

Upper Permian floras of the Dolomites

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The upper Permian floras of the Dolomites can be regarded as one of the richest and most interesting worldwide. It provides significant information on the climate prevailing at that time, but also on the state of development, particularly of the gymnosperms. Effectively we encounter many highly evolved conifers like the Araucarian-progenitor *Ortiseia* (*Ortiseia leonardii*, *Ortiseia visscheri*, *Ortiseia jonkeri*, *Ortiseia zanettii*), but also Abietaceae-ancestors (*Majonica alpina*, *Majonica clementwesterhofae* n. sp.). A secondary rule in play is that other conifers like *Ulbeus vicietus* nov. comb. (probably a progenitor of today's *Taxodium*-conifers), *Ullmannia edwardsae* n. sp., probably a forefather of the extant *Taxaceae*-tribe or *Voltzia sjerpii* nov. comb. belong to the *Cryptomeria*-family. Interesting is the evolution of *Ginkgoites munchisonae* n. sp. having many affinities with modern Ginkgo-trees. Also fully evolved cycads were present with *Zamia*-like *Nilssonia brandtii*, or *Cycas* resembling *Macrotaeniopteris wachtleri* nov. comb. and *Taeniopteris*. Interesting is the apparition of archaic *Pernerina pasubi* having cycas-like multiseeded fertile organs. True ferns were present with *Angiopterites munchisonii* gen. nov. n. sp. and *Sphenopteris* sp. Together with the Pteridospermatophyta *Lepidopteris martinsii* and *Scythophyllum* sp. as well as the horsetails *Neocalamites behnkeae* and *Equisetites siberi* they prove that the climate in the Upper Permian of the Dolomites varied considerably. This changed effectively in direction to the late Permian and the Permo-Triassic catastrophe. For several million years the flora vanished only to appear under totally new circumstances in the Early-Middle Triassic.

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Late Permian (Wuchiapingian, about 260 mio years), Seceda - Gröden-Valley, Northern Italy

Some Upper Permian landscapes of the Dolomites were dominated by more cold adapted gymnosperms. Left grows the Abietaceae *Majonica clementwesterhofae*. On the twigs lie isolated seed scales and winged seeds from decaying cones. In the middle is visible a branchlet of *Ginkgoites munchisonae* with berries, below appear a decaying male cone. On the right side sprout the character conifer, the Araucaria ancestor *Ortiseia leonardii* with male and female cones and some shed one seeded scales.

In the Late Permian, the Dolomites were located near the equator. They were washed by the Tethys Ocean, which is reflected in the fossil deposits of marine life by the presence of nautiloids. However, if one compares the Late Permian flora of the Dolomites with its richness in conifers, it remember more that of a today's Northern Tropic circle, such as Southern China or Northern Vietnam, or also New Caledonia, located on the Tropic of Capricorn between 19rd and 23rd latitude. Therefore, it can be supposed that in the Late Permian the climate on the Equator was something colder than today. Not all layers in the Grödnert Sandstone are coeval and some differences in the plant assemblage can be explained by time-differences. However, the presence of Marattiaceae (*Angiopterites*) and cycads (*Macrotaeniopteris*, *Nilssonia*) are subtropical climate indicators characterized by hot summers and mild winters with infrequent frost. Nevertheless, some fossil sites like the Bletterbach-gorge and especially the Seceda in the Gröden-Valley indicate that there were also colder periods in direction to the late Wuchiapingian-stage. In these localities we encounter a dominance of conifers, which is even more confirmed that they are sometimes the only flora elements that are found.

Components of the Grödnert-Sandstone flora:

Sphenophyta

Neocalamites behnkeae (WACHTLER 2015)
Equisetites siberi (WACHTLER 2015)

Pteridophyta

Angiopterites murchisonii (WACHTLER, 2021)
Sphenopteris sp.

Pteridospermatophyta

Lepidopteris martinsii (WACHTLER, 2013)
Scythophyllum sp.

Cycadophyta

Macrotaeniopteris wachtleri (PERNER, 2015)
Nilssonia brandtii (WACHTLER, 2015)
Taeniopteris sp.
Pernerina pasubi (WACHTLER, 2015)

Ginkgophyta

Ginkgoites murchisonae (WACHTLER 2021)

Coniferophyta

Ortiseia leonardii (FLORIN, 1964)
Ortiseia visscheri (CLEMENT-WESTERHOF, 1984)
Ortiseia jonkeri (CLEMENT-WESTERHOF, 1984)
Ortiseia zanettii (WACHTLER, 2015)
Majonica alpina (CLEMENT-WESTERHOF, 1987)
Majonica clementwesterhofae (WACHTLER, 2021)
Voltzia sjerpii (CLEMENT-WESTERHOF, 1987)
Ulbeus vicetinus (DE ZIGNO 1862, WACHTLER 2017)
Ullmannia edwardsae (WACHTLER, 2021)

Sphenophyta

The horsetails play no major role in the Upper Permian plant world dominated by the gymnosperms. Only in the Vicentinian Dolomites their populations are slightly more abundant, while at the Seceda or in the Bletterbach they were rare. Nevertheless, two completely different horsetail families were present. One Equisetaceae-species (*Equisetites siberi*) with its rounded strobili, and one of the last Calamitaceae (*Neocalamites behnkeae*) known before its extinction, characterised by its elongated sporangiophores and bracts clawing the sporangia. Both horsetails document that the Upper Permian was in no case so desertic as previously thought.

Neocalamites behnkeae (WACHTLER, 2015)

Etymology

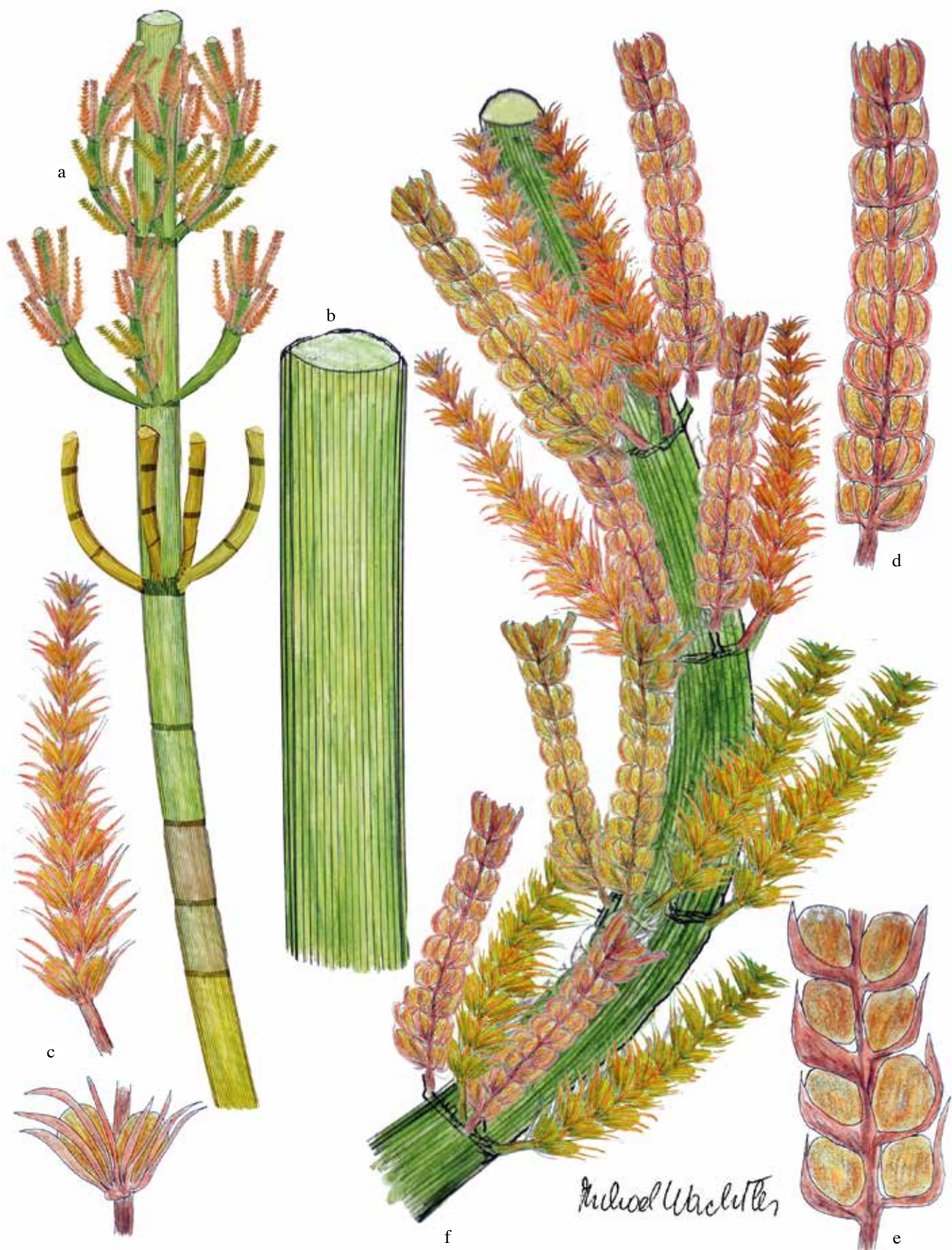
Honouring Christa Behnke, (Niederhöchstadt, Germany), preparator for the Museum of Natural Sciences in Brussels and collector of plant fossils.

Holotype

PAS 693; **Paratype:** PAS 210 (fertile organ);
Repository: Coll. Wachtler, Dolomythos-Museum, Innichen

Description

Stem: Main stems up to 5 cm wide with widely separated tangential striae. Lateral stems forking at an angle of 45 degrees or



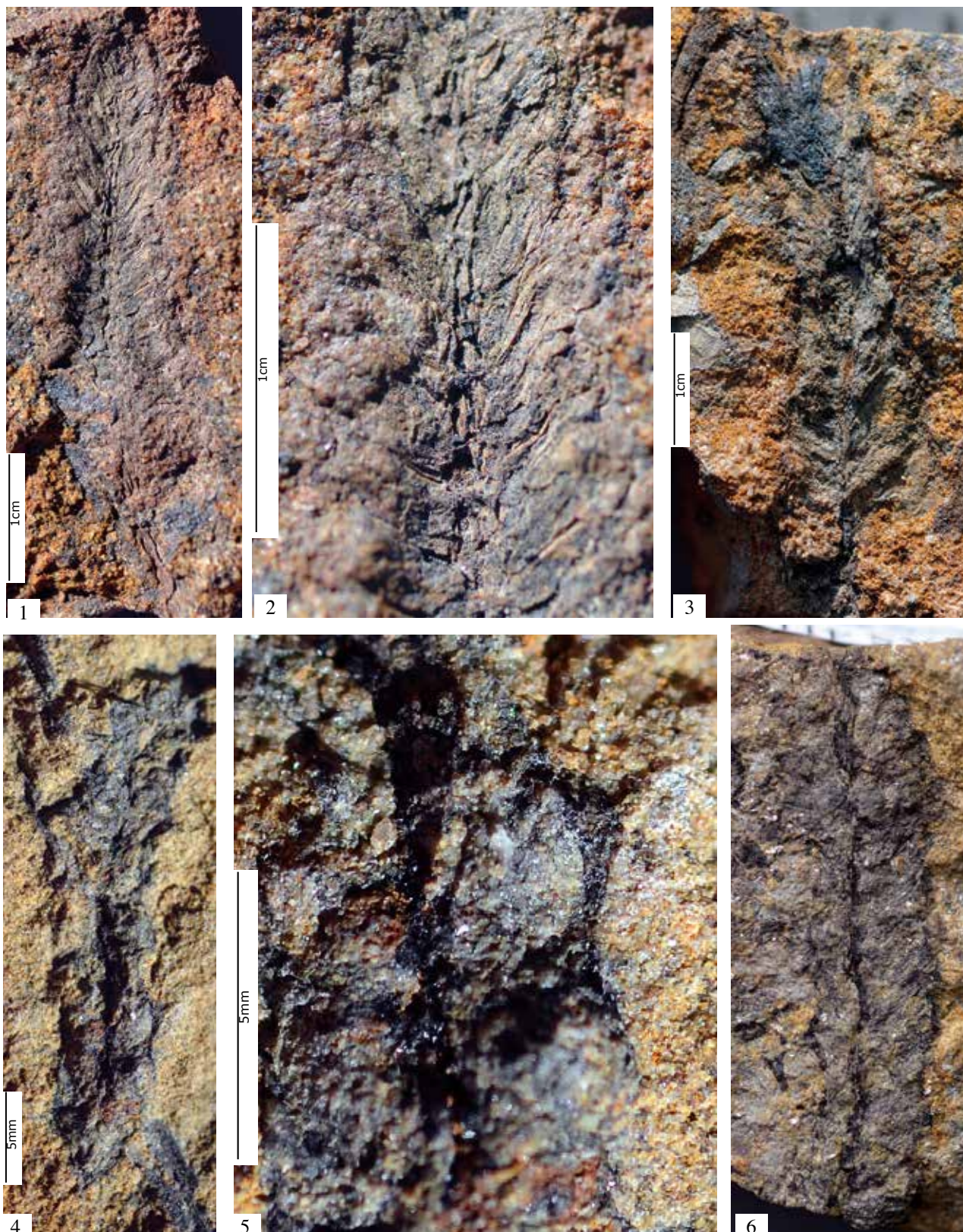
***Neocalamites behnkeae*. Reconstructions (Late Permian, Wuchiapingian)**

a. Whole plant, b. Apical part of a stem; c. Juvenile strobilo and detail; d. Adult cone; e. Mature sporangiophore; f. Suggested plant with lateral fertile shots



***Neocalamites behnkeae*. Stems and branchlets (Late Permian, Wuchiapingian)**

1. Stem (CUEC 449, Cuecenes); 2. Part of a branching stem (PAS 693, designed holotype); 3. Stem with distinctive large tangential striae (PAS 378); 4. Stem with narrow tangential striae (PAS 33); 5. Branching stem (PAS 421); 6-7. Leaflets and detail (PAS 710); 8-9. Detail of the longitudinal ribs (PAS 434, PAS 28); Valli del Pasubio, Ariche, Coll. Michael Wachtler, Dolomythos-Museum.



***Neocalamites behnkeae*. Stems and branchlets (Late Permian, Wuchiapingian)**

1-2. Juvenile sporangiophore and detail of the bracts (PAS 210, paratype); 3. Strobilo (PAS 727); 4-5. Adult mainly decomposed strobilo and detail of the sporangia (PAS 301); 6. Sporangiophore (PAS 442); All Valli del Pasubio, Ariche, Coll. Michael Wachtler, Dolomythos-Museum.

less, mostly with narrow longitudinal ribs. They are only scarcely more slender than the main stem. The ribs pass without or only suggested interruption through the node. Branchlets of the last order with several times forking leaves.

Fertile parts: Strobili are from 3 cm to 8 cm long, but only 0.5 to 1 cm wide. The elongated and pointed bracts claw densely the elliptical to rounded sporangiophores (PAS 210, paratype; PAS 727, PAS 301, PAS 442).

Taxonomic notes

Neocalamites behnkeae constitutes the dominant horsetail from the Ariche-locality in the Valley of Pasubio (Southern Dolomites). Although sometimes fragmented they can be recovered in fair numbers, often characterized by their forking main and secondary stems (Wachtler, 2015). Several features distinguish them from *Equisetites siberi*, the other horsetail recovered in the Late Permian Gröden Formation found especially in the nearby Contrada Ulbe (Recoaro). The typical telescope-like internodes are only sometimes betoken while in *Equisetites siberi* they are closely spaced and distinctively noticeable. The secondary stems are very pronounced, being usually only slightly more slender than the main stem, whereas this phenomenon is not recognizable in *Equisetites siberi*. The remarkable and frequently found strobili, being of *Calamites*-type, also stand in contrast to an insertion in the *Equisetites*-group. The stems and branchlets of *Neocalamites behnkeae* have some resemblances with Late Carboniferous *Calamites equisetiformis* bearing widely separated longitudinal ribs on the main stems and narrow spaced tangential striae on the secondary branchlets. But also Early Permian (Kungurian) *Neocalamites tregiovensis* from the Val di Non (Wachtler, 2012, 2015) develop widely spaced longitudinal ribs on the main axis. The whorls of the secondary branchlets are different from *Neocalamites tregiovensis* or Late Carboniferous *Calamites multiramis* (*Annularia stellata*) and vaguely resemble Late Carboniferous *Calamites equisetiformis*.

***Equisetites siberi* (WACHTLER, 2015)**

Etymology

Named after Hans-Jakob "Kirby" Siber, outstanding individual in worldwide palaeontology.

Holotype

ULBE 130 (stem and strobilus); **Paratype:** ULBE 96 (whorls); **Repository:** Coll. Wachtler, Dolomythos-Museum, Innichen

Description

Stem and branchlets: Main stems stocky, from 5 to 10 cm wide with sometimes closely spaced apical nodes (ULBE 13, ULBE 45). Lateral branchlets arranged in whorls fused into nodal sheaths (ULBE 88). These slender, about 8-10 cm long. Leaf sheath consisting of spine-like teeth as found in many Triassic *Equisetites* specimens (CUEC 415). In juvenile specimens the nodes are much more separated. Longitudinal ridges relatively closely spaced in juvenile, as well as in an mature stage.

Fertile parts: Strobili rounded consisting of an arrangement of peltate shields. About 5 cm long, 3-4 cm wide, segmented in several peltate sporangiophores, each about 1 cm, quadrate, rounded on the edges.

Taxonomic notes

Although the heyday of the *Equisetitaceae* comes in the Triassic, where they were widespread and dominate largely the landscape with their huge appearance, they were a common reality beginning from the Carboniferous. Just in the Westphalian Yorkshire coal deposits of Great Britain we encounter with *Equisetites hemingwayi*, a horsetail being in appearance very close to modern *Equisetum* (Kidston, 1901). Other Early Permian occurrences include *Equisetites vaujolyi* (Zeiller, 1895) with its up to 6 cm long leaves, 0.6 cm wide with a single vein per leaf, or *Equisetites geraschi* (Perner & Wachtler, 2015) from Niederhausen in the Saar-Nahe-basin. Whereas in *Equisetites siberi* the lateral axis is slender, in Lower Permian *Equisetites geraschi* they were huge, reaching circumferences of 4 cm. Otherwise the organisation between Permian and Triassic giant horsetails, like *Equisetites mougeotii* or *Equisetites arenaceus*, exhibits few differences. Probably *Equisetites siberi*, as well as the Triassic species could reach a main stem-size of about 10 cm and grow 2-3 metres high. Fertile organs were born on the main axis or on secondary lateral branches in aggregations of many strobili (Wachtler, 2016), what makes them different considerably from the extant one, with only one apically growing sporangiophore.



***Equisetites siberi*. Reconstructions (Late Permian. Wuchiapingian)**

a. Stem with strobili, b. Apical part of a stem (ULBE 84; ULBE 13); c. Juvenile stem (ULBE 88); d. Two strobili; e. Isolated strobilus (ULBE 84); f. Sporangophore



***Equisetites siberi*. Stems and branchlets (Late Permian., Wuchiapingian)**

1-2. Stem with strobilus and detail of the strobilus (ULBE 130, designed holotype); 3-4. Two juvenile stems evidencing longitudinal ribs and nodes (ULBE 88); 5. Two adult stems (ULBE 98); All Ulbe, Recoaro; Coll. Michael Wachtler, Dolomythos-Museum



***Equisetites siberi*. Stems and branchlets (Late Permian, Wuchiapingian)**

1. Stem with lateral whorls of shoots (ULBE 96, paratype); 2. Extra-long stem (ULBE 48); 3. Stem with close-spaced internodes (ULBE 84); 4-5. Apical parts of a stems (ULBE 43, ULBE 13); 6. Stem evidencing well the tangential striae (ULBE 46); All Ulbe, Recoaro; 7. Apical part of a huge stem (CUEC 430); 8. Detail of a leaf sheath (CUEC 415); Cuccenes, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum

The horsetails *Equisetites siberi* and also *Neocalamites benckea*, can be regarded as good climatic indicators of this part of Pangea lying near the equator and washed by the Thethys-ocean. In net contradiction to the general opinion of an arid climate in that time can be assumed that there were enough swamps and fresh water lakes in which the horsetails, but also cycads could settle.

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Pteridospermatophyta

In the Upper Permian localities of the Dolomites, several fragmented sterile leaves as well as *Peltaspermum* shields of the enigmatic seed ferns have been found. Due to the poor conservation only a generic classification could be done.

Peltaspermum sp. (SCHIMPER, 1869)

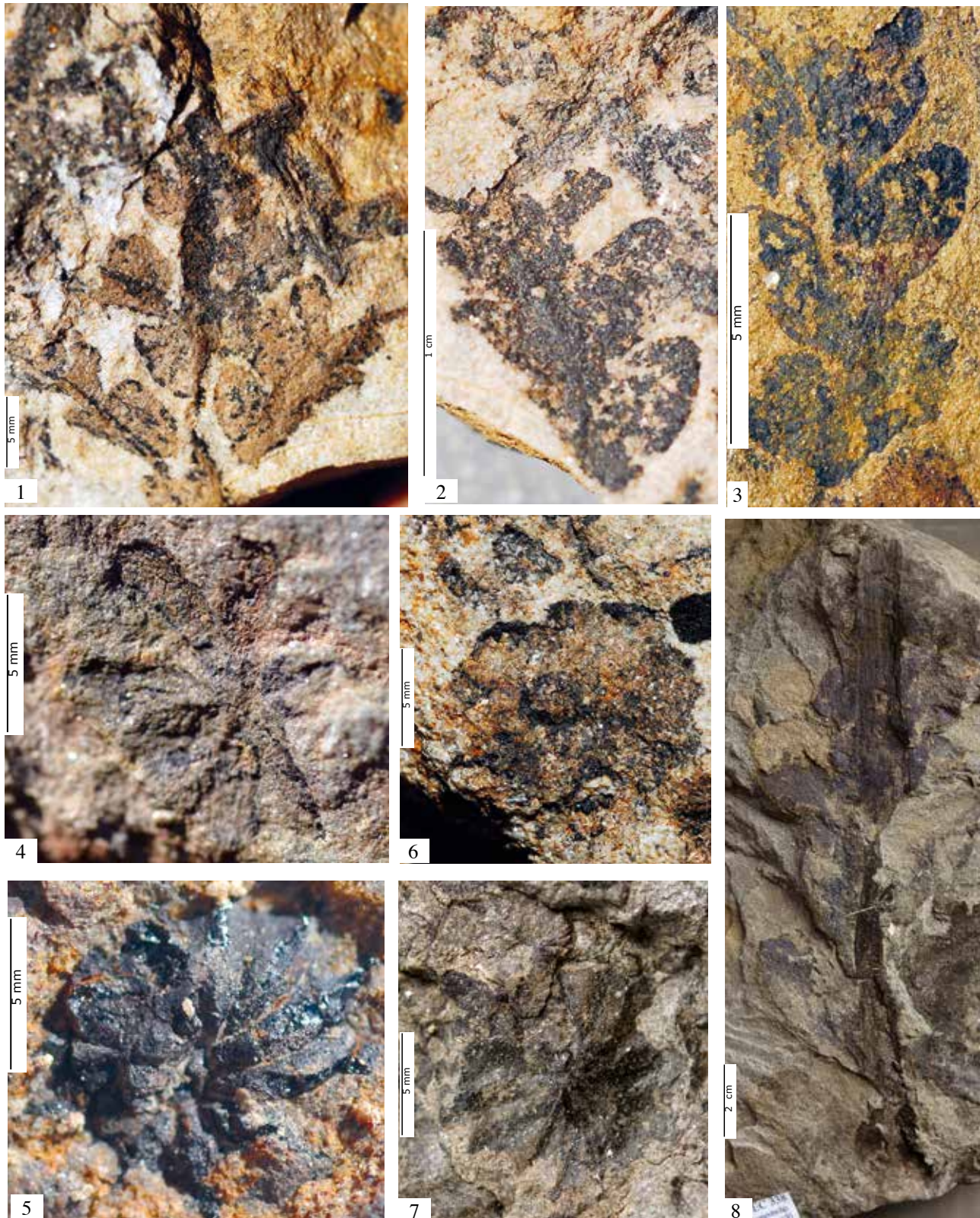
2015 - *Lepidopteris* sp. WACHTLER p. 159-160

Taxonomic notes

Sometimes shield-like segmented fructifications were found in the Grödner Sandstone, that can be regarded as irrefutable evidence of a group of seedferns classified as Peltaspermales. Unfortunately, till now only badly preserved sterile fronds were recovered that make precise classification difficult.

The persistence of the Peltaspermales from the Carboniferous-Permian border well into the Triassic-Jurassic makes them one of the longest existing pteridosperm lineages (Wachtler, 2015). This very interesting group of plants reveals a special problem in palaeobotany: the term *Peltaspermum* pertains to the female organs, while the foliage is often referred to using other names, such as *Wachtlerophyllum*, *Autunia*, *Rachyphyllum*, or *Lepidopteris* in the Permian, and *Scythophyllum* or *Thinnfeldia* in the Triassic (Perner & Wachtler, 2013).

Starting in the late Lower Permian, the Peltaspermales diminished their size, probably due to the climate, which became hostile. This trend towards miniaturization continued throughout the rest of the Permian. *Lepidopteris martinsii* from the Upper Permian Zechstein generate leaflets that were small-sized, as well as the *Peltaspermum* organs. The *Peltaspermum* heads increased their size only starting in the Lower Triassic with *Scythophyllum bergeri*. If the rarely found *Peltaspermum* shields in the Grödner Sandstone pertain to *Lepidopteris* or *Scythophyllum* is difficult to estimate, because it seems—judging in base of the rarely encountered and badly conserved pinulas—both seed-fern genera were present. Therefore the generic name *Peltaspermum* sp. was adopted. The fructifications were rounded, about 1 cm in diameter, umbrella-shaped, and about 10 times segmented in pods that included the seeds. The leaves of *Lepidopteris*-fronds found in the Grödner Sandstone of the Dolomites (especially Ulbe, Recoaro) were fleshly, pinnate, equipped with some indistinguishable veins hidden by a thick cuticle. More rich in *Lepidopteris* (*Peltaspermum*) *martinsii* fronds and frag-



Seed-ferns: *Peltaspermum*, *Scytophyllum*, *Lepidopteris* (Late Permian, Wuchiapingian)

1-3. *Lepidopteris* sp. Fronds, leaves, pinnulas (ULBE 71A-B, ULBE 55, all Ulbe); 4-6. *Peltaspermum* (fertile organs) (PAS 558, PAS 415 all Ariche, Valli del Pasubio, ULBE 73, Ulbe, Recoaro); 7. *Peltaspermum* sp. (CUEC 344, Cuecenes, Gröden Valley); 8. *Scytophyllum* sp. (CUEC 338, Cuecenes, Gröden Valley); all Coll. Michael Wachtler, Dolomythos-Museum

mented fertile peltate shields furnishing cuticle crop out in the Bletterbach-gorge. Some doubtful *Scythophyllum*-fronds were also present on the base of the Seceda.

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Pteridophyta

Ferns are not common in the Upper Permian Grödnert Sandstone of the Dolomites. Although often even alate seeds of conifers or other small parts in good quality were found, small fern pinnules were completely missing in it. The only exception is the locality Ariche in the Valli del Pasubio, where apart from the richness in cycads, a highly interesting fern will be found: *Angiopterites munchisonii* nov. gen. n. sp. It has with its sporangia borne on the underside of the pinnules, very close to the margin, in clusters of several opposite pairs many similarities with today's *Angiopteris* ferns inserted in the family of Marattiaceae. This discovery is extremely important because *Angiopteris*-ferns can be regarded as a good indicator of a wet and moderately warm climate.

The other fern, *Sphenopteris* constitutes one of the most dominant flora elements and sometimes the only certain fern of the European Middle to Late Permian.

Sphenopteris sp.

Sphenopteris sp. WACHTLER, 62-67

Rarely isolated fern-fronds occur in the Grödnert Sandstone that have similarities with Upper Permian *Sphenopteris dichotoma*, known mainly from the European Zechstein (Wachtler, 2015). Till not better material will be recovered only a classification as *Sphenopteris* sp. is justifiable. Unmistak-

able evidence we have in the Early Permian Tregiovo-Formation of the Dolomites with *Sphenopteris battistii* (Wachtler, 2015). Why the ferns declined so much in the Permian after a peak in the Carboniferous and further arose Triassic must be studied, because other water-loving plants like cycads and horsetails were not in danger of becoming extinct.

Angiopterites nov. gen. (WACHTLER, 2021)

Etymology

The name refers to an ancestor of today's *Angiopteris* ferns.

Diagnosis

Bipinnate fronds forming pinnules with serrulate margins. Sporangia attached in clusters along a vein near the apex.

Angiopterites munchisonii nov. gen. n. sp. (WACHTLER, 2021)

Holotype

PAS 93 (fertile frond) Paratype: PAS 390 (sterile frond), Valli del Pasubio, Ariche; **Repository:** Coll. Wachtler, Dolomythos-Museum, Innichen

Etymology

Honouring the British geologist Roderick Impey Murchison (1792-1871), name-giver of the Permian period, which with his wife Charlotte made several fruitful researches in the Dolomites.

Diagnosis

Fern with bipinnate fronds. Pinnules with veins that are free and forked once near the petiole. The elongated sporangia are clustered near the margin.

Description

Sterile leaves: Pinnules up to 3 cm wide, the margins are serrate towards the apical part, the apex is acuminate. The veins arise from the rachis and usually divide once at the base (PAS 390, paratype, PAS 682), in rare cases also twice.

Fertile leaves: Pinnules mostly identical to the sterile, up to 3 cm wide. The margin



Ferns: *Sphenopteris* sp. (Late Permian, Wuchiapingian)

1-2. Small parts of fronds (PAS 658, PAS 201); Ariche, Valli del Pasubio; all Coll. Michael Wachtler, Dolomythos-Museum

is crenulate, the preserved part of the pinnula of holotype PAS 93 is 8 cm long, but probably the entire length could reach a length of 15 till 25 cm. From the midrib sprout relatively massive veins that fork once in close proximity of the base. The sporangia develop in elliptic double-rows near the margin on the apical part of the veins. They are elongated, and about 1 mm long.

Discussion

It is believed that the marattioids ferns originated early in the fossil record, probably just in the Devonian-Carboniferous. But the various genera of the Marattiaceae, such as *Angiopteris*, *Marattia*, *Ptisana*, *Eupodium*, *Christensenia*, *Danaea* known as eusporangiate ferns are not so uniform as often believed (Murdock, 2008a). Fully developed *Danaea*-ancestors are known from the Triassic with *Danaeopsis dolomitica* (Anisian) and especially *Danaeopsis marantacea* (Ladinian) recovered in beautiful fronds from the German locality Ilsfeld (Wachtler, 2016). This suggests that their evolution-lines separated just in the Carboniferous.

Today the genus *Angiopteris* (occurring from Madagascar, India, Japan, Australia and

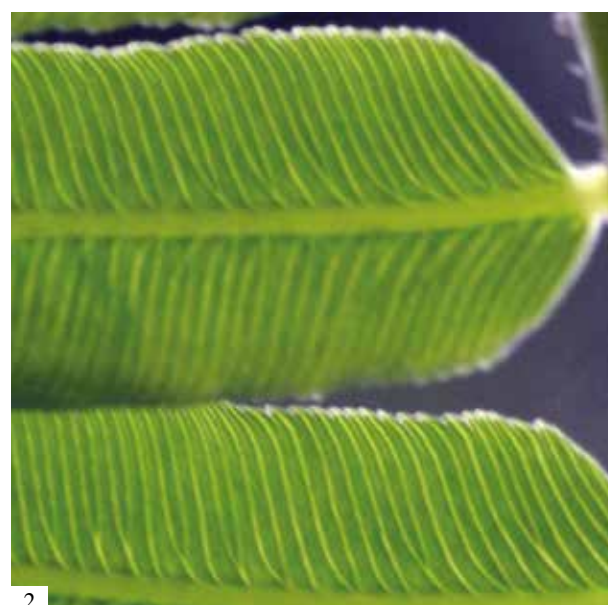
some Pacific islands) is known with huge bi-pinnate rarely once- or three-pinnate leaves that can measure up to 9 metres in length (*Angiopteris teysmanniana* from Java). The pinnae and pinnules are placed alternately. Veins are free and forked once or twice. Ten species are recognised as valid (Christenhusz, 2007). The single pinnae are up to 1.2 metres long and 40 centimetres wide, whereas the pinnules are till 20 centimetres long. The sporangia are clustered in short double-rows of three to seven with no indusium attached along a vein near its apex.

What are the closest fossil relatives of *Angiopteris*? In the Early Permian, frequent ferns like *Scolecopteris* (Perner & Wachtler, 2013) or Triassic *Asterotheca* (Wachtler, 2016) have to be discharged due to their different system of synangia. In late Permian, *Qasimia schyfsmae* (Hill et al., 1985) from central Saudi Arabia the sporangia cover the whole underside between the venation reaching from the base till the edge. In that there are more similarities with the *Danaeopsis*-species from the Triassic (*Danaeopsis dolomitica* and *Danaeopsis marantacea*). Moreover, in these two time different species the sporangia are on the underside between the venation in two rows reaching almost to the edge

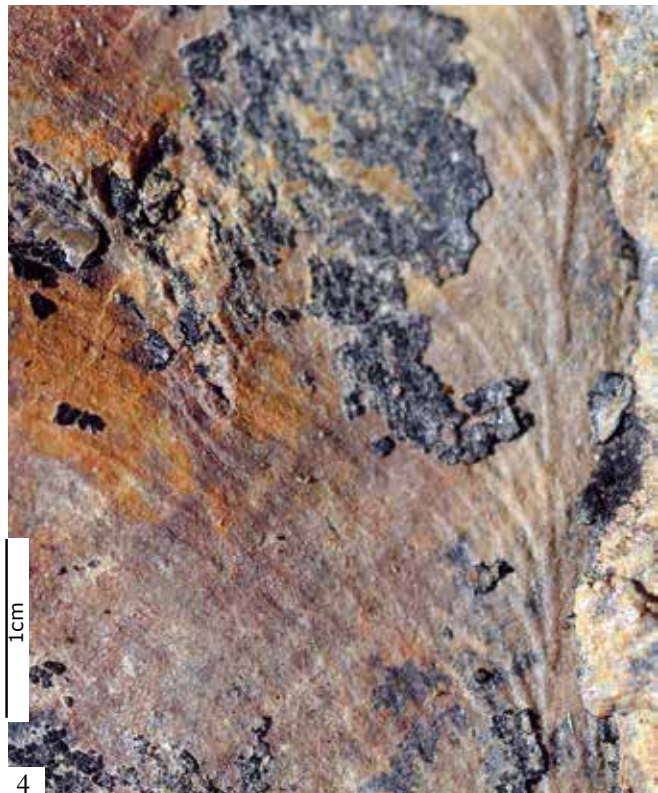
(Wachtler, 2016) what is not the case in *Angiopterites murchisonii*, generating their sporangia only on the margin. The fertile organisation of the thought Marattiaceae *Rothwellopteris pectopteroides* from the Late Permian of South China is not known enough to make considerations about their Marattialean classification. In the plethora of described Paleozoic ferns *Angiopterites murchisonii* correspond, due to their sterile, but especially their fertile arrangement of the sporangia probably like no other to the blueprint of extant *Angiopteris*-ferns. Interestingly in the Triassic of the Dolomites with its richness in ferns it was no longer found.

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1-2. *Angiopteris palmiformis*. 1. Sporangia arranged on the underside of the pinnules, very close to the margin, in clusters of opposite pairs. 2. Sterile frond with the dividing veins close to the rachis. 3. *Angiopteris evecta*. Frond.



***Angiopterites murchisonii* gen. nov. n. sp. (Late Permian, Wuchiapingian)**

1-2. Two fertile pinnules and detail of the sporangia close to the margin with the dividing veins close to the rachis (PAS 93, designed holotype); 3. Sterile leaf evidencing the dividing veins near the mid-vein (PAS 390, paratype); 4. Other sterile frond (PAS 682); all Ariche, Valli del Pasubio; Coll. Michael Wachtler, Dolomythos-Museum

Cycadophyta

In the Upper Permian Grödnert Sandstone of the Dolomites we encounter with certainty between three till four different Cycadales, all based on different fertile organs. Most of them are a continuation and evolution from the Early Permian on. *Nilssonia brandtii* will be found in splendid male and female cones, which allow a classification as Zamiaceae ancestors. *Macrotaeniopteris wachtleri* and *Taeniopteris* sp. can, thanks to the properties of their fertile organs inserted as *Cycas*-progenitors. The greatest difficulties are posed by the categorization of the cycad-like plant *Pernerina pasubi* (Wachtler, 2015) and their fertile organs. The seed-arrangement allows a consideration as macrosporophyll of a *Cycas*-plant like *Macrotaeniopteris wachtleri*, but their fronds are contradictory.

Macrotaeniopteris wachtleri nov. comb. (PERNER, 2015, WACHTLER, 2021)

Bjuvia wachtleri, PERNER, 2015 pp. 132-137

Etymology

Honouring Michael Wachtler, discoverer and describer of many Alpine fossil floras.

Holotype

PAS 650, Valli del Pasubio, Ariche;
Repository: Coll. Wachtler, Dolomythos-Museum, Innichen

Description

Leaves: Cycad with oblong entirely margined leaves, but also often irregularly lacerated. Foliage ends tapered. Lateral veins arise at 80–90° from the rachis, to prosecute straight and parallel, without



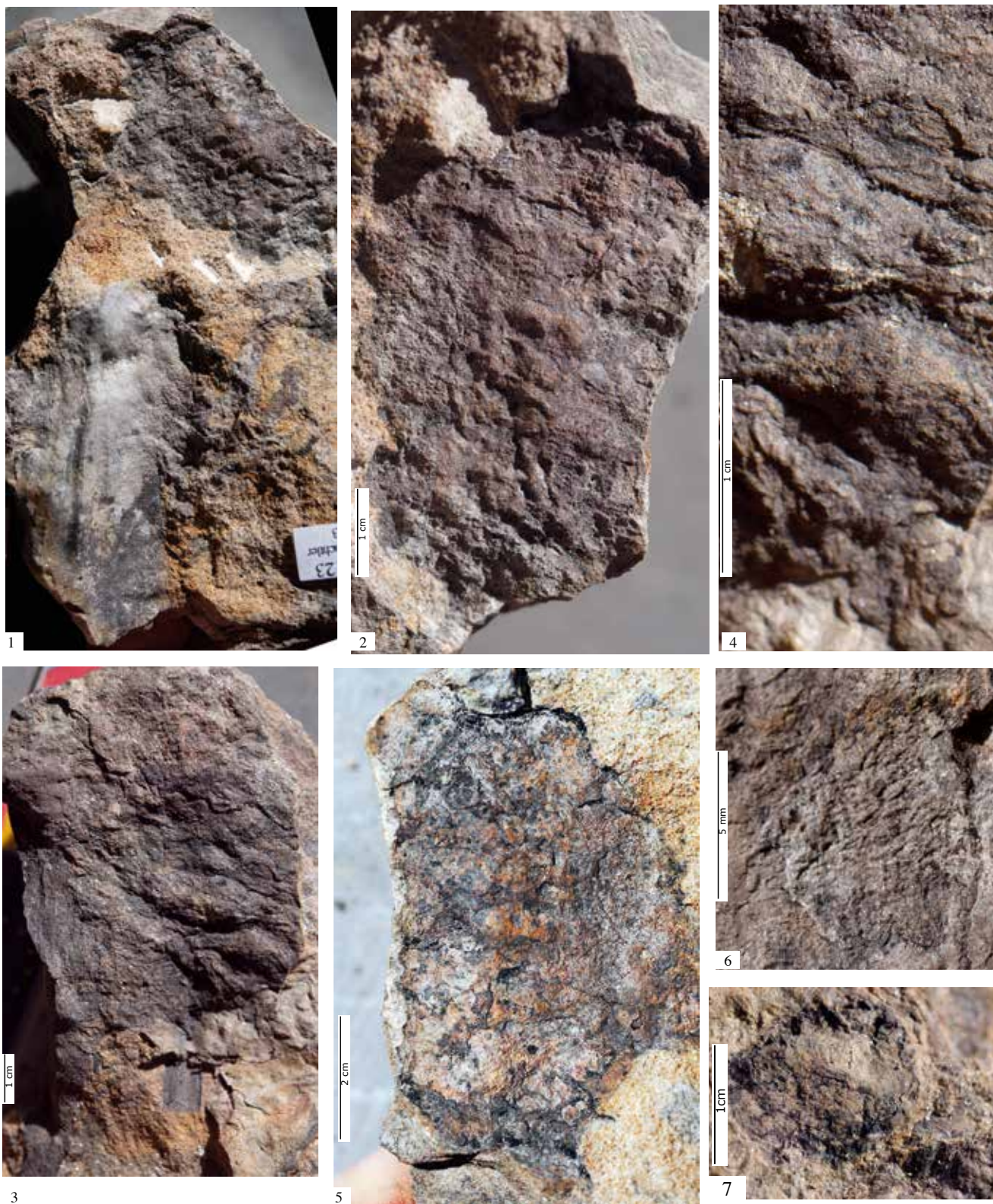
Taeniopteris sp. Leaves (Late Permian, Wuchiapingian)

1-3. Single leaves (PAS 347, PAS 489, PAS 750); Ariche, Valli del Pasubio; all Coll. Michael Wachtler, Dolomythos-Museum



***Macrotaeniopteris wachtleri*. Leaves (Late Permian, Wuchiapingian)**

1-3. Parts of leaves (PAS 798, PAS 96, PAS 100); 4. Detail of an apical side of a leaf with parallel veins (PAS 110); 5-6. Apical part of a frond with a decaying male cone on the upper side (PAS 650, designed holotype); Ariche, Valli del Pasubio; all Coll. Michael Wachtler, Dolomythos-Museum



***Androstrobus*. Male cycad cones belonging to *Macrotaeniopteris* or *Taeniopteris* (Wuchiapingian)**

1-2. *Taeniopteris* leaf and male cone (PAS 123); 3-4. Male cone and detail of the microsporophyll (PAS 683); 5. Male cone (PAS 123); 6-7. Isolated microsporophylls (PAS 650 designed holotype; PAS 734); Ariche, Valli del Pasubio; all Coll. Michael Wachtler, Dolomythos-Museum



***Macrotaeniopteris wachtleri*. Reconstructions (Late Permian. Wuchiapingian)**

a. Whole plant with a male cone (PAS 650, PAS 683), d. Entire frond (PAS 798, PAS 96, PAS 100, PAS 110); Microsporophyll (PAS 734)

forking till the end of the lateral margin. The density of the veins is about 20 to 25 per centimetre. Probably the leaves reached a size from 30 to 50 cm by a symmetrical wide from 15 till 20 cm for each part (PAS 650).

Male cones: They are bulbous till globose, about 6-8 cm long, 4-5 cm wide, equipped with a short peduncle. The microsporophylls are about 1 cm in diameter with many elongated pollen sacs on their lower surface.

Female organs: Till now difficult to establish, but of *Dioonites*-type. It can not be ruled out that the female organ described as *Pernerina pasubi* has some similarities. The seeds arranged like chains on two rows on a fertile blade are a characteristic of *Macrotaeniopteris*, *Taeniopteris* or *Bjuvia* cycads.

Taxonomic notes

When this cycad was described first (Perner, 2015) it was classified as *Bjuvia wachtleri*. Because the name *Bjuvia* (Florin, 1933) especially for Permian cycads with huge entire to irregular lacerated fronds resembling today's banana-leaves can be regarded as synonymous with *Macrotaeniopteris* this new combination has proven to be more useful. The same is valid for *Macrotaeniopteris tridentina* from the Early Permian (Kungurian) of the Dolomites (Wachtler 2021) as well for *Macrotaeniopteris multinervis* from the Early Permian (Sakmarian) Rotliegend, Perner & Wachtler, 2015).

Effectively from the Early Permian on we encounter two different lines of cycas-like ancestors: *Taeniopteris* characterized by its smaller entire leaves and *Macrotaeniopteris* with bigger leaves. As better evidenced in the Triassic (Wachtler, 2010, Wachtler, 2016) both cycas-like genera can be distinct by their distinct leaves but also by their macrosporophylls. Especially in the Dolomites both are a frequent flora-element beginning from the Early Permian till the Middle Triassic.

Usually in the Triassic, these leaves can be associated with *Dioonites* (Rühle von Lilienstern, 1928) female organs (Wachtler, 2016), resembling extant megasporophylls of the genus *Cycas*. They were in *Macrotaeniopteris-Bjuvia* huge with many macrosporophylls assembled together, holding up to 40 seeds for each

row ending in a stunted feather-like sterile appendix, while *Taeniopteris* generate less sporophylls equipped with a few seeds, but distinct by an aesthetic feather-like apex. Similar megasporophylls with two rows of seeds united on a fruit-leaf and ending in a feather-like structure are not preserved in this form in the late Permian of the Dolomites. But the enigmatic *Pernerina pasubi* megasporophylls, being frequent in the same layers, correspond to the blueprint, that parental affinities with *Macrotaeniopteris* are possible.

From the Early Permian till the Early Triassic *Macrotaeniopteris* and *Taeniopteris* underwent gradually an evolutionary change. Their sterile leaves and megasporophylls did not originate at the same height as today's cycads but sprout extending upwards around a central axis. Only beginning from the Middle Triassic *Taeniopteris angustifolia* they adapt to today's (Wachtler, 2016).

Difficulties arose to distinct *Nilssonia*-leaves being especially in the Early Permian similar to *Macrotaeniopteris*. But their fronds were more oblong and more slender evidencing mainly the same width from the base till the apex. The parallel veins are also farther apart in *Nilssonia*. The biggest difference, however, consist in the completely different female organs, being in *Nilssonia brandtii* similar to extant *Zamia*-cones.

Pernerina pasubi (WACHTLER, 2015)

Pernerina pasubii, WACHTLER, 2015 pp. 138-143

Etymology

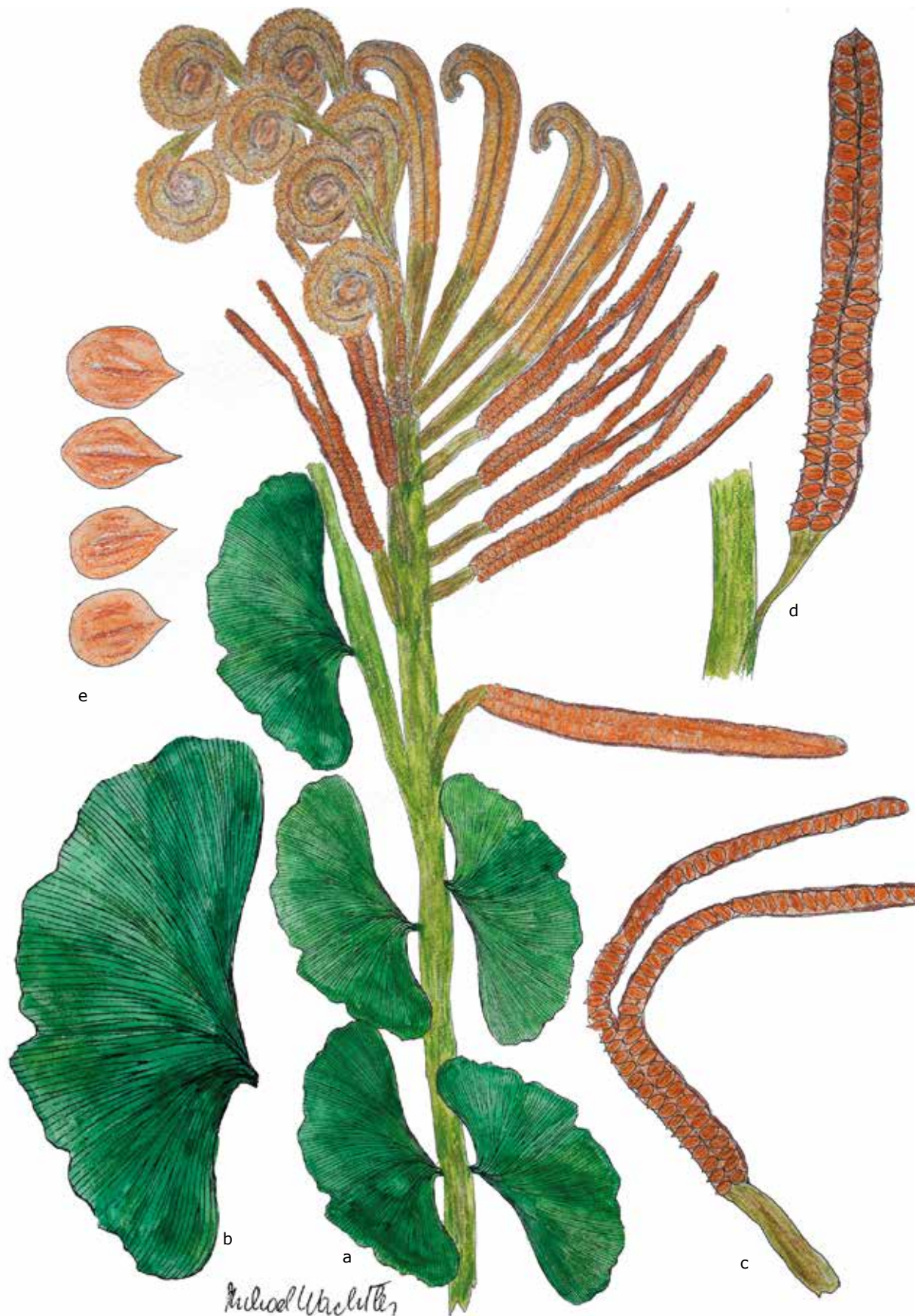
The genus-name honours Thomas Perner, paleobotanist and discoverer of many fossil plants all over the world. The species name remember the locality Valli del Pasubio in the Vicentinian Dolomites.

Holotype

PAS 660, Paratype PAS 499 (fructification), Valli del Pasubio, Ariche; **Repository:** Coll. Wachtler, Dolomythos-Museum, Innichen

Description

Leaves: Entire plant low growing. Foliage larger (about 4 cm) than long (2 cm) attached to the main rachis only in the middle. The clearly visible veins fork on the base irregularly to prosecute than mainly undivided



***Pernerina pasubi*. Reconstructions (Late Permian. Wuchiapingian)**

a. Whole plant (PAS 660, holotype; PAS 431); b. Single leaf (PAS 660, c. Megasporophyll (PAS 480); d. Megasporophyll connected with a branchlet (PAS 432); e. Single seeds (PAS 499)

till the end. In that it is very similar to a ginkgo-leaf (PAS 660, holotype).

Female organs: Megasporophyll beginning with an about 2 cm long sterile petiole. Seeds than attached chain-like in two rows on the from the ovule hidden leaf (PAS 480, PAS 432). The ovules are elliptic, only 1 mm long (PAS 499). About 20 ovules on each row form a megasporophyll.

Taxonomic notes

Pernerina pasubi constitutes the most enigmatic plant of the variegated Ariche-Upper Permian flora. A detailed insertion in one of the known plant groups is difficult, but it has great similarities with the cycads, especially with Triassic *Dioonites*-megasporophylls (Wachtler, 2015), where the seeds are also inserted on a fruit-leaf. The feather-like apical structure, characteristic for *Dioonites* is missing in *Pernerina*. The attached leaves of *Pernerina* have no affinities with those of *Macrotaeniopteris* or *Taeniopteris* but nevertheless also today's *Cycas*-plants have divergent leaf shapes like *Cycas micholitzii*, *Cycas multipinnata*, *Cycas multifrondis* or *Cycas debaoensis*.

Another solution could go in the direction of the *Sagenopteris*-seedferns of the Triassic. But the leaves are not organized in groups of four and the venation of *Pernerina* - although forking several times - is not net-like. The leaves have some similarities with ginkgo-foliage, but their seeds are coated by an aril, being in that different from *Pernerina*. In summary can be stated that we have the same problem as in Early Permian cycad-like *Wachtleropteris*: *Pernerina* constitutes probably an archaic evolutionary *Cycas*-like plant.

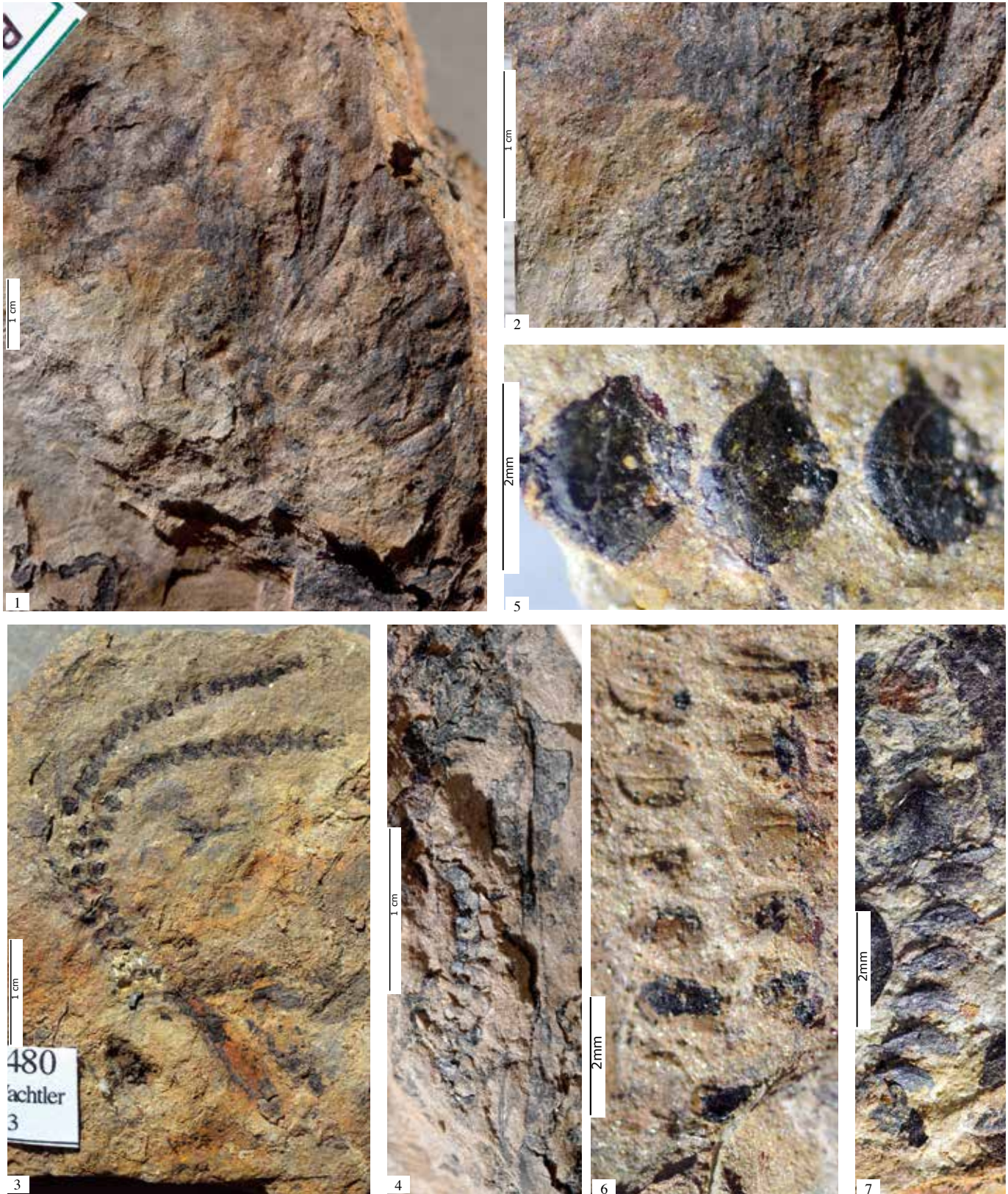
Taeniopteris sp.

Sometimes in the Upper Permian deposits of the Dolomites were recovered tongue-shaped leaves equipped with an entire margin ending in a tapered to rounded apex. Mostly they belong to *Taeniopteris*, distinct from *Macrotaeniopteris wachtleri* due to its smaller leaves. *Taeniopteris eckardtii* is a common flora-element in the coeval Upper Permian Zechstein. Frequent is also *Taeniopteris simplex* in the Early-Middle Triassic from the Dolomites as well as *Taeniopteris nonensis* in the Early Permian. Therefore, it can be expected that *Taeniopteris* occurs also in the Late Permian Grödnert Sandstone.



Pernerina pasubi. Leaves and fertile parts

1-2. Leaves and a megasporophyll connected on the same branchlet (PAS 660, designed holotype); Ariche, Valli del Pasubio; all Coll. Michael Wachtler, Dolomythos-Museum



***Pernerina pasubi*. Fertile parts (Late Permian, Wuchiapingian)**

1-2. Whole cone with enrolled sporophyll (PAS 431); 3. Megasporophyll with a chain of seeds (PAS 480); 4. Sporophyll connected with a stem (PAS 432); 5-7. Detail of the seeds (PAS 499, PAS 432, PAS 519); Ariche, Valli del Pasubio; all Coll. Michael Wachtler, Dolomythos-Museum

***Nilssonia brandtii* (WACHTLER, 2015)**

Nilssonia brandtii, WACHTLER, 2015 pp. 144-149

Etymology

The species name honours Silvio Brandt, Halle, profound researcher and describer of European Upper Permian fossils.

Holotype

PAS 681, **Paratype:** PAS 536 (male cone) PAS 35 (female cone), Valli del Pasubio, Ariche; **Repository:** Coll. Wachtler, Dolomitos-Museum, Innichen

Description

Leaves: Cycad with geometrically segmented fronds. Leaves arising at right angles crossed by never forking veins. The leaves generate about 20 lateral, undivided veins per cm, arising at 80–90° from the rachis (PAS 681, PAS 322, PAS 98).

Male cones: Of morphogenus *Androstrombus*-type. Cones in best cases 15 cm long, with a width of 4 cm, of which the peduncle measures about 2–3 cm. The cone itself is slender, ending tapered. The microsporophylls are aggregated densely around the main axis. They are hexagonal, up to 1 cm long, holding rounded 1 mm wide pollen sacs on the underside (PAS 536, paratype, PAS 54, PAS 809, 740, PAS 746).

Female cones: Of *Thetydostrobos*-type. They are bulkier and do not reach the same length as the male cones with only a short peduncle. The cones are about 10 cm long, the megasporophylls can reach a consistable size of 1.3 cm. They are hexagonal, and densely covered with tiny hairs or trichomes. The two seeds on each scale are exposed on the lower part of the megasporophyll (PAS 35, paratype, PAS 542, PAS 745).

Taxonomic notes

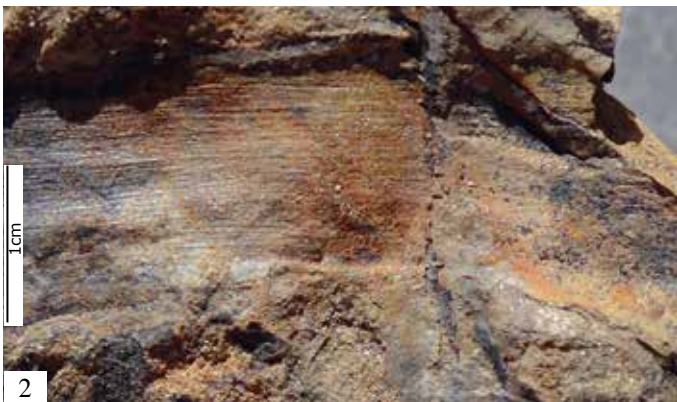
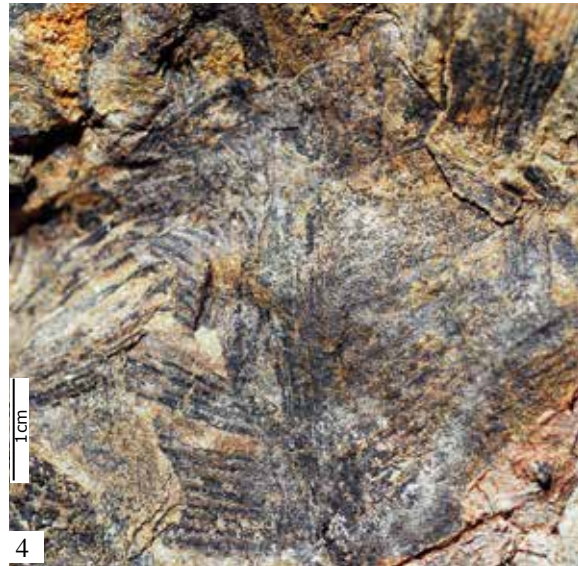
From the Early Permian on we encounter just two different types of cycads. One (*Macrotaeniopteris*, *Taeniopteris*)—conducting to the extant genus *Cycas*—characterized by their entire, sometimes naturally lacerated leaves and equipped with a tuft of featherlike megasporophylls holding on the basal part in two rows a fair amount of seeds and the other (*Nilssonia*, *Pseudoctenis*) with geometrically segmented fronds, bulky

female and slender male cones resembling the large group of today's *Zamia*-cycads. In the Upper Permian of the Dolomites we have from the *Zamia*-ancestor line at least one, maybe also two representatives (with *Pseudoctenis*), classified till now only as *Nilssonia brandtii*. This evolution-way continues then in a spectacular spreading in the Early Triassic where all lineages were in large numbers present.

For a long time, little attention was paid to the unsightly cones, but only from them we can deduce what family and in what numbers they were present. Whereas cycad-cones are rare in other Permo-Triassic fossil sites, in the Upper Permian Ariche-locality we have a multiplicity of gymnosperm-cones, not only from cycads but also from conifers.

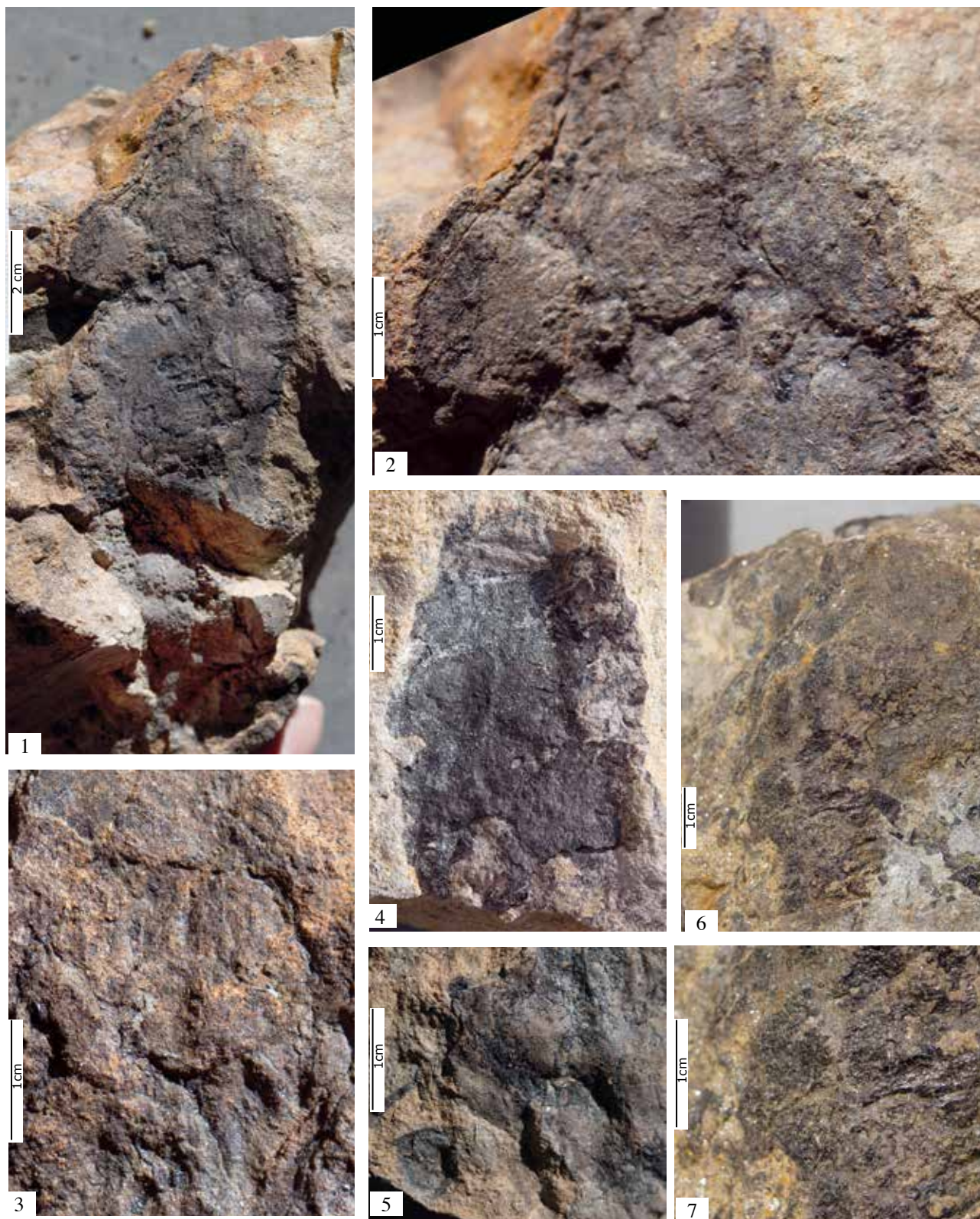
Well preserved fronds, twigs or leaves are otherwise rare. Probably the somewhat greater distance between the growing place and the deposition may be the cause. In the Early-Middle Triassic layers of the Dolomites they were of seawater beach-fossilisation, whereas in the Upper Permian sediments they were deposited in freshwater lakes. *Nilssonia*-female cones can be distinct by a hexagonal tessellated pattern of megasporophylls in which single scales reach a consistable diameter of 1.5 cm. In well preserved specimen, they are densely covered by tiny hairs or trichomes. The two seeds on each scale usually cannot be seen due to the closed sporophyll, but sometimes the shadows of the elliptic ovules are exposed on the lower part of the megasporophylls. Since it is not always clear if they belong to *Nilssonia* or *Pseudoctenis* foliage the morphoname *Thetydostrobos* for female fossil cones of the *Zamia*-type was given.

More complex is the situation for the male cones, being also in extant uniform in all known cycads. For fossil pollen cones the morphogenus name *Androstrombus* (Wachtler, 2010, 2013) was introduced. Usually *Nilssonia* held slender and elongated pollen organs, whereas *Macrotaeniopteris* (*Bjuvia*) and *Taeniopteris* had smaller and more rounded cones. In summary, it can be said that the cycads play an important rule especially in the Upper Permian locality Ariche in the Vicentian-Dolomites and less in other places like the Bletterbach (Kustatscher et al., 2014) or the Seceda-mountain.



***Nilssonia brandtii*. Leaves (Late Permian, Wuchiapingian)**

1. Part of a frond (PAS 681, designed holotype); 2-3. Detail of the leaves and veins (PAS 322, PAS 98); 4. Apical part of a frond with clearly visible veins (PAS 103); 5. Frond evidencing the strong rachis (PAS 119); all Ariche, Valli del Pasubio; all Coll. Michael Wachtler, Dolomythos-Museum



***Nilssonia brandtii*. Female cones (Late Permian, Wuchiapingian)**

1. Completely preserved female (*Tethyostrobus*) cone in connection with *Nilssonia*-fronds and detail of the megasporophylls (PAS 35, paratype); 3. Detail of a megasporophyll (PAS 542); 4. Female cone (PAS 745); 5. Megasporophyll with shed seed (PAS 661); 6-7. Megasporophyll with lateral exposed seed (PAS 804); all Ariche, Valli del Pasubio; all Coll. Michael Wachtler, Dolomythos-Museum



***Nilssonia brandtii*. Male cones (Late Permian, Wuchiapingian)**

1. Completely preserved male cone (*Androstrobus*) with leaves on the same slab (PAS 536, paratype); 2. Entire male cone (PAS 54); 3. Juvenile not mature male cone (PAS 809); 4-5. Male cones (PAS 740, PAS 746); 6. Detail of the open microsporangia (PAS 746); all Ariche, Valli del Pasubio; all Coll. Michael Wachtler, Dolomythos-Museum



***Nilssonia brandtii*. Reconstructions (Late Permian. Wuchiapingian)**

a. Whole female plant with a female cone (PAS 35) b. Megasporophyll outside (PAS 542, PAS 35); c. Detail of a pinnula ((PAS 681, PAS 322, PAS 98), d. male cone (PAS 536)

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Ginkgophyta

Just on the Carboniferous-Permian border we encounter two separated Ginkgoalean lineages: a *Baiera*-line characterized by their needle like lobed foliage and a *Ginkgoites*-line evidenced by their more or less fan-shaped leaves with a repeatedly forking vein structure—typical of modern Ginkgoales. The late Permian (Lopingian) from the Dolomites is rich in plant layers, especially conifers (*Ortiseia*, *Majonica*), but after them came in relative frequency just the Ginkgophyta, largely before the cycads and other plant-families. The richest places for the Ginkgoales are Cuecenes at the base of the Seceda-mountain in the Gröden-Valley, the Bletterbach-gorge located between the hamlets Radein and Aldein (Bauer et. al., 2014), they are scarcely present and Ariche near the Valli del Pasubio in the Venetian Dolomites. Especially on the Seceda they occur in several horizons within the Grödner Sandstone connected with pollen organs and seeds/ovules.

Ginkgoites murchisonae n. sp. (WACHTLER, 2021)

Etymology

The species-name is dedicated to the misunderstood British geologist and fossil collector Charlotte Murchison (née Hugonin, 1788–1869). She accompanied her husband Roderick Impey Murchison during his travels, studies, and fieldwork, working alongside him and visiting several times the Dolomites. Although Charlotte contributed in many of Roderick Murchinson's work she was refused as co-author because women were even forbidden to enter higher schools at the time.

Holotype

PAS 558, **Paratypes:** PAS 446 (seeds), Cuecenes-Seceda, Gröden Valley; **Repository:** Coll. Wachtler, Dolomythos-Museum, Innichen

Diagnosis

Foliage divided into several forking segments, sometimes elongated till fan-shaped, connected together by a petiole. Subtle veins cross the linear, entire margined lobed

leaves. Seeds oval rounded, with the lower side having a pointed apex. Suggested pollen-organs small-sized cone-like.

Description

Foliage: Leaves variegated reaching from slightly lobed (CUEC 549) till deeply incised laminas. These divided into more segments, reaching from two-times bilobed (CUEC 558, designed holotype) till usually four times, but reaching also five lobes (CUEC 543). Petiole slender, about 2 till 4 cm long (CUEC 446, designed paratype, CUEC 557), from which sprout the more times bilobed segments, each of them more or less being symmetrical. Single laminas longer than wide, with entire margin being from 5 cm (CUEC 558) till 7 cm (CUEC 446), reaching in extreme cases also 10 cm. These crossed by parallel, till sometimes forking veins. Some leaves wedge-shaped, reaching on the apex a width of 3 cm (CUEC 343). The apex is rounded convex till slightly tapered.

Female fructifications: Ovules/seeds till 1.5 cm long, 1 cm wide (CUEC 506, CUEC 538, CUEC 544, CUEC 563, CUEC 565),

sometimes in mass-occurrences, tapered on the apex, basically concave. Sometimes a mid-ridge is visible (CUEC 538, CUEC 572), as well as parts of the fleshy aril (CUEC 356, CUEC 572). Seldom they are equipped with a connecting stalk (CUEC 572, CUEC 565). Usually the slender and sometimes long stalks can be collected isolated (CUEC 559) or in the ginkgo-seed debris (CUEC 571). As in living ginkgo the mature seeds and stalks become separated from each other during the composting process.

Pollen organs: Till 5 cm long, 0.7 cm wide, characterised by many small-sized bracts (CUEC 541).

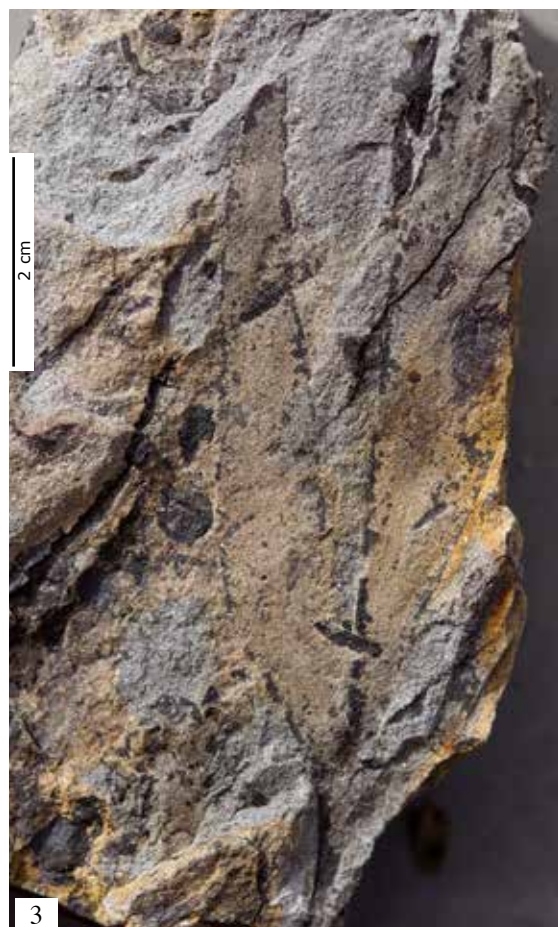
Discussion

Strangely in the Permian of the Dolomites we encounter just fully evolved ginkgophyta and this not only refers to the fan-shaped foliage, but also to their fertile parts or their distinctness of long and short spur shoots that include collar-like ring from which the leaves emanate, just as on modern ginkgos, and the two upright ovules that form together. Leaves probably growing as short



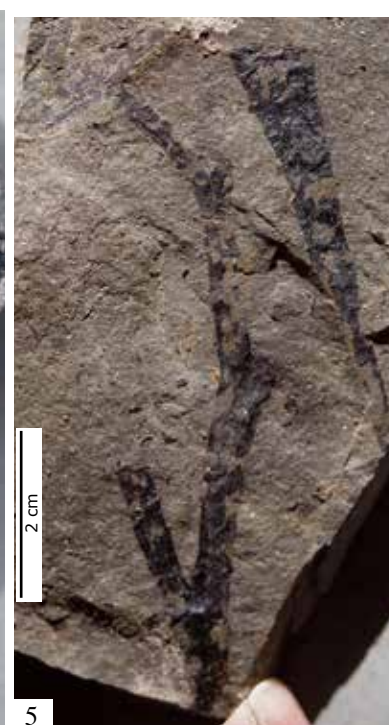
Ginkgoites munchisonae: rotten stalks and seeds

1-2. Rotten fruits and shed stalks, becoming separated each other in the decomposition process (CUEC 571, CUEC 559); 4. Squashed *Ginkgoites*-seeds. 3. Seed/Ovule with connecting stalk and midrib (CUEC 572).



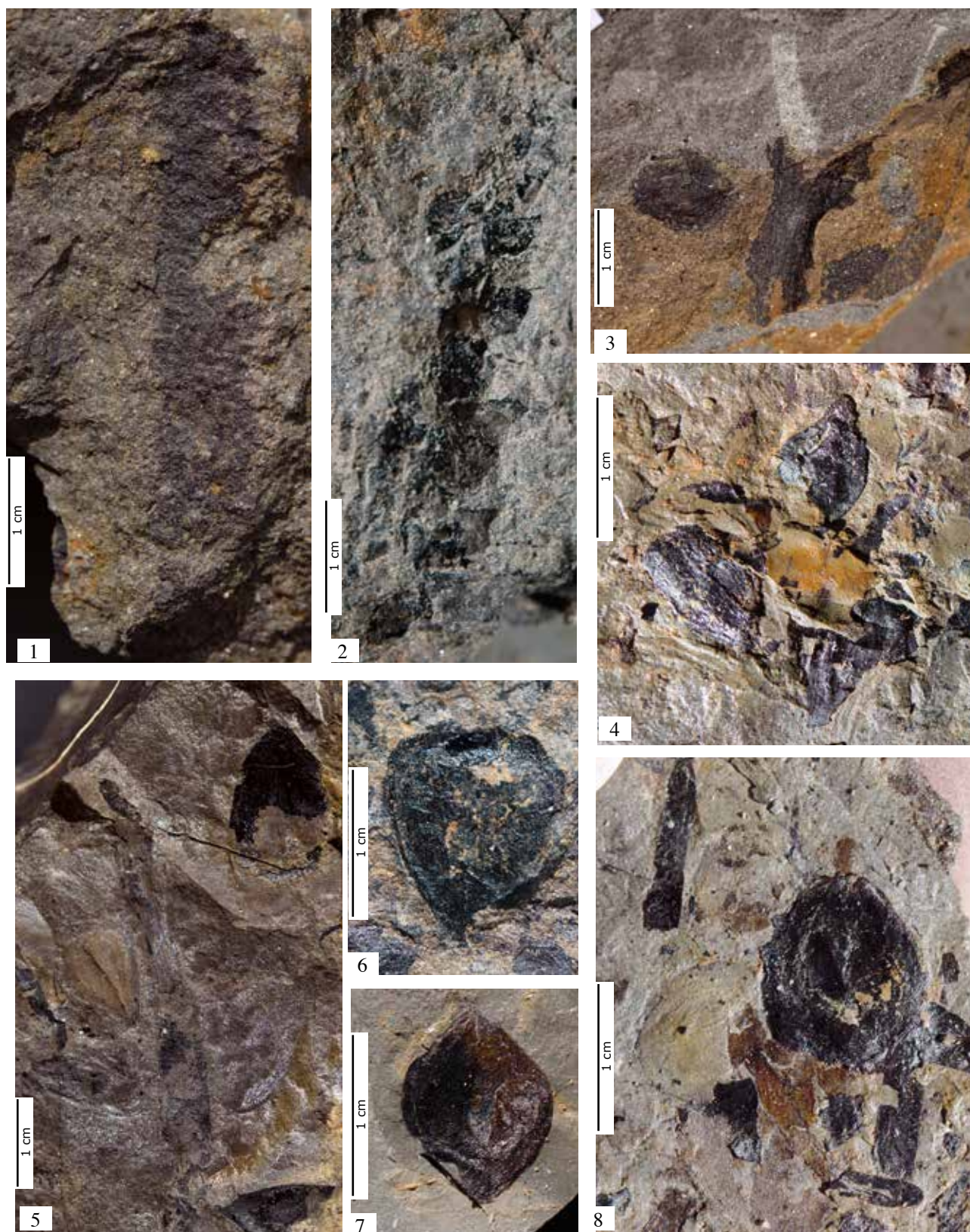
***Ginkgoites munchisonae*. Leaves and seeds (Late Permian, Wuchiapingian)**

1. Four lobed leaf (Designed holotype CUEC 558); 2-3. Leaf with accompanying seeds (Designed paratype CUEC 446); 4. Two-lobed broad leaf (CUEC 343); 5. Leaf with seed (CUEC 343); all Cuecenes, Gardena Valley, Coll. Michael Wachtler, Dolomythos Museum



***Ginkgoites murchisonae*. Leaves and branchlets (Late Permian, Wuchiapingian)**

1. Twig with several leaves (CUEC 543); 2. Slightly two-lobed leaf with details of the venation (CUEC 549); 3. Four-lobed leaf (CUEC 557); 4. Leaf with seeds (CUEC 554); 5. Stem with leaves (CUEC 528); all Cuecenes, Gardena Valley, Coll. Michael Wachtler, Dolomythos Museum



***Ginkgoites murchisonae*. Male cones and seeds (Late Permian, Wuchiapingian)**

1. Suggested juvenile male cone (CUEC 541); 2. Adult male cone (CUEC 524); 3. Seed (CUEC 356); 4-5. Agglomeration of seeds (CUEC 506, CUEC 538); 6-7. Isolated seeds (CUEC 544, CUEC 563); 8. Two seeds (CUEC 565); all Cuecenens, Gardena Valley, Coll. Michael Wachtler, Dolomythos Museum

shoots are usually unlobed, those of the long shoots against are deeply dissected.

Early Permian (Kungurian) *Ginkgoites pohli* from the Italian Dolomites manifest still a transition-mode between the *Baiera*- and the *Ginkgoites*-type whereas Upper Permian *Ginkgoites murchisonae* evidences just a tendency and resemblances with today's maidenhair trees. This line can then be traced over many millions of years from Upper Permian *Ginkgoites murchisonae*, over Middle Jurassic *Ginkgoites huttonii* or Cretaceous *Ginkgoites sibirica*, till reaching modern times with Paleogene *Ginkgo cranei* from North Dakota. After the Paleogene-Eocene, they are just so evolved that there are hardly any more differences to today's (Seward, 1919; Crane, 2015).

Late Permian *Ginkgoites murchisonae* therefore fills together with coeval *Baiera digitata* from the European Zechstein, a gap in the evolution of the first Ginkgoales. The question why the Dolomites settled the future *Ginkgo biloba*-concept in the late Permian remains unresolved, whereas in the German localities the *Baiera*-blueprint can be traced for many million years till the Triassic-Jurassic.

Usually in the Early Permian Tregiovo, spring-like flora-elements from *Ginkgoites pohli* like immature seeds or short shoots can be found more, whereas in the Upper Permian Grödnert Sandstone is a frequency of an autumnal *Ginkgoites murchisonae* seed-agglomeration.

An important question to resolve is the climate in the Permian. Today ginkgo-trees grow in the temperate regions of the world, like many parts of Europe, the United States, as well as Eastern Asia with China and Japan. They do not survive in too cold areas like the Northern States of the world or on the other extreme in too high temperatures with water poverty. Egypt, Sicily or Florida are not adequate, as well as Norway, Siberia or Alaska. It can therefore be suggested that a similar mild climate we had sometimes but not always over the Permian in the Dolomites. *Ginkgoites* then vanished completely during the Triassic. Therefore, it can be supposed that the climate was tropical and hot and only on the Triassic-Jurassic border the circumstances were again suitable for the ginkgos.

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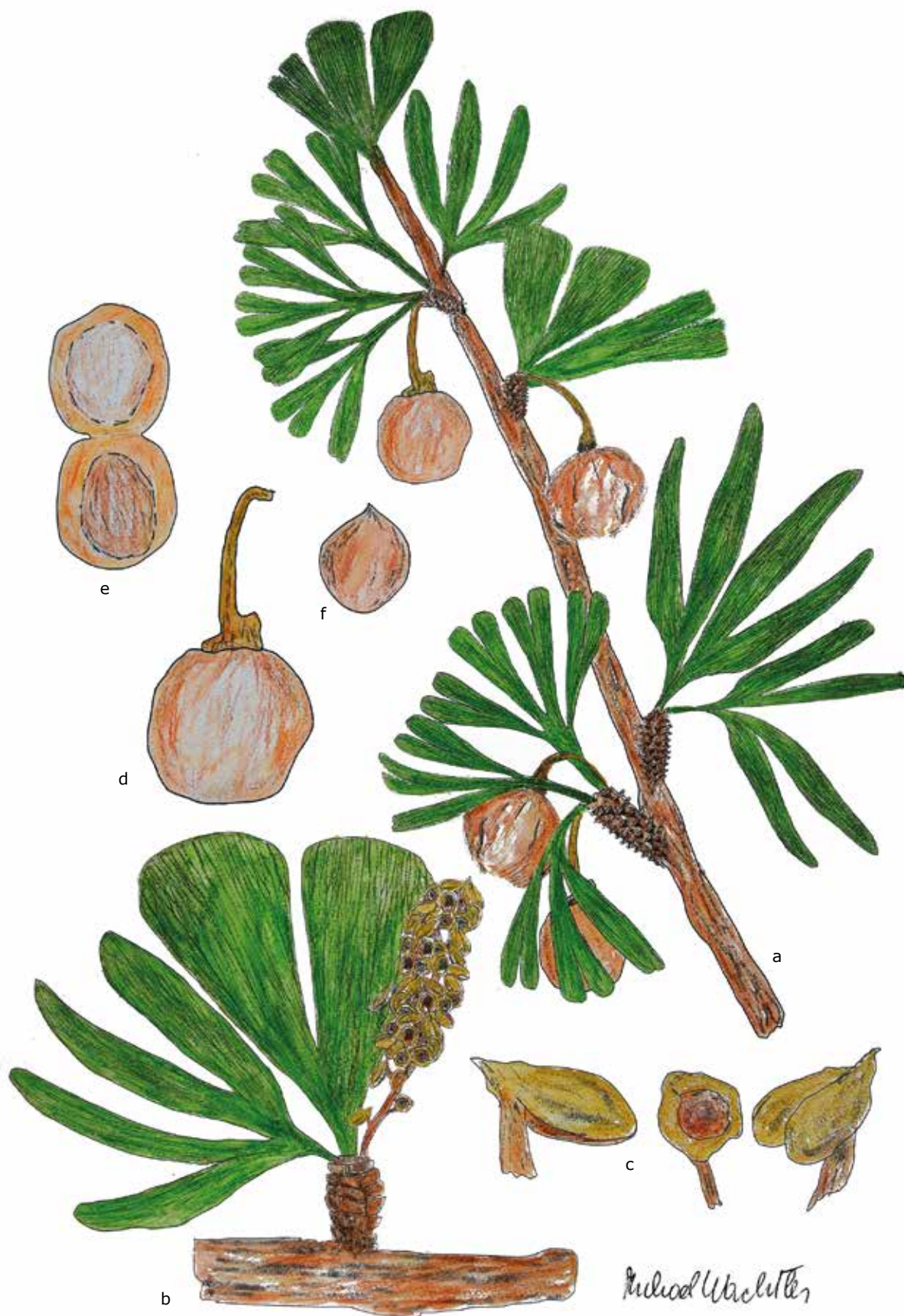
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Coniferophyta

Conifers are the most widespread group of plants in the Grödnert Sandstone in terms of species-number, as well as in quantity. Within them two are dominant: *Ortiseia* and *Majonica*. They are so common that even subspecies with different characteristics could be established. They belong to slightly time-different layers or they developed different characteristics as it can be seen today on the variegated *Araucaria* plant society in New Caledonia. While *Ortiseia* due to its features can be regarded as ancestor of the *Araucariaceae*, *Majonica* with its alate seeds and projecting bracts may be considered as progenitor of the *Abietaceae*. Less common are the *Voltziales* (*Voltzia sjerpii*), the *Taxodium*-cypresses (*Ulbeus vicetinus*) and the *Taxaceae* (*Ullmannia edwardsae*).

Araucaria-ancestors

An interesting group inside the conifer-families are represented by the *Araucarias*. Now they are restricted to the Southern hemisphere, but for a long period—from the Earliest Permian till the Triassic-Jurassic—they were widespread on the Northern part of the globe. One feature that distinguishes them from other conifers are their one-



***Ginkgoites murchisonae*. Reconstructions. (Late Permian. Wuchiapingian)**

a. Shoot with several berries (CUEC 558, holotype, CUEC 446, CUEC 543, CUEC 549, CUEC 557); b. Male cone on a branchlet (CUEC 541, CUEC 524); c. Isolated microsporophylls (juvenile and mature); d. Berry (CUEC 572); e. Open berry evidencing the aril (CUEC 571); f. Seed (CUEC 544, CUEC 563, CUEC 565)

seeded megasporophyll in contrast to many other conifers like the Pinaceae, Piceaceae, Abietaceae, which bear two, mostly alate seeds on their scales or the three or more seeded *Cryptomeria*-conifers and Sequoias. The Araucarias are also distinct by their huge pollen cones with on the upper part of the microsporophyll dorsiventrally hanging pollen sacs and bulbous female cones.

Since Upper Permian *Ortiseia* (*leonardii*) was established by Rudolf Florin 1964, diverse species covering the whole Permian were found and described (Clement-Westerhof, 1984; Wachtler, 2012, 2015). Therefore, this conifer can be regarded as one of the best-known Permian conifers. When they were discovered, it was not clear for a long time which family they should be placed in. Only after intensive and lengthy studies, based on hundreds of fertile specimens, Michael Wachtler succeeded in proving that these can be regarded as the earliest ancestor of the Araucarias (Wachtler, 2012, 2015). In the Permian, they developed their characterising features, such as their elongated and long bracted pollen organs and bulbous female cones, as well as their symmetrical arranged foliage branchlets. An interesting feature is the evolving of their one-seeded scales. In the beginning and during the whole Permian, various minute sterile leaves covered densely the seed scale, probably to protect the seed from predators. After maturity the scale and within them the seed was shed entirely. Clearly as Araucaria-conifers, recognizable conifers we encounter begin from the Carboniferous-Permian border with *Ortiseia uhli* from the Kasimovian/Gzhelian Saar-Nahe-Basin in Germany, although also from the Carinthian Alps representatives are known from this time. After that the recoveries moved to the Southern Alps, especially the Dolomites. Artinskian *Ortiseia dasdanai* was followed by Kungurian *Ortiseia daberii*. In the late Permian we then have the Dolomites a great diversity with slightly different features, probably also due to geological time differences, like *Ortiseia leonardii*, *Ortiseia jonkeri*, *Ortiseia zanettii* or *Ortiseia visscheri*.

The conifer *Ortiseia* can be regarded as the typical Alpine Permian plant-genus. Strangely being just present in the Carboniferous-Permian Saar-Nahe-Basin,

unmistakable findings in the otherwise rich Late Permian Zechstein deposits are only sparsely recorded. They were described by Helmuth Ullrich (1964) as *Culmitzschia florinii* being in that only a synonym of *Ortiseia*. The most widespread conifer there are (*Pseudo*)*Voltzia liebeana* additionally to *Ullmannia*, which due to their archaic fruit-berries can be classified as a Taxaceae.

After the Permian-Triassic border Araucariaceae mostly changed their blueprint. The only clearly identifiable representative, evidencing a little the old feature of the sterile leaflets surrounding the seed-scale we encounter with *Ortiseia collii* in Early Middle Triassic (Anisian) sediments on the Balearic islands (Mallorca, Estellencs) in Spain (Juárez & Wachtler, 2015).

Moreover, in the Dolomites the Ortiseiaceae can be followed from the Anisian till the Carnian period (*Araucarites churchillae*, *Araucarites gilbertae*, *Araucarites spinosa*) but in a modified form. The twigs were than formed sometimes (*Araucarites spinosa*) as spreading pseudo-whorls with second till third order branches of unequal length with rigid leathery pungent needles as extant *Araucaria araucana*. On the Triassic-Jurassic border, the last *Araucarites* species disappeared from the Northern hemisphere to enlarge their areas on the Southern globe. Especially in the Jurassic Cerro Cuadrado in Argentina they were fossilized in stupend specimen during a volcanic eruption. Their rounded, globose female cones have just many similarities with the extant one.

***Ortiseia leonardii* (FLORIN, 1964)**

1964 *Ortiseia leonardii*, FLORIN, Pl. 1-3

1984 *Ortiseia leonardii* (Florin), CLEMENT-WESTERHOF
Pl. I-XI pp. 122-135

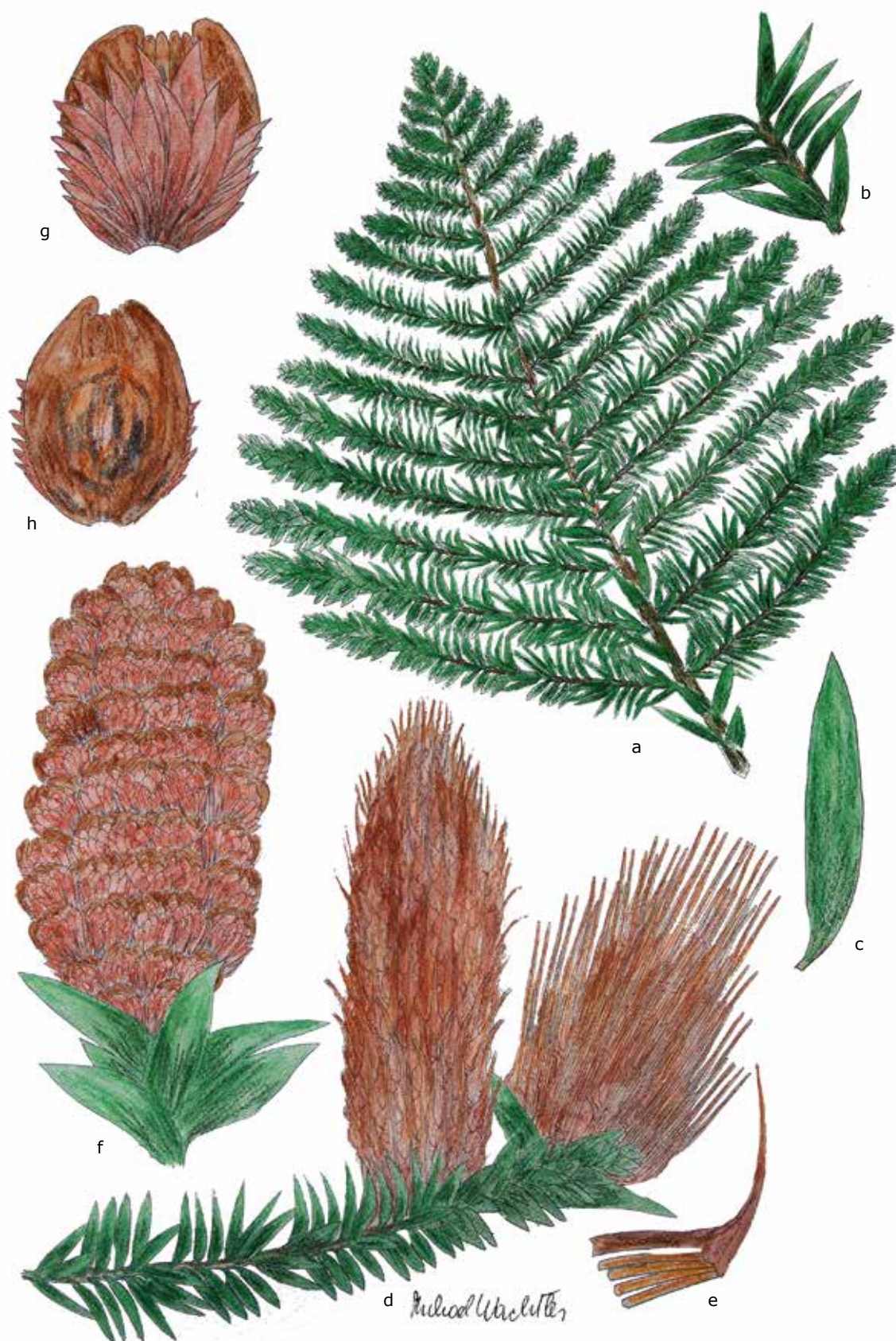
2015 *Ortiseia leonardii* WACHTLER, pp. 103-109

Etymology

Honouring the Italian geologist and paleontologist Piero Leonardi (1908–1998).

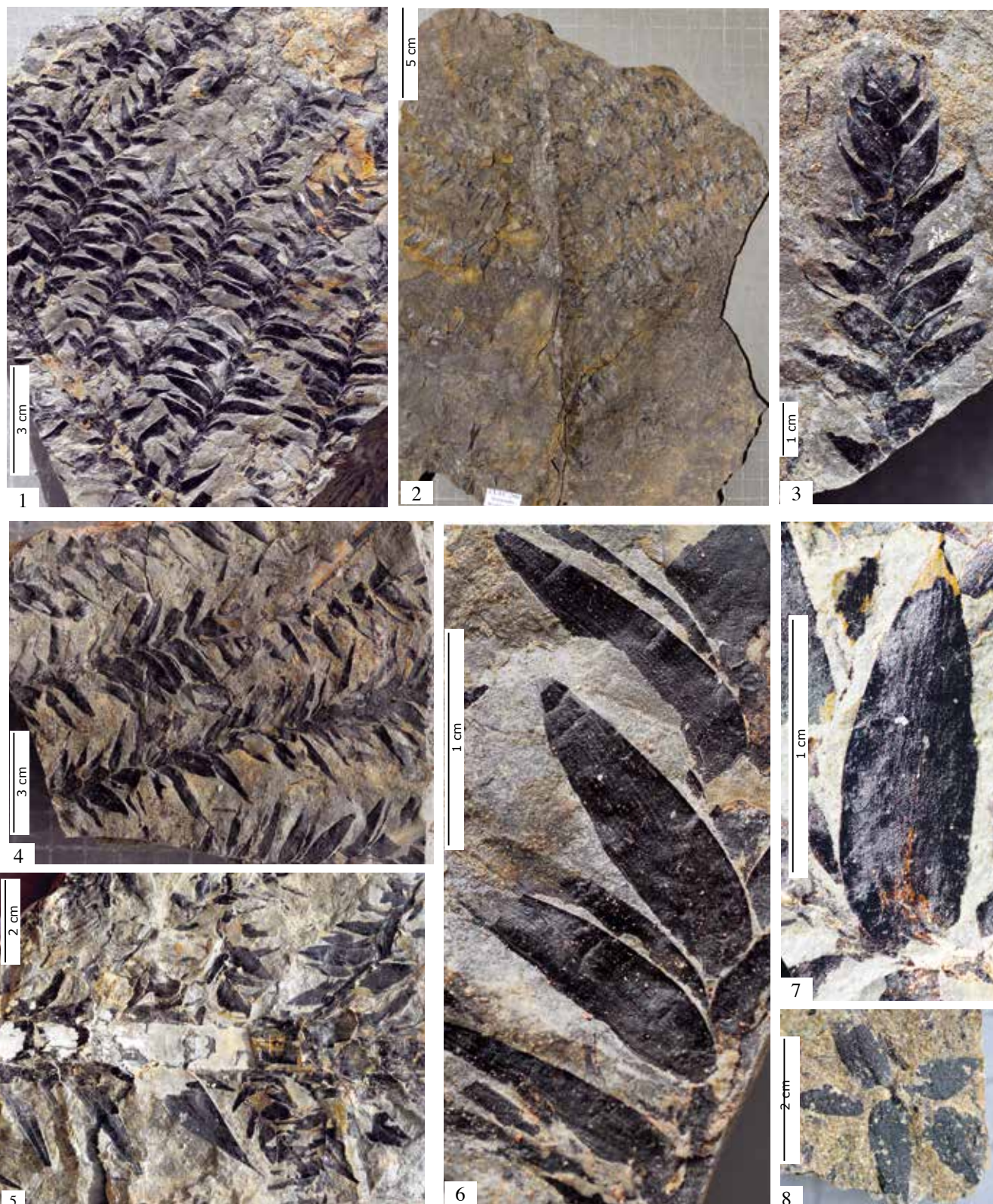
Description

Branchlets and leaves: Conifer with pinnately branched lateral shoot system. Leaves from leathery to awl-shaped and lanceolate with an acute to obtuse apex. Leaf base slightly contracted with nearly invisible grooves across the entire foliage.



***Ortiseia leonardii*. Reconstructions (Late Permian. Wuchiapingian)**

a. Branchlet (CUEC 63); b. Detail of a twig (CUEC 78); c. Single leaf (CUEC 43); d. Male cones on a twig (CUEC 60, CUEC 484, CUEC 246, CUEC 150, CUEC 93, CUEC 129); e. Microsporophyll (CUEC 156); f. Female cone (CUEC 201, CUEC 327; CUEC 322); g. Seed scale abaxial side (CUEC 112, CUEC 57); h. Seed scale, adaxial side (CUEC 425, CUEC 34)



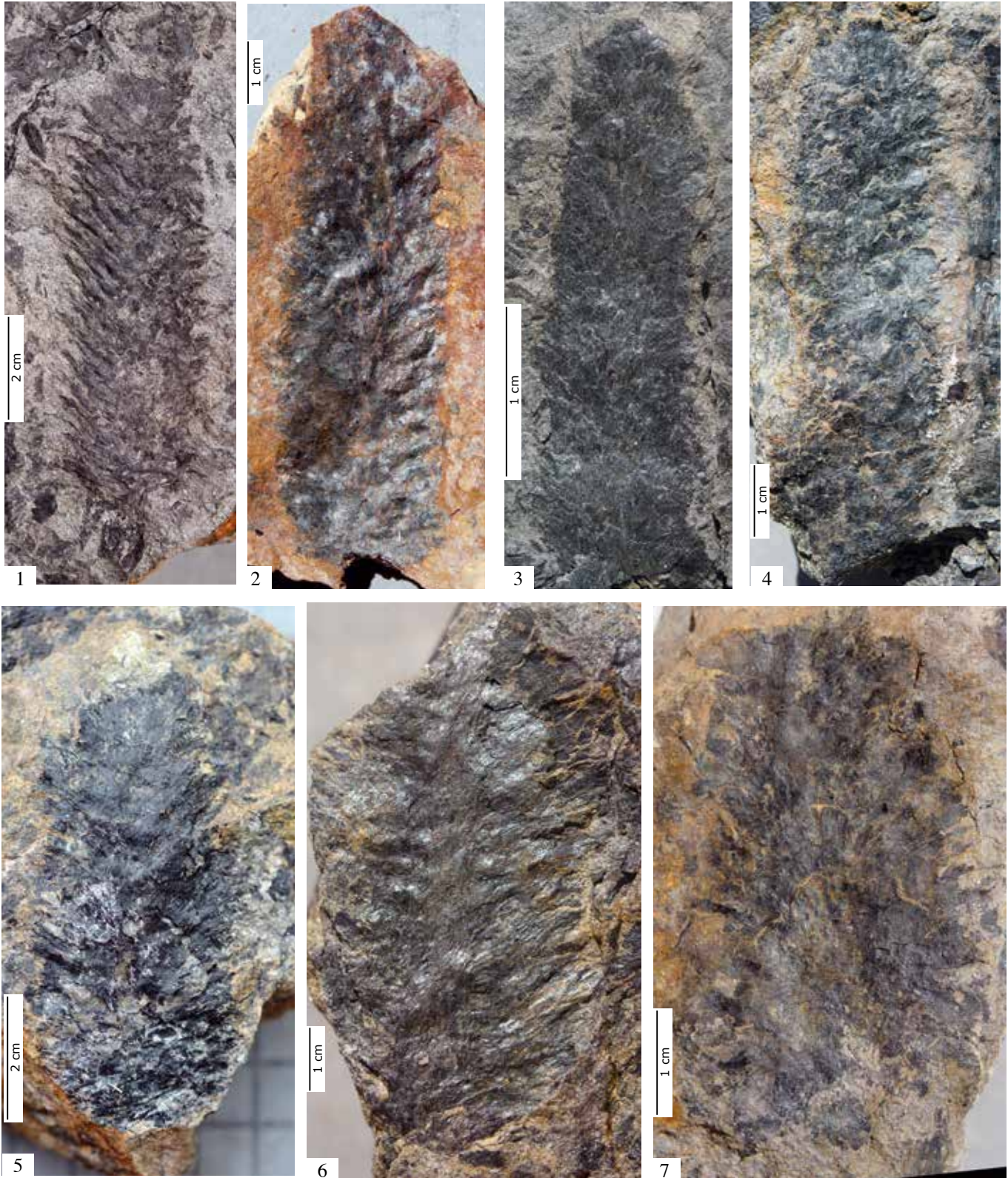
***Ortiseia leonardii*. Twigs and branchlets (Late Permian. Wuchiapingian)**

1. Branchlet (CUEC 63); 2. Twig (CUEC 260); 3. Apical part of a twig (CUEC 69); 4. Detail of a twig (CUEC 78); 5. Leaves on a main stem (CUEC 73); 6-7. Single leaves. Detail (CUEC 78, CUEC 43); 8. Apical part of a branchlet (CUEC 206); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum.



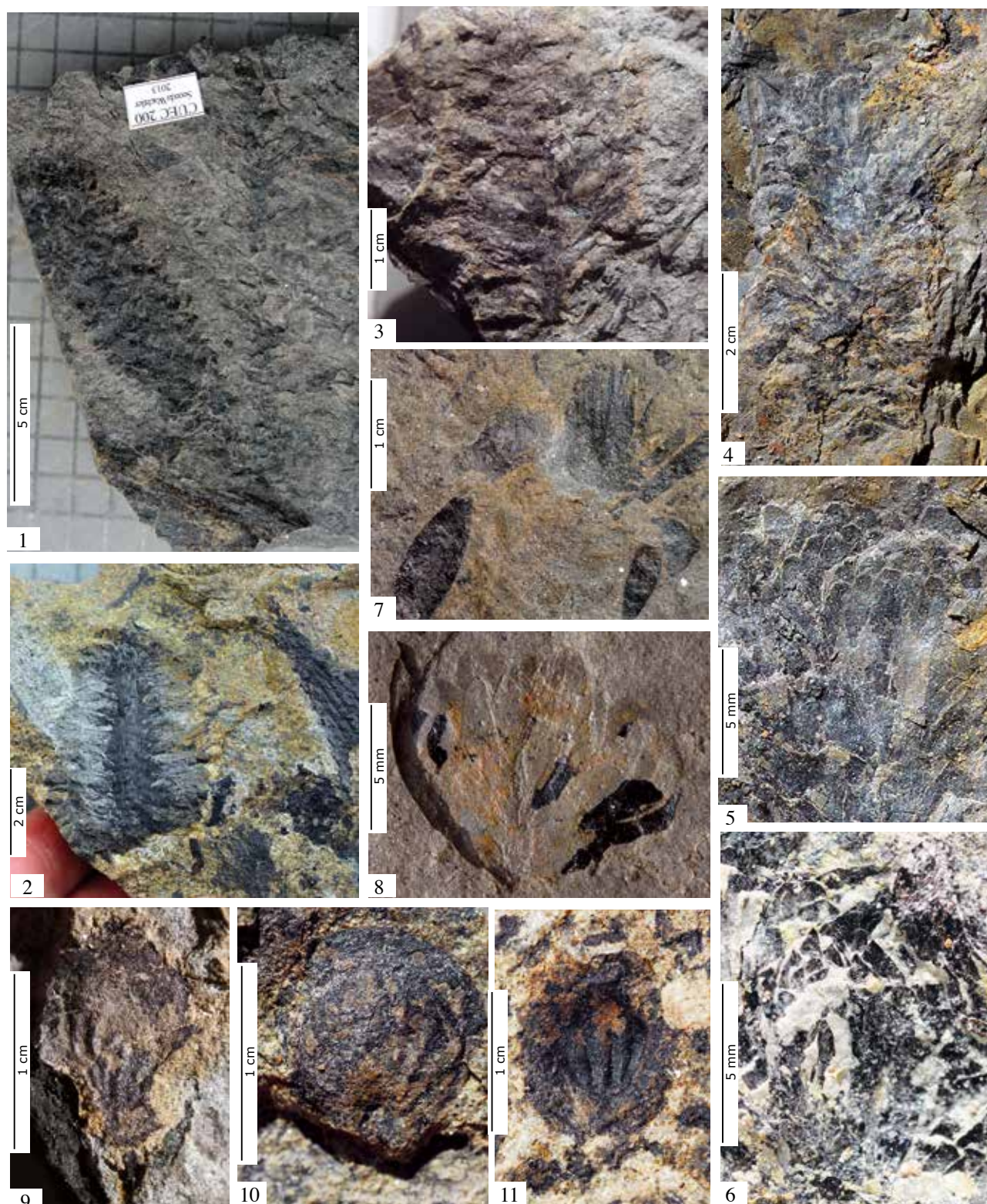
***Ortiseia leonardii*. Male cones and microsporophylls (Late Permian. Wuchiapingian)**

1. Juvenile male cone (CUEC 60); 2. Two male cones (CUEC 484); 3-4. Male adult cones (CUEC 246, CUEC 150); 5-6 Male cones. Note the long bracts (CUEC 93, CUEC 129); 7-8. Male cones. Detail of the bracts and microsporophylls (CUEC 330, CUEC 192); 9. Detail of the dorsiventrally hanging microsporophylls (CUEC 156); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum.



***Ortiseia leonardii*. Female cones (Late Permian. Wuchiapingian)**

1-4. Several elongated female cones (CUEC 371, CUEC 316, CUEC 329, CUEC 326); 5-7. Several bulbous female cones (CUEC 201, CUEC 327; CUEC 322); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum.



***Ortiseia leonardii*. Female cones and seed scales (Late Permian. Wuchiapingian)**

1. Female cone, attached on a branchlet (CUEC 200); 2. Female and part of a male cone (CUEC 190); 3. Female cone with slight arching of the seeds (CUEC 419); 4-5. Young female cone and detail of two megasporophylls, abaxial view. The ovules are hidden behind the sterile leaves (CUEC 112); 6. Detail of one juvenile megasporophyll in a cone. The ovule lies mainly invisible in the background (CUEC 57); 7. Seed and *Ortiseia*-leaves (CUEC 158); 8. Juvenile scale with detail of the protective leaves (CUEC 568); 9-11. Seeds evidencing the merged protective foliage (CUEC 425, CUEC 34, CUEC 11); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomymthos-Museum.

Single leaves are normally from 1.0 till 1.5 cm long and at the base up to 0.5 to 0.8 cm wide (CUEC 63).

Male cones: Slender, up to 10 cm long, about 2 cm wide, with an axis bearing numerous spirally arranged and overlapping microsporophylls. Young cones characterised by microsporophylls with extremely long bracts up to 1.5 cm, adult cones partially losing this characteristic. Pollen sacs araucaroid, with a fair number of pollen sacs hanging from the outer lower margin towards the main axis (CUEC 484, CUEC 246).

Female: From long elongated (about 10 cm long and 2 to 2.5 cm wide, (CUEC 371, CUEC 316), till bulky to round bodied (at least 5 cm long and 2.5 to 3.5 cm wide, (CUEC 201, CUEC 327). Cone axis holding spirally arranged seed scales. Various minute sterile leaves cover the coalesced seed scale densely on the outer side. Seed scales, 1.2–1.5 cm long, 1.0 cm wide dropped after maturity as one unit. No distinct and overlapping bract recognizable. Ovule/seed approximately in the middle, up to 1 cm long and 0.5–0.7 cm wide.

Taxonomic notes

This first discovered single-seed bearing *Ortiseia* closes a chapter in the understanding of modern Araucariaceae. The upright standing male and female cones and the arrangement and appearance of the twigs and leaves can be considered typical of all Araucariaceae. The *Ortiseia* ovulate seed scale is composed of three different merged units: a number of sterile protective leaflets surrounded a barely segmented scale. A single, nut-like, and relatively large ovule without wings was embedded in the middle of the seed scale. After maturity the scale including the seed was shed entirely. From the Triassic on the protective leaves merged than completely, that today we can hardly recognise anything of the original blueprint.

The branches indeed extended in the Permian pinnately. Their structure was similar to that of modern *Araucaria heterophylla*, the Norfolk Pine. Only in the Triassic we encounter then in the Alps the first rope-like branchlets like in *Araucaria araucana*.

All different *Ortiseia* species from the late Permian of the Southern Alps can be attributed to some slight age-differences. Probably *Ortiseia leonardii* is slightly older than

the other one, but unambiguous evidence can not be provided. From the much more evolved and, in contrast to the other sites, species rich Ariche-locality it seems that it must be the youngest, possessing a lot of Early Triassic plant affinities like abundant cycadophyte as well as sphenophyta.

Interestingly on the locus typicus Seceda/Cuecenes two different types female cones of *Ortiseia leonardii* can be found within the same strata and location. One elongated form and one bulbous. It can hardly be assumed that they belong to two different species, too close to each other they are found. More can be assumed that, depending on the branch position or height of the tree, they formed different cone shapes. Otherwise, their scales were identical.

The male cones featured remarkably long microsporophyll-bracts that extended well beyond the elongated scales especially when young. The male cones were slender and could reach lengths of up to 10 cm.

Ortiseia jonkeri (CLEMENT WESTERHOF, 1984)

1984 *Ortiseia jonkeri* CLEMENT-WESTERHOF PI. XX-XXI pp. 142-160

2015 *Ortiseia jonkeri* WACHTLER, pp. 110-114

Etymology

Honouring the Dutch palaeobotanist Frits Jonker.

Description

Branchlets and leaves: Widely spaced and symmetrically spreading out to the sides with slightly imbricate leaves. Foliage awl-shaped incurved to triangular reaching about 1 cm in length and 0.5–0.7 in width.

Male cones: Fully grown cones reach a length of 4.5 cm–8 cm and about 2–3 cm in width. They are elongated and slender, sometimes bulging in the middle. From the axis sprout numerous spirally arranged and overlapping microsporophylls that usually reach a length of 0.5 cm. The microsporophylls end in a short-pointed bract of about 0.5 cm (ULBE 59, ULBE 62, ULBE 07).

Female cones: From round-bodied, 2.5 cm length and 2 cm in width till elongated with a maximum 5 cm length and 3 cm width. Cone axis holding spirally arranged seed



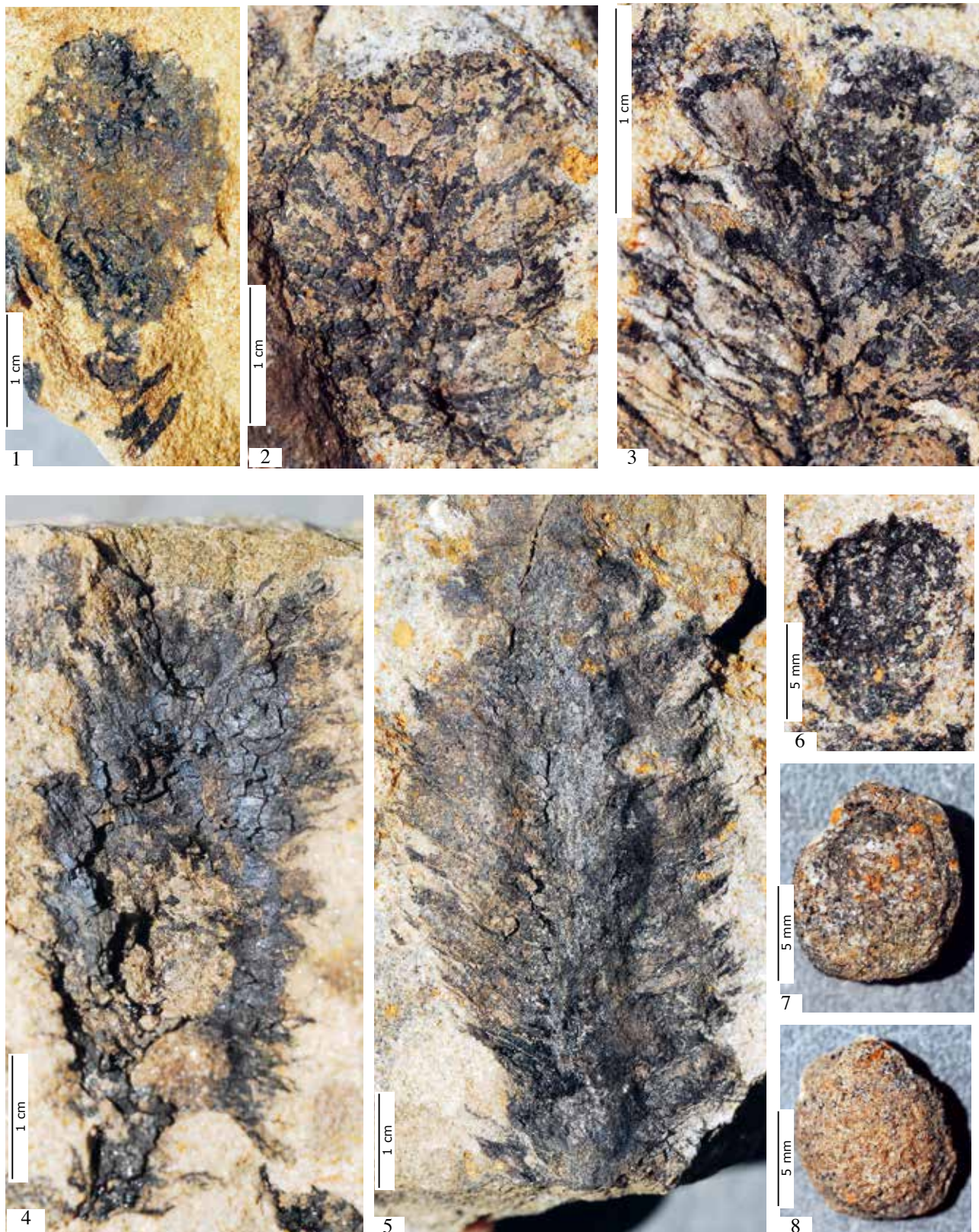
***Ortiseia zanettii*. Reconstructions (Late Permian. Wuchiapingian)**

a. Male cone ((PAS 304, PAS 637, PAS 704); b. Microsporophyll outside; c. Microsporophyll with hanging pollen sacs (PAS 94, PAS 219 paratype); d. Female cone (PAS 379, paratype, PAS 69, PAS 12); e. Juvenile ovule outside (PAS 428); f. Adult scale abaxial view (PAS 77, 408); g. Mature scale (PAS 554, PAS 364, PAS 352); h. Scale overhead view (PAS 6, 89, 80); all Ariche, Valli del Pasubio; Coll. Michael Wachtler, Dolomythos-Museum.



***Ortiseia jonkeri*. Male cones (Late Permian. Wuchiapingian)**

1. Isolated needle (ULBE 140); 2. Juvenile male cone (ULBE 63); 3. Juvenile male cone (ULBE 59); 4. Pollen cone evidencing the outer part and the microsporophylls from the inner side (ULBE 62); 5. Semi-destroyed old male cone (ULBE 07); 6. Detail of the axis (ULBE 12); 7. Microsporophylls from the lateral side (ULBE 10); all Ulbe, Recoaro; Coll. Michael Wachtler, Dolomythos-Museum.



***Ortiseia jonkeri*. Female cones (Late Permian. Wuchiapingian)**

1. Juvenile female cone attached to the branchlet (ULBE 61); 2. Mature female cone with seeds ready to be released (ULBE 18); 3. Apical part of a female cone (ULBE 67); 4. Female cone evidencing the bushy protective leaves (ULBE 15); 5. Fully grown female cone (ULBE 66); 6. Isolated seed scale with impressions of the outer side covering leaflets (ULBE 35); 7-8. Isolated seed inner side (adaxial) and outside (abaxial) (ULBE 40); all Ulbe, Recoaro; Coll. Michael Wachtler, Dolomythos-Museum.

scales, bearing on their inner side the ovuliferous seeds. They are composed of various minute and elongated sterile leaves surrounding the seed scale. The scale holds only one rounded to slightly elongated ovule/seed in the approximate middle. Seed scales 1.2–1.5 cm long, dropped after maturity as a single unit. No visible projecting bract. Seeds about 1 cm long, 0.6–0.8 cm wide, surrounded by fleshy protective leaves (ULBE 66).

Taxonomic notes

Apart from Clement-Westerhof's locus typicus the stone cutterly Cortiana in the Valli del Pasubio, unfortunately now closed and completely overgrown with dense vegetation, *Ortiseia jonkeri* was also recovered in the hamlet Ulbe near Recoaro (Wachtler, 2015). The site is characterized by its richness in male and female cones.

Ortiseia jonkeri differs with its shorter bracts of the microsporophylls from *Ortiseia leonardii* (0.5 cm against 1 cm). The aspect of the female cones is nearly identical till a little more small-sized. More discrepancies can be seen with *Ortiseia zanettii* from the nearby Ariche locality with its huge male cones and stocky microsporophylls.

Ortiseia zanettii (WACHTLER, 2015)

2015 *Ortiseia zanettii* WACHTLER, pp. 115–122

Etymology

Named after Feruccio Zanetti, the owner of the terrain, where *Ortiseia zanettii* is common, who generously allowed the material to be collected.

Description

Branchlets and leaves: Slightly awl-shaped to linear, 1 cm long foliage. Fine slender leaves covering the main stem (PAS 755).

Male cones: Massive, up to 10 cm long, about 2.5 to 3 cm wide, elongated, having mainly the same size all over the cone. Microsporophylls up to 1 cm long and 0.5 cm wide, enlarged with a short broad apex. Pollen sacs, with clearly recognizable close hanging microsporophylls from the lower apical part towards the main axis (PAS 94, PAS 304; PAS 60).

Female cones: Round bodied to elongated, 3.5–5 cm long, 2–3 cm wide. Cone axis holding spirally arranged seed scales. These are 1.5 cm long and 0.8 cm wide, covered on the outer side with various minute sterile protective leaves. Scale, holding a 1.0 cm long and 0.5 cm wide nutlike ovule/seed embedded deeply approximately in the middle of the scale. Scale and seed dropped after maturity as a single unit. No visible distinct bract (PAS 379, PAS 69, PAS 12).

Taxonomic notes

Ortiseia zanettii stands apart from the till now described Late Permian *Ortiseia leonardii*, *Ortiseia visscheri* and *Ortiseia jonkeri* due to its distinctive huge pollen cones. They are much more massive than those of *Ortiseia leonardii* or *Ortiseia jonkeri*, and are the only ones where it is easily possible to recognise the typical blueprint of all extant Araucarias: the pollen sacs hanging from the apical lower side dorsiventrally to the main axis. Therefore, the discovery of *Ortiseia zanettii* is important to understand the evolving line of Araucariaceae and to prove that they have hardly changed in the last 300 million years. This does not mean that other *Ortiseia*-species did not have this characteristic, but it is more difficult to see. *Ortiseia zanettii* is the dominant conifer together with *Majonica alpina* from the by Michael Wachtler discovered locality Ariche in the Vicentian Dolomites. There pollen, as well as seed cones and scales can be recovered in large quantities.

Surprisingly, and in net contrast to the abundant and beautiful preserved branches and leaves at the Seceda-Cuecenes locality where *Ortiseia leonardii* is the dominant conifer, in the locus typicus for *Ortiseia zanettii*—the Contrada Ariche (Valli del Pasubio)—well-preserved leaves and branches are rare, while both female and male cones are abundant and also well maintained.

It is a mystery why they are missing whilst others, like fragile Cycad-leaves, were found in quite good quality and quantity. Probably the Araucariaceae and Abietaceae were flooded from a longer distance into a former lake which caused the delicate branches to be largely destroyed. Otherwise, the seed scales of *Ortiseia* owing to their robustness, and the winged seeds of *Majonica* due to their ability to fly, were deposited for



***Ortiseia zanettii*. Male cones (Late Permian, Wuchiapingian)**

1. Juvenile male cone attached on a twig (PAS 94, designed holotype); 2. Entire juvenile pollen cone (PAS 304); 3. Pollen cone with short bracts (PAS 637); 4. Juvenile male cone (PAS 704); 5. Semi destroyed male cone (PAS 60); 6. Old pollen cone without pollen sacs (PAS 57); all Ariche, Valli del Pasubio; Coll. Michael Wachtler, Dolomythos-Museum



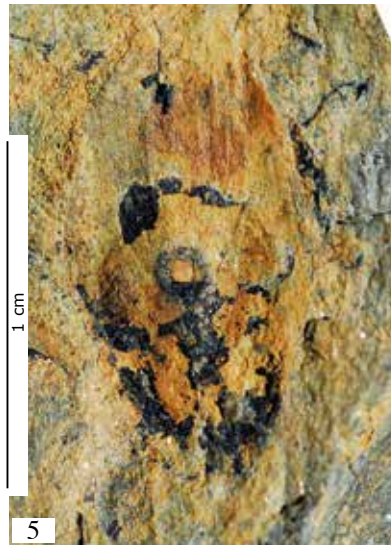
***Ortiseia zanettii*. Male cones (Late Permian. Wuchiapingian)**

1. Microsporophyll with hanging pollen sacs (PAS 94); 2. Microsporophyll evidencing well the hanging pollen sacs (PAS 219 Paratype); 3. Deposit of three adult male cones (PAS 56); all Ariche, Valli del Pasubio; Coll. Michael Wachtler, Dolomythos-Museum



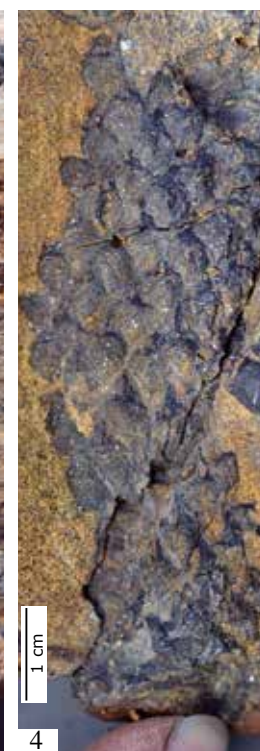
***Ortiseia zanettii*. Female cones (Late Permian. Wuchiapingian)**

1. Fully grown female cone (PAS 379, paratype); 2. Naturally broken female cone (PAS 69); 3. Mature female cone, ready to release the seeds (PAS 12); 4. Young female cone (PAS 659); 5. Juvenile seed scale evidencing the protective leaves (PAS 428); all Ariche, Valli del Pasubio; Coll. Michael Wachtler, Dolomythos-Museum



***Ortiseia zanettii*. Ovules and seeds (Late Permian. Wuchiapingian)**

1-3. Ovules outside (PAS 554, PAS 364, PAS 352); 4-6. Ovules overhead view and inner face (PAS 6, PAS 89, PAS 80); 7-8. Seeds obverse and reverse view (PAS 77, 408); all Ariche, Valli del Pasubio; Coll. Michael Wachtler, Dolomythos-Museum



***Ortiseia zanettii*. Ecology (Late Permian. Wuchiapingian)**

1. Slab with two female cones (a = lateral view, b. overview), c. twig, d. single seed (PAS 363); 2. Deposit of a male (a) and female (b) *Ortiseia*-cone, and several *Ortiseia* seed-scales (PAS 345); 3. Isolated twig (PAS 755); 4. Strange twig with hardened leaves (PAS 549); all Ariche, Valli del Pasubio; Coll. Michael Wachtler, Dolomythos-Museum

the most part intact in the fine mud and sediment that even the finest structures are still recognizable today.

Although in almost all palaeobotanical literature the visual aspect of Paleozoic-Mesozoic pollen cones is defined as uniform, it can be established that it is not so. The huge Permian *Ortiseia-Araucaria* cones stand in net contrast to the small *Majonica-Abies* pollen cones and, in almost the same manner, to the dwarfish male cones of *Férovalentinia-Pinus*. Also the isolated, rounded valves with a lobed rim, and a number of radial ridges originating from a short basal column described as *Brinkia cortianensis* or *Brinkia kerpiana* (Kustatscher et. al., 2019) are nothing other than seed scales belonging to *Ortiseia visscheri*, *Ortiseia jonkeri* or *Ortiseia leonardii* and therefore the name can only be regarded as synonymous. Such seed scales can be found in the hundreds together with *Ortiseia* female cones and *Ortiseia* twigs.

There are fewer differences between *Ortiseia zanettii* and the other *Ortiseia*-species in the look of their ovuliferous organs. Their coalesced seed-scale concept with various sterile tapered minute leaves, which serve to cover the seed scale, survived in slightly modified form till today's Araucarias.

Abietaceae-ancestors

In 1987, the Dutch researcher Johanna Clement-Westerhof recognized in Upper Permian sediments of the Bletterbach-gorge (South-Tyrol) the first winged seed conifers naming them *Majonica alpina*. Probably due to the scarce material from Bletterbach, the only locality where Clement-Westerhof's *Majonica*-material was recovered, she was not able to capture the true potential of her discovery. *Majonica* holds not only one winged lateral seed, as suggested in the publication (Clement-Westerhof, 1987) but symmetrical-ly equal on the lobed seed scale's two-winged seed protected on the outer side by a projecting bract. Thus, she was not able to recognise that she has found the ancestors of the Abietaceae because today's firs (*Abies*) exhibits approximately this feature.

Influenced by Rudolf Florin's mega-work about Permian conifers (Florin, 1938–1945), Clement-Westerhof proposed to include the genera *Majonica*, additionally to the new classified *Dolomitia* (the seed scale from a *Voltzia* conifer) and *Pseudovoltzia* in the new family—the Majonicaceae. This was a doubt-

ful and not understandable decision, because the alate *Majonica*-seeds and the wingless and small-sized ovate *Voltzia*-seeds equipped with a basal horny micropylar appendix are too different. Additionally, all Voltziales bear from three till more seeds on each scale, whereas the winged Majonicaceae as precursors of the Abietaceae only two.

After intense research and the recovering of hundreds and hundreds of specimen Michael Wachtler (2013, 2015) was able to explore the real nature of this alate seeds and scales, as well as their (mostly decayed female cones) and relatively small-sized (not so dwarfish as today) pollen cones. The specimen came from continuous successions—beginning from the Carboniferous-Permian border and than following till the Permo-Triassic border, to vanish there surprisingly—making possible to elaborate an interesting evolving-process. Now it can be established that the progenitors of the Abietoidea played on the Euramerican landmass—a dominant rule and later evolutionary stages occur only marginally in the following 200–300 million years.

Majonica alpina (CLEMENT WESTERHOF, 1987)

1987 *Majonica alpina*, CLEMENT WESTERHOF, pp. 375-402

2015 *Majonica alpina*, WACHTLER, pp. 123-131

Etymology

Named from Johanna Clement-Westerhof after her family.

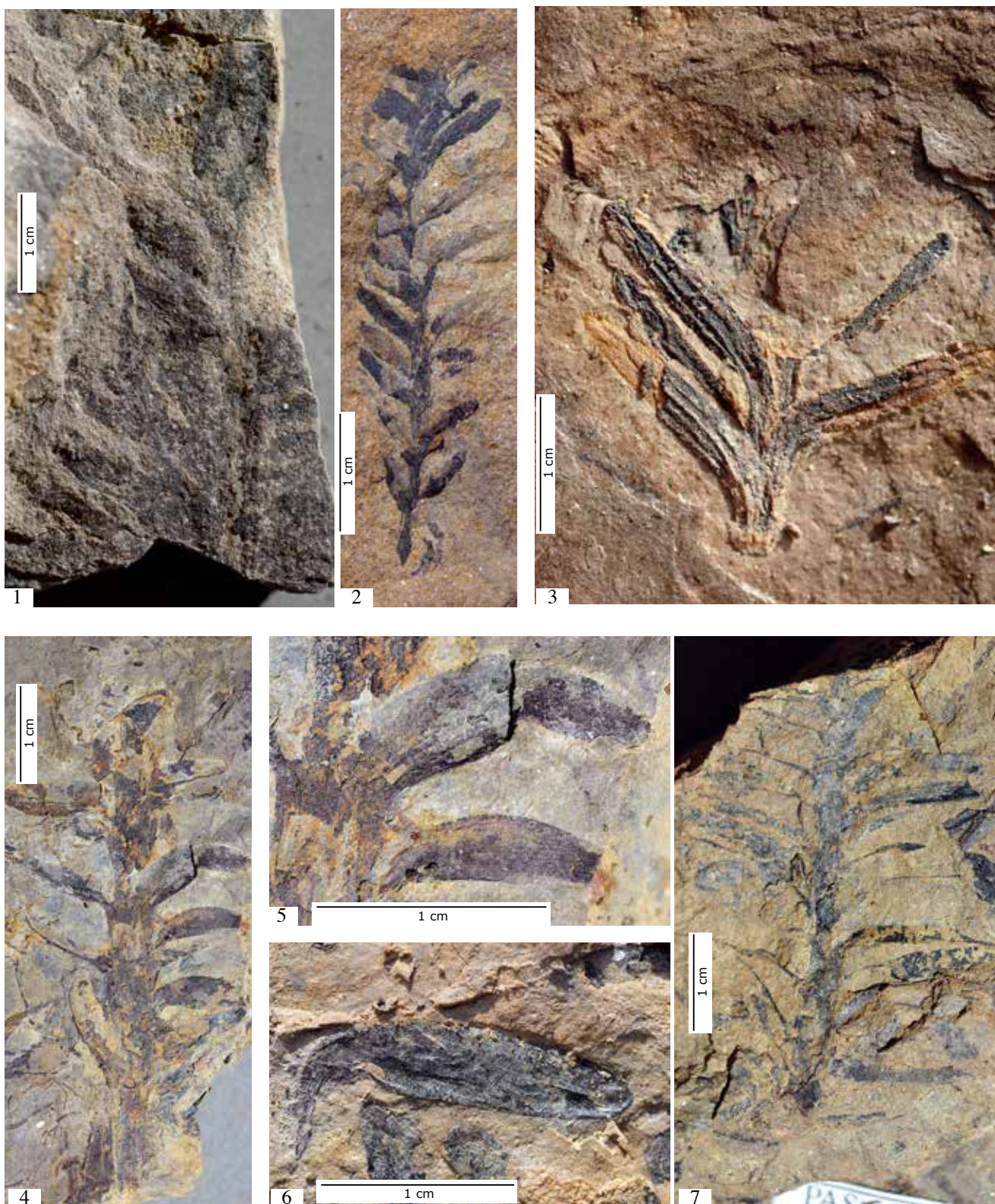
Holotype

Prep. 755, Laboratory of Palaeobotany and Palynology of the State University of Utrecht, The Netherlands, (Plate I, 1), Butterloch

Description

Branchlets and leaves: Shoots irregularly branched with sometimes heterophyllous leaves. These linear, up to 1.5 cm long and 0.3 cm wide, sometimes quadrangular with an obtuse apex, probably because growing in summerdry exposition. Other with a lanceolate shape, subtle resin canals indicated. Leaves do not overlap each other.

Male cones: Up to 3.5 cm long and 1.5 cm wide (but usually smaller), solitary spreading or aggregated together on a short shoot. Covered densely with minute peltate microsporophylls (PAS 157, PAS 522, PAS 59, PAS 204, PAS 628).



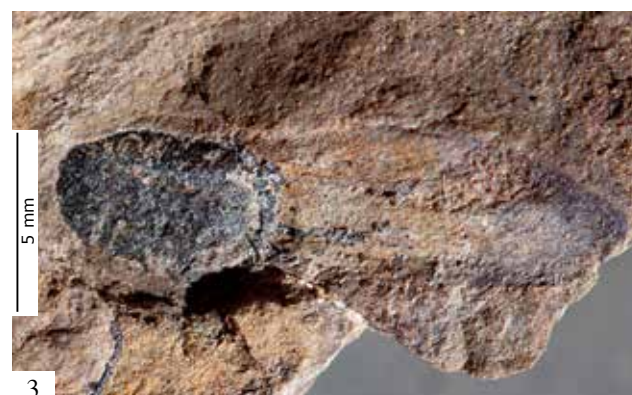
***Majonica alpina*. Female cones (Late Permian. Wuchiapingian)**

1. Branchlet (PAS 631); 2. Apical twig (PAS 800); 3. Detail of a leaf with the ascending needles and the striae (PAS 716) 4-5. Shot and detail of the needles (PAS 603); 6. Single ascending leaf PAS 520); 7. Part of a twig with longer needles PAS 561); all Ariche, Valli del Pasubio, Vicenza; Coll. Michael Wachtler, Dolomythos



***Majonica alpina*. Female cones (Late Permian. Wuchiapingian)**

1. Young female cone (PAS 346); 2-3. Female cone with long bracts (PAS 759); 4. Semi-adult female cone (PAS 317); 5-7. Female cones (PAS 784, PAS 743, PAS 791); 8. Decomposed female cone, upper side-view (PAS 13); 9. Decomposed female cone with detail of the bracts (PAS 380); 10. Female cone (PAS 711); all Ariche, Valli del Pasubio, Vicenza; Coll. Michael Wachtler, Dolomythos



***Majonica alpina* Winged seeds (Late Permian. Wuchiapingian)**

1-8. Various winged seeds evidencing their diversity (PAS 714, PAS 706, PAS 335, PAS 530, PAS 553, PAS 811, PAS 548, PAS 563); all Ariche, Valli del Pasubio, Vicenza; Coll. Michael Wachtler, Dolomythos-Museum.

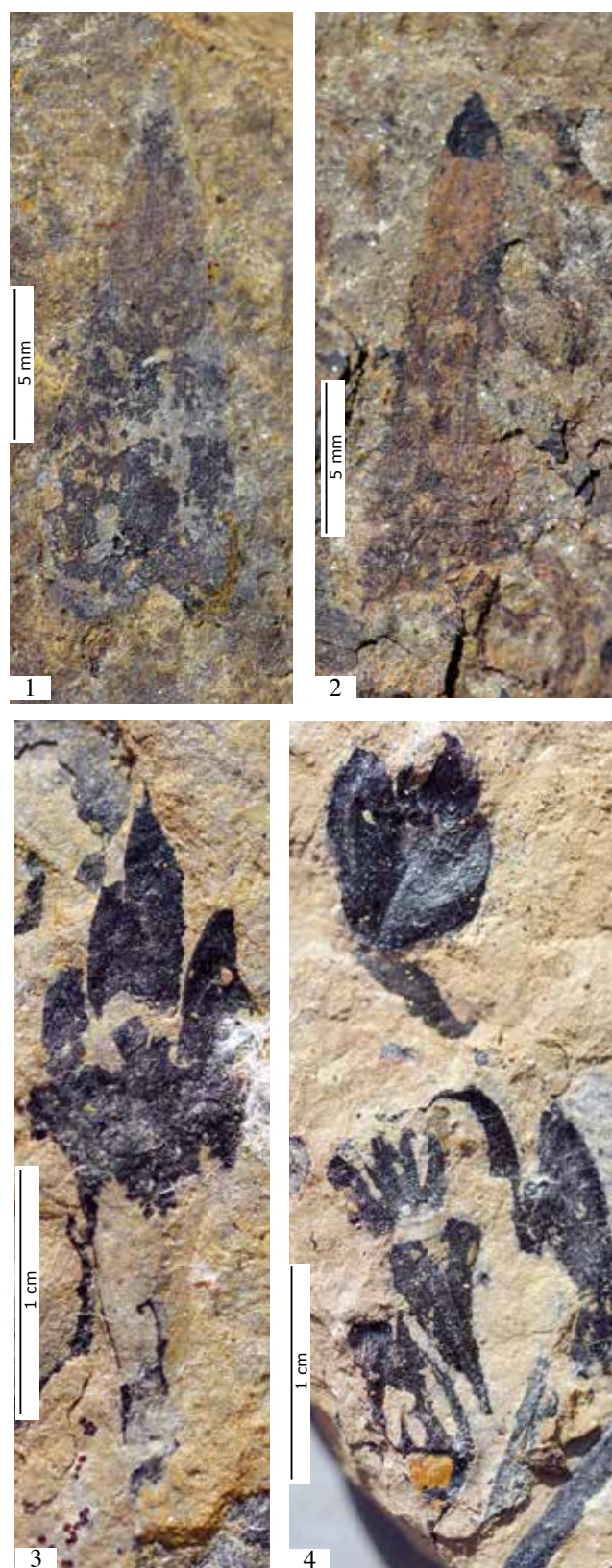
Female cones: Young female cones with sometimes also 3–4 cm long bracts covering mostly the seed scale. Mature cones about 8 cm long and slender, 2–3 cm wide. Cone disintegrating at maturity when drying, so only some isolated scales remain on the basal part, as encountered in today's Abietoidea. Bracts composed of one central cover-leaf and not connected with the primary bract, a several times segmented appendix, composed of about 4–5 small-sized sterile leaves. Physical seed scale mirror-like double lobed, about 1.5 cm long, 1.0 cm wide, reniform, with a small hump in the middle. Scales with one winged seed on each side covering two thirds of the scale from the basal part. Seeds till 0.5 cm long, cuneate and angular, wings till 0.7 cm long ending cuneate till slightly tapered.

Taxonomic notes

Based on excellent cuticular analyses Johanna Clement-Westerhof (1987) described first *Majonica alpina* from the Bletterbach-gorge near Aldein-Radein. By finding isolated seeds equipped with a wing, she determined that it was different from all other previously found conifers but she was unable to draw any more correct conclusions due to the incomplete material. When in 2015 Michael Wachtler began to investigate the remnants of *Majonica*, he based his researches on another hitherto unknown fossil site in the Vicentinian Dolomites: Contrada Ariche in the Valli del Pasubio.

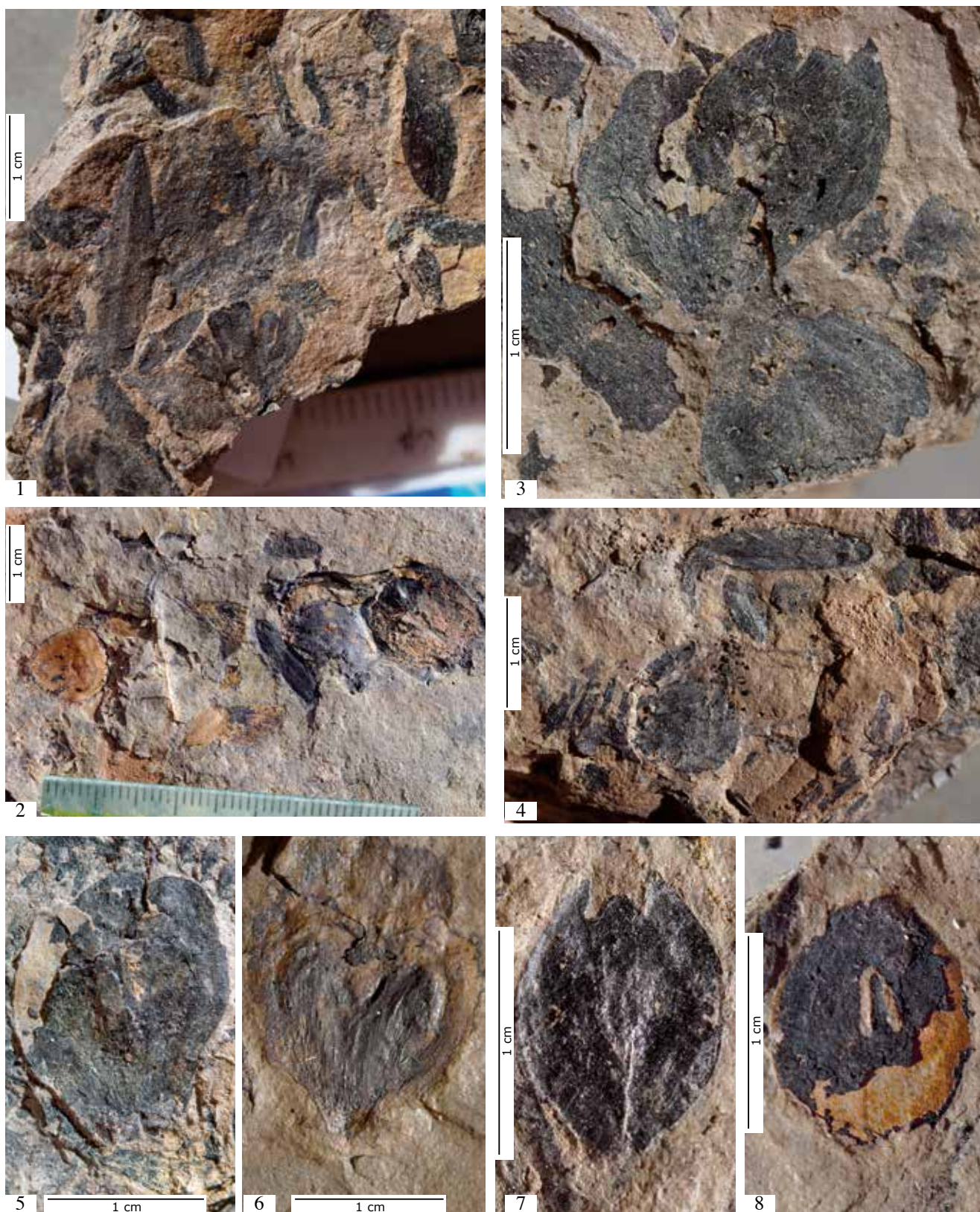
Majonica alpina constitutes at the Ariche-locality together with *Ortiseia zanettii* the most widespread conifer-genus. In some silty and fine-mud layers its excellent conservation status reveals the organisation of all delicate fertile parts well. That it is the same species as in Bletterbach is confirmed by the recovery not only of the alate seeds, but also what Clement-Westerhof designated as "ovuliferous dwarf-shoot", that effectively is a sterile part of the bract.

With *Majonica* ends an about 50 million years old glorious evolving concept of the *Abies*-progenitors, beginning in the Carboniferous (Kasimovian) with archaic *Gomphostrobus bifidus* and *Wachtlerina bracteata*, that was then prosecuted with Early Permian (Artinskian) *Majonica suessi* over Kungurian *Majonica ambrosii* till Upper Permian *Majonica alpina*. In the beginning



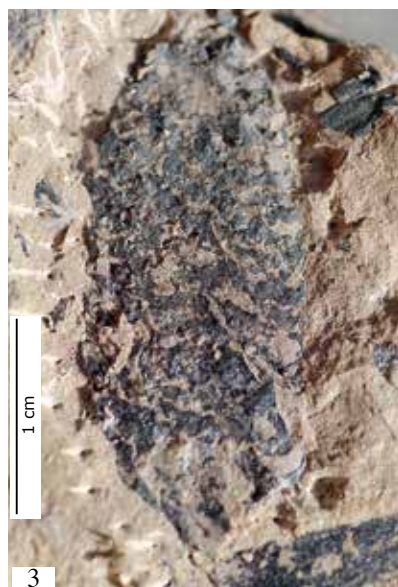
Majonica alpina. Bracts and seed scales (Late Permian. Wuchiapingian)

1-2. *Majonica alpina*. Isolated bract cusp (PAS 601, PAS 619); 3. Bract adaxial side (interior) (PAS 540); 4. Bracts and seed scale (PAS 506), all Ariche, Valli del Pasubio, Vicenza; Coll. Michael Wachtler, Dolomythos



***Majonica alpina*. Bracts and seed scales (Late Permian. Wuchiapingian)**

1. Bract cusp, bract appendix, seed scale and seed (PAS 262); 2. Several seed scales with one beautiful conserved winged seed and a bract (PAS 714); 3. Decomposed cone with seeds and seed scales (PAS 657); 4. Scale and leaf (PAS 520); 5-6: Seed scales seed-side (PAS 519, PAS 709); 7-8. Seed scales outer side with shadow of the bract (PAS 525, PAS 707); all Ariche, Valli del Pasubio, Vicenza; Coll. Michael Wachtler, Dolomythos



***Majonica alpina*. Pollen cones (Late Permian. Wuchiapingian)**

1. Twig with several male cones (PAS 157); 2. Pollen cone and seed scale (PAS 522); 3. Detail of the male cone (PAS 522); 4. Isolated pollen cone (PAS 59); 5. Detail of the microsporophylls with pollen dust (PAS 204); 6-7. Broken pollen cone and detail of the microsporophylls (PAS 628); all Ariche, Valli del Pasubio, Vicenza; Coll. Michael Wachtler, Dolomythos



***Majonica alpina*. Reconstructions (Late Permian. Wuchiapingian)**

a. Branchlet with female cone (PAS 759); b. Seed scale abaxial side (PAS 506, PAS 262); c. Covering micro-bracts (PAS 506, PAS 262); d. Seed scale adaxial side with two winged seeds (PAS 519, PAS 709); e. Winged seeds (PAS 714, PAS 706, PAS 335, PAS 530, PAS 553, PAS 811, PAS 548, PAS 563); f. Male cones (PAS 157); g. Leaves (PAS 716)

the Abietaceae-ancestors still developed symmetrical branches (*Wachtlerina*) that just in the Early Permian (*Majonica suessi*) changed to the same plagiotropic disposition as we encounter today. On the end of the Permian then, for inexplicable reasons, these fir ancestors disappeared mostly for many millions of years, only to reappear in almost the same form in the Eocene again.

Understanding the original structure of the seed scales is not easy due to its great complexity. Only by examining hundreds of isolated fertile parts was it possible to understand the exact construction plan. The seed scales of *Majonica* are composed of several parts: 1. A long sterile projecting bract, that could reach a length of 2 till 4 cm, especially in a juvenile stage; 2. Another sterile bract appendix composed of several closely aggregated micro-leaves; 3. A seed scale in the form of two linked lobes with a small additional lobe in the middle; 4. Two distinct alate seeds with basally on the wing attached ovules. Each covers a lobe.

Today the two lobed scales are totally fused, that the original dents are no longer visible. But these lobes give clear indications that probably in the Devonian there were two separate fruit-blades generating on each a seed. The seed scales were shed after maturity, but not in its present form, where it is mainly impossible to find entire cones. That sometimes complete female cones are found proves that in the Permian sometimes the cones decayed on the soil. Therefore, today's *Pseudotsuga*-conifers with its similar bracted female cones, which in contrast to the Abietaceae did not dissolve on the tree, developed at that time and from then on went its own way. Interestingly also the *Ortiseia*-conifers as *Araucaria*-ancestors shed in the Upper Permian mostly their upright growing cones entirely, whereas today they disintegrate on the tree. Therefore, it can be assumed that Abietaceae and *Araucarias* developed from a common ancestor between the Devonian and the Carboniferous.

Other alike looking conifers like the spruces (*Picea*) already from the Devonian-Carboniferous took their own line of development. Spruces or cedars had probably their origin on other continents, like the former Siberian-Angara landmass. Early Permian *Kungurodendron* from the Ural mountains as *Picea*-progenitor or *Stukenbergia* (Wachtler, 2020) as

archaic Cedar has better conditions to be considered as ancestor of these families. Strangely all these conifer-tribes made a rapid development just in the Early Permian and then remained nearly unchanged to the present. Another question that arises is which of today's fir species shows the most original traits. All Abietaceae with a spatulate bract and a long caudate cusp like *Abies alba*, *Abies bracteata*, *Abies procera* or *Abies delavayi* have resemblances with Permian *Majonica*, although the indentation of the two lobes today is in no species recognizable. Moreover, the two distinct bract-leaves, that were shed separately in *Majonica* are in no extant fir recorded, because they are inseparably merged and fused together. But the majority of the features of *Majonica* correspond to extant firs. *Majonica alpina* is not the only species recorded in the Upper Permian sediments of the Dolomites. *Majonica clementwesterhofae* is similar, but evidence another slightly different bract-concept. The reasons may be attributed to some age-different deposition.

***Majonica clementwesterhofae* n. sp. (WACHTLER, 2021)**

Holotype

CUEC 509, Dolomythos Museum, Innichen, Coll. Wachtler

Locus typicus

Cuecenes, Seceda, Gröden-Valley, Dolomites. Upper Permian (Wuchiapingian)

Additional material

Scales and seeds: CUEC 504, (CUEC 504, CUEC 531, CUEC 499, CUEC 501, CUEC 146, CUEC 421, CUEC 516, CUEC 441. Seeds: CUEC 511, CUEC 603, CUEC 519, CUEC 613, CUEC 616, CUEC 631, CUEC 542, CUEC 605; Leaves and twigs: CUEC 489, CUEC 601, CUEC 608, CUEC 503, CUEC 348, CUEC 405

Repository

All Wachtler Collection, Museum Dolomythos, Innichen

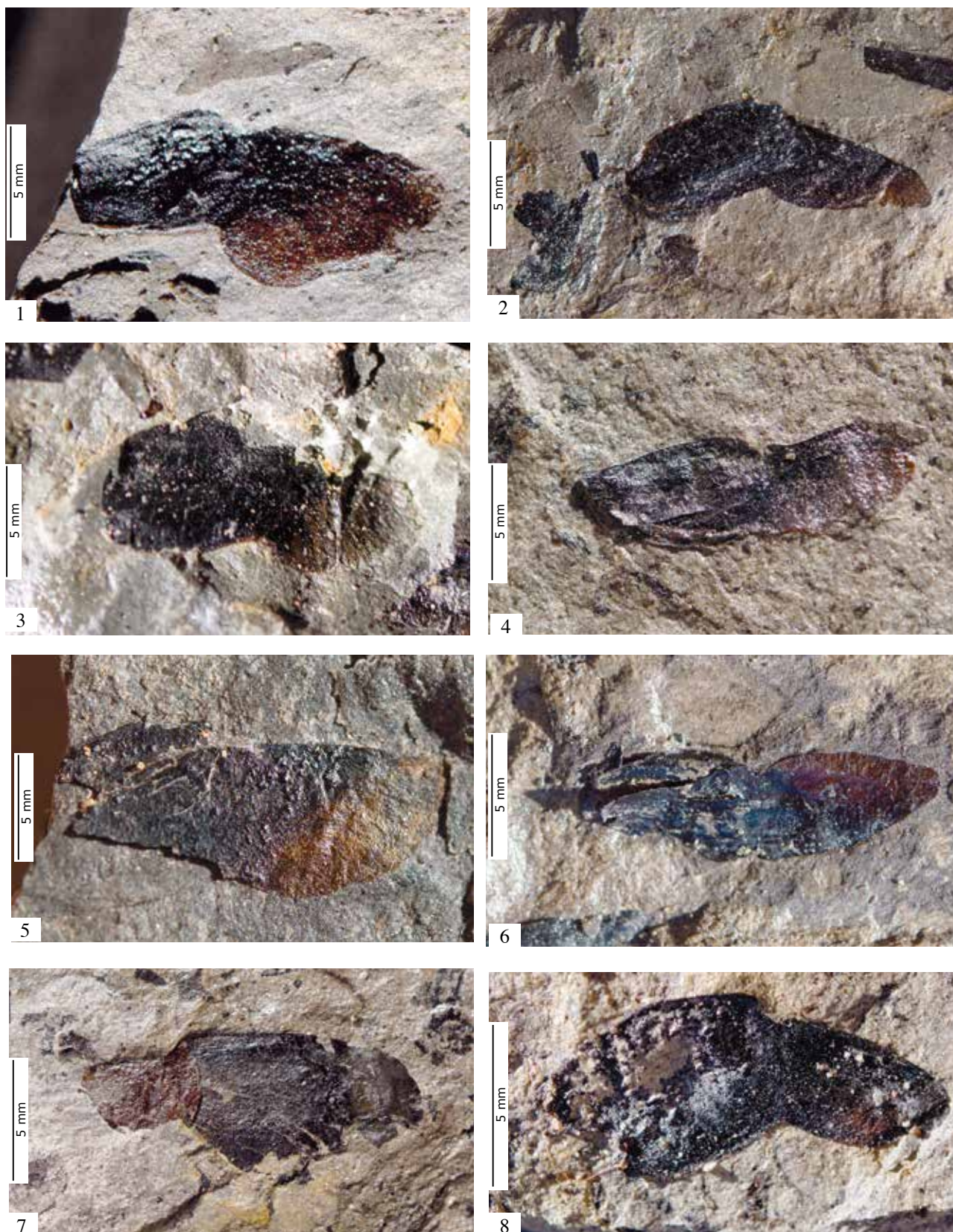
Etymology

In honour of the Dutch palaeobotanist Johanna A. Clement-Westerhof which described the Permian floras of the Dolomites and recognized the first winged-seed conifer.



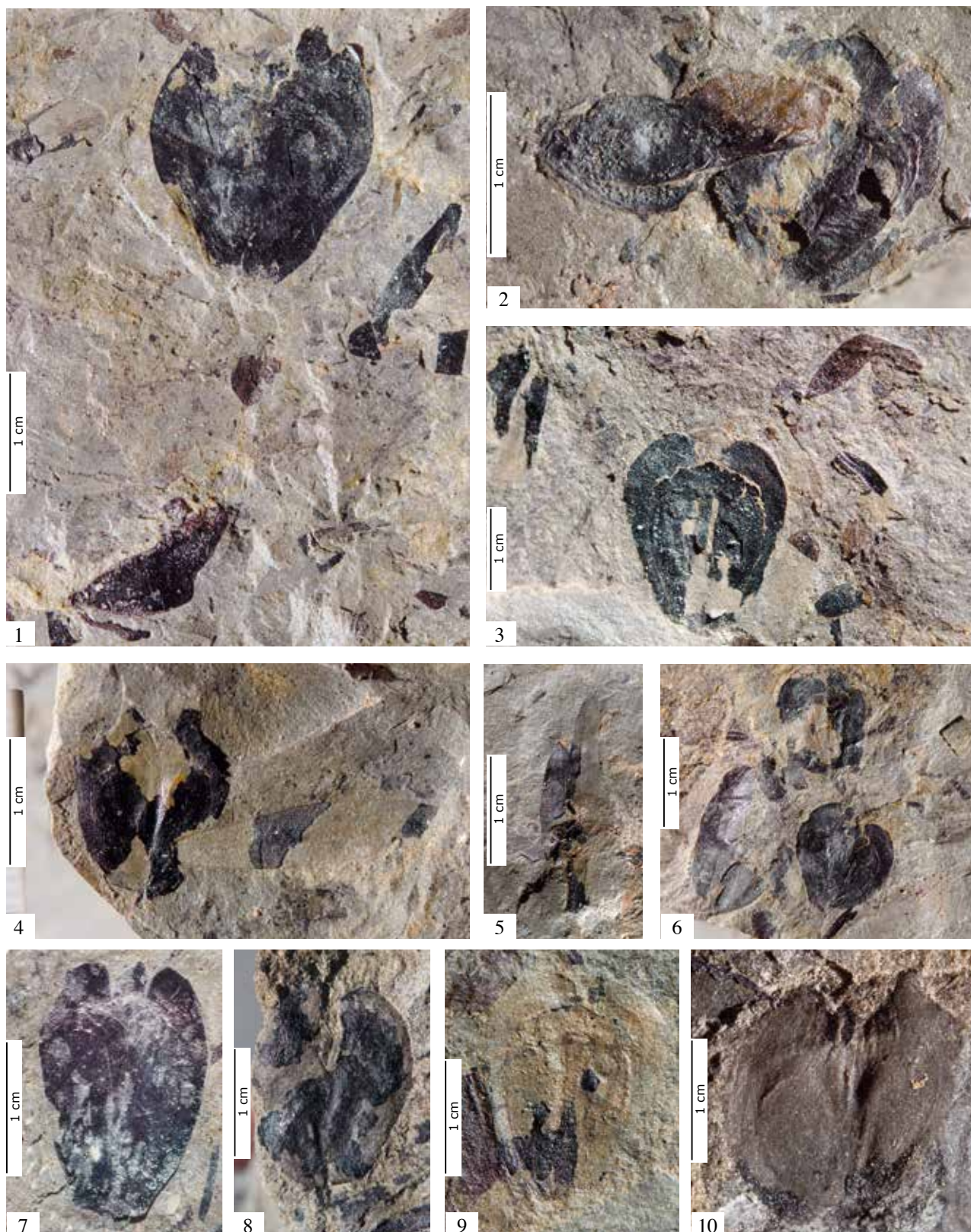
***Majonica clementwesterhofae*. Twigs and male cones (Late Permian. Wuchiapingian)**

1. Branchlet (CUEC 601); 2-3. Twig with ascending leaves and detail (CUEC 489); 4. Juvenile twig (CUEC 500); 5. Twig with ascending leaves and prominent striae on the leaves (CUEC 608); 6. Apical part of a twig (CUEC 503); 7-8. Male cones (CUEC 348, CUEC 405); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum



***Majonica clementwesterhofae*. Winged seeds (Late Permian. Wuchiapingian)**

1-8. Various winged seeds evidencing their diversity (CUEC 511, CUEC 603, CUEC 519, CUEC 613, CUEC 616, CUEC 631, CUEC 542, CUEC 605); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum



***Majonica clementwesterhofae*. Seed scales (Late Permian. Wuchiapingian)**

1. Scale and seed, front-seed-side (CUEC 509, designed holotype); 2. Scale and seed, adaxial seed-side (CUEC 504); 3. Scale and leaf (CUEC 504); 4. Scale and bract (CUEC 531); 5. Isolated bract (CUEC 499); 6. Several bracts, reverse and front side (CUEC 501); 7-8. Scales reverse side, partially with impressions of the cover-leaves (CUEC 146, CUEC 421); 9-10. Scales front side with shadows of the winged seeds (CUEC 516, CUEC 441); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum

Diagnosis

Conifer with slender plagiotropic branches, leaves descending, spirally arranged, slightly curved, seed scales with two winged seeds and equipped with an abaxial protruding bract, pollen cones globose.

Description

Branches and leaves: Twigs irregularly branched with lateral spreading slanting secondary shoots. The leaves were arranged all around the twigs, but mostly to the sides. They are sessile, linear till little curved and flat, rounded at the apex, with one or two resin ducts (CUEC 241, CUEC 489, CUEC 500, CUEC 608).

Male cones: Globular till conic, from 2.0 till 3.0 cm long and 1.5-2.0 cm wide. Microsporophylls shortly bracted (CUEC 348, CUEC 405).

Female cones: Decaying after maturity. Cone scales a little broader than wide, with two curved blunt horns at the apex. Till 2 cm long, highest width 1.8 cm (CUEC 500, holotype). Abaxial side characterized by a till 2 cm long bract, scale partially covered with micro-leaves (CUEC 146, CUEC 421). Protruding bract not directly connected with the scale; therefore shed independently. Winged seeds in pairs on each scale. Size of the seeds till 7 mm, wings till 8 mm long, from poorly (CUEC 511), till well developed (CUEC 519).

Taxonomic notes

Comparing the two Lopingian Abietaceae-ancestors *Majonica clementwesterhofae* and *Majonica alpina* there are not many but nevertheless some differences that justify the splitting in two separate species. In *Majonica clementwesterhofae* the wings of the seeds are only partially evolved, in *Majonica alpina* they have mainly the disposition of today's Abies-conifers. Also the dwarfish sterile leaves that cover the outside are inseparably connected with the seed scale in *Majonica clementwesterhofae*, but form an independent appendix in *Majonica alpina*. Main bract, seed scale and winged seeds can therefore be found separately in the sediments (Wachtler, 2015). It seems that *Majonica clementwesterhofae* represents the more archaic form.

Also the with *Majonica* furthermore widespread *Ortiseia*-species in the Gröden-

Formation like *Ortiseia leonardii* (Seceda, Gröden-Valley; Florin, 1964), *Ortiseia jonkeri* (Cortiana, Valli del Pasubio; Clement-Westerhof, 1984; Wachtler, 2015), *Ortiseia vissheri* (Clement-Westerhof, 1984; Bletterbach, Aldein) and *Ortiseia zanettii* (Ariche, Valli del Pasubio; Wachtler, 2015) can be distinguished by little, but recognizable differences probably based on some age different deposition.

Another question is, how the originally described *Majonica alpina* (Clement-Westerhof, 1987) from the Bletterbach (Aldein-Radein) can be inserted? Unfortunately, as holotype was classified part of a shoot (Prep. 755, Laboratory of Palaeobotany and Palynology of the State University of Utrecht) that in all cases is more doubtful than a seed scale. Especially the real fertile parts (Prep. 738, 742, 743) are not seed scales but only sterile bract-appendixes. But unmistakable Prep. 746, p. 389 represents a winged seed. Based on all of these facts can be stated that they resemble mostly those from Ariche (Valli del Pasubio) (Wachtler, 2015) and not *Majonica clementwesterhofae*. It is common in certain layers of the Seceda, but stands in the background of the widespread *Ortiseia leonardii*. Otherwise, it is also more difficult to recognize, because the twigs were not shed entirely as in *Ortiseia*, but remain for a long time on the tree, as in today's Abietaceae. Therefore, only small end-parts of the shoots can be found. This is also valid for the female cones, decaying mostly on the tree and are only torn down in their entirety after violent storms. Only in the finest mud well preserved seeds or scales give enough information about this species.

Taxodium-ancestors

In Upper Permian (Wuchiapingian) sediments of the Southern Alps conifer-like twigs and cones were recovered that have affinities with today's *Taxodium* conifers (Bald cypresses). The history about the discovery and research is complex. In 1854, the German geologist Carl Friedrich Freiherr von Schauroth figured a conifer from Recoaro with the name *Palissya massalongi*. Baron Achille de Zigno published again (1862) the same drawing and changed the name to *Taxites massalongi*. Additionally, he described another species with *Taxites vicetinus*. Although in the early days of



***Majonica clementwesterhofae*. Reconstructions (Late Permian. Wuchiapingian)**

a. Branchlet (CUEC 601, CUEC 489); b. Pollen cone (CUEC 348, CUEC 405); c. Twig with decaying female cone; d. Seed scale adaxial side with two winged seeds (CUEC 509, designed holotype, CUEC 504); e. Winged seeds (CUEC 511, CUEC 603, CUEC 519); f. Seed scale abaxial view (CUEC 146, CUEC 421); Main bract (CUEC 499); h. Secondary bract (CUEC 146)

research at Recoaro Triassic strata were often mixed with Permian strata, they are described as coming from the lower layers of the sandstone, meaning the Upper Permian Grödner Sandstone (*Si trova negli strati più bassi dell'arenaria inferiore nella valle del Prak presso Recoaro*).

De Zigno figured the specimen of table IX, fig. 3, 4, 5, 6 correspond effectively some *Taxodium*-ancestors, whereas, the other can belong to same *Ortiseia* or *Majonica* branchlet. De Zigno adopted the confusing name "*vicetinus*", that later was sometimes changed to "*Taxites vicentinus*" and belonging to Triassic sediments (Kustatscher et al., 2019). But up to this point we have not been able to solve anything about the classification of this conifer, because the conifer *Taxites (langsdo.rfii)* was introduced by Brongniart, 1828) for conifers from the Tertiary and did not correspond to the blue print of the Permian one. In 2017, Michael Wachtler instituted therefore the new genus-name *Ulbeus*, remembering the main place of discovery near Recoaro, for conifer-twigs characterized by short shoots with needles spreading distichously and alternately to either side in one plane. The seed cones are spherical and woody holding a few scales. Nevertheless, it is necessary to add further modifications due to new findings.

***Ulbeus vicetinus* nov. comb. (WACHTLER 2017, DE ZIGNO 1862)**

Etymology

From the hamlet Ulbe, forming part of the small town Recoaro in the Italian Southern Dolomites-Mountains where most of the new conifer-genus were recovered. The species name refers to the Italian Province Vicenza.

Holotype

ULBE 122; **Paratype** ULBE 146, female cone (Coll. Wachtler, Dolomythos Museum, Innichen, Südtirol)

Description

Branchlets and leaves: Characterised by short and long shoots spreading distichously. Short shoots, about 5 cm to 7 cm long and planate. The leaves are arranged in two ranks, with decurrent needles disposed alternately, linear, nearly straight, decreasing toward the

apex, about 1 till 1.5 cm long, 0.1–0.2 cm wide. They are longest below or near the middle, of the short shoot, margins parallel, entire, apex acute and pungent, sometimes a midrib is visible (ULBE 122, designed holotype, ULBE 123, ULBE 148, ULBE 145).

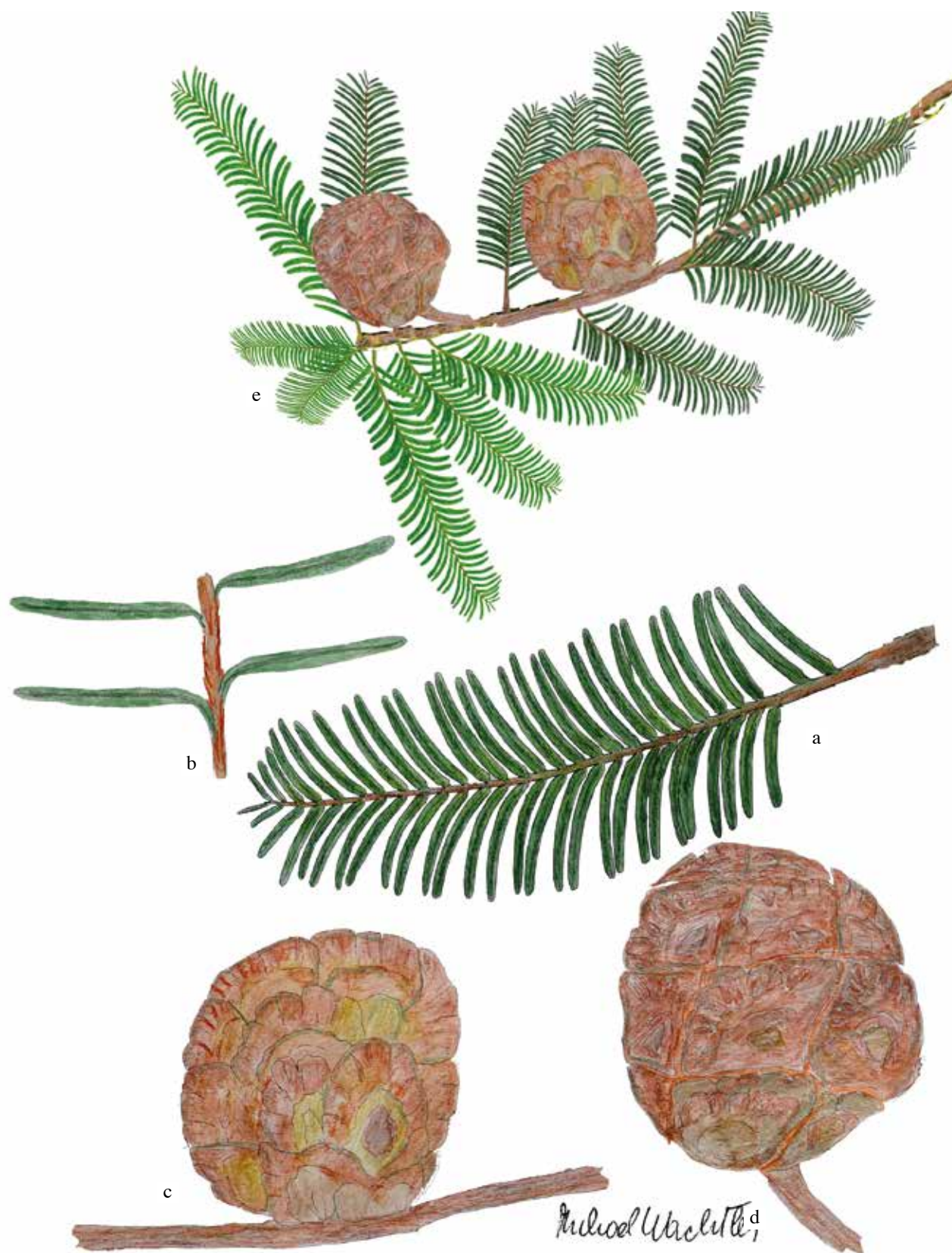
Pollen cones: Not known.

Seed cones: Rounded to ovoid, about 1.5 cm, terminal near the end, or sessile on the shoots. They are composed of several mainly four-sided bract-scales. Cone bract-scales thick and woody, nearly of unequal size, looking four-sided, bracts included on the scale (ULBE 146, paratype, ULBE 151, ULBE 150, ULBE 144).

Remarks

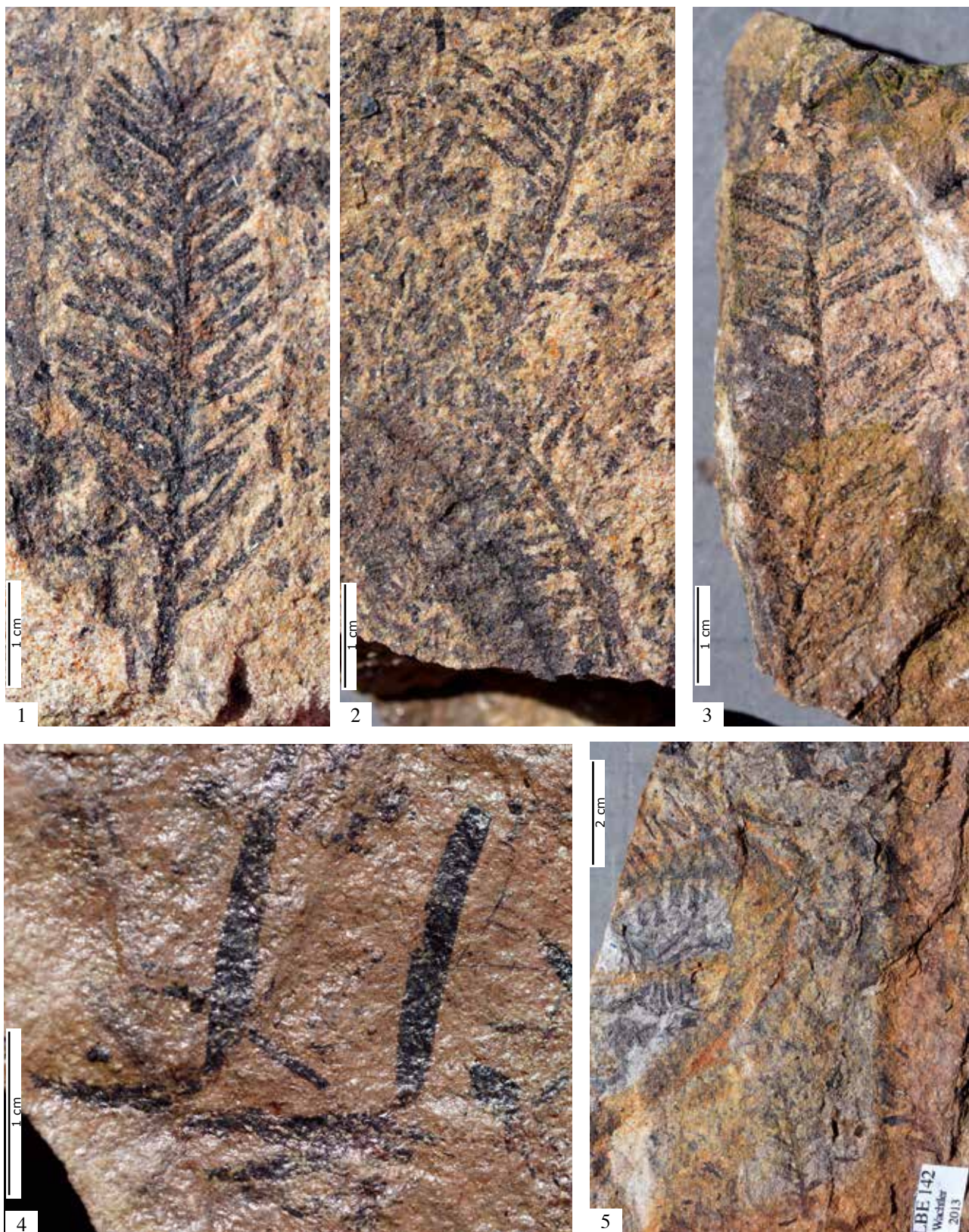
Ulbeus vicetinus leaves and cones can be compared with several existing conifers today like *Metasequoia*, *Sequoia* or *Taxodium*. Since the foliage is disposed distichous in opposite pairs along the branches in *Metasequoia*, but grow distichously and alternately in *Sequoia* and *Taxodium*, the first one can be discharged as *Ulbeus*-progenitor, having alternately arranged leaves. Whereas the long and short shoots in *Sequoia* and *Taxodium* are mainly equal, also here the leaves give some indication about the differences. They are not narrowed at the base and sessile with an obtuse apex in *Sequoia*, and narrowed at the base, short decurrent and petiolate, with an acute apex in *Taxodium*. *Sequoia* has more elongated cones with more seed scales, whereas *Taxodium* is characterized by its spherical female fructifications holding only a few scales. Therefore, with some doubt *Ulbeus vicetinus* can be inserted as potential *Taxodium*-ancestor and only in a second choice as *Sequoia*.

Today the conifer *Taxodium* grows in river flood plains and swamps. The two main species *Taxodium distichum* (*Taxodium ascendens* is a variety) and *Taxodium mucronatum* are distributed in the Southeastern United States and Mexico (Farjon, 2005), whereas *Sequoia* is restricted to the Pacific coast in California and Oregon. From the Late Cretaceous fossils belonging probably to *Taxodium (Margeriella cretacea)* are recorded from California (Taylor et al., 2009). The first description about leaves of this type is seen in Brongniart, 1828, as *Taxites*



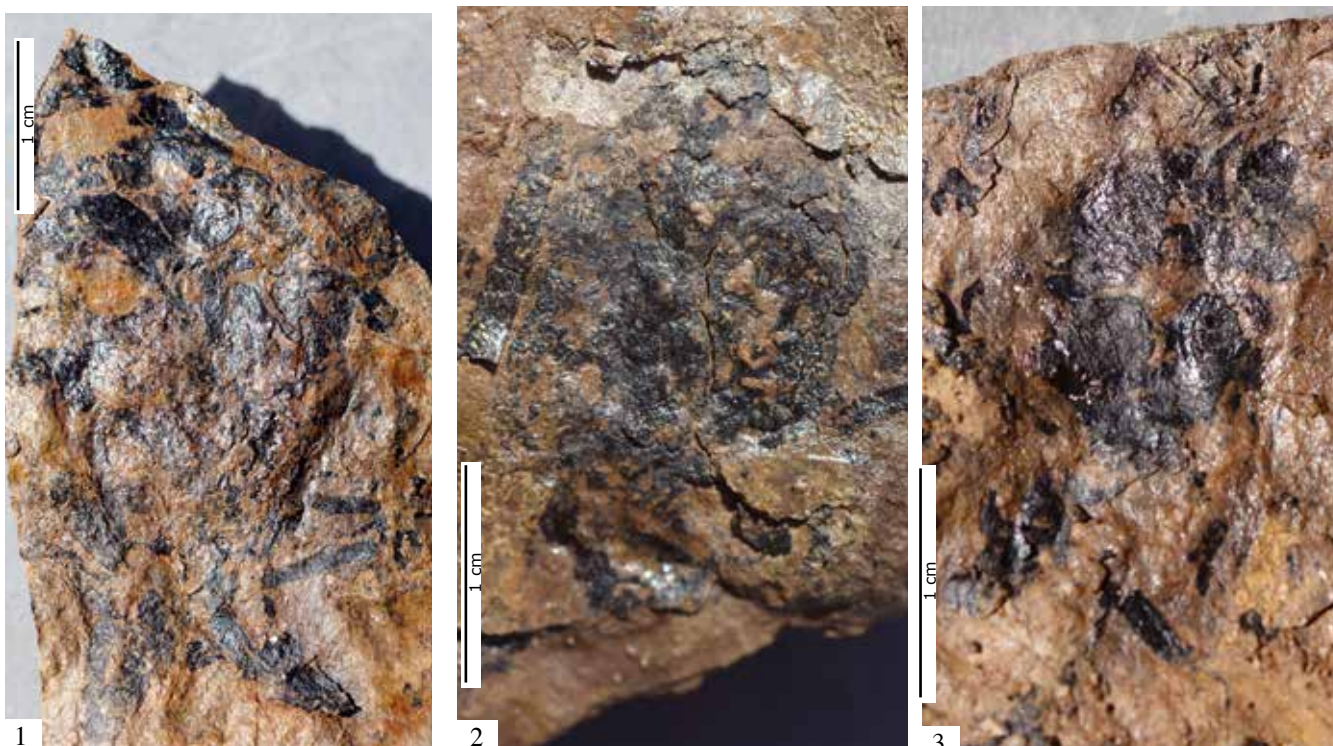
***Ulbeus vicetinus*. *Taxodium*-ancestor. Reconstructions (Late Permian. Wuchiapingian)**

a. Isolated twig (ULBE 122 designed holotype); b. Single needles (ULBE 145, PAS 716); c. Juvenile female cone (ULBE 150); 4. Adult female cone (ULBE 146); e. Entire branchlet with cones



***Ulbeus vicetinus*. Twigs and needles (Late Permian, Wuchiapingian)**

1. Short shoot (ULBE 122, designed holotype); 2. Short and long shoot (ULBE 123); 3. Branchlet (ULBE 148); 4. Detail of the decurrent needles (ULBE 145); 5. Isolated branchlets (PAS 142, (All Ulbe, Recoaro), Coll. Wachtler, Dolomythos Museum



***Ulbeus vicetinus* - Cones (Late Permian, Wuchiapingian)**

1. Female cone (ULBE 146, paratype); 2. Female cone sitting on a branchlet (ULBE 150); 3. Female cone (ULBE 144); All Ulbe, Recoaro, , Coll. Wachtler, Dolomythos Museum

langsдорffii from the Tertiary of Europe, now classified as *Sequoia langsдорffii*. After that Oswald Heer applied the name *Taxodium dubium* for fossils previously inserted as *Taxodites dubius* from Tertiary fossil sites in Switzerland and other parts of Europe (Heer, 1868). But also, some of these figured specimens represent more *Sequoia* leafy shoots than *Taxodium* progenitors (Chaney, 1950).

Otherwise, Upper Cretaceous conifers from the Yukon Valley in Alaska classified as *Sequoia rigida* with needles distichously arranged resemble more *Taxodium* than *Sequoia*. It can be regarded as first reliable evidence of *Taxodium* conifers in the Cretaceous (Chaney, 1950).

With these emerge another legitimate question: why do we have, in the Late Permian, relatively complete and equal looking *Taxodium*- (or *Sequoia*) conifers, with shoots, needles and cones formed in mainly the same manner as today? And why do we have a gap in the Triassic? One consideration can be that especially in Middle Europe the climate became more wet in the Late Permian, but not so

tropical as compared in the Triassic. Also, other conifers like coeval *Abies*-progenitor *Majonica*, or *Pinus*-ancestor *Fèrovalentinia* were widespread in Permian sediments near the Tethys-ocean, but are not further recorded in the Triassic, then dominated by a multitude of ferns or strangely also lycopods. It is certain that in some areas of the world all these conifers, survived to spread than in the Cretaceous.

Taxaceae-ancestors

Some conifers from the Upper Permian Dolomites are characterised by their berry-like seed cones distally clustered in groups. They have same vague resemblances with *Ullmannia*, mainly known from the European Later Permian Zechstein. All the appearance of these conifers reminds some Taxaceae-ancestors like *Cephalotaxus* or *Torreya*.

***Ullmannia edwardsae* n. sp. (WACHTLER, 2021)**

Holotype

CUEC 230 (twig and attached ovule), Dolomythos Museum, Innichen, Coll. Wachtler

Locus typicus

Cuecenes, Seceda, Gröden-Valley, Dolomites;
Upper Permian (Wuchiapingian)

Additional material

Branchlets: CUEC 223 CUEC 227, CUEC 229,
CUEC 243, CUEC 251, CUEC 258, CUEC 297
CUEC 306

Etymology

Honouring the English novelist, journalist, traveller and Egyptologist Amelia Ann Blanford Edwards (also known as Amelia B. Edwards, 1831-1892). In her book "A Midsummer Ramble in the Dolomites(1873), later entitled "Untrodden Peaks and Infrequent Valleys" she described the journey with her travelling companion Miss Lucy Renshaw (1833-1919) through the then little-known Dolomites. It was her aim in this book to present the history, botany and geology of the Dolomites as well as the art, culture, customs and traditions of the inhabitants.

Diagnosis

Conifer with plagiotropic branches, leaves shortly stalked and ascending spreading on pectinately short shoots. Female cones berry like elongated, coated by a fleshy aril. Pollen cones small sized and shortly bracted.

Description

Branches and leaves: Twigs spreading plagiotropic (CUEC 258, CUEC 243, CUEC 251). Leaves shortly stalked (CUEC 251), ascending, spirally inserted, spreading comb-like pectinately on lateral shoots. They are linear and rounded at the apex, with two hidden stomatal veins.

Male cones: Sitting apically on short shoots, till 2 cm long, 1 cm wide (CUEC 226, CUEC 300). Microsporophylls equipped with short bracts.

Female cones: Seed cones berry-like, clustered groups between the foliage (CUEC 230, designed holotype). Ovules obovoid till ellipsoid, probably surrounded by a fleshy aril. They are connected with the short shoots by short sterile leaves or bracts (CUEC 295). The length varies from 0.5 till 1.0 cm, the width is 0.5 till 0.7 cm.

Discussion

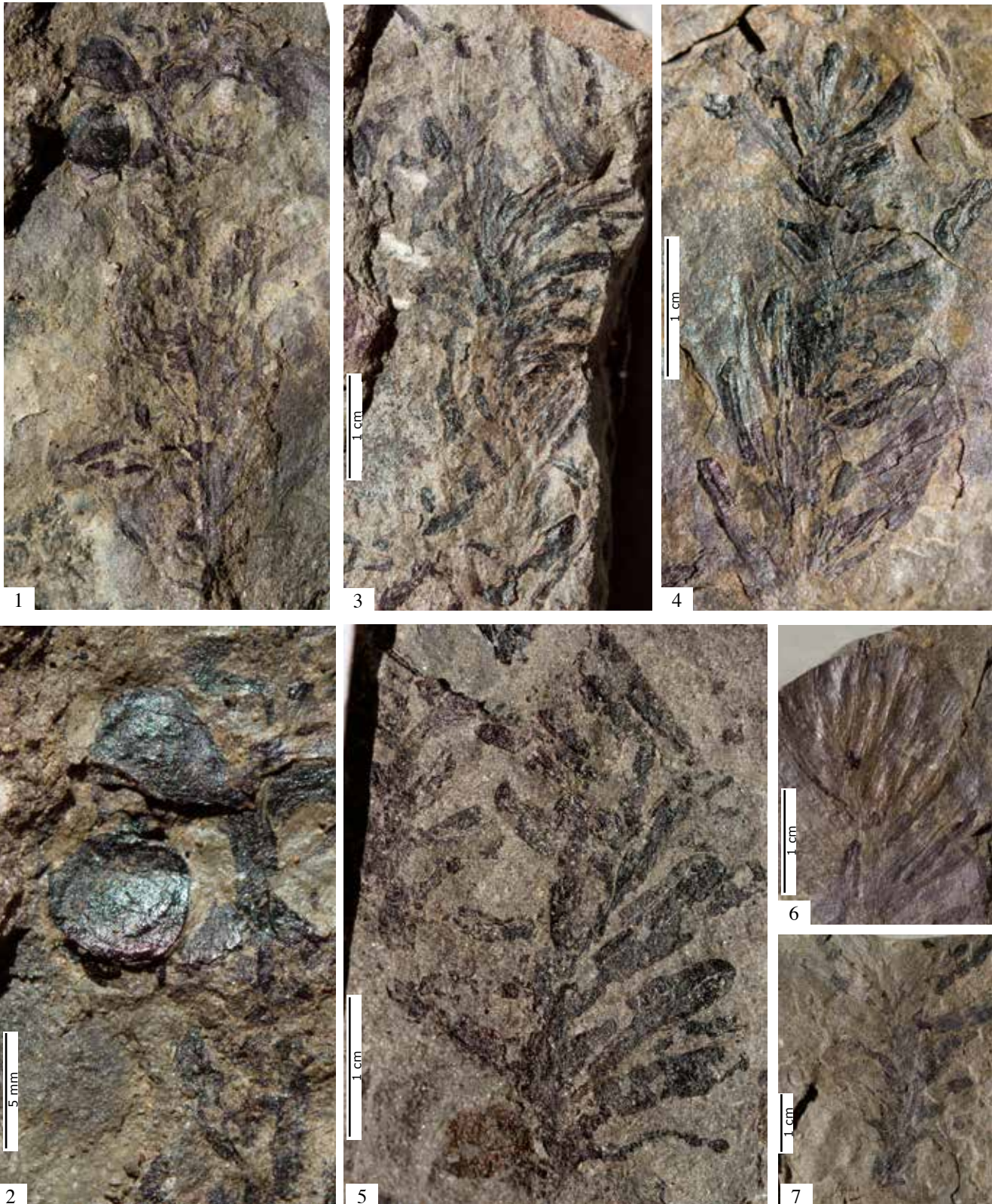
Just in 1850 the German palaeobotanist Heinrich Göppert (1800-1884), based on the abundance of plant-fossils found in the

German-English Copper Shale (Zechstein), described the conifer *Ullmannia*. Göppert honoured the mineralogist and curator of the "Hessische Mineralien-Cabinett" at Marburg Johann Christoph Ullmann (1771-1821). He classified three species: *Ullmannia bronnii* (pag. 185-189, plate 20 fig. 1-26), *Ullmannia frumentaria* (pag. 189-190, pl 21, fig. 1-3), and *Ullmannia lycopioides* (pag. 100-191, pl. 21, fig. 4-6). Göppert was not able to insert them with certainty in one of the existing conifer-families doubting between Araucarias and Cupressinaceae. Later also female organs were found in connection with the branchlets. Together with the conifer *Pseudovoltzia*, the berry-seeded *Ullmannia* can be regarded as abundant character-conifer from the Upper Permian Zechstein. Amazingly conifers with berry-like seed cones, like today's Taxaceae must have evolved at the same time as the conifers began to form. There is no other way to explain the cones coated by a fleshy aril of the Ullmanniaceae in the Permian.

They were composed of bunches of berry-like fruits. If they are not fully mature, it is possible to clearly see the structure of the cone, which is surrounded by sterile bracts. When they grow, they merge to form a fleshy fruit body, probably similar to the fruit of modern *Torreya* or *Taxus*. A short bract was generally present. The berries themselves dropped when they reached maturity. The male cones were relatively small (only up to two centimetres long) with pollen sacs on the bottom side. The vegetative twigs of the Ullmanniaceae spread wide apart and forked several times. They were equipped with slender, lanceolate needles.

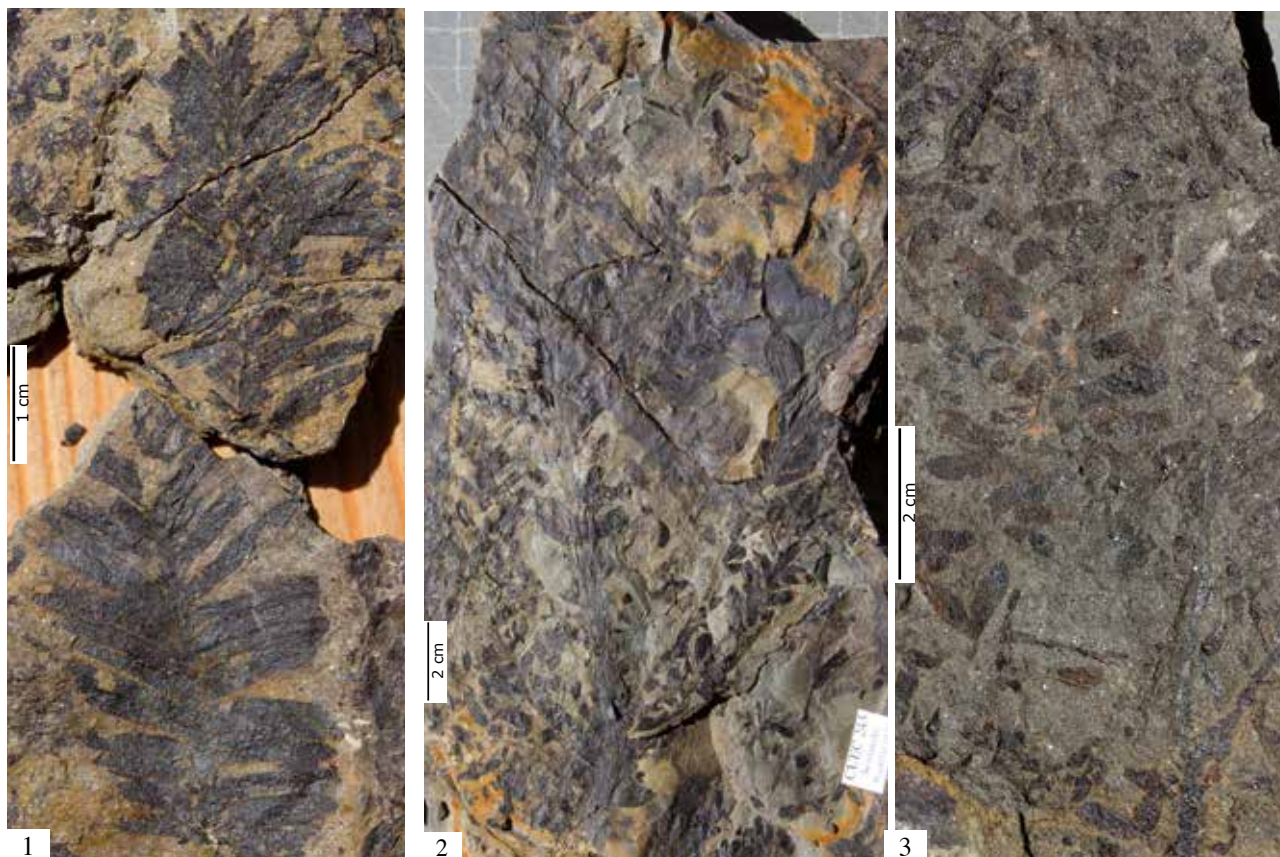
Till now there was a strange gap in the fossil record between the Upper Permian of the Alps and the Central European Copper shale (Zechstein). Plants, especially conifers being abundant in the Zechstein like *Pseudovoltzia* and *Ullmannia* were mainly absent in the Alpine Late Permian, whereas frequently found conifers remains there like *Majonica* or *Ortiseia* were seldom in the Zechstein. One explanation is due to the scarcity of research activities in the Dolomites, whereas especially in Germany a intense mining activity unearthed a lot of good material, not only plant fossils, but also fishes and vertebrates.

Nevertheless, it can now be assumed that the wing-seeded *Majonica* (Abietaceae-ancestor) and *Ortiseia* (Araucaria-progenitor) were widespread in the Late Permian of the Alps, and



***Ullmannia edwardsae* n. sp. Twigs and seeds (Late Permian, Wuchiapingian)**

1-2. Branchlet and attached seed-berries (CUEC 230, designed holotype); 3-4. Twigs (CUEC 223 CUEC 227); 5. Ramifying branchlet (CUEC 251); 6. Apical part of a twig (CUEC 229); 7. Branchlet (CUEC 227); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum



***Ullmannia edwardsae* n. sp. Twigs (Late Permian, Wuchiapingian)**

1. Detail of the needles (CUEC 306); 2. Ramifying branchlet (CUEC 258); 3. Carpet of leaves (CUEC 297); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum.

rarely found in the Zechstein, with a few remains described as *Culmitzschia florinii* (Ullrich, 1964), probably better classified as *Ortiseia florinii*, whereas *Pseudovoltzia liebeana* of the Zechstein found a rare counterpart in the Alps as *Voltzia sjerpii* (Clement-Westerhof, 1987).

Till now *Ullmannia* was completely missing in the Alps. But based on findings on the Seceda-mountain a presence of berry-seeded conifer-cones can be assumed. *Ullmannia edwardsae* is not widespread in the Upper Permian of the Alps and due to this fact also difficult to recognize. Only in one isolated layer on the right side of the Seceda it is common enough to find out that their blueprint varies from other gymnosperms. Within the Alpine plant assemblage it is also difficult to separate from *Ulbeus vice-tinus*, having a similar foliage, but being planate with leaves arranged in two ranks and not spirally inserted as in *Ullmannia*. Otherwise, the seeds of *Ginkgoites murchisonae* can be confused with *Ullmannia* seed cones. But due to the fact that *Ginkgoites murchisonae* foliage was never found in this sediments it can be assumed that it was not present.

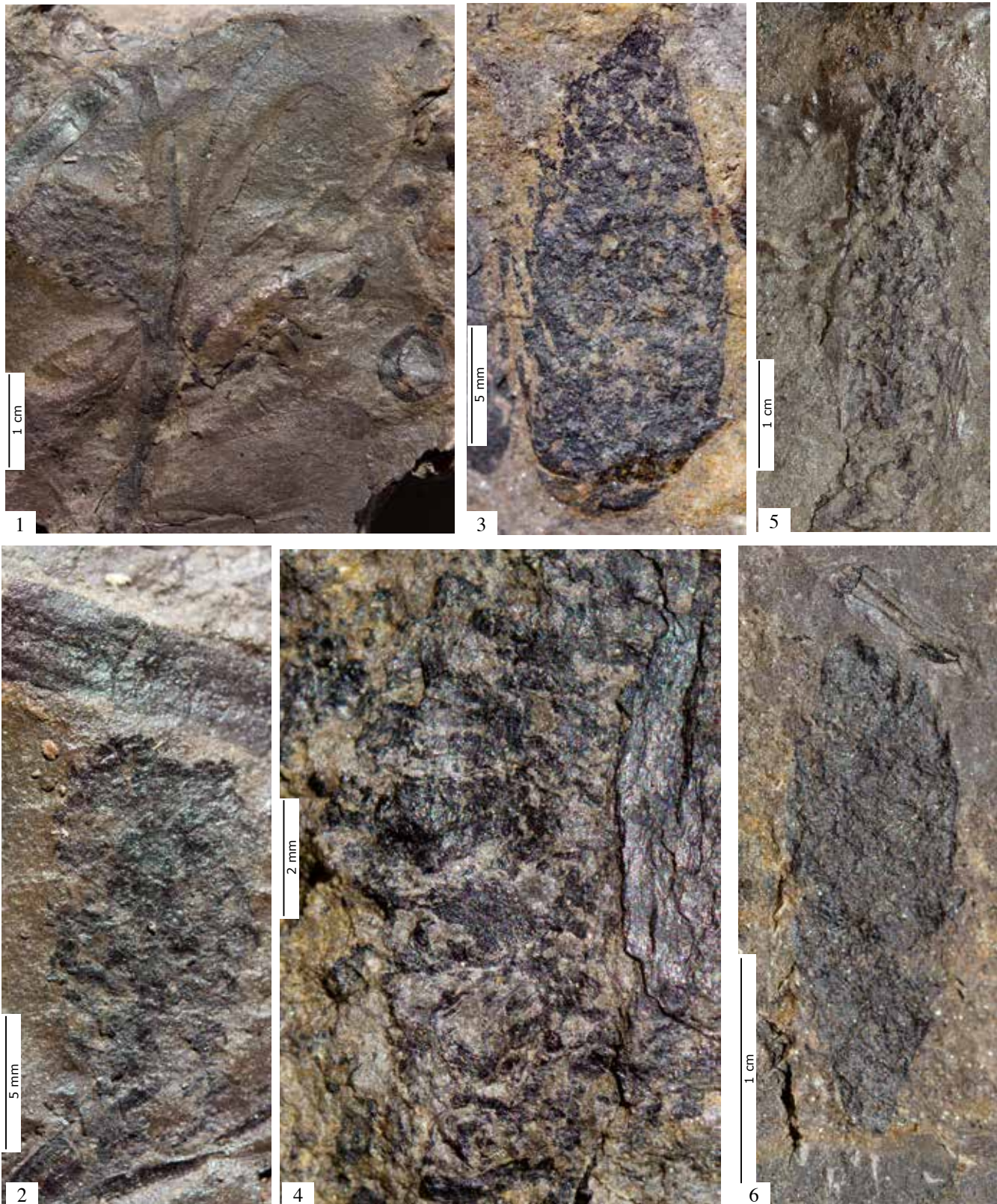
More seeded Upper Permian conifer-scales

In the Upper Permian Wuchiapingian we encounter in Europe at least two different *Voltzia*-types. *Pseudovoltzia liebeana* can be regarded as character-conifer of the German Late Permian Zechstein, but it has a long and checkered history behind it. Described in 1862 as a fern-pinnula *Cyclopteris liebeana* by the German palaeontologist Hanns Bruno Geinitz (1814–1900), he changed his opinion in 1880 and declared the prominent seed scales as belonging to a conifer—*Voltzia liebeana*. It was than in 1927, Rudolf Florin who changed it somewhat unfortunately to *Pseudovoltzia liebeana*. Although criticized especially by the very hard working Hans-Joachim Schweitzer (1996) it can be stated: there are some reasons to regard *Pseudovoltzia liebeana* as an own genus due to the fact that the scales hold for other *Voltziales* unusual huge seeds and also their foliage-type is very differently from all other species in the Permian or the Triassic. Otherwise, their three-seeded lobes with dorsiventrally hanging seeds are a typical feature of *Voltzia* and also their male, araucaroid-like cones.



***Ullmannia edwardsae* n. sp. Seed cones (Late Permian, Wuchiapingian)**

1-5. Several seed cones in the various versions (CUEC 295, CUEC 237, CUEC 238, CUEC 256, CUEC 259); 6. Seed cone attached on a twig (CUEC 331); 7. Carpet of seeds (CUEC 233); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum.



***Ullmannia edwardsae* n. sp. Seed cones (Late Permian, Wuchiapingian)**

1-2. Pollen cone attached on a stemlet, on the right side seed-cone, and detail of the male cone (CUEC 226); 3. Male cone (CUEC 300); 4. Detail of the microsporophylls (CUEC 313); 5. Pollen cone (CUEC 253); 6. Male cone (CUEC 298); all Cuecenes-Seceda, Gröden-Valley; Coll. Michael Wachtler, Dolomythos-Museum

Another Voltziaceae from the Dolomites was named by Johanna Clement-Westerhof (1987) in honour of her father *Pseudo(Voltzia) sjerpii*. To complicate the research Clement-Westerhof introduced for *Voltzia*-seed scales found isolated the new genus name *Dolomitia (cittertiae)* also from the same locality Bletterbach. Additionally, she created a new family composed of the genera *Majonica*, *Dolomitia* and *Pseudovoltzia* (Clement-Westerhof, 1987). Because science should solve problems, not create them can be established: The genus *Majonica* (Clement-Westerhof, 1987) is characterized by their winged seeds and is so far away as the Abietaceae and the Sequoias today.

Voltzia sjerpii and *Pseudovoltzia liebeana* have a different foliage type and also their seed scales are remarkably different. Because the ovuliferous scales of *Voltzia sjerpii* resemble those of Early Permian *Voltzia viallii* and Early-Middle Triassic *Voltzia rietscheli* from the Dolomites the most appropriate name will be *Voltzia sjerpii*. Therefore, also the genus-name *Dolomitia* is superfluous, being nothing other than a typical *Voltzia*-seed scale. Nevertheless, Late Permian *Voltzia sjerpii* is interesting in connecting Artinskian *Voltzia triumphilina*, Kungurian *Voltzia vialli* with the Triassic Voltziaceae from the Dolomites like *Voltzia rietscheli* till Late Triassic *Voltzia carinthica* (Wachtler, 2016).

***Voltzia sjerpii* nov. comb. (CLEMENT-WESTERHOF, 1987, WACHTLER, 2021)**

1987 *Pseudovoltzia sjerpii* CLEMENT-WESTERHOF, Dyas,
II, pp. 390-394 pl. VII-VIII

Etymology

The species was named in memory of Clement-Westerhof's father Jan Sjerp Westerhof.

Description

Branchlets and leaves: Shoots bearing spirally arranged bifacial leaves, not or slightly overlapping; shape ovate or (narrow) triangular, apex obtuse (especially in smaller leaves) to acute. Observed length 0.4–1.2 cm, width up to 0.4 cm. Leave base cushions rhomboid, slightly decurrent and, so far as observed, completely covering the axes.

Male cones: Not known.

Female cones: Seed scales bilaterally symmetrical, provided with many sterile leaves and three fertile scales of which two are laterally emerging and recurved and one median on the adaxial side, all showing basally on their abaxial

surface a place of ovule attachment. Basal part of scale-stalk relatively short.

Taxonomic notes

Conclusions were made to regard the Voltziaceae as an important missing link between the most archaic and more developed conifers (Clement-Westerhof, 1987). This theory can not be followed because the Voltziaceae appeared on the Carboniferous-Permian border together with other highly evolved conifers. They accompanied mainly unchanged gymnosperms (Araucaria-, Abietaceae-, Pinaceae-, Ginkgo-, Cycad-ancestors in a long travel for about hundred million years till the end of the Triassic. It seems that they were pushed to the brink of extinction due to the Raibl-catastrophe in the Carnian-stage. Late Triassic *Voltzia carinthica* was characterized by its small-sized seed scales and dwarfish female cones. If this is so, then *Cryptomeria japonica* has all the requirements to be considered the last representative of this genus. That this possibility exists can be confirmed that as in *Pseudovoltzia liebeana* as well in modern *Cryptomeria japonica* we encounter more regularly grown through female cones (Uhl & Brandt, 2004). These are twigs that enter the cone, proliferate them and sprout out, a feature that is mainly unknown in most conifers, but occurs interestingly in fair amounts in *Cryptomeria*.

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