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The Campanian Grünbach Flora of Lower Austria: palaeoecological interpretations

By Jiří Kvaček[1] and Alexei Herman[2]

(With 2 text-figures and 2 plates)

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Abstract

Palaeoecology of Grünbach wetlands is reconstructed based on fossil plant morphology, anatomy and taphonomic observations. Five plant communities have been reconstructed: aquatic plant community, swamp-semiaquatic plant community, juglandaceous and palm wetland forest, riparian community and mesophytic forest community.

Introduction

The Grünbach Flora comes from the Lower Campanian coal-bearing strata of the Grünbach Formation (Gosau Group) in the Grünbach - Neue Welt Basin in the Northern Calcareous Alps in Austria. It represents one of a few till now described Late Cretaceous antracophilous floras in the Northern Hemisphere. The coalseams of the Grünbach Formation have been exploited from the second half of the 19th century until the 1960s. Numerous well-preserved plant fossils from beds accompanying the coal seams are housed in natural history collections 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.

Several important taxa of the flora were described by Ettingshausen (1852) and Unger (1850, 1852, 1867). The flora was later briefly discussed by Krasser (1906) and Kerner-Marilaun (1934). A project of monographic description of the flora was initiated by Dr. H. Kollmann from the Natural History Museum in Vienna in 1999. Till now several papers on this flora were published by present authors (e.g. Herman & J. Kvaček 2002a, b; J. Kvaček & Herman 2004). This paper is focused on plant palaeoecology and description of plant communities.

The Grünbach Flora, in contrast to numerous floras coming from clastic sediments (compare Uličný et al. 1997), has unique taxonomic composition. It is rich in monocots, particularly pandans, as well as ferns. During our field excavations in Grünbach we learned that pandan leaf remains are most abundant fossils in the locality.

[1] Dr. Jiří Kvaček, National Museum, Prague, Vaclavské nám. 68, 115 79, Praha 1, Czech Republic. – e-mail: jiri.kvacek@nm.cz

[2] Dr. Alexei Herman, Geological Institute, Russian Academy of Sciences, 7 Pyzhevskii Pereulok, 119017 Moscow, Russia. – e-mail: herman@ginras.ru

Material

Plant fossils (more than 1000 specimens) from the Grünbach Formation are stored in the Natural History Museum, Vienna (NHM), Geological Survey, Vienna, Institute of Palaeontology (University of Vienna), the Styrian Provincial Joanneum Museum (Graz), National Museum, Prague (NMP) 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, and in the Department of Palaeontology of the NMP, collection numbers beginning with K. Plant remains are represented by leaf impressions, compressions, fructifications and fossil wood.

The Grünbach Flora is moderately diverse, comprising approximately 52 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 in a dump near Grünbach village carried out in 2001 and 2003.

Stratigraphic position and age of the Grünbach Flora

The Grünbach Formation ("Coal-bearing Series" according to PLÖCHINGER 1961) is represented by interbedding coalseams and freshwater/nearshore marine clastic sediments (conglomerates, sandstones, and coaly siltstones). Plant fossils are the most common palaeontological remains in the Grünbach Formation. Foraminifers from the Grünbach Formation at Maiersdorf NE of Grünbach belong to the *Globotruncana elevata* Zone (Lower Campanian) and the nannofossil association can be assigned to the Campanian UC 15 Zone (HRADECKÁ & al. 2000). DRAXLER (*in* SUMMESBERGER 1997), who studied palynological spectra from a measured section of the Grünbach Formation in the Segen Gottes coal mine in Grünbach, identified 29 species of moss, lycopod, fern, gymnosperm and angiosperm spores and pollen. She 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).

The Early Campanian age of the Grünbach Flora is based on foraminifers from the Grünbach Formation and on the correlation of plant-bearing deposits with the underlying Maiersdorf Formation (PLÖCHINGER 1961, SUMMESBERGER & al. 2000) and the overlying Piesting Formation (SUMMESBERGER 1997; CHRISTENSEN 1998; HRADECKÁ & al. 2000; SUMMESBERGER & al. 2002; TRÖGER & al. 2001) yielding stratigraphically important marine fossils and palynomorphs.

Plant communities

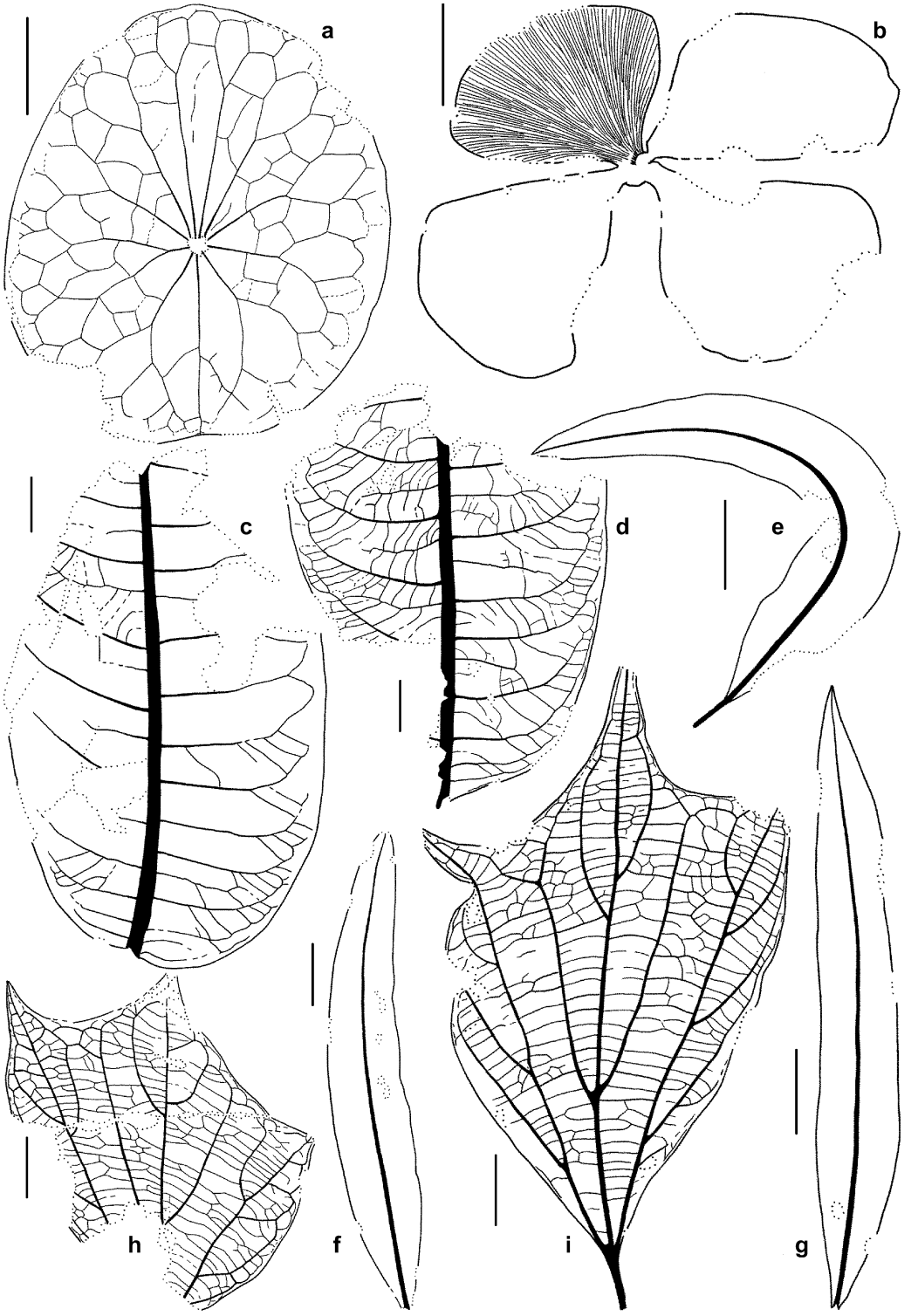
Interpretation of the Grünbach plant communities is based on plant morphology (leaf size, shape and texture), anatomy (cuticular characters, aerenchymatic tissues of water plants), the autecology of some taxa (such as *Marsilea*, water plants, palms, pandans), their abundance and taphonomic observations. The latter have been limited, because a section in the abandoned coal mine is not accessible. Nevertheless, taphonomic observations showed constant association of particular plant remains on one hand-specimen as well as associations of particular plants and sedimentary types. Degree of degradation and decomposition

of fossil leaves was used as evidence of fossil plant transportation. Using these criteria the following plant communities composing the Grünbach Flora could be reconstructed.

Aquatic plant community includes two water plants: *Nelumbites* and *Quereuxia*. *Nelumbites* has round or elliptic, entire-margined, peltate, floating leaves (Fig. 1a) with well-developed aerenchyma (Pl. 1, fig. 1). *Quereuxia* is represented by small triangular or elliptic leaves forming leaf rosettes (Pl. 1, fig. 2). The leaves of *Nelumbites* and leaf rosettes of *Quereuxia* with leaflets still attached are well preserved and show low mechanical degradation which is an evidence of short transportation of leaf material. Aquatic plant remains are abundant, therefore we assume the presence of the extensive shallow water environment in Grünbach.

Swamp/semiaquatic plant community is dominated by pandans with elongated leaves. *Pandanites trinervis* (ETTINGSHAUSEN) J. KVAČEK & HERMAN is characterized by strap-like, parallel-veined, typically armed leaves, which are M-shaped in transverse section (Pl. 1, fig. 4). Many leaves show armed keels, attenuate apices and auriculate bases (J. KVAČEK & HERMAN 2004). Leaf accumulations of *Pandanites trinervis* are typical for this locality (Pl. 2, fig. 4). These plants probably formed monodominant stands in swampy environment and were the main coal-forming biomass. In all probability the community also included semi-aquatic herbaceous monocots (*Araciphyllites* etc.), horsetails *Equisetites* and ferns such as *Marsilea* (Fig. 1b) and *Cladophlebis* (Pl. 1, fig. 3). *Araciphyllites* possesses parallel venation emerging from a multistranded costa (J. KVAČEK & HERMAN 2004). Palm trees with *Sabalites* leaves could occur there forming groups similar to recent hammocks. *Sabalites longirhachis* (UNGER) J. KVAČEK & HERMAN is characterized by costapalmate, entire, lanceolate leaves with a long rhachis (Pl. 2, fig. 1). It should be emphasized 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 including palms and pandans (UHL & DRANSFIELD 1987: Pl.34D).

Juglandaceous and palm wetland forest was dominated by plants with *Sapindophyllum* leaves of probably juglandaceous affinity, palms *Sabalites* and conifers *Geinitzia*. *Sapindophyllum pelagicum* (UNGER) VELENOVSKÝ is represented by compound leaves consisting of entire-margined, petiolate, elliptic leaflets with brochidodromous venation (Figs. 1c,d). Fossil *Sapindophyllum* 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* and twigs of physiognomically evergreen conifer *Geinitzia* occurring in the same type of sediment as *Sapindophyllum* 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 hook-like keeled leaves (Pl. 2, fig. 3). 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 *Pandemophyllum* (?) were also common here (Figs. 1e-g). 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 *Gymnogramme*, *Monheimia*, *Cladophlebis*, *Onychiopsis* and angiosperms *Myricophyllum*, *Grevilleophyllum*, *Menispermites* etc.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Riparian community was dominated by platanoid trees, *Credneria* being the most numerous among them. *Credneria* leaves are entire-margined, trilobed, with acute base, actinodromous primary veins and brochidodromous secondary veins (Figs. 1h, i). Their leaves and leaf fragments are usually preserved in coarser-grained sandstones and sandy siltstones reflecting a high-energy depositional environment (Pl. 2, fig. 2). The second common plant of this community is a fern "*Pecopteris*" *striata* STERNBERG. 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*, which fossil leaves usually show a significant mechanical degradation.

Mesophytic forest community consisted probably of conifers *Pagiophyllum*, *Podozamites* and perhaps some angiosperms (*Leguminosites*). *Pagiophyllum* shows delicate shoots with hook-like 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 envrionemnt. Rare *Podozamites* plants were probably mixed with *Pagiophyllum* trees. Plant remains recorded from this community are often fragmentary and uncommon.

Discussion: reconstruction of the Grünbach vegetation.

The Grünbach Flora includes palms (*Sabalites*) and numerous lauraceous angiosperms (*Pandemophyllum* (?), *Grevilleophyllum* (?) etc.), therefore we interpret it as a typical flora of the Euro-Sinian Region which was characterised by a subtropical climate (VAKHRAMEEV 1991). The rich shallow-marine fauna of the Campanian – Maastrichtian part of the Gosau Group belongs to the Theia Realm. Physiognomic CLAMP analysis of the Grünbach Flora shows that its plants experienced a humid sub-tropical to oceanic mesothermal frostless climate with warm/hot summers and short relatively dry, but not arid, seasons (HERMAN & J. KVAČEK 2002a). The conclusion on the high humidity of the climate is corroborated by the extensive coal accumulation in the Grünbach Formation and by lack of sclerophyllous plants in the Grünbach Flora. 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.). 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.

Fig. 1: Fossil plants of the Grünbach Flora, dominated in different plant communities (scale bars represent 1 cm). (**a**) *Nelumbites* sp., NHM 1970/1396/0156; (**b**) *Marsilea* sp. (venation is shown schematically), NHM 1999B0057-0509; (**c**, **d**) *Sapindophyllum pelagicum* (UNGER) VELENOVSKÝ, NHM 1999B0057-0283, NHM 1999B0057-0281; (**e - g**) *Pandemophyllum* (?) *proteoides* (UNGER) comb. nov., NHM 1999B0057-0347, NHM 1999B0057-0363, NHM 1999B0057-0339; (**h**, **i**) *Credneria* aff. *senonensis* (KNOBLOCH) NĚMEJC & Z. KVAČEK, NHM 1999B0057-0125, NHM 1999B0057-1801.

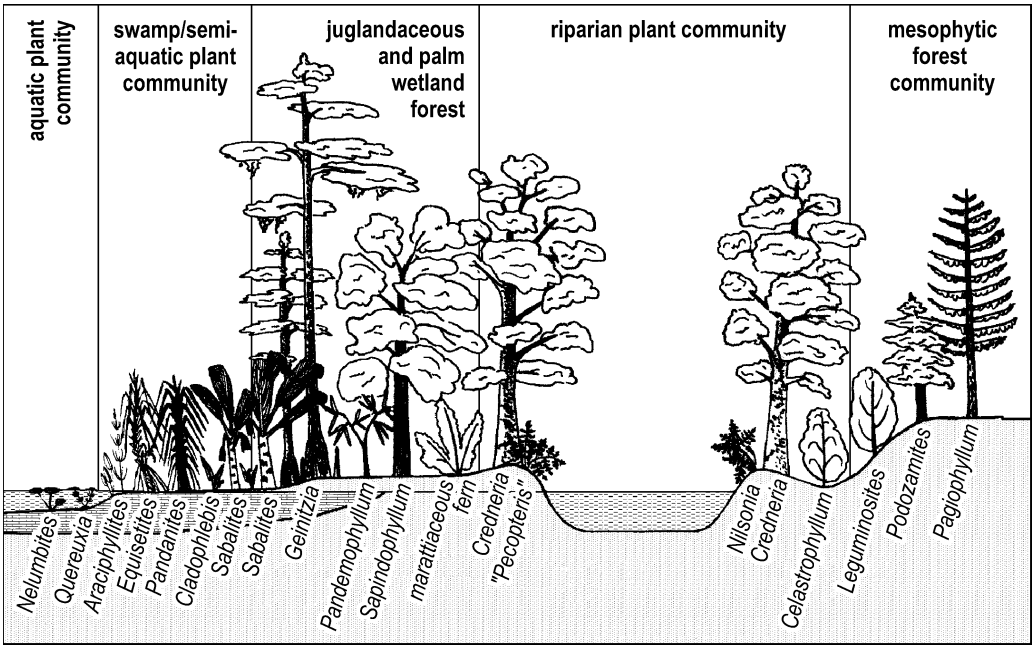

Fig. 2: Reconstruction of the Grünbach wetland vegetation.

From our observations we can reconstruct the following landscape existed during the accumulation of the plant-bearing Grünbach Formation (Fig. 2). In coastal lowlands and plains of an island, large open bodies of shallow fresh water (ponds and oxbow lakes) with floating *Quereuxia* and *Nelumbites* leaves were surrounded by swampy lowlands inhabited by community dominated by pandans and ferns with palm hammocks. 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 depending on the soil wetness and exposition to the sun. Small rivers or streams probably crossed this lowland. Their margins were inhabited by riparian plant community composed mainly of ferns "*Pecopteris*" and numerous shrubs or trees of platanoid angiosperms. Away from lakes, swamps and rivers, in drier places, mesophytic predominantly coniferous forest existed.

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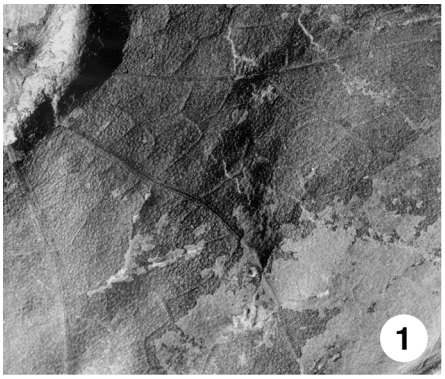
Plate 1

Fig. 1: ***Nelumbites*** **sp.**
Detail of leaf showing well-developed aerenchyma (cell-like microstructure); Grünbach, Lower Campanian, Inv. NHM 1999B0057-0494; x 3 natural size.

Fig. 2: ***Quereuxia angulata*** **(LESQUEREUX) KRYSHTOFOVICH**
Grünbach, Lower Campanian, Inv. NHM 1999B0057-0315; x 2.2 natural size.

Fig. 3: ***Cladophlebis*** **sp.**
Grünbach, Lower Campanian, Inv. NHM 1999B0057-0560; x 0.82 natural size.

Fig. 4: ***Pandanites trinervis*** **(ETTINGSHAUSEN) J. KVAČEK & HERMAN**
Grünbach, Lower Campanian, Inv. NHM 1999B0057-0239; x 0.5 natural size.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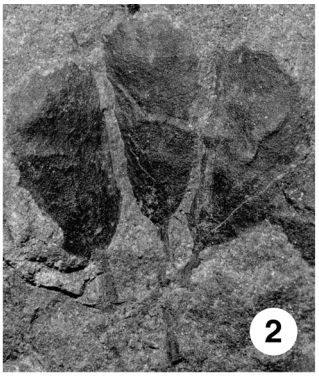
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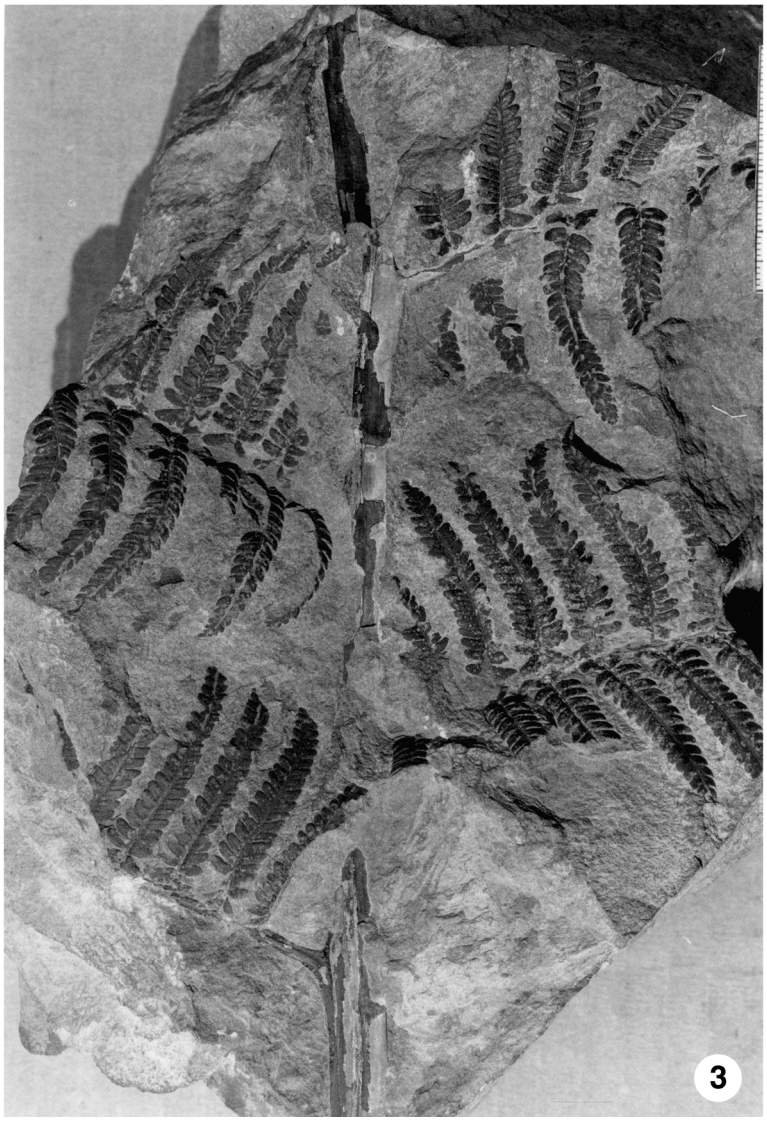
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Plate 2

Fig. 1: ***Sabalites longirhachis*** **(UNGER) J. KVAČEK & HERMAN**
Grünbach, Lower Campanian, Inv. NHM 1999B0057-0533; x 0.55 natural size.

Fig. 2: ***Credneria*** **ex gr.** ***senonensis*** **(KNOBLOCH) NĚMEJC & Z. KVAČEK**
Enrolled fossil leaf in coarse-grained probably alluvial sandstone; Grünbach, Lower Campanian, Inv. NHM 1999B0057-0314; x1.1 natural size.

Fig. 3: ***Geinitzia formosa*** **HEER**
Grünbach, Lower Campanian, Inv. NHM 1999B0057-1800; x 1.2 natural size.

Fig. 4: Leaf accumulation typical of the Grünbach locality.
Prevailing remains are fossil leaves of *Pandanites trinervis* (ETTINGSHAUSEN) J. KVAČEK & HERMAN. Grünbach, Lower Campanian, NMP K 451; x 0.75 natural size.


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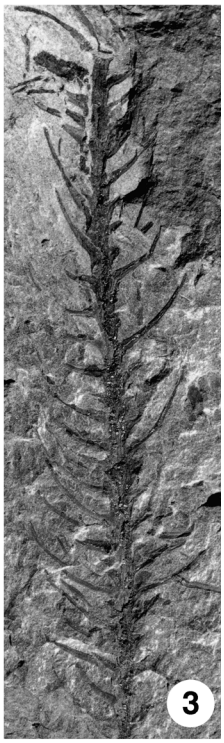
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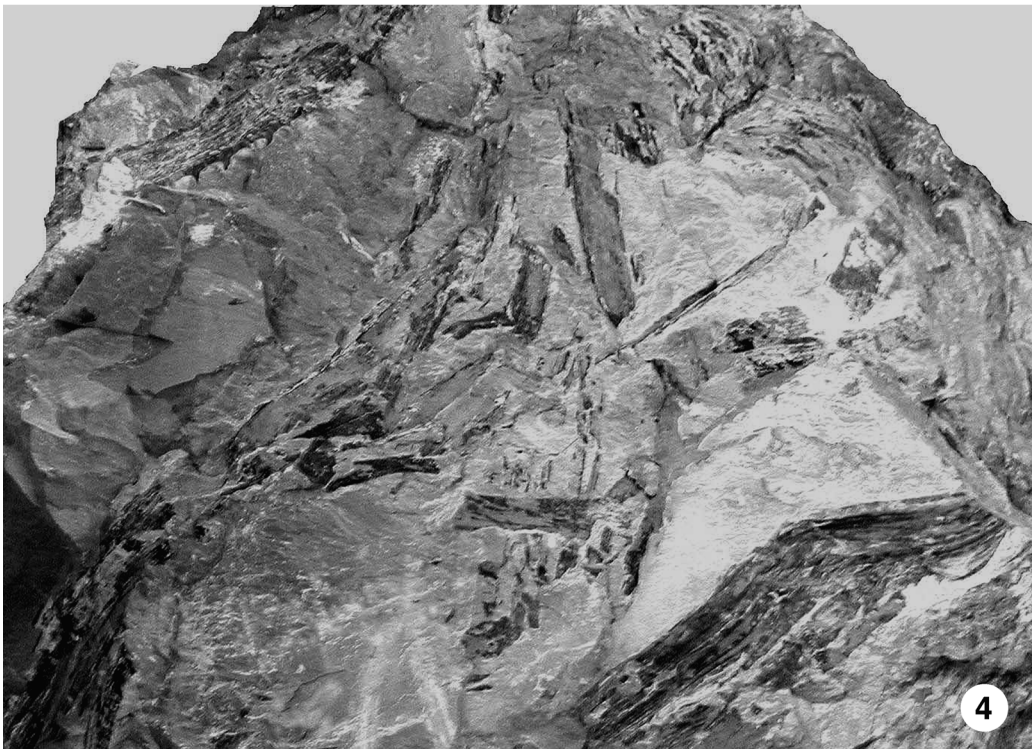
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