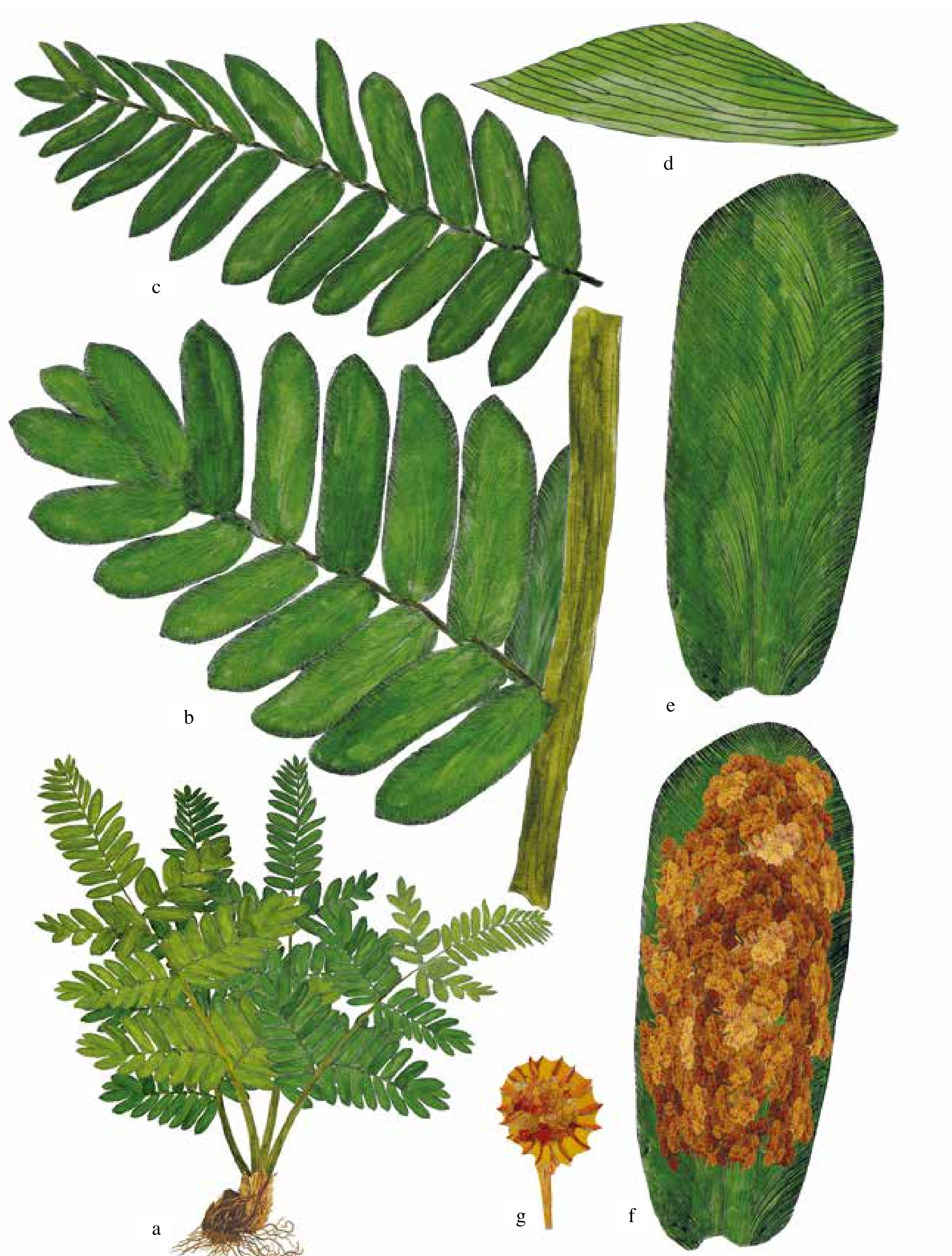
The classification as *Aneimidium klipsteini* could have been valid if it had been a precursor of today's Anemia ferns, mostly found in the Neotropics with very different tropophylls and sporophylls. But this is not the case: fertile and sterile leaves are similar, with the spores covering a large area of the underside of the fertile leaves. Pott, Guhl, Lehmann (2013) also got no further in their monographic work on the clay pits around Duingen (Coppengrave), in which they identified the sterile leaves as *Zamites* sp. or *Otozamites klipsteini,* and the fertile ones as *Cycadolepis* sp. and classified them as Cycadophytes. The genus name *Cyclopteris* can be excluded because it was a fern widespread primarily in the Upper Carboniferous, with similar leaves but large sori, often covered by an indusium which does not apply to those from the Early Cretaceous (Wachtler, 2023).

Now the genus *Elaphoglossum,* the so-called tongue ferns, would be shortlisted. They populate the tropics and subtropics worldwide with around 700 species. They are low-growing ferns, usually composed of an 8-15 cm long, slender petiole which bears a single leaf. The spores develop within a half to three-quarter closed ring-like annulus and cover almost the entire underside of the leaves. *Elaphoglossum* ferns differ therefore considerably due to the lack of a long petiole and the formation of true three-pinnate fronds in the Lower Cretaceous fern.



Dunker, 1846: *Cyclopteris klipsteini* pl. IX, fig. 7, *Cyclopteris mantelli* pl. IX, fig. 4+6

Schenk; 1871, *Aneimidium klipsteini,* fig. XXVI, fig. 7, XXXI fig. 6. The specimens come from Duingen



***Wiedenrothia klipsteini*. Early Cretaceous. Reconstructions**

a. Whole plant; b. Part of a frond; c. Frond; d. Detail of a pinnula with veins; e. Fertile little pinnula upper view; f. Fertile pinnula bottom view; g. Sporangia

Since not one hypotheses applies to this fern from the Wealden of Central Europe, it makes sense to introduce a new genus name and who would be more deserving of being honored with it than the long-time researcher of the Wealden in northwest Germany, Kurt Wiedenroth.

Etymology

Dedicated to the explorer of the Early Cretaceous of northwest Germany Kurt Wiedenroth from Garbsen (Lower Saxony). Throughout his life, his interest in paleontology was primarily plant fossils and ammonites. His collections found their way into, among others, the Berlin Nature Museum, the Dolomythos Museum (Innichen, Italy), and the geoscientific collection of the University of Bremen.

Diagnosis

Fronds tri-pinnate, pinnules leathery and tongue-like, sporangia with annulus located on the underside.

Wiedenrothia klipsteini nov. comb Wachtler 2024

Research history

1846 *Cyclopteris klipsteini* Dunker p. 11, pl. IX, fig. 6

1846 *Cyclopteris mantelli* Dunker p. 10, pl. IX, fig. 4-5
1852 *Cyclopteris mantelli* Ettinghausen p. 10, fig. III, fig. 13-16

1869 *Aneimidium mantelli* Schimper p. 486, fig. XXXI, fig 13

1871 *Aneimidium klipsteini* Schenk p. 213, fig. XXVI, fig. 7, XXXI fig. 6 Duingen

2014 Z*amites sp. Otozamites klipsteinii* Pott, Guhl, Lehmann Pl V, Fig. 6

Holotype

DUING 19, Dolomythos-Museum, Innichen, Italien

Stratigraphy

Early Cretaceous, Bückeberg-Formation (Berriasium-Valanginium)

Description

Whole plant: Low-growing fern with tripinnate tongue-shaped fronds.
Sterile fronds: Individual pinnules located opposite each other on the frond, up to 6 cm long, reaching 3 cm wide, slightly tapering to rounded (DUING 19, holotype, DUING

***Wiedenrothia klipsteini*. Early Cretaceous**
1. Fertile pinnula (DUING 350, Coll. Garbermann); 2. Detail of a fertile pinnula with sporangia (DUING 19, holotype, Coll. Wachtler); all Duingen

Wiedenrothia klipsteini. Early Cretaceous. Whole plant and leaves

1-3. Various fronds (Coll. Wiedenroth, Natural History Museum Berlin); 4. Partially fertile frond (DUING 19, designated holotype); 5-6. Fertile pinnules (DUING 354, Coll. Garbermann); 7. Isolated pinnula (DUING 386, Coll. Garbermann); 8. Pinnula with detail of the delicate veining (DUING 57, Coll. Wachtler, Dolomythos Museum); all Duingen

386). Fitting tightly to the petiole, partially clawing it. Leaf veins delicate, arising from the base of the leaf, dividing sporadically and ending at the edge of the leaflets (DUING 57).

Fertile fronds: Like the sterile fronds, sori are located in larger numbers on the underside of the pinnules (DUING 354, DUING 350, DUING 19). Sporangia with annulus, carrying the spores inside and releasing them when ripe.

Remarks

Wiedenrothia klipsteini from the German Wealden around Duingen is one of those enigmatic plants that appeared out of nowhere in the fossil record, although it has not been possible to draw conclusions about today's descendants. Although several modern-day ferns come close, such as *Elaphoglossum*, the so-called tongue ferns, there are equally separating factors that exclude closer relationships. Although the enigmatic fern *Cyclopteris,* which was widespread in Europe during the Carboniferous period, would actually have great similarities in terms of leaf shape, the similarities end there, as there are too great differences in their fertile systems (Wachtler, 2023).

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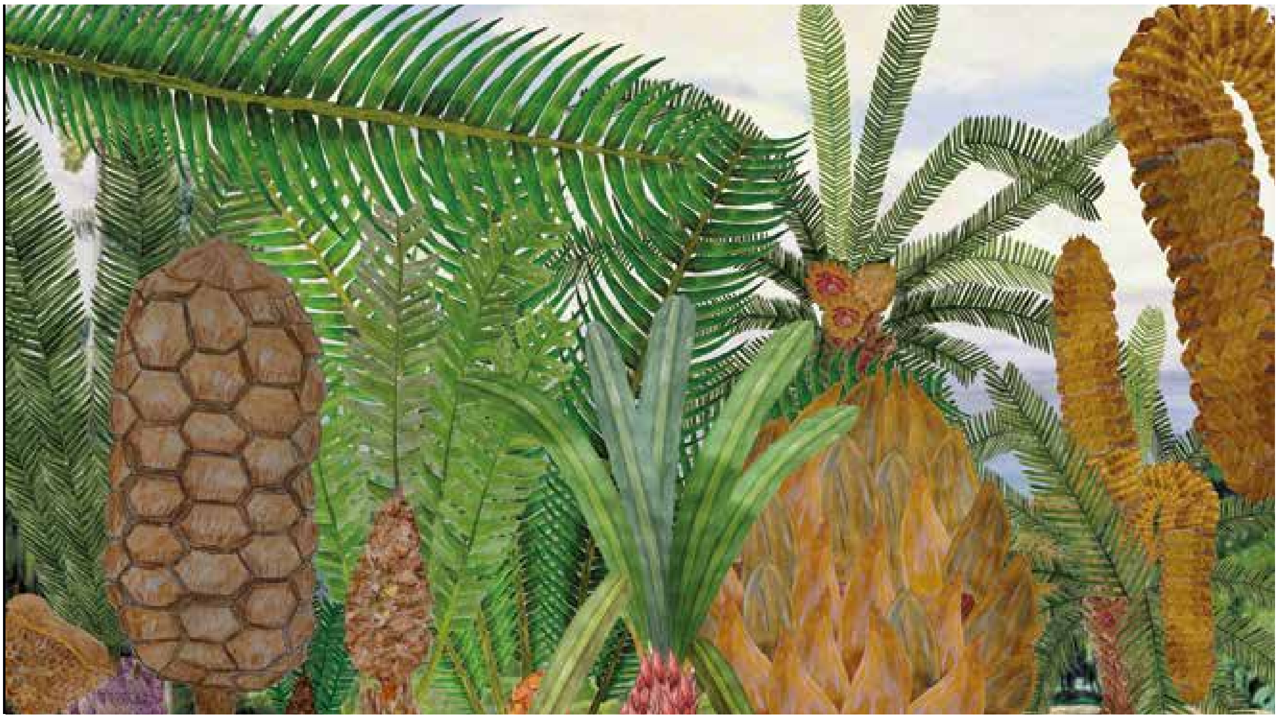

Michael Wachtler

The Lower Cretaceous Flora of Central Europe
A 140 million year old living world

The sediments from the Lower Cretaceous (Berrasian), known as German Wealden, mainly from the clay pits around Duingen, have fascinated researchers since the early 19th century due to their abundance of fossils. Sparsely occurring horsetails (Equisetites sp.), and ferns (*Dennstaedtites geinitzii* nov. comb., as well as *Wiedenrothia klipsteini,* nov. gen.), but a large number of well-preserved gymnosperms such as ginkgos (*Ginkgoites pluripartitus*), conifers (especially *Sphenolepis sternbergiana*, but also T*sugites garbermannii* n. sp., and *Tsugites linkii* nov. comb.), as well as numerous genera of cycads, formed a floral community that was relatively poor in species but abundant in quantity. The highlight is the large number of plant remains from a family, which has been classified under a variety of names, but above all as Bennettitales. Although these were sometimes associated with the beginning of the angiosperms, well-preserved new finds show that they belong to the cycads and are related to today's genus Dioon (*Dioonites dunkerianum, Dioonites lyellanum* nov. comb.). There are also Zamia cycads (*Zamites aequalis, Ctenis humboldtianum, Nilssonia foamburgense, Ceratozamites kurwius* nov. gen.) and sparse ancestors of the genus Cycas (*Taeniopteris beyrichii*). A club moss, *Seppeltia bockii* gen. n. sp. stands somewhat isolated there. Although we are on the arising of flowering plants appearing a little later everywhere, there is no evidence of their appearance or at least possible lines of development in the Lower Cretaceous of Europe. Their rapid appearance must therefore have other reasons, as happened at the Carboniferous-Permian boundary with the equally sudden spread of gymnosperms (conifers, cycads, ginkgos): climate change and, in the case of angiosperms, the emergence of birds as ideal seed dispersers.

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