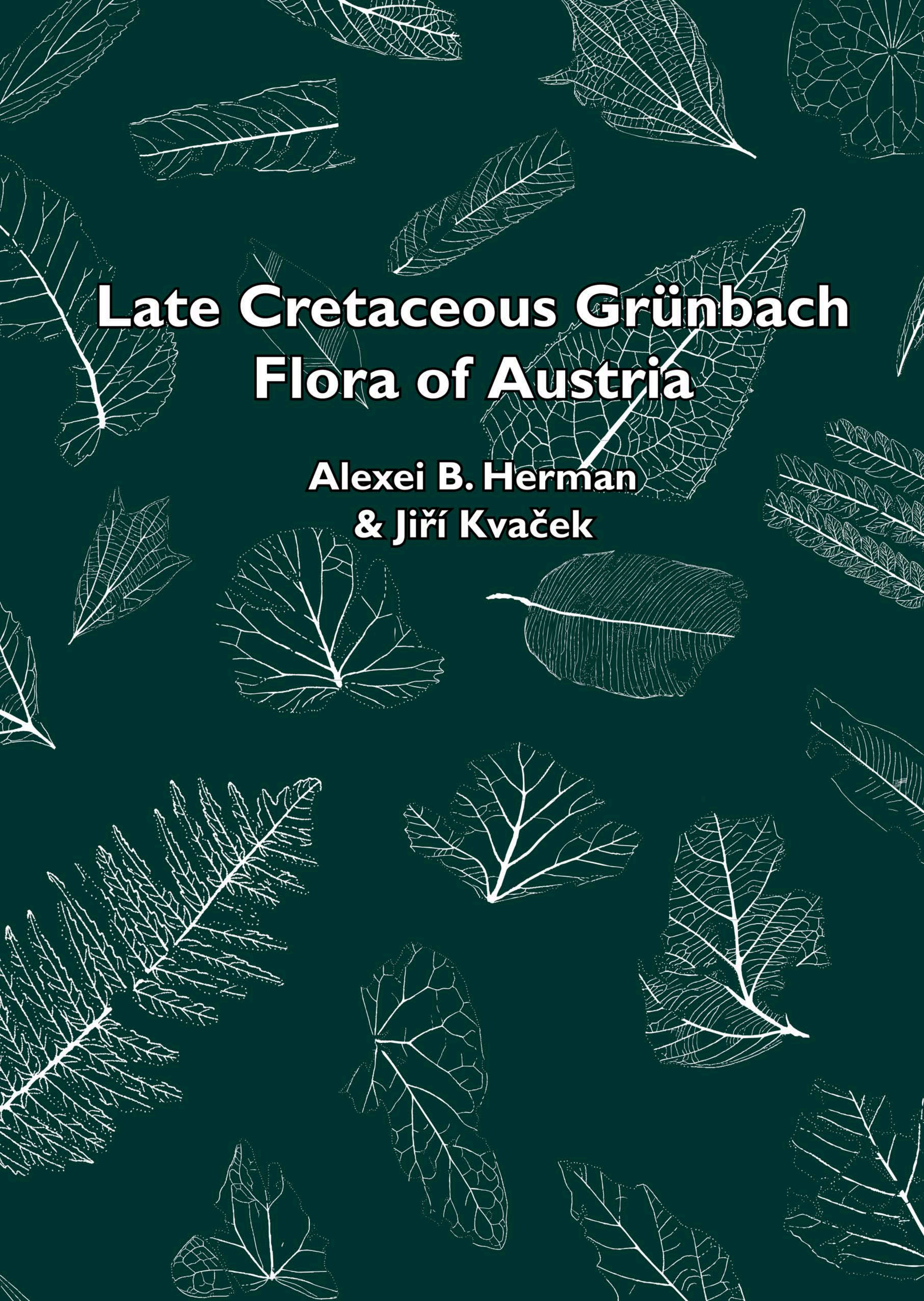

Late Cretaceous Grünbach Flora of Austria

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Late Cretaceous Grünbach Flora of Austria

by Alexei B. Herman and Jiří Kvaček

(With 61 text-figures, 1 table and 36 plates)

Abstract

The Grünbach flora coming from the Grünbach Formation (Neue Welt Basin) is comprehensively described and revised. 53 taxa are recognized and analysed based on morphological and anatomical methods. The following new names are introduced: *Cladophlebis gosauensis* J. Kvaček & Herman, nov. spec., *Gosauopteris danaeoides* J. Kvaček & Herman, nov. gen. et nov. spec., *Marsileaceaephyllum campanicum* J. Kvaček & Herman nov. spec., *Microphyllopteris austriaca* J. Kvaček & Herman, nov. spec., *Monheimia ungeri* J. Kvaček & Herman nov. spec., *Sphenopteris gruenbachiana* J. Kvaček & Herman, nov. spec., *Sphenopteris heterophylla* (Unger) J. Kvaček & Herman, comb. nov., *Sphenopteris ungeri* J. Kvaček & Herman, nov. spec., *Gruenbachia pandanoides* J. Kvaček & Herman, nov. gen. et nov. spec., *Theiaiphyllum kollmannii* Herman & J. Kvaček, nov. gen. et nov. spec., *Brasenites krasseri* Herman & J. Kvaček, nov. spec., *Celastrophyllum johannae* Herman & J. Kvaček, nov. spec., *Compositiphyllum serratum* Herman & J. Kvaček, nov. gen. et nov. spec., *Compositiphyllum ovale* (Vakhrameev) Herman & J. Kvaček, comb. nov., *Compositiphyllum retinerve* (Herman) Herman & J. Kvaček, comb. nov., *Ettingshausenia gruenbachiana* Herman & J. Kvaček, nov. spec., *Grebenkia europaea* Herman & J. Kvaček, nov. spec., *Juglandiphyllites pelagicus* (Unger) Herman & J. Kvaček, comb. nov., *Leguminosites mucronatus* Herman & J. Kvaček, nov. spec., *Menispermites ettingshausenii* Herman & J. Kvaček, nov. spec., *Menispermites summesbergeri* Herman & J. Kvaček, nov. spec., *Dicotylophyllum proteoides* (Unger) Herman & J. Kvaček, comb. nov., *Ternstroemites* (?) *neueweltensis* Herman & J. Kvaček, nov. spec., *Viburniphyllum austriacum* Herman & J. Kvaček, nov. spec., *Viburniphyllum ermanniorum* Herman & J. Kvaček, nov. spec.

The flora is compared with other similar European Late Cretaceous floras. Palaeoecological and palaeoclimatological interpretations based on the CLAMP and NRL methods are summarized.

Contents

Introduction

The Grünbach Flora comes from the Lower Campanian coal-bearing strata of the Grünbach Formation which form part of the Gosau Group in the Grünbach – Neue Welt Basin in the Eastern Calcareous Alps, Lower Austria. The coal seams of the Grünbach Formation were exploited from the second half of the 19th century until the 1960s (text-fig. 1), but mining was extremely difficult in this highly tectonised basin and was finally abandoned as uneconomic.

Numerous well-preserved plant fossils from beds accompanying the coal seams are housed at geological museums in Austria and the Czech Republic. The main collections are stored in Vienna at the Natural History Museum and in the Austrian Geological Survey. The latter one is of particular importance housing the type specimens described by UNGER (1850, 152) and ETTINGSHAUSEN (1852).

Although collected since the 19th century, this collection had never been studied monographically. A few fossil plants had been described (UNGER 1850, 1852; ETTINGSHAUSEN 1852) and some Grünbach plants were preliminarily identified and labelled in the collection by ETTINGSHAUSEN in 1879, KRASSER in 1904-1906 and KERNER-MARILAUN in 1934. However, all these descriptions and identifications were in need of revision.

The Grünbach Flora represents one of the few known Late Cretaceous antracophilous (mire) floras in the Northern Hemisphere. However, information on the Grünbach Flora published in scientific literature is very limited, and this rich, exceptionally important, well-preserved and well-collected flora is almost unknown within the palaeobotanical community. It is remarkable that VAKHRAMEEV (1991), in his review of the Jurassic and Cretaceous floras and climates of the Earth, did not list the Grünbach Flora among the Senonian floras of the European Province, whereas in his earlier book (VAKHRAMEEV et al. 1970) he only referred to finds of palms *Palmophyllum longirhachis* in the uppermost Cretaceous of Austria.

In 1999 the authors began to study the Grünbach plant fossils (HERMAN & J. KVAČEK 2000, 2002a, b; HERMAN et al. 2002; HERMAN 2004a, b; J. KVAČEK & HERMAN 2004a, b). Our research is based on a study of the existing plant fossil collections mentioned above as well as on our field collecting from spoil heap near Grünbach Village undertaken in 2001, 2003 and 2005 (text-fig. 2). This study was initiated by Dr. H. KOLLMANN of the Natural History Museum in Vienna. The present publication represents the results of our monographic investigation and description of the Grünbach Flora and is structured as follows: At the beginning of this publication we present a historical analysis of research on the Grünbach Flora, the material studied and methods used, geological setting and age of the plant-bearing beds. Then we discuss the systematic composition of the Grünbach Flora and describe the fossil plants that comprise the flora. The palaeopalynological chapter is based on data published by DRAXLER (in SUMMESBERGER 1997) and SVOBODOVÁ (HRADECKÁ et al. 2000). This is followed by a comparison of the Grünbach Flora with other European Cretaceous floras and a discussion of the palaeofloristic and phytogeographic significance of the Grünbach Flora with ecological and palaeoclimatic interpretations. Finally, we present the main conclusions of our study.

Chapter 1 Historical Analysis

Although collected from the early 19th century, the Grünbach Flora had never been studied monographically. Geological investigations of the Gosau Group in the Grünbach – Neue Welt area started early in the 19th century (BOUÉ 1833; ZITTEL 1866; SUESS 1881). The first fossil plant to be described from the Grünbach Formation (part of the Gosau Group) was *Flabellaria longirhachis* UNGER and *Geinitzia reichenbachii* (GEINITZ) HOLLICK & JEFFREY (= *Geinitzia cretacea* ENDLICHER; UNGER 1850). Two years later UNGER (1852) published illustrations of this plant. Specimens

Text-fig. 1: View of the abandoned Segen Gottes coal mine in Grünbach Village. Photo by A.B. HERMAN 2002.

Text-fig. 2: View of old coal mine spoil heap in Grünbach Village, with Schneeberg Mountain in the background. Photo by J. Kvaček 2003.

studied and depicted by Unger are kept in the Austrian Geological Survey (Geologische Bundesanstalt). Later Ettingshausen (1852) published a monograph on fossil representatives of the genus *Pandanus* in which he included pandanaceous leaves from Grünbach: *Pandanus austriacus* Ettingshausen, *P. trinervis* Ettingshausen and *P. pseudoinermis* Ettingshausen. Most of his type material is also stored in the abovementioned collection.

Several important taxa from the Grünbach Flora were described by Unger (1867): *Pecopteris zippei* Corda, *P. striata* Sternberg, *Hymenophyllites heterophyllus* Unger, *H. macrophyllus* Goeppert, *Microzamia gibba* Corda, *Cunninghamites dubius* Sternberg, *Phyllites ehrlichi* Unger, *Ph. proteoides* Unger, *Ph. reussi* Unger, and *Ph. pelagicus* Unger. At least some specimens of this material are kept at the Institute of Palaeontology, University of Vienna.

Ettingshausen (in 1879), Krasser (in 1904-1906) and Kerner-Marilaun (in 1934) preliminarily identified and labelled some fossil plants in the collection stored at the Department of Geology and Palaeontology at the Natural History Museum, Vienna. However, all these identifications needed revision.

The Grünbach flora was briefly discussed by Krasser and Kerner-Marilaun. Krasser (1906) in his short paper presented the following generic list of the Grünbach Flora based on the collection in the Natural History Museum, Vienna: *Coniopteris*, *Cladophlebis*, *Thinnfeldia*, *Danaea*, *Marattia*, *Lygodium*, *Matonia* (similar to *M. sarmentosa*), *Alsophila*, *Marsilea*, *Trapa*, *Geinitzia*, *Podocarpus*, *Cordaites* (?), *Juglandites*, *Rhamniphyllum*, *Callicarpiphyllum*, *Salix*, *Quercus*, *Ulmus*, *Grevillea*, *Banksia*, *Proteophyllum*, *Pisonia*, *Brasenia*, *Platanus*, *Palaeocassia*, *Sapindus*, *Sapindophyllum*, *Hedera*, *Cussonia*, *Viburnum*, *Pandanus*, *Arundo* (?), *Flabellaria*. He mentioned that *Alsophila*, marattiacean ferns, *Geinitzia*, *Salix*, *Sapindophyllum* and *Flabellaria* were the most abundant plants in the flora. Kerner-Marilaun (1934) discussed the climatic conditions experienced by the Grünbach Flora and included the same list as that in Krasser's publication.

In the geological monograph by Thenius (1962), the following fossil plants from the Grünbach Flora are mentioned (p. 58): marattiaceous ferns *Matonia*, gymnosperms *Geinitzia* and angiosperms, the most characteristic being *Pandanus* and "*Flabellaria*" palm leaves reflecting, according to Thenius, a tropical climate. Leaf drawings of "*Flabellaria*" *longirhachis*, *Geinitzia cretacea* and "*Credneria*" are shown on plate IV of this book. In his later publication, Thenius (1983) extended the list of genera comprising the Grünbach Flora (pages 50-52): *Flabellaria*, *Pandanus*, *Grewillea*, *Banksia*, *Proteophyllum*, *Populus*, *Quercus*, *Ulmus*, *Salix*, *Platanus*, *Viburnum*, *Hedera*, *Sapindus*, *Brasenia*, *Geinitzia*, *Danaea*, *Marattia*, *Matonia*, *Alsophila*, *Lygodium*, *Marsilea*. In this publication, there are photographs of *Pandanus* and *Flabellaria longirhachis* (text-fig. 27) as well as a reconstruction of the Grünbach vegetation made by Pap in 1980 (text-fig. 26). Berger (1966) described single specimen of a fern trunk *Neopsaronius turnovskyi* Berger from the Campanian-Maastrichtian Flysch (locality Wien-Hütteldorf). Knobloch (1977) referred to several plants (*Pandanus austriacus*, *Geinitzia cretacea)* from Grünbach. Kollmann & Summesberger (1982) also mentioned fossil plants from the Grünbach Flora in the abandoned Segen Gottes coal mine at Grünbach: *Equisetites*, *Matonia*, *Coniopteris*, *Thinnfeldia*, *Podozamites*, *Geinitzia*, *Ginkgo*, *Brasenia*, *Flabellaria* and *Pandanus*. These authors also made the following observation (Kollmann & Summesberger 1982, p. 96): "Unfortunately, the rich flora has never been described. Only Krasser has identified the material of the Museum of Natural History in Vienna. A new effort is made now by H. Walther and F. Schaarschmidt to make a scientific investigation of the beautifully preserved flora". We are not aware of any further studies on the Grünbach flora by Waltlher and Schaarschmidt.

In a discussion on the palaeoclimatic interpretation of the Grünbach – Neue Welt Basin, Summesberger (1997) suggested that presence of palms ("*Flabellaria*"), palm-like trees (e.g. "*Pandanus*") and large-leaved ferns in the Grünbach Flora reflects a warm and humid climate without a distinct winter period, whereas leaves of "*Ginkgo*", "*Platanus*", "oaks", "elm trees" and other possibly deciduous plants indicate dry land conditions in nearby regions.

Palynological samples from a measured section of the Grünbach Formation in the Segen Gottes coal mine of Grünbach, collected by Plöchinger (1961), were studied by I. Draxler (*in* Summesberger 1997). She identified 29 species of moss, lycopod, fern, gymnosperm and angiosperm spores and pollen and emphasised that the most characteristic elements of the palynoflora were pollen of the *Normapolles* group. Svobodová (*in* Hradecká et al. 2000), who studied palynological samples from the Grünbach Formation (Coal-Bearing Series) and Piesting Formation (*Inoceramus* Marl) in the surroundings of Grünbach, also mentioned the presence of prevailing triporate angiosperm pollen from the *Normapolles* group in these sediments.

A monographic description of the Grünbach Flora was initiated by Dr. H. Kollmann from the Natural History Museum in Vienna in 1999. To date, several papers and conference abstracts on this flora have been published by the present authors. In these publications we have discussed our preliminary data on taxonomic composition, palaeofloristics and palaeoclimatology of the Grünbach Flora (Herman & J. Kvaček 2000, 2002a, b; Herman et al. 2002; Herman 2004a, b), palaeoecology of the Grünbach wetland vegetation and plant communities (J. Kvaček & Herman 2004a) and monocotyledonous plants of the Grünbach Flora (J. Kvaček & Herman 2004b, 2005) such as *Lysichiton austriacus* (J. Kvaček & Herman) Bogner et al., *Pandanites trinervis* (Ettingshausen) Kvaček et Herman, *Sabalites longirhachis* (Unger) Kvaček et Herman and unnamed monocotyledon (Monocotyledon gen. et sp. indet.).

In this current publication we present the results of our monographic study of the Grünbach Flora.

Chapter 2 Material and Methods

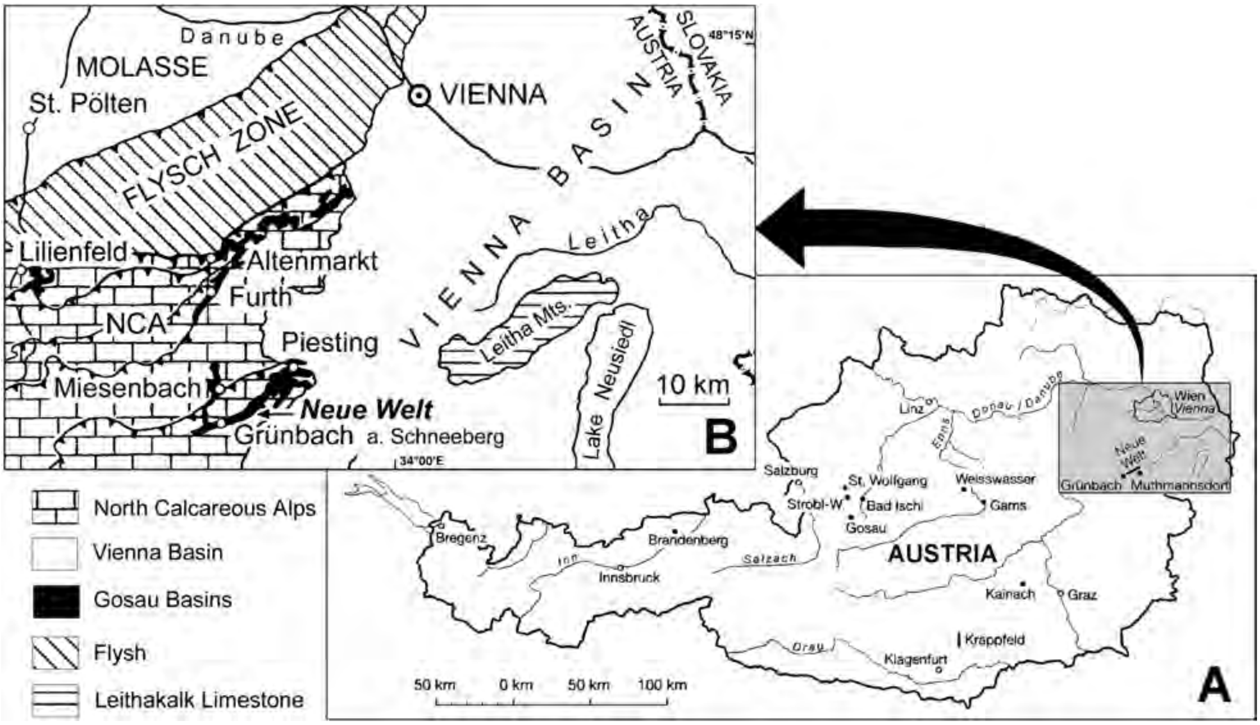
Plant fossils (over 1000 specimens) from the Grünbach Formation, described in this publication, come mostly from old coal mines and their spoil heaps from vicinity of Grünbach: Segen Gottes Schacht or Josefin Schacht in Grünbach (the majority of specimens), from Richardbau Schacht in Klaus and Unter and Ober Höflstein near Grünbach (some specimens). Smaller collections come from other localities within the Neue Welt Basin, probably quarries, in Dreistätten, Muthmannsdorf, Felbering, Frankenhof and Maiersdorf. Majority of the specimens were gathered by five collectors: Steiner, Legthaler, Wirth, Fürst, and Franke in period 1900-1910. The collections are stored in the Department of Geology and Palaeontology of the Naturhistorisches Museum Wien (Natural History Museum, Vienna; NHMW), the Geologische Bundesanstalt (the Austrian Geological Survey, Vienna; GBA), the Institute of Palaeontology (University of Vienna; IPUW), the Styrian Provincial Joanneum Museum (Graz), and the Narodni Muzeum (National Museum, Prague; NMP). Most of the material described is housed in the Department of Geology and Palaeontology of the NHMW, under the collection No. 1999B0057/....

Plant remains are represented by leaf impressions, compressions, fructifications and fossil wood. Fine details of venation and morphology are preserved in the fossil leaves and they show little evidence of long distance transport or decay prior to burial. Some of the material yields fragments of cuticles.

All descriptions of leaf morphology are based on direct observations made using a dissecting microscope. To highlight the venation of fossil leaves we used oblique lighting. Although leaf compressions appeared to be well-preserved, cuticles obtained after maceration were poor. Fragments of coalified material obtained by sampling were first treated with SCHULZE‘s reagent followed by a low concentration of potassium hydroxide. Due to the high grade of coalification and chemical change, probably caused by the high calcium carbonate content of the surrounding rock, it was only possible to recover small pieces of cuticle. In an attempt to improve the procedure, the oxidation time was increased from 3 to 48 hours. Best results were obtained if samples were treated for 10 to 24 hours in SCHULZE's reagent. The cuticles were examined using an Olympus BX 50 light microscope and photographed using an Olympus Camedia C-5050 digital camera.

Our study required photography of all the plant fossils and construction of an electronic database. After cleaning, the specimens were photographed under low angle incident light using 35 mm Ilford FP4 Plus film in a Contax 167MM SLR camera with a Zeiss S-Planar T* 2.8/60 macro lens, and black and white prints (12.5 x 20 or 20 x 25 cm) were made. Leaf drawings were made from some of the photographs. First, the leaf outlines and venation were drawn directly on the photographs, and then the photographic image was bleached away using an aqueous solution of potassium iodide and iodine. Afterwards, the bleached image was conventionally fixed leaving an ink drawing that was used for subsequent study. Photographs and ink drawings of fossil plants were scanned using Epson 1670 scanner, saved on CDs and processed using Adobe Photoshop 7.0 software. Some specimens were photographed using an Olympus Camedia C-5050 digital camera.

The electronic database created using Apple Works 6.0 software now comprises 1219 records. They include information on localities, plant taxonomy and nomenclature (generic and specific names, author(s), previous identification) as well as collection information (drawer No, block No and specimen No) and reference to photographic image(s) (film and frame numbers) and line drawing(s).



Text-fig. 3: Sketch map of the Austrian occurrences of the Gosau Group (A) (Strobl.-W. – Strobl-Weissenbach) (after Summesberger et al., 2000) and position of the Grünbach – Neue Welt Basin in the Eastern Alps, Austria (B) (simplified from Summesberger 1997).

Methods of palaeoclimatic analysis of the flora are described in Chapter 9 of this publication.

Chapter 3 Geological setting and age

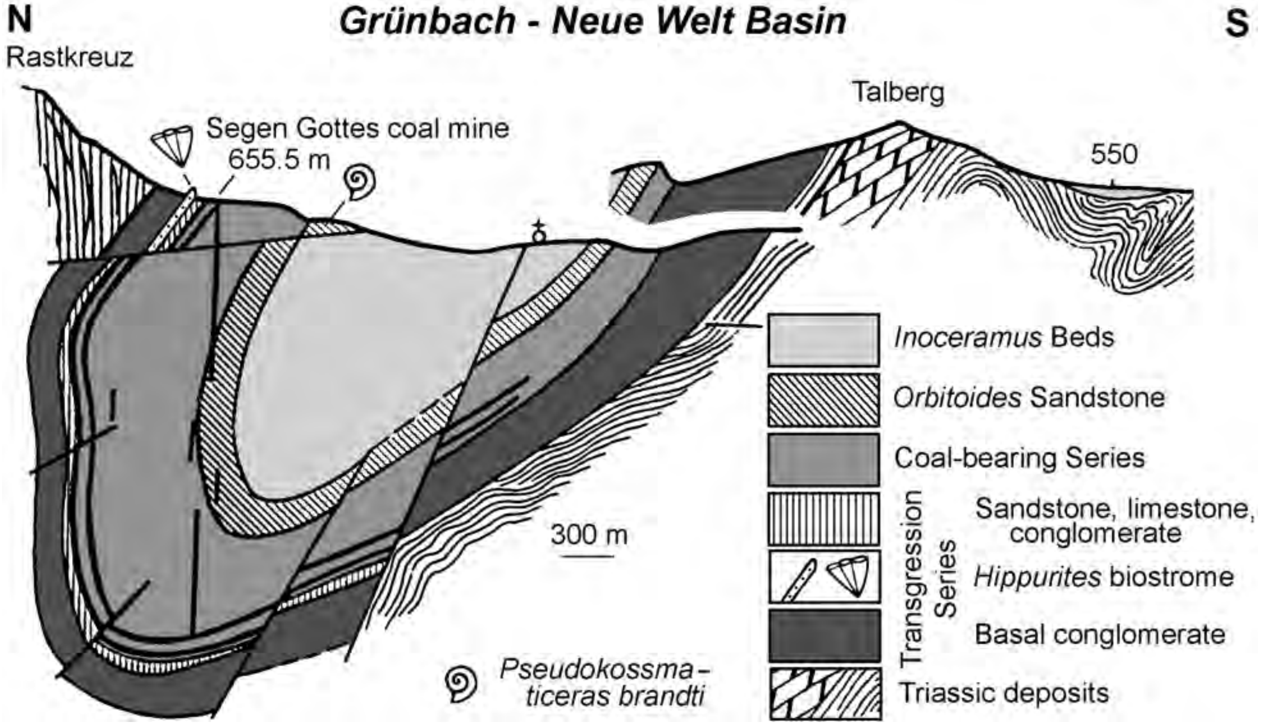
The Grünbach Flora comes from the Grünbach Formation forming part of the Gosau Group in the Grünbach – Neue Welt Basin in the Eastern Calcareous Alps, Lower Austria. This group derives its name from the village of Gosau in Upper Austria. The Upper Cretaceous to Palaeogene Gosau Group unconformably overlies folded and faulted Permian to Lower Cretaceous rocks. Numerous Gosau basins, widespread in the Austrian territory (text-fig. 3A), are filled by predominantly clastic sediments of the synorogenic Gosau Group which represents a distinct sedimentary cycle (Suess 1881, Kühn 1947, Plöchinger 1961, Summesberger 1997; Summesberger et al. 2000, 2002). The rich shallow-marine fauna of the Campanian-Maastrichtian part of the Gosau Group belongs to the Theian Realm (Kollmann 2000).

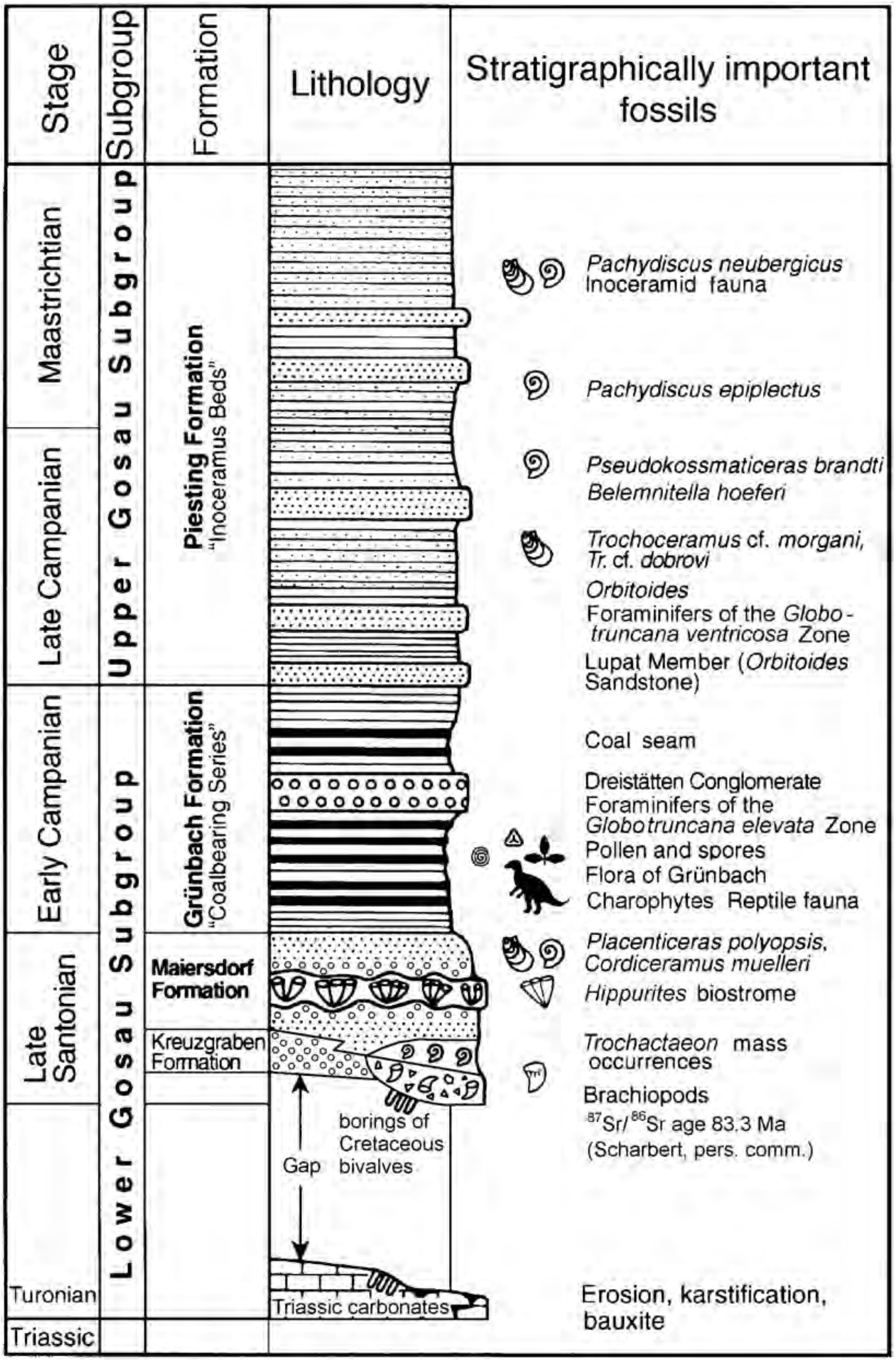
The Grünbach – Neue Welt Basin (text-fig. 3B) is one of the largest Gosau basins. It represents a syncline (Grünbach Syncline) (text-fig. 4) with an overturned northwest limb (Plöchinger 1961). The Brezova Series in the Little Carpathians (Slovakia) could denote the emerged north-eastern end of the Grünbach – Neue Welt Basin (Summesberger 1997). The predominantly terrigenous clastic infill of the basin (Gosau Group) consists of six lithostratigraphic units of Late Santonian to Eocene age (Summesberger 1997; Summesberger et al. 2002): the Kreuzgraben Formation (Upper Santonian), Maiersdorf Formation (Upper Santonian), Grünbach Formation (Lower Campanian), Piesting Formation (Upper Campanian – Maastrichtian), Zweiersdorf Formation (Danian – Paleocene) and Willendorf Formation (Eocene). The three formations of Late Santonian to Maastrichtian age, with a combined thickness of several hundred metres, are discussed below (text-fig. 5).

Maiersdorf Formation ("Transgression Series" according to Plöchinger 1961). This consists of conglomerates, breccias, sandstones, limestones and marls with rudist biostromes, gastropod accumulations (*Nerinea*, *Trochactaeon*) and brachiopod limestones. Although palaeontological data from these deposits are scarce, the Late Santonian age of the Maiersdorf Formation is based on finds of *Hippurites* (rudist biostrome near Grünbach) as well as *Placenticeras polyopsis* (Dujardin) and *Cordiceramus muelleri* Petrascheck (Plöchinger 1961, Summesberger et al. 2000, 2002). A poorly preserved nannofossil assemblage from the brachiopod limestone in the Piesting S section suggests nannofossil standard zone CC16-17 (*Marthasterites furcatus*, *Calculites* cf. *obscurus*) of a (late) Santonian to earliest Campanian age (Summesberger et al. 2002). This age is corroborated by isotope dating of brachiopod shells (Kollmann et al. 2000; Summesberger et al. 2002): the Sr^{87}/Sr^{86} data indicate an age of 83.3±0.5 Ma (S. Scharbert unpublished data). Strontium isotope study of rudists in the Grünbach area provides ages of 84.0 Ma and 84.8 Ma (Steuber 2004). The sediments of the Maiersdorf Formation reflect a Late Santonian marine transgression in the Grünbach – Neue Welt – Piesting area providing evidence of fully marine, shallow water conditions (Summesberger et al. 2002).

Grünbach Formation ("kohleführende Serie" or "Coal-bearing Series" according to Plöchinger1961). This is represented by interbedded coal seams and freshwater/nearshore marine clastic sediments (conglomerates, sandstones, siltstones and silty clays) (Summesberger et al. 2000, 2002). The coal seams of the Grünbach Formation were exploited from the second half of the 19th century until the 1960s (Text-figs 1, 2). According to Plöchinger (1961), there are at least eight coal seams in the Grünbach Formation of Grünbach interbedding with silty clays containing numerous plant fossils (text-fig. 6). Foraminifers and calcareous nannofossils are rare, probably due to brackish water depositional conditions. Foraminifers from the Grünbach Formation at Maiersdorf belong to the *Globotruncana elevata* Zone (Lower Campanian), whilst nannofossil association can be assigned to the Campanian UC 15 Zone (Hradecká et al. 2000). Draxler (*in* Summesberger 1997) studied palynological samples from a measured section of the

Text-fig. 4: Cross-section through the syncline of the Grünbach – Neue Welt Basin (after Plöchinger 1961).





Text-fig. 5: Section of the Gosau Group in the Grünbach – Neue Welt Basin in the Eastern Alps, Austria (simplified from Summesberger & al. 2000) and the stratigraphic position of the plant-bearing beds of the Grünbach Flora.

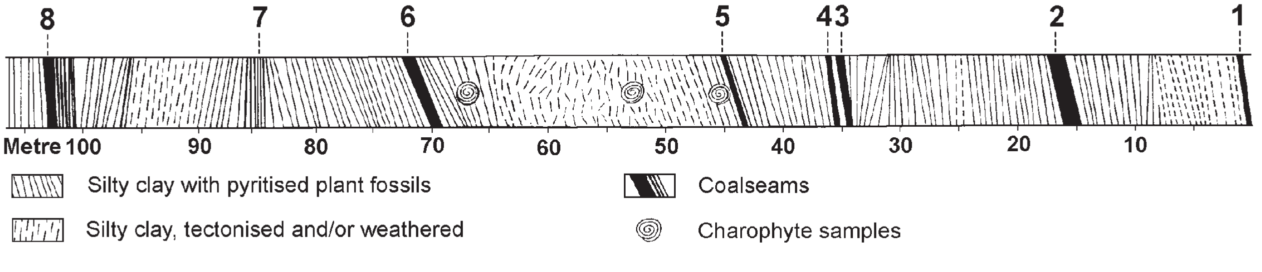
Grünbach Formation in the Segen Gottes coal mine of Grünbach (text-fig. 6) and identified 29 species of moss, lycopod, fern, gymnosperm and angiosperm spores and pollen, noting that the most characteristic elements of the palynoflora were pollen of the *Normapolles* group. A rich reptile fauna is also known from this formation at Muthmannsdorf where carnosaur, iguanodon, pterosaur, scelidosaur, crocodile and turtle remains have been found (Bunzel 1871-1873, Seeley 1881, Buffetaut 1979, Wellnhofer 1980, Summesberger 1997).

The Grünbach Formation reflects prevailing alluvial, lacustrine to brackish water depositional environments with possible rare marine transgressions. The dominating palaeogeography during accumulation of the plant-bearing deposits of the Grünbach Formation is that of a large island of unknown relief, at least temporarily connected to the continent. Coal formation was common in the swampy, low relief basin. Terrestrial freshwater swamps and shallow water sediments indicate a deltaic plain under warm and humid climate conditions. This was inhabited by rich vegetation and a reptile fauna including dinosaurs, pterosaurs and crocodiles.

Piesting Formation ("Inoceramenschichten", "Inoceramenmergel" or "*Inoceramus* Beds" according to Plöchinger 1961 and Summesberger 1997). This consists predominantly of silty to sandy marls, marly sandstones, sandstones and siltstones with marine fossils of Late Campanian and Maastrichtian age (Summesberger et al. 2000, 2002). Foraminifers from the Piesting Formation at Grünbach can be attributed to the *Globotruncana ventricosa* Zone (lower part of the Upper Campanian). However, the majority of the Piesting Formation yields Late Campanian – Maastrichtian foraminifers (Hradecká et al. 2000). Large *Orbitoides* foraminifers are very common in the so-called *Orbitoides* Sandstone ("Orbitoidensandstein", originally "Orbituliten Sandstein": Summesberger et al. 2002) in the lower part of the formation. Nannofossil associations from the Piesting Formation belong to the UC 16, UC 17 and UC 18- ?UC 19 Zones which characterise the Campanian – Lower Maastrichtian stratigraphic interval (Hradecká et al. 2000). The Late Campanian ammonite *Pseudokossmaticeras brandti* (Redtenbachter) occurs at Grünbach (Plöchinger 1961) (text-fig. 5), the early Maastrichtian *Pachydiscus epiplectus* (Redtenbachter) at Muthmannsdorf (Summesberger 1997; Summesberger et al. 2002), and the late Campanian belemnite *Belemnitella hoeferi* (Schloenbach) at Grünbach (Christensen1998). Triporate angiosperm pollen of the *Normapolles* group allows Hradecká et al. (2000) to assign some samples from the Piesting Formation near Grünbach to the Upper Campanian.

A rich fauna recently discovered in the Piesting Formation comes from two closely situated outcrops belonging to the type section of the formation. The outcrop at the road cut south of Piesting, which represents the lower part of the section, yields *Trochoceramus* cf. *morgani* and *T.* (?) cf. *dobrovi*, proving an uppermost Campanian (or uppermost Campanian – lowermost Maastrichtian) age (Tröger et al. 2000, 2001), and chron 32N according to palaeomagnetic investigations (Summesberger et al. 2002). The second

Text-fig. 6: Section through the Grünbach Formation ("Coal-bearing Series") of Grünbach showing coal seams, palynological samples taken by Plöchinger (numbers) and samples with charophytes (after Plöchinger 1961).



outcrop from the higher part of the section at Piesting sports field contains diverse Lower Maastrichtian inoceramids; the ammonite *Pachydiscus neubergicus* from the same locality indicates Lower to lower Upper Maastrichtian (Tröger et al. 2000, 2001, Kollmann et al. 2000; Summesberger et al. 2002). The poorly preserved nannoflora is considered to belong to the standard zone CC 24 (early Maastrichtian). A palaeomagnetic study of the section suggests that it may correlate with Chron 31R just above the Campanian-Maastrichtian boundary (Tröger et al. 2000, Summesberger et al. 2002). The sediments of the Piesting Formation provide evidence of a fully marine, shelf to deeper marine depositional environment (Summesberger et al. 2002).

The Early Campanian age of the plant-bearing beds of the Grünbach Flora (text-fig. 5) is therefore based on foraminifers, spores and pollen from the Grünbach Formation and on the correlation of these deposits with the underlying Maiersdorf and the overlying Piesting formations which contain stratigraphically important marine fossils.

Chapter 4 Systematic Composition

The Grünbach Flora has a relatively large number of plant megafossil taxa, with 53 species identified to date, representing Equisetopsida (1 species), Polypodiopsida (11 species), Cycadopsida (1 species), Pinopsida (4 species), Liliopsida (6 species), and Magnoliopsida (30 species). The most characteristic representatives of the Grünbach Flora are shown in text-figs 7 and 8.

In addition to the above-mentioned groups of fossil plants, which will be described in detail in the following chapters (Text-figs 9 to 53 and Plates 1 to 36), several other fossil remains are represented including poorly preserved impressions of unknown thalli (Herman & J. Kvaček 2002a), charophytes (Plöchinger 1961) and unidentified seeds, which are not described in this study. Palynomorphs are described briefly in a separate chapter.

From the available material we have identified the following macrofossils:

Equisetopsida
Equisetites sp.
Polypodiopsida
Gosauopteris danaeoides J. Kvaček & Herman, nov. gen. et nov. spec.
Monheimia ungeri J. Kvaček & Herman, nov. spec.
Microphyllopteris austriaca J. Kvaček & Herman, nov. spec.
Coniopteris sp.
Cladophlebis gosauensis J. Kvaček & Herman, nov. spec.
Raphaelia lobifolia (Corda in Reuss) Knobloch
Sphenopteris gruenbachiana J. Kvaček & Herman, nov. spec.
Sphenopteris heterophylla (Unger) J. Kvaček & Herman, comb. nov.
Sphenopteris ungeri J. Kvaček & Herman, nov. spec.

Text-fig. 7: Floral picture of the Grünbach Flora, Polypodiopsida: A, B – *Cladophlebis gosauensis* J. Kvaček & Herman, nov. spec., C, D – *Sphenopteris gruenbachiana* J. Kvaček & Herman, nov. spec., E, F – *Microphyllopteris austriaca* J. Kvaček & Herman, nov. spec., G – *Raphaelia lobifolia* (Corda in Reuss) Knobloch, H – *Marsileaceaephyllum campanicum* J. Kvaček & Herman, nov. spec., I, J – *Gosauopteris danaeoides* J. Kvaček & Herman, nov. gen. et nov. spec., K – *Sphenopteris ungeri* J. Kvaček & Herman, nov. spec., L – *Monheimia ungeri* J. Kvaček & Herman, nov. spec.; Cycadopsida: M – *Nilsonia* cf. *holyi* J. Kvaček; Pinopsida: N – *Podozamites* cf. *lanceolatus* (Lindley & Hutton) Harris, O – *Geinitzia formosa* Heer, NHMW 1970/1396/1648, P – *Geinitzia reichenbachii* (Geinitz) Hollick & Jeffrey, NHMW 1970/1396/1800, Q – *Pagiophyllum* sp., GBA 2006/64/39; Liliopsida: R, S, T – *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, U – *Sabalites longirhachis* (Unger) J. Kvaček & Herman, V – *Lysichiton austriacus* (J. Kvaček & Herman) Bogner et al., W, X, Y, Z – *Theiaiphyllum kollmannii* Herman & J. Kvaček, nov. gen. et nov. spec.; Grünbach (scale bar represents 1 cm); for specimen numbers, except O and P, see text-figures 9 to 24.

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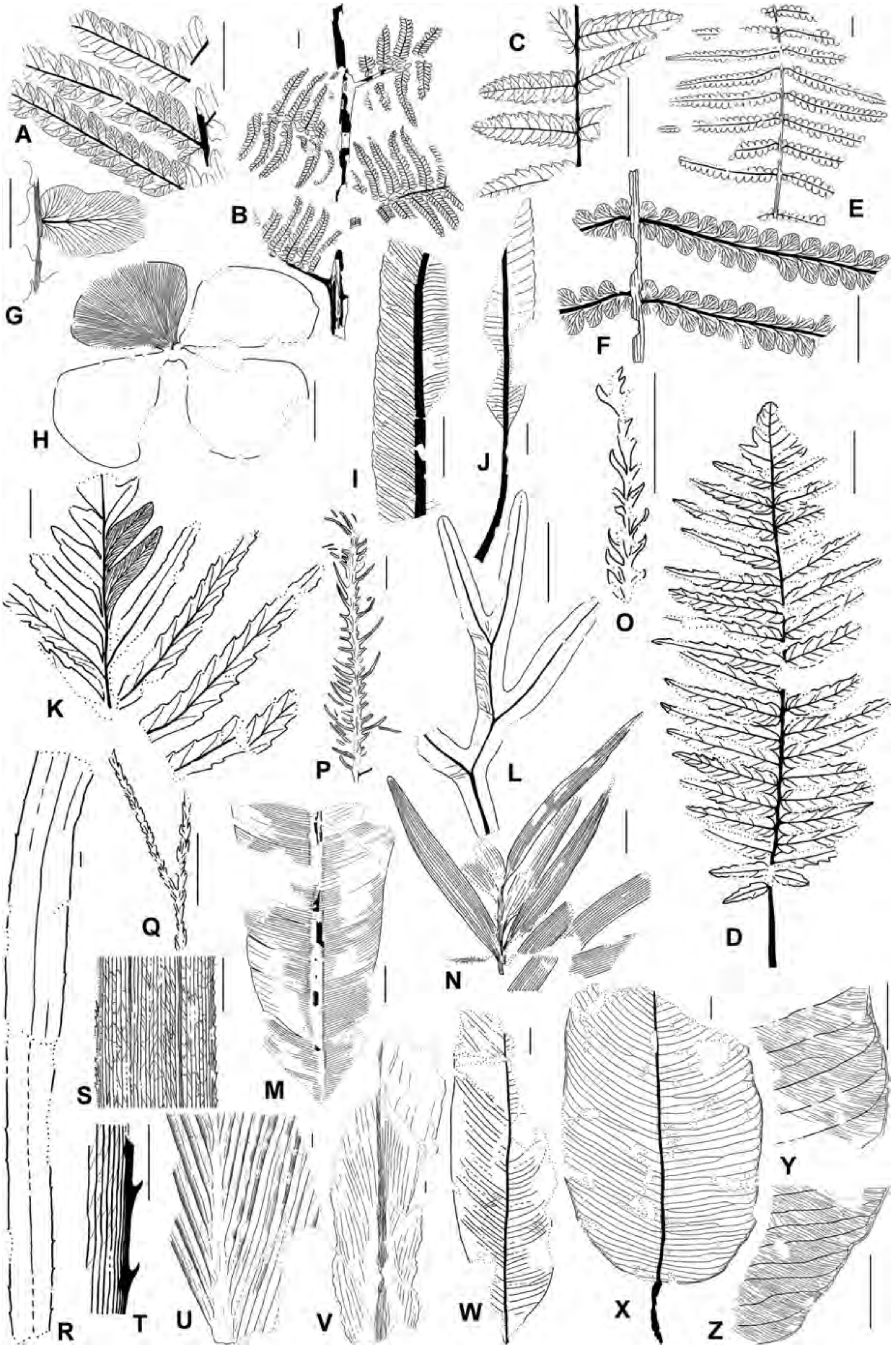
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Sphenopteris sp.
Marsileaceaephyllum campanicum J. Kvaček & Herman nov. spec.
Cycadopsida
Nilsonia cf. *holyi* J. Kvaček
Pinopsida
Geinitzia formosa Heer
Geinitzia reichenbachii (Geinitz) Hollick & Jeffrey
Pagiophyllum sp.
Podozamites cf. *lanceolatus* (Lindley & Hutton) Harris
Liliopsida
Lysichiton austriacus (J. Kvaček & Herman) Bogner et al.
Pandanites trinervis (Ettingshausen) J. Kvaček & Herman
Gruenbachia pandanoides J. Kvaček & Herman, nov. gen. et nov. spec.
Sabalites longirhachis (Unger) J. Kvaček & Herman
Theiaiphyllum kollmannii Herman & J. Kvaček, nov. gen. et nov. spec.
Monocotyledon gen. & sp. indet.
Magnoliopsida
Brasenites krasseri Herman & J. Kvaček, nov. spec.
Celastrophyllum johannae Herman & J. Kvaček, nov. spec.
Celastrophyllum sp.
Compositiphyllum serratum Herman & J. Kvaček, gen. et nov. spec.
Debeya insignis (Hosius & Marck) Knobloch
Ettingshausenia gruenbachiana Herman & J. Kvaček, nov. spec.
Ettingshausenia cf. *laevis* (Velenovský) J. Kvaček & Váchová
Ettingshausenia sp.
Grebenkia europaea Herman & J. Kvaček, nov. spec.
Juglandiphyllites pelagicus (Unger) Herman & J. Kvaček, comb. nov.
Leguminosites mucronatus Herman & J. Kvaček, nov. spec.
Menispermites ettingshausenii Herman & J. Kvaček, nov. spec.
Menispermites summesbergeri Herman & J. Kvaček, nov. spec.
Myricophyllum serratum (Velenovský) Velenovský
Myricophyllum sp. cf. *M. zenkeri* (Ettingshausen) Heer
Quereuxia angulata (Newberry) Kryshtofovich
Rogersia sp.
Ternstroemites (?) *neueweltensis* Herman & J. Kvaček, nov. spec.
Viburniphyllum austriacum Herman & J. Kvaček, nov. spec.
Viburniphyllum ermanniorum Herman & J. Kvaček, nov. spec.
Dicotylophyllum proteoides (Unger) Herman & J. Kvaček, comb. nov.
Dicotylophyllum sp. 1
Dicotylophyllum sp. 2
Dicotylophyllum sp. 3
Dicotylophyllum sp. 4
Dicotylophyllum sp. 5
Dicotylophyllum sp. 6

Text-fig. 8: Floral picture of the Grünbach Flora, Magnoliopsida: A – *Menispermites ettingshausenii* Herman & J. Kvaček, nov. spec., B – *Menispermites summesbergeri* Herman & J. Kvaček, nov. spec., C, D – *Ettingshausenia gruenbachiana* Herman & J. Kvaček, nov. spec., E – *Ettingshausenia* cf. *laevis* (Velenovský) J. Kvaček & Váchová, F – *Ettingshausenia* sp., G – *Quereuxia angulata* (Newberry) Kryshtofovich, NHMW 1999B0057/0315, H – *Dicotylophyllum* sp. 7, I, J, K – *Dicotylophyllum proteoides* (Unger) Herman & J. Kvaček, comb. nov., L, M – *Leguminosites mucronatus* Herman & J. Kvaček, nov. spec., N – *Celastrophyllum* sp., O, P – *Juglandiphyllites pelagicus* (Unger) Herman & J. Kvaček, comb. nov., Q – *Debeya insignis* (Hosius & Marck) Knobloch, R – *Myricophyllum* sp. cf. *M. zenkeri* (Ettingshausen) Němejc, S – *Myricophyllum serratum* (Velenovský) Velenovský, T – *Brasenites krasseri* Herman & J. Kvaček, nov. spec., U – *Dicotylophyllum* sp. 4, V – *Dicotylophyllum* sp. 3, W – *Ternstroemites* (?) *neueweltensis* Herman & J. Kvaček, nov. spec., X, Y – cf. *Dicotylophyllum* sp. 7, Z – *Rogersia* sp., AA, AB – *Viburniphyllum ermanniorum* Herman & J. Kvaček, nov. spec., AC – *Viburniphyllum austriacum* Herman & J. Kvaček, nov. spec., AD – *Grebenkia europaea* Herman & J. Kvaček, nov. spec., AE – *Dicotylophyllum* sp. 2, AF – *Dicotylophyllum* sp. 5, AG – *Dicotylophyllum* sp. 1, AH – *Compositiphyllum serratum* Herman & J. Kvaček, nov. gen. et nov. spec., AI – *Juglandiphyllites pelagicus* (Unger) Herman & J. Kvaček, comb. nov. , AJ – *Dicotylophyllum* sp. 6, AK – *Celastrophyllum johannae* Herman & J. Kvaček, nov. spec.; Grünbach (scale bar represents 1 cm); for specimen numbers, except G, see text-figures 25 to 53.

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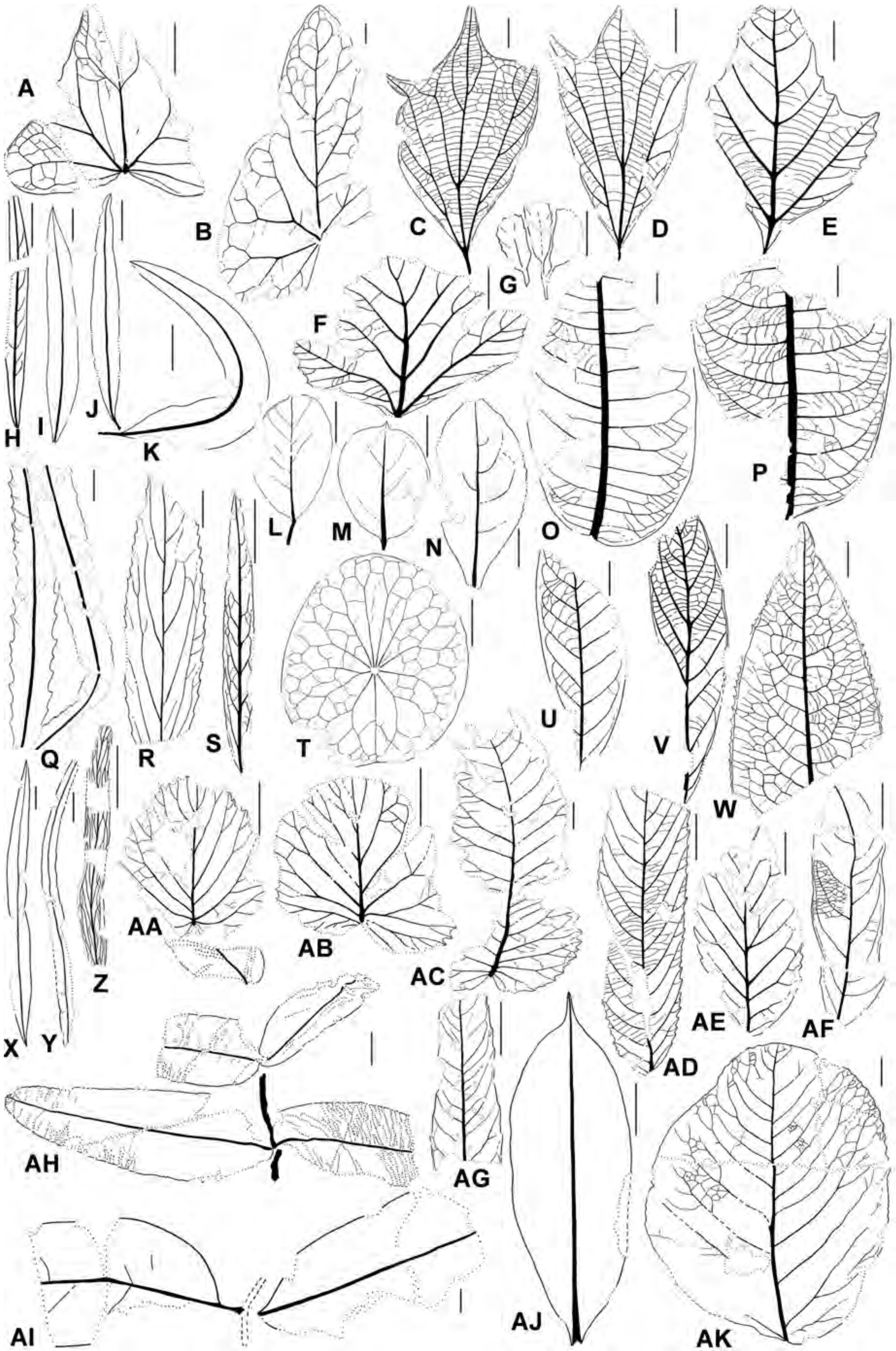
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Dicotylophyllum sp. 7
Ceratoxylon sp.

Equisetopsida. Horsetails are rare and represented by a single specimen assigned to the genus *Equisetites* Sternberg.

Polypodiopsida. Ferns are represented by 11 species (text-fig. 7, A-L) showing certain affinities to the families ?Marattiaceae, Matoniaceae, ?Schizaeaceae, Gleicheniaceae, Dicksoniacae, and Marsileaceae. Ferns are assigned to eight genera *Gosauopteris* J. Kvaček & Herman, nov. gen., *Monheimia* Debey & Ettingshausen, *Microphyllopteris* Arber, *Coniopteris* Brongniart, *Cladophlebis* Brongniart, *Raphaelia* Debey & Ettingshausen, *Sphenopteris* (Brongniart) Sternberg, and *Marsileaceaephyllum* Nagalingum. *Coniopteris* and *Monheimia* possess reproductive structures, but only *Monheimia* has preserved spores *in situ*. Spores of the dispersed genus *Matonisporites* and the arrangement of sori indicate well-pronounced affinities of *Monheimia* with Matoniaceae. Other fern remains are present only in the sterile state and are mostly classified in terms of morphogenera.

Cycadopsida. Cycads are represented only by the genus *Nilsonia* Brongniart (text-fig. 7, M). Its presence in a European Campanian flora is surprising and is considered to be unique. The closest records of *Nilsonia* in the Campanian-Maastrichtian are found in Canada (Bell 1957), Alaska (Hollick 1930), Northeastern Russia (Herman 1991, 1999, 2004c) and Sakhalin Island (Krassilov 1979).

Pinopsida. Conifers comprising four species are represented by two main groups: Geinitziaceae and *Podozamites* Group. A single taxon, *Podozamites* C. Braun in Münster (text-fig. 7, N), is assigned to the *Podozamites* Group. It is recorded by one unique, but well-preserved specimen representing a relatively late occurrence for the genus. Two species of the genus *Geinitzia* Endlicher are assigned to the family Geinitziaceae (text-fig. 7, O, P). A few other sterile conifer twigs are described as the morphogenus *Pagiophyllum* Heer (text-fig. 7, Q).

Liliopsida. Monocotyledons are represented by six genera. Five genera are based on sterile foliage and one on reproductive structure. Three taxa of sterile foliage bear significant diagnostic characters and can be identified with recent families and even genera. The fossil species of the recent genus *Lysichiton* Schott (text-fig. 7, V) represents the family Araceae. Genera *Pandanites* Tuszon (text-fig. 7, R, S, T) based on leaves and *Gruenbachia* J. Kvaček & Herman, nov. gen. based on reproductive structures bear unequivocal characters of the Pandanaceae. The morphogenus *Sabalites* Saporta (text-fig. 7, U) represents a member of the Arecaceae. The remaining two taxa, one of which is described as a new genus *Theiaiphyllum* Herman & J Kvaček, nov. gen., (text-fig. 7, W, X, Y, Z) are of unknown systematic affinity.

Magnoliopsida. Dicotyledonous angiosperms are mostly recorded as leaf impressions or compressions (text-fig. 8). Thirty species were identified. They belong to genera *Brasenites* Wang & Dilcher, *Celastrophyllum* Goeppert**,** *Compositiphyllum* Herman & J. Kvaček nov. gen., *Debeya* Miquel, *Ettingshausenia* Stiehler, *Grebenkia* Lebedev, *Juglandiphyllites* Boulter & Z. Kvaček, *Leguminosites* Bowerbank, *Menispermites* Lesquereux, *Myricophyllum* Saporta, *Quereuxia* Kryshtofovich, *Rogersia* Fontaine, *Ternstroemites* E.W. Berry, *Viburniphyllum* Nathorst, *Dicotylophyllum* Saporta, and *Ceratoxylon* Velenovský & Viniklář. They are assigned to 18 genera, representing 17 genera of sterile foliage and one reproductive structure. There are only five genera of dicots which show enough characters to be compared with recent natural taxa of the suprageneric level. The genus *Ettingshausenia* Stiehler carries unequivocal characters of the family Platanaceae. The leaf impression *Celastrophyllum johannae* can be assigned on the basis of its cuticle to the hamamelid clade. Venation of the genus *Juglandiphyllites* resembles some juglandoids. This assumption is supported by high representation of *Normapolles* pollen in the sediment (Draxler in Summesberger 1997), which is usually considered to represent pollen of ancestors of the family Juglandaceae. The modern affinity of the genus *Brasenites*, comprising sterile foliage of an aquatic plant, is probably close to the modern genus *Brasenia* of the Cabombaceae within the Nymphales (Wang & Dilcher 2006). The genus *Quereuxia* Kryshtofovich is comparable to the family Trapaceae (e.g. McIver & Basinger 1993). Angiosperm fructification of unknown origin is assigned to the genus *Ceratoxylon*.

Approach to identification of fossil angiosperm leaves. The attribution of Cretaceous angiosperms (mostly leaf remains) to extant genera or higher taxa long prevailed in palaeobotany, and partially this tradition is still used. The selection of an appropriate living equivalent on the basis of leaf macromorphology is not a very difficult task because of the huge diversity of leaves in the modern angiosperms. However, angiosperms that are fairly distant from a systematic point of view may have very similar leaves. Therefore, the determination of fossil leaves within the scope of the system of the extant angiosperms is very subjective and may lead to misinterpretation and significant loss of information (Krassilov 1979). Moreover, this approach has resulted in the mistaken assumptions that most angiosperms in the Cretaceous were represented by extant genera and, therefore, had long evolved, and that palaeobotanical data were nearly useless for revealing the phylogeny of these plants. Recent studies (primarily those of the reproductive structures of Cretaceous angiosperms) have shown that Cretaceous angiosperms were very peculiar, differed in most cases significantly from modern plants, and actually reflect the early evolution of this group.

The validity of the assignment of Cretaceous fossil leaves to extant genera or higher taxa was questioned as early as the end of the 19th century. When leaf remains that resembled leaves of extant plants were only loosely determined (due to observed differences, unusual combination of characters, or insufficient preservation of fossil material), the endings *-phyllum* or *-ites* were added to the most relevant modern generic name. A genus of this type was believed to correspond to several extant genera, or an extant family, or even an order. Although the endings *-phyllum* and *-ites* imply that the fossil plants in question have certain differences from their extant analogues and, therefore, the application of such names is unequivocally better than the assignment of Cretaceous fossils directly to extant taxa, the problem has persisted: such genera are frequently regarded as closely related to the relevant extant genera and are often placed together with them in higher taxa in the system of modern angiosperms.

However, numerous examples show that the assignment of Cretaceous leaves to modern genera and families is erroneous or, at least, needs more support. According to the evocative metaphor of Meyen, we operate like the man who found a nut on the railway line and claimed to have found a steam locomotive: in fact an assignment of fossil leaf to a modern genus or family implies (as a rule, unjustifiably) that all other, usually unknown, organs of the fossil plant are the same as in living representatives of this taxon. However, as a rule we lack any proof of such implication.

It is clear that for the Cretaceous angiospermous leaves we need to use a morphological classification of leaves that is independent from the system of modern plants. This morphological system should be based on observed features of leaf morphology rather than on weak and often erroneous hypotheses about the morphology of the whole plant. Krassilov (1979, p. 43) noticed that “only an inductive system with clear diagnoses of the taxa (each taxon includes leaves of a definite morphological type rather than those resembling leaves of a particular extant genus) and consistent application of the principle of priority to names can provide a common language and reduce the loss of information.” Such a classification does not depend on the system of modem plants: there is no unambiguous correspondence between taxa of the morphological system and taxa that were established to describe whole plants. To put it differently, a genus of the morphological system may occur in more than one genus (or even family) of whole plants and, vice versa; the latter may be supplied by leaves belonging to more than one genus of the morphological system.

The inclusion of dispersed fossil leaves of a particular morphotype in one genus, as an alternative for traditional assignment of fossil angiosperm leaves to taxa of modern plants on the basis of superficial resemblance, seems to be the most effective key for the identification of Cretaceous angiosperm leaves. As Meyen (1987, p. 252) noticed, "... the main goal of this system is to choose leaves of plants that are worth comparing with the fossils being studied." This approach allows a palaeobotanist to trace the appearance of a particular leaf morphotype, its geological history, and proportions of particular leaf morphotypes within certain time intervals and certain fossil floras.

Chapter 5 Systematic Palaeontology

Equisetopsida
Equisetales
Equisetaceae

Genus *Equisetites* Sternberg, 1833

Type: *Equisetites muensteri* Sternberg 1833, p. 43, pl. 16, figs 1-5 (for details see J. Kvaček & Straková 1997).

Equisetites sp.

(pl. 1, figs 9, 10)

2002a *Equisetites* sp. Herman & J. Kvaček, p. 7, pl. 1, fig. 4.

Material: NHMW 1999B0057/0252.

Occurrence: Grünbach am Schneeberg, Austria.

Description: The only specimen available (pl. 1, figs 9, 10) represents a compressed stem 135 mm long and 28 mm wide. The axis shows rather irregular longitudinal grooves (approximately 10 per 1 cm), but no ridges. There are two nodes preserved. The central, better-preserved node exhibits numerous rounded scars. It is estimated there were originally about 30 scars per node. The scars are 2 mm in diameter (pl. 1, fig. 10). Another node is situated at the end of the fragment. The only complete internode between the mentioned nodes is straight, slightly contracted at both ends measuring 67 mm in length.

Comparison and discussion: We assign the present material to the genus *Equisetites* Sternberg in accordance with Watson & Batten (1990) and contrary to Harris (1961) assuming that the fossil material does not correspond with all the necessary diagnostic characters of the recent genus *Equisetum*, particularly with regard to reproductive organs.

Considering the incompleteness of the material we could not assign the fossil to any known species. We were even unable to determine if the scars in the nodal area represent places of attachments of leaves or branches.

The present material is larger than *Equisetites* sp. from the Senonian of South Bohemia (Němejc & Z. Kvaček 1972, pl. 1, figs 2-4, 9, 12). That differs from *Equisetites* sp. in having a much smaller diameter main axis and in having teeth in the nodal area. *E. lyellii* (Mantell) Seward (Watson & Batten 1990, Text-figs 15-34) differs from the present material also in being much smaller in size. *Equisetites burchardii* Dunker (Watson & Batten 1990, Text-figs 1-6) differs from the present material in having whorls of eight leaves and in size of the axis. *Equisetum arcticum* Heer from the Palaeogene of Spitzbergen (Heer 1870) and *Equisetum fluviatoides* McIver & Basinger from the Palaeocene of Saskatchewan, Canada (McIver & Basinger 1993) are smaller and differs from *Equisetites* sp. in having well-pronounced ridges on the axes.

Polypodiopsida
? Maratiales
? Marattiaceae

Genus *Gosauopteris*
J. Kvaček & Herman, nov. gen.

Type: *Gosauopteris danaeoides* J. Kvaček & Herman, nov. spec.

Diagnosis: Leaves – (fronds or pinnae) simple, serrate, with long, robust and basally expanded petiole. Venation pinnate with regularly distributed lateral veins. Tertiary veins forming irregular reticulum.

Etymology: Derived from a name of the Gosau Group.

Comparison and discussion: The genus *Gosauopteris* is similar to some species of the extant genus *Danaea* Sm. (Marattiaceae), particularly to *D. simplicifolia* Rudge and *D. carrillensis* Christ, which also have entire lamina with a long petiole expanded at its base (Tryon & Tryon 1982). Venation pattern of *Gosauopteris* is different from *Danaea* Smith, consisting of three grades of laterals. *Gosauopteris* shows thicker veins, running usually to the leaf margin or dichotomizing near the leaf margin, thinner veins dichotomizing, anastomosing and third grade laterals forming a reticulate pattern. Combination of pinnate and reticulate venation is quite unusual among ferns. In the Marattiaceae it occurs in the genus *Christensenia* (*Kaulfussia*). The genus *Gosauopteris* also has an expanded base of its petiole, a character which is confined to the families Marattiaceae, Osmundaceae and Plagiogyriaceae. A laterally expanded base occurs very rarely also in some members of the Dryopteridaceae. Although we did not record any fertile specimen, we suggest associating the genus *Gosauopteris* with the Marattiaceae based on a combination of characters: entire lamina bearing teeth and expanded base of its petiole. *Gosauopteris* differs from Marattiaceae in having three orders of veins. The Marattiaceae has an extended fossil record going back to the Carboniferous (Mamay 1950, Stidd 1974). The genera *Angiopteris* and *Marattia* are reported from the Jurassic of Yorkshire (Harris 1961, Van Konijnenburg-van Cittert 1966). Simple leaved members of the Marattiaceae are unknown from the fossil record. It is not ruled out that our specimens could also be parts of larger fronds as it occurs at the recent *Angiopteris erecta* which has pinnate fronds consistsing of petiolate pinnae. On the other hand we cannot confirm this fact because all our specimens were found as simple leaves.

Sterile leaves of extant genera *Oleandra* (Dryopteridaceae tribe Oleandreae), *Elaphoglossum* (Dryopteridaceae tribe Bolbitideae), *Asplenium* (Aspleniaceae), *Anetium* (Vittariaceae) and *Niphidium* (Polypodiaceae) are similar to *Gosauopteris* in the shape of the lamina, but the presence of an indumentum, in the case of first two genera, absence of three vein orders and absence of any reproductive structures in *Gasauopteris* prevent closer comparison.

Sometimes, if lacking teeth, similar fronds of sterile fossil foliage were reported under the name *Taeniopteris* Brongniart, 1832 (= *Oleandrium* Schimper, 1869) as in the case of *Taeniopteris* (*Marattia*) *muensteri* Goeppert, 1903 (Andrews et al. in Boureau 1970). Morphogenus *Taeniopteris* Brongniart differs from *Gosauopteris* in the absence of teeth, in having shorter petiole and, more regular lateral veins, usually forking from their base and lacking any tertiary venation.

The genus *Danaeites* Goeppert 1836, although used for Cretaceous ferns, is based on Carboniferous fertile plant remains of clear maratiaceous affinity from Silesia, which are of completely different gross-morphology. *D. asplenioides* Goeppert (1836, pl. 19, figs 4, 5) differs from *Gosauopteris* in having very small pinnules arranged in bipinnately divided fronds. The genus *Marantoidea* Jaeger 1827 (≡ *Danaeopsis* Heer 1864 nom illegit., non *Danaeopsis* Presl 1845) differs from *Gasauopteris* in having veins forked near the rachis and entire margin of pinnae (Webb 2001, Van Konijnenburg – van Cittert et al. 2006). The genus *Angiopteridium* Schimper 1869 (= *Marattiopsis* Schimper 1874) based on the type *Angiopteridium muensteri* (Goeppert) Schimper differs from *Gosauopteris* in having pinnate fronds with sessile pinnule lacking three orders of veins.

Marattites Marion & Laurent is based on the species *M. desideratus* Marion & Laurent 1898 (pl. 1, fig. 1) from the Cretaceous of Romania. It represents a poorly preserved fragment of pinnula, which does not show any leaf margin and seems to lack any important diagnostic character.

Gosauopteris danaeoides J. Kvaček & Herman nov. spec.

(pl. 1, figs 1-8, pl. 5, fig. 10; pl. 31, fig. 1a;
Text-figs 7 I, J, 9)

1906 *Marattia* sp. Krasser, p. 1.
1906 *Danaea* sp. Krasser, p. 1.

Etymology: Derived from the genus *Danaea*, which is similar in gross morphology.

Holotype: NHMW 1999B0057/0469a

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg.

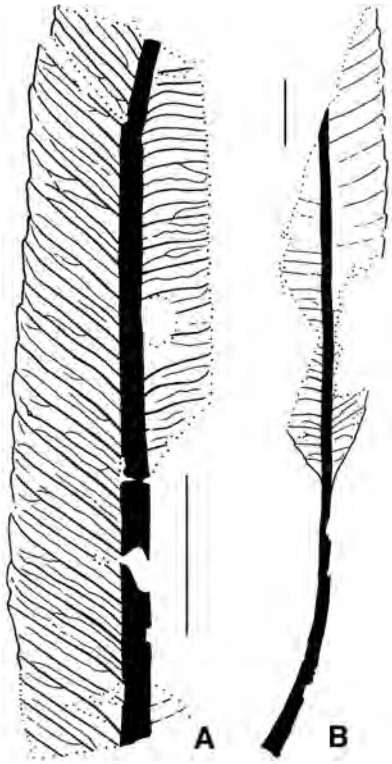
Material: GBA: 2006/60/02-2006/60/04, …/06, 2006/60/07, …/09 to …/12, …/14 to …/20, …/23, …/24, …/27, …/31, …/34, …/39, …/41, …/42, …/44, …/45, 2006/69/02, 2006/69/09, 2006/70/02
NHMW: 1853/0003/0034, …/0035, …/0037, …/0038, …/0043, …/0046, …/0049, …/0053, …/0055, 1999B0057/0002, …/0050, …/0086, …/0087, …/0088, …/0091, …/0092, …/0093, …/0094, …/0095b, …/0096, …/0099, …/0100c, …/0101a, …/0118a, …/0125, …/0133, …/0162, …/0236, …/0253, …/0278, …/0346, …/0423b, …/0447a, …/0448b, …/0464, …/0465, …/0466, …/0467, …/0468, …/0469a,b, …/0471a, …/0472, …/0473, …/0474b, …/0475a, …/0476, …/0477a, …/0479, …/0481, …/0482, …/0483a, …/0484, …/0485, …/0549, …/0554, …/0570, …/0580, …/0581, …/0582, …/0583, …/0584b, …/0593
IPUW: 8 unnumbered specimens in the University of Vienna.

Occurrence: Grünbach am Schneeberg, Dreistätten, Muthmannsdorf, Frankenhof.

Diagnosis: Fronds simple, lanceolate. Frond lamina serrate with acute or rounded apex, cuneate base and long robust petiole. The petiole with expanded base. Venation pinnate showing robust main vein and simple regularly distributed lateral veins, which are of three orders. Lateral veins terminating in teeth or in sinuses between teeth. Third order veins delicate linking the lateral veins and forming a reticulate pattern.

Description: The holotype (pl. 1, fig. 1) represents a basal part of a leaf with a long and robust petiole (lamina: 67 x 15 mm, petiole: 25 x 1.5-2.5 mm). It shows well-pronounced pinnate venation, all three orders of veins and a characteristic dentate margin.

The other material consists of numerous fragments of leaves. Although the leaf remains of this fern are the most common fossils at the locality, complete leaves are rare (pl. 5, fig. 10). The material consists of simple leaf fronds, which are lanceolate to linear lanceolate, displaying acute or rarely rounded apices (pl. 1, figs 5, 8). Their base is usually cuneate (pl. 1, fig. 1, text-fig. 9). The characteristic long petiole is preserved at the specimens No. GBA 2006/60/07, 2006/60/15, 2006/60/29, 2006/60/41. The frond margin is dentate to serrate (pl. 1, fig. 2). Teeth are small, usually shorter than 1 mm, rounded to acute. Size of the leaf lamina varies (80-160 x 8-23 mm). The frond has characteristic pinnate venation with mid-vein (1-2 mm thick) running to the apex. Lateral



Text-fig. 9: *Gosauopteris danaeoides* J. Kvaček & Herman, nov. gen. et nov. spec., A – NHMW 1999B0057/0447a, B – holotype NHMW 1999B0057/0469a, Grünbach (scale bar represents 1 cm).

veins are distributed 1-2 mm apart from each other, leaving the mid vein at angles of 60-80°. There are three orders of the laterals. The first order is more robust running to the margin of the lamina, terminating in teeth or in sinuses between teeth (pl. 1, figs 2, 7, text-fig. 9) and sometimes dichotomizing or anastomosing in the margin. Second order veins run usually parallel to the first order, but frequently leave or join the lateral veins of first order (pl. 1, fig. 7). Well-preserved leaves show lateral veins of first and second order linked with delicate veins of third order forming a reticulate pattern with other laterals (pl. 1, figs 2, 3).

Notes on ecology: Small entire leaves, leathery lamina and robust petioles suggest that this species is adapted to relatively dry conditions and may be epiphytic.

Comparison and discussion: This taxon is very typical for the Grünbach Formation and according to our knowledge it was not recorded in any other Cretaceous locality out of the Neue Welt Basin. There are several names associated with *Gosauopteris danaeoides*. The names *Blechnum braunii* Ettingshausen (GBA 2006/60/02), *Polypodites blechnoides* Ettingshausen, *Polypodites dryandroides* Ettingshausen are written on several old labels in the collection of GBA demonstrating problems with their identification. *Polypodites blechnoides* Ettingshausen and *Polypodites dryandroides* Ettingshausen were probably never validly published. *Blechnum braunii* Ettingshausen, 1854, pl. 14, fig. 2 is described from the Eocene of Croatia. Its similarity to *Gosauopteris danaeoides* is only superficial. There is only one order of veins, which are forking in the base and are much less pronounced. For comparison with recent material and similar fossil genera see the discussion of the genus. Similar leaf to *Gosauopteris danaeiodes* is described by Knobloch (1999) from the Cenomanian of the Czech Republic as "*Acrostichum*" *touchovicense* Knobloch (1999, pl. 1, figs 6, 12, pl. 12, figs 4, 7). Although similar in having comparably large laminae and long petioles, it differs from *Gosauopteris danaeiodes* by the absence of any teeth and having only one order of veins. The holotype with a preserved apical part (Knobloch 1999, pl. 1, fig. 6) shows an obtuse apex and a midvein which does not reach its margin. Another similar leaf is *Danaeites schlotheimii* Debey & Ettingshausen, 1859a from the Cretaceous of Aachen. It differs from *G. danaeoides* in having entire-margined lamina and peculiar ribs (remains of synagia?).

Gleicheniales
Matoniaceae

Genus *Monheimia*
Debey & Ettingshausen, 1859a

Type: *Monheimia polypodioides* Debey & Ettingshausen, 1859a, p. 211, pl. 3, figs 34-36, pl. 4, figs 1, 2, 21.

Discussion: The genus *Monheimia* is described from the Santonian of Aachen in Germany. Type material is preserved as leaf compressions, therefore detailed study of sori and their spores was not possible. It was not even very clear from the original illustrations whether the fertile fronds represent the same species. The species *Monheimia aquisgranensis* was discussed by Knobloch (1999) and used for the material coming from the Cenomanian of the Czech Republic. Knobloch (1999) hesitated to include fertile material in this genus and labelled it as: "? *Monheimia* sp. vel ? *Laccopteris* sp. vel ? *Microdictyon* sp.". *Monheimia aquisgranensis* was also described from the Ripley Formation in Tennessee, U.S.A. by Berry (1925). The depicted material is fragmentary but does remind *Monheimia* in venation pattern.

The present material confirms that sterile and fertile fronds belong together, bearing reproductive structures including spores *in situ* and suggests an association of the genus with the family Matoniaceae, particularly with the genus *Phanerosorus* Copeland. *Monheimia* and *Phanerosorus* show the same type of sori and very similar arrangement of sterile fronds. *Monheimia* differs from *Phanerosorus* in having numerous dichotomously divided pinnules giving the pinnules a rather different outline. From other genera of the Matoniaceae (*Phlebopteris* Brongniart 1836, *Matonidium* Schenk 1871, *Selenocarpus* Schenk 1867, *Piazopteris* Lorch 1967, *Delosorus* Skog 1988, *Weichselia* Stiehler 1857, *Carolopteris* Debey & Ettingshausen, 1859a) *Monheimia* differs in having several times dichotomously divided lamina with terminally situated sori.

Monheimia ungeri
J. Kvaček & Herman, nov. spec.

(pl. 1, figs 11-15, pl. 2, figs 1-6,
pl. 3, figs 1-10; Text-figs 7L, 10)

Etymology: In honour of Franz Unger, the outstanding Austrian palaeobotanist, who published the first descriptions of the Grünbach Flora.

Holotype: NHMW 1999B0057/0564 (pl. 2, figs 1-5, pl. 3, figs 1-10).

Stratum typicum: Grünbach Formation, Lower Campanian.

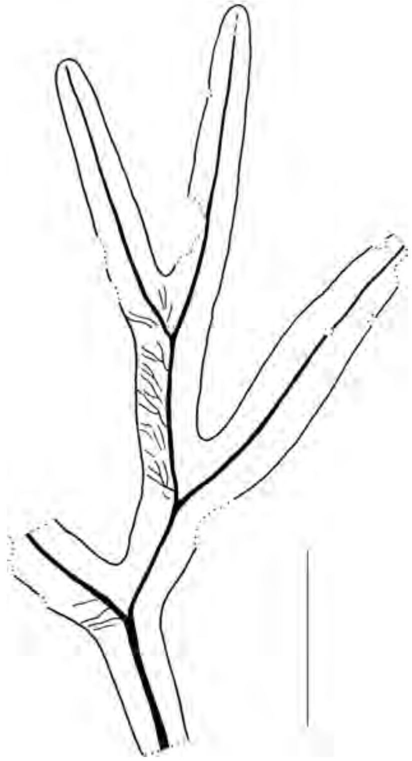
Locus typicus: Grünbach am Schneeberg.

Material: GBA: 2006/60/75
NHMW: 1970B1396-1644, 1999B0057/0084, …/0449, …/0453, …/0454, …/0561, …/0565, …/0609, …/0101d.

Occurrence: Grünbach am Schneeberg, Muthmannsdorf.

Diagnosis: Probably pinnately compound frond, bearing deeply lobed dichotomizing pinnules. Venation pinnate, mid vein robust, lateral veins delicate, dichotomizing and anatomizing several times. Sori rounded, arranged in two rows on both sides of midvein, confined to the terminal part of the pinnules. Sporangia wedge-shaped or nearly rounded, arranged radially, about 50 per sorus. Spores tetrahedral, smooth with well-pronounced trilete mark.

Description: The holotype (part and counterpart, pl. 2, figs 1-5) shows fragments of a probably compound frond (37 x 62 mm, 30 x 70 mm). Each fragment shows several pinnules attached decussately to a possibly common short rachis (pl. 2, fig. 1). Lamina of the pinnula is lobed, dichotomizing 7-12 times (3-5 x 40-70 mm). Its base is acute, terminal portions of lobes are rounded. All parts are attached or closely placed to a 12 mm short basal rachis 1 mm in diameter (pl. 2, fig. 1). Pinnules show pinnate venation with a robust mid vein dichotomizing several times (pl. 1, figs 11, 13; pl. 2, figs 3, 6). The secondary veins are delicate, dichotomizing several times, sometimes anatomizing, leaving the mid vein at angles of 45° (pl. 2, fig. 3, text-fig. 10). Rounded sori occur in terminal lobes of pinnules (pl. 2, fig. 3). They are arranged in two rows running parallel on both sides



Text-fig. 10: *Monheimia ungeri* J. Kvaček & Herman, nov. spec., NHMW 1999B0057/0449, Grünbach (scale bar represents 1 cm).

of the mid-vein (pl. 2, fig. 2, pl. 3, fig. 6), but they can also be arranged singly (pl. 3, fig. 5). Sori are about 1.5-1.8 mm in diameter, densely distributed on lower side of the lamina, sometimes so dense that they form a paved-like pattern (pl. 2, figs 2, 4). Sporangia rounded, 250-300 µm in diameter (pl. 3, fig. 1). There are 45-60 per sorus, forming a radial structure covered by persistent umbrella-shaped indusium attached centrally (pl. 3, figs 5, 6, 9). Spores 50-60 µm in diameter, rounded tetrahedral with smooth walls. Trilete mark well-pronounced (pl. 3, figs 3, 4, 8, 9). If macerated, sporangia frequently decompose liberating complete or incomplete tetrads (pl. 3, figs 2, 7).

Other type material consists of several fragments of sterile fronds and pinnules. The largest specimen (pl. 1, fig. 12) shows two pinnules decussately arranged on a possibly common axis. Each pinnulae is 70 mm long and 70 mm broad in its broadest place. Specimen No. NHMW 1999B0057/561 shows a small isolated pinnula (25 x 33 mm) dichotomizing three times (pl. 1, fig. 14). Lobes of the pinnulae lamina are 2-3 mm broad. Other fragments of pinnules (pl. 1, figs 11, 13, 15, pl. 2, fig. 6) show variation indicating quite a high degree of heterophylly in the species.

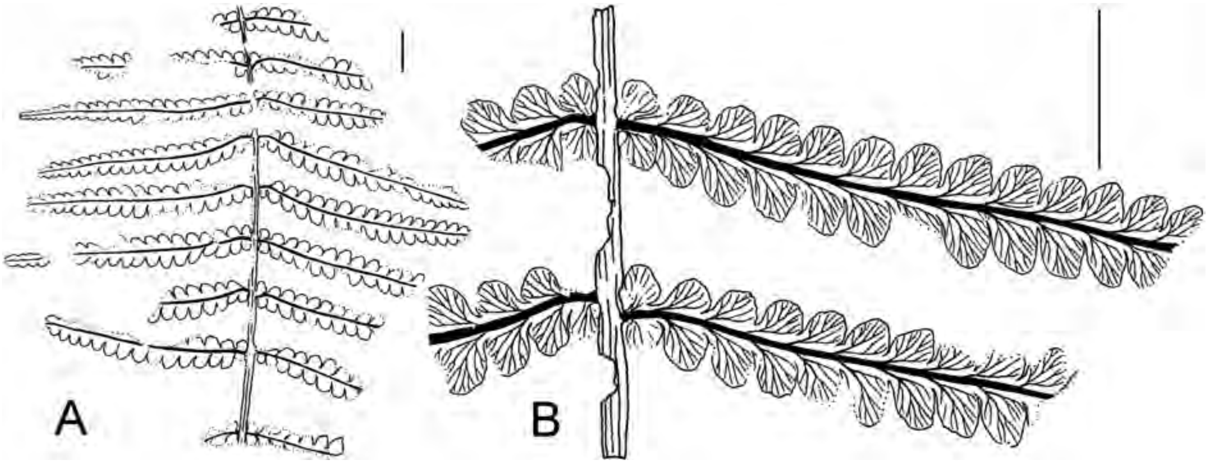
Comparison and discussion: *Monheimia ungeri* differs from *Monheimia polypodioides* Debey & Ettingshausen, 1859a, pl. 3, figs 34, 36, pl. 4, figs 1, 2, 21 in having pinnules rather regularly pinnately divided and in having sori distributed on all the abaxial surfaces of the pinnulae lamina.

M. ungeri differs from *Monheimia aquisgranensis* Debey & Ettingshausen from the Santonian of Aachen in Germany (Debey & Ettingshausen 1859a, pl. 4, figs 3-10) in having larger pinnules and in having sori closely adpressed to each other.

Monheimia cf. *aquisgranensis* Debey & Ettingshausen is reported from the Cenomanian of the Czech Republic by Knobloch (1999). It is associated with reproductive structures identified as "? *Monheimia* sp. vel ? *Laccopteris* sp. vel ? *Microdictyon* sp." (Knobloch 1999). This material displays pinnulae laminae 2-3 mm wide and sori which are not confined to terminal parts of pinnules (compare Knobloch 1999, pl. 6, fig. 10). *Monheimia ungeri* differs in having broader pinnules (usually 3-4 mm) and in having sori terminally.

Similar fronds to *Monheimia ungeri* were described by Rüffle & Knappe (1988) from the Santonian of Quedlinburg as *Laccopteris rigida* Heer. Although these leaves do not have terminally arranged sori, those figured on the text-fig. 1, top right (Rüffle & Knappe 1988) show similarities in the gross-morphology of the lamina.

Reproductive structures of *Monheimia ungeri* show important characters: arrangement of sori, umbrella-shaped indusium, wedge-shaped sporangia and *Matonisporites* spores, which unequivocally associate this genus with the Matoniaceae.



Text-fig. 11: *Microphyllopteris austriaca* J. Kvaček & Herman, nov. spec., A, B – holotype NHMW 1999B0057/0559, Grünbach (scale bar represents 1 cm)

? Gleicheniaceae

Genus *Microphyllopteris* Arber, 1917

Type: *Microphyllopteris pectinata* Arber 1917, pl. 7, figs 5, 9, 11.

Discussion: After detecting that the genus *Gleichenites* Goeppert (1836) is based on Palaeozoic seed-ferns Cantrill & Nagalingum (2005) recommended that the genus *Microphyllopteris* Arber (1917) should be used for sterile Mesozoic fern foliage similar to the extant genus *Gleichenia*. Although Seward (1926) emended the diagnosis of the genus *Gleichenites* and numerous later workers (Herbst 1962, Van der Burgh & Van Konijnenburg-van Cittert 1984) followed him (but see also Berry 1924), its type *G. linkii* Goeppert does not show diagnostic characters of the Gleicheniaceae. Goeppert (1836, p. 181 and 182) mentions this species first, also in the protologue, and it seems to be a clearly declared type of the genus. However, other species also described by Goeppert (1836) are of the same systematic affinity – seed ferns. Due to the above mentioned problems Crabtree (1988) decided to designate a new genus *Gleicheniaceaphyllum* for sterile fossil foliage of the Gleicheniaceae. It shows pseudodichotomy and resting bud as diagnostic characters. Although *Microphyllopteris* also includes some material of Mesozoic seed ferns (this fact is difficult to confirm due to poor preservation of the type material). Nagalingum & Cantrill (2006) retained its use particularly because it is very useful as a morphogenus accommodating various foliage of gleicheniaceous (but not only gleicheniaceous) affinity. It is characterised by fragmentary preservation of a frond lacking pseudodichotomy and a resting bud.

Microphyllopteris austriaca
J. Kvaček & Herman nov. spec.

(pl. 4, figs 1-8; Text-figs 7E,F, 11)

Etymology: Derived from the name of the country where it was found.

Holotype: NHMW 1999B0057/0559, (pl. 4, figs 1-3; text-fig. 11).

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

Material: GBA: 2006 60/82, 2006/60/83

NHMW: 1970/1396/458, …/1631, …/1650, …/1651, …/1652, 1999B0057/0084a, …/0257, …/0403, …/0406, …/0407, …/0408, …/0409, …/0410, …/0411, …/0415, …/0416a, …/0417,

…/0418, …/0420, …/0421, …/0422, …/0423a, …/0426, …/0427, …/0428, …/0431, …/0432, …/0438, …/0439, …/0444b, …/0559, …/0566, …/0588, …/0589, …/0593, …/0595, …/0596, …/0602, …/1795, …/1627.

Occurrence: Grünbach am Schneeberg, Muthmannsdorf, Austria.

Diagnosis: Frond bipinnate, secondary pinnae linear lanceolate inserted opposite or sub-opposite to the primary axis at an angle near to 90°. Pinnules rounded or slightly elongated irregularly, undulate to entire-margined with rounded apex and decurrent base. Pinnules inserted decussately, having pinnate venation.

Description: The holotype (pl. 4, fig. 1) shows a portion of a bipinnate frond with S-shaped secondary pinnae. It shows the main rachis 1-1.5 mm wide and grooved (pl. 4, fig. 2). Its secondary linear lanceolate pinnae (6-10 x 30–55 mm) are inserted opposite to sub-opposite to the rachis at an angle near to 90°. They show 6-18 pairs of pinnules inserted decussately or semi-decussately (pl. 4, fig. 2). Pinnules (2-3 x 2-4 mm) are rounded or slightly elongated with serrate margin (pl. 4, fig. 3, text-fig. 11). Their apex is usually rounded, base short decurrent. Pinnules often do not diminish in size along the secondary pinna except in the terminal part near to the apex. The mid vein of the pinnulae does not reach the apex, terminating with dichotomy into two laterals (pl. 4, fig. 3, text-fig. 11). Secondary veins in the base of each pinnulae are semi-decussately arranged, the secondary vein is conspicuously large and aligned in a terminal direction, running nearly parallel to the axis of the secondary the pinna (pl. 4, fig. 3, text-fig. 11). All secondary veins leave the mid vein at an angle of 30°.

The specimen no. NHMW 1999B0057/0595 (pl. 4, fig. 5) represents a part of a bipinnate frond 135 mm long, 40 mm wide. Secondary pinnae are short (3-5 x 3-20 mm) and are inserted semi-decusately at angles of 80-90°. Pinnules are rounded, undulate, sometimes nearly entire-margined, base short decurrent (1-2 x 2-3 mm). Pinnules in terminal parts of pinnae appear gradually united forming lobate laminae. Pinnules occurring in the terminal third of secondary pinnae show conspicuous structures resembling circinate venation in pinnae of juvenile fronds.

Other type material consists of fragments of fronds, which are always bipinnate. They are more than 120 mm long and 100 mm wide. Terminal parts of fronds show lanceolate outline (pl. 4, figs 7, 8). Size of the fronds can be estimated based on frond fragments.

Discussion: *Microphyllopteris austriaca* nov. spec. differs from other species of the genus *M. petinata* Arber, *M. gleichenioides* (Oldham & Morris) Walkom, *M. unisora* Cantrill & Nagalingum) in having pinnule and pinnae arranged decusately. *M. unisora* Cantrill & Nagalingum (2005) differs from *M. austriaca* in having asymmetrically placed primary vein, which is leaving the rachis in angle 45°.

Microphyllopteris austriaca is similar to *Gleichenia zippei* (Corda) Heer, *G. delicatula* Heer from the Cenomanian of Bohemia (Velenovský 1888) and *Didymosorus comtoniifolius* Debey & Ettingshausen and *D.gleichenioides* Debey & Ettingshausen and *D. varians* Debey & Ettingshausen (1859a). It differs in having pinnules with decurrent bases and an asymetrically placed primary vein.

Circinate venation of pinnules resemble fronds described as *Microtaenia variabilis* Knowlton (1918, pl. 29, figs 1-4) from the Cretaceous of Wyoming. This character is, however, interpreted here as juvenile foliage (personal communication van Konijnenburg-van Cittert 2007).

Dicksoniaceae

Genus *Coniopteris* Brongniart, 1849

Type: *Pecopteris murrayana* Brongniart 1835, p. 358, pl. 126, figs 1-5 ≡ *Coniopteris murrayana* Brongniart, 1849, p. 75, Jurassic, Yorkshire, United Kingdom.

Coniopteris sp.

(pl. 9, figs 4-6)

Occurrence: Grünbach am Schneeberg.

Material: NHMW 1970B01396/1563.

Description: A fragment of a bipinnate fern frond 61 mm long, 30 mm wide (pl. 9, Figs 4-6). Primary axis 1 mm in diameter bearing alternately attached secondary pinnae. They are lanceolate in outline (4-6 x 17-22 mm) and pinnately divided. Pinnules are rhomboidal (2-3 x 3-4 mm), dentate, and attached to the secondary axis by a short petiole. Possible sporangia are born on margins of pinnules (pl. 9, fig. 6). Venation is difficult to observe. It seems to be dichotomizing from its base. The occurrence of the remains of three fragmentary fronds on one hand specimen, and the direction of their secondary pinnae suggests, that the frond may be larger and tripinnate (compare pl. 9, fig. 4).

Comparison and discussion. This type of fern frond is very rare in the collection, being represented by only one specimen. It is assigned to the genus *Coniopteris* on the basis of its pinnulae shape and the arrangement of possible sori. It was impossible to get any spores *in situ* from the places where possible sori are developed. Therefore its identification remains open.

Polypodiales incertae sedis

Genus *Cladophlebis* Brongniart, 1849

Type: *Neuropteris albertsii* Dunker, 1846, p. 8, pl. 7, fig. 6 (≡ *Cladophlebis albertsii* (Dunker) Brongniart, 1849, p. 107), Lower Cretaceous, Germany.

Cladophlebis gosauensis J. Kvaček & Herman, nov. spec.

(pl. 5, figs 1-6; Text-figs 7A, B, 12)

1867 *Pecopteris zippei* Corda; Unger, p. 649, pl. 2, figs 1, 1*

Etymology: Derived from the name of the stratigraphic unit – the Gosau Group.

Holotype: described here NHMW 1999B0057/0560 (pl. 5, figs 1, 2; text-fig. 12A).

Stratum typicum: Grünbach Formation, Lower Campanian.

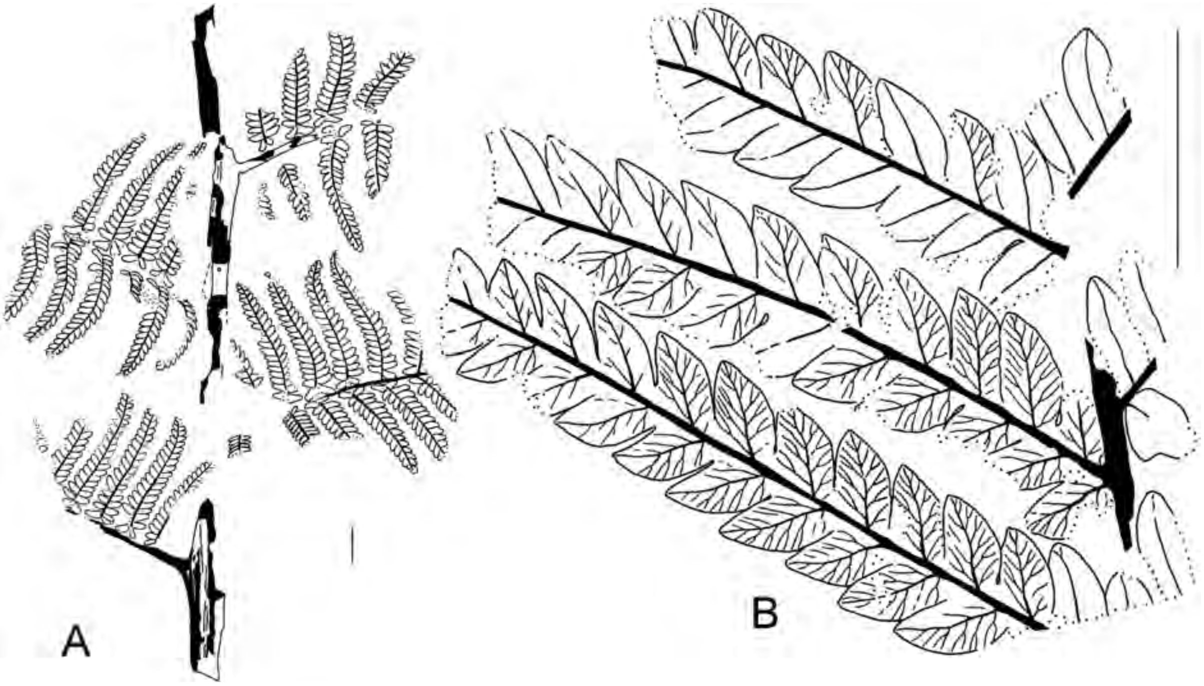
Locus typicus: Grünbach am Schneeberg.

Material: GBA: 2006/60/58, …/60, …/65, …/80, …/84
NHMW: 1970/1396/1655, 1999B0057/0095a, …/0101b, …/0118b, …/0394b, …/0424, …/0434, …/0436, …/0437, …/0441, …/0442, …/0443, …/0444a, …/0446, …/0560, …/0585, …/0592, …/0594, …/0597, …/72.197.

Occurrence: Grünbach am Schneeberg, Muthmannsdorf, Austria.

Diagnosis: Tripinnate frond, main rachis robust. Secondary pinnae inserted alternately to the main rachis. Tertiary pinnae linear-lanceolate, straight or S-shaped. Pinnules lanceolate bearing short decurrent bases and acute apices. Central and terminal pinnules inserted at angles of 60°, basal inserted at angle of 90°. The most basal pair expanded and oriented backwards in basal part forming small extra lobe.

Description: The holotype represents by far the best preserved specimen (pl. 5, fig. 1, text-fig. 12A). It shows a large fragment of a tripinnate frond. The main rachis is smooth or with fine longitudinal striae, 6-10 mm in diameter. The largest fragment of the rachis is 200 mm long (pl. 5, fig. 1). Secondary pinnae are arranged alternately on the primary axis which is 1-3



Text-fig. 12: *Cladophlebis gosauensis* J. Kvaček & Herman, nov. spec., A – holotype NHMW 1999B0057/0560, B – NHMW 1999B0057/0446, Grünbach (scale bar represents 1 cm).

mm in diameter. They are not completely preserved. We assume they were probably lanceolate in outline (pl. 5, fig. 1). The largest secondary pinna is 120 mm long. Tertiary pinnae are linear lanceolate, straight or S-shaped (pl. 5, fig. 2) and arranged decussately or semi-decussately on the secondary axis (1-0.5 mm in diameter). However, some specimens (pl. 5, fig. 5) have secondary pinnae arranged alternately. Their length varies usually between 40-90 mm. Central and terminal pinnules are lanceolate (1-2 x 3-5 mm), with shortly decurrent bases and acute apices, being arranged alternately (pl. 5, figs 2, 4, 6) at angles of 60°. Basal pinnules are usually inserted at an angle of 90° to the axis. The most basal pinnules, placed next to the secondary rachis, are expanded sometimes forming an extra lobe (pl. 5, fig. 6). They are conspicuously oriented backwards. Venation of the pinnules is pinnate with mid-vein terminating in the apex. Lateral veins are typically 5-7 on each side, dichotomizing once. Other type material is represented by fragments of secondary fronds, which show fine details of pinnules and their venation (pl. 5, figs 4, 3, 6) and variation within the frond gross-morphology. Particularly important are specimens numbered NHMW 1999B0057/0444a (pl. 5, fig. 5) showing acute terminal part of the secondary pinna and NHMW 1999B0057/0446 (text-fig. 12B) displaying fine venation of frond pinnules.

Comparison and discussion: *Cladophlebis gosauensis* differs remarkably from *Gleichenia zippei* Corda in Reuss, as primarily identified Unger (1867), in having tripinnate fronds lacking typical dichotomous topology. The fronds have a very robust construction indicating they were born on a large arborescent plant, probably on a tree fern.

Some specimens of *Cladophlebis gosauensis* in GBA bear labels with a name *Sphenopteris pichleri* Schenk. This species was described by Schenk (1875-76, pl. 29, figs 2-5) from the Gosau Group in Brandenberg of North Tyrol. The species differs from *Cladophlebis gosauensis* in having denatate decurrent pinnules.

From most of the representatives of the genus, *Cladophlebis gosauensis* differs in having basal pinnule broad, forming small extra lobe and oriented backwards. In this character it resembles the extant genus *Cyathea* J.E Smith (Cyatheaceae). It shows a very similar shape, venation and the same orientation of the basal pinnules (compare e.g. Tryon & Tryon 1982, text-figs 24.7, 25.10, 25.11). Modification of the basal pinnulae also occurs in *Eboracia lobifolia* (Phillips) Thomas (Harris 1961, text-figs 62, 63) and *Dicksonia kendalii* Harris (1961, text-fig. 66) fern taxa from the Jurassic of Yorkshire, both of which are assigned to the Dicksoniaceae. They differ from *C. gosauensis* in having bipinnate fronds and in a larger size of the basal pinnules. *Eboracia lobifolia* differs, additionally, in having waved margins of pinnules and second basal pinnule is smaller than other ones.

Cladophlebis gosauensis shows similarities in shape and venation of its pinnules to the fern fragment described by Rüffle & Knappe (1988) as cf. *Cladophlebis arctica*. It differs from *C. gosauensis* in absence of modified basal pinnules. Unfortunately, the specimen is too incomplete to be compared in detail.

In shape of the pinnules and their venation *Cladophlebis gosauensis* resembles *Cladophlebis frigida* (Heer) Seward from the Lower Cretaceous of Greenland (Heer 1882, pl. 6, fig. 5b, pl. 10, figs 1-4, pl. 7, fig. 2; Seward 1926) and from the Cenomanian of the Czech Republic (Velenovský 1888, Frič & Bayer 1901, 1903), but it differs in having basal pinnules that are slightly larger having an extra lobe which is oriented backwards.

Genus *Raphaelia* Debey & Ettingshausen, 1859a

Type: *Raphaelia neuropteroides* Debey & Ettingshausen 1859a, p. 220, pl. 4, figs 23-28, pl. 5, figs 18-20, Upper Cretaceous, Aachen, Germany.

The genus was described by Debey & Ettingshausen (1859a) from the Santonian of Aachen. It is known from several Cretaceous localities in Europe (e.g. Knobloch 1999) and characterised by simple or bipinnate pinnae bearing rounded, serrate pinnulae with contracted base. Its pinnate are of "neuropterid" venation – the main vein of each pinnulae terminates below the pinnulae apex. *Raphaelia* resembles slightly Jurassic genus *Eboracia* Thomas 1911 and some Jurassic species of *Dicksonia* L'Héritier 1789. However, pinnae of *Raphaelia* have contacted, cordate base with short petiole. The genus *Neuropteridiumi* Schimper in Schimper & Schenk 1879 differs form *Rapahelia* in having robust rachis, regular arrangement of pinnae which are lacking any petioles (for more discussion, see Van Konijnenburg-van Cittert et al. 2006).

Raphaelia lobifolia (Corda in Reuss) Knobloch

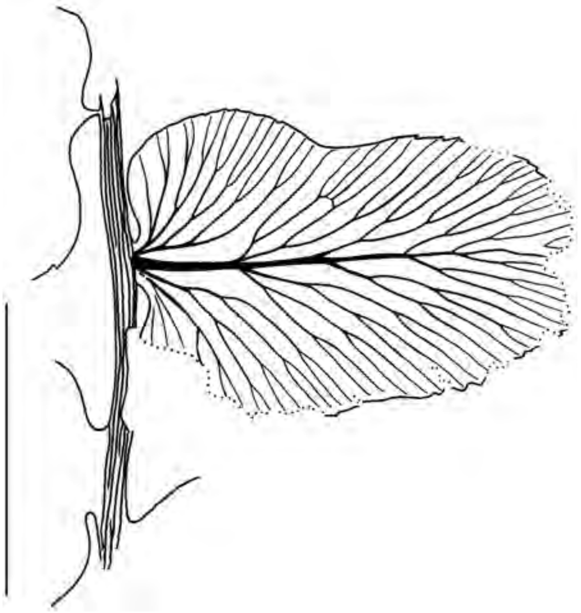
(pl. 8, figs 8-11, pl. 9, figs 1-3; Text-figs 7G, 13)

1846 *Pecopteris lobifolia* Corda in Reuss, p. 95, pl. 49, figs 4-5.
1889 *Osmundophyllum cretaceum* Velenovský, p. 6, pl. 2, fig. 21.
1900 *Gymnogramme bohemica* Bayer, p. 45, text-figs 14, 14a, pl. 2, fig. 2.
1901 *Pecopteris lobifolia* Corda in Reuss; Frič & Bayer, p. 83.
1901 *Raphaelia woldrichii* Mařík, p. 3, pl. 1, figs 3-8.
1999 *Raphaelia* cf. *lobifolia* (Corda in Reuss) Knobloch, p. 34, pl. 5, figs 6-10, pl. 7, figs 1b, 4b.

Material: NHMW: 1999B0057/0160, .../0255, .../0275, .../0368, .../0425, .../0435b, .../0445a, .../0455, .../0456, .../0457, .../0458, .../0459c, .../0460, .../0461, .../0462, .../0463, .../0562, .../0598, .../0600, .../0601, .../0603, .../1795.

Occurrence. Höflein, Grünbach am Schneeberg.

Description: The material consists of numerous small fragments of bipinnate or simple pinnate fronds. The largest fragment No. NHMW 1999B0057/0603 shows a bipinnate frond 8 cm long and 7 cm wide (pl. 8, fig. 9). The main rachis (2 mm wide) bears both pinnules (pl. 8, fig. 8) and simple pinnate pinnae (pl. 8, fig. 9). Fragments of pinnae (No. NHMW 1999B0057/0456, 1999B0057/0562, pl. 8, figs 10, 11, text-fig. 13) show the main rachis 1-2 mm wide bearing decussately or alternately arranged pinnules leaving the rachis at angles of nearly 90°. Pinnulae



Text-fig. 13: *Raphaelia lobifolia* (Corda in Reuss) Knobloch, NHMW 1999B0057/0456, Grünbach (scale bar represents 1 cm).

margin is serrate, apex rounded, base cordate (pl. 8, fig. 8). Shape and size of the pinnules vary from elongate rounded (10-15x12-18 mm) to lanceolate (16 x 36 mm). Large lanceolate pinnules are pinnately lobed consisting of 1-4 pairs of lobes (pl. 9, fig. 3). Terminal pinnules are trilobed (pl. 9, figs 1, 2). Venation of the pinnulae is pinnate. It shows the main vein of the pinnulae, stout at base, terminating below the pinnulae apex. Lateral veins are semi-decussately arranged, dichotomizing 1-4 times (text-fig. 13). Fertile material is unknown.

Comparison and discussion: Fragments of sterile fronds described here are identified as *Raphaelia lobifolia* (Corda in Reuss) Knobloch. The taxon was designated by Corda and published in Reuss (1846) on material from the locality Mšeno from the Cenomanian of the Czech Republic. The type material is lost or of unknown repository, therefore we relied on illustrations by Corda (in Reuss 1864, pl. 49, figs 4, 5) and other material from the Cenomanian of the Czech Republic published by Knobloch (1999) as *Raphaelia* cf. *lobifolia*. The material is typified by large serrate pinnules with numerous dichotomously branched secondaries and cordate base. The present material is also very similar to *Filicites* sp. 6 described by Němejc & Z. Kvaček (1975) from the Senonian of South Bohemia, Czech Republic.

Genus *Sphenopteris* (Brongniart) Sternberg, 1825

Syn.: *Filicites* sect. *Sphenopteris* Brongniart, 1822, p. 33

Type: *Filicites* (*Sphenopteris*) *elegans* Brongniart, 1822, p. 33, pl. 2, fig. 2 ≡ *Sphenopteris elegans* (Brongniart) Sternberg, 1825, p. 15, Carboniferous, Silesia, Poland.

Discussion: The genus is used as a morphogenus in a broad sense, accommodating sterile foliage of fern-like fronds with deeply dissected pinnae or, in other words, with pinnae bearing basally fused pinnules with “sphenopterid” venation.

Sphenopteris heterophylla (Unger) J. Kvaček & Herman comb. nov.

(pl. 5, figs 7-9; text-fig. 14)

Basionym: *Hymenophyllites heterophyllus* Unger, 1867, Kreidepflanzen aus Österreich, p. 650, pl. 2, figs 3, 4.

Neotype: Designated here. GBA 2006/60/79, pl. 5, figs 7-9.

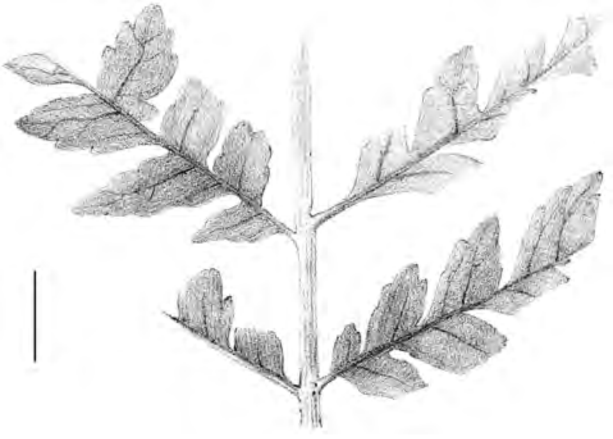
Stratum typicum: Upper Santonian – Lower Coniacian.

Locus typicus: St. Wolfgang am Wolfgangsee, Austria.

Material: GBA 2006/60/79.

Occurrence: Muthmannsdorf.

Emended diagnosis: Frond bipinnate, of unknown shape. Secondary pinnae linear lanceolate, alternately arranged on the main axis where interspaced



Text-fig. 14: *Sphenopteris heterophylla* (Unger) J. Kvaček & Herman, comb. nov., illustration from Unger 1867, pl. 2, figs 3, 4 (scale bar represents 1 cm).

with dentate, decurrent pinnules. Pinnules of the secondary pinnae lanceolate with dentate margin, acute apices and shortly decurrent base. Venation generally pinnate, midvein supplemented with two or three veins arising from the base and running parallel to the main vein (odontopteroid venation).

Description: The neotype (pl. 5, figs 7-9) shows bipinnate fronds of unknown shape and size being preserved in fragments. Main axis bears secondary alternately arranged pinnae interspaced with dentate, decurrent pinnules (pl. 5, fig. 7). The secondary pinnae are linear lanceolate over 72 mm long, bearing alternately arranged pinnules. Each pinnulae is dentate with a decurrent base and an acute apex, typically 5-10 x 10-20 mm (pl. 5, figs 8, 9). Venation generally pinnate, each pinnulae is entered by two or three main veins with several secondaries terminating in teeth. Beside the lost holotype, there is only one specimen available for the study, which we suggest to keep as a neotype.

Nomenclatural remarks: The type material of *Hymenophyllites heterophyllus* Unger was not found in the collections of the Naturhistorisches Museum and the Geologische Bundesanstalt. It is still not ruled out that it will be found in the collections of the University of Vienna, however, we already tried to find it there. Because the original material is still of unknown repository we decided to select a neotype which displays all the morphological chcaracters of the original material (compare text-fig. 14), although it does not come from the type locality.

Comparison and discussion: The genus *Hymenophyllites* Goeppert, 1836 is based on Palaeozoic filicalean fronds now classified under the morphogenus *Sphenopteris* (Brongniart) Sternberg. Material of *Sphenopteris heterophylla* is exceptional in several points. It was previously described by Unger (1867) but since that time there has been only one more specimen collected. It differs as far as we know from all members of the genus in specific, rather irregular, venation. Some of its pinnules are fused and entered by more than one main vein (two or three) giving the pinnules a rather odontopteroid character. In this character *S. heterophylla* resembles a cycad foliage *Mesenea bohemica* (Corda in Reuss) J. Kvaček from the Cenomanian of the Czech Republic (J. Kvaček 1999). The material in hand does not have any cuticle preserved that could help us to resolve the problem.

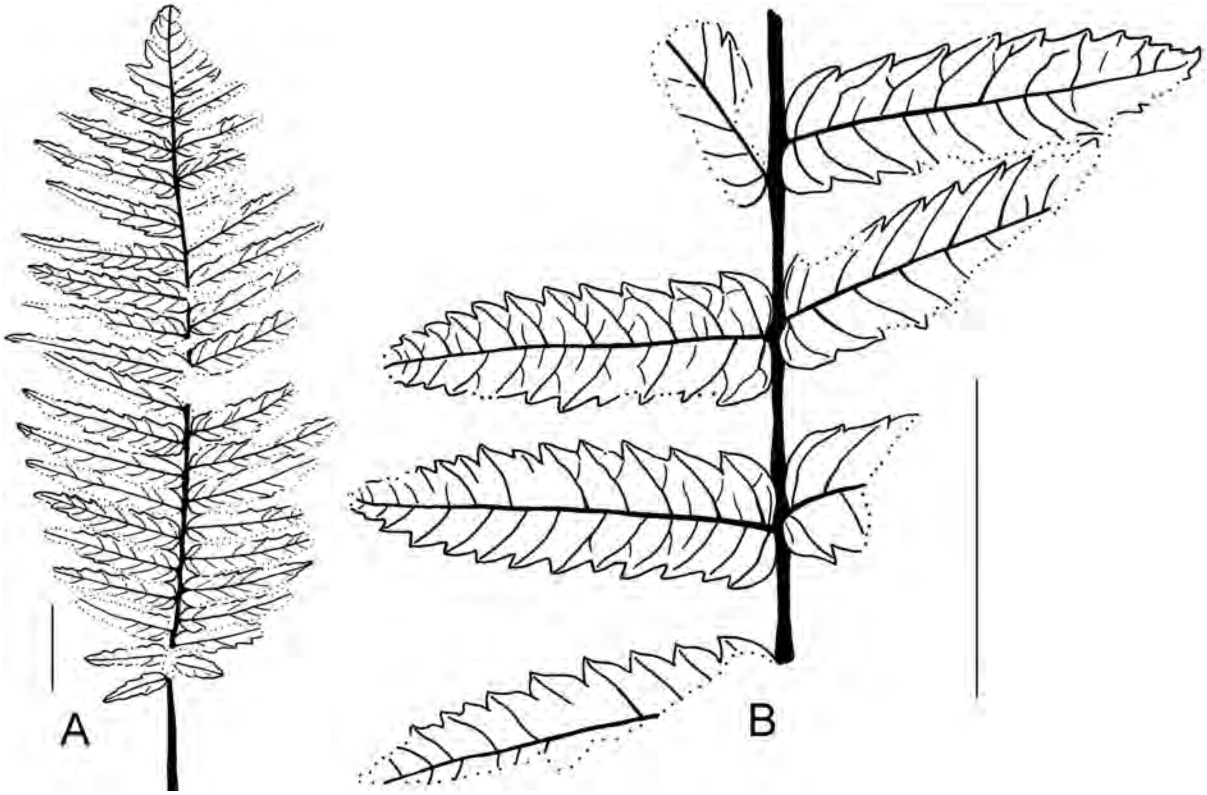
Sphenopteris heterophylla differs from *Sphenopteris pichleri* Schenk (1875-76, pl. 29, figs 2-5, Gosau Group in Brandenberg of North Tyrol) in having odontopteroid type of venation and more robust frond physiognomy. In gross morphology *S. heterophylla* resembles the sterile fronds of *Coniopteris hymenophylloides* (Brongniart) Seward (e.g. Harris 1961). Particularly similar are specimens of *S. heterophylla* described by Sze (1931) from the Chinese Liassic (Sze 1931, pl. 5, fig. 1). On the other hand *C. hymenophylloides* differs remarkably from *S. heterophylla* in the pinnulae venation pattern as mentioned above.

Sphenopteris gruenbachiana
J. Kvaček & Herman, nov. spec.

(pl. 6, figs 1-10; Text-figs 7C, D, 15)

Etymology: Derived from the type locality.

Holotype: NHMW 1999B0057/0586, (pl. 6, figs 5, 6).



Text-fig. 15: *Sphenopteris gruenbachiana* J. Kvaček & Herman, nov. spec., A – NHMW 1999B0057/0552, B – NHMW 999B0057/0398, Grünbach (scale bar represents 1 cm).

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg.

Material: GBA: 2006/60/59, …/61, 2006/64/07, …/10, …/40, 2006/69/12, 2006/70/02.
NHMW 1861/0001/0095, …/0037, 1861/0003/0042, …/46, …/49, 1970/1396/1792, 1999B0057/0060a, …/0063b, …/0096, …/0196b, …/0213, …/0214, …/0215a, …/0238, …/0242, …/0247, …/0341b, …/0384, …/0385, …/0386, …/0387, …/0388, …/0389, …/0390, …/0391, …/0392, …/0393, …/0394a, …/0395a, …/0396, …/0397, …/0398, …/0399, …/0400, …/0401b, …/0402, …/0404, …/0405, …/0412, …/0414, …/0419, …/0429, …/0430, …/0433a, …/0440, …/0445b, …/0447b, …/0466, …/0469a, …/0471b, …/0475b, …/0483b, …/0501b, …/0550, …/0552, …/0585, …/0586, …/0587, …/0590, …/0591, …/1628,…/1791, …/1793.
IPUW: 4 unnumbered specimens.

Occurrence: Grünbach am Schneeberg, Dreistätten, Muthmannsdorf.

Diagnosis: Fronds simply pinnate, oval to linear lanceolate in outline, with acute apex and rounded base having a short petiole. Pinnulae sessile, linear-lanceolate, dentate, with acute apex and cordate base. Pinnules arranged decussately on the main rachis. Venation pinnate; secondary veins simple or forking, accompanied by one or two intersecondaries. Secondary veins ending in acute or attenuate teeth.

Description: The holotype (pl. 6, figs 5, 6) represents a basal fragment of simply pinnate frond (27x75 mm). It shows serrate, lanceolate pinnules (4-5 x 10-30) with acute apices and cordate bases. They are attached decussately to the primary axis. Teeth are acute, sometimes attenuate, gradually diminishing to the pinnulae apex. Each tooth is less than

1 mm long. Venation is pinnate with well-pronounced mid-vein and 10-14 secondaries terminating in teeth (pl. 6, fig. 6). The secondary veins are simple, forking or irregularly pinnately divided. The type material consists of several complete leaves and numerous fragments. They are of two types: elliptical and linear-lanceolate in outline. The most complete leaf is No. NHMW 1999B0057/0552 (37 x 90 mm) showing broadly elliptical outline. The frond has an acute apex, rounded base, and a short petiole (pl. 6, fig. 9, text-fig. 15A). A narrower type is represented by a specimen No. GBA 2006/64/07, which is linear lanceolate 10-17 x 92 mm with semidecusately arranged pinnules (pl. 6, fig. 2). Similar frond showing decussately arranged pinnules is depicted on pl. 6, fig. 1. Although fern fronds vary in length, their mean size is about 9 mm (maximal length recorded – 11 mm No NHMW 1999B0057/0238). Narrower fronds are usually dissected to their apex, broader fronds have fused terminal pinnules, which are nearly obtuse in outline (pl. 6, figs 3, 8). Pinnules of the fronds are quite uniform in shape. They vary slightly in length (2-4 x 6-20 mm). The best preserved fragments (NHMW 1999B0057/0398, NHMW 1999B0057/1628) show pinnules with clear cordate bases (pl. 6, fig. 10, Text-fig 15B). Their venation is pinnate with the main vein and secondaries well-pronounced (text-fig. 15). It is interesting to note, that the secondary veins in basal part of the pinnules usually dichotomise, whereas higher secondaries are predominantly simple. Secondary veins are usually accompanied by one or two thin and short intersecondaries (text-fig. 15B).

Comparison and discussion: This taxon seems to be according to our knowledge unique for the Grünbach Formation (its occurrences out of the basin recorded in collections of GBA are very probably misinterpreted due to mixed locality labels). Taxa which slightly resemble *Sphenopteris gruenbachiana* are mentioned and discussed below. *Sphenopteris gruenbachiana* differs from *Cladophlebis browniana* (Dunker) Seward from the Lower Cretaceous of Germany (Seward 1894, pl. 7, fig. 4 who synonymized also *Pecopteris virginiensis* Fontaine, 1889, *Cladophlebis crenata* Fontaine, 1889, *C. alata* Fontaine, 1889, *C. petiolata* Fontaine, 1889) in having cordate bases of pinnules and simple secondaries. It also differs in the presence of intersecondary veins. *S. gruenbachiana* is similar in gross-morphology of the frond to *Cladophlebis jelisejevii* Kryshtofovich 1958, but differs in having pinnules with cordate bases, smaller teeth and in having intersecondaries. The gross-morphology of *S. gruenbachiana* resembles also *Sphenopteris nauckhoffiana* (Heer) Halle from the Late Cretaceous of Greenland (Pattorfik, Heer 1880, pl. 1, fig. 9, Halle 1913), but it differs in having more pronounced cordate bases to the pinnules, in having uniform marginal teeth and the presence of intersecondaries.

Sphenopteris ungeri
J. Kvaček & Herman nov. spec.

(pl. 7, figs 1-7; Text-figs 7K, 16)

1867 *Pecopteris striata* Presl in Sternberg; Unger, p. 650, pl. 2, fig. 2.

Etymology: In honour of Franz Unger, the outstanding Austrian palaeobotanist, who recorded the fossil for the first time.

Stratum typicum: Grünbach Formation, Lower Cretaceous.

Locus typicus: Grünbach am Schneeberg.

Holotype: NHMW 1999B0057/0517, (pl. 7, figs 2, 7).

Material: GBA: 2006/64/39
NHMW: 1999B0057/0515, .../0516, .../0517, .../0518, .../0519, .../0522, .../0523, .../0568, .../0569.

Occurrence: Grünbach am Schneeberg, Austria.

Diagnosis: Frond bipinnate, secondary pinnae linear lanceolate inserted sub-opposite to the primary axis at an angle of 30-45°. Pinnules lanceolate, entire-

Text-fig. 16: *Sphenopteris ungeri* J. Kvaček & Herman, nov. spec., GBA 2006/64/39, Grünbach (scale bar represents 1 cm).

margined, with attenuate apices and decurrent bases. Pinnules frequently fused in their basal parts. In distal parts of frond pinnules fused completely forming lamina with dentate or entire margin. Venation of pinnules pinnate; primary axis not reaching the apex of pinnulae; dichotomously branched secondary veins inserted at steep angles.

Description: The holotype, a leaf compression, represents a part of a bipinnate frond (55 x 123 mm, pl. 7, fig. 7) showing secondary pinnae, linear lanceolate (2-4 x 40-70 mm), attached alternately or semidecussately to the main axis (0.5 mm in diameter). Pinnules of the secondary pinnae are lanceolate, entire-margined (3-5 x 8-10 mm) with attenuate or acute apices and decurrent bases. Numerous pinnules are partly united in their base (pl. 7, fig. 2). Venation is pinnate, with a middle vein that is very inconspicuous and bearing lateral veins dichotomizing once or twice, leaving the main vein at angles of 30° (pl. 7, fig. 2). Although the holotype is a good leaf compression, it was impossible to prepare its cuticle, which is a common condition among true ferns. On this rather indirect character we consider the plant to be of fern affinity and not related to the genus *Pecopteris*. Other type material consists of fragments of fronds. The specimens NHMW 1999B0057/0522 and NHMW 1999B0057/568 show terminal parts of fronds (pl. 7, figs 3, 5, 6) with fused terminal pinnules. A well-preserved leaf impression of the terminal part of the frond from the Geologische Bundesanstalt (pl. 7, figs 1, 4) shows fused terminal pinnules, which are strongly decurrent and with well-pronounced venation.

Comparison and discussion: Careful comparison between the present material and the holotype of *Pecopteris striata* Presl in Sternberg (1838, pl. 37, fig. 3) revealed a large difference among both taxa. The holotype of *Pecopteris striata* Presl in Sternberg, although fragmentarily preserved, has the typical pecopterid frond arrangement. It shows a pinnulae with a rounded apex, no decurrent base and well-pronounced pinnate venation. It definitely differs from the leaves of *Sphenopteris ungeri* described by Unger as *Pecopteris stricta* (Unger 1867). Therefore we decided to introduce a new taxon.

Sphenopteris ungeri represents a type of sterile foliage which is quite common in the Upper Cretaceous. Fronds of this type were described under several generic names belonging to recent ferns *Asplenium* – e.g. *A. foersteri* Debey & Ettingshausen (e.g. Velenovský & Viniklář 1929, pl. 17, figs 5, 6, pl. 20, fig. 6, pl. 22, fig. 8), *Thyrsopteris* – *T. capsulifera* Velenovský (e.g. Velenovský 1888, pl. 1, figs 6-12), *Anemia* – *A.* cf. *fremontii* Knowlton (e.g. Knobloch 1999, pl. 1, fig. 8, pl. 3, figs 1-8).

Sphenopteris cretacea Velenovský & Vinklář (1929, pl. 17, figs 1-4) from the Cenomanian of the Czech Republic and *Asplenium dicksonianum* Heer from the Cretaceous of Greenland (Heer 1882, pl. 32) differ from *Sphenopteris ungeri* in having very narrow pinnules with one or two marginal teeth. Venation and fusion of terminal pinnules in both above mentioned species are very similar to the present material. *Anemia* cf. *fremontii* Knowlton (Knobloch, 1999, p. 29, pl. 1, fig. 8, pl. 3, figs 1-8) and *Onychiopsis capsu-*

lifera (Velenovský) Nathorst (e.g. Velenovský 1888, Frič & Bayer 1901, 1903, text-fig. 12) differ from *Sphenopteris ungeri* in having usually long pinnules without attenuate apices.

Present studies in the Cenomanian of the Czech Republic show that this type of foliage is found in association with spores of the family Schizaeaceae (e.g. Pátová & J. Kvaček 2006). All above mentioned taxa of sterile foliage are probably closely related representing sterile foliage of various ferns from the Schizaeaceae. Without fertile material and inspection of spores *in situ* their systematic relationship must remain open.

Additionally, *Sphenopteris ungeri* is macroscopically similar to leaves of *Mesenea bohemica* (Corda in Reuss) J. Kvaček (= *Kirchnera arctica* (Heer) Velenovský). It differs from *M. bohemica* in having an entire-margined pinnulae and an attenuate apex (Velenovský 1888, Frič & Bayer 1901, 1903, text-fig. 27, text-fig. 28). The crucial difference between these two taxa is in the presence of cycadoid cuticle in *Mesenea bohemica* (J. Kvaček 1999, pls 3-5), which places *Mesenea* into the cycads.

Sphenopteris sp.

(pl. 4, figs 9, 10)

Material: NHMW 1999B0057/0356a.

Occurrence: Grünbach am Schneeberg.

Description: A fragment of a bi-pinnate fern frond 3 cm long showing two alternately attached fragments of secondary pinnae (pl. 4, fig. 10). Secondary pinnae leave the rachis at angles of 30°, bearing lanceolate pinnules (2 x 6 mm) with acute apices and decurrent bases. Venation is poorly preserved and difficult to trace.

Comparison and discussion: This piece of sterile fern foliage is too fragmentary to be assigned to any particular species. We assign it to the genus *Sphenopteris* considering the fact that it has dissected pinnae bearing pinnula with decurrent and partly fused bases.

There are several good candidates for comparison. Foliage of similar frond gross-morphology was assigned to species *Sphenopteris cretacea* Velenovský & Viniklář (1929, pl. 17, figs 1-4) and *Asplenium foersteri* Debey & Ettingshausen by Bayer (compare Bayer in Frič & Bayer, 1901, 1903, text-fig. 15) both from the Cenomanin of Bohemia. Another very similar species is *Onychiopsis capsulifera* (Velenovský) Nathorst (Velenovský 1888, Bayer in Frič & Bayer, 1901, 1903, text-fig.12) from the Cenomanian of Bohemia.

Salviniales

Marsileaceae

Genus *Marsileaceaephyllum* Nagalingum, 2007

Type: *Marsilea johnhallii* Skog & Dilcher, 1992, p. 983, figs 1-11 ≡ *Marsileaceaephyllum johnhallii* (Skog & Dilcher) nagalingum, 2007, p. 44.

Discussion. Identification of members of the Marsileaceae is based mostly on reproductive structures (*Regnellidium upatoiensis* Lupia et al. 2000 from the Santonian Eutaw Formation, USA). The genus *Marsileaceaephyllum* was introduced by nagalingum (2007) to accommodate fossils plants which resemble sterile leaves of *Marsilea* Linnaeus, but differs in lacking reproductive organs. *Marsileaceaephyllum* differs profoundly from the recent genus *Regnellidium* Lindmann and *Regnellites* Yamada & Kato (2002) from the Upper Jurassic to Lower Cretaceous of Japan in having four pairs of leaflets forming a typical rosette. Cretaceous records of *Marsileaceaephyllum* have grown in number during the last two years. Except *Marsileaceaephyllum johnhallii* described from the Dakota Formation (Skog & Dilcher 1992), there are also *M. lobatum* Nagalingum, 2007 and *M.* sp. B from the Alexander Island of Antarctica, *M.* sp. C from Australia and *Marsileaceaephyllum mahisensis*

Hu et al. (2008) from the Early Cretaceous of the Middle East.

Tertiary records come form the Eocene of Wyoming (*M*. sp. A sensu Nagalingum 2007, see also Rich et al. 2001) The genus *Fortuna* McIver & Basinger (1993) also shows rosettes consisting of fours leaflets. It differs from *Marsileaceaephyllum* in having leaflets with reticulate venation, more orders of veins, marginal teeth and glands and aerenchymatous texture.

The doubtful fossil *Marsilidium speciosum* Schenk (1871, p. 225, pl. 26, figs 3, 3a) from the Lower Cretaceous of Germany, which has dichotomous venation, differs from *Marsileaceaephyllum* in having hexafoliate leaves with dentate leaflets and rachis as in the genus *Sphenophyllum*. *Sphenoglossum quadrifolium* Emmons (1856, pl. 1, fig. 2) from the Triassic of North Carolina, although resembling *Marsileaceaephyllum*, is based on material, which is very doubtful and is probably of no biological affinity.

Marsileaceaephyllum campanicum
J. Kvaček & Herman, nov. spec.

(pl. 8, figs 1-7; text-figs 7H, 17)

1906 *Marsilea* sp. Krasser, p. 2.
1910 *Marsilea nathorstii* Krasser in Seward, p. 474, nom. inval.
2004b *Marsilea* sp. J. Kvaček & Herman, p. 93, fig. 1b.

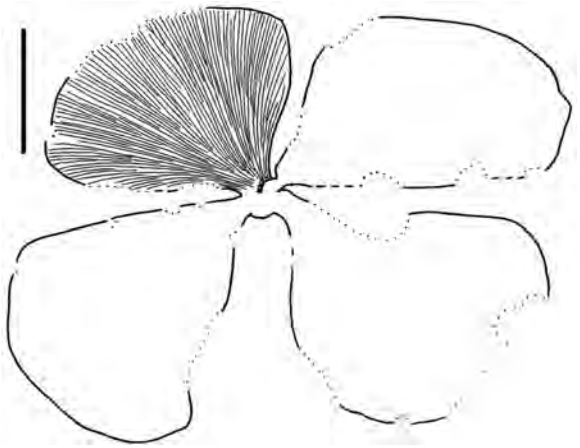
Etymology: Derived from the name of the stratigraphic stage, where the fossil comes from.

Holotype: NHMW 1999B0057/0509a (pl. 8, fig. 2; text-fig. 17)

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

Material: NHMW: 1999B0057/0250, …/0265, …/0285, …/0288, …/0413, …/0448a, …/0452, …/0508b, …/0509a, …/0599, …/0604, …/0605, …/0606, …/0607, …/0608.



Text-fig. 17: *Marsileaceaephyllum campanicum* J. Kvaček & Herman, nov. spec., holotype NHMW 1999B0057/0509a, Grünbach (scale bar represents 1 cm).

Occurrence: Grünbach am Schneeberg.

Diagnosis: Petioles bearing four terminal leaflets, leaflets wedge-shaped, entire-margined, base cuneate, apex rounded, lateral margins straight to convex. Venation dichotomous, rarely anastomosing, with inconspicuous marginal vein.

Description: The holotype (pl. 8, fig. 2) represents a complete rosette of four wedge-shaped leaflets. Each leaflet shows radially arranged and dichotomously branched veins. Other type material consists of several fragments of complete (pl. 8, fig. 3) or incomplete rosettes (pl. 8, figs 1, 4) and isolated leaflets (pl. 8, figs 5, 6, 7). Wedge-shaped leaflets (12-40 x 14-44 mm) are radially attached to a petiole. Distal margin of the leaflet is rounded, obtuse, entire-margined and usually slightly undulate. Leaflet venation is regularly dichotomous consisting of simple, forking or rarely anatomising veins of one order (pl. 8, fig. 6). The intramarginal vein, the common character of the genus *Marsilea*, is in the present material inconspicuous and rarely preserved (pl. 8, figs 4, 6). In the present material usually two veins are joined in the marginal parts suggesting the existence of an inconspicuous intramarginal vein. The specimen No. NHMW 1999B0057/0250 (pl. 8, fig. 4) shows a

Text-fig. 18: *Marsilea aegyptiaca* Willd. NHMW herbarium, modern (scale bar represents 1 cm).

rarely preserved fragment of the petiole 9 mm long and 1 mm in diameter. No attached fertile material has been found.

Discussion: Diagnostic characters of *Marsileaceaephyllum campanicum*, leaflets and their arrangement and venation are very similar to the recent representatives of the genus *Marsilia*, the main difference is that we do not have any record of reproductive structures. The second difference between *M. campanicum* and *Marsilea* is the size of the leaves; generally leaves of *Marsilea* species are smaller. For comparison we depicted extant *Marsilea aegyptiaca* Willdenow (text-fig. 18), which also forms comparatively large leaflets and which shows diagnostic characters of living *Marsilea* (Kramer 1990b).

Marsileaceaephyllum campanicum differs from *Marsileaceaephyllum johnhallii* from the Cenomanian of Dakota, USA (Skog & Dilcher 1992) in having entire-margined leaflets, dichotomising venation and an inconspicuous marginal vein. *M. campanicum* differs from *M. lobatum* Nagalingum, 2007 from the Albian of the Alexander Island (Antarctica) in having nearly entire-mrgined leaflets and dichotomizing venation. *M. campanicum* differs from *M. mahisensis* Hu et al., 2008 from the Albian of the Middle East in having larger leaves, nearly entire-margined lamina and dichotomising venation. Other previously published species of fossil Marsileaceae are questioned by Skog & Dilcher (1992) and considered here as doubtful.

The genus *Fortuna marsilioides* (Bell) McIver & Basinger, 1993 differs from *Marsilea* in having reticulate venation of leaflets, more orders of veins and marginal teeth. The only specimen of *Fortuna* comparable to *Marsileaceaephyllum campanicum* is figured by McIver & Basinger (1993) in pl. 45, fig. 4. It represents a rosette of four leaflets with poorly preserved venation.

Regnellites nagashimae Yamada & Kato 2002 from the Late Jurassic to Early Cretaceous of Japan and *Regenellidium diphyllum* Lindmann differ from *M. campanicum* in having only two leaflets per leaf.

Marsilidium speciosum Schenk (1871, p. 225, pl. 26, figs 3, 3a) from the Lower Cretaceous of Germany differs from *Marsileaceaephyllum campanicum* in having hexafoliate leaves with dentate leaflets and rachis as in the genus *Sphenophyllum*.

Cycadopsida
Cycadales
Nilssoniaceae

Genus *Nilsonia* Brongniart, 1824

Type: *Nilsonia brevis* Brongniart, 1824, p. 218, pl. 12, figs 4, 5.

The genus is characterized by entire-margined or dissected elongate lamina bearing cuticle with straight walled ordinary cells and haplocheilic stomata.

Nilsonia cf. *holyi* J. KVAČEK & KNOBLOCH

(pl. 9, figs 7, 8, pl. 34, figs 1, 2; text-fig. 7M, 19)

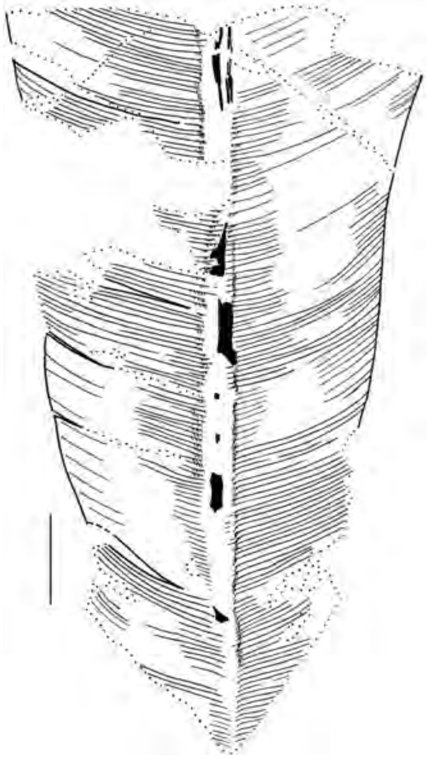
1997 *Nilsonia holyi* J. KVAČEK & KNOBLOCH, p. 46, pl. 1, figs 1-5, pl. 2, figs 4-6, text-figs 2a,b.
2002a *Nilsonia* sp., HERMAN & J. KVAČEK, p. 8, text-fig 1a.

Material: NHMW 1999B0057/0079.

Occurrence: Grünbach am Schneeberg, Austria.

Description: The only specimen available represents a fragment of the basal part of the leaf. The leaf lamina is entire-margined showing a cuneate base, which is incompletely preserved. The leaf fragment is 8 cm long and 4 cm wide. Rare lamina ruptures, simulating segmentation parallel to lateral veins, occur on left leaf margin. The lamina is attached to upper part of the midrib, which is 4-4.5 mm wide. Lateral veins are not forked, slightly curved upwards, simple, emerging from the midrib at an angle of 80°. A few small remains of cuticle adhering to the midrib were obtained for cuticle preparations. Pl. 34, figs 1, 2 show only ordinary cells with straight anticlinal walls and possible rounded trichome base (pl. 34, fig. 1).

Comparison and discussion: Based on morphological characters – lamina attached to the upper side of rhachis, unforked veins and cuticular characters – straight anticlinal walls, we distinguished the genus *Nilsonia* (Cycadales) from *Nilssoniopteris* NATHORST (Bennettitales).



Text-fig. 19: *Nilsonia* cf. *holyi* J. KVAČEK, NHMW 1999B0057/0079, Grünbach (scale bar represents 1 cm).

The lack of well preserved cuticle and the incompleteness of the material, particularly the lack of an apical part of the lamina, prevent us assigning the leaf with certainty to any known species. Using morphological characters in common (entire-margined leaves with lamina ruptures simulating segmentation, similar venation pattern, size and also geographic proximity) we assign the material to the species *Nilsonia holyi* from the Cenomanian of Bohemia (Czech Republic, J. KVAČEK & KNOBLOCH 1997). Other species of *Nilsonia* with entire-margined laminae could be also considered: *Nilsonia yukonensis* HOLLICK from the Upper Cretaceous of Alaska (HOLLICK 1930), *Nilsonia orientalis* from the Jurassic of Siberia (HEER 1878), *Nilsonia tenuinervis* Seward and *N. thomasii* HARRIS from the Jurassic of Yorkshire (HARRIS 1964), *N. johnstrupii* HEER from the Lower Cretaceous of Greenland (HEER 1882).

Pinopsida
Geinitziaceae

Genus *Geinitzia* ENDLICHER, 1847 emended HARRIS, 1969

Type: *Araucarites reichenbachii* GEINITZ, 1842, p. 98, pl. 24, fig. 4 ≡ 1909 *Geinitzia reichenbachii* (GEINITZ) HOLLICK & JEFFREY, 1909, p. 38, pl. 5, figs 7-10, pl. 8, figs 3, 4, pl. 16, figs 2-4, pl. 17, figs 1-4, pl. 18, figs 1-4.

Emended diagnosis: Twigs with helically arranged leaves. Each leaf falcate – curved towards the apex of the twig, subdecurrent, with keel, triangular in transversal section (compare Harris 1969, contrary to Kunzmann 1999).

Discussion: We understand the genus as a morphogenus of sterile twigs of taxodioid affinity according to Harris (1969) and contrary to Kunzmann (1999). Endlicher (1847) defined the genus *Geinitzia* based on his diagnosis of three taxa: *Sedites rabenhorstii* Geinitz, 1842, *Araucarites reichenbachii* Geinitz, 1842 and *Cryptomeria primaeva* Corda in Reuss, 1846. Unfortunatelly, this is not in agreement with current understanding of the ICBN. Following the rules Kunzmann (1999) suggested selecting *Araucarites reichenbachii* Geinitz as a basis for a revision of the genus. The original type specimen of *Araucarites reichenbachii* described by Geinitz (1842) is of unknown repository and very probably lost. In such a case it is necessary to select a lectotype or neotype of *A. reichenbachii*. This issue was discussed by Kunzmann (1999). It is beyond the scope of this publication to deal with the problem in detail.

Comparison: *Geinitzia* differs from *Elatocladus* and *Cunninghamites* in having needles mostly falcate, curved with a keel and clearly quadrangular in transversal section (compare Harris 1979). *Elatocladus* and *Cunninghamites* have straight, flat leaves without any keel (J. Kvaček 1999, Kunzmann 1999). Genus *Cryptomeriopsis* Stopes & Fuji (1910) was emended by Van der Ham et al. 2001 and is used as a morphogenus for sterile taxodiaceous shoots with known epidermal anatomy. *Paracryptomeria* Srinivasan & Friis (1989) is another genus used for coniferous shoots with known epidermal characters. Both of the latter genera are not appropriate for the present material, because it is based mostly on shoot gross morphology only. Very limited information on the epidermal anatomy is available. Velenovský (1885a) used the genus *Sequoia* for these taxa. Sterile twigs of the studied material do not show any generic character of *Sequoia* and associated ovuliferous cones argue even more against this assumption.

Geinitzia reichenbachii
(Geinitz) Hollick & Jeffrey

(pl. 10, figs 6-10, pl. 34, figs 3, 4; text-fig. 7P)

1842 *Araucarites reichenbachii* Geinitz, p. 98, pl. 24, fig. 4.
1847 *Geinitzia cretacea* Endlicher, p. 17.
1847 *Geinitzia cretacea* Endlicher, p. 280.
1868 *Sequoia reichenbachii* (Geinitz) Heer, p. 83, pl. 43, figs 1d, 2b, 5a.
1869 *Sequoia reichenbachii* (Geinitz) Heer, p. 8, pl. 1, figs 1-9.
1885a *Geinitzia cretacea* Endlicher; Velenovský, p. 15, pl. 8, figs 3, 11, 12, pl. 9, figs 1, 2.
1885a *Sequoia reichenbachii* (Geinitz) Heer; Velenovský 1885a, p. 15, pl. 8, figs 3, 11, 12, pl. 9, figs 1, 2.
1898 *Sequoia reichenbachii* (Geinitz) Velenovský; Bayer in Frič, p. 71, text-fig. 96.
1909 *Geinitzia reichenbachii* (Geinitz) Hollick & Jeffrey, p. 38, pl. 5, figs 7-10, pl. 8, figs 3, 4, pl. 16, figs 2-4, pl. 17, figs 1-4, pl. 18, figs 1-4.

Stratum typicum: Bílá Hora Formation, Turonian.

Locus typicus: Dresden – Strehlen, Saxony, Germany.

Material: GBA: 2006/64/17, …/18, …/26, …/44, …/32, …/36, …/37, 2006/68/03, 2006/69/08. NHMW: 1970/1396/1800, 1999B0057/0122b, …/0129, …/0140, …/0152, …/0181, …/0209b, …/0210, …/0211, …/0217, …/0218a, …/0219, …/0220, …/0221, …/0222, …/0223, …/0224, …/0225, …/0226, …/0228, …/0229, …/0230, …/0231, …/0232, …/0233, …/0234, …/0325a, …/0558, …/0563a, …/0571, …/0573, …/0801. IPUW: 2 unnumbered specimens.

Occurrence. Grünbach Formation (Lower Campanian): Grünbach am Schneeberg, Frankenhof, Austria; Dresden Strehlen, Germany; Klikov, Zliv, Czech Republic.

Typification: For discussion of the type material see Kunzmann (1999).

Description: The material studied consists of numerous fragments of twigs, which show helically arranged shortly decurrent needles. Needles with a keel are straight or falcate, emerging from the twig at angles of 40-90°. They are usually 15-20 mm in length (No. GBA 2006/64/18) and 0.5-1.2 mm in width. Their base is usually wider (2-3 mm). Needles are rhomboidal in cross section (pl. 10, fig. 9). Each needle shows a rhomboidal leaf base (pl. 10, fig. 8, No. NHMW 1999B0057/221), which grows with age in a similar way to recent conifers. Observed axes of leafy twigs reach a width 1.5-15 mm in diameter depending on the age of the twig (max. diameter recorded in the specimen No. NHMW 1999B0057/0571. Twigs documenting the phylotaxy and needle morphology are shown on plate 10, figs 6-10.

Fragments of cuticle were separated from the specimen No. NHMW 1999B0057/0221. It shows isodiametric to elongate polygonal cells (10-20 x 30-60 μm) with straight anticlinal walls (pl. 34, figs 3, 4). Stomatal aparati oval 50 x 25 μm (pl. 34, fig. 4).

Discussion: *Geinitzia reichenbachii* is one of the most widespread Late Cretaceous conifers. It was described from numerous Late Cretaceous localities in the Northern Hemisphere under various names: *Geinitzia cretacea* Endlicher, *Seqoia reichenbachii* (Geinitz) Heer, *Sequoia rigida* Heer etc. Morphology of its shoot is similar to the recent *Athrotaxis cupressoides* D. Don (Farjon 2005), however, its ovuliferous cones are not available for closer comparison.

Geinitzia reichenbachii has always been found without any attached ovuliferous cone. Therefore it represents a pure morphogenus for coniferous twigs. In the Grünbach Flora, twigs assigned to *G. reichenbachii* bear helically arranged needles, which are rhomboidal in cross section along the entire needle, having needles comparatively longer than *G. formosa*.

Geinitzia reichenbachii was described from various localities in Europe. Velenovský (1885a) described this conifer from numerous sites in the Bohemian Cenomanian. Similar occurrences are known from Poland (Karczmarz & Popiel 1966 pl. 1, fig. 2), Belgium (*Sequoites primaeva*, Stockmans 1946), the Netherlands (*Sequoia reichenbachii*, Kräusel 1922) and Romania (*Geinitzia cretacea*, Givulescu & Lacatusu 1978, Givulescu et al. 1980), (*Sequoia rigida*, Bozzi 1888). More records of *G. reichenbachii* from various localities in Italy are mentioned by Gomez et al. 2002). *Geinitzia reichenbachii* is also known from North America. It is e.g. described by Raubeson & Gensel (1991) from the Black Creek Formation in North Carolina.

Geinitzia formosa Heer

(pl. 11, figs 1-12; text-fig. 7O)

1852 *Geinitzia cretacea* Endlicher; Unger, p. 93, pl. 34, fig. 6.
1871b *Geinitzia formosa* Heer, p. 6, pl. 2, figs 1-6.
? 1975 *Geinitzia cretacea* Endlicher sensu Unger; Němejc & Z. Kvaček, p. 27, text-figs 5-7, pl. 2, figs 2, 6-8, pl. 3, fig. 1, pl. 16, figs 1-3, pl. 17, figs 1-6.
1999 *Geinitzia formosa* Heer; Kunzmann, p. 114, text-fig. 22, pl. 26, figs 1-8, pl. 27, figs 5-10, pl. 28, figs 1-6.

Neotype: Designed by Kunzmann (1999) UW 3936, Würzburg University.

Material: GBA: 2006/64/38.
NHMW: 1861/0003/0096, 1970/1396/1648, …/1660, 1999B0057/0100a, …/0208, …/0215b, …/0227, …/0234, …/0244, …/0284a, …/0286, …/0547, …/0557, …/0574, …/0575, …/0576, …/0577, …/0578.

Occurrence: Grünbach Formation (Lower Campanian): Grünbach am Schneeberg, Austria; Quedlinburg, Germany; Zliv, Bohemia, Czech Republic.

Diagnosis: For emended diagnosis see Kunzmann (1999).

Description: The material studied consists of numerous fragments of twigs and several ovuliferous cones, one of which is born terminally on a twig (pl. 11, fig. 7). Fragments of sterile twigs show helically arranged shortly decurrent needles. Needles with a keel are s-shaped or curved upwards to the twig apex, emerging from the twig at angles of 20-40°. They are usually 2-10 mm in length (maximal recorded length 11 mm – no. NHMW 1999B0057/0208) and 0.2-0.8 mm in width. Needles are rhomboidal in cross section in basal part and triangular in cross section in apical part. Each needle shows a rhomboidal leaf base (pl. 11, fig. 2, nos NHMW 1999B0057/0547, 1999B0057/0576). Axes of leafy twigs reach a width of 0.5-5 mm in diameter (max. diameter recorded in the specimen no. NHMW 1999B0057/0576).

Ovuliferous cones of *Geinitzia formosa* are elongate, cylindrical bearing helically arranged bracts. Each bract consists of a massive stalk and a head. The only complete specimen of the ovuliferous cone No. NHMW 1999B0057/0575 reaches 63 mm in length and 16 mm in width. The number of bracts per cone is about 40 (pl. 11, figs 8, 10). Bracts are 15-17 mm long having a stalk 4-5 mm in diameter and a head 7-8 mm in diameter. Each head is flat rhomboidal and sometimes possibly polygonal with a small mucro in its centre (pl. 11, fig. 12, NHMW 1999B0057/0575). The ovuliferous cone born on a twig is not completely preserved, being 51 mm in length and 17 mm in diameter. It shows about 32 bracts 5-7 mm long.

Cuticle removed from the specimen No. NHMW 1999B0057/0575 is poorly preserved showing elongate ordinary cells (5-12 x 20-25 μm) with straight anticlinal walls and very poorly preserved stomata.

Comparison and discussion: *Geinitzia formosa* differs from *G. reichenbachii* in having shorter needles, which are frequently s-shaped. The needles of *G. formosa* are rhomboidal only their basal parts, they are triangular apically. Ovuliferous cones attached to or associated with sterile twigs have the appearance of those described by Heer (1871b) and Kunzmann (1999) from the Santonian of Quedlinburg. The studied ovuliferous cones are of similar size range as the cones demonstrated by Kunzmann (1999, pl. 26). *G. formosa* differs from *G. schlotheimii* Kunzmann, Knoll & Gaipl (2003) described from the Aachenian Santonian in having smaller ovuliferous cones with smaller number of ovuliferous cone scales. Comparison with the material described by Němejc & Z. Kvaček (1975) from the Santonian of Bohemia is difficult because of the lack of any ovuliferous cone attached or associated with the Bohemian material and very poorly preserved cuticle of the Austrian material; sterile twigs from both localities are very similar in gross-morphology, and due to this reason we assign the Bohemian twigs to the same species.

Pinopsida incertae sedis

Genus *Pagiophyllum* Heer, 1881

Type: *Pachyphyllum cirinicum* Saporta in Thiolliére 1873, p. 37 ≡ *Pagiophyllum cirinicum* (Saporta) Heer, 1881, p. 11, pl. 10, fig. 6.

The genus *Pagiophyllum* was emended by Harris (1969) as a morphogenus for sterile coniferous twigs having needles helically arranged, and with the length exceeding the width of the leaf cushion and with a base which does not narrow.

Pagiophyllum sp.

(pl. 10, figs 3-5)

Material: GBA 2006/64/42.

Occurrence: Grünbach Formation (Lower Campanian), Grünbach am Schneeberg (Josefifloetz).

Description: The only specimen available for the present study represents a leafy twig bearing helically arranged needles. Each needle is shortly decurrent, as broad as its cushion, curved upwards, sometimes s-shaped, 1-2.5 mm long and 0.5-0.8 mm wide. Its free part is longer than, or equal to, the basal part attached the twig. The length of each needle exceeds breadth of the leaf cushion.

Comparison and discussion: Morphology of the leafy twig shows characters fitting the morphogenus *Pagio-*

phyllum as redefined by Harris (1969). Its free leaf portion is longer than the width of the cushion (Harris 1979). The case of the present material is very near to an arbitrary boundary between genera *Brachyphyllum* and *Pagiophyllum*. *Brachyphyllum* sp. published by Van der Ham et al. (2003) is quite similar to the presently described material. Similar twigs were described under several names: e.g. *Cyparissidium cretaceum* Schenk (1875-76) from the Gosau Group in northern Tyrol (locality of Brandenberg), *Cyparissidium gracile* Heer and *Glyptostrobus europeus cretaceus* from the Bohemian Cenomanian by Velenovský (1885a). Due to uniformity of the sterile foliage among conifers, particularly Cupressaceae s. l., it is difficult or even impossible to identify more accurately such twigs, therefore we avoid attempting to associate these remains with any species name.

Genus *Podozamites* (Brongniart) C. Braun in Münster, 1843

Type: *Zamites distans* Presl in Sternberg 1838: 196, pl. 41, fig. 1 ≡ *Podozamites distans* (Presl in Sternberg) C. Braun in Münster 1843: 28, 36.

Podozamites cf. *lanceolatus* (Lindley & Hutton) Harris

(pl. 10, figs 1, 2; Text-figs 7N, 20)

1885a *Podozamites lanceolatus* (Lindley & Hutton) Heer; Velenovský p. 11, pl. 2, figs 1-19, 24.
1975 *Podozamites* aff. *lanceolatus* (Lindley & Hutton) Heer; Němejc & Z. Kvaček, p. 19, pl. 2, fig. 1.
1997 *Lindleycladus* cf. *lanceolatus* (Lindley & Hutton) Heer; Knobloch & J. Kvaček, p. 581, text-figs 9a-c, e-h.
2002a *Lindleycladus* cf. *lanceolatus* (Lindley & Hutton) Heer; Herman & J. Kvaček, p. 8, text-fig 1a.

Material: NHMW 1999B0057/0246.

Occurrence: Grünbach am Schneeberg.

Description: The only hand specimen available shows a twig with five mostly incompletely preserved leaves attached (pl. 10, figs 1, 2). Near 4 virtually attached leaves, there are five more leaf fragments arranged in a position which corresponds with their possible attachment to a part of the same twig which is not preserved (pl. 10, fig. 1). The twig is 1.5-2 mm wide, showing ridges. Each leaf is entire-margined, long lanceolate with an obtuse apex and acute base. The length of leaves is 50-57 mm, width varies from 3 mm to 6 mm. There are 11-12 simple veins running from base parallel to the leaf margin (pl. 10, fig. 2). The veins do not fork in the leaf base; therefore vein density in basal and apical parts of a leaf is higher than in its central part. The specimen is a seemingly well-preserved leaf compression, but all attempts to prepare a cuticle preparation failed. The coal matter was always completely dissolved during the maceration process and no cuticle was obtained.

Text-fig. 20: *Podozamites* cf. *lanceolatus* (Lindley & Hutton) Harris, NHMW 1999B0057/0246, Grünbach (scale bar represents 1 cm).

Comparison and discussion: Although our specimen is morphologically very similar to *Lindleycladus lanceolatus* (Lindley & Hutton) Harris, particularly to *Lindleycladus* cf. *lanceolatus* (Lindley & Hutton) Harris described by Knobloch & J. Kvaček (1997, Text-figs 9a-c, e-h) from the Cenomanian of Moravia, a lack of cuticle does not allow us to assign this specimen to the genus *Lindleycladus*. We understand the species *lanceolatus* in its broad sense i.e. it accommodates all impressions showing lanceolate, parallel veined leaves attached to a long twig. Similar leaves are known from the middle Jurassic to Upper Cretaceous. In the Cenomanian of Bohemia VELENOVSKÝ (1885a) described a similar leaf under the name *P. lanceolatus* from the locality of Bohdánkov (VELENOVSKÝ 1885a, pl. 2, figs 11-19). KNOBLOCH & J. KVAČEK (1997, Text-figs 9a-c, e-h) recorded a very similar leaf from the Cenomanian of Moravia, locality Velké Opatovice. A leaf fragment from the Senonian of south Bohemia (NĚMEJC & Z. KVAČEK 1972, pl. 2, fig. 1) represents another occurrence of this taxon. The genus *Lindleycladus* is also known from the Early Cretaceous of Brazil (KUNZMANN et al. 2004).

Notes on ecology: it is interesting to note that there are three additional isolated leaf fragments occurring on the same hand specimen. This fact documents the local abundance of this foliage type. Unfortunately, we lack any information about its position in the sedimentary succession.

The species is interpreted according to our experience from other floras, e.g. of the Peruc-Korycany Formation, as representing a mesophytic upland forest.

Magnoliophyta
Liliopsida

Monocots are well represented in Grünbach. They are mostly recorded as foliage (4 species), but also as reproductive structures (1 species). Members of the Pandanaceae and the Arecaceae represent one of the earliest occurrences of these groups in the fossil record. The descriptive terminology of monocot leaf morphology and venation used here was that published by HICKEY & PETERSON (1978) and MAYO & al. (1996).

Arales
Araceae

Genus *Lysichiton* SCHOTT, 1857

Type: *Dracontium camtschatcense* LINNAEUS 1753, p. 968 ≡ *Lysichiton camtschatcensis* (LINNAEUS) SCHOTT 1857, p. 62.

Discussion. The recent genus *Lysichiton* which belongs to the subfamily Orontioideae of the Araceae differs from *Araciphyllites* WILDE et al., 2005 of the subfamily Aroideae in having less dense secondary veins and nearly quadrangular areoles. As pointed out by BOGNER et al. (2007), foliage of *Lysichiton* is so characteristic that they were able to identify the fossil with the recent genus. *Lysichiton* is characterised by oblong leaves with midcosta reaching the leaf apex and lateral primaries arising successively along its length. Its higher-order venation is more or less regularly transverse-reticulate, forming elongate rectangular meshes (BOGNER et al. 2007).

Lysichiton austriacus
(J. KVAČEK & HERMAN) BOGNER, JOHNSON, Z. KVAČEK & UPCHURCH

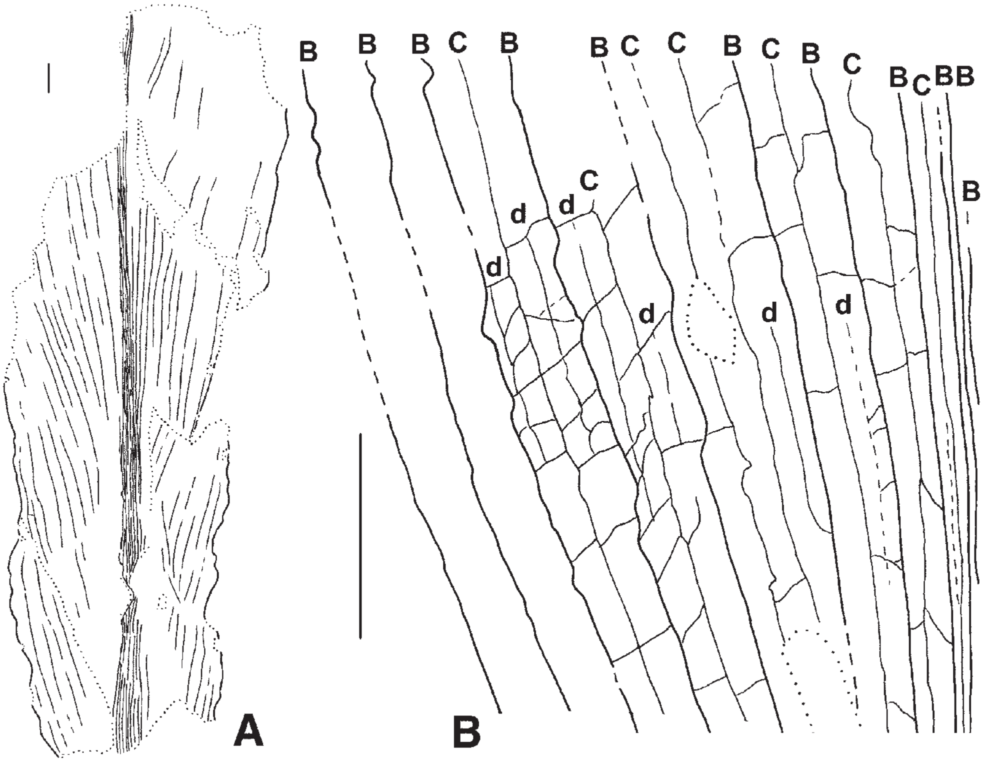
(pl. 12, figs 1, 2, 4; text-figs 7V, 21)

2004a *Araciphyllites austriacus* J. KVAČEK & HERMAN, p. 327, text-fig. 3; pl. 1, figs 1, 2, 4, nom. inval.
2005 *Araciphyllites austriacus* J. KVAČEK & HERMAN, p. 4, text-figs 1-2A, B.
2007 *Lysichiton austriacus* (J. KVAČEK & HERMAN) BOGNER, JOHNSON, Z. KVAČEK & UPCHURCH, p. 142.

Holotype: NHMW 1999B0057/0183.

Occurrence: Grünbach am Schneeberg, Segen Gottes Schacht.

Emended diagnosis: Leaf blade simple, entire-margined; midrib multistranded massive, deeply impressed, venation pinnate, eucamptodromous,



Text-fig. 21: *Lysichiton austriacus* (J. Kvaček & Herman) Bogner et al., holotype NHMW 1999B0057/0183, A – leaf outline and venation, B – detailed venation, Grünbach (scale bar represents 1 cm).

primary lateral veins consisting of several weakly differentiated vein subsets, higher-order venation arranged more or less in regular transverse reticulate pattern between them, forming areoles.

Description: The only specimen available is the holotype (pl. 12, fig. 2). It shows thin, lanceolate elongate leaf lamina 260 mm long, narrowing from more than 100 mm in the terminal part to 60 mm in the basal part. The leaf margin is entire, slightly undulate in the basal part. The midrib narrows from the base (12 mm wide) to the apex (3 mm in width). The primary laterals are arranged in three poorly differentiated orders. They emerge at an angle of about 10° from a multistranded midcosta (text-fig. 21, pl. 12, fig. 2). Each order has veins of specific width: B – 0.12 – 0.10 mm, C – 0.08-0.06 mm, d – 0.05-0.03 mm. Spacing of the parallel veins varies from 0.8 to 1.2 mm. Higher-order venation is more or less regularly reticulate between them. Transverse veins vary in width (0.10 – 0.03 mm); they seem to form two width orders 0.08-0.06 mm and 0.05-0.02 mm. The first set frequently connects two adjacent veins “C”, the second connects veins “d”. Both transverse vein orders are straight or curved, sigmoidal or s-shaped, spaced 0.5-2.8 mm apart. They are perpendicularly or obliquely oriented to the primary laterals (text-fig. 21B, pl. 12, fig. 4).

Comparison and discussion: *Lysichiton austriacus* shows a multistranded midrib, lateral primaries arising successively along its length and higher-order venation of regularly transverse-reticulate pattern forming elongate rectangular meshes (Bogner et al. 2007) – characters, which fit well with the diagnosis of *Lysichiton*.

Lysichiton austriacus differs from *Araciphyllites tertiarius* (Engelhardt) Wilde et al. (2005) in having numerous closely placed secondary veins and rectangular alveoles.

The species *Lysichiton americanus* (pl. 12, figs 3, 5), in particular, is remarkably similar to *L. austriacus* showing a multistranded midrib, similar arrangement of secondary veins and rectangular aleveoles (Mayo et al. 1997). *L. austriacus* differs from *L. americanus* in having a higher number of lateral vein orders and two orders of transversal veins. The similarity of *L. austriacus* to other recent monocotyledon families is less pronounced. Members of the Alismataceae, Hydrocharitaceae and Limnocharitaceae differ from *L. austriacus* in lacking acrodromous venation with reticulate secondaries and a simple midrib.

Pandanales
Pandanaceae

Genus *Pandanites* Tuzson, 1913, emended J. Kvaček & Herman, 2004a

(non *Pandanites* Dorf 1942, p. 46, nom. illegit.)

Pandanophyllum Kryshtofovich, 1929, p. 120(1364), nom. illegit. (non *Pandanophyllum* Hasskarl ex Steudel, 1855, p. 134)

Type: *Pandanites acutidens* Tuzson, 1913, p. 219, pl. 15, fig. 6.

For emended diagnosis of the genus *Pandanites* and discussion of the genus see J. Kvaček & Herman (2004a). *Pandanites* only superficially recalls fossil leaves *Desmiophyllum* Unger 1850 (Van Konijnenburg – van Cittert 1992) and *Dammarites* Presl in Sternberg 1838 (Hluštík 1976, 1977b). However, both types of leaves do not show M-shape of leaves if transversally sectioned and therefore have nothing in common with the genus *Panadanites*.

Pandanites trinervis (Ettingshausen) J. Kvaček & Herman

(pl. 13, figs 1-4; pl. 14, figs 1-5; pl. 15, figs 1-6, 9; pl. 16, figs 1-5; text-figs 7R,S, T, 22, 56)

1852 *Pandanus trinervis* Ettingshausen, p. 494, pl. 26, fig. 1.
1852 *Pandanus austriacus* Ettingshausen, p. 492, pl. 23, fig. 1.
1852 *Pandanus pseudo-inermis* Ettingshausen, p. 493, pl. 24, figs 1, 2; pl. 25, fig. 1.
2004a *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, text-fig. 4, pl. 2, figs 1-4, pl. 3, figs 1-5, pl. 4, figs 1-9, pl. 5, figs 1-5.

Holotype: GBA 1852/02/01, Ettingshausen 1852, pl. 26, fig. 1 (J. Kvaček & Herman 2004a).

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Dreistätten, Austria.

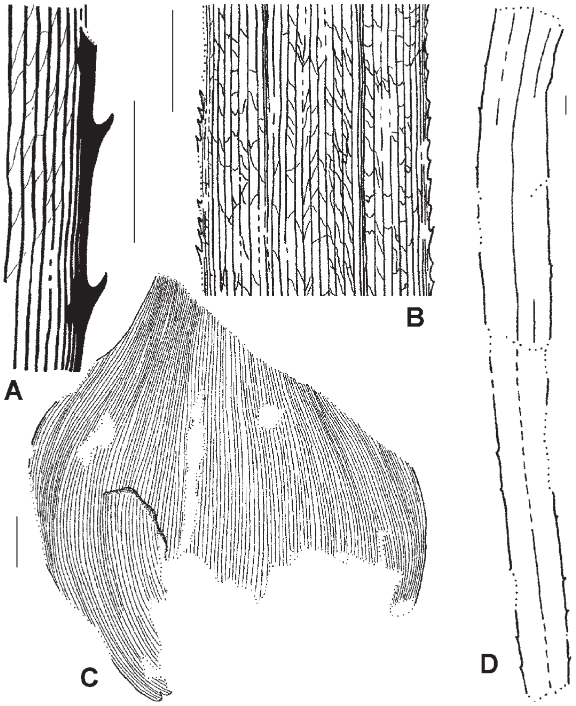
Material: GBA: 1852/02/02, …/03, 1852/03/05b, 2001/06/02, …/03, …/04, …/09, 2006/60/20, …/24, …/26, …/39, …/41, …/53, …/54, …/56, …/57, …/64, …/66, …/67, …/69, …/70, …/71, …/74, …/76, …/77, 2006/64/03, …/10, …/19, …/22, …/30, …/31, …/33, …/34, …/41, …/45; 2006/68/02, …/05, 2006/69/01, 2006/70/01, 2006/75/39A,B.
NHMW: 1853/0003/0034, …/0037, …/0038, …/0041, …/0043, …/0053, …/0054, …/0055,1970/1396/614, 1999B0057/0031, …/0041, …/0061, …/0102a, …/0151, …/0154 to …/0156, …/0158, …/0165, …/0166, …/0167, 0168, 0169, …/0171, …/0172, …/0173, …/0176 to …/0178, …/0180b, …/182, …/0184, …/0186b, …/187, …/0188, …/0190, …/0192, …/193, …/0196a, …/0197, …/0202, …/0204, …/0209a, …/0213, …/0239, …/0259a, …/0260, …/0280, …/0284b, …/0285, …/0289, …/0331a, …/0364a, …/0394c, …/0435a, …/0474a, …/, …/0528, …/0529, …/0534 – 0546, …/0549, …/0563b, …/0584a.
NMP: K 418, K 419
IPUW: several unnumbered specimens.

Occurrence: Austria: Grünbach Formation, Gosau Group, Early Campanian: Dreistätten, Grünbach am Schneeberg, Muthmannsdorf, Frankenhof; St. Wolfgang-Tiefengraben, Geistthal: Gosau Group, ?Campanian, Austria; Romania: Rusca Montana; Maastrichtian.

Diagnosis: For emended diagnosis of *Pandanites trinervis* see J. Kvaček & Herman (2004a).

Description: The holotype of *Pandanites trinervis* (pl. 13, fig. 1) shows three leaf fragments in a position suggesting their original emergence from a shoot. Each of the fragments is linear, with marginal spines 1 mm long, relatively regularly distributed at distances of 3-5 mm apart on both leaf margins. There is only one vein order parallel to the margin (distance between veins 0.3-0.5 mm). Thin transverse veins connect primaries at oblique, or rarely right, angles (pl. 13, fig. 4).

There are numerous specimens of leaves of *P. trinervis* in the collection of NHMW and GBA showing various parts of leafy shoots, leaf apices, bases and leaf margins. The whole terminal parts of branches are shown in specimens No. NHMW 1999B0057/0179, 1999B0057/0176, 1999B0057/0192, GBA 2006/64/25. Their leaves are spirally inserted (pl. 15, fig. 1). The longest preserved leaf fragment is 396 mm long and 28-40 mm wide (pl. 14, fig. 1). The maximum width of the lamina among the studied leaves is 94 mm (No. NHMW 1999B0057/0280). Several transversally broken specimens show M-shape sections of leaves (pl. 14, figs 3, 4). The sheathing leaf base of *P. trinervis* varies in shape. Some specimens show a more open base (NHMW 1999B0057/0193, 1999B0057/0543 and GBA 2001/06/02), others are nearly auriculate (NHMW 1999B0057/0285, text-fig. 22C, pl. 14, fig. 5). The apex is attenuate showing a drip-tip (pl. 14, fig. 2). Nearly all leaves are to some degree armed with spines, but leaf fragments without spines are also common. Basal parts of leaves, similar to recent members of the family, have usually no spines (compare pl. 14, figs 5, 6). The spines occur on margins (pl. 16, figs 2, 4, 5) and abaxial face of the midrib (pl. 15, fig. 2). Considerable variation in the size of marginal spines (0.5-3 mm) and their spacing (2-20 mm) are documented in pl. 15, figs 3, 4, and pl. 16, figs 2-6. The midrib is well pronounced possibly being sclerified. Similarly fibres occur in the middle of each half of the leaf lamina (section located in the region of "M" sinuses). The fibres are preserved, e.g., in the holotype (pl. 13, figs 1, 4) and in the specimens NHMW 1999B0057/0154 (pl. 16, figs 1, 2), NHMW 1999B0057/0528, GBA 2006/64/31, running parallel to veins, and seemingly showing a second, thicker, order of veins (pl. 13, fig. 4; pl. 16, fig. 3).



Text-fig. 22: *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, A – NHMW 1999B0057/0041, leaf margin and fine venation near margin, B – NHMW 1999B0057/0154, leaf venation, C – NHMW 1999B0057/0285, leaf base, venation shown schematically, D – largest leaf fragment NHMW 1999B0057/0239, Grünbach (scale bar represents 1 cm).

Venation of many leaves is not easily discernible due to the thick coal matter. Only some specimens (e.g. the holotype), which were probably naturally macerated before fossilisation, show the venation clearly (pl. 13, fig. 4; pl. 16, figs 1-4). Leaf lamina of all specimens exhibit only one order of veins (0.05-0.3 mm thick). Delicate obliquely or perpendicularly orientated veins (0.01 mm thick) run transversally to the main order (pl. 16, fig. 4; text-figs 22A, B). The density of veins is usually 16-30 per cm. Narrower parts of leaves show typically higher vein density than the wider parts. The lowest density, 8 veins per cm, was recorded in the specimen No. GBA 2001/06/02.

Cuticles, although seemingly well preserved, are difficult to prepare. The specimen NHMW 1999B0057/0541 provides an example of an exceptionally well-preserved leaf compression, from which cuticles of both leaf sides were obtained. The adaxial cuticle shows elongate ordinary cells (5-12 x 25-65 μm) with straight or curved anticlinal walls 2-5 mμ thick (pl. 15, fig. 5) and isodiametric cells resembling crystal cavities (10 x 10 μm). Isolated tetracytic stomata, which sometimes occur in short rows (pl. 15, fig. 5), have two lateral subsidiary cells and two unspecialised polar cells (guard cells 3-5 x 20-25 μm; subsidiary cells 10-15 x 15-34 μm). The abaxial cuticle shows wide intercostal bands and narrow costal bands of 5-20 cells. Intercostal bands consist of isodiametric or elongate ordinary cells (5-12 x 16-55 μm) and numerous longitudinally orientated tetracytic stomata. Each stoma typically consists of two guard cells (2-3 x 12-15(25) μm) and four unspecialised subsidiary cells (pl. 15, fig. 9), two of which are in lateral (7-12 x 25-40 μm) and two in polar (10-20 x 15-25(45) μm) positions. In some stomata one lateral cell may be replaced by two smaller ones. The hypodermis consists of isodiametric polygonal cells.

Comparison and discussion: Ettingshausen (1852) described three species of pandan-like leaves from Grünbach: *Pandanus trinervis*, *P. austriacus*, *P. pseudo-inermis*. We have selected *P. trinervis* as the most typical and the best preserved among the described species. The holotype of *Pandanus austriacus* is currently of unknown repository and that of *P. pseudo-inermis* is poorly preserved. Considering the figure and Ettingshausen's description, it can be seen that there are small differences between *P. austriacus* and *P. trinervis* e.g. size of spines and thickness of veins, which we consider to be within the scope of variation within the species. The basal parts of larger leaves of recent pandans also show bigger spines. The thickness of veins and their number seem to be very variable within *Pandanus* leaves in general. In *Pandanites trinervis* vein thickness varies from 0.6 to 0.2 mm, and their density ranges from 8 to 20 veins per cm, depending on the position in the leaf.

The thicker vein order described in *P. pseudo-inermis* and three thick parallel strands in *P. trinervis* do not appear to be true veins. During our studies more than 70 specimens from three collections were inspected. We found out that preservation and degree of decomposition before burial controls the appearance of pandanoid fossil leaves (J. Kvaček & Herman 2004a). We decided to run an experiment lasting one year on maceration of recent *Pandanus* leaves in KOH. The leaf parenchyma gradually degraded and the leaf became progressively more translucent, but its sclerotic fibres were not affected, becoming more clearly visible. Therefore we suggest that the three veins of *P. trinervis* and also the thicker veins of *P. pseudo-inermis* actually represent fibres, which became more pronounced in certain stages of natural maceration in water (J. Kvaček & Herman 2004a).

There are several occurrences of pandans in the Cretaceous of the Gosau Group in Austria (Summesberger, pers. comm., 2002). One locality in the vicinity of the village of Geistthal (Gosau Group) was described by Knobloch (1977) who assigned fragments of fossil leaves to "*Pandanus*" *austriacus* (Nos NMP K 118, NMP K 119). The specimens were compared to *Pandanites trinervis*. Although the leaves are poorly preserved and not showing good marginal spines, their slightly M-shaped transversal sections allows interpreting them as poorly preserved leaves of *P. trinervis*. Other localities with recorded *Pandanites trinervis* are St.Wolfgang (J. Kvaček 2007b), Aigen near Salzburg, Kainach and Gams near Hieflau. Study of this material will be an object of another paper.

Pandanites acutidens Tuzson (1913), although known only from the illustration by Tuzson (1913), is treated here as conspecific with *P. trinervis*. It shows a leaf of similar M-shaped transversal section, the same venation pattern and well-preserved marginal spines. Other *Pandanus*-like leaves were described from the Maastrichtian of Rusca Montana in Romania by Petrescu & Dusa (1980). All of them: *Pandanus spinatissimus* Petrescu & Dusa 1980, *P. barburi* Petrescu & Dusa 1980, *P. tenuissimus* Petrescu & Dusa 1980 were invalidly published as *nomina nuda*. They probably represent various fragments of one taxon, which corresponds in gross morphology to *Pandanites trinervis*.

Pandanophyllum ahnertii Kryshtofovich from the Aptian of Siberia (Kryshtofovich 1929, pl. 59, figs 1-3, age confirmed by Krassilov 1967) exhibits linear leaves with doubtful marginal spines and an M-shaped transversal section of lamina. After inspection of the type material in All-Russian Geological Prospecting Institute (VNIGRI) in St. Petersburg (JK, 2004), it become clear that *Pandanophyllum ahnertii* is a very doubtful taxon. Its lamina is very narrow and difficult to interpret. The material is very fragmentary, representing probably a fragment of an axis or doubtful leaf fragment.

Pandanites corsonii Dorf from the Maastrichtian of the Rocky Mountains (Dorf, 1942, pl. 3, fig. 1) shows characters similar to *P. trinervis* including M-shaped cross section of leaf lamina and venation pattern. It is difficult to find significant differences between these two fossil leaves. A minor difference is in the size of marginal spines. *P. trinervis* has marginal spines 0.5-3 mm long, while *P. corsonii* has spines 5-6 mm long. The latter also lacks spines on the abaxial surface of the midrib, although it is not easy to clarify this character in the fossil state, a problem already experienced in our studies of *Pandanites trinervis*.

Another, probable new, *Pandanites* is recorded by Upchurch & Mack (1998) from the Maastrichtian of New Mexico. The authors mention, without any illustration, presence of “three longitudinal folds” within an armed leaf. This combination of characters is typical for transversely M-shaped pandanoid foliage.

Comparison of leaf epidermal structure of *Pandanites trinervis* and recent representatives of the genus *Pandanus* shows similarity in general appearance, but differences in details. Stomata of recent representatives of the genus, e.g. *Pandanus veitchii* Dall and *P. edulis* Thou are surrounded by specialised subsidiary cells differentiated into small, more isodiametric, thickly cutinised polar cells (compare Tomlinson 1965). Subsidiary polar cells of *Pandanites trinervis* (pl. 15, fig. 9) are not usually specialised (compare pl. 15, figs 8 and 9). Unspecialised polar cells are confined to some recent, usually basal members of the genus *Pandanus* and to the genus *Sararanga* (Tomlinson 1965).

The family Pandanaceae shows numerous ancestral characters and is considered to be quite ancient among Monocotyledons (Cox et al., 1995). It consists of four living genera: *Pandanus* Linnaeus (700 species in Indo-Pacific region), *Freycinetia* Gaudichaud-Beaupré (200 species in Austral-Asian region), *Sararanga* Hemsley (2 species in the Philippines and Melanesia) (Stone et al. 1998), and *Martellidendron* Callmander et al. 2003 (7 species in Madagascar). The genus *Sararanga* is considered to be the most basal in the pandanoid clade (Dahlgren et al., 1985; Hotton et al., 1994). Within the genus *Pandanus* there are about 60 sections occurring mostly in Old world tropics from West Africa to Polynesia. Both *Martellidendron* and *Sararanga* show reticulate pollen grains with small lumina (Callmander, 2001); characters which are regarded as ancestral not only within the family, but for all monocotyledons and angiosperms (e.g. Walker & Walker 1984). However, the situation in the Pandanaceae is more complex, according to the last study (Callmander et al. 2003) the genus *Martellidendron* is more related to *Freicinetia*.

Occurrence of fossil pandans in the Late Cretaceous together with ancestral characters recorded in the recent representatives [as, for example, absence of style, incompletely sealed carpels (Stone et al. 1998)], and molecular data (Soltis et al. 2000), support the assumption of great antiquity of the family.

Genus *Gruenbachia* J. Kvaček & Herman, nov. gen.

Type: *Gruenbachia pandanoides* J. Kvaček & Herman nov. spec.

Etymology: After Grünbach village in Lower Austria.

Diagnosis: Globular infructescences/inflorescences consisting of radially arranged multicarpelate units. Each unit consisting of several basi-medially fused carpels.

Discussion: The globular infructescences/inflorescences *Gruenbachia* are compared to the female reproductive structures of the recent Pandanaceae. Although microscopic details including structure of pollen grains are missing, we suggest that there are enough characters to unequivocally identify the taxon. Particularly important are clear delimitations of carpels/fruitlets into phalanges and also their characteristic apical extensions. Additionally, globular infructescences are attached to the axis, triangular in perpendicular section which is typical for monocots, and the fructifications occur in intimate association with leaves of *Pandanites trinervis*.

Gruenbachia differs from similar radially aggregated inflorecences/infructescenses of Platanaceae and Altingiaceae and *Sparganium* in having clear basi-medial fusion of carpels/fruitlets into units. Additional characters are triangular axis and association with extremely abundant foliage of *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman.

Among fossil reproductive structures most similar to *Gruenbachia* seems to be the genus *Viracarpon* Sahni (1934) from the Deccan Beds in India. *Viracarpon* differs from *Gruenbachia* first of all in mode of preservation; it is preserved as a permineralised fructification. It consists of syncarps each containing six carpels. The carpels are completely or partly fused, but in a different way than in *Gruenbachia*. *Gruenbachia* shows basi-medial fusion of carpels whereas *Viracarpon* shows medio-apical fusion of carpels (Namburdi & Tidwell 1978). Other characters are difficult to compare due to the different form of preservation.

Five species of *Viracarpon* were described: *V. hexaspermum*, *V. elongatum*, *V. tenue* (Sahni, 1964), *V. chitaleyi* (Patil, 1972) and *V. sahnii* (Chitaley & al., 1969), which is usually considered synonymous with *V. hexaspermum*, showing very similar characteristics.

Revision by Bande & Awasthi (1986) concluded that *Viracarpon* does not belong to Pandanaceae and its affinity still remains unknown.

Pandanusocarpon umariense Bonde 1990 from the Eocene of the Deccan Intertrapean Beds of India represents an isolated perminerlized single seeded fruit. Except for its globose shape and general fruit structure it does not show any resemblance to the Pandanaceae (Bonde 1990).

Other fossil reproductive structures are less similar to *Gruenbachia*. Heads of platanoid infructescences (*Platanus laevis* Knobloch & Mai 1986, *Sparganium dinosauri* Velenovský & Viniklář 1926, pl. 21, fig. 8 – interpreted here also as an impression of a Platanaceae pistilate flower) differ from *Gruenbachia* in having fruitlets separate, never fused basally. The axis on which they are born is oval, not triangular in transversal section. *Sparganiocarpus terminalis* Velenovský & Viniklář (1929) represents an elongate reproductive structure which differs profoundly from *Gruenbachia* in its arrangement of individual fruitlets on a robust axis and lacking any sign of phalanges. *Antocephale* Bayer (Z. Kvaček 1992) also shows radially arranged units, but none of the structures show the formation of phalanges. Moreover *Gruenbachia* shows quite sharp fruit apices, which are basi-medially fused.

Similarity of *Gruenbachia* to the recent representatives of the family is most pronounced in the genus *Pandanus*. The most significant character in common among *Gruenbachia* and *Pandanus* is the presence of phalanges – polydrupes. Fruits forming phalanges are frequently recorded in section *Pandanus*. Particularly important are species with phalanges fused only in basal part. This character is typical for species of *Pandanus* growing now in south-east Asia.

Gruenbachia pandanoides J. Kvaček & Herman, nov. spec.

(pl. 16, figs 7-10)

Etymology: Demonstrating similarities to the recent family Pandanaceae.

Holotype: NHMW 1999B0057/0179 (pl. 16, fig. 9).

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

Material: GBA: 2006/60/61, 2006/69/01.
NHMW: 1999B0057/0163, …/0179, …/0216, …/0264a, …/0401, …/0567.

Occurrence: Grünbach am Schneeberg, Muthmannsdorf, Austria.

Diagnosis: Globular inflorescences/infructescences attached to an axis triangular in cross section. Inflorescence/infructescence consisting of numerous, radially arranged multicarpelate units (phalanges). If sectioned in the polar region there are 5-8 units (phalanges) per infructescence. Each unit consisting of about ten basi-medially fused carpel/fruitlets. Apical parts of each carpel/fruitlet straight and spiny giving the whole head an echinate appearance.

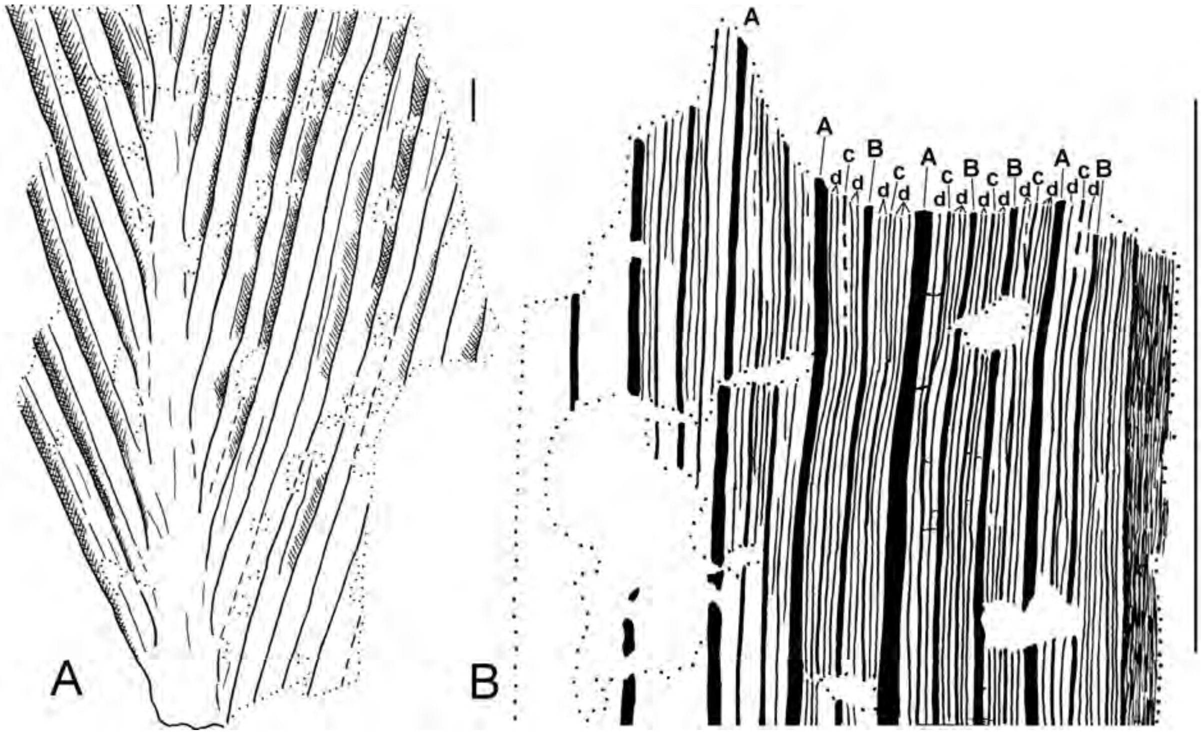
Description: The holotype (pl. 16, fig. 9) shows half of a floral head born on a short peduncle. The axis, which is triangular in cross section, is 5 mm wide and more than 23 mm long. Pistilate inflorescences/infructescences of the holotype are preserved in one half. It is globose 20 mm in diameter. Units, which are interpreted as carpels are fused basally and arranged in groups. Distal parts of units are dissected into 4-5 mm long fibrous apices.

The specimen No. GBA 2006/69/01 shows that the heads were attached to the triangular axis in distance 40 mm from each other. Complete heads (pl. 16, figs 7-10) are oval to elongated, 20-40 mm in diameter, consisting of radially arranged highly elongated units interpreted as carpels (about 10 mm in length, pl. 16, fig. 9, pl. 16, fig. 10). The units (carpels) are aggregated into further units, of which there are 5-8 per infructescence, if sectioned in the polar region (pl. 16, fig. 10). The carpel units are basi-medially fused. The apex of each unit is extended in usually two or three spines, which are sometimes filamentous with a spiny tip.

The best-preserved head (No. NHMW 1999B0057/0264a, pl. 16, fig. 10) shows numerous (about 50) radially arranged units. The head is ovoid 43 mm long, 27 mm wide. Each unit is 9-10 mm long, free apical parts are 4-5 mm long.

Comparison and discussion: On a species level, it is possible to compare *Gruenbachia pandanoides* with five species of *Viracarpon*: *V. hexaspermum*, *V. elongatum*, *V. tenue* (Sahni, 1964), *V. chitaleyi* (Patil, 1972) and *V. sahnii* (Chitaley & al., 1969). All of them are preserved as perminerlized fruits showing fused syncarps each containing six carpels. The carpels are completely or medio-apically fused (Namburdi & Tidwell 1978). In this character they differ from *Gruenbachia pandanoides* which has fruitlets fused basaly or basi-medially.

As mentioned above, the genus *Panadanus* is the most similar living taxon to *Gruenabchia*. Pandans with fruits basally fused in phalanges are represented by species, which are native to south-east Asia,



Text-fig. 23: *Sabalites longirhachis* (Unger) J. Kvaček & Herman, A – NHMW 1999B0057/0533, leaf outline and venation, B – NHMW 1999B0057/0528, detail of venation: AddcddBddcdd[Bddcdd]A, veins ‘d’ and some veins ‘c’ shown schematically, Grünbach (scale bar represents 1 cm).

particularly Indonesia: *P. archboldianus* Merrill & L.M. Perry, 1939, *P. affinis* Kurz, *P. gibbsianus* Martelli, *P. polycephalus* Lamarck 1785, *P. aurantiacus* Ridl. Some of the pandans from there have elongate, spiny drupes and spherical fruiting heads – cephali (*P. archboldianus*, *P. affinis*, *P. gibbsianus*, *P. aurantiacus*). *Pandanus affinis*, *P. aurantiacus* and *P. polycephalus* have numerous heads per fruiting axis as the fossil *Gruenbachia* (pl. 16, fig. 6). Very similar in structure of the fructification is *P. hendersonii* St. John from Anamba Islands, Indonesia (St. John 1965b). *Gruenbachia* shows reproductive structures consisting of units very similar to the phalanges of *P. archboldianus*, *P. affinis*, *P. gibbsianus*, *P. aurantiacus* (compare pl. 16, fig. 6). The linear shape of subunits of *Gruenbachia* resembles similarly shaped drupes of *P. pendens* (St. John 1965a).

Arecales
Arecaceae

Genus *Sabalites* Saporta, 1865, emended Read & Hickey, 1972

Type: *Flabellaria major* Unger 1842, p. 42, pl. 14, fig. 2 ≡ *Sabalites major* (Unger) Saporta, 1865, p. 83, pl. 2.

Syn: *Geonomites* Lesquereux 1878: 115, pro parte, (non *Geonomites* de Visiani, 1864: 456). *Juranyia* Tuzson, 1908: 1.

The genus was emended by Read & Hickey (1972), who also selected a new lectotype (contrary to Andrews 1970). Our understanding of the genus is in line with the concept of fossil record of palms summarized by Harley (2006) and Harley (in Dransfield et al. 2008).

Sabalites longirhachis (Unger) J. Kvaček & Herman

(pl. 17, figs 1-4, pl. 18, pl. 19,
figs 1-4; text-figs 7U, 23)

1850 *Flabellaria longirhachis* Unger, p. 332.
1852 *Flabellaria longirhachis* Unger; Unger, p. 91, pl.31, pl. 32, fig. 1.
1908 *Juranyia hemiflabellata* Tuzson, p. 1, pl. 1, figs 1, 2 (non pl. 2, fig. 3).
1913 *Juranyia hemiflabellata* Tuzson; Tuzson p. 222, pl. 17, fig. 1.
1965 *Palmophyllum longirhachis* (Unger) Baikovskaya, p. 373, pl. 1, fig. 2 ("*longirachis*").
2002 *Sabalites longirhachis*(Unger) Castells, nom. inval., p. 135. pl. 38, figs 1, 2, pl. 39, fig. 1, pl. 46, fig. 3.
2004a *Sabalites longirhachis* (Unger) J. Kvaček & Herman, p. 341, text-fig. 5, pl. 6, pl. 7, figs 1-4, pl. 8, figs 1-4.

Lectotype: Designated by J. Kvaček & Herman (2004a) No. GBA 1852/03/05a; figured by Unger, 1852 pl. 31; refigured here in pl. 17, fig. 3.

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Muthmannsdorf, Austria.

Material: GBA: 1852/03/05a, …/11, 2001/06/01, …/04, …/05, …/06, …/08, …/09, 2006/60/01, …/41, …/43, …/46, …/47, …/49 to …/52, …/55, …/62, …/63, …/67, …/68, …/72, …/78, 2006/64/01, 2006/64/02, …/28.
NHMW: 1970/1396/625, 1978/1991, 1999B0057/0051, …/0149, …/0150, …/0159, …/0235, …/0370, …/0524, …/0525, …/0526, …/0527, …/0528, …/0530, …/0531, …/0532, …/0533, …/0534, …/0536.
IPUW: 8 unnumbered specimens.

Occurrence: Grünbach Formation, Lower Campanian: Muthmannsdorf, Grünbach am Schneeberg, Felbering, Maiersdorf, Austria; Romania: Rusca Montana near Caransebes (Banat); Maastrichtian.

Diagnosis: For emended diagnosis see J. Kvaček & Herman (2004a).

Notes on nomenclature: The name *Sabalites longirhachis* (Unger) J. Kvaček & Herman is valid in contrary to the earlier published name *Sabalites longirhachis* (Unger) Castells (2002) who invalidly published the combination (see Mc Neill et al. 2006, art. 33.4, 33.5). Castells (2002) did not indicate a basionym as required in Art. 33.4 of the Vienna Code.

Description: The lectotype (pl. 17, fig. 3) is a leaf impression representing an almost complete leaf. It was broken in two parts of which the basal part has not been available for the present study and is of unknown repository. The apical part shows a portion of a leaf 320 mm long and 170 mm wide. The costa is 12-14 mm wide and the leaf segments vary from 5 to 10 mm in width. The second Unger type specimen (No. GBA 1852/03/11) shows a fragment of a leaf base with a costa 18 mm wide (pl. 17, fig. 2).

A complete leaf lamina is not preserved in any of the specimens studied, but numerous fragments of leaf margins (e.g. NHMW 1999B0057/0149) indicate that the leaf lamina was undivided and lanceolate (pl. 19, figs 1, 4). The largest specimen studied (pl. 18), shows the lamina 380 mm long and 200 mm wide. The maximum width of the lamina, 240 mm, has been recorded in the specimen NHMW 1999B0057/0150. A leaf base with the petiole and a complete leaf apex is not preserved in any specimen studied. The specimen NHMW 1999B0057/0149 (pl. 19, fig. 4) shows a leaf lamina near its base. The specimen No. GBA 2001/06/01 shows several marginal segments partly free (pl. 19, fig. 1) and may represent a fragment close to the leaf apex.

A long and massive costa narrows gradually to the apex and is typically 19 – 30 mm wide. In the apical part of a leaf the costa is narrow and covered on the adaxial part with decurrent bases of leaf segments (pl. 18). It is possible to observe a clear induplicate splitting in marginal parts of the specimen No. GBA 2001/06/01. The specimen No. NHMW 1999B0057/0149 (pl. 19, fig. 4) represents an abaxial part of the lamina showing induplicately split segments from the opposite side. Each segment is V-shaped in transversal section showing four parallel vein subsets and the midvein. Segment width is typically about 10 mm. In some cases the width can vary within one leaf lamina, e.g. from 6 mm to 16 mm (NHMW 1999B0057/0530). Some leaf fragments from the collection of the University of Vienna (without numbers) have segments at least 19 mm wide. The parallel veins of different orders follow the formula AddCddBddCdd(BddCdd)A. Veins of lower orders (C, d) can vary in number (text-fig. 23B, pl. 19, fig. 3), particularly "d" veins, which, although typically two in number, can vary from one to three. The width of veins of different orders is as follows: A: 0.4-0.2 mm, B: about 0.1 mm, C: about 0.08 mm, d: about 0.02 mm. Spacing of the parallel veins varies from 0.2 to 0.02 mm. Transverse veins are difficult to observe, since they are irregularly spaced, extremely fine, about 0.01 mm wide, and perpendicularly or obliquely orientated to the parallel venation.

The cuticle is very thin and difficult to prepare. Cuticle preparations were extracted from the specimen NHMW 4191970 from Maiersdorf (pl. 19, fig. 2). The cell structure shows elongated ordinary cells 8-10 x 30-50 μm with straight anticlinal walls and circular tetracytic stomata (pl. 19, fig. 2) – subsidiary cells 7-17 x 5-7 μm; guard cells 8-10 x 2-5 μm.

Comparison and discussion: In the revision of *Sabalites longirhachis* (J. Kvaček & Herman 2004a) we have followed the classification introduced by Read & Hickey (1972), and therefore have used the generic name *Sabalites* instead of *Palmophyllum* Conwentz (1886). The generic name *Palmophyllum* was used by Baikovskaya (1965) for similar Romanian material from the Maastrichtian of Transylvania. *Juranyia hemiflabellata* Tuzson (1908, pl. 1, figs 1, 2) from the Maastrichtian of Rusca Montana, Transylvania in Romania is very similar to, or even conspecific with *Sabalites longirhachis*. Considering that we are dealing with a palm leaf morphotaxon of limited systematic value, we have suggested keeping both leaf-types in one species (J. Kvaček & Herman 2004a). The type material of *Juranyia hemiflabellata* is of unknown repository and we were able to study the only available specimen housed in the Natural History Museum, London (No. V.24132).

Specimens of *Sabalites longirhachis* described by Castells (2002) from the Upper Cretaceous of Catalonia, as far as we can recognize from simplified drawings, resemble the type material of *S. longirhachis* in size and shape. All specimens show undissected laminas and well pronounced costa. Specimens of *Sabalites longirhachis* described by Marmi et al. (2008) come from the same basin (lower Maastrichtian) as the latter but different localities (Fumanya and Pinyes) in the eastern Pyrenees. They show complete leaves with long petioles.

Geonomites imperialis (Dawson) Bell from the Campanian of the Nanaimo Group in British Columbia, Canada (Bell 1957, pl. 22, fig. 5, pl. 23, fig. 2, pl. 24, fig. 3) and *Genomites schimperi* Lesquereux from the Campanian-Maastrichtian of the Ripley Formation in Georgia, U.S.A. (Berry 1878, pl. 2) are very similar or even identical to *Sabalites longirhachis*. They show a similarly long costa with an undivided lamina, but slightly differs from *S. longirhachis* in subtle characters such as long decurrent bases of leaf segments.

The oldest unequivocal record of a palm leaf is *Sabalites carolinensis* Berry (1914, pls 5, 6) from the Coniacian – Early Santonian of South Carolina, USA. It differs from *S. longirhachis* in having a shorter costa and narrow wedge-shaped segments, which ultimately split.

Among other species of the genus *Sabalites*, the present taxon is most similar to *Sabalites tenuirachis* (Lesquereux) Read & Hickey from the Palaeocene of the Raton Formation in New Mexico (Lesquereux, 1878, pl. 11, fig. 1). Besides the stratigraphic and geographic difference it differs slightly in leaf morphology; Lesquereux (1878: 117) states: “the rays seem to become free or cut from each other towards their points”. In this character *S. tenuirachis* differs from most specimens of *S. longirhachis* that we have studied.

Sabalites ungeri (Lesquereux) Dorf (Lesquereux, 1878, pl. 11, fig. 2) from the Palaeocene of the Raton Formation, New Mexico is also similar to *S. longirhachis* in gross morphology of its leaf, but differs from *Sabalites longirhachis* in having a robust striated costa. All other palm leaves of the genus *Sabalites*, as far as we know, have a very short costa in comparison with the material at hand.

Liliopsida incertae sedis

Genus *Theiaiphyllum*
Herman & J. Kvaček, nov. gen.

Derivatio nominis: After *Theia* (Greek myth.) – sister of Thetis, a Nereid in Greek mythology.

Type: *Theiaiphyllum kollmannii* Herman & Kvaček, nov. spec.

Species included: only the type.

Diagnosis: Leaves simple, unlobed; leaf base round to narrow cuneate, leaf apex narrow acute; leaf margin entire. Venation pinnate brochidodromous. Secondary veins numerous, thin, simple, connecting the upper secondary vein and forming brochidodromous loops close to the leaf margin. Tertiary veins very thin, oblique to secondary veins, percurrent or rarely ramified-percurrent, forming small loops very close to the leaf margin.

Comparison and discussion: Although pinnate venation with numerous simple secondary veins and closely-spaced, slightly sinuous, percurrent tertiary venation and intramarginal veins typical of *Theiaiphyllum kollmannii* nov. gen. et nov. spec. are known in several angiosperm taxa, both monocots and dicots (Myrtaceae, Chrysobalanaceae, Rhamnaceae, Fagaceae, Dipterocarpaceae, Ochnaceae and some other families), we believe that the shape and venation of these leaves, particularly the thin venation forming small loops close to the leaf margins, allow us to assign this plant, with some uncertainty, to monocotyledons.

Theiaiphyllum kollmannii
Herman & J. Kvaček, nov. spec.

(pl. 20, figs 1-7, pl. 21, figs 1-6; text-fig. 24)

Derivatio nominis: In honour of Heinz A. Kollmann, a distinguished Austrian geologist and palaeontologist.

Holotype: NHMW 1999B0057/0237 (pl. 21, figs 1-5, text-fig. 24, D-F).

Stratum typicum: Grünbach Formation, Lower Campanian.

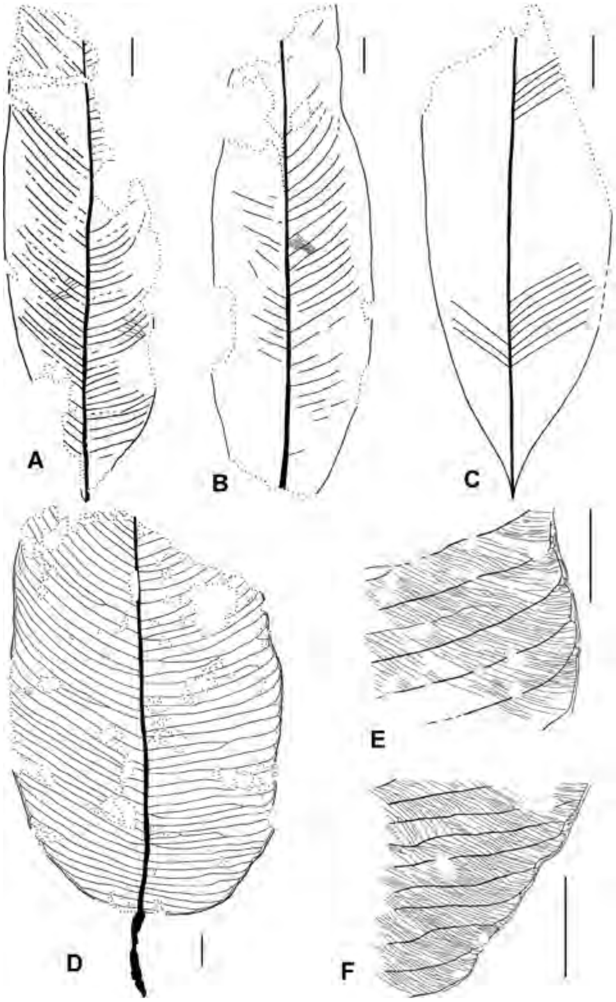
Locus typicus: Grünbach am Schneeberg, Austria.

Material: GBA: 2001/06/07.
NHMW: 1970/1396/1642, 1999B0057/0024,
.../0027, .../0034, .../0038, .../0039, .../0040,
.../0042, .../0043, .../0048, .../0049, .../0053,
.../0065, .../0068, .../0073, .../0074, .../0082,
.../0237, .../0243, .../0245, .../0303, .../0470a.

Occurrence: Grünbach am Schneeberg, Austria.

Diagnosis: As for the genus.

Description: Although numerous in the collection, leaves are preserved incompletely: usually the basal parts of the leaves are better preserved than their apical parts, and only two leaf apices are known. Leaves



Text-fig. 24: *Theiaiphyllum kollmannii* Herman & J. Kvaček, nov. gen. et nov. spec., A – NHMW 1999B0057/0245, B – NHMW 1999B0057/0048, C – NHMW 1999B0057/0068, D, E, F – holotype NHMW 1999B0057/0237: D – leaf outline and venation, E, F – detailed venation, Grünbach (scale bar represents 1 cm).

medium to large in size, simple, unlobed, elliptic to narrow elliptic, symmetric or slightly asymmetric, entire-margined. Due to the incomplete preservation leaf length is unknown but was probably 10 to 25 cm, leaf width 2.5 to 9 cm. Leaf lamina elliptic to narrow elliptic in general outline, being broadest in the middle part of the leaf. Leaf base round (pl. 21, fig. 1) to narrow cuneate (pl. 20, fig. 1), sometimes slightly decurrent. Leaf apex narrow acute (pl. 20, fig. 5). Leaf margin entire, usually slightly undulate. Petiole stout, poorly preserved, up to 28 mm long and 2.5 mm thick (pl. 21, fig. 1).

Venation pinnate brochidodromous. Midvein strong, thick, straight, running to leaf apex, approximately 0.8 to 1.8 mm thick in its basal part, narrowing towards the apex. Numerous thin closely spaced secondary veins emerge from the midvein at an angle of 50-90°, the most developed of them being in the middle part of the leaf lamina. Secondary veins usually opposite or almost opposite in the lower part of the leaf, simple, curving upwards or almost straight, connecting to the upper secondary vein and forming simple brochidodromous loops or even an intramarginal vein close to leaf margin (pl. 21, figs 2-4; text-fig. 24, D-F). Sometimes the secondary vein connects to an adjacent secondary vein or rarely divides into two secondaries (text-fig. 24, D). Tertiary veins very closely-spaced, very thin, oblique to secondary veins, forming an angle of 45-50°, percurrent or rarely ramified-percurrent, straight or slightly sinuous (Pl., 20, figs 2, 4, 7; Pl., 21, figs 2-6; text-fig. 24, A, B, E, F), forming small loops or cells very close to leaf margin (pl. 21, figs 2, 3; text-fig. 24, E, F). Higher order venation unknown.

Comparison and discussion: Leaves of *Theiaiphyllum kollmannii* nov. gen. et nov. spec. figured on pl. 20 and pl. 21 differ in their outline and vary in the form of apex and base. However, they possess similar venation: strong midvein, numerous thin closely spaced pinnately arranged secondary veins, slightly curving upwards (pl. 20, figs 1, 2, 5-7; pl. 21, figs 1-4), and very characteristic tertiary venation (pl. 20, figs 4, 7; pl. 21, figs 2-5): very closely-spaced, very thin, oblique to secondary veins, forming an angle of 45-50°, percurrent or rarely ramified-percurrent.

Tertiary venation in *Theiaiphyllum kollmannii* nov. gen. et nov. spec. is similar to *Haemanthophyllum cordatum* Golovneva from the Maastrichtian – Lower Paleocene of North-eastern Russia (Golovneva 1987, p. 1127, pl. 1, figs 1, 2, 4, 5, pl. 2, fig. 2, text-figs 1-5; Herman & Spicer 1995, text-fig. 3a, 3b) and *Haemanthophyllum kamtschaticum* Budantsev (Budantsev 1983, p. 139, pl. 63, figs 1-4) from the Paleocene of Kamchatka and Northern Alaska. However, leaf lamina outline and first and second order venation in *Theiaiphyllum kollmannii* are completely different from those observed in *Haemanthophyllum*.

Among dicots, *Theiaiphyllum kollmannii* nov. gen. et nov. spec. is most similar to *Ficus densinervis* Hosius & Marck from the Senonian of Westfalen (Hosius & Marck 1880, p. 135, pl. 25, figs 10-12). This species is characterised by elliptic to narrow elliptic entire-margined leaves, narrow cuneate leaf base and pinnate brochidodromous venation with numerous closely spaced secondary veins and percurrent tertiary venation. However, the new species differs from *F. densinervis* in having both cuneate and round leaf base, thinner secondary veins and tertiary veins emerging more obliquely from the secondary veins, particularly near the leaf margin. Unfortunately, poor preservation of the Westfalian samples does not allow more detailed comparison of these two species. *Ficus glascoena* Lesquereux from the latest Albian – Cenomanian Dakota Formation in North America (Lesquereux 1891, p. 76, pl. 13, figs 1, 2) has large entire-margined leaves with a stout midvein and numerous thin pinnately-arranged closely spaced secondary veins. However, *Theiaiphyllum kollmannii* differs from this species in having both cuneate and round leaf base and simple and usually curving-upwards secondary veins. Again, poor preservation of *Ficus glascoena* does not allow more detailed comparison of these species, particularly in tertiary and higher order venation patterns. *Ficus protogaea* Heer (Heer 1874, p. 108, pl. 29, fig. 2 b, pl. 30, figs 1-8) from the Late Cretaceous of Greenland resembles *Theiaiphyllum kollmannii* nov. gen. et nov. spec. in having elliptic to narrow elliptic entire-margined leaves with pinnate brochidodromous venation and numerous thin secondary veins. However, tertiary venation in *T. kollmannii* is percurrent or rarely ramified-percurrent and therefore different from the orthogonal-reticulate venation observed in *Ficus protogaea*.

Theiaiphyllum kollmannii nov. gen. et nov. spec. resembles *Yammelehia superba* Krassilov from the Turonian of Negev, Israel (Krassilov et al. 2005, p. 121, pl. 18, figs 1-5, text-fig. 19), having large elliptic to narrow elliptic leaves with round to narrow cuneate base, stout petiole, entire leaf margin, prominent midvein and numerous parallel thin secondary veins. However, it differs from this plant in having totally different tertiary venation which is percurrent or rarely ramified-percurrent in *Theiaiphyllum kollmannii* and forms a reticulum consisting of areoles in *Yammelehia superba*.

Eucalyptus angusta Velenovský from the Cenomanian Peruc-Korycany Formation in Czech Republic (Velenovský 1885b; Frič & Bayer 1901, p. 144, fig. 111) possesses secondary venation similar to that of *Theiaiphyllum kollmannii* nov. gen. et nov. spec. with numerous closely spaced secondary veins emerging from the midvein at an angle of 45-50°. However, the tertiary venation of the new species is not typical of *Eucalyptus*. Moreover, the leaves of *E. angusta* are oblong-lanceolate, almost linear, whereas the leaves of *Theiaiphyllum kollmannii* nov. gen. et nov. spec. are elliptic to narrow elliptic. Another species from the Cenomanian of Czech Republic, *Myrsinophyllum varians* Velenovský (Velenovský 1889; Frič & Bayer 1901, p. 154, fig. 123) also has closely spaced secondary veins but differs from the new species in leaf size, leaf shape and venation near the leaf margin where secondary veins in *M. varians* become irregularly ramified.

Monocotyledon gen. et sp. indet.

(pl. 21, figs 7, 8)

2004a Monocotyledon gen. et sp. indet. J. Kvaček & Herman, p. 348, pl. 9, figs 1, 2.

Material: NHMW 1999B0057/0537.

Occurrence: Grünbach am Schneeberg, Josefi Schacht, Austria.

Description: The only specimen available shows several leaf fragments or fragments of one large entire-margined leaf without apex or base. The largest fragment (250 x 95 mm) with enrolled margins and without any midrib (pl. 21, fig. 7) shows parallel venation pattern with four vein orders arranged according to the formula AdCdBdCdA (pl. 21, fig. 8). Transversal veins are conspicuously thick (pl. 21, fig. 8), of approximately the same thickness as the vein subset B. They connect at right angles and at regular distances with veins of order A, crossing veins B,C and d. The distance between transversal veins is 2-7 mm; veins of order A are approximately 2 mm apart. Thickness of veins: A – 0.3-0.35 mm; B – 0.1 mm; C – 0.07 mm; d – 0.05 mm.

Discussion: This monocotyledon leaf is similar to the specimen described by Dorf (1942) from the uppermost Cretaceous of the Rocky Mountains (U.S.A.) as *Typha* sp. The Dorf specimen shows similar venation pattern with three or four vein subsets. It is also similar in the arrangement of transversal veins connecting with veins of higher subsets (A or B). A similar specimen was depicted by Hickey (1977, pl. 11, figs 2, 3) from the Early Eocene of North Dakota, USA. *Typha* sp. differs from the specimen from Grünbach in having thinner transversal veins with irregular distribution.

Magnoliopsida

Genus *Brasenites*
Wang & Dilcher, 2006

Type: *Brasenites kansense* Wang & Dilcher, 2006, p. 394, figs 7, 8

The genus *Brasenites* was recently established by Wang & Dilcher (2006, p. 394) with the only species (type of the genus) *B. kansense* Wang & Dilcher from the Upper Albian Dakota Formation, Barton County, Kansas, USA. The diagnostic characters of the genus are suborbiculate to orbiculate lamina shape, peltate central leaf base (petiole inserted in the center of the leaf), entire leaf margin, and bisymmetrical actinodromous primary venation. Wang & Dilcher (2006, p. 394) believe that ‘the modern affinity of this genus is probably close to the modern genus *Brasenia* of the Cabombaceae within the Nymphales on the basis of the similar morphological features shared by the living and fossil leaves’. Wang & Dilcher (2006) also show that *Brasenites* possesses some similarities with genera *Nelumbo* and *Nelumbites*, however, it differs decidedly in having a shield leaf shape, a peltate central leaf base and a bisymmetrical actinodromous primary venation pattern.

Brasenites krasseri
Herman & J. Kvaček, nov. spec.

(pl. 27, figs 1-7, pl. 36, figs 5, 6; Text-figs 25)

Derivatio nominis: After palaeobotanist F. Krasser who preliminary studied the Grünbach Flora (Krasser 1906).

Holotype: Designated here. NHMW 1970/1396/1559 (pl. 27, fig. 1; text-fig. 25).

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

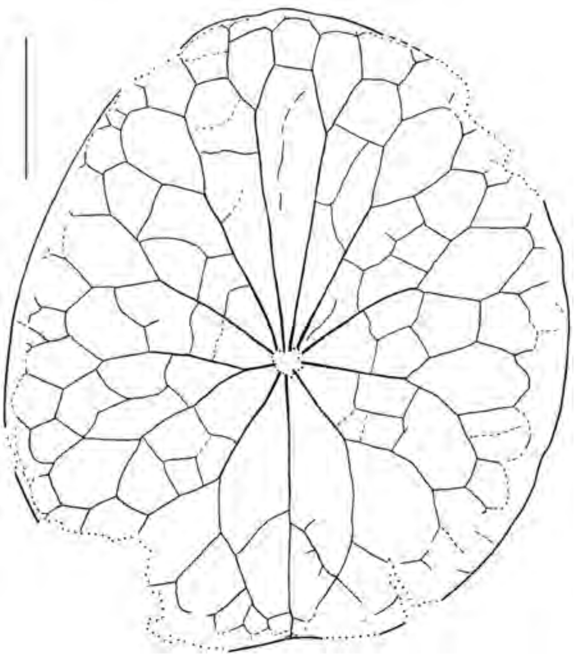
Material: NHMW: 1970/1396/156e, 1999B0057/248, .../0251, .../0452, .../0486, .../0487, .../0488, .../0489, .../0490, .../0491, .../0492, .../0493, .../0494, .../0495, .../0496, .../0497, .../0498, .../0499, .../0500, .../0501a, .../0502, .../0503, .../0504, .../0505, .../0506, .../0507, .../0508a, .../0509b, .../0510, .../0511, .../0556.

Occurrence: Austria, Grünbach am Schneeberg; Grünbach Formation, Lower Campanian.

Diagnosis: Leaves peltate, small or medium, simple, unlobed, eliptic (suborbiculate) to round (orbiculate), symmetric, entire-margined, slightly funnel-shaped near the region of the petiole attachment. Leaf base shallow cordate or round, apex round. Petiole attaching to the leaf lamina in its central part. Venation bisymmetrical actinodromous, 11 to 15 primary veins going from the place of the petiole attachment radially, bifurcating, forming, together with tertiary veins, a series of polygonal loops towards leaf margin. The central primary vein going to leaf apex forks and does not reach leaf margin, the central primary vein going to leaf base extends nearly to the leaf margin. Third to sixth order venation orthogonal-reticulate. Small round to polygonal cells on leaf surface represent aerenchyma imprints.

Description: Leaves peltate, small to medium in size, simple, unlobed, elliptic (suborbiculate) to round (orbiculate), symmetric, entire-margined. Leaf length from 4.0 cm to approximately 12.3 cm, leaf width from 3.7 cm to approximately 7.7 cm. Leaf lamina peltate, usually broadly elliptic in general outline (pl. 27, figs 1, 4; text-fig. 25), but sometimes elliptic or round, being broadest in the middle part of the leaf. Leaf base shallow cordate (text-fig. 25) or round, leaf apex round (pl. 27, figs 1, 2; text-fig. 25). Leaf margin entire, sometimes slightly undulate. Petiole poorly preserved, thick, attached to the leaf lamina in its central part. The leaf lamina is slightly funnel-shaped near the region of the petiole attachment (pl. 27, fig. 5).

Primary venation bisymmetrical actinodromous, with 11 to 15 primary veins going from the region of the petiole attachment radially towards leaf margin. Primary veins 0.2-0.3 mm thick, straight or curved, repeatedly bifurcating. The most developed are primary veins going to both the leaf apex and base, with the former being straight and the latter – curved. The central primary vein going to the leaf apex forks and does not reach the leaf margin, the central primary vein going to leaf base extends nearly to the leaf margin (text-fig. 25). The secondary veins arising from forked primary veins forming, together with tertiary veins, a series of polygonal loops near the leaf margin (brochidodromous venation – text-fig. 25). Tertiary veins very thin, orthogonal-reticulate (pl. 27, figs 3, 6; text-fig. 25), forming small loops near the leaf margin (text-fig. 25). Fourth to sixth order venation orthogonal-reticulate (pl. 27, fig. 3).



Text-fig. 25: *Brasenites krasseri* Herman & J. Kvaček, nov. spec., holotype NHMW 1787 (=1970/1396/1559), Grünbach (scale bar represents 1 cm).

Sometimes impressions of small, approximately 0.2 mm in diameter, round to polygonal cells (protuberances) are observed on leaf surface, probably representing the imprint of aerenchymous tissue or air lacunae in the mesophyll (pl. 27, figs 6, 7). Therefore, judging from the leaf morphology and the presence of aerenchyma, this species represents floating leaves of a water plant.

Cuticle removed from the specimen NHMW 1999B0057/0494 shows isodiamtetric, angular ordinary cells (12-20 x12-22 μm) and curved anticlinal walls 2-2.5 μm in thickness (pl. 36, figs 5, 6).

Comparison and discussion: This species was first identified as *Nelumbites* sp. (Kvaček & Herman 2004) but later we assigned it to *Brasenites* (Herman &

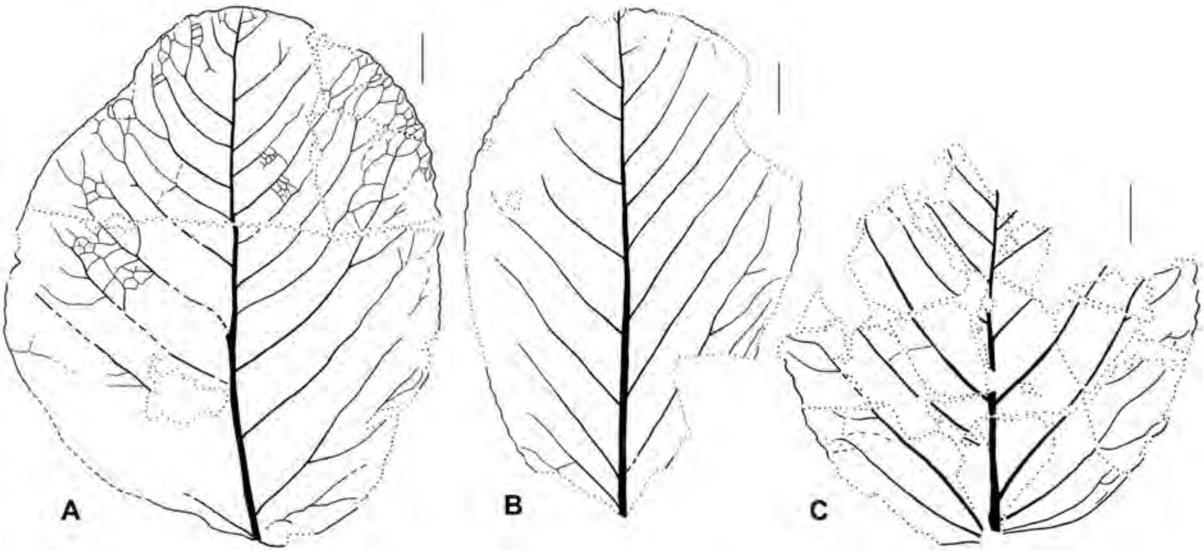
Kvaček 2007). Wang & Dilcher (2006) characterize *Brasenites* in presence of a shield leaf shape, a peltate central leaf base, a bisymmetrical actinodromous primary venation pattern, and lamina consisting of small rounded cells (protuberances). All the later mentioned features are typical for the *Brasenites krasseri* which explains its assignment to this genus.

Brasenites krasseri is very similar to the type of the genus *B. kansense* Wang & Dilcher from the Upper Albian Dakota Formation, Barton County, Kansas, USA (Wang & Dilcher 2006, p. 394, figs 7, 8) in leaf shape and venation. *B. krasseri*, however, has bigger range of leaf size which includes also small leaves (4 x 3.7 cm) not typical for *B. kansense*. However, the main difference between these species is in their venation: *B. krasseri* possess 11 to 15 primary veins whereas *B. kansense* has 11 primary veins; the central primary vein going to leaf apex in *B. krasseri* forks and does not reach leaf margin, whereas this vein in *B. kansense* extends to the leaf margin; alternatively, the central primary vein going to leaf base in *B. krasseri* is stout and extends nearly to the leaf margin, but in *B. kansense* this vein is short and thin.

Among modern plants, *Brasenites krasseri* is similar to floating leaves of genera *Brasenia* (pl. 27, fig. 8) and *Nelumbo* L. Krasser (1906, p. 2) even assigned this plant to *Brasenia*, but unfortunately this taxonomic suggestion was not supported by finds of associated reproductive organs typical for *Brasenia*. Fossil leaves described from the early Cretaceous Buarcos Flora of Portugal as *Braseniopsis venulosa* Saporta and *B. villarsioides* Saporta have a reticulate venation pattern (Saporta 1894, p. 192, 195, pl. 34, figs 1-4, pl. 35, fig. 9) which is very different from that characteristic for the genus *Brasenites*.

Among other fossil angiosperms, the new species has some similarities with representatives of the genus *Nelumbites*. This genus was first described by Berry (1911) for fossil leaves similar to the modern genus *Nelumbo* Linnaeus. Representatives of this genus are characterised by round or elliptic peltate leaves with entire, sometimes undulate leaf margins and actinodromous, often radially symmetric, venation (whereas *Brasenites* has bisymmetrical actinodromous venation) with primary veins going from the region of the petiole attachment in the central or occasionally lower part of the leaf lamina towards leaf margin. The type of the genus *Nelumbites*, *N. virginensis* (Fontaine) Berry from the Albian Patapsko Formation in Maryland and Virginia, USA (Fontaine 1889, p. 321, pl. 161, figs 1, 1a, 2; Berry 1911, p. 463, pl. 82, figs 3-5), possess peltate entire-margined leaves with shallowly cordate leaf bases, actinodromous primary veins and orthogonal-reticulate tertiary and higher order venation similar to those observed in *Brasenites krasseri*. However, leaves of *Nelumbites virginensis* are significantly bigger than *Brasenites krasseri*. Moreover, the latter species differs from *Nelumbites virginensis* by having more numerous primary veins, with the lower veins being as well developed as the upper ones, and by having the petiole attachment in the central part of the leaf lamina.

N. tenuinervis (Fontaine) Berry from the Albian Patapsko Formation of the Atlantic coast of North America (Fontaine 1889, p. 322, pl. 172, fig. 8; Ward 1905, p. 497, pl. 109, figs 2, 3; Berry 1911, p. 464, pl. 82, figs 1, 2), the Albian Kyzylshen Formation in Kazakhstan (Vakhrameev 1952, p. 184, pl. 12, fig. 9-11, text-fig. 39) and the Turonian-Coniacian Arman and Naraulíisk formations in the North-eastern Russia (Filippova & Abramova 1993, p. 123, pl. 4, fig. 10, pl. 102, fig. 7) is characterised by round peltate entire-margined leaves, which differs from *Brasenites krasseri* by its smaller size of leaf lamina, more distinct midvein and fewer primary veins and by the attachment of their petioles usually in the lower part of the leaf but not in its central part. *B. krasseri* differs from *Nelumbites minimus* Vakhrameev from the Albian Kyzylshen Formation in Kazakhstan (Vakhrameev 1952, p.183, pl. 12, figs 5-8, text-figs 37, 38) by the bigger size of the leaves, petiole attachment in the central part of the leaf lamina, and more numerous primary veins.



Text-fig. 26: *Celastrophyllum johannae* Herman & J. Kvaček, nov. spec., A – holotype NHMW 1970/1396/1613, B – NHMW 1970/1396/1614, C – NHMW 1999B0057/0157, Grünbach (scale bar represents 1 cm).

Brasenites krasseri differs from *Nelumbites aravensis* Krassilov from the Turonian of Negev, Israel (Krassilov et al. 2005, p. 99, pl. 9, figs 1-5, pl. 10, figs 1-4, pl. 11, figs 1-3) in having smaller leaves with less numerous primary veins. Moreover, the latter species has dimorphic leaf laminae (funnel-shaped with nearly central petiole insertion and flat with eccentric petiole insertion) – the feature which is not observed in *Brasenites krasseri*.

Genus *Celastrophyllum* Goeppert, 1854

Type: *Celastrophyllum attenuatum* Goeppert, 1854, p. 52, pl. 14, fig 89.

Celastrophyllum johannae Herman & J. Kvaček, nov. spec.

(pl. 22, figs 1-9, pl. 35, figs 1-3; text-fig. 26)

Derivatio nominis: In honour of Johanna Kovar-Eder, a distinguished Austrian palaeobotanist.

Holotype: Designated here. NHMW 1970/1396/1613, pl. 22, figs 5, 6; text-fig. 26, A.

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Austria, Grünbach am Schneeberg, Austria.

Material: GBA: 2006/64/43, 2006/69/10, …/11. NHMW: 1970/1396/1614, 1999B0057/0001, …/0153, …/0157, …/0267, …/0273, …/0377.

Occurrence: Austria, Grünbach am Schneeberg, Muthmannsdorf; Grünbach Formation, Lower Campanian.

Diagnosis: Leaves medium, simple, unlobed, elliptic to broadly elliptic, asymmetric, with dentate-crenate margins. Leaf base broadly round, asymmetric, apex broadly round. Leaf margin dentate to crenate, teeth with round, apressed or acute apices. Sinuses between teeth shallow, round. Venation pinnate craspedodromous. Midvein prominent, stout, straight, supporting up to 15 pairs of thin secondary veins. Tertiary and quaternary venation orthogonal-reticulate.

Description: Leaves medium in size, simple, unlobed, asymmetric, with dentate-crenate margin. Leaf length approximately 7-10.5 cm, leaf width 5.8-8.6 cm. Leaf lamina elliptic (pl. 22, fig. 1; text-fig. 26, B) or broadly elliptic (pl. 22, fig. 5; text-fig. 26, A), asymmetric, the maximum width being in the middle part of the leaf. Leaf base broadly round (pl. 22, figs 2, 5, 7; text-fig. 26, A, C), often asymmetric, apex broadly round (pl. 22, figs 1, 5, 7; Text-figs 26, A, B). Leaf margin dentate to crenate (pl. 22, figs 3, 4, 6; Text-figs 26, A, B), marginal teeth (pl. 22, figs 3, 4, 6) simple, 1.0-1.8 mm in height, with round, apressed or acute apices curving upwards. Sinuses between teeth shallow, broad, round. Petiole incompletely preserved, up to 3 mm thick (pl. 22, fig. 7).

Venation pinnate craspedodromous. Midvein prominent, stout, straight, running to the leaf apex, approximately 1-1.7 mm thick in its basal part, rapidly narrowing towards leaf apex. Up to 15 pairs of secondary veins emerging from the midvein at an angle of 40-50°, with the third to fifth pair (from the leaf base) being most developed. Secondary veins much narrower than the midvein, straight, undulate or slightly curving upwards, lower opposite or almost opposite, dividing up to 2-3 times with all branches terminating in the marginal teeth (text-fig. 26). Tertiary veins poorly preserved, very thin, orthogonal-reticulate (text-fig. 26, A). Near the leaf margins, tertiary veins, together with terminal parts of secondary veins, form irregular loops or cells (text-fig. 26, A). Quaternary venation orthogonal-reticulate (text-fig. 26, A).

Cuticle removed from the specimen NHMW 1999B0057/0153 shows thick adaxial cuticle bearing isodiametric ordinary cells (12-30 x 20-38 μm) with straight anticlinal walls 1-2 μm thick (pl. 35, fig. 1). The abaxial cuticle is even thicker showing polygonal ordinary cells (20-35 x 35-50 μm) and irregularly scattered paracytic stomata and rounded trichome bases covering one cell (pl. 35, fig. 2). Subsidiary cells are quadrangular (12-18 x 18-38 μm) seemingly less cutinised than the ordinary cells, guard cells 5 x 15-25 μm in size (pl. 35, fig. 3). The surface of the abaxial cuticle is ornamented showing psilate structure.

Comparison and discussion: *Celastrophyllum johannae* nov. spec. is most similar to *C. orientalis* Filippova from the Turonian-Coniacian Arman Formation of North-eastern Russia (Filippova & Abramova 1993, p. 157, pl. 8, fig. 2, pl. 102, fig. 1) in leaf size, crenate leaf margin and craspedodromous venation with thin undulating secondary veins and reticulate tertiary veins. However, *C. johannae* nov. spec. has bigger and rounder leaves and more oblique, curving upwards, secondary veins. *Celastrophyllum johannae* nov. spec. resembles *C. ensifolium* Lesquereux from the Late Cretaceous of North America (Lesquereux 1874, p. 108, pl. 21, figs 2, 3) which has similar marginal teeth and venation, but the new species is characterised by rounder and broader leaves with upward curving secondary veins.

A poorly preserved leaf of *Alniphyllum kefersteinii* (Unger) Bayer from the Senonian of South Bohemia (Němejc 1957, p. 104, pl. 10, figs 3, 3a, text-fig. 4) is much smaller, although the leaf base and venation have some similarities with the new species. The outline of the leaf lamina and venation of *Celastrophyllum johannae* nov. spec. resembles those of *Populus hyperborea* Heer from the Late Cretaceous of Greenland (Heer 1874, p. 106, pl. 27, fig. 8 d, pl. 29, fig. 6-9, pl. 30, fig. 2 b) but the new species, unlike *P. hyperborea*, has a dentate to crenate leaf margin. *Quercus ellsworthiana* Lesquereux from the Late Cretaceous of North America (Lesquereux 1874, p. 65, pl. 6, fig. 7) differs from *Celastrophyllum johannae* nov. spec. by having a more elongate leaf lamina and a distinctly undulate leaf margin. *Ficus deflexa* Lesquereux from the latest Albian – Cenomanian Dakota Formation in North America (Lesquereux 1891, p. 80, pl. 3, fig. 13) has, unlike *Celastrophyllum johannae*, entire-margined leaf lamina.

***Celastrophyllum* sp.**

(pl. 22, fig. 10, pl. 34, figs 5, 6; text-fig. 27)

Material: NHMW: 1999B0057/0070, …/0262a.

Occurrence: Grünbach am Schneeberg; Grünbach Formation, Lower Campanian, Austria.

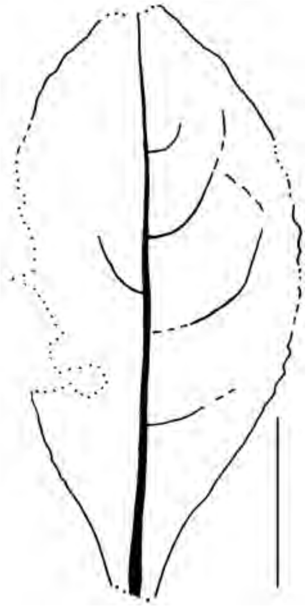
Description: In the collection there are two incomplete and poorly preserved leaf compressions belonging to this species. Leaves small, simple, unlobed, symmetric, with a dentate margin. Leaf length from 3.6 cm to approximately 9.5 cm, leaf width from 1.7 to 2.7 cm. Leaf lamina elliptic in shape, with the maximum width being in the lower part of the leaf. Leaf base narrow cuneate, decurrent, symmetric. Apex not preserved, probably narrow acute. Leaf margin dentate, marginal teeth small, simple, triangular, with acute or round apices, 0.3-0.5 mm in height. Sinuses between teeth round. Petiole not preserved.

Venation pinnate brochidodromous. Midvein straight, terminating at leaf apex, approximately 0.7-0.8 mm thick in its basal part, narrowing towards the apex. More than 4 (6-8?) pairs of rare secondary veins emerging from the midvein at an angle of 70-90°, the most developed being found in the middle part of the leaf lamina. Secondary vein simple, curving upwards, connecting to the upper secondary vein and forming loops at some distance (approximately 1.5 mm) from the leaf margin. Tertiary veins, higher order venation, and venation near leaf margin, not preserved.

Cuticle removed from the specimen NHMW 1999B0057/0262 is delicate and poorly preserved. The cuticle is penetrated by many fungal mycelia, which blur the cuticle pattern (pl. 34, fig. 6). Ordinary cells are isodiametric and poorly preserved. Possible stoma anomocytic (pl. 34, fig. 5).

Comparison and discussion: Small size, elliptic leaf shape, decurrent base, dentate leaf margin and brochidodromous venation allow us to assign this species to the genus *Celastrophyllum* GOEPPERT. However, poor sample preservation prevents specific identification of these leaves.

Celastrophyllum sp. differs from *C. latifolium* FONTAINE from the early Cretaceous Patapsco Formation in North America (WARD 1905, p. 559, pl. 116, fig. 6; BERRY 1911, p. 477, pl. 40, fig. 7; DOYLE & HICKEY, 1976, fig. 7) and the Cenomanian-Coniacian Krivorechenskaya and Arman Formations of North-eastern Russia (FILIPPOVA & ABRAMOVA 1993, p. 156, pl. 35, fig. 1, pl. 41, fig. 6) in having a dentate leaf margin, cuneate leaf base and more regular secondary venation. *C. acutidens* FONTAINE from the Lower Cretaceous Potomac Group of Virginia and Maryland, USA (WARD 1905, p. 529, pl. 113, figs 7, 8) differs from *Celastrophyllum* sp. described here by having larger leaves with bigger and more numerous marginal teeth.



Text-fig. 27: *Celastrophyllum* sp., NHMW 1999B0057/0262a, Grünbach (scale bar represents 1 cm).

"*C.*" *ovale* VAKHRAMEEV from the Middle Albian of Kazakhstan (VAKHRAMEEV 1952, p. 144, pl. 37, figs 6, 7, text-figs 57, 58) has more round leaves (leaflets). "*C.*" *retinerve* HERMAN from the Turonian Valizhgen Formation of North-western Kamchatka, Russia (HERMAN 1991, p. 97, pl. 9, figs 1-5, pl. 10, figs 4-8, text-fig. 3) differs from *Celastrophyllum* sp. in having bigger marginal teeth and reticulate venation. Moreover, the latter two species probably featured compound leaves and should therefore be excluded from the genus *Celastrophyllum*.

Bresciphyllum cretaceum VELENOVSKÝ from the Cenomanian Peruc Flora of the Czech Republic (VELENOVSKÝ

1889, Frič & Bayer 1901, p. 160, text-fig. 131) possesses a similar leaf shape and venation, but *Celastrophyllum* sp. differs from this species in having a smaller leaf size, secondary veins emerging from the midvein at an angle of 70-90° and a dentate rather than serrate leaf margin.

Genus *Compositiphyllum* Herman & J. Kvaček, nov. gen.

Derivatio nominis: After *compositus* (Lat.) – compound and *phyllum* (Gr.) – leaf.

Type: *Compositiphyllum serratum* Herman & Kvaček, nov. spec.

Species included: type *Compositiphyllum serratum* Herman & Kvaček, nov. spec.; *Compositiphyllum retinerve* (Herman) Herman & Kvaček, comb. nov. (basionym: *Celastrophyllum retinerve* Herman, 1987, p. 100, pl. 10, figs 4-8, text-fig. 3; see also Herman 1991, p. 97, pl. 9, fig. 1-5, text-fig. 27) from the Turonian of North-western Kamchatka; *Compositiphyllum ovale* (Vakhrameev) Herman & Kvaček, comb. nov. (basionym: *Celastrophyllum ovale* Vakhrameev, 1952, p. 244, pl. 37, figs 6, 7, text-figs 57, 58) from the Middle Albian of Kazakhstan; *Compositiphyllum* sp. (*Celastrophyllum* sp.: Upchurch 1984, p. 524, fig. 2) from the Lower Cretaceous Potomac Group in North America.

Diagnosis: Leaves pinnately compound, leaflets sessile or sometimes with short petiolules, opposite. Leaflets simple, unlobed, round to elliptic or narrow elliptic, with broadly acute, round or cordate, usually asymmetric base and acute apex. Leaflet margin crenate, dentate or serrate, marginal teeth with acute or round apices, of different size but usually small. Venation pinnate brochidodromous, tertiary and higher order venation reticulate.

Comparison and discussion: The new genus differs from other genera described for fossil compound or probably compound leaves (*Dalembia* Lebedev & Herman, *Debeya* Miquel, *Juglandiphyllites* Boulter & Z. Kvaček, *Platanites* Forbes, *Sapindophyllum* Ettingshausen, *Sapindopsis* Fontaine, *Scheffleraephyllum* Filippova, *Sorbites* Filippova, etc.) in having pinnately compound leaves with simple, unlobed, usually sessile leaflets, crenate, dentate or serrate leaflet margins and pinnate brochidodromous venation with reticulate tertiary and higher order veins.

We include four species of fossil compound leaves in this genus, all of which are morphologically similar to each other in leaf morphology, leaflet shape, margin and venation. Fossil material from these provides evidence that the leaves were pinnately compound. However, Vakhrameev (1952) interpreted two “leaf” impressions of *Celastrophyllum ovale* situated opposite each other as leaves belonging to one shoot, and Upchurch (1984) described his specimen of *Celastrophyllum* sp. as a leaf lacking a distinct petiole, but with an associated stem fragment (which is most probably the common petiole of the compound leaf with sessile leaflets). Herman (1987, 1991) described the impressions of *Celastrophyllum retinerve* as leaves or, most probably, leaflets of pinnately compound leaves. The plant fossils from Grünbach provide strong evidence that the species described below is represented by compound leaves.

Compositiphyllum serratum Herman & J. Kvaček, nov. spec.

(pl. 23, figs 1-9, pl. 34, figs 7-9; text-fig. 28)

Derivatio nominis: After *serratum* (Lat.) – serrate.

Holotype: NHMW 1999B0057/0033 (pl. 23, figs 1-3, 9, pl. 34, figs 7-9; text-fig. 28, A).

Stratum typicum: Grünbach Fm., Lower Campanian.

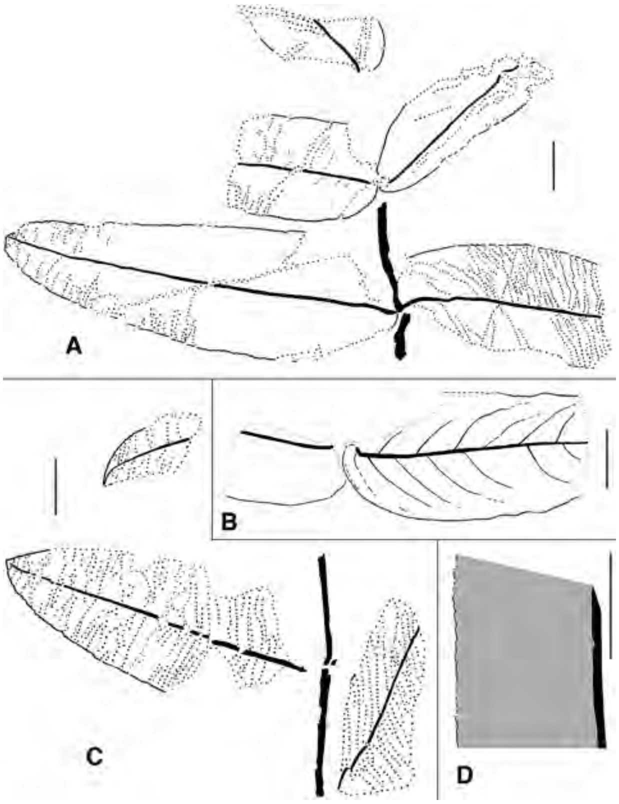
Locus typicus: Grünbach am Schneeberg, Austria.

Material: NHMW: 1999B0057/0028, …/0033 (counterpart …/0028), …/0069, …/0186a, …/0257a, …/0257b.

Occurrence: Austria, Grünbach am Schneeberg; Grünbach Formation, Lower Campanian.

Diagnosis: Leaves pinnately compound, leaflets sessile, opposite, small, simple, unlobed, narrow ovate, narrow elliptic or elliptic, symmetric or asymmetric, with serrate margin. Leaflet base cordate or auriculate, usually asymmetric, apex broadly acute. Marginal teeth very small, simple, triangular, with acute apices. Venation pinnate brochidodromous. Midvein stout and straight, numerous secondary veins very narrow, simple, emerging from the midvein at an angle of 45-90°, curving upwards, connecting to the upper secondary vein and forming loops. Tertiary veins very thin, ramified-percurrent to reticulate, higher order venation reticulate.

Description: Leaves pinnately compound (pl. 23, figs 1, 2, 4; Text-figs 28, A, B, C). Leaflets sessile, i.e. attached to the petiole directly by their bases, opposite (pl. 23, fig. 2; Text-figs 28, A, B). Leaflets small, simple, unlobed, narrow ovate, narrow elliptic or elliptic, symmetric or asymmetric, with serrate margin. Leaflet length 6.0-10.6 cm, leaflet width 2.5-3 cm. Leaflet lamina usually narrow ovate, sometimes elliptic or narrow elliptic in general outline, being broadest in the lower and sometimes middle part of the leaflet. Leaflet base cordate or auriculate (pl. 23, figs 2, 3, 6; Text-figs 28, A, B), usually asymmetric. Leaflet apex broadly acute (pl. 23, figs 1, 4-6; text-fig. 28, A, C). Leaf margin serrate. Marginal teeth very small, 0.2-0.3 mm in height, simple, triangular, with acute apices (pl. 23, figs 7-9; text-fig. 28, D). Sinuses between teeth round or acute. Petiolule is absent. Common petiole of leaf strong, up to 2.5 mm thick (pl. 23, figs 1, 4; Text-figs 28, A, C).



Text-fig. 28: *Compositiphyllum serratum* Herman & J. Kvaček, gen. & sp. nov., A – holotype NHMW 1999B0057/0033, B – NHMW 1999B0057/0257b, C – NHMW 1999B0057/0069, D – holotype NHMW 1999B0057/0033, detail of leaf margin with very small teeth, Grünbach (scale bar represents 1 cm).

Venation pinnate brochidodromous (pl. 23, fig. 6; text-fig. 28, B). Midvein stout and straight, terminating at leaflet apex, up to 2.5 mm thick in its basal part, narrowing towards apex. Numerous (more than 15-20) pairs of secondary veins emerging from the midvein at an angle of 45-90°, the most developed of them being in the middle part of the leaflet lamina. Secondary veins very thin, simple, curving upwards, connecting to the upper secondary vein and forming loops at some distance from the leaflet margin (pl. 23, figs 6-8). Tertiary veins very thin, ramified-percurrent to reticulate, higher order venation reticulate (pl. 23, figs 7, 8).

Cuticle removed from the holotype shows adaxial cuticle with ordinary cells 6-20 x 20-30 μm. Anticlinal walls are straight (pl. 34, fig. 9).

Abaxial cuticle shows ordinary cells 8-20 x 20-38 μm with straight anticlinal walls. Stomatal apparati are difficult to observe, stomatal chamber 15-20 x 25-32 μm (pl. 34, figs 8, 9).

Comparison and discussion: In its leaf shape and venation, *C. serratum* nov. spec. bears most resemblance to *Compositiphyllum* sp. (*Celastrophyllum* sp. UPCHURCH 1984) but differs in having much smaller marginal teeth, more numerous secondary veins and a wider angle between midvein and secondary veins. *Compositiphyllum ovale* (VAKHRAMEEV) HERMAN & KVAČEK, comb. nov. (basionym: *Celastrophyllum ovale* VAKHRAMEEV 1952, p. 244-245, pl. 37, fig. 6, 7, text-figs 57, 58) has smaller and rounder leaflets with crenate margin, bigger marginal teeth, fewer and more irregular secondary veins. The new species differs from *Compositiphyllum retinerve* (HERMAN) HERMAN & J. KVAČEK, comb. nov. (basionym: *Celastrophyllum retinerve* HERMAN 1987, p. 100-101, pl. 10, figs 4-8, text-fig. 3) in having more elongate sessile (without petioles) leaflets with cordate or auriculate, but not round or broadly acute, base, much smaller marginal teeth and a smaller distance between brochidodromous loops of secondary veins and the leaflet margin.

Genus *Debeya* MIQUEL, 1853

Type: *Debeya serrata* MIQUEL, 1853, p. 38, pl. 1, fig. 1

Debeya insignis (HOSIUS & MARCK) KNOBLOCH, 1964

(pl. 24, figs 1-3; text-fig. 29)

1880 *Dewalquea insignis* HOSIUS & MARCK, p. 172, pl. 32, figs 111-113, pl. 33, fig. 109, pl. 34, fig. 110.
1890 *Dewalquea insignis* HOSIUS & MARCK; LANGE, p. 671, pl. 34, fig. 8.
1957 *Dewalquea insignis* HOSIUS & MARCK; NĚMEJC, p. 106, pl. 12, figs 1, 2, pl. 13, figs 2-5, text-fig. 5.
1964 *Debeya insignis* (HOSIUS & MARCK) KNOBLOCH, p. 147.
1975 *Debeya insignis* (HOSIUS & MARCK) KNOBLOCH; NĚMEJC & KVAČEK, p. 48, pl. 8, fig. 4, pl. 9, figs 2, 4-7, pl. 10, figs 1, 3, 5, 6, pl. 11, fig. 4, pl. 22, figs 1-5, text-fig. 18 (see also synonymy in this publication).

Material: NHMW: 1999B0057/0065, .../0101c, .../0126, .../0180A, .../0241, .../0356b.

Occurrence: Senonian of Westfalen, Aachen and South Bohemia; Austria, Grünbach am Schneeberg, Grünbach Formation, Lower Campanian.

Description: Leaves small in size, probably palmately compound, unlobed, symmetric, with dentate margin. All leaflets in the collection are incomplete, therefore leaflet length is unknown but was approximately 7-9 cm, leaflet width 0.5 -1.6 cm. Leaflet lamina linear to oblong lanceolate in general outline, being broadest in the middle part of the leaf. Leaflet base narrow cuneate and slightly decurrent, symmetric, leaflet apex not preserved. Leaflet margin dentate or serrate, entire in the basal part of the leaf. Marginal teeth simple, up to 1.7 mm in height, triangular (text-fig. 29, A) or hook-like (text-fig. 29, B) in shape, with acute or round curving-upwards apices. Size of the marginal teeth often varies within one leaflet. Sinuses between teeth round. Petiole is poorly preserved in two specimens.

Venation pinnate craspedodromous. Midvein stout, prominent, straight, terminating at leaflet apex, approximately 0.5-1 mm thick in its basal part, narrowing towards leaf apex. Secondary veins poorly preserved, very thin, numerous, emerging from midvein at an angle of approximately 70° or less, slightly upwards curving and terminating in marginal teeth (text-fig. 29, A). Higher order venation and venation near leaflet margin not preserved.

Comparison and discussion: Although in the collection there are no remains of compound leaves with leaflets attached, in sample NHMW 1999B0057/0180a (pl. 24, fig. 2; text-fig. 29, A) two leaflets are situated close to each other with their bases pointing in one direction. Therefore we suggest that these fossils represent a fragment of a compound leaf. This is corroborated by a close similarity between the Grünbach material and the fossil leaflets of *Debeya insignis* described from the Senonian of Westfalen (HOSIUS & MARCK 1880), Aachen (LANGE 1890) and South Bohemia (NĚMEJC 1957; NĚMEJC & KVAČEK 1975). Therefore we assign the Grünbach leaflets to *D. insignis* (HOSIUS & MARCK) KNOBLOCH.

D. coriacea (VELENOVSKÝ) KNOBLOCH from the Cenomanian Peruc-Korycany Formation in the Czech Republic (Velenovský 1884, Frič & Bayer 1901, p. 159, figs 129, 130) and the Senonian of South Bohemia (Němejc & Kvaček 1975, p. 53, pl. 10, fig. 2, pl. 12, fig. 1, text-fig. 81m) has palmately compound leaves with dentate-margined leaflets. However, *D. insignis* from Grünbach, unlike *D. coriacea*, has linear to oblong lanceolate, but not elliptic or narrow elliptic, leaflets and numerous, sometimes hook-like, marginal teeth in all leaflet lamina, but not restricted to the upper half.

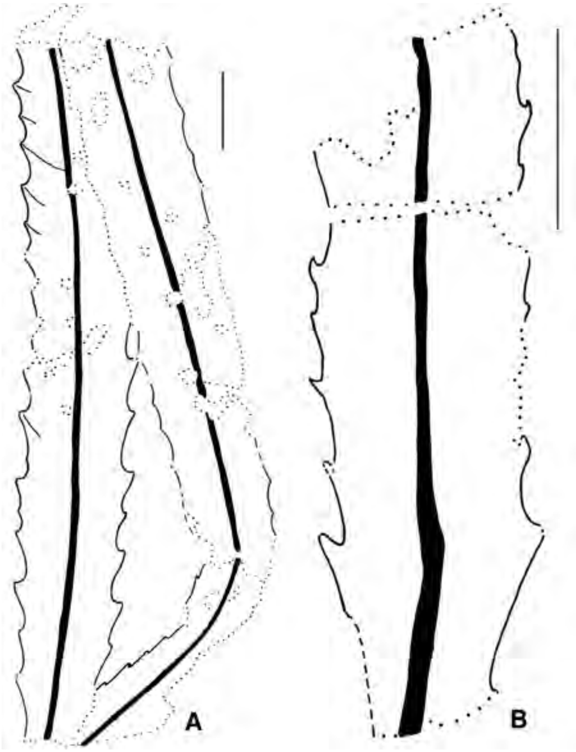
D. haldemiana (Saporta & Marion) Knobloch from the Senonian of Westfalen (Hosius & Marck 1880, p. 173, pl. 33, figs 116, 117, pl. 34, figs 115, 118-122, pl. 35, fig. 114) and South Bohemia (Němejc & Kvaček 1975, p. 52, pl. 10, fig. 4, pl. 11, fig. 3, text-fig. 8k) and *D. (Dewalquea) pentaphylla* Velenovský from the Cenomanian Peruc Flora of Czech Republic (Velenovský 1884, Frič & Bayer 1901, p. 158, fig. 128) differ from *D. insignis* in having entire-margined leaflets.

Leaflets from Grünbach are morphologically similar to *Proteophyllum lanceolatum* Němejc & Kvaček leaves from the Senonian of South Bohemia (Němejc & Kvaček 1975, p. 37, pl. 5, figs 3-11, pl. 6, figs 2, 3, 5, 7-9, pl. 18, figs 1-5, text-fig. 9), for which cuticular features are known. Lack of cuticles and poor preservation of venation in our material do not allow a detailed comparison of the leaflets from Grünbach with *P. lanceolatum*.

Genus *Ettingshausenia* Stiehler, 1857

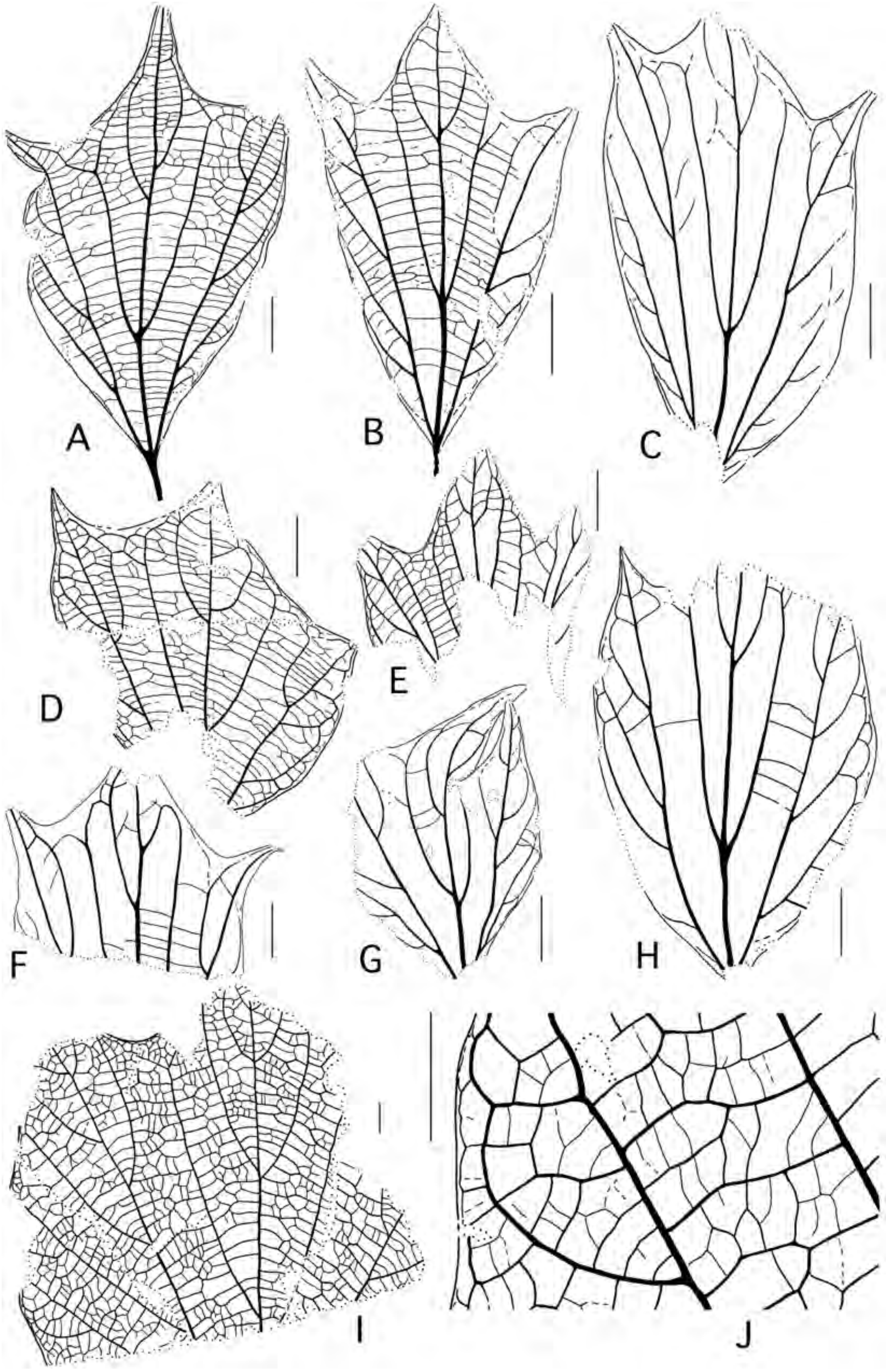
Type: *Credneria cuneifolia* Bronn 1837, p. 583, pl. 28, fig. 11 ≡ *Ettingshausenia cuneifolia* (Bronn) Stiehler, 1857, p. 66.

Emended diagnosis (Maslova et al. 2005): Leaf blades vary from entire triangular and pentagonal hexangular, rhomboidal or oval rhomboidal, without lobes or with vestigial lobes, to leaf blades with two to six lateral lobes. Leaf lamina often asymmetric. Leaf base usually cuneate and decurrent on the petiole. If the leaf base is truncate or cordate, the region of the leaf base adjacent to the petiole forms a small wedge. Peltate base occasionally present. Leaf apex acute or, more rarely, obtuse. Leaf margin dentate-incised; more rarely leaf entire-margined. Leaf venation craspedodromous or palinactinodromous, with developed lateral basal veins. Tertiary venation percurrent or ramified-percurrent.



Text-fig. 29: *Debeya insignis* (Hosius & Marck) Knobloch, A – NHMW 1999B0057/0180a, B – NHMW 1999B0057/0065, Grünbach (scale bar represents 1 cm).

Discussion: The genus *Ettingshausenia* with the type *E. cuneifolia* (Bronn) Stiehler was proposed by Stiehler (1857, p. 66). The type was initially described by Bronn (1837, p. 583, pl. 28, fig. 11) as *Credneria cuneifolia* Bronn from the Cenomanian of Niederschöna in Germany. Here we use the generic name *Ettingshausenia* for dispersed fossil *Platanus*-like leaves which cannot be assigned to the modern genus *Platanus* L. due to the lack of associated reproductive organs (Maslova et al. 2005).



Text-fig. 30: *Ettingshausenia gruenbachiana* Herman & J. Kvaček, nov. spec., A – holotype NHMW 1999B0057/1801, B – NHMW 1999B0057/0279, C – NHMW 1999B0057/0302, D – NHMW 1999B0057/0125, E – NHMW 1999B0057/0297, F – NHMW 1999B0057/0296, G – NHMW 1999B0057/0312, H – NHMW 1999B0057/0306, I, J – NHMW 1999B0057/0258: I – large leaf fragment, J – detailed venation, Grünbach (scale bar represents 1 cm).

Ettingshausenia gruenbachiana **Herman & J. Kvaček, nov. spec.**

(pl. 24, figs 4-11, pl. 25, fig. 1,
pl. 35, figs 5, 6; text-fig. 30)

Derivatio nominis: After Grünbach Village in Lower Austria.

Holotype: Designated here. NHMW 1970/1396/1649 (=1999B0057/1801), almost complete leaf (pl. 24, fig. 5, text-fig. 30, A).

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

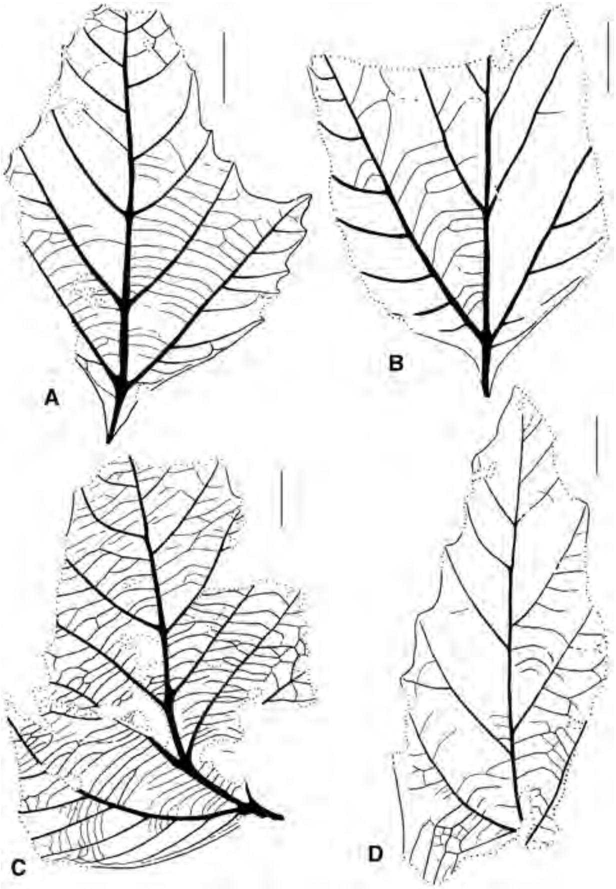
Material: NHMW 1999B0057/0125, …/0135, …/0242, …/0258, …/0262b, …/0279, …/0292, …/0294, …/0296, …/0297, …/0300, …/0301, …/0302, …/0305, …/0306, …/0307, …/0309, …/0310, …/0311, …/0312, …/0313, …/0314.

Occurrence: Grünbach am Schneeberg, Maiersdorf; Grünbach Formation, Lower Campanian, Austria.

Diagnosis: Leaves small to large, obovate, simple, trilobate, often asymmetric, entire-margined, petiolate. Leaf base narrow cuneate, never peltate, apex acute to slightly attenuate. Two lateral lobes in the upper part of a leaf triangular, with acute to attenuate apices. Venation palmately-pinnate brochidodromous with strong basal veins emerging from leaf base. Suprabasal secondary veins rare, brochidodromous, obliquely emerging from primary veins at an angle of 20° or less and curving upwards. Tertiary veins percurrent or ramified-percurrent, quaternary veins percurrent to orthogonal-reticulate, tertiary venation near leaf margin looped.

Description: Leaves small to large in size, simple, trilobate, often asymmetric, entire-margined. Leaf length from 5-5.5 (text-fig. 30, G) to approximately 25 cm (text-fig. 30, I), leaf width from 4 to approximately 15 cm. Leaf lamina (including lobes) obovate in general outline, being broadest in the upper part of the leaf. Leaf base narrow cuneate but not decurrent, symmetric (pl. 24, figs 5, 6, pl. 25, fig. 1; text-figs 30, A, B). A few specimens possess well-preserved basal parts of the leaf lamina, none of which has a peltate leaf base. Leaf apex acute to slightly attenuate (pl. 24, figs 4-6; text-figs 30, A, B, D, G). Two lateral lobes in the upper part of the leaf are well-developed (pl. 24, figs 5-7; text-fig. 30, B) or small (pl. 25, fig. 1; text-fig. 30, C). Lobes triangular in shape, broad or narrow, with acute to attenuate apices. Lateral lobes within one leaf are often of different size and shape (pl. 24, fig. 4; pl. 25, fig. 1; text-figs 30, C, D). Sinuses between lateral lobes and leaf apex (apical lobe) are broad, usually shallow (pl. 24, figs 4, 5; text-figs 30, A, D), rarely deep (pl. 24, figs 6, 10; text-figs 30, B, G), round. Leaf margin entire. Petiole poorly preserved, 1.2 mm thick and more than 8 mm in length.

Venation palmately-pinnate brochidodromous. Midvein stout, straight, terminating leaf apex, approximately 0.8 mm thick in its basal part, narrowing towards the apex. Two lateral basal veins stout, approximately of the same width as the midvein, straight (pl. 24, fig. 4; text-figs 30, D, H) or slightly curved (pl. 24, figs 5, 7; text-figs 30, A, F) in their distal parts, emerging from leaf base and terminating at the lateral lobe apices. Suprabasal secondary veins rare, brochidodromous, obliquely emerging from midvein and basal veins at an angle of 20° or less and curving upwards. Two, rarely three, pairs of opposite or almost opposite secondary veins emerge from the midvein. Three to five abaxial and usually one adaxial secondaries emerge from each lateral basal vein. There are no infrabasal secondary veins. Tertiary veins prominent, straight or slightly curved, percurrent or ramified-percurrent (pl. 24, figs 4, 5, 9, 10; text-figs 30, A, D, I), nearly perpendicular to



Text-fig. 31: *Ettingshausenia* cf. *laevis* (Velenovský) J. Kvaček & Váchová, A – NHMW 1999B0057/0263a, B – NHMW 1999B0057/0295, C – NHMW 1999B0057/0263b, D – NHMW 1999B0057/0293, Grünbach (scale bar represents 1 cm).

the secondary veins. Quaternary veins percurrent to orthogonal-reticulate (pl. 24, fig. 8; text-figs 30, J). Tertiary venation forming loops along leaf margin (pl. 24, figs 8, 11; text-fig. 30, J).

The best cuticle preserved was removed from the specimen No. NHMW 1999B0057/0279 and is of medium thickness (pl. 35, figs 5, 6). Adaxial cuticle is thicker, consisting of polygonal ordinary cells (6-15 x 10-25 μm), anticlinal walls straight or slightly curved 1-3 μm. Abaxial cuticle is thin with nearly invisible ordinary cells with slightly sinuous anticlinal walls. Stomatal complexes (20-25 x 30-35 μm) consisting of two well pronounced guard cells (pl. 35, figs 5, 6), circular trichome bases (12 μm in diameter) consisting of several cells (pl. 35, fig. 6).

Comparison and discussion: *Ettingshausenia gruenbachiana* nov. spec. differs from the majority of fossil *Platanus*-like leaves by its trilobate shape and entire margin of the leaf lamina. *Ettingshausenia senonensis* (Knobloch) J. Kvaček & Váchová from the Senonian of South Bohemia (Knobloch 1964; Němejc & Kvaček 1975, J. Kvaček & Váchová 2006) bears most resemblance to the new species. *E. gruenbachiana* nov. spec. differs from *E. senonensis* in having trilobate leaves and not five lobes present in *E. senonensis*. The lobes in *E. gruenbachiana* are small and triangular in shape whereas *E. senonensis* has bigger usually ellipsoidal lobes. The new species possesses shallower sinuses and does not have the additional small 'second order' lobes typical of *E. senonensis*. The leaf base in *E. gruenbachiana* is cuneate but never peltate, whereas *E. senonensis* has both cuneate and peltate bases. Secondary veins in the new species are fewer and emerge more obliquely from the primary (midvein and lateral basal) veins.

Credneria purkynei Velenovský & Viniklář from the Cenomanian of the Czech Republic (Velenovský & Viniklář 1927, p. 19, pl. 8, figs 5-8, pl. 12, fig. 7) is very similar to *Ettingshausenia senonensis*. As Němejc & Kvaček (1975, p. 58) noted, 'morphologically both are hardly to be distinguished from each other'. This species differs from *E. gruenbachiana* by the same features which allow us to differentiate the latter and *E. senonensis*.

Several species of the genus *Credneria* were described from the Santonian of Quedlinburg and the Senonian of Westfalen in Germany (*C. integerrima* Zenker, *C. acuminata* Hampe, *C. denticulata* Zenker, *C. subtriloba* Zenker, *C. triacuminata* Hampe, *C. westfalica* Hosius, *C. tenuinervis* Hosius, etc.), including the type of the genus *C. integerrima* Zenker (Zenker 1833; Hosius & Marck 1880; Richter 1905; etc.), but they probably all belong to one highly polymorphic species (Němejc & Kvaček 1975). *Ettingshausenia gruenbachiana* nov. spec. differs from the *Credneria* leaves from Quedlinburg and Westfalen in its smaller size, narrower obovate leaf shape, cuneate leaf base, narrower triangular lateral lobes and entire leaf margin.

Platanervia integrifolia Krassilov from the Turonian of Negev, Israel (Krassilov et al. 2005, p. 113, pl. 16, figs 1-7, text-fig. 18) has broadly rhomboidal leaves with cuneate bases, entire margin and palmately-pinnate venation similar to those in *Ettingshausenia gruenbachiana* nov. spec. The latter species, however, differs from *Platanervia integrifolia* in having distinct lateral lobes, well-developed stout basal veins and acute to attenuate leaf and lateral lobe apices.

'Sassafras' acutilobum Lesquereux from the Cenomanian Peruc Flora of the Czech Republic (Velenovský 1884, Frič & Bayer 1901, p. 130, fig. 93) resembles *Ettingshausenia gruenbachiana* nov. spec. in its trilobate leaf shape but has different secondary and, particularly, tertiary venation which is not typical for platanoid leaves.

Ettingshausenia cf. *laevis* (Velenovský) J. Kvaček & Váchová, 2006

(pl. 25, figs 2-4; pl. 32, figs 5, 6,
pl. 35, fig. 4; text-fig. 31)

1882	*Credneria laevis* Velenovský, p. 6, pl. 1, fig. 4, pl. 2, figs 2-6.
1889	*Platanus laevis* (Velenovský) Velenovský, p. 16, pl. 1, figs 1, 2.
1901	*Platanus laevis* (Velenovský) Velenovský; Frič & Bayer, p. 132, fig. 98.
2006	*Ettingshausenia laevis* (Velenovský) J. Kvaček & Váchová, p. 83, text-figs 2a, 3ab.

Material: NHMW: 1999B0057/0090, …/0123c, …/0135, …/0263a, …/0263b, …/0293, …/0295, …/0304.

Occurrence: Czech Republic; Peruc-Korycany Formation, Cenomanian; Austria, Grünbach am Schneeberg; Grünbach Formation, Lower Campanian.

Description: Leaves small in size, simple, trilobate, symmetric, with dentate margin. Leaf length from 7 cm (pl. 25, fig. 2; text-fig. 31, A) to approximately 12 cm, leaf width from 5.3 cm (pl. 25, fig. 2; text-fig. 31, A) to approximately 9 cm. Leaf lamina rhomboidal in shape, the maximum width being in the middle part of a leaf (pl. 25, fig. 2; text-fig. 31, A). Leaf base narrow cuneate and decurrent, symmetric, apex narrow acute. Two small lateral lobes, considerably smaller than the middle lobe (apical part of the leaf), triangular in shape, situated in the middle part of the leaf lamina (pl. 25, figs 2, 3; text-figs 31, A, C). Sinuses between lobes and apical part of the leaf shallow, broad, round (pl. 25, fig. 2; text-fig. 31, A). Leaf margin dentate, marginal teeth simple, triangular, slightly curving upwards, with broadly acute or round apices, 1-1.6 mm in height. Sinuses between teeth round. Petiole poorly preserved (pl. 25, fig. 3; text-fig. 31, C), approximately 1.8 mm thick.

Venation palmately-pinnate craspedodromous. Midvein stout, straight, terminating at the leaf apex, approximately 0.6 – 0.8 mm thick in its basal part, narrowing towards the leaf apex. Two stout lateral basal veins, of approximately the same width as the midvein or slightly thinner, straight, emerging from the midvein 5 – 8 mm above the leaf base and terminating at the lateral lobe apices (pl. 25, figs 2-4; text-figs 31, A-C). Suprabasal secondary veins craspedodromous, occasionally camptodromous, emerging from the midvein and basal veins at an angle of 30-40° and going to the marginal teeth. Rarely suprabasal secondary veins almost perpendicular to the basal vein (pl. 25, fig. 4; text-fig. 31, B). More than 5 (approximately 7) pairs of secondary veins emerge from a midvein, situated opposite each other in the lower part of the leaf (pl. 25, figs 2, 3; text-figs 31, A, C). Nine or more abaxial secondaries emerge from each lateral basal vein (pl. 25, figs 2-4; text-figs 31, A-C). There are no prominent adaxial secondaries going from lateral basal veins. Usually one thin and short camptodromous infrabasal secondary vein emerges from a midvein (pl. 25, figs 2-4; text-figs 31, A-C). Tertiary veins prominent, slightly curved, percurrent or ramified-percurrent. Quaternary venation

Text-fig. 32: *Ettingshausenia* sp., NHMW 1999B0057/0298, Grünbach (scale bar represents 1 cm).

and venation near leaf margins poorly preserved.

Cuticle removed from the specimen No. NHMW 1999B0057/0135 is medium thick (pl. 35, fig. 4). Adaxial cuticle is thicker, consisting of polygonal ordinary cells (7-18 x 18-50 μm), anticlinal walls straight or slightly curved 1-3 μm in thickness. Abaxial cuticle is thin with nearly invisible ordinary cells with slightly sinuous anticlinal walls. Stomatal complexes (12-15 x 20-25 μm) consisting of two well pronounced guard cells (pl. 35, fig. 4). Simple and compound circular trichome bases are present.

Comparison and discussion: The fossil species which bears most similarity to the material described here is *Ettingshausenia laevis* (Velenovský) J. Kvaček & Váchová from the Cenomanian Peruc-Korycany Formation in the Czech Republic (Velenovský 1882; Frič & Bayer 1901, p. 132, fig. 98; J. Kvaček & Váchová 2006). Incomplete preservation of the Grünbach fossil leaf material does not allow us to assign this species to *E. laevis* with confidence. However, these leaves obviously differ from the other species of the Grünbach Flora possessing platanoid morphology, *E. gruenbachiana* nov. spec., in having a distinctly dentate leaf margin.

The species which bears most resemblance to *E.* cf. *laevis* is *Platanus newberryana* Heer from the Late Cretaceous of North America, Greenland, Alaska, Kazakhstan and North-eastern Russia (Capellini & Heer 1866, p. 16, pl. 1, fig. 4; Lesquereux 1874, p. 72, pl. 8, figs 2, 3, pl. 9, fig. 3; Hollick 1930, p. 83, pl. 47, fig. 3; Vakhrameev 1952, p. 222, pl. 24, fig. 2, pl. 25, fig. 2; Herman 1991, p. 69, pl. 3, fig. 1, pl. 5, fig. 1; and others), which differs from *E. cf. laevis* in having smaller and narrower lateral lobes and a shorter but wider middle (apical) lobe. Trilobed leaves of *Platanus primaeva* Lesquereux from the latest Albian and Late Cretaceous of North America, Kazakhstan, Western Siberia, Alaska and North-western Kamchatka (Lesquereux 1874, p. 69, pl. 7, fig. 2; Lesquereux 1891, p. 72, pl. 8, fig. 7, pl. 9, figs 1-4, pl. 10, fig. 1; Hollick 1930, p. 84, pl. 51, fig. 2; Vakhrameev 1952, p. 218, pl. 27, figs 2, 3, pl. 28, fig. 2, pl. 29, fig. 2, pl. 30, figs 1, 2, pl. 31, figs 1, 2, text-fig. 50; Herman 1991, p. 70, pl. 3, fig. 2) are broader and have fewer secondary veins and marginal teeth.

A further species similar to *Ettingshausenia* cf. *laevis* is *Platanus reynoldsii* Newberry from the latest Cretaceous and Tertiary of Asia and North America (Newberry 1898; Krassilov 1976; Moiseeva 2003; Moiseeva & al. 2004; Maslova & al. 2005; and others). However, unlike *Ettingshausenia* cf. *laevis*, it possesses both abaxial and adaxial secondary vein branches going from the lateral basal veins towards the margins of the lateral lobes. Moreover, this species usually has smaller and more numerous marginal teeth and a broader middle lobe. Variability of this species also differs from that typical of *Ettingshausenia* cf. *laevis*.

***Ettingshausenia* sp.**

(pl. 25, fig. 5; text-fig. 32)

Material: NHMW 1999B0057/0298.

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Description: This species is represented by a single fossil leaf within the collection (pl. 25, fig. 5; text-fig. 32). It is small, simple, trilobate, symmetric, with a dentate margin. Leaf length unknown, leaf width approximately 6.5 cm. Leaf lamina ovate in shape, the maximum width being in the lower part of the leaf. Leaf base broadly cuneate, asymmetric, apex not preserved. Two lateral lobes well developed but smaller than the middle lobe (apical part of the leaf), probably triangular in shape, situated in the lower part of the leaf lamina. Sinuses between lateral lobes and apical part of the leaf unknown. Leaf margin dentate, marginal teeth simple, triangular, with acute apices, 0.5-0.8 mm in height. Sinuses between teeth round. Petiole not preserved. Venation palmately-pinnate craspedodromous. Midvein stout, approximately 1.2 mm thick in its basal part, rapidly narrowing towards the apex. Two basal veins stout, approximately 1 mm thick in their basal parts, emerging from the midvein 1-5 (?) mm above the leaf base and going to the lateral lobe apices. Suprabasal secondary veins emerging from midvein and lateral basal veins at an angle of 30-45° and terminating at the marginal teeth. More than four pairs of secondary veins emerge from a midvein, being opposite in the lower and middle parts of the leaf. Eight or more abaxial and three or more prominent adaxial secondaries emerge from each lateral basal vein. There are no infrabasal secondary veins. Tertiary veins thin, percurrent or ramified-percurrent, slightly curved. Quaternary venation and venation near leaf margins poorly preserved.

Comparison and discussion: The leaf under consideration bears some similarities with *Ettingshausenia* cf. *laevis* described above (trilobed leaf with cuneate base, dentate leaf margin, two stout lateral basal veins, opposite secondary veins and percurrent tertiary venation characteristic of platanoid leaves), but differs from this species in having a relatively broader leaf lamina, ovate leaf shape with maximum width in the lower part of the leaf, asymmetric broad leaf base and possibly better developed lateral lobes. The midvein in *Ettingshausenia* sp. is thicker, than in *E.* cf. *laevis*, lateral basal veins are stronger and have both abaxial and prominent adaxial secondaries emerging from them. These features prevent assignment of the leaf to *E.* cf. *laevis*, but poor preservation of the single specimen does not allow specific identification of the leaf.

The specimen described possesses some similarities with several species of platanoid morphology, such as *Platanus embicola* Vakhrameev from the Upper Albian-Cenomanian of Kazakhstan (Vakhrameev 1952, p. 214, pl. 22, figs 4, 5, pl. 23, figs 1-3 pl. 24, fig. 1, pl. 25, fig. 1, text-fig. 49), *P. primaeva* Lesquereux from the Upper Cretaceous of Kazakhstan, Western Siberia, Alaska, North-western Kamchatka and North America (Lesquereux 1874, p. 69, pl. 7, fig. 1, pl. 26, fig. 2; Hollick 1930, p. 84, pl. 51, fig. 2; Vakhrameev 1952, p. 218, pl. 27, figs 2, 3, pl. 28, fig. 2, pl. 29, fig. 2, pl. 30, figs 1, 2, pl. 31, figs 1, 2, text-fig. 50; Herman 1991, p. 70, pl. 3, fig. 2) and *P. velenovskyana* Krasser from the Cenomanian Peruc Flora of the Czech Republic (Velenovský 1882, Frič & Bayer 1901, p. 131, figs 95, 96). Again, poor preservation of the *Ettingshausenia* sp. leaf does not allow detailed comparison with these species.

Genus *Grebenkia* E. Lebedev, 1986

Type: *Viburnum anadyrense* Kryshtofovich 1958, p. 65, pl. 13, figs 2, 3; text-figs 51, 52 ≡ *Grebenkia anadyrensis* (Kryshtofovich) E. Lebedev, 1986, p. 136, text-figs1-3.

Grebenkia europaea
Herman & J. Kvaček, nov. spec.

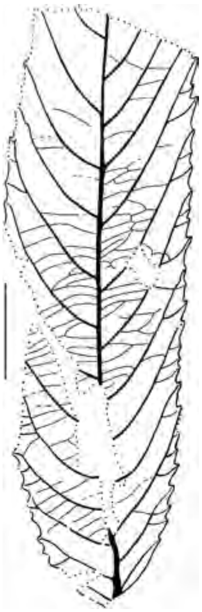
(pl. 25, figs 6, 7; text-fig. 33)

Derivatio nominis: After Europe.

Holotype: Designated here. NHMW 1999B0057/0277 (pl. 25, figs 6, 7; text-fig. 33).

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Austria, Grünbach am Schneeberg.



Text-fig. 33: *Grebenkia europaea* Herman & J. Kvaček, nov. spec., holotype NHMW 1999B0057/0277, Grünbach (scale bar represents 1 cm).

Material: NHMW 1999B0057/0114, …/0123a, …/0271, …/0308.

Occurrence: Austria, Grünbach am Schneeberg; Grünbach Formation, Lower Campanian.

Diagnosis: Leaves small, simple, unlobed, oblong-elliptic, symmetric or slightly asymmetric, with dentate margin. Leaf base narrow or broad cuneate, apex acute. Leaf margin dentate, marginal teeth small, simple, triangular, curving upwards, with acute apices, intervening sinuses round. Occasionally 1-3 smaller teeth are present between two larger teeth. Venation pinnate craspedodromous. Midvein straight, terminating at leaf apex, secondary veins numerous, up to 20 pairs emerging from the midvein, forking up to three times, all branches terminating in marginal teeth. Tertiary veins thin, straight or slightly curved, percurrent or ramified-percurrent.

Description: Leaves small in size, simple, unlobed, symmetric or slightly asymmetric, with dentate margin (pl. 25, figs 6, 7; text-fig. 33). Leaf length from 4.5-5.5 cm to approximately 10-12 cm, leaf width from 1.7 cm to approximately 2.3 cm. Leaf lamina oblong-elliptic in general outline, broadest in the middle part of the leaf. Leaf base narrow or broad cuneate, symmetric or slightly asymmetric, leaf apex acute. Leaf margin dentate (pl. 25, fig. 7), marginal teeth simple, small, triangular in shape, curving upwards, with acute apices, 0.4-1.2 mm in height. Occasionally 1 or 2, rarely 3, smaller teeth occur between two larger teeth. Sinuses between teeth round. Petiole not preserved.

Venation pinnate craspedodromous. Midvein straight, terminating at leaf apex, approximately 0.4 mm thick in its basal part, narrowing towards leaf apex. Secondary veins numerous, emerging from the midvein at an angle of 70° in the basal part of the leaf and 40-50° in the apical part and curving upwards. Up to 20 pairs of secondary veins emerge from the midvein, the most developed being in the middle part of the leaf lamina. Secondary veins fork basiscopically up to three times with all branches terminating in marginal teeth. Tertiary veins thin, straight or slightly curved, percurrent or ramified-percurrent (pl. 25, fig. 7; text-fig. 33), oblique to the secondary veins. Higher order venation and venation near leaf margin not preserved.

Comparison and discussion: *Grebenkia europaea* nov. spec. is similar to the type of the genus *G. anadyrensis* (Kryshtofovich) E. Lebedev from the Upper Albian-Cenomanian Krivorechenskaya Formation and the Turonian Valizhgen Formation of North-eastern Russia, in synonymy of which we also include two species: *G. kryshtofovichii* E. Lebedev from the Krivorechenskaya and Valizhgen formations and *G. acuminata* Filippova from the Krivorechenskaya Formation (Kryshtofovich 1958, p. 65, pl. 13, figs 2, 3, text-figs 51, 52; Lebedev 1986, p. 136-138, text-figs1-3; Filippova 1989, p. 86, pl. 10, figs 3-5; Herman 1991, p. 130, pl. 8, fig. 6, pl. 11, fig. 6; Filippova & Abramova 1993, p. 174-175, pl. 33, figs 2, 3, pl. 39, figs 2-5, pl. 110, fig. 2), in having oblong-elliptic leaves with irregular dentation, pinnate craspedodromous venation and percurrent or ramified-percurrent tertiary veins. However, *G. europaea* has smaller, narrower and more elongate leaves and a larger number of secondary veins.

G. europaea nov. spec. has some similarities in leaf shape and venation with *Viburniphyllum whymperi* (Heer) Herman from the Upper Cretaceous and Tertiary of North America, Greenland, Sakhalin Island and North-eastern Russia (Heer 1871a, p. 475, pl. 46, fig. 1b; Heer 1878, p. 111, pl. 54, fig. 1; Kryshtofovich & Baikovskaya 1960, p. 112, pl. 21, fig. 4; Baikovskaya 1956, pl. 11, fig. 4; Herman 1991, p. 114, pl. 11, fig. 9b, pl. 13, figs 5-7) but differs from this species in having irregular marginal teeth and percurrent to ramified-percurrent tertiary veins emerging obliquely from the secondaries – features typical of the genus *Grebenkia*.

Genus *Juglandiphyllites*
Boulter & Z. Kvaček, 1989

Type : *Juglandiphyllites ardtunensis* Boulter & Z. Kvaček, 1989, p. 95, pl. 19, figs 1-3.

The genus *Juglandiphyllites* has been established for pinnately compound leaves from the Paleocene flora of the Isle of Mull. It is based on *Juglandiphyllites ardtunensis* Boulter & Z. Kvaček (holotype No. V. 25133,1) housed in the Natural History Museum, London. Leaflets of the compound leaves are (Boulter & Z. Kvaček, 1989, p. 94) 'ovate to elliptical, acute-obtuse to slightly cordate, mostly asymmetrical at the base, entire-margined to serrate, venation camptodrome to craspedodrome, secondaries slightly curved, at least at the leaflet base, at wider angles on one side of the midvein than on the other, regularly spaced. Intersecondaries partly present, teeth asymmetrically triangular to falcate, non-glandular, usually sharp, sinuses angular, sharp, secondaries and external veins entering the teeth, mostly submedially, tertiaries weakly to distinctly percurrent, more or less widely spaced'. Boulter & Z. Kvaček (1989) emphasised that the margin of these leaflets can be entire to serrate, a range often found in the same genus or even in species of modern Juglandaceae.

The genus *Sapindophyllum* Ettingshausen is based on a Tertiary (Eocene) leaf remain *Sapindophyllum spinulosodentatum* Ettingshausen 1869, p. 26, pl. 46, fig. 27 from the locality of Kučlín (Czech Republic), which is determined as *Engelhardia orsbergensis* (Z. Kvaček personal communication 2008). Therefore the genus *Sapindophyllum* can not be used for leaves of general juglandoid affinity and morphology. It differs from *Juglandiphyllites pelagicus* in having serrate margin, lanceolate lamina and finely pinnate venation. Other generic names proposed for leaves with similar morphology, *Juglandophyllum* Schenk and *Judlandiphyllum* Nathorst, cannot be used because they have been invalidly published (see Boulter & Z. Kvaček 1989).

Juglandiphyllites pelagicus (Unger)
Herman & J. Kvaček, comb. nov.

(pl. 30, figs 1-4a, 5, 6, pl. 31, figs 1b-3, pl. 36, figs 1-4; text-figs 8O, P, AI, 34)

Basionym: *Phyllites pelagicus* Unger, 1850, Genera et species plantarum fossilium, p. 503.

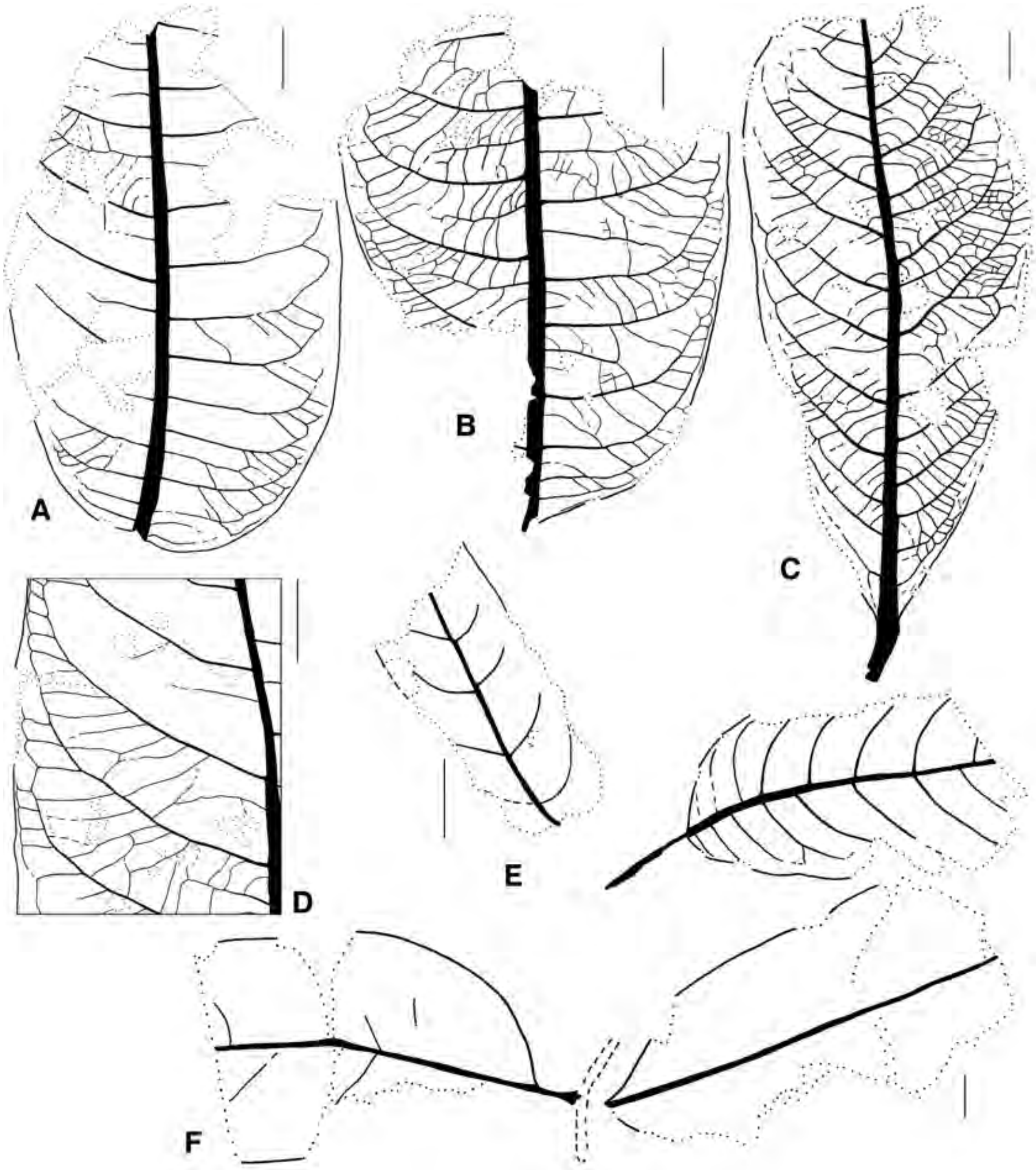
1867 *Phyllites pelagicus* Unger, p. 653, pl. 2, fig. 13.
1884 *Sapindophyllum pelagicum* (Unger) Velenovský, p. 7, pl. 7, fig. 9, pl. 8, figs 6-9.
1901 *Sapindophyllum pelagicum* (Unger) Velenovský; Frič & Bayer, p. 138.

Holotype: GBA 2006/07/01, pl. 30, figs 1, 2; text-fig. 34C (Unger 1867, pl. 2, fig. 13).

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

Material: GBA: 2006/60/26, …/32, …/62, 2006/64/01, …/02, …/04, …/06, …/11, …/15, …/17, …/19, …/20, …/23, …/24, …/27, …/29, …/33. NHMW: 1853/0003/0052, 1999B0057/0005, …/0006, …/0007, …/0008, …/0009, …/0010, …/0011, …/0012, …/0013, …/0014, …/0015, …/0016, …/0017, …/0018, …/0019, …/0020, …/0021, …/0022, …/0023, …/0025, …/0026, …/0029, …/0031, …/0032, …/0035, …/0036,



Text-fig. 34: *Juglandiphyllites pelagicus* (Unger) Herman & J. Kvaček, comb. nov., A – NHMW 1999B0057/0283a, B – NHMW 1999B0057/0281, C – holotype GBA 2006/07/01, D – NHMW 1999B0057/0282a, detailed venation, E – NHMW 1999B0057/0052, two leaflets, F – NHMW 1999B0057/0061, two leaflets possibly attached to the common petiole, Grünbach (scale bar represents 1 cm).

…/0037, …/0041, …/0042, …/0045, …/0046, …/0047, …/0050, …/0051, …/0052, …/0054, …/0055, …/0057, …/0058, …/0059, …/0060b, …/0061, …/0062, …/0064, …/0066, …/0067, …/0071, …/0072, …/0077, …/0080, …/0081, …/0083, …/0084, …/0085, …/0102b, …/0103, …/0117, …/0134, …/209c, …/0212a, …/0236, …/0261, …/0276, …/0281, …/0282a, …/0283a, …/360b, …/0373, …/0380, …/0512.

Occurrence: Czech Republic, Peruc-Korycany Formation, Cenomanian; Austria, Grünbach am Schneeberg, Muthmannsdorf, Dreistätten, Grünbach Formation, Lower Campanian.

Description: Leaves probably pinnately compound (Text-figs 34 E, F). Leaflets small to medium in size, simple, unlobed, narrow to broadly elliptic, symmetric or asymmetric, entire-margined. Leaflet length from

5-5.5 cm to approximately 17 cm or more (up to 25? cm), leaflet width from 2.5-2.7 cm to approximately 10 cm. The holotype (pl. 30, fig. 1, text-fig. 34C) represents an entire-margined leaflet with cuneate base and broad short petiole. Leaflet lamina usually elliptic but sometimes narrow elliptic (pl. 30, fig. 4a) or broadly elliptic (pl. 30, fig. 3; pl. 31, fig. 3) in general outline, being broadest in the middle part of the leaflet. Leaflet base broadly round (text-fig. 34A) or broadly cuneate (text-fig. 34B), occasionally narrow cuneate (text-fig. 34C), often asymmetric. Leaflet apex (pl. 30, fig. 5; pl. 31, fig. 4) narrow to broadly acute or round, sometimes slightly attenuate. Leaflet margin entire, sometimes slightly undulate (pl. 30, fig. 2; pl. 31, fig. 2). Petiolule rarely preserved, 1 cm or less in length and 1 mm in width (text-fig. 34C). Common petiole of leaf not preserved.

Venation pinnate brochidodromous. Midvein stout and straight, running towards leaflet apex, up to 2.5 mm thick in its basal part, narrowing towards the apex. At least 12-15 (up to 25 ?) pairs of secondary veins emerge from the midvein at an angle of 60-90°, more usually at 80-90°, the most developed being in the middle part of the leaflet lamina (Text-figs 34 A-C). Secondary veins opposite or almost opposite in the lower part of the leaflet, thin, simple, curving upwards, connecting to the upper secondary vein and forming a series of loops towards the leaflet margin. There is usually one intersecondary vein between two secondaries (Text-figs 34 A-C); the intersecondary vein is shorter and thinner than adjacent secondary veins. Tertiary veins very thin, percurrent to ramified-percurrent, straight or slightly curved (pl. 30, fig. 2; Text-figs 34 A-D), forming small loops near the leaf margin (pl. 30, fig. 2; Text-figs 34 A-C). Higher venation orders orthogonal-reticulate (Text-figs 34 C, D).

Poorly preserved cuticle (probably adaxial) removed from the specimen NHMW 1999B0057/0282a shows ordinary cells (7-12 x 12-20 μm) (pl. 36, figs 1, 2, 4). Anticlinal walls are straight, 2-3 μm in thickness. Cuticle shows circular trichome bases and resin bodies 20-50 μm (pl. 36, figs 1, 2, 4). Possible stomata were observed in some places, where small bits of abaxial cuticle are preserved (pl. 36, fig. 1, arrowed) and pl. 36, fig. 3 (NHMW 1999B0057/0084). They are small 17 x 12 μm and quite difficult to observe.

Comparison and discussion: The morphology of the leaflets described here conforms with the generic diagnosis of *Juglandiphyllites* (see above).

J. pelagicus is similar to the type of the genus, *J. ardtunensis* Boulter & Z. Kvaček from the Paleocene flora of the Isle of Mull (Boulter & Z. Kvaček 1989, p. 95, pl. 19, figs 1-3), in having an elliptic leaflet shape, asymmetrical leaflet base, an entire margin and slightly curved secondary veins. However, *J. pelagicus* usually has bigger and wider leaflets, acute or round, a sometimes slightly attenuate leaflet apex without the drip-tip observed in *J. ardtunensis*, partly present intersecondary veins and distinct percurrent to ramified-percurrent, but not irregularly-reticulate, tertiary venation. *J. finlayi* (Johnson) Boulter & Z. Kvaček from the Paleocene flora of the Isle of Mull (Boulter & Z. Kvaček 1989, p. 96, pl. 19, fig. 4) differs from *J. pelagicus* in having narrower leaflets with a coarsely double dentate leaf margin.

Juglandites primordialis Lesquereux from the latest Albian – Cenomanian Dakota Formation in North America (Lesquereux 1891, p. 70, pl. 35, fig. 15) has leaf shape and venation similar to those of *Juglandiphyllites pelagicus*. The latter, however, differs from the Dakota species in having a larger number of secondary veins. Unfortunately, poor preservation of *Juglandites primordialis* does not allow more detailed comparison of these species.

Sapindus apiculatus Velenovský from the Cenomanian Peruc Flora of Czech Republic (Velenovský 1884; Frič & Bayer 1901, p. 137, fig. 102) differs from *Juglandiphyllites pelagicus* in having much smaller and narrower leaflets with acute to slightly attenuate apices and acute bases. Moreover, *J. pelagicus* leaflets have distinct petiolules which were not observed in *Sapindus apiculatus*. *S. morrisonii* Lesquereux from the Late Cretaceous of North America (Lesquereux 1883, p. 83, pl. 16, figs 1, 2) has compound leaves with entire-margined leaflets, but differs from *Juglandiphyllites pelagicus* in having narrower leaflets with acute, but never broadly round, bases. *Ficus macrophylla* Lesquereux from the latest Albian – Cenomanian Dakota Formation in North America (Lesquereux 1891, p. 76, pl. 11, fig. 1) has large entire-margined leaves with primary and secondary venation similar to those in *Juglandiphyllites pelagicus*, but the latter species differs in its smaller size, curving-upwards secondary veins and percurrent to ramified-percurrent but not orthogonal-reticulate tertiary venation.

Two species from the Upper Cretaceous of Kazakhstan, *Juglans aktjubensis* Vakhrameev (Vakhrameev 1952, p. 179, pl. 11, fig. 4, text-fig. 34) and *Ficus embensis* Vakhrameev (Vakhrameev 1952, p.180, pl. 11, figs 5, 5a, text-fig. 35) bear some similarities in leaf shape to *Juglandiphyllites pelagicus* but differ from this species in having both smaller leaf (leaflet ?) size and secondary and tertiary venation.

J. pelagicus is one of the most abundant species in the Grünbach Flora. Most of the material is represented by isolated leaflets. A small number of samples (NHMW 1999B0057/052, …/0061, …/0117) show two or three leaflets which bases are situated close to each other as if attached to a common petiole (text-figs 34 E, F). We have not found undisputed evidence of two or more leaflets still attached, forming a compound leaf. However, there are several indications that *J. pelagicus* was indeed a compound leaf. They are: (1) finds of two or three leaflets together with their bases situated close to each other; (2) *J. pelagicus* leaflets usually have asymmetric bases and short petiolules typical of leaflets of compound leaves; (3) sometimes fossil leaflets form a leaf accumulation (leaf mat) similar to those producing by modern dicots synchronously shedding leaflets of their compound leaves, and (4) *J. pelagicus* is morphologically similar in its leaflet shape and venation to modern and fossil Juglandaceae plants with compound leaves.

The latter is corroborated by palynological data: Draxler (in Summesberger 1997), who studied palynological spectra from the Grünbach Formation in Grünbach, emphasised that the most characteristic element of the palynoflora is pollen of the *Normapolles* group; this pollen is considered to be of juglandaceous affinity (Friis 1983; Sims et al. 1999). However, *J. pelagicus* is the only fossil plant with leaves of juglandaceous morphology in the Grünbach Flora. Although the evidence mentioned above is not beyond question, we believe that *J. pelagicus* most probably represents a fossil plant of juglandaceous affinity with compound leaves and *Normapolles* pollen.

Modern deciduous dicots with compound leaves usually drop their leaves intact only when the temperature suddenly falls below freezing point; in other cases they drop individual leaflets (D. Ferguson pers. comm. 2004). This explains why *J. pelagicus* is not found intact: the climate experienced by the Grünbach Flora was most probably subtropical and frost-free (Herman & Kvaček 2002a).

Genus *Leguminosites* Bowerbank, 1840

Type: *Leguminosites subovatus* Bowerbank, 1840, p. 125, pl. 17, figs 1, 2.

Leguminosites mucronatus
Herman & J. Kvaček, nov. spec.

(pl. 26, figs 3-5; text-fig. 35)

Derivatio nominis: After *mucronatus* (Lat.) – sharp-pointed.

Holotype: NHMW 1999B0057/0270a (with counterpart 1999B0057/270b), almost complete leaf (pl. 26, figs 3, 4; text-fig. 35B).

Stratum typicum: Grünbach Fm., Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

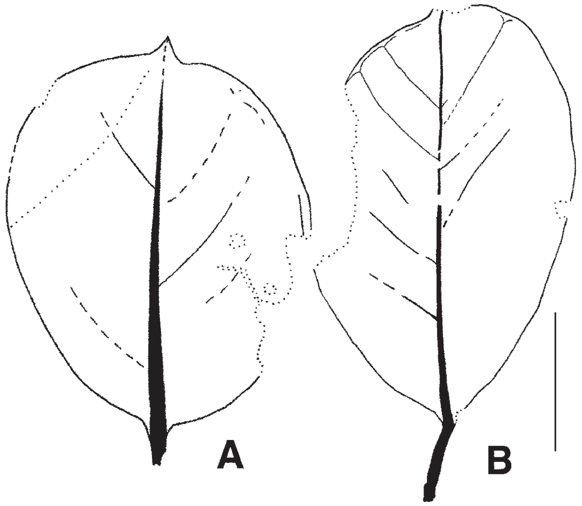
Material: NHMW 1999B0057/0240.

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Diagnosis: Leaf small, simple, unlobed, broadly obovate or broadly elliptic, asymmetric, entire-margined. Leaf base broadly cuneate or broadly round, slightly decurrent, symmetric, leaf apex mucronate. Venation pinnate brochidodromous. Midvein stout, straight, terminating at leaf apex and rapidly narrowing towards it. 7-10 pairs of very narrow secondary veins emerging from the midvein, secondary veins simple, straight or slightly upwards-curving, connecting to the upper secondary vein and forming loops along and very close to the leaf margin. Distal parts of the secondary veins suggest a very thin intramarginal vein situated close to the leaf margin.

Description: Two specimens belonging to this species are represented by impressions of almost complete leaves (pl. 26, figs 3-5; text-fig. 35). Leaves small, simple, unlobed, broadly obovate or broadly elliptic, asymmetric, entire-margined. The bigger leaf (holotype: pl. 26, figs 3, 4; text-fig. 35B) is 3.1 x 1.8 cm, the smaller leaf 2.8 x 2.1 cm, with maximum width of the leaf lamina situated in the upper or middle part of the leaf. Leaf base broadly cuneate (holotype) or broadly round, slightly decurrent, symmetric, leaf apex mucronate. Leaf margin entire. Petiole 0.8 mm thick and not less than 5.5 mm in length.

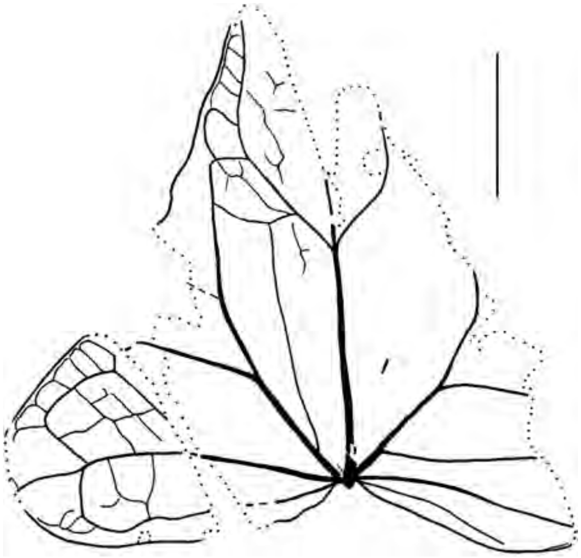
Venation pinnate brochidodromous. Midvein stout, straight, terminating at the leaf apex, approximately 0.6-1 mm thick in its basal part, rapidly narrowing towards the leaf apex. 7 to 10 pairs of very thin secondary veins emerge from the midvein at an angle of 30-45°, the most developed being in the middle or upper part of the leaf lamina. Secondary veins simple, straight or slightly upwards-curving, connecting to the upper secondary vein, forming loops along and very close to the leaf margin. Distal part of secondary vein, forming a brochidodromous loop, almost perpendicular to the secondary vein itself and nearly parallel to the leaf margin (text-fig. 35). These parts approximate a very thin intramarginal vein situated close to the leaf margin. Tertiary veins and higher order venation are not preserved.



Text-fig. 35: *Leguminosites mucronatus* Herman & J. Kvaček, nov. spec., A – NHMW 1999B0057/0240, B – holotype NHMW 1999B0057/0270a, Grünbach (scale bar represents 1 cm).

Comparison and discussion: Leaf shape, size and venation allow us to assign this species to the genus *Leguminosites* Bowerbank. *L. mucronatus* nov. spec. differs from *L. schachschachensis* Shilin from the Senonian of Kazakhstan (Shilin & Romanova 1978, p. 70, pl. 16, fig. 5, pl. 17, fig. 5, pl. 22, fig. 7) in having a smaller leaf size, mucronate but not slightly emarginate leaf apex and brochidodromous loops of secondary veins situated very close to the leaf margin.

Several species of *Leguminosites* (*L. atanensis* Heer, *L. phaseolites* Heer, *L. prodromus* Heer, *L. cassiaeformis* Heer, *L. coronilloides* Heer, *L. amussus* Heer) were described by Heer (1874, p. 118-119, pl. 32, fig. 19, pl. 34, figs 6-14) from the Upper Cretaceous of Greenland. They differ from *L. mucronatus* nov. spec.



Text-fig. 36: *Menispermites ettingshausenii* Herman & J. Kvaček, nov. spec., holotype NHMW 1999B0057/0089a, Grünbach (scale bar represents 1 cm).

in having more elongate elliptic leaves and secondary veins forming brochidodromous loops at some distance from the leaf margin, whereas in the new species the leaves are broadly obovate or broadly elliptic and the secondary vein loops are situated very close to the leaf margin. Moreover, *L. amussus* is characterised by a cordate leaf base, and *L. atanensis* – by a round leaf apex. These features are not typical of *L. mucronatus* nov. spec.

L. mucronatus nov. spec. differs from *L. acuminata* Filippova from the Cenomanian of Chukotka (Northeastern Russia) (Filippova & Abramova 1993, p. 145, pl. 6, fig. 6, pl. 39, fig. 1) in having a smaller leaf size, rounder leaves, mucronate apex and very thin secondary veins. *L. ovalifolius* Heer from the Upper Albian of Kazakhstan (Vakhrameev 1952, p. 233, pl. 18, fig. 3) is similar to the new species in leaf size and shape and very thin secondary veins but differs from it in having a slightly emarginate leaf apex and craspedodromous venation.

The new species differs from *L. hymenophyllus* Lesquereux from the latest Albian – Cenomanian Dakota Formation in North America (Lesquereux 1891, p. 152, pl. 55, figs 7-9, pl. 56, fig. 3) by having smaller broadly obovate to broadly elliptic leaves with mucronate leaf apex and brochidodromous loops of the secondary vein situated close to the leaf margin; these features are not typical for *L. hymenophyllus*.

Genus *Menispermites* Lesquereux, 1874

Type: *Menispermites obtusiloba* Lesquereux, 1874, p. 94, pl. 25, figs 1, 2, pl. 26, fig 3.

Menispermites ettingshausenii Herman & J. Kvaček, nov. spec.

(pl. 26, fig. 2, pl. 36, fig. 7; text-fig. 36)

Derivatio nominis: After famous European palaeobotanist C. von Ettingshausen.

Holotype: NHMW 1999B0057/0089a, pl. 26, fig. 2; text-fig. 36.

Stratum typicum: Grünbach Fm., Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

Material: Only the holotype.

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Diagnosis: Leaf small, simple, trilobate, broadly triangular, symmetric, entire-margined. Leaf base cordate. Two lateral lobes in the lower part of the leaf well-developed, broad, round-triangular. Sinuses between lateral lobes and apical part of the leaf broad, shallow, round. Venation palmate brochidodromous. Midvein straight, two pairs of basal veins emerging from the leaf base. The basal vein of the upper pair forks with one branch going to the apical part of the leaf forming a loop, the other branch going to the lateral lobe also forming a loop. The basal vein of the second pair goes to the lateral lobe apex. One pair of infrabasal veins thin, short. One or two secondary veins brochidodromous, emerging from the midvein and the lower basal vein, curving upwards and forming loops. Tertiary veins thin, orthogonal-reticulate, forming loops along leaf margin. Quaternary venation orthogonal-reticulate.

Description: The only specimen (the holotype) is represented by an incomplete leaf (pl. 26, fig. 2, text-fig. 36). Leaf small, simple, trilobate, broadly triangular in general outline, probably symmetric, entire-margined. Leaf length approximately 4.6 cm, leaf width approximately 4.7 cm, being broadest in the lower part of leaf. Leaf base cordate, leaf apex not preserved. Two lateral lobes (only one is preserved) well-developed, broad, round-triangular in shape, situated in the lower part of the leaf. Sinuses between lateral lobes and apical part of the leaf broad, shallow, round. Leaf margin entire, sometimes slightly undulate. Petiole not preserved.

Venation palmate brochidodromous. Midvein straight, going to leaf apex, approximately 0.6 mm thick in its basal part, narrowing towards leaf apex. There are two pairs of lateral basal veins, the uppermost pair being most developed. Lateral basal veins emerging from leaf base, straight in their proximal parts and curving in distal parts, 0.5 mm thick (upper pair), 0.4-0.3 mm thick (lower pair). Basal vein of the upper pair forks about half-way to the leaf margin, one branch going to the middle lobe (apical part of the leaf), connecting with a suprabasal secondary vein forming a loop, and the other branch going to the lateral lobe, connecting with a secondary vein emerging from the lower basal vein, also forming a loop. Basal vein of the second pair going to the lateral lobe apex. One pair of infrabasal veins thin, short, connecting with the secondary vein, emerging from the lower basal vein, and forming a loop. One or two (?) suprabasal secondary veins brochidodromous, obliquely emerging from the midvein at an angle of 35-40°, curving upwards, forking once and forming loops. One or two secondary veins brochidodromous, emerging from the lower basal vein at an angle of 45-60°, curving upwards and also forming loops. Tertiary veins thin, orthogonal-reticulate, forming loops along the leaf margin. Quaternary venation poorly preserved, orthogonal-reticulate.

Cuticle of *Menispermites ettingshausenii* is fragile, although quite thick, with well-developed hypodermis (pl. 36, fig. 7). Ordinary cells are polygonal (20-25 x 8-15 μm) anticlinal walls straight or slightly curved 2-3 μm in thickness (pl. 36, fig. 7). Stomata were not observed.

Comparison and discussion: *Menispermites ettingshausenii* Herman & J. Kvaček, nov. spec. is similar to *M. salinensis* Lesquereux from the Late Cretaceous of North America (Lesquereux 1874, p. 95, pl. 20, figs 2, 4) which also has trilobate broadly triangular leaves. However, *M. salinensis* leaves are larger and have an undulate to crenate leaf margin, whereas *M. ettingshausenii* is entire-margined.

The new species resembles *M. cuspidentatus* Krassilov from the Turonian of Negev, Israel (Krassilov et al. 2005, p. 86, pl. 4, figs 1, 2, pl. 5, figs 1-4), with a broadly triangular leaf shape and cordate base, but differs from this species in having a smaller size, distinct lateral lobes and entire leaf margin.

Menispermites summesbergeri **Herman & J. Kvaček, nov. spec.**

(pl. 26, fig. 1; text-fig. 37)

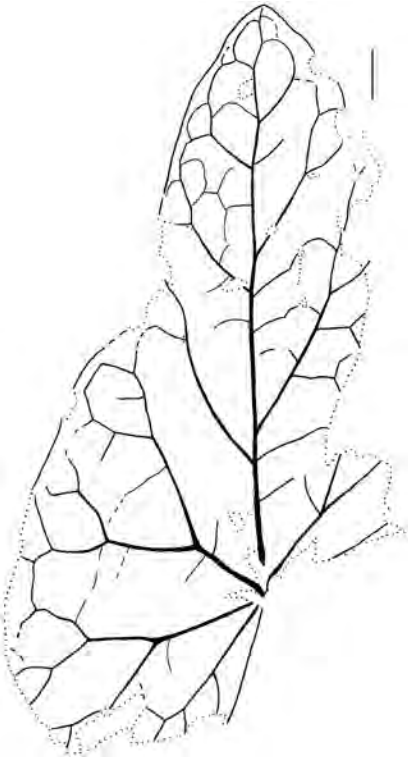
Derivatio nominis: After Herbert Summesberger, a distinguished Austrian geologist and palaeontologist.

Holotype: Designated here. NHMW 1999B0057/0555 (pl. 26, fig. 1; text-fig. 37).

Stratum typicum: Grünbach F.m, Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

Material: Only the holotype.



Text-fig. 37: *Menispermites summesbergeri* Herman & J. Kvaček, nov. spec., holotype NHMW 1999B0057/0555, Grünbach (scale bar represents 1 cm).

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Diagnosis: Leaf large, simple, trilobate, broadly triangular, entire-margined. Leaf base deeply cordate, apex narrow, round. Two large lateral lobes, broad, probably round, situated in the lower part of the leaf; sinuses between these and the apical part of the leaf broad, shallow, round. Venation palmate brochidodromous. Midvein straight, 3 pairs of lateral basal veins emerging from the leaf base and running to the lateral lobe, the uppermost pair being the most developed. Basal veins forking up to three times, forming loops along the leaf margin. 3-4 suprabasal secondary veins brochidodromous, obliquely emerging from the midvein, forking once and forming loops along the leaf margin. Tertiary veins percurrent to orthogonal-reticulate, forming loops along the leaf margin.

Description: The single specimen (holotype) is represented by an incomplete leaf (pl. 26, fig. 1; text-fig. 37). Leaf large, simple, trilobate, broadly triangular in general outline, probably symmetric or slightly asymmetric, entire-margined. Leaf length approximately 15.3 cm, leaf width approximately 11.5 cm, with maximum width situated in the lower part of the leaf lamina. Leaf base deeply cordate, leaf apex narrow, round. Two lateral lobes (only one is preserved) well-developed, big, broad, probably round, situated in the lower part of the leaf. Sinuses between the lateral lobes and the apical part of the leaf broad, shallow, round. Leaf margin entire. Petiole not preserved.

Venation palmate brochidodromous. Midvein straight, going to leaf apex, approximately 1-1.2 mm thick in its basal part, narrowing towards the apex. There are three pairs of lateral basal veins, the uppermost pair being the most developed. Basal veins emerging from leaf base and going to the lateral lobe, straight in their lower (adaxial) parts, 1 mm thick (upper pair), 0.7 mm thick (middle pair) and 0.5 mm thick (lower pair), forking up to three times and forming loops along the leaf margin. Suprabasal secondary veins rare, brochidodromous, obliquely emerging from the midvein at an angle of 20-45°, straight or slightly curving upwards, forking once and forming loops along leaf margin. Three secondary veins emerge from the midvein on the right-hand side of the leaf and four on the left side. Tertiary veins thin, percurrent or ramified-percurrent to orthogonal-reticulate, nearly perpendicular to the primary and secondary veins. Tertiary veins forming loops along the leaf margin. Quaternary venation not preserved.

Comparison and discussion: This species, like *M. ettingshausenii* Herman & J. Kvaček described above, possess a trilobate, broadly triangular, entire-margined leaf with palmate brochidodromous venation, but differs from it in having a bigger leaf lamina, deeply cordate base and three pairs of lateral basal veins. All lateral basal veins in *M. summesbergeri* go to the lateral lobe, whereas in *M. ettingshausenii* the basal vein of the upper pair forks about half-way to the leaf margin, one branch going to the apical part of the leaf and the other branch going to the lateral lobe. Lateral basal veins in *M. summesbergeri* fork up to three times and form loops along the leaf margin, but in *M. ettingshausenii* the basal vein of the second pair goes straight to the lateral lobe apex, and tertiary veins form a series of loops along the leaf margin, features not observed in *M. summesbergeri*.

M. summesbergeri resembles *M. obtusiloba* Lesquereux from the Late Cretaceous of North America (Lesquereux 1874, p. 94, pl. 22, fig. 1, pl. 25, figs 1, 2, pl. 26, fig. 3) which has a similar trilobate, broadly triangular leaf with palmate venation, but the new species is characterised by a deeply cordate base, more numerous secondary veins and an entire leaf margin, whereas the margin in *M. obtusiloba* is undulate rather than entire. *M. septentrionalis* Hollick from the Cenomanian-Turonian of the Yukon River basin, Alaska (Hollick 1930, p. 79, pl. 42, figs 3, 4), has a cordate leaf base and venation, similar to those of *M. summesbergeri*. The latter, however, differs from the Alaskan species due to its trilobate and broadly triangular leaf with a deeply cordate base.

M. summesbergeri differs from *M. cuspidentatus* Krassilov from the Turonian of Negev, Israel (Krassilov et al. 2005, p. 86, pl. 4, figs 1, 2, pl. 5, figs 1-4), in having a deeply cordate leaf base and entire margin.

Genus *Myricophyllum* Saporta, 1862

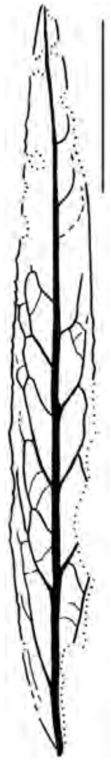
Type: *Myricophyllum gracile* Saporta, 1862, p. 255, pl. 10, fig. 1.

Myricophyllum serratum (Velenovský) Velenovský, 1889

(pl. 26, figs 8-10; text-fig. 38)

1883 *Myrica serrata* Velenovský, p. 9, pl. 2, figs 1-8.
1889 *Myricophyllum serratum* (Velenovský) Velenovský, p. 16, 50, 53, 58.
1901 *Myrica serrata* Velenovský; Frič & Bayer, p. 113, fig. 70.
1957 *Myricophyllum serratum* (Velenovský) Velenovský; Němejc, p. 104, pl. 12, fig. 4b, pl. 13, fig. 1, text-fig. 3.

Material: NHMW: 1999B0057/0336a, b, .../0337.



Text-fig. 38: *Myricophyllum serratum* (Velenovský) Velenovský, NHMW 1999B 0057/0336a, Grünbach (scale bar represents 1 cm).

Occurrence: Czech Republic, Peruc-Korycany Formation, Cenomanian; Czech Republic, Senonian; Austria, Grünbach am Schneeberg, Grünbach Formation, Lower Campanian.

Description: Leaves small in size, simple, unlobed, symmetric, with serrate margin. Leaf length from 4.4 to approximately 7.0 cm, leaf width from 0.5 to 0.8 cm. Leaf lamina narrow lanceolate in general outline, maximum width is in the middle part of the leaf. Leaf base narrow cuneate, symmetric, leaf apex narrow, acute (text-fig. 38). Leaf margin serrate, marginal teeth simple, very small, triangular in shape, slightly curving upwards, with acute apices (pl. 26, fig. 9). Sinuses between teeth shallow, broad, round. Petiole poorly preserved. Venation pinnate brochidodromous. Midvein straight, running to leaf apex, approximately 0.3 mm thick in its basal part, narrowing towards the leaf apex. Secondary veins numerous, emerging from the midvein at an angle of 25-30° in the basal part of a leaf and 45-60° in the apical part (text-fig. 39). Up to 15 (?) pairs of secondary veins emerge from the midvein, the most developed being in the middle part of the leaf lamina. Secondary veins opposite in the lower and middle parts of the leaf, simple, curving upwards, connecting with the upper secondary vein and forming oblique loops at some distance from the leaf margin (pl. 26, fig. 9; text-fig. 38). Tertiary veins within these loops are thin, straight or slightly curved, percurrent (text-fig. 38). Tertiary veins near the leaf margin form loops, from the abaxial parts of which short veins run towards the marginal teeth. Higher order venation not preserved.

Comparison and discussion: This species differs from *Myricophyllum* sp. cf. *M. zenkeri* (Ettingshausen) Velenovský described below in having smaller and narrower leaves with a serrate margin, very small marginal teeth and brochidodromous venation. In comparison with *Myrica taldysaica* Shilin from the Senonian of Kazakhstan (Shilin & Romanova 1978, p. 60, pl. 11, fig. 4, pl. 12, figs 2, 4, 6, 7, pl. 22, figs 4, 5), *Myricophyllum serratum* has smaller and narrower leaves with distinctly brochidodromous venation. In leaf shape, serrate margin and venation *M. serratum* resembles *Myrica dakotensis* Lesquereux from the Late Cretaceous of North America (Lesquereux 1883, p. 35, pl. 4, fig. 9). However, *Myricophyllum serratum* has narrower leaves with smaller marginal teeth. This species also differs from *Myrica* (?) *trifoliata* Newberry from the latest Albian-Cenomanian Dakota Group in North America (Newberry 1898, p. 37, pl. 14, fig. 2) in the same manner.

M. serratum differs from *Myrica cretacea* Heer (Heer 1871b, p. 10, pl. 3, figs 2a, b, c; Kräusel 1922, pl. 1, fig. 17, pl. 2, fig. 6) and *M. schenkiana* Heer (Heer 1871b, p. 11, pl. 3, figs 1) from the Santonian of Quedlinburg, Germany (Heer 1871b) and the Netherlands (Kräusel 1922) in having narrower leaves with smaller marginal teeth. Two other species of the genus *Myrica* from the Senonian of Germany (Westfalen), *M. primaeva* Hosius & Marck and *M. leiophylla* Hosius & Marck (Hosius & Marck 1880, p.155, pl. 28, figs 46, 47) have narrow leaf laminas comparable to that of *Myricophyllum serratum*, but differ from this species in having bigger marginal teeth.

Myricophyllum sp. cf. *Myricophyllum zenkeri* (Ettingshausen) Němejc, 1957

(pl. 26, figs 6, 7; text-fig. 39)

1874 *Myrica zenkeri* (Ettingshausen) Heer, p. 108, pl. 31, fig. 2.
1901 *Myrica zenkeri* (Ettingshausen) Heer; Frič & Bayer, p. 113, fig. 69 (see also synonymy in this publication).
1952 *Myrica zenkeri* (Ettingshausen) Heer; Vakhrameev, p. 177, pl. 11, figs 1, 2, pl. 41, fig. 4.
1957 *Myricophyllum zenkeri* (Ettingshausen) Němejc, p. 102, pl. 11, figs 1-3, 3a, 3b, text-fig. 2.
1978 *Myrica zenkeri* (Ettingshausen) Heer; Shilin & Romanova, p. 57, pl. 11, figs 2, 3, pl. 12, figs 1, 5.

Material: NHMW: 1999B0057/0097, …/0098a (counterpart).

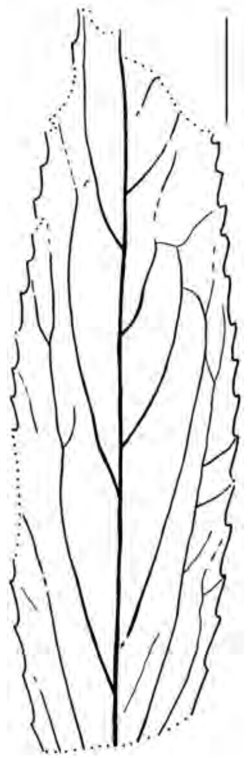
Occurrence: Czech Republic, Peruc-Korycany Formation, Cenomanian; Czech Republic, Klikov Formation, Senonian; Upper Cretaceous of Greenland; Upper Cretaceous of Kazakhstan; Austria, Grünbach am Schneeberg, Grünbach Formation, Lower Campanian.

Description: The only incompletely preserved leaf impression (pl. 26, figs 6, 7; text-fig. 39) belongs to this species. Leaves small in size, simple, unlobed, symmetric, with dentate margin. Leaf length unknown, probably about 10 cm, leaf width 2.2 cm. Leaf lamina oblong elliptic in general outline, being broadest in the middle part of the leaf. Leaf base and apex not preserved. Leaf margin dentate, marginal teeth simple, triangular in shape, curving upwards, with acute apices, approximately 0.6 mm in height (pl. 26, fig. 7). Sinuses between teeth round. Petiole not preserved. Venation pinnate craspedodromous and brochidodromous. Midvein thin, straight, approximately 0.3 mm thick in its basal part, narrowing towards the apex. 5 or 6 secondary veins preserved in each side of the leaf fragment. Secondary veins obliquely emerging from the midvein at an angle of 20-35°, curving upwards, connecting with the upper secondary vein and forming oblique loops at some distance from the leaf margin, or forking basiscopically up to 5 times with all branches terminating in marginal teeth. Higher order venation and venation near leaf margin not preserved.

Comparison and discussion: Poor preservation of this single leaf impression (leaf base and apex are missing) prevents a precise specific identification of this leaf. However, leaf shape, dentate margin and venation allow it to be assigned to the genus *Myricophyllum* Saporta.

The species described here exhibits some features similar to those of *M. zenkeri* (Ettingshausen) Velenovský from the Cenomanian Peruc-Korycany Formation of the Czech Republic (Velenovský 1883; Frič & Bayer 1901, p. 113, fig. 69) and the Senonian of South Bohemia (Němejc 1957, p. 102, pl. 11, figs 1-3, 3a, 3b, text-fig. 2): oblong elliptic leaf lamina, dentate leaf margin with triangular upwards-curving teeth. Venation is similar in leaves from Grünbach and the Czech Cenomanian and Senonian, but in our specimen secondary veins emerge more obliquely from the midvein. *M. zenkeri* (Heer 1874, p. 108, pl. 31, fig. 2) from the Cretaceous of Greenland is too poorly preserved for comparison with our specimen.

M. sp. cf. *M. zenkeri* described here differs from *Myrica schenkiana* Heer from the Santonian of Quedlinburg, Germany (Heer 1871b, p. 11, pl. 3, figs 1) by having fewer secondary veins which emerge more obliquely from the midvein. *M.* sp. cf. *M. zenkeri*, in comparison to *Myrica dakotensis* Lesquereux from the Late Cretaceous of North America (Lesquereux 1883, p. 35, pl. 4, fig. 9), has broader leaves with more oblique secondary veins. *M. longa* Heer from the latest Albian – Cenomanian Dakota Formation in North America (Lesquereux 1891, p. 67, pl. 3, figs 1-6) has, unlike *M.* sp. cf. *M. zenkeri*, entire-margined leaves. The Grünbach specimen differs from *Myrica taldysaica* Shilin from the Senonian of Kazakhstan (Shilin & Romanova 1978, p. 60, pl. 11, fig. 4, pl. 12, figs 2, 4, 6, 7, pl. 22, figs 4, 5) in having bigger marginal teeth.



Text-fig. 39: *Myricophyllum* sp. cf. *M. zenkeri* (Ettingshausen) Němejc, NHMW 1999B0057/0097, Grünbach (scale bar represents 1 cm).

Genus *Quereuxia* Kryshtofovich, 1953

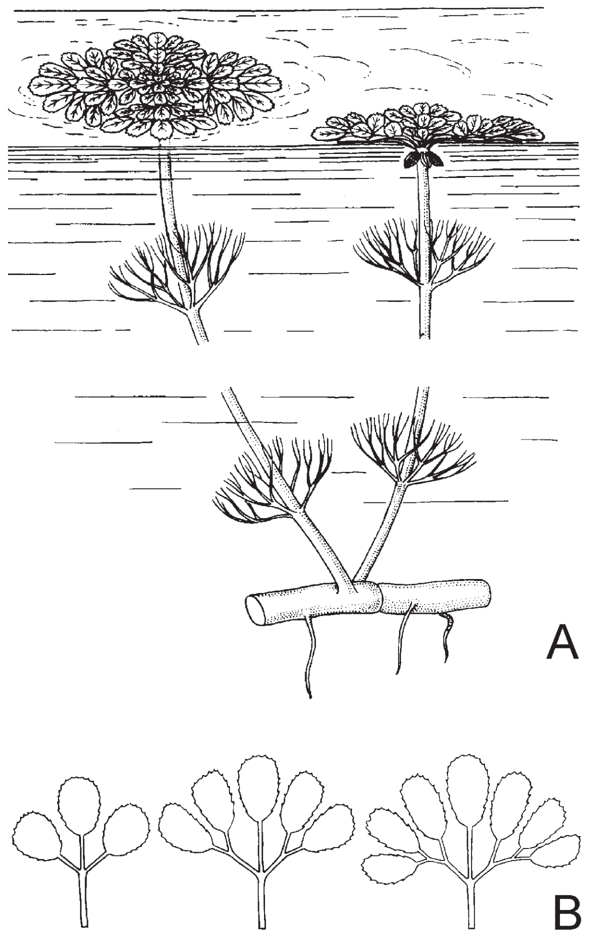
Type: *Neuropteris angulata* Newberry, 1861, p. 131, pl. 3, fig. 5 ≡ *Quereuxia angulata* (Newberry) Kryshtofovich, 1953, p. 23, pl. 3, figs 1, 11.

Quereuxia angulata (Newberry) Kryshtofovich, 1953

(pl. 27, figs 9-14; text-fig. 40)

1861 *Neuropteris angulata* Newberry, p. 131, pl. 3, fig. 5.
1953 *Quereuxia angulata* (Newberry) Kryshtofovich, p. 23, pl. 3, figs 1-11, pl. 4, figs 1-8, text-figs 3, 4 (see synonymy in this publication).
1988 *Quereuxia angulata* (Newberry) Kryshtofovich; Samylina, p. 89, pl. 19, fig. 4b, pl. 34, figs 1-16, pl. 35, figs 15b-21, text-figs 17, 18 (see complete synonymy in this publication).
1991 *Quereuxia angulata* (Newberry) Kryshtofovich; Herman, p. 130, pl. 13, figs 10-12.
1994 *Quereuxia angulata* (Newberry) Kryshtofovich; Golovneva, p. 96, pl. 9, fig. 9, pl. 58, figs 1-8.

Material: NHMW: 1970B1396/1661, 1999B0057/0218b, …/0254, …/0272, …/0315, …/0316, …/0317, …/0318, …/0319, …/0320, …/0321, …/0322, …/0323, …/0324, …/0325b,



Text-fig. 40: *Quereuxia angulata* (Newberry) Kryshtofovich, A – reconstruction of the whole plant, B – schematic reconstruction of compound leaves (modified from Samylina 1988).

…/0326, …/0327, …/0329, …/0330, …/0381.

Occurrence: Late Cretaceous and Tertiary of Europe, Asia and North America.

Description: In the collection there are impressions of floating leaf rosettes (pl. 27, fig. 14), fragments of the rosettes, individual leaves (pl. 27, figs 12, 13) and leaflets (pl. 27, figs 9-11). The biggest rosette 4 cm in diameter consists of approximately 15-17 leaflets (pl. 27, fig. 14), the largest leaflets being situated in the peripheral part of the rosette and the smallest ones in its central part. Leaves palmately compound, consisting of three or more leaflets (text-fig. 40A). Leaflets small, simple, unlobed, obovate, broadly obovate to broadly elliptic, symmetric or asymmetric, dentate-margined (pl. 27, figs 9-11). Leaflet length from 0.45 to 1.6 cm, leaflet width from 0.4 to 1.2 cm. Leaflet lamina usually broadly obovate or obovate in general outline, being broadest in the upper half of the leaflet, but sometimes broadly elliptic with maximum width situated in the middle part of the lamina, usually symmetric but occasionally asymmetric. Leaflet base acute, broadly acute or round, leaflet apex round (pl. 27, figs 9-11). Leaflet margin entire in the lower part of the lamina and dentate to crenulate in its upper part. Petioles and petiolules poorly preserved, the latter being thin, more than 2 mm in length. Venation poorly preserved, pinnate-palmate craspedodromous, with numerous thin simple secondary veins running from the leaflet base or midvein to the leaflet margin (pl. 27, figs 9-11).

Comparison and discussion: This species is known from numerous Late Cretaceous (post Turonian) and Paleogene floras of Eurasia and North America. Samylina (1988) published a reconstruction of the whole plant with floating leaf rosettes *Quereuxia angulata*, underwater leaves, fruits and roots (text-fig. 40A). The material described in this study is only represented by floating leaves.

Leaves of *Q. flabellata* Golovneva from the latest Maastrichtian of the Rarytkin Range, North-eastern Russia (Golovneva 1994, p. 97, pl. 15, figs 6, 11) have leaf margin and venation similar to those observed in *Q. angulata*, but *Q. flabellata* leaves are simple, they are bigger than *Q. angulata* leaflets and have a fan-shaped leaf outline. *Q. rotundifolia* Golovneva from the latest Maastrichtian of the Rarytkin Range (Golovneva 1994, p. 97, pl. 19, fig. 2) also has simple leaves which are bigger than *Q. angulata* leaflets and have peltate bases.

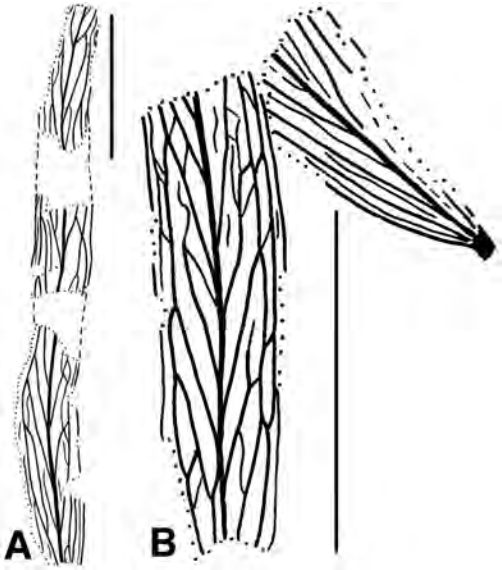
Genus *Rogersia* Fontaine, 1889

Type: *Rogersia longifolia* Fontaine, 1889, p. 287, pl. 139, fig. 6, pl. 144, fig. 2

The genus *Rogersia* was first described by Fontaine (1889, p. 287) who gave the following generic diagnosis: "Leaves long, narrow, and willow-like, wedge-shaped at base, acute, with a very strong midvein and very slender primary nerves; these go off very obliquely and diverge very slowly from the midrib, running for a long distance nearly parallel with the margins of the leaves; they anatomize with branches sent off from other nerves of like grade higher up to form very long, irregularly shaped, and lax meshes; ultimate reticulation oblong, sub-rhombic, of quite uniform dimension." Fontaine (1889) assigned two species to this genus: *R. longifolia* Fontaine and *R. angustifolia* Fontaine.

Rogersia sp.

(pl. 27, figs 15, 16; text-fig. 41)



Text-fig. 41: *Rogersia* sp., A – NHMW 1999B0057/0089b, B – NHMW 1999B0057/0089c, Grünbach (scale bar represents 1 cm).

Material: NHMW: 1999B0057/0089b, …/0089c.

Occurrence: Austria, Grünbach am Schneeberg; Grünbach Formation, Lower Campanian.

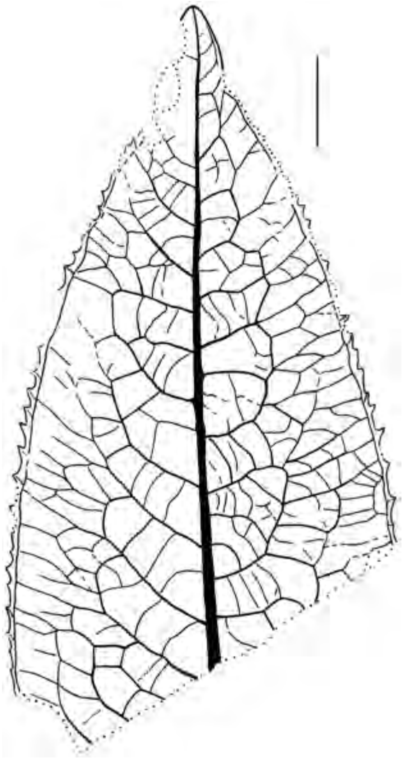
Description: Several incompletely preserved specimens belong to this species (pl. 27, figs 15, 16; text-fig. 41). Leaves very small, simple, unlobed, linear, symmetric, entire-margined. Leaves of unknown length, but more than 3-4 cm, width 0.4-0.5 cm. Leaf lamina linear in outline, being broadest in the middle part of the leaf. Leaf base narrow cuneate (pl. 27, fig. 15; text-fig. 41B), leaf apex not preserved. Leaf margin entire. Petiole not preserved. Venation pinnate brochidodromous. Midvein distinct, straight or slightly undulate, going to the leaf apex. Numerous (more than 8 pairs) thin secondary veins emerging from the midvein at a very low angle of 15-25°, connecting to the other secondaries and forming long oblique loops (pl. 27, figs 15, 16; Text-figs 41 A, B). Tertiary and higher order venation not preserved.

Comparison and discussion: These leaves are similar to *Rogersia angustifolia* Fontaine from the Lower Cretaceous of North America (Fontaine 1889, p. 288, pl. 143, fig. 2, pl. 149, figs 4, 8, pl. 150, figs 2-7; Doyle & Hickey, 1976, fig. 4) in having linear entire-margined leaves with narrow cuneate base, and pinnate brochidodromous venation with secondary veins forming oblique loops. However, *Rogersia* sp. is much smaller than *R. angustifolia* and has a relatively thin midvein and more regular secondary venation. *Rogersia* sp. differs from *Rogersia longifolia* Fontaine from the Lower Cretaceous of North America (Fontaine 1889, p. 287, pl. 139, fig. 6, pl. 144, fig. 2, pl. 150, fig. 1, pl. 159, figs 1, 2) in having much smaller leaves with a relatively thinner midvein.

Myrtophyllum angustum (Velenovský) Knobloch from the Cenomanian of the Czech Republic (Knobloch 1999, p. 49, pl. 10, fig. 7, pl. 12, fig. 3) resembles *Rogersia* sp. in having oblong entire-margined leaves. However, *Myrtophyllum angustum* has bigger and broader leaves with more regular pinnate brochidodromous venation.

Genus *Ternstroemites* E.W. Berry, 1916

Type: *Ternstroemites eolignitica* E.W. Berry, 1916, p. 294, pl. 76, figs 1, 2, pl. 78, fig. 5



Text-fig. 42: *Ternstroemites* (?) *neueweltensis* Herman & J. Kvaček, nov. spec., holotype NHMW 1999B0057/0030, Grünbach (scale bar represents 1 cm).

Ternstroemites (?) *neueweltensis* **Herman & J. Kvaček, nov. spec.**

(pl. 29, figs 8-10; text-fig. 42)

Derivatio nominis: After Neue Welt Basin in Lower Austria.

Holotype: NHMW 1999B0057/0030 (pl. 29, figs 8-10; text-fig. 42).

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

Material: Only the holotype.

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Diagnosis: Leaves large, simple, unlobed, probably elliptic, symmetric, with serrate margin. Leaf apex narrow acute. Leaf margin serrate, marginal teeth small, simple, triangular, curving upwards, with acute apices. Venation pinnate brochidodromous, with distinct intramarginal vein and sometimes intersecondary veins. Midvein strong and straight, secondary veins numerous, emerging from the midvein at an angle of 60-90°, thin, simple, curving upwards, connecting with the upper secondary vein and forming loops approximately half-way to the leaf margin. From these loops, thin and nearly-straight branches run towards leaf margin and join a very thin intramarginal vein situated close to the leaf margin. From the intramarginal vein short thin branches go to the marginal teeth. Tertiary veins are very thin, percurrent to ramified-percurrent.

Description: One incompletely preserved specimen (holotype) represents this species. Leaf large, simple, unlobed, probably elliptic, leaf lamina symmetric, with serrate margin. Leaf of unknown length, but probably 14-18 cm, width 4.6-4.7 cm. Leaf lamina probably elliptic in general outline, being broadest in the middle part of the leaf. Leaf base not preserved, leaf apex narrow acute with a round extremity (pl. 29, fig. 8; text-fig. 42). Leaf margin serrate. Marginal teeth small, simple, triangular, curving upwards, with acute apices, 0.8-1.2 mm in height (pl. 29, fig. 9; text-fig. 42). Sinuses between teeth round. Petiole not preserved.

Venation pinnate brochidodromous, with a distinct thin intramarginal vein. Midvein strong and straight, going to leaf apex, up to 1.2 mm thick in the preserved part of the leaf and probably thicker in its basal (unknown) part, narrowing towards the leaf apex. Secondary veins numerous, 13 are preserved, emerging from the midvein at an angle of 60-90°, the most developed probably situated in the middle part of the leaf lamina. Secondary veins thin, simple, curving upwards, connecting with the upper secondary vein and forming brochidodromous loops approximately half-way to the leaf margin (pl. 29, figs 8, 10; text-fig. 42). From these loops, thin and nearly-straight branches run towards the leaf margin, sometimes forming additional loops, and joining a very thin but distinct intramarginal vein situated close to the margin (pl. 29, fig. 10; text-fig. 42). From this vein, short and thin simple branches go to the marginal teeth. Sometimes (but not always) there is one intersecondary vein between two secondaries; it is shorter and thinner than the adjacent secondary veins (pl. 29, fig. 8; text-fig. 42). Tertiary veins are very thin, percurrent to ramified-percurrent, straight or slightly curved. Higher order venation not preserved.

Comparison and discussion: Elliptic shape of the leaf lamina, serrate leaf margin and pinnate brochidodromous venation with stout midvein, intersecondary veins and short branches going from brochidodromous loops/intramarginal vein to marginal teeth allow us to assign this species to the genus *Ternstroemites* Berry. However, the presence of an intramarginal vein is not typical of this genus, therefore we cannot consider the generic determination of the species with certainty.

T. neueweltensis nov. spec. differs from the type of the genus *Ternstroemites*, *T. eoligniticus* Berry from the Eocene of southeastern North America (Berry 1916, p. 294, pl. 76, figs 1, 2, pl. 78, fig. 5) in having a narrow acute, but not attenuate, leaf apex, smaller marginal teeth and distinct intramarginal veins. The new species differs from *T. harwoodensis* (Dawson) Bell from the Coniacian Valizhgen Formation in North-western Kamchatka (Herman 1991, p. 88, pl. 7, figs 2-4, text-fig. 22) and the Campanian Nanaimo Group in Vancouver Island (Bell 1957, p. 68, pl. 59, fig. 4, pl. 60, figs 1, 3, pl. 61, fig. 4, pl. 62, fig. 1) in having shorter and less pronounced numerous secondary veins and distinct intramarginal veins.

Ternstroemia crassipes Velenovský from the Cenomanian Peruc Flora of the Czech Republic (Velenovský 1884, Frič & Bayer 1901, 140, fig. 107) resembles *Ternstroemites neueweltensis* nov. spec. in its elliptic leaf shape, brochidodromous venation and dentate leaf margin, but the Czech Cenomanian species does not have a distinct intramarginal vein; moreover, marginal teeth in this species are much bigger, and secondary veins form brochidodromous loops at a shorter distance from the leaf margin than in *T. neueweltensis*.

Genus *Viburniphyllum*
Nathorst, 1886

Type: *Viburnum giganteum* Saporta, 1868, p. 370, pl. 30, figs 1, 2 ≡ *Viburniphyllum giganteum* (Saporta) Nathorst, 1886, p. 52.

Viburniphyllum austriacum
Herman & J. Kvaček, nov. spec.

(pl. 31, figs 5-7; text-fig. 43)

Derivatio nominis: After Austria.

Holotype: NHMW 1999B0057/0382 (pl. 31, figs 5-7; text-fig. 43).

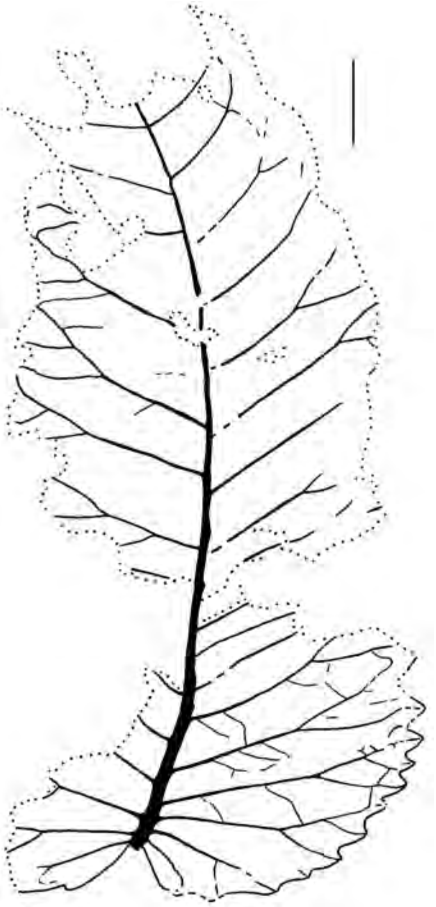
Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

Material: Only the holotype.

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Diagnosis: Leaf medium, simple, unlobed, narrow elliptic or narrow ovate, slightly asymmetric, with dentate margin. Leaf base cordate, asymmetric. Leaf margin dentate, marginal teeth simple, triangular, straight, with acute apices. Sinuses between teeth deep, triangular, round. Venation pinnate craspedodromous. Midvein prominent, straight, rapidly narrowing towards leaf apex. More than 17 pairs of secondary veins emerging from the midvein. Secondary veins thin, straight or slightly curving upwards,



Text-fig. 43: *Viburniphyllum austriacum* Herman & J. Kvaček, nov. spec., holotype NHMW 1999B0057/0382, Grünbach (scale bar represents 1 cm).

dividing up to three times. Tertiary veins percurrent or ramified-percurrent.

Description: The single specimen (holotype) is represented by an incomplete leaf impression (pl. 31, figs 5-7; text-fig. 43). Leaves medium in size, simple, unlobed, slightly asymmetric, with dentate margin. Leaf length unknown, approximately 12-13 cm, leaf width approximately 6.2 cm. Leaf lamina narrow elliptic or narrow ovate, the maximum width being in the lower or middle part of the leaf. Leaf base cordate, asymmetric (pl. 31, figs 5, 7; text-fig. 43), apex not preserved. Leaf margin dentate, marginal teeth simple, triangular, straight, with acute apices, 1.4-2.3 mm in height (pl. 31, fig. 6; text-fig. 43). Sinuses between teeth deep, triangular, round. Petiole not preserved. Venation pinnate craspedodromous. Midvein prominent, straight, going to leaf apex, approximately 1.8 mm thick in its basal part, rapidly narrowing towards the leaf apex. More than 17 pairs of secondary veins emerging from the midvein at an angle of 75-90°, the third to seventh pair (from the leaf base) being the most developed. Secondary veins much thinner than the midvein, straight or slightly curving upwards, lower opposite, dividing up to three times with all branches terminating in the marginal teeth (pl. 31, fig. 5; text-fig. 43). Tertiary veins poorly preserved, thin, curved, emerging from the secondary veins at an angle of 45-80°, percurrent or ramified-percurrent (text-fig. 43). Quaternary veination and venation near the leaf margin not preserved.

Comparison and discussion: *Viburniphyllum basicordatum* Herman from the Campanian Bystrinskaya Formation in North-western Kamchatka (Herman 1991, p. 110, pl. 12, figs 6-8, text-figs 32, 33) possesses narrow elliptic or narrow ovate leaf lamina with a cordate base similar to *V. austriacum* nov. spec. but differs from the new species in having a smaller leaf size, distinctly pinnate-palmate venation with strong lateral basal veins, a more oblique angle between the midvein and secondary veins and pronounced percurrent tertiary venation. *V. alnoides* (Hollick) Herman from the Campanian of Alaska (Hollick 1930, p. 71, pl. 38, fig. 4) and North-western Kamchatka (Herman 1991, p. 109, pl. 12, fig. 5) has a relatively narrow round or slightly cordate leaf base not typical of the new species.

Viburnphyllum lesquereuxii Ward from the latest Albian – Cenomanian Dakota Formation in North America (Lesquereux 1891, p. 122, pl. 52, figs 8-10) has a round to cordate leaf base and leaf margin and venation similar to those observed in *Viburniphyllum austriacum*. However, the latter has a narrower leaf lamina with a deeply cordate base, smaller marginal teeth and more numerous secondary veins.

Viburniphyllum ermanniorum **Herman & J. Kvaček, nov. spec.**

(pl. 32, figs 1, 2; text-fig. 44)

Derivatio nominis: In honour of Oskar and Friederike Ermann (Vienna) who are generous sponsors of the Earth sciences at the Natural History Museum in Vienna.

Holotype: NHMW 1999B0057/0269 (pl. 32, fig. 1; text-fig. 44A).

Stratum typicum: Grünbach Formation, Lower Campanian.

Locus typicus: Grünbach am Schneeberg, Austria.

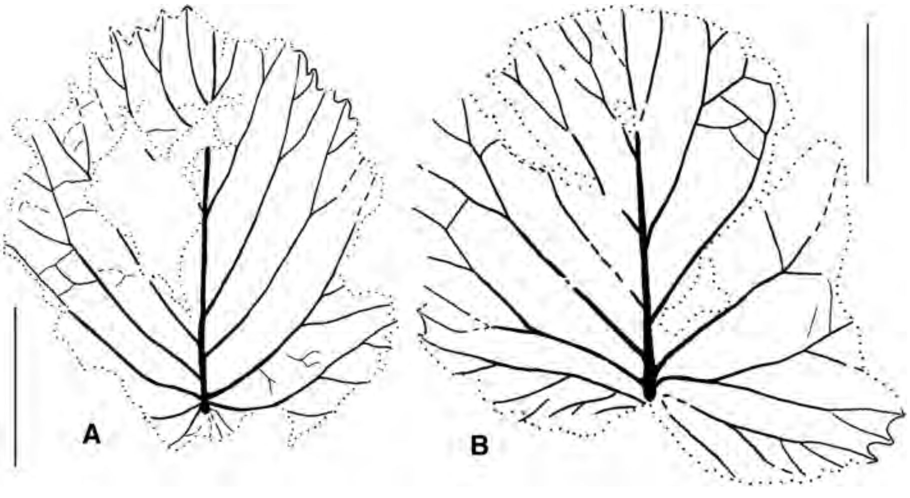
Material: GBA: 2006/64/10, 2006/64/13.
NHMW: 1999B0057/0266, …/0268.

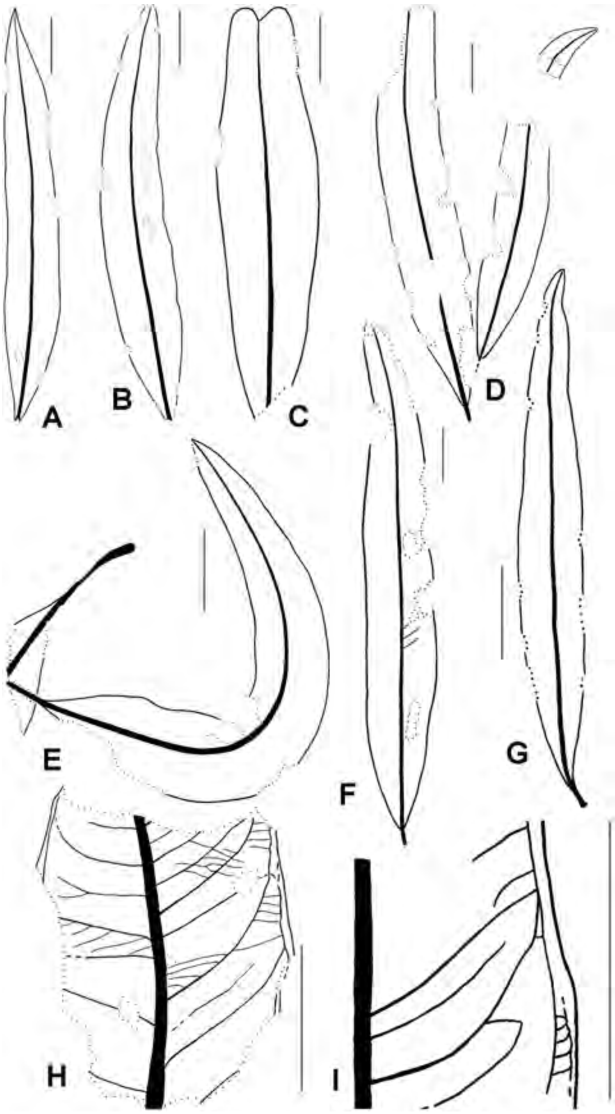
Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Diagnosis: Leaf small, simple, unlobed, round, symmetric or slightly asymmetric, with dentate margin. Leaf base deeply cordate, symmetric, apex probably round. Leaf margin dentate, marginal teeth relatively big, simple, triangular, straight, with narrow acute, sometimes slightly attenuate, or narrowly round apices. Sinuses between teeth deep, round. Venation pinnate to palmately-pinnate craspedodromous. Midvein straight, supporting 8-10 pairs of secondary veins. Basal veins opposite, straight or slightly curving upwards, dividing 2-3 times. Suprabasal secondary veins craspedodromous, dividing 1-2 times. Upper infrabasal secondary veins almost as strong as the basal veins, lower infrabasal veins thin and short. Tertiary veins thin, straight or slightly curved, percurrent or ramified-percurrent.

Description: Leaves small in size, simple, unlobed, symmetric or slightly asymmetric, with dentate margin. Leaf length approximately 3 cm (pl. 32, fig. 1; text-fig. 44A) or slightly more, up to approximately 4 cm (text-fig. 44B), leaf width from 2.7 cm (pl. 32, fig. 1; text-fig. 44A) to approximately 5 cm. Leaf lamina round in shape with leaf width slightly less or slightly more than leaf length, the maximum width being in the middle part of the leaf. Leaf base deeply cordate, symmetric, apex poorly preserved, probably round (pl. 32, fig. 1; text-fig. 44A). Leaf margin dentate, marginal teeth relatively big, simple, triangular, straight, with narrow acute, sometimes slightly attenuate, or narrowly round apices, 1.2-1.8 mm in height. Sinuses between teeth deep, round. Petiole not preserved.

Text-fig. 44: *Viburniphyllum ermanniorum* Herman & J. Kvaček, nov. spec., A – holotype NHMW 1999B0057/0269, B – NHMW 1999B0057/0268, Grünbach (scale bar represents 1 cm).





Text-fig. 45: *Dicotylophyllum proteoides* (Unger) Herman & J. Kvaček, comb. nov., A – NHMW 1999B0057/0339B, B – NHMW 1999B0057/0363a, C – NHMW 1999B0057/0001, D – NHMW 1999B0057/0161a, b, E – NHMW 1999B0057/0347a, F – NHMW 1999B0057/0164a, G – NHMW 1999B0057/0354a, H – NHMW 1999B0057/0217a, venation, I – NHMW 1999B0057/0001, detailed venation, Grünbach (scale bar represents 1 cm).

Venation pinnate to palmately-pinnate craspedodromous. Midvein straight, going to leaf apex, approximately 0.5 – 0.7 mm thick in its basal part, rapidly narrowing towards the leaf apex. 8-10 pairs of secondary veins emerging from the midvein, the third pair (from the leaf base) being the most developed (basal veins) (pl. 32, fig. 1; text-fig. 44A). Basal veins opposite, approximately 0.3 mm thick, emerging from the midvein 1 – 1.2 mm above the leaf base at an angle of 75-90°, straight or slightly curving upwards, dividing 2-3 times with all branches terminating in the marginal teeth. Suprabasal secondary veins craspedodromous, emerging from the midvein at an angle of 20 (upper veins) to 60° (lower veins), curving upwards, dividing once or twice, all branches terminating in the marginal teeth. Upper infrabasal secondary veins almost as strong as the basal ones, dividing up to 3 times (pl. 32, fig. 1; text-fig. 44 A, B). Lower infrabasal secondary veins thin and short. Tertiary veins thin, straight or slightly curved, percurrent or ramified-percurrent (pl. 32, fig. 1; text-fig. 44A). Quaternary venation and venation near leaf margins not preserved.

Comparison and discussion: *Viburniphyllum ermanniorum* nov. spec. differs from the other representatives of this genus in having small round leaves with deeply cordate bases. From *Viburniphyllum austriacum* Herman & J. Kvaček, nov. spec. it differs in angular shape of lamina and steeper secondary veins. *V. lebedevii* Vakhrameev & Herman (Herman 1991, p. 112, pl. 12, figs 1-4, text-figs 34, 35) and *V. basicordatum* Herman (Herman 1991, p. 110, pl. 12, figs 6-8, text-figs 32, 33) from the Coniacian – Campanian of North-western Kamchatka also possess a cordate leaf base but have much larger leaves. Moreover, *V. lebedevii* only has a slightly cordate base and *V. basicordatum* has an oblong-elliptic leaf lamina.

Viburnum inaequilaterale Lesquereux and *V. grewiopsideum* Lesquereux from the latest Albian – Cenomanian Dakota Formation in North America (Lesquereux 1891, p. 119-120, pl. 21, figs 2-4) have leaf shape, venation and margin similar to *Viburniphyllum ermanniorum*, but differ in their bigger size and acute, rather than deeply cordate, leaf bases. *Viburnites crassus* Lesquereux and *V. masoni* Lesquereux from the latest Albian – Cenomanian Dakota Formation in North America (Lesquereux 1891, p. 124-125, pl. 45, figs 1-5) are characterised by round leaves with leaf margin and venation similar to those in *Viburniphyllum ermanniorum*. However, the latter has a smaller size and a deeply cordate leaf base not typical of the above-mentioned Dakota species.

Genus *Dicotylophyllum*
Saporta, 1894

Type: *Dicotylophyllum cerciforme* Saporta, 1894, p. 147, pl. 26, fig. 14 (Cretaceous of Portugal).

Here we use the generic name *Dicotylophyllum* as a formal name for dispersed fossil dicotyledonous leaves of unknown affinity. Sometimes this is due to the poor preservation of the material studied, but sometimes the leaves which we describe under the name *Dicotylophyllum* differ significantly from all other known leaf morphotypes. Nevertheless, our material is not of a sufficiently high quality to enable the assignment of a new genus to these dispersed leaves.

Eight species are attributed to the genus *Dicotylophyllum*. Seven have informal specific names and are numbered from 1 to 7.

Dicotylophyllum proteoides (Unger) Herman & J. Kvaček, comb. nov.

(pl. 28, figs 1-15, pl. 29, figs 1-7, pl. 36, fig. 8; text-figs 45, 46)

Basionym: *Phyllites proteoides* Unger, 1867, Kreidepflanzen aus Österreich, p. 652, pl. 2, fig. 11.

1867 *?Phylliyes reussii* Unger, p. 653, pl. 2, fig. 12.
2004b *Pandemophyllum* J. Kvaček & Herman, p. 93.
2004b *Pandemophyllum* (?) *proteoides* (Unger) J. Kvaček & Herman, p. 95, text-figs 1 e-g, nom inval.

Neotype: designated here. NHMW 1999B0057/0339A (pl. 28, fig. 2).

Stratum typicum: Grünbach Formation, Lower Campanian.

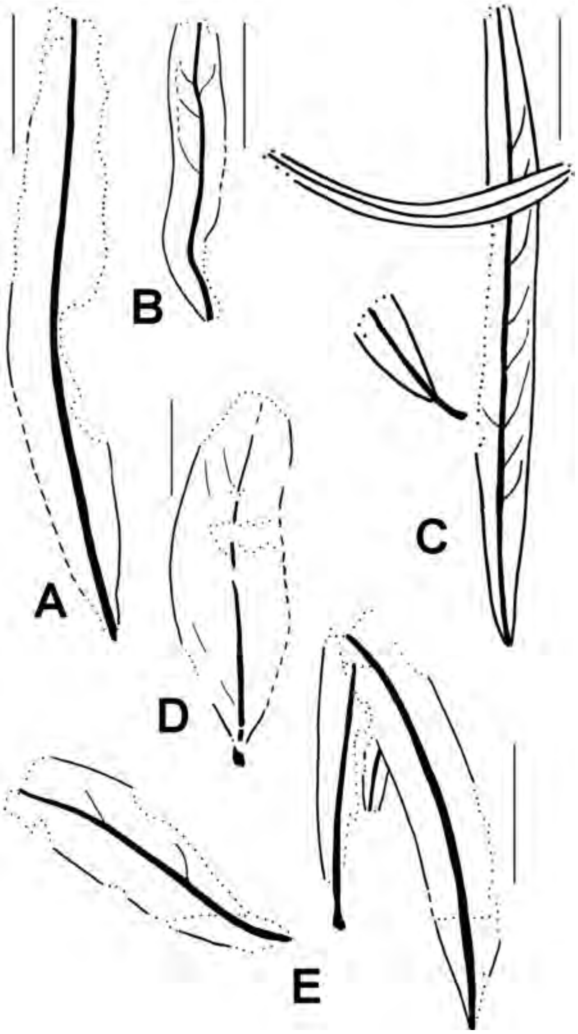
Locus typicus: Austria, Grünbach am Schneeberg.

Material: GBA: 2006/60/28, 2006/64/17
NHMW: 1861/0001/0095, 1970B1396/1638, …/1657, 1999B0057/0001, …/0056, …/0058, …/0059, …/0063a, …/0078, …/0104, …/0122a, …/0140, …/0142a,b, …/0153, …/0161, …/0164a,b, …/0217a, …/0259b, …/0264b, …/0283b,c, …/0284c, …/0331b, …/0332, …/0333, …/0334, …/0335, …/0338, …/0339b, 1970/1396/459b,c, …/0341a, …/0343, …/0344a,b, …/0345a,b, …/0347a-c, …/0348, …/0349, …/0350, …/0351, …/0352a,b, …/0353, …/0354a-c, …/0355a,b …/0356c, …/0357, …/0358, …/0359a, …/0360a, …/0361a,b …/0362, …/0363a,b, …/0364b, …/0470b, …/0371, …/0395b, …/0416b, …/0477b, …/0478, …/0480, …/0512, …/1788, …/1641, …/2037, …/2038.

Occurrence: Austria, Grünbach am Schneeberg, Frankenhof, Muthmannsdorf; Grünbach Formation, Lower Campanian.

Description: The neotype shows simple, unlobed, lanceolate, symmetric, entire-margined lamina. It is 12 x 85 mm in size with the base cuneate and the apex acuminate. Its midvein is stout, venation pinnate, secondary veins very difficult to observe leaving the midrib in angle of 60°.

Other leaves vary in length from 4.5-6 cm to approximately 12-13 cm, and width from 0.3-1 cm to approximately 2.5 cm. Leaf lamina lanceolate in outline, being broadest in the middle section or occasionally in the lower 1/3 of the leaf. Leaf base narrow cuneate, leaf apex narrow acute (pl. 28, figs 2, 4, 6, 7a; Text-figs 45A-E, G, 46 A-E; note that the emarginate leaf apex in text-fig. 45C is probably damaged). Leaf margin entire. Petiole short, 0.4-1 cm in length and 0.5-0.8 mm in width (text-fig. 45G). Venation pinnate camptodromous. Midvein stout and straight, terminating at the leaf apex, up to 0.8 mm thick in its basal part, narrowing towards the apex. Numerous secondary veins emerge from the midvein at an



Text-fig. 46: *Dicotylophyllum proteoides* (Unger) Herman & J. Kvaček, comb. nov., A – NHMW 1999B0057/0344b, B – NHMW 1999B0057/0347c, C – NHMW 1999B0057/0164b, D – NHMW 1999B0057/2038, E – NHMW 1999B0057/0344c, Grünbach (scale bar represents 1 cm).

angle of 40-80°, the most developed of them being in the middle part of the leaf lamina. Secondary veins thin, simple, curving upwards (pl. 29, fig. 3, text-fig. 46 B, C), connecting with the upper secondary vein and, together with tertiary veins, forming a series of small loops between the upper tertiary vein and the nearby leaf margin (pl. 28, figs 13, 15; text-fig. 45 H). Occasionally there is one intersecondary vein between two secondaries; it is shorter and thinner than the adjacent secondary veins (text-fig. 45 I). Tertiary veins are very thin, percurrent, straight, forming small loops near the leaf margin (Text-figs 45 H, I). Higher orders veins form a reticulum with small areoles (pl. 28, figs 12, 13). Cuticle removed from the specimen NHMW 1999B0057/0383 is extremely poorly preserved, showing remains of ordinary cells (pl. 36, fig. 8).

Comparison and discussion: *Dicotylophyllum proteoides* is one of the most abundant species in the Grünbach Flora. Leaves belonging to this species often form a leaf accumulation on bedding planes (pl. 28, fig. 1, pl. 29, figs 1, 2, 7). The fine venation of the leaves described here recall in some respect the genus *Pandemophyllum* Upchurch & Dilcher from the Cenomanian of Dakota (Upchurch & Dilcher 1990).

Many elongated entire-margined leaves with a very simple morphology similar to that of *Dicotylophyllum proteoides* have been described by different authors from the Late Cretaceous of the Northern Hemisphere: *Proteoides acuta* Heer, *P. daphnogenoides* Heer, *P. grewilliaeformis* Heer (Capellini & Heer 1866, p. 17, pl. 4, figs 7-11), *P. lancifolius* Heer, *P. ilicoides* Heer (Heer 1871b, p. 12-13, pl. 3, figs 5-8), *P. longus* Heer (Heer 1874, p. 110, pl. 29, fig. 8 b, pl. 31, figs 4, 5), *Laurophyllum aquisgranense* Lange (Lange 1890, p. 669, pl. 34, fig. 4), *Mytrophyllum* cf. *angustum* (Velenovský) Knobloch (Krassilov et al. 2005, p. 120, pl. 12, fig. 3), *Salix proteaefolia* Lesquereux (Lesquereux 1874, p. 60, pl. 5, figs 1-4) and others. *Laurus plutonia* Heer from the latest Albian – Cenomanian Dakota Formation in North America (Lesquereux 1891, p. 91, pl. 13, figs 5, 6) is characterised by leaf shape and venation similar to these of *D. proteoides*. The latter, however, differs from this species in having thinner and more regularly arranged secondary veins. The morphological simplicity of these leaves makes it very difficult to distinguish them. If its cuticle is not clearly preserved and if in particular paracytic stomata are not unequivocally present, it is difficult to assign the leaf type to lauroid foliage. This statement is in contrary to our previous preliminary determinations of this kind of leaf (compare Herman & Kvaček 2002, Kvaček & Herman 2004b).

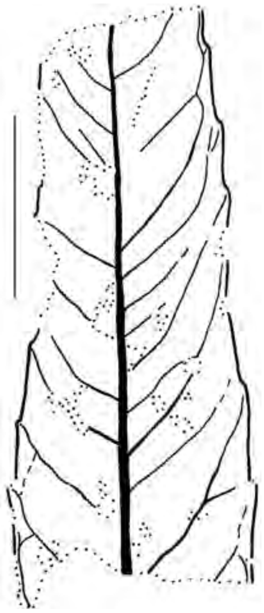
Dicotylophyllum sp. 1

(pl. 32, figs 3, 4; text-fig. 47)

Material: NHMW: 1999B0057/0282b, …/0336c.

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Description: Leaves small, simple, unlobed, linear, symmetric, with dentate margin. Leaf margin dentate or serrate. Marginal teeth small, simple, triangular or hook-like in shape, apressed, with acute or round curving-upwards apices. Sinuses between teeth are shallow, broad, round. Venation pinnate craspedodromous. Midvein straight, secondary veins numerous, thin, curving upwards and terminating in marginal teeth. Tertiary veins ramified-percurrent, higher order venation orthogonal-reticulate.



Text-fig. 47: *Dicotylophyllum* sp. 1, NHMW 1999B0057/0282b, Grünbach (scale bar represents 1 cm).

Two incomplete leaves represent this species. Leaves small in size, simple, unlobed, symmetric, with dentate margin. Leaf length is unknown due to poor preservation but is approximately 10-12 cm, leaf width 1.1-1.4 cm. Leaf lamina linear in general outline, probably broadest in the middle part of the leaf (pl. 32, fig. 3; text-fig. 47). Leaf base and apex not preserved. Leaf margin dentate or serrate. Marginal teeth small, simple, 0.3-0.5 mm in height, triangular or hook-like in shape, apressed, with acute or round curving-upwards apices (pl. 32, fig. 4; text-fig. 47). Sinuses between teeth shallow, broad, round. Petiole not preserved. Venation pinnate craspedodromous. Midvein straight, going to leaf apex, approximately 0.5 mm thick in its basal part, narrowing towards leaf apex. Secondary veins numerous, thin, emerging from midvein at an angle of approximately 35-60°, curving upwards and terminating in marginal teeth (pl. 32, fig. 3; text-fig. 47). Occasionally the secondary vein connects to the upper secondary vein forming a brochidodromous loop. Tertiary veins ramified-percurrent. Higher order venation orthogonal-reticulate.

Comparison and discussion: *Dicotylophyllum* sp. 1 is similar to *Debeya insignis* (Hosius & Marck) Knobloch from the Grünbach Formation described above in leaf shape, a dentate or serrate leaf margin with hook-like teeth and pinnate craspedodromous venation with numerous secondary veins. However, it differs from *Debeya insignis* in having bigger leaves and smaller, apressed marginal teeth.

Proteophyllum lanceolatum Němejc & Kvaček from the Senonian of South Bohemia (Němejc & Kvaček 1975, p. 37, pl. 5, figs 3-11, pl. 6, figs 2, 3, 5, 7-9, pl. 18, figs 1-5) is characterised by broadly linear to oblong lanceolate leaves with a toothed or serrate margin, prominent midvein and straight or slightly curved thin secondaries. This species, however, differs from *Dicotylophyllum* sp. 1 due to its larger size and its tertiary venation, which forms a fine network composed of irregular and rather large, slightly elongated and mostly quadrangular meshes, parallel to the secondaries.

Text-fig. 48: *Dicotylophyllum* sp. 2, NHMW 1999B0057/0098b, Grünbach (scale bar represents 1 cm).

***Dicotylophyllum* sp. 2**

(pl. 32, figs 7, 8; text-fig. 48)

Material: NHMW 1999B0057/0098b, …/0051, …/0071.

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Description: Leaves small, simple, unlobed, oblong elliptic, symmetric or slightly asymmetric, with dentate margin. Leaf base narrow round, symmetric or slightly asymmetric. Leaf margin dentate, marginal teeth simple, triangular, curving upwards, with round apices. Sinuses between teeth narrow, round. Venation pinnate craspedodromous. Midvein prominent, straight, secondary veins numerous, straight or slightly curving upwards, forking once or twice with all branches terminating in marginal teeth. Sometimes two secondary veins emerge from one point forming a characteristic "fork". Tertiary veins poorly preserved, thin, percurrent.

Leaves small in size, simple, unlobed, symmetric or slightly asymmetric, with dentate margin. Leaf length is unknown due to incomplete preservation of leaf impressions but was probably 5-7 cm or slightly more, leaf width approximately 1.8 to 2.7 cm. Leaf lamina oblong elliptic in general outline, probably being broadest in the middle part of the leaf. Leaf base narrowly round, symmetric or slightly asymmetric (pl. 32, figs 7, 8; text-fig. 48), leaf apex unknown. Leaf margin dentate, marginal teeth simple, triangular in shape, 1-1.2 mm in height, curving upwards, with round apices (pl. 32, fig. 7; text-fig. 48). Sinuses between teeth narrow, round. Petiole not preserved.

Venation pinnate craspedodromous. Midvein prominent, straight, approximately 0.6-0.8 mm thick in its basal part, narrowing towards the leaf apex. Secondary veins prominent, numerous, emerging from the midvein at an angle of 40-50° in the basal part of the leaf, straight or slightly curving upwards. Sometimes two secondary veins emerge from one point in the midvein, or the secondary vein divides into two branches of the same order soon after emerging from the midvein, forming a characteristic "fork" (pl. 32, figs 7, 8; text-fig. 48). Well-developed secondary veins in the middle part of leaf forking once, rarely twice, all branches terminating in marginal teeth (pl. 32, figs 7, 8; text-fig. 48). Tertiary veins poorly preserved, thin, percurrent. Higher order venation and venation near leaf margin not preserved.

Comparison and discussion: This species resembles *Myrica thulensis* Heer (Heer 1874, p. 107, pl. 31, fig. 1) from the Late Cretaceous on Greenland and *Dryophyllum cretaceum* Debey (Lange 1890, p. 665, pl. 33, figs 5-8) from the Senonian of Aachen, Germany, with its oblong elliptic leaf shape, dentate margin and pinnate craspedodromous venation. However, secondary veins in *Dicotylophyllum* sp. 2 fork once or twice, and sometimes a secondary vein divides into two branches of the same order soon after emerging from the midvein, whereas the secondary veins in *Myrica thulensis* and *Dryophyllum cretaceum* are simple.

Quercophyllum pseudodrymejum (Velenovský) Němejc from the Senonian of South Bohemia (Němejc & Kvaček 1975, p. 54, pl. 8, fig. 3, pl. 9, figs 1, 3) differs from *Dicotylophyllum* sp. 2 by virtue of its decurrent cuneate leaf base, simple secondaries and prominent percurrent to ramified-percurrent tertiary venation. *Quercophyllum gracile* (Debey) Němejc from the Senonian of Klikov, South Bohemia (Němejc 1961, p. 12, pl. 2, figs 1a, 2-4, text-fig. 1) possesses leaf shape and venation similar to those observed in *Dicotylophyllum* sp. 2 but differs from this species in having a cuneate leaf base and bigger marginal teeth. *Dicotylophyllum* sp. 2 resembles *Viburniphyllum austriacum* described here in overall leaf shape, size and shape of marginal teeth and pinnate venation, but differs in shape of leaf base (narrow round in *Dicotylophyllum* sp. 2 and distinctly cordate in *Viburniphyllum austriacum*) and sharper angle of the secondary veins emerging from the primary one.

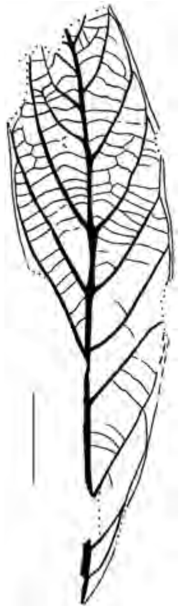
Dicotylophyllum sp. 3

(pl. 32, fig. 9; text-fig. 49)

Material: NHMW 1999B0057/0121, …/0123b.

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

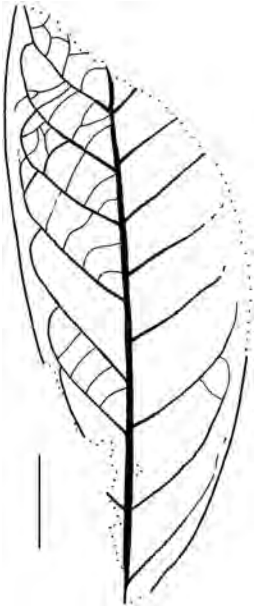
Description: Leaves small, simple, unlobed, lanceolate, symmetric, entire-margined. Leaf base narrow cuneate, symmetric. Leaf margin entire, slightly undulate. Venation pinnate brochidodromous. More than 10 pairs of secondary veins emerge from the midvein, secondary veins opposite in lower and middle parts of the leaf, simple or forking once, curving upwards and forming loops close to the leaf margin. Tertiary veins thin, straight or slightly curved, percurrent or ramified-percurrent.



Text-fig. 49: *Dicotylophyllum* sp. 3, NHMW 1999B0057/0123b, Grünbach (scale bar represents 1 cm).

Leaves small, simple, unlobed, lanceolate, symmetric, entire-margined (pl. 32, fig. 9; text-fig. 49). Leaf length approximately 7.5-10 cm, leaf width from 1.6-1.7 cm. Leaf lamina lanceolate in general outline, being broadest in the middle part of the leaf. Leaf base narrow cuneate, symmetric, leaf apex not preserved (pl. 32, fig. 9; text-fig. 49). Leaf margin entire, slightly undulate. Petiole not preserved. Venation pinnate brochidodromous. Midvein straight, running to the leaf apex, approximately 0.7 mm thick in its basal part, narrowing towards the apex. Secondary veins emerging from midvein at an angle of 35-45°. More than 10 (probably 13-15) pairs of secondary veins emerging from the midvein, the most developed being in the middle part of the leaf lamina (pl. 32, fig. 9; text-fig. 49). Secondary veins opposite in lower and middle parts of the leaf, simple or forking once, curving upwards, connecting with the upper secondary vein and forming oblique loops close to the leaf margin. Tertiary veins thin, straight or slightly curved, percurrent or ramified-percurrent, almost perpendicular to the midvein and the secondary veins (pl. 32, fig. 9; text-fig. 49). Higher order venation and venation near leaf margin not preserved.

Comparison and discussion: Leaf shape, pinnate curving-upwards secondary veins and percurrent or ramified-percurrent tertiary venation of *Dicotylophyllum* sp. 3 resemble those of *Quercophyllum pseudodrymejum* (Velenovský) Němejc from the Senonian of South Bohemia (Němejc & Kvaček 1975, p. 54, pl. 8, fig. 3, pl. 9, figs 1, 3). The latter, however, has a dentate leaf margin and craspedodromous rather than brochidodromous secondary venation. *Dicotylophyllum saliciforme* Němejc from the Senonian of Klikov,



Text-fig. 50: *Dicotylophyllum* sp. 4, NHMW 1999B0057/0044, Grünbach (scale bar represents 1 cm).

South Bohemia (Němejc 1961, p. 32, pl. 8, figs 1-4, text-fig. 10) possesses leaf shape and secondary and tertiary venation similar to those characteristic of *Dicotylophyllum* sp. 3 described here. The latter differs from *D. saliciforme* by brochidodromous rather than camptodromous venation.

Dicotylophyllum sp. 4

(pl. 32, fig. 10; text-fig. 50)

Material: NHMW: 1999B0057/0044.

Occurrence: Austria, Grünbach am Schneeberg; Grünbach Formation, Lower Campanian.

Description: Leaf small, simple, unlobed, lanceolate, slightly asymmetric, entire-margined. Leaf base narrow cuneate. Venation pinnate brochidodromous, more than 8 pairs of secondary veins emerging from the midvein, opposite or almost opposite, simple, curving upwards and forming prominent loops at a distance of approximately 1-1.5 mm from the leaf margin. Tertiary veins thin, straight or slightly curved, percurrent or sometimes ramified-percurrent.

The only incompletely preserved specimen is represented by a small, simple, unlobed, lanceolate, slightly asymmetric, entire-margined leaf (pl. 32, fig. 10; text-fig. 50). Leaf of unknown length, but approximately 8-10 cm, width 2.4 cm. Leaf lamina lanceolate in general outline, being broadest in the middle part of the leaf. Leaf base narrow cuneate, leaf apex not preserved (pl. 32, fig. 10; text-fig. 50). Leaf margin entire. Petiole not preserved. Venation pinnate brochidodromous. Midvein straight, terminating at leaf apex, approximately 0.8 mm thick in its basal part, narrowing towards the leaf apex. Secondary veins emerging from midvein at an angle of 45-60°. More than 8 (probably 13-15) pairs of secondary veins emerging from the midvein, the most developed (thickest and longest) in the middle part of the leaf lamina (pl. 32, fig. 10; text-fig. 50). Secondary veins opposite or almost opposite, simple, curving upwards, connecting with the upper secondary vein and forming prominent loops at some distance (approximately 1-1.5 mm) from the leaf margin. Tertiary veins thin, straight or slightly curved, percurrent or sometimes ramified-percurrent, almost perpendicular to the midvein and the secondary veins (pl. 32, fig. 10; text-fig. 50). Higher order venation and venation near the leaf margin not preserved.

Comparison and discussion: This species is very similar to *Dicotylophyllum* sp. 3 Herman & J. Kvaček described above, and initially we had assigned both to one species. However, *Dicotylophyllum* sp. 4 differs distinctly from *Dicotylophyllum* sp. 3 in the second order venation: its secondary veins are shorter and form prominent loops at a distance of approximately 1-1.5 mm from the leaf margin, whereas in *Dicotylophyllum* sp. 3 they are longer and form more oblique loops close to the margin.

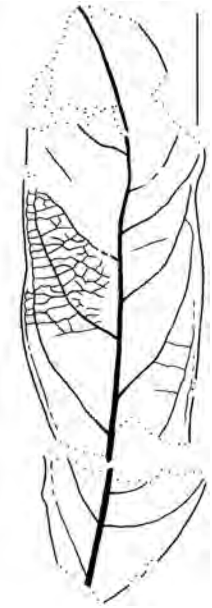
Dicotylophyllum sp. 5

(pl. 33, figs 1-3; text-fig. 51)

Material: NHMW: 1999B0057/0054, .../0282c.

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Description: Leaves small, simple, unlobed, lanceolate, symmetric, entire-margined. Leaf base narrow cuneate, leaf apex narrow acute. Venation pinnate brochidodromous to camptodromous. Midvein straight, terminating at the leaf apex, more than 8 pairs of secondary veins emerging from the midvein. Secondary veins simple, curving upwards, connecting with the upper secondary vein, forming loops close to the leaf margin, or forming, together with tertiary veins, a series of small loops near the leaf margin between this and the upper secondary vein. Tertiary veins thin, orthogonal-reticulate, forming small loops or cells near the leaf margin. Higher order venation orthogonal-reticulate.



Text-fig. 51: *Dicotylophyllum* sp. 5, NHMW 1999B0057/0054, Grünbach (scale bar represents 1 cm).

Two incompletely preserved fossil leaves represent this species. Leaves small, simple, unlobed, lanceolate, symmetric, entire-margined. Leaves of unknown length, but approximately 6-7 cm, width 1.6-1.7 cm. Leaf lamina lanceolate in general outline, broadest in the middle part of the leaf. Leaf base narrow cuneate, leaf apex narrow acute (pl. 33, figs 1-2; text-fig. 51). Leaf margin entire, slightly undulate. Petiole not preserved. Venation pinnate brochidodromous to camptodromous (pl. 33, figs 1-3; text-fig. 51). Midvein straight (some undulations of the midvein in the leaf shown in text-fig. 53 are due to deformation of the sample), running to the leaf apex, approximately 0.5 mm thick in its basal part, narrowing towards the apex. More than 8 (probably 10-12) pairs of secondary veins emerging from the midvein at an angle of 35-60°, the most developed being found in the middle part of the leaf lamina. Secondary veins opposite or almost opposite in the lower part of the leaf, simple, curving upwards, connecting with the upper secondary vein and forming loops close to the leaf margin (brochidodromous venation – text-fig. 51). Sometimes a secondary vein, together with tertiary veins, form a series of small loops between the upper secondary vein and the nearby leaf margin (camptodromous venation – text-fig. 51). Tertiary veins thin, orthogonal-reticulate (pl. 33, figs 1-3; text-fig. 51), form small loops or cells near the leaf margin (pl. 33, figs 1, 3; text-fig. 51). Fourth and fifth order venation orthogonal-reticulate (pl. 33, fig. 3).

Comparison and discussion: The most characteristic feature of this species, distinguishing it from other leaf morphotypes in the Grünbach Flora, is the reticulate tertiary and higher order venation. This type of venation may suggest a lauracean affinity for *Dicotylophyllum* sp. 5. In a leaf shape, entire margin and pinnate venation it is similar to *Dicotylophyllum* sp. 3, but differs in having thinner secondary veins and distinct reticulate tertiary venation (pl. 33, figs 1, 3) whereas *Dicotylophyllum* sp. 3 has percurrent to ramified-percurrent tertiary venation.

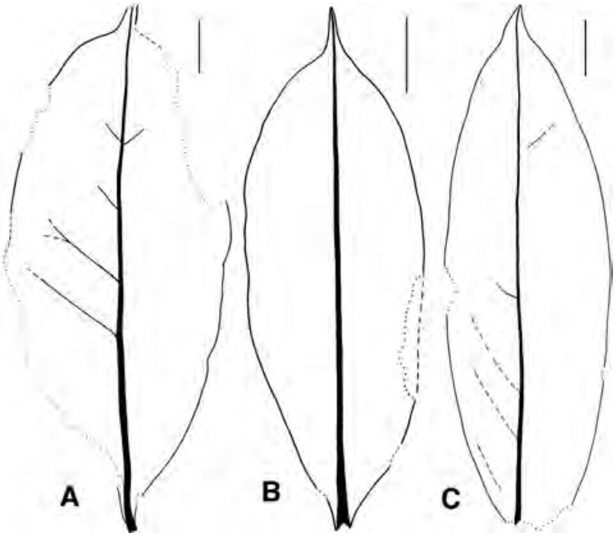
***Dicotylophyllum* sp. 6**

(pl. 31, fig. 4; pl. 33, figs 4, 5; text-fig. 52)

Material: NHMW: 1999B0057/0075, …/0042-1, …/0076, …/0135b.

Occurrence: Grünbach am Schneeberg, Austria; Grünbach Formation, Lower Campanian.

Description. Leaves small to medium, simple, unlobed, oblong elliptic, symmetric or slightly asymmetric, entire-margined. Leaf lamina of thin texture,



Text-fig. 52: *Dicotylophyllum* sp. 6, A – NHMW 1999B0057/0075, B – NHMW 1999B0057/0135b, C – NHMW 1999B0057/0042-1, Grünbach (scale bar represents 1 cm).

base narrow to broad cuneate, slightly decurrent, apex attenuate. Venation pinnate, with 8-12 pairs of thin, straight, simple or once-forking secondary veins.

Leaves small to medium in size, simple, unlobed, symmetric or slightly asymmetric, entire-margined (pl. 31, fig. 4, pl. 33, figs 4, 5, text-fig. 52). Leaf length from 6.0 to 10.4 cm, leaf width from 3.0 to 4.3 cm. Leaf lamina of thin texture, oblong elliptic in general outline, being broadest in the middle part of the leaf. Leaf base narrow to broad cuneate, slightly decurrent, symmetric (text-fig. 52B) or slightly asymmetric (Text-figs 52 A, C). Leaf apex distinctly attenuate, tip narrow, forming a driptip (pl. 31, fig. 4; pl. 33, figs 4, 5; Text-figs 52 A, B) or broad (text-fig. 52C). Leaf margin entire, sometimes slightly undulate. Petiole not preserved. Venation pinnate, probably camptodromous or brochidodromous. Midvein straight, terminating at leaf apex, approximately 0.9-1.4 mm thick in its basal part, narrowing towards the leaf apex. Secondary veins poorly preserved, thin, emerging from midvein at an angle of 40-50°, simple or forking once, straight. Probably 8-12 pairs of secondary veins emerging from the midvein (Text-figs 52 A, C). Higher order venation and venation near leaf margin not preserved.

Comparison and discussion: The most prominent and characteristic feature of this species is the attenuate leaf apex. The only other entire-margined species in the Grünbach Flora with an attenuate apex is *Leguminosites mucronatus* Herman & Kvaček, nov. spec. described above, which is much smaller and possesses a broad elliptic or obovate leaf lamina. *Dicotylophyllum* sp. 6 differs from *Theiaiphyllum kollmannii* Herman & Kvaček, nov. gen. et nov. spec. in having thin leaf texture, distinctly attenuate apex and less numerous secondary veins. *Diospyros anceps* Lesquereux from the Late Cretaceous of North America (Lesquereux 1874, p. 89, pl. 6, fig. 6) has elongate entire-margined leaves, but *Dicotylophyllum* sp. 6 differs from this species due to its larger leaves with a more pronounced attenuate leaf apex.

***Dicotylophyllum* sp. 7**

(pl. 25, figs 8-14, pl. 30, figs 4b,c;
pl. 35, figs 7, 8; text-fig. 53)

Material: NHMW: 1999B0057/0009, …/0059b,c …/0100b, …/0256, …/0282, …/0289, …/0290, …/0291, …/0342, …/0566, …/0572, …/0579.

Occurrence: Grünbach am Schneeberg, Austria, Grünbach Formation, Lower Campanian.

Description: Leaves small, simple, unlobed, linear, symmetric, entire-margined. Leaf length from 3 to approximately 13 cm, leaf width from 0.3-0.4 to approximately 0.8 cm. Leaf lamina relatively narrow, strip-like, linear in outline, broadest in the middle part of the leaf. Leaf base narrow cuneate, leaf apex narrow acute (pl. 25, figs 9, 10, 12; text-fig. 53A). Leaf margin entire. Petiole not preserved. Venation pinnate, probably camptodromous. Midvein distinct, straight, terminating at the leaf apex. Secondary veins numerous, very thin, closely spaced, emerging from the midvein at a very sharp angle and running almost parallel to the midvein (pl. 25, fig. 11). Higher orders of venation not preserved. Cuticle removed from the specimen NHMW 1999B0057/0100 is delicate and poorly preserved. The cuticle is penetrated by many mycelia of fungi, which blur the cuticle pattern (pl. 35, fig. 7). Ordinary cells are isodiametric (7-12 x 12-18 μm) and poorly preserved, also poorly preserved anomocytic stomata(15 x 20 μm) (pl. 35, fig. 8).

Comparison and discussion: *Dicotylophyllum* sp. 7 described here is similar in leaf shape and venation to *Grevilleophyllum constans* (Velenovský) Velenovský from the Cenomanian Peruc-Korycany Formation in the Czech Republic (*Grevillea constans* Velenovský 1883; Frič & Bayer 1901, p. 123, fig. 85). However, its cuticle is very different. Although poorly preserved, it does show anomocytic stomata which are very different from paracytic stomata of *Grevilleophyllum constans*. The leaf also resembles *Proteophyllum laminarum* Velenovský from the Cenomanian and Seno-nian of the Czech Republic (Velenovský 1889, Frič & Bayer 1901, p. 118, fig. 76; Němejc & Kvaček 1975, p. 40, pl. 6, figs 1, 4, 6, pl. 7, figs 1, 2, 4, 6, pl. 19, figs 1-6, text-figs 10-12) in having narrow entire-margined leaves with pinnate venation and numerous thin closely spaced secondary veins. However, *P. laminarum* has a relatively wider leaf lamina and possibly brochidodromous venation, whereas the venation in *Dicotylophyllum* sp. 7 is probably camptodromous, and its secondary veins are thinner, emerging from the midvein at a sharper angle.

Genus *Ceratoxylon* Velenovský & Viniklář, 1931

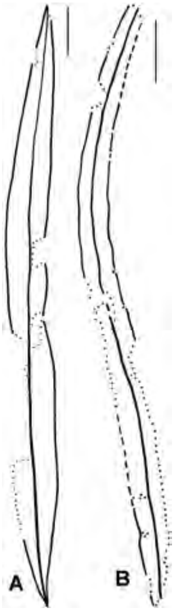
Type: *Ceratoxylon laterale* Velenovský & Viniklář, 1931, p. 13, 73, pl. 28, figs 3-7 from the Cenomanian of the Czech Republic.

Ceratoxylon sp.

(pl. 33, figs 6-9)

Material: NHMW 1999B0057/0551, …/0553.

Occurrence: Grünbach Formation (Lower Campanian), Grünbach am Schneeberg, Austria.



Text-fig. 53: *Dicotylophyllum* sp. 7, A – NHMW 1999B0057/0256, B – NHMW 1999B0057/0100b, Grünbach (scale bar represents 1 cm).

Description: There are three specimens preserved on two slabs in the collection. The best-preserved specimen (No. NHMW 1999B0057/0551, pl. 33, fig. 6) shows a compound inflorescence. The main axis (0.5-1.2 mm in diameter) is bearing helically arranged secondary axes (0.5 mm in diameter). Each secondary axis shows helically placed units (2-2.5 x 0.8-1 mm) in axils of bracts 2 mm long. Detailed structure of units is not known.

Comparison and discussion: Genus *Ceratoxylon* accommodates compound reproductive structures of unknown affinity. The present inflorescence is compared to *Ceratoxylon laterale* Velenovský & Viniklář from the Peruc-Korycany Formation of the Bohemian Cretaceous Basin (Velenovský & Viniklář 1931, pl. 28, figs 3-7) and *C. minus* Němejc from the Santonian of the South Bohemian Basins (Němejc 1961, pl. 1, figs 7-10. The present material is similar to the *C. laterale* in arrangement of secondary axes, but differs in details of units. The units of the present material do not show bifurcations and are supported by a bract. *Ceratoxylon minus* Němejc (1961, text-fig. 11) is similar to the present material in size and shape of units. Preservation of the present material does not allow precise comparison.

Chapter 6 Palaeopalynology

Spores and pollen from the plant-bearing deposits of the Grünbach Formation at Grünbach were studied by Draxler (in Summesberger 1997) and Svobodová (in Hradecká et al. 2000). Here we present their results as they were published.

Fifteen samples were collected by Dr. Benno Plöchinger from a measured section of the Coal-bearing Series in the coal-mine of Grünbach. The samples are under study now and are the best accessible palynological material. Samples from the surface contain badly preserved pollen and spores only.

Preliminary list of morphogenera and species of pollen and spores:

Sphagnaceae
Stereisporites sp.
Lycopodiaceae
Retitriletes sp. (*Lycopodium* sp.)
Camarozonosporites sp.
Filicatae
Cyathidites sp.
Leiotriletes sp. (*Lygodium* sp.)
Gleicheniidites senonicus Ross.
Cicatricosisporites sp.
Appendicisporites tricuspidatus Weyland & Greif.
Polypodiaceoisporites sp.
Echinatisporites sp.
Angiospermae
Dicotyledoneae
"*Normapolles*"
Oculipollis sp.
Oculipollis parvoculus Goczan
Oculipollis zaklinskaiaiae Goczan
Semioculipollis sp.
Longanulipollis sp.
Hungaropollis sp.
Krutzschipollites sp.
Suemegipollis sp.
Extremipollis sp.
Pseudoplicapollis sp.
Laudaypollis sp.
Momipetes sp. (similar to *Engelhardtia*)
Tricolpopollenites sp. (at least 5 taxa)
Tricolpopollenites sp. (at least 3 taxa)
Monocotyledoneae
Arecipites sp. (Palmae)
Gymnospermae
Pityosporites sp. (at least 2 taxa, *Pinus*, *Cathaya*?)
Taxiodiaceaepollenites sp.
Reworked:
Circitlina sp. (Upper Triassic)
Ovalipollis sp. (Upper Triassic)
Lueckisporites sp. (Upper Permian)
Illinites sp. (Upper Permian).

Discussion: The most characteristic elements are pollen from the "*Normapolles*" group of ancient angiosperms. They are of small to medium size (25-50 μm) and have complex protruding apertures. The distribution in the sequence varies. The pollen from the "*Normapolles*" group are reported from the Upper Santonian and Campanian of Hungary (Goczan 1964; Goczan, Groot, Krutzsch & Pacltová 1967; Kedves, 1989, Goczan & Siegl-Farkas 1990). *Complexiopollis complicatus*, characteristic in the Upper Santonian of the Ajka Coal Formation, and other morphospecies of *Complexiopollis* recorded from different localities of the Gosau-Group (Turonian-Santonian; Siegl-Farkas 1994) are absent in the Grünbach samples.

Arecipites sp. can be related to *Palmae*, also recorded as leaves. The large spores of Pteridophyta (*Leiotriletes* sp., *Appendicisporites tricuspidatus*, *Cicatricosisporites* sp.) are similar to the Schizaeaceae. This family is distributed today in tropical and subtropical climates. For most of the specimens of Angiospermae, for the "*Normapolles*" group, and for different others not mentioned in detail here, no direct correlation can be made to modern plants based on the present stage of knowledge. (Draxler in Summesberger 1997 p. 80-81).

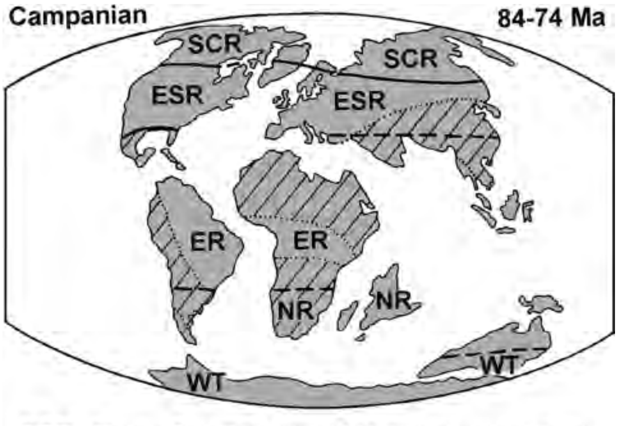
"The interdisciplinary study of selected outcrops of the Late Cretaceous fine-clastic sediments in the Grünbach-Neue Welt Gosau Group, eastern part of the Northern Calcareous Alps gave new foraminiferal, nannoplankton and palynological data. Maceration of samples from the Coal-Bearing Series and Inoceramus Marl yields assemblages of prevailing angiosperm pollen and marine microplankton in addition to scolecodonts and chitinous linings of foraminifers. On the base of the association of triporate angiosperm pollen of the *Normapolles* group – *Pseudopapillollis praesubhercynicus*, *Oculopollis* spp., *Suemegipollis germanicus* some of the Inoceramus Marl samples in the surroundings of Grünbach can be attributed to the Late Campanian. The biostratigraphically important species *Pyxidinopsis bakonyensis* of the Campanian age was recorded in a sample of the Coal-Bearing Series at Maiersdorf." (Hradecká et al. 2000, p. 51).

Chapter 7 Palaeofloristics and Phytogeography

7.1 Phytogeographic Significance

The Grünbach Flora is a typical flora of the Euro-Sinian palaeophytogeographic region (text-fig. 54, Vakhrameev 1991). It also belongs to the Southern Laurasian Province according to Batten (1984) and Crane (1987) and to the *Normapolles* Province by Herngreen & Chlonova (1981). It is situated on the southern margin of the *Normapolles* region (text-fig. 55) and contains a certain amount of palm pollen (Draxler in Summesberger 1997) indicating transmission to the Equatorial Province.

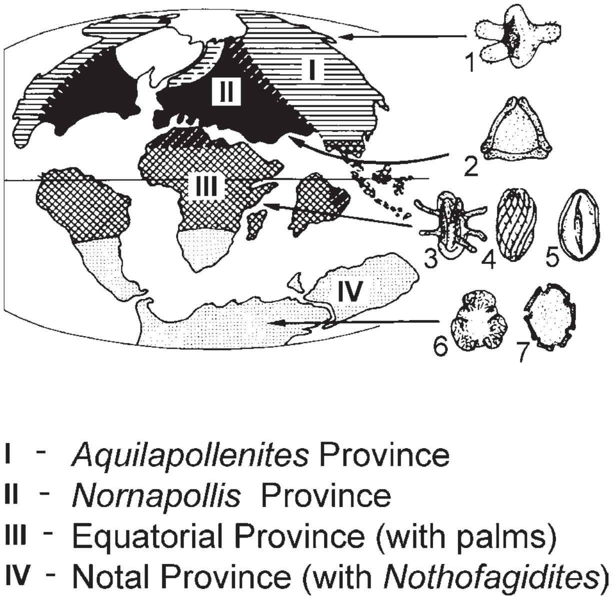
The Santonian-Maastrichtian floras of Europe have several features in common. They share the conifer *Geinitzia*, platanoids and palms *Sabalites*. During the Late Cretaceous *Geinitzia formosa* Heer interestingly replaces the conifer *Cunninghamites lignitum* (Sternberg) J. Kvaček (= *Cunninghamia elegans* Corda in Reuss) of similar ecological amplitude. In Europe, finds of *Geinitzia formosa* are recorded from the Campanian of Grünbach (present study), from the Santonian of Quedlinburg and Blankenburg, from the Santonian of Aachen (Kunzmann et al. 2003) and from the Santonian of Scania (Kunzmann & Friis 1999).



Text-fig. 54: Campanian phytogeographic and palaeoclimatic regions of the world (modified from Vakhrameev, 1991): SCR – Siberian-Canadian Region of the warm temperate climate, ESR – Euro-Sinian Region of the subtropical climate, ER – Equatorial Region of the tropical climate, NR – Austral (Notal) Region of the subtropical climate, WT – warm temperate belt of the South Hemisphere (existed since Santonian); shaded are arid and semiarid areas.

Monocots are one of the most significant group of the Grünbach Flora. The genus *Sabalites* from there represents the most northerly occurrence of palms in Laurasia. Since palms are usually confined to southern Europe, their presence has important climatic implications (see Chapter 9. Palaeoclimatic Interpretations). *Sabalites longirhachis* is described from Grünbach (J. Kvaček & Herman 2004a), from the Maastrichtian of Romania (Tuzson 1908, 1913, 1914), from the Campanian-Maastrichtian localities Bagnols, Fuveau near Rhone in France (Saporta 1890) and from Isona locality in Spain (Castells 2002). Fossil palms from Late Cretaceous are also known from the Turonian of Israel (Krassilov et al. 2005), the Campanian of Canada (Bell 1957) and Maastrichtian of USA (Dorf 1938).

Occurrences of *Pandanites trinervis* appear to be restricted to Alp-Carpathian localities and are there-



Text-fig. 55: Palaeofloristic provinces in Late Cretaceous (mostly Senonian) based on palynological data (modified from Herngreen & Chlonova, 1981 and Vakhrameev, 1991); main pollen types are: 1 = *Aquilapollenites*, 2 = *Trudopollis* (from *Nornapolles* group), 3 = *Elaterosporites*, 4 = *Ephedripites*, 5 = *Psilamonocolpites* (palm-like pollen), 6 = *Microcachrydites* (Podocarpaceae), 7 = *Nothofagidites*.

fore of palaeoecological significance (see Chapter 8. Palaeoecological Interpretations). *P. trinervis* occurs in masses in the Campanian of Grünbach (J. Kvaček & Herman 2004a) and St. Wolfgang (J. Kvaček 2007). There are further occurrences of this taxon in the Maastrichtian of Banat, Romania (Petrescu & Dusa 1980). These distinctive fossils were additionally recorded in the Maastrichtian (?) of the Rocky Mountains, USA (Dorf 1938), where they form a similar assemblage to Grünbach together with palms (*Sabalites* spp.), other monocots (*Canna* ? *magnifolia* Knowlton, "*Typha*" sp.), *Equisetum* sp., and platanoid plants (*Credneria protophylloides* Knowlton).

Another interesting plant of the Grünbach Flora is the genus *Nilsonia*, which is usually considered as a boreal element (Vakhrameev 1991). *Nilsonia* occurs e.g. in the Flora of the Nanaimo Group (Campanian of British Columbia, Canada, Bell 1957). It is present as three species, *N. vancouverensis* (Dawson) Bell, *N. cuneata* (Newberry) Chaney, *N. serotina* Heer. The flora also contains leaf impressions of palms *Genomites imperialis* (Dawson) Bell which are almost identical to *Sabalites longirhachis* (J. Kvaček & Herman 2004a). It is interesting to note that palms considered as subtropical-tropical indicators occur there again with the boreal element *Nilsonia*. This unique co-occurrence has been found exclusively in the Campanian Nanaimo Group and at Grünbach. Platanoids are generally also considered as elements of the Late Cretaceous temperate forest of the Northern Hemisphere (Vakhrameev 1991). They are present in the Grünbach Flora as three species of *Ettingshausenia*. Other elements such as Equisetaceae, Marsileaceae and water lilies are quite cosmopolitan taxa and their occurrence is of lower phytogeographical significance.

7.2 Palaeofloristic Comparison

Although there is no direct equivalent to the Grünbach Flora, the floras that most resemble it in terms of plant content are from the Gosau Formation (Unger 1867, Schenk 1876, Tyroff 1984, Hradecká et al. 2006, 2007, J. Kvaček 2007b), Maastrichtian of Romania (Tuzson 1908, 1913, 1914; Baikovskaja 1965; Petrescu & Dusa 1980), the Maastrichtian of Spain (Castells 2002), the Senonian (Němejc 1957, 1961, 1968; Němejc & Kvaček 1975) and the Cenomanian of the Czech Republic (Velenovský 1882, 1883, 1884, 1885a,b, 1889; Frič & Bayer 1901, 1903; Velenovský & Viniklář 1924, 1926, 1929, 1931; Hluštík 1974, 1976, 1877a,b, 1978, 1980, 1986a,b; Hluštík & Konzalová 1976a,b; Knobloch 1971, 1973, 1974, 1978, 1985, 1986, 1987a,b; 1994a,b, 1999; Knobloch & Mai 1986, 1991; J. Kvaček 1992a,b, 1994, 1995, 1997a,b, 1999, 2000, 2003, 2006, 2007; Kvaček & Knobloch 1997; J. Kvaček & Pacltová 2001; Kvaček et al. 2005, 2006; J. Kvaček & Váchová 2006; Z. Kvaček 1983, 1991, 1992). Other significant comparable floras have been described from Poland (Geinitz 1849-50, Velenovský 1882, 1883, 1884, 1885a,b; Karczmarz & Popiel 1966, 1971), Aachen Formation – Germany, Belgium (Göppert 1842; Debey

1848; Debey & Ettingshausen 1859a, b, Ubaghs 1885, 1887; Lange 1890; Stockmans 1946; Knobloch & Mai 1986; Gottwald 2000; Meijer 2000; Kunzmann et al. 2003), Westphalia (Hosius & V.D. Marck 1880), Bayern (Gothan 1941), Quedlinburg (Heer 1871b, Richter 1904, 1905, Kunzmann 1999, Rüffle & Trostheide 2000), Maastrichtian type area – Netherlands, Belgium (Miquel 1853; Kräusel 1922, 1923; Van der Ham et al. 2001, 2003a,b, 2004; Van der Ham & van Konijnenburg-van Cittert 2004), Sweden (Friis 1983, 1984, 1985, 1990; Friis & Skarby 1982; Skarby 1986; Friis et al 1988; Srinivasan & Friis 1989; Eklund et al. 1997; Kunzmann & Friis 1999; Schönenberger & Friis 2001; Leng et al. 2005), Italy (Bozzi 1888, 1891), Romania (Givulescu & Lacatusu 1978; Givulescu et al. 1980, Givulescu 1981), Bulgaria (Zeiller 1905, Hartung 1939, Hartung & Gothan 1939, Tenčov & Černjavska 1965), Hungary (Knobloch & Mai 1986, Rákosi & Brabacka 2000), Slovenia (Dobruskina et al. 1999), Croatia (Kerner 1895), and Crimea (Krassilov 1984).

Due to palaeoecological conditions which indicate a peaty swamp habitat, the Grünbach Flora represents a unique case with few counterparts in the Late Cretaceous. Apart from a few small localities in the Alps (Gosau Group – St. Wolfgang: Unger 1867, J. Kvaček 2007b, Geistthal near Gratz: Knobloch 1977), the Maastrichtian flora of Romania bears the closest resemblance. It is situated in the Transylvanian Region of Banat near the Iron Gate of the River Danube and is found in several localities (Rusca Montana, Hateg) which are mentioned in short reports by Tuzson (1908, 1913, 1914), Baikovskaja (1965) and Petrescu & Dusa (1980). The sedimentary conditions (M. Popa personal communications 2003, 2005) and floristic content of these Romanian localities are similar to those at Grünbach. The most characteristic elements of both floras are represented by the palm *Sabalites longirhachis* and *Pandanus trinervis*. Pandans are particularly important since they are good indicators of wetland habitats (see Chapter 8. Palaeoecological Interpretations). The localities in both Austria and Romania were exposed on tectonically active islands during the Alpine-Carpathian orogeny.

The Maastrichtian Flora of Isona in Catalonia, Spain, recently described by Castells (2002), appears to have numerous parallels with the Grünbach Flora. Unfortunately, closer comparison of both floras is difficult due to inadequate illustrations of the Catalonian flora and the language barrier. In general, there may be similarities with *Equisetum-Equisetites*, *Podozamites*, *Sabalites*, *Debeya*. Identification of both species of *Nilsonia* (Castells 2002, pl. 6, figs 2-4) is considered to be dubious, although presence of the genus in Spain cannot be entirely dismissed. This flora may potentially be of interest, but needs to be revised and studied in detail.

The Senonian flora of the Czech Republic described by Němejc (1938, 1956, 1957, 1961, 1968), Němejc & Z. Kvaček (1975) and Knobloch (1964) shares several features with the Grünbach Flora. The conifers *Geinitzia* and *Podozamites*, angiosperms *Platanus-Ettingshausenia*, and *Debeya* are recorded in both floras. Palynospectra of both localities are rich in *Normapolles* pollen (compare Draxler in Summesberger 1997 and Pacltová 1956, 1958, 1961, 1963; Zetter et al. 2002).

The Senonian flora of Westphalen (Hosius & V.D. Marck 1880) is found in several localities in Germany and is mainly represented by angiospems. It shares the following taxa with the Grünbach Flora: *Quercus castanoides* Hosius & V.D. Marck – *Grebenkia*, *Ettingshausenia-Credneria*, *Debeya*. The Senonian flora of Quedlinburg was described by Heer (1871b), Richter (1904, 1905) and is mentioned in, for example, Kunzmann (1999), Rüffle & Trostheide (2000). It comes from sandstones interbedded with mudstone lenses and is palaeoecologically similar to the Aachen Flora, sharing the following taxa with the Grünbach Flora: *Sphenopteris* (*Asplenium dicksonianum*), *Geinitzia*, *monocots*, *Debeya*, *Myricophyllum* and *Platanus-Ettingshausenia*.

The flora from the Santonian of Idzigow (Kieslingswalde) was described by Geinitz (1850), partially by Velenovský (1882, 1883, 1884, 1885b) and comprehensively by Bayer (in Frič 1897, 1898). It is preserved in sandstones of fluvial origin containing a few remains of ferns and conifers together with numerous angiosperms. It shares the following taxa with the Grünbach Flora: *Geinitzia reichenbachii* and *Ettingshausenia*.

The Santonian flora of Aachen (Göppert 1842; Debey 1848; Debey & Ettingshausen 1859a, b, Ubaghs 1885, 1887; Lange 1890; Stockmans 1946; Knobloch & Mai 1986; Gottwald 2000; Meijer 2000; Kunzmann et al. 2003) occurs in sandstones and is interpreted as reflecting a flood plain environment. The Aachen flora of Belgium was described by Stockmans (1946). A meaningful comparison was constrained by Stockmans' simplified illustrations, however, the flora does show some similarities with the Grünbach Flora, namely sharing the genera *Monheimia*, *Sphenopteris/Adiantites forsteri*, *Raphaelia*, *Geinitzia*, *Myricophyllum/Dryandroides*, and *Debeya* (Debey & Ettingshausen 1859a, b; Lange 1890; Kräusel 1923; Knobloch 1972; Kunzmann et al. 2003).

The Late Cretaceous flora of Maastrichtian type area in the Netherlands and Belgium (Miquel 1853; Kräusel 1922; Van der Ham et al. 2001, 2003a,b, 2004; Van der Ham & van Konijnenburg-van Cittert 2004) shows limited similarities. It shares following genera with the Grünbach flora: *Debeya*, *Pagiophyllum*, and *Myricophyllum/Myrica*.

Less similarities are shared with the Late Cretaceous flora of Sweden particularly due to its different mode of preservation (Friis 1983, 1984, 1985, 1990; Friis & Skarby 1982; Skarby 1986; Friis et al 1988; Srinivasan & Friis 1989; Eklund et al. 1997; Kunzmann & Friis 1999; Schönenberger & Friis 2001; Leng et al. 2005). The only shared taxon with the Grünbach Flora is the conifer *Geinitzia* which is represented in Scania by seeds (Kunzmann & Friis 1999).

Localities of Turonian-Maastrichtian age in France are poorly documented in literature. Information about them is scattered in several, usually short, contributions (e.g. Laurent, 1932; Marion 1890; Saporta 1862, 1890; Ducreux et al. 1982; Gomez 1994; Gomez et al., 2003; Marmi et al. 2008). Material from French Campanian-Maastrichtian, which includes also equivocal records of pandans (*Pandanus amarylifolius* Roxburgh, locality Ambone near Toulouse) need major revision, but was not available for the present study.

Small florules from Hungary, Bulgaria, Croatia, Slovenia and Italy (for references see above) have only few taxa in common with the Grünbach Flora, particularly conifers (*Geinitzia*, *Pagiophyllum*).

Although quite distant in age, the Cenomanian flora of the Czech Republic shares numerous taxa with Grünbach Flora. This may be due to several reasons. 1. The Czech flora represents the best preserved well-studied and well-described flora in Europe and therefore serves as a model, influencing the identification of other European floras. 2. Its own diversity generates a higher probability of finding similar (sister) plants. The flora has been described by many authors, the most important work being undertaken by Velenovský (1882, 1883, 1884, 1885a, b, 1888, 1889), Bayer (in Frič & Bayer 1901, 1903), and Velenovský & Viniklář (1926, 1927, 1929, 1931). The flora was revised and, additionally, described by Hluštík (1972, 1974, 1976, 1977ab, 1978, 1980, 1986), Knobloch (1974, 1978, 1999), Knobloch & Mai (1986), Z. Kvaček (1983) and J. Kvaček (1994, 1995, 1997a,b, 1999, 2000a,b, 2003, 2006, 2007a), J. Kvaček & Knobloch (1997), Eklund & J. Kvaček (1998), J. Kvaček & Dilcher (2000), J. Kvaček & Pacltová (2001), Kvaček & Eklund (2003), Kvaček et al. (2005), and Kvaček et al. (2006). The following taxa are common to the Cenomanian Flora of the Czech Republic and the Grünbach Flora: *Monheimia*, *Sphenopteris*, *Rapahelia*, *Nilsonia*, *Podozamites*, *Geinitzia*

(J. Kvaček & Dilcher 2000), *Platanus-Ettingshausenia*, *Debeya*, *Juglandiphyllites* (=*Sapindophyllum*).

Fossil palms are known from the Turonian of Southern Negev, Israel (Krassilov et al. 2005). However, the taxonomic composition of this flora is different from that of the Grünbach Flora and probably reflects hotter and more arid environment.

Although similar in age, the Pautut (Santonian/Campanian) Flora of Greenland (Boyd 1992, 1994) is quite different from the Grünbach Flora and except superficial resemblance of fern fronds of the broad morphogenus *Sphenopteris* and elongate entire-margined leaves of angiosperms, it shows no shared taxa.

On the other hand, the more distantly situated Cretaceous floras of North America do show similarities to the Grünbach Flora. The Maastrichtian (?) flora of the Rocky Mountains (Dorf 1938) shares quite a number of genera: *Pandanites*, *Sabalites*, *Ettingshausenia/Credneria*, *Myricophyllum/Myrica*, *Celastrophyllum/Celastrus*, *Viburniphyllum/Viburnum* and *Leguminosites*.

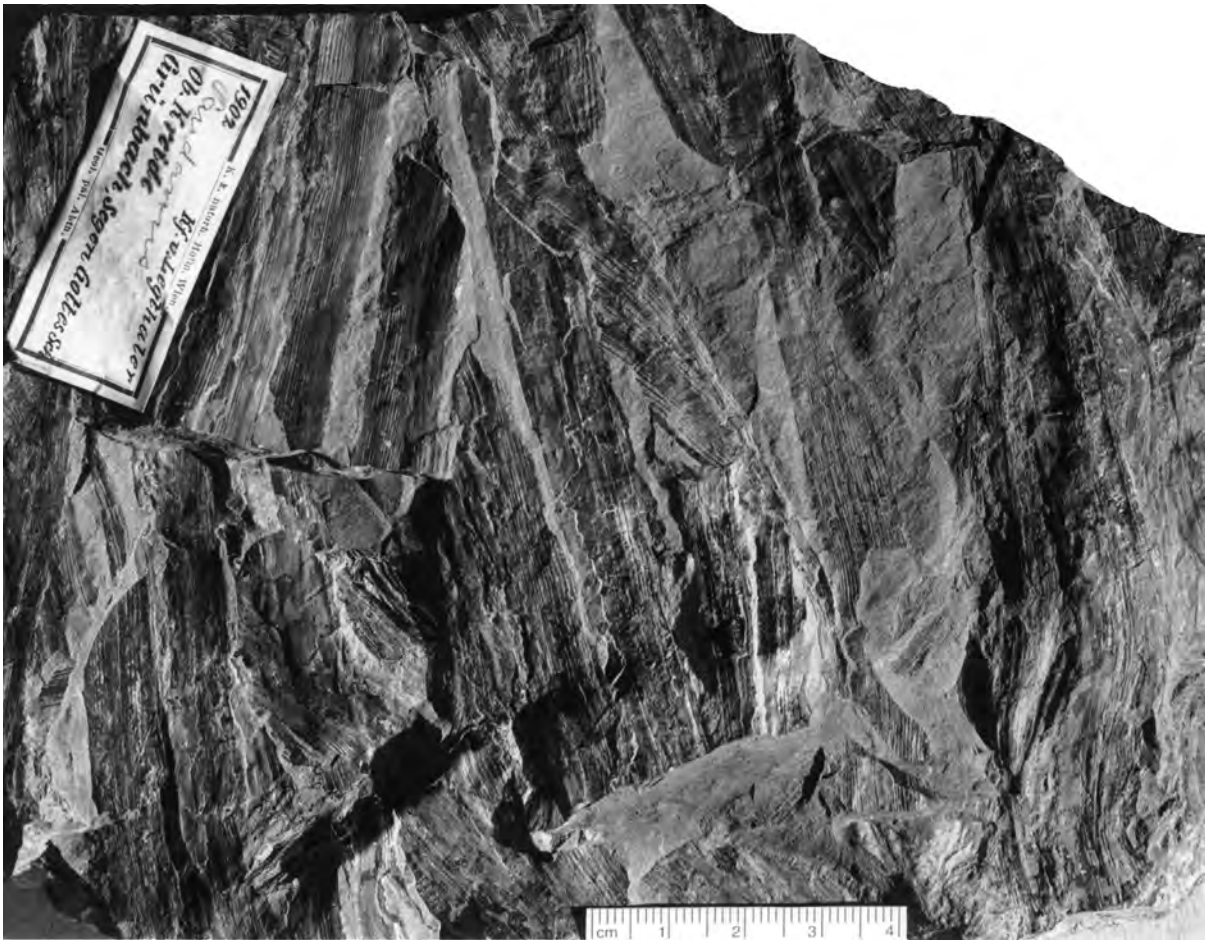
Another flora bearing similarities to the Grünbach Flora has been studied and described within the Campanian Nanaimo Group, Vancouver Island, British Columbia, Canada (Bell 1957). This flora is quite rich in taxa and contains only two fossil plants that are also present in the Grünbach Flora. These comprise palm leaves described as *Genomites imperialis* (Dawson) Bell which are almost identical to *Sabalites longirhachis* (J. Kvaček & Herman 2004a) and genus *Nilsonia*. It is interesting to note that palms considered as subtropical-tropical indicators are found in the Nanaimo Group together with *Nilsonia* (*N. vancouverensis* (Dawson) Bell, *N. cuneata* (Newberry) Chaney, *N. serotina* Heer), which is usually interpreted as a boreal element. This unique co-occurrence has been found exclusively in the Campanian Nanaimo Group and at Grünbach.

Chapter 8 Palaeoecological Interpretations

The Grünbach Flora represents one the few Late Cretaceous mire floras in the Northern Hemisphere that have been studied to date. This chapter focuses on plant palaeoecology and descriptions of plant communities. The Grünbach Flora, in contrast to numerous other floras found in clastic sediments, has a unique taxonomic composition (compare Uličný et al. 1997). It is rich in monocots, particularly pandans, together with ferns. The Grünbach Flora is moderately diverse, comprising 53 plant taxa belonging to Equisetopsida, Polypodiopsida, Cycadopsida (Cycadales), Pinopsida, Liliopsida, and Magnoliopsida. Our taphonomic observations are based on extensive studies of plant fossil collections and on field observations from a spoil heap near Grünbach village carried out in 2001 (Herman, Kvaček and Summesberger), 2003 (Kvaček) and 2005 (Herman, Kvaček and Eder). From field excavations in Grünbach it became apparent that the most abundant fossils in the locality were represented by pandan leaf remains.

8.1 Plant communities

Interpretation of the Grünbach plant communities is based on plant morphology (leaf size, shape and texture), anatomy (cuticular characters, aerenchymatic tissues of water plants), the autecology of some taxa (such as *Marsileaceaephyllum*, water plants, palms, pandans), together with their abundance and taphonomic observations. The latter were restricted due to lack of access to a section in the abandoned coal mine. Nevertheless, our observations have demonstrated that particular plant fossils are often found together. Also we have observed constant associations of particular plant fossils and sedimentary facies. The amount of degradation and decomposition of fossil leaves was used as evidence of fossil plant transportation. Using these criteria, the following plant communities comprising the Grünbach Flora were reconstructed.



Text-fig. 56: Leaf accumulation typical of the Grünbach locality. Prevailing remains are fossil leaves of *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, Grünbach, Lower Campanian.

Aquatic plant community includes two water plants: *Brasenites* and *Quereuxia*. *Brasenites* has round or elliptic, entire-margined, peltate, floating leaves with well-developed aerenchyma. *Quereuxia* is represented by small triangular or elliptic leaves forming leaf rosettes. The leaves of *Brasenites* and leaf rosettes of *Quereuxia* with leaflets still attached are well preserved and show low mechanical degradation, providing evidence of short transportation of leaf material. Aquatic plant remains are abundant, suggesting the presence of an extensive shallow water environment at Grünbach.

Swamp/semiaquatic plant community is dominated by pandans with elongated leaves. *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman is characterised by strap-like, parallel-veined, typically armed leaves, which are M-shaped in transverse section. Many leaves show armed keels, attenuate apices and auriculate bases (J. Kvaček & Herman 2004a). Leaf accumulations of *Pandanites trinervis* are typical for this locality (text-fig. 56). These plants probably formed monodominant stands in a swampy environment and constituted the main coal-forming biomass. It is believed that the community also included semi-aquatic herbaceous monocots (*Lysichiton* etc.), horsetails *Equisetites* and ferns such as *Marsileaceaephyllum* and *Cladophlebis*. *Lysichiton* has parallel venation emerging from a multistranded costa (J. Kvaček & Herman 2004a, J. Kvaček & Herman 2005). Palm trees with *Sabalites* leaves may occur there, forming groups similar to recent *Sabal* or hardwood hammocks in Florida. *Sabalites longirhachis* (Unger) J. Kvaček & Herman is characterised by costapalmate, entire, lanceolate leaves with a long rhachis. It should be emphasised that recent habitats similar to those reconstructed for the Grünbach Flora occur in the peat-swamp forests of Sumatra. Although more tropical, they show a similar floral composition, particularly with the presence of palms and pandans (Uhl & Dransfield 1987, pl. 34D).

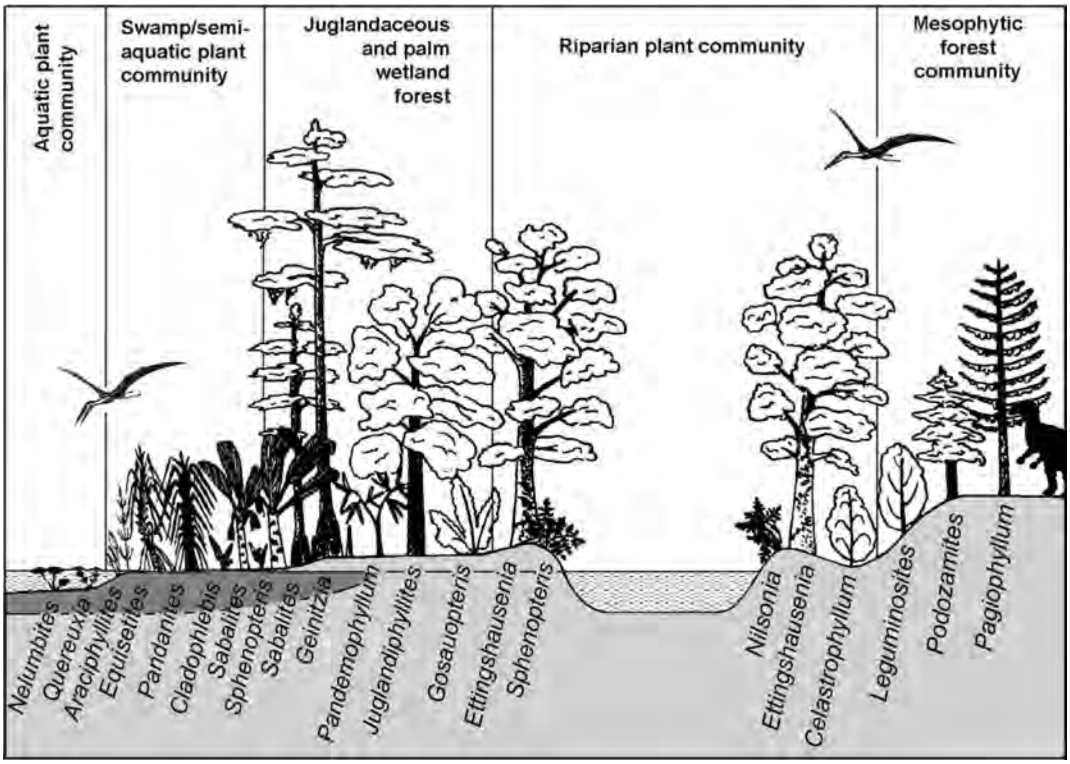
Juglandaceous and palm wetland forest was dominated by plants with *Juglandiphyllites* leaves of probably juglandaceous affinity, palms *Sabalites* and conifers *Geinitzia*. *Juglandiphyllites pelagicum* (Unger) Velenovský is represented by compound leaves consisting of entire-margined, petiolate, elliptic leaflets with brochidodromous venation. Fossil *Juglandiphyllites* leaflets are rarely attached forming compound leaves. This is caused probably by deciduousness of these plants which in a frostless climate usually drop their individual leaflets, but not primarily by transportation of a leaf material. Leaves of *Sabalites* occurring in the same type of sediment as *Juglandiphyllites* could not be transported for long distances: usually they, being heavy, fall close to the trees and could have become fragmented before (and during) transport. *Geinitzia formosa* Heer shows rigid shoots with falcate keeled leaves. One specimen demonstrates an elongate taxodioid ovuliferous cone attached to a leafy shoot. Long entire-margined, lanceolate leaves of various, but mainly small, sizes belonging to *Dicotylophyllum* sp. were also common here. They probably grew preferentially on drier soils and/or southern slopes. Ferns of possibly marattiaceous affinity were a typical component of this plant assemblage. This plant community was probably taxonomically the most diverse and included some other species, such as various ferns *Microphyllopteris*, *Monheimia*, *Cladophlebis*, *Onychiopsis* and angiosperms *Myricophyllum*, *Menispermites* etc.

Riparian community was dominated by platanoid trees, *Ettingshausenia* being the most numerous among them. *Ettingshausenia* leaves are entire-margined, trilobed, with acute base, actinodromous primary veins and brochidodromous secondary veins. Their leaves and leaf fragments are usually preserved in coarser-grained sandstones and sandy siltstones reflecting a high-energy depositional environment. The second common plant of this community is a fern *Sphenopteris ungeri* J. Kvaček et Herman. Its fronds are bipinnate, pinnules are elongate or triangular in shape and possess a well-pronounced venation. Other possible components of the riparian community are *Raphaelia*, *Nilsonia* and *Celastrophyllum*, the leaves of which usually show significant mechanical degradation.

Mesophytic forest community consisted probably of conifers *Pagiophyllum*, *Podozamites* and perhaps some angiosperms (*Leguminosites*). *Pagiophyllum* shows delicate shoots with falcate leaves. Comparing *Podozamites* fossils from the Grünbach Flora to similar plants from the Cenomanian locality Bohdánkov in Bohemia where they are classified as members of mesophytic forest (Kvaček unpublished data), we conclude that they could be assigned to the same mesophytic forest environment. Rare *Podozamites* plants were probably mixed with *Pagiophyllum* trees. Plant remains recorded from this community are often fragmentary and uncommon.

8.2 Reconstruction of the Grünbach vegetation

The dominating palaeogeographic situation during accumulation of the plant-bearing deposits of the Grünbach Formation is that of a large island with unknown relief, at least temporarily connected to the continent (Kollmann pers. comm.). The connection to the main land is also supported by fossil remains of vertebrates (Kroh pers. comm.). Terrestrial freshwater peat swamps and shallow water sediments indicate a relatively large deltaic plain. The presence of relict plants in the Grünbach Flora (*Nilsonia*, *Podozamites*) probably reflects the existence of the flora in an ‚island refuge‘. The relict plants could have persisted there due to geographic isolation and buffering in their original environment.



Text-fig. 57: Reconstruction of the Grünbach wetland vegetation and main plant communities (modified from J. Kvaček & Herman 2004).

From our observations we can reconstruct the following landscape that existed during the accumulation of the plant-bearing Grünbach Formation (text-fig. 57). In coastal lowlands and plains, large open bodies of shallow fresh water (ponds and oxbow lakes) with floating *Quereuxia* and *Brasenites* leaves were surrounded by swampy lowlands inhabited by community dominated by pandans and ferns with palms. Plants with *Pandanites* leaves probably formed monodominant stands in this swampy environment. Wetland juglandaceous forest with palms and evergreen conifers *Geinitzia* was developed along shores of the lakes, ponds and swamps. Wetland forest was taxonomically diverse and probably not uniform with the degree of heterogeneity depending on the soil wetness and exposure to the sun. Small rivers or streams probably crossed this lowland. Their margins were inhabited by riparian plant community composed mainly of ferns *Sphenopteris* and numerous shrubs or trees of platanoid angiosperms. Away from lakes, swamps and rivers, in drier places, mesophytic predominantly coniferous forest existed.

Chapter 9 Palaeoclimatic Interpretations

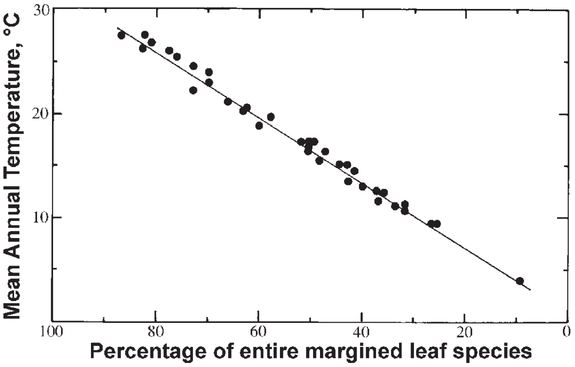
Palaeoclimatic analysis of the Grünbach Flora using the Nearest living relative, leaf margin analysis and Climate Leaf Analysis Multivariate Program approaches allowed us to reconstruct both qualitative and quantitative palaeoclimatic parameters experienced by the flora and check the hypothesis that the Grünbach Flora existed 1000 km south of the present day position of the Neue Welt Basin.

9.1 Palaeobotanical Methods of Palaeoclimatic Analysis

Nearest Living Relative (NLR) approach is one traditionally used by palaeobotanists for palaeoclimate analysis. The technique relies on the accurate identification of the nearest living relatives of the ancient plants composing a fossil flora, and the ancient climate is extrapolated from the climatic requirements of the living plants. The NLR approach usually works quite well for Quaternary and Neogene floras, and it is sometimes applicable for Palaeogene floras, but the antiquity of Cretaceous and older floras usually precludes its use. Apart from the difficulties of finding a relative at the species level for which climatic tolerances are the narrowest, the technique implies that climatic requirements of plant (or animal) taxa were not affected by evolution and are constant throughout the geologic time. Clearly this cannot be true. Therefore, in our interpretation of the Grünbach Flora we can use the NLR approach only as data additional to other kinds of palaeoclimatic analysis, keeping in mind that this technique could provide us with imprecise or even incorrect data.

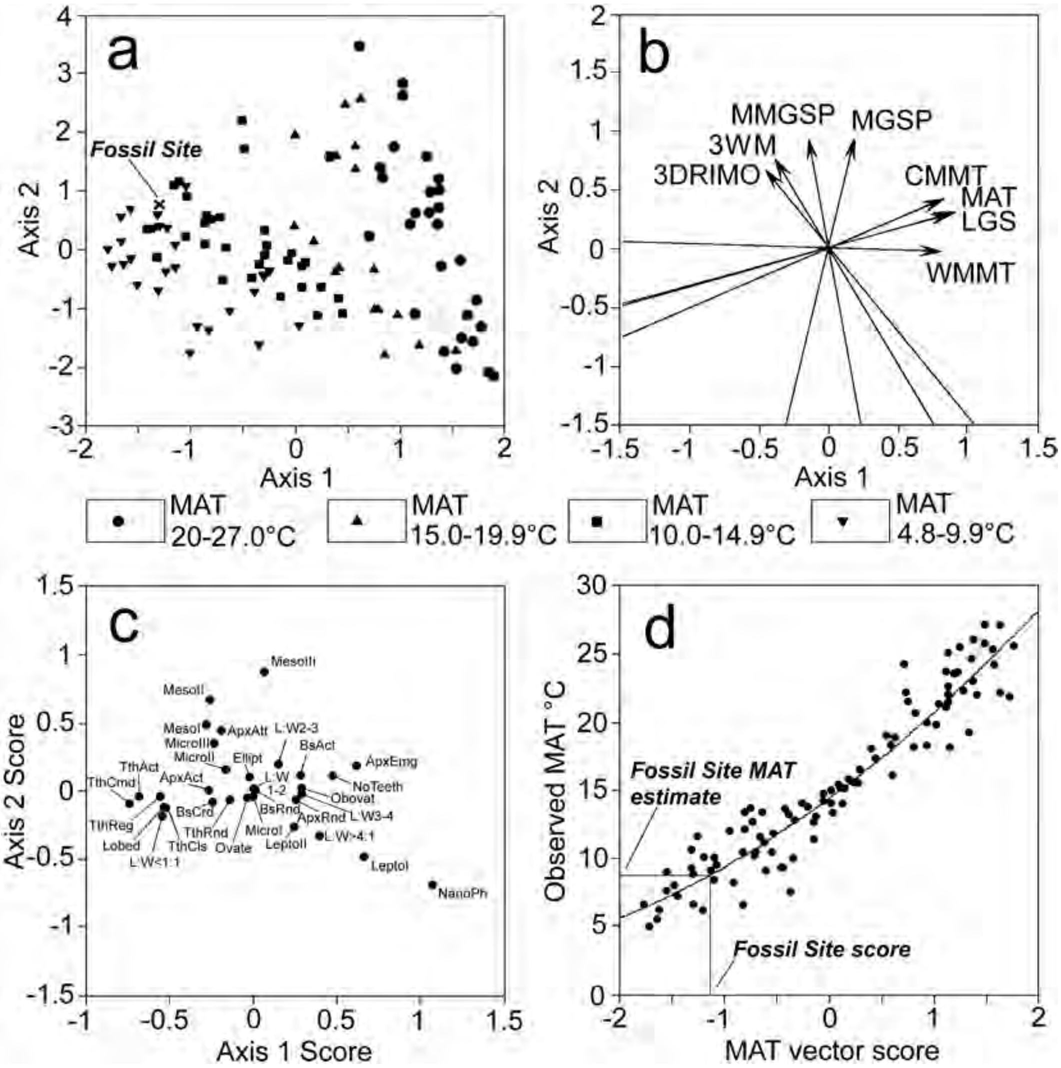
Leaf Margin Analysis (LMA). It is much safer to reconstruct past climates using taxonomically independent morphological or anatomical features characterising adaptations to particular environmental constraints. An early attempt at quantifying physiognomic characters in terms of climatic data was that of Bailey & Sinnot (1915).They examined the margin characteristics of woody dicot leaves and noted that there was a good direct relationship between the proportion of taxa with entire margins and mean annual temperature: entire margins are characteristic of warm climates and toothed margins of cool climates. By plotting the proportions of entire margined to toothed margined leaves in a flora, a clear relationship with mean annual temperature is apparent. Text-fig. 58 shows such a relationship for South-eastern Asian plants (Wolfe 1979). In an ideal situation the ratio of leaf margins in a fossil flora with a high diversity of dicot leaf species in it could yield a reliable mean annual temperature experienced by the plants at the time they grew.

The LMA has been used extensively for Tertiary and even Cretaceous material but the method has some serious limitations. Firstly, there is an underlying assumption that water is not limiting to growth in any of the taxa used in leaf margin analysis. If, however, drought is a factor, then leaf size tends to be diminished and teeth can be lost so giving an abnormally warm climatic signal. Secondly, because the morphology of a leaf is always a compromise between conflicting constraints (for example the advantage of having a large leaf surface area for light interception is moderated by evapotranspirational stresses and structural costs) a single character analysis provides only a partial, and possibly erroneous, climatic signal. However, we use the LMA in our interpretation of the Grünbach Flora in order to compare its result with data provided by other kinds of palaeoclimatic analysis of the flora.



Text-fig. 58: Plot of mean annual temperature (MAT) against the percentage of leaf margin types (from Wolfe 1979).

Climate Leaf Analysis Multivariate Program (CLAMP). In an attempt to overcome the above mentioned limitations and to obtain palaeoclimatic data from the leaf flora Wolfe (1993, 1995) developed a multi-character leaf physiognomic technique. Correspondence Analysis, a multivariate statistical ordination tool, was used to analyse 29 leaf characters found in modern taxa from present day vegetation at 103 sites for which climatic conditions were known from the meteorological observations. Wolfe was able to identify those characters that were most strongly correlated with climatic variables. These variables included mean annual, warm month mean, and cold month mean temperatures, mean annual, mean growing season, mean monthly growing season, and precipitation during the three consecutive driest months. Wolfe called this database and multivariate



Text-fig. 59: Results of CLAMP analysis using CANOCO; a – distribution of modern and fossil sites in axis 1/axis 2 space as defined by leaf characteristics; b – the environmental vectors in axis 1/axis 2 space; vectors: 3DRIM – precipitation during the three consecutive driest months, 3WM – precipitation during the three consecutive wettest months, MMGSP – mean monthly growing season precipitation, MGSP – mean growing season precipitation, CMMT – cold month mean temperature, MAT – mean annual temperature, LGS – length of the growing season, WMMT – warm month mean temperature; c – the distribution of leaf characters in axis 1/axis 2 space; leaf characters: ApxAct – apex acute, ApxAtt – apex attenuate, ApxEmg – apex emarginate, ApxRnd – apex round, BsAct – base acute, BsCord – base cordate, BsRond – base round, Ellipt – leaf elliptic, LeptoI – leptophyll I, LeptoII – leptophyll II, Lobed – lobed leaf, L:W<1:1 – length to width ratio less than 1:1, L:W1-2 – length to width ratio from 1:1 to 2:1, L:W2-3 – length to width ratio from 2:1 to 3:1, L:W3-4 – length to width ratio from 3:1 to 4:1, L:W>4:1 – length to width ratio more than 4:1, MesoI – mesophyll I, MesoII – mesophyll II, MesoIII – mesophyll III, MicroI – microphyll I, MicroII – microphyll II, MicroIII – microphyll III, NanoPh – nanophyll, Noteeth – no teeth, Obovat – leaf obovate, Ovate – leaf ovate, TthAct – teeth acute, TthCls – teeth close, TthCmd – teeth compound, TthReg – teeth regular, TthRnd – teeth round; d – MAT vector scores plotted against observed MAT values (modified from Herman, 2004b).

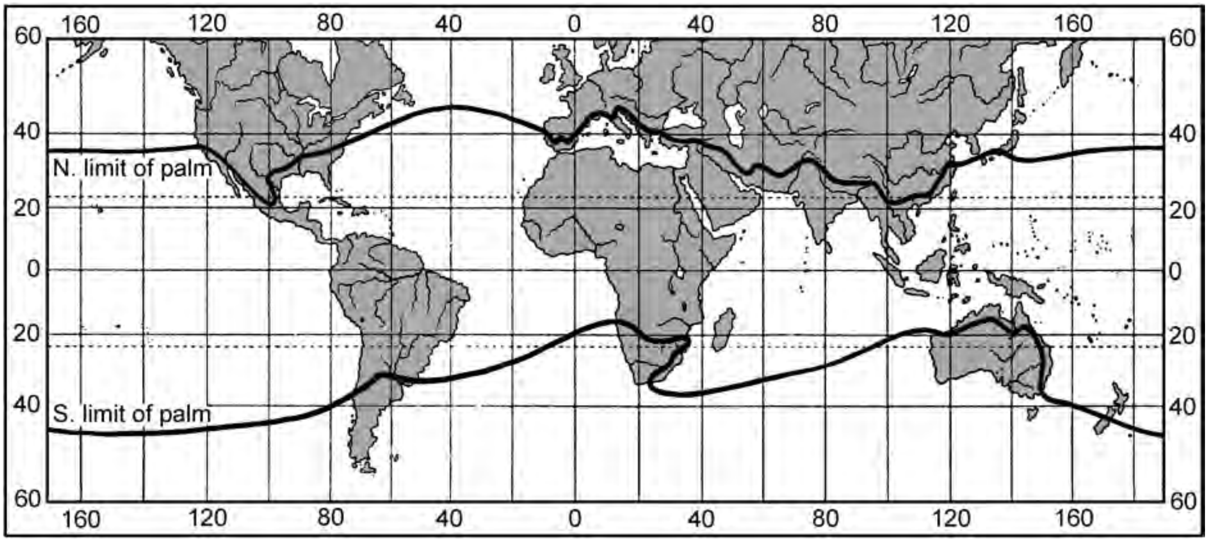
analysis Climate-Leaf Analysis Multivariate Program (CLAMP).

We have used the CLAMP methodology presented in Wolfe (1993) with some modifications. In CLAMP the architecture of woody dicot leaves from modern day vegetation growing under known climatic conditions is used as a reference data set against which to compare the architecture of leaves found in a fossil assemblage. There are now several of these datasets and they vary in size, geographical and climatic coverage. Here for comparability and appropriateness we use 173 modern vegetation sites (before we used dataset consisting of 103 sites: Herman & J. Kvaček 2002a, b). Most of these sites are from the Northern Hemisphere (dataset PHYSG3AR, see http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html) scored for 31 leaf characters (their definitions are in: Wolfe 1993, 1995; Herman & Spicer 1996, 1997; see also http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html) and correlated with 8 climate variables. These variables are: mean annual temperature (MAT), warm month mean temperature (WMMT), cold month mean temperature (CMMT), mean growing season precipitation (MGSP), mean monthly growing season precipitation (MMGSP), precipitation during three consecutive wettest months (3WM), precipitation during the three consecutive driest months (3DRIM), and length of the growing season (LGS). To be statistically reliable CLAMP requires the scoring of at least 20 leaf morphotypes at any given site. Whereas Wolfe (1993) originally used the indirect ordination engine of Correspondence Analysis, and consequently had to use subjective methods to position the climate vectors, we now use Canonical Correspondence Analysis (CANOCO) (Ter Braak 1986, 1987-92) which is a direct ordination technique that explicitly positions the climate vectors (Kovach & Spicer 1995; Herman & Spicer 1996, 1997). CANOCO is used to identify and calibrate correlations between angiosperm leaf characters and climate variables.

CANOCO is a direct ordination method here used to order site, leaf character and environmental data in multidimensional space simultaneously; sites being ordered by their character scores, and characters by their distribution among the sites. The sites are, therefore, arranged relative to one another in multidimensional space using the physiognomic characters of the vegetation at that site; environmental data are not used to position the sites. Text-fig. 59a shows 31-dimensional leaf character space collapsed to two dimensions. Axes 1 and 2 represent the two axes of greatest variation in the data so the plot is the least distorted projection from 31 dimensional space. The dots represent each of the 145 vegetation samples (28 subalpine sites are excluded) positioned relative to its neighbours based on the characters that are possessed by the leaves of at least 20 woody dicots in that vegetation.

The dots (text-fig. 59a) are coded to demonstrate that they are arranged according to the MAT experienced at each sample site; a mean annual temperature vector appears to run from left (low MATs) to right (high MATs). CANOCO explicitly positions the environmental vectors within this physiognomically defined vegetation space (text-fig. 59b). Text-fig. 59c shows the positions of leaf characters as defined by their distribution between the different vegetation sites. An imaginary line connecting “NoTeeth” and “Teeth Compound” dots (text-fig. 59c) lies close to the MAT vector (text-fig. 59b) confirming that leaf margin characteristics do indeed correlate with MAT and that leaf margin analysis is actually a more primitive version of CLAMP. The “leaf size” line going from Nanophyl (small leaf) to MesoIII (large leaf) (text-fig. 59c) lies close to precipitation vectors (text-fig. 59b) as we would expect.

Text-fig. 59a shows a fossil site (in this instance it is a Turonian flora from the Novaya Sibir Island, Arctic Russia) positioned in the leaf character space side by side with modern vegetation sites. The characteristics of the fossil leaves were scored in the same way as the modern leaves and added to the statistical



Text-fig. 60: Distribution of modern palms (modified from Philip's School Atlas… 2002)

analysis as "passive" samples. This means that their inclusion in the analysis did not disturb the structure of the "physiognomic space" as defined by the modern leaves. The position of the fossil site relative to those of the modern sites with known climates allows us to estimate, with a measurable degree of precision, the ancient climatic conditions under which the fossil flora grew. To do this, the environmental vectors (text-fig. 59b) are calibrated using modern sites with known climates. Text-fig. 59d shows the relationship between distance along the MAT vector, in arbitrary units, and the observed MAT, for modern sites. The position of the fossil site along the MAT vector can be used to determine the ancient MAT by seeing where the vector position intercepts the regression line. Alternatively, an equation describing the regression curve can be used to calculate the unknown MAT.

The scatter of dots about the regression line indicates a statistical uncertainty of being able to estimate the correct MAT. In this instance one standard deviation of the residuals about the regression line is 1.8°C.

9.2 Results and Discussion

In the nearest living relative (NLR) analysis of the Grünbach Flora four taxa are particularly important (Herman & J. Kvaček, 2007): palms (Arecaceae: fossil genus *Sabalites*), pandans (Pandanaceae: fossil genus *Pandanites*) and ferns probably belonging to the families Schizaeaceae (spores *Leiotriletes* sp., *Appendicisporites tricuspidatus*, *Cicatricosisporites* sp.) and Matoniaceae (*Monheimia* with spores *Matonisporites* preserved *in situ*). Palms are also recorded as pollen *Arecipites* sp. (Draxler in Summesberger 1997). Palms *Sabalites longirhachis* (Unger) J. Kvaček & Herman and pandans *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman are abundant in the Grünbach Flora whereas ferns are less numerous.

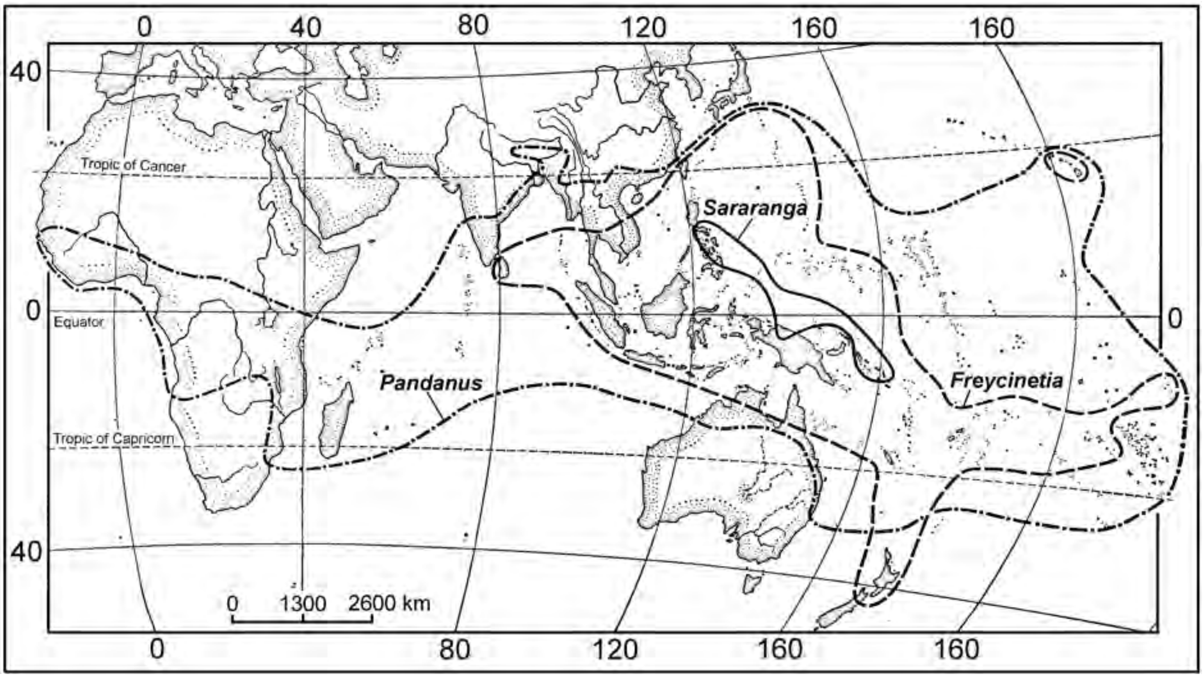
The family Arecaceae (palms) consists of 190 (up to 240 according to some authors) recent genera with 2000 (3400 ?) recent species (Imkhanitskaya 1982; Uhl & Dransfield 1987, Dransfield & Uhl 1998, Dransfield et al. 2008). Palms are widespread in the tropical, subtropical and warm temperate regions of all continents (text-fig. 60), but are the most abundant and diverse in South-East Asia and tropical South America. A limited number of species are known from warm temperate regions in which they may reach a latitude of 44° N (Imkhanitskaya 1982). The most northerly palm *Chamaerops humilis* occurs in northern Africa, southern Portugal and Malta; *Trachycarpus fortunei* H. Wendl reaches a latitude of 35° N in Korea and Japan but can survive in Scotland where it is used as an introduced plant in parks and gardens. This palm can tolerate short periods of winter frost up to -18° C (data from the Nikita Botanical Garden, Ukraine). The most northerly American palm, *Sabal minor*, occurs in the south-eastern USA and reaches North Carolina.

Pandanaceae (pandans) is a typical Palaeotropic family consisting of four recent genera: *Pandanus* L. (700 species in the Indo-Pacific region), *Freycinetia* Gaudichaud-Beaupré (200 species in the Austral-Asian region), *Sararanga* Hemsley (2 species in the Philippines and Melanesia) (Grushvitskii 1982; Stone et al. 1998) and *Martellidendron* Callmander et al. 2003 (7 species in Madagascar). Pandans are considered to be good indicators of climate. These evergreen plants usually occur in tropical and subtropical climates, but also in warm temperate forests such as those of Southern Japan (text-fig. 61). They grow in humid coastal habitats and on islands, from which it can be assumed that they require a high water supply provided by rainfall or by ground water in swamps. The latter case is probably applicable to *Pandanites trinervis* found in the Grünbach coal swamp.

Draxler (in Summesberger 1997) pointed out that large fern spores *Leiotriletes* sp., *Appendicisporites tricuspidatus*, *Cicatricosisporites* sp. from the plant-bearing deposits of Grünbach were similar to the family Schizaeaceae. Today this family is distributed mostly in tropical and subtropical climates, only a few species being known from the temperate regions of North and South America, South Africa, Japan, New Zealand and Tasmania (Popova 1978; Tryon & Tryon 1982; Kramer 1990a).

Fern spores *Matonisporites* were found *in situ* in sori of *Monheimia* fern foliage. Both *Matonisporites* spores and *Monheimia* are supposed to belong to Matoniaceae. Today this family occurs in tropical and subtropical rainy climates in South-eastern Asia – in Kalimantan, Sumatra, Malaysia Peninsula, Moluccas and New Guinea (Gladkova 1978; Kramer 1990b). However, geological record of Matoniaceae shows that in Jurassic this family was distributed also in subtropical and warm temperate climates of Europe, Northern Africa, North America and Australia (Osnovy Paleontologii... 1963; Van Konijneneburg-Van Cittert 1993).

Text-fig. 61: Distribution of modern pandans (modified from Grushvitskii 1982)



Therefore, co-occurrence of palms, pandans and possible representatives of the family Schizaeaceae and Matoniaceae in the Grünbach Flora is thought to indicate that the flora experienced a humid and hot or warm frost-free climate which could be classified as tropical, subtropical or, less plausibly, warm temperate (Herman & J. Kvaček, 2007).

Leaf margin analysis (LMA) of 27 non-aquatic dicot leaf morphotypes from the Grünbach Flora shows (Herman & J. Kvaček, 2007) that 48 % (13 species: *Menispermites ettingshausenii*, *M. summesbergeri*, *Ettingshausenia gruenbachiana*, *Juglandiphyllites pelagicum*, *Dicotylophyllum proteoides*, *Leguminosites mucronatus*, *Rogersia* sp., *Dicotylophyllum* sp. 3, sp. 4, sp. 5, sp. 6, sp. 7) have leaves or leaflets with entire margins. This indicates that the estimated mean annual temperature experienced by the Grünbach Flora is 16°C (text-fig. 58).

Physiognomic analysis of the Grünbach Flora using the CLAMP technique is now based on a new revised fossil plant taxonomy (Herman & J. Kvaček, 2007) whereas in our previous study (Herman & J. Kvaček 2002a, b) we used a preliminary taxonomy as at that time the monographic study of the flora was not finished yet. In the present study 27 dicot leaf morphotypes were scored for as many of the 31 characters as were preserved. The scoring results (percentage of characters preserved) are:

Leaf margin (is preserved in all 27 morphotypes): leaves lobed – 5.6 %; leaves with no teeth – 48.1 %; teeth regular – 48.1 %; teeth close – 40.7 %; teeth round – 16.7 %; teeth acute – 35.2 %; teeth compound – 1.9 %.

Leaf size (is preserved in 25 morphotypes): nanophyll – 0 %; leptophyll I – 0 %; leptophyll II – 2 %; microphyll I – 26 %; microphyll II – 41.3 %; microphyll III – 16.6 %; mesophyll I – 8.6 %; mesophyll II – 5.3 %; mesophyll III – 0 %.

Leaf apex (is preserved in 14 morphotypes): emarginate – 0 %; round – 35.7 %; acute – 39.3 %; attenuate – 25 %.

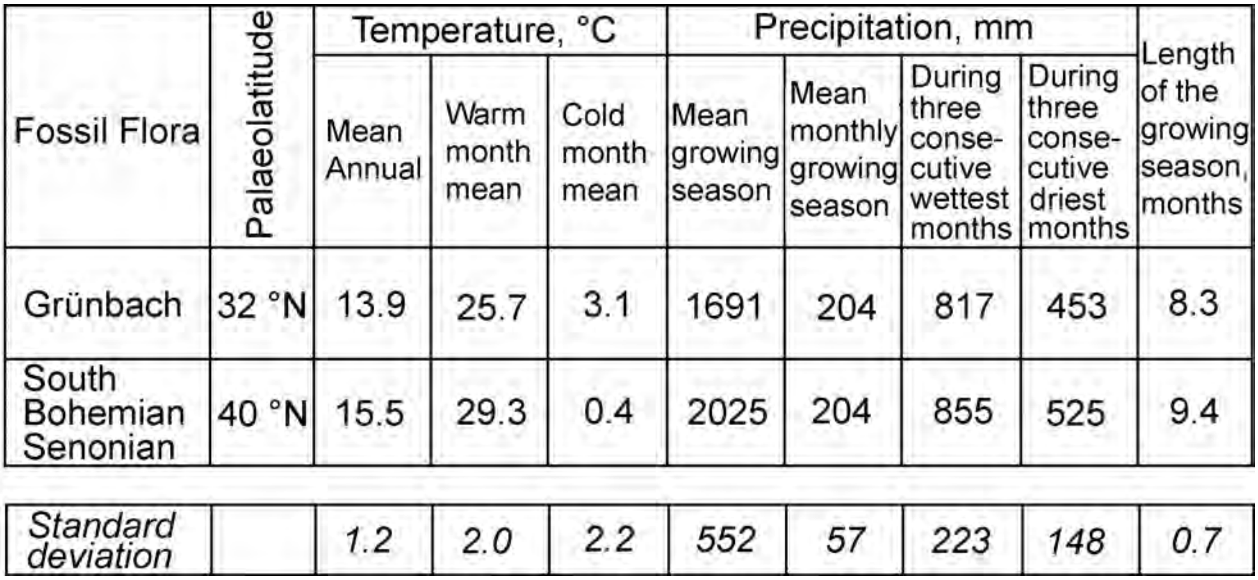
Leaf base (is preserved in 23 morphotypes): cordate – 21.7 %; round – 15.2 %; acute – 63.0 %.

Leaf length to with ratio (is preserved in 21 morphotypes): less than 1:1 – 7.1 %; 1:1 to 2:1 – 25.4 %; 2:1 to 3:1 – 18.2 %; 3:1 to 4:1 – 11.1 %; more than 4:1 – 38.1 %.

Leaf shape (is preserved in 25 morphotypes): obovate – 10 %; elliptic – 74 %; ovate – 16 %.

CLAMP analysis of the Grünbach Flora yielded (Table) a MAT of 13.9°C, a WMMT of 25.7°C, a CMMT well above freezing at 3.1°C, a LGS of 8.3 months, a MGSP of 1691 mm, a MMGSP of 204 mm, 3WM of 817 mm and 3DRIM of 453 mm (Herman & J. Kvaček, 2007). Therefore, it can be concluded from LMA and CLAMP (which give similar estimates of the mean annual temperature), that the Grünbach Flora experienced a humid subtropical climate with hot summers and short relatively dry, but not arid, seasons. Here we use the modified Köppen classification of global climates (The Times atlas 1996) defining the humid subtropical climate, or climate Ca, as a “rainy climate with mild winters: coolest month above 0°C (32°F), but below 18°C (64.4°F); warmest month above 22°C (71.6°F)”. NLR analysis of the Grünbach Flora also supports this conclusion.

This is corroborated by lithological climate indicators (bauxites of the Gosau Group: see text-fig. 5) and by the presence of large foraminifers, rudists, corals and a reptile fauna in the Santonian-Campanian of the Neue Welt Basin (Summesberger 1997) together with finds of *Neopsaronius* tree fern trunks in the Senonian flysh of Austria (Berger 1966, Vakhrameev 1991). The invertebrate fauna of the Gosau Group belongs to the Tethyan (or Theian: Kollmann 2000) palaeobiogeographic realm (Kauffman 1973, Sohl 1987) which is considered to reflect both tropical and subtropical



Fossil Flora	Palaeolatitude	Temperature, °C			Precipitation, mm				Length of the growing season, months
		Mean Annual	Warm month mean	Cold month mean	Mean growing season	Mean monthly growing season	During three conse-cutive wettest months	During three conse-cutive driest months	
Grünbach	32 °N	13.9	25.7	3.1	1691	204	817	453	8.3
South Bohemian Senonian	40 °N	15.5	29.3	0.4	2025	204	855	525	9.4
Standard deviation		*1.2*	*2.0*	*2.2*	*552*	*57*	*223*	*148*	*0.7*

Table 1. Estimated climate data for the Senonian (Santonian – Campanian) floras of Grünbach and South Bohemia (modified from Herman, 2004b).

climates. The suggested high humidity of the climate experienced by the Grünbach Flora is corroborated by the extensive coal accumulation in the Grünbach Formation and by the lack of sclerophyllous plants in this flora.

The Grünbach Flora includes pandans (*Pandanites*), palms (*Sabalites*) and numerous angiosperms with narrow entire-margined leaves (*Dicotylophyllum proteoides*, *Dicotylophyllum* sp. 7), which, according to Vakhrameev (1991), can be interpreted as a flora typical of the Euro-Sinian phytogeographic region (see text-fig. 54) characterised by a subtropical climate. The conclusion that the Grünbach Flora experienced a humid subtropical climate is also in a good agreement with geological data on the Campanian climatic belts of the Earth (Chumakov 2004; Herman 2004b) and with Late Cretaceous computer climate modelling using Atmospheric General Circulation model (Valdes et al. 1999; Herman 2004b).

Palaeomagnetic directions from the Gosau K/T boundary beds in the Elendgraben near Salzburg, Austria, indicate a palaeolatitude of 32°N for the Gosau Basin (Preisinger et al. 1986). A recent palaeomagnetic investigation of Grünbach yielded a palaeolatitude approximately 1000 km south of the present day position of its plant-bearing deposits (Summesberger 1997, Scholger pers. comm. 2001). To check this hypothesis we compared results for the Grünbach palaeoclimate with those obtained from CLAMP analysis of the Senonian flora of Zliv, Klikov and Hluboká in the South Bohemia (Czech Republic) (Němejc 1957, 1961; Knobloch 1964; Němejc & Kvaček 1975).

Despite some differences in taxonomic composition and angiosperm leaf physiognomy between these two floras, almost identical palaeoclimatic results were obtained, both for palaeotemperatures and precipitation (Table). All differences in the estimates are within the possible error of the method. Therefore, our CLAMP results do not support the hypothesis that the Grünbach Flora existed 1000 km south of the present day position of the Neue Welt Basin. However, our data cannot be used as an argument against this hypothesis, because both the Czech Senonian and the Grünbach floras reflect the climates of two relatively small islands (or sometimes peninsulas) the climates of which were considerably influenced by the warm Tethys Ocean. Moreover, it cannot be assumed that these floras are of the same age; the Grünbach Flora may reflect a relatively cooler time interval within the Senonian and could therefore have occupied a more southerly position, despite the similarity in temperatures.

Conclusions

The Grünbach Flora comes from the Grünbach Formation forming part of the Gosau Group in the Grünbach – Neue Welt Basin in the Eastern Calcareous Alps, Lower Austria. Although collected since the early 19th century, the Grünbach Flora had never been studied monographically and was in need of revision. The Early Campanian age of this flora is based on foraminifers, spores and pollen from the Grünbach Formation and on the correlation of these deposits with the underlying Maiersdorf and the overlying Piesting formations which contain stratigraphically important marine fossils.

The Grünbach Flora comprises 53 macrofossil species, representing Equisetopsida (1 species belonging to *Equisetites* Sternberg), Polypodiopsida (11 species belonging to genera *Cladophlebis* Brongniart, *Coniopteris* Brongniart, *Gosauopteris* J. Kvaček & Herman, nov. gen., *Marsileaceaephyllum* Nagalingum, *Microtaenia* Knowlton, *Monheimia* Debey & Ettingshausen, *Raphaelia* Debey & Ettingshausen and *Sphenopteris* (Brongniart) Sternberg), Cycadopsida (1 species belonging to *Nilsonia* Brongniart), Pinopsida (4 species belonging to *Podozamites* C. Braun in Münster, *Geinitzia* Endlicher and *Pagiophyllum* Heer), Liliopsida (6 species belonging to *Lysichiton* Schott, *Pandanites* Tuszon, *Gruenbachia* J. Kvaček & Herman, nov. gen., *Sabalites* Saporta, *Theiaiphyllum* Herman & J. Kvaček, nov. gen., and Monocotyledon gen. & sp. indet.), and Magnoliopsida (30 species belonging to genera *Brasenites* Wang & Dilcher, *Celastrophyllum* Goeppert, *Compositiphyllum* Herman & J. Kvaček, *Debeya* Miquel, *Ettingshausenia* Stiehler, *Grebenkia* Lebedev, *Juglandiphyllites* Boulter & Z. Kvaček, *Leguminosites* Bowerbank, *Menispermites* Lesquereux, *Myricophyllum* Saporta, *Quereuxia* Kryshtofovich, *Rogersia* Fontaine, *Ternstroemites* E.W. Berry, *Viburniphyllum* Nathorst, *Dicotylophyllum* Saporta, *Ceratoxylon* Velenovský & Viniklář). Within the fossil flora of Grünbach, four genera (*Gosauopteris*, *Gruenbachia*, *Theiaiphyllum* and *Compositiphyllum*) and 27 species are new.

Spores and pollen from the Grünbach Formation at Grünbach were studied by Dŕaxler (in Summesberger 1997) and Svobodová (Hradecká et al. 2000). The most characteristic feature of the palynoflora is pollen from the "*Normapolles*" group.

The Grünbach Flora represents one of the few known Late Cretaceous mire floras in the Northern Hemisphere. Due to the palaeoecological conditions, which indicate a peaty swamp habitat, the Grünbach Flora represents a unique case with few counterparts in the Late Cretaceous. Although there is no direct equivalent to the Grünbach Flora, the floras that most resemble it in terms of plant content are from the Maastrichtian of Romania, the Maastrichtian of Spain, the Senonian and the Cenomanian of the Czech Republic. The Grünbach Flora includes pandans, palms and numerous angiosperms with narrow entire-margined leaves which, according to Vakhrameev (1991), can be interpreted as a flora typical of the Euro-Sinian phytogeographic region. The Grünbach Flora also belongs to the Southern Laurasian Province (Batten 1984; Crane 1987) and to the *Normapolles* Province (Herngreen & Chlonova 1981). The presence of relict plants in the Grünbach Flora (*Nilsonia*, *Podozamites*) probably reflects the existence of the flora in an ‚island refuge'.

The following plant communities comprising the Grünbach Flora were reconstructed on the basis of plant morphology, anatomy, the autecology of some taxa and taphonomic observations: aquatic, swamp/semiaquatic, juglandaceous and palm wetland, riparian and mesophytic forest. The dominating palaeogeographic environment during the accumulation of the Grünbach Formation is that of a large island, temporarily connected to the continent. In the coastal lowlands and plains of the island, large open bodies of shallow fresh water (ponds and oxbow lakes) with floating dicots were surrounded by swampy lowlands inhabited by a community dominated by pandans and ferns with palm hammocks. A wetland juglandaceous forest with palms and evergreen conifers was developed along the shores of the lakes and swamps. Small rivers or streams may have crossed this lowland, their margins populated by a riparian plant community composed mainly of *Sphenopteris* ferns, and shrubs or trees of platanoid angiosperms. At a distance from the lakes, swamps and rivers mesophytic predominantly coniferous forest prevailed.

Palaeoclimatic analysis of the Grünbach Flora using the nearest living relative (NLR), leaf margin analysis (LMA) and Climate Leaf Analysis Multivariate Program (CLAMP) approaches allows us to reconstruct both qualitative and quantitative palaeoclimatic parameters experienced by the flora (Herman & J. Kvaček, 2007). It can be concluded from the NLR approach (using palms Arecaceae: *Sabalites*, pandans Pandanaceae: *Pandanites* and ferns probably belonging to the families Schizeaceae: spores *Leiotriletes* sp., *Appendicisporites tricuspidatus*, *Cicatricosisporites* sp. and Matoniaceae: *Monheimia* with *Matonisporites* spores preserved *in situ*), LMA (13 dicot species, or 48 %, have leaves or leaflets with entire margins) and CLAMP that the Grünbach Flora experienced a humid subtropical frost-free climate with hot summers and short relatively dry, but not arid, seasons. Physiognomic analysis of the Grünbach Flora using the CLAMP technique yielded a mean annual temperature of 13.9°C (16°C using LMA), a warm month mean temperature of 25.7°C, a cold month mean temperature well above freezing at 3.1°C, a growing season length of 8.3 months, a mean growing season precipitation of 1691 mm, a mean monthly growing season precipitation of 204 mm, precipitation during the three consecutive wettest months of 817 mm and precipitation during the three consecutive driest months of 453 mm. The Grünbach Flora can be interpreted as a flora typical of the Euro-Sinian phytogeographic region characterised by a subtropical climate. Our CLAMP results do not support the previously held hypothesis that the Grünbach Flora existed 1000 km south of the present day position of the Neue Welt Basin.

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Plates

Plate I

Figs 1-4: *Gosauopteris danaeoides* J. Kvaček & Herman, gen. & sp. nov., Grünbach am Schneeberg.

1 = holotype, NHMW 1999B0057/0469a, x 1.1, leaf fragment showing long petiole
2 = NHMW 1999B0057/0466, x 2.1, detail of venation
3 = NHMW 1999B0057/0253, x 1.5, detail of venation
4 = NHMW 1999B0057/0472, x 1.2
5 = NHMW 1999B0057/0253, x 0.8, three leaf fragments, one of which showing attenuate apex
6 = NHMW 1999B0057/0584b, x 0.8
7 = detail of venation NHMW1999B0057/0095, x 1.3
8 = NHMW 1999B0057/0582, x 0.9

Figs 9, 10: *Equisetites* sp., Grünbach am Schneeberg.

9 = NHMW 1999B0057/0252, x 0.4, node arrowed
10 = NHMW 1999B0057/0252, x 0.7, detail

Fig. 11-15: *Monheimia ungeri* J. Kvaček & Herman, sp. nov., - vegetative parts of frond, Grünbach am Schneeberg.
11 = NHMW 1999B0057/0454, x 3
12 = NHMW 1999B0057/0565, x 1.4
13 = NHMW 1999B0057/0449, x 2.5
14 = NHMW 1999B0057/0561, x 1.3
15 = NHMW 1999B0057/0565, x 1.9


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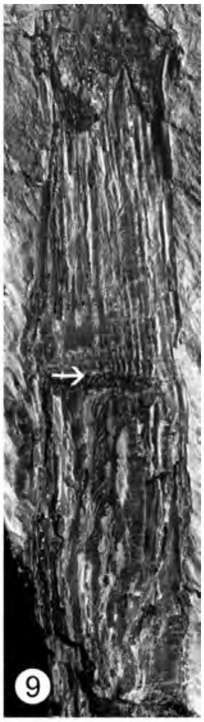
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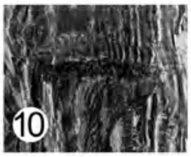
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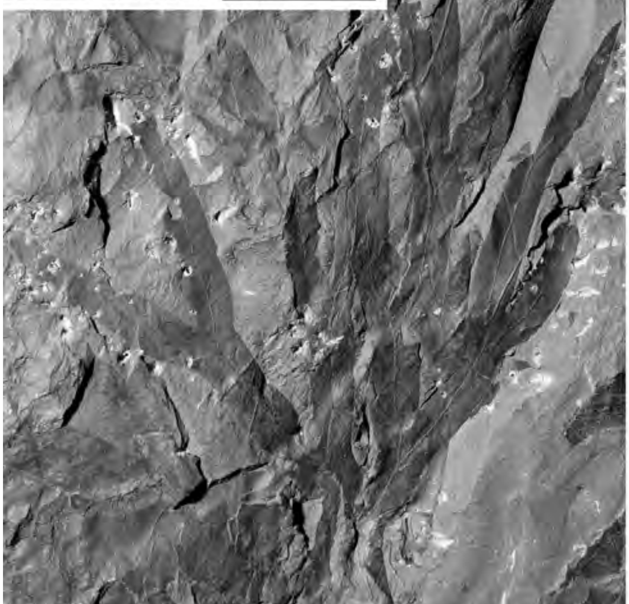
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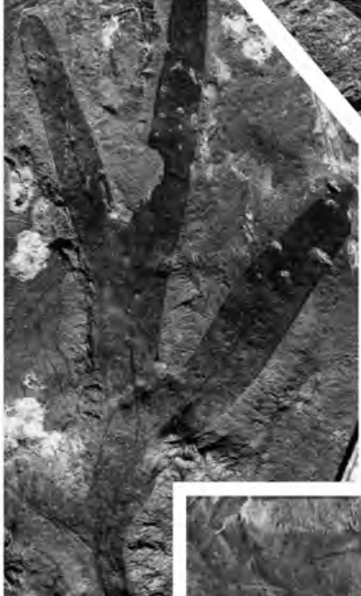
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Plate I

Plate 2

Figs 1-6: *Monheimia ungeri* J. Kvaček & Herman, nov. spec., Grünbach am Schneeberg.

1 = holotype, NHMW 1999B0057/0564, x 1.5, frond with vegetative and reproductive parts
2 = holotype, NHMW 1999B0057/0564, x 3.9, detail of reproductive part of frond showing rows of sori
3 = holotype, NHMW 1999B0057/0564, x 3.4, detail
4 = holotype, NHMW 1999B0057/0564, x 2.4, reproductive part of the frond
5 = holotype, NHMW 1970B1396-1644, x 0.9, counterpart of Fig. 1
6 = NHMW 1999B0057/0249, x 2.5, part of a frond with venation

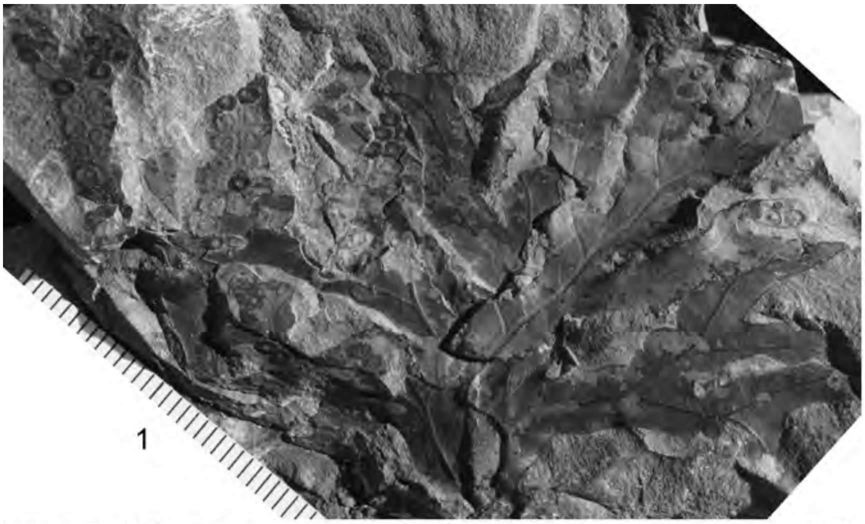
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Plate 2

Plate 3

Figs 1-10: *Monheimia ungeri* J. Kvaček & Herman, nov. spec. – holotype, Grünbach am Schneeberg.

1 = NHMW 1999B0057/0564, x 105 macerated wedge-shaped sporangium showing mass of spores
2 = NHMW 1999B0057/0564, x 180 tetrade of spores
3 = NHMW 1999B0057/0564, *Matonisporites* spore, x 550
4 = NHMW 1999B0057/0564, *Matonisporites* spore, x 550
5 = NHMW 1999B0057/0564, sorus with radial striation, x 16
6 = NHMW 1999B0057/0564, detail of Plate 2, fig. 4, row of sori, x 14.3
7 = NHMW 1999B0057/0564, broken tetrade of spores, SEM
8 = NHMW 1999B0057/0564, *Matonisporites* spore, SEM
9 = NHMW 1999B0057/0564, ventral view of sorus, SEM
10 = NHMW 1999B0057/0564, *Matonisporites* spore, SEM

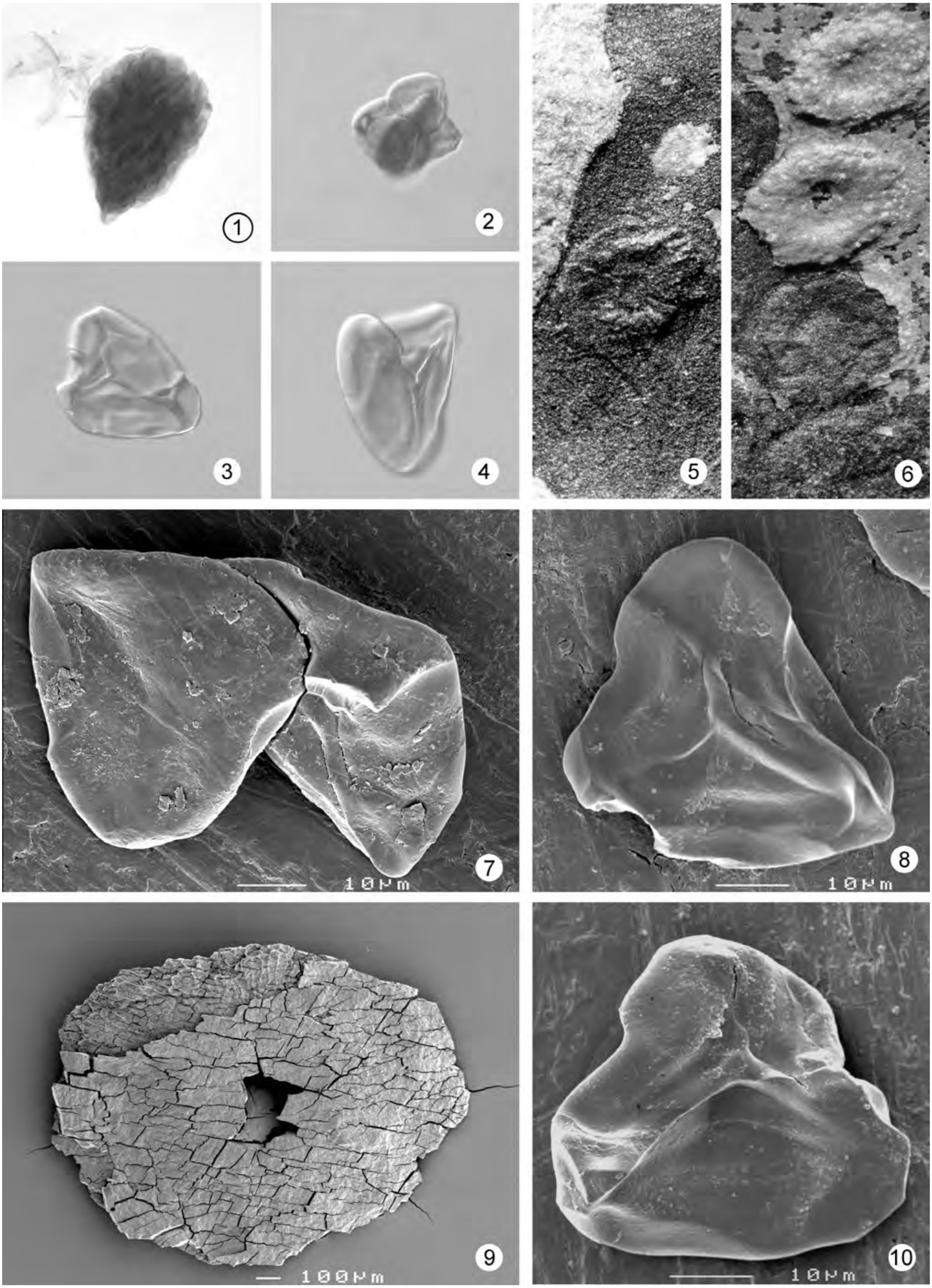


Plate 3

Plate 4

Figs 1-8: *Microphyllopteris austriaca* J. Kvaček & Herman, nov. spec., Grünbach am Schneeberg.

1 = holotype, NHMW 1999B0057/0559, x 0.8
2 = holotype, NHMW 1999B0057/0559, x 2.1, detail
3 = holotype, NHMW 1999B0057/0559, x 4.6, detail showing venation
4 = NHMW 1999B0057/0595, x 1.4
5 = NHMW 1999B0057/0406, x 3.6, frond with circinate vernation of juvenile pinnules
6 = NHMW 1999B0057/0409, x 2.7
7 = NHMW 1999B0057/0589, x 0.7
8 = NHMW 1999B0057/0438, x 1.6, apical part of frond

Figs 9-10: *Sphenopteris* sp. - frond fragment, Grünbach am Schneeberg.

9 = NHMW 1999B0057/0356a, x 0.6
10 = NHMW 1999B0057/0356a, x 2.1

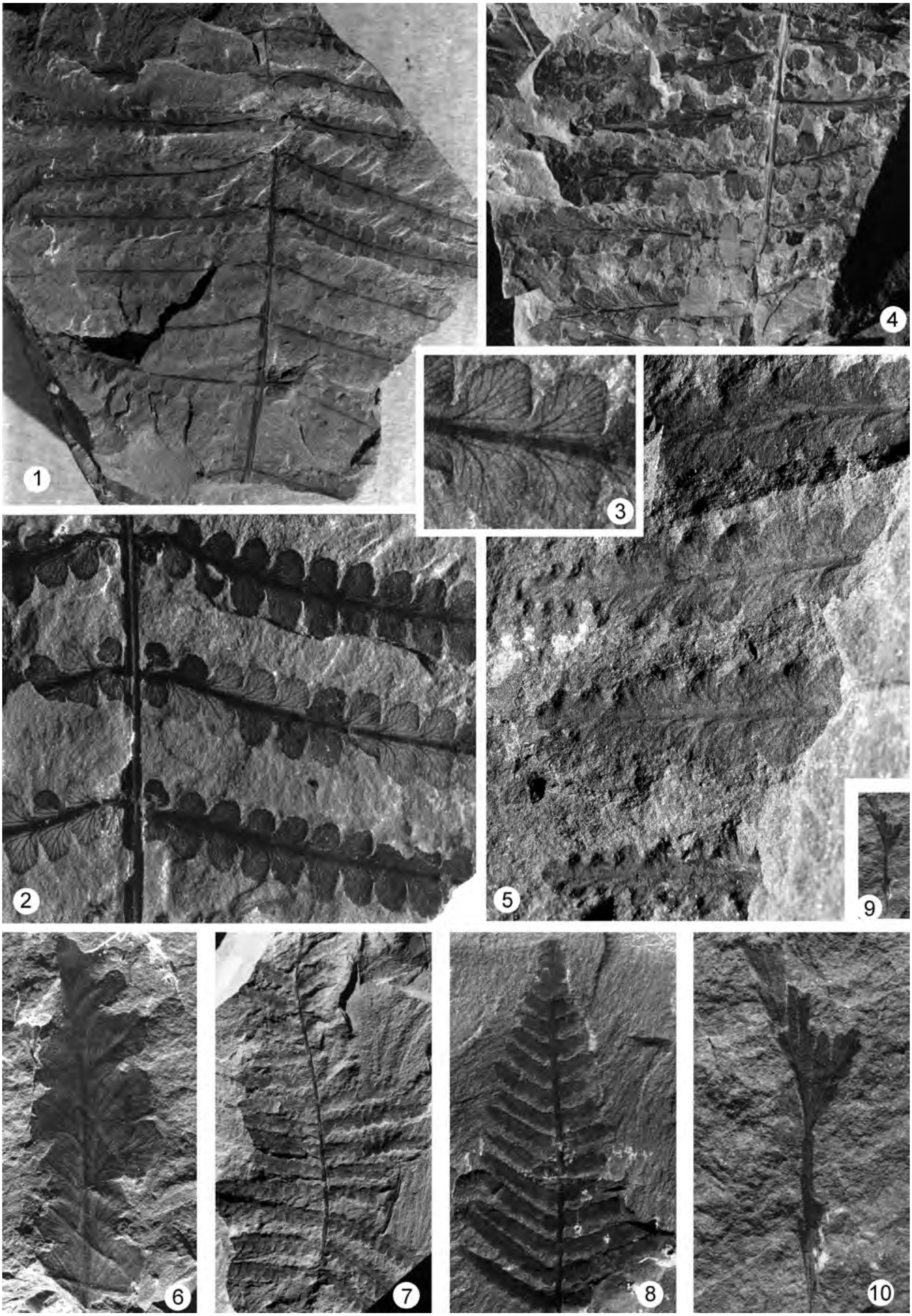


Plate 4

Plate 5

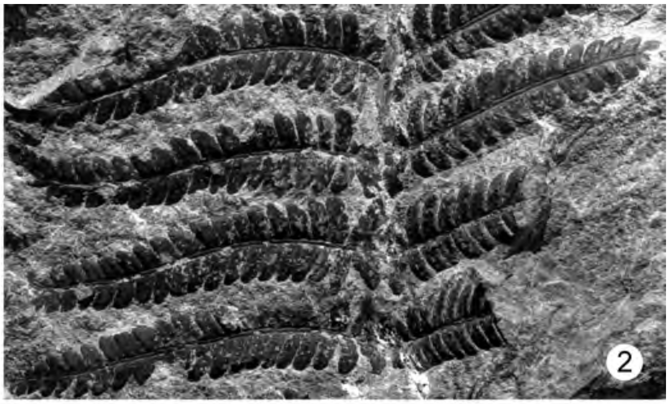
Figs 1-6: *Cladophlebis gosauensis* J. Kvaček & Herman, nov. spec., Grünbach am Schneeberg.

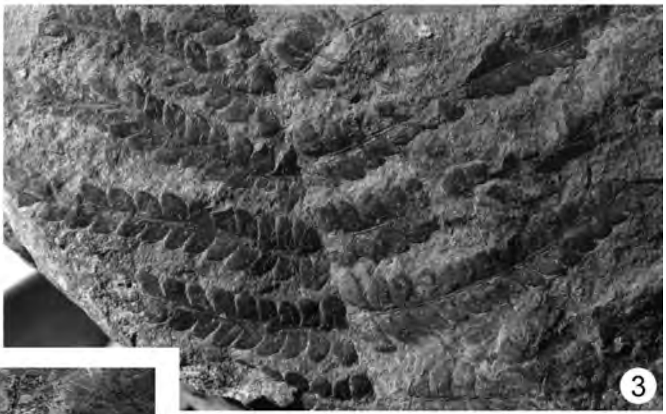
1 = holotype, NHMW 1999B0057/0560, x 0.5
2 = holotype, NHMW 1999B0057/0560, x 1.2, detail
3 = NHMW 1999B0057/0441, x 1.2
4 = NHMW 1999B0057/0446, x 2.3
5 = NHMW 1999B0057/0444a, x 1.4
6 = NHMW 1999B0057/0441, x 2.0

Figs 7-9: *Sphenopteris heterophylla* (Unger) J. Kvaček & Herman, comb. nov., Muthmannsdorf.

7 = GBA 2006/60/79, x 0.8
8 = GBA 2006/60/79, x 0.9
9 = GBA 2006/60/79, x 1.6

Fig. 10: *Gosauopteris danaeoides* J. Kvaček & Herman, nov. gen. et nov. spec.,
Grünbach am Schneeberg. NHMW 1999B0057/0583, x 1.0





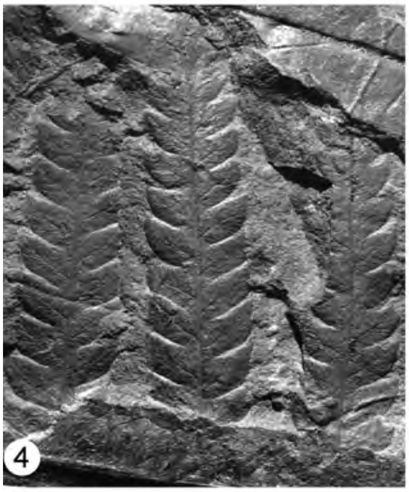


Plate 5

Plate 6

Figs 1-10: *Sphenopteris gruenbachiana* J. Kvaček & Herman, nov. spec., Grünbach am Schneeberg.

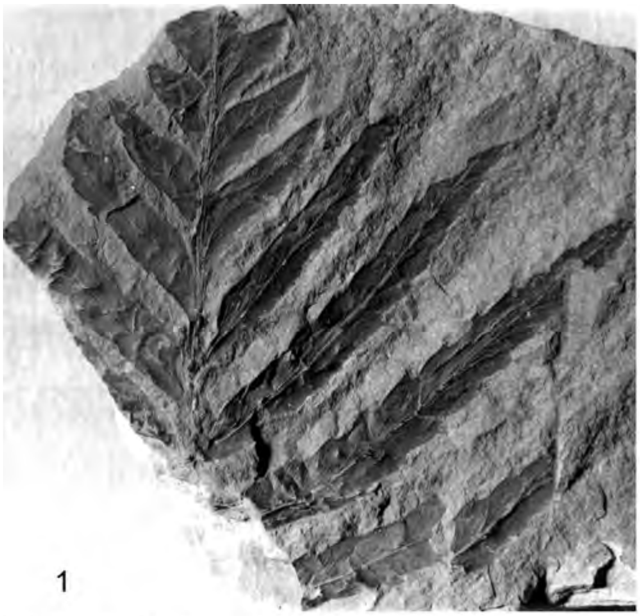
1 = NHMW 1999B0057/0238, x 0.7
2 = GBA 2006/64/07, x 1.1
3 = NHMW 1999B0057/0390, x 2.5
4 = NHMW 1999B0057/0397, x 1.8
5 = holotype, NHMW 1999B0057/0586, x 1.1
6 = holotype, NHMW 1999B0057/0586, x 2.0
7 = NHMW 1999B0057/0585, x 1.2
8 = NHMW 1999B0057/0550, x 0.9
9 = NHMW 1999B0057/0552, x 1.5
10 = NHMW 1999B0057/1628, x 2.0

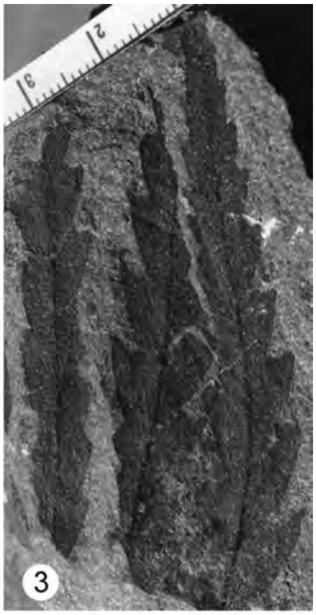
Plate 6

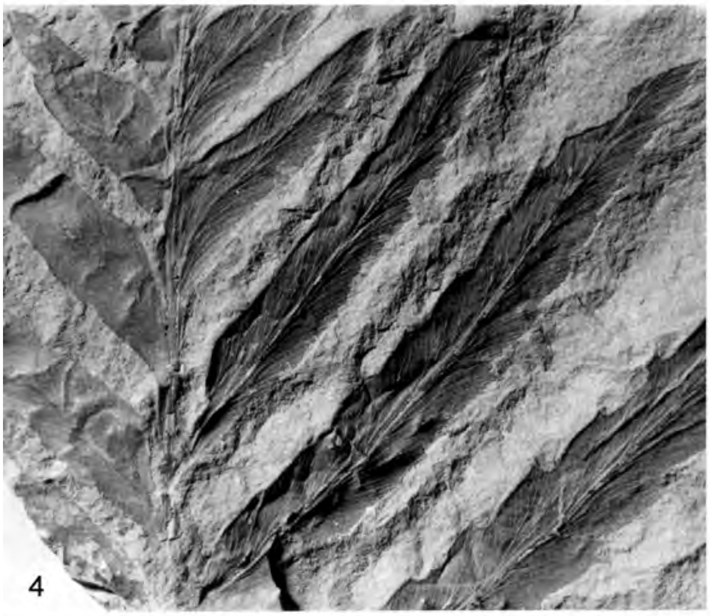
Plate 7

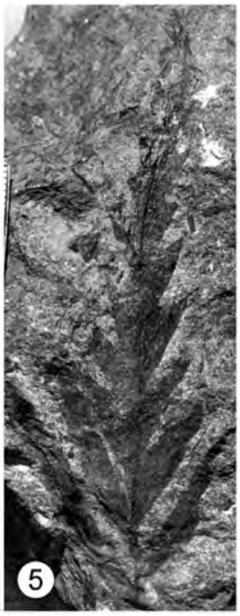
Figs 1-8: *Sphenopteris ungeri* J. Kvaček & Herman, nov. spec., Grünbach am Schneeberg.

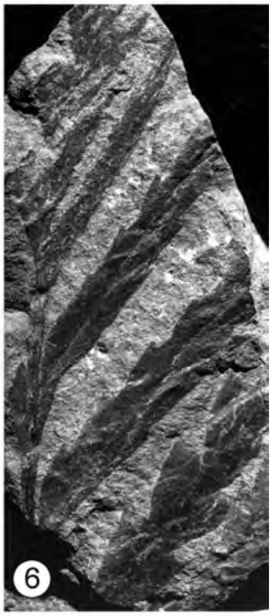
1 = GBA 2006/64/39, x 1.2
2 = holotype, NHMW 1999B0057/0517, x 2.7, detail of Fig. 7 showing leaf margin and venation
3 = NHMW 1999B0057/0522, x 1.2
4 = GBA 2006/64/39, x 2.1, detail of Fig. 1 showing leaf margin and venation
5 = NHMW 1999B0057/0522, x 0.9
6 = NHMW 1999B0057/0568, x 1.1
7 = holotype, NHMW 1999B0057/0517, x 1.5











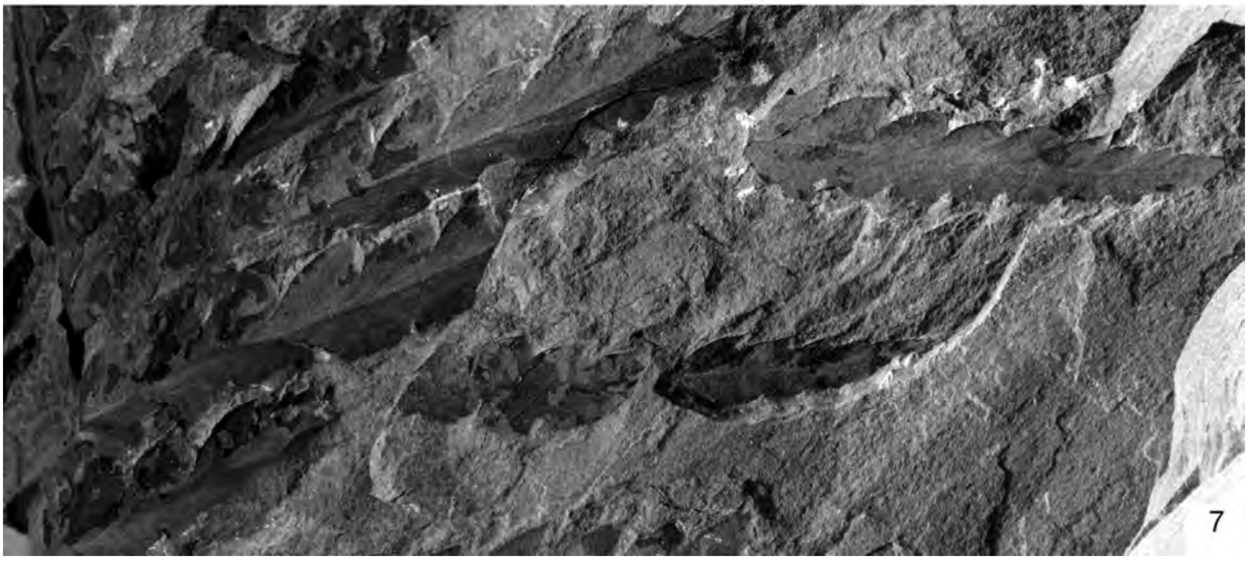


Plate 7

Plate 8

Figs 1-7: *Marsileaephyllum campanicum* J. Kvaček & Herman, sp. nov., Grünbach am Schneeberg.

1 = NHMW 1999B0057/0605, x 1.1
2 = holotype, NHMW 1999B0057/0509a, x 1.2, four leaves forming a rosette
3 = NHMW 1999B0057/0606, x 1.6, four leaves forming a rosette
4 = NHMW 1999B0057/0250, x 0.9
5 = NHMW 1999B0057/0448a, x 1.5
6 = NHMW 1999B0057/0509, x 1.8
7 = NHMW 1999B0057/0265, x 0.9

Figs 8-11: *Raphaelia lobifolia* (Corda in Reuss) Knobloch, Grünbach am Schneeberg.

8 = NHMW 1999B0057/0562, x 1.8
9 = NHMW 1999B0057/0603, x 1.4
10 = NHMW 1999B0057/0456, x 2.4
11 = NHMW 1999B0057/0562, x 2.7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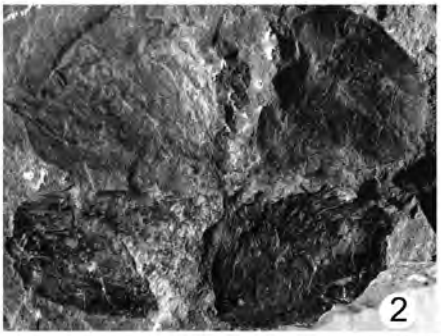
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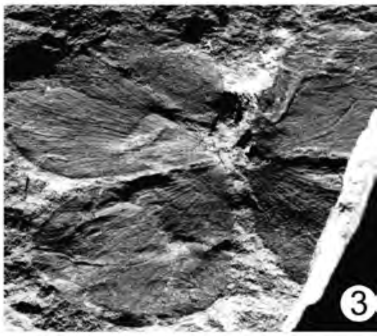
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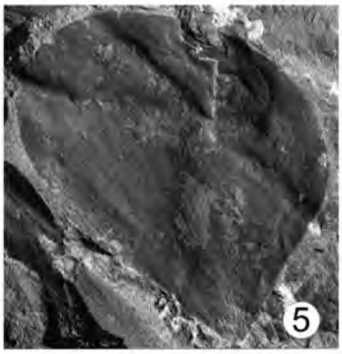
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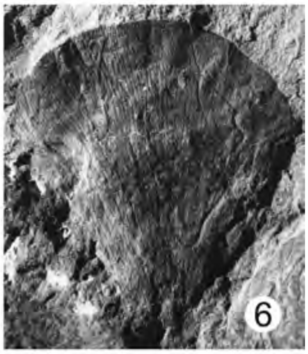
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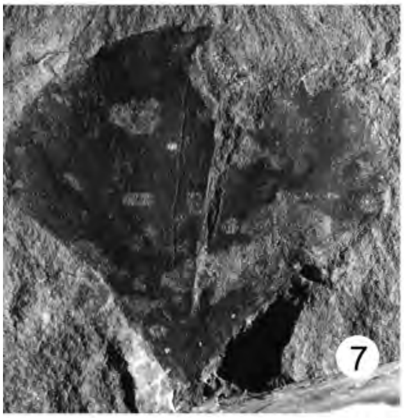
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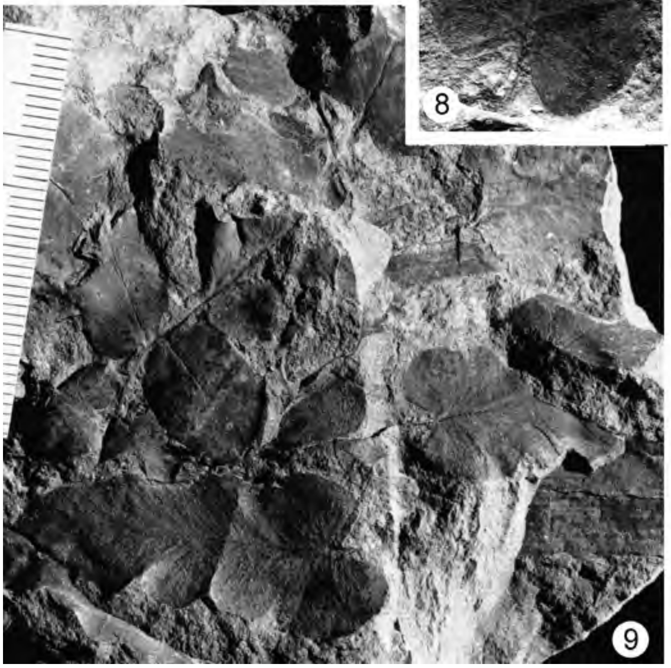
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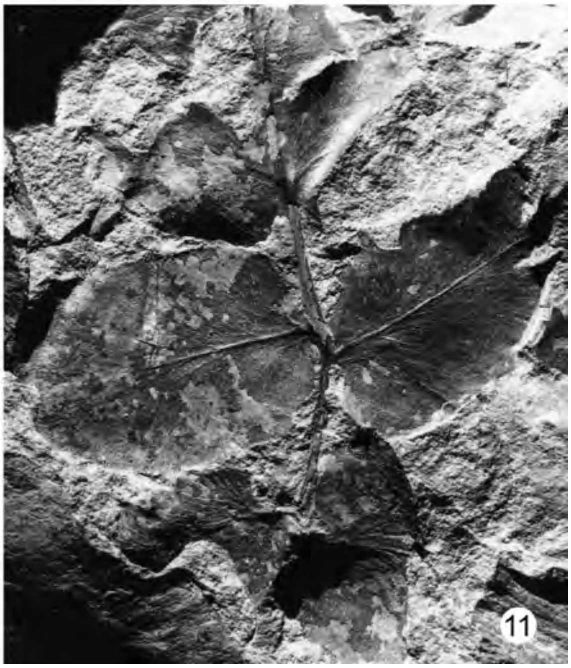
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Plate 8

Plate 9

Figs 1-3: *Raphaelia lobifolia* (Corda in Reuss) Knobloch, Grünbach am Schneeberg.

1 = NHMW 1999B0057/0603, x 2.4
2 = NHMW 1999B0057/0457, x 3.4
3 = NHMW 1999B0057/1795, x 2

Figs 4-6: *Coniopteris* sp., Grünbach am Schneeberg.-

4 = NHMW 1970B01396/1563, x 1.2
5 = NHMW 1970B01396/1563, x 3
6 = NHMW 1970B01396/1563, x 20

Figs 7-8: *Nilsonia* cf. *holyi* J. Kvaček, Grünbach am Schneeberg.

7 = NHMW 1999B0057/0079, x 1
8 = NHMW 1999B0057/0079, x 4.7, detail of leaf margin and venation

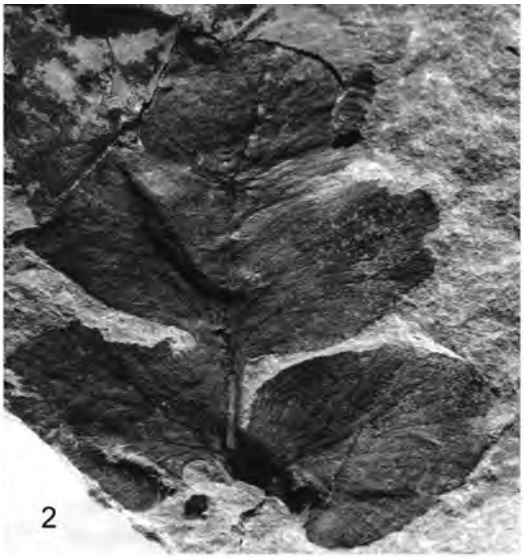


Plate 9

Plate 10

Figs 1-2: *Podozamites* cf. *lanceolatus* (Lindley & Hutton) Harris, Grünbach am Schneeberg.

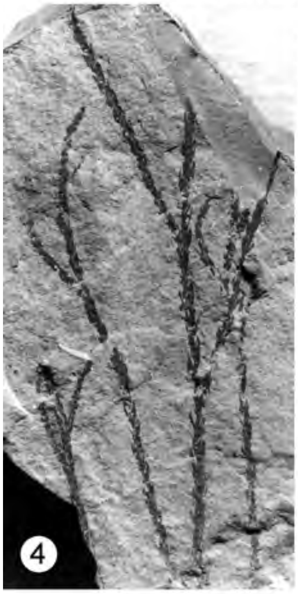
1 = NHMW 1999B0057/0246, x 1.2
2 = NHMW 1999B0057/0246, x 1.8, detail

Figs 3-5: *Pagiophyllum* sp., Grünbach am Schneeberg.

3 = GBA 2006/64/42, x 2.7, detail of Fig. 4 showing scale-like leaves
4 = GBA 2006/64/42, x 1.3
5 = unnumbered specimen in University of Vienna, x 1.3

Figs 6-10: *Geinitzia reichenbachii* (Geinitz) Hollick & Jeffrey.

6 = NHMW 1970B1396-1800, x 0.9
7 = unnumbered specimen in University of Vienna, x 0.7
8 = NHMW 1999B0057/0221, x 1.1
9 = NHMW 1999B0057/0217b, x 2.1, Grünbach am Schneeberg
10 = GBA 2006/68/03, x 1.2, Frankenhof, Neue Welt



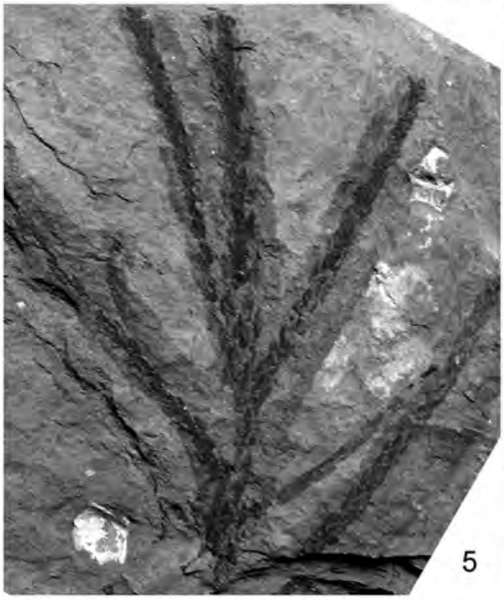
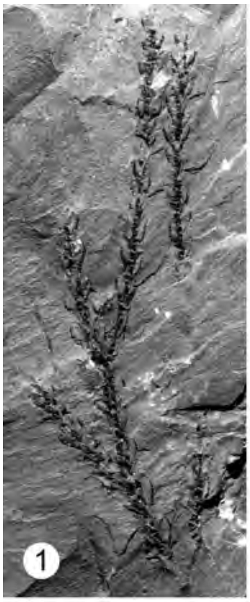


Plate 10

Plate 11

Figs 1-12: *Geinitzia formosa* Heer, Grünbach am Schneeberg.

1 = NHMW 1999B0057/0577, x 1.4
2 = NHMW 1999B0057/0547, x 1.4
3 = NHMW 1970/1396/1660, x 1.8
4 = NHMW 1970/1396/1660, x 2.7, detail of Fig. 3
5 = NHMW 1999B0057/0563a, x 0.5
6 = NHMW 1999B0057/0576, x 0.6
7 = NHMW 1999B0057/0578, x 0.9, cone attached to a leafy shoot
8 = NHMW 1999B0057/0578, x 1.3, cone, detail of Fig. 7
9 = NHMW 1999B0057/0212b, x 1.8, cone
10 = NHMW 1999B0057/0575, x 1.4, cone
11 = NHMW 1999B0057/0575, x 2.3, detail of Fig. 10
12 = NHMW 1999B0057/0575, x 4.6, detail of Fig. 10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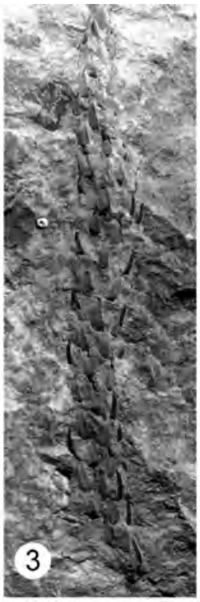
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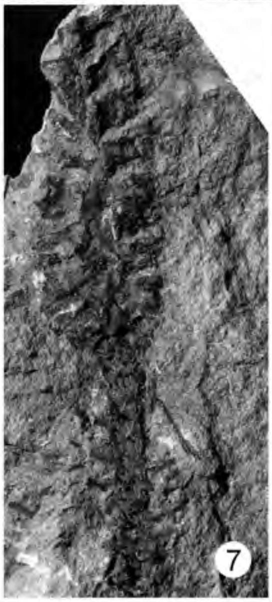
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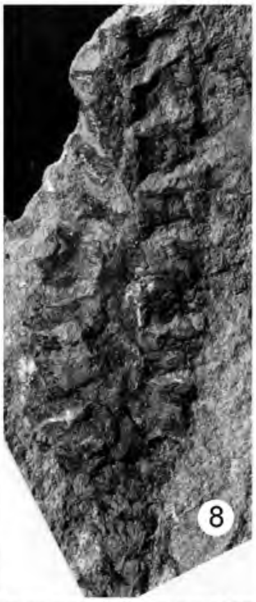
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12

Plate 11

Plate 12

Figs 1-2, 4: *Lysichiton austriacus* (J. Kvaček & Herman) Bogner et al., Grünbach am Schneeberg.

1 = holotype, NHMW 1999B0057/0183, x 3.6, detail of venation, note
multistranded costa on right and sharp angle of outgoing veins
2 = holotype, NHMW 1999B0057/0183, x 0.7
4 = holotype, NHMW 1999B0057/0183, x 5.5, venation with areoles

Figs 3, 5: *Lysichiton americanus* Hultén & H. St. John, Recent plant, portion of leaf in translucent light.

3 = veins near costa, x 3.6
5 = detail of venation with alveoles, x 5.5


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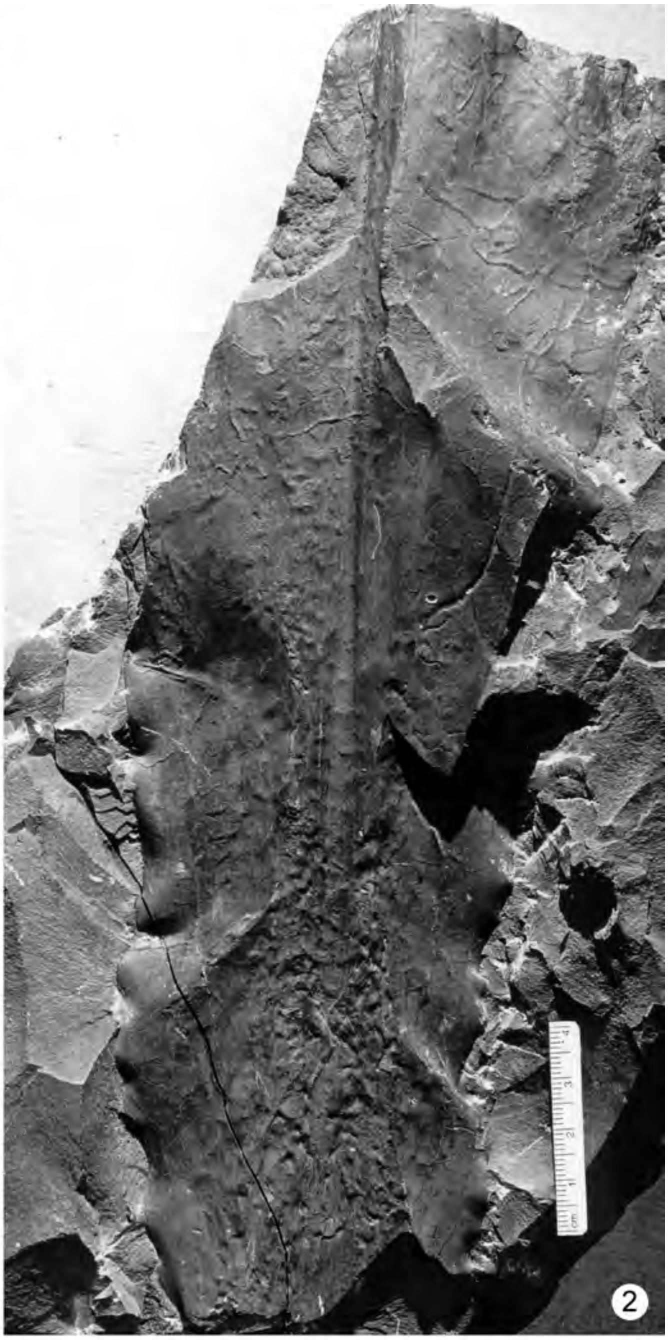

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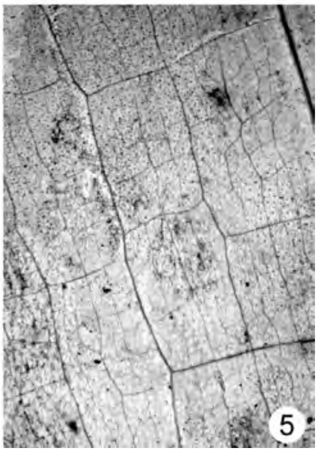
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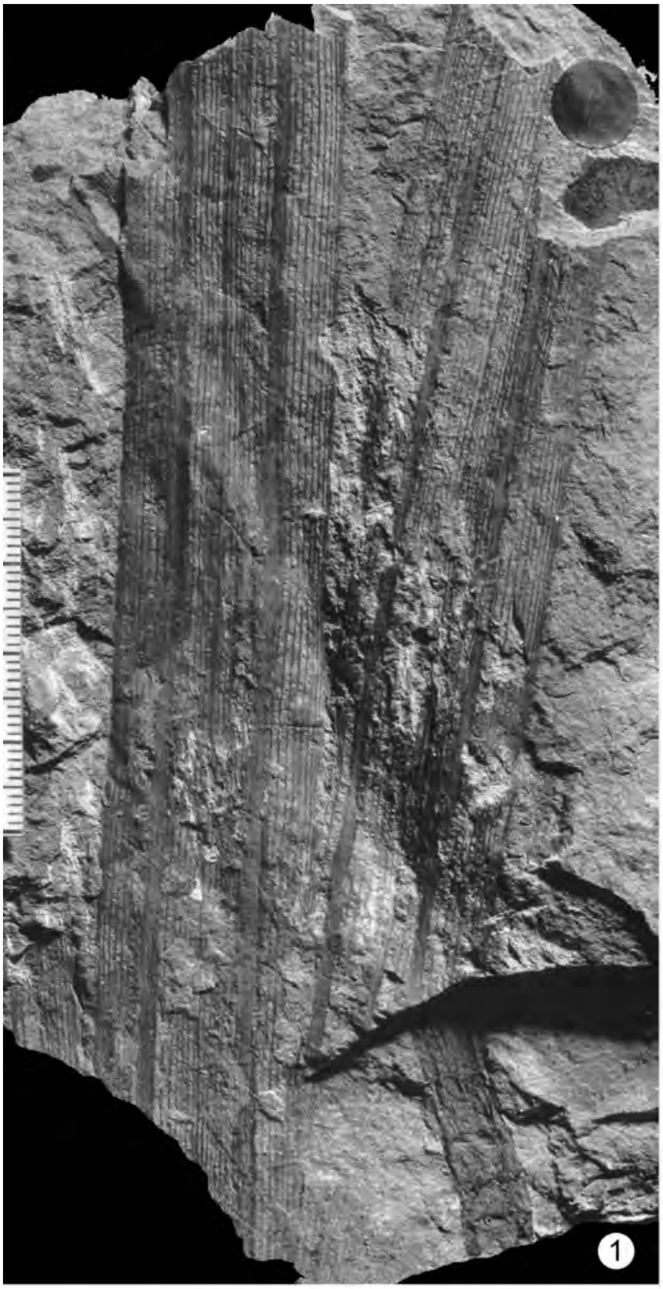
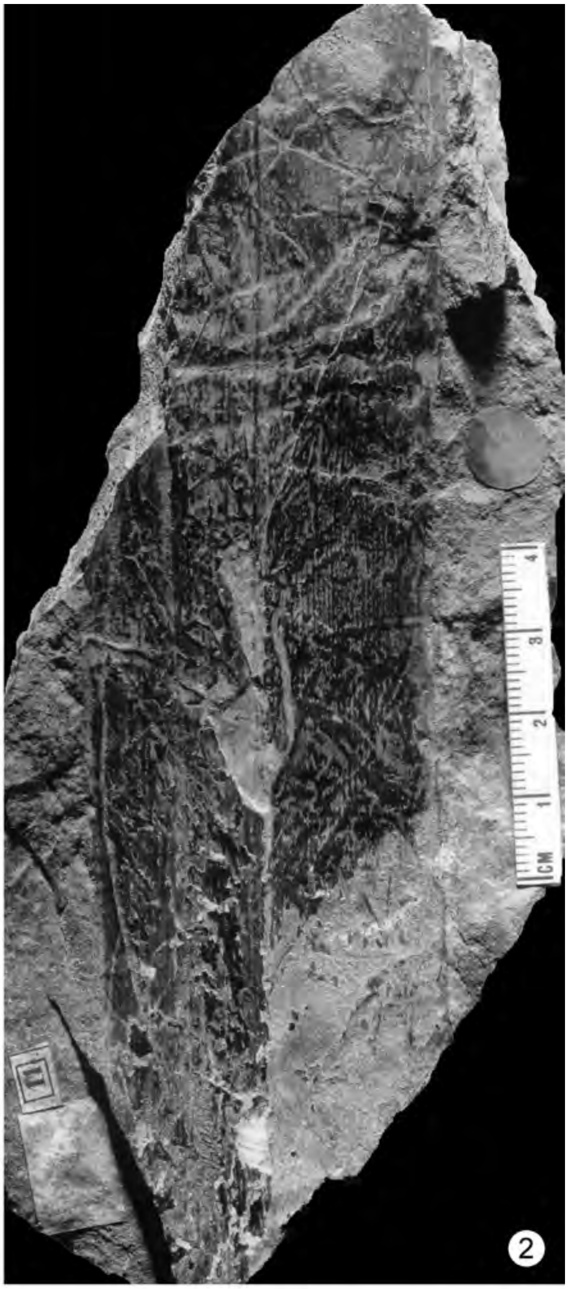
Plate 12

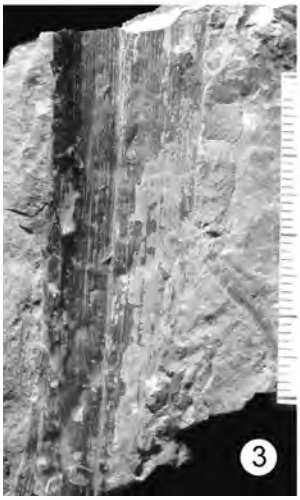
Plate 13

Figs 1-4: *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, Grünbach am Schneeberg.

1 = holotype, Ettingshausen, 1852, pl. 26 (IV), fig. 1, GBA 1852/02/01, x 1.2
2 = syntype of *Pandanus pseudo-inermis* Ettingshausen, 1852, pl. 25 (II), fig. 1, GBA 1852/02/02, x 1.1
3 = syntype of *Pandanus pseudo-inermis* Ettingshausen, 1852, pl. 24 (II), fig. 2, GBA 1852/02/03, x 1.1
4 = holotype, GBA 1852/02/01, x 4.4, detail of venation







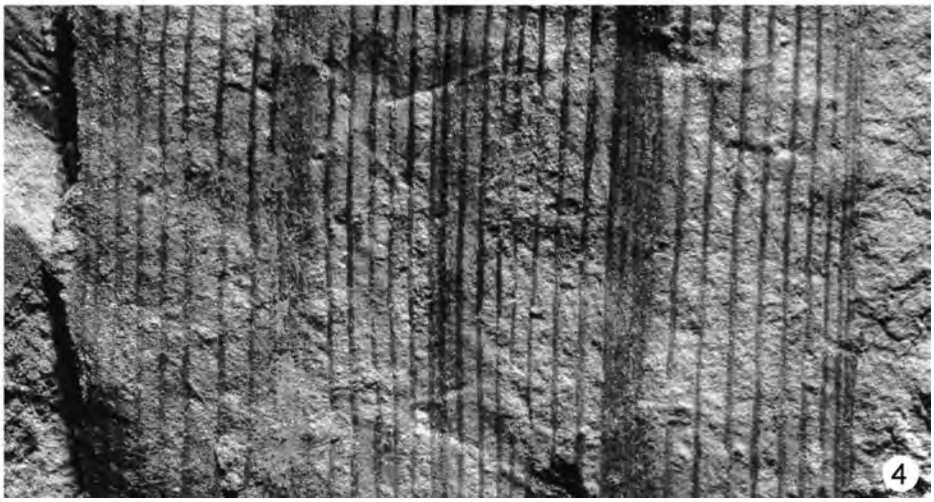


Plate 13

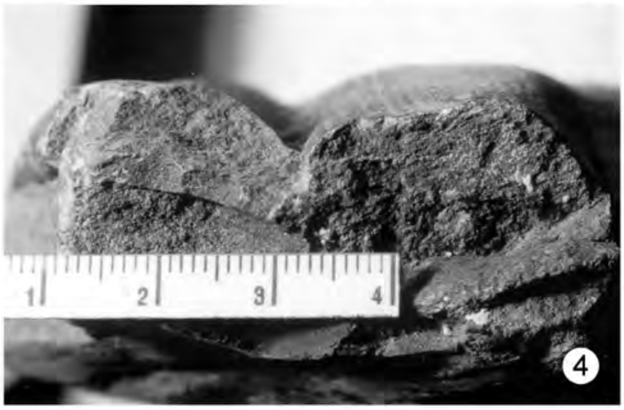
Plate 14

Figs 1-5: *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, Grünbach am Schneeberg.

1 = NHMW 1999B0057/0239, x 0.6, the longest leaf fragment armed with infrequent spines
2 = NHMW 1999B0057/0584a, x 0.7, attenuate leaf apex
3 = NHMW 1999B0057/0102a, x 3.6, M-shaped transversal section of leaf
4 = GBA 2001/06/02, x 1.5, M-shaped transversal section of leaf base
5 = NHMW 1999B0057/0285, x 1.2, auriculate leaf base

Fig. 6: *Pandanus tectorius* Soland ex Parkinson.

6 = NHMW herbarium, x 0.7, auriculate leaf base, modern, Hawaiian Islands.



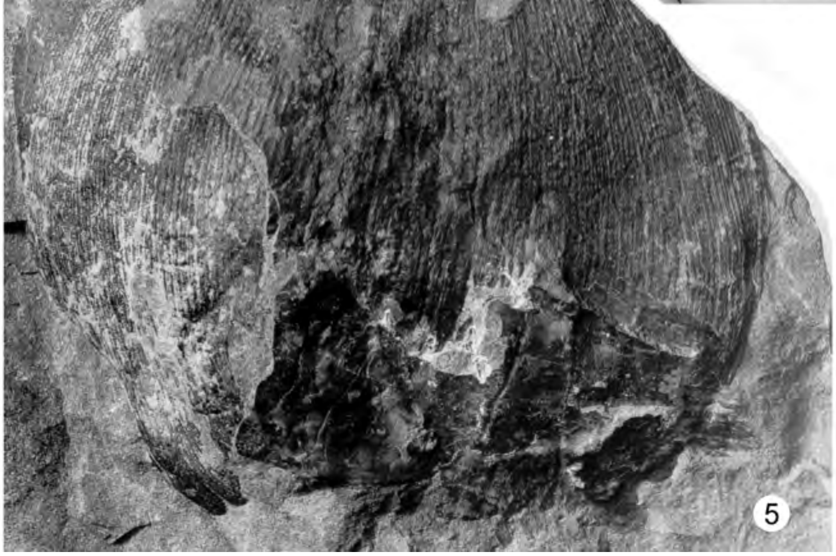


Plate 14

Plate 15

Figs 1-6, 9: *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, Grünbach am Schneeberg.

1 = NHMW 1999B0057/0176, x 1.2, leafy branch with three or more leaves attached
2 = NHMW 1999B0057/0549, x 5.9, spine on abaxial side of midrib
3 = NHMW 1999B0057/0534, x 3.6, large marginal spines
4 = NHMW 1999B0057/0549, x 2.6, delicate marginal spines
5 = NHMW 1999B0057/0541b, x 240, adaxial cuticle, stoma arrowed
6 = NHMW 1999B0057/0541c, x 240, abaxial cuticle, stomata arrowed
9 = NHMW 1999B0057/0541c, x 470, stoma

Figs 7-8: *Pandanus edulis* Thou, Recent.

7 = abaxial cuticle, x 240
8 = stoma, x 470

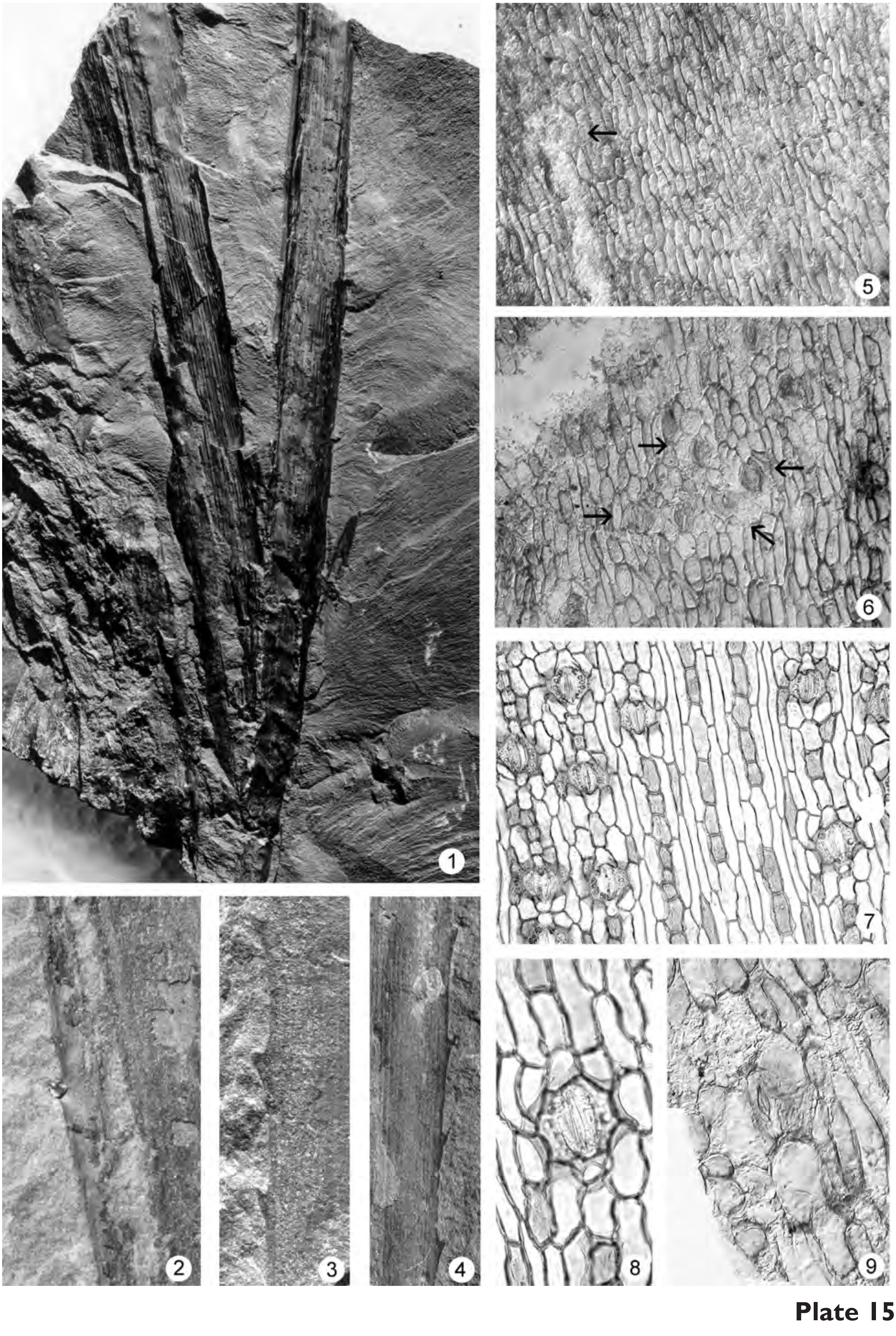


Plate 15

Plate 16

Figs 1-5: *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, Grünbach am Schneeberg.

1 = NHMW 1999B0057/0154, x 0.8, leaf fragment
2 = NHMW 1999B0057/0154, x 2.0, detail of Fig. 1 showing leaf
margin with marginal spines and venation
3 = GBA 2001/006/0004, x 1.5, venation
4 = NHMW 1999B0057/0041, x 3.9, large marginal spines and venation near leaf margin
5 = NHMW 1999B0057/0239, x 1.8, large but rare marginal spines

Fig. 6: *Pandanus gibbsianus* Martinelli.

6 = Herbarium Bogor, Indonesia, BO-1566456, coll. Meijer, No. 1989, loc. Nunukan, East Borneo, head-like infructescence showing basally fused fruitlets forming phalanges, modern, x 0.7.

Figs 7-10: *Gruenbachia pandanoides* J. Kvaček & Herman, nov. gen. et nov. spec., Grünbach am Schneeberg.

7 = NHMW 1999B0057/0163, x 1.1
8 = NHMW 1999B0057/0216, x 1.4
9 = holotype, NHMW 1999B0057/0179, x 1.4
10 = NHMW 1999B0057/0264a, x 1.2

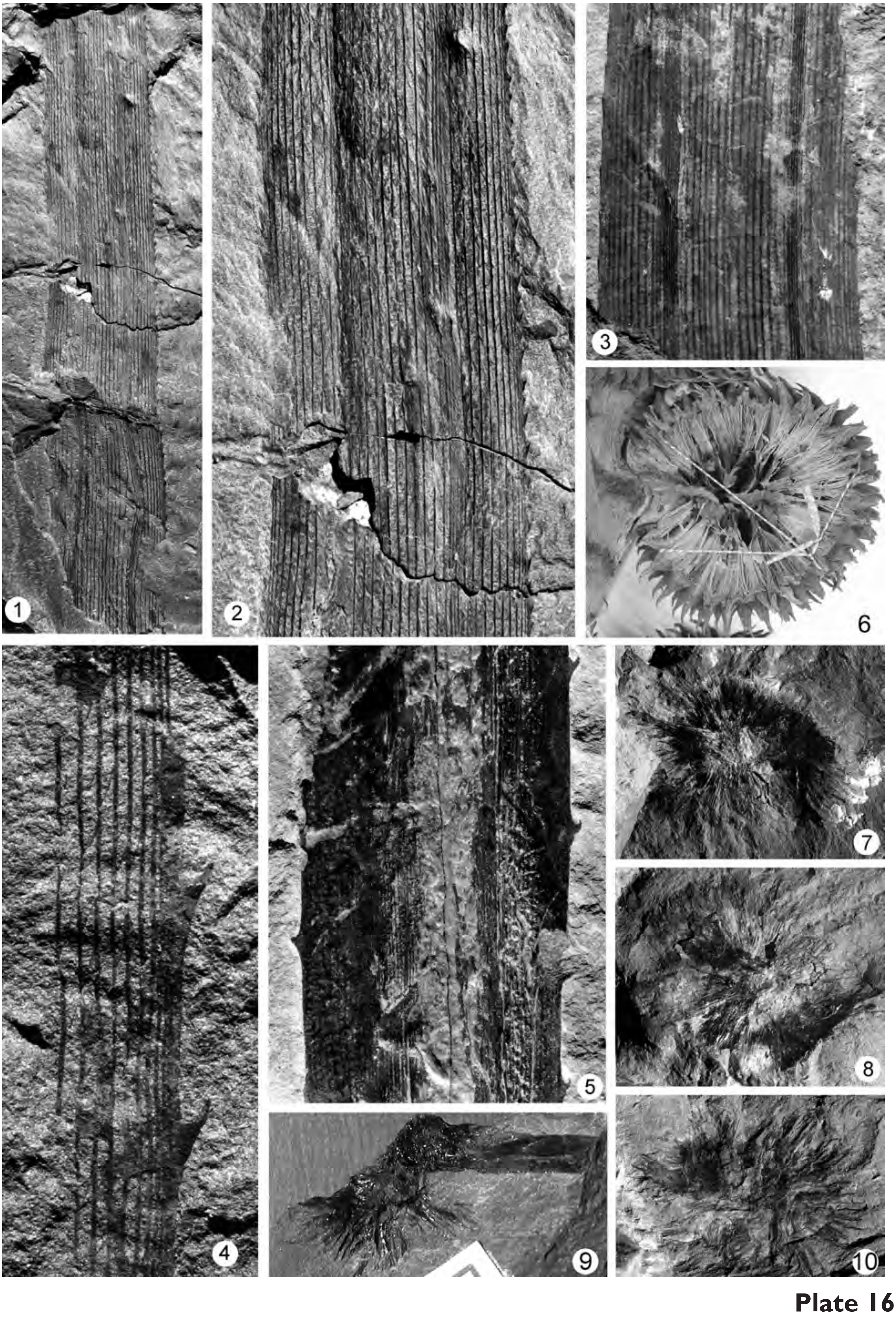


Plate 16

Plate 17

Figs 1-4: *Sabalites longirhachis* (Unger) J. Kvaček & Herman, Grünbach am Schneeberg.

1 = NHMW 4191970, x 0.7, leaf fragment showing costa, Maiersdorf
2 = GBA 1852/03/11, x 0.6, basal part of leaf, Muthmannsdorf
3 = lectotype, GBA 1852/03/05a, x 0.5, Muthmannsdorf
4 = NHMW 1999B0057/0533, x 0.8, basal part of leaf

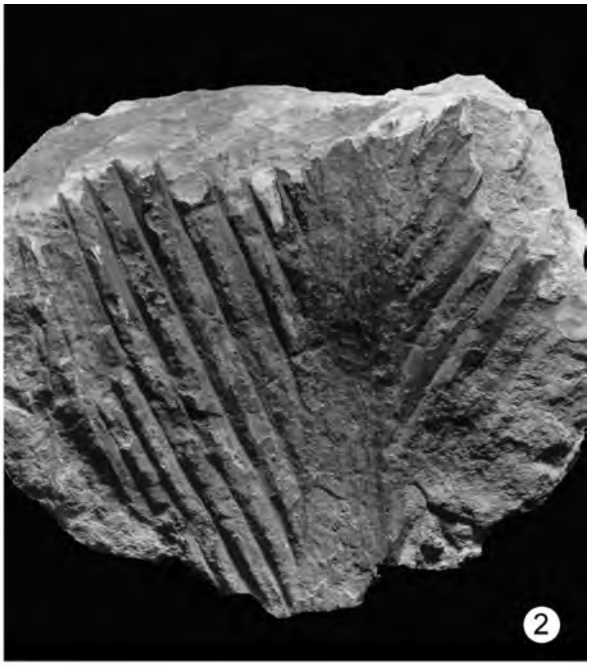


Plate 17

Plate 18

Sabalites longirhachis (Unger) J. Kvaček & Herman, Grünbach am Schneeberg.

NHMW 1999B0057/0235, x 0.6, apical part of leaf

Plate 18

Plate 19

Figs 1-4: *Sabalites longirhachis* (Unger) J. Kvaček & Herman.

1 = GBA 2001/06/01, x 0.6, leaf margin, Grünbach am Schneeberg
2 = NHMW 4191970b, x 300, abaxial cuticle showing stomata (arrowed), Maiersdorf
3 = NHMW 1999B0057/0528, x 3.6, detail of venation, Grünbach am Schneeberg
4 = NHMW 1999B0057/0149, x 0.6, basal part of leaf, Grünbach am Schneeberg

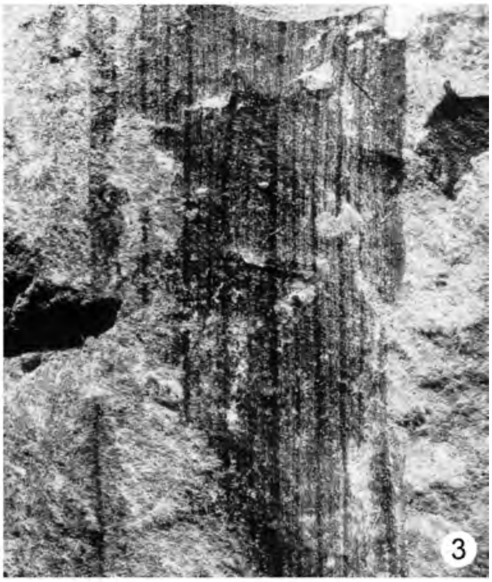


Plate 19

Plate 20

Figs 1-7: *Theiaiphyllum kollmannii* Herman & J. Kvaček, nov. gen. et nov. spec., Grünbach am Schneeberg.

1 = NHMW 1999B0057/0068, x 1.2, leaf with decurrent base
2 = NHMW 1999B0057/0024, x 1.4
3 = NHMW 1999B0057/0243, x 0.8
4 = NHMW 1999B0057/0053, x 5.0, detail of secondary and tertiary venation
5 = NHMW 1970/1396/1642., x 1.0, two leaf fragments, one of which showing attenuate leaf apex
6 = NHMW 1999B0057/0048, x 0.9
7 = NHMW 1999B0057/0048, x 2.5, detail of Fig. 6 showing secondary and tertiary venation

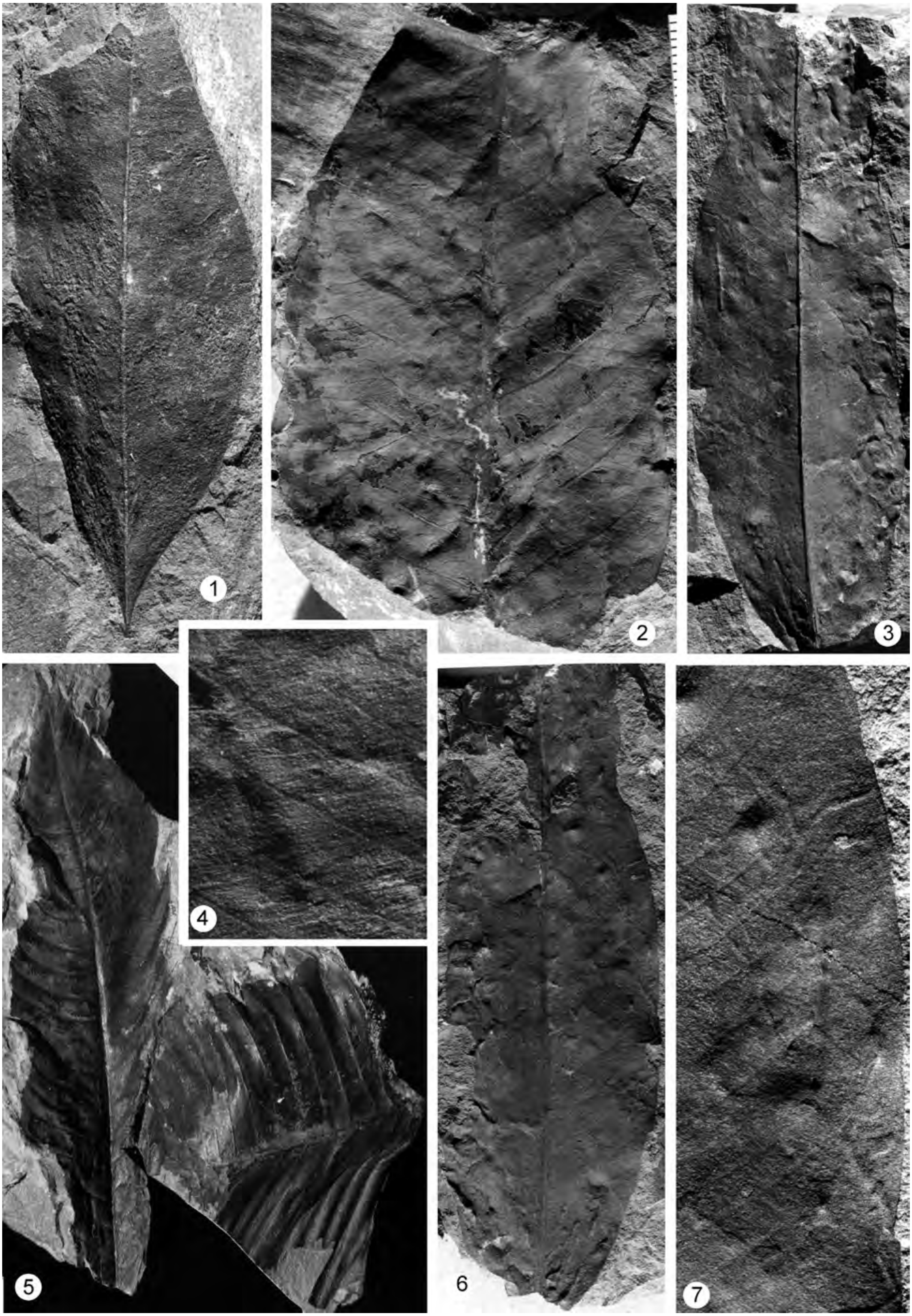


Plate 20

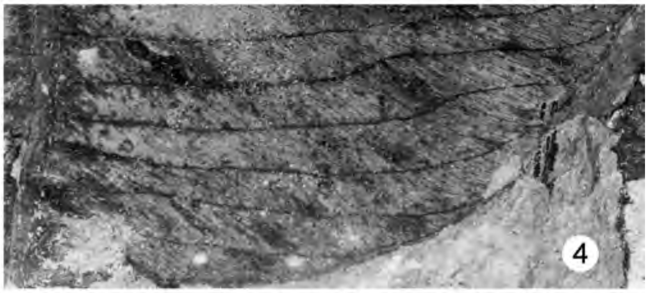
Plate 21

Figs 1-6: *Theiaiphyllum kollmannii* HERMAN & J. KVAČEK nov. gen. et nov. spec., Grünbach am Schneeberg.

1 = holotype, NHMW 1999B0057/0237, x 0.8
2 = holotype, NHMW 1999B0057/0237, x 3.5, detail of Fig. 1 showing leaf margin and fine venation near leaf base
3 = holotype, NHMW 1999B0057/0237, x 3.4, detail of Fig. 1 showing leaf margin and fine venation
4 = holotype, NHMW 1999B0057/0237, x 2.3, detail of Fig. 1 showing leaf margin and fine venation near leaf base
5 = holotype, NHMW 1999B0057/0237, x 4.6, detail of Fig. 1 showing fine venation in the middle part of leaf lamina
6 = NHMW 1999B0057/0245, x 5.2, leaf fragment showing fine venation

Figs 7-8: Monocotyledon gen. & sp. indet., Grünbach am Schneeberg.

7 = NHMW 1999B0057/0537, x 0.9, leaf fragment
8 = NHMW 1999B0057/0537, x 3.6, detail of Fig. 7 showing venation



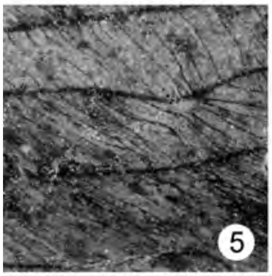


Plate 21

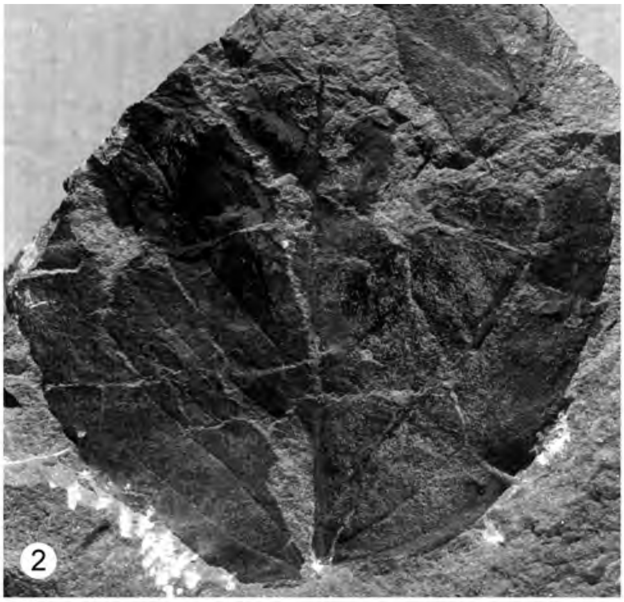
Plate 22

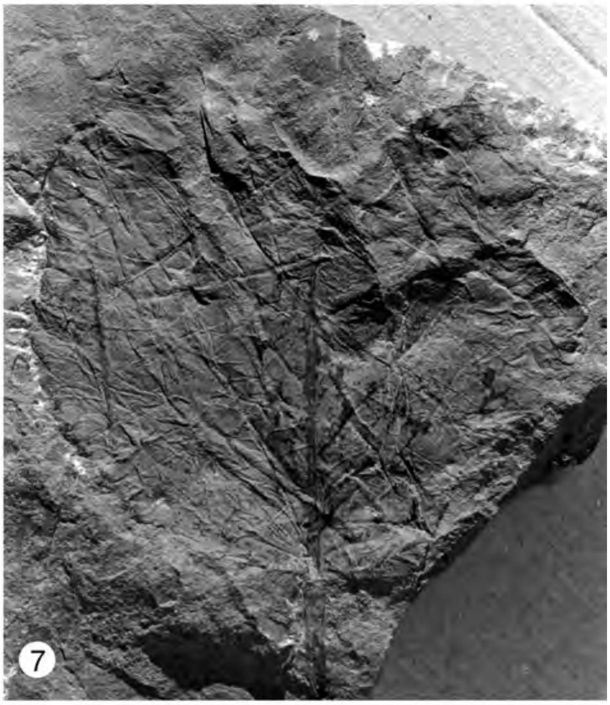
Figs 1-9: *Celastrophyllum johannae* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

1 = NHMW 1970/1396/1614, x 0.7
2 = NHMW 1999B0057/0157, x 1.1
3 = NHMW 1999B0057/0157, x 2.7, detail of Fig. 2 showing marginal teeth
4 = NHMW 1999B0057/0157, x 1.8, detail of Fig. 2 showing marginal teeth
5 = holotype, NHMW 1970/1396/1613, x 0.8
6 = holotype, NHMW 1970/1396/1613, x 2.7, detail of Fig. 5 showing marginal teeth
7 = NHMW 1999B0057/0153, x 0.9
8 = NHMW 1999B0057/0267, x 1.0
9 = NHMW 1999B0057/0377, x 0.7

Fig. 10: *Celastrophyllum* sp., Grünbach am Schneeberg.

10 = NHMW 1999B0057/0262a, x 1.6





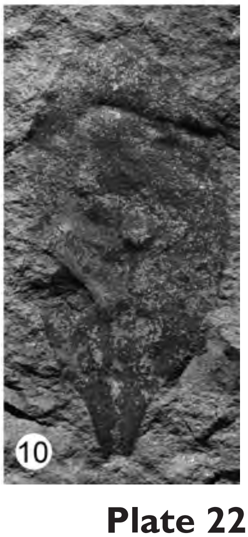


Plate 22

Plate 23

Figs 1-9: *Compositiphyllum serratum* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

1 = holotype, NHMW 1999B0057/0033, x 0.9, fragment of compound leaf with five leaflets
2 = holotype, NHMW 1999B0057/0033, x 1.8, detail of Fig. 1 showing bases of two leaflets attached to a common petiole of the leaf
3 = holotype, NHMW 1999B0057/0033, x 3.4, detail of Fig. 1 showing leaflet margin with very small teeth
4 = NHMW 1999B0057/0069, x 1.2, leaflet attached to a common petiole of the leaf
5 = NHMW 1999B0057/0186a, x 1.5, leaflet apical part
6 = NHMW 1999B0057/0257a, x 0.9, completely preserved leaflet
7 = NHMW 1999B0057/0257a, x 3.6, detail of Fig. 6 showing leaflet margin with very small marginal teeth and well preserved venation
8 = NHMW 1999B0057/0257a, x 2.3, detail of Fig. 6 showing leaflet margin with very small marginal teeth and venation
9 = holotype NHMW 1999B0057/0033, x 5.9, detail of Fig. 1 showing leaflet margin with very small teeth

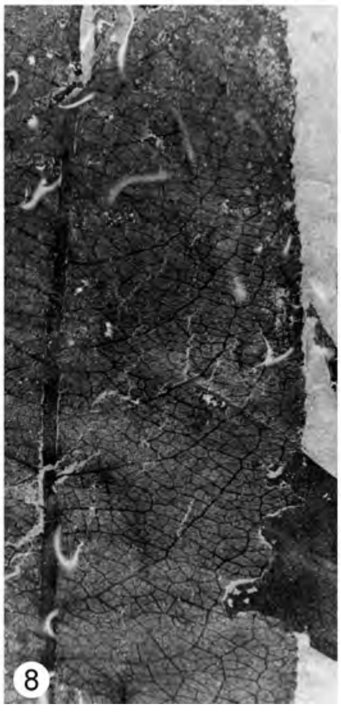


Plate 23

Plate 24

Figs 1-3: *Debeya insignis* (Hosius & Marck) Knobloch, Grünbach am Schneeberg.

1a, 1b = NHMW 1999B0057/0101c, x 1.3, two leaflets
2 = NHMW 1999B0057/0180a, x 0.9, two leaflets with closely situated bases
probably forming palmately compound leaf
3 = NHMW 1999B0057/0065, x 2.0, leaflet with rare hook-like marginal teeth

Figs 4-11: *Ettingshausenia gruenbachiana* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

4 = NHMW 1999B0057/0125, x 1.4
5 = holotype, NHMW 1999B0057/1801 (=1970/1396/1649), x 0.9
6 = NHMW 1999B0057/0279, x 1.5
7 = NHMW 1999B0057/0296, x 1.1, leaf apical part with two lateral lobes
8 = NHMW 1999B0057/0258, x 1.6, leaf fragment showing entire margin and details of venation
9 = NHMW 1999B0057/0314, x 0.9
10 = NHMW 1999B0057/0297, x 2.1
11 = NHMW 1999B0057/0297, x 3.1, detail of Fig. 10 showing sinus between lobes and
details of venation

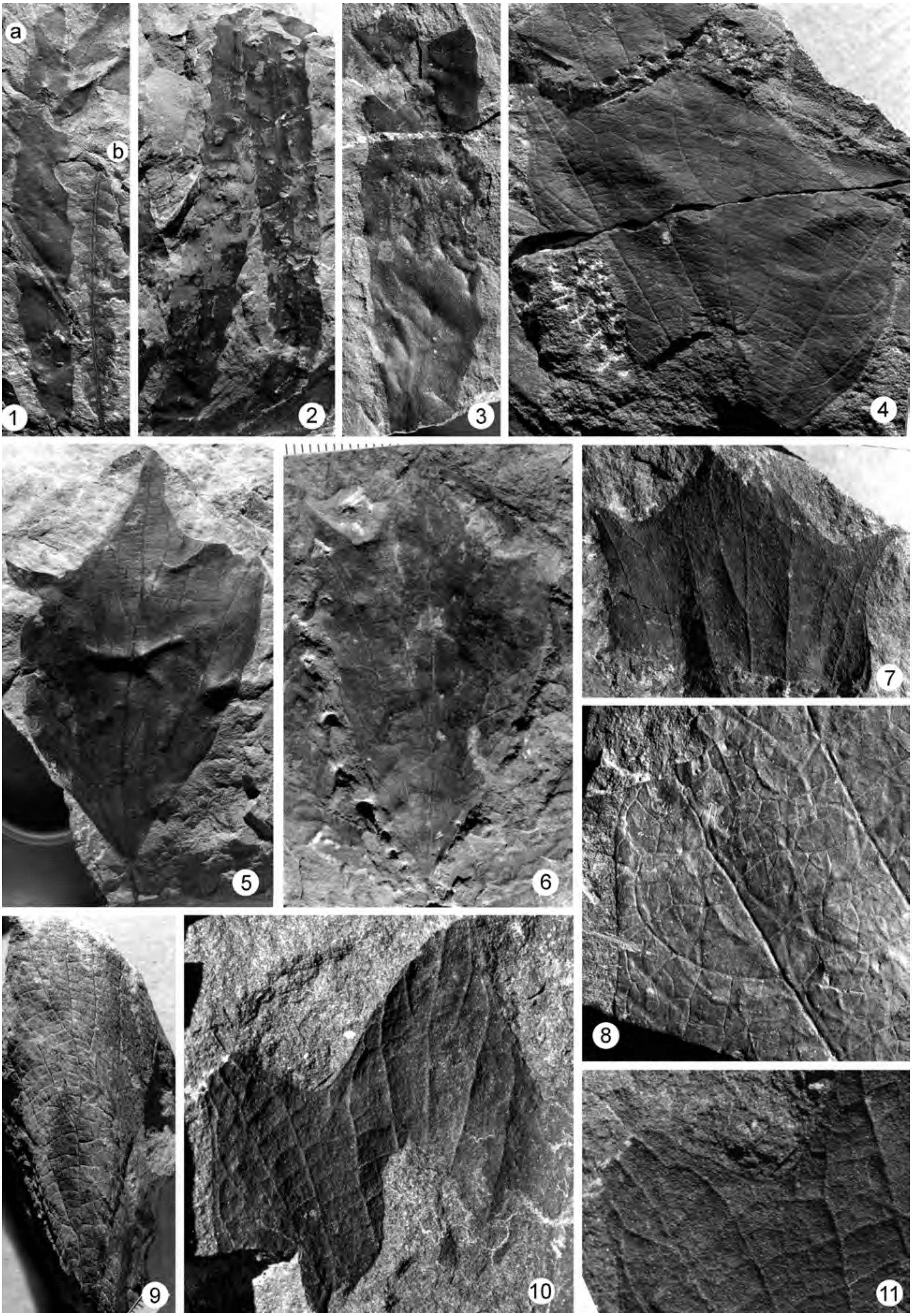


Plate 24

Plate 25

Fig. 1: *Ettingshausenia gruenbachiana* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

1 = NHMW 1999B0057/0302, x 1.3

Figs 2-4: *Ettingshausenia* cf. *laevis* (Velenovský) J. Kvaček & Váchová, Grünbach am Schneeberg.

2 = NHMW 1999B0057/0263a, x 1.3
3 = NHMW 1999B0057/0263b, x 1.0
4 = NHMW 1999B0057/0295, x 1.3

Fig. 5: *Ettingshausenia* sp., Grünbach am Schneeberg.

5= NHMW 1999B0057/0298, x 1.5

Figs 6-7: *Grebenkia europaea* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

6 = holotype NHMW 1999B0057/0277, x 1.4
7 = holotype NHMW 1999B0057/0277, x 3.2, detail of Fig. 6 showing leaf margin and venation

Figs 8-14: *Dicotylophyllum* sp. 7., Grünbach am Schneeberg.

8 = NHMW 1999B0057/0100b, x 0.8
9 = NHMW 1999B0057/0256, x 0.6
10 = NHMW 1999B0057/0566a, x 0.9
11 = NHMW 1999B0057/0566b, x 2.7, detail of Fig. 10 showing thin, closely spaced secondary veins emerging from the midvein at a very sharp angle
12 = NHMW 1999B0057/0566c, x 2.3
13 = NHMW 1999B0057/0579, x 1.5
14 = NHMW 1999B0057/0289, x 1.8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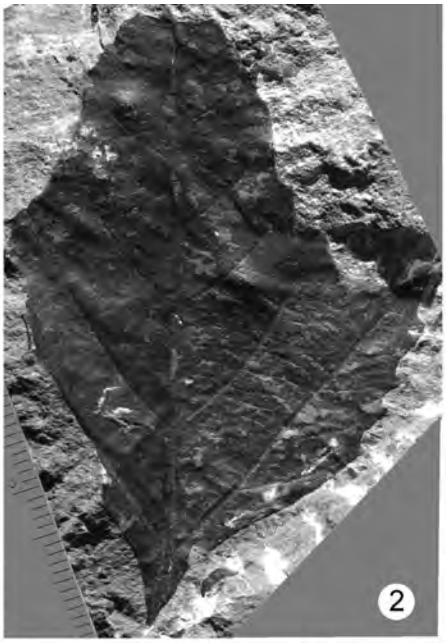
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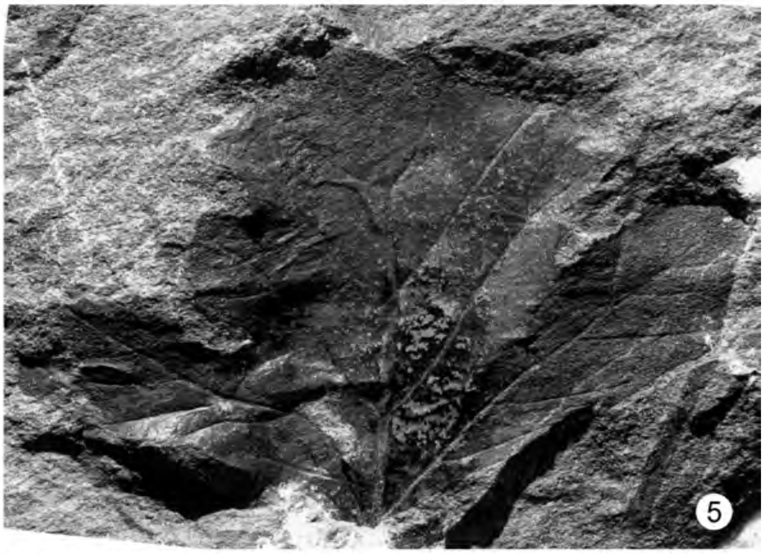
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Plate 25

Plate 26

Fig. 1: *Menispermites summesbergeri* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

1 = holotype, NHMW 1999B0057/0555, x 0.8

Fig. 2: *Menispermites ettingshausenii* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

2 = holotype, NHMW 1999B0057/0089a, x 2.2

Figs 3-5: *Leguminosites mucronatus* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

3 = holotype, NHMW 1999B0057/0270a, x 1.3
4 = holotype counterpart, NHMW 1999B0057/0270b, x 1.4
5 = NHMW 1999B0057/0240, x 1.5

Figs 6-7: *Myricophyllum* sp. cf. *M. zenkeri* (Ettingshausen) Němejc, Grünbach am Schneeberg.

6 = NHMW 1999B0057/0097, x 1.5
7 = NHMW 1999B0057/0097, x 4.1, detail of Fig. 6 showing leaf margin

Figs 8-10: *Myricophyllum serratum* (Velenovský) Velenovský, Grünbach am Schneeberg.

8 = NHMW 1999B0057/0336a, x 2.1
9 = NHMW 1999B0057/0336b, detail of Fig. 8 showing leaf margin and venation, x 5.2
10 = NHMW 1999B0057/0337, x 1.9


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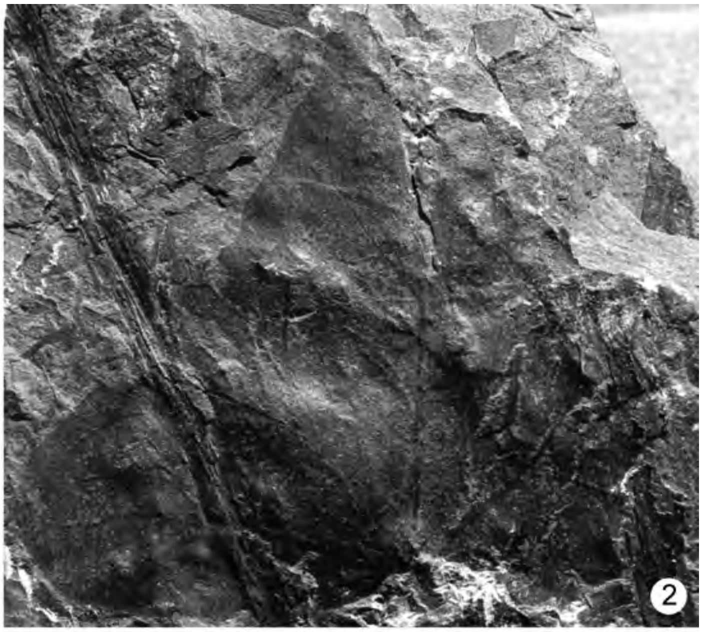
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Plate 26

Plate 27

Figs 1-7: *Brasenites krasseri* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

1 = holotype, NHMW 1999B0057/1787 (=1970/1396/1559), x 1.5
2 = NHMW 1999B0057/0248, x 1.2
3 = NHMW 1999B0057/0499, x 6.1, detail of venation
4 = NHMW 1999B0057/0493, x 0.8
5 = NHMW 1999B0057/0494, x 1.2
6 = NHMW 1999B0057/0494, x 3.1, detail of Fig. 5 showing venation and round to polygonal cells on leaf surface probably representing imprint of an aerenchimous tissue
7 = NHMW 1999B0057/0494, x 6.1, detail of Fig. 5 showing round to polygonal cells probably representing imprint of an aerenchimous tissue

Fig. 8: *Brasenia* sp., modern.

8 = elliptic peltate leaf, x 1.5

Figs 9-14: *Quereuxia angulata* (Newberry) Kryshtofovich, Grünbach am Schneeberg.

9 = NHMW 1999B0057/0316, x 1.6, leaflet
10 = NHMW 1999B0057/0321, x 1.6, leaflet
11 = NHMW 1999B0057/0316, x 1.4, leaflet
12 = NHMW 1999B0057/0326, x 1.1, four leaflets forming palmately compound leaf
13 = NHMW 1999B0057/0315, x 1.3, three leaflets attached forming palmately compound leaf
14 = NHMW 1970B1396-1661, x 0.9, two leaf rosettes with numerous leaflets of different sizes

Figs 15-16: *Rogersia* sp., Grünbach am Schneeberg.

15 = NHMW 1999B0057/0089b, c, x 2.5, two incompletely preserved leaves
16 = NHMW 1999B0057/0089c, x 2.2, two or three incompletely preserved leaves

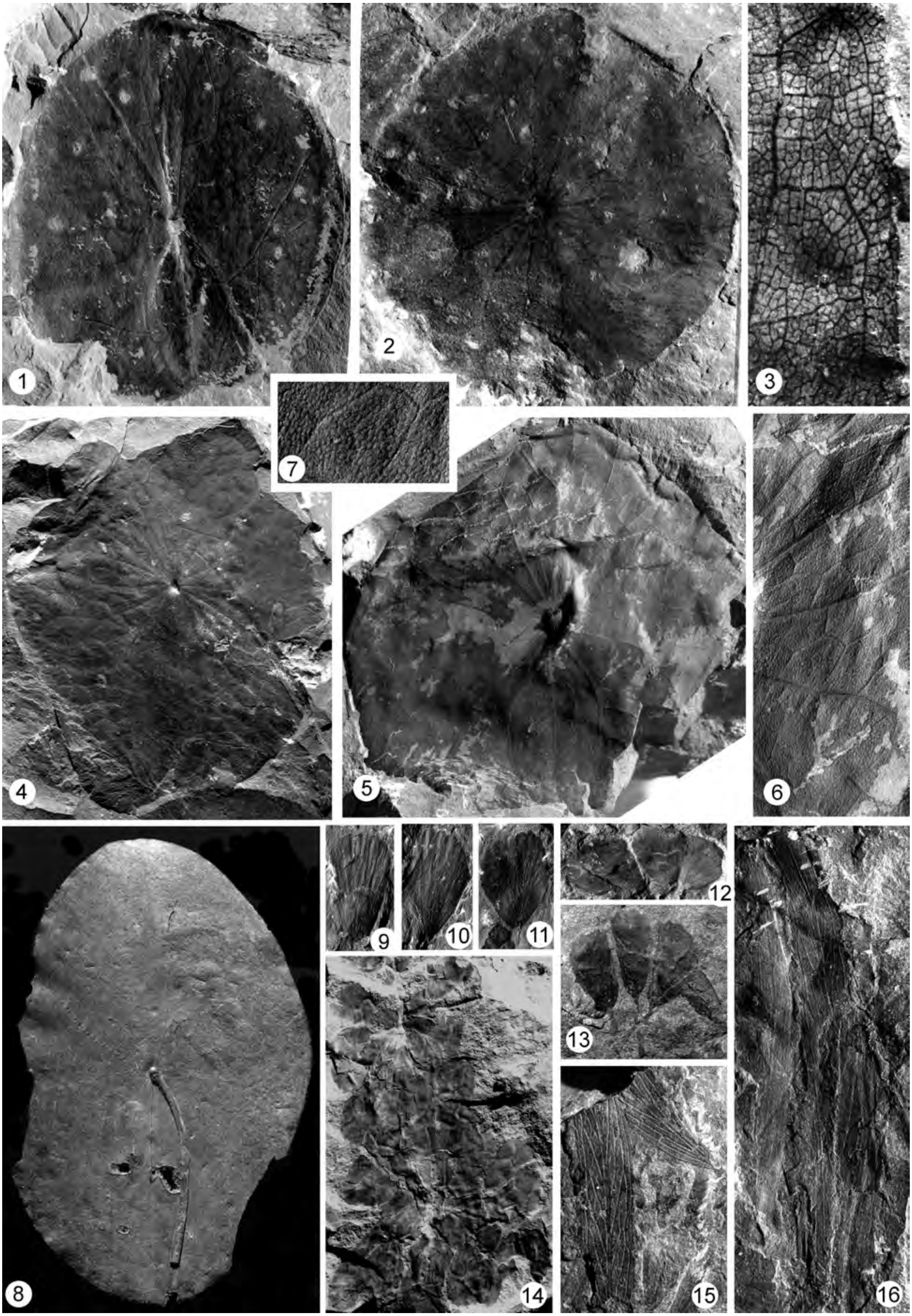

Plate 27

Plate 28

Figs 1-15: *Dicotylophyllum proteoides* (Unger) Herman & J. Kvaček, comb. nov., Grünbach am Schneeberg.

1 = NHMW 1999B0057/0259b, x 0.8, leaf accumulation, subparallel orientation of leaves probably reflects their transportation prior to burial
2 = neotype, NHMW 1999B0057/0339A, x 1.0
3 = NHMW 1999B0057/0164a, x 0.8
4 = NHMW 1999B0057/0339B, x 1.0
5 = NHMW 1999B0057/0354b, x 0.8
6 = NHMW 1999B0057/0354a, x 1.8
7a-c = NHMW 1999B0057/0347a-c, x 1.5
8a = NHMW 1999B0057/0352a, x 0.7
8b = NHMW 1999B0057/0352b, x 0.7
9 = NHMW 1999B0057/0395b, x 1.5
10 = NHMW 1999B0057/0001, x 2.1, detail of Fig. 11 showing venation
11 = NHMW 1999B0057/0001, x 1.2, leaf with damaged apex
12 = NHMW 1999B0057/0161d, x 4.1, detail of Fig. 13 showing venation
13 = NHMW 1999B0057/0161d, x 1.9
14 = NHMW 1999B0057/0338, x 1.5
15 = NHMW 1999B0057/0217a, x 3.6, leaf fragment showing venation


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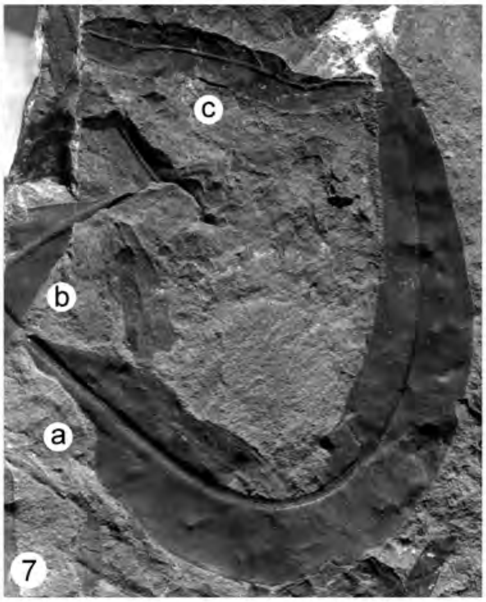
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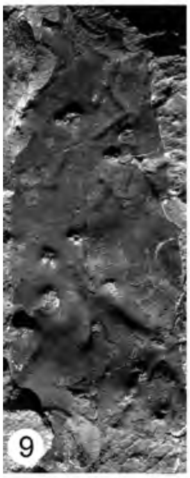
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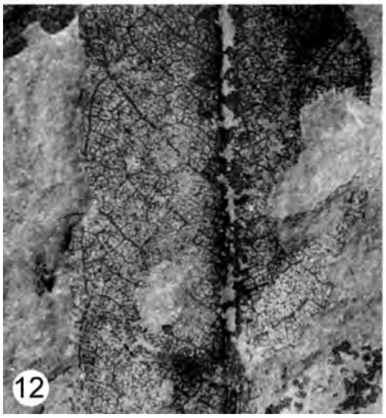
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Plate 28

Plate 29

Figs 1-7: *Dicotylophyllum proteoides* (Unger) Herman & J. Kvaček, comb. nov., Grünbach am Schneeberg.

1= NHMW 1999B0057/0359b, x 1.3, leaf accumulation
2 = NHMW 1999B0057/0335, x 1.5, several leaves
3 = NHMW 1999B0057/0351, x 4.4, leaf fragment showing venation
4 = NHMW 1970/1396/459b,c, x 1.2, two leaves
5 = NHMW 1999B0057/0059d,e, x 1.5, two leaves
6 = NHMW 1999B0057/0370, x 1.3
7 = NHMW 1999B0057/0344b,c, x 1.8, several leaves

Figs 8-10: *Ternstroemites* (?) *neueweltensis* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

8 = holotype, NHMW 1999B0057/0030, x 1.4
9 = holotype, NHMW 1999B0057/0030, x 1.8, detail of Fig. 8 showing marginal teeth and venation
10 = holotype, NHMW 1999B0057/0030, x 1.8, detail of Fig. 8 showing venation and distinct intramarginal vein

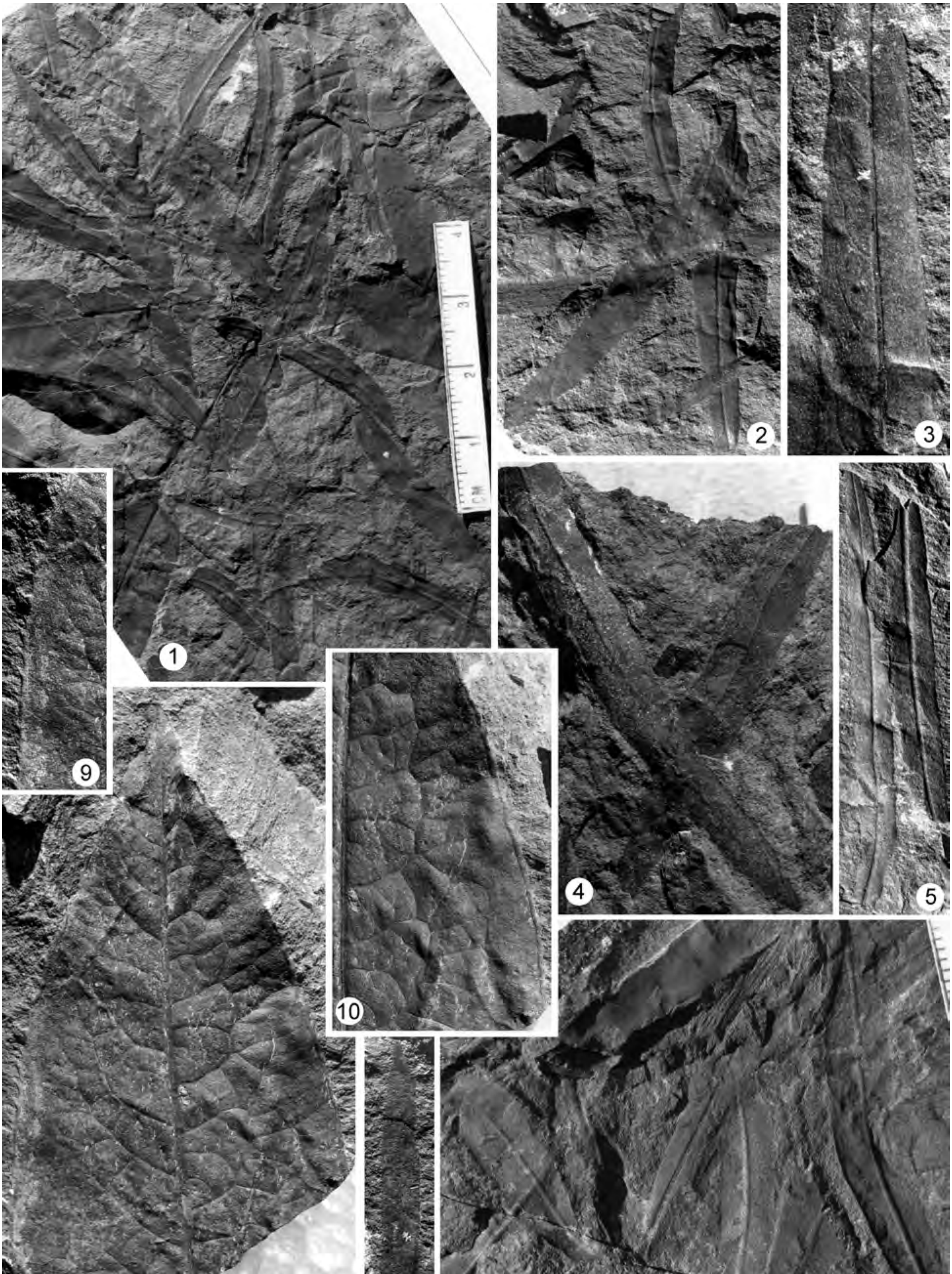


Plate 29

Plate 30

Figs 1-4a, 5-6: *Juglandiphyllites pelagicus* (Unger) Herman & J. Kvaček, comb. nov., Grünbach am Schneeberg.

1 = holotype Unger, 1867, pl. II, fig. 13, GBA 2006/07/01, x 0.8
2 = holotype GBA 2006/07/01, x 2.4, detail of Fig. 1 showing leaf margin and venation
3 = NHMW 1999B0057/0281, x 1.1
4a = NHMW 1999B0057/0059, x 0.9
5 = NHMW 1999B0057/0018, x 1.8
6 = NHMW 1999B0057/0077, x 1.2

Figs 4b,c: *Dicotylophyllum* sp. 7., Grünbach am Schneeberg.

4b, 4c = NHMW 1999B0057/0059b,c, x 0.9

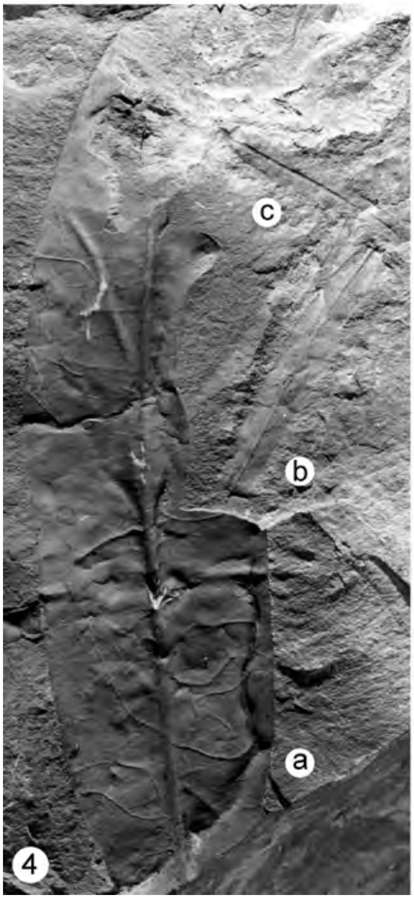


Plate 30

Plate 31

Fig. 1a: *Gosauopteris danaeoides* J. Kvaček & Herman, nov. gen. et nov. spec., Grünbach am Schneeberg.

1a = NHMW 1999B0057/0236, x 0.8

Figs 1b-3: *Juglandiphyllites pelagicus* (Unger) Herman & J. Kvaček, comb. nov., Grünbach am Schneeberg.

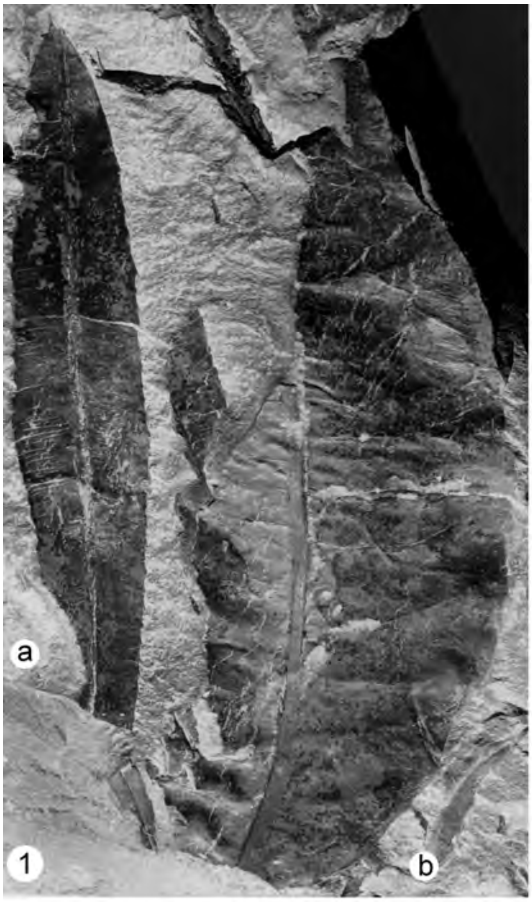
1b = NHMW 1999B0057/0236, x 0.8
2 = NHMW 1999B0057/0282a, x 2.7, detail showing leaf margin and venation
3 = NHMW 1999B0057/0283a, x 1.3

Fig. 4: *Dicotylophyllum* sp. 6, Grünbach am Schneeberg.

4 = NHMW 1999B0057/0075, x 1.2

Figs 5-7: *Viburniphyllum austriacum* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

5 = holotype, NHMW 1999B0057/0382, x 0.9
6 = holotype, NHMW 1999B0057/0382, x 1.6, detail of Fig. 5 showing leaf margin and venation
7 = holotype, NHMW 1999B0057/0382, x 2.7, detail of Fig. 5 showing leaf base, margin and venation



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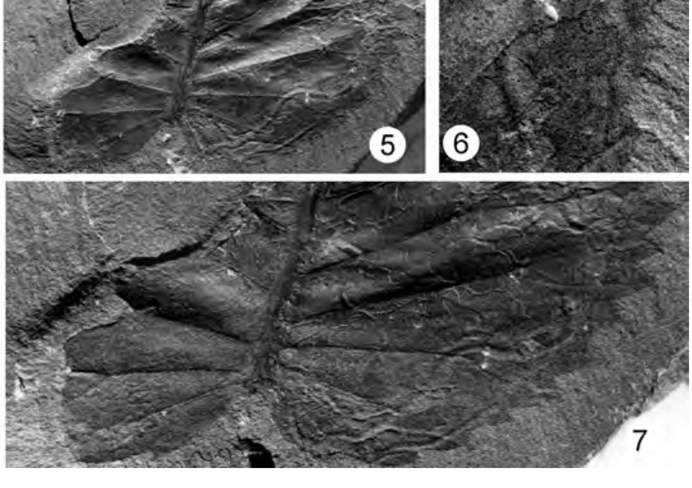
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Plate 32

Figs 1-2: *Viburniphyllum ermanniorum* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

1 = holotype, NHMW 1999B0057/0269, x 2.4
2 = NHMW 1999B0057/0266, x 2.3

Figs 3-4: *Dicotylophyllum* sp. 1, Grünbach am Schneeberg.

3 = NHMW 1999B0057/0282b, x 1.5
4 = NHMW 1999B0057/0282b, x 4.8, of Fig. 3 showing leaf margin and venation

Figs 5-6: *Ettingshausenia* cf. *laevis* (Velenovský) J. Kvaček & Váchová, Grünbach am Schneeberg.

5 = NHMW 1999B0057/0293, x 0.9
6 = NHMW 1999B0057/0293, x 1.8, detail of Fig. 5 showing leaf margin and venation

Figs 7-8: *Dicotylophyllum* sp. 2, Grünbach am Schneeberg.

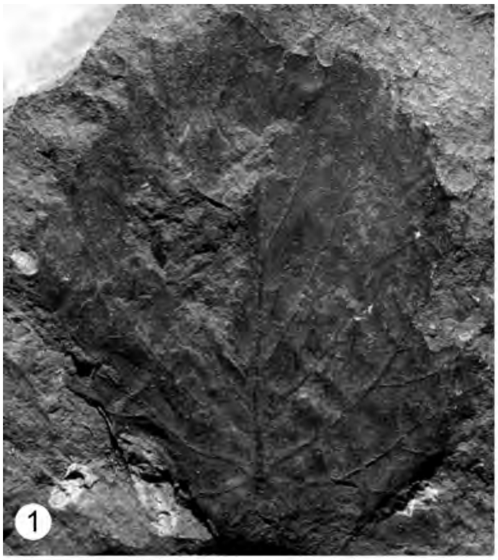
7 = NHMW 1999B0057/0098b, x 1.5
8 = NHMW 1999B0057/0071, x 1.6

Fig. 9: *Dicotylophyllum* sp. 3, Grünbach am Schneeberg.

9 = NHMW 1999B0057/0123b, x 1.2

Fig. 10: *Dicotylophyllum* sp. 4, Grünbach am Schneeberg.

10 = NHMW 1999B0057/0044, x 1.3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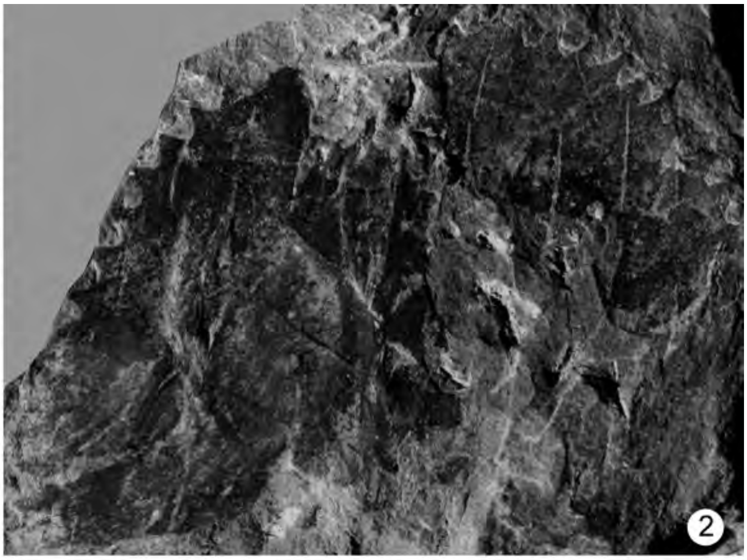
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Plate 32

Plate 33

Figs 1-3: *Dicotylophyllum* sp. 5, Grünbach am Schneeberg.

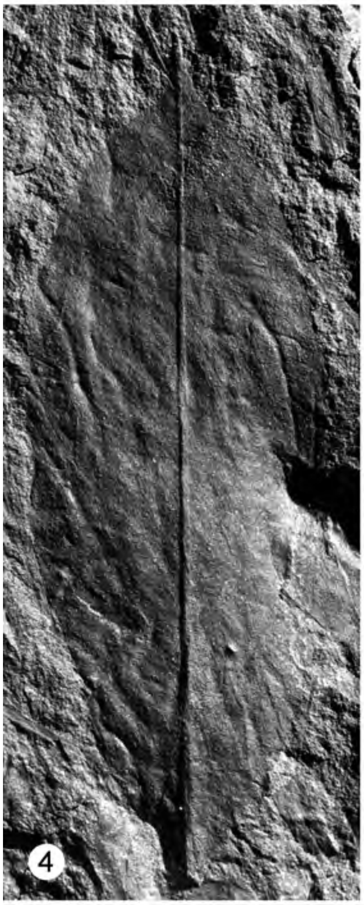
1 = NHMW 1999B0057/0282c, x 4.2, apical part of the leaf
2 = NHMW 1999B0057/0054, x 1.5
3 = NHMW 1999B0057/0054, x 6.1, detail of Fig. 2 showing leaf margin and venation

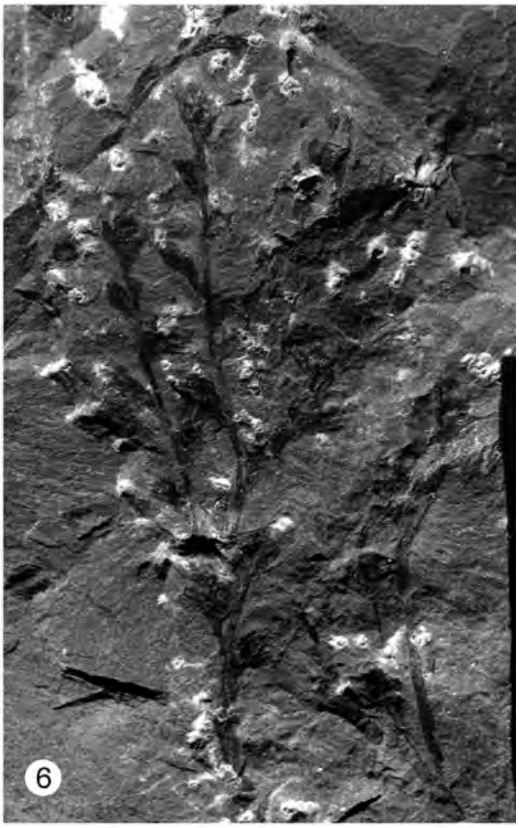
Figs 4-5: *Dicotylophyllum* sp. 6, Grünbach am Schneeberg.

4 = NHMW 1999B0057/0135b, x 1.6
5 = NHMW 1999B0057/0042-1, x 1.2

Figs 6-9: *Ceratoxylon* sp., Grünbach am Schneeberg.

6 = NHMW 1999B0057/0551, x 2.7
7 = NHMW 1999B0057/0551, x 2.1
8 = NHMW 1999B0057/0553, x 5.9
9 = NHMW 1999B0057/0551, x 4.1





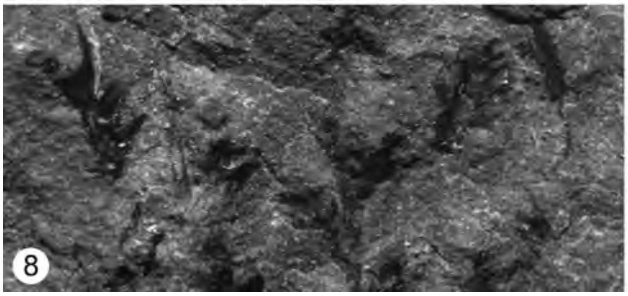


Plate 33

Plate 34

Figs 1-2: *Nilsonia* cf. *holyi* J. Kvaček, Grünbach am Schneeberg.

1 = NHMW 1999B0057/0079, x 180, cuticle showing ordinary cells and possible trichome base
2 = NHMW 1999B0057/0079, x 180, cuticle showing ordinary cells

Figs 3-4: *Geinitzia reichenbachii* (Geinitz) Hollick & Jeffrey, Grünbach am Schneeberg.

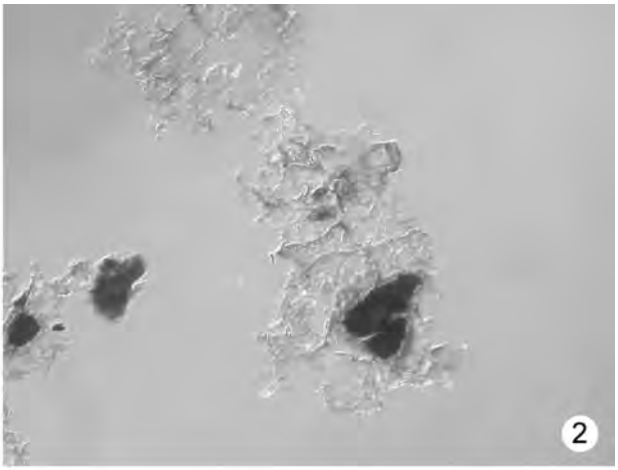
3 = NHMW 1999B0057/0221, x 180, cuticle showing stomata
4 = NHMW 1999B0057/0221, x 180, cuticle showing ordinary cells and one stoma

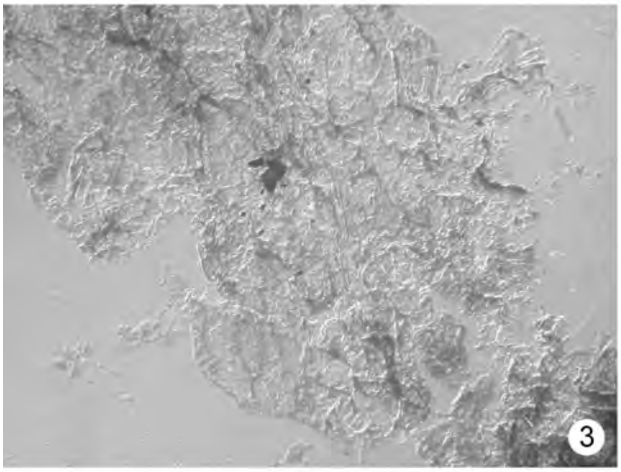
Figs 5-6: *Celastrophyllum* sp., Grünbach am Schneeberg.

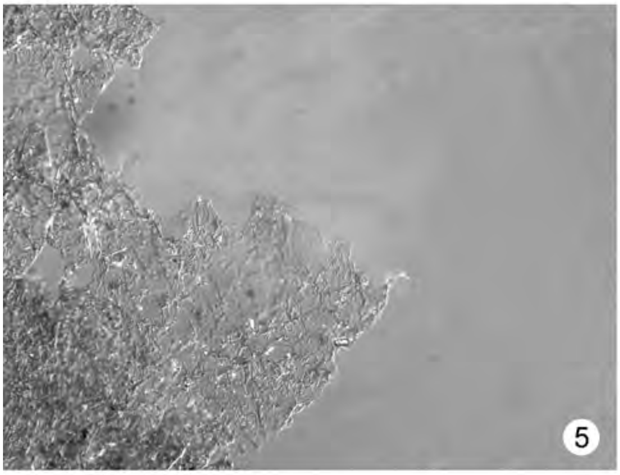
5 = NHMW 1999B0057/0262aa, x 180, cuticle showing possible stoma
6 = NHMW 1999B0057/0262ab, x 180, cuticle showing possible stoma

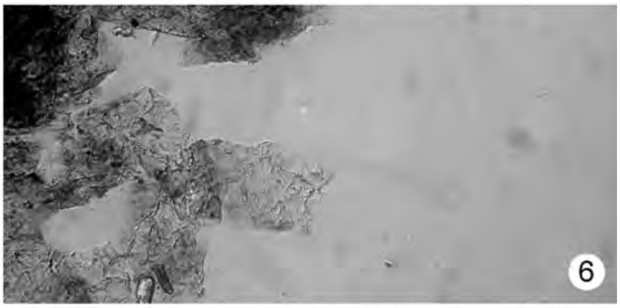
Figs 7-9: *Compositiphyllum serratum* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

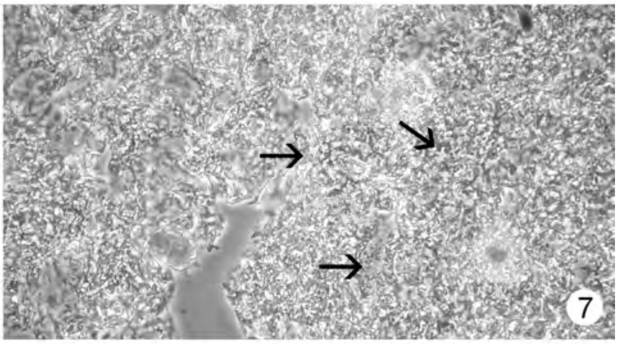
7 = holotype, NHMW 1999B0057/0033, x 180, abaxial cuticle showing three possible stomata (arrowed), phase contrast (PhC)
8 = holotype, NHMW 1999B0057/0033, x 180, abaxial cuticle showing possible stoma (arrowed)
9 = holotype, NHMW 1999B0057/0033, x 180, adaxial cuticle

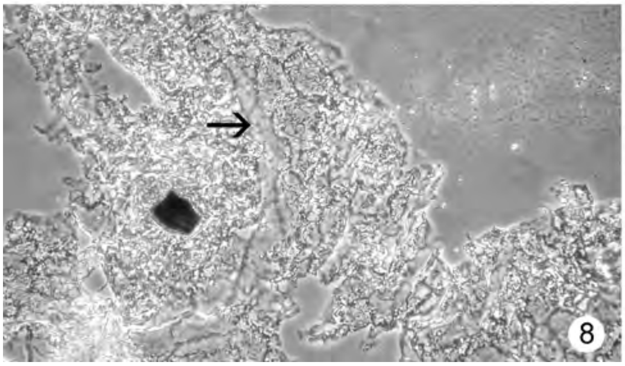












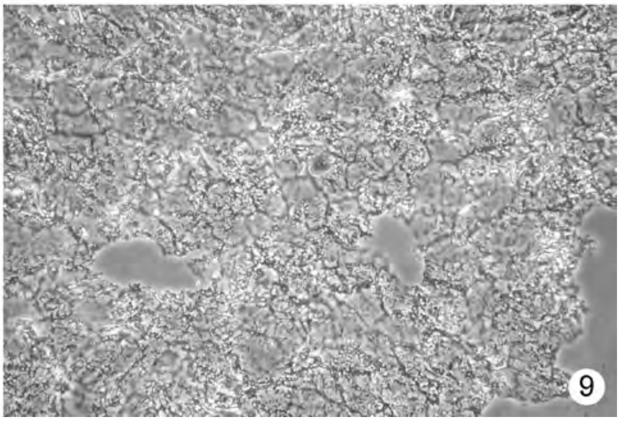


Plate 34

Plate 35

Figs 1-3: *Celastrophyllum johannae* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

1 = NHMW 1999B0057/0153, x 180, adaxial cuticle
2 = NHMW 1999B0057/0153, x 180, abaxial cuticle, p - papilla, t - trichome base, s - stoma
3 = NHMW 1999B0057/0153, x 180, abaxial cuticle showing numerous stomata

Fig. 4: *Ettingshausenia* cf. *laevis* (Velenovský) J. Kvaček & Váchová, Grünbach am Schneeberg.

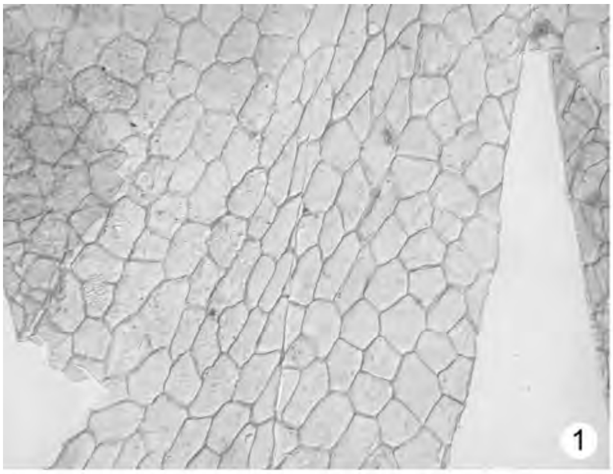
4 = NHMW 1999B0057/0135a, x 180, abaxial cuticle showing stomata (arrowed)

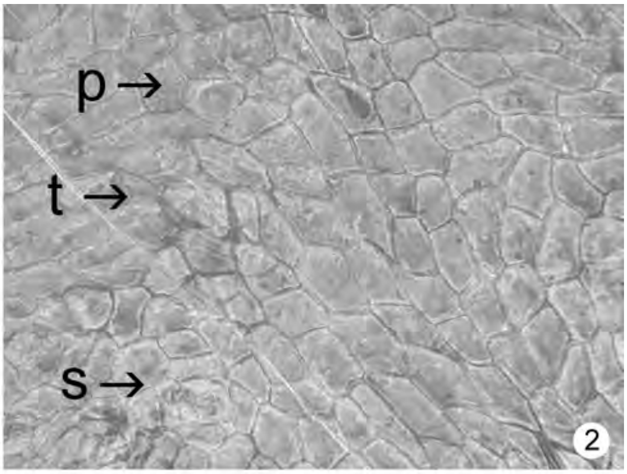
Figs 5-6: *Ettingshausenia gruenbachiana* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

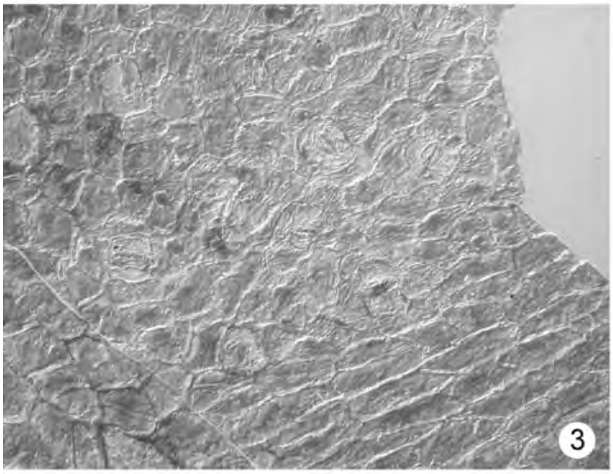
5 = NHMW 1999B0057/0279a, x 180, abaxial cuticle showing
stomata and trichome bases, s - stoma, t - trichome base
6 = NHMW 1999B0057/0279b, x 180, abaxial cuticle showing stomata and trichome bases, PhC

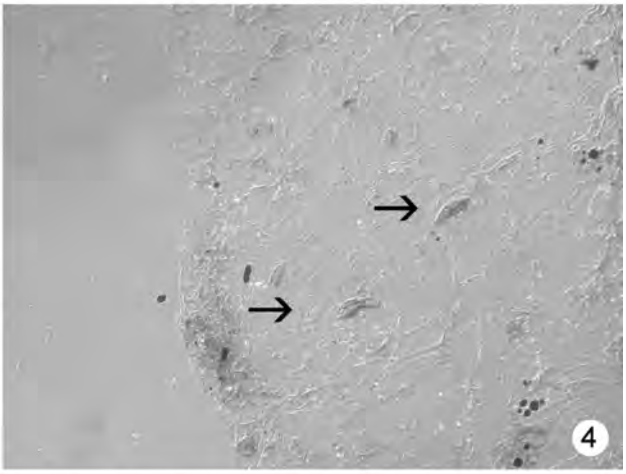
Figs 7-8: *Dicotylophyllum* sp. 7, Grünbach am Schneeberg.

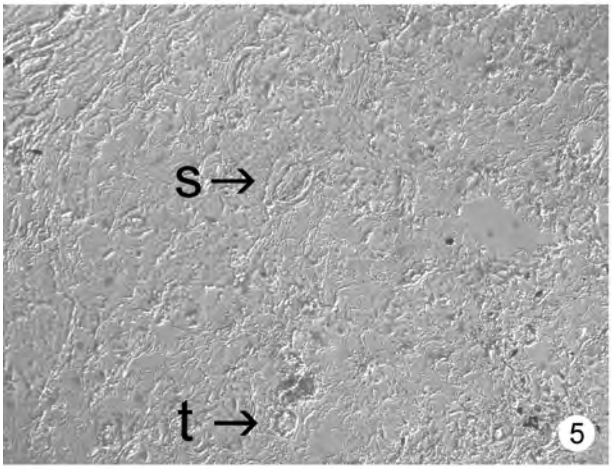
7 = NHMW 1999B0057/0100b, x 180, abaxial cuticle showing possible stomata (arrowed), PhC
8 = NHMW 1999B0057/0100b, x 180, abaxial cuticle showing possible stomata (arrowed)

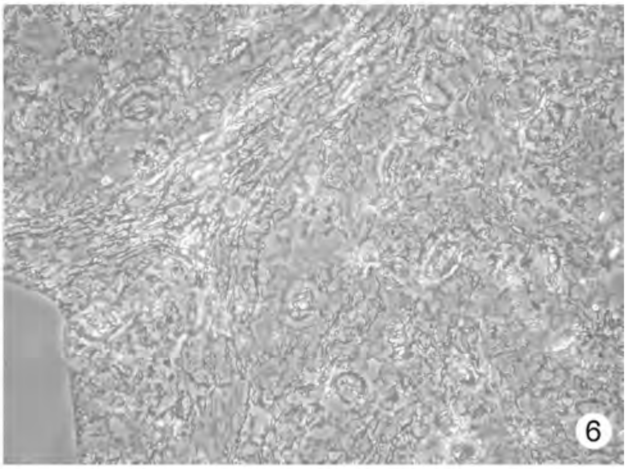


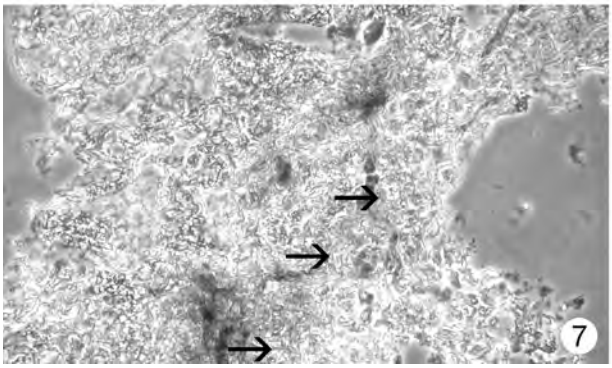












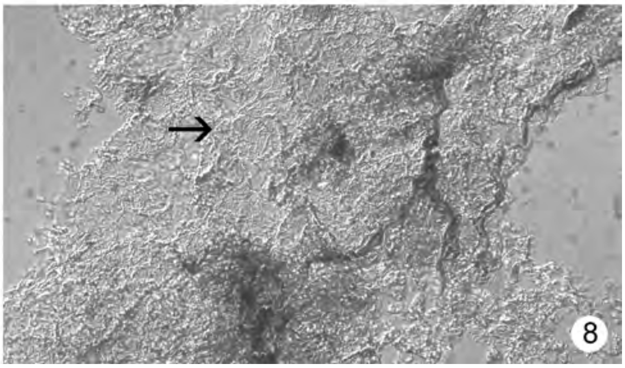


Plate 35

Plate 36

Figs 1-4: *Juglandiphyllites pelagicus* (Unger) Herman & J. Kvaček, comb. nov., Grünbach am Schneeberg.

1 = NHMW 1999B0057/0282aa, x 180, cuticle showing stoma (arrowed), PhC
2 = NHMW 1999B0057/0282aa, x 180, cuticle showing ordinary cells
3 = NHMW 1999B0057/0282aa, x 180, cuticle showing ordinary cells
4 = NHMW 1999B0057/0282ab, x 180, cuticle showing resin bodies, PhC

Figs 5-6: *Brasenites krasseri* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

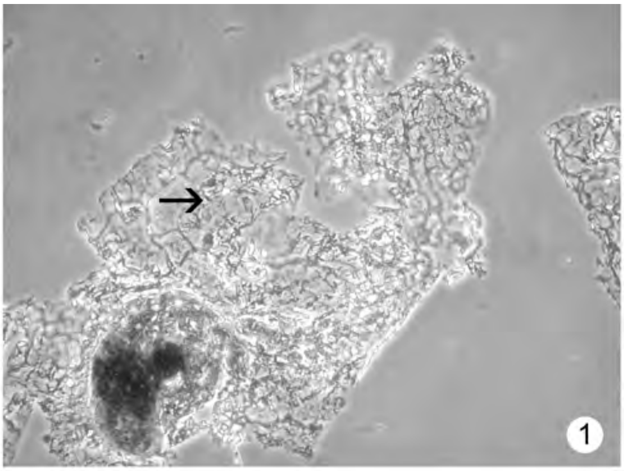
5 = NHMW 1999B0057/0494a, x 180, adaxial cuticle showing ordinary cells, PhC
6 = NHMW 1999B0057/0494a, adaxial cuticle showing ordinary cells, x 180

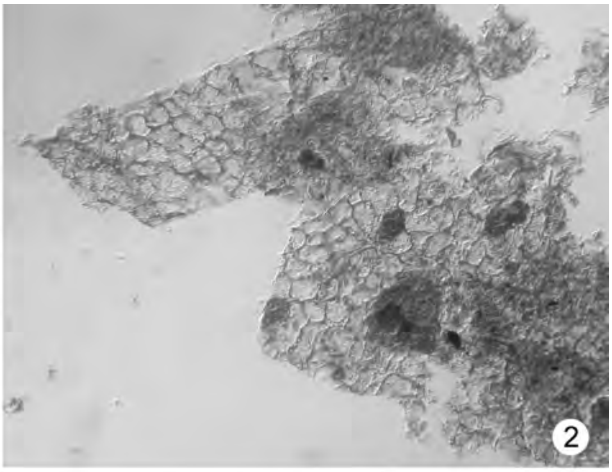
Fig. 7: *Menispermites ettingshausenii* Herman & J. Kvaček, nov. spec., Grünbach am Schneeberg.

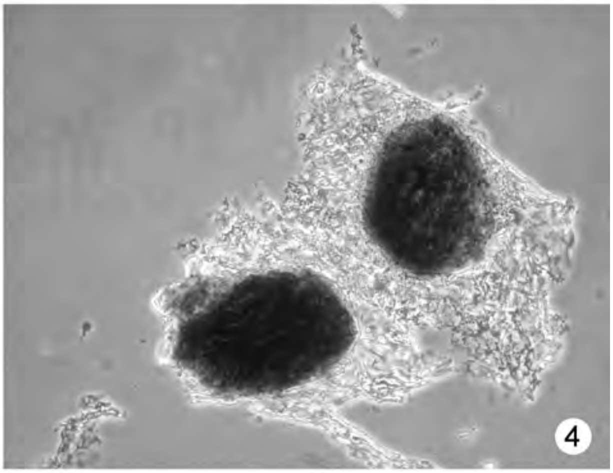
7 = holotype, NHMW 1999B0057/089, x 180, cuticle fragment showing possible stoma

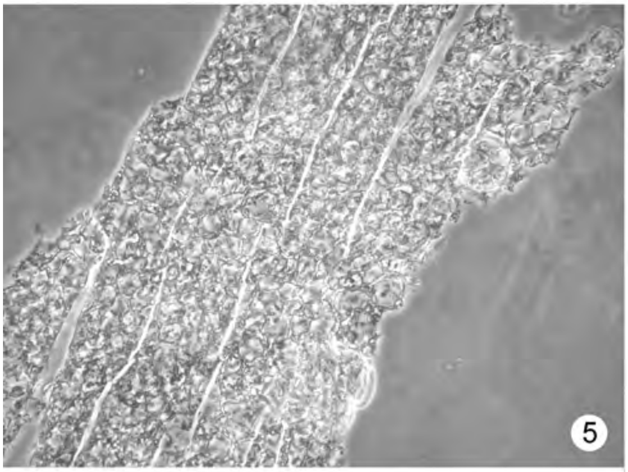
Fig. 8: *Dicotylophyllum proteoides* (Unger) Herman & J. Kvaček, comb. nov., Grünbach am Schneeberg.

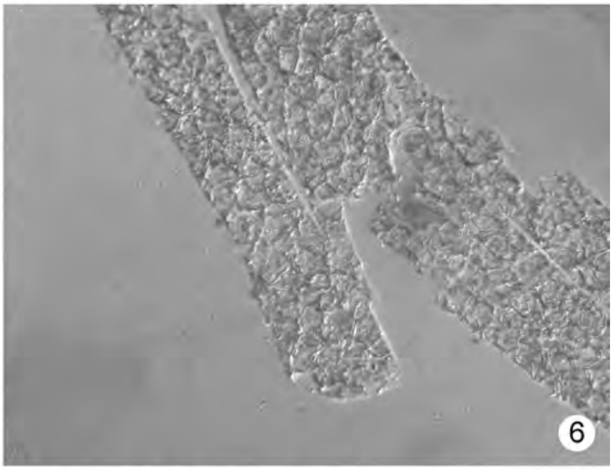
8 = NHMW 1999B0057/0338, x 180, cuticle showing ordinary cells

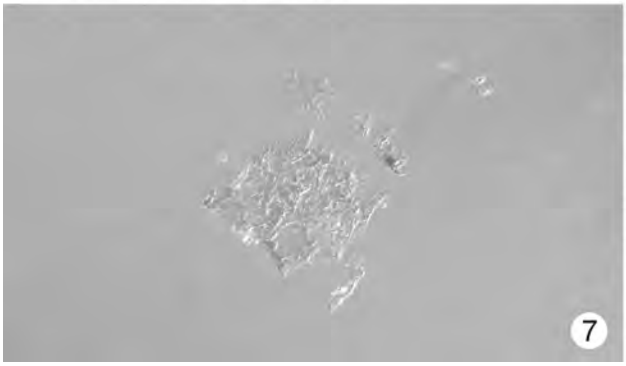












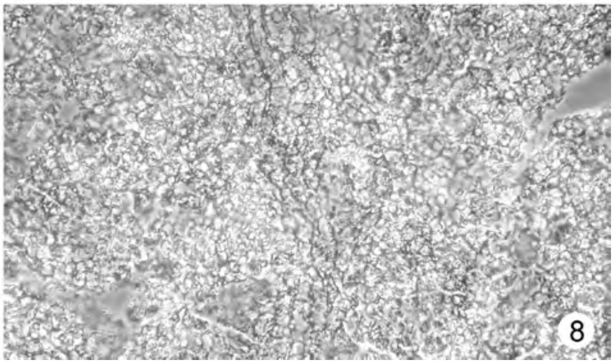


Plate 36

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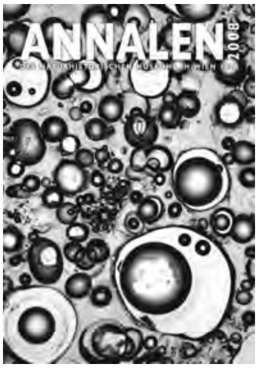
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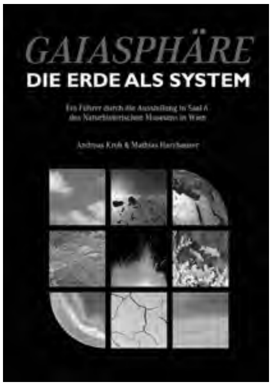

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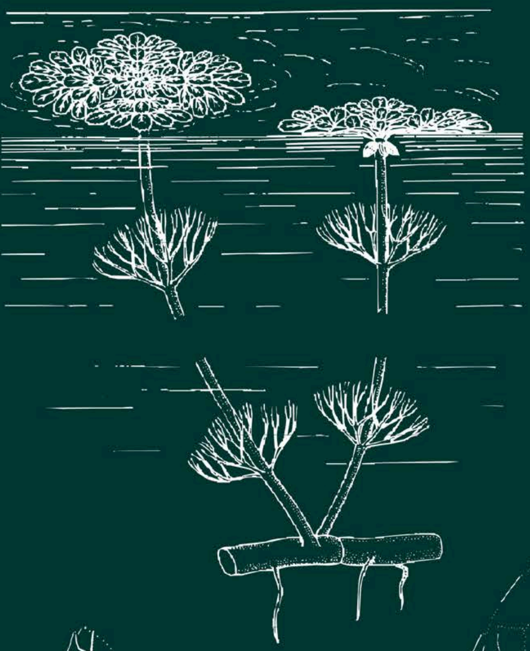

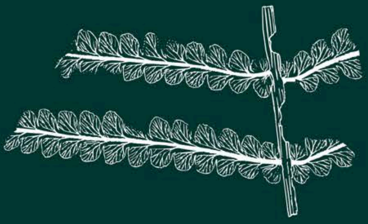

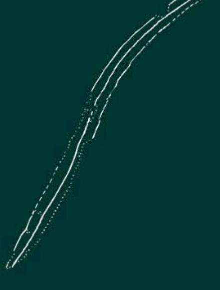

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