

Michael Wachtler. Important discoveries

***Megachirella wachtleri*, the ancestor of snakes and lizards**

In 1999, Michael Wachtler recovered a partially preserved reptile-skeleton from the Kühwiesenkopf (Prà della Vacca) in the Pragser Dolomites. It was described by Silvio Renesto and Renato Posenato in 2003 as *Megachirella wachtleri*. Immediately, the importance of this fossil was recognized as pertaining to the crown group of squamata and also the lepidosauromorpha. But only in 2018, a group of scientists under the overall control of Tiago Simões were able to classify *Megachirella wachtleri* as the oldest known stem squamate by using the new high-resolution microfocus X-ray computed tomography data. This paper deals with the exciting found-history of *Megachirella* and the chronological course of research.

The more than 242-million-year-old fossil, *Megachirella wachtleri*, is the most ancient ancestor of all modern lizards and snakes, iguanas, chameleons, geckos, known as squamates. *Megachirella* is about 75 million years older than what was thought were the oldest fossil squamata in the world.

The birth of first dinosaurs

The Dolomites are rich in Paleozoic-Mesozoic ichno-associations, which can be followed in the rock-sediments from the Early Permian till the Middle Triassic. In 2007, Michael Wachtler discovered a new fossil site with interesting ichnospecies on the Piz da Peres mountain holding an exhausting near-shore paleoecosystem with numerous tetrapod tracks. Especially the new *Sphingopus ladanicus*-trackways were interesting because they showed a clear tendency towards bipedalism with a functionally three-toed pes as is possible in the synapomorphies of basal dinosaurs. These characters are interpreted as possible synapomorphies of basal dinosaurs. Therefore, the tracks of *Sphingopus ladanicus* can be interpreted as dinosauroid and not dinosaurian. More realistic would be to indicate them as 'ancestors' of dinosaurs or more exactly an affiliated evolutionary-line.

Wachtlerosaurus

In 2017 Michael Wachtler discovered a small-sized Middle Triassic archosaur in the Dolomites. It was described by Thomas Perner as *Wachtlerosaurus ladanicus*. The skeleton was mostly complete; the skull is characterized by its powerful teeth, the ribs are slender. The animal would have adapted to a climbing and arboreal lifestyle with the miniaturization of body size to evade predation. It is not easy to insert *Wachtlerosaurus* in one of the known families. Since very little is known about the phylogenetically earliest members of the Avemetatarsalia, this new animal helps to fill a gap in the knowledge.

Der Farn Wachtleria

Wachtleria nobilis, discovered by Michael Wachtler and described by the Austrian palaeontologist Georg Kandutsch is the oldest known ancestor of the Lindsaeaceae, a tropical to subtropical fern family part of the Polypodiales. The Lindsaeaceae includes about 200 species distributed across South America, East Asia and New Zealand. *Wachtleria nobilis* highlights all the features of today's Lindsaeaceae with their slender stipes and fertile leaves with sori grouped on the outer margins of the leaves.

An important fern and a famous woman geologist

The fern *Gordonopteris lorigae* was first found in beautiful and well-preserved specimens on the Kühwiesenkopf by Michael Wachtler. It is named after the Scottish geologist, palaeontologist and politician Marie Ogilvie Gordon (1864 – 1939). She was the first woman to be awarded a Doctor of Science from University of London and the first woman to be awarded a PhD from the University of Munich. She was also a supporter and campaigner for the rights and equality of children and women.

The species name *lorigae* honours Prof. Dr Carmela Loriga Broglio (1929–2003), one of the pioneers of Triassic geology in the Dolomites.

The golden age of clubmosses

Although extant lycophytes constitute a modest group of herbaceous plants, they have played an enormous role in the history of land vegetation, extending over 400 million years. They dominated the vegetation around the world and were the largest known living organisms in the Carboniferous. Therefore, discoveries of new missing links not only throw light on the evolution of this important family but help us to understand climatic and palaeoecological cataclysms in the past. The giant Lycophyta dominated the swamp-jungles in the Carboniferous and it was thought that they declined in a relatively short time on the Permian border. Astonishingly, the clubmosses experienced a new golden age all over the Triassic, although – with regard to their size – on a lower level. And the Dolomites play a major role in the understanding of lycophytes.

The enigma of the scale trees

One arborescent lycopod, probably descended from the Carboniferous Lepidodendrales, is represented by *Lycopia dezanchei*, first discovered and described by Michael Wachtler. It constitutes a highly interesting plant and a direct descendant of giant *Lepidodendron*, because it has ancestral affinities. It seems that some of the arborescent Lycophyta crossed the Permian by reducing their size and survived till the Mesozoic to occupy ecological niches. Extant Lycopodiales and *Lycopia* show a comparable root system with a reptant stem and rootlets, as well terminal strobili.

The last Sigillaria-lycopods

It was thought that the other big group of Carboniferous Lycophyta, the Sigillariaceae, died out at the beginning of the Permian. Due to new discoveries in the Dolomites it can be stated that they played –although on a dwarfish base– an important role for understanding Triassic vegetation and its evolution in the Jurassic. *Sigillcampeia*, honouring Edith Campeï the first finder, was characterised by its bonsai-like growth, and give a deep insight into the blueprint, growth and fertilisation of this lycopod family. It is also interesting that the cones hold microsporangiate and also macrosporophylls with only one huge sporangia, that in other cases could also be regarded as a seed.

Another interesting genus is represented by *Eocyclotes alexawachtleri*, characterized by a short stem and ending in a closely spaced foliage forming a rosette around which are arranged numerous tongue-like sporophylls. This lycopod was first found in the Braies Dolomites by Alexa Wachtler.

Ancestors of today's quillworts

Present-day *Isoetes*, commonly known as quillworts, have 192 recognised species, all over the world, and occupy mostly aquatic or semi-aquatic slow-moving waters. They are heterosporous. Triassic *Isoetites brandneri*, discovered for the first time by Michael Wachtler in the Braies Dolomites, one of the oldest ancestors and is comparable with today's *Isoetes*.

The origin of gymnosperms

The slow evolution of life is an indisputable scientific principle. However, it seems that all of today's widespread plant tribes were already present at the Carboniferous–Permian boundary and that their common ancestors can be largely dated back to the Devonian. This means that the origins of gymnosperms and angiosperms should be found there. In the earliest Permian (and probably before) all the features of the gymnosperms were highly developed; hence, in the following 300 million years they changed only slightly. The straight evolution line to modern-day Araucariaceae was clearly defined in the Permian. The one-seeded genus *Ortiseia* had the same structural appearance as modern-day Araucarias, while wing-seeded *Majonica* represented the firs. Also the *Pinus* ancestor *Fèrovalentinia* was widespread in the Early Permian, as well as the typical three-, four- (or more) lobed seed scales of

the Voltziaceae, which were potential progenitors of today's Cupressaceae. The typical blueprint of the Ginkgoales was in the same way already defined in the Paleozoic (*Baiera*), and even fully evolved Cycadales like *Bjuvia*, *Taeniopteris* or *Nilssonia* could be encountered. The cycad-like *Wachtleropteris* or rudimentary conifer *Perneria* can be regarded as real living fossils in the Permian. The double Y-lobed leaves and seed scales of *Perneria* are the last memory of a common plant origin in the Devonian, where all tribes hold this feature. This blueprint can be observed in its hidden form in all modern-day floras.

The mother of all cycads

The origins and evolution of the cycads have fascinated palaeobotany researchers for decades. This is probably due to their early origins - with ancestors extending back more than 300 million years into the Carboniferous - and because the plants that developed from them or parallel to them could enable researchers to gain knowledge of the evolution of the flowering plants.

The cycads still living today consist of 11 genera and 305 species, which make them the second largest group of gymnosperms after the conifers. They spread over the tropics and sub-tropics north and south of the equator, and Central America is considered the region with the greatest diversity of cycads. The palm ferns are generally divided into three large families: the Cycadaceae, the Stangeriaceae, and the Zamiaceae. All cycads exhibit a plethora of common features. They all have separate sexes, with male and female fructifications located on separate plants. With the exception of the genus *Cycas*, all species developed similar male and female cones that are easy to differentiate from those of other plants and were located individually or in groups at the tip of the stem between the fronds.

Many of our efforts to understand the evolution of the Cycadales are hampered by the poor fossil record, although there is worldwide interest in understanding the evolution and origin of this mysterious plant group.

In the 1990s Michael Wachtler began intensive research into fossil cycads, first in the Alps and then all over Europe. So it was possible to recover sufficient remains from the Early Permian through the whole Triassic and till today. Furthermore, fossil Cycadophyta from other parts of the world were studied and compared to obtain indications about evolutionary trends. Therefore it is now possible to view their unusual story through time in a new light.

But where should we look for the starting point of the Cycadophyta? Their multiovulate or biovulate sporophylls were already fully developed on the Carboniferous–Permian border, therefore a slow transition cannot be deduced or has to be sought between the Devonian and the Carboniferous.

After their appearance between the Carboniferous and Permian, they became more numerous, remaining nearly unchanged in the development from the Permian to the Triassic. For a long time, the doctrine has held that the genus *Cycas* can be considered the most primitive based on the unusual structure of their macrosporophylls, and that all others were derived from it through reduction. Fossil finds, however, indicate that the *Cycas* and *Zamia* groups developed almost simultaneously, ever since the Palaeozoic era.

Wachtleropteris valentini - honouring Michael Wachtler and Ferruccio Valentini – discovered in sediments from Early Permian, represents the most rudimental cycad gymnosperm. The shrubby plant was equipped with leaves that extended upwards on a stem and branched twice, which is not typical for today's cycads, and each of the leaves split into two independent branches. The leaves were tongue-shaped and have a pronounced midrib. The arrangement of the cones on the end of a pinnate leaf identifies them as gymnosperms. They can therefore be classified as "last representatives of a very old and primitive species having cycadalean affinities" from the Devonian until the Permian.

From the Permian and all through the Triassic we then encounter isolated wedge-shaped appendices holding two ovules/seeds on the lower shield surface. They belong to cycadalean progenitors, like *Nilssonia*, *Apoldia* or *Pseudoctenis*, and have an amazing resemblance to today's *Zamia* species.

With its irregular but still recognisably segmented fronds, *Nilssonia perneri* from Tregiovo can be considered a potential ancestor of the cycads from the Zamiaceae-line. There are enough parental affinities to regard the Early Permian *Nilssonia perneri* as the precursor of the Upper Permian *Nilssonia brandtii* or Middle Triassic *Nilssonia primitiva*, both from the Dolomites.

Additionally, from the Permian and especially in the Triassic, feathered cycad megasporophylls with multiple seeds/ovules attached on the lower side of an often closed or semi-open fruit-blade are found. They were classified as *Taeniopteris* or *Bjuvia*. Strangely enough, many ancestors of the cycads hold more or less large entire fronds that may have been torn several times due to the rigours of nature, like today's banana leaves. They pertain to the other big group of modern-day cycads: the *Cycas* family.

The enigmatic ginkgo

Ginkgo biloba tree stands like a recluse among the flora of today and is still surrounded by mystery. Its evolutionary history is also astonishing since it has been a witness to the history of the Earth from the Early Permian to today. Today's ginkgo leaves are fan-shaped with veins radiating out into the leaf blade. On the Carboniferous–Permian border indeed their leaves were irregularly lobed and needle-like. Surprisingly, we can establish that the Early Permian *Baiera pohli* from Tregiovo, described first by Michael Wachtler can be regarded - due to its inchoate and irregular branching system - as the most primitive ginkgo so far recorded, with affinities to some progymnosperm plants from the Devonian. But it has all of the features of real ginkgos: these characteristics include a collar-like ring from which the leaves emanate, and two ovules/seeds aggregated together. The ovules did not hang from the end of a distinctive stalk like those on a modern ginkgo, however, but were held by a modified leaf segment.

The search for the most primitive conifer

Which ancestors of the gymnosperms from the Carboniferous-Permian transition are the most likely candidates for being the first ancestor of all conifers? Which fossil finds exhibit the most primitive features? Which species has the best prerequisites suggesting that all other conifers are derived from it? These questions are some of the most difficult to answer in the history of the evolution of plants. No other species of conifer exhibits such primitive features as *Perneria thomsonii* from the Carboniferous-Permian transition. In many regards, with their double-Ypsilon terminal leaves and pointy-tipped emergences in the lower part, they are reminiscent of the progymnosperms from the Devonian. It can thus be considered certain that the cones of the most primitive conifers were not inflorescences, but individual pinnate to tetrapinnate (at the most) leaves on which one to several (at the most up to eight) seeds could form instead. Based on *Perneria*, it is possible to derive many of the later lines of development such as the Araucaria-like *Ortiseia*, conifers bearing winged seeds like *Wachtlerina* or *Majonica*, the first pines with their earliest representative *Fèrovalentinia*, and even the primitive ginkgo trees.

Fèrovalentinia and the origin of the Pines

Just like almost every other family of conifers, the modern Pinoideae, which are generally referred to as pines or *Pinus*, had already experienced an explosive development by the time of the transition from the Carboniferous to the Permian that brought them close to the modern pines in a very short time. Strangely enough, the multi-lobed and lacinate individual leaves of its Devonian ancestors played a role again in this case: they became longer, forming the long and slender needles we are familiar with today. The cones, in contrast, became extremely woody and had virtually reached their modern appearance during the Lower Permian.

The subfamily of the Pinoideae today consists of about 110 species that almost exclusively inhabit the northern hemisphere. They form monoecious trees or even bushes, and colonise the most

inhospitable regions, including the highest mountains, due to their tenaciousness. They like to grow in the company of other pines and can cover extensive areas. Their needles rarely grow alone (except for *Pinus monophylla*), but usually in bundles of two to five, sometimes even in groups of eight, whereas the base of the needles is surrounded by a fascicle sheath. The seeds form in pairs on an ovuliferous scale and can either be winged, as on the Scots pine (*Pinus sylvestris*), or nut-like as on the Swiss pine (*Pinus cembra*). The cones themselves can reach lengths from just a few centimetres, as on the mountain pine (*Pinus mugo*) or the Colorado pinyon (*Pinus edulis*), to 60 centimetres on the sugar pine (*Pinus lambertiana*). The male pollen cones are usually small and grow in bunches arranged in a helix near the base of long, young shoots.

The incredibly rapid rate at which development must have occurred at the beginning of the Permian, a rate which was never achieved again, can also be traced based on the development and divergence of the pine-like trees. Early Permian *Fèrovalentinia wachtleri*, fossils of which have been found in the Southern Alps can be regarded as most ancient pine. The astonishing changes that must have taken place in the short period of about five million years can be seen on pine trees found just a few kilometres away in Tregiovo, which came from an later stage. In the meantime, the pines had clearly diverged along several lines. *Valentinia angelellii* still exhibited relatively short-needled, lacinate leaves, while *Valentinia cassinissi*, in contrast, was characterised by long-needled, bushy bundles similar to the modern, five-needle Swiss pine (*Pinus cembra*). The seed cones, however, only changed marginally, and have stayed that way until today.

An interesting feature of the needles of these early pines is their striking similarity to the ginkgo leaves of that period. It is especially difficult to differentiate them from Permian ginkgophyte *Sphenobaiera*. It is therefore possible to derive a relationship between the ginkgos and the pines.

The astonishing Development of Conifers with Winged Seeds

Conifers with cones that were characterised by winged seeds appeared for the first time in the earliest part of the Lower Permian (*Wachtlerina bracteata*). They did not form a homogeneous group in the Permian, but it is certainly possible to draw parallels to the modern fir trees. The formation of winged seeds led to their inexorable rise, as their seedlings could travel long distances.

Their woody seed cones are composed of numerous, spirally arranged ovuliferous scales which bear winged seeds on their upper surface that are only attached at the base. Certain species such as the Douglas fir (*Pseudotsuga menziesii*) or the bristlecone fir (*Abies bracteata*) are characterised by cover bracts that extend far beyond the ovuliferous scales, a feature of many Palaeozoic conifers.

The variety in appearance of these winged seeds today demonstrates the different ways in which they have developed since the earliest stages of the Permian. It is certain that winged seeds had formed by the beginning of the evolution of conifers, and that the ability to spread seeds carried by the wind over long distances became a model for success. This model was no less advanced than the nuts offered by other conifers to animals as food. The Upper Permian *Majonica alpina*, a winged-seeded conifer, which was classified for the first time by the Dutch palaeobotanist Johanna Clement-Westerhof (1987) based on fossil finds from the Dolomites, was a milestone in the history of research of the plant kingdom. But Michael Wachtler recognized after intense researches that just before we have with Early Permian *Majonica suessi* and *Cassinisia ambrosii*, firs with the same features.

Their woody seed cones are composed of numerous, spirally arranged ovuliferous scales which bear two-winged seeds on their upper surface that are only attached at the base. Many *abies*-species are characterised by sterile cover bracts that extend far beyond the ovuliferous scales, a feature of many Palaeozoic conifers. Although this type of aliform seed has only been preserved in rare cases, and even then only in the finest sediments, it has still been possible to collect enough evidence for this important step in evolution. It is certain that winged seeds had formed by the beginning of the evolution of conifers, and that the ability to spread seeds carried by the wind over long distances became a model for success. This direction line was no less advanced than the nuts offered by other conifers to animals as food. We can only speculate, but a series of distinct characteristics indicate

that in the Carboniferous–Permian border Araucariaceae and Abietoidaceae were still so closely related as to give some difficulties in telling them apart.

Ortiseia or the birth of Araucarias

The family of the Araucariaceae today consists of three living genera: *Araucaria*, *Agathis* and *Wollemia* (first discovered only in 1994). They are almost completely endemic to the Southern hemisphere. From the Permian to the Triassic, however, their ancestors dominated extensive parts of the Earth. In contrast to other conifers, they are distinguished by slender pollen sacs that hang freely from the end of the microsporophyll towards the rachis of the cone. The female cones are usually globular, and most can reach significant sizes, with diameters of up to 30 cm, like those of *Araucaria bidwillii*. The seed scales themselves differ greatly from those of other conifers: they contain only one single seed, and in many species they are merged with the ovuliferous scales, forming an inseparable unit. Upon maturity, the cones drop their seeds and scales one by one. The noticeably regular structure of the crown, with more or less equally distributed branches, makes the Araucariaceae unique in the world of conifers. This is why it can be assumed that their ancestors also exhibited these properties. In fact, almost all the characteristics appeared, albeit in slightly modified forms, in the earliest stages of the Permian.

Ortiseia can be considered as ancestor of all Araucarias. They were just widely present in all Early Permian with *Ortiseia uhli* (Niederhausen) or *Ortiseia triumphilina* (Collio) and *Ortiseia daberi* (Tregiovo). All these conifers were characterised by their stout, bulbous or also sometimes elongated female cones. The single seed scale was surrounded by a plethora of sterile dwarfish leaflets. Over the course of millions of years, the sterile leaflets merged with the scale and seed to form a unit like those found on the modern Araucarias. A single, nut-like, and relatively large seed without wings was attached to the middle of the seed scale. The seed was released upon maturity together with the seed scale. The male cones were slender and could reach lengths of up to 10 cm. They featured remarkably long microsporophylls that extended well beyond the cone, especially when young, and the hanging pollen sacs were attached on the upper side of the microsporophyll, as seen well in *Ortiseia zanettii* (from the Upper Permian of the Dolomites). This single-seed bearing *Ortiseia* closes one chapter in the understanding of modern *Araucaria*. The upright standing male and female cones and the arrangement and appearance of the twigs and leaves can be considered typical of all Araucariaceae. The evolution was partially completed by the time of the Permian in the form of *Ortiseia*, or in the Triassic by *Araucarites* and they are barely recognisable in the *Araucaria* of today.

The ancestors of the larches (*Larix*)

The evolution of the important conifer family *Larix* was in the past shrouded by questions. It can be now stated that they were already present from the Early–Middle Triassic. *Wachtlerolarix weissii*, in particular, has all the features of today's larches, such as small-sized seed cones, needles clustered on short shoots and small male strobili borne solitarily from the apex of short shoots. The origin of the larches' typical false whorls lies in a reduction and compression of the needles of a twig to a bundle. In contrast to the evolution of the genus *Pinus* (*Fèrovalentinia*) with its 2–3–5 regularly assembled needles, which occurred in the Early Permian, the larch family has a different development history also demonstrated by their irregularly bundled leaves. The larches have their origin in a reduction and compression from a shoot to a bundled short shoot. For this reason, the number of leaves in each tuft varies considerably. It seems that over time a reduction from normal shoots to short shoots must have occurred independently several times, as seen in the extant *Cedrus*, *Larix*, *Pseudolarix* or *Sciadopitys*. The reduction to this bundled short shoot never occurred in *Metasequoia glyptostroboides* or in *Taxodium distichum* although progenitors were also already present in the Permian.

The evolution of the berry-seeded conifers

Some modern Cupressoideae, such as *Torreya*, *Cephalotaxus* and *Calocedrus*, are normally characterised by thick, fleshy, berry-like fruits. For a long time no satisfying answer could be given about their development. Amazingly, these conifers evolved at the same time as the other conifers began to form and in the same way as the first Araucarias (*Ortiseia*): sterile micro-leaves began to coat the seed, forming a fleshy aril. There is no other way to explain the berry-like cone structure of the conifer *Ullmannia* in the Upper Permian. Early–Middle Triassic *Kandutschia kuehnii* has the same blueprint. If the berry held only one seed inside, which is often difficult to determine, then these can be considered as an ancestral line to the present-day *Torreya*, *Cephalotaxus* and *Taxus*.

The beginning of the Cupressaceae

Some living conifers hold three or more seeds on each scale. Today, they play only a minor role in the conifer kingdom. At the Carboniferous–Permian border, three- and more-seeded conifers were widespread, and they were categorised as Voltziales. Although this important group is often regarded as leading to all modern-day conifers, particularly in the Mesozoic, it is not so.

As first certain *Voltzia* conifer can be regarded *Seymourina niederhauseni*, originating in the Earliest Permian. Female cones were extraordinarily tall, sometimes 25 cm in length, while male cones reached a length of about 10 cm. A fair number of dwarfish, sterile tapered leaves surrounded the scales. The seed scales were divided into three or more fertile rounded lobes and additionally they were equipped sometimes on the outside with a projecting sterile bract. Ovules/seeds were collocated and hung inverted from the upper side of each lobe. From the Early Permian until the Late Permian similar Voltziales conifers, mostly the three-lobed varieties, are found. In the Upper Permian Zechstein basin, the type-conifer *Pseudovoltzia liebeana* is encountered. Most *Voltzia* cones disintegrate at maturity on the tree. In the Triassic, a Voltziales conifer explosion occurred in Europe, with many arborescent to shrubby subgenera and species that usually held three lobes and were three-seeded (many *Voltzia* species) but could be as much as five-lobed and five-seeded (*Aethophyllum*, *Swedenborgia*).

The vegetative branches were not uniform. Some held slender, geometrically regular branchlets with falcate needles, others were characterised by their rope-like protruding twigs, irregularly and sparsely branched and armoured by leathery triangular leaves. Elongated, slender needles about 20 cm long pertain to *Aethophyllum stipulare* but some were also thorny (*Agordia*). In the Alpine Voltziales, a consistent line can be followed from the Early–Middle Triassic (Anisian) *Voltzia unescoensis*, *Voltzia agordica* and *Voltzia rietscheli*, till Middle Triassic *Voltzia dolomitica* or Late Triassic (Carnian) *Voltzia carinthica*.

It may be that these widespread and influential Voltziales disappeared completely at the Triassic–Jurassic border, or that they survived in some extant form. Some genera in the fairly inhomogeneous family of the Cupressaceae can otherwise be accepted as possible *Voltzia* descendants. The usually three- or more-seeded *Cryptomeria*, *Cunninghamia* or *Sequoiadendron*, but also the *Juniper* tree, can be regarded as the most likely potential relatives of the Voltziales.

The large and globally ranging group of the Cupressaceae (or cypress) family unfortunately represents an arbitrarily put together system of conifers, such as Cunninghamioideae, Taiwanioideae, Athrotaxidoideae, Sequoioideae, Taxodioideae, Callitroideae and the super-group of Cupressoideae with the genera *Juniper* and *Cupressus*.

Many of the forerunners of widespread conifer families seem to be now already occupied. This is true of the Araucariaceae (occupied with *Ortiseia* as the most likely potential ancestor), the Abietaceae (*Majonica*) and Piceoideae (*Estrellencia*), the Pinoideae *Pinus* (with Early Permian *Fèrovalentinia*), the Cephalotaxaceae and *Taxus* (*Ullmannia*, *Kandutschia*), and the Laricoideae (*Wachtlerolarix*). Other genera from the Cupressaceae remain, such as *Taiwania* or *Glyptostrobus*. Early–Middle Triassic *Alpia anisica* or the Ladinian *Alpia ladinica*, as well as the Late Triassic *Pusteria maribelae*, with its needle- or awl-like foliage and small cones, have some similarities with them and can be seen as descendants.

The origin of angiosperms

Researches initiated by Michael Wachtler will attempt to explain the strange angiosperm-genesis with new theories based on surprising new findings. His study deals with the beginning and propagation of all angiosperms in the Early Permian period from the deciduous trees, over herbaceous flowers and grasses, and will give interpretations on why they could evolve in isolation and why probably the worldwide climate change due to an immense catastrophe in the Permo-Triassic boundary caused a quasi-extinction of the first angiosperms and retarded their spreading all over the world for a long time.

The evolution of flowering plants represents till now one of the central questions of natural science. The angiosperm fossil record confirmed in the 19th century the rich radiation of flowering plants between the Early and Middle-Late Cretaceous, but not before. Our present knowledge about angiosperms is based on the dogma that first appeared the family of Magnoliaceae than any other flowering plant. We do not usually take into consideration that the genesis of angiosperms could happen in a different way of evolution, maybe a more unexpected step.

Just Darwin was extremely distressed by the abrupt origin and fast spreading of the flowering plants in the Cretaceous in complete contrast to his theory about the slow evolution of plants and animals through millions of years. Therefore, he speculated a slow and long evolution on an extinct or destroyed landscape or a lost continent. All these ended then in the famous letter about the "*abominable mystery*" which Darwin wrote to Joseph Hooker on 22 July 1879.

If we are able to find flora-elements maybe on a "dark continent" prior to the Cretaceous with many of these properties, we come nearer to the answer of the "abominable mystery."

Some of the theories about isolated landmasses were evolved by the Austrian geologist Eduard Suess. In his "*Antlitz der Erde*" (The Face of the Earth) in 1885, he hypothesized that in the Paleozoic era, there was one big landmass on the southern hemisphere that he called the Gondwana – from an Indian tribe, the Gonds – comprising Africa, South America, India and Australia. In the north, he located two big paleo-continents: North-America connected to Europe, which he called the Atlantis, and the other, he named Angara after a Siberian river, comprising parts of today's Russia with the Urals and Siberia. He baptized the ocean separating this landmass as the Tethys. It was just a modern opinion based on connected land-bridges, several years before Alfred Wegener elaborated his continental drift theory in 1912.

The Angaran landmass, from the Carboniferous till the Early Cretaceous period, was located north of Europa and North America and therefore, different climatic conditions had prevailed there. Isolated from the other landmasses, this community remained unique for millions of years. Strangely the origin of angiosperms based on the fossil record can be dated back in the Angara-landmass to the Carboniferous-Permian era. In the early Permian sediments from Chekarda and Matvévo in the Ural-region, many different "flowers" could be found. Till now little attention was given to the inner details of these inflorescences. Considerable differences exist between the plethora of fructifications. Some had five petals as many of today's flowers like the Rosaceae (cherries, apricots, and plums). Others had six petals, or even more more.

Several "flowers" from Early Permian sediments in the Urals evidences well a diverse stamen with anthers and a gynoecium, also with the impressions of some ovules. It is surprising, and speaks for the extraordinary preservation in these Matvévo layers, that the slender filament as well the anther with the pollen sacs are visible. In the Early Permian period, several angiosperm lineages such as deciduous trees comprising maples, oaks, ash trees or stone-fruits as well as herbaceous flowers and grasses, dicots and monocots, were present. Once "invented" the bisexual flower, composed of stamen and carpel with surrounding petals, sepals or tepals, all further lineages can be deduced. The Magnolia theorem as being the most primitive plant and an evolution of all angiosperms from them cannot be reconstructed. Accompanied with the ascension of flowering plants, we have a coeval rising of all insect groups.

The spreading of diverse lineages of angiosperms in the Early Permian Angara-Land is therefore equally mysterious or not, as the coeval diffusion of gymnosperms in the Euro-American landmass with several subordinated tribes such as conifers, cycads or ginkgos. This coevolution in the Early Permian period simplifies the understanding of angiosperm development considerably, especially when it can be based on solid arguments and facts due to compound findings.

All these big evolution steps on the Carboniferous-Permian border are till now recorded only from old Angara-Land. If the hypothesis of the hermaphroditic flowers can be proved by Paleozoic findings the "Magnolia-theory," collapsed like a house of cards. Once the hermaphroditic flower was created, all further developments and segmentations could be deduced easily. Why could this not happen in the Carboniferous-Permian border? The way to the stamen, composed of a sterile filament and the pollen-generating anther, was as difficult and inventory as the pollen-bract-cone of gymnosperms. These are valid also for the ovary of angiosperms, in contrast to the manifold seed- and cone-peculiarities of the gymnosperms.

It is more difficult to elaborate a hypothesis about the movement of all gymnosperms and angiosperms in the following million years. Why we have the astonishing worldwide propagation of angiosperms beginning from the Cretaceous and not before? What happened to the angiosperm ancestors of Angara from the Early Permian till the Cretaceous?

If we have mostly all flowering plant tribes in the Early Permian Angara-Land, why could they not radiate all over the landmass when Pangaea assembled to one global continent? 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. Today, basaltic lava covers about 2 million square kilometres there, but the original extension is estimated at about 7 million square kilometres approximately in the region from Siberia over the former Angara-continent.

If this global catastrophe happened really, and this is based on facts and documented by analyses from the extinction of many animal tribes. Angara was the most involved landmass and therefore, it is plausible that this landscape suffered more than all others. It can be suggested that only with difficulties the angiosperms survived on some isolated refuges and that too on a restricted and marginal level. Probably for a long time, till the Cretaceous, they were not able to expand on a large scale. In this case, the most involved victims of these mother of all catastrophes were the angiosperms.

First paleobotanical researches in the Dolomites

Michael Wachtler recovers primitive fossilised cycads and conifers. These residuals document how this interesting genus has come into being. The cycadees or fern palms belong to one of the oldest plant families. He describes them together with the Dutch professor Han van Konijnenburg – van Cittert in 2000.

The discovery of the Fossilagerstätte Kühwiesenkopf and Piz da Peres

In 1999 Michael Wachtler discovered the new fossil site Kühwiesenkopf and Piz da Peres. On the base of the Kühwiesenkopf Michael Wachtler recovered a part of a reptile described later by Silvio Renesto and Renato Posenato as *Megachirella wachtleri*. It is now regarded as ancestor of all squamates including snakes and lizards. Soon it was classified as "Garden Eden of the primitive times". After the big Permian-Triassic- Catastrophe during which about 90% of all creatures died out, a lot of new plants, fishes and land animals developed in this place.

Discovery of the quickly worldwide known "fossil repository Tregiovo" in the Trentino Dolomites

In the mountains of Trentino, Michael Wachtler in cooperation with the forest-man Fèro Valentini, discovers in 2012 the new fossil site Tregiovo with enigmatic fossils. There 275 million years ago - in a savannas-like biocoenosis were deposited innumerable unknown plants. Inserted in the fossilised plant remains we have frequent animal footprints from lacertoid reptiles (Dromopus), which found sufficient surviving resources in this biocenosis.

The great find of gold

In 2008 on Monte Rosa Michael Wachtler, with the twins Mario and Lino Pallaoro, Federico Morelli, Maurizio Petti and Georg Kandutsch make the biggest gold discovery in the Alps in modern days. They found 30 kg of native gold. They started off from a forgotten map by a Swiss scientist.

Genera and species honouring Michael Wachtler

Megachirella wachtleri nov. gen. n. sp. RENESTO & POSENATO, 2002

Wachtleria nobilis nov. gen. n. sp. KANDUTSCH, 2011

Wachtleropteris valentinii gen. nov. n. sp. PERNER, 2013

Wachtlerina bracteata nov. gen. n. sp. PERNER, 2013

Calamites wachtleri n. sp. PERNER, 2013

Wachtlerophyllum schaalii gen. nov. sp. n. (PERNER, 2015)

Bjuvia wachtleri n. sp. (PERNER, 2015)

Feroyalentia wachtleri sp. nov. (PERNER, 2015)

Wachtlerolarix weissii gen. nov. n. sp. PERNER, 2016

Wachtlerosaurus ladinicus gen. nov. n. sp. PERNER, 2018

Genera and species first discovered or described by Michael Wachtler

Michael Wachtler first described as individual author or together with other researchers from Spain, Italy, USA, Germany, Holland, Austria **42 new genera and 125 new species** (till December 2018). Five genera, and four species take as a tribute for his merits in scienc his name.

Invertebrates

Megachirella wachtleri nov. gen. n. sp. RENESTO & POSENATO, 2002

Wachtlerosaurus ladinicus gen. nov. n. sp. PERNER, 2018

Insects

Angaroptera nicolaswachtleri nov. gen. n. sp. WACHTLER, 2017

Ichnogenera

Sphingopus ladinicus n. sp. AVANZINI & WACHTLER, 2012

Polichaete

Burocratina kraxentrougeri gen. n. n. sp. WACHTLER & GHIDONI, 2018

Lecanorales

Ragazzonia schirollii gen. nov. sp. nov. (WACHTLER, 2015)

Lycophyta

Eocyclotes alexawachtleri nov. gen. n. sp. WACHTLER, 2019

Sigillcampeia nana nov. gen. n. sp. WACHTLER, 2016

Sigillcampeia blau n. sp. WACHTLER, 2016

Selaginellites perneri n. sp. WACHTLER, 2016

Selaginellites zollwegii n. sp. PERNER & WACHTLER, 2013

Lycopodia dezanchei nov. gen. n. sp. WACHTLER, KUSTATSCHER, VAN KONIJNENBURG, 2011

Lycopodostrobos gaeae nov. gen. n. sp. WACHTLER, 2011

Isoetites brandneri n. sp. WACHTLER, KUSTATSCHER, VAN KONIJNENBURG, 2011

Lepacyclotes bechstaedtii n. sp. WACHTLER, KUSTATSCHER, VAN KONIJNENBURG, 2011

Selaginellites leonardii n. sp. WACHTLER, KUSTATSCHER, VAN KONIJNENBURG, 2011

Selaginellites venieri n. sp. WACHTLER, 2011

Sphenophyta

Calamites kinneyana n. sp. WACHTLER, 2017
Equisetites siberi sp. nov. WACHTLER, 2015
Neocalamites behnkeae sp. nov. WACHTLER, 2015
Equisetites geraschi sp. nov. PERNER & WACHTLER 2015
Calamites wachtleri n. sp. PERNER, 2013
Equisetostachys richthofeni nov. sp. WACHTLER, 2011
Neocalamites tregiovensis n. sp. WACHTLER, 2011

Coniferophyta

Araucarites weissii n. sp. WACHTLER, 2019
Ulbia vicentina n. sp. WACHTLER, 2017
Agordia ungeri gen. nov. sp. nov. WACHTLER, 2016
Voltzia rietscheli n. sp. WACHTLER, 2016
Voltzia carinthica n. sp. WACHTLER, 2016
Pusteria maribelae gen. nov. sp. nov. WACHTLER, 2016
Kandutschia kuehnii gen. nov. sp. n. WACHTLER, 2016
Wachtlerolarix weissii nov. gen. sp. n. PERNER, 2016
Wachtlerolarix anisica sp. n. PERNER, 2016
Farjonia campeiae nov. gen. n. sp. WACHTLER, 2016
Farjonia preseglii n. sp. WACHTLER, 2016
Swedenborgia nissleri WACHTLER, 2016
Estellensia saezii nov. gen. n. sp. JUÁREZ & WACHTLER, 2015
Ortiseia collii n. sp. JUÁREZ & WACHTLER, 2015
Majonica hansonii n. sp. (WACHTLER & PERNER, 2015
Ortiseia uhli n. sp. WACHTLER & PERNER, 2015
Ortiseia zanettii n. sp. WACHTLER, 2015
Ferovalentinia wachtleri sp. nov. PERNER, 2015
Ferovalentinia angelellii sp. nov. WACHTLER, 2015
Ferovalentinia cassinisi sp. nov. WACHTLER, 2015
Ortiseia triumphilina nov. comb. WACHTLER, 2015
Majonica suessi sp. nov. WACHTLER, 2015
Perneria thomsonii nov. gen. n. sp. WACHTLER, 2013
Seymourina niederhauseni nov. gen. n. sp. PERNER & WACHTLER, 2013
Wachtlerina bracteata nov. gen. n. sp. PERNER, 2013
Voltzia unescoensis n. sp. WACHTLER, 2011
Willsiostrobos unescoensis nov. sp. WACHTLER, 2011
Tirolstrobos unescoensis nov. gen. n. sp. WACHTLER, 2011
Voltzia agordica comb. nov. WACHTLER, 2011
Willsiostrobos kostneri n. sp. WACHTLER, 2011
Tirolstrobos agordicus n. sp. WACHTLER, 2011
Voltzia dolomitica n. sp. WACHTLER & VAN KONIJNENBURG, 2000
Willsiostrobos dolomiticus n. sp. WACHTLER, 2011
Tirolstrobos dolomiticus n. sp. WACHTLER, 2011
Alpia anisica gen. nov. sp. nov. WACHTLER, 2011
Alpianthus anisicus gen. et sp. nov. WACHTLER, 2011
Dolomitostrobos anisicus gen. et sp. nov.
Alpia ladinica n. sp. WACHTLER & VAN KONIJNENBURG, 2000
Voltzia pragsensis n. sp. WACHTLER & VAN KONIJNENBURG, 2000
Dolomitostrobos ladinicus n. sp. WACHTLER, 2011

Schizolepis ungeri n. sp. WACHTLER, 2011
Alpianthus ungeri sp. nov. WACHTLER, 2011
Dolomitostrobis bellunensis sp. nov. WACHTLER, 2011
Albertia alpina n. sp. WACHTLER, 2011
Pusterostrobis haidingeri gen. et sp. nov. WACHTLER, 2011
Darneya schaurothi n. sp. WACHTLER, 2011
Cassinisia ambrosii n. sp. WACHTLER, 2012
Trentia treneri gen. et sp. WACHTLER, 2012
Albertia scopolii n. sp. WACHTLER, 2012
Seymourina viallii n. sp. WACHTLER, 2015
Ortiseia daberii n. sp. WACHTLER, 2013
Dolomitia nonensi, n. sp. WACHTLER, 2013

Pteridosperma

Sagenopteris nadalii n. sp. JUÁREZ & WACHTLER, 2015)
Pernerina pasubi gen. nov. sp. nov. WACHTLER, 2015
Wachtlerophyllum schaalii gen. nov. sp. nov. PERNER, 2015)
Hurumia lingulata nov. gen. PERNER & WACHTLER, 2013
Peltaspermum dammannii n. sp. PERNER & WACHTLER, 2013
Rachiphyllum hauptmannii n. sp. PERNER & WACHTLER, 2013
Peltaspermum meyeri n. sp. WACHTLER, 2013
Peltaspermum bornemannii n. sp. KUSTATSCHER, WACHTLER, VAN KONIJNENBURG, 2007
Pteruchus deznigii n. sp. WACHTLER, 2011
Sagenopteris keilmannii n. sp. WACHTLER, 2011
Caytonia fedelii n. sp. WACHTLER, 2011
Lugardonia paradoxa nov. gen. n. sp. KUSTATSCHER, VAN KONIJNENBURG, 2009

Pteridophyta

Daenaepsis alpina sp. n. WACHTLER, 2016
Sphenopteris battistii sp. n. WACHTLER, 2015
Scolecopteris lothii n. sp. PERNER & WACHTLER, 2013
Todites muelleri n. sp. PERNER & WACHTLER, 2013
Scolopendrites grauvogelii n. sp. KUSTATSCHER, WACHTLER, VAN KONIJNENBURG, 2006
Scolopendrites scolopendrioides n. sp. KUSTATSCHER, WACHTLER, VAN KONIJNENBURG, 2006
Gordonopteris lorigae nov. gen. n. sp. KUSTATSCHER, WACHTLER, VAN KONIJNENBURG, 2006
Ladinopteris kandutschii nov. gen. n. sp. WACHTLER, 2011

Ginkgophyta

Baiera perneri n. sp. WACHTLER, 2013
Baiera pohli n. sp. WACHTLER, 2013

Cycadophyta

Olangocarpus dolasillae Gen. nov. sp. n. WACHTLER 2016
Nilssonia faustinii WACHTLER, 2016
Androstrobis donai n. sp. WACHTLER, 2016
Androstrobis elongatus n. sp. WACHTLER, 2016
Nilssonia brandtii sp. nov. WACHTLER, 2015
Bjuvia wachtlerei sp. nov. PERNER, 2015
Wachtleropteris valentinii n. sp. WACHTLER, 2012, PERNER, 2013
Nilssonia perneri sp. nov. WACHTLER, 2013

Pizperesia tannae gen. nov. n. sp. WACHTLER, 2010
Pizperesia raetiae gen. nov. n. sp. WACHTLER, 2010
Taeniopteris simplex nov. gen. n. sp. WACHTLER, 2010
Nilssonia primitiva n. sp. WACHTLER, 2010
Dioonitocarpidium cycadea n. sp. WACHTLER, 2010
Bjuvia olangensis n. sp. WACHTLER, 2010
Dioonitocarpidium lorezzi n. sp. WACHTLER, 2010
Thetydostrobus marebbeii gen. nov. sp. nov. WACHTLER, 2010
Pseudecten braiesensis n. sp. WACHTLER, 2010
Bjuvia dolomitica n. sp. WACHTLER & VAN KONIJNENBURG, 2000
Apoldia wengensis n. sp. WACHTLER & VAN KONIJNENBURG, 2000
Nilssonia perneri n. sp. WACHTLER, 2012
Bjuvia trentina n. sp. WACHTLER, 2012

Proangiospermales

Matvéeva perneri gen. nov. sp. n. WACHTLER 2017
Naugolnykhia matvévoi gen. nov. sp. nov. WACHTLER 2017
Lyswaia nicolaswachtleri gen. nov. sp. nov. WACHTLER 2017
Krasnaia dammannii gen. nov. sp. nov. WACHTLER 2017
Taezhnoeia geraschi gen. nov. sp. nov. WACHTLER 2017

Michael Wachtler Scientific contributions

Year 2018

- 98) **Perner T., 2018:** A new interesting archosaur from the Ladinian (Middle Triassic) of the Dolomites (Northern Italy)
97) **Wachtler M., 2018:** A new reptile from the Middle Triassic (Anisian) of Piz da Peres (Dolomites - Northern Italy)
96) **Wachtler M., 2018:** A fossil polychaete worm from the Illyrian of the Dolomites (Northern Italy)
95) **Wachtler M., 2018:** Early-Middle Triassic vertebrate tracksites from the Dolomites (Northern Italy)
94) **Wachtler M., 2018:** *Megachirella wachtleri* and the origin of squamates - The history of discovery
93) **Wachtler M., 2018:** The marine reptile *Neusticosaurus* from the Eastern Alps

Year 2017

- 92) **Wachtler M., Valentini F., 2017:** La Flora Fossile del Permiano Inferiore di Tregiovo. Un interessante periodo nell'evoluzione delle piante, in Atti I. Conferenza, Revò 22-23- Agosto 2015, Coord. Francesco Angelelli
91) **Wachtler M., 2017:** Early Permian Origin and Evolution of Angiosperms - The Flowering of Angara-Land
90) **Wachtler M., 2017:** The insect-variety of Angaran Early Permian
89) **Wachtler M., 2017:** The evolution of horsetails from Permian Angara-Land till Euramerica
88) **Wachtler M., 2017:** Early Permian ferns from the Fore-Urals.....
87) **Wachtler M., 2017:** Early Permian conifers from Angara-Land and their role in the gymnosperm-evolution
86) **Wachtler M., 2017:** The origin of the *Taxodium*-conifers in the Permian

Year 2016

- 85) **Wachtler M., (2016):** A strange rising of the lycophyta in the European 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
- 84) **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
- 83) **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
- 82) **Wachtler M., (2016):** The development of horsetails in the Mesozoic. 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
- 81) **Wachtler M., (2016):** Early-Middle Triassic (Anisian) ferns from the Dolomites (Northern Italy). 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
- 80) **Wachtler M., (2016):** Middle Triassic (Ladinian) Ferns in an European context. 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
- 79) **Wachtler M., (2016):** Triassic Seed ferns from the Dolomites (Northern Italy). 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
- 78) **Wachtler M., (2016):** A short history about the evolution of gymnosperms. In: Wachtler M., Perner T., Fossil Triassic Plants from Europe and their Evolution, Volume 1: Conifers and Cycads, Dolomythos Museum, Innichen, South Tyrol, Italy, p. 3-16
- 77) **Michael Wachtler:** Early Triassic progenitors of the conifers *Abies* and *Picea*. In: Wachtler M., Perner T., Fossil Triassic Plants from Europe and their Evolution, Volume 1: Conifers and Cycads, Dolomythos Museum, Innichen, South Tyrol, Italy, p. 17-29
- 76) **Thomas Perner (2016):** : Origin of the larches - The genus *Larix* in the Triassic. In: Wachtler M., Perner T., Fossil Triassic Plants from Europe and their Evolution, Volume 1: Conifers and Cycads, Dolomythos Museum, Innichen, South Tyrol, Italy, p. 30-39
- 75) **Wachtler M., (2016):** Where is the origin of the berry-seed cone conifers? In: Wachtler M., Perner T., Fossil Triassic Plants from Europe and their Evolution, Volume 1: Conifers and Cycads, Dolomythos Museum, Innichen, South Tyrol, Italy, p. 40-45
- 74) **Wachtler M., (2016):** The conifer *Albertia* in the Alpine Trias. In: Wachtler M., Perner T., Fossil Triassic Plants from Europe and their Evolution, Volume 1: Conifers and Cycads, Dolomythos Museum, Innichen, South Tyrol, Italy, p. 46-50
- 73) **Wachtler M., (2016):** What is related with the Cupressaceae? Conifers of doubtful evolutionary tendencies from the Early-Middle Triassic. In: Wachtler M., Perner T., Fossil Triassic Plants from

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65) **Wachtler, M., (2016):** Die mitteltriasische Flora von Ilsfeld (Ladin, Erfurt-Formation) S. 3-13; in Wachtler M., 2016. The Middle Triassic Flora of Ilsfeld (Germany) Ladinian, Erfurt Formation - Die mitteltriasische Flora von Ilsfeld (Deutschland) Ladin, Erfurt-Formation, Published by Dolomythos Museum, Innichen, South Tyrol, Italy.

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