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Early Campanian Grünbach flora of Austria: systematic composition and palaeoclimatic interpretations

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ABSTRACT. The Early Campanian flora from the Grünbach Formation in the Grünbach-Neue Welt Basin in Lower Austria comprises 53 species, representing Equisetopsida, Polypodiopsida, Cycadopsida, Pinopsida, Liliopsida and Magnoliopsida. Palaeoclimatic analysis of the Grünbach flora using the nearest living relative (palms Arecaceae: *Sabalites*, pandans Pandanaceae: *Pandanites*, and ferns probably belonging to the families Schizaeaceae and Matoniaceae), leaf margin analysis (13 dicot species, or 48% have leaves or leaflets with entire margins) and Climate Leaf Analysis Multivariate Program (CLAMP) approaches allows us to conclude that the Grünbach flora experienced a humid subtropical frost-free climate with hot summers and short relatively dry, but not arid, seasons.

KEY WORDS: fossil flora, palaeoclimate, CLAMP, Lower Campanian, Austria

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 (Fig. 1). The coal seams of the Grünbach Formation were exploited from the second half of the 19th century until the 1960s, 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, 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 studied monographically. A few fossil plants had been described (Unger 1850, 1852, Ettingshausen 1852) and some other plants were preliminarily identified and labelled in the collection by Ettingshausen in the year 1879, by Krasser in the years 1904–1906 (Krasser 1906), and Kerner-Marilaun (1934) in the year 1934.

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. In 1999 the authors began to study the Grünbach plant fossils (Herman & Kvaček 2000, 2002a, b, Herman et al. 2002, Herman 2004a, b, Kvaček & Herman 2004a, b, 2005). Our research is based on a study of the existing plant fossil collections mentioned above as well as on our field observations from a dump near Grünbach village undertaken in 2001, 2003 and 2005. This study was initiated by Dr. H. Kollmann of the Natural History Museum in Vienna. The present publication

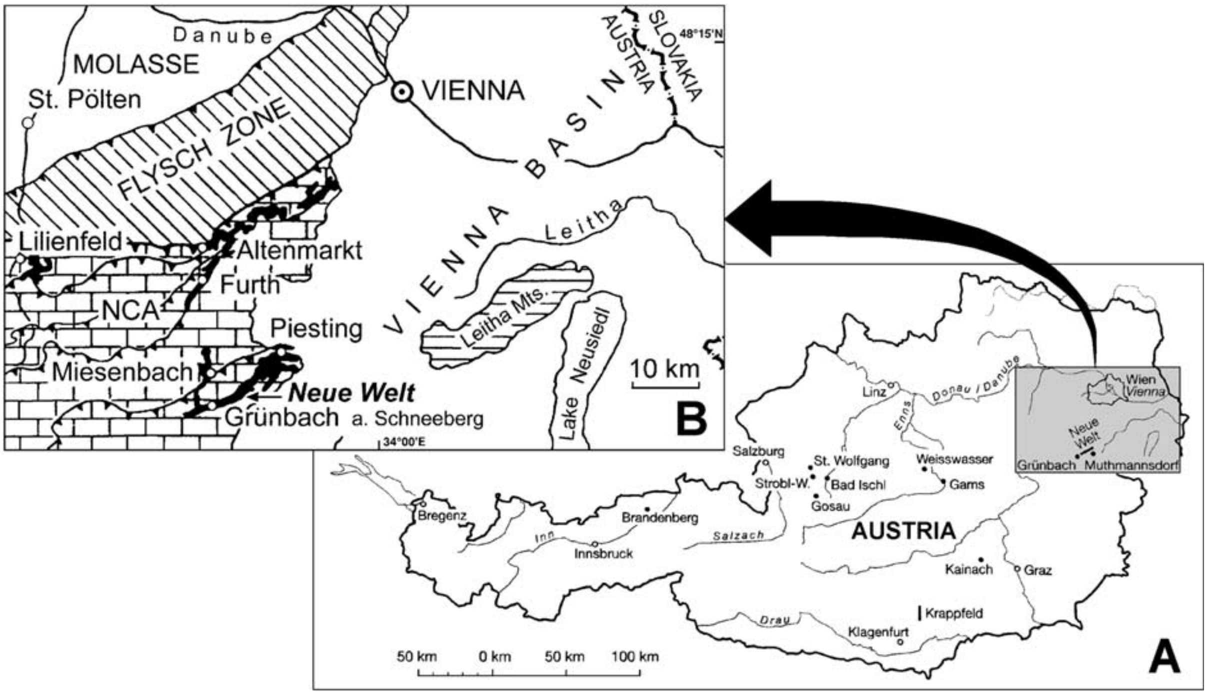

Fig. 1. A – Sketch map of the Austrian occurrences of the Gosau Group: Strobl-W. – Strobl-Weissenbach (after Summesberger et al. 2000); **B –** position of the Grünbach – Neue Welt Basin in the Eastern Alps, Austria (after Summesberger 1997, simplified)

represents some results of our investigation of the Grünbach flora. Plant taxa designeted here contain also new genera and species formally described as gen. n. and sp. n. in a monograph which is currently in press (Herman & Kvaček in press).

SYSTEMATIC COMPOSITION AND AGE OF THE GRÜNBACH FLORA

The Grünbach flora has a relatively large number of plant macrofossil taxa, with 53 species identified to date, representing Equisetopsida (1 species), Polypodiopsida (11), Cycadopsida (1), Pinopsida (4), Liliopsida (6), and Magnoliopsida (30). The most characteristic representatives of the Grünbach flora are shown in Figs 2 and 3. In addition to the above-mentioned groups of fossil plants, several other fossil remains are represented including poorly preserved impressions of unknown thalli (Herman & Kvaček 2002a), charophytes (Plöchinger 1961) and unidentified seeds.

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

Polypodiopsida. Ferns are represented by 11 species (Fig. 2: A–L) showing certain affinities to the families Matoniaceae, Schizaeaceae, Dicksoniacae, Dennstaediaceae and Marsileaceae. Ferns are assigned to eight genera *Cladophlebis* Brongniart*, Coniopteris* Brongniart*, Gosauopteris* J. Kvaček & Herman, *Marsilea* L.*, Microtaenia* Knowlton*, Monheimia* Debey & Ettingshausen*, Raphaelia* Debey & Ettingshausen and *Sphenopteris* Sternberg. *Coniopteris*, *Monheimia* and *Microtaenia* possess reproductive structures, but only *Monheimia* has preserved spores *in situ*. Spores of *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 classified in terms of morphogenera except *Marsilea* which, although preserved as sterile foliage, provides sufficient diagnostic characters to be assigned with a high degree of probability to the recent genus.

Cycadopsida. Cycads are represented only by the genus *Nilsonia* Brongniart (Fig. 2: M). Its presence in a European 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), North-eastern Russia (Herman & Lebedev 1991, Herman 1999, 2004c) and Sakhalin Island (Krassilov 1979).

Pinopsida. Conifers comprising four spe-

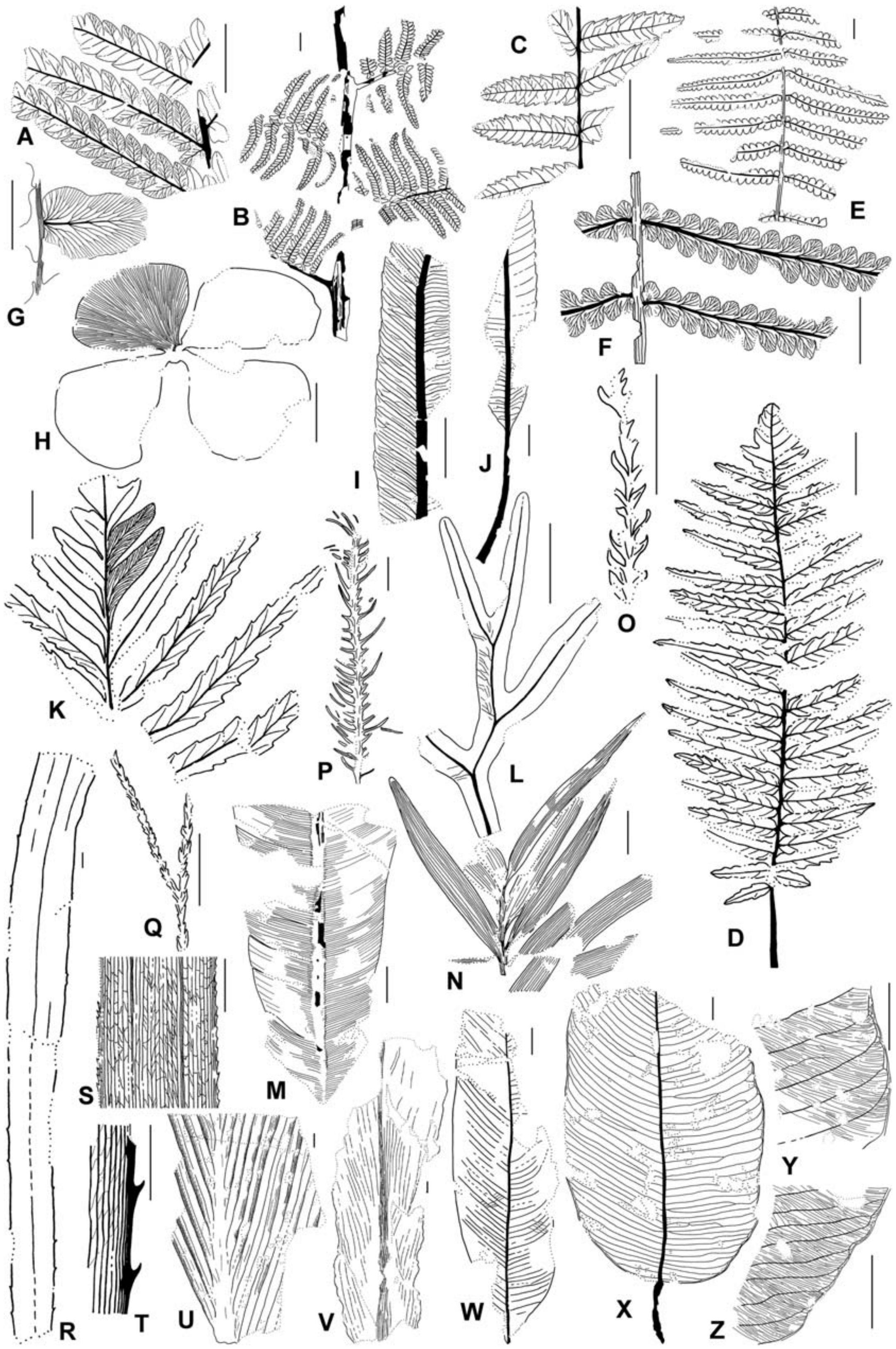

Fig. 2. Floral picture of the Grünbach flora, Polypodiopsida: **A, B** – *Cladophlebis gosauensis* J. Kvaček & Herman, **C, D** – *Sphenopteris gruenbachiana* J. Kvaček & Herman, **E, F** – *Microtaenia austriaca* J. Kvaček & Herman, **G** – *Raphaelia lobifolia* (Corda in Reuss) Knobloch, **H** – *Marsilea campanica* J. Kvaček & Herman, **I, J** – *Gosauopteris danaeoides* J. Kvaček & Herman, **K** – *Sphenopteris ungerii* J. Kvaček & Herman, **L** – *Monheimia ungerii* J. Kvaček & Herman, Cycadopsida: **M** – *Nilsonia* cf. *holyi* J. Kvaček; Pinopsida: **N** – *Podozamites* sp. cf. *Lindleycladus lanceolatus* (Lindley & Hutton) Harris, **O** – *Geinitzia formosa* Heer, **P** – *Geinitzia reichenbachii* (Geinitz) Hollick & Jeffrey, **Q** – *Pagiophyllum* sp., unnumbered specimen from the Geologische Bundesanstalt; Liliopsida: **R, S, T** – *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, **U** – *Sabalites longirhachis* (Unger) J. Kvaček & Herman, **V** – *Araciphyllites austriacus* J. Kvaček & Herman, **W, X, Y, Z** – *Theiaiphyllum kollmannii* Herman & J. Kvaček, Grünbach; scale bar – 1 cm

cies are represented by two main groups: *Podozamites* Group and Curpessaceae s.l. A single taxon, *Podozamites* C.F.W. Brown (Fig. 2: 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 Cupressaceae s.l. (Fig. 2: O, P). A few other sterile conifer twigs are described here as the morphogenus *Pagiophyllum* Heer (Fig. 2: 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. The genus *Araciphyllites* Wilde et al. (Fig. 2: V) is assigned to the Araceae. It is particularly close to the genus *Lysichiton*. Genera *Pandanites* Tuszon (Fig. 2: R, S, T) based on leaves and *Grunbachia* J. Kvaček & Herman, based on reproductive structures bear unequivocal characters of the Pandanaceae. Morphogenus *Sabalites* Saporta (Fig. 2: U) bears unequivocal characters of the Arecaceae. The remaining two taxa, one of which is described as a new genus *Theiaiphyllum* Herman & J. Kvaček (Fig. 2: W, X, Y, Z) are of unknown systematic affinity.

Magnoliopsida. Dicotyledonous angiosperms are mostly recorded as leaf impressions or compressions (Fig. 3). Thirty species were identified. They belong to genera *Brasenites* Wang & Dilcher, *Celastrophyllum* Goeppert, *Compositiphyllum* Herman & J. Kvaček, *Debeya* Miquel, *Ettingshausenia* Stiehler, *Grebenkia* Lebedev, cf. *Grevilleophyllum* Velenovský, *Juglandiphyllites* Boulter & Z. Kvaček, *Leguminosites* Bowerbank, *Menispermites* Lesquereux, *Myricophyllum* Saporta, cf. *Pandemophyllum* Upchurch & Dilcher, *Quereuxia* Kryshtofovich, *Rogersia* Fontaine, *Ternstroemites* E.W. Berry, *Viburniphyllum* Nathorst, *Dicotylophyllum* Saporta, *Ceratoxylon* Velenovský & Viniklář. They are assigned to 18 genera, representing 17 genera of sterile foliage (see above) and one reproductive structure *Ceratoxylon*. 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* Herman & J. Kvaček 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. Angiosperm fructification of unknown origin is assigned to the genus *Ceratoxylon*.

The Upper Cretaceous to Paleogene Gosau Group unconformably overlies folded and faulted Permian to Lower Cretaceous rocks. Numerous Gosau basins, widespread in the Austrian territory, are filled by predominantly clastic sediments of the synorogenic Gosau Group which represents a distinct sedimentary cycle (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 is one of

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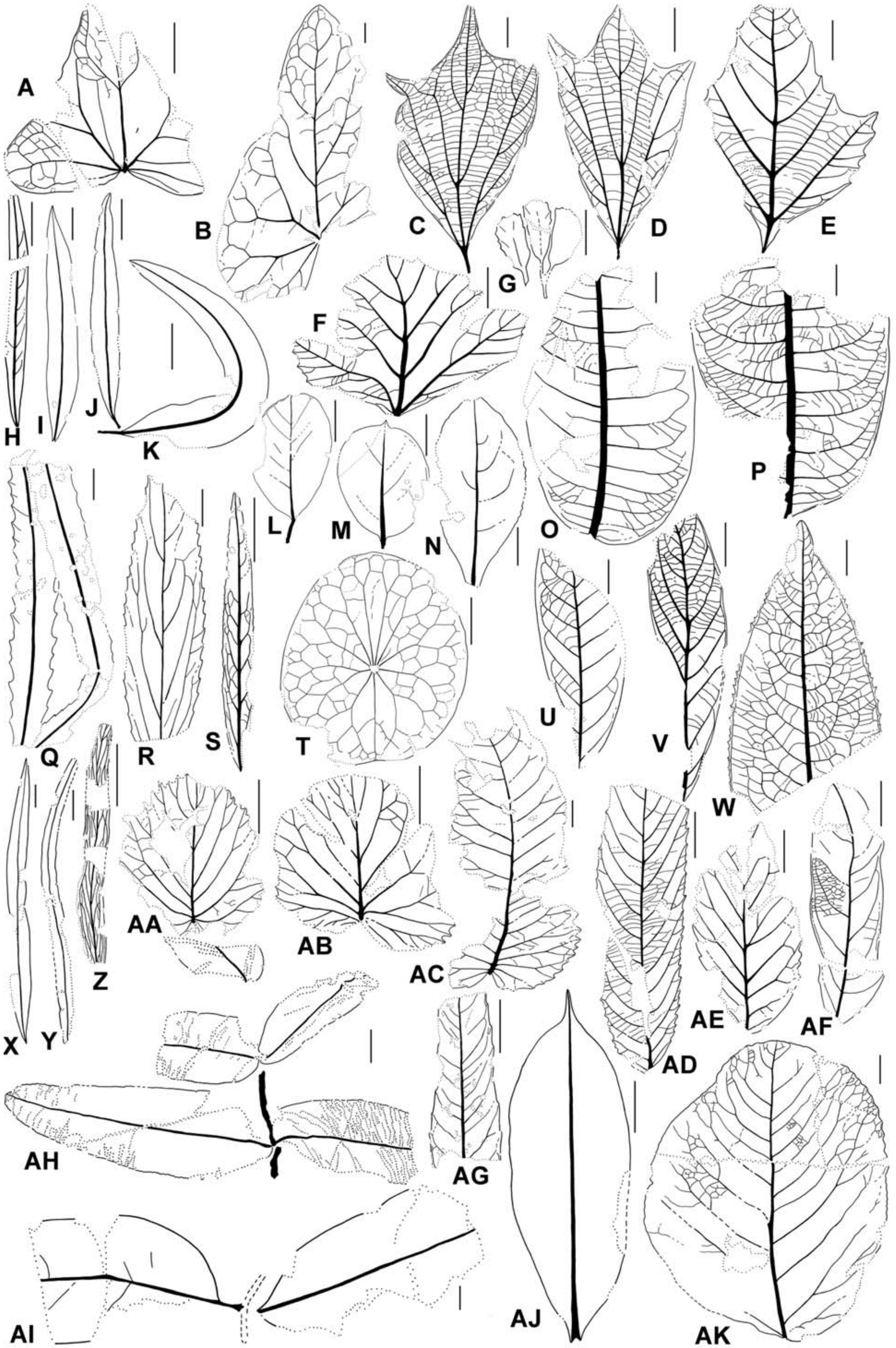
Fig. 3. Floral picture of the Grünbach flora, Magnoliopsida: **A** – *Menispermites ettingshausenii* Herman & J. Kvaček, **B** – *Menispermites summesbergerii* Herman & J. Kvaček, **C, D** – *Ettingshausenia gruenbachiana* Herman & J. Kvaček, **E** – *Ettingshausenia* cf. *laevis* (Velenovský) Herman & J. Kvaček, **F** – *Ettingshausenia* sp., **G** – *Quereuxia angulata* (Newberry) Kryshtofovich, **H** – *Pandemophyllum* (?) sp., **I, J, K** – cf. *Pandemophyllum proteoides* (Unger) Herman & J. Kvaček, **L, M** – *Leguminosites mucronata* Herman & J. Kvaček, **N** – *Celastrophyllum* sp., **O, P** – *Juglandiphyllites pelagicus* (Unger) Herman & J. Kvaček, **Q** – *Debeya insignis* (Hosius & Marck) Knobloch, **R** – *Myricophyllum* sp. cf. *M. zenkeri* (Ettingshausen) Heer, **S** – *Myricophyllum serratum* (Velenovský) Němejc, **T** – *Brasenites krasserii* Herman & J. Kvaček, **U** – *Dicotylophyllum* EM-2 Herman & J. Kvaček, **V** – *Dicotylophyllum* EM-1 Herman & J. Kvaček, **W** – *Ternstroemites* (?) *neueweltensis* Herman & J. Kvaček, **X, Y** – cf. *Grevilleophyllum constans* (Velenovský) Velenovský, **Z** – *Rogersia* sp., **AA, AB** – *Viburniphyllum ermannii* Herman & J. Kvaček, **AC** – *Viburniphyllum austriacum* Herman & J. Kvaček, **AD** – *Grebenkia europeica* Herman & J. Kvaček, **AE** – *Dicotylophyllum* DM-2 Herman & J. Kvaček, **AF** – *Dicotylophyllum* EM-3 Herman & J. Kvaček, **AG** – *Dicotylophyllum* DM-1 Herman & J. Kvaček, **AH** – *Compositiphyllum serratum* Herman & J. Kvaček, **AI** – *Juglandiphyllites pelagicus* (Unger) Herman & J. Kvaček, **AJ** – *Dicotylophyllum* EM-4 Herman & J. Kvaček, **AK** – *Celastrophyllum johannae* Herman & J. Kvaček, Grünbach; scale bar – 1 cm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the largest Gosau basins. 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 Early Campanian age of the plant-bearing beds of the Grünbach 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 (Summesberger 1997, Summesberger et al. 2002).

PALAEOBOTANICAL METHODS OF PALAEOCLIMATIC ANALYSIS

Palaeoclimatic analysis of the Grünbach flora using the nearest living relative, leaf margin analysis and Climate Leaf Analysis Multivariate Program approaches allows us to reconstruct both qualitative and quantitative palaeoclimatic parameters experienced by the flora.

Nearest Living Relative (NLR) approach is one traditionally used by palaeobotanists for palaeoclimate analysis. This technique relies on accurate identification of the nearest living relatives of the ancient plants comprising a fossil flora, the ancient climate being extrapolated from the climatic requirements of the living plants. The NLR approach usually works quite well for Quaternary and Neogene floras, and is sometimes applicable to Paleogene 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 the climatic requirements of plant (or animal) taxa were not affected by evolution and remained constant throughout geologic time. Clearly this is untenable. Therefore, when interpreting the Grünbach flora, the NLR approach can only be used in conjunction with other forms of palaeoclimatic analysis, bearing in mind that this technique could provide us with imprecise or even incorrect data.

Leaf Margin Analysis (LMA). This provides a more reliable method of reconstructing past climates using taxonomically independent morphological or anatomical features reflecting adaptations to particular environmental constraints. An early attempt at quantifying physiognomic characters in terms of climatic data was that of Bailey and 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. Figure 4 shows such a relationship for south-eastern Asian plants (Wolfe 1979). In an ideal situation, for a fossil flora with a high diversity of dicot leaf species, the ratio of leaf margins could yield a reliable mean annual temperature as experienced by the plants.

The LMA has been used extensively for Tertiary and for some Cretaceous material (Krassilov 1979, Herman 2004b) but the method has some serious limitations. First, 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 the number of teeth can be reduced 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

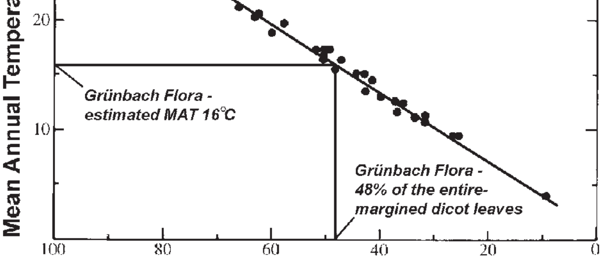

Fig. 4. Plot of mean annual temperature (MAT) against the percentage of leaf margin types (from Wolfe 1979).

a large leaf surface area for light interception is moderated by evapo-transpirational stresses and structural costs), a single character analysis provides only a partial, and possibly erroneous, climatic signal. Nevertheless, LMA has been used 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.

Climate Leaf Analysis Multivariate Program (CLAMP). In an attempt to overcome the above-mentioned limitations and to obtain palaeoclimatic data from 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 106 sites for which climatic conditions were known from meteorological observations. Wolfe (l.c.) 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 (1993) called this database and its multivariate 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 the dataset comprising 144 modern vegetation sites (previous studies used the dataset consisting of 103 sites: Herman & Kvaček 2002a, b). Most of these sites are from the northern hemisphere (dataset PHYSG3br, see http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html) scored for 31 leaf characters and correlated with 8 climate variables. This dataset lacks samples belonging to the "alpine nest": it is usually better to use this dataset unless winter temperatures below freezing are suspected for the fossil flora. We used the following leaf characters (their definitions are in: Wolfe 1993, 1995, Herman & Spicer 1996, 1997; http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html).

Leaf margin: leaves lobed; leaves with no teeth; teeth regular; teeth close; teeth round; teeth acute; teeth compound.

Leaf size: nanophyll; leptophyll I; leptophyll II; microphyll I; microphyll II; microphyll III; mesophyll I; mesophyll II; mesophyll III.

Leaf apex: emarginate; round; acute; attenuate.

Leaf base: cordate; round; acute.

Leaf length to with ratio: less than 1:1; 1:1 to 2:1; 2:1 to 3:1; 3:1 to 4:1; more than 4:1.

Leaf shape: obovate; elliptic; ovate.

The climate variables used in the analysis are:

- mean annual temperature (MAT), °C;
- warm month mean temperature (WMMT), °C;
- cold month mean temperature (CMMT), °C;
- mean growing season precipitation (MGSP), mm;
- mean monthly growing season precipitation (MMGSP), mm;
- precipitation during three consecutive wettest months (3WM), mm;
- precipitation during the three consecutive driest months (3DRIM), mm;
- length of the growing season (LGS), months.

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 created by ter Braak (1986, 1987–92) the Canonical Correspondence Analysis (CANOCO) 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. Figure 5a 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

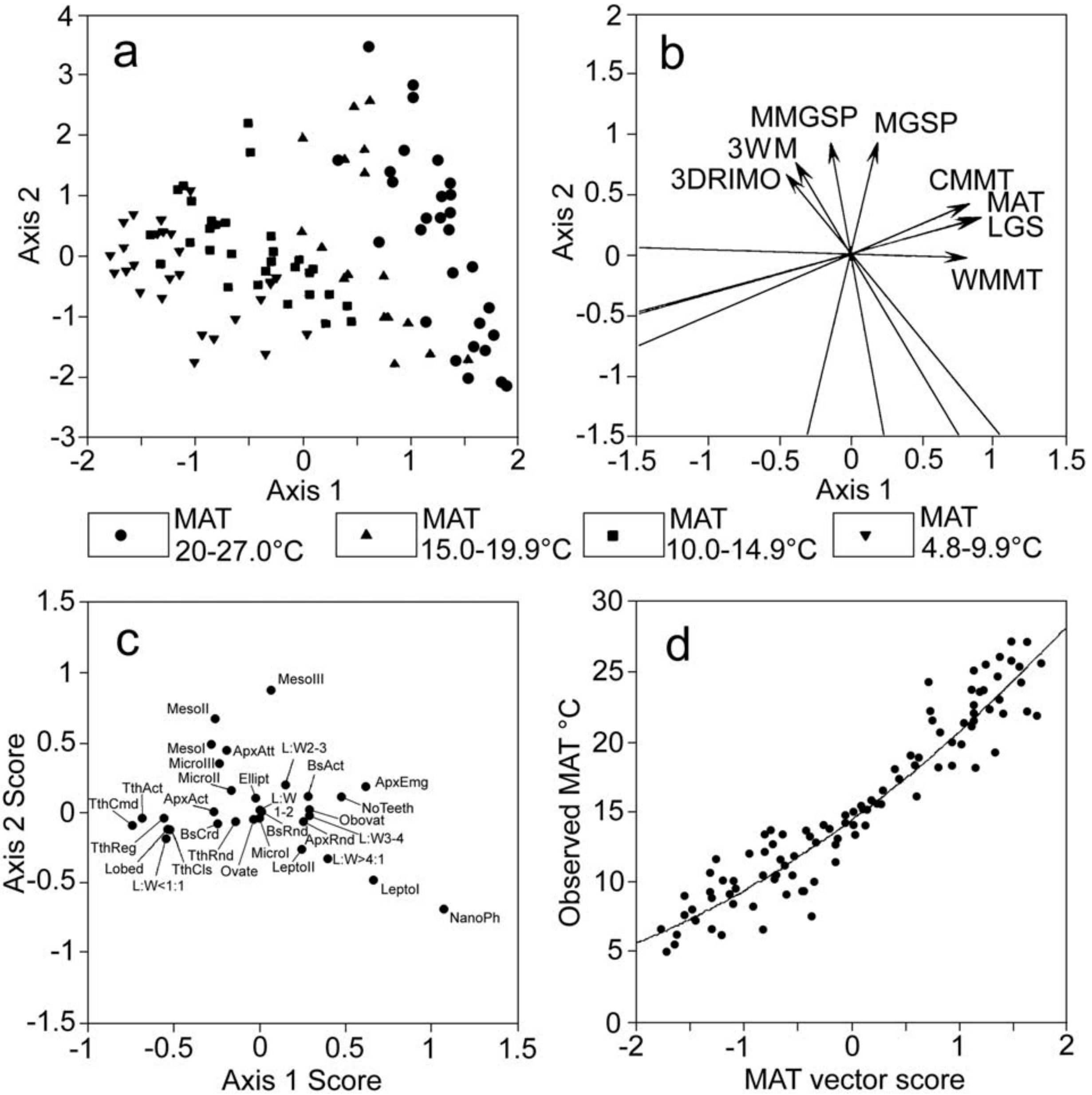

Fig. 5. Results of CLAMP analysis using CANOCO; **a** – distribution of modern and fossil sites in axis 1/axis 2 space as defined by leaf characteristics; **b** – the environmental vectors in axis 1/axis 2 space; vectors: **3DRIM** – precipitation during the three consecutive driest months, **3WM** – 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).

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 (Fig. 5a) 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. 5b). Figure 5c 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 (Fig. 5c) lies close to the MAT vector (Fig. 5b) 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; Fig. 5c) lies close to precipitation vectors (Fig. 5b) as would be expected.

Figure 5a shows a fossil site (in this case it is a Turonian flora from Novaya Sibir Island, Arctic Russia, taking as an example) 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 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 (Fig. 5b) are calibrated using modern sites with known climates. Figure 5d 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 the 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.

PALAEOCLIMATIC INTERPRETATIONS OF THE GRÜNBACH FLORA: RESULTS AND DISCUSSION

In the nearest living relative (NLR) analysis of the Grünbach flora four taxa are particularly important: palms (Arecaceae: fossil genus *Sabalites*, Pl. 1), pandans (Pandanaceae: fossil genus *Pandanites*, Pl. 2, figs 6–9) and ferns probably belonging to the families Schizaeaceae (spores *Leiotriletes* sp., *Appendicisporites tricuspidatus*, *Cicatricosisporites* sp.) and Matoniaceae (*Monheimia* with spores *Matonisporites* preserved *in situ*, Pl. 2, figs 1–5). Palms are also recorded as pollen *Arecipites* sp. (Draxler in Summesberger 1997). Palms *Sabalites longirhachis* (Unger) J. Kvaček & Herman and pandans *Pandanites trinervis* (Ettinghausen) 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). Palms are widespread in the tropical, subtropical and warm temperate regions of all continents (Fig. 6), 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 is a typical palaeotropic family consisting of three recent genera: *Pandanus* L. – 700 species in the Indo-Pacific region, *Freycinetia* Gaudichaud-Beaupré – 200 species in the Austral-Asian region, and *Sararanga*

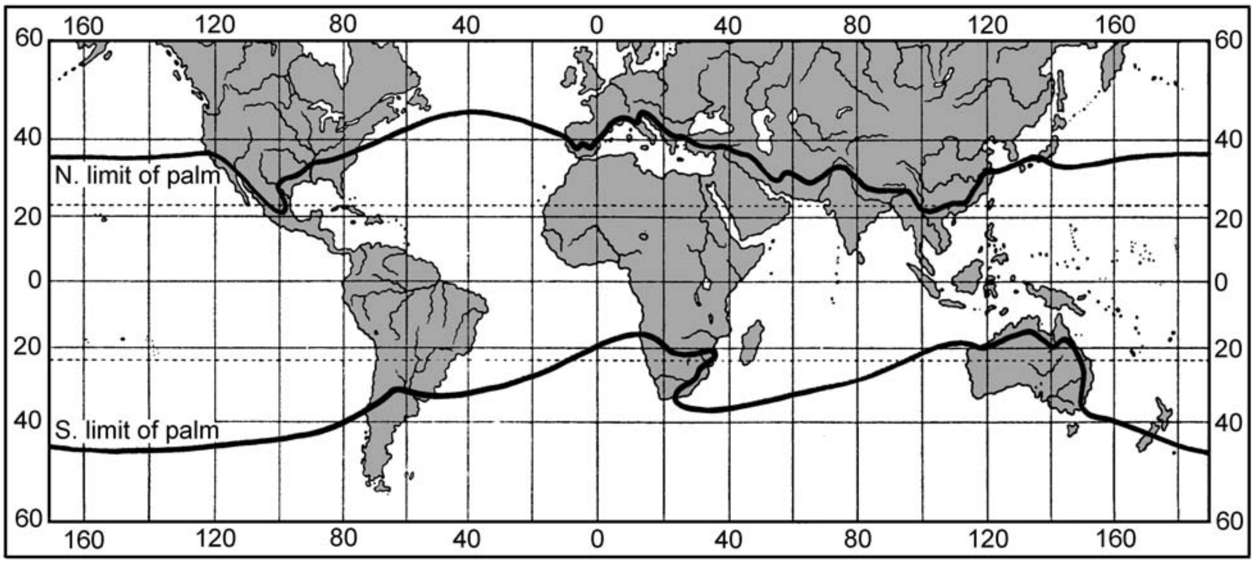

Fig. 6. Distribution of modern palms (modified from Philip's School Atlas, 2002)

Hemsley – 2 species in the Philippines and Melanesia (Grushvitskii 1982, Stone et al. 1998). 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 (Fig. 7). 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 spores of 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*

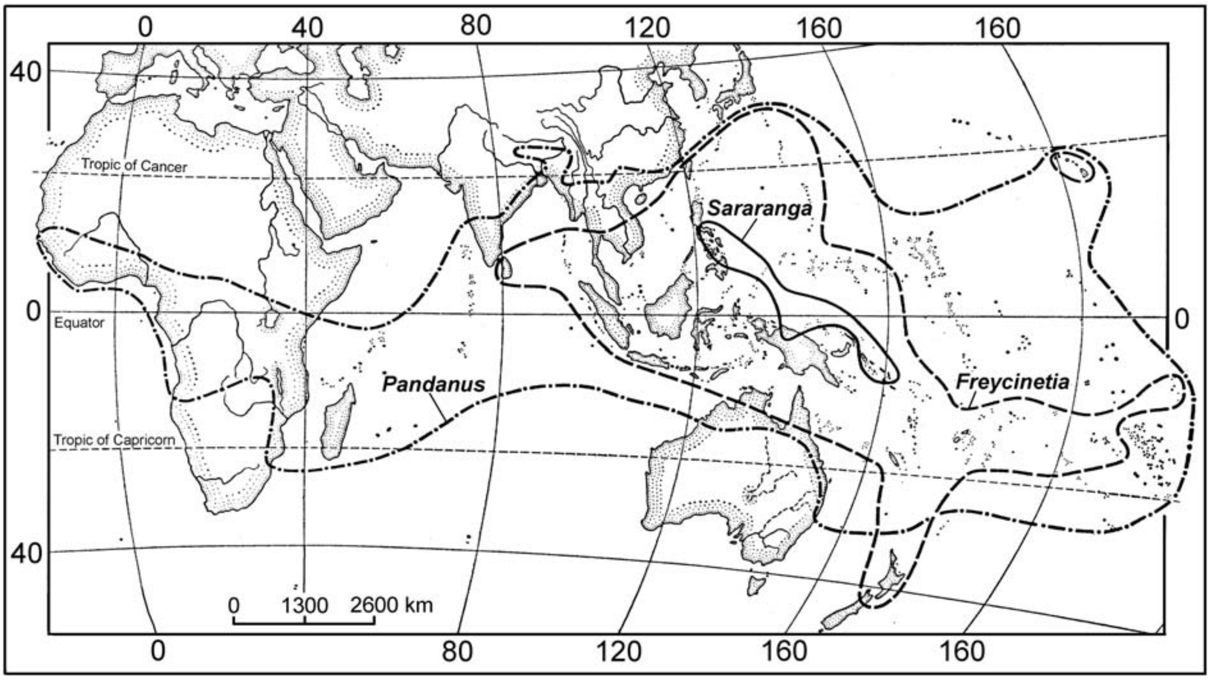

Fig. 7. Distribution of modern pandans (modified from Grushvitsky 1982)

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 (Vakhrameev et al. 1963, van Konijnenburg-van Cittert 1993).

Therefore, co-occurrence of palms, pandans and possible representatives of the families 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.

Leaf margin analysis (LMA) of 27 non-aquatic dicot leaf morphotypes from the Grünbach flora shows that 48% (13 species: *Menispermites ettingshausenii*, *M. summesbergerii, Ettingshausenia gruenbachiana, Juglandiphyllites pelagicum, Pandemophyllum proteoides, Pandemophyllum* (?) sp., *Leguminosites mucronata, Grevilleophyllum* cf. *constans*, *Rogersia* sp., *Dicotylophyllum* EM-1, *Dicotylophyllum* EM-2, *Dicotylophyllum* EM-3, and *Dicotylophyllum* EM-4) have leaves or leaflets with entire margins. This indicates that the estimated mean annual temperature experienced by the Grünbach flora is about 16°C (see Fig. 4).

Physiognomic analysis of the Grünbach flora using the CLAMP technique is now based on a new revised fossil plant taxonomy whereas in our previous study (Herman & 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 the 31 characters. 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 width 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 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. 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 Köppen (1931) classification of global climates modified (The Times Atlas of the world 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) and by the presence of large foraminifers, rudists, corals and a reptile fauna in the Santonian-Campanian of the Grünbach-Neue Welt Basin (Summesberger 1997) together with finds of *Neopsaronius* tree fern trunks in the Senonian flysh of Austria (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 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 (*Pandemophyllum* (?), *Grevilleophyllum* (?) etc.), which, according to Vakhrameev (1991), can be interpreted as a flora typical of the Euro-Sinian phytogeographic region (Fig. 8) characterized 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).

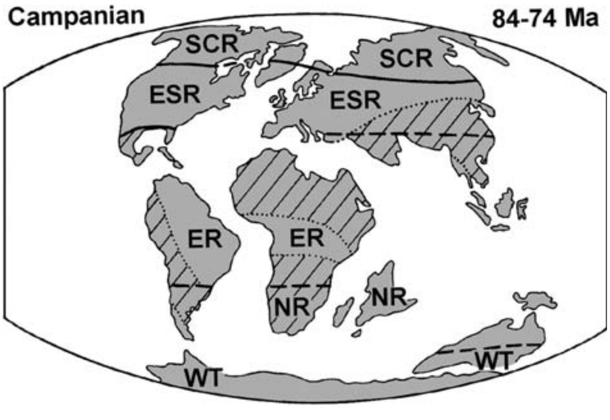

Fig. 8. Campanian phytogeographic and palaeoclimatic regions of the world (modified from Vachrameev 1991): **SCR** – Siberian-Canadian Region of the warm temperate climate, **ESR** – Euro-Sinian Region of the subtropical climate, **ER** – Equatorial Region of the tropical climate, **NR** – Austral (Notal) Region of the subtropical climate, **WT** – warm temperate belt of the southern hemisphere (existed since Santonian); shaded are arid and semiarid areas

CONCLUSIONS

The Grünbach flora comes from the Grünbach Formation forming part of the Gosau Group in the Grünbach-Neue Welt Basin in Lower Austria. The Early Campanian age of the plant-bearing beds of the Grünbach 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 species, representing Equisetopsida (1 species belonging to *Equisetites*), Polypodiopsida (11 species belonging to genera *Cladophlebis, Coniopteris, Gosauopteris*, *Marsilea*., *Microtaenia, Monheimia, Raphaelia* and *Sphenopteris*, Cycadopsida (1 species belonging to *Nilsonia*), Pinopsida (4 species belonging to *Podozamites*, *Geinitzia* and *Pagiophyllum*), Liliopsida (6 species belonging to *Aracephyllites*, *Pandanites*, *Grunbachia*, *Sabalites*, *Theiaiphyllum*, and Monocotyledon gen. et sp. indet.), and Magnoliopsida (30 species belonging to genera *Celastrophyllum*, *Compositiphyllum*, *Debeya, Ettingshausenia*, *Grebenkia*, cf. *Grevilleophyllum*, *Juglandiphyllites*, *Leguminosites*, *Menispermites*, *Myricophyllum*, *Brasenites*, cf. *Pandemophyllum*, *Quereuxia*, *Rogersia*, *Ternstroemites*, *Viburniphyllum*, *Dicotylophyllum*, and *Ceratoxylon)*.

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. It can be concluded from the NLR approach (using palms Arecaceae: *Sabalites*, Pandanaceae: *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*), 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.

This is corroborated by lithological climate indicators and by the presence of large foraminifers, rudists, corals and a reptile fauna in the Santonian and Campanian of the Neue Welt Basin as well as *Neopsaronius* tree fern trunk remains in the Senonian flysh of

Austria. The suggested high humidity of the climate is corroborated by the extensive coal accumulation in the Grünbach Formation. The Grünbach flora can be interpreted as a flora typical of the Euro-Sinian phytogeographic region characterised by a subtropical climate.

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PLATES

Plate 1

Sabalites longirhachis (Unger) J. Kvaček & Herman, apical part of a large leaf, × 0.6, NHMW 1999B0057-0235

Plate 1

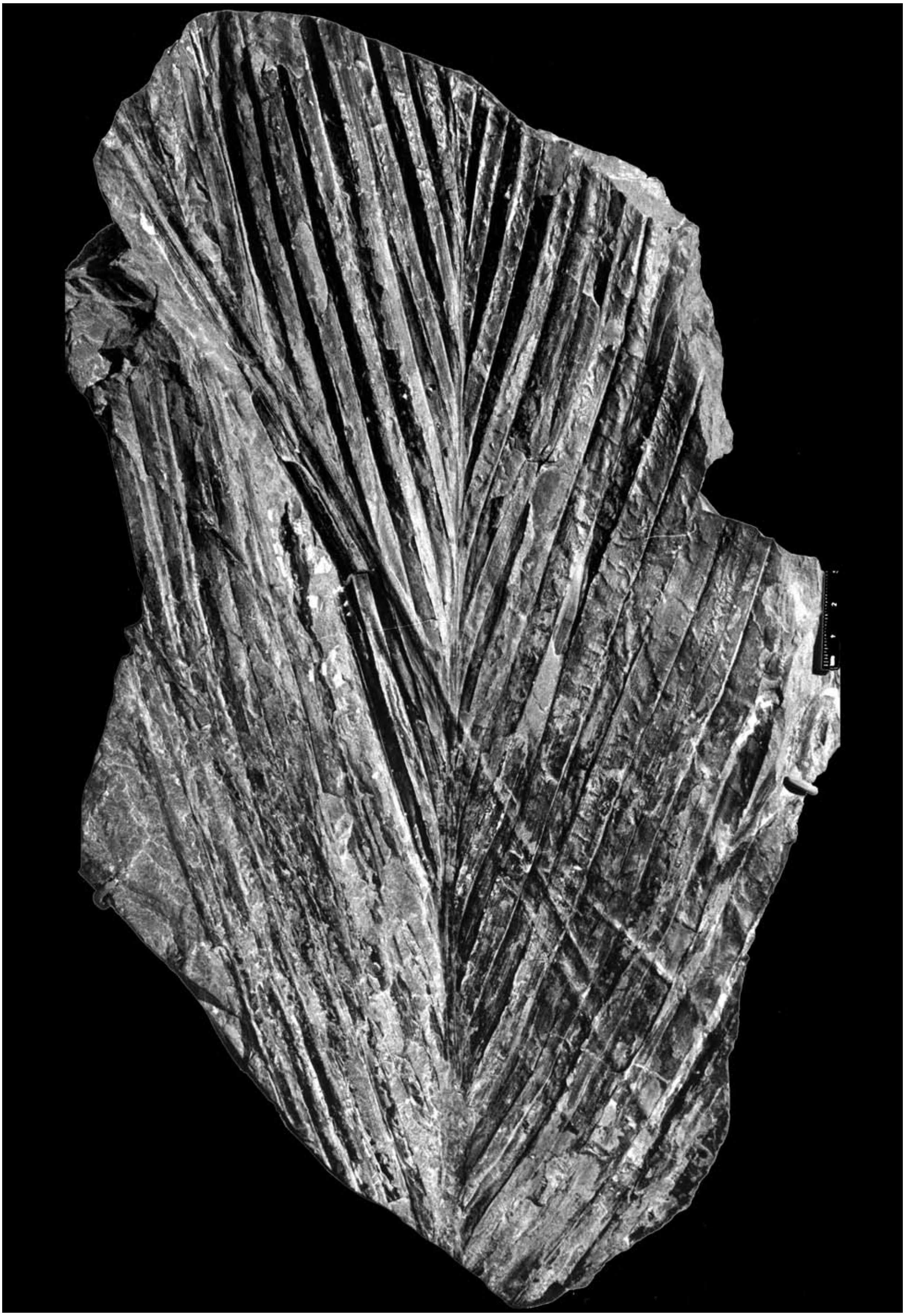
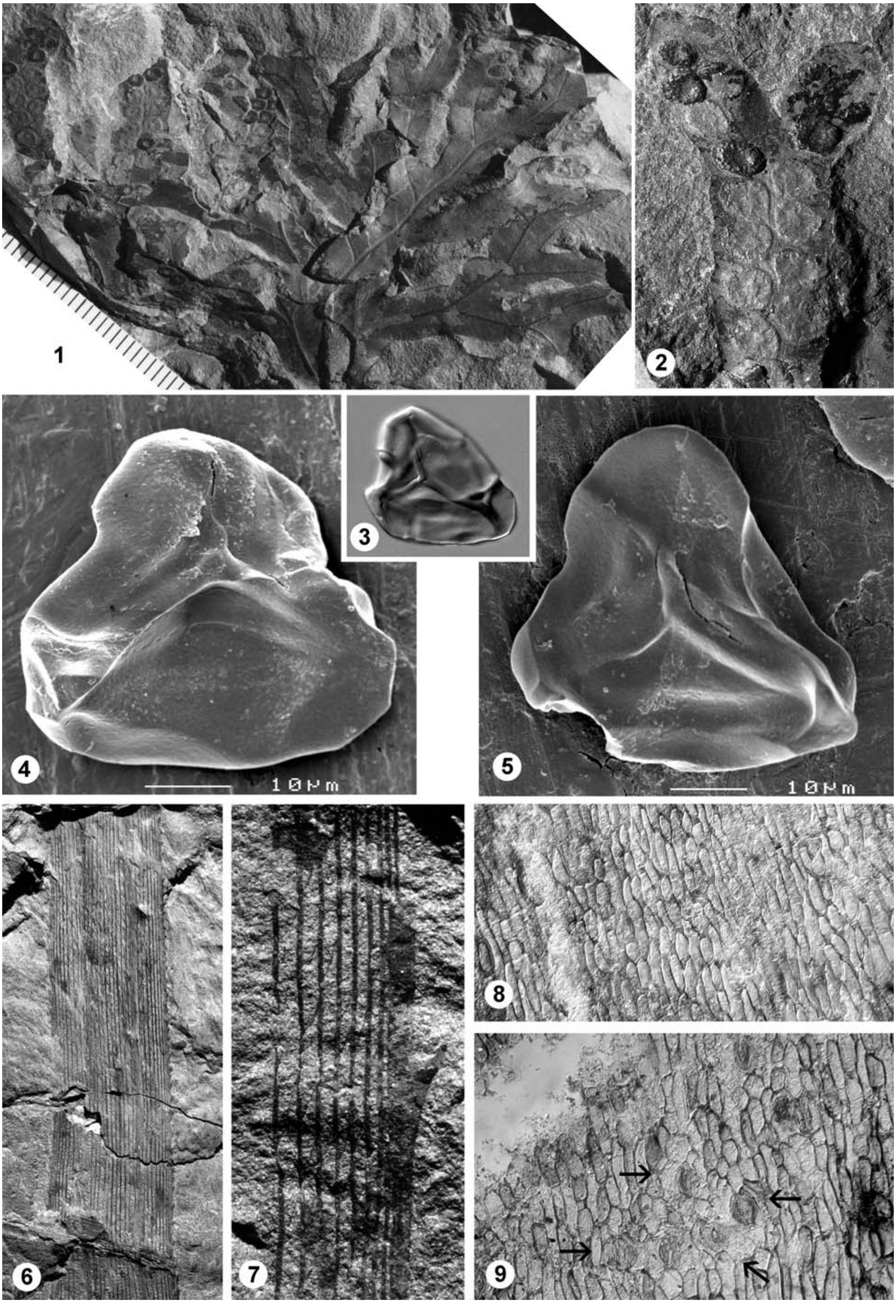


Plate 2

1. *Monheimia ungerii* J. Kvaček & Herman, frond with vegetative and reproductive parts, × 1.7, NHMW 1999B0057-0564
2. *Monheimia ungerii* J. Kvaček & Herman, detail of reproductive part of the frond showing rows of sori, × 4.3, NHMW 1999B0057-0564
3. *Matonisporites* spore, × 600, NHMW 1999B0057-0564
4. *Matonisporites* spore, SEM, NHMW 1999B0057-0564
5. *Matonisporites* spore, SEM, NHMW 1999B0057-0564
6. *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, leaf fragment, × 0.9, NHMW 1999B0057-0154
7. *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, large marginal prickles and venation near leaf margin, × 4.3, NHMW 1999B0057-0041
8. *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, adaxial cuticle, × 260, NHMW 1999B0057-0541b
9. *Pandanites trinervis* (Ettingshausen) J. Kvaček & Herman, abaxial cuticle, stomata arrowed, × 260, NHMW 1999B0057-0541c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