Acta Palaeobotanica 51(2): 127–179, 2011

Biodiversity and the reconstruction of Early Jurassic flora from the Mecsek Mountains (southern Hungary)

MARIA BARBACKA

Hungarian Natural History Museum, Department of Botany, H-1476, P.O. Box 222, W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland; e-mail: barbacka@bot.nhmus.hu

Received 15 June 2011; accepted for publication 27 October 2011

ABSTRACT. Rich material from Hungary's Early Jurassic (the Mecsek Mts.) was investigated in a palaeoenvironmental context. The locality (or, more precisely, area with a number of fossiliferous sites) is known as a delta plain, showing diverse facies, which suggest different landscapes with corresponding plant assemblages. Taphonomical observations proved that autochthonous and parautochthonous plant associations were present. The reconstruction of the biomes is based on the co-occurrence of taxa and their connection with the rock matrix and sites in the locality, as well as the environmental adaptation of the plants expressed in their morphology and cuticular structure. The climatic parameters were confirmed as typical for the Early Jurassic by resolution of a palaeoatmospheric CO_2 level based on the stomatal index of one of the common species, *Ginkgoites marginatus* (Nathorst) Florin.

Plant communities were differentiated with the help of Detrended Correspondence Analysis (DCA); the relationship between taxa and sites and lithofacies and sites, were analysed by Ward's minimal variance and clustered with the help of the UPGMA algorithm.

These methods aided the recognition of five phytocoenoses in the Mecsek delta: swamp, dominated by the pteridosperm *Komlopteris* associated with cheirolepidiaceous and other conifers and ginkgophytes; swamp areas along river banks with conifers; seasonally drier floodplain colonised by cycads, bennettites and sphenophytes; wetter floodplain with dominant *Ginkgoites marginatus*; highly disturbed, well-drained islands occupied mainly by ferns; and relatively dry areas dominated by *Sagenopteris* and associated with cycads and ferns.

KEYWORDS: plant assemblages, palaeoecology, statistic methods, Early Jurassic, Hungary

INTRODUCTION

Fossil plants and their responses to palaeoenvironments, their assemblages and mutual interactions have met with increasing interest from the second half of the 20th century onwards. Based on taxonomic studies, which are the starting point for palaeoecological patterns, different methods were provided for trying to understand the functional mechanisms active in palaeo-communities.

Individual localities with their specific conditions of plant preservation offer varied opportunities for palaeoecological reconstructions. To reach this aim, different methods, from very simple listing of plants that give information about the content of plant assemblages, through investigations of plant adaptation as expressed in their morphology and cuticular structure, up to modern mathematic modelling and statistical analyses are used in palaeobotany.

The Early Jurassic flora from the Mecsek Mts. (South Hungary) has been collected and studied since 1989 (Barbacka 1992, 1994a,b, 2001, 2002, 2009). The flora now consists of 55 species. Taxonomical studies were often supplemented with taphonomical remarks and followed by environmental conclusions. The environmental hypotheses were mainly based on supposed plant adaptations to differentiated conditions. Working on the fossil flora from

Hungary, certain tendencies were observed in the regular repetition of species co-existing on the same rock slabs, and possible relations between taxa and their location within the area, as well as between taxa and the type of rock.

The aim of the present paper, based on all available data, is to introduce the Hungarian fossil plant sites in an ecosystem model showing differentiated plant co-existence, interrelations of plant species and rock type, and the real distribution of plant assemblages. The objectivity of the results is provided by statistic methods. Such analyses are rather rarely used in palaeobotany, because they need a large record appropriate for statistics and proof of the autochthonous or parautochthonous origin of the material.

The obtained results can be applied to a revision of the plant assemblage-environment relationship, and may form a basis for updating palaeoecological models based on palynological analyses. It can also contribute to the general knowledge of Jurassic plant assemblages and supply data for comparative studies.

PART 1

Geological and Paleoenviromental Background

GEOLOGY AND PALAEOGEOGRAPHY

The Early Jurassic plant macrofossil locality in Hungary is confined to the Mecsek Coal Formation (Hetényi in Császár 1997) in the Mecsek Mountains (Pécs and Komló regions, southern Hungary) and closely connected with coal mining. The coal-bearing area extends in a N – S direction, for a distance of about 20–30 km, from Nagymányok to Pécs (Fig. 1). The mining region occupies about 350–400 km^2. The beginning of coal mining in Hungary dates back more than 200 years. After the most intense exploitation period between 1960 and 1990, the underground mines were closed, and in 2004, open mining also came to an end.

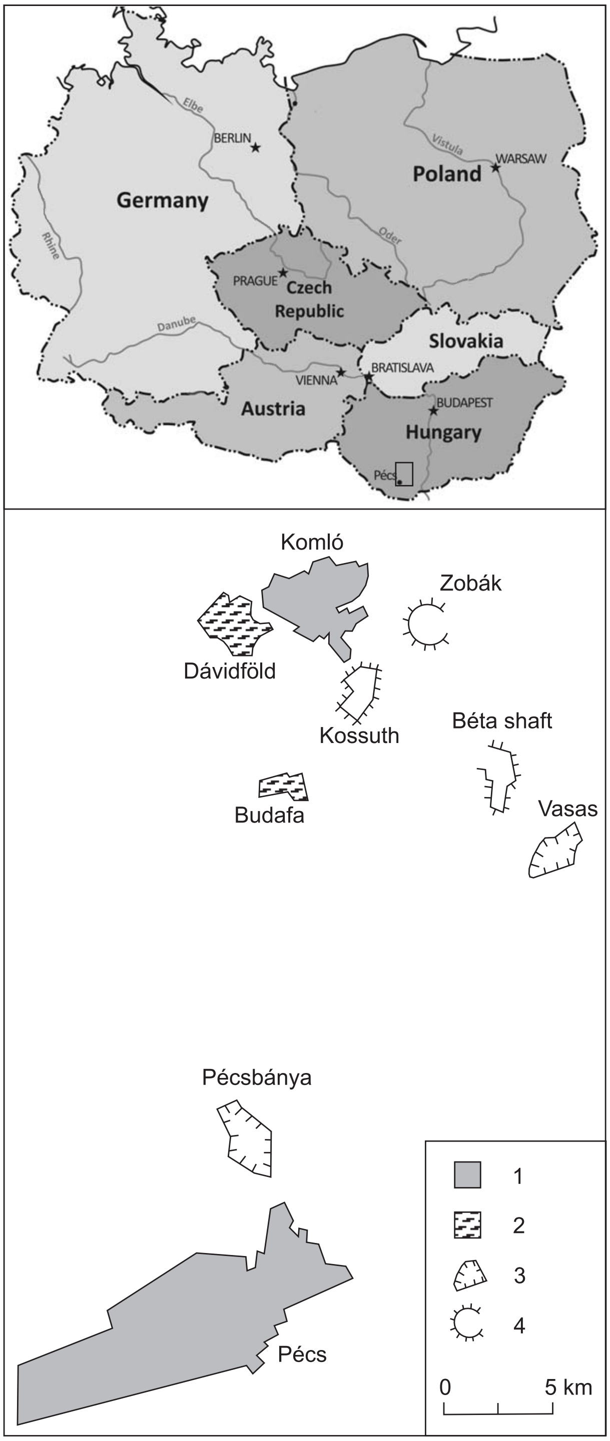


Fig. 1. Map of sites in the Mecsek Mts. locality (A. Sojka drawing): **1** – settlements, **2** – dumps, **3** – open mines, **4** – shafts

The age of coal measures were determined as Early Liassic (Hantken 1878) and narrowed down to the Hettangian by subsequent geological (Paál-Solt 1969, Nagy & Nagy 1969), palaeontological (Földi 1967, Nagy 1970, Szente 1992) and palynological (Góczan 1956) investigations.

The Mecsek Coal Formation, which is the most interesting from a palaeobotanical viewpoint, comprises the Upper Triassic and the Lower Jurassic sequences consisting of sandstone, claystone, mudstone and coal. The coal seams occur mainly in the middle and upper parts of the sequence, which are dated as

Early Jurassic (Landis et al. 2003), but thin coal seams appear already in the fluvial succession of the latest Rhaetian. At the beginning of the Liassic, fluvial–lacustrine–palustrine sedimentation continued, with paralic coal-swamp deposits becoming predominant in the later phase of the sedimentary record.

The formation is built of a cyclic alternation of arkosic sandstone, siltstone, claystone and coal seams. The thickness and carbonization degree of the coal deposits are diversified due to asymmetry in the depository basin caused by unequal subsidence (Fig. 2): according to Nagy (1969) the thickness is at its lowest near Nagymányok (120 m), gradually increasing southward to Pécs (1000–1200 m thick). This asymmetry, observed also in the Upper Triassic Karolina völgy Sandstone Formation, is a result of non-uniform extension of the half-graben (Nagy 1969). In the Alpine-Carpathian region, Lower Liassic, coal bearing siliciclastic sequences, showing features similar to those of the Mecsek Zone, are classified as “Gresten Facies” – a characteristic facies of the southern margin of the European shelf of the Tethys (Haas 2001).

Beginning from the basal (Late Rhaetian) part of the Mecsek Coal Formation the facies show a well expressed trend of environment changes: delta – limnic – lacustrine – delta – lagoonal – plain marine – lagoonal – plain marine (Nagy 1969). During the Hettangian sedimentation, it was mainly fluvial with channel, flood plain and swamp facies. Further up the sequence, coquinas of brackish-water molluscs appear in increasing frequency. The Lower Sinemurian member of the formation may have been deposited in a tidal-flat marsh environment. In the middle member of the Mecsek Coal Formation, thin (0.5–1.5 m) rhyolitic tuffite interlayers occur (Haas 2001).

Plant beds sometimes alternate with mollusc-bearing marine sublittoral layers in the same horizons of the succession. In the upper member of the Mecsek Coal Formation, crinoids appear, indicating a temporary establishment of “normal salinity” marine conditions.

The coal formation is overlain by fine-grained sandstone and dark-grey shale with thinning upward sandstone interlayers (Vasas Marl). In the lower part of the succession,

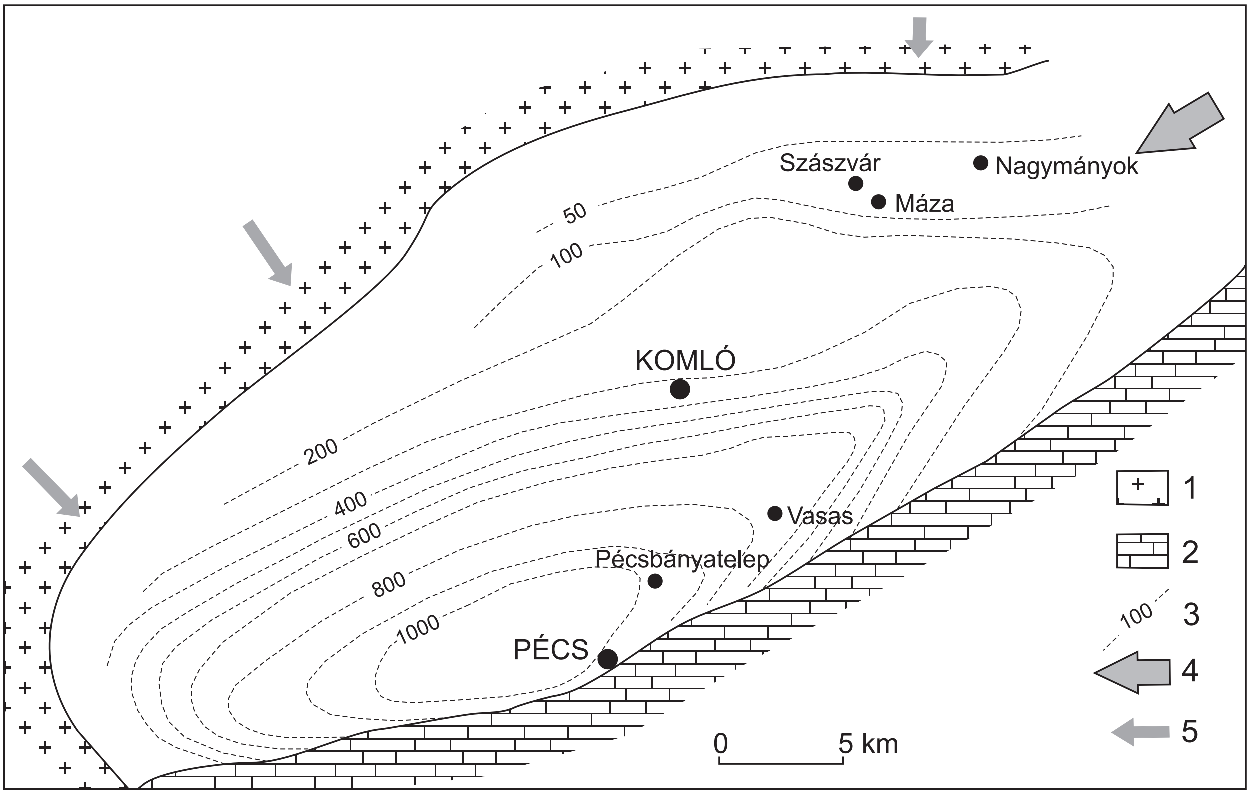


Fig. 2. Map of the Mecsek basin (modified, after Nagy 1969): **1** – granitoid denudated area (sedimentary basin margine), **2** – carbonate denudated area (sedimentary basin margine), **3** – isolines of hypothetical basin thickness, **4** – direction of the sea current, **5** – direction of granitoid clast transport

Liogryphaea beds occur which may have formed in a very shallow marine environment. Locally, other bivalves and crinoids, as well as sporadic poorly preserved plant remains, also occur.

The upper part of the formation is rich in molluscs, echinoderms, brachiopods and foraminifera, indicating a deeper marine ramp environment of normal salinity. The entire sequence suggests transgression and a gradual deepening of the sea. The rise in sea-level and the resultant retreat of the shoreline may have caused a decrease in terrigenous input, because the delta system diverged from the study area.

According to Némedi Varga (1998) the coal-bearing succession can be subdivided into three major units and several subunits:

1. The lowermost unit (Rhaetian) is divided into two parts:

1.1. The lower part showing laminated, paludal (river channel – floodplain) facies: grey to dark-grey siltstones, black shales and thin coal seams. The overlying bed contains layers of a phyllopod *Isaura hungarica* Vadász.

1.2. In the upper part of this section, a limnic facies dominates, represented by nonlaminated green-grey siltstones with occasional rootlet tracks, shale and subordinate sandstones.

2. The middle section (Hettangian) contains the thickest coal seams; the coal production is the most intensive therein and almost entirely limited to them. They are strongly variable in thickness and very difficult to follow because of the presence of foldings, flexures and reverse faults. The middle section is divided into five levels:

2.1. Limnic level a, with thin coal seams and predominating siltstones and shales, subordinately sandstone intercalations;

2.2. Limnic level b, with dominant sandstones, subordinately siltstones, without coal seams;

2.3. Limnic, with thick coal seams, dominating siltstones, shales, sandstones (in some areas), and a rhyolitic tuffite layer at Pécs;

2.4. Limnic – paralic transitional level. Dominant siltstones – sandstones, without coal seams, containing a tuffite layer with phyllopods (*Howellites princetonensis* var. *minor* Nagy) indicating freshwater environments;

2.5. Paralic transitional level with coal seams of medium thickness; dominant siltstones and shales.

3. The uppermost section (Lower Sinemurian) is of paralic type, characterized by thin coal seams that were not suitable for coal production. In the southern part of the basin, the facies is heterotypic, coastal, marine, with grey calcareous siltstones, fine- and coarse grained sandstones and marls. The uppermost section is subdivided into three parts:

3.1. The lower part, without coal seams, represents marine facies with syngenetic deformations created by sandstones with crinoids and “wormtracks”;

3.2. The middle part is a typical paralic succession of shales, aleurolites and sandstones with thin coal seams;

3.3. The upper part is of transitional type, with siltstones and sandstones.

Nagy & Nagy (1969) and Némedi Varga (1995, 1998) interpreted this section as paralic, open-lagoon, coastal and marine environments in a transgressive context. Nagy & Nagy (1969) accepted the deltaic character of the deposits, and suggested a river delta-plain leading to lagoon systems.

The changes of facies in the sedimentary series vary at particular sites within the same locality (shafts and open mines, Fig. 3). The stratigraphic sequences may strongly differ from each other at short distances as a result of the tectonic activity associated with strong subsidence, which produced flexures and folds. Consequently, data from different shafts are often of local significance only (e.g. see Nagy & Nagy 1969).

FACIES IN WHICH FOSSIL PLANT REMAINS WERE COMMON

In the Mecsek Mts. the facies sequence includes small cycles beginning from Early Hettangian limnic, up to Early Sinemurian, marine (Fig. 4). Plant remains are mostly associated with a Hettangian paludal (river channel – flood plain) facies.

At Pécsbánya and Vasas this part of the sequence is the thickest (almost equally thick) and starts in the Hettangian, while at Komló (Kossuth shaft) it begins in the early Sinemurian and narrows towards the NW of the sedimentary basin.

Changes are not only observed in the thickness of the sedimentary cycle. Near Pécsbánya and Vasas deltaic and floodplain facies dominate, with regularly repeated swamp

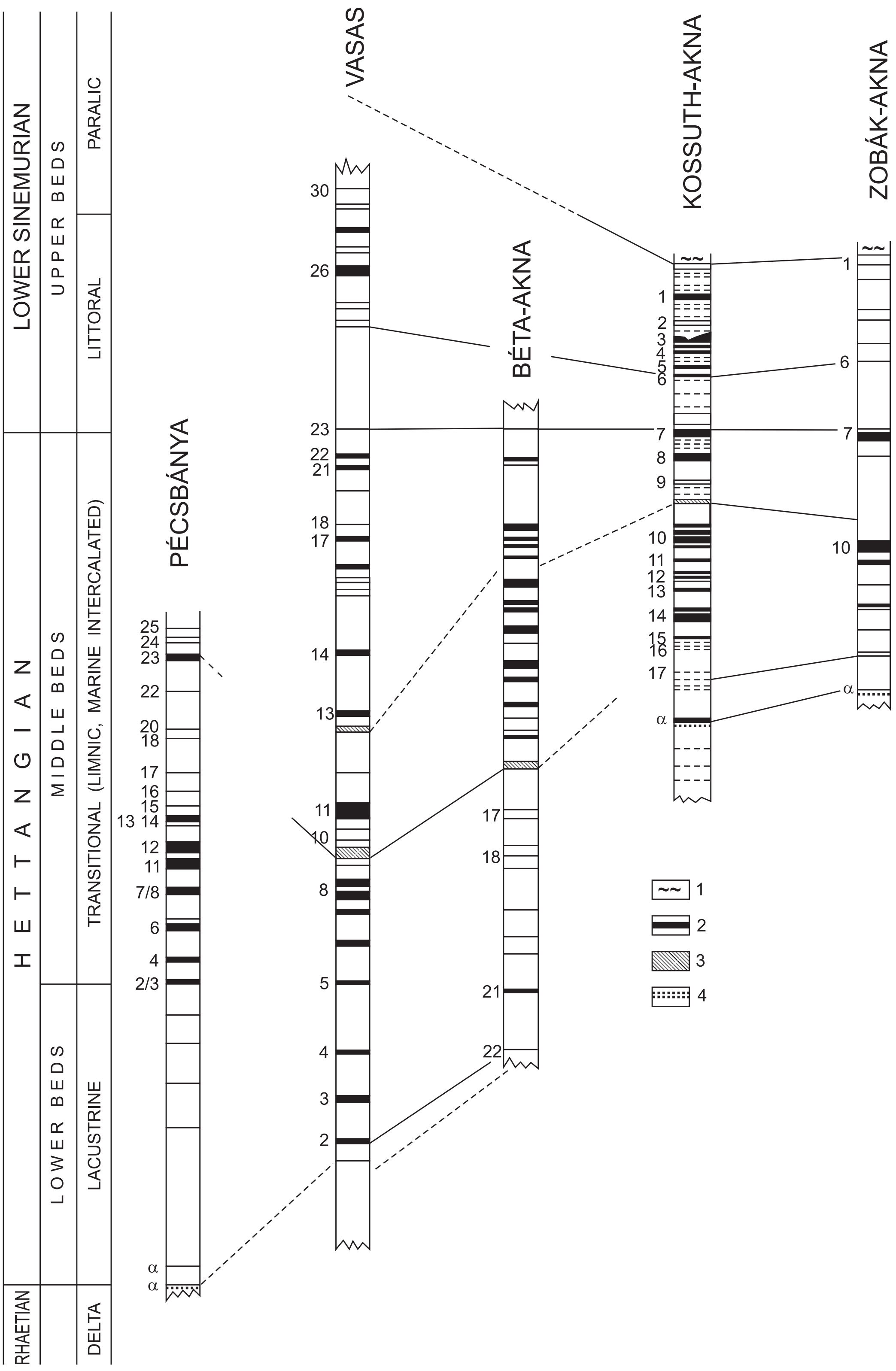


Fig. 3. The Mecsek Mts., sequences of different sites (modified, after Nagy 1969): **1** – overlying complex, **2** – coal seams with their serial numbers, **3** – tuffite, **4** – underlying complex

facies. In the Late Hettangian they are interrupted by a thin marine facies followed then by floodplain. Near the Komló-Béta shaft, the deltaic facies are only in the lower half of the sequence (Hettangian), which also contains cyclic swamp facies, and in the Early Sinemurian it turns into floodplain alternating with swamp and lagoon. The Komló-Kossuth shaft shows an increase in swamp facies alternating with floodplain.

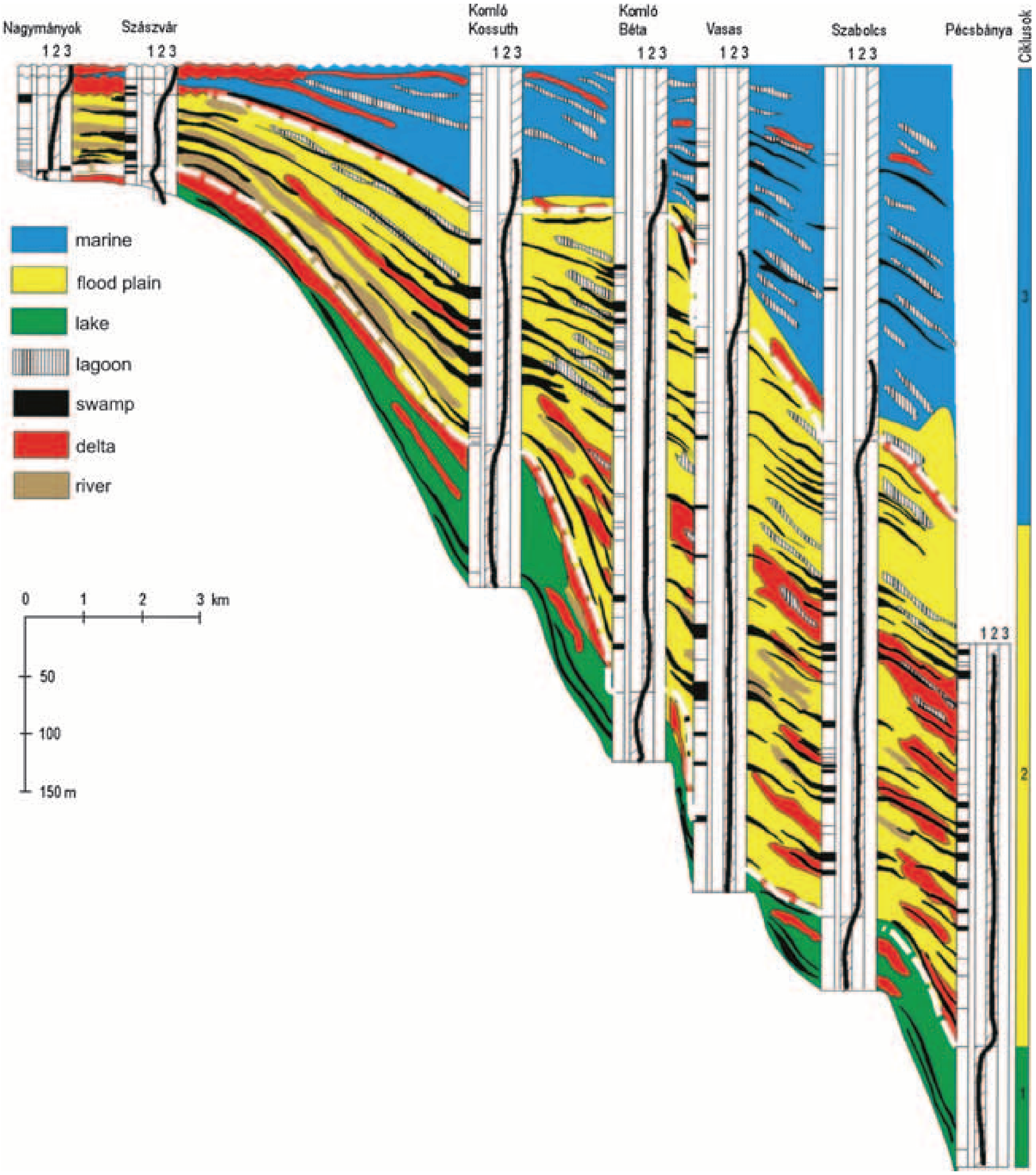


Fig. 4. Facies in the Mecsek Mts. locality (modified, after Nagy 1969)

PALAEOENVIRONMENT

The Mecsek delta plain (today's coal field area) was situated in the Jurassic at the latitude of today's Spain (Csontos & Vörös 2004, fig.23), the climate was generally stable, warm and wet during the whole period of the Jurassic (Vakhrameev 1991). According to the global palaeogeography, the main continents still formed one supercontinent (Golonka 2000), thus differences in plant content between particular localities only partly depended on climatic zones and floristical provinces. The main groups of plants, even at a generic level, were present all over the world. It seems, however, that plant specific diversification observed at the various fossil plant sites might be partly caused by local conditions like palaeogeographic position, altitude above sea level, intensity of solar radiation, distance from fresh-water and sea coasts, air humidity, moisture, type and quality of soil. The taxonomic content of the plant cover depended on adaptation to these conditions, and on the strength of competition between species.

The Mecsek Mts. flora grew in specific conditions characterized by short-term cycles as a consequence of the dynamic character of the delta plain. Oscillation in the water level, the flooded area, new areas formed by deposited sand, cyclic devastation and creation have made the territory interesting for the palaeobotanist (see also the figure in Thomas & Cleal 1993, p. 29).

PALAEONTOLOGY AND PALYNOLOGY

The coals generally contain monospecific bivalve assemblages of *Unio vizeri* Nagy accompanied by phyllopods, both indicating predominantly freshwater deltaic environments. They alternate with subordinate strata containing diverse gastropods and bivalves, indicating marine paralic environments (e.g. *Coelesina* and *Gryphea*). The bivalves from Pécsbánya are usually characteristic of lagoonal associations, except for the two genera, *Plagiostoma* and *Ceratomya*, which are characteristic of near-shore marine environments (Szente 1995). In a vertical direction the coal deposits show a tendency towards transition from freshwater limnic or deltaic facies to lagoonal or marine paralic facies, which are also heteropic facies at the same time.

Among terrestrial vertebrates, the Grallator-type footprint, *Comlosaurus carbonis* Kordos, were found in both open mines, Vasas and Pécsbánya (Kordos 1983, Ősi et al. 2011).

The palynological investigations in the Mecsek Mts. locality that started in the 1960s, were of interest to the mining industry, constituted a basis for the designation of the Triassic/Jurassic boundary and helped to correlate the distinct coal seams (Bóna 1963, 1969, 1979, 1983, 1995, Bóna et al. 1995). Based on rich palynological assemblages, Bóna (1983) established that the coal deposits were Upper Hettangian – Lower Sinemurian in age, and intercalated between the Uppermost Triassic (Rhaetian) strata and the coal measures of the Bucklandian Zone (Lower Sinemurian).

Bóna (1963) proposed the first, and still used, palaeoenvironmental model with three vegetation zones:

(1) the swamp zone (dominant allochthonous saccate conifer pollen grains

(2) the flat marsh zone (allochthonous saccate conifer pollen grains and autochthonous *Calamospora* (Sphenophyta)

(3) the marshland forest zone (fern spores, and pollen grains from seed ferns, Podozamitaceae and Palissyaceae.

A detailed palynofacies analysis focusing on palaeoenvironment and palaeoclimate was addressed for the first time by Ruckwied et al. (2008). They proved that the palynomorph assemblages represent a typical Rhaetian/Hettangian microflora. The Upper Rhaetian part of the sedimentary series is dominated by bisaccate pollen grains, trilete spores and pollen of the *Circumpolles* group, and by a small amount of *Corollina* spp. Up-section, a striking increase in trilete spores, mainly species of the spore genera *Concavisporites* and *Deltoidospora*, was recognized.

They also noted the sudden increase in *Dictyophyllum harrisii* within the Triassic/Jurassic boundary interval, followed by a peak abundance of *Inaperturopollenites* spp. This signal is repeated up-section in a small-scale cyclic pattern characteristic of the entire Hettangian sedimentary series following swamp – fluvial changes.

Within the small-scale cycles, river elements of the palynomorph assemblage (*Conbaculatisporites mesozoicus*, *Concavisporites* spp., *Deltoidospora* spp., *Stereisporites* spp., *Todisporites* spp., *Vitreisporites pallidus*) dominate in fluvial sandstones, whereas swamp elements (predominantly *Dictyophyllum* spp., *Inaperturopollenites* spp.) are characteristic of the coal beds; deltaic sand- and siltstones show a nearly equal amount of both groups, i.e. river and swamp elements, pointing to both the standing and agitated water bodies of the delta plain.

Götz et al. (2011) made a palaeoecological reconstruction of the Mecsek locality according to the model proposed by Abbink (1998). This model was discussed in relation with the macroflora and its adaptation to different types of environment (see also page 162).

PART 2

Reconstruction of the Environment Based on Plant Macroremains

PALAEOATMOSPHERIC CO_2 COCENTRATION

Palaeobotanical climate proxy methods complementing geological and geochemical approaches in palaeoclimatic studies are now well-established (Beerling 1999, Poole & Kürschner 1999, Mosbrugger 1999). The response of plants to external conditions and their inherent adaptation mechanisms make it possible to monitor changes in atmospheric pCO_2 on the basis of leaf structures. In the last decades, a method that uses cuticle characteristics has been developed. Stomatal parameters have proved particularly useful, because stomata density is closely related to atmospheric composition and displays an inverse correlation to pCO_2 (Woodward 1987).

An estimation of palaeoatmospheric CO_2 concentration is possible using parameters such as the stomatal density (SD), stomatal index (SI), and its relation to the nearest living equivalent species (NLEs), defined as the stomatal ratio (SR). A detailed discussion of this method is provided by Beerling and Royer (2002a, b).

Numerous previous studies have investigated the SD and SI for different plant groups from different time intervals of Earth's history, from the oldest land plants (McElwain & Chaloner 1995, McElwain 1998) up to modern plants. For the Mesozoic, mostly gymnosperms have been used, including Cycadales (e.g. *Ctenis* and *Nilssonia*: McElwain Chaloner 1995, McElwain et al. 1999), Bennettitales (*Anomozamites* and *Pterophyllum*: Steinthorsdottir et al. 2011), Pteridospermales (*Stenopteris*: McElwain et al. 1999, McElwain 1998, *Lepidopteris, Tatarina, Rhachiphyllum*: Retallack 2001, Bonis et al. 2010), Coniferales (*Brachyphyllum* and *Pagiophyllum*: McElwain 1998) and Ginkgoales (*Baiera*, *Ginkgoites, Ginkgo*: Xie et al. 2006, Beerling et al. 1998). Ginkgoales represent an especially suitable group, because of its wide occurrence, commonly well-preserved cuticle and continuous presence in global flora from the Palaeozoic up to the present. The recent *Ginkgo biloba*, the only NLE for Ginkgoales, has been extensively studied for its SI from different localities. Both dried material from herbaria, and freshly collected material were studied (Royer et al. 2001), as well as samples growing under controlled experimental conditions in ambient and elevated CO_2 (e.g. Beerling et al. 1998).

The species *Ginkgoites marginatus* from the Hettangian *Thaumatopteris* zone (Nagy 1961) of the Mecsek Mts. was selected for stomatal measurements. According to Beerling and Royer (2002a), the SI is species-dependent, so data from the same species should be compared.

Samples for investigation were restricted mainly to Pécsbánya, where 22nd horizon was most productive for macrofloral remains.

The best preserved 18 samples of *Ginkgoites marginatus* from the Mecsek Mts. were studied. Ginkgoales are represented in the Hungarian locality by three genera and five species; their richness is mainly manifested mainly in the high numbers of specimens. The most common is *Ginkgoites marginatus*. Usually it has a cuticle well-preserved for determination, but for our study, the quantity of the material was limited to the best samples only. A lot of leaves have cuticles partly damaged by pyrite, which made the cell outlines unrecognizable; other samples have cuticles too delicate for preparing satisfactory large pieces. The cuticle pieces were collected in each case from the middle part of the leaf and prepared in Schulze solution followed by 3% KOH. In some cases, unprepared cuticle pieces were examined under a fluorescent microscope. Only the lower cuticle was used for examination. Epidermal cells, including the subsidiary cells, were counted according to the method described by Jones & Rowe (1999) and Kürschner (1996). The counting was done on microphotographs – for each sample as many counts as possible depending on the size and quality of cuticle: this amounted to 116 measurements of 18 specimens. The investigated cuticle area was 300×300 µm = 0.09 mm^2 (the minimum area for SI calculation is 0.03 mm^2 – Jones & Rowe 1999). This area was chosen because it was possibly the largest fragment of cuticle within a stomatal band. SD was calculated from the same parts of cuticle.

SI was calculated according to Salisbury's equation (Jones & Rowe 1999) $SI = [SD/(ED+SD)] \times 100$, where SI – stomatal index, SD – stomatal density (number of stomata/area), ED – number of epidermal cells/area.

The atmospheric CO_2 level was estimated as 600 ppm × SR when SR is the Stomatal Ratio, i.e. SI of the nearest living equivalent divided by SI of fossil plant: SR = SI of NLEs/SI fossil. Carboniferous standardization was used after Berner and Kothavala (2001).

SI for the extant *Ginkgo biloba* was used according to Beerling and Royer (2002a), as 9.1 at 350 ppm.

The statistical test employed was the InStat 997: GraphPad InStat Demo, Version 3.00 for Win95/NT. GraphPad Software Incl., San Diego.

RESULTS AND INTERPRETATION

The mean value of stomatal density for Hungarian specimens is 4.23, and the mean SI = 4.96.

Based on the obtained SI values, the palaeoatmospheric CO_2 concentration was calculated and presented on Table **1**.

Table 1. *Ginkgoites marginatus* – SI, SD and SR values for Hungary; SD and SI counted for 0.09 mm^2 cuticle areas

Ginkgoites marginatus, Hungary	
number of specimens/ measurements	18/116
SI average (mean)	4.96
Std deviation	1.056
Std error	0.2488
Minimum	3.220
Maximum	6.328
Median	5.053
Lower 95% CI	4.437
Upper 95% CI	5.487
SD	2.30–6.30
SD average	4.23
SR	1.83

As shown on Table 2, the SI values obtained from recent *Ginkgo biloba* by different authors vary even at the same CO_2 ppm level, which may cause fluctuation in estimations of palaeo CO_2 level. To avoid inaccuracy during comparison of different data, in the present paper (Table 3) the SI of *G. biloba* = 9.1 at 350 ppm was used after Beerling and Royer (2002a), which is the nearest to the mean value of accessible records at 350 ppm.

The gained SI and pCO_2 level data were compared with those from other localities and time slices, measured on different species belonging to the Ginkgoales. The list of species and their SI is given according to Beerling and Royer (2002a), supplemented with data published later. For instance, measurements were completed on *Ginkgoites marginatus* from Sweden and its SI estimated by Beerling et al. (1998). The value of SI given by the authors for the Early Jurassic is 5.7, which is a little higher than the value for the Hungarian specimens, but the difference is not significant. There is also a record for the Late Triassic, which shows a higher value (= 6.5), which denotes a slight increase in pCO_2 at the Triassic-Jurassic transition (see also Beerling et al. 1998, McElwain et al. 1999, Bonis et al. 2010). Comparing all the data from Table 3, it can be observed that SI values of different species from the same localities correspond well with each other. The level of pCO_2 during the Mesozoic fluctuates generally between 666 and 1162, except for two peaks at 2100 (China Middle Jurassic – *G. yimanensis*) and 1606 (China E. Cretaceous – *G. coriacea* (Chen et al. 2001). The pCO_2 value for the Hungarian Early Jurassic is placed among the higher values above 1000 ppm in the curve given by Beerling and Royer (2002a, p. 546). These data also fit into the curve of CO_2 and temperature trends over the past 300 million years given by Kürschner (2001).

The Hungarian data confirm the Hettangian climate of this locality as typical for this period, without significant local oscillation.

Table 2. *Ginkgo biloba*, SI values according to different authors and possibly fluctuation in pCO_2 in Hungary estimated on the bases of these values

	Beerling et al. (1998) 350 ppm	Beerling et al. (1998) 560 ppm	Royer et al. (2001)	McElwain et al. (1999)	Chen et al. (2001)	Retallack (2001) 350 ppmv	Retallack (2001) ppmv 560 ppmv	Beerling & Royer (2002) 300 ppmv	Beerling & Royer (2002) 350 ppmv
SI of *Ginkgo biloba*	8.7	8.0	12.1	11.33	9.3	9.7	8.0	12.1	9.1
SR	1.75	1.61	2.44	2.28	1.88	1.95	1.61	2.44	1.83
palaeoatmospheric CO_2 level	1050	966	1464	1368	1128	1170	966	1464	1100

Table 3. SI values for the Mesozoic ginkgoalean species (on the basis of Beerling and Royer 2002), pCO_2 level was estimated using Si of NLE *Ginkgo biloba* = 9.1 at 350 ppm (after Beerling & Royer 2002)

Study	Species of the genus *Ginkgoites*	Locality	Period	SI	CO_2 level
Beerling et al. (1998)	*G. troedssonii*	Sweden	Late Triassic (Rhaetian)	5.9	925
	G. marginatus	Sweden	Late Triassic (Rhaetian)	6.5	840
	G. marginatus	Sweden	Early Jurassic	5.7	958
	G. huttoni	Yorkshire	Middle Jurassic	5.6	975
McElwain et al. (1999)	*G. obovata*	Sweden	Late Triassic (Rhaetian)	4.7	1162
	G. obovata	Sweden	Late Triassic (Rhaetian)	6.8	803
	G. acosmia	Greenland	Late Triassic (Rhaetian)	8.5	642
Chen et al. (2001)	*G. obrutschewii*	China	Early Jurassic	6.7	815
	G. yimanensis	China	Middle Jurassic	2.6	2100
	G. huttoni	Yorkshire	Middle Jurassic	5.5	993
	G. coriacea	China	Early Cretaceous	3.4	1606
Retallack (2001)	*G. matatiensis*	S. Africa	Late Triassic (Carnian)	8.2	666
	G. telemachus	S. Africa	Layte Triassic (Carnian)	7.6	718
	G. lunzenzis	Austria	Late Triassic (Carnian)	6.7	815
	G. troedssonii	Sweden	Late. Triassic (Rhaetian)	6.0	910
	G. manchurica	China	Late Jurassic (K-Tit.)	7.4	738
	G. manchurica	China	Early Cretaceous (Berr.)	5.0	1092
	G. coriacea	China	Early Cretaceous (Val-Haut)	6.2	881
	G. polaris	Antarctica	Early Cretaceous (Barr.)	6.7	815
Beerling & Royer (2002)	*G. dahlii*	Norway	Middle Jurassic	4.5	1213
Xie et al. (2006)	*G. chilinense*	China	Middle Jurassic. (Bajocian)	5.3	1030
	G. obrutschewi	China	Middle Jurassic. E. Bajocian	5.9	925
	G. huttoni	China	Early Jurassic. Aalenian	6.1	895
	G. aganzhenense	China	Early Jurassic. (Pliensbachian)	5.8	941
present paper	*G. marginatus*	Hungary	Early Jurassic (Hettangian)	4.96	1100

STATISTIC ANALYSES

DATA COLLECTION AND THEIR DESCRIPTION

The fossil plant macroremains from the Hettangian–Sinemurian Karolinavöldi Coal Formation of the Mecsek Mountains were collected from 1950 in the shafts of Béta, Kossuth and Zóbak, in the open mines of Pécsbánya, Rücker and Vasas and the dumps of Budafa and Dáviföld the Komló and Pécs regions, Southern Hungary (Fig. 1). They are found in layers between exploited coal lenses, whose thickness varies from a few centimetres to several dozen meters; they are usually preserved in siltstone and its varied forms like grey siltstone, micaceous grey siltstone, brown siltstone with a high level of organic matter and the form containing mica and foliated siltstone and the form with mica, foliated siltstone with a high crystal sulphur content, very fine grained siltstone and fine laminated siltstone and the form with crystal sulphur, and sandstone.

The present study is based on all leaf species from the Mecsek Mts. stored in the palaeobotanical collection in the Hungarian Natural History Museum, Department of Botany. The collection at the moment contains more than 5000 hand specimens.

The remains are represented mostly by complete or incomplete leaves, but also by leafy shoots (conifers), fragments of axes, simple or branched, seeds, roots, and occasional fructifications. The remains are distributed on rock slabs in various directions, from one to several on each slab; often slabs of the fine laminated siltstone are entirely covered by plant compressions; the fossil leaves are also present in between rock lamellas. The number of different taxa represented on particular slabs usually varies from 1 to 3, but often rises to 5.

The aim of the study was to detect relationships between plant species in the community and their coexistence in ecosystems, clarify possible plant segregation into groups dependent on local landscapes, on the kind of rocks and on the site in the depository basin, with the aid of numerical methods. The acquired data are used for a model of the delta ecosystem. Personal observations during whole period of collection (1989–2003) confirmed that the same species in the same combinations repeated independently on level on particular sites. This fact allows assumption that collected samples cover all depositional subtypes and assemblages of the Mecsek Coal Formation.

Specimens used for the study were larger than 10 cm, and possibly represented more than one plant remain on a rock surface. Data were collected from both sides of slabs and they were treated separately.

The following features were recorded into the database:

(1) the site of collection (name of shaft, open mine, dump);

(2) the names of all species on the slab. In some cases, data only regard the generic level: *Sagenopteris* is partly undeterminable due to its cuticle being poorly preserved, and the genus is generally quite uniform in environmental tolerance, and *Brachyphyllum* was found in small amounts; both species, *B. mamillare* and *B. crucis*, show no differences either in rock *matrix* or in co-occurrence, so they are handled together. Also, *Pagiophyllum* was used for analysis as a genus, since *P. peregrinum* is very common, and occurs together with the rare *P. ordinatum*. *Coniopteris hymenophylloides*, *Sphenopteris* sp., *Pachypteris banatica*, *Pseudoctenis* sp., *Ctenis* sp., and *Geinitzia* sp. were not included into data base for the analyses, because they occur only as single specimens not associated with other taxa.

The state of preservation and fragmentation of some ginkgoalean and equisetalean remains made them undeterminable at a specific level, but they were found in such large amounts, that they cannot be omitted. They are indicated in the material as indeterminable ginkgophytes and *Equisetites* sp., independent of the determined species from those groups;

(3) length of remains. When the remain was fragmented by rock breaking, but it was obviously fossilized as a larger piece, the length is given as "more than" × cm. In the case of very dense and numerous fragments, the measurements were done on the fragments that were easily distinguishable and a length was given from × to y. The term "large" used in the text always means a size over 6 cm in length.

(4) type of remain (leaf, stalk, cone, etc.);

(5) type of rock.

MACROFOSSILS AND PLANT ASSEMBLAGE

The basic character of the fossil flora of the Mecsek Mts. was determined by environmental changes typical for delta plains: riverside–swamp–lake–lagoon. Such alternations induced changes in the plant cover of the area. The ecosystem was influenced by both damaging and creating processes caused by fluctuations in the water level or changes in the riverbed.

Plant fossils have been sporadically collected in the Mecsek Mts. since the beginning of the 19th century, when the coal mining started. Later, lists of plant fossils were recorded in a number of publications (among others Stúr & Böck 1874, Hantken 1878, Kleidorfer 1898, Hofmann 1907, Némedi Varga 1998, Wein 1952), as supplementary data for the geological documentation needed for commercial mining. The first short description of the macroremains was given by Nagy (1961). The taxonomic revision of the described taxa and systematic work on the continuously collected material has been carried out by Barbacka (1992, 1994a,b, 2001, 2002, 2009).

The remains mostly occur in the Hettangian deposits which are richest in coal seams, in between the coal seams, and are predominantly preserved in siltstone, fine laminated siltstone and, rarely, in sandstone. From a palaeoecological aspect, the coal seams can be regarded as one unit. Therefore, this is treated as one locality with several sites (shafts, open mines and dumps).

Generally, the plant remains from the Mecsek Mts. are characterized by quite a high generic variability, while the species diversity in each genus is low. Almost all the main plant groups occur in the flora; each group is represented by a number of genera, usually up to 5, with the exception of the fern genera, represented by up to 9. The number of species in each genus varies from usually 1 up to 3 in only four genera: *Cladophlebis*, *Sagenopteris*, *Nilssonia*, *and Brachyphyllum*. Table 4 shows the complete list of taxa (leaves only).

SHORT CHARACTERIZATION OF THE FLORA ELEMENTS IN THE MECSEK LOCALITY

Horsetails are represented by two genera, *Equisetites* (*E. columnaris* – Pl. 1, fig. 1, and *E. muensteri*) and *Neocalamites* (*N. carcinoides*, see Barbacka 2009). Both genera are

Table 4. List of leaf taxa described from the Mecsek Mts. so far

SPHENOPHYTA	*Equisetites columnaris* (Brongniart) Phillips
	Equisetites muensteri Sternberg
	Equisetites sp.
	Neocalamites carcinoides Harris
PTERIDOPHYTA	
Marattiaceae	*Marattiopsis hoerensis* Schimper
Osmundaceae	*Cladophlebis denticulata* (Brongniart) Fontaine
	Cladophlebis haiburnensis (Lindley et Hutton) Brongniart
	Cladophlebis roesserti (Schenk) Saporta
	Todites goeppertianus (Münster) Krasser
	Todites princeps (Presl) Gothan
Matoniaceae	*Phlebopteris angustiloba* (Presl) Hirmer et Hörhammer
	Phlebopteris sp.
Dipteridaceae	*Clathropteris meniscoides* Brongniart
	Dictyophyllum nilssonii (Brongniart) Göppert
	Dictyophyllum rugosum Lindley et Hutton
	Thaumatopteris brauniana Popp
Dicksoniaceae	*Coniopteris hymenophylloides* (Brongniart) Seward
	Sphenopteris sp.
PTERIDOSPERMATOPHYTA	
Caytoniales	*Sagenopteris hallei* Harris
	Sagenopteris nilssoniana Brongniart
	Sagenopteris pilosa Barbacka
incerte sedis	*Komlopteris nordenskioeldii* (Nathorst) Barbacka
	Pachypteris banatica (Humml) Doludenko
	Ptilozamites cycadea (*Ctenozamites cycadea*) (Berger) Schenk
CYCADOPHYTA	
Cycadales	*Bjuvia simplex* Florin
	Ctenis sp.
	Nilssonia obtusa (Nathorst) Harris
	Nilssonia polymorpha Schenk
	Nilssonia revoluta Harris
	Pseudoctenis sp.
Bennettitales	*Anomozamites marginatus* (Unger) Nathorst
	Pterophyllum subaequale Hartz
GINKGOPHYTA	
Ginkgoales	*Baiera furcata* (Lindley & Hutton) Braun
	Ginkgoites marginatus (Nathorst) Florin
	Ginkgoites minuta (Nathorst) Harris
	Sphenobaiera leptophylla (Harris) Florin
	Sphenobaiera longifolia (Pomel) Florin
CONIFEROPHYTA	
Coniferales	*Elatocladus* sp.
	Geinitzia sp.
Cheirolepidiaceae or Araucariaceae	*Brachyphyllum crucis* Kendall
	Brachyphyllum mamillare Lindley & Hutton
	Brachyphyllum papareli Saporta emend. Thévenard
Cheirolepidiaceae	*Hirmeriella airelensis* Muir et van Konijnenburg-van Cittert
	Pagiophyllum ordinatum Kendall emend. Harris
	Pagiophyllum peregrinum (Lindley et Hutton) Schenk emend. Kendall
Podocarpaceae	*Podozamites lanceolatus* Lindley et Hutton
	Podozamites sp.
Incertae sedis	*Desmiophyllum* sp.

common and numerous specimens have survived as large fragments. In the case of *Equisetites*, besides stems, the underground rhizomes together with roots in their growing position have been preserved, which suggests undisturbed conditions in fine, muddy soil.

Neocalamites is rarer than *Equisetites.* It is supposed that it occurred in a different habitat, possibly dryer than *Equisetites* (Barbacka 2009).

Ferns are the richest group, being represented by 14 species from five families (see

Table 4). Except for the Dicksoniaceae, which have a very fine structure and are small, ferns from the Mecsek Mts. have large, palmately dissected fronds (often exceeding 1 m) with long pinnate segments or toothed or incised margins; the species of Marattiaceae, Osmundaceae and Dicksoniaceae are pinnate. Usually large fragments, or even whole fronds were preserved, but they had always been fragmented during mining processes, or erosion. Thus, the specimens contain fragments of rachises with pinnules, fragments of segments and often complete leaf bases. Extended fronds with a large surface area correspond with humid and warm conditions (van Konijnenburg-van Cittert 2002).

Four genera are represented by more than one species and usually these species differ significantly from each other. In the genus *Cladophlebis*, *C. haiburnensis* has the widest pinnules, with entire margins and rounded apices. Pinnules of *C. denticulata* (Pl. 2, fig. 3) are elongated, relatively narrow and dentate in different degrees, apex acute or subacute. *C. roessertii* (Pl. 2, fig. 4) is the smallest, and its pinnules are narrow, elongated, shorter than 1 cm, margins entire and apex acute (Barbacka & Bodor 2008).

Todites goeppertianus (Pl. 1, fig. 2) and *T. princeps* (Pl. 2, fig. 1) differ in their whole structure. The former is large and its fronds and pinnules resemble *C. haiburnensis* in size and shape. *T. princeps* has small fine fronds with minute pinnules (ca. 0.5 cm long). Reduced size can sometimes be a sign of arid circumstances, althrough *C. hymenophylloides* and *Sphenopteris* sp. certainly are not of a xeromorphic type. The fronds of *Phlebopteris angustiloba* (Pl. 1, fig. 3) are not large, and the pinnules are very narrow (0.5 cm or less in width), and touching each other. *Phlebopteris* sp. (Pl. 2, fig. 2) has larger fronds and more delicate, long, sparse pinnules.

The two species of *Dictyophyllum* differ in the same manner from each other. *D. nilssonii* (Pl. 1, fig. 5) has long segments with incisions, while those of *D. rugosum* (Pl. 1, fig. 6) are long and relatively narrow (ca 2 cm), elongated, more sparsely arranged and often incised. Their apex is acute. The lamina substance is thicker than in *D. nilssonii*. Two other genera from the same family occur as a single species: *Thaumatopteris brauniana* and *Clathropteris meniscoides* (Pl. 1, fig. 4). Both have large fronds. Segments of *C. meniscoides* are very long, toothed, while *T. brauniana* has long, narrow pinnules (up to 1.5 cm wide).

The rarest are representatives of Dicksoniaceae, *Coniopteris hymenophylloides* (1 specimen) and *Sphenopteris* sp. (17 specimens), and two species from Osmundaceae, *C. roessertii* (16 specimens), and *T. princeps* (14 specimens). The remaining two species, *Todites goeppertianus* and *Clathropteris meniscoides* are very common, but the number of co-occurring specimens is relatively low.

Pteridosperms are very widespread in the Mecsek locality, although the number of their taxa is low. The commonest is *Komlopteris nordenskioeldii* (Pl. 2, figs. 5, 7), which is one of the dominant elements in the Mecsek community. This seed fern has pinnate leaves about 20 cm in length with varied pinnules attached to the rachis, most often with a narrowed base. This type of adherence is quite fragile, but despite that, leaves are very often found whole, or as rachis fragments with pinnules. Leaves of this species often remained preserved as debris, in finely laminated aleurolite, also crowded between lamellas. The structure of the leaves shows an adaptive specialization (shade leaves with thin cuticle and sun leaves with thick ones, Barbacka & van Konijnenburg-van Cittert 1998, Guignard et al. 2001), but the general structure of its stomata suggests an adaptation to wet habitats (Barbacka 1994c). The cuticles vary in the presence and number of multicellular hair bases, whose structure is very similar to the secreting glands (hydatodes) of recent *Gonocaryum* (Icacinaceae, see Hejnowicz 1980). Their function is connected with the secretion of superfluous water (Barbacka 1994b, Barbacka et al. 2010). Possibly, the plant was a tree (Barbacka & van Konijnenburg-van Cittert 1998).

The genus *Sagenopteris* (Pl. 3, fig. 1) is represented by three species (Barbacka 1992), recognizable only by cuticle details. Its seemingly compound leaves with a rather short petiole and usually four (rarely five) nearly oval pinnules are rather small – the size of developed leaf varies from 5 to 15 cm. The structure of the leaf is always very delicate, the pinnules' place of attachment is very thin and easily breaks, but still complete or almost complete leaves are often found in addition to numerous separate pinnules. The cuticle is always thin and the stomata have large and exposed guard cells. Species from the Mecsek Mts. often have numerous hair bases. The cuticle structure suggests adaptation to high air humidity.

Ptilozamites (*Ctenozamites*) *cycadea* (Pl. 2, fig. 6) is common. Its large, bipinnate leaves are quite strong and coriaceous. Small pinnules (up to 3 cm) join to the rachis with their whole base. The cuticle is thick, sometimes a little thinner (sun and shade leaves effect? Barbacka & van Konijnenburg-van Cittert 1998) and the stomata are strongly protected by cuticle thickenings which restrict the stomatal pit to a very small opening. Guard cells are large and well cutinised. These features are of a xeromorphic type.

Pachypteris banatica, excluded from the analyses, is very rare, almost unique (3 specimens found). The pinnate leaves have small pinnules (up to 1.5 cm) with a thick cuticle; the stomata are varied, protected by papillae or by a slightly thickened ring, with sunken guard cells. The morphology and cuticle (presence of glands) suggest xeromorphic or halophytic tolerance (Barbacka 1994 a,c).

The most widespread cycad genera in the Mecsek locality are *Nilssonia* and *Bjuvia* (Barbacka 2001). All species of *Nilssonia*, *N. polymorpha* (Pl. 3, fig. 2), *N. obtusa* and *N. revoluta* have elongated leaves with entire or almost entire margins (*N. polymorpha* is more or less irregularly pinnate). This type of leaf grows in clusters from short branches (*Nilssoniocladus* Kimura & Sekido). In most cases they are found as complete leaves; only the largest species has fragmented remains. The leaves often form debris in fine laminated aleurolite, frequently crowded between laminas. These plants were probably of the shrub type (see reconstruction of similar species, Watson & Cusack 2005, text fig. 33). Species from the Mecsek Mts. differ from each other in their size and with regard to their cuticles. The smallest is *N. revoluta,* whose leaves are narrow (less than 1 cm) and do not exceed 9 cm in length. Its cuticle is thick and stomata small, surrounded by a cutinised ring. These features may be regarded as xeromorphic. *N. obtusa* is of medium size, its leaves are up to 17 cm long, and the cuticle is thinner than in *N. revoluta*. The stomata have thicker subsidiary cells than ordinary cells (sometimes papillae) and numerous one-cell hair bases occur on the cuticle. This species shows transitional features between xeromorphic *N. revoluta* and the finest *N. polymorpha*, which has the largest leaves of the three species. The length of its leaves is estimated at up to 30 cm (no whole leaf preserved), and width at up to 5.6 cm. The cuticle is very fine, with thin stomata with hollow papillae on subsidiary cells and occasional hair bases. This species shows features mostly related to wet conditions.

Bjuvia simplex (Pl. 3, fig. 3) is very common. Its very large leaves resemble those of recent bananas. Because of their size, the leaves are always found in fragments, sometimes forming debris. The cuticle is moderately thick, and stomata are small and surrounded by a thickened ring (sometimes papillae). The large surface of the leaf blade, which is exposed to allow intensive evaporation, signals rather wet conditions and is justified by the need to protect the stomata, since the plant is large with leaves placed on the top of a high stem (see reconstruction, Florin 1933, text fig. 32).

Pseudoctenis sp. and *Ctenis* sp. are very rare, only a few fragments being collected, so they were not used in the analyses. They have pinnate leaves with a rather thick cuticle and thickenings around the stomatal pit.

Bennettites are only represented by two species belonging to two genera: *Anomozamites marginatus* and *Pterophyllum subaequale*. They are not numerous in the locality and their leaves are mainly found as large fragments. Their leaves are pinnate with narrow segments and both species are rather small in their categories. Their cuticles are moderately thick and do not show any special adaptive features. Usually bennettites are connected with rather dry conditions (Abbink 1998, Abbink et al. 2004).

Ginkgophytes are very numerous (Barbacka 2002); especially abundant are *Ginkgoites marginatus* (Pl. 3, fig. 4) and *Baiera furcata* (Pl. 3, fig. 6). *Sphenobaiera longifolia* (Pl. 3, fig. 5) and *S. leptophylla* are less common. In most cases, the leaves were preserved complete; even leaves of such fine plants as *Sphenobaiera leptophylla* or *S. longifolia*. Ginkgophytes in the Mecsek often form debris, but even in these cases, fragmentation is not strong.

All taxa from this locality are characterized by relatively narrow segments (2–5 mm in different taxa). The broadest segments belong to *Ginkgoites marginatus*, up to 17 mm in the form with two lobes. They have thin to moderately thick cuticles with papillae on the subsidiary cells or at least thickenings around the stomatal pit in all species, sometimes also on the ordinary cells.

Ginkgoites minuta, not used in the analyses, is very rare, being found only once, and all the leaves came from the same slab. Its morphology differs from other ginkgophytes from this locality in its size (it is much smaller), thicker cuticle and in the presence of resin bodies. In all the other species, resin bodies were not observed, even in *Sphenobaiera leptophylla*, which was described by Harris (1935). It seems that their presence may depend on the environment (Barbacka 2002).

The conifers are strongly dominated by *Elatocladus* sp. (Pl. 3, fig. 9). The genera *Brachyphyllum*, represented by three species (*B. mamillare, B. papareli* and *B. crucis*), as well as *Pagiophyllum* (Pl. 3, fig. 8) with its two species (*P. peregrinum* and *P. ordinatum*) are not very common, but often co-occurred with other taxa. They are commonly preserved in large shoot fragments, often branched, but in debris the fragments can be rather small (1–2 cm or even separated leaves). Their morphology is different: *Elatocladus* sp. has needle-like leaves of very fine structure; its cuticle is thin and unsuitable for preparation. It is usually interpreted as living in wet conditions. *Brachyphyllum* and *Pagiophyllum* have thick and small leaves adjacent to their shoots, their cuticle is thick and sunken guard cells are protected by a thickened cuticular ring suggesting the xeromorphic character of these plants (Thévenard et al. 2005).

Some other coniferalean taxa are present in the locality, like *Geinitzia* sp. and *Podozamites schenkii* (Pl. 3, fig. 7). Both genera are fine in structure, having a thin cuticle unsuitable for preparation. *Geinitzia* (not used in the analysis) is found as branched shoots and, similarly to *Elatocladus*, *Podozamites* is usually preserved as rather large fragments, in contrast to its fine shoots and leaves with narrow bases. They are usually associated with wet conditions (Harris 1979).

DEGREE OF FRAGMENTATION, AUTOCHTONOUS ORIGIN OF THE REMAINS

High numbers of samples allow the analysis of different degrees of remains fragmentation, which is inevitable even in autochthonous or parautochthonous flora. Figure 5A-N shows categories of size/type of preservation for the fourteen most abundant species (over 30 specimens), from particular groups. The following categories were considered: large fragments (above 6 cm), debris (numerous fragments between 2–6 cm), litter (a crowd of large fragments or complete/almost complete leaves, in between rock lamellae as well), and small fragments (separate, below 6 cm). Leaves, which may have been preserved complete, i.e. *Komlopteris* or *Sagenopteris*, have additional categories like “complete” or “pinnae”, and ginkgophytes have a category for “segments”.

The state of preservation of macroremains proves that most of them are autochthonous or parautochthonous in origin and there were good conditions for fossilization (the presence of cuticles and their good state). As it issues from Fig. 5A-N the autochtonic character of the flora may be proved by:

a. domination of large and undamaged fragments

b. fragile attachments of pinnules in compound fronds or leaves are in most cases undamaged

c. conifer shoots (mainly *Elatocladus*) are very often preserved in branching state and often with male or female cones attached

d. occurrence of underground rhizomes of *Equisetites* with thin roots in growing position

e. predominance of monospecific debris in which leaves are often complete (Ginkgoales) or fragments are relatively large (e.g. separate, but entire pinnules).

MULTIVARIATE ANALYSIS

The data encompass the species composition of 1122 palaeontological samples, which were classified into types of rock substratum according to the geological criteria. Generally, 37 species of plant and 10 types of rock substratum were recognized. The occurrence of species in samples was coded in a nominal, binary 0–1 scale, i.e. as absence/presence data.

Additionally, each sample was characterized regarding the type of rock substratum. Nominal variables (types of rock substratum) were represented by a series of dummy variables each representing a category y_{ik} = 1 or 0, depending on whether sampling unit i belongs or not to category k. The data set prepared in the form of data matrix was then used for the clustering and ordination.

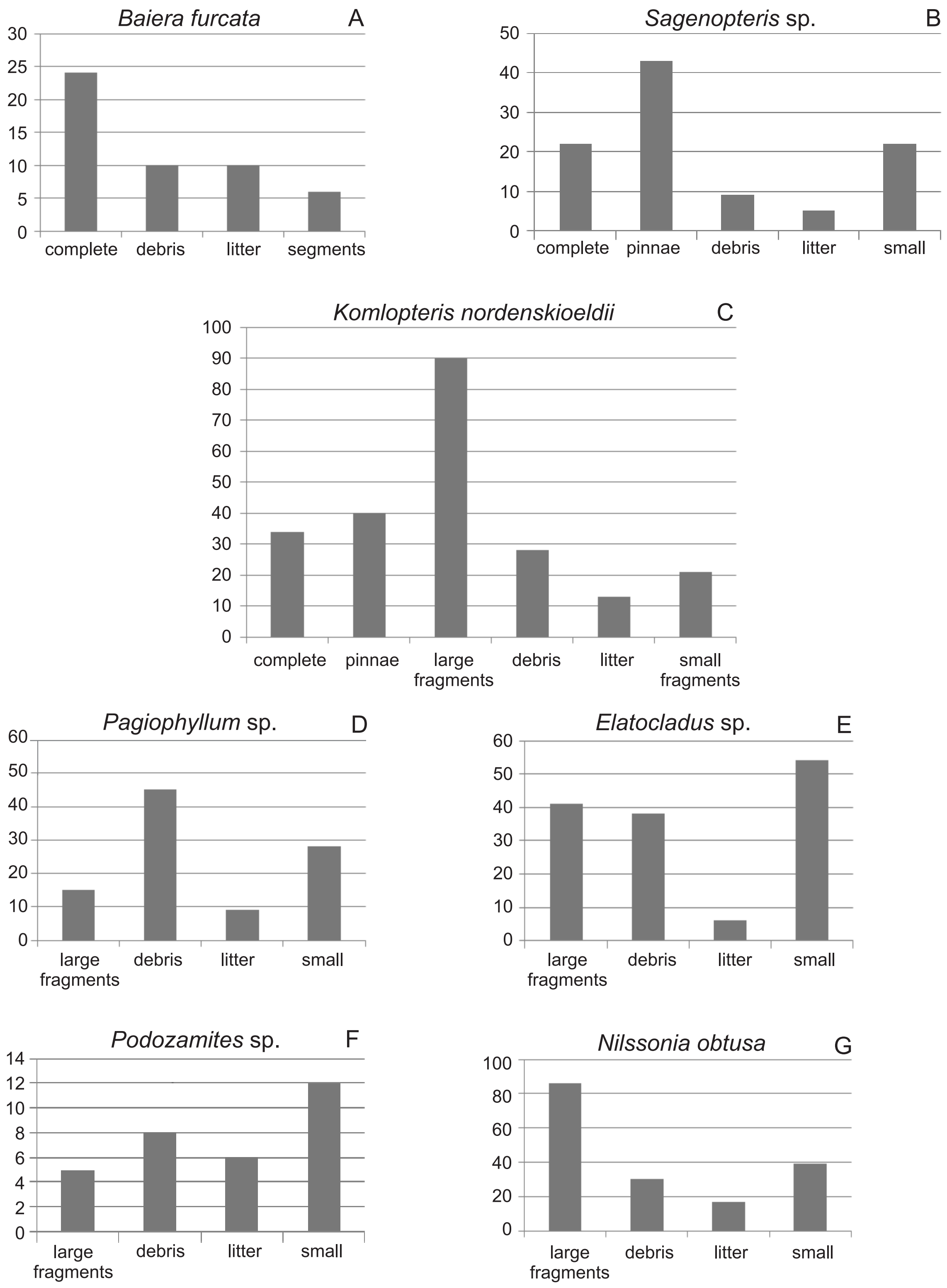


Fig. 5A-N. Degree of leaf fragmentation in selected species

Clustering

The palaeontological samples originated from 7 sites (Fig. 1). In each site the occurrence of species and the type of rock substratum were evaluated, and their presence was coded in the nominal, binary 0–1 scale, forming a synthetic table. Then, the sites were classified according to the species occurrence. Additionally, the relationships between the type of substratum and species were coded in the nominal, binary 0–1 scale and displayed in the form of a data

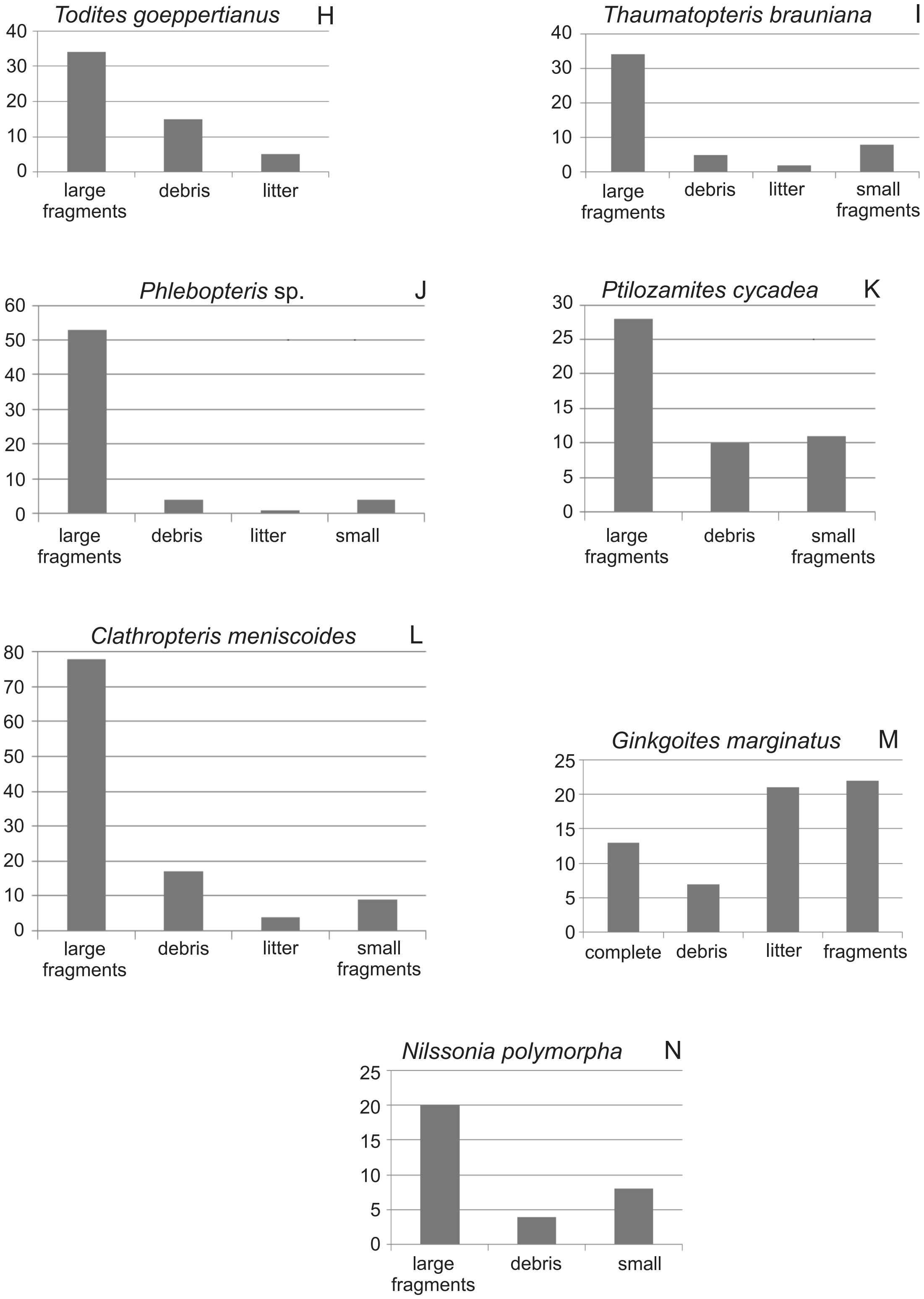


Fig. 5. Continued

matrix. The matrix was then used for the classifying of species and rock substratum in respect of their occurrence in particular sites. A UPGMA algorithm (Sokal & Michener 1958) was used, implemented in the NTSYSpc program (Rohlf 2000–2005).

Ordination

To display the relationships between the samples and species, and to show joint occurrence of species in the samples, a Detrended Correspondence Analysis was used (DCA – Hill

Gauch 1980). This is a heuristic modification of CA design (Hill 1973) to remedy both the edge effect and the arch effect, which distort the original distances among the samples. The edge effect is removed in DCA by non-linear rescaling of the axis. The arch effect, a more serious problem in CA, is removed in DCA by the heuristic method of "detrending-by-segments", which was used in the present analysis. DCA is popular, especially in field ecology; however it may be used in all types of data, given that they are reasonably representative of sections of the major underlying environmental gradients. The main premise is that each species displays a unimodal (Gaussian) distribution in two or more dimensions, defined by the specific species' responses to the hypothetical environmental gradients (Ter Braak & Prentince 1988). In particular, in the context of the present study, it means that groups of species had similar patterns of ecological response to the underlying environmental gradients, and that the patterns have been preserved, or at least not seriously disturbed, in the palaeobotanical samples. The groups of species with the uniform type of response (deduced from their joint occurrence) are considered as having similar ecological requirements, thus forming ecological groups.

The length of gradient for DCA Axis 1 amounted to 10.19 standard deviation, and the percentage of variance accounted for 4.0% and 3.7% of the variance of DCA Axis 1 and Axis 2, respectively. The inspection of the DCA results showed that five species were outliers (see Results). The length of gradient of the reduced data set for DCA Axis 1 amounted to 8.06 standard deviation, and the percentage of variance accounted for 4.6% of the Axis 1, and 4.3% of the Axis 2. The samples that differ by 4 standard deviations are to be expected to have no species in common. Total inertia equaled to 19.494. The distribution of species along the DCA Axis 1 and Axis 2 is displayed in Figure 6.

RESULTS

The DCA analysis was applied for species co-occurrence and separation of plant groups presumably growing together in the same ecological niches. Fig. 6 shows the obtained distribution of species along Axis 1 and Axis 2, as well as groups formed by both the first and second axes.

In the first step, out of the 37 examined species, six species were removed by the used programm as outliers: *Clathropteris meniscoides*, *Todites goeppertianus*, *Todites princeps*, *Podozamites schenkii, Podozamites* sp. and *Neocalamites carcinoides*, thus the final analysis was carried out on 31 species.

The lowest scores on Axis 1 are possessed by *Nilssonia revoluta*, *Cladophlebis denticulata* and *Anomozamites marginatus*, forming a distinct cluster, together with *Sagenopteris* sp., *Marattiopsis hoerensis* and *Nilssonia obtusa* (Fig. 6). The position at the opposite extreme along Axis 1 is occupied by *Equisetites muensteri*. The gradient along Axis 1 divides the plant species into three clusters (see also Table 5).

On Axis 2, the lowest DCA score is possessed by *Thaumatopteris brauniana*, and *Nilssonia polymorpha* shows the highest value. The gradient along the axis also groups species into three clusters, which occupy equal parts of the axis (Fig. 6).

Axes 1 and 2 enable a distinction to be made between five groups of plants, including the monospecific *Ginkgoites marginatus* group (Fig. 6, Tab. 5). The percentage of plant groups in the particular samples is shown in Fig. 7A–D.

INTERPRETATION OF RESULTS AND DISCUSSION

DCA Ecogroups

The DCA ordination provides an opportunity for the study of species co-occurrence within the same samples, and, assuming the autochthonous or parautochthonous character of the flora, it may be interpreted as their joint occurrence in similar ecological conditions. Taxa showing the closest association along the Axes 1 and 2 are grouped into five clusters, i.e. five putative ecological groups. The groups are named from the dominant taxon and show their centre of occurrence along the DCA Axis 1 and 2 (Fig. 6A).

The many factors which may determine the origin of plant assemblages include: palaeogeographic position, altitude above sea level, marine transgressions and regressions, distance from the sea coast (influence of salty

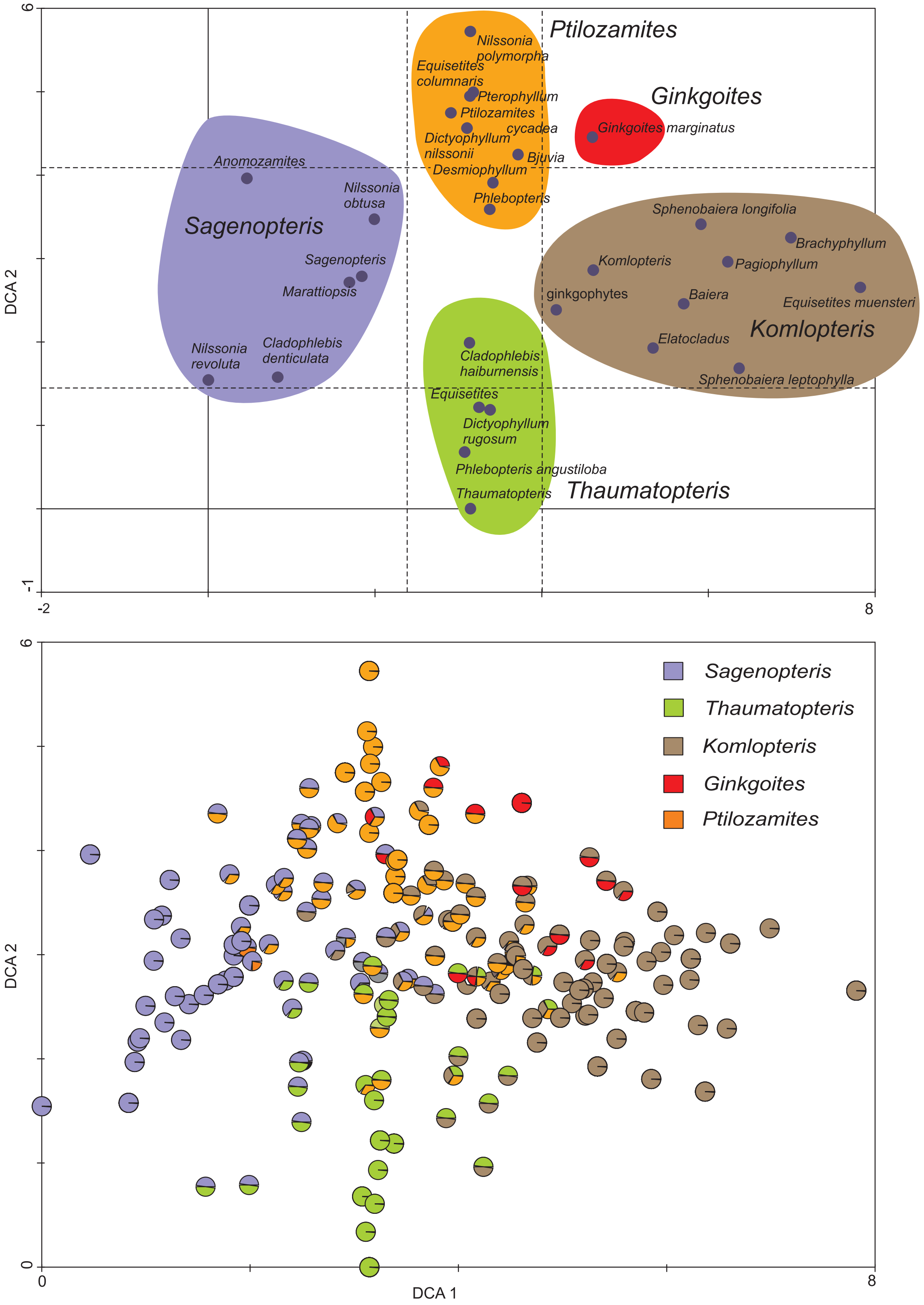


Fig. 6. A. DCA: ecogroups, B – ecogroups with extended niches

water), distance from a fresh-water reservoir, air humidity, type of soil, its moisture and quality, succession and competition.

Since the taxa are in this case from the same area, the first two factors may be omitted and only local environmental changes are considered as a possibility.

Considering the delta environment and changes typical of such a landscape, the most probable factors strongly influencing changes

Table 5. Groups of taxa obtained in DCA analysis according to Axis1, Axis 2 and Axes 1/2 (following the gradient)

	Axis 1	Axis 2	Axes 1/2
1	*Nilssonia revoluta* *Cladophlebis denticulata* *Marattiopsis hoerensis* *Sagenopteris* sp. *Nilssonia obtusa* *Anomozamites marginatus*	*Thaumatopteris brauniana* *Phlebopteris angustiloba* *Dictyophyllum rugosum* *Equisetites* sp.	*Nilssonia revoluta* *Anomozamites marginatus* *Cladophlebis denticulata* *Marattiopsis hoerensis* *Sagenopteris* sp. *Nilssonia obtusa*
2	*Thaumatopteris brauniana* *Phlebopteris angustiloba* *Dictyophyllum rugosum* *Equisetites* sp. *Cladophlebis haiburnensis* *Phlebopteris* sp. *Desmiophyllum* sp. *Bjuvia simplex* *Dictyophyllum nilssonii* *Ptilozamites cycadea* *Pterophyllum subaequale* *Equisetites columnaris* *Nilssonia polymorpha*	*Nilssonia revoluta* *Cladophlebis denticulata* *Sphenobaiera leptophylla* *Elatocladus* sp. *Cladophlebis haiburnensis* ginkgophytes *Baiera furcata* *Marattiopsis hoerensis* *Sagenopteris* sp. *Equisetites muensteri* *Komlopteris nordenskioeldii* *Pagiophyllum* sp. *Brachyphyllum* sp. *Sphenobaiera longifolia*	*Thaumatopteris brauniana* *Phlebopteris angustiloba* *Equisetites* sp. *Dictyophyllum rugosum* *Cladophlebis haiburnensis*
3	unidentified ginkgophytes *Komlopteris nordenskioeldii* *Ginkgoites marginatus* *Elatocladus* sp. *Baiera furcata* *Sphenobaiera longifolia* *Pagiophyllum* sp. *Sphenobaiera leptophylla* *Brachyphyllum* sp. *Equisetites muensteri*	*Nilssonia obtusa* *Phlebopteris* sp. *Desmiophyllum* sp. *Anomozamites marginatus* *Bjuvia simplex* *Ginkgoites marginatus* *Dictyophyllum nilssonii* *Ptilozamites cycadea* *Pterophyllum subaequale* *Equisetites columnaris* *Nilssonia polymorpha*	*Nilssonia polymorpha* *Equisetites columnaris* *Pterophyllum subaequale* *Ptilozamites cycadea* *Dictyophyllum nilssonii* *Bjuvia simplex* *Desmiophyllum* sp. *Phlebopteris* sp.
4			*Ginkgoites marginatus*
5			*Komlopteris nordenskioeldii* *Elatocladus* sp. *Baiera furcata* *Sphenobaiera longifolia* *Pagiophyllum* sp. *Brachyphyllum* sp. *Sphenobaiera leptophylla* *Equisetites muensteri*

in floristic composition are the moisture gradient of (Axis 1) and degree of environmental stability (Axis 2). The degree of disturbance may influence floristic changes detectable in the fossil state in two ways: by selection of taxa that adapt to given conditions and by plant succession stopped at different levels by flood or other catastrophic events, which is manifested in the contents of particular groups and adaptation of their components.

Presuming that in a delta plain a large territory is well watered, the gradient of Axis 1 possibly follows humidity in the present case from the relatively less wet regions to wet, swampy zones. The morphology and cuticular structure of plants change along this axis in correspondence with this supposition.

The appearance of the groups in relation to both axes fits in to a curve of normal distribution with lower extreme values and higher moderate values (Fig. 8A wetness gradient – blue and stability gradient – red). It corresponds well with ecological rules, when the most diverse populations are connected with moderate conditions, while extreme conditions need higher specialization, which restricts the number of taxa. It implies from Fig. 8A that in both cases (Axes 1 and 2) the dry and disturbed conditions characterised by low values restricted the number of taxa to a higher degree than in case of the opposite values, i.e. wet and more stable.

The quantitative contribution of particular groups in the plant cover displays the reverse trend (Fig 8B). The *Komlopteris* group and the *Sagenopteris* group (they show the opposite tendencies on Axis 1) are most rich in specimens. The groups from the medium values of Axis 1 are not so numerous. If the biomass is proportional to the extension of environments, it would mean that in the Mecsek delta territory, floodplains and swamps dominated, as well as more drained territories, while highly disturbed or the most stabile, moderated wet areas were smaller, although more diverse.

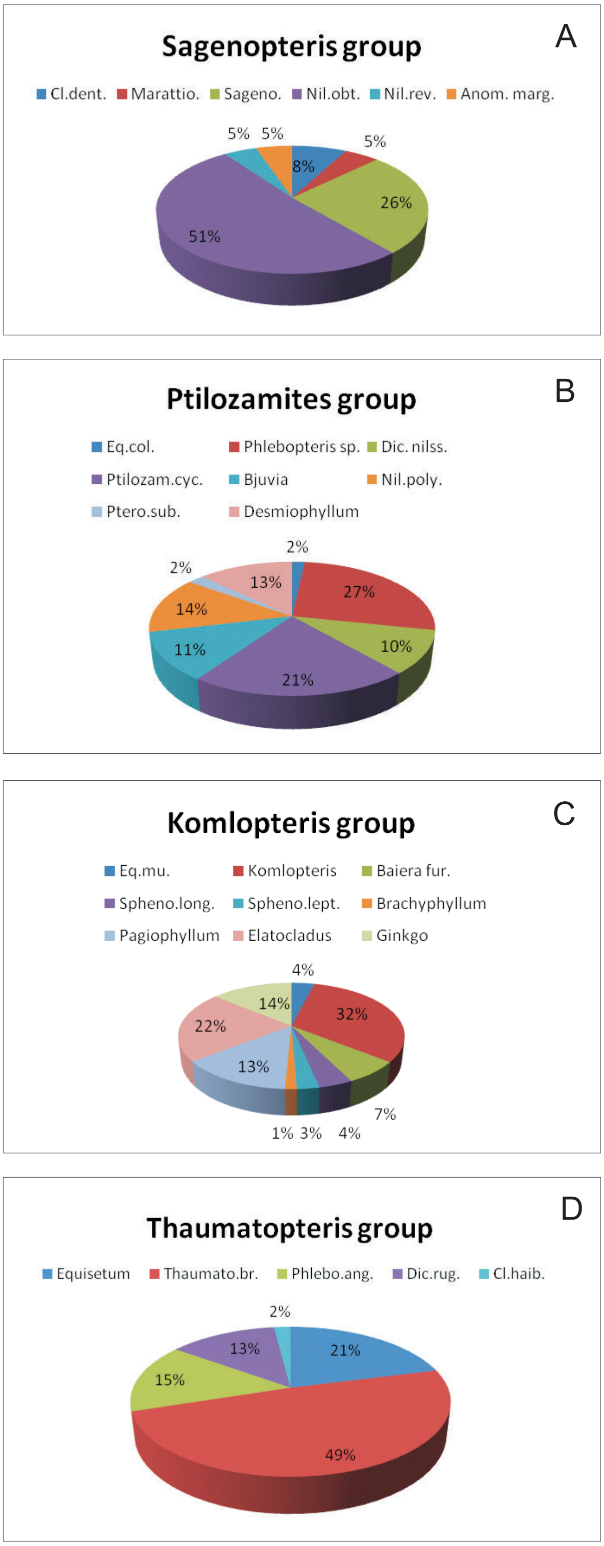


Fig. 7. A-D. – Percentage of taxa in particular ecogroups

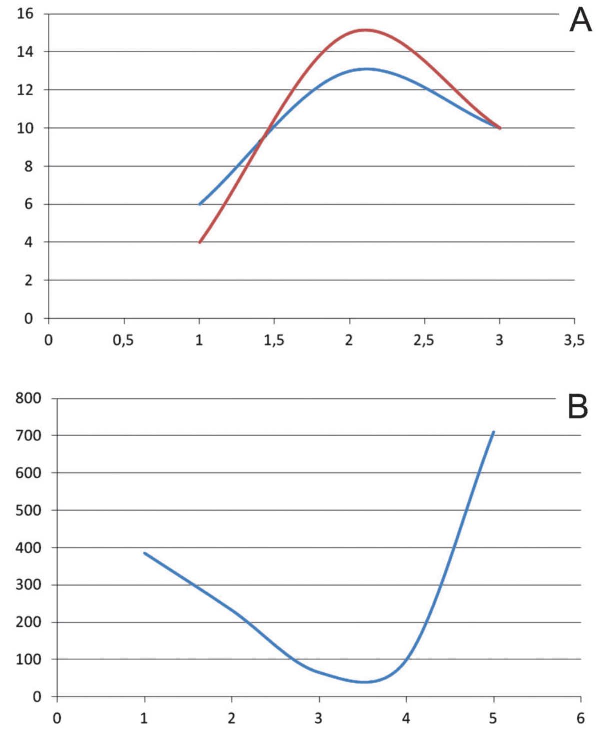


Fig. 8. A. Distribution of taxa amount along Axis 1 (wetness gradient – blue) and 2 (stability gradient – red) according to DCA; B – Distribution of specimens amount along Axis 1

DCA – Extension of Niches

The segregation of taxa according to the extent of their ecological profiles is in compliance with the given environmental circumstances, so they form distinct ecogroups. Axes 1 and 2 form a space in which particular taxa are distributed according to their putative ecological adaptations (Fig. 6B). It is worth noticing that, although all the ecogroups tend to extend and overlap with each other, none of the taxa extended along the entire gradient either that of Axis 1, or that of Axis 2.

Additional DCA analyses for particular species give more detailed information on their predilections and show the scope of their environmental tolerance, i.e. may define their niches (Figs 9–13). It is natural that overlapping niches do not fully follow the groups separated on the grounds of maximum occurrence of taxa and that taxa with wide niches can occur in more than one ecogroup. The widest niches were occupied by 5 species: *Komlopteris nordenskioeldii*, *Elatocladus* sp., *Sagenopteris* sp., *Phlebopteris* sp. and *Dictyophyllum* *nilssonii*, while *Brachyphyllum* sp. and *Equisetites columnare* show the narrowest niches. The niches of *Sphenobaiera leptophylla* and *Nilssonia revoluta* are not very restricted, but quite distinctive and only overlap each with other to a minimal degree.

Taxa reaching the opposite sides of the Axis 1, presumably representing the moisture gradient, belong to completely different types of environment, and *Nilssonia revoluta* and *Brachyphyllum* sp., in particular, are mutually exclusive. *Nilssonia revoluta* occupies an exceptional niche, since it extends to presumably drier and more disturbed surroundings (Fig. 9), while the narrow occurrence of *Brachyphyllum* sp. (Fig. 12) can be explained by its high specialisation. *Equisetites muensteri*, which expands to maximally wet conditions, has a wider adaptation and co-occurs with more taxa (Fig. 12).

Some species with xeromorphic features, like *Brachyphyllum* sp., *Pagiophyllum* sp., *Ptilozamites cycadea* or *Bjuvia simplex*, show their maxima in presumably wet environment, but their niches extend towards dry habitats (Figs 12 and 11 respectively). On the other hand, xeromorphic features occur not only in ancient plants living in strict arid conditions, but also in semi-arid sites, which are seasonally or periodically dry (Batten 1974). In the recent biomes, several plants living in wet conditions, e.g. in high peat bogs, also displayed xeromorphic features due to physiological dryness.

Taxa co-occurrence based on extended niches

Based on the range of niches, all possible co-occurrences of taxa within the Mecsek delta were determined (Table 6).

The amount of possible combinations of taxa is high, but certain tendencies are noticeable. Most strikingly, none of the ferns, cycads and bennettites occurs together with *Brachyphyllum*. *Cladophlebis denticulata* does not co-occur with any ginkgophytes, similarly to *Phlebopteris*, although the latter may occur with *Ginkgoites marginatus*. *Thaumatopteris brauniana* does not co-occur with bennettites, and the majority of ginkgophytes. Also, *Nilssonia revoluta* avoids ginkgophytes; the other cycads co-occur only with *G. marginatus*. Generally, besides *Brachyphyllum*, which has exceptionally few combinations, some ferns, ginkgophytes and cycads do not combine with each other.

Most combinations show both species of *Dictyophyllum*, *Phlebopteris* sp., *Komlopteris nordenskioeldii* and *Elatocladus* sp., and also *Desmiophyllum* sp. (see also Fig. 14).

DESCRIPTION OF RECONSTRUCTED LANDSCAPES

Based on the DCA ecogroups, the following environmental types were distinguished within the delta landscape of the Mecsek locality:

1. Moderately disturbed, relatively dry (non-flooded) inland areas, which correspond to the occurrence of the *Sagenopteris* group.

Dominant element. *Sagenopteris* sp.

This habitat mostly seems to correspond to the "upland" widely applied in palaeoecological reconstructions, here used according to Batten's definition (Baten 1974, p. 446), in that case probably only minimally raised, yet high enough not to be flooded. In this habitat, taxa are highly spread: from dry and disturbed conditions favouring *Nilssonia revoluta* and *Cladophlebis denticulata*, passing towards areas of higher moisture, where *N. obtusa* and *Marattiopsis hoerensis* began to appear, while *Sagenopteris* sp. and *Anomozamites marginatus* were attracted to conditions of heightened stability.

The majority of species listed in this group justifies their position on the Axis 1 as representing the driest conditions in the Mecsek ecosystem. *Nilssonia revoluta* has the narrowest leaves among the *Nilssonia* species with entire margins, and possess bulges on the subsidiary cells; features which were interpreted by Harris (1964) as xeromorphic. Its niche is rather narrow and within the drier interval extends towards the more disturbed condition (Fig. 9). *Cladophlebis denticulata* has relatively narrow and elongated pinnules with dentate margins. Its niche continues towards more dry and disturbed circumstances (Fig. 9). *Anomozamites marginatus*, a bennettite with thick, small and short pinnules and *Nilssonia obtusa* with its moderately thick cuticle and narrow entire leaves also corresponds with the suggested type of environment. Its occurrence expands towards a less disturbed section.

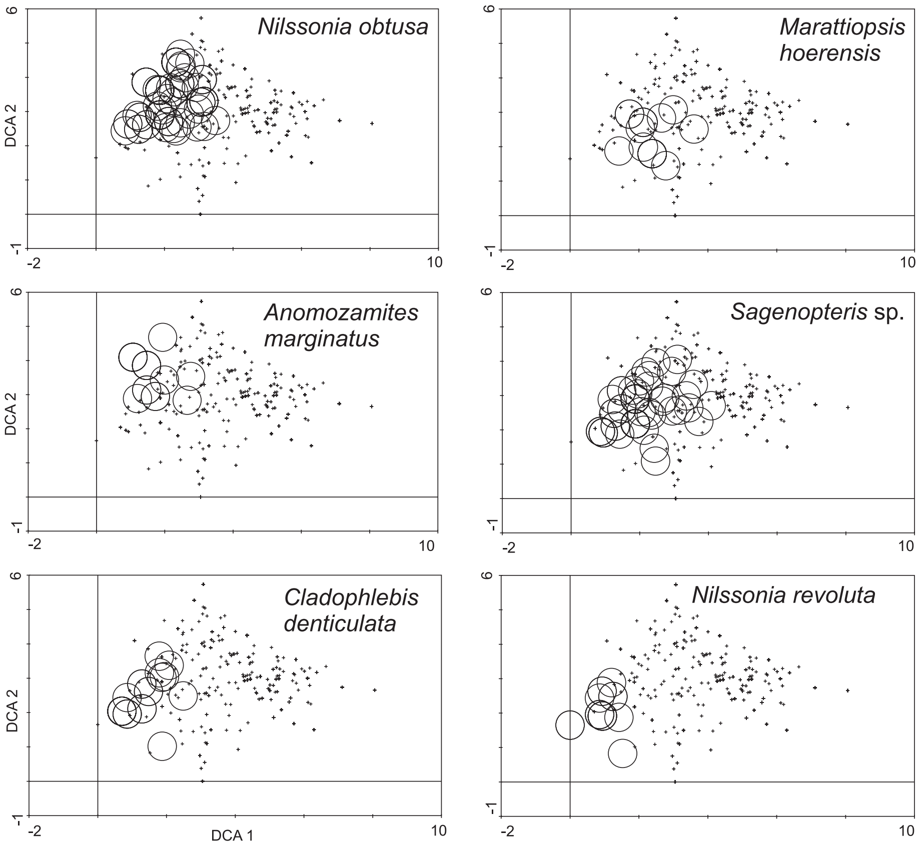


Fig. 9. DCA for species from *Sagenopteris* group

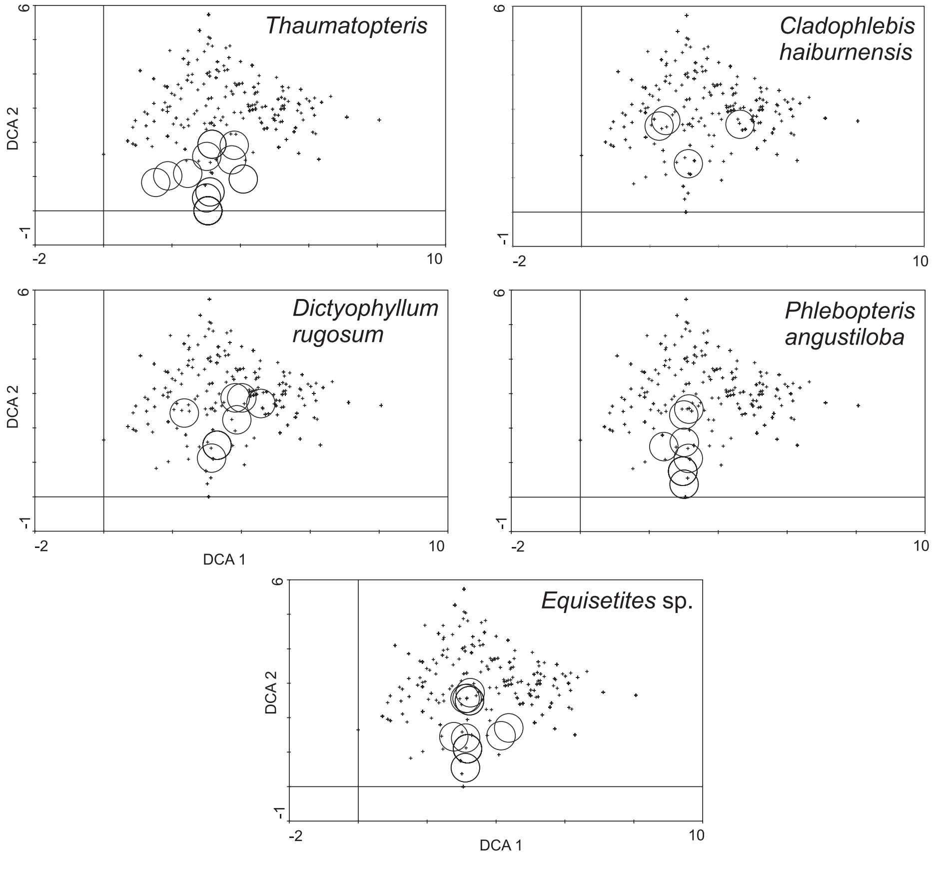


Fig. 10. DCA for species from *Thaumatopteris* group

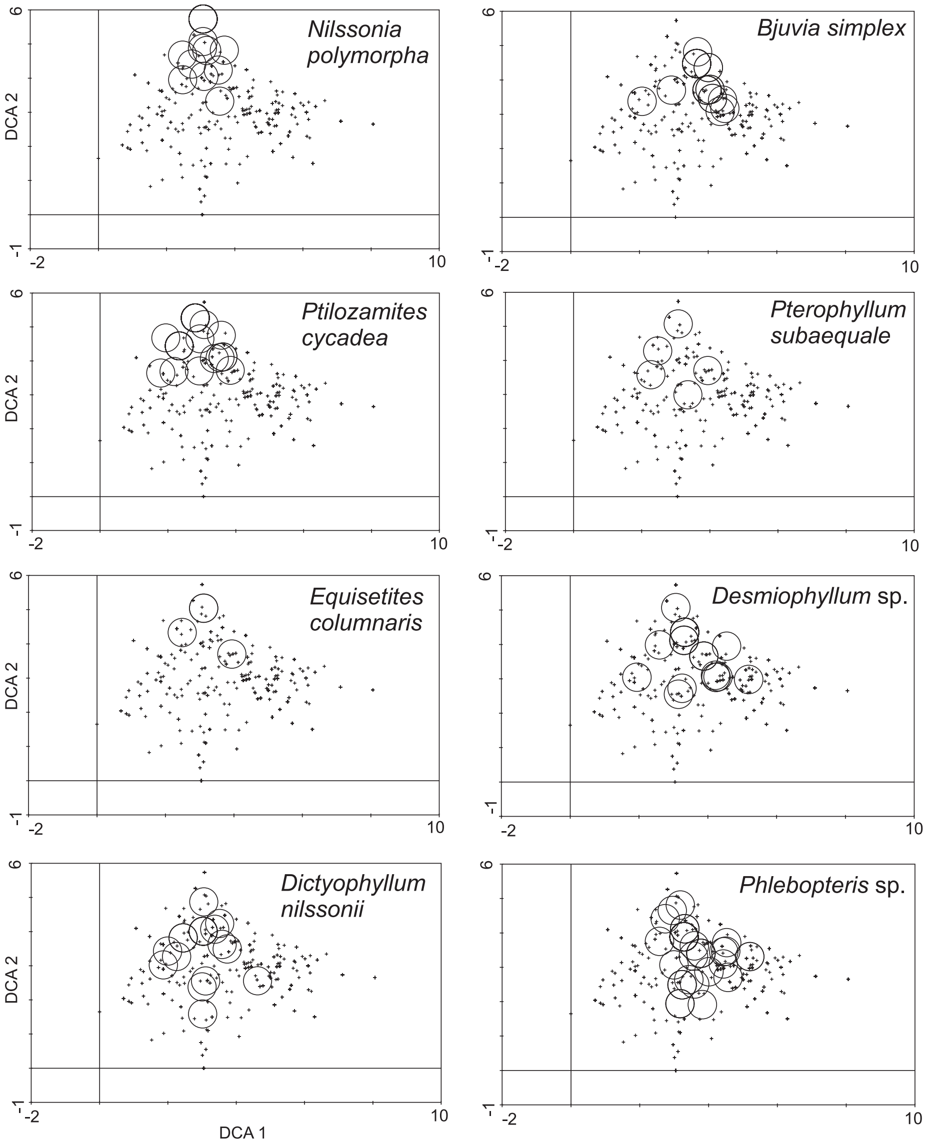


Fig. 11. DCA for species from *Ptilozamites* group

What is surprising is the presence of *Marattiopsis hoerensis* and *Sagenopteris* sp., which are characterized by rather delicate leaves. *Sagenopteris* has a thin cuticle and exposed guard cells; *Marattiopsis* is usually connected with warm, moist circumstances (van Konijnenburg-van Cittert 2002, Wang 2002). Its recent relative *Marattia* grows in the shaded floors of wet tropical forests (Thomas 1985), and also often along river banks (van Konijnenburg-van Cittert pers. com.) which is here confirmed by its niche stretching towards wetter and more disturbed environments. The range of *Sagenopteris* is much expanded, and also occupies territories, which are variably disturbed, reaching moderately wet areas. The structure of both the genera *Marattiopsis* and *Sagenopteris* suggests a preference for shaded places with high air humidity, and not necessarily a high concentration of moisture in the soil. This way they may be imagined as understorey, or a climbing form, in the case of *Sagenopteris*. The suggested shrub or tree appearance of the latter (Harris 1964, Gordenko 2008) would have been more justified if sun leaves had been found. The described trunk of *Sagenopteris* does not exclude it from a climbing life style (e.g. extant genus *Hedera*). This fact would explain such a wide co-occurrence of *Sagenopteris*, always living in the shadow of other plants.

The other taxa, which are possible in this type of environment because of the range of their niches, are: *Ptilozamites cycadea*, *Bjuvia simplex*, *Cladophlebis haiburnensis*, and *Dictyophyllum rugosum*.

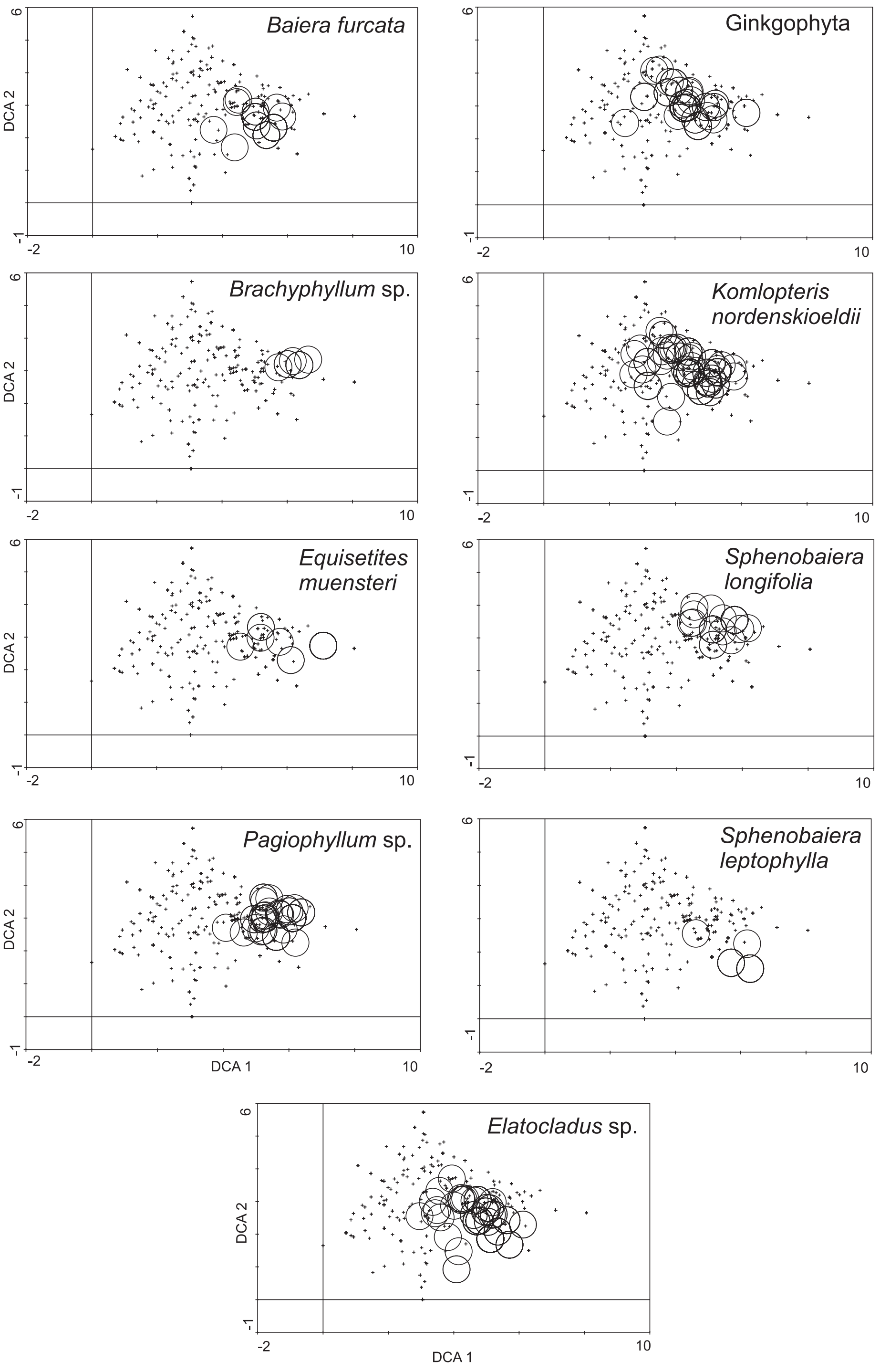


Fig. 12. DCA for species from *Komlopteris* group

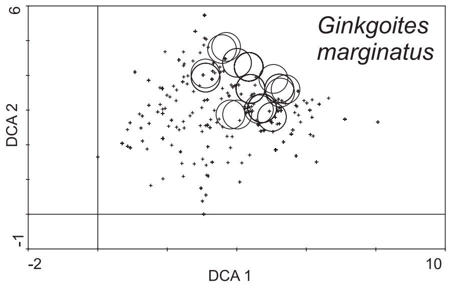


Fig. 13. DCA for *Ginkgoites marginatus*

Table. 6. Taxa co-occurrence based on extended niches. Explanation of colours: dark blue – sphenophytes, light brown – ferns, green – seed ferrns, violet – cycads, blue – bennettites, brown – gikgophytes, grey – conifers.

	Equisetites columnaris	*Equisetites muensteri*	*Marattiopsis hoerensis*	*Cladophlebis haiburnensis*	*Cladophlebis denticulata*	*Phlebopteris angustiloba*	*Phlebopteris* sp.	*Dictyophyllum nilssonii*	*Dictyophyllum rugosum*	*Thaumatopteris brauniana*	*Sagenopteris* sp.	*Komlopteris nordenskioeldii*	*Ptilozamites cycadea*	*Nilssonia polymorpha*	*Nilssonia obtusa*	*Nilssonia revoluta*	*Bjuvia simplex*	*Anomozamites marginatus*	*Pterophyllum subaequale*	*Ginkgoites marginatus*	*Sphenobaiera longifolia*	*Sphenobaiera leptophylla*	*Baiera furcata*	*Desmiophyllum* sp.	*Elatocladus* sp.	*Brachyphyllum* sp.	*Pagiophyllum* sp.
Equisetites columnaris	+	–	+	–	+	–	+	+	–	_	+	+	+	+	+	–	+	+	+	+	+	–	–	+	+	–	–
Equisetites muensteri	–	+	–	+	+	–	+	+	+	–	+	+	–	–	+	–	+	–	–	+	+	+	+	+	+	+	+
Marattiopsis hoerensis	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	+	+	+	–	+
Cladophlebis haiburnensis	–	+	+	+	+	+	+	+	+	+	+	+	–	–	+	+	+	+	+	+	+	+	+	+	+	–	+
Cladophlebis denticulata	–	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	–	–	–	–	+	+	–	–
Phlrbopteris angustiloba	–	–	+	+	+	+	+	+	+	+	+	+	–	–	+	–	–	+	+	+	–	–	–	+	+	–	–
Phlebopteris sp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+
Dictyophyllum nilssonii	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	–	+	+	+	+	–	+
Dictyophyllum rugosum	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+
Thaumatopteris brauniana	–	–	+	+	+	+	+	+	+	+	+	+	–	–	+	+	–	–	–	–	–	–	+	+	+	–	–
Sagenopteris sp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	+	+	+	–	+
Komlopteris nordenskioeldii	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+
Ptilozamites cycadea	+	–	+	–	+	–	+	+	+	–	+	+	+	+	+	–	+	+	+	+	–	–	–	+	+	–	–
Nilssonia polymorpha	+	–	+	–	–	–	+	+	+	–	+	+	+	+	–	+	+	+	+	+	–	–	–	+	+	–	+
Nilssonia obtusa	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	–	–	–	+	+	–	+
Nilssonia revoluta	–	–	+	+	+	–	–	–	+	+	+	–	–	+	+	+	+	+	–	–	–	–	–	+	–	–	–
Bjuvia simplex	+	+	+	+	+	–	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+
Anomozamites marginatus	+	–	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	–	–	–	+	+	–	–
Pterophyllum subaequale	+	–	+	+	+	+	+	+	+	–	+	+	+	+	+	–	+	+	+	+	+	–	+	+	+	–	+
Ginkgoites marginatus	+	+	+	+	–	+	+	+	+	–	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+
Sphenobaiera longifolia	+	+	–	+	–	–	+	–	+	–	–	+	–	–	–	–	+	–	+	+	+	+	+	+	+	+	+
Sphenobaiera leptophylla	–	+	–	+	–	–	+	+	+	–	–	+	–	–	–	–	+	–	–	+	+	+	+	+	+	–	+
Baiera furcata	–	+	+	+	–	–	+	+	+	+	+	+	–	–	–	–	+	–	+	+	+	+	+	+	+	+	+
Desmiophyllum sp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+
Elatocladus sp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+
Brachyphyllum sp.	–	+	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	+	+	–	+	–	+	+	+
Pagiophyllum sp.	–	+	+	+	–	–	+	+	+	–	+	+	–	+	+	–	+	–	+	+	+	+	+	+	+	+	+

Taxa that were not used in the analyses but could be attributed to this habitat are: *Todites goeppertii*, *Todites princeps*, and *Clathropteris meniscoides.* Only 3 specimens of *Todites goeppertianus* (total number 69) were associated with *Nilssonia obtusa*. Therefore, since the niche of *N. obtusa* extends from medium wet to drier habitats, it is probable that *T. goeppertianus* also belong to this group. This is justified by the presence of *Cladophlebis*, which is closely relative to *Todites* (Harris 1961). It is also probable that its niche extended towards more disturbed areas, where they formed monospecific thickets.

No specimens of *Todites princeps* were associated with other plants. The small amount of these in the locality suggests a narrow niche. The morphology, although fine, suggests adaptation to rather dry conditions, according to its relatively thick rachis and rigid appearance (see also Barbacka & Bodor 2008). Schweitzer (1978) discussed the lifestyle of this species as possibly being epiphytic (after Harris 1961) or living on periodically dried clay (after Weber 1968). Its strongly distinct occurrence in the Mecsek locality rather suggests the last solution.

The majority of *Clathropteris meniscoides* did not associate with other taxa, but some samples showed co-occurrence (18% of studied specimens). Single fragments occurred with *Anomozamites marginatus*, *Sagenopteris* sp., *Phlebopteris* sp., *P. angustiloba*, *Elatocladus* sp., *Thaumatopteris brauniana*, *Dictyophyllum rugosum*, and *Komlopteris nordenskioeldii*, but it was mostly associated with *Nilssonia obtusa* (10 specimens). Considering the types of niche characteristic of these species, the niche of *Clathropteris meniscoides* could extend to medium wet and medium disturbed habitats.

Four selected taxa were analysed from a taphonomical point of view: *Sagenopteris* sp. (Fig. 5B), *Clathropteris meniscoides* (Fig. 5L), *Todites goeppertianus* (Fig. 5H), *Nilssonia obtusa* (Fig. 5G). All of them show significant dominance of large fragments; in the case of *Sagenopteris* separated pinnae are most abundant. The amount of debris specimens is not very high, and production of litter was rather low.

Remarks. Generally conifers are often connected with drier conditions (Batten 1974, Kustatscher et al. 2010, Abbink 1998, Abbink et al. 2004, Wang et al. 2005) and also treated as indicators of seasonally dry vegetation (Falcon-Lang et al. 2009). Cheirolepidiaceae are often assigned to drier habitat (including the seasonally dry) as drought resistant, thermophilous plants (e.g. Batten 1974, Nguyen et al. 1999, Abbink 1998, Abbink et al. 2004). Other groups often connected with dry environments are cycads and bennettites (Batten 1974, Abbink et al. 2004).

Caytoniales, which in the Mecsek Mts. are at their maximum extent in rather dry conditions, appeared to have a very wide tolerance. In a deltaic environment, they are usually placed into transitions between the floodplain and backswamp peats, or moist, lush, generally warm and wet habitats (Abbink 1998, Abbink et al. 2004, Hesselbo et al. 2003). However, Thorn (2001) interpreted many Caytoniales as occurring in dry habitat with conifers, arborescent ferns, lycopods and bryophytes.

Ferns and sphenophytes are not considered as typical of dry conditions, but are sometimes mentioned (Batten 1974). For the ferns, this mostly regards Matoniaceae, which have leaves protected by a resistant cuticle (van Konijnenburg-van Cittert & van der Burgh 1996, Abbink et al. 2004, van Konijnenburg-van Cittert 2002). They mentioned species of *Phlebopteris* as being tolerant to semiarid conditions, similarly to Hesselbo et al. (2003), who stressed that the same was true for Osmundaceae.

2. Highly disturbed short-lived, moderately wet territories formed by alluvial deposits (islands, peninsulas, forelands), fully damaged by river flood, occupied by pioneer plants from the group *Thaumatopteris*.

The dominant species. *Thaumatopteris brauniana*.

The *Thaumatopteris* group exclusively consists of Sphenophyta and Pteridophyta. Taxa of this group show very close moisture values, but are spread along the stability gradient of the environment. *Thaumatopteris brauniana*, *Equisetites* sp., *Dictyophyllum rugosum*, and *Cladophlebis haiburnensis* show their maximal appearance in this habitat. Other possible taxa whose niches reach these territories are also mainly pteridophytes: *Phlebopteris angustiloba*, *Cladophlebis denticulata*, *Dictyophyllum nilssonii*, *Phlebopteris* sp., *Marattiopsis hoerensis*, and *Clathropteris meniscoides*.

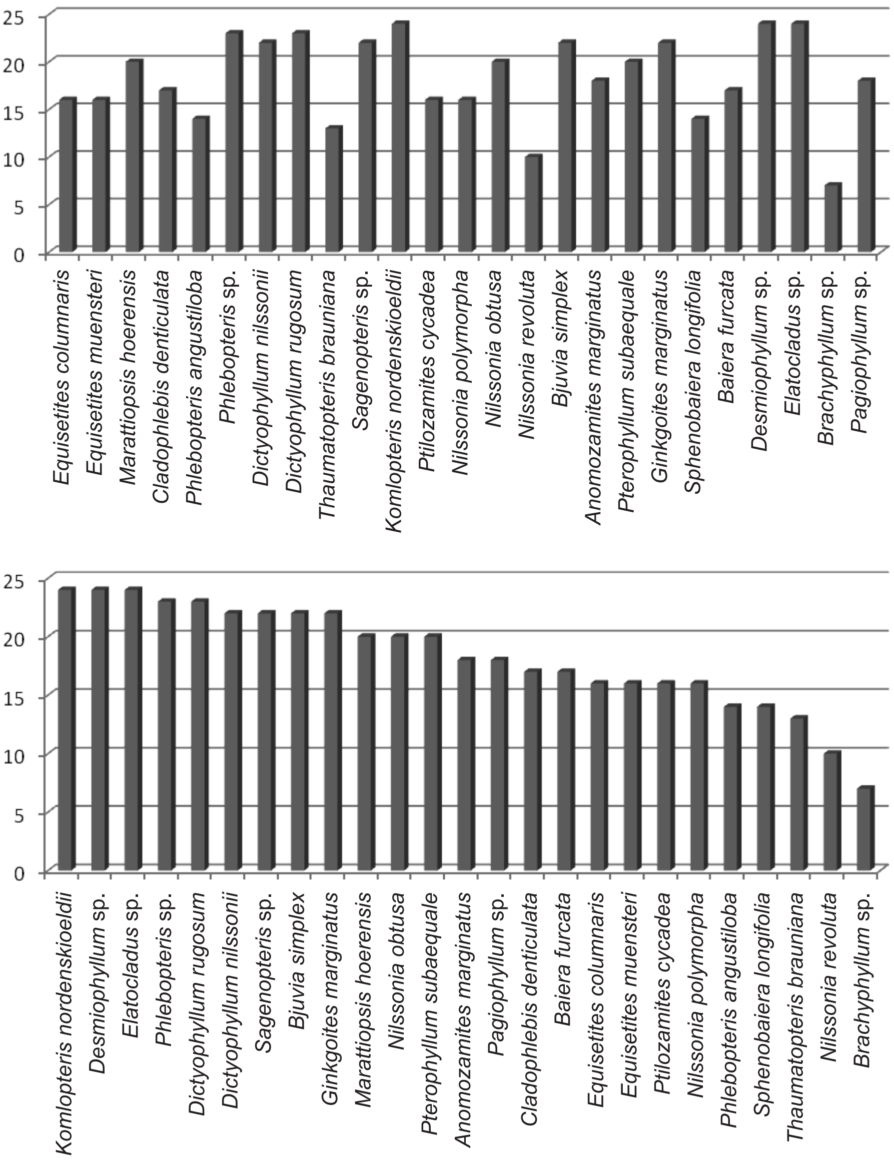


Fig. 14. Degree of co-occurence of particular taxa: A – according to taxonomy, B – in order of range of charge

The composition of this assemblage is typical of disturbed areas, since pteridophytes and sphenophytes, which are here the main elements, tend to occupy new territories as pioneer plants, and often occur in a stage of early succession (Thomas 1985). From the other plant groups, *Komlopteris nordenskioeldii*, *Sagenopteris* sp., *Baiera furcata*, and *Elatocladus* sp. tend to appear in this early colonized stage as well (or as the next succession stage in these areas).

Coniopteris hymenophylloides and *Sphenopteris* sp., which were not used in the analyses, always occur alone. Their morphology, slender rachises and fine pinnules suggest medium wet to wet habitats.

Thaumatopteris brauniana was mainly preserved in large fragments with a minimal tendency for production of debris or litter (Fig. 5 I). Other species of ferns (compare Fig. 5 H, J, L) also show the same type of fragmentation. In this type of habitat, when areas are quickly covered by water and sand, fragmentation of such a type is not remarkable. Observations of the Hungarian records correspond with the Iranian ones that were regarded by Schweitzer (1978) as forming extended thickets, or in association with *Dictyophylum nilssonii* or species from the genus *Sagenopteris*.

Remarks. By analogy with their contemporary species, ferns and sphenophytes may often be regarded as pioneer plants colonizing disturbed habitats. Bomfleur and Kerp

(2010) discussed this predilection with regard to Dipteridaceae. They concluded that „*Clathropteris/Polyphacelus* locally became dominant elements during the early phase of colonization of disturbed sites after catastrophic volcanic events" (Bomfleur & Kerp 2010, p. 151). Thomas (1985) considered ferns as a usual element of conifer dominated open forests, but rarely as a strictly dominant factor. He pointed out Dicksoniaceae and Cyatheaceae together with horsetails as forming monospecific thickets as a stage of succession (see also Retallack 1977). Apart from ferns, Francis et al. (2008) also included liverworts, mosses, cycadophytes and angiosperms in the disturbed flora, and regarded *Taeniopteris* as forming thickets in disturbed clearings.

3. Moderately disturbed swamp occupied by the *Komlopteris* ecogroup.

Dominant element. *Komlopteris nordenskioeldii.*

This ecogroup occupies a habitat continuously passing from moderately wet to swampy, occasionally submerged areas. Here gymnosperms show their maximum occurrence accompanied by *Equisetites muensteri*, which reaches the highest value on Axis 1. The majority of them show leaf structures characteristic of wet conditions. To this group belongs *Komlopteris nordenskioeldii* with exposed stomata (Barbacka 1994b) and a type of hydatodes, as well as *Elatocladus* sp. connected usually with a wet, even swampy habitat, and all species of ginkgophytes from this locality. Their cuticles are either moderately thick (*Ginkgoites* and *Baiera*) or rather thin (*Sphenobaiera*). All forms found in the Mecsek Mts. have papillate cuticles, at least around the stomatal pit (Barbacka 2002). According to Zhou (2009, p. 16), the Mesozoic ginkgophytes are often associated with plants adapted to "different climates from hot and dry to wet and temperate, from coastal plain and lowland to inland riparian/swamp environments". Sun et al. (2008, p. 220) measured the stomatal index and carbon isotope for the Middle Jurassic *Ginkgo* leaves, and concluded that "the fossil *Ginkgo* in a 'green house' world is more efficient in water use than the living *Ginkgo*".

Other plants, whose niches extend to this habitat, do not reach the maximum moisture, but rather extend only to slightly wetter conditions. These are: *Ginkgoites marginatus*, *Pterophyllum subaequale*, *Ptilozamites cycadea*, *Dictyophyllum nilssonii, D. rugosum*, *Cladophlebis haiburnensis*, *Phlebopteris* sp., *Sagenopteris* sp., and *Desmiophyllum* sp. Finally, taxa that probably appeared there as well are the earlier discussed *Coniopteris hymenophylloides*, *Sphenopteris* sp., and *Clathropteris meniscoides,* as well as some taxa which were not used in the analysis: *Ginkgoites minuta*, *Geinitzia* sp., and *Podozamites* sp. *Ginkgoites minuta*, similar to all other ginkgophytes, is placed in the *Komlopteris* group and so is *Geinitzia* sp., which is comparable to *Elatocladus* sp. Both species of *Podozamites* may probably also be included in this group, since they are usually connected with wet conditions.

Members of this assemblage show differences in remains fragmentation (Fig. 5). *Komlopteris nordenskioeldii* and *Baiera furcata* possess the high amount of large fragments or complete leaves usual for the locality, while conifers like *Elatocladus* sp., *Pagiophyllum* sp., and *Podozamites* sp. are much more fragmented: the highest in number are specimens with small fragments, or debris with a relatively low production of litter. This situation would be justified when those conifers also grew along the swampy river banks and a portion of their fragments would be destroyed by river stream. The other taxa possibly preferred the swampy surroundings of stagnant water (lakes, canals, river branches with a slow stream).

Remarks. Usually equisetes and ferns were attributed to swamp (floodplain) or marsh (van Konijnenburg-van Cittert 2002, 2008, van Konijnenburg-van Cittert & van der Burgh 1989, 1996, Kustatscher et al. 2010, Krassilov 1973, Batten 1974, Abbink et al. 2004). Krassilov (1973) revealed *Equisetites* as forming monospecific thickets in marshes, and he also ascribed *Dictyophyllum*, *Todites*, and *Elatides* to this habitat. *Elatides* was also attributed to moist lowland by Abbink et al (2004), and *Geinitzia* and *Brachyphyllum* were attributed to the same by Nguyen et al. (1999). Marattiales, Osmundaceae, Dipteridaceae, Dicksoniaceae and others were interpreted as understorey, either in marshes or along riverbanks (van Konijnenburg-van Cittert 2002, Abbink et al. 2004, and Hesselbo et al. 2003 without

Osmundaceae). In the Mecsek Mts., only two species of *Dictyophyllum*, one species of *Cladophlebis* and *Phlebopteris* sp., which show fine frond structure, partly occupy the wetter territories, but none of them are abundant in the areas with maximum moisture.

Chun (1996) discussed a swamp-lake environment of the Lower Mesozoic in Korea with the dominancy of *Dictyophyllum* and *Clathropteris* species together with *Cladophlebis*, *Pterophyllum*, *Anomozamites*, and *Nilssonia* as well as ginkgophytes. Out of the Hungarian species of bennettites and cycads, only one, *Pterophyllum subaequale* expanded to a wetter canopy. Considering that the composition of this canopy complemented by other taxa extended to this habitat, it corresponds well with the lush, moist vegetation from Sutherland (van Konijnenburg-van Cittert & van der Burgh 1996).

Popa and van Konijnenburg-van Cittert (2006, p. 207) interpreted seed ferns from the genera of *Sagenopteris*, *Pachypteris*, *Ctenozamites* (*Ptilozamites*), and *Komlopteris* as being „swamp margin plants" together with conifers, when cycads together with ferns were considered as growing „in the final phase of peat swamp development". It agrees with earlier Popa' s suggestions (Popa 1997) that seed ferns of *„Thinnfeldia"* group were associated with swamp areas.

All species of Hungarian *Sphenobaiera* were found in swampy habitat, although Retallack (1977) in his reconstruction regarded the genus as xerophytic. In the Kimmeridgian flora from Sutherland, the ginkgophytes, *Brachyphyllum*, *Elatocladus* together with *Nilssonia*, *Pterophyllum*, and *Sphenopteris* are attributed to upland forest (van Konijnenburg-van Cittert & van der Burgh 1996). Similarly to the Hungarian locality, Batten (1974) interpreted conifers as growing along river banks.

According to Abbink et al. (2004) as well as van Konijnenburg-van Cittert (2008), river SEG was also favourable for ferns, especially from the families Osmundaceae, Dicksoniaceae, Schizaceae, Dipteridaceae, Cyatheaceae, and Pteridaceae, a finding which is not excluded in the case of the Mecsek flora, however, it is not confirmed either.

A little unexpectedly, the genera *Pagiophyllum* and *Brachyphyllum* in the Mecsek Mts. are limited to highly watered areas contrary to their xerophytic micro- and macromorphology (Thévenard et al. 2005). However, according to recent opinions, Cheirolepidiaceae are found in very variable environments, from dry to swampy and coastal (Vakhrameev 1970, 1991, Alvin 1982, Hesselbo et al. 2003, Greb et al. 2006, Wang et al. 2005, Popa & van Konijnenburg-van Cittert 2006); and details of their cones confirm adaptation to wet conditions (Barbacka et al. 2007). Since the genus *Brachyphyllum* is not homogeneous and certain species can be of Cheirolepidiaceae or Araucariaceae affiliation (van Konijnenburg-van Cittert & Morgans 1999), it is only possible to indicate that the *Brachyphyllum* from the Mecsek locality shows a very low tolerancy and is strongly restricted to a narrow niche within the swamp, reaching maximum wetness on Axis 1, and probably occasionally in submerged areas.

4. Weakly disturbed, moderately wet canopy – *Ptilozamites* group.

Dominant species. *Ptilozamites cycadea.*

The *Ptilozamites* group is the most diverse compared with representatives of different plant groups, showing here their maximum frequency: horsetails – *Equisetites columnaris*; ferns – *Dictyophyllum nilssonii* and *Phlebopteris* sp.; seed ferns – *Ptilozamites cycadea*; cycads – *Bjuvia simplex* and *Nilssonia polymorpha*; bennettites – *Pterophyllum subaequale*; as well as *Desmiophyllum* sp.(*incertae sedis*, probably Gnetales). Other taxa whose niches extend to this habitat are: *Nilssonia obtusa*, *Komlopteris nordenskioeldii*, *Anomozamites marginatus*, *Sagenopteris* sp., and *Ginkgoites marginatus.*

The composition of this assemblage unites taxa usually connected with both wetter and drier conditions. *Nilssonia polymorpha*, displaying a relatively narrow niche limited to this environment (Fig. 10), was generally regarded as being connected with wet conditions, similarly to *Desmiophyllum*, which has a delicate cuticle. Contrary to this, *Bjuvia simplex* with its rather thick cuticle and stomata protected by a thickened ring shows adaptation to dry surroundings. It may be a sign of periodical dryness, but its tall stature and large leaves at the top also suggest that these leaves might have been exposed to sun, therefore, their protection is justified even in water-rich areas.

The other species with typical xeromorphic features is *Ptilozamites cycadea*, which has coriaceous and rather small pinnules, and stomata protected by a small, very thick cuticular ring on the upper surface that narrows the opening. The guard cells are also thick, although large. Nevertheless, xeromorphic features occur not only in plants living in arid circumstances, but also in seasonally or periodically dry ones (Rees et al. 2000).

Equisetites columnaris from the Hungarian locality is, compared with *E. muensteri*, characterized by smaller, narrower stems, which possibly may be the effect of adaptation to survival in unfavourable circumstances. Taxa not used in the analysis but attributed to this environment are: *Neocalamites hoerensis*, *Cladophlebis roessertii*, *Ctenis* sp., and *Pseudoctenis* sp..

Neocalamites carcinoides shows a low co-occurrence. On single specimens, it is found together with *Equisetites* sp., *Bjuvia simplex*, *Nilssonia obtusa*, *Sagenopteris* sp., *Ginkgoites* sp., *Ptilozamites cycadea*, and on 8 specimens with *Komlopteris nordenskioeldii*. *Cladophlebis roessertii* occurs together with *Nilssonia obtusa* and *Phlebopteris* sp. on two specimens; possibly, it can be placed in the same environment. *Pseudoctenis* sp. and *Ctenis* sp. are very rare and are not associated with any other taxa. Their morphology, which is similar to that of *Bjuwia simplex*, may allow their placement in the same group.

The degree of fragmentation of selected species from this ecogroup (*Nilssonia polymorpha*, *Phlebopteris* sp., *Ptilozamites cycadea*, (Fig. 5 J, K, N) shows a predominance of large fragments in comparison with small fragments or debris. Litter production is minimal, probably because of the nature of the plants.

Remarks. This habitat is the most mixed with regard to the structural adaptation of the composing taxa. According to Wnuk and Pfefferkorn (1984, p. 348), “coexistence of mesomorphic and xeromorphic species in the same community suggests that distributions are being controlled by microenvironmental factors”, which may mean that small, better drained places exist in the canopy occupied by such types of plant. These authors also indicated that xeromorphy is not connected exclusively with dryness, but can also be viewed as a response to light intensity, which in consequence induces succession of plants with such tolerancy.

Ptilozamites cycadea, which here is the dominant element, was rather interpreted as growing in dry conditions, which is clear from its xeromorphic structure. Also, carbon-cycle interpretations of Yorkshire flora placed the genus *Ctenozamites* (*Ptilozamites*) in rather dry conditions (Hesselbo et al. 2003, Kustatscher et al. 2010) even in the coastal zone. This canopy, similarly to the drier one, groups cycads and bennettites as displaying here their maximum frequency. Cycads are often connected with rather wet circumstances (Abbink et al. 2004), especially *Nilssonia* with entire margins (Vakhrameev 1991). However, this study demonstrates that, even within this type of leaves, the preferences of particular species might be different. In Batten (1974), cycads co-occurred with ginkgophytes and conifers, they were located also together with bennettites in open forest, while Kustatscher et al. (2010) located cycads (including *Bjuvia* and *Nilssonia*) in lowland together with pteridosperms (including *Sagenopteris*). All of these compositions are similar to those in the Mecsek locality. However, Thorn (2001) mentioned that in New Zealand (Middle Jurassic) cycads occur far from the other gymnosperms. In this canopy, both species of Mecsek bennettites meet, since their niches overlap at the border of habitats. Their preference corresponds with those described by Gordenko (2008), who interpreted her bennettitalean records as mesophytic.

According to Bomfleur and Kerp (2010), *Clathropteris* may occur in a bennettitalean dominated assemblage forming herbaceous understorey in open vegetation dominated by Bennettitales. In the Hungarian assemblages, *Clathropteris* co-occurred with *Nilssonia obtusa* and *Dictyophyllum rugosum*, which means that its niche extends rather in the direction of more disturbed territories, while the bennettitalean/cycad assemblage tends toward stability.

Thorn (2001) placed arborescent and herbaceous ferns as well as cycads into a damp area, pointing that cycads grew far from the other gymnosperms (Coniferales and Caytoniales).

The *Neocalamites* assigned here forms mainly monospecific thickets, which is uderstandable because of its size and biology. Probably its growth was similar to *Calamites*, whose expansive and thick rhizomes excluded all other plants from the habitat (Thomas 1985).

5. Weakly disturbed wetland – *Ginkgoites* group.

This type of environment is predominated by *Ginkgoites marginatus*, which is at its maximum expanse here. It is in the same moisture range as the highly wet, swampy habitat of the *Komlopteris* group, but with a tendency toward more stable circumstances. Other species occurring in these surroundings are: *Komlopteris nordenskioeldii*, *Sphenobaiera longifolia*, *Elatocladus* sp., *Ptilozamites cycadea*, *Pterophyllum subaequale*, *Desmiophyllum* sp., *Phlebopteris* sp., and *Equisetites columnaris*. The fragmentation of *Ginkgoites marginatus* (Fig. 5M) differs from that of *Baiera furcata* (Fig. 5A) in having more fragmented leaves and the highest production of litter out of all species from the locality. In this aspect, *Sphenobaiera longifolia* shows a transition between both species. This very high litter production can be explained by relatively stable (the niche of *Ginkgoites marginatus* extends towards even more stable, Fig. 13), and highly wet circumstances; thus, fallen leaves (ginkgophytes were deciduous) had good conditions for fossilization in this state.

Remarks. Compositionally, this environment shows a transition between moderately disturbed swamp and less disturbed, moderately wet habitats, where apart from the dominant *Ginkgoites marginatus* some elements of both canopies are present. The monospecific dominancy of *Ginkgoites* may be explained by analogy with *Ginkgo biloba*, which shows moderate allelopathy. Nam (Nam et al. 1997) revealed that its leaves produce substances that, after falling, dissolve in soil and inhibit the development of seeds of certain other trees.

The canopy occupied by *Ginkgoites marginatus* well corresponds with the statement that during the Mesozoic Ginkgoales preferred “stable and ecologically saturated” places Zhou (2009, p. 15), while Abbink et al. (2004) also ascribed ginkgophytes to wetland. Francis et al. (2008) interpreted stable wetland as being covered by araucarian conifers, ferns and cycads, while Hesselbo et al. (2003) stated that in the Yorkshire Jurassic more ginkgophytes were associated with wet than dry conditions, although they occurred in both types of habitat. Popa & van Konijnenburg-van Cittert (2006) supposed Ginkgoales (including *Sphenobaiera longifolia*) as upland representatives.

THE COASTAL ZONE

The possible species appearing in this environment are *Pachypteris banatica* and possibly *Brachyphyllum* sp., while *Pachypteris banatica*, occurred alone (three specimens only). Its semi xeromorphic features (Barbacka 1994c) and the fact, that another species from this genus (*P. papillosa*) was regarded as a halophytic plant, imply that this species might be placed in the coastal zone. The genus *Brachyphyllum*, particularly *B. crucis* of which a few specimens are known from the Mecsek locality,was also presumed to be tolerant of salty habitats (Harris 1979, Abbink 1998, Abbink et al. 2004, van Konijnenburg-van Cittert & Morgans 1999).

Remarks. Sometimes equisetes are attributed to a coastal/tidally influenced habitat (Batten 1974, Gee et al. 2003). Usually Cheirolepidiaceae are known as being tolerant to salty soil and interpreted as a type of mangrove (Batten 1974, Nguyen et al. 1999). Kustatscher et al. (2010) interpreted *Ptilozamites sandbergeri* as a potential halophytic plant, placing it into the coastal zone together with lycopods. *Pachypteris* is generally known as a genus with some halophytic species (Harris 1964, van Konijnenburg-van Cittert & van der Burgh 1996, van Konijnenburg-van Cittert 2008, Abbink et al. 2004).

GENERAL REMARKS

The Mecsek locality represents typical lowland vegetation with a diverse, but not species-rich, flora which fits in with the general rules of wetland ecology presented by Wing and DiMichele (1995). The proposed habitats and taxa connected with them were dynamic to a certain degree. Fluctuation in water levels was the factor, which mostly influenced changes and the succession of vegetation. Since plant associations within groups were based exclusively on taxa co-occurrence which was rather stable, these changes were of minor significance.

Generally, in the Mecsek delta the circumstances of medium to less wetness appeared to be optimal for ferns, for which all species are found in these categories. The environmental preferences of ferns are known to be shady, warm and humid (van Konijnenburg-van Cittert 2002, Wang 2002), but unexpectedly, here they avoid very wet or swampy surroundings.

All cycads prefer less disturbed places, and all ginkgophytes together with conifers are grouped in richly irrigated places. Seed ferns show the widest tolerance.

Plant distribution in the presented model reveals differences in environmental preferences between species within genera. In most cases, different species of the same genus show maximum growth in different niches excluding species of *Sphenobaiera*, which are at their maximum extent in the same niche. The niches of some species intersect, so they may occur together, like *Phlebopteris*, *Dictyophyllum*, *Cladophlebis*, and two of the three species of *Nilssonia*, (*N. obtusa–N. revoluta*, and *N. polymorpha- N. revoluta*), as well as some species whose niches are completely separate, like those belonging to *Equisetites*, as well as *Nilssonia polymorpha* with N. *obtusa*.

DELTA ENVIRONMENT

For better understanding of ecosystems, a study of the extant Danube delta can reveal the location of particular plant groups in a hypothetical biome. A complex study of this delta has been carried out during the last decade (Gâştescu et al. 1998, Szilassi 2004, Hanganu et al. 2002). Within the Danube delta, the following ecosystems were recognised:

– coastal lagoons

– standing brackish and salt waters

– channels and canals with active or free water circulation

– standing fresh water: lakes with active or reduced change of water table

– wetlands: flooded reed beds, floating reed beds, riparian formations, frequently flooded river levees

– forests (dunes, floodplains)

– shrubs and herbaceous vegetation (calcareous cliffs, predeltaic fields, low marine levees)

– open places with little or no vegetation (dunes, beaches)

If an attempt is made to situate the Jurassic ecogroups on a delta model using existing ecosystems similar to those of Danube delta, the habitat of the *Sagenopteris* group is most similar to those of the marine levees – these are slightly raised territories perpendicular to the main branches of the river. Recently, in the Danube delta these levees were covered by oak forests. The ecological conditions of the territory are diverse and strongly depend on fluctuation in water levels.

The *Ptilozamites* group would possibly correspond with the ecosystem of calcareous cliff in the Danube delta. Specific morphohydrographic conditions provided an environment for diverse flora adapted to semi-arid conditions and high insolation.

The most extended, swampy area with the *Komlopteris* group is comparable with wetland, probably encompassing lakeside terrain, or on a riparian formation on the river levees along the channels or in depressions. These are territories that, dependent on water level, may be periodically submerged. The group could occasionally reach the slopes of the marine levees, too.

The *Thaumatopteris* group could be placed on territories, which are mostly disturbed, at the riverbanks, on easily damageable alluvial deposits or newly formed islands, possibly also forming floating islands (Dr. M. Dorothei pers. com.), extending also to river levees or swamp. The percentages of particular groups in the plant cover (Fig. 15) and thus putative proportions among environments within the hypothetic delta suggest that swamps occupied the largest territories, followed by marine levees and drier territories, then cliffs and semi-arid areas, the smallest territory being occupied by highly disturbed zones and floating islands. Habitat containing *Ginkgoites marginatus* can be treated as transition between swamp and semi-arid areas.

Deltas have a mosaic character and environments can change even within small areas, and also within short time intervals (seasonal changes). Such changes were also indicated by

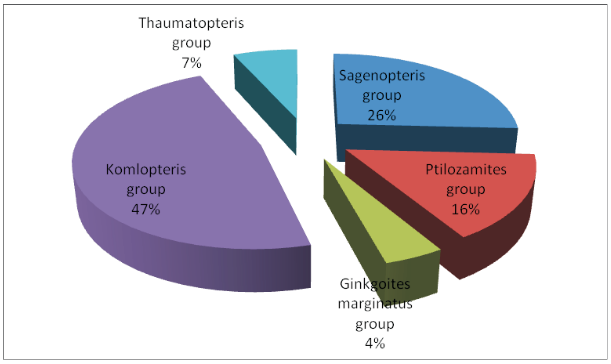


Fig. 15. The percentages of particular groups in the plant cover

pollen analysis (see Götz et al. 2011). Alteration from fern-dominated to conifer-dominated assemblages was also observed by Batten (1974) and Wang et al. (2005). Fluctuations in water level (at the rivers, channels and lakes) and changes in salinity (influence of sea movements) may cause plant taxa to alternate in short cycles (too short to be visible in the fossil state). In this case, the general content of eco-groups would be plus minus constant, but within them there would certainly not be any cases in which all taxa occurred together in the same time.

RELATIONS BETWEEN TAXA, TYPE OF ROCK OR SITE IN THE LOCALITY

All leaf taxa and distinctive rock types containing plant fragments were used in the analysis of the associations between taxa and rock types (in previous analyses not all taxa were considered). It seems that the obtained relationships do not follow the order of the ecogroups, which means that connections between type of rock and taxa are insignificant. Although, macroscopically, ten types of rock were distinguished, microscopic examination proved that a lot of them have similar structures which enable them to unite within the same facies, thus rock types were simplified to 4 categories (Table 7). Similarly to the previous analysis, taxa do not seem to be in close connection with a given type of facies.

Three lithofacies can be distinguished in the rock unit in which most plant remains were found. Sandstones could represent environments containing higher energy depositional conditions, like channels; siltstones could represent environments of low, episodically higher depositional energy, like alluvial plain or delta plain; and fine lamellated siltstones could originate in more distal environments, like lakes and swamps. The presence of calcite cementation perpendicular to lamination provides evidence for carbonated pedogenic levels whose presence might indicate a semi-dry or dry climate, at least in the lower part of the sequence.

The occurrence of calcite molusc shells indicates a lack of acidification (at least temporal) of the water in the basin, which should be expected in a humid climate. On the other hand, the presence of coal seams and rich floral remains points to a humid climate. This paradox can be explained by local hydrological conditions, i.e. permanently high humidity and a high water table only in restricted depressions with dense vegetation and peat accumulation, while drier, seasonal climate dominated in the surrounding land. Therefore, it can be suggested that the occurrence of coal deposits in this setting is not connected with an overall humid climate, but either with humid periods or differentiated topography characterized by locally wetter depressions (Pieńkowski, pers. com.). Mineralogical studies generally confirm associations between sandstones and channels (the presence of Ostracoda), between siltstones and periodically dried floodplain, and between laminated siltstones and swamps (Bodor pers. com.).

Associations between rocks and sites group two open mines Vasas and Pécsebánya and two shafts – Zobák and Béta and separate them from the dumps (Fig. 16). More interesting are associations between taxa and substrate. It is noticeable from Table 7 that plant groups do not really follow a certain rock type. There are two taxa with completely opposite trends: *Brachyphyllum* sp. which has a limited niche in one group appeared in all types of rocks, while *Cladophlebis haiburnensis* occurs only in one type of rock, but belongs to three assemblages. It may be interpreted that for *Brachyphyllum* sp., habitat wetness and given ecogroup were the main factors that influenced its distribution, and not the type of environment: floodplain, swamp, or channel. Contrary to this, *Cladophlebis haiburnensis* seems to favour certain types of environment (here lakes or swamps), but might belong to more ecogroups tolerating this type of habitat. Data from Tables 7 and 8 suggest that local conditions varied within small areas and were mixed to a high level, while most of the plants show a wide tolerance.

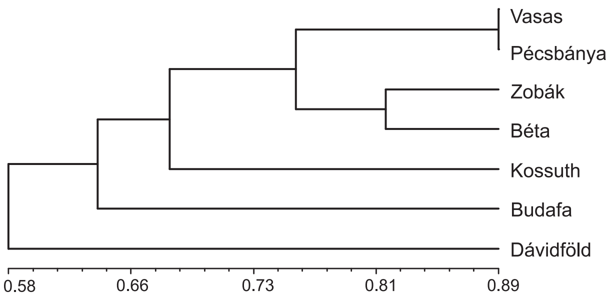


Fig. 16. Relationships between rocks and sites, UPGMA analysis

Table 7. Association between substrate and taxa in relation to ecogroups and facies. 1 – *Sagenopteris* group, 2 – *Thaumatopteris* group, 3 – *Ptilozamites* group, 4 – *Ginkgoides* group, 5 – *Komlopteris* group

Species	Grey silt	Fol silt	Fine lam. silt.	Sandst.	Groups
	river or delta floodplain	lakes or swamps		channels	
Anomozamites marginatus	X	X			1, 3
Baiera furcata	X	X	X		2, 5
Bjuvia simplex	X	X	X		1, 3
Brachyphyllum sp.	X	X	X	X	5
Cladophlebis denticulata	X	X	X		1, 2
Cladophlebis haiburnensis		X			1, 2, 5
Clathropteris meniscoides	X	X		X	2, 5
Dictyophyllum nilssonii	X	X			2, 3, 5
Dictyophyllum rugosum	X	X			1, 2, 5
Elatocladus sp.	X	X	X		2, 4, 5
Equisetites columnaris	X				3, 4
Equisetites muensteri	X	X		X	5
Ginkgoides minuta	X				5
Ginkgoites marginatus	X	X	X		3, 4
Komlopteris nordenskioeldii	X	X	X		2, 3, 4, 5
Marattiopsis hoerensis	X	X	X		1, 2
Neocalamites carcinoides	X	X			3
Nilssonia obtusa	X	X	X		1, 3
Nilssonia polymorpha	X	X	X		3
Nilssonia revoluta	X	X	X		1
Pagiophyllum sp.	X	X	X	X	5
Phlebopteris angustiloba	X	X		X	2
Phlebopteris sp.	X	X		X	2, 3, 4, 5
Podozamites sp.	X			X	5
Pterophyllum subaequale	X	X	X		3, 4, 5
Ptilozamites cycadea	X	X	X		1, 3, 4, 5
Sagenopteris sp.	X	X	X		1, 2, 3, 5
Sphenobaiera leptophylla		X	X		5
Sphenobaiera longifolia	X	X			4, 5
Thaumatopteris brauniana	X	X		X	2
Todites goeppertianus	X	X	X	X	1
Todites princeps	X	X			1

Figure 17 illustrates the association between taxa and sites. On the basis of this analysis, the most similar sites appeared to be Vasas (an open mine) and Budafa (a dump), which proves that unproductive rocks from Vasas were mostly transported to Budafa (so in further analyses they are united into one site). A similar situation pertains with the Zobák shaft, Kossuth shaft and Dávidföld (a dump – but this dump is connected with more shafts, some of which are unknown, so is omitted from further discussion). Based on the cladogram, similarities divide the sites into two groups: Pécsbánya–Béta shaft–Vasas+Budafa and Kossuth shaft–Zobák shaft. These groups generally correspond to the geographical distinction between the region of Komló and region of Pécs. Turning back to Figure 4, it

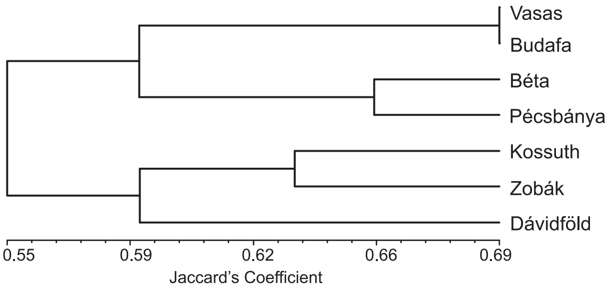


Fig. 17. Relationships between taxa and sites, UPGMA analysis

can be observed that passing from Pécsbánya towards Komló, the delta facies comes to an end at the Béta shaft, so in this region floodplain dominated, with less river facies than in the region of Pécs. The macrofloral composition of both zones noticeably follows this distinction in proportion to particular components: the Komló region is generally richer in plants, and its main disproportions regard increased amounts of *Komlopteris nordenskioeldii, Ptilozamites cycadea*, *Bjuvia simplex*, ginkgophytes, and *Elatocladus* sp., thus dominant elements of the *Komlopteris* and *Ptilozamites* ecogroups, but slightly fewer ferns, *Sagenopteris*, and the genus *Nilssonia* (*Sagenopteris* and *Thaumatopteris* ecogroups). This implies that the region of Komló could have been wetter and less disturbed, while the region of Pécs was could have been more disturbed and drier (Fig. 18 F, G).

The distribution of the main floristic components in particular sites is shown in Figure 18A–F. Two neighbouring sites, nearest to the opposite sides of the border between the regions represent quite different compositions. In the Béta shaft, ferns predominate (Fig. 18D), while in Kossuth, it is the *Komlopteris* ecogroup (Fig. 18A), which is dominant. The Zobák shaft lies between the Kossuth shaft and Szászvár in a NW direction. Here again, river and delta facies appear, but evidently floodplain dominates. As far as plant composition is concerned, this resulted in a relatively low percentage of all elements with a predominance of ferns, *Ptilozamites cycadea* and species from the genus *Nilssonia*. Also *Ginkgoites marginatus* occurs here in higher numbers (ecogroup *G. marginatus*, low disturbance and moderate wetness). The proportion of other taxa ranges between 2–7% (Fig. 18B).

Pécsbánya is most exposed to the South, where the delta facies dominates alternately with the floodplain. Here the Cheirolepidiaceae and *Desmiophyllum* are absent and ginkgophytes are rare. *Komlopteris* is at less than 5 %, but the ferns, *Nilssonia* and *Elatocladus*, dominate. It seems that the *Thaumatopteris* ecogroup is dominant (disturbed and moderately wet habitat), and elements occur from wet and drier habitats that tolerate disturbance (Fig. 18C). Cheirolepidiaceae (*Pagiophyllum*) are most abundant at Vasas and the Zobák shaft, where alluvial facies are most developed (Fig. 18E,B respectively). It can be observed that richness in floral elements depends on facies changes. Pécsbánya (Fig. 18C) and Béta (Fig. 18D) are considerably poorer and there, the influence of the deltaic facies is higher.

COMPARISON OF MECSEK PLANT ASSEMBLAGE OBTAINED USING TWO METHODS: THE SEGS MODEL AND DCA CO-OCCURRENCE MODEL

The reconstruction of the Mecsek palaeoenvironment started with palynological investigations, first of all made by Bóna (1963, 1969). He distinguished three zones according to palynomorph occurrence: a deep water zone which was characterised by allochthonous pollen and spores transported by wind from land; shallow swamp and swamp forest with allochthonous gymnosperm pollen and autochthonous horsetail spores; and inshore areas with mainly conifer pollen (Lachkar et al. 1984).

New investigations based on microfloral data were provided by Ruckwied et al. (2008). The authors dealt mainly with the Triassic–Jurassic boundary and from this point of view distinguished environmental types characteristic of the Upper Triassic as upland and river which turn into warmer lowland and drier lowland at the lowermost Hettangian.

The authors also pointed out difficulties in reconstruction based on microremains alone, which often appear in problems of association between palynomorphs and mother plants, as well as in the unknown tolerance of plants to stress or disturbance. The next attempt to reconstruct the palaeoecology in the Mecsek locality was based on micro and macroremains (Götz et al. 2011). The authors discussed changes in the palynomorph assemblages reflecting a long term trend from river dominated to swamp dominated elements, as well as small-scale cyclic changes of deltaic–swamp–river dominated elements. This way, temporal changes were detected, in which habitat types proposed by Abbink (1998), Abbink et al. (2001, 2004) were represented by different frequency of palynomorphs through the Rhaetian and Hettangian (Götz et al. 2011, fig. 8).

According to Abbink's environmental types (Abbink 1998, Abbink et al. 2001, 2004) and the corresponding SEGs (Sporomorph Ecogroups) he proposed, a model of the Mecsek vegetation was discussed. According to figure 8 from Götz et al. (2011), the participation of sporomorphs

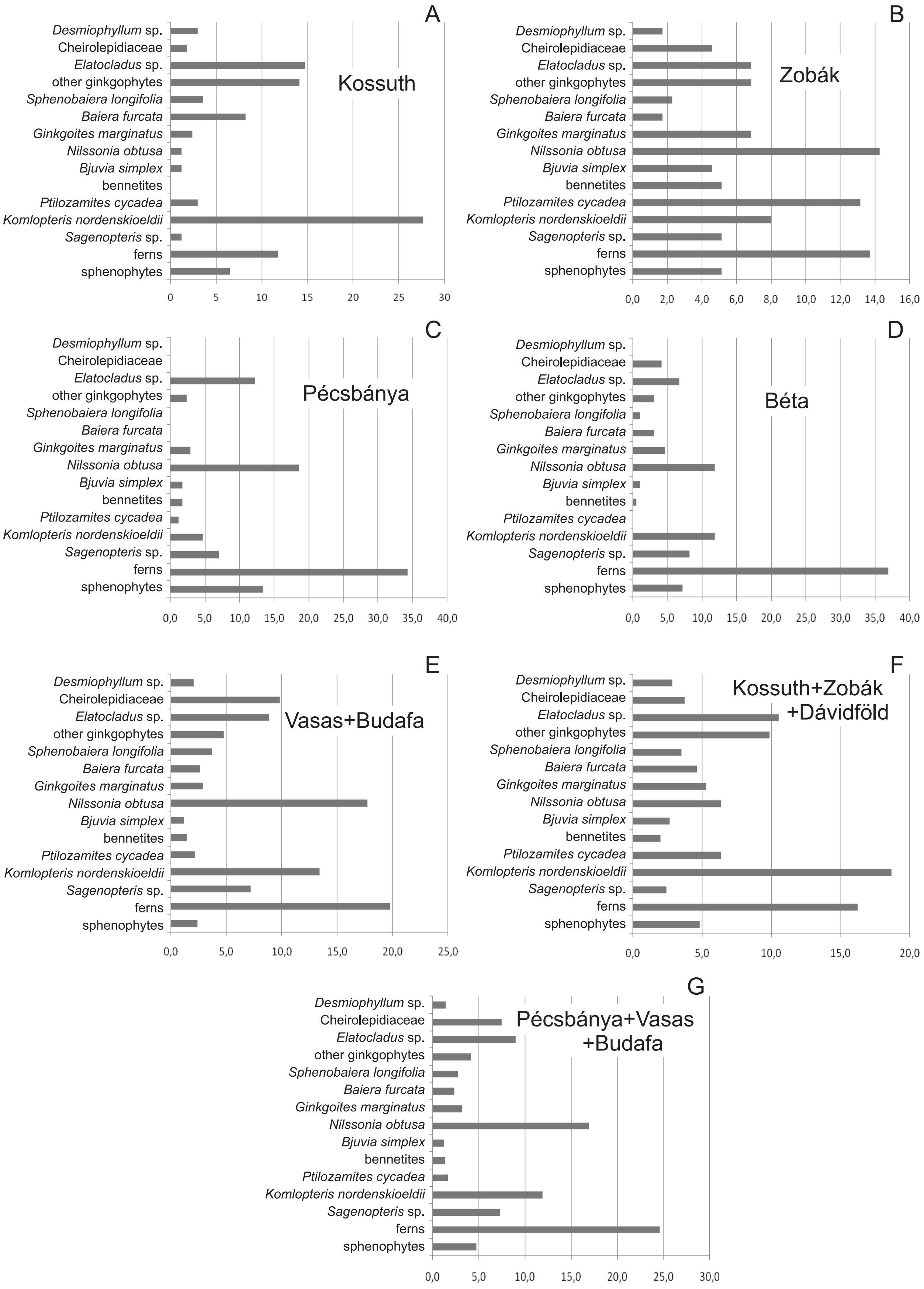


Fig 18. A-F. Percentage of taxa in particular sites

characteristic of upland is very low during the Hettangian. Drier lowland shows medium and fluctuated contribution values, the warmer lowland and wetter lowland show maximum values, and the elements of river deposits show the most variable values. The microfloral assemblages and their environmental connections were discussed in relation to sporomorph – mother plant combinations,with a macroflora adaptability approach.

Table 8 contains a comparison of both models. The DCA co-occurrence model includes all taxa according to their niches in their widest meaning, complemented by taxa which were not considered in the analysis. The names of habitats used by Götz et al. (2011), after Abbink (1998), Abbink et al. (2001, 2004), with small modifications, are changed according to local conditions which better correspond with the suggested reconstruction and in the table are supplemented by two additional habitats. The environmental types do not correspond with each other in each category, but were collated based on their definitions. Both models in general outline correspond with each other. The most similar is the composition of the swamp ("wetter lowland"), although the present model does not contain the cycads and *Pachypteris* (which in this case were placed in the coastal habitat) suggested by the SEG model. The preferences of cycads and ginkgophytes are different. In seasonally dried floodplain ("drier lowland") in the present model the Cheirolepidiaceae are completely absent and the participation of Dicksoniaceae is doubtful. The most different is the "river", which in both models does not contain any common taxa. The "highland" (drier inland or levees) is also different in having only two common elements.

GENERAL DISCUSSION

In the last decades, palaeoecological reconstructions have become very popular. They encompass very different types of investigation, based on plants and animal assemblages in a locality (Lerner et al. 2009), evidence of fossil micro- and megaflora (Thorn 2001, Bercovici et al. 2009), analyses of palaeosols (Sheldon & Tabor 2009), analyses of peats (DiMichele & Phillips 1994), sedimentology (Shao et al. 2003), complex sedimentology, palaeozoological and palaeobotanical data (DiMichele & Beall 1990, DiMichele et al. 2008), sedimentology and macroflora (Falcon-Lang et al. 2009), coal-ball investigations (Galtier 1997), stomatal index calculation (for references see page 134, about SI, this paper) and carbon isotope and stomatal CO_2 densities (Hesselbo et al. 2003).

Investigations consider biotic changes over long periods (DiMichele et al. 2008, Greb et al. 2006), or focus on a given period or locality. Many reconstructions have been made for the Palaeozoic, mainly Carboniferous or Permian wetlands (Di Michele & Phillips 1994, DiMichele et al. 2006, DiMichele & Gastaldo 2008, Libertin et al. 2009, Bercovici et al. 2009), or coal swamps (Phillips & Peppers 1984, Phillips et al. 1985, Thomas & Cleal 1993), providing good records for such investigations.

Well-documented and detailed reviews of wetlands and their role as ecosystem over a time period were given by Greb et al. (2006) and of their taphonomy by Gastaldo et al. (1995).

Special methods were applied for sporomorph analyses based on familiar ordinary plant adaptations and comparisons with extant relatives (Abbink 1998, Abbink et al. (2001, 2004).

The Jurassic (or closely related period from Late Triassic to pre-angiosperm Cretaceous) ecosystems have also been worked up using different methods (Batten 1974, van Konijnenburg-van Cittert & van der Burgh 1996, Abbink 1998, Nguyen et al. 1999, Thorn 2001, Shao et al. 2003, Hesselbo et al. 2003, Abbink et al. 2004, McElwain et al. 2007, Sun et al. 2008, Jansson et al. 2008, Francis et al. 2008, Gordenko 2008, Kustatscher et al. 2010).

The general rule in those studies was to mainly use a generic or higher systematic level for plant taxonomy and in this way certain interpretations were generalized. Taxonomy of fossils is often problematic and analyses on a specific level may be regarded as running a risk of producing false results, particularly in the mathematic models (Rees et al. 2000, 2002). Palynological studies cannot also be used for specific analyses, because sporomorphs are not specialized to such a degree.

It ensues that floristical compositions of different landscapes are more or less universal.

The present analysis, which in most cases was based on species, showed that this method can provide interesting results, showing that

Table 8. Comparison of assemblages obtained by using two methods of paleoecological reconstruction (SEGs and DCA co-occurrence model). Taxa in systematic order. Names written in bold – taxa showing maximum frequency in the present model. Underlined – taxa not attributed to given habitat by SEGs. Interrupted underline – taxa which niches extend to the given habitat, or not used in analysis but attributed as possible elements

Abbink's model	Analysis of sporomorph/macroflora (Götz et al. 2011)	Present model – taxa coocurrence	Present paper
wetter lowland	Sphenophyta Osmundaceae (*Todites*, *Cladophlebis*) *Pachypteris* (Corystospermales) (*Komlopteris*, *Ptilozamites*) Cycadales Ginkgoales Dicksoniaceae (*Sphenopteris*, *Coniopteris*) Bennettitales Dipteridaceae (*Clathropteris*, *Thaumatopteris*, *Dictyophyllum*) Coniferales (*Elatocladus*, *Geinitzia*)	***Komlopteris nordenskioeldii*** ***Baiera furcata*** ***Sphenobaiera longifolia*** ***Sphenobaiera leptophylla*** ***Equisetites muensteri*** ***Elatocladus sp.*** ***Pagiophyllum sp.*** ***Brachyphyllum* sp.** *Ginkgoites marginatus* *Pterophyllum subaequale* *Ptilozamites cycadea* *Dictyophyllum nilssonii* *Dictyophyllum rugosum* *Cladophlebis haiburnensis*, *Phlebopteris* sp. *Sagenopteris* sp. *Desmiophyllum* sp. *Coniopteris hymenophylloides* *Sphenopteris* sp. *Ginkgoites minuta* *Genitzia* sp. *Clathropteris meniscoides* *Podozamites* sp.	swamp (swampy floodplain)
river	pteridosperms (*Komlopteris*, *Ptilozamites*) *Sphenopteris* Dipteridaceae (*Clathropteris*, *Thaumatopteris*) Caytoniales (*Sagenopteris*)	*Elatocladus* sp. *Pagiophyllum* sp. *Podozamites* sp.	swamps along the river banks
warmer lowland	Osmundaceae (*Todites*, *Cladophlebis*) *Pachypteris* (Corystospermales) *Komlopteris*, *Ptilozamites*) Sphenophyta Coniferales (*Elatocladus*) Dicksoniaceae (*Sphenopteris*, *Coniopteris*) Cycadales Ginkgoales Dipteridaceae (*Clathropteris*, *Thaumatopteris*, *Dictyophyllum*) Bennettitales	***Thaumatopteris brauniana*** ***Equisetites* sp.** ***Dictyophyllum rugosum*** ***Cladophlebis haiburnensis*** ***Phlebopteris angustiloba*** *Baiera furcata* *Elatocladus* *Cladophlebis denticulata* *Dictyophyllum nilssonii* *Komlopteris nordenskioeldii Marattiopsis hoerensis* *Sagenopteris* sp. *Phlebopteris* sp. *Clathropteris meniscoides* *Coniopteris hymenophylloides?* *Sphenopteris* sp.?	disturbed areas (small islands, floating islands, river banks)
drier lowland	Cycadales Cheirolepidiaceae bennettitales pteridosperms (*Komlopteris*, *Ptilozamites*) Dicksoniaceae (*Sphenopteris*, *Coniopteris*)	***Nilssonia polymorpha*** ***Pterophyllum subaequale*** ***Ptilozamites cycadea*** ***Bjuvia simplex*** ***Dictyophyllum nilssonii*** ***Equisetites columnaris*** ***Desmiophyllum* sp.** ***Phlebopteris* sp.** *Nilssonia obtusa* *Komlopteris nordenskioeldii* *Anomozamites marginatus* *Sagenopteris* sp. *Ginkgoites marginatus* *Neocalamites hoerensis* *Cladophlebis roessertii* *Ctenis* sp. *Pseudoctenis* sp.	weakly disturbed moderately wet (cliffs, seasonally semi-arid habitats)

Table 8. Continued

Abbink's model	Analysis of sporomorph/macroflora (Götz et al. 2011)	Present model – taxa coocurrence	Present paper
highland	*Caytoniales*(*Sagenopteris*) Ginkgoales Cheirolepidiaceae Coniferales (*Geinitzia*) pteridosperms (*Komlopteris*, *Ptilozamites*)	***Sagenopteris sp.*** ***Nilssonia revoluta*** ***Anomozamites marginatus*** ***Cladophlebis denticulata*** ***Marattiopsis hoerensis*** ***Nilssonia obtusa*** *Ptilozamites cycadea Bjuvia simplex* *Cladohlebis haiburnensis* *Dictyophyllum rugosum* *Todites goeppertian* *Todites princeps* *Clathropteris meniscoides*	drier areas (marine levees)
		Ginkgoites marginatus *Komlopteris nordenskioeldii*, *Sphenobaiera longifolia*, *Elatocladus* sp., *Ptilozamites cycadea*, *Pterophyllum subaequale*, *Desmiophyllum* sp., *Phlebopteris* sp., *Equisetites columnaris*	weakly disturbed wetland
		Pachypteris banatica? *Brachyphyllum* sp.?	coastal

different species of the same genus often tend to choose different life conditions.

Numerous environmental reconstructions were based on the sporomorph ecotype in Abbink's model, or in the case of macroflora, on structural adaptations of plants and comparison with their extant relatives. Since most remains were preserved in wetland circumstances (Greb et al. 2006), and these remains provided most information thanks to their state of preservation (grossmorphology and cuticle), the majority of reconstructions regard this ecosystem and consequently, types of environments in different localities are comparable. The classic model of wetland, or delta plain, contains territories as proposed by Abbink (1998): upland, lowland, river, pioneer, coastal and tidally-influenced areas, which are usually slightly modified, depending on local surroundings.

Abbink (1998, Abbink et al. 2001, 2004) in creating his model, studied macrofloral assemblages and their possible attribution to a given type of canopy. Since then, Abbink's model has become popular not only in palynology, but also in macroflora research.

The common feature for these reconstructions was the study of a macroflora at a generic level, due to lack of sufficient information on the ecological requirements of different species within one genus, as well as to taxonomical uncertainties. This was especially important in the use of multivariate analyses (Rees et al. 2002). On the other hand, the preferences of genera are easier to interprete and generalize.

The standard reconstructions of plant assemblages rarely consider the wide tolerance of plants, instead placing certain taxa in quite narrow environmental categories. The multivariate analyses, though used in palaeobotany for more than 30 years (Spicer & Hill 1979), have so far been employed for more general databases. Jasper et al. (2010) applied a DCA method which appeared to be suitable for palaeoecological reconstructions. The authors differentiated plant associations (miospores) depending on the environment of the Duckmanian wetland.

The CA multivariate analysis of the Permian floras/climates over the world was applied by Rees et al. (2000, 2002) as a method of providing the best available proxy for the original vegetation. The authors documented global geographic patterns of Permian climate parameters using fossil floras and climate-sensitive sediments based on co-occurrences and distribution patterns of fossil leaves at a generic level. This way, an arrangement of fossil genera from 644 localities in the Northern Hemisphere was obtained. The authors used a mathematical method for grouping plants of the same parameters and tracing their association with sedimentological and palaeoclimatological patterns over the world. The present investigation tried to group plants in a similar way, based on their co-occurrence, but in a much narrower context, within one locality area.

When making a mathematic model for palaeoecological reconstructions, some factors that influence the state of a flora, but cannot be considered in the analysis, should be taken into account.

Time. The palaeoenvironment developed and changed according to the cycles mentioned above over a long time. Development of a single stratum in the Mecsek Coal Formation was estimated as taking ca 7000 years. In the region of Pécs, the development time for the entire coal measure was estimated as 4.5 million years (Nagy 1969). In spite of such a long period and accidental gathering, the flora seems to be quite compact (species assemblages may persist for a million years – DiMichele 1994), which has also been proved by palynological records. Its low variability suggests that during this time its elements have not changed to a high degree. It can be assumed that coexistence of given species was nearly constant since it was caused by environmental conditions and not by temporal factors. However, time as a factor cannot be entirely overlooked.

The casual character of records. In the open mines, the remains were collected at different points of the entire sequence, but not continuously from consecutive strata. In the Mecsek Coal Formation, the beds with plant remains were distributed sparsely as irregular lenses and not as continuous sequences that were caused partly by a process of biostratinomy, and partly by tectonic activity. A portion of the material was collected from the dump heaps. Although the collecting was accidental in character, co-occurrence of given taxa shows the same tendencies and does not vary much.

Circumstances of fossilization. Most taxa are of autochthonous or parautochthonous character, according to Gastaldo's definition (Gastaldo et al. 1995). This is revealed by the good state of the remains, unbroken large fragments, often almost complete compound leaves, branching shoots and delicate pinnules etc. However, there are also slabs with broken and crowded fragments, which is unavoidable during a long time period, and may have been caused by the character of the delta and natural powerful events like storms, hurricanes, and so on. Contrary to this, it is worth noticing that detritus or litter in most cases is monospecific, which suggests that its deposition in each case is rather restricted to small basins. Generally, large swampy territories and numerous lakes provided good conditions for the fossilization of plants growing together or close to each other.

The analyses employed in the presented investigations provided very interesting results. They were mainly used to demonstrate how it is possible to apply statistic methods to the interpretation of relationships between fossil taxa and environmental changes from a given locality. The other question was how the results could help in reconstructing the palaeoecology and what type of information can be detected for understanding mechanisms functioning in plant communities. Based on plant co-occurrence, we obtained signs of regularity in the grouping of taxa into assemblages, which may be interpreted as a response to local conditions. Group of plants segregated by this method are clearly interpretable and fit in with our knowledge about the ecology of the delta.

CONCLUSIONS

1. A DCA method appeared appropriate for the reconstruction of a palaeoenvironment based on the co-occurrence of taxa.

2. Such investigations may be used not only at a generic (or higher) level, but also at a specific level, which can help to detect the varied tolerance of different species belonging to the same genus.

3. Using a DCA method, it was possible to separate five plant associations whose composition depended on environmental circumstances like soil moisture and stability/disturbance of their living areas. The same type of analysis made for particular species shows their wider extension within the whole community, which made it possible to define the range of their ecological tolerance as well as determine all possible combinations of taxa within a given type of environment.

4. Association between rock matrix and taxa, as well as between taxa and site within the locality proved that in the Mecsek locality, the biodiversity of the areas displaying

a dominance of delta facies was poorer than those in which alluvial facies predominated.

5. Comparison with the environmental reconstruction of the same locality obtained on the basis of sporomorphs and macroflora remains shows that most similar results regarded the plant compositions of swamps and warmer lowland (here interpreted as moderately wet, highly disturbed areas). The contents of other environmental categories significantly diverge in both methods.

ACKNOWLEDGEMENTS

I would like to express my thanks to Ass. Prof. Józef Mitka for his assistance and help in statistic analyses of my material. I am very grateful Bodor Emese, who helped to collect the database and made thin sections for mineralogical analysis of rocks and Dr. György Szakmány for help in this analysis. I also thank very much Prof. Johanna van Konijnenburg-van Cittert, Prof. Mihai Popa and Prof. Leon Stuchlik, for critically reading the manuscript and their suggestions, Prof. Géza Császár and Prof. Krzysztof Birkenmajer for remarks on the geological part, and prof. Grzegorz Pieńkowski for his help in facies interpretation. I am very grateful prof. Botond Kiss and Dr. Mihai Dorotfei for materials about Danube delta and suggestions concerning plant ecology of delta, as well as M.S. Agnieszka Sojka for help in drawing and editing figures.

REFERENCES

ABBINK O. 1998. Palynological investigations in the Jurassic of the North Sea region. LPP Contributions Series 8. LPP Foundation, Utrecht.

ABBINK O., TARGARONA J., BRINKHUIS H. & VISSCHER H. 2001. Late Jurassic to earliest Cretaceous palaeoclimatic evolution of the southern North Sea. Global and Planetary Change, 30: 231–256.

ABBINK O., van KONIJNENBURG-van CITTERT J.H.A. & VISSCHER H. 2004. A sporomorph ecogroup model of the Northwest European Jurassic – Lower Cretaceous: concepts and framework. Geol. Mijnbouw, 83: 17–38.

ALVIN K.L. 1982. Cheirolepidiaceae: biology, structure and paleoecology. Rev. Palaeobot. Palynol., 37: 71–98.

BARBACKA M. 1992. The Liassic seed ferns of the Mecsek Mountains (S. Hungary): 257–263. In: J. Kovar-Eder (ed.), Palaeovegetational Development in Europe and Regions Relevant to Its Palaeofloristic Evolution. Proc. Pan. Eur. Palaeobot. Conf. Vienna, 19–23 Sept. 1991.

BARBACKA M. 1994a. *Pachypteris banatica* from the Mecsek Mountains Liassic. Acta Palaeobot., 34(1): 5–19.

BARBACKA M. 1994b. *Komlopteris* Barbacka nov. gen., a segregate from *Pachypteris* Brongniart. Rev. Palaeobot. Palynol., 83: 339–349.

BARBACKA M. 1994c. Reconstructions of stomata of *Komlopteris* and *Pachypteris* and their adaptation to climate. Annls. Hst.-Nat. Mus. Natural. Hung., 86: 5–11.

BARBACKA M. 2001. The cycads of Hungarian Liassic. Rev. Paléobiol., 20(2): 525–541.

BARBACKA M. 2002. The Liassic Ginkgoales from the Mecsek Mountains, Hungary. Rev. Paléobiol., 21(2): 697–715.

BARBACKA M. 2009. Sphenophyta from the Early Jurassic of the Mecsek Mts., Hungary. Acta Palaeobot., 49(2): 221–231.

BARBACKA M. & BODOR E. 2008. Systematic and palaeoenvironmental investigations of fossil ferns *Cladophlebis* and *Todites* from the Liassic of Hungary. Acta Palaeobot., 48(2): 133–149.

BARBACKA M. & van KONIJNENBURG-van CITERT J.H.A. 1998. Sun and shade leaves in two Jurassic species of Pteridosperms. Rev. Palaeobot. Palynol., 103: 209–221.

BARBACKA M., ZIAJA J. & WCISŁO-LURANIEC E. 2010. Taxonomy and palaeoecology of the Early Jurassic macroflora from Odrowąż, central Poland. Acta Geol. Pol., 60(3): 373–392.

BARBACKA M., ZIAJA J., WCISŁO-LURANIEC E. & REYMANÓWNA M. 2007. *Hirmeriella muensteri* (Schenk) Jung from Odrowąż (Poland), with female and male cones, and in situ *Classopolis* pollen grains. Acta Palaeobot., 47(2): 339–357.

BATTEN D.J. 1974. Wealden palaeoecology from the distribution of plant fossils. Proc. Geol. Ass., 85(4): 433–458.

BEERLING D.J. 1999. Stomatal density and index: theory and application: 251–256. In: Jones T.P. & Rowe N.P. (eds), Fossil plants and spores: modern techniques. The Geological Society, London.

BEERLING D.J. & ROYER D.L. 2002a. Fossil plants as indicators of the Phanerozoic global carbon cycle: Ann. Rev. Earth Planet. Sci., 30: 527–556.

BEERLING D.J. & ROYER D.L. 2002b. Reading a CO_2 signal from fossil stomata. New Phytologist, 153: 387–397.

BEERLING D.J., McELWAIN J.C. & OSBORNE C.P. 1998. Stomatal response of the "living fossil" *Ginkgo biloba* L. to changes in atmospheric CO_2 concentrations. Jour. Exper. Botany, 49(326): 1603–1607.

BERCOVICI A., DIEZ J.B., BROUTIN J., BOURQUIN S., LINOL B.,VILLANUEVA-AMADOZ E.U., LÓPEZ-GÓMEZ J. & DURAND M. 2009. A palaeoenvironmental analysis of Permian sediments in Minorca (Balearic Islands, Spain) with new palynological and megafloral data. Rev.Palaeobot. Palynol., 158(2009): 14–28.

BERNER R.A. & KOTHAVALA Z. 2001. Geocarb III: A revised model of atmospheric CO_2 over Phanerozoic time. Am. Journ. Sci., 301: 182–204.

BOMFLEUR B. & KERP H. 2010. The first record of the dipterid fern leaf *Clathropteris* Brongniart from Antarctica and its relation to *Polyphacelus stormensis* Yao, Taylor et Taylor nov. emend. Rev. Palaeobot. Palynol., 160(3–4): 143–153.

BÓNA J. 1963. A mecseki liász feketekőszéntelepek távol-azonosítására irányuló palynológiai vizsgálatok (Palynological investigations of Liassic coal measures, their correlation and identification). Földt. Közl., 93: 15–23.

BÓNA J. 1969. Palynologie. In: Nagy E. (ed.), Unterlias-Kohlenserie des Mecsek-Gebirges Geologie. Ann. Hung. Geol. Inst., 51: 683–707.

BÓNA J. 1979. Tele-identification of coal seam groups by palynological methods within the Mecsek Lower Liassic Coal Measures. Földtani Kutatás, 22: 29–32 (in Hungarian).

BÓNA J. 1983. Palynological studies on the Upper Triassic and Lower Liassic of the Mecsek Mountains. Őslénytani Viták, 29: 47–57 (in Hungarian with English abstract).

BÓNA J. 1995. Palynostratigraphy of the Upper Triassic formations in the Mecsek Mts. (Southern Hungary). Acta Geol. Hung., 38(4): 319–354.

BÓNA J., NAGY E. & NÉMEDI VARGA Z. 1995. A Mecseki Kőszin Formació kőzetei, növényi maradványai és makrofaunája (Rocks, plant fossils and macrofauna of the Mecsek Black-Coal Formation): 233–261. In: Némedi Varga Z. (ed.), Mecseki feketekőszén kutatása és bánya- földtana. Miskolci Egyetem Központi Könyvtár és Levéltár, Miskolc (in Hungarian).

BONIS N.R., van KONIJNENBURG-van CITTERT J.H.A. & KÜRSCHNER W.M. 2010. Changing CO_2 conditions during the end-Triassic inferred from stomatal frequency analysis on *Lepidopteris ottonis* (Goeppert) Schimper and *Ginkgoites taeniatus* (Braun) Harris. Palaeogeogr. Palaeoclimat. Palaeoecol., 295: 146–161.

Ter BRAAK C.J.F. & PRENTICE I.C. 1988. A theory of gradient analysis. Adv. Ecol. Res., 18: 271–317.

CHEN L.Q., CHENG-SEN LI, CHALONER W.G., BEERLING D.J., SUN Q.G., COLLINSON M.E. & MITCHELL P.L. 2001. Assessing the potential for the stomatal characters of extant and fossil *Ginkgo* leaves to signal atmospheric CO_2 change. Am. Jour. Bot., 88(7): 1309–1315.

CHUN H.Y. 1996. Paleofloristic assemblages through geological time in Korea. Chemosphere, 33(9): 1705–1735.

CSÁSZÁR G. (ed.). 1997. Basic litostratigraphic units of Hungary. Charts and short descriptions. The Geological Institute of Hungary, Budapest.

CSONTOS L. & VÖRÖS A. 2004. Mesozoic plate tectonic reconstruction of the Carpathian region. Palaeogeogr. Palaeoclimat. Palaeoecol., 210: 1–56.

DiMICHELE W.A. 1994. Ecological patterns in time and Space. Paleobiology, 20(2): 89–92.

DiMICHELE W.A. & BEAL S.B. 1990. Flora, fauna, paleoecology of the Brazil Formation of Indiana. Rocks Miner., 65: 244–250.

DiMICHELE W.A. & GASTALDO R.A. 2008. Plant paleoecology in deep time. Ann. Missouri Bot. Gard., 95: 144–198.

DiMICHELE W.A. & PHILLIPS T.L. 1994. Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica Palaeogeogr. Palaeoclimat. Palaeoecol., 106(1994): 39–90.

DiMICHELE W.A., KERP H., TABOR N.J. & LOOY C.V. 2008. The so-called "Paleophytic–Mesophytic" transition in equatorial Pangea – Multiple biomes and vegetational tracking of climate change through geological time. Palaeogeogr. Palaeoclimat. Palaeoecol., 268(2008): 152–163.

DiMICHELE W.A., TABOR N.J., CHANEY D.S. & NELSON W.J. 2006. From wetlands to wet spots: Environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras. Geol. Soc. Am. Special Paper, 399(2006): 223–248.

FALCON-LANG H.J., NELSON W.J., ELRICK S., LOOY C.V., AMES P.R. & DiMICHELE W.A. 2009. Incised channel fills containing conifers indicate that seasonally dry vegetation dominated Pennsylvanian tropical lowlands. Geology, 37(10): 923–926.

FLORIN R. 1933. Studien über die Cycadales des Mesozoikums. Kung. Sv. Vet. Akad. Handl., 12(5): 1–134.

FÖLDI J. 1967. A Mecsek hegységi felsószinemuri képzódmények szintezési lehetósége (Zusammenfassung: Gliederungsmöglichkeiten in den Obersinemurischen Bildungen des Mecsek-Gebirges). Föld. Ins. Évi Jelentése, 1965: 133–148.

FRANCIS J.E., ASHWORTH A., CANTRILL D.J., CRAME J.A., HOWE J., STEPHENS R., TOSOLINI A.-M. & THORN V. 2008. 100 Million Years of Antarctic Climate Evolution: Evidence from Fossil Plants: 19–28. In: Cooper A.K., Barrett P.J., Stagg H., Storey B., Stump E., Wise W., and the 10 th ISAES editorial team (eds), Antarctica: A Keystone in a Changing World. Proceedings of the 10th International Symposium on Antarctic Earth Sciences. Washington, DC: The National Academies Press.

GALTIER J. 1997. Coal-ball floras of the Namurian-Westphalian of Europe. Rev. Palaeobot. Palynol., 95(1997): 51–72.

GASTALDO R.A., PFEFFERKORN H.W. & DiMICHELE W.A. 1995. Taphonomic and sedimentologic characterization of roof-shale floras. Geol. Soc. Am. Memoir, 185: 341–351.

GÂŞTESCU P., OLTEAN M., NICHERSU I. & CONSTANTINESCU A. 1998. Ecosistems of the Romanian Danube Delta Biosphere Reserve (map sc. 1: 75 000 and text-book). Institute of Geography, Institute of Biology, Danube delta Institute, Institute for Inland Water Management and Waste Water Treatment (RIZA/The Netherlands).

GEE C.T., MEYER C.A. & van KONIJNENBURG-van CITTERT J.H.A. 2003. The first unequivocal sphenophytes from the Late Jurassic of northwestern Switzerland (late Oxfordian Vellerat Formation) – palaeobotany and implications for facies interpretation. Cour. Forsch.-Inst. Senckenberg, 241: 97–109.

GÓCZAN F. 1956. A komlói liász feketekószéntelepek azonositására irányuló pollenanalitikai vizsgálatok (Pollen analysis as a method for coal layers identification in the Liassic of Komló). Földt. Int. Évk., 45(1): 135–166 (in Hungarian).

GOLONKA J. 2000. Cambrian-Neogene plate tectonic maps. Wydawnictwo Uniwersytetu Jagiellońskiego, Kraków.

GORDENKO N.V. 2008. Middle Jurassic Flora of the Peski Locality (Moscow Region). Systematics, Paleoecology, and Phytogeography. Paleont. Jour., 42 (12): 1285–1382.

GÖTZ A.E., RUCKWIED K. & BARBACKA M. 2011. Palaeoenvironment of the Late Triassic (Rhaetian) and Early Jurassic (Hettangian) Mecsek Coal Formation (south Hungary): implications from macro and microfloral assemblages. Palaeobiodiv. Palaeoenviron., 91: 75–88.

GREB S.F., DiMICHELE W.A. & GASTALDO R.A. 2006. Evolution and importance of wetlands in earth history. Geol. Soc. Am. Special Paper, 399 (2006): 1–40.

GUIGNARD G., BÓKA K. & BARBACKA M. 2001. Shade and sun leaves? Cuticle ultrastructure of *Komlopteris nordenskioeldii* (Nathorst) Barbacka. Rev. Palaeobot. Palynol., 114(3–4): 191–208.

HAAS J. 2001 (ed.). Geology of Hungary. Eötvös University Press, Budapest.

HANGANU J., DUBYNA D., ZHMUD E., GRIGORAŞ I., MENKE U., DROST H., ŞTEFAN N. & SÂRBU I. 2002. Vegetation of the Biosphere Reserve Danube Delta with Transboundary Vegetation Map, 1:161.000, Danube Delta National Institute Romania, Institute of Botany and Denube Delta Biosphere Reserve Ukraine and RIZA The Netherlands.

HANTKEN M. 1878. A Magyar Korona Országáinak széntelepei és szénbányászata. (Coal mines and coal production in the countries of the Hungarian Crown). Légrády Testvérek, Budapest.

HARRIS T.M. 1935. The fossil flora of Scoresby Sound East Greenland, part 4: Ginkgoales, Coniferales, Lycopodiales and isolated fructifications. Medd. om Grønland, 112(1): 1–176.

HARRIS T.M. 1961. The Yorkhire Jurassic flora. I: Thallophyta – Pteridophyta. Trustees of the British Museum, London.

HARRIS T.M. 1964. The Yorkshire Jurassic Flora. II: Caytoniales, Cycadales & Pteridosperms. Trustees of the British Museum (Natural History), London.

HARRIS T.M. 1979. The Yorkshire Jurassic Flora. V: Coniferales. Trustees of the British Museum, London.

HEJNOWICZ Z. 1980. Anatomia i histogeneza roślin naczyniowych (Anatomy and histogenesis of vascular plants). PWN, Warszawa. (in Polish).

HESSELBO S.P., MORGANS-BELL H.S., McELWAIN J.C., REES P. MCA, ROBINSON S.A. & ROSS C.E. 2003. Carbon-Cycle Perturbation in the Middle Jurassic and Accompanying Changes in the Terrestrial Paleoenvironment. The Jour. Geol., 111: 259–276.

HILL M.O. 1973. Reciprocal averaging: an eigenvector method for odination. J. Ecol., 61: 237–249.

HILL M.O. & GAUCH H.G. 1980. Detrended Correspondence Analysis: an improved ordination technique. Vegetatio, 42: 47–58.

HOFMANN K. 1907. Adatok a Pécsi-hegység geológiájához (Data for the geology of Pécs'Moutains) Földt. Közl., 37(4–5): 111– 116 (in Hungarian).

JANSSON I.-M., McLOUGHLIN S., VAJDA V. & POLE M. 2008. Early Jurassic flora from the Clarence-Moreton Basin, Australia. Rev. Palaeobot. Palynol., 150(1–4): 5–21.

JASPER K., HARTKOPF-FRÖDER C., FLAJS G. & LITTKE R. 2010. Palaeoecological evolution of Duckmantian wetlands in the Ruhr Basin (western Germany): A palynological and coal petrographical analysis. Rev. Palaeobot. Palynol., 162(2010): 123–145.

JONES T.P. & ROWE N.P. (eds), 1999. Fossil Plants and Spores. Modern Techniques. Geol. Soc. London.

KLEIDORFER F. 1898. (translated to Hungarian by LITSCHAUER, A.) Pécsvidéke ásványszenet tartalmazó liász-hegysége(The Liassic mountains containing black coal) OMBKE, Selmecbánya.

van KONIJNENBURG-van CITTERT J.H.A. 2002. Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia. Rev. Palaeobot. Palynol., 119(2002): 113–124.

van KONIJNENBURG-van CITTERT J.H.A. 2008. The Jurassic fossil plant record of the UK area. Proceed. Geol. Assoc., 119: 59–72.

van KONIJNENBURG-van CITTERT J.H.A. & van der BURGH J. 1989. The flora from the Kimmeridgian (Upper Jurassic) of Culgower, Sutherland, Scotland. Rev. Palaeobot. Palynol., 61: 1–51.

van KONIJNENBURG-van CITTERT J.H.A. & van der BURGH J. 1996. Review of the Kimmeridgian flora of Sutherland, Scotland, with reference to the ecology and in situ pollen and spores. Proceed. Geol. Assoc., 107: 97–105.

van KONIJNENBURG-van CITTERT J.H.A. & MORGANS H.S. 1999. The Jurassic flora of Yorshire. The Palaeontological Association, London.

KORDOS, L. 1983. Fontosabb szórványleletek a MÁFI gerinces-gyűjteményében (8. közlemény). Dinosaurus lábnyomok (*Komlosaurus carbonis* n. g. n. sp.) a mecseki liászból (Most important casual records in the Vertebrata collection of the Geological Institute of Hungary. Dinosaurus' legprints.) Ann. Hung. Geol. Inst., 1983: 503–511.

KRASSILOV V.A. 1973. Climatic changes in Eastern Asia as indicated by fossil floras. I. Early Cretaceous. Palaeogeogr. Palaeoclimat. Palaeoecol., 13: 261–273.

KUSTATSCHER E., van KONIJNENBURG-van CITTERT J.H.A. & ROGHI G. 2010. Macrofloras and palynomorphs as possible proxies for palaeoclimatic and palaeoecological studies: A case study from the Pelsonian (Middle Triassic) of Kühwiesenkopf/Monte Prà della Vacca (Olang Dolomites, N-Italy). Palaeogeogr. Palaeoclimat. Palaeoecol., 290: 71–80.

KÜRSCHNER W.M. 1996. Leaf stomata as biosensors of palaeoatmospheric CO_2 levels. LPP Contributions Series 5, LPP Foundation, Utrecht.

KÜRSCHNER W.M. 2001. Leaf sensor for CO_2 in deep time. Nature, 411: 247–248.

LACHKAR G., BÓNA J. & PAVILLON M.J. 1984. The Liassic Gresten Facies: palynological data and Paleogeographical significance. Acta Geol. Hung., 27(3–4): 409–416.

LANDIS E.R., ROHRBACHERA T.J., BARKERA C.E., FODOR B. & GOMBAR G. 2003. Coalbed gas in the Mecsek Basin, Hungary. Intern. Jour. Coal Geol., 54(2003): 41– 55.

LERNER A.J., LUCAS S.G., SPIELMANN J.A., KRAINER K., DiMICHELE W.A., CHANEY D.S., SCHNEIDER J.W., NELSON J. & IVANOV A. 2009. The biota and paleoecology of the Upper Pennsylwanian (Missourian) Tinajas locality, Socorro County. New Mexico Geological Society Guidebook, 60 th Field Conference, Geology of the Chupadera Mesa Region, 2009: 267–280.

LIBERTIN M., DAŠKOVÁ J., OPLUŠTIL S., BEK J. & EDRESS N. 2009. A Palaeoecological model for a vegetated early Westphalian intramontane valley (Intra- Sudetic basin, Czech Republic). Rev. Palaeobot. Palynol., 155(2009): 175–203.

McELWAIN J.C. 1998. Do fossil plants signal palaeoatmospheric CO_2 concentration in the geological past? Phil. Trans. R. Soc. Lond., B, 353: 83–96.

McELWAIN J.C. & CHALONER W.G. 1995. Stomatal density and index of fossil plants track atmospheric carbon dioxide in the Paleozoic. Ann. Bot., 76: 389–395.

McELWAIN J.C., BEERLING D.J. & WOODWARD F.I. 1999. Fossil Plants and Global Warming at the Triassic-Jurassic Boundary. Science, 285: 1386–1390.

McELWAIN J.C., POPA M.E., HESSELBO S.P., HAWORTH D.M. & SURLYK F. 2007. Macroecological responses of terrestrial vegetation to climatic and atmospheric change across the Triassic/Jurassic boundary in East Greenland. Paleobiology, 33: 547–573.

MOSBRUGGER V. 1999. The nearest living relative method: 261–266. In: Jones T.P. & Rowe N.P. (eds), Fossil plants and spores: modern techniques. The Geol. Soc. London.

NAGY E. 1969. Paläogeographie. In: Nagy E. (ed.), Unterlias-Kohlenserie des Mecsek-Gebirges, Geologie. Ann. Inst. Geol. Publ. Hung., 51(2): 307–317.

NAGY E. & NAGY J. 1969. Stratigraphie. In: Nagy E. (ed.), Unterlias-Kohlenserie des Mecsek-Gebirges, Geologie. Ann. Inst. Geol. Publ. Hung. 51(2): 280–287.

NAGY I.Z. 1961. Liassic remains of the Mecsek Mountains. Ann. Inst. Geol. Publ. Hung., 49(2): 609–613.

NAGY I.Z. 1970. Lower Liassic Molluscs from the Mecsek Mts., Hungary. Ann.. Hist.-Nat. Mus. Natn. Hung., 62: 65–98.

NAM S.J., KIM K.U., SHIN D.H. & HWANG S.J. 1997. Identification of biologiocally active substatnces from *Ginkgo biloba* L. Kor. J. Weed Sci., 17(4): 421–430.

NÉMEDI VARGA Z. 1995. A pécsi feketekőszén-terület földtani és hegységszerkezeti viszonyai (The area of Coal-Formation near Pécs and its geological relations): 39–64. In: Némedi Varga Z. (ed.), Mecseki feketekőszén kutatása és bánya földtana. (Investigations of black coal and geology of coal measures in the Mecsek Mts.). Miskolci Egyetem Központi Könyvtár és Levéltár, Miskolc.

NÉMEDI VARGA Z. 1998. A Mecsek- és a Villányi-Egység jura képződményeinek rétegtana (The stratigraphy of the Jurassic units of the Mecsek Mountains and Villányi Mountains): 319–336. In: Bérci I. & Jámbor A. (eds), Magyarország geológiai képződményeinek rétegtana (The stratigraphy of the Hungarian geological units). A MOL Rt és a MÁFI kiadványa Budapest 1998 (in Hungarian).

NGUYEN TU T.T., BOCHERENS H., MARIOTTI A., BAUDIN F., PONS D., BROUTIN J., DERENNE S. & LARGEAU C. 1999. Ecological distribution of Cenomanian terrestial plants based on $^{13}C/^{12}C$ ratios. Palaeogeogr. Palaeoclimat. Palaeoecol. 145: 79–93.

ŐSI A., PÁLFY J., MAKÁDI L., SZENTESI Z., GULYÁS P., RABI M., BOTFALVAI G. & HIPS K. 2011. Hettangian (Early Jurassic) Dinosaur Tracksites from the Mecsek Mountains, Hungary. Ichnos, 18: 79–94.

PAÁL-SOLT M. 1969. Kohlenpetrographie. In: Nagy E. (ed.), Unterlias-Kohlenserie des Mecsek-Gebirges, Geologie. Ann. Inst. Geol. Publ. Hung., 51(2): 473–575.

PHILLIPS T.L. & PEPPERS R.A. 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. Intern. Jour. Coal Geol., 3(3): 205–255.

PHILLIPS T.L., PEPPERS R.A. & DiMICHELE W.A. 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. Intern. Jour. Coal Geol., 5(1985): 43–109.

POOLE I. & KÜRSCHNER W.M. 1999. Stomatal density and index: the practice: 257–261. In: Jones T.P.

& Rowe N.P. (eds), Fossil plants and spores: modern techniques. The Geol. Soc. London.

POPA M.E. 1997. Corystospermal pteridosperms in the Liassic continental deposits of Romania. Acta Palaeont. Roman., 1: 81–87.

POPA M.E. & van KONIJNENBURG-van CITTERT J.H.A. 2006. Aspects of Romanian Early-Middle Jurassic palaeobotany and palynology. Part VII. Successions and floras. Progr. Nat. Sci., 16: 203–212.

REES P. MCA, ZIEGLER A.M. & VALDES P.J. 2000. Jurassic phytogeography and climates: New data and model comparisons: 297–318. In: Huber B.T., Macleod K.G. & Wing L. (eds), Warm climates in Earth History. Cambridge University Press, Cambridge.

REES P. MCA, ZIEGLER A.M., GIBBS M.T., KUTZBACH J.E., BEHLING P.J. & ROWLEY D.B. 2002. Permian Phytogeographic Patterns and Climate Data/Model Comparisons. The Jour. Geol., 110: 1–31.

RETALLACK G.J. 1977. Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. Alcheringa, 1: 247–277.

RETALLACK G.J. 2001. A 300-million-year record of atmospheric carbon dioxide from fossil plant cuticles. Nature, 411: 287 – 290.

ROHLF F.J. 2000–2005. NTYS-pc. Numerical taxonomy and multivariate analysis, version 2.1. Exeter Software, Setauket, New York, USA.

ROYER D.L., SCOTT L.W., BEERLING D.J., JOLLEY D.W., KOCH P.L., HICKEY L.J. & BERNER R.A. 2001. Palaeobotanical evidence for near present-day levels of atmospheric CO_2 during part of the Tertiary. Science, 292: 2310–2313.

RUCKWIED K., GÖTZ A.E., PÁLFY J. & TÖRÖK Á. 2008. Palynology of a terrestrial coal-bearing series across the Triassic/Jurassic boundary (Mecsek Mts., Hungary). Central Europ. Geol., 51(1): 1–15.

SCHWEITZER H.J. 1978. Die Räto-Jurassichen Floren des Iran und Afghanistans. 5. *Todites princeps*, *Thaumatopteris brauniana* und *Phlebopteris polypodioides*. Palaeontographica, B, 168(1–3): 17–60.

SHAO L., ZHANG P.,HILTON J., GAYER R., WANG Y., ZHAO C. & LUO Z. 2003. Paleoenvironments and paleogeography of the Lower and lower Middle Jurassic coal measures in the Turpan-Hami oil-prone coal basin, northwestern China. AAPG Bulletin, 87(2): 335–355.

SHELDON N.D. & TABOR N.J. 2009. Quantitative paleoenvironmental and paleoclimatic reconstruction using paleosols. Earth Sci. Rev., 95(1–2): 1–52.

SOKAL R.R. & MICHENER C.D. 1958. A statistical method for evaluating systematic relationships. Univ. Kansas Sci. Bull., 38: 1409–1438.

SPICER R. & HILL C.R. 1979. Principal components and correspondence analyses of quantitative data from a Jurassic plant bed. Rev. Palaeobot. Palynol., 28(1979): 273–299.

STEINTHORSDOTTIR M., BACON K.L., POPA M.E., BOCHNER L. & McELWAIN J.C. 2011. Bennettitalean leaf cuticle fragments (here *Anomozamites* and *Pterophyllum*) can be used interchangeably in stomatal frequency-based palaeo-CO_2 reconstructions. Palaeontology, 54: 867–882.

STÚR D. & BÖCK J. 1874. Neueste Ausbeute an fossilen Pflanzenresten in der Umgegend von Fünfkirchen. Verh. K.K. Geol. Reichsanst., 5: 115–118.

SUN B-N, XIE S.-P., YAN D.-F. & CONG P.-Y. 2008. Fossil plant evidence for Early and Middle Jurassic paleoenvironmental changes in Lanzhou area, Northwest China. Palaeoworld, 17: 215–221.

SZENTE I. 1992. Early Jurassic Mollucs from the Mecsek Mountains (S. Hungary). A preliminary study. Ann. Univ. Sci. Budapest, Sect. Geol., 29: 325–343.

SZENTE I. 1995. Bivalvia from the Bathonian (Middle Jurassic) of the Mecsek Mts., Hungary. Ann. Univ. Sci. Budapest., Sect. Geol., 30: 93–109 and 221–224.

SZILASSI P. 2004. A Duna-delta természeti földrajza és környezeti próblémai (Geography and environmental problems of Danube delta). Földrajzi Értesítő, 53(3–4): 183–201 (in Hungarian).

THÉVENARD F., GOMEZ B. & DAVIERO-GOMEZ V. 2005. Xeromorphic adaptations of some Mesozoic gymnosperms. A review with palaeoclimatological implications. Comptes Rendus. Palevol, 4(2005): 67–77.

THOMAS B.A. 1985. Pteridophyte success and past biota – a palaeobotanist's approach. Proceed. Roy. Soc. Edinburgh, 86B: 423–430.

THOMAS B.A. & CLEAL C.J. 1993. The coal measures forests. National Museum of Wales, 1993.

THORN V. 2001.Vegetation communities of a high palaeolatitude Middle Jurassic forest in New Zealand. Palaeogeogr. Palaeoclimat. Palaeoecol., 168(2001): 273–289.

VAKHRAMEEV V.A. 1970. Pattern of distribution and Palaeoecology of Mesozoic conifers Cheirolepidiaceae. Paleontol. Journ., 1(1970): 19–34.

VAKHRAMEEV V.A. 1991. Jurassic and Cretaceous floras and climates of the Earth. Cambridge University Press, Cambridge, New York, Port Chester, Melbourne, Sydney.

WANG Y. 2002. Fern ecological implications from the Lower Jurassic in Western Hubei, China. Rev. Palaeobot. Palynol., 119: 125–141.

WANG Y., MOSBRUGGER V. & ZHANG H. 2005. Early to Middle Jurassic vegetation and climatic events in the Qaidam Basin, Northwest China. Palaeogeogr. Palaeoclimat. Palaeoecol., 224(1–3): 200–216.

WATSON J. & CUSACK H.A. 2005. Cycadales of the English Wealden. Monograph of the Palaeontological Society, London.

WEBER R. 1968. Die fossile Flora der Rhät-Lias-Übergangsschichten von Bayreuth (Oberfranken) unter besonderer Berücksichtigung der Coenologie. Erlanger Geol. Abh., 72: 1–73.

WEIN G. 1952. A komlói bányaföldtani kutatások legújabb eredményei (The newest results of Komló's mine geological investigations). Földtani Közlöny, 82: 337–348.

WING S.L. & DiIMICHELE W.A. 1995. Conflict between Local and Global Changes in Plant Diversity through Geological Time. PALaios, 5(10): 551–564.

WNUK C. & PFEFFERKORN H.W. 1984. The life and paleoecology of Middle Pennsylwanian medullosan pteridosperms based on an in situ assemblage from the Bernice basin (Sullivan country, Pennsylvania, USA). Rev. Palaeobot. Palynol., 41(1984): 329–351.

WOODWARD F.I. 1987. Stomatal numbers are sensitive to increases in CO_2 from pre-industrial levels. Nature, 327: 617–618.

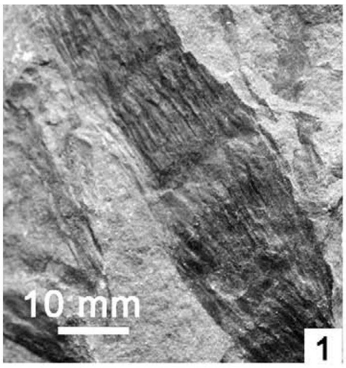
XIE S., SUN B., YAN D., XIAO L. & WEI L. 2006. Leaf cuticular characters of *Ginkgo* and implications for palaeoatmospheric CO_2 in the Jurassic. Progr. Natural Sci., 16 (Special Issue): 258–263.

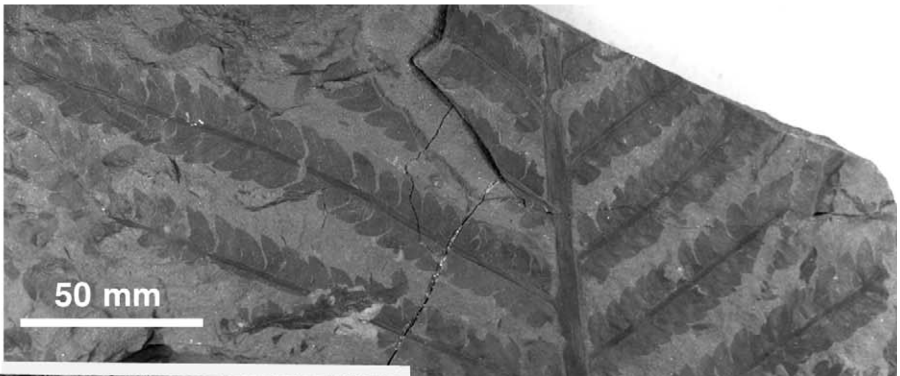
ZHOU Z-Y. 2009. An overview of fossil Ginkgoales. Palaeoworld, 18(1): 1–22.

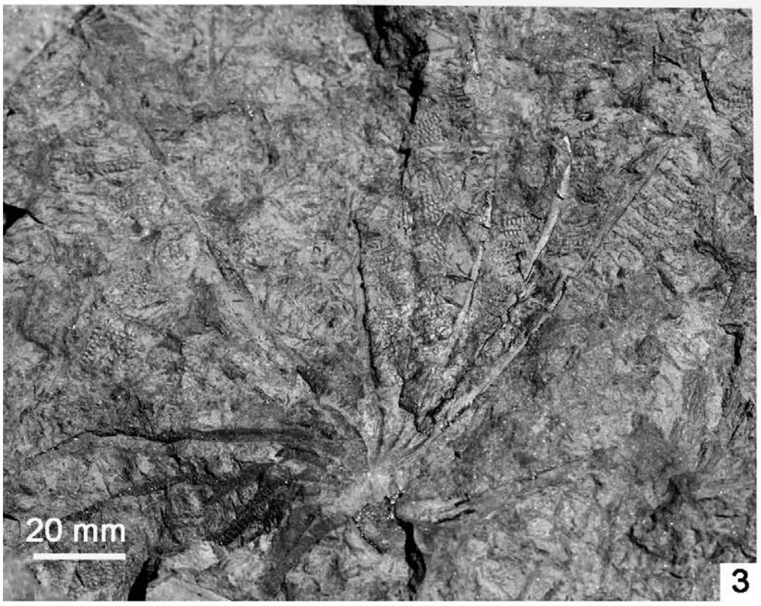
PLATES

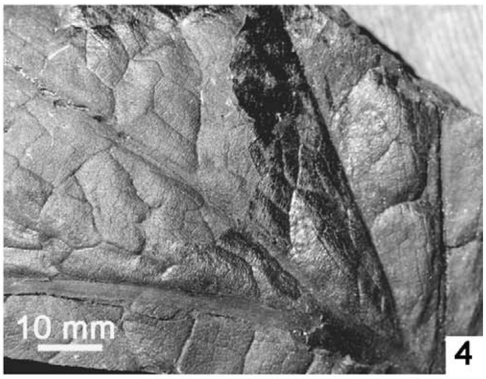
Plate 1

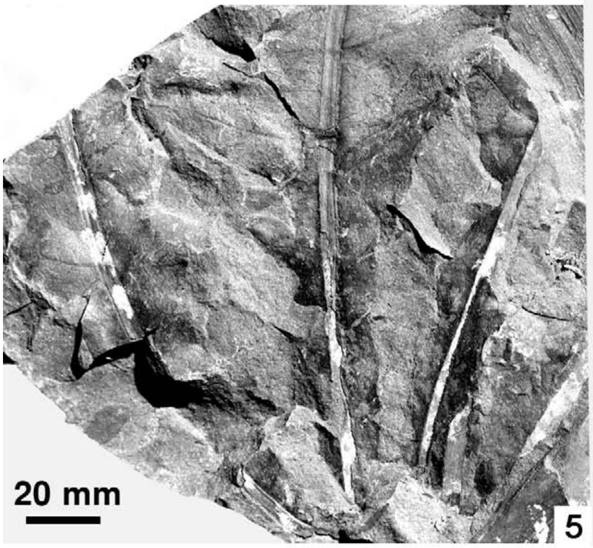
1. *Equisetites columnaris*, No BP 96.144.1.
2. *Todies goeppertianus*, No BP 89.224.1.
3. *Phlebopteris angustiloba*, leaf base, No BP 89.440.1.
4. *Clathropteris meniscoides*, fragment of leaf base, No BP 89.315.1.
5. *Dictyophyllum nilssonii*, near the leaf base, No BP 96.80.2.
6. *Dictyophyllum rugosum*, No BP 94.273.1.


10 mm
1


50 mm
2


20 mm
3


10 mm
4


20 mm
5

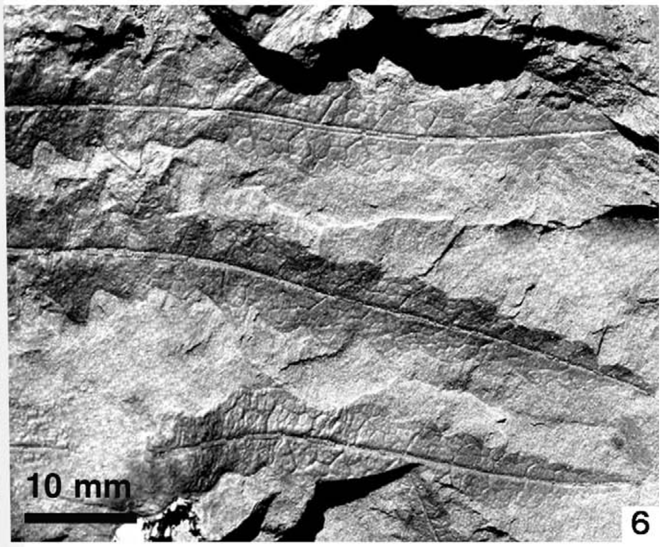
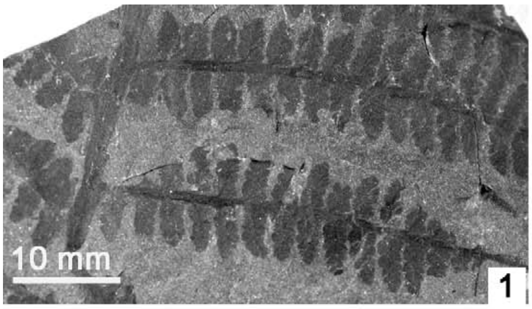
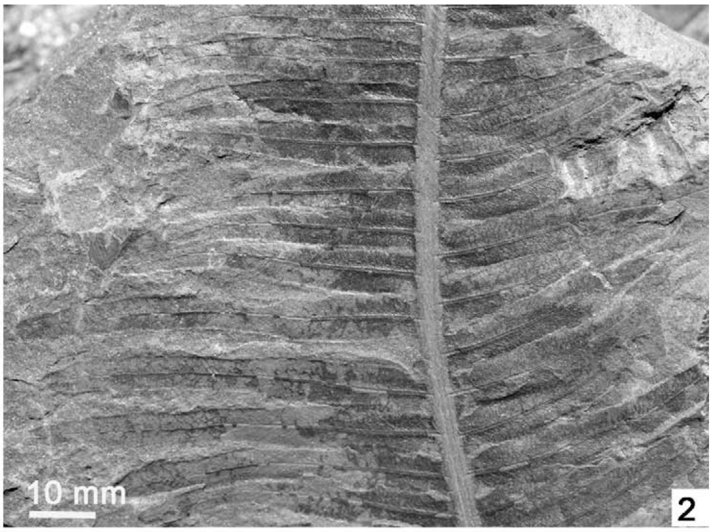

10 mm
6

Plate 2

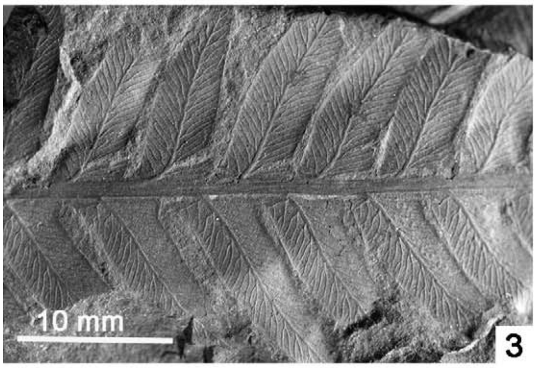
1. *Todites princeps*, No BP 94.692.1.
2. *Phlebopteris* sp. No BP 96.239.1.
3. *Cladophlebis denticulata*, No BP 2004.1040.1.
4. *Cladophlebis roessetii*, No BP 2004.1002.1.
5. *Komlopteris nordenskioeldii*, shade leaf, No BP 89.368.1.
6. *Ptilozamites cycadea*, No BP 94..1.
7. *Komlopteris nordenskioeldii*, sun leaf, No BP 89.275.1.



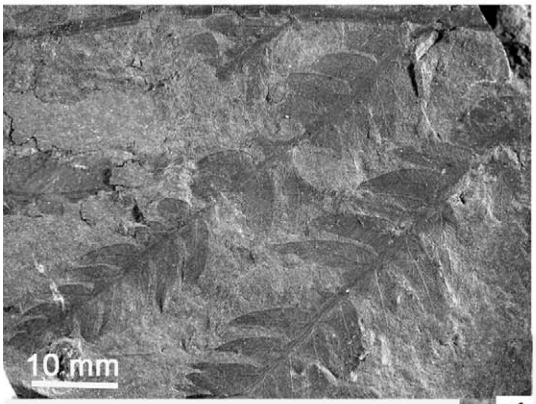
1



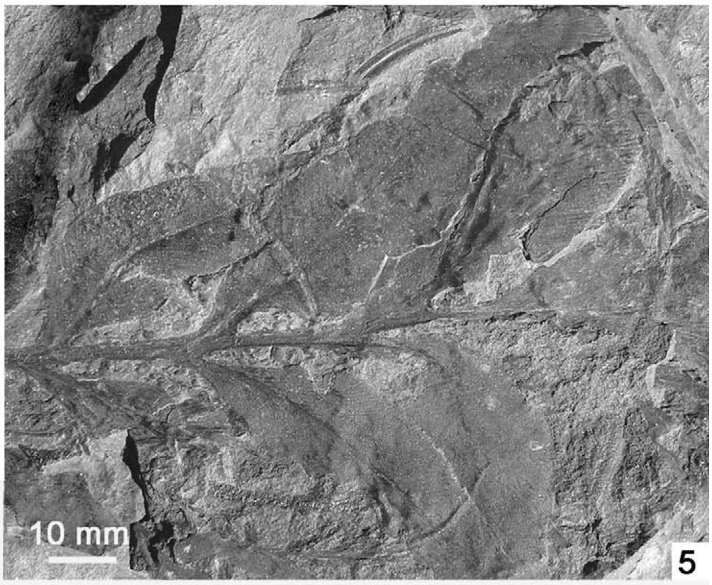
2



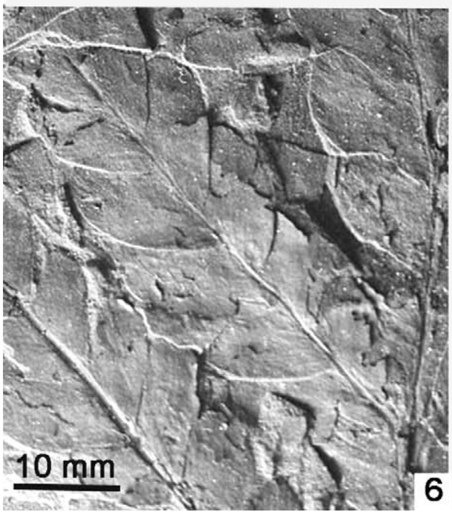
3



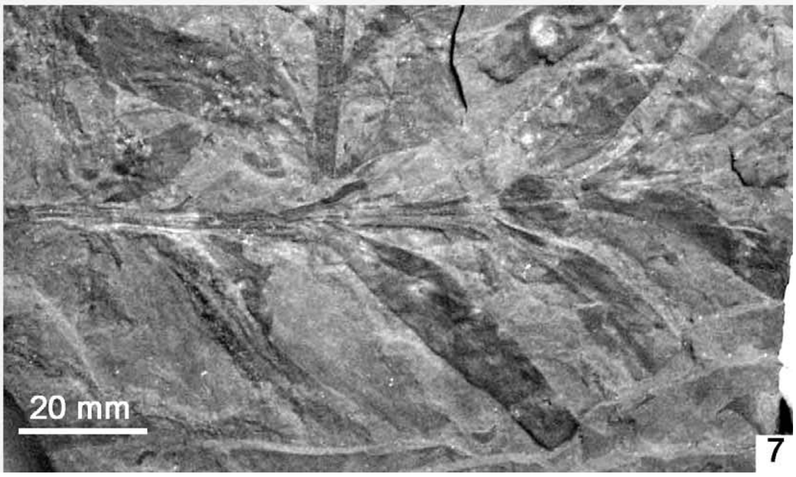
4



5



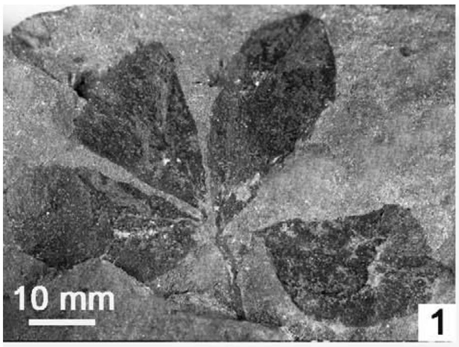
6



7

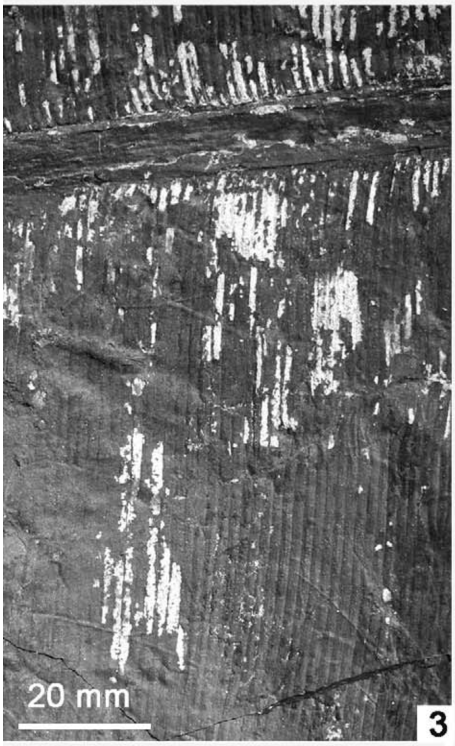
Plate 3

1. *Sagenopteris nilssoniana*, No BP 89.385.1.
2. *Nilssonia polymorpha*, No BP 94.879.1.
3. *Bjuvia simplex*, No BP 98.1054.1.
4. *Ginkgoites marginatus*, No BP 2011.230.1.
5. *Sphenobaiera longifolia*, BP 94.989.1.
6. *Baiera furcata*, No BP 98.596.1.
7. *Podozamites schenkii*, No BP 89.35.1.
8. *Pagiophyllum* sp. No BP 98.1216.1.
9. *Elatocladus* sp. No BP 2000.1202.1.

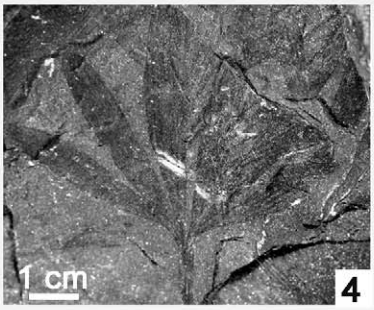


1

2

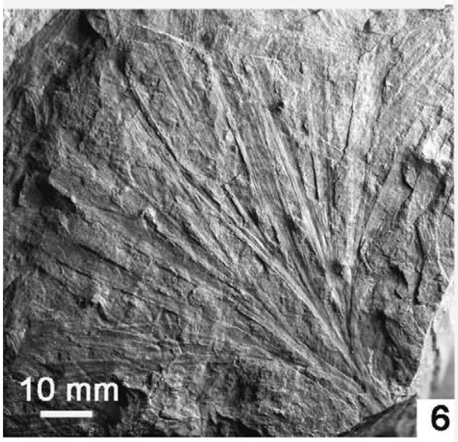


3



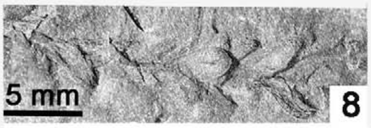
4

5

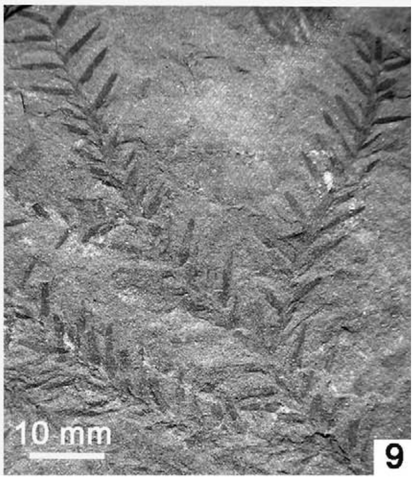


6

7



8



9