Early–Middle Triassic (Anisian) ferns from the Dolomites (Northern Italy)

by
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Abstract

After a heyday in the Carboniferous, followed by a strange decline in the Permian, beginning from the Early–Middle Triassic, a new rising of the ferns could be observed. Several families, still widespread today, like the Marattiales, Osmundaceae and also the Lindsaeceae and the tree ferns colonized the Northern hemisphere and help to trace indications of a humid moderately warm climate. This research examines the rise of the Pteridophyta in the Alps and puts them in a context with other European Triassic fern associations. Some of them, like *Anomopteris, Neuropteridium, Danaeopsis, Cladophlebis*, play a major role in large parts of the Northern hemisphere. Due to some differences with the Middle Triassic fern *Danaeopsis marantacea* Anisian *Danaeopsis dolomitica n.sp* was classified as a new species. Others can till now be identified as endemic for the Alps, in Early–Middle Triassic times a part of the supercontinent Pangaea near to the ocean. This is valid for ferns like *Gordonopteris lorigae, Ladinopteris kandutschi*i, probably belonging to the Marattiales or the Osmundaceae, and *Wachtleria nobilis*, an interesting precursor of the Lindsaeaceae.

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Key words: fossil ferns, Dolomites, Italy, Early-Middle Triassic, Anisian

A fern community in the Early-Middle Triassic of the Dolomites: a. *Danaeopsis dolomitica*; b. *Neuropteridium elegans*; c. *Ladinopteris kandutschii*; d. *Cladophlebis rhombifolia*; e. *Wachtleria elegans*; f. *Gordonopteris lorigae*; g. *Neuropteridium voltzii*; h. *Anomopteris mougeotii*

Especially in the area around the Piz da Peres in the Pragser Dolomites, with the surrounding mountains like the Kühwiesenkopf, Hochalpenkopf and Fünffingerspitze, in several slightly time different layers, well preserved fossil plant beds are found. In the lower strata, Cycadophyta, Sphenophyta, Coniferales, and Lycodophyta form with the Filicales a homogeneous unit, in the uppermost layers the variegated Lycophyta-association composed of *Lycopia dezanchei, Isoetites brandneri, Lepacyclotes bechstaedtii, Selaginellites leonardii,* and *Selaginellites venier*i mostly disappear, whereas new fern genera like *Anomopteris mougeotii, Ladinopteris kandutschii* and *Wachtleria nobilis* were recorded in fair amounts. *Neuropteridium elegans, Neuropteridium voltzii, Danaeopsis dolomitica, Gordonopteris lorigae* and *Cladophlebis rhhombifolia* are widespread everywhere in Anisian sediments of the Dolomites.

The Marattiales

The Marattiaceae are represented today by about 260 extant species placed today in six genera: *Angiopteris, Christensenia, Danaea, Eupodium, Marattia* and *Ptisana.* They have a long fossil record beginning from the Devonian–Carboniferous border until the present and have changed little over the whole of this period. The Marattiaceae grow in tropical to subtropical forests where the temperature and air humidity remain high throughout the year.
The leaves are generally large and leathery, and from one- (*Danaea*) to three-pinnate. With its sometimes over 6 m long fronds, the group of Marriataceae present problems for palaeobotanists due to the necessarily fragmented nature of most specimens. The sporangia –and this is a distinction from all other ferns with the exception of the Ophioglossales– are usually fused in round or elongate synangia, where a thin part of the sporangium dries and shrinks to form a pore through which the spores fall, except in Angiopteris where the sporangia are almost free. Fertile parts of the Marattiales are known from the Carboniferous–Permian as *Scolecopteris*, and in the Triassic as *Asterotheca.* Usually three to five, but mostly four sporangia, lacking an annulus, are fused there to one synangium. They are attached on the lower parts of each leaflet and, due to the fact of the higher resistance of the fossilised large, thick-walled synangia, they are usually also clearly visible.
The only fern from the Early–Middle Triassic (Anisian) Dolomites that can be with certainty inserted in the order of Marattiales is *Danaeopsis*. The extant genus Danaea is distinguished from other genera by long synangia that are sunken into a thickened lamina of the fertile fronds. The fronds are dimorphic, with the fertile pinna more contracted and clearly stalked, while sterile pinna are sessile. We have a beginning with *Danaeopsis dolomitica* followed by the heyday with *Danaeopsis arenacea* in the Middle Triassic (Ladinian) with thier huge fronds, clearly evidencing two rows of sporangia sunken between the veins on their lower parts. In the Anisian of the Dolomites they were not widespread, and usually have smaller fronds.

The Osmundaceae

The Osmundales are regarded as a primitive group intermediate between eusporangiate and leptosporangiate ferns because they possess a mixture of sporangial features from both types. Today, the family is represented by the three genera Osmunda, Todea and Leptopteris. Fertile and sterile pinnae are usually markedly different, with the sporangia –scattered on the abaxial surface– borne on highly reduced non-photosynthetic pinnae. The first representatives of the Osmundales are recorded from the Carboniferous–Permian border with some *Todites* species (*Todites muelleri)*. They were characterised by tripinnate fertile fronds with deeply dissected lobate pinnules and round apexes.
In the Early Triassic the presumed progenitors of the Osmundaceae like *Anomopteris mougeotii, Gordonopteris lorigae, Neuropteridium* and *Cladophlebis rhombifolia* were variegated and bear distinctive features. *Anomopteris mougeotii* can be regarded as the most cosmopolitan representative pterophyta in the Lower Triassic, extending from Spain to China. Strangely, this widespread fern was very uniform and without apparent sub-species covered large areas of the Northern hemisphere in the shadow of the omnipresent conifers. Due to the small desiccated leaves, *Anomopteris mougeotii* was probably adapted for longer periods of dryness.

Today‘s ferns with an old fossil record

a. Today‘s *Danaea alata*. Fertile part with the sunken synangia covering all the plant-width. b-c. The fern *Marattia laevis.* Note the different venation on fertile and sterile leaflets. d-e. Extant *Todea barbara*-ferns. The sporangia cover the lower side of the leaflets; f-g. *Todea barbara* a fern belonging to the family of the Osmundaceae.

Osmunda regalis, the kingfern is one of the most representative fern of this genus

Lindsaea stricta a fern growing in the Amazonian jungle. First representatives we have in the Early Triassic of the Dolomites.

Another representative of the Osmundaleans in the Early Triassic, *Gordonopteris lorigae* from the Dolomites, also has small leaves, but apparently not as dwarfish as *Anomopteris mougeotii*, unlike which it was also tripinnate and had no aphlebia. Ferns probably also belonging to the Osmundaceae were *Neuropteridium* and *Cladophlebis*. *Neuropteridium* is recorded in two subspecies *N. voltzii* and *N. elegans* in the Dolomites, appearing in almost equal quantities (Wachtler, 2011). It was low-growing with a bulbous stem and very distinct fertile and sterile fronds. Of all this fern genus, *Cladophlebis* is the most difficult to obtain an exact insertion. Similar fronds are described all over the Triassic–Jurassic in many sometimes confusing forms like *Cladophlebis, Anotopteris* or *Acrostichites*. Because the leaflets evidence a narrow mid-rib as is typical for *Cladophlebis,* this genus name was accepted.
The insertion of *Ladinopteris kandutschii* is unclear, but it probably has to be regarded as Osmundales. The leaves are sometimes leathery, the sporangia deeply sunken on the lower part of the leaf and aggregated around the mid-vein.

The Lindsaeaceae

Wachtleria nobilis was probably an ancestor of the Lindsaeaceae, and certainly has a striking resemblance to this tropical to subtropical fern family inserted in the order of Polypodiales. The Lindsaeaceae comprise about 200 species distributed across South America, East Asia and New Zealand. The main genus *Lindsaea* is characterised by up to 30 cm long slender and erect stipes. The fronds were simple to dissect; veinlets free or sometimes anastomosing, the lamina margin thickened and decurrent. The sori were arranged towards the upper and outer margin and have the indusium attached to the disc. *Wachtleria nobilis* evidence all the features of today's Lindsaeaceae with their slender stipes and fertile leaves with sori grouped on the outer margins of the leaves.

Systematic Paleontology

Class: Filicopsida BOWER, 1899
Order: Marattiales Prantl, 1874
Family: Danaeaceae Agardh, 1822
Genus *Danaeopsis* Heer 1864

Taxonomic notes

In 1864, the German palaeontologist August Schenk introduced the name *Danaeopsis marantacea,* referring to Oswald Heer (1864) as the first describer, who without a description or a diagnosis had only chosen the name *Danaeopsis* as a possibility for this fern. Following the nomenclature rules, the first given name *Marantoidea* (1827) from the German Georg Friedrich Jaeger took priority. Unfortunately, in the meantime the genus name *Danaeopsis* for this Triassic character fern became so deeply rooted and widely known that it was generally accepted (Zijlstra et al., 2010).

Danaeopsis dolomitica n. sp. WACHTLER 2016

Type horizon and age

Dolomites, Early-Middle Triassic (Anisian)

Holotype:

PIZF 123

Paratype:

PIZF 561 (Fertile pinnula)

Material

PIZF 33, 257, 1416, 292, PIZ 230, 564, 566

Repository

Coll. Wachtler, Dolomythos Museum, Innichen, Südtirol

Etymology

After the Dolomites, where this fern was first found.

Locality

All over the Dolomites, especially on Piz da Peres and Kühwiesenkopf

Diagnosis

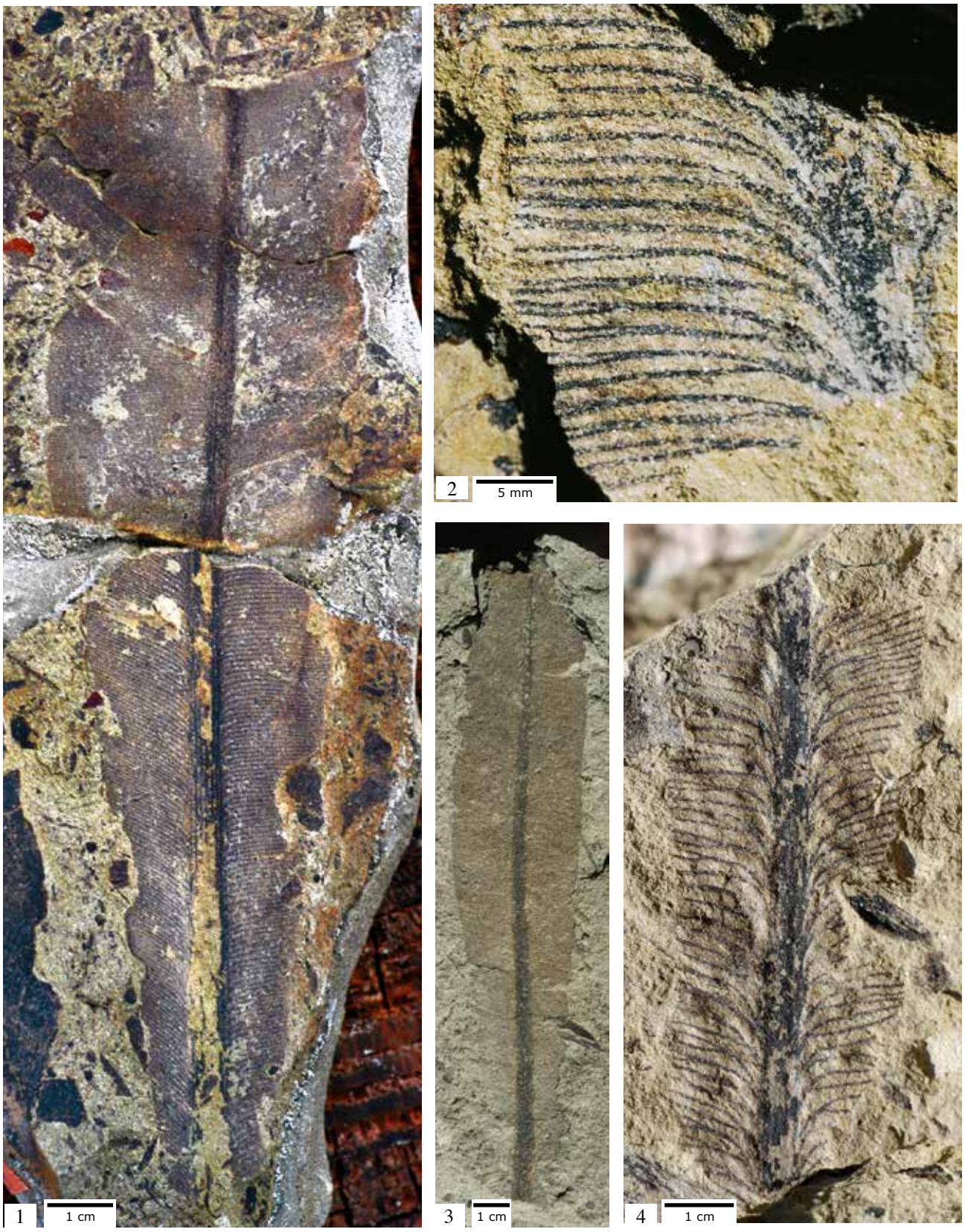
Bipinnate fern with dimorphic fronds. Sterile pinnae forking usually once, sometimes twice. Fertile, evidencing on the lower part two rows of sporangia covering the whole blade.

Description

Fronds: Bipinnate, entire-leaved with sterile pinnae bigger than fertile ones.
Sterile pinnules: Lateral leaves from 10 to 20 cm, and up to 4 cm in width (PIZF 33). Secondary veins arising directly from a broad midrib (2–4 mm wide, forking usually only once at the beginning and only in rare cases twice (PIZF 257, 123, 292). The veins reach the margin more or less perpendicularly at a concentration that varies in the specimens from 8 to 16 cm.
Fertile pinnules: Fertile pinnae similar to sterile, but smaller, with a short stipe, holding on the lower part between each pair of secondary veins, two rows of sporangia. This is inserted over almost the whole pinna.

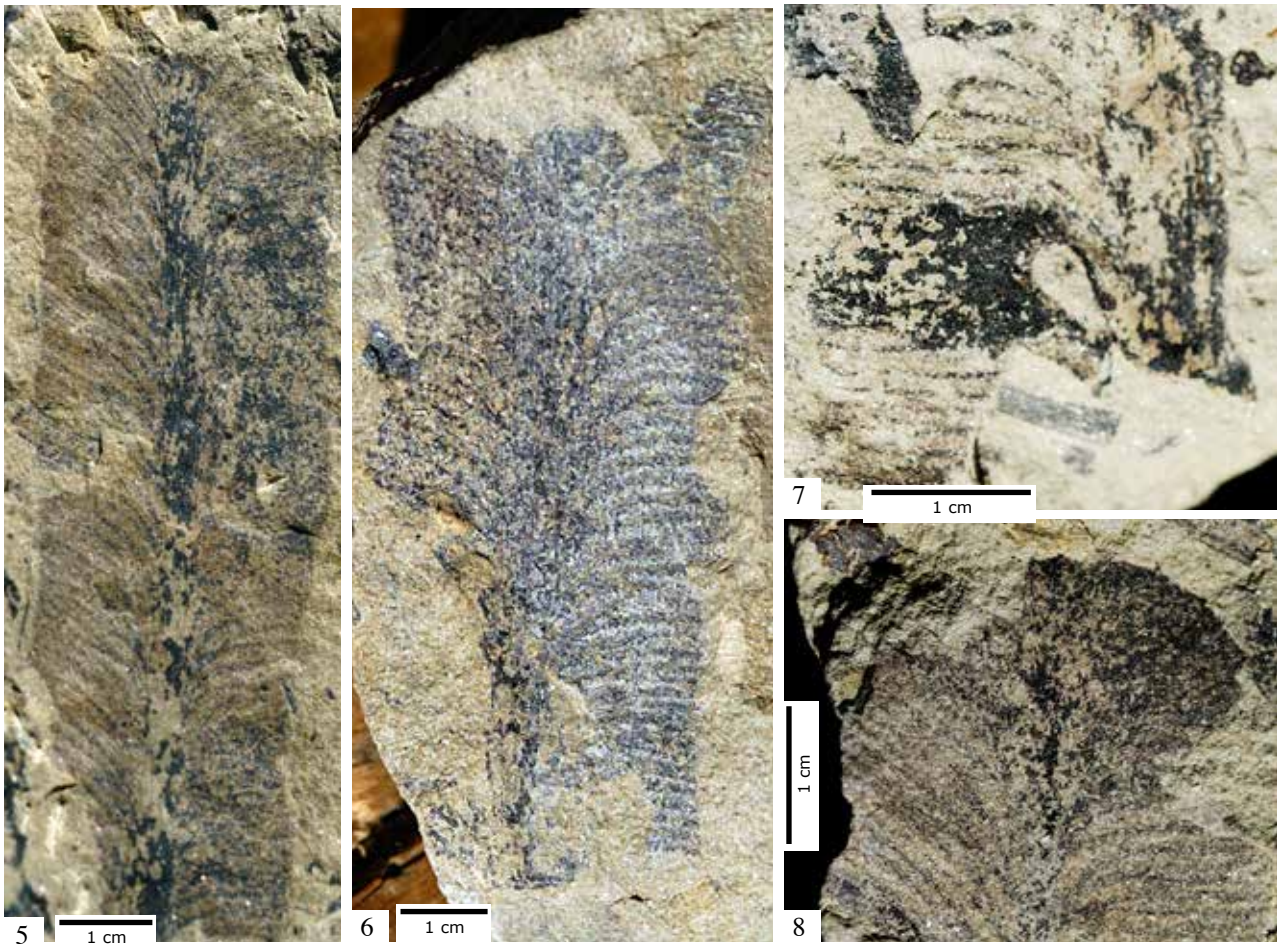
Remarks

Anisian *Danaeopsis dolomitica* resembles in the structure of their bipinnate fronds, the dimorphic fertile and sterile leaves and their forking veins Ladinian *Danaeopsis marantacea*. But there are also conspicuous differences. One of them is the noticeably smaller fronds, reaching in *Danaeopsis marantacea* as much as 1 m width (in the German locality of Ilsfeld isolated pinnae are recorded with a size of 40–50 cm and a width of 7 cm), whereas in *Danaeopsis dolomitica* the largest reach 20 x 5 cm, but they usually have a size of 10 x 3 cm). Also the venation is different (Wachtler, 2011). They fork much more in *Danaeopsis marantacea*, evidencing in some specimens, especially on the upper part of the pinna, a reticulate venation, whereas in the older *Danaeopsis dolomitica* the veins fork only at the base and then only rarely again time (Wachtler, 2016). All these features -independently a ten million years separation- make it reasonable to introduce a new species name. Evolving trends in the direction of *Danaeopsis marantacea* can be easily undertaken. The biggest difference from the common cycadalean fronds otherwise lies in their forking venation. In the Permian we have no clearly identified ancestor.



***Danaeopsis dolomitica* n. sp. (Early-Middle Triassic) Sterile and fertile leaves**

1. Part of a pinna (PIZF 33); 2. Detail of a pinna, forking two times (PIZ 257*);* 3. Part of a pinna (PIZF 1416*);* 4. Sterile pinna (Designed holotype PIZ 123*,* all Coll. Wachtler, Dolomites, Anisian)



***Danaeopsis dolomitica* n. sp. (Early-Middle Triassic) Fertile fronds**

5-8. Fertile pinnules (Paratype PIZ 561, 230, 564, 566, all Coll. Wachtler, Dolomites, Anisian)

The fern appeared apparently from nothing and so *Danaeopsis dolomitica* represents the oldest known species.

About 20 species of the fern genus *Danaeopsis* have been encountered, reaching a global distribution, and ranging from the Early Triassic to the Rhaeto-Liassic. Parental affinities were established with the Marattiales and its living sub-group Danaea (Christenhusz, 2007). Their dimorphic leaves, the smaller fertile pinnae, attached to the main rachis with a short stipe, the synangia inserted over the whole leaf in two rows, and their entire pinna, connected in a sessile way to the rachis, are indications of close parental affinities.

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***Danaeopsis dolomitica* n. sp. (Early-Middle Triassic) Reconstructions**

a. Whole plant, b. Single frond, c. Sterile pinna (PIZ 257), d. Fertile part of a pinna (PIZ 561), e. Synangia arranged in two rows

Systematic Paleontology
Class: Filicopsida BOWER, 1899
Order: Osmundales BERCHTOLD & PRESL, 1820

Genus *Anomopteris* BRONGNIART 1828

Taxonomic notes

This fern was named by Adolphe Th. Brongniart, one of the pioneers of palaeobotany, as *Anomopteris* (anomalous fern), because for him it differed from all recent and fossil ferns.

Anomopteris mougeotii BRONGNIART 1828

Type horizon and age

Dolomites, Early-Middle Triassic, Anisian, Pelson-Illyrian (243 - 241 Mya)

Description

Fronds: The bipinnate fronds may reach a length of 1 m and are supported by a thick rachis (about 5–10 mm), from which long slender, linear pinnae (ca. 20 cm) arise perpendicularly. Typical leaves, called aphlebiae, at the base of each pinna are a distinguishing characteristic. Complete fronds may reach a length of 1 m and 20–40 cm wide.
Leaves: Small pinnules, closely spaced but not in contact, arise perpendicularly and vary in size from 1.5 x 2 mm to 2 x 3 mm. Venation is usually difficult to observe. Secondary veins arise from a strong midrib, usually forking once.
Fertile leaves: The lower surface of the fertile parts of the pinnules is covered with sporangia. Spores round, trilete, 25–40 µm in diameter with a punctate exospore.

Diagnosis, remarks and ecology

The botanical affinity of this fern remains unclear, although the fertile pinnules including the spores have all the characteristics of the Osmundaceae, with the exception of an aphlebia at the base of each pinna that has never been recorded in the Osmundaceae. Juvenile fronds were in the past described as *Pecopteris sulziana* and only meticulous research demonstrated that it was only a juvenile growing stage of *Anomopteris mougeotii* (Grauvogel & Grauvogel, 1980).
Anomopteris mougeotii can be regarded as the characteristic fern not only of the European Early–Middle Triassic, but also the complete Northern hemisphere at that time. It is common in the German Buntsandstein, recorded in extraordinarily complete specimens from the Vosges and other localities in France (Grauvogel-Stamm & Grauvogel, 1980), Spain (Juárez & Wachtler, 2015), found in the Dolomites (Konijnenburgh – van Cittert J.H.A et al. 2006, Wachter, 2011), and extends as far as the Lower Triassic of China (Wang et al., 1978).
It is abundant in the Anisian strata from the Dolomites. Interestingly, *Anomopteris* was never recorded in the lower parts of the Kühwiesenkopf but is widespread in the upper layers. The reason is not completely clear because other ferns like *Neuropteridium* and *Gordonopteris* are well inserted in the lower floras. More than other plants, it could be defined as a strata-marker for Early–Middle Triassic layers in the Northern hemisphere.

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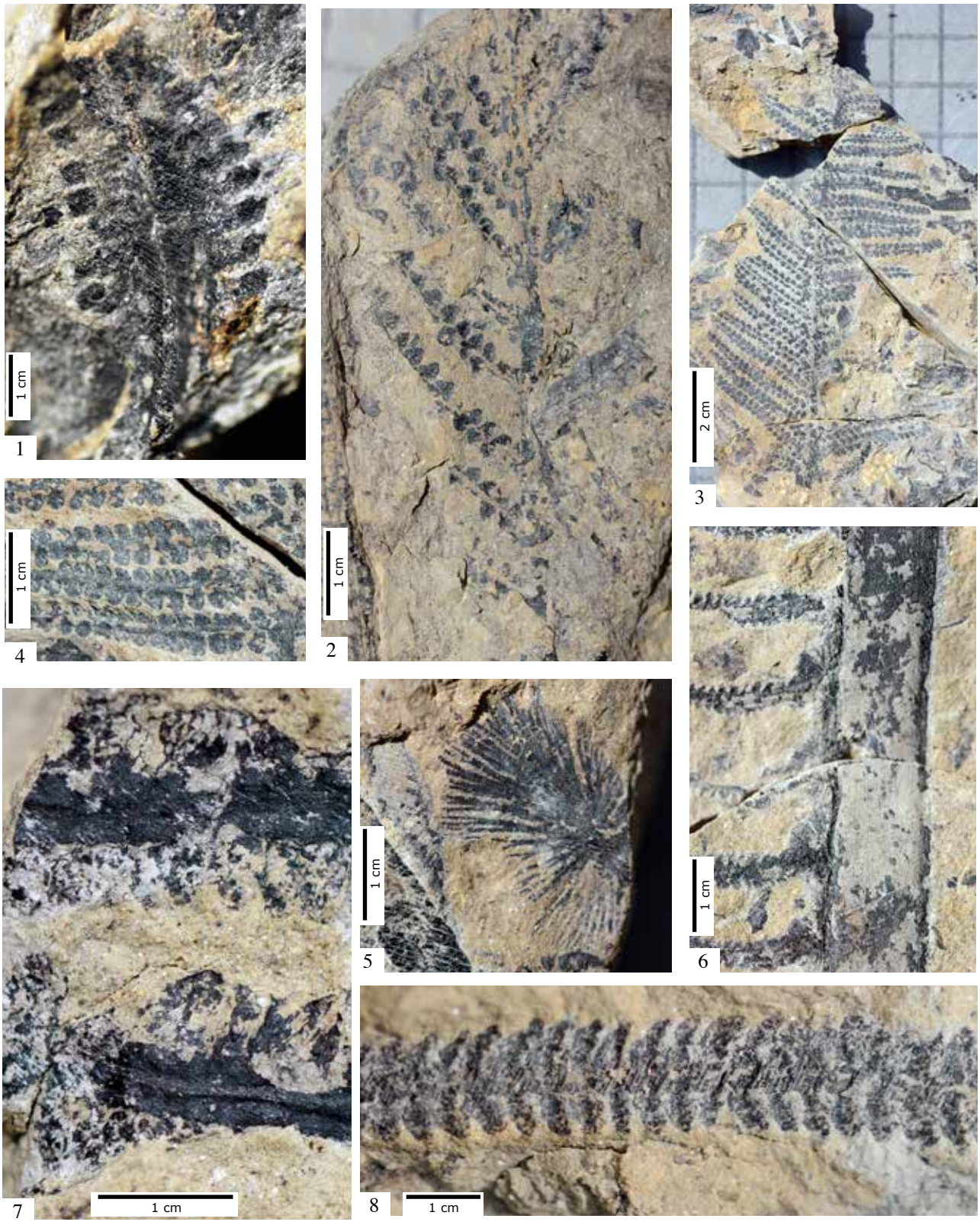
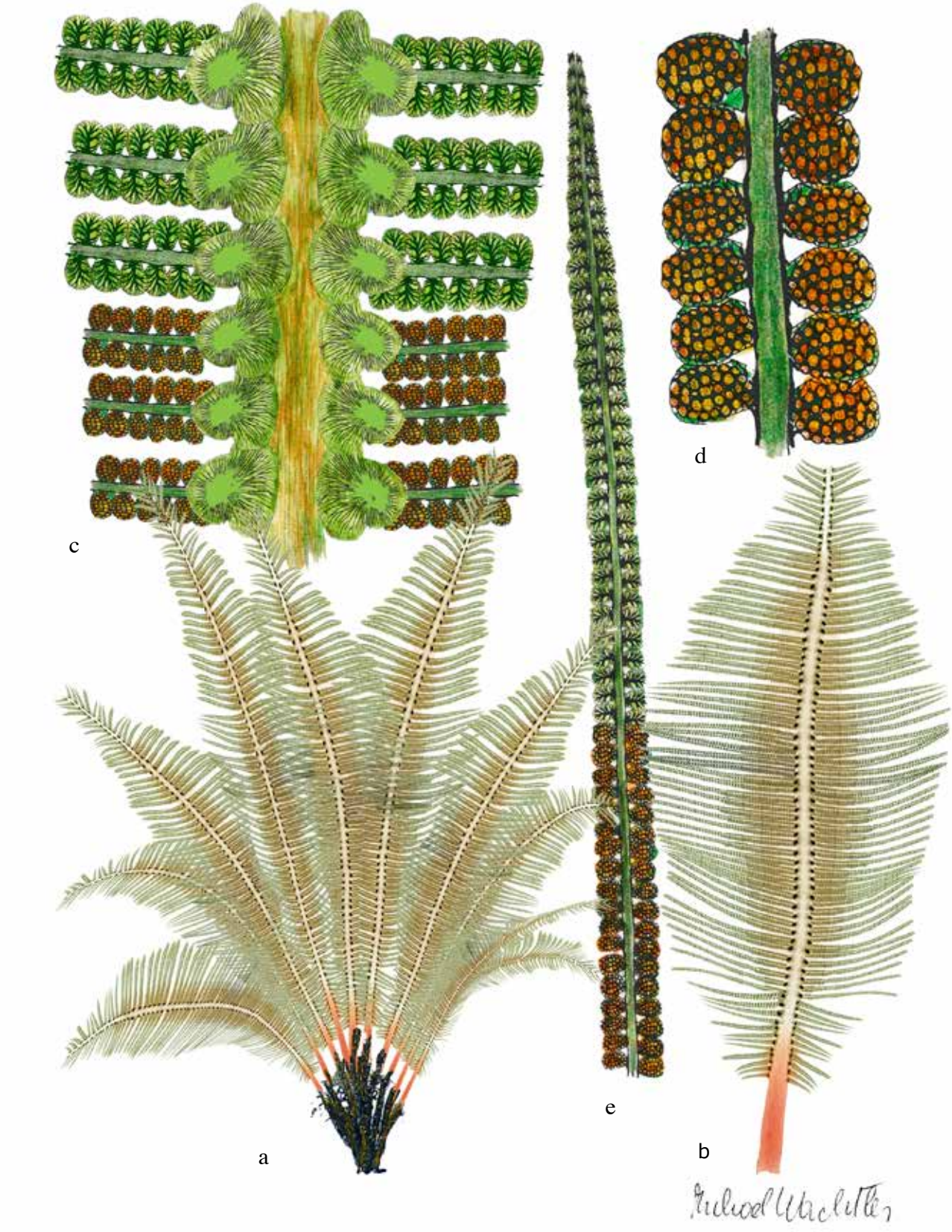


Anomopteris mougeotii (Early-Middle Triassic) Sterile and fertile leaves

1. Juvenile frond with enrolled pinnae (PIZF 107); 2. Juvenile frond (*Pecopteris sulziana*) (PIZF 240); 3-4. Juvenile frond and detail (PIZF 210); 5. Typical aphlebia attached on the main rachis (PIZF 208); 6. The consistent main rachis and the lateral pinnae (PIZF 135); 7. Fertile pinnules (PIZF 236); Aggregation of fertile pinnules (PIZF 142 all Coll. Wachtler, Dolomites, Anisian)

Anomopteris mougeotii (Early-Middle Triassic) Sterile and fertile leaves

1. Mainly entire frond fragment, Kühwiesenkopf (KÜH 1197*); 2*. Detail showing the aphlebia on both sides of the rachis (6 x 2 cm), (Piz da Peres PIZ 256, all Coll. Wachtler, Dolomites, Anisian)



***Anomopteris mougeotii* (Early-Middle Triassic) Reconstructions**

a. Whole plant, b. Single bipinnate frond, c. Rachis and aphlebia upper part sterile leaves, lower fertile, d. Fertile part of a pinnae, e. Fertile pinnae.

Systematic Paleontology

Class: Filicopsida BOWER, 1899
Order: Osmundales BERCHTOLD & PRESL, 1820

Gordonopteris VAN KONIJNENBURG-VAN CITTERT, KUSTATSCHER, WACHTLER, 2006

Taxonomic notes

The genus *Gordonopteris* was first found on the Kühwiesenkopf and is named after the Scottish researcher Marie Ogilvie Gordon, one of the pioneers of Triassic palaeobotany in the Dolomites.

Gordonopteris lorigae VAN KONIJNENBURG-VAN CITTERT, KUSTATSCHER, WACHTLER, 2006

Etymology

Honouring Prof. Dr Carmela Loriga Broglio, who was the first leader of the project on the fossil fauna and flora from Kühwiesenkopf.

Type horizon and age

Dolomites, Lower to Middle Triassic, Anisian, Pelson-Illyrian (243 - 241 Mya)

Holotype

KÜH 633, (Coll. Wachtler, Natural History Museum Südtirol, Bozen)

Description

Fronds: This fern is characterised by its tripinnate fronds, which probably exceeded 1 m in length, being about 1 m long and 20 cm wide. The rachis of the first order broad, smooth. Main pinnae arising alternately to sub-oppositely at angles of 45–60 degrees, pinnae of the second order usually growing sub-oppositely at 60–90 degrees. The pinnae of the first order relatively long, with the neighbouring pinnae in close contact, but never overlapping. Rachis of first order about 12 mm wide, smooth. Second-order pinnae arising at 60–90 degrees, relatively short up to 4–5 cm long, in close contact, but also never overlapping. Evidence suggests its classification as a tree fern.
Leaves: Pinnules of the third order are small (usually c. 2–3 x 2–3 mm), attached by their entire base, rounded in outline with a neuropterid venation forking once after branching from the midvein.
Fertile leaves: Fertile pinnules are distinguished by a reduced, completely rounded lamina, with more or less rounded sporangia on the lower side. Spores globose, trilete, 43–62 µm in diameter, with a finely punctate exine.

Diagnosis, remarks and ecology

The fern *Gordonopteris* is one of the common elements in the Early–Middle Triassic flora of the Dolomites Konijnenburgh-van Cittert et al., 2006, Wachtler, 2011). Beautiful and well-preserved specimens are found everywhere, showing in detail all parts of the frond and also the subtle venation of the small pinnae. Its botanical affinity is not yet resolved, but the arrangement of the sporangia suggests a relationship with the Osmundaceae or the Marattiales. A difference from another common Early–Middle fern *Anomopteris,* apart from the missing aphlebia, is that the frond is tripinnate and not bipinnate.

Citations

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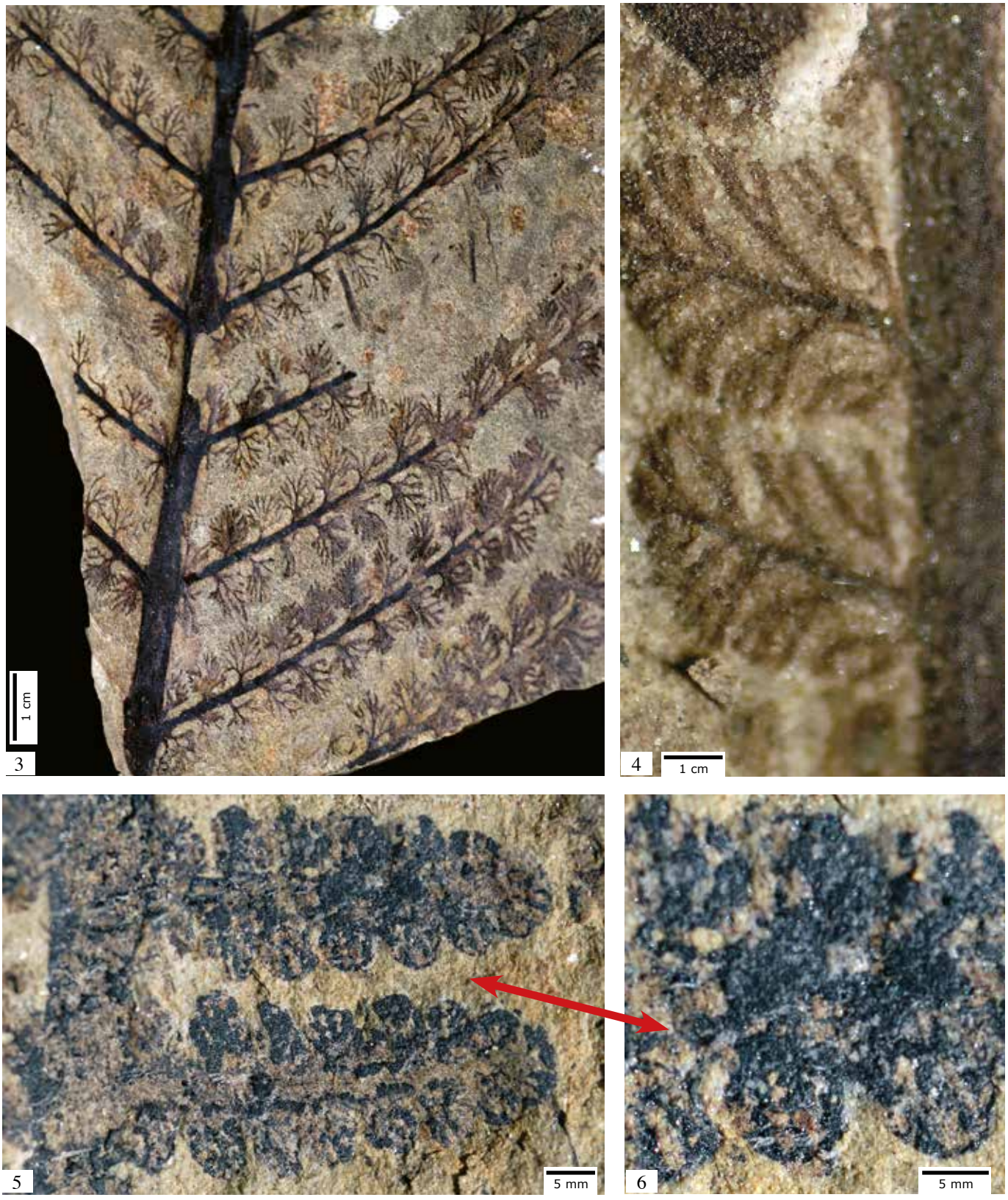
Wachtler, M., 01/2011): Ferns and seedferns from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, 57-79, Innichen

***Gordonopteris lorigae* (Early-Middle Triassic) Sterile and fertile leaves**

1 - 2. Especially well-preserved mainly complete frond and detail of the fertile parts (46 x 37 cm) (*Holotype* KÜH 633) Coll. Wachtler, Anisian, Kühwiesenkopf



***Gordonopteris lorigae* (Early-Middle Triassic) Sterile and fertile leaves**

3. Especially well-preserved section of a sterile frond (10 x 8 cm) (PIZ 252); 4. Two pinnulae showing the vein-forking habitus (PIZ 116); 5. Fertile pinnulae (5 x 2 cm) (PIZ 239*);* 6. Detail of sporangia on the surface (2 x 2 cm) (PIZ 239) All Coll. Wachtler, Anisian, Piz da Peres

***Gordonopteris lorigae* (Early-Middle Triassic) Sterile and fertile leaves**

a. Suggested whole plant; b. Single tripinnate frond (PIZ 252); c. Fertile pinnae (PIZ 239); d. Sterile pinnae (PIZ 116)

Systematic Paleontology
Class: Filicopsida BOWER, 1899
Order: Osmundaceae

Genus *Ladinopteris* WACHTLER 2011

Taxonomic notes

Ladinopteris is named after the Ladins, the people who live in this area.

Ladinopteris kandutschii WACHTLER 2011

Type horizon and age

Dolomites, Early-Middle Triassic, Anisian, Pelson-Illyrian (243 - 241 Mya)

Holotype

PIZF 1101 (Coll. Wachtler, Natural History Museum Südtirol, Bozen)

Etymology

Ladinopteris kandutschii is named after Georg Kandutsch, an Austrian palaeobotanist and researcher.

Description

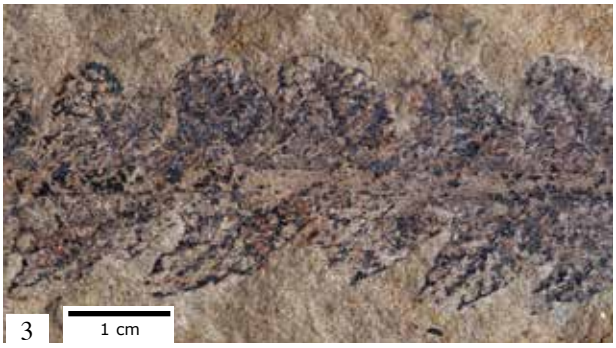
Plant: Robust, leathery bipinnate fern with a consistent hairy rachis from which long slender, linear pinnae arise perpendicularly. Entire fronds may have reached lengths of over 1 m.
Sterile fronds: Bipinnate ovate to elliptic frond. Pinnules small, triangular to oblong with a strong mid-vein from which almost invisible lateral veins originate, forking once. The rachis is 1–1.5 cm thick at the base, subtle hairs covering the stipe. Secondary pinnae arise perpendicularly, pointing slightly upwards, narrowly oblong, 20–30 cm x 8–10 mm wide. Most of the leaves are apparent, seldom overlapping.
Pinnules: The rachis of the single leaves is 1–1.5 mm wide and relatively small, pinnules are sessile, oblong to triangular (2–4 x 1.5–2.5 mm), arising perpendicularly from the rachis. The venation consists of a pronounced mid-rib, secondary veins (in the majority of cases four on each side of the pinnules) arising from the mid-vein and forking once. They end near the margin, but are mostly undeveloped. Margin pointed to slightly rounded.
Fertile fronds: Sori or sporangia on the under-surface. Sporangia numerous (20–40 on each pinnule), large, spherical, clustered along the veinlets of the pinnules.

Diagnosis, remarks and ecology

Bipinnate fern with hairy rachis, secondary pinnae arising perpendicularly. Pinnules small and sessile with a typical consistent sunken mid-rib and almost invisible lateral veins (Wachtler, 2011).
Ladinopteris kandutschii was probably well adapted to shady sites under the conifer vegetation. With their sunken mid-ribs and leathery appearance, the fronds show a superficial resemblance to *Anomopteris mougeotii.* However, the pointed triangular leaves are completely different from the small rounded *Anomopteris* pinnule. Maybe some relationship can be found in the Triassic fern *Asterotheca*, widespread in the German Ladinian. Another consistent difference is the complete absence of aphlebiae. It is also difficult to determine the relationship with any extant fern species. The arrangement of the sporangia otherwise tends more to the ancient group of the Marattiales.

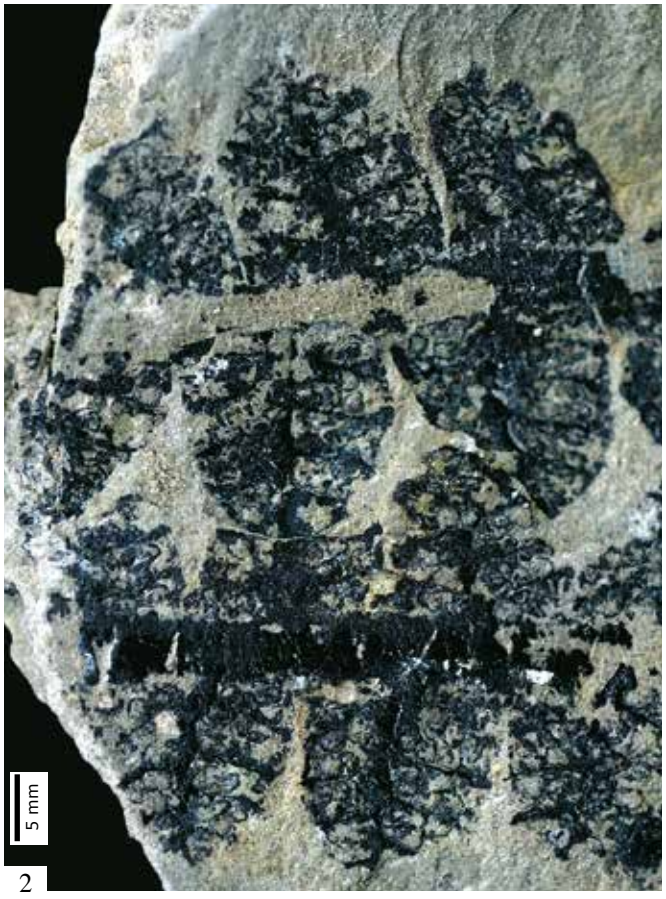
Citations

Wachtler, M., (01/2011): Ferns and seedferns from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, 57-79, Innichen.



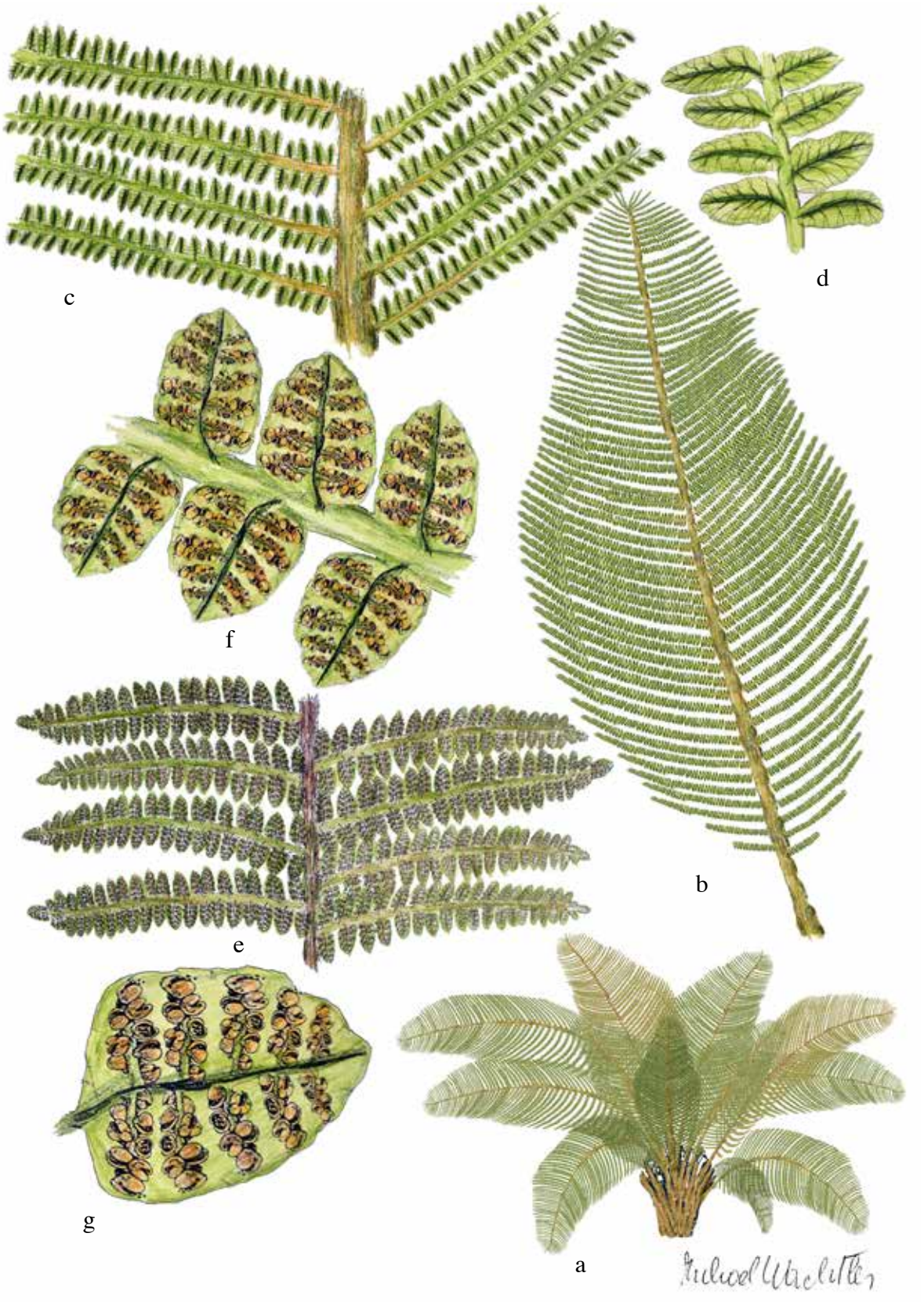
***Ladinopteris kandutschii* (Early-Middle Triassic) Sterile and fertile leaves**

1. Mainly entire bipinnate frond (60 x 40 cm) and details of the pinnules with a strong midrib and the hairy rachis (8 x 5 cm) (Piz da Peres, Holotype PIZF 1101); 3. Several pinnules, rounded on the upper side, pointed on the lower (PIZ 219 3 x 1.5 cm) 4. Several pinnules (15 x 5 cm) (PIZ 246), All Coll. Wachtler, Anisian, Piz da Peres



***Ladinopteris kandutschii* (Early-Middle Triassic) Sterile and fertile leaves**

1. Part of a frond (15 x 10 cm) (Paratype PIZ 49); 2. Fertile pinnules (PIZ 249 Paratype); 3. Part of a sterile terminal frond showing the vein system (PIZ 37) All Coll. Wachtler, Anisian, Piz da Peres



***Ladinopteris kandutschii* (Early-Middle Triassic) Reconstructions**

a. Whole plant; b. Single bipinnate frond (PIZ 1101); c. Sterile pinnae (PIZ 37); d. Sterile leaflets; e. Part of a fertile frond (PIZ 49); f. Fertile pinnules (PIZ 249); g. Fertile pinnae.

Systematic Paleontology

Order Filicales, Bower, 1899
Family Osmundaceae Berchtold & Presl, 1820

Neuropteridium SCHIMPER 1879

Taxonomic notes

The genus was recognised for the first time by Brongniart (1828) in the Vosges as *Neuropteris elegans*, but in 1844, Schimper and Mougeot included all the previously known Triassic *Neuropteris* species in the genus *Neuropteridium* to distinguish them from the Carboniferous *Neuropteris* species, which are characterised by bipinnate fronds. The fertile parts were for a long time thought to be a separate species, known as *Scolopendrites* (Goeppert, 1836). The connection between *Scolopendrites* and *Neuropteridium* was only recognized in 1879 and 1890 by Wilhelm Schimper and August Schenk. In the Dolomites are known two different species of *Neuropteridium: Neuropteridium elegans* and *Neuropteridium voltzii.* They are equally widespread and common.

Neuropteridium elegans BRONGNIART 1828, SCHIMPER 1879

Fertile pinnules called *Scolopendrites grauvogelii,* Van Konijnenburg-Van Cittert, Kustatscher, Wachtler, 2006

Type horizon and age

Dolomites, Europe, China, Lower to Middle Triassic, Anisian, Pelson-Illyrian (243 - 241 Mya)

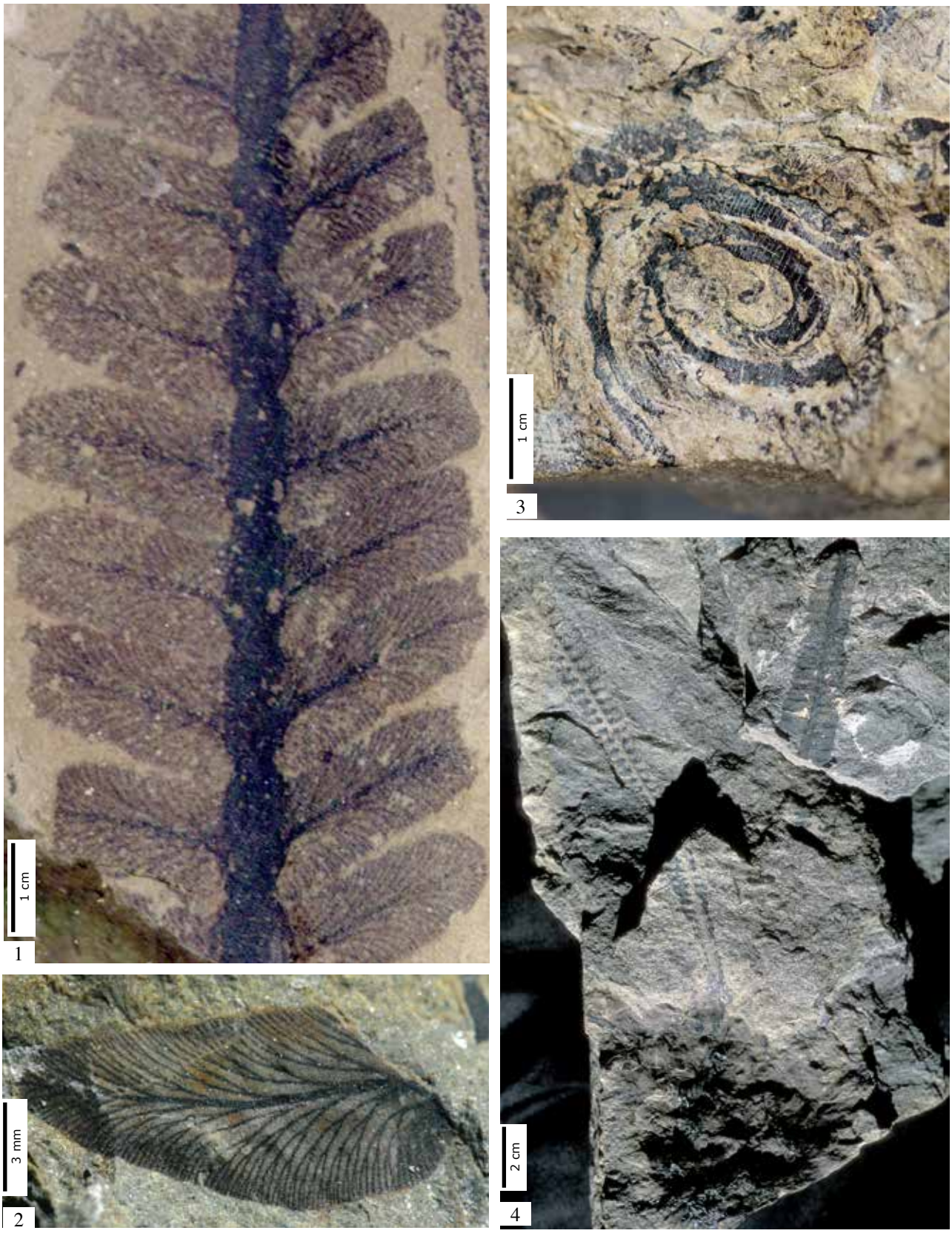
Rhizom: Global to ovoid, up to 8–12 cm long, about 5 cm wide, from which sprout the simply pinnate fronds. The number of fronds is usually small, from 6 to 10.
Fronds: The fertile fronds were up to 15–25 cm long, characterised by a 2–3 cm long petiole and an up to 20 cm long stipe, from which the pinnules arise more or less perpendicularly. Basal pinnules small (from 4 x 2–3 mm) but increase rapidly in size, before decreasing again towards the apex. The rachis in the middle part of the frond is c. 3 mm thick while it decreases to 1 mm towards the apex.
Pinnules: Leaves with typical neuropterid venation, arising more or less perpendicularly from the rachis with a clear mid-rib that extends about one-half to two-thirds of the pinnule length and the secondary veins that diverge and fork up to three times. Usually contracted at their base. The leaves are usually 2–3 cm long and 8–12 mm wide.
Fertile pinnules: Of *Scolopendrites grauvogelii*-type. Simply pinnate, fertile fern fronds arising from a rhizome; fronds with relatively narrow rachis and densely placed hanging pinnules. The rachis is generally narrow (0.6–3.0 mm). The complete lower side of pinnules is covered with globular sporangia. The sporangia are more or less circular in outline, with a diameter of around 300–400 µm. Spores trilete, circular in equatorial outline, c. 35–45 µm in diameter, exospore scabrate to granulate.

Neuropteridium voltzii BRONGNIART 1828, SCHIMPER 1879

Fertile pinnules called *Scolopendrites scolopendrioides*, (Brongniart, 1828; Goeppert 1836), comb. nov. (Van Konijnenburg-Van Cittert, Kustatscher, Wachtler, 2006)

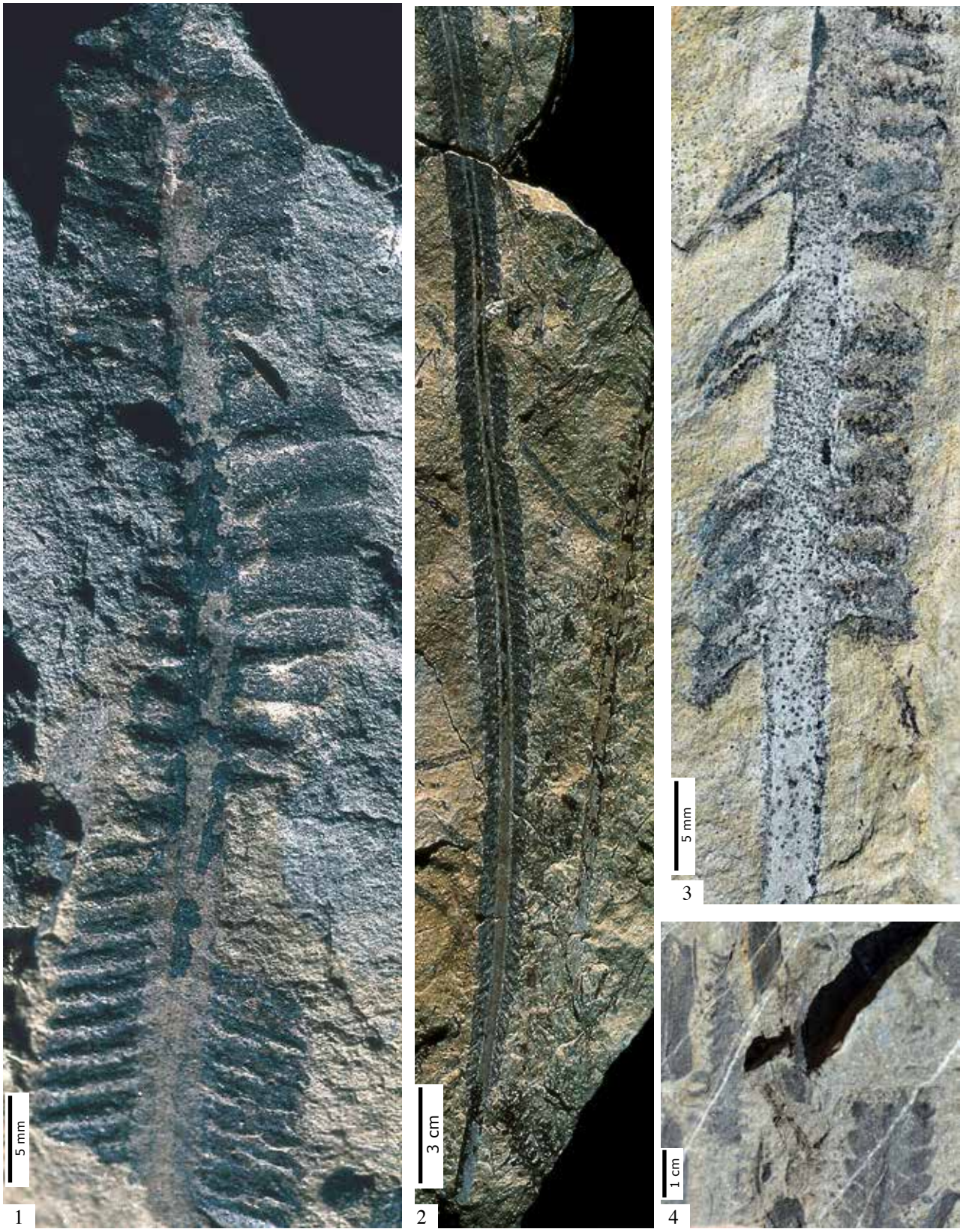
Description

Rhizom: Global to ovoid, up to 8–15 cm long, about 5–8 cm wide, from which simply pinnate fronds sprout.
Fronds: Long, reaching a length of almost 1 m with a broad rachis (up to 1 cm wide) and pinnules but their width is usually only 1 cm.
Leaves: Pinnules attached almost by their whole base and are only slightly auriculate; their apex is rounded–acute. The leaves are usually 4–5 cm long and 8–12 mm wide, but they can be even longer (perhaps up to 8 cm). The pinnule base is slightly contracted; the apex is roundly acute. The venation is neuropterid, with a clear mid-rib extending about two-thirds of the pinnule length. Secondary veins are numerous and fork several, but mostly 2–3, times.
Fertile pinnules: Of *Scolopendrites scolopendrioides* type. Pinnate fronds arising



***Neuropteridium elegans* (Early-Middle Triassic) Sterile fronds**

1.) Part of a pinnate frond (10 x 4 cm) (KÜH 972); 2. Single pinnula (1.5 x 1 cm) (PIZ 516*); 3.* Young enrolled frond (PIZF 248); 4. Fronds attached to a rhizome fragment *(*KÜH 220) All Coll. Wachtler, Anisian, Kühwiesenkopf and Piz da Peres



Neuropteridium elegans* (Early-Middle Triassic) Fertile fronds *(Scolopendrites grauvogelii)

1. Fertile fond fragment 7,5 cm long with a basal *Scolopendrites* part and an apical *Neuropteridium elegans* part (*Scolopendrites grauvogelii.* Holotype. KÜH 222); 2. Fertile frond of *Neuropteridium elegans* (*Scolopendrites grauvogelii (KÜH 971);* 3. Fertile frond of *Neuropteridium elegans* (2 x 2 cm) (PIZ 231); 4. Sterile and fertile frond of *Neuropteridium elegans* (ALP 14) All Coll. Wachtler, Anisian, Kühwiesenkopf and Piz da Peres

***Neuropteridium elegans*. Fertile fronds *(Scolopendrites grauvogelii)*. Reconstructions**

a. Whole plant with sterile and fertile fronds *(Scolopendrites grauvogelii)*, b. Entire frond, (PIZ 516), c. Detail of the leaves and the rachis, d. Single leave with neuropterid venation, e. Fertile frond *Scolopendrites grauvogeli*i.

from a rhizome. Rachis 4–6 mm holding the usually hanging pinnules. The whole lower surface of the fertile pinnules is covered with sporangia. Sporangia are oval and cover the whole lower surface of the pinnules. Spores trilete, circular in equatorial outline, with a diameter of 35–45 µm and the exospore is scabrate to granulate.

Diagnosis, remarks and ecology

In 1828 Adolphe Brongniart, figured on pl. 67, fig. 1, a frond fragment from the Vosges, over 20 cm long with a rachis c. 5 mm wide and pinnules that arise more or less perpendicularly. The pinnules are 4–5 cm long and 8–10 mm wide with a constricted base and a pointed apex. He named it *Neuropteris voltzii. Neuropteridium elegans* and *Neuropteridium voltzii* elegans occur together, not only in the Dolomites, but also in the German and French Buntsandstein floras. The difference between *Neuropteridium voltzii* and *N. elegans* lies mainly in the width of the rachis (much thicker in *N. voltzii* than in *N. elegans*) and the length and shape of the pinnules (longer but smaller and more pointed in *N. voltzii,* broader but shorter and rounded in *N. elegans*). The *Neuropteridium* species can be attributed with caution to the Osmundaceae. *Neuropteridium* occupied a wide-ranging habitat and constitutes one of the characteristic ferns of the European Early Triassic Buntsandstein with a distribution that extends to China. Fertile and sterile pinnae are very different; the sporangia evolve on highly reduced pinnae.

The rachis of the fronds is usually broader than in *Neuropteridium elegans*, with a width of 3–6 mm in the frond fragments. Pinnules are up to c. 5 cm longer than in *Neuropteridium elegans* with more or less the same width (4–9 mm), resulting in a much greater length/width ratio.

The nomenclatural history of the fertile fern genus, characterised by hanging pinnules on which the lower surface is completely covered with sporangia, is rather complicated. Brongniart (1828b,c) described material from the Vosges under the name *Filicites scolopendrioides.* Goeppert (1836, p. 276) later created the generic name *Scolopendrites* for this material, and therefore, the legitimate name for the fertile pinnules of *Neuropteridium voltzii* is *Scolopendrites scolopendrioides*.

The two fertile pinnules, *Scolopendrites grauvogelii* for *Neuropteridium elegans* and *Scolopendrites scolopendrioides* for *Neuropteridium voltzii,* are macromorphologically difficult to distinguish although the main characteristic in this respect is the thickness of the rachis (narrower than in *S. scolopendrioides*). In *Neuropteridium elegans* the fertile pinnules were usually slightly smaller than in *Scolopendrites scolopendrioides (Neuropteridium voltzii)*, with a mean length of 4–8 mm (8–11 in *S. scolopendrioides)*, and a mean width of 2–3 mm as in *Scolopendrites scolopendrioides*. The sporangia were more or less circular in outline, with a diameter around 300–400 µm, whereas in *Scolopendrites scolopendrioides* they are oval and c. 600 · 200 µm. Just as in *Scolopendrites scolopendrioides,* the spores are trilete, circular in equatorial outline, with a diameter of 35–45 µm, and the exospore is scabrate to granulate. When sporangia are present the difference is easy to observe, in *Scolopendrites grauvogelii* they are circular and those in *Scolopendrites scolopendrioides* are oval and twice as large. The spores of the two species are indistinguishable.

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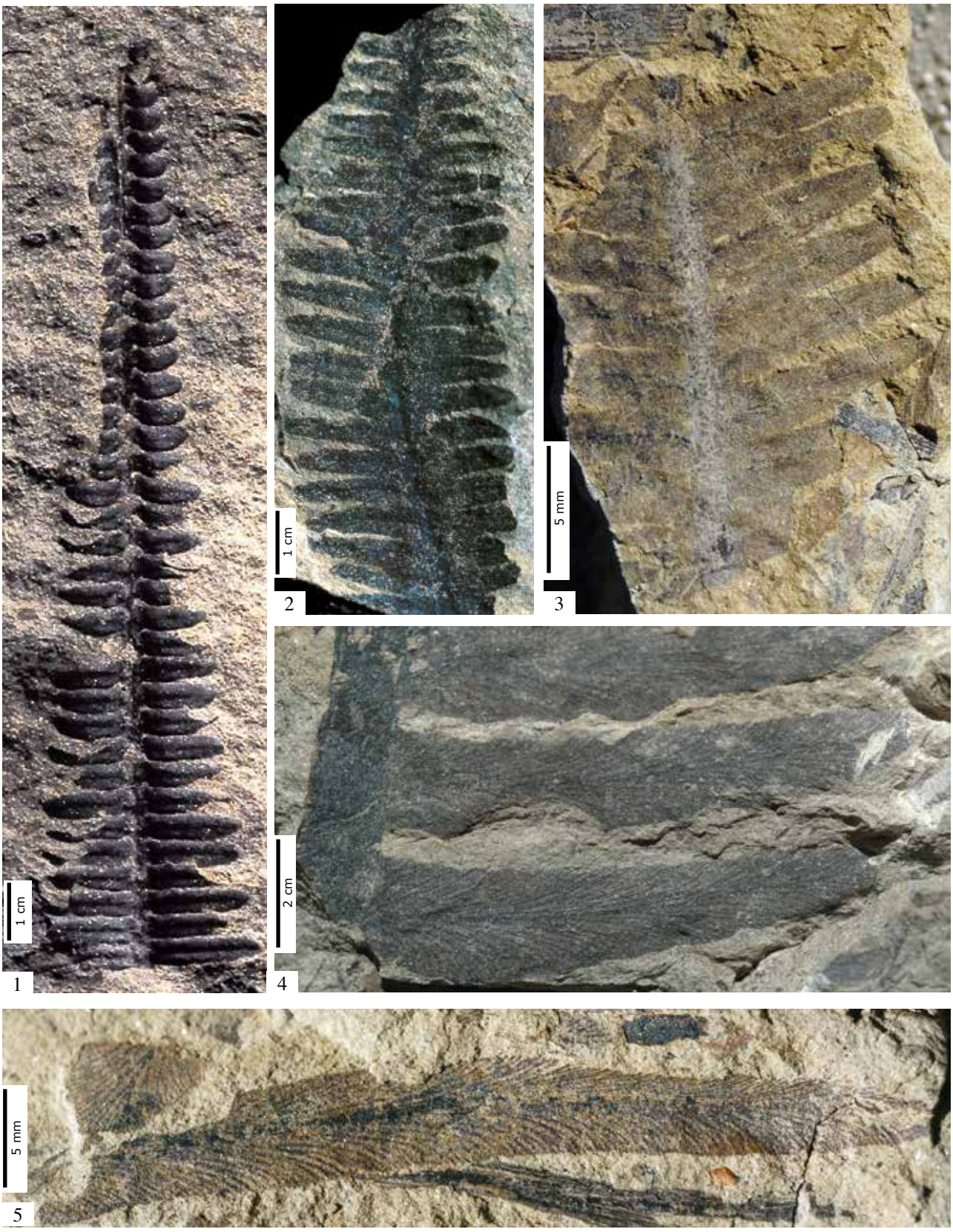

***Neuropteridium voltzii* (Early-Middle Triassic) Sterile fronds**

1. Mainly complete frond (KÜH 973*);* 2. Part of a pinnate frond (7 x 8 cm) (KÜH 976*);* 3. Frond (PIZ 559); 4. Part of a frond (KÜH 2161); 5. Extraordinarily long single pinnula (5 x 1 cm) (PIZ 228*).* All Coll. Wachtler, Anisian, Kühwiesenkopf and Piz da Peres

***Neuropteridium voltzii*. Fertile fronds (*Scolopendrites scolopendrioides)* (Early-Middle Triassic)**

1. Fertile frond of *Neuropteridium voltzii* (*Scolopendrites scolopendrioides* KÜH 810*); 2-3.* Fertile frond of *Neuropteridium voltzii* and detail of the pinnae (*Scolopendrites scolopendrioides* PIZ 501)*;* 4. Typical rhizome of *Neuropteridium* (PIZ) All Coll. Wachtler, Anisian, Kühwiesenkopf

***Neuropteridium voltzii* (Early-Middle Triassic) Reconstructions**

a. Whole plant *with sterile and fertile fronds (Scolopendrites scolopendrioides)*, b. *Entire frond,* (PIZ 56), c. Single leave with neuropterid venation, d. Fertile frond *Scolopendrites scolopendrioides, e. Detail of the lower basis covered with sporangia.*

Systematic Paleontology

Order FILICALES, BOWER, 1899
Family Osmundaceae
Genus *Cladophlebis* (Brongniart, 1849)

Taxonomic notes

When Adolphe Brongniart in 1828 described for the first time *Neuropteris gaillardotii* from the French Muschelkalk he gave two illustrations: one pinnule with several times forking veins without a visible mid-rib (pl. 74, fig. 3a) and one with a mid-rib (pl. 74, fig. 3) as typical for *Cladophlebis remota*. The first one was later changed to *Todites gaillardotii*, due to some affinities with the Todea ferns and being confined with roundish leaflets. The second, in addition to its delicate mid-rib and forking secondary veins, also characterised by pinnules with a more acutely angled apex, was classified further as *Cladophlebis*.

Cladophlebis rhombifolia PRESL 1838, BRONGNIART 1849

Type horizon and age

Dolomites, Lower to Middle Triassic, Anisian, Pelson-Illyrian (243 - 241 Mya)

Description

Whole plant: Bipinnate to tripinnate fern, with fronds up to 80 cm long, holding a slender rachis (5–8 mm) from which up to 20 cm long pinnae arise alternately at an angle of 45 degrees.
Sterile pinnules: Single leaflets (1–1.5 cm long and 5–8 mm wide) normally attached with only part of their base or mid-rib at an angle of 30–60 degrees. Pinnules slightly falcate to triangular ovate, sometimes demonstrating an undulating margin. In some specimens the pinnules tend to have a more acute apex. The venation consists of a midrib that does not reach the apex, and twice-forking secondary veins arising at c. 60 degrees.
Fertile pinnules: Pinnae reduced, sometimes involute or undulated with sporangial attachment areas at the end of the secondary veins.

Diagnosis, remarks and ecology

Cladophlebis has been recorded as a rare element in Europe from the Lettenkeuper (Ladinian) and Schilfsandstein (Carnian) from Germany.
Triassic fern foliage is often difficult to classify. Isolated pinnules, mainly fertile, have been attributed to genera such as *Pecopteris, Neuropteris* and *Cladophlebis, Anotopteris* or *Speirocarpus.* But evaluating all the facts for fronds and pinnulas of this time, the classification *Cladophlebis* can be regarded as effective. Because *Cladophlebis remota* is restricted to Ladinian plant-sites in Europe (Lettenkeuper, Hauptsandstein in Germany, Wengen Formation in the Dolomites), for this fern, which was collected in fair amounts in the Anisian of the Dolomites, the name *Cladophlebis rhombifolia* was chosen. In this sense, *Acrostichites rhombifolia,* known from the German Buntsandstein, will be regarded as synonymous.
Single pinnules or parts of fronds could be confused with *Neuropteridium*. A distinctive characteristic compared to the similar *Neuropteridium* pinnules, apart from their tripinnate appearance and the attachment only by the mid-rib, is that they are slightly falcate to triangular ovate and grow upwards. Similar-looking ferns from Early and Middle Triassic floras in Europe have been described due to their pecopterid form under the name *Cladophlebis distans* (Presl, 1838) Frentzen, 1922, or *Anotopteris distans* (Presl, 1838) Schimper, 1869. But since many are based on poorly preserved material or of insufficient quality, they are difficult to determine.

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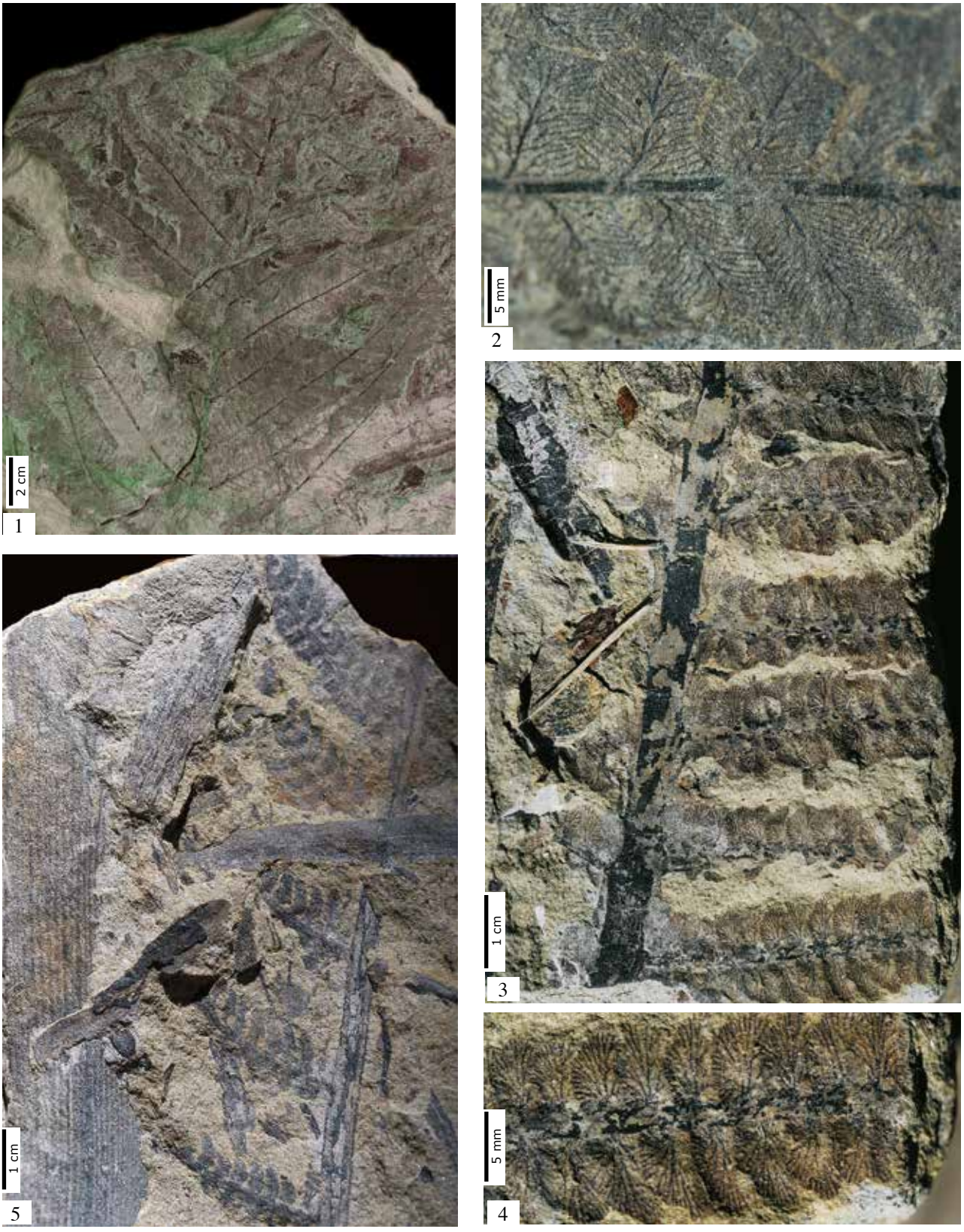

***Cladophlebis rhombifolia* (Early-Middle Triassic) Sterile and fertile fronds**

1-2. Part of a bipinnate frond (30 x 20 cm, and single pinnules (4 x 2 cm (PIZF 1102); 3. Part of a juvenile frond (8 x 5 cm PIZ 531); 4. Juvenile pinnules (5 x 1.2 cm, PIZ 531;) 5. Fertile frond (10 x 5 cm KÜH 1402); All Coll. Wachtler, Anisian, Kühwiesenkopf

***Cladophlebis rhombifolia* (Early-Middle Triassic) Sterile and fertile fronds**

6. Mainly entire frond (PIZF 268); 7. Part of a frond evidencing the slightly falcate, upwards growing leaflets (KÜH 574); 8. Part of a frond (KÜH 1405). All Coll. Wachtler, Anisian, Kühwiesenkopf and Piz da Peres

***Cladophlebis rhombifolia* (Early-Middle Triassic) Reconstructions**

a) Whole plant, b) Single bipinnate frond (PIZF 1102), c) Sterile pinnae (PIZF 1102), d) Part of a fertile frond (KÜH 1402).

Systematic Paleontology

Order Filicales Bower, 1899
Family: Lindsaeaceae Dryander 1793

*Wachtleria (*Kandutsch, 2011)

Taxonomic notes

Named after Michael Wachtler, who discovered the fossil site extending from Piz da Peres to Kühwiesenkopf and carried out extensive palaeontological research in the Dolomites.

Wachtleria nobilis KANDUTSCH 2011

Type horizon and age

Dolomites, Early-Middle Triassic, Anisian, Pelson-Illyrian (243 - 241 Mya)

Holotype

PIZ 303 (Coll. Wachtler, Natural History Museum Südtirol, Bozen)

Etymology

Nobilis, Latin name for elegant

Diagnosis

Dimorphic small fern with slender fronds, leaves shortly stalked or attached at the inner, lower corner, wedge-shaped. Veins flabellately forked. Sori extending along the outer margin of the leaves, protected by a narrow flap.

Description

Plant: Pinnate fern with slender linear stipe, linear and glabrous lamina, pinnae shortly stalked or decurrent on raised edge of the rachis, asymmetrically wedge-shaped to fan-shaped, sometimes lobed. Veins forking several times, mid-rib absent.
Fronds: Stipe slender, 20–40 cm long, the first 10–15 cm without pinnae. Stipes are 3–5 mm wide, with a single vascular strand. They are linearly erect and long in proportion to the thickness of the rachis.
Pinnae: Pinnae usually wider than long, 2 cm x 1.5 cm, asymmetrically arranged on a stalk, wedge-shaped to fan-shaped, decurrent on raised edge of the rachis. The venation arises from the lower basal angle of the pinnae, the mid-vein is undeveloped, forking several times, other veins arise directly from the rachis. The secondary veins end near the margin. The margin of the pinnae is delicate, frequently flattened or lobed.
Fertile fronds: Sterile pinnae taller, deflexed on the outer margin. Sori in the form of a continuous line of sporangia covered by the reflexed leaf margin. The fertile pinnules measure about 2.5 x 2 cm; the sporangia are arranged in a row and are protected by the inrolled leaflet margin. The sori are protected by indusia, which open towards the margin.

Diagnosis, observations and ecology

The fern *Wachtleria nobilis* is not very rare especially on Piz da Peres. In certain lenses it is the most abundant fern, although well-preserved specimens are rare due to their fragility. Conservation is possible only in very fine siltstones but in such cases this small fern offers spectacular insights into the variety of this ancient fern world.
Wachtleria has a striking resemblance to today's Lindsaeaceae, especially *Lindsaea linearis.* This family with its 200 extant species is considered to be among the most primitive of those included among modern ferns. The Lindsaeaceae are widespread, particularly in the tropics. As root-climbing epiphytes, Lindsaeaceae from the Early Cretaceous are recorded only from the roots, and not from their foliage (Schneider et al., 2001).

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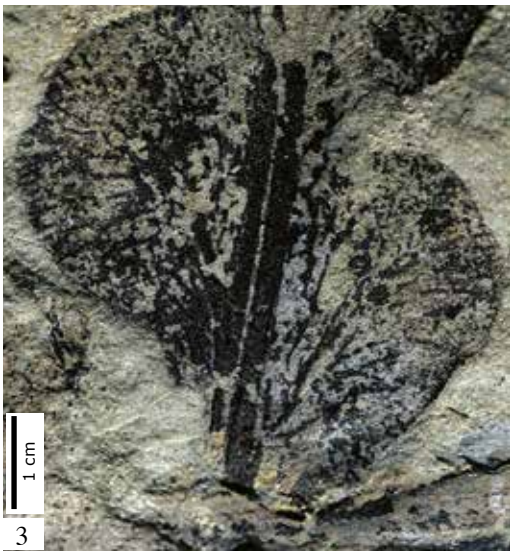
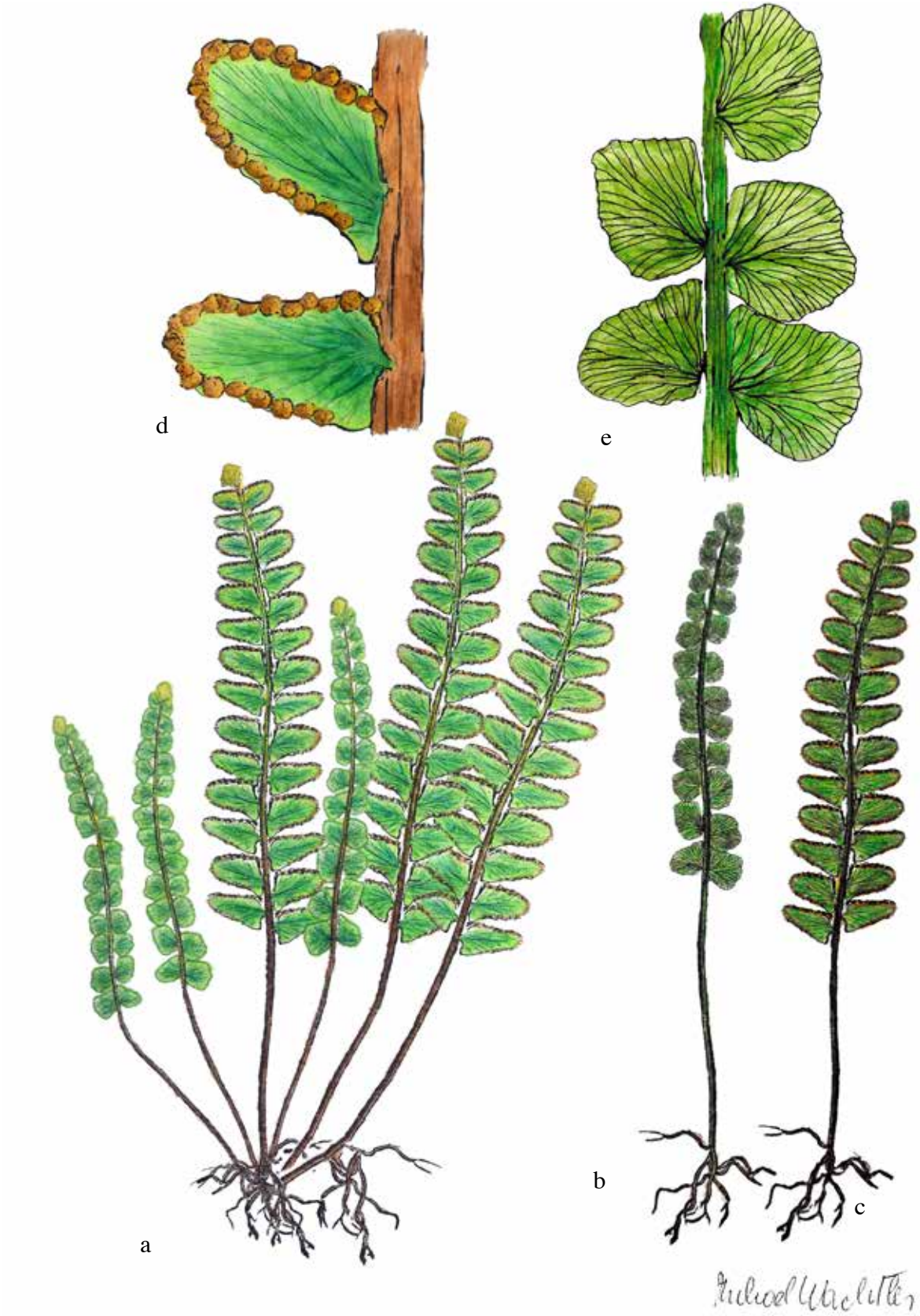


***Wachtleria nobilis* (Early-Middle Triassic) Sterile and fertile fronds**

1. Part of a sterile pinnae (PIZ 303 Holotype); 2. Detail of a fertile pinnae, seen from the surface (PIZ 303, Holotype. 3. Part of a sterile pinnae, showing attachment of pinnules (PIZ 303). All Coll. Wachtler, Anisian, Piz da Peres

Wachtleria nobilis (Early-Middle Triassic) Sterile and fertile fronds

4. Several sterile pinnae showing the slender stems (30 x 14 cm, PIZ 311); 5. Part of a fertile pinnae. The sporangia are arranged in a row on the margin (8 x 4 cm PIZ 520); 6) Part of a sterile pinnae, showing the attachment of pinnules (PIZ 520, all Coll. Wachtler, Anisian, Piz da Peres)



***Wachtleria nobilis* (Early-Middle Triassic) Reconstructions**

a) Whole plant, b) Single frond sterile (PIZ 311), c) Single frond fertile, d) Fertile part (PIZ 520), e) Sterile pinnae-detail (PIZ 303).

The beauty of Triassic ferns (Early-Middle Triassic)

1. Young evolving fern-like plant with fine hairs on juvenile circinate fronds and on the stem system (KÜH 2104); 2. Juvenile involute fern-frond, probably belonging to *Gordonopteris* (PIZ 271; 3. A fern-frond with feeding traces (PIZF 66); 4. Aphlebia from *Anomopteris mougeotii* upper unusually upper side view (PIZ 195); 5-7. Several pinnulas looking equal, but they belong to different fern-species: 5. *Neuropteridium grandifolium?* (PIZ 220), 6. *Neuropteridium voltzii* (PIZ 156), 7. *Neuropteridium elegans* (PIZ 124). All Coll. Wachtler, Anisian, Piz da Peres and Kühwiesenkopf