

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

by MICHAEL WACHTLER



DoloMythos

Published by the Dolomythos Museum, Innichen, South Tyrol, Italy January 2012

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

Editorial staff: Edith Campei, Michael Wachtler

Dolomythos is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be sent to: Museum Dolomythos Rainerstraße 11 39038 Innichen Italy mail: info@dolomythos.com

Print: Technolab Communication srl, TLAB Editrice Viale Pecori Giraldi, 20/B 36061 Bassano del Grappa (VI) - IT www.technolab.it Wachtler M.: The Genesis of plants Preliminary researches about the Early-Middle Triassic Fossil Floras from the Dolomites - A Compendium; ISBN 978-88-904127

Please cite this articles as:

Wachtler, M., (12/2011): Lycophyta from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), in "The Genesis of plants Preliminary researches about the Early-Middle Triassic Fossil Floras from the Dolomites - A Compendium" Dolomythos, Innichen. p. 165 - 211

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

by

Michael Wachtler P. P. Rainerstrasse 11, 39038 Innichen, Italy, e-mail michael@wachtler.com

Abstract

Although the most dominant group of plants in the Carboniferous, Lycophyta currently inhabit the shadows of more successful plants. Therefore, discoveries of new missing links not only throw light on the evolution of this important family, but also help us understand climatic and paleoecological cataclysms in the past. Four different genera containing five new species from the Early-Middle (Anisian) Triassic age in the Eastern Alps are described here. They were well preserved and enabled the determination of their preferred living habitat and symbiosis to other plants and animals due to their abundance and detailed stratigraphical classification. Surprisingly, the most abundant form was the sub-arborescent club moss Lycopia dezanchei gen. et sp. nov., exhibiting dichotomous branching and creeping root horizons. They could act as an intermediate form between Carboniferous Lepidodendrales and extant Lycopodiales. The fertile morphogenus was the homosporous Lycopodostrobus gaiae gen. et sp. nov. Extant Sellaginella-like forms were represented by Selaginellites leonardii sp. nov., with its heterosporous strobili and Selaginellites venierii sp. nov., with characteristic anisophyllous shoots. Another group of extant Lycophyta, the Isoetales, were represented by Isoetites brandneri sp. nov., resembling mostly extant Isoëtes and Lepacyclotes bechstaedtii sp. nov., with its bulbous corpus. Never recorded in these Anisian strata was the most enigmatic Early Triassic lycophyte, Pleuromeia sternbergii. Surprisingly, in the near but slightly older Werfen strata of the Carinthia, it still constitutes the dominant plant assemblage. This work compares the living conditions in the Early-Middle Triassic age and develop information and solutions about the rapid extinction of the historic and often discussed Pleuromeiales.

Online: December 2011. Key words: fossil lycophyta, Dolomites, Italy, Early-Middle Triassic, Anisian.

Remarks

This study summarises fifteen years of my lonely and dangerous work in the mountains of the Eastern Alps in which I made a lot of interesting discoveries. In long-lasting studies, cataloguing and descriptions, I tried to shed more light on a lost world. I thought that all this could be useful for humanity to understand more about our past. Unfortunately, one day, the authorities confiscated and removed all my specimens from my house, damaging a large part of my research. My computers, photos and notations were also sequestered and taken away, the cataloguing labels changed to cover the traces of my findings and studies, and my name cancelled from my collection and anonymised. Many photos and annotations were based on my older archives and a large part of these studies lacked further cuticle analyses and pollen preparation. I apologise for this and hope to make a revised version for when my country learns to appreciate science.

Although agreeing with some parts of the content of "Lycophytes from the Middle Triassic (Anisian) locality Kühwiesenkopf (Monte Prà della Vacca) in the Dolomites (northern Italy)" (2010), this publication was, however, never fully authorised by Michael Wachtler and edited under unacceptable pressure, with several formerly-agreed conditions of a reciprocal contract not being maintained. Therefore, in my opinion, the right authorship for this work has to be read as MICHAEL WACHTLER, EVELYN KUS-



Fig. 1: Fossil-plant bearing localities in the Eastern Southern Alps. Orange: carboniferous fossil points; yellow: Permian fossil points; red: Early Triassic - Olenekian fossil points; and green: Early-Middle Triassic (Anisian) fossil points.

TATSCHER, JOHANNA H. A. VAN KONIJNEN-BURG-VAN CITTERT or it has to be seen as an illegal publication or one without agreement from all authors. Michael Wachtler regrets the pronounced interdiction of research by the authorities, as well as police force, attempting to exercise his intellectual research rights.

Localities

The fossil plant-rich Piz da Peres area covers about 8 km of the Northern part of the Dolomite Mountains, starting from the western side of Piz da Peres over the Ladinian village of St. Vigil and reaching the Kühwiesenkopf over the hamlet of Prags. It traverses several mountains, which the native people refer to as a big mountain sundial. Starting from the Kühwiesenkopf, we have the "Zehner" (Tenner) "Elfer" (Elevener) and "Zwölfer" (Twelver), also called Hochalpenkopf, the "Einser" (Oner), also called Maurerkopf, and the "Zweier"(Twoer). Other mountains with fossil plant lenses are the Flatschkofel and the Drei-Fingerspitze. The main fossil plant lenses lie in the sometimes-exposed open rock slopes that are occasionally interrupted by shrubs and woods in which the layers cannot be traced. Other places important for the comprehension of Early Triassic lycophyte evolution lie in the neighbouring Carinthian Mountains, where the Induan/ Olenekian Werfen layers hold a rich Pleuromeia-dominated flora. Usually, the recovered specimens are well preserved and give a deep insight into the ecosystems after the Permian-Triassic boundary.

Paleobiology and paleoecology

During the Early Triassic age, the Eastern-Southern Alps were located near a beach close to a shallow water basin. The high sedimentation rate suggests frequent storm events (hurricanes). After intense volcanic activities in the Lower Permian, their first, not yet, marine deposited cycles contributed to the Gröden-Formation during the Upper Permian. During the following Early Triassic age, the now oceanic-influenced sediments contributed to the Werfen-Formation. They consist of a strongly varying sequence of mixed terrigenous siliciclastic and carbonatic lithofacies (BRANDNER ET AL., 2009). Since the 19th century, the Werfen-Formation has been divided into two sections: one beginning from the Permian-Triassic boundary subdivided into Tesero-, Mazzin-, Andraz-, Seis-Member and Gastropodenoolith, which are characterised by an abundance of the scallop-like bivalve mollusc Claraia especially found in the Seis-Member, and the other composed of Campill-, Val Badia-, Cencenighe- and San Lucano-Member, showing an increase in terrigenous input. Hemipelagic terrigenous and subordinate carbonate sediments were deposited continuously, while storm events also sometimes delivered a lot of plant debris. These basin sediments, with a conspicuous clastic input, continue until the Anisian Dont Formation (=Pragser Schichten sensu PIA, 1937). The fine silty marine Werfen layers reach 500 metres in thickness in the Northern Alps, and 200 metres in the Southern Alps (BRANDNER ET AL., 2009).



Fig. 2: The Piz da Peres fossil area. It covers about 8 km from Piz da Peres to Kühwiesenkopf, around a mythical sundial of the native people. Zehner = Tenner, Elfer = Elevener, Zwölfer = Twelver, Einser = Oner, Zweier = Twoer. The main plant fossil lenses lie on open rock.

The Campill-Val Badia Member in the Eastern Southern Alps could be correlated with the Middle Buntsandstein, or more detailed Volpriehausen-Hardegsen-Formation of Germany (about 249.7 to 245.9 \pm 0.7 Mya old) stretching from Induan to Olenekian.

While the South Tyrolean Werfen-Formation has not revealed to date any determinable plant species, the nearby Gailtaler Alps and other mountain chains in Carinthia display well fossilised floras (Ulrichberg-Klagenfurt, Wunderstätten-St. Paul, Nötsch-Villach, Golsernock-Stockenboi and Laas-Kötschach-Mauthen). They are characterised by а dominance of the lycophyte Pleuromeia sternbergii, accompanied by the sphenophyte Equisetites and some isolated Voltzia remains (THIEDIG & KABON, 2011) and can therefore be defined as a vegetation-rich, but species-poor flora.

The locality Bleiriese-Golsernock, discovered in 2011 by Georg Kandutsch, Helmut Prasnik and Michael Wachtler, exhibits abundant and well-preserved Pleuromeia sternbergii material, accompanied by Equisetites mougeotii. It is remarkable that other plant groups like ferns, seed ferns, conifers or cycads are till now missing. The sub-arborescent lycophyte *Pleuromeia*, dominant worldwide during the Early Triassic period, seems to have been effectively extinct during the Olenekian-Anisian boundary (RETALLACK G., 1975). Ecological support is given by the slightly younger Anisian Formations of the Dolomites where rich lycophyte assemblages (Lycopia dezanchei, Isoetites brandneri, Lepacyclotes bechstaedtii, Selaginellites leonardii and *Selaginellites venierii*) are common. In spite of intensive research, a total absence of *Pleuromeia* has to be accepted. The giant horsetail *Equisetites mougeotii* has been recovered in the Werfen-Formation (Campill-Val Badia Member), as well as in the following successions from Anisian to Ladinian and Carnian, showing only minimal changes in its aspect and reproduction cycles. Most Carinthian Triassic localities are situated inside crowded vegetation below the forest line (in the Dolomites, mainly all fossil plant-bearing horizons lie over

the forest limit); therefore, only newly built forest trails enable the exploration of underlying rocks. Sufficient Early Triassic plant layers have been opened over the years and the excavated fossil slabs



Exploring the newly discovered Olenekian fossilisedplant point Bleiriese-Golsernock in the Gailtaler Alps.



Open lying isolated tree-trunks, root-horizons and ripple marks from Kühwiesenkopf - main plant layer.

give a good insight into ancient habitat systems. All the findings mainly show predominance of the lycophyte *Pleuromeia sternbergii*, identical to the Central German Buntsandstein one. It could be assumed that vast areas of the Northern hemisphere in the Early Triassic were colonised by only one plant species. The *Pleuromeia* monocultures are effectively strange when compared to the almost exploding diversity of the Anisian landscapes that followed a little later. The theory of the commonly thought vegetationpoor and arid Permian landscapes has to be revised. New discoveries in the Dolomites (Bletterbach, Tregiovo) suggest an extraordinary abundance of humidity-loving horsetails (Equisetites), ferns and seed ferns (*Callipteris*),



Kühwiesenkopf - Main plant lenses

conifers, cycadophyta (*Taeniopteris*) and gingkophyta (*Sphenobaiera*). Therefore, comparisons with today's Okavango-delta with its seasonal floodings, salt islands and associated salt-resistant plants, and semiarid zones facilitate the understanding of this ancient landscape.

The Kühwiesenkopf lycophyte paradise

The Anisian Dont Formation, consisting of a carbonate-terrigenous sequence more than 200 metres thick, reaches the most distinguished development in the Braies Dolomites. The main plant-bearing horizon on Kühwiesenkopf lays circa 75 metres above a massive carbonate platform attributed to the Bythinian-Anisian Gracilis Formation (DE ZANCHE ET AL. 1992; BROGLIO LORIGA ET AL. 2002; VAN KONIJNENBURG-VAN CITTERT ET AL. 2006).

One club moss-rich layer on Kühwiesenkopf has enabled, like in a few other places worldwide, an inimitable insight into a contiguous beach more than 240 million years old. This main lens can be prosecuted for a total of 214 metres, of which the middle 52 metres are covered by a dense forest where no rocks protrude. On the right side, there are plant layers 42.5 metres long and onemetre thick. There is also the presence of the only terrestrial reptile, *Megachirella wachtleri* (RENESTO, 2003). The lenses hold a variegated flora containing equal proportion of lycophyta, conifers, cycadophyta, ferns and seed ferns.

After the overgrowing patch of forest, the layers crop out for 119.5 metres, interrupted once by a geological fault that elevates the lenses 25 metres high. These beddings are characterised by a rich fish assemblage belonging to five different families (*Dipteronotus, Saurichthys, Bobasatrania, Gyrolepis* and coelacanths), of which the first three genera have never or only rarely been recorded in the Early Triassic (TINTORI A. ET AL. 2001). Most of the fish skeletons have been found in a narrow, only three-metre long section in the middle. The preservation of invertebrates in this area can be related to the very rapid burial events made by heavy storms and flood deposits originating from terrestrial domains.

All the fishes seem to be well adapted to live near the coastline. Dipteronotus sp., known only from a dozen specimens in Europe, is one of the best indicators of strong fresh water influx in the Middle Triassic. Saurichthys sp., widespread in the Thetydalean ocean in the Triassic period, was an able predator. It is generally encountered in sediments of marine environments, as well as sporadically in rocks of brackish or continental origin. Bobasatrania sp., found nearly worldwide from Madagascar to Cina, Greenland, Svalbard and Canada in Early Triassic beds, was another predator, but in comparison to Saurichtys sp., it was a steady swimmer, scrunching with great accuracy its preys with a battery of minute teeth. Gyrolepis sp. has been found in sediments of marine coastal environments, especially in the Ladinian Fossillagerstätte of Monte San Giorgio. The skeletons of the coelacanths recovered allow, with caution, the insertion of the species Heptanema (known from the Western Alps) in the Middle Triassic. The ichthyofauna attests a marine depositional environment with a very strong influx from nearby land, testified by a huge amount of plant remains.

In the whole section, apart from the ubiquitous ferns, seed ferns, conifers abundant cycadophyta species, and there is the most complete club moss association. The most abundant is the subarborescent Lycopia dezanchei, followed



by Isoetites brandneri, Lepacyclotes

bechstaedtii and Selaginellites leonardii.

Apart from Isoetites brandneri and

Lepacyclotes bechstaedtii, which have

never been recorded in the other layers

of Kühwiesenkopf, Hochalpenkopf or Piz

Kühwiesenkopf: Lower lens layer demonstrating the Megachirella finding point, the plant lenses (especially lycophyta) and the fish-basin. Total length: 214 metres.

da Peres, Lycopia dezanchei is found everywhere and in large quantities, whereas Selaginellites leonardii is much more abundant in the Wachtler gorge in the west side of Piz da Peres, with another species, Selaginellites venierii, holding anisophyllous foliage.

All in all, we have to do it with an ancient marine depression probably near a highly saline coastline or also influenced by geothermal events such as hot springs or heated soils offering the best requirements for lycopods to predominate over other plant families. Whether several storm events burst the plants in this depression or overflooding at the coastline will be determined by some fossilised root horizon.

Just below this main Kühwiesenkopf horizon, a bank of nodular and bioclastic limestone contains a rich marine epifaunal assemblage, dominated by brachiopods (Punctospiriferella fragilis, Tetractinella trigonella, Mentzelia mentzelii, Spiriferina-paläotypus and Angustothyris angustaeformis) and bivalves (Mysidioptera cainalloi, Neomorphotis compta, Entolium discites, Newaagia noetlingi, Pleuromya cf. musculoides, P. brevis and Neoschizodus? sp. Others, such as Plagiostoma striatum, Pseudoplacunopsis fissistriata and Prospondylus comptus have been found only in the plant bearing deposit, or in fossiliferous horizons located in the upper part of the formation (Parallelodon esinensis, Pteria? sp., Entolium kellneri and Chlamys (Praechlamys) cf. schroeteri) (PO-SENATO, 2008).

After this fish- and club moss-rich section, this lens becomes abruptly increasingly thinner to the end in well-preserved ripplemarks that wedge into the mainly sterile and plant-free horizons. Although other layers in Kühwiesenkopf and Piz da Peres are rich in club mosses, they never reach the abundance of this lens. Furthermore, extant club moss communities are known from stress-conditioned biocenosis, like the Tepuis of Venezuela or some high-plateau in the Andes. Such marine-near and also different genera-rich lycophyte zones are unknown nowadays. The richness of all plant families in this Anisian stratum, from conifers to ferns and cycadophyta, does not allow extraordinary conclusions to be made about global cataclysms or totally different living conditions during that period.

Materials and methods

To date (2011), the Lycophyta fossil record is characterised by:

Pleuromeia sternbergii (about 200 species) only known from the Olenekian strata in Carinthia

Lycopia dezanchei (about 200 pieces) Lycopodostrobus gaiae (about 10 pieces) Isoetites brandneri (about 50 pieces) Lepacyclotes bechstaedtii (about 10 pieces) Selaginellites leonardii (about 20 pieces) Selaginellites venieri (2 pieces)

Repository

Most of the macrofossil plant collection is stored at the Natural History Museum Südtirol, Bozen. The remainder of the collection is in the Museum Dolomythos, Innichen, or in the collection of Georg Kandutsch, Arriach (Carinthia).

Specimens were photographed under natural light using Nikon D200, Lenses AF MICRO NIKKOR 60 mm 1:2.8 D and AF-S NIKKOR 17-35 mm 1:2.8 D for larger pieces. The digital images were processed using Adobe Photoshop CS version 12.1.

Explanation of the table on the next pages:

Like an expulsion from the Garden Eden, we have the biggest modifications in plant kingdom at the Carboniferous-Permian boundary. Surprisingly, mainly all plant families developed during this time.

In the Permian, we encounter an impoverished and decreasing number of plant families.

From the Early Triassic onwards, we have a general recovery and mutation of all plant associations.

From a cycadophyte-related group originates the protoangiosperms as the true cycads. In Early Triassic, we have the division of "feather-sporophyll"-bearing cycads like extant *Cycas* and strobili-holding cycads like *Bowenia*, *Ceratozamia*, *Dioon*, *Encephalartos*, *Stangeria* and *Zamia*.

The conifers split into the araucarian line (Voltziales) and pinaceae-cupressaceae line (Alpiales).

Seed ferns were dominated for a long time by *Peltas-permum-Scytophyllum-Thinnfeldia* and a *Sagenopteris* line. Both seemed to disappear at the Jurassic-Cretaceous boundary without leaving any extant descendants.

Equisetaceae diminished from the Triassic period to present.

Lycophyta remained all the time mainly unmodified in the Isoetaceae and Selaginellaceae, whereas Lycopia met the same fate as Equisetites. It was reduced to surviving as Lycopodiales. The Pleuromeiales became extinct in a very short time after the Early Triassic.





SYSTEMATIC PALAEONTOLOGY Division LYCOPHYTA Order PLEUROMEIALES Family PLEUROMEIACEAE

GENUS Pleuromeia CORDA in GERMAR 1852

The lycophyte *Pleuromeia* constitutes one of the best-described and most interpreted plants in paleobotany. It was found in the first decade of the nineteenth century in the German Buntsandstein and described by the Czech botanist Karl Joseph Corda in 1852. After that, a lot of similar species or subspecies were recovered around the world from France, Spain and Austria to Russia, China, Japan, Argentina and Australia.

Pleuromeia sternbergii (MÜNSTER 1842), CORDA in GERMAR 1852

1839 Sigillaria sternbergii MÜNSTER, P. 47, PL 3, FIG. 10 1852 Pleuromeia sternbergii (MÜNSTER) CORDA in GERMAR, p. 184

1904 Pleuromeia sternbergii (MÜNSTER) CORDA in PO-TONIE, n. 38

1904 Pleuromeia sternbergii (MÜNSTER) CORDA in MÄGDEFRAU, p. 119, pl. III-VII

2011 Pleuromeia sternbergii (MÜNSTER) CORDA in THIEDIG & KABON, p. 203 – 224

2011 Pleuromeia sternbergii (MÜNSTER) CORDA in KANDUTSCH & WACHTLER

Type localities

Carinthia: Bleiriese-Golsernock, Laaser Wald – Kötschach-Mauthen, Ulrichberg - Klagenfurt, St. Paul Mountains, Rottensteiner Kreuz, Wunderstätten, Dobratsch, Waidischbach

Type horizon and age

Lower Triassic, Induan-Olenekian, Werfen Formation

Repository

Georg Kandutsch Collection, Arriach - Carinthia, Museum Dolomythos - Innichen (South Tyrol)

Diagnosis

Sub-arborescent lycophyte with unbranched, erect trunk. Rhyzomorphic roots are typi-

cally four-lobed and the stem in the lower part is covered with traces of scars from fallen leaves. Foliage in the upper part is lanceolatic, displaying a prominent mid-vein and attached on their enlarged basis to the stem. Cones are well defined, sitting terminally and solitary on the axis. Sporophylls have a circular to oval lamina and a large globose sporangium covering nearly all the adaxial surface. They contain either microspores or megaspores.

Discussion

This description tried to work out only new stratigraphical and paleoecological phenomena from the not so well-known fossil deposits in the Eastern Alps and left behind detailed specifications indicating only some references (TAYLOR ET AL. 2009; GRAUVO-GEL-STAMM, 1993; GRAUVOGEL-STAMM & LUGARDON, 2001; RETALLACK, 1975).

The consistent *Pleuromeia* findings from Carinthia comes from the Induan-Olenekian Werfen-Formation (Campill-Val Badia-Member), corresponding to the German Mittlerer Buntsandstein (THIEDIG & KABON, 2011; KANDUTSCH & WACHTLER, 2011). In contrast to the continental German deposits, they belong to a marine environment with accompanying casts and impressions of seashells like *Neoschizodus* and *Bakevellia* sp.

The horizon newly discovered by Georg Kandutsch, Helmuth Prasnik and Michael Wachtler in 2011 on the forest trail of Bleiriese-Golsernock near the Upper Carinthian locality of Stockenboi revealed an especially rich and well-preserved sternbergii Pleuromeia vegetation, accompanied by the giant horsetail Equisetites mougeotii. It was interesting that other plant groups like ferns, seed ferns, cycads and conifers were absent. About 200 specimens were recovered from the locality Bleiriese-Golsernock and some from the Laaser Wald near Kötschach-Mauthen, including typical four-lobed rhizomes, stems bearing leaf scars, leaves and cones with mega- and microsporophylls. They confirmed that we have to do it with a mainly in pure stands growing plant.

The location near the ancient Tethys Ocean confirmed once more that the Pleuromeiales occupied a wide-ranging habitat, growing as a coastal halophyte as well as an inland



- 1) GOL 30. Pleuromeia sternbergii. Several stems from juvenile plants.
- 2) GOL 22. Pleuromeia sternbergii. Part of a lower stem fragment with cleavage impressions.
- 3) GOL 05. Pleuromeia sternbergii. Typical four-lobed rhizomorphous root.
- 4) GOL 14. Pleuromeia sternbergii. Internal part of a stem with outstanding leaf fragments from the upper side.
- 5) GOL 02. Pleuromeia sternbergii. Single leaf with mid-vein.

xerophyte in the Early Triassic German Basin, perhaps also in a desert or stormy environment. Surprisingly, this lycophyte, which dominated the floras of the lower Triassic, did not survive the Olenekian-Anisian boundary because a club mossrich vegetation was encountered (*Lycopia dezanchei, Isoetites brandneri, Lepacyclotes bechstaedtii, Selaginellites leonardii* and *S. venierii*) in the slightly younger Anisian strata around the neighbouring Piz da Peres, but no *Pleuromeia* was found.

Of interest are therefore the reasons why the outstanding giant club moss *Pleuromeia* became extinct in a geologically short time, whereas the giant horsetail *Equisetites*, which occupied the same ecological niches, passed unchanged on to the following periods. Since quillworts like *Isoetites* and *Selaginella*like club mosses have been recorded from the Early Triassic, and the creeping and dichotomising Lycopiales of Anisian strata have a completely different structural composition, we could not hypothesise an apparent successor of Pleuromeia. We can only vaguely argue that maybe Carboniferous Sigillaria have some similarities. It seems that the Pleuromeiales came from nothing and disappeared without leaving any trace. This appears strange because in the Eastern-Southern Alps, we have a mainly continuous fossil plant record on a small area from the Carboniferous over Permian and Triassic periods. It is dissatisfying to establish Pleuromeia as a pioneer plant after the Permian-Triassic cataclysm. A lot of other plants like the Peltaspermales, Coniferales, Cycadophyta and Equisetales survived, also mainly unmodified by these supposedly alldestroying catastrophes.



Pleuromeia sternbergii. (a) Entire plant (b) leaf-arrangement on the upper side, (c) leaf-arrangement on the lower side, (d) internal part of the stem, (e) root system, (f) entire strobilus and (g) megasporophyll.



6) GOL 01. Pleuromeia sternbergii. Strobilus with attached part of the stem.

7) GOL 01 Pleuromeia sternbergii. Detail of the cone with macrospore.

- 8) GOL 22 Pleuromeia sternbergii. Single sporangium.
- 9) GOL 22 Pleuromeia sternbergii. Single sporangium.
- 10) GOL 04 Pleuromeia sternbergii. Cone with microspores.
- 11) GOL 21 Pleuromeia sternbergii. Cone with microspores.

SYSTEMATIC PALAEONTOLOGY Division LYCOPHYTA Order ISOETALES Prantl, 1874 Family ISOETACEAE Reichenbach 1828

Genus Isoetites MÜNSTER, 1842

The Isoetaceae are a group of widespread lycophytes currently occurring in temperate regions, as well as at high altitudes in tropical regions. Known as quillworts, these perennial plants, superficially resembling grasses, grow mostly submerged in shallow water or in wet soils or flood plains. A habitat of permanent or temporary lakes, riverbanks and saliniferous lagoons could also be true for their ancestors.

The generic name Isoetites, for fossilised quillworts, was first introduced by Georg Graf zu MÜNSTER (1842, p. 107-8, pl. IV, fig. 4) in the description of the specimen Isoetites crociformis from the Lower Jurassic of Daiting near Monheim. He chose this name to express the resemblance of the tuberous stem and elongated leaves to those of the extant Isoëtes. This concept to use the name *Isoetites* for quillwort-resembling fossil forms has gradually become accepted; the same happened for the generic term Equisetites for horsetails being similar to extant Equisetes. All in all, this herbaceous lycophyte has evolved very little from Early Triassic to the present.

Isoetites brandneri WACHTLER et. al., 2010

2010 Isoetites brandneri; Wachtler et al. Pl 2 - 4

Holotype

KÜH035

Paratypes

KÜH634 corm, KÜH011 microspores, KÜH751 megaspore

Material

KÜH 030, KÜH 041, KÜH 062, KÜH 459, KÜH 246

Etymology

After Rainer Brandner, who studied the geology and stratigraphy of the Braies Dolomites.

Type localities

Kühwiesenkopf

Type horizon and age

Lower to Middle Triassic, Anisian, Pelson-Illyrian

Diagnosis

Low-growing herbaceous lycophytes, which resemble extant quillworts. Plant displays a small corm-like stem, leaves and rhizomorphous roots are attached close together. Foliage is spreading and protruding, single leaves are narrowly erect and ending as lanceolate. Heterosporous sporangia are embedded on the spoon-shaped basis of the leaves. Megasporangia occur on the outer leaf bases and microspores on the interior part.

Description

Roots: Holotype KÜH 035, a mostly entire plant (at all 15 cm high), shows in the lower part the organisation of the 3.7 cm long roots. They do not have traditional roots, but some of its leaves are modified to act like rhizomorphs. The roots are not creeping or protruding, but try to claw compactly in the soil substrate.

Stems: Bulbous to reduced, or completely missing. An indeterminate number of fertile to vegetative leaves form on the lower part a rounded short corm (KÜH 035).

Leaves: Tufted, erect to somewhat lax. Leaves narrowly cylindrical at the tips and gradually widen towards the base (until 0.6 cm), where they abruptly expand and flatten into a spoon-like form. Usually a fold in the middle part of the leaves can be noted. They can reach a length of 15 cm, leaving rhomboidal leaf scars on the stem when released. On KÜH 035, several leaves arise spirally, up to 8 cm long and 0.5 cm wide, from the base of the 4 cm long corm. Leaves narrow constantly until they reach a width of 0.3 cm in the middle and end apically lanceolate. KÜH 1246 shows the organisation of Isoetites brandneri from the upper side. Two plants growing close together display stems that measure 1.35 cm and 1.15 cm, the closely arranged rolling and papery leaves varying from 0.3 to 0.35 cm in width. Leaf cuticles are 2.5 to 3.0-µm



1) KÜH 035. *Isoetites brandneri* sp. nov. Holotype. Complete plant with roots.

2) KÜH 002. Isoetites brandneri sp. nov. Old stem fragment covered by leaf scars.

3) KÜH 011. Isoetites brandneri sp. nov. Paratype. The specimen yield immature microspores.

thick, both on the upper and lower side. Most of the leaves are fertile with sporangia of two kinds embedded in the leaf bases.

Epidermis is thick on the upper and lower side. Epidermal cells are isodiametric in the central part, uncommonly more elongated near the margins. Abaxial epidermal cells are protected by papillae. Stomata are in irregular rows, sunken and covered partially by papillae of the surrounding 5 to 7 subsidiary cells. Adaxial epidermis occur with few or no stomata and epidermal cells without papillae. Variations of the "normal" epidermis occur sometimes (KÜH 751, KÜH 004, KÜH 035).

Sporangia: Plants hold two kinds of sporophylls. Each sporangium is solitary and embedded in the hollowed leaf bases. Megasporangia occur in the outer leaf bases, while the following circle of leaves bear microsporangia and the innermost leaves are sterile. Megasporangia are large. Some immature groups of spores have been extracted from KÜH 011 and mature megaspores from KÜH 751. In KÜH 011, the microspores are reniform and up to 35 to 40 µm in diameter. They could belong to the dispersed genus Aratrisporites. Several oval to circular megaspores, 270 to 300 µm in diameter, have been found in the cuticle slides (KÜH 751). Megaspores are convolute to verrucate with a thick spore. The ornamentation reduces proximally in height. The trilete aperture is delicate, only a few times indicated by plicae (WACHTLER ET AL. 2010).

Remarks

Although many specimens are difficult to interpret because their leaves could easily be confused with those of a lot of other plants, especially when lacking fertile parts, compressions of Triassic Isoetaceae are known around the world. It is therefore possible to suggest that the origins of this characteristic heterosporous shortstemmed lycopod date back to the Carboniferous if not to the Devonian time. Beginning from the Early Triassic (Olenekian) with *Isoetes beestonii*, which is known from Australia (Blackwater – Queensland, Coal Cliff Sandstone) (RETALLACK, 1997), as well as *Isoetites brandneri* from the Anisian layers in the European Alps and *Isoetites sagittatus* from the late early Triassic of North China (WANG, 1991), this plant varies only in minimum details.

Closely related species to *Isoetites* are probably *Lepacyclotes bechstaedtii* found in the same Anisian sediments and *Lepacyclotes* (Annalepis) zeilleri recorded from the younger Ladinian deposits in Europe. The Pleuromeiaceae and Carboniferous Sigillaria could eventually be added to this group of single-standing lycopods. They stand anyway in discrepancy to the Lyopodiales bearing creeping and protruding roots, such as Lycopiaceae, Selaginellaceae and Carboniferous Lepidodrendales.

SYSTEMATIC PALAEONTOLOGY Division Lycophyta Order Isoeteales PRANTL, 1874 Family Isoetaceae REICHENBACH, 1828

Genus Lepacyclotes EMMONS, 1856

Lepacyclotes has to be regarded as a worldwide ranging low-growing bulbed lycophyte. It has been recorded from the Early-Middle Triassic (Anisian) beds in China as Lepacyclotes (Isoetes) ermayinensis (WANG, 1991), from the coeval sediments of Kühwiesenkopf in the Dolomites as Lepacyclotes bechstaedtii, from the Middle to Later Triassic as Lepacyclotes (Tomiostrobus) convexus (BRIK, 1952) in Kazakhstan, and as Lepacyclotes zeilleri from the Middle Triassic (Ladinian) sites in the Lettenkohle in France, Germany and the Wengen-Formation in the Dolomites.

Lepacyclotes bechstaedtii WACHTLER ET AL., 2010

2010 Lepacyclotes bechstaedtii; Wachtler et al. Pl 5 - 6

Holotype

KÜH 1285

Paratypes

KÜH 007, KÜH 547

Material

KÜH 2142



4) KÜH 1246. *Isoetites brandneri* sp. nov. Two plants growing very closely together.
5) KÜH 030. *Isoetites brandneri* sp. nov. Detail of the enlarged leaf bases containing sporangia.
6) KÜH 025. *Isoetites brandneri* sp. nov. View from the upper side.

Etymology

After Thilo Bechstädt, who studied with Rainer Brandner the geology and stratigraphy of the Braies Dolomites.

Type localities

Kühwiesenkopf

Type horizon and age

Lower to Middle Triassic, Anisian, Pelson-Illyrian

Diagnosis

Low-growing lycophyta with closely-spaced foliage forming a rosette. Leaves are oblong and thickened, ending acuminate to triangular with sterile leaves holding central costae. Sporophylls with elongated sporangium occur in the basal part. Corm is quadrilobate.

Description

Roots: KÜH 2142 shows part of the 3 cm long rhyzomorphs. They resemble those of *Isoetites* and are quite different from the protruding and creeping roots of *Lycopia*.

Stem: Lepacyclotes bechstaedtii spread into large clusters by forming 4 to 10 cm high and wide rosettes. Holotype KÜH 1285 shows a mainly complete preserved sidefaced plant. From a 2 cm high stem, with a diameter of 1.1 to 1.5 cm, arise spirally the closely-spaced fertile and sterile leaves. The whole plant was 4.5 cm. KÜH 007, as well as KÜH 547 evidence compressed rosettes from the upper side, both have a total diameter of 7 cm.

Leaves: The oblong leaves open flattish and are 1.6 to 1.7-cm long and 0.7 to 1 cm wide. The adaxial surface is flat to concave, broader in the middle and ends in a mucronate three-cornered structure. The basal leaves from KÜH 007 are up to 2 cm long, 0.6 cm wide and with a central costa. Only small cuticle fragments (KÜH 2122 and KÜH 007) are obtained. The normal epidermal cells are elongated (40 to 50 x 10 μ m), with papillae on one side and without on the other. A few stomata are irregularly distributed on both epidermal sides. They show simple stomata with large and elongated guard cells (WACHTLER ET AL., 2010).

Sporophylls: The plant holds sterile and fertile leaves, which are difficult to separate because they are always densely packed. KÜH 547 displays an isolated sporophyll 1.5 cm long and 0.8 cm wide, with a central elongated fertile part that is 0.9 cm long and 0.5 cm wide. It has a putative quadrilobate corm.

Remarks

In 1856, the American geologist Ebenezer EMMONS described leaf circlets from the Late Triassic (Carnian) Pekin-Formation in North Carolina as Lepacyclotes circularis and several detached scales as Lepacyclotes ellipticus. For a long time, the specimen passed unobserved in the U.S. National Museum. In 1910, the French palaeontologist Paul FLICHE named some isolated and disarticulated sporophylls Annalepis zeilleri. These fertile parts have also been misunderstood and regarded as araucarian seed scales (GRAUVOGEL-STAMM & LUGARDON, 2001). The confusion increased when similar rosette-like structures or elongated triangular sporophylls were described from other parts of the world as Tomiostrobus, Skilliostrobus or Cylostrobus (RETALLACK, 1997). Finally, Lea Grauvogel-Stamm and Philippe Duringer in 1983 cognised that the scales of Annalepis zeilleri were sporophylls belonging to the lycopsids with megaspores of Tennellisporites and microspores assignable to Aratrisporites. Although the first described Lepacyclotes found in considerable numbers lack clearly identified spores, but are abundantly associated with them, the resemblance of the fossilised specimen and especially the sporophylls suggest that we have to do it with a conspecific group of herbaceous lycophyta, with Lepacyclotes (EM-MONS, 1856) having priority over the other one.

Discussion

Several low growing Triassic lycophyta are known from a lot of locations worldwide. Difficulties occur in differentiating if we have to do it with detached fertile parts from sub-arborescent club mosses or small-sized plants to be inserted into a wider group of Isoetaceae-like forms.



- 1) KÜH 1285. Lepacyclotes bechstaedtii sp. nov. Holotype. Mainly complete plant seen from the lateral side.
- 2) KÜH 2142. Lepacyclotes bechstaedtii sp. nov. Plant with crowded foliage.
- 3) KÜH 547. Lepacyclotes bechstaedtii sp. nov. Paratype. Plant seen from the upper side.
- 4) KÜH 007. Lepacyclotes bechstaedtii sp. nov. Paratype. Specimen with an inner circle of elongated leaf fragments.

Different fructifications from the Lower Triassic of Australia, belonging probably sub-arborescent lycophytes, have to described as Tomiostrobus, been Cylostrobus, Austrostrobus, Lycostrobus and Skilliostrobus. Most are regarded as a synonym of Tomiostrobus (RETALLACK 1997, TAYLOR ET AL. 2009). This is valid for Takhtajanodoxa mirabilis from the Siberian deposits. Although all these sporophylls have some affinities with Lepacyclotes producing even the same microspores of dispersed genus Aratrisporites - they differ in having a distal elongated limb and bluntly pointed to mucronate ending tips (GRAUVOGEL-STAMM & LUGARDON, 2001). Furthermore, Tomiostrobus is characterised by a short stem (RETALLACK, 1997).

The genus *Lepacyclotes* was a worldwideranging Mesozoic lycophyta, found from the Alps to China and Australia and appearing in the Early-Middle Triassic until the Triassic, when it began to disappear on the border with the Jurassic. The Isoetales, in contrast, was just present in the earliest Triassic in Australia as *Isoetes beestonii* and slightly later as *Isoetites brandneri*, remaining only marginally modified until the present.

While the Pleuromeiales with their unbranched erect stem have only vague affinities, some fossilised remains especially from Australia, India and Siberia could be more closely related to *Lepacyclotes*. However, this is only valid if all this morphogenus for fructifications is not regarded as terminal cones of other shrubby or bushy plants.

Anisian *Lepacyclotes bechstaedtii* was much smaller than Ladinian *Lepacyclotes (Annalepis) zeilleri*, bearing sporophylls up to 5 cm long and 2 cm wide and reaching a plant size of 15 cm. *Lepacyclotes circularis* described by Emmons has nearly the same size as that of *Lepacyclotes zeilleri*. Some affinities persist with coeval *Lepacyclotes ermayensis* holding elongated sporophylls with triangular mucronate tips.

No extant plants have enough affinities with *Lepacyclotes. Stylites andicola*, found in extremely crowded colonies on a moist and limy substrate around the margins of glaciers at an elevation of 4,750 metres in Peru, also share resemblances with *Lepacyclotes*, but much more with *Isoëtes*. Others, like South American *Isoëtes novo-granadensis* or Tasmanian *Isoëtes gunnii*, have

reduced leaves but bear more resemblances with Isoetaceae. In all of them, the leaves have a relatively short upper leaf zone and a sheathing base comprising two-thirds or more of the total leaf length. In Isoëtes novo-granadensis, the up to 5-cm long triangular foliage is arranged in a half-buried rosette. The stems are generally fleshly and buried completely in marshes or swamps. Lepacyclotes bechstaedtii and Isoetites brandneri have only been found in the Kühwiesenkopf "Dead Fish-Basin", together with the other lycophytes Lycopia dezanchei and Selaginellites leonardii. The latter two are common in other parts of the Piz da Peres area. The basin harbours abundant skeletons of fish like coelacanths, Gyrolepis, Bobasatrania, Dipteronotus and Saurichtys, as well as being unusually rich in land plants. Besides the lycophytes and some isolated Equisetites mougeotii, it is rich in ferns like Neuropteridium or Gordonopteris, seed ferns such as Scytophyllum and Sagenopteris, conifers like Voltzia and Alpia, as well as several cycadophyta species like Bjuvia and Nilssonia and some enigmatic proto-angiospermales. Therefore, it is difficult to deduce globally active theories about extraordinary climatic changes from the plant assemblage. More reasonable would be the notion of a salt-saturated soil with frequently ephemeral ponds as well as overflooded marshlands, where Lepacyclotes and *Isoetites* occupied the most exposed places. This is the preferred living space for extant Isoëtes species worldwide, which further supports the idea that this plant never abandoned its ecological niche and ancestral living habitat in 300 million years.



Isoetites brandneri: (a) Entire plant (KÜH 035), (b) megasporophyll and microsporophyll with leaves and (c) lateral side showing the arrangement of fertile parts.

Lepacyclotes bechstaedtii: (a) Entire plant (KÜH 1285), (b) interior view of the plant (KÜH 1285), (c) upper view ((KÜH 007) and (d) single sporophyll.

SYSTEMATIC PALAEONTOLOGY Division LYCOPHYTA Order SELAGINELLALES Prantl, 1874 Family SELAGINELLACEAE Willkomm, 1854

Genus Selaginellites ZEILLER, 1906

Extant Selaginellaceae belong to a widely distributed family of herbaceous lycopods, welladapted to various climate conditions and soil types. Some species can resist extreme weather, such as those prevalent in alpine or artic circles. They can also colonise barren and dry deserts. One of the most well-known, *Selaginella lepidophylla*, is called the resurrection plant because it can survive years without rainfall.

They reach their highest diversity in tropical areas under the forest canopy, protected from direct sunshine or around riverbanks, marshes or waterfalls. All extant Selaginellaceae are included in one large genus of about 700 species. The presence or absence of leaves of two distinct sizes has been used as a criterion for subdividing extant Sellaginellaceae (KORALL & KENRICK, 2002). Anisophylly is characteristic of the subgenera Heterostachys and Stachygynandrum, whereas Tetragonostachys, Selaginella and *Ericetorum* are isophyllous. Selaginellaceae are delimited from herbaceous Lycopodiaceae by their heterosporous fructifications in contrast to the isosporous Lycopods.

The earliest fossil evidence of Selaginellaceae comes from the Carboniferous (Visean 345.3 to 328.3 Ma) and from the late Carboniferous (Selaginellites gutbieri), when branching stems that bore minute leaves were widespread in coal measure floras. Surprisingly, in that time, isophyllous and anisophyllous species coexisted (THOMAS 1992, 1997). Although fossil Selaginellas are known from such a long time ago, their remains are very rare, often despite their inconspicuousness and fragility. Renè Zeiller instituted the genus Selaginellites in 1906 for fossil heterosporous lycopods resembling recent Selaginellas. Even if Paleozoic-Mesozoic *Selaginellites* are presumably congeneric with Selaginella, this classification concept has become largely accepted. A delimitation to other Lycopodaceae is that Selaginellites is restricted to heterosporous species, whereas Lycopodites includes isosporous taxa and other species that are not known to be heterosporous (ZEILLER, 1906).

Selaginellites leonardii sp. nov. WACHT-LER ET AL. 2010

Holotype

KÜH 1140

Paratype

KÜH 956

Material

PIZ 622, PIZ 623, KÜH523, PIZ 563, PIZ 165

Etymology

Remembering Piero Leonardi, a pioneer in the research on the geology of the Dolomites

Type localities

Piz da Peres, Kühwiesenkopf

Type horizon and age

Early-Middle Triassic, Anisian, Pelson

Diagnosis

Stems branch dichotomously and are regularly or irregularly forked or branched. Leaves tightly appressed to ascending on the stems. Foliage structure linear-lanceolate to slightly falcate at the marginal ranks. Strobili with clusters of overlapping sporophylls are arranged spirally to decussately. Sporophylls ovate, differentiated from vegetative sterile leaves. Heterosporous sporangia in the axils of sporophylls are divided into compact tetrads of trilete microspores, while megaspores are oval to circular with thick spore walls.

Description

Vegetative branches: Stems are densely cespitose, ascending, slightly to greatly branched, up to 5 cm high and with dichotomising axes without an appartenent decrease in the thickness of lateral branches. PIZ 622 is a good example of a mainly complete specimen. It shows an erect, many-branched stem holding juvenile and adult shoots. Some of the ultimate branchlets are merely short spurs, slightly enlarged at the tip and only a few millimetres in length. The thickness of the



- 1) PIZ 622. Selaginellites leonardii. Mainly complete branch.
- 2) PIZ 623. Selaginellites leonardii. Branches show dichotomous forking.
- 3) KÜH 956. Selaginellites leonardii. Paratype. Axes evidence slightly enlarged short spurs.
- 4) KÜH 1140. Selaginellites leonardii. Holotype. Minute axes.
- 5) PIZ 165. Selaginellites leonardii. Sterile branch.

branches varies from 1.2 to 1.8 mm in PIZ 623.

Leaves: On juvenile shoots of PIZ 563, leaves are 1 to 3 mm long and protruding, a little awl-shaped, displaying a subtle needle-like characteristic. Adult branchlets are covered with several rows of minute appressed, narrowly lanceolate and highly overlapping leaves. In that manner, they are mostly invisible, suggesting naked shoots (PIZ 622, PIZ 623, KÜH 1140, KÜH 956 and PIZ 165).

Strobili: Holotype KÜH 1140 shows two compact heterosporous strobilus fragments, preserved on slightly different horizons in the block, but not in organic connection with the vegetative parts. The complete larger strobilus $(1.7 \times 0.3 \text{ cm})$ bears helically to decussately arranged micro- and macrosporophylls, which are aligned in four irregular vertical files (1.5 to 2 x 1 to 1.2 mm). They are ovate with a long, acuminate apex (about 2 mm long) and an entire margin and are therefore completely different from the sterile leaves, which are minute and acicular. PIZ 622 display in the lower part a semi-destroyed strobilus attached to a branchlet. Strobili, in comparison to the shoots and the dimension of the whole plant, are extraordinarily long. Maceration of sporophyll fragments gave small cuticle pieces with isodiametric cells and sporangia containing masses of immature, in situ microspores and megaspores. The microspores are mostly organised in immature, compact tetrads containing spores approximately 46 (42.5 to 50) µm in diameter. Well-developed, separated trilete microspores are 56 (45 to 62.5) µm in diameter, proximally with a punctate (possibly granulate) or smooth (psilate) spore wall and distally rugulate. Several oval to circular megaspores of 312 x 356 (270 to 340 x 300 to 410) µm in diameter have been found dispersed in the sediment; clusters of megaspores have been extracted from the sporophylls. Megaspores are psilate to punctate, with a 10-µm thick spore wall. The trilete aperture is delicate or not well-developed, and only rarely indicated by plicae. Megaspores, and to a lesser degree microspores, are found both in the lower and upper part of cone fragments. During maceration, an entire sporophyll with adhering sediment yielded a small cluster of megaspores and an entire immature mass of microspores, suggesting that the sporophylls were probably distributed in rows of microsporophylls and megasporophylls (WACHTLER ET AL. 2010).

Selaginellites venieri sp. nov. WACHT-LER, 2011

Holotype

PIZ 548

Material

PIZ 548B counterplate

Etymology

For Umberto Venier, which dedicate his life for searching fossil plants in the Eastern Alps.

Type localities

Piz da Peres

Type horizon and age

Early-Middle Triassic, Anisian, Pelson

Diagnosis

Cespitose low-growing lycopod with a dichotomising axis. Leaves anisophyllous, characterised by their opposite pairs of dorsal and ventral leaves that differ in size and form. The larger leaves are attached laterally and the smaller ones medially on the upper surface. Leaves mostly entire to minutely denticulate.

Description

Vegetative branches: Erect plant, dichotomously branched, with leaves crowded throughout the stem. *Selaginellites venieri* is characterised by their anisophyllous morphology, with its leaves in two ranks and the ventral or lateral set smaller than the dorsal set.

Vegetative leaves: Both median and lateral leaves are 2-pairs ranked, closely imbricate, narrowly rounded at the tip, strongly oblique to the axis, and ascending at an approximately 45° angle. The lateral side is 1.8 to 2.2 mm long and 0.5 to 0.7 mm wide,



6) KÜH 1140. *Selaginellites leonardii*. Holotype. Heterosporous strobilus.
7) KÜH 1140. *Selaginellites leonardii*. Holotype. Heterosporous strobilus. Detailed.
8) PIZ 622. *Selaginellites leonardii*. Badly conserved, but attached strobilus.
9) PIZ 563. *Selaginellites leonardii*. Shrub with well-preserved or juvenile leaves.
10) PIZ 563. *Selaginellites leonardii*. Detail of subtle leaves.

while the central part is 0.6 to 0.8 mm long and 0.5 to 0.7 mm wide. The surface area of the external standing leaves is therefore about three times greater than that of the smaller internal leaves (PIZ 548). Anisophylly is typical for many species of extant *Selaginella* species.

Discussion

At least two quite different *Selaginella* species formed part of the Early-Middle Triassic

ecosystem in the Dolomites. The isophyllous *Selaginellites leonardii*, characterised by their same-sized leaves, and the anisophyllous *Selaginellites venieri*, with its possession of two sets of different foliage on the same rank. Unfortunately, only a few, sometimes, poorly preserved Triassic heterosporous *Selaginellites* species are currently known, most of them found in Upper Triassic (Rhaetian) rocks in Arizona (*Selaginella anasazia*), Greenland (*Selaginellites pola*-



Selaginella venieri: a) Part of a branch, b) evidencing the arrangement of the anisophyllous leaves



Selaginella leonardii: (a) Entire twig, (b) part of an ultimate branch, (c) sporophyll and (d) internal part of a sporophyll displaying macro- and microsporangia.

ris), Sweden (Selaginellites hallei and Lycopodites scanicus) and China (Selaginellites yunnanensis). They have some affinities with Selaginellites leonardii and Selaginel-

lites venieri, but not enough to classify them as conspecific. The most closely resembling species to *Selaginellites leonardii* is Rhae-



PIZ 548. Selaginellites venieri. Holotype. Branch with anisophyllous leaves.
 PIZ 548. Selaginellites venieri. Holotype. Detail of the anisophyllous leaves.

tian *Selaginellites hallei*, but it bears much smaller strobili.

It is not possible - with the dried characteristic, its close-fitted needles and also, in parts, the naked stems of *Selaginellites leonardii* - to trace parallels within all the extant Selaginella species. The well-known *Selaginella lepidophylla* has some similarities, but exhibits a much more equipped leaf arrangement and is also anisophylous in contrast to the isophyllous *Selaginellites leonardii*.

It would therefore be conducive to compare the living parts and the visual nature of Early Triassic and extant Selaginellaceae. *Selaginellites leonardii* is found mainly at two points in Piz da Peres: in the lower strata of Kühwiesenkopf and in the slightly younger layers of the Piz da Peres Wachtler gorge. The species at these two sites are remarkably common, in association with *Selaginellites venieri*, and occur in almost the same manner amidst a variegated flora consisting of conifers, ferns, seed ferns, cycads and horsetails. To understand the desiccated disposition of *Selaginellites leonardii*, it would be much more reasonable to search them in local ecological phenomena and not to use them to diagnose global or even catastrophic events. This spike-moss found its preferred habitat probably in some rocky, sunexposed, up-rushed coastal zone.

Other is the situation for *Selaginellites venieri*. A habitat in the shadow of the other plants like today's anisophyllous Selaginellaceae could be likely accepted. The ecological advantages of double-sized leaves are still unknown. Nonetheless, heterophyllous foliage characterises most Early Triassic plants like conifers (*Voltzia heterophylla* and *Schizolepis ungeri*), seed ferns (*Scytophyllum bergeri*) and cycado-phyta.

SYSTEMATIC PALAEONTOLOGY Division LYCOPHYTA Subdivision LYCOPHYTINA Kenrick & Crane, 1997 Order LYCOPIALES Wachtler, 2011 Family LYCOPIACEAE Wachtler, 2011

Genus Lycopia WACHTLER ET AL., 2010

Diagnosis

Sub-arborescent to arborescent lycophyte, stems are wide creeping and rooting at irregular intervals. Main stems are dichotomously or anisotomously branched. Leaves herbaceous, acicular, entire and spreading on the apical part. Strobili terminal and solitary on a short stalk, bearing spirally-arranged sporophylls. Sporangia are adaxially near the sporophyll base.

Etymology

After their insertion as lycophyte and commemorating Julius Pia, and Austrian geologist and director of the Natural History Museum of Vienna, who during the First World War conducted intensive research in the Braies Dolomites.

Lycopia dezanchei Wachtler et. al., 2010

2004 Lycophyta gen indet. sp. indet.; Kustatscher ET AL., p. 131, pl. 1, fig. 4.
2010 Lycopia dezanchei; Wachtler ET AL. Pl 7, Fig 1, pl. 8, Fig. 1 - 4

Holotype

KÜH 1425

Material

PIZ 97, KÜH 1423, KÜH 1424, KÜH 655, KÜH192, KÜH529, KÜH0641, KÜH1115, KÜH1322

Etymology

After Vittorio De Zanche, who made extensive and detailed studies about the stratigraphy in the Dolomites.

Type localities

Kühwiesenkopf, Piz da Peres, Val Duron

Type horizon and age

Dont Formation, Richthofen Conglomerate, Morbiac Limestone. Lower to Middle Triassic, Anisian, Pelson-Il-

lyrian

Diagnosis

Sub-arborescent lycophyte with wide creeping rhizomes, rooting at irregular intervals and covered by subtle hairy appendices. Main stems erect, isophyllous, sparsely leafy, branching dichotomously and anisotomously, bearing spirally-arranged foliage. Leaves are lanceolate to elongated, maintaining an uniform width. Cuticle is thick and epidermal cells isodiametric to rectangular. Stomata are sunken and protected by the papillae. Cones are of *Lycopodostrobus gaiae*-type, with long helically-arranged decreasing sporophylls on a central axis. Sporangia are borne adaxially at the sporophyll base.

Description

Roots: Rhizomes grow mainly prostrate along the ground, from which branches the main and erect stems. Two root fragments (KÜH 1162 is 48 cm long and 13.5 cm wide, while KÜH 2438 is 40 cm long and 14 cm wide) display alternate arising stems. The rhizomes are densely covered with 2 to 5 mm long hairy rootlets and subtle 1 mmwide pit marks. On KÜH 1162, the main stems arising reach a diameter of 4 cm and arise in a dorsolateral position.

Stems: Stems are of considerable size, the fragment of KÜH 1423 is up to 60 cm long and 7 cm wide. Sometimes on the lower part, they are covered with rhomboidal cleavage compressions, a result of abscised leaves (KÜH 1229). Branches are sparsely leafy, isophyllous and covered with spirally-arranged, long, simple leaves especially in the upper part. A dichotomy resulting in daughter axes of approximately equal diameter (KÜH 1264) as well as anisotomous systems with one structurally dominant branch have been noted (KÜH 1424). Leaves display a tendency to be bushy on the apical part and are downwardly curved.

Leaves: On the base, the leaves are densely appressed and sometimes also scale-like. On older or larger stems, rhomboidal leaf



1) KÜH 1425 (PAL 1264). Lycopia dezanchei (Holotype) Isotomous forking apical stem fragment Kühwiesenkopf.
 2) PIZ 97. Lycopia dezanchei. Stem fragment with long leaves. Piz da Peres.

scars from released foliage are typical. In the higher parts, the foliage is spreading and protruding. Leaves are herbaceous, lanceolate to elongated, with an entire margin showing one central unbranched vein or costa. It extends through the entire length of the leaf. They taper only slightly from the base to the apex. The length of the leaves varies from 15 to 30 cm on apical mature tree crowns, and their width ranges from 0.4 to 0.7 cm (KÜH 1423). Thick leaf cuticle is amphistomatic, while normal epidermal cells are isodiametric to rectangular (25 to 30 x 40 to 50 µm). Stomata are sunken and protected by papillae.

Strobili: Cones are terminal and solitary on a short stalk, cylindrical, up to 10 cm long and 3.5 to 4 cm wide. Sporophylls are scalelike and overlapping, broadly ovate to deltoid, narrowing to an extralong pointed tip. Sporangia are borne adaxially near the sporophyll base and are homosporous.

Genus *Lycopodostrobus* nov. gen. WACHTLER, 2011

Diagnosis

Strobili of Triassic Lycopodiales with helically arranged homosporous sporophylls. Sporophyll scales end in a long pointed appendage. Sporangia occur adaxially on the lower leaf axils.

Etymology

After their affinity to the strobili of the Lycopodiales.

Lycopodostrobus gaiae nov. sp. WACHTLER, 2011

Holotype

PIZ 98

Paratype

KÜH 1262

Material

PIZ 99, PIZ 213, KÜH 1426, PIZ 317, KÜH 778, KÜH 1276

Etymology

After Gaia, the primordial Earth goddess in ancient Greek mythology

Type localities

Piz da Peres, Kühwiesenkopf

Type horizon and age

Dont Formation, Richthofen Conglomerate, Morbiac Limestone. Lower to Middle Triassic, Anisian, Pelson-Il-

Diagnosis

lyrian

Elongated strobili with long gradually tapering sporophylls. Spores are homosporous and clustered on the upper side near the apex. Sporophylls encase the cone at a juvenile stage to become increasingly protruding when mature.

Description

Several lycophyta cones at all growth stages were recovered from Piz da Peres. They help elucidate the evolution of club moss cones from the Palaeozoic to the present. While the mostly mature cones from Kühwiesenkopf yielded no in situ spores, four juvenile to semi-fully grown strobili from Piz da Peres exhibited the position of the spores inside the sporophylls. Holotype PIZ 98, with 7-cm long preserved parts, shows the organisation of these strobili well. The estimated length of the cone body of Lycopodostrobus gaiae probably reached 10 to 20 cm in length (KÜH 1276: 15.5 cm long) and 3 to 4 cm in width. The cones can continue for a further 5 cm, showing a characteristic tapering appendix. PIZ 213 represents a juvenile specimen with a cone length of 5 cm, held by a 1-cm long stalk. Sporophylls are attached at an angle of about 80 degrees to the cone apex. The single sporophylls are complete, with a triangular to slightly lanceolate ending and 2 to 5-cm long pointed prolongations. In mature cones (KÜH 1262 and KÜH 1426), the characteristic appendices become increasingly protruding, whereas in juvenile forms, they tend to encase the cones. The spore-bearing zone, probably reniform, lies on the adaxial side of the sporophyll



3) KÜH 1423. Lycopia dezanchei. Extraordinarily long stem fragment.

4) KÜH 655. Lycopia dezanchei. Root segmented with subtle hairs.

5) KÜH 1424. Lycopia dezanchei. Bifurcating anisotomous apical stem fragment with bushy leaves.

near the axis and is 10 to 15 mm long and 5 mm wide.

Remarks

Michael Wachtler first discovered *Lycopia* in 1999 on the slopes of Kühwiesenkopf in the Braies Dolomites. In the following years, he collected other materials from Piz da Peres and finally some badly preserved specimens from Val Duron belonging to the younger Morbiac Limestone of the Illyrian age, which enhanced knowledge on the appearance and living habitat of this interesting lycophyte. *Lycopia* constitutes one of the most common flora elements in the Anisian strata of the Dolomites and was in sub-arborescent competition with conifers (*Voltzia, Alpia* and *Albertia*) and giant horsetails (*Equisetites*).

It should not be completely discarded that Triassic Lycopia has some affinity with extant Lycopodiales as well as Carboniferous Lepidodendrales. If the descendants of Triassic Equisetites are observed in the Carboniferous Calamites, this is not so misleading. Most Lepidodendrales are thought to have become extinct in Europe and North America at the end of the Carboniferous, whereas in China, they persisted into the Middle Permian.

A large number, probably more than 350 *Lepidodendron* species, has been described since the genus was first recognized by Kaspar Graf von Sternberg in 1820. Most species are based either on fragments of large stems lacking leaves or on generally smaller branches with foliage still attached. Only rarely does good evidence of a connection between leafy shoots, main axis fragments and still fertile organs exist (CHALONER & MEYER-BERTHAUD, 1983). A feature of Lepidodendron is their expanded pyramidal and also diamondshaped decurrent leaf base. This is most evident when the leaf has been abscised and a characteristic leaf cushion remains, called "Blattpolster" by older authors in German.

Comparing *Lycopia* to other Triassic lycopsida, such as *Isoetites* or *Lepacyclotes*, they have to be immediately discharged because of their herbaceous characteristic, their non-protruding rhizome structure and non-dichotomising branching system. This is also the main difference between arborescent Pleuromeiales, which are characterised by their non-forking stems. Differences in the root system (four-lobed tap root-like in *Pleuromeia* versus creeping and protruding) and different heterosporous sporangia from the homosporous structure of *Lycopia dezanchei* are other distinguishing features.

It seems that *Lycopia* stands were isolated among the Mesozoic lycophyta, occupying mostly the ecological niche of *Pleuromeia*. which was never recorded in the Early-Middle Triassic strata of Piz da Peres, but was very abundant in the Induan-Olenekian Werfen-Formation of the neighbouring Carinthia and in the global distribution during the Early Triassic.

The generic name Lycopodites was introduced to describe the isophyllous to anisophyllous leaves of the suggested Lycophyta, ranging from Devonian till Pleistocene (TAY-LOR ET AL. 2009). Especially for Palaeozoic fossils, it is nearly impossible to distinguish minute branches from the distal twigs of Lepidodendrales, particularly while the attached reproduction organs are missing. Lycopodites amazonica described from the Middle Devonian of Brazil and Oxrodia gracilis from the Mississippian of Scotland are thought to represent herbaceous lycopsids. Others, like Synlycostrobus tyrmensis and Onychiopsis psilotoides, belong to younger Cretaceous deposits and can therefore be regarded as the descendants of Lycopia.

Many more affinities have been discovered with the extant group of Lycopodiales. Extant Lycopodiales are represented by four genera (about 480 species in Lycopodium, 430 species in Huperzia, 41 species in Lycopodiella and ones species in Phylloglossum. All are homosporous, generally dichotomously branched and represent small herbaceous plants. Their stems arise adventitiously from a horizontal rhizome. The Lycopodiales have a global distribution, but their favoured habitat spans mainly from temperate to subarctic regions.

Both extant Lycopodiales and Lycopia show a comparable root system with a reptant stem and rootlets. Lycopia also bears either aboveground or underground running rhizomes or lateral branches. The abscised leaf cushions are pyramidal in Lepidodendron and more rhomboidal in Lycopia, but similar in every case. The robot-like structure of Lepidodendron, commonly called Stigmaria,



- 1) PIZ 98. Lycopodostrobus gaiae (Holotype). Suggested strobilus of Lycopia dezanchei.
- 2) PIZ 98. Lycopodostrobus gaiae (Holotype). Detail of sporophylls .
- 3) PIZ 99. Lycopodostrobus gaiae. Strobilus with sporophylls.
- 4) PIZ 213. Lycopodostrobus gaiae. Strobilus with attached sterile leaves of Lycopia dezanchei on the lower part.
- 5) KÜH 1262. Lycopodostrobus gaiae. Mature strobilus bearing spatiolate sporophylls.

resembles the rhizomes of *Lycopia* in many parts, with its shallow propagation structure and helically-arranged lateral appendages. In *Stigmaria* and *Lycopia*, the appendages are abscised during plant growth, leaving small subtle circular scars in *Lycopia* and bigger ones in *Stigmaria*.

Lepidodendron and Lycopia hold apically dichotomising axes and do not have ligulate leaves. The organography of branching was fundamentally dichotomous in extinct Lepidodendron, varying from equal to unequal. When unequal, overtopping would have occurred, leading to a determinate branch. The same could be stated for Triassic Lycopia as well as the recent Lycopodiales. Both also bear homosporous strobili. Lycopia could be considered a "Giant Lycopod" in the same manner as the "Giant horsetails Equisetites" from the same Anisian strata.

Lepidostrobus is a loosely defined morphogenus, named and briefly described by Alexandre BRONGNIART after a cone determined for the first time by Parkinson (1804) and currently stored in the London Natural History Museum. For the next 150 years, all cones that even vaguely fitted BRONGNI-ART's criteria were included there (BRACK-HANES, S.D. & THOMAS, B.A., 1983). Since the holotype yielded only microsporangia, but bisporangiate cones were found in Lepi*dodendron*, a distinction was made that the morphogenus *Flemingites* has to be used for that kind of strobilus, whereas Lepidostrobus should only include microsporangiate strobili (TAYLOR ET AL. 2009).

Although never found in complete organic connection, Lycopodostrobus gaiae strobili constitute the fertile organ of Lycopia dezanchei. The cone morphology is comparable with that of Carboniferous Lepidostrobus cones belonging to Lepidodendron. They are characterised by their homosporous strobili borne on distal branches in the crown of the tree. Such strobili found in the Stephanian sediments on Stangnock in Carinthia also bear typical protruding leafy appendices. Only the size of Triassic *Lycopodostrobus* is smaller, reaching half of the Carboniferous one in the best cases.

Compared to the extant Lycopodiopsida, the Isoetales and Selaginellas have to be eliminated because of their totally different composition, root system and mainly heterosporous reproduction. The discovery of abundant material of Isoetaceae and Selaginellaceae in the Anisian layers consolidates the argument that other relatives have to be searched for.

Altogether, *Lycopia* constitutes a highly interesting plant and, if not a direct descendant of giant *Lepidodendron*, it could at least be integrated into the same family. It seems that the arborescent lycophyte crossed the Permian by reducing their size enormously and survived the Mesozoic by further decreasing its size to occupy ecological niches as dormant dwarfs, maybe increasing in size when circumstances changed.

General discussion

Why I conducted this research

Since 1990, I spent most of my time in the mountains around Piz da Peres. First, I had to learn how to walk and then hear the sound of the past, at least to see inside the rocks. This took years and years of hard work. Only after that, I felt mature enough to understand the rocks. At the end, the rocks began to tell me their living history. Thus, I discovered a lot of new and, at that time, unknown fossils. I often read in books the manner in which I can understand the past, but the best way is by exploring and searching until you have the missing links in your hand. These are then the incontrovertible arguments for understanding how life evolved or how they could have evolved. Unfortunately, we now live in a time when many scientists perform their studies in the privacy of their own home and not in nature. Although cladistic analyses on a writing desk can be useful, they are nothing against many years of studying in the wilderness.

All that time, I lied in wet soil or scrambled onto exposed rocks. Avalanches buried me, I was struck by lightning, and I suffered from cold and heat. However, I felt like a free man, something that I could not affirm from the people in the valleys, who had to carry out often nonsensical work. Sometimes, my absence from normal life was noticed and the police put pressure on me with their guns. I saw villages expanding and an increasing number of ski slopes that restricted the areas I was investigating.



Lycopia dezanchei: (a) Entire plant, (b) root horizon, (c) stem, (d) *Lycopodostrobus gaiae*: Cone with open sporophylls, (e) sporophyll displaying microsporangia, (f) closed sporophyll, (g) single leaf, (h) single shoot, (i) isotomous growth pattern and (j) anisotomous forking stem with one part more dominant than the other.

Shortly, the authorities imposed a research ban on me and punished me. However, I never suffered from boredom or desperation. I said to myself that if I helped to decode only one drop of water in the big ocean of science, my life was just worth living.

The significance of lycopods in the past Although extant lycophytes constitute a modest group of herbaceous plants, they have played an enormous role in the history of land vegetation and have the longest fossil record of any vascular plant, extending over 400 million years from the Early Devonian, maybe from the late Silurian until the present (CLEAL & THOMAS, 2009). They dominated vegetation around the world and were the largest known living organisms in the Carboniferous. The oldest representatives of the group are found in the Early Devonian with Baragwanathia and Drepanophycus (SCHWEITZER, 1990). The presence of lycopods - from herbaceous to arborescent - can be traced continuously from then until the present. All the characteristics that typify Lycopodium today, such as creeping, dichotomous and anisotomous branching,

numerous spirally-arranged microphylls, and reproduction by spores produced in large sporangia borne adaxially to the leaves, remain remarkably unchanged from the oldest member of the group (HUEBER, 1983). Selaginellaceae has also been recorded in the Carboniferous, whereas the oldest members of Isoetaceae have only been recorded as far back as the Early Triassic in Australia *(Isoetes beestonii;* RETALLACK, 1975); the Alps *(Isoetites brandneri;* WACHTLER ET AL. 2010). Certainly they have to date further back because just in that time of global distribution.

The modification of landscape from the Carboniferous to the Triassic

An impoverished flora after the Carboniferous. In a geologically short time, the dominant giant lycophyta disappeared completely. In the lower Permian, only isolated remains were found (Rotliegend: *Subsigillaria brardii* and *Lepidostrobus*) (BARTHEL, 2009). This is also valid for the Alps, where only some doubtful *Stigmaria ficoides* roots



An entirely recovered *Sigillaria* stem from the Carinthian Stangnock area with a diameter of up to one metre (Collection Georg Kandutsch).

from the Early Permian Laas-Formation and Wunderstätten have been published (FRITZ ET AL. 1990; WANK & PRINZ, 1994).

Huge delta swamps in the Early Triassic. In the Early Triassic, big parts of Europe and other landscapes consisted of enormous flat basins and delta swamps. The palaeoecological milieu was more humid with an intertonguing of river channels and floodplains and lakes (MADER, 1990). This would have been consistent with the presence of Pleuromeia and the abundant richness of humidloving Equisetacea (Equisetites mougeotii), whereas other plants (the ferns Anomopteris mougeotii and Neuropteridium, the conifer Voltzia heterophylla, and the seed fern Scytophyllum bergeri) filled the niches of drier landscapes or higher-lying areas. Thus, the dominance of *Pleuromeia* and *Equisetites* is explainable without catastrophism theories. The short heyday of Pleuromeiales. The lycophyte Pleuromeia sternbergii is recorded extensively in the Induan-Olenekian and constitutes one of the most well-known



Upper Carboniferous *Selaginellites gutbieri* with two attached bisporangiate cones and well developed planar branching ovate to lanceolote leaves with acute apices. Westfal D. Zwickau. Collection Jürgen Meyer, Zwickau

global plant species in that period, ranging from the Carinthian mountains (Gailtaler Alps, Karawanken), Germany (*Pleuromeia sternbergii*), over the Caspian Sea to Wladiwostok, China and Japan (*Pleuromeia rossica, P. obrutschewii, P. epicharis, P. jiaochengensis and P. hattai*), even occurring in Australian locations from the former



Lepidostrobus sp. cone from Carboniferous (Upper Stephanian) Carinthian Stangnock, belonging to *Lepidodendron* (Collection Georg Kandutsch).

Compared to the Carboniferous *Lepidodendron* cones, Lycopia strobili were nearly as large, but from half to one-third smaller in length. The composition of long and protruding leafy appendices on sporophylls is surprisingly similar. Gondwana continent (*P. longicaulis*). As stated by other authors (RETALLACK, 1975; LOOY ET AL. 1999; TAYLOR ET AL. 2009), the Pleuromeiales apparently came from nothing, dominated the planet for a short geological time and became completely extinct on the Olenekian-Anisian boundary. It is also possible that they are the descendants of Carboniferous Sigillariaceae. Tracing an evolutionary line from Pleuromeiales to any extant lycopods like *Isoëtes* is highly improbable because Isoetales co-inhabited with Pleuromeiales in the Early Triassic.

The irresistible ascension of land plants in the Early-Middle Triassic. After nearly 50 million years of a difficult time for plants beginning from the Early Permian to the Early Triassic, we relive the rise and spread of mainly all extant plants in the Anisian. A lot of new-age ferns (*Gordonopteris, Marantoidea, Ladinopteris, Sphenopteris, Anomopteris, Wachtleria and Neuropteridium*) belonging to the Marattiacea, Gleichenaceae, Osmundacea or Lindsaeaceae were highly diffused. This is also valid for the conifers dividing them in Voltziaceae and Alpiaceae, which evolved into mainly all conifers present nowadays like Araucarians, Pinaceae and Cupressaceae. There was an enormous diversification of the cycadophyta (Bjuvia and Nilssonia), with a splitting of mainly all living cycad genera and a rise in an unusual group of proto-angiospermales (Ladinia and Pizperesia). Moreover, the lycophyta (Lycopia, Isoetites and Selaginellites) and sphenophyta (Equisetites) maintained their ecological niche, even though very reduced in size and diffusion. Only the Peltaspermales (Scytophyllum, Sagenopteris), although highly present in the Early-Middle Triassic, seemed to not have survived the Jurassic-Creataceous boundary.

The importance of the new lycopod species from Piz da Peres. The discovery of



The Induan-Olenekian (249.7 to 245 million years) Carinthian *Pleuromeia* area: (1) *Pleuromeia sternbergii* and (2) *Equisetites mougeotii*. In the background: The conifers *Voltzia heterophylla, Alpia,* the fern *Neuropteridium,* the seed fern *Scytophyllum* and *Anomopteris.*

several new species and one new genus of Lycophytes in the lower Middle Triassic of the Southern Alps shed some interesting light on the evolution of this group. The Triassic was a time of important radiation and change in several key morphological characteristics of this group. After the predominant position of giant Lycopods in the Carboniferous, there was a decline in the Permian and a much reduced level of radiation of dwarf lycopods in the Early Triassic, with nearly all groups present then still extant now.

Possible geothermal events as a cause of this unusual lycophyta assemblage. The early Middle Triassic Kühwiesenkopf Dead-Fish basin is distinguished by their variegated club moss association. Special reasons for this local environment could lie in local geothermal features such as hot springs, lakes, fumaroles, geysers, heated soils or hot streams. These distinctive environmental conditions allowed unusual plant assemblages and combinations of floras, like the club moss vegetation capable of surviving high-stress conditions of soil mineralisation and temperature. However, marked differences in vegetation composition and physiognomy were not so distinctive to deduce further speculations regarding global catastrophic events.

The invariability of Isoetaceae. The quillworts maintained their aspect mainly unvaried at least from the Early Triassic until today. Their evolutionary line traces more to the group of Carboniferous Sigillariaceae than the Lepidodendrales, even though this hypothesis is not completely acceptable. Moreover, this evolutionary line began in the Carboniferous or even the Devonian. It is, however, suggested that there is a close relationship between Triassic *Isoetites (brandneri*) and *Lepacyclotes (bechstaedtii)*.

The early polypetalous diversification of Selaginellales. In the Early Triassic, we



The Anisian (245 to 237 million years) Kühwiesenkopf Dead-Fish-Rift with the Lycopod coast: (1) Lycopia dezanchei with (2) Lyopodostrobus gaiae, (3) Selaginella leonardii, (4) Selaginella venieri, (5) Lepacyclotes bechstaedtii, (6) Isoetites brandneri and (7) Equisetites mougeotii. In the fish basin: Saurichtys, Bobasatrania, Dipteronotus and coelacanths. In the background: Neuropteridium elegans, Neuropteridium voltzii, Voltzia unescoensis, Gordonopteris lorigae, Alpia anisica, Bjuvia olangensis, Scytophyllum bergeri, Sagenopteris keilmannii and Aethophyllum stipulare.

Early-Middle Triassic lycophyta from the Alps

Pleuromeiales



Pleuromeia sternbergii Olenekian - Early Triassic



Isoetites brandneri Anisian - Early Middle Triassic



Early-Middle Triassic lycophyta from the Alps

Selaginellales

Lycopodiales



Selaginellites venieri Anisian - Early Middle Triassic

Lycopia dezanchei Anisian - Early Middle Triassic

encounter Selaginella species with isotophyllous (*Selaginellites leonardii*) and also anisophyllous leaves (*Selaginellites venieri*). The advantage of one or the other could not be explained satisfactorily. Furthermore, there is currently a nearly equal distribution of anysophyllos genera like *Heterostachys* and *Stachygynandrum*, or isophyllous species such as *Tetragonostachys*, *Selaginella* or *Ericetorum*. Their heterosporophylly is an old attribute, still remaining unvaried. The same is true for their often branching and low-growing characteristics.

The interesting evolution of *Lycopia.* One of the most surprising discoveries involved the sub-arborescent *Lycopia dezanchei*. It seems to have the same reduction history as the *Equisetites*. Both were widespread in the Early-Middle Triassic floras of Tethydealan Dolomites and can be defined as "Giant horsetails" or "Giant Lycopods". In addition, both have extant *Lycopodium* and Equisetes as their direct descendants and probably originated in the colossal Lepidodendron or Calamites trees of the Carboniferous. In contrast to Isoetites or Selaginellites, which were always small-sized, they became smaller over the million years until today as dwarf scrubbed plants in the copse of other vegetation. Astonishingly, Lycopia resembling lycopods were, until now, never recorded from other parts of the world or in the Early Triassic and following periods. Other midget characteristics have been noted in the Early Triassic, with the shrubby Voltzia conifer Aethophyllum stipulare in contrast to the arborescent Voltziales, as well as the current enormous difference in the growing habitus of giant Sequoia and shrubby dwarf pines.

The showdown of the dinosaurs. The Anisian layers of Piz da Peres also hold a rich ichnofauna dominated by Archosauriformes (*Chirotherium, Brachychirotherium*)



Lycopods are distributed all over the world. Club mosses like *Lycopodium* are homosporous, but spike mosses like Selaginellaceae and quillworts are heterosporous, with female spores larger than the male ones. Left: *Huperzia dentata*, right: *Lyopodium clavatum*.

and *Isochirotherium*) and some dinosauromorpha (*Sphingopus ladinicus* n. sp.; AVAN-ZINI & WACHTLER, 2011). The emergence of the dinosaurs was therefore linked to the transformation of vegetation. The increasingly widespread bushlands benefitted tetrapods, which were able to elevate themselves and walk two-legged. *Sphingopus*, with its reduced forelegs and three-clawed hind leg, achieved all the properties of true dinosaurs that followed a little later. In this Early Triassic, there was the dawn of a long-lasting alliance and partnership between animals and plants.

References

AMERON, H. W. J., van BOERSMA M. (1974). Vorläufige Untersuchungsergebnisse an älteren und neu aufgesammelten jungpaläozoischen Pflanzenfunden der Ostalpen (Österreich). – Carinthia II, 84: 9–15, Klagenfurt.

AMERON, H. W. J. van, BOERSMA, M. NIEDERMAYR,

G., (1976). Bericht über erste Pflanzenfunde aus der Trias-Basis der westlichen Gailtaler Alpen bei Kötschach (Kärnten, Österreich), Carinthia II, S. 103-112 Klagenfurt.

ANDREWS, H. N. (1961). Studies in Palaeobotany. Wiley and Sons Ed., New York and London, 487 pp.

ASH, S. R. (1972). Late Triassic plants from the Chinle Formation in North-Eastern Arizona. Palaeontology, 15(4), 598-618.

ANDREWS, H. N. (1979). Skilliostrobus gen. nov., a new lycopsid cone from the early Triassic of Australia. Alcheringa, 3, 73-89.

AVANZINI M., WACHTLER, M. (2011). *Sphingopus ladinicus* isp. nov, from the Anisian of Pragser Dolomiten (Southern Alps, Italy), in press.

BALME, B. E. 1963. Plant microfossils from the Lower Triassic of Western Australia. Paleontology, 6 (1), 12-40.

BANERJI, J. (1989). Some Mesozoic plant remains from Bhuj Formation with remarks on the depositional environment of beds. The Palaeobotanist, 37, 159-168.

BARTHEL, M. (2009). Die Rotliegendflora des Thüringer Waldes. – Veröffentlichungen des Naturhistorischen Museums Schleusingen

BECHSTÄDT, T. H. AND BRANDNER, R. (1970). Das Anis

Left: The recent club moss *Lycopodiella cernua* is found throughout the tropics and subtropics. It occurs along forest fringes, in young secondary forest, often in swamp margins, in grassland, on moist cliff-faces, hillsides and mountain slopes. Right: Anisophyllous *Selaginella kraussiana*.

zwischen St. Vigil und dem Höhlensteintal (Pragser und Olanger Dolomiten, Südtirol), Festband D. Geol. Inst., 300-Jahr-Feier Univ. Innsbruck, pp. 9-103.

BLANCKENHORN, M. (1886). Die fossile Flora des Buntsandsteins und des Muschelkalks der Umgegend von Commern. Palaeontographica, 32B, 117-153.

BRANDNER, R., HORACEK, M., KEIM, L., SCHOLGER, R. (2009). The Pufels/Bulla road section: deciphering environmental changes across the permian-Triassic boundary to the Olenekian by integrated litho-, magneto- and isotope stratigraphy. A field trip guide. In: GEO.ALP 6, S. 116 - 132.

BOCK, W. (1962). A study on fossil Isoetes. Journal of Paleontology, 36, 53-59.

BOSE, M.N. and ROY, S.K. (1964). Studies on the upper Gondwana of Kutch - 2. Isoetaceae. Paleobotanist, 12, 226-227

BRACK-HANES, S.D., THOMAS, B.A., (1983). A re-examination of Lepidostrobus Brongniart, Botanical journal of the Linnean Society.

BROGLIO LORIGA, C., FUGAGNOLI, A., VAN KONI-JNENBURG-VAN CITTERT, J. H. A., KUSTATSCHER, E., POSENATO, R. and WACHTLER, M. (2002). The Anisian macroflora from the Northern Dolomites (Monte Prà della Vacca/Kühwiesenkopf, Braies): a first report. Rivista Italiana di Paleontologia e Stratigrafia, 108, 381-390.

BROWN, R.W., (1939). Some American fossil plants belonging to the Isoetales. Journal of the Washington Academy of Sciences, 29 (16), 261-269.

BROWN, R.W. 1958. Paleobotany. – New occurrences of the fossil quillworts called Isoetites. Journal of the Washington Academy of Sciences, 48 (11), 358-361.

CANTRILL, D. J., WEBB, J. A. (1998). Permineralized pleuromeid lycopsid remains from the Early Triassic Arcadia Formation, Queensland, Australia. Review of Palaeobotany and Palynology, 102, 189-211.

CASSINIS, G., PEROTTI C. R. (2007). A stratigraphic and tectonic review of the Italian Southern Alpine Permian, Palaeoworld 16 – 140- 172

CHALONER, W. (1967). Lycophyta. In: BOUREAU, E. (Ed), Traité de Paleobotanique. Tome II. Bryophyta, Psilophyta et Lycophyta. Masson et Cie Editeurs. Paris, p. 437–802, 845 pp.

CHALONER. W. G., MEYER-BERTHAUD. B.(1983). Leaf and stem growth in the Lepidodendrales. Botanical Journal of the Linnean Society. 86, 135-48.

CLEAL, C. J. & THOMAS, B. A. (2009). Introduction to plant fossils. Cambridge University Press, Cambridge, 237 pp.

COLLINSON, M. E. (1991). Diversification of modern heterosporous pteridophytes. In BLACKMORE, S. and BARNER, S. H. (eds.). Pollen and Spores. Systematic Association Special Volume, 44, 119-150 (Clarence Press, Oxford).

COUPER, R. A. 1958. British Mesozoic microspores and pollen grains a systematic and stratigraphic study. Palaeontographica, 103B, 75-179.

DAUGHERTY, L. H. (1941). The Upper Triassic Flora of Arizona. Carnegie Institute, Washington Publications, 526, 1-108.

DE ZANCHE, V., FRANZIN, A., GIANOLLA, P., MIETTO, P., SIORPAES, C. (1992). The Piz da Peres Section (Valdaora-Olang, Pusteria Valley, Italy): a reappraisal of

the Anisian stratigraphy in the Dolomites. Eclogae Geologicae Helveticae, 85, 127–143.

DE ZANCHE, V., GIANOLLA, P., MIETTO, P., SIORPAES, C., VAIL, P. R. 1993. Triassic sequence stratigraphy in the Dolomites (Italy). - Mem. Sci. Geol., 45: 1 – 27.

DOBRUSKINA, I. A. (1974). Triassic Lepidophytes. Paleontogical Zhurnal, 3, 111-124.

DOBRUSKINA, I. A. (1985). Some problems of the systematics of the Triassic lepidophytes. Paleontogical Zhurnal, 19(3), 74-88.

EMMONS, E., (1856). Geological report of the Midland Counties of North Carolina. George P. Putnam and Co., New York, 352 pp.

EMMONS, E., (1857). American Geology, part 6. Sprague, Albany, New York, 152 pp.

ERKAN, E. (1977). Uran- und gipsführendes Permoskyth der östlichen Ostalpen, 1 Jahrb. Geol. B.-A. Band 120, Heft 2 S. 343—400 Wien.

FLICHE, P. (1910). Flore fossile du Trias en Lorraine et Franche-Comté. Ed. Berger-Levrault, Paris, Nancy, 297 pp.

FONTAINE, W.M. (1883). Contributions to the Knowledge of the Older Mesozoic Flora of Virginia. United States Geological Survey Monograph, 6, 1-144.

FRENTZEN, K. (1914). Die Flora des Bundsandsteins Badens. Mitteilungen des Großherzolichen Badischen Geologischen Landesanstalt, 8, 63-158.

FRITZ, A. BOERSMA, M., KRAINER, K. (1990). Steinkohlenzeitliche Pflanzenfossilien aus Kärnten.-Carinthia II, Sonderheft

FUGAGNOLI, A., POSENATO, R. (2004). Middle Triassic (Anisian) benthic Foraminifera from the Monte Prà della Vacca/Kühwiesenkopf section (Dont Fm, Braies Dolomites, Northern Italy). Bollettino della Società Paleontologica Italiana, 43 (3), 347-360.

GEYER, G. (1901). Geologische Aufnahmen im Weissenbachthale, Kreuzengraben und in der Spitzegelkette (Oberkärnten). Verhandlungen der k. k. geologischen Reichsanstalt, Wien.

GÖTZINGER, M. (1985). Mineralisationen in den Gutensteiner Schichten (Anis) in Ostösterreich, Arch. f. Lagerst.forsch. Geol. B.-A. ISSN 0253-097X Band 6 S.183-192 Wien, Juni 1985

GRAUVOGEL-STAMM, L. (1978). La flore du Grès à Voltzia (Buntsandstein supérieur) des Vosges du Nord (France). Sciences Géologiques, Mémoirs, 50, 1-225.

GRAUVOGEL-STAMM, L. 1993. Pleuromeia sternbergii (Münster) Corda from the Lower Triassic Germany – further observations and comparative morphology of its rooting organ. Review of Palaeobotany and Palynology, 77, 185-212.

GRAUVOGEL-STAMM, L., DURINGER, P. (1983). Annalepis zeilleri Fliche 1910 emend., un organe reproducteur de Lycophyte de la Lettenkohle de l'Est de la France. Morphologie, spores in situ et paléoécologie. Geologische Rundschau, 72, 23-51.

GRAUVOGEL-STAMM, L., LUGARDON, B. (2001). The Triassic Lycopsids *Pleuromeia* and *Annalepis*: Relationships, Evolution, and Origin. American Fern Journal, 91 (3), 115-149.

HALLE, T. G. (1907). Einige krautartige Lycopodiaceen paläozoischen und mesozoischen Alters. Kungliga Svenska Vetenskapsakademiens Handlingar, 7 (5), 1-17. HARRIS, T. M. (1935). The fossil Flora of Scoresby Sound, East Greenland. Meddelelser om Grønland, 112, 1-176.

HUEBER FM. (1983). A new species of *Baragwanathia* from the Sextant Formation (Emsian) Northern Ontario, Canada. Journal of the Linnean Society (Botany) 86, 57-79.

KARRFALT, E., (1986). New observations on the structure and development of Nathorstianella. Review of Palaeobotany and Palynology, 47, 1-8.

KANDUTSCH G., WACHTLER M. (2011). Fossile Pflanzen der Frühen Trias aus den Gailtaler Alpen, in press

KELBER, K.-P., HANSCH, W. (1995). Keuperpflanzen. Die Enträtselung einer über 200 Millionen Jahre alten Flora. Museo, 11, 1-157.

KELBER, K.-P. (1999). Neue Befunde über die Schachtelhalme des Keupers.- In: Hauschke, N. &

Wilde, V. (eds.): Trias - Éine ganz andere Welt, III.14: 355-370; (Verl. Dr. F. Pfeil), München.

KENRICK, P., CRANE, P.R. (1997). The Origin and Early Diversification of Land Plants: A Cladistic Study. Smithsonian Institution Press, Washington DC, 441 pp.

KELBER, K.-P., VAN KONIJNENBURG-VAN CITTERT, J. H. A. (1998). Equisetites arenaceus from the Upper Triassic of Germany with evidence for reproductive strategies. Review of Palaeobotany and Palynology, 100, 1–6. KRASSILOV, V. A., ZAKHAROV, Y. D. (1975). *Pleuromeia*

from the Lower Triassic of the Far East of the U.S.S.R. Review of Palaeobotany and Palynology, 19, 221-232.

KRASSILOV, V. A. (1978). Mesozoic lycopods and ferns from the Bureja basin. – Palaeontographica, Abt. B., 166 (1-3): 16-29.

KUSTATSCHER, E., WACHTLER, M. VAN KONIJNEN-BURG-VAN CITTERT, J. H. A. (2007). Horsetails and seedferns from the Middle Triassic (Anisian) locality Kühwiesenkopf (Monte Prà della Vacca) in the Dolomites (Northern Italy). Palaeontology, 50 (5), 1277– 1298.

LEE, H. H. (1951). On some *Selaginellites* remains from the Tatung Coal series. Science Record, 4 (2), 193-196.

LESCHIK, G. (1955). Die Keuperflora von Neuwelt bei Basel. II. Die Iso- und Microsporen. Schweizer Paläontologische Abhandlungen, 72, 1-70.

LINDLEY, J., HUTTON, W. (1836). The fossil flora of Great Britain. London, 208 pp.

LOOY, C. V., COLLINSON, M. E., VAN KONIJNENBURG-VAN CITTERT, J. H. A., VISSCHER, H., BRAIN, A. P. R. (2005). The ultrastructure and botanical affinity of end-Permian spore tetrads. - Int. J.Plant Sci., 166(5): 875-887.

LUGARDON, B., GRAUVOGEL-STAMM, L., DOBRUSKINA, I., (2000). Comparative ultrastructure of the megaspores of the Triassic lycopsid Pleuromeia rossica Neuburg. – Compt. Rend. Acad. Scienc., ser. II, fasc. A, Scienc. Terr. Plan., 330 (7), 501–508.

LUNDBLAD, B. (1948). Selaginelloid Strobilus from East Greenland (Triassic). Meddlilser fra Dansk Geologish Forening Kobenhavn, 11 (3), 351-363.

LUNDBLAD, B. (1950a). Studies in the Rhaeto-Liassic Floras of Sweden: I: 1 Pteridophyta, Pteridospermae, and Cycadophyta from the mining district of NW Scania. Kungliga Svenska Vetenskapsakademiens Handlingar, ser. 4, 1 (8), 5-82.

LUNDBLAD, B. (1950b). On a fossil Selaginella from the

Rhaetic Hyllinge, Scania. Svenska Botaniisk Tidskrift, 44 (3), 475-487.

MADER, D. (1990). Palaeoecology of the flora in Buntsandstein and Keuper in the Triassic of Middle Europe. [2 vols.]. Fischer, Stuttgart. 1582 pp. 71 fig. 103 plts.

MÄGDEFRAU, K. (1931). Zur Morphologie und phylogenetischen Bedeutung der fossilen Pflanzengattung Pleuromeia. Beiheften zum Botanischen Centralblatt, 48 (2), 119-140.

MÄGDEFRAU, K. (1956). Paläobiologie der Pflanzen, Stuttgart 1968

MENG FANSONG, (1996). Middle Triassic Lycopsids flora of South China and its palaeoecological significance. Palaeobotanist India, 45, 334-343.

MENG FANSONG (1998). Studies on Annalepis from Middle Triassic along the Yangtze Valley and its bearing on the Origin of Isoetes. Acta Botanica Sinica, 40 (8), 768-774.

MENG FANSONG, ZHANG ZHENLAI, NIU ZHIJUN and CHEN DAYOU (2000). Primitive lycopsid flora in the Yangtze Valles of China and systematics and evolution of Isoetales. 70-85. In: Changsha = Science and Technology Press, Hunan Province, 87 pp.

MENNING M., HENDRICH A. (2002). Stratigraphische Tabelle von Deutschland. Deutsche Stratigraphische Kommission

MOUGEOT, A. (1849). Observations sur le Caulopteris Lesangeana (Schimper et Mougeot) et nécessité de créer pour ce végétal fossile un genre nouveau dédié à Lesaing. Annales de la Societé d'Emulation des Vosges, 7, 7-16.

MOSTLER, H. (1972). Die permoskythische Transgressions-Serie der Gailtaler Alpen. — Mitt. Ges. Geol. Bergbaustud., 20, S. 143—149, Wien.

MÜNSTER G., (1842). Beiträge zur Petrefacten-Kunde, Band 5, In Commission der Buchner'schen Buchhandlung.

NATHORST, A. G. (1908). Paläobotanische Mitteilungen, 3. *Lycostrobus scotti,* eine grosse Sporophyllähre aus den rätischen Ablagerungen Schonens. Kungliga Svenska Vetenskapsakademiens Handlingar, 43,1–9.

PASSONI, L., VAN KONIJNENBURG-VAN CITTERT, J. H. A., (2003). New taxa of fossil Carnian plants from Mount Pora (Bergamasc Alps, Northern Italy). Review of Paleobotany and Palynology, 123, 321-346.

PIA, J. (1937). Stratigraphie und Tektonik der Pragser Dolomiten in Südtirol, Wien. Selbstverl.. 1937. XV, 248 S. : Ill., graph. Darst., Kt..

PIGG, K. B. (1992). Evolution of Isoetalean Lycopsids. Annals of the Missouri Botanic Garden, 79, 589-612.

PIGG, K. B. (2001). Isoetalean Lycopsid Evolution: from the Devonian to the Present. American Fern Journal, 91 (3), 99-114.

POSENATO, R. (2008). Anisian (Middle Triassic) bivalves from the Dolomites. N. Jb. Geol. Paläont. Abh.2008, vol. 247/1, p. 93–115, Stuttgart, January

POTONIÉ, H. (1902). Pleuromeiacae. In: Enger A (ed.),

Die natürlichen Pflanzenfossilien von Engler, Teil 4, 754-756, Leipzig.

POTONIÉ, H. (1904). Abbildungen und Beschreibungen fossiler Pflanzen-Reste der paleozoischen und mesozoischen Formationen, Königliche Preussische Geologische Landes-Anstalt und Bergakademie, II, 38-39, 1-15. RENESTO S., POSENATO R. (2003). A new Lepidosauromorph reptile from the Middle Triassic of the Dolomites (Northern Italy). Rivista Italiana di Paleontologia e Stratigrafia, 109(3), p. 463-474.

RETALLACK, G. J., (1975). The life and times of a Triassic lycopod. Alcheringa 1, 3-29. ISSN 0311-5518.

RETALLACK, G. J. (1997). Earliest Triassic origin of Isoetes and Quillwort evolutionary radiation. Journal of Palaeontology, 71 (3), 500-521.

RETALLACK, G. J., METZGER, C. A., GRAVER, T., JAHREN, A. H., SMITH, R. M. H., SHELDON, N. D. (2006): Middle-Late Permian mass extinction on land. – Geol. Soc. Amer. Bull., 118: 1398-1411.

ROTHWELL, G.W., ERWIN, D.M. (1985). The rhizomorph apex of Paurodendron; implications for homologies among the rooting organs of Lycopsida. American Journal of Botany, 72, 86–98.

SCHIMPER, W. P. (1869). Traité de Paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel. I. J. B. Baillère et Fils éd., Paris, 738 pp.

SCHIMPER, W. P., MOUGEOT, A. (1844). Monographie des Plantes fossiles du Grès Bigarré de la Chaine des Vosges. Ed. G. Engelmann, Leipzig, 83 pp.

SCHWEITZER H.-J. (1990). Pflanzen erobern das Land. Kleine Senckenberg-Reihe Nr. 18, Frankfurt am Main.

SCHWEITZER, H.-J., VAN KONIJNENBURG-VAN CITTERT, J. H. A. AND VAN DER BURGH, J., (1997). The Rhaeto-Jurassic flora of Iran and Afghanistan. 10. Bryophyta, Lycophyta, Sphenophyta, Pterophyta-Eusporangiatae and - Protoleptosporangiatae.Palaeontographica, 243B, 103-192.

SENOWBARI-DARYAN, B., ZÜHLKE, R., BECHSTÄDT, T., FLÜGEL, E. (1993). Anisian (Middle Triassic) Buildups of the Northern Dolomites (Italy): The Recovery of Reef Communities after the Perm/Triassic Crisis. Facies, 28, 181-256.

SEWARD, A. C. (1910). Fossil Plants II – A Textbook for students of Botany and Geology. Cambridge University Press, Cambridge, 624 pp.

SEWARD, A. C. (1913). A British Fossil Selaginella. New Phytologist, 12 (3), 85-88.

SEWARD, A. C. (1917). Fossil plants, III Pteridospermae, Cycadofilices, Cordaitales, Cycadophyta. University Press, Cambridge, 559 pp.

SEWARD, A. C. (1931). Plant life through the ages – A geological and botanical retrospect. University Press, Cambridge, 603 pp.

SKOG, J. E., HILL, C. R. (1992). The Mesozoic herbaceous lycopsids. Annals of the Missouri Botanical Garden, 79 (3), 648-675.

SNIGIREVSKAYA, N. S. (1980). Takhtajanodoxa Snig., a new link in evolution of lycopsids. In ZHILIN S.G. (ed.) Systematika i evolyutsiya vysshikh rastenii, Nauka, Leningrad, 45-53, 122 pp. [In Russian]

SPIEKER, T. (1854). *Pleuromeia*, eine neue fossile Pflanzengattung und ihre Arten, gebildet aus *Sigillaria sternbergi* Münst. des bunten Sandsteins zu Bernburg. Zeitschrift für die Gesammten Naturwissenschaften, 1852 (3), 177-191.

TAYLOR, W. A. (1989). Megaspore wall organization in Selaginella. - Pollen et Spores, 31: 251-288.

TAYLOR, T.N., TAYLOR, E. J. (1993). The Biology and

Evolution of plants. Prentice-Hall Inc., Englewood Cliffs, New Jersey (USA), 982 pp.

TAYLOR W.C., HICKEY R.J. (1992). Habitat, evolution, and speciation in Isoetites. Annals of the Missouri Botanical Garden, 79, 613-622.

TAYLOR, T.N., TAYLOR, E.L., KRINGS M. (2009). Paleobotany. The Biology and Evolution of Fossil Plants. Burlington MA, London, San Diego CA, New York NY, Elsevier/Academic Press Inc., xxi + 1230 pp.

THIEDIG, F., KABON, H. (2011). Neue fossile Pflanzenfunde von Pleuromeia sternbergii CORDA aus den Werfener Schichten (Olenekium-Stufe, Unter-Trias) im Oberostalpin Kärntens, Carinthia, Klagenfurt. 203-224.

THOMAS, B. A. (1992). Paleozoic herbaceous lycopsids and the beginnings of extant Lycopodium sens. lat. and Selaginella sens. lat. – Ann. Miss. Bot. Garden, 79: 624-631.

TINTORI A., POSENATO R., KUSTATSCHER E., Michael WACHTLER M. (2001). New Triassic fish faunas from paralic environments in the Alps. 3. International Meeting on Mesozoic fishes, Serpiano (CH)

TOLLMANN, A. (1968). Beitrag zur Frage der Skyth-Anis-Grenze in der zentralalpinen Fazies der Ostalpen. Verh. Geol. B.-A., Jg. 1968, S. 28–45, Wien.

TOLLMANN, A. (1968). Tektonische Karte der Nördlichen Kalkalpen, 2. Teil. — Mitt. Geol. Ges. Wien, 61 124—181, Taf. 1, Wien 1969.

TOLLMANN, A. (1972). Die Neuergebnisse über die Trias-Stratigraphie der Ostalpen. — Mitt. Ges. Geol. Bergbaustud., 21, 65—113, Innsbruck.

TOWNROW, J.A. (1968). A fossil Selaginella from the Permian of New South Wales. - J. Linn. Soc. London Bot., 61: 13-23.

TRYON, R. M., TRYON, A. F. (1982). Ferns and allied plants. Springer-Verlag, New York, USA, 875 pp. VAN KONIJNENBURG-VAN CITTERT, J. H. A., KUS-TATSCHER, E., WACHTLER, M. (2006). Middle Triassic (Anisian) ferns from the locality Kühwiesenkopf (Monte

Prà della Vacca) in the Dolomites (Northern Italy). Palaeontology, 49 (5), 943-968.

WACHTLER, M., (2010). About the origin of Cycads and some enigmatic Angiosperm-like fructifications from the Early-Middle Triassic (Anisian) Braies Dolomites (Northern Italy), Dolomythos, 1: 3-55, Innichen.

WACHTLER, M., KUSTATSCHER E., VAN KONIJNEN-BURG-VAN CITTERT J.H.A. (2010). Lycophytes from the Middle Triassic (Anisian) locality Kühwiesenkopf (Monte Prà della Vacca) in the Dolomites (Northern Italy). – Palaeontology, 53(3)

WACHTLER, M., (2011). Ferns and seed ferns from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, 57-79, Innichen

WACHTLER, M., (2011). Seed ferns from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, 88-104, Innichen.

WACHTLER, M., (2011). Evolutionary lines of conifers from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, 3-72 Innichen.

WANG Qi (2008). Proposal to conserve the name Pleuromeia with that spelling (fossil lycopsida). TAXON, 57 (2), 659-660.

WANG ZIQIANG, WANG LIXIN (1990). New plant as-

semblages from the bottom of the Mid-Triassic Ermaying Formation. Shanxi Geology, 5 (4), 303-318.

WANG ZIQIANG (1991). Advances on the Permo-Triassic lycopods in North. China. I. An Isoetes from the mid-Triassic in Northern Shaanxi. province. Palaeontographica, Abt. B, 222 (1-3), 1-30.

WANK, M., PRINZ, G., (1994). Ein Schuppenbaumgewächs bei Wunderstätten (St. Pauler Berge, Kärnten), Carinthia II, S. 467-468.

WARCH, A. (1979). Perm und Trias der nördlichen Gailtaler Alpen. - Carinthia II, Sh. 35, 111 S., Klagenfurt

WHITE, M. E. (1981). Cyclomeia undulata (Burges) gen et comb. nov., a Lycopod of the early Triassic strata of New South Wales. Records of the Australian Museum, 33 (16), 723-734.

WOOD, G. R., BEESTON, J. W. (1986). A late Permian lycopod cone Skilliostrobus sp. cf. S. australis Ash 1979 from Queensland. Geological Survey of Queensland, Publications, 387, 41-49.

ZEILLER, R. (1906). Bassin houiller et Permien de Blanzy et du Creusot. II. Flore fossile. Études Gîtes Minéraux de la France. - 265 pp., Ministère des Travaux 1979 from Queensland. Geological Survey of Queensland, Publications, 387, 41-49.