Permo-Triassic climate catastrophes as basis for the birth of new life forms

by Michael Wachtler
P. P. Rainerstrasse 11, 39038 Innichen, Italy; E-mail: michael@wachtler.com
Collaboration: Nicolas Wachtler; E-mail: nicolas@wachtler.com

Abstract

Several times in the course of Earth's history, climate cataclysm has considerably changed the planet, at the same time offering the ecological niche for the emergence of new life-forms. One of the best ways to examine these changes are modifications in the plant world. In the Eastern Alps, especially in the Dolomites from the Carboniferous over the whole Permian and Triassic, we have a mainly uninterrupted succession of sediments that contain abundant plant fossils. In the Late Carboniferous, an immense cataclysm, probably the foothills of the Late Paleozoic Ice Age affecting the former Southern globe Gondwana continent, in particular changed the horsetail-fern dominated flora. In the early Permian period, the Alps were located at about the tenth latitude to the south, the extremely cold climate reached its peak and created room for the evolution of conifers, such as the first Abietaceae, Pinoidea, Araucariaceae, all sub-tribes of the cycads and also the ginkgos. After a short blossoming in the Late Permian, another disaster, the Permo-Triassic catastrophe, probably a consequence of the huge volcanic phenomena in Siberia, transformed the whole plant kingdom once more. Beginning from the Early Triassic, the flora recovers, offering the possibility for paradisiac conditions for the first evolution and propagation of many fern families, lycopods, gymnosperms and horsetails. This prosecuted till the Late Triassic when the Raibl-Cataclysm reduced the plant kingdom again. This publication explains the changes during these periods and attempts to provide answers about the causes and consequences.

May 2021

Key words: Permian floras, Triassic floras, Dolomites, climate catastrophes, gymnosperm evolution, fern evolution

Late Permian (Wuchiapingian, about 260 mio years), Ariche - Valli del Pasubio, Northern Italy

In the Upper Permian many plants, especially the gymnosperms were fully evolved. Left below sprout the cycad ***Macrotaeniopteris wachtleri*** with male cones. Followed by the interesting cycad ***Pernerina pasubi*** with megasporophylls, after that the *Zamia*-like cycad ***Nilssonia brandtii*** with a male cone and its two seeded female cones. On the right side is an ***Angiopterites murchisonii*** fern. In the left upper part grows the last Calamitaceae recorded in Earth-history ***Neocalamites benckeae***. In the rich conifer assemblage dominates the Araucariaceae ***Ortiseia zanettii*** with female and male cones. After that on the right side a twig with female cones and decaying seed scales of the fir-ancestor ***Majonica alpina.***

Plants can be regarded as one of the most efficient climate indicators from the past that are only rarely recorded, even more meaningful than terrestrial animals , and marine life that could cover considerable distances, even cross oceans. The vegetation is fixed in one place and could not escape when the climatic conditions changed, only retiring and making place for other better adapted flora elements. Since plants can be found frequently in the same layers, they can provide a good overview of the diversity of life of the past.

One of the most significant areas in the world which allow in-depth study of the changes in the vegetation over many million years are the Dolomites. From the Carboniferous over the whole Permian and Triassic, many plant lenses crop out and can be tracked over many kilometres. They offer an interesting overview about the radical changes over eons; sometimes, they can tell stories of immense natural disasters and climate cataclysm. Additionally, coeval but distantly growing plant assemblages can offer valuable hints regarding the climate differences over the hemispheres. An Alpine Permian or Triassic biocoenosis can be different from a simultaneously deposited found in Germany or France, not to examine a flora from America (although the continents were merged together in the Paleozoic) and not to compare with continents that in ancient times were separated, like the Angara landmass, today's Ural region or the Southern hemisphere Gondwana area.

What is important in studying fossil plants is not just the visual nature of sterile leaves or branchlets but the stratigraphical placement of their fertile parts. Unfortunately, less attention was often paid by the collectors to cones, seed scales or sporangia, whereas decorative-looking twigs from various localities enjoyed priority, which increased the

Late Carboniferous (Moscovian, about 310 mio years)

The landscape is dominated by a horsetail-fern assemblage with ***Acitheca polymorpha*** (left), ***Ptychocarpus unitus,*** (middle) and ***Marattiopsis feminaeformis*** (right). In the background grow ***Calamites incisum*** (left), ***Calamites multiramis*** (middle) and ***Calamites equisetiformis*** (right). All were found together in one layer at the Krone/Corona mountain in the Eastern Alps.

collection but complicated the real classification or the answer to how a plant contributed to an evolutionary way (Wachtler, 2013).

The Late Carboniferous tropical pluvial heyday

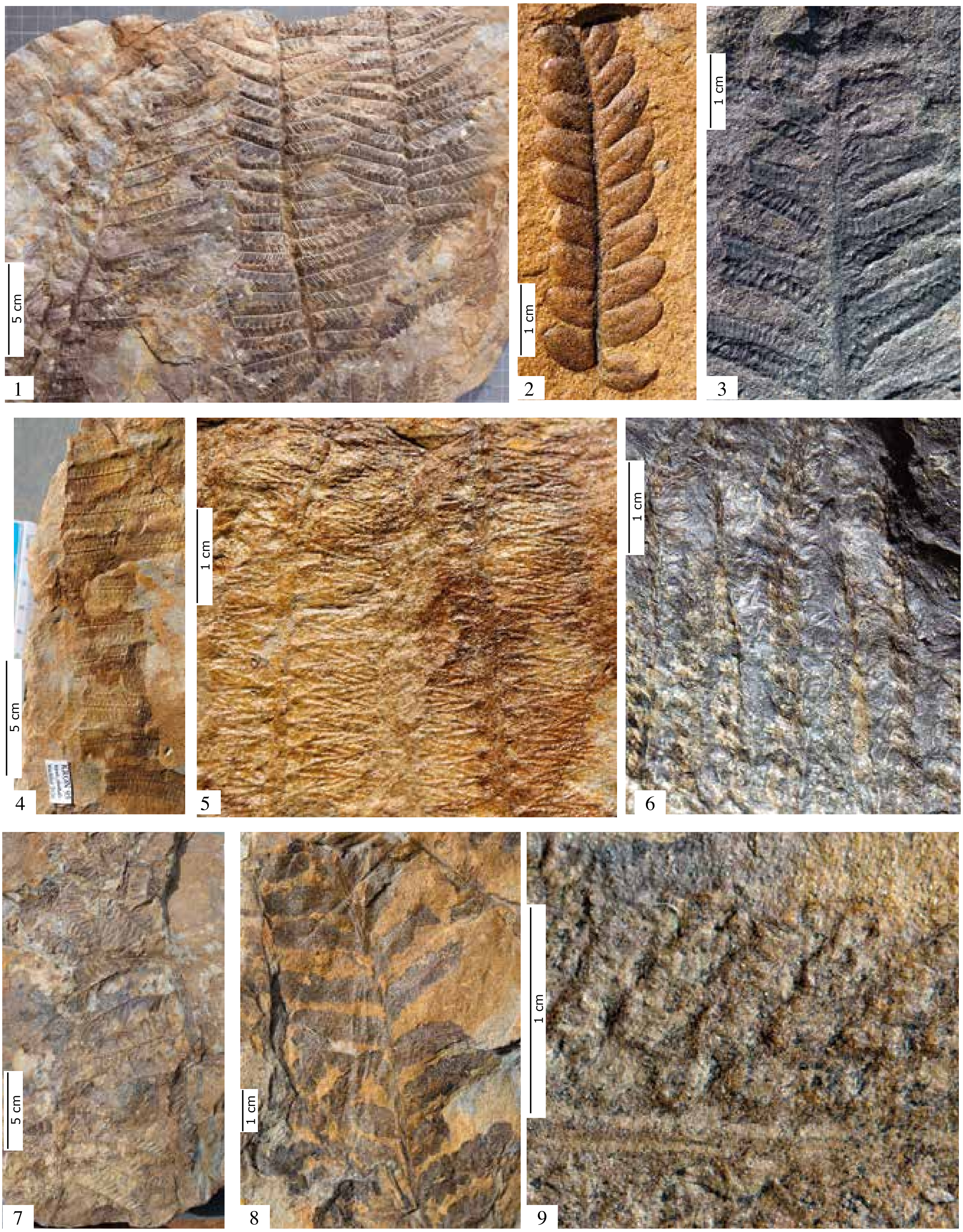
In the Carnian Alps, in many places, fossil plants from the Late Carboniferous crop out. The area was located in that time at the tenth parallel south of the equator. Beginning from the Late Devonian on, about 360 million years ago—the giant Southern continent Gondwana was positioned over the South Pole and was covered by an immense ice shield. This lasted for about 65 million years till the end of the Carboniferous. But strange things happened during the Late Paleozoic Ice Age as well. About 90% of all coal reserves of the entire world were deposited especially in the Late Carboniferous equatorial regions (McGhee, 2018). But what followed at the end of the Carboniferous? All over the equatorial regions, we encounter first a vanishing of the big club-moss trees (*Lepidodendron* and *Sigillaria*). In one of the worldwide fossil sites par excellence—the Krone/Corona located between the Austrian and Italian border—in the upper parts, the giant club mosses had just mostly become extinct, but water-loving horsetails (Calamitaceae) and tropical ferns dominated the Late Carboniferous (Moscovian) vegetation.

Late Carboniferous Krone (Corona)

The Dammann-Gerasch-Perner-Wachtler-research zone. A single layer was investigated over a length of 15 metres. Three different Calamitaceae (***Calamites equisetiformis, Calamites incisum, Calamites multiramis*** with its branchlets and fertile organs) lived here closely together. They were accompanied by several tropic ferns (***Acitheca polymorpha*** (*Angiopteris*), ***Marattiopsis feminaeformis*** (Marrattiales), ***Ptychocarpus unitus*** (*Psaronius-Scolecopteris*-ferns).

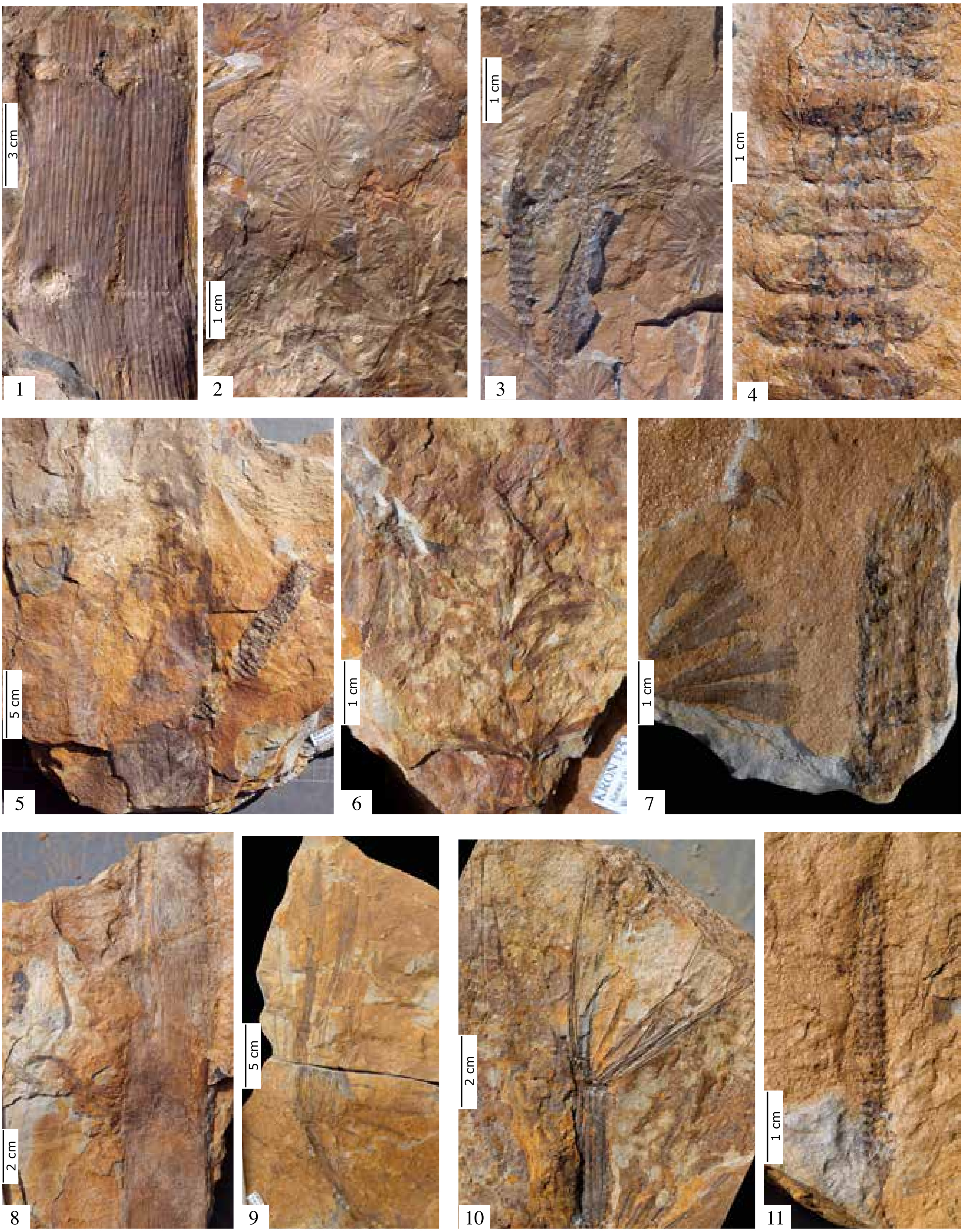
The Dolomites 300 Mio years ago (dinosaurpictures.org)

To make a coeval comparison was opened on the Krone, the Dammann-Gerasch-Perner-Wachtler research site. The objective was to collect all possible plants and their fertile parts, from a 15 metre long and 1- to 1.5-metre-wide area. Interestingly, the layer was dominated by three *Calamites* horsetails and three Pteridophyta, belonging mostly to the Marattiaceae. In the same coeval layer, ***Calamites equisetiformis*** (known as *Asterophyllites equisetiformis* branchlets) with their subtle sporangiophores, ***Calamites incisum*** (with sporangiophores described as *Macrostachya infundibuliformis, Palaeostachya*, and stems classified as *Calamites cistii* or *Calamites schuetzeiformis*, and branchlet-leaves known as *Sphenophyllum incisum, Sphenophyllum longifolium*) and ***Calamites multiramis*** (with branchlets known as *Annularia stellata, Annularia sphenophylloides*, and fertile organs described as *Calamostachys tuberculata*) were encountered together (Fritz et al., 1990). A layer underneath, which had already been investigated a few years earlier, revealed in particular *Calamites multiramis* with well preserved *Annularia stellata* leaves and fertile organs. This is also valid for a closely upper laying deposit on the Austrian side of the frontier, excavated in 1985 by the Museo Friulano di Storia Naturale (Kustatscher et al., 2019), which yielded amazing *Calamites*



Ferns from the Krone fossil site (Late Carboniferous, Moscovian)

1-3. ***Acitheca polymorpha***: 1. Entire fronds (KRON 108); 2. Single sterile pinnula (KRON 99); 3. Fertile pinnula (KRON 51); 4-6. ***Marattiopsis feminaeformis;*** 4. Part of a whole frond (KRON 95); 5. Single sterile pinnula (KRON 95); 6. Fertile pinnula with synangia; 7-9. ***Ptychocarpus unitus,*** 7. Frond (KRON 113); 8. Sterile pinnula (KRON 129); 9. Fertile pinnula (KRON 33); Coll. Michael Wachtler, Dolomythos-Museum.



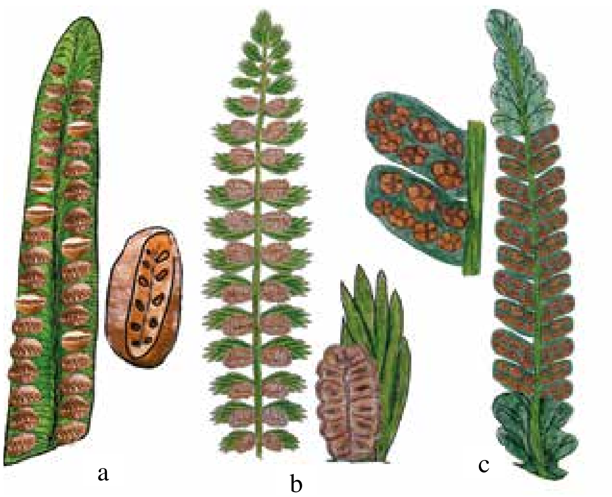
Horsetails *(Calamites)* (Late Carboniferous, Moscovian)

1-4. ***Calamites multiramis***: 1. Stem (KRON 44); 2. Lateral branchlets (*Annularia stellata*, KRON 23); 3. Sporangiophores *Calamostachys tuberculata* (KRON 35); 4. Detail of the sporangia (KRON 06) 5-7. ***Calamites incisum;*** 5. Stem with attached sporangiophore (KRON 69); 6. Lateral branchlet (*Sphenophyllum incisum,* KRON 125); 7. Leaf and sporangiophore (KRON 121); 8-11. ***Calamites equisetiformis;*** 7. Stem with attached sporangiophores (KRON 85); 9. Lateral branchlet (KRON 131); 10. Lateral branchlet (KRON 112); 11. Sporangiophore (KRON 79); Coll. Michael Wachtler, Dolomythos-Museum.

Different *Calamites*-sporangiophores from *the Krone/Corona mountain*
a. Calamites multiramis (Isolated parts: *Annularia stellata, Calamostachys tuberculata); b.* ***Calamites incisum*** (Isolated parts: *Calamites cistii, Calamites schuetzeiformis*, *Sphenophyllum incisum, Sphenophyllum longifolium, Macrostachya infundibuliformis, Palaeostachya; c.* ***Calamites equisetiformis*** (Isolated parts: *Asterophyllites equisetiformis)*

multiramis (Annularia stellata) remains and *Acitheca polymorpha*-ferns; however, in this research, less attention was given to their fertile parts.
Three characteristic ferns can be encountered in this layer: The most common is ***Acitheca polymorpha***, due to its sporangia clustered in sori along the lateral veins near the margin affinities with extant *Angiopteris* ferns.
The second fern ***Marattiopsis feminaeformis*** (often classified as *Pecopteris feminaeformis*) is also widespread and fits well in the concept of the extant Marattiaceae, although their crown-like leaflets are different. Another fern ***Ptychocarpus unitus*** (sometimes described as *Pecopteris unita*) can be classified due to its sporangia accumulation into synangia as an eusporangiate fern having parental affinities with Palaezoic *Psaronius, Scolecopteris* or *Asterotheca*. Extant descendants are difficult to establish, although the synangia resemble most archaic *Psilotum* ferns.

In which geological age can the declining of the big *Lepidodendron, Sigillaria* and *Calamites*-trees be inserted? The localities Stangnock and Königsstuhl in the Nockberge mountains are rich in huge clubmosses and horsetails, additionally to well-preserved seed ferns (*Alethopteris serlii* and *Pachytesta gigantea*-cupulas). A Bashkirian-Moscovian age is probable for this older flora. Gradually, *Lepidodendron* and *Sigillaria* became extinct. In the Kronalpe/Corona, we encounter the last huge club mosses only till the field road from the Austrian Kronalm to the Italian Casera, about 100 metres below the classic fossil site, where ferns and *Calamites* horsetails dominate, and the clubmosses *Sigillaria* and *Lepidodendron* were not present. The seed ferns were rare, but the first conifers also did not appear. Therefore, a Moscovian age for the Krone fossil site is plausible.
Only over the Rattendorfer Alm (Grenzlandschichten, Italian-Austrian border), we encountered for the first time, but conifers (*Ortiseia* sp.) only rarely. If the beginning of the conifers is coeval with the Middle-European fossil sites, then a late Carboniferous Kasimovian/Gzehlian age is suggested there.
What was the reason for a relatively faster decline of the plant world? Till the Moscovian, the Alpine landscape can be regarded as tropic, with an abundance of Marattiaceae and water-lowing horsetails.



Different fertile ferns fr*om the Krone/ Corona mountain*
a. ***Acitheca polymorpha***; b. ***Marattiopsis feminaeformis;*** c. ***Ptychocarpus unitus***

In a relatively quick succession, the Calamitaceae and the ferns were pushed back and in the Kasimovian appeared the first conifers. But this is not enough: over the Gzhelian-Asselian-Sakmarian, we have in the Eastern Alps for about 20 million years no fossil record till the Artinskian. In the Artinskian, we encounter a flora vegetating on the edge of survival as rare before and after – no horsetails, no ferns, no clubmosses, but only prickly conifers, like Abietaceae-, Araucariaceae and Pinoidea ancestors and some isolated lichens.

The fact is that an immense climate catastrophe must have influenced the equatorial regions in the Late Carboniferous. Strangely, the Late Paleozoic Ice Age, restricted on the Southern globe, ended gradually till the Carboniferous-Permian border. However, it changed the equatorial climate furthermore for a long time, maybe by cold currents from the south—like today's Humboldt current, that flows north along the western coast of South America from southern Chile (about 45th parallel south) till Peru (about 4th parallel south), reaching mainly the Equator)—with uncharacteristic water temperatures of 16 °C instead of the normal 25 °C for tropical waters; it is responsible for the aridity of the Atacama Desert and the coastal areas of Peru and Ecuador. Other possible reasons for this climate catastrophe could also be a change in the orbital circle from a more elliptic or more circular till the agglomeration of the big Gondwana landmasses on the South Pole. It seems that this Late Paleozoic Ice Age was not bipolar but mostly concentrated on the Southern hemisphere.

The Alpine-Artinskian wasteland catastrophe

In the Artinskian, about 290 million years ago, the Dolomite were located directly on the equator. But the climate was overthroated by storms and arctic cold in the winter months, which caused the conifer-leaves to fall off. Nevertheless, it was a great time of evolution of the new conifer families. The first *Pinus* ancestors, ***Fèrovalentinia wachtleri***, began to spread, and the Abietaceae progenitors ***Majonica suessi***, the first Aracaurias ***Ortiseia dasdanai*** with ***Voltzia triumpilina*** (probably an extant *Cryptomeria* is a descendant) evolved.

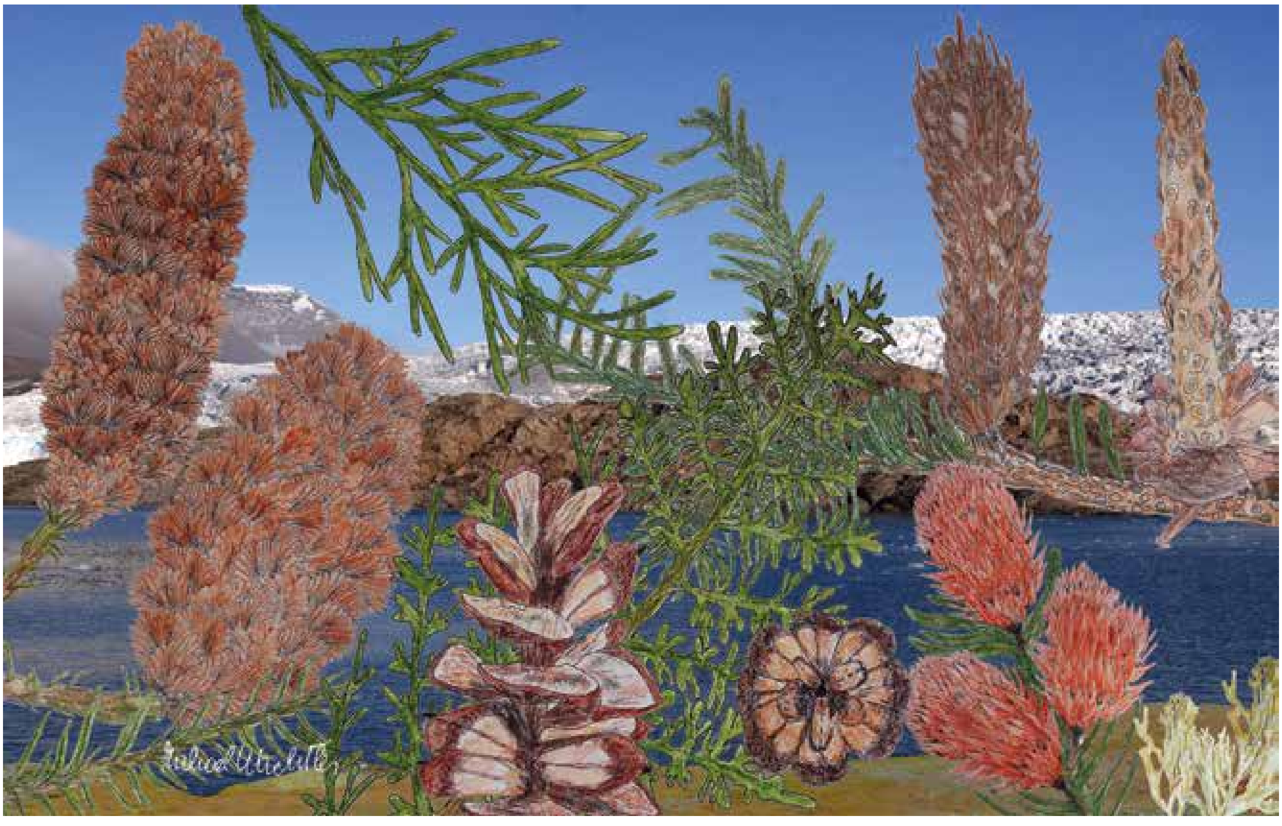
The ferns were dominating in the Late Carboniferous with tropic Marattiales; seed ferns vanished along with the horsetails. Gradually, some of them recovered later in the Kungurian, but at a lower level, to disappear like the Calamitaceae on the Permian-Triassic border forever. Otherwise, low-growing carpets of lichens were widespread (***Ragazzonia schirollii***).

The Dolomites had to suffer more than other Middle European regions, proven by a greater fern-richness in coeval fossil sites in Germany or France as they were part of the big Euramerican landmass. The most Northern parts of earth were in the Early Permian Artinskian untouched or only

The most primitive *Pinus*-ancestor

Artinskian *Ferovalentinia wachtleri* (branchlet and female cone (COL 236, COL 126, Monte Dasdana) represents till now the most archaic Pinoidea (Coll. Wachtler).

partially touched by the influences of the Gondwana Ice Age.
Interestingly, at 45 degrees north of the Angara continent, part of today's Ural region, a plethora of angiosperm-ancestors, horsetails, ferns and mainly the whole spectrum of insects could evolve. From the Silurian-Devonian period, Siberia and the Urals occupied a position apart from other landmasses, throughout the Carboniferous till the Permian. This position was between the 30th and 60th north latitude (today's position of Paris is about the 48th latitude; New York's is about the 41st latitude. Therefore, this northern Angara-landmass—for a long time, till the Triassic period—formed an isolated continent with independent floras and faunas (Wachtler, 2020).
On the Angara-continent, a unique development of angiospermic plants and insects occurred during the Early Permian. Interestingly, almost all the dominating insect families today were just present there and inside them were many potential pollinators. The Meganisoptera, the Megasecoptera, as well as modern looking mayflies, the Orthoptera, the Blattodea, the Plecoptera (stoneflies), ancient book-lices, the Neuroptera, the beetles and the Cicada were recorded. We encountered many well-preserved scorpionflies or the crown-group of the Acercaria, caddisflies and perfectly preserved Arachnida. About the presence of the Lepidoptera (butterflies) and the Hymenoptera, the sawflies, wasps, bees, ants, as well as the true flies (Diptera) cast a shadow of doubt, but it can be stated that some fossilised insects indicate this direction.
In the plant kingdom, we recorded just aggregated fruits, including Magnolia-like, and, surprisingly, their flowers. There were different kind of spikes, typically to grasses, and fruits resembling the Campanulaceae and Phytolaccaceae. Pappus, florets and capitula from the Asteraceae were present. Extensive presence of samaras from almost five dif-



Early Permian (Artinskian, about 287 mio years) Collio, Northern Italy

Within a few million years, the landscape changed from its abundance of horsetails and ferns to a reduced lichen conifers plant society. On the left, the first Araucaria ancestor ***Ortiseia dasdanai*** with female cones, in the middle a *Pinus* progenitor, the prickly ***Férovalentinia wachtleri,*** on the right the first firs ***Majonica suessi*** with its decaying female and small-sized pollen cones, far right below the lichen ***Ragazzonia schirollii.***

ferent broad-leaved trees like maples, elms or ashes can be found. Moreover, acorns or nuts, typically from oaks or hazelnuts, and different drupes from stone fruits were encountered (Perner & Wachtler, 2020). Although the flowers today, just like in the past, are small-sized, different development stages were discovered. Mostly, they have clearly defined carpels and stamen incorporated in the same plant.
Summarizing the equatorial European regions additionally to the Southern landmass from the Early Permian till the Artinskian suffered extremely through an icy climate catastrophe, whereas the Northern hemisphere was only partially influenced by this cataclysm. But it was the birthplace or the evolving fertile ground for the gymnosperms (conifers, cycads, ginkgos) and angiosperms on the Angara-continent.

The Dolomites 280 Mio years ago (dinosaurpictures.org)

The Kungurian flourishing

In the Early Permian Kungurian period, the climate changed considerably in the equa-

The most primitive ginkgos

It is difficult to accept that from Kungurian ***Ginkgoites pohli*** (leaves (TRE 297, seed/ovule TRE 45, Tregiovo) evolved in succession just till the late Permian the gingkoales. The collar on the base of the leaves and the berry-like seeds were fully developed in the Early Permian (Coll. Valentini)

The most primitive cycad

Kungurian *Wachtleropteris valentinii* (leaves (TRE 333, Tregiovo)) represents till now the most archaic cycad (Coll. Wachtler).

torial areas. In a relatively rapid geological time the equatorial region passed from a cold climatic to a subtropical zone. This Kungurian life biotic community can be defined as the first fully developed gymnosperm plant assemblage. Strangely all the gymnosperms (conifers, cycads, ginkgos) appeared fully evolved in the Early Permian and could be instantaneously recognized as Abietaceae, Araucariaceae, Pinoidea, Cycas, Zamia or Gingko-ancestors. They modified their appearance in the following 280 million years only marginally and opposed in that a theory of a slow and gradual evolution of the life.

In the European fossil sites appear the first unequivocal cycads and interestingly contemporaneously with the two lines that today populate the Earth: the more seeded Cycas-line and the two seeded *Zamia*-line. The first were present in the Alps with ***Macrotaeniopteris tridentina*** and ***Taeniopteris nonensis***, the second as ***Nilssonia perneri***. Strangely we encounter in the Dolomites a "last of the Mohicans"-taxa in the form of ***Wachtleropteris valentinii***, an extremely archaic cycad remembering some Devonian plants.
The Ginkgoales were just widely present with ***Ginkgoites pohli.*** They exhibited all

Early Permian (Kungurian, about 280 mio years), Tregiovo, Northern Italy

Within a very short time the arctic climate changed again to subtropical. Left lower part the seed ferns ***Autunia*** and ***Lepidopteris meyeri,*** after the fern ***Sphenopteris battistii***. A variety of gymnosperm-families suddenly developed. In the middle is visible first the most archaic cycad-progenitor ***Wachtleropteris valentinii*** with male and female cones, after that a more evolved ***Taeniopteris nonensis*** and ***Macrotaeniopteris tridentina***. On the right is a *Zamia*-cycad ***Nilssonia perneri***. Upper part in the middle left: A branchlet of the Abietaceae ***Majonica ambrosii*** with a male cone. Left upper part: The giant horsetail ***Neocalamites tregiovensis,*** in the middle sprout the first gingko ***Ginkgoites pohli*** with its seeds and a male organ. After following a branchlet of the Araucariacea ***Ortiseia daberi.*** On the right side is visible a male and a female cone with seed scales of Voltzia ***viallii.***

the features of today's *Ginkgo biloba*, like leaves coated by a collar and berry-like ovules/seeds. Beginning from the Kungurian, the Pinoidea began to diversify in the five bundled ***Férovalentinia cassinisi***, and the irregularly from one, two, till three grouped ***Férovalentinia angelellii***. Other frequent conifers were the Araucariaceae with ***Ortiseia daberi,*** the Abietaceae with ***Majonica ambrosii*** and ***Voltzia viallii***. Poorly represented were the ferns with ***Sphenopteris battistii***, additionally to some *Peltaspermum*-seed-ferns (***Lepidopteris meyeri, Autunia***) or the horsetails with ***Neocalamites tregiovensis.***

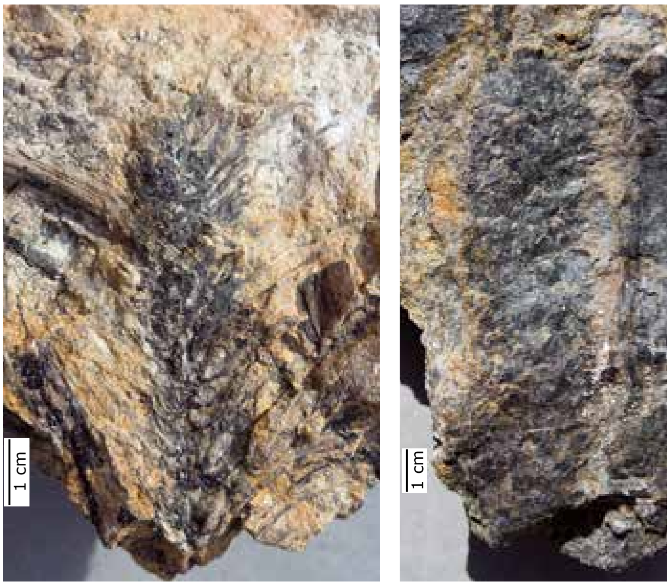
The Dolomites 260 Mio years ago (dinosaurpictures.org)

The Late Permian recovery

The late Permian (Wuchiapingian) is distinguished by two interesting European flora-zones. A Middle-North European Zechstein (Copper slate) community characterized by ***Baiera digitata***-gingkos, the Taxaceae ***Ullmannia frumentaria, Pseudovoltzia liebeana*** and ***Taeniopteris eckardtii-***cycads with some isolated ***Sphenopteris dichotoma*** ferns and ***Peltaspermum martinsii*** seed ferns and an Alpine area with the dominating Araucarian-progenitors *Ortiseia* (***Ortiseia leonardii, Ortiseia visscheri, Ortiseia jonkeri, Ortiseia zanettii***), but also Abietaceae-ancestors (***Majonica alpina, Majonica clement-westerhofae***). A highlight is the evolution of ***Ginkgoites murchisonae*** having many affinities with modern Ginkgo-trees. Also fully evolved cycads were present with Zamia-like ***Nilssonia brandtii,*** or Cycas resembling ***Macrotaeniopteris wachtleri.*** The apparition of archaic ***Pernerina pasubi*** is interesting, bearing cycas-like multiseeded fertile organs. True ferns were rarely encountered with ***Angiopterites murchisonii*** and ***Sphenopteris***. In the Late Permian Alps, we have also a fair amount of horsetails like ***Equisetites siberi*** and with ***Neocalamites behnkeae*** the last survivor of the Calamitaceae is recorded.

Whereas, in the Late Permian Zechstein ***Ortiseia florinii*** and *Majonica* sp. were present but seldom, the same occurred in the Alps with ***Voltzia sjerpii*** and the Taxaceae ***Ullmannia edwardsae*** being present, but rare. For the last time, the late Paleozoic plant community especially in the Dolomites dominating Araucaria-ancestors *Ortiseia*, Abietaceae *Majonica,* and ginkgos reached its heyday, whereas all other plant families like ferns, lycopods or horsetails stood in the background.

The upper Permian (Wuchiapingian) floras of the Dolomites can be regarded as one of the richest and most interesting worldwide



Late Permian Firs and Araucarias

In the Wuchiapingian the firs and araucarias were fully evolved. Left: Female cone of *Majonica alpina* (PAS 750, Ariche, Valli del Pasubio); right *Ortiseia leonardii* (CUEC 326, Cuecenes, Seceda), both Wuchiapingian, Late Permian, all coll. Wachtler and proof that the climate in that time in the straightly on the equator lying Dolomites was not as hostile to life as it is often assumed.

The Permo-Triassic catastrophe

Beginning from the latest Permian over the Triassic border the climate changed in a short time and their repercussions were equal as the Carboniferous-Permian cataclysm. In the Dolomites, with their uninterrupted succession of layers from the Permian over the whole Triassic this can be examined perfectly. Especially on the Seceda mountain in the Gröden-Valley many slightly time different plant lenses crop out. Till a certain point. Abruptly commence layers of gypsum from drying or silting up of the inshore water. Within a few million years the climate changed from subtropic with cycads and also Marattiaceae ferns to a desertic hostile climate with no more fossil plants recorded, and this happened worldwide. An audacious hypothesis can be searched in the largest known volcanic events of the last 500 million years of earth's geological history—the forming of Siberian Traps, spanning one million years between the Permian–Triassic boundary, about 251 to 250 million years ago. Moreover, today the basaltic lava covers about two million square kilometres, but the original extension is estimated to be about seven million square kilometres approximately in the region from Siberia over the former Angara-continent (Benton et al., 2010; Wachtler, 2020).

If this global catastrophe really happened, and this is based on facts and documented by analyses from the extinction of many life tribes, Angara was the most evolved landmass and after them also the global landscape suffered. It can be suggested that only with great difficulty did the Palaeo-angiosperms survive on some isolated refuges and that too on a restricted and marginal level on the Angara-landmass. However, in Europe the climate changed considerably between the Permian and the Triassic. For many million years the Pinus-conifers and also the Abietaceae, as well as the Ginkgoales disappeared from the fossil record.

The Dolomites on the Permo-Triassic boundary. The life-world was extinct, extended salt-deposits, testimonies of a desert climate cover the landscape. All unusual conditions for an area lying near the equator.

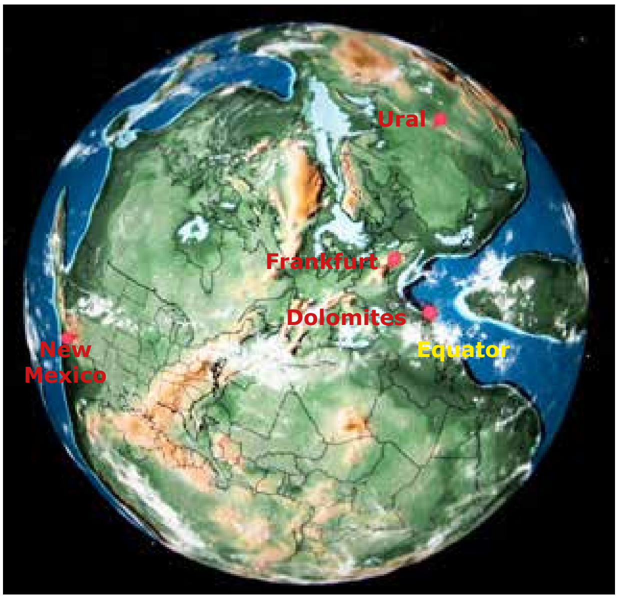
If we have mostly all flowering plant tribes in the Early Permian Angara-Land and also mainly all gymnosperms just in the Permian, why could they not radiate all over the landmass when Pangaea assembled to one global continent? From the Triassic till the Cretaceous, the time of worldwide appearance of angiosperms, but also a reemerging of the Pinoideae and Abietaceae, probably obstacles, such as high mountain ranges or extremely consolidated endemic floras were too high to allow a global distribution of the insects and flowering plants on one side and many gymnosperms tribes on the other. But the main cause was the lack of wide-ranging seed dispersers like birds. Nowadays, birds can travel thousands of kilometres over the highest mountain ranges and within a short time. The first birds appeared in the Upper Jurassic (Tithonian), about 150 million years ago, the worldwide propagation of many plants, especially the angiosperms we encounter in the Early Cretaceous. All this can not be a coincidence.

The slow Early Triassic recovering

Astonishingly the first plants to recover after the Permo-Triassic cataclysm were the club-mosses and the horsetails. Especially the lycophyte ***Pleuromeia sternbergii***, one of the best-described and most interpreted Early Triassic plants recorded extensively in the Early Triassic (Induan–Olenekian) in Europe and in other subspecies reaching till Russia, China and Japan. Surprisingly it seems that *Pleuromeia*, which dominated the floras of the Lower Triassic, did not survive the Olenekian–Anisian boundary, whereas the giant horsetail ***Equisetites,*** which occupied the same ecological niches, passed unchanged on to the following periods.

The Triassic plant life explosion

The Early-Middle Triassic (Anisian) saw a global climate improvement. Quickly a tropical till subtropical biota began to dominate in the Dolomites. For the first time after the Late Carboniferous, we encounter an extraordinary rich fern-community with several completely different and new families of Pteridophyta. Tribes, still present today, like the *Danaea*-ferns (***Danaeopsis dolomitica*** and ***Danaeopsis marantacea***), the Osmundaceae (***Neuropteridium***



The Dolomites 240 Mio years ago (dinosaurpictures.org)

The last Sigillarias

Anisian *Sigillcampeia nana* (PIZ 1000, stem with attached leaves, Piz da Peres) represents one of the last Sigillariaceae (Coll. Wachtler)

Early-Middle Triassic fern-community (Anisian, about 245 mio years), Piz da Peres

A variegated tropical till subtropical flora with many different fern-families dominates: Left the ***Anomopteris mougeotii,*** than follow the two Osmundaceae ***Neuropteridium elegans*** and ***Neuropteridium voltzii.*** After that grow the oldest *Danaea*-fern recorded ***Danaeopsis dolomitica*** and right the most archaic *Lindsaea*-fern ***Wachtleria nobilis***. In the background, on the left the two tree ferns ***Gordonopteris lorigae*** and ***Ladinopteris kandutschii*** flourish.

voltzii and ***Neuropteridium elegans***), the Lindsaeceae (***Wachtleria nobilis***) additionally to tree-ferns parented with the Cyatheaceae (***Gordonopteris lorigae*** and ***Ladinopteris kandutschii***) began to flourish. Other in the Early-Middle Triassic (Anisian) widespread ferns like ***Anomopteris mougeotii*** or ***Cladophlebis rhombifolia*** have apparently no living counterparts. Moreover, the seed ferns reappeared largely with ***Scytophyllum bergeri*** and the enigmatic ***Sagenopteris keilmannii*** and prosecuted their way all over the Triassic.

The cycads, just present in the Permian began to become invasive. Especially in the Early-Middle Triassic the *Cycas*-cycads (***Bjuvia olangenis, Taeniopteris simplex***) maintained largely their Permian features meaning leaves and megasporophylls arranged spirally on an axis. Only beginning from the Middle Triassic (***Taeniopteris angustifolia***) the multi-seeded megasporophylls and fronds changed to planate as today's *Cycas*. Strangely the entire leaf, lacerated often by storms remained in the Northern hemisphere till the late Triassic, a feature that today within the geometrically segmented fronds of the cycads is not anymore recorded.

Various and widespread in that time were also the biovulate cycads with ***Nilssonia primitiva*** and ***Pseudoctenis braiesensis***, resembling extant *Zamia*-cycads. Their female and male cones did not change many from the Permian till today.

The conifer assemblage varied considerably in the Anisian with a dominance of the Voltziales. For the first time emerged *Glyptostrobus*-ancestors (***Alpia anisica***), larches ***(Wachtlerolarix***), Cupressaceae (***Pusteria***), whereas the Araucariaceae (***Araucarites churchillae***), dominating in the Permian were present, but pushed in the background. Also the horsetails found largely their place in the European plant as-

Early-Middle Triassic lycopod community (Anisian, about 245 mio years), Piz da Peres

The interesting club-moss plant assemblage: Left the enigmatic ***Eocyclotes alexawachtleri,*** followed by the low growing parented ***Lepacyclotes bechstaedtii,*** behind the Isoetaceae ***Isoetites brandneri***. In the middle ***Sigillcampeia nana,*** one of the last representatives of the *Sigillaria*-trees, on the right the arborescent ***Lycopia dezanchei***, probably the last descendant of the *Lepidodendron* club mosses and the Selaginellaceae ***Selaginellites leonardii.***

semblages (***Equisetites aenaceus, Schizoneura merianii***).
One of the most interesting peculiarities in the Early Triassic Dolomites is represented by the reemerging of a plethora of arborescent till small growing lycopods. Especially interesting is the tree-shaped ***Lycopia dezanchei***. Their appearance and also their cone-like strobili resemble some Bonsai-shaped *Lepidodendron*-trees. *Lycopia dezanchei,* as well as the small arborescent ***Eocyclotes alexawachtleri*** disappeared within a short time. Others like ***Lepacyclotes bechstaedtii*** and ***Sigillcampeia nana*** survived till the end of Triassic. They can be regarded as the last descendants of the huge *Sigillaria* clubmosses. The Selaginellaceae ***Selaginellites leonardii*** and ***Isoetites brandneri*** survived till today. However, not completely resolved is the abundance of lycopods in the Early Triassic. It can probably be due to the extremely saline soils.

The Dolomites were located in the Anisian at about the tenth latitude north within a tropical environment. Never before have we encountered such a richness in different gymnosperms, ferns, lycopods and horsetails. The climate must have been pleasant in all respects. But this paradisiacal period lasted only a couple of million years, because towards the Middle Triassic (Ladinian) the vegetation became poorer again.

The Late Triassic Raibl cataclysm

The flora impoverished continuously till the Late Triassic (Carnian), when another catastrophe, the Raibl-Cataclysm pushed back the rich flora assemblages from the Early Mesozoic. No ferns were furthermore recorded in the Eastern Alpine Raibl sediments, no cycads, seed ferns, rarely horsetails occurred. Only a plethora of different lycopods, such as leafless ***Selaginellites perneri*** and ***Sigillcampeia blaui*** form vast plant-carpets. Moreover, in this time the only reasons for the emerging of lycopods can be searched in saline soils.

Additionally, the conifers were common and well preserved, but had a reduced and extremely prickly character like ***Araucarites spinosa, Voltzia carinthica,*** or shrubby cypresses (***Pusteria maribelae***). Sometimes appeared larch progenitors (***Wachtlerolarix weissii***). The vegetation was as reduced as in the Early Permian (Artinskian), about 50 million years earlier.

But why did we have in the Julian period—ranging only a few million years—such a reduced vegetation? The Raibl-Flora, that can be followed in the Lienz-Dolomites over many kilometres, was miserable and xerophytic in all parts—not the conservation, but the richness. We encountered lenses extending for hundreds of meters where mainly one mimicry and leafless *Selaginellites perneri* species can be found in contradiction to the earlier Ladinian flora and the later Rhäto-Liassic plant assemblages.

It was supposed (Simms & Ruffell, 1989) that the cataclysm was created by massive basalt formations in British Columbia (Wrangellia Terrane), spewing out huge volumes of lava over hundred thousands of years, around 232 million years ago. The palaeobotanical fossil record during the Carnian sustained a dry and extremely arid climate on the Paleo-Tethys beaches of this region, whereas before and after this is not ascertainable.

After this "Raibl-Cataclysm" the vegetation recovered in a short time leading to a normally tropical wet climate on the Triassic-Jurassic border. Strangely the dinosaurs experienced its full bloom and dominated the Earth for about 150 million years and together with them also the birds and later the flowering plants.

Early-Middle Triassic gymnosperm-community (Anisian, about 245 mio years), Piz da Peres

The gymnosperms with cycads and conifers were widespread. The ginkgoales were missing: Left two fertile female cycas ***Bjuvia olangensis***; in the middle another parented cycas ***Taeniopteris simplex***, right the Zamiaceae ancestors ***Nilssonia primitiva*** and ***Pseudoctenis braiesensis*** with female cones, shed seed scales and male cones. In the background left grows the conifer ***Voltzia rietscheli*** and on the right side the *Glyptostrobus* progenitor ***Alpia anisica.***

The Lienz Dolomites (Lavanter Alm). For kilometres crop out plant rich sediments, which give indications of a extremely reduced flora, the Raibl-cataclysm (Foto Michael Wachtler).

The Dolomites 220 Mio years ago (dinosaurpictures.org)

Late Triassic (Karnian, about 232 mio years), Lienz Dolomites Northern Italy

During the Carnian, especially the Julian stage another catastrophe - the Raibl cataclysm - reduced the plant kingdom. Especially the club moss ***Selaginellites perneri*** (middle) became dominant, ferns, ginkgos and cycads were missing completely. It was accompanied by another lycopod ***Sigillcampeia blaui,*** (below left) the last small-sized survivor of the huge *Sigillaria*-trees from the Carboniferous. The conifers remained in the background and were characterized by leathery or prickly leaves. Left ***Araucarites spinosa***, in the middle at the top the spiny Cupressaceae ***Pusteria maribelae***, right one of the last Voltziaceae ***Voltzia carinthica.***

The Raibl-cataclysm and its richness in lycopods

Carpets of the clubmoss ***Selaginellites perneri*** (Entire plants LAV 26, strobili LAV 32) dominate in the Late Permian (Carnian) Dolomites. Such a reduced flora indicates extreme weather conditions.

References

Benton, M. J., Sennikov, A. G., Newell, A. J., 2010. Murchison's first sighting of the Permian, at Vyazniki in 184; Proceedings of the Geologists' Association, vol. 121, pp. 313 - 318. https://doi.org/10.1016/j.pgeola.2010.03.005

Fritz, A., Boersma, M., Krainer, K., 1990. Steinkohlenzeitliche Pflanzenfossilien aus Kärnten. Carinthia II, Sh. 49, 109–132, Klagenfurt

Kustatscher, E., Nowak, H., Opluštil, S., Pšenička, J., Muscio, M. & Simonetto, L., 2019. The Carboniferous flora of the Carnic Alps: state of the art. – Gortania, 30: 33–47.

McGhee, G., 2018. Carboniferous Giants and Mass Extinction: The Late Paleozoic Ice Age World, New York: Columbia University Press. ISBN: 9780231180962

Perner T., 2015. *Ferovalentinia wachtleri* n. sp. from the Early-Permian, a conifer-species on the base of all Pinoideae; in Wachtler M., Perner T., 2015. Fossil Permian plants from Europe and their evolution. Rotliegend and Zechstein-Floras from Germany and the Dolomites. Published by Dolomythos Museum, Innichen, South Tyrol, Italy; Oregon Institute of Geological Research, Portland, OR, (USA), ISBN 978-88- 908815-4-1; pp. 83-88

Simms, M. J.; Ruffell, A. H. 1989. Synchronity of climatic change and extinctions in the Late Triassic. Geology. 17: 265–268.

Wachtler M., 2015. Interesting conifer-evolution in the Early-Permian (Artinskian) Collio Flora (Brescian Alps - Northern Italy); in Wachtler M., Perner T., 2015. Fossil Permian plants from Europe and their evolution. Rotliegend and Zechstein-Floras from Germany and the Dolomites. Published by Dolomythos Museum, Innichen, South Tyrol, Italy; Oregon Institute of Geological Research, Portland, OR, (USA), ISBN 978-88-908815-4-1; pp. 68-82

Wachtler M., 2015. The Lower Permian (Sakmarian/ Artinskian) Collio-Flora from Val Trompia (Southern-Alps, Italy); in Wachtler M., Perner T., 2015. Fossil Permian plants from Europe and their evolution. Rotliegend and Zechstein-Floras from Germany and the Dolomites. Published by Dolomythos Museum, Innichen, South Tyrol, Italy; Oregon Institute of Geological Research, Portland, OR, (USA), ISBN 978-88- 908815-4-1, pp. 45-51

Wachtler M., 2016. *Sigillaria*-Lycopods in the Triassic. In: Wachtler M., Perner T., Fossil Triassic Plants from Europe and their Evolution, Volume 2: Lycopods, horsetails, ferns, Dolomythos Museum, Innichen, South Tyrol, Italy, p. 3-16

Wachtler M., 2016. Fossil Triassic *Selaginella* species from the Dolomites. In: Wachtler M., Perner T., Fossil Triassic Plants from Europe and their Evolution, Volume 2: Lycopods, horsetails, ferns, Dolomythos Museum, Innichen, South Tyrol, Italy, p. 3-16

Wachtler M., 2020. The Evolution of the First Flowers - Early Permian Angiosperms p. 17-42; In Wachtler M., Perner, T. (eds.), 2020: The Origin and Evolution of Angiosperms - Early Permian Flowering plants. ISBN 978-88-944100-4-4

Wachtler M., Perner T., 2020. Insect and Flowering Plant Interactions in the Permian p. 149-190; In Wachtler M., Perner, T. (eds.), 2020: The Origin and Evolution of Angiosperms - Early Permian Flowering plants. ISBN 978-88-944100-4-4