



FERNS AND SEED FERNS FROM THE
EARLY-MIDDLE TRIASSIC (ANISIAN)
PIZ DA PERES (DOLOMITES – NORTHERN ITALY)

by
MICHAEL WACHTLER



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Italy
mail: info@dolomythos.com

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¹ Michael Wachtler, P. P. Rainerstrasse 11, 39038 Innichen, Italy, e-mail michael@wachtler.com.

² Georg Kandutsch, Hinterwinkl, 9543 Arriach, Austria, e-mail Alpdoc@aon.at

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by

Michael Wachtler

P. P. Rainerstrasse 11, 39038 Innichen, Italy, e-mail michael@wachtler.com

Abstract

From 1999 to 2010 Michael Wachtler passed the summers on Piz da Peres, a distinctive mountain between the lovely Dolomitian localities Olang and San Vigilio di Marebbe. The author recovered large quantities of well-preserved ferns and seed ferns. Some ferns, such as *Anomopteris mougeotii*, *Neuropteridium elegans*, *N. voltzii*, *Marantoidea arenacea*, and *Sphenopteris schoenleiniana*, and the seed fern *Scytophyllum bergeri*, were known from other Early-Middle Triassic localities (German Basin, France, etc.), and others had been discovered earlier by Michael Wachtler on the nearby Kühwiesenkopf in the Braies Dolomites (*Gordonopteris lorigae*, *Ladinia simplex*) and published on several occasions (Van Konijnenburg-Van Cittert et al., 2006; Kustatscher et al., 2007; Wachtler, 2010). Given the richness of the Piz da Peres layers, especially in ferns and seed ferns, further work was carried out on new ferns such as *Ladinopteris kandutschii* n. sp. and *Wachtleria nobilis* nov. gen. n. sp. and new seed ferns such as *Sagenopteris keilmannii* n. sp., with its suggested ovulate organ *Caytonia fedelei*, and an enigmatic seed fern pollen organ named *Pteruchus dezignii* n. sp. The aim of the present work was to examine in more detail the palaeoecology of this beautiful Garden Eden, providing an insight into the interactions between plants and animals, especially insects, and climatic changes in the Early Triassic.

Online: January 2011.

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

Methodology and Palaeobiology

The Kühwiesenkopf is famous for its interesting lycophyte flora (Kustatscher et al., 2009), and the large cycad vegetation that is unlike anything seen elsewhere (Wachtler, 2010). The fossil lenses of Piz da Peres are particularly rich in well-preserved ferns and seed ferns, although interesting Cycadophyta, Sphenophyta, Coniferales and Lycodophyta have also been recovered. On Piz da Peres the Filicales and the Coniferales form the dominant flora. However the conifers are only represented by two *Voltzia* species, whereas the ferns are represented by many different genera and species. Another interesting feature of this locality is the seasonal changes in flora that are evident

in the different plant lenses. It is therefore possible to examine the palaeoecology of several plant habitats and growth stages. Because the subtle sediments and layers on Piz da Peres open like a diary of the past, changes in stages and living conditions can be implied.

The fern *Gordonopteris lorigae*, first described from Kühwiesenkopf (Van Konijnenburg-Van Cittert et al., 2006), and previously thought to be endemic to the Alpine Trias, was found in every plant layer. *Anomopteris mougeotii* was also frequent, along with the low growing ferns *Neuropteridium elegans* and *N. voltzii* known from the German Buntsandstein and the French Grés à *Voltzia*. Another frequent genus, which has yet to be recovered elsewhere,

was *Ladinopteris kandutschii* n. gen. n. sp. Its ideal habitat seems to be as shrubby under dense conifer trees, especially *Voltzia recubariensis*. All these ferns belong to the Osmundaceae, an ancient fern group with ancestors going back to the Palaeozoic. Another study carried out by Georg Kandutsch deals with a group of ferns that have no relationship with the Osmundaceae or whose affinity is unclear. *Wachtleria nobilis* n. gen. n. sp., a fern bearing a striking resemblance to extant Lindsaeaceae, had a restricted distribution. Fern species that are common in the European Trias, like *Sphenopteris schoenleiniana* or *Marantoidea arenacea*, were also present, while other ferns were present as such small specimens or at such a low frequency that they are not discussed here.

Of the pteridosperms the most abundant was *Scytophyllum bergeri*, belonging to the group of Peltaspermales with its seed-bearing shield-like organs *Peltaspermum bornemannii*. Also present was a new pollen organ with the parental characters of Peltaspermales and Corystospermales: *Pteruchus deznii* n. sp. It is not clear if this belong to *Scytophyllum bergeri* or to another as yet unidentified seed fern. The seed fern *Sagenopteris keilmannii* n. sp., belonging to the Caytonales, but never recorded so far was common but not numerous. It was possible to attribute a new female reproductive structure to this seed fern: *Caytonia fedelei* n. sp. Other pteridosperms were not in evidence with any certainty, because the increasingly numerous cycads from the Bjuvia group were occupying their habitats.

It was possible to assemble almost all parts of the plants and to determine their life-cycles, although new information continued to provide surprises throughout the study.

Some measurements were only approximate, and the study lacks accurate pollen and cuticle analysis, because in an arbitrary act by the authorities all specimens from the Wachtler collection (5,000 in total) were confiscated in December 2010 and taken away in circumstances that are not common in highly developed democracies. So it was not possible to finish all planned studies and make them available to the public in a normal scientific way.

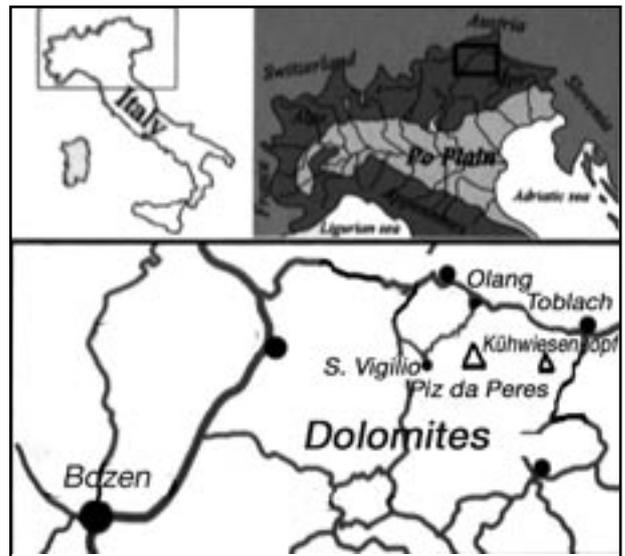


Fig. 1: Map of the Braies Dolomites area in Northern Italy with Piz da Peres and Kühwiesenkopf.

Conclusions/Significance

The discovery of this 241.5-million-year-old fern world adds new insights into the evolution of the modern plant system. *Gordopteris*, *Neuropteridium*, *Ladinopteris* and *Anomopteris* probably belonged to the Osmundaceae, an old fern group with ancestors found until the Upper Permian. *Wachtleria* was probably an ancestor of the Lindsaeaceae. The classification of other ferns remains in doubt: *Marantoidea* could be inserted into the Marattiales, another old family with representatives up until the Carboniferous. The fossil plants from Piz da Peres and Kühwiesenkopf yield in many aspects a totally new vegetation paragenesis, known from no other part of the world. Transition plants ranging from the Carboniferous-Permian to the present can be found, such as horsetails and lycopods. Very well could be observed the down of the once dominating giant *Lepidodendron* and *Calamites* of Palaeozoic. *Lycopia dezanchei* (Kustatscher et. al. 2009) and *Equisetites mougeotii* (Kustatscher et. al. 2007) occurring in the Early-Middle Triassic beds were still arboreal. The extant horsetails and club mosses are only small and creeping. It is possible to relive the rise of the modern vegetation with the emergence of rapidly propagating cycads, the modern ferns, taking over the reign of

the conifers as the dominant plants in the giant woods. Further search of cladistic and phylogenetic characteristics in the literature could be useful, even though following the advice given by the famous palaeobotanist family, E. and T. Taylor (2009), has proven more than successful:

"In our opinion, it will be more productive if there were (given) greater attention directed at mining the rock record in the hope of discovering more informative and new specimens, than to continue to construct new phylogenies using the same, often ambiguous characters."

New fossil records from Piz da Peres could also provide answers to unresolved problems.

Introduction

The Anisian fossil beds that extend from Braies Valley throughout the locality of Olang as far as San Vigilio di Marebbe in Val Badia and extending to La Val and the Fassa Valley have their origins in a marine fluvial environment. In certain areas the so-called Dont Formation, in which most of the specimens were found, is more than 200 m thick (Broglia Loriga et al., 2002). Within this are irregular lens-shaped plant horizons that may reach about one metre in high.

Extraordinarily well-preserved fossils were collected by Michael Wachtler over 20 years from the silty, clayey lenses, particularly from the slightly younger Ladinian plant beds, and are summarised in Wachtler & Van Konijnenburg-Van Cittert (2000), in which new conifer species (*Voltzia dolomitica*, *Voltzia ladinica*) and new Cycadophyta (*Bjuvia dolomitica*, *Sphenozamites wengensis*) were established. In the last ten years a systematic investigation of the Early-Middle Triassic Anisian layers has revealed exceptional findings of invertebrates, vertebrates and plants that have allowed the reconstruction of a spreading and flourishing palaeoecological system after the Permian/Triassic crisis. The different sand- and limestone-layers were especially rich, ranging from red to yellow, grey and green at the base of Piz da Peres West. Since Michael Wachtler spent months and months searching in this dangerous gorge, which is prone to rock falls, the local farmers have given the locality the name "Wachtler Schlucht"

(Wachtler gorge). This name is used herein to specify a rock system of no more than 500 m long and 200 m high, encircled by dense stands of conifers (spruces, mountain pines, stone pines), with little human activity.

Reconstruction of the Peres Plant Beds

Throughout the Dont Formation, which was laid down in the Pelsonian age, the sedimentological deposits comprise a typical succession of marine transgression and alluvial coastal habitats with ancient beach-near plains and forests. These conditions persisted for no more than one million years. Deposition took place in several different sub-milieus.

Fluvial channels: Rivers brought plants from inland. In this case the plant remains were fragmentary, disarticulated and difficult to identify.

Coastal storm events: Several lenses were 20 cm thick and contained randomly orientated plant remains throughout the whole sediments. They also contained marine biota such as gastropods (*Loxonema*), epibysate bivalves (*Neomorphotis compta*, *Plagiostoma* etc.), and a few brachiopods and ammonites (Posenato, 2008). Fish (*Saurichtys*, *Bobasatrania*, *Dipteronotus*, coelacanths, Tintori, 2002), invertebrates (*Megachirella wachtleri*, Renesto, 2003), archosaur teeth and rhynchosaur skeletons were occasionally found. The highly abundant terrestrial plants in the deposit had their origin in gravitative flows, probably caused by extreme events such as storms or tsunamis. The plants would have been buried suddenly under a carpet of sand near the place in which they were originally growing and were not transported long distances. This was particularly evident in the lower layers of Kühwiesenkopf, in the *Equisetites* beds of Piz da Peres West and the plant beds of Piz da Peres/Furcia. These layers usually consist of greyish coloured sandstone, which takes its colour from the tiny plant remains (Gall et al., 1993). The liberated mass of water would have submerged the vegetation growing along the beaches. Plants in these lenses, especially fern and cycad fronds, but also conifer twigs, are often large-sized and complete, but are sometimes only preserved with minimum detail.



Fig. 2: Plant-bearing horizons on Piz da Peres West: (1) *Equisetites* point, (2) Wachtler gorge, (3) Forest fossil point.

Temporary standing waters due to normal coastal events: Silty-clayey lenses up to several decimetres thick, containing more or less preserved plants in some layers, and indeterminable chaffs in the other have their origin in different sedimentary deposits over the course of an indefinable period of time. This is the case for the upper layers of Kühwiesenkopf, but especially in “Wachtler gorge” on Piz da Peres. These silty-clayey deposits are mainly yellow to orange with fine sand fractions. The details and impressions of the plants are extraordinarily well-preserved, such that even delicate veins and fructifications are visible.

On Piz da Peres West in particular, a succession of coarse-grained rounded detritus is not uncommon. They are then overlain by different strata containing more or less well-preserved plants. In most cases the 10 cm (at its maximum) thick layer in the middle contains the most well-preserved plants, whereas the upper substrate only contains a mixture of chaff. The plants are incorporated into the rocks without preferential orientation.

Palaeoecology and Palaeoclimatology

Consistent differences exist between the various fossil beds. The slightly older plant lenses from the lower stratas of Kühwiesenkopf, overlying the top of the Early Anisian (Aegean) carbonates (Lower Serla Dolomite), could be defined as *Lycopia-Bjuvia-Voltzia-Neuropteridium* beds. In detail, there is a Lycophyta-association dominated by the arboriscent *Lycopia dezanchei*,



Fig. 3: Piz da Peres – Fossil point, Wachtler gorge: a) Fern bed, b) *Voltzia* bed, c) Lycopod bed.

then *Isoetites brandneri*, *Lepacyclotes bechstaedtii* and *Selaginellites leonardii*. Such a range of lycopophyta was not found in any other area. Of the Coniferales there are two to three as yet undefined *Voltzia* genera and the low-growing arboriscent *Aethophyllum stipulare*. The fossil record suggests that one is a special heterophyllous form of *Voltzia*, whereas the other, with its acicular needles, resembles *Voltzia ladinica* from the Ladinian of the Dolomites. *Voltzia recubariensis* is not present or only as an ancestral form. Sphenophyta (*Equisetites mougeotii*) are present but not dominant, along with some doubtful *Neocalamites* sp. and *Echinostachys-Schizoneura* (Kustatscher et al., 2007). A number of cycad genera and sub-genera are dominant: *Ladinia simplex*, *Bjuvia primitiva*, *Bjuvia olangensis* and *Nilssonia braiensis* (Wachtler, 2010). The ferns exist as a *Gordonopteris-Neuropteridium* association with *Neuropteridium elegans*, *N. voltzii* and *Gordonopteris lorigae*. *Marantoidea arenacea* and *Sphenopteris schoenleiniana* are present, but rare. *Anomopteris* is lacking, along with *Ladinopteris kandutschii*. The seed ferns include *Scyto-phyllum bergeri* and *Sagenopteris keilmannii*. *Pleuromeia*, a typical Lycophyta from the German Buntsandstein, is absent.

The upper layers of Kühwiesenkopf and Piz da Peres, overlain by the lower beds of the Late Anisian (Illyrian) carbonates from the Contrin Formation (Bechstädt & Brandner, 1970; de Zanche et al., 1992), are characterised by rich fern and seed fern assemblages: *Anomopteris mougeotii*, *Ladinopteris kandutschii* and *Gordonopteris*

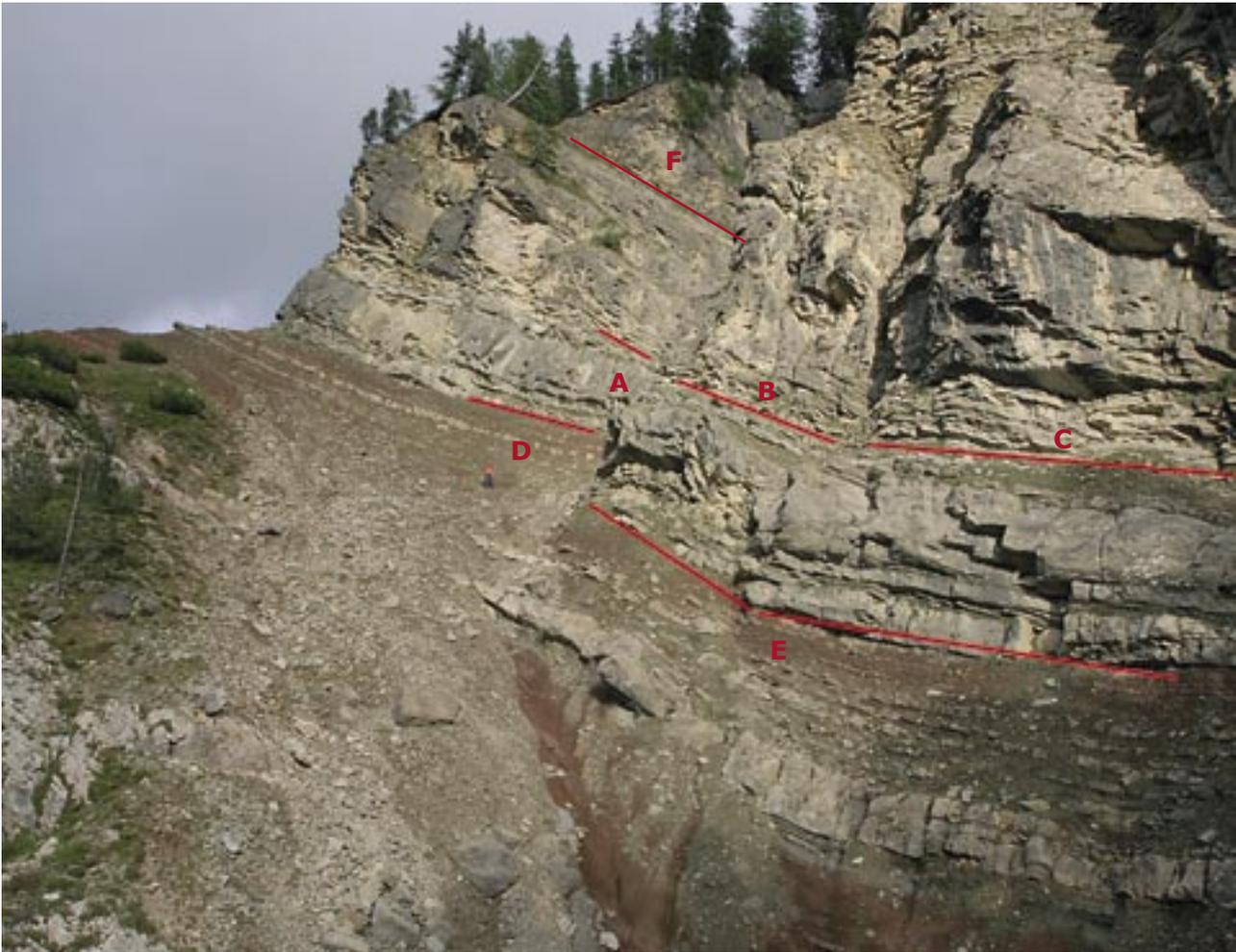


Fig. 4: Piz da Peres – Fossil point, Wachtler gorge. Detail. Precipice. A) Anthesis vegetation: Cycads, ferns, seed ferns. B) Anthesis vegetation: Ferns, seed ferns. C) Anthesis vegetation: Voltzia beds, sometimes *Ladinopteris*. D: Anthesis vegetation: Ferns, seed ferns. E) Plant chaff, poorly preserved. F) Upper layers.

lorigae as well as *Scythophyllum bergeri* and *Sagenopteris keilmannii* are typical. *Wachtleria nobilis* is restricted to an area on Piz da Peres West. *Voltzia recubariensis* is generally the dominant conifer. Cycads of the *Bjuvia*-type are common; Lycophyta such as *Lycopia dezanchei* and the small *Selaginellites leonardii* are present, but restricted in number.

It is worth going into more detail about the plant paragenesis on Piz da Peres West. Apart from locality 1, Fig. 2, where the vegetation could be defined as monophyletic giant horsetail vegetation, probably with a new giant *Equisetites* species and some inarticulate skeletons of invertebrates (?*Rhyncosaurus*, ?archosaurs), the most interesting assemblages are in the various plant lenses in the Wachtler gorge. Fig. 4 A–C clearly shows the plant abundance in

the Early-Middle Triassic in a restricted area. Of special interest is the insight that is possible into different microclimates: namely solar-exposed areas versus shady wooded areas. The plant layers A–C are 50 metres long. In the first 30 metres there are a few conifers and lycophyta (only the tiny *Selaginellites leonardii* is abundant). In order of frequency we found: *Gordonopteris lorigae*, *Anomopteris mougeotii*, *Bjuvia olangensis*, *Scythophyllum bergeri*, *Equisetites mougeotii*, *Ladinopteris kandutschii*, *Nilssonia braiesensis*, *Bjuvia primitiva*, *Sagenopteris rhoifolia*, *Marantoidea arenacea*, *Sphenopteris schoenleiniana*, *Wachtleria nobilis*, and *Voltzia ladinica*. Archosaur teeth and reptile skeletons were also recovered.

Moving to the right in the same layer there is a *Voltzia recubariensis* bed (E) that con-

Lycophyta	
<i>Lycopodium dezanchei</i> nov. gen. n. sp.	endemic
<i>Isoetes brandneri</i> n. sp.	endemic
<i>Lepacyclotes bechstaedtii</i> n. sp.	endemic
<i>Selaginellites leonardii</i> n. sp.	endemic
Sphenophyta	
<i>Equisetites mougeotii</i>	
<i>Equisetites</i> n. sp. in press n. sp.	endemic
<i>Schizoneura-Echinostachys paradoxa</i>	
Coniferophyta	
<i>Voltzia recubariensis</i>	endemic
<i>Voltzia ladinica</i> n. sp.	endemic
<i>Voltzia</i> n. sp. in press n. sp.	endemic
<i>Aethophyllum stipulare</i>	
Pteridospermatophyta	
<i>Scythophyllum bergeri</i>	
<i>Sagenopteris keilmannii</i> n. sp.	endemic
Cycadophyta	
<i>Ladinia simplex</i> nov. gen. n. sp.	endemic
<i>Bjuvia primitiva</i> n. sp.	endemic
<i>Bjuvia olangensis</i> n. sp.	endemic
<i>Nilssonia braiensis</i> n. sp.	endemic
Pteridophyta	
<i>Neuropteridium elegans</i>	
<i>Neuropteridium voltzii</i>	
<i>Gordonopteris lorigae</i> nov. gen. n. sp.	endemic
<i>Anomopteris mougeotii</i>	
<i>Ladinopteris kandutschii</i> nov. gen. n. sp.	endemic
<i>Wachtleria nobilis</i> nov. gen. n. sp.	endemic
<i>Marantoidea arenacea</i>	
<i>Sphenopteris schoenleiniana</i>	
Dubious	
<i>Cladophlebis</i>	
<i>Neocalamites</i>	
<i>Ptilozamites</i>	
<i>Albertia</i>	

Fig. 5: List of the plants till now recovered and diagnosed with certain reliability.

tains 95% of all plant fossils at this locality. Only a few *Ladinopteris kandutschii* fronds are present, and no other plants. *Lycopodium dezanchei* on the other hand is common in the Lycopod beds (Fig. 3C), where the rocks end and the extant forest begins. *Wachtleria nobilis* was found in monoculture on the place Fig. 3 A. The forest-fossil point shown in Fig. 2, locality 3, is rich in well-preserved *Ladinia simplex* and *Bjuvia primitiva* leaves. Because it is only 2 metres wide and the plants seem to have been mouldy it could once have been a restricted brackish water area. In all – between Kühwiesenkopf and Piz da Peres – about 30 different plants have been recovered to date (for details see list), half of them endemic or discovered in this area for the first time. This confirms that the ancient beaches and lagoons of this Anisian Fossilagerstätte, although covering only a relatively small area, supported a wide variety of plants.

Repository

Wachtler's plant collection is stored at the Naturmuseum Südtirol in Bozen/Bolzano (Italy) and in the Museum Dolomythos at Innichen (San Candido). All items have the specimen code "KÜH" (for Kühwiesenkopf) or "PIZ" (for Piz da Peres) followed by a serial number.

Materials and Methods

This study is based on more than 4,000 rock slabs ranging from only a few centimetres up to one metre or more in thickness.

To date (2010) the fern fossil record is comprised of:

Gordonopteris: about 400 pieces

Neuropteridium: about 300 pieces

Anomopteris: about 300 pieces

Ladinopteris: about 150 pieces

Wachtleria: about 50 pieces

Marantoidea: about 30 pieces

Scythophyllum and *Peltaspernum*: about 400 pieces

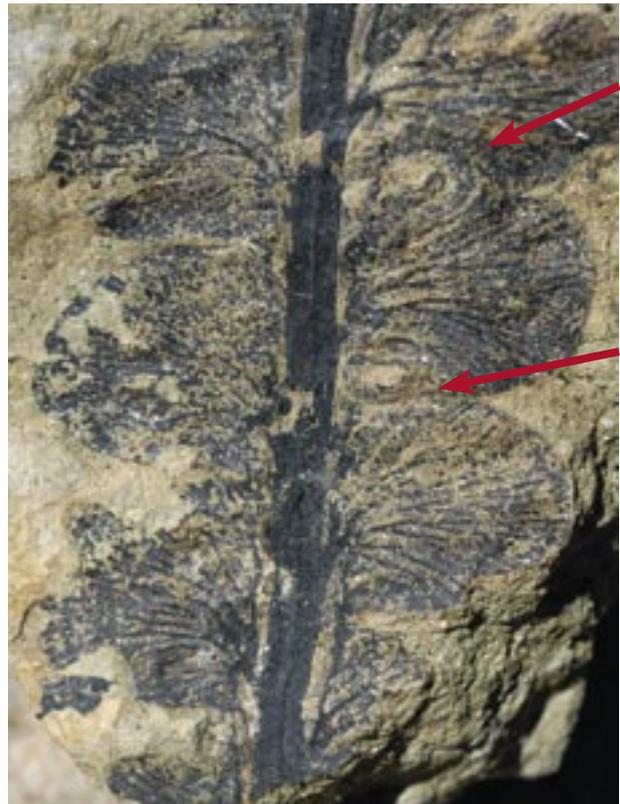
Sagenopteris: about 100 pieces.

These specimens were photographed under natural light using a Nikon D200 camera, with the following lenses: AF MICRO NIKKOR 60 mm 1:2.8 D and AF-S NIKKOR 17-35 mm 1:2.8 D for larger pieces. The digital images were processed using Adobe Photoshop CS version 8.0.

Interactions between animals and plants



Neuropteridium leaflet with marginal feeding traces of insects.



Coprolites produced by insects from a *Wachtleria* frond.

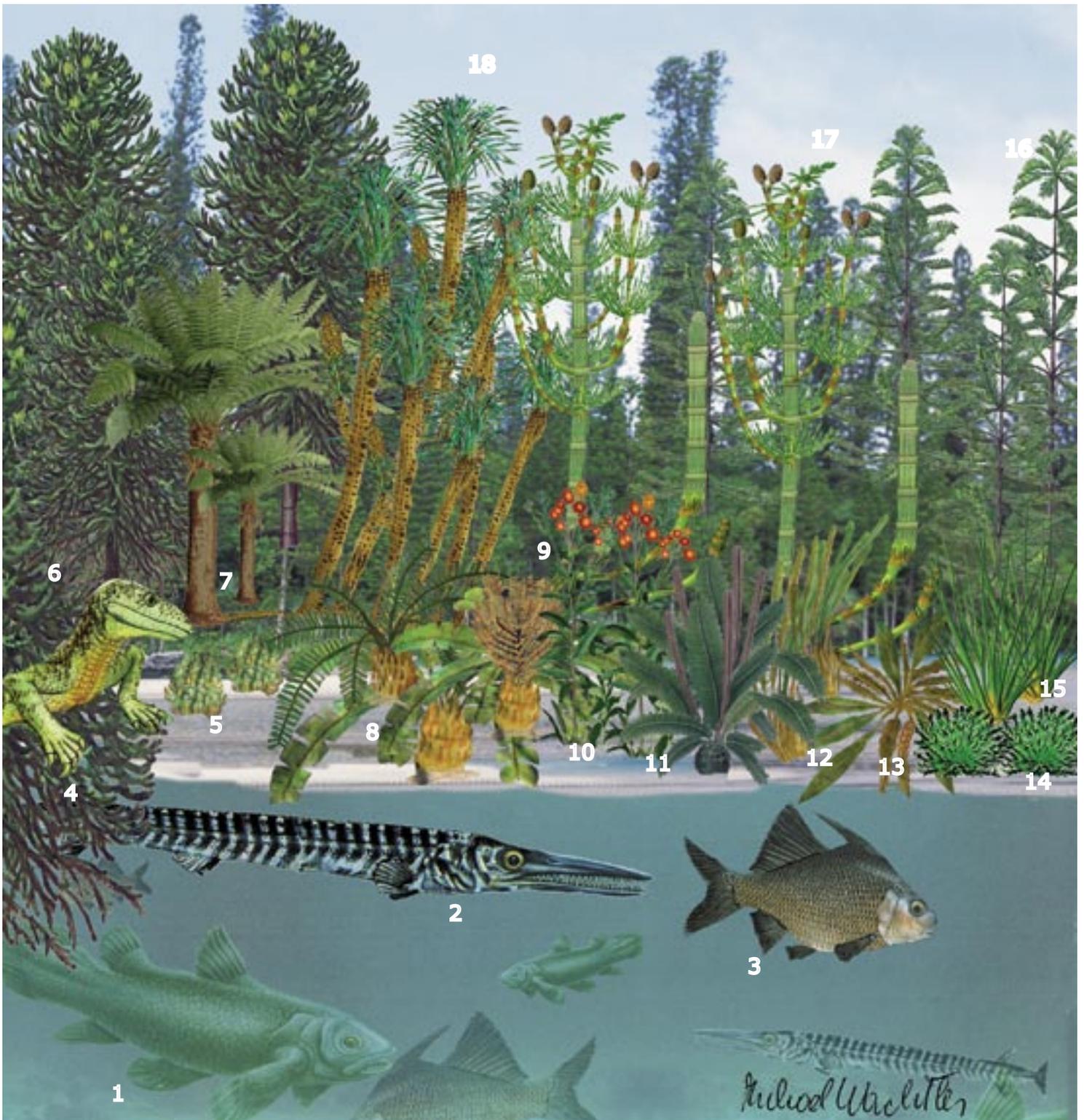


A beetle (Coleoptera) near a petiole of *Wachtleria*. An intensive and complex plant-pollinator relationship developed in the Early-Middle Triassic.



Leaflet with marginal feeding traces. Right: Typical juvenile involute *Gordonopteris* frond.





The Anisian landscape from Kühwiesenkopf in the Dolomites (241 million years ago). Reconstruction based on the findings of Michael Wachtler 1999–2009: 1) *Coelacanth*; 2) *Saurichtys*; 3) *Dipteronotus*; 4) *Megachirella wachtleri* (reptile); 5) *Lepacyclotes bechstaedtii* (lycopod); 6) *Voltzia* (conifer); 7) *Gordonopteris lorigae* (fern); 8) *Bjuvia olangensis* (cycad); 9) *Scytophyllum bergeri* (seed fern); 10) *Bjuvia olangensis* and *Dioonitocarpidium cycadea* (cycad); 11) *Neuropteridium elegans* (fern); 12) *Pizperesia* (cycad); 13) *Ladinia simplex* (cycad); 14) *Selaginellites leonardii* (lycopod); 15) *Isoetites brandneri* (lycopod); 16) *Voltzia ladinica* (conifer); 17) *Equisetites mougeotii* (horsetail); 18) *Lycopia dezanchei* (lycopod).

Ferns and seed ferns from the Piz da Peres



Gordonopteris lorigae



Scytophyllum bergeri



Sagenopteris keilmannii



Ladinopteris kandutschii



Marantoidea arenacea



Anomopteris mougeotii



Neuropteridium elegans



Wachtleria nobilis

Order FILICALES Bower, 1899
Family probably OSMUNDACEAE Bercht. and Presl, 1820
Genus *GORDONOPTERIS* Van Konijnenburg-Van Cittert et al., 2006

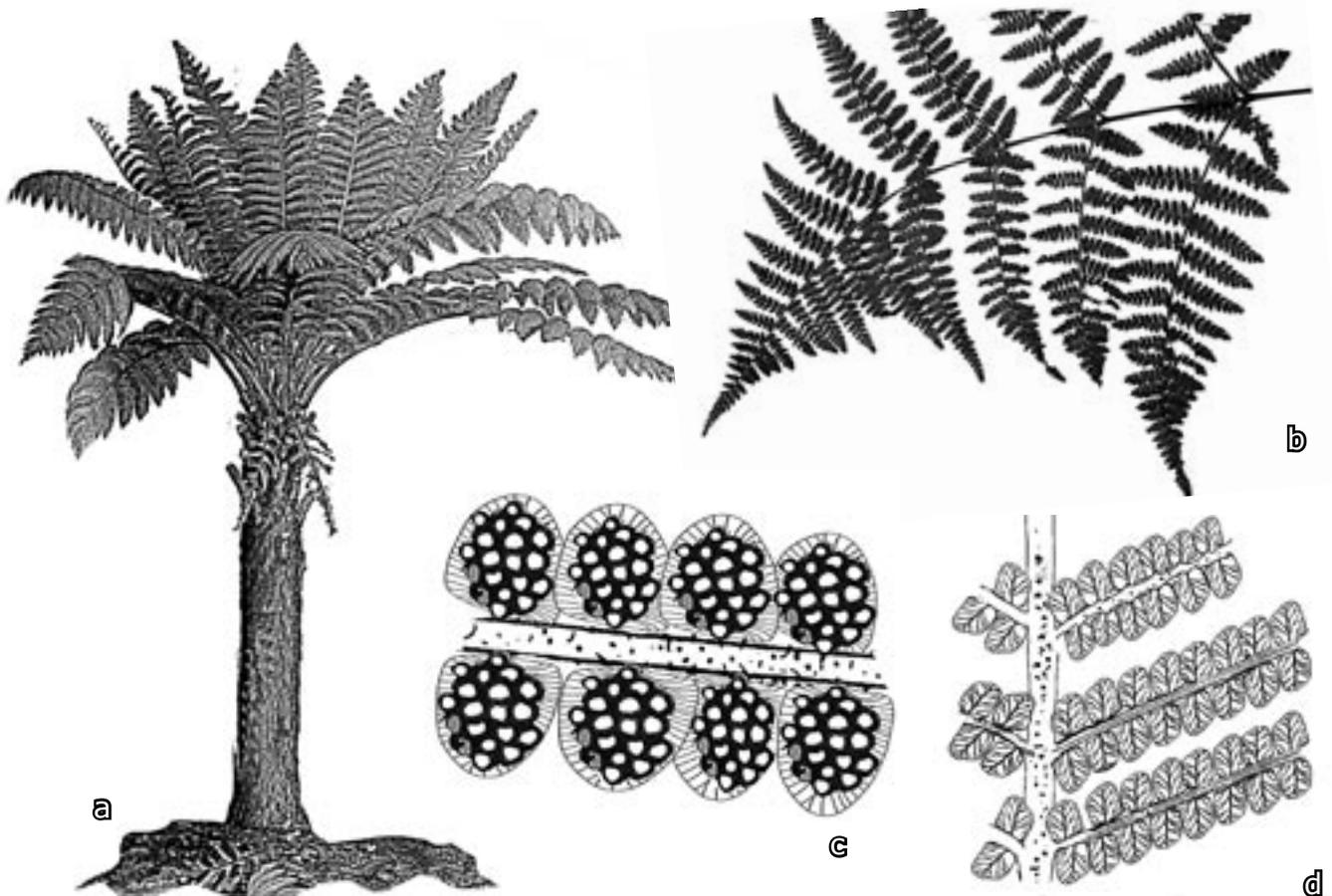
Gordonopteris lorigae

(Van Konijnenburg-Van Cittert et. al., 2006)

Description.

Gordonopteris lorigae was first found and described from the nearby Kühwiesenkopf (Van Konijnenburg-Van Cittert et al., 2006) and is one of the most common and typical ferns on Piz da Peres. 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. *Gordonopteris lorigae* is characterised by its tripinnate fronds, which probably exceeded one metre in length. Evidence suggests its classification as a tree fern. The pinnae of the first order arise alternately to sub-oppositely at angles of 45–60 degrees, and the pinnae of the second order usually grow sub-oppositely at 60–90 degrees (PIZ 252). They are relatively short (20–45 mm long and 4–5 mm wide). 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 (PIZ 116). 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 (PIZ 239).



Gordonopteris lorigae – a) Suggested whole plant; b) Single tripinnate frond (PIZ 252); c) Fertile pinnules (PIZ 239); d) Sterile pinnules (PIZ 116)



1



2



3



4

- 1) PIZ 252 *Gordonopteris lorigae*. Especially well-preserved section of a sterile frond (10 x 8 cm)
- 2) PIZ 116 *Gordonopteris lorigae*. Two pinnulae showing the vein-forking habitus (3 x 2 cm)
- 3) PIZ 239 *Gordonopteris lorigae*. Fertile pinnulae (5 x 2 cm)
- 4) PIZ 239 *Gordonopteris lorigae*. Detail of sporangia on the surface (2 x 2 cm)

Order FILICALES Bower, 1899
Family unknown, possibly OSMUNDACEAE
Genus ANOMOPTERIS Brongniart 1828

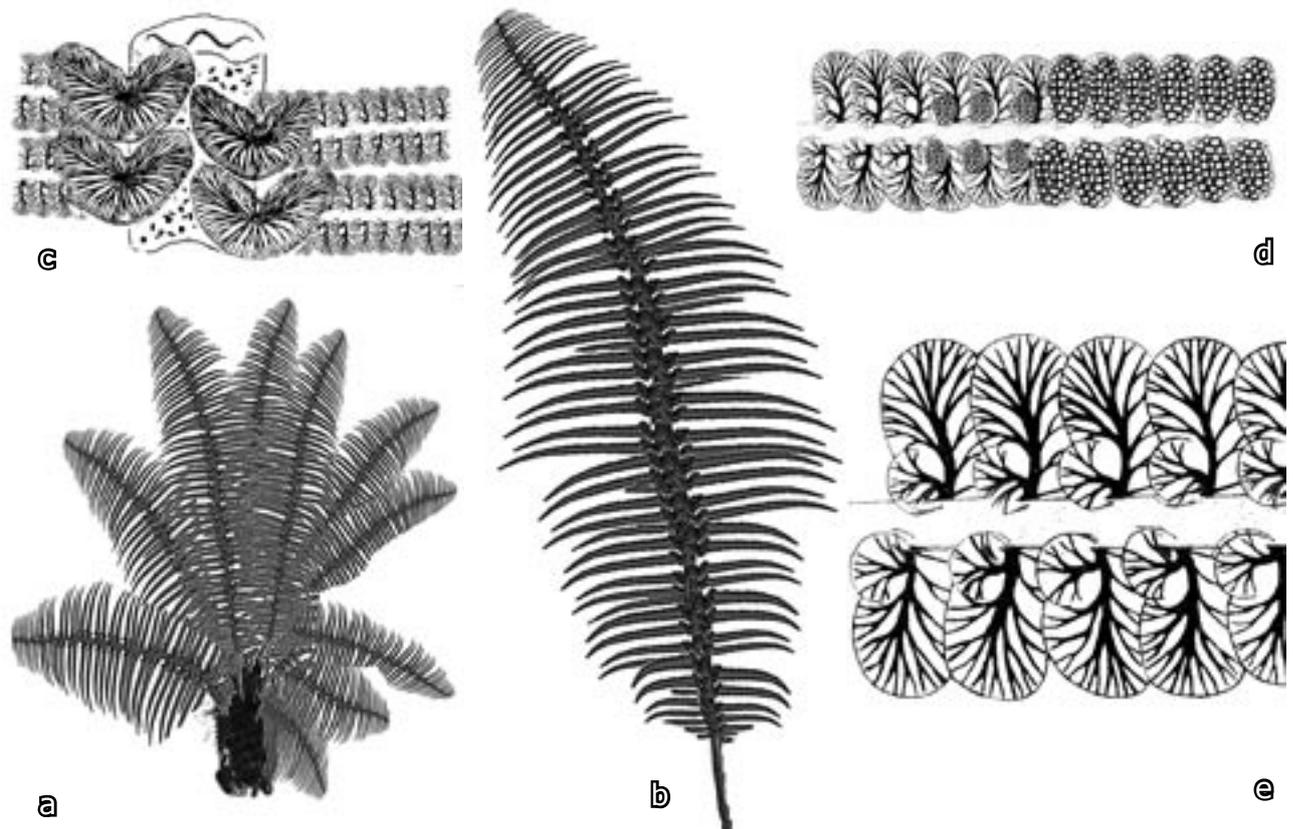
***Anomopteris mougeotii* Brongniart,
1828**

2006 *Anomopteris mougeotii* - Van Konin-
jnenburg-Van Cittert, p. 961, pl. 4, fig. 1, 3.

Description.

This fern was named by Brongniart – one of the pioneers of palaeobotany – as *Anomopteris* (anomalous fern), because for him it differed from all recent and fossil ferns. Its botanical affinity remains unclear, although the fertile pinnules including the spores have all the characters of the Osmundaceae, with the exception that an aplebia at the base of each pinna, the presence of a terminal sporangial annulus and the W-shaped frond outline have

never been recorded from the Osmundaceae. *Anomopteris* is one of the typical ferns of the German Buntsandstein (Frentzen, 1915), but is also recorded from the Vosges and other localities in France (Grauvogel-Stamm and Grauvogel, 1980), and extends as far as the Lower Triassic of China (Wang et al., 1978). It is abundant in the Anisian Stratas from Piz da Peres. The bipinnate fronds may reach a length of one metre 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 aplebia, at the base of each pinna are a feature. 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 visible only in the best-preserved specimens. Secondary veins arise from a strong midrib, usually forking once. The lower surface is covered with sporangia. Spores round, trilete, 25–40 µm in diameter with a punctate exospore.



Anomopteris mougeotii – Suggested fern structure: a) Whole plant, b) Single bipinnate frond, c) Rachis and aplebia, d) Fertile pinnae, e) Sterile pinnae.



- 1) PIZ 256 *Anomopteris mougeotii*. Part of a frond (15 x 10 cm)
- 2) PIZ 256 *Anomopteris mougeotii*. Detail showing the aplebia on both sides of the rachis (6 x 2 cm)
- 3) PIZ 395 *Anomopteris mougeotii*. Detail of the pinna (6 x 1.5 cm)
- 4) PIZ 515 *Anomopteris mougeotii*. Single pinnule showing strong midrib, from which secondary veins arise, forking once.
- 5) PIZ 218 *Anomopteris mougeotii*. Fertile pinnae (8 x 2.5 cm)
- 6) PIZ 218 *Anomopteris mougeotii*. Detail of fertile pinnules (4 x 1 cm)

Systematic Palaeontology
Order FILICALES Bower, 1899
Family unknown, possibly Osmundaceae or
Gleicheniaceae

Genus *Ladinopteris* gen. nov. WACHTLER

Generic diagnosis

Bipinnate fern with hairy rachis, secondary pinnae arising perpendicularly. Pinnules small and sessile with a typical consistent sunken midrib and almost invisible lateral veins. Unprotected sporangia not grouped in sori attached to the veins.

Etymology

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

Ladinopteris kandutschii WACHTLER, n. sp.

Holotype

PIZF 1101
Paratypes
PIZ 49, PIZ 249 (fertile part)
Material
PIZ 37, PIZ 219, PIZ 246

Etymology

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

Type localities

Piz da Peres, seldom Kühwiesenkopf

Type horizon and age

Dont Formation
Lower to Middle Triassic, Anisian, Pelson

Repository

Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

Diagnosis

Robust, leathery bipinnate fern with a consistent hairy rachis from which long slender, linear

pinnae arise perpendicularly. Pinnules small, triangular to oblong with a strong midvein from which originate almost invisible lateral veins, forking once. Spore sacs (or sporangia) on the under surface clustered along fine veins.

Description

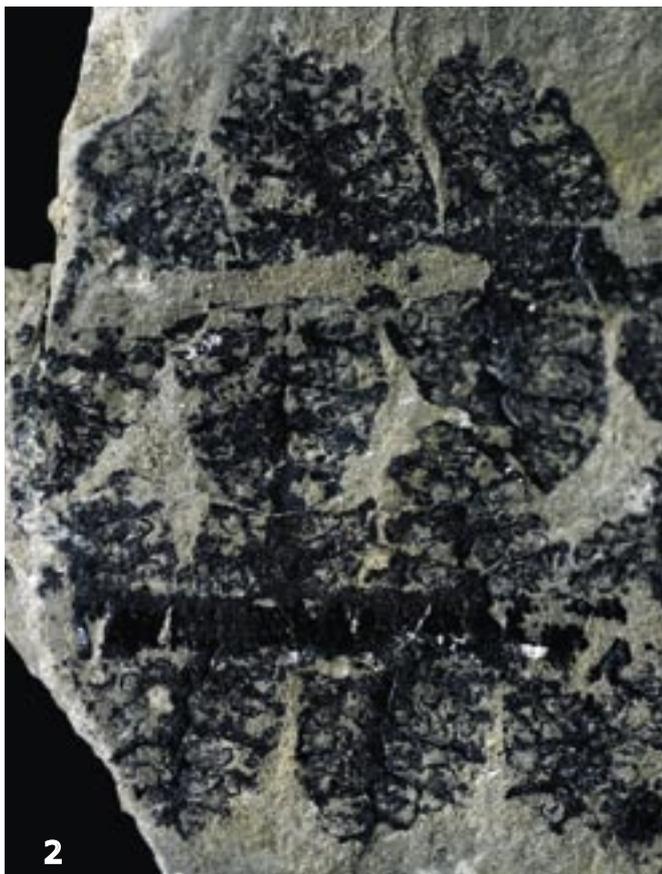
Fronde: The most complete specimen (PIZF 1101) is 60 cm long, 40 cm wide and has a bipinnate ovate to elliptic frond. Entire leaves may have reached lengths of over one metre. The rachis is 1.2 cm thick at the base, subtle hairs cover the stipe. Secondary pinnae arise perpendicularly, pointing slightly 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 midrib, secondary veins (in the majority of cases four on each side of the pinnules) arising from the midvein and forking once. They end near the margin, but are mostly undeveloped and are apparent only in well-preserved specimens (PIZ 37). Margin pointed to slightly rounded, sometimes both on the same secondary pinnae (PIZ 219).

Fertile fronds: Sporangia numerous (20–40 on each pinnula), large, spherical, not grouped into sori but clustered along the veinlets of the pinnules. Four to six sporangia are attached to each secondary vein.

Remarks

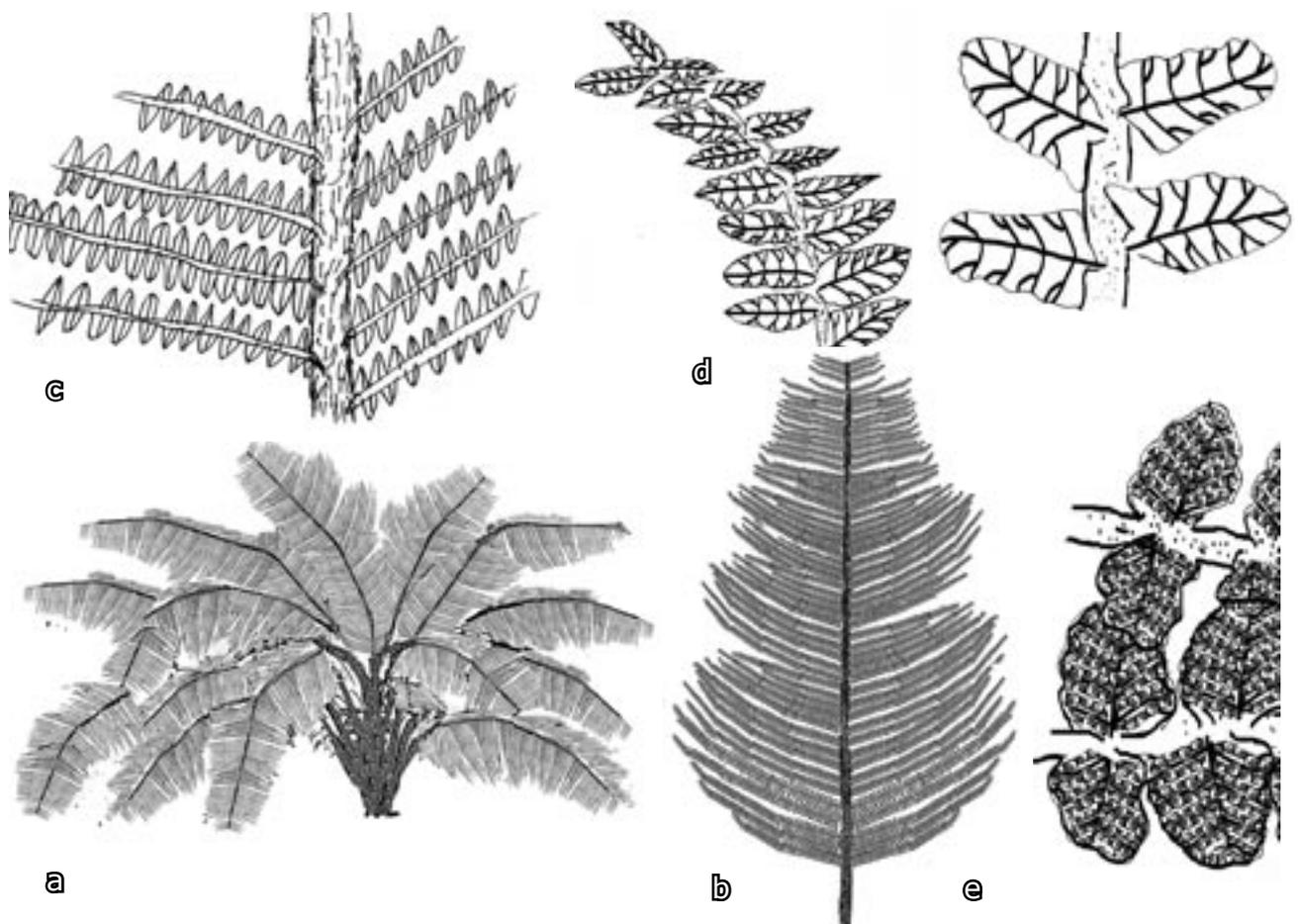
Ladinopteris kandutschii is common in the Piz da Peres flora. Interestingly this fern is found in typical *Voltzia recubariensis* beds, normally being the only other plant. This fern was probably well adapted to shady sites under the conifer vegetation. With their sunken midribs and leathery appearance the fronds show a superficial resemblance to *Anomopteris mougeotii*. However, the pointed triangular leaves are completely different from the small-sized rounded *Anomopteris* pinnule. Another consistent difference is the complete absence of aphaebias. Ferns with a rough resemblance were described from the Triassic of the Dolomites and placed in the morphogenus *Cladophlebis*: Leonardi (1968) mentioned *Cladophlebis ruetimeyeri*, and



- 1) PIZ 49 *Ladinopteris kandutschii*. Part of a frond (15 x 10 cm)
- 2) PIZ 249 *Ladinopteris kandutschii*. Fertile pinnules (3 x 2 cm) (Paratype)
- 3) PIZ 37 *Ladinopteris kandutschii*. Part of a sterile terminal frond showing the vein system (7 x 3 cm)

Wachtler & Van Konijnenburg (2000) *C. leuthardii*. Several *Cladophlebis*-species were also described from the Triassic of France and Germany (Fliche, 1910). None of them have revealed their exact relationship. In most cases they are too badly preserved, or belong to other ferns that are also found in the Anisian Piz da Peres. All also lack the triangular pinnula with the strong midrib. It is also difficult to determine the relationship to any extant fern species. Based on their leathery and minute pinnules they most resemble the Gleichenaceae. The primary upper frond stem branches fork two or three times in the Gleichenaceae, whereas this is never observed in *Ladinopteris*. On the other hand both ferns are covered with numerous, conspicuous bundles of short bristles. Heer (1904) and Schenk (1867) described some Gleicheniaceae from the German Triassic Schilfsandstein and Rhaetian: *Gleichenia*

gracilis and *Gleichenia microphylla*. Based on the descriptions of Schmidt (1928) they seem to be true Gleichenaceae with pinnae that fork several times. Schmidt noted two to four perfect rings of sporangia on each pinnula. The organisation of the sporangia is therefore totally different from that of *Ladinopteris*, in which the pinnules are also rounded. A relationship with other Triassic ferns is not apparent, and thus *Ladinopteris kandutschii* probably forms part of a new endemic tribe of the Anisian Alpine Trias vegetation. The arrangement of the sporangia otherwise tends to give more affinity with the ancient group of Osmundaceae. Since many Osmunda-like ferns have been found at Piz da Peres it is possible that they were the most frequent fern group at this time. If this theory is valid *Ladinopteris* was the most shade-adapted fern in the Anisian palaeo-ecosystem.



Ladinopteris kandutschii – Suggested fern structure. a) Whole plant, b) Single bipinnate frond (PIZ 1101), c) Portion of the rachis (PIZ 1101), d) Sterile pinnae (PIZ 37), e) Fertile pinnae (PIZ 249)



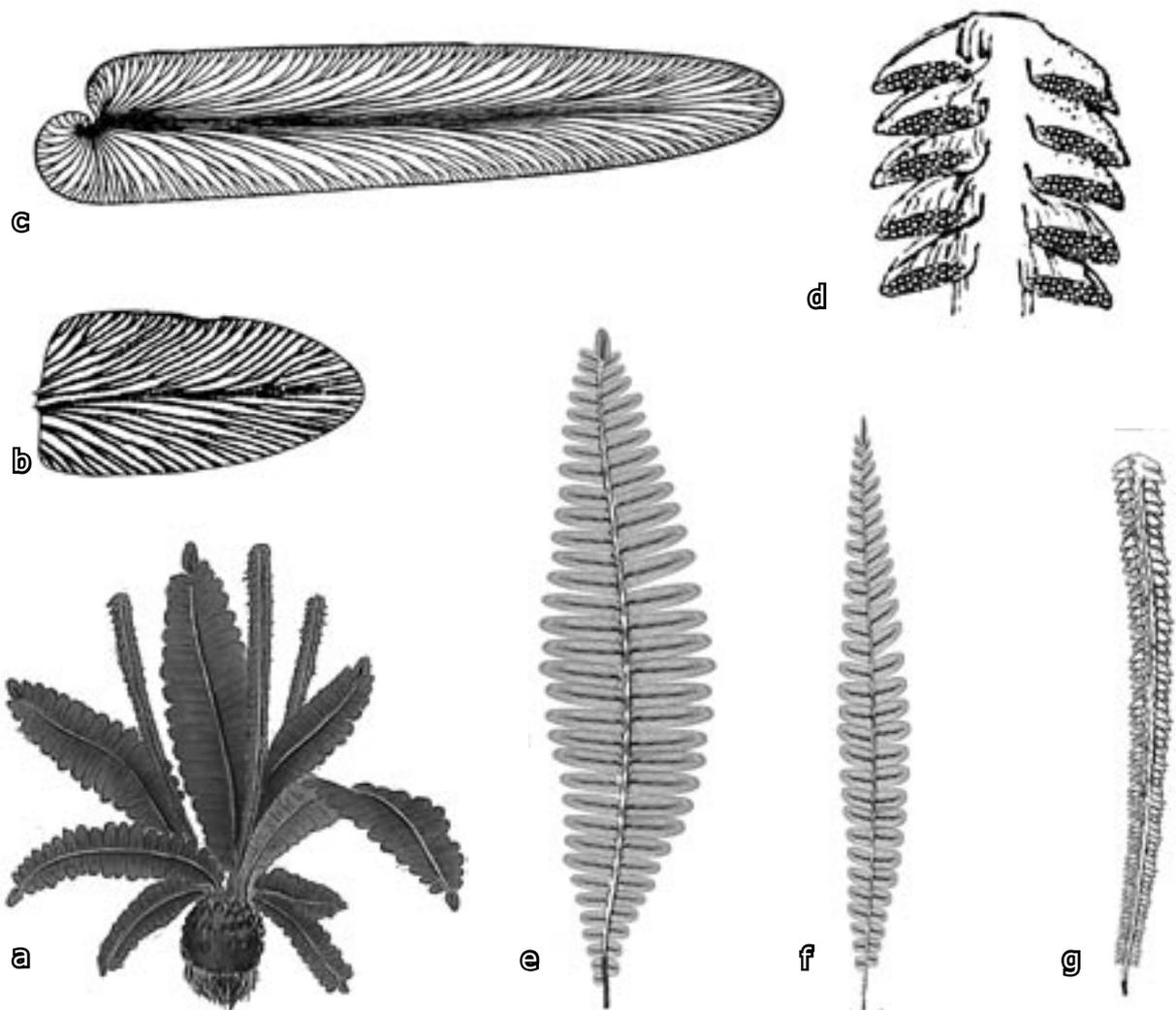
- 4) PIZF 1101 *Ladinopteris kandutschii*. Holotype. Mainly entire bipinnate frond (60 x 40 cm)
 5) PIZF 1101 *Ladinopteris kandutschii*. Details of the pinnules with a strong midrib and the hairy rachis (8 x 5 cm)
 6) PIZ 219 *Ladinopteris kandutschii*. Several pinnules, rounded on the upper side, pointed on the lower (3 x 1.5 cm)
 7) PIZ 246 *Ladinopteris kandutschii*. Several pinnules (15 x 5 cm)

Order FILICALES Bower, 1899
 Family ?OSMUNDACEAE Bercht. and Presl, 1820

**Genus NEUROPTERIDIUM
 Schimper, 1879**

As in the nearby Kühwiesenkopf two species of *Neuropteridium* were noted: *Neuropteridium elegans* and *Neuropteridium voltzii*. They are equally common. Several *Neuropteridium* species from the German Basin (*N. grandifolium*, *elegans*, *voltzii*, *intermedium*, *imbricatum*, *bergense*) could probably also

be reduced to only two or three species: *N. grandifolium*, *elegans* and *voltzii*. The fern *Neuropteridium* is one of the typical plants of the Early-Middle Triassic floras in Europe, and has been recorded from various localities in Germany and France, with a distribution that extends to China. The genus was recognised for the first time by Brogniart (1828) in the Vosges, whereas the fertile parts were for a long time thought to be a separate species, known as *Crematopteris* (Schimper & Mougeot, 1844). Detailed studies from Kühwiesenkopf yielded proof that *Crematopteris* (an illegitimate name,



Neuropteridium – Suggested fern structure: a) Whole plant *Neuropteridium elegans*, b) *Neuropteridium elegans* – single pinnula (PIZ 516), c) *Neuropteridium voltzii* – single pinnula (PIZ 156), d) *Scolopendrites* sp. fertile frond, e) *Neuropteridium voltzii* – entire frond, f) *Neuropteridium elegans* entire frond, *Scolopendrites* entire fertile organ.



- 1) PIZ 125 *Neuropteridium elegans*. Part of a pinnate frond (10 x 4 cm)
- 2) PIZF 56 *Neuropteridium voltzii*. Part of a pinnate frond (7 x 8 cm)
- 3) PIZ 516 *Neuropteridium elegans*. Single pinnula (1.5 x 1 cm)
- 4) PIZ 156 *Neuropteridium voltzii*. Single pinnula (2 x 1 cm)
- 5) PIZ 228 *Neuropteridium voltzii*. Extraordinarily long single pinnula (5 x 1 cm)

because Goeppert created the species *Scolopendrites* in 1836) was nothing other than the fertile frond of *Neuropteridium*.

Neuropteridium was a small fern, bearing a typical ovoid rhizome, rarely found with attached fronds. Usually 6 (PIZ 176) to 12 (specimen found in the Vosges) simply pinnate sterile fronds originate from one rhizome, along with totally different-looking fertile fronds called *Scolopendrites*. Only accurate analysis on isolated fructifications can doubtless attest to which *Neuropteridium* genera the fertile parts pertain. On Piz da Peres the fronds are occasionally well-conserved, showing all leaf veins in the maximum detail. Because the entire lower surface of the fertile pinnules is covered with sporangia, it is suggested that the fern *Neuropteridium* probably also belonged to the family Osmundaceae.

***Neuropteridium elegans*
(Brongniart, 1828) Schimper, 1879**

2006 *Neuropteridium elegans*; Van Konijnenburg-Van Cittert, p. 946.

Neuropteridium elegans was characterised from a 2–3 cm long petiole and an up to 20 cm long stipe, from which the pinnules arise more or less perpendicularly. The basal pinnules are small (from 4 x 2–3 mm) but increase rapidly in size to 15–20 x 6–7 mm before decreasing again towards the apex. The venation is typically neuropterid with a clear midrib that extends about one half to two-thirds along the pinnule and secondary veins that diverge and fork up to three times (PIZ 516). 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 in length but smaller and more pointed in *N. voltzii*, broader but shorter and rounded in *N. elegans*).

***Neuropteridium voltzii*
(Brongniart, 1828) Schimper, 1879**

2006 *Neuropteridium voltzii*; Van Konijnenburg-Van Cittert, p. 949.

Neuropteridium voltzii has longer (up to 7 cm PIZ 228) but narrower (4–6 mm) pinnules than *N. elegans*, resulting in a much larger length/width ratio. The pinnules are attached by almost their entire base, the apex is roundly acute. The venation is neuropterid with a clear midrib extending along about two-thirds of the pinnule. Secondary veins are numerous and fork two to three times (PIZ 156).

**Genus SCOLOPENDRITES
Goeppert, 1836**

***Scolopendrites scolopendrioides*
(Van Konijnenburg-Van Cittert, 2006)**

The fertile frond of the *Neuropteridium* ferns is characterised by hanging fertile pinnules, called *Scolopendrites*, on which the complete lower surface is covered with sporangia. As demonstrated above in the Anisian flora from Kühwiesenkopf two different species were noted: *S. scolopendrioides* belonging to the fern *Neuropteridium voltzii* and *S. grauvogelii*, the fertile form of *Neuropteridium elegans*.

***Scolopendrites grauvogelii*
(Van Konijnenburg-Van Cittert, 2006)**

The two *Scolopendrites* species are difficult to distinguish. The main difference lies in the shape and size of the sporangia (oval and twice as large, diameter about 600 x 200 µm) in *S. scolopendrioides*, whereas in *S. grauvogelii* they are round with a diameter of about 300–400 µm. The pinnules in *S. grauvogelii* are usually also somewhat shorter than in *S. scolopendrioides*. The spores of the two species are indistinguishable. They are trilete, circular in equatorial outline, with a diameter of approximately 35–45 µm. PIZ 176 is particularly interesting. This specimen shows a complete young *Neuropteridium* fern, probably *N. elegans*, with a rhizome, two fertile and four sterile fronds.



6) PIZ 176 *Neuropteridium elegans* – *Scolopendrites grauvogelii*. Entire juvenile plant with sterile and fertile fronds and an ovoid root system (12 x 7 cm)

7) PIZ 231 *Scolopendrites grauvogelii*. Fertile frond of *Neuropteridium elegans* (9 x 4 cm)

8) PIZ 501 *Scolopendrites scolopendrioides*. Fertile frond of *Neuropteridium voltzii* (2 x 2 cm)

OTHER FERNS FROM THE EARLY-MIDDLE TRIASSIC (ANISIAN) PIZ DA PERES (DOLOMITES – NORTHERN ITALY)

by
Georg Kandutsch
Hinterwinkl, 9543 Arriach, Austria, e-mail Alpdoc@aon.at

Abstract

Although most of the ferns from the Early-Middle Triassic Anisian layers of Piz da Peres probably belonged to the fern group Osmundaceae, as described elsewhere (Wachtler, 2011), there are other ferns whose classification is not yet clear. One small fern, *Wachtleria nobilis* gen. n. sp. nov., with an astonishing resemblance to the extant Lindsaeaceae, is described and its habitat analysed in this article. Other ferns with undefined affinities, including *Marantoidea arenacea*, which is only known from the German Keuper, as well as *Sphenopteris schoenleiniana*, are also mentioned. For the detailed geology and palaeoecology of Piz da Peres see previous work on the locality (Broglio, 2002; Van Konijnenburg-Van Cittert, 2006; Kustatscher, 2007; Wachtler 2010, 2011).

Online: January 2011.

Key words: fossil ferns, Dolomites, Italy, Middle Triassic, Anisian.

PTERIDOPHYTA incertae sedis

Genus SPHENOPTERIS Sternberg, 1825

Sphenopteris schoenleiniana (Brongniart, 1835) Presl, 1838

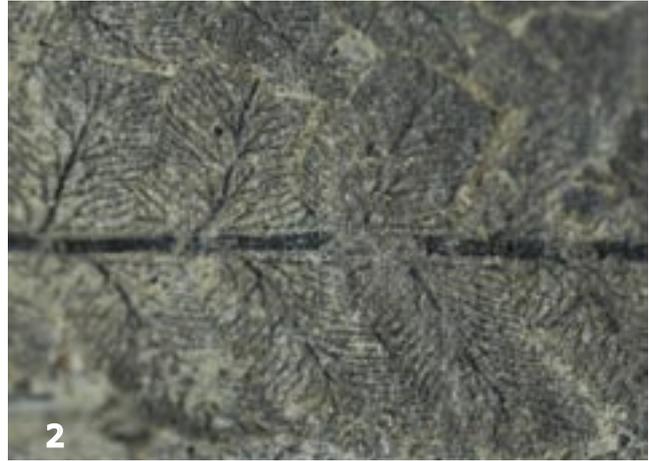
2006 *Sphenopteris schoenleiniana* (Van Konijnenburg-Van Cittert, p. 959).

Description.

Bipinnate to tripinnate fern, probably paripinnate, with fronds up to 80 cm long, with a slender rachis (5–8 mm) from which up to 20 cm long pinnae with equally slender ramifications (1–3 mm) fork perpendicularly. Pinnules (1–1.5 cm long and 3–5 mm wide) normally attached with only part of their base or midrib at an angle of 30–60 degrees. Pinnules slightly falcate to triangular ovate, demonstrating an undulating margin. The venation consists of a midrib that does not reach the apex, and twice-forking (PIZF 1102, PIZ 531) secondary veins

arising at c. 60 degrees. Fertile pinnae reduced, sometimes involute. Sporangial attachment areas at the end of the secondary veins. Single pinnulae or parts of fronds could be confused with *Neuropteridium*. A distinctive characteristic compared to the similar *Neuropteridium* pinnules, apart from their attachment only by the midrib, is that they are slightly falcate to triangular ovate and grow upwards. The most complete specimen (PIZF 1102) is 30 cm long and 25 cm wide.

Sphenopteris schoenleiniana has been recorded as a rare element in Europe from the 'Lettenkohle' (Ladinian) and 'Schilfsandstein' (Carnian) from Germany (Schenk 1864; Frentzen 1922a, b; Schmidt 1928; Kelber and Hansch, 1995). A similar species is *Acrostichites rhombifolia*, known from the German Buntsandstein. However, the pinnules seem to be smaller than in *Sphenopteris*. The 'pecopterid' form closely resembles *Cladophlebis ruetimeyeri*. The two species often occur in the same locality, but since they have never been found within one frond or attached to one rhizome, it is difficult to place them in one or the other genus.



- 1) PIZF 1102 *Sphenopteris schoenleiniana*. Part of a bipinnate frond (30 x 20 cm)
- 2) PIZF 1102 *Sphenopteris schoenleiniana*. Single pinnules (4 x 2 cm)
- 3) PIZ 531 *Sphenopteris schoenleiniana*. Part of a juvenile frond (8 x 5 cm)
- 4) PIZ 531 *Sphenopteris schoenleiniana*. Juvenile pinnules (5 x 1.2 cm)
- 5) KÜH 1402 *Sphenopteris schoenleiniana*. Fertile frond (10 x 5 cm)

Order MARATTIALES Prantl, 1874
Family MARATTIACEAE Bercht. and Presl,
1820

Marantoidea arenacea (Jaeger 1827)

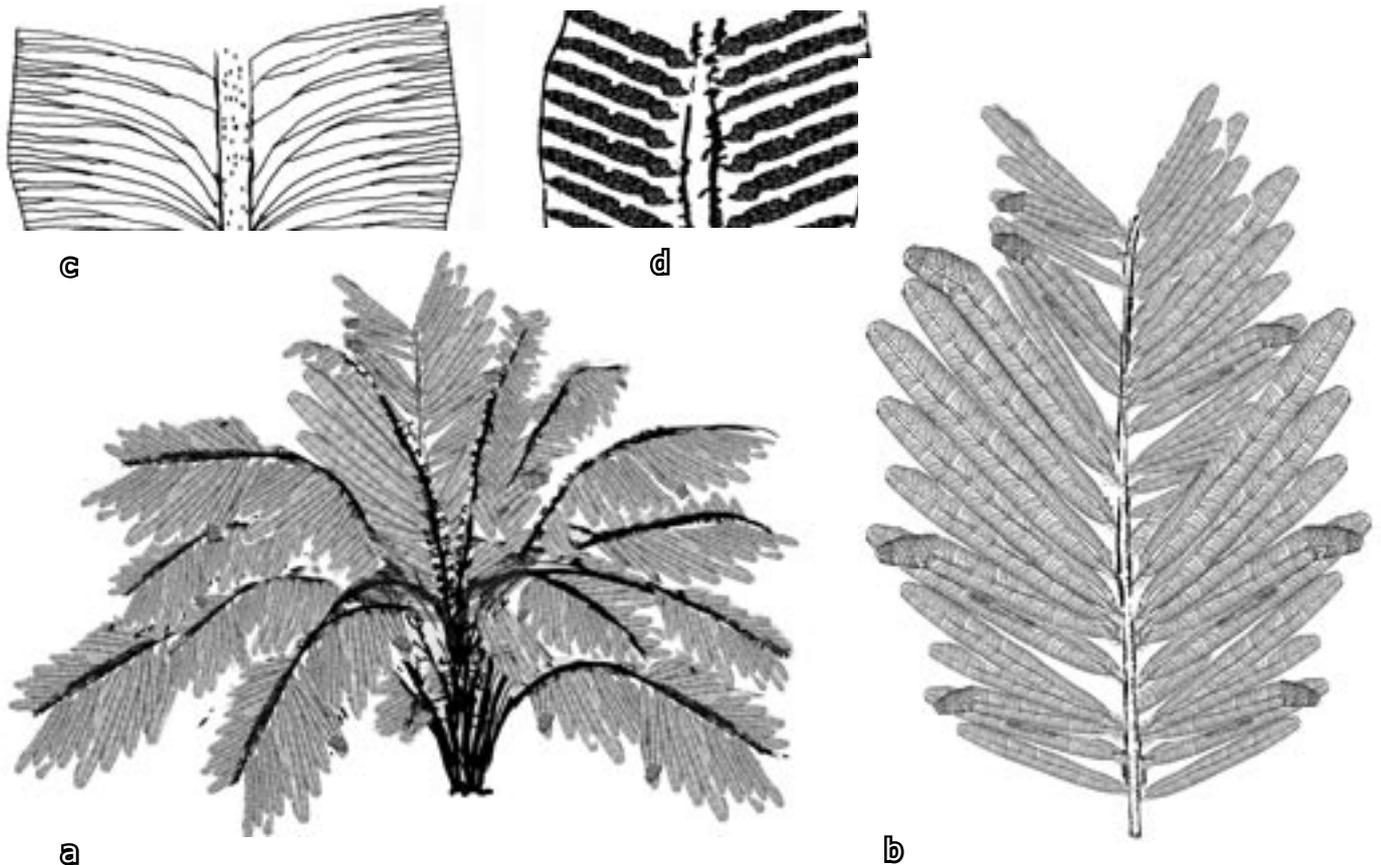
2006 *Marantoidea* sp. (Van Konijnenburg-
Van Cittert, p. 956, pl. 4, fig. 2, 4)

Description.

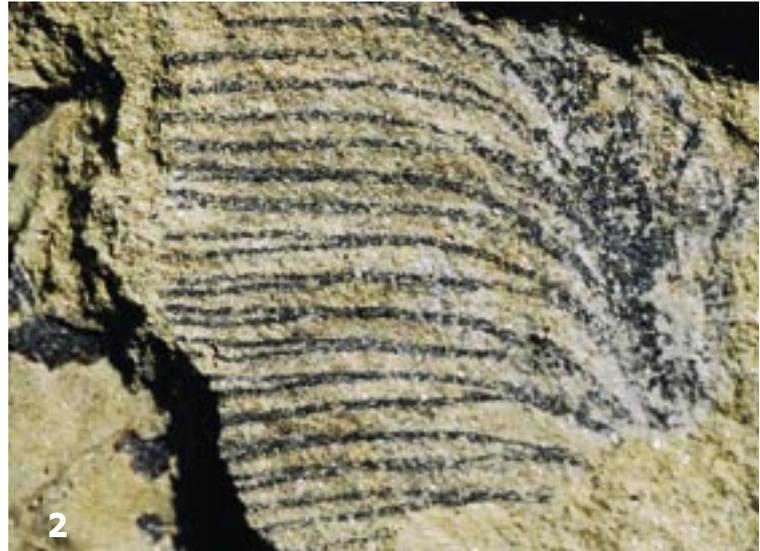
The fern *Marantoidea arenacea* is not rare on Piz da Peres, but complete fronds have not been found to date. The largest single leaves reach approximately 15 cm (PIZ 33). More or less entire *Marantoidea* fronds are known from the German Keuper under the name *Danaeopsis*. However, Presl (1838) created this genus illegitimately for material that had previously been described as *Marantoidea arenacea* by Jaeger (1827) and therefore leaves from Piz da Peres were also

given this term (Van Konijnenburg-Van Cittert, 2006). Parental affinities were established with the Marattiales, especially with *Angiopteris* and *Archangiopteris* (Kelber, 1995). *Marantoidea arenacea* from the German Keuper holds its sporangia in rows on the side veins. Because they are free and not connate to synangia they are classified as eusporangiate.

None of the pinnules from Piz da Peres is complete, but some reach from 10 to 15 cm in length, and up to 4 cm in width. They differ from the common cycadalean fronds, because secondary veins arise from a broad midrib (2.5–4 mm wide) at an angle of 70 degrees. These veins fork once or twice, usually near the midrib and once near the outer margin (PIZ 257). The veins reach the margin more or less perpendicularly at a concentration that varies between 8 and 16/cm. Some *Marantoidea* fragments (PIZ 561) appear to be the fertile part of a frond, but spores were not found.



Marantoidea arenacea – Suggested fern structure. a) Whole plant, b) Single frond, c) Sterile pinna (PIZ 257), d) Fertile part of a pinna (PIZ 561)



- 1) PIZF 33 *Marantoidea arenacea*. Part of a pinna (14 x 6 cm)
- 2) PIZ 257 *Marantoidea arenacea*. Detail of a pinna, forking two times (3 x 2.5 cm)
- 3) PIZF 1416 *Marantoidea arenacea*. Part of a pinna (12 x 4 cm)
- 4) PIZ 561 *Marantoidea arenacea*. Part of a fertile pinna (6 x 3 cm)

Order FILICALES Bower, 1899
Family unknown, possibly LINDSAEACEAE Dry-
ander 1793

***Wachtleria* gen. nov. KANDUTSCH**

Generic 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.

Etymology

Named after Michael Wachtler, who discovered the Fossilagerstätte Piz da Peres - Kühwiesenkopf and carried out extensive palaeontological research in the Dolomites.

***Wachtleria nobilis* KANDUTSCH sp. nov.**

Holotype

PIZ 303
Paratypes
PIZ 520 (fertil part), PIZ 311 stipes
Material
PIZ 305, PIZ 167, PIZ 217, GSTATTL 1 + 2.

Etymology

Nobilis, latin name for elegant.

Type localities

Piz da Peres, Gstattl - Prags

Type horizon and age

Dont Formation
Lower to Middle Triassic, Anisian, Pelson.

Repository

Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

Diagnosis

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, midrib absent. Fertile pinnae deflexed on the outer margin. Sorus in the form of a continuous line of sporangia covered by the reflexed leaf margin.

Description

Fronds: Stipe slender, 20–40 cm long, the first 10–15 cm without pinnae. PIZ 311 shows several delicate, up to 30 cm long stipes with attached sterile pinnules on the 3 mm rachis. PIZ 303 is the best-preserved specimen with fertile and sterile fronds on the same slab. Stipes are 5 mm wide, with a single vascular strand. They are linearly erect and long in proportion to the thickness of the rachis. The leaves touch each other and are shortly stalked, especially in specimen GSTATTL1.

Fertile fronds: PIZ 303 shows several well-preserved sterile leaves and one fertile leaf from the upper side. Sterile pinnae taller, flexed on the margin to cover the sporangia. One of the pinnae on specimen PIZ 303 clearly shows the flexion used to protect the sori arranged on the margin. The best-preserved fertile frond (PIZ 520) shows the underside of a frond. Each pinnula measures 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. On slab PIZ 520 two sporangia on the third pinna are open, showing that they have shed their spores. KÜH 444 could also belong to *Wachtleria* or is closely related.

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 (PIZ 303). The venation arises from the lower basal angle of the pinnae, the midvein 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.

Remarks

The fern *Wachtleria nobilis* is not very rare on Piz da Peres West. In certain lenses it is

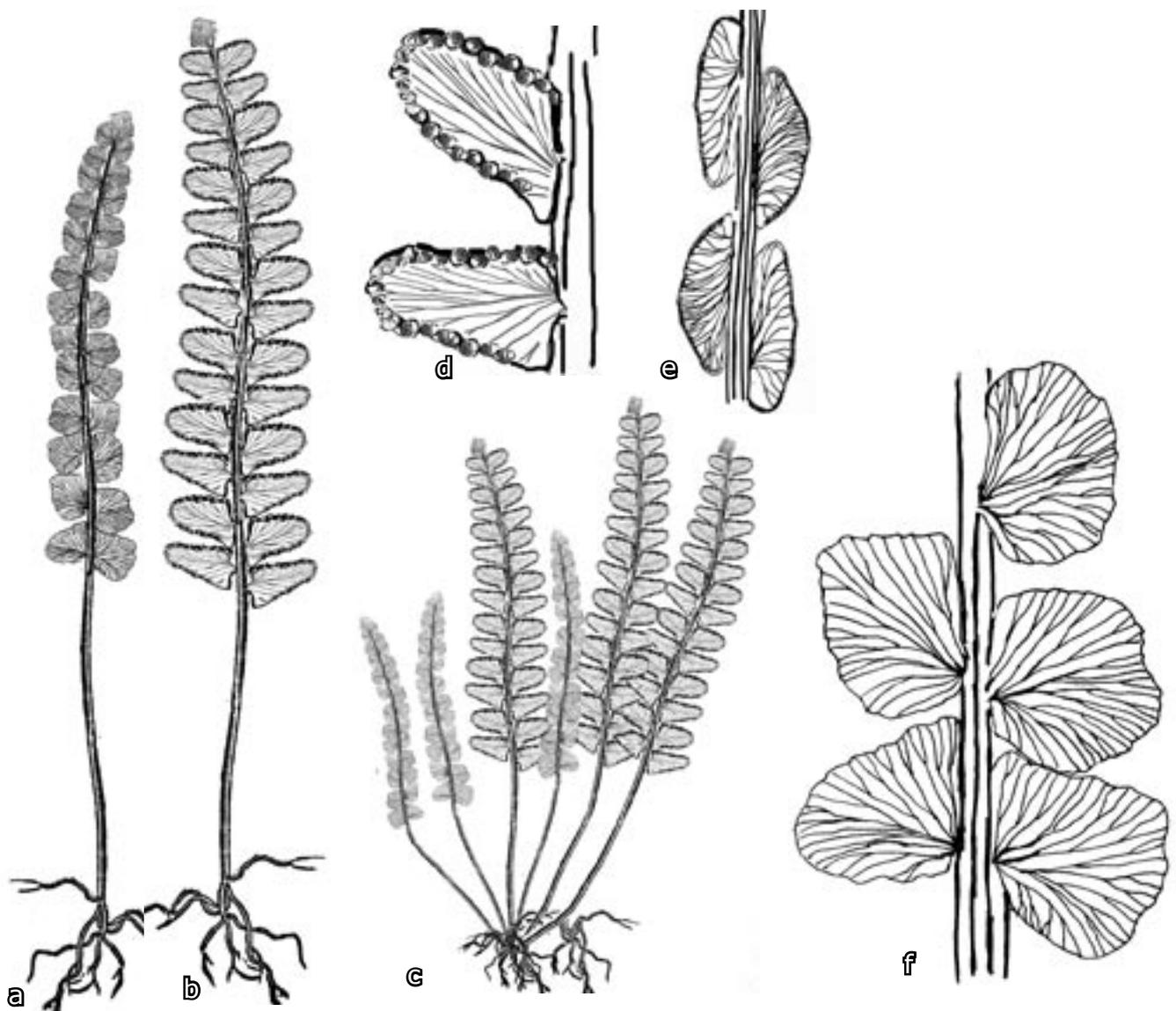


- 1) PIZ 303 *Wachtleria nobilis*. Holotype. Part of a sterile pinnae (10 x 4 cm)
- 2) PIZ 303 *Wachtleria nobilis*. Holotype. Part of a fertile pinnae, seen from the surface (6 x 3 cm)
- 3) PIZ 303 *Wachtleria nobilis*. Holotype. Part of a sterile pinnae, showing attachment of pinnules (2.5 x 3 cm)

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 (Duncan et al., 1986). 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). In the literature on Early and Middle Triassic floras, only *Neopteridium curvinerve* (Wang and Wang, 1990) from Scythian sediments in China could have some resemblance. Their pinnules are triangular with an obtusely pointed apex and wide base. Apart from the close-meshed venation, the more or less rhomboidal pinnules and the missing fertile parts, the material differs from *Wachtleria*. The genus *Neopteridium* is also thought to pertain to the osmundaceous ferns.



Wachtleria nobilis – Suggested fern structure: a) Single frond sterile (PIZ 311), b) Single frond fertile, c) Whole plant, d) Fertile part (PIZ 520), e) Fertile pinnae surface (PIZ 303), f) Sterile pinnae (PIZ 303).



4) PIZ 311 *Wachtleria nobilis*. Several sterile pinnae showing the slender stems (30 x 14 cm)

5) PIZ 520 *Wachtleria nobilis*. Part of a fertile pinnae. The sporangia are arranged in a row on the margin (8 x 4 cm)

6) PIZ 520 *Wachtleria nobilis*. Part of a sterile pinnae, showing the attachment of pinnules (2,5 x 3 cm)

SEED FERNS FROM THE EARLY-MIDDLE TRIASSIC (ANISIAN) PIZ DA PERES (DOLOMITES – NORTHERN ITALY)

by

Michael Wachtler

P. P. Rainerstrasse 11, 39038 Innichen, Italy, e-mail michael@wachtler.com.

Abstract.

Two different seed fern species are common on Piz da Peres: *Scytophyllum bergeri*, belonging to the Peltaspermales and *Sagenopteris keilmannii* n. sp., a seed fern belonging to the Caytonales, easily recognisable because of its meshed and reticulated leaves. Their suggested ovulate organs were recovered from both, along with probable microsporophylls from *Scytophyllum*. *Caytonia fedelei* n. sp. is thought to be the ovulate organ of *Sagenopteris keilmannii* n. sp. Since *Sagenopteris keilmannii* n. sp. constitutes perhaps the earliest record of this genus, their fructifications are of special interest and could give new insights into the evolution of the Caytonales. *Peltaspermum bornemannii*, the ovuliferous macrosporophyll of *Scytophyllum bergeri*, is described in detail, as well as *Pteruchus deznignii* n. sp., which is cautiously suggested to be a new pteridosperm pollen-bearing organ belonging to *Scytophyllum*.

Online: January 2011.

Key words: Seed ferns, Dolomites, Italy, Middle Triassic, Anisian.

Description.

Unlike the Carboniferous pteridosperms, the so-called Mesozoic seed ferns have never been considered to represent a natural group, but instead have been regarded historically as separate orders or families with uncertain affinities. Three major groups of Mesozoic seed ferns have been established: Caytonales, Peltaspermales and Corystospermales. However, only their Mesozoic age and the presence of ovule-bearing sporophylls and pollen organs unite them (Taylor, 2006). In the Early-Middle Triassic seed ferns *Scytophyllum* and *Sagenopteris* from Piz da Peres we have two interesting shrubby plants that are transition forms between the Palaeozoic and Mesozoic. Whereas *Scytophyllum bergeri* appears to have originated from some callipteroid Palaeozoic seed fern, this is not the case for *Sagenopteris*. Its Paleozoic ancestors remain obscure.

Historically the Peltaspermales were thought to be exclusively Mesozoic. However, more recently it was proven that they were widespread and abundant in the Permian vegetation, appearing at least as early as the late Carboniferous. In the last decennia actin-

omorphous *Peltaspermum* megasporophylls have been recorded from various Eurameria, Angara and Cathaysia fossil sites, which attest to their global diffusion beginning from the late Carboniferous. Although the cupula-like shields are easily assignable to the Peltaspermales the origin of their microsporophylls is more complicated. Usually the Peltaspermales are thought to have pollen organs of the *Antevisia*-type. This is true for *Lepidopteris* fronds, one of the type-fossils of the Gondwana flora. Male fructifications have never been recorded for *Scytophyllum*. Since the newly discovered microsporophylls from Piz da Peres that are attributable to *Scytophyllum bergeri* have nothing in common with *Antevsia* pollen organs, the microsporophyll was cautiously inserted into the pollen-bearing group of *Pteruchus*. Until further investigations clarify the situation, *Pteruchus deznignii* from Piz da Peres will be described as an enigmatic pollen organ with both peltasperm and corystosperm characteristics. The persistence of the Peltaspermales well into the Mesozoic makes this one of the longest existing of the pteridosperm lineages originating in the Palaeozoic (Kerp et al., 2001).

Order PELTASPERMALES Taylor, 1981
Family PELTASPERMACEAE Pilger and Melchior, in Melchior and Werdermann 1954

Scytophyllum bergeri **Bornemann, 1856**

Scytophyllum bergeri (Kustatscher et. al. 2007)

Description.

Scytophyllum bergeri bears paripinnate fronds, with an axis sometimes covered by scales. The leaves are attached opposite each other or alternately and arise from a primary rachis with a short petiole or are broadly to obliquely attached. Leaves variable, from lanceolate to elongated, reaching substantial lengths, entire to lobed, sometimes with incisions resembling small pinnules. The longest leaves reach 18 cm by 3 cm (PIZ 243). They are attached opposite each other or alternately and arise from a primary rachis with a short petiole or are broadly to obliquely attached. The leaves often have a leathery, lacerated consistency; only in young or in apical leaves are they tiny and entire. The variability in the leaves suggests an adaptation to sun or shade. The apex is usually rounded, the margin in full-grown leaves undulating (PIZ 243). Apical leaves are often paripinnate (PIZ 51), the axis covered by leaf scales. The venation on the midrib is distinct, the secondary and tertiary veins only sometimes visible. PIZ 51 clearly shows the composition of the veins. From a strong midvein arise tiny mostly invisible lateral veins, which fork several times. KÜH 2173 shows a graft, in which three to four seedlings, each bearing young *Scytophyllum* leaves, arise from a root system. This suggests that *Scytophyllum* was more of a shrub than a small tree, probably reaching one or two metres in height.

Remarks

The seed fern *Scytophyllum bergeri* with its ovuliferous organ *Peltaspermum bornemannii* is a common fossil in the Piz da Peres area and is easily recognised by its leaf-

lets. Unfortunately the fossilised leaf tends to peel away from the stone slab following recovery of the specimen.. The best way to recover them is to fix the pinnae with hair spray without exposing them to sunlight. Another interesting property is that the fronds glow in ultraviolet light. The ancestor of *Scytophyllum* was probably a Callipteroid seed fern, possibly *Autunia conferta*, an important Permian fossil that has been recorded from the nearby Carinthian Kötschach-Mauthen (Amerom, H. et. al., 1976) and also from the Upper Permian of the Bletterbach Gorge in the Dolomites. (*P. martinsii* - Vörding B., 2008).

It is not clear how the callipterids survived beyond the Permo-Triassic crisis. The ancestral subgroup of Peltaspermales can be traced to the callipterids, represented by the genera *Autunia* and *Rhachiphyllum*. Fronds of *Autunia conferta* were relatively compact, up to 80 cm in length in species from the Rotliegend (DiMichele, 2005). Callipterid fronds were also paripinnate, with alethopteroid, sphenopteroid and flabeliform pinnules. Typical intercalary pinnae (Zwischenfiedern) were situated on the primary rachis. Pinnules varied in shape, from profoundly lobed to entire-margined. However, some *Scytophyllum* leaves looked more like a frond with pinnules. The slightly lateral-forking midveins also suggest pinnae (KÜH 2173, KÜH 1196). Specimens similar in gross morphology to *Scytophyllum*, named *Supaia thinnfeldioides*, occurred in the Permian. They had linear, lanceolate pinnules with acute to rounded apices, well-developed midveins extending almost to the apex, and high-angle lateral veins, thus most resembling the Piz da Peres *Scytophyllum* leaves. In addition, the scales on the main rachis could be interpreted as reduced incalary pinnae (Zwischenfiedern) (PIZ 243, KÜH 963). If the assumption of small *Callipteris* bipinnate frond-accretion versus fused and therefore now elongated *Scytophyllum* pinnula is true, we thus have another well-documented example of rapid changes in a extremely short period of time in the Piz da Peres plant assemblage, in addition to the cycadean *Bjuvia*. Because many plants from the Early-Middle Triassic Piz da Peres appear to have changed rapidly, climatic or atmospheric events were probably the catalyst.

Genus *PELTASPERMUM* Harris, 1937

Peltaspermum bornemannii
(Kustatscher et. al., 2007)

Description

The seed-bearing organ of *Scytophyllum bergeri*, classified as *Peltaspermum bornemannii*, consists of an axis, bearing alternate branches, which dichotomize several times and bore terminal, peltate and lobed discs with ovules on the lower surface. These seed-bearing fructifications are usually isolated, but one specimen (PIZ 521) showed aggregation of lateral branches with typical segmented shields on a central axis. Ten axes are apparent, with two umbrella-shaped discs, 15 mm in diameter, attached. The lower surface of the cupulate head reveals 15–16 distinctive ribs, that taper and end on an inner ring with a central depression. In the whole vessel-like depression protected by leaf-like membranes there is space for about 20–40 small (5 mm) rounded to elongated seeds. Full-grown discs could reach a diameter of 25 mm (PIZF 8, PIZF 47). This suggests that the mature seeds were dropped or ejected after maturity from the cupulas. PIZF 47 shows an almost mature disc, KÜH 2148 a shield with exposed seeds. The upper surface (KÜH 2172) is attached to the axis by a marginal 5 mm thick petiole and is completely flat and plain. Only small and irregular swellings from the seeds are visible (KÜH 2008).

Remarks

Like *Scytophyllum*, *Peltaspermum bornemannii* also has its ancestor in Permian fructifications. The most closely related was probably *Peltaspermum martinsii*. Although smaller and with only 9–10 ribs and containing only half the seeds it shows all the characteristics of the Triassic *Peltaspermum*. The main difference between the Palaeozoic *Peltaspermum martinsii* and Anisian-Mesozoic *P. bornemannii* lies in the wedge-shaped radially arranged ribs on a central axis. They were often distinct from each other in the Palaeozoic, whereas in the Mesozoic

Peltaspermum bornemannii the single ribs were fused together. The Palaeozoic saw the beginning of the worldwide radiation of the Peltaspermales with their manifold leaf- and frond-systems, distinguishable in every case by their typical peltate disks.

Order CAYTONIALES Thomas, 1925
Order ?PELTASPERMALES-CORYSTOSPERMALES

Genus *Pteruchus* Thomas, 1933

***Pteruchus dezzignii* WACHTLER, sp. nov.**

Holotype.

PIZ 105

Etymology

Named after Baron Achille de Zigno, an Italian palaeobotanist of the 19th century, who searched in the Anisian Stratas of Recoaro.

Type locality

Piz da Peres

Type horizon and age

Dont Formation.
Lower to Middle Triassic, Anisian, Pelson

Repository

Natural History Museum Südtirol, Bozen.

Diagnosis

Microsporophyll consisting of leaf-like pinnales arranged on a central axis with a basal stalk and a distal flattened head. Pollen sacs attached on the abaxial surface of each pinna.

Description

Although *Scytophyllum bergeri* forms one of the most common leaf impressions on Piz da Peres, and the associated ovuliferous organs *Peltaspermum bornemannii* are also numerous, pollen organs have never been recovered with certainty. Only one, with its



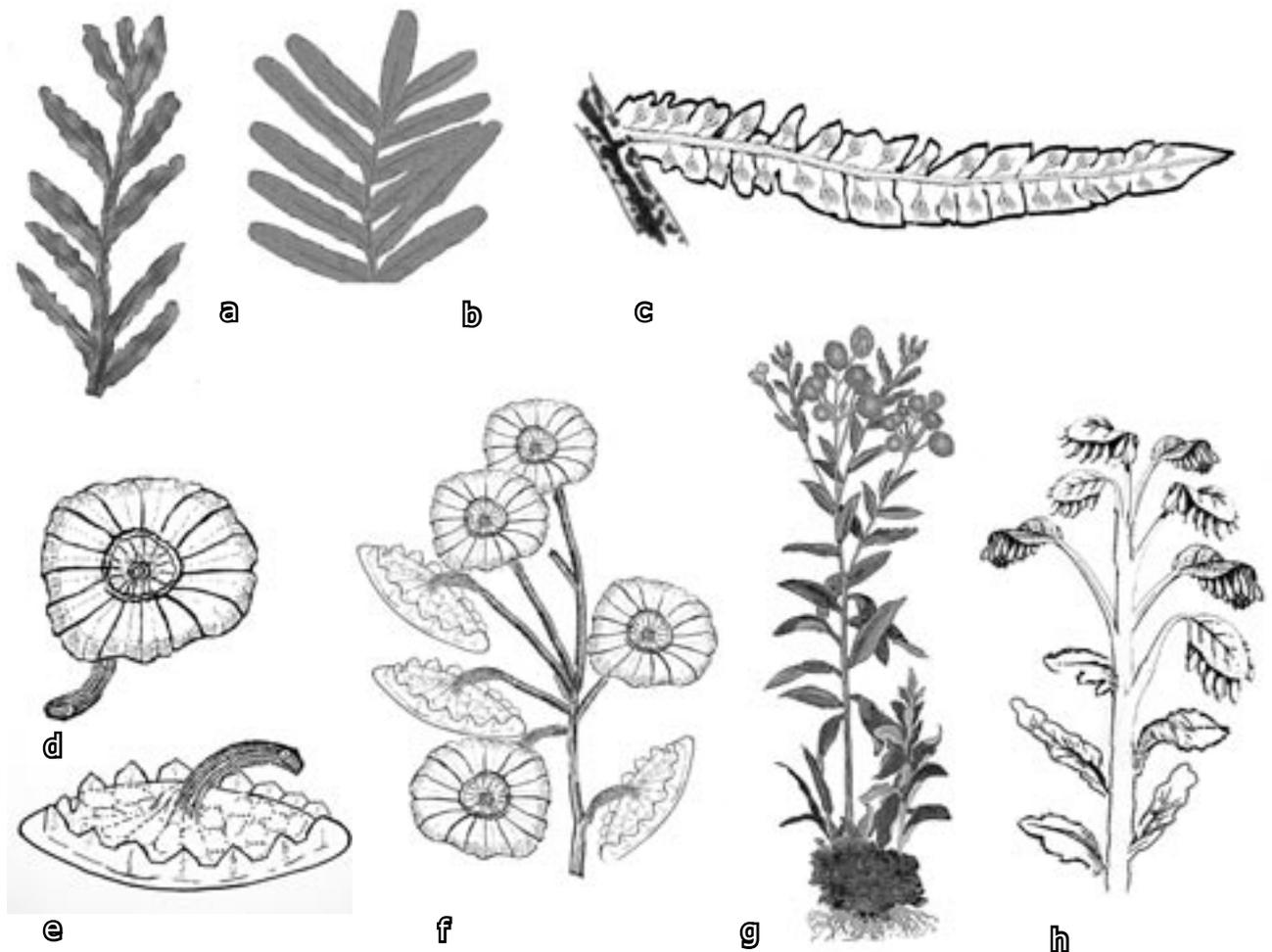
- 1) PIZ 243 *Scytophyllum bergeri*. Part of a huge pinnate frond (15 x 20 cm)
- 2) PIZ 51 *Scytophyllum bergeri*. Pinnae showing a distinct midvein (12 x 10 cm)
- 3) KÜH 2173 *Scytophyllum bergeri*. Young plant with rhizome (15 x 8 cm)

attached foliage and overlying pollen substance is thought to belong to *Scytophyllum*. Until further analysis its exact affiliation will remain enigmatic. PIZ 105 consists of an 8 cm long axis that holds four to five small sterile leaves on the lower part. Their habitus and the typical mode of cuticle peeling suggest their classification as *Scytophyllum bergeri*. Eight fertile pinnae with an entire margin arise sub-oppositely to alternately on the upper side of the rachis. The microsporophyll laminae are ovate, up to 1 cm long and 0.8 cm wide, with entire margins and a slightly irregular surface. The venation of the lamina is indistinguishable. The abaxial side of the flattened leaves holds approximately 20 elongated pollen sacs in one row. Exactly how many rows of pollen sacs

there are is not clear, but four have been estimated, along with 80 pollen sacs. The pollen sacs are up to 2 mm long, 0.5 mm wide. The entire surface of the slab is covered with pollen grains.

Remarks

The pollen organs from Peltaspermales, to which *Scytophyllum* is thought to belong, are usually of the *Antevsia*-type. They include branched axes that bear a lateral group of 4–12 elongated pollen sacs at their distal tips (Taylor, 2009). Surprisingly *Pteruchus deznii* has no affinity with *Antevsia*, but bears a close resemblance to the pollen organs from another Mesozoic seed fern group: the *Corystospermales*. These also have pol-



Scytophyllum bergeri – Suggested reconstruction: a) Leaf type (KÜH 1195), b) Leaf type (KÜH 479), c) Leaf (KÜH 2172), d) *Peltaspermum bornemannii* ovuliferous organ, lower part (PIZF8), e) *Peltaspermum bornemannii* ovuliferous organ upper part (KÜH 2172), f) *Peltaspermum bornemannii* ovuliferous organ (PIZ521), g) *Scytophyllum bergeri* + *peltaspermum bornemannii* – whole plant, h) *Pteruchus deznii* pollen organ (PIZ 105).



- 4) PIZ 521 *Peltaspermum bornemannii*. Mostly complete ovuliferous organs (8 x 7 cm)
 5) PIZ 521 *Peltaspermum bornemannii*. Detail of the lower surface (2.5 x 2.5 cm)
 6) PIZF 8 *Peltaspermum bornemannii*. Another fruiting body. Seeds immature, born under each lobe (2.5 x 2.5 cm)
 7) PIZ 47 *Peltaspermum bornemannii*. Almost mature fruiting body (2.5 x 2.5 cm)
 8) KÜH 2148 *Peltaspermum bornemannii*. Shield with mature seeds (2 x 2 cm)



Pteruchus deznigii – Holotype (PIZ 105). Entire slab and detail of two leaves with attached pollen sacs under the surface.

len organs, with an axis bearing numerous, helically arranged microsporophylls, each of which terminates in a distally flattened head. They are known particularly from the Southern hemisphere and from Antarctica, with its *Dicroidium* foliage, and throughout the European Jurassic as *Thinnfeldia*. There therefore appear to be two possible solutions: either this pollen organ has nothing to do with *Scytophyllum* and pertains to an as yet unknown foliage type, or the Corystospermales constitutes a sister group of the Peltaspermales with closely related species in the Early Triassic. The fossil record would also support this, because Peltaspermales are more plausible ancestors of corystosperms such as *Thinnfeldia* and *Dicroidium* (Retallack, 2000) than peltasperms such as *Lepidopteris* and *Scytophyllum*. For instance, seed ferns from the early Triassic, Coal Cliff Sandstone of New South Wales, Australia, bear leaves referred to as *Thinnfeldia callipteroides*, a typical corystosper-

mian plant; however, the stomatal apparatus of the leaves is cyclocytic with papillate subsidiary cells, distinct from the doubly cyclocytic non-papillate subsidiary cells of Middle to Late Triassic *Thinnfeldia*, and identical to the stomatal apparatus of *Lepidopteris*, the most typical of all Peltaspermales. Several authors (Rothwell and Serbet, 1994; Taylor, 2009) have suggested that the corystosperms may be a monophyletic group including *Callistophyton*, *Caytonia*, the glossopterids, and *Peltaspermum*. *Thinnfeldia rhomboidales* leaves also bear an astonishing resemblance to *Scytophyllum bergeri*. Meanwhile the Peltaspermales, with its different subgroups such as *Lepidopteris*, *Tatarina*, *Vittaeophyllum*, *Pursonia* and *Scytophyllum*, formed a varied and large group. Phylogenetic analysis (Nixon et al., 1994) indicates that *Lepidopteris* is a sister group to the Corystospermales. However, further fossil records will be required to confirm or reject these assumptions.



9) KÜH 2172 *Peltaspermum bornemannii*. Scytophyllum leaf and attached fructification lobe (12 x 5 cm)
 10) KÜH 2172 *Peltaspermum bornemannii*. Detail of the head, immature seeds under the surface (2.5 x 3 cm)
 11) PIZ 243 *Peltaspermum bornemannii*. Fructing body seen from the head (2.5 x 2.5)
 12) KÜH 2008 *Peltaspermum bornemannii*. Fructing shield from the head (25 x 3 cm)

Order CAYTONIALES Thomas, 1925
Family CAYTONIACEAE Thomas, 1925
Genus *Sagenopteris*, 1838 C. PRESL in
STERNBERG, vol. II, 7/8

Sagenopteris keilmannii

WACHTLER, sp. nov.

2007 *Sagenopteris* sp.; Kustatscher et. al.,
pp. 1277 - 1298, Text figs. 4 A-B

Holotype

PIZ 1103

Paratypes

PIZ 256, PIZ 172

Material

PIZF 258

Etymology

Named after Johannes Keilmann, who supported and developed palaeontology in the 20th century.

Type localities

Piz da Peres, seldom Kühwiesenkopf

Type horizon and age

Dont Formation

Lower to Middle Triassic, Anisian, Pelson

Repository

Natural History Museum Südtirol, Bozen,
Museum Dolomythos Innichen.

Diagnosis

Leaves palmately compound on a petiole, consisting of several ovoid to lanceolate leaflets, sometimes undulating on the margin. Each leaflet with a distinguishable midrib from which originate lateral veins that initially branch dichotomously, then with anastomosing lateral veins. This subsequent branching forms a complex reticulate venation pattern.

Description

The most complete specimen, 20 cm long and 15 cm wide (PIZF 1103), shows three to four 8 to 12 cm long, and 5 cm wide, lanceolate, slightly midribbed leaflets attached to the same petiole. The typical obliquely elongated to irregular meshes are obvious. The arrangement of two to four leaves was probably normal for this *Sagenopteris* species. PIZ 172 shows that the leaves could reach a considerable size. On this slab there are two leaflets, one 15 cm by 7 cm, the other one only 4.5 x 5 cm. PIZ 258 also shows two leaves on the same slab, but these are staggered and do not arise at the same point. Of interest is that the young leaves were nearly as large as long. As well as PIZ 172, PIZ 256 also shows a young leaflet. It can be assumed that growth mainly involved length and not width. Leaves were fragile, yielding cuticles with difficulty, often lacerated on the margins, ovoid with no defined apex. Palynological samples yielded *Vitreisporites pallidus*, a bisaccate pollen grain that is typical of the Caytoniales to which *Sagenopteris* is thought to belong (Kustatscher et al., 2007). Ovulate organs classified as *Caytonia* and suggested to pertain to *Sagenopteris* were also found nearby.

Remarks

Sagenopteris leaves pertain to the second most common seed fern after *Scythophyllum bergeri* in the Piz da Peres area. Caytonales, into which *Sagenopteris* leaves were inserted, were first described in 1925, when the British palaeobotanist Hamshaw Thomas described *Sagenopteris phillipsii* leaf compressions from mid-Jurassic beds of Cayton Bay, Yorkshire. The co-occurrence of the pollen-organ *Caytonanthus* (Harris, 1937) and ovule-bearing cupules of *Caytonia* (Thomas, 1925) suggested that these organs and leaves pertain to the same plant. *Sagenopteris* from the Middle-Late Jurassic and Early Cretaceous floras of both northern and southern hemispheres (Taylor, 2006) were subsequently found to be common with a worldwide distribution. However, to date only a few pre-Rhaetian (latest Triassic) Caytonales leaves have been recovered. *Sagenopteris keilmannii* currently constitutes the oldest known material of this

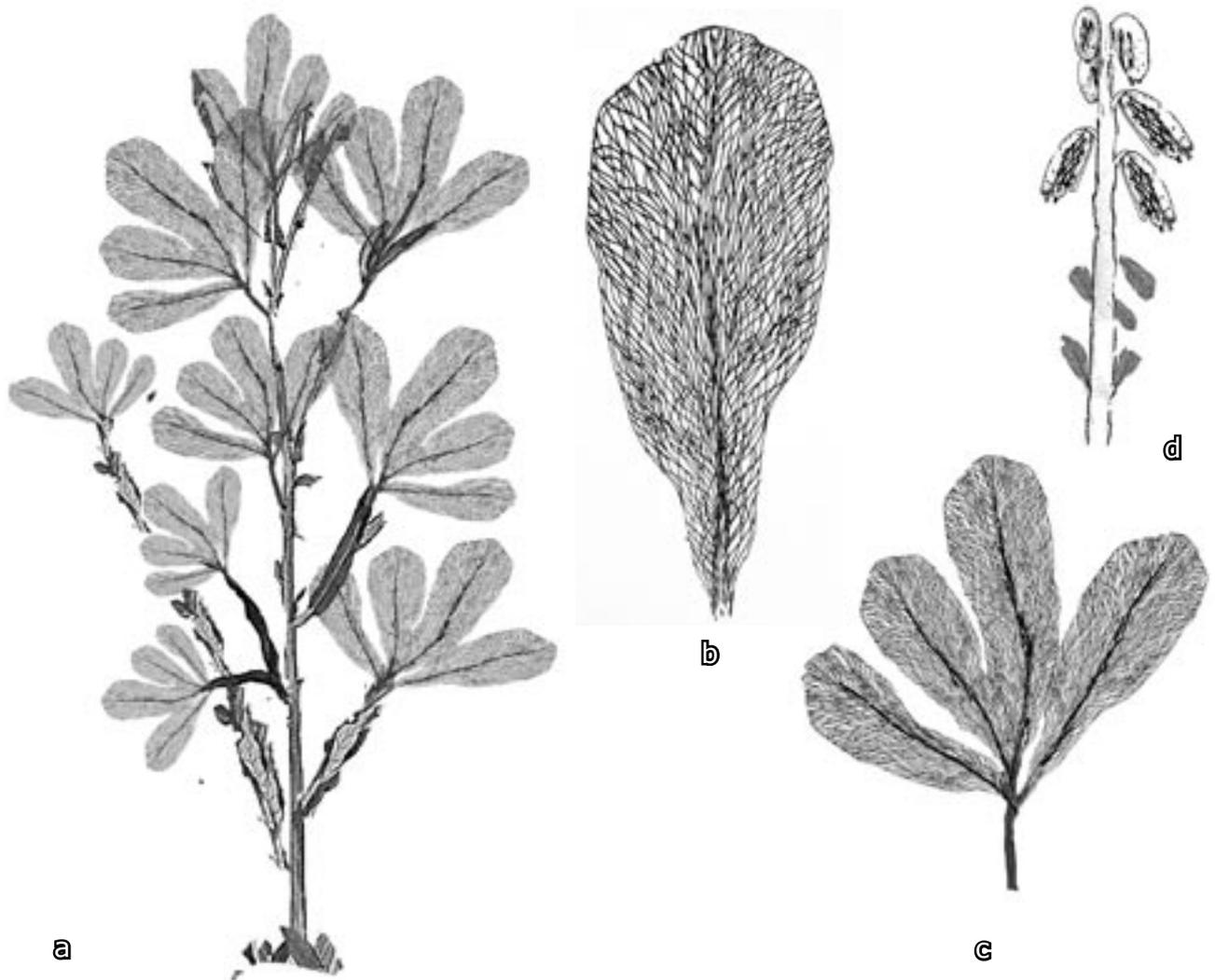


1) PIZF 1103 *Sagenopteris keilmannii*. Holotype. Entire frond (20 x 15 cm)

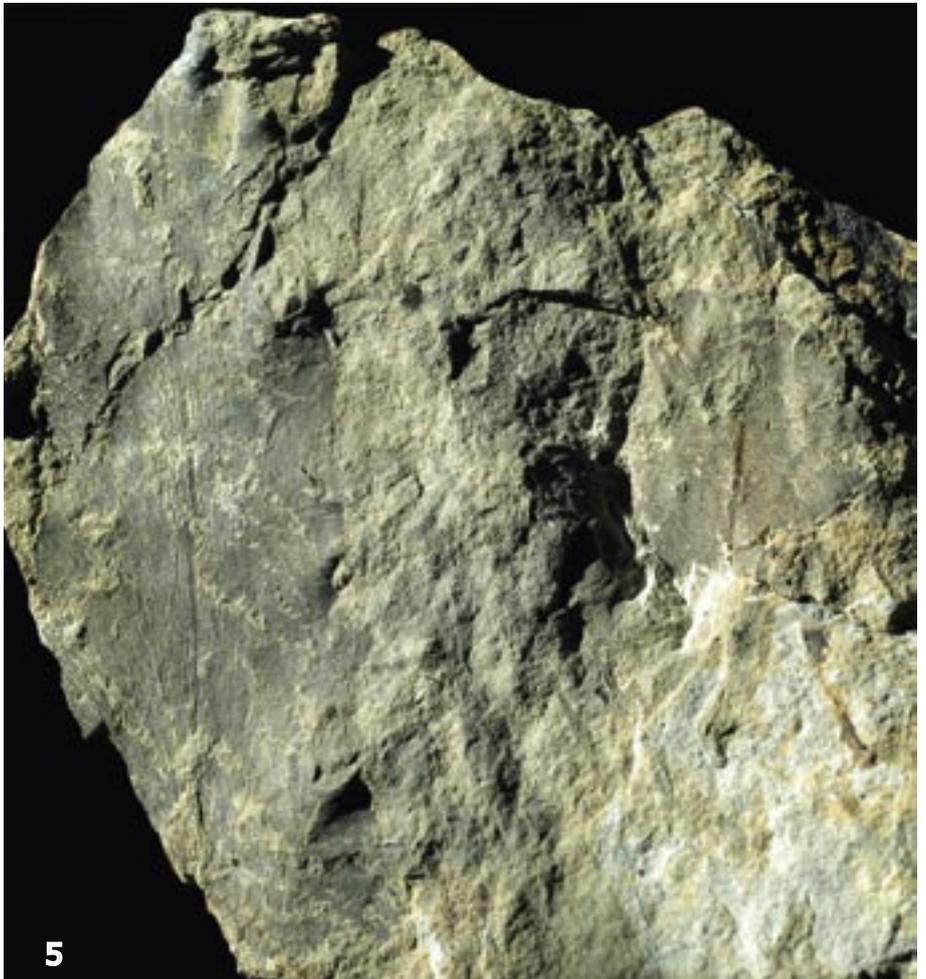
seed fern genus. Apart from its age there are other substantial differences. *Sagenopteris nilssonii* (Brongniart, 1825) and *S. rhoifolia*, Presl, from Rhaetian-Liassic (late Triassic) localities in Germany (Bayreuth, Bamberg) and *S. semicordata* from the Carnian Flora of Sinsheim, along with *S. serrata*, differ from the Anisian specimens in having a more gracile rachis and smaller leaflets. They usually reach a length of 7 cm, with a maximum of 10 cm. Astonishingly single *S. keilmannii* leaves could reach a length of 15 cm and a width of 8 cm. *S. phillipsii* also yields a thick cuticle, unlike *S. keilmannii*. In addition, the midvein is usually more consistent in the Jurassic *Sagenopteris* species, whereas

the vein structure is more delicate in the Anisian *Sagenopteris*. In contrast to other specimens, *Sagenopteris* leaves from Piz da Peres are more rounded on the apex, sometimes lacerated and flattened on the margin. In this sense there are sufficient indications that it is a primitive *Caytonia* species, probably with an evolving status or representing a transition plant between the Palaeozoic and Mesozoic.

It is believed that *Sagenopteris keilmannii* was more of a shrub than a small tree, which fits well with the seed fern community of the Anisian Piz da Peres, composed mainly by Peltaspermales (*Scytophyllum*) and Caytonales (*Sagenopteris*).



Sagenopteris keilmannii – Suggested reconstruction: a) Whole plant, b) Single leaf (PIZF 1103), c) Entire frond PIZF 1103, d) *Caytonia fedelei*, Female ovule organ (PIZ 190)



- 2) PIZF 1103 *Sagenopteris keilmannii*. Detail of a leaflet (5 x 4 cm)
3) PIZ 256 *Sagenopteris keilmannii*. Detail of a young leaf (7 x 5 cm)
4) PIZ 258 *Sagenopteris keilmannii*. Two leaflets on an axis (15 x 8 cm)
5) PIZ 172 *Sagenopteris keilmannii*. Two leaflets on a slab: large 15 x 7 cm, small 4.5 x 5 cm

Order CAYTONIALES Thomas, 1925
Family CAYTONIACEAE Thomas, 1925
Genus Caytonia, Thomas, 1925

Caytonia fedelei WACHTLER, sp. nov.

Holotype

PIZ 190

Paratype

PIZ 206

Etymology

Named after Paolo Fedele, who collected many fossil plants in the Dolomites.

Type localities

Piz da Peres

Type horizon and age

Dont Formation
Lower to Middle Triassic, Anisian, Pelson

Repository

Natural History Museum Südtirol, Bozen,
Museum Dolomythos Innichen.

Diagnosis

Stalked cupules arise on an axis in subopposite pairs. Each multiovulate cupule containing the seeds is recurved downwards.

Description

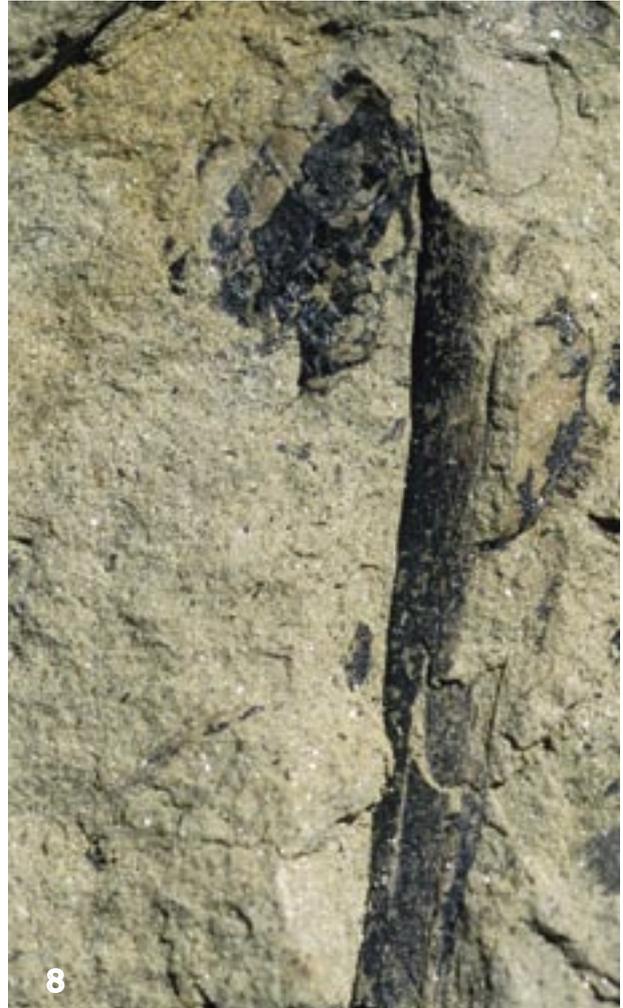
Caytonia fedelei exhibits a slender axis (PIZ 190), about 7 cm long, bearing sub-oppositely arranged cupules, and each recurved downwards toward the main axis. Cupules are approximately 10 mm long, 3–4 mm wide and hold between 8 and 14 ovules. Ovules are attached to a midrib on the inside of the potentially fleshy, berry-like cupules. Seeds are ~2.0 mm long and radially symmetrical with a slender cavity in the centre. PIZ 190 bears a total of ten upward-

ly recurved cupules on the upper part, and several small leaves at the base, resembling *Sagenopteris* leaflets. Each cupula is attached to a delicate stalk on the axis, suggesting that the cupules were shed at maturity. PIZ 190 appears to contain small and poorly developed ovules, and the ovulate structure consists of cup-like inrolled flaps. Mature ovulate organs are apparent in PIZ 206. One clearly shows the cupula containing 10–12 ovules, each with a pit. The open lip at the base suggests that the seeds were mature enough to be discharged.

Remarks

The first phylogenetic analyses (Thomas, 1925) considered the cupule of *Caytonia* to be homologous with the anatropous, bitegmic ovule of the angiosperms. Later it was conclusively ascertained that the seed-bearing unit *Caytonia* was a cupule, not a carpel, and that it functioned like a gymnosperm. Since the early descriptions of the Caytoniales, which were based on specimens from the Jurassic of Europe and Greenland, their range has been extended geographically and stratigraphically. Ovulate reproductive organs have been described from various Jurassic localities of Europe, Australia, the Cretaceous of Siberia and the Antarctic (Taylor, 2006). *Caytonia* was wind-pollinated and had characteristic small wind-dispersed bisaccate pollen.

The main difference between *Caytonia fedelei* and Caytonales is that, apart from its younger age, the cupules do not have a lip-like projection toward the point of attachment, but are directed downwards. They are also more elongated than rounded, as in *C. nathorstii*, *C. thomasi* and *C. sewardii*. In that sense *C. fedelei* seems to be rather more primitive and at the beginning of a developmental stage. Its ovulate organs have no affinity to the other group of seed ferns, the Peltaspermales, including *Scytosphyllum bergeri* and its female fructification *Peltaspermum bornemannii*, an umbrella-like cupula, and is therefore easily recognisable, occurring abundantly on Piz da Peres.



- 6) PIZ 190 *Caytonia fedelii*. Holotype. Female ovule-bearing axis (7 x 3 cm)
 7) PIZ 190 *Caytonia fedelii*. Detail of two cupulas (2 x 2 cm)
 8) PIZ 206 *Caytonia fedelii*. Single cupula on an axis showing the seeds inside (5 x 3 cm)
 9) PIZ 206 *Caytonia fedelii*. Detail of one cupula with approximately 12 seeds and the open lip (1 x 1 cm)

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