

The Conifers in the Carnian Raibl beds of the Lienz Dolomites

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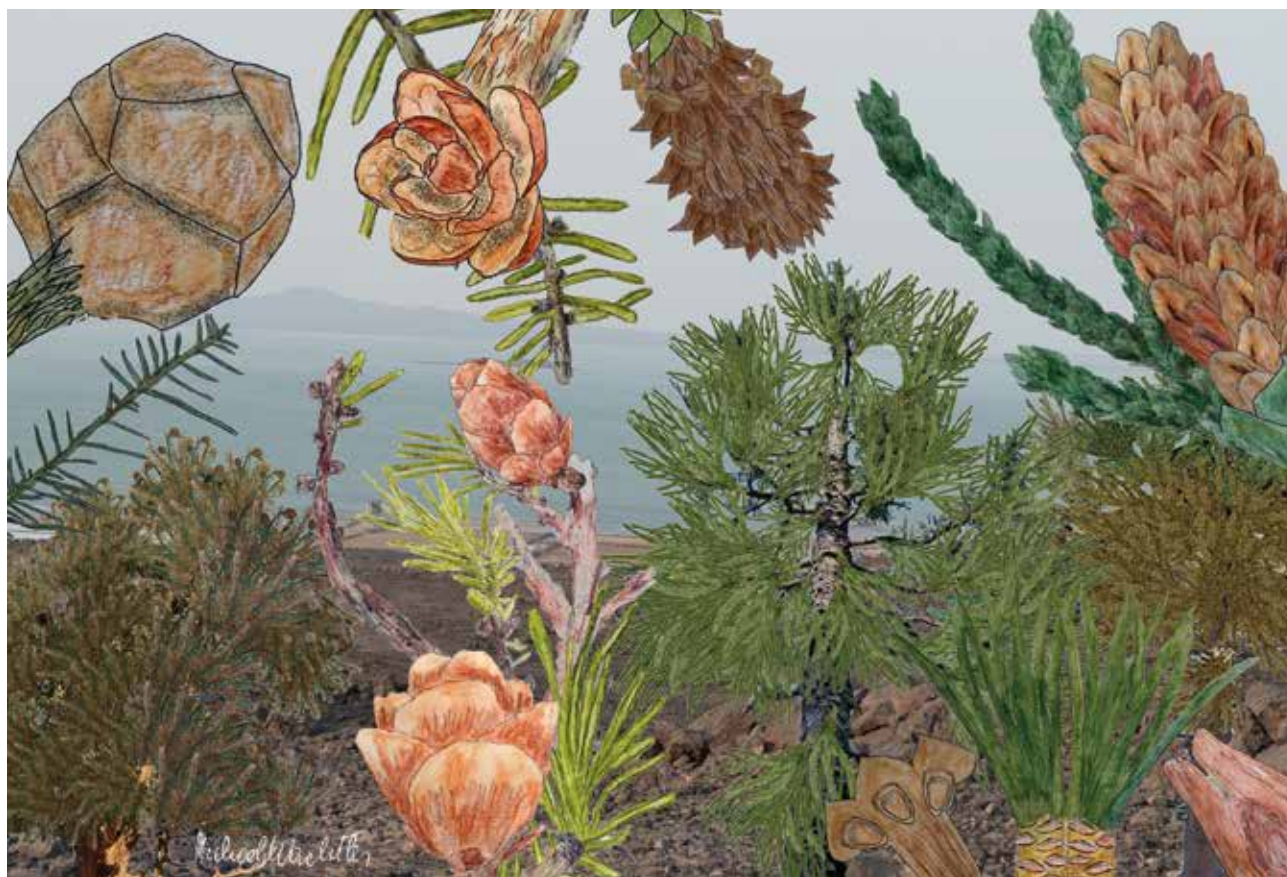
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In the extremely reduced and live-hostile Upper Triassic (Carnian) Raibl sediments of the Lienz Dolomites we encounter at least four different conifer families. *Voltzia carinthica*, one of the last Voltziaceae recorded, characterized by their scales with three lobes, holding on each one small-sized seed, and probably parented with the extant genus *Cryptomeria*, *Araucarites spinosa* a representative of the Northern hemisphere Araucarias, that can be distinguished by their one seeded scales, *Pusteria maribelae*, a forefather of the Cypress-family and *Wachtlerolarix weissii*, that has resemblances with today's larches. All can be regarded as frequent in the hundreds of meters outcropping layers of the Raibl Formation in the Lienz Dolomites. Strangely all evidence withered, thorny and extremely reduced characteristics, maybe to be attributed to catastrophic climate events.

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Key words: Araucariaceae, Voltziaceae, Cupressaceae, Larches, Raibl Formation, Carnian, Lienz Dolomites, Conifer evolution, Raibl Cataclysm, palaeoclimatology, Carnian Pluvial Event



A Late Triassic (Carnian) offshore conifer landscape of the Lienz Dolomites (Raibl cataclysm)

On the left side grow ***Pusteria maribelae*** conifers, after that are visible cones and twigs of the larch ancestor ***Wachtlerolarix weissii***, followed by ***Voltzia carinthica***. On the right side sprout a twig with a female cone of ***Araucarites spinosa***. In the understory is recognizable the clubmoss ***Sigillcampeia blaii***.

The Voltziaceae represent one of the most frequent conifer-families in the Permo-Triassic of Europe. A typical feature are their three- (*Voltzia*) till five-lobed seed scales (*Swedenborgia*) with dorsiventrally hanging seeds. In the Earliest Permian (Perner & Wachtler, 2013) they could also hold more lobes and seeds (about ten or more). *Voltzia* cones were huge in the Permian, reaching from 10 to 20 cm, but reduced their size gradually in the Triassic. Their scales were shed after maturity. Moreover, their branchlets changed from the symmetrical planate in the Early-Middle Permian to the sparsely and irregularly branched in the Late Permian (*Pseudovoltzia*) and over the whole Triassic. One of the last real Voltziaceae that we encounter in the world fossil record is represented by Upper Triassic *Voltzia carinthica*. It constitutes a common conifer element in the Carnian Raibl sediments of the Eastern Dolomites from Raibl till the Lienz Dolomites. One interesting feature are their dwarfish seed scales, that reach with maximum 10 mm only half the size of their Lower-Middle Triassic relatives, and also their cones were in contrast to the Permian and Early-Middle Triassic small-sized.

Although being so frequent in the Triassic can not be established without doubt which extant conifer could be a living successor, but today's *Cryptomeria* has with its three-lobed seed scales composing a dwarfish cone the best possibilities. Especially if we compare seed scales and suggested cones of *Voltzia carinthica* than the resemblances are astonishing. Moreover, their twigs have common similarities. Differences constitute the cones of *Cryptomeria* which are shed entirely and do not disaggregate.

All Voltziaceae can be easily distinguished by their three lobed scales, giving place for three seeds that were dorsiventrally hanging from the upper side of each distinct lobe. Usually the seed scales were found isolated in the sediments. Probably most of the cones dissolved just on the tree or at least on the soil. Complete cones especially in the Triassic are rarely recorded (Wachtler, 2016a, b). Although they were often brought in connection with *Araucaria*-trees, seed scales and female cones are too different to justify a closer relationship. But due to similar twigs and also pollen cones a distinction between the Triassic *Araucarites*-conifers is not easy.



1-2. Several *Voltzia carinthica* seed scales and seeds. The scales are only 10 mm in size, the seeds 2 mm, ZOC 24, Zochenpass, Coll. Wachtler, Dolomythos



***Voltzia carinthica*. Reconstructions (Late Triassic, Carnian)**

a. Seed scale, inner side with seeds (SEE 15); b. Single seed (ZOC 24); c. Seed scale with shed seeds; d. Seed scales abaxial side; e. Female cone (SEE 30); f. Pollen cone (SEE 38); g. Isolated leaf and twig (ZOC 132); h. Mainly complete branchlet (ZOC 102); i. Tree



***Voltzia carinthica*. Twigs and leaves (Late Triassic, Carnian)**

1. Twig (SEE 24, holotype, Seekofel); 2. Often diverging branchlet (ZOC 102, Zochenpass); 3. Part of a twig (ZOC 82)
All Coll. Wachtler, Dolomythos Museum; Lienz-Dolomites



1



2



3



4



5



6

***Voltzia carinthica*. Juxtaposed shoots (Late Triassic, Carnian)**

1-2. Twig with acuminate leaves on the main twig and rounded on the secondary branchlet (ZOC 63); 4. Twig with pointed foliage on the main twig and a branching small shoot with rounded needle (ZOC 61); 4-5. Twig with a secondary branchlet with decaying needles (ZOC 71); 6. Shoot with shed needles on the secondary branchlet (ZOC 73); (All Coll. Wachtler, Zochenpass, Lienz-Dolomites)



***Voltzia carinthica*. Twigs and cones (Late Triassic, Carnian)**

1-2. Detail of the leaves (ZOC 133, SEE 64; 3. Detail of leaves (ZOC 132); 4-5. Pollen cones (SEE 38, SEE 46); 6. Decaying female cone (SEE 30); All Coll. Wachtler, Dolomythos Museum; Lienz-Dolomites



***Voltzia carinthica*. Seed scales (Late Triassic, Carnian)**

1. Several isolated seed scales (SEE 15, paratype); 2. Seed scale with impressions of a seed (arrow) (SEE 15); 3. Seed scale (SEE 15); 4. Seed scale adaxial view (SEE 30); 5. Detail of a seed scale (ZOC 35); 6-7. Two distinct seed scales on a slab with one shed seed (ZOC 24); 8. Seed scale (SEE 61); All Coll. Wachtler, Seekofel, Zochenpass, Lavant Luggauer Törl, Lienz-Dolomites

***Voltzia carinthica* WACHTLER 2016**

Type horizon and age

Dolomites, Late Triassic, Carnian (225 Mya)

Holotype

SEE 24 (Leaves) Coll. Wachtler, Dolomythos-Museum, Innichen), **Paratype:** SEE 15 (Seed scales)

Etymology

Named after the latin name Carinthia for the Austrian County Kärnten

Description

Branchlets: Shoots irregularly protruding, massive and widely spreading, but sparsely branched.

Leaves: Needles densely spirally arranged, armoured and leathery, broadly spear-headed to pointedly egg-shaped. They are flat but a little bowed outward around the midline. Leaves are from 6 mm to 10 mm in length and 0.5 to 0.8 mm in width.

Pollen cones: From 5–7 cm, 2–3 cm width, consisting of an axis with spirally arranged microsporophylls holding slightly upwardly curved peltate shields. Pollen sacs attached to the outer lower edges of the microsporophylls, directed towards the main spindle.

Seed cones: Decaying after maturity, probably only till 5 cm long (SEE 30). Ovuliferous scales with three fused and apically rounded till tapered lobes. Some sterile microleaves sprouting on the outer side, a feature of many Triassic *Voltzia* seed scales. Scales robust, till 10 mm long, apically 7–8 mm width, with a broad and long peduncle. Peduncle having half the size or more from the entire scale. On each lobe, one seed is embedded on the upper part of the scales. The seeds are about 2 mm long and elongated with a small basal micropyle.

Diagnosis, remarks and ecology

Voltzia carinthica constitutes a common flora element of the Late Triassic Raibl sediments. Not easy is the distinction only based on their branchlets, that sometimes can be confused with those of *Araucarites spinosa*.

However, the last one is more robust and leathery. No difficulties arose when isolated seed scales are found. Comparing *Voltzia carinthica* with Early till Middle Triassic Voltziaceae like *Voltzia rietscheli* or *Voltzia agordica* especially the seed scales can be distinct by their dwarfism. As only extant representative can probably be regarded *Cryptomeria japonica* or *Cryptomeria fortunei* having mostly the same character of the cones, but also their branchlets. More distant is the conifer *Cunninghamia*, evidencing also three seeded scales, but being different from *Voltzia*.

Genus ARAUCARITES Presl, 1838 (in Sternberg, 1838)

Taxonomic notes

The genus name *Araucarites* was first introduced by Karl Presl in 1838 "*Versuch einer geognostisch-botanischen Darstellung der Vorwelt*", Vol 2. edited by **Kaspar Maria Graf Sternberg**, although just in 1837 **Stephan Ladislaus Endlicher** proposed the name for Araucarian fossil wood, but without going in further details (Zijlstra & van Konijnenburg-van Cittert, 2000).

Another attempt was made in 1850 by **Heinrich Göppert** in his "*Monographie der fossilen Coniferen*" in which he described wood, leaves and cones from more *Araucarites* species of various geological periods reaching from the Carboniferous till the Oligocene. Later it became evident that the term *Araucarites* can only be used for fossilised conifers holding one seed sunken seed on each scale. Therefore, many species (like *Araucarites recubarensis* (Massalongo ex De Zigno, 1862), or *Araucarites agordicus* (Unger, 1850) were transferred to *Voltzia species* (Wachtler, 2016), because it became obvious that they hold three seeds on each fertile scale.

The first real Araucaria progenitors originated on the Carboniferous-Permian border (Perner & Wachtler, 2015) with *Ortiseia uhli*. They were than frequent in the Early Permian Dolomites (*Ortiseia dasdanai*, *Ortiseia daberii*) and especially in the Upper Permian with *Ortiseia leonardii* (Florin, 1964), *Ortiseia jonkeri* (Clement-Westerhof, 1984), or *Ortiseia zanettii* (Wachtler, 2015). Inter-



Cryptomeria japonica resembles in some details the Voltziaaceae. The more-lobed bract and the three seeds for each scale are the same. 1. Tree; 2. Branchlet; 3. Male cone; 4. Female cone; 5. Single bract outside; 6. Single bract inner side. 7. Juvenile cone; 8. *Cryptomeria fortunei*, branchlet with seed cones.

estingly all Permian *Ortiseia*-*Araucarias* hold as main distinctive feature ovulate scales that were composed of an agglomeration of many minute sterile leaves completely surrounding the once-segmented seed blade and the only one submerged seed. In the Permian the Araucarian ancestors hold bulbous till elongated female cones.

After the Permian Triassic border in the Araucaria ancestors the agglomeration of many sterile leaves disappeared and a once-lobed scale generating one seed remained. During the whole Triassic we encounter than isolated shed *Araucarites* seed scales (Anisian *Araucarites churchillae*, Ladinian *Araucarites gilbertae*). After that the globose seed cones found a continuation in the southern hemisphere, whereas the Northern hemisphere *Araucarias* vanished.

In the Alps we can found from the Anisian over the Ladinian till the Carnian frequently one-lobed seed scales with an equal long sterile bract holding one seed. Only rarely entire bulbous till mostly elongated cones can be found, because their cones decayed just on the tree. In the Carnian of the Lienz Dolomites one *Araucarites* species is common so that the habitat, and its blue print can be studied well.

***Araucarites spinosa* n. sp. WACHTLER 2020**

Holotype

ZOC 99 (cone and scales) Coll. Wachtler, Dolomythos Museum, Innichen, Südtirol

Paratype

ZOC 116 (twig); LAV 91 (Seed scale)

Etymology

After the Latin name "spinosus", meaning thorny, due to the prickly leaves.

Diagnosis

Conifer trees with spreading twigs, foliage rigid and leathery, cones elongated till only slightly bulbous, scales oblong, one seed inserted in a lobed scale.

Description

Branchlets and leaves: Twigs spreading with hardened lateral branches of unequal length ZOC 116, paratype, SEE 59, LAV 61, LAV 69). Foliage awl-shaped and densely arranged around the shoot, 10 mm long, 0,7



Araucaria araucana shoot and seed scales of *Araucaria heterophylla*. They have affinities with *Araucarites* from the Upper Triassic. The lobes of the scales merged to one unit in the Triassic, that today the evolutionary development is not more visible. Originally many microleaves coated a lobed fertile scale.



***Araucarites spinosa* n. sp. Reconstructions (Late Triassic, Carnian)**

a. Female cone (LAV 99); b. Seed scales outside (ZOC 42, LAV 95); c. Seed scales inner side with the sunken seed (LAV 91, ZOC 24, SEE 51); d. Male cone (ZOC 45) e. Microsporophyll; f. Leaves; g. Twig (ZOC 116); h. Tree.



***Araucarites spinosa* n. sp. Twigs (Late Triassic, Carnian)**

1. Twig (ZOC 116, paratype); 2-5. Branchlets (SEE 59, LAV 61, ZOC 85, LAV 69); 6-7. Detail of the needles (ZOC 114, ZOC 117); All Coll. Wachtler, Seekofel, Zochenpass, Lavant Luggauer Törl, Lienz-Dolomites)



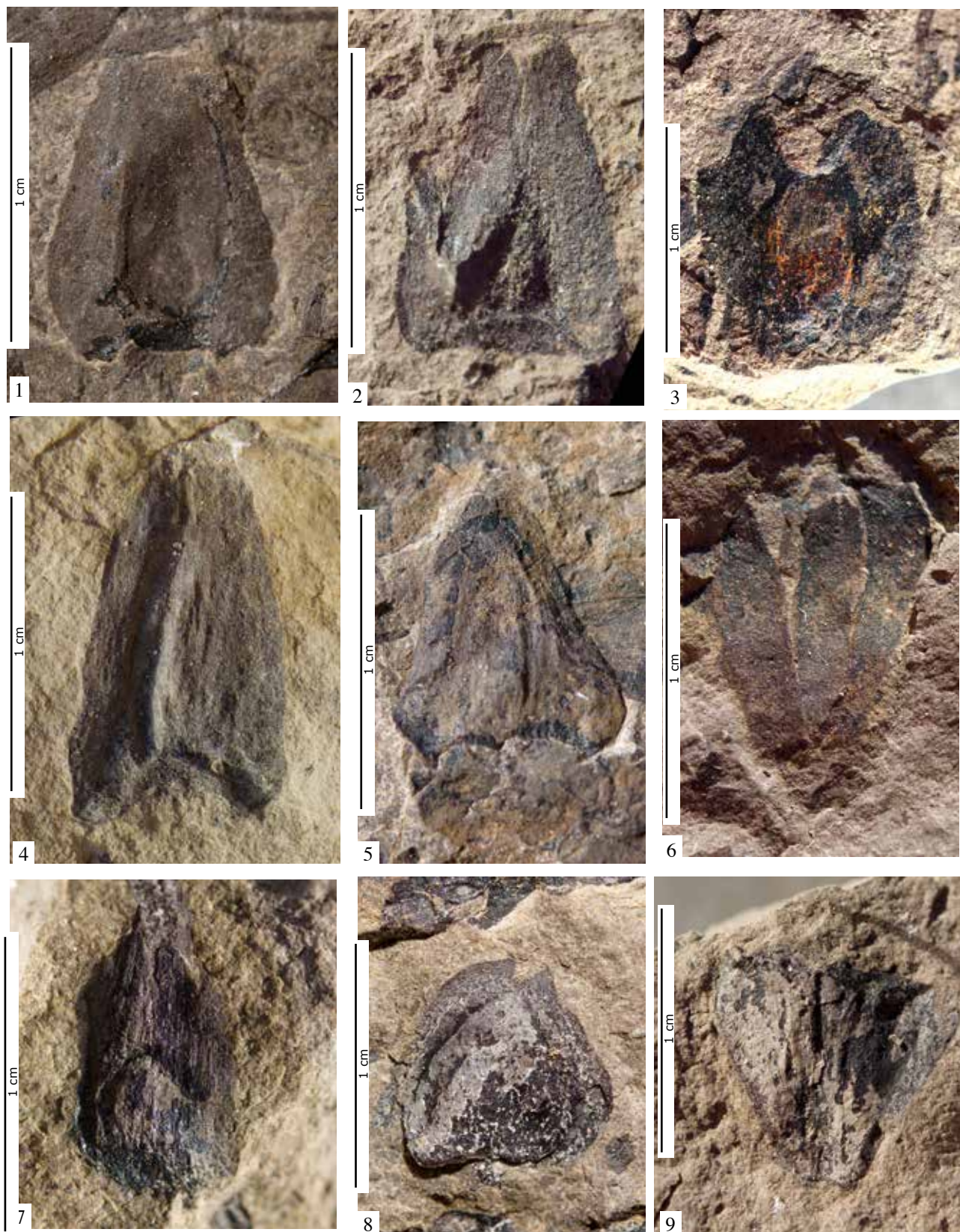
***Araucarites spinosa* n. sp. Female and male cones (Late Triassic, Carnian)**

1-2. Mature female cone and detail of an isolated scale (Designed holotype LAV 99) 2. Two female cones (SEE 61; Coll. Karl Weiss); Decaying male cone (ZOC 45); (Coll. Wachtler, Seekofel, Zochenpass, Lavant Luggauer Törl, Lienz-Dolomites)



***Araucarites spinosa* n. sp. Female cones, twigs (Late Triassic, Carnian)**

1-2. Two cones with isolated seed scales (ZOC 45); 3-4. Female cone (or twig) and isolated seed scale (LAV 63) (All Coll. Wachtler, Zochenpass, Lavanter Alm, Lienz-Dolomites)



***Araucarites spinosa* n. sp. Seed scales (Late Triassic, Carnian)**

1. Seed scale (LAV 91, Paratype); 2. Isolated seed scale, (ZOC 24); 3. Seed scale with well evidenced seed (SEE 51); 4-6 Seed scales outside (ZOC 42, LAV 95, HOCH 01); 7-9. Other blue prints of seed scales (ZOC 81, ZOC 125, ZOC 10); Zochenpass, Lavant Luggauer Törl, Hochstadel, Seekofel, Lienz-Dolomites; All Coll. Wachtler, Dolomythos-Museum

mm broad on the base (ZOC 117), tapering to a pungent apex. Single leaves lanceolate leathery and coriaceous, with entire margin. Surface smooth.

Pollen cones: Standing solitary on the branchlets, densely surrounded by the microsporophylls (ZOC 45).

Ovuliferous cones: Cones ovoid (SEE 61) till elongated (LAV 99 holotype), 5-7 cm long, about 4-5 cm broad.

Seed scales: From 10 till 12 mm long, at the base 8 mm wide, gradually narrowing to the apex (LAV 91, paratype, ZOC 24, SEE 51, ZOC 42). Scale generating a sunken elongated seed covered by a short sterile bract.

Diagnosis, remarks and ecology

Araucarites conifers are frequent in the Carnian Raibl beds of the Eastern Alps, especially in the Lienz Dolomites, whereas only a few came from the Rio del Lago Formation near Dognà in the Julian Alps. Because the first described Raibl beds near Raibl (Cave del Predil) evidence a different flora with cycads, conifers, ferns, it can be suggested that the widespread Raibl layers in the Lienz Dolomites pertain to a younger development.

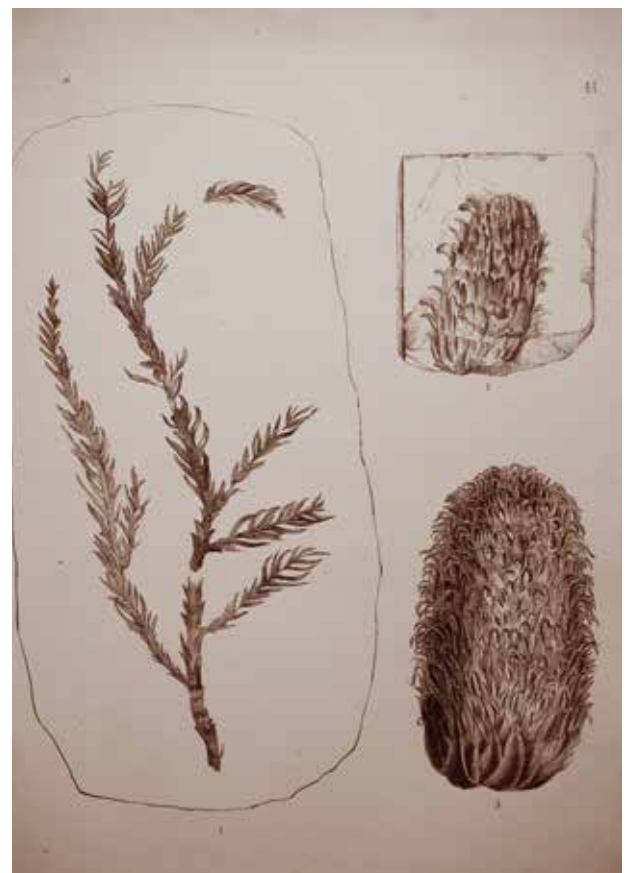
In the past mostly all Araucarian like twigs were classified as belonging to the Voltziaceae but this is misleading because as seen especially in the Carnian Formation, we encounter two different - but resembling - branchlets. One here described as *Araucarites spinosa* pertain due to their one-seeded scales effectively to some Araucaria-ancestor, the other to *Voltzia*, because bearing three lobed scales with three small-sized seeds. In the Raibl beds the differences are obvious. *Araucarites spinosa* was equipped by pendulous branchlets with rigid and coriaceous, mostly leathery leaves. *Voltzia carinthica* had also pendulous branchlets, but the foliage was imbricate and lanceolate.

The separation between the Voltziales and the Araucarias occurred just on the Carboniferous-Permian border. From that time, they lived for many million years in a coexistence, because we can find in the same beds in Germany (Niederhausen) (Perner & Wachtler, 2014) and in the Early Permian Alps twigs, cones and seed scales

of both conifers. It seems that in the Jurassic the Araucarias became extinct in the Northern hemisphere and survived only on the Southern globe.

Another mainly coeval *Araucarites* species is recorded from the Upper Triassic Chinle Formation in the Petrified Forest (Southwestern United States). Effectively *Araucarites rudicula*-cones have some resemblances with *Araucarites spinosa* but the seed scales are not segmented but they contract distally to a mucronate tip. No foliage is recorded from there. Indeed *Araucarites rudicula* helps to understand the Upper Triassic morphology of the famous *Araucarioxylon arizonicum* trunks that form the Petrified Forest National Park in Arizona (Axsmith & Ash, 2006.)

Whereas over the whole Permian in the Alps Araucaria ancestors especially *Ortiseia* play a fundamental role in the conifer fossil re-



Araucarites from Goeppert 1850 "Monographie der Fossilen Coniferen", Plate 44. 1. Twig of *Araucarites sternbergii* (*goepperti*) from Bad Häring Tyrol (Oligocene); 2. Strobilus from *Araucarites goepperti*, Bad Häring. 3. Cone of extant *Araucaria imbricata*

cord, they stand in the Triassic behind the widespread *Voltzia*-conifers. Moreover, their blueprint changed considerably. Whereas the branches in the Permian spread nearly horizontally forming two symmetrical rows of branchlets like today's *Araucaria heterophylla*, in the Late Triassic their foliage branches resembled mostly *Araucaria araucana* from South America. Moreover, their seed cones experience a drastic development between the Permo-Triassic border. Whereas the Permian *Ortiseia*-*Araucarias* were characterized by their dwarfish microleaves surrounding completely the seed scale, this feature disappeared beginning from the Early Triassic, because these subtle foliage merged to one completely the scale covering unit.

Today's *Araucaria* seed scales hold one seed that is merged totally with the ovoid to oblong scale and bract. Interestingly the European Triassic *Araucarites* species hold on one side the feature of the Permian with the one lobed scale and on the other a, the scale not overprojecting bract. Today's *Araucaria* cones are globose, Paleozoic and Mesozoic *Araucarites* cones were from bulbous elongated till considerably elongated. From the Early Middle Triassic (Anisian) we encounter in the Dolomites frequently this lobed scales, whereas entire cones can only rarely be found.

Another discussion arose if the frequent found shoots with partially detached scales (ZOC 45, LAV 63, but also ZOC 21, ZOC 45, ZOC 44, ZOC 22) represent decaying cones or branchlets with losing leaves. Sometimes they are accompanied by unquestionable seed scales (ZOC 45, LAV 63). Cautiously they can be allocated as decaying *Araucarites* cones. Otherwise they have to be classified with their tapering mould in the middle of the blade as dried and decaying apical shoots.

From all *Araucaria* ancestors beginning from the Permian over the Triassic *Araucarites spinosa* is by far the most dried up, spinous and leathery representative. With the other conifers (*Voltzia carinthica*, *Pusteria maribelae*) and clubmosses (*Selaginellites perneri*, *Sigillcampeia blauti*) they are another indication of the live hostile, nearby deadly circumstances that prevailed in the Upper Triassic (especially Early Julian stage) of Europe.

Upper Triassic larches

The evolution of the important conifer family *Larix*, or the larches, was until now shrouded in mystery. Through fortunate circumstances in Upper Triassic layers (Carnian) of the Lienz-Dolomites (Eastern Alps), the first unquestionable ancestors could be recovered. *Wachtlerolarix weissii* can be classified as a transition form on the base of the Laricoideae. A more primordial species *Wachtlerolarix anisica* from the Anisian of the Prager Dolomites (Pelsonian) can otherwise be regarded as Coniferophyta, lying probably at the crown base of the larch-progenitors. *Wachtlerolarix weissii* holds all features of today's larches like small-sized seed cones, needles clustered on short shoots, and small male strobili borne on the apex of short shoots. It can be established that the origin of the larches' typical false whorls lie in a reduction and compression of the needles of a twig to a bundle. In contrast to the evolution of the genus *Pinus* (*Fèrovalentinia*) with its 2–3–5 regularly assembled needles – occurring already in the Early Permian – the larch family has therefore a different evolutionary history manifested also by its irregularly bundled leaves.

Wachtlerolarix weissii PERNER 2016

Type horizon and age

Lienz-Dolomites, Late Triassic, Carnian (235–228 Mya)

Holotype

SEE 04 (Coll. Wachtler, Dolomythos Museum, Innichen, Südtirol); **Paratype:** SEE 07 (Female cone), SEE 40 (Male cone) (Coll. Wachtler, Dolomythos Museum, Innichen, Südtirol)

Description

Branchlets: Slender, bark smooth, sometimes with ridges and grooves. Foliage of two types: long shoots with well-separated leaves and short shoots on condensed buds bearing a tuft of needles. Leaves of the main branch irregularly long, from 1 to 4 cm, short shoots in tufts inserted

in buds, up to 0.5 cm wide, 2 cm long holding this from the base until the tapered to rounded apex, keeled in the middle.

Pollen cones: Dwarfish usually 0.5 cm up to a maximum of 1 cm length, solitary or in groups (pairs). Two pollen sacs hanging on the lower side.

Seed cones: Rounded to ovoid, small-sized – usually 1 cm long, 0.5–1 cm wide, composed of a few scales, no additional bracts

visible. Seeds two on each scale, short-winged. Seed cones sitting on the main branchlets, connected with a small bud.

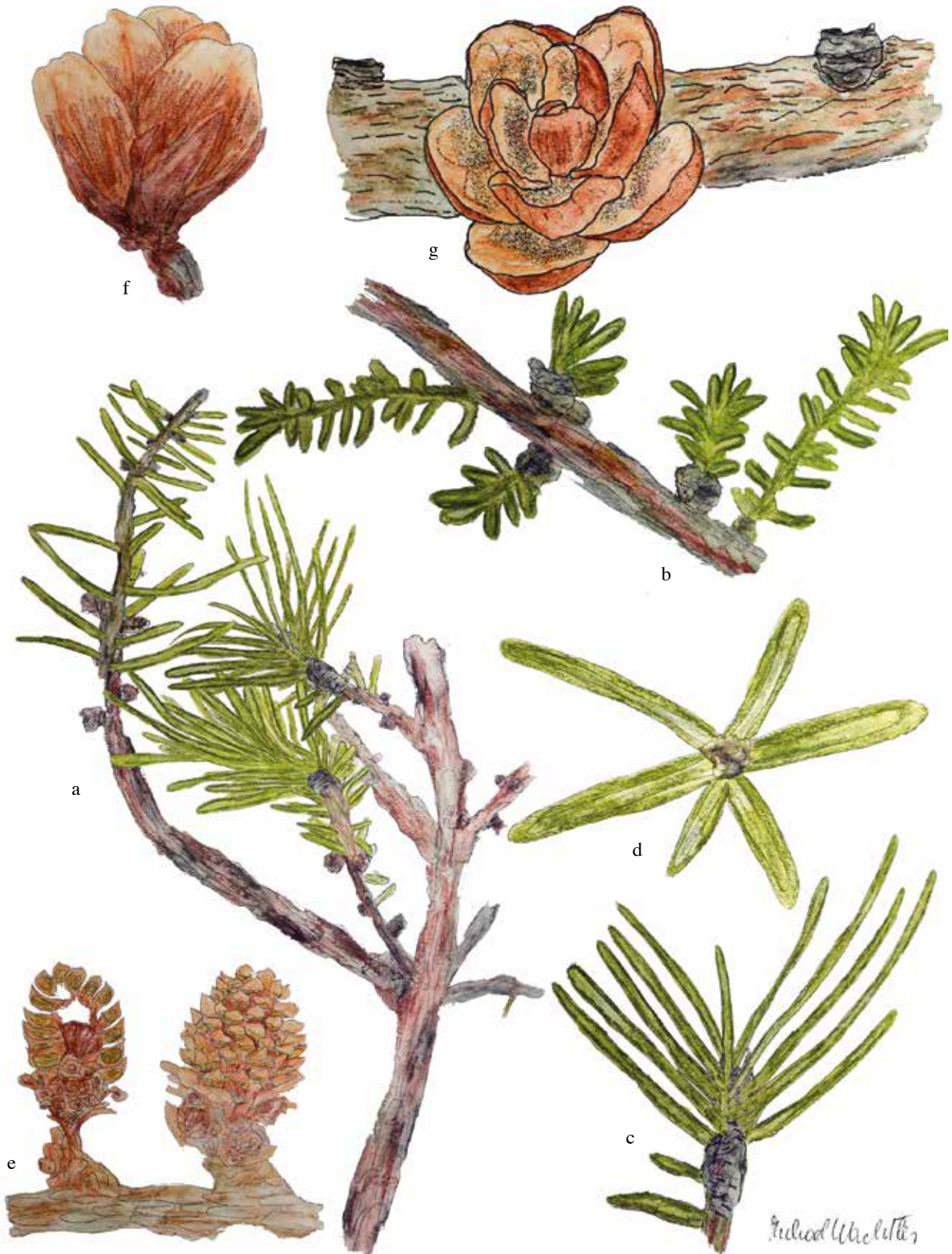
Diagnosis, remarks and ecology

Probably knowing nothing about the recent discovery of the ancestors of the *Pinus* family (Wachtler, 2015, Perner, 2015), a presumption could arise that today's genera *Pinus* and *Larix* have the same origin.



The larches today

1. *Larix laricina*. Tuft of needles seen from above. 2. *Larix decidua*. Lateral view of the needle-bundles. 3. Pollen cone. 4. Short shoots. 5. Juvenile cone with bracts. 6-7. *Larix gmelinii*. Female cone, lateral view and upper side. 8. *Larix decidua*. Isolated seed scale.



***Wachtlerolarix weissii*. Reconstructions (Late Triassic, Carnian)**

a. Part of a branchlet with short and long shoots (SEE 09); b. Detail of the short shoots ((SEE 04, holotype); c. Lateral view of a long shoot (SEE 10); d. Overview (SEE 57); e. Pollen cones the left broken in the middle, the other from outside (SEE 40); f-g. Seed cones (SEE 07, SEE 26).



***Wachtlerolarix weissii*. Branchlets and needles (Late Triassic, Carnian)**

1-2. Branchlet bearing partially normal-sized and short shoots. Detail of a short shoot (SEE 04, designed holotype); 3. Needles bundled in a tuft (SEE 56); 4. Apical shoot with long needles (SEE 08); 5. Branchlet with long and apical short shoots bearing a tuft of needles (SEE 49); 6. Lateral and above view of a whorls of leaves. Note the keeled needles (SEE 57); 7. Short shoot (SEE 10); All Coll. Wachtler, Seekofel, Lienz-Dolomites)



***Wachtlerolarix weissii*. Female cones (Late Triassic, Carnian)**

1. Cone on a twig (SEE 26) 2. Cone with needles; 3. Open cone evidencing the single seed scales (SEE 07 Paratype); 3. Seedling with sprouting needles some minute root (SEE 36); 4. Female cone seating on a branchlet (SEE 06); 5. Exemplary preserved male cones with one broken in the middle evidencing the microsporophylls and one entire cone (SEE 40, Paratype); 6. Two pollen cones (SEE 47); All Coll. Wachtler, Seekofel, Lienz-Dolomites

However, observing in detail the fossil record it is clear that both originate not only in totally different times (*Férovalentinia-Pinus* in Early Permian, *Wachtlerolarix-Larix* in the Triassic), but the development is based on different prerequisites (Wachtler, 2016). The first, *Férovalentinia*, can still be followed back to the dichotomy of Devonian ancestors, revealing in that sense a geometrically concept from (1)-2-3-5 leaves for each bundle. The second have their origin in a reduction and compression

from a shoot to a bundled short shoot, as is typical for today's larches. For this reason, the amount of leaves for each tuft varies considerably.

It seems that in *Wachtlerolarix weissii* the needles are fused in a slightly smaller number as in extant larches. In Early Triassic *Wachtlerolarix anisica*, the branchlets are still reasonably developed; only with difficulty can parental affinities with the larches be observed. In Late Triassic *Wachtlerolarix weissii*, all components



Cypresses of the world

1. Twig of *Cupressus macrocarpa*; 2. Twig of *Cupressus cashmeriana*; 3. Male cone of *Cupressus sempervirens*; 4. Twig and female cone of *Cupressus arizonica*; 5. Female cone of *Cupressus sempervirens*; 6. Open immature cone of *Cupressus sempervirens*; 7. Mature cones of *Cupressus macrocarpa*.

indicate in direction of the Laricoideae. Additionally, *Wachtlerolarix anisica* in the Early–Middle Triassic sediments of the Pragser Dolomites plays only a subordinate role in the plant assemblage dominated by *Voltzia* and *Araucarites* and especially by ferns and cycads.

On the Seekofel in the Lienz-Dolomites of Carnian age, *Wachtlerolarix weissii* is the most common plant together with other two conifers *Araucarites spinosa* and *Voltzia carinthica* – and strangely the lycopod *Sigill-campeia blauti*.

In comparison with today's larches, the female fructifications resemble mostly some small-sized cone bearer like *Larix laricina* (Tamarack larch) with its only 1–2.3 cm (0.4–0.9 inch) long cones holding 12–25 seed scales. Moreover, the male cones—being between 0.5 cm and 0.8 cm in length—have amazing resemblances with extant larches' pollen organs. The bark is just the same, tight and flaky, and short shoots, a feature of all larches, are present. The most unambiguous difference we have is in the needles, being in *Wachtlerolarix weissii* more leave-like, rounded on the apex in contrast to the tapered needles of today's larches. The leaves/needles are produced sometimes, but not always, in dense clusters on woody spur shoots. In addition, in the Triassic larch progenitors the needles were keeled abaxially and rounded adaxially. Considerations can be made about the relationship of the palaeo-larches.

Today in the artificial group of the Pinaceae we include conifers like *Abies*, *Pinus*, *Picea*, *Larix* or *Tsuga*, being distant in their evolving process. It is totally different what we can deduce from the fossil record being separated from each other just in the Permian period. Probably with coeval *Pusteria maribelae*, pertaining to the Cupressaceae, a relationship is possible.

How far *Wachtlerolarix* is more related to *Larix* or *Pseudolarix*, is not so easy to establish. The blueprint of the seed cone resembles more *Larix*, while the aggregation of the pollen cones have some similarities with *Pseudolarix*. It seems that, over time, a reduction from normal shoots to short shoots must have occurred independently several times as seen in extant *Cedrus*, *Larix*, *Pseudolarix*, *Cathaya* or *Sciadopitys*.

Upper Triassic Cypresses

Today the cypresses are distributed throughout warm-temperate and subtropical regions from North America, reaching till Honduras. They grow around the Mediterranean from North Africa, over Middle East and South Europe and reach till the Himalaya and China. Usually they have a shrub like character, but they grow also to tall trees. The leaves are spreading usually small and scale-like, and appressed to the branch on older branchlets. The pollen cones are small, reaching only 2 till 3 mm, the seed cones grow solitary on short branchlets. The seed scales are peltate, quadrangulate, rhombic or polygonal in outline, often with well developed umbos (Farjon, 2005).

Pusteria maribelae WACHTLER 2016

Etymology

After the Pustertal, where the fossil site is located.

Holotype

LAV 40; branchlet with attached cone (Coll. Wachtler, Dolomythos Museum, Innichen, Südtirol)

Description

Branchlet and leaves: Shrublike with rugged or shrivelled bark. Twigs forking irregularly covered with densely appressed needles. Foliage needle-like, tiny, hard, acute, easily decaying, probably due to their dried-up character.

Pollen cones: Not known.

Seed cones: Ovoid or globose, till 2 cm long with 8–10 seed scales. Held by a till 1 cm long short branchlet covered with pointed needles. Scales densely fused together, peltate till polygonal in outline, smooth on the outside, but no umbo visible. Seeds about 1 mm, oval, small flattened.

Diagnosis, remarks and ecology

In the Carnian we encounter with *Pusteria maribelae* just fully evolved cypresses. They are frequent in the Raibl Formation

of the Lienz Dolomites and manifest just all the features of the extant *Cupressus*-genus. Abundant *Pusteria* conifers are found everywhere in the Carnian Lienz Dolomites. They grow there with the conifers *Araucarites spinosa* and *Voltzia carinthica*, and in the middle of *Selaginellites perneri* carpets or the clubmoss *Sigillcampeia blauti*. Seldom they can be encountered together with the larch ancestor *Wachtlerolarix*.

The origin of this cypress family must lie at least in the Early Triassic, because some conifer twigs have striking resemblances with *Pusteria maribelae*, but they were in that time seldom.

Due to their prickly and hard needles, their rugged bark a desertic climate is proposed. Although being found with marine shells, what let suppose a marine nearshore

environment all features suggest that there were no abundant rainfalls all over the year. This is also based on the fact that *Pusteria* hold extremely dried branchlets with only a few needles. In that they resemble some desertic cypresses from Arizona or New Mexico.

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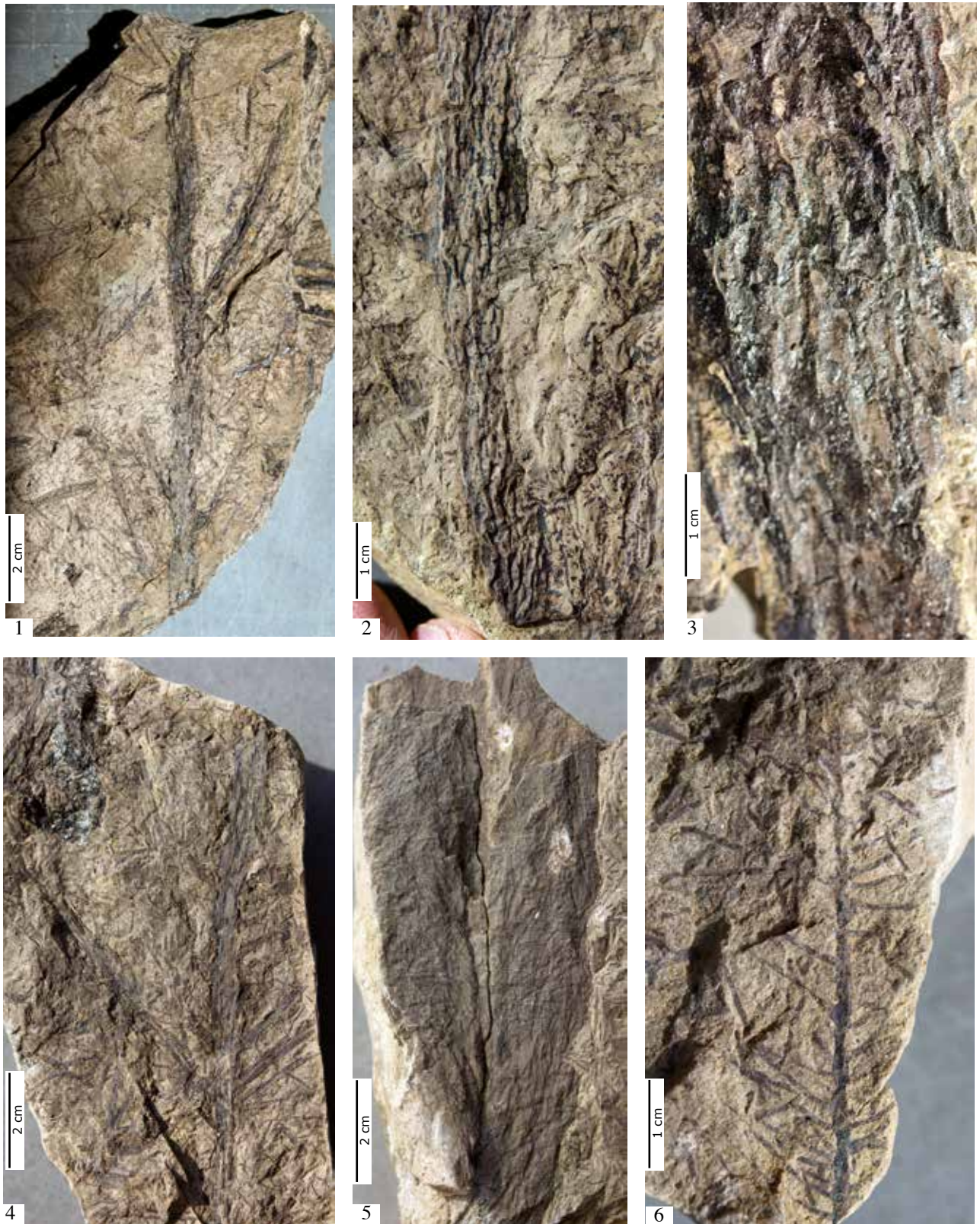
***Pusteria maribelae* Cypress-Conifer. Cones (Late Triassic, Carnian)**

1. Branchlet with to female cones (LAV 111); 2. Detail of the ovoid seed cone with the polygonal seed scales (LAV 111); Coll. Wachtler, Lavanter Alm, Lienz-Dolomites)



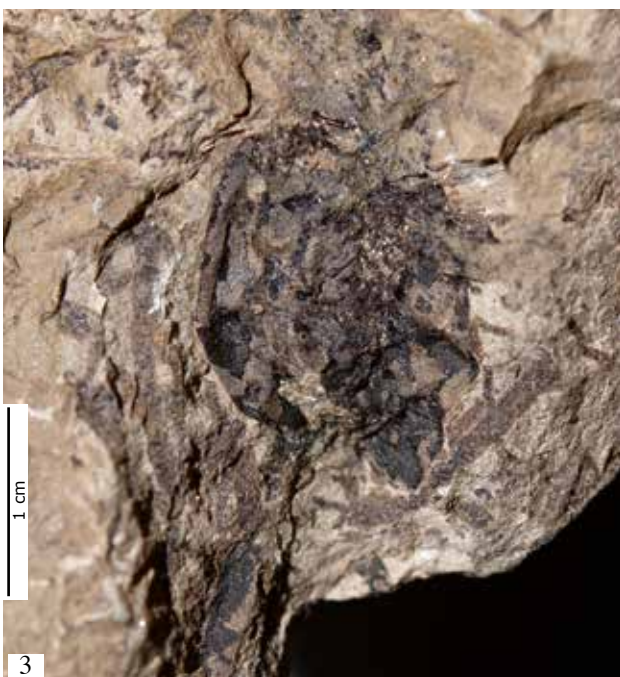
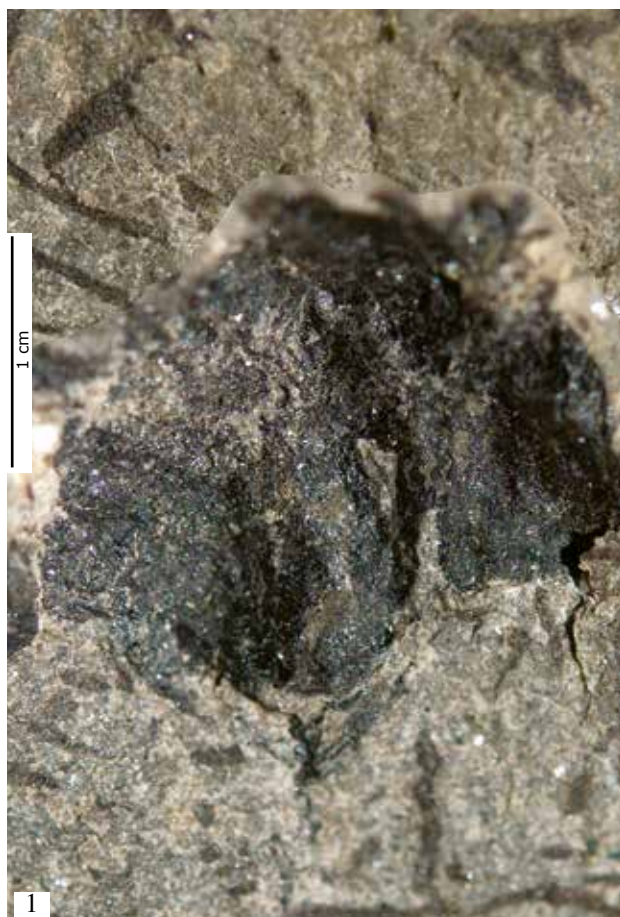
***Pusteria maribelae*. Reconstructions (Late Triassic, Carnian)**

a. Branchlet of the last order (LAV 108); b. Branchlet with two female cones (LAV 111); c. Twig (LAV 40); d. Stem (LAV 100); e. Suggested entire plant



***Pusteria maribelae* Cypress-Conifer. Branchlets and needles (Late Triassic, Carnian)**

1. Branchlet with a female cone on the upper side (LAV 40 holotype); 2. Stemlet with furrowed bark (LAV 100); 3. Stem and detail of the bark (LAV 46); 4. Branchlet (LAV 110); 5. Twig of the last order (LAV 105); 6. Branchlet of the last order (LAV 108); All Coll. Wachtler, Lavanter Alm and Lavant Luggauer Törl, Lienz-Dolomites)



***Pusteria maribelae* Cypress-Conifer. Cones (Late Triassic, Carnian)**

1-2. Seed cones with seeds (LAV 42, LAV 103); 3. Seed cone (LAV 30); 4. Seed cone (Hochstadel 02); 5. Seed cone from the holotype (LAV 40); All Coll. Wachtler, Lavanter Alm, Lavant Luggauer Törl and Hochstadel, Lienz-Dolomites)

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