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

by

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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 Selaginella-like forms were represented by *Selaginellites leonardii* sp. nov., with its heterosporous strobili and *Selaginellites venieri* sp. nov., with characteristic anisophyllous shoots. Another group of extant Lycophyta, the Isoetales, were represented by *Isoetites brandnleri* 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 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-
TATSCHER, JOHANNA H. A. VAN KONIJNENBURG-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” (Elevenner) 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 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 Pleuroomeia-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 Dorn 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).
The Campill-Val Badia Member in the Eastern Southern Alps could be correlated with the Middle Buntsandstein, or more detailed Volpriehausen-Hardeggen-Formation of Germany (about 249.7 to 245.9 ± 0.7 Ma 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 a 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* and *Voltzia* remains. It is remarkable that other plant groups like ferns, seed ferns, conifers or cycads are still 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 succesions 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
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 vegetation-poor 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*),

Open lying isolated tree-trunks, root-horizons and ripple marks from Kühwiesenkopf - main plant layer.
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 semi-arid 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 CITTERN 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 one-metre 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 *Saurichthys 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 Fossilagerstätte 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 and abundant cycadophyta species, there is the most complete club moss association. The most abundant is the sub-arborescent *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 venieri*, 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 lycopsids 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 deposits, or in fossiliferous horizons located in the upper part of the formation (*Parallelodon esinensis*, *Pteria? sp.*, *Entolium kellneri* and *Chlamys (Praechlamys) cf. schroeteri*) (PONSENATO, 2008).

After this fish- and club moss-rich section, this lens becomes abruptly increasingly thinner to the end in well-preserved ripple-marks 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)
- *Lycopodostrubus 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 *Bowiea, Ceratozamia, Dioon, Encephalartos, Stangeria* and *Zamia*.

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

Seed ferns were dominated for a long time by *Peltaspermum-Scythophyllum-Thuinfeldia* 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.
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 PONTIE, 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


#### Type horizon and age

Lower Triassic, Induan-Olenekian, Werfen Formation

#### Repository

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

#### Diagnosis

Sub-arborescent lycophyte with unbranched, erect trunk. Rhyzomorphic roots are typically four-lobed and the stem in the lower part is covered with traces of scars from fallen leaves. Foliage in the upper part is lanceolate, 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; GRAUVOGEL-STAMM, 1993; GRAUVOGEL-STAMM & LUGARDON, 2001; RETALLACK, 1975).

The consistent *Pleuromeia* findings from Carinthia comes from the Induan-Olenekian Werfen-Formation (Campill-Val Badia-Membe), 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 *Pleuromeia sternbergii* 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.
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.
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 moss-rich vegetation was encountered (*Lycopodia 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 Lycopoidales 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 dissatisfaction 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 all-destroying 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.
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-Ilyrian

**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 short-stemmed 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) (RETTALLACK, 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 Lycopodiales bearing creeping and protruding roots, such as Lycopiaceae, Selaginellaceae and Carboniferous Lepidodendrales.

**SYSTEMATIC PALAEONTOLOGY**

Division Lycophyta
Order Isoetales 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-Ilyrian

**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 *Lycopodium*.

**Stem:** *Lepacyclotes bechstaedti* spread into large clusters by forming 4 to 10 cm high and wide rosettes. Holotype KÜH 1285 shows a mainly complete preserved side-faced 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 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.

**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 µm), 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 circulalis* 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* (EMMONS, 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 bechstaedti* sp. nov. Holotype. Mainly complete plant seen from the lateral side.
2) KÜH 2142. *Lepacyclotes bechstaedti* sp. nov. Plant with crowded foliage.
3) KÜH 547. *Lepacyclotes bechstaedti* sp. nov. Paratype. Plant seen from the upper side.
4) KÜH 007. *Lepacyclotes bechstaedti* sp. nov. Paratype. Specimen with an inner circle of elongated leaf fragments.
Different fructifications from the Lower Triassic of Australia, belonging probably to sub-arborescent lycophytes, have been described as Tomiostrobus, Cylastrobus, 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 worldwide-ranging 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 (An nalepis) 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 fleshy and buried completely in marshes or swamps. Lepacyclotes bechstaedtii and Isoetites brandneri have only been found in the Küh wiesenkopf “Dead Fish-Basin”, together with the other lycophytes Lycopia dezanchei and Selaginellites leonardi. 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, Dipterontus and Saurichyts, 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 bechstaeeldii: (a) Entire plant (KÜH 1285), (b) interior view of the plant (KÜH 1285), (c) upper view (KÜH 007) and (d) single sporophyll.
Genus Selaginellites ZEILLER, 1906

Extant Selaginellaceae belong to a widely distributed family of herbaceous lycopods, well-adapted to various climate conditions and soil types. Some species can resist extreme weather, such as those prevalent in alpine or arctic 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 Selaginellaceae (KORALL & KENRICK, 2002). Anisophyllly 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. WACHTLER 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 apparente 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 leonardi. Mainly complete branch.
5) PIZ 165. Selaginellites leonardi. 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 x 0.3 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 trilette 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 trilette 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 immature mass of microspores, suggesting that the sporophylls were probably distributed in rows of microsporophylls and megasporephyls (WACHTLER ET AL. 2010).

**Selaginellites venieri sp. nov. WACHTLER, 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 denticate.

**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,
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 leonardi, 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 (Selaginellaanasazia), 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 Lyco-

podites scanicus) and China (Selaginellites yunnanensis). They have some affinities with Selaginellites leonardii and Selaginell-

ites venieri, but not enough to classify them as conspecific. The most closely resembling species to Selaginellites leonardii is Rhae-
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 anisophyllous 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, sun-exposed, 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 cycadophyta.
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-Illrian

Diagnosis
Sub-arborescent lycophyte with wide creeping rhizomes, rooting at irregular intervals and covered by subtile 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 mm-wide 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.

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 scale-like 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-IIlyrian

**Diagnosis**

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.
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 diamond-shaped decurrent leaf base. This is most evident when the leaf has been absised and a characteristic leaf cushion remains, called "Blattpolster" by older authors in German. Comparing *Lycopia* to other Triassic lycopods, 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 (TAYLOR 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 absised 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*,

2) PIZ 98. *Lycopodostrobus gaiae* (Holotype). Detail of sporophylls.


4) PIZ 213. *Lycopodostrobus gaiae*. Strobilus with attached sterile leaves of *Lycopis dezanchei* on the lower part.

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 *Equi-
setites*” from the same Anisian strata. *Lepidostrobus* is a loosely defined morpho-
genus, 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 *Lepidostro-
bus* 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 Selaginellales 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 brandii* 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).
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 humid-loving 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 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. ji-aochengensis and P. hattai*), even occurring in Australian locations from the former
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 lycopsids 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 Marattiaceae, Gleichenaceae, Osmundaceae 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 (*Lyco-pia, 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-Cretaceous boundary.

**The importance of the new lycopod species from Piz da Peres.** The discovery of...
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 florals, like the club moss vegetation capable of surviving high-stress conditions of soil mineralization 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
Early-Middle Triassic lycophyta from the Alps

**Pleuromeiales**

*Pleuromeia sternbergii*
Olenekian - Early Triassic

*Megasporophyll*  
*Whole plant*

*Pleuromeia sternbergii*  
Adaxial view

**Isoetales**

*Isoetites brandneri*
Anisian - Early Middle Triassic

*Adaxial view*

*Lepacyclotes bechstaedtii*
Anisian - Early Middle Triassic
Early-Middle Triassic lycophyta from the Alps

**Selaginellales**

- **Selaginellites venieri**  
  Anisian - Early Middle Triassic
- **Selaginellites leonardi**  
  Anisian - Early Middle Triassic

**Lycopodiales**

- **Lycopia dezanchei**  
  Anisian - Early Middle Triassic
encounter Selaginella species with isoto-
phyllous (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 anysophyllous genera like Heterostachys
and Stachygynandrum, or isophyllous spe-
cies such as Tetragonostachys, Selaginella
or Eriocarpus. 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 discover-
ies involved the sub-arborescent Lycopia
dezanchei. It seems to have the same re-
duction 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
Equisetites as their direct descendants and
probably originated in the colossal Lepido-
dendron or Calamites trees of the Carbon-
iferous. In contrast to Isoetites or Selagin-
ellites, 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. Oth-
er 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
habit 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 Archosauroid-
formes (Chirotherium, Brachychotherium

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: Lycopodium clavatum.
and Isochirotherium) and some dinosauro-
morphs (Sphingopus ladinicus n. sp.; AVAN-
ZINI & WACHTLER, 2011). The emergence
of the dinosaurs was therefore linked to the
transformation of vegetation. The increas-
ingly widespread bushlands benefitted tetra-
pods, 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 Trias-
sic, there was the dawn of a long-lasting al-
liance and partnership between animals and
plants.

References
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 Galttal Alpen bei Kötschach
(Kärnten, Österreich), Carinthia II, S. 103-112 Klagen-
furt.
ASH, S. R. (1972). Late Triassic plants from the Chinle
Formation in North-Eastern Arizona. Palaeontology,
15(4), 598-618.
ANDREWS, H. N. (1979). Skiliiostrobus gen. nov., a
new lycopsid cone from the early Triassic of Australia.
Alcheringa, 3, 73-89.
AVANZINI M., WACHTLER, M. (2011). Sphingopus la-
diniclus 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 envi-
ronment of beds. The Palaeobotanist, 37, 159-168.
Waldes. – Veröffentlichungen des Naturhistorischen Mu-
seums Schleusingen

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


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


