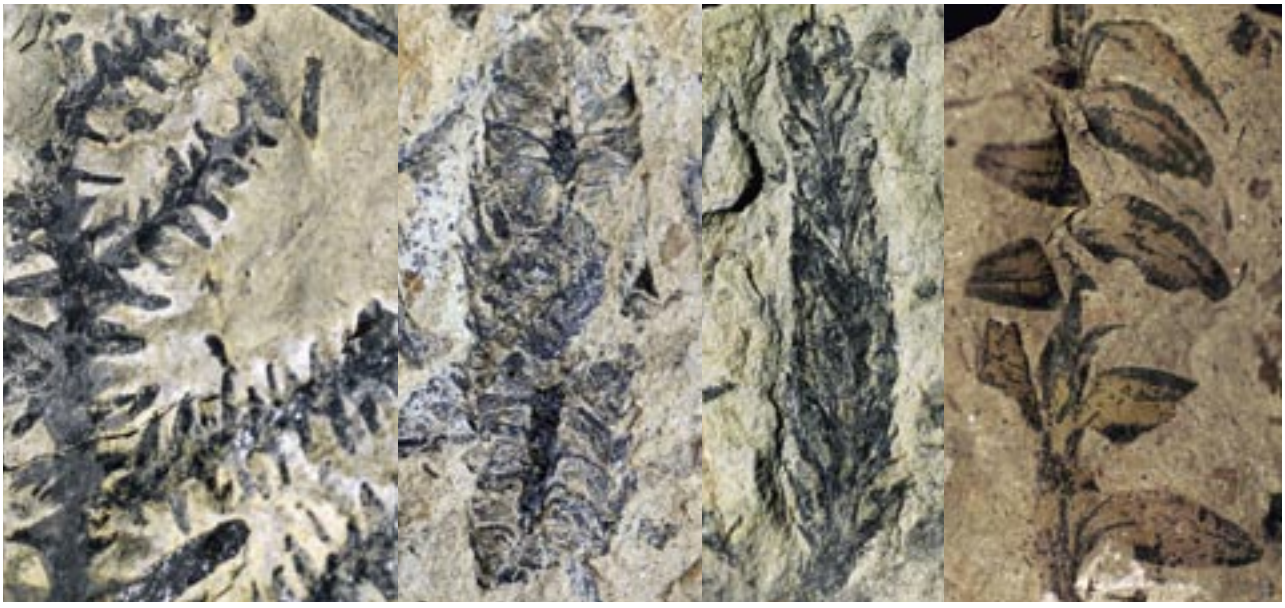
EVOLUTIONARY LINES OF CONIFERS

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

by
MICHAEL WACHTLER



Dolomythos

Published online by the Dolomythos Museum, Innichen, South Tyrol, Italy.

Dolomythos includes results of original research on systematic, evolutionary, morphological and ecological biology, including paleontology. Syntheses and other theoretical papers, based on research, are also welcome. Dolomythos is intended primarily for papers by the staff of the Dolomythos Museum or on research using material in this Museum.

Editorial staff: Edith Campei, Michael Wachtler

Dolomythos is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be sent to:

Museum Dolomythos
Rainerstraße 11
39038 Innichen
Italy
mail: info@dolomythos.com

Print: Technolab Communication srl, TLAB Editrice
Viale Pecori Giraldi, 20/B
36061 Bassano del Grappa (VI) - IT
www.technolab.it
ISBN 978-88-904127

Please cite this articles as:
Wachtler, M., (06/2011): Evolutionary lines of conifers from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, 3-72 Innichen.

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Abstract

The conifers built some of the dominant plant assemblages of the Early-Middle Triassic floras in the Dolomites. New discoveries, especially of their fructifications, suggest that their evolving lines had to be interpreted in a new manner. The key to understanding all extant conifers lies in the reinterpretation of ancient cone structures and, perhaps less importantly, in their foliage-composition.

One substantial group of the newly discovered conifers pertains to the Voltziales, a group with a worldwide distribution. *Voltzia unescoensis* n. sp. is thought to have borne male cones of *Willsiostrobus unescoensis* nov. sp. and female fructifications of the morphogenus *Tirolstrobus unescoensis* nov. gen. n. sp. *Voltzia agordica* comb. nov., known from research by FUCHS, UNGER AND HAUER (1850) and first described as *Araucarites agordica* was largely dominant. The name replaced the mainly coeval description *Araucarites recubariensis* (1862). The morphogenus for the male cones is *Willsiostrobus kostneri* n. sp., and for the seed cones it is *Tirolstrobus agordicus* n. sp. *Aethophyllum stipulare*, just known from the German Buntsandstein, is recorded for the first time in the Alpine Trias. It was a low-growing shrubby conifer. Its more lobed female bract scales are characteristically Voltzialean. Also, pollen organs of *Willsiostrobus acuminatus* belonging to *Aethophyllum* were found in the Anisian strata of the Dolomites. Based on new discoveries, the seed cones of *Voltzia dolomitica*, found in the Ladinian strata and therefore younger in age, were interpreted in detail. This will increase the knowledge about the developmental stages of Mesozoic conifers. The pollen cones of *Willsio–strobus dolomiticus* n. sp., as well as other *Willsiostrobus* cones from Euramerian floras, only bore the characteristics of extant Araucarias. Seed cones belonging to *V. dolomitica* were of the *Tirolstrobus dolomiticus* n. sp. type, with large-sized fructifications generating three-lobed bracts and two seeds holding on to separate minute-scale stalks. The distinguishing marks of a female cone assembly, more lobed connate bracts and separate seed scales, were observed in many Alpine Voltziales up until the Carnian *Voltzia haueri* and the Norian *Voltzia seefeldensis*, and also in most of the Voltziales in the Northern hemisphere. Therefore, they probably have to be dismissed as direct progenitors of extant Araucarias. The origin of all Araucarias is probably to be found in some Early Mesozoic conifers of the southern globe.

Different backgrounds were noted for two other interesting conifers that were recorded for the first time: *Alpia anisica* gen. et sp. nov. and *Schizolepis ungeri* n. sp. Whereas *Alpia anisica* bore needle-like acicular foliage, sometimes with some heterophyllous aspects, *Schizolepis ungeri* was characterized by its juxtaposed branching system, with small-sized apressed juvenile needles and dominant outwards spreading lunate adult foliage on the same shoot. The fertile organs of *Alpia* and *Schizolepis* had some parental affinities. Male cones of *Alpianthus anisicus* gen. et sp. nov. (for *Alpia anisica*) and *Alpianthus ungeri* sp. nov. (for *Schizolepis ungeri*) were composed of a cluster of small-sized pollen cones with pollen sacs on the lower surface of the microsporophylls. These features are reminiscent of the extant Pinaceae or Cupressaceae. The same was observed for the female cones: *Dolomitostrobus anisicus* gen. et sp. nov. (for *A. anisica*) and *Dolomitostrobus bellunensis* sp. nov. (for *S. ungeri*), with their

entire partially fused bract scales embedding just one seed, which have no closer parental structures with coeval Voltziaceae or extant Araucariaceae. If this concept is valid, a split between "Old-World Conifers" (Cupressaceae, Pinaceae) and "New-World Conifers" (Araucariaceae, Podocarpaceae) occurred between the Permian and the Early Triassic. The evolutionary line of Alpia anisica led to Ladinian *Alpia ladinica* nov. comb., with its seed cones of *Dolomitostrobus ladinicus* n. sp., and to other Carnian conifers, such as *Alpia (Voltzia) raiblensis*.
Another conifer that was difficult to interpret is Albertia alpina n. sp., with its sword-shaped leaves. Albertia, also known from the Vosges and the German Buntsandstein, developed interesting giant pollen cones of the *Darneya schaurothi* n. sp. type, whereas the female cones (*Pusterostrobus haidingeri* gen. et sp. nov.) were small-sized and globose.
Astonishingly, the early Mesozoic conifers were characterized by a heterophyllous to juxtaposed foliage, which changed considerably between juvenile and adult leaves. This had nothing to do with heterophyllous shadow or sun-exposed shoots. In this context, the nomenclature for sterile foliage in many other conifer families of that time must be revised.
As noted for other plant clades such as the lycopods, horsetails, cycads and ferns on the borderline of the Carboniferous-Permian, and not, as previously supposed, between the Permian-Triassic, "the mother of all catastrophes" occurred in the plant kingdom. An addiction to an impressive dwarfism captured almost all of the families. In a short geological time scale they lost more than two thirds of their size. The conifers – as the most established successors of the Cordaitales or some other progymnosperm ancestor – appeared to be the biggest losers on first appearance. Half meter-sized leaf tufts were reduced to needles no bigger than a few centimetres. However, with this change they became the global leaders in the tree kingdom, and remained virtually unmodified for more than 250 million years. Other interesting features also occurred: many plants increased their fertile/sterile organ ratio enormously to become virtual sex bombs. The conifers were not an exception. *Albertia*, with its huge pollen cones, and *Schizolepis* with its large quantities of pollen and seed cones, followed the common trend in the plant kingdom.

Online: July 2011
Key words: fossil conifers, Dolomites, Italy, Early-Middle Triassic, Anisian, Ladinian.

History

The first knowledge about plant fossils in the Triassic Dolomitian beds came from the Italian naturalist Antonio Tommaso CATULLO (Belluno 1782 - Padova 1869), who mentioned in his 1827 published main work "Saggio di Zoologia fossile delle provincie austro-venete" some plant localities, like the Val Imperina near Agordo, without describing or illustrating in detail his discoveries.
The Austrian imperial mine manager Wilhelm FUCHS collected in Agordo between 1834-1835 and from 1838 to 1844 paleontological material. In his "Die Venetianer Alpen. Ein Beitrag zur Kenntniss der Hochgebirge" he described the geological settings of these mountains, and consigned several plant slabs – due to his poor knowledge about fossil flora – to the Austrian pioneer of paleobotany Franz UNGER, who in his "Genera et species Plantarum fossilium" (1850), made a first generic diagnosis about *Araucarites agordicus* from the "rothen Sandstein" (red sandstone) of the Imperina-Valley. In the same year, Austrian geologist Franz von HAUER, in "Ueber die vom Herrn Bergrath W. Fuchs in den Venetianer Alpen gesammelten Fossilien" (Wien), classified several other fossils from the FUCHS-collection and reproduced, mainly beneath, from the "Bunter Sandstein, Myacitensandstein", UNGER's previously described *Araucarites agordicus*. On one of the two specimens he pictured a male cone, with its typical appearance, next to the conifer shoot.
Around the same time the Italian paleobotany pioneer Abramo MASSALONGO collected first fossil plants from several localities around the bathing resort Recoaro in the Venetian Alps (Monte Spitz, Rovegliana, Val del Rotolone, Prak,Lichelere (Ricchelere)). Unfortunately, his publication was interrupted due to his death (1824-1860), which occurred at the young age of only 36 years.

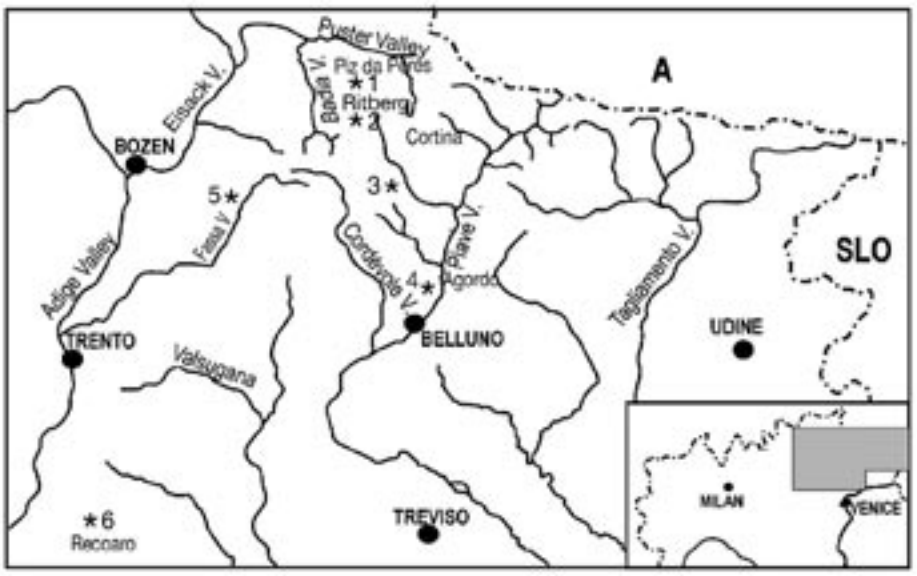


Fig. 1: Map of the Dolomites showing the localities of the different plant fossils:
1) Piz da Peres (Kühwiesenkopf)
2) Ritberg – La Val
3) Zonia – Selva di Cadore
4) Val Imperina – Agordo
5) Val Duron – Fassa
6) Recoaro

In the middle of the nineteenth century, a highpoint in the interest in fossil plants that has not been reached since originated in this part of the Southern Alps. After MASSALONGO, the German palaeontologist Carl Friedrich Freiherr von SCHAUROTH published his paleontological research in Veneto in "Übersicht der geognostischen Verhältnisse der Gegend von Recoaro im Vicentinischen" (Wien, 1855), in which he featured an ill-preserved conifer and named it *Pallissya massalongi*.
MASSALONGO's Recoaro material was handed to his research fellow Barone A. DE ZIGNO, who completed the studies and commemorated him in diverse aspects. Based on Massalongo's former drawings and notices in 1862, DE ZIGNO produced a comprehensive monograph entitled "Sulle Piante Fossili del Trias di Recoaro", in which he adopted all of the original names given by MASSALONGO and honoured him with previously undescribed collection material such as *Araucarites massalongi* and *Taxites massalongi*. Probably knowing nothing about UNGER and HAUER's previously edited works he named an abundant conifer *Araucarites recubariensis* in commemoration of the old Roman name for Recoaro. Because *Araucarites recubariensis* is suggested as being conspecific with *A. agordicus*, and also because the male cones illustrated have the same appearance, *Araucarites agordicus* (established 1850) has priority over *A. recubariensis* (1862) and thus the right denomination could only be *Voltzia agordica* (UNGER, 1850).
The next important researcher in the Southern Alpine Early-Middle Trias floras was German paleontologist A. SCHENK, who in his exhaustive work "Ueber die Pflanzenreste des Muschelkalkes von Recoaro" (1868) described and reproduced different *Voltzia recubariensis* shoots, lamenting the total absence of other plant genera such as ferns. Based on related studies, older authors, especially SCHENK (1868), had no problem recognizing that the strata around Recoaro could be related to the "Buntsandstein" and "Muschelkalk" in Germany and the Vosges, observing similar plants such as the conifers *Aethophyllum, Voltzia heterophylla* and *Albertia*. Unfortunately, after this heyday, the interest in Early Triassic Alpine flora declined for about 150 years.
In 1999, Michael WACHTLER discovered new, rich Anisian fossil plant assemblages, mainly around the Piz da Peres, a distinctive mountain between the localities of Prags, Olang and St. Vigil in the Northern Dolomites. Whereas the Recoaro-plant assemblage, as well as Val Imperina-Agordo, is obviously dominated by conifers, the 150 km distant Piz da Peres flora is excessively abundant in different plant families with no predominant genera, varying from ferns to seed ferns, cycads, lycopods, horsetails and conifers. Following this, M. WACHTLER also discovered plant fossil sites in Anisian layers in other parts of the Dolomites (Ritberg – Wengen, Val Imperina – Agordo, Zonia – Selva di Cadore, Val Duron – Fassa).
Although some of DE ZIGNO's (or MASSALONGO's) material has become dispersed, the excellent drawings from this Italian non-

1850: *Araucarites agordicus* in HAUER F., "Ueber Die Vom Herrn Bergrath W. Fuchs in Den Venetianer Alpen Gesammelten Fossilien", Plate 1, Fig. 16. Original book courtesy of Michael Wachtler.

academic and self-taught palaeontologist, as well as SCHENK's plates and HAUER'S illustrations in particular, leave no doubt that some of the old material from Agordo and Recoaro, as well as the newly discovered material, belong to the same species.

Geology and Paleobiology

The Anisian Early-Middle Triassic plant layers in the Dolomites begin in the late Bithynian (*Gracilis* formation – lower layers on Kühwiesenkopf), proceed to the so-called Dont-Formation, of Pelsonian age (Kühwiesenkopf upper layers, Piz da Peres, Ritberg-La Val, Agordo-Val Imperina, Recoaro), where the most abundant plant sediments are deposited, continue in the Illyrian Richthofen conglomerate (Piz da Peres-Furcia rhyncosaur track beds, Val Duron rhyncosaur track beds) and reach sometimes the Buchenstein-strata (Fassanian to Langobardian) on Piz da Peres-Furcia.

After this a change in the vegetation is obvious: we observed traditional Dolomitian-Ladinian plant assemblages such as *Bjuvia dolomitica, Sphenozamites wengensis, Voltzia dolomitica, Alpia (Voltzia) ladinica, Pelourdea vogesiaca* and *Equisetites arenacea* (WACHTLER & VAN KONIJNENBURG-VAN CITTERT, 2000; KUSTATSCHER et. al., 2004). Excluding the conifers *Pelourdea vogesiaca* and *Elatocladus*, which were only encountered in Alpine Ladinian strata, we had to classify these taxa as evolving stages of Anisian vegetation.

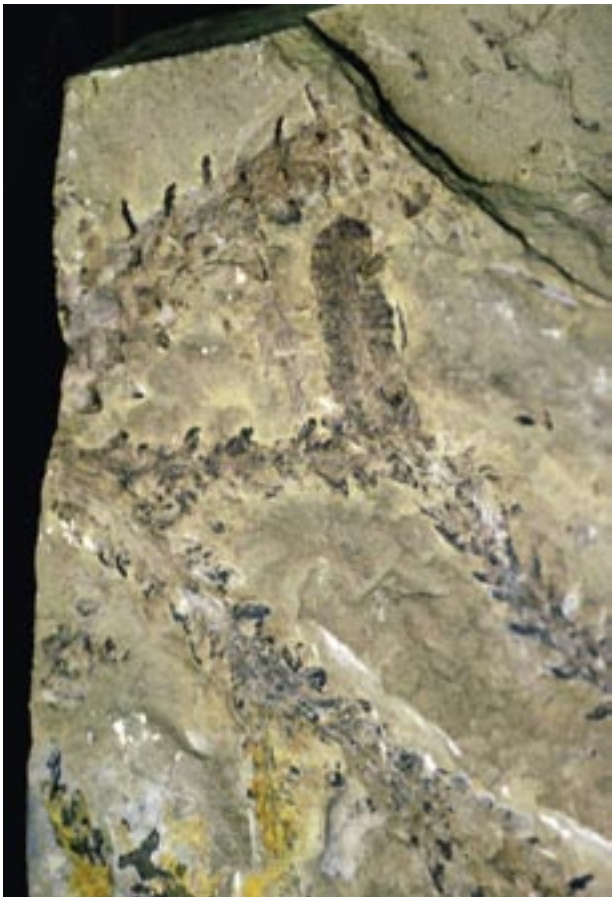
With the exception of the lower segments of the Kühwiesenkopf, characterized by their slightly different flora (lacking *Anomopteris mougeotii, Albertia alpina, Voltzia agordica* and Schizolepis ungeri), all of the other strata (Piz da Peres, Kühwiesenkopf upper layers, Ritberg-La Val, Agordo – Val Imperina, Recoaro) hold with *Voltzia agordica* mainly the same guide-fossil. If the plant assemblages constitute a time marker than the Dont Formation of Piz da Peres, the Voltago Conglomerate and the *Voltzia* beds of Recoaro (DE ZANCHE et al., 1993, GIANOLLA et al., 1998) pertain to the Pelsonian. The upper *Rhyncosauroides* track layers with their plant assemblages from Piz da Peres (Furcia) and the site of the Val Duron (Fassa) must then be inserted in the Early-Middle Illyrian. All of these former marine beds were characterized by shales, siltstones and sandstones, intercalated by brownish dolomites, grey marly limestones and marls (BARBIERI et al., 1980), and hold from a few centimetres to one metre and more-thick fossil-plant lenses. Only in Agordo-Val Imperina, with marine and beach sediments inserted between older metamorphic rocks, did we find a coeval but different geological origin. As noticed by the older authors (DE ZIGNO, 1862, SCHENK, 1868) several fossil plant sites of the Dolomites were dominated by conifers. This is valid for the localities around Recoaro as well as Agordo – Val Imperina and Ritberg – La Val. Also, some layers on Piz da Peres (west side, Wachtler gorge layer 2, Piz da Peres – Furcia) hold rich conifer beds.

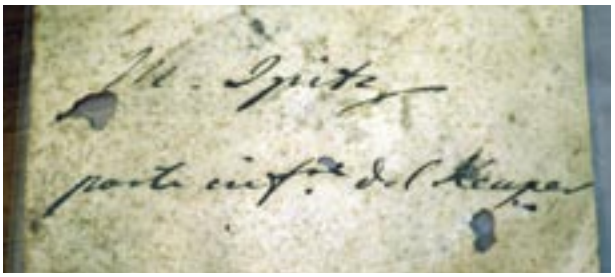
The composition of the rich and diversified floras from Kühwiesenkopf and Piz da Peres, with their predominance of cycads, fern trees, ferns conifers, lycopods and equisetaceae, indicates a warm and humid tropical climate.

Paleoecology and Paleoclimatology

The Val Imperina Schizolepis country

In the Val Imperina, near the small town of Agordo, ancient metamorphic rocks gave origin of the long-lasting mining activities at the "Linea della Valsugana" (an impor-





1862: *Araucarites recubariensis* in DE ZIGNO, A., "Sulle piante fossili del Trias di Recoaro raccolte dal Prof. A. Massalongo", Memorie dell'I. R. Istituto Veneto di Scienze, lettere ed arti, Volume 11. Plate V. Original book courtesy of Michael Wachtler.

Right: Specimen from Massalongo's collection with attached pollen cone and original description by A. De Zigno: "M. Spitz - posti del Keuper" (Monte Spitz – localities of the Keuper), Courtesy of Museo di Geologia e Paleontologia, Padova.

tant fault representing the geological border of the Dolomites). Red and yellow to greyish sandstones, a result of the erosion of an ancient coastline, are intercalated by massive bands of calcareous rocks. An interesting plant site lies just behind the old extraction complex of the Val Imperina. The fossil plant vegetation here mainly consists of conifers; ferns (*Sphenopteris*), cycads (*Bjuvia*) and *Equisetites* could only be observed in some isolated layers. In 1850, Franz Unger described *Araucarites agordicus* – the first fossil plant from the Dolomites – in this valley.
Unfortunately, the plant-fossil layers are densely overgrown by a nearby impenetrable scrubland that, according to old photographs, was not there in the nineteenth century. Following the descriptions of the mine manager Wilhelm FUCHS on one of the few vegetation-free points, in 2011 Michael Wachtler discovered a new exciting place completely filled by only one conifer, in this work described as *Schizolepis ungeri* WACHTLER, 2011, (honouring the father of Austrian paleobotany, F. UNGER).
Exactly 1 m2 of the 20 cm-thick fossil sediments was removed. It contained – sandwiched, but deposited during one storm event – leaves, stems, and male and female organs of only one conifer, *Schizolepis*. The pollen cones largely dominated the seed cones, characteristic of a spring-time-vegetation. From the seldomly seen 100% monophyletic *Schizolepis* vegetation, the life cycle

1868: *Araucarites recubariensis* in SCHENK, A., "Über die Pflanzenreste des Muschelkalks von Recoaro. Geognostische – paläontologische Beiträge", 58-87. Plate 11. Original book courtesy of Michael Wachtler.

of this conifer could be perfectly restored: branches bearing large-sized adult leaves, from 1.5 to 2 cm long, transitional foliage and juvenile leaves on the same branchlets (only 2 mm-5 mm long) were the characteristics of this very interesting tree, with pollen organs and seed cones that have striking resemblances to today's Cupressaceae.

The Piz da Peres ancient coastline world

One of the most exciting places for conifer fossils is the Wachtler gorge plant layer 2 on Piz da Peres (Fig. 2). Here, the plant abundance of the Early-Middle Triassic is clearly revealed in a restricted area. Plant layer 2 provides a unique opportunity to study an intact ancient paleoecosystem, beginning with shell-covered marine biota, across to a still-water area containing *Voltzia agordica* – the most dominant offshore-growing conifer – changing to the miscellaneous plant assemblage of the closer outback. The vertical stratification here tells us a lot about the flooding cycles that occurred in that time. Thus, it is worth describing this amazing Early-Triassic coastline in more detail:

The plant lense 2 A-2D is a total of 87 m long. All the strata lay over a conglomerate layer containing 10 cm-sized, mainly rounded, detritus. From left to right it begins with 15 m-long brackish water sedimentations and marine biota well-adapted to these conditions such as *Neoschizodus laevigatus elongatus* (POSENATO, 2008). This bivalve was found throughout the entire position 2A, sometimes alternating between isolated gastropods (*Naticella costata, Loxonema obsoletum*) and poorly preserved plants, mainly stems or the hardest parts of the trees. Adjacent begins the 11 m-long section 2B that is evidence of a shallow water ecosystem with from the waves totally destroyed marine biota. The plants here are only rarely recognizable.

A monophyletic *Voltzia agordica*-floral assembly (2C) follows after the deposits for 20 m, which suggests that this conifer was especially well adapted to the stormy coastal conditions, and formed virtually the only forestal vegetation. Many male cones and typically dispersed lobed bracts from disintegrated female cones were found. Only some isolated *Ladinopteris kandutschii* fern or *Equisetites mougeotii*-horsetail remains were observed.

Gradually, after a 10 m-long mainly sterile area, the beds change to sediments with an extremely diversified flora. This lasts for about 26 m before the plant layers get more and more filmy until they totally disapear in the sterile calcareous rocks (2D). Well-preserved entire to mainly entire parts of ferns (*Gordonopteris lorigae, Anomopteris mougeotii, Ladinopteris kandutschii, Marantoidea arenacea, Sphenopteris schoenleiniana, Wachtleria nobilis*), seed ferns (*Scytophyllum bergeri, Sagenopteris keilmannii*), cycads (*Ladinia simplex, Pizperesia tannae, Pizperesia raetiae, Bjuvia primitiva, Bjuvia olangensis, Nilssonia braiesensis)*, conifers (V*oltzia agordica, Alpia anisica, Albertia alpina, Aethophyllum stipulare*), equisetales (*Equisetites mougeotii)* and lycopods (*Selaginellites brandneri, Lycopia dezanchei*) were observed. Very occasionally, remains from reptiles (*Rhyncosaurus*) and primitive archosaurs were observed. As observed else-

Early-Middle Triassic fossil plant localities in the Dolomites

Recoaro - Monte Spitz

Agordo - Val Imperina

Fassa - Val Duron

Selva di Cadore - Zonia

Olang - Furcia/Piz da Peres

Marebbe - Piz da Peres

Prags - Kühwiesenkopf

La Val - Ritberg

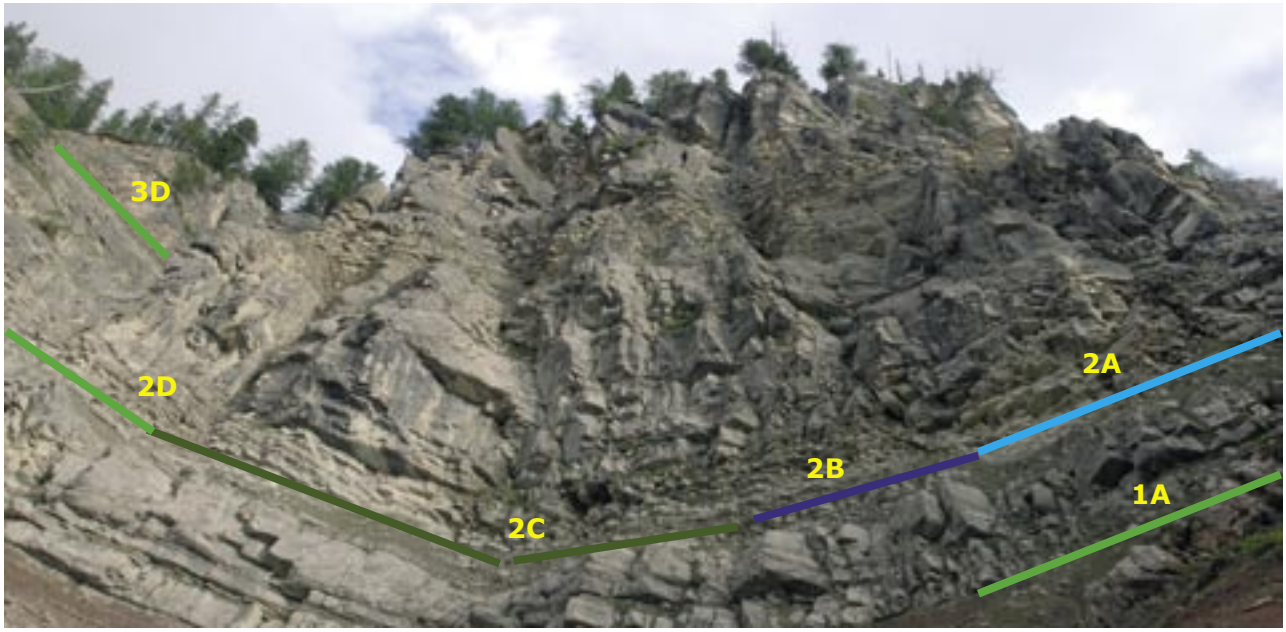


Fig. 2: Piz da Peres, Wachtler gorge: The ancient coastline world
2A) Shell layer: brackish water shells (*Neoschizodus laevigatus elongates, Naticella costata, Loxonema obsoletum*)
2B) Plant chaff layer: fragmented and poorly preserved plants
2C) *Voltzia agordica* layer: conifer monoculture, only some isolated *Ladinopteris*-ferns
2D) Diverse plant layer: rich in different genera (equisetales, ferns, seed ferns, lycopods, conifers, cycads)

Reconstruction of the ancient coastline from Piz da Peres:
2D) Diverseness plant layer: *Alpia anisica (1), Albertia alpina* (2), (conifers); *Lycopia dezanchei (3), Selaginellites leonardii* (4) (lycopods); *Gordonopteris lorigae (5), Neuropteridium elegans (6), Neuropteridium voltzii (7), Anomopteris mougeotii (8), Wachtleria nobilis (9), Marantoidea arenacea (10), Sphenopteris schoenleiniana* (12) (ferns); *Scytophyllum bergeri (12), Sagenopteris keilmannii* (13), (seed ferns); *Pizperesia tannae (14), Ladinia simplex (15), Bjuvia primitiva (16), Bjuvia olangensis (17), Nilssonia braiensis* (18), (cycads)

2C) *Voltzia agordica* layer: *Voltzia agordica* (19) conifer monoculture, *Ladinopteris kandutschii (20), Equisetites mougeotii* (21), Archosaur remains (22), *Rhyncosaurus* skeletons (23)

2A, B) Shell layer, plant chaff layer: Brackish water shells (*Neoschizodus laevigatus elongates (24), Naticella costata (25), Loxonema obsoletum* (26), Fragmented and poorly preserved plants

1) *Neoschizodus laevigatus elongates*, 2) *Loxonema obsoletum*, 3) *Naticella costata*

4) conglomerate-layer from 2D, 5) root horizon from 2C

where (Piz da Peres – Furcia, Ritberg – La Val), the conifer *Voltzia agordica* effectively built the immediate coastal vegetation in this Anisian strata, with the fern *Ladinopteris* in the brushwood.
The thickness of the layer varies from 2.60 m (2A) to only a few centimetres (2D). The base is formed by a massive conglomerate bank. The conservation of the conifers and all of the other plants is particularly good. In such a quiet water area, the plants were immediately buried by fine sands. Because of this, well-maintained plants could be only observed in areas with displacement not far from the original growing zone.

The Kühwiesenkopf conifer woods

There are two predominant plant layers on Kühwiesenkopf: one is in the lower part of the late Bithynian and the other is in the upper part of the so-called Dont Formation of the Pelsonian-Illyrian age. They were characterized by their slightly different plant assemblages.
In the lower sediments, the dominant *Voltzia agordica* is replaced by a slightly different progenitor: *Voltzia unescoensis.* This is almost equally present in the conifer vegetation with another characteristic conifer *Alpia anisica*; the shrubby conifer *Aethophyllum stipulare* is present, but only occasionally. The conifer *Albertia alpina* was not observed in the lower strata; perhaps it arrived later from the German basin, as well as the fern *Anomopteris mougeotii*, which was lacking until now in the lower strata.

The Recoaro, La Val and Selva di Cadore sites

Further old and known sites are found in the area of Recoaro. As described in the work by Massalongos and De Zignos (1862), the plant fossil sites lay on the base of Monte Spitz, Rovegliana (near the locality of Mondonuovo) and Rotolone. The flora here is dominated by conifers with *Voltzia agordica* (ex *recubariensis*), *Albertia* and *Aethophyllum stipulare*, and only some isolated horsetails and ferns.
The site of Zonia (Selva di Cadore) has a conspicuously diverse flora with conifers, ferns, seed ferns, cycads, equisetales and lycopodiales, whereas Ritberg-La Val could be also defined as monophyletic conifer country.

Morphology and Phylogeny of the Conifers

It is thought that the earliest remains attributed to conifers (*Swillingtonia denticulata*) occur in the Westphalian B strata of England, which are about 310 million years old (SCOTT, 1974, SCOTT & CHALONER, 1983). The fusinized leafy twigs resemble just those attributed to *Walchia* in younger strata. Anatomically preserved remains of conifer stems are known from Westphalian C strata of England, dating back 308 million years (GALTIER et al., 1992). They show well-preserved piths and primary and secondary xylems, that clearly distinguish them from cordaitalean remains. There are no doubts that they represent conifers. In the Late Pennsylvanian flora of Hamilton, Kansas, at least three species of *Walchia* (MAPES & ROTHWELL, 1988) and one *Emporia*-species were found (MAPES & ROTHWELL, 1984).

Although most early conifers look from their outer appearances like the extant conifer, their cones were quite different. Rudolf FLORIN's (1938-1945) detailed studies proposed that all Paleozoic female conifer cones can be distinguished by their spirally arranged dwarf-shoot complexes. He established the doctrine that the progenitors of the conifers had to be looked for in the Cordaitales, a group of gymnosperms that can be traced from the Lower Carboniferous into the Permian (TAYLOR T. N. & TAYLOR E. 1993).

Directly evolving lines were established, mainly based on the compound dwarf-shoot cone assemblages, from Carboniferous Cordaitales to the Permian conifers *Walchia, Ernestiodendron, Otovicia* and *Ortiseia (Culmitzschia*) to the Mesozoic Voltziales, which have a closely related seed cone composition. From this originated the hypothesis that all living conifers evolved from this line by a gradual fusion of their dwarf shoots into one single non-lobed bract-scale.

However, this theory cannot explain the phylogeny of another group of important Paleozoic conifers, the Ullmaniaceae, especially known from the Middle-Upper Permian Euramerian flora. Their fertile organs substantially differ from those of other Permian conifers. The ovulate cones of *Ullmannia* bore spirally arranged, entire ovuliferous scales and only held one substantial single seed on their adaxial surface (TAYLOR T. N. & TAYLOR E. 1993). The differences in the male cone types in modern conifers were also completely disregarded in FLORIN's concept. Araucarian pollen cones differ greatly from Cupressaceae or Pinaceae, with their catkin-like small-sized male pollen cones. Another alternative theory is that modern families may have directly evolved from different Paleozoic ancestors, and that the "mother of all conifers" must have come way before the progymnosperms, such as the Archaeopteridales or Aneurophytales (CLEMENT-WESTERHOF, J., 1988).

Materials and Methods

Up until now (2010), the conifer-fossil record has been characterized by:

Voltzia unescoensis (about 60 pieces)
Male cone: *Willsiostrobus unescoensis* (about 10 pieces)
Female cone: *Tirolstrobus unescoensis* (about 10 pieces)

Voltzia agordica (about 400 pieces)
Male cone: *Willsiostrobus kostneri* (about 40 pieces)
Female cone: *Tirolstrobus agordicus* (whole cones and about 50 single bract scales)

Aethophyllum stipulare (about 10 pieces)
Male cone: *Willsiostrobus acuminatus* (1 piece)
Female cone: ?

Albertia alpina (about 100 pieces)
Male cone: *Darneya alpina* (about 5 pieces)
Female cone: *Pusterostrobus haidingeri* (about 5 pieces)

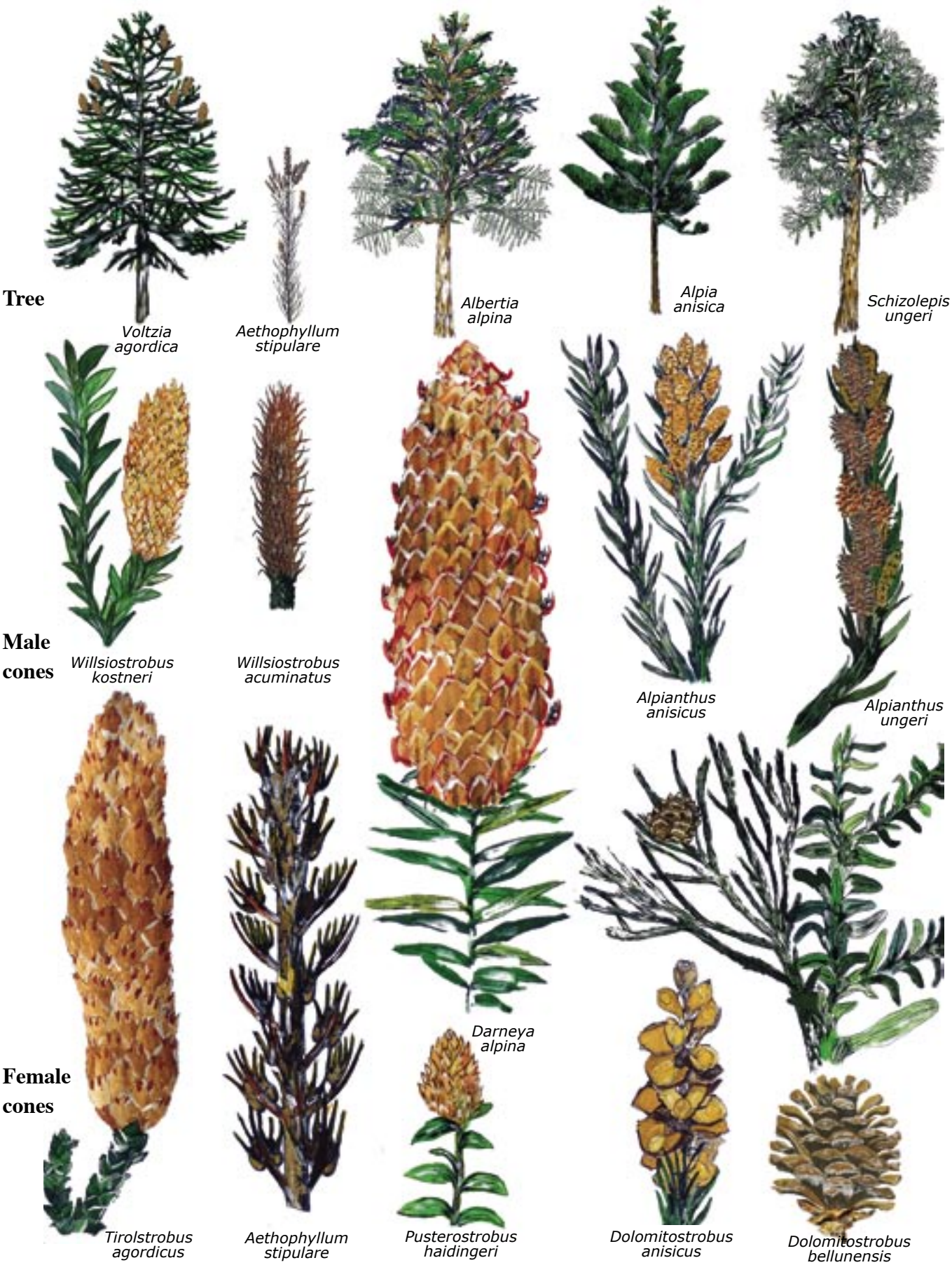
Alpia anisica (about 200 pieces)
Male cone: *Alpianthus anisicus* (about 5 pieces)
Female cone: *Dolomitostrobus anisicus* (about 10 pieces)

Schizolepis ungeri (about 200 pieces)
Male cones: *Alpianthus ungeri* (20 pieces)
Female cones: *Dolomitostrobus bellunensis* (about 5 pieces)

Repository

Most of the macrofossil plant collection is stored at the Natural History Museum Südtirol, Bozen. The remainder of the collection is in the Museum Dolomythos Innichen.

Specimens were photographed under natural light using a Nikon D200 from Nikon Corporation, Tokio, lenses: AF MICRO NIKKOR 60 mm 1:2.8 D and AF-S NIKKOR 17-35 mm 1:2.8 D for larger pieces. The digital images were processed using Adobe Photoshop CS version 8.0.



Reconstruction of the Early-Middle Mesozoic coniferales from the Dolomites: *Voltzia agordica, Aethophyllum stipulare* (after Grauvogel-Stamm), *Albertia alpina, Alpia anisica, Schizolepis ungeri.* Male and female cones, half their natural size.

The Alpine Voltziales

Division CONIFEROPHYTA
Order VOLTZIALES
Family VOLTZIACEAE
Genus Voltzia Brongniart, 1828

Voltzia unescoensis sp. nov. WACHTLER, 2011

Holotype

KÜH 1422

Paratypes

KÜH 58, KÜH 263

Material

KÜH 271, KÜH 266, KÜH 259

Etymology

After the United Nations Educational, Scientific and Cultural Organization, which included the Dolomites in the UNESCO World Nature heritage in order to conserve their beauty.

Type localities

Kühwiesenkopf

Type horizon and age

Lower Triassic, Anisian, Bythinian-Pelsonian

Diagnosis

Upright-growing conifer with sweeping branches. Ultimate shoots absent or very short near the apex of the penultimate branches. Leaves partly overlapped each other, slighty heterophyllous, from triangular to elongated, or falcate, with a more or less acute apex. Male cones single at the tips of branchlets, elongated – ellipsoid. Microsporophylls ended in a typical scale head. Each peltum holds several pollen sacs on two rows of the lower surface, which are as long as the sporophyll pedicle and lay in the opposite direction to the main cone axis. Seed cones with more-lobed bracts, connate at the base. Seeds attached on subtle scale stalks.

Description

Vegetative branches: The holotype of *Voltzia unescoensis* (KÜH 1422) consists of a penultimate leafy shoot, 30 cm long, 20 cm wide, with six slightly curved knurls. Branches aslender, widely spaced out to the sides and densely clothed with but not hidden by the foliage. They bore tripinnate branchlets only at and near the tips (KÜH 263).

Vegetative leaves: The foliage is often heterophyllous, also on the same branches. There are leaves evidencing a triangular aspect, with a broad basis and a pointed apex (KÜH 58), and another one that is slightly lunate (KÜH 271). They partly overlapped each other; the leaves were small sized, varying from 3 to 6 mm long and 2 to 3 mm wide.

Pollen cones: Of the *Willsiostrobus unescoensis* type. Male cones 4 to 6 cm long, 2 to 2.5 cm thick, ellipsoid to cylindrical, growing laterally on the tips of the branches. Each microsporophyll is positioned in a dense and imbricate spiral on the cone axis. A triangular peltum holds several pollen sacs on its abaxial face in two rows that hang parallel and free in the direction of the main cone axis.

Seed cones: Of the *Tirolstrobus unescoensis* type. The three-lobed bracts arise from the main cone axis. Two tiny scale stalks originate separately from or near to the main axis and each holds one small-sized seed embedded in the upper surface.

Willsiostrobus unescoensis sp. nov. WACHTLER, 2011

Holotype

KÜH 1193

Paratypes

KÜH 1412, KÜH 785

Material

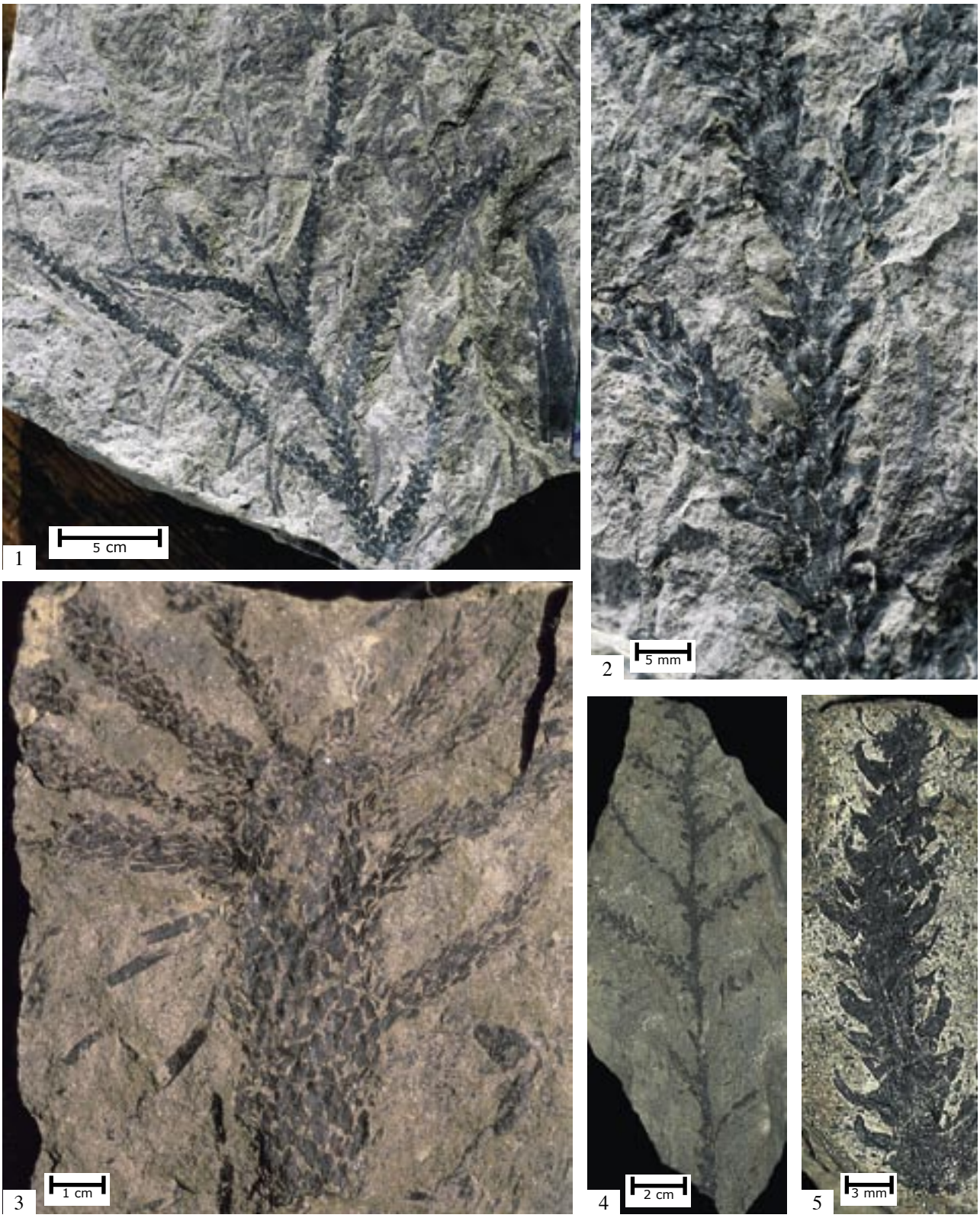
KÜH 776, KÜH 1317, KÜH 872

Type horizon and age

Lower Triassic, Anisian, Bythinian-Pelsonian

Diagnosis

Ovoid to cucumber-shaped pollen cones. Microsporophylls with a distal portion ending



1) KÜH 1422 *Voltzia unescoensis* (holotype). Slender branches with densely and spirally arranged leaves
2) KÜH 1422 *Voltzia unescoensis*. Detail of the shoot and arrangement of the leaves
3) KÜH 58 *Voltzia unescoensis*. Part of a storm-damaged shoot with secondary developed branches
4) KÜH 263 *Voltzia unescoensis*. Slender shoot
5) KÜH 271 *Voltzia unescoensis*. Detail of the foliage

in a flattened and obtuse angled apex. They are strongly curved and overlap the adjacent sporophyll. Pollen sacs arranged on the lower surface of the peltate microsporophyll and recurved to the cone axis.

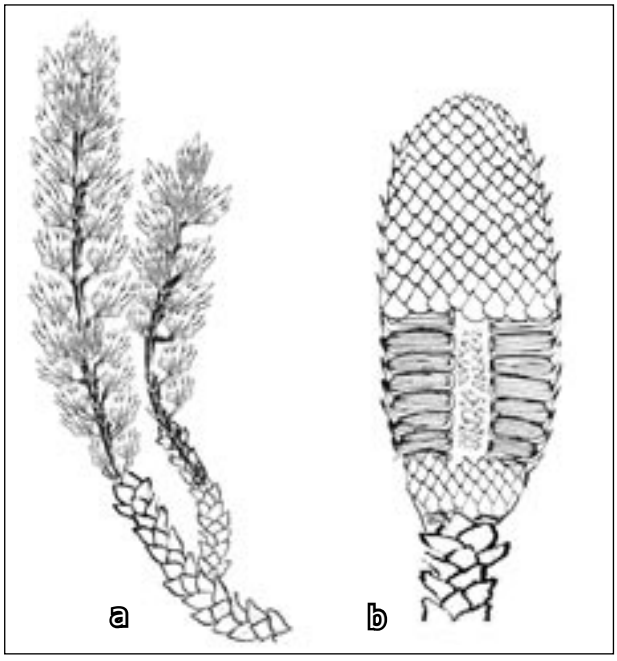
Description

The holotype KÜH 1193 consists of a 5 cm long, 2.6 cm thick, mainly entire male cone with attached peltate protecting bracts. A typical upwards-curved pointed spine sprouts from each peltum. On the lower part of the cone, elongated pollen sacs with dispersing pollen grains are evidenced. The paratypes KÜH 1412 and KÜH 785 show the interior structure of a pollen cone. The microsporophylls, from 7 to 10 mm long, were dispersed in a dense and imbricate spiral on the cone axis. On the abaxial side of the peltate shield the cylindrical pollen sacs hang in parallel, free from the main stalk.

Tirolstrobus gen. nov. WACHTLER, 2011

Generic diagnosis

Female conifer cones, cylindrical to elongated, born on ultimate branches. Bracts more lobed, but connate at the basis with separate seed scales, each holds one small-sized seed on the distal end.



Voltzia unescoensis. a) Suggested reconstruction of a young female cone (KÜH 365) b) *Willsiostrobus unescoensisis*. Male cone of *Voltzia unescoensis* (KÜH 1193)

Etymology

Named after the Alpine country Tirol, were the region in which they were found lies.

Tirolstrobus unescoensis sp.nov. WACHTLER, 2011

Holotype

KÜH 365

Paratype

KÜH 367

Etymology

Name honours the United Nations Educational, Scientific and Cultural Organization

Type horizon and age

Lower Triassic, Anisian, Bythinian-Pelsonian

Diagnosis

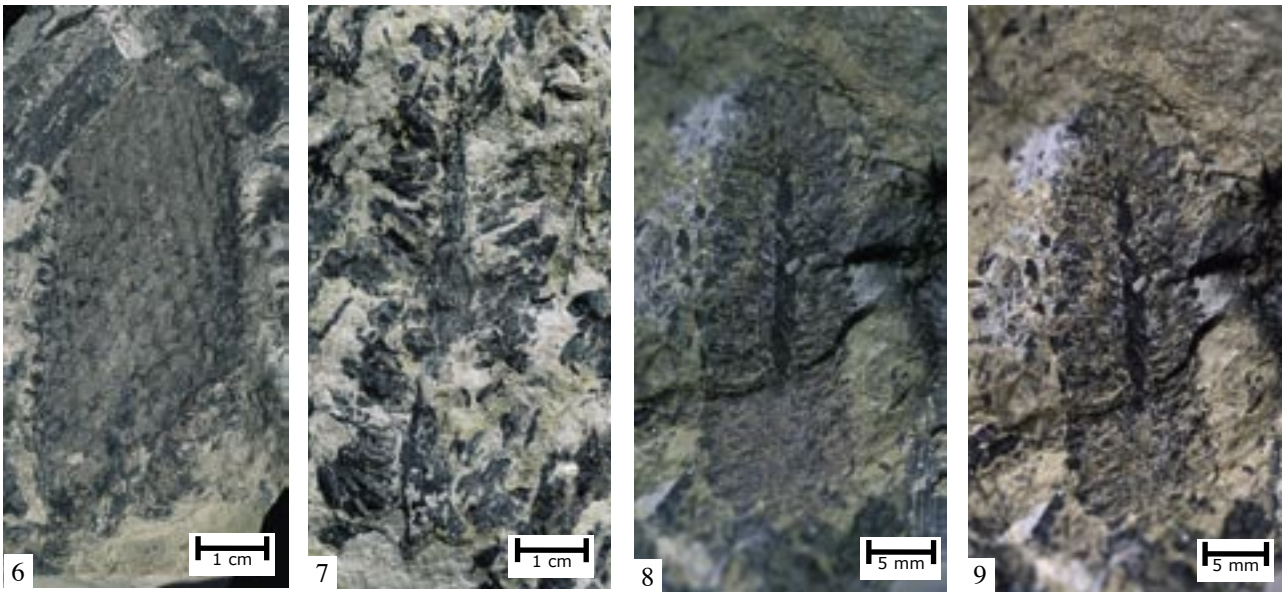
Erect, elongated conifer cones, bearing helically arranged three-lobed close-knitted bracts. Separate two-seed scales, each holds one small-sized rounded seed on the upper surface.

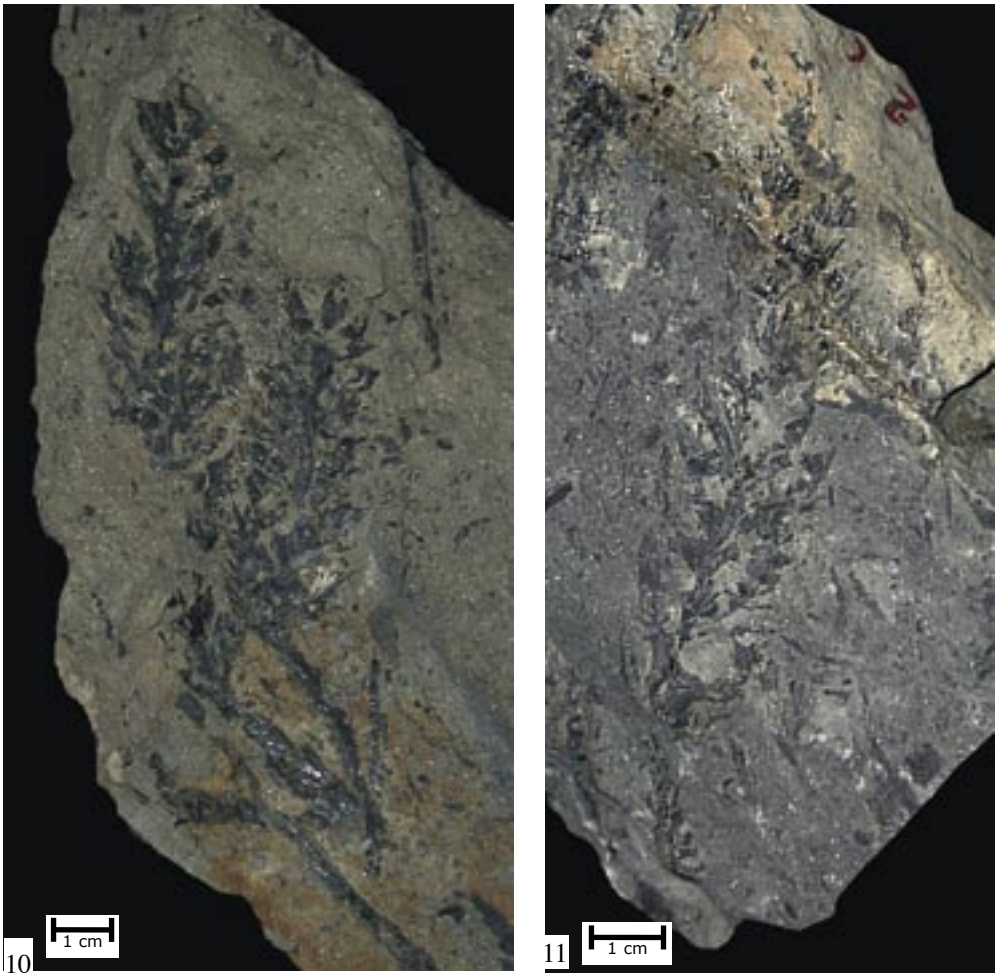
Description

Holotype KÜH 365 has the typical features of young immature Voltzialean seed organs. The cones are not yet ligneous, but just show the more lobed bract-scales. The bigger of the two cones is 9 cm long, 2 cm wide, and the smaller one has a length of 5 cm. Cone KÜH 367 is 8 cm long, 2 cm wide and is also from the same juvenile typus. Two seeds embedded on separate scales pertain to each fertile bract-scale. Usually, the sterile bracts were released at maturity and the seeds were only dispersed after this.

Voltzia agordica UNGER, 1850

1850 *Araucarites agordicus*, UNGER
1850 *Araucarites agordicus*; HAUER, Pl. III, Fig. 16
1859 *Auracarites recubariensis*; MASSALONGO, unpublished
1862 *Auracarites recubariensis*; DE ZIGNO, Pl. V, Figs. 1, 2; Pl. VI, Figs. 1-4, Pl. VII, Figs. 1-3





6) KÜH 1193 *Willsiostrobus unescoensis*. Mostly entire male cone with outer protective scales
7) KÜH 1412 *Willsiostrobus unescoensis*. Male cone
8) KÜH 872 *Willsiostrobus unescoensis*. Male cone
9) KÜH 785 *Willsiostrobus unescoensis*. Male cone
10) KÜH 365 *Tirolstrobus unescoensis*. Two young female cones on a shoot with typical three-lobed bract scales
11) KÜH 367 *Tirolstrobus unescoensis*. Young female cone of the Voltzialean type

1868 *Auracarites recubariensis*; SCHENK, table 8, Fig. 7
2008 *Voltzia recubariensis*; WACHTLER, Pl. 4, Figs. 5, 6

Material

PIZF 45, PIZ 187, PIZ 24, PIZ 19, PIZ 32, PIZF 9

Type localities

Agordo, Recoaro, Piz da Peres, Kühwiesenkopf, Ritberg

Type horizon and age

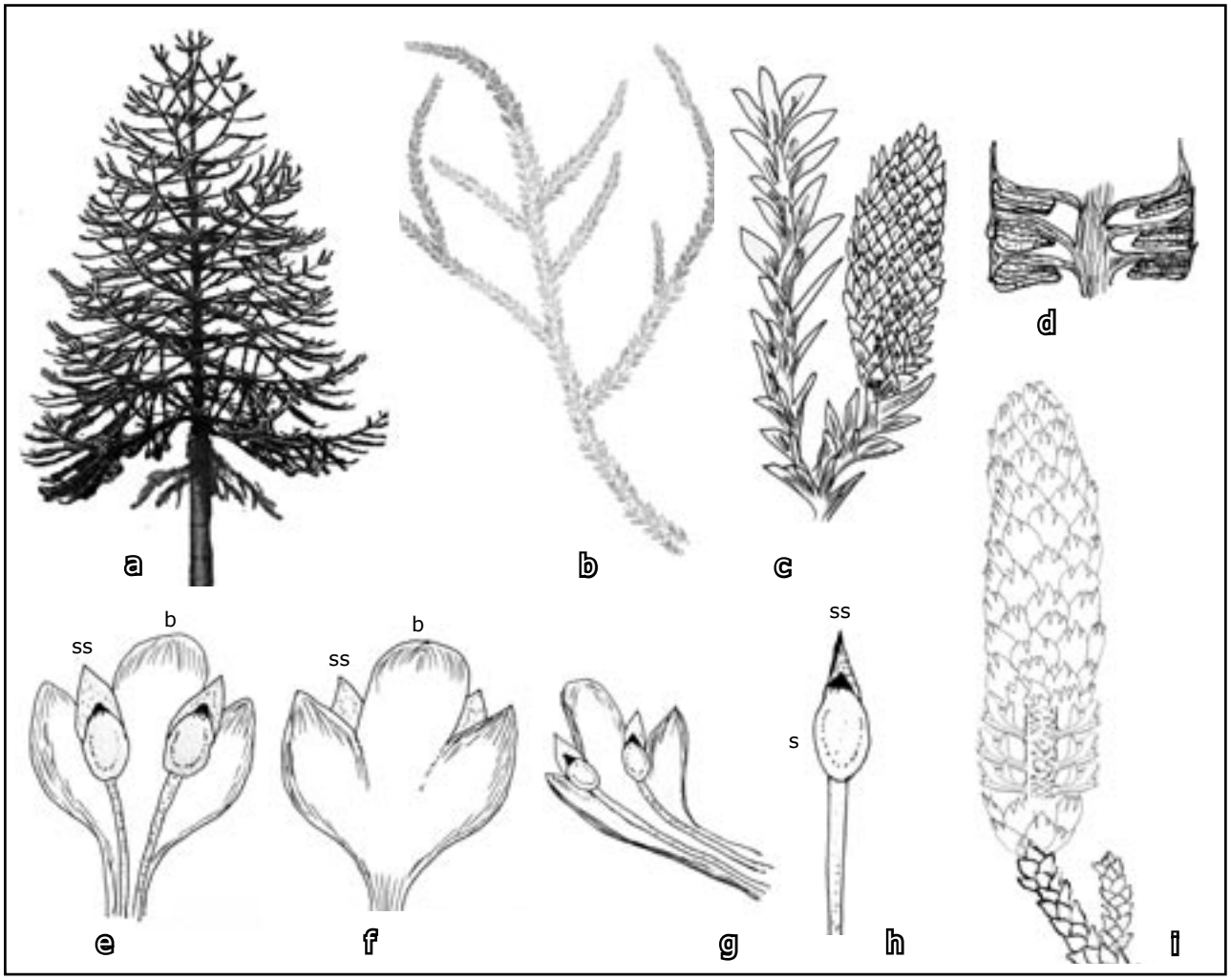
Lower to Middle Triassic, Anisian, Pelson-Illyrian

Diagnosis

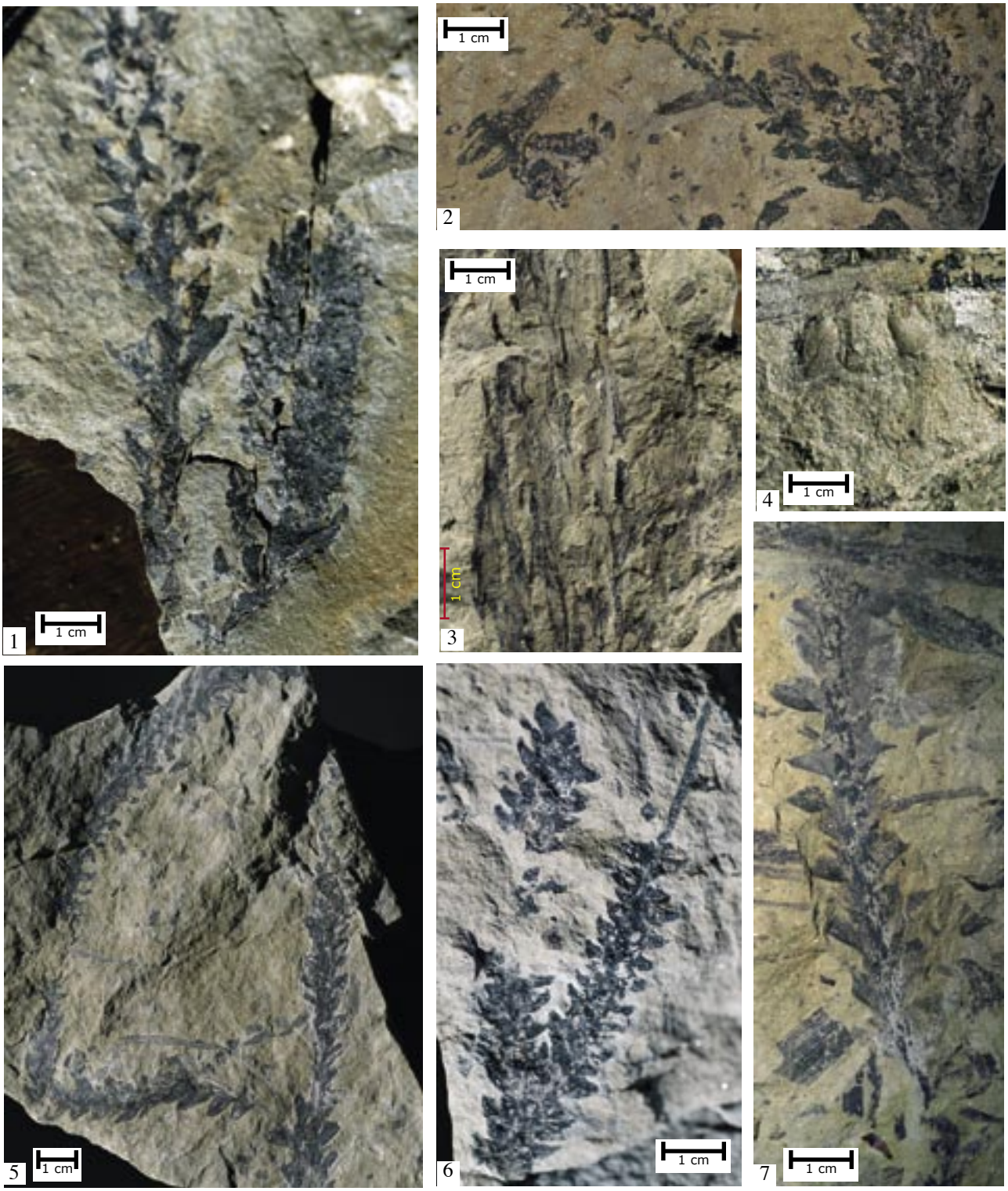
Conifer with widely spread branches. Shoots well spaced and coarse. Leaves thick, tough and scale like, triangular, broad at the base, with sharp edges and a pointed apex. Male cones elongated with peltate microsporophylls, holding several pollen sacs, recurved to the main axis, on their abaxial outer edges. Seed cones with three-lobed adnate bracts, two seeds attached on separate scales.

Description

Vegetative branches: *Voltzia agordica* had a straight trunk, decurrent bark (PIZ 26, PIZ 25) and pendulous twigs. PIZ 19 shows evi-



Voltzia agordica – Suggested reconstruction of the conifer: a) tree, b) sterile shoot, c) *Willsiostrobus kostneri* – male cone of *Voltzia agordica* (PIZF 45), d) *Willsiostrobus kostneri*: microsporophylls with pollen sac arrangement, e) *Tirolstrobus agordicus*: Seed-scale interior, f) Bract-scale: outer side, g) Bract-scale: lateral side (PIZ 20) h) T*irolstostrobus agordicus: single seed-scale with seed,* i) T*irolstostrobus agordicus* – female cone of *Voltzia agordica* (ss = seed-scale, s = seed, b = bract-scale)



1) PIZF 45 *Voltzia agordica* (holotype). Shoot with attached male cone of the *Willsiostrobus kostneri* type
2) PIZ 187 *Voltzia agordica*. Ultimate branch with isolated seed scale
3) PIZ 24 *Voltzia agordica*. Part of a stem with a decayed female cone of the *Tirolstrobus agordicus* type and two seeds
4) PIZ 24 *Voltzia agordica*. Detail from Fig. 3 showing two seeds on tiny holding scales
5) PIZ 19 *Voltzia agordica*. Part of a slender shoot
6) PIZ 32 *Voltzia agordica*. Mostly decomposed shoot
7) PIZF 9 *Voltzia agordica*. Detail of the broad spearhead to the pointed leaves

dence of irregularly diverging, drooping and sweeping branches.
Vegetative leaves: From the stem more or less rope-like shoots develop. They diversify by irregularly protruding smaller lateral branchlets (PIZF 45). The glossy leaves completely cover each branch, closely overlapping each other. The leaves are triangular shaped and broadened on the rachis. On older trees, the leaves became especially leathery and thick, with sharp margins and pointed tips (PIZ 32). The single leaves were usually from 4 to 8 mm long, and 3 to 4 mm wide.
Pollen cones: Of the *Willsiostrobus kostneri* type. Male cones occurred laterally on the tips of ultimate branches. Microsporophylls are found in a dense and imbricate spiral on the cone axis. They are peltate and hold six to eight cylindrical pollen sacs on their lower edges that are parallel to and free from the stalk. *Willsiostrobus kostneri* cones are to be considered as a morphogenus belonging to Voltzia agordica because they were found in the same monophyletic strata.
Seed cones: Of the *Tirolstrobus agordicus* type. From a main cone axis arise three-lobed sterile bracts that are strongly adnate on the lower basis. Two other fertile scales sprouting from or near to the main cone axis each protect one rounded to elongated seed (PIZ 20). The cones usually decayed after maturity, losing the bracts that were often found separately as isolated organs. Only after this were the seeds released.

Willsiostrobus kostneri sp. nov. WACHTLER, 2011

1850 *Araucarites agordicus*; HAUER, Pl. III, Fig. 16b
1859 *Auracarites recubariensis*; MASSALONGO, unpublished
1862 *Auracarites recubariensis*; DE ZIGNO, Pl. V, Fig. 3; Pl. VI, Fig. 5
1868 *Auracarites recubariensis*; SCHENK, Pl. 11
2008 *Voltzia recubariensis*; WACHTLER, Pl. 4, Fig. 6

Holotype

PIZF45

Paratypes

PIZ 128, RIT 76AB

Material

PIZ 30, PIZ 42, PIZ 212, PIZ 28, PIZ 22

Etymology

Named after Josef Kostner (1872-1954), researcher and faithful guide of the geologist Maria Ogilvie-Gordon

Type localities

Agordo, Recoaro, Piz da Peres, Kühwiesenkopf, Ritberg

Type horizon and age

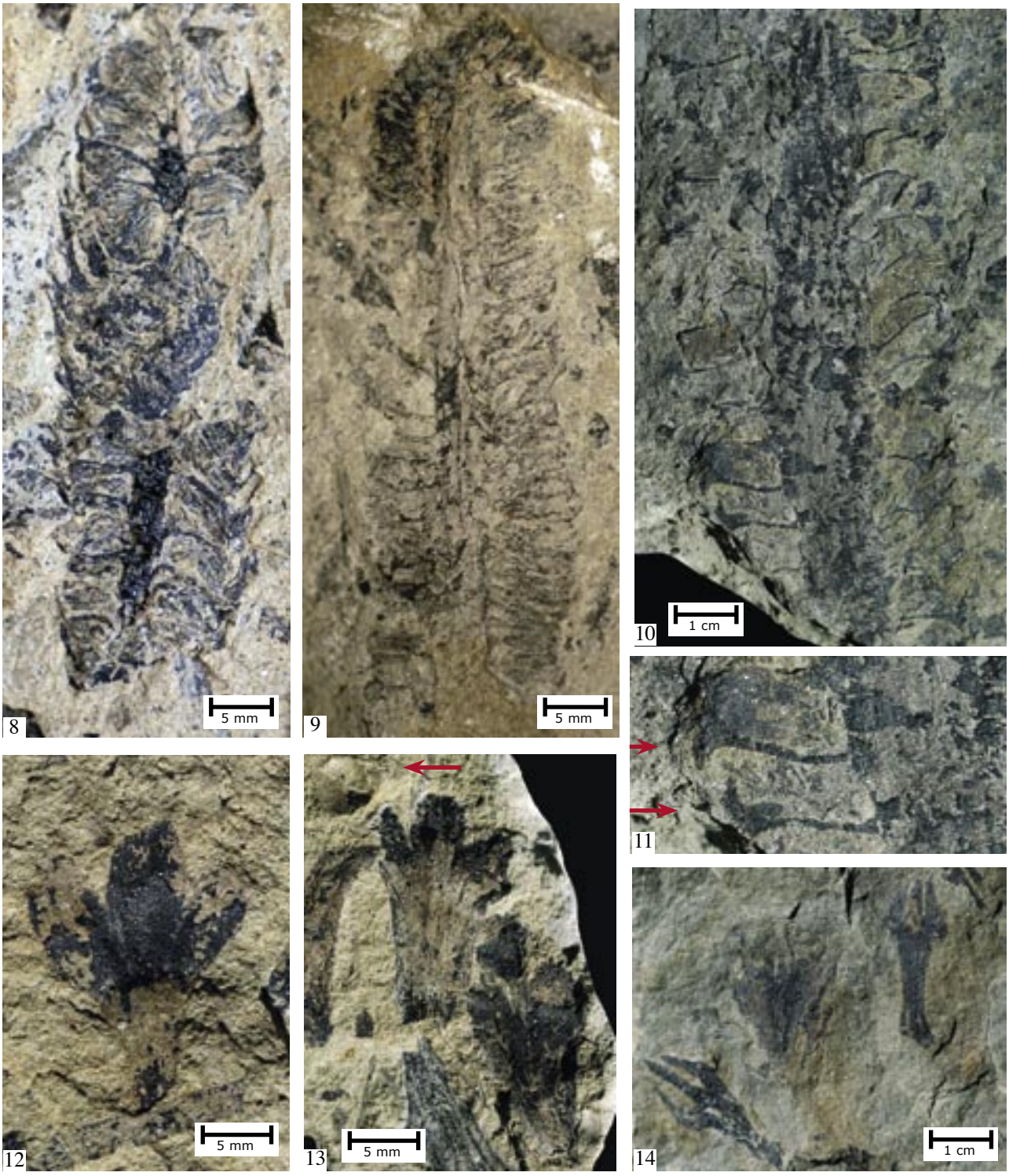
Lower to Middle Triassic, Anisian, Pelson-Illyrian

Diagnosis

Elongated pollen cones with peltate microsporophylls densely and spirally dispersed on a central cone axis. Each peltum holds several pollen sacs on the lower side as long as the sporophyll pedicle, which is curved in the direction of the cone axis.

Description

Willsiostrobus kostneri male conifer cones were found in abundance in the Anisian strata of the Southern Alps. The cylindrical to elongated cone, 6 cm long by 2 cm wide, of the holotype PIZF 45 from Piz da Peres/Furcia is attached to an ultimate shoot of Voltzia agordica. The peltate microsporophylls hold the pollen sacs on the lower part, which are directed towards the cone axis, similar to the extant Araucarias. Paratype PIZ 128 shows the shield-like peltum that abaxially holds six to eight pollen sacs recurved to the main axis, which is as long as the sporophyll pedicle. Each 8 mm-long microsporophyll ends in a terminal, strongly curved rhomboidal distal portion overlapping the adjacent peltum with a short spine. Pollen cone RIT 76 shows densely arranged bracts on the upper part of the outer side and on the lower part open pollen sacs. Microsporophyll cones are especially abundant in monophyletic Voltzia beds such as Ritberg – La Val, Piz da Peres/Furcia, and in Wachtler's gorge on the Eastern Piz da Peres on point 2C were *Voltzia agordica* covered almost 95% of the vegetation. Materials PIZ 212, PIZ 30, PIZ 28, PIZ 128 and many more were picked up in these lay-



8) PIZ 128 *Willsiostrobus kostneri*. Whole cone clearly showing the arrangement of the six pollen sacs on two rows
9) RIT 76 *Willsiostrobus kostneri*. Whole cone with the pollen sacs on the lower surface of each scale
10) PIZ 20 *Tirolstrobus agordicus*. Whole, mainly decayed cone, with two paired seeds attached
11) PIZ 20 *Tirolstrobus agordicus*. Detail of the seed arrangement with a rudimentary wing attached
12) PIZ 228 *Tirolstrobus agordicus*. Single bract
13) PIZ 43 *Tirolstrobus agordicus*. Two scale bracts with one isolated seed on the upper left margin
14) PIZ 21 *Tirolstrobus agordicus*. Several scale bracts showing the adnate scales with pointed lobes

ers, suggesting that pollen cones were much more frequent than female cones.

Tirolstrobus agordicus sp. nov. WACHTLER, 2011

Holotype

PIZ 20

Paratypes

PIZ 21 (scale-bract), RIT 169, PIZ 43

Material

PIZF 3, PIZF 5, RIT 109, PIZ 187

Etymology

Named after the southern Dolomitian locality of Agordo

Type localities

Piz da Peres, Kühwiesenkopf, Ritberg

Type horizon and age

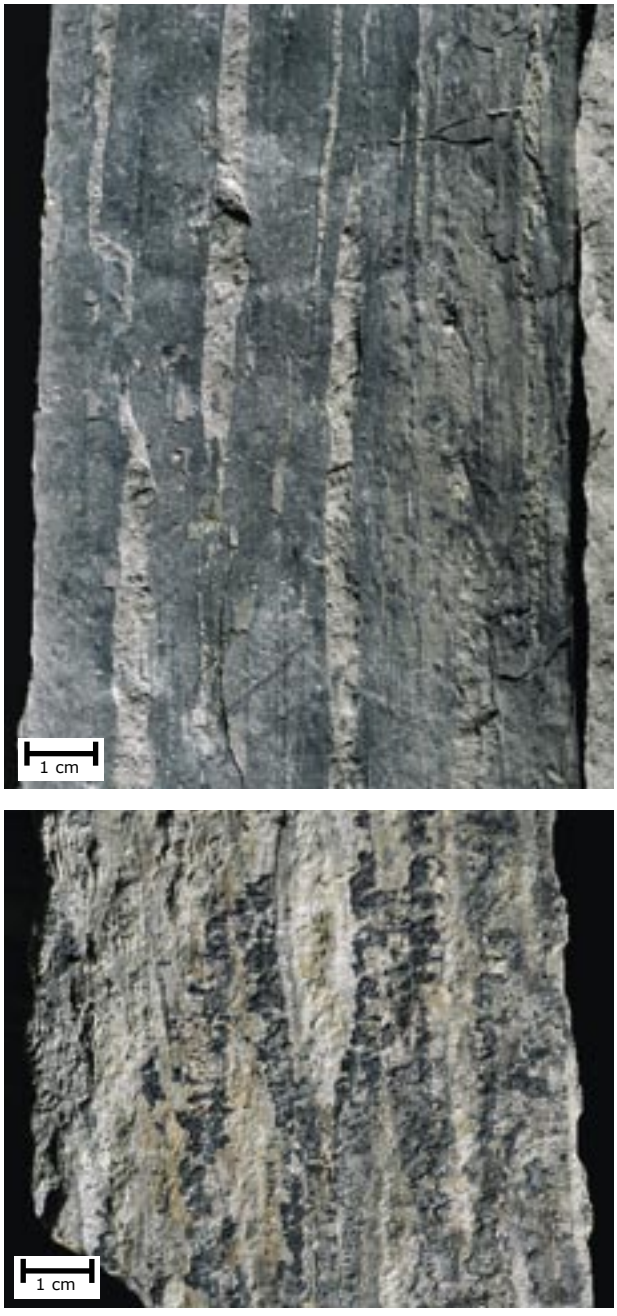
Lower to Middle Triassic, Anisian, Pelson-Illyrian

Diagnosis

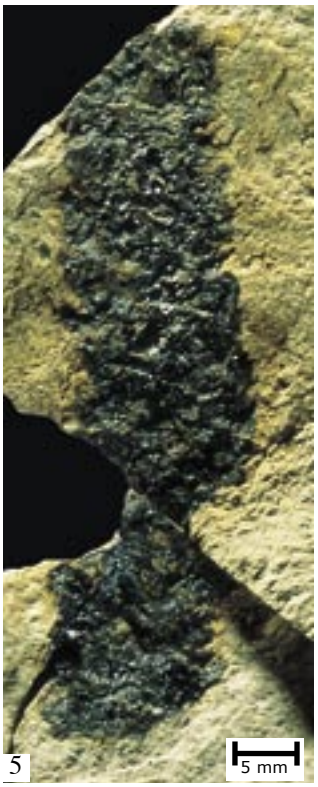
Elongated seed cones with numerous bract scales arranged in dense spirals along a spindle. Bracts were three-lobed and strongly connate. Two separate, tiny, stalked seed scales ending with a pointed wing; each holds one elongated small-sized seed. The cones disintegrated after maturity.

Description

The holotype PIZ 20 is a mature, mostly decayed cone with most of the sterile bracts dispersed. Of interest is, most of the small seeds were still attached to the minute stalked scales where the main sterile and adnate bracts had just been released. In fact, the abundant *Voltzia agordica* beds contain innumerable, dispersed, typical lobed bracts, only sometimes with adjacent seeds. Paratype PIZ 21 is a good example of the numerous cone scale complexes that were found isolated in the sediments. The symmetrical three pointed scale-like units reach a length of 2 to 3 cm. The stalk is sharply truncated at the base, as though abscised. Two small-sized seeds embedded on the upper side of each of the two seed scales suggest a five-lobed structure of the bract scales. Adult *Tirolstrobus* cones were massive, up to 15 cm long by 4 cm wide. Because young and adult cones usually lie in different seasonal strata, the life cycle of *Voltzia* cones probably had 2-3 year intervals. *Tirolstrobus agordicus* should be viewed as a morphogenus of *Voltzia agordica*.



Voltzia agordica: Outer (PIZ 26) and inner (PIZ 25) structure of a stem



1) WRI 01 *Tirolstrobus dolomiticus*. Young female cone, Ritberg – La Val
2) WSW 54 *Voltzia dolomitica*. Shoot with decayed seed cone *Tirolstrobus dolomiticus*. Prags – Seewald
3) WSW 01 *Tirolstrobus dolomiticus*. One decaying cone and leaves of Voltzia dolomitica. Prags – Seewald
4) WIK 03 *Willsiostrobus dolomiticus*. Male cone of *Voltzia dolomitica*. Prags – Innerkohlbach
5) WRI 08 W*illsiostrobus dolomiticus*. Male cone. Ritberg La Val

Voltzia dolomitica WACHTLER, 2000

? 1927 *Voltzia recubariensis* GORDON, P. 67, Pl. 8, Fig. 7
? 1953 *Pagiophyllum* (?) LEONARDI, P. 18, Pl. 3, Fig. 8, 10, Pl. 4, Fig. 2
1998 *Voltzia* sp. STINGL & WACHTLER, p. 79
2000 *Voltzia dolomitica* WACHTLER & VAN KONIJNENBURG, Pl. 7 Figs. 1 - 4, Pl. 8 Figs. 1-6

Material

WSW 201, WRI 025, WRI 28, WSW 54

Type localities

Seewald, Innerkohlbach, Sarlköfele – Prags, Ritberg – Wengen

Type horizon and age

Middle Triassic, Upper Ladinian-Langobardian

Diagnosis

Conifer with branches in one plane. Foliage of the penultimate and ultimate shoots spirally arranged, overlapping each other. Leaves distinctively armoured, scale-like triangular, apex more or less acute. Male cones with peltate microsporophylls, pollen sacs hanging on their edges and recurved to the main axis. Female cones robust, with more lobed bract-scales bearing two small-sized seeds.

Description

Voltzia dolomitica constitutes the most abundant conifer species from the Ladinian Wengen formation. Material WSW 201 represents a mainly entire shoot with protruding, slightly falcate branches bearing broadly ovate leaves. The foliage is triangular and leathery with a sharply pointed apex. They are closely set and spread out from all sides of the shoot. Leaves vary in size between 6 to 10 mm by 3 to 5 mm width on the penultimate shoot and 5 to 8 and 2 to 4 mm width on the ultimate shoots (WACHTLER & VAN KONIJNENBURG, 2000).

Willsiostrobus dolomiticus sp. nov. WACHTLER, 2011

2000 *Voltzia dolomitica* WACHTLER & VAN KONIJNENBURG, p. 7, Fig. 8, p. 10, Fig. 5

Holotype

WIK 003

Paratype

WRI 008

Type localities

Seewald, Innerkohlbach – Prags, Ritberg – Wengen

Type horizon and age

Middle Triassic, Upper Ladinian-Langobardian

Diagnosis

Small-sized male cones with upwardly curved peltate shields. Pollen sacs attached to the outer lower edges of the microsporophylls, directed towards the main spindle.

Description

Only two, poorly conserved, male cones were found. One (WIK 003) is 4.5 cm long, 1.2 cm wide. It consists of an axis with spirally arranged microsporophylls. The stalk is 6 to 7 mm long and the microsporophyll head ca. 1 mm wide and 1 mm long. The other one, which was classified as *V. ladinica* cone in a previous work (WACHTLER & VAN KONIJNENBURG, 2000), is suggested as belonging to *V. dolomitica* due to its habitus. It is 6 cm long and 1.2 cm thick. For statistical reasons, and mainly for the isolated male pollen cones found in the Ladinian Wengen Formation, the new morphogenus *Willsiostrobus dolomiticus* will be introduced.

Tirolstrobus dolomiticus WACHTLER, 2011

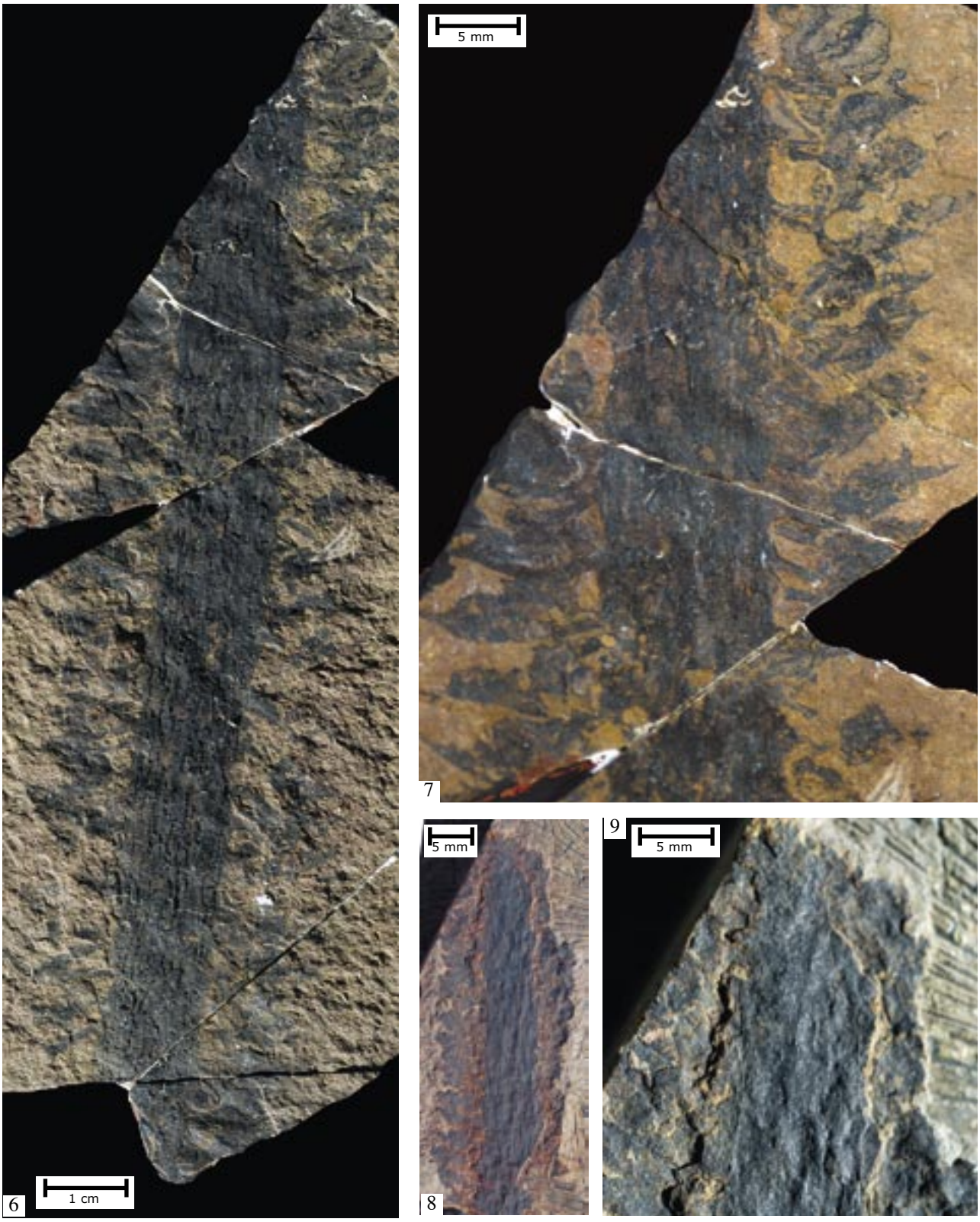
2000 *Voltzia dolomitica*; WACHTLER & KONIJNENBURG-VAN CITTERT, Pl. 7 Fig. 3, Pl. 8, Figs. 1, 3

Holotype

WSW 200

Paratypes

WSW 201, WSW 203, WRI 01, WWS 01 (young cone)



6) WSW 200 *Tirolstrobus dolomiticus* (holotype). Mostly complete adult female cone. Prags – Seewald

7) WSW 200 *Tirolstrobus dolomiticus*. Detail of the cone with the lobed bract scales and the attached seeds. Prags – Seewald

8) WSW 201 *Tirolstrobus dolomiticus*. Upper part of an adult cone. Prags – Seewald

9) WSW 201 *Tirolstrobus dolomiticus*. Detail of the bracts on the upper part of the cone. Prags – Seewald

Etymology

Named after the Dolomite mountains

Type localities

Prags – Seewald, Prags Innerkohlbach, Ritberg – Wengen

Type horizon and age

Middle Triassic, Upper Ladinian-Langobardian

Diagnosis

Elongated robust seed cones with numerous cone scales arranged in dense spirals along a main axis. Three-lobed sterile bracts closely fused on the lower part. Two separate scales each hold one minuscule seed. The cones disintegrated after maturity.

Description

Three mainly perfect adult cones and several juvenile strobili of *Tirolstrobus dolomiticus* were found. Material WSW 200 shows a mature cone with several open scale bracts and attached seeds. Two small seeds (0.5 cm to 0.5 cm) are embedded on separate tapered scales. The cones were 15 to 20 cm in length with a width of 5 cm. The cone spindle is massive. The sterile bracts are three lobed with one slightly longer pointed apex in the middle. The younger cones are much smaller, not ligneous (WRI 01, WSW 01), reaching a length of 5 to 6 cm and a width of 3 to 4 cm (WACHTLER & VAN KONIJNENBURG, 2000). Their appearance agrees with the concept of characteristic seed cones of the Voltziales.

Aethophyllum stipulare BROGNIART, 1828

1828 *Aethophyllum stipulare*; BRONGNIART, Pl. 18, Fig.1
1844 *Aethophyllum stipulare*; SCHIMPER & MOUGEOT, Pl. XIX
1862 *Aethophyllum foetterlianum*; DE ZIGNO, Pl. III and IV
1891 *Aethophyllum stipulare*; SCHENK (in ZITTEL) p. 393
1942 Aethophyllum speciosum; MÄGDEFRAU, p. 209, Fig. 177
1973 *Aethophyllum stipulare*; GRAUVOGEL-STAMM & GRAUVOGEL, p. 143, Figs. 1-3
1978 *Aethophyllum stipulare*; GRAUVOGEL-STAMM, L. p. 75, Figs. 13-20

Diagnosis

Low-growing, bushy conifer from the Ansian-Scythian plant assemblages of German and Alpine Trias. Extraordinarily long, but narrow parallel-nerved leaves. Female and male cones arranged on terminal branches.

Description

Shrubby conifer, up to 1.5-2 m high, stem diameter 2 cm, occasionally branched. Foliage 5 to 30 cm long, 0.2 to 0.9 cm width, with parallel-veined leaves (3 to 7 nerves each) that are linear and sessile. *Aethophyllum stipulare* shares no similarities with any living conifer and stands isolated in the Triassic plant assemblages, although the arrangement of the male and female cones suggests a classification in the Voltziales with an undergroup of the Aethophyllaceae. Fossilized remains (GRAUVOGEL-STAMM & GRAUVOGEL, 1973) suggest that plants only 30-50 cm high could be fertile. Male cones were about 5 cm long, 1.5 cm broad and of the *Willsiostrobus acuminatus* type. Female cones extraordinarily long, up to 22 cm, 3.5 cm broad, characterized by 5 to 7 horn-like pointed appendages, each holding one seed.

Remarks

The shrubby conifer *Aethophyllum* has a long and changing history behind it. In 1828, BRONGNIART described a new plant genus from the *Voltzia* Sandstones (Upper Buntsandstein) of the Vosges and first classified it into the Monocotyledons. UNGER (1850), however, put the plant into the Typhaceae, a classification that was also followed by DE ZIGNO (1862). In 1891, SCHENK considered *Aethophyllum* as a fertile part of the Equisetales, with a close resemblance to *Schizoneura paradoxa.* MÄGDEFRAU (1942) agreed with this concept, and introduced the new subspecies *Aethophyllum speciosum*. The extensive research of GRAUVOGEL-STAMM (1973, 1978), based on new material, described this plant as a low-growing bushy conifer, with male pollen organs of the morphogenus *Willsiostrobus acuminatus* and elongated female cones with

1) KÜH 2150 *Willsiostrobus acuminatus.* Whole male cone
2) KÜH 2150 *Willsiostrobus acuminatus.* – Aethophyllum stipulare. Part of the sterile base
3) KÜH 2150 *Willsiostrobus acuminatus*. Abaxial view of the cone

horn-like projections, each bearing a single recurved ovule.

The fossil record of the conifer *Aethophyllum* in the Dolomites is sparse; one reason is that isolated leaves could easily be confused with *Lycopia* or *Equisetites* foliage. The fact that the shrubby conifer was present anyway in the Alpine Trias was proven by the recovery of male *Aethophyllum* cones of the *Willsiostrobus acuminatus* type and descriptions and illustrations by MASSALONGO and, especially, DE ZIGNO (1862) in the Middle of the nineteenth century over the Recoaro flora. MASSALONGO described the new genus *Aethophyllum foetterlianum*, which was reproduced by DE ZIGNO (Plates III and IV) in his work about the Triassic fossil plants of Recoaro. The five specimens show a striking resemblance to *Aethophyllum stipulare* from the Buntsandstein of Vosges. Therefore, it could be suggested that we should consider it as the same species, and *Aethophyllum stipulare* (BRONGNIART, 1828) has priority over *A. foetterlianum* because it was established first.

Plates III and IV from DE ZIGNO, A., 1862. "Sulle piante fossili del Trias di Recoaro raccolte dal prof. A. Massalongo" Memorie dell'I. R. Istituto Veneto di scienze, lettere ed arti, Volume 11. Venezia.

DE ZIGNO described *Aethophyllum foetterlianum* as a new species, but it is probably conspecific with *Aethophyllum stipulare.*

Willsiostrobus acuminatus GRAUVOGEL-STAMM, 1978

1844 *Amentum Coniferae* SCHIMPER & MOUGEOT, Pl. XXIIB
1973 *Masculostrobus acuminatus,* GRAUVOGEL-STAMM & GRAUVOGEL, p. 101-114, Figs. 1-3
1978 *Willsiostrobus acuminatus*, GRAUVOGEL-STAMM, p. 84, Figs. 18-20

Diagnosis

Pollen organs comparable to many Voltzialean cones composed of hypopeltate and hyposporangiate microsporophylls bearing free sporangia.

Description

Material KÜH 2150, holds the most complete *Willsiostrobus acuminatus* cone from the Dolomites. The well-preserved ellipsoid cone is 6.5 cm long and 1.5 cm thick; the helically arranged peltate microsporophylls hold several elongated pollen sacs as long as the sporophyll pedicle on the lower surface. The cone is nearly mature, showing a cluster of pollen grains. Each peltate shield ends in a typical, up to 2.0 cm long anther, which distinguishes it from the other male cones of the Voltziales. This pointed, final filament was also eponymous for this species of cones.

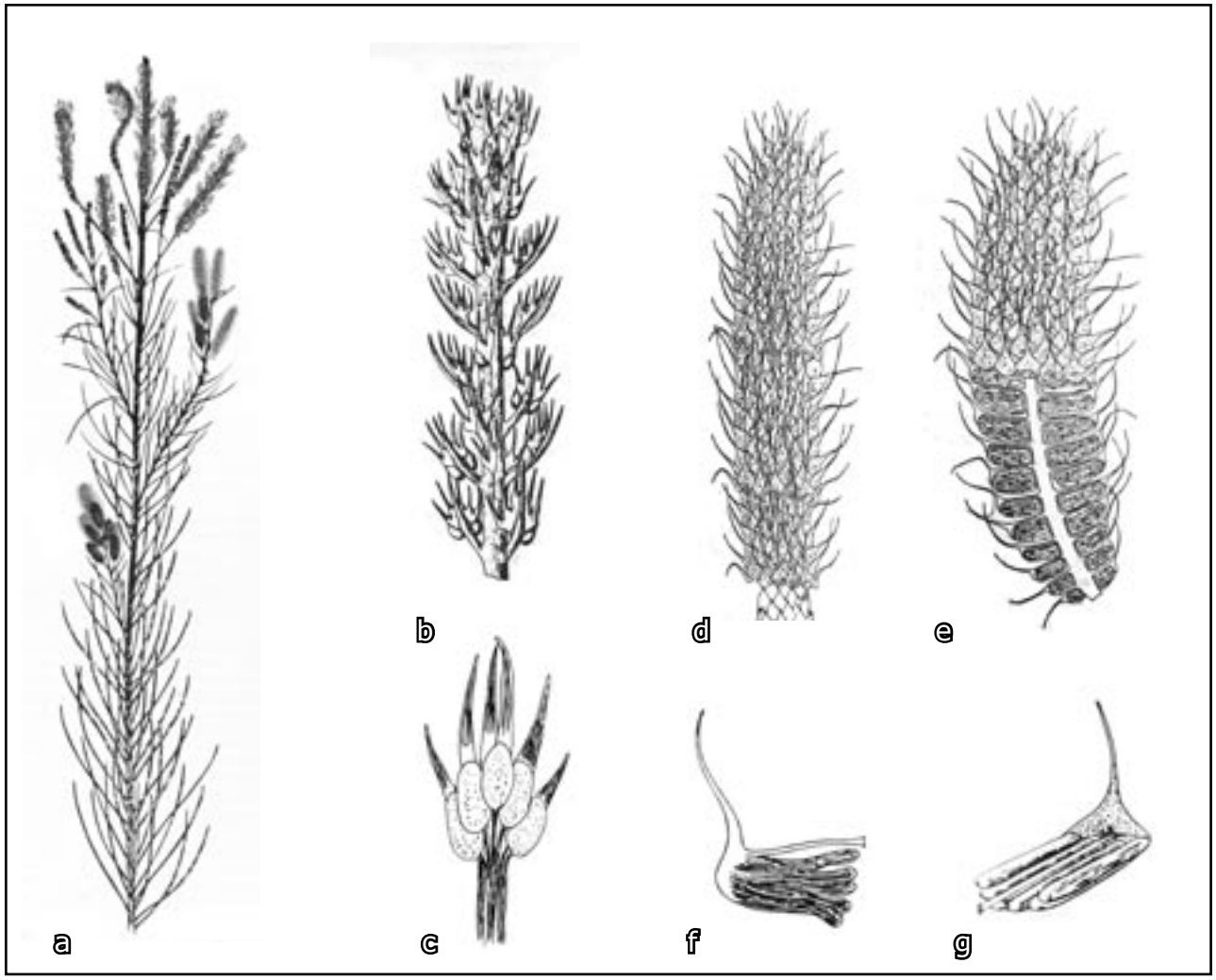
Remarks

In 1973, Lea Grauvogel-Stamm first proposed the classification as *Masculostrobus* (SEWARD 1911) *acuminatus*, and then she introduced the genus *Willsiostrobus* (GRAUVOGEL-STAMM 1978) for peltate male conifer-cones of the Triassic with pollen sacs hanging from the lower distal end in the direction of the main axis. Pollen cones of *Aethophyllum stipulare* have eusaccate pollen and a proximal tetrad mark in addition to a distal aperture (GRAUVOGEL-STAMM & GRAUVOGEL, 1973, GRAUVOGEL-STAMM 1978).

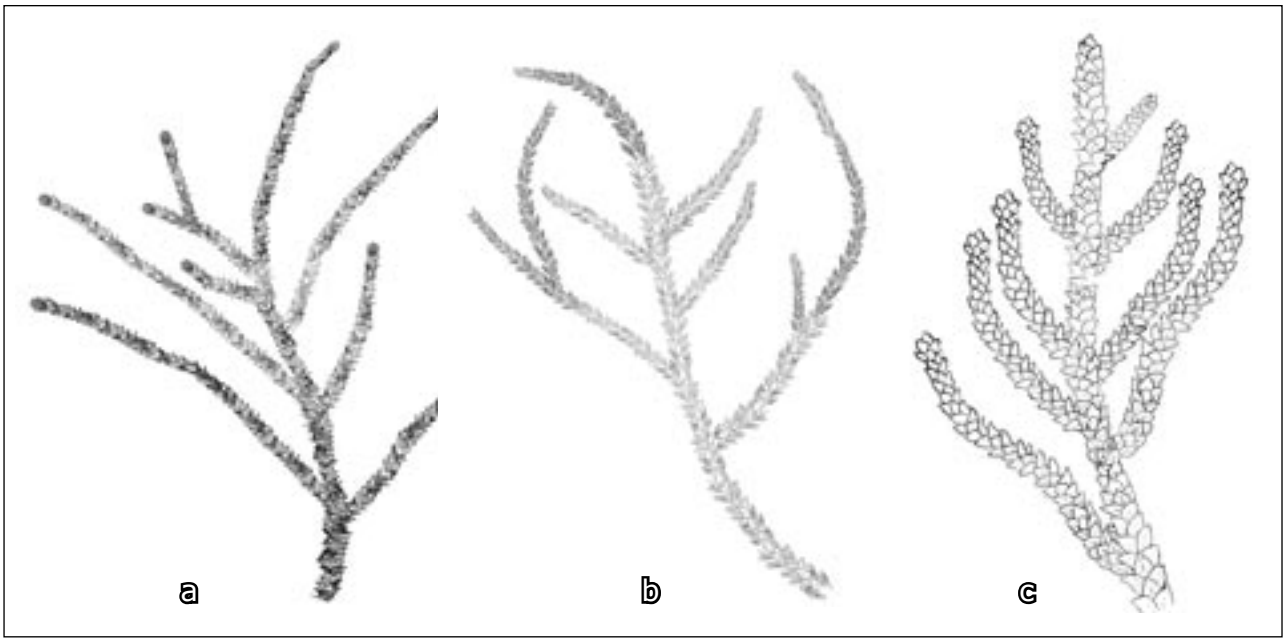
General remarks

The "Voltziales" were a primitive but "nebulous" conifer group ranging from the Late Palaeozoic into the Mesozoic (TAYLOR, 1988; TAYLOR & GRAUVOGEL-STAMM, 1995). Because the sterile foliage of all conifers was nearly the same from the late Carboniferous/Early Permian, precise knowledge of the fertile organs plays a fundamental role in the knowledge of conifers. The Permo-Triassic pollen cones of the Voltziales at this time had a structure similar to the extant Araucarias. Another important distinguishing feature is the structure of female cones. Most of the Permian conifers, such as the Walchiaceae, differ from the Mesozoic Voltziaceae by their ovuliferos dwarf-shoot complexes, which are compunds of a specific number of individual bract-seed scales. Only Permian Majonicaceae, especially *Pseudovoltzia*, reached the stage of fusion of their bract-seed scales to form single flat scales and could therefore be regarded as the closest relatives of Triassic Voltziales.

The assumption of a consecutive development line from the Voltziales to the extant Araucarias could be accepted for the branching patterns and also the pollen organs, but it is not so easy for the female cones with their more-lobed bract scales. In fact, up until the Carnian and Norian, distinctive three to five lobed bract-seed scales of the Voltziales were found, which suggests that



Aethophyllum stipulare – Suggested reconstruction of the conifer: a) whole plant, b) female cone, c) single bract, d) Willsiostrobus acuminatus – male cone of Aethophyllum stipulare (KÜH 2150), e) *Willsiostrobus acuminatus*: male cone showing the arrangement of the pollen sacs, f) *Willsiostrobus acuminatus*: microsporophyll with pollen sacs. g) *Willsiostrobus acuminatus*: microsporophyll and pollen sacs, lateral view. (After GRAUVOGEL-STAMM, 1978)



Evolving stage of the Triassic Voltziales. a) Shoot of *Voltzia unescoensis* (Pelsonian-Early Triassic) b) Shoot of *Voltzia agordica* (Illyrian to Early-Middle Triassic). c) Shoot of *Voltzia dolomitica* (Ladinian (Fassanian-Langobardian) Middle Triassic). The same is also valid for *Voltzia haueri* (Carnian (Julian-Tuvalian) and *Voltzia seefeldensis* (Norian (Alaunian-Sevatian)

there was no conspicuous change to the totally fused and entire form of fertile scales – a characteristic of Early Jurassic up until extant female Araucarian cones. In this aspect, the evolving stage of the Alpine Voltziales – and probably most of the Northern hemisphere Voltziales – seems to cease effectively and reach a dead end. Therefore, the progenitor of all Araucarias should be looked for in Southern hemisphere *Voltzia* relatives, and not in the exhausted group of the Old World conifers.

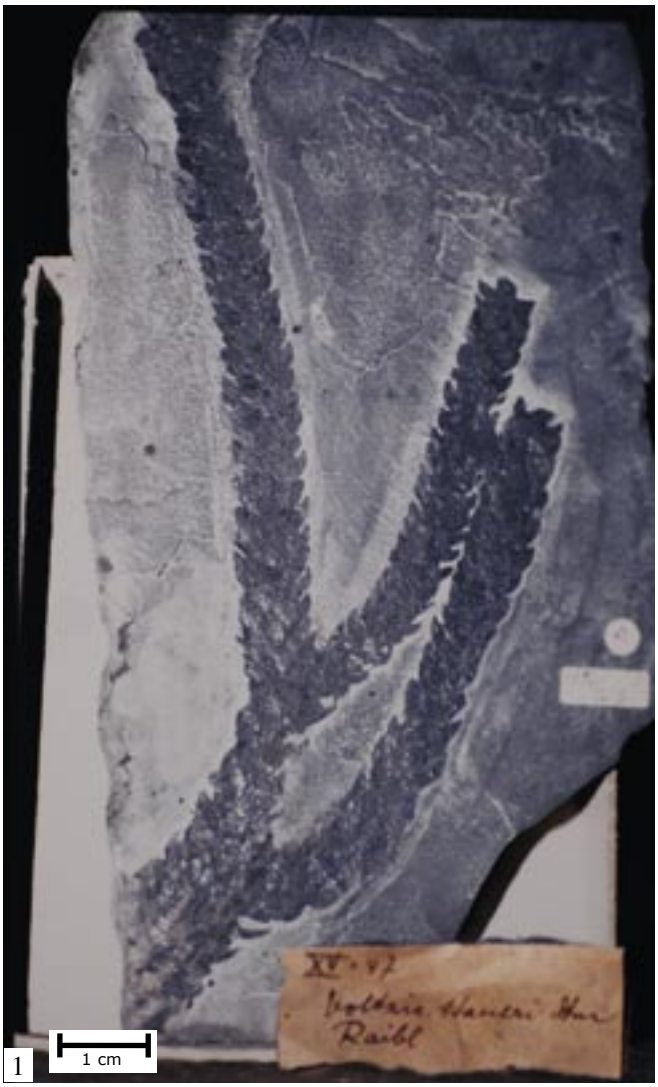
Vegetative branches and leaves

Interesting details emerged from tracking the evolving lines of the Dolomitian Voltziales, mainly based on observations about newly discovered material that covered more than 25 million years from Early till Middle-Late Triassic. Whereas the older Anisian *Voltzia unescoensis* and *Voltzia agordica* were characterized by a rope-like structure of the main branches and small-sized, hard but not leathery leaves, the Ladinian *Voltzia dolomitica* (WACHTLER & VAN KONIJNENBURG-VAN CITTERT, 2000) only bore thick-walled armoured leaves on massive shoots. Therefore, they displaced the sweeping branches of the Anisian Voltziales. In this evolutionary context, another line could be traced to the Carnian (Julian-Tuvalian) *Voltzia haueri* (DOBRUSKINA et al. 2001) from the Southern Alps locality of Raibl, and to the Norian (Sevatian) *Voltzia seefeldensis* from the North Tyrolean locality of Seefeld, where the leaves once again become armoured. Their heavy protruding shoots resemble the extant *Araucaria araucana*.

The paleoecological insertion of the Early Mesozoic *Aethophyllum stipulare* is difficult to interpret. As a low-growing shrubby conifer with elongated leaves, it does not fit the concept of normal conifer trees. Although *Aethophyllum* male and female cones have a Voltzialean morphology, a classification in the family of Aethophyllaceae – under the order of Voltziales – would be more reasonable.

Pollen cones

Although comprising an important feature in the distinction of coeval conifers, in the past, pollen cone assembly was often neglected. In HAUERS (1850) illustration of *Voltzia agordica*, one male cone was reproduced but its true character was not mentioned. DE ZIGNO (1862) also illustrated



1) *Voltzia haueri* (Stur). Old specimen collected at Raibl. Geologische Bundesanstalt Vienne

2) *Voltzia haueri* (Stur). Old specimen described as *Voltzia heterophylla*. Geologische Bundesanstalt Vienne

Voltzia (recubariensis) agordica foliage and male organs, also without going into more detail about them.

Lea GRAUVOGEL-STAMM, in her exhaustive works about the Early-Middle Triassic conifers from the Vosges, established several basic morphogenus types that are partly valid for the Alpine Trias (GRAUVOGEL-STAMM, L., 1969, GRAUVOGEL-STAMM, L & GRAUVOGEL, L., 1973 GRAUVOGEL-STAMM, L., 1978, GRAUVOGEL-STAMM, L., SCHAARSCHMIDT, F., 1978). She created the genus *Willsiostrobus* for Triassic male Voltziales cones (GRAUVOGEL-STAMM, 1978); for statistical reasons, this concept was widened to include the Alpine Voltziales. Up until now, *Willsiostrobus kostneri, W. unescoensis and W. dolomiticus* were rated as having typical Alpine Triassic conifer pollen organs due to their different foliage and fructifications, and *W. cordiformis, W. ligulatus, W. rhoimboidalis, W. willsi* and *W. bromsgrovensis* (GRAUVOGEL-STAMM & SCHMIDT, 1978) were proposed for material from the Upper Buntsandstein of Vosges in France. All of the cones consist of a central axis surrounded by numerous helically arranged, flattened microsporophylls. Each sporophyll has an upturned distal segment that overlaps the sporophyll above and a small basal projection that partially covers the pollen sacs. On the abaxial surface of the microsporophylls, attached to the peltum, several elongated pollen sacs grow in the direc-

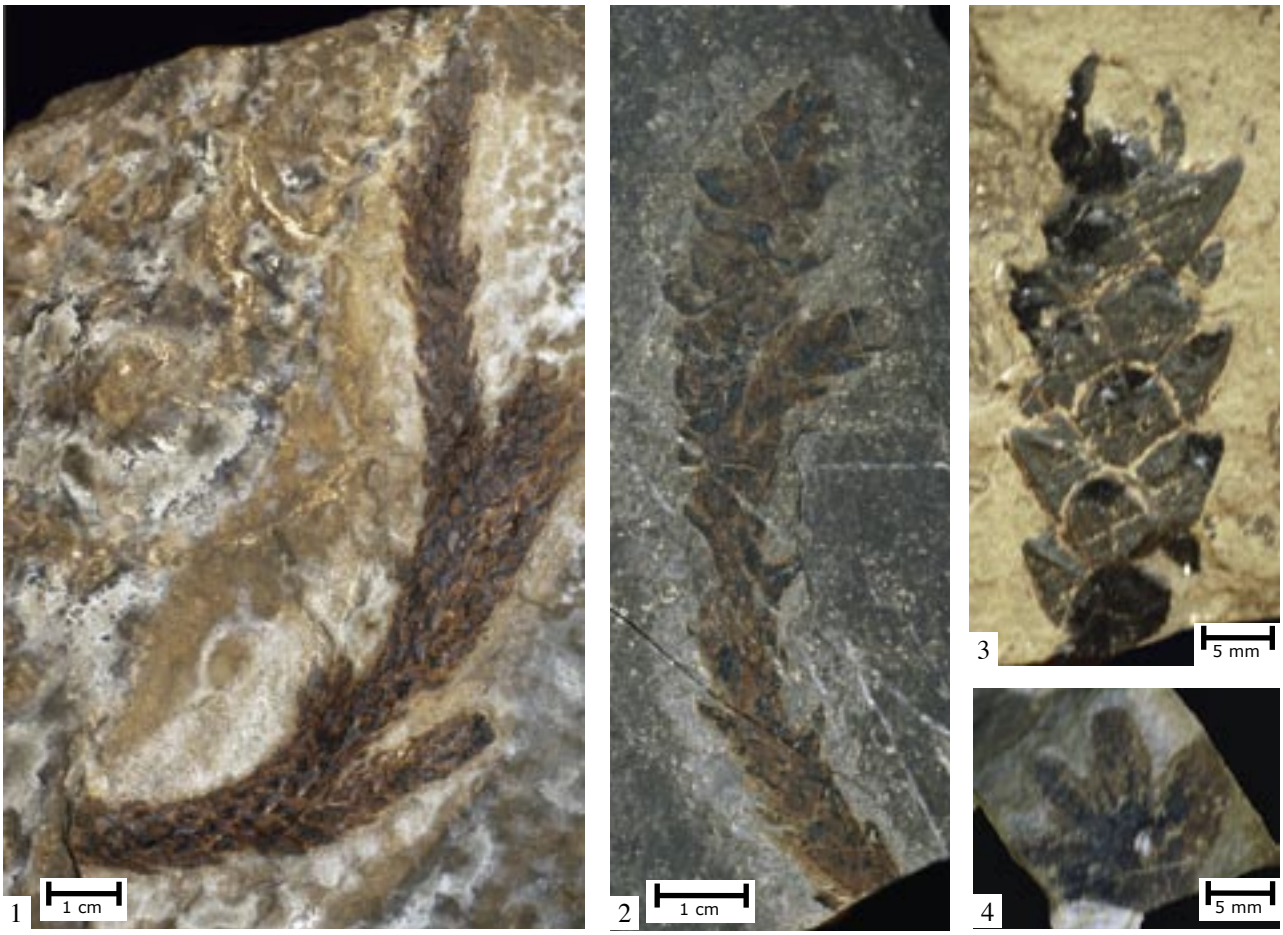
tion of the central axis. The male cones of the Triassic Voltziales look like those of many modern Araucarians, but not extant Cupressaceae or Pinaceae.
An evolutionary line can also be found in the Alpine *Willsiostrobus* cones. *Willsiostrobus unescoensis* cones were an elongated ovoid shape, whereas the pollen organs of *W. kostneri* had an elongated to cylindrical appearance. Ladinian *W. dolomiticus* seemed to have the smallest pollen cones. This smaller size reflects a difference between the Mesozoic Voltziales, which only rarely exceeded 6 cm in length, whereas the extant *Araucaria* cones could reach a length of about 15 cm. Furthermore, Araucarian pollen organs are usually slightly curved, which has never been noted for Alpine Voltziales.
Until further investigations determine whether or not the foliage and pollen organs of Alpine *Aethophyllum* pertain to *Aethophyllum stipulare* and the morphogenus *Willsiostrobus acuminatus*, the Alpine species will be regarded as the same species.

Seed cones

Tirolstrobus-seed cones can be defined by their distinctive lobed and connate bract scales as being typically Voltzialean. The juvenile cones were about half the size of fully-grown cones and were not ligneous. Therefore, it can be assumed that several Voltzialean cones worldwide belong to the same species and are only in the different stages of growth. The cones usually began to decay upon maturity, first releasing the sterile bracts and then freeing the hanging, small-sized seed scales. The size difference between *T. unescoensis, T. agordicus* and *T. dolomiticus* was minimal.

Discussion

Questions primarily arise about the direct progenitors of the Mesozoic Voltziales. Rich Permian megafloras were found in several localities of the Dolomites (Bletterbach, Cuencenes-Gardena) but also in the Vicentinian Alps, as well as the German Basin. Upper Permian *Ortiseia*, first found in the Dolomites, has to be eliminated as a progenitor due to its large number (20-30) of sterile and only one single fertile scale (CLEMENT-WESTERHOF, 1988). The same is valid for the Walchiaceae, with its large number of sterile scales. However, another established order fulfils many criteria of the Voltziales: the Majonicaceae, with its type genera *Majonica, Dolomitia* and, especially, *Pseudovoltzia*. This family is characterized by its peculiar organization of fertile scales: they were just arranged in one plane. *Majonica* and *Dolomitia* were found in the Dolomites, but are also recorded from siltstone layers of the Upper Permian Zechstein in Thuringia in Germany and from other parts of the Northern hemisphere. In *Dolomitia*, the sterile and fertile scales were also moderately connate. In *Pseudovoltzia* some ovuliferous dwarf shoots were just partially fused and thus resembled Mesozoic Voltziales. Furthermore, *Pseudovoltzia liebeana* (FLORIN 1927) pertains to the characteristic conifers of the European Upper Permian; *Pseudovoltzia sjerpii* was limited to the Vicentinian Alps. Therefore, Mesozoic Voltzean female cones can be taken as a continuation of an evolutionary trend from the Palaeozoic Majonicaceae.
For the male pollen cones, the following names were introduced: *Willsiostrobus rhomboidalis* (GRAUVOGEL-STAMM & SCHAARSCHMIDT, 1978), which was thought to belong to *Pelourdea* (ex *Yuccites) vogesiaca*, and *Willsiostrobus acuminatus* (GRAUVOGEL-STAMM & GRAUVOGEL, GRAUVOGEL-STAMM & SCHAARSCHMIDT 1978), which was the male cone structure of the bushy *Aethophyllum stipulare*. Furthermore, *Willsiostrobus wilsii* (TOWNROW GRAUVOGEL-STAMM & SCHAARSCHMIDT 1978) is suggested as being the pollen cone of *Voltzia heterophylla*. In contrast, there are many doubts about *Willsiostrobus cordiformis, W. denticulatus* and *W. ligulatus*. Apart from the male cones, which have been described over the years, many *Voltzia* species have only been classified based on their sterile foliage. In addition to the better known *Voltzia heterophylla, Pelourdea vogesiaca* and *Aethophyllum stipulare*, other known species are: *Voltzia rigida, V. elegans, V. brevifolia, V. coburgensis, V. acutifolia, V. remkerslebensis, V. koeneni, V. weisssmanni, V. fraasi, V. argillacea*. If some species like *Voltzia coburgensis* could be interpreted as being a developing line from the former one, like *Voltzia heterophylla*, many of the others are probably just



1) *Voltzia seefeldensis*. Shoot from the Norian fish beds in Seefeld. Collection Welzl-Müller
2) *Voltzia seefeldensis*. Vegetative shoot from the fish beds in Seefeld. Collection Welzl-Müller
3) *Voltzia seefeldensis*. Arrangement of the leathery leaves. Seefeld. Collection Welzl-Müller
4) *Voltzia seefeldensis*. Single, more-lobed bract scale. Seefeld. Collection Welzl-Müller

synonyms. Detailed cuticle analysis and/or further knowledge of the fructifications pertaining to each foliage type could enable a firm classification.
Assured references for *Pelourdea vogesiaca*, with its foliage that was up to 15 cm long, and which resembled extant *Agathis*-conifers, are missing in the Anisian strata. Furthermore, this species pertains to the dominant flora of the Ladinian plant assemblages in the Dolomites.
The delimitation of *Albertia, Schizolepis* and *Alpia* was easier, since they developed totally different pollen and seed organs. Astonishingly, in the Early Triassic, many completely different conifer families evolved that hold – apart from their leave type – totally different kinds of pollen structures and ovule arrangements.
A tendency towards heterophylly, with adult and juvenile leaves showing diverse aspects, even on the same shoots is representative of primitive conifers; regarding this aspect, the typical Buntsandstein conifer *Voltzia heterophylla* does not stand alone in the Mesozoic conifer kingdom. In other families, such as the newly created Alpiaceae, the heterophylly is just as well pronounced, especially in *Schizolepis*.
With increased knowledge of the Mesozoic Voltziales we could determine further interesting details about the phylogeny of ancient conifers, even though any changes to their long and unaltered assemblage, especially of the female fructifications, will confront many well-established theories about the Euramerian Voltziales as the "mothers of all conifers".

The conifer *Albertia* in the Alpine Trias

Division CONIFEROPHYTA
Order ALBERTIALES
Family ALBERTIACEAE
Genus *Albertia* SCHIMPER & MOUGEOT, 1844

Albertia alpina WACHTLER, 2011

1844 *Albertia*; SCHIMPER & MOUGEOT, Pl. XVI, Fig. A1
1885 *Albertia*; RENAULT, Pl. 7, Fig. 14
1891 *Voltzia;* SCHENK, p. 274, 279, Fig. 198 g
1944 *Voltzia rigida*; FLORIN, p. 492, Pl. CLXXXI-CLXXXII, Fig. 6

Holotype

PIZ 175

Paratypes

KÜH 1406, RIT 57, PIZ 185, PIZ 178

Material

PIZ 387, PIZ 390

Etymology

From the Alps where it was found

Type localities

Piz da Peres, Kühwiesenkopf, Ritberg

Type horizon and age

Early-Middle Triassic, Anisian, Pelson

Diagnosis

Sword-shaped conifer leaves, standing straight out from the twigs or angled forwards a little. Male cones robust with peltate pollen organs consisting of microsporophylls arranged spirally on a peduncle, bearing their pollen sacs on its lower surface. Seed cones globose with lobed seed scales.

Description

Vegetative branches: Medium growing conifer with elongated branches. Shoots spread irregularly with decurrent leaves on the axis.

Vegetative leaves: Holotype PIZ 175 – part of an adult twig – is 18 cm long with leaves from 1 to 2.5 cm long, 0.5 to 0.8 cm wide, ending in a long, stiff point. The leaves are long and lanceolate, sharply pointed on the edges. The leaves only occasionally overlap the next ones. A distinct midrib is observable on the lower leaves. Decurrent leaves with a clear midrib could easily be seen on RIT 57. Juvenile foliage is usually arrayed radially around the branchlets (PIZ 305, KÜH 1406). They are up to 1.5 cm long, 0.5 to 0.8 cm wide. They were also spread out, but smaller (1 to 3 cm long), lanceolate or triangular-ovate, flattened and coriaceous (PIZ 178).
Pollen cones: Of the *Darneya schaurothi* type. Male cones consistently 15 to 20 cm long, 4 to 6 cm wide. The holding stalks diverge from a massive cone axis, which ends in a long falcate to flexuous appendage. The subtle microsporophylls are arranged on this second axis, bearing the pollen sacs on their lower surfaces.
Seed cones: Of the *Pusterostrobus haidingeri* type. Female cones ovoid to subglobose, spherical, from 2 to 4 cm long, 2 to 4 cm wide. Scale bracts elongated, ending in three-pointed tips, generating one seed.

Darneya schaurothi WACHTLER, 2011

1973 *Voltziostrobus schimperi*; GRAUVOGEL, p. 38
1969 *Darneya peltata* SCHAARSCHMIDT & MAUBEUGE, p. 378, Fig. 1, Pl. 1
1979 *Darneya peltata* GRAUVOGEL-STAMM, SCHAARSCHMIDT & MAUBEUGE, p. 19, Pl. 4

Holotype

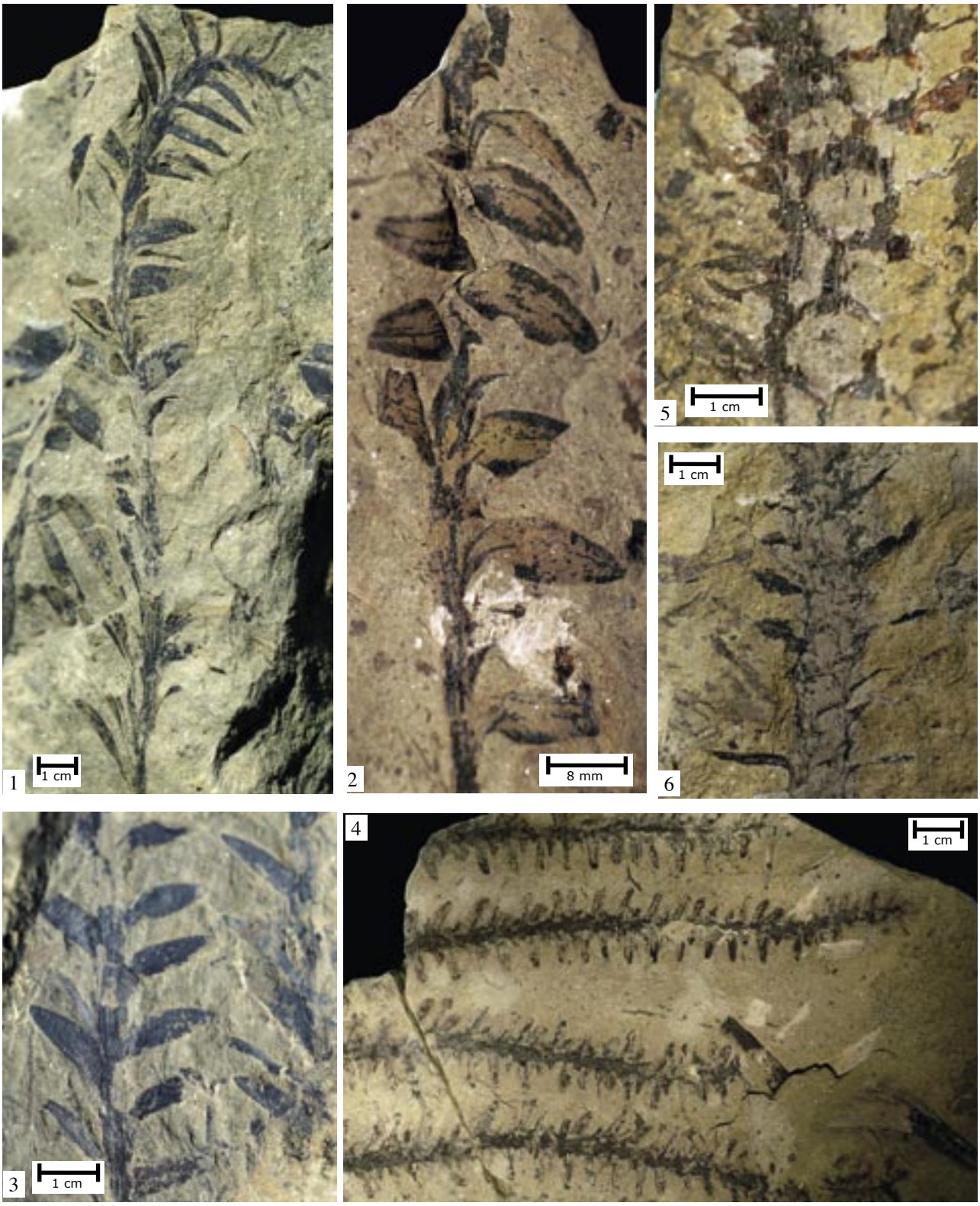
PIZ 603

Paratype

PIZ 229, PIZ 583

Etymology

Named after Carl Friedrich Freiherr von SCHAUROTH (1818-1893), palaeontologist and paleobotanist, (who named *Voltzia coburgensis*). He performed intensive research studies in the Dolomites and the Vicentinian Alps around Recoaro.



1) PIZ 175. *Albertia alpina* (holotype). Part of an adult branch with the pointed elongated leaves
2) RIT 57 *Albertia alpina*. Single leaves evidencing strong mid-veins
3) PIZ 178. *Albertia alpina*. Detail of the leaves
4) PIZ 390 *Albertia alpina*. Part of a juvenile shoot
5) PIZ 387 *Albertia alpina*. Part of a stem
6) PIZ 185 *Albertia alpina*. Part of a shoot

Type localities

Piz da Peres

Type horizon and age

Early-Middle Triassic, Anisian, Pelson

Diagnosis

Elongated bulky pollen cones borne on a central axis with spirally arranged pollen organs. Around this second central axis, ending in a long lunate sterile scale, sprout minute microsporophylls, which hold two pollen sacs on their lower surfaces.

Description

Paratype PIZ 583 constitutes an almost entire pollen cone of *Darneya schaurothi*. It has a length of 18 cm and a width of 6 cm; thus, it is obvious that *Darneya* pollen cones could reach a total length of between 15 and 20 cm. Paratype PIZ 229, and especially holotype PIZ 603, clearly show the composition of *Darneya schaurothi* pollen cones, with its robust central axis. The preserved part of PIZ 229 is 6 cm long and 4 cm wide, and bears the typical clustered pollen-structures of *Darneya*. Holotype PIZ 603 was chosen because it shows in detail the composition of the single pollen organs. On a second minute axis, ending in a long, covering shield, minute microsporophylls, up to 1 mm long, grow in a spiral and close arrangment. Each holds two pollen sacs on the lower surface.

Pusterostrobus gen. nov. WACHTLER, 2011

Generic diagnosis

Small, single female conifer cones, mostly spherical, borne on ultimate branches. Bract scales pointed, each holding one seed

Etymology

Named after the Puster Valley in the Dolomites

Pusterostrobus haidingeri WACHTLER, 2011

Holotype

KÜH 1288

Paratype

PIZ 601

Material

KÜH 1312, KÜH 1264

Etymology

Named after Wilhelm von HAIDINGER (1795-1871), Austrian geologist and founder of the Federal Geological Office (Geologische Bundesanstalt) or GBA in Vienna, from which the major part of the paleontological research in the Dolomites began in the nineteenth century

Type localities

Kühwiesenkopf, Piz da Peres

Type horizon and age

Early-Middle Triassic, Anisian, Pelson

Diagnosis

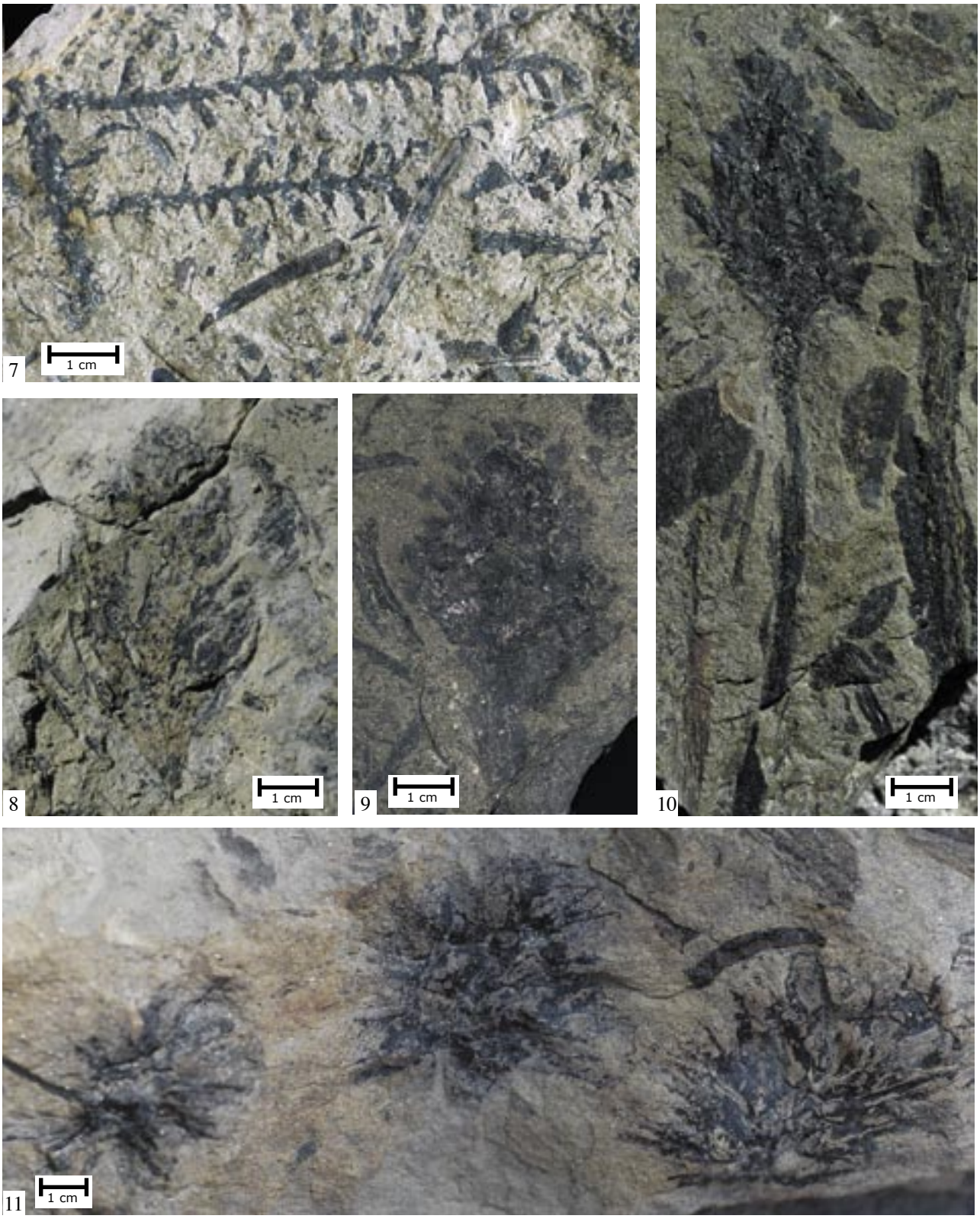
Female cones, spherical when immature, slightly elongated in the adult stage, grow upright on fertile shoots. Scale bracts are long with a pointed tip.

Description

Holotype 1288 shows three young *Pusterostrobus* cones on the upper side. They were spherical to elongated with a size ranging from 2 to 3 cm in length and 2 to 3 cm in width, bearing mainly entire, oblong-elliptic or oblong-ovate bract scales. They hold only one wingless ovule, fused onto the scale. The materials KÜH 1312 and KÜH 1264 are good examples of other young *Pusterostrobus* cones showing their spherical to elongated habitus. Approximately 6 cm of the branch still has some leave attached, so it can be seen that *Pusterostrobus* is a morphogenus of *Albertia alpina*. Paratype PIZ 601 is an older cone, with 5 mm-long seeds inside the scales. The bract scales are more lobed; therefore, this paratype is of Voltzialean disposition.

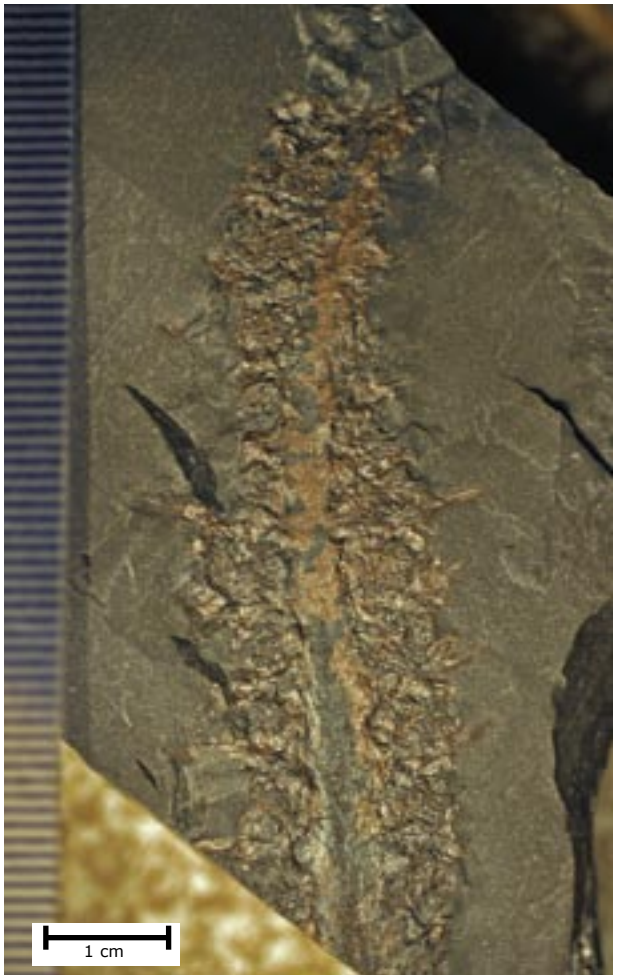
General remarks

Vegetative branches and leaves: Leaves from *Albertia* have been recognized since the nineteenth century (SCHIMPER & MOUGEOT,



7) KÜH 1406 *Albertia alpina*. Part of a sterile shoot
8) PIZ 601. *Pusterostrobus haidingeri*. Female cone
9) KÜH 1064. *Pusterostrobus haidingeri*. Immature female cone
10) KÜH 1312. *Pusterostrobus haidingeri*. Immature female cone
11) KÜH 1288. *Pusterostrobus haidingeri* (holotype). Three cones seen from the upper side with open seeds

1844; RENAULT, 1885) as pertaining to an enigmatic conifer group known only from isolated remains in the Grés a Voltzia of the French Vosges. Several successive authors noted that the pollen organs described as *Darneya peltata* actually belonged to *Albertia* (SCHAARSCHMIDT & MAUBEUGE, 1969; GRAUVOGEL-STAMM & SCHAARSCHMIDT & MAUBEUGE, 1979). *Albertia* was estimated to be a shrubby low-growing conifer. Abundant findings from the Kühwiesenkopf and Piz da Peres showed that *Albertia alpina* was an arborescent conifer, which, from its external appearance, looked like extant *Araucaria bidwillii*. The foliage of *Albertia alpina* could be sometimes be confused with the foliage of *Voltzia agordica*, but the assembly of the shoots is quite different. The foliage of *V. agordica* is short and broad, (4 to 8 mm long, 3 to 4 mm wide) completely covering each branch, closely overlapping each other. The leaves of *Albertia alpina* are decurrent, needle-like, elongated, sword-shaped and only overlap occasionally. The leaves could reach consistent lengths of 2 cm and more. The difference in *Alpia anisica* shoots – occurring in the same layers – persists in their symmetrical branches with falcate curved needles, which are also much thinner. This is also valid for *Schizolepis ungeri.* Otherwise, *Aethophyllum* was a shrubby conifer with very long needles, which could not be confused with another species. Leaves and shoots like those of *Albertia* were recorded from the Permian and classified as *Archaeopodocarpus germanicus*, *Ullmannia bronni* or *Culmitzschia florinii* (TAYLOR T.N., GRAUVOGEL-STAMM L., 1995), but further insertions are not valid without connections to their fertile organs.

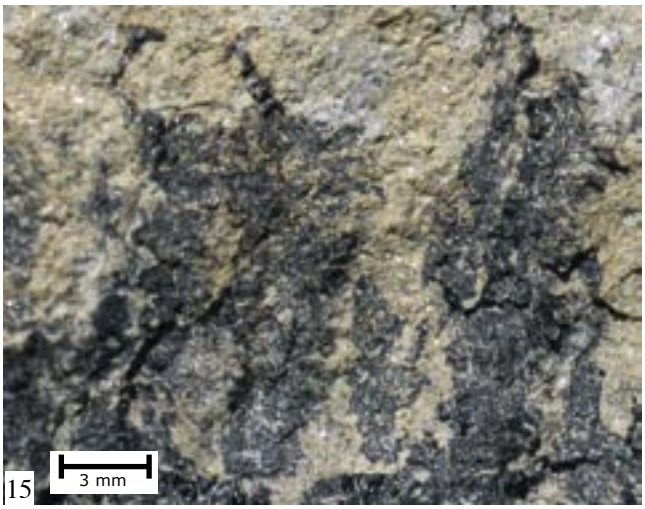


Suggested male cone of *Albertia/Darneya* from the lower Rotliegend (Lower Permian), Steinbruch Cabarz, near Tabarz, Germany (Collection Stephan Brauner WP 5924, classified as a conifer shoot). Courtesy of the Natural History Museum Schloss Bertholdsburg Schleusingen.

Pollen cones: Several *Darneya* species were described from the Anisian Grés a Voltzia of Vosges. The most common, *Darneya dentata* (GRAUVOGEL-STAMM, 1978, TAYLOR T.N.; GRAUVOGEL-STAMM L., 1995), attributed to Albertia of the Vosges, was only about 7.0 cm long and from 1.5 to 2.0 cm wide. The male organs have a completely different organization, giving the appearance of one cone with peltate microsporophylls up to 20 mm long and 5-7 mm wide. The pollen sacs were arranged on the upper side of the leaf-like sporophyll (GRAUVOGEL-STAMM, 1978). A microsporophyll from the Vosges provided pollen grains with two sacs, corresponding to the dispersed species *Triadispora falcata* KLAUS. *Darneya peltata* (SCHAARSCHMIDT & MAUBEUGE, 1969) was from 3 cm to 10 cm long and 2 to 4.5 cm wide, and *D. mougeottii* (GRAUVOGEL-STAMM, 1969), the biggest of the Grés a Voltzia of the Vosges, reached a length of 11 cm and a width of 4.5 cm.

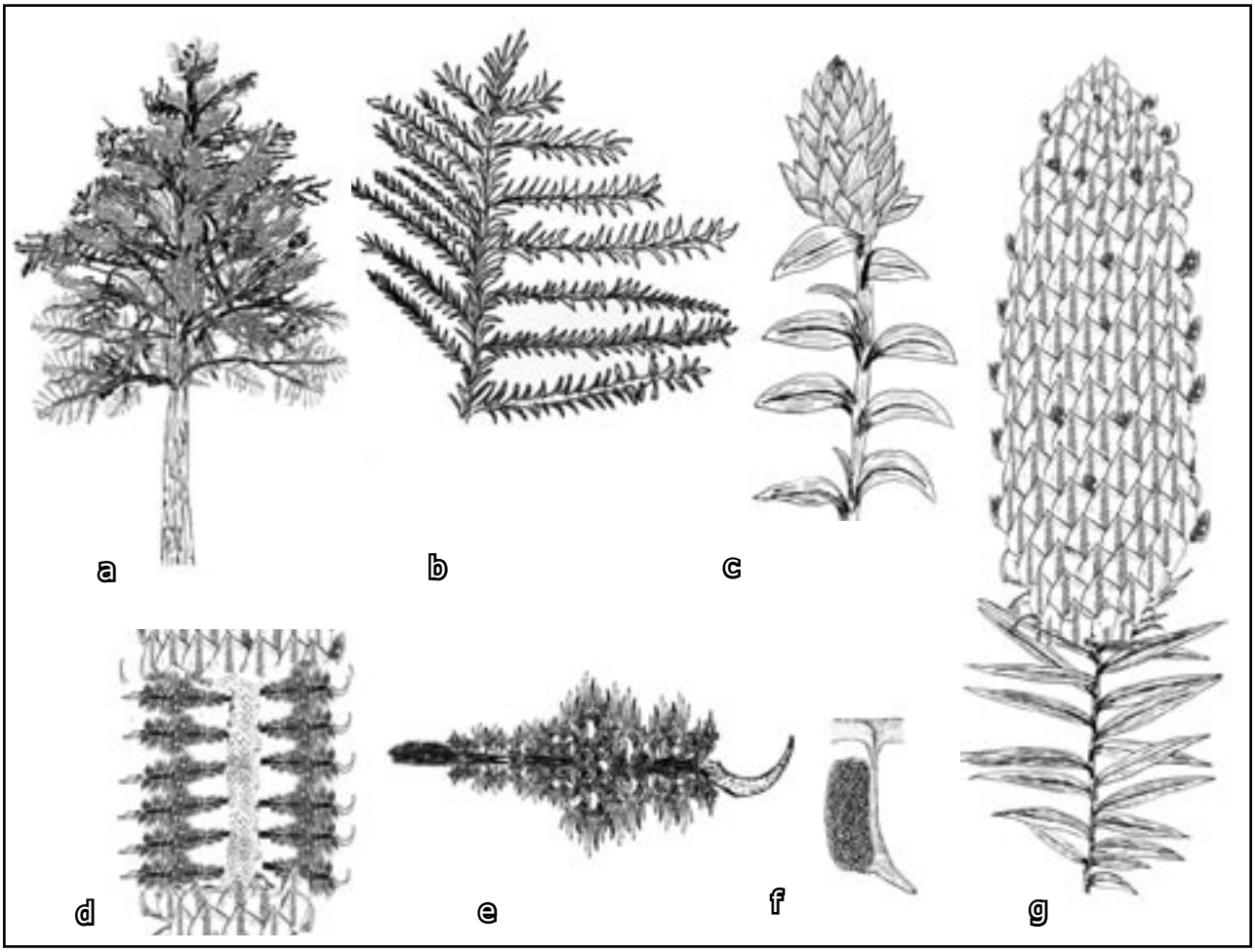
Darneya alpina pollen cones were therefore more consistent. *Darneya peltata* only bore a few elongated pollen sacs, whereas *D. alpina* had a 1 to 3 cm-long axis with spirally aggregated microsporophylls on a subtle peduncle. In this manner, they formed another micro-cone.

The male cones of *Darneya* (morphogenus for *Albertia*), *Willsiostrobus* (morphogenus for Mesozoic Voltziales) and *Alpianthus* (morphogenus for Alpiales) reveal differ-

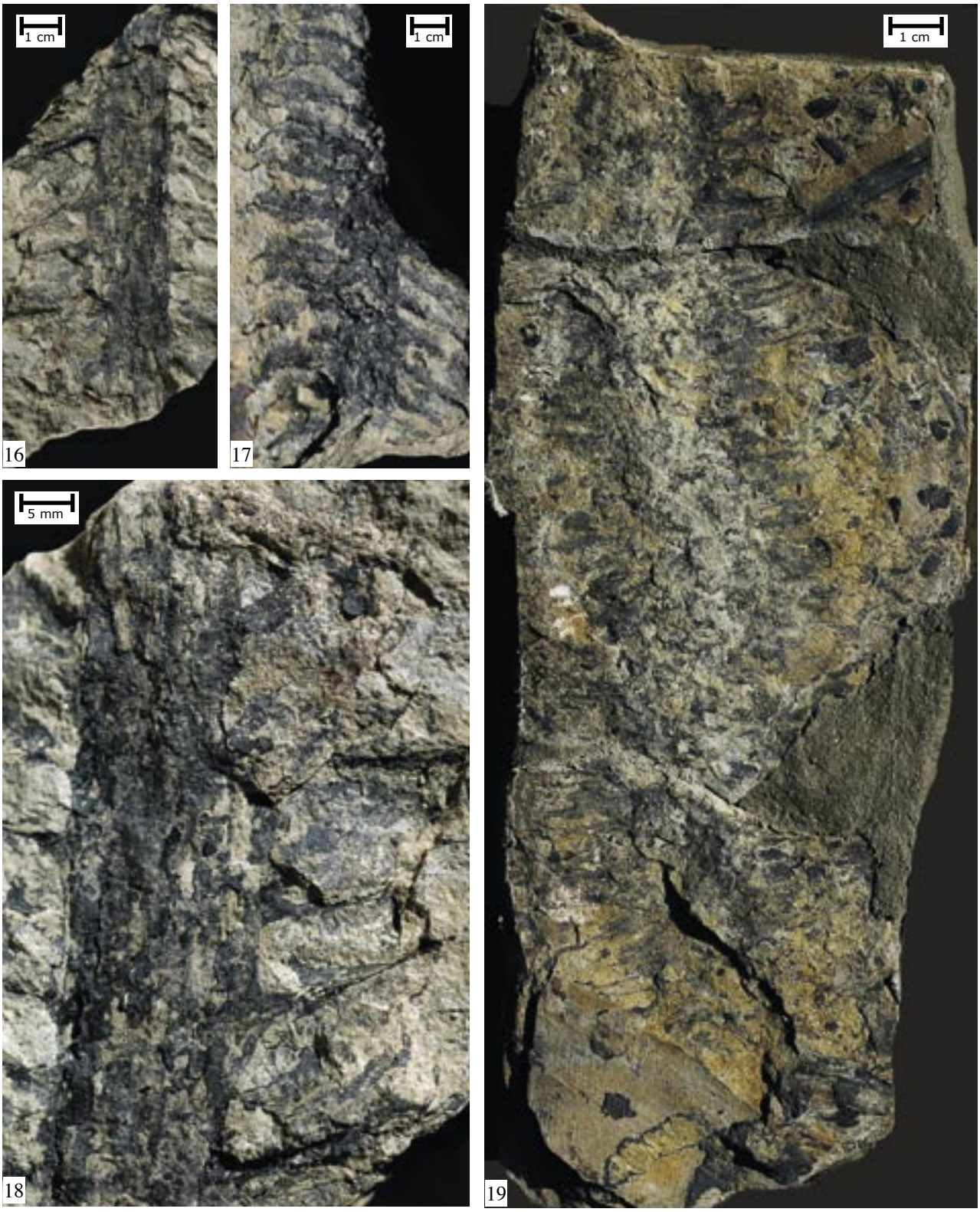


12) PIZ 603 *Darneya schaurothi* (holotype). Pollen cone with clustered microsporangia
13) PIZ 603 *Darneya schaurothi* (holotype). Detail of the the falcate termination of the covering scales
14) PIZ 603 *Darneya schaurothi* (holotype). Single pollen microsporophyll with the minute pollen sacs
15) PIZ 229 *Darneya schaurothi*. Detail of the pollen sacs arranged around the central axis

ent kinds of pollen organ organizations. The Willsiostrobus cones, with the microsporophylls attached to the distal lower edge, had a structure similar to the cones of the extant Araucariaceae. The difference between *Alpianthu*s and *Alpia anisica* and *Schizolepis ungeri* is obvious. Pollen organs of *Alpia* and *Schizolepis* are composed of several catkin-like upright growing and stalked micro-cones bearing the pollen sacs on the lower surface of minute microleaves. Regarding this feature, the *Darneya*-pollen cones stand isolated in the Early Mesozoic conifer assemblages.
It is difficult to establish the Permian progenitor for *Darneya alpina*, although one specimen classified as "conifer remains" from the Lower Permian in the Schleusingen Museum has all the outer aspects of a male *Darneya* cone. The microsporophylls consistently rise from the main axis in almost the same manner. Their distal parts also end in a long and pointed spine. Therefore, based on the sterile leaves and fructification from the Lower and Upper Permian, an early devolving line of this conifer family is suggested.
Seed cones: *Pusterostrobus* cones were usually small-sized and spherical. Megasporophylls from *Voltzia agordica*, known as *Tirolstrobus*, were much longer (15-20 cm), elongated and cylindrical. The bract scales were also mainly lobed. Female cones of *Alpia anisica* (named *Dolomitostrobus anisicus*) consist of entire rounded ovuliferous scales with only one consistent seed and are therefore also easily distinguishable from *Albertia*.



Albertia alpina – Suggested reconstruction of the conifer: a) whole plant, b) juvenile sterile shoot, c) Pusterostrobus haidingeri, immature female cone of Albertia alpina, d) *Darneya schaurothi*, part of a male cone with attached microsporophylls (PIZ 603), e) Darneya schaurothi - male fructification showing the attachment of pollen clusters, f) *Darneya schaurothi,* single pollen sac, g) *Darneya schaurothi*, entire male cone (PIZ 583)



16) PIZ 229 *Darneya schaurothi*. Part of a pollen cone
17) PIZ 229 *Darneya schaurothi*. Another part of the same cone
18) PIZ 229 *Darneya schaurothi*. Detail showing the wooden axis
19) PIZ 583 *Darneya schaurothi*. Mostly entire pollen cone. At 18 cm in length, it was a pollen bomb for the conifers

Division CONIFEROPHYTA
Order ALPIALES
Family ALPIACEAE

Alpia gen. nov. WACHTLER, 2011

Generic diagnosis

Mesozoic conifers with slender spreading shoots. Twigs with different juvenile and adult foliage characteristic. Leaves ranging from needle-like incurved and falcate, sticking straight out from the branchlets, changing to a quite narrow decussate foliage. Pollen organs with several catkin-like cones bearing minute microsporophylls. Pollen sacs on the lower surface. Female cones spherical in youth, to globose-elongated in the adult stage. Bract-seed scales partially fused, ligneous, ovuliferous scales non-lobed, most with one seed.

Etymology

After the Alps, where this Triassic conifer was native

Alpia anisica, sp. nov. WACHTLER, 2011

Holotype

PIZ 411 (Branch)

Paratypes

PIZ 40, PIZ 233, KÜH 1040, KÜH 1192, KÜH 991 (heterophyllous leaves)

Material

KÜH 697, PIZ 385, PIZ 233, PIZ 40, PIZ 132, KÜH 1312, KÜH 1264, PIZ 147, PIZ 356

Etymology

From the Anisian strata where they were found

Type localities

Piz da Peres, Kühwiesenkopf

Type horizon and age

Early-Middle Triassic, Anisian, Pelson

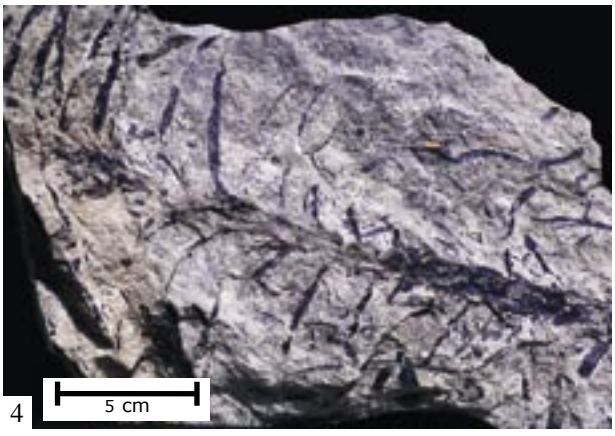
Diagnosis

Medium-growing conifer with symmetrical bipinnate branches arising at right angles from the main trunk. Shoots bearing flattened falcate and narrow needles, sharply pointed at the apex. Heterophyllous leaves present. Small-sized pollen cones developing in groups between sterile leaves. Globose to elongated seed cones with one bulky, nut-like seed embedded in the upper surface of an entire, non-lobed, rounded seed scale.

Description

Vegetative branches: Holotype PIZ 411 from Piz da Peres – Wachtler gorge – was chosen because of its typically falcate and

PIZ 356 *Alpia anisica*. Mostly entire shoot (reconstructed in parts), Piz da Peres

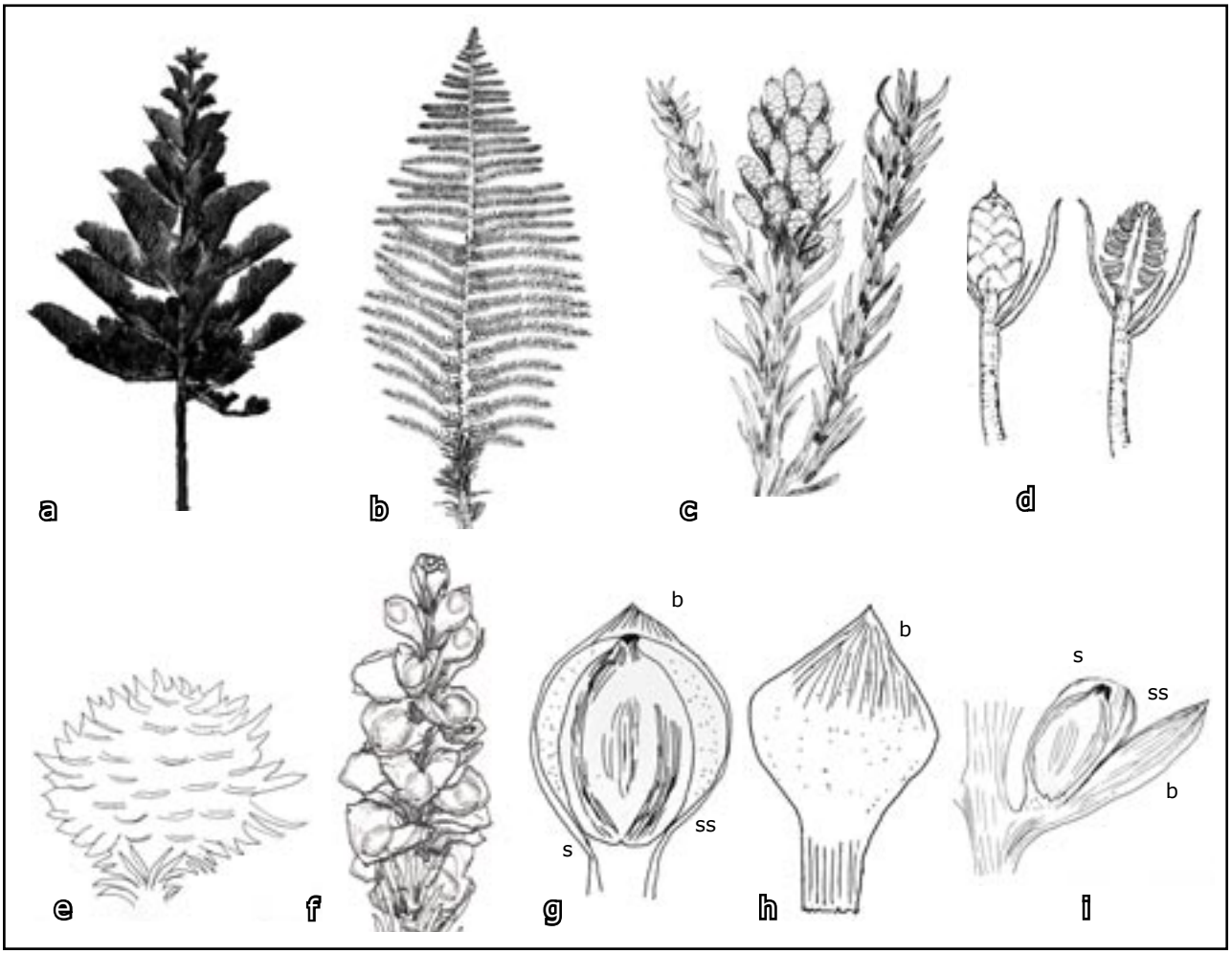


1) KÜH 1040 *Alpia anisica*. Weather-destroyed branch, Kühwiesenkopf lower strata
2) KÜH 1192 *Alpia anisica*. Shoot with regular needle-like leaves, Kühwiesenkopf lower strata
3) KÜH 991 *Alpia anisica*. Heterophyllous leaves on a branch. Needles up to 5 cm long, Kühwiesenkopf lower strata
4) KÜH 697 Alpia anisica. Detail of a heterophyllous twig, Kühwiesenkopf lower strata

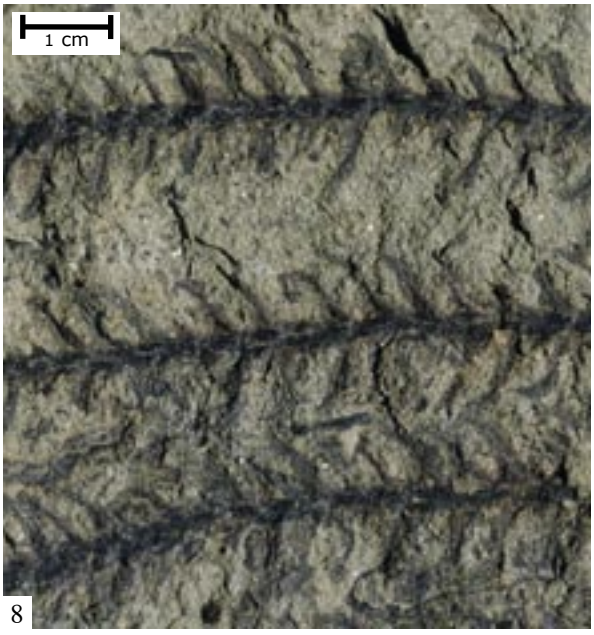
pointed subtle needles. PIZ 356, also from Piz da Peres – 60 cm long, 40 cm wide – shows the habitus of a mostly entire shoot, with geometrically opposing to slightly subopposing, non-forked branchlets. The main branch axis is covered with 3 to 5 cm-long leaves, which are sparsely spaced from one another. Even though the vegetative shoots of the lower Kühwiesenkopf layers are a little older in age, they only differ in some details; only further analysis would show whether or not another Alpia subspecies has to be formed. Some of the material especially KÜH 1040, demonstrate a greater tendency towards heterophylly, also shown by KÜH 697 and KÜH 991, which have twigs with 5 cm-long needles and a width of 1 mm.

Vegetative leaves: Needles lanceolate, awl-shaped, incurved and decurrent, reaching a length of 1 to 2.5 cm, with a thickness at the base of only 1 mm (holotypes PIZ 411, PIZ 233, PIZ 40). On older branches and the main axis, some of the leaves reached a length of 3-6 cm. They were stiff and hard, scale-like or transitional between being claw- and scale-like, occasionally tightly overlapping. The reason for this heterophyllous aspect presumably has nothing to do with shade or sun exposed orientations but rather with the typical characteristic of Alpiaceae of forming juxtaposed juvenile and adult foliage on the same branches. Paratype KÜH 1040 exhibits a large twig (24 cm long, 20 cm wide) with broken limbs from storm or environmental influences.

Pollen cones: Of the *Alpianthus anisicus* type. *Alpia ansica* holds small-sized catkin-like pollen cones in the axils of sterile leaves.



Alpia anisica – Suggested reconstruction of the conifer: a) whole tree, b) complete twig, c) *Alpianthus anisicus* – male cone of *Alpia anisica* (PIZ 42), d) male cone with detail of the pollen sacs, e) *Dolomitostrobus anisicus* – immature female cone (KÜH 1249), f) *Dolomitostrobus anisicus* – decaying adult female cone (PIZ 514), g) Seed-scale interior, h) Bract-scale: outer side, i) Bract-scale: lateral side (ss = seed-scale, s = seed, b = bract-scale)



5) PIZ 411 *Alpia anisica* (holotype). Part of a shoot
6) PIZ 385 *Alpia anisica*. Detail of a main shoot with falcate needles
7) PIZ 233 *Alpia anisica*. Last order shoot
8) PIZ 40 *Alpia anisica*. Detail of a main shoot with falcate needles

Seed cones: Of the *Dolomitostrobus anisicus* type. Female cones spherical in youth, opening to an elongated cone, with rounded, entire ovuliferous seed scales, with one consistently embedded fleshly seed, which fills most of the length and width of the scale. The cone decayed after maturity.

Alpianthus gen. nov. WACHTLER, 2011

Generic diagnosis

Male organs consisting of a cluster of small-sized pollen cones. Each catkin-like cone is attached to a main axis with spirally arranged bud scales with pollen sacs on the lower surface of the microsporophylls.

Etymology

After the Dolomite mountains, where rich fossilized conifer sites were discovered.

Alpianthus anisicus, sp. nov. WACHTLER, 2011

Holotype

PIZ 132

Paratype

PIZF 42, KÜH 1423

Material

KÜH 1417

Etymology

After the Anisian strata, where they were found

Type localities

Piz da Peres, Kühwiesenkopf

Type horizon and age

Early-Middle Triassic, Anisian, Pelson

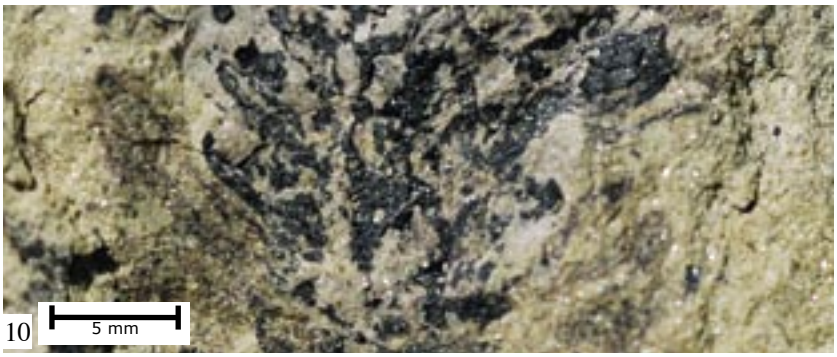
Diagnosis

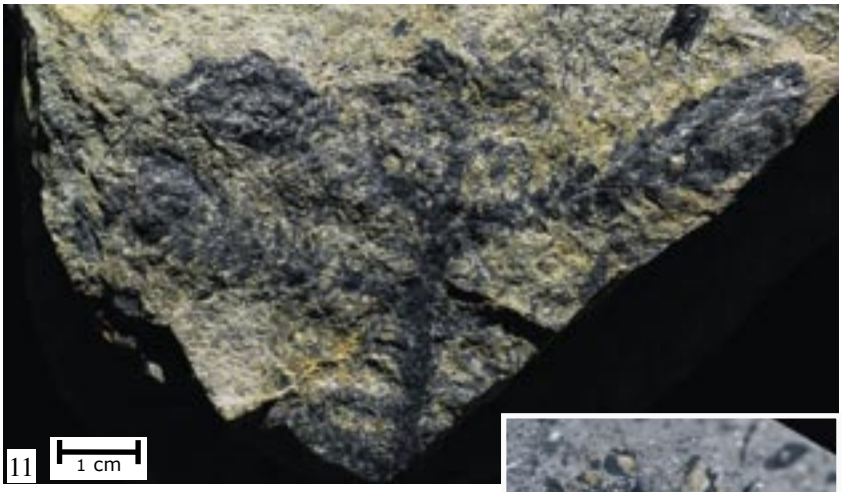
Male fructifications with small-sized pollen organs sprouting in the axils or between ordinary leaves. Micro-cones cylindrical to elongated and attached to slim stalks, with spirally arranged microsporophylls on the upper part, holding the pollen sacs on their abaxial side.

Description

Holotype PIZ 132 shows the features of an *Alpianthus anisicus* male cone releasing pollen grains. The slender pollen cones originate between ordinary, sterile, incurved leaves. The entire fertile compound is 4 cm long and 1.5 cm wide. The real pollen organ sprouts from a 5 to 8 mm-long slender stalk and forms a cylindrical to elongated, 0.3 to 0.7 cm long, 1-3 mm wide structure. The pollen scales, closed when immature, hold their pollen sacs on the lower surface. Paratype PIZF 42 and material KÜH 1417 show fully-grown male cones with leaves of the *Alpia anisica* type. KÜH 1423 is a good example how the pollen cones were arranged on the shoots.

Alpia anisica. PIZ 517 Part of a stem





9) PIZ 132 *Alpianthus anisicus* (holotype). Pollen-bearing cone
10) PIZ 132 *Alpianthus anisicus* (holotype). Detail of stalked microsporophylls
11) KÜH 1423 *Alpianthus anisicus.* Several juvenile male cones on a shoot from Kühwiesenkopf – lower strata
12) PIZF 42 *Alpianthus anisicus*. Male cone with *Alpia anisica* foliage
13) KÜH 1417 *Alpianthus anisicus*. Pollen-bearing cone with attached shoot
14) KÜH 202 *Alpianthus anisicus*. Pollen-bearing cone with attached shoot from Kühwiesenkopf – lower strata

Dolomitostrobus gen. nov. WACHTLER, 2011

Generic diagnosis

Female conifer cones: spherical when immature, globose to elongated with sparsely ovuliferous scales in the adult stage. Bract-seed scales partially fused, entire and non-lobed, generating one to two seeds.

Etymology

Named after the region where found: the Dolomites

Dolomitostrobus anisicus WACHTLER, 2011

Holotype

PIZ 514

Paratypes

PIZ 410, KÜH 1249 (immature female cone), PIZ 188, PIZ 147 (seed)

Material

PIZ 139, PIZF 48, PIZ 232

Etymology

Named after the Anisian, the geological time period from when they were found.

Type localities

Piz da Peres, Kühwiesenkopf, Ritberg

Type horizon and age

Early to Middle Triassic, Anisian, Pelson

Diagnosis

Globular to elongated conifer seed cones with mostly entire, rounded, non-lobed seed scales arranged in spirals along an axis. Single nut-like seeds embedded on the upper side of a partially fused bract scale.

Description

Juvenile *Dolomitostrobus anisicus* cones are globose with a size ranging from 2 to 3 cm in length and 2 to 3 cm wide. The most complete cone branch is KÜH 1249AB, where four juvenile cones are attached to a single shoot. They are encased on 2.5 cm-long sterile leaves on each side; the fertile scales are closely coated in the strobilus. Holotype PIZ 514 shows a semi-mature seed cone with 16-20 fertile bract scales, containing more or less rounded to slightly elongated seeds embedded in the upper surface of each scale. The cone is 6 cm long, 3 cm wide; each seed scale has a length between 0.7 and 1 cm. A good example for a mature cone holding seeds is PIZ 188. Each cone scale is composed of a bract-scale complex with the partially fused bracts as long as the seed scales. Each non-lobed seed scale consistently has seeds that mainly fill the whole scale. The single, fleshy, nut-like seeds (1 cm long, 0.8 cm wide) were embedded in the upper surface in the tissue of the scale. Paratype PIZ 188 is a mostly decayed cone, with only 12 scales, showing three seeds. All of the others had just been shed. Material PIZ 139 exhibits a mostly three-dimensional cone when viewed from the outer side. The bract ends are tapered, showing no indication of a lobed structure. Seed cone PIZ 410AB is mostly spherical, 5 cm long and 5 cm wide, and is directly attached to a shoot with leaves of *Alpia anisica*. An example of an entire fossilized seed is PIZ 147. The seed is 1.2 to 0.7 cm long, with two emarginations in the middle.

Alpia ladinica, comb. nov. WACHTLER, 2000

2000 *Voltzia ladinica* WACHTLER & VAN KONIJNENBURG, p. 10, Figs. 1-5, p. 11, Figs. 1-5

Holotype

WRI 31 (branch holding one immature female cone)

Paratype

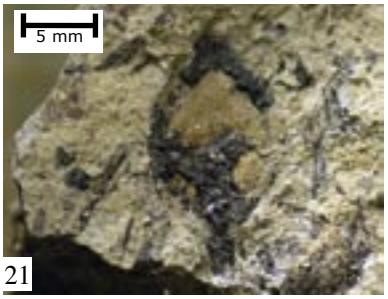
WSW 46

Material

Shoot, Museum de Gherdeina

Etymology

From the Ladinian strata, where it was found



15) KÜH 1249 *Dolomitostrobus anisicus*. Four young female cones on a twig
16) PIZ 514 *Dolomitostrobus anisicus*(holotype). Female cone with seeds
17) PIZ 514 *Dolomitostrobus anisicus* (holotype). Entire scale holding one large-sized seed
18) PIZ 410 *Dolomitostrobus anisicus*. Female cone belonging to *Alpia anisica*
19) PIZ 188 *Dolomitostrobus anisicus*. Almost decayed female cone with seeds
20) PIZ 139 *Dolomitostrobus anisicus*. Mature cone from the outer side
21) PIZ 147 *Dolomitostrobus anisicus*. One isolated seed: 1.3 cm - 0.7 cm wide
22) PIZF 48 *Dolomitostrobus anisicus*. One isolated seed. 1.7 cm - 0.7 cm wide

Voltzia heterophylla. Old specimen collected at Raibl, Carnian. Geologische Bundesanstalt Vienne. The specimen probably belongs to an evolving line of Alpia.

Type localities

Seewald – Braies, Ritberg – La Val, Val Gardena

Type horizon and age

Middle-Triassic, Upper Ladinian-Langobardian

Diagnosis

Characteristic conifer of the Ladinian with incurved falcate and quite narrow needles on young trees and sometimes with a tendency towards strong heterophylly of the needles on fully-grown plants. Seed cones with entire non-lobed ovuliferous scales, holding one seed.

Description

Most details were documented in a previous work about the Ladinian flora of the Dolomites (WACHTLER & KONIJNENBURG – VAN CITTERT, 2000). With the finding of abundant material from the Anisian, this conifer could be seen in a new light. Therefore, the former classification as *Voltzia ladinica* could not be sustained for the following reasons: although the foliage of many conifers is almost the same, there are consistent differences in the structural concept of the cones. Mesozoic female Voltziales cones were characterized by their more-lobed bract scales, usually with small-sized seeds. This detail would be replaced in *Alpia ladinica* by their entirely non-lobed seed scales, each holding only one seed. Therefore, for this group of conifers, it was reasonable to establish a new family: the Alpiaceae.

Dolomitostrobus ladinicus WACHTLER, 2011

2000 *Voltzia ladinica*, WACHTLER & VAN KONIJNENBURG, p. 10, Figs. 1-2

Holotype

WSW 52

Paratype

WRI 31AB

Etymology

Named after the Ladinian, an important geological time period

Type localities

La Val – Ritberg, Prags Seewald

Type horizon and age

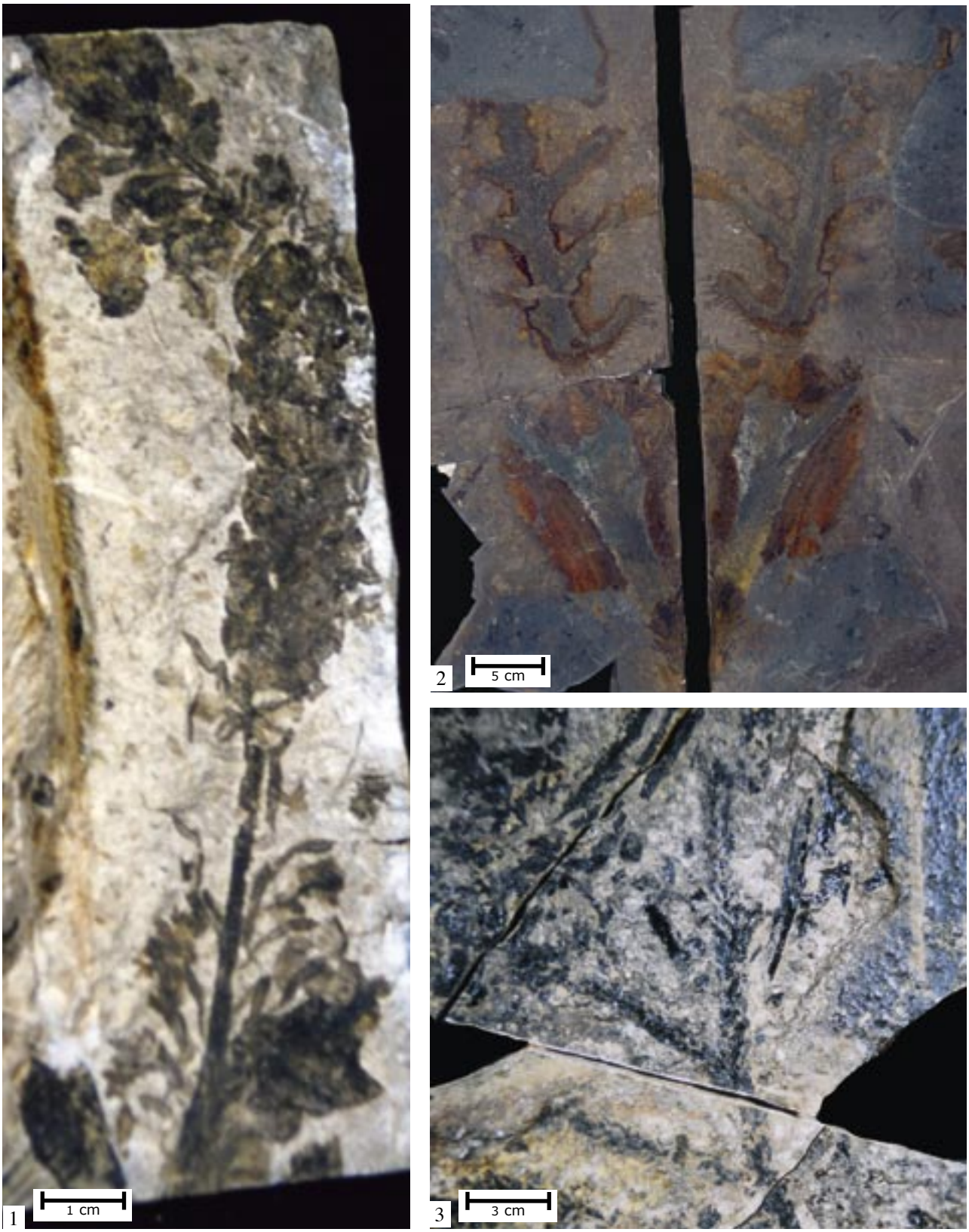
Middle-Triassic, Upper Ladinian-Langobardian

Diagnosis

Female conifer cones, globose when immature, elongated when mature, with mostly entire non-lobed cone scales arranged in spirals along an axis. Single seeds.

Description

Holotype WSW 52 – a semi-mature female cone – is 8 cm long, 1.5 cm wide and bears several bract scale units that are mostly rounded and entire. The megasporophyll shows some attached seeds on the fertile scales. The rounded to elongated seeds mostly fill the entire scale.



1) WSW 52 *Dolomitostrobus ladinicus* (holotype). Detail of a female cone.
2) *Alpia ladinica* (Museum de Gherdeina). Part and counterpart. Shoot with normal and heterophyllous leaves.
3) WRI 31 *Alpia ladinica* (holotype). Branch with one juvenile cone attached to the upper left shoot.

General remarks

Vegetative branches and leaves: As in the Alpine Voltziales, and also in other characteristic Alpine Mesozoic conifer groups, such as the Alpiaceae, we have an interesting evolutionary tendency from *Alpia anisica* across *Alpia (Voltzia) ladinica* (WACHTLER & KONIJNENBURG – VAN CITTERT, 2000) to Carnian *Alpia (Voltzia) raiblensis* (DOBRUSKINA et al., 2001) from the Raibl-strata on the Austrian-Italian boarder. Flexuous, decurrent and narrow needles characterize all of these conifers. Beginning with the Ladinian *Alpia ladinica*, there is also a tendency for tripinnate shoots, a novelty that would never be observed in older *Alpia anisica*. Although the similarity between foliage types in the conifers is not a distinguishing attribute, the most important feature for establishing a new family, compared to the Voltziaceae, was the completely different structural plan of the female and male cones. Regarding this feature, they resemble extant Pinaceae and Cupressaceae more than the Araucariaceae.

Pollen cones: *Alpianthus* pollen cones totally differ from the peltate microsporophylls of the Voltziales, as well the extant Araucarians, by holding several pollen sacs on the lower edge, curved in the direction of the cone axis. *Alpianthus* male cones formed catkin-like clusters in the axils of sterile leaves. Like extant Pinaceae, this could be defined as an *Alpianthus* cone conglomeration, with the formation of a one cone-complex.

Seed cones: In contrast to the three-lobed bracts of the Mesozoic Voltziales, such as coeval *Voltzia agordica*, with small-sized seeds embedded on tiny scales, *Alpia anisica* usually holds only one substantial and fleshy nut-like seed. The generalization that all ancient conifers evolved from a compound dwarf shoot, as reported in the exhaustive works of Rudolf FLORIN (1931, 1951, 1955), could not be evidenced in *Dolomitostrobus* and has to be revised. Regarding this feature, they have a striking resemblance to Paleozoic *Ullmannia* seed cones. Therefore, it is more probable that the Ullmaniaceae and Alpiaceae evolved from one group of archaic conifers where one compound dwarf shoot generated one female cone, whereas in the Voltziales one dwarf shoot only evolved one bract-seed scale and therefore a cone was formed from innumerable dwarf shoots.

Order ALPIALES
Family SCHIZOLEPISACEAE
Genus Schizolepis, BRAUN, 1847

1846 *Voltzia schizolepis*, BRAUN, p. 158
1847 *Schizolepis liaso-keuperianus*, BRAUN, p. 86
1871 *Schizolepis braunii*, SCHENK, (1865b-67), p. 179, Pl. XLIV, Figs. 1-8
1897 *Schizolepis cylindrica*, NATHORST, Pl. 2, Figs. 1-2
1919 *Schizolepis braunii*, SEWARD, p. 439
1995 *Schizolepis liasokeuperianus*, KELBER & HANSCH, Fig. 275

Schizolepis ungeri, sp. nov. WACHTLER, 2011

Holotype

AGO 01

Paratypes

AGO 70 (stem), AGO 14, AGO 49, AGO 66, AGO 2 (male cones), AGO 4, AGO (female cones)

Material

AGO 68 (roots), AGO 70, AGO 72, AGO 65 (stems), AGO 67, AGO 73

Etymology

After Franz Unger, the father of Austrian paleobotany, who described the first plants in the Dolomites

Repository

Museo Civico, Belluno

Type locality

Val Imperina – Agordo

Type horizon and age

Early-Middle Triassic, Anisian, Pelson

Diagnosis

Large branching, multipinnate conifers with juxtaposed juvenile and adult foliage. The leaves come in two forms: adult shoots hold falcate, strongly outwards spreading leaves, juvenile twigs produce narrow, needle-like, close fitted and more or less appressed

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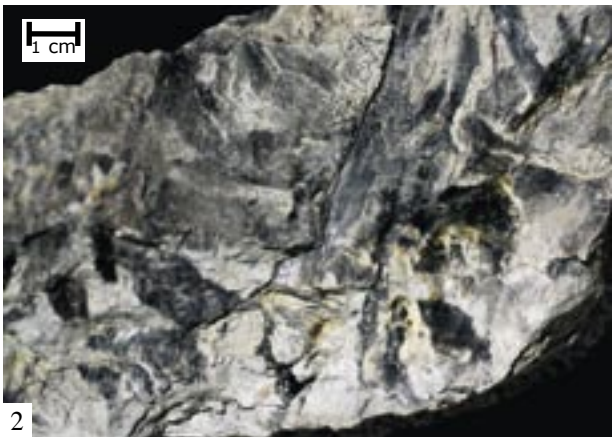

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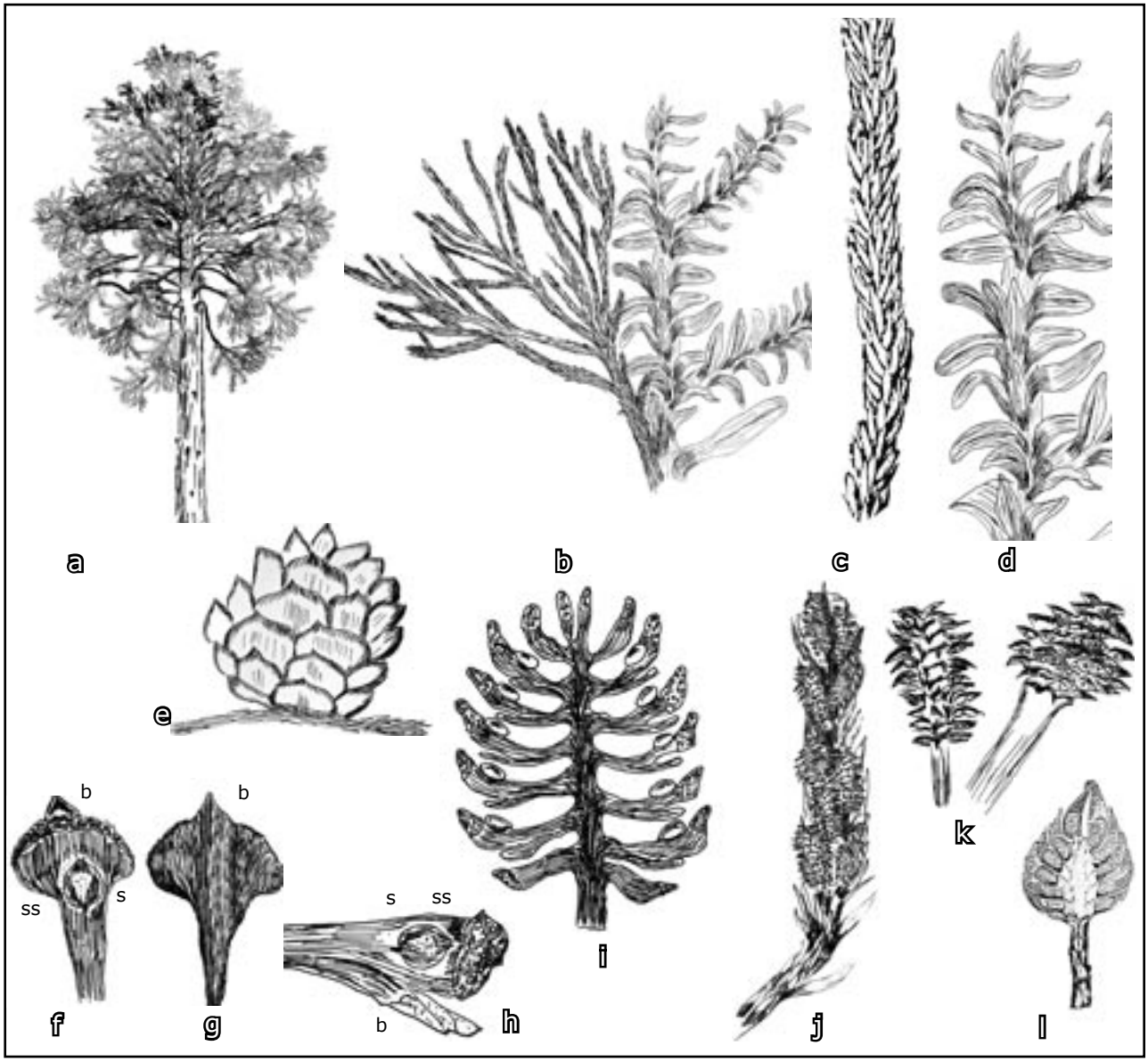
1) AGO 1 *Schizolepis ungeri* (holotype). Slab clearly showing the two types of leaves
2) AGO 68 *Schizolepis ungeri*. Part of a root system
3) AGO 70 *Schizolepis ungeri*. Stem with bark and peeled cortex
4) AGO 72 *Schizolepis ungeri*. Inner structure of a trunk
5) AGO 65 *Schizolepis ungeri*. Stem fragment

leaves. Male organs are terminal, cylindrical with several catkin-like pollen cones. Microsporophylls hold the pollen sacs on their lower surface. Female cones globose, holding a few, partially fused bract-seed scales. The ovuliferous scales are tapered, fleshy and generate small-sized seeds.

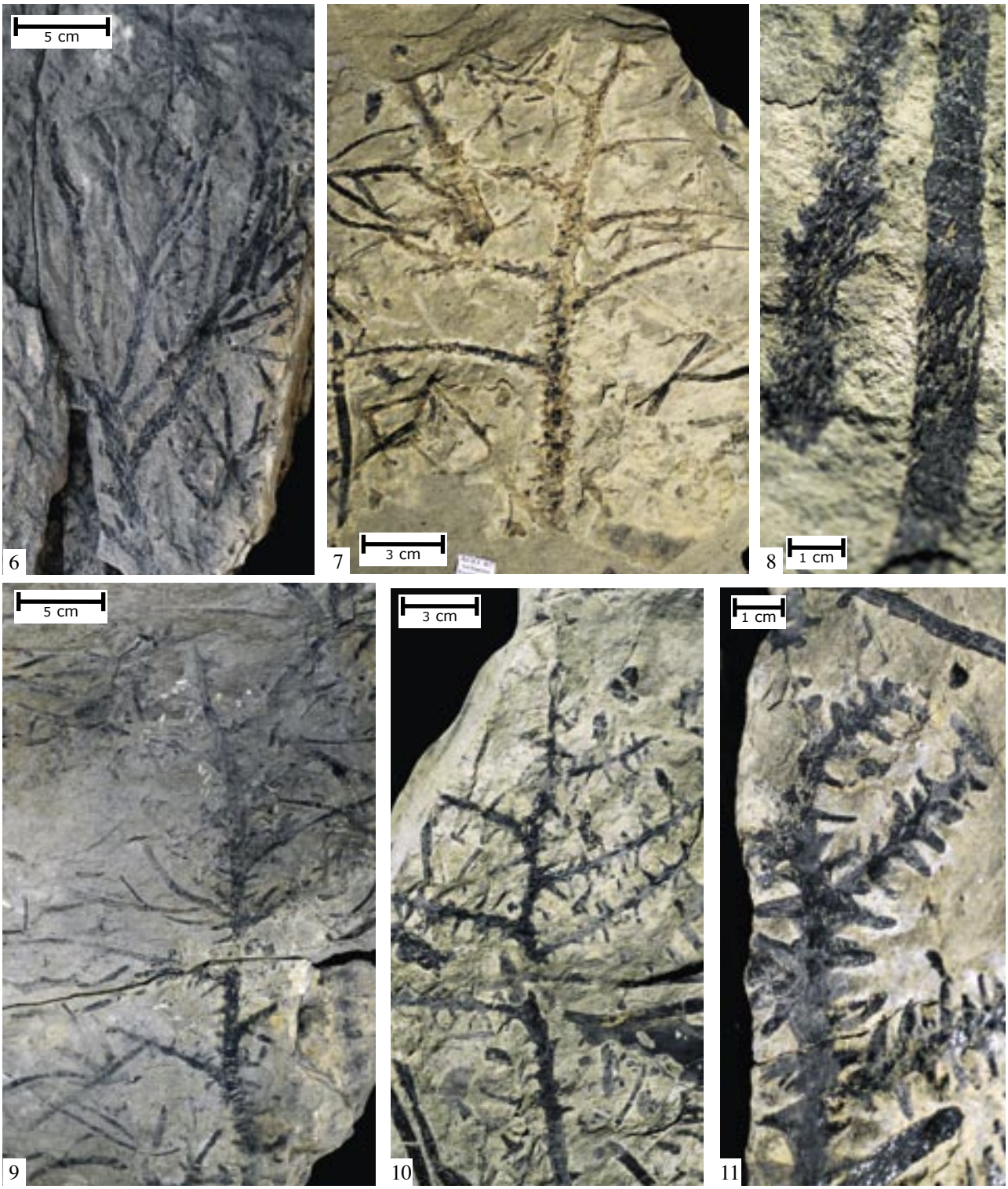
Description

Vegetative branches: Foliage sprays with mature leaves are sparsely branched with flattened and protruding needles; shoots with juvenile leaves are multipinnate, with needle-like foliage closely appressed to the twigs. Holotype AGO 01 clearly shows the two patterns of shoots.

Vegetative leaves: Branchlets bearing adult foliage with leaves 1 to 2 cm-long and 0.5 cm-wide leaves. They were falcate, sharply triangular, loosely spreading outwards, broader at the base and sharply pointed on the apex. Good examples are AGO 66 and AGO 49. On some shoots (AGO 67, AGO 73), a crossover



Schizolepis ungeri – Suggested reconstruction of the conifer: a) whole plant, b) sterile shoot with juvenile and adult foliage (AGO 01), c) juvenile foliage (AGO 14, d) adult foliage (AGO 66) e) *Dolomitostrobus bellunensis* – juvenile cone (AGO 48) f) Seed-scale interior, g) Bract-scale: outer side, h) Bract-scale: lateral side (ss = seed-scale, s = seed, b = bract-scale) i) *Dolomitostrobus bellunensis* – mature female cone of *Schizolepis ungeri* (AGO 60), j) *Alpianthus ungeri* – male cone of *Schizolepis ungeri* (AGO 3), k) *Alpianthus ungeri* – mature pollen cones AGO 18) l) *Alpianthus ungeri* single pollen cone, inside view.



6) AGO 1 *Schizolepis ungeri* (holotype). Shoot with juvenile leaves, which were subtle, needle-like and pressed against the twig

7) AGO 67 *Schizolepis ungeri*. Example of a branchlet with transitional juvenile and adult leaves

8) AGO 14 *Schizolepis ungeri*. Detail of a branch with juvenile foliage

9) AGO 73 *Schizolepis ungeri*. Branchlet with adult and juvenile leaves

10) AGO 49 *Schizolepis ungeri*. Branchlet with adult leaves

11) AGO 66 *Schizolepis ungeri*. Detail of adult, sharp pointed and falcate foliage

from one foliage stage to another could be seen. Juvenile leaves are subtle, decurrent, linear and mostly pressed against the twig. They are only up to 5 mm long, 0.1 mm wide (AGO 14), close attached to and encasing the axis, giving the appearance of a glossy shoot. The shoots do not reach more than 4-5 mm in thickness and fork several times. A mostly entire branch of this type is visible on AGO 1 (right side).

Pollen cones: Of the *Alpianthus ungeri* type. Entire male fructifications, 5 to 7 cm long, 1 cm wide, consisting of a cluster of cylindrical pollen organs, generating 12 to 14 microsporophylls, each ca. 1 mm in width, with denticulate margins. Microsporangia are abaxially borne.

Seed cones: Of the *Dolomitostrobus bellunensis* type. Female cones are spherical in the juvenile stage, mostly globose, seated at the outer margins or nearer the base of foliage sprays with juvenile leaves. Mature cones are subglobose, with a few widely spread triangular to slightly pointed ligneous scales. One to two seeds are generally embedded in the upper surface of each scale.

Alpianthus ungeri, sp. nov. WACHTLER, 2011

Holotype

AGO 03

Paratypes

AGO 02, AGO 06, AGO 56

Material

AGO 53, AGO 13

Etymology

After Franz Unger, pioneer of Paleobotany in the old Austrian Empire

Type locality

Val Imperina Agordo

Type horizon and age

Early-Middle Triassic, Anisian, Pelson

Diagnosis

Male conifer fructifications consisting of several small-sized pollen cones sprouting from the axils of specialized reproductive shoots. Each cylindrical pollen cone is attached to a long, slender stalk, which holds spirally arranged, more or less umbrella or shield-shaped microsporophylls with the pollen sacs on the abaxial side.

Description

Holotype AGO 03 presents an entire cone on a shoot of *Schizolepis ungeri*. The whole fructification is 5 cm long and 1 cm wide, whereas the regular catkins, attached to a 5 mm-long 1 mm-thick stalk are from 5 to 10 mm long and 4 to 6 mm wide (AGO 03, AGO 06, AGO 31). Several microsporophylls lie closely appressed on the central axis, holding the attached pollen sacs on the lower surface. On AGO 06, six rows, each holding from 4 to 8 microsporophylls, were observed. Material AGO 13 is a mostly decayed pollen cone, whereas AGO 56 and AGO 53 show a slightly pointed extension on the apex of each minute pollen cone. The small-sized pollen cones are densely closed in the juvenile stage; the microsporophylls open when they are mature to release their pollen grains. Usually, entire male organs do not exceed a length of 5 to 8 cm by 0.8 to 1.2 wide.

Dolomitostrobus bellunensis, sp. nov. WACHTLER, 2011

Holotype

AGO 60

Paratypes

AGO 04, AGO 48, AGO 66 (seed)

Material

AGO 10, AGO 61, AGO 82

Etymology

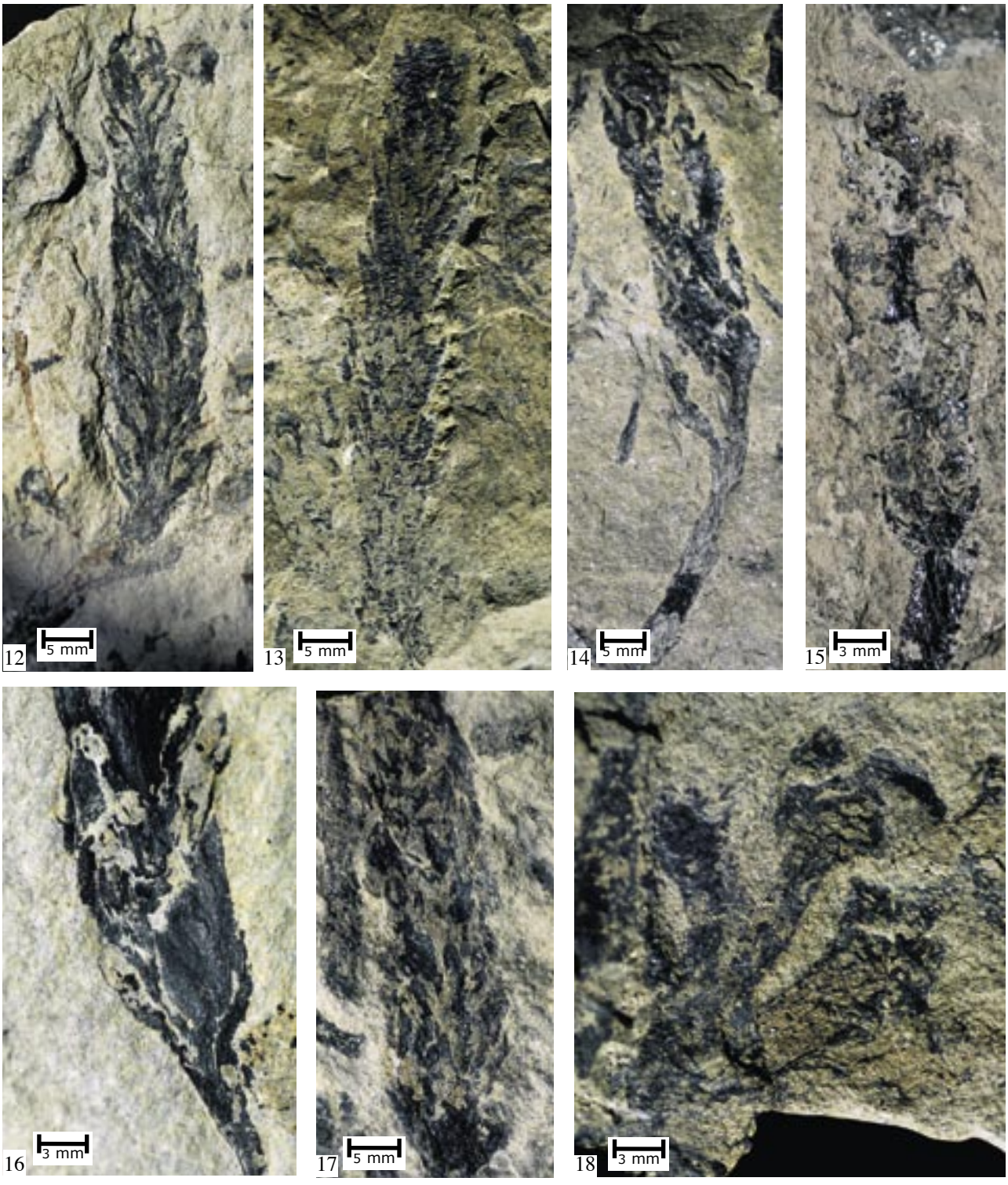
After the northern Italian province of Belluno, where the cones were found

Type locality

Val Imperina Agordo

Type horizon and age

Early-Middle Triassic, Anisian, Pelson



12) AGO 3 *Alpianthus ungeri* (holotype). Example of an almost mature pollen organ
13) AGO 2 *Alpianthus ungeri*. Entire pollen organ
14) AGO 53 *Alpianthus ungeri*. Male organ with the catkin-like pollen cones
15) AGO 13 *Alpianthus ungeri*. Mostly decayed pollen organ
16) AGO 31 *Alpianthus ungeri*. Detail of the pollen catkin
17) AGO 56 *Alpianthus ungeri*. Lower part of the pollen cones
18) AGO 6 *Alpianthus ungeri*. Three pollen cones with open pollen sacs attached

Diagnosis

Seed cones nearly spherical, with densely closed bract scales when immature, opening and mainly spreading outwards when mature. Cone scales elongated, slender on the base with a mostly triangular and entire head on the face, with one to two seeds embedded in the upper surface of a partially fused bract scale. Seeds are embedded in the upper surface of an entire, rounded to pointed ovuliferous scale.

Description

Good examples of juvenile *Dolomitostrobus bellunensis* seed cones are shown by AGO 48 and AGO 10. They were seated on juvenile *Schizolepis ungeri* foliage and at this stage are spherical and closed. Normally they are 2 to 3 m long and wide. Holotype AGO 60 and also AGO 04 show cones that are ready to shed their seeds. On AGO 04 – which represents an undeveloped cone – the scale bracts could be seen from the upper side. A 1 cm-long stalk opens to a 5 to 7 mm-wide and 3 to 5 mm-long triangular shield. One seed for each scale is held by a minute stalk. Paratype AGO 60 consists of a fully-grown female cone, where some of the seeds have just been released. Only 10 bract scales were observed. The seed scales end in entire, non-lobed margins, which are obtusely pointed, ligneous and fleshly. Examples of dispersed seeds are AGO 86 and AGO 82. The seeds could reach a length of 5 to 7 mm and a width of 3 to 5 mm.

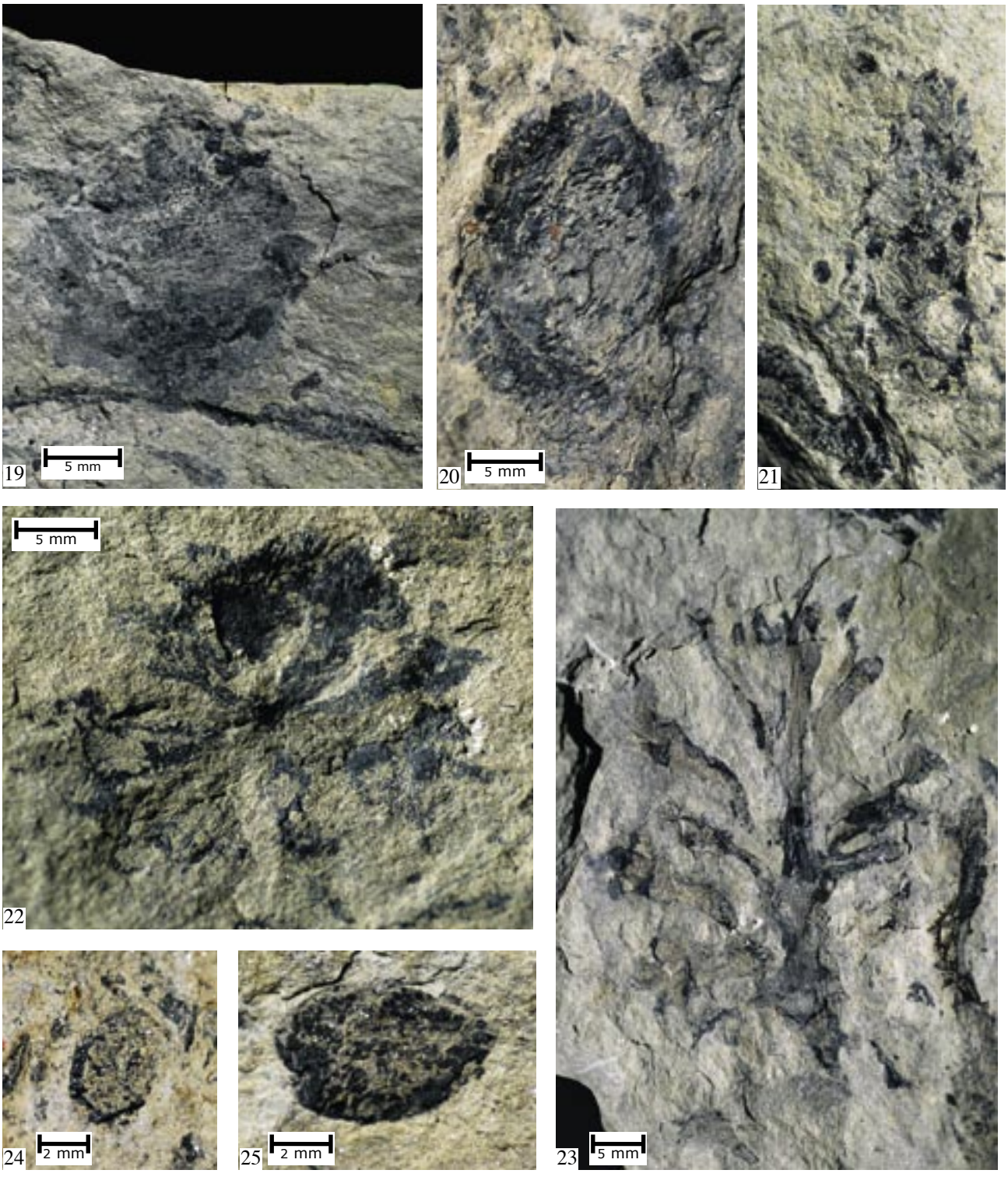
Discussion

BRAUN introduced the genus *Schizolepis (liasokeuperianus*) in two publications (1846 and 1847) for a conifer with acuminated leaves and scale-like cones that was found in rhaetic-liassic rocks near Veitlahm in Baviera. In his "Die fossile Flora der Grenzschichten des Keupers und Lias Frankens" (1871), A. SCHENK – another pioneer of German paleobotany – established the species *Schizolepis braun*i for material found in the same place where BRAUN had described his conifers, and illustrated leaves, shoots and stems on plate XLIV and Figures 1-6 and part of a female cone, with the suggested one or two-lobed scales and attached seeds, in Figures 7 and 8. Because the two conifers are thought to be synonymous, *Schizolepis liasokeuperianus* was validated by several authors who recognized that this conifer was a common floral element of Northern hemisphere Jurassic rocks (KELBER & HANSCH, 1995, WANG et. al. 1997)). Isolated detached branchlets and leaves have been found to be numerous in sediments, but complete shoots or cones have rarely been found. *Schizolepis* was suggested to hold spirally arranged, bilobate, with one till two seed bearing scales in the bract axils.

Some doubt arose because other authors (especially SEWARD, 1919a) restricted the term *Schizolepis* to only female cones or cone scales from the Rhaetic beds in Germany, Sweden and Poland, from Middle Jurassic floras or incomplete strobili found in the Upper Jurassic or Wealden strata in Spitzbergen, whereas the genus *Pityophyllum* was established for vegetative shoots. This form of genus was first introduced by Swedish researcher A. G. NATHORST (1897) for sterile leaves and branches discovered during his long stays in Spitzbergen. Because there is no reason to suppose that all of the older authors (BRAUN 1846, 1847, UNGER 1850, SCHENK 1871) connected only female fructifications to this genus, the term *Schizolepis* is used here for vegetative shoots and leaves of an interesting conifer, only known incompletely until now.

Meanwhile, *Schizolepi*s was investigated in many areas of the Northern globe from Turkestan, South Russia and Mongolia to China and Europe (Portugal, Poland, England, Germany), and is thought to have occurred from the Early Permian to the Jurassic. As with the female cones, leaves were created by many different species, showing how problematic a clear classification is when based on poorly known material without connection to fertile or sterile material (*Schizolepis follini*, NATHORST; *S. cylindrical*, NATHORST, from Spitzbergen; *S. moelleri*, SEWARD; *S. retroflexa*, SCHENK; S. pedicelata TURUTANOVA-KEYOVA, from Russia; *S. beipiaoensis*, ZHENG; *S. shangyuanensis*, ZHENG, from China; *S. daohugouensis*, ZHANG et. al. from Mongolia).

Most of the authors confirmed a phylogenetic position for *Schizolepis* between the Voltziales and the extant Pinaceae (WANG et. al. 1997), and identified the bilobed seed scales as a further developmental line from



19) AGO 48 *Dolomitostrobus bellunensis*. Juvenile globose female cone
20) AGO 10 *Dolomitostrobus bellunensis*. Juvenile female cone
21) AGO 61 *Dolomitostrobus bellunensis*. Semi-adult cone
22) AGO 4 *Dolomitostrobus bellunensis*. Female cone with juvenile seeds
23) AGO 60 *Dolomitostrobus bellunensis* (holotype). Mature female cone with some seeds embedded in the seed scales
24) AGO 82 *Dolomitostrobus bellunensis*. Dispersed seed
25) AGO 78 *Dolomitostrobus bellunensis*. Dispersed seed

the three to the five-lobed scales of *Voltzia*. Therefore, *Schizolepis* was inserted in the enigmatic group of Voltziales (STEWART, ROTHWELL, 1993). Also, evolutionary lines were traced to other extant conifers, such as by MILLER (1988): "It is clear, however, that the fossil genera A*ethophyllum, Pachylepis, Pseudovoltzia, Schizolepis* and *Swedenborgia* are closely related to the Cupressaceae and Taxodiceae and may represent an ancestral complex."

NATHORST (1897) emphasized the fact that the *Schizolepis* trees were composed of long and short shoots and that the leaves on the short branches were densely packed, whereas on the long shoots they were spread out and spaced. Even these two foliated shoots pertain to one of the main characteristics of *Schizolepis* and contribute to the misunderstanding of this conifer. The classification of conifers based only on sparsely found sterile shoots is very delicate, because even the same tree can show extreme variations. Thus, many classifications of Triassic and Jurassic gymnosperms must be viewed with this in mind. The arrangement and assembly of fructifications, not those of foliage structure, provide the only definitive indications of to which group they belong.

Therefore, the rich and monophyletic plant assemblages of the Val Imperina essentially contribute towards resolving the increasing conditions and reproduction patterns that are characteristic of this conifer. As stated in other studies on the Dolomites, several coniferales effectively belong to the Voltziales because of their characteristics cones (*Voltzia unescoensis, Voltzia agordica, Aethophyllum*). The male cones mostly resemble extant Araucarians, and, if the female more-lobed bract scales have found a way to fuse together, then this is valid also for the female cones. Classification of *Schizolepis* into the Voltziales would be excluded based on the fructification structures alone.

Another group of Mesozoic conifers have features in common with *Schizolepis*: the newly established order of Alpiales. Male and female cones of *Alpia anisica* from the Dolomites have a striking resemblance to *Schizolepis ungeri* and suggest a common evolutionary line to the extant Pinaceae or Cupressaceae. Whereas indexing as Cupressaceae is suggested for *Schizolepis*, a resemblance of *Alpia* to the Pinaceae is more convincing.

Both *Alpia* and *Schizolepis* hold several small-sized catkin-like pollen cones between sterile foliage, alluding that one larger cone was present. The different arrangement of the male cones provides another reason for suggesting that the dividing line between Southern World Araucarians and Northern Wold Pinaceae and Cupressaceae was just completed in the Early Triassic.

Despite having almost the same type of construction of ovuliferous pollen organs, there are some decisive differences between the co-existing *Schizolepis ungeri* and *Alpia anisica*: In *S. ungeri*, the clustered pollen organs have more of an entire cone characteristic than *A. anisica*. Differences were also noted in the seed organs. *Alpia anisica* bears one 1.5 - 1 cm-sized fleshly seed that almost completely fills the whole scale. In contrast, *S. ungeri* holds one to two smaller-sized seeds in each scale. The seed scale is also formed from an elongated ligneous pedicle, whereas in *Alpia* the ovuliferous scales are without or only have a short stalk. In both cases, the bract scales are mainly fused together at maturity and are entire and not bilobed or even three lobed, as suggested for most of the Jurassic *Schizolepis* cones. The entire female partially fused bract scales have all the ground features of Pinaceae and Cupressaceae.

Although *A. anisica* had heterophyllous leaves, they varied notably from those of *S. ungeri*. Their juxtaposed foliage with closed, fitted, petite needles on multibranching juvenile shoots and falcate protruding leaves on adult twigs are characteristic of *S. ungeri*.

Juxtaposed juvenile and adult foliage on the same branches is a characteristic of some extant coniferales such as *Juniperus chinensis* and *Xanthocyparis (Cupressus) vietnamensis*, suggesting a strong parental relationship between Early-Middle Mesozoic *Schizolepis* and Cupressaceae.

In conclusion, it could be stated that *Alpia anisica* and *Schizolepis ungeri* were probably Early-Middle Triassic related conifers, bearing all the significant features of extant Pinaceae and Cupressaceae. Therefore, a division between most of today's Southern Hemisphere dominating scale-foliated Araucarians and Northern globe Pinaceae and Cupressaceae with their needle-like leaves took place between the Permian and the Early Triassic.

Triassic Alpine conifers

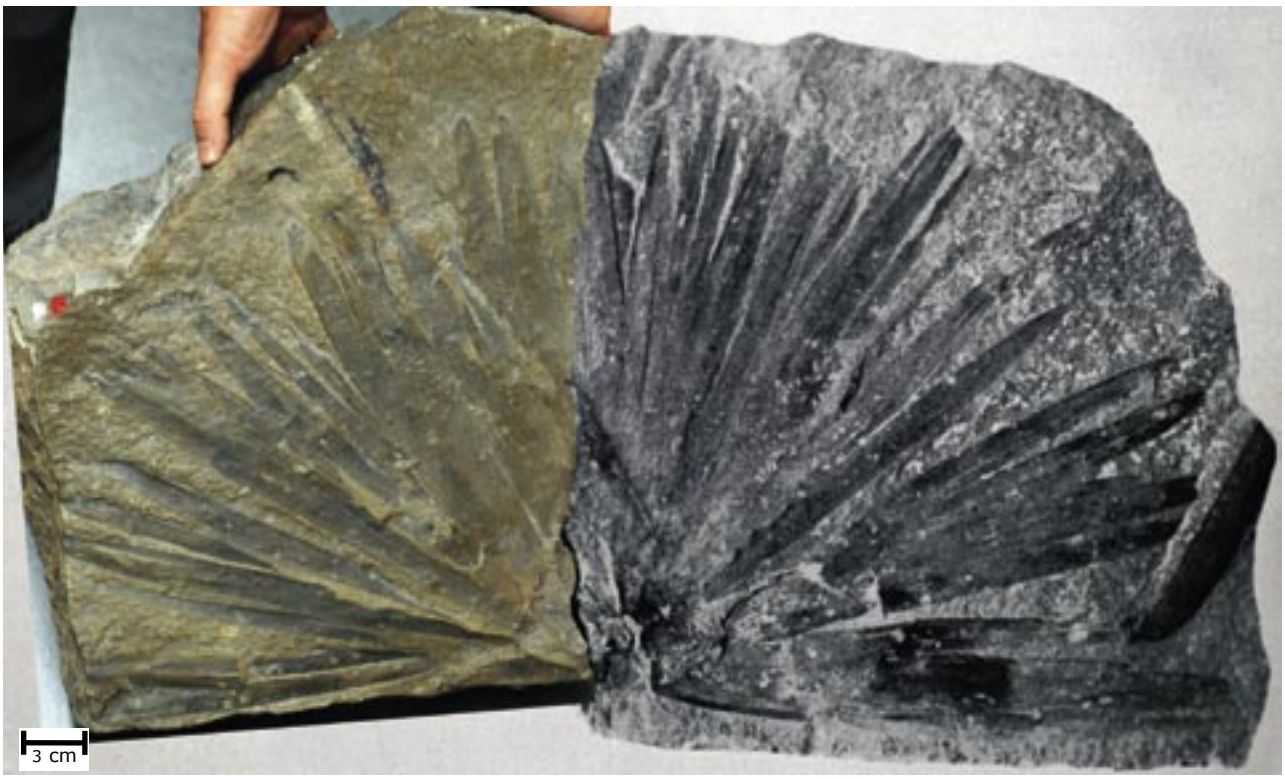
With the finding of adequate sterile and fertile material in the Dolomites the previously difficult comprehension of Mesozoic conifers can be viewed with new insights. In fact, this includes several groups of completely different pollen, seed cone and tree developments. FLORIN (1931-1951) proposed that all coniferales have their origin in the Lower Carboniferous-Lower Permian Cordaitales. Other authors were also motivated to include progymnosperms in their consideration. From this arose the question about the direct progenitors of Mesozoic conifers.

The Permian conifers

The Walchiaceae (GÖPPERT 1865, SCHIMPER 1870): Genera included in the Euramerian Walchiaceae are the Upper Carboniferous-Lower Permian *Walchia, Ernestiodendron, Otovicia* and Upper Permian *Ortiseia*, (CLEMENT-WESTERHOF, 1988), whereas *Culmitzschia* seems to be closely related to, if not synonymous with, *Ortiseia*. Leaves were bifacial and spirally arranged, with consistent ovuliferous cones, sometimes 20-25 cm long, with a high number of fertile dwarf shoots provided with 10 to 30 sterile and 1 to 3 fertile scales. Fertile and sterile seed-scales were not, or were only slightly, connate at the base. The form genera are *Walchiostrobus* for seed cones and *Walchianthus* for pollen organs.

The Majonicaceae (CLEMENT-WESTERHOF, 1987): Genera included are Upper Permian *Majonica, Dolomitia* and *Pseudovoltzia*. They were characterized by their compound ovuliferous dwarf shoots provided with 1 to 15 sterile and 2 to 3 fertile scales, each bearing a single inverted ovule on its abaxial surface. Fertile and sterile scales were moderately to considerably connate, especially in *Pseudovoltzia* (CLEMENT-WESTERHOF, 1988).

The Ullmanniaceae (ZIMMERMANN, 1959): These Upper Permian conifers hold compound, up to 6 cm-long ovuliferous cones, generating entire, mostly rounded, non-lobed seed scales in which one seed was

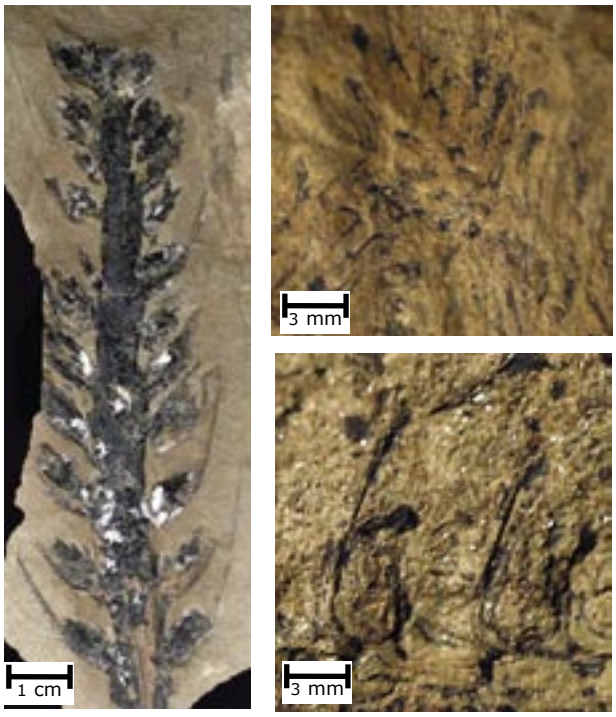


Cordaites principalis, Upper Carboniferous, Wettin. Entire leave tuft. Half of the original figure by K. Mägdefrau in "Paläobiologie der Pflanzen", courtesy of the Institute for Geosciences, Halle (Saale)

consistently embedded. Only one bract and seed scale were partially fused together. Pollen cones were of the small-sized *Strobilifer frumentarius* type, up to 3 cm long, with pollen sacs on the abaxial part. Although WEIGELT (1928) put *Ullmannia frumentaria* in the Podocarpaceae, renaming it *Archaeopodocarpus germanicus*, this opinion is to reconsider. The Ullmaniaceae should probably be defined as an important transitional group of Permian conifers in an evolutionary line to Early Mesozoic Alpiaceae and extant Cupressaceae and Pinaceae.
Other Permian coniferales were Pennsylvanian **Thucydiaceae, Bartheliaceae** and **Emporiaceae**, especially known from the USA, and the Gondwanan Permian families **Ferugliocladaceae** and **Buriadiaceae**.

The different Early-Middle Triassic Alpine conifer lines

The Voltziaceae (BRONGNIART, 1828): They were characterized by scale-like leaves, generating pollen cones with peltate shields and pollen sacs attached to the lower edge of each microsporophyll, with seed cones with more-lobed bract scales, resembling individual dwarf shoots.
The Albertiaceae (SCHIMPER & MOUGEOT, 1844): They generated sword-like leaves with globose to subglobose seed cones and giant pollen cones with clustered pollen organs.
The Alpiaceae (WACHTLER 2011): These include the genera *Alpia* and *Schizolepis.* They hold heterophyllous, juxtaposed needle-like leaves with spherical to elongated seed cones, generating only a few, partially fused bract scales. The seed scale was entire and non-lobed. Male cones were generated in the axils of sterile leaves with catkin-like fructifications, with small-sized microsporophylls and pollen sacs on their lower surface.



Left: *Cordaianthus*, male fructification of *Cordaites*, Crockhey, Westphalian. Right: *Walchiastrobus gothani*. Oberhof, 219/14. Florin, 1937. Detail of single ovuliferous dwarf shoots. Right, below: *Walchianthus* sp. Oberhof, 221/18. Suggested as belonging to *Walchia arnhardtii* by R. Florin, 1937. Detail of single microsporophylls. Specimen courtesy of the Natural History Museum, Schloss Bertholdsburg, Schleusingen

Summary

1. The Carboniferous-Permian boundary: origins of a new plant world

The Carboniferous-Permian border, not the Permian-Triassic cataclysm, was the most important period for the evolution and formation of most extant plants. The cycads and many new fern families arose in this time period, whereas others, such as the dominant *Lepidodendron, Sigillaria* and *Calamites*, minimized and totally changed their appearance. Also, the conifers originated and were formed between the Upper Carboniferous-Permian-Early Triassic, and remained almost unchanged for 250 million years. A general climate change was probably the catalyst of this general modification of the whole plant kingdom, which has not happened since. We have not had an extinction event in the sense of an irreversible loss of families, but there has been a complete transformation of the plants. No explicit crisis progenitors could be defined: all of the lycopods, horsetails, conifers, ferns, cycads and seed ferns battled together through this time. In the Early Mesozoic, they were present in the landscape in almost equal numbers.

2. The general dwarfism between the Permian and Lower Triassic

From the Upper Carboniferous to the Permian, a common dwarfism occurred throughout

1) *Walchia piniformis*, Oberhof. No.. 216/13. Old specimen described and illustrated as *Lebachia laxifolia* by R. Florin, Palaeontographica, Pl. LXXXV. Courtesy of the Natural History Museum, Schloss Bertholdsburg Schleusingen

2) *Walchia piniformis*, Oberhof. No. 214/11. Old specimen described as *Lebachia piniformis* by R. Florin in 1937. Courtesy of the Natural History Museum, Schloss Bertholdsburg, Schleusingen

3) *Walchianthus* sp. Male cone of *Walchia*. Lochbrunnen Oberhof. WP 1866

4) *Walchianthus* sp. Male cone of *Walchia* (suggested as pertaining to *Lebachia parvifolia* by R. Florin. Oberhof, 221/3

5) *Walchiostrobus* sp. Young female cone of *Walchia*, suggested as pertaining to *Lebachia parvifolia* by R. Florin. 220/19

6) *Walchistrobus fasciculatus*. Female cone of *Walchia*. 219/19. All specimens courtesy of the Natural History Museum, Schloss Bertholdsburg, Schleusingen

most of the plant kingdom. The colossal Carboniferous *Lepidodendron* trees were modified to the Early Triassic arborescent *Lycopia*; other lycophyta such as *Sigillaria* lost their tree aspect to form *Isoeites* or *Pleuromeia*, or even gnomish *Selaginellites*. The giant horsetail *Calamites* changed to *Equisetites*. Extreme dwarfism occurred in the ferns: their leaves became reduced to a few millimetre-sized *Anomopteris, Ladinopteris* and *Gordonopteris* foliage, and the Early Triassic *Neuropteridium* and *Wachtleria* formed a few petite fronds. This happened to the cycads, Permian *Taeniopteris* and Early Triassic *Ladinia* and proceeded to the seed ferns like the dwarfish Peltaspermum *Callipteris*. In a short geological time period most of the vegetation lost more than two thirds of its original size. Also, the progenitors of the conifers were no exception. The miniaturization of leaves from half-metre sized tuft-like *Cordaites* leaves to the nanoid needles of the first Walchiaceae and almost all extant conifers were impressive. They were reduced to one tenth or even less of their original size. Interestingly, this did not result in a total extinction of clades, but a strange transformation to a smaller-sized growth habitus occurred. The reason for this minimization was not the Permian-Triassic catastrophe, because this dwarfism only began in the Lower Permian and proceeded until the Early Triassic. In fact, none of the intensive research in the Anisian strata of the Dolomites yielded tree trunks larger than 10 to 15 cm in diameter Therefore, the theory that the Early Triassic was manifested by widely divergent but extremely small-sized vegetation was established. This was very different to Permian floras, which were also stunted in growth but had a lower species diversity.

3. The conifers: a dwarf shoot theory is not enough

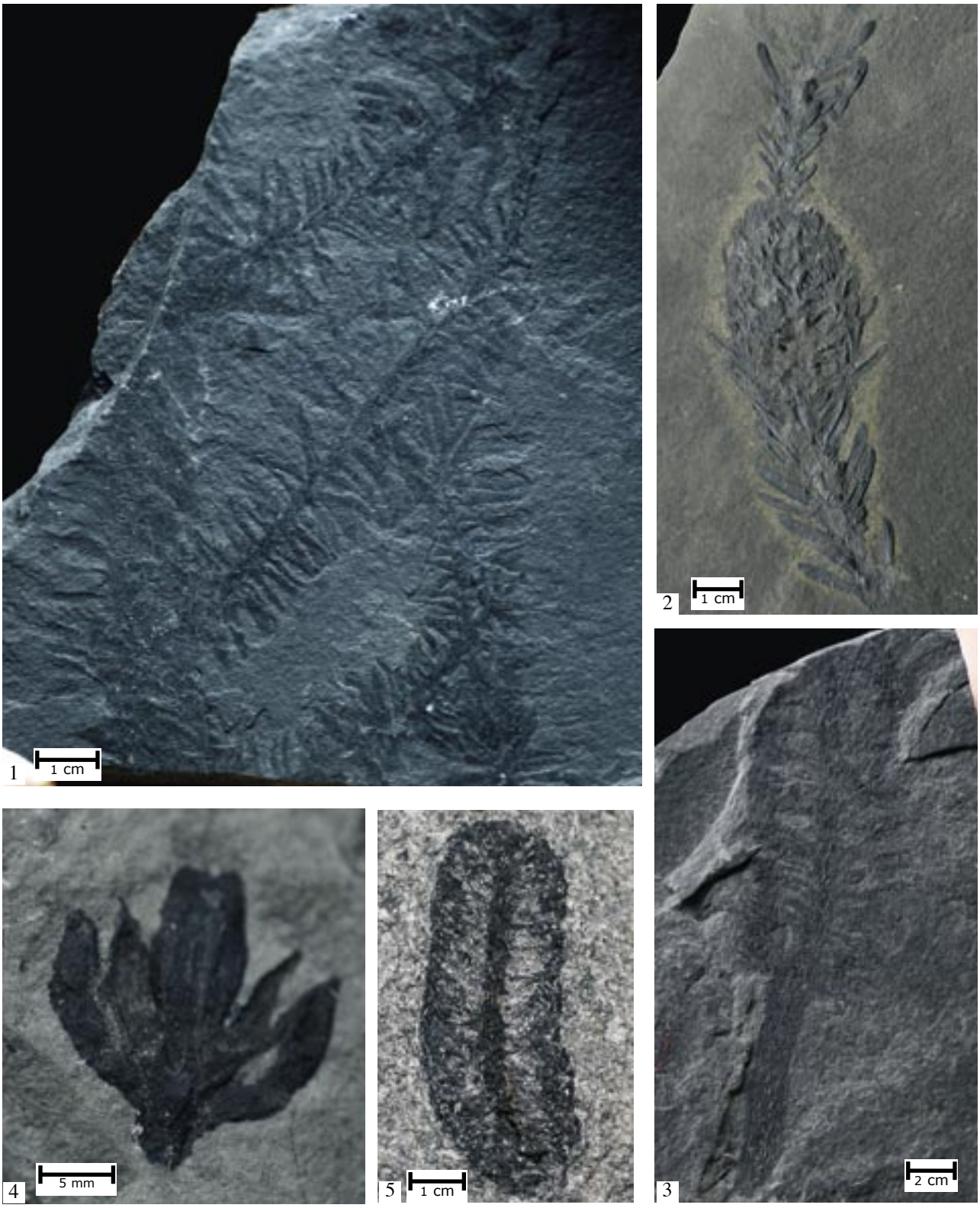
As suggested by other authors (CLEMENT-WESTERHOF, 1988), phylogenetic considerations about the conifers are firstly to be based on the interpretation of their reproductive organs and only secondly on the organization of their foliage, which mainly remained unchanged from the Permian to the present. FLORIN's (1931-1955) most established theory – that all conifers initially bore ovuliferous dwarf-shoot compounds and that all modern conifer seed cones originated by the fusion of more and more of their innumerable bract scales – was supported by many researchers. This doctrine explained the evolutionary stages of several Paleozoic conifers like *Walchia, Ortiseia, Otovicia, Ernestiodendron, Majonica, Dolomitia* and *Pseudovoltzia*, and also the Mesozoic Voltziales. But this concept did not take into consideration the important family of Permian Ullmanniaceae or the newly established family of Early-Middle Triassic Alpiaceae. Their Upper Carboniferous-Lower Permian ancestor is unknown; parental affinities with the cordaitales are possible, but not obligatory.

4. The two-way female cone origin-theory: single versus multiple dwarf-shoot cones

Within the conifers, we can presume that a minimum of two different seed cone evolutionary stages occurred. The Paleozoic Ullmaniaceae, as well as the Mesozoic Alpiaceae, were characterized by small-sized female cones and a reduced number of fertile scales, with entire, but fused seed scales and bracts, giving no indication of a coalescence of dwarf shoots into one single unit. The group of Voltziales usually held voluminous female cones, some up to 20 cm and more sized, with more-lobed bract scales. Therefore, it could be assumed that in the Walchiaceae, Majonicaceae and Voltziaceae a specific number of fertile dwarf shoots generated one cone, whereas in the Ullmaniaceae and Alpiaceae one fertile dwarf shoot formed one single cone. Thus two plausible evolutionary concepts could be established: one from the Upper Permian Ullmanniaceae across the Alpiaceae to the few bract-scales generating extant Cupressaceae and Pinaceae, and the other from descendants of the Upper Permian Majonicaceae and the Early Triassic Voltziaceae, to the many ovuliferous scale-bearing Araucariaceae and other related Southern hemisphere conifer groups.

5. The two-way male cone origin theory: catkin cones versus edge-held pollen sacs

Often ignored in theories is the important rule of the male cones. Male cones differed considerably between the Permian-Triassic Voltziales, Ullmaniaceae, Albertiaceae



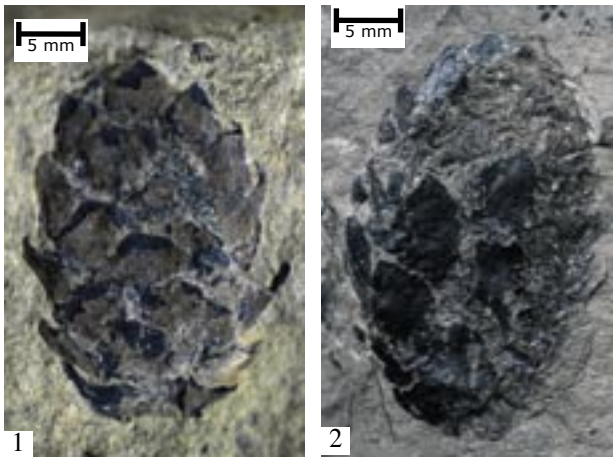
1) *Pseudovoltzia liebeana*. Sterile shoot, reproduced by Weigelt 1928, plate XXXIV, Fig. 11, Unterkopf, Eisleben. Courtesy of the Institute for Geosciences, Halle (Saale)

2) *Pseudovoltzia liebeana*. Young female cone with apical proliferation, Kamsdorf. Collection Silvio Brandt, Halle (Saale)

3) *Pseudovoltzia liebeana*. Mature female cone. Courtesy of the Institute for Geosciences, Halle (Saale)

4) *Pseudovoltzia liebeana*. Single bract scale. Collection Silvio Brandt, Halle (Saale)

5) *Pseudovoltzia liebeana*. Male cone. Collection Silvio Brandt, Halle (Saale)



1) *Strobilifer frumentarius.* Male cone suggested as belonging to *Ullmannia frumentaria*. Coll. Silvio Brandt, Halle (Saale)

2) *Strobilifer frumentarius*. Male cone suggested as belonging to *Ullmannia frumentaria*. Coll. Silvio Brandt, Halle (Saale)

and Alpiaceae, as well as between the extant Araucarian bulk-pollen cones and the catkin-like fructifications of the Cupressaceae and Pinaceae. On their voluminous male cones, the extant Araucarias held the pollen sacs on the outer lower edge of peltate microsporophylls, recurved towards the main axis. This feature of the cones of *Araucarias* did not differ much from the Mesozoic *Willsiostrobus* cones of the Voltziales. The progenitor of the Cupressaceae and Pinaceae male cones is to be looked for in the Alpiaceae with *Alpia* or *Schizolepis*. These were characterized by small-sized catkin cones, arranged in specific numbers between sterile foliage. As with the seed cone concept, the one pollen-cone compound of Voltziaceae versus the one single cone of Alpiaceae concept could also be adopted here. One enigmatic conifer group comprises the Albertiaceae, which aere mainly characterized by their giant pollen cones with innumerable pollen sacs arranged on a main axis like a Christmas tree. From this arose the question of how the Carboniferous-Lower Permian cordaitales or other ignote progenitors or successors changed their pollen cone concept so much.

6. The dawn of sexuality

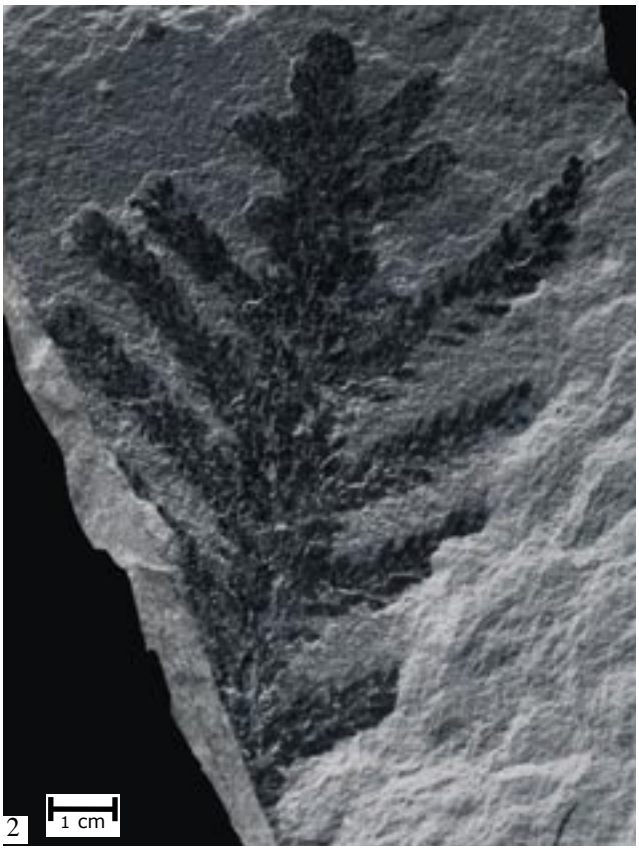
Whereas most of the plants between the Carboniferous-Permian-Early Triassic reduced in size, the number or size of sex organs increased immensely, and some became virtual sex bombs. The conifer *Albertia* had pollen cones that were more than 20 cm in length, and a high number of fertile cones characterized the Voltziales and Alpiaceae. In certain species like the fern *Neuropteridium*, but also in cycads like *Bjuvia*, the percentage of fertile/sterile organs reached a 1:1 ratio. This remained to the present day, whereas in Early Carboniferous flora the fertile organs stayed in background compared to their sterile foliage.

7. Juxtaposed juvenile and adult foliage on the same shoots

A character of most Paleozoic-Mesozoic plants, also achieved in some extant conifers, was the development of juxtaposed juvenile and adult foliage on the same shoots. In particular, *Schizolepis ungeri*, but also *Alpia anisica*, produced larger sized adult and close fitted and more or less appressed juvenile foliage on the same branches. This habitus was preserved in some extant Cupressaceae such as *Juniperus chinensis* and *Xanthocyparis (cupressus) vietnamensis*, and could, with difficulty, be explained by sun or shade exposure. It has also been suggested that many of the foliage types from the Permian and Triassic (see *Walchia piniformis* and other minimally diverging leaves of subspecies, and also *Ullmannia frumentaria* and *Ullmannia bronnii* and *Voltzia heterophylla*, for example) correspond to the same taxa. But other clades such as the cycadophyta *Taeniopteris* or *Ladinia*, with their sharply pointed or rounded leaves, and *Scytophyllum*, with its tongue- and frond-like foliage, have the same feature. The reasons for this characteristic trait might be due to adverse environmental conditions.

8. Proliferation of cones

The progression through cones and the return to normal vegetative shoots, as seen in some extant conifer cones (*Abies koreana*, FARJON, 2008; *Picea abies*, *Cryptomeria japonica,* especially *Cunninghamia lanceolota,* UHL & BRANDT 2004), had already occurred in the Upper Permian *Pseudovoltzia liebeana*, as well as in *Voltzia hexagona* and the Thucydiaceae (HERNANDEZ-CASTILLO et. al. 2001). Some authors suggested (UHL & BRANDT 2004) that this was a trait of ancient conifers and rather than modern ones, where it is only rarely detected.



1) *Ullmannia frumentaria*. Sterile shoot, coll. Pangert. Courtesy of the Institute for Geosciences, Halle (Saale)

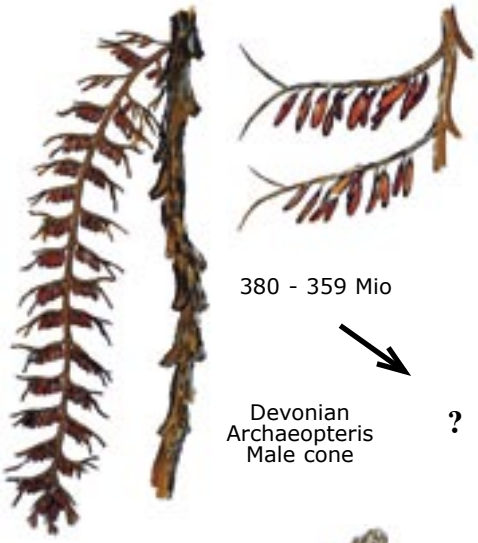
2) *Ullmannia frumentaria*. Sterile shoot, Mansfelder Mulde. Coll. Silvio Brandt, no. 184, Halle (Saale)

3) *Ullmannia frumentaria*. Seed cone, illustrated by Weigelt p. 113 as fruit of *Archaeopodocarpus*. Courtesy of the Institute for Geosciences, Halle (Saale)

4) *Ullmannia frumentaria*. Seed cone, legendary specimen illustrated by H. B. Geinitz, 1880, pl. 5 and lost during the War.

5) *Ullmannia frumentaria*. Seed cone resembling Geinitz's specimen. Coll. Silvio Brandt, Halle (Saale)

The enigmatic evolution of male conifer cone



380 - 359 Mio

Devonian
Archaeopteris
Male cone

?

359 - 294 Mio

Carboniferous
Cordaitanthus
Male cone

?

310 - 275 Mio

An evolution line from Permian Walchia, Majonica (Pseudovoltzia) to Mesozoic Voltzia and extant Araucariaceae could be accepted

Lower Permian Walchianthus
Male cone

?

An evolution line from Permian Ullmannia to Mesozoic Schizolepis - Alpia and extant Pinaceae and Cupressaceae- could be possible

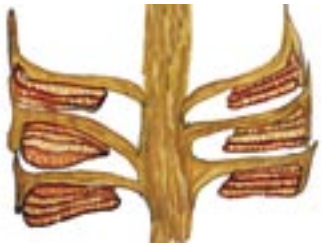
260 - 251 Mio

Upper Permian Ullmannia
Male cone

?

Pseudovoltzia, Upper Permian
male cone - single pollen

251 - 203 Mio



Lower Triassic Voltzia
Male cone

Schizolepis
Male cone

Lower Triassic Alpia
Male cone

Extant

Extant Araucaria
Male cone

Extant Pine
Male cone

The enigmatic evolution of female conifer cone

Cordaites
Female cone

359 - 294 Mio ?

?

An evolution line from Permian Walchia, Majonica (Pseudovoltzia) to Mesozoic Voltzia and extant Araucariaceae could be possible

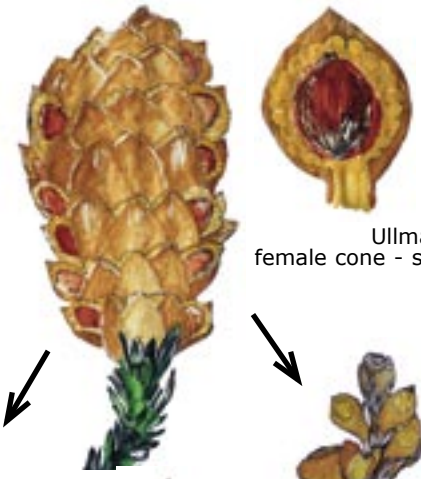
An evolution line from Permian Ullmannia to Mesozoic Schizolepis - Alpia and extant Pinaceae and Cupressaceae- could be accepted

310 - 275 Mio

Walchia, Lower Permian
female cone - single seed scale

Pseudovoltzia, Upper Permian
female cone - single seed scale

260 - 251 Mio



Ullmannia
female cone - single seed scale

251 - 203 Mio

Voltzia
female cone - single seed scale

Schizolepis
female cone - single seed scale

Alpia
female cone - single seed scale

Extant

Extant Araucaria
Female cone

Extant Pine
Female cone

Extant Abies
Female cone

9. The origin of the Araucarias. Are any Euramerian Voltzia-ancestors lurking there?

The Voltziales of the Northern hemisphere were characterized by their more-lobed bract scales, which ranged from the Early to the Late Triassic (*Voltzia agordica, Voltzia dolomitica, Voltzia haueri*, and also *Voltzia coburgensis*, for example). Even though the pollen cones of Voltziales were mainly the same as those of extant Araucarias, it can be assumed that the progenitor of all Araucarias must be looked for in the Voltziales, although some Gondwanian parents were probably able to fuse their bract scales between the Permian-Early Triassic.

10. The origin of the Cupressaceae and Pinaceae. Similarities between the Ullmanniaceae and the Alpiaceae

A development line from *Alpia* to the Pinaceae and *Schizolepis* to the Cupressaceae is plausible based on their male and female fructifications. Both held small-sized pollen cones interspersed between sterile leaves. Whereas *Schizolepis* female cones were globose and only held a limited number of scales with a thickened end, like the extant Cupressaceae, the *Alpia* seed cones were elongated and almost entirely fused to form rounded bract scales, suggesting an affinity with the extant Pinaceae.

Information

All of the studies lack pollen and cuticle analyses because the authorities and police force confiscated and removed all of these specimens – based on a more year's work – from my house. The fossil slabs were thrown together and carried away on a truck in such a manner that they were irrevocably destroyed. My computers, photos and notations were also sequestered and brought away. So many photos and annotations are based on older archives of mine that, unfortunately, I occasionally had to choose holotypes for some species that were not ideal. I apologise for this and now just plan a revised version for when my country learns to appreciate science.

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