ABOUT THE ORIGIN OF CYCADS
AND SOME ENIGMATIC ANGIOSPERM-LIKE
FRUCTIFICATION FROM THE
EARLY-MIDDLE TRIASSIC (ANISIAN)
BRAIES DOLOMITES (NORTHERN ITALY)

by

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by
Michael Wachtler

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Abstract

Background.
The fossil record of Cycadales and early Angiosperm-like fructifications is fragmentary. Many of our efforts to understand the evolution of this enigmatic plant group are hampered by the poor fossil record. Beginning from 1999 the author recovered large quantities of well-preserved cycadalean remains and also other enigmatic strobili and fructifications in Early Middle to Middle Triassic (Anisian) sediments. Therefore it was possible to view their unusual story in a new light.

Methodology and Paleobiology.
Several Anisian Cycads and other fructifications with sometimes unknown affinity were described and the paleobiology of the habitat investigated. Peresia tannae gen. nov. n. sp. is an enigmatic fructification with spirally free arranged hammer like pollen-scales on the upper part of a branch and flowerlike structures on the lower part. The single organs give the idea of densely reduced and compressed small fern-fronds. Peresia raetiae gen. nov. n. sp. bears microleaves with aggregated sporangia on the lower surface, near the apex. However, its fleshy wedge-shaped scales resemble single male cycad scales. Ladinia simplex n. gen. n. sp. is suggested to be a transition form between ferns and cycads. It bears entire leaves with an acuminate to rounded apex. Cataphyll-like sterile leaves and ovule-bearing organs with two rows of ovules on the abaxial surface form the megasporophyll. Bjuvia primitiva n. sp. is thought to be a real cycad with small, whole to sometimes-frayed leaves. Bjuvia olangensis sp. nov. was the largest growing cycad in the Early-Middle Triassic Dolomites. It produced huge, lacerated to segmented leaves. The stems ended in a single strong taproot and branching coralloid roots. Dioonitocarpidium cycadea n. sp. and Dioonitocarpidium loretzi n. sp. are female sporophylls belonging to Bjuvia primitiva and Bjuvia olangensis. Thetydostrobus marebbei gen. nov. sp. nov. is suggested to be the male cycadalean cone pertaining to Bjuvia. It resembles modern cycad-strobili with its microsporophylls arranged spirally on a central axis and microsporangia on the lower surface, near the apex. Nilssonia braiesensis n. sp. has clear-segmented leaflets leading to the typical foliage-system of today’s Cycadales.

Conclusions/Significance.
This 241.5 million year old world represents the most complete ancient cycadalean world ever found. All the main parts of cycads, such as the leaves, stems, roots, male and female strobili, but also the juvenile and mature life-circuit as well as animal association and also possible parental plants, were
discovered in large quantities. Research on their characteristics allows a fairly complete reconstruction of the life history and associated habitat. It is of particular importance to phylogenetic and cladistic studies that in the Early to Middle Triassic the evolution-cycle of cycads was nearly finished and they differed only in small details from the extant species. The approach to the relationships in cycad evolution and the early angiosperm habitat were studied and hypotheses established. Future studies and new fossil records would provide more clarity about several questions concerning unresolved problems.

Online: May 2010.

Key words: fossil cycads, early angiosperms, Dolomites, Italy, Middle Triassic, Anisian.

Introduction.

The geological and paleontological richness of the Braies Dolomites has been well known since 1875 when the German geologist Hermann Loretz described various marine invertebrates (brachiopods, molluscs). He was supervised by Edmund von Mojsisovis (1882) with his basic work about ammonoids. But the most widely accepted long-standing research was edited by Julius Pia in 1937 (Stratigraphie und Tektonik der Pragser Dolomiten in Südtirol). Further studies (Bechstädt and Brandner, 1970; De Zanche et al., 1992) completed the knowledge about this area in the Eastern part of the Dolomites, which UNESCO included in the world heritage list in 2009 for its geological beauty.

Surprisingly until 1999 only a few plant fragments were described from this extensive area between the Braies Valley and the Gadertal Valley. (Fig. 1) That year Michael Wachtler discovered the first rich plant horizon under the crest of Kühwiesenkopf. (Fig. 2a) In subsequent years he extended his research to the nearby Hochalpenkopf, Maurerkopf, Flatschkofel, Dreifingerspitze, all over the borough of Olang, then around the Piz da Peres mountain up to Marebbe (Fig. 2b) covering a distance of over 20 km. Everywhere inside this area in typical Anisian (lower Middle Triassic) successions he found plant fossil bearing levels. They contained rich Early Mesozoic floras, but also reptile remains, new ichnofaunas, and also marine biota (e.g. bivalves, brachiopods, ammonoids and fish skeletons). The first results were published in 2002 (Broglio Loriga et al.).

Geological age.

In the area studied the plant-bearing beds begin about 75 m above a massive carbonate platform previously known as ‘Algenwollenkalk’, and now attributed to the Gracilis Formation (De Zanche et al. 1992; Gianolla et al. 1998). The following, so-called Dont Formation, is more than 200 m thick and bears several lens-shaped plant horizons that reach a consistent thickness of about one metre. They alternate with silty and marly limestone or carbonate layers, in which only sparse terrestrial plant remains occur. All the successions were deposited in an original basin, lagoonal, peritidal or continental habit. Studies on brachiopods (Bechstädt and Brandner 1970) and foraminifers (Fugagnoli and Posenato 2004) suggest a Pelsonian age for the studied section; integrated studies between palynomorphs and ammonoids narrow the time interval for the deposition of the fossiliferous horizon down to the boundary between the Middle and Upper Pelsonian (Kustatscher et al. 2006).

But also in the slightly younger Richthofen Conglomerate (Avanzini, Gianolla and Neri, 2007) and Morbiac Dark Limestone (Delfrati and Farabegoli, 2000), both Illyrian in age, plant-remains could be found, often inside rich ichnofaunas also containing dinosauro-morph trample layers.

Over the years an extraordinary rich plant assemblage has come to the surface with several highlights as its abundance of Lycophytes with four new species up to now (Isoetites brandneri, Lepacyclotes bechstaedtii, Selaginellites leonardii) and especially the arborescent Lycopodium dezanchei as an interesting connecting link between Carboniferous and recent lycopodales. But also Sphe- nophyta (Equisetites) and Coniferales (several Voltzia-genera, Aethophyllum), as well as new fern species (Gordonopteris lorigae) were discovered. Up to now more than 30 different plants document the importance of this novel ‘Fossillagerstätte’. Some, such as the ferns Neuropteridium and Anomopteris,
or seedferns like Sagenopteris and Scythophyllum, were already known from the lower Triassic to lower Middle Triassic floras from the German Basin. Other very common species in the German Buntsandstein like the Lycophyte Pleuromeia are as yet completely absent in the Braies Dolomites.

One of the most significant plant assemblages in the Piz da Peres territory belongs to the group of Cycadophyta. They are present in these Anisian strata – in contrast to other areas – in an enormous abundance and variety, and occupy nearly 25% of all flora-elements. Over the years, based on systematic research, it was possible to compile an important collection of nearly all the significant parts of primitive Cycadales, beginning from the roots, to stems and cataphylls, different leaf types and the up to now enigmatic male and female cones. Because of the worldwide interest in the evolution and the origin of this mysterious plant group this work looks in detail at the fossil cycads from the Piz da Peres area.

Repository.

Wachtler’s plant collection is stored at the Naturmuseum Südtirol in Bozen/Bolzano (Italy) or in the Museum Dolomythos at Innichen (San Candido). They all have the specimen code “KÜH” (for Kühwiesenkopf) or PIZ (For Piz da Peres) followed by a serial number.

Materials and Methods.

The research is based on more than 1,000 rock-slabs of cycadalean parts ranging from only a few centimetres up to one metre or more. Only in rare cases, and with further evolution, Cycad-leaves get cuticles.

Up to now (2009) the Cycad-fossil record is characterized by:

- Bjuvia primitiva leaves: about 400 pieces
- Bjuvia olangensis: about 300 pieces
- Nilssonia braiesensis: about 50 pieces
- Ladinia simplex: about 200 pieces
- Bjuvia trunks: about 10 pieces
- Dioonitocarpidium: about 30 pieces, (including about 10 whole cones)
- Thetydostrobus: (about 10 pieces)
- Peresia: (about 20 pieces, mostly single scales)

With a long-lasting sense of observation and statistical analysis an interesting Early-Mesozoic life-world could be understood. In this rapidly changing world, open questions were posed to define until when one leaf or fertile organ could be left in one genera and when it may be reasonable to put it in another. However, the enormous number of slabs was useful. Whereas in other places only a few poorly preserved parts were recovered, the Piz da Peres-area brought innumerable Cycad parts to light.

In any case, comparison with specimens from several museums and other localities in Europe was helpful, where fertile and sterile material could be re-examined. This also counts for all the valuable literature that has been produced over the centuries by many researchers. Analysis and new hypothesis from other authors (Crane, 1988, Grimm, 1999) about cladism and developmental pathways of cycads between early origins and their present-day counterparts was very useful. Further analysis would enlarge the scope of knowledge about this early paradise.

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 8.0.

Systematics.

Paleoecology and Paleoclimatology.

Much observational research has been conducted by the author over many years, leading to the recognition of some interesting paleo-ecological and paleo-environmental effects. One of the most surprising diagnoses on this ancient, over 241 million year old habitat, was the diversification that occurred in an extremely short time. This could be noted not only on plants, but the layers accompanying rich ichnofauna also made a rapid transformation. Newly discovered dinosauromorph to dinosauriformes tracks and skeletons suggest that in this time a complete modification of terrestrial life occurred. It is not the purpose of this publication to go into more detail about a previous Permo-Triassic crisis but rapid mutations and variations are, in fact, clear.

Some lens-shaped layers understandably contain a higher percentage of cycads. Conifer-rich strata contain few cycad leaves. The rock fall precipices of the western part from Piz da Peres contains, in some layers, a typical rainy season anthesis with a dominance of male pollen-organs. More young plants and fructifications were found there. The long-ranging mountain from Kühwiesenkopf to Drei Fingerspitze, on the other hand, was richer in fully-grown female organs as well as large cycadalean leaves.

Fig. 2: Plant-bearing horizons on Kühwiesenkopf (a) and Piz da Peres (b).
The life cycle of female strobili is usually much longer than that of males. When pollination has finished cycad sporophyll decays and is destroyed by the environment or animals. The female cone, on the other hand, continues to develop until the seeds are mature enough to be released. This seasonal variation was useful for the classification and understanding of the primitive evolution of male strobili.

Many cycad leaves bear traces of have been eaten by small animals, probably insects. It may be suggested that insect-pollination occurred and was a new development in evolution and an advantage to other plants. (Stevenson, D.W., et. al., 1999.) Marks and aggregations have been found on several cycad leaves that could be interpreted as coprolites.

In the Early Permian numerous large land plants like *Sigillaria, Calamites, Lepidodendron* vanished, creating empty ecological niches. They were replaced in the Triassic by shrubby to low growing lycophytes (*Lycopia* and *Isoetites*). The same occurred in the German Buntsandstein Basin with the also bushy lycophyte *Pleuromeia*. The big horsetail trunks (*Calamites*) now consist of moderately growing *Equisetites*. The Palaeozoic ferns like *Pecopteris* were replaced in the Middle-Triassic Piz da Peres landscape by low growing ferns like *Anomopteris, Neuropteridium*, and *Gordonopteris*, the seedferns *Alethopteris, Odontopteris, Neuropteris, Sphenopteris* by the Triassic genera *Scythophyllum* and *Sagenopteris*. Most of the large wood plants now consist of conifers from the *Voltzia* group. Above all, the rapidly expanding cycadophytes became more and more dominant. Also in the intercontinental Central European Basin we have nearly the same situation and often the same plants, although this massive Cycadophyta flora is missing. The evolutionary event caused by the elimination of the large land plants of previous times let a group of dinosaurs morph animals develop who, by increasing their height with erected bodies, were more able to survey the landscape. They could therefore reach more of the nutritious plants than the others. In the dark and dense woods of the Carboniferous period all that was a disadvantage.

Just as important as insect pollination was the new strategy of the small compressed and gradually fusing fertile microleaves as a basis for all Cycad cones and probably the origin of angiosperm ascension. A new repository for pollen and ovules was invented. The new order of Peresiaceae constitutes a new milestone in plant evolution. Through them it is not only possible to understand the formation of male and female cycad cones but also the evolution of bisexual flowers divided into stamen and carpel. Observing the paleoecological environment it can be deduced that the flora and fauna was changing more rapidly than has ever been seen since in the subsequent millions of years. The causes of all this have been a strange mystery until now.

**Characters of higher gymnosperms.**

The history of the evolution of “higher” seed plants, like cycads, bennettitales and angiosperms is one of the most exciting chapters in fossil records. They have many characteristics, which are unique in the plant kingdom. The only certainty is that their ancestors are to be found in Paleozoic ferns or seedferns. Up to now researchers have argued whether higher gymnosperms have more elements from ferns (like Marattiales) or seedferns (the most commonly mentioned group are the Medullosaceae). But only new fossil findings could contribute to determining evolution tendencies. (Kenrick, P. and Crane, P.R., 1997).

Cycads have a fossil record that dates back at least 250 million years, making them the oldest crown-clade of seed plants. There is some controversy over older cycad fossils that date Permian and the late Carboniferous period, although the extent to which it radiated is unknown because relatively few fossil specimens have been found (Brenner, E. et. al. 2003). The cycads had their heyday during the Mesozoic era, and have been declining in terms of richness in species and ecological importance ever since. They are paradoxical in that they obtusely have some primitive fern-like features and other characteristics that until now were considered advanced (Jones, 2002).

The earliest convincing record of bennettitaleans comes from the Late Triassic period (Molteno Formation in South Africa and Lunz, Austria.)
Some authors date back the origin of angiosperm-like plants to the Triassic period although their triumphal procession did not start before the Cretaceous period. It is central to any discussion of angiosperm evolution precisely which characteristics constitute an angiosperm and what features may be considered preangiospermic. Both questions remain difficult to resolve and find simple answers to.

Details used to separate angiosperms from other seed plants include the enclosed nature of the ovary, the presence of flowers, vessels in the xylem and in the phloem, double fertilization, bitegmic ovules (with two integuments) and the presence of endosperm and tectate pollen. (Taylor Th. N., Taylor E., 1993). In any case, angiosperms are the most dominant group in today’s flora and a success story in the plant kingdom.

In contrast to the multitudinous angiosperms, modern cycads now include only eleven genera and 292 species distributed across the warm, tropical and subtropical environments of the Americas, Africa and Australasia. In any case, they are the most species-rich group of gymnosperms after conifers (Zgurski et. al., 2008). Virtually all extant genera have restricted geographical ranges, which reflect both relict and endemic distributions. Cycads are long-living, perennial, unisexual plants, which develop cones and reproduce seeds and are characterized by a large crown of compound leaves and a stout trunk. (Jones, 2002)

The living cycads are placed in three families: the Cycadaceae, the Stangeriaceae and the Zamiaceae.

Female cones consisting of loosely organised sporophylls and lacking a central axis characterize the Cycadaceae. They bear their ovules on the margins of a basal stalk-like structure.

The Stangeriaceae contains two genera: Stangeria, with its pinnate, fern-like leaves and Bowienia with bipinnate leaves. In both genera cataphylls are absent or produced only erratically. The family of the Zamiaceae is divided into two subfamilies, the Encephalartoideae and the Zamioideae. All Zamiaceae have cataphylls, flat leaflets and cones borne terminally or laterally on the main stem. The seeds are attached above the sporophyll stalk (Jones 2002).

The main characteristics of Cycads, sometimes also unique in the plant kingdom, are:

**Monophyletic group.** It is suggested that all cycads derive from a single, common ancestor.

**Dioecious plants.** All cycads are unisexual, having male and female reproductive parts on different plants. The unisexual system, with male and female cones on different plants, is one of the main characteristics of cycads and was the origin of a new efficient reproduction-system.

**Presence of cycasin.** All extant genera of cycads produce the mythylazoxymethanol glycoside cycasin. This compound is not known to occur in any other gymnosperm. (Crane P. 1988)

**Girdling leaf traces:** In all cycads some leaf traces arise from the stele on the side of the stem opposite the leaf that they supply. This is also unique in gymnosperms.

**Leaves:** The leaves of all cycads expect Bowenia are pinnate and lack a terminal segment. Only Bowenia leaves are bipinnate.

**Simple ovulate cone.** All extant cycads produce simple, clearly defined clusters of megasporophylls (cones) and in all genera except Cycas the cones are determinate. The sporophylls are usually biovulate or multiovulate.

**Trichomes.** All extant cycads have branched or unbranched small hairs on the apex of the cones or emerging leaves.

**Ppetiole.** All leaves of cycads have a basal woody structure.

**Microsporangia on lower surface.** The microsporophylls of cycads are flattish and obovate in their outline and each one bears microsporangia on its lower surface.

**Roots.** All cycads basically produce two types of roots. A primary thickened, fleshy and elongated taproot and special, upwards growing, branched roots, known as coralloid roots. These roots contain symbiotic cyanobacteria, which can fix nitrogen from the atmosphere.

**Stem.** Cycads have a stem or trunk, which becomes larger, as the plant gets older. These structures range from being subterranean and almost tuberous or bulbous. Cycads stems are pachycaulous.
Suggested evolving-concepts of Paleozoic-Early Mesozoic Cycads

Female cones - Dioonitiocarpidium

Male and female cones - Peresia

Peresia
Evolving of female plant

Peresia
Evolving of male - female plant

Ladinia-taeniopteroid female cone-evolving

Ladinia - Peresia male - female evolving

Bjuvia-Dioonitiocarpidium female cone

Bjuvia - Thetydostrobus male cone

Bjuvia-Nilssonia Cycas plant
Systematic Paleontology
Subdivision: Filicales? Bower, 1899
Pteridospermophyta? F.Oliver & D.H.Scott 1904
Order unknown
Family indet.
Genus *Peresia* gen. nov. WACHTLER, M.

Generic diagnosis.
Enigmatic fructifications with fertile appendices suggesting reduced microfronds, distally sprouting from slender stems.

Etymology.
The genus is named after the Piz da Peres Mountain in the Dolomites, where they were first found.

*Peresia raetiae* WACHTLER, sp. nov.

Holotype.
PIZ 155

Paratypes.
PIZ 617, (microleaves) PIZ 209 (sporangia)

Material.
PIZ 620, PIZ 111, PIZ 557, PIZ 614

Etymology.
Named after Celtic-Raetic goddess Raetia, Mother Nature.

Type localities.
Piz da Peres

Type horizon and age.
Dont-Formation.
Lower to Middle Triassic, Anisian, Pelson

Repository.
Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

Diagnosis.
Scale-like appendices arranged helically on a central axis. Single round-bodied scales made up of several microleaves on a combined stalk, distally covered by unbranched trichomes. Elongated pollen sacs on the lower surface of the apex.

Description.
**Sporophyll:** Scales arranged helically on up to 12 cm-long stalks. PIZ 155 consist of a 12 cm-long, 0.5 cm-wide not completely preserved axis from which three pollen-scales branch. Distance from each organ to the other on the same side 5 mm. Rupture nipples suggest that many fertile scales occur on both sides of the stalk. This could be observed also on other pieces (PIZ 620).

**Fertile scales:** Up to 30 mm-long, at apex 20 mm-wide scales. Stalk 5 mm-wide perpendicular from a central axis, enlarging continuously up to 1 cm before crossing over to the spore-bearing zone. The scales on the apex bulge, suggesting a hammer-like appearance. (PIZ 209, PIZ 613).

**Microleaves:** 10 - 5 mm x 2 - 3 mm containing 4-6 microspores on the lower surface aggregated on two rows at a median axis. About 10 to 12 microleaves form an entire fertile scale. On the lower surface of each 8 - 10 mm-long 1 – 2 mm-wide micro-leaf (PIZ 617) several microsporangia could be observed. The distal surface of each micro-leaf is covered with a ramentum of filamentous trichoms. They are unbranched. (PIZ 617, PIZ 557, PIZ 111).

**Microsporangia:** Elongated 1 mm x 0.5 mm on the apex of microleaves forming a dense 4 to 8 mm-wide cluster all over the scale. Microsporangia on the abaxial part of microleaves.

Remarks.
Up to 20 parts and entire strobili of *Peresia raetiae* were found. Because no other similar
1) PIZ 155 *Peresia raetiae*. Sporophyll with 3 attached scales. Slab 6 x 6 cm. Scales 20 mm, petiole 90 mm.
2) PIZ 155 *Peresia raetiae*. Single scale covered with trichomes - 20 mm x 15 mm at apex. 5 mm at base.
3) PIZ 620 *Peresia raetiae*. Scale 30 mm long. 25 mm at apex 3 mm scale stalk.
4) PIZ 620 *Peresia raetiae*. Entire sporophyll, stalk 80 mm x 2 mm with attached scales.
pollen organs are known on the fossil record, comparisons are difficult. If they are viewed with their fleshy corpus, they look like a solitary Cycas scale. Although Thetydostrobus, occurring in the same strata, forms a clearly defined cone, whereas Peresia raetiae consists only of loosely arranged scales on a stalk. Other perceptions are obtained if we suggest that Peresia scales are an initial stage of the cone-forming process for the male Cycadales fructification. With the Thetydostrobus cone, Peresia scales also divide the hairy apex. Sometimes Cycadalean Thetydostrobus also seems to be formed of densely arranged microleaves and not made up of a single scale like today’s cycads.

**Systematic Paleontology**

Subdivision: Filicales? Bower, 1899
Pteridophyta?
Order unknown
Family indet.

*Peresia tannae* WACHTLER, sp. nov.

**Holotype.**

PIZ 553.

**Paratype.**

PIZ 207.

**Etymology.**

*Peresia tannae* is named after Tanna, the queen of rocks in old Ladinian myths.

**Type localities.**

Piz da Peres

**Type horizon and age.**

Dont-Formation.
Lower to Middle Triassic, Anisian, Pelson.

**Repository.**

Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

**Diagnosis.**

Shrubby plant with scale-like appendices distally sprouting from slender stems. Upper part of branch holding scales with microsporangia, lower part with flowerlike fructifications. Single scales made up of microleaves with isolated ovules on the abaxial side.
1) PIZ 617 *Peresia raetiae*. Scale 20 mm x 18 mm. Microsporangia at leaf-like structure on apex.
2) PIZ 111 *Peresia raetiae*. Single scale 20 mm x 20 mm
3) PIZ 613 *Peresia raetiae*. Single scale, bearing (female?) ovules laterally on the microleaf. 18 mm x 17 mm
4) PIZ 209 *Peresia raetiae*. Scale 30 mm x 18 mm, 4 mm basal stalk. Abaxial part with pollen bearing portion at apex (3 mm) Pollen 1 mm x 0.5 mm
5) PIZ 557 *Peresia raetiae*. Scale 30 mm x 20 mm with leaf-like organs, fertile part on upper side.
6) PIZ 209 *Peresia raetiae*. Abaxial part with pollen-bearing portion at apex (20 mm a 3 mm) Pollen 1 mm x 0.5 mm
Description.

**Plant:** Up to 20 cm-tall bush with frequently forking slender branches. Fertile organs sprout distally on each twig. The shrub is divided into an upper zone with microsporophylls and a lower zone with budlike to flowerlike organs.

**Petiole:** Up to 30 slender sprigs, 2 mm-thick, but up to 5 cm-long covered with nipples or short leaves (PIZ 553). On each a single fertile organ.

**Sporophylls:** Fertile scales arranged distally, subdivided into an upper part with typical wedge-shaped fructifications containing microsporangia and lower branches with a flower-like arrangement of megasporangia.

**Fertile scales:** Upper hammer-like microsporangia-structures 8 mm-long to 15 mm-wide, lower megasporangia-scales 15 mm-long, 12 mm-wide.

**Microsporangia:** On the apex of upper part forming a dense 6 mm-broad cluster all over the scale. Microsporangia on the abaxial part of the microleaves.

**Macrosporangia:** Microleaves of the flower 10 - 5 mm long x 1 -3 mm containing 4-6 sporangia on the lower surface aggregated on two rows at a median axis. About 12 microleaves form an entire flower. Sporangia on lower part 1 mm x 0.5 mm.

**Fig. 5:** *Peresia tannae* evolving-phases.

1. Scale with microspores from the upper part of fructification. (PIZ 553)
2 -3. Flower-like ovulous organs from the lower part. (PIZ 553)
4. Structure of *Peresia tannae*. Single leaflets arranged to form a fertile bouquet.
1) PIZ 553 *Peresia tannae*. Sporophyll with fertile aggregates arranged distally on each single branch. Microsporangia-scales on the upper part, megasporangia on the lower part. Picture detail 13 x 7 cm.

2) PIZ 553 *Peresia tannae*. Five sporophylls distally attached on slender stems, including one microsporophyll on the upper side, and four flower-like macrosporophylls.

3) PIZ 553 *Peresia tannae*. Part of branch with unusually verrucous surface. (15 x 2 mm)
Remarks.

Until further studies provide more information about the Peresiaceae group, it is difficult to find out to which plant group these sporophylls could pertain. The upper wedge-shaped organs have close affinities with *Peresia raitae*. But the structure is quite different. On *Peresia tannae* sporophylls were held by slender branches, in *P. raitae* the stem is corpulent and suggests more affinities as a primitive and incomplete fused Cycad sporophyll. *Peresia raitae* also bears more trichoms than *Peresia tannae*. *Peresia raitae* was also never seen with divided micro- and suggested megasporangia-organs on the same sporophyll. Together they have fertile organs that resemble reduced and compressed fronds and together they bear their sporangia on the abaxial side of the scales. They have no affinity to Peltaspermales (*Sagenopteris, Scythophyllum*), which are common in these strata. It also appears that the Peresiaceae with their sporangia-leaves have more affinities to ferns (such as Marattiales or their fertile fronds *Scolecospernis*) than to seedferns.

Another widely distributed group in the Middle Mesozoic are the Bennettitales. Striking resemblances with the bennettitalean female “flower” *Williamsonia gigas* (see PIZ 553) and male organ *Weltrichia sol* (see PIZ 207) are not to be dismissed. A direct link to this group is not to be excluded. However, it could maybe presumptuous to say that these shrubs have more affinities with angiosperms than any other Mesozoic plant group. The upper pollen-bearing organs could be interpreted as primitive stamen and the lower as rudimental carpels. If *Peresia raitae* were able to fuse and compress the structure to the cycadalean cone, then *Peresia tannae* was probably able to make the first step towards real angiosperms. Meanwhile it could be stated that, in this rapid changing Early Triassic world, several plant groups and also animals were trying to evolve or mutate, hence surprising alternative solutions to the Paleozoic past emerged.
1) PIZ 553 *Peresia tannae*. Microsporophyll (15 mm wide x 8 mm long) covered with microspores from the upper part of fructification.

2) PIZ 553 *Peresia tannae*. Other microsporophyll (10 mm wide x 4 mm long) covered with microspores from the upper part of fructification.

3) PIZ 553 *Peresia tannae*. Macrosporophyll (12 mm wide x 14 mm long) covered with sporangia from the lower part of fructification.

4) PIZ 553 *Peresia tannae*. Macrosporophyll (10 mm wide x 14 mm long) covered with sporangia from the lower part of fructification.

5) PIZ 553 *Peresia tannae*. Sporophyll (10 mm wide x 15 mm long) covered with sporangia from the lower part of fructification.
Systematic Paleontology
Subdivision: Filicales? Bower, 1899
Pteridophyta?
Order unknown
Family indet.

Genus *Ladinia* gen. nov. Wachtler, M.

Generic diagnosis.
Seed-bearing plant with sterile and fertile foliage. Leaves with entire margin and tapered to rounded apex. Secondary veins arising almost perpendicularly from the rachis, unforked and parallel. Female sporophyll consisting of ovule-bearing organs on the abaxial surface.

Etymology.
After the people of Ladins, the original population of the Dolomites mountains in northern Italy.

*Ladinia simplex* WACHTLER, sp. nov.

Holotype.
KÜH 2118

Paratypes.
KÜH 885

Material.
KÜH 2030, PIZ 332, PIZ 158, KÜH 2151, PIZ 133, KÜH 2140

Etymology.
Named after its elementary arrangement of leaves and attached fertile organs.

Type localities.
Kühwiesenkopf, Piz da Peres

Type horizon and age.
Dont-Formation
Lower to Middle Triassic, Anisian, Pelson

Repository.
Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

Diagnosis.
*Ladinia simplex* bears entire acuminate, sometimes papery, sterile leaves, often divided into forking midveins and secondary veins arising almost perpendicularly unforked and parallel from the rachis. The sporophylls consist of compact sterile cataphyll-like foliage and leaves with loosely arranged ovule-bearing organs on two rows on the abaxial surface without forming a cone.

Description
**Plant:** Low-growing shrub, foliage erected or obliquely spreading laterally, (KÜH 885) about 15 sterile leaves, crossing over to 10 - 15 distally arranged fertile sporophylls. (KÜH 2118)
**Roots and stems:** More fernlike than cycadalean. (KÜH 660)
**Leaves:** Sterile leaves on a short 1 – 2 cm-long and 5 mm-wide stalk, linear to lanceolate, 8 to 15 cm long and 1-3 cm wide, margin usually entire, not lacerated or folded. Leaves ending sometimes in a pointed apex, (PIZ 133) or slightly rounded (KÜH 2140, PIZ 332). Rachis 5 mm reducing uniformly to the apex. Sometimes on the position of a single rachis several forking median veins occur towards the apex (KÜH 2030). Secondary veins arising almost perpendicularly from the rachis, unforked and parallel; vein concentration at the margin 20-30 per cm (PIZ 158).
**Sporophylls:** Cataphyll-like leaves settled between fertile and sterile foliage, leathery, condensed, 0.5 to 1 cm wide, about 5 cm long, sharply pointed with dorsal spines, bearing no middle-constriction or only slight emargination. Median rachis barely visible. Sterile leaves ending gradually. They are narrower (up to 0.8 cm wide) (KÜH 2118), shorter (5-10 cm long) and more com-
1) KÜH 885 *Ladinia simplex*. 5 sterile leaves 10 x 2 cm.

2) KÜH 2118 *Ladinia simplex*. About 10 fertile leaves overlie several sterile leaves. Detail 14 x 10 cm

3) KÜH 2118 *Ladinia simplex*. Detail of the fertile sporophylls. 10 - 14 small seeds on two rows.
pact. Venation is difficult to see. They bear on the lateral final sides tiny (max 5 mm long) spines. Fertile ovules attached to the abaxial surface of the rachis in two rows, 3 mm wide x 2 mm long. Sporophylls growing from a massive 1 cm long stalked petiole.

Remarks.

*Ladinia simplex* was included only as a probable ancestor and not as a real cycad due to its fernlike character. The rachis is divided, looking like accidentally formed median veins. The leaves are often thin and fragile, of taeniopteroid-type and yield no cuticle. Compared with *Bjuvia*, *Ladinia*-foliage is generally smaller, never lacerated, leaves often spread laterally and not upwards. Only the vein concentration is 20-30 per cm approximately, as high as in Anisian *Nilssonia* and *Bjuvia*. The adnate megasporophyll is suggested as being more primitive. The fertile leaves of *Ladinia* do not form a cone like *Bjuvia-Dioonitocarpidium*, a central axis is missing, also the featherlike structure, or consists only of casual arranged spikes. Only fine spines could be highlighted. They could be interpreted as the beginning of a rudimental featherlike structure and a means of protection against damage from insects or other animals. The sporophylls do not have the typical constriction of *Dioonitocarpidium*, but only show a first sign. The number of megasporophyll-leaves in Ladinia is reduced (6-8 compared to 8-14 in *Dioonitocarpidium cycadea* and up to 60 in *Dioonitocarpidium loretzi*). The seeds are smaller than in *Dioonitocarpidium*. Hence *Ladinia simplex* could be defined more as a fern than a cycadalean transition plant. It must be considered that Cycads do not evolve from seedferns like Medullosaceae as suggested in literature, but from the pterophyta. The constant enlarging of seeds from *Ladinia simplex* to *Bjuvia primitiva* could be a sign for understanding the emerging of cycad-like plants. In many cases *Ladinia*-leaves were found aggregated together (KÜH 885, KÜH 2218, PIZ 17, PIZ 160), which in *Bjuvia* only occurs in rare circumstances. Although cycadales mostly have the appearance of single leaves, the original concept probably lies in a pinna like today’s *Stangeria*. For unknown reasons from the Paleozoic to Early Mesozoic one sterile pinna become more dominant and formed larger laterally erected sprouting foliage. Evidence for that theory still evident in extant Cycadales is the simultaneous growth of a corona of leaves.

![Fig. 7: 1) Suggested reconstruction of *Ladinia simplex*. 2) Single female sporophyll. Different foliage of *Ladinia simplex*: 3) Entire pointed apex (PIZ 133, PIZ 332), 4) Entire – rounded, midveins dichotomously branched (KÜH 2140).](image)
1) PIZ 332 Ladinia simplex. Leaf showing slightly pointed apex (6 x 2 cm)
2) KÜH 2140 Ladinia simplex-leaf with rounded apex. 83 x 3 cm
3) PIZ 340 Ladinia simplex. Short petiole and basal leaf-system Detail 8 cm
4) PIZ 160 Ladinia simplex. Two leaves attached on the basis
5) KÜH 2030 Ladinia simplex. Lower abaxial part of the leaf showing dichotomously branched midveins and unforked lateral veins.
1) KÜH 660 *Ladinia simplex*. Several leaves with stem. Slab 20 cm
2) KÜH 661 *Ladinia simplex*. Several leaves, slab 15 cm
Taxonomy

Systematic Paleontology
Subdivision: Cycadophytina
Class Cycadopsida Brongniard, 1843
Order Cycadales Dumortier, 1829
Suborder Bjuvia FLORIN 1933

Bjuvia primitiva n. sp.

Holotype.
KÜH 230.

Paratype.
KÜH 132.

Material.
KÜH 155, PIZ 579, KÜH 182, KÜH 877.

Etymology.
Because of its primitive character as a transition form to other Cycadales.

Type localities.
Kühwiesenkopf, Piz da Peres

Type horizon and age.
Dont-Formation, Richthofen Conglomerate, Morbiac Limestone.
Lower to Middle Triassic, Anisian, Pelson-Ilyrian

Repository.
Natural History Museum Südtirol, Bozen, Museum Dolomithos Innichen.

Diagnosis.
Cycadalean-like plant with whole oblong leaves, sometimes lacerated, rounded to a U-shape at the apex. Secondary veins arising at a right angle from the upper side of the rachis to the margin, unforked and parallel. Usually short petiole. Leaves erected.

Description.
Leaves: Foliage of Bjuvia primitiva is usually 15 - 25 cm long and 5-10 cm wide. The leaves are oblong, often slender, sometimes segmented. The apex varies from rounded to U or V-shaped, but never acuminate (KÜH 182, KÜH 877). Secondary veins arise at a right angle from the upper side of the rachis to the margin (PIZ 579). The veins are unforked and parallel; vein concentration at the margin: 20-30/cm. The leaves may sometimes be folded.

Petiole: Short, (1-3 cm) 5 mm wide, with gradually beginning leaflets (PIZ 533). Foliage growing continuously from the rachis, but soon reaching the maximum width, than continuing with the same width up to the apex.

Male cones: Thetydostrobus fructifications were found together with Bjuvia primitiva.

Female cones: Complete female cones and also isolated sporophylls belonging to Dioonitocarpidium cycadea were found together with Bjuvia primitiva.

Remarks.
Bjuvia primitiva is common in the Anisian Braies flora and is surprising mainly due to

![Different foliage of Bjuvia primitiva](image)

1) Slightly lacerated U-Shaped (KÜH 155),
2) Lacerated - V-shaped (KÜH 230)
its behavioural modifications. *Bjuvia primitiva* differs from *Bjuvia olangensis* occurring in the same strata because of its smaller size. *Bjuvia olangensis* (KÜH 2140, PIZ 41) is much bigger, more segmented, the apex linear and not U- to V-shaped. It differs from Anisian *Ladinia simplex* of the same place due to its more consistent leaves, that are never acuminate on the apex. Otherwise *Bjuvia primitiva* could be seen as a transitional form between *Ladinia* and consistently growing *Bjuvia olangensis*. Until accurate cuticle-analysis or other research ascertains the exact distinction, problems are anticipated.

*Bjuvia primitiva* resembling leaves were described with different names from several localities in Germany. Schmidt (1928) mentions *Danaeopsis angustifolia* (classifying it as *Marattiaceae*) from Keuper, but because of its never furcating parallel veins, it probably has a greater cycadalean affinity. However, fairly similar taeniopterid foliage found from Permian to Triassic (*Taeniopteris multinervis, Taeniopteris coriacea*) could only be used as a morphospecies of primarily sterile leaves (Remy and Remy, 1975). Therefore this form genus has to be dismissed as a possibility for comparison.

The leaves differ from Ladinian *Bjuvia dolomitica* (Wachtler and Van Konijnenburg-van Cittert, 2000) due to their higher fragrance. Cuticles are difficult to obtain, whereas in the Ladinian *Bjuvia dolomitica* it was not a problem. The vein concentration is again 14-18 per cm for Bjuvia dolomitica and 20 to 30 for Bjuvia primitiva. Certain *Nilssonian* leaves from Lunz in Austria of Carnian age also have *Bjuvia* affinities. In Rhaetian *Bjuvia simplex* the vein concentration decreases further to 12-14 cm. Bjuvia simplex also forks on the rachis. (Florin R., 1933).

Even though extant Cycads, with their mathematical segmented leaf system have totally different leaves, with the knowledge of *Bjuvia primitiva* it is possible to demonstrate that leaf types of modern cycads probably originate from an entire single leaf passing through varying degrees of casually lacerating foliage to the perfect pinnate leaves of *Nilssonia* and extant Cycads. Surprisingly, the over 240 million year old Dolomite-Anisian Bjuvias bears all the features of modern Cycads. From the root system to the cycas-like megasporophyll arrangement (probably Dioonitocarpidium cycadea) and the male strobilus of *Thetydostrobus*-type, found in the same strata, we have an extraordinary analogy with extant cycads.
1) KÜH 132 Bjuvia primitiva. Open and lacerated leaf 10 x 6 cm
2) KÜH 230 Bjuvia primitiva. Open and lacerated leaf 15 x 6 cm
3) KÜH 155 Bjuvia primitiva. Leaf apex (4 x 2 cm)
4) KÜH 470 Bjuvia primitiva. Folded leaf 12 x 3 cm
5) PIZ 579 Bjuvia primitiva. Leaf segment with parallel vein-system (2 cm)
6) KÜH 877 Bjuvia primitiva. Leaf with V-shaped apex. (6 cm x 6 cm)
Systematic Palaeontology
Subdivision: Cycadophytina
Class Cycadopsida Brongniard, 1843
Order Cycadales Dumortier, 1829
Suborder Bjuvia FLORIN 1933

*Bjuvia olangensis* n. sp.

**Holotypes.**
KÜH 130 (leaves), KÜH 2218 (stem).

**Paratypes.**
KÜH 2031 (leaves), KÜH 2221 (stem)

**Material.**
PIZ 111, KÜH 2225, PIZ 552, KÜH 2220

**Etymology.**
Named after the locality of Olang in Pustertal Valley, (Dolomites). The mountains over this borough were crossed by the plant-bearing horizons.

**Type localities.**
Kühwiesenkopf, Piz da Peres

**Type horizon and age.**
Dont-Formation, Richthofen Conglomerate, Morbiac Limestone.
Lower to Middle Triassic, Anisian, Pelson-Ilyrian

**Repository.**
Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen

**Diagnosis.**
*Bjuvia olangensis* is the biggest of several cycadalean-like plants of this Anisian Braies-Dolomites Fossilagerstätte. The leaves are almost lacerated, often folded, on the apex normally torn, only rarely slightly U-shaped. The petiole is long and bare. The suggested trunk is bulbous, with a massive main root and additional “coralloid roots”.

**Description**

**Leaves:** *Bjuvia olangensis*-foliage reaches a length at least 50 cm with a width of 40 cm (KÜH 2225, KÜH 2223). In the youth stadium the leaves were whole, tending towards significant leaf shredding, and to a greater or lesser degree of being torn and folded, when they were fully grown. Only sometimes the leaves tend to be mathematically segmented (KÜH 2226). The apex often looks cropped. Delicate secondary veins arise almost perpendicularly from the rachis, unforked and parallel. The concentration of the veins varies from 20 (PIZ580) to 30 (PIZ552) per cm.

**Petiole:** Bare, sometimes up to 20 cm long, to up to 10 mm - 15 mm wide. (KÜH 2031)

**Trunk:** The stem can reach a length of 15 cm and 11 cm in circumference, (KÜH2218) passing over to the root system. The trunk is covered by characteristic persistent girdling leaf traces, which change in the upper part to a "leaf armour" of tightly packed, helically arranged shaped leaves. (KÜH 2113) They are wide (up to 12 mm) but relatively short (3-4 cm) with no evident petiole and vena- tion (KÜH 2220) and form a crown-like ring. (KÜH2221) Only the last leaves are much longer (7-8 cm) but only 7 mm wide, well-shaped and bear an indefinitely median rip and could interpreted as cataphylls. The entire trunk and root system is up to 24 cm long.

**Roots:** The main root is thick and fleshy, solid, 9 cm long, 7-8 cm wide, from which small, sometimes upwards growing, often branched secondary roots ramify, (KÜH2218) resembling the typical “coralloid roots” of today’s cycads. They can reach a length of 3 cm x 1 cm.

**Male cones:** Probably *Thetydostrobus marebbel*.

**Female cones:** Suggested macrosporophyll *Dioonitocarpidium loretzi*, found near Bjuvia-leaves.

**Remarks**

The *Bjuvia olangensis* leaves were among the largest in the Lower to Middle Triassic...
1) KÜH 2225 Bjuvia olangensis. Big slab (70 x 50 cm)
2) KÜH 2223 Bjuvia olangensis. Several leaves on a big slab (100 x 40 cm)
3) KÜH 130 Bjuvia olangensis. Two leaves seen from the lateral side Petiole 12 cm, Leaves 32 cm
4) KÜH 2031 Bjuvia olangensis. Leaf showing the laceration of leaflets. Leaf 35 cm
of the Dolomites and seemed to be a transition point between *Bjuvia primitiva* and the following Ladinian up to Rhaetian *Bjuvias*. The *Bjuvia* leaves were disproportionately large, therefore the single, huge foliage tends to overlap and lacerate irregularly like the current Musa-fronds (Banana plant). The leaf shredding tends towards clearly defined segmentation resembling the *Nilssonia* leaf type. Therefore it is sometimes difficult to decide whether it is to be classified with *Nilssonia* or *Bjuvia*.

In the German Basin plant-fossils with entire Cycad-leaves were classified as *Nilssonia polymorpha*. (Schmidt M., 1928) Without going into more details on leaf types, it could be said that in the Middle Triassic many Cycadales-affiliated leaves coexisted and only the missing cuticle analysis and also the poor sporophyll record prevented more definite classification. *Phasmatocycas*, ovule-bearing organs with suggested taeniopteroid leaves from the Upper Carboniferous period of North America as possible ancestors of Cycads, were contested by other authors (Axsmith B. 2003), because pteridospermal affinities are evident. *Leptocycas* from the Upper Triassic beds in North Carolina has a slender stem with a crown of loosely arranged, pinnately compound leaves of *Pseudoctenis*-type towards the apex. Since it is from a younger age and totally different assembly it has to be dismissed.

From the same time as *Bjuvia olangensis* *Antarcticycas schopfi*-stems are known with their suggested pollen-organs *Delemaya spinulosa* and leaves of *Yelchophyllum omegapetiolaris*-type (Hermsen E. 2009) from the Fermouw Formation (Early-Middle Triassic- Anisian) of the Antarctica. They were found in permineralized conservation. The only 3 cm-long, 8 mm-wide male cone, different leaf type, and also the root and stem system are quiet different from *Bjuvia olangensis*. But a closer or further affinity cannot be completely excluded.

Fig. 9: Different leaves of *Bjuvia olangensis*:
1) Sometimes lacerated (KÜH 2223);
2) Lacerated - flattened (KÜH 2223);
3-4) Irregular cycad-like (KÜH 2225), (KÜH 553)
1) KÜH 2218 *Bjuvia olangensis*. Entire trunk, 24 cm x 11 cm with taproot and coralloid roots.
2) KÜH 2218 *Bjuvia olangensis*. Detail showing coralloid roots.
3) KÜH 2220 *Bjuvia olangensis*. Detail of trunk apex with leaves (3 cm).
4) KÜH 2221 *Bjuvia olangensis*. Detail of leaves and cataphylls.
5) KÜH 2221 *Bjuvia olangensis*. Trunk with leaves and cataphylls 12 cm.

Wachtler, M.: Origin of Cycadales
Systematic Palaeontology
Subdivision: Cycadophytina
Class Cycadopsida Brongniard, 1843
Order Cycadales Dumortier, 1829
Suborder Bjuvia FLORIN 1933

Nilssonia braiesensis n. sp.

Holotypes.
KÜH 897.

Paratype.
KÜH 900.

Material
KÜH 670, PIZ 180, KÜH 2170, PIZ 24.

Etymology.
Named after the Braies Valley (Pragser Tal), which is especially rich in plant fossils.

Type localities.
Kühwiesenkopf, Piz da Peres.

Type horizon and age.
Dont-Formation, Richthofen Conglomerate, Morbiac Limestone.
Lower to Middle Triassic, Anisian, Pelson-Illlyrian

Repository.
Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

Diagnosis.
Nilssonia braiesensis leaves are petiolate, pinnate and distinctly separate each from each other. The lamina is subdivided into numerous, irregularly oppositely to sub-oppositely, positioned segments, whose ends normally truncate to obtuse. From a varying degree of strong rachis, secondary parallel veins arise perpendicularly on the leaves, without forking to the margin. Petiole long and bare.

Description.

Leaves: The foliage of Nilssonia braiesensis can reach at least 30 cm in height and up to around 20 cm in width. (KÜH 900, KÜH 897) Pinnate leaflets are attached oppositely (KÜH 2170) to sub-oppositely, (KÜH 900) almost perpendicularly to the rachis. The length of the segments continuously decreases towards the apex of the leaf. They normally end slightly cropped or U-shaped. The width of the individual segments may vary considerably, some segments being twice as wide as others and can reach a total width of up to 10 cm. The segments are sometimes irregular, oblong, ending more or less lanceolate shaped. Veins arise parallel and unforked from the adaxial side of the rachis to the margin. (15 – 30 veins/cm). The leaf segments sometimes tend to be folded. A varying leaf structure even on the same plant can be observed (KÜH 897)

Petiole: Relatively consistent (KÜH 897 with 9 cm) and bare without spines or prickles. Diameter approximately from 5 to 10 mm.

Male cones: Suggested from Thetydostrobus-group

Female cones: Suggested from Dioonitocarpidium group.

Remarks.
Narrow, nearly band-like or oblong-oval leaves with irregularly segmented lamina and segments, attached to the upper side of the rachis were attributed to the genus Nilssonia (Pott, C., Kerp, H., Krings, M., (2007a). The macromorphological features correspond well with those seen in typical representations of this common Mesozoic foliagetype. Additional characteristics include a fine, parallel venation everywhere with unforked veins. Nilssonia braiesensis differs from the well-known Nilssonia leaves of Carnian Lunz not only in terms of its different geological period but also from a more primitive nature. Strong mathematically arranged leaflets are not developed and leaf modification occurs even on the same plant.
1) KÜH 897 *Nilssonia braiesensis*: Several aggregated leaves with long petiole (9 cm high
2) KÜH 670 *Nilssonia braiesensis*: Detail of venation and segment distance (Detail 3 cm)
3) KÜH 900 *Nilssonia braiesensis*: Alternate opposite standing leaves (15 x 5 cm)
The same is also valid for many leaves classified up to now as *Pterophyllum* (e.g. *Pterophyllum jaegeri*) and now considered to be of bennettitalean foliage. However, many cycadalean and bennettitalean leaves are macromorphologically similar, and can usually be distinguished only in terms of epidermal anatomy. Until new analysis solves this problem many doubts remain.

On the other hand, the first unquestionable fossil record of Bennettitales is reported from Carnian deposits (Pott, C., McLoughlin, S. Lindström, A., 2009). The great disparity in age therefore suggests the cycadalean origin of these leaves. The dominance of Cycadalean leaf forms in the Anisian strata of the Dolomites dismisses the Bennettitaceae origin as well. It may also be more likely that most pinnate leaves from the Ladinian Dolomites belong to a further development of Anisian *Nilssonia* and not to *Pterophyllum jaegeri* as believed up to now. (Wachtler, M., Van Konijnenburg-van Cittert, J.H.A., 2000). *Nilssonia braiesensis* indicates that Nilssoniales evolved much earlier in the Triassic than previously thought. (Pott C. et al., 2007)

The genera *Yuania*, *Tingia*, and *Plagiozamites*, once included in the Cycadales, are now placed with the *Noeggerathiales*, an order attributed to the progymnosperms. (Pott C. et. al., 2009)

*Pseudoctenis*, another characteristic cycadalean foliage element of the Rhaetian (uppermost Triassic) and Jurassic floras from Europe, was often historically used in an arbitrary way where no valid generic diagnosis existed. (Pott, C., Kerp, H., Krings, M., 2007b). Apart from its younger age, they differ in the segment form, which is never basiscopically decurrent. Therefore it could be more conducive to suggest a relationship with other *Bjuvia* leaves of these strata, because macromorphological relationships are obvious. Sometimes it may also be a problem to distinguish *Bjuviaolangensis* leaves from *Nilssonia braiesensis*, especially when they are almost clearly lacerated. But they lack the nearly mathematical segmentation typical of *Nilssonia*-pinnas.

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Fig. 10: Different leaves of *Nilssonia braiesensis*:
1) Sub-oppositely - undulated (KÜH 900);
2) Cycadlike - irregular (KÜH 897)
3) *Nilssonia braiesensis*. Reconstruction of the whole plant.
Traces of animal remain on cycads.
1) PIZ 338. Animal feeding on a Bjuvia leaf
2) PIZ 335. Traces from unidentified insects.
3) KÜH 1409. Nibbled cycad foliage.
4) KÜH 2171. Animal remains.
Evolution of cycadalean leave-type in the Anisian Dolomites

It is suggested that most primitive and ancestral leave-type of the fern-cycadalean ancestor was single-entire, acuminate and on a short petiole (*Ladinia simplex*). (PIZ 133, KÜH 2140). It originated from an taeniopteroid Stangeria-Bowenia-like pinna of an unknown Paleozoic ancestor.

Cycad-character was reached with *Bjuvia primitiva* with it oblong, sometimes lacerated, on the apex U- to V-shaped leaves. Petiole is just more pronounced. (KÜH 882, KÜH 2217, PIZ 182, KÜH 877).

*Bjuvia olangensis* foliage was just fully lacerated till slightly segmented, distally V-shaped to flat. Leaves where big, with a long massive petiole. (KÜH 2223, KÜH 2226). Today's cycadalean foliage-form was reached by *Nilssonia braiesensis*. Leaves were mathematically segmented (KÜH 2170).

Slightly younger (Ladinian) *Sphenozamites wengensis* (WSW 06, WRI 21) from Dolomites shows just extant *Zamia furfuracea* foliage.

The begin from a single entire leaflet of all extant cycads is obvious from the rich material found in the Early-Middle-Triassic in Dolomites, more doubts remain what was the activator of all this rapid enhancement of single Cycad-leaves.

Fig. 11: Evolution from Cycad-leaves in the Lower-Middle Triassic:
1) *Ladinia simplex* - entire, papery and acuminate. (PIZ 133 - PIZ 332).
2 + 3) *Bjuvia primitiva* - Entire to lacerated, rounded at apex or slightly U-shaped. (KÜH 2140 - KÜH 155)
3 + 4) *Bjuvia olangensis* - Lacerated to segmented, U to V-shaped at apex (KÜH 2223)
5) *Nilssonia braiesensis* - Clearly segmented (KÜH 897)
6) *Sphenozamites wengensis* - oblong and obtuse (WSW 06 - WRI 21)
Evolving of leaf-type in Anisian of Dolomites

1) PIZ 133 *Ladinia simplex*-leaf with pointed apex. 3 x 1.5 cm
2) KÜH 882 *Bjuvia primitiva* leaf with round apex. Leaf lacerated
3) KÜH 2217 *Bjuvia primitiva* leaf with U-shaped apex.
4) KÜH 533 *Bjuvia primitiva* leaf slightly lacerated
5) KÜH 2223 *Bjuvia olangensis*. Leaf sometimes lacerated, apex U-shaped. 30 x 10 cm
6) KÜH 2226 *Bjuvia olangensis*. Leaf often lacerated to segmented. 20 x 15 cm
7) KÜH 2170 *Nilssonia braiesensis*. Leaf clearly segmented. 10 x 10 cm
Systematic Palaeontology
Subdivision: Cycadophytina
Class Cycadopsida Brongniard, 1843
Order Cycadales Dumortier, 1829
Suborder Bjuvia FLORIN 1933

*Dioonitocarpidium cycadea* n. sp.

**Holotype.**
KÜH 2109

**Paratypes.**
KÜH 753.

**Material.**
KÜH 2137, KÜH 2108 KÜH, PIZ 581, PIZ 141, PIZF 6.

**Etymology.**
*Dioonitocarpidium cycadea* is named after its resemblance to today's megasporophyll of Cycas.

**Type localities.**
Kühwiesenkopf, Piz da Peres

**Type horizon and age.**
Dont-Formation, Richthofen Conglomerate, Morbiac Limestone.
Lower to Middle Triassic, Anisian, Pelson

**Repository.**
Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

**Description.**

**Female cones:** 12 - 18 cm long, 8 - 10 cm wide. (KÜH 2109, PIZ 581, KÜH 753) with several (8 to 16) leaf-like megasporophylls, spirally arranged on a central axis. Lower leaflets of the cone sterile, replaced in succession by fertile sporophylls.

**Peduncle:** 4 - 6 cm long, 1 cm wide with sterile cataphyll-like pointed narrow leaves. (PIZ 581, KÜH 2109)

**Megasporophylls:** Consisting of a basal short, 1 cm-long petiole, a proximal fertile part and a finishing sterile featherlike structure. (KÜH 2137, PIZF 6). Length ratio about 1:4:3 (petiole: fertile part: sterile part). The fertile and sterile parts were divided by a constriction. The seeds enfolded on the abaxial surface of the fertile part by a downwards lapping leaf. Seed bearing region about 3 to 7 cm long, from 2 to 12 ovules on each row, increasing in number to the apex. Leaflet divided from a sometimes forking midvein, which ends on the apex. Distal feather-leaves oblong to ovate with leaf-segments on either side. (KÜH 2137: about 40 microleaves on each side). Microleaf segments directed obliquely upwards, 1 mm wide at base, with acute apices, and divided by a single undivided vein (PIZ 141). Single veined leaflets hairy.

**Ovules:** Closely pressed without space on the abaxial part of the lamina, orientated at right angles to the midvein. Seeds varying considerably from 2 mm to 7 mm long, 2 to 5 mm wide.

**Plant:** Probably due to its size *Dioonitocarpidium cycadea* belongs to *Bjuvia primitiva*. It is also suggested that Anisian Cycads bear more than one cone (PIZ 581).

**Remarks:**
In 1938 Rühle von Lilienstern introduced the genus *Dioonitocarpidium (pennaefomae)* for single cycadalean megasporophylls from Unterkeuper (Ladinian). He based his studies on a previously described (1928) slab classified as *Dioonites pennaeformis*. Even though no entire fossilized cone was ever found, he drew an entire cone probably influenced by modern cycadales, in his "Die Lebewelt unserer Trias". The illustration, based on a hypothetical Triassic female cone with accompanying pointed whole *Taeniopteris* leaves, amazingly corresponded to *Bjuvia-Cycads*. 

36 Dolomythos, 2010
1) KÜH 2109 *Dioonitocarpidium cycadea*. Female cone (10 x 8 cm) with ca. 14 sporophylls. 6 to 14 seeds on two rows on the abaxial surface of the sporophyll.

2) KÜH 2109 *Dioonitocarpidium cycadea*. Detail of the lower part of the sporophyll, with 3 seeds attached on one row.

3) PIZ 581 *Dioonitocarpidium cycadea*. Slab (22 x 12 cm) containing two female cones. The smaller one holds 8 sporophylls and the bigger one 14. Seed size only 5 x 5 mm
Till now only single megasporophylls were found. This counts for Ladinian *Dioonitocarpidium moroderi* (Kustatscher, E., Wachtler, M. & Van Konijnenburg-Van Cittert, J. H. A. 2004), as well as nearly equally old *Schozachia donaea* (Rozynek, B. 2008) from German Keuper and also *Dioonitocarpidium keuperianum*, from the Upper Triassic (Carnian) fossil deposit of Lunz in Austria. In all these cases it is to be presumed that they pertain to cycadales and have parental affinities to *Dioonitocarpidium cycadea*. The difference lies, apart from their younger fossil age, in the slightly bigger and more developed megastrobili-leaves. The fact that only single megaleaves have been found in other places suggests that the attachment to the central axis was no longer as strong as in *Dioonitocarpidium cycadea*. The Jurassic genus *Beania* with its loose spikes has a totally different cone construction, that cannot therefore be compared with any *Dioonitocarpidium*-cone.

Doubtful cycadalean megasporophylls are just bequeathed from Paleozoic. *Lesleya* known from Mississippian to Late Permian in Europe and North America is probably a sterile taeniopteroid foliage genus. (Taylor T. N. Taylor E. L. Krings M., 2008). Fertile female strobili were put inside *Phasmatocycas kansana*. Axsmith et. al. (2003) suggested that Upper Carboniferous *Spermopteris* or Lower Permian *Phasmatocycas* are “decidedly less cycad-like than previously believed.” They also have only little resemblance with *Dioonitocarpidium cycadea*. *Primocycas chinensis* from the lower Permian in China with its featherlike apex and laterally attached ovules is thought to be a cycad macrosporophyll. (Zhu, J., Du, X., 1981) The difference from Anisian *Dioonitocarpidium* lies in the fact that in *Primocycas chinensis* the megasporophyll is palmate on the apex. Also the seeds are attached at a distance on both sides of the leaf and are not abaxial. The evolving-concept of cycads would therefore be totally different. From *Primocycas* it is also unknown how the entire cone was formed. Approximately 30 species of Taeniopteroid leaves were described by the Permian of China. Further studies reported that several belong to ferns. (Pott C. et. al. 2009) Some of them could be considered as ancestors of Thetydalean cycads.

It can be considered that also in *Dioonitocarpidium* cones, a single pinna was the basis of female cones. (KÜH 2109, PIZ 581).
1) KÜH 753 *Dioonitocarpidium cycadea*. Complete cone.

2) KÜH 2137 *Dioonitocarpidium cycadea*. Single sporophyll adaxial side with featherlike apex. (8 cm)

3) PIZ 2108 *Dioonitocarpidium cycadea*. Fertile part of sporophyll containing 7 seeds on each side of midrib. (8 x 5 mm one seed)

4) PIZ 141 *Dioonitocarpidium cycadea*. Feather-part of sporophyll

5) PIZF 6 *Dioonitocarpidium cycadea*. Fertile part of sporophyll containing 12 seeds on each row. (3 x 0,5 cm), ovules 3 x 2 mm.
Systematic Palaeontology
Subdivision: Cycadophytina
Class Cycadopsida Brongniard, 1843
Order Cycadales Dumortier, 1829
Suborder Bjuvia FLORIN 1933

**Dioonitocarpidium loretzi** n. sp.

**Holotype.**
KÜH 758

**Paratype.**
KÜH 534.

**Etymology.**
*Dioonitocarpidium loretzi* is named after Hermann Loretz who was the first to study the palaeontology of Kühwiesenkopf and the Braies Dolomites in 1875.

**Type localities.**
Kühwiesenkopf
Type horizon and age.
Dont-Formation.
Lower to Middle Triassic, Anisian, Pelson-Illrian

**Repository.**
Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

**Diagnosis.**
Cycadalean cone consisting of loosely organised sporophylls arranged spirally on a central axis. On consistent peduncle sterile leaves. Megasporophylls bearing ovules on the lower abaxial side on two rows. Sporophylls with a terminal feather-like apex.

**Description.**
**Female cones:** 20 - 30 cm long, 10 - 15 cm wide (KÜH 758). Up to 60 sporophylls spirally arranged on a central axis with a terminal feather-like apex, bearing two rows of ovules on the abaxial surface. Sometimes up to 20 seeds on each row. In the youth stadium (KÜH 534) megasporophylls pressed together and erected.

**Peduncle:** 4 - 6 cm long, 1 to 1.3 cm wide with sterile cataphyll-like leaves. (KÜH 534)

**Megasporophylls:** 1 cm wide, 5 to 15 cm long. Ovules on the lower surface enfolded from a downlapping leaf. Seed-bearing region about 8 to 10 cm long, from 2 to 30 ovules on each row, increasing in number towards the apex. Lower sporophylls often sterile, cataphyll-like. Featherlike apex covering apical part of approximately 1/3 of entire sporophyll.

**Ovules:** Closely pressed on the abaxial part of the lamina, orientated at right angles to the midvein. From 2 mm to 4 mm long, 3 to 6 mm wide.

**Remarks.**
Coequal *Dioonitocarpidium cycadea* from the same strata bears fewer megaleaves (60 to 8-14) and also fewer ovules on each megasporophyll (40 to 6-14 on each row). Therefore it could be suggested that *Dioonitocarpidium loretzi* is a further development of *Dioonitocarpidium cycadeae*. Differences between other *Dioonitocarpidium*-megasporophylls were just described under *D. cycadeae*.

It is therefore worth comparing Dioonitocarpidium female cones with extant Cycas. The differences lie in the much smaller ovules, (2-3 x 1.5-2 cm in *Cycas revoluta* compared to 0.2 – 0.4 x 0.3 – 0.6 cm in *Dioonitocarpidium*). The seeds are also embedded on the lower surface and not laterally as in Cycas. The megaleaves are more fragile and arranged around a central axis whereas the Cycas cone lacks any cone axis and consists of a circle of cabbage-like clusters of loosely arranged sporophylls (Jones, 2002). Otherwise it is clear that *Dioonitocarpidium* has a striking resemblance with today's Cycas cones. The evolution of the female cones of other extant Cycadales, like Zamia, Dioon, Stangeria and others, could only in part be explained by *Dioonitocarpidium*. It is not clear whether there has been a reduction in ovule numbers from *Dioonitocarpidium* cones to the usual two or a *Peresia*-like solution, where various micro-fronds have fused to form cycadaelean-like scales with macrosporangia and later a complete cone.
1) KÜH 534 Dioonocarpidium loretzi. Young immature female cone. (22 x 8 cm)
2) KÜH 758 Dioonocarpidium loretzi. Cone with minimum 60 sporophylls. Each could contain up to 40 seeds on two rows. (18 x 10 cm)
**Systematic Paleontology**

Subdivision: Cycadophytina  
Class Cycadopsida Brongniard, 1843  
Order Cycadales Dumortier, 1829

**Genus Thetydostrobus gen. nov.**  
WACHTLER

**Generic diagnosis.**

Cycadalean male cone from Lower Middle Triassic. Ovoid cone on a peduncle with microsporophylls arranged spirally on a central axis. Microsporangia distally arranged on lower surface.

**Etymology.**

The genus *Thetydostrobus* is named after the Tethys-ocean that existed between the continents Gondwana and Laurasia during the Mesozoic era.

*Thetydostrobus marebbei* WACHTLER, sp. nov.

**Holotype.**  
PIZ101

**Paratypes.**  
KÜH2222, KÜH 392.

**Material.**  
PIZ 530, PIZ 28.

**Etymology.**

*Thetydostrobus marebbei* is named after the Ladinian locality San Vigilio di Marebbe.

**Type localities.**  
Kühwiesenkopf, Piz da Peres

**Type horizon and age.**

Dont-Formation.  
Lower to Middle Triassic, Anisian, Pelson

**Repository.**

Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

**Diagnosis.**

Male cycadalean cones developing from a peduncle. Ovoid to cylindrical densely closed by rhomboidal scales. Pollen-bearing organs wedge-shaped, microsporangia on the lower surface. Scale apex with trichoms.

**Description.**

**Peduncle:** A 2 – 3 cm-long peduncle crosses over to an 8 – 15 cm-long cone from which 30 to 100 sporophylls arise perpendicularly.  
**Cones:** Usually cylindrical to ovoid-cylindrical (PIZ 101). Cones in youth closed, (PIZ 28) in adulthood open dispersing their pollen grains. (KÜH 2222) Pollen cone PIZ 101 is 6 cm long and 3 cm wide, each sporophyll 1 cm to 0.5 cm. It belongs to a juvenile stadium. Male cone PIZ 530, 4 x 3 cm highlights very well pointed hairs on the apex. PIZ 28 represents a well conserved peduncle. The scales are covered with trichomes. Male reproductive structure KÜH2222 shows more adult stadium with open pollen sacs, to sori aggregated. This cone is 10 cm long and 4 cm wide. KÜH 392 belongs to an old, semi-destroyed male cone. It is suggested that all cones belong to Bjuvia.  
**Male-sporophylls:** Usually 2-3 cm long, on the apex 1-1.5 cm by 0.5 - 0.8 cm wide. Microsporophylls distally rhomboid, covered on the apex with fine hairtips. Pollen sacs on the lower surface, visible to the naked eye, ellipsoid to spheroidal.

**Remarks.**

The Cycadalean pollen cones fossil record is unfortunately poor. One belongs to
1) KÜH 2222 Thetydostrobos marebbei. Mature pollenorgan 10 x 4 cm
2) PIZ 101 Thetydostrobos marebbei. Male cone 6 x 3 cm.
3) PIZ 2222 Thetydostrobos marebbei. Mature cone showing pollen coming out
4) PIZ 101 Thetydostrobos marebbei. Lateral part showing the sporophylls (10 x 5 mm)
Lasiosstrobus, a permineralized Upper Carboniferous reproductive organ, but due to its poor preservation it could also be interpreted as fertile conifer or ginkgo-organ (Taylor T. N., Taylor E. L., 1993). Androstrobus, a cylindrical pollen cone from the Middle Jurassic, found in Yorkshire, England, just younger in age, from an exterior view could have some similarities with Dolomite-Anisian Thetydostrobus. Further studies could ascertain whether there has really been evolution from Thetydostrobus to Androstrobus.

A male cone found attached to stem apex with Nilssonian-like leaves, named Holozamites hongtaoi (Wang Y. D., et al. 2005) from the Chinese Yangcaogou Formation (Upper Triassic) has more affinities to Thetydostrobus. The cone is cycadalean, but seems to be more developed than Thetydostrobus. There are more affinities with fertile scales from the Anisian Dolomites described below as Peresia raetiae. They bear a fertile leaf-like zone on the distal part of the stalk. Although the individual scales are clearly separated on the axis each from each other and therefore we cannot define it as real cycadalean male cone, it is worth making some considerations. Peresia is made up of connate fertile pinnate foliage. These microleaves were fern-like with sac-like structures arranged in sori. The crowding of several microleaves made them inflated and convex. They already showed the habitus of current male Cycads-scales, with their distally formed trichomes, microsporangia on the lower (abaxial) surface of the wedge-shaped scales. Some enigmatic problems can therefore be resolved more easily. The male cone of Cycads is nothing other than an aggregation of scale-fernfronds that initially originated on a discontinuous base until the point when they became very closely aggregated. Peresia raetiae seems to be the last non-cycadalean fructification, Thetydostrobus marebbei the first real male cycadalean-cone. Further studies will provide evidence of which Bjuvia species the Thetydostrobus cone belongs to. Bjuvia was with the utmost probability dioecious and, like today’s cycads, had a specific time of year to produce male cones. Hence so-called “springtime-vegetation” in some strata of Piz da Peres rich in cycadalean male cones. A decomposition process began just after pollination and therefore well-preserved male cones are rare.
1) PIZ 530 *Thetydostrobus marebbei*. Male cone (5 x 3 cm + 2 cm petiole) Partially covered with hairs on the lower part. Single sporophyll about 10 x 5 mm

2) PIZ 530 *Thetydostrobus marebbei*. Lower part with hairy apical spines 2 mm long

3) KÜH 392 *Thetydostrobus marebbei*. Decomposed male cone

4) PIZ 28 *Thetydostrobus marebbei*. Lower part with petiole
Discussion

This Early-Middle Triassic flora of the Braies Dolomites constitutes an interesting primitive Cycadalean-bennettitalean-preangiosperm plant association. Although the Bjuvia-assemblage could be defined as “very similar” to today’s cycads, the group of Peresiaceae could only be defined as “angiospermous, but not angiosperms” and also “bennettitalean, but not bennettitalean”. The evolution of Peresia probably constitutes the main condition for the development of cycads and angiosperms. Or, ferns, cycads and angiosperms are more closely related than was thought up to now. In this form angiosperms could be regarded as merely specialized cycadophytas, in which Bennettitales and Cycadales have to be seen in the same context.

It is difficult to say what happened after the Permo-Triassic crisis. None of the big plant-groups vanished. Horsetails survived as well as ferns, conifers, and club mosses. But all they changed consistently: they reduced in size, especially club mosses and horsetails. The decreasing of all plant-parts was probably a factor that led to the beginning of cycads and angiosperms.

**Climatic change:** The Triassic world was marked by a temperate climate. *Antarcticycas* documents that also on the Poles there was enough warming to allow a cycad to live. The impenetrably dense Carboniferous forests were now replaced by big savannas and shrubby bushes. The oxygen content probably also changed.

**Insect life.** The leaves of *Bjuvia* and *Ladinia* show traces of having been bitten by insects or animals (PIZ 338, PIZ 335, KÜH 1409, KÜH 217). It is difficult to know if they descend from insects, pollinators or small reptiles but it is to be assumed that Cycad-Angiosperm evolution was co-influenced by the ascension of pollinators.

**Dinosaur age.** Dolomite-Anisian plant-beds also bear many archosaurier remains and track ways. Some of them (*Archaeo-Parachirotherium*) were classified as dinosauriformes or closely related to primitive dinosaurs. Primitive snake and lizard-skeletons (*Megachirella wachtleri*), were also found together with Piz da Peres plant-assemblage.

**Characters**

**Peresiaceae. General features.**

It is now to be established which important plant revolutions could have been introduced by the Peresiaceae.

**Taeniopteroid ferns.** The Peresiaceae are a group of Early Triassic enigmatic fructifications. They evolved between the Palaeozoic and Mesozoic and diversified in a short time to several lines of “higher” seed plants.

**Kinship of cycads and angiosperms.** The fusion of distal microleaves helps not only to form Cycad cones but also flower evolution and stamen-carpel. The Permian-Trias-
Bisexual flower. Certain Peresiaceae were dioecious (PIZ 155, PIZ 620) others monoecious (PIZ 553). One line leads to cycads, the other to Bennettialean and angiosperms.

Origin of stamen. Distal Peresiaceae micro-pinnas, aggregated and compressed, formed the stamen of the angiosperms (PIZ 553). The pollen organs lie on the apical abaxial part of the leaves.

Origin of carpel. Taeniopteroid micro-pinnas on the lower part of Peresia-fructification were compressed and forced to grow upwards rather than outwards due to lack of space and formed flowerlike structures with integuments. On the lower surface of these fertile leaves the sporangia grouped together or reduced in number, even becoming infertile, giving their biomass to the others.

Unisexual pollen-cone evolution. Some Peresiaceae aggregated fertile fronds on a stalk and formed by compressing the first cycad cones (PIZ 617, PIZ 111).

Pollination. Both wind- and self-pollination was therefore possible.

Cycadales. General features.

With the new Anisian Cycadophyta the phylogeny of Cycads has to be seen in another context. The established doctrine of the genus Cycas as the most primitive must be reviewed. The leaf structure from Stangeria resembles most the Palaeozoic-Triassic ancestor; the fertile part of Cycads could have evolved from Bowenia-like spirally arranged bipinnate fronds. Short scale-like male and female cones as ancestors of all modern cycads evolved at the same time as Cycas megasporophylls. Therefore it is superfluous to talk about more primitive or derived properties.

Cycads were in this case as conservative as conifers throughout all the millions of years in their morphology, anatomy, ecology, physiology and adaptive capacities. They have in fact not changed much since the early Mesozoic.

In a surprisingly short time all the aspects of today’s cycads were formed, from the composition of coralloid roots to the trunk with scars and pits from dropped leaves, cataphylls and even the male and female strobili. The evolution of real Cycads was nearly finished in the Early-Middle Triassic. Over the next 240 million years and more, only a few details changed.

Based on Anisian cycad fossil records, the following theories can be put forward:

Monophyletic genesis. The ancestor of all Cycadales is to be sought in Carboniferous-Permian pteridophyta. There are several reasons that the foliage of the Palaeozoic ancestor belongs to a taeniopteroid bipinnate fern with several forking midribs and lateral veins towards the margin. Fern-progenitors could be highlighted by arrangements of microsporangia in sorus-groups, constantly on the abaxial side lying sporangia and also the circinate vernation. The first real Cycads are to be searched for among the Permo-Triassic boundary.

Single leaf-evolution. All extant Cycad leaves except Stangeria and Bowenia originate from the modifying and increasing of a pina with entire flat lanceolated single leaves. The transition to real cycadophyta occurred in the Early Triassic from oblong, sharp pointed single Ladinia-leaves (PIZ 133, PIZ 332) to U-shaped Bjuvia-leaf types at the apex. With an increase in leaf dimensions, (KÜH 2140) probably to give adequate rigidity in extreme winds, the leaves became more deflected and folded (KÜH 470). This came hand in hand with a varying degree of casually ripped and segmented foliage type. (KÜH 2226, KÜH 2217, PIZ 182). Finally they changed to a nearly mathematical segmentation typical of Nilssonia (KÜH 897, KÜH 670). In a relatively short time the typical Cycad segmented pinnate leaf was formed.

Reduced leaves. Cataphylls in extant Cycads are the last remains from the ancient entire oblong to acuminate pungent foliage and evolved also just in the Early-Middle Triassic as an means of defence against insects and animals. They also represent a transition system from sterile to fertile leaflets. (KÜH 2221)

Primary taproot system. Early Triassic Cycadales formed a main massive taproot.

Coralloid roots. Right from the start Cycads had coralloid roots and a strong pillar-shaped root (KÜH 2218). White spheres between Triassic Bjuvia-coralloid roots sug-
gest that cyanobacteria already lived at that time in symbiosis with cycads.

**Bulbous stems.** Early Mesozoic stems were just tuberous, unbranched and terminated by an apical meristem. Like extant cycads the surface of the trunk was tough and bark-like from the persistent bases of fallen leaves (KÜH 2218, KÜH 2220). A more primitive pre-cycadalean stem-system consists of a loose adhesion and combination from different single leaves (Ladinia).

**Unisexual performance.** All Early Mesozoic cycads were already like extant dioecious ones. Male and female sporophylls were born on different plants. Megasporophylls found together suggest that ancient Cycads sometimes bore various strobili on the same plant.

**Two-way megasporophyll-evolution.** Female sporophylls evolved in two ways in the early Triassic. From big pinnate fertile leaves (Dioonitocarpidium - Cycas) and from smaller bipinnate fertile leaves (Peresia - All other extant Cycads).

**Dioonitocarpidium-cone Cycads.** Early cycads produced a crown of macrosporophylls on a stalk-like axis. The seeds were attached to the lower surface of the sporophyll. Each fertile leaf enclosed from 2 to 20 ovules in two rows. Ancient cycads bear seeds, just slightly bigger than sporangia. A featherlike apex finished off the sporophyll leaf. Intermediate forms (Ladinia) showed that the featherlike structure originated as a spine arrangement to prevent animals or insects biting them. Dioonitocarpidium-cones feature only marginal differences with extant Cycas. (KÜH 2118, KÜH 534, KÜH 758, KÜH 2108, PIZ 141)

**Peresia-cone Cycads.** Peresia raetiae-type scales (PIZ 613) suggest that the evolution of female cones of all Cycads except Cycas occurred in the same way as male cones by mimetizing and compressing bipinnate leaflets.

**Male Cycas cones.** The origin of all extant male pollen organs lies in a compressed micro-pinna with extended helically arranged microsporophylls (Peresia). The entire pollen-scale was a loose arrangement of many individual small-sized pollen-leaves. (PIZ 155, PIZ 620, PIZ 553). Microsporangia were arranged in the upper part on the lower surface. For several reasons, probably due to weather conditions or for animal protection separate pollen stalks tended to fuse forming a cone (Thetydostrobus). The cone-building processes were completed in the Early Triassic.

**Distally orientated trichomes.** Early Triassic cycads produced trichomes on young leaves and especially on the distal part of sporophyll microleaves. They were apparently unbranched (PIZ 207, PIZ 617).
Conclusions.

We can now document a part of history of an extraordinary plant-assemblage with many links that had been missing until now. It will be particularly important to phylogenetic studies that Paleozoic fernfronds were able to reduce their sterile foliage to single leaves and consequently to turn back into segmented pinna. Equally interesting is the fact that the male and female cone evolved from single fronds to aggregated scales and after that to compressed cones. Synangia and sporangia turned into pollen organs and ovule-bearing sporophylls. At the same time other plants, the genus *Peresia*, began to form from their fronds bisexual “flowers” with pollen-organs and ovule bearing carpels. They only coexisted for a short time, before each continued along its own path, one becoming angiosperms and the other cycads. The great invention was the fusing of their fronds to pollen and ovule-scales on one side and protected stamen and carpels on the other. Hence, the location of Piz da Peres has given us deep insight into a remote paradise of primordial times.

Acknowledgments.

I would first like to thank the beautiful nature that has given me so much satisfaction. From 1995 when I discovered the first new cycad *Bjuvia dolomitica* until now I have learned so many things about the time and relativity of human values. When I stood as “time-walker” on Piz da Peres I completely forgot about the busy, hasty and stressful life in the lower valleys. For weeks and months I searched for an abominable phantom: the discovery of all the parts of the plants. The parts came out and formed part of the mosaic. I was led along the wrong tracks and then corrected. The search for the male organs drove me mad. One day I found the first poorly preserved one. Another day, many weeks later, another one. The individual Cycad pieces were put together. New traces opened. In the summer I forgot about humanity and turned into another being. I did not discover how to make big money, but I walked inside nature, as people are seldom allowed to do.
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