Ann. Naturhist. Mus. Wien	103 A	1–21	Wien, März 2002

Campanian Grünbach Flora of Lower Austria: preliminary floristics and palaeoclimatology

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(with 4 text-figures, 1 table and 3 plates)

Manuscript submitted on May 4, 2001,
the revised manuscript accepted on October 24, 2001

Abstract

The Grünbach Flora comes from the Grünbach Formation of the Gosau Group in the Grünbach - Neue Welt Basin in the Eastern Calcareous Alps, Lower Austria. The Early Campanian age of this flora is based on correlation of plant-bearing deposits with marine biostratigraphy. The Grünbach Formation sediments reflect a terrestrial freshwater swamp palaeoenvironment. The Grünbach Flora consists of approximately 60 plant taxa belonging to algae, possible liverworts, horsetails, ferns, cycadophytes, conifers, monocots, aquatic dicots, terrestrial dicots, angiosperm fructifications, fossil woods and possible root remains. Although there is no direct equivalent of the Grünbach Flora, the closest floras are those from the Senonian and the Cenomanian of the Czech Republic and Germany. Physiognomic analysis of the Grünbach Flora using the CLAMP (Climate Leaf Analysis Multivariate Program) technique yielded a mean annual temperature of 15.3°C, a warm month mean temperature of almost 22°C, a cold month mean temperature well above freezing at 8.8°C, a length of the growing season of 8.6 months, a mean annual precipitation of 1373 mm, a mean monthly growing season precipitation of 95 mm, a mean growing season precipitation of 840 mm, and a precipitation during 3 consecutive driest months of 164 mm. Therefore, the Grünbach Flora experienced a humid sub-tropical to maritime mesothermal climate with warm/hot summers and short relatively dry season during the summers.

Introduction

The Grünbach Flora comes from the Grünbach Formation ("Coal-bearing Series" according to PLÖCHINGER 1961) of the Gosau Group in the Grünbach - Neue Welt Basin in the Eastern Calcareous Alps, Lower Austria (Fig. 1). The coalseams of the Grünbach Formation have been exploited from the second half of the 19th century until the 1960s. Mining was extremely difficult in the 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, the Czech Republic and Great Britain, but the main collection is stored at the Natural History Museum in Vienna. Although collected since the 19th century, this collection had never been described monographically. Only

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a few fossil plants were described in detail: *Flabellaria longirhachis* UNGER, *Geinitzia cretacea* ENDLICHER (UNGER 1850, 1852), *Pandanus austriacus* ETTINGSHAUSEN, *P. trinervis* ETTINGSHAUSEN and *P. pseudoinermis* ETTINGSHAUSEN (ETTINGSHAUSEN 1852). In 1879 ETTINGSHAUSEN (not published), in 1904-1906 KRASSER and in 1934 KERNER-MARILAUN preliminarily identified and labelled some fossil plants in the collection (KRASSER 1906, KERNER-MARILAUN 1934), but all these identifications need revision. KNOBLOCH (1977) mentioned several plants (*Pandanus austriacus, Geinitzia cretacea)* from the Grünbach Flora. In 1999 the authors began to study the Grünbach plant fossils (HERMAN & KVACEK 2000). The present paper represents our preliminary results on composition, palaeofloristic comparison and palaeoclimatology of the Grünbach Flora.

Material and methods

Plant fossils (more then 1000 specimens) from the Grünbach Formation are stored at the Naturhistorisches Museum (NHM, Vienna), Geologische Bundesanstalt (Geological Survey, Vienna), Institute of Palaeontology (University of Vienna), the Styrian Provincial Joaneum Museum (Graz), Narodni Museum (National Museum, Prague) and British Museum of Natural History (London). The material described in this paper is housed in the Department of Geology and Palaeontology of the NHM, collection No 1999B0057.

Plant remains are represented by leaf impressions, compressions, fructifications and fossil wood. The fossils preserve fine details of venation and morphology and show little evidence of leaves having undergone long distance transport or decay prior to burial. Some of the material yield fragments of cuticles.

Our study required photography of all plant fossils and construction of electronic database. After cleaning, the specimens were photographed under low angle incident light using 35 mm Ilford FP4 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. The leaf outlines and venation were drawn directly on the photographs. Afterwards, the photographic image was bleached away using an aqueous solution of potassium iodide and iodine. The bleached image was then conventionally fixed leaving an ink drawing that was used for subsequent study.

The electronic database created using Claris Works 5.0 software consists now of 1087 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.

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 KOH. Due to the high grade of coalification and chemical change caused probably by high content of calcium carbonate in the surrounding rock it was only possible to get small pieces of cuticle. The time for oxidation was changed from 3 to 48 hours to gain a suitable procedure timing. Best results were obtained if samples were treated 10 to 24 hours in SCHULZE 's reagent. The cuticles were examined using a light microscope Olympus BX 50. Physiognomic analysis of the Grünbach Flora using the CLAMP (Climate Leaf Analysis

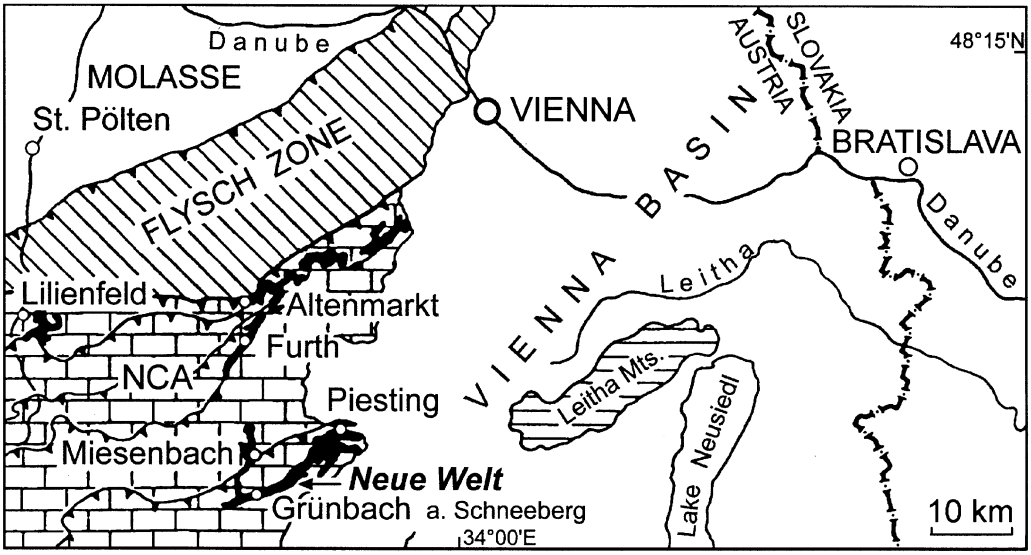


Fig. 1: Position of the Grünbach - Neue Welt Basin in the Eastern Alps, Austria (simplified from SUMMESBERGER 1997).

Multivariate Program) technique allowed us to reconstruct quantitative palaeoclimatic parameters experienced by the flora. We have used the CLAMP methodology presented in WOLFE (1993) with some modifications (HERMAN & SPICER 1997). 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. We have used 103 modern Northern Hemisphere vegetation sites scored for 31 leaf characters (WOLFE 1993, HERMAN & SPICER 1996, 1997) and correlated with 8 climate variables. These variables are: mean annual temperature (MAT), warm month mean temperature (WMMT), cold month mean temperature (CMMT), mean annual precipitation (MAP), mean growing season precipitation (MGSP), mean monthly growing season precipitation (MMGSP), precipitation during the three consecutive driest months (3DRIMO), 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.

Foliar physiognomic techniques employ a Canonical Correspondence Analysis (CANOCO) (TER BRAAK 1986, 1987-92) 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. Fig. 2a 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 103 vegetation samples positioned relative

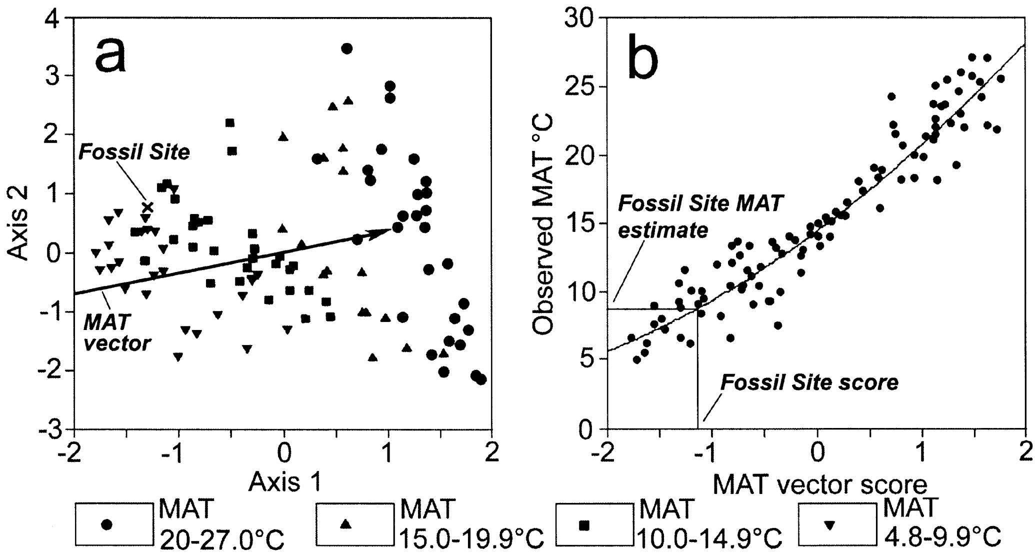


Fig. 2: Results of CLAMP analysis using CANOCO. (**a**) distribution of modern sites and an arbitrary fossil site in axis 1/axis 2 space as defined by leaf characteristics and the position of the MAT vector in this space; (**b**) MAT vector scores plotted against observed MAT values.

to its neighbours based on the characters that are possessed by the leaves of at least 20 woody dicots in that vegetation.

Fig. 2 shows how we can identify and calibrate correlations between leaf characters and one of the climate variables - in this instance, mean annual temperature. The dots (Fig. 2a) 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 (Fig. 2a: MAT vector). Fossil sites are positioned in the leaf character space side by side with modern vegetation sites (Fig. 2a shows an arbitrary fossil site).The characteristics of the fossil leaves were scored in the same way as the modern leaves and added to the statistical 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 are calibrated using modern sites with known climates. Fig. 2b 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.

Biostratigraphy of the Gosau Group in the Grünbach – Neue Welt Basin and age of the Grünbach Flora

The Grünbach - Neue Welt Basin of the Eastern Alps (see Fig. 1) is one of the largest Gosau basins. It represents a syncline (Grünbach Syncline) with an overturned limb (PLÖCHINGER 1961). The predominantly terrigenous clastic fillings of the basin (Gosau Group) consist of five lithostratigraphic units of Late Santonian to Eocene age; the three lower units represent the Cretaceous part of the Gosau Group (SUMMESBERGER 1997, SUMMESBERGER & al. 2000) (Fig. 3). Their thickness is several hundred metres.

Maiersdorf Formation ("Transgression Series" according to PLÖCHINGER 1961). It consists of conglomerates, breccias, sandstones with rudist biostromes, gastropod accummulations (*Nerinea*, *Trochactaeon*) and brachiopod limestones. 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 & al. 2000). This dating is corroborated by isotope study (probably Upper Santonian according to Sr^{86}/Sr^{87} data: KOLLMANN & al. 2000).

Grünbach Formation ("Coal-bearing Series" according to PLÖCHINGER 1961). It is represented by interbedding coalseams and freshwater/nearshore marine clastic sediments (conglomerates, sandstones, coaly siltstones). Plant fossils (the Grünbach Flora) are the most common palaeontological remains in the Grünbach Formation. Foraminifers from the Grünbach Formation at Maiersdorf belong to the *Globotruncana elevata* Zone (Lower Campanian) and nannofossil association can be assigned to the Campanian UC 15 Zone (HRADECKÁ & al. 2000). DRAXLER (*in* SUMMESBERGER 1997), who studied palynological samples from a measured section of the Grünbach Formation in the Segen Gottes coal mine of Grünbach and identified 29 species of moss, lycopod, fern, gymnosperm and angiosperm spores and pollen, emphasised that the most characteristic elements of the palynoflora are pollen of the *Normapolles* group. A rich reptile fauna is also known from this formation at Muthmannsdorf where carnosaur, iguanodon, pterosaur, scelidosaur and crocodile remains have been found (BUNZEL 1871-1873, SUMMESBERGER 1997).

Piesting Formation ("Inoceramus Beds" according to PLÖCHINGER 1961). It consists predominantly of sandstones and siltstones with marine fossils of Late Campanian and Maastrichtian age. Foraminifers from the Piesting Formation at Grünbach can be attributed to the *Globotruncana ventricosa* Zone (lower part of the Upper Campanian). However, the major part of the Piesting Formation yields Late Campanian - Maastrichtian foraminifers (HRADECKÁ & al. 2000). Large foraminifers *Orbitoides* are very common in the so called *Orbitoides* Sandstone 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 & al. 2000). The Late Campanian ammonite *Pseudokossmaticeras brandti* (REDTENBACHER) occurs at Grünbach, the Early Maastrichtian *Pachydiscus epiplectus* (REDTENBACHER) at Muthmannsdorf (SUMMESBERGER 1997), and the Late Campanian belemnite *Belemnitella hoeferi* (SCHLOENBACH) at Grünbach (CHRISTENSEN 1998).Triporate angiosperm pollen of the *Normapolles* group allow HRADECKÁ & al. (2000) to assign some samples from the Piesting Formation near Grünbach to the Upper Campanian.

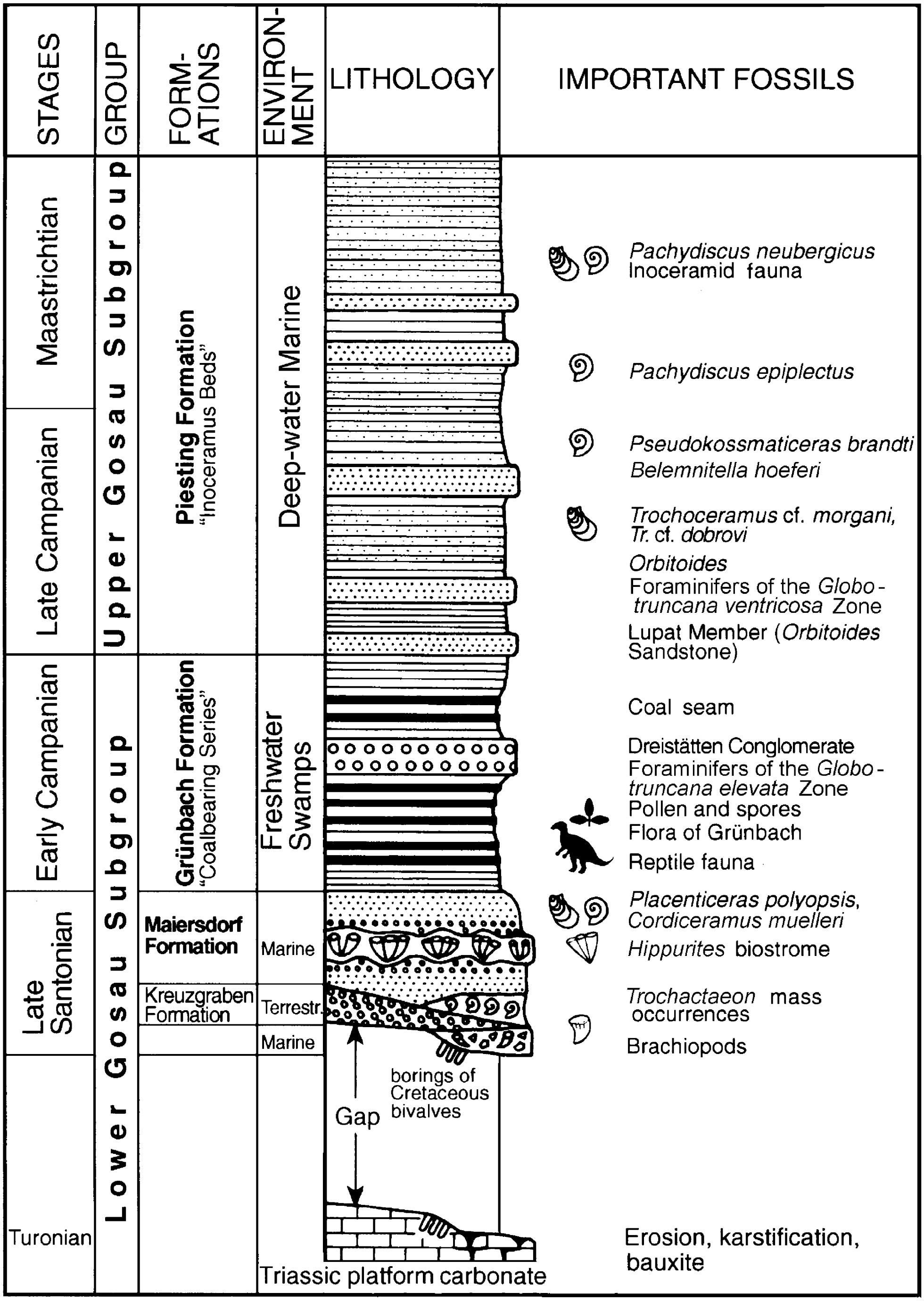


Fig. 3: Section of the Gosau Group in the Grünbach - Neue Welt Basin in the Eastern Alps, Austria (simplified from SUMMESBERGER & al. 2000) and the stratigraphic position of the plant-bearing beds of the Grünbach Flora.

A rich fauna recently discovered from the Piesting Formation at the sports field of Piesting yields diverse Maastrichtian inoceramids; the ammonite *Pachydiscus neubergicus* from the same locality indicates Lower to lower Upper Maastrichtian (TRÖGER & al. 2000, KOLLMANN & al. 2000). The poorly preserved nannoflora belongs most probably to the standard zone CC 24 (Early Maastrichtian). The palaeomagnetic study of the section demonstrates that it probably correlates with Chron 31R just above the Campanian-Maastrichtian boundary (TRÖGER & al. 2000). The neighboured outcrop at the roadcut S near Piesting yielded *Trochoceramus* cf. *morgani* and *T.* cf. *dobrovi* of latest Campanian - Early Maastrichtian age (TRÖGER & al. 2000).

The Early Campanian age of the Grünbach Flora is therefore based on foraminifers, spores and pollen from the Grünbach Formation and on the correlation of plant-bearing deposits with the underlying Maiersdorf and the overlying Piesting Formations yielding stratigraphically important marine fossils.

The rich shallow-marine fauna of the Campanian-Maastrichtian part of the Gosau Group belongs to the Theian Realm (KOLLMANN, 2000). The dominating palaeogeographic situation during accummulation of the plant-bearing deposits of the Grünbach Formation is that of large island with unknown relief, at least temporary connected to the continent. Terrestrial freshwater swamps and shallow water sediments indicate a relatively large deltaic plain under warm and humid climate conditions. It was inhabited by carnosaurs, iguanodons, pterosaurs, scelidosaurs and crocodiles (BUNZEL 1871 - 1873).

Systematics of the Grünbach Flora

The Grünbach Flora is relatively rich in the number of fossil plants consisting of approximately 60 taxa belonging to algae, possible Hepaticopsida, Equisetopsida, Polypodiopsida, Cycadopsida (Cycadales), Pinopsida (twigs and cones), Liliopsida, Magnoliopsida (aquatic and terrestrial dicot leaves, angiosperm fructifications).

Several kinds of fossils recalling monopodial thalli are only putatively assigned to algae. Remains of liverworts showing agregates of dichotomously branching thalli are preliminarily assigned to the genus *Thallites* WALTON.

Equisetopsida. Stem with a node showing remains of leaf sheaths was assigned to the genus *Equisetites* STERNBERG (Pl. 1, fig. 4).

Polypodiopsida. More then 8 different species of ferns were recorded. *Cladophlebis* sp. 1 shows bipinnate fronds bearing ovate-lanceolate slightly forward curved entire-margined pinnules 3-5 mm long; *Cladophlebis* sp. 2 (Pl. 1, fig. 1) shows simply or perhaps bipinnate fronds bearing lanceolate pinnae with serrate margins; venation of the pinnule is pinnate, each secondary vein ends in a marginal teeth. *Coniopteris* sp. has bipinnate fronds bearing wedge-shaped pinnules. *Gleichenites* (= *"Gymnogramme"*) shows bipinnate fronds with ovate slightly decurrents pinnules.

Another fern provisionally assigned by KRASSER (1906) to the recent genus *Marattia* (Pl. 1, fig.3) is a characteristic element of the Grünbach Flora. Morphologically diverse lanceolate, serrate leaves of this fern ranging up to 8 cm in length are attached to long petioles. Leaf venation is pinnate with well pronounced secondary veins. This fern is almost certainly of marattialean affinity, but we are not absolutely sure that it belongs to the genus *Marattia*.

An interesting element of the flora is *Marsilea* L., the most complete specimens of which show four leaflets arranged in a rosette. Each leaflet is wedge-shaped entire-margined with dichotomous venation. Morphological similarity of this fern to modern representatives of *Marsilea* allows us to assign this fossil plant to the recent genus with a high degree of certainity.The genus *Monheimia* DEBEY & ETTINGSHAUSEN originally described from the Upper Cretaceous of Germany is also present in the Grünbach Flora. It shows dichotomously branched lamina sometimes with terminally arranged sori.

Cycadopsida. The most unusual feature of the flora is the occurrence of a cycad *Nilsonia* sp. (Fig. 4a). This typically Jurassic and Lower Cretaceous genus has in the Grünbach Flora its stratigraphically latest record in Europe. In North-eastern Asia *Nilsonia* is abundant in some Santonian - Campanian floras (HERMAN 1999). The only specimen shows lower part of the entire-margined lamina with characteristic unforked densely arranged secondaries. Its lamina is typically attached to the upper part of the midrib. Therefore, morphologically this leaf is very similar to typical *Nilsonia*. Unfortunately, this determination is not evidenced by the epidermal study: the preservation of a cuticle obtained after maceration was too poor.

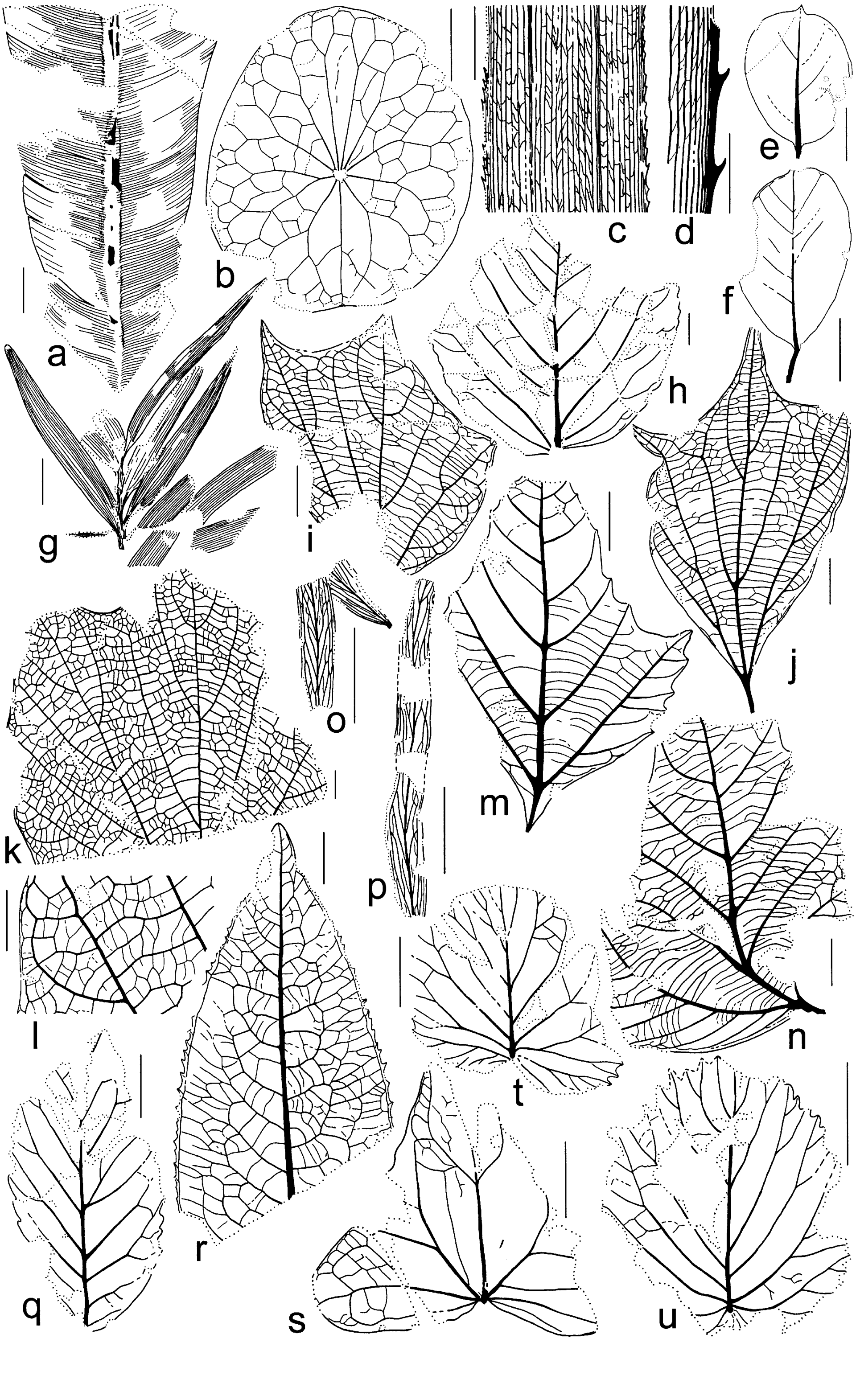
Pinopsida. The conifers *Lindleycladus* HARRIS and possibly *Podozamites* C.F.W. BRAUN may represent other archaic taxa. *Lindleycladus* cf. *lanceolatus* (LINDLEY & HUTTON) HARRIS (Fig. 4g) shows at least 8 lanceolate leaves helically arranged on an axis. Each leaf is 5 - 6 cm long showing parallel venation.

The most frequent conifer in the Grünbach Flora is *Geinitzia* cf. *cretacea* ENDLICHER represented by twigs with needles 1.5 - 2 cm long; several twigs have terminally born ovuliferous cones (4 - 5 cm long) attached. They show helically arranged peltate cone scales. Additionally, there are 3 other probably taxodiaceous species (*Cyparissidium* sp., *Pagiophyllum* sp. and *Brachyphyllum* sp.) represented by twigs with shorter scale-like leaves attached.

Liliopsida. Monocotyledons are represented by 3 genera (KVACEK & HERMAN, in preparation): *Pandanites* TUZSON, *Sabalites* SAPORTA and *Zingiberopsis* HICKEY & PETERSON.

Pandanites trinervis (ETTINGSHAUSEN) KVACEK & HERMAN (KVACEK & HERMAN, in preparation) is by far the most common fossil plant in the collection (Figs. 4c, d; Pl. 1, fig. 2). Our field observations demonstrate that this species probably composed a monodominant community. It is represented by numerous broken lanceolate leaves showing typical M-shape in a transversal section. There are numerous spines on the leaf margins and on an abaxial side of a midrib. Basal parts of leaves show auricles, apex is acute.

Fig. 4: Selected fossil plants of the Grünbach Flora (scale bars represent 1 cm). (**a**) *Nilsonia* sp., NHM 1999B0057/0079; (**b**) "*Brasenia*" sp., NHM 1970/1396/0156; (**c**), (**d**) *Pandanites trinervis* (ETTINGSHAUSEN) KVACEK & HERMAN, NHM 1999B0057/0154, NHM 1999B0057/0041; (**e**), (**f**) "*Pyrus* " sp., NHM 1999B0057/0240, NHM 1999B0057/0270; (**g**) *Lindleycladus* cf. *lanceolatus* (LINDLEY & HUTTON) HARRIS, NHM 1999B0057/0246; (**h**) *Viburniphyllum* sp. 1, NHM 1999B 0057/0157; (**i - l**) *Platanus* aff. *senonensis* (KNOBLOCH) KNOBLOCH, NHM 1999B0057/0225, NHM 1999B0057/0180A, NHM 1999B0057/0258, (detail of leaf margin and venation); (**m**), (**n**) *Platanus laevis* (VELENOVSKY) VELENOVSKY, NHM 1999B0057/0263A, NHM 1999B0057/0263B; (**o**), (**p**) *Grevilleophyllum* sp., NHM 1999B0057/0089A, NHM 1999B0057/0089B; (**q**) *Quercophyllum ("Castanea")* sp., NHM 1999B0057/0098; (**r**) *Dicotylophyllum* sp., NHM 1999B0057/0030; (**s**) *Menispermites* sp., NHM 1999B0057/0089; (**t**), (**u**) *Viburniphyllum* sp. 2, No. NHM 1999B0057/0268, NHM 1999B0057/0269.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Large but incompletely preserved palm leaves belong probably to the genus *Sabalites* SAPORTA (Pl. 2). Leaves consist of undivided palmately arranged rays attached to long, deltoid, gradually tapering rachis. Single leaf impression showing parallel venation belongs probably to *Zingiberopsis*. It is very similar to *Z. riggauensis* KNOBLOCH described from Cenomanian-Turonian deposits of Germany (KNOBLOCH, 1979).

Magnoliopsida. Dicotyledonous angiosperms are mostly recorded as leaf impressions or compressions. Laurales are represented by the genera *Myrtophyllum* HEER and *Grevilleophyllum* VELENOVSKY (Figs. 4o, p); the latter showing elongately elliptical, entire-margined leaves, the venation is pinnate brochidodromous.

Platanoid leaves are represented by two species of *Platanus* L. (Figs. 4i - n). They both show lobed palmately divided lamina but differ from each other in leaf shape, venation (camptodromous or craspedodromous) and margin (entire or dentate). Aquatic angiosperms assigned to the genera *Quereuxia* KRYSHOTOFOVICH and *Brasenia* SCHREBER (Fig. 4b) are characteristic for the Grünbach Flora. *Quereuxia* is represented by compound leaves or separate leaflets and several poorly preserved rosettes of leaves. Each leaflet is wedge-shaped with a dentate margin and craspedodromous to nearly actinodromous venation. Round or elliptic peltate leaves assigned provisionally to *Brasenia* show a lamina with an entire margin, petiole inserted nearly centrally, primary venation actinodromous.

One of the most abundant components of the flora is *Sapindophyllum* ETTINGSHAUSEN. Small, entire-margined, mucronate leaves with brochidodromous venation are assigned provisionally to the recent genus *Pyrus* L. (Figs. 4e, f). Pinnately compound leaves probably belong to the genus *Sapindopsis* FONTAINE.

Other angiosperm taxa are less numerous in the collection. They are assigned to the following taxa: *Quercophyllum* FONTAINE (Fig. 4q), *Magnoliaephyllum?* SEWARD, *Citrophyllum ?* UPCHURCH & DILCHER (Pl. 3), *Debeya* MIQUEL, *Dicotylophyllum* SAPORTA (Fig. 4r), *"Dryandra"* R. BROWN, *Menispermites* LESQUEREUX (Fig. 4s), *Ternstroemites* BERRY, *Viburniphyllum* NATHORST (Figs. 4h, t, u), etc. Angiosperm fructifications are assigned to the genus *Ceratoxylon* VELENOVSKY et VINIKLÁR and also, traditionally, to *Sparganium* L. Some carbonatized seeds and fruits are not yet identified.

As to the number of species, the Grünbach Flora is dominated by angiosperms (about 70 %) followed by ferns, conifers and other groups of plants. The relatively large number of relict plants in the Grünbach Flora (*Nilsonia*, *Lindleycladus*, possibly *Podozamites*) probably reflects the existence of the flora in an 'island refuge': these plants could survive there due to geographic and/or environmental isolation of the area.

The Grünbach Flora is a typical flora of the Euro-Sinian palaeophytogeographic region (VAKHRAMEEV 1991). Although there is no direct equivalent of the Grünbach Flora, taxonomically the most similar floras are those from the Senonian of the Czech Republic (NEMEJC 1957, 1961, NEMEJC & KVACEK 1975) and probably the Maastrichtian of Romania (TUZSON 1914). The taxodiaceous conifer *Geinitzia cretacea* is shared by the Grünbach Flora and the Czech Senonian flora, but the most pronounced similarities are in angiosperm taxa: *Myrtophyllum, Grevilleophyllum, Platanus, Magnoliaephyllum, Quercophyllum* and *Debeya* are recorded in both floras. *Pandanites* and *Sabalites* occur in both Grünbach Flora and the Maastrichtian flora of Romania.

The Senonian flora of Quedlinburg (RÜFFLE & TROSTHEIDE 2000) is also similar to the Grünbach Flora in having such taxa as *Geinitzia cretacea, Zingiberopsis, Platanus, Myrtophyllum, "Quercus"* (*Quercophyllum*) and probably *Monheimia*.

Several Turonian or Campanian fossil plants have been described from the Tambergau locality in the Obersulzbach Valley, Upper Austria (TYROFF 1984). Although these plants come from the Gosau Group (KOLLMANN & SUMMESBERGER, pers. comm. 2001), only a few taxa are common in this flora and the Grünbach Flora: *Coniopteris*, *Geinitzia cretacea* (= *Sequoia reichenbachii* (GEINITZ) HEER and *Geinitzia formosa* HEER) and *Myrtophyllum*.

Some taxa of the Grünbach Flora are also known from the Cenomanian Peruc-Korycany Flora of Bohemia (FRIC & BAYER 1902, Z. KVACEK 1983, J. KVACEK & KNOBLOCH 1997, J. KVACEK & DILCHER 2000). These floras yield identical (or similar) species among the genera *Nilsonia, Lindleycladus, Geinitzia, Myrtophyllum, Grevilleophyllum, Magnoliaephyllum, Platanus, Sapindopsis, Debeya, "Dryandra"* etc.

CLAMP analysis of the Grünbach Flora

Physiognomic analysis of the Grünbach Flora (28 dicot leaf morphotypes were scored for as many of the 31 characters as were preserved) using the CLAMP technique yielded (Table 1) a mean annual temperature of 15.3°C, a warm month mean temperature of almost 22°C, a cold month mean temperature well above freezing at 8.8°C, a growing season length of 8.6 months, a mean annual precipitation of 1373 mm, a mean monthly growing season precipitation of 95 mm, a mean growing season precipitation of 840 mm, and a precipitation during 3 consecutive driest months of 164 mm. Therefore, the Grünbach Flora experienced a humid sub-tropical to marine mesothermal climate (climates Ca and Cb according to Köppen's classification) with warm/hot summers and short relatively dry, but not arid, seasons. This is corroborated by lithological climate indicators (bauxites of the Gosau Group: see Fig. 3) as well as by the presence of large foraminifers, rudists, corals and a reptile fauna in the Santonian-Campanian of the Neue Welt Basin. The invertebrate fauna of the Gosau Group belongs to the Tethyan (or Theian: KOLLMANN 2000) palaeobiogeographic realm (KAUFFMAN 1973, SOHL 1987) which probably reflects not exclusively tropical but also sub-tropical climates.

Palaeomagnetic directions from the Gosau K/T boundary beds in the Elendgraben near Salzburg, Austria indicate a palaeolatitude of the Gosau Basin of 32°N (PREISINGER et al. 1986). A recent palaeomagnetic investigation of Grünbach yielded a palaeolatitude about 1000 km south of the present day position of the plant-bearing deposits (SUMMESBERGER 1997, SCHOLGER, pers. comm. 2001). To check this hypothesis we decided to compare the Grünbach palaeoclimate with those obtained from CLAMP analysis of the Senonian flora of Zliv, Klikov and Hluboka in the Czech Republic (NEMEJC 1961, NEMEJC & KVACEK 1975).

Despite some differences in taxonomic composition and angiosperm leaf physiognomy in these two floras, we obtained similar palaeoclimatic results, both for palaeotemperatures and precipitation (Table 1). 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 climates

Tab. 1: Climate data for the Early Campanian Grünbach Flora and the Senonian flora of Zliv, Klikov and Hluboka, the Czech Republic.

Climate data for the Senonian (Santonian-Campanian) floras of Eurasia

FOSSIL FLORA	Palaeolatiude	Mean Annual Temperature (°C)	Warm Month Mean Temperature (°C)	Cold Month Mean Temperature (°C)	Mean Annual Precip. (mm)	Mean Growing Season Precip. (mm)	Mean Monthly Growing Season Precip. (mm)	Precip. during 3 Consecutive Driest Month (mm)	Length of Growing Season (months)
ZLIV, KLIKOV, HLUBOKA Senonian	40°N	15.6	22.2	9.0	1284	780	88.6	144.1	8.7
GRÜNBACH Early Campanian	32°N	15.3	21.8	8.8	1373	840	95.2	164.1	8.6
Standard Deviation		1.8	3.1	3.3	430	280	23	70	1.1

of two relatively small islands (or sometimes peninsulas) the climates of which were considerably influenced by the warm Tethys Ocean. Moreover, we cannot be sure that these floras are of the same age; the Grünbach Flora may reflect a relatively cooler time interval within the Senonian and therefore could have had a more southerly position despite the similarity of temperature.

Conclusions

The Early Campanian Grünbach Flora existed in a large island or peninsula with unknown relief. Plants inhabited freshwater swamp, lacustrine, floodplane and river delta environments.

The Grünbach Flora consists of approximately 60 taxa belonging to algae, possible Hepaticopsida, Equisetopsida, Polypodiopsida, Cycadopsida (Cycadales), Pinopsida (twigs and cones), Liliopsida, Magnoliopsida (aquatic and terrestrial dicot leaves, angiosperm fructifications). Based on the number of species, the Grünbach Flora is dominated by angiosperms (about 70 % of species) followed by ferns, conifers and other groups of plants. Large number of relict plants in the Grünbach Flora (*Nilsonia*, *Lindleycladus*, possible *Podozamites*) probably survived until Early Campanian due to geographic and/or environmental isolation of the flora in an 'island refuge'.

The Grünbach Flora is a typical flora of the Euro-Sinian Region. Although there is no direct equivalent of the Grünbach Flora, the Senonian and Cenomanian floras of the Czech Republic and Germany are the closest to the Grünbach Flora.

CLAMP analysis of the Grünbach Flora shows that its plants experienced a humid subtropical to marine mesothermal climate with warm/hot summers and short relatively dry, but not arid, seasons. 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 can not be used as an argument against this hypothesis, because both the Czech Senonian and the Grünbach floras reflect climates of two islands the climates of which were considerably influenced by the warm Tethys Ocean.

Acknowledgements

We are extremely grateful to Dr. H. KOLLMANN from the Museum of Natural History in Vienna for logistical and financial support which made this work possible and for the useful discussions. Our warm thanks go to Dr. H. SUMMESBERGER who discussed with us the Cretaceous geology and stratigraphy of the Neue Welt Basin, provided us with publications and organised field excursion to the vicinity of Grünbach. We also thank Dr. J. EDER for her help with the collection, literature, useful discussions and kind hospitality, Prof. R.A. SPICER who helped us with CLAMP analysis and Prof. Z. KVACEK for the discussion on fossil plant taxonomy.

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Plate 1

Fig. 1: *Cladophlebis* sp.
Grünbach, Lower Campanian, Inv. NHM 1999B0057/0238; x1 natural size.

Fig. 2: *Pandanites trinervis* (Ettingshausen) Kvacek & Herman
Grünbach, Lower Campanian, Inv. NHM 1999B0057/0239; x2 natural size.

Fig. 3: *Marattia* sp.
Grünbach, Lower Campanian, Inv. NHM 1999B0057/0236; x1 natural size.

Fig. 4: *Equisetites* sp.
Grünbach, Lower Campanian, Inv. NHM 1999B0057/0252; x1 natural size.

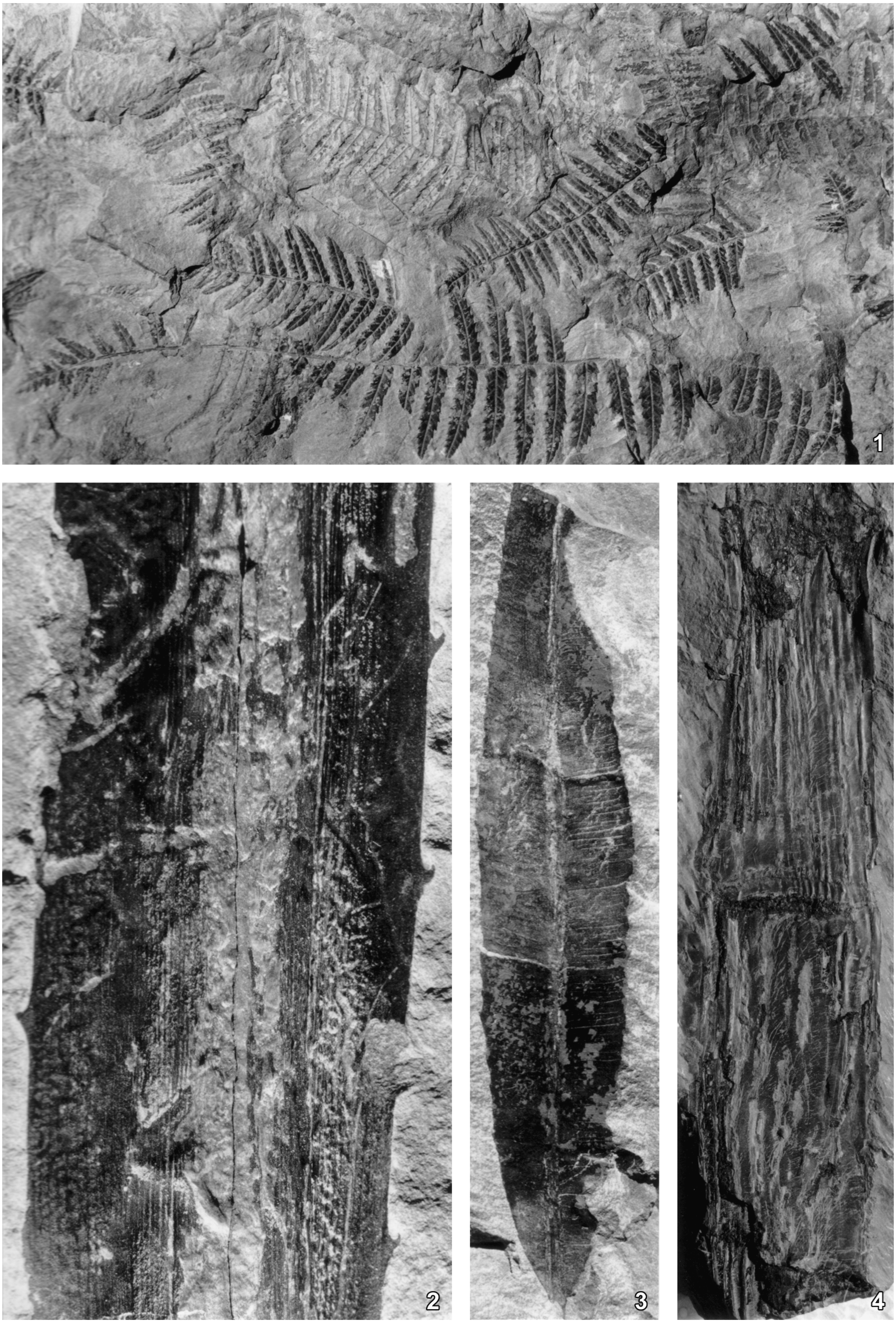
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Plate 2

Sabalites longirhachis **(Unger) Kvacek & Herman**
Grünbach, Lower Campanian, Inv. NHM 1999B0057/0235; x0.5 natural size.

Plate 3

***Citrophyllum* (?) sp.**
Grünbach, Lower Campanian, Inv. NHM 1999B0057/0237; x1 natural size.


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