The evolution of the Araucariaceae in the Triassic

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The Araucariaceae played over the whole Permian with the genus *Ortiseia* a prominent role within the gymnosperms. Their only one seed merged with the scale made them easily recognizable between other conifers, like the winged seed bearing Majonicaceae or the more seeded Voltziaceae. Another distinguishing feature in the Permian were their bulbous till elongated cones and the outer side of the seed scales covering small-sized protective leaves. Interestingly, beginning from the Triassic the Araucariaceae changed their blueprint: the plethora of protective leaves fused to form one single bract, the seed scales were shed almost exclusively on the tree, that entire cones can be found extreme rarely. The Triassic Araucariaceae progenitors developed symmetrically flat branchlets but also rope-like irregularly spreading twigs. All these features we encounter during the whole Triassic beginning from Early-Middle Triassic *Araucarites churchillae* n. sp., over Ladinian *Araucarites gilbertae* n. sp. till Late Triassic (Carnian) *Araucarites spinosa* n. sp.

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Araucarites churchillae **(Anisian, Early-Middle Triassic)**

An Anisian landscape with the Araucaria-ancestor ***Araucarites churchillae****:* Left: A male tree with cones and microsporophyll. Right a female tree with a female cone and some shed seed scales.

The Triassic of the Dolomites was characterized by a quick spreading of many plant families after the Permo-Triassic cataclysm. Moreover, about 50 million years lasting reduction of the plant world during the whole Permian, where only the gymnosperms (conifers, cycads, ginkgos) can be encountered largely, ended in the Early-Middle Triassic. During the whole Permian, but especially in the Late Permian we encounter two different European biotic communities: an Alpine dominated by Araucariaceae (*Ortiseia*) and Abietaceae (*Majonica*) and a Northern European characterized by Voltziaceae (*Pseudovoltzia)* and Taxaceae (*Ullmannia*). Rarely a moderate exchange took place.

Moreover, the Ginkgoales split into two separate families: *Ginkgoites* especially in the Dolomites and *Baiera* in the Northern European Zechstein (Wachtler, 2021). The *Pinus* ancestors (*Férovalentinia*) boomed in the Alps in the Early Permian, to disappear mostly after that period, only to re-emerge in the Eocene.

In the Early Triassic the landscape changed considerably. From the nothing appeared a multitude of ferns (*Anomopteris, Neuropteridium, Danaeopsis, Wachtleria, Ladinopteris, Anotopteris, Gordonopteris, Cladophlebis, Symopteris, Todites, Asterotheca, Chiropteris*) being progenitors of many extant Pteridophyta tribes like *Osmunda, Lindsaea, Danaea, Cyathea, Dipteris* or *Marattia.* They were accompanied by strange seed ferns (*Sagenopteris, Scytophyllum)* and lycopod survivors from the Carboniferous-Permian like S*igillcampeia, Lycopia, Eocyclotes, Lepacyclotes, Pleuromeia* till also in the present surviving genera like *Selaginellites* and *Isoetites* and horsetails (*Equisetites, Schizoneura*). The conifers played only a background role in the Early Triassic, whereas other gymnosperms like the cycads (*Nilssonia, Pseudoctenis, Bjuvia, Taeniopteris*) were widespread.

Due to rich plant lenses, stretching for many kilometres especially in the Dolomites and based of thousands and thousands specimen an exact classification also for the conifers was made easier. Within them one conifer—*Voltzia*—prevailed over the whole Triassic (Wachtler, 2016). It can be distinct from other conifers by their more-lobed seed scales, bearing three or more small-sized seeds. Mostly they hold three dorsiventrally hanging seeds on each scale (*Voltzia*-species), but they could arrive till five seed-lobes for each scale like in *Aethophyllum* or *Swedenborgia* (Wachtler, 2016). The scale-lobes could be tapered (*Voltzia agordica, Aethophyllum stipulare* or *Swedenborgia nissleri*), but also rounded (*Voltzia rietscheli, Voltzia dolomitica, Voltzia carinthica)*.

Other reasonably distinguishable conifers spread in the Late Triassic (Carnian) with the larch-progenitors *Wachtlerolarix* and a prickly dried up Cupressaceae-ancestor *Pusteria*. The same is valid for *Alpia*, a two seeded conifer having resemblances with extant *Glyptostrobus*, today reduced to the subtropical southeastern China, northern Vietnam and eastern Laos. Another enigmatic conifer is represented by Early-Middle Triassic *Albertia,* characterised by strangely arranged pollen sacs and huge male cones (probably the greatest ever recorded), which seems to have no descendants today. All these mentioned conifers are relatively good known also in their fertile parts.

Now we need to focus on other more problematic Triassic conifers. What happened with the Araucariaceae (*Ortiseia*), Abietaceae (*Majonica*) or Taxaceae (*Ullmannia*) so widespread in the European Permian? But also the Ginkgoales (*Gingkoites, Baiera*) or the Pinoidea (*Férovalentinia*)?

In the Early-Middle Triassic we encounter isolated berry-fruits (*Kandutschia kuehnii)* having resemblances to the Taxaceae, but their rare occurrence is far from a well-documented result.

Then we have all over the Triassic isolated seed scales that are bilobed and additionally equipped with a short bract. In that they have resemblances with Permian *Ortiseia* or *Majonica* scales. Moreover, in the Permian it is not easy to tell apart isolated *Majonica* and *Ortiseia* seed scales. Only the abundance of material with isolated alate seeds and single ovules, symmetrical and plagiotropic branchlets, elongated big and small sized male cones help to get an accurate picture about the two conifer-families.

In 2016, I described a conifer scale with an accompanying winged seed (PIZ 752, holotype) as *Farjonia campeiae*, honouring Aljos Farjon, senior scientific officer for the Royal Botanic Gardens, Kew, and the world's premier conifer taxonomist. Furthermore, I figured several pinnately branched shoots as

***Araucarites churchillae*. Reconstructions (Anisian, Early-Middle Triassic)**

a. Female tree; b. Entire twig (PIZ 356);c. Detail of a branchlet (PIZ 652, PIZ 233, PIZ 40); d. Single leaf; e. Female cone (PIZ 699); f. Seed scale adaxial side with merged seed (PIZF 986, PIZ 991, PIZ 683); Seed scale abaxial side with short bract (PIZF 124, PIZF 247, PIZ 754); h. Male cone ((PIZ 656, PIZ 737); i. Isolated microsporophyll (PIZ 733)

belonging to *Farjonia* (PIZ 652, PIZ 233, PIZ 40, PIZ 356). This was probably a mistake and could better be classified as *Araucarites,* whereas the seed scale holotype with the winged seed could be maintained as *Farjonia campeiae.*
From the Middle Triassic (Upper Ladinian), I described additionally a new conifer with plagiotropic branchlets as *Farjonia presegliei* (PRE 50 holotype). This genus could also be maintained, having effectively resemblances with Abietaceae-ancestors. Especially because by later researches palmate branchlets were recorded that can be classified as *Araucarites* (Wachtler, 2011, 2015, 2016). It can be supposed that also—but in minor number—Abietaceae, as well as Araucariaceae were present in the Alpine plant assemblages.

Araucaria-ancestors

To bring order in the evolution of Triassic conifers the following system will be proposed.

Araucarites churchillae sp. nov. WACHTLER 2021

Type horizon and age

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

Holotype

PIZ 652 Branchlet Coll. Wachtler, Naturmuseum Südtirol, Bozen

Paratype

PIZ 690 Seed scale Coll. Wachtler, Dolomythos-Museum, Innichen

Material

Branchlets: PIZ 233, PIZ 40, PIZ 356; Female cones and seed scales: PIZ 699, (PIZF 124, PIZF 247, PIZ 754, PIZ 658)

Etymology

In honour of Anna Churchill née Maitland-Laurie, a woman of artistic and musical talent, which accompanied her husband George Cheetham Churchill (1822–1906) through the Dolomites. The book "The Dolomite Mountains", the account of a journey by the two English naturalists, Gilbert and Churchill was published in 1864 and first introduced this name in Europe.

Diagnosis

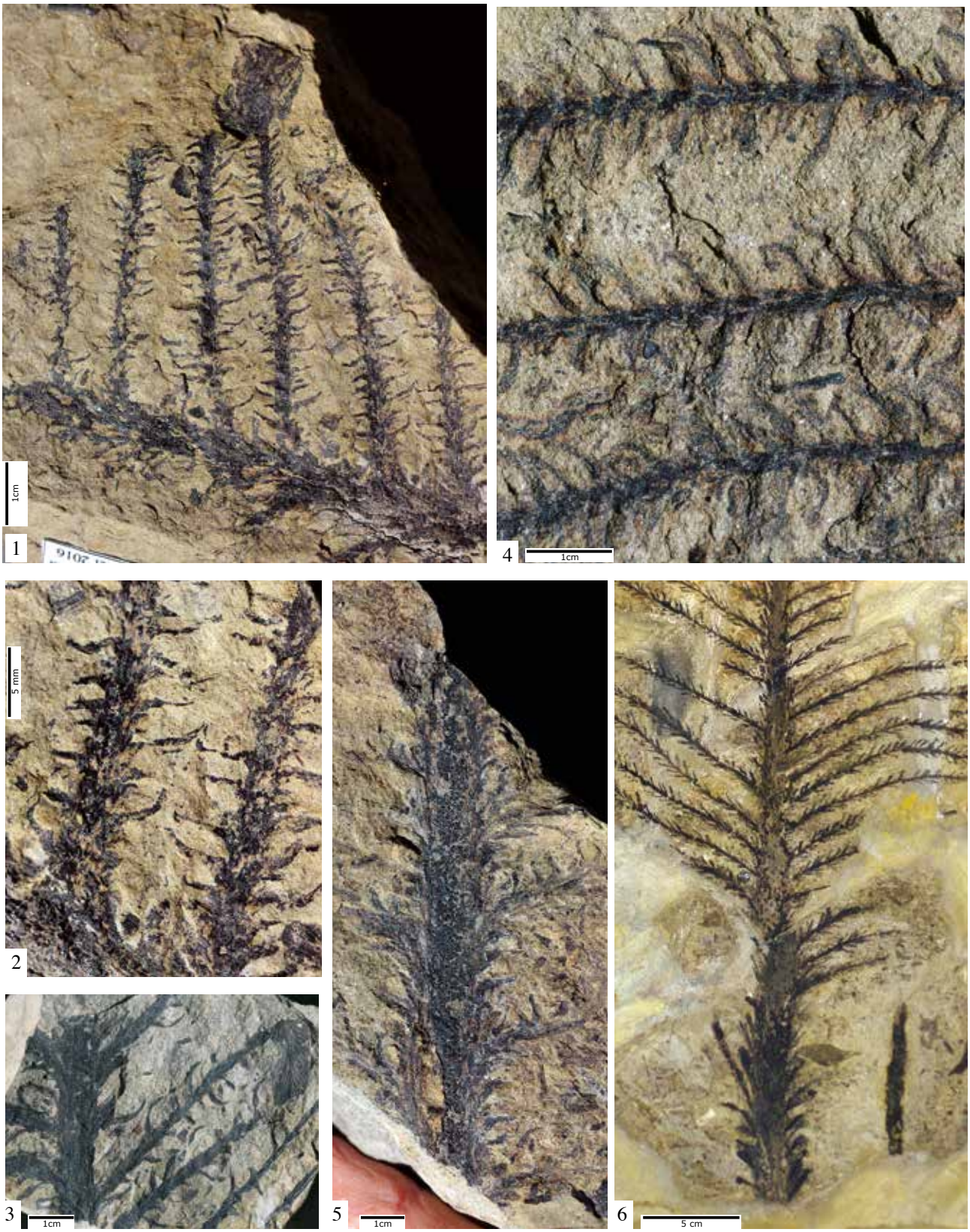
Arborescent conifers with evenly spaced combs of branchlets. Leaves are awl-shaped. Female cones bulbous, seed scales bilobed, additionally equipped with one short bract having in the middle one sunken seed. They are usually shed after maturity. Pollen cones araucaroid with from the upper part of the microsporophyll dorsiventrally hanging pollen sacs.

Description

Vegetative branches and leaves: Conifer with symmetrical bipinnate branches arising at right angles from the main trunk. Branchlets geometrically opposing to slightly subopposing (PIZ 652, PIZ 233). Needles lanceolate, awl-shaped, incurved and decurrent, reaching a length of 1 to 1.5 cm, with a thickness at the base of only 0.1 cm. The main branch axis is covered with 3- to 5-cm-long leaves, which are sparsely spaced (PIZ 40). They were stiff and hard, bent inward especially on the apical part.
Pollen cones: Male fructifications elongated, about 3–5 cm long. Microsporophylls bracted with several from the outer side to the main axis hanging pollen sacs (PIZ 656, PIZ 733, PIZ 737).
Seed cones: Female cones spherical in youth, up to 5 cm long (PIZ 699), but decaying at maturity; thus only in rare cases can entire cones be recovered. Dispersed seed scales are frequent, reaching a length of about 1.5 cm and a width of 0.7 to 1 cm. They were equipped with a pointed sterile median bract partially overlaying the two outer lobes (PIZF 124, PIZF 247, PIZ 754). Adaxial side evidencing only one elongated and sunken seed (PIZ 690, PIZF 986, PIZ 991, PIZ 683).

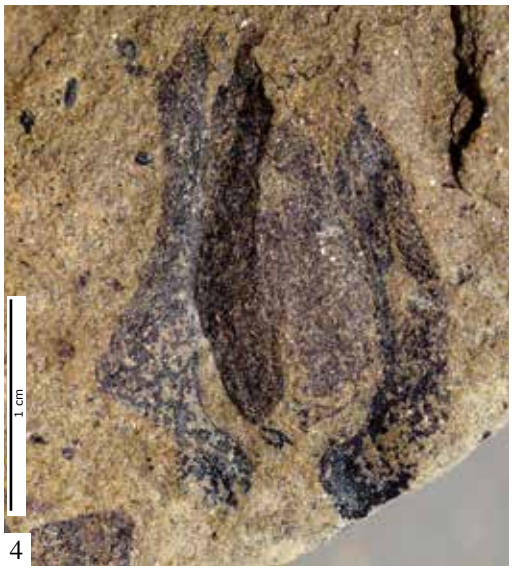
Discussion

From the Carboniferous-Permian border on we encounter on the Euramerican landmass an uninterrupted succession of a conifer-family, that due to the variety of characteristic female and male cones, isolated shed seed scales, pinnately



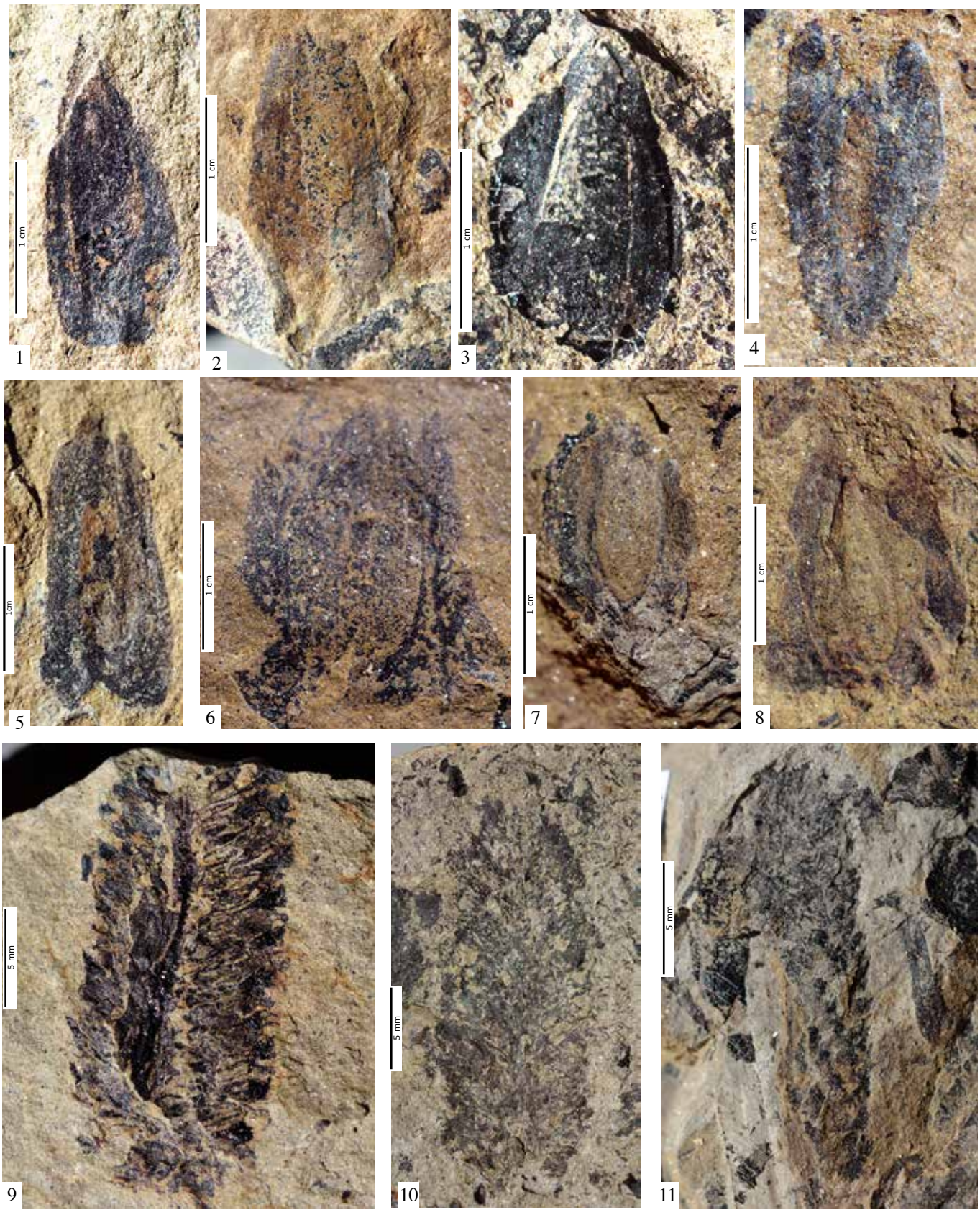
***Araucarites churchillae* n. sp. Branchlets (Anisian, Early-Middle Triassic)**

1-2. Part of a twig and detail of the needles (designed holotype, PIZ 652); *3.* Part of a branchlet *(*PIZ 233); 4. Detail of a main shoot with falcate needles (PIZ 40) 5. Main branchlet (PIZ 663); 6. Detail of a twig (PIZ 356) (all Coll. Wachtler, Piz da Peres-Wachtler gorge Miara, Anisian, Pelsonian)



***Araucarites churchillae* n. sp. cones and seed scales (Anisian, Early-Middle Triassic)**

1. Juvenile not decomposed cone (PIZ 699); 2. Detail of the single scales (PIZ 699); 3. A seed-scale carpet (PIZF 195); 3. Two isolated seed scales, the left one outer side, the right inner view (PIZ 690) 4. Seed scale with impression of the seed (PIZ 717); All Coll. Wachtler, Piz da Peres Miara, Anisian, Illyrian)



***Araucarites churchillae* n. sp. Isolated seed scales and seeds (Anisian, Early-Middle Triassic)**

1-4. Isolated seed scales abaxial (PIZF 124, PIZF 247, PIZ 754, PIZ 658); 5-8. Isolated seed scales inside (adaxial) with seeds (PIZF 78, PIZF 986, PIZ 991, PIZ 683); 9-10. Mostly entire male cones (PIZ 656, PIZ 737); 11. Male cone (PIZF 187; All Coll. Wachtler, Piz da Peres Miara, Anisian, Illyrian)

***Araucarites churchillae*. Male cone**

Detail of the microsporophyll with pollen sacs (PIZ 733)

branched shoots can easily be classified as Araucariaceae-ancestors. The first appearance we have in the Kasimovian/ Gzhelian (Late Carboniferous) Saar-Nahe-Basin in Germany with *Ortiseia uhli*, then their main recovery-places moved in the Early Permian to the Eastern Alps with Artinskian *Ortiseia dasdanai,* followed by Kungurian *Ortiseia daberi*. In the late Permian we have than in the Dolomites a great diversity with *Ortiseia leonardii, Ortiseia jonkeri, Ortiseia zanettii* and *Ortiseia visscheri* distinct by little variations, probably due to time different sedimentations.

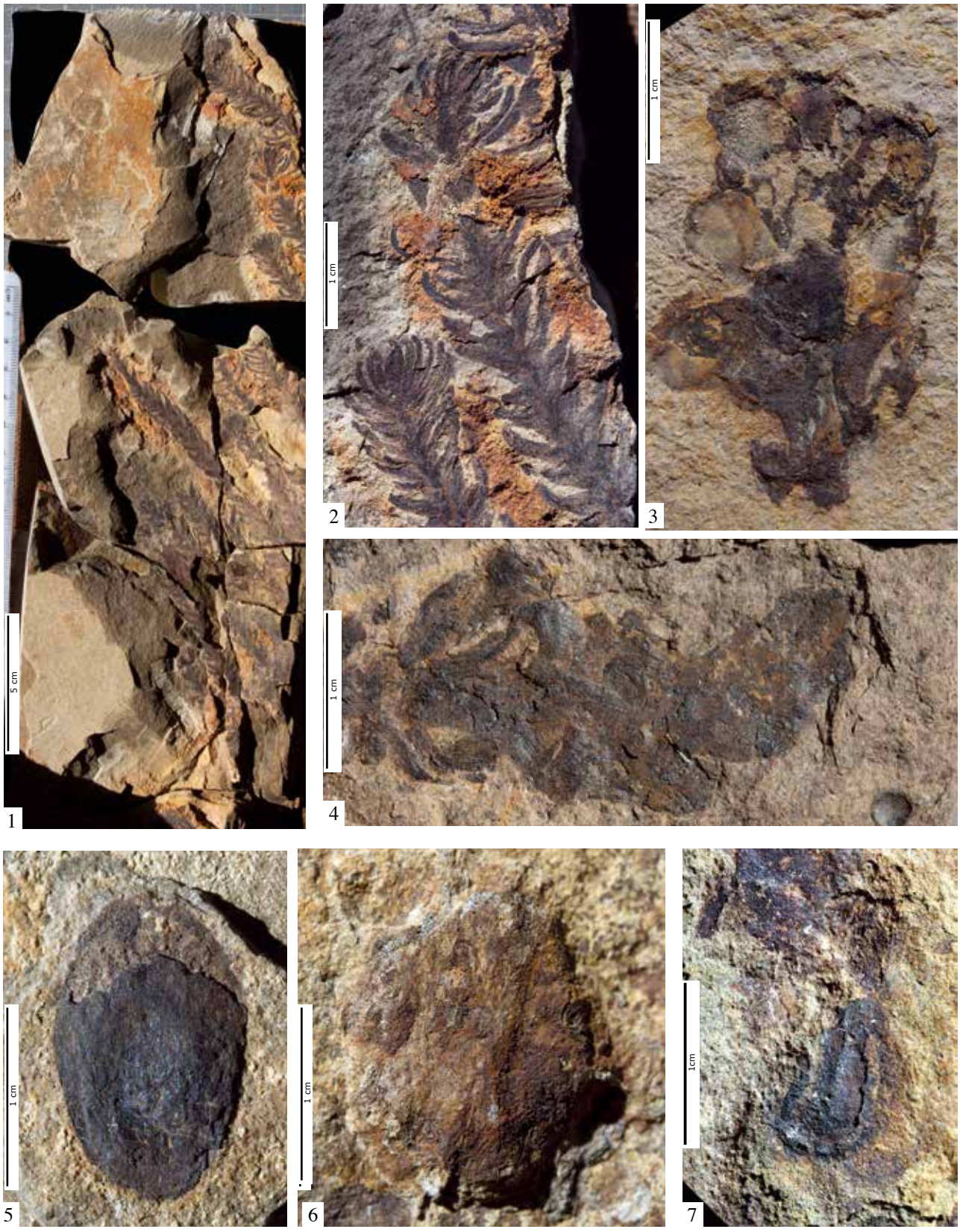
Some peculiarities of these Araucariaceae were so characteristic to facilitate a classification also over the different time epochs and to delimit them against other conifer families. The most archaic megasporophyll of all Araucarian-ancestors consisted in a seed scale surrounded by a plethora of sterile dwarfish leaflets. Only one single seed evolved, merged and sunk in the middle of the scale. It can be assumed that most part of the cones decayed on the soil. This conclusion can be drawn because many completely preserved cones are found in the sediments. It is different to extant Araucarias which decay on the tree.

Permian Araucarian progenitors carried huge elongated pollen cones, with especially in the juvenile specimen long bracts (*Ortiseia leonardii)*. Several pollen sacs were hanging from the upper part of the microsporophyll in direction to the main axis. All over the Permian we encounter symmetrically plane arranged branchlets like today`s *Araucaria heterophylla.* During the Triassic the Araucariaceae changed considerably and two different branchlet systems were present: pinnately branched shoots, with slightly falcate leaves and as novelty also plagiotropic twigs being divergent from the main axis like extant *Araucaria araucana*.

Unfortunately in that they can be confused easily with another conifer-tribe having similar characteristics: The Voltziales. They generate similar male cones with from the upper part of the microsporophyll dorsiventrally hanging pollen sacs. It seems that especially in the Permian the pollen-bracts of the Voltziaceae were shorter and more robust. Moreover, their foliage structure was very much alike with their irregularly spreading branchlets.

Therefore, for decades the frequent in the Triassic found Voltziaceae were regarded as ancestors of the Araucariaceae. Only the mostly isolated found seed scales give strong clues to completely different evolving systems beginning from the Late Carboniferous border on (Wachtler, 2016).

Aracaurites churchillae fits with its pinnately branched twigs well in the evolving scenery of the Permian *Araucaria*-ancestors *Ortiseia.* The main differences lay in their seed scales where the many protective leaves on the outer side of the scales from the Permian merged to form in the Triassic only one pointed median sterile bract as in today's Araucarias, although sometimes the original blue print can be barely seen (PIZ 986). The only one sunken seed in the middle was shed entirely with the scale. All these features remained than over the whole Triassic— where the *Araucarites*-species played an important role in the Northern hemisphere (Ladinian *Araucarites gilbertae*, Carnian *Araucarites spinosa*) till their disappearing on the Triassic-Jurassic border.



***Araucarites gilbertae* n. sp. (Ladinian, Middle Triassic)**

1. Branchlet and detail of the leaves (PRE 90, designed holotype); 3. Part of a female cone (PRE 76); 4. Apical part of a branchlet with a female cone (PRE 41); 5-6. Seed scale abaxial side (PRE 80, PRE 100); 7. Seed scale adaxial side evidencing one sunken seed (PRE 06); All Coll. Wachtler, Preseglie (Brescian Alps), Langobardian

Araucarites gilbertae, sp. nov. WACHTLER 2021

Type horizon and age

Dolomites, Middle Triassic, Upper Ladinian-Fassanian-Langobardian (238 - 235 Mya)

Holotype

PIZ 652 branchlet, Coll. Wachtler, Dolomythos Museum, Innichen, Südtirol

Etymology

In honour of Susan Gilbert née Green (1809–1871), which accompanied her husband Josiah Gilbert (1814–1893) through the Dolomites. The book "The Dolomite Mountains", of the two English naturalists, Gilbert and Churchill was published in 1864 and first introduced the name "Dolomites" worldwide.

Diagnosis

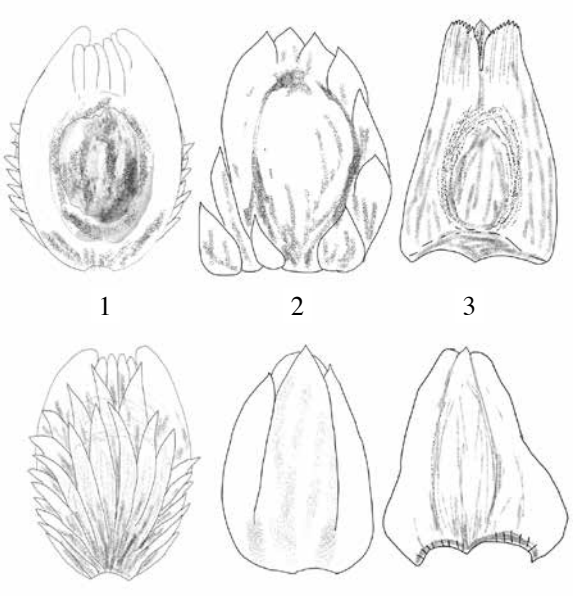
Conifer with pinnately branched twigs. Leaves are falcate. Female cones bulbous, seed scales equipped with one merged seed shed after maturity.

Description

Vegetative branches and leaves: Twigs spreading symmetrically, needles awl-shaped and falcate (PRE 90, designed holotype), from 1 to 1.5 cm long.
Pollen cones: Not known with security, because similar to Voltzia male cones.
Seed cones: Female cones bulbous (PRE 41), but decaying at maturity; Seed scales, reaching a length of about 1.5 cm and a width of 0.7 till 1 cm, generating only one sunken seed (PRE 80, PRE 100, PRE 06).

Discussion

Like in the Anisian sediments, as well as in the Carnian a fair amount of isolated seed scales were recovered, that have due to its only one with the scale merged seed all the features to be inserted as *Araucarites.* Additionally, also evenly spaced combs of branchlets with awl-shaped can be found, that have resemblances with *Aracaurites churchillae* from the Anisian layers of the Dolomites. Although the palaeoflora from Preseglie in the Brescian Alps is dominated by *Voltzia* and several cycads (*Bjuvia, Taeniopteris, Nilssonia*), other conifers were present. Unfortunately, due to the scarcity of fertile organs more precise classifications are sometimes difficult.



Araucaria-seed scales: The Permo-Triassic-change

1. Ortiseia leonardii (Wuchiapingian); 2. Araucarites churchillae (Anisian); 3. Araucarites spinosa (Carnian). The Araucaria-ancestors remained mainly unmodified all over the Permian and changed considerable beginning from the Early Triassic. Top: Adaxial side, bottom abaxial side.

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