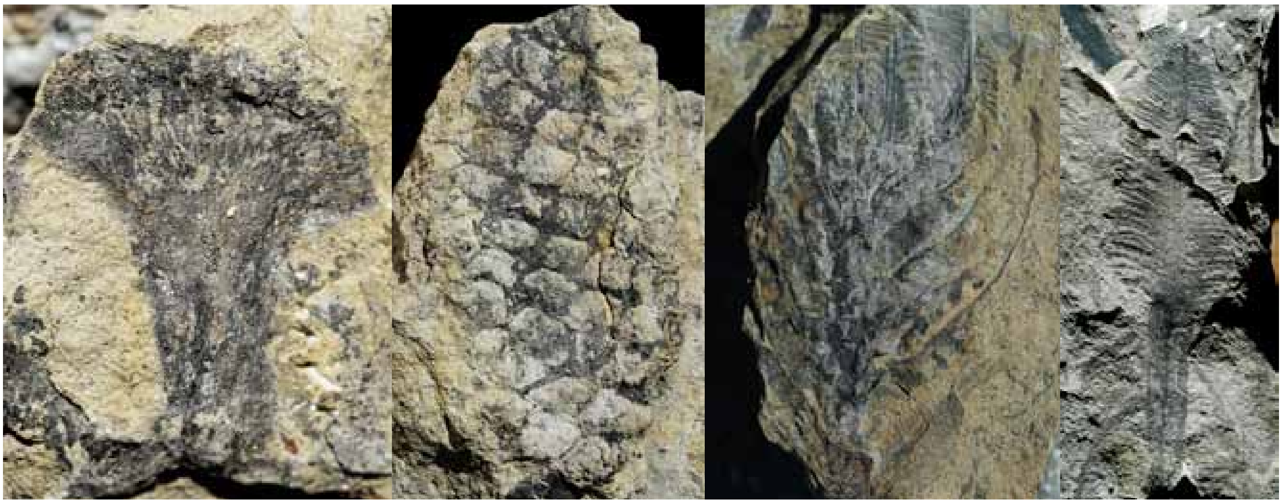
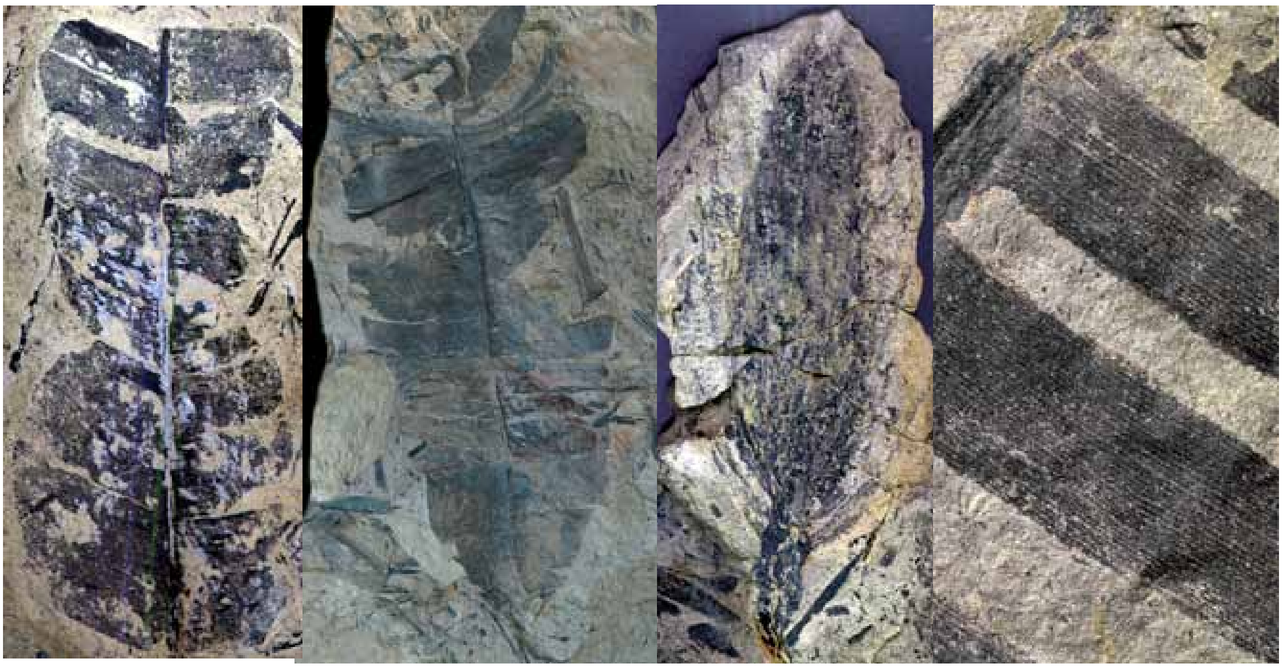


ABOUT THE ORIGIN OF CYCADS AND SOME ENIGMATIC ANGIOSPERM-LIKE FRUCTIFICATIONS FROM THE EARLY-MIDDLE TRIASSIC (ANISIAN) BRAIES DOLOMITES (NORTHERN ITALY)

by

MICHAEL WACHTLER



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

by
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Abstract

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. Since 1999 the author has recovered large quantities of well-preserved cycadalean remains and other enigmatic strobili and fructifications from Early Middle to Middle Triassic (Anisian) sediments. Therefore it is now possible to view their unusual story in a new light.

Several Anisian Cycads and other fructifications with sometimes unknown affinity were described and the palaeobiology of the habitat investigated. *Pizperesia tannae* gen. nov. sp. n. is an enigmatic fructification with free spirally arranged hammer-like pollen scales on the upper part of a branch and flower-like structures on the lower part. The single organs give the impression of densely reduced and compressed small fern fronds. *Pizperesia raetiae* gen. nov. sp. n. 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. sp. n. 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 sp. n. 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 consist in a single strong taproot and branching coralloid roots. *Dioonitocarpidium cycadea* sp. n. and *Dioonitocarpidium loretzi* sp. n. are female sporophylls belonging to *Bjuvia primitiva* and *Bjuvia olangensis*. *Thetydostrobus marebbei* gen. nov. sp. n. is thought 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* sp. n. has clearly segmented leaflets resembling the typical foliage of extant Cycadales.

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

Introduction

The geological and palaeontological 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 MOJSISOVICS (1882), who worked on ammonoids. However, the most widely accepted long-standing study was edited by JULIUS PIA in 1937 (*Stratigraphie und Tektonik der Pragser Dolomiten in Südtirol*). Further studies (BECHSTÄDT & BRANDNER, 1970;

DE ZANCHE ET AL., 1992) added to the knowledge about this area in the Eastern Dolomites, which UNESCO included in the world heritage list in 2009 for its geological beauty.

Surprisingly, until 1999 only a few plant fragments had been described from the Piz da Peres area, which lies between the Braies Valley and the Gadertal Valley (Fig. 1). In 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 and Dreifingerspitze, across the borough of Olang, then around the Piz da Peres mountain up to Marebbe (Fig. 2b), covering a distance of over 20 km. Everywhere within this area he found plant fossil-bearing levels in typical Anisian (lower Middle Triassic) successions. These contained rich Early Mesozoic floras, but also reptile remains, new ichnofaunas and marine biota (e.g. bivalves, brachiopods, ammonoids and fish skeletons). The first results were published in 2002 (BROGLIO LORIGA ET AL.).

Geological age

In this area the plant-bearing beds begin about 75 m above a massive carbonate platform previously known as 'Algenwellenkalk', and now attributed to the Gracilis Formation (DE ZANCHE ET AL., 1992; GIANOLLA ET AL., 1998). The adjacent, so-called Dont Formation is more than 200 m thick and bears several lens-shaped plant horizons that reach a thickness of about one metre. These alternate with silty and marly limestone or carbonate layers, in which only sparse terrestrial plant remains occur. All successions were deposited in an original basinal, lagoonal, peritidal or continental habit.

Studies on brachiopods (BECHSTÄDT & BRANDNER, 1970) and foraminifers (FUGAGNOLI & POSENATO, 2004) suggest a Pelsonian age for the studied section; integration of studies of palynomorphs and ammonoids has narrowed the time interval for the deposition of the fossiliferous horizon down to the boundary between the Middle and Upper Pelsonian (KUSTATSCHER ET AL., 2006). However, plant remains have also been found in the slightly younger Richthofen Conglomerate (AVANZINI ET. Al. 2007) and Morbiac Dark Limestone (DELFRATI & FARABEGOLI, 2000), both Illyrian in age, often inside rich ichnofaunas also containing dinosauromorph trample layers.

Over the years an extraordinarily rich plant assemblage has come to the surface, featuring highlights such as its abundance of lycophytes, with five new species identified to date (*Isoetites brandneri, Lepacyclotes bechstaedtii, Selaginellites leonardii, Selaginellites venieri* and the arborescent *Lycopia dezanchei*, an interesting link between Carboniferous and recent lycopodales). In addition, Sphenophyta (*Equisetites*) and Coniferales (several *Voltzia and Alpia genera*), as well as new fern genera (*Gordonopteris, Wachtleria, Ladinopteris*) have been discovered. To date more than 30 different plants, the most new species, document the importance of this novel 'Fossillagerstätte'. Some, such as the ferns *Neuropteridium* and *Anomopteris*, or seed ferns 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 from the Braies Dolomites.

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

Conclusions/Significance

This 241.5-million-year-old world represents the most complete ancient cycadalean world ever found. All the main parts of cy-

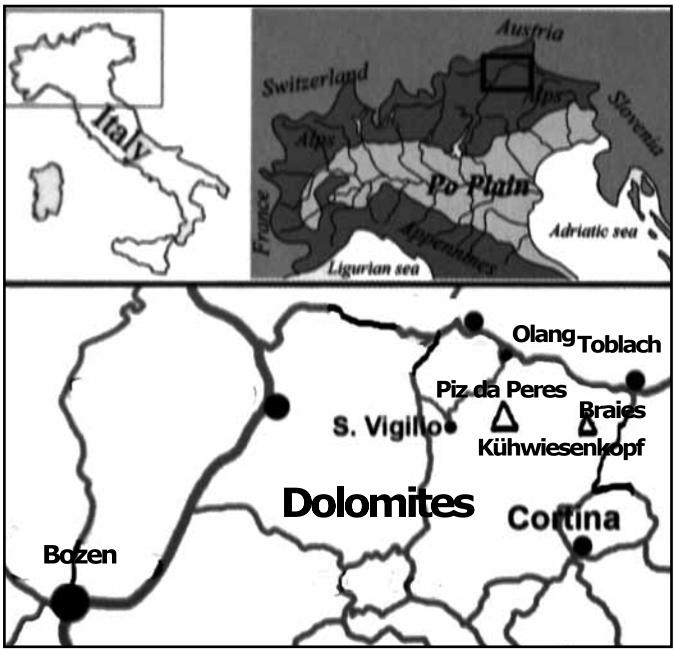


Fig. 1: Map of the Braies Dolomites area in Northern Italy with Piz da Peres and Kühwiesenkopf.

cads, such as the leaves, stems, roots, male and female strobili, along with the juvenile and mature life cycle, animal associations and also the possible parental plants, were discovered in large quantities. Research on their characteristics has allowed a fairly complete reconstruction of their life history and associated habitat. It is of particular importance to phylogenetic and cladistic studies that in the Early to Middle Triassic the evolution of cycads was almost complete such that they differed only in small details from the extant species. The relationships between cycad evolution and the early angiosperm habitat were studied and hypotheses established. Future studies and new fossil records will provide more clarity on unresolved problems.

Observation and statistical analysis of these specimens were used to develop an understanding of the Early-Mesozoic plant-universe. In this rapidly changing world, it is often difficult to determine when one leaf or fertile organ should be left in one genera and when it may be reasonable to move it to another. However, the enormous number of slabs was useful in this sense. Whereas at other sites only a few poorly preserved parts were recovered, the Piz da Peres area has yielded innumerable cycad parts. Comparison with specimens from several museums and other sites in Europe was also helpful, especially when fertile and sterile material could be re-examined. The same is true for all the valuable literature that has been produced over the centuries by many researchers. Analysis and new hypotheses from other authors (CRANE, 1988, GRIMM, 1999) about cladism and the developmental pathways of cycads between their early origins and their present-day counterparts were also very useful. Further analysis would enlarge our knowledge about this early paradise.

Repository

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

Materials and Methods

The study was 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, do cycad leaves have cuticles.

To date (2010) 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
Pizperesia: about 20 pieces, mostly single scales

Specimens were photographed under natural light using a Nikon D200 camera, with AF MICRO NIKKOR 60 mm 1:2.8 D and AF-S NIKKOR 17-35 mm 1:2.8 D lenses for larger specimens. The digital images were processed using Adobe Photoshop CS version 5.1.

Fig. 2: Plant-bearing horizons on Kühwiesenkopf (a) and Piz da Peres (b).

Systematics

Palaeoecology and Palaeoclimatology

Much observational research has been conducted by the author over many years, leading to the recognition of various interesting palaeoecological and palaeoenvironmental effects. One of the most surprising diagnoses regarding this ancient, over 241-million-year-old habitat, was that diversification occurred within an extremely short period of time. This was noted not only for plants, but also the layers accompanying the rich ichnofauna. Newly discovered dinosauromorph to dinosauriformes tracks and skeletons suggest that complete modification of terrestrial life occurred during this period. It is beyond the scope of this publication to go into more detail about a previous Permo-Triassic crisis, but nevertheless, rapid mutations and variations are, in fact, clear.

Some lens-shaped layers understandably hold a higher percentage of cycads. Conifer-rich strata contain few cycad leaves. The rock fall precipices of the western part of 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 mountain extending from Kühwiesenkopf to Drei Fingerspitze was richer in fully-grown female organs as well as large cycadalean leaves.

The life cycle of female strobili is usually much longer than that of males. When pollination has finished the 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 is useful for the classification and understanding of the primitive evolution of male strobili.

Many cycad leaves bear signs of having been eaten by small animals, probably insects. Insect pollination may have occurred and would have been a new development in evolution and an advantage to other plants (STEVENSON et al., 1999). Marks and aggregations were found on several cycad leaves that could be interpreted as coprolites.

In the Early Permian numerous large land plants like *Sigillaria, Calamites* and *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 bushy lycophyte *Pleuromeia*. The large horsetail trunks (*Calamites*) were replaced with moderately growing *Equisetites*. The Palaeozoic ferns like *Pecopteris and Sphenopteris* were replaced in the Middle-Triassic Piz da Peres landscape by low growing ferns like A*nomopteris, Neuropteridium* and *Gordonopteris*, and the seed ferns *Alethopteris, Odontopteris and Neuropteris* by the Triassic genera *Scythophyllum* and *Sagenopteris*. Most of the large woody plants were eventually replaced by conifers from the *Voltzia* group. Above all, the rapidly expanding cycadophytes became more and more dominant. A similar situation has been observed in the intercontinental Central European Basin, often with the same plants, although the large cycadophyta flora is missing. The evolutionary event caused by the elimination of the large land plants of previous times allowed a group of dinosauromorph animals to develop who, by increasing their height with erect bodies, were more able to survey the landscape. They could therefore reach more of the nutritious plants than other animals. In the dark and dense woods of the Carboniferous period that was a disadvantage.

Just as important as insect pollination was the new strategy involving small compressed and gradually fusing fertile microleaves as a basis for all Cycad cones and probably the origin of the angiosperms. A new repository for pollen and ovules was invented. The new order of *Pizperesiaceae* constituted a 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 stamens and carpels.

By observing the palaeoecological environment it can be deduced that the flora and fauna changed more rapidly than it has done in the subsequent millions of years. The causes of such changes have remained a mystery.

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 the fossil record. They have many characteristics that are unique in the plant kingdom. The only certainty is that their ancestors are to be found in the Palaeozoic ferns or seed ferns. Researchers continue to argue over whether higher gymnosperms have more elements from ferns (like Marattiales) or seed ferns (the most commonly mentioned group are the Medullosaceae). Only new fossil findings will resolve this issue (KENRICK & CRANE, 1997).

Cycads have a fossil record that dates back at least 270 million years, making them the oldest crown-clade of seed plants. There is some controversy over older true cycad fossils from the Early Permian or the late Carboniferous period, although the extent to which they radiated is unknown because relatively few fossil specimens have been found (BRENNER 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 have some primitive fern-like features and other characteristics that until now have been 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 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 which may be considered preangiospermic. Both questions remain difficult to resolve.

The features used to separate angiosperms from other seed plants include the enclosed nature of the ovary, the presence of flowers, vessels in the xylem and phloem, double fertilization, bitegmic ovules (with two integuments) and the presence of endosperm and tectate pollen (TAYLOR AND TAYLOR, 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 11 genera and 292 species distributed across the warm, tropical and subtropical environments of the Americas, Africa and Australasia. However, 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 via seeds and are characterized by a large crown of compound leaves and a stout trunk (JONES, 2002).

The living cycads are divided among three families: the Cycadaceae, the Stangeriaceae and the Zamiaceae.

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

The Stangeriacea contains two genera: Stangeria, with its pinnate, fern-like leaves, and Bowenia 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 Zamiodeae. 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, some of which are also unique in the plant kingdom, are as follows:

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

Dioecious. 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 and efficient reproductive 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, 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 to 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.

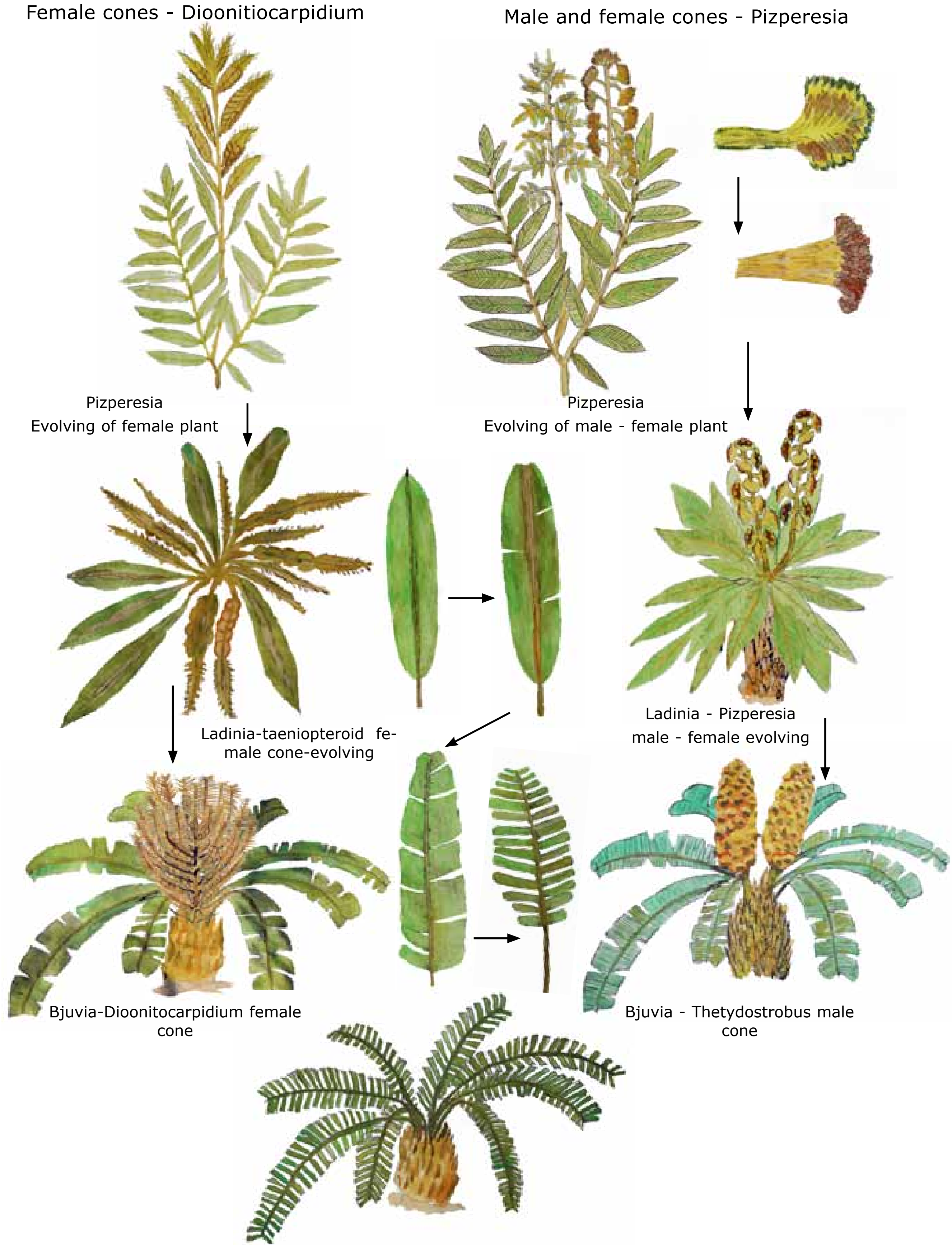
Petiole. All leaves of cycads have a basal woody structure.

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 ages. These structures could be subterranean, almost tuberous or bulbous. Cycads stems are pachycaulous.

Suggested evolution of Palaeozoic-Early Mesozoic Cycads



Systematic Paleontology

Subdivision: Filicales? BOWER, 1899
Pteridospermophyta? F. OLIVER & D.H. SCOTT 1904
Order unknown
Family indet.

Genus *Pizperesia* gen. nov. WACHTLER, 2010

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 it was first found.

Pizperesia raetiae sp. nov. WACHTLER, 2010

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, Kühwiesenkopf

Type horizon and age

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

Repository

Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

Diagnosis

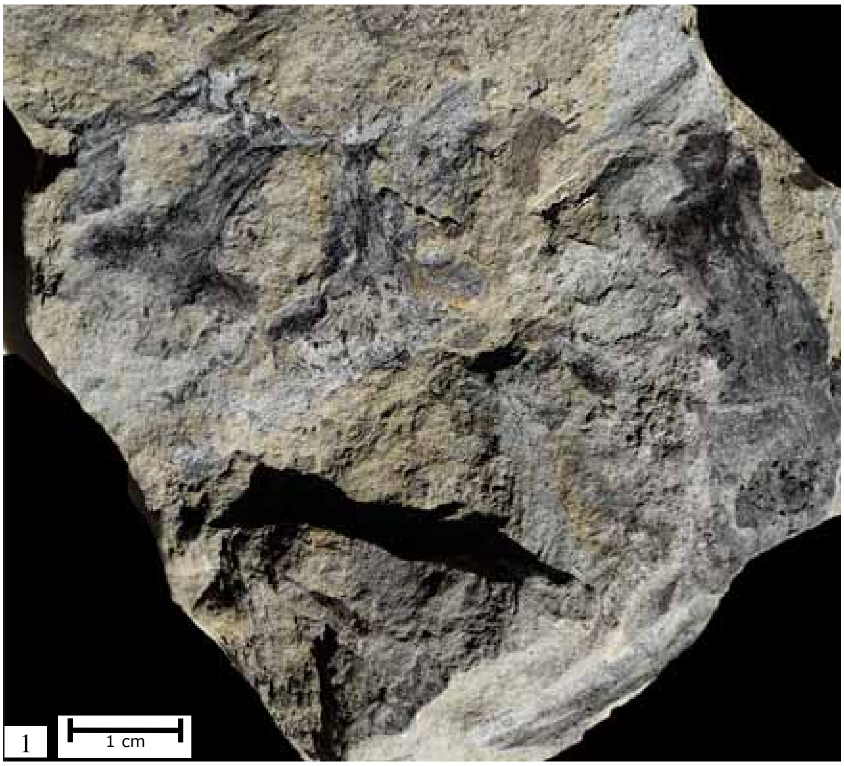
Scale-like appendices arranged helically on a central axis. Single round-bodied scales made up of several microleaves on a combined stalk, distally covered by unbranched trichomes. Elongated pollen sacs on the lower surface of the apex.

Description

Sporophyll: Scales arranged helically on up to 12 cm-long stalks. PIZ 155 consists of a 12 cm-long, 0.5 cm-wide incompletely preserved axis from which three pollen scales branch. The distance from each organ to the other on the same side is 5 mm. Rupture nipples suggest that many fertile scales occurred on both sides of the stalk. This was also observed on other specimens (PIZ 620).
Fertile scales: Up to 30 mm-long scales, reaching 20 mm wide at apex. 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 to 6 microspores on the lower surface aggregated in two rows along the median axis. About 10 to 12 microleaves form an entire fertile scale. Several microsporangia were observed on the lower surface of each 8–10 mm long, 1–2 mm wide micro-leaf (PIZ 617). The distal surface of each microleaf is covered with a ramentum of filamentous, unbranched trichomes (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 partial and entire strobili of *Pizperesia raetiae* were found. Since no other similar pollen organs are known from 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, *Pizperesia raetiae* consists only of loosely ar-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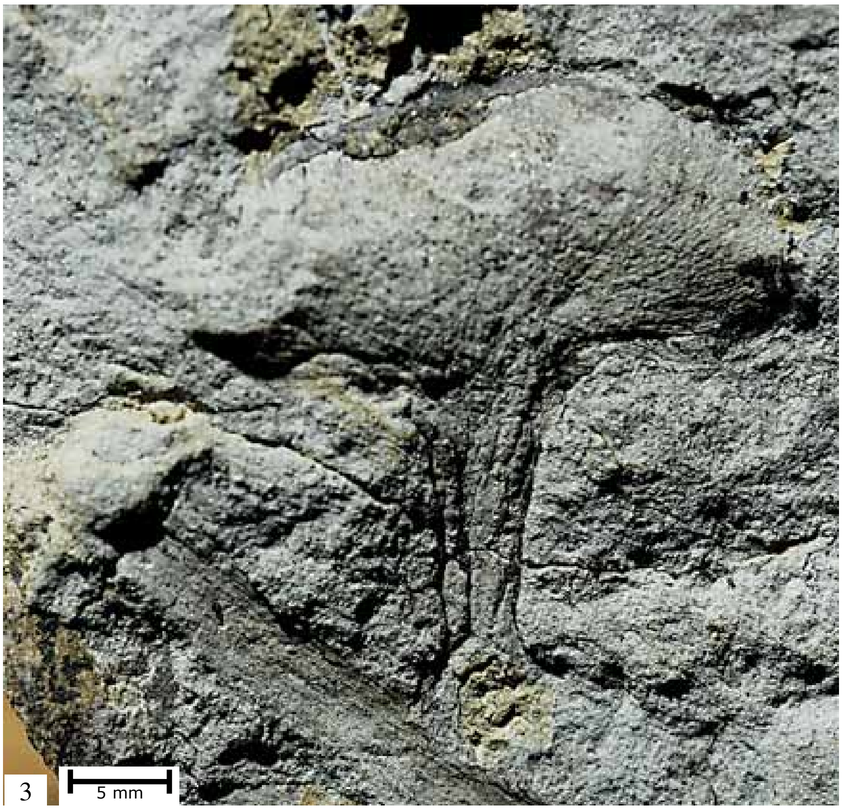
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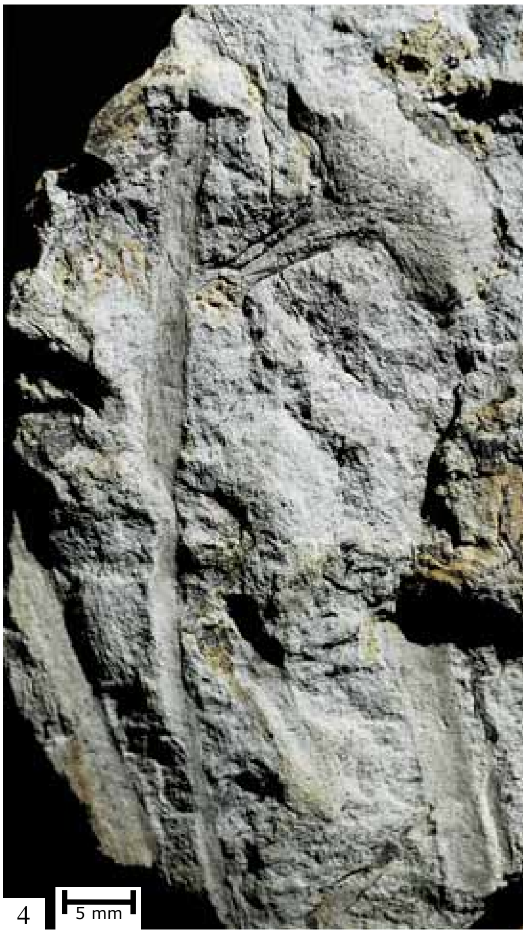
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1) PIZ 155 *Pizperesia raetiae*. Holotype. Sporophyll with three attached scales and one attached Ladinia leave on the upper side. Slab 6 x 6 cm. Scales 20 mm, petiole 90 mm.

2) PIZ 155 *Pizperesia raetiae*. Single scale covered with trichomes – 20 mm x 15 mm at apex, 5 mm at base.

3) PIZ 620 *Pizperesia raetiae*. Scale 30 mm long, 25 mm at apex, 3 mm scale stalk.

4) PIZ 620 *Pizperesia raetiae*. Entire sporophyll, stalk 80 mm x 2 mm with attached scales.

ranged scales on a stalk. Another possibility is that Pizperesia scales are an initial stage of the cone-forming process of the male Cycadales fructification. Like the *Thetydostrobus* cone, *Pizperesia* scales also divide at the hairy apex. Sometimes Cycadalean *Thetydostrobus* also seems to be formed of densely arranged microleaves and not by a single scale like today's cycads.

Systematic Paleontology

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

Pizperesia tannae **sp. nov. WACHTLER, 2010**

Holotype

PIZ 553

Paratype

PIZ 207

PIZ 413 *Pizperesia raetiae*. Scale 20 mm x 18 mm. Sporophyll evidencing in difference to the other the impression of two macro-seeds, like most of extant female cycad cones (Dioon, Encephalartos, Macrozamia).

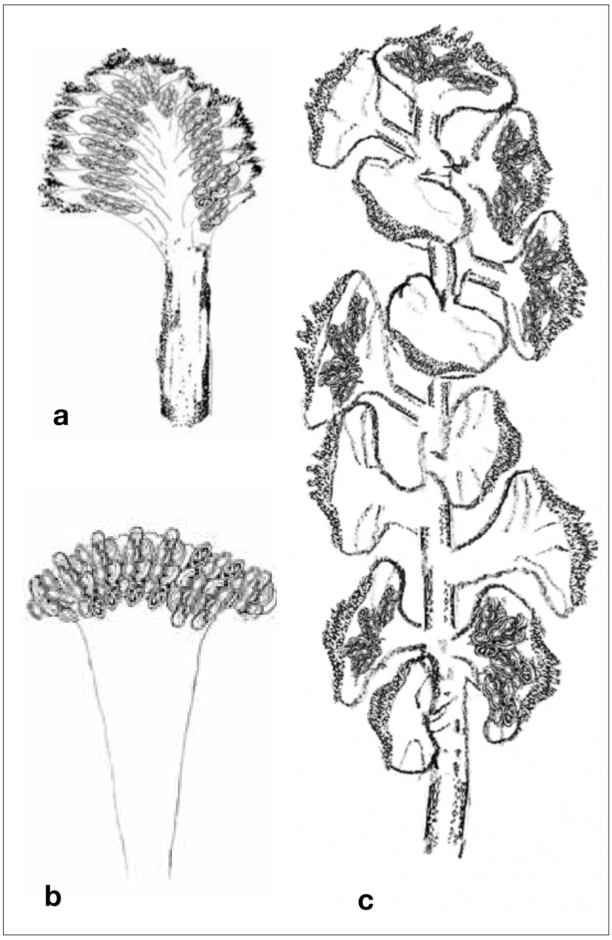

Fig. 4: Different types of *Pizperesia raetiae* scales.

1. Single leaflets arranged to form a fertile bouquet. Microsporangia aggregated on a median rachis of each leaflet (PIZ 617).
2. Fused leaflets and elongated microsporangia on the abaxial side (PIZ 209).
3. Suggested construction of *Pizperesia* fructification (PIZ 620).

Etymology

Pizperesia 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


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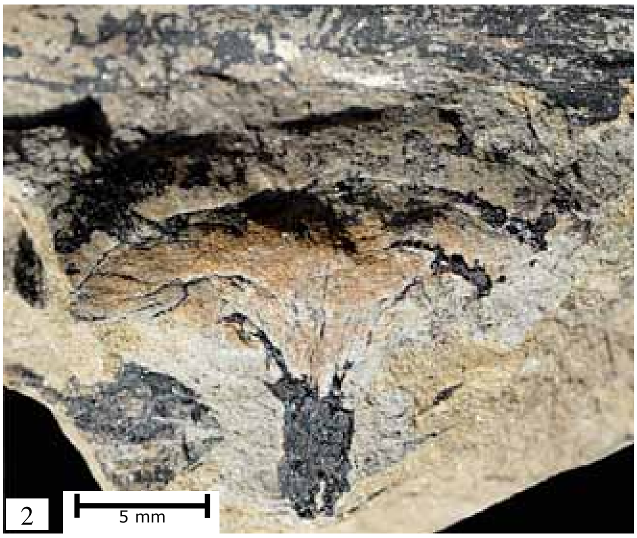
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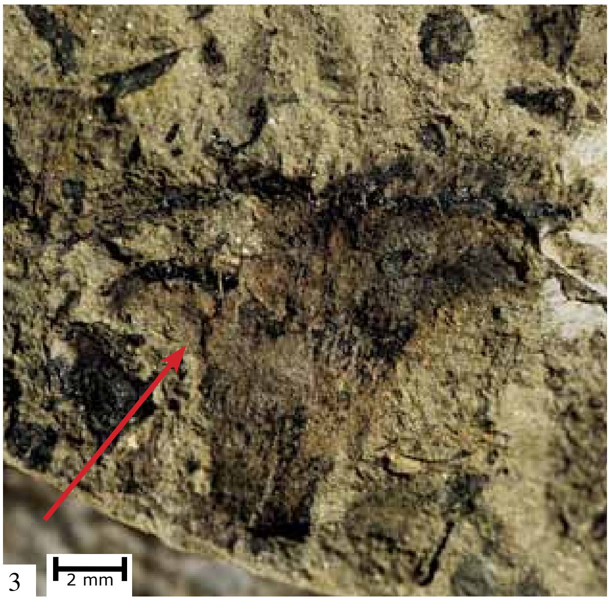
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1) PIZ 617 *Pizperesia raetiae*. Paratype. Scale 20 mm x 18 mm. Microsporangia on leaf-like structure at apex.

2) PIZ 111 *Pizperesia raetiae*. Single scale (20 mm x 20 mm).

3) PIZ613 *Pizperesia raetiae*. Single scale, bearing (female?) ovules laterally on the microleaf. 18 mm x 17 mm.

4) PIZ 209 *Pizperesia raetiae*. Paratype. 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 *Pizperesia raetiae*. Scale 30 mm x 20 mm with leaf-like organs, fertile part on upper side.

6) PIZ 209 *Pizperesia raetiae*. Abaxial part with pollen-bearing portion at apex (20 mm x 3 mm). Pollen 1 mm x 0.5 mm.

Diagnosis

Shrubby plant with scale-like appendices distally sprouting from slender stems. Upper part of branch holding scales with microsporangia, lower part with flower-like fructifications. Single scales made up of microleaves with isolated ovules on the abaxial side.

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 bud-like to flower-like 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 the upper part forming a dense 6 mm broad cluster

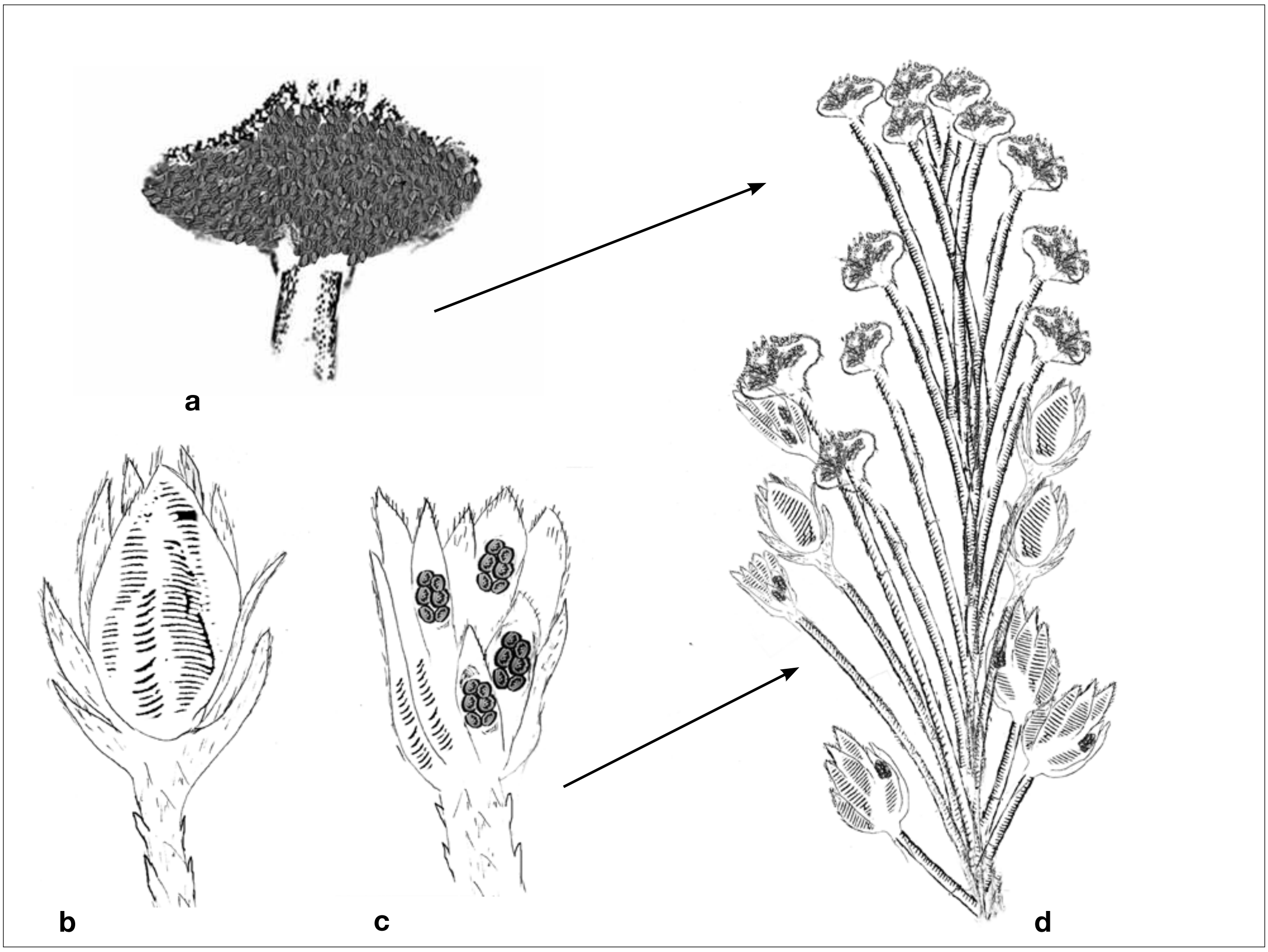
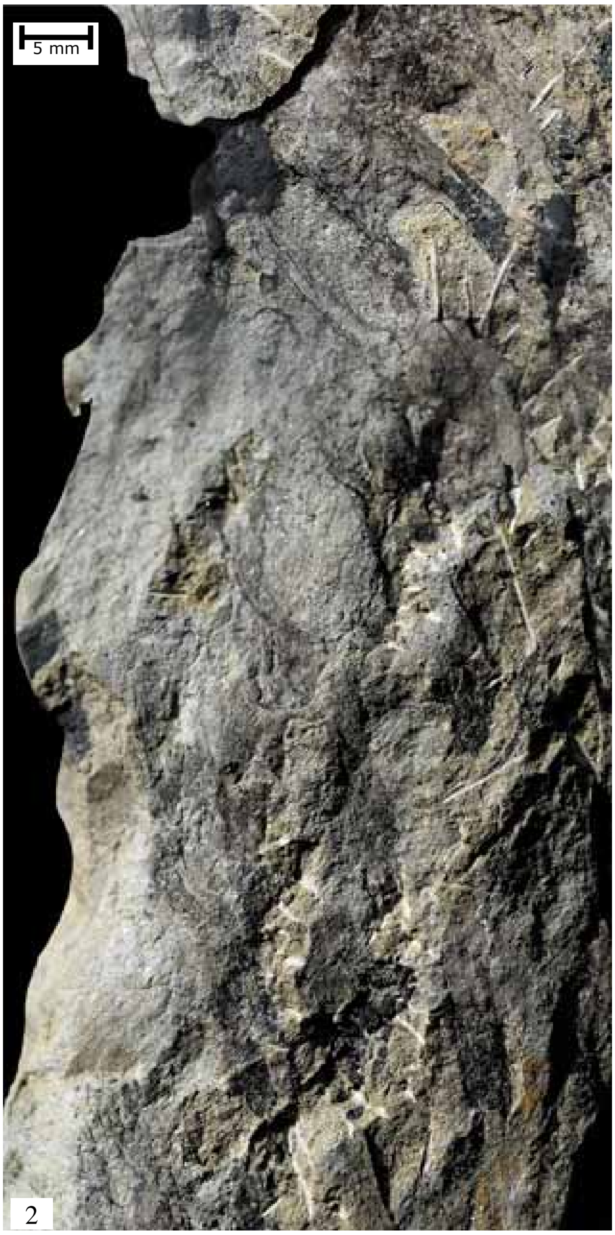


Fig. 5: Evolving phases of *Pizperesia tannae*.

1. Scale with microspores from the upper part of fructification (PIZ 553).

2 –3. Flower-like ovuliferous organs from the lower part (PIZ 553).

4. Structure of *Pizperesia tannae*. Single leaflets arranged to form a fertile bouquet.



1) PIZ 553 *Pizperesia tannae*. Holoype. 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 *Pizperesia tannae.* Five sporopylls distally attached on slender stems, including one microsporophyll on the upper side, and four flower-like macrosporophylls.

3) PIZ 553 *Pizperesia tannae*. Part of branch with unusually verucous surface (15 x 2 mm).

4) PIZ 207 *Pizperesia tannae*. Scale 20 mm x 18 mm, 8 mm basal stalk. Adaxial part showing the upwards growth of leaves.

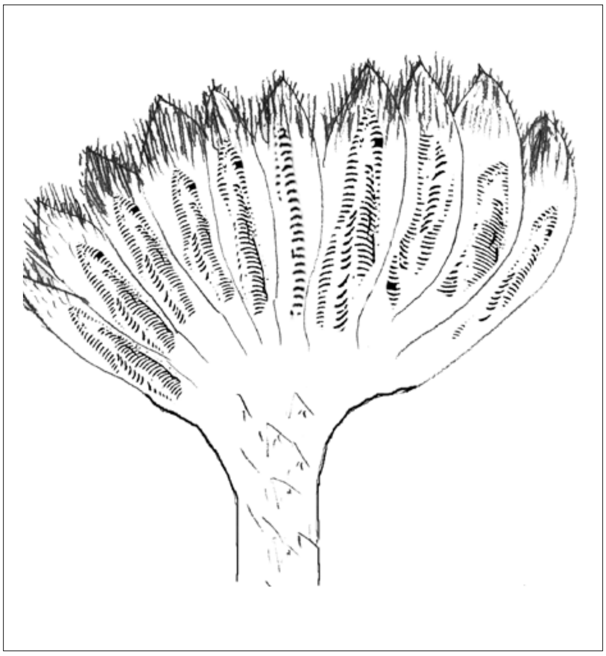


Fig. 6: *Pizperesia tannae*: Fused leaflet adaxial view. Clearly visible aggregated leaflets and unbranched trichomes (Bennettitalean female "flower") (PIZ 207).

all over the scale. Microsporangia on the abaxial part of the microleaves.

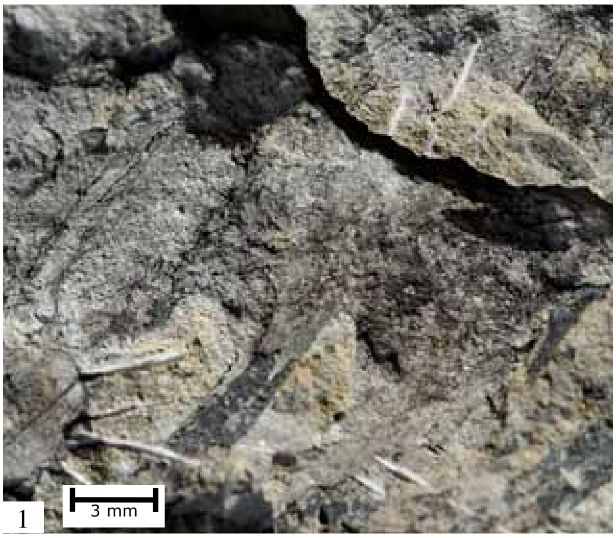
Macrosporangia: Microleaves of the flower 10–5 mm long x 1–3 mm containing 4 to 6 sporangia on the lower surface aggregated in two rows along the median axis. About 12 microleaves form an entire flower. Sporangia on lower part 1 mm x 0.5 mm.

Remarks

Until further studies provide more information about the Pizperesiaceae group, it is difficult to determine to which plant group these sporophylls could pertain. The upper wedge-shaped organs have close affinities with *Pizperesia raetiae*. However, the structure is quite different. On *Pizperesia tannae* the sporophylls are held by slender branches, but in *P. raetiae* the stem is corpulent and suggests more affinities with a primitive and incompletely fused Cycad sporophyll. *Pizperesia raetiae* also bears more trichomes than Pizperesia tannae. Pizperesia raetiae has also never been seen with divided micro- and suggested megasporangia-organs on the same sporophyll. Together they have fertile organs that resemble reduced and compressed fronds, and 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 Pizperesiaceae with their sporangia-leaves have more affinity to ferns (such as *Marattiales* or their fertile fronds *Scolecopteris*) than to seed ferns.

Another widely distributed group in the Middle Mesozoic were 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 cannot be ruled out.

However, it may be 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 stamens and the lower as rudimental carpels. If *Pizperesia raetiae* were able to fuse and compress the structure to form the cycadalean cone, then *Pizperesia tannae* was probably able to make the first step towards real angiosperms.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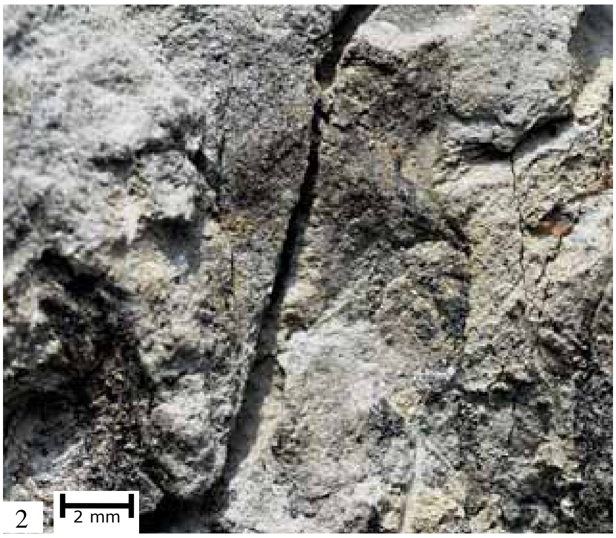
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1) PIZ 553 *Pizperesia tannae*. Microsporophyll (15 mm wide x 8 mm long) covered with microspores from the upper part of fructification.

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

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

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

5) PIZ 553 *Pizperesia 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, 2010

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 sp. nov. WACHTLER, 2010

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

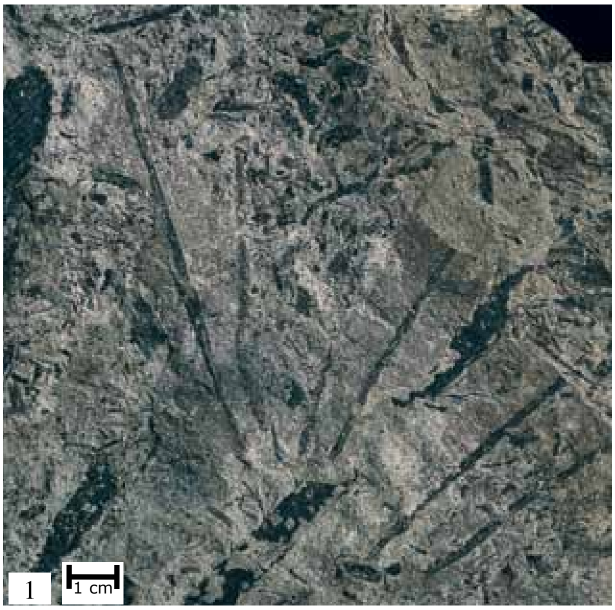
Ladinia simplex bears entire acuminated, sometimes papery, sterile leaves, often divided into forking midveins and secondary veins arising almost perpendicularly unforked and parallel from the rachis. The sporophylls consist of compact sterile cataphyll-like foliage and leaves with loosely arranged ovule-bearing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

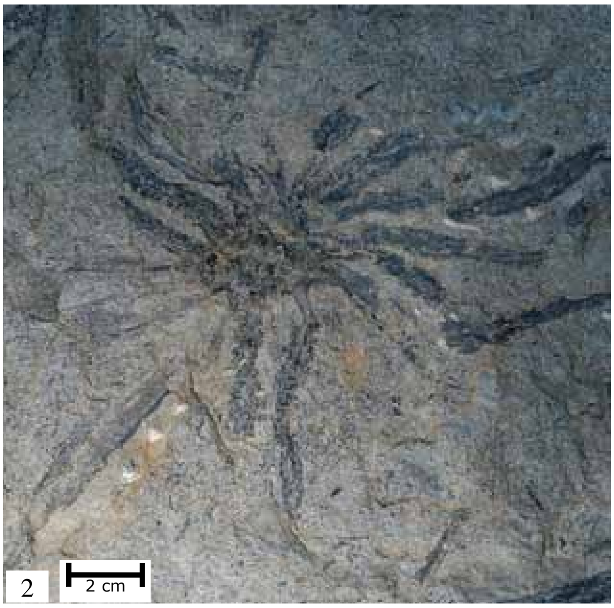
Description

Plant: Low-growing shrub, foliage erect or obliquely spreading laterally (KÜH 885), with about 15 sterile leaves becoming 10–15 distally arranged fertile sporophylls (KÜH 2118).
Roots and stems: More fern-like than cycadalean (KÜH 660).
Leaves: Sterile leaves on a short 1–2 cm long and 5 mm wide stalk, linear to lanceolate, 8–15 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 in the position at the site 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 to 30 per cm (PIZ 158).
Sporophylls: Cataphyll-like leaves located 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 narrow (up to 0.8 cm wide), 5–10 cm long and compact. Venation is difficult to see. Spines on the lateral sides. (KÜH 2118), 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





1) KÜH 885 *Ladinia simplex*. Paratype. Five sterile leaves
2) KÜH 2118 *Ladinia simplex*. Holotype. About 10 fertile leaves overlie several sterile leaves. Detail 14 x 10 cm.
3) KÜH 2118 *Ladinia simplex*. Detail of the fertile sporophylls. Ten to 14 small seeds in two rows.

cycad due to its fern-like character. The rachis is divided, resembling 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, at approximately 20 to 30 per cm, is high as in Anisian *Nilssonia* and *Bjuvia*.

The adnate megasporophyll is suggested to be more primitive. The fertile leaves of *Ladinia* do not form a cone like *Bjuvia-Dioonitocarpidium*, the central axis is missing along with the feather-like structure, or it consists only of casually arranged spikes. Only fine spines are visible. They could be interpreted as being the beginning of a rudimental feather-like 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 of a slight constriction. The number of megasporophyll leaves in *Ladinia* is reduced (6 to 8 compared to 8 to 14 in *Dioonitocarpidium cycadea* and up to 60 in *Dioonitocarpidium loretzi*). The seeds are smaller than in *Dioonitocarpidium*.

Hence *Ladinia simplex* could be thought of more as a fern than a cycadalean transition plant. It must be noted that Cycads did not evolve from seed ferns like Medullosaceae, as suggested in the literature, but from the pterophyta. The constant enlarging of seeds from Ladinia simplex to *Bjuvia primitiva* could indicate the emergence of cycad-like plants.

In many cases *Ladinia* leaves were found aggregated (KÜH 885, KÜH 2218, PIZ 17, PIZ 160), which in *Bjuvia* only occurs in rare circumstances. Although cycadales mostly appear as single leaves, the original concept probably lies in a pinna like today's *Stangeria*. For unknown reasons one sterile pinna became more dominant during the Palaeozoic to Early Mesozoic and formed larger laterally erect sprouting foliage. Evidence for that theory that can still be seen in extant Cycadales is the simultaneous growth of a corona of leaves.

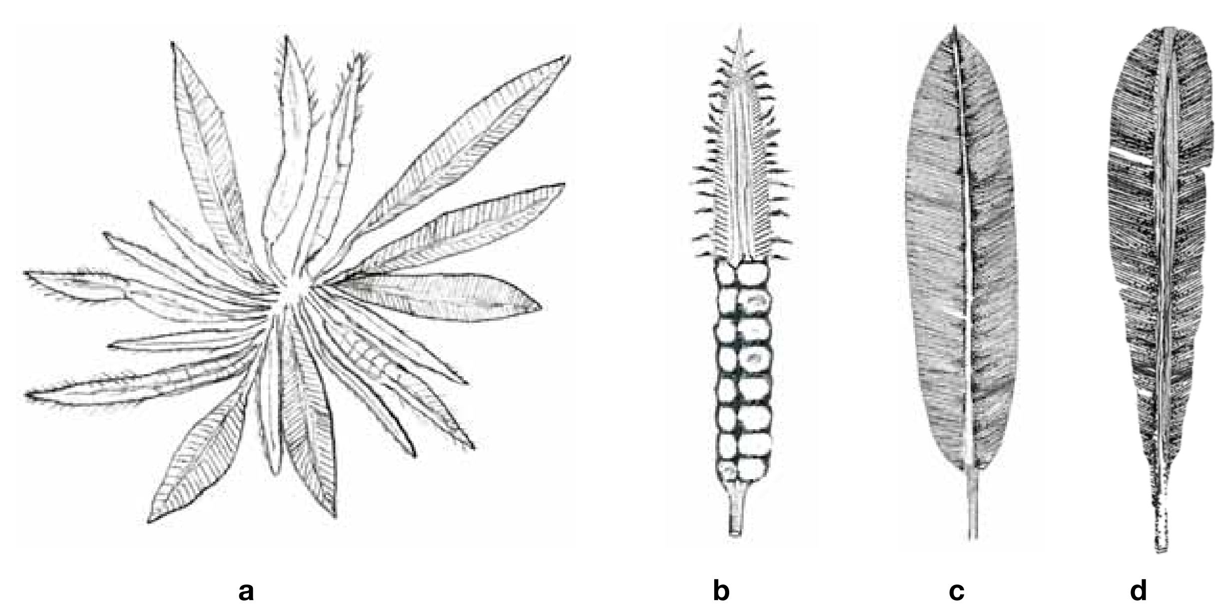


Fig. 7: 1) Suggested reconstruction of *Ladinia simplex*. 2) Single female sporophyll.
Different foliage of *Ladinia simplex*:
3) Entire pointed apex (PIZ 133, PIZ 332).
4) Entire, rounded, midveins dichotomously branched (KÜH 2140).

1) PIZ 332 *Ladinia simplex*. Leaf showing slightly pointed apex (6 x 2 cm).
2) KÜH 2140 *Ladinia simplex* leaf with rounded apex (8 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 at the base.
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.

Systematic Paleontology

Subdivision: Cycadophytina
Class Cycadopsida BROGNIART, 1843
Order Cycadales DUMORTIER, 1829

Genus *Bjuvia* FLORIN, 1933

Bjuvia, named after Upper Triassic discoveries of Sweden bears entire leaves, like the current Musa-fronds (banana plant), in contrast to the ubiquitous pinnate fronds of living cycads.

Bjuvia primitiva sp. nov. WACHTLER, 2010

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-Illyrian.

Repository

Natural History Museum Südtirol, Bozen, Museum Dolomythos 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 erect.

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 per cm. The leaves are sometimes folded.
Petiole: Short (1–3 cm), 5 mm wide, with gradually developing leaflets (PIZ 533). Foliage growing continuously from the rachis, but soon reaching the maximum width, then continuing at the same width up to the apex.
Male cones: *Thetydostrobus* fructifications were found together with *Bjuvia primitiva*.
Female cones: Complete female cones and isolated sporophylls belonging to *Dioonitocarpidium cycadea* were found together with *Bjuvia primitiva*.

Remarks

Bjuvia primitiva is common in the Anisian Braies flora and shows some surprising

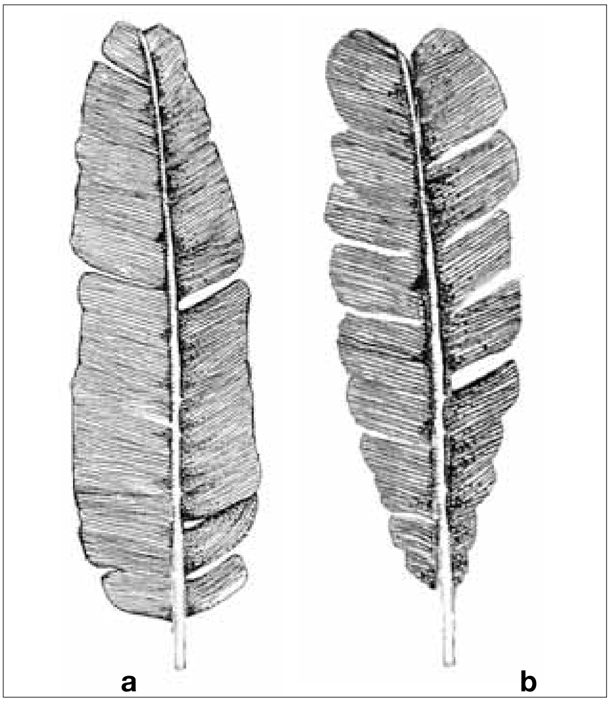


Fig. 8: Different foliage of *Bjuvia primitiva*:

1) Slightly lacerated U-shaped leaf (KÜH 155).

2) Lacerated V-shaped leaf (KÜH 230).

1) KÜH 2225 Young involute *Bjuvia* leaf

2) KÜH 2171. Leaf of *Ladinia simplex*

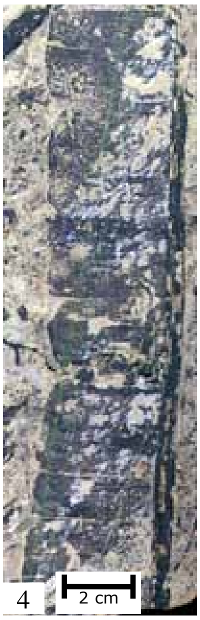
modifications. *Bjuvia primitiva* differs from *Bjuvia olangensis* occurring in the same strata because of its smaller size. *Bjuvia olangensis* (KÜH 2140, PIZ 41) is much larger, more segmented, and the apex is linear and not U - to V-shaped. It differs from Anisian *Ladinia simplex* from the same site due to its more consistent leaves, which are never acuminate at the apex. Otherwise *Bjuvia primitiva* can be thought of as a transitional form between Ladinia and the widespread *Bjuvia olangensis*. Until accurate cuticle analysis or other research ascertains the exact distinction, problems with its classification will remain.

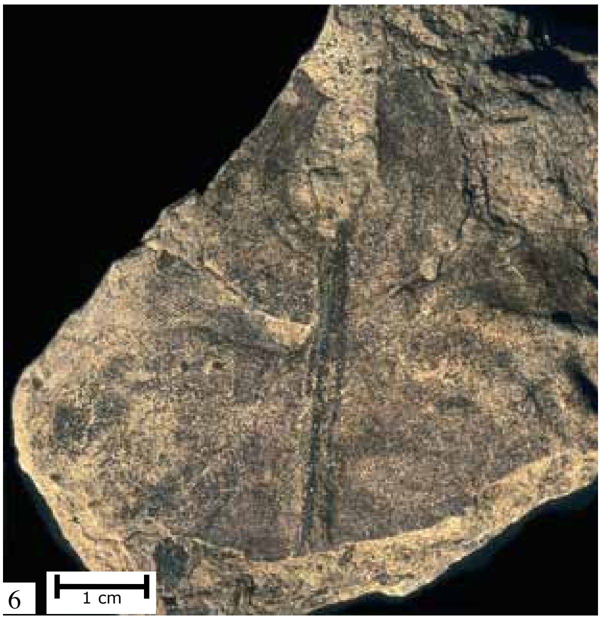
Bjuvia primitiva-type leaves have been described with different names from several localities in Germany. SCHMIDT (1928) mentioned *Danaeopsis angustifolia* (classifying it as Marattiaceae) from Keuper, but because of its non-furcating parallel veins, it probably has a greater cycadalean affinity. For fairly similar taeniopterid foliage found from the Permian to Triassic (T*aeniopteris multinervis, Taeniopteris coriacea*) classified mainly as a morphospecies of primarily sterile leaves its often difficult to establish which one belongs to true cycads. (REMY & REMY, 1975).

The leaves differ from Ladinian *Bjuvia dolomitica* (WACHTLER & VAN KONIJNENBURG-VAN CITTERT, 2000) due to their higher levels of fragility. Cuticles are difficult to obtain, whereas in the Ladinian *Bjuvia dolomitica* this is not a problem. The vein concentration is 14 to 18 per cm for *Bjuvia dolomitica* and 20 to 30 for *Bjuvia primitiva*.

Certain Nilssonian leaves of Carnian age from Lunz in Austria also have affinity with *Bjuvia*. In Rhaetian *Bjuvia simplex* the vein concentration is reduced to 12 to 14 per cm. In addition the rachis of *Bjuvia simplex* forks (FLORIN, 1933).

Even though extant Cycads, with their mathematically segmented leaf system, have totally different leaves, using knowledge of *Bjuvia primitiva* it is possible to demonstrate that the leaf types of modern cycads probably originated from an entire single leaf, passing





1) KÜH 132 *Bjuvia primitiva*. Paratype. Lacerated leaf (10 x 6 cm)
2) KÜH 230 *Bjuvia primitiva*. Holotype. Lacerated leaf (15 x 6 cm)
3) KÜH 155 *Bjuvia primitiva*. Leaf and apex
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)

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* bear all the features of modern Cycads. From the root system to the Cycas-like megasporophyll arrangement (probably *Dioonitocarpidium* cycadea) and the male strobilus of the *Thetydostrobus*-type, found in the same strata, they show an extraordinary similarity to extant cycads.

Bjuvia olangensis sp. nov. WACHTLER 2010

Holotype

KÜH 130 (leaves), KÜH2218 (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-Illyrian

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 Fossillagerstätte. 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 (PIZ 580) to 30 (PIZ 552) 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, (KÜH 2218) 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 venation (KÜH 2220) and form a crown-like ring. (KÜH 2221) 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, (KÜH 2218) resembling the typical "coralloid roots" of today's cycads. They can reach a length of 3 cm x 1 cm.
Male cones: Probably *Thetydostrobus marebbei.*
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 of the Dolomites and seemed to be a tran-

1) KÜH 2225 *Bjuvia olangensis*. Large slab (70 x 50 cm).
2) KÜH 2223 *Bjuvia olangensis*. Several leaves on a large slab (100 x 40 cm).
3) KÜH 130 *Bjuvia olangensis*. Holotype. 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.

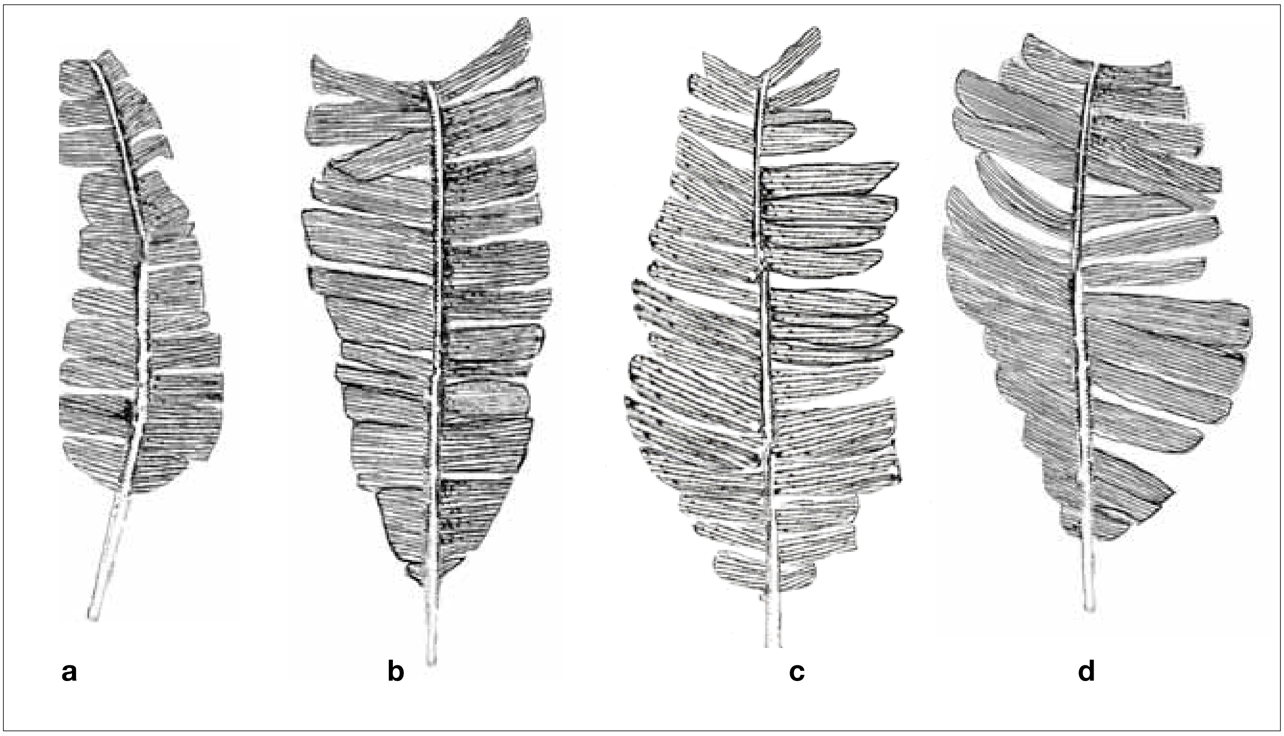


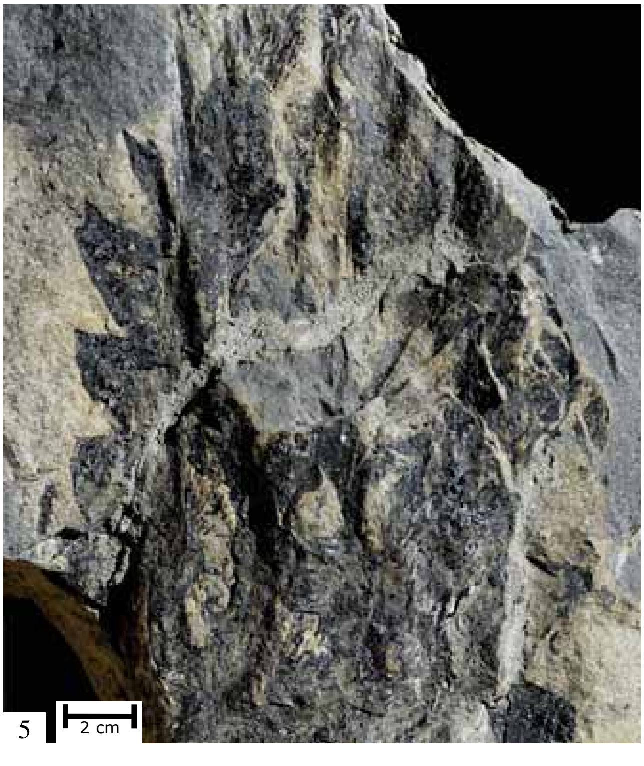
Fig. 9: Different leaves of *Bjuvia olangensis*:
1) Slightly lacerated (KÜH 2223).
2) Lacerated and flattened (KÜH 2223).
3–4) Irregular cycad-like (KÜH 2225), (KÜH 553).

sition 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. 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.



1) KÜH 2218 *Bjuvia olangensis*. Holotype stem. 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
4) KÜH 2221 *Bjuvia olangensis*. Detail of leaves and cataphylls
5) KÜH 2221 *Bjuvia olangensis*. Trunk with leaves and cataphylls (12 cm)

Systematic Palaeontology

Subdivision: Cycadophytina
Class Cycadopsida BROGNIART, 1843
Order Cycadales DUMORTIER, 1829

Genus *Nilssonia* BRONGNIART, 1825

The genus *Nils(s)onia* was introduced by A. BROGNIART for once-pinnate leaves from the Lower Jurassic of Scania in Sweden characterised by a prominent venation. The most important feature used to distinguish *Nilssonia* leaves from *Pterophyllum,* belonging to Bennettitales is the insertion of the leaf segments to the rachis. They are inserted to the upper side in *Nilssonia*, while they are laterally inserted in *Pterophyllum* (POTT & KRINGS, 2010).

Nilssonia braiesensis sp. nov. WACHTLER, 2010

Holotype

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-Illyrian

Repository

Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

Diagnosis

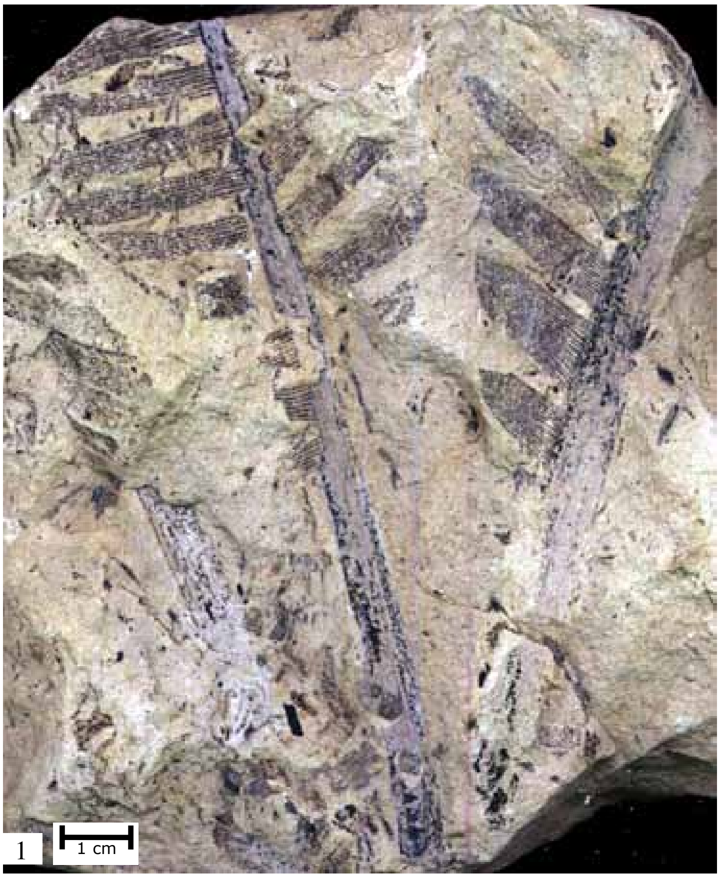
Nilssonia braiesensis leaves are petiolate, pinnate and distinctly separate from each other. The lamina is subdivided into numerous, irregularly oppositely to subоppositely positioned segments, whose ends are normally truncate to obtuse. From a strong rachis, secondary parallel veins arise perpendicularly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

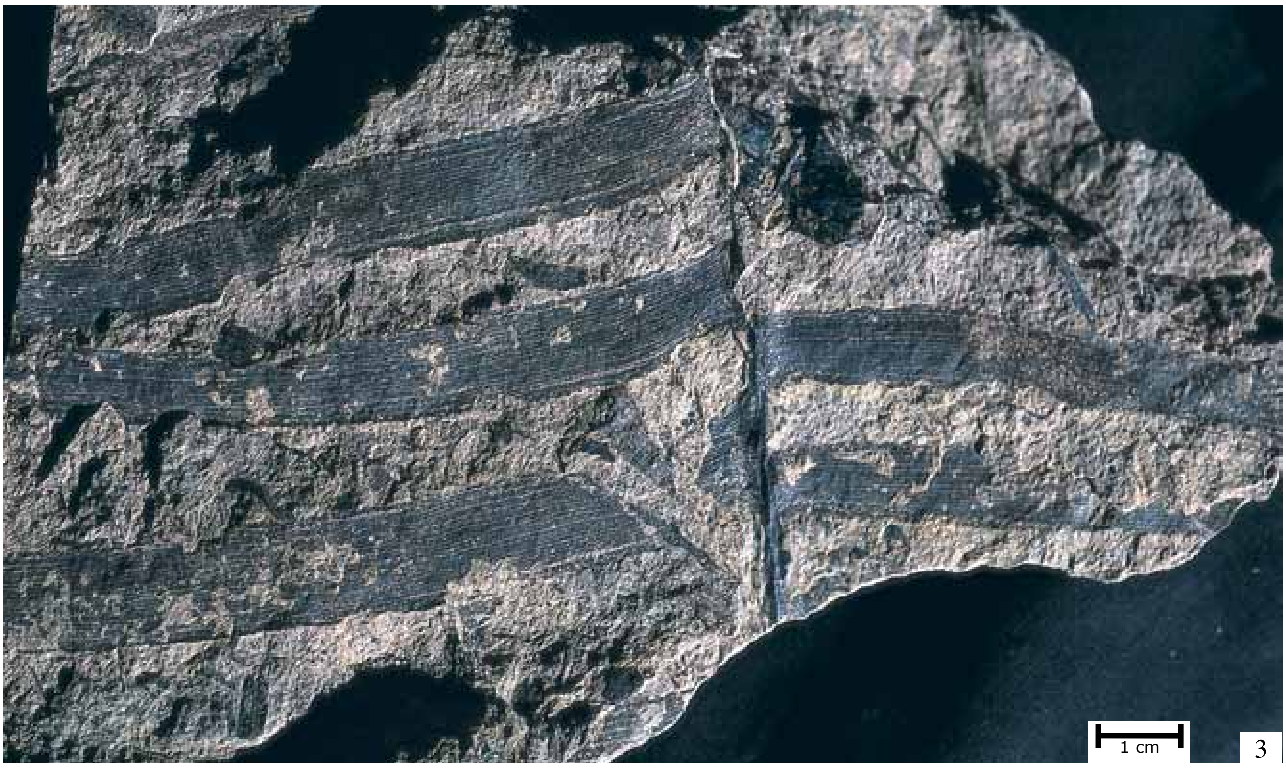
Description

Leaves: The foliage of *Nilssonia braiesensis* can reach at least 30 cm in length and up to 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 to 30 veins/cm). The leaf segments sometimes tend to be folded. Variation in leaf structure can be observed even on the same plant (KÜH 897).
Petiole: Relatively consistent (KÜH 897, 9 cm) and bare without spines or prickles. Diameter approximately 5 to 10 mm.
Male cones: Suggested from *Thetydostrobus* group.
Female cones: Suggested from *Dioonitocarpidium* group.

Remarks

Narrow, almost 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 ET. AL., 2007a). The macromorphological features correspond well with those seen in typical representations of this common Mesozoic foliage type. Additional characteristics include fine, parallel venation everywhere with unforked veins.
Nilssonia braiesensis differs from the well-known *Nilssonia* leaves of the Carnian Lunz not only in terms of its different geological period but also its more primitive nature. Strong mathematically arranged leaflets are





1) KÜH 897 *Nilssonia braiesensis*. Holotype. 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).

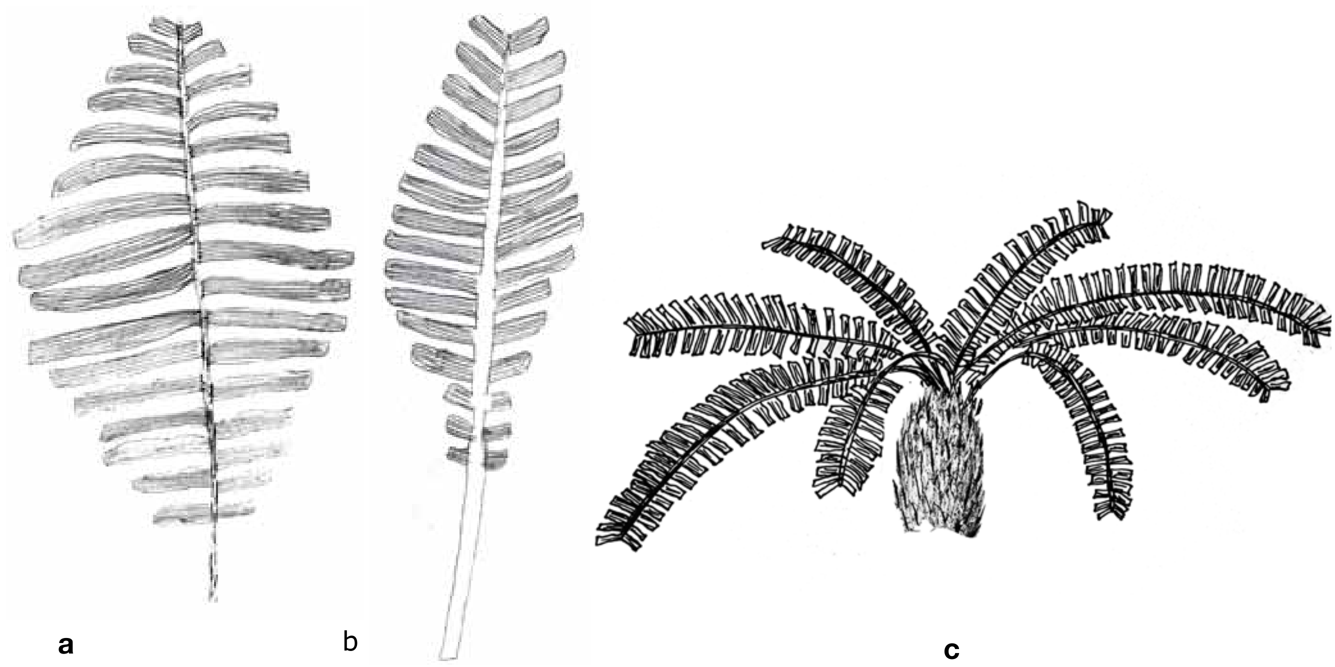


Fig. 10: Different leaves of *Nilssonia braiesensis*:
1) Sub-oppositely undulating (KÜH 900).
2) Cycad-like and irregular (KÜH 897).
3) *Nilssonia braiesensis.* Reconstruction of the whole plant.

not developed and leaf modifications occur even on the same plant.

The same is true for many leaves currently classified as *Pterophyllum* (e.g. *Pterophyllum jaegeri*) and now considered to be 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 resolves this issue many doubts remain.

The till now first unquestionable fossil record of bennettitaleans was found in the Carnian deposits (POTT ET. AL., 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 also rules out their bennettitalean origin. It is 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 to date (WACHTLER & VAN KONIJNENBURG-VAN CITTERT, 2000). *Nilssonia braiesensis* indicates that the Nilssoniales evolved much earlier in the Triassic than previously thought (POTT 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 ET. AL., 2009). *Pseudoctenis,* another characteristic cycadalean foliage element of the Rhaetian (uppermost Triassic) and Jurassic floras from Europe, has historically been used in an arbitrary way when no valid generic diagnosis existed (POTT ET. AL., 2007b). Apart from its younger age, it differs in the form of its segments, which are never basiscopically decurrent.

Therefore it would be more appropriate to suggest a relationship with other *Bjuvia* leaves of these strata, because the macromorphological similarities are obvious. Furthermore, it is sometimes difficult to distinguish *Bjuvia olangensis* leaves from *Nilssonia braiesensis*, especially when they are lacerated like a frond. However, they lack the almost mathematical segmentation typical of *Nilssonia* pinnae.

Traces of animal remains 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 leaf-type in the Anisian Dolomites

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

Cycad characteristics were shown by *Bjuvia primitiva* with its oblong, sometimes lacerated U- to V-shaped leaves. The petiole are more pronounced (KÜH 882, KÜH 2217, PIZ 182, KÜH 877).

Bjuvia olangensis foliage was completely lacerated to slightly segmented, distally V-shaped to flat. Leaves were large, with a long thick petiole (KÜH 2223, KÜH 2226).

Today's cycadalean foliage-type was shown by *Nilssonia braiesensis*. Leaves were mathematically segmented (KÜH 2170).

Slightly younger (Ladinian) *Sphenozamites wengensis* (WSW 06, WRI 21) from the Dolomites showed extant *Zamia furfuracea* foliage. That all today's cycads originated from a plant with a single entire leaflet is obvious from the rich material found in the Early-Middle-Triassic in the Dolomites, but doubts remain as to the cause of the rapid enhancement diversification of single cycad leaves.

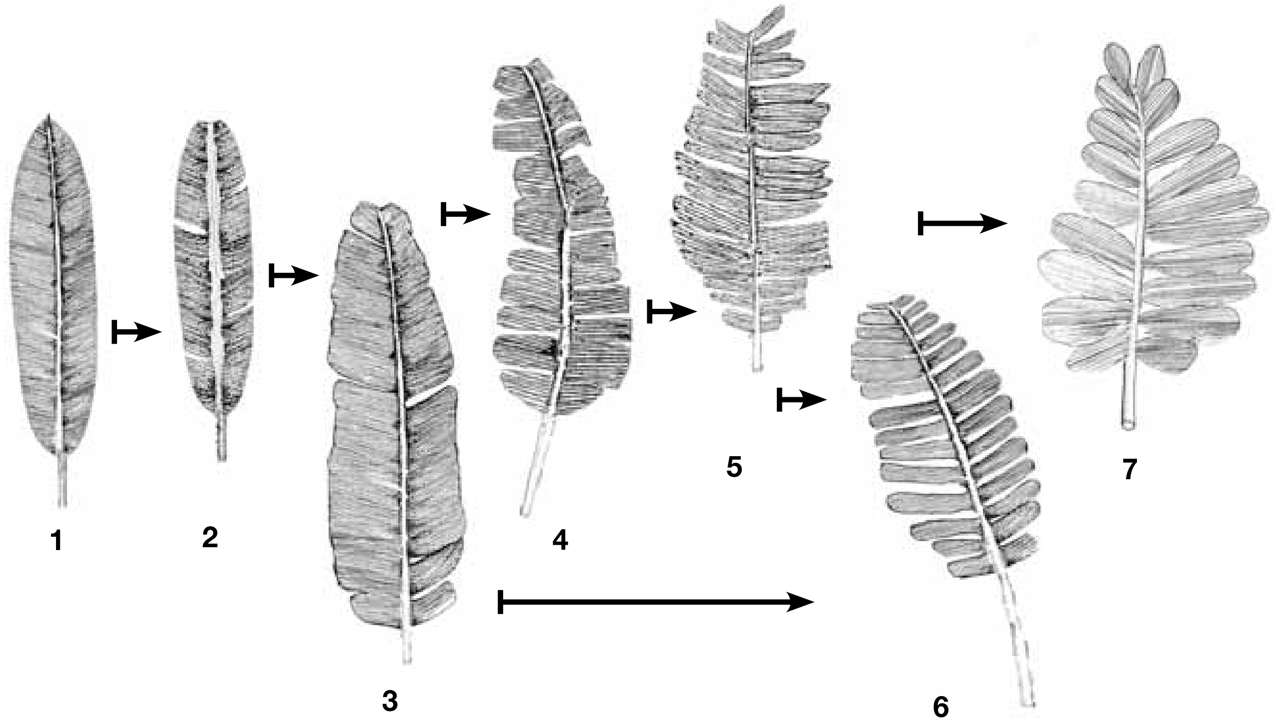
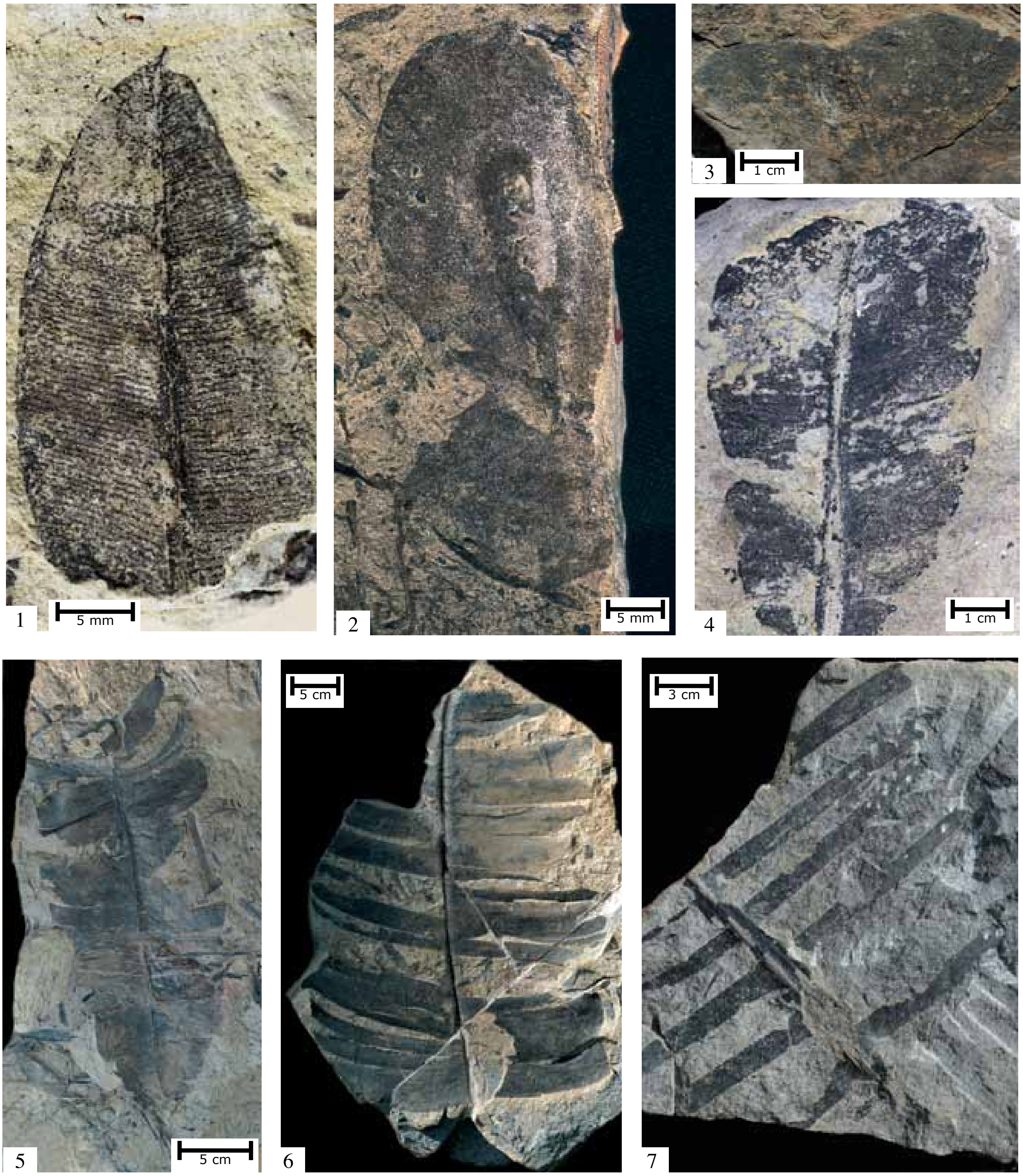


Fig. 11: Evolution of cycad leaves in the Lower-Middle Triassic:
1) *Ladinia simplex* – Entire, papery and acuminate (PIZ 133 - PIZ 332).
2 + 3) *Bjuvia primitiva* – Entire to lacerated, rounded at apex or slightly U-shaped (KÜH 2140 – KÜH 155).
3 + 4) *Bjuvia olangensis* – Lacerated to segmented, U- 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 leaf types in the Anisian 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 BRONGNIART 1843
Order Cycadales DUMORTIER, 1829

Genus Dioonitocarpidium RÜHLE VON LILIENSTERN, 1938

In 1938 RÜHLE VON LILIENSTERN introduced the genus *Dioonitocarpidium (pennaeforme)* 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, showed an amazing resemblance to *Bjuvia* cycads.

Dioonitocarpidium cycadea sp. nov. WACHTLER, 2010

Holotype

KÜH 2109

Paratype

KÜH 753.

Material

KÜH 2137, KÜH 2108, KÜH 2107, 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.

Diagnosis

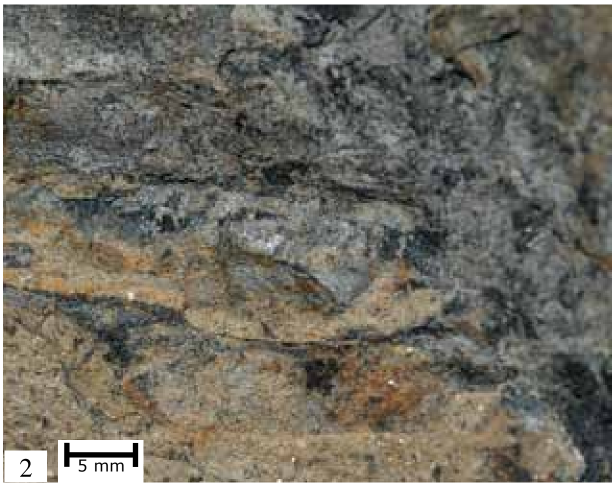
Dioonitocarpidium cycadea cones consist of loosely organized sporophylls arranged more or less spirally on a central axis. Sterile leaves on the base of the consistent peduncle. Megasporophylls bearing several seeds on the lower abaxial side in two rows. Sporophylls with a terminal feather-like apex.

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 short basal, 1 cm-long petiole, a proximal fertile part and a terminal sterile feather-like structure (KÜH 2137, PIZF 6). Length ratio about 1:4:3 (petiole:fertile part:sterile part). The fertile and sterile parts are divided by a constriction. The seeds are enfolded on the abaxial surface of the fertile part by a downwards curving leaf. Seed-bearing region about 3 to 7 cm long, from 2 to 12 ovules in each row, increasing in number to the apex. Leaflet divided from an occasionally forking midvein, which terminates at the apex. Distal feather-like 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 spaced on the abaxial part of the lamina, orientated at right angles to the midvein. Seeds varying considerably in size from 2 mm to 7 mm long, 2 to 5 mm wide.
Plant: Based on its size *Dioonitocarpidium cycadea* belongs to Bjuvia primitiva. It is also suggested that Anisian cycads bore more than one cone (PIZ 581).

Remarks

To date in most cases only single megasporophylls of Dioonitocarpidium have been found. This is valid for Ladinian *Dioonito-*



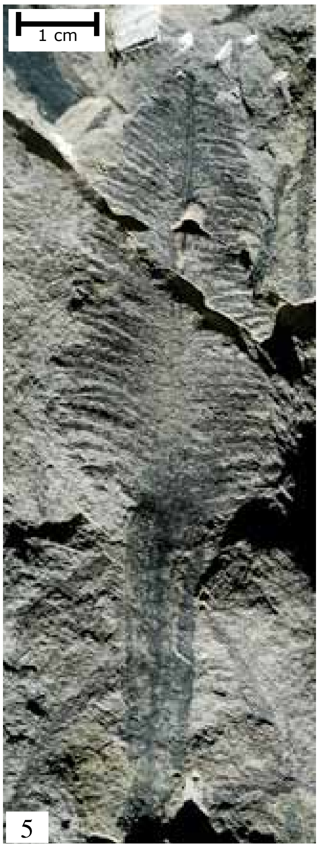
1) KÜH 2109 *Dioonitocarpidium cycadea*. Holotype. Female cone (10 x 8 cm) with ca. 14 sporophylls. Six to 14 seeds in two rows on the abaxial surface of the sporophyll

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

3) PIZ 581 *Dioonitocarpidium cycadea*. Slab (22 x 12 cm) containing two female cones. The smaller one holds 8 sporophylls and the larger one 14. Seed size only 5 x 5 mm

carpidium moroderi (KUSTATSCHER ET AL., 2004), as well as the almost equally old Schozachia donaea (ROZYNEK, 2008) from the German Keuper and also *Dioonitocarpidium keuperianum* from the Upper Triassic (Carnian) fossil deposit of Lunz in Austria. All of these cases are presumed to pertain to cycadales and have parental affinities to *Dioonitocarpidum cycadea*. The difference between these and *D. keuperianum* lies, apart from their younger fossil age, in their slightly larger and more developed megastrobili leaves. The fact that only single megaleaves have been found at other sites 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, and therefore cannot be compared with any *Dioonitocarpidium* cone.



5) KÜH 2137 Dioonitocarpidium cycadea. Single sporophyll adaxial side with feather-like apex (8 cm).

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

Doubtful cycadalean megasporophylls are just known from the Palaeozoic. *Lesleya* from the Mississippian to Late Permian in Europe and North America is probably a sterile taeniopteroid genus (TAYLOR ET AL., 2008). Fertile female strobili were placed within *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 bear only a vague resemblance to *Dioonitocarpidium cycadea*.

Primocycas chinensis from the lower Permian in China with its feather-like apex and laterally attached ovules is thought to be a cycad macrosporophyll (ZHU & DU, 1981). It differs from the Anisian *Dioonitocarpidium* in the fact that in *Primocycas chinensis* the megasporophyll is palmate at the apex. In addition, the seeds are attached non touching each other on both sides of the leaf and are not abaxial. From *Primocycas* it is also unclear as to how the entire cone was formed. Approximately 30 species of taeniopteroid leaves have been described from the Permian of China. Further studies have reported that several belong to the ferns (POTT ET AL., 2009). Some could be considered as ancestors of Thetydalean cycads.

It is suggested that, in *Dioonitocarpidium* cones, a single pinna formed the basis of the female cones (KÜH 2109, PIZ 581).

Dioonitocarpidium loretzi sp. nov. WACHTLER, 2010

Holotype

KÜH 758

Paratype

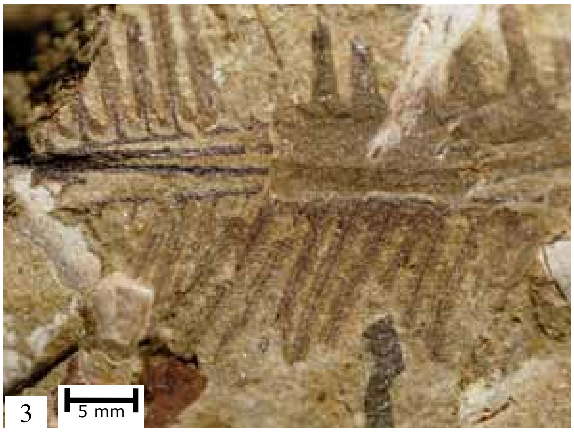
KÜH 534.

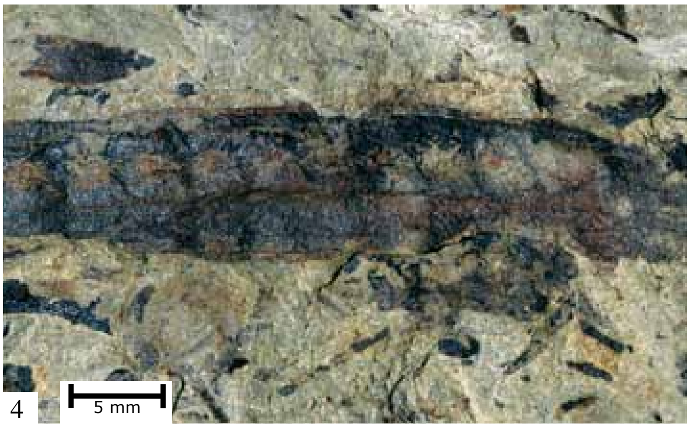
Etymology

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





1) KÜH 753 *Dioonitocarpidium cycadea*. Paratype. Complete cone.

2) KÜH 2107 *Dioonitocarpidium cycadea*. Complete cone.

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

4) PIZF 6 *Dioonitocarpidium cycadea*. Fertile part of sporophyll containing 12 seeds in each row (3 cm in length x 0.5 cm wide, ovules 3 x 2 mm).

Type horizon and age

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

Repository

Natural History Museum Südtirol, Bozen, Museum Dolomythos Innichen.

Diagnosis

Cycadalean cone consisting of loosely organized sporophylls arranged spirally on a central axis. On stout peduncle sterile leaves. Megasporophylls bearing ovules on the lower abaxial side in 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 in each row. In the juvenile stage (KÜH 534) megasporophylls pressed together and erected.
Peduncle: 4–6 cm long, 1–1.3 cm wide with sterile cataphyll-like leaves (KÜH 534).
Megasporophylls: 1 cm wide, 5–15 cm long. Ovules on the lower surface enfolded by a downward curving leaf. Seed-bearing region about 8 to 10 cm long, from 2 to 30 ovules in each row, increasing in number towards the apex. Lower sporophylls often sterile, cataphyll-like. Feather-like apex covering apical third of entire sporophyll.
Ovules: Closely pressed spaced on the abaxial part of the lamina, orientated at right angles to the midvein. From 2 to 4 mm long, 3 to 6 mm wide.

Remarks

Coeval *Dioonitocarpidium cycadea* from the same strata bear fewer megaleaves (8 - 14 in *D. cycadea* versus 60 in *D. loretzi*) and also fewer ovules on each megasporophyll (6-14 in *D. cycadea* each row, versus 40 in *D. loretzi)*. Therefore *Dioonitocarpidium loretzi* may have developed from *Dioonitocarpidium cycadeae*. Differences compared to other *Dioonitocarpidium* megasporophylls were described under *D. cycadeae*.
It is therefore worth comparing *Dioonitocarpidium* female cones with extant *Cycas*. Differences can be seen 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

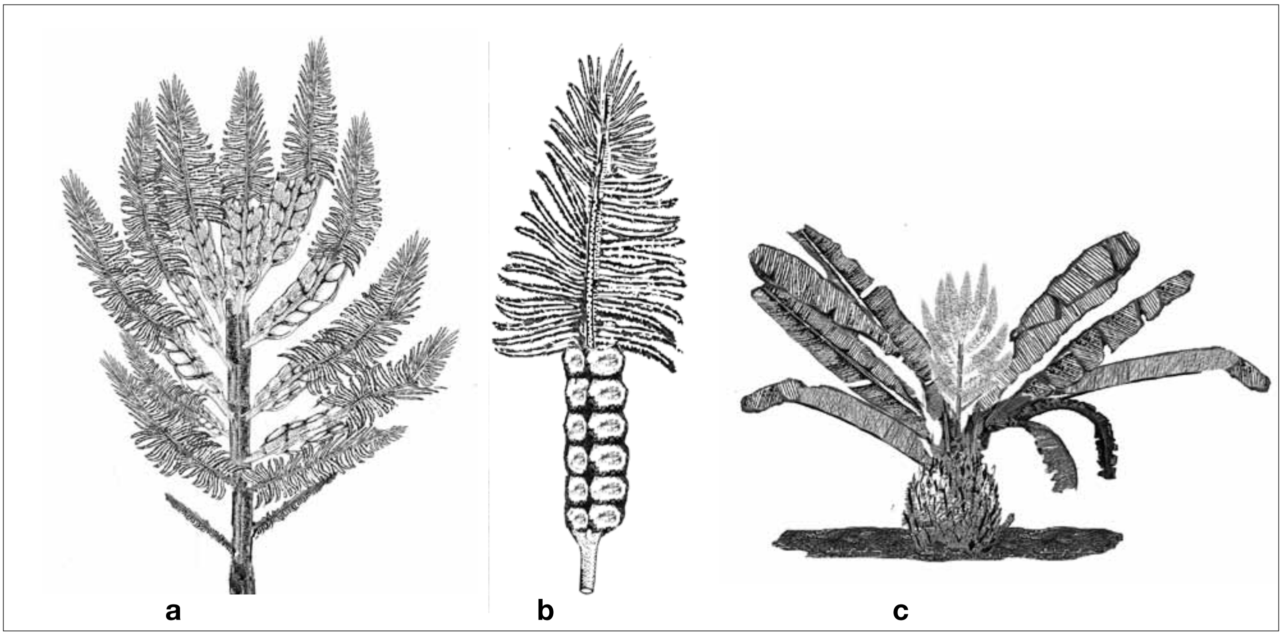


Fig. 12: 1) Suggested female cone Dioonitocarpidium cycadea. 2) *Dioonitocarpidium cycadea* – single megasporophyll – abaxial side. 3) Entire Bjuvia plant.

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 *Dioonitocarpidium* has a striking resemblance to extant 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 *Pizperesia*-like solution, where various micro-fronds have fused to form cycadaelean-like scales with macrosporangia and later a complete cone.

1) KÜH 534 *Dioonitocarpidium loretzi*. Paratype. Young immature female cone (22 x 8 cm).

2) KÜH 758 *Dioonitocarpidium loretzi.* Holotype. Cone with minimum 60 sporophylls. Each could contain up to 40 seeds in two rows (18 x 10 cm).

Systematic Paleontology

Subdivision: Cycadophytina
Class Cycadopsida BROGNART, 1843
Order Cycadales DUMORTIER, 1829

Genus *Thetydostrobus* gen. nov. WACHTLER, 2010

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 sp. nov. WACHTLER, 2010

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 coverred by rhomboidal scales. Pollen-bearing organs wedge-shaped, microsporangia on the lower surface. Apex of scales covered with trichomes.

Description

Peduncle: A 2–3-cm-long peduncle support an 8–15-cm-long cone from which 30 to 100 sporophylls arise perpendicularly.
Cones: Usually cylindrical to ovoid-cylindrical (PIZ 101). Cones are closed when juvenile (PIZ 28), opening in adulthood to disperse 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, clearly demonstrates the pointed hairs on the apex. PIZ 28 represents a well conserved peduncle. The scales are covered with trichomes. Male reproductive structure KÜH 2222 is a more adult stadium with open pollen sacs, and aggregated sori. This cone is 10 cm long and 4 cm wide. KÜH 392 belongs to an old, semi-destroyed male cone. All cones are suggested to belong to *Bjuvia.*
Male sporophylls: Usually 2–3 cm long, and 1–1.5 cm by 0.5–0.8 cm wide at the apex. Microsporophylls distally rhomboid, covered at the apex with fine hairs. Pollen sacs on the lower surface, visible to the naked eye, ellipsoid to spheroidal.

Remarks

The fossil record of cycadalean pollen cones is unfortunately poor. One belongs to *Lasiostrobus*, a permineralized Upper Carboniferous reproductive organ, but due to its poor preservation it could also be interpreted as a fertile conifer or ginkgo organ (TAYLOR & TAYLOR, 1993).
Androstrobus, a cylindrical pollen cone from the Middle Jurassic, found in Yorkshire, England, and slightly younger in age, from the exterior could have some similarities with the Dolomite-Anisian *Thetydostrobus*. Further studies will be required to ascertain whether *Androstrobus* really evolved from Thetydostrobus.

1) KÜH 2222 *Thetydostrobus marebbei.* Paratype. Mature pollen organ 10 x 4 cm.
2) PIZ 101 *Thetydostrobus marebbei.* Holotype. Male cone 6 x 3 cm.
3) PIZ 2222 *Thetydostrobus marebbei.* Mature cone showing pollen being released.
4) PIZ 101 *Thetydostrobus marebbei.* Lateral part showing the sporophylls (10 x 5 mm).

A male cone found attached to a stem apex with *Nilssonia*-like leaves, named *Holozamites hongtaoi* (WANG 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 also affinities with fertile scales from the Anisian Dolomites described below as *Pizperesia raetiae*. They bear a fertile leaf-like zone on the distal part of the stalk. Although the individual scales are clearly separated from each other on the axis and therefore we cannot define it as a real cycadalean male cone, it is worth noting the following. *Pizperesia* 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.

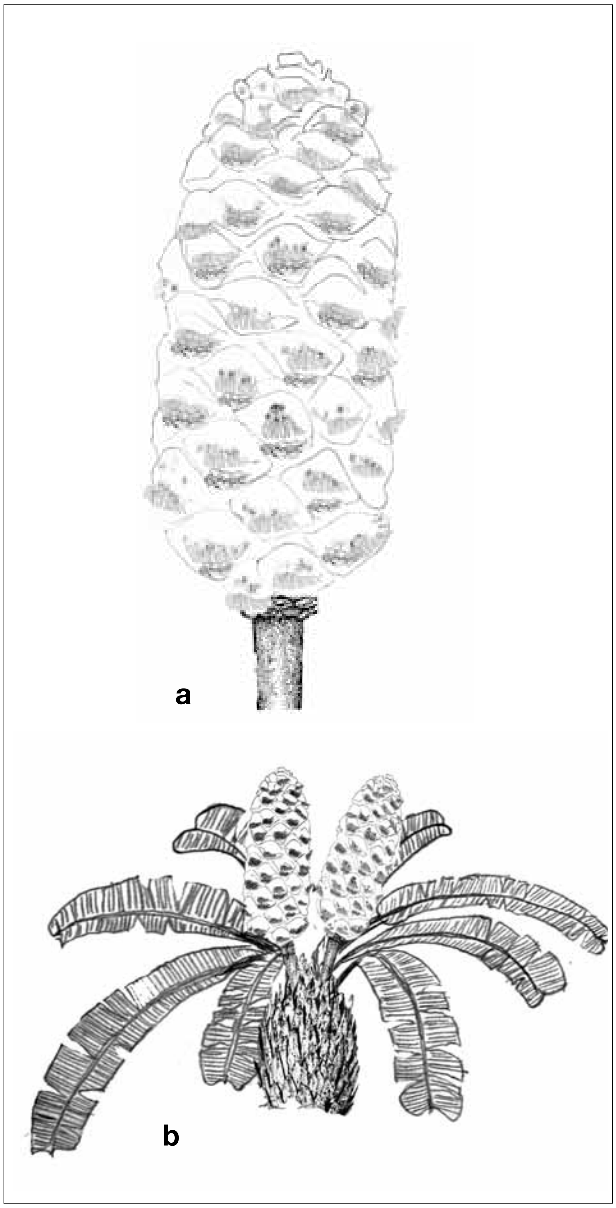
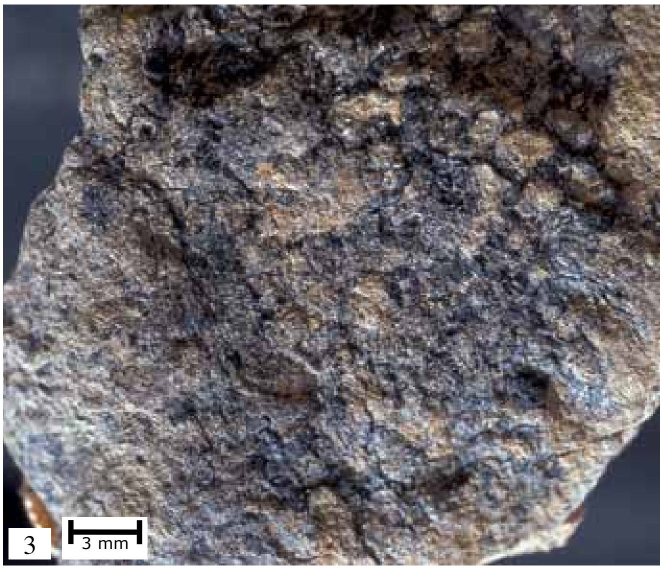


Fig. 13: Reconstruction of *Thetydostrobus marebbei* cone. Differences with extant cycad male cones are minimal.

Bjuvia primitiva with male cone *Thetydostrobus marebbei.*

They showed the habitus of extant male cycad scales, with their distally formed trichomes, and microsporangia on the lower (abaxial) surface of the wedge-shaped scales. Some enigmatic problems can therefore be resolved. The male cycad cone is nothing other than an aggregation of scale-fern fronds that initially originated on a discontinuous base and subsequently became closely aggregated. *Pizperesia raetiae* seems to be the last non-cycadalean fructification, and *Thetydostrobus marebbei* the first real male cycadalean cone.

Further studies will be required to determine to which *Bjuvia* species the *Thetydostrobus* cone belongs. *Bjuvia* was almost certainly dioecious and, like today’s cycads, produced male cones at a specific time of year. Hence the so-called “springtime-vegetation” in some strata of Piz da Peres that are rich in cycadalean male cones. Decomposition would have begun 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.* Paratype. 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 described as "very similar" to today's cycads, the group of Pizperesiaceae could only be described as "angiospermous, but not angiosperms" and also "bennettitaloid, but not bennettialean".

The evolution of *Pizperesia* probably constitutes the origin for the development of cycads and angiosperms. In other words, ferns, cycads and angiosperms are more closely related than was previously thought.

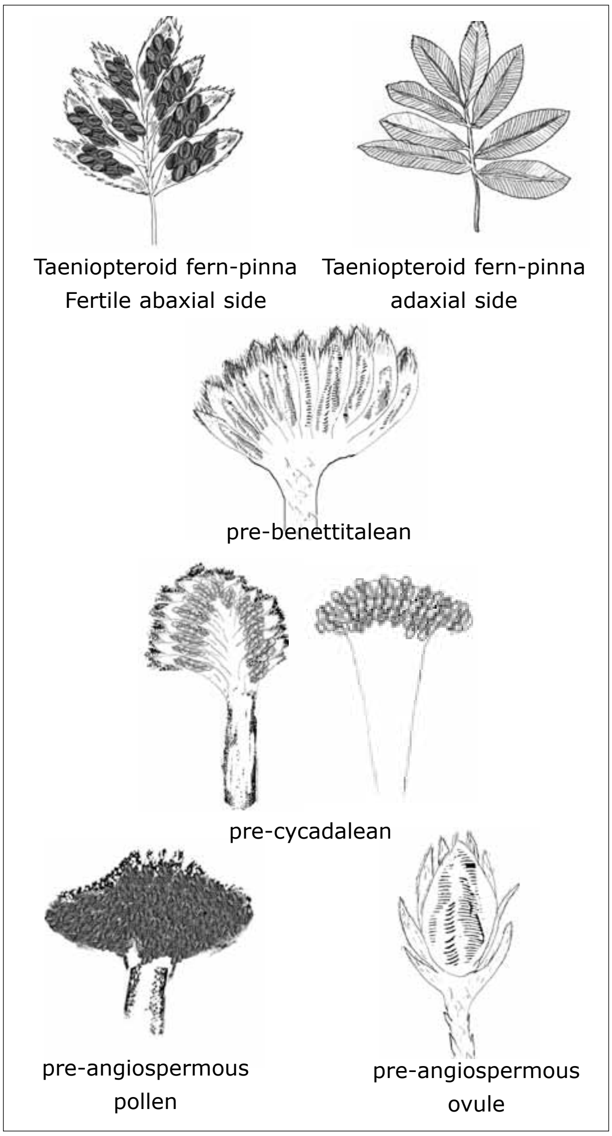


Fig. 14: Evolution of *Pizperesia* from reduced fern fronds.

Thus angiosperms could be regarded as merely specialized cycadophytas, as could Bennettitales and Cycadales.

It is difficult to say in what changed the clime between the Permian and Triassic. None of the large plant groups vanished. Horsetails survived as well as ferns, conifers, and club mosses. But all they changed in the same way: they decreased in size, especially club mosses and horsetails. The decrease in size 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* indicates that even at the Poles there was enough warmth to allow a cycad to live. The impenetrably dense Carboniferous forests were replaced by large savannas and shrubby bushes. The atmospheric 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 whether they were insects, pollinators or small reptiles but it is assumed that cycad-angiosperm evolution was influenced by the ascension of pollinators.

Dinosaur age. Dolomite-Anisian plant-beds also bear many archosaurier remains and tracks. Some of them (*Sphingopus ladinicus sp. nov.*) have been classified as dinosauriformes or are closely related to primitive dinosaurs. Primitive snake and lizard skeletons (*Megachirella wachtleri gen. nov. sp. n.*) have also been found together with the Piz da Peres plant assemblage.

Characters

Pizperesiaceae. General features

We can now establish which important plant revolutions may have been introduced by the Pizperesiaceae.

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

Kinship of cycads and angiosperms. The fusion of distal microleaves helped not only to form cycad cones but also flowers and the stamen-carpel system. The Permian-Triassic boundary was essential for both plant groups.

Bisexual flowers. Certain Pizperesiaceae were dioecious (PIZ 155, PIZ 620) and others monoecious (PIZ 553). One line led to cycads, the other to bennettitaleans and angiosperms.

Origin of stamen. Distal Pizperesiaceae 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 the *Pizperesia* fructification were compressed and forced to grow upwards rather than outwards due to the lack of space and formed flower-like structures with integuments. On the lower surface of these fertile leaves the sporangia grouped together or were reduced in number, even becoming infertile, giving their biomass to other sporangia.

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

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

Cycadales. General features

Given the new Anisian Cycadophyta the phylogeny of cycads can be seen in another context. The established doctrine of the genus Cycas as the most primitive must be reviewed. The leaf structure of *Stangeria* shows the closest resemblance to the Palaeozoic-Triassic ancestor; the fertile part of cycads could have evolved from *Bowenia*-like spirally arranged bipinnate fronds. The short scale-like male and female cones that are the 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 over millions of years in terms of their morphology, anatomy, ecology, physiology and adaptive capacities. They have in fact not changed much since the early Mesozoic. All the aspects of today's cycads were formed in a surprisingly short time, from the development of coralloid roots to the trunk with scars and pits from fallen leaves, cataphylls and even the male and female strobili. The evolution of real cycads was almost complete by 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 the Carboniferous-Permian pteridophyta. The foliage of the Palaeozoic ancestor is thought to belong to a taenopteroid bipinnate fern with several forking midribs and lateral veins towards the margin. Fern progenitors could be assumed by the arrangement of microsporangia on the abaxial side of the leave, as well as the circinate venation. The first real cycads should be sought at the Permo-Triassic boundary.

Single leaf evolution. All extant cycad leaves except *Stangeria* and *Bowenia* originated via the modification and increase in size of a pinna with entire, flat, lanceolate, 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 randomly ripped and segmented foliage (KÜH 2226, KÜH 2217, PIZ 182). Finally the almost mathematical segmentation typical of *Nilssonia* (KÜH 897, KÜH 670) developed. In a relatively short time the typical segmented pinnate leaf of cycads was formed.

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

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

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

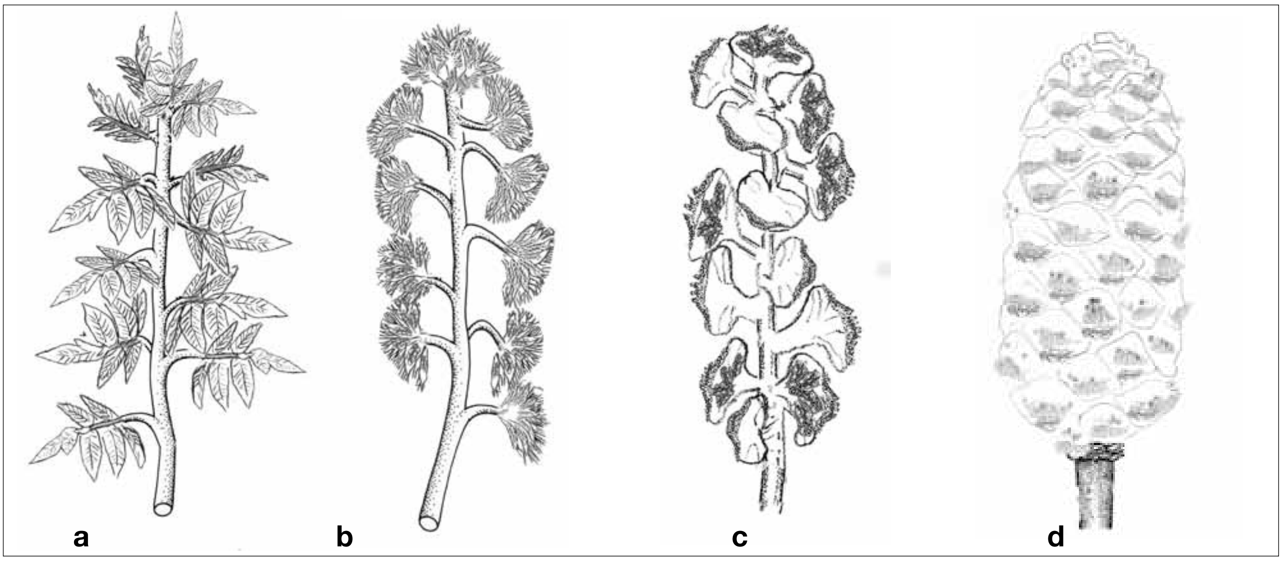


Fig. 4: Suggested construction and fusion of *Pizperesia* fructification to male–female cycad cone. 1. Open fern-leaves like those of extant *Stangeria* and *Bowenia*. 2. (PIZ 155) Scale with aggregated leaflets and unbranched trichomes. 3. (PIZ 620) Leaflets fused to scales and further compression to form a cone. 4. (PIZ 101) Male cycad cone *Thetydostrobus marebbei.*

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

Unisexual performance. All Early Mesozoic cycads were 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 large pinnate fertile leaves (*Dioonitocarpidium* to *Cycas*) and from smaller bipinnate fertile leaves (*Pizperesia* to 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 bore seeds only slightly larger than sporangia. A feather-like apex finished off the sporophyll leaf. Intermediate forms (*Ladinia*) show that the feather-like structure originated as spines to prevent grazing by animals or insects. Dioonitocarpidium cones show only marginal differences to extant Cycas (KÜH 2118, KÜH 534, KÜH 758, KÜH 2108, PIZ 141).

Pizperesia-cone cycads. *Pizperesia 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 minimizing 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 (*Pizperesia*). 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 regions on the lower surface. For several reasons, probably due to weather conditions or defence against animals, 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).

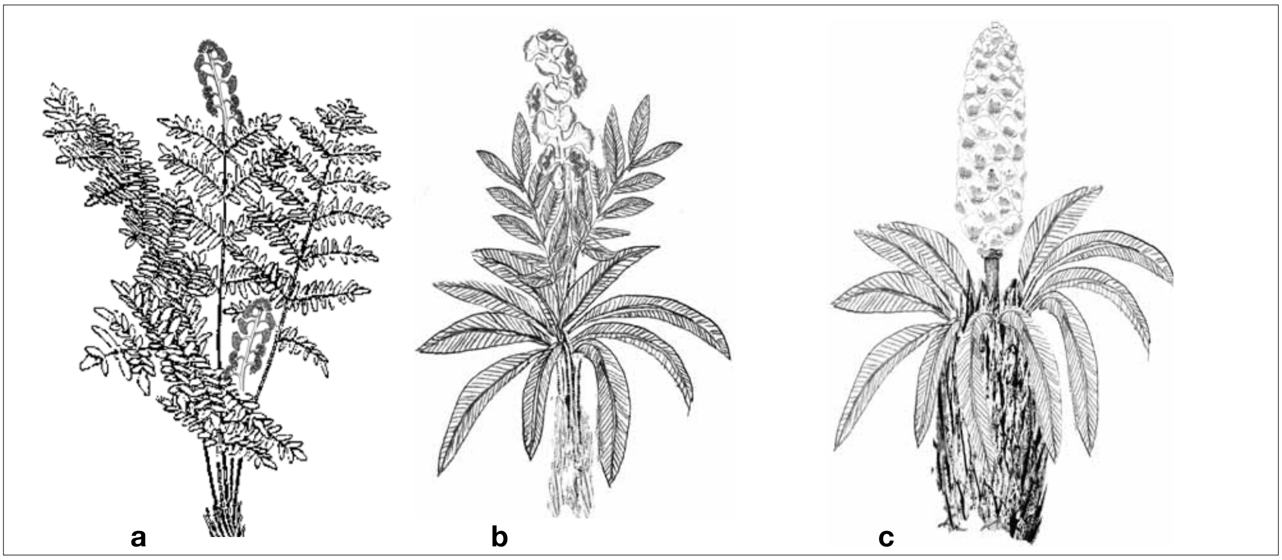


Fig. 15: Evolution of Cycas plant. 1) Pinnate to bipinnate fern. 2) Compression of distal part to single scales (*Pizperesia raetiae*). 3) Fusing of scales to a cone and lower pinnae to single leaves or cataphylls.

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 time and the relativity of human values. When I stood as a “time-traveller” on Piz da Peres I completely forgot about the busy, rushed and stressful life in the lower valleys. For weeks and months I searched for an abominable phantom: the discovery of all parts of the plants. The parts were revealed and formed part of the mosaic. I was led along 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 pathways opened. In the summer I forgot about humanity and turned into another being. I did not discover how to make lots of money, but I walked inside nature, as people are seldom allowed to do.

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