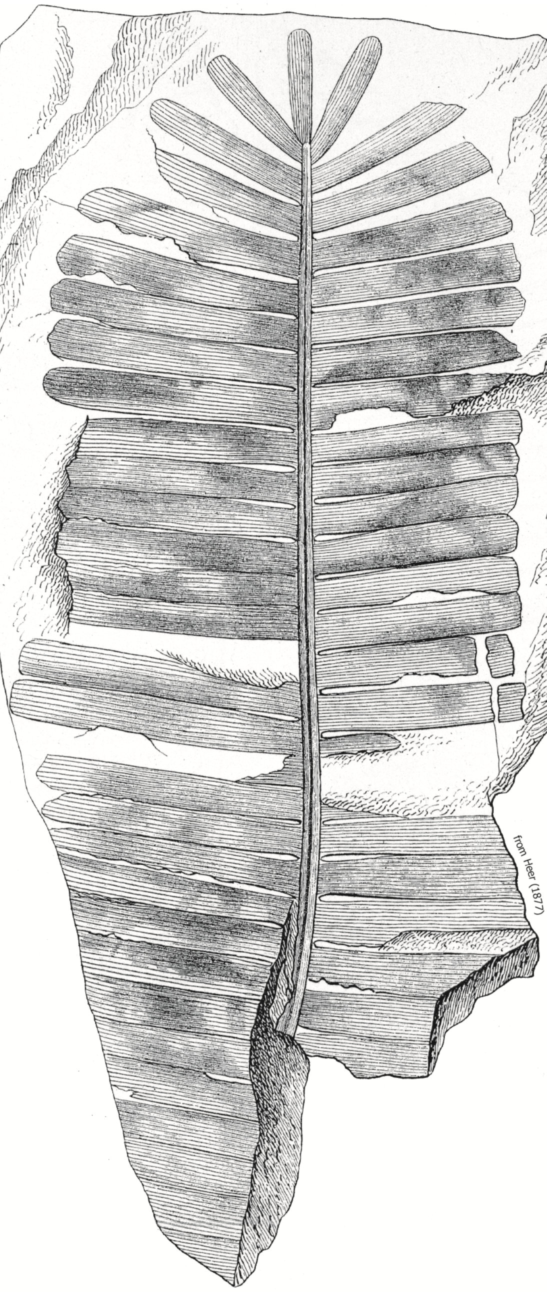
CUTICULAR ANALYSIS OF GYMNOSPERM FOLIAGE FROM THE CARNIAN (UPPER TRIASSIC) OF LUNZ, LOWER AUSTRIA



from Heer (1877)

Christian Pott
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Fach Paläontologie (Paläobotanik)

CUTICULAR ANALYSIS OF GYMNOSPERM FOLIAGE FROM THE CARNIAN (UPPER TRIASSIC) OF LUNZ, LOWER AUSTRIA

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Dekan	Prof. Dr. Hans Kerp
Erster Gutachter	Prof. Dr. Hans Kerp
Zweiter Gutachter	PD Dr. Michael Krings
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CONTENTS

INTRODUCTION

Studies of fossil plants have a long tradition. Palaeobotany as a research field was established at the latest with the release of the monumental publication of Sternberg (1820–1838). Other early fundamental releases were published in the following 30 years (Schlotheim 1820, 1822; Brongniart 1825, 1828, 1849; Lindley & Hutton 1831–1837; Braun 1843; Unger 1845, 1850; Bronn 1848; Ettingshausen 1851; Miquel 1851), the so-called "Golden Age" of Palaeobotany (Cleal et al., 2005). One of these works provided the first illustrations of plant fossils from Lunz (von Ettingshausen, 1851). The work on fossil plants from Lunz thus has a long tradition, too.

For most of the time, work on fossil plants was restricted to describing and classifying species, which at that time were mainly grouped together in so-called form- or morphotaxa. This type of categorisation enduringly complicates the inclusion of fossil plants in modern systematic and phylogenetic analyses. One of the first ecological considerations on a fossil flora was provided by Heer (1865); today ecological interpretation plays a major role in the evaluation of fossil floras. Nevertheless, the establishment of systematic inventories must not be disregarded or underestimated, since they provide a fundamental basis for subsequent ecological interpretation even if only the diversity of a flora is relevant. Systematic studies also contribute considerably to the understanding of systematics and evolution of the modern floral assemblages.

The present work provides a detailed documentation of the macromorphology and epidermal anatomy of the sterile foliage fossils from a diverse and rich Late Triassic (Carnian) megaflora in the Northern Calcareous Alps of Lower Austria. The flora from Lunz represents one of only a few well-preserved megafloras of the Alpine Triassic, and is one of the most suitable floras for the analysis of the floral development in Late Triassic deposits from the Alps. The here presented results form an integral part of the general intention to produce a comprehensive characterisation of the flora from Lunz. The constitutive topic of this study is to characterise and diagnose the excellently preserved gymnospermous leaf remains from Lunz. Based on the establishment of sound diagnoses that incorporate macromorphological and epidermal features, the currently confusing taxonomy and resulting incomplete or unreproducible typification of the foliage types is reviewed and corrected, revised or completed, where necessary. In addition to the detailed diagnoses, illustrations of the individual forms and species are provided. This appeared to be particularly necessary, since illustrations of Lunz fossils are generally rare in previous publications. Detailed analysis of the macromorphology and epidermal anatomy along with the investigation of large sample sets of fossils, are required in order to establish high-confidence species and their ordinal and generic allocation (see chapters 1–3, 5–6) as well as to consider intraspecific variations.

Based primarily on the results mainly obtained from cuticular analysis, questions concerning the palaeoecology of the plants (i.e. assumptions of environments and environmental variables by means of adaptations of the plants as well as plant/insect-interactions) can be assessed. They may provide new data and insights into the life habits and ecological characteristics of the plants (see chapters 4, 7–8). Analysing as many species as possible from a single flora contributes to detailed conclusions with regard to the palaeoecology, substantiated by the concordance of the adaptations of the plants. Additional information from sedimentological and palaeozoological data can be used to further substantiate the significance of the adaptive nature of the epidermal and idiocuticular features.

Several aspects make the Lunz flora particularly interesting and suitable for these investigations:

—The flora from Lunz is palaeobotanically significant, since it represents one of only a few megafloras from the Alpine Triassic (Kerp 2000). Moreover, the Lunz flora is one of the oldest fossil floras that includes representatives of the extinct bennettitaleans (Cleal 1993). The flora is of stratigraphical importance in that it contributes fundamentally to the correlation of the German and Alpine facies of the European Triassic. The enabling of age-dating of other Late Triassic floras of Europe and North America that are not correlated with marine fossils supports the stratigraphic value of this flora (cf. Dobruskina 1998).

—The availability of a large number of fossils facilitates the work on the Lunz flora, and provides possibilities for large-sample investigations. They are necessary to reconstruct intraspecific variation or specific discriminations. With more than 4000 specimens (Dobruskina 1998; personal observation), the Lunz flora is one of the richest Late Triassic floras of the northern hemisphere. Almost all fossil remains are preserved as impressions or compressions.

—The preservation of the fossils is exceptional for compressions; moreover, the compressed remains yield excellently preserved cuticles. The fossils come from coal mines, and consequently never underwent weathering or other destructive forces, since they were directly sold from the mines to the museums. Cuticles can easily be removed from the rock and processed.

—With more than 70 species recorded to date (Dobruskina 1989, 1998), including sphenophytes, ferns, cycadaleans, bennettitaleans, conifers and ginkgophytes, the Lunz flora represents one of the most diverse Late Triassic floras. The most remarkable feature of this flora is the abundance of compressed cycadophyte (i.e. Cycadales and Bennettitales) reproductive structures and foliage. Several detailed studies exist that focus on the numerous and diverse fertile cycadophyte remains (Krasser 1916, 1917, 1919; Kräusel 1948, 1949, 1953). In contrast, the innumerable specimens of sterile foliage have not received much scholarly attention to date. This is partly due to the fact that the fossils are spread among collections throughout Europe.

—Unfortunately, this aggravates work on the Lunz flora and its collections: Due to the fact that the Lunz collection was partitioned, and the fossils were sold to collections and museums throughout Europe, no systematic survey existed to date that provides a synoptic and well-illustrated species list. Consequently, the various 19th and early 20th century collectors, traders and curators, who labelled most of the fossils, along with the early scholars studying the material, unintentionally created considerable confusion with regard to the scientific names given to the different foliage types based on macromorphology. This confusion remains to date, and renders establishing a trustworthy inventory of the plants in the Lunz flora a difficult task. This aspect underscores the need for a detailed systematic study to clarify the composition and nature of this highly diverse flora so that the Lunz flora may furthermore serve as the standard for Triassic floras of the northern hemisphere as proposed by Dobruskina (1989, 1998).

LOCALITY, MATERIAL AND METHODS

Locality.—The material comes from the area around Lunz-am-See in the Northern Calcareous Alps of Lower Austria, approximately 100 km west of Vienna. The plant fossils were collected from several localities located in a slender belt (WSW–ENE) between Lunz-am-See and Vienna (Figure 1). Most of the fossils were collected in coal mines that were active in the late 19th and early 20th centuries. Detailed outcrop positions are indicated in Figure 1. The outcrop conditions around Lunz-am-See are poor today, since coal mining finally ceased after WWII

(1958), and none of the localities is accessible to date. Fossils can still be found on some of the old spoil tips and "outcrops" produced by small creeks around Lunz-am-See (personal observation). However, this material is strongly weathered, and usually not suitable for cuticular analysis. As a result, this study is entirely based on material kept in various European museum collections. To date, approximately 4000 plant fossils from Lunz are known in the several collections. Additional 15 000 specimens are said to be stored in The Natural History Museum London (J. Eder, personal communication, 2004).

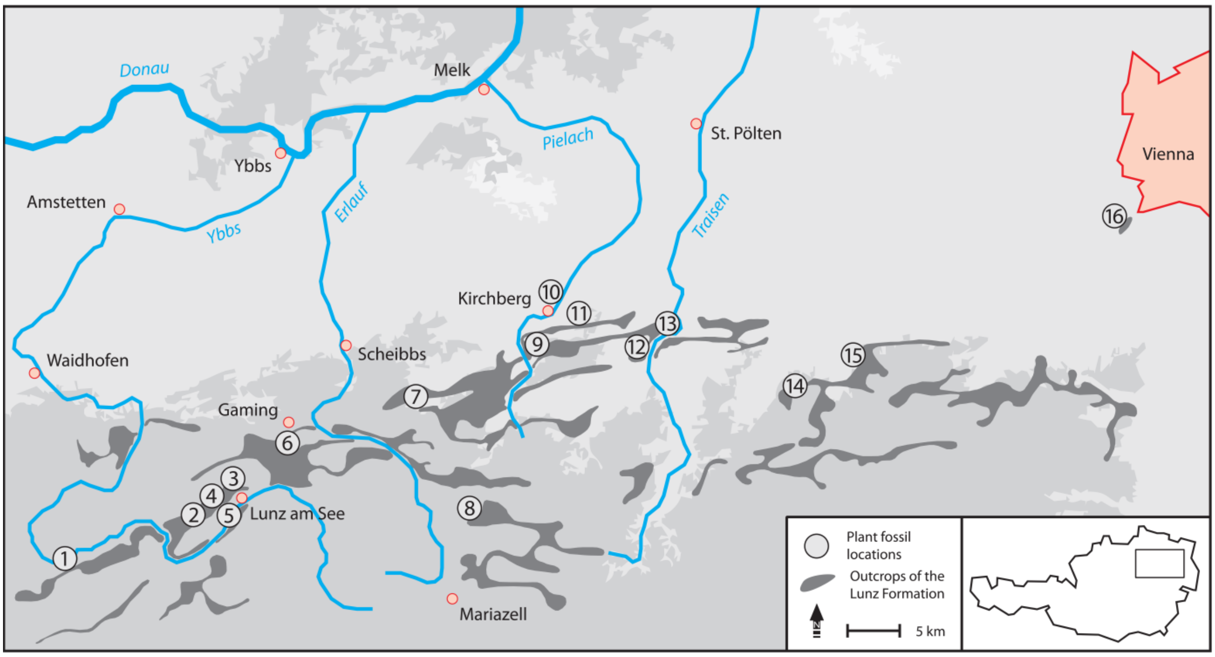

Figure 1. Map with the position of Lunz-am-See in Lower Austria, the outcrops of the 'Lunzer Schichten' and the localities where Lunz plant fossils were found (after Dobruskina 1998). 1, Hollenstein/Ybbs; 2, Ahornberg; 3, Holzapfel; 4, Pramelreith; 5, Lunz am See; 6, Gaming; 7, St. Anton/Jeßnitz; 8, Wienerbrück; 9, Loich; 10, Kirchberg/Pielach; 11, Tradigist; 12, Schrambach; 13, Lilienfeld; 14, Kleinzell; 15, Ramsau; 16, Kaltenleutgeben.

Material.—The Lunz plant fossils from the following collections formed the basis of this study: The Geological Survey of Austria, Vienna, Austria (1784 specimens); the Natural History Museum, Vienna, Austria (956 specimens); the State Museum Joanneum, Graz, Austria (263 specimens); the Natural History Museum, Stockholm, Sweden (171 specimens); the Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands (120 specimens); the Natural History Museum Senckenberg, Frankfurt, Germany (67 specimens); the State Museum of Lower Austria, St. Pölten, Austria (42 specimens); the State Collections of Natural History, Dresden, Germany (32 specimens); the Palaeobotany Research Group, Münster, Germany (31 specimens); the Naturalis Museum of Natural History, Leiden, The Netherlands (at least 24 specimens). As a result, a total amount of more than 3500 specimens could be considered for this study.

Methods.—The different collections mentioned above were studied on location. More than two thirds of the hand specimens were photographed with a high-resolution Nikon D100 digital camera using polarised light to increase contrast (cf. Schaarschmidt 1973) (Figure 2). This resulted in more than 2800 digital images. The use of polarised light and high resolution imaging revealed several details (venation, raised surface structures) that are hardly visible to the naked eye. A number of rock and cuticle samples (>350) was selected for cuticular analysis. Moreover, several hand specimens (>250) were loaned for other analyses (e.g. epifluorescence microscopy). Cuticles were prepared according to procedures outlined in Kerp (1990) and Kerp & Krings (1999). Rock samples with plant remains were dissolved in hydrofluoric acid (40% HF) in order to remove the sediment, or the plant remains were picked from the rock surface. Cuticles were macerated according to the standard procedure using Schulze's reagent (35% HNO_3 with a few crystals of $KClO_3$) and 5–10% potassium hydroxide (KOH). Macerated cuticles were washed in distilled water, gently dehydrated in pure glycerine, and finally mounted in permanent glycerine-jelly microscope slides.

More than 2800 microscopic slides were produced. Slides are stored in the collection of the Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Universität Münster, Germany, and in the relevant museum collections; the accession numbers for figured slides are indicated in the figure captions of the relevant papers.

Cuticle preparations were studied and documented by three different microscopy methods: Most of the samples were analysed with a Leitz Diaplan light microscope with Nomarski interference contrast, and photographed with a mounted Nikon DS-5M digital camera. In addition, small and brittle samples not suitable for maceration were analysed under incident UV-fluorescence. The use of a scanning electron microscope on some cuticles, mainly those of *Glossophyllum florinii*, revealed several details that were not visible with normal light microscopy or required opacity of the sample to demonstrate surface structures of the cuticles.

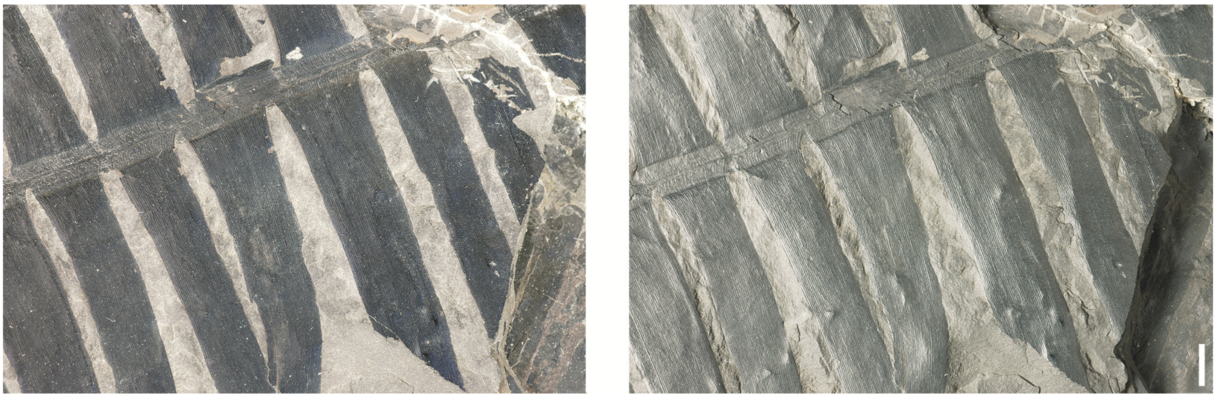

Figure 2. Pictures demonstrating the effect of using polarised light and filters (*left*: with filters; *right*: without filters); specimen NHMW 2006B0008/0033, *Nilssonia sturii*; scale bar — 5 mm.

GEOLOGICAL SETTING

The fossils come from the 'Lunzer Sandstein', which forms the upper part of the Lunz beds. The Lunz Formation (= Lunz beds or Lunzer Schichten) consists basally of sandstones, followed by marine marls gradually grading upwards into terrestrial sands, shales and coal. The coal-bearing part of the sequence is overlain by marls and with a sandstone layer at the top. The plant fossils occur in the shales associated with the coal beds. Exact age dating of the Lunz Formation is still a problem because adequate biostratigraphic markers such as ammonoids and conodonts are absent. Recent studies focussing on regional and facies-spanning correlations of biostrati-graphically well-established sections within the Hallstatt and Reifling Intraplatform Basins (Hornung & Brandner 2005) suggest that the Lunz Formation is positioned within the upper part of the Reingraben Formation (T. Hornung, personal communication, 2006). As a result, the Lunz Formation is probably late Julian (Julian 2/II) in age. Palynological studies indicate a Carnian (Bharadwaj & Singh 1964) and, more detailed, a Julian age (Dunay & Fisher 1978; Hochuli & Frank 2000) of the Lunz Formation. The Opponitzer Limestone, the upper sub-unit of the Lunzer Schichten, has been dated as Tuvalian by Dunay and Fisher (1978). An illustrated profile of the Lunzer Schichten is provided by Verloop (1908).

GEOGRAPHY AND CLIMATE DURING THE CARNIAN

Geography.—The Carnian is the earliest stage of the Late Triassic, dating from 228 to 216.5 Ma. It comprises two regional stages, the Julian (228–225 Ma) and the Tuvalian (225–216.5 Ma) (ICS 2005). The Carnian might be considered the heyday of Pangaea (Wing & Sues 1992), when all of the present continents together formed the supercontinent Pangaea. The land mass was surrounded by the Panthalassic Ocean, a single global ocean. With the Palaeo-Tethys, the global ocean had a western branch at equatorial latitudes. The later northern and southern continents Laurasia and Gondwana started to drift apart along an east-west-oriented rift system in its western part, which gave rise to the narrow and shallow Tethys seaway. In the Early Jurassic, this seaway became the precursor of the Central Atlantic Ocean. In the Carnian, the developing seaway was already well-established, although the prograding rift had not completely broken through to the west (Blakey, 2005).

Climate.—The Triassic was a period dominated by continental processes. Environmental variables were strongly different to modern levels: Carbon dioxide was reaching a temporal maximum (250–300% of modern levels; Berner & Kothavala 2001; Ghosh et al. 2005), while the oxygen concentration had a temporal minimum (at about 75% of modern levels; Berner 1999). The poles were not covered by ice caps like today. In general, the climate in the tropics of the Carnian was mostly arid (Hay et al. 1982). Simms and Ruffell (1989) postulated a "pluvial event", which interrupted the general arid climate of the Late Triassic. Several studies supported this change to humid conditions between the Julian and the beginning of the Tuvalian (e.g. Hochuli & Frank 2000; Roghi 2004; Stefani et al. 2004; Buratti & Cirilli 2007). The nature of this event is still discussed (Visscher et al. 1994; Olsen 1997). Moreover, this event is sporadically believed to be an artifact that was caused by the migration of continents of the Tethyan area across the equatorial climatic zone (Kent & Olsen 2000). The apparent climate change from arid to humid and back to arid simply reflects the drift of the continents in a northward direction (Wing & Sues 1992; Kent & Olsen 2000; Olsen & Rainforth 2001). Hence, a zonal climate was already established in the Late Triassic. An equatorial tropical belt comparable to the today's one was well-developed at Carnian times (Kent & Tauxe 2005). The regions along the shores of the Tethyan rift passed through this narrow climatic zone in only a few million years when Pangaea drifted slowly to the north; and consequently, the equatorial belt comprised of specific and mostly endemic ecosystems moved to the south. That region is today characterised by the only poorly known Late Triassic deposits of the south-eastern United States and northern Africa (Kent & Olsen 2000; Olsen & Rainforth 2001).

A SHORT HISTORY OF RESEARCH ON PLANT FOSSILS FROM LUNZ

The 19th century.—Plant fossils from Lunz were discovered nearly 160 years ago. The first illustration of plants from this flora was provided by Ettingshausen (1851). Since 1871, the Lunz plant fossils were studied more intensively. Studies were carried out until today with several interruptions. The first scholar studying plant fossils from Lunz was Dionysus Stur (1827–1893), who published three essays concerning the Lunz flora (Stur 1871, 1885, 1888). He was the first who showcased the plant fossils from Lunz to a general scientific public.

After Stur's sudden death, the Lunz fossils received only little scientific attention for more than ten years. During this time, mining foreman Josef Haberfelner (1830–1913) made sure that Lunz fossils became unforgettable; moreover, he arranged that Lunz fossils became more known throughout Europe. He organised the professional excavation of the fossils, and sold them to various natural history museums. In dispersing the fossils all over Europe, Haberfelner unconsciously complicated the study of this flora.

The 20th century.—In the following years, Fridolin Krasser (1865–1922) started to work on the Lunz flora. He revised part the work of Stur, and published several essays, in which he processed the handwritten notes of Stur with regard to ferns and cycadophyte foliage (Krasser 1909a, 1909b, 1909c). Later, he addressed himself to the fertile organs contained in the Lunz flora. Besides the excellent preservation of the fossils it was the presence of these fertile elements of Cycadales and Bennettitales that caused the illustriousness and, in fact, the significance of this flora. In the last years of WWI, Krasser published two benchmark papers on cycadophyte reproductive structures from Lunz (Krasser 1917, 1919). He also was the first, who used cuticular analysis in the analysis of the Lunz fossils.

However, work on the Lunz fossils rested for only a short time after Krasser's sudden death. In 1920, Richard Kräusel (1890–1966) released his first publication on some plant fossils from Lunz (Kräusel 1920). In the following years, he primarily worked on a flora of the same age, i.e. the flora from Neuewelt near Basel, Switzerland (Kräusel 1943, 1952, 1961; Kräusel & Leschik 1955, 1959; Kräusel & Schaarschmidt 1966). He thoroughly compared this flora with Lunz, and consequently, also studied plant fossils from Lunz (Kräusel 1920, 1943, 1948, 1949, 1953). Moreover, the work of Kräusel also focussed on the reproductive structures from Lunz. His studies resulted in several essays in which he copiously described putative bennettitalean and cycadalean reproductive organs and ginkgophytes (Kräusel 1943, 1948, 1949, 1953). He thereby revised some of Krasser's views, mainly when Florin's fundamental work on stomatal apparati of gymnosperms was released in 1933. In this important work, Florin described a critical aspect for the discrimination of bennettitalean from cycadalean foliage based on epidermal features (Florin 1933a). This was adopted by most of the contemporary palaeobotanists. Later, Kräusel turned to sterile foliage, but was not able to continue this work due to his death. His last publication focussing on the Lunz flora appeared in 1966, and dealt with pinnate bennettitalean foliage. Whenever possible, he considered cuticles of the Neuewelt and Lunz plants during his work.

Following Kräusel's death, work on the plant fossils from Lunz was abandoned for a longer period, until, in the 1990s, Inna Dobruskina (*c. 1932) addressed herself to the Lunz flora during her work on Eurasian Triassic floras. Three publications on the history and research of the Lunz flora were published between 1988 and 1998 (Dobruskina 1988, 1989, 1998). They include a relatively good overview and several synoptic "species" lists based on literature research. After this, it seemed that Mrs. Dobruskina has closed her studies on the Lunz flora.

Several other authors attended themselves to the Lunz flora since 1920, and released a few papers concerning specimens or taxa from that flora. Noteworthy are the works of A. G. Nathorst (1906, 1908), K. Frentzen (1922a, 1922b), C. R. Florin (1933c) and J. Langer (1943, 1945). The latter classified some of the specimens of the Lunz flora as ″endangered″ or "lost", and described a few specimens that were disregarded so far. Palynological, stratigraphical and age-dating studies were carried out by J. H. Verloop (1908), D. C. Bharadwaj and H. P. Singh (1957, 1964), R. F. Dunay and M. J. Fisher (1978) and G. Roghi (in process).

The 21st century.—Since 2004, a comprehensive study including extensive cuticular analyses is conducted at the Palaeobotany Research Group of the University Münster. Several papers focussing on the sterile bennettitalean and cycadalean foliage were submitted in 2005 and 2006. The present thesis is based on this research.

BENNETTITALES VS. CYCADALES

Bennettitaleans and cycadaleans represent the main focus of the present study. They are critical elements in the Lunz flora, and consequently intensively discussed later. Therefore, a short introduction that includes a closer look at the differences of the macromorphology of the leaves, reproductive modes and strategies, evolutionary history and the fossil relatives of these two orders of gymnosperms seems to be convenient.

Fundamental differences.—The Cycadales and Bennettitales are two orders of superficially similar gymnosperms, which, however, show a number of fundamental differences, notably in the structure of the reproductive organs.

Cycads are thought to be the most primitive of the living seed plants; the ancestors might be found among the extinct seed ferns (pteridosperms). Cycads are dioecious. The micro- and macrosporophylls in all cycad genera and species are reduced fertile leaves that are, with the exception of female *Cycas* plants, arranged in determinate shoots or cones. Both types of cones (pollen and seed cones) are produced terminally at the stem apices of male and female plants, respectively. In female *Cycas* plants, the megasporophylls are also born terminally at the stem apex, however, they are not arranged in a strobilus like in the other genera (i.e. *Encephalartos*, *Dioon*, *Zamia*, etc.). They rather form a cone-like cluster. *Cycas* megasporephylls represent a plesiomorphic type of a cycad megasporophyll on which the possible derivation from ancestral sterile leaves is traceable. Up to eight ovules are arranged in two rows laterally inserted at the basal part (the stalk) while the apical part is laminar with a more or less reduced pinnate architecture. The derived megasporophylls of the other genera are arranged in strobili (e.g. *Dioon*, *Encephalartos*, etc.), and produce only a single pair of ovules. The ovules are borne abaxially close to the inner part of the a-pex. The distal part of the sporophylls is reduced to form a peltate shield that covers the ovules. In combination with the adjacent megasporophylls, it forms a hermetically sealed outer surface of the seed cone (cf. Norstog & Nicholls 1997).

Cycad microsporophylls are always arranged in cones in all extant genera and species. The microsporangia are positioned on the abaxial surface of the sporophylls. Microsporophylls of *Cycas* species produce a thousand microsporangia, while the number of sporangia produced is gradually reduced from *Dioon* through *Encephalartos*, *Stangeria* and *Bowenia* to *Zamia* from about 700 to 25 microsporangia. Cycads are pollinated by wind or by beetles (i.e. weevils) (cf. Norstog & Nicholls 1997).

Intact seed cones of fossil cycads (i.e. *Androstrobus*, *Beania*; Harris 1964) are present as well as individual sporophylls (e.g. the megasporophyll *Dioonitocarpidium*). Mamay (1976) proposed a hypothetical evolution of the cycad megasporophyll from a *Spermopteris* type of fertile pteridosperm leaves. This implies that the strobilar megasporophylls of modern cycads represent a derived (apormorphic) type of an ancestral foliar megasporophyll of the *Dioonitocarpidium* or *Cycas* type. However, Axsmith et al. (2003) qualified the fertile nature of the *Spermopteris* fossil, which was typified by sterile specimens of a taeniopterid form. These authors assigned Mamay's *Spermopteris* specimens to the genus *Phasmatocycas*, which has been interpreted as a primitive cycad megasporophyll. Alternatively, Gao Zhi-Feng and Thomas (1989a) proposed two evolutionary lineages of the evolution in modern cycad megasporophylls. The first lineage leads from a *Crossozamia* megasporophyll and cone axis through *Beania* cones to the strobilar megasporophylls of the extant *Zamia* type. In the second lineage, it is proposed that modern *Cycas* megasporophylls separately evolved from *Crossozamia* megasporophylls. From this opinion, it may be inferred that the two types of modern cycad sporophylls are homologous.

Conversely, reproductive structures of the Bennettitales are not arranged in cones or strobili. Rather, male and female reproductive parts are arranged in "flowers" that show a superficial resemblance to bisexual angiosperm flowers. Bennettitales are predominantly monoecious, they are traditionally divided in two families, the Cycadeoidaceae (=Bennettitaceae) and the Williamsoniaceae. The two families are distinguished primarily by their growth habit. Most Cycadeoidaceae produce unbranched, massive and spheric trunks. The reproductive organs are born deeply sunken between remaining leaf bases (cataphylls) on the trunk. Williamsoniaceae are characterised by slender, arborescent stems (e.g. *Bucklandia*) with the reproductive structures exposed in branch axills. The Williamsoniaceae consist of two groups, sporadically treated as own families, the Williamsoniaceae and the Wielandiellaceae. Nowadays, these two groups are united in the Williamsoniaceae, which are supposed to be older than the Cycadeoidaceae (Alvin et al. 1967).

Bennettitaleans assigned to the Williamsoniaceae are mostly monoecious; they possess bisexual (*Williamsoniella* type) or unisexual (i.e. male *Weltrichia* type or female *Williamsonia* type) "flowers". The female part of the "flower" is composed of a cylindrical receptacle that bears alternating stalked ovules and interseminal scales. The ovules are characterised by a micropyle that overarches the gynoecial rind. The male portion of the "flower" consists of a circle of microsporangia bearing sporophylls. It surrounds the female part in bisexual "flowers". Microsporangia are arranged in synangia on the adaxial side of the sporophylls or are enclosed in the microsporophylls with adaxial openings (*Williamsoniella*). The "flower", may it be unisexual or bisexual, is surrounded by one or more circles of sterile bracts (e.g. *Cycadolepis*). Reconstructions of the differrent "flower" types are given in Crane (1985) and Watson and Sincock (1992). The pollination of bennettitalean "flowers" remains elusive. Bennettitalean "fruits" are generally allocated to the genus *Bennetticarpus* that is comprised of cone-like structures containing several seed-bearing scales spirally arranged around a central axis (Harris 1969).

While there are numerous extant cycads (11 genera with approximately 305 species; Hill et al. 2004), the Bennettitales represent an extinct group of plants. However, the stomata of some extant Gnetopsida (Welwitschiaceae and Gnetaceae), a group of plants suggested to be closely related to the once widespread Bennettitales, resemble the bennettitalean stomatal type (see below) (Florin 1933b; Martens 1971). Even if some scholars suggest that phylogenetic relationships between bennettitaleans and extant gnetaleans, gymnosperms and angiosperms exist, they remain controversially discussed (Crane 1985; Nixon et al. 1994; Donoghue & Doyle 2000; Doyle 2006).

On the general evolution of the seed-bearing habit refer to Taylor and Taylor (1993) and Norstog and Nicholls (1997).

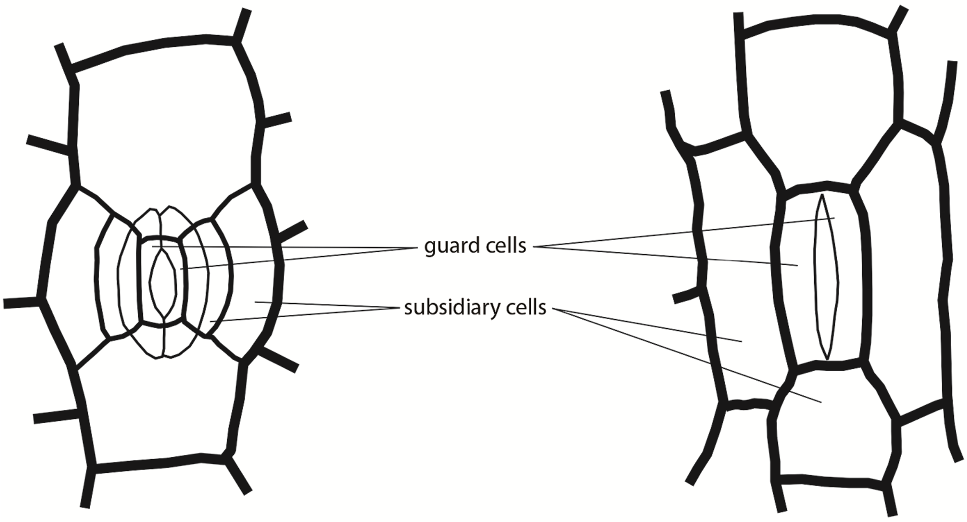

Figure 3. Schematic line-drawing of a syndetocheilic (*left*) and a haplocheilic (*right*) stoma.

Foliage.—Cycadalean and bennettitalean foliage is often macromorphologically similar, and thus can usually only be distinguished based on epidermal anatomy. Thomas and Bancroft (1913) first distinguished cycadalean and bennettitalean foliage in this way. Especially significant in the discrimination of the two foliage types is the stomatal morphology. Bennettitalean leaves are characterised by syndetocheilic stomata, while cycadalean leaves possess haplocheilic stomata (Figure 3). These termini were introduced by Florin (1933b, p. 14), and refer to the development and the resulting morphotype of the stomatal apparatus. Syndetocheilic stomata separate the Bennettitales from all other groups of plants with the exception of representatives of *Welwitschia* and *Gnetum* (see above).

The order and number of cell divisions during stomatal ontogeny is responsible for the formation of the two distinct stomatal types: In a syndetocheilic stoma, the initial mother cell divides two times. The two guard cells originate from the resulting median cell, while the subsidiary cells originate from the two outer cells. This stomatal type is considered as the apomorphic type. Haplocheilic stomata are composed of two guard cells that originate from one mother cell, while the subsidiary cells originate from adjacent epidermal cells. This type is analogically considered to be the plesiomorphic type (Figure 3).

Three leaf genera are generally accepted to be typical for Mesozoic cycadalean foliage: *Ctenis*, *Nilssonia* and *Pseudoctenis* (Taylor & Taylor 1993; Norstog & Nicholls 1997; Watson & Cu-sack 2005). Typical Mesozoic foliage assigned to the Bennettitales is allocated to clearly more genera. The most widespread genera are *Anomozamites*, *Nilssoniopteris*, *Otozamites*, *Pseudocycas*, *Pterophyllum*, *Ptilophyllum*, *Sphenozamites* and *Zamites* (Figure 4) (Taylor & Taylor 1993; Watson & Sincock 1992).

Bennettitales or Cycadeoidales?—The most common placement of this group (its status ranges from a division to an order) is as an order within the class Cycadopsida (Cleal & Rees 2003). The ordinal names Bennettitales and Cycadeoidales are based on the generic names Bennettites Carruthers, 1870 and Cycadeoidea Buckland ex Lindley et Hutton, 1932, respectively (Watson & Sincock 1992). Cycadeoidales is widely used by North American palaeobotanists while European authors mostly use the name Bennettitales. It is generally accepted that both names are synonyms for a single group (order) of plants. The different usage maintains considerable confusion to date. Watson and Sincock (1992) discussed the priority problem, and provided evidence for the priority of Bennettitales Engler, 1892 over Cycadeoidales Arnold, 1947 even if the familial rank of Cycadeoidaceae Buckland, 1829 has priority over Bennettitaceae Engler, 1892.

THE CUTICLES

Another critical element of this study are the cuticles of the seed plants from Lunz. In order to avoid many repetitions, the reader is referred to Kerstiens (1996), Riederer and Müller (2006) and to Chapter 6 of this work for further detailed information about the structure, functions and adaptative possibilities as well as the importance of the cuticles for the plant and its interactions with the environment.

The cuticle is a critical element in the controlled exchange of substances between the outside world and the internal tissues of vascular plants. Its protective effectiveness against excessive water loss is of special importance for the growth and life of the plant. Moreover, the cuticle provides protection from various deleterious environmental influences, including UV-radiation, mechanical injuries, dust particles and phytopathogenic microorganisms (Martin 1964; Campbell et al. 1980; Allen et al. 1990). A heavily cutinised epidermis may prohibit piercing-and-sucking arthropods from penetrating the surface, and thus function in herbivory abatement. In addition, the cuticles of many extant plants display special structures either of wax coating (epicuticular waxes) or as surface micro-reliefs that may also function in protecting the plant. Epicuticular waxes are found in all vascular plants (Neinhuis & Barthlott 1997), whereas surface ornaments primarily occur in angiosperms (Barthlott & Ehler 1977; Barthlott 1980; Barthlott & Ziegler 1981) and some gymnosperms (e.g. Florin 1936). Both characteristics are effective as passive defence mechanisms against herbivores and phytopathogenic microorganisms, and can serve as adaptations to particular (extreme) abiotic habitat conditions (e.g. Chapman 1976; Suzuki 1980; Hutchings & Saenger 1987; Western 1988).

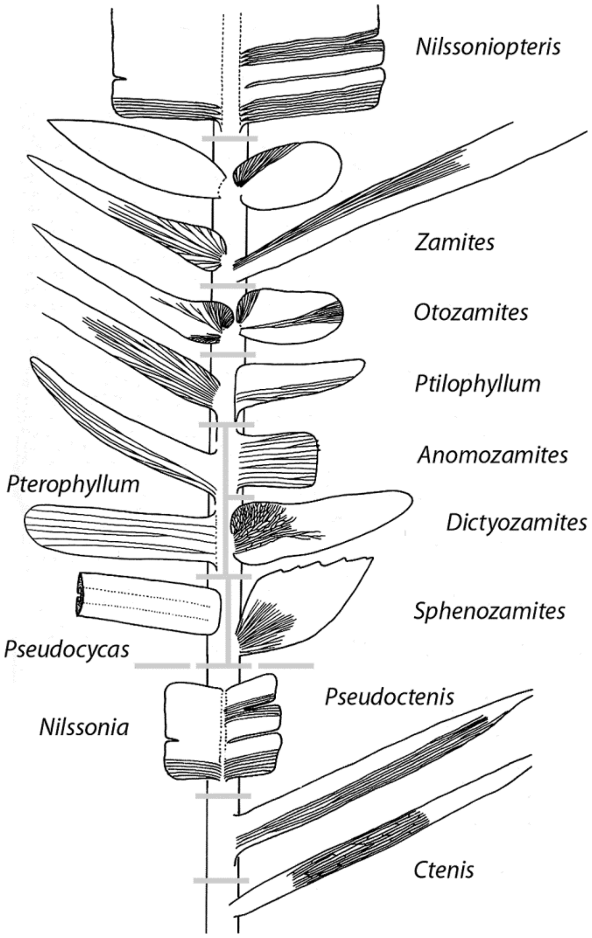

Figure 4. Details of leaf segment morphology and venation of bennettitalean and cycadalean leaf form-genera (modified after Watson & Sincock 1992; Watson & Cusack 2005).

The cuticles of many fossil seed plants are highly resistant, and often survived fossilisation and diagenesis almost unchanged morphologically. Fossil cuticles are highly informative, and consequently obviously useful in the taxonomy of fossil seed plants (e.g. Krings & Kerp 2000; Kerp & Krings 2003). They are also important with regard to palaeobiological and palaeoecological considerations (e.g. Krings et al. 2003a, 2003b). As a result, the analysis of fossil cuticles has become a major focus of palaeobotanical research (Kerp 1990).

SECTION I — BENNETTITALES

The order Bennettitales was established by Engler (1892, p. 61). Historically, it was widely believed that the representatives of Bennettitales are close relatives of the extant Cycadales (e.g. Morris 1841; Miquel 1851; Steinmann 1903). More recently, however, a number of fundamental differences between cycads and bennettitaleans have been elaborated, which suggest that the two groups of plants are not closely related (Schuster 1931; Crane 1985; Watson & Sincock 1992; Taylor & Taylor 1993). The two groups were formerly grouped together in the 'cycadophytes'. The current systematic position of the Bennettitales has repeatedly been discussed. Recent cladistic analyses substantiate that Cycadales and Bennettitales are not closely related, although individual workers do not entirely agree on the position of the Bennettitales (e.g. Crane 1985; Nixon et al. 1994; Rothwell & Serbet 1994; Donoghue & Doyle 2000; Doyle 2006; Hilton & Bateman 2006). The origin of the Bennettitales and their relationships to the other lineages of fossil and extant seed plants remain controversial (Norstog & Nicholls 1997; Doyle 2006), due in part to the fact that many of the reproductive structures attributed to the Bennettitales continue to be incompletely understood (Norstog & Nicholls 1997; Rothwell & Stockey 2002; Stockey & Rothwell 2003).

The earliest persuasive records of bennettitaleans come from the Late Triassic. The bennettitalean representatives from the Lunz flora thus range among these earliest bennettitaleans in the fossil record (Cleal 1993; Kelber 1998; Kelber & Nitsch 2005). Bennettitaleans were abundant in the Early–Middle Jurassic, and became extinct in the Early Cretaceous.

Bennettitaleans reported from pre-Carnian localities have to be addressed very carefully. Cuticles of pre-Carnian species are often not preserved or unknown. The accommodation of species like *Pterophyllum cutelliforme* (Sze 1936; Ke-Qin Sun 2006), *P. cotteanum* (Geinitz 1873; Barthel 1976), *P. blechnoides* (Geinitz 1873), *P. samchokense* (Kawasaki 1931), *P. daihoense* (Kawasaki 1931, 1934; Ke-Qin Sun 2006) and *P. eratum* (Gu & Zhi 1974) from the Upper Carboniferous and Permian of China, Korea and Germany in the genus *Pterophyllum* remains equivocal.

CHAPTER 1

Proposal to conserve the name *Pterophyllum* (Foss., Bennettitales) with a conserved type

Christian Pott, Hans Kerp, Johanna H.A. van Konijnenburg-van Cittert & Gea Zijlstra

Taxon 56: 966–967 (2007)

Abstract.—Brongniart introduced the name *Pterophyllum* for a genus comprising two species of fossil pinnate leaves, *P. minus* and *P. majus*, from the uppermost Triassic of southern Sweden and assigned them to the Cycadaceae. He (l.c.: 216. 1825) also discussed the cycadalean nature of *Algacites filicoides* Schloth. (Nachtr. Petrefaktenk.: 47. 1822), which had originally been interpreted as an alga, but did not classify the latter species in *Pterophyllum* or in another genus for pinnate cycad-like foliage. Three years later Brongniart (Prodr. Hist. Vég. Foss.: 95. 1828) gave a new, largely identical diagnosis of *Pterophyllum* to which he attributed six species; two others were mentioned as doubtful. In addition to *P. minus* and *P. majus* he listed four names under *Pterophyllum*, two of them being *nomina nuda* (*P. meriani*, *P. williamsonis*). He transferred *Algacites filicoides* Schloth. and *Osmundites pectinatus* Jaeger (Pflanzenverst. Bausandstein Stuttg.: 29. 1827) to *Pterophyllum* but he did not adopt the original specific epithets and renamed them as *P. longifolium* and *P. jaegeri* respectively, these latter names thus being illegitimate. Nathorst subsequently transferred *P. minus* (Kongl. Svenska Vetenskapsakad. Handl. ser. 2. 16(7): 19. 1878) and *P. majus* (Beitr. Foss. Fl. Schwedens: 21. 1878) to the genus *Anomozamites* Schimper 1870 (Traité Paléont. Vég. II: 140. 1870), a genus of the Bennettitales. This implies that without conservation, *Pterophyllum* (typified on either *P. minus* or *P. majus*), has to replace *Anomozamites*, whereas for the genus in the sense as enlarged by Brongniart in 1828, no name is available. *Pterophyllum* is still widely used as a morphogenus for pinnate leaves and the generic diagnosis has been emended by Harris (Yorksh. Jurassic Fl. III: 92. 1969) and Watson & Sincock (Bennettitales Engl. Wealden: 108. 1992) to include only species with syndetocheilic stomata of the bennettitalean type.

(l.c.) in their pl. 25. Thus the type of *S. paradoxa* is that of *C. erectus*, and *C. nutans* (pl. 26 in Schimper & Mougeot) becomes a taxonomic synonym of these names. It appears that no original material of Brongniart still exists, and moreover, the specimens investigated by Schimper & Mougeot are lost as well. Therefore, Grauvogel-Stamm (l.c.: 70) designated a neotype, the specimen cited above. This specimen is illustrated in Grauvogel-Stamm (l.c.: t. 6, f. 1 and text fig. 5). At present this unnumbered specimen still is housed in Maison Grauvogel, a small natural history museum in Ringendorf, near Strasbourg. In the near future it will probably be moved to the Musée de l'Institut de Géologie de Strasbourg, France.

(1791) Proposal to conserve the name *Pterophyllum* (fossil *Bennettitales*) with a conserved type

Christian Pott[1,6], Ian M. Miller[2,6], Hans Kerp[1], Johanna H.A. van Konijnenburg-van Cittert[3,4] & Gea Zijlstra[5]

[1] *Forschungsstelle für Paläobotanik, Geologisch-Paläontologisches Institut, Hindenburgplatz 57, 48143 Münster, Germany. christian.pott@uni-muenster.de (author for correspondence)*
[2] *Denver Museum of Nature and Science, 2001 Colorado Blvd., Denver, Colorado 80205-5798, U.S.A.*
[3] *National Natural History Museum Naturalis, P.O. Box 9517, 2300 RA Leiden, The Netherlands*
[4] *Laboratory of Palaeobotany and Palynology, Budapestlaan 4, 3584 CD Utrecht, The Netherlands*
[5] *Nationaal Herbarium Nederland, Utrecht University branch, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands*
[6] *The conclusions of this proposal were reached independently by research groups led by C. Pott and I. Miller. The current proposal is a collaborative effort between these groups.*

(1791) ***Pterophyllum*** Brongn. in Ann. Sci. Nat. (Paris) 4: 211. Feb 1825 ('1824'), nom. cons. prop.
Typus: *P. longifolium* Brongn. (Prodr. Hist. Vég. Foss.: 95. Dec 1828) nom. illeg. (*P. filicoides* (Schloth.) Zeiller, *Algacites filicoides* Schloth.), typ. cons. prop.

Brongniart (l.c.: 216. 1825) introduced the name *Pterophyllum* for a genus comprising two species of fossil pinnate leaves, *P. minus* and *P. majus*, from the uppermost Triassic of southern Sweden and assigned them to the *Cycadaceae*. He also discussed the cycadalean nature of *Algacites filicoides* Schloth. (Petrefaktenkunde Nachträge: 47. 1822), which had originally been interpreted as an alga, but did not assign this species to *Pterophyllum* or to any other cycadalean genus despite its pinnate cycad-like foliage. Three years later, Brongniart (Prodr. Hist. Vég. Foss.: 95. 1828) gave a new, largely identical diagnosis of *Pterophyllum* to which he attributed six species; two others were mentioned as doubtful. In addition to *P. minus* and *P. majus* he listed four names under *Pterophyllum*, two of them being nomina nuda (*P. meriani*, *P. williamsonis*). He transferred *Algacites filicoides* Schloth. and *Osmundites pectinatus* Jaeger (Pfl.-Versteiner.: 29. 1827) to *Pterophyllum* but he did not adopt the original specific epithets and instead renamed them as *P. longifolium* and *P. jaegeri*, respectively, these latter names thus being illegitimate. Nathorst subsequently transferred *P. minus* and *P. majus* (in Öfv. Kongl. Vetenskaps-Akad. Handl. 1: 34. 1876) to the genus *Anomozamites* Schimper 1870 (Traité Paléont. Vég. 2: 140. 1870). Accepting this transfer implies that without conservation, *Pterophyllum* (typified on either *P. minus* or *P. majus*), has to replace *Anomozamites*, whereas for the genus in the enlarged sense of Brongniart (1828), no name is available. *Pterophyllum* is still widely used as a morphogenus for pinnate leaves and the generic diagnosis has been emended by Harris (Yorksh. Jurassic Fl. 3: 92. 1969) and Watson & Sincock (Bennettitales Engl. Wealden: 108. 1992) to include only species with syndetocheilic stomata of the bennettitalean type.

The *Cycadales* and *Bennettitales* are two groups of superficially similar gymnosperms that possess several fundamental differences. Members of both groups display a similar growth habit, and the foliage is often macromorphologically very similar. However, leaves with preserved cuticles can be distinguished on the basis of epidermal anatomy. The reproductive structures of *Cycadales* and *Bennettitales* are very dissimilar. Collectively, this evidence indicates that the two groups are not closely related, a conclusion supported by cladistic analysis. However, researchers do not entirely agree on the phylogenetic position of the *Bennettitales*, e.g., Crane (in Ann. Missouri Bot. Gard. 72: 716–793. 1985; in Cladistics 1: 329–348. 1985), Nixon & al. (in Ann. Missouri Bot. Gard. 81: 484–533. 1994), Rothwell & Serbet (in Syst. Bot. 19: 443–482. 1994), Doyle (in J. Torrey Bot. Soc. 133: 169–209. 2006), and Hilton & Bateman (in J. Torrey Bot. Soc. 133: 119–168. 2006).

The order *Bennettitales* was not established until 1892 by Engler (Syllabus: 61. 1892). Thomas & Bancroft (in Trans. Linn. Soc. London, Bot. 8: 155–203. 1913) first distinguished cycadalean and bennettitalean foliage based on epidermal anatomy.

Algacites filicoides was described by Schlotheim in 1822 (l.c.: 47. 1822), who figured a single specimen from the Carnian (Upper Triassic) of Neuewelt near Basel (Switzerland) (l.c.: pl. IV, fig. 2. 1822) that is now kept in the Museum für Naturkunde der Humboldt-Universität zu Berlin. Zeiller (Bassin Houill. Blanzy Creusot: 196. 1906) replaced *Pterophyllum longifolium* by *P. filicoides*, thus making the correct new combination. However, he illustrated a cuticle of a specimen from the type locality that does not show the typical stomata. Thomas (in J. Linn. Soc., Bot. 47: 407. 1930) illustrated cuticles with stomata from the Carnian of Lunz (Austria) and thereby emended *Pterophyllum filicoides*. Although the latter name is legitimate, it was hardly ever adopted by subsequent authors; the species is mostly still referred to as *P. longifolium* (see: Jongmans & Dijkstra, Foss. Cat. 56: 2716–2718. 1963; Dijkstra & van Amerom, Foss. Cat. 91: 594. 1985). Andrews (in Bull. U.S. Geol. Surv. 1300: 179. 1970) claimed to select *P. longifolium* as type of *Pterophyllum*, disregarding the fact that it was not eligible, not being an original (1825) species; he also neglected *Algacites filicoides* Schloth., the name which it replaced and *P. filicoides*, the correct new combination.

Jongmans & Dijkstra (l.c.: 2691–2744. 1963) and Dijkstra & van Amerom (l.c.: 588–601. 1985) list ca. 265 species of *Pterophyllum*. The genus is clearly in need of revision. The few species reported from the Upper Carboniferous and Permian (e.g., Geinitz, Dyas 2: 146. 1862; Renault & Zeiller, Étud. Commentry Fl. Foss.: 619. 1890) can no longer be accommodated in *Pterophyllum*, either because their cuticles do not show the bennettitalean epidermal anatomy (Zeiller, l.c.: 198, fig. B'. 1906) or because cuticles are not known in these fossils. The earliest unequivocal occurrence of *Pterophyllum* with cuticle has been reported from the Carnian and the youngest stratigraphic occurrence is in the Lower Cretaceous. The geographical distribution of *Pterophyllum* is largely restricted to the northern hemisphere, from North America across Europe to eastern Asia.

Several species previously assigned to *Pterophyllum* do not show the typical bennettitalean epidermal anatomy and have been transferred to other genera (e.g., *Anomozamites* Schimper, *Nilssonia* Nathorst; Thomas, l.c.: 389–415. 1930; Pott & al. in Rev. Palaeobot. Palynol. 143: 197–217. 2007). On the other hand, detailed studies of species of cycad-like foliage with cuticle preservation, previously assigned to other genera, necessitated their transfer to *Pterophyllum* (Watson & Sincock, l.c.: 108–121. 1992). Even when a critical revision of the genus *Pterophyllum* results in a reduction of the number of species, *Pterophyllum* is still a major constituent of Mesozoic northern hemisphere floras. Especially in Upper Triassic floras *Pterophyllum* is often the dominant taxon, for example in the very rich floras of Lunz and Neuewelt.

In accordance with Art. 14.9 of the ICBN (McNeill & al. in Regnum Veg. 146. 2006), we propose to conserve the generic name *Pterophyllum* Brongniart 1825 with *Pterophyllum longifolium* Brongn. nom. illeg. (*P. filicoides* (Schloth.) Zeiller, *Algacites filicoides* Schloth.) as type. Rejection of this proposal would require the renaming of a considerable number of *Pterophyllum* species for which no alternative generic name is currently available, and would make it necessary to replace *Anomozamites* by *Pterophyllum*. This would lead to considerable confusion, particularly because the name *Pterophyllum* is not only frequently used in (palaeo)botanical but also in geological literature, including textbooks (e.g., Vakhrameev, Jur. Cretac. Fl. 1991; Benton, Foss. Record. 1993; Stewart & Rothwell, Paleobotany. 1993; Taylor & Taylor, Biol. Foss. Pl. 1993; Dobruskina, Triassic Fl. Eurasia. 1994).

CHAPTER 2

Revision of the *Pterophyllum* species (Cycadophytina: Bennettitales) in the Carnian (Late Triassic) flora from Lunz, Lower Austria

Christian Pott, Johanna H. A. van Konijnenburg-van Cittert, Hans Kerp & Michael Krings

Review of Palaeobotany and Palynology 147: 3–27 (2007)

Abstract.—A revision of the genus *Pterophyllum* from the famous Late Triassic flora of Lunz in Lower Austria based on macromorphology, biometry, and epidermal anatomy is presented. Two distinct species, *Pterophyllum filicoides* and *P. brevipenne*, are recognised. Other *Pterophyllum* "species" described from Lunz by D. Stur and F. Krasser in the late 19th and early 20th centuries are interpreted as conspecific with either of these two species; others represent cycadalean foliage assignable to the genus *Nilssonia*. Full-grown *P. filicoides* leaves are more than 45 cm long and oblong to broadly oval in outline; the lamina is subdivided into narrow leaf segments up to 11 cm long. Full-grown leaves of *P. brevipenne* are considerably smaller than those of *P. filicoides*, and lanceolate to spatulate in outline; the lamina is subdivided into leaf segments up to 2.7 cm long. *Pterophyllum* is by far the most common element in the Lunz flora. Moreover, the species from Lunz range among the earliest representatives of this genus in the fossil record. This suggests that certain Bennettitales locally became significant elements of the vegetation relatively early in their evolutionary history.

Keywords.—*Pterophyllum*, plant fossils, Bennettitales, epidermal anatomy, Lunz (Austria), cuticular analysis.

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Revision of the *Pterophyllum* species (Cycadophytina: Bennettitales) in the Carnian (Late Triassic) flora from Lunz, Lower Austria

Christian Pott [a,*], Johanna H.A. van Konijnenburg-van Cittert [b,c], Hans Kerp [a], Michael Krings [d]

[a] *Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, D-48143 Münster, Germany*

[b] *National Natural History Museum Naturalis, P.O. Box 9517, 2300 RA Leiden, The Netherlands*

[c] *Laboratory of Palaeobotany and Palynology, Budapestlaan 4, 3584 CD Utrecht, The Netherlands*

[d] *Bayerische Staatssammlung für Paläontologie und Geologie und GeoBio Center^{LMU}, Richard-Wagner-Straße 10, D-80333 Munich, Germany*

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Abstract

A revision of the genus *Pterophyllum* in the famous Late Triassic flora of Lunz, Lower Austria, based on macromorphology, biometry, and epidermal anatomy is presented. Two distinct species, *Pterophyllum filicoides* and *Pterophyllum brevipenne*, are recognized. Other *Pterophyllum* "species" described from Lunz by D. Stur and F. Krasser in the late 19th and early 20th centuries are interpreted as conspecific with either of these two species; others represent cycadalean foliage assignable to the genus *Nilssonia*. Full-grown *P. filicoides* leaves are more than 45 cm long and oblong to broadly oval in outline; the lamina is subdivided into narrow leaf segments up to 11 cm long. Full-grown leaves of *P. brevipenne* are considerably smaller than those of *P. filicoides*, and lanceolate to spatulate in outline; the lamina is subdivided into leaf segments up to 2.7 cm long. *Pterophyllum* is by far the most common element in the Lunz flora. Moreover, the species from Lunz range among the earliest representatives of this genus in the fossil record. This suggests that certain Bennettitales locally became significant elements of the vegetation relatively early in their evolutionary history.

Keywords: *Pterophyllum*; plant fossils; Bennettitales; epidermal anatomy; Lunz (Austria); cuticular analysis

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1. Introduction

The Carnian (early Late Triassic) flora of Lunz in Lower Austria contains several morphotypes of segmented or entire-margined to coarsely segmented leaves, most of which have historically been interpreted as belonging to the bennettitalean foliage morphogenus *Pterophyllum* Brongniart, 1825 ('1824') (Stur, 1885; Krasser, 1909b). Brongniart (1825) introduced *Pterophyllum* for pinnate cycadophyte leaves. Stur (1885) refers 17 foliage types from Lunz to the genus *Pterophyllum*, however, without giving diagnoses, descriptions, or illustrations of the fossils. As a result, the names introduced by this author remained nomina nuda until Krasser (1909b), based on Stur's handwritten notes, provided a more formal classification, which

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* Corresponding author. Tel.: +49 251 8323934; fax: +49 251 8321739.

E-mail address: christian.pott@uni-muenster.de (C. Pott).

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includes brief diagnoses of the individual taxa and a short discussion, but still lacks illustrations of the material.

Although cuticular analysis is known to provide a wealth of information useful in determining the systematic affinities of many foliage fossils (e.g., Florin, 1933; Watson and Sincock, 1992; Watson and Cusack, 2005), it has largely been neglected in studies of the Lunz flora. Data on the epidermal anatomy of *Pterophyllum* leaves from Lunz had been unavailable, with the exception of a few cuticles described by Kräusel and Schaarschmidt (1966). However, their descriptions are incomplete, and hence not useful as a basis for accurately identifying further specimens that may be similar in gross morphology. As a result, circumscription of the foliage types from Lunz assigned to *Pterophyllum* by Krasser (1909b) continues to be vague, and thus the systematic affinities of these fossils remain uncertain.

A recent thorough reinvestigation of the Lunz flora based on macromorphological and cuticular analyses revealed that the body of fossils conventionally placed in the genus *Pterophyllum* (cf. Stur, 1885; Krasser, 1909b) is in need of a revision because it includes both bennettitalean and cycadalean foliage. The cycadalean foliage has formally been excluded from *Pterophyllum* by Pott et al. (2007a), and transferred to *Nilssonia*. Entire-margined to coarsely segmented foliage has been transferred to *Nilssoniopteris* (Pott et al., in press-b). The present paper provides detailed descriptions of the macromorphology and epidermal anatomy of the bennettitalean foliage retained in *Pterophyllum*. Based on our results, we propose that, in the Lunz flora, the morphogenus *Pterophyllum* is represented by only two distinct species, i.e. *Pterophyllum filicoides* and *Pterophyllum brevipenne*. Other *Pterophyllum* "species" described by Stur (1885) and Krasser (1909b) are interpreted as conspecific with either of these two species based on epidermal anatomy.

2. *Pterophyllum* Brongniart, 1825 ('1824')

Pterophyllum is a morphogenus of bennettitalean foliage comprised of segmented leaves with laterally inserted, almost parallel-sided leaf segments, a striate rachis and epidermal anatomies that display syndetocheilic stomata (Thomas, 1930; Florin, 1933; Harris, 1969; Van Konijnenburg-van Cittert et al., 2001). Brongniart (1825) introduced the name *Pterophyllum* for a genus comprising two species of fossil pinnate leaves, *P. minus* and *P. majus*, from the uppermost Triassic of southern Sweden, and assigned them to the Cycadaceae. He also discussed the cycadalean nature of *Algacites filicoides* Schlotheim, 1822 from the Late Triassic flora of Neuewelt (Switzerland), which had originally been interpreted as an alga (Schlotheim, 1822), but did not classify the latter species in *Pterophyllum* or in another genus for pinnate cycad-like foliage. Later, in 1828, Brongniart gave a new, largely identical diagnosis of *Pterophyllum* to which he attributed six species; two others were mentioned as doubtful (Brongniart, 1828). He transferred *A. filicoides* Schlotheim, 1822 and *Osmundites pectinatus* Jaeger, 1827 to *Pterophyllum* but did not adopt the specific epithets and renamed them as *Pterophyllum longifolium* and *Pterophyllum jaegeri*, these latter names thus being illegitimate. Nathorst subsequently transferred *P. minus* and *P. majus* to the genus *Anomozamites* Schimper, 1870 (Nathorst, 1878a,b). Because the two species on which Brongniart (1825) originally established the genus *Pterophyllum* are now classified in another genus, the generic name *Pterophyllum* Brongniart, 1825 ('1824') is illegitimate. However, *Pterophyllum* is still widely used as a morphogenus for pinnate leaves. The generic diagnosis has been emended by Harris (1969) and Watson and Sincock (1992) to include only bennettitalean foliage characterized by syndetocheilic stomata.

In accordance with ICBN (Greuter et al., 2000) Art. 14, Pott et al. (in press-a) proposed to conserve the generic name *Pterophyllum* Brongniart, 1825 ('1824') with the type species *P. filicoides* (Schlotheim, 1822) Zeiller, 1906 (basionym *Algacites filicoides* Schlotheim, 1822). Andrews (1970) selected *P. longifolium* Brongniart, 1828 as the type species of *Pterophyllum*, thereby disregarding the nomenclatural changes made by Zeiller (1906) and validated by Thomas (1930).

3. Geological setting, material, and methods

The material was collected in the late 19th and early 20th centuries from several active coalmines around Lunz-am-See in the Northern Calcareous Alps, Lower Austria, approximately 100 km west of Vienna (Fig. 1). The Lunz flora represents one of the richest and most diverse Late Triassic floras of the Northern Hemisphere and consists of sphenophytes, ferns, and a variety of gymnosperms, including cycadaleans, bennettitaleans, coniferophytes and putative ginkgophytes (Dobruskina, 1989, 1998).

The fossils occur in the "Lunzer Sandstein", which is part of the Lunz beds. The Lunz Formation (= Lunzer Schichten) consists of sandstones at basis, followed by marine marls gradually grading upwards into terrestrial

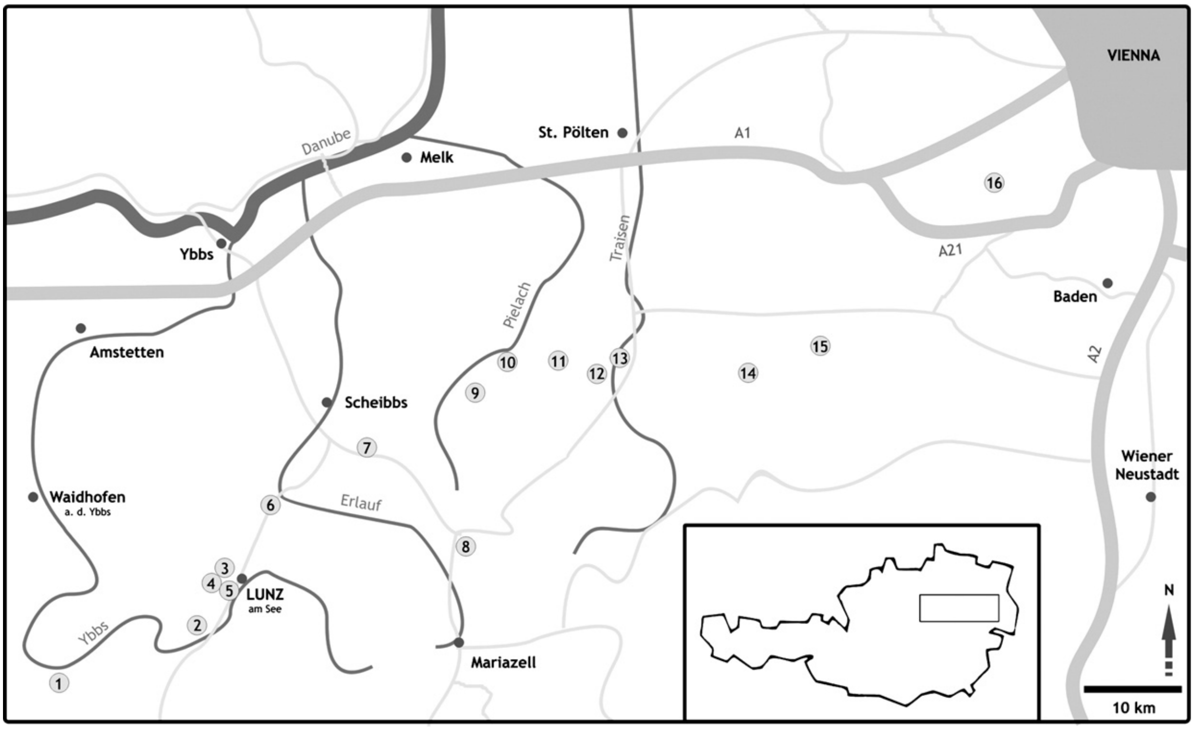

Fig. 1. Map showing the position of Lunz-am-See in Lower Austria and the localities where Lunz plant fossils were found (1) Hollenstein an der Ybbs; (2) Ahornberg; (3) Holzapfel; (4) Pramelreith; (5) Lunz am See; (6) Gaming; (7) Sankt Anton an der Jessnitz; (8) Wienerbruck; (9) Loich; (10) Kirchberg an der Pielach; (11) Tradigist; (12) Schrambach; (13) Lilienfeld; (14) Kleinzell; (15) Ramsau; (16) Kaltenleutgeben.

sands, shales, and coal. The coal-bearing part of the sequence is overlain by marls and with a sandstone layer at the top. The plant fossils occur in the shales associated with the coal beds. Exact age dating of the Lunz Formation continues to be a problem due to the lack of adequate biomarkers such as ammonoids and conodonts. Recent studies focusing on regional and facies-spanning correlations of biostratigraphically well-established sections of the Hallstatt Basin and the Reifling Intraplatform Basin (Hornung and Brandner, 2005) suggest that the Lunz Formation ought to be integrated within the upper part of the Reingraben Formation (T. Hornung personal communication, 2006). Taking this into account, the Lunz Formation probably is late Julian (Julian 2/II) in age. Palynological studies indicate a Carnian (Bhardwaj and Singh, 1964) and Julian age (Dunay and Fisher, 1978; Roghi, 2004). The Opponitzer Limestone, the upper sub-unit of the Lunzer Schichten, has been dated as Tuvalian by Dunay and Fisher (1978).

The plant fossils from Lunz are usually preserved as impressions or compressions, the latter often with excellently preserved cuticles. Cuticles were prepared according to procedures outlined in Kerp (1990), and Kerp and Krings (1999). Rock samples with plant remains were dissolved in hydrofluoric acid (HF) in order to remove the sediment, or the plant remains were picked from the rock surface. Cuticles were macerated according to the standard procedure using Schulze's reagent (35% HNO_3 with a few crystals of $KClO_3$) and 5–10% Potassium hydroxide (KOH). Macerated cuticles were washed in distilled water, gently dehydrated in pure glycerine, and finally mounted in permanent glycerine-jelly microscope slides. Slides are stored in the collections of the relevant museums; accession numbers are indicated in the figure captions.

Hand specimens were photographed with a Nikon D 100 digital camera; in order to increase contrast, cross-polarization (i.e. polarized light sources together with a polarizing filter over the camera lens) was used. Cuticles were analysed with a Leitz Diaplan microscope and photographed with a Nikon DS-5M digital camera.

The material used in this study is deposited in the following collections:

GBA	Geologische Bundesanstalt, Wien (Geological Survey of Austria, Vienna, Austria),
JOA	Landesmuseum Joanneum, Graz (State Museum Joanneum, Graz, Austria),
MNB	Museum für Naturkunde, Berlin (Museum of Natural History, Berlin, Germany),

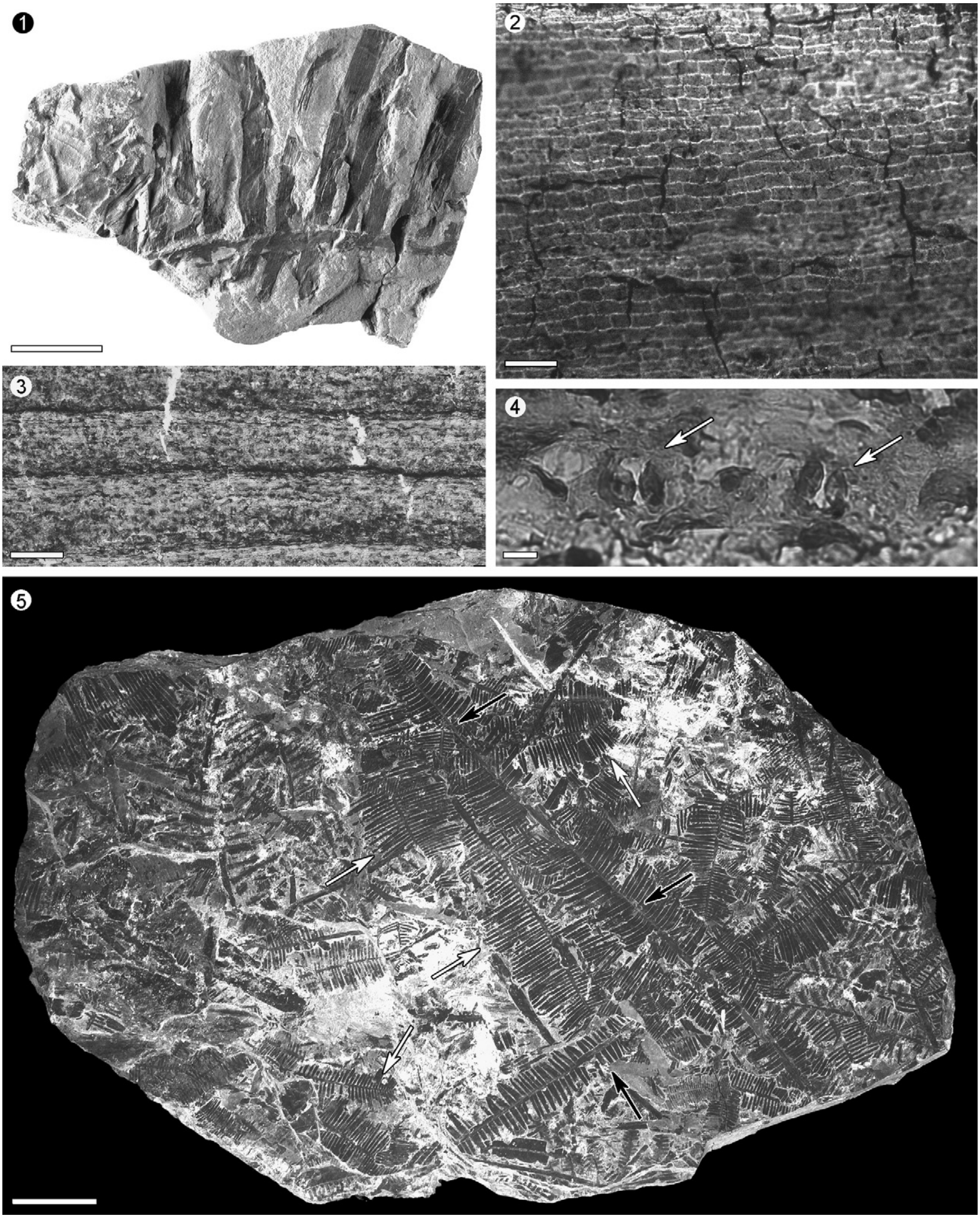

Plate I.

NAT	National Naturhistorisch Museum Naturalis, Leiden (Museum of Natural History, Leiden, The Netherlands),
NHM	Naturhistorisches Museum, Wien (Museum of Natural History, Vienna, Austria),
NRM	Naturhistoriska Riksmuseet, Stockholm (Museum of Natural History, Stockholm, Sweden),
PBO	Forschungsstelle für Paläobotanik, Münster (Palaeobotany Research Group, Münster, Germany),
RUU	Laboratory of Palaeobotany and Palynology, University Utrecht, The Netherlands,
SPO	Niederösterreichisches Landesmuseum, St. Pölten (State Museum of Lower Austria, St. Pölten, Austria).

4. Taxonomy

Order: Bennettitales Engler, 1892
Family: unknown
Genus: *Pterophyllum* Brongniart, 1825 (‘1824’)

Pterophyllum filicoides (Schlotheim, 1822) Zeiller, 1906
Plates I, 1–4; II–IV

Synonymy and selected references

1822	*Algacites filicoides,* von Schlotheim, Nachträge Petrefactenkunde, pp. 46–48, pl. IV, fig. 2
1827	*Osmundites pectinatus,* Jaeger, Pflanzenversteinerungen Bausandstein Stuttgart, pp. 29–32, pl. V, fig. 6, pl. VII, figs. 1–5
1828	*Pterophyllum longifolium,* Brongniart, Prodrome, p. 95, no ill.
1828	*Pterophyllum jaegeri,* Brongniart, Prodrome, p. 95, no ill.
1865	*Pterophyllum longifolium,* Heer, Urwelt der Schweiz, p. 52, pl. III, fig. 6
1877	*Pterophyllum longifolium,* Heer, Flora Fossilis Helvetiae, pp. 80–82, pl. XXX, figs. 7,8, pl. XXXIII, XXXV, XXXVI, figs. 1,2
1885	*Pterophyllum longifolium,* Stur, Flora der Lunzer-Schichten, p. 99, no ill.
1885	*Pterophyllum approximatum,* Stur, Flora Lunzer-Schichten, p. 99, no. ill.
1903	*Pterophyllum longifolium,* Leuthardt, Keuperflora von Neue Welt, pp. 16–18, pl. V, figs. 4,5, pl. VI, fig. 3, pl. VII, figs. 2,3, pl. VIII, figs. 1,2, pl. IX, figs. 1,2, pl. X, figs. 1–3
1906	*Pterophyllum filicoides,* Zeiller, Blanzy et Creusot, p. 196, fig. A.
1909b	*Pterophyllum longifolium,* Krasser, Kenntnis Flora Lunzer Schichten, pp. 116–119, no ill.
1909b	*Pterophyllum jaegeri,* Krasser, Kenntnis Flora Lunzer Schichten, pp. 116–119, no ill.
1930	*Pterophyllum filicoides,* Thomas, Cuticle Structure of Mesozoic Cycadean Fronds, pp. 406–409, pl. 20, figs 3–5, text—fig. 13
1932	*Pterophyllum filicoides,* Harris, Fossil Flora Scoresby Sound III, p. 47, no ill.
1966	*Pterophyllum longifolium,* Kräusel and Schaarschmidt, Keuperflora Neuewelt, pp. 5–17, pl. 2, 5, figs. 1,2
1967	*Pterophyllum filicoides,* Barnard, Upper Triassic plants from the Kalawch River, pp. 7–31, fig. 2
1992	*Pterophyllum filicoides,* Watson and Sincock, Bennettitales English Wealden, p. 108, no ill.

Holotype: MB.Pb.2006/189 (Plate I, 1) — Schlotheim, E.F. von, 1822. Nachträge zur Petrefactenkunde. Becker’sche Verlagsbuchhandlung, Gotha, pp. 46–48, pl. IV, fig. 2. We here provide the first ever photographic illustration of the holotype specimen (Plate I, 1).
Repository: Palaeobotanical Collection of the Museum für Naturkunde, Berlin.
Material studied: More than 250 specimens from the collections of NHM, GBA, NRM, RUU, JOA, SPO, PBO and NAT.
Locality: Lunz-am-See, Lower Austria.
Stratum: Lunzer Schichten, Julian, middle Carnian, Triassic.

Plate I.

1. *Pterophyllum filicoides*, holotype (MNB, MB.Pb.2006/189; courtesy of S. Schultka, Berlin), scale bar = 10 mm, locality: Neuewelt, Basel, Switzerland [originally named *Algacites filicoides*];
2. *Pterophyllum filicoides*, surface view of adaxial cuticle of holotype (MNB, MB.Pb.2006/189; by epifluorescence microscopy), scale bar = 100 μm, locality: Neuewelt, Basel, Switzerland [originally named *Algacites filicoides*];
3. *Pterophyllum filicoides*, fragment of abaxial cuticle from holotype (MNB, MB.Pb.2006/189/001), scale bar = 200 μm, locality: Neuewelt, Basel, Switzerland [originally named *Algacites filicoides*];
4. *Pterophyllum filicoides*, fragment of abaxial cuticle from holotype with syndetocheilic stomata (arrows; MB.Pb.2006/189/001), scale bar = 10 μm, locality: Neuewelt, Basel, Switzerland [originally named *Algacites filicoides*];
5. Large Lunz specimen (NHM, 2006B0008/0049) with unaligned leaves of *Nilssonia*, black arrows, (cf. Pott et al., 2007a) and *Pterophyllum*, white arrows, scale bar = 100 mm, locality: Lunz-am-See, Austria.

Description

Leaves are petiolate, impari-segmented, regular, oblong to broadly oval in outline, obtuse rounded at apex, up to 47 cm long and 20 cm wide (incomplete leaves). The prominent petiole measures up to about 1/5th of the overall length of the leaf (Plate II, 1–3). Besides these large leaves several tiny leaves occur, which are up to 10 cm long and display identical leaf architecture but with narrow rachides. The lamina is subdivided into numerous long and narrow, parallel-sided to spateolate leaf segments, which are oppositely positioned (Plate II, 1–9). The length of the individual segments varies depending on the position in the leaf; leaf segments are up to 101.6 mm long and 2–9 mm wide. The proximal leaf segments are short. Segment length slightly increases toward the middle of the leaf,

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Plate II. *Pterophyllum filicoides*
(macromorphology) 1.–7. Several slabs displaying excellently preserved compressed leaves, scale bars = 20 mm — locality: Lunz-am-See, Austria;

1. NRM, S148576 [originally labelled *P. brevipenne*];
2. NRM, S148240 [originally labelled *P. brevipenne*];
3. NRM, S148314 [originally labelled *P. brevipenne*];
4. GBA, 1909/003/0442 [originally labelled *P. longifolium*];
5. GBA, 1909/003/0531 [originally labelled *P. longifolium*];
6. GBA, 1909/003/0462 [originally labelled *P. longifolium*];
7. NHM, 1887/0001/0033 [originally labelled *P. longifolium*];
8. Leaf that probably grew under shadowy conditions (NHM, 1885/D/4049), scale bar = 10 mm, locality: Lunz-am-See, Austria [originally labelled *P. jaegeri*];
9. Detail of a leaf with laterally inserted leaf segments and venation (NRM, S148568), scale bar = 5 mm, locality: Lunz-am-See, Austria — [originally labelled *P. longifolium*];
10. Detail of Plate II, fig. 9, focusing on the bifurcate venation (arrows), scale bar = 5 mm.

Plate III. *Pterophyllum filicoides*
(cuticles) — locality: Lunz-am-See, Austria. (see on page 10)

1. Cuticle section of the apex of a leaf segment (NHM, 1885/C/5854/0008), scale bar = 50 μm [originally labelled *P. jaegeri*];
2. Detail of Plate III, fig. 1, scale bar = 50 μm;
3. Adaxial cuticle, overview (NHM, 2006B0008/0013/0001), scale bar = 100 μm [originally labelled *P. longifolium*];
4. Adaxial cuticle, overview (PBO, 0/0062), scale bar = 100 μm [originally labelled *P. longifolium*];
5. Adaxial cuticle, overview, with syndetocheilic stoma (arrow; PBO, 0/0056), scale bar = 100 μm [originally labelled *P. longifolium*];
6. Syndetocheilic stoma of adaxial cuticle (PBO, 0/0056), scale bar = 50 μm [originally labelled *P. longifolium*];
7. Abaxial cuticle, overview (PBO, 0/0049), scale bar = 100 μm [originally labelled *P. longifolium*];
8. Abaxial cuticle, overview (PBO, 0/0048), scale bar = 100 μm [originally labelled *P. longifolium*];
9. Abaxial cuticle, overview at base of leaf segment with cuticular striae (NHM, 1884/0000/0021/0007), scale bar = 100 μm [originally labelled *P. brevipenne*].

Plate IV. *Pterophyllum filicoides*
(abaxial cuticle details) — locality: Lunz-am-See, Austria. (see on page 11)

1. Stoma with different cutinisation of guard cells (GBA, 1909/003/0518/0005), scale bar = 10 μm [originally labelled *P. longifolium*];
2. Intercostal field with stomata and sinuous cell walls (GBA, 1909/003/0518/0005), scale bar = 20 μm [originally labelled *P. longifolium*];
3. Stoma with different cutinisation of guard cells (GBA, 1909/003/0518/0005), scale bar = 10 μm [originally labelled *P. longifolium*];
4. Syndetocheilic stoma (NHM, 2006B0008/0025/0002), scale bar = 10 μm [originally labelled *Pterophyllum* sp.];
5. Stoma with different cutinisation of guard cells (GBA, 1909/003/0518/0005), scale bar = 10 μm [originally labelled *P. longifolium*];
6. Sunken stoma (GBA, 1909/003/0518/0005), scale bar = 10 μm [originally labelled *P. longifolium*];
7. Intercostal field with cuticular striae directed towards the stomata (NHM, 1884/0000/0021/0007), scale bar = 20 μm [originally labelled *P. brevipenne*];
8. Stoma with different cutinisation of guard cells (GBA, 1909/003/0518/0005), scale bar = 10 μm [originally labelled *P. longifolium*];
9. Cells of intercostal field with sinuous cell walls (GBA, 1909/003/0518/0005), scale bar = 10 μm [originally labelled *P. longifolium*];
10. Cells of intercostal field with sinuous cell walls (GBA, 1909/003/0518/0005), scale bar = 10 μm [originally labelled *P. longifolium*];
11. Hollow papilla (PBO, 0/0047), scale bar = 10 μm [originally labelled *P. longifolium*];
12. Hollow papilla at the end of an epidermal cell (NHM, 2006B0008/0013/0001), scale bar = 10 μm [originally labelled *P. longifolium*];
13. Long and hollow papillae between stomata (PBO, 0/0048), scale bar = 20 μm [originally labelled *P. longifolium*];
14. Sinuous cell walls (GBA, 1909/003/0518/0005), scale bar = 10 μm [originally labelled *P. longifolium*],
15. Sinuous cell walls (GBA, 1909/003/0518/0005), scale bar = 10 μm [originally labelled *P. longifolium*].

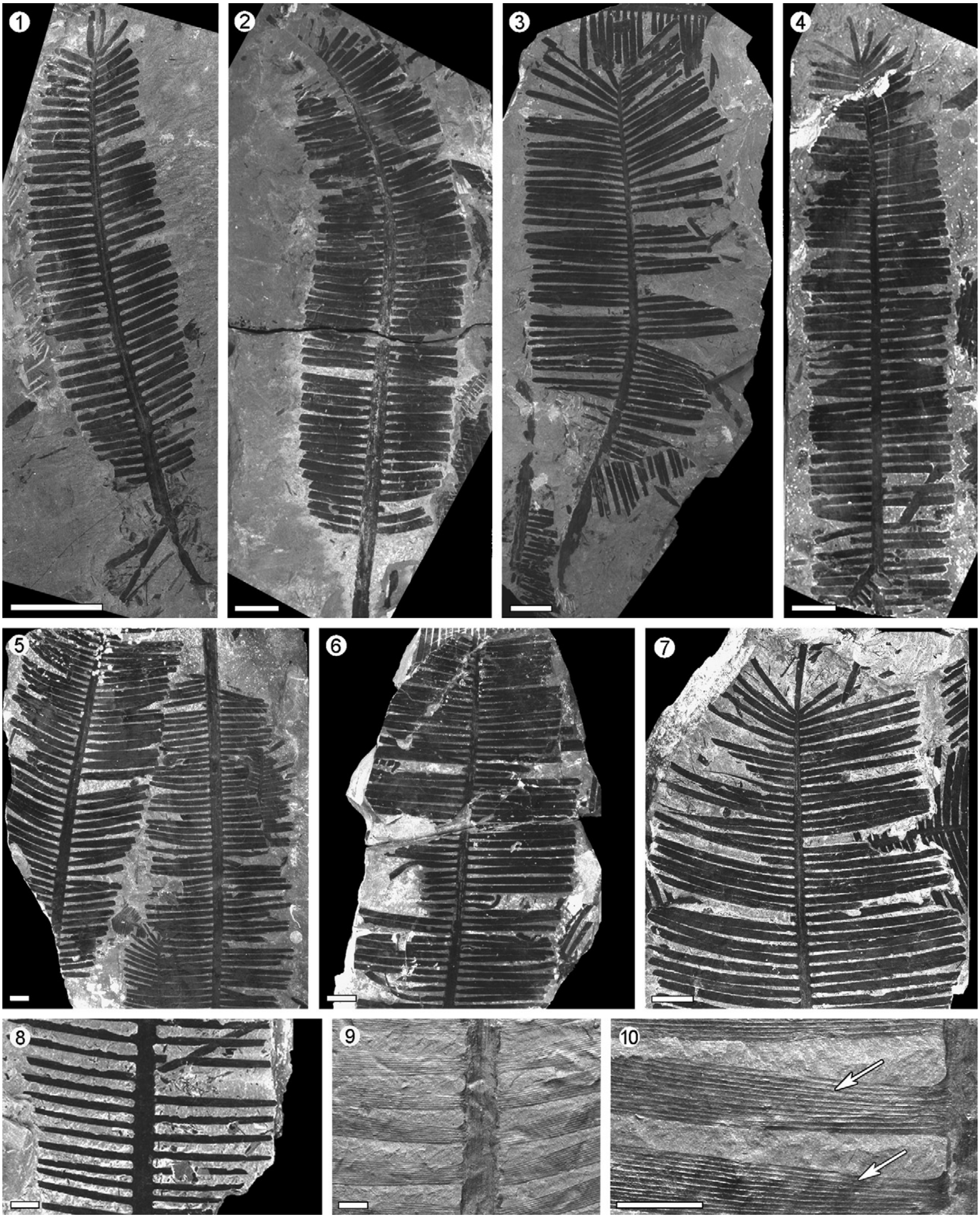

Plate II.

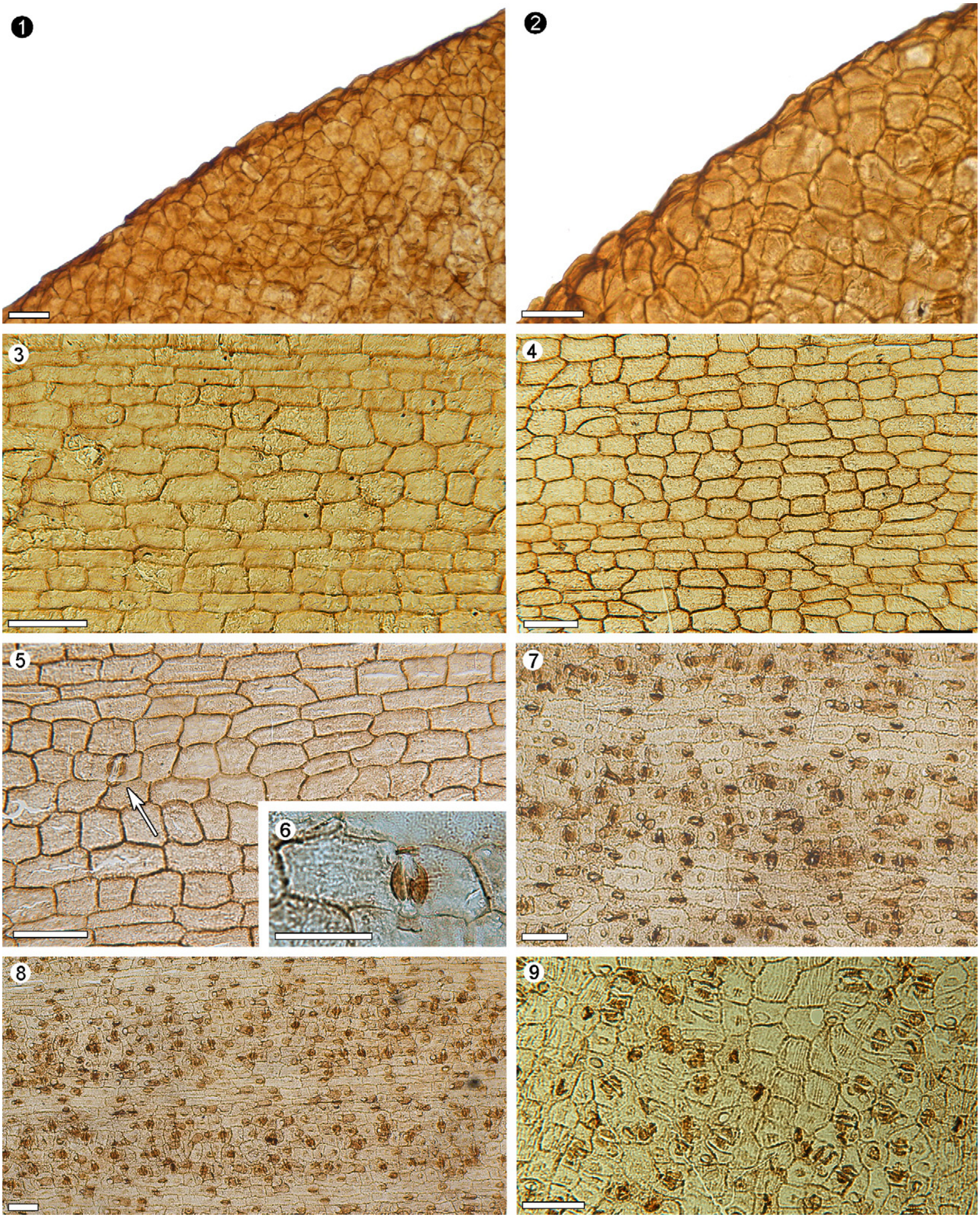

Plate III (*caption on page 8*).

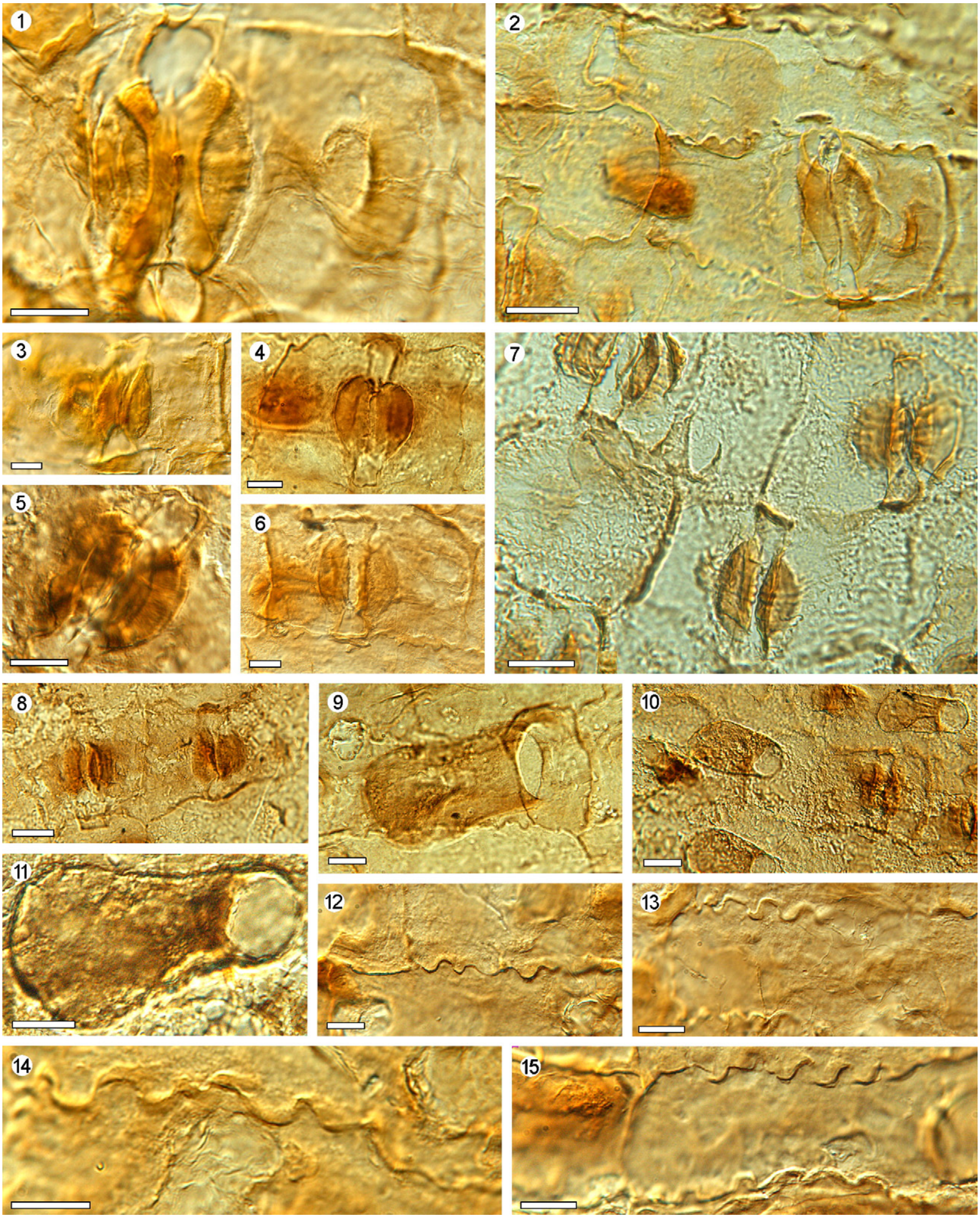

Plate IV (*caption on page 8*).

and then gradually decreases toward the leaf tip. The leaf segments are basally more or less constricted (Plate II, 2, 5–6). The basal constriction is usually prominent in segments positioned in the proximal portion of the leaf, but rather indistinct or absent in distally positioned segments. Leaf segment apices are obtuse to acutely rounded. The length/width-ratio, a feature that is often used to discriminate individual species, is always larger than 7:1; in some specimens, it reaches up to 22:1. The distance between the individual leaf segments is regular within a single leaf; however, intraspecific variations may occur between different leaves.

The segments insert laterally to the prominent and longitudinally striate rachis (Plate II, 9). Leaves that display wide spaces between the individual leaf segments (e.g., Plate II, 8) probably represent shade leaves. The distal five leaf segments form the apex (Plate II, 1, 4, 7). The terminal leaf segment does not differ in shape from the laterally positioned segments. Numerous parallel veins enter each of the segments (Plate II, 9–10) and usually bifurcate once close to the segment base (Plate II, 10). Occasionally additional bifurcations occur in the proximal portion of the segment. Veins positioned close to the lateral segment margins do not fork.

The leaves are amphistomatic but with only a few stomata on the adaxial surface, and produce robust cuticles; costal and intercostal fields are distinguishable on both sides of the leaf. Occurrence of stomata is limited to the intercostal fields. The adaxial cuticle is slightly thicker than the abaxial cuticle, displaying thickened edges between the anticlinal and periclinal cell walls.

Adaxial cuticle — epidermal cells positioned above the veins are narrow, rectangular, and elongate to isodiametric in outline, 45–145 μm long and 22.5–42.5 μm wide. Anticlinal cell walls are straight. Cells of intercostal areas are isodiametric (square) to broadly rectangular in outline, 37.5–90 μm long and 30–62.5 μm wide. Anticlinal and periclinal cell walls are smooth (Plate III, 3–6). The diacytic stomatal complexes are syndetocheilic, 37.5–50.5 μm long and 20–35 μm wide. Stomata are only occasionally present (Plate III, 5–6) and arranged in an open chain within a line of cells located in the middle of the intercostal fields. Stomatal pores (12.5–22.5 μm long) are oriented perpendicularly to the veins. Two rectangular subsidiary cells overarch the pit mouth, and thus form a slightly sunken stoma (Plate III, 6).

Abaxial cuticle — costal fields are composed of 3–4 lines of epidermal cells (Plate III, 7–8). The cells above the veins are morphologically similar to those seen in the adaxial epidermis, but possess more delicate walls, are narrow, rectangular, and elongate to isodiametric in outline, 55–145 μm long and 22.5–50 μm wide. Anticlinal cell walls are usually straight, but may occasionally also display faint and irregular undulations (Plate IV, 12–15). Periclinal walls are smooth, surface ornamentation is present but difficult to observe clearly (Plate IV, 7). Cells often bear a long and hollow papilla (50–62.5 μm long) positioned in one of the cell corners (Plate IV, 9–11). Intercostal fields are 200–300 μm wide, with isodiametric to broadly rectangular cells. Epidermal cells are 30–80 μm long and 25–62.5 μm wide and often bear a small and solid papilla (or cuticular thickening). Anticlinal cell walls are straight. Stomata are syndetocheilic, 37.5–55 μm long and 20–30 μm wide (Plate IV, 1–8). They are orientated perpendicularly to the veins. The pores measure 15–20 μm. The diacytic stomata possess two rectangular subsidiary cells that overhang the pit mouth, and thus form a slightly sunken stoma (Plate IV, 7). The kidney-shaped guard cells possess heavily cutinized central portions of the dorsal walls, while the polar ends are weakly cutinized (Plate IV, 3–7).

Remarks

Long and narrow individual leaf segments characterize *Pterophyllum filicoides*. The taxon can be distinguished macromorphologically from *P. brevipenne* (see below) by its much wider lamina, greater length of the individual leaf segments, and the occurrence of an apical leaf segment that is morphologically similar to the lateral leaf segments. *Pterophyllum filicoides* was originally described as *Algacites filicoides* by von Schlotheim (1822), who figured a single specimen from the Carnian (Upper Triassic) of Neuewelt near Basel (Switzerland). Zeiller (1906) introduced the combination *P. filicoides* without explicitly indicating the basionym. He illustrated a cuticle of a specimen from the type locality that, however, does not show the typical stomata. Thomas (1930) illustrated cuticles with stomata from the Carnian of Lunz (Austria) and validated the combination *P. filicoides*. Although the latter name is legitimate, it was hardly used by subsequent authors; rather, the species is usually still referred to as *P. longifolium* (see: Jongmans and Dijkstra, 1963; Dijkstra and Van Ameron, 1985). Our analysis of the holotype of *P. filicoides* from Neuewelt revealed that the epidermal anatomy of this specimen is identical to that seen in the material from Lunz (Plate I, 2–4).

Based on the epidermal anatomy of the material from Lunz, *Pterophyllum jaegeri* is regarded as conspecific, and thus a younger synonym of *P. filicoides* (Thomas 1930; Harris, 1932; Barnard, 1967; this study). *Pterophyllum jaegeri* was established based on material from the Keuper (Upper Triassic) near Stuttgart as *Osmundites pectinatus* by Jaeger (1827). The author gave a very detailed description and illustrated six specimens under this name, five pinnate leaves and one stem portion; however, it is unlikely that the fern-like stem illustrated on Jaeger's pl. VII, fig. 6 really belongs to the foliage. Plant fossils from the Keuper of Stuttgart do not yield cuticles; hence, the affinities of the type material of *P. jaegeri* remain equivocal. Harris (1932) and Barnard (1967) placed also *P. brevipenne* in *P. filicoides*. However, the latter author only studied a single *Pterophyllum* specimen from Lunz and assumed that all *Pterophyllum* leaves from Lunz have the same epidermal anatomy. *Pterophyllum inaequale*, illustrated by Fontaine (1883) from the Mesozoic flora of Virginia, is apparently identical to *P. filicoides*; however, only the very schematic illustration (Fontaine, 1883, pl. 36, fig. 1) is accessible and determination of the affinities remains difficult.

The cycadalean *Pseudoctenis santajuanensis* leaves described by Nielsen (2005) from the Carnian Santa-Juana-Formation of Chile, South America, are superficially almost identical to the *Pterophyllum filicoides* leaves from Lunz and Neuewelt. Moreover, based on the descriptions provided by Nielsen (2005), the material is rather assignable to *P. filicoides*. Nielsen (2005) listed several features considered as characteristic for *P. santajuanensis*, which seem, however, to be typical for *Pterophyllum*. Unfortunately, the epidermal anatomy of *P. santajuanensis*, which could be used to determine the bennettitalean or cycadalean affinity of this taxon, remains unknown.

Pterophyllum approximatum (Plates VIII, 1; IX, 4–6), *P. jaegeri* (Plates VIII, 4–5; IX, 1), and *P. longifolium* (Plates II, 4–7; III, 1–7; IV, 1–3, 5–6, 8–15) introduced by Stur (1885) and described by Krasser (1909b) from Lunz are interpreted as conspecific with *P. filicoides* because the epidermal anatomy of these forms from Lunz is identical to that seen in *P. filicoides*.

Pterophyllum brevipenne Kurr *ex* Schenk, 1864, emend. Plates V–VII

Synonymy and selected references

1864 *Pterozamites brevipennis,* Kurr *ex* Schenk, Flora des Keupers und der rhaetischen Formation, p. 65, pl. V, fig. 1
1865 *Pterophyllum brevipenne,* Heer, Urwelt der Schweiz, p. 52, pl. III, fig. 1
1871 *Pterophyllum merianii,* Stur, Geologie der Steiermark, p. 250, no ill.
1877 *Pterophyllum brevipenne,* Heer, Flora Fossilis Helvetiae, p. 82, pl. XXXIV, figs. 1–8, pl. XXXVI, fig. 3
1885 *Pterophyllum brevipenne,* Stur, Flora der Lunzer-Schichten, p. 99, no ill.
1885 *Pterophyllum rectum,* Stur, Flora der Lunzer-Schichten, p. 99, no ill.
1885 *Pterophyllum* cf. *pulchellum,* Stur, Flora der Lunzer-Schichten, p. 99, no ill.
1885 *Pterophyllum haberfelneri,* Stur, Flora der Lunzer-Schichten, p. 99, no ill.
1885 *Pterophyllum macrophyllum,* Stur, Flora der Lunzer-Schichten, p. 99, no ill.
1903 *Pterophyllum brevipenne,* Leuthardt, Keuperflora von Neue Welt, pp. 19–20, pl. V, figs. 6–8, pl. X, fig. 1
1909b *Pterophyllum brevipenne,* Krasser, Kenntnis Flora Lunzer Schichten, pp. 116–119, no ill.
1966 *Pterophyllum brevipenne,* Kräusel and Schaarschmidt, Keuperflora Neuewelt, pp. 5–17, pl. 1, figs. 1–4, pl. 4, figs. 1,2, pl. 5, figs. 3–5

Holotype: Schenk's specimen — Schenk, A. (1864). Beiträge zur Flora des Keupers und der rhätischen Formation. Berichte der Naturforschenden Gesellschaft zu Bamberg, 7, 1–91, p. 65, pl. V, fig. 1.
Remark: The holotype specimen, along with most other specimens of that collection, which was kept in the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany, was lost during WWII (M. K.). As a result, this species requires selection of a neotype according to IBCN § 9.6.
Neotype: NHM 1884/D/1209 (Plate V, 1).
Repository: Museum of Natural History, Vienna.

Description of the neotype

The neotype is an impari-segmented, petiolate leaf, which is spatulate in overall outline. Leaf segments are all complete except for those left below. The leaf is 14.8 long, 3.2 cm wide at the apex and 1.5 cm wide at the insertion of the basal leaflets. The incomplete petiole is 8 mm long. The rachis is finely longitudinally striated and gradually tapers from 4.1 to 1.8 mm in width. The apical leaflet is incompletely preserved (5.9 mm long); the left side of the leaf bears 39 leaflets, of which 37 are preserved; the right side 34 leaflets, of which 33 are preserved. The leaflets gradually increase in length in apical direction. They are 0.5–1.8 cm long, having a constant width of 3.0–3.5 mm. The leaflets are inserted laterally to the rachis at angles of 70°–90°; the apical ones at the lowest angle. Leaflets are broadly inserted; they are only slightly contracted at the base, parallel-sided, and obtusely rounded at the apices. The venation is dense and consists of fine parallel veins; veins basally fork once, additional bifurcations occur sporadically (Plate V, 1).

Material studied: More than 70 specimens from the following collections: GBA, NHM, NRM, RUU, JOA, and NAT.
Locality: Lunz-am-See, Lower Austria.
Stratum: Lunzer Schichten, Julian, middle Carnian, Triassic.
Remarks: The specimen mentioned in an unpublished manuscript by Kurr cannot clearly be identified, but it is very likely that it is the same specimen that was later figured by Schenk (1864). *Pterozamites brevipennis* is the original name, which was introduced by Kurr (*manuscriptum*) and validly published by Schenk (1864). The latter author gave a detailed description and figured a single specimen. Information on the type locality is missing. Heer (1865, 1877) subsequently transferred *Pterophyllum brevipennis* to the genus *Pterophyllum*. *P. brevipenne* has often been regarded as "sub-species" or synonym of *P. longifolium* or *P. jaegeri* (e.g. Heer, 1877). Cuticles are known from specimens from Neuewelt and Lunz (Kräusel and Schaarschmidt, 1966), but the specific diagnosis has not been emended to date to include information about the epidermal anatomy.

Emended diagnosis

Leaves petiolate, impari-segmented, lanceolate to spatulate in outline, apex obtuse rounded; lamina subdivided into short, parallel-sided leaf segments, oppositely positioned and laterally inserted to the rachis; leaf segments with several simply forked parallel veins; leaves amphistomatic but with less stomata on the adaxial than on the abaxial surface, epidermal cells rectangular to isodiametric, cell walls straight; stomata sunken, syndetocheilic, arranged in rows in intercostal fields; guard cells with prominent dorsal thickenings and radial striae; abaxial epidermal cells with long hollow and delicate papillae.

Description

Leaves are petiolate, impari-segmented, regular oblong to more lanceolate or spatulate to inverted-conical in outline, obtusely rounded apically (Plate V, 1, 3–6). The largest leaf portions at hand are up to 22.7 cm long and 6 cm wide. Petioles are basally widened and shorter than 1/10th of the length of the entire leaf (Plate V, 3). Besides the large leaves several tiny leaves occur, which are up to 10 cm in length and display identical leaf architecture but with very tiny rachides. The lamina is subdivided into numerous narrow and short, spateolate leaf segments, oppositely positioned and closely spaced. The length of the individual leaf segments varies depending on their position. They are up to 27 mm long and 2.5–5 mm wide. Proximal leaf segments are short, but increasing in length to the apical third of the leaf. The distally following leaf segments gradually decrease towards the rounded apex (Plate V, 1, 3–4, 6). The proximal one or two leaf segments often lack counterparts on the opposite side of the rachis (Plate V, 1, 3). The leaf segments are usually broadly attached to the rachis, but may occasionally display a profound basal constriction. They are bluntly rounded apically. The length/width-ratio of the leaf segments ranges from 6:1 to 4:1. It is always smaller than 7:1.

The segments insert laterally to the prominent and longitudinally striate rachis (Plate V, 7). The distance between individual leaf segments remains more or less the same within a single leaf, but may vary slightly between individual leaves. The apical portion of the leaf usually consists of three, sometimes up to five, leaf segments; the terminal segment usually differs in morphology from the laterally positioned segments in that it is more rounded in outline (Plate V, 3–4) and apically distinctly wider. Numerous parallel veins enter the leaf segments (Plate V, 7–8). They usually bifurcate near the segment base (Plate VI, 3); however, the veins positioned near the lateral segment margins may show bifurcations elsewhere. Additional bifurcations may sporadically occur; however, the occurrence of additional bifurcations is not limited to the proximal portion of the segment as in *Pterophyllum filicoides* (see above).

Plate V. *Pterophyllum brevipenne*
(macromorphology) 1.–6. Several slabs showing excellently preserved compressed leaves, scale bars = 10 mm — locality: Lunz-am-See, Austria.

1. NHM, 1884/D/1209, neotype [originally labelled *P. pulchellum*];
2. NHM, 1885/D/4086 [originally labelled *P. rectum*];
3. NRM, S148237 [originally labelled *P. rectum*];
4. NRM, S148423 [originally labelled *P. haberfelneri*];
5. NHM, 1884/0000/0034 [originally labelled *P. rectum*];
6. NHM, 1887/0001/0030 [originally labelled *P. macrophyllum*];
7. Detail of a leaf with laterally inserted leaf segments and venation (NHM, 1885/D/4060), scale bar = 5 mm, locality: Lunz-am-See, Austria [originally labelled *P. macrophyllum*];
8. Detail of a leaf, showing insertion and venation of the leaf segments (NHM, 1885/D/4086), scale bar = 5 mm, locality: Lunz-am-See, Austria [originally labelled *P. rectum*].

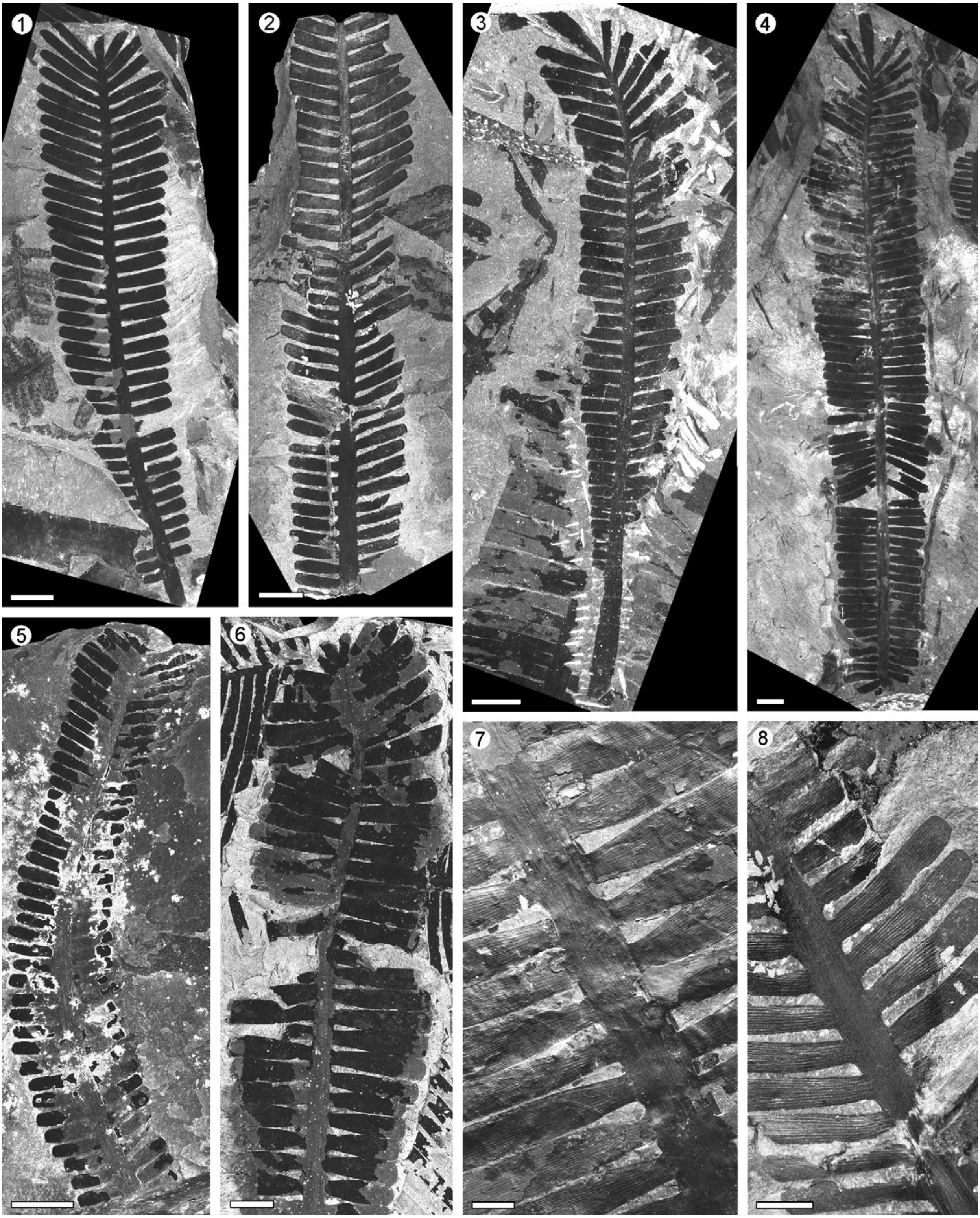

Plate V.

The leaves are amphistomatic but with less stomata on the adaxial than on the abaxial surface, and have robust cuticles; costal and intercostals fields are distinguishable on both sides of the leaf. The cuticle of the adaxial side is slightly thicker than the abaxial cuticle, having thickened edges between the anticlinal and periclinal walls.

Adaxial cuticle — epidermal cells above the veins are rectangular to isodiametric, 42.5–85 µm long and 27.5–47.5 µm wide (Plate VI, 5, 7). Anticlinal cell walls are smooth. Cells of intercostal areas are isodiametric (square) to broadly rectangular, 32.5–57.5 µm long and 30–52.5 µm wide. Anticlinal cell walls are smooth. In contrast to *Pterophyllum filicoides*, the periclinal walls are always straight in *P. brevipenne*; sinuous walls or faint undulations are lacking. Stomata are syndetocheilic with two diacytic subsidiary cells, 37.5–50 µm long and 20–27.5 µm wide (Plate VI, 5–8). A few stomata are present, arranged in an open chain within a cell line located in the centre of the intercostal field; their density is distinctly higher than that seen in *P. filicoides* (Plate III, 5; VI, 5, 7). Stomatal pores (15.0–17.5 µm long) are orientated perpendicularly to the veins. The two rectangular subsidiary cells form a slightly sunken stoma by overhanging the pit mouth. Papillae or trichome bases are absent.

Abaxial cuticle — cells over the veins are similar to those of the adaxial side, but with more delicate walls, and narrow, rectangular to isodiametric in shape, 42.5–102.5 µm long and 22.5–45 µm wide. Costal fields are composed of 3–4 lines of cells (Plate VII, 1, 3). Anticlinal cell walls are straight. Periclinal walls are smooth; ornamentation is present but difficult to observe in detail (Plate VII, 5, 6, 8, 12). Epidermal cells often bear a terminal long and hollow papilla (40–57.5 µm long; Plate VII, 10–11) Intercostal areas are 175–250 µm wide, individual epidermal cells isodiametric to broadly rectangular, 25–50 µm long and 30–50 µm wide (Plate VII, 1, 3). The epidermal cells within the stomatal zones often bear irregular solid cuticular thickenings (Plate VII, 2–3). Anticlinal cell walls are straight, not undulating as in *Pterophyllum filicoides*. Stomata are confined to intercostal areas, syndetocheilic, 37.5–50 µm long and 20–30 µm wide (Plate VII, 1, 3, 4–7, 9, 12). The stomatal pores (12.5–20 µm) are oriented perpendicularly to the veins. The two rectangular subsidiary cells are diacytic, slightly overhanging the pit mouth, and thus form a slightly sunken stoma. The kidney-shaped guard cells exhibit heavily cutinized central portions of the dorsal walls, while the polar ends are weakly cutinized (Plate VII, 7, 9).

Remarks

Pterophyllum brevipenne is characterized by relatively short leaf segments, a terminal leaf segment that morphologically differs considerably from the lateral segments, and by the slender overall outline of the leaves. In several studies, *P. brevipenne* is regarded as having been introduced by Kurr (1845: *Flora der Juraformation*). However, Kurr neither mentioned *P. brevipenne* in this publication nor is there any appropriate figure suggesting an apparently similar species or specimen. This also applies to the rare edition of 1846 (Kurr, 1846). Rather, the form was originally described and illustrated as *P. brevipennis* in an unpublished manuscript by Kurr, which was later published by Schenk (1864). The genus *Pterozamites* in its original description includes *Pterophyllum* as a “sub-genus” (Braun, 1843), which led Schenk (1864) to accommodate this form in *Pterozamites*. Later, Schimper (1870) regarded *Pterozamites* as a separate genus besides *Pterophyllum*. According to Schimper, *Pterozamites* is characterized by leaf segments that insert to the upper side of the rachis, as in *Nilssonia* leaves (Schimper, 1870, p. 145; Pott et al., 2007a). Heer (1865, 1877) subsequently transferred *P. brevipennis* correctly to the genus *Pterophyllum*, which is characterized by leaf segments that are laterally inserted to the rachis.

Plate VI. *Pterophyllum brevipenne*
(cuticles) — locality: Lunz-am-See, Austria.

1. Cuticle section of the apex of a leaf segment (NHM, 1885/D/4087/0001), scale bar = 100 µm [originally labelled *P. rectum*];
2. Detail of Plate VI, fig. 1, scale bar = 100 µm;
3. Abaxial cuticle, overview of leaf segment base with bifurcating vein courses (GBA, 2006/004/0003/0001), scale bar = 200 µm [originally unlabelled];
4. Rachis cuticle, showing cell pattern and a single stoma (GBA, 1909/003/0379/0005), scale bar = 50 µm [originally labelled *P. brevipenne*];
5. Adaxial cuticle, overview (NHM, 1885/D/4087/0003), scale bar = 100 µm [originally labelled *P. brevipenne*];
6. Adaxial cuticle, syndetocheilic stoma (NHM, 1885/D/4087/0004), scale bar = 10 µm [originally labelled *P. rectum*];
7. Adaxial cuticle, overview (GBA, 2006/004/0003/0002), scale bar = 100 µm [originally unlabelled];
8. Adaxial cuticle, syndetocheilic stoma (NHM, 1885/D/4087/0004), scale bar = 20 µm [originally labelled *P. rectum*].

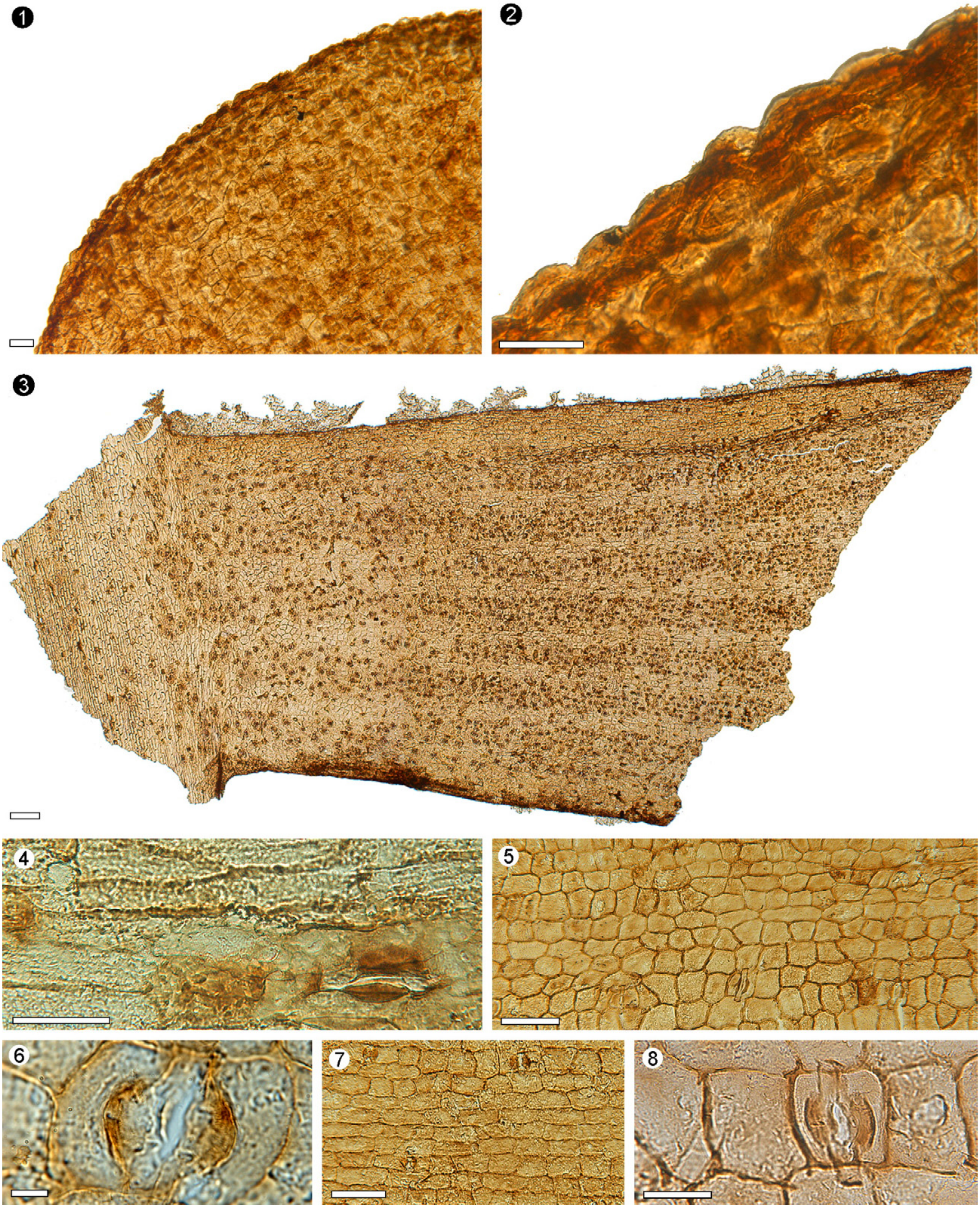

Plate VI.

Based on the macromorphology and epidermal anatomy of the original set of specimens of *Pterophyllum rectum* (= *merianii*), *P. macrophyllum, Pterophyllum haberfelneri*, *Pterophyllum merianii*, and *Pterophyllum pulchellum* (= *merianii*) from Lunz, all these "species" names are actually synonyms of *P. brevipenne*. As a result, leaves from Lunz previously assigned to *P. rectum* (Plates V, 2–3, 5, 8; VIII, 3; VI, 1–2, 6, 8; VII, 3, 10), *P. macrophyllum* (Plates V, 6–7; VIII, 7; IX, 9–10), *P. haberfelneri* (Plates V, 4; IX, 7–8), *P. merianii* (Plate VIII, 6), and *P. pulchellum* (Plates V, 1; IX, 2–3, 11–12) by Stur (1885) and Krasser (1909b) are placed in the synonymy of *P. brevipenne*. *Pterophyllum rectum, P. haberfelneri* and *P. macrophyllum* are nomina nuda introduced by Stur (1885). *Pterophyllum rectum* refers to the specimens that Stur earlier regarded as *P. merianii* (Stur, 1871; Krasser, 1909b, p. 118). The epidermal anatomies of *P. rectum, P. haberfelneri* and *P. macrophyllum* are identical to that seen in *P. brevipenne* (Plates VI, 1–2, 4–6, 7; VII, 1–3; IX, 7–10). *P. merianii* is also a nomen nudum introduced by Brongniart (1828) based on specimens from Neuewelt. The species was figured and described by Heer (1877), but was often regarded as questionable (Schenk, 1864, 1866; Leuthardt, 1903; Krasser, 1909b; Kräusel and

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Plate VII. *Pterophyllum brevipenne*
(abaxial cuticle) — locality: Lunz-am-See, Austria.

1. Overview (NHM, 1884/0000/0028/0004), scale bar = 100 µm [originally labelled *P. brevipenne*];
2. Apical portion of leaf segment with cuticular bars (NHM, 1884/0000/0028/0004), scale bar = 20 µm [originally labelled *P. brevipenne*];
3. Detail of abaxial cuticle with intercostal field and papillae (NHM, 1885/D/4087/0004), scale bar = 50 µm [originally labelled *P. rectum*];
4. Syndetocheilic stoma (NHM, 1884/0000/0028/0004), scale bar = 10 µm [originally labelled *P. brevipenne*];
5. Overview of a leaf segment base with cuticular striate pattern (GBA, 1909/003/0379/0006), scale bar = 100 µm [originally labelled *P. brevipenne*];
6. Cuticular striae directed towards the stomata (GBA, 1909/003/0379/0006), scale bar = 20 µm [originally labelled *P. brevipenne*];
7. Syndetocheilic stoma (NHM, 1884/0000/0028/0004), scale bar = 10 µm [originally labelled *P. brevipenne*];
8. Periclinal cell wall with striae (GBA, 1909/003/0379/0002), scale bar = 10 µm [originally labelled *P. brevipenne*];
9. Adjacent stomata (GBA, 1909/003/0379/0003), scale bar = 10 µm [originally labelled *P. brevipenne*];
10. Two adjacent hollow papillae (NHM, 1885/D/4087/0002), scale bar = 10 µm [originally labelled *P. rectum*];
11. Hollow papillae (NHM, 1884/0000/0028/0004), scale bar = 10 µm [originally labelled *P. brevipenne*];
12. Cuticular striae originating from a stoma (GBA, 1909/003/0379/0006), scale bar = 10 µm [originally labelled *P. brevipenne*].

Plate VIII. Specimens assigned to *Pterophyllum filicoides* and *P. brevipenne*, originally labelled with Stur's original species names, scale bars = 10 mm— locality: Lunz-am-See, Austria. (see on page 20)

1. *P. filicoides* (NHM, 1885/D/4069) [originally labelled *P. approximatum*];
2. *P. brevipenne* (NHM, 1884/D/1207) [originally labelled *P. brevipenne*];
3. *P. brevipenne* (NHM, 1885/D/4087) [originally labelled *P. rectum*];
4. *P. filicoides* (GBA, 1909/003/0401) [originally labelled *P. jaegeri*];
5. *P. filicoides* (NHM, 1884/D/1196) [originally labelled *P. jaegeri*];
6. *P. brevipenne* (GBA, 1909/003/0574) [originally labelled *P. merianii*];
7. *P. brevipenne* (NHM, 1885/D/4064) [originally labelled *P. macrophyllum*].

Plate IX. Cuticles of specimens with original species names that are now assigned to *Pterophyllum filicoides* and *P. brevipenne* — locality: Lunz-am-See, Austria. (see on page 21)

1. *P. filicoides*, adaxial and abaxial cuticle (NHM, 1885/C/5854/0010), scale bar = 200 µm [originally labelled *P. jaegeri*];
2. *P. brevipenne*, abaxial cuticle (NHM, 1884/D/1209/0002), from neotype, scale bar = 200 µm [originally labelled *P. pulchellum*];
3. Detail of Plate XI, fig. 2, scale bar = 100 µm;
4. *P. filicoides*, abaxial cuticle (NHM, 1885/D/4069/0005), scale bar = 200 µm [originally labelled *P. approximatum*];
5. Detail of Plate IX, fig. 4, scale bar = 50 µm;
6. *P. filicoides*, adaxial cuticle (NHM, 1885/D/4069/0008), scale bar = 100 µm [originally labelled *P. approximatum*];
7. *P. brevipenne*, abaxial cuticle (GBA, 1909/003/0383/0008), scale bar = 200 µm [originally labelled *P. haberfelneri*];
8. Detail of Plate IX, fig. 7, scale bar = 100 µm;
9. *P. brevipenne*, abaxial cuticle (NHM, 2006B0008/0014/0002), scale bar = 200 µm [originally labelled *P. macrophyllum*];
10. Detail of Plate IX, fig. 9, scale bar = 50 µm;
11. *P. brevipenne*, abaxial cuticle (NHM, 1883/C/3875/0005), scale bar = 100 µm [originally labelled *P. pulchellum*];
12. *P. brevipenne*, adaxial cuticle (NHM, 1883/C/3875/0005), scale bar = 200 µm [originally labelled *P. pulchellum*].

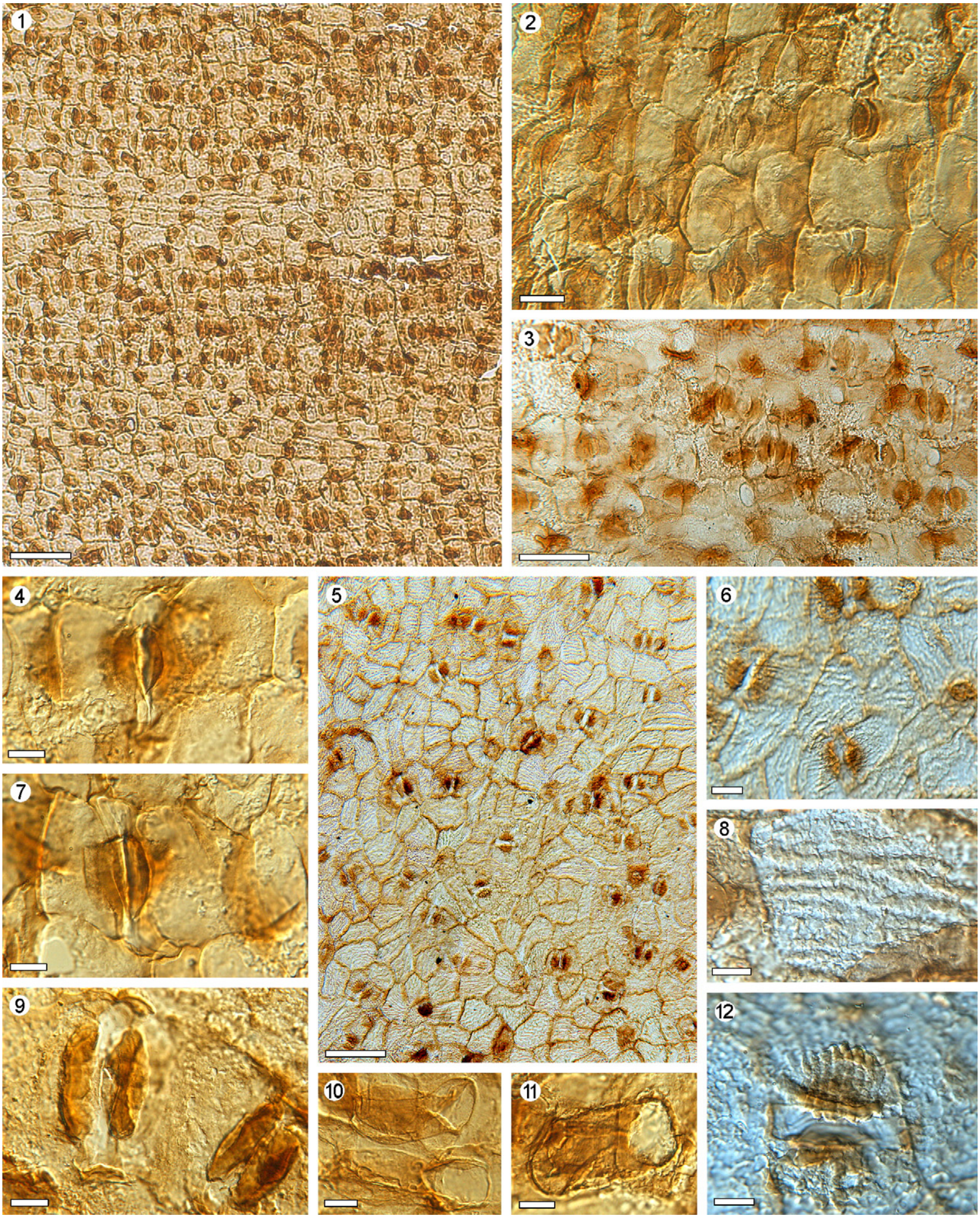

Plate VII.

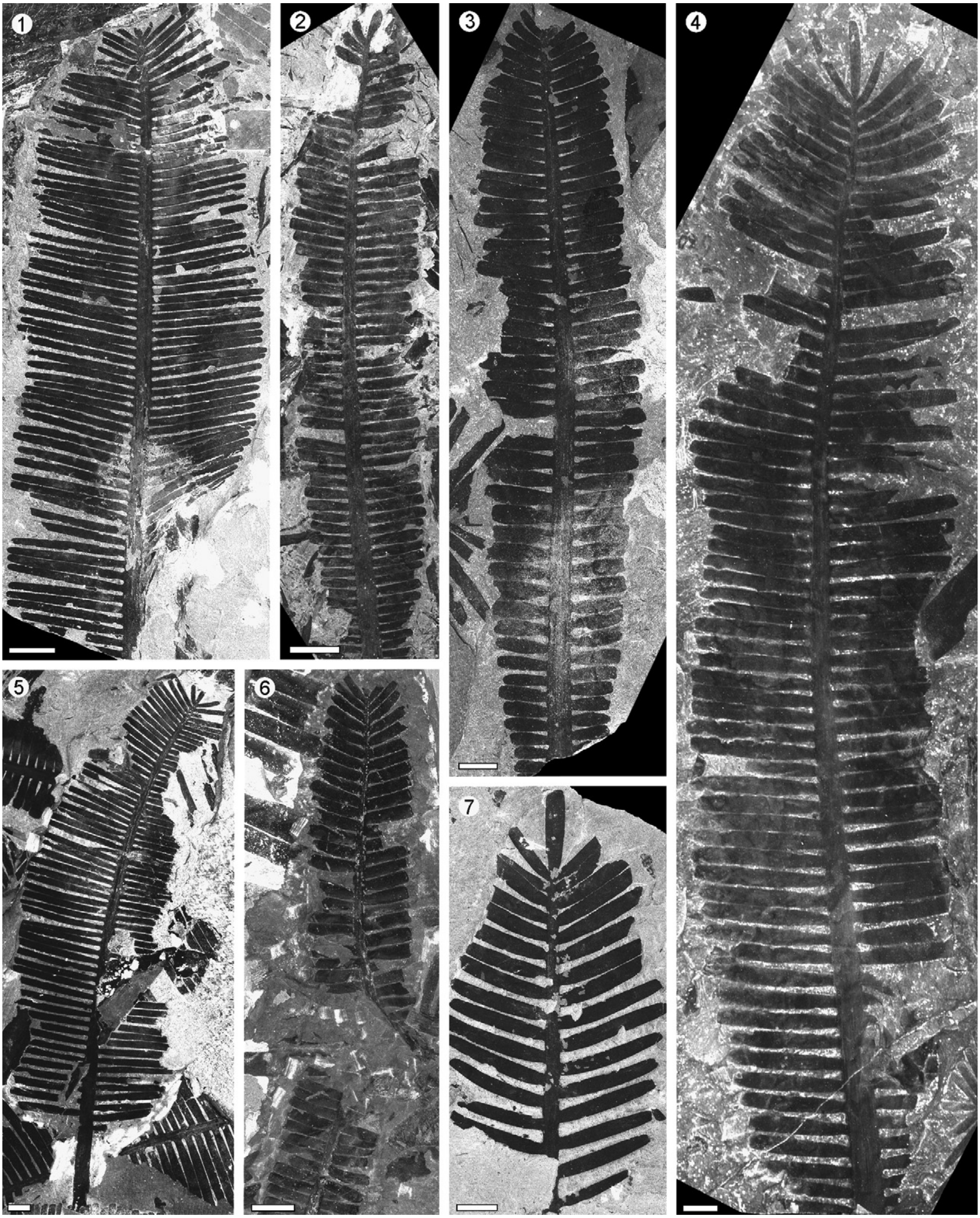

Plate VIII (*caption on page 18*).

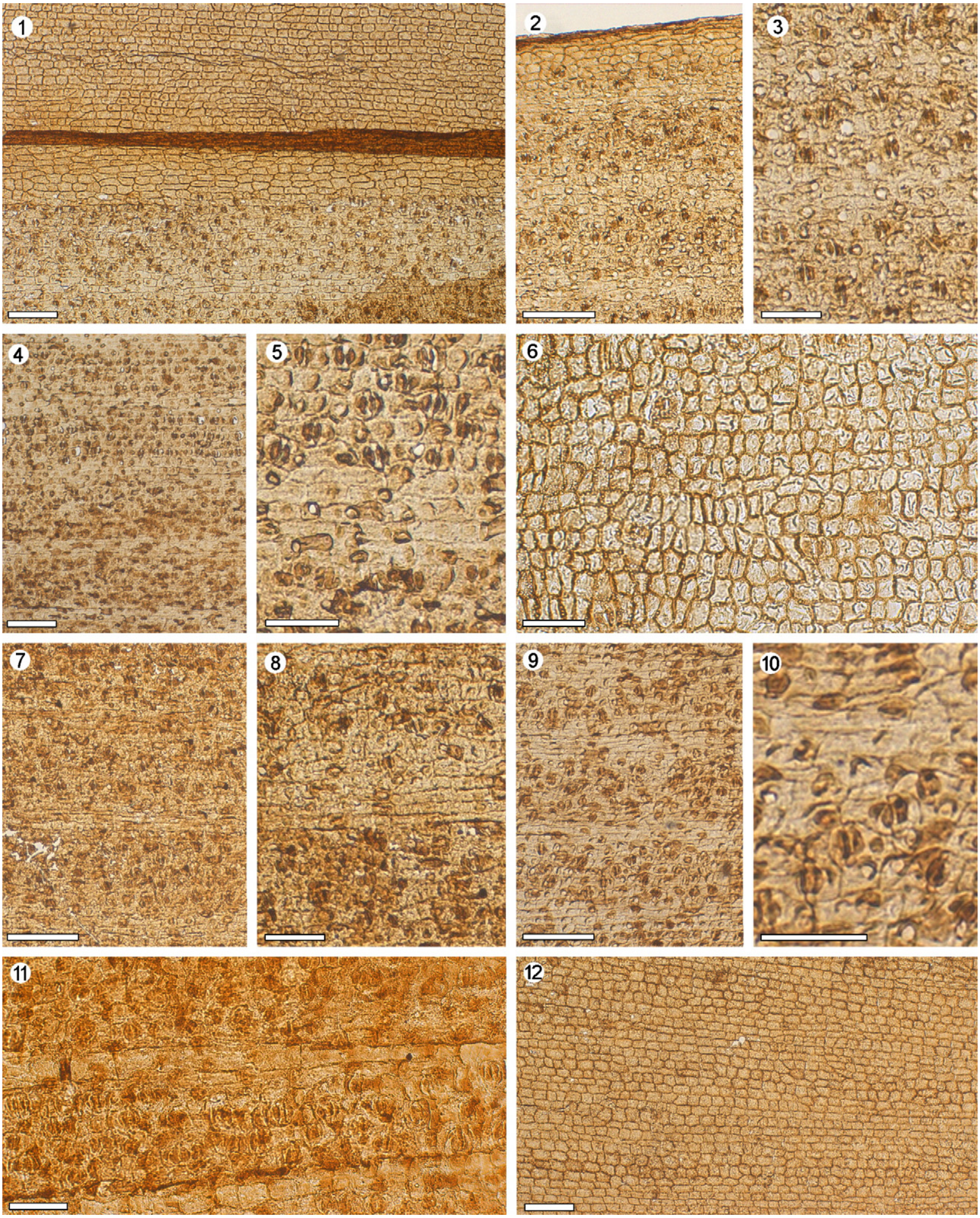

Plate IX (*caption on page 18*).

Table 1
Macromorphology and epidermal features used in the distinction of *Pterophyllum filicoides* and *P. brevipenne*

		Pterophyllum filicoides	*Pterophyllum brevipenne*
Macromorphology			
Length up to		47.0 cm	22.7 cm
Width up to		20.3 cm	6.0 cm
Leaf segment length up to		10.2 cm	2.7 cm
Leaf segment width		2.0–9.0 cm	2.5–5.0 mm
Length/width ratio		22–7:1	6–4:1
Bifurcation of veins in the segments		limited to basal portion	not limited to basal portion
Apex composed of		5 segments	usually 3 segments
apical and lateral segments		identical in outline	different in outline
Adaxial epidermial anatomy			
Costal fields	epidermal cell lengths	45.0–145.0 μm	42.5–85.0 μm
	epidermal cell widths	22.5–42.5 μm	27.5–047.5 μm
	anticlinal cell walls	straight	straight
Intercostal fields	epidermal cell lengths	37.5–90.0 μm	32.5–057.5 μm
	epidermal cell widths	30.0–62.5 μm	30.0–52.5 μm
	anticlinal cell walls	straight	straight
	stoma length	37.5–50.5 μm	37.5–50.0 μm
	stoma width	20.0–35.0 μm	20.0–27.5 μm
Abaxial epidermal anatomy			
Costal fields	width	3–4 cell lines	3–4 cell lines
	epidermal cell lengths	55.0–145.0 μm	42.5–102.5 μm
	epidermal cell widths	22.5–50.0 μm	22.5–45.0 μm
	anticlinal cell walls	slightly sinuous	straight
Intercostal fields	width	200–300 μm	175–250 μm
	epidermal cell lengths	30.0–80.0 μm	25.0–50.0 μm
	epidermal cell widths	25.0–62.5 μm	30.0–50.0 μm
	anticlinal cell walls	straight	straight
	stoma length	37.5–55.0 μm	37.5–50.0 μm
	stoma width	20.0–30.0 μm	20.0–30.0 μm
	papilla height	50.0–62.5 μm	40.0–57.5 μm
	cuticular applications	absent	present, irregularly distributed

Schaarschmidt, 1966). *Pterophyllum pulchellum* is a younger synonym of *P. merianii* (Heer, 1877).

5. Comparison of *Pterophyllum filicoides* and *P. brevipenne*

Long and narrow leaf segments characterize *Pterophyllum filicoides* (length/width ratio 22–7:1), while similarly narrow, but distinctly shorter segments are the main character of *P. brevipenne* (length/width ratio 6–4:1). The epidermal cells of *P. brevipenne* are always smaller than those seen in *P. filicoides* (Table 1). However, the ranges overlap, and thus the size of the epidermal cells cannot be used as a reliable character in the separation of the two species. The adaxial epidermal anatomy displays features that are more useful in discriminating the two species. For example, stomata occur only very occasionally in *P. filicoides*, and the distance between the individual stomata arranged in a single longitudinal row is distinctly higher in *P. filicoides* (Plate III, 5) than in *P. brevipenne* (Plate VI, 5, 7). The adaxial epidermal cells in *P. brevipenne* appear to be more closely arranged and rather square to upright rectangular (Plate VI, 5), while they are longer, and thus narrower, in *P. filicoides* (Plate III, 3–5). Even if this latter character is less clearly definable when averaging the cell lengths, it still presents a noteworthy difference between the two species that contributes to the distinction of the epidermal anatomies. There are also discriminating features provided by the abaxial epidermis. The anticlinal cell walls show undulations in *P. filicoides* (Plate IV, 2, 6, 9, 12–15), while they are always straight in *P. brevipenne*. The abaxial cuticle displays an additional discriminating character: In *P. brevipenne,* the outer periclinal cell walls of the cells in intercostal fields possess irregularly distributed cuticular applications or thickenings (Plate VII, 2–3), which are absent from *P. filicoides* (Plate III, 7–9).

The preceding brief comparison of *Pterophyllum filicoides* and *P. brevipenne* demonstrates that cuticle structure and epidermal anatomy contain a complement of features significant for species discrimination in *Pterophyllum*. However, it has to be taken into account that cuticle structure and epidermal anatomy may vary considerably within a single leaf segment, i.e. between proximal and distal portions of the segment. In the *Pterophyllum* species from Lunz, the regular arrangement of cells and epidermal derivatives gradually disappears toward the segment base (Plates III, 9; VII, 5) and tip (Plates III, 1–2; VI, 1–2; VII, 2). Thus, a cuticular preparation from the mid portion of a leaf segment is required in any case to obtain reliable data. Discrimination of individual species based entirely on fragmentary cuticles from segment bases or tips is difficult.

6. Further species names used for *Pterophyllum* leaves from Lunz

Stur (1885) introduced several additional *Pterophyllum* species names, which were not discussed above or addressed in Pott et al. (2007a, in press-b):

(a) *Pterophyllum cteniforme* Stur is resumed neither by Stur (1888) nor Krasser (1909b). Only a single specimen labelled *P. cteniforme* was found in the studied collections (NRM, S148565). However, this specimen belongs to *Dioonitocarpidium* and was correctly identified as *D. keuperianum* by Kräusel (1953).

(b) *Pterophyllum pectiniforme* Stur was neither retrieved by Krasser (1909b) nor did the studied collections contain any specimens labelled *P. pectiniforme*. As a result, this species has to be regarded as dubious since it was never validly diagnosed or illustrated.

(c) *Pterophyllum haidingeri* Goepp. (Stur, 1871) is conspecific with *Taeniopteris haidingeri* Göppert mnsc. nec Ettingshausen (Stur, 1885). *Taeniopteris haidingeri* was transferred to *Macrotaeniopteris* by Krasser (1909a,b) and recently to *Nilssoniopteris* by Pott et al. (in press-b). However, it remains unresolved whether the material from Lunz is conspecific with Unger's (1845) *P. haidingeri* Göppert *manuscr.*, because Jongmans and Dijkstra (1960, 1963), disregarding Unger (1845), did not relate Stur's *Pterophyllum* (= *Macrotaeniopteris*) *haidingeri* Göppert *ms.* and *P. haidingeri* Unger, although the latter species apparently also occurs in the Lunzer Schichten near Gaming/Lower Austria (Unger, 1845, 1848). Unger (1845) gave no descriptions and illustrations of *P. haidingeri* Göppert *manuscr.* and later (1848) named the taxon *P. haidingeri* Unger.

7. Discussion

The historical species inventory of the Carnian flora from Lunz, Lower Austria, compiled by Stur (1871, 1885) and Krasser (1909b) includes 17 different *Pterophyllum* species. Although neither Stur nor Krasser illustrated any of the fossils that formed the basis for the specific diagnoses and descriptions, the taxonomical novelties presented by these authors were readily accepted as "sound" species, and are still widely used today. However, the lack of illustrations made scrutiny of the accurateness of the diagnoses and descriptions difficult, and over time created considerable confusion. This confusion remains to date and renders establishing a trustworthy updated inventory of the *Pterophyllum* species from Lunz a difficult task. Moreover, the separate status of some of the species has repeatedly been questioned, and difficulties with regard to assigning additional specimens to the individual species have been noted. As a result, Frentzen (1922) and Dobruskina (1998), among other scholars, speculated that there are probably significantly fewer *Pterophyllum* species in the Lunz flora than listed in the historical inventory.

During the last 2 years, more than 500 compression specimens of *Pterophyllum* foliage from Lunz, including the original suites of specimens studied by Stur and Krasser, were (re-)examined with regard to macromorphology, biometry, and epidermal anatomy. As a result, an extensive set of new data became available that formed the basis for the reassessment of the genus *Pterophyllum* in the Lunz flora presented in this paper. The new data indicate that the number of *Pterophyllum* species in this flora actually is considerably lower than previously thought, and thus support the hypothesis advanced by Frentzen (1922) and Dobruskina (1998). Only two distinct *Pterophyllum* species, i.e. *P. filicoides* and *P. brevipenne*, are recognized. Other *Pterophyllum* "species" described by Stur (1885) and Krasser (1909b) are interpreted as conspecific with either of these two species based on identical epidermal anatomies: *P. approximatum*, *P. jaegeri*, and *P. longifolium* are conspecific with *P. filicoides* and *P. macrophyllum, P. rectum* (= *merianii*)*, P. haberfelneri, P. merianii,* and *P. pulchellum* (= *merianii*) are conspecific with *P. brevipenne*. The differences in leaf macromorphology, used by Stur and Krasser to discriminate these taxa from one another, are within the range of normal intraspecific variation. Still other foliage types from Lunz conventionally assigned to *Pterophyllum* (e.g., *P. riegeri*, *P. neuberi*, and *P. irregulare*) display haplocheilic stomata, and thus represent cycadalean foliage. These taxa have recently been transferred to the genus *Nilssonia* (Pott et al., 2007a).

The Lunz flora is characterized by a large number of plants that represent typical elements of younger Mesozoic (i.e. Rhaetian, Jurassic and Cretaceous) floras, including *Pterophyllum, Nilssonia*, *Nilssoniopteris* and *Pseudoctenis* (Pott et al., 2007a,b, in press-b). Among these elements, *Pterophyllum* is particularly interesting because leaves assignable to this genus represent by far the most common fossils from Lunz (Plate I, 5). Moreover, the representatives of the genus *Pterophyllum*, along with several other types of bennettitalean foliage (e.g., *Nilssoniopteris*) from this flora, range among the earliest bennettitaleans in the fossil record (Cleal, 1993; Kelber, 1998; Kelber and Nitsch, 2005). A remarkably high proportional abundance of bennettitalean foliage fossils has also been recorded for the Keuper flora of Neuewelt in Switzerland (Leuthardt, 1903). On the other hand, in Keuper floras from southern Germany the proportional abundance of bennettitalean foliage is distinctly lower that that recorded for Lunz and Neuewelt (e.g. Schenk, 1865–1867).

The genus *Pterophyllum* was originally described as a morphogenus for bipinnate cycad-like leaves (Brongniart, 1828) and has been redefined to include only leaves with typical bennettitalean cuticles (Harris, 1969; Watson & Sincock, 1992). If cuticles are unknown, the attribution of segmented leaves to the genus *Pterophyllum* is, however, hardly possible. The genus was widespread in the Late Triassic and Early Jurassic; the earliest unequivocal fossils are from the Carnian (Upper Triassic) of Lunz and Neuewelt (this study; Leuthardt, 1903), while the latest stratigraphical occurrence has been recorded for the Early Cretaceous (Kelber, 1998).

Pterophyllum species reported from pre-Carnian localities must be addressed very carefully. Cuticles of pre-Carnian *Pterophyllum* species are often not preserved or unknown. Hence, the accommodation of species like *P. cutelliforme* (Sze, 1936; Ke-Qin Sun, 2006), *P. cotteanum* (Geinitz, 1873; Barthel, 1976), *P. blechnoides* (Geinitz, 1873), *P. samchokense* (Kawasaki, 1931), *P. daihoense* (Kawasaki, 1931, 1934; Ke-Qin Sun, 2006) and *P. eratum* (Gu and Zhi, 1974) from the Upper Carboniferous and Permian of China, Korea and Germany in *Pterophyllum* remains equivocal. However, even if cuticles are known, some species have incorrectly been assigned to *Pterophyllum*. *Pterophyllum grandeuryi* and *P. fayolii*, described by Zeiller (1906) from the Upper Carboniferous of Blanzy et Creusot, France, rather resemble species that are now accommodated in *Pseudoctenis* based on macromorphology (Pott et al., 2007b). The abaxial cuticle portions of *P. grandeuryi* figured by Zeiller (1906, Fig. B', p. 198) are characterized by haplocheilic stomata, which is definitely a cycadalean feature. Consequently, a very critical revision of pre-Carnian *Pterophyllum* representatives is mandated.

The geographical distribution of *Pterophyllum* is largely restricted to North America, Europe, and Asia (cf. Jongmans and Dijkstra, 1963). With regard to Lunz and Neuewelt, it is particularly interesting that the abundance of *Pterophyllum* in these floras depicts an abrupt mass occurrence because stratigraphically older deposits have to date only sporadically produced *Pterophyllum* fossils with often unknown cuticles (e.g., Schenk, 1866; Stur, 1885; Dobruskina et al., 2001; Kustatscher et al., 2004). What makes this feature even more significant is the fact that not only shows the genus *Pterophyllum* an abrupt mass occurrence in the Lunz and Neuewelt floras, but also other bennettitalean foliage taxa such as *Nilssoniopteris* occur in abundance in these floras, while they are missing or rare elements in stratigraphically older floras (Pott et al., in press-b). This suggests that *Pterophyllum*, along with several other bennettitaleans, locally became significant elements of the vegetation relatively early in their evolutionary history. However, the precise circumstances that provided for the sudden success of the bennettitaleans in Lunz and Neuewelt remain elusive.

It is possible that the relatively poor record of plant fossils from earlier Triassic deposits, along with misinterpretation and/or misidentification of fossils from earlier floras, depict a biased picture of the early evolutionary history of *Pterophyllum* and other bennettitaleans. On the other hand, certain changes in the biology and/or ecology of some bennettitaleans may have occurred during the Late Triassic that facilitated sudden local mass occurrences of these plants. For example, alternative or improved reproduction and dispersal strategies may have evolved that enabled rapid colonization of new habitats by large numbers of individuals. Although most cycadophyte reproductive structures from Lunz (e.g., *Haitingeria*, *Westersheimia*) suggest that these plants were wind-pollinated, it has been hypothesized that, from the Late Triassic onwards, beetles became increasingly important as pollinators for several groups of bennettitaleans (Crowson, 1981; Lawrence and Newman, 1982). This hypothesis is based primarily on the fact that the earliest representatives of the modern beetles appeared in the early Late

Triassic, and subsequently evolved into diverse lineages during the middle and late Late Triassic (i.e. Cupedidae, Trachypachidae, and Staphylinoidea; cf. Grimaldi and Engel, 2005). Since the early evolutionary history of modern beetles, especially the reticulated beetles (Cupedidae), seems parallel to that seen in the Bennettitales, it is possible that closer co-evolutionary relationships existed between beetles and Bennettitales. Noteworthy in this context is the discovery of small insect eggs from Lunz that are structurally similar to eggs produced by modern reticulated beetles and exclusively occur on *Nilssoniopteris* leaves (Pott et al., submitted for publication). The increasing diversity of cupedids and other beetles during the Late Triassic may have provided beetle-pollinated bennettitaleans with a reproductive advantage over wind-pollinated forms. This advantage may eventually have resulted in mass occurrences of certain bennettitaleans. An alternative hypothesis with regard to the sudden proliferation of bennettitaleans concerns the appearance of bisexual bennettitalean “flowers”. In bisexual plants, both male and female reproductive structures co-occur in one individual, and thus this individual is twice as effective as, for instance, a dioecious cycad, and thus bisexuality may considerably increase the rate of reproduction. In addition, larger plant-feeding land vertebrates became increasingly abundant during the Late Triassic (e.g., Benton, 2004), and thus may also have affected reproduction and dispersal in the Bennettitales. Some of these plant-feeding animals perhaps ingested bennettitalean seeds. If these seeds were capable of passing through the alimentary canal unscathed, plant-feeding vertebrates may have contributed to long-distance dispersal of bennettitaleans, and thus assisted in the colonization of new areas.

8. Concluding remark

Although the Late Triassic ecosystems of the Alpine realm are regarded as significant with regard to the evolution of plant life in the Mesozoic (Dobruskina, 1998), and thus have received considerable attention in the past, our understanding of the actual diversity and complexity of these ecosystems, and the biology and ecology of the individual constituents remain incomplete. The revision of the genus *Pterophyllum* in the Lunz flora presented in this paper, along with several other recently conducted studies on the seed plants from Lunz (Pott et al., 2007a,b, in press-a, b), demonstrate how integrated analyses of compression fossils based on both macromorphology and epidermal anatomy are capable of broadening our understanding of the vegetation that grew in these ancient landscapes. The systematic analysis of the *Pterophyllum* species from Lunz contributes to a more accurate depiction of the individual components of this flora, and underscores how a reassessment of old material can provide a more sharply focused concept of an ancient ecosystem. The results obtained provide a template to not only interpret (newly discovered) isolated parts of these plants from other floras with regard to their morphology and systematic affinities, but also function and ecological context. This approach offers new avenues of investigation of both the plants and the ecosystems in which they lived. Such information is important as it relates to the identification of disarticulated plant fossils, especially foliage types, since structural and morphological features are the basis of generic and specific identifications.

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References

Andrews, H.N., 1970. Index of generic names of fossil plants, 1820–1965. U.S. Geol. Surv. Bull. 1300.

Barnard, P.D.W., 1967. Upper Triassic plants from the Kalawch River, Northeast Afghanistan. Fossils of North-east Afghanistan, Italian Expeditions to the Karakorum (K2) and Hindu Kush, Scientific Reports. Brill, Leiden, pp. 25–40.

Barthel, M., 1976. Ergebnisse der floristischen neubearbeitung des Rotliegenden in Sachsen. Z. Geol. Wiss. 4, 921–933.

Benton, M.J., 2004. Origin and interrelationships of dinosaurs. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. University of California Press, Berkeley, pp. 11–30.

Bhardwaj, D.C., Singh, H.P., 1964. An Upper Triassic miospore assemblage from the coals of Lunz, Austria. The Palaeobotanist 12, 28–44.

Braun, F.R., 1843. Beiträge zur Urgeschichte der Pflanzen. Beiträge zur Petrefacten-Kunde, pp. 1–46.

Brongniart, A., 1825. (‘1824’). Observations sur les végétaux fossiles renfermés dans les grès de Hoer en Scanie. Ann. Sci. Nat. 4, 200–224.

Brongniart, A., 1828. Prodrome d’une Histoire des Végétaux Fossiles. Levrault, Paris.

Cleal, C.J., 1993. Gymnospermophyta. In: Benton, M.J. (Ed.), The Fossil Record, vol. 2. Chapman & Hall, London, pp. 795–808.

Crowson, R.A., 1981. The Biology of the Coleoptera. Academic Press, London.

Dijkstra, S.J., Van Ameron, H.W.J., 1985. Fossilium Catalogus II: Plantae — Pars 91: Filicales, Pteridospermae, Cycadales, incertae sedis, vol. 2. Kugler Publications, Amsterdam. Supplement.

Dobruskina, I.A., 1989. The alpine Lunz-Flora — a standard flora for the carnian stage of the Triassic. Int. Geol. Rev. 31, 1209–1215.

Dobruskina, I.A., 1998. Lunz flora in the Austrian Alps — a standard for Carnian floras. Palaeogeogr. Palaeoclimatol. Palaeoecol. 143, 307–345.

Dobruskina, I.A., Jurkovsek, B., Kolar-Jurkovsek, T., 2001. Upper Triassic flora from "Raibl beds" of Julian Alps (Italy) in Karavanke Mts. (Slovenia). Geologija 44, 263–290.

Dunay, R.F., Fisher, M.J., 1978. The Carnian palynofloral succession in the Northern Calcarous Alps, Lunz-am-See, Austria. Pollen Spores 20, 177–187.

Florin, R., 1933. Studien über die Cycadales des Mesozoikums. Kunglika Svenska Vetenskapsakademiens Handlingar, vol. 12, pp. 1–134.

Fontaine, W.M., 1883. Contributions to the Knowledge of the Older Mesozoic Flora of Virginia. Government Printing, Washington.

Frentzen, K., 1922. Keuperflora und Lunzer Flora. Centralblatt für Mineralogie. Geol. Paläontol. 1, 23–28.

Geinitz, E., 1873. Versteinerungen aus dem Brandschiefer der unteren Dyas von Weissig bei Pillnitz in Sachsen. Neues Jahrbuch für Mineralogie. Geol. Paläontol. 691–704.

Grimaldi, D., Engel, M.S., 2005. Evolution of the Insects. Cambridge University Press, Cambridge.

Greuter, W., McNeill, J., Burdet, H.-M., Demoulin, V., Filgueiras, T.S., Nicolson, D.H., Silva, P.C., Skog, J.E., Trehane, P., Turland, N.J., Hawksworth, D.L., 2000. International Code of Botanical Nomenclature (St. Louis Code). Regnum Vegetabile, vol. 138. Koeltz Scientific Books, Königstein.

Gu, Zhi, 1974. Palaeozoic Plants from China. Scientific Press, Beijing.

Harris, T.M., 1932. The fossil flora of Scoresby Sound East Greenland — Part 3: Caytoniales and Bennettitales. Medd. Grønl. 85, 1–133.

Harris, T.M., 1969. The Yorkshire Jurassic Flora III. Bennettitales. Trustees of the British Museum (Natural History), London.

Heer, O., 1865. Die Urwelt der Schweiz. Schultheß, Zürich.

Heer, O., 1877. Flora Fossilis Helvetiae. Wurster & Comp, Zürich.

Hornung, T., Brandner, R., 2005. Biochronostratigraphy of the Reingraben turnover (Hallstatt facies belt): local black shale events controlled by regional tectonics, climatic change and plate tectonics. Facies 51, 460–479.

Jaeger, G.F., 1827. Über die Pflanzenversteinerungen welche in dem Bausandstein von Stuttgart vorkommen. Metzler, Stuttgart.

Jongmans, W., Dijkstra, S.J., 1960. Fossilium Catalogus II: Plantae – Pars 44: Filicales, Pteridospermae, Cycadales. Junk, 's-Gravenhage.

Jongmans, W., Dijkstra, S.J., 1963. Fossilium Catalogus II: Plantae — Pars 56: Filicales, Pteridospermae, Cycadales. Junk, 's-Gravenhage.

Kawasaki, S., 1931. The flora of the Heian System — Part 2 (Atlas). Bull. Geol. Surv. Chosen (Korea) 6 (2) Plates 16–99.

Kawasaki, S., 1934. The flora of the Heian System — Part 2. Bull. Geol. Surv. Chosen (Korea) 6 (4), 47–311.

Ke-Qin Sun, 2006. The Cathaysia flora and the mixed Late Permian Cathaysian-Angaran floras in East Asia. J. Integr. Plant Biol. 48, 381–389.

Kelber, K.-P., 1998. Phytostratigraphische Aspekte der Makrofloren des süddeutschen Keupers. Doc. Nat. 117, 89–115.

Kelber, K.-P., Nitsch, E., 2005. Paläoflora und Ablagerungsräume im unterfränkischen Keuper. Jahresber. Mitt. Oberrhein. Geol. Ver. 87, 217–253.

Kerp, H., 1990. The study of fossil gymnosperms by means of cuticular analysis. Palaios 5, 548–569.

Kerp, H., Krings, M., 1999. Light microscopy of cuticules. In: Jones, T. (Ed.), Fossil Plants and Spores: modern techniques. Geological Society, London, pp. 52–56.

Krasser, F., 1909a. Die Diagnosen der von Dionysius Stur in der obertriadischen Flora der Lunzerschichten als Marattiaceenarten unterschiedenen Farne. Sitz.ber. Kais. Akad. Wiss., Abt 1 (118), 13–43.

Krasser, F., 1909b. Zur Kenntnis der fossilen Flora der Lunzer Schichten. Jahrb. Kais.-K. Geol. Reichanst. 59, 1–26.

Kräusel, R., 1953. Ein neues *Dioonitocarpidium* aus der Trias von Lunz. Senckenbergiana 34, 105–108.

Kräusel, R., Schaarschmidt, F., 1966. Die Keuperflora von Neuewelt bei Basel — IV. Pterophyllen und Taeniopteriden. Schweiz. Paläontol. Abh. 84, 3–44.

Kurr, J.G., 1845. Beiträge zur fossilen Flora der Juraformation Württembergs. Gutenberg'sche Buchdruckerei, Stuttgart.

Kurr, J.G., 1846. Beiträge zur fossilen Flora der Juraformation Württembergs. Beck & Fränkel, Stuttgart.

Kustatscher, E., Wachtler, M., Van Konijnenburg-van Cittert, J.H.A., 2004. A number of additional and revised taxa from the Ladinian flora of the Dolomites, Northern Italy. GeoAlp 1, 57–69.

Lawrence, J.F., Newman, A.F., 1982. Evolution and classification of beetles. Ann. Rev. Ecolog. Syst. 13, 261–290.

Leuthardt, F., 1903. Die Keuperflora von Neuewelt bei Basel — I. Teil, Phanerogamen. Abh. Schweiz. Paläontol. Ges. 30, 1–23.

Nathorst, A.G., 1878a. Beiträge zur fossilen Flora Schwedens — Über einige rhätische Pflanzen von Pålsjö in Schonen. Schweitzerbart'sche Verlagsbuchhandlung, Stuttgart.

Nathorst, A.G., 1878b. Bidrag till Sveriges fossila flora. — II. Floran vid Högenäs och Helsingborg. K. Sven. Vetensk.Akad. Handl. 16, 1–53.

Nielsen, S.N., 2005. The Triassic Santa Juana Formation at the lower Biobío River, South Central Chile. J. South Am. Earth Sci. 19, 547–562.

Pott, C., Kerp, H., Krings, M., 2007a. Morphology and epidermal anatomy of *Nilssonia* (cycadalean foliage) from the Upper Triassic of Lunz (Lower Austria). Rev. Palaeobot. Palynol. 143, 197–217.

Pott, C., Kerp, H., Krings, M., 2007b. *Pseudoctenis cornelii* nov. spec. (cycadalean foliage) from the Carnian (Upper Triassic) of Lunz, Lower Austria. Annalen 2006 des Naturhistorischen Museums Wien, vol. 108A, pp. 39–55.

Pott, C., Miller, I. M., Hickey, L. J., Kerp, H., Van Konijnenburg-van Cittert, J. H. A., Zijlstra, G., in press-a. Proposal to conserve the name *Pterophyllum* (fossil Bennettitales) with a conserved type. Taxon.

Pott, C., Krings, M., Kerp, H., in press-b. The first record of *Nilssoniopteris* (fossil Gymnospermophyta, Bennettitales) from the Carnian (Upper Triassic) of Lunz, Lower Austria. Palaeontology.

Pott, C., Labandeira, C.C., Krings, M., Kerp, H., submitted for publication. Fossil insect eggs and ovipositional damage on bennettitalean leaf cuticles from the Carnian (Upper Triassic) of Austria. Journal of Paleontology.

Roghi, G., 2004. Palynological investigations in the Carnian of the Cave del Predil area (Julian Alps, NE Italy). Rev. Palaeobot. Palynol. 132, 1–35.

Schenk, A., 1864. Beiträge zur Flora des Keupers und der rhätischen Formation. Ber. Nat.Forsch. Ges. Bamberg VII, 1–91.

Schenk, A., 1865–1867. Die fossile Flora der Grenzschichten des Keupers und Lias Frankens. Kreidel, Wiesbaden.

Schenk, A., 1866. Bemerkungen über einige Pflanzen der Lettenkohle und des Schilfsandsteins. Würzbg. Nat.Wiss. Z. VI, 49–63.

Schimper, W.P., 1870. Traité de Paléontologie Végétale, vol. 3. Baillière et Fils, Paris. 1869–1874.

von Schlotheim, E.F., 1822. Nachträge zur Petrefactenkunde. Becker'sche Verlagsbuchhandlung, Gotha.

Stur, D., 1871. Geologie der Steiermark. Verlag des geognostisch-montanen Vereines für Steiermark, Graz.

Stur, D., 1885. Die obertriadische Flora der Lunzer-Schichten und des bituminösen Schiefers von Raibl. Denkschr. Kais. Akad. Wiss. 3, 93–103.

Stur, D., 1888. Die Lunzer (Lettenkohle-)Flora in den "older mesozoic beds of the Coal-Field of Eastern Virginia". Verh. Kais.-K. Geol. Reichanst. 10, 203–217.

Sze, H.C., 1936. Über einen Vorläufer von Pterophyllen in der unteren Shihhotze Serie in Shansi. Bull. Geol. Soc. China 15, 467–472.

Thomas, H.H., 1930. Further observations on the cuticle structure of Mesozoic cycadean fronds. J. Linn. Soc. Lond., Bot. 48, 389–415.

Unger, F., 1845. Über das relative Alter der Steinkohlen-Formation in Österreich. Österr. -Kais. Privil. Wien. Ztg. 20.01.1845.

Unger, F., 1848. Die Lias-Formation in den nordöstlichen Alpen von Österreich. Neues Jahrbuch für Mineralogie, Geognosie. Geol. Petrefact. 47, 279–291.

Van Konijnenburg-van Cittert, J.H.A., Mikuz, V., Pavsic, J., 2001. *Pterophyllum* (Cycadopsida) from Carnian beds in Poljane valley (Slovenia). Geologija 44, 317–323.

Watson, J., Cusack, H.A., 2005. Cycadales of the English Wealden. The Palaeontographical Society, London.

Watson, J., Sincock, C.A., 1992. Bennettitales of the English Wealden. The Palaeontographical Society, London.

Zeiller, R., 1906. Bassin Houiller et Permien de Blanzy et du Creusot — Fascicule II: Flore fossile. Imprimerie nationale, Paris.

CHAPTER 3

The first record of *Nilssoniopteris* (fossil Gymnospermophyta, Bennettitales) from the Carnian (Upper Triassic) of Lunz, Lower Austria

Christian Pott, Michael Krings & Hans Kerp

Palaeontology 50: 1299–1318 (2007)

Abstract.—The Carnian (Late Triassic) flora of Lunz in Lower Austria is famous for the abundance of well-preserved bennettitalean and cycadalean foliage and reproductive structures. However, only the fertile remains have been studied in detail to date. Recently completed systematic macromorphological and cuticular analyses of leaf fossils from Lunz revealed that several forms previously accommodated in the genus *Macrotaeniopteris* do not represent ferns, but rather Bennettitales assignable to the genus *Nilssoniopteris*. We describe three species of *Nilsoniopteris*, which represent the first record for this genus from Lunz, and one of the earliest accounts of *Nilssoniopteris* in the northern hemisphere. The following new combinations are introduced: *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909a) comb. nov., *N. angustior* (Stur ex Krasser, 1909a) comb. nov., and *N. lunzensis* (Stur ex Krasser, 1909a) comb. nov. The discovery of *Nilssoniopteris* further substantiates the significance of the Lunz flora as one of the richest and most diverse early Late Triassic floras from the northern hemisphere.

Keywords.—Cuticle, *Macrotaeniopteris*, *Taeniopteris*, fossil plants, Carnian, Triassic, Lunz.

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FIRST RECORD OF *NILSSONIOPTERIS* (GYMNOSPERMOPHYTA, BENNETTITALES) FROM THE CARNIAN (UPPER TRIASSIC) OF LUNZ, LOWER AUSTRIA

by CHRISTIAN POTT*, MICHAEL KRINGS† *and* HANS KERP*

*Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, D-48143 Münster, Germany; e-mails: christian.pott@uni-muenster.de, kerp@uni-muenster.de

†Bayerische Staatssammlung für Paläontologie und Geologie und GeoBio-Center^{LMU}, Richard-Wagner-Straße 10, D-80333 Munich, Germany; e-mail: m.krings@lrz.uni-muenchen.de

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Abstract: The Carnian (Late Triassic) flora of Lunz in Lower Austria is famous for an abundance of well-preserved bennettitalean and cycadalean foliage and reproductive structures. However, only the fertile remains have been studied in detail to date. Recently completed systematic macromorphological and cuticular analyses of leaf fossils from Lunz revealed that several forms previously accommodated in the genus *Macrotaeniopteris* do not represent ferns but rather Bennettitales assignable to the genus *Nilssoniopteris*. We describe three species of *Nilssoniopteris*, which represent the first records for this genus from Lunz, and one of the earliest accounts of *Nilssoniopteris* in the Northern Hemisphere. The following new combinations are introduced: *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909*a*) comb. nov., *N. angustior* (Stur ex Krasser, 1909*a*) comb. nov. and *N. lunzensis* (Stur ex Krasser, 1909*a*) comb. nov. The discovery of *Nilssoniopteris* further substantiates the significance of the Lunz flora as one of the richest and most diverse early Late Triassic floras from the Northern Hemisphere.

Key words: cuticle, *Macrotaeniopteris*, *Taeniopteris*, fossil plants, Carnian, Triassic, Lunz.

THE well-known Carnian (early Late Triassic) flora from Lunz in Lower Austria contains several morphotypes of elongate, entire-margined to coarsely pinnate leaves, most of which have historically been interpreted as belonging to marrattialean ferns (Krasser 1909*a*). The earliest record in the literature of these leaf types is in a species list (Stur 1885); however, no diagnoses, descriptions or illustrations were given. In this list, Stur (1885) referred six foliage morphotypes to the genus *Taeniopteris* Brongniart, 1828. The names given by Stur, however, remained *nomina nuda* until Krasser (1909*a*), based on Stur's handwritten notes, provided diagnoses for the taxa and a short discussion, but without illustrating the material. He also transferred the six species to the morphogenus *Macrotaeniopteris* Schimper, 1869. *Macrotaeniopteris* was introduced by Schimper (1869) for entire-margined fronds previously accommodated in *Taeniopteris auct. nec* Brongniart. Schimper assigned *Macrotaeniopteris* to the Marattiales, but subsequent studies (e.g. Florin 1933*a*) revealed that some forms, e.g. several specimens described as *M. gigantea* Schimper, 1869, in fact represent cycadalean foliage.

Although cuticular analysis is known to provide a wealth of information useful in determining the systematic affinities of many late Palaeozoic and Mesozoic compression foliage fossils (e.g. Harris 1932; Florin 1933*a*, *b*; Kerp 1990; Watson and Sincock 1992; Krings and Kerp 2000; Krings *et al.* 2005; Watson and Cusack 2005), it has largely been neglected in studies of the Lunz flora. Data on the epidermal anatomy of the proposed *Macrotaeniopteris* leaves were absent, with the exception of a few fragmentary cuticles described by Kräusel (1920). However, Kräusel's descriptions are incomplete and, hence, not very useful as a tool for accurately identifying further specimens that may be similar in overall appearance. As a result, the circumscription of the six foliage types from Lunz assigned to *Macrotaeniopteris* by Krasser (1909*a*) continued to be vague, and thus the affinities of these fossils (e.g. fern or seed plant foliage) remained uncertain.

A recent detailed reinvestigation of the Lunz flora based on macromorphological and cuticular analyses (see Pott *et al.* 2005, 2007*a*, *b*, *d*) revealed that the foliage

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types previously referred to *Macrotaeniopteris* (marrattialean foliage) actually represent bennettitalean foliage assignable to the morphogenus *Nilssoniopteris* Nathorst, 1909 emend. Boyd, 2000; three distinct species of *Nilssoniopteris* are recognized. In this paper, we provide detailed descriptions of these species, and the new combinations *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909*a*) comb. nov., *N. angustior* (Stur ex Krasser, 1909*a*) comb. nov. and *N. lunzensis* (Stur ex Krasser, 1909*a*) comb. nov. are introduced. These *Nilssoniopteris* taxa represent the first unequivocal record of this genus for the flora from Lunz, and one of the earliest accounts of *Nilssoniopteris* in the Northern Hemisphere.

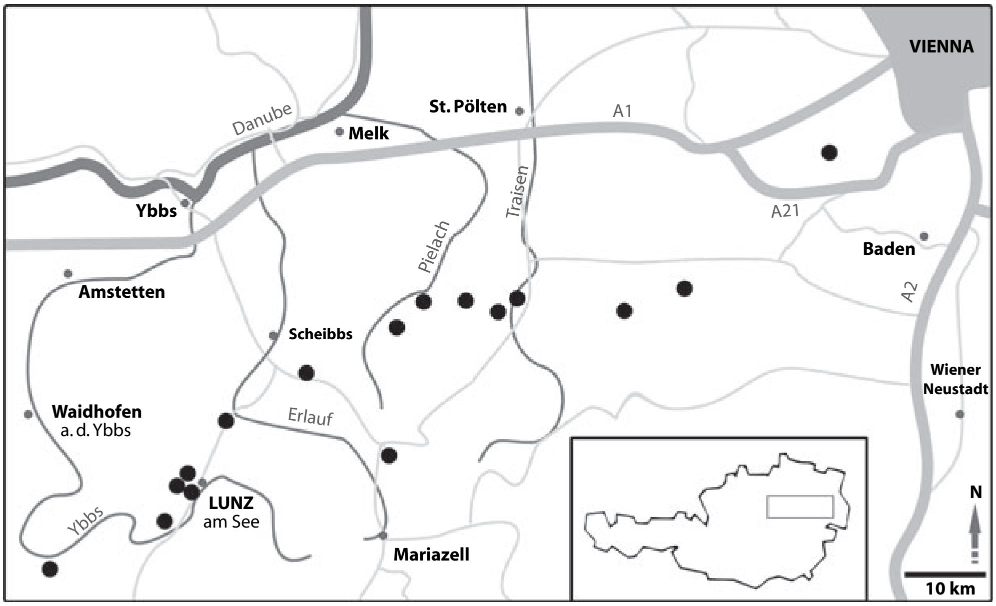
MATERIAL AND METHODS

Geological setting and material

The material comes from the area around Lunz-am-See in the Northern Calcareous Alps of Lower Austria, approximately 100 km west of Vienna (Text-fig. 1). The material was collected in the late nineteenth and early twentieth centuries from several active coal-mines. With more than 4000 specimens, the Lunz flora is one of the richest Late Triassic floras of the Northern Hemisphere. Moreover, with more than 70 species recorded to date (Dobruskina 1989, 1998, Pott *et al*., 2007*a*, *b*, *d*), including sphenophytes, ferns, cycadaleans, bennettitaleans, conifers and ginkgophytes, the Lunz flora also represents one of the most diverse Late Triassic floras.

The outcrop conditions around Lunz-am-See are poor today since coal-mining ceased after World War II. Some of the old spoil tips still exist, but are not easily accessible; moreover, the material from these spoil tips is strongly weathered and usually unsuitable for cuticular analysis. As a result, this study is based entirely on material kept in various European museum collections.

The fossils occur in the ‘Lunzer Sandstein’, which is part of the Lunz beds. The Lunz Formation (= Lunzer Schichten) consists of sandstones at the base, followed by marine marls gradually grading upwards into terrestrial sands, shales and coal. The coal-bearing part of the sequence is overlain by marls and with a sandstone layer at the top. The plant fossils occur in the shales associated with the coal beds. Exact age dating of the Lunz Formation is still a problem because adequate biomarkers such as ammonoids and conodonts are lacking. Recent studies focusing on regional and facies-spanning correlations of biostratigraphically well-established sections within the Hallstatt and Reifling Intraplatform basins (Hornung and Brandner 2005) have suggested that the Lunz Formation is positioned within the upper part of the Reingraben Formation (T. Hornung, pers. comm. 2006). As a result, it is probably late Julian (Julian 2/II) in age. Palynological studies have indicated Carnian (Bhardwaj and Singh 1964) and Julian (Dunay and Fisher 1978) ages. The Opponitzer



TEXT-FIG. 1. Index map showing the region around Lunz-am-See with the localities from which Lunz plants have been recovered in the past.

Limestone, the upper subunit of the Lunzer Schichten, was dated by Dunay and Fisher (1978) as Tuvalian.

Cuticular analysis and documentation

The plant fossils from Lunz occur as impressions or compressions, the latter often with excellently preserved cuticles. The latter were prepared according to procedures outlined in Kerp (1990), and Kerp and Krings (1999). Rock samples with plant remains were dissolved in hydrofluoric acid (HF) in order to remove the sediment, or they were picked from the rock surface. Cuticles were macerated according to the standard procedure using Schulze's reagent (35 per cent HNO_3 with a few crystals of $KClO_3$) and 5–10 per cent potassium hydroxide (KOH). Macerated cuticles were washed in distilled water, gently dehydrated in pure glycerine, and finally mounted in permanent glycerine-jelly microscope slides. The slides are stored in the relevant museum collections; accession numbers are indicated in the figure captions.

Hand specimens were photographed with a Nikon D 100 digital camera using polarized light to increase contrast (cf. Schaarschmidt 1973). Cuticles were analysed with a Leitz Diaplan microscope with Nomaski interference contrast and photographed with a Nikon DS-5M digital camera.

Abbreviations. GBA, Geologische Bundesanstalt, Wien (Geological Survey of Austria, Vienna); NHM, Naturhistorisches Museum, Wien (Natural History Museum, Vienna); NRM, Naturhistoriska Riksmuseet, Stockholm (Museum of Natural History, Stockholm); RUU, Laboratory of Palaeobotany and Palynology, University of Utrecht, The Netherlands; JOA, Landesmuseum Joanneum, Graz (State Museum Joanneum, Graz, Austria).

SYSTEMATIC PALAEONTOLOGY

Subdivision CYCADOPHYTINA *sensu* Cleal and Rees, 2003
Class GNETOPSIDA *sensu* Cleal and Rees, 2003
Order CYCADEOIDALES (=BENNETTITALES) Wieland, 1916
Family unknown

Genus NILSSONIOPTERIS Nathorst, 1909 emend. Boyd, 2000

Type species. Nilssoniopteris tenuinervis Nathorst, 1909 (see Cleal *et al.* 2006) from the Rhaetian of Höör, Scania, Sweden.

Emended diagnosis. Strap-shaped leaf falling from stem at maturity, petiolate, lamina undivided, lobed to completely dissected down to the rachis, attached laterally or to adaxial surface of midrib, leaving part of the upper surface of the midrib exposed. Veins free, simple or forked, ending at margin. Cuticle with syndetocheilic stomata; epidermal cell walls straight or usually sinuous.

Remarks. Nathorst (1909) introduced *Nilssoniopteris* for entire-margined cycadophyte leaves from the Jurassic of Europe. However, he did not designate a type species for the genus. Therefore, it was not validly published. Cleal *et al.* (2006) validated it by designating a type. Harris (1932) introduced the genus *Taeniozamites* for entire-margined taeniopterid leaves that are characterized by a bennettitalean epidermal anatomy. Later, Florin (1933*a*) placed *Taeniozamites* in the synonymy of *Nilssoniopteris*. The synonymy of *Nilssoniopteris* and *Taeniozamites* is widely accepted today, with *N. tenuinervis* as the type species (Cleal *et al.* 2006).

With regard to macromorphology, some *Nilssoniopteris* fossils may resemble *Anomozamites* Schimper, 1870 (bennettitalean foliage). Typical representatives of *Nilssoniopteris* display an entire-margined lamina. However, some specimens from Lunz have a lamina that is partially lobed or dissected down to the rachis. Fully pinnate leaves are traditionally assigned to *Anomozamites.* However, several authors, e.g. Harris (1969) and Boyd (2000), have illustrated intermediate leaf types. Unfortunately, the information available on the epidermal anatomy of *Anomozamites* (see Harris 1969) is incomplete and does not provide features useful in the discrimination of *Anomozamites* from *Nilssoniopteris*. Boyd (2000) emended the diagnosis of *Nilssoniopteris* to include the lobed leaves that are intermediate between *Nilssoniopteris* and *Anomozamites* and display bennettitalean epidermal anatomy. In this paper, Boyd's emendation of the generic diagnosis for *Nilssoniopteris* is expanded to include also leaves that are dissected down to the rachis.

Nilssoniopteris haidingeri (Stur ex Krasser, 1909*a*) nov. comb.
Plates 1–2

Basionym. Macrotaeniopteris haidingeri Krasser, 1909*a*: Krasser, F. 1909*a*. Die Diagnosen der von Dionysius Stur in der obertriadischen Flora der Lunzerschichten als Marattiaceenarten unterschiedenen Farne. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Wien*, *Abteilung 1*, **118**, 13–43.

v. *1885* *Taeniopteris haidingeri* Göppert *ms. nec* Ettingshausen; Stur, p. 97.
v. *1885* *Taeniopteris latior* Stur, p. 97.
v. 1909*a* *Macrotaeniopteris latior* Krasser, p. 39 (no illustration).
v. 1909*a* *Macrotaeniopteris haidingeri* Krasser, pp. 40–41 (no illustration).
v. *1909b* *Macrotaeniopteris latior* Krasser, p. 109 (no illustration).

v. *1909b* *Macrotaeniopteris haidingeri* Krasser, p. 109 (no illustration).

? 1920 *Taeniopteris* sp. Kräusel, p. 207, pl. 11, figs 4–5 (cuticle).

Comment on synonymy. The synonymy given above is based on the set of specimens originally studied by Stur (1885) and Krasser (1909*a*), which is today stored in the collections of the GBA.

Types. Lectotype, GBA 1909/002/0247 (Pl. 1, fig. 7). Epitype, GBA 1909/002/0232 (Pl. 1, fig. 1).

Remarks. The species was originally named *Taeniopteris haidingeri* (Stur 1885; *nomen nudum*) and later transferred to *Macrotaeniopteris haidingeri* by Krasser (1909*a*). Krasser provided a detailed diagnosis, but did not figure any specimens. Because no holotype was designated, specimen GBA 1909/002/0247 is selected here as the lectotype. This specimen belongs to the original set of fossils studied by Stur (1885) and Krasser (1909*a*, *b*), and yields cuticles that display syndetocheilic stomata (Pl. 2, figs 2–3). The specimen GBA 1909/002/0232 is selected as an epitype because it shows several macroscopic features more clearly than the lectotype. Moreover, it is one of the specimens that Stur undoubtedly analysed. The label in Stur's handwriting reads '*Taeniopteris haidingeri(ana)*'. The epitype specimen does not yield cuticles suitable for analysis.

Repository. Palaeobotanical Collection of the Geologische Bundesanstalt, Vienna.

Material. 65 specimens from the NHM, GBA, NRM, JOA and RUU collections.

Emended diagnosis. Leaves large, lanceolate in outline; lamina often basally divided into squarish parallel-sided segments of unequal width, apex obtuse-rounded; insertion of lamina to rachis lateral; individual lamina segments with several delicate, basally bifurcating parallel veins; leaves amphistomatic with robust cuticles; costal and intercostal fields distinct on abaxial, but indistinct on adaxial side of the leaf; epidermal cells isodiametric, sometimes rectangular, anticlinal cell walls straight; stomata restricted to intercostal fields, syndetocheilic, with two subsidiary cells; guard cells with prominent, crescent dorsal thickenings; epidermal cells of abaxial intercostal fields bear short papillae.

Description

The leaves are large (up to nearly 60 cm long and 15 cm wide), petiolate (petioles rarely preserved), entire-margined or partially pinnate, almost regular, broadly oval or oblong to lanceolate in outline, the apex obtuse-rounded (Pl. 1, figs 1–5). The rachis is markedly striate. The lamina is usually coarsely divided into several squarish segments that are opposite to subopposite in position (Pl. 1, figs 1, 3, 5) and insert laterally to the rachis (Pl. 1, figs 5–6). Segmentation is typically more profound in the proximal portion of the lamina. Segments are 2–4 cm long and 3–13 cm wide, and generally increase in length toward the leaf apex; some may taper distally and become slightly wider proximally. The width of the individual segments varies considerably; some are more than twice as wide as others (Pl. 1, figs 2–4). The distance between adjacent leaf segments remains the same within a single leaf, unless the segments are widened basally. Numerous parallel veins enter each segment and run straight to the apex. The veins usually fork twice in the basal part of the segment (Pl. 1, fig. 6).

The leaves are amphistomatic; however, stomatal density is considerably higher on the abaxial side of the leaf. The leaves have robust cuticles. Costal and intercostal fields are distinct on the abaxial (Pl. 2, fig. 2), but indistinct on the adaxial (Pl. 2, fig. 1) side of the leaf.

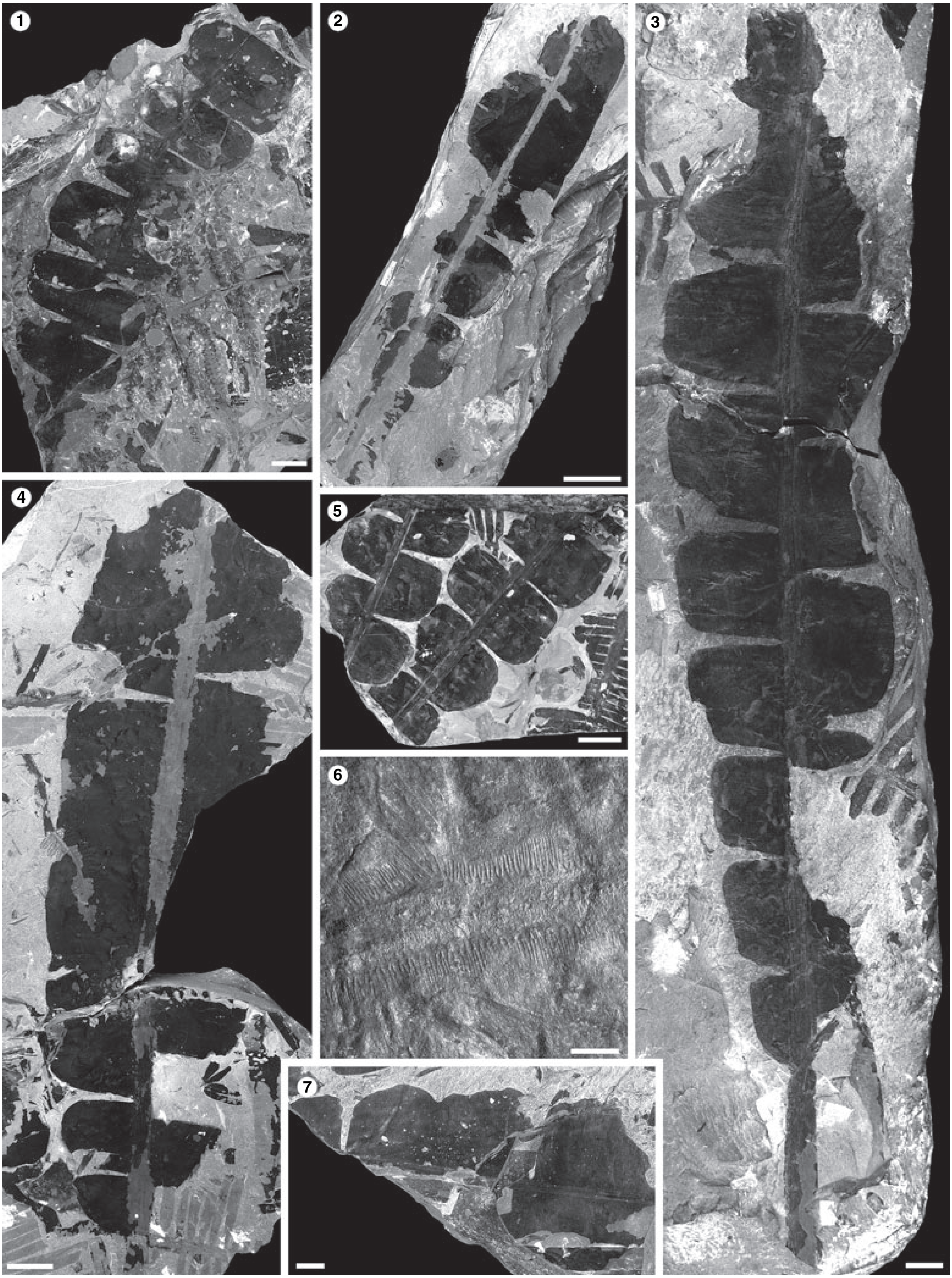
Adaxial epidermal anatomy. The cuticle of the adaxial side is slightly thicker than that of the abaxial side. The epidermal cells are rectangular and elongate to isodiametric in outline, 25–62·5 μm long and 22·5–35 μm wide (Pl. 2, fig. 1). Anticlinal walls are smooth. Stomata only occur close to the rachis. Stomatal apparatuses are syndetocheilic and diacytic, 45·5–52·5 μm long and 25–32·5 μm wide (Pl. 2, fig. 9). Stomatal pores (12·5–20 μm in diameter) are orientated perpendicular to the veins. Two rectangular subsidiary cells partly overarch the pit mouth and create a slightly sunken stoma (cf. Pl. 2, figs 7–8). Subsidiary cells are often slightly more cutinized than the normal epidermal cells. Papillae or trichome bases are absent.

Abaxial epidermal anatomy. The abaxial epidermis shows a clear differentiation into costal and intercostal fields (Pl. 2, figs 2–3). Costal fields are composed of 6–7 rows of cells (Pl. 2, fig. 5) and lack stomata and papillae. The individual cells are 25–65 μm long and 20–40 μm wide, possess delicate walls, and are rectangular and elongate to isodiametric in outline. Anticlinal cell walls are straight. Periclinal walls are smooth, surface ornamentation is present but rarely easily recognized. Intercostal fields are composed of 3–5 rows of cells. Individual cells are isodiametric or sometimes rectangular in outline, 25–52·5 μm long, 17·5–32·5 μm wide, and possess rounded 'corners'. They often bear a small, solid papilla (Pl. 2, figs 4–6).

EXPLANATION OF PLATE 1

Figs 1–7. *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909*a*) comb. nov., Lunz, Lower Austria. 1, GBA 1909/002/0232, epitype. 2, NHM 1885/D/3995. 3, NHM 1884/D/1203. 4, NHM 2006B0008/0027. 5, NHM 2006B0008/0042. 6, GBA 1909/002/0277, showing the forking of the veins close to the rachis. 7, GBA 1909/002/0247, lectotype. Scale bars represent 2 cm in 1, 4, 7; 3 cm in 2; 1 cm in 3, 5; 5 mm in 6.

PLATE 1



POTT *et al.*, *Nilssoniopteris*

Anticlinal cell walls are straight. Stomata are regularly distributed within the intercostal fields, syndetocheilic, 37·5–55 μm long and 17·5–30 μm wide (Pl. 2, figs 2–8). The stomatal pores (12·5–20 μm in diameter) are orientated perpendicular to the veins (Pl. 2, fig. 6). The two rectangular subsidiary cells are 20–45 μm wide and long, diacytic, and by overarching the pit mouth, create a sunken stoma (Pl. 2, figs 7–8). Each subsidiary cell bears a small, solid papilla that overarches the pit mouth (Pl. 2, fig. 8). The dorsal walls of the kidney-shaped guard cells possess strongly cutinized, crescentic central parts, whereas the polar ends are only weakly cutinized (Pl. 2, fig. 8). The arrangement of epidermal cells in distinct rows gradually disappears towards the rachis. The epidermal cells positioned close to the lamina margin are much smaller than the cells located in the middle portion of the lamina.

Discussion. This foliage type is assigned to *Nilssoniopteris* because essential macromorphological features (e.g. the nearly band-like or oblong-oval outline of the entire-margined or lobed leaves and lateral insertion of the lamina to a massive rachis) correspond well to those seen in typical representatives of the genus (Harris 1969; Boyd 2000). In addition, the venation is similar, especially with regard to the parallel lateral veins that fork twice near their base. Furthermore, the epidermal anatomy, characterized by syndetocheilic stomata, justifies accommodation of this species in *Nilssoniopteris* (Harris 1969; Boyd 2000).

Macrotaeniopteris latior Krasser, 1909*a* is placed in the synonymy of *Nilssoniopteris haidingeri*. The separate status of *M. latior* is questionable. The main character used to discriminate *M. latior* from *M. haidingeri* is the outline of the lamina that, according to Krasser (1909*a*), is entire-margined in *M. latior* and 'lobed' in *M. haidingeri*. However, several specimens exist that can be regarded as intermediate between these two forms (e.g. Pl. 1, figs 2, 4). The most complete specimens of *N. haidingeri* show that the distal part of the lamina is entire-margined and lobation is restricted to the middle and lower portions of the leaf. Because the epidermal anatomy of both forms is identical, they are regarded as conspecific.

Taeniopteris gigantea Schenk, 1867 from the Rhaeto-Liassic of Franconia, Germany (Schenk 1867), displays superficial similarities to *N. haidingeri*. However, the epidermal anatomy of *T. gigantea* from the Rhaeto-Liassic of Scania, Sweden, clearly differs from that of *N. haidingeri* in having haplocheilic stomata (Florin 1933*a*). Florin (1933*a*) provided a detailed description of the epidermal anatomy of *T. gigantea* and transferred this species to the genus *Bjuvia* Florin, 1933. Leaves with haplocheilic stomata are excluded from the Bennettitales *per definitionem* (Florin 1933*a*).

Other species that resemble *N. haidingeri* include *Pterophyllum hanesianum* Harris, 1932 from the Rhaetian of Greenland, *N. major* (Lindley and Hutton, 1833) Harris, 1946 from the Jurassic of Yorkshire (Harris 1969), *Taeniozamites jourdyi* (Zeiller, 1903) Harris, 1932 from the Rhaetian of Greenland, and *Macrotaeniopteris lata* (Oldham and Morris, 1863) Feistmantel, 1877 from the Jurassic of India.

Pterophyllum hanesianum was described from the Rhaetian of Greenland based on fragmentary specimens (Harris 1932). Leaf outline and length remain unknown to date. Leaf segments are distinctly narrower than those seen in *N. haidingeri*. Consequently, a closer comparison of *P. hanesianum* to *N. haidingeri* remains difficult. Subsidiary cells of *P. hanesianum* are more thickly cutinized than normal epidermal cells whereas they are not especially cutinized in *N. haidingeri*; on the other hand, the subsidiary cells of *P. hanesianum* bear a papilla that is similar to papillae found on the subsidiary cells of *N. haidingeri*.

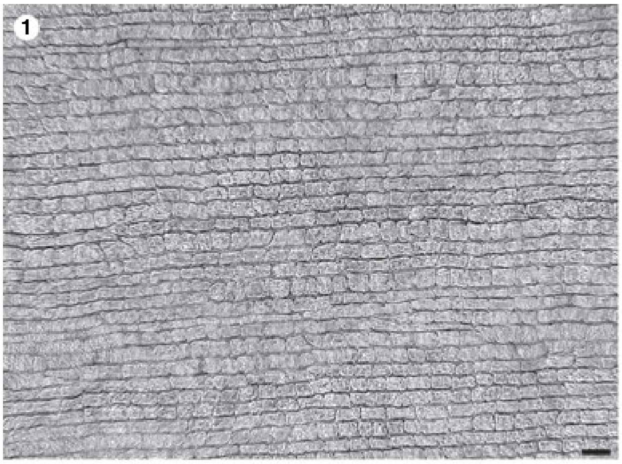
Nilssoniopteris major is similar to *N. haidingeri* with regard to leaf outline and attachment of the lamina, as well as venation pattern. It clearly differs in having much smaller leaves (i.e. usually 15 cm long). Moreover, the anticlinal cell walls are strongly sinuous and not straight as in *N. haidingeri*, and the stellate trichomes that are typical for *N. major* do not occur in *N. haidingeri*. Rather, the absence of hair bases in the *N. haidingeri* cuticles from Lunz indicates that these leaves were entirely glabrous with the exception of small papillae.

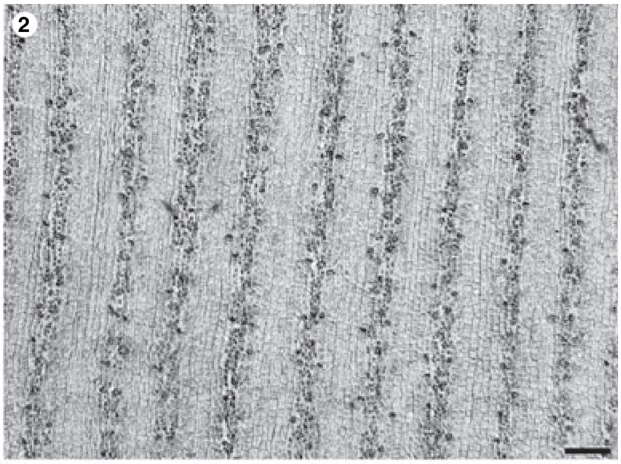
Taeniozamites jourdyi displays similarities to *N. haidingeri* in general leaf outline and size of the individual leaf segments. The stomatal morphology in both species is similar, but the epidermal cells of *T. jourdyi* possess sinuous anticlinal walls and the leaves bear trichomes.

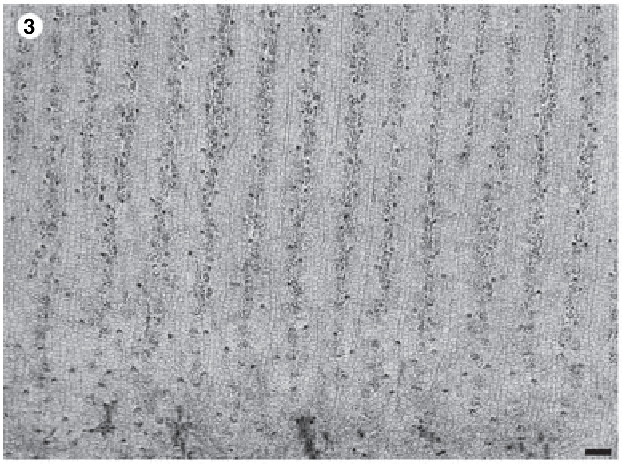
EXPLANATION OF PLATE 2

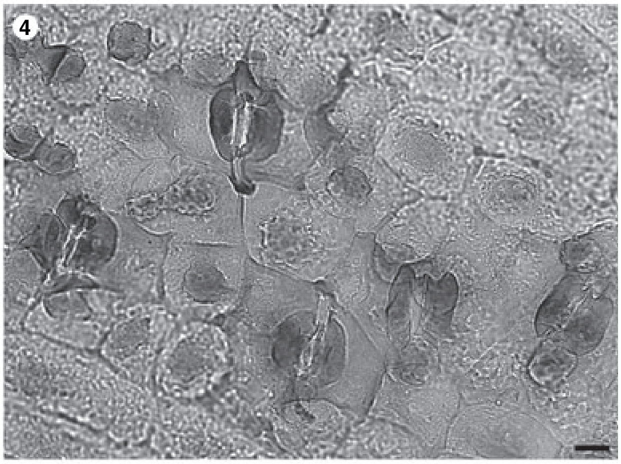
Figs 1–7. *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909*a*) comb. nov., Lunz, Lower Austria. 1, JOA 63874/0004, adaxial cuticle, overview. 2, GBA 1909/002/0247/0005, abaxial cuticle, overview. 3, GBA 1909/002/0247/0008, abaxial cuticle, venation pattern close to rachis (lower part of image). 4, NHM 1885/D/3983/0003, abaxial cuticle, arrangement of stomata in intercostal field. 5, NHM 1885/D/3983/0003, abaxial cuticle, two intercostal fields with several stomata. 6, NHM 1885/D/3983/0003, abaxial cuticle, intercostal field with several stomata. 7, NHM 1885/D/3983/0003, abaxial cuticle, single stoma with overarching papillae. 8, NHM 1885/D/3983/0003, abaxial cuticle, single stoma with overarching papillae. 9, GBA 1909/002/0247/0002, adaxial cuticle from lectotype with two adjacent stomata. Scale bars represent 50 μm in 1, 5–6; 200 μm in 2–3; 10 μm in 4, 7–9.

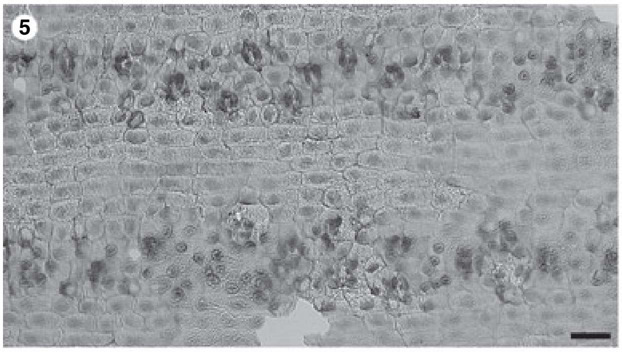
PLATE 2

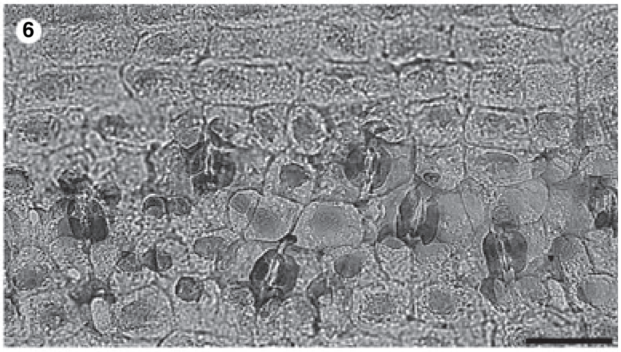


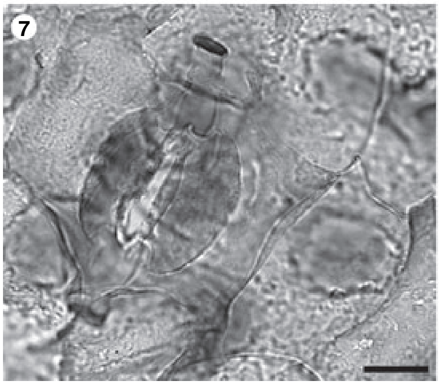


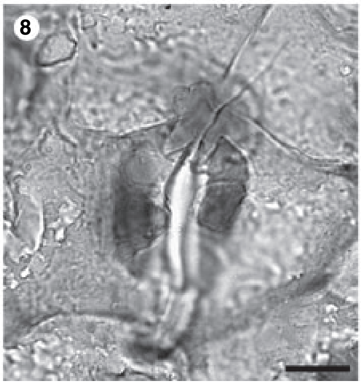


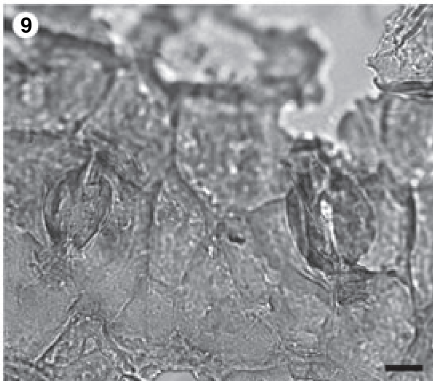












POTT *et al.*, *Nilssoniopteris*

Macrotaeniopteris lata, a common species in the Jurassic of the Rajmahal Hills flora of India, closely resembles entire-margined specimens of *N. haidingeri* in outline and dimensions. However, specimens with a segmented lamina have not been recorded to date.

Nilssoniopteris musafolia Barnard, 1965 (Schweitzer and Kirchner 2003) from the Rhaeto-Liassic of Iran shows some resemblance in basic morphology to *N. haidingeri*, but since cuticles of the former are not available, closer comparison is impossible at present.

Distribution. Lunzer Schichten, Julian, middle Carnian; Lunz-am-See, Lower Austria.

Nilssoniopteris angustior (Stur ex Krasser, 1909*a*) comb. nov.
Plates 3–4

Basionym. Macrotaeniopteris angustior Krasser, 1909*a*: Krasser, F. 1909*a*. Die Diagnosen der von Dionysius Stur in der obertriadischen Flora der Lunzerschichten als Marattiaceenarten unterschiedenen Farne. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Wien*, *Abteilung 1*, **118**, 13–43.

v. *1885* *Taeniopteris angustior* Stur, p. 97.
v. *1885* *Taeniopteris simplex* Stur, p. 97.
v. *1885* *Taeniopteris parvula* Stur, p. 97.
v. 1909*a* *Macrotaeniopteris simplex* Krasser, pp. 38–39 (no illustration).
v. 1909*a* *Macrotaeniopteris angustior* Krasser, pp. 39–40 (no illustration).
v. 1909*a* *Macrotaeniopteris parvula* Krasser, p. 40 (no illustration).
v. 1909*b* *Macrotaeniopteris simplex* Krasser, p. 109 (no illustration).
v. 1909*b* *Macrotaeniopteris angustior* Krasser, p. 109 (no illustration).
? 1920 *Macrotaeniopteris simplex* Krasser; Kräusel, pp. 206–209, text-fig. 5; pl. 10, figs 1–3 (cuticle).

Types. Lectotype, GBA 1909/002/0193 (Pl. 3, fig. 7). Epitype, GBA 1909/002/0186 (Pl. 3, fig. 1).

Remarks. The species was originally named *Taeniopteris angustior* by Stur (1885; *nomen nudum*) and later transferred to *Macrotaeniopteris angustior* by Krasser (1909*a*). Krasser provided a detailed diagnosis, but did not illustrate any specimens. Because no holotype was designated, specimen GBA 1909/002/0193 is selected here as the lectotype. This specimen belongs to the original set of fossils studied by Stur (1885) and Krasser (1909*a*, *b*), and yields cuticles that display syndetocheilic stomatal apparatuses (Pl. 4, fig. 3). The specimen GBA 1909/002/0186 is selected as an epitype because it shows several macroscopic features more clearly than the lectotype. Moreover, it is one of the specimens that Stur undoubtedly analysed. The label in Stur's handwriting reads '*Taeniopteris angustior*'. The epitype specimen does not yield cuticles suitable for analysis.

Repository. Palaeobotanical Collection of the Geologische Bundesanstalt, Vienna.

Material. 65 specimens from the NHM, GBA, NRM and JOA collections.

Emended diagnosis. Leaves petiolate, oblong to lanceolate in outline, apex acute; insertion of lamina to rachis lateral; venation dense, veins parallel, forking twice close to rachis. Leaves amphistomatic with robust cuticles; costal and intercostal fields not differentiated; epidermal cells isodiametric to rectangular, anticlinal cell walls straight; stomata irregularly arranged in rows, syndetocheilic, with two subsidiary cells, guard cells with prominent, crescent-shaped dorsal thickenings; abaxial epidermal cells with long hollow papillae.

Description

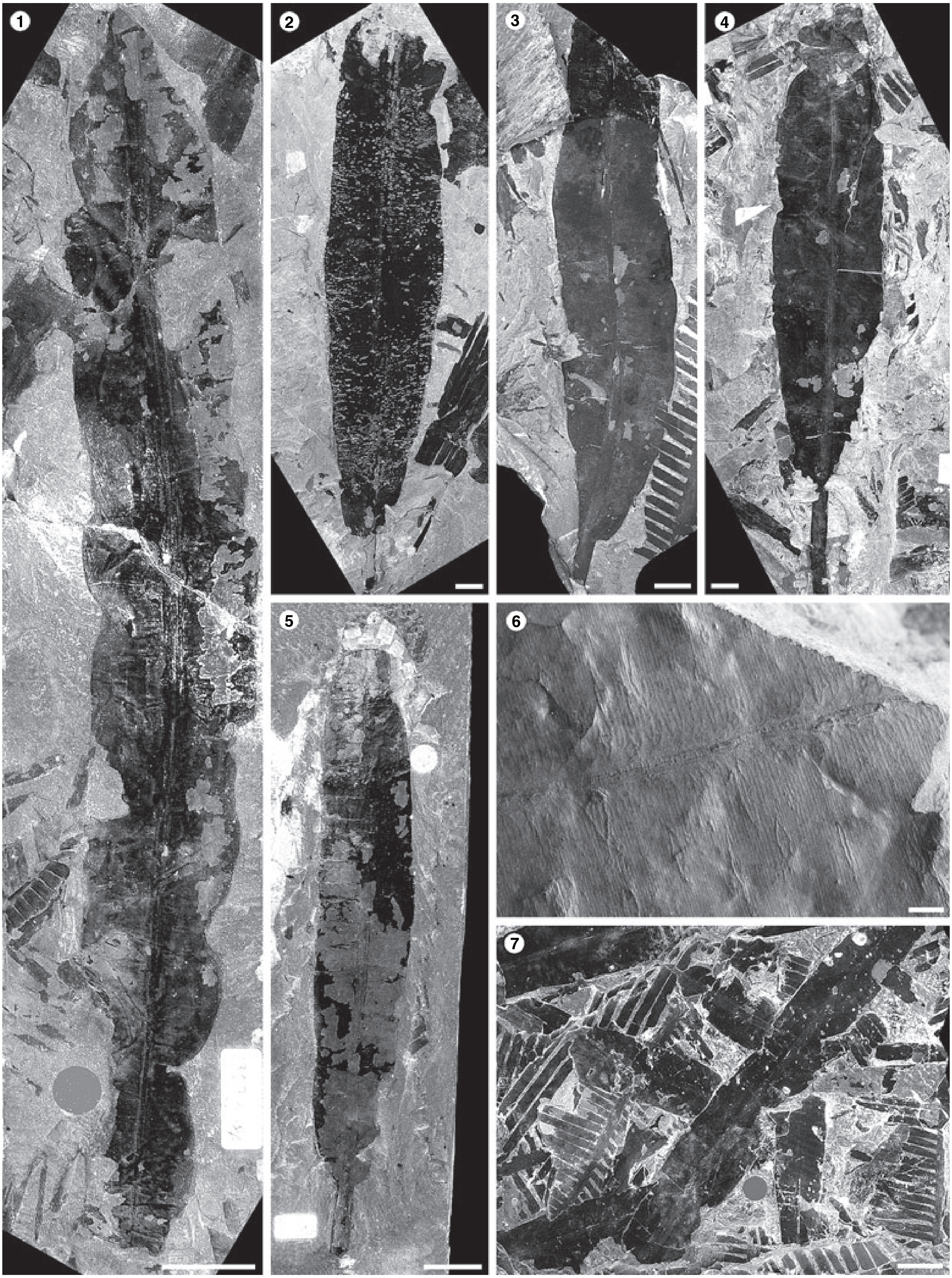
The leaves are relatively large (largest fragments up to 29·0 cm long and 5·2 cm wide), petiolate, narrow, oblong to lanceolate in outline, with acute apices (Pl. 3, figs 1–5). The lamina is not subdivided into segments, but occasionally growth aberrations of the leaf margin occur that resemble weak lobations (Pl. 3, fig. 1), or the lamina is locally torn apart, as in extant *Musa* leaves. The lamina is inserted laterally to the striate rachis (Pl. 3, fig. 6). It is very narrow close to the petiole, but then rapidly increases in width (Pl. 3, figs 2–5). Numerous parallel veins enter perpendicular to the lamina and run straight to the margin (Pl. 3, fig. 6). The veins usually fork twice close to the rachis (Pl. 3, fig. 6); additional bifurcations may occasionally occur.

The leaves are amphistomatic; however, stomatal density is considerably higher on the abaxial side of the leaf. The leaves have relatively thin cuticles; nevertheless, large pieces of cuticle can easily be obtained. Costal and intercostal fields are not clearly differentiated. However, an alternation of stomatiferous and non-stomatiferous areas occurs on the abaxial side (Pl. 4, figs 4–6).

EXPLANATION OF PLATE 3

Figs 1–7. *Nilssoniopteris angustior* (Stur ex Krasser, 1909*a*) comb. nov., Lunz, Lower Austria. 1, GBA 1909/002/0186, epitype. 2, NHM 1885/D/1212. 3, NHM 1887/0001/0009. 4, NRM S148256. 5, GBA 1909/002/0187. 6, GBA 1909/002/0218, showing forking of the veins close to the lamina. 7, GBA 1909/002/0193, lectotype. Scale bars represent 2 cm in 1, 5, 7; 1 cm in 2–4; 2 mm in 6.

PLATE 3



POTT *et al.*, *Nilssoniopteris*

Adaxial epidermal anatomy. The cuticle of the adaxial side is slightly thicker than that of the abaxial side. The epidermal cells are isodiametric, usually rectangular, 27·5–70 μm long and 22·5–42·5 μm wide (Pl. 4, fig. 1). Anticlinal cell walls are smooth and well cutinized. Stomata occur sporadically in areas close to the rachis (Pl. 4, figs 2–3); the stomatal apparatuses are identical to those seen in the abaxial epidermis (cf. Pl. 4, figs 7–9). Virtually every epidermal cell possesses a distinct central cuticular thickening on the outer periclinal wall (Pl. 4, figs 4–5); trichomes or hair bases are absent.

Abaxial epidermal anatomy. Epidermal cells are usually rectangular to isodiametric in outline, but may also be slightly elongated or rounded, 20–62·5 μm long and 20–40 μm wide (Pl. 4, fig. 4). Anticlinal cell walls are straight, with triangular cuticular thickenings in the cell corners. Periclinal walls are smooth; nearly every cell bears a central cuticular thickening, 10–17·5 μm in diameter (Pl. 4, fig. 4). This feature becomes more distinct towards the margin of the lamina (Pl. 4, figs 4, 6). Stomata and subsidiary cells are arranged in long rows, orientated perpendicular to the rachis; they alternate with non-stomatiferous bands of cells (Pl. 4, figs 3, 6). This alternation is irregular and does not concur with the venation pattern. Stomatal bands are composed of 1–3 rows of cells (Pl. 4, figs 4–6). The stomata are 32–45 μm long and 15–25 μm wide, syndetocheilic, sunken (Pl. 4, figs 7–9), and consist of the pair of guard cells and two rectangular subsidiary cells (25–50 μm long and 27·5–50 μm wide; Pl. 4, figs 7–9). Subsidiary cells cover the peripheral portions of the guard cells and form a small, slit-like stomatal pit (diacytic stomatal apparatus). Pores (12·5–17·5 μm in diameter) are orientated perpendicular to the cell rows. The dorsal walls of the kidney-shaped, sunken guard cells possess strongly cutinized, crescent-shaped central parts and distinct radial striae (Pl. 4, figs 7–8). However, a small peripheral portion and the polar ends of the guard cells are weakly cutinized. Long hollow papillae (37·5–52·5 μm long) are irregularly scattered across the abaxial epidermis (Pl. 4, fig. 5; arrows).

Discussion. This foliage type is assigned to *Nilssoniopteris* because macromorphological features (i.e. the nearly band-like or oblong-oval outline of the entire-margined or lobed leaves and the lateral insertion of the lamina to a robust rachis) correspond well with those seen in typical representatives of this genus (Harris 1969; Boyd 2000). Additional typical nilssoniopterid features of *N. angustior* include the delicate parallel venation composed of veins that fork twice near the rachis (Harris 1969; Boyd 2000), and syndetocheilic stomata.

We place *Macrotaeniopteris simplex* Krasser, 1909*a* and *M. parvula* Krasser 1909*a*, which have both been described from Lunz, in the synonymy of *Nilssoniopteris angustior*. These forms were originally distinguished from *N. angustior* based on differences in the forking pattern of the veins (Krasser 1909*a*). However, our large set of specimens indicates that this is not a consistent feature; several specimens display intermediate venation patterns. Moreover, the epidermal anatomies of *N. angustior*, *Macrotaeniopteris simplex* (see Kräusel 1920) and *M. parvula* are identical.

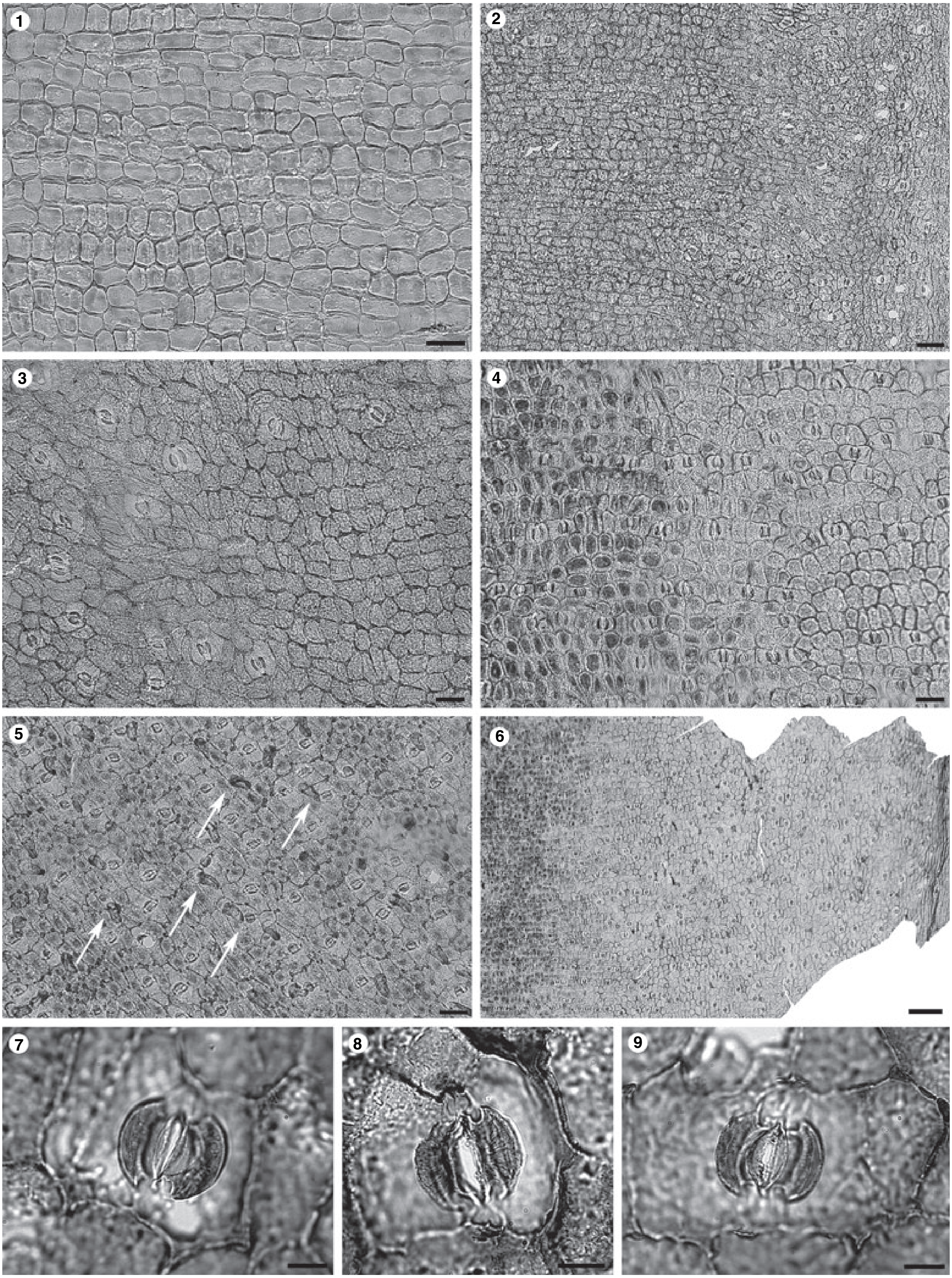
Macrotaeniopteris magnifolia (Rogers, 1843) Schimper, 1869 from the Carnian of Virginia (Fontaine 1883; Cornet and Olson 1990) closely resembles *N. angustior* in basic morphology, especially with regard to the dimensions, leaf form and venation. However, its epidermal anatomy has not been described to date, and hence its relationship to *N. angustior* remains elusive.

Other forms that are similar in gross morphology to *N. angustior* include *N. tenuinervis* (Nathorst, 1880) Nathorst, 1909 (= *N. vittata* Harris, 1969) and *N. pristis* Harris, 1969 from the Jurassic of Yorkshire (Harris 1969). *Nilssoniopteris tenuinervis* is the type species of the genus *Nilssoniopteris* (Cleal *et al.* 2006). The epidermal anatomy of both taxa is typical for bennettitalean foliage, and characterized by syndetocheilic stomata and strongly sinuous anticlinal cell walls. However, the latter do not occur in *N. angustior*. Stomata in *N. tenuinervis* are less regularly orientated than those seen in *N. angustior* and often adjusted transversely whereas they are orientated perpendicularly in *N. angustior*. Moreover, the leaves of *N. tenuinervis* and *N. pristis* are distinctly less wide (1·0–3·0 cm) than those produced by *N. angustior*. Leaf margins of *N. pristis* are finely denticulate, whereas *N. tenuinervis* and *N. angustior* possess entire-margined leaves.

EXPLANATION OF PLATE 4

Figs 1–7. *Nilssoniopteris angustior* (Stur ex Krasser, 1909*a*) comb. nov., Lunz, Lower Austria. 1, GBA 1909/002/0090/0002, adaxial cuticle, overview. 2, NHM 1885/D/3966/0004, adaxial cuticle, arrangement of stomata close to the rachis (right side of image). 3, GBA 1909/002/0193/0013, adaxial cuticle of lectotype, arrangement of stomata close to rachis (left side). 4, NHM 1884/0015/0010, abaxial cuticle, middle portion of the lamina, epidermal cells with papillae on the left side, cells without papillae on the right side of image. 5, NHM 1887/0001/0009/0004, abaxial cuticle, overview with papillae (arrows). 6, NHM 1884/0015/0009, abaxial cuticle, overview of portion of lamina between rachis (right) and margin (left). 7, NHM 1884/0015/0012, abaxial cuticle, stoma with radial striae on guard cells. 8, NHM 1884/0015/0012, abaxial cuticle, stoma. 9, NHM 1884/0015/0012, abaxial cuticle, stoma showing radial striae on guard cells. Scale bars represent 50 μm in 1, 3–5; 100 μm in 2; 200 μm in 6; 10 μm in 7–9.

PLATE 4



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Another related form from the Jurassic of Yorkshire is *N. major*, but the leaf outline of its foliage corresponds better to that seen in *N. haidingeri* (see above).

Gnaedinger and Herbst (2004) described several *Taeniopteris* species from the Upper Triassic El Tranquilo Group in Patagonia, Argentina, that are morphologically similar to *N. angustior*. However, they did not provide information on the epidermal anatomy; thus, a closer comparison of these Patagonian fossils to *N. angustior* is impossible at present. They have to be retained in *Taeniopteris* until material suitable for cuticular analysis becomes available (cf. Cleal and Rees 2003).

Forms that morphologically resemble *N. angustior* have also been reported from the Carnian Molteno Formation of South Africa (Anderson and Anderson 1989). However, the affinities of these fossils remain elusive because the morphology of the stomatal apparatuses has not been documented. As a result, they must also be retained in the morphogenus *Taeniopteris* for the time being.

The epidermal anatomy of *N. schenkiana* Barnard, 1965 from the Rhaeto-Liassic of Iran (Barnard 1965; Schweitzer and Kirchner 2003) closely resembles that of *N. angustior*, but trichome bases are absent in the latter species and a comparison of the papillae with the trichomes of *N. schenkiana* remains problematic. Moreover, leaves of *N. schenkiana* are notably smaller than those of *N. angustior*.

Distribution. Lunzer Schichten, Julian, middle Carnian; Lunz-am-See, Lower Austria.

Nilssoniopteris lunzensis (Stur ex Krasser, 1909*a*) comb. nov.
Plates 5–6

Basionym. Macrotaeniopteris lunzensis Krasser, 1909*a*: Krasser, F. 1909*a*. Die Diagnosen der von Dionysius Stur in der obertriadischen Flora der Lunzerschichten als Marattiaceenarten unterschiedenen Farne. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Wien*, *Abteilung 1*, **118,** 13–43.

v. *1885* *Taeniopteris lunzensis* Stur, p. 97.
v. 1909*a* *Macrotaeniopteris lunzensis* Krasser, pp. 41–42 (no illustration).
v. *1909b* *Macrotaeniopteris lunzensis* Krasser, pp. 109–110 (no illustration).

Types. Lectotype, GBA 1909/002/0315 (Pl. 5, fig. 6). Epitype, GBA 1909/002/0302 (Pl. 5, fig. 5).

Remarks. The species was originally named *Taeniopteris lunzensis* by Stur (1885; *nomen nudum*) and later transferred to *Macrotaeniopteris lunzensis* by Krasser (1909*a*). Krasser provided a detailed diagnosis, but did not illustrate specimens. Because no holotype was designated, specimen GBA 1909/002/0315 is selected here as the lectotype. This specimen belongs to the original set of fossils studied by Stur (1885) and Krasser (1909*a*, *b*). It yields cuticles that display syndetocheilic stomatal apparatuses (Pl. 6, fig. 10). Specimen GBA 1909/002/0302 is selected as an epitype because it shows several macroscopic features more clearly than the lectotype. Moreover, it is one of the specimens that Stur undoubtedly analysed. The label in Stur's handwriting reads '*Taeniopteris lunzensis*'. The epitype specimen does not yield cuticles suitable for analysis.

Repository. Palaeobotanical Collection of the Geologische Bundesanstalt, Vienna.

Material. 30 specimens from the NHM, GBA, NRM, RUU collections.

Emended diagnosis. Leaves relatively small, petiolate, imparipinnate, lanceolate to broadly oval in outline, apex obtuse rounded; lamina subdivided into broad, parallel-sided segments. Leaf segments variable in width, irregularly opposite in position, inserted laterally to rachis; veins parallel, once or twice forked. Leaves amphistomatic, lacking a clear differentiation into costal and intercostal fields; epidermal cells rectangular to isodiametric, anticlinal cell walls straight; stomata syndetocheilic, sunken, loosely arranged in rows; guard cells with prominent dorsal thickenings and radial striae; adaxial and abaxial epidermal cells bear small, solid papillae.

Description

The leaves are relatively small (up to 17·2 cm long and 6·2 cm wide), petiolate (petioles up to 2·0–2·5 cm long and 4–6 mm wide), imparipinnate, lanceolate to oval in overall outline (Pl. 5, figs 1, 3–6, 8). The rachis is marked by longitudinal striae and the lamina is subdivided into individual segments, which insert laterally to the rachis (Pl. 5, figs 2, 7). Leaf segments are broadly attached, slightly decurrent, irregularly to regularly opposite in position (Pl. 5, figs 1, 3, 6, 8), and up to 32·0 mm long and between 4·4 mm and 17·5 mm wide. The apex is round and formed by the uppermost three leaf seg-

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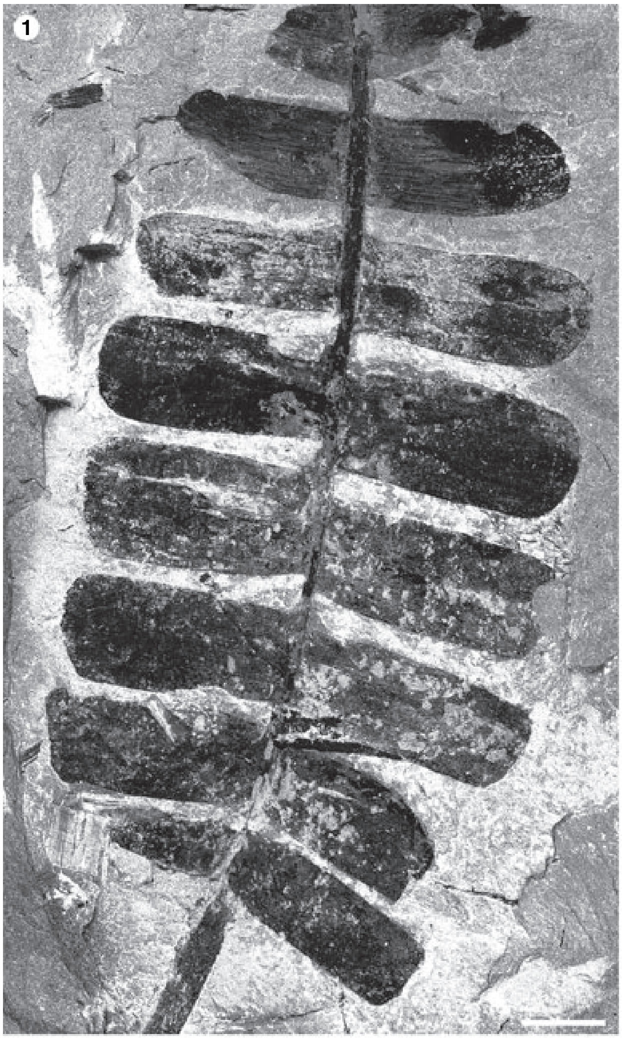
EXPLANATION OF PLATE 5

Figs 1–8. *Nilssoniopteris lunzensis* (Stur ex Krasser, 1909*a*) comb. nov., Lunz, Lower Austria. 1, NHM 1888/0001/0018. 2, NHM 1886/0001/0019. 3, GBA 1909/002/0317. 4, NHM 1887/0001/0013/0001. 5, GBA 1909/002/0302, epitype. 6, GBA 1909/002/0315, lectotype. 7, NHM 1884/0027. 8, NHM 2006B0008/0021. Scale bars represent 1 cm in 1, 3–4, 6, 8; 5 mm in 2, 5, 7.

PLATE 5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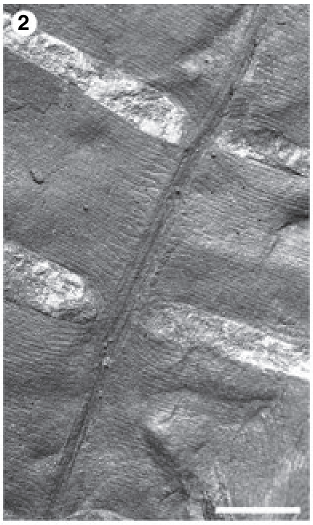
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8

ments (Pl. 5, figs 1, 3–6, 8). The basal leaf segments are short and broad; more distally positioned segments are only slightly longer than the basal ones. Individual leaf segments are more or less rectangular in outline and obtusely rounded apically (Pl. 5, figs 1, 3–6, 8). Basal segments are 2–3 times broader than the apical ones. Distances between individual segments remain consistent within a single leaf. The apical leaf segment differs from the lateral segments in being much narrower; however, it is rarely preserved (Pl. 5, figs 4–6, 8). It extends from the tip of the rachis; the subterminal segments insert at acute angles (Pl. 5, figs 4–6). Numerous parallel veins enter each leaf segment (Pl. 5, figs 2, 7). The veins usually fork once or twice immediately after entering the segment (Pl. 5, figs 2, 7). Additional forking occasionally occurs, but is limited to the proximal one-third of the segment.

The leaves are amphistomatic; however, stomatal density is considerably higher on the abaxial side of the leaf. They have well-developed cuticles; costal and intercostal fields are not clearly differentiated, but an alternation of stomatiferous and non-stomatiferous areas is visible (Pl. 6, figs 2–4).

Adaxial epidermal anatomy. Epidermal cells are isodiametric, typically rectangular, not or only slightly elongated, 45–60 μm long and 22·5–30 μm wide (Pl. 6, fig. 1). Anticlinal cell walls are smooth and well cutinized. Stomata occur sporadically on the adaxial side (Pl. 6, fig. 2). They are distributed regularly and identical to those of the abaxial side. The adaxial cuticle is slightly thicker than the abaxial cuticle. A central idiocuticular thickening may occur on the epidermal cells.

Abaxial epidermal anatomy. Epidermal cells are usually rectangular to squarish, but some may be slightly elongated or rounded, 25–57·5 μm long and 25–35 μm wide. Anticlinal cell walls are straight, with triangular cuticular thickenings in the corners (Pl. 6, fig. 6). Nearly every normal epidermal cell bears a central cuticular thickening 12·5–17·5 μm in diameter (Pl. 6, figs 3, 8). The periclinal thickenings are more distinct towards the leaf margin. Stomata are arranged in long rows that are orientated perpendicular to the rachis. The stomatiferous rows alternate with non-stomatiferous bands of cells; however, this alternation is irregular and does not concur with the venation pattern. Stomatal bands consist of 1–3 rows of cells (Pl. 6, figs 3–4, 7). The stomata are 32·5–42·5 μm long and 17·5–25 μm wide, syndetocheilic, sunken (Pl. 6, figs 5, 10–14) with two rectangular subsidiary cells (Pl. 6, fig. 7). Subsidiary cells partly cover the guard cells and form a small, slit-like stomatal pit (diacytic stomatal apparatus). Pores (15–22·5 μm in diameter) are orientated perpendicular to the cell rows (Pl. 6, fig. 3). The dorsal walls of the kidney-shaped, sunken guard cells show strongly cutinized, crescent-shaped central portions and distinct radial striae (Pl. 6, figs 11–14). However, a small peripheral portion and the polar ends of the guard cells are weakly cutinized. Hollow papillae (18–20 μm long) are irregularly distributed in the abaxial epidermis (Pl. 6, figs 4, 9).

Discussion. Macrotaeniopteris lunzensis is transferred to *Nilssoniopteris* based on gross-morphological characters, i.e. laminar, laterally attached leaf segments and veins that fork close to the rachis (cf. Cleal and Rees 2003), and epidermal features. However, segmented leaf architecture, a similar stomatal morphology, and long papillae are also known to occur in species of *Pterophyllum* Brongniart, 1825. *Nilssoniopteris lunzensis* is similar in gross morphology to that seen in *Pterophyllum inconstans* Goeppert 1843, a species reported from Germany, Vietnam, Japan and China (Schenk 1867; Zeiller 1903; Yabe 1925; Sze and Lee 1952). However, the epidermal anatomy of *N. lunzensis* clearly differs from that of *P. inconstans* in that the epidermis of the latter has sinuous anticlinal cell walls, and the distribution of stomata is even less regular (Schenk 1867). Zeiller (1903), Yabe (1925) and Sze and Lee (1952) figured excellently preserved macrofossils of *P. inconstans*, but did not study the cuticles.

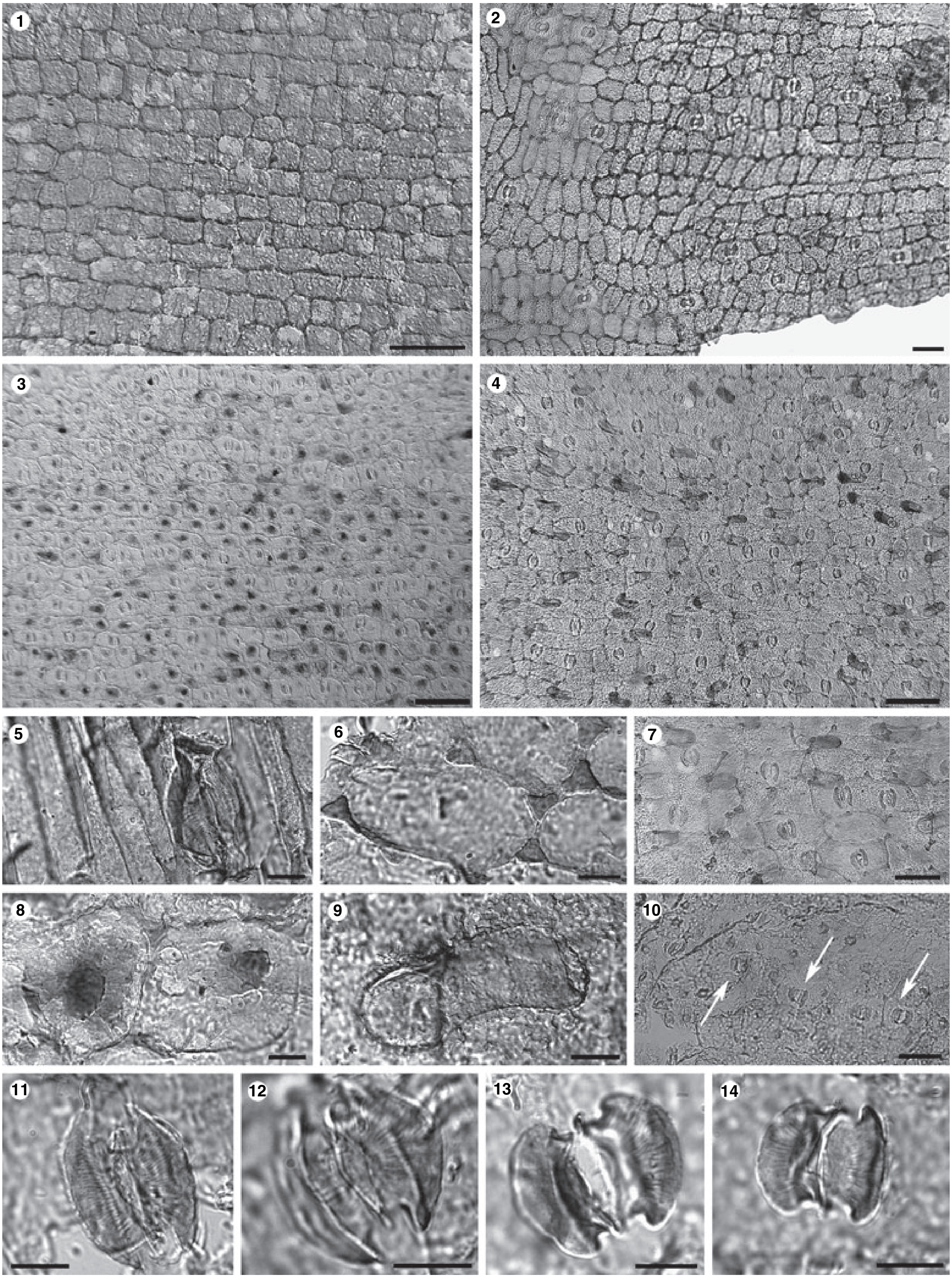
Leaves of *Pterophyllum braunsii* Schenk, 1867, from the Liassic of Franconia (Germany), are superficially similar in outline to those of *N. lunzensis*, but their epidermal anatomy is unknown to date (Schenk 1867). *Nilssoniopteris lunzensis* also resembles *P. princeps* Oldham and Morris, 1863 from the Jurassic of India. These authors assumed that their fossils belong to the cycads. However, their epidermal anatomy is still unknown.

Nilssoniopteris lunzensis also resembles *Anomozamites nilssonii* (Phillips, 1829) Harris, 1969 from the Jurassic of Yorkshire in both size and macromorphology (Harris 1969). However, they clearly differ in their epidermal

EXPLANATION OF PLATE 6

Figs 1–14. *Nilssoniopteris lunzensis* (Stur ex Krasser, 1909*a*) comb. nov., Lunz, Lower Austria. 1, NHM 1885/D/4021/0001, adaxial cuticle, overview. 2, NRM 148318/0001, adaxial cuticle, arrangement of stomata close to the rachis. 3, NRM S148543/0004, abaxial cuticle, overview. 4, NHM 1885/D/4021/0001, abaxial cuticle, with stomata and papillae scattered regularly between epidermal cells. 5, NRM S148318/0001, portion of rachis with stoma. 6, NRM S148318/0002, abaxial cuticle, epidermal cells with thickened edges. 7, NHM 1885/D/4021/0001, abaxial cuticle, stomata and long papillae. 8, NRM S148543/0004, abaxial cuticle, epidermal cells with central cuticular thickening. 9, NHM 1885/D/4021/0001, abaxial cuticle, single papilla. 10, GBA 1909/002/0315/0013, abaxial cuticle of lectotype with syndetocheilic stomata (arrows). 11, NRM S148318/0001, abaxial cuticle, stoma with radial striae on guard cells. 12, NRM S148318/0001, abaxial cuticle, stoma with radial striae on guard cells. 13, NRM S148543/0004, abaxial cuticle, stoma with radial striae on guard cells. 14, NRM S148543/0004, abaxial cuticle, stoma with radial striae on guard cells. Scale bars represent 100 μm in 1, 3–4; 50 μm in 2, 7, 10; 10 μm in 5–6, 8–9, 11–14.

PLATE 6



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anatomy: *N. lunzensis* has straight anticlinal cell walls, whereas in *A. nilssonii* the anticlinal walls are sinuous. The arrangement and orientation of the stomata, and the size of the subsidiary cells, are features that also clearly distinguish the two species.

Distribution. Lunzer Schichten, Julian, middle Carnian; Lunz-am-See, Lower Austria.

GENERAL DISCUSSION

Classification of impression/compression foliage fossils based exclusively on macromorphology is generally speculative and results in an artificial system of morphotaxa that does not necessarily reflect biological relationships. The assignment of several foliage types previously accommodated in the marattialean fern genus *Macrotaeniopteris* to the bennettitalean foliage genus *Nilssoniopteris* based on a combination of macromorphological and epidermal characters demonstrates the value of cuticular analysis in determining more accurately the systematic position of compression fossils based on biological criteria.

Nilssoniopteris is included in the Bennettitales based on epidermal features, including sinuous anticlinal epidermal cell walls, which are regarded as typical for bennettitaleans, and syndetocheilic stomata, which are interpreted as an autapomorphy of the entire group. The latter feature separates the Bennettitales from all other groups of seed plants, including the Cycadales (Florin 1933*a*). However, the stomata of some extant Gnetopsida (Welwitschiaceae Caruel, 1876; Gnetaceae Blume, 1833), a group of plants suggested to be closely related to the once widespread Bennettitales, resemble the bennettitalean stomatal type (Florin 1933*a*; Martens 1971).

It is interesting to note that the leaves of all *Nilssoniopteris* species from Lunz are amphistomatic (although with fewer stomata on the adaxial than on the abaxial side of the leaf), since amphistomy has also been recorded for several other plants from Lunz, including the enigmatic ginkgophyte *Glossophyllum florinii* Kräusel, 1943 (Pott *et al.* 2007*c*), most, if not all, *Pterophyllum* species (Pott *et al.* 2007*d*), and the cycadaleans *Nilssonia lunzensis* Stur ex Pott, Kerp and Krings, 2007 and *N. riegeri* (Stur ex Krasser, 1909*a*) Pott, Kerp and Krings, 2007 (Pott *et al.* 2007*a*). In extant plants, amphistomy tends to be more common among plants with thick leaves that thrive in xeric habitats (Parkhurst 1978; Fahn and Cutler 1992). The presence of stomata on both sides of the leaf is interpreted as an adaptation to reduce the internal diffusion distance of CO_2 in thick leaves (see Parkhurst *et al.* 1988). On the other hand, Mott *et al.* (1982) stated that amphistomy is characteristic for plants living in high-light environments and possessing high photosynthetic capacities, and may represent an adaptation to allow high stomatal conductances, which are necessary to take advantage of high photosynthetic capacities.

The *Nilssoniopteris* species from Lunz have syndetocheilic stomata, but none displays sinuous anticlinal epidermal cell walls. This concurs with a hypothesis advanced by Gothan and Weyland (1973) that early members of the Bennettitales had not yet evolved sinuous anticlinal cell walls. The *Pterophyllum* (bennettitalean foliage) species from Lunz generally lack distinctly sinuous anticlinal cell walls (Pott *et al.* 2007*d*). However, one of these species displays a possible precursory wall type characterized by faint undulations. Sinuous anticlinal cell walls are believed to have a stabilizing effect on the leaf, and thus may have been effective as an adaptation to certain environmental conditions (e.g. sustained wind), or as a protective mechanism against foliage-feeding arthropods. The leaves of all *Nilssoniopteris* species from Lunz possess papillate surfaces; however, form and spatial arrangement of papillae varies greatly. Long and hollow papillae are randomly arranged on the abaxial surfaces in *N. angustior* and *N. lunzensis*, while short, solid papillae are produced by nearly every epidermal cell of both sides of the leaf in these species, or papillae are restricted to the intercostal fields of the abaxial surface (covering the stomatiferous areas) in *N. haidingeri*. Epidermal papillae modify the physical properties of the leaf surface (Barthlott and Ehler 1977). Their restriction to the stomatiferous areas in *N. haidingeri* suggests a functional adaptation in response to ecological conditions. The precise nature of this adaptation, cannot, however, be determined at present.

Nilssoniopteris is a common element in Jurassic floras, and known to occur in several parts of the world, including Sweden, the United Kingdom (Nathorst 1909; Lundblad 1950; Harris 1969; Watson and Sincock 1992), Iran and Afghanistan (Sadovnikov 1989; Schweitzer and Kirchner 2003), China (Barale *et al.* 1998), and Greenland (Harris 1932; Boyd 2000). The fossil record of the genus in North America is somewhat scanty (see Ash 1989). We provide here the earliest record of *Nilssoniopteris* from the Triassic of Europe. Several *Taeniopteris* leaves resembling *Nilssoniopteris* have been reported from the Triassic and Jurassic of the Southern Hemisphere (Anderson and Anderson 1989; Gnaedinger and Herbst 2004; Cantrill and Hunter 2005). However, for none of these leaves has the epidermal anatomy been documented to date; thus, proposed affinities with the Bennettitales are speculative.

Along with the Neuewelt flora near Basel, Switzerland (Leuthardt 1901, 1903; Kräusel and Leschik 1955; Kräusel and Schaarschmidt 1966), the Lunz flora undoubtedly represents one of the richest and most diverse Carnian floras of the Northern Hemisphere (Dobruskina 1989, 1994, 1998). It is interesting to note that *Nilssoniopteris* has not been reported from Neuewelt or from any other Middle–Late Triassic flora, e.g. Raibl, north-east Italy (Schenk 1866; Stur 1885; Dobruskina 1994); Mount Pora, Bergamasc Alps, northern Italy (Passoni and van Konijnenburg-van Cittert 2003); Heilgersdorf near Coburg, Germany (Kelber and Hansch 1995); Wengen Formation, northern Italy (Wachtler and van Konijnenburg-van Cittert 2000). However, some of these floras contain leaves assigned to *Taeniopteris*, *Macrotaeniopteris*, *Bjuvia* and *Anomozamites*, which may be macromorphologically similar to the *Nilssoniopteris* species from Lunz. Unfortunately, the epidermal anatomy of these forms is often unknown, and renders a more accurate assessment of their affinities a difficult task.

According to Norstog and Nicholls (1997), the cycadophytes comprise two orders of plants, the Cycadales and Bennettitales. Both are quite similar with regard to growth habit and foliage morphology. However, the reproductive organs are distinctly different, which indicates that they are not closely related (Crane 1988; Doyle 2006). Sterile leaves of bennettitaleans and cycadaleans are distinguishable on epidermal features; especially significant is the morphology of the stomatal apparatuses, which are syndetocheilic in the former and haplocheilic in the latter (Florin 1933*a*). The Bennettitales are an enigmatic group of gymnosperms characterized by complex reproductive structures, some of which are not fully understood to date (see Norstog and Nicholls 1997; Rothwell and Stockey 2002; Stockey and Rothwell 2003). The origin and relationships of the Bennettitales to other fossil and extant groups of gymnosperms remain largely elusive. The Lunz flora is important in this context because it contains a remarkable array of male and female cycadophyte reproductive structures (Krasser 1917, 1919; Kräusel 1948, 1949, 1953). Although these have been studied in some detail, no persuasive evidence as to their relationship to the various cycadalean and bennettitalean foliage types has been demonstrated to date. Only a single fertile structure, namely *Dioonitocarpidium* (Schenk, 1867) Rühle von Lilienstern, 1928, has been tentatively correlated with sterile foliage, originally described as *Danaeopsis angustifolia* but later transferred to *Taeniopteris* (Rühle von Lilienstern, 1928). However, Kelber and Hansch (1995) rejected this reconstruction. *Dioonitocarpidium* may represent a macrosporophyll, probably with affinities in the Cycadales (Harris 1961; Kustatscher *et al.* 2004). Kustatscher *et al.* (2004) correlated a *Dioonitocarpidium* specimen from the Ladinian of northern Italy with cycadalean *Bjuvia* foliage. However, both correlations are based solely on co-occurrence of *Dioonitocarpidium* and sterile foliage in the same bedding planes.

The lack of evidence for reconstructing whole-plant taxa in the Lunz flora is in part a result of the fact that only isolated plant parts are preserved; reproductive structures in organic connection to leafy twigs or stems have never been found. Moreover, cycadophyte stems or branches are generally rare in the Lunz flora, and reproductive structures and leaves were not normally persistent, but periodically shed from the source plant as part of the natural life cycle. Consequently, only analyses of the epidermal anatomy of both sterile leaves and reproductive structures from Lunz may provide clues for reconstructing whole-plant taxa. During our re-investigation of the Lunz flora (Pott *et al.* 2005), we have gathered information on the epidermal anatomy of the cycadalean genera *Nilssonia* Brongniart, 1825 (Pott *et al.* 2007*a*) and *Pseudoctenis* Seward, 1911 (Pott *et al.* 2007*b*), and the bennettitalean genera *Nilssoniopteris* (this paper) and *Pterophyllum* (Pott *et al.* 2007*d*). As a result, we now know the epidermal anatomy of all cycadophyte taxa in the Lunz flora. This provides an excellent data set for further research focusing on the assignment of the reproductive structures to their respective foliage. Our approach in the near future will be to analyse the cuticles from the cycadophyte reproductive structures in order to compare these with the epidermal anatomy of the foliage.

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REFERENCES

ANDERSON, J. M. and ANDERSON, H. M. 1989. *Palaeoflora of Southern Africa – Molteno Formation (Triassic), Volume 2 – Gymnosperms*. Balkema, Rotterdam, 567 pp.

ASH, S. R. 1989. The Upper Triassic Chinle flora of the Zuni Mountains, New Mexico. *New Mexico Geological Society Guidebook, 40th Field Conference, South Eastern Colorado Plateau*, pp. 225–230.

BARALE, G., THÉVENARD, F. and ZHOU, Z. 1998. Discovery of *Nilssoniopteris* in the Middle Jurassic Yima Formation of Henan, central China. *Geobios*, **31**, 13–20.

BARNARD, P. D. W. 1965. Flora of the Shemshak Formation. Part 1. Liassic plants from Dorud. *Rivista Italiana di Paleontologia e Stratigrafia*, **71**, 1123–1168.

BARTHLOTT, W. and EHLER, N. 1977. *Raster-Elektronenmikroskopie der Epidermis-Oberflächen von Spermatophyten*. Steiner, Wiesbaden, 105 pp.

BHARDWAJ, D. C. and SINGH, H. P. 1964. An Upper Triassic miospore assemblage from the coals of Lunz, Austria. *Palaeobotanist*, **12**, 28–44.

BLUME. C. L. V. 1833. *De novis quibusdam plantarum familiis expositio et olim iam expositarum enumeration*. Lugduno-Batava, Leiden, 32 pp.

BOYD, A. 2000. Bennettitales from Early Cretaceous floras of West Greenland: *Pterophyllum* and *Nilssoniopteris*. *Palaeontographica, Abteilung B*, **255**, 47–77.

BRONGNIART, A. 1825. Observations sur les végétaux fossiles renfermés dans les grès de Hoer en Scanie. *Annales des Sciences Naturelles*, **4**, 200–224.

—— 1828. *Prodrome d'une Histoire des Végétaux Fossiles*. Levrault, Paris, viii + 823 pp.

CANTRILL, D. J. and HUNTER, M. A. 2005. Macrofossil floras of the Latady Basin, Antarctic Peninsula. *New Zealand Journal of Geology and Geophysics*, **48**, 537–553.

CARUEL, T. 1876. Sulla struttura fiorale e le affinità di varie famiglie dicotiledoni inferiori. *Nuovo Giornale Botanico Italiano*, **11**, 10–24.

CLEAL, C. J. and REES, P. M. 2003. The Middle Jurassic flora from Stonesfield, Oxfordshire, UK. *Palaeontology*, **46**, 739–801.

—— —— ZIJLSTRA, G. and CANTRILL, D. J. 2006. A clarification of the type of *Nilssoniopteris* Nathorst (fossil Gymnospermophyta, Bennettitales). *Taxon*, **55**, 219–222.

CORNET, B. and OLSON, P. E. 1990. *Early to middle Carnian (Triassic) flora and fauna of the Richmond and Taylorsville basins, Virginia and Maryland, U.S.A.* Virginia Museum of Natural History, Martinsville, 83 pp., 21 pls.

CRANE, P. R. 1988. Major clades and relationships in the 'higher' gymnosperms. *In* BECK, C. (ed.). *The origin and evolution of gymnosperms*. Columbia University Press, New York, NY, 504 pp.

DOBRUSKINA, I. A. 1989. The alpine Lunz-Flora – a standard flora for the Carnian Stage of the Triassic. *International Geological Review*, **31**, 1209–1215.

—— 1994. *Triassic floras of Eurasia*. Springer, Wien, 422 pp.

—— 1998. Lunz flora in the Austrian Alps – a standard for Carnian floras. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **143**, 307–345.

DOYLE, J. A. 2006. Seed ferns and the origin of angiosperms. *Journal of the Torrey Botanical Society*, **133**, 169–209.

DUNAY, R. F. and FISHER, M. J. 1978. The Carnian palynofloral succession in the Northern Calcarous Alps, Lunz-am-See, Austria. *Pollen et Spores*, **20**, 177–187.

FAHN, A. and CUTLER, D. F. 1992. Xerophytes. *In* BRAUN, H. J., CARLQUIST, S., OZENDA, P. and ROTH, I. (eds). *Handbuch der Pflanzenanatomie. Spezieller Teil, Band XIII, Teil* 3. Gebrüder Borntraeger, Berlin/Stuttgart, ix + 176 pp.

FEISTMANTEL, O. 1877. Jurassic (Liassic) flora of the Rajmahal Group in the Rajmahal Hills. *Memoirs of the Geological Society of India, Palaeontologia Indica, Series II*, **II**, 53–162.

FLORIN, R. 1933*a*. Studien über die Cycadales des Mesozoikums (Bennettitales, pp. 11–31). *Kungliga Svenska Vetenskapsakademiens Handlingar, Tredje Serien*, **12**, 1–134.

—— 1933*b*. Über *Nilssoniopteris glandulosa* n. sp., eine Bennettitacee aus der Juraformation Bornholms. *Arkiv för Botanik*, **25A**, 1–19.

FONTAINE, W. M. 1883. *Contributions to the knowledge of the Older Mesozoic Flora of Virginia.* Government Printing, Washington, DC, xii + 144 pp., 54 pls.

GNAEDINGER, S. and HERBST, R. 2004. Pteridophylla del Triásico del Norte Chico de Chile. I. El género *Taeniopteris* Brongniart. *Ameghiniana*, **41**, 91–110.

GÖPPERT, H. R. 1843. Ueber die fossilen Cykadeen überhaupt, mit Rücksicht auf die in Schlesien vorkommenden Arten. *Uebersicht der Arbeiten und Veränderungen der Schlesischen Gesellschaft für Vaterländische Kultur*, 114–144.

GOTHAN, W. and WEYLAND, H. 1973. *Lehrbuch der Paläobotanik*. BLV, München, 677 pp.

HARRIS, T. M. 1932. The fossil flora of Scoresby Sound East Greenland – Part 3: Caytoniales and Bennettitales. *Meddelelser om Grønland*, **85**, 1–133.

—— 1946. Liassic and Rhaetic plants collected in 1936–38 from East Greenland. *Meddelelser om Grønland*, **114**, 1–40.

—— 1961. The fossil cycads. *Palaeontology*, **4**, 313–323.

—— 1969. *The Yorkshire Jurassic Flora III*. Trustees of the British Museum (Natural History), London, vi + 186 pp., 7 pls.

HORNUNG, T. and BRANDNER, R. 2005. Biochronostratigraphy of the Reingraben turnover (Hallstatt facies belt): local black shale events controlled by regional tectonics, climatic change and plate tectonics. *Facies*, **51**, 460–479.

KELBER, K. P. and HANSCH, W. 1995. Keuperpflanzen. Die Enträtselung einer über 200 Millionen Jahre alten Flora. *Museo*, **11**, 1–157.

KERP, H. 1990. The study of fossil gymnosperms by means of cuticular analysis. *Palaios*, **5**, 548–569.

—— and KRINGS, M. 1999. Light microscopy of cuticules. 52–56. *In* JONES, T. P. and ROWE, N. P. (eds). *Fossil plants and spores: modern techniques.* Geological Society, London, 396 pp.

KRASSER, F. 1909*a*. Die Diagnosen der von Dionysius Stur in der obertriadischen Flora der Lunzerschichten als Marattiaceenarten unterschiedenen Farne. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Wien, Abteilung 1*, **118**, 13–43.

—— 1909*b*. Zur Kenntnis der fossilen Flora der Lunzer Schichten. *Jahrbuch der Kaiserlich-Königlich Geologischen Reichsanstalt*, **59**, 101–126.

—— 1917. Studien über die fertile Region der Cycadophyten aus den Lunzer-Schichten: Mikrosporophylle und männliche Zapfen. *Denkschriften der Kaiserlichen Akademie der Wissenschaften (Wien), Mathematisch-Naturwissenschaftliche Klasse*, **94**, 489–553.

—— 1919. Studien über die fertile Region der Cycadophyten aus den Lunzer Schichten: Makrosporophylle. *Denkschriften der Kaiserlichen Akademie der Wissenschaften (Wien), Mathematisch-Naturwissenschaftliche Klasse*, **97**, 1–32.

KRÄUSEL, R. 1920. Über einige Pflanzen aus dem Keuper von Lunz (Nieder-Österr.). *Jahrbuch der Preußischen Geologischen Landesanstalt*, **41**, 192–209.

—— 1943. Die Gingkophyten der Trias von Lunz in Niederösterreich und von Neue Welt bei Basel. *Palaeontographica, Abteilung B*, **87**, 59–93.

—— 1948. *Sturiella langeri* nov. gen., nov. sp., eine Bennettitee aus der Trias von Lunz (Nieder-Österreich). *Senckenbergiana*, **29**, 141–149.

—— 1949. Koniferen und andere Gymnospermen aus der Trias von Lunz, Nieder-Österreich. *Palaeontographica, Abteilung B*, **89**, 35–82.

——1953. Ein neues *Dioonitocarpidium* aus der Trias von Lunz. *Senckenbergiana*, **34**, 105–108.

—— LESCHIK, G. 1955. Die Keuperflora von Neuewelt bei Basel – I. Koniferen und andere Gymnospermen. *Schweizer Paläontologische Abhandlungen*, **71**, 1–27.

—— and SCHAARSCHMIDT, F. 1966. Die Keuperflora von Neuewelt bei Basel – IV. Pterophyllen und Taeniopteriden. *Schweizer Paläontologische Abhandlungen*, **84**, 3–44.

KRINGS, M. and KERP, H. 2000. A contribution to the knowledge of the pteridosperm genera *Pseudomariopteris* Danzé-Corsin nov. emend. and *Helenopteris* nov. gen. *Review of Palaeobotany and Palynology*, **111**, 145–195.

——KLAVINS, S. D., DIMICHELE, W. A., KERP, H. and TAYLOR, T. N. 2005. Epidermal anatomy of *Glenopteris splendens* Sellards nov. emend., an enigmatic seed plant from the Lower Permian of Kansas (U.S.A.). *Review of Palaeobotany and Palynology*, **136**, 159–180.

KUSTATSCHER, E., WACHTLER, M. and VAN KONIJNENBURG-VAN CITTERT, J. H. A. 2004. A number of additional and revised taxa from the Ladinian flora of the Dolomites, northern Italy. *Geo.Alp*, **1**, 57–69.

LEUTHARDT, F. 1901. Beiträge zur Kenntnis der Flora und Fauna der Lettenkohle von Neuewelt bei Basel. *Eclogae Geologicae Helvetiae*, **7**, 125–128.

—— 1903. Die Keuperflora von Neuewelt bei Basel – I. Teil Phanerogamen. *Abhandlungen der Schweizer Paläontologischen Gesellschaft*, **30**, 1–23.

LINDLEY, J. and HUTTON, W. 1831–37. *The fossil flora of Great Britain, or Figures and descriptions of the vegetable remains found in a fossil state in this country. Volumes I–III.* James Ridgway and Sons, London, 49 pp. (Vol. I), 54 pp. (Vol. II), 72 pp. (Vol. III) + Atlas of 76 pls.

LUNDBLAD, A. B. 1950. Studies in the Rhaeto-Liassic floras of Sweden. I. Pteridophyta, Pteridospermae and Cycadophyta from the mining district of NW Scania. *Kungliga Svenska Vetenskapsakademiens Handlingar, Fjärde Serien*, **1**, 1–82.

MARTENS, P. 1971. *Les Gnétophytes*. Gebrüder Borntraeger, Berlin, 295 pp.

MOTT, K. A., GIBSON, A. C. and O'LEARY, J. W. 1982. The adaptive significance of amphistomatic leaves. *Plant, Cell and Environment*, **5**, 455–460.

NATHORST, A. G. 1880. Berättelse, afgifven till Kongl. Vetenskaps-Akademien, om en med understöd af allmänna medel utföd vetenskaplig resa till England. *Kongliga Vetenskapsakademiens Förhandlingar*, **5**, 23–84.

——1909. Über die Gattung *Nilssonia* Brongn. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **43**, 3–37.

NORSTOG, K. J. and NICHOLLS, T. J. 1997. *The biology of the Cycads*. Cornell University Press, Ithaca, NY, xi + 363 pp.

OLDHAM, T. and MORRIS, J. 1863. Fossil flora of the Rajmahal Series in the Rajmahal Hills. *Memoirs of the Geological Society of India, Palaeontologia Indica, Series II*, 1–52.

PARKHURST, D. F. 1978. The adaptive significance of stomatal occurrence on one or both surfaces of leaves. *Journal of Ecology*, **66**, 367–383.

—— WONG, S. C., FARQUHAR, G. D. and COWAN, I. R. 1988. Gradients of intercellular CO_2 levels across the leaf mesophyll. *Plant Physiology*, **86**, 1032–1037.

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

PHILLIPS, J. 1829. *Illustrations of the geology of Yorkshire etc. Part 1. The Yorkshire coast*. xii + 184, pp., 14 pls.

POTT, C., KERP, H. and KRINGS, M. 2005. Kutikularanalyse triassischer Samenpflanzen von Lunz, Niederösterreich. *Berichte des Institutes für Erdwissenschaften der Karl-Franzens-Universität Graz*, **10**, 95–96.

—— —— —— 2007*a*. Morphology and epidermal anatomy of *Nilssonia* (cycadalean foliage) from the Upper Triassic of Lunz (Lower Austria). *Review of Palaeobotany and Palynology*, **143**, 197–217.

—— —— ——2007*b*. *Pseudoctenis cornelii* nov. spec. (cycadalean foliage) from the Carnian (Upper Triassic) of Lunz, Lower Austria. *Annalen 2006 des Naturhistorischen Museums Wien*, **108A**, 39–55.

—— KRINGS, M. and KERP, H. 2007*c*. A surface microrelief on the leaves of *Glossophyllum florinii* (?Ginkgoales) from the Upper Triassic of Lunz, Austria. *Botanical Journal of the Linnean Society*, **153**, 87–95.

——VAN KONIJNENBURG-VAN CITTERT, J. H. A., KERP, H. and KRINGS, M. 2007*d*. Revision of the *Pterophyllum* species (Cycadophytina: Bennettitales) in the Carnian (Late Triassic) flora from Lunz, Lower Austria. *Review of Palaeobotany and Palynology*, doi: 10.1016/j.revpalbo.2007.03.005.

ROGERS, W. B. 1843. On the age of the coal rocks of eastern Virginia. *Reports of the First, Second, and Third Meetings of the Association of American Geologists and Naturalists, at Philadelphia in 1840 and 1841, and at Boston in 1842. Embracing its Proceedings and Transactions*, 298–316.

ROTHWELL, G. W. and STOCKEY, R. A. 2002. Anatomically preserved *Cycadeoidea* (Cycadeoidaceae), with a reevaluation of systematic characters for the seed cones of Bennettitales. *American Journal of Botany*, **89**, 1447–1458.

RÜHLE VON LILIENSTERN, H. 1928. *Dioonites pennaeformis* Schenk, eine fertile Cycadee aus der Lettenkohle. *Paläontologische Zeitschrift*, **10**, 91–107.

SADOVNIKOV, G. N. 1989. *Taeniopteris*, *Nilssoniopteris* and *Nilssonia* in the late Triassic flora of Iran. *Paleontological Journal*, **23**, 95–100.

SCHAARSCHMIDT, F. 1973. Pflanzenfossilien in ungewöhnlichem Licht. *Natur und Museum*, **103**, 247–253.

SCHENK, A. 1865–67. *Die Fossile Flora der Grenzschichten des Keupers und Lias Frankens*. Kreidel, Wiesbaden, 232 pp., 45 pls.

—— 1866. Über die Flora der schwarzen Schiefer von Raibl. *Würzburger Naturwissenschaftliche Zeitschrift*, **6**, 10–20.

SCHIMPER, W. P. 1869. *Traité de Paléontologie Végétale. Tome Premier*. Baillière et Fils, Paris, 738 pp., 56 pls.

—— 1870–72. *Traité de Paléontologie Végétale. Tome Second*. Baillière et Fils, Paris, 968 pp., 38 pls.

SCHWEITZER, H. J. and KIRCHNER, M. 2003. Die rhätojurassischen Floren des Iran und Afghanistans. 13. Cycadophyta III. Bennettitales. *Palaeontographica, Abteilung B*, **264**, 1–166.

SEWARD, A. C. 1911. The Jurassic flora of Sutherland. *Transactions of the Royal Society of Edinburgh*, **47**, 643–709.

STOCKEY, R. A. and ROTHWELL, G. W. 2003. Anatomically preserved *Williamsonia* (Williamsoniaceae): evidence for bennettitalean reproduction in the Late Cretaceous of western North America. *International Journal of Plant Science*, **164**, 251–262.

STUR, D. 1885. Die obertriadische Flora der Lunzer-Schichten und des bituminösen Schiefers von Raibl. *Denkschriften der Kaiserlichen Akadademie der Wissenschaften (Wien)*, **3**, 93–103.

SZE, H. C. and LEE, H. H. 1952. Jurassic plants from Szechuan. *Palaeontologica Sinica*, **135**, 16–38.

WACHTLER, M. and VAN KONIJNENBURG-VAN CITTERT, J. H. A. 2000. The fossil flora of the Wengen Formation (Ladinian) in the Dolomites (Italy). *Beiträge zur Paläontologie*, **25**, 105–141.

WATSON, J. and CUSACK, H. A. 2005. Cycadales of the English Wealden. *Monograph of the Palaeontographical Society* (Publication no. 622, issued as part of Vol. 158 for 2004), 189 pp., + 10 pls.

—— and SINCOCK, C. A. 1992. Bennettitales of the English Wealden. *Monograph of the Palaeontographical Society* (Publication no. 588, issued as part of Vol. 145 for 1991), 228 pp., + 23 pls.

WIELAND, G. R. 1916. American fossil cycads, II. Taxonomy. *Carnegie Institution of Washington Publication*, **34**, 1–277.

YABE, H. 1925. Notes on some Mesozoic plants from Japan, Korea and China, in the collection of the Institute of Geology and Paleontology of Tôhoku Imperial University. *Scientific Reports of the Tôhoku Imperial University, Sendai, Japan, Second Series (Geology)*, **7**, 1–28.

ZEILLER, R. 1903. *Flore fossile des gîtes de charbon du Tonkin.* Ministère des travaux publics, Paris, 328 pp. + atlas (56 pls).

CHAPTER 4

Circinate vernation in cycadeoidalean foliage of the genus *Pterophyllum*

Christian Pott & Michael Krings

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Abstract.—The Cycadeoidales are Mesozoic gymnosperms with entire or pinnate leaves and complex reproductive structures. Although many forms superficially resemble cycads, particularly with regard to foliage macromorphology, cycadeoidaleans and cycads are today believed to be not closely related. Cuticular analysis of cycadeoidalean foliage from the Carnian (Upper Triassic) of Austria reveals that *Pterophyllum filicoides* displays circinate vernation in the form of inwardly coiled leaf segments, which are strikingly similar to immature leaf segments seen in extant *Cycas* species. This discovery represents the first record of circinate vernation in the Cycadeoidales, and may suggest that cycadeoidalean leaves resemble those of cycads not only with regard to macromorphology but also development.

Keywords.—Cycadeoidales; Cycadales; fossil foliage; cuticular analysis; Lunz (Austria); Carnian (Upper Triassic); ontogeny

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First record of circinate vernation in bennettitalean foliage

Christian Pott, Münster and **Michael Krings,** München

With 2 figures

Pott, C. & Krings, M. (2007): First record of circinate vernation in bennettitalean foliage. – N. Jb. Geol. Paläont. Abh., **245**: 315–321; Stuttgart.

Abstract: The Bennettitales are Mesozoic gymnosperms with entire or pinnate leaves and complex reproductive structures. Although many forms superficially resemble cycads, particularly with regard to foliage macromorphology, bennettitaleans and cycads are not believed to be closely related at this time. Cuticular analysis of bennettitalean foliage from the Carnian (Upper Triassic) of Austria reveals that *Pterophyllum filicoides* displays circinate vernation in the form of inwardly coiled leaf segments, which are strikingly similar to immature leaf segments seen in extant *Cycas* species. This discovery represents the first record of circinate vernation in the Bennettitales and may suggest that bennettitalean leaves resemble those of cycads not only with regard to macromorphology but also development.

Key words: *Pterophyllum,* Carnian, Triassic, cuticular analysis, vernation, Bennettitales, Cycadales, Lunz (Austria), ontogeny.

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1. Introduction

The Bennettitales Engler (= Cycadeoidales Arnold) are Mesozoic (Triassic–Cretaceous) gymnosperms with entire or simple pinnate leaves and complex reproductive structures. The origin of the Bennettitales and relationships to the other lineages of fossil and extant seed plants remain controversial (Norstog & Nicholls 1997; Doyle 2006), due in part to the fact that many of the reproductive structures attributed to the Bennettitales continue to be incompletely understood (Norstog & Nicholls 1997; Rothwell & Stockey 2002; Stockey & Rothwell 2003). It was once widely believed that the Bennettitales are close relatives of the Cycadales DuMortier (e. g. Morris 1841; Miquel 1851; Steinmann 1903). More recently, however, a number of fundamental differences between cycads and bennettitaleans, notably with regard to the reproductive biology, have been elaborated, which suggest that the two groups of plants are not closely related (Schuster 1931; Taylor & Taylor 1993). Cladistic analyses generally support this hypothesis (e. g. Nixon et al. 1994; Rothwell & Serbet 1994; Doyle 2006; Hilton & Bateman 2006). Nevertheless, the Bennettitales and Cycadales are very similar with regard to foliage macromorphology and, as a result, the sterile leaves of many fossil bennettitaleans and cycadaleans are only distinguishable based on epidermal features; especially significant is stomatal morphology, which is syndetocheilic in the former and haplocheilic in the latter group of plants (Florin 1933). In syndetocheilic stomata the guard and subsidiary cells all have their origin from a single initial, while in haplocheilic

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stomata guard and subsidiary cells originate from different initials (TAYLOR & TAYLOR 1993).

The macromorphological similarities of cycadalean and bennettitalean foliage raise the question as to whether these resemblances are superficial and restricted to overall architecture, or that the leaves of both groups of plants also display similar development. However, comments about leaf development in the Bennettitales are rare in the literature and to date are based exclusively on macroscopic observations. For example, particularly small leaves assigned to *Pterophyllum* BRONGNIART have variously been regarded as immature based on the difference in size compared to large *Pterophyllum* leaves in the same bedding planes (e.g. HEER 1877; KRASSER 1909; KRÄUSEL & SCHAARSCHMIDT 1966).

Recent systematic cuticular analysis of the bennettitalean foliage fossils from the Carnian (Late Triassic) flora of Lunz in Austria has produced new information about leaf development in the Bennettitales in the form of immature *Pterophyllum filicoides* (SCHLOTHEIM) ZEILLER leaves displaying circinate vernation similar to that seen in certain extant cycads. Although the discovery of circinate vernation in *Pterophyllum* is not totally unexpected because it is a condition shared by many groups of 'more primitive plants', it has not been previously documented in bennettitaleans.

2. Material and methods

The fossils come from the area around Lunz-am-See, a city located in the Northern Calcareous Alps of Lower Austria, approximately 100 km west of Vienna. They were collected during the late 19th and early 20th centuries, mainly by J. HABERFELNER, a mining foreman from Lunz-am-See. The fossils occur in the "Lunzer Sandstein", which is part of the Lunz Formation (= Lunzer Schichten). Recent palynological studies indicate that the Lunz Formation is late Julian (Carnian, Late Triassic) in age (ROGHI 2004). Detailed information about the geological setting, sedimentology and palaeontology of the Lunz Formation can be found in DUNAY & FISHER (1978) and DOBRUSKINA (1998).

A total of 246 compression fossils of *Pterophyllum filicoides* were studied macroscopically and by cuticular analysis according to procedures outlined in KERP & KRINGS (1999). In addition, bulk macerations (cf. HARRIS 1926) of smaller slabs containing remains of *P. filicoides* were conducted. More than 300 cuticle slides were prepared and analysed microscopically. Cuticles were analysed with a Leitz Diaplan microscope and photographed with a Nikon DS-5M digital camera. Specimens and cuticle slides are stored in the collection of the Museum of Natural History (NHMW), Vienna, Austria; accession numbers are indicated in the figure caption.

3. Results

Pterophyllum filicoides is among the most abundant fossils in the Lunz flora. Leaves are once pinnate and display considerable size range; the smallest complete leaves are 15 cm long and 4.5 cm wide and have a relatively narrow rachis (Fig. 1A), while the largest specimens measure 50 cm long and 20 cm wide and possess a robust rachis (Fig. 1B). Corresponding epidermal anatomy establishes that all these leaves belong to *P. filicoides* (see POTT et al. (in press), for detailed information on the architecture and epidermal anatomy of *P. filicoides*). None of the compression fossils and cuticles obtained thereof shows evidence of circinate vernation. However, one of the bulk macerations yielded some 30 leaf segments displaying circinate vernation, i.e. the distal portion is inwardly coiled up to four times (Fig. 1C-F). Most of the specimens represent detached segments with coiled distal

Fig. 1. Macromorphological and epidermal features of *Pterophyllum* leaves. **A.** Small *Pterophylulm filicoides* leaf; specimen NHMW 1887/I/0027; bar = 10 mm. **B.** Large and mature *P. filicoides* leaf; specimen NHMW 1887/I/0033; bar = 10 mm. **C.** Reassembled immature *P. filicoides* leaf; bracket indicates portion of rachis with coiled leaf segments in organic connection; slides NHMW 2006B0008/0010/0001–0007, 0009–0010, 0016–0017, 0019–0021, 0026, 0029–0030, 0034, 0041, 0045, 0047–0048, 0051, 0053, 0055; bar = 5 mm. **D-F.** Inwardly coiled leaf segments; slides (D) NHMW 2006B0008/0010/0030, (E) NHMW 2006B0008/0010/0001, (F) NHMW 2006B0008/0010/0003; bars = 500 µm. **G.** adaxial (upper half) and abaxial (lower half) cuticle of *P. filicoides*; slide NHMW 2006B0008/0010/0014; bar = 100 µm. **H.** Detail of Fig. 1F, showing adaxial (above) and abaxial (below) cuticle and hence establishes that the leaves are inwardly coiled; slide NHMW 2006B0008/0010/0003; bar = 100 µm.

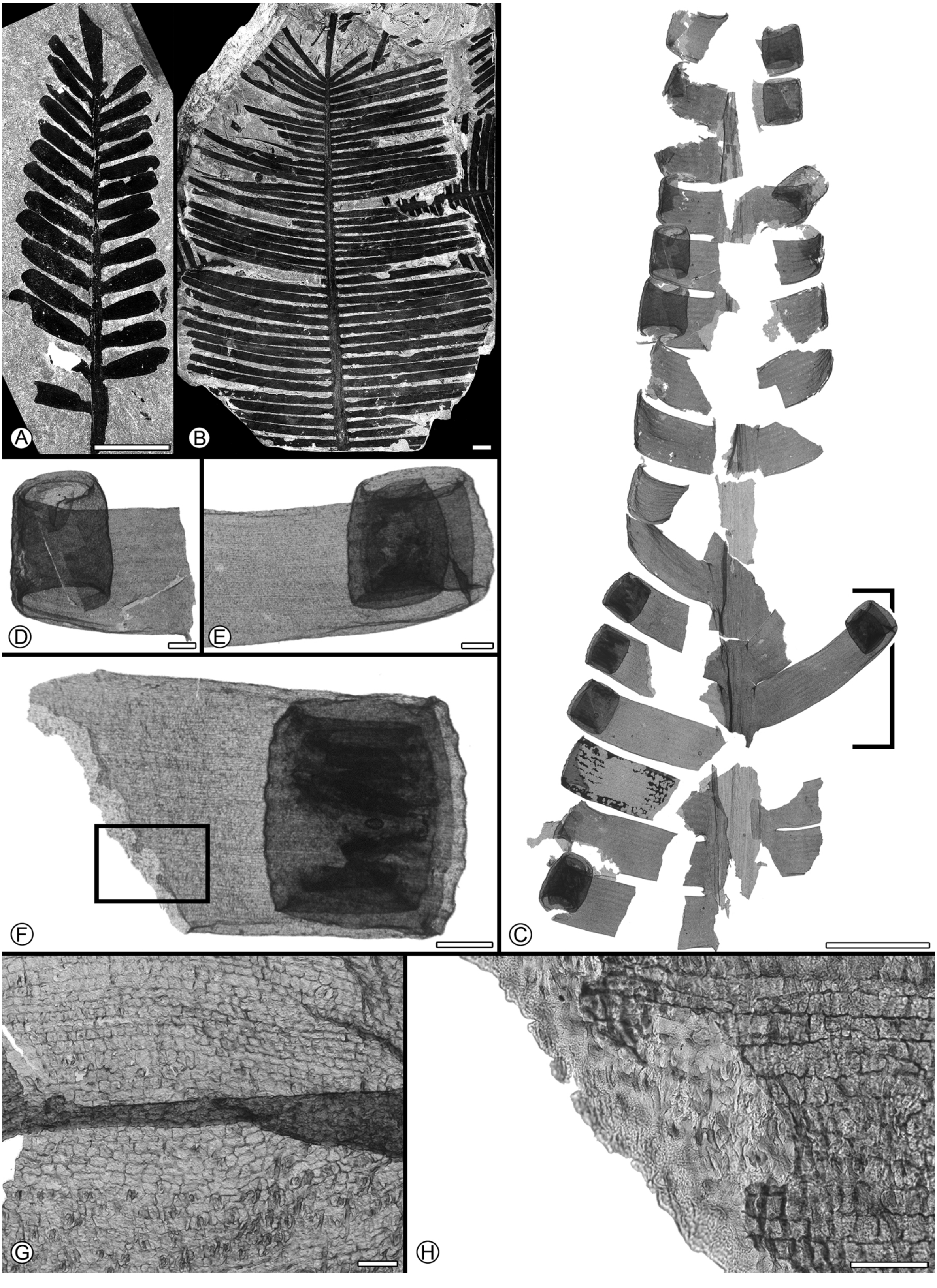

Fig. 1 (Legend see p. 316)

portions, but some show several coiled segments still attached to portions of a rachis up to 2.5 mm wide (Fig. 1C, bracket). Since all of the coiled leaf segments come from a single, relatively small slab, they probably belong to a single immature leaf. Part of this leaf is reassembled in Figure 1C based on the most likely arrangement (e.g. with regard to rachis width) of the fragments obtained from that slab. The largest immature leaf segments are 7.5 mm long and 2.5 mm wide and thus considerably smaller than the segments seen in large, full-grown leaves (up to 102 mm long and 9 mm wide) of the same species. Moreover, spacing of the segments appears to be slightly closer than that seen in full-grown *P. filicoides* leaves. The immature leaf segments are slightly inclined toward the leaf tip (Fig. 1C), while, in mature leaves, the segments are usually arranged more or less perpendicularly to the rachis (Fig. 1B). Reassembly of the immature leaf (Fig. 1C) suggests that uncoiling of the segments is more advanced proximally in the leaf, while distally positioned segments are still largely coiled. The epidermal anatomy of the coiled leaf segments (Fig. 1G-H) corresponds to that seen in mature *P. filicoides* leaves. Leaves are amphistomatic; distinct costal and intercostal areas are visible on both sides. Adaxial and abaxial side of the leaf can be clearly distinguished by the number of stomata; while stomata are rare on the adaxial side (Fig. 1G, upper half of image), they occur in abundance in the abaxial intercostal fields (Fig. 1G, lower half of image). Stomata are syndetocheilic and morphologically identical on both sides of the leaf.

4. Discussion

Pterophyllum filicoides from the Upper Triassic of Lunz provides the first evidence for circinate vernation in bennettitalean foliage. Epidermal anatomy indicates that the leaves are inwardly curved. Coiling is compact and regular, which substantiates that the fossils do not represent fragments of desiccated and/or wilted mature leaves, but rather were immature at the time of fossilisation. The former would result in recurved leaf segments or an irregular inward curvature or coiling of the segments. The immature leaf segments of *P. filicoides* are strikingly similar to leaf segments seen in immature (elongating) leaves of certain extant cycads, e.g. species in the genus *Cycas* L. (cf. NORSTOG & NICHOLLS 1997: fig. 2.20-2.22). As in *Cycas,* uncoiling of the *P. filicoides* leaf segments seems to initially occur in the proximal

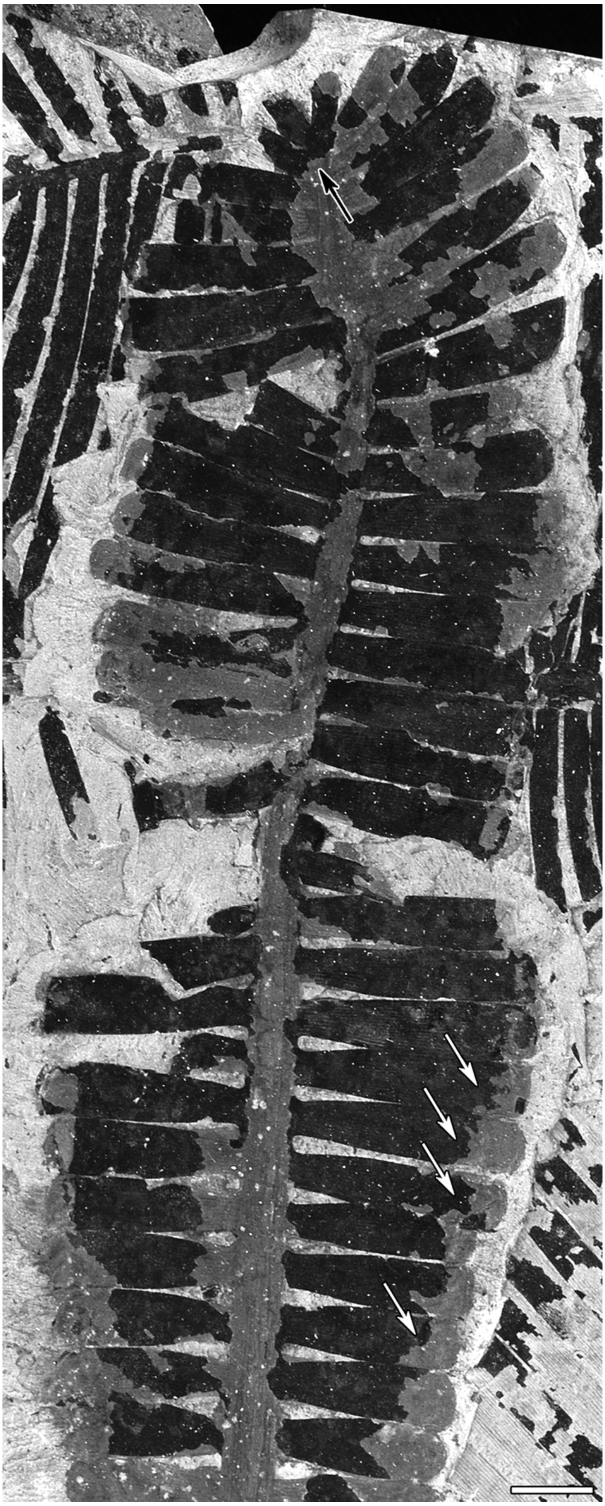

Fig. 2. Small, probably immature *Pterophyllum* leaf; black arrow indicates short and stout terminal segments; white arrows indicate consistent absence of coaly substance on the distal parts of lateral segments; specimen NHMW 1887/I/0030; bar = 10 mm.

portion of the leaf and subsequently proceed to the upper segments.

Large and mature *Pterophyllum filicoides* leaves (Fig. 1B) are up to 50 cm long and characterised by a robust rachis up to 15 mm wide. Several of the cuticle preparations contain coiled leaf segments attached to a relatively delicate rachis (Fig. 1C, bracket). Since these cuticles were obtained exclusively by bulk maceration, it cannot be determined whether the rachis of immature leaves is generally delicate and becomes robust during elongation and maturation, or the portions of immature leaves with delicate rachises come from a small leaf, perhaps produced by a very young *P. filicoides* plant. It is interesting in this context that particularly small *Pterophyllum* leaves have historically often been interpreted as immature (see above). However, this interpretation is based exclusively on the size difference between the small and large *Pterophyllum* leaves of similar architecture that occur in the same bedding planes, but does not include the presence of special immaturity features such as coiled leaf segments or incomplete development in the small leaves. Our study shows that circinate vernation is just barely recognisable in hand specimens. Rather, cuticles are required to determine immaturity, and they reveal that many of the small *Pterophyllum* leaves in the Lunz flora are mature. On the other hand, particularly small *Pterophyllum* leaves have also been regarded as belonging to small-leaved species by various authors (e.g. Heer 1877; Stur 1885; Krasser 1909). Based on cuticular analysis, Pott et al. (in press) demonstrate that several of the small *Pterophyllum* leaves from Lunz belong to *P. filicoides*. The fact that they are several times smaller than the large leaves of the same species suggests that heterophylly may have been a characteristic feature of *P. filicoides* and perhaps bennettitaleans in general.

Heterophylly may arise by two fundamentally different mechanisms (Steeves & Sussex 1989): The first is an expression of programmed ontogenetic changes in leaf size and shape (i.e. heteroblastic development), while the second includes the occurrence of different leaves as a result of adaptation. Because the mechanisms underlying heterophylly in *Pterophyllum filicoides* remain elusive, it is impossible to assign a specific functional or ecological significance to intraspecific variation of leaf size in these plants. For example, the small leaves may have been produced by juvenile *P. filicoides* plants and thus reflect heteroblastic development. On the other hand, it is also possible to envision that, in favourable conditions, mature *P. filicoides* plants produced large leaves, while small leaves only developed during (intermittent) periods of unfavourable conditions where they were more advantageous than large leaves. Small leaves were perhaps produced during periods of drought in order to minimise water loss via transpiration but, at the same time, maintain a minimum of photosynthetic activity.

Since distally coiled leaf segments have been documented only in cuticle preparations and have not yet been recognised macroscopically, it is interesting to determine if there are any macroscopical clues that may help distinguish immature from small mature *Pterophyllum* leaves based on hand specimens alone. One such feature is perhaps the degree of development of the terminal leaf segments. In some of the small leaves, these segments appear comparatively short and stout (Fig. 2, black arrow), while in others they look like miniature versions of the terminal leaf segments present in large mature leaves (Fig. 1A). Moreover, in some of the compressions, the coaly substance covering the distal portion of the leaf segments is consistently missing, while elsewhere in the segments the coaly film is well-preserved (Fig. 2, white arrows). However, it cannot be determined at present whether this is due to breaking off of the coiled distal portions of the segment or merely represents a preservational artefact.

Another question concerns the distribution of circinate vernation in the various lineages of bennettitaleans. In extant cycads, the group of plants that perhaps represents the best modern analogue with regard to leaf development, the pattern of vernation greatly varies among genera (Norstog & Nicholls 1997). The vernation pattern documented for *Pterophyllum filicoides* corresponds best to that seen in extant *Cycas* species. However, it cannot be determined at present whether the rachis in *P. filicoides* was erect, inflexed or reflexed on emergence. The fact that vernation greatly varies among cycad genera argues against proposing circinate vernation for all bennettitalean foliage types. Since evidence for coiled bennettitalean rachises has not been produced to date, we speculate that circinate vernation in these plants was perhaps restricted to the leaf segments, but did not include the rachis and thus may have occurred exclusively in pinnate leaves such as *Pterophyllum,* whereas entire foliage types (e.g. *Nilssoniopteris* Nathorst) were more likely conduplicately folded in the leaf bud.

5. Concluding remarks

Circinate vernation occurs in the Late Triassic bennettitalean foliage taxon *Pterophyllum filicoides* and appears to be similar to that seen in certain extant cycads. This discovery actually is not surprising since circinate vernation is a feature shared by many groups of 'more primitive' plants; nonetheless, circinate vernation has not previously been documented for bennettitaleans. The data presented here provide a template to not only interpret isolated parts of these plants from other floras with regard to morphology and systematic affinities, but also function and, in some instances, relationships to stages of the growth of the plants. This approach offers a new avenue of investigation of fossil plants based on hitherto underrepresented structural and developmental features.

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References

Dobruskina, I. A. (1998): Lunz flora in the Austrian Alps – a standard for Carnian floras. – Palaeogeography, Palaeoclimatology, Palaeoecology, **143**: 307-345.

Doyle, J. A. (2006): Seed ferns and the origin of angiosperms. – Journal of the Torrey Botanical Society, **133**: 169-209.

Dunay, R. F. & Fisher, M. J. (1978): The Carnian palynofloral succession in the Northern Calcarous Alp, Lunz-am-See, Austria. – Pollen et Spores, **20**: 177-187.

Florin, R. (1933): Zur Kenntnis der Spaltöffnungsapparate der Bennettitales. – Kungliga Svenska Vetenskapsakademiens Handlingar, Tredje Serien, **12**: 11-31.

Harris, T. M. (1926): Note on a new method for the investigation of fossil plants. – New Phytologist, **25**: 58-60.

Heer, O. (1877): Flora Fossilis Helvetiae. – VIII + 182 pp.; Zürich (J. Wurster & Comp.).

Hilton, J. & Bateman, R. M. (2006): Pteridosperms are the backbone of seed-plant phylogeny. – Journal of the Torrey Botanical Society, **133**: 119-168.

Kerp, H. & Krings, M. (1999): Light microscopy of fossil cuticules. – In: T. P. Jones & N. P. Rowe (Eds.): Fossil Plants and Spores: Modern Techniques, p. 52-56; London (The Geological Society).

Krasser, F. (1909): Zur Kenntnis der fossilen Flora der Lunzer Schichten. – Jahrbuch der kaiserlich-königlich geologischen Reichsanstalt, **59**: 1-26.

Kräusel, R. & Schaarschmidt, F. (1966): Die Keuperflora von Neuewelt bei Basel, IV., Pterophyllen und Taeniopteriden. – Schweizerische Paläontologische Abhandlungen, **84**: 3-44.

Miquel, F. A. W. (1851): Over de rangschikking der fossiele Cycadaceae. – Tijdschrift voor de wisen natuurkundige Wetenschapen, **4**: 205-227.

Morris, J. (1841): Remarks upon the recent and fossil Cycadaceae. – The Annals and Magazine of Natural History, Zoology, Botany and Geology, **7**: 110-120.

Nixon, K. C., Crepet, W. L., Stevenson, D. & Friis, E M. (1994): A reevaluation of seed plant phylogeny. – Annals of the Missouri Botanical Garden, **81**: 484-533.

Norstog, K. J. & Nicholls, T. J. (1997): The Biology of the Cycads. – XIII + 365 pp.; Ithaca (Cornell University Press).

Pott, C., Van Konijnenburg-van Cittert, J. H. A., Kerp, H. & Krings, M. (in press): Revision of the *Pterophyllum* species (Cycadophytina: Bennettitales) in the Carnian (Late Triassic) flora from Lunz, Lower Austria. – Review of Palaeobotany and Palynology, doi:10.1016/j.revpalbo.2007.03.005.

Roghi, G. (2004): Palynological investigations in the Carnian of the Cave del Predil area (Julian Alps, NE Italy). – Review of Palaeobotany and Palynology, **132**: 1-35.

Rothwell, G. W. & Serbet, R. (1994): Lignophyte phylogeny and the evolution of spermatophytes: A numerical cladistic analysis. – Systematic Botany, **19**: 443-482.

Rothwell, G. W. & Stockey, R. A. (2002): Anatomically preserved *Cycadeoidea* (Cycadeoidaceae), with a reevaluation of systematic characters for the seed cones of Bennettitales. – American Journal of Botany, **89**: 1447-1458.

Schuster, J. (1931): Über das Verhältnis der systematischen Gliederung, der geographichen Verbreitung und der paläontologischen Entwicklung der Cycadeen – Teil Trias. – Botanisches Jahrbuch, **64**: 189-197.

Steeves, T. A. & Sussex, I. M. (1989): Patterns in Plant Development, 2nd edition. – XVI+388 pp.; Cambridge (Cambridge University Press).

Steinmann, G. (1903): Einführung in die Paläontologie. – 466 pp.; Leipzig (Engelmann).

Stockey, R. A. & Rothwell, G. W. (2003): Anatomically preserved *Williamsonia* (Williamsoniaceae): Evidence for bennettitalean reproduction in the Late Cretaceous of Western North America. – International Journal of Plant Sciences, **164**: 251-262.

Stur, D. (1885): Die obertriadische Flora der Lunzer-Schichten und des bituminösen Schiefers von Raibl. – Denkschriften der kaiserlichen Akademie der Wissenschaften (Wien), **3**: 93-103.

TAYLOR, T. N. & TAYLOR, E. L. (1993): The Biology and Evolution of Fossil Plants. – XXII + 982 pp.; Englewood Cliffs (Prentice Hall).

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Addresses of the authors:

CHRISTIAN POTT, Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, D-48143 Münster, Germany;
E-mail: christian.pott@uni-muenster.de.

MICHAEL KRINGS, Bayerische Staatssammlung für Paläontologie und Geologie und GeoBio-Center^{LMU}, Richard-Wagner-Straße 10, D-80333 Munich, Germany;
E-mail: m.krings@lrz.uni-muenchen.de.

SECTION II — CYCADALES

Even if the first cycad species was validly described by Linnæus (1753, p. 1188) (i.e. *Cycas circinalis*), representatives of this group were already known to science since 1682 when H. A. van Rheede tot Draakestein figured a specimen from the Malabar coast, Kerala, India (Van Rheede tot Draakestein, 1682, pl. 19). However, the order Cycadales was not established until 1829 (Dumortier 1829). Recently, Cycadales comprise about 305 extant species and a number of extinct genera and species (Hill et al. 2004). The first widely accepted true cycads are known from the Triassic, although several possible cycadalean forms were described from the Carboniferous and Permian (e.g. Zhu Jia-Nan & Du Xiang-Ming 1981; Gao Zhi-Feng & Thomas 1989a, 1989b). Nevertheless, cycadalean foliage is relatively rare in pre-Carnian strata. Cycadaleans reported from pre-Carnian localities have to be addressed very carefully because cuticles are often not preserved or unknown.

Living cycads mainly thrive in dry habitats in tropical areas between 35° N and 35° S. The genus *Cycas* is the only with a broad geographical range. It can be used to infer that a tendency for living in the upper and lower tropics is present in cycads. This is likely to assume because these areas are indicated by a drier climate with relatively cool winters. Cycads require some rainfall, but appear to be partly xerophytic. Some are known to survive in semi-desert climates, and to grow in sand or on rock. Some cycad species are also able to grow in full sun or shade, and some are salt tolerant.

CHAPTER 5

Morphology and epidermal anatomy of *Nilssonia* (cycadalean foliage) from the Upper Triassic of Lunz (Lower Austria)

Christian Pott, Hans Kerp & Michael Krings

Review of Palaeobotany and Palynology 143: 197–217 (2007)

Abstract.—The Carnian flora from Lunz (Lower Austria) ranks among the richest and most diverse fossil floras from the Upper Triassic. It is one of the first modern Triassic floras with bennettitaleans. Although this flora is often referred to in the literature, modern taxonomic studies are mostly absent; only some of the reproduction structures have been studied in detail. Many of the plant remains yield excellently preserved cuticles. During a systematic study of the *Pterophyllum* leaves from Lunz, it appeared that several species previously accommodated in that taxon, have to be transferred to other genera. This paper deals with four species that are transferred to *Nilssonia* (cycadalean foliage); the macromorphology and epidermal anatomy are described and discussed. The following new combination is introduced: *Nilssonia riegeri* (Stur ex Krasser 1909) nov. comb. Two new species are described (i.e. *Nilssonia lunzensis* and *N. neuberi*) based on material originally mentioned in a species list as *Ctenis lunzensis* Stur nom. nud. and *Pterophyllum neuberi* Stur nom. nud. The diagnosis for a fourth species, *Nilssonia sturii* Krasser 1909, is emended. The *Nilssonia* species from Lunz range among the earliest representtatives of the genus *Nilssonia*.

Keywords.—*Nilssonia*, cuticular analysis, Carnian, fossil cycads, Austria, palaeoecology.

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Morphology and epidermal anatomy of *Nilssonia* (cycadalean foliage) from the Upper Triassic of Lunz (Lower Austria)

Christian Pott [a],*, Hans Kerp [a], Michael Krings [b]

[a] *Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, D-48143 Münster, Germany*
[b] *Bayerische Staatssammlung für Paläontologie und Geologie und GeoBio-Center^{LMU}, Richard-Wagner-Straße 10, D-80333 Munich, Germany*

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Abstract

The Carnian flora from Lunz (Lower Austria) ranks among the richest and most diverse fossil floras from the Upper Triassic. It is one of the first modern Triassic floras with bennettitaleans. Although this flora is often referred to in the literature, modern taxonomic studies are mostly absent; only some of the reproductive structures have been studied in detail. Many of the plant remains yield excellently preserved cuticles. During a systematic study of the *Pterophyllum* leaves from Lunz, it appeared that several species previously accommodated in that taxon have to be transferred to other genera. This paper deals with four species that are transferred to *Nilssonia* (cycadalean foliage); the macromorphology and epidermal anatomy are described and discussed. The following new combination is introduced: *Nilssonia riegeri* nov. comb. Two new species are described (i.e. *Nilssonia lunzensis* and *Nilssonia neuberi*) based on material originally mentioned in a species list as *Ctenis lunzensis* Stur nom. nud. and *Pterophyllum neuberi* Stur nom. nud. The diagnosis for a fourth species, *Nilssonia sturii* Krasser, is emended. The *Nilssonia* species from Lunz range among the earliest representatives of the genus *Nilssonia*.

Keywords: *Nilssonia*; cuticular analysis; Carnian; fossil cycads; Austria; palaeoecology

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1. Introduction

The very rich and diverse Carnian flora from Lunz (Austria) is dominated by pinnate leaves, most of which are attributed to the Bennettitales. Only a few fossils have been assigned to *Ctenis* Lindley et Hutton, a genus of cycadalean foliage (Stur, 1885); however, the cycadalean nature was presumed only based on macromorphology. The best method to discriminate cycadalean from bennettitalean foliage is by cuticular analysis (Florin, 1933; Watson and Sincock, 1992; Watson and Cusack, 2005). Thus far, no unequivocal representatives of cycadalean foliage, recognized based on cuticles, have been reported from Lunz, with the exception of several cycadalean megasporophylls assigned to *Dioonitocarpidium* Rühle von Lilienstern by Kräusel (1953).

Stur (1871) was the first who mentioned pinnate cycad-like foliage from Lunz, and in 1885, he published a long list of taxa. However, none of these two publications includes descriptions and illustrations. Stur's list (1885) includes 17 *Pterophyllum* species, 13 of which

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* Corresponding author. Tel.: +49 251 8323934; fax: +49 251 8321739.
E-mail address: christian.pott@uni-muenster.de (C. Pott).

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are new names. Moreover, the list also contains two new names for *Ctenis* species. All the new names introduced by Stur (1885) are nomina nuda. Krasser (1909) published a classification of the taxa based on Stur's handwritten notes, giving short descriptions of the taxa accompanied by a brief discussion. Because Krasser (1909) could not find the specimens originally assigned to *Ctenis* by Stur, he did not deal with the material allocated to *Ctenis*. Krasser (1909) classified the *Pterophyllum* species into six groups, but his classification is difficult to follow. *Pterophyllum* is now generally accepted as a type of bennettitalean foliage (e.g., Boyd, 2000). Krasser (1909) was the first who reported *Nilssonia* from the Lunz flora, by renaming *Pterophyllum irregulare* Stur *Nilssonia sturii* Krasser. However, *P. irregulare* (non *P. irregulare* Nathorst) is a nomen nudum. Krasser (1909) only gave a brief description of the species without illustrations and did not study cuticles.

Although *Pterophyllum* leaves from Lunz are shown in many museum exhibitions and are illustrated in many textbooks and popular articles (e.g., Potonié, 1899; Schmidt, 1928; Bachmayer and Kollmann, 1969; Turek et al., 1990; GBA, 2002), a modern revision of the genus that includes cuticular analyses is still absent.

A new revision of the Lunz flora, focusing on foliage taxa, reveals that several species previously assigned to *Pterophyllum* actually represent cycadalean leaves. The cycadalean nature of these fossils is evidenced by epidermal anatomy, notably the morphology of the stomatal complexes. Based on leaf morphology and epidermal anatomy, these forms are accommodated in *Nilssonia* Brongniart. Four species are described here that represent the first unequivocal cycadalean leaves from Lunz.

2. Material and methods

The material studied comes from the Upper Triassic of Lunz in the Northern Calcareous Alps of Lower Austria, approximately 100 km west of Vienna (Fig. 1). The material was collected during the late 19th and early 20th centuries in coalmines at several localities in the area around Lunz-am-See. With more than 30,000 specimens, the Lunz flora is one of the richest and most diverse Late Triassic floras of the Northern Hemisphere. The flora consists of sphenophytes, ferns, and numerous gymnosperms (i.e., ?ginkgophytes, cycadaleans, bennettitaleans and coniferophytes); to date more than 70 taxa have been reported. The most up-to-date overviews were published by Dobruskina (1989, 1998), however, these papers are essentially based on older publications.

The Lunz Formation (Lunzer Schichten) is subdivided into three units (Verloop, 1908). The middle unit is named Lunzer Sandstein and consists of sandstones at the base overlain by marine marls gradually grading upwards into terrestrial sands, shales and coal. The coal-bearing part of the sequence is overlain by marls and with a sandstone layer at the top of the subunit. The plant fossils occur in the shales associated with the coal beds.

The lower unit of the Lunzer Schichten (=Reingrabener Schiefer) is dated as Julian based on the occurrence of ammonoids (Krystyn, 1978). Palynological studies indicate a Carnian (Bhardwaj and Singh, 1964) and a Julian age (Dunay and Fisher, 1978). The Opponitzer Limestone, the upper subunit of the Lunzer Schichten was dated as Tuvalian (Dunay and Fisher, 1978).

Outcrops in the area around Lunz are today poor since coal mining finally ceased after World War II. Spoil tips are not well accessible and most of the material is strongly weathered. The old specimens are stored in museum collections throughout Europe (see Appendix).

Almost all remains are preserved as impressions or compressions, the latter often with excellently preserved cuticles. Cuticles were prepared according to procedures summarized in Kerp (1990), and Kerp and Krings (1999). Samples with plant remains were dissolved in hydrofluoric acid in order to obtain cuticles, or cuticles were picked directly from the rock surface. Cuticles were macerated according to the standard procedure using Schulze's reagent (35% HNO_3 with a few crystals of $KClO_3$) and 5–10% potassium hydroxide. Macerated cuticles were washed in distilled water, gently dehydrated in pure glycerine, and afterwards mounted in permanent glycerine-jelly on microscope slides. Slides are stored in the collection of the Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Universität Münster, Germany; accession numbers are given in the figure captions.

Hand specimens were photographs with a Nikon D 100 digital camera; in order to increase contrast cross-polarization (i.e. polarized light sources with polarizing filter over the camera lens) was used. Cuticles were analysed with a Leitz Diaplan light microscope equipped with a Nikon DS-5M digital camera.

3. Taxonomy

Subdivision: Cycadophytina
Class: Cycadopsida
Order: Nilssoniales
Genus: *Nilssonia* Brongniart (1825)

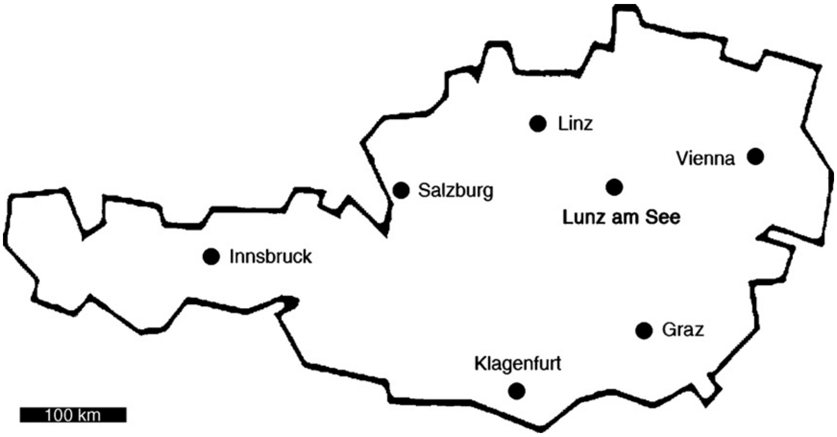

Fig. 1. Position of Lunz-am-See in the Northern Calcareous Alps, Lower Austria.

Remark on the orthography of the generic name *Nilssonia*: Brongniart (1825) introduced the genus *Nilsonia* for leaves from the Lower Jurassic of Scania (Sweden). Brongniart (1825, p. 204), mentioned that the genus was named after M. Nilson. Nathorst (1909) commented that the name was misspelled because the family name is Nilsson, and he corrected the generic name. The spelling *Nilsonia* is a typographical error (Schweitzer et al., 2000). The spelling *Nilssonia* is today widely accepted in the literature (e.g., Harris, 1932, 1964; Schweitzer et al., 2000; Watson and Cusack, 2005).

Nilssonia sturii Krasser (1909) emend.
Plates I, II, 1–3 and III

Selected references

1885 *Pterophyllum irregulare* Stur, Flora Lunzer-Schichten, p. 99 (nom. nud.)
non 1879 *Pterophyllum irregulare* Nathorst, Om Floran i Skånes kolförande Bildningar, p. 68, Plate XVII, Fig. 1
1909 *Pterophyllum irregulare* Krasser, Kenntnis Flora Lunzer Schichten, pp. 116–120, no ill.
1909 *Nilssonia sturii* Krasser, Kenntnis Flora Lunzer Schichten, pp. 120–121, no ill.
1917 *Nilssonia sturii* Seward, Fossil Plants, p. 576, no ill.

Lectotype: GBA 1909/003/0388 (Plate I, 4).

Comment: The name *Nilssonia sturii* was introduced by Krasser (1909) who gave a very brief diagnosis but did not illustrate any specimens of the species. Because no holotype was designated, the specimen GBA 1909/003/0388 is here selected as the lectotype. This specimen belongs to the original set of fossils studied by Stur (1885) and Krasser (1909); originally labelled *Pterophyllum irregulare* by Stur (1885).

Repository: Palaeobotanical Collection of the Geologische Bundesanstalt, Vienna.

Emended diagnosis

Leaves petiolate, pinnate, lanceolate in outline, distally tapering; lamina subdivided into parallel-sided to tapering leaf segments, variable in width, with rounded apices; oppositely to sub-oppositely positioned, inserted to the adaxial (upper) side of the rachis, each with several unforked, delicate parallel veins. Leaves hypostomatic with delicate cuticles, epidermal cells narrow, polygonal to rectangular, anticlinal cell walls straight. Stomatal apparati monocyclic and actinocytic, in intercostal fields; guard cells with prominent dorsal thickenings. Abaxial epidermis with short hollow papillae.

Description

Leaves are petiolate, pinnate (segmented), of almost regular, oblong, more or less lanceolate shape, apex unknown. Lamina subdivided into numerous, irregularly oppositely positioned segments (Plate I, 1–8). Length of segments continuously decreases towards the apex of the leaf. Segments are clearly crescent-to sword-shaped, all of same shape, distally tapering, slightly widened at the base. The width of the individual segments may vary considerably, some segments being twice as wide as others (Plates I, 1–6 and II, 2–3). The distance between the individual segments remains the same within a single leaf, unless the segments are widened basally. Segments are attached to the upper side of the rachis (Plates I, 5,9 and II, 1,3).

Numerous parallel, non-bifurcated veins enter the segments and run straight to the apex (Plate I, 5–9). In adaxial surface view, the prominent rachis is nearly completely covered by the leaf segment bases (Plate I, 4–6, 8–9). The leaf apex is not preserved. The proximal part of the leaf consists of a naked petiole, which is, however, rarely preserved. The petiole may reach a length of up to 17.1 cm.

Incomplete leaves are up to 54.5 cm long and 26.2 cm wide. The length of the leaf segments varies according to their position within the leaf, the longest being up to 13.2 cm. Within a single leaf, the width of segments may vary considerably, ranging from 6.7 mm up to 18.8 mm at their base.

Leaves are hypostomatic and have delicate cuticles. Costal and intercostals fields are distinguishable on the abaxial (Plate III, 1) but not on the adaxial side of the leaf (Plate III, 2).

Adaxial cuticle — The cuticle of the adaxial side is very delicate and difficult to macerate. Epidermal cells are polygonal or rectangular in outline, elongate with acute or pointed ends, 35–80 μm long and 20–37.5 μm wide. Anticlinal cell walls are smooth. Stomata are absent on the adaxial side, which does not show any other special features, neither cuticular thickenings nor trichome bases or papillae (Plate III, 2).

Abaxial cuticle — The abaxial cuticle is thin, but slightly thicker than the adaxial cuticle. The epidermis shows a clear differentiation into costal and intercostal fields. Costal fields are composed of about 3 to 4 lines of cells (Plate III, 1) without stomata and trichome bases; cells are narrow, rectangular, or polygonal to isodiametric in outline, slightly elongate, acute, 25–62.5 μm long and 15–25 μm wide. Anticlinal cell walls are straight and periclinal walls are smooth. Every second or third cell bears a short, thick-walled, hollow papilla (20–25 μm in diameter) positioned at the end of the cell (Plate III, 1, 4, 8, 10). Intercostal fields are

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Plate I. *Nilssonia sturii* Krasser (1909) emend. (see on page 201)

1. well preserved leaf with irregularly faced leaf segments (NHM, 1886/0001/0014), scale bar = 1 cm;
2. well preserved leaf displaying irregularly faced leaf segments (GBA, 1909/003/0400), scale bar = 2 cm;
3. well preserved leaf with well recognisable character of the leaf segments (NHM, 1884/D/1202), scale bar = 1 cm;
4. well preserved leaf showing different sizes of the leaf segments, lectotype, originally labelled *Pterophyllum irregulare* by Stur (1885) (GBA, 1909/003/0388), scale bar = 1 cm;
5. detail of central part of a leaf with leaf segments inserted to the upper side of the rachis (NHM, 1886/0001/0014), scale bar = 1 cm;
6. apical part of a well preserved leaf with the leaf segments decreasing in length towards the leaf apex (NRM, S148681), scale bar = 1 cm;
7. central part of a large and well preserved leaf (GBA, 1909/003/0392), scale bar = 2 cm;
8. large and excellently preserved leaf portion (NHM, 2006B0008/0033), scale bar = 1 cm;
9. detail of a leaf with covered rachis and simple veins (NHM, 2006B0008/0012), scale bar = 2 mm.

Plate II. *Nilssonia sturii* Krasser (1909) emend. and *Nilssonia riegeri* (Stur ex Krasser, 1909) nov. comb. (see on page 202)

1. *N. sturii*, central part of a leaf with leaf segments inserted to the upper side of the rachis (NHM, 2006B0008/0033), scale bar = 5 mm;
2. *N. sturii*, apical part of an excellently preserved leaf with the leaf segments decreasing in length towards the leaf apex (NHM, 1885/D/4027), scale bar = 1 cm;
3. *N. sturii*, central part of a leaf with leaf segments inserted to the upper side of the rachis (NRM, S148246), scale bar = 1 cm;
4. *N. riegeri*, central part of a leaf with several lanceolate leaf segments (GBA, 1909/003/0585), scale bar = 1 cm;
5. *N. riegeri*, excellently preserved leaf displaying the delicate architecture of this species, lectotype (GBA, 1909/003/0589), scale bar = 1 cm;
6. *N. riegeri*, central part of a leaf with leaf segments inserted to the upper side of the rachis, lectotype (GBA, 1909/003/0589), scale bar = 5 mm.

Plate III. *Nilssonia sturii* Krasser (1909) emend. (see on page 203)

1. abaxial cuticle, overview displaying cell pattern with short papillae and stomata (GBA, 1909/002/0518/0007), scale bar = 50 μm;
2. adaxial cuticle, overview of cell pattern (GBA, 1909/002/0518/0004), scale bar = 50 μm;
3. abaxial cuticle, stoma with strongly cutinized guard cells (GBA, 1909/002/0518/0007), scale bar = 50 μm;
4. abaxial cuticle, overview showing the arrangement of cells, stomata, and papillae (GBA, 1909/002/0518/0006), scale bar = 50 μm;
5. abaxial cuticle, haplocheilic stoma with strongly cutinized parts of the guard cells (GBA, 1909/002/0518/0006), scale bar = 20 μm;
6. abaxial cuticle, haplocheilic stoma with surrounding subsidiary cells forming an actinocytic stomatal apparatus (NHM, 2006B0008/0035/0002), scale bar = 20 μm;
7. abaxial cuticle, haplocheilic stoma with surrounding subsidiary cells forming an actinocytic stomatal apparatus (NHM, 2006B0008/0035/0001), scale bar = 10 μm;
8. abaxial cuticle, short, hollow, and strongly cutinized papilla (GBA, 1909/002/0518/0006), scale bar = 10 μm;
9. abaxial cuticle, haplocheilic stoma with radial striae on the walls of the guard cells (NHM, 2006B0008/0035/0001), scale bar = 10 μm;
10. abaxial cuticle, short, hollow, and strongly cutinized papilla (GBA, 1909/002/0518/0006), scale bar = 10 μm.

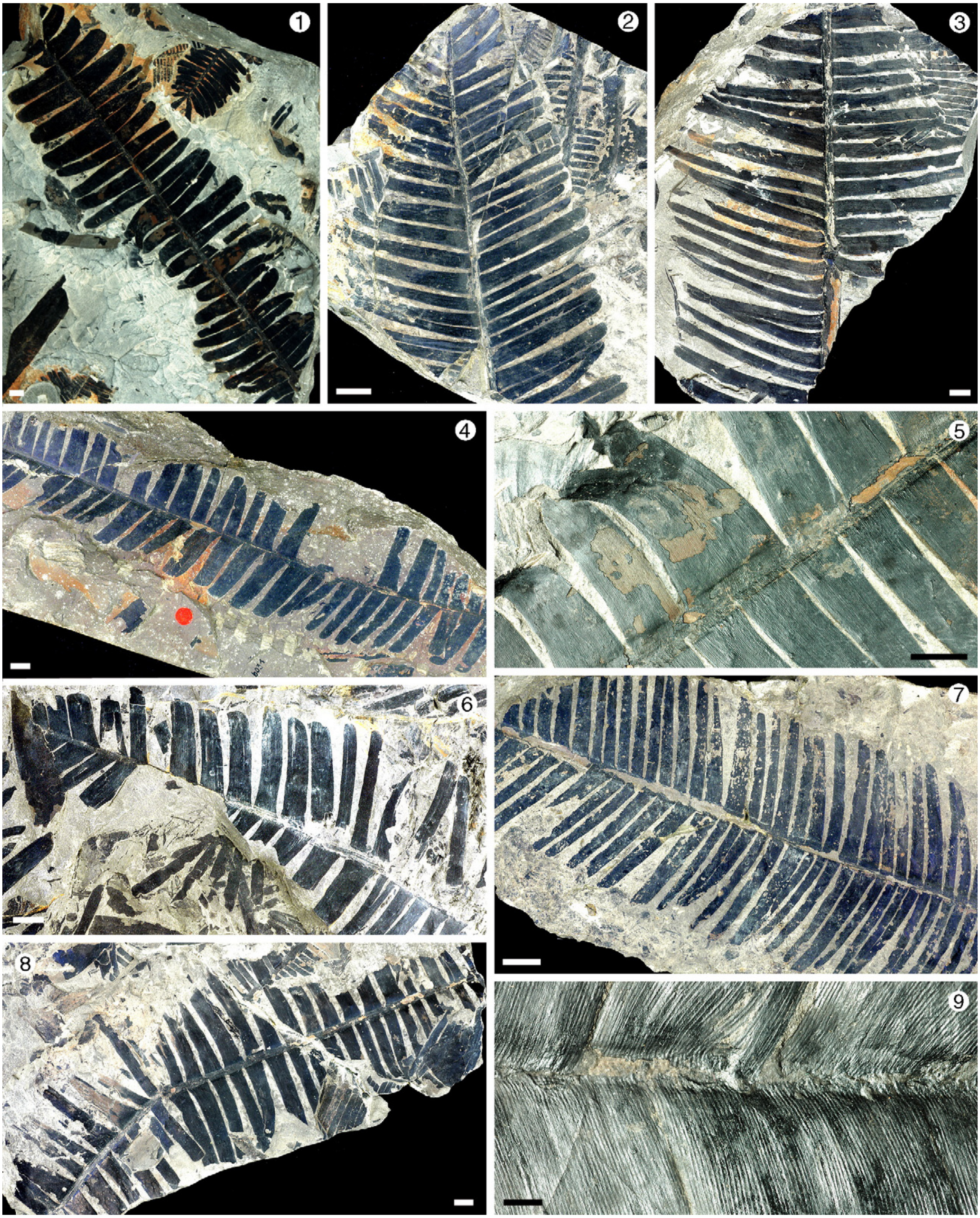

Plate I (*caption on page 200*).

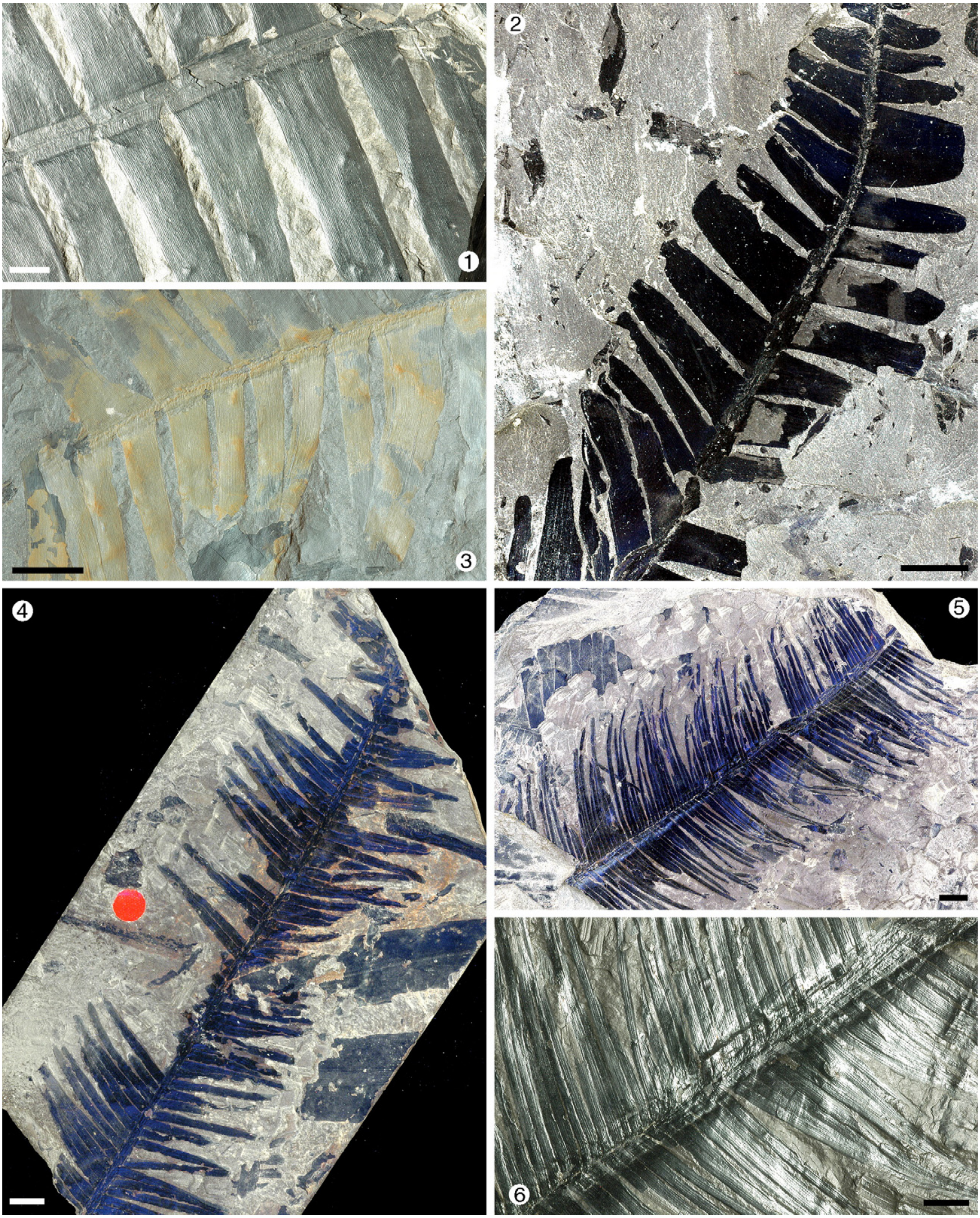

Plate II (*caption on page 200*).

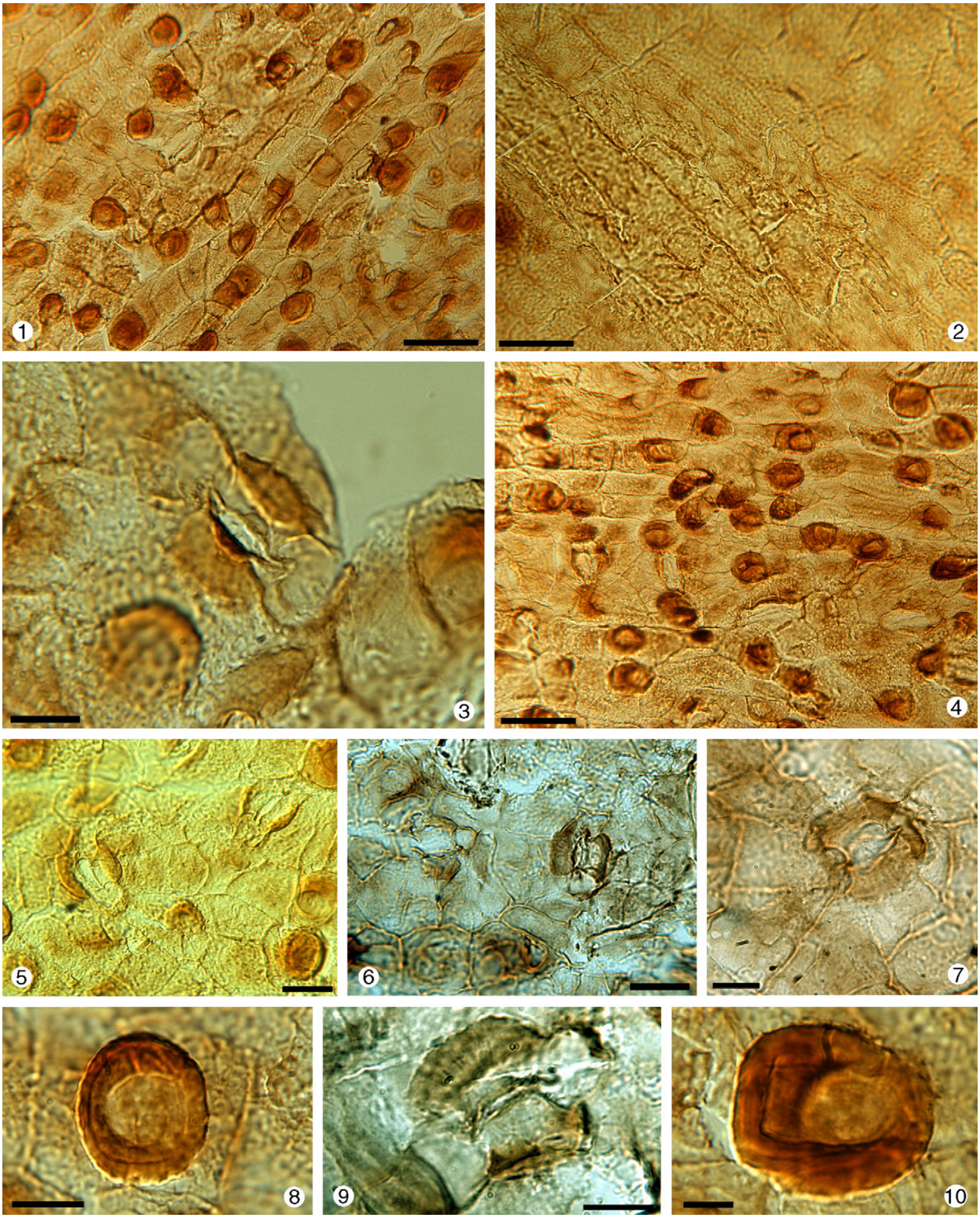

Plate III (*caption on page 200*).

100–150 μm wide; cells are polygonal and isodiametric to broadly rectangular or slightly elongate (Plate III, 1, 4), ranging from 15–40 μm long to 12.5–30 μm wide. Anticlinal cell walls are straight. Stomata are regularly distributed but irregularly oriented within the intercostal fields. Actinocytic stomatal apparati are mono- to diacyclic, 32.5–45 μm long and 15–22.5 μm wide, with 6 to 8 trapezoid to rectangular subsidiary cells (Plate III, 3, 5–7, 9). The stomatal pores vary in length from 10–17.5 μm. The kidney-shaped guard cells are not sunken. The central parts of the dorsal walls are strongly cutinized, whereas the ventral part and the polar ends of the guard cells are weakly cutinized (Plate III, 3, 5–7, 9).

Locality: Lunz-am-See, Lower Austria.
Source Strata: Lunzer Schichten, Julian, middle Carnian, Triassic.
Material studied: Approximately 60 specimens from the following collections: NHM, GBA, NRM, RUU, JOA, SPO.

Remarks

The leaf remains described above are assigned to the genus *Nilssonia* because macromorphological features (e.g. narrow, nearly band-like or oblong-oval, irregularly segmented lamina and segments, attached to the upper side of the rachis and covering it) correspond well with those seen in typical representatives of this genus (Van Konijnenburg-van Cittert et al., 2001; Watson and Cusack, 2005). Additional characters include a short distance between the segments, and a fine, parallel venation with unforked veins (Schimper and Schenk, 1890; Nathorst, 1909; Harris, 1964). Leaf variability as shown by the Lunz specimens (Plates I, 1–2 and II, 1–2) is typical for *Nilssonia* (Nathorst, 1909; Harris, 1932, 1964; Schweitzer et al., 2000).

The leaf morphology of the Lunz material is superficially similar to that of the *Nilssonia tenuicaulis*-complex, as has already been stated by Krasser (1909) and Seward (1917). These authors, however, did not figure Lunz material. The leaves from Lunz here described as *Nilssonia sturii* are much larger than those of *N. tenuicaulis* Seward, as was already mentioned by Krasser (1909). According to Harris (1943), *N. tenuicaulis* leaves reach a maximum length of 20.0 cm, although he later states that the leaves must have been larger (Harris, 1964). Nevertheless, *N. tenuicaulis* is still smaller than *N. sturii*. Moreover, both species also differ considerably with regard to epidermal anatomy (cf. Dower et al., 2004). The density of papillae in *Nilssonia tenuicaulis* is lower than in *Nilssonia sturii* (Plate III, 1, 4); in *N. tenuicaulis* papillae occur only occasionally (Harris, 1943). Harris (1943) also describes small resin bodies for *N. tenuicaulis* that do not occur in *N. sturii*.

Pterophyllum irregulare described and illustrated by Nathorst (1879) from the Rhaeto–Liassic of Bjuv (Sweden) is very different from *Nilssonia sturii*, in having more slender leaf segments; the name *P. irregulare* Stur is a nomen nudum, used for the species later named *N. sturii* (Krasser, 1909).

Several of the specimens originally assigned to *Ctenis* (and *Ctenophyllum* Schimper) by Stur (1885) and Krasser (1909), kept in the collections of NHM, GBA and NRM, can be identified as *Nilssonia sturii*. None of these specimens shows anastomosing veins, which is a typical feature for *Ctenis*.

Nilssonia riegeri (Stur ex Krasser, 1909) nov. comb.
Plate II, 4–6
Basionym: *Pterophyllum riegeri*, (Stur, 1888 nomen nudum) Krasser (1909) — Krasser, F., 1909. Zur Kenntnis der fossilen Flora der Lunzer Schichten. Jahrbuch der kaiserlich-königlich geologischen Reichsanstalt 59, 1–26.

References

1871 *Pterophyllum riegeri* Stur, Geologie der Steiermark, p. 250, (nom. nud.)
1885 *Pterophyllum riegeri* Stur, Flora Lunzer-Schichten, p. 99, (nom. nud.)
1888 *Pterophyllum riegeri* Stur, Lunzer Flora in Virginia“, p. 8, (nom. nud.)
1909 *Pterophyllum riegeri* Krasser, Kenntnis Flora Lunzer Schichten, pp. 119–121, no ill.

Lectotype: GBA 1909/003/0589 (Plate II, 5)
Comment: The name *Pterophyllum riegeri* was introduced by Stur (nomen nudum) and validated by Krasser (1909), who gave a very brief diagnosis but did not illustrate the specimens. Because no holotype was designated, the specimen GBA 1909/003/0589 is here selected as the lectotype. This specimen belongs to the original set of fossils studied by Stur (1885) and Krasser (1909); originally labelled *Pterophyllum riegeri* by Stur (1885).

Repository: Palaeobotanical Collection of the Geologische Bundesanstalt, Vienna.

Diagnosis

Leaves slender pinnate, overall outline lanceolate; lamina subdivided into narrow segments of equal width, tapering towards their apex, apices rounded; leaf segments insert to the upper side of the rachis; each segment with several simple, delicate parallel veins. Leaves amphistomatic with delicate cuticles; costal and intercostals fields distinguishable on the abaxial, but not on the adaxial side of the leaf. Epidermal cells narrow, polygonal to rectangular, cell walls straight; stomata haplocheilic, arranged in intercostal fields; guard cells with prominent dorsal thickenings; abaxial epidermis with short hollow papillae.

Description

Leaves are oblong to lanceolate in outline, pinnate, leaf segments densely spaced. Lamina subdivided into numerous, irregularly faced, narrow and lanceolate segments; (Plate II, 4–5). Segments attached to the upper side of the rachis. They cover most of the adaxial surface of the rachis (Plate II, 6). Individual segments gradually decrease in length towards the apex of the leaf; individual segments taper towards their apex, resulting in an irregular outline of the leaf. Leaf segments narrow, basally slightly expanded, apex rounded. Segments almost equal in width, bent slightly towards the leaf apex, more than five times as long as broad. Five to eight parallel, non-bifurcated veins enter the segments at a somewhat acute angle (Plate II, 4–6). Petiole not preserved.

Incomplete leaves are up to 16.0 cm long and 8.9 cm wide. The length of the leaf segments varies depending on their position within the leaf; they are up to 5.2 cm long; their width ranges from 1.7 mm to 3.3 mm.

Leaves are amphistomatic with delicate cuticles. Costal and intercostals fields are distinguishable on the abaxial, but not on the adaxial side of the leaf.

Adaxial cuticle — Epidermal cells are polygonal or rectangular, elongate with acute or pointed ends. The adaxial cuticle of *Nilssonia riegeri* is largely similar to that of *Nilssonia sturii*, morphologically as well as with regard to cell sizes, but *N. riegeri* differs from *N. sturii* in having a few stomata on the adaxial side. Hollow papillae occur occasionally but in some instances may be reduced to thickenings of the periclinal walls.

Abaxial cuticle — Cells over veins are narrow, rectangular or polygonal to isodiametric in shape, slightly elongate, acute. Costal fields are composed of about 2 to 3 lines of cells. The abaxial cuticle of *Nilssonia riegeri* is largely similar to that of *Nilssonia sturii*, morphologically as well as with regard to cell sizes. Periclinal walls are smooth; short, thick-walled, hollow papillae-bearing cells are scattered regularly between the normal epidermal cells. The monocyclic stomata are regularly distributed within the intercostal fields and oriented irregularly. Stomata are surrounded by an actinocytic ring of 6 to 8 trapezoid to rectangular subsidiary cells. The kidney-shaped guard cells are surficial. The central parts of the dorsal walls are strongly cutinized, whereas their ventral parts and the polar ends are only weakly cutinized.

Locality: Lunz-am-See, Lower Austria.
Source Strata: Lunzer Schichten, Julian, middle Carnian, Triassic.
Material studied: Five specimens from the following collections: GBA, NRM

Remarks

Krasser (1909) originally described the specimens studied here and gave a short diagnosis. Although he noticed some characteristic features (insertion of the leaf segments, venation) that are typical for *Nilssonia*, he assigned the material to *Pterophyllum riegeri*, thereby following Stur (1885). Cuticular analysis clearly demonstrates that the specimens cannot be retained in *Pterophyllum*, a genus for bennettitalean foliage, but rather belong to the Cycadales. Based on the pinnate nature of the leaf, the insertion of the individual leaf segments, the venation pattern and the epidermal anatomy, this species is assigned to *Nilssonia*.

Cuticles of *Nilssonia riegeri* are very similar to those of *Nilssonia sturii* and it is difficult to distinguish both species based on the cuticles. However, *N. riegeri* leaves are amphistomatic, whereas those of *N. sturii* are hypostomatic. Moreover, the overall morphology of the leaves is quite different in that *N. riegeri* leaves are much smaller and possess narrower leaf segments.

Nilssonia riegeri appears to be a relatively rare species. Only five specimens have been recorded to date. Unfortunately, not all of these specimens yield well preserved cuticles, because some are covered with varnish and cuticles are strongly oxidized.

Nilssonia riegeri is quite similar to *Nilssonia feriziensis* Fakhr from the Rhaeto–Jurassic flora of the Kerman Basin, Iran (Schweitzer et al., 2000), but much smaller; cuticles of the latter species are not known.

Nilssonia lunzensis Stur ex Pott, Kerp and Krings nov. spec.
Plates IV and V, 1–2

Selected references

1885 *Ctenis lunzensis* Stur, Flora Lunzer-Schichten, p. 98 (nom. nud.)
1885 *Ctenis angustior* Stur, Flora Lunzer-Schichten, p. 98 (nom. nud.)
1909 *Ctenis lunzensis* Krasser, Kenntnis Flora Lunzer Schichten, p. 113 (nom. nud.)
1909 *Ctenophyllum lunzense* Krasser, Kenntnis Flora Lunzer Schichten, p. 113 (nom. nud.)

Holotype: GBA 1909/003/0196 (Plate IV, 6)
Epitype: NRM, S148602 (Plate IV, 5)

Repository: Palaeobotanical collection of the Geologische Bundesanstalt, Vienna

Diagnosis

Leaves imparipinnate, broad-lanceolate to acute-oval in outline; leaf subdivided into tongue-shaped segments of unequal width. Leaf segments strongly decurrent at the base, tapering towards the apices, apices rounded; leaf segments inserted to the upper side of the rachis, several delicate veins enter each segment and run straight towards the apex. The leaf apex consists of a large terminal segment, rhomboidal in outline. Leaves amphistomatic, cuticles delicate. Epidermal cells elongate, rectangular to isodiametric in outline; anticlinal cell walls straight; stomata sunken; stomatal apparati monocyclic, arranged in intercostal fields.

Description

Leaves imparipinnate, individual segments attached to the upper side of the rachis, strongly decurrent basiscopically and tapering towards the apices, resulting in a rather open appearance of the leaf (Plate IV, 1–2, 4–9). The unequal widths of the individual segments, some twice as wide as the adjacent ones, create an irregular appearance (Plate IV, 1–2, 5–7, 9). The overall outline of the leaf is oblong to pointed-oval. Segment length gradually decreases towards the leaf apex. The leaf apex consists of a large terminal segment that is rhomboidal in outline (Plate IV, 5, arrow). Leaf segments are more than twice as long as wide and bent towards the leaf apex. The apices of the individual segments are obtuse-rounded. Numerous parallel veins enter the segments at an angle of ca. 80°, and run straight towards the apex without bifurcating (Plate IV, 3, 8); each vein consists of two thin vascular strands. The petiole is unknown.

Incomplete leaves are up to 24.6 cm long and 13.9 cm wide. Individual leaf segments are up to 85 mm long and 16.8 to 42.1 mm wide; their length varies depending to their position within the leaf.

Leaves are amphistomatic; cuticles are very delicate and difficult to macerate. A differentiation into costal and intercostal fields occurs in the adaxial and abaxial epidermis.

Adaxial cuticle — Cells over veins are elongate, rectangular to isodiametric in outline, occasionally ending acutely, 55–105 μm long and 25–37.5 μm wide. Anticlinal cell walls are smooth. Cells of intercostal fields are isodiametric, polygonal to broadly rectangular in outline, ending acutely, 45–95 μm long and 30–60 μm wide. Anticlinal cell walls are smooth and heavily cutinized (Plate V, 3, 7, 11–12). The periclinal walls sometimes show faint longitudinal striae. Stomata are

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Plate IV. *Nilssonia lunzensis* nov. spec. (see on page 207)

1. detail of central part of a leaf, epitype (NRM, S148602), scale bar = 1 cm;
2. large and well preserved leaf showing characters of the leaf segments (NHM, 2006B0008/0031), scale bar = 1 cm;
3. detail of a leaf, showing vein courses of overlapping leaf portions, cf. text (GBA, 1909/003/0196), scale bar = 5 mm;
4. central part of a well preserved leaf (GBA, 1909/002/0208), scale bar = 1 cm;
5. excellently preserved leaf with recognisable apical region, epitype (NRM, S148602), scale bar = 1 cm;
6. central part of a well preserved leaf, holotype (GBA, 1909/003/0196), scale bar = 2 cm;
7. a part of an excellently preserved leaf (NHM, 1883/C/5900), scale bar = 1 cm;
8. detail of a leaf, with leaf segments inserted at the upper side of the rachis and well recognisable vein courses (NHM, 1885/D/4020), scale bar = 5 mm;
9. upper part of a leaf showing vein courses (GBA, 1909/003/0195), scale bar = 5 mm.

Plate V. *Nilssonia lunzensis* nov. spec. (see on page 208)

1. adaxial cuticle, overview of cell pattern (NRM, S148241/0006), scale bar = 100 μm;
2. abaxial cuticle, overview of cell pattern with stomata (NRM, S148241/0006), scale bar = 100 μm;
3. adaxial cuticle, overview with densely arranged epidermal cells (NRM, S148241/0001), scale bar = 100 μm;
4. adaxial cuticle, with haplocheilic stoma (NRM, S148241/0006), scale bar = 50 μm;
5. adaxial cuticle, showing cuticular bars (NRM, S148241/0002), scale bar = 10 μm;
6. abaxial cuticle, sunken stoma (NRM, S148241/0006), scale bar = 10 μm;
7. adaxial cuticle, epidermal cells with solid cell walls (NRM, S148241/0001), scale bar = 50 μm;
8. adaxial cuticle, sunken stoma (NRM, S148241/0002), scale bar = 10 μm;
9. adaxial cuticle, sunken stoma (NRM, S148241/0002), scale bar = 10 μm; 1
10. adaxial cuticle, stoma with monocytic arranged subsidiary cells (NRM, S148241/0002), scale bar = 20 μm;
11. adaxial cuticle, epidermal cells with solid cell walls (NRM, S148241/0001), scale bar = 10 μm;
12. adaxial cuticle, epidermal cells with solid cell walls (NRM, S148241/0001), scale bar = 10 μm.

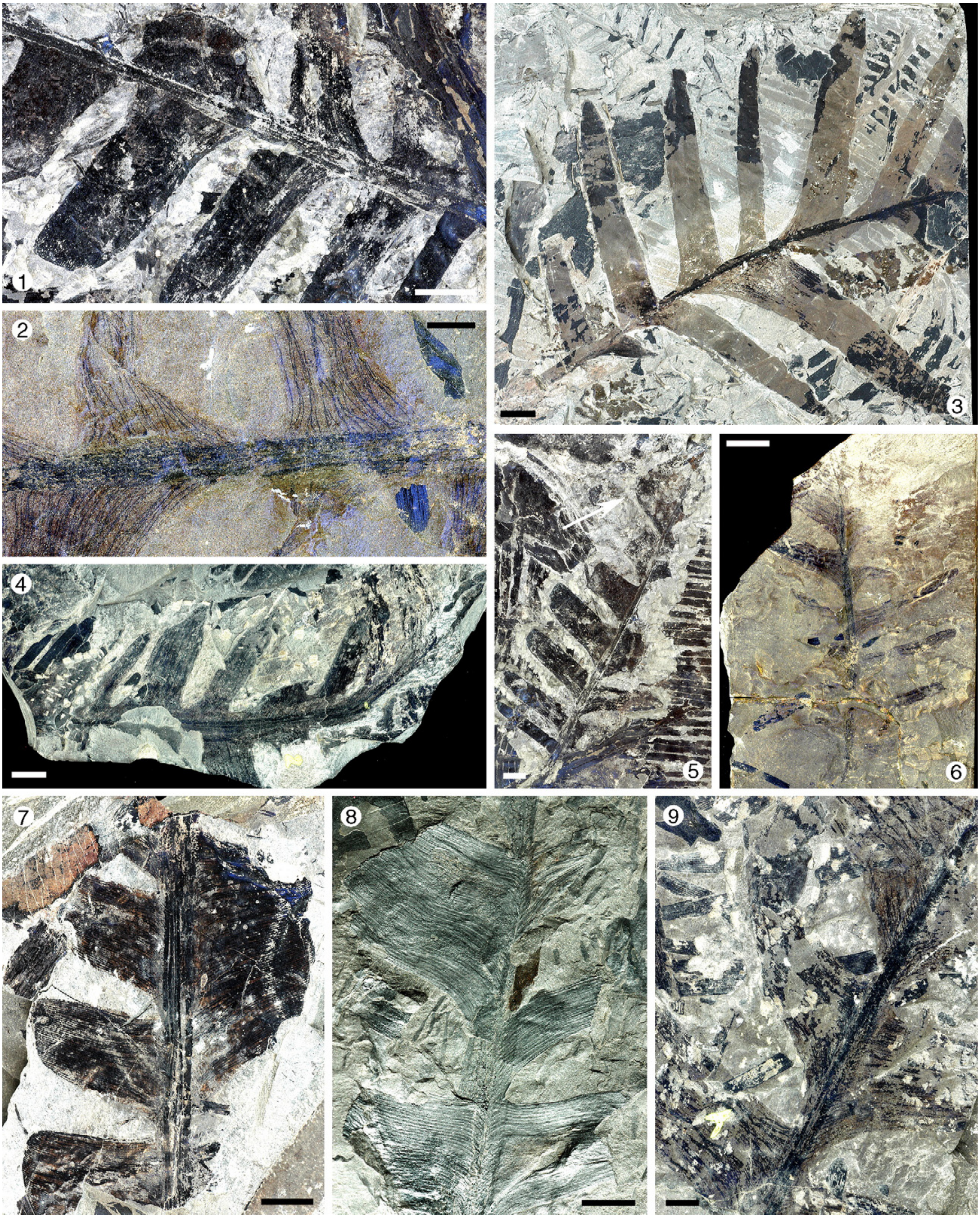


Plate IV (*caption on page 206*).

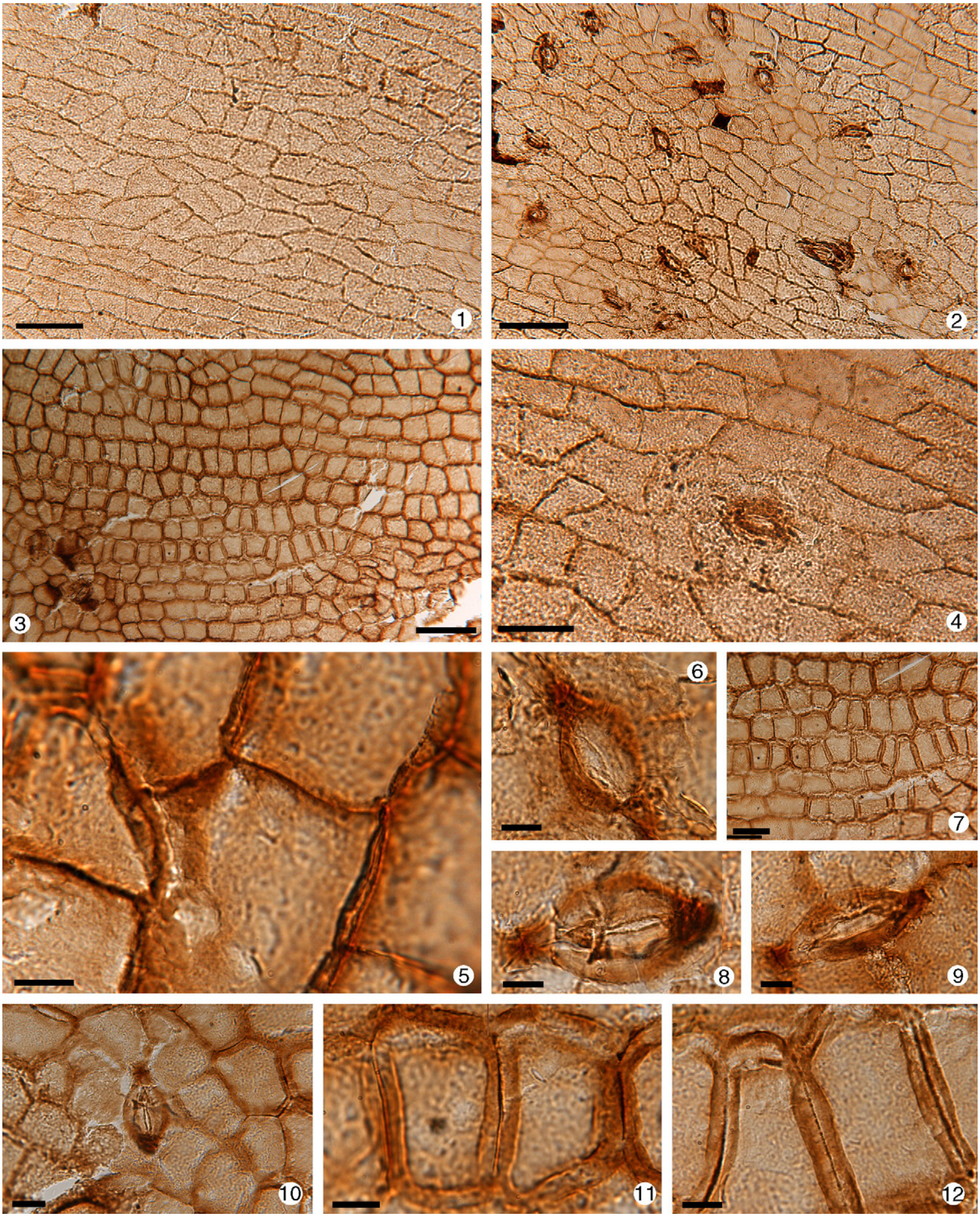


Plate V (*caption on page 206*).

confined to the intercostal fields, irregularly oriented, 55–80 µm long and 22.5–32.5 µm wide; they are monocyclic with a ring of 6 to 7 polygonal subsidiary cells. The stomata are slightly sunken, with pores of 15–22.5 µm in length. Papillae and trichomes are absent (Plate V, 1, 4, 5).

Abaxial cuticle — Costal fields are composed of about 3 to 4 lines of cells. Epidermal cells are similar in outline and size to those of the adaxial side; however, cutinisation of the anticlinal walls is weaker. Cells are narrow, elongate, rectangular in outline, with straight anticlinal walls (Plate V, 2, 4), 50–115 µm long and 20–40 µm wide. Periclinal walls are normally smooth, but longitudinal striae may occasionally be present. Intercostal fields are 200–225 µm wide, cells rectangular to acutely ending, polygonal or isodiametric, irregularly oriented (Plate V, 2), 35–80 µm long and 17.5–45 µm wide. Anticlinal cell walls are straight. Stomatal apparati irregularly oriented, monocyclic, 45–65 µm long and 20–35 µm wide, with 6 to 7 polygonal subsidiary cells encircling the stomatal pit; stomata sunken (Plate V, 6, 8–9, 10), stomatal pores 12.5–17.5 µm long. Papillae may occur in the proximal portion of the segments; trichome bases are absent.

Locality: Lunz-am-See, Lower Austria.
Source Strata: Lunzer Schichten, Julian, middle Carnian, Triassic.
Material studied: Approximately 30 specimens from the following collections: NHM, GBA, NRM, RUU, JOA

Remarks

The leaf morphology and epidermal anatomy, especially the shape of the stomatal apparati, justify the accommodation of this species in the genus *Nilssonia*. Many of the specimens included here in *Nilssonia lunzensis* were originally labelled as *Ctenis lunzensis* by Stur (1871, 1885) and Krasser (1909). However, this latter name is a nomen nudum because the species was never validly described. The assignment to *Ctenis* was based on the presumed anastomosing venation (Krasser, 1909). However, careful re-examination of Stur's and Krasser's original material revealed that the specimens do not show anastomosing veins. Some of the leaf segments were folded during embedding in the sediment and, as a result, leaf parts overlap each other (Plate IV, 3). The veins of the underlying leaf portion are often still visible in the overlying leaf segment, which suggests the presence of anastomosing veins. Therefore, these anastomoses are regarded as a taphonomic feature, which does not allow assignment of the material to the genus *Ctenis*. Several specimens from the collection of the Geologische Bundesanstalt in Vienna were labelled by Stur as *Ctenophyllum lunzense*. However, the genus *Ctenophyllum* is no longer used and, according to Seward (1917), is a synonym of *Pseudoctenis* Seward. According to Krasser (1909), these are the specimens referred to as *C. lunzensis* by Stur in his 1885 paper. *Ctenis* differs from *Nilssonia* in having laterally inserted leaf segments.

Nilssonia lunzensis differs from the other *Nilssonia* species from Lunz in having more loosely arranged leaf segments; a comparison of the *Nilssonia* species from Lunz is presented in Table 1.

A species closely resembling *Nilssonia lunzensis* is *Nilssonia kendallii* Harris from the Middle Jurassic of Yorkshire, UK (Harris, 1964). Although *N. kendallii* shows a similar gross morphology and the cuticles also are superficially similar, this species has much smaller leaves and the resin bodies and papillae mentioned by Harris (1964) for *N. kendalii* are missing in *N. lunzensis*.

Nilssonia acuminata Göppert from the Rhaeto–Liassic of Franconia (Germany) is another species that shows some similarity to *Nilssonia lunzensis* (Schenk, 1867). However, leaves of this species apparently also have resin bodies, which were interpreted as sporangia by Schenk (1867).

Nilssonia neuberi Stur ex Pott, Krings and Kerp nov. spec.
Plate VI

Nomenclatural remarks: The name *Pterophyllum neuberi*, from which the specific epithet is derived, was introduced by Stur (1885) as a nomen nudum. Krasser (1909) gave a very brief description and placed this species in the synonymy of *Ctenophyllum grandifolium* Fontaine (1883), thereby transferring the latter species to *Pterophyllum*. Cornet and Olson (1990), and probably not aware of Krasser's (1909) paper, again transferred *C. grandifolium* to *Pterophyllum*. Cornet and Olson (1990) refigured one of the very schematic drawings of Fontaine (1883). Because Fontaine's illustrations are schematic and do not show essential details such as the venation, we feel that a comparison of the Lunz material to Fontaine's specimens, which have never been illustrated photographically, is not possible. Therefore, a new species based on the material studied by Stur (1885) and Krasser (1909) is formally proposed here.

Selected references
1885 *Pterophyllum neuberi* Stur, Flora Lunzer-Schichten, p. 99, (nom. nud.)
1909 *Pterophyllum grandifolium* Krasser, Kenntnis Flora Lunzer Schichten, p. 115–120, no ill.
1990 non *Pterophyllum grandifolium* Cornet and Olson, Flora Richmond and Taylorsville Basins, p. 52, pl. 18.

Table 1
Macromorphological and epidermal features of the Nilssonia species from Lunz

		Nilssonia sturii	*Nilssonia riegeri*	*Nilssonia lunzensis*	*Nilssonia neuberi*
Leaf morphology	outline	pinnate; lanceolate to tapering	slender pinnate; oblong to lanceolate	imparipinnate; oblong to pointed-oval	regularly pinnate, very large, strong
	distance of segments	densely spaced	densely spaced	loosely spaced, irregular	regular and loose
	leaf apex	rounded, triangular apical segment	unknown	large terminal rhomboidal segment	unknown
	leaf base	petiolate	unknown	unknown	unknown
	leaf length up to	54.5 cm (incomplete leaf)	16.0 cm (incomplete leaf)	24.6 cm (incomplete leaf)	52.5 cm (incomplete leaf)
	leaf width up to	26.2 cm	8.9 cm	13.9 cm	39.3 cm
	attachment of leaf segments	to upper side of rachis, completely covering the rachis	to the upper side of rachis, covering most of the rachis	to the upper side of rachis, covering most of the rachis	to upper side of rachis, completely covering the rachis
	outline of leaf segments	crescent- to sword-shaped; of variable widths	fine lanceolate, narrow, tapering towards apex; of equal widths	tapering towards apex, bent upwards, variable widths	narrow and grass-like, linear, of equal widths
	bases of leaf segments	slightly widened	slightly expanded	strongly decurrent	slightly widened
	apices of leaf segments	obtuse-rounded	pointedly rounded	obtuse-rounded	obtuse-rounded to cut-off
	length of leaf segments up to	13.2 cm	5.2 cm	8.5 cm	23.3 cm
	basal width of leaf segments	6.7-18.8 mm	1.7-3.3 mm	16.8-42.1 mm	12.3-26.4 mm
	vein entrance	at right angle	at slightly acute angle	at an angle of ca. 80°	at right angle
	veins	numerous, parallel, non bifurcate	five to eight, parallel, non bifurcate	numerous, parallel, marked by two thin lines, non bifurcate	numerous, parallel, densely spaced, non bifurcate
Stomaty	stomaty	hypostomatic	amphistomatic	amphistomatic	hypostomatic
	stomatal type	mono- to diacyclic (haplocheilic)	monocyclic (haplocheilic)	monocyclic (haplocheilic)	monocyclic (haplocheilic)
Adaxial epidermal anatomy	costal and intercostal fields	not distinguishable	not distinguishable	distinguishable	not distinguishable
	epidermal cells (costal fields)	polygonal or rectangular, elongate with acute or pointed ends	polygonal or rectangular, elongate with acute or pointed ends	elongate, rectangular to isodiametric	rectangular elongate
	dimensions (length × width)	35-80 µm × 20-37.5 µm	35-80 µm × 20-37 µm	55-105 µm × 25-37.5 µm	67.5-142 µm × 27.5-32 µm
	anticlinal / periclinal walls	smooth / smooth	smooth / smooth	smooth / smooth	smooth / smooth
	epidermal cells (intercostal fields)			isodiametric, polygonal to broad-ly rectangular, ending acute	
	dimensions (length × width)			45-95 µm × 30-60 µm	
	stomata		rarely present; type, size and shape see abaxial cuticle	slightly sunken	
	distribution			intercostal fields, regular	
	dimensions (length × width)			55-80 µm × 22.5-32.5 µm	
	subsidiary cells			6-7, polygonal	
	stomatal porus			15-22.5 µm; irregular oriented	
	hair bases, papillae	absent	hollow papillae or cuticular thickenings rarely present	absent	absent
Abaxial epidermal anatomy	costal/intercostal fields	distinguishable	distinguishable	distinguishable	distinguishable
	costal fields	3-4 lines of cells	2-3 lines of cells	3-4 lines of cells	9-10 lines
	epidermal cells (costal fields)	narrow, rectangular, or polygonal to isodiametric, elongate, acute	narrow, rectangular, or polygonal to isodiametric, elongate, acute	narrow, elongate, rectangular	narrow, rectangular or elongate to isodiametric
	dimensions (length × width)	25-62.5 µm × 15-25 µm	25-60 µm × 15-25 µm	50-115 µm × 20-40 µm	c. 20-30 µm wide
	anticlinal walls	straight	straight	straight	straight
	periclinal walls	smooth	smooth	smooth, striae may be rare	smooth
	intercostal fields	100-150 µm wide	100-150 µm wide	200-225 µm wide	350-375 µm wide
	epidermal cells (intercostal fields)	polygonal and isodiametric to broad rectangular or slightly elongate	polygonal and isodiametric to broad rectangular or slightly elongate	rectangular to acute ending, polygonal or isodiametric, irregular	cell dimensions and outline are not recognizable
	dimensions (length × width)	15-40 µm × 12.5-30 µm	15-40 µm × 12.5-30 µm	35-80 µm × 17.5-45 µm	cell dimensions and outline are not recognizable
	anticlinal walls	straight	straight	straight	cell dimensions and outline are not recognizable
	stomata	not sunken	not sunken	sunken	slightly sunken
	distribution	intercostal fields, regular	intercostal fields, regular	intercostal fields	intercostal fields, regular
	orientation	irregular	irregular	irregular	irregular
	dimensions (length × width)	32.5-45 µm × 15-22.5 µm	32.5-45 µm × 15-23 µm	45-65 µm × 20-35 µm	40-50 µm × 17-25 µm
	subsidiary cells	6-8, rectangular to trapeziod	6-8, rectangular to trapeziod	6-7, polygonal	unidentifiable
	stomatal porus	10-17.5 µm	10-17 µm	12.5-17.5 µm	unidentifiable
	hair bases, papillae	short, thick-walled, hollow papilla on every 2nd or 3rd cell	thick-walled, hollow papillae scattered regularly	papillae very rare; trichome bases absent	some cells bearing a thick-walled hollow papilla

Holotype: GBA 1909/003/0576 (Plate VI, 1)
Epitype: GBA 2006/004/0014 (Plate VI, 5)

Repository: Palaeobotanical collection of the Geologische Bundesanstalt, Vienna

Diagnosis

Leaves large, robust, subdivided into long, parallel-sided, irregularly alternating segments with rounded apices. Leaf segments insert to the upper side of the rachis. Each segment with several, non-bifurcated, parallel, delicate veins. Leaves hypostomatic, cuticles thin. Epidermal cells on both leaf sides elongate to rectangular with straight anticlinal cell walls. Epidermis of the abaxial side differentiated into costal and intercostals fields; stomata restricted to the intercostal fields. Stomatal apparati haplocheilic; guard cells with prominent dorsal thickenings and radial striae. Abaxial epidermis with a few short hollow papillae.

Description

Leaves are large and robust, regularly pinnate; leaf segments widely spaced (Plate VI, 1–3, 5); individual leaf segments slightly decurrent, insert to the upper side of the rachis, long and narrow, hardly tapering towards their tips. The striate rachis is remarkably thin. Leaf petiole and apex unknown. Venation dense, consisting of a large number of parallel, non-bifurcated veins that enter the leaf segments at 90° angles (Plate VI, 5).

Incomplete leaves are up to 52.5 cm long and 39.3 cm wide. The length of the leaf segments varies depending on their position within the leaf; leaf segments may be up to 23.3 cm long and 12.3–26.4 mm wide.

The leaves are hypostomatic and have very delicate cuticles. Costal and intercostals fields are distinguishable only on the abaxial side.

Adaxial cuticle — Unfortunately, cuticles are rather poorly preserved. Cells are rectangular, elongate, 67.5–142.5 μm long and 27.5–32.5 μm wide. Anticlinal cell walls are smooth as far as visible. Periclinal walls are smooth.

Abaxial cuticle — Cells over the veins are narrow, rectangular or elongate to isodiametric in outline; dimensions are difficult to ascertain, cells are about 20–30 μm wide (Plate VI, 6, 9). Costal fields are composed of 9 to 10 lines of cells (Plate VI, 9). Anticlinal cell walls are straight, periclinal walls smooth, some bearing a thick-walled hollow papilla. Intercostal fields are 350–375 μm wide, individual cells not recognizable. Stomata are regularly distributed in the intercostal fields, randomly oriented, monocyclic, 40–50 μm long and 17–25 μm wide (Plate VI, 4, 6–9). Stomata are slightly sunken, guard cells with radial striae on the dorsal walls (Plate VI, 4, 8). Dorsal walls are strongly cutinized in the central part, but the small polar ends are only weakly cutinized.

Locality: Lunz-am-See, Lower Austria.
Source Strata: Lunzer Schichten, Julian, middle Carnian, Triassic.
Material studied: About 30 specimens from the following collections: GBA, NRM

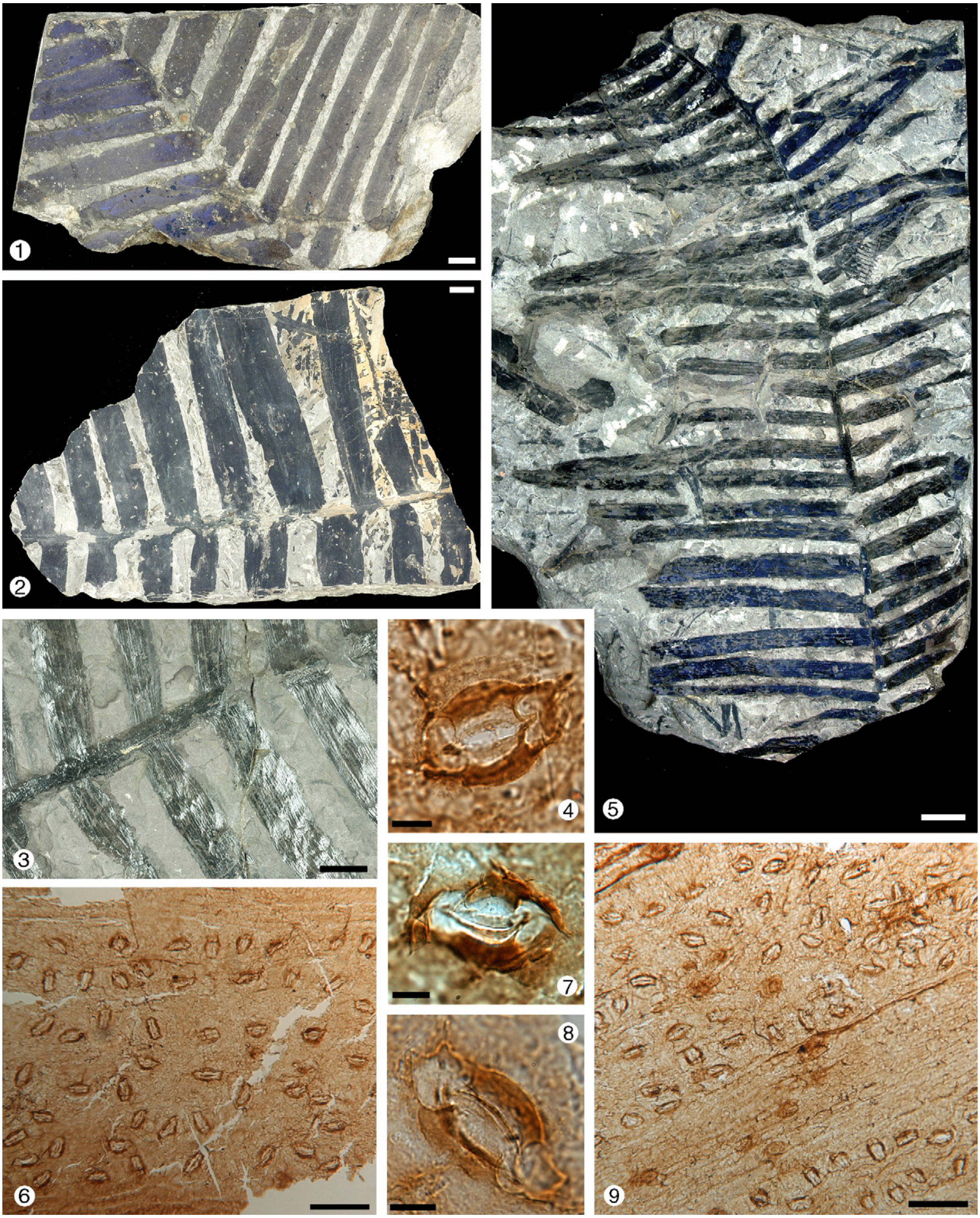
Remarks

The leaf architecture and epidermal anatomy, particularly the insertion of the leaf segments and the morphology of the stomatal apparati justify the accommodation of this species in the genus *Nilssonia*. *Nilssonia neuberi* can easily be distinguished from other *Nilssonia* species by its large dimensions (Plate VI, 1, 5).

The material from Lunz originally labelled as *Pterophyllum neuberi* cannot be assigned to *Pterophyllum* because this latter genus is a type of bennettitalean foliage. The material here assigned to *Nilssonia neuberi* has haplocheilic stomata that are typical for cycadalean leaves (Florin, 1933; Watson and Cusack, 2005). Although only cuticles can give definite proof for the generic assignment of this type of pinnate foliage, it cannot be denied that some *Pterophyllum* species are superficially similar to *N. neuberi*. If no cuticles are available, generic assignments remain speculative. This latter category includes several species from the Upper Triassic and Jurassic, which either have been assigned to *Pterophyllum*, *Pseudoctenis* or *Nilssonia*.

Pterophyllum braunsii Schenk looks somewhat similar but the insertion of the leaf segments is not clear and cuticles are unknown (Schenk, 1867). Leaf segments attached to the upper side of the rachis and non-bifurcated veins that are typical features for *Nilssonia* characterize *Pterophyllum robustum* Compter from the Keuper (Upper Triassic) of Franconia, southern Germany (Compter, 1894; Rühle von Lilienstern, 1933; Kelber and Hansch, 1995). The size of the leaves (Compter, 1874, 1894; Kelber and Hansch, 1995, Fig. 155) is similar to that of *Nilssonia neuberi*. Compter (1894) discussed the assignment of *P. robustum* to *Pterophyllum,* whereas Kelber (1998) suggested that this species might be assignable to *Pseudoctenis*.

Nilssonia princeps Oldham et Morris from the Rajmahal Group (Jurassic) of India is another species that is very similar to *Nilssonia neuberi* (Seward, 1917; Sahni and Rao, 1931, 1934). This species was originally described as *Pterophyllum princeps* (Oldham and Morris, 1863; Feistmantel, 1877) and assigned to the cycads. Menendez (1952) gave a detailed description of *N. princeps* from the Rhaetian Llantenes flora of Argentina.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Nilssonia princeps is characterized by very large leaves with segments that insert to the upper side of the rachis and non-bifurcated, densely spaced veins. The epidermal anatomy of *N. princeps* is unknown. However, the leaf segments of *N. princeps* are always shorter than those of *N. neuberi*.

4. Discussion

As has already been mentioned before, only cuticles can give definite proof for the assignment of isolated pinnate foliage to the Cycadales or Bennettitales. If cuticles are unavailable, assignments remain speculative and result in an artificial system of morphotaxa that do not necessarily reflect biological relationships. The assignment of several foliage morphotypes previously accommodated in the bennettialean foliage morphogenus *Pterophyllum* to the cycadalean foliage morphogenus *Nilssonia* based on a complement of macromorphological and epidermal characters demonstrates the value of cuticular analyses in more accurately depicting the systematic position of compression foliage fossils based on biological criteria.

However, even if the generic assignment to *Nilssonia* is clear, individual species within this genus are often difficult to discriminate because they are highly variable (Nathorst, 1909; Harris, 1932; Boyd, 2000; Schweitzer et al., 2000). Moreover, morphologically very similar species may show distinct differences in the epidermal anatomy (Schweitzer et al., 2000). According to these latter authors, species can only be adequately characterized by studying several complete leaves. The Carnian flora of Lunz includes a considerable number of large leaf remains with well preserved cuticles, and thus enables the characterisation of the four *Nilssonia* species described above.

The Lunz flora is dominated by bennettitaleans, e.g., *Pterophyllum*. In addition, cycadaleans such as the here described species of *Nilssonia* are common. Other typical elements include marattialean and osmundalean ferns (e.g., *Asterotheca* Presl ex Corda, *Speirocarpus* Stur), and sphenopsids (*Equisetites* Sternberg, *Neocalamites* Halle). Conifers have been recorded, but are rare. More than 70 taxa have to date been reported from the Lunz flora (Dobruskina, 1998). Although several other rich floras have been reported from the Carnian [e.g. Neuewelt near Basel, Switzerland (Heer, 1865; Leuthardt, 1901, 1903; Kräusel and Leschik, 1955, 1959; Kräusel and Schaarschmidt, 1966), Raibl, NE-Italy (Bronn, 1858; Schenk, 1866; Stur, 1885), Franconia, S-Germany (Kelber and Hansch, 1995)], the Lunz flora still remains the richest and most diverse Late Triassic flora of the Northern Hemisphere (Dobruskina, 1989, 1994, 1998).

The here reported species of *Nilssonia* are the oldest well-documented representatives of the genus. *Nilssonia* is known from Lunz, but has not been recorded for more or less coeval floras such as Neuewelt and Raibl. However, cuticular studies with regard to coeval floras primarily focussed on fertile organs and not on sterile foliage. Without cuticles, it is difficult, if not impossible, to distinguish between bennettitalean and cycadalean leaves. Broglia Loriga et al. (2002) briefly mentioned the occurrence of *Nilssonia* in the Anisian flora from the Kühwiesenkopf in the Dolomites (N-Italy). Schenk (1867) reported two *Nilssonia* species from the Upper Keuper (Rhaetian) of Franconia, and Ash (2001) mentioned a *Nilssonia* species from the Upper Triassic Chinle Formation of North America. *Nilssonia* is very common in the Jurassic, and known from various parts of the world, e.g., Europe (Nathorst, 1879, 1909; Lundblad, 1950; Harris, 1964; Kvacek, 1995; Kelber, 1998; Watson and Cusack, 2005), Iran and Afghanistan (Sadovnikov, 1989; Schweitzer et al., 2000), India (Sahni and Rao, 1931, 1934), Japan (Yabe, 1925), Greenland (Harris, 1932, 1946; Boyd, 2000).

Within the Triassic of the paratropics several phases in the development of the flora can be recognized. Earliest Triassic floras were dominated by lycopsids (*Pleuromeia* Corda ex Giebel). In the early Anisian a conifer-dominated flora with *Voltzia* Brongniart, *Pelourdea* Seward and *Aethophyllum* Brongniart appeared.

Plate VI. *Nilssonia neuberi* nov. spec.

1. central part of a well preserved leaf, holotype (GBA, 1909/003/0576), scale bar = 1 cm;
2. part of an excellently preserved leaf (NRM, S148579), scale bar = 1 cm;
3. detail of a leaf, with leaf segments inserted at the upper side of the rachis, epitype (GBA, 2006/004/0014), scale bar = 1 cm;
4. abaxial cuticle, stoma with strongly cutinized dorsal walls of the guard cells (NRM, S148579/0007), scale bar = 10 µm;
5. very large and excellently preserved leaf, epitype (GBA, 2006/004/0014), scale bar = 3 cm;
6. abaxial cuticle, overview showing arrangement pattern of stomata (NRM, S148579/0004), scale bar = 100 µm;
7. abaxial cuticle, stoma with strongly cutinized dorsal walls of the guard cells (NRM, S148579/0004), scale bar = 10 µm;
8. abaxial cuticle, stoma with strongly cutinized dorsal walls of the guard cells (NRM, S148579/0004), scale bar = 10 µm;
9. abaxial cuticle, overview showing arrangement pattern of stomata and vein courses (NRM, S148579/0007), scale bar = 100 µm.

Ladinian floras include a number of elements also known from the Anisian, e.g., the lycopsid *Annalepis zeilleri* Fliche, the fern *Anomopteris mougeotii* Brongniart, together with *Pelourdea vogesiaca* Schimper et Mougeot and several species of *Voltzia*. New elements include the conifer *Elatocladus* Halle, the fern *Cladophlebis* Brongniart and several types of cycadalean foliage, e.g., *Bjuvia* Florin and *Sphenozamites* (Brongniart) Miquel (Kerp, 2000). Although the earliest unequivocal bennettitalean fossils (*Pterophyllum jaegeri* [Schlotheim] Brongniart) have been reported from the Ladinian, it is a rare element (Kelber and Hansch, 1995). Bennettitaleans did not become common until the Carnian, when they were dominant, at least locally like in Lunz (Kelber, 1998; Pott et al., subm.).

The major floristic change took place after the Carnian and before the Rhaetian. Rhaetian floras show a much more modern aspect than Carnian floras, and are characterized by the first major occurrence of a number of leptosporangiate ferns, e.g., Dipteridaceae and Matoniaceae, and conifers, e.g., Cheirolepidiaceae (Hirmeriellaceae) (Kelber and Hansch, 1995; Kerp, 2000). Putative Cheirolepidiaceae have been reported from the Chinle Formation (Carnian) of North America, e.g., *Pagiophyllum* (Ash, 1970), but Cheirolepidiaceae are never common before the Rhaetian (Cleal, 1993). This is also evidenced by the palynological record. Although cheirolepidiaceous pollen is known from older Triassic strata, the first real abundance of *Corollina* (*Classopollis*) has been recorded for the Rhaetian (Visscher and Brugman, 1981; Traverse, 1988).

The earliest Dipteridaceae (e.g., *Clathropteris* Brongniart) have been described from the middle Carnian of Franconia (Kelber and Hansch, 1995), and this genus is also known from Lunz (Stur, 1885). The earliest Matoniaceae (*Phlebopteris* Brongniart) are known from the Carnian Chinle Formation of North America (Ash et al., 1982; Ash, 2005). However, altogether Rhaetian floras are much more similar to Jurassic floras than to older Triassic floras (Kelber and Hansch, 1995, Kelber, 1998). Unfortunately, very little is known about the Norian vegetation because diverse Norian macrofloras are very rare, and most Norian floras are dominated by conifers (Kelber and Hansch, 1995; Ash, 1999).

Although the fossils *Nilssonia* from Lunz do not represent the earliest record of the genus it is noteworthy that *Nilssonia*, a genus traditionally regarded as a typically Jurassic group, is represented by four different species. In addition, *Nilssonia* is relatively common in the Lunz flora. The earliest Cycadales have been described from the Lower Permian of China (Zhu and Du, 1981; Gao and Thomas, 1989a,b). Nevertheless, cycadalean foliage is relatively rare in pre-Carnian strata.

During the Carnian, Lunz was positioned at a palaeolatitude of c. 30° N (Scotese, 2003; Blakey, 2005). According to reconstructions of Scotese (2003), the climate in this region was cool temperate to locally arid. Palaeogeographical reconstructions show that the Lunz flora grew in a lowland setting. The coal-bearing beds are intercalated between fully marine beds. The presence of coal seams indicates that the environment was stable for longer periods of time, enabling the accumulation of large amounts of plant material (Kerp, 2000). The preservation of the large amounts of peat, which were later altered into coal, requires special conditions, including minimal oxidation and bacterial decay. These latter conditions are usually reached in peat bogs with a high groundwater table, reduced oxygen supply and low pH values. The abundance of ferns and sphenophytes, the latter often occurring in monotypical associations, indeed indicate humid to very humid environments. The abundance of very large randomly oriented and well preserved leaves suggests minimal transport of the plant material.

The Lunz flora contains a number of elements that are regarded as typical for younger Mesozoic floras, i.e. Rhaetian (Nathorst, 1876, 1878–1886; Johansson, 1922; Harris, 1946; Lundblad, 1950; Kelber, 1998) and younger. Lunz is one of the earliest occurrences of the bennettitaleans, notably the morphogenus *Pterophyllum* (Cleal, 1993; Kelber, 1998, 2005). Moreover, the Lunz flora contains very early representatives of the bennettitalean genus *Nilssoniopteris* Nathorst (Pott et al., subm.). The description of the cycadalean foliage morphogenus *Nilssonia* further substantiates the significance of the Lunz flora with regard to a more complete understanding of the vegetational changes and evolutionary innovations that occurred during the Middle to Late Triassic, especially the first appearances of genera that are very common and widespread in the Rhaetian–Jurassic.

As a result, the Lunz flora obviously represents a mixture, in which typical elements of older Mesozoic, i.e. pre-Rhaetian, floras co-occur with forms that are characteristic constituents of younger and more modern, post-Carnian floras. A number of recent studies indicate that several plant groups and genera evolved much earlier in the Triassic than previously thought (Wachtler and Van Konijnenburg-van Cittert, 2000; Broglia Loriga et al., 2002; Passoni and Van Konijnenburg-van Cittert, 2003; Kustatscher et al., 2004; Kustatscher and Van Konijnenburg-van Cittert, 2005). Therefore, it may be concluded that, within the Triassic, a major floral turnover did not occur, but rather the floral composition changed gradually.

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Appendix A

Abbreviations used in the text are as follows:

GBA — Geologische Bundesanstalt, Wien (Geological Survey of Austria, Vienna, Austria),
NHM — Naturhistorisches Museum, Wien (Museum of Natural History, Vienna, Austria),
NRM — Naturhistoriska Riksmuseet, Stockholm (Museum of Natural History, Stockholm, Sweden),
MNB — Museum für Naturkunde, Berlin (Museum of Natural History, Berlin, Germany),
RUU — Laboratory of Palaeobotany and Palynology, University Utrecht, The Netherlands,
NAT — Nationaal Naturhistorisch Museum Naturalis, Leiden (Museum of Natural History, Leiden, The Netherlands),
JOA — Landesmuseum Joanneum, Graz (State Museum Joanneum, Graz, Austria),
SPO — Niederösterreichisches Landesmuseum, St. Pölten (State Museum of Lower Austria, St. Pölten, Austria),
PBO — Forschungsstelle für Paläobotanik, Münster (Palaeobotany Research Group, Münster, Germany).

References

Ash, S.R., 1970. *Pagiophyllum simpsonii*, a new conifer from the Chinle Formation (Upper Triassic) of Arizona. Journal of Paleontology 44, 945–952.

Ash, S., 1999. An Upper Triassic upland flora from North Central New Mexico, U.S.A. Review of Palaeobotany and Palynology 105, 183–199.

Ash, S., 2001. New cycadophytes from the Upper Triassic Chinle Formation of the southwestern United States. Paleobios 21, 15–28.

Ash, S., 2005. A new Upper Triassic flora and associated invertebrate fossils from the basal beds of the Chinle Formation, near Cameron, Arizona. Paleobios 25, 17–34.

Ash, S., Litwin, R.J., Traverse, A., 1982. The Upper Triassic fern *Phlebobteris smithii* (Daugherty) Arnold ant its spores. Palynology 6, 203–219.

Bachmayer, F., Kollmann, H.A., 1969. Schätze im Boden—Bilder aus Österreichs Vergangenheit, 2nd edn. Naturhistorisches Museum Wien, Wien.

Bhardwaj, D.C., Singh, H.P., 1964. An Upper Triassic miospore assemblage from the coals of Lunz, Austria. Palaeobotanist 12, 28–44.

Blakey, R., 2005. Global Earth History. Published online at http://jan.ucc.nau.edu/~rcb7/RCB.html. Last hit: 21.03.2006.

Boyd, A., 2000. Bennettitales from Early Cretaceous floras of West Greenland: *Pterophyllum* and *Nilssoniopteris*. Palaeontographica Abteilung B Paläophytologie 255, 47–77.

Broglia Loriga, C., Fugagnoli, A., Van Konijnenburg-van Cittert, J.H.A., Kustatscher, E., Posenato, R., Wachtler, M., 2002. The Anisian macroflora from the Northern Dolomites (Monte prà della Vacca/Kühwiesenkopf, Braies): a first report. Rivista Italiana di Paleontologia e Stratigrafia 108, 381–390.

Brongniart, A., 1825. Observations sur les Végétaux fossiles renfermés dans les Grès de Hoer en Scanie. Annales des Sciences Naturelles 4, 200–224.

Bronn, H.G., 1858. Beiträge zur Triasischen Fauna und Flora der bituminösen Schiefer von Raibl, nebst Anhang über die Kurr'sche Sippe *Chiropteris* aus dem Lettenkohlen-Sandsteine. Schweizerbart, Stuttgart.

Cleal, C.J., 1993. In: Benton, M.J. (Ed.), Gymnospermophyta. The Fossil Record, vol. 2. Chapman and Hall, London.

Compter, G., 1874. Ein Beitrag zur fossilen Keuperflora. Nova Acta der kasierlichen Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher 37, 10–13.

Compter, G., 1894. Die fossile Flora des unteren Keupers von Ostthüringen. Zeitschrift für Naturwissenschaften 37, 205–230.

Cornet, B., Olson, P.E., 1990. Early to Middle Carnian (Triassic) Flora and Fauna of the Richmond and Taylorsville Basins, Virginia and Maryland, U.S.A. Virginia Museum of Natural History, Martinsville.

Dobruskina, I.A., 1989. The alpine Lunz-flora — a standard flora for the carnian stage of the Triassic. International Geological Review 31, 1209–1215.

Dobruskina, I.A., 1994. Triassic Floras of Eurasia. Springer, Wien.

Dobruskina, I.A., 1998. Lunz flora in the Austrian Alps — a standard for Carnian floras. Palaeogeography, Palaeoclimatology, Palaeoecology 143, 307–345.

Dower, B.L., Bateman, R.M., Stevenson, D.W., 2004. Systematics, ontogeny, and phylogenetic implications of exceptional anatomically preserved cycadophyte leaves from the Middle Jurassic of Bearreraig Bay, Skye, Northwest Scotland. Botanical Review 70, 105–120.

Dunay, R.F., Fisher, M.J., 1978. The Carnian palynofloral succession in the Northern Calcarous Alp, Lunz-am-See, Austria. Pollen et Spores 20, 177–187.

Feistmantel, O., 1877. Jurassic (Liassic) flora of the Rajmahal Group in the Rajmahal Hills. Memoirs of the Geological Society of India, Palaeontologia Indica Serie II 53–162.

Florin, R., 1933. Studien über die Cycadales des Mesozoikums. Kungliga Svenska Vetenskapsakademiens Handlingar, Tredje Serien 12, 1–134.

Fontaine, W.M., 1883. Contributions to the Knowledge of the Older Mesozoic Flora of Virginia. Government Printing, Washington.

Gao, Z., Thomas, B.A., 1989a. Occurrence of earliest cycads in the Permian of China and its bearing on their evolution. Chinese Science Bulletin 34, 766–769 [in Chinese].

Gao, Z., Thomas, B.A., 1989b. A review of fossil cycad megasporophylls, with new evidence of *Crossozamia* Pomel and its associated leaves from the Lower Permian of Taiyuan, China. Review of Palaeobotany and Palynology 60, 205–223.

Geologische Bundesanstalt Wien, GBA, 2002. Rocky Austria-Eine bunte Erdgeschichte von Österreich. Geologische Bundesanstalt Wien, Wien.

Harris, T.M., 1932. The fossil flora of Scoresby Sound East Greenland — Part 3: Caytoniales and Bennettitales. Meddelelser om Grønland 85, 1–133.

Harris, T.M., 1943. Notes on the Jurassic Flora of Yorkshire. Annals and Magazine of Natural History, Series II 10, 838–854, 7–9.

Harris, T.M., 1946. Liassic and Rhaetic plants collected in 1936–38 from East Greenland. Meddelelser om Grønland 114, 1–40.

Harris, T.M., 1964. The Yorkshire Jurassic Flora II. Trustees of the British Museum (Natural History), London.

Heer, O., 1865. Die Urwelt der Schweiz. Schulthess, Zürich.

Johansson, N., 1922. Die rhätische Flora der Kohlengruben bei Stabbarp und Skromberga in Schonen. Kungliga Svenska Vetenskapsakademiens Handlingar 63, 1–78.

Kelber, K.-P., 1998. Phytostratigraphische Aspekte der Makrofloren des süddeutschen Keupers. Documenta Naturae 117, 89–115.

Kelber, K.-P., 2005. Beyond the Permian–Triassic extinction events: the highly diverse lower Keuper flora (Ladinian, Triassic) of southern Germany. Workshop on Permian–Triassic Palaeobotany and Palynology Bolzano/Bozen (Italy), June 16–18, 2005, Abstract Book.

Kelber, K.-P., Hansch, W., 1995. Keuperpflanzen. Die Enträtselung einer über 200 Millionen Jahre alten Flora. Museo 11, 1–157.

Kerp, H., 1990. The study of fossil gymnosperms by means of cuticular analysis. Palaios 5, 548–569.

Kerp, H., 2000. The modernization of landscapes during the Late Paleozoic–Early Mesozoic. In: Gastaldo, R.A., DiMichele, W.A. (Eds.), Phanerozoic Terrestrial Ecosystems. Paleontological Society Papers, pp. 79–113.

Kerp, H., Krings, M., 1999. Light microscopy of cuticules. In: Jones, T. (Ed.), Fossil Plants and Spores: Modern Techniques. Geological Society, London, pp. 52–56.

Krasser, F., 1909. Zur Kenntnis der fossilen Flora der Lunzer Schichten. Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt 59, 1–26.

Kräusel, R., 1953. Ein neues *Dioonitocarpidium* aus der Trias von Lunz. Senckenbergiana 34, 105–108.

Kräusel, R., Leschik, G., 1955. Die Keuperflora von Neuewelt bei Basel-I. Koniferen und andere Gymnospermen. Schweizer Paläontologische Abhandlungen 71, 1–27.

Kräusel, R., Leschik, G., 1959. Die Keuperflora von Neuewelt bei Basel-III. Equisetaceen. Schweizer Paläontologische Abhandlungen 77, 5–19.

Kräusel, R., Schaarschmidt, F., 1966. Die Keuperflora von Neuewelt bei Basel-IV. Pterophyllen und Taeniopteriden. Schweizer Paläontologische Abhandlungen 84, 5–79.

Krystyn, L., 1978. Eine neue Zonengliederung im alpin-mediterranen Unterkarn. In: Zapfe, H. (Ed.), Beiträge zur Biostratigraphie der Tethys-Trias. Springer, Wien.

Kustatscher, E., Van Konijnenburg-van Cittert, J.H.A., 2005. The Ladinian flora (Middle Triassic) of the Dolomites: palaeoenvironmental reconstructions and palaeoclimatic conclusions. GeoAlp 2, 31–52.

Kustatscher, E., Wachtler, M., Van Konijnenburg-van Cittert, J.H.A., 2004. A number of additional and revised taxa from the Ladinian flora of the Dolomites, Northern Italy. GeoAlp 1, 57–69.

Kvacek, J., 1995. Cycadales and Bennettitales leaf compressions of the Bohemian Cenomanian, central Europe. Review of Palaeobotany and Palynology 84, 389–412.

Leuthardt, F., 1901. Beiträge zur Kenntnis der Flora und Fauna der Lettenkohle von Neuewelt bei Basel. Eclogae Geologicae Helvetiae 125–128.

Leuthardt, F., 1903. Die Keuperflora von Neuewelt bei Basel-I. Teil Phanerogamen. Abhandlungen der Schweizer Paläontologischen Gesellschaft 30, 1–23.

Lundblad, A.B., 1950. Studies in the Rhaeto–Liassic floras of Sweden. I. Pteridophyta, Pteridospermae and Cycadophyta from the mining district of NW Scania. Kungliga Svenska Vetenskapsakademiens Handlingar, Fjärde Serien 1, 1–82.

Menendez, C.A., 1952. La Flora Mesozoica de la Formacion Llantenes. Revista del Instituto Nacional de Investigacion de las Ciencas Naturales 11, 147–261.

Nathorst, A.G., 1876. Anmärkningar om den fossilen floran vid Bjuf i Skåne. Öfversigt af Konglika Vetenskaps-Akademiens Förhandlingar 1, 29–41.

Nathorst, A. G., 1878–1886. Om floran i Skånes kolförande bildningar-I. Floran vid Bjuf. Sveriges Geologiska Undersökning Serie C 27, 33, 85, 1–126.

Nathorst, A.G., 1879. Om floran i Skånes kolförande bildningar-I. Floran vid Bjuf (andra häftet). Sveriges Geologiska Undersökning. Ser. Ca, Avhandlingar Och Uppsatser 335, 55–82.

Nathorst, A.G., 1909. Über die Gattung *Nilssonia* Brongn. Kungliga Svenska Vetenskapsakademiens Handlingar 43, 3–37.

Oldham, T., Morris, J., 1863. Fossil Flora of the Rajmahal Series in the Rajmahal Hills. Memoirs of the Geological Society of India, Palaeontologia Indica Series II 1–52.

Passoni, L., Van Konijnenburg-van Cittert, J.H.A., 2003. New taxa of fossil Carnian plants from Mount Pora (Bergamasc Alps, Northern Italy). Review of Palaeobotany and Palynology 123, 321–346.

Potonié, H., 1899. Lehrbuch der Pflanzenpalaeontologie mit besonderer Rücksicht auf die Bedürfnisse des Geologen. Dümmler, Berlin.

Rühle von Lilienstern, H., 1933. Die Pflanzenwelt des unteren Keupers. Mitteilungen der Gemeinde der Steinsburgfreunde 2, 12–22.

Sadovnikov, G.N., 1989. *Taeniopteris*, *Nilssoniopteris* and *Nilssonia* in the Late Triassic flora of Iran. Paleontological Journal 23, 95–100.

Sahni, B., Rao, A.R., 1931. On some Jurassic plants from the Rajmahal Hills. Journal and Proceedings of the Asiatic Society of Bengal (New Series) XXVII 183–208.

Sahni, B., Rao, A.R., 1934. *Rajmahalia paradoxa* gen. et sp. nov. and other Jurassic plants from the Rajmahal Hills. Proceedings of the Indian Academy of Sciences, I 258–269.

Schenk, A., 1866. Über die Flora der schwarzen Schiefer von Raibl. Würzburger Naturwissenschaftliche Zeitschrift VI, 10–20.

Schenk, A., 1867. Die fossile Flora der Grenzschichten des Keupers und Lias Frankens. Kreidel, Wiesbaden.

Schimper, W., Schenk, A., 1890. Palaeophytologie. In: Zittel, K.A. (Ed.), Handbuch der Palaeontologie. Oldenbourg, München, pp. 211–232.

Schmidt, M., 1928. Die Lebewelt unserer Trias. Hohenlohe'sche Buchhandlung, Öhringen.

Schweitzer, H.-J., Kirchner, M., Van Konijnenburg-van Cittert, J., 2000. The Rhaeto–Jurassic flora of Iran and Afghanistan. 12. Cycadophytina II. Nilssoniales. PAlaeontographica Abteilung B Paläophytologie 254–263.

Scotese, C.R., 2003. Paleomap Project. Published online at www.scotese.com. Last hit: 21.03.2006.

Seward, A.C., 1917. Fossil Plants. Hafner, New York. reprint 1969.

Stur, D., 1871. Lunzer Sandstein. In: Direction des geognostisch-montanen Vereines für Steiermark (Ed.), Geologie der Steiermark. Verlag des geognostisch-montanen Vereines für Steiermark, Graz, pp. 242–316.

Stur, D., 1885. Die obertriadische Flora der Lunzer-Schichten und des bituminösen Schiefers von Raibl. Denkschriften der kaiserlichen Akademie der Wissenschaften Wien 3, 93–103.

Stur, D., 1888. Die Lunzer (Lettenkohle-)Flora in den "older mesozoic beds of the Coal-Field of Eastern Virginia". Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt Wien 10, 203–217.

Traverse, A., 1988. Paleopalynology. Unwin Hyman, Boston.

Turek, V., Marek, J., Benes, J., 1990. Fossilien. Aventinum, Praha.

Van Konijnenburg-van Cittert, J.H.A., Mikuz, V., Pavsic, J., 2001. *Pterophyllum* (Cycadopsida) from Carnian beds in Poljane valley (Slovenia). Geologija 44, 317–323.

Verloop, J.H., 1908. Profil der Lunzer Schichten in der Umgebung von Lunz. Zeitschrift der Deutschen Geologischen Gesellschaft 60, 81–88.

Visscher, H., Brugman, W.A., 1981. Ranges of selected palynomorphs in the Alpine Triassic of Europe. Review of Palaeobotany and Palynology 34, 115–128.

Wachtler, M., Van Konijnenburg-van Cittert, J.H.A., 2000. The fossil flora of the Wengen Formation (Ladinian) in the Dolomites (Italy). Beiträge Zur Paläontologie 25, 105–141.

Watson, J., Cusack, H.A., 2005. Cycadales of the English Wealden. Monograph of the Palaeontographical Society 1–189.

Watson, J., Sincock, C.A., 1992. Bennettitales of the English Wealden. Monograph of the Palaeontographical Society 1–228.

Yabe, H., 1925. Notes on some Mesozoic plants from Japan, Korea and China, in the collection of the Institute of Geology and Paleontology of Tôhoku Imperial University. The Scientific Reports of the Tôhoku Imperial University, Sendai, Japan — 2nd Series (Geology) 7, 1–28.

Zhu, J., Du, X., 1981. A new cycad — *Primocycas chinensis* gen. et sp. nov. discovers from the Lower Permian in Shanxi, China and its significance. Acta Botanica Sinica 23, 401–404 [in Chinese].

CHAPTER 6

Pseudoctenis cornelii nov. spec. (cycadalean foliage) from the Carnian (Upper Triassic) of Lunz, Lower Austria

Christian Pott, Hans Kerp & Michael Krings

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Abstract.—*Pseudoctenis* (cycadalean foliage) is a characteristic element of Rhaetian (uppermost Triassic) and Jurassic floras from Europe. Here we describe a new species, *Pseudoctenis cornelii*, from the Carnian flora of Lunz in Lower Austria that provides the earliest persuasive evidence for this genus in the European Triassic. The new species is included in *Pseudoctenis* based on macromorphology and epidermal anatomy; a particularly significant feature is sunken, haplocheilic stomata, partially closed by overarching papillae. *Pseudoctenis cornelii* displays features that are consistent with those extant plants adaptated to life in (seasonally) dry environments.

Keywords.—Cuticular analysis, Cycadales, foliage, Carnian, Triassic flora, palaeoecology.

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Pseudoctenis cornelii nov. spec. (cycadalean foliage) from the Carnian (Upper Triassic) of Lunz, Lower Austria

By Christian POTT[1], Hans KERP[1] and Michael KRINGS[2]

(With 1 textfigure and 3 plates)

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Zusammenfassung

Die Gattung *Pseudoctenis* (Cycadeenbeblätterung) ist ein charakteristisches Element rhätischer (oberste Trias) und jurassischer Floren in Europa. Aus der Flora von Lunz in Niederösterreich wird eine neue Art, *Pseudoctenis cornelii*, beschrieben, die den ältesten sicheren Nachweis der Gattung *Pseudoctenis* aus der europäischen Trias darstellt. Die neue Art wird auf der Basis makromorphologischer und epidermal-anatomischer Merkmale zu *Pseudoctenis* gestellt; besonders wichtig sind die eingesenkten, haplocheilen Spaltöffnungen, die von Papillen der umgebenden Nebenzellen überdeckt sind. *Pseudoctenis cornelii* weist Merkmale auf, die in ganz ähnlicher Weise bei heutigen, an ein Leben in (saisonal) trockenen Lebensräumen angepassten Pflanzen ausgebildet sind.

Schlüsselwörter: Kutikularanalyse, Cycadales, Beblätterung, Karn, Triassische Flora, Paläoökologie

Abstract

Pseudoctenis (cycadalean foliage) is a characteristic element of Rhaetian (uppermost Triassic) and Jurassic floras from Europe. Here we describe a new species, *Pseudoctenis cornelii*, from the Carnian flora of Lunz in Lower Austria that provides the earliest persuasive evidence for this genus in the European Triassic. The new species is included in *Pseudoctenis* based on macromorphology and epidermal anatomy; a particularly significant feature is sunken, haplocheilic stomata, partially closed by overarching papillae. *Pseudoctenis cornelii* displays features that are consistent with those extant plants adaptated to life in (seasonally) dry environments.

Keywords: Cuticular analysis, Cycadales, foliage, Carnian, Triassic flora, palaeoecology

Introduction

The famous Carnian flora from Lunz in Lower Austria is one of only a few well-preserved floras from the Alpine Triassic (CLEAL 1993; DOBRUSKINA 1998). One of the remarkable features of this flora is the abundance of compressed cycadophyte (i.e. Cycadales and Bennettitales) reproductive structures and foliage. While several detailed studies exist that focus on the fertile cycadophyte remains (KRASSER 1917, 1919; KRÄUSEL 1948,

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[1] Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, 48143 Münster, Germany. – e-mail: christian.pott@uni-muenster.de

[2] Bayerische Staatssammlung für Paläontologie und Geologie und GeoBio-Center^{LMU}, Richard-Wagner-Straße 10, 80333 Munich, Germany

1949, 1953), the innumerable foliage specimens have not received much scholarly attention to date. This is due in part to the fact that the fossils are spread among collections throughout Europe. Moreover, the various 19th and early 20th century collectors, traders, and curators, who labelled most of the fossils, along with the early scholars studying the material, unintentionally created considerable confusion with regard to the scientific names given to the different foliage types based on macromorphology. This confusion remains to date and renders establishing a trustworthy inventory of the plants that lived in the Lunz area during the Carnian a difficult task.

Cuticles are known to provide a wealth of information useful in the taxonomy of compression seed plant fossils, but also important with regard to paleobiological and paleoecological considerations (e.g., KERP 1990; MCELWAIN & CHALONER 1996). Although cuticular analysis has long since proven to provide a more complete understanding of many ancient seed plants, it has largely been neglected in studies of the cycadophyte foliage from Lunz. To fill this gap, we have initiated a research project that focuses on seed plant cuticles from Lunz. In the course of the last two years, detailed information on the epidermal anatomy of most of the proposed "species" has been gathered. As a result, we now have an extensive set of heretofore largely unavailable data based on epidermal features to interpret this famous flora.

Our cuticle studies of the Lunz cycadophytes revealed that the status of many of the foliage "species", which were established based exclusively on macromorphological features, is not supported by the epidermal anatomy. On the other hand, the studies also produced evidence for the occurrence in the Lunz flora of a few taxa that are new to science. We here describe the macromorphology and epidermal anatomy of *Pseudoctenis cornelii*, a new cycadalean foliage species from Lunz. This species provides the earliest persuasive evidence for the genus *Pseudoctenis* SEWARD in the European Triassic. *Pseudoctenis cornelii* is compared to other species in the genus, and some hypotheses with regard to the palaeoautecology are offered based on the adaptative significance of macromorphological and epidermal features.

The genus *Pseudoctenis* SEWARD

The cycadalean foliage genus *Pseudoctenis* is a common element of several Rhaetian (uppermost Triassic) and many Jurassic floras in Europe (SEWARD 1911, 1917; HARRIS 1932, 1964). SEWARD (1911) introduced the genus for *Zamites*-type leaves from the Jurassic of Sutherland, Great Britain. However, this author did not provide a generic diagnosis, but only a comparison to *Ctenis* LINDLEY et W. HUTTON (cycadalean foliage). Although *Ctenis* and *Pseudoctenis* are similar in macromorphology, SEWARD (1911) notes that they are easily distinguishable based on the occurrence of anastomoses in the venation of *Ctenis*. HARRIS (1950) concurs with SEWARD in that the *Ctenis-Pseudoctenis* series consists of two distinct groups.

Nevertheless, the genus *Pseudoctenis* historically often was used in an arbitrary way because no valid generic diagnosis existed. As a result, through the years, numerous foliage specimens were accommodated in genera such as *Pterophyllum* BRONGNIART, *Ctenophyllum* SCHIMPER, and *Zamites* BRONGNIART, although they actually belonged to *Pseudoctenis*. However, this changed when HARRIS (1932) described epidermal features of *Pseudoctenis spectabilis* Harris, *P. depressa* Harris, and *P. lanei* Thomas from the Jurassic of Yorkshire. The epidermal anatomy establishes the cycadalean affinities of *Pseudoctenis* based on the presence of haplocheilic stomata, a feature that generally discriminates cycadalean from bennettitalean foliage (Florin 1933). Stomatal morphology is especially valuable in distinguishing *Pseudoctenis* leaves from those bennettitalean foliage types that are similar in macromorphology, e.g., certain taxa in *Pterophyllum* and *Zamites*. Harris (1932, 1964) provides a diagnosis for *Pseudoctenis* that includes both macromorphological and epidermal characters. Nevertheless, the validity of *Pseudoctenis* Seward remains technically problematical because the original study (Seward 1911) does not include a diagnosis, and useful cuticles cannot be obtained from the type specimen (cf. Harris 1964).

Geological setting, material and methods

The material comes from Lunz in the Northern Calcareous Alps of Lower Austria, and was collected during the late 19th century from several coal mines in the area around Lunz-am-See, approximately 100 km west of Vienna (fig. 1). Coal mining in the Lunz area ceased after World War II., and collection of new material is today limited to the old spoil tips; however, spoil tip fossils are usually strongly weathered. The fossils occur in the "Lunzer Sandstein", which is part of the Lunz beds. The Lunz Formation (= Lunzer Schichten) consists of sandstones at basis, followed by marine marls gradually grading upwards into terrestrial sands, shales, and coal. The coal-bearing part of the sequence is overlain by marls and with a sandstone layer at the top. The plant fossils occur in the shales associated with the coal beds. The exact age of the Lunz Formation remains a problem to date since adequate biomarkers such as ammonoids and conodonts are missing. However, a recent correlation of biostratigraphically well-established sections in the Hallstatt and Reifling Intraplatform Basins (Hornung & Brandner 2005) suggests that the Lunz Formation may be correlated with the upper part of the Reingraben Formation (T. Hornung, pers. comm.). Taking this into account, the Lunz Formation is approximately late Julian (Julian 2/II) in age. Palynological studies indicate a Carnian (Bharadwaj & Singh 1964) and Julian age (Dunay & Fisher 1978). The Opponitzer Limestone, the upper sub-unit of the Lunzer Schichten, has been dated as Tuvalian by Dunay & Fisher (1978).

The *Pseudoctenis cornelii* specimens are kept in the collections of the Natural History Museum Vienna (NHMW), and the Geological Survey of Austria (GBA), Vienna, under accession numbers NHMW 1887/0001/0032 and 1887/0001/0033, and GBA 1909/002/0355, 1909/003/0195, and 1909/003/0783.

Cuticles were prepared according to procedures outlined in Kerp (1990), and Kerp & Krings (1999). Pieces of rock with identifiable plant remains were dissolved in hydroflouridic acid (HF), and subsequently macerated according to the standard procedure using Schulze's reagent (HNO_3 with a few crystals of $KClO_3$) and 5–10 % Potassium hydroxide. Macerated cuticles were washed in distilled water, gently dehydrated in pure glycerine, and finally mounted in permanent glycerine-jelly microscope slides. Slides are deposited in the collection of the Natural History Museum Vienna (Austria); accession numbers are indicated in the figure captions.

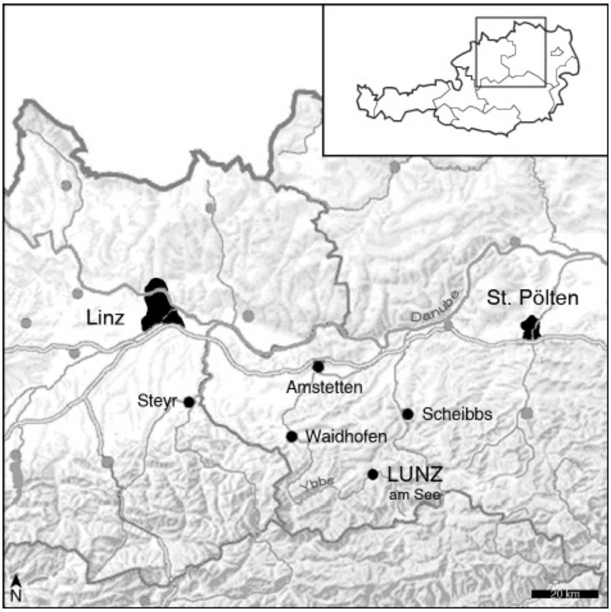

Fig. 1: Geographical position of Lunz-am-See in the Northern Calcareous Alps of Lower Austria.

Hand specimens were photographed with a Nikon D 100 digital camera; in order to increase contrast, cross-polarization (i.e. polarized light sources together with a polarizing filter over the camera lens) was used. Cuticles were analysed with a Leitz Diaplan microscope and photographed with a Nikon DS-5M digital camera.

Abbreviations:

NHMW – Naturhistorisches Museum Wien, Österreich
GBA – Geologische Bundesanstalt, Wien, Österreich

Systematic part

Division Gymnospermophyta (= Gymnospermae, auct.)
Subdivision Cycadophytina sensu CLEAL & REES, 2003
Class Cycadopsida MEYEN, 1984
Order Cycadales DUMORTIER, 1829
Genus *Pseudoctenis* SEWARD, 1911 emend. HARRIS, 1964

***Pseudoctenis cornelii* nov. spec.**

Plates 1–3

Holotype: NHMW 1887/0001/0033 (pl. 1, fig. 1)

Paratypes: GBA 1909/002/0355 (pl. 1, fig. 4), GBA 1909/003/0195 (pl. 1, fig. 5), GBA 1909/003/0783 (pl. 1, fig. 3), NHMW 1887/0001/0032.

Type locality: Lunz-am-See, Lower Austria.

Stratum typicum: Lunzer Schichten, Carnian (Upper Triassic).

Diagnosis: Leaves pinnate; lamina subdivided into narrow, tongue-shaped leaf segments, oppositely positioned and inserted laterally to the rachis, tapering, tips rounded; each leaf segment with several parallel veins; veins may fork once; leaves with delicate cuticles, hypostomatic, epidermal cells rectangular to isodiametric, cell walls undulate; stomata sunken, haplocheilic, occurring in intercostal fields; guard cells with prominent dorsal thickenings; subsidiary cells bear small hollow papillae that partially cover the guard cells; normal abaxial epidermal cells may bear short hollow papillae.

Etymology: The specific epithet is proposed in honour of the biologist Arne CORNELIUS (1980–2001), a friend and colleague of the first author, who was murdered during a research trip to Sabah, Borneo, Malaysia.

Description: The material consists of leaf fragments up to 14.5 cm long; based on the material at hand we estimate that adult leaves of *Pseudoctenis cornelii* were up to 70 cm long. The pinnate blade is elliptical, with its widest spread reaching well over 15 cm. The blade has a somewhat lax appearance because spacing of the leaf segment is relatively loose (pl. 1, figs 1–5). The rachis is massive and straight, up to 10 mm wide and roughly marked with longitudinal striae. Tongue-shaped leaf segments extend from the rachis at angles between 80° and 90°. They are oppositely to sub-oppositely positioned, polymorphous (size and shape strongly depend on the position in the leaf), generally oblong in outline, tapering, and with rounded tips. The largest leaf segments occur in the middle portion of the blade where they may be > 70 mm long and up to 6.5 mm wide. In the proximal portion of the blade, the leaf segments are shorter, up to 25 mm long, and 4–5.3 mm wide, and narrower in proportion to their length. Toward the leaf tip, leaf segment size gradually decreases. The segments are wholly adherent to the rachis and basiscopically decurrent. The venation is conspicuous. Seven to twelve parallel veins enter each leaf segment from the rachis (pl. 1, figs 2, 4). The veins may fork once, shortly after entering the leaf segment. Further forking of the veins in more distal portions of the leaf segments does not occur (pl. 1, fig. 2).

The leaves are hypostomatic and produce fine cuticles. Both the adaxial and abaxial epidermis are differentiated into costal and intercostals fields. The adaxial epidermal cells overlying the veins are rectangular or elongate to isodiametric in outline, and 55–140 µm long and 32.5 to 47.5 µm wide. The anticlinal walls are slightly undulated (pl. 3, figs 4–8, 10). The epidermal cells in the adaxial intercostal fields are rectangular in outline, isodiametric, and generally smaller (between 50 and 87.5 µm long and 30 to 42.5 µm wide) than those seen in the costal fields. The anticlinal cell walls are slightly undulated to sinuous (pl. 3, figs 4–8, 10). Surface ornamentations are not visible, but cuticular thickenings may occur within the individual curves of the sinuous anticlinal walls. The outer periclinal cell walls are delicate and possess a smooth surface. Papillae or trichome bases are absent from the adaxial epidermis.

The abaxial costal fields are composed of 4 to 6 rows of epidermal cells. The epidermal cells over the veins possess delicate walls. The cells are narrow, rectangular or elongate to isodiametric in outline, typically ending acutely, 55–98 µm long and 20–33 µm wide. The anticlinal cell walls are slightly sinuous (pl. 2, figs 2, 9); the outer periclinal walls are smooth. The intercostal fields are broad, between 350 and 450 µm wide, and composed of polygonal to broadly rectangular, isodiametric cells (pl. 2, figs 1, 2, 9) that are up to 55 µm long and between 20 and 37.5 µm wide. Some of the cells bear a small hollow papilla (12–16 µm in diameter). Stomata are confined to the intercostal fields (pl. 2, figs 2, 9). They are haplocheilic, 40-55 µm long and 16–25 µm wide, regularly scattered across the intercostal fields, randomly oriented, and surrounded by 4 to 6 subsidiary cells forming a ?monocyclic stomatal apparatus. The exact form of the subsidiary cells is not discernible. Each subsidiary cell bears a small hollow papilla that overarches the pit mouth and covers the sunken guard cells (pl. 2, figs 1, 3–8, 10).

Remarks: A variety of names, including *Pterophyllum longifolium* BRONGNIART, 1828, *P. riegeri* STUR ex KRASSER, 1909, and "*Ctenophyllum lunzense* STUR", occur on the historic labels attached to the five *Pseudoctenis cornelii* hand specimens, and indicate that different opinions existed with regard to the affinities of the specimens. However, macromorphology and epidermal anatomy do not support placement of the specimens in either of these taxa. Rather, the new species can be referred to the genus *Pseudoctenis* based on a complement of macromorphological and epidermal features, including laterally inserting narrow leaf segments with parallel venation that lacks anatomoses and haplocheilic stomata with sunken guard cells, partly covered by papillae extending from the subsidiary cells. However, *P. cornelii* differs from the typical Jurassic *Pseudoctenis* species in that sinuous anticlinal walls characterize the epidermal cells. Moreover, heavily cutinized rings produced by the subsidiary cells typically surround the sunken guard cells in *Pseudoctenis* (cf. HARRIS 1964); such rings are not developed in *P. cornelii*. Apart from these distinguishing features, the epidermal anatomy of *P. cornelii* closely resembles that seen in *Pseudoctenis* sp. A from the Jurassic of Yorkshire (HARRIS 1964: fig. 38). This author obtained cuticles from an isolated leaf segment, which is nearly identical in size and shape to the leaf segments of *P. cornelii*. HARRIS (1964) states that *Pseudoctenis* sp. A differs from all other *Pseudoctenis* species from the Jurassic of Yorkshire. As a result, this author eventually (HARRIS 1974) assignes *Pseudoctenis* sp. A to *Eretmophyllum whitbiense* THOMAS, 1913 (a member of the Ginkgoales, cf. THOMAS 1913). However, the ginkgoalean affinities of *Pseudoctenis* sp. A remain questionable based on the fragmentary nature of HARRIS' specimen.

With regard to macromorphology, *Pseudoctenis cornelii* closely resembles *Pterophyllum braunianum* GÖPPERT, 1843 var. α from the Rhaeto-Liassic of Franconia (SCHENK 1867: pl. 38). This poorly understood taxon is characterized by loosely spaced, crescent-shaped leaf segments with slightly widened bases that insert laterally into the rachis. However, vein density of *P. braunianum* var. α is apparently slightly lower than that of *P. cornelii* (i.e. 7–12 veins in *P. cornelii* [see above] vs. 5–6 veins in *P. braunianum* var. α [according to SCHENK 1867]). Unfortunately, SCHENK (1867) does not provide a detailed description of the stomata. This aspect would be highly significant since the epidermal anatomy of *P. braunianum* var. α (SCHENK 1867: pl. 38, fig. 9) generally corresponds well to that seen in *P. cornelii*.

A second, superficially very similar form is *Pseudoctenis harringtoniana* BONNETTI, 1968 from the lower Carnian of the Molteno Formation of South Africa (ANDERSON & ANDERSON 1989: pls 169–172). However, documentation of the epidermal anatomy of *P. harringtoniana* remains incomplete to date, and hence a closer comparison of this form to *P. cornelii* is impossible at present.

The epidermal anatomy of *Pseudoctenis cornelii* resembles that seen in *Nilssonia syllis* Harris, 1964 and *N. compta* (Phillips, 1829) Bronn, 1848 (Harris 1964: figs 19, 23). Nevertheless, *P. cornelii* cannot be assigned to *Nilssonia* Brongniart based primarily on the fact that the leaf segments arise laterally in *P. cornelii*, while *Nilssonia* leaf segments are attached to the upper side of the rachis (cf. Schweitzer & Kirchner 1998; van Konijnenburg-van Cittert et al. 2001; Watson & Cusack 2005).

Discussion

The discovery of a new foliage type in the Lunz flora, and subsequent assignment of this type to the cycadalean foliage morphogenus *Pseudoctenis* based on a complement of macromorphological and epidermal characters clearly demonstrates the value of cuticular analyses in more accurately depicting the systematic position of compression foliage fossils.

The genus *Pseudoctenis* is a common element in several Rhaetian (uppermost Triassic) and many Jurassic floras from Europe (Seward 1911, 1917; Harris 1932, 1964; Lundblad 1950; Schweitzer & Kirchner 1998), but has to date not been documented persuasively from older deposits. As a result, the new species *P. cornelii* from the Carnian of Lunz represents the earliest unequivocal evidence for the genus from the European Triassic, with the possible exception of *Pterophyllum braunianum* var. α (Schenk, 1867). However, one putative *Pseudoctenis* species, i.e. *P. middridgensis* Stoneley, 1958, comes from the Upper Permian (Thuringian) of England (Stoneley 1958). *Pseudoctenis middridgensis* is based on a single specimen that yields only small, ill-preserved cuticle fragments from the rachis, and Stoneley (1958: p. 323) notes that, in the absence of adequate knowledge of the epidermal anatomy, assignment of this fossil to *Pseudoctenis* must be considered provisional. While the oldest compelling *Pseudoctenis* fossils in the northern Hemisphere come from the upper Carnian, the earliest evidence for this genus in the southern Hemisphere is from the lower Carnian (e.g., from the Molteno Formation, cf. Anderson & Anderson 1989). Reports of *Pseudoctenis* from other early Late Triassic floras (e.g., from the Santa Juan Formation, cf. Leppe & Moisan 2003; Nielsen 2005) are questionable because the macromorphology of the fossils closely corresponds to that of certain *Pterophyllum* species, and data on the epidermal anatomy are missing.

It is interesting to note that the Lunz flora contains a number of elements that are regarded as typical for modern Mesozoic (i.e. Rhaetian, Jurassic, and Cretaceous) floras. Foremost among these are the bennettitaleans. The representatives from Lunz of the bennettitalean foliage morphogenus *Pterophyllum* are among the oldest in the fossil record (Cleal 1993; Kelber 1998, 2005). Moreover, the Lunz flora contains very early representatives of the cycadalean genus *Nilssonia* (Pott et al., 2007a) and the bennettitalean genus *Nilssoniopteris* Nathorst (Pott et al., in press). The discovery of the cycadalean foliage morphogenus *Pseudoctenis* at Lunz adds yet another typical Jurassic element to this list, and, as a result, further substantiates the significance of the Lunz flora with regard to a more complete understanding of the vegetational changes and evolutionary innovations that occurred in this area during the Mid- to Late Triassic/Early Jurassic transition.

The foliage macromorphology and epidermal anatomy of *Pseudoctenis cornelii* display several features that may have been effective as adaptations to life under conditions with (seasonal) moisture limitation. The strong linear venation of *P. cornelii*, along with a markedly striate rachis, may have been effective in directing rainwater (freshwater) toward the base of the frond. Unfortunately, no supporting microstructures in the form of leaf surface micro-reliefs (cf. Pott et al., 2007b) are recognizable from the cuticles. Moreover, the excellent preservation of the cuticles may suggest that the leaves of *P. cornelii* were coriaceous and perhaps similar to the leaves of modern cycads, oleander, sea lavender, or rubber trees, which are adapted to life in moisture limited and/or saline environments (Fahn & Cutler 1992). The sunken stomata, partly closed by a ring of densely spaced papillae that extend from the subsidiary cells, suggest windy and dry conditions because, in extant plants, sunken stomata that are partially covered by papillae, are often associated with a xeromorphic epidermis, and found in plants that live under arid conditions (Hutchings & Saenger 1987). It is interesting to note in this context that, in *P. cornelii*, the stomatal apparati are characterized by papillae that overarch the stomatal pit, whereas all Jurassic *Pseudoctenis* species possess a heavily cutinized ring produced by the subsidiary cells around the stomatal pits. Harris (1964) regards this ring as a characteristic feature of the Jurassic representatives of *Pseudoctenis*. It is possible to envisage that the densely spaced papillae may have fused over time to form a massive ring, which was perhaps more effective as an adaptation.

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References

Anderson, J.M. & Anderson, H.M. (1989): Molteno Formation (Triassic), Vol. II: Gymnosperms. – 567 pp. – Rotterdam (Balkema).

Bharadwaj, D.C. & Singh, H.P. (1964): An Upper Triassic miospore assemblage from the coals of Lunz, Austria. – The Palaeobotanist **12**: 28-44.

Bonnetti, M.I.R. (1968): Las especies del género *Pseudoctenis* en la flora Triásica de Barreal (San Juan). – Ameghiniana **5**: 433-446.

Brongniart, A. (1828): Prodrome d'une histoire des végétaux fossiles. – VIII+223 pp. – Paris (Levrault).

Bronn, H.G. (1848): Index palaeontologicus oder Uebersicht der bis jetz bekannten fossilen Organismen. Erste Abtheilung, zweite Hälfte. – 604 pp. – Stuttgart (Schweizerbart).

Cleal, C.J. (1993): Gymnospermophyta. In: Benton, M.J. (ed.): The Fossil Record, vol. 2. – p. 795-808. – London (Chapman & Hall).

––– & Rees, P.M. (2003): The Middle Jurassic flora from Stonesfield, Oxfordshire, UK. – Palaeontology **46**: 739-801.

Dobruskina, I.A. (1998): Lunz Flora in the Austrian Alps – a standard for Carnian floras. – Palaeogeography, Palaeoclimatology, Palaeoecology **143**: 307-345.

Dumortier, B.C.J. (1829): Analyse des familles des plantes, avec l'indication des principaux genres qui s'y rattachent. – 104 pp. – Tournay (J. Casterman aîné).

Dunay, R.F. & Fisher, M.J. (1978): The Karnian palynofloral succession in the Northern Calcarous Alps, Lunz-am-See, Austria. – Pollen et Spores **20**: 177-187.

Fahn, A. & Cutler, D.F. (1992): Xerophytes. – IX+176 pp. – Stuttgart (Borntraeger).

Florin, R. (1933): Studien über die Cycadales des Mesozoikums (Bennettitales, pp. 12-30). – Kungliga Svenska Vetenskapsakademiens Handlingar **12**: 4-134.

Göppert, H.R. (1843): Ueber die fossilen Cykadeen überhaupt, mit Rücksicht auf die in Schlesien vorkommenden Arten. – Uebersicht der Arbeiten und Veränderungen der schlesischen Gesellschaft für vaterländische Kultur: 114-144.

Harris, T.M. (1932): The fossil flora of Scoresby Sound East Greenland – Part 3: Caytoniales and Bennettitales. – Meddelser om Grønland **85**: 1-133.

––– (1950): Notes on the Jurassic Flora of Yorkshire, 46-48. Annals and Magazine of Natural History, Series 12, **3**: 1001-1030.

––– (1964): The Yorkshire Jurassic Flora **II**. – VIII+191 pp. – London (Trustees of the British Museum (Natural History)).

––– (1974): The Yorkshire Jurassic Flora **IV**. – 150 pp. – London (Trustees of the British Museum (Natural History)).

Hornung, T. & Brandner, R (2005): Biochronostratigraphy of the Reingraben Turnover (Hallstatt Facies Belt): Local black shale events controlled by regional tectonics, climatic change and plate tectonics. Facies **51**: 460-479.

Hutchings, P. & Saenger, P. (1987): Ecology of Mangroves. – 389 pp. – St Lucia (University of Queensland Press).

Kelber, K.-P. (1998): Phytostratigraphische Aspekte der Makrofloren des süddeutschen Keupers. – Documenta naturae **117**: 89-115.

––– (2005): Beyond the Permian-Triassic extinction events: the highly diverse Lower Keuper flora (Ladinian, Triassic) of Southern Germany. – Workshop on Permian-Triassic Paleobotany and Palynology Bolzano/Bozen (Italy), June 16-18, 2005.

Kerp, H. (1990): The Study of fossil gymnosperms by means of cuticular analysis. – Palaios **5**: 548-569.

––– & Krings, M. (1999): Light microscopy of cuticules. In: Jones, T. (ed.): Fossil Plants and Spores: modern techniques. – pp. 52-56 – London (Geological Society).

Krasser, F. (1909): Zur Kenntnis der fossilen Flora der Lunzer Schichten. – Jahrbuch der kaiserlich-königlich geologischen Reichsanstalt **59**: 1-26.

––– (1917): Studien über die fertile Region der Cycadophyten aus den Lunzer-Schichten: Mikrosporophylle und männliche Zapfen. – Denkschriften der kaiserlichen Akademie der Wissenschaften (Wien), Mathematisch-Naturwissenschaftliche Klasse **94**: 489-553.

––– (1919): Studien über die fertile Region der Cycadophyten aus den Lunzer Schichten: Makrosporophylle. – Denkschriften der kaiserlichen Akademie der Wissenschaften Wien **97**: 1-32.

Kräusel, R. (1948): *Sturiella langeri* nov. gen., nov. sp., eine Bennettitee aus der Trias von Lunz (Nieder-Österreich). – Senckenbergiana **29**: 141-149.

—— (1949): Koniferen und andere Gymnospermen aus der Trias von Lunz, Nieder-Österreich. – Palaeontographica Abt. B, **89**: 35-82.

—— (1953): Ein neues *Dioonitocarpidium* aus der Trias von Lunz. – Senckenbergiana **34**: 105-108.

LEPPE, M. & MOISAN, P. (2003): Nuevos registros de Cycadales y Cycadeoidales del Triásico superior del río Bíobío, Chile. – Revista Chilena de Historia Natural **76**: 475-484.

LUNDBLAD, A.B. (1950): Studies in the Rhaeto-Liassic floras of Sweden. I. Pteridophyta, Pteridospermae and Cycadophyta from the mining district of NW Scania. – Kungliga Svenska Vetenskapsakademiens Handlingar **1**: 1-82.

MCELWAIN, J.C. & CHALONER, W.G. (1996): The fossil cuticle as a skeletal record of environmental change. – Palaios **11**: 376-388.

MEYEN, S.V. (1984): Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. – Botanical Review **50**: 1-111.

NIELSEN, S.N. (2005): The Triassic Santa Juana Formation at the lower Biobío River, south central Chile. – Journal of South American Earth Sciences **19**: 547-562.

PHILLIPS, J. (1829): Illustrations of the Geology of Yorkshire; or, A Description of the Strata and Organic Remains of the Yorkshire Coast: Accompanied by a Geological Map, Sections, and Plates of the Fossil Plants and Animals. – 192 pp. – York (Thomas Wilson).

POTT, C., KERP, H. & KRINGS, M. (2007a): Morphology and epidermal anatomy of *Nilssonia* (cycadalean foliage) from the Upper Triassic of Lunz (Lower Austria). – Review of Palaeobotany and Palynology **143**: 197-217.

—— , KRINGS, M. & KERP, H. (2007b): A surface micro-relief on the leaves of *Glossophyllum florinii* (?Ginkgoales) from the Upper Triassic of Lunz, Austria. – Botanical Journal of the Linnean Society **153**: 87-95.

—— , KRINGS, M. & KERP, H. (in press): The first record of *Nilssoniopteris* (fossil Gymnospermophyta, Bennettitales) from the Carnian (Upper Triassic) of Lunz, Lower Austria – Palaeontology.

SCHENK, A. (1867): Die fossile Flora der Grenzschichten des Keupers und Lias Frankens. – XXIV+232 pp. – Wiesbaden (C. W. Kreidel).

SCHWEITZER, H.-J. & KIRCHNER, M. (1998): Die rhäto-jurassischen Floren des Iran und Afghanistans. 11. Pteridospermophyta und Cycadophyta, I. Cycadales. – Palaeontographica Abt. B, **248**: 1-85.

SEWARD, A.C. (1911): The Jurassic flora of Sutherland. – Transactions of the Royal Society of Edinburgh **47**: 643-709.

—— (1917): Fossil Plants III, (Reprint of 1969). – VIII+656 pp. – New York (Hafner).

STONELEY, H.M.M. (1958): The Upper Permian flora of England. – Bulletin of the British Museum (Natural History) Geology **3**: 293-337.

THOMAS, H. (1913): On some new and rare Jurassic plants from Yorkshire - *Eretmophyllum*, a new type of Ginkgoalean leaf. – Proceedings of the Cambridge Philosophical Society **17**: 256-262.

VAN KONIJNENBURG-VAN CITTERT, J.H.A., MIKUZ, V. & PAVSIC, J. (2001): *Pterophyllum* (Cycadopsida) from Carnian beds in Poljane valley (Slovenia). – Geologija **44**: 317-323.

Verloop, J.H. (1908): Profil der Lunzer Schichten in der Umgebung von Lunz. – Zeitschrift der Deutschen Geologischen Gesellschaft **60**: 81-88.

Watson, J. & Cusack, H.A. (2005): Cycadales of the English Wealden. – Monograph of the Palaeontographical Society, London – 189 pp., 10 pls. – No. 622, issued as Vol. 158 for 2004.

Plate 1

***Pseudoctenis cornelii* nov. spec.**

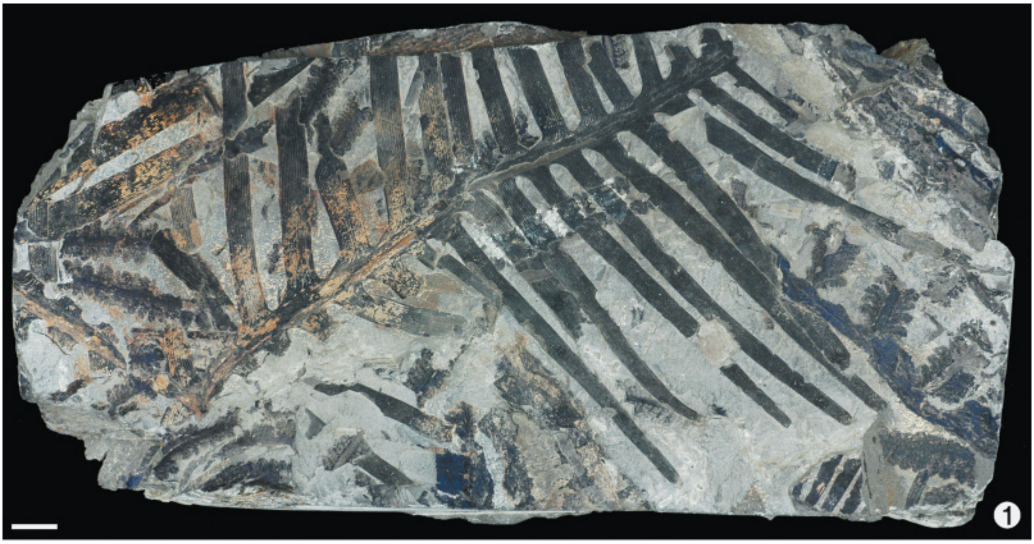
Fig. 1: NHMW 1887/0001/0033 (Holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Mid portion of a leaf – scale bar = 1 cm

Fig. 2: NHMW 1887/0001/0033 (Holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Detail of fig. 1 – scale bar = 5 mm

Fig. 3: GBA 1909/003/0783
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Proximal portion of a leaf – scale bar = 1 cm

Fig. 4: GBA 1909/002/0355
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Detail of a mid portion of a leaf, showing vein courses – scale bar = 5 mm

Fig. 5: GBA 1909/003/0195
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Detail of a median portion of a leaf, showing vein courses – scale bar = 5 mm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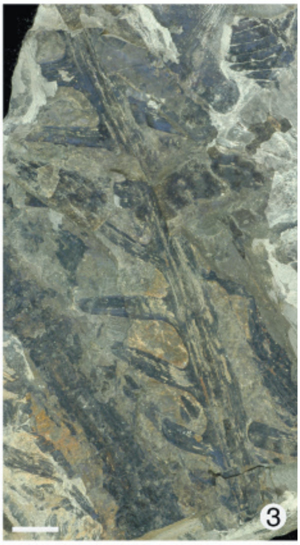
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Plate 2

***Pseudoctenis cornelii* nov. spec. – abaxial cuticle**

Fig. 1: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Abaxial cuticle, detail of intercostal field – scale bar = 50 µm

Fig. 2: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Abaxial cuticle, overview – scale bar = 100 µm

Fig. 3: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Abaxial cuticle, stoma with overarching papilla, view from inside – scale bar = 10 µm

Fig. 4: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Abaxial cuticle, papillae overarching a stoma – scale bar = 10 µm

Fig. 5: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Abaxial cuticle, stoma, view from the inside – scale bar = 10 µm

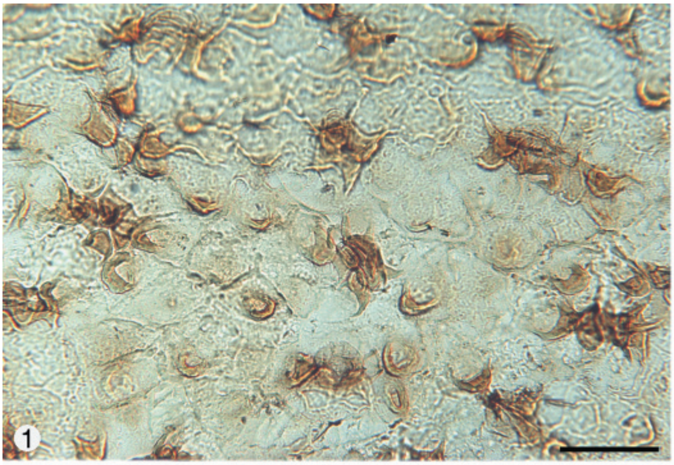
Fig. 6: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Abaxial cuticle, two adjacent stomata with papillae – scale bar = 10 µm

Fig. 7: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Abaxial cuticle, papillae overarching stoma – scale bar = 10 µm

Fig. 8: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Abaxial cuticle, stoma, view from the inside – scale bar = 10 µm

Fig. 9: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Abaxial cuticle, overview with costal and intercostal fields – scale bar = 50 µm

Fig. 10: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Abaxial cuticle, detail of intercostal field – scale bar = 20 µm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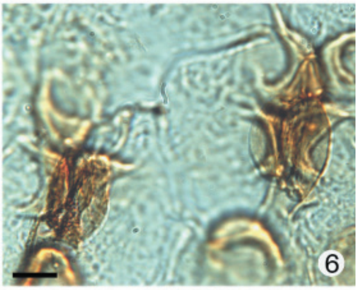
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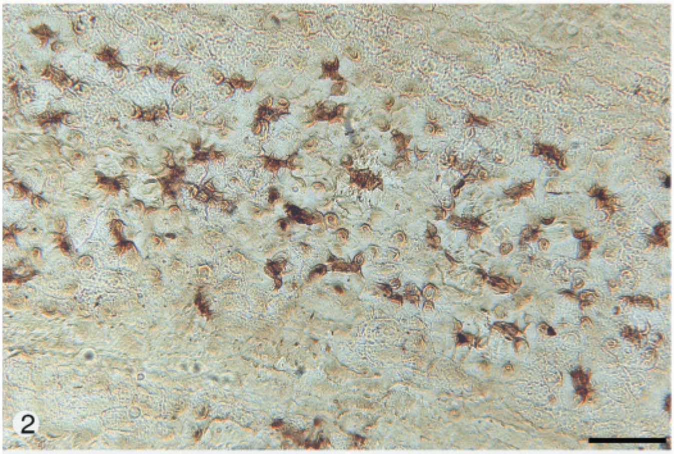
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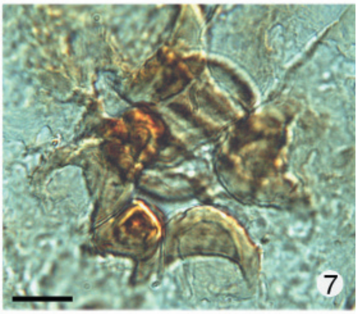
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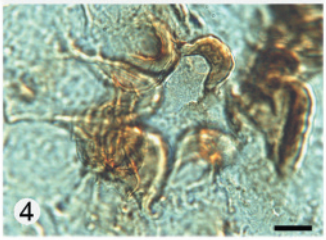
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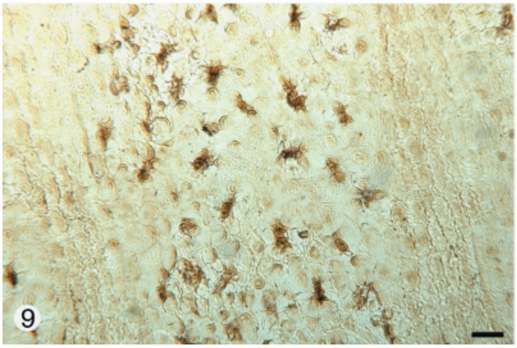
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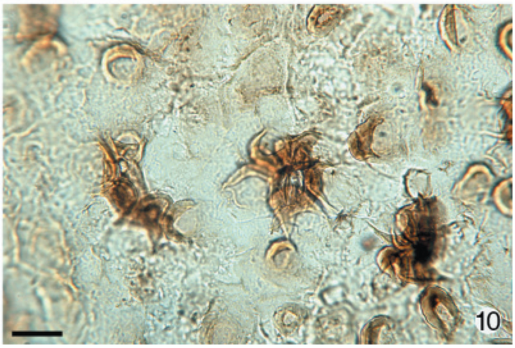
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Plate 3

Pseudoctenis cornelii nov. spec. – adaxial cuticle

Fig. 1: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Adaxial cuticle, overview – scale bar = 100 µm

Fig. 2: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Adaxial cuticle, showing the sinuous anticlinal cell walls – scale bar = 20 µm

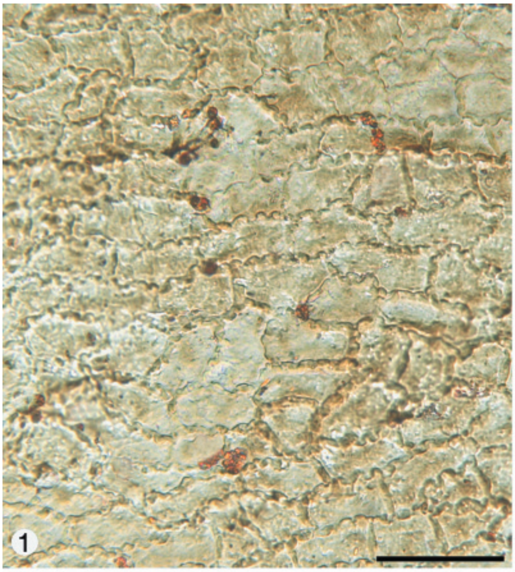
Fig. 3: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Adaxial cuticle, epidermis with sinuous anticlinal cell walls – scale bar = 20 µm

Fig. 4: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Adaxial cuticle, epidermal cells with sinuous anticlinal cell walls – scale bar = 10 µm

Fig. 5: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Adaxial cuticle, epidermal cell with sinuous anticlinal walls – scale bar = 10 µm

Fig. 6: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Adaxial cuticle, detail with sinuous anticlinal cell walls – scale bar = 20 µm

Fig. 7: NHMW 2007B0002/0005 (from holotype)
Upper Triassic, Carnian, Lunz-am-See, Lower Austria
Adaxial cuticle, overview – scale bar = 20 µm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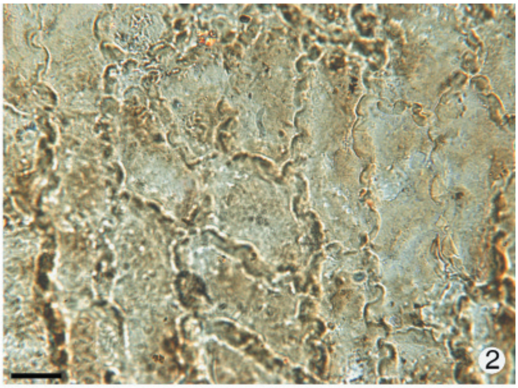
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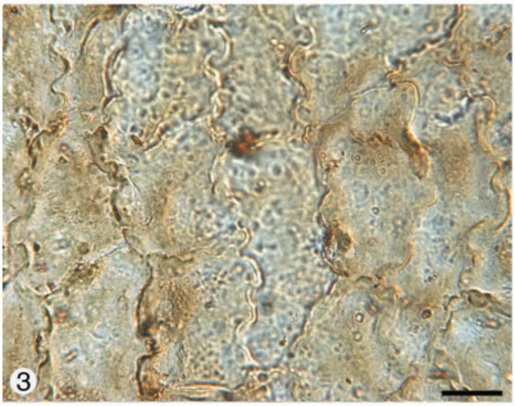
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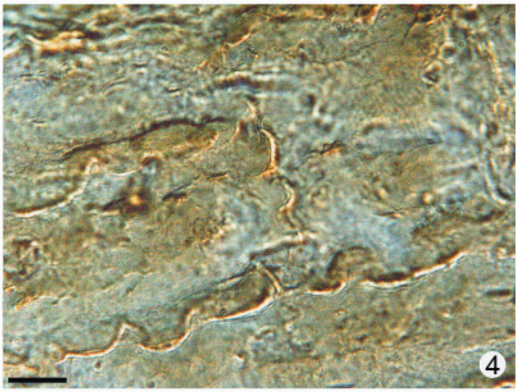
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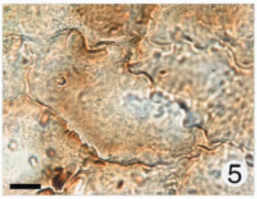
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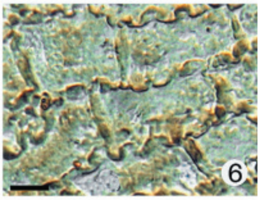
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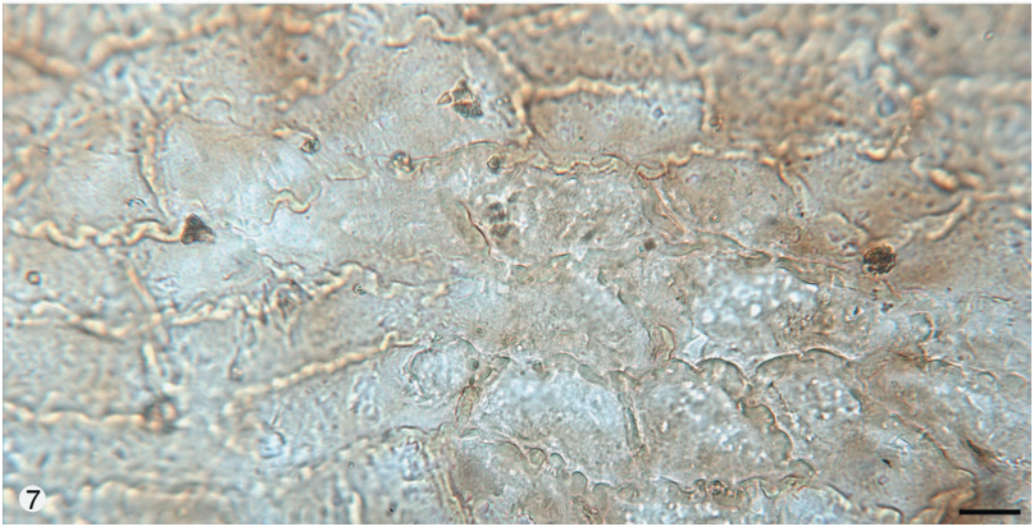
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SECTION III — ECOLOGY

Inferring ecological implications from fossil plants is always to be done carefully, since the fossil record of a palaeoecosystem is always incomplete, and a variety of factors has to be considered in reconstructing relevant palaeoecosystems or the ecological background of the plants. Information on the environment and ecological interactions of plants with their environment or plant/animal-interactions are provided not only by the plants themselves or the cuticles, but also by palaeontological, sedimentological and palynological data.

The reconstruction of the palaeoecology (i.e. biotic and abiotic habitat conditions) of the plants by means of analysis of fossil cuticles is mainly based on the examination of epidermal and idiocuticular features. Numerous adaptations to distinct environmental conditions are recognisable in epidermal patterns or cause obvious epidermal adaptations.

Therefore, the adaptive relevance of these characters, their adaptive qualities and distribution among the individual plant, within the species and among genera needs to be pointed out. The knowledge of these aspects within extant plants is an evident factor to reason the way of living of fossil plants and their ecological requirements. It has also to be considered that differrent patterns of life may cause different ecological requirements even if plants thrive in the same ecosystem.

CHAPTER 7

A surface micro-relief on the leaves of *Glossophyllum florinii* (?Ginkgoales) from the Upper Triassic of Lunz, Austria

Christian Pott, Michael Krings & Hans Kerp

Botanical Journal of the Linnean Society, 153: 87–95 (2007)

Abstract.—The cuticles of many extant seed plants display distinct surface microreliefs, which represent adaptations to certain habitat conditions or mechanical defences against herbivores and phytopathogenic microorganisms. Although micro-reliefs have variously been noted in fossil cuticles, hypotheses relating to the effectiveness of these structures in fossil plants have not been advanced to date. A surface microrelief composed of longitudinally orientted idiocuticular striae occurs on the leaves of the enigmatic Carnian (Late Triassic) gymnosperm (?ginkgophyte) *Glossophyllum florinii* Kräusel from the Northern Calcareous Alps of Lower Austria. Most striae originate from the tips of the papillae on the stomatal subsidiary cells. The *G. florinii* surface micro-relief may have 1) reduced leaf wettability; 2) produced or enhanced the self-cleaning effect of the leaf; 3) prevented the formation of a water film on the leaf surface; and/or 4) mechanically stabilised the leaf.

Keywords.—Adaptation, Carnian, cuticular analysis, ecology, idiocuticular striae, Northern Calcareous Alps, papillae, stomata.

Botanical Journal of the Linnean Society, 2007, **153**, 87–95. With 19 figures

A surface microrelief on the leaves of *Glossophyllum florinii* (?Ginkgoales) from the Upper Triassic of Lunz, Austria

CHRISTIAN POTT[1]*, MICHAEL KRINGS[2] and HANS KERP[1]

[1]*Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, D-48143 Münster, Germany*
[2]*Bayerische Staatssammlung für Paläontologie und Geologie und GeoBio-Center^{LMU}, Richard-Wagner-Straße 10, D-80333 Munich, Germany*

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The cuticles of many extant seed plants display distinct surface microreliefs, which represent adaptations to certain habitat conditions or mechanical defences against herbivores and phytopathogenic microorganisms. Although microreliefs have variously been noted in fossil cuticles, hypotheses relating to the effectiveness of these structures in fossil plants have not been advanced to date. A surface microrelief composed of longitudinally orientated idiocuticular striae occurs on the leaves of the enigmatic Carnian (Late Triassic) gymnosperm (?ginkgophyte) *Glossophyllum florinii* Kräusel from the Northern Calcareous Alps of lower Austria. Most striae originate from the tips of the papillae on the stomatal subsidiary cells. The *G. florinii* surface microrelief may have (1) reduced leaf wettability, (2) produced or enhanced the self-cleaning effect of the leaf, (3) prevented the formation of a water film on the leaf surface, and/or (4) mechanically stabilized the leaf. © 2007 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2007, **153**, 87–95.

ADDITIONAL KEYWORDS: adaptation – Carnian – cuticular analysis – ecology – idiocuticular striae – Northern Calcareous Alps – papillae – stomata.

INTRODUCTION

The cuticle is a critical element in the controlled exchange of substances between the outside world and the internal tissues of vascular plants; especially important is its protective effectiveness against excessive water loss. Moreover, the cuticle provides protection from various deleterious environmental influences, including UV-radiation, mechanical injuries, dust particles, and phytopathogenic microorganisms (Martin, 1964; Campbell, Huang & Payne, 1980; Allen *et al*., 1990). A heavily cutinized epidermis may also function in herbivory abatement by prohibiting piercing-and-sucking arthropods from penetrating the surface. In addition, the cuticles of many extant plants display special structures either in the form of wax adcrustations (epicuticular waxes) or as surface microreliefs (i.e. ornamentations of the cuticle) that may also function in protecting the plant. The former are found in all vascular plants (Neinhuis & Barthlott, 1997), whereas the latter occur primarily in angiosperms (Barthlott & Ehler, 1977; Barthlott, 1980; Barthlott & Ziegler, 1981) and some gymnosperms (e.g. Florin, 1936). Epicuticular waxes are produced either exclusively during leaf development and expansion, or during the entire lifetime of the leaf (Rentschler, 1971; Neinhuis, Koch & Barthlott, 2001). Surface microreliefs are formed during the growth of the leaf (Barthlott, 1980) or develop as a result of continued growth of the cuticle after cell expansion has ceased. Both epicuticular waxes and surface microreliefs are effective as passive defences against herbivores and phytopathogenic microorganisms, and can serve as adaptations to particular (extreme) abiotic

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*Corresponding author.
E-mail: christian.pott@uni-muenster.de

habitat conditions (e.g. Chapman, 1976; Suzuki, 1980; Hutchings & Saenger, 1987; Western, 1988).

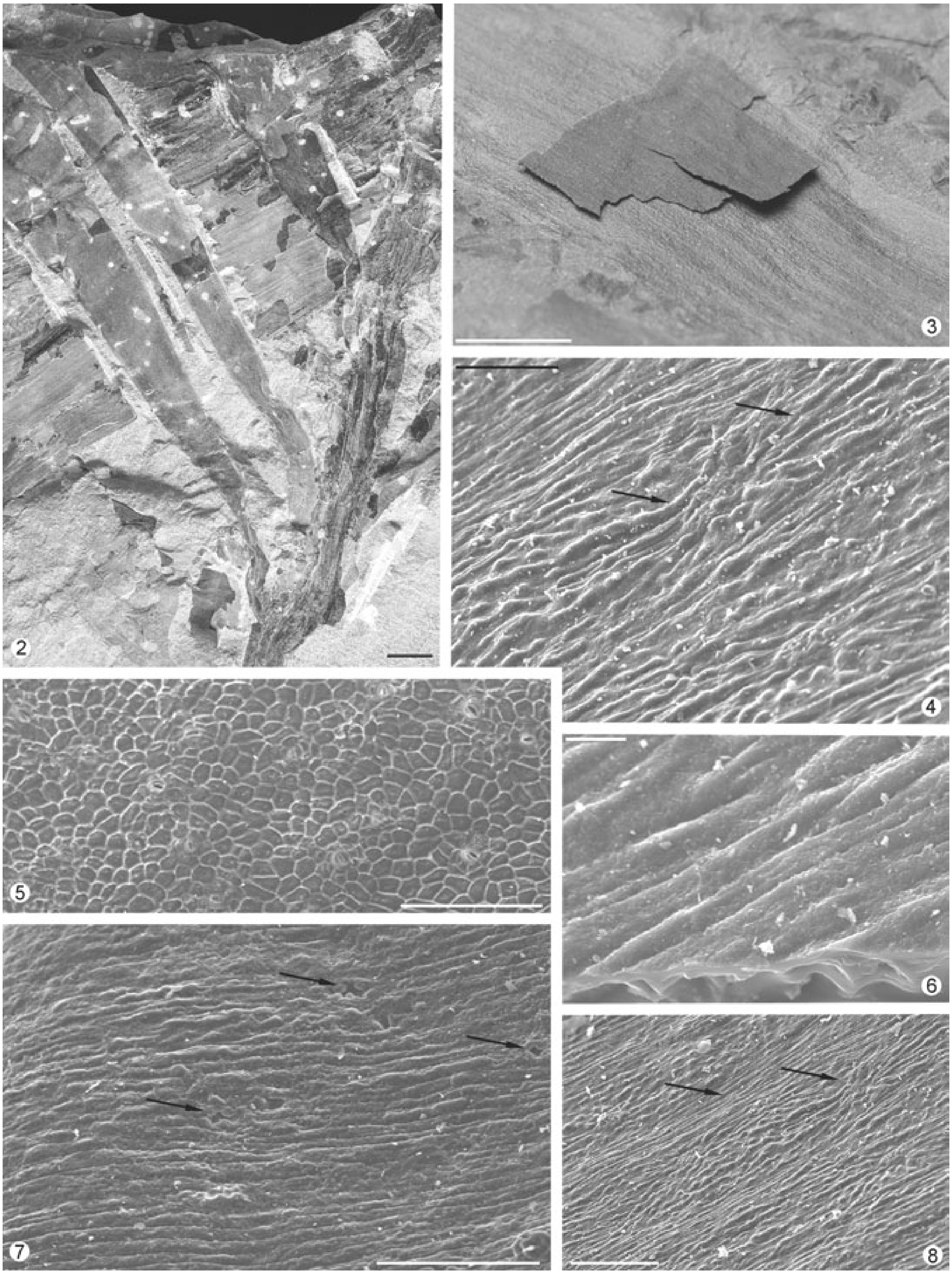
The cuticles of many ancient seed plants are highly resistant, and often survive fossilization and diagenesis almost unchanged morphologically. It has been established that cuticles provide a wealth of information useful in the taxonomy of fossil seed plants (e.g. Cleal & Shute, 1995; Krings & Kerp, 2000; Kerp & Krings, 2003), and are also important with regard to palaeobiological and palaeoecological considerations (e.g. Krings *et al*., 2003a, 2003b). As a result, the analysis of fossil cuticles has become a major focus of palaeobotanical research (Kerp, 1990). Although the occurrence of surface microreliefs has variously been noted in fossil cuticles (e.g. Florin, 1936; Dobruskina, 1998; Denk & Velitzelos, 2002), detailed descriptions of these ornaments and their spatial arrangement are scarce, and hypotheses relating to the mechanical and ecological function(s) in fossil plants have not been advanced to date.

Here we describe a surface microrelief in the form of longitudinally orientated idiocuticular striae that occurs on the leaves of the enigmatic Late Triassic leaf taxon *Glossophyllum florinii* Kräusel 1943 [= *Arberophyllum* Doweld (Doweld, 2000)] from the Lunzer Sandstein in the Northern Calcareous Alps of lower Austria. Compressed leaves and leaf fragments of *G. florinii* (Figs 1, 2) are common in the Lunzer Sandstein and usually yield excellently preserved cuticles (Figs 2, 3). The macromorphology and epidermal anatomy of *G. florinii* were originally described and reconstructed by Kräusel [1943: fig. 4 (re-illustrated in Fig. 1)]. This author assigned the species to the gymnosperm order Ginkgoales based on epidermal anatomy. It is possible, however, that there are also other groups of plants where these leaves might be housed, e.g. conifers [such as *Pelourdea* Seward (= *Yuccites* WP Schimper et Mougeot)] or early gnetophytes. *Glossophyllum* forms an isolated taxon that differs in various morphological traits from other members in the Mesozoic ginkgophytes, including *Ginkgoites* Seward, *Baiera* Braun and *Sphenobaiera* Florin (Tralau, 1968; Dobruskina, 1998). The most characteristic features of *Glossophyllum* are tongue-shaped leaves that lack petioles and subepidermal secretory cavities. The occurrence of a surface microrelief in *G. florinii* represents the first record for cuticle ornamentation in a Triassic putative ginkgophyte. The *G. florinii* microrelief is discussed with regard to mechanical and ecological function(s).

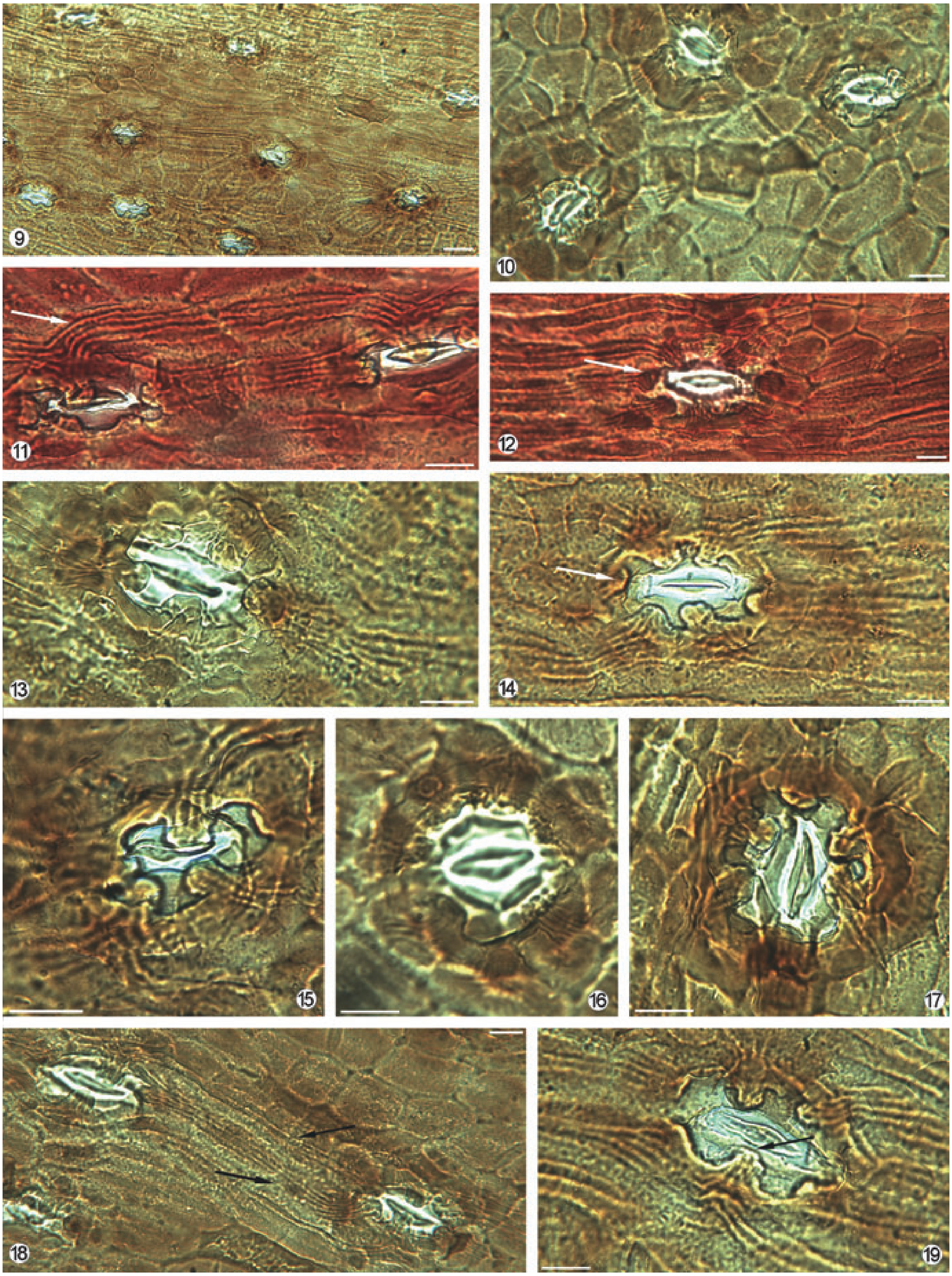
GEOLOGICAL SETTING, MATERIAL AND METHODS

The specimens of *Glossophyllum florinii* come from the famous Late Triassic flora of Lunz in the Northern Calcareous Alps of lower Austria. They were collected during the late 19th and early 20th centuries from several localities (mostly spoil tips of coal mines) in the area around Lunz-am-See, *c.* 100 km west of Vienna (cf. Dobruskina, 1998: fig. 2). The Lunz flora is one of the most important fossil floras of the Carnian (early Late Triassic) in Europe (Dobruskina, 1989). The plant fossils (impressions and compressions) come from the so-called Lunzer Sandstein, which is part of the Lunz beds (Verloop, 1908: fig. 1). Based on the marine invertebrates that occur in the strata positioned directly above and below the Lunzer Sandstein (the Reingrabener Schiefer and Opponitzer Schichten, respectively) the Lunzer Sandstein was correlated with the stratotype of the Carnian; Krystyn (1978) places the Lunzer Sandstein in the upper part of the early Carnian (i.e. Julian). The Lunz flora is palaeobotanically significant because it represents one of only a few well-preserved floras of the alpine Triassic, and is one of the oldest fossil floras with bennettitaleans (Cleal, 1993). The flora is diverse, including sphenophytes, ferns, ginkgophytes, coniferophytes, and cycadophyte foliage; the most remarkable aspect is the abundance of fertile cycadophyte remains (Krasser, 1909a, 1909b, 1917, 1919). Additional information on the composition of the Lunz flora can be found in Dobruskina (1989, 1998).

Figure 1. Reconstruction of a *Glossophyllum florinii* twig. Scale bar = 1 cm. From Kräusel (1943: fig. 4) with permission; http://www.schweizerbart.de.



Figures 2–8. Habitus and epidermal surface features of *Glossophyllum florinii* from the Upper Triassic of Lunz, lower Austria. Fig. 2. Leafy branch of *G. florinii*; specimen no. 1889-VI-08. Scale bar = 5 mm. Fig. 3. Piece of cuticle on the surface of a *G. florinii* leaf fossil; specimen no. S148334. Scale bar = 5 mm. Fig. 4. Surface view of an abaxial cuticle segment, showing idiocuticular striae radiating from a stoma (arrows). Scale bar = 100 μm. Fig. 5. Adaxial cuticle viewed from the inside. Scale bar = 200 μm. Fig. 6. Edge of a piece of cuticle, showing the idiocuticular nature of the striae. Fig. 7. Surface view of a cuticle segment from the adaxial side, showing well-defined striae and sunken stomata in the upper part (arrows). Scale bar = 200 μm. Fig. 8. Surface view of an abaxial cuticle segment, showing delicate striae (arrow) and cuticular striae radiating from a stoma (arrow). Scale bar = 200 μm.



Figures 9–19. Epidermal anatomy of *Glossophyllum florinii* from the Upper Triassic of Lunz, lower Austria. Fig. 9. Abaxial epidermal cell pattern (intercostal field), overview; slide no. 0–0005. Scale bar = 50 μm. Fig. 10. Three stomatal complexes; slide no. 0–0005. Scale bar = 20 μm. Figs 11, 12. Stomatal complex with radiating cuticular striae (arrow); slide no. 0–0012. Scale bars = 20 μm. Figs 13, 14. Stomatal complexes displaying papillae (arrow) and striae; slide no. 0–0005. Scale bars = 20 μm. Figs 15–17. Stomatal complexes; slide no. 0–0005. Scale bars = 20 μm. Fig. 18. Two adjacent stomatal complexes interconnected by bundles of striae (arrows); slide no. 0–0005. Scale bar = 20 μm. Fig. 19. Stomatal complex displaying papillae and striae (arrow); slide no. 0–0005. Scale bar = 20 μm.

The material used in this study comes from the collections of the Laboratory of Palaeobotany and Palynology, University Utrecht, the Netherlands (accession numbers 243, 17858A, 17930), the Museum of Natural History Vienna, Austria (accession numbers A6025, 1883-C-5923, 1885-D-3893, 1885-D-3969, 1885-D-3971, 1885-D-4055, 1886-I-4, 1886-I-22, 1887-I-24, 1889-VI-08, 1889-VI-20, 1944-I-4), and the Museum of Natural History Stockholm, Sweden (accession numbers S148223, S148234, S148334, S148522, S148596, S148660).

Cuticles were prepared according to procedures outlined in Kerp (1990), and Kerp & Krings (1999). Plant remains were picked from the rock surface using a preparation needle, and macerated according to the standard procedure using Schulze's reagent (HNO_3 with a few crystals of $KClO_3$). Macerated cuticles were washed in distilled water, gently dehydrated in pure glycerine, and subsequently mounted in permanent glycerine-jelly on microscope slides. In order to increase contrast, some cuticles were stained with Sudan III. Permanent cuticle slides are deposited in the slide collection of the Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Universität Münster, Germany, under accession numbers PBO0-0005, PBO0-0006, PBO0-0009, and PBO0-0012. For SEM analysis, small pieces of cuticle were picked from the rock, dried on a precision heating plate, and subsequently sputter-coated with coal. The cuticles were analysed with a Leitz Diaplan light microscope and JEOL 840 scanning electron microscope and photographed digitally. Images were processed in Photoshop 7.0.

DESCRIPTION

Glossophyllum florinii leaves posses a thick and leathery appearance and are amphistomatic. On the abaxial side, stomatiferous costal and nonstomatiferous intercostal fields are well-defined. The costal fields are between 60 and 90 μm wide, and consist of 2–3 rows of isodiametric, polygonal to rectangular epidermal cells. The intercostal fields (Fig. 9) are between 120 and 140 μm wide, and consist of 4–10 rows of isodiametric to rectangular cells. The anticlinal cell walls are straight and the outer periclinal walls smooth, producing only faint idiocuticular striae. Stomata are distributed regularly in the costal fields; stomatal pores are randomly orientated. Stomatal density on the abaxial side measures up to 35–48 stomata mm^{-2}. The stomatal density of the adaxial side is considerably lower, up to 22–36 stomata mm^{-2}. The adaxial cuticle is thicker than the lower cuticle, and composed of well-defined longitudinally orientated rows of elongate, isodiametric or polygonal epidermal cells (Fig. 5), up to 50 μm wide and 80 μm long. The outer periclinal walls of the ordinary epidermal cells are smooth. The anticlinal cell walls are straight. Stomata are scattered across the epidermis, and stomatal complexes are similar in structure to those seen on the abaxial side (Fig. 5); however, orientation of the stomatal pores is more regular. The individual stomatal complexes on the adaxial and abaxial side are separated from one another by one to several ordinary epidermal cells (Figs 9, 10, 18). However, they are usually interconnected by idiocuticular striae. The stomatal complex is oval to round in shape, 30–35 μm wide and 48–55 μm long. The guard cells are sunken, 8–15 μm wide and 45–50 m long, and possess prominent circum-poral thickenings (Figs 13–17). Apertures are typically slit-like and shorter (usually some 40 μm in length) than the length of the pit mouth (Figs 16, 17). The guard cells are surrounded by 5–7 subsidiary cells, which are regular in shape and size; it is not possible to distinguish polar from lateral subsidiaries. The subsidiary cells are more heavily cutinized than the normal epidermal cell (Fig. 17). A distinct and solid papilla extends from each subsidiary cell and overarches the pit mouth [Figs 13–15, 19 (arrow)]. For more details on the epidermal anatomy of *G. florinii*, refer to Kräusel (1943).

Glossophyllum florinii leaves show a surface microrelief consisting of elevated striae and depressions (Figs 9, 11, 12, 18); the relief is typically much more prominent on the adaxial side of the leaf (Figs 7, 8). SEM reveals that the striae are composed exclusively of cuticle material (Figs 4, 6), and hence represent idiocuticular structures (cf. Barthlott & Ehler, 1977: fig. 63c). The width of the individual striae ranges between 3 and 10 μm. Virtually all striae are primarily orientated in longitudinal direction (i.e. parallel to the leaf lateral margins; Figs 4, 7, 8 [arrow]), and thus form a very regular pattern (Figs 8, 11, 12); bifurcating striae are rarely observed. The distance between two neighbouring striae (i.e. the depression) is between 1 and 3 μm wide. Most striae originate from the tips of the papillae on the stomatal subsidiary cells [Figs 12, 14, 15, 17, 19 (arrows)], and, from there, radiate in an outward direction across the subsidiary cells. Striae that initially do not run longitudinally, curve after a short distance and, as a result, also become orientated parallel to the lateral leaf margins (Fig. 12). Adjacent stomatal complexes are usually interconnected by up to 3 bundles of ornaments, each consisting of 4–5 parallel striae [Figs 8, 11 (arrow), 18 (arrows)]; these striae are not necessarily orientated parallel to the lateral leaf margins. The striae that originate from stomatal complexes in the proximal portion of the leaf usually fuse with those that are given off from above positioned stomatal complexes (Figs 4, 7, 9). As a result, the total number of longitudinally orientated striae on the leaf surfaces remains more or less constant. The striae are never restricted to individual epidermal cells, but instead consistently continue across the borders of the cells, even where different cell types (e.g. stomatal subsidiary and normal epidermal cells) occur next to one another (Figs 9, 12).

DISCUSSION

The surface microrelief on the leaves of *Glossophyllum florinii* represents the first account for cuticle surface ornaments in a Triassic putative ginkgophyte. Although the epidermal anatomy of *G. florinii* has been studied in detail by Kräusel (1943), this surface feature has not previously been recorded. Surface ornaments have been noted in a number of other fossil ginkgophytes. For example, Florin (1936) describes surface 'striations' on a number of ginkgophyte cuticles from the Wealden (lower Cretaceous) of the Franz-Josef-Land archipelago that are similar to the striae seen in *G. florinii*. This author compares the striations with the cuticular foldings that occur on the pinnules of the extant cycad *Stangeria* Moore and the fossil *Ctenis* Lindley et Hutton. Denk & Velitzelos (2002) report 'striations' from Cenozoic representatives of the Ginkgoales. However, neither of these studies offers hypotheses with regard to the ecological and mechanical functions of the surface microreliefs. The sole extant representative of the ginkgophytes, *Ginkgo biloba* L., displays a distinct surface microrelief in the form of longitudinally orientated striae (pers. observ.). Along with acute epicuticular wax structures, the striae are effective in reducing leaf wettability (Neinhuis & Barthlott, 1997). We are not aware of any study that records cuticle ornaments similar to those seen in *G. florinii* for a fossil or extant representative of the other two plant groups (e.g. conifers or the gnetophytes) that have variously been considered as a repository for *G. florinii*.

Modern plants with thick leathery foliage, comparable to that seen in *G. florinii*, grow predominantly in (seasonally) arid regions (i.e. xeromorphic plants) or in environments characterized by elevated to high soil and ground water salinity (i.e. salt-resistant glycophytes and halophytes). The Late Triassic palaeolatitudinal position of the Lunz area (*c.* 30°N) in the Northern Calcareous Alps of Austria suggests that the Lunz flora grew in a paratropical environment (Scotese, 2003). According to Stur (1885), the Lunz flora was located in a hillside region of the Bohemian mountains; there, close to the coast of the Tethys Ocean, it was influenced by marine climate. The occurrence of a heavily cutinized epidermis and deeply sunken stomata that are partially covered by papillae extending from the subsidiary cells [Figs 7, 10, 11–19 (arrows)] in several plant taxa from the Lunz flora, support the hypothesis that the Lunz flora grew in a (seasonally) dry and/or coastal (i.e. salinity-affected) environment. Moreover, it is likely that the Lunz palaeoecosystem was subjected to sustained wind, which often occurs in coastal and near-coast environments, and was an open-canopy, high-light habitat. The fact that the leaves of *G. florinii* are amphistomatic may be positively correlated with their thick, leathery nature. It has been noted that amphistomy tends to be more common amongst extant plants that possess thick leaves and thrive in xeric habitats (Parkhurst, 1978; Fahn & Cutler, 1992). The presence of stomata on both sides of the leaf is interpreted as an adaptation to reduce the internal diffusion distance of CO_2 in thick leaves (e.g. Parkhurst *et al.*, 1988). On the other hand, Mott, Gibson & O'Leary (1982) state that amphistomy is characteristic for plants living in high-light environments (e.g. coastal areas) and possessing high photosynthetic capacities, and may represent an adaptation to allow the high stomatal conductances necessary to take advantage of high photosynthetic capacities. Stomatal conductance is a numerical measure of the rate of passage of either water vapour or carbon dioxide through the stomata. It plays an important role in the plant-atmosphere water exchange. Diffusion of CO_2 into the mesophyll of leaves and water vapour from the leaf to the atmosphere is mainly driven by the stomatal aperture, which is controlled by a complex system of physiological processes. An increased uptake of CO_2 may cause higher photosynthetic rates for a more effective exploitation of the high-light conditions.

Several considerations can be offered on the effectiveness of the *G. florinii* surface ornamentation. One particularly interesting aspect with regard to the protective effectiveness of cuticle surface ornaments concerns the reduction of leaf wettability (Barthlott & Neinhuis, 1997). Water droplets possess a high surface tension due to the strong intermolecular forces of the water molecules that cause their spherical shape. It has been established from extant plants that the minute, air-filled spaces between surface ornaments or epicuticular wax crystals reduce the contact zone between a water droplet and the leaf surface. As a result, in leaves with surface ornaments, the contact area is reduced considerably because the water droplets only contact the upper tips of the ornaments, but do not adhere firmly to the leaf surface, and thus the surface tension of the droplets is retained and they are much easier repelled (Rentschler, 1971; Juniper, 1991). Thus, it is possible to envisage that the *G. florinii* surface microrelief functioned in reducing the wettability of the leaves. This hypothesis is supported by the presence of microrelief on the entire leaf surface that is especially well-developed on the adaxial side. Moreover, the ornamented leaves of the extant *Ginkgo biloba* are effective in reducing leaf wettability (see above).

A significant side effect of surface microreliefs in the form of parallel striae is the cleaning of the leaf surface. Dust particles that continuously accumulate on all leaf surfaces are washed off by water running off the leaf (Barthlott & Ehler, 1977; Campbell *et al*., 1980; Barthlott & Neinhuis, 1997). On smooth surfaces, dust particles are usually only rearranged by effluent water, whereas on ornamented surfaces these contaminants are washed off by the water droplets rolling off the leaves. Because this phenomenon was noted in the Sacred Lotus (*Nelumbo nucifera* Gaertn.), it is commonly termed 'the Lotus effect' (Barthlott & Neinhuis, 1997). The self-cleaning effect is of great significance because dust particles on leaf surfaces adversely affect plants (Pal *et al*., 2002). For example, dust may raise the surface temperature of the leaves, which considerably increases the transpiration rate (Eller, 1977). In xeric and windy environments in particular, dust contamination is a major adverse effect on plant life. In addition, the air in coastal habitats is saline. In combination with sustained wind and a high evaporation rate, salt particles remaining on the leaves can cause injuries to the tissue. Plants affected by high salt concentrations often appear dark green in the early stages, but rapidly develop marginal yellowing and necrosis of older leaves (Delahaut & Hasselkus, 1999). Salt crystals on the leaf surfaces may cause, among other things, dehydration of the epidermis and internal tissues. It is possible that the self-cleaning effect of leaves removes not only dust particles, but also salt crystals. Pioneer plants with self-cleaning leaves growing in dusty, coastal environments would have a competitive advantage over those without. The *G. florinii* surface microrelief may have been effective in self-cleaning of its leaves. However, it is likely that this effect was not as sophisticated as the well-known consummate structures in *Nelumbo nucifera* Gaertn., *Brassica oleracea* L., or *Tropaeolum majus* L., based on the structure and spatial arrangement of the surface ornaments in *G. florinii*.

The surface microrelief of *G. florinii* may also have provided some protection from phytopathogenic microorganisms, especially fungi. Fungal spores are disseminated by air and accumulate on leaf surfaces where they germinate and eventually infest the internal tissues directly through the cuticle and epidermis or through stomatal pores (Martin, 1964; Cowling & Horsfall, 1980; Suzuki, 1980; Juniper, 1991). Self-cleaning leaves may protect the plant from phytopathogenic fungi by removing the spores from the surface. It is interesting to note that epiphyllous fungi have been discovered on *Pterophyllum* Brongn. leaves from the Lunz flora (Schaarschmidt, 1966). However, epiphyllous fungi have not yet been documented for *G. florinii*.

The idiocuticular striae on the *G. florinii* leaves are almost exclusively orientated in a longitudinal direction, parallel to the lateral leaf margins. This may have facilitated the flow of rainwater longitudinally from all areas of the lamina to the leaf base and tip. If the striae were arranged differently (e.g. in transverse direction or forming a reticulate pattern), water would not be directed to the leaf base and tip, but would rather run off laterally (striae arranged in transverse direction) or remain on the surface (reticulate pattern). As a result, the surface microrelief in *G. florinii* may have prevented the formation of a water film on the surface, and thus ensured continuous CO_2 uptake (Barthlott & Neinhuis, 1997). It is known from extant plants that the presence of a water film on the leaf surfaces and liquid water in the antechambers of sunken stomata may reduce the uptake of CO_2 by up to four times (Smith & McClean, 1989).

Apart from the effectiveness in protecting the plant from deleterious environmental influences, the *G. florinii* surface microrelief may also have possessed a mechanical function. For example, it is known from extant plants that certain surface ornaments strengthen the leaf (Kurer, 1917; Barthlott & Ehler, 1977). This may be especially significant in plants that thrive in areas where considerable changes in water availability result in alterations of the leaf shape. For example, if *G. florinii* lived in a seasonally dry environment, it is possible that shrinkage of the leaves occurred due to turgor loss during periods of water limitation. Here the surface ornament may have enabled leaves to reestablish their turgid form once water became available again.

It is impossible at present to assign a particular ecological or mechanical function to the surface microrelief of *G. florinii* leaves, but comparisons with extant plants provide at least some general ideas about the possible effectiveness of this feature. Further studies of the epidermal anatomy of seed plants from the Lunzer Sandstein will provide insights into the distribution among the taxa and diversity of surface ornaments in this flora. Along with data on the epidermal anatomy of the plants and information gathered from palaeozoological and sedimentological studies, this may ultimately lead to a more complete understanding of the adaptative significance of surface ornaments in this Late Triassic flora, and the quality of the biotic and abiotic ecological parameters that shaped the environment in which the Late Triassic plants from the Lunzer Sandstein lived.

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REFERENCES

Allen EA, Hoch HC, Steadman JR, Stavely RJ. 1990. Influence of leaf surface features on spore deposition and the epiphytic growth of phytopathogenic fungi. In: Andrews JH, Hirano SS, eds. *Microbial ecology of leaves*. New York: Springer, 87–110.

Barthlott W. 1980. Development and micro-morphology of complex cuticular fold patterns on floral trichomes of *Antirrhinum* L. (Scrophulariaceae). *Berichte der Deutschen Botanischen Gesellschaft* **93:** 379–390.

Barthlott W, Ehler N. 1977. *Raster-Elektronenmikroskopie der Epidermis-Oberflächen von Spermatophyten*. Wiesbaden: Steiner.

Barthlott W, Neinhuis C. 1997. Purity of the Sacred Lotus, or escape from contamination in biological surfaces. *Planta* **202:** 1–8.

Barthlott W, Ziegler B. 1981. Systematic applicability of seed coat micro-morphology in orchids. *Berichte der Deutschen Botanischen Gesellschaft* **94:** 267–273.

Campbell CL, Huang JS, Payne GA. 1980. Defense at the perimeter: the outer walls and the gates. In: Horsfall JG, Cowling EB, eds. *Plant disease: an advanced treatise, 5. How plants defend themselves*. New York: Academic Press, 103–120.

Chapman VJ. 1976. *Mangrove vegetation*. Vaduz: Cramer.

Cleal CJ. 1993. Gymnospermophyta. In: Benton MJ, ed. *The fossil record*, Vol. 2**.** London: Chapman & Hall.

Cleal CJ, Shute CH. 1995. A synopsis of neuropterid foliage from the Carboniferous and Lower Permian of Europe. *Bulletin of the Natural History Museum London (Geology)* **51:** 1–52.

Cowling EB, Horsfall JB. 1980. How plants defend themselves. In: Horsfall JG, Cowling EB, eds. *Plant disease: an advanced treatise, 5. How plants defend themselves*. New York: Academic Press, 1–16.

Delahaut KA, Hasselkus ER. 1999. *Salt injury to landscape plants*. Madison: University of Wisconsin-Extension. A2970.

Denk T, Velitzelos D. 2002. First evidence of epidermal structures of Ginkgo from the Mediterranean Tertiary. *Review of Palaeobotany and Palynology* **120:** 1–15.

Dobruskina IA. 1989. The alpine Lunz flora – a standard flora for the Carnian stage of the Triassic. *International Geological Review* **31:** 1209–1215.

Dobruskina IA. 1998. Lunz flora in the Austrian Alps – a standard for Carnian floras. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143:** 307–345.

Doweld AB. 2000. *Arberophyllum*, a new generic name for *Glossophyllum* Kräusel, 1943 (Ginkgophyta). *Paleontological Journal* **34:** 674–675.

Eller B. 1977. Road dust induced increase of leaf temperature. *Environmental Pollution* **13:** 99–107.

Fahn A, Cutler DF. 1992. Xerophytes. In: Braun HJ, Carlquist S, Ozenda P, Roth I, eds. *Handbuch der Pflanzenanatomie. Spezieller Teil, Band XIII, Teil* 3. Berlin/Stuttgart: Gebr. Borntraeger.

Florin R. 1936. Die fossilen Gingkophyten aus Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters. II. Allgemeiner Teil. *Palaeontographica* **B82:** 1–72.

Hutchings P, Saenger P. 1987. *Ecology of mangroves*. St Lucia: University of Queensland Press.

Juniper BE. 1991. The leaf from the inside and the outside: a microbe's perspective. In: Andrews JH, Hirano SS, eds. *Microbial ecology of leaves*. New York: Springer, 21–42.

Kerp H. 1990. The study of fossil gymnosperms by means of cuticular analysis. *Palaios* **5:** 548–569.

Kerp H, Krings M. 1999. Light microscopy of cuticles. In: Jones TP, Rowe NP, eds. *Fossil plants and spores: modern techniques*. London: Geological Society, 52–56.

Kerp H, Krings M. 2003. Kutikularanalytische Befunde zur Abgrenzung der *Odontopteris minor* f. *zeilleri* Potonié von *Odontopteris reichiana* Gutbier. *Courier Forschungsinstitut Senckenberg* **241:** 31–42.

Krasser F. 1909a. Die Diagnosen der von Dionysius Stur in der obertriadischen Flora der Lunzerschichten als Marattiaceenarten unterschiedenen Farne. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften (Wien), Abteilung* **1 (118):** 13–43.

Krasser F. 1909b. Zur Kenntnis der fossilen Flora der Lunzer Schichten. *Jahrbuch der Königlich-Kasierlichen Geologischen Reichsanstalt* **59:** 1–26.

Krasser F. 1917. Studien über die fertile Region der Cycadophyten aus den Lunzer-Schichten: Mikrosporophylle und männliche Zapfen. *Denkschiften der Kaiserlichen Akademie der Wissenschaften (Wien), Mathematisch-Naturwissenschaftliche Classe* **94:** 489–553.

Krasser F. 1919. Studien über die fertile Region der Cycadophyten aus den Lunzer Schichten. Makrosporophylle. *Denkschriften der Kaiserlichen Akademie der Wissenschaften (Wien), Mathematisch-Naturwissenschaftliche Classe* **97:** 1–32.

Kräusel R. 1943. Die Ginkgophyten der Trias von Lunz in Nieder-Österreich und von Neue Welt bei Basel. *Palaeontographica* **B87:** 59–93.

Krings M, Kerp H. 2000. A contribution to the knowledge of the pteridosperm genera *Pseudomariopteris* Danzé-Corsin nov. emend. & *Helenopteris* nov. gen. *Review of Palaeobotany and Palynology* **111:** 145–195.

Krings M, Kellogg DW, Kerp H, Taylor TN. 2003a. Trichomes of the seed fern *Blanzyopteris praedentata*: implications for plant–insect interactions in the Late Carboniferous. *Botanical Journal of the Linnean Society* **141:** 133–149.

Krings M, Kerp H, Taylor TN, Taylor EL. 2003b. How Paleozoic vines and lianas got off the ground: on scrambling and climbing Carboniferous-Early Permian pteridosperms. *The Botanical Review* **69:** 204–224.

Krystyn L. 1978. Eine neue Zonengliederung im alpinmediterranen Unterkarn. *Schriftenreihe der Erdwissenschaftlichen Kommission der Österreichischen Akademie der Wissenschaften* **4:** 67–75.

Kurer GA. 1917. Kutikularfalten und Protuberanzen an Haaren und Epidermen und ihre Verwendung zur Differenzialdiagnose offizineller Blätter. PhD thesis, University of Bern. Zürich: Leemann.

Martin JT. 1964. Role of cuticle in the defense against plant disease. *Annual Review of Phytopathology* **2:** 81–100.

Mott KA, Gibson AC, O'Leary JW. 1982. The adaptive significance of amphistomatic leaves. *Plant, Cell and Environment* **5:** 455–460.

Neinhuis C, Barthlott W. 1997. Characterization and distribution of water-repellent, self-cleaning plants. *Annals of Botany* **79:** 667–677.

Neinhuis C, Koch K, Barthlott W. 2001. Movement and regeneration of epicuticular waxes through plant cuticles. *Planta* **213:** 427–434.

Pal A, Kulshreshtha K, Ahmad KJ, Behl HM. 2002. Do leaf surface characters play a role in plant resistence to autoexhaust pollution? *Flora* **197:** 47–55.

Parkhurst DF. 1978. The adaptive significance of stomatal occurrence on one or both surfaces of leaves. *Journal of Ecology* **66:** 367–383.

Parkhurst DF, Wong SC, Farquhar GD, Cowan IR. 1988. Gradients of intercellular CO_2 levels across the leaf mesophyll. *Plant Physiology* **86:** 1032–1037.

Rentschler I. 1971. Die Wasserbentzbarkeit von Blattoberflächen und ihre submikroskopische Wachsstruktur. *Planta* **96:** 119–135.

Schaarschmidt F. 1966. Ein Ascomycet in *Pterophyllum*. *Schweizerische Paläontologische Abhandlungen* **84:** 67–79.

Scotese CR. 2003. *Paleomap project*. http://www.scotese.com.

Smith WK, McClean TM. 1989. Adaptive relationship between leaf water repellency, stomatal distribution, and gas exchange. *American Journal of Botany* **76:** 465–469.

Stur D. 1885. Die obertriadische Flora der Lunzer-Schichten und des bituminösen Schiefers von Raibl. *Denkschriften der Kaiserlichen Akademie der Wissenschaften* **3:** 93–103.

Suzuki H. 1980. Defenses triggered by previous invaders: fungi. In: Horsfall JG, Cowling EB, eds. *Plant disease: an advanced treatise, 5. How plants defend themselves*. New York: Academic Press, 319–332.

Tralau H. 1968. Evolutionary trends in the genus *Ginkgo*. *Lethaia* **1:** 63–101.

Verloop JH. 1908. Profil der Lunzer Schichten in der Umgebung von Lunz. *Zeitschrift der Deutschen Geologischen Gesellschaft* **60** (Monatsbericht 4)**:** 81–88.

Western RA. 1988. Adaptations of plants to a desert environment. *Emirates Natural History Group Bulletin* **36:** 17–23.

CHAPTER 8

Fossil insect eggs and egg imprints on bennettitalean leaf cuticles from the Carnian (Upper Triassic) of Austria

Christian Pott, Michael Krings & Hans Kerp

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Abstract.—Small eggs and egg imprints on *Nilssoniopteris* (bennettitalean foliage) leaf cuticles from the Carnian of Austria provide a rare insight into insect egg morphology and oviposition in the Late Triassic. The eggs are attached to the abaxial leaf surface, arranged in circles, and may have been produced by beetles or sawflies, wasps or allied basal Hymenoptera. The imprints are rhomboidal in outline and surrounded by a narrow elevated margin. They occur on the ad- and abaxial cuticle and coincide when both cuticles are superimposed, which indicates that the eggs were injected into the interior of the leaf. It is likely that these structures result from dragonfly or damselfly oviposition. The eggs exclusively occur on *N. haidingeri* leaves, while egg imprints are only found on *N. angustior*. This suggests that some kind of host specificity existed, perhaps related to specific preferences in larval diet.

Keywords.—Mesozoic insects, Odonata, Coleoptera, Symphyta, plant/insect interactions, Lunz, cuticular analysis.

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FOSSIL INSECT EGGS AND OVIPOSITIONAL DAMAGE ON BENNETTITALEAN LEAF CUTICLES FROM THE CARNIAN (UPPER TRIASSIC) OF AUSTRIA

CHRISTIAN POTT,[1] CONRAD C. LABANDEIRA,[2] MICHAEL KRINGS,[3] AND HANS KERP[1]

[1]Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, D-48143 Münster, Germany, <christian.pott@uni-muenster.de>, <kerp@uni-muenster.de>; [2]National Museum of Natural History, Department of Paleobiology, MRC-121, P.O. Box 37012, Washington, D.C. 20013-7012, <labandec@si.edu>; and [3]Bayerische Staatssammlung für Paläontologie und Geologie und GeoBio-Center^{LMU}, Richard-Wagner-Straße 10, D-80333 Munich, Germany, <m.krings@lrz.uni-muenchen.de>

ABSTRACT—Two types of evidence for insect ovipositional activity (i.e., actual egg chorions and ovipositional damage) occur on *Nilssoniopteris* (bennettitalean foliage) leaf cuticles from the Carnian of Austria and provide a rare direct insight into insect egg morphology and oviposition in the Late Triassic. The egg chorions have exclusively been found on *N. haidingeri* leaves, where they are attached to the outer surface of the abaxial cuticle; one specimen suggests that the eggs were arranged in circles. It is impossible at present to determine the affinities of the eggs; possible producers may be beetles, dragonflies, sawflies, or other allied basal Hymenoptera. Ovipositional damage occurs on *N. angustior* leaves in the form of lenticular egg impressions surrounded by a narrow, elevated margin. The impressions are visible on the ad- and abaxial cuticle, and coincide when both cuticles are superimposed, which indicates that the eggs producing these impressions were injected into the interior of the leaf. Producers of eggs that may have caused these damages are perhaps dragonflies or damselflies. The restricted occurrence of the two types of ovipositional activity suggests that some kind of host specificity existed, perhaps related to specific preferences in larval diet.

INTRODUCTION

PLANTS AND animals today display a wide variety of more or less intimate direct interactions. For example, plants serve as habitat, diet, shelter, and mating arenas for animals, and as hosts for eggs, larvae, and pupae, especially of arthropods. On the other hand, insects and several other groups of animals such as bats and birds are essential in the reproductive biology and dispersal of many plants. With this recognition of the biological and ecological significance of extant plant/animal interactions, a sound understanding of the evolutionary history of these interactions, including the roles they have played in biological and ecological processes in the past, is critical in documenting the complexity and evolution of both ancient and modern ecosystems. Moreover, fossilized plant/animal interactions may offer insights into the behavior of ancient animals and provide information on the autecology of ancient plants (e.g., Krings et al., 2003).

A wealth of information about plant/insect interactions in the fossil record has been gathered to date. However, most of the reports focus on insect damage on plants (e.g., chew marks, stylet probes, and wood borings; e.g., Labandeira, 1997, 2005), which is often easily recognizable in compression specimens or permineralizations, and on feeding specializations indicated by external insect structure such as mouthpart morphology (e.g., Labandeira and Beall, 1990). Documentation of aspects relative to the reproductive biology of ancient insects is comparatively rare. This is particularly true of egg morphology and ovipositional behavior. Although fossil insect eggs and egg remains (e.g., egg impressions or scars on plant stems and leaves) have occasionally been recorded (e.g., Grauvogel-Stamm and Kelber, 1996; Van Konijnenburg-van Cittert and Schmeißner, 1999; Béthoux et al., 2004), these structures are not normally preserved well enough to permit detailed evaluation. Ovipositional behavior is generally difficult to reconstruct based on fossils.

The Mesozoic fossil record has yielded numerous examples of plant/animal interactions in the form of damage on plants caused by phytophagous or polleniphagous insects (e.g., Kelber and Geyer, 1989; Grauvogel-Stamm and Kelber, 1996; Ash, 1997, 1999, 2005) Labandeira, 1997, 2002; Scott et al., 2004). Moreover, distinctive lenticular scars on Mesozoic plant fossils caused by ovipositor insertion of insect eggs (ovipositional scars) have been described from various stems of *Equisetites* Sternberg, 1833 and *Calamites* Brongniart, 1828; the eggs are generally interpreted as having been produced by Protodonata or Odonata (Kelber and Geyer, 1989; Grauvogel-Stamm and Kelber, 1996; Béthoux et al., 2004; Ash, 2005). Similar ovipositional scars have been recorded for *Taeniopteris* Brongniart, 1828 leaves from the Ladinian of France and Lower Keuper of Germany, and interpreted as caused by Odonata (Grauvogel-Stamm and Kelber, 1996). *Schmeissneria* (Presl, 1833) Kirchner and Van Konijnenburg-van Cittert, 1994 leaves from the Jurassic of Germany display surface structures that have been interpreted as Odonata egg remains (Van Konijnenburg-van Cittert and Schmeißner, 1999). These latter two records are based on impression fossils and hence do not permit detailed analysis. As a result, insect egg morphology and ovipositional behavior in the Mesozoic remains poorly understood.

In this paper we provide a detailed evaluation and photographic documentation of insect eggs and ovipositional damage in the form of egg impressions on Late Triassic *Nilssoniopteris* Nathorst, 1909 emend. Pott, Krings, and Kerp, 2007 (Bennettitales) leaf cuticles from the Carnian of Lunz in Lower Austria. These fossils represent the first record for actual insect eggs and egg impressions obtained by means of cuticular analysis, and offer rare insights into insect egg morphology, ovipositional behavior, and host responses to oviposition in the Late Triassic. Although insect diversity is believed to have been high during the Late Triassic (Labandeira and Sepkoski, 1993; Scott et al., 2004; Ash, 2005; Béthoux et al., 2005; Grimaldi and Engel, 2005, p. 46) and probably akin to today (Anderson et al., 1998), no fossil insect remains have previously been documented from the Lunz paleoecosystem. Thus, the fossils presented here also represent the first record of insects from this famous Carnian paleoecosystem.

GEOLOGY, MATERIAL, AND METHODS

The fossils containing the insect eggs and egg impressions on bennettitalean foliage come from the area around Lunz-am-See in the Northern Calcareous Alps of Lower Austria, approximately 100 km west of Vienna, and were collected in the late 19th and early 20th centuries from several active coal mines (Fig. 1). The Lunz flora represents one of the richest and most diverse Late Triassic floras of the Northern Hemisphere and is one of the earliest Triassic plant assemblages of the Northern Hemisphere dominated by Cycadales and Bennettitales (Dobruskina, 1989, 1998).

The fossils occur in the 'Lunzer Sandstein,' which is part of the Lunz beds. The Lunz Formation (=Lunzer Schichten) consists of sandstones at its base, followed by marine marls gradually grading upwards into terrestrial sands, shales, and coal. The coal-bearing part of the sequence is overlain by marls and displays a sandstone layer at the top. The plant fossils occur in the shales that are associated with the coal beds. Determination of the exact

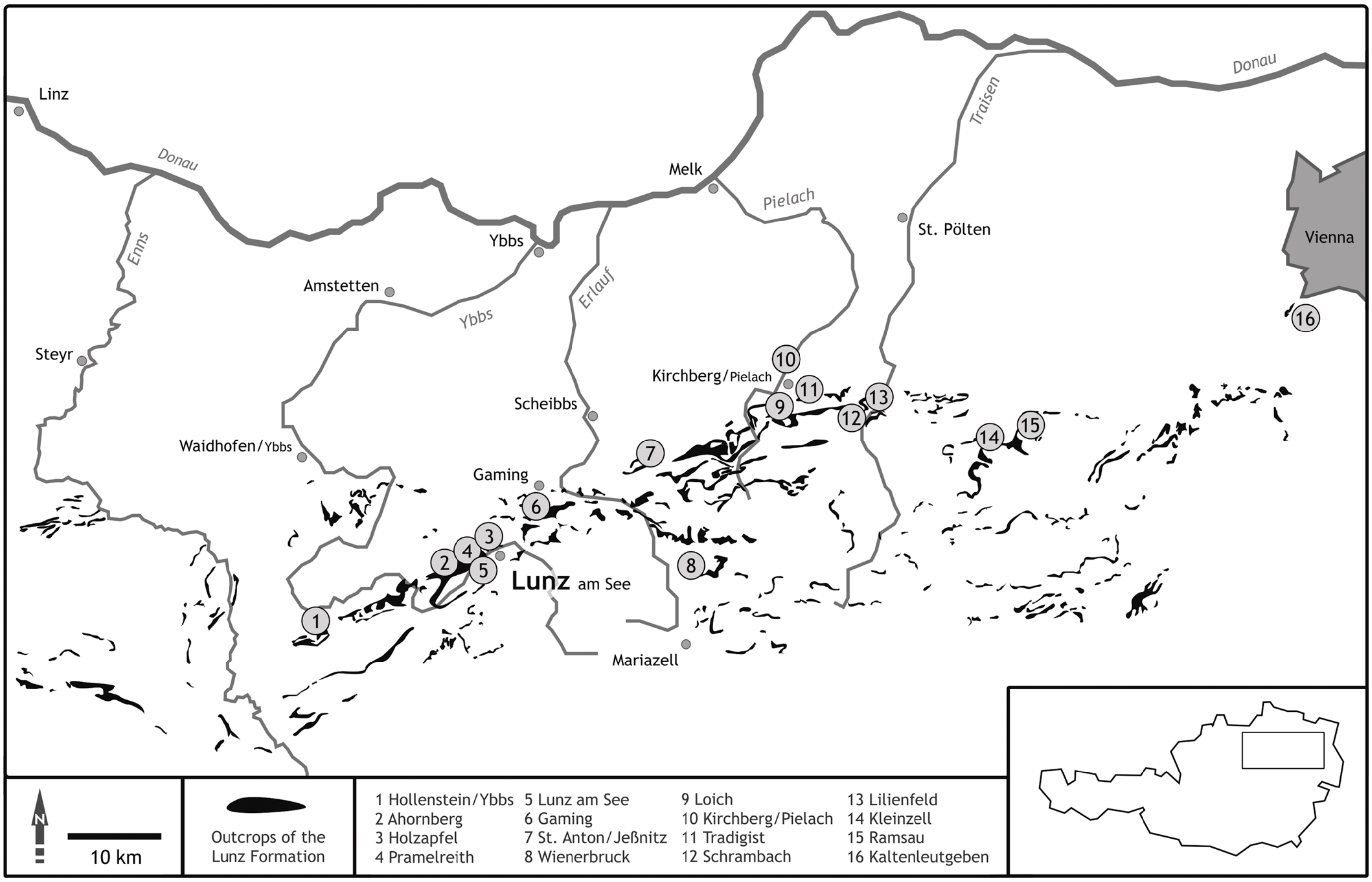


FIGURE *1*—Outcrops and locations from where the Lunz plant fossils have been collected during the 19th and early 20th centuries.

age of the Lunz Formation remains difficult due to the lack of adequate biomarkers such as ammonoids or conodonts. Recent studies of the Hallstatt and Reifling Intraplatform Basins (Hornung and Brandner, 2005) suggest that the Lunz Formation correlates with the upper part of the Reingraben Formation (T. Hornung, personal commun.), and thus is approximately upper Julian (Julian 2/II; Lower Carnian; c. 225 Ma) in age (Gradstein et al., 2004; Hornung, 2006).

The plant fossils from Lunz are usually preserved as compressions, often with excellently preserved cuticles. Cuticles were prepared according to procedures outlined in Kerp (1990), and Kerp and Krings (1999). Rock samples with plant remains are dissolved in hydrofluoric acid (48% HF) in order to remove the sediment. Cuticles are macerated according to standard procedure using Schulze's reagent (35% HNO_3 with a few crystals of $KClO_3$) and 5–10% potassium hydroxide (KOH). Macerated cuticles are washed in distilled water, gently dehydrated in pure glycerin, and finally mounted in permanent glycerin-jelly microscope slides. Slides are stored in the relevant museum collections; accession numbers are indicated in the figure captions.

Hand specimens were photographed with a Nikon D 100 digital camera; in order to increase contrast, cross-polarization (i.e., polarized light sources together with a polarizing filter over the camera lens) was used. Cuticles were analyzed with a Leitz Diaplan microscope and photographed with a Nikon DS-5M digital camera.

RESULTS AND DISCUSSION

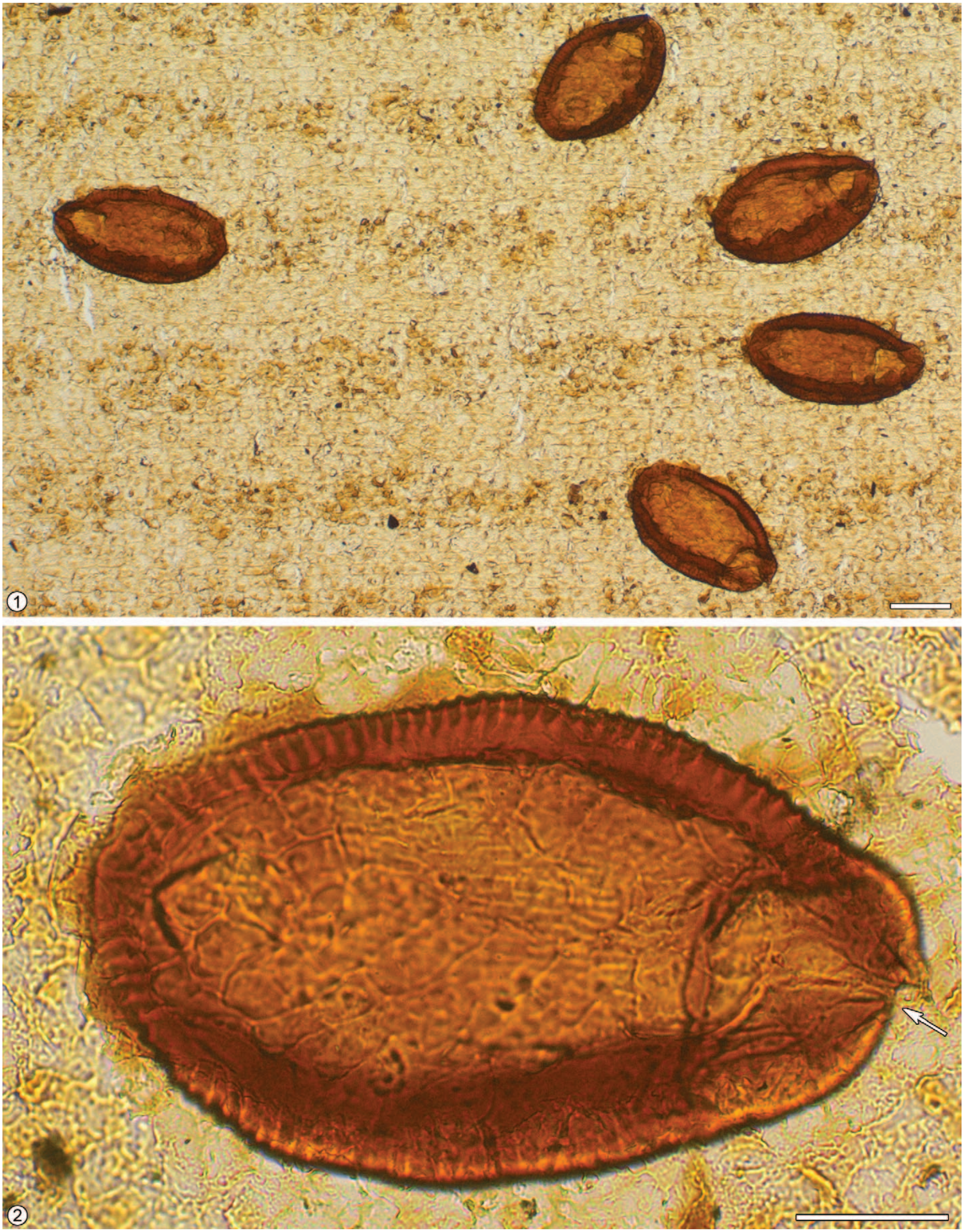
The morphogenus *Nilssoniopteris* accommodates foliage in the gymnosperm order Bennettitales, an extinct group of seed plants characterized by cycad-like leaves and complex reproductive structures that was widespread and diverse in the Late Triassic and Jurassic but vanished during the Cretaceous (Kelber, 1998). A detailed description of the macromorphology, cuticles, and epidermal anatomy of the *Nilssoniopteris* species considered here can be found in Pott, Krings, and Kerp (2007). The descriptions given below of the leaf morphology and epidermal anatomy are limited to a brief summary of features significant in the context of insect oviposition.

INSECT CHORIONS ON LEAVES OF *NILSSONIOPTERIS HAIDINGERI* (STUR EX KRASSER, 1909) POTT, KRINGS AND KERP, 2007

Figures 2.1–2.2, 3.1–3.7, 4, 5.1

Leaves.—Leaves of *Nilssoniopteris haidingeri* are up to 60 cm long and 15 cm wide, almost regular broadly oval or oblong to lanceolate in outline, entire-margined or partially pinnate (Fig. 5.1). The lamina is usually coarsely divided into oppositely to sub-oppositely positioned squarish segments that insert laterally to the rachis. Numerous proximally bifurcating parallel veins enter each lamina segment and run straight to the margin. The leaves have robust cuticles. Costal and intercostal fields are distinct on the abaxial, but indistinct on the adaxial side of the leaf. Intercostal fields are characterized by epidermal cells that bear solid papillae.

Chorions.—A total of 15 small, dorsiventrally compressed chorions have been discovered on cuticles of three different *Nilssoniopteris haidingeri* specimens. All chorions display approximately the same size and morphology, which indicates that they were produced by the same kind of insect. In the following description, the micropylar end of the chorions to the leaf surface is called 'proximal tip,' while the opposite represents the distal tip; the surfaces of the chorions are termed ventral (i.e., the side oriented toward the leaf surface) and dorsal. The chorions are oval in outline, slightly compressed dorsiventrally, between 280 and 310 μm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long and 150–180 μm wide (Figs. 2.1–2.2, 3.1, 3.3). They are attached to the outer surface of the abaxial (lower) cuticle. Eggs attached to the adaxial (upper) leaf surface have not been found to date. The chorions possess a massive lateral rim that is crenulate and characterized by prominent intercalary septae (Figs. 3.5–3.6, 4). Between the individual septae, the lateral rim shows shallow depressions (Figs. 2.2, 3.5–3.6, 4). The dorsal and ventral surfaces of the chorion are less massive (e.g., Fig. 2.2) and marked by distinct longitudinal striae that occur on the inner side of the chorion (Figs. 2.2, 3.1). The ventral side displays a near-rectangular proximal area that is thin-walled and surrounded by a stronger cutinized ''wall'' (Figs. 3.3, 3.3–3.4, 4). On the opposite dorsal side, the massive lateral rim is proximally interrupted and displays a distinct aperture, which is embraced by two lips formed by the lateral rim (Figs. 2.2, 3.2, 3.4, arrows, 4).

Around the lateral margins of the eggs, a narrow and incomplete ring composed of accumulated cutin occurs on the leaf surface (Figs. 2.2, 3.1, 3.3, 3.5, arrows, 4). Focusing through the objects reveals that, beneath the eggs, the papillae of the normal epidermal cells and stomatal subsidiary cells are either dissolved or the entire space between leaf surface and chorion is filled with cutin or another substance secreted by the leaf (Fig. 3.7).

The spatial distribution of the chorions on the leaf surface is preserved in one of the cuticle preparations: This specimen (Fig. 2.1) suggests that the eggs are arranged in circles of approximately 1.5 mm in diameter; all eggs are oriented with their micropylar tips towards the centre of the circle (Figs. 2.1, 3.1). Arrangement of the eggs does not concur with structural details of the leaf epidermis and cuticle (i.e., no arrangement along the veins); the eggs may occur on costal and intercostal fields (Fig. 2.1).

Comments.—The thin-walled trapezoidal proximal area visible on the ventral side of the chorions is interpreted as the hatching aperture (e.g., Figs. 3.3–3.4, 4). The surrounding ''wall'' is composed of the remains of the chorion that were folded apart by the hatchling during hatching (Fig. 3.4, arrow). Presence of this feature indicates that the eggs have already hatched and only the chorions are preserved as fossils. The eggs were oriented horizontally on the leaf surface, rather than perpendicularly (i.e., standing upright) based on the fact that massive cutinization occurs around the entire outer margin (Figs. 3.3, 3.4, 3.7, 4) and in the spaces between the eggs and leaf surface. The massive cutinization beneath and around the eggs suggests that the eggs remained on the leaf surface for a longer period of time, and were gradually incorporated into the leaf cuticle. This may reflect a response of the leaf epidermis to the presence of the eggs. Alternatively, adcrustration of additional cuticular materials may have been induced by certain chemicals on the chorion in order to more firmly glue the eggs to the leaf surface during development of the hatch. The massive lateral crenulate flange with intercalary septae, along with the longitudinal striae on the inner surfaces of the dorsal and ventral sides of the chorion, supports the hypothesis that the eggs remained on the leaf for a longer period of time since they indicate that the chorions were relatively robust. Robustness of the chorions could not be explained if hatching of the larvae occurred after only a few days. Moreover, the fact that the chorions are robust strengthens the interpretation that they were deposited onto the outer surface of the leaf (Wesenberg-Lund, 1943, p. 79). The orifice embraced by lips occurring proximally on the dorsal side (Figs. 3.2, 3.4, 4) may represent a gas-exchange device (aeropyle) for the encapsulated embryo, and/or may form part of the hatching aperture.

Affinities.—Detailed evidence for egg morphology and ovipositional behavior of ancient insects is virtually absent from the fossil record. Moreover, no insect imago or larva has been documented from Lunz to date that could provide insights into insect abundance and diversity in this Late Triassic paleoecosystem. As a result, we are confined in assessing the affinities of the chorions from Lunz to comparisons with extant insect groups for which egg morphology and ovipositional behavior have been documented, along with information about the fossil record of these extant insect groups. Assignment of the chorions to a particular insect family or genus is impossible at present. However, morphology, size, and spatial arrangement on the leaf surface permit speculation about affinities with basal Hymenoptera (i.e., Symphyta) or Coleoptera, two orders of insects that were well established and diverse by the Late Triassic (Rasnitsyn, 1969; Ponomarenko, 1977, 1992; Labandeira and Sepkoski, 1993; Grimalid and Engel, 2005).

During the Late Triassic, four major clades of insects had ovipositors capable of piercing plant tissue, particularly stems and leaves. These were the Odonata, particularly zygopteran damselflies; the Orthoptera such as phytophagous members of the Saltatoria; the basalmost clade of the Hymenoptera, the sawflies of the Tenthredinoidea; and the Coleoptera, especially some early-derived clades of the Polyphaga (Labandeira, 2006). All of these taxa have been recorded for Triassic strata, and thus may have occurred in the habitats, in which *Nilssoniopteris haidingeri* lived.

In the following paragraphs, we discuss each of these four groups and present a hypothesis with regard to the producers of the chorions based on plant damage features, ovipositor structure, and general habitat type frequented by each of the four ovipositor-bearing insect clades.

Several extant species in the basal Hymenoptera (e.g., members of the Tenthredinidae and Pamphilidae), are known to attach their eggs to abaxial leaf surfaces (Hinton, 1981, p. 705). Others, such as the Xyelidae and Tenthredinidae, have laterally compressed ovipositors with sawtooth ridges or rows of cutting denticles that are used to insert eggs endophytically (Burdick, 1961; Labandeira, 2006). The majority of the latter forms inject the eggs into leaves, rachides, and twigs. The Symphyta form the basal grade of the Hymenoptera (Rasnitsyn, 1988, 2000; Schulmeister, 2002, 2003a, 2003b; Grimaldi and Engel, 2005, p. 409). They are primitive phytophages, widespread in cool to temperate regions. The phylogenetically oldest family in the suborder Symphyta, the Xyelidae, still exists today with some 50 species; it represents one of the eight oldest insect families. Xyelidae are abundant in the fossil record; the group can be traced into the Late Triassic (Rasnitsyn, 1969; Carpenter, 1992; Grimaldi and Engel, 2005, p. 409). During the Mesozoic, xyelids apparently were more widely distributed, and occurred in distinctly warmer climates, than seen in the extant species of this family (Grimaldi and Engel, 2005, p. 410). Most extant xyelids liberate their eggs into staminate cones or needles of Pinaceae (Burdick, 1961; Blank et al., 2005), and the larvae subsequently feed on pollen or within buds (Burdick, 1961). It is possible that oviposition in cones is a derived mode, and the earliest forms generally deposited their eggs on leaves. Blank (2002) suggests that the earliest Xyelidae did not exclusively feed on pollen, but they were at best facultatively pollen-iphagous. However, no feeding traces (cf. Ash, 2005) were observed on or in any of the *Nilssoniopteris* leaves from Lunz.

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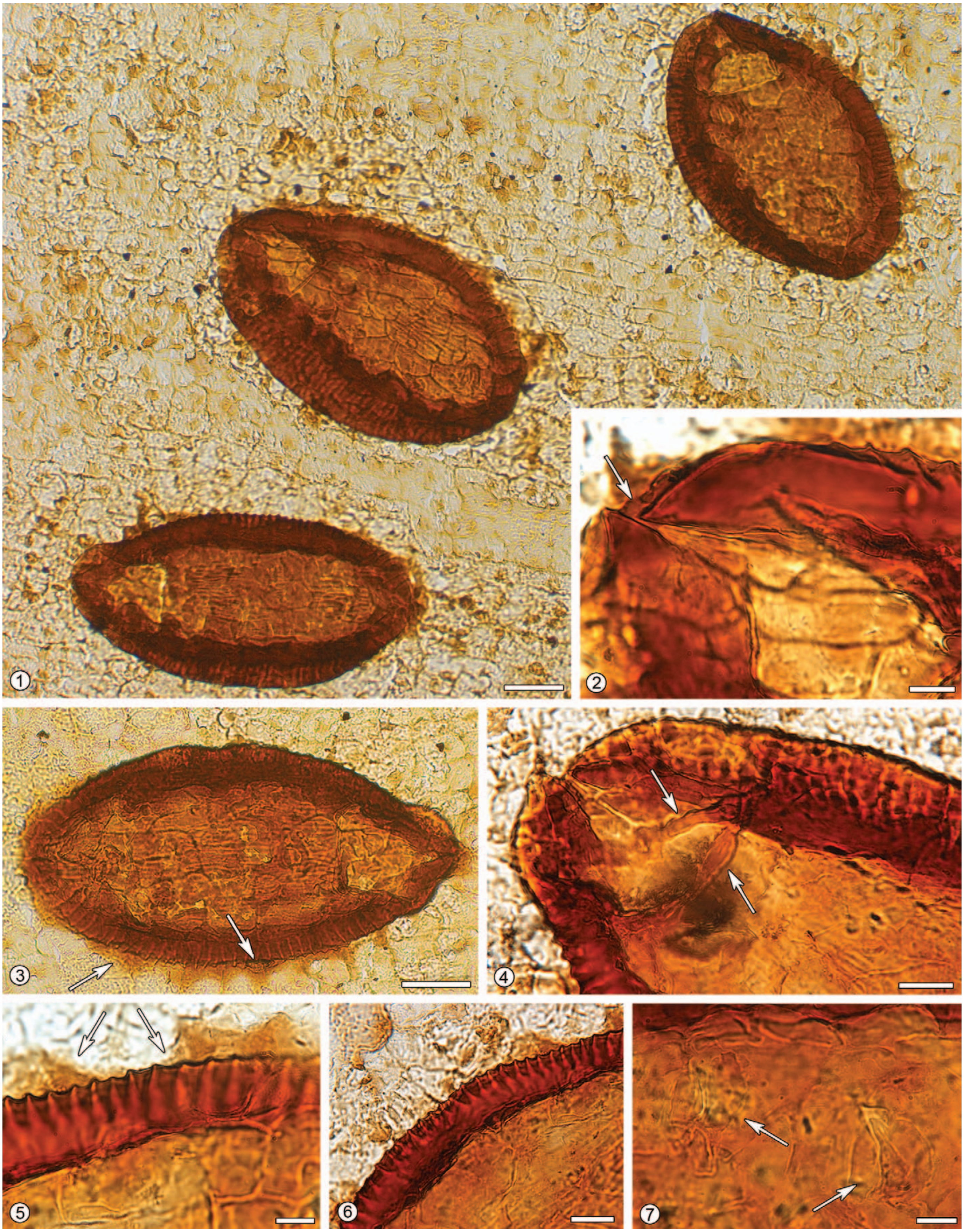
FIGURE 2—Eggs on cuticles of leaves of *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909) Pott, Krings et Kerp, 2007 (†Bennettitales). *1,* Large cuticle segment. Note the small oval eggs arranged in a circle. Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 100 μm. *2,* Detail of Fig. 2.1, focusing the morphology of the eggs. Note the heavy cutinizations around the lateral margin of the egg and the well-recognizable micropyle (arrow). Scale bar = 50 μm.



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Blank (2002) also suggests that larvae of the earliest Hymenoptera did not feed endobiontically like the larvae of most derived xyelids. Eggs of some extant Xyelidae (e.g., *Pleroneura* Konow, 1897) are similar in size to the chorions from Lunz (Burdick, 1961).

Besides Hymenoptera, the eggs on the *Nilssoniopteris haidingeri* leaf cuticles may also have been produced by Coleoptera (beetles). Coleoptera today represent the largest order of insects. Most beetles liberate their eggs into soil, soil burrows, or wood, or attach the eggs to the abaxial surfaces of leaves (Crowson, 1981, p. 360–362). A few species are known that inject their eggs into living leaf tissues, but these are mostly members of the Phytophaga group (Cerambycidae, Chrysomelidae, Curculionidae and related lineages). Phytophagan beetles are a relatively derived group that is believed to have originated during the earlier Jurassic (Carpenter, 1992; Zherikhin and Gratshev, 1995; Gratshev and Zherikin, 2003). Thus, it is rather unlikely that they produced the eggs on *N. haidingeri*.

The Coleoptera is an ancient insect lineage, depicted by an extensive fossil record that can be traced into the late Paleozoic (Lawrence and Newman, 1982). The major radiation, however, occurred after the Permo-Triassic extinction event (Carpenter, 1992; Labandeira and Sepkoski, 1993; Grimaldi and Engel, 2005, p. 360). Many extinct groups of beetles, most belonging to the Archecoleoptera and Myxophaga, have been described based on well-preserved fossils. Some of these lineages survived the Permian/Triassic boundary and became extinct toward the end of the Jurassic (Crowson, 1981, p. 661–664; Carpenter, 1992; Grimaldi and Engel, 2005, p. 361). A comparison of the material from Lunz with the eggs and ovipositional behavior of these ancient groups of beetles is impossible because only imagines and/or larvae of these forms have been described. On the other hand, a number of extant beetle families can be traced into the Middle Triassic. For example, the earliest representatives of rove beetles (Staphylinoidea, Polyphaga group) have been recorded for the Middle Triassic (Fraser et al., 1996). Rove beetles thrive on the ground and feed on small arthropods or other soil-inhabiting animals. Although egg size and egg morphology in extant *Staphylinus* Linnaeus, 1758 (Szujecki, 1966; Hinton, 1981, p. 117) correspond well with that seen in the fossils, it is rather unlikely that these insects produced the eggs from Lunz because most extant staphylinids liberate their eggs into soil.

The Trachypachidae include six extant species, but the group was more diverse in the Late Triassic to Late Jurassic (Ponomarenko, 1977, 1992; Grimaldi and Engel, 2005, p. 366). Trachypachids are small, carabid-like animals with ancestral adephagan characters. They represent a basal sister group to the Carabidae. Trachypachid beetles live in riparian to dry habits and feed on the ground. Little is known about their biology. Nevertheless, based on the fact that they were present in the Late Triassic, and the extant species live in habitats comparable to that interpreted for the Lunz paleoecosystem, it cannot be excluded that members of this group produced the eggs on *Nilssoniopteris haidingeri*. However, the larvae of extant trachypachids usually live on the ground.

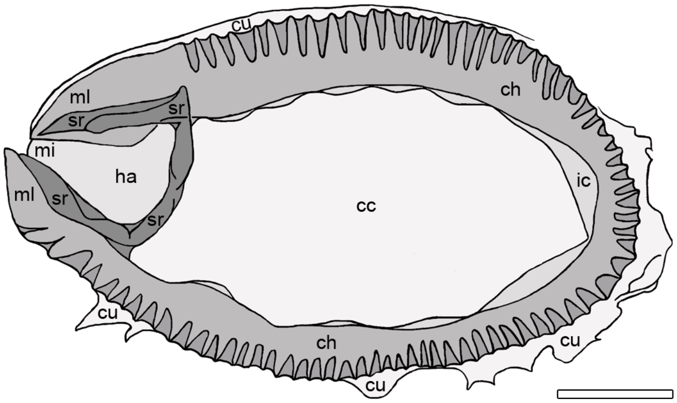

FIGURE *4*—Schematic line drawing of an egg based on Figs. 2.1–2.2 and 3.1–3.7. Abbreviations: cc—central chamber; ch—chorion; cu—accumulated cutinizations around the chorion; ha—hatching aperture; ic—inner chorionic layer; mi—micropyle; ml—micropylar lips; sr—shell remains of hatching aperture folded apart during the hatching process; for details see text. Scale bar = 50 μm.

The Cupedidae (reticulated beetles) are related to the Archostemata, a taxon commonly regarded as the basal suborder of the beetles (Crowson, 1962; Grimaldi and Engel, 2005, p. 363–365; Jingjing Tan et al., 2006). The extant Cupedidae represent relicts of a once diverse lineage. The fossil record indicates that the group was particularly diverse during the Late Triassic to Early Cretaceous (Carpenter, 1992). Today the reticulated beetles include some 30 species in nine genera. Larvae are wood-borers that typically live in moderately firm and dry, fungus-infested woods; adults live beneath the bark of trees or on leaves. Extant reticulated beetles occur in forests and woodland; they can be found in rainforest as well as arid grassland and open woodland ecosystems. The eggs of extant reticulated beetles (Crowson, 1962) closely resemble the fossils from Lunz with regard to size and surface structures. Unfortunately, Hinton (1981, p. 649 ff.), in his fundamental work on the biology of insect eggs, does not detail the morphology of either Cupedidae or Trachypachidae eggs.

It has variously been suggested that cupedid beetles played a major role in the reproductive biology (i.e., as pollinators) of the Bennettitales (Crowson, 1981, p. 600 and 665; Lawrence and Newton, 1982), because the diversity pattern through time of the Cupedidae seems parallel to that seen in the Bennettitales (cf. Sitte et al., 1998; Grimaldi and Engel, 2005, p. 361). Moreover, the morphology of certain flower-like bennettitalean reproductive structures (e.g., Wieland, 1916; Delevoryas, 1968; Rothwell and Stockey, 2002; Stockey and Rothwell, 2003) strongly suggests insect rather than wind pollination (Stockey and Rothwell, 2003). Interactions between bennettitaleans and cupedids were perhaps not restricted to pollination. Rather, the beetles may also have benefited from other parts of the plants (i.e., wood, leaves). This hypothesis is supported by the fact that Jurassic representatives of cupedid beetles have been shown to have lived in the wood of certain Bennettitales (Ponomarenko, 2003).

Other possible producers of the eggs include dragonflies. Most modern odonatan taxa, particularly zygopterans such as the Coenagrionidae, insert eggs into plant tissue with laterally compressed

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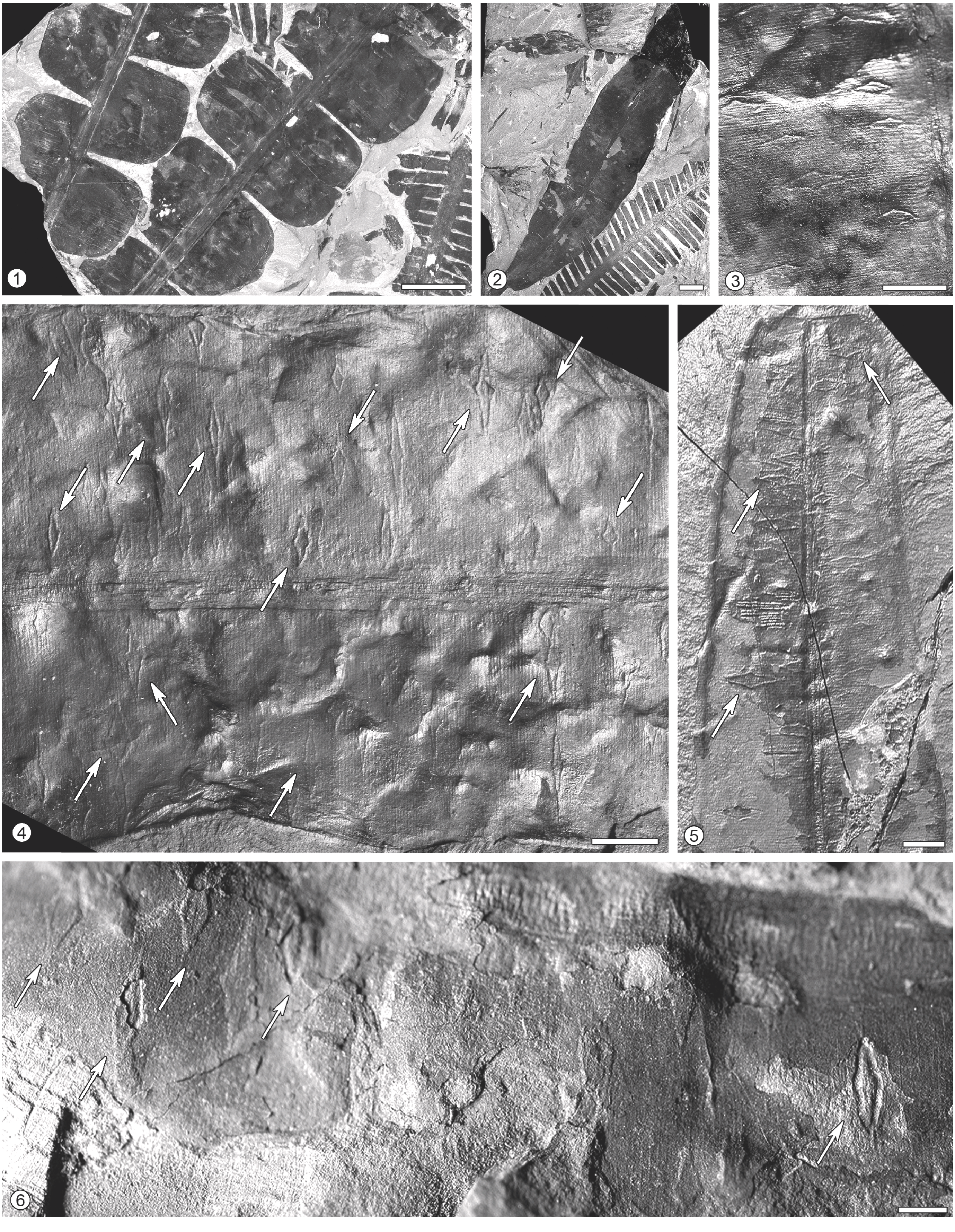
FIGURE 3—Eggs on cuticles of leaves of *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909) Pott, Krings et Kerp, 2007 (†Bennettitales). *1,* Detail of Fig. 2.1, focusing on some of the eggs. Scale bar = 50 μm. *2,* Close up of hatching aperture and micropyle (arrow) embraced by two lips. Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 10 μm. *3,* Details of Fig. 2.1, showing the morphology of the eggs. Note heavy cutinizations around the lateral margin of the eggs (arrow). Scale bar = 50 μm. *4,* Close up of hatching aperture with putative shell remains folded apart by the hatching embryo (arrow). Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 20 μm. *5,* Close-up, focusing on the crenulate margin. Arrows indicate heavy cutinizations around the margins of the chorion. Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 10 μm. *6,* Structure of crenulate margin, overview. Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 50 μm. *7,* Two stomata (arrows) that occur in the leaf epidermis beneath one of the eggs. Slide GBA 1909/002/0250/0006 deposited in the Geological Survey of Austria, Vienna (Austria). Scale bar = 10 μm.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sawtooth ovipositors that superficially resemble that of tenthredinids (Labandeira, 2006). The eggs are inserted either completely into plant tissue, foliar or stem, or partially with about half of the egg emergent. A few groups in the Anisoptera, however, attach their eggs to plant surfaces. Eggs partially inserted or attached to surfaces usually leave characteristic ellipsoidal to ovoidal marks surrounded by callus or other scar material, with disorganized tissue within, often appearing as a shallow crater (Labandeira, 2002). The shape and general appearance of the chorions is similar to that of exophytic Odonata. Endophytic eggs are typically more elongate (roughly four times longer than wide) and often slightly curved. The chorion from Lunz appear to have only a single terminal micropyle, assuming the dorsal structure alluded to is in fact an aeropyle or related to the hatching process; its position is certainly very different from the micropyle in modern odonatan eggs. In all extant Odonata, the eggs have at least two terminal or subterminal micropyles, and the more plesiotypic taxa have numerous micropyles (e.g., Sahlén, 1994, 1995). Hatching usually involves complete or nearly complete separation of a terminal ‘cap,’ not a longitudinal split. No odonatan eggs have been described that have a lateral crenulate flange as seen in the chorions from Lunz. Finally, arrangement of the eggs in a partial circle (Fig. 2) is not typical of the modern Odonata species laying eggs externally on leaves; these are most often deposited in irregular masses (Corbet, 2004, p. 36). Eggs inserted into plant tissue usually are much larger (i.e., 1.5 to 2.0 mm long) than the eggs from Lunz, but eggs produced by species that deposit onto plant surfaces typically are only about 0.5 mm long (Schiemenz, 1957), and thus similar in size with the eggs from Lunz. In addition, the arrangement of the eggs in circles adds support to the hypothesis that dragonflies produced the eggs (Wesenberg-Lund, 1943, p. 70–71). Some, but not all, endophytic species, including some Lestidae (Matushkina and Gorb, 2000) place their eggs in a radial pattern, but neither the morphology nor position on the leaf suggests that the eggs from Lunz were endophytic.

Size, morphology, and ovipositional marks surrounded by callus or other scar material with disorganized tissue, along with the insect groups present during the Late Triassic, it is possible to speculate that a cupedid or related beetle most likely produced the chorions on *Nilssoniopteris haidingeri*.

EGG IMPRESSIONS ON LEAVES OF *NILSSONIOPTERIS ANGUSTIOR* (STUR EX KRASSER, 1909) POTT, KRINGS AND KERP, 2007
Figures 5.2–5.6, 6.1–6.8

Leaves.—Leaves of *Nilssoniopteris angustior* (Fig. 5.2) are oblong to lanceolate in outline, up to 30 cm long and 5 cm wide. The lamina is usually entire-margined and inserts laterally to a prominent rachis. Numerous basally bifurcating parallel veins enter the lamina and run straight to the margin. The leaves have delicate to massive cuticles; an alternation of stomatiferous and non-stomatiferous areas occurs on the abaxial side. Stomata occur sporadically in adaxial lamina areas close to the midrib. Stomata and subsidiary cells of the abaxial lamina are arranged in rows that alternate with non-stomatiferous bands of cells; however, this alternation is irregular and does not concur with the venation pattern.

Impressions.—Of the 65 specimens at hand of *Nilssoniopteris angustior*, 22 specimens are marked by one to several regularly rhomboidal impressions (Fig. 5.3–5.6), which are 3–6 mm long and 1–2 mm wide. Impressions may occur on the adaxial (upper) and abaxial (lower) side of the leaf. However, in compressions that expose the adaxial side of the leaf, the impressions are surrounded by a narrow raised margin, and hence clearly demarcated from the surrounding epidermis (Fig. 5.3–5.5), while impressions on the abaxial side lack this feature (Fig. 5.6). The impressions are consistently oriented parallel to the lateral veins and perpendicular to the rachis (Fig. 5.3–5.5). They usually occur near the rachis (Fig. 5.5–5.6), but impressions close to the leaf margin have also been found (Fig. 5.4).

Cuticle preparations of individual impressions and vicinity reveal that the impressions congruently occur on both the adaxial and abaxial side (Fig. 6.1), i.e., ad- and abaxial imprint areas coincide when both cuticles are superimposed. However, ad- and abaxial impressions display characteristic structural differences (Fig. 6.1–6.6), which are especially well recognizable in the mirror-inverted imprint shown in Fig. 6.1 (grey and white arrows). On the adaxial side, the leaf cuticle is distinctly thinner along the margin of the impression, which is also recognizable in the compression specimens (e.g., Fig. 5.4), whereas the central region of the impression area is normally cutinized (Fig. 6.3, 6.5). Cell forms and sizes, as well as spatial arrangement of the epidermal cells, correspond to those seen outside the imprint area, and the individual epidermal cells within the impression area are not unnaturally distorted (Fig. 6.5). Delicateness of the cuticle along the margin of the adaxial impressions often causes tearing of the cuticle (Fig. 6.1, grey arrow). On the other hand, the abaxial imprint area is characterized by a considerably thinner cuticle within the rhomboid (Fig. 6.1, white arrow, 6.2, 6.4). A narrow band consisting of heavily cutinized epidermal cells marks the border line of the impression area (Fig. 6.4, 6.6). Close to this marginal scar, the epidermal cells within the imprint area are distinctly deformed (Fig. 6.6); the general epidermal cell pattern, however, is not affected.

Comments.—The impressions described here are structurally similar to the rhomboidal impressions or lenticular scars documented on *Schmeissneria* leaves from the Lower Jurassic of Germany by Van Konijnenburg-van Cittert and Schmeißner (1999). These authors interpret the impressions as egg impressions. However, detailed analyses of the leaf cuticle and epidermal anatomy within and outside of the imprint area, have not been provided because these fossils are preserved as impressions. Nevertheless, based on the corresponding in basic structure and spatial arrangement between the impressions described here and the structures detailed by Van Konijnenburg-van Cittert and Schmeißner (1999), we interpret the impressions on *Nilssoniopteris angustior* leaves from Lunz as impressions caused by insect eggs. With regard to the lenticular shape, prominent marginal scar and comparatively flat center, and arrangement parallel to venation, the impressions from Lunz are similar to impressions seen on various leaves from the Upper Triassic Molteno Formation (South Africa), and on glossopterid leaves from the Clouston Farm Site (Permian) in South Africa.

The fact that the impressions are visible on both surfaces of

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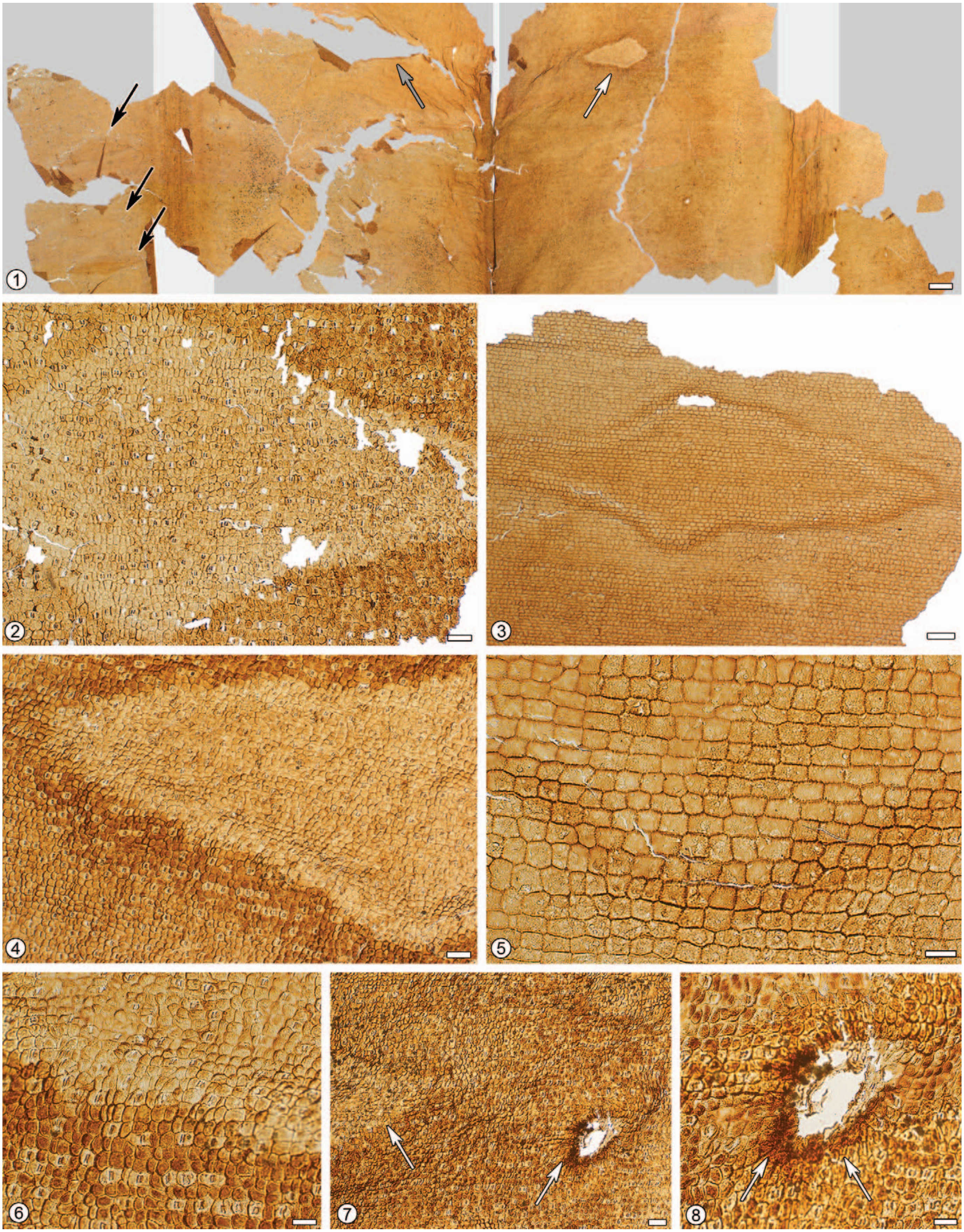
FIGURE 5—Leaves of *Nilssoniopteris haidingeri* (Stur ex Krasser, 1909) Pott, Krings et Kerp, 2007, and *Nilssoniopteris angustior* (Stur ex Krasser) Pott, Krings et Kerp, 2007 (†Bennettitales). *1, Nilssoniopteris haidingeri*, Specimen NHM 2006B0008/0042; deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 10 mm. *2, Nilssoniopteris angustior*. Specimen NHM 1887/I/0009; deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 10 mm. *3–5,* Rhomboidal impressions on leaves of *Nilssoniopteris angustior*. View from the adaxial side, showing the raised outer margins of the imprint areas. Specimens NHM 1884/0015 (Fig. 5.3), and NHM 1884/0015 (Fig. 5.4), deposited in the Museum of Natural History, Vienna (Austria), and GBA 1909/002/0185 (Fig. 5.5), deposited in the Geological Survey of Austria, Vienna (Austria). Scale bars = 5 mm (Fig. 5.3, 5.4), and 10 mm (Fig. 5.5). *6,* Rhomboidal impressions on *Nilssoniopteris angustior*. View from the abaxial side; carbonaceous material removed. Specimen RUU 17895 deposited in the Laboratory of Palaeobotany and Palynology, Utrecht (The Netherlands). Scale bar = 5 mm.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the leaf, and coincide when both cuticles are superimposed, indicates that the eggs were deposited into the interior leaf tissues. Moreover, one specimen suggests that insertion of the eggs into the leaves occurred from the abaxial side: Several circular injuries, 70–300 μm in diameter, occur in the cuticle close to the impressions (Fig. 6.7–6.8). These injuries may have been caused by an insect ovipositor (cf. Wesenberg-Lund, 1943, figs. 63–65). Each of the injuries is surrounded by heavily cutinized epidermal cells (Fig. 6.8), which likely represent a post-trauma wound response of the leaf (i.e., wound callus formation).

The abnormal shape of the epidermal cells within the abaxial impression area is indicative of mechanical distortion as a result of oviposition or egg growth. Moreover, the plant cuticle within the abaxial impression area became considerably thinner in response to the presence of the eggs in the interior. The mechanisms underlying the alteration of the cuticle thickness cannot be determined. It is possible that certain chemicals exuded from the eggs, or injected during oviposition, have dissolved part of cuticle. This may eventually have facilitated hatching of the naiads or larvae. However, leaf surface openings produced by the escaping larvae, or evidence for larval feeding activity in the interior of the leaves, have not been observed. The heavily cutinized marginal scar, which occurs around the abaxial impression areas (e.g., Fig. 6.4) may represent a form of defense reaction of the plant, or was produced by the plant to protect and stabilize the epidermis in this area of the leaf (Peeters, 2002).

Affinities.—Van Konijnenburg-van Cittert and Schmeißner (1999) attribute the egg impressions on *Schmeissneria* leaves from the Lower Jurassic of Germany and on leaves of various plants from the Carnian of South Africa, respectively, to the Odonata (dragonflies and damselflies). This is based primarily on the characteristic distribution pattern and macroscopic appearance of the structures. However, since the Triassic and Jurassic impressions are larger (i.e., 0.8 × 3 mm in diam.) than those caused by extant members in the Odonata, they are interpreted as having been caused by representatives in this group of insects that were larger than the extant species. The egg impressions from Lunz correspond well to those described by Van Konijnenburg-van Cittert and Schmeißner (1999).

The impressions from Lunz are up to 5 times larger than those described by Van Konijnenburg-van Cittert and Schmeißner (1999). Taking this into account, it is likely that they were produced by still larger members in the Odonata. Two suborders of the Odonata are known from the Triassic: the Archizygoptera, which survived the Permian/Triassic boundary, and the Triassolestoidea (Anisozygoptera), which first appeared in the Late Triassic (Carpenter, 1992). Both groups are extinct today. The latter group is related to the extant damselflies and characterized by a transversely elongate head and absence of epiprocts in adults (Grimaldi and Engel, 2005, p. 184). Extant damselflies inject the eggs into leaves of aquatic plants or plants overarching inshore waters (Wesenberg-Lund, 1943, p. 70–71; Hinton, 1981, p. 486 ff.). Several species in the Odonata (e.g., emerald damselflies of the genus *Lestes* Leach, 1815) exclusively inject the eggs into plants growing above or outside the water (e.g., *Alisma* Linnaeus 1753 species) (Wesenberg-Lund, 1913). After hatching, the naiads drop into the water. Eggs of extant Odonata are considerably smaller than the eggs outlined by the impressions on *N. angustior* from Lunz. Nevertheless, the mode of oviposition displayed by extant Odonata, along with the typical spatial arrangement of the eggs, may suggest that the egg impressions from Lunz have been caused by eggs belonging to Odonata (Schiemenz, 1957; Wesenberg-Lund, 1943, p. 70–71; Hinton, 1981, p. 486 ff.; Hellmund and Hellmund, 1996; Corbet, 2004, p. 21–22; Van Konijnenburg-van Cittert and Schmeissner, 1999). However, it cannot be ruled out that the damages have other origins, but pupae or mining is less likely because evidence for mines or other external damage is lacking in the hand specimens as well as in the cuticles.

These egg impressions provide additional information regarding the ecology of the plants producing *Nilssoniopteris angustior* foliage: the hatching naiads of dragonflies have to reach water immediately to complete development, which implies that these plants have grown near inshore waters, perhaps with branches or leaves overhanging the water surface.

DISCUSSION AND CONCLUSIONS

Insect eggs and/or egg impressions have variously been described from the Mesozoic fossil record. However, evidence based on cuticular analysis has not been produced to date. The material presented here provides the first detailed documentation of fossil insect eggs and egg impressions based on cuticle preparations.

It is impossible at present to determine the affinities of the eggs and egg impressions from Lunz, due primarily to the fact that detailed information on the morphology and distribution on/in leaves of other fossil and extant insect eggs is rare. The material at hand demonstrates that insect eggs liberated onto or into leaves characteristically affect the structure of the plant surface, especially with regard to cuticle thickness. Such characteristic alterations in cuticle thickness may be used in future studies to detect insect oviposition activity from plant cuticles, even if the eggs themselves are not preserved, and thus provide an innovative means to gather data about the composition and ecology of ancient ecosystems.

The fossils from Lunz also demonstrate that different modes of oviposition can be reconstructed based on how the presence of the eggs has affected the leaf cuticle. The coinciding ad- and abaxial impressions on leaves of *Nilssoniopteris angustior* (Fig. 6.1) suggest that insect eggs were placed into interior leaf tissues by an insect with an elongate ovipositor or abdomen as seen in extant dragonflies (Wesenberg-Lund, 1943, p. 70–71, figs. 56–57). Circular injuries occurring in the abaxial cuticle may have been inflicted by a penetrating long ovipositor (Fig. 6.7–6.8).

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FIGURE 6—Ovipositional damage on leaf cuticles of *Nilssoniopteris angustior* (Stur ex Krasser) Pott, Krings et Kerp, 2007 (†Bennettitales). *1,* Overview of a large cuticle segment. The cuticle segment is opened with the interior side up; for orientation background columns are given, indicating (from left to right) right adaxial cuticle (grey); central vascular bundle (white); left adaxial cuticle (grey); leaf margin (white); left abaxial cuticle (grey); central vascular bundle (white); right abaxial cuticle (grey). The grey and white arrows indicate mirror-inverted imprint areas on the adaxial (grey arrow, inner area of the imprint torn off) and abaxial cuticle (white arrow); black arrows indicate additional imprint areas on the adaxial cuticle). Slide NHM 1884/0015/0003 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 1 mm. *2,* Abaxial cuticle, showing a rhomboidal imprint characterized by a weakly cutinized inner and normally cutinized outer area. Slide NHM 1884/0015/0016 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 100 μm. *3,* Adaxial cuticle, showing a rhomboidal imprint; note the differences in cuticle thickness. Slide NHM 1884/0015/0007 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 200 μm. *4,* Abaxial cuticle, showing a rhomboidal imprint. Detail of the inner area and heavily cutinized margin of the imprint area. Slide NHM 1884/0015/0003 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 100 μm. *5,* Close up of a detail of Fig. 6.3. Scale bar = 50 μm. *6,* Detail of a rhomboidal imprint, showing the epidermal cell pattern with distorted cells and heavily cutinized outer margin. Slide NHM 1884/0015/0003 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 50 μm. *7,* Abaxial cuticle, showing a rhomboidal imprint (arrow) and a circular injury perhaps caused by an insect ovipositor. Note the wound-callus formation around the damaged area. Slide NHM 1884/0015/0002 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 100 μm. *8,* Close-up on one of the circular injuries in the leaf surface. Slide NHM 1884/0015/0002 deposited in the Museum of Natural History, Vienna (Austria). Scale bar = 50 μm.

Wound callus formation around the injuries indicates that the surfaces were pierced while the leaf was alive. On the other hand, the eggs deposited onto the abaxial leaf surfaces of *N. haidingeri* (Fig. 2.1–2.2) are suggestive of an insect that did not pierce the leaf surface for oviposition, and thus might have had a reduced ovipositor. If these eggs were not preserved, the characteristic alteration of the abaxial cuticle in the form of massive cutinizations beneath and around the eggs would still document deposition of the eggs onto the abaxial leaf surface.

It is interesting to note that the eggs and egg impressions on *Nilssoniopteris* seem to display host-specificity. During the last two years, we have analyzed cuticles of all taxa of Cycadales and Bennettitales from Lunz based on a large sample set consisting of approximately 2,500 cuticle preparations of about 350 leaves of 10 species of the genera *Pterophyllum*, *Nilssoniopteris*, *Nilssonia*, and *Pseudoctenis* (Pott et al., 2007a, 2007b; Pott, Krings, and Kerp, 2007; Pott, Van Konijnenburg-van Cittert et al., 2007). However, egg impressions were found exclusively on leaves of *N. angustior* (Fig. 5.2), while the eggs only occur on cuticles of *N. haidingeri* (Fig. 5.1). It is possible to envisage that this host-specificity reflects certain preferences in larval diet or differences in the spatial (topographical) distribution of the host plants. For example, the hatch of extant Odonata that emerges from eggs deposited outside the water immediately drops down into the water where the naiads further develop (Corbet, 2004, p. 69–71); naiads that fail to reach the water shortly after hatching will perish after only a short period of time. Therefore, successful reproduction in Odontata requires that the eggs are liberated on plants that grow close to open water. If the impressions on *N. angustior* were produced by Odonata eggs, these plants must have grown in close proximity to a body of water. Assuming a cupedid origin of the actual eggs on leaves of *N. haidingeri*, those plants may have grown elsewhere but accessible for arboreal or ground beetles. Host plant specificity is stated to have been manifest in all possible degrees in herbivorous beetles (Crowson, 1981, p. 585).

Although cuticular analysis is long since known to represent a valuable means of extracting biological information from compression fossils that is useful in taxonomy but also important with regard to paleobiological and paleoecological considerations, cuticular analysis has rarely been applied in the decipherment of plant/animal interactions. The results presented here document that fossil cuticles may provide features with regard to the reproductive biology of ancient insects such as egg morphology, spatial arrangement of eggs, modes of oviposition, and host-specificity. Because compression fossils are much more abundant than permineralizations, they represent a copious source of information about plant/insect associations (e.g., Anderson et al., 1998; Scott et al., 2004; Labandeira, 2005). This source, however, has remained largely untapped to date. The cycadophytes from Lunz may serve as template for future studies of ancient insect activities on foliage based on fossil cuticles.

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REFERENCES

ANDERSON, J. M., R. KOHRING, AND T. SCHLÜTER. 1998. Was insect biodiversity in the Triassic akin to today?—A case study from the Molteno Formation (South Africa). Entomologia Generalis, 23(1/2):15–26.

ASH, S. 1997. Evidence of arthropod-plant interactions in the Upper Triassic of the Southwestern of the United States. Lethaia, 29:237–248.

ASH, S. 1999. An Upper Triassic *Sphenopteris* showing evidence of insect predation from Petrified Forest National Park, Arizona. International Journal of Plant Science, 160(1):208–215.

ASH, S. 2005. A new Upper Triassic flora and associated invertebrate fossils from the basal beds of the Chinle Formation, near Cameron, Arizona. PaleoBios, 25(1):17–34.

BÉTHOUX, O., J. GALTIER, AND A. NEL. 2004. Earliest evidence of insect endophytic oviposition. Palaios, 19:408–413.

BÉTHOUX, O., F. PAPIER, AND A. NEL. 2005. The Triassic radiation of the entomofauna. Comptes Rendus Palevol, 4:609–621.

BLANK, S. M. 2002. Biosystematics of the extant Xyelidae with particular emphasis on the Old World taxa: (Insecta: Hymenoptera). Ph.D. dissertation, Freie Universität, Berlin, 200 p.

BLANK, S. M., A. SHINOHARA, AND B.-K. BYUN. 2005. The East Asian *Xyela* species (Hymenoptera: Xyelidae) associated with Japanese Red Pine (*Pinus densiflora*; Pinaceae) and their distribution history. Insect Systematics & Evolution, 36:259–278.

BRONGNIART, A. 1828. Prodrome d'une histoire des végétaux fossiles. Levrault, Paris, VIII+223 p.

BURDICK, D. 1961. A taxonomic and biological study of the genus *Xyela* Dalman in North America. University of California Publications in Entomology, 17:285–355.

CARPENTER, F. M. 1992. Arthropoda 4—Superclass Hexapoda, p. 279–337. *In* R. L. Kaesler (ed.), Treatise on Invertebrate Palaeontology. The Geological Society of America and the University of Kansas, Boulder, Colorado.

CORBET, P. S. 2004. Dragonflies: Behaviour and Ecology of Odonata. Cornell University Press, Ithaca, XXXIV+829 p.

CROWSON, R. A. 1962. Observations on the beetle family Cupedidae, with descriptions of two new fossil forms and a key to the recent genera. The Annals and Magazine of Natural History, Zoology, Botany and Geology (13. Series), 5:147–157.

CROWSON, R. A. 1981. The Biology of the Coleoptera. Academic Press, London, XII+802 p.

DELEVORYAS, T. 1968. Investigations of North American cycadeoids: Structure, ontogeny and phylogenetic considerations of cones of Cycadeoidea. Palaeontographica Abt. B, 121(4–6):122–133.

DOBRUSKINA, I. A. 1989. The alpine Lunz-Flora—A standard flora for the carnian stage of the Triassic. International Geological Review, 31:1209–1215.

DOBRUSKINA, I. A. 1998. Lunz flora in the Austrian Alps—A standard for Carnian floras. Palaeogeography, Palaeoclimatology, Palaeoecology, 143: 307–345.

FRASER N. C., D. GRIMALDI, P. E. OLSON, AND B. J. AXSMITH. 1996. A Triassic Lagerstätte from eastern North America. Nature, 380:615–619.

GRADSTEIN, F., J. OGG, AND A. SMITH. 2004. A Geologic Time Scale. Cambridge University Press, Cambridge, XX+589 p.

GRATSHEV, V. G. AND V. V. ZHERIKHIN. 2003. The fossil record of weevils and related beetle families (Coleoptera, Curculionoidea). Acta zoologica cracoviensia, 46:129–138.

GRAUVOGEL-STAMM, L. AND K.-P. KELBER. 1996. Plant-insect interactions and coevolution during the Triassic in Western Europe. Paleontologia Lombarda, Nuova Serie, 5:5–23.

GRIMALDI, D. AND M. S. ENGEL. 2005. Evolution of the Insects. Cambridge University Press, Cambridge, XVI+755 p.

HELLMUND, M. AND W. HELLMUND. 1996. Zum Fortpflanzungsmodus fossiler Kleinlibellen (Insecta, Odonata, Zygoptera). Paläontologische Zeitschrift, 70(1/2):153–170.

HINTON, H. E. 1981. Biology of the Insect Eggs (Volumes 1–3). Pergamon, Oxford, XXIV+1125 p.

HORNUNG, T. 2006. Die Reingrabener Wende in der Halleiner Salzbergfazies (distale Hallstattfazies)—biostratigraphische Daten. Geo. Alp, 3:9–21.

HORNUNG, T. AND R. BRANDNER. 2005. Biochronostratigraphy of the Reingraben turnover (Hallstatt facies belt): Local black shale events controlled by regional tectonics, climatic change and plate tectonics. Facies, 51:460–479.

JINGJING TAN, DONG REN, AND CHUNGKUN SHIH. 2006. First record of fossil *Priacma* (Coleoptera: Archostemata: Cupedidae) from the Jehol Biota of western Liaoning, China. Zootaxa, 1326:55–68.

KELBER, K.-P. 1998. Phytostratigraphische Aspekte der Makrofloren des süddeutschen Keupers. Documenta naturae, 117:89–115.

KELBER, K.-P. AND G. GEYER. 1989. Lebensspuren von Insekten an Pflanzen des Unteren Keupers. Courier Forschungs-Institut Senckenberg, 109:165–174.

KERP, H. 1990. The study of fossil gymnosperms by means of cuticular analysis. Palaios, 5:548–569.

KERP, H. AND M. KRINGS. 1999. Light microscopy of cuticules, p. 52–56. *In* T. Jones, Fossil Plants and Spores: Modern Techniques. Geological Society, London.

KIRCHNER, M. AND J. H. A. VAN KONIJNENBURG-VAN CITTERT. 1994.

Schmeissneria microstachys (Presl 1833) Kirchner et Van Konijnenburg-van Cittert comb. nov. and *Karkenia hauptmannii* Kirchner et Van Konijnenburg-van Cittert sp. nov., plants with ginkgoalean affinities from the Liassic of Germany. Review of Palaeobotany and Palynology, 83:199–215.

Konow, F. W. 1897. Ueber die Xyelini (Tenthredinidarum tribus). Entomologische Nachrichten, 23:55–58.

Krings, M., D. W. Kellogg, H. Kerp, and T. N. Taylor. 2003. Trichomes of the Seed Fern *Blanzyopteris praedentata*: Implications for plant-insect interactions in the Late Carboniferous. Botanical Journal of the Linnean Society, 141:133–149.

Krasser, F. 1909. Die Diagnosen der von Dionysius Stur in der obertriadischen Flora der Lunzerschichten als Marattiaceenarten unterschiedenen Farne. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Wien, Abt. 1, 118:13–43.

Labandeira, C. C. 1997. Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. Annual Review of Ecology and Systematics, 28: 153–193.

Labandeira, C. C. 2002. The history of associations between plants and animals, p. 26–261. *In* C. M. Herrera and O. Pellmyr (eds.), Plant-Animal Interactions: An Evolutionary Approach. Blackwell Science, London.

Labandeira, C. C. 2005. Insect leaf-mining in Late Triassic gymnospermous floras from the Molteno Formation of South Africa. Salt Lake City Annual Meeting (October 16–19, 2005). Geological Society of America Abstracts with Programs, 37(7):15.

Labandeira, C. C. 2006. Silurian to Triassic plant and insect clades and their associations: new data, a review, and interpretations. Arthropod Systematics & Phylogeny, 64:53–94.

Labandeira, C. C. and B. S. Beall. 1990. Arthropod terrestriality, p. 214–256. *In* D. G. Mikulic (ed.), Arthropod Paleobiology (Short Courses in Paleontology, Number 3). University of Tennessee Press (for the Paleontological Society), Knoxville, TN.

Labandeira, C. C. and J. J. Sepkoski. 1993. Insect diversity in the fossil record. Science, 261:310–315.

Lawrence, J. F. and A. F. Newman. 1982. Evolution and classification of beetles. Annual Review of Ecology and Systematics, 13:261–290.

Leach, W. E. 1815. Entomology, p. 57–172. *In* D. Brewster (ed.), The Edinburgh Encyclopaedia—Volume 9. William Blackburn, Edinburgh.

Linnaeus, C. 1753. Species plantarum, exhibentes plantas rite cognitas, ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas. Volume 1. Laurentii Salvii, Stockholm, XV+784 p.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Edicio decima, reformata. Laurentii Salvii, Stockholm, 824 p.

Matushkina, N. A. and S. N. Gorb. 2000. Patterns of endophytic egg-sets in damselflies (Odonata, Zygoptera). Vestnik zoologii Supplement, 14(2): 152–159. (In Russian)

Nathorst, A. G. 1909. Über die Gattung *Nilssonia* Brongn. Kungliga Svenska Vetenskapsakademiens Handlingar, 43:3–37.

Peeters, P. J. 2002. Correlations between leaf structural traits and the densities of herbivorous insect guilds. Biological Journal of the Linnean Society, 77:43–65.

Ponomarenko, A. G. 1977. Suborder Adephaga, p. 17–104. *In* L. V. Arnold'di, V. V. Zherikhin, L. M. Nikritin, and A. G. Ponomarenko (eds.), Mezozoiskie Zhestkokrylye. Akademia Nauk SSSR, Trudy Paleontologicheskogo Instituta 161. Nauka Publishers, Moscow.

Ponomarenko, A. G. 1992. Suborder Adephaga, p. 19–142. *In* L. V. Arnold'di, V. V. Zherikhin, L. M. Nikritin, and A. G. Ponomarenko (ed.), Mesozoic Coleoptera. Smithsonian Institution Libraries, Washington, D.C. (English translation of Ponomarenko, 1977)

Ponomarenko, A. G. 2003. Palaeontological discoveries of beetles (http://www.zin.ru/animalia/coleoptera/eng/syst4.htm), last hit: 2 November 2007.

Pott, C., H. Kerp, and M. Krings. 2007a. *Pseudoctenis cornelii* nov. spec. (cycadalean foliage) from the Carnian (Upper Triassic) of Lunz, Lower Austria. Annalen des Naturhistorischen Museums Wien, 109A:1–17.

Pott, C., H. Kerp, and M. Krings. 2007b. Morphology and epidermal anatomy of *Nilssonia* (cycadalean foliage) from the Upper Triassic of Lunz (Lower Austria). Review of Palaeobotany and Palynology, 143:197–217.

Pott, C., M. Krings, and H. Kerp. 2007. The first record of *Nilssoniopteris* (fossil Gymnospermophyta, Bennettitales) from the Carnian (Upper Triassic) of Lunz, Lower Austria. Palaeontology, 50,1299–1318.

Pott, C., J. H. A. van Konijnenburg-van Cittert, H. Kerp, and M. Krings. 2007. Revision of the *Pterophyllum* species (Cycadophytina: Bennettitales) in the Carnian (Late Triassic) flora from Lunz, Lower Austria. Review of Palaeobotany and Palynology, 147:3–27.

Rasnitsyn, A. P. 1969. Origin and evolution of the lower Hymenoptera. Trudy Paleontologicheskii Instituta (Akademiya Nauk SSSR), 123:1–196. (In Russian)

Rasnitsyn, A. P. 1988. An outline of evolution of the hymenopterous insects. Oriental Insects, 22:115–145.

Rasnitsyn, A. R. 2000. Testing cladograms by fossil record: The ghost range test. Contributions to Zoology, 69(4):251–258.

Rothwell, G. W. and R. A. Stockey. 2002. Anatomically preserved *Cycadeoidea* (Cycadeoidaceae), with a reevaluation of systematic characters for the seed cones of Bennettitales. American Journal of Botany, 89:1447–1458.

Sahlén, G. 1994. Ultrastructure of the eggshell of *Aeshna juncea* (L.) (Odonata, Aeshnidae). International Journal of Insect Morphology and Embryology, 23(4):345–354.

Sahlén, G. 1995. Eggshell ultrastructure in *Onychogomphus forcipatus unguiculatus* (van der Linden) (Odonata, Gomphidae). International Journal of Insect Morphology and Embryology, 24(3):281–286.

Schiemenz, H. 1957. Die Libellen unserer Heimat. Franckh'sche Verlagshandlung, Stuttgart, 154 p.

Schulmeister, S. 2002. Simultaneous analysis of the basal lineages of Hymenoptera (Insecta) using sensitivity analysis. Cladistics, 18:455–484.

Schulmeister, S. 2003a. Review of morphological evidence on the phylogeny of basal Hymenoptera (Insecta), with a discussion of the ordering of characters. Biological Journal of the Linnean Society, 79:209–243.

Schulmeister, S. 2003b. Simultaneous analysis of basal Hymenoptera (Insecta): Introducing robust-choice sensitivity analysis. Biological Journal of the Linnean Society, 79:245–275.

Scott, A. C., J. M. Anderson, and H. M. Anderson. 2004. Evidence of plant-insect interactions in the Upper Triassic Molteno Formation of South Africa. Journal of the Geological Society of London, 161:401–410.

Sitte, P., H. Ziegler, F. Ehrendorfer, and A. Bresinsky. 1998. Strasburger Lehrbuch der Botanik. Fischer, Stuttgart, 1007 p.

Sternberg, K. M. G. von. 1820–1838. Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. Fleischer, Spurny, Leipzig and Prague, Volume I, 144+XLII p., Volume II, 80 p.

Stockey, R. A. and G. W. Rothwell. 2003. Anatomically preserved *Williamsonia* (Williamsoniaceae): Evidence for bennettitalean reproduction in the Late Cretaceous of Western North America. International Journal of Plant Science, 164(2):251–262.

Szujecki, A. 1966. Notes on the appearance and biology of eggs of several *Staphylinidae* (*Coleoptera*) species. Bulletin de l'Académie Polonaise des Sciences, Cl. II, 14(3):169–175.

Van Konijnenburg-van Cittert, J. H. A. and S. Schmeissner. 1999. Fossil insect eggs on Lower Jurassic plant remains from Bavaria (Germany). Palaeogeography, Palaeoclimatology, Palaeoecology, 152:215–223.

Wesenberg-Lund, C. 1913. Fortpflanzungsverhältnisse: Paarung und Eiablage der Süßwasserinsekten. Fortschritte der naturwissenschaftlichen Forschung, 8:161–286.

Wesenberg-Lund, C. 1943. Biologie der Süßwasserinsekten. Gyldendalske Boghandel, Copenhagen, and Springer, Berlin, VIII+682 p.

Wieland, G. R. 1916. American Fossil Cycads, Volume II—Taxonomy. Carnegie Institution, Washington, VII + 277p., 58 pls.

Zherikhin, V. V. and V. G. Gratshev. 1995. A comparative study of the hind wing venation of the superfamily Curculionoidea with phylogenetic implicatons, p. 634–777. *In* J. Pakaluk and S. A. Slipinski (eds.), Biology, Phylogeny, and Classification of Coleoptera. Papers celebrating 80th Birthday of Roy A. Crowson, Volume 2, Muzeum i Instytut Zoologii PAN, Warszawa.

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DISCUSSION

The broad range of topics presented in the preceding chapters reflects the value of cuticular analyses in the study of compressed foliage fossils, not only with regard to the taxonomy of many fossil plants from Lunz, but also with regard to the phylogenetic consequences. The latter, in turn, may affect considerations about the reconstruction of the evolutionary history and relationships of Late Triassic seed plants. The consequences thereof are not restricted to the Lunz flora or the Carnian period. They also may affect other taxa and groups as well as the correlation of different organ morphotaxa of the same deposit (i.e. sterile leaves and reproductive structures), and thus the reconstruction of natural taxa (“natural units”). Moreover, our view of the floral development in the Late Triassic and younger periods may change. Comparisons of the Lunz flora to other coeval floras may add to the phytogeographical trends that occurred in the early–middle Mesozoic.

Plant cuticles may reflect various aspects relative to environmental interactions or influences that control the plants in their ecosystem. Comparisons of the ecological features of the cuticles of extant plants with fossil cuticles may provide the possibility to interpret the palaeobiology and -ecology of the fossil plant and environment in which they lived. Palaeoecological interpretation of the Lunz flora based on the results obtained from cuticular analysis is one of the main aspects addressed in the following sections.

THE FLORA FROM LUNZ AND ITS ECOLOGICAL AND ENVIRONMENTAL IMPLICATIONS

Lunz at Carnian times.—Reconstructions by Scotese (2003) and Blakey (2005) suggest that the Lunz flora was situated at the northern shore of the Tethys seaway, distinctly north of the equator, at palaeo-latitudes between the Tropic of Cancer and about 30° N. Today, the regions of the Tropics are covered by deserts, which delimit the tropics north- and southwards; the adjacent sub-equatorial areas represent semi-humid tropics.

The extreme land-sea distribution during the Carnian produced a climate characterised by “mega-monsoons” (Kutzbach & Gallimore 1989). Monsoons primarily are large-area air circulation processes accompanied secondarily by high humidity transported by strongly directional winds. The dry climates that were typical for the Early and Middle Triassic became gradually more influenced by strong seasonal rainfall, and developed more distinct climatic zonation. However, Late Triassic deposition of evaporites is interpreted as indicative of arid climatic regimes (Hay et al. 1982; Olsen 1997). This has to be regarded questionable, since these areas were either located near to the equator or in the rift valley of the western Tethys (Olsen & Rainforth 2001), and may thus only represent local or regional climatic conditions. Hence, they may cause a bias in the interpretation of overall Carnian climates. In contrast, it may be considered that the Carnian climate was possibly characterised by only seasonal aridity (which may have supported the production of evaporites, but mainly is evidenced by the presence of red beds; Sheldon 2005), alternating with seasonal rainfalls, particularly if the climate is believed to have been more zonal in the Late Triassic (Wing & Sues 1992). According to reconstructions provided by Scotese (2003), the climate in the rift region was warm temperate to locally arid.

The Carnian seas were characterised by extremely low and relatively stable sea levels, which persisted since the end of the Permian (Haq et al. 1987). In the late Carnian, first signs occur of a constant rise of the sea level reaching its maximum in the Middle Cretaceous (Haq et al. 1987; Olsen 1997). The seas in the region were shallow, and intensive and large-area evaporation may have occurred due to (seasonally) higher temperatures of the water surface, which result in extensive deposition of evaporites. The drying-out may not generally indicate an arid or dry climate but may, on the other hand, have increased the salinity of the seaway.

Despite of everything mentioned above about Carnian climate and its discussion, several features suggest an overall humidity of the environment in the period and the region where the Lunz flora grew (e.g. Bharadwaj & Singh 1964; Hochuli & Frank 2000; Roghi 2004). First, the composition of the Lunz flora includes a number of ferns and sphenophytes, which require humid environments, and often occur in monotypical associations. Moreover, ferns require liquid water for reproduction. A humid environment has also been suggested for the flora from the Raibl Group in the Southern Alps based on the composition of the spore assemblage (Roghi 2004). Palaeogeographical reconstructions show that the Lunz flora may have grown in a lowland setting (Blakey 2005). The coal-bearing beds are intercalated between fully marine beds. This suggests that marine and freshwater periods alternated in this area that may be interpreted as a paralic basin. In fact, Stremme (1911) hypothesised that the coals from Lunz are paralic. Continental (fluvial) deposition close to marine sedimentation is today widely present in large, tidal-influenced estuaries (or deltas) with meandering riverbeds and decreased flow velocities or lentic water bodies (Chu Wang 1984). The development of tidal blind channels or lagoons that have had a similar appearance to recent delta systems (Hood 2006) is a typical character of estuarine systems. The abundance of very large randomly oriented and well-preserved leaves in the Lunz flora suggests minimal transportation of the plant material. The plants consequently may have grown close to (inshore) waters where the leaves directly were shed into water, and did not drift far away. The rifting seaway may have produced estuarine systems with temporary marine flooding and evaporation that did not have any sound influence on the climate.

Dipnoans.—The occurrence of flying dipnoans (lungfishes) in the marine layers of the Lunz Formation (Teller 1891; Abel 1906), whose modern relatives, however, dwell in distinct shallow freshwater habitats, supports the periodical presence of seawater and a paralic basin that periodically provided environmental conditions for those specially adapted fish species (Sawyer 1972). Lungfishes can survive for longer periods of time in very little or even without water. They can periodically stay out of water and breathe in the air, and thus are adapted to lagoonal environments. Both marine and freshwater fossils of dipnoans (lungfishes) are known (Abel 1906; Dasch & Campbell 1970).

Adaptations of the plants.—The presence of xerophytic epidermal and cuticular features in most of the plants from the Lunz flora may suggest that the plants lived in xeric habitats. This may at first not be consistent with the inferred overall humidity in the Carnian Lunz region. However, these features may also be interpreted as stress-induced adaptations that indicate the presence of sustained winds and/or saline air (Krings & Kerp 1998), which are typical in coastal or estuarine areas. Plants that do not grow directly in tidal flats but close to seawater may also be adapted to salinity transported by wind. Moisture availability in coastal habitats may have been further reduced by intensive solar radiation (high-light environment) and the osmotic effect of elevated soil and ground water salinity. The strong linear venation of the leaves of some plants (i.e. *Glossophyllum florinii* and *Pseudoctenis cornelii*), along with striate rachides, may have been effective in directing rainwater (freshwater) toward the base of the leaf. The preservation of the cuticles and their robustness may suggest that the leaves of several of these plants were coriaceous and perhaps similar to the leaves of modern cycads, oleander, sea lavender or rubber trees. The latter are adapted to a drier or saline environment (Fahn & Cutler 1992).

Nearly all of the taxa described in the preceding chapters display sunken or slightly sunken stomata. Moreover, several have stomata that are covered by overarching papillae. The papillae provide for the reduction of excessive water loss through the stomata, which may be caused by persistent wind. Sunken stomata that are partially covered by papillae are often associated with other xeromorphic features in extant plants, and found in plants that live under arid conditions (Hutchings & Saenger 1987). Papillae are present on the leaf surfaces of nearly all analysed taxa, and may additionally have reduced wind speed directly on the leaf surface. It is very likely that the adaptations to xeric habits also have been developed due to the seasonal aridity, which is suggested to have affected the plants in the Lunz ecosystem. For example, many extant epiphytic orchids also display certain xeric adaptations (sunken stomata, robust cuticles), but often lived in humid environments of the tropics and sub-tropics. They are exposed to seasonal aridity or drought stress due to their epiphytic pattern of living.

Today, the regions of the Tropics, where the Lunz flora was located during the Carnian, are characterised by a distinct seasonal climate with a long dry season and a short rainy season. This climate may be considered to have also been present comparatively in the Carnian. Hence, adaptations to seasonal aridity, independent from duration, are inevitable for the plants but do not exclude the presence of a more humid environment in general.

The formation of micro-relief structures on the leaves of several plants (e.g. *Pterophyllum filicoides*, *P. brevipenne* and *Glossophyllum florinii*) may then again represent an adaptation to increased humidity and seasonal rainfall. The surface ornaments may have reduced leaf wettability to prevent the formation of a water film on the leaf surfaces, which could adversely affect the uptake of CO_2 (Barthlott & Neinhuis 1997), and thus decrease the efficiency of the photosynthetic activity. The longitudinal orientation of the striae possibly enabled the directed water run-off of the leaf. The water was either directed to the plant (apex) if the leaves were positioned upright or oriented to the leaf apex and away from the plant if the leaves were hanging down. In addition, surface ornaments may have provided for or enhanced the self-cleaning effect of the leaves (Barthlott & Ehler 1977; Pal et al. 2002). Remaining dust particles may increase the surface temperature of the leaves (Eller 1977), while salt particles may cause irreparable injuries to the leaf tissue (Delahaut & Hasselkus 1999). If the running-off of water droplets is facilitated, the harmful effects of such particles remaining on the leaf surface are reduced because they were washed off by the repelling water droplets. The latter is, in turn, an adaptation to air contamination caused by wind, wave spume or marine evaporation.

Another aspect contributing to the suggestion of an estuarine or tidal habit is the presence of matoniaceous and gleicheniaceous ferns (Stur 1885; Krasser 1909a). They are construed to indicate pioneer plant vegetation in coastal areas due to their comparable adaptations (Van Konijnenburg-van Cittert 2002). The presence of ferns in the Lunz flora indeed may be interpreted as pioneer plant vegetation in a lagoonal lowland setting.

Insects.—The presence of possible odonate eggs on the leaves of *Nilssoniopteris* plants suggests that these leaves overhang open water surfaces because odonate larvae must drop directly into water after hatching. Hence, these plants must have been more or less tree-like (possibly members of the Williamsoniaceae) with longer branches that overhung the water surface. Larvae of extant Odonata develop in freshwater. This may indicate that freshwater bodies must have been present in the region. Imagos of Odonata are also mainly confined to humid environments or open waters, respecttively. Though the detection of egg shells assigned to reticulated beetles on leaves of another species of *Nilssoniopteris* does not directly point to a humid environment, it substantiates the presence of humidity because cupedid beetles are today often found in large numbers on rainforest trees. Moreover, it is interesting to note that the eggs and imprints on *Nilssoniopteris* leaves seem to display a kind of host specificity. Host specificity (e.g. in herbivorous beetles) is today particularly abundant in the Tropics (Ødegaard 2003).

Bennettitalean ecology.—The exact ecological requirements of bennettitaleans remain unknown. Bennettitaleans are quite similar to cycads in overall morphology. Extant cycads grow in the more arid regions of the tropics and sub-tropics with cold winters; they are able to grow on sand or rock, one species even as an epiphyte. They are mainly adapted to xeric habits. Some species are halophytic or accept Salinity in their environment (Norstog & Nicholls, 1997). Presupposed that the macromorphological similarity is an adaptation to surrounding climatic and environmental factors, it is possible to envision that bennettitaleans may have had similar ecological requirements as cycads. The analysis of the Lunz flora yielded several results suggesting that bennettitaleans may have had other, perhaps more advanced demands on their environment (as mentioned above: seasonal humidity, swampy habits or habits close to inshore waters, acceptance of direct salinity- or periodical water-stress in lowland coastal habitats) (cf. Cleal & Rees, 2003).

Stability of the environment.—Presence of coal seams indicates that the environment in the Carnian Lunz area was stable for longer periods of time, which enabled the accumulation of large amounts of plant material. Today the most stable (continental) environments are found in the Tropics. Large amounts of coal originate from peat, which may be formed mainly in non-marine environments but also may undergo marine ingressions. Formation of peat requires special conditions, including minimal oxidation and bacterial decay. The latter usually occur in swamps or peat-bogs with a high groundwater table, reduced oxygen supply and low pH values.

Species in an unstable environment must first adapt to the changing environment before they can specialise. As a consequence, the community initially is relatively poor in species number. Under stable environmental conditions, which may include regular seasonal changes, species may adapt to one another. This process effects specialisation and occupation of many almost non-overlapping ecological niches, and allows the coexistence of many species (Sanders 1968). Hence, stable environments favour specialisation and increasing biodiversity. The Lunz flora shows a relatively high species diversity and number of individual species of different plant groups along with relatively high intrageneric diversity concerning ferns, seed plants, ginkgophytes and conifers (Stur 1885, 1888; Krasser 1909a, 1909b; Kräusel 1943, 1949, 1952; Dobruskina 1998). It may indicate that relatively stable environmental conditions have perhaps controllled the Lunz ecosystem.

Conclusive remarks.—Summarising the various aspects concerning adaptation of the plants and the surrounding parameters (i.e. climate, habitat, environmental and ground conditions and plant/environment-interactions), and relating these aspects to comparable extant ecosystems in similar latitudes, it may be suggested that the Lunz flora grew in a relatively stable environment. This environment may have been characterised by a humid climate with intermittent or seasonal periods of drought. It is suggested that the plants thrived in an estuarine lowland setting close to a lentic freshwater lagoon. The lagoonal site may have been part of a riverine delta system with aerial marine influences and sustained windy conditions.

In modern semi-arid to arid areas, wetlands are particularly significant with regard to preserving biodiversity (Bacon 1997). This function is important not only within wetlands, but also surrounding ecosystems (cf. Greb et al. 2006).

Interpretation of the flora from Lunz as kind of sub-tropical rainforest-like floras is unsupported. However, Burnham and Johnson (2004) compiled a set of parameters that characterise tropical rainforests, and may be recognisable in fossil plant assemblages. Several of these parameters are present in the Lunz flora and its inferred palaeoecology. The parameters of Burnham and Johnson (2004) include (1) plants growing in low elevations; (2) relatively high species diversity within the flora; (3) a higher abundance of large-leaved plants along river (freshwater!) meanders; (4) high abundance of large-leaved plants in general and plants with entire-margined mesophyllous leaves; and (5) increased diversity of plant/animal-interactions. High biomass production and sequential shedding of leaves are the only two parameters that cannot be directly documented in fossil floras.

THE HIGH ABUNDANCE OF BENNETTITALEANS IN LUNZ AND THE RADIATION OF THE BENNETTITALES

What makes the Lunz flora even more signifycant is the high abundance of bennettitaleans. This is reflected by several species at least two genera (i.e. *Pterophyllum* and *Nilssoniopteris*) that depict an abrupt mass occurrence of bennettitaleans. Stratigraphically older deposits have to date only sporadically contributed to the fossil record of these two genera. The bennettitaleans from Lunz are not only representted by one or two fossils; rather, the leaves of *Pterophyllum* and *Nilssoniopteris* are the most abundant fossils in the Lunz assemblage. This suggests that several bennettitaleans locally became relevant elements of the vegetation early in their evolutionary history. However, the factors that caused or facilitated this sudden success of the bennettitaleans remain elusive. It seems that the contemporaneous flora from Neuewelt produces similar abundances (personal observation). The early evolutionary history or the high abundance of bennettitaleans may produce a biased picture, since it may be related to the relatively poor record of plant fossils from lower Triassic deposits. It cannot be excluded that earlier representatives of the bennettitaleans may be discovered in future, but to date no certain fossils or similar mass occurrences are known. Misinterpretation or misidentification of fossils from earlier floras may perhaps add to this problem.

On the other hand, biological factors may have played a major role in the sudden success of the bennettitaleans in the Late Triassic:

Flowers.—Certain changes in the biology or ecology of some bennettitaleans may have occurred during the Late Triassic that enabled the sudden local high abundance. This possibly resulted in an “explosive adaptive radiation” that may form the basis for rapid evolutionary changes in the Bennettitales. Alternative or improved reproduction and dispersal strategies may have evolved that allowed rapid colonisation of new habitats, ecological niches or regions by large numbers of individuals. One important hypothesis with regard to the sudden increase of bennettitaleans concerns the appearance of bisexual bennettitalean “flowers”. In bisexual plants, both male and female reproductive structures co-occur in one individual. Thus, this individual plant is twice as effective as, for instance, a dioecious cycad. Bisexuality may thereby considerably increase the rate of reproduction. The work on the fructifications in the Lunz flora, their relation to Bennettitales as well as their adaptive functionality is still in progress. Wind-pollination is suggested to be the ancestral mode of pollination in gymnosperms, but the derived mode in angiosperms (Owens et al. 1998). Hence, wind-pollinated bennettitalean “flowers” may be an additional indicative for the Bennettitales from Lunz to be one of the earliest occurrences of bennettitaleans.

Beetles.—It has been hypothesised that, since the Late Triassic, beetles became increasingly important as pollinators for several groups of bennettitaleans (Crowson 1981; Lawrence &

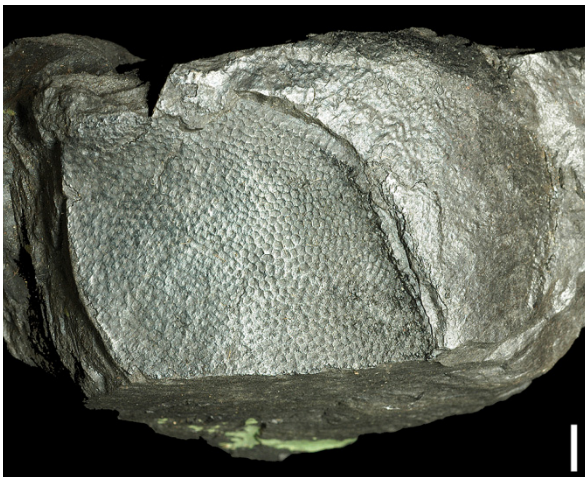

Figure 5. *Bennetticarpus wettsteinii* with possible dehiscence area; specimen SPO F/0072; scale bar — 5 mm.

Newton 1982). This is based primarily on the fact that the earliest representatives of the modern beetles appeared in the early Late Triassic, and subsequently diversified during the middle and late Late Triassic (i.e. Cupedidae, Trachypachidae and Staphylinoi-dea; cf. Grimaldi & Engel 2005; Labandeira 2006). Since the pattern of the early evolution of modern beetles, especially the reticulated beetles (Cupedidae), seems parallel to that seen in the Bennettitales, it seems plausible to suggest that closer co-evolutionary relationships existed between the beetles and Bennettitales (Sitte et al. 1998; Grimaldi & Engel 2005). Noteworthy in this context is the discovery of small insect eggs on several leaf fossils from Lunz. The egg shells are structurally similar to eggs produced by modern reticulated beetles. The increasing diversity of cupedids and other beetles during the Late Triassic may have provided beetle-pollinated bennettitaleans with a reproductive advantage over wind-pollinated forms that may have been common in Cycadales. This advantage may eventually have resulted in contemporary evolutionary success of certain bennettitaleans.

Vertebrates.—Larger plant-feeding land vertebrates became increasingly abundant during the Late Triassic (e.g. Benton 2004). They may also have affected reproduction and dispersal of the Bennettitales. Some of these plant-feeding animals might perhaps have fed on bennettitalean “fruits”. Several of the reported “fruits” assigned to *Bennetticarpus* had the size of apples, and may have had a sarcotestal rind. One of the *Bennetticarpus* “fruits” shows a possible dehiscence area (Figure 5), and thus is assumed to have been shed at maturity. Sarcotestae in extant fruits are mostly colourful, and often produce a distinct odour to attract larger animals. It is possible that *Bennetticarpus* and other Carnian “fruits” of bennettitaleans may have profited from similar strategies. If the seeds remain intact after having passed through the digestive tract, plant-feeding vertebrates may have contributed to the long-distance dispersal of bennettitaleans, and thus assisted in the colonisation of new territories.

Concluding hypothesis.—The presumed “explosive adaptive radiation”, along with a reproducetive and dispersal advantage of the bennettitalean species, significantly may have affected the floristic composition of this region. Overall diversity of adjacent regions on several taxonomic levels may have been increased. The several aspects summarised above including possible advantageous adaptations to the prevailing environmental conditions may have affectted the development of the bennettitaleans in their early history, and provided a basis for the evolutionary success of this group of plants. This may also have had phytogeographical consequences for contemporary and later floral developments in the Late Triassic (Rhaetian) and the Lower–Middle Jurassic of Laurasia.

RESEMBLANCE TO YOUNGER MESOZOIC AND JURASSIC FLORAS

The Lunz flora contains a number of elements that are regarded as typical for Rhaetian and Lower–Middle Jurassic floras (Nathorst 1876, 1878–1886; Johansson 1922; Harris 1932a, 1932b, 1946, 1961–1979; Lundblad 1950; Kelber 1998). Typically Rhaetian and Jurassic seed plants are represented by members of the Cycadales (i.e. *Pseudoctenis*, *Nilssonia* and *Ctenis*), Bennettitales (i.e. *Pterophyllum*, *Anomozamites*, *Ptilozamites*, *Otozamites* and *Nilssoniopteris*, Ginkgoales (i.e. *Ginkgo*, *Sphenobaiera* and *Baiera*) and Coniferales (i.e. *Brachyphyllum*, *Pagiophyllum* and *Stachyotaxus*). Lunz provides to date the first unequivocal appearances of genera, which are very common and widespread in the Rhaetian–Jurassic (i.e. *Nilssonia*, *Pseudoctenis*, *Pterophyllum* and *Nilssoniopteris*). It is remarkable that some of these genera are each represented by several species in the Carnian from Lunz: *Nilssonia* is representted by up to four species, *Nilssoniopteris* is comprised of three sound species, and *Pterophyllum* is represented by two distinct species. *Pseudoctenis cornelii*, the only species of this genus from Lunz, represents the earliest unequivocal evidence for this genus from the European Triassic.

Conifers, which have not been included in this study, are represented by one species of the genus *Stachyotaxus* in the flora from Lunz (Stur 1885; Kräusel 1949) and by another in the flora from Neuewelt (Kräusel 1952). *Stachyotaxus* is relatively common in the Rhaetian of Greenland and Scania (Harris 1935; Johansson 1922). Unfortunately, the epidermal anatomy of *Stachyotaxus* from Lunz is poorly known to date. Thus, its systematic position remains unclear to date; Kräusel (1949, 1952) avoided the discussion, and only assigned the form to the conifers. The Lunz fossils macromorphologically resemble extinct as well as extant members of the Araucarian tribe (Cantrill 1992; Jones et al. 1995; Chambers et al. 1998). Araucarians had their maximum diversity in the Jurassic and Cretaceous, when they still were globally distributed. The allocation of the reported ginkgophytes from Lunz (*Ginkgoites*, ?*Desmiophyllum*; Kräusel 1943) remains also unclear, since their epidermal anatomies are also unknown to date.

It was generally suggested that a major floristic change took place after the Carnian and before the Rhaetian (Kerp 2000) because Rhaetian floras show a much more modern aspect than Carnian floras. Rhaetian floras are much more similar to Jurassic floras than to older Triassic floras (Kelber & Hansch 1995; Kelber 1998). This is also reflected in the evolutionary history of ferns and conifers: The first major occurrence of leptosporangiate ferns (e.g. Dipteridaceae and Matoniaceae) or conifers (e.g. members of the Cheirolepidiaceae) was in the Rhaetian (Alvin 1982; Kelber & Hansch 1995; Kerp 2000). This is also evidenced by the palynological record, as the first real abundance of cheirolepidiaceous pollen is recorded from the Rhaetian (Visscher & Brugman 1981; Traverse 1988). However, this may be weakened by the following observations:

Earliest Dipteridaceae already occur in the Middle Triassic of eastern Australia (Herbst 1979; Webb, 1982) with the earliest European occurrences in the middle Carnian of Franconia (Kelber & Hansch 1995). Representatives of this family are also known from Lunz (Stur 1885). Moreover, other representatives of Gleicheniopsida have been recorded from the Carnian of Lunz (i.e. Matoniaceae and Gleicheniaceae; Stur 1885) as well as from the Carnian Chinle Formation of North America (Ash et al. 1982; Ash 2005). In addition, putative cheirolepidiaceous conifers have been reported from Carnian strata (i.e. *Pagiophyllum* form the Chinle Formation of North America; Ash 1970). Other conifers have already rarely been present in Carnian floras (see above). Consequently, there exist several indications for a more gradual floristic change in the Late Triassic floras that must not be overlooked.

Unfortunately, Norian vegetation is only poorly known because Norian macrofloras are very rare. In addition, most Norian floras are dominated by conifers (Kelber & Hansch 1995; Ash 1999).

Depicting the analogies between the Lunz flora and its pre-Rhaetian and post-Carnian relatives reveals that a gradual change in the composition of Late Triassic (Carnian–Rhaetian) floras is more likely than a major floristic turnover that has been suggested by several scholars (e.g. Kelber & Hansch 1995; Kelber 1998; Kerp 2000). To what extent the environmental changes in the Late Carnian contributed to these changes, can only be estimated based on comparisons with developments in comparable extant ecosystems. Most studies on recent floristic changes mainly deal with invasions of dominating alien species, and therefore, are only sparsely suitable for comparison.

The high abundance, not only of the bennettitalean representatives but also of the *Nilssonia* species, and the relatively common occurrence of these species in the Lunz (and perhaps Neuewelt) flora add another aspect to the significance of these floras concerning a more complete understanding of the vegetational changes, evolutionnary innovations and major phytogeographical and developmental processes in the Late Triassic. Local mass occurrence is a basis for the establishment of successfully reproducing populations, which then, in a period of more stable environmental conditions, have the potential to colonise different ecological niches. Establishment of niches again provides further diversification of the relevant plant groups. A comparison with several Rhaetian and Jurassic floras, in which, indeed, several genera show a greater diversity than in the Lunz flora, contributes to the estimation of evolutionary and adaptive processes that generated the outstanding success of several groups of plants.

Concluding remark.—As a result, the Lunz flora apparently represents a mixture, in which typical elements of older Mesozoic, i.e. pre-Rhaetian, floras co-exist with forms that are characteristic elements of younger and more modern, post-Carnian floras. In addition, several recent studies suggest that several plant groups and genera evolved much earlier in the Triassic than previously thought (Wachtler & Van Konijnenburg-van Cittert 2000; Broglio Loriga et al. 2002; Passoni & Van Konijnenburg-van Cittert 2003; Kustatscher et al. 2004; Kustatscher & Van Konijnenburg-van Cittert 2005). Therefore, it may be concluded that, within the Triassic, the floral composition changed gradually instead of a major floral turnover.

FUTURE PERSPECTIVES I: FRUCTIFICATIONS AND WHOLE-PLANT-TAXA

Overview.—The most remarkable aspect of the Lunz flora is the relatively high portion and diversity of male and female fertile cycadophyte remains. The Lunz flora has yielded a wide variety of well-preserved fossils described as fructifications assigned to cycadalean, bennettitalean and ginkgoalean species, respectively (Krasser 1916, 1917, 1919; Kräusel 1943, 1948, 1949, 1953; Langer 1943, 1945). The most reputed fossils are *Diooniticarpidium*, *Haitingeria*, *Westersheimia*, Sturiella, *Bennetticarpus*, ?*Pramelreuthia* and ?*Antholithus*. A bias is recognised in the allocation of these fossils: Distinct cycadaleans are represented only by two species of macrosporophylls of the genus *Dioonitocarpidium* (i.e. *D. keuperianum* and *D. liliensternii*). This does not really concur with the very common occurrence of cycadalean foliage from Lunz. In contrast, bennettitalean reproductive structures are represented by a wider morphological diversity [i.e. distinct: *Haitingeria krasseri* (male), *Bennetticarpus wettsteinii* (female, "fruit"), *Sturiella langeri* (bisexual "flowers"); putative: *Westersheimia pramelreuthensis* (male), *Pramelreuthia haberfelneri* (male)], which much better matches the wide variety and high abundance of bennettitalean leaf fossils. *Antholithus* is to date assigned to the Ginkgoales (Kräusel 1943; Xiu-Qun Liu et al. 2006), but its allocation is not accepted throughout (Fry 1955; Taylor et al. 2006).

The allocation of the only admissible sterile ginkgophyte leaf morphotaxon *Glossophyllum florinii* remains elusive, too (Doweld 2000).

Potentials.—The allocation of the fructifications from Lunz to the various plant groups is not entirely clarified, and often continues to be debated (e.g. Langer 1943; Crane 1985; Ash & Litwin 1996). The problem in assigning the reproductive structures to sterile foliage is due primarily to the facts that cuticles remain unknown for most of the reproductive structures. Others structurally do not fit general bennettitalean fructifycation systems or represent isolated parts of "flowers". However, it has to be taken in account that the bennettitaleans from Lunz seem to be the earliest distinct record of this plant group, and thus their reproductive structures may represent precursory forms of the established bennettitalean reproductive structures that are known from several Jurassic deposits (e.g. Harris 1932a, 1932b, 1969). There are several indications that most of the "fruits" and "flowers" were shed at maturity, and hence are found as isolated parts. The main focus of the forthcoming studies and analyses of Lunz plants includes clarification of the epidermal anatomy of the reproductive structures. Based on these results, the isolated sterile and fertile parts will be combined and reconstructions of the reproductive structures may be possible. Moreover, the exact knowledge of the structural composition of the cycadophyte fertilia contributes to or allows assumptions of reproductive modes (i.e. zoochoric or anemochoric) and strategies.

Whole-plant-taxa.—When including the results from the cuticular analyses of the present study, it is also possible to reconstruct so-called whole-plant taxa (Kerp 1990). The reconstruction of whole-plant-taxa is one of the most important aims of palaeobotanical research. Systematic as well as phylogenetic observations require the consideration of the individual species as complete biological units. Therefore, "natural units" (i.e. sound species and not morphotaxa) are required. Since most of the parts of fossils plants are found isolated, a reconstruction of the source plant is necessary. The reconstructions also allow different palaeobiological and -ecological implications of the individual plants, species and the entire flora. Because most of the seed plants display characteristic epidermal anatomies, the knowledge of the epidermal anatomy is inevitable. Affiliation of leaves and reproductive structures to one and the same individual plant or species is often only possible based on correspondences in the epidermal anatomy of leaves and reproductive structures.

Assignments of the sterile leaves and the relating fructifications have never been conducted for Lunz plant fossils before. This may be due to the fact that no detailed study of the sterile leaves was present to date, and epidermal anatomies of most of the plants remained unknown. The results of the present study now provide an extensive set of heretofore largely unavailable data for the reconstruction of seveal of the seed plants in the Lunz flora. In the light of the phylogeny and radiation of the Bennettitales, the Lunz flora receives distinct significance with regard to the knowledge of whole plants, their growth habit and reproductive modes. Reconstructions may furthermore contribute to the understanding of the phylogeny and the palaeobiology of other plants from Lunz.

FUTURE PERSPECTIVES II: SYSTEMATICS AND ECOLOGY

Ferns.—The Lunz flora also comprises several ferns and fern allies (Stur 1885; Krasser 1909a, 1909c) that are known to science in the form of Latin diagnoses, and contain several new genera and species. No figures illustrate these taxa to date, and consequently, they are practically unknown. The systematic clarification of the fern and sphenophyte taxa from Lunz is important, and will be one of the forthcoming projects concerning the research of the Lunz flora. Moreover, the investigation of the fern flora may add additional details to the understandding of the environmental conditions that affected the growth and the interactions of the Lunz plant assemblage, since ferns have distinct environmental requirements (cf. Van Konijnenburg-van Cittert 2002). Moreover, most ferns and fern allies from Lunz represent herbaceous plants that colonised the ground whereas most of the seed plants along with some putative tree ferns (e.g. *Asterotheca merianii*) or large sphenophytes (i.e. *Neocalamites*) seem to have been arborescent representatives. However, the size and habit of the cycadophytes from Lunz was not comparable to extant trees or large cycads, but rather to smaller shrubs or smaller to medium cycads like *Encephalartos*, *Zamia* or *Chigua* representatives.

Table I. Synopsis of the taxa names given by Stur (1885) and Krasser (1909a, 1909b) with their previous affinities and their revised names and affinities by means of the present study.

Order	Present study	Krasser 1909a, 1909b	Affinities	Stur 1885
Bennettitales	*Pterophyllum filicoides*	*Pterophyllum jaegeri*	cycadophyte*	
		Pterophyllum longifolium	cycadophyte*	*Pterophyllum longifolium*
		Pterophyllum approximatum	cycadophyte*	*Pterophyllum approximatum*
	Pterophyllum brevipenne	*Pterophyllum brevipenne*	cycadophyte*	*Pterophyllum brevipenne*
		Pterophyllum rectum	cycadophyte*	*Pterophyllum rectum*
			cycadophyte*	*Pterophyllum merianii* (Stur 1871)
		Pterophyllum pulchellum	cycadophyte*	*Pterophyllum pulchellum*
		Pterophyllum haberfelneri	cycadophyte*	*Pterophyllum haberfelneri*
		Pteropyhllum macrophyllum	cycadophyte*	*Pteropyhllum macrophyllum*
	Nilssoniopteris haidingeri	*Macrotaeniopteris haidingeri*	marattialean fern	*Taeniopteris haidingeri*
		Macrotaeniopteris latior	marattialean fern	*Taeniopteris latior*
	Nilssoniopteris angustior	*Macrotaeniopteris angustior*	marattialean fern	*Taeniopteris angustior*
		Macrotaeniopteris simplex	marattialean fern	*Taeniopteris simplex*
			marattialean fern	*Taeniopteris parvula*
	Nilssoniopteris lunzensis	*Macrotaeniopteris lunzensis*	marattialean fern	*Taeniopteris lunzensis*
		Pterophyllum lunzense	cycadophyte*	*Pterophyllum lunzense*
Cycadales	*Nilssonia sturii*	*Nilssonia sturii*	cycadophyte*	*Pterophyllum irregulare*
		Pterophyllum guembelii	cycadophyte*	*Pterophyllum guembelii*
	Nilssonia riegeri	*Pterophyllum riegeri*	cycadophyte*	*Pterophyllum riegeri*
	Nilssonia lunzensis	*Ctenis lunzensis*	gleicheniacean fern	*Ctenis lunzensis*
			gleicheniacean fern	*Ctenis angustior*
		Ctenophyllum lunzense	gleicheniacean fern	
		Pterophyllum pichleri	cycadophyte*	*Pterophyllum pichleri*
		Pterophyllum haueri	cycadophyte*	*Pterophyllum haueri*
	Nilssonia neuberi	*Pterophyllum grandifolium*	cycadophyte*	*Pterophyllum neuberi*
	Pseudoctenis cornelii		putative cycadalean	"*Ctenophyllum lunzense* " (on labels)
not traceable		*Pterophyllum taxinum*	cycadophyte*	*Pterophyllum cteniforme*
			cycadophyte*	*Pterophyllum pectiniforme*
			cycadophyte*	*Pterophyllum haidingeri* (Stur 1871)

* The name *Pterophyllum* suggests bennettitalean, the name *Nilssonia* cycadalean affinities of the fossils

The value of cuticular analyses.—Cuticular analysis contributes considerably to the systematics of fossil plants, and may also be important in inferring the phylogeny of seed plants. The description of high-confidence bennettitalean species, the differentiation between cycadalean and bennettitalean species and the resulting discovery of the cycadalean representatives demonstrates the value of cuticular analysis. The phylogenetical significance of species is the higher the more complete the ascertainable information about the species is. Moreover, this study revealed that the information gathered from the cuticles produces the best results in combination with the macromorphological traits of the plants (i.e. the discrimination between *Nilssonia* and *Pterophyllum* species).

The cuticle studies revealed that the status of many of the foliage "species", which were established based exclusively on macromorphological features, is not supported by the epidermal anatomy. Stur (1871, 1885) and Krasser (1909a, 1909b) gave in their lists and descripttions 15–18 cycadophyte species (mainly *Pterophyllum* species; the name *Pterophyllum* at least suggests bennettitalean affinities of these fossils). Indications for the cycadalean nature of some of these fossils are only found in Krasser (1909b) with the renaming of *Pterophyllum irregulare* into *Nilssonia sturii*. Today, only two sound *Pterophyllum* species and five cycadalean species are present in the Lunz flora. The bennettitaleans are in turn completed by three distinct *Nilssoniopteris* species (Table I), which were previously classified as marattialean ferns (Stur 1885; Krasser 1909a). Former ferns (i.e. *Macrotaeniopteris*) are now accommodated in the bennettitaleans, several former putative bennettitalean species are now assigned to the cycadaleans. The taxonomy of compression plant fossils has consequently to be treated very carefully without considering the cuticles, mainly if cuticles are obviously present. This is also reflected in the incongruity in defining distinct generic characters to discriminate foliage (morpho-)genera, which caused considerable confusion in the past.

These changes may have distinct effects on derived phylogenies of gymnosperms when foliage is included in the analyses (cf. Rayfield et al. 2005). Assessing the allocation of the fertile elements from Lunz to (1) different orders and genera and (2) to the foliage, may also contribute to clarifying the origin and radiation of Late Triassic gymnosperms. The taxonomic and systematic changes will be included in forthcoming analyses inferring phylogenetic relationships of the Lunz plants including the fertile elements and possible whole-plant-taxa.

Juvenile leaves.—Another aspect that may have some influence on our understanding of the relationship between bennettitaleans and cycadaleans may be the first ever record of the development of a bennettitalean leaf. The mode of development is similar to that seen in extant cycads (e.g. *Cycas circinalis*). Development of leaves is an ontogenetically determined process. The macromorphological similarities between cycadalean and bennettitalean foliage raise the question as to whether the correspondence is superficial and restricted to overall architecture, or the leaves of both groups of plants also display similar development, and consequently, a derived character (apomorphy). To what extent this apomorphy influences new phylogenies that infer the relationships of Bennettitales and Cycadales in relation to other seed plant groups remains to be seen, when the feature is included in phylogenetic analyses. This again emphasises the importance of the Lunz flora itself as well as underlines the consequences of cuticular analyses. Further cuticular investigations may possibly reveal additional information of the development of the leaves of other genera (e.g. *Leguminanthus*).

Quality and quantity.—Several fossil floras show a high degree of generic diversity through different plant groups and orders. However, these genera often are represented by only a single or two species, which in turn are often represented by one

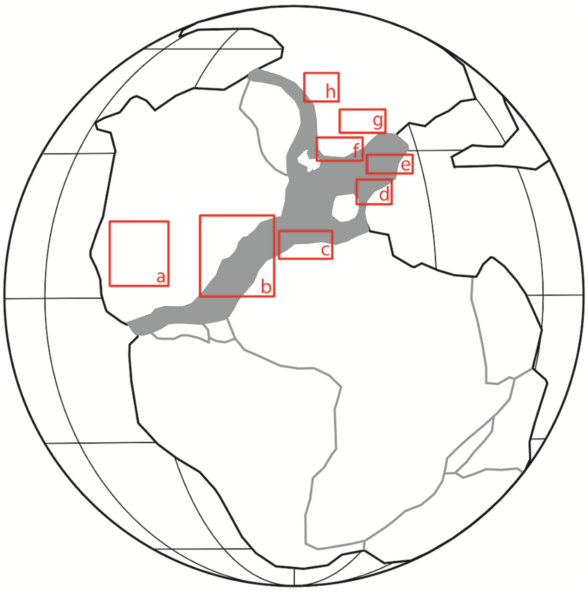

Figure 6. Mesozoic rifting area within the supercontinent Pangaea (mean Late Triassic), with the locations and localities mentioned in the text (modified after Kent & Olson 2000; Rayfield et al. 2005). a, Chinle Formation; b, Newark Supergroup; c, region of Essaouira; d, Raibl Group; e, Lunz Formation; f, Neuewelt; g, southern Germany; h, Scania, Sweden.

or two fossils. It cannot be denied that this also applied to the (former) classification of fossils in the Lunz flora. Consequently, this depicts a biased view of the composition of the flora. The quantity and relative abundance of representatives of a distinct flora is often not mentioned, and thus diversity is inferred only based on counting reported and described genera and species that do often not reflect the real composition of the relevant flora (cf. the abundance of the *Pterophyllum* and *Nilssonia* representatives in the Lunz). The consequence is that, for instance, for the Lunz flora, a high abundance of bennettitaleans can be documented even if the number of species is low. This will probably also be reflected in the flora from Neuewelt near Basel; the study of this flora will be included in the following investigations on the Lunz plant assemblage. Thus, considering of the number of fossils of each genus or species adds other useful information, i.e. before the background of assuming environmental circumstances or the reproductive potential of a fossil flora and its consequential impacts on the floral composition of slightly younger floras. In addition, the possibilities to compare several coeval floras or floras of different ages can be generally more standardised.

Floral exploration.—The Tethys seaway was a part of the Mesozoic rifting within the supercontinent of Pangaea (Kent & Olsen 2000). Several other early Mesozoic rift or coastal basins from the northern hemisphere are well-known [i.e. the Newark Supergroup Basin along the United States east coast including the Fundy Basin of Nova Scotia (e.g. Fowell & Traverse, 1995; Wade et al. 1996; Olsen 1997; Kent & Tauxe 2005), the Western Morocco Synrift Basin close to Essaouira in southern Morocco (e.g. Piqué & Laville 1993; Le Roy et al. 1997; Olsen 1997) and the Carnian successions in the Northern (Lunz, Neuewelt) and Southern Alps (Cave del Predil, Raibl)] (cf. Figure 6). All these successions are of comparable or related age (e.g. Traverse 1985), and some of them have yielded relatively well-preserved plant fossils. Based on detailed systematic and palaeoecological analyses of these floras an overall comparison can be inferred. Consequently, differences or similarities in the composition of the floras between and within groups of plants can be documented. Hence, the floras may biostratigraphically be comparable and very useful in the correlation of North American and European sections. The comparison of the assumed environmental requirements of the individual floras contributes not only to the understanding of the floral development during the early Late Triassic, but also to overall reconstructions of climatic situations within this period and region and the ongoing discussion of the “pluvial event” or the more zonal climate of the Julian–Tuvalian times.

Neuewelt.—The most important flora that will be studied following the Lunz flora (cuticular analyses, taxonomic review, palaeoecological considerations) is the coeval flora from Neuewelt near Basel, Switzerland (e.g. Heer, 1877; Leuthardt 1903, 1904; Kräusel & Leschik 1955, 1959; Kräusel & Schaarschmidt 1966). This flora is also composed of several bennettitaleans, ferns, sphenophytes and ginkgophytes, partly with identical or very similar species as in Lunz. Additional relevant features of this flora are the apparent conformity of the sediment that preserved the fossils, the similar state of presservation of the fossils and of the quite similar abundance of the material. For instance, cycadaleans from Neuewelt are similarly sparsely reported as they were previously from Lunz. Marattialean ferns are known from Neuewelt that resemble the *Nilssoniopteris* species from Lunz (Leuthardt 1904). The present re-investigation conspicuously converted the picture of the Lunz flora. It will be interesting to see whether a re-investigation of the flora from Neuewelt produces a similar shift in the depiction of that flora. The Neuewelt flora is also important because it comprises some of the earliest reports on fossil plants from the Alpine realm (e.g. Brongniart 1828, 1849; Heer 1865; Leuthardt 1903).

Raibl.—The area of the 'Raibler Schichten', now the Raibl Group in north-eastern Italy, is one of the important objects of research regarding the stratigraphy and geology of the Southern Julian Alps (Roghi 2004). It is very suitable for the stratotype of the Carnian. Within the Raibl Group, a relatively rich and diverse fossil macroflora is known since Bronn (1858) provided the first release about the fossils from the Cave del Predil area near Raibl (Schenk 1866; Dobruskina et al. 2001). Stur (1885) already compared the Lunz flora with the Raibl flora, but further studies on the Raibl flora were not undertaken. Since the age of these strata is well-known, and palaeoclimatological considerations have already been made (Hochuli & Frank 2000; Roghi 2004), it represents a slightly older flora that is suitable for comparison with the Lunz flora. Unfortunately, no cuticular information of Raibl plants is available to date. Other related floras that have to be consulted in this context are the recently discovered Triassic plant localities of Mount Pora (Passoni & Van Konijnenburg-van Cittert 2003) and Monte Pra Della Vacca in the Dolomites, northern Italy (Kustatscher et al. 2004; Kustatscher & Van Konijnenburg-van Cittert 2005).

Newark.—Floras of the same period that were found in North American deposits are also of high relevance. The floras from the Newark Supergroup Basin (Early Carnian) at the eastern coast of the United States were similarly located close to the Tethys seaway, but closer to the equator than the Lunz flora. Major works on the Newark Supergroup plant megafossils were done by Fontaine (1883), Bock (1969) and, more recently, by Ash (1980, 2005), Ash et al., (1982) and Axsmith and Kroehler (1989). The fossil floras of the north-eastern United States appear to be quite well comparable to the floras from Switzerland and Austria regarding composition and diversity. However, hardly any cuticular studies on the plant fossils from Newark have been carried out so far (Ash 1980). Investigations of the North American floras including cuticular analyses will provide new insights mainly in systematics and palaeoecology of these floras, and make these floras more comparable to the floras of the European Alps.

Chinle.—In contrast to the floras from the Newark Basin, the floras from the late Carnian–Norian Chinle Formation (Arizona, New Mexico, Utah and Colorado; Ash 1980) were located far away from the coast of the Tethys seaway (Rayfield at al. 2005). Palaeobotanical work on the Chinle Formation was mainly conducted by Ash (1970, 1989, 1999, 2001, 2005) and Ash and Litwin (1996). The Newark Supergroup and the Chinle Formation can be well correlated via palynological data (Litwin & Traverse, 1991). The two locations with probably different environmental influences (marine vs. continental, riparian) render both floras significantly interesting and their correlation to European Alpine floras an obvious task to infer environmental influences on the floral development within the Middle–Late Triassic. A comparison to Rhaetian floras from southern Germany and southern Sweden may complete the picture of the floral development and perhaps diversification patterns.

Some unconformity and systematic incongruity aspects between North American and European Middle–Late Triassic plant megafossils render the comparison of the floras a difficult task (e.g. Rayfield et al. 2005), but highlights the need for a standardised systematic approach as a base for further comparisons. As Rayfield et al. (2005) pointed out, the correlation of North American and western European floras from Early Triassic deposits fails due to unconformity and peerlessness in taxonomy and/or systematics. These authors did not find any megafloral genera that are spatially widespread or temporally restricted to Middle–Late Triassic stages across North America and Europe. This may perhaps change a little, if the representatives of the different genera may become more comparable when cuticular studies are included in the systematic analyses of the plants.

Essaouira.—Unfortunately, no Triassic floras are known from the North African (i.e. Moroccan) deposits of the High Atlas to date because this area is only scarcely studied (e.g. Le Roy et al. 1997).

A standard flora?—If, as Dobruskina (1989, 1998) tried to establish, the Lunz flora may serve as a standard for Carnian (and perhaps slightly older and younger) floras of Laurasia as are the floras of the Molteno Formation for the Carnian of Gondwana (Anderson & Anderson 1989), a complete inventory of this flora is required, and the comparability to other floras has to be ensured. The latter can only be successful if comparable information on all the relevant floras is made available. Compiling differentiated and detailed information of macromorphological and epidermal characters of the individual species as well as of quantity and quality of the fossils in combination with a more or less synoptic catalogue will provide a crucial template for ongoing investigations on the floral development of the Middle–Late Triassic in Western Europe and south-central North America. If the Lunz flora may serve as a standard, will be revealed by the ongoing analyses of the Lunz flora itself and by the investigations of several adjacent and coeval floras.

Conclusive remark.—The present study documents the importance and usefulness of cuticular analyses for the understanding of fossil floras and their constituents. Mainly the taxonomic or systematic revisions that became necessary after the analysis of the cuticles of the Lunz plant fossils demonstrate the significance of cuticular analysis. The excellent preservation of the cuticles that contributed to several differrent environmental (i.e. plant/animal-interactions and interactions of plants with their unenlivened environment) implications as well as to inferences of the local climate and habitats is in almost the same manner noteworthy. This becomes even more essential if plant fossils and floras are consulted in comparisons and interpretations that span continents or temporal periods.

SUMMARY

The main object of this study was to produce a thorough re-investigation of the sterile foliage of gymnosperm seed plants (i.e. Cycadales and Bennettitales) from the Upper Triassic of Lower Austria by means of cuticular analysis. The previous taxonomic characters and systematic affinities of the Lunz fossils were hardly traceable. While the well-known fertile remains from the Lunz flora have already been intensively studied, the sterile remains, which are of excellent preservational condition, and yield well-preserved cuticles, did not receive much scholarly attention to date. Moreover, by the professional selling of the fossils in the late 19th century, the confusion in labelling of the fossils was even increased because no suitable detailed (and illustrated) work existed for classifying the fossils uniformly.

The results obtained by cuticular analysis were used to (1) clarify the taxonomy of the leaf fossils that (2) revise the material and (3) reconstruct aspects of the palaeoecosystem and palaeoenvironmental conditions of the region where the Lunz flora thrived.

In detail, several taxonomic revisions were conducted: The status of many of the foliage “species”, which were established based exclusively on macromorphological features, is not supported by epidermal anatomy. The first scholars studying Lunz plant fossils, Stur and Krasser, listed 15–18 cycadophyte species that now are either assigned to *Nilssonia* and *Pseudoctenis* (cycadalean foliage) or remain in *Pterophyllum* (bennettitalean foliage). Bennettitalean and cycadalean foliage is primarily distinguished by the morpho-type of the stomata. As a result of the revision, only two clearly defined *Pterophyllum* species (i.e. *P. filicoides* and *P. brevipenne*) and five cycadalean species (i.e. *Nilssonia sturii*, *N. neuberi*, *N. lunzensis*, *N. riegeri* and *Pseudoctenis cornelii*) are present in the Lunz flora. *Pseudoctenis cornelii* is a species that is new to science and represents the earliest record of this genus. The bennettitaleans are, in turn, completed by three distinct *Nilssoniopteris* species (i.e. *N. haidingeri*, *N. angustior* and *N. lunzensis*), which were previously classified as marattialean ferns. The taxonomic work also proved the name of the genus *Pterophyllum*, which is one of the dominating cycadophyte morphogenera of the Mesozoic, being invalid. A proposal to conserve the name was posted during this study.

Among various adaptations of the plants to distinct habitat and environmental conditions that became recognisable from the cuticles, several other aspects were revealed by the cuticular studies that may contribute to the reconstruction of the assumed surroundings where the Lunz plants lived. A surface pattern of raised striae was discovered on the leaves of *Glossophyllum florinii*. It is interpreted i.a. to reduce the wettability of the leaves, and thus enforce the controlled run-off of water droplets. Dragonflies and beetles are supposed to be the origin of insect eggs and impressions that were found on the cuticles of *Nilssoniopteris* representatives. The presence of these eggs allows conclusions on plant/insect-interactions that may have occurred during the Triassic as well as on the putative habitat of the plants, because dragonfly larvae have to drop into freshwater where they develop. Therefore, these leaves must have overhung open water surfaces of freshwater bodies.

The cuticular investigations also revealed the first record of a juvenile (emerging) leaf of a bennettitalean (i.e. *Pterophyllum filicoides*). The development of the leaves of bennettitaleans was previously unknown. This aspect may influence our view of the relationships between Cycadales and Bennettitales if it is included in phylogenetic analyses of the higher seed plant groups.

Summarising the several aspects of the adaptations of the plants and the surrounding factors including climate, habitat, environmental and ground conditions and interactions of the plants

with their environment (i.e. plant/animal-interactions), and relating them to comparable extant ecosystems of similar latitudes, it may be suggested that the Lunz flora grew in a relatively stable environment characterised by a humid climate with seasonal droughts. The plants thrived in an estuarine lowland setting close to a freshwater lagoon. The lagoonal site was perhaps part of a riverine delta system with aerial marine influences and sustained windy conditions that enforced the xeric adaptations of the plants.

Ongoing studies include the investigation of the fertile elements of Cycadales and Bennettitales, that may contribute to the raise and radiation of the Bennettitales and the investigation and description of the ferns that are present in the Lunz flora. Comparison of the Lunz flora with other adjacent and coeval floras contributes to infer possible large area floral developments in the early Late Triassic as well as to the gradually floral changing in the Late Triassic–Middle Jurassic.

LITERATURE CITED

Abel O. 1906. Fossile Flugfische. Jahrbuch der Geologischen Reichsanstalt Wien 56: 1–93.

Allen EA, Hoch HC, Steadman JR, Stavely RJ. 1990. Influence of leaf surface features on spore deposition and the epiphytic growth of phytopathogenic fungi. In: Andrews JH, Hirano SS, editors. Microbial Ecology of Leaves. New York: Springer, pp. 87–110.

Alvin KL. 1982. Cheirolepiadaceae: Biology, structure and paleoecology. Review of Palaeobotany and Palynology 37: 71–98.

Alvin KL, Barnard PDW, Harris TM, Hughes NF, Wagner RH, Wesley A. 1967. Gymnospermophyta. In: Harland WB, Holland CH, House MR, Hughes NF, Reynolds AB, Rudwick MJS, Satterthwaite GE, Tarlo LBH, Willey EC, editors. The fossil record. Special Publication of the Geological Society of London 2: 247–267.

Anderson JM, Anderson HM. 1989. Palaeoflora of Southern Africa, Molteno Formation (Triassic) - Gymnosperms (excluding *Dicroidium*). Rotterdam: Balkema. 567 p.

Arnold CA. 1947. An introduction to paleobotany. New York: MacGraw-Hill. XI+403 p.

Ash SR. 1970. *Pagiophyllum simpsonii*, a new conifer from the Chinle Formation (Upper Triassic) of Arizona. Journal of Paleontology 44(5): 945–952.

Ash SR. 1980. Upper Triassic floral zones of North America. In: Dilcher DL, Taylor TN, editors. Biostratigraphy of fossil plants. Stroudsburg: Dowden, Hutchinson and Ross, pp. 153–170.

Ash S. 1989. The Upper Triassic Chinle flora of the Zuni Mountains, New Mexico. New Mexico Geological Society Fieldbook, 40th Field Conference, Southeastern Colorado Plateau: 225–230.

Ash S. 1999. An Upper Triassic upland flora from North Central New Mexico, U.S.A. Review of Palaeobotany and Palynology 105: 183–199.

Ash S. 2001. New cycadophytes from the Upper Triassic Chinle Formation of the southwestern United States. PaleoBios 21(1): 15–28.

Ash S. 2005. A new Upper Triassic flora and associated invertebrate fossils from the basal beds of the Chinle Formation, near Cameron, Arizona. PaleoBios 25(1): 17–34.

Ash S, Litwin RJ. 1996. Two new species of the pinnate microsporophyll *Pramelreuthia* from the Upper Triassic of the southwestern United States. American Journal of Botany 83(8): 1091–1099.

Ash S, Litwin RJ, Traverse A. 1982. The Upper Triassic fern *Phlebobteris smithii* (Daugherty) Arnold ant its spores. Palynology 6: 203–219.

Axsmith BJ, Kroehler PA. 1989. Upper Triassic *Dinophyton* zone plant fossils from the Stockton Formation in Southeastern Pennsylvania. The Mosasaur 4: 45–47.

Axsmith BJ, Serbet R, Krings M, Taylor TN, Taylor EL, Mamay SH. 2003. The enigmatic Paleozoic plants *Spermopteris* and *Phasmatocycas* reconsidered. American Journal of Botany 90(11): 1585–1595.

Bacon PR. 1997. Wetlands and biodiversity. In: Hails AJ, editor. Wetlands, biodiversity and the Ramsar Convention - The role of the convention on wetlands in the conservation and wise use of biodiversity. Cambridge, UK: IUCN Publications, Ramsar Convention Library. 196 p.

Barthel M. 1976. Ergebnisse der floristischen Neubearbeitung des Rotliegenden in Sachsen. Zeitschrift für geologische Wissenschaften 6: 921–933.

Barthlott W. 1980. Morphogenese und Mikromorphologie komplexer Cuticular-Faltungsmuster an Blüten-Trichomen von *Antirrhinum* L. (Scrophulariaceae). Berichte der deutschen Botanischen Gesellschaft 93: 379–390.

Barthlott W, Ehler N. 1977. Raster-Elektronenmikroskopie der Epidermisoberflächen von Spermatophyten. Tropische und subtropische Pflanzenwelt 19: 1–105.

Barthlott W, Neinhuis C. 1997. Purity of the Sacred Lotus, or escape from contamination in biological surfaces. Planta 202: 1–8.

Barthlott W, Ziegler B. 1981. Mikromorphologie der Samenschalen als systematisches Merkmal bei Orchideen. Berichte der deutschen Botanischen Gesellschaft 94: 267–273.

Benton MJ. 2004. Origin and relationships of Dinosauria. In: Weishampel DB, Dodson P, Osmólska H, editors. The Dinsosauria. Berkeley: University of California Press, pp. 7–19.

Berner RA. 1999. Atmospheric oxygen over Phanerozoic time. Proceedings of the National Academy of Sciences 96: 10955–10957.

Berner RA, Kothavala Z. 2001. Geocarb III: A revised model of atmospheric CO_2 over Phanerozoic time. American Journal of Science 301: 182–204.

Bhardwaj DC, Singh HP. 1957. *Asterotheca meriani* (Brongn.) Stur and its spores from the Upper Triassic of Lunz (Austria). The Palaeobotanist 5(2): 51–55.

Bharadwaj DC, Singh HP. 1964. An Upper Triassic miospore assemblage from the coals of Lunz, Austria. The Palaeobotanist 12: 28–44.

Blakey R. 2005. Global earth history. Published online at http://jan.ucc.nau.edu/ ~rcb7/RCB.html. Last access: 26.02.2007.

Bock W. 1969. The American Triassic flora and global distribution. North Wales, Pennsylvania: Geological Center. 406 p.

Braun CFW. 1843. Beiträge zur Urgeschichte der Pflanzen. Beiträge zur Petrefacten-Kunde(6): 1–46.

Broglia Loriga C, Fugagnoli A, Van Konijnen-burg-van Cittert JHA, Kustatscher E, Posenato R, Wachtler M. 2002. The Anisian macroflora from the Northern Dolomites (Monte prà della Vacca/Kühwiesenkopf, Braies): A first report. Rivista Italiana di Paleontologia e Stratigrafia 108: 381–390.

Brongniart A. 1825. Observations sur les végétaux fossiles renfermés dans les grès de Hoer en Scanie. Annales des Sciences Naturelles 4: 200–224.

Brongniart A. 1828. Prodrome d'une histoire des végétaux fossiles. Paris: Levrault. VIII+223 p.

Brongniart A. 1849. Tableau des genres végétaux fossiles considérés sous le point de vue de leur classification géologique. Dictionnaire Universel d'Histoire Naturelle. Paris: Renard, Martinet et C^{ie}. 127 p.

Bronn HG. 1848. Index palaeontologicus. Stuttgart: Schweizerbart. 1381 p.

Bronn HG. 1858. Beiträge zur Triasischen Fauna und Flora der bituminösen Schiefer von Raibl, nebst Anhang über die Kurr'sche Sippe *Chiropteris* aus dem Lettenkohlen-Sandsteine. Stuttgart: E. Schweitzerbart'sche Verlagshandlung und Druckerei. 63 p.

Buckland W. 1829. On the Cycadeoideae, a family of fossil plants found in the oolite quarries of the Isle of Portland. Transactions of the Geological Society, London 2: 395–401.

Buratti N, Cirilli S. 2007. Microfloristic provincialism in the Upper Triassic Circum-Mediterranean area and palaeogeographic implication. Geobios: in press.

Burnham RJ, Johnson KR. 2004. South American palaeobotany and the origins of Neotropical rainforests. Philosophical Transactions of the Royal Society of London B 359: 1595–1610.

Campbell CL, Jeng-Sheng Huang, Payne GA. 1980. Defense at the perimeter: The outer walls and the gates. In: Horsfall JG, Cowling EB, editors. Plant disease and advanced treatise. New York: Academic Press, pp. 103–120.

Cantrill DJ. 1992. Araucarian foliage from the Lower Cretaceous of Southern Victoria, Australia. International Journal of Plant Science 153(4): 622–645.

Carruthers W. 1870 (1868). On fossil cycadean stems from the secondary rocks of Britain. Transactions of the Linnean Society of London 26: 675–708.

Chambers TC, Drinnan AN, McLoughin S. 1998. Some morphological features of Wollemi Pine (*Wollemia nobilis*: Araucariaceae) and their comparison to Cretaceous plant fossils. International Journal of Plant Science 159(1): 160–171.

Chapman VJ. 1976. Mangrove Vegetation. Vaduz: Cramer. 447 p.

Chu Wang F. 1984. The dynamics of a river-bay-delta system. Journal of Geophysical Research 89(C5): 8054–8060.

Cleal CJ. 1993. Gymnospermophyta. In: Benton M, editor. The fossil record. London: Chapman & Hall, pp. 795–808.

Cleal CJ, Lazarus M, Townsend A. 2005. Illustrations and illustrators during the 'Golden Age' of palaeobotany: 1800–1840. In: Bowden AJ, Burek CV, Wilding R, editors. History of palaeobotany: Selected essays. London: The Geological Society, pp. 41–61.

Cleal CJ, McAllister Rees P. 2003. The Middle Jurassic flora from Stonesfield, Oxfordshire, UK. Palaeontology 46(4): 739–801.

Crane PR. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. Annals of the Missouri Botanical Garden 72: 716–793.

Crowson RA. 1981. The Biology of the Coleoptera. London: Academic Press. XII+802 p.

Dasch EJ, Campell KSW. 1970. Strontium-Isotope evidence for marine or freshwater origin of fossil dipnoans and arthrodires. Nature 227: 1159–1159.

Delahaut KA, Hasselkus ER. 1999. Salt injury to landscape plants. Madison: University of Wisconsin-Extension A2970.

Dobruskina IA. 1988. Collections of the Lunz flora in Graz. Mitteilungen der Abteilung für Geologie und Paläontologie des Landesmuseums Joanneum 47: 19–26.

Dobruskina IA. 1989. The alpine Lunz-Flora - a standard flora for the Carnian stage of the Triassic. International Geological Review 31: 1209–1215.

Dobruskina IA. 1998. Lunz flora in the Austrian Alps - a standard for Carnian floras. Palaeogeography, Palaeoclimatology, Palaeoecology 143: 307–345.

Dobruskina IA, Jurkovsek B, Kolar-Jurkovsek T. 2001. Upper Triassic flora from "Raibl beds" of Julian Alps (Italy) in Karavanke Mts. (Slovenia). Geologija 44(2): 263–290.

Donoghue MJ, Doyle JA. 2000. Seed plant phylogeny: Demise of the anthophyte hypothesis? Current Biology 10: 106–109.

Doweld AB. 2000. *Arberophyllum* - a new generic name for *Glossophyllum* Kräusel, 1943 (Ginkgophyta). Paleontological Journal 34: 674–675.

Doyle JA. 2006. Seed ferns and the origin of angiosperms. Journal of the Torrey Botanical Society 133: 169–209.

Dumortier BC. 1829. Analyse des familles des plantes, avec l'indication des principaux genres qui s'y rattachent. Tournai: J. Casterman. 104 p.

Dunay RF, Fisher MJ. 1978. The Carnian palynofloral succession in the Northern Calcarous Alp, Lunz-am-See, Austria. Pollen et Spores 20(1): 177–187.

Eller BM. 1977. Road dust induced increase of leaf temperature. Environmental pollution 19: 99–107.

Engler A. 1892. Syllabus der Vorlesungen über specielle und medicinisch-pharmaceutische Botanik. Berlin: Gebr. Borntraeger. XXIII+184 p.

Ettinghausen C von. 1851. Beiträge zur Flora der Vorwelt. Naturwissenschaftliche Abhandlungen 4(1): 65–99.

Fahn A, Cutler DF. 1992. Xerophytes. Berlin: Gebr. Borntraeger. XII+176 p.

Florin R. 1933a. Studien über die Cycadales des Mesozoikums. Kungliga Svenska Vetenskapsakademiens Handlingar 12(5): 1–134.

Florin R. 1933b. Zur Kenntnis der Spaltöffnungsapparate der Bennettitales. Kungliga Svenska Vetenskapsakademiens Handlingar, Tredje Serien 12(5): 11–31.

Florin R. 1933c. Die Spaltöffnungsapparate der *Williamsonia*-, *Williamsoinella*- und *Wielandiella*-Blüten (Bennettitales). Arkiv för Botanik 25A(15): 1–20.

Florin R. 1936. Die fossilen Gingkophyten aus Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters. II. Allgemeiner Teil. Palaeontographica Abt. B 82: 1–72.

Fontaine WM. 1883. Contributions to the knowledge of the older Mesozoic flora of Virginia. Washington: Government Printing. 144 p.

Fowell SJ, Traverse A. 1995. Palynology and age of the upper Blomidon Formation, Fundy basin, Nova Scotia. Review of Palaeobotany and Palynology 86: 211–233.

Frentzen K. 1922a. Die Keuperflora Badens. Verhandlungen des naturwissenschaftlichen Vereins in Karlsruhe 28: 1–76.

Frentzen K. 1922b. Keuperflora und Lunzer Flora. Centralblatt für Mineralogie, Geologie und Paläontologie 1: 23–28.

Fry WL. 1955. Notes on the generic name for cordaitean cones. Bulletin of the Torrey Botanical Club 82(6): 486–490.

Gao Zhi-Feng, Thomas BA. 1989a. A review of fossil cycad megasporophylls, with new evidence of *Crossozamia* Pomel and its associated leaves from the Lower Permian of Taiyuan, China. Review of Palaeobotany and Palynology 60: 205–223.

Gao Zhi-Feng, Thomas BA. 1989b. Occurrence of earliest cycads in the Permian of China and its bearing on their evolution. Chinese Science Bulletin 34(9): 766–769.

Geinitz E. 1873. Versteinerungen aus dem Brandschiefer der unteren Dyas von Weissig bei Pillnitz in Sachsen. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Paläontologie: 691–704.

Ghosh P, Bhattacharya SK, Ghosh P. 2005. Atmospheric CO_2 during the Late Paleozoic and Mesozoic: Estimates from Indian soils. In: Baldwin IT, Caldwell MM, Heldmaier G, Jackson RB, Lange OL, Mooney HA, Schulze E-D, Sommer U, Ehleringer JR, Dearing MD, Cerling TE, editors. A history of atmospheric CO_2 and its effects on plants, animals, and ecosystems. Berlin: Springer, pp. 8–34.

Greb SF, DiMichele WA, Gastaldo RA. 2006. Evolution and importance of wetlands in earth history. In: Greb SF, DiMichele WA, editors. Wetlands through time. Boulder, Colorado: The Geological Society of America, Specieal Paper 399, pp. 1–40.

Grimaldi D, Engel MS. 2005. Evolution of the insects. Cambridge: Cambridge University Press. XVI+755 p.

Gu and Zhi. 1974. Palaeozoic plants from China. Beijing: Scientific Press. IV+278 p.

Haq BU, Hardenbol J, Vail PR. 1987. Chronology of fluctuating sea levels since the Triassic. Science 235: 1157–1166.

Harris TM. 1932a. The fossil flora of Scoresby Sound, East Greenland - Part 2: Description of seed plants *incertae sedis* together with a discussion of certain cycadophyte cuticles. Meddelelser om Grønland 85(3): 1–112.

Harris TM. 1932b. The fossil flora of Scoresby Sound, East Greenland - Part 3: Caytoniales and Bennettitales. Meddelelser om Grønland 85(5): 1–133.

Harris TM. 1935. The fossil flora of Scoresby Sound, East Greenland - Part 4: Ginkgoales, Coniferales, Lycopodiales and isolated fructifications. Meddelelser om Grønland, 112: 1–176.

Harris TM. 1946. Liassic and Rhaetic plants collected in 1936–38 from East Greenland. Meddelelser om Grønland 114(9): 1–40.

Harris TM. 1961–1979. The Yorkshire Jurassic Flora. Trustees of the British Museum (Natural History). Vol. I, 212 p.; II, 191 p.; III, 186 p.; IV, 150 p.; V, 166 p.

Harris TM. 1964. The Yorkshire Jurassic Flora - Part II. Caytoniales, Cycadales & Pteridosperms. London: Trustees of the British Museum (Natural History). 191 p.

Harris TM. 1969. The Yorkshire Jurassic Flora - Part III. Bennettitales. London: Trustees of the British Museum (Natural History). 186 p.

Hay WW, Behensky JF, Barron EJ, Sloan II JL. 1982. Late Triassic–Liassic palaeoclimatology of the proto-central north Atlantic rift system. Palaeogeography, Palaeoclimatology, Palaeoecology 40: 13–30.

Heer O. 1865. Die Urwelt der Schweiz. Zürich: Schulthess. XXIX+622 p.

Heer O. 1877. Flora fossilis Helvetiae. Zürich: J. Wurster & Comp. VI+182 p.

Herbst R. 1979. Review of the Australian Dipteridaceae. Proceedings of the Linnean Society of New South Wales 103: 7–21.

Hill KD, Stevenson DW, Osborne R. 2004. The world list of cycads. The Botanical Review 70(2): 274–298.

Hilton J, Bateman RM. 2006. Pteridosperms are the backbone of seed-plant phylogeny. Journal of the Torrey Botanical Society 133(1): 119–168.

Hochuli PA, Frank SM. 2000. Palynology (dinoflagellate cysts, spore-pollen) and stratigraphy of the Lower Carnian Raibl Group in the eastern Swiss Alps. Eclogae Geologicae Helvetiae 93: 429–443.

Hood WG. 2006. A conceptual model of depositional, rather than erosional, tidal channel development in the rapidly prograding Skagit River Delta (Washington, USA). Earth Surface Processes and Landforms 31: 1824–1838.

Hornung T, Brandner R. 2005. Biochronostratigraphy of the Reingraben turnover (Hallstatt facies belt): local black shale events controlled by regional tectonics, climatic change and plate tectonics. Facies 51: 460–479.

Hutchings P, Saenger P. 1987. Ecology of mangroves. St Lucia: University of Queensland Press. 388 p.

International Commission on Stratigraphy (ICS). 2005. International stratigraphic chart.

Johansson N. 1922. Die rhätische Flora der Kohlengruben bei Stabbarp und Skromberga in Schonen. Kungliga Svenska Vetenskapsakademiens Handlingar 63(5): 1–78.

Jones WG, Hill KD, Allen JM. 1995. *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae. Telopea 6(2–3): 173–176.

Kawasaki S. 1931. The flora of the Heian System - Part 2 (Atlas). Bulletin of the Geological Survey of Chosen (Korea) 6(2): plates 16–99.

Kawasaki S. 1934. The flora of the Heian System - Part 2. Bulletin of the Geological Survey of Chosen (Korea) 6(4): 47–311.

Kelber K-P. 1998. Phytostratigraphische Aspekte der Makrofloren des süddeutschen Keupers. Documenta naturae 117: 89–115.

Kelber K-P, Hansch W. 1995. Keuperpflanzen. Die Enträtselung einer über 200 Millionen Jahre alten Flora. Museo 11: 1–157.

Kelber K-P, Nitsch E. 2005. Paläoflora und Ablagerungsräume im unterfränkischen Keuper. Jahresberichte und Mitteilungen des oberrheinischen geologischen Vereins 87: 217–253.

Kent DV, Olsen PE. 2000. Magnetic polarity, stratigraphy and paleolatitude of the Triassic–Jurassic Blomidon Formation in the Fundy basin (Canada): Implications for early Mesozoic tropical climate gradients. Earth and Planetary Science Letters 179: 311–324.

Kent DV, Tauxe L. 2005. Corrected Late Triassic latitudes for continents adjacent to the North Atlantic. Science 307: 240–244.

Ke-Qin Sun. 2006. The Cathaysia flora and the mixed Late Permian Cathaysian-Angaran floras in East Asia. Journal of Integrative Plant Biology 48(4): 381–389.

Kerp H. 1990. The study of fossil gymnosperms by means of cuticular analysis. Palaios 5: 548–569.

Kerp H. 2000. The modernization of landscapes during the Late Paleozoic–Early Mesozoic. In: Gastaldo RA, DiMichele WA, editors. Phanerozoic terrestrial ecosystems: Paleontological Society Papers, pp. 79–113.

Kerp H, Krings M. 1999. Light microscopy of cuticules. In: Jones T, editor. Fossil plants and spores: Modern techniques. London: Geological Society, pp. 52–56.

Kerp H, Krings M. 2003. Kutikularanalytische Befunde zur Abgrenzung der *Odontopteris minor* f. *zeilleri* Potonié von *Odontopteris reichiana* Gutbier. Courier Forschungs-Institut Senckenberg 241: 31–42.

Kerstiens G, 1996. Plant cuticles - An integrated functional approach. Oxford: BIOS Scientific Publishers. XIV+337 p.

Krasser F. 1909a. Die Diagnosen der von Dionysius Stur in der obertriadischen Flora der Lunzerschichten als Marattiaceenarten unterschiedenen Farne. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Wien, Abt. 1 118: 13–43.

Krasser F. 1909b. Zur Kenntnis der fossilen Flora der Lunzer Schichten. Jahrbuch der Kaiserlich-Königlich Geologischen Reichsanstalt 59(1): 1–26.

Krasser F. 1909c. Übersicht über die Marattiaceen der Lunzer Flora. Anzeiger der Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse, 07. Jänner 1909: 5–7.

Krasser F. 1916. Studien über die fertile Region der Cycadophyten aus den Lunzer Schichten: Mikrosporophylle und männliche Zapfen. Anzeiger der Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse 27: 335–354

Krasser F. 1917. Studien über die fertile Region der Cycadophyten aus den Lunzer-Schichten: Mikrosporophylle und männliche Zapfen. Denkschriften der kaiserlichen Akademie der Wissenschaften (Wien), Mathematisch-Naturwissenschaftliche Klasse 94: 489–553.

Krasser F. 1919. Studien über die fertile Region der Cycadophyten aus den Lunzer Schichten: Makrosporophylle. Denkschriften der kaiserlichen Akademie der Wissenschaften (Wien), Mathematisch-Naturwissenschaftliche Klasse 97: 1–32.

Kräusel R. 1920. Über einige Pflanzen aus dem Keuper von Lunz (Nieder-Österr.). Jahrbuch der Preußischen Geologischen Landesanstalt 41(1): 192–209.

Kräusel R. 1943. Die Gingkophyten der Trias von Lunz in Niederösterreich und von Neue Welt bei Basel. Palaeontographica Abt. B 87: 59–93.

Kräusel R. 1948. *Sturiella langeri* nov. gen., nov. sp., eine Bennettitee aus der Trias von Lunz (Nieder-Österreich). Senckenbergiana 29(1): 141–149.

Kräusel R. 1949. Koniferen und andere Gymnospermen aus der Trias von Lunz, Nieder-Österreich. Palaeontographica Abt. B 89: 35–82.

Kräusel R. 1952. *Stachyotaxus sahnii* nov. spec., eine Konifere aus der Trias von Neuewelt bei Basel. The Palaeobotanist 1: 285–288.

Kräusel R. 1953. Ein neues *Dioonitocarpidium* aus der Trias von Lunz. Senckenbergiana 34(1): 105–108.

Kräusel R. 1961. Ein Fund fruchtender Gymnospermenreste im Keuper von Neuewelt bei Basel. Eclogae Geologicae Helvetiae 53(2): 693–694.

Kräusel R, Leschik G. 1955. Die Keuperflora von Neuewelt bei Basel - I. Koniferen und andere Gymnospermen. Schweizer Paläontologische Abhandlungen 71: 1–27.

Kräusel R, Leschik G. 1959. Die Keuperflora von Neuewelt bei Basel - III. Equisetaceen. Schweizer Paläontologische Abhandlungen 77: 5–19.

Kräusel R, Schaarschmidt F. 1966. Die Keuperflora von Neuewelt bei Basel - IV. Pterophyllen und Taeniopteriden. Schweizer Paläontologische Abhandlungen 84: 3–44.

Krings M, Kellogg DW, Kerp H, Taylor TN. 2003a. Trichomes of the seed fern *Blanzyopteris praedentata*: Implications for plant-insect interactions in the Late Carboniferous. Botanical Journal of the Linnean Society 141: 133–149.

Krings M, Kerp H. 1998. Epidermal anatomy of *Barthelopteris germarii* from the Upper Carboniferous and Lower Permian of France and Germany. American Journal of Botany 85(4): 553–562.

Krings M, Kerp H. 2000. A contribution to the knowledge of the pteridosperm genera *Pseudomariopsis* Danzé-Corsin nov. emend. and *Helenopteris* nov. gen. Review of Palaeobotany and Palynology 111: 145–195.

Krings M, Kerp H, Taylor TN, Taylor EL. 2003b. How Paleozoic vines and lianas got off the ground: On scrambling and climbing Carboniferous–Early Permian pteridosperms. The Botanical Review 69(2): 204–224.

Kustatscher E, Van Konijnenburg-van Cittert JHA. 2005. The Ladinian flora (Middle Triassic) of the Dolomites: palaeoenvironmental reconstructions and palaeoclimatic conclusions. Geo.Alp 2: 31–52.

Kustatscher E, Wachtler M, Van Konijnenburg-van Cittert JHA. 2004. A number of additional and revised taxa from the Ladinian flora of the Dolomites, Northern Italy. Geo.Alp 1: 57–69.

Kutzbach JE, Gallimore RG. 1989. Pangaean climates: Megamonsoons of the megacontinent. Journal of Geophysical Research 94(D3): 3341–3357.

Labandeira CC. 2006. The four phases of plant-arthropod associations in deep time. Geologica Acta 4(4): 409–438.

Langer J. 1943. Über einige Stücke aus der Keuperflora von Lunz (Niederdonau). Berichte des Reichamts für Bodenforschung: 52–58.

Langer J. 1945. Über einige Stücke aus der Liasflora von Steiersorf und der Keuperflora von Lunz. Jahrbuch der Geologischen Bundesanstalt Wien 1/2: 21–33.

Lawrence JF, Newton AF. 1982. Evolution and classification of beetles. Annual Review of Ecology and Systematics 13: 261–290.

Le Roy P, Piqué A, Le Gall B, Aït Brahim L, Morabet AM, Demnati A. 1997. Les bassins côtiers triasico–liasiques du Maroc occidental et la diachronie du rifting intra-continental de l'Atlantique central. Bulletin de la Société géologique de France 168(5): 637–648.

Leuthardt F. 1903. Die Keuperflora von Neuewelt bei Basel - I. Teil Phanerogamen. Abhandlungen der Schweizer Paläontologischen Gesellschaft 30: 1–23.

Leuthardt F. 1904. Die Keuperflora von Neuewelt bei Basel - II. Teil Kryptogamen. Abhandlungen der Schweizer Paläontologischen Gesellschaft 31: 25–48.

Lindley J, Hutton W. 1831–1837. The Fossil flora of Great Britain, or figures and descriptions of the vegetable remains found in a fossil state in the country. London: Ridgway. Vol. I, 224 p.; II, 208 p.; III, 208 p.

Linnæus C. 1753. Species plantarum, exhibentes plantas rite cognitas, ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas. Tomus I. Stockholm (Holmiæ): Laurentii Salvii. XV+784 p.

Litwin RJ, Traverse A, Ash SR. 1991. Preliminary palynological zonation of the Chinle Formation, southwestern U.S.A., and its correlation to the Newark Supergroup (eastern U.S.A.). Review of Palaeobotany and Palynology 68: 269–287.

Lundblad AB. 1950. Studies in the Rhaeto–Liassic floras of Sweden. I. Pteridophyta, Pteridospermae and Cycadophyta from the mining district of NW Scania. Kungliga Svenska Vetenskapsakademiens Handlingar, Fjärde Serien 1(8): 1–82.

Mamay SH. 1976. Paleozoic origin of the cycads. Geological Survey Professional Paper 934, 1–48.

Martens P. 1971. Les gnétophytes. Berlin: Gebr. Borntraeger. 295 p.

Martin JT. 1964. Role of cuticle in the defense against plant disease. Annual Review of Phytopathology 2: 81–100.

Miquel FAW. 1851. Over de rangschikking der fossiele Cycadaceae. Tijdschrift voor de wis- en natuurkundige Wetenschapen 4: 205–227.

Morris J. 1841. Remarks upon the recent and fossil Cycadaceae. The Annals and Magazine of Natural History, Zoology, Botany and Geology 7: 110–120.

Nathorst AG. 1876. Anmärkningar om den fossila floran vid Bjuf i Skåne. Öfversigt af Konglika Vetenskaps-Akademiens Förhandlingar 1: 29–41.

Nathorst AG. 1878–86. Om floran i Skånes kolförande bildningar. Sveriges Geologiska Undersökning Serie C 27, 33, 85: 1–126.

Nathorst AG. 1906. Über *Dictyophyllum* und *Camptopteris spiralis*. Kungliga Svenska Vetenskapsakademiens Handlingar 41(5): 3–24.

Nathorst AG. 1908. Paläobotanische Mitteilungen 4.–6. Kungliga Svenska Vetenskapsakademiens Handlingar 43(6): 1–24.

Neinhuis C, Barthlott W. 1997. Characterization and distribution of water-repellent, self-cleaning plant surfaces. Annals of Botany 79: 667–677.

Nixon KC, Crepet WL, Stevenson D, Friis EM. 1994. A reevaluation of seed plant phylogeny. Annals of the Missouri Botanical Garden 81(3): 484–533.

Norstog KJ, Nicholls TJ. 1997. The Biology of the cycads. Ithaca: Cornell University Press. 363 p.

Ødegaard F. 2003. Taxonomic composition and host specificity of phytophagous beetles in a dry forest in Panama. In: Basset Y, Novotny V, Miller SE, Kitching RL, editors. Arthropods of Tropical forests - Spatio-temporal dynamics and resource use in the canopy. Cambridge: Cambridge University Press, pp. 220–236.

Olsen PE. 1997. Stratigraphic record of the Early Mesozoic breakup of Pangea in the Laurasia-Gondwana rift system. Annual Review of Earth and Planetary Sciences 25: 337–401.

Olsen PE, Rainforth EC. 2001. The "Age of Dinosaurs" in the Newark Basin, with special reference to the lower Hudson Valley. In: Gates AE, Olsen PE, editors. Geology of the Lower Hudson Valley - New York State Geological Asscoiation Field Trip Guide Book. Albany: New York State Geological Association, New York State Museum, p. 59–176.

Owens JN, Takaso T, Runions CJ. 1998. Pollination in conifers. Trends in Plant Science 3(12): 479–485.

Pal A, Kulshreshtha K, Ahmad KJ, Behl HM. 2002. Do leaf surface characters play a role in plant resistence to auto-exhaust pollution? Flora 197: 47–55.

Passoni L, Van Konijnenburg-van Cittert JHA. 2003. New taxa of fossil Carnian plants from Mount Pora (Bergamasc Alps, Northern Italy). Review of Palaeobotany and Palynology 123: 321–346.

Piqué A, Laville E. 1993. Les séries triasiques du Maroc, marquers du rifting atlantique. Comptes Rendus des Séances de l'Académie des Sciences, Paris, Série II - Mécanique, Physique, Chimie, Sciences de la Terre et de l'Univers 314: 1215–1220.

Rayfield EJ, Barretti PM, McDonnell RA, Willis KJ. 2005. A Geographical Information System (GIS) study of Triassic vertebrate biochronology. Geological Magazine 142(4): 327–354.

Riederer M, Müller C. 2006. Biology of the plant cuticle. Oxford: Blackwell Publishing. XVIII+438 p.

Roghi G. 2004. Palynological investigations in the Carnian of the Cave del Predil area (Julian Alps, NE Italy). Review of Palaeobotany and Palynology 132: 1–35.

Rothwell GW, Serbet R. 1994. Lignophyte phylogeny and the evolution of spermatophytes: A numerical cladistic analysis. Systematic Botany 19(3): 443–482.

Rothwell GW, Stockey RA. 2002. Anatomically preserved Cycadeoidea (Cycadeoidaceae), with a reevaluation of systematic characters for the seed cones of Bennettitales. American Journal of Botany 89(9): 1447–1458.

Sanders HL. 1968. Marine benthic diversity: a comparative study. The American Naturalist 102(925): 243–282.

Sawyer WH. 1972. Lungfishes and amphibians: Endocrine adaptation and the transition from aquatic to terrestrial life. Federation Proceedings 31(6): 609–614.

Schaarschmidt F. 1973. Pflanzenfossilien in ungewöhnlichem Licht. Natur und Museum 103(7): 247–253.

Schenk A. 1866. Über die Flora der schwarzen Schiefer von Raibl. Würzburger naturwissenschaftliche Zeitschrift 6: 10–20.

Schlotheim EF von. 1820. Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung einer Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert. Gotha: Becker'sche Verlagsbuchhandlung. 437 p.

Schlotheim EF von. 1822. Nachträge zur Petrefactenkunde. Gotha: Becker'sche Verlagsbuchhandlung. 100 p.

Schuster J. 1931. Über das Verhältnis der systematischen Gliederung, der geographischen Verbreitung und der paläontologischen Entwicklung der Cycadeen - Teil Trias. Botanisches Jahrbuch 64: 189–197.

Scotese, CR. 2003. Paleomap Project. Published online at www.scotese.com. Last access: 26.02.2007.

Sheldon ND. 2005. Do red beds indicate paleoclimatic conditions?: A Permian case study. Palaeogeography, Palaeoclimatology, Palaeoecology 228: 305–319.

Simms MJ, Ruffell AH. 1989. Synchroneity of climatic change and extinctions in the Late Triassic. Geology 17: 265–268.

Sitte P, Ziegler H, Ehrendorfer F, Bresinsky A. 1998. Strasburger - Lehrbuch der Botanik. Stuttgart: Fischer. 1007 p.

Stefani M, Brack P, Gianolla P, Keim L, Mastandrea A, Maurer F, Neri C, Preto N, Ragazzi E, Riva A, Roghi G, Russo F. 2004. Triassic carbonate platforms of the Dolomites, carbonate production, relative sea-level fluctuations and the shaping of the depositional architecture. Fieldtrip Guidebook, 32nd Int. Geol. Congress, Florence, August 20–28, P44: 1–64.

Steinmann G. 1903. Einführung in die Paläontologie. Leipzig: W. Engelmann. 466 p.

Sternberg KMG von. 1820–1838. Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. Leipzig und Prag. Vol. I, 144+XLII; II, 80 p.

Stockey RA, Rothwell GW. 2003. Anatomically preserved *Williamsonia* (Williamsoniaceae): Evidence for bennettitalean reproduction in the Late Cretaceous of Western North America. International Journal of Plant Science 164(2): 251–262.

Stremme H. 1911. Über paralische und limnische Kohlenlager und Moore. International Journal of Earth Sciences 2(1): 13–25.

Stur D. 1871.Geologie der Steiermark. Graz: Verlag des geognostisch-montanen Vereines für Steiermark. XXXI+654 p.

Stur D. 1885. Die obertriadische Flora der Lunzer-Schichten und des bituminösen Schiefers von Raibl. Denkschriften der Kaiserlichen Akademie der Wissenschaften (Wien) 3: 93–103.

Stur D. 1888. Die Lunzer (Lettenkohle-)Flora in den "older Mesozoic beds of the Coal-Field of Eastern Virginia". Verhandlungen der Kaiserlich-Königlich Geologischen Reichsanstalt 10: 203–217.

Suzuki H. 1980. Defenses triggered by previous invaders: fungi. In: Horsfall JB, Cowling EB, editors. Plant disease and advanced treatise. New York: Academic Press, pp. 319–332.

Sze HC. 1936. Über einen Vorläufer von Pterophyllen in der unteren Shihhotze Serie in Shansi. Bulletin of the Geological Society of China 15(4): 467–476.

Taylor EL, Taylor TN, Kerp H, Hermsen EJ. 2006. Mesozoic seed ferns: Old paradigms, new disxoveries. Journal of the Torrey Botanical Society 133(1): 62–82.

Taylor TN, Taylor EL. 1993. The biology and evolution of fossil plants. Englewood Cliffs: Prentice Hall. 982 p.

Teller FJ. 1891. Über den Schädel eines fossilen Dipnoërs, *Ceratodus sturii* nov. spec., aus den Schlichten den oberen Trias der Nordalpen. Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt Wien 15: 1–39.

Thomas HH, Bancroft N. 1913. On the cuticles of some recent and fossil cycadean fronds. Transactions of the Linnean Society of London: Botany 8(5): 155–204.

Traverse A. 1985. Paleopalynological insights on dating of the Newark Supergroup rocks and their correlation with European sections. The American Association of Petroleum Geologists Bulletin 69(9): 1450.

Traverse A. 1988. Paleopalynology. Boston: Hyman. XXIII+600 p.

Unger F. 1845. Synopsis plantarum fossilium. Leipzig: Voss. 329 p.

Unger F. 1850. Genera et species plantarum fossilium. Vindobonæ: Braumüller. XL+627 p.

Van Konijnenburg-van Cittert JHA. 2002. Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia. Review of Palaeobotany and Palynology 119: 113–124.

Van Rheede tot Draakestein HA. 1678–1693 (1682). Hortus Indicus Malabaricus. Amsterdam. 12 Volumes, 1595 p.

Verloop JH. 1908. Profil der Lunzer Schichten in der Umgebung von Lunz. Zeitschrift der Deutschen Geologischen Gesellschaft 60(4): 81–88.

Visscher H, Brugman WA. 1981. Ranges of selected palynomorphs in the alpine Triassic of Europe. Review of Palaeobotany and Palynology 34(1):115–128.

Visscher H, Van Houte M, Brugman WA, Poort RJ. 1994. Rejection of a Carnian (Late Triassic) “pluvial event” in Europe. Review of Palaeobotany and Palynology 83: 217–226.

Wachtler M, Van Konijnenburg-van Cittert JHA. 2000. The fossil flora of the Wengen Formation (Ladinian) in the Dolomites (Italy). Beiträge zur Paläontologie 25: 105–141.

Wade JA, Brown DE, Traverse A, Fensome RA. 1996. The Triassic–Jurassic Fundy Basin, eastern Canada: Regional setting, stratigraphy and hydrocarbonate potential. Atlantic Geology 32(3):189–231.

Watson J, Cusack HA. 2005. Cycadales of the English Wealden. Monograph of the Palaeontographical Society, London 158: 1–189. (Publ. No. 622).

Watson J, Sincock CA. 1992. Bennettitales of the English Wealden. Monograph of the Palaeontographical Society London 145: 1–228. (Publ. No. 588).

Webb JA. 1982. Triassic species of *Dictyophyllum* from eastern Australia. Alcheringa 6: 79–91.

Western RA. 1988. Adaptations of plants to a desert environment. Bulletin of the Emirates Natural History Group 36: 17–23.

Wing SL, Sues H-D, Tiffney BH, Stucky RK, Weishampel DB, Spicer RA, Jablonski D, Badgley CE, Wilson MVH, Kovach WL. 1992. Mesozoic and early Cenozoic terrestrial ecosystems. In: Behrensmeyer AK, Damuth JD, DiMichele WA, Potts R, Sues HD, Wing SL, editors. Terrestrial ecosystems through time: Evolutionary paleoecology of terrestrial plants and animals. Chicago: University of Chicago. p 327–416.

Xiu-Qun Liu, Cheng-Sen Li, Yu-Fei Wang. 2006. The pollen cones of *Ginkgo* from the Early Cretaceous of China, and their bearing on the evolutionary significance. Botanical Journal of the Linnean Society 152: 133–144.

Zhu Jia-Nan, Du Xian-Ming. 1981. A new cycad - *Primocycas chinensis* gen. et sp. nov. discovered from the Lower Permian in Shanxi, China and its significance. Acta Botanica Sinica 23(5): 401–404.

"Taxonomische Klassifikationen sind niemals richtig oder falsch; sie sind lediglich mehr oder weniger sinnvoll und akzeptabel."
(Peter F. Yeo, Cambridge, UK).

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APPENDIX

Abbreviations used for the museums and collections mentioned in the text:

GBA	Geologische Bundesanstalt, Wien (Geological Survey of Austria, Vienna, Austria)
JOA	Landesmuseum Joanneum, Graz (State Museum Joanneum, Graz, Austria)
MNB	Museum für Naturkunde, Berlin (Museum of Natural History, Berlin, Germany)
NAT	Nationaal Naturhistorisch Museum Naturalis, Leiden (Museum of Natural History, Leiden, The Netherlands)
NHM	Naturhistorisches Museum, Wien (Museum of Natural History, Vienna, Austria)
NRM	Naturhistoriska Riksmuseet, Stockholm (Museum of Natural History, Stockholm, Sweden)
PBO	Forschungsstelle für Paläobotanik, Münster (Palaeobotany Research Group, Münster, Germany)
RUU	Laboratory of Palaeobotany and Palynology, University Utrecht, The Netherlands
SNB	Naturmuseum Senckenberg, Frankfurt am Main (Museum of Natural History, Frankfurt, Germany)
SPO	Niederösterreichisches Landesmuseum, St. Pölten (State Museum of Lower Austria, St. Pölten, Austria)

Table II. List of accession numbers of the specimens stored in the different collections that contributed to this study.

NHM Wien	NHM Wien	NHM Wien	GBA Wien	GBA Wien	GBA Wien
1878-VI-9957	1885-D-3862	1887-I-27	GBA 1909/02/204	GBA 1909/02/340	GBA 1909/03/467
1878-VI-9980	1883-D-3893	1887-I-30	GBA 1909/02/208	GBA 1909/02/344	GBA 1909/03/490
1878-VI-9990	1885-D-3935	1887-I-32	GBA 1909/02/211	GBA 1909/02/345	GBA 1909/03/494
1882-C-3061	1885-D-3958	1887-I-33	GBA 1909/02/212	GBA 1909/02/354	GBA 1909/03/505
1882-C-3064	1885-D-3966	1887-I-34	GBA 1909/02/215	GBA 1909/02/355	GBA 1909/03/506
1882-C-3068	1883-D-3969	1887-I-34-2	GBA 1909/02/216	GBA 1909/02/369	GBA 1909/03/508
1882-C-5066	1885-D-3971	1887-VI-17	GBA 1909/02/225	GBA 1909/02/371	GBA 1909/03/512
1883-C-3875	1885-D-3972	1888-I-18	GBA 1909/02/228	GBA 1909/02/375	GBA 1909/03/518
1883-C-5197	1885-D-3982	1889-VI-04	GBA 1909/02/232	GBA 1909/02/518	GBA 1909/03/531
1883-C-5852	1885-D-3983	1889-VI-05	GBA 1909/02/233	GBA 1909/03/018	GBA 1909/03/540
1883-C-5854	1885-D-3994	1889-VI-08	GBA 1909/02/234	GBA 1909/03/096	GBA 1909/03/550
1883-C-5863	1885-D-3995	1889-VI-11	GBA 1909/02/235	GBA 1909/03/195	GBA 1909/03/568
1883-C-5864	1885-D-4020	1889-VI-16	GBA 1909/02/236	GBA 1909/03/197	GBA 1909/03/570
1883-C-5866	1885-D-4021	1889-VI-18	GBA 1909/02/237	GBA 1909/03/198	GBA 1909/03/572
1883-C-5867	1885-D-4022	1889-VI-20	GBA 1909/02/238	GBA 1909/03/199	GBA 1909/03/574
1883-C-5870	1885-D-4023	1944-I-44	GBA 1909/02/239	GBA 1909/03/201	GBA 1909/03/575
1883-C-5872	1885-D-4024	2006B0008/0001	GBA 1909/02/240	GBA 1909/03/202	GBA 1909/03/576
1883-C-5877	1885-D-4026	2006B0008/0002	GBA 1909/02/246	GBA 1909/03/204	GBA 1909/03/577
1883-C-5880	1885-D-4027	2006B0008/0010	GBA 1909/02/247	GBA 1909/03/205	GBA 1909/03/578
1883-C-5893	1885-D-4029	2006B0008/0012	GBA 1909/02/248	GBA 1909/03/370	GBA 1909/03/580
1883-C-5896	1885-D-4034	2006B0008/0013	GBA 1909/02/249	GBA 1909/03/371	GBA 1909/03/581
1883-C-5900	1885-D-4035	2006B0008/0014	GBA 1909/02/250	GBA 1909/03/375	GBA 1909/03/582
1883-C-5902	1885-D-4043	2006B0008/0015	GBA 1909/02/251	GBA 1909/03/376	GBA 1909/03/583
1883-C-5904	1885-D-4049	2006B0008/0016	GBA 1909/02/254	GBA 1909/03/377	GBA 1909/03/584
1883-C-5907	1885-D-4050	2006B0008/0020	GBA 1909/02/254	GBA 1909/03/378	GBA 1909/03/585
1883-C-5909	1885-D-4054	2006B0008/0021	GBA 1909/02/256	GBA 1909/03/379	GBA 1909/03/587
1883-C-5912	1885-D-4055	2006B0008/0022	GBA 1909/02/266	GBA 1909/03/380	GBA 1909/03/588
1883-C-5914	1885-D-4056	2006B0008/0025	GBA 1909/02/269	GBA 1909/03/382	GBA 1909/03/589
1883-C-5919	1885-D-4060	2006B0008/0026	GBA 1909/02/270	GBA 1909/03/383	GBA 1909/03/592
1883-C-5923	1885-D-4061	2006B0008/0027	GBA 1909/02/271	GBA 1909/03/385	GBA 1909/03/594
1883-C-5925	1885-D-4063	2006B0008/0028	GBA 1909/02/272	GBA 1909/03/386	GBA 1909/03/720
1884-15	1885-D-4064	2006B0008/0031	GBA 1909/02/273	GBA 1909/03/387	GBA 1909/03/749
1884-16	1885-D-4068	2006B0008/0033	GBA 1909/02/274	GBA 1909/03/388	GBA 1909/03/762
1884-20	1885-D-4069	2006B0008/0034	GBA 1909/02/275	GBA 1909/03/389	GBA 1909/03/763
1884-21	1885-D-4071	2006B0008/0035	GBA 1909/02/277	GBA 1909/03/391	GBA 1909/03/779
1884-22	1885-D-4075	2006B0008/0039	GBA 1909/02/280	GBA 1909/03/392	GBA 1909/03/783
1884-26	1885-D-4077	2006B0008/0040	GBA 1909/02/281	GBA 1909/03/393	GBA 1909/03/851
1884-27	1885-D-4084	2006B0008/0042	GBA 1909/02/282	GBA 1909/03/394	GBA 1909/03/909
1884-28	1885-D-4086	2006B0008/0044	GBA 1909/02/302	GBA 1909/03/396	GBA 1909/03/930
1884-30	1885-D-4087		GBA 1909/02/303	GBA 1909/03/397	GBA 1909/03/931
1884-31	1885-D-4091	**GBA Wien**	GBA 1909/02/304	GBA 1909/03/398	GBA 1909/03/932
1884-34	1885-D-4095	GBA 1909/02/064	GBA 1909/02/305	GBA 1909/03/399	GBA 1909/03/933
1884-D-1192	1885-D-4100	GBA 1909/02/090	GBA 1909/02/306	GBA 1909/03/400	GBA 1909/03/934
1884-D-1193	1885-D-4109	GBA 1909/02/145	GBA 1909/02/307	GBA 1909/03/401	GBA 1909/03/935
1884-D-1194	1885-D-5973	GBA 1909/02/183	GBA 1909/02/308	GBA 1909/03/402	GBA 1909/03/936
1884-D-1195	1886-I-03	GBA 1909/02/184	GBA 1909/02/309	GBA 1909/03/403	GBA 1909/03/940
1884-D-1196	1886-I-04	GBA 1909/02/185	GBA 1909/02/310	GBA 1909/03/404	GBA 1909/03/941
1884-D-1198	1886-I-08	GBA 1909/02/186	GBA 1909/02/311	GBA 1909/03/407	GBA 1909/03/956
1884-D-1202	1886-I-14	GBA 1909/02/187	GBA 1909/02/312	GBA 1909/03/410	GBA 1909/03/966
1884-D-1203	1886-I-17	GBA 1909/02/188	GBA 1909/02/315	GBA 1909/03/426	GBA 2006/004/0003
1884-D-1205	1886-I-19	GBA 1909/02/189	GBA 1909/02/316	GBA 1909/03/440	GBA 2006/004/0006
1884-D-1206	1886-I-22	GBA 1909/02/190	GBA 1909/02/317	GBA 1909/03/441	GBA 2006/004/0008
1884-D-1207	1887-D-1200	GBA 1909/02/191	GBA 1909/02/321	GBA 1909/03/442	GBA 2006/004/0011
1884-D-1208	1887-I-09	GBA 1909/02/192	GBA 1909/02/327	GBA 1909/03/443	GBA 2006/004/0014
1884-D-1209	1887-I-11	GBA 1909/02/193	GBA 1909/02/331	GBA 1909/03/445	
1884-D-1210	1887-I-12-2	GBA 1909/02/195	GBA 1909/02/332	GBA 1909/03/451	**NRM Stockholm**
1884-D-1211	1887-I-13-1	GBA 1909/02/196	GBA 1909/02/336	GBA 1909/03/454	S148220
1884-D-4067	1887-I-13-2	GBA 1909/02/197	GBA 1909/02/337	GBA 1909/03/456	S148223
1885-C-5910	1887-I-24	GBA 1909/02/199	GBA 1909/02/338	GBA 1909/03/462	S148228
1885-D-1212	1887-I-25	GBA 1909/02/203	GBA 1909/02/339	GBA 1909/03/466	S148230

Table II. (condinued).

NRM Stockholm	NRM Stockholm	NRM Stockholm	RUU Utrecht	NAT Leiden	IOA Graz
S148231	S148471	S148668	17867	5100	63756
S148232	S148483	S148671	17870	5101	63765
S148233	S148495	S148679	17872	J1195/a	63772
S148234	S148502	S148681	17874	J1195/b	63781
S148237	S148505	S148685	17877	J1197	63795
S148238	S148512	S148686	17880	RGM15529	63796
S148240	S148522	S148687	17882	RGM18074	63797
S148242	S148523	S148690	17885	RGM231654	63802
S148244	S148534		17886	THDB 6643	63807
S148245	S148536	**RUU Utrecht**	17887	THDB 6918	63814
S148246	S148543	243	17889	THDB 8623	63816
S148256	S148550	246	17890	THDB12213	63817
S148257	S148560	349	17894	THDB6906	63818
S148258	S148568	415	17895	THDB6908	63821
S148287	S148575	2894	17896	THDB6916	63824
S148314	S148576	8281	17901	THDX5099	63829
S148318	S148577	8285	17902		63863
S148323	S148578	8287	17903	**IOA Graz**	63874
S148324	S148579	8292	17904	62718	63879
S148331	S148583	17847	17908	63649	63881
S148332	S148584	17849	17912	63656	63883
S148334	S148586	17850	17914	63663	63884
S148353	S148588	17851	17919	63672	63888
S148420	S148594	17852	17920	63682	63900
S148422	S148596	17853	17925	63688	63901
S148423	S148597	17854	17930	63690	63904
S148435	S148598	17856	17937	63693	63916
S148437	S148599	17857	17939	63694	63927
S148448	S148601	17858	17940	63726	without number
S148449	S148602	17859	17943	63731	without number
S148451	S148608	17862	18066	63737	
S148454	S148657	17864		63741	**SPO St. Pölten**
S148468	S148660	17865	**NAT Leiden**	63742	F/0042
S148470	S148666	17866	1458	63745	F/0049

CURRICULUM VITAE

Christian Pott
Diplom Biologe

geboren am 04. Februar 1977 in Münster/Westfalen

Familienstand	ledig
Eltern	Klaus Pott und Birgit Pott, geb. Bayer

Schulbildung

09/1983 – 06/1987	Johannes-Grundschule, Altenberge
08/1987 – 06/1996	Städtisches Gymnasium Paulinum, Münster Hochschulreife (Abitur) am 04. Juni 1996 in Münster

Zivildienst

07/1996 – 07/1997	Vogelwart und Mitglied der Nationalparkwacht Niedersächsisches Wattenmeer, Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz (NLWKN), Norden, Außenstelle Spiekeroog

Studium

10/1997 – 03/2003	Studium der Biologie, Paläontologie und Systematik an der Westfälischen Wilhelms-Universität Münster
05/2002 – 02/2003	Diplomarbeit am Zoologischen Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Sektion Ornithologie [Betreuung: Dr. R. van den Elzen]

Prüfungen

Diplom	im Fach Biologie am 07. April 2003 (Westfälische Wilhelms-Universität Münster)

Promotionsstudiengang

seit 04/2003	Promotionsstudium Biologie an der Westf. Wilhelms-Universität Münster

Beginn der Dissertation

06/2004	am Geologisch-Paläontologischen Institut und Museum der Westfälischen Wilhelms-Universität Münster [Betreuung: PD Dr. Michael Krings, Bayerische Staatssammlung für Paläontologie und Geologie und GeoBio-Center^{LMU}, München, und Prof. Dr. Hans Kerp, Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut und Museum der Westfälischen Wilhelms-Universität, Münster]

Tätigkeiten

04/2001 – 08/2001	Durchführung der botanischen Exkursionen im Umkreis von Münster und Kontrolle der angefertigten Herbare, Institut für Botanik und Botanischer Garten der Westfälischen Wilhelms-Universität Münster

10/2000 – 02/2003	Netzwerkadministration im Institut für Evolution und Ökologie der Tiere der Westfälischen Wilhelms-Universität Münster, währenddessen Betreuung der Studentenkurse Datenverarbeitung in der Biologie und Molekular-phylogenetische Analysenmethoden
10/2002 – 02/2007	jeweils im Winterhalbjahr Betreuung von studentischen Exkursionen an die deutsche und niederländische Küste zum Thema Vogelzug und Überwinterungsstrategien im Auftrag des Instituts für Evolution und Ökologie der Tiere der Westfälischen Wilhelms-Universität Münster
seit 04/2003	freiberufliche Autorentätigkeit für Bibliographisches Institut F. A. Brockhaus, Mannheim und Verlag Eugen Ulmer, Stuttgart
seit 06/2004	Wissenschaftlicher Mitarbeiter an der Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut und Museum der Westfälischen Wilhelms-Universität Münster (DFG-Förderung KR 2125/3-1)

Münster, 15. März 2007 ______________________________

EIDESSTATTLICHE ERKLÄRUNG

Hiermit versichere ich, dass ich die vorgelegte Dissertation selbst und ohne unerlaubte Hilfe angefertigt, alle in Anspruch genommenen Quellen und Hilfsmittel in der Dissertation angegeben habe und die Dissertation nicht bereits anderweitig als Prüfungsarbeit vorgelegen hat.

Münster, 15. März 2007 ______________________________

REMARK

REMARK TO THIS EDITION

The present volume is a reformatted but unchanged version of my original dissertation. This version has been edited in February 2015, and has been completed with the final versions of the papers constituting the PhD thesis.

Papers marked with an asterisk (*) on the **CONTENTS** page were, when the thesis was submitted, *Submitted* to the journals, where they were also published later; papers marked with two asterisks (**) were accepted for publication and *In press* in the specified journal; and the paper marked with three asterisks (***) has been *Submitted* to the *American Journal of Botany* at the moment, when the thesis was submitted, but has later been published in the specified journal.

The *Proposal to conserve the name* Pterophyllum *(Foss., Bennettitales) with a conserved type* (**CHAPTER 1**) has been adopted by the Nomenclature Committee for Fossil Plants and accepted during the Nomenclature session at the XVIII International Botanical Congress, 23-30 July 2011, Melbourne, Australia, with ‘unanimous agreement among the Committee members’ (Taxon 60: 902–905 [2011]).

Stockholm, 24 February 2015 ____________________________