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Relationships between ecosystems and plant assemblages as responses to environmental conditions in the Lower Jurassic of Hungary and Romania

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ABSTRACT. Two Early Jurassic localities, the Mecsek Mts in Hungary and Anina in Romania, are similarly significant and both floras are of autochthonous/paraautochthonous origin. In the Early Jurassic the Hungarian locality was a delta plain; the Romanian locality was an intramontane depression filled predominantly by a braided river system. The floristic composition of the two localities (52 genera, 120 species), although superficially similar (25 common genera), differs at species level (only 9 common species) as well as in the proportions of taxa in major plant groups. These differences can be explained by differences in environmental conditions resulting from palaeogeographic and topographic factors. Based on previous and recent studies, alpha diversity as well as statistically (DCA, PCA) differentiated ecogroups are compared and discussed. For common species, the GLM method was used to classify them to particular environmental response types. Their environmental requirements in both ecosystems are evaluated. Some of the shared species showed different preferences at the localities, explainable by their broad ecological tolerance.

KEYWORDS: macroflora, palaeoecology, Early Jurassic, Hungary, Romania

INTRODUCTION

A comparison of Hungarian and Romanian Early Jurassic localities is of interest to us, since these localities are close to each other, the straight-line distance being ca 370 km. Both floras are of autochthonous/paraautochthonous origin, associated with coal-bearing deposits, and with similar modes of

preservation (Popa 1998, Barbacka 2011). Both of them have been systematically sampled for more than 20 years. There are exhaustive lists of taxa recognised so far, and the geological settings are well known (Barbacka 1991, 1992, 1994a, b, 1997, 2000, 2001, 2002, 2009, Barbacka & Bodor 2008, Bodor & Barbacka 2008,

Givulescu & Popa 1994, 1998, Kędzior & Popa 2013, Nagy & Nagy 1969, Popa 1992, 1997a, b, 1998, 2000a, b, 2001a, b, 2005, 2014, Popa & Kędzior 2008, Popa & Van Konijnenburg-van Cittert 1999, 2006, Popa & Meller 2009, Thévenard & Barbacka 2000). Statistical studies of both localities have distinguished plant ecogroups (Barbacka 2011, Barbacka et al., MS.). In the present work we applied statistical methods to both localities in order to compare their ecological backgrounds and plant environmental responses. Although they are palaeogeographically close, they differ in their taxonomical composition and type of geological setting.

The Hungarian locality in the Mecsek Mts is a typical delta plain (facies: delta – limnic – lacustrine – delta – lagoonal – plain marine – lagoonal – plain marine), which is Hettangian and earliest Sinemurian in age. The reconstructed palaeoenvironment was characterised as a system of river channels with river levees and marine barriers, crevasse splays, swampy areas, lakes, and channels (Nagy & Nagy 1969, Paál-Solt 1969, Barbacka 2011). Detrended correspondence analysis (DCA) of floral composition (based on co-occurrence of taxa on the same slabs) gave five ecogroups interpreted as depending on the two most important factors – moisture and degree of disturbance (Barbacka 2011):

1. *Sagenopteris* group. Moderately disturbed, relatively dry (non-flooded) inland areas (*Nilssonia revoluta*, *Anomozamites marginatus*, *Cladophlebis denticulata*, *Marattiopsis hoerensis*, *Sagenopteris* sp., *Nilssonia obtusa*).

2. *Thaumatopteris* group. Highly disturbed, short-lived, moderately wet areas formed by alluvial deposits (islands, peninsulas, forelands), fully damaged by river flooding, occupied by pioneer plants (*Thaumatopteris brauniana*, *Phlebopteris angustiloba*, *Equisetites* sp., *Dictyophyllum rugosum*, *Cladophlebis haiburnensis*)

3. *Ptilozamites* group. Weakly disturbed, moderately wet canopy (*Nilssonia polymorpha*, *Equisetites columnaris*, *Pterophyllum subaequale*, *Ptilozamites cycadea*, *Dictyophyllum nilssonii*, *Bjuvia simplex*, *Desmiophyllum* sp., *Phlebopteris* sp.)

4. *Ginkgoites* group. Weakly disturbed wetland (*Ginkgoites marginatus*).

5. *Komlopteris* group. Moderately dis-

turbed swamp (*Komlopteris nordenskiöldii*, *Elatocladus* sp., *Baiera furcata*, *Sphenobaiera longifolia*, *Pagiophyllum* sp., *Brachyphyllum* sp., *Sphenobaiera leptophylla*, *Equisetites muensteri*).

Anina (formerly known as Steierdorf) is a historical coal mining centre in the middle area of the Reșița Basin, where the plant-bearing Steierdorf Formation reaches 250 m thickness (Bucur 1991, 1997, Popa & Kędzior 2008, Popa 2009). The Steierdorf Formation is coal-bearing, yielding eight bituminous coal seams, Hettangian-Sinemurian in age. The Steierdorf Formation is formed mainly by a braided river system occurring in a depression during the Hettangian-Sinemurian, where mires, lakes, flood plains next to levees, and river channels occurred (Popa 2009, Kędzior & Popa 2013). For plant ecology, PCA was performed (based alike in Mecsek on co-occurrence of taxa in the same hand specimen), revealing four ecogroups whose taxonomical composition depended mainly on the moisture/disturbance gradient and the temperature gradient (Barbacka et al. in prep).

1. *Podozamites* group, in moderately wet and disturbed habitat, not influenced by temperature (*Podozamites paucinervis*, *Sphenobaiera* sp. and *Pinites* sp.).

2. *Schizoneura* group. Lower temperature and higher moisture/higher disturbance, a typical flood plain association (*Neocalamites (Schizoneura) carcinoides*, *Dictyophyllum nilssonii*, *Cladophlebis nebbensis*, *C. haiburnensis*, *Dictyophyllum nervulosum*, *Coniopteris murrayana*, *Matonia braunii*, *Thaumatopteris brauniana*).

3. *Zamites* group. Higher temperature and higher moisture, probably swampy in its last, closing moments, when it was filled up with sediment (*Zamites schmiedelii*, *Baiera* sp., *Ptilophyllum* sp., *Cladophlebis denticulata*, *Geinitzia* sp., *Ginkgoites* sp., *Komlopteris nordenskiöldii*, *Ptilozamites cycadea*).

4. *Nilssonia* group. Relatively dry, moderately warm and undisturbed conditions corresponding with levees, which were the highest-elevation relief forms in the basin (*Nilssonia* sp. 1).

Since the climate of the Jurassic is known to have been relatively stable (Vakhrameev 1991), microclimatic, palaeotopographic, or palaeogeographic factors influenced the floristic composition of particular localities. A genus-level

cluster analysis of European Jurassic localities (Barbacka et al. 2014) placed the Reșița Basin (including Anina) and the Mecsek Mts in the same branch: Reșița was paired with Yorkshire (UK) and Mecsek with Scoresby Sound (Greenland), all being of the river-delta type of environment. On species level, Reșița and Mecsek were in different clades, confirming a significant difference in their plant composition. Similarity of genus composition accompanied by dissimilarity of species content is not an unusual combination, as observed in a statistical approach to Mecsek flora (Barbacka 2011). The same genera can occur in different habitats, but species of the same genus almost always occupy different ecological niches (Barbacka 2011).

In this paper we discuss the presumed taxonomical similarity between the two floras and the mechanisms governing local floristical changes, in the light of environmental variation.

MATERIAL AND METHODS

The comparison of the two floras from the Mecsek Mts and Anina localities was based on samples stored at the Hungarian Natural History Museum (3256 samples belonging to 42 taxa, collected by Barbacka since 1989) and samples stored at the University of Bucharest and the National Geological Museum (1384 samples belonging to 89 taxa, collected by Popa since 1990).

Alpha diversity was estimated based on complete lists of taxa based on vegetative plant remains with quantitative values. Since the studied material from Mecsek contains twice as many specimens as that from Anina, the values are given as percentages, making the data comparable.

Taxa determined as 'sp.' are assigned letters for Anina (sp. A, sp. B) and numbers for Mecsek (sp. 1, sp. 2).

STATISTICAL ANALYSES

We used palaeobotanical databases of the 3256 samples from Mecsek and 1384 samples from Anina for the calculations. First the data were ordinated separately for the two localities by principal coordinate analysis (PCoA). Their distribution along axis 1 and axis 2 was influenced by the similarities and differences in taxonomical composition. The data are for taxa based on vegetative plant remains that co-occurred with at least one other taxon in the

same slab. The taxa were coded as binary (0-1) variables (for details see Barbacka 2011, Barbacka et al. 2014, Barbacka et al. in prep). In order to estimate the responses of particular taxa along PCoA axis 1 and axis 2 we applied a logistic regression model, the General Linear Model (GLM) using the logit link. A binomial distribution of the response variable was assumed (Agresti 2007). In that way the response variables (species) were related to a predictor – sample loadings along PCoA axis 1 and axis 2 (Barbacka et al. in prep, Fig. 2). Forward (stepwise) selection starting from the null model was used to find the fitted model for the particular species, based on the F-test criterion and corresponding I-type error based on 499 runs. The calculations were performed with CANOCO 5 (ter Braak & Šmilauer 2012). Finally, seven species common to the two sites were considered (see Table 1). GLMs for the two localities revealed the response of the species along the two PCoA axes and thus enabled us to classify them to particular response types. The group responses were interpreted as common occurrence in similar ecological conditions, that is, forming the putative ecological groups.

RESULTS

ALPHA DIVERSITY

The flora from Anina appears to be more diverse than the flora from the Mecsek Mts. It contains 48 genera and 88 species belonging to 9 plant groups (Popa 1992, 1998, 2000a, b, 2009, Popa & Van Konijnenburg-van Cittert 2006, Popa & Meller 2009), as compared with 29 genera and 42 species from 8 plant groups (including one *incertae sedis*) in Mecsek (Barbacka 1991, 1992, 1994a, b, 1997, 2000, 2001, 2009, 2011, Barbacka & Bodor 2008, Thévenard & Barbacka 2000; Table 1, Fig. 1A, B). The plant groups represented in both localities correspond to each other; lycopods and Czekanowskiales additionally occur in the material from Anina, while *Desmiophyllum* sp. (*incertae sedis*) is present in the material from Mecsek. The two localities have 25 genera in common but only 9 species in common.

In terms of plant taxonomical groups, sphenophytes are represented in Anina by 2 genera and 3 species, representing 13% of the total

Table 1. List of species in Mecsek and Anina localities. Common species in bold letters

Taxon	Anina	Mecsek	Taxon	Anina	Mecsek
<i>Aninopteris formosa</i> Popa	1		<i>Komlopteris</i> sp.	1	
<i>Anomozamites marginatus</i> (Unger) Nathorst		31	<i>Kylikipteris arguta</i> Lindley et Hutton	20	
<i>Baiera furcata</i> (Lindley et Hutton) Braun		57	<i>Kylikipteris</i> sp.	1	
<i>Baiera</i> sp.	2		<i>Marattia (Marattiopsis) intermedia</i> (Münster) Kilpper	4	
<i>Bjuvia simplex</i> Florin		28	<i>Marattia (Marattiopsis)</i> sp.	3	
<i>Bjuvia</i> sp.	2		<i>Marattiopsis hoerensis</i> (Schimper) Thomas		45
<i>Brachyphyllum</i> sp. 1		18	<i>Matonia braunii</i> (Göppert) Harris	70	
<i>Brachyphyllum</i> sp. 2	1		<i>Neocalamites (Schizoneura) carcinoides</i> Harris	142	46
<i>Cladophlebis</i> cf. <i>aktashensis</i> Turutanova- Ketova	2		<i>Neocalamites</i> sp. A	8	
<i>Cladophlebis denticulata</i> (Bron- gniart) Fontaine	65	58	<i>Nilssonsonia obtusa</i> (Nathorst) Harris		181
<i>Cladophlebis haiburnensis</i> Lindley et Hutton	30	36	<i>Nilssonsonia polymorpha</i> Schenk		30
<i>Cladophlebis nebbensis</i> (Brongniart) Nathorst	58		<i>Nilssonsonia revoluta</i> Harris		18
<i>Cladophlebis roessertii</i> (Schenk) Saporta		17	<i>Nilssonsonia</i> sp. A	78	
<i>Cladophlebis</i> sp.	119		<i>Nilssonsonia</i> sp. B	9	
<i>Cladophlebis</i> sp. X	6		<i>Nilssonsonia</i> sp. C	26	
<i>Clathropteris meniscoides</i> Bron- gniart	1	194	<i>Nilssoniopteris</i> sp.	4	
<i>Coniopteris hymenophylloides</i> (Bron- gniart) Seward		2	<i>Osmundopsis</i> cf. <i>sturi</i> (Raciborski) Harris	2	
<i>Coniopteris murrayana</i> Brongniart	8		<i>Otozamites</i> sp. A	1	
<i>Coniopteris</i> sp. A	1		<i>Otozamites</i> sp. B	1	
<i>Coniopteris</i> sp. B	52		<i>Pachypteris banatica</i> (Humml) Doludenko		1
<i>Ctenis</i> cf. <i>grandifolia</i> Fontaine	12		<i>Pachypteris rhomboidalis</i> (Ettingshau- sen) Doludenko	1	
<i>Ctenis</i> sp.		1	<i>Pachypteris speciosa</i> (Ettingshausen) Andrae	64	
<i>Cupressinocladus</i> sp.	2		<i>Pachypteris</i> sp.	2	
<i>Czekanowskia rigida</i> Heer	1		<i>Pagiophyllum</i> sp. 1		127
<i>Desmiophyllum</i> sp.		76	<i>Pagiophyllum</i> sp. A	6	
<i>Dicksonia</i> sp.	6		<i>Pagiophyllum</i> sp. B	7	
<i>Dictyophyllum nervulosum</i> Kilpper	5		<i>Phlebopteris angustiloba</i> (Presl) Hirmer et Hörhammer	1	75
<i>Dictyophyllum nilssonii</i> (Brongniart) Göppert	60	56	<i>Phlebopteris formosa</i> Givulescu et Popa	9	
<i>Dictyophyllum rugosum</i> Lindley et Hutton		48	<i>Phlebopteris polypodioides</i> Brongniart	1	
<i>Dictyophyllum</i> sp.	2		<i>Phlebopteris</i> sp. 1		112
<i>Eboracia lobifolia</i> (Philips) Thomas	1		<i>Phlebopteris</i> sp. A	4	
<i>Elatides</i> sp.	6		<i>Phlebopteris woodwardii</i> Leckenby	18	
<i>Elatocladus</i> sp. 1		366	<i>Phoenicopsis angustifolia</i> Heer	7	
<i>Elatocladus</i> sp. A	13		<i>Phoenicopsis</i> sp.	10	
<i>Equisetites columnaris</i> Brongniart		53	<i>Pinites</i> sp.	37	
<i>Equisetites muensteri</i> (Sternberg) Harris		56	<i>Podozamites distans</i> (Braun) Presl	7	
<i>Equisetites</i> sp. 1		24	<i>Podozamites lanceolatus</i> (Lindley et Hut- ton) Braun		1
<i>Equisetites</i> sp. A	12		<i>Podozamites paucinervis</i> Boersma et Van Konijnenburg-van Cittert	43	
<i>Geinitzia</i> sp.	17		<i>Podozamites</i> sp. 1		29
<i>Ginkgoites marginatus</i> (Nathorst) Florin		121	<i>Podozamites</i> sp. A	11	
<i>Ginkgoites minuta</i> (Nathorst) Harris		1	<i>Pseudoctenis</i> sp. 1		1
<i>Ginkgoites</i> sp. 1		93	<i>Pseudoctenis</i> sp. A	1	
<i>Ginkgoites</i> sp. A	41		<i>Pseudocycas</i> sp.	2	
<i>Hausmannia buchii</i> (Andrae) Seward	5		<i>Pterophyllum brevipenne</i> Kurr	6	
<i>Hausmannia</i> cf. <i>dentata</i> Oishi	2		<i>Pterophyllum longifolium</i> Brongniart	7	
<i>Hausmannia</i> sp.	1		<i>Pterophyllum subaequale</i> (Hartz) Harris		9
<i>Isoetes</i> sp.	1		<i>Pterophyllum</i> sp.	24	
<i>Komlopteris nordenskiöldii</i> (Nathorst) Barbacka	2	552	<i>Ptilophyllum</i> sp.	22	
			<i>Ptilozamites cycadea</i> (Berger) Schenk	2	140
			<i>Ptilozamites leckenbyi</i> (Leckenby) Nathorst	1	

Table 1. Continued

Taxon	Anina	Mecsek
<i>Raphaelia</i> sp.	2	
<i>Sagenopteris</i> sp. 1		312
<i>Sagenopteris</i> sp. A	13	
<i>Solenites</i> sp.	5	
<i>Sphenobaiera dragastanii</i> Givulescu	1	
<i>Sphenobaiera grandis</i> Kilpper	3	
<i>Sphenobaiera leptophylla</i> (Harris) Florin		21
<i>Sphenobaiera longifolia</i> (Pomel) Florin		31
<i>Sphenobaiera spectabilis</i> (Nathorst) Florin	2	
<i>Sphenobaiera</i> sp.	54	
<i>Sphenopteris</i> sp.		2
<i>Storgaardia johanna</i> nomen nudum	1	
<i>Storgaardia spectabilis</i> Harris	3	
<i>Storgaardia</i> sp.	8	
<i>Thaumatopteris brauniana</i> Popp	18	94
<i>Thaumatopteris</i> sp.	21	
<i>Todites goepertianus</i> (Münster) Krasser		78
<i>Todites princeps</i> Presl		15
<i>Todites</i> sp.	1	
<i>Zamites aninaensis</i> (Semaka) Givulescu	3	
<i>Zamites schmidelii</i> Presl	34	
<i>Zamites</i> sp.	14	
Taxa	89	42
summa of samples	1384	3256

number of specimens. In Mecsek, sphenophytes account for 2 genera, 4 species and a 5% share (Figs 2A, B, 3). The genera are the same but the species are different. For Mecsek, 3 species of *Equisetites* were noted (*E. columnaris*, 29.6% of sphenophytes; *E. muensteri*, 31.3%; *Equisetites* sp. 1, 13.4%) and one species of *Neocalamites* (*Schizoneura*) *carcinoides*, 25.7%. For Anina there was one species, *Equisetites* sp. A (7.4% of sphenophytes) and 2 species of *Neocalamites*, but only one of them, *N. carcinoides* (named here *Schizoneura carcinoides*), occurred in a significant amount (87.7%).

Lycophytes were recorded only from Anina, as one specimen of *Isoetites* sp.

Ferns (Fig. 4) are the most diverse in both localities. In Anina they are represented by 16 genera and 35 species (Popa 1997a, 2001a, Popa 2005, Givulescu & Popa 1994, 1998, Popa & Van Konijnenburg-van Cittert 1999), and the total number of specimens constitutes 43.4% of all the material (Fig. 2A, B); ferns dominated the whole assemblage. In Mecsek, 9 genera and 14 species of fern were recorded (Barbacka 2011, Barbacka & Bodor 2008, Bodor & Barbacka 2008), and the specimens formed 25.5% of all collected samples, the second biggest group besides seed ferns. Four

common species (of the total 9) were ferns, but their shares differed between the two assemblages: *Cladophlebis denticulata* (Anina 10.8% of ferns, Mecsek 6.9%), *Clathropteris meniscoides* (Anina 1 specimen, Mecsek 23.3% of all ferns), *Dictyophyllum nilssonii* (Anina 10%, Mecsek 6.7%), and *Phlebopteris angustiloba* (Anina 1 specimen, Mecsek 9% of ferns).

Seed ferns (Fig. 5) are not very numerous in Anina, represented by 4 genera and 8 species (Popa 1997b, Popa 2000a), but they have a 6.7% share of the total number of specimens (Fig. 2A, B). In Mecsek the same 4 genera include 4 species (Barbacka 1991, 1992, 1994a, b, 1997) but their share is 30.8% of the total number of specimens, indicating their dominance in the flora. In Anina the individual species are not frequent and the most numerous one is *Pachypteris speciosa* (74.4% of all seed ferns), while *Komlopteris nordenskioeldii* is represented by a single specimen. In Mecsek,

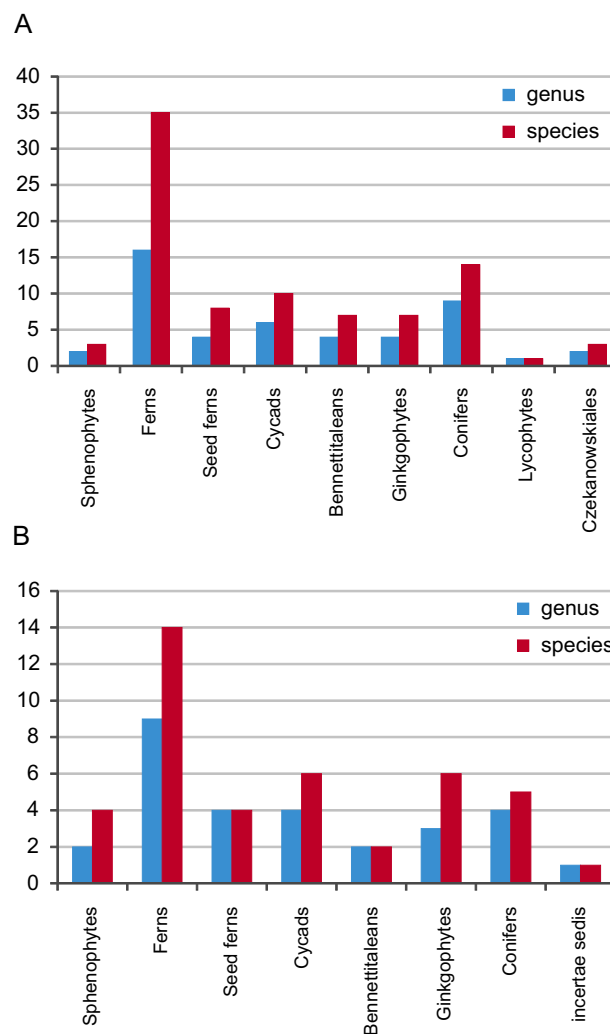


Fig. 1. Numbers of genera and species from the major taxonomical plant groups (A) in Anina, (B) in Mecsek

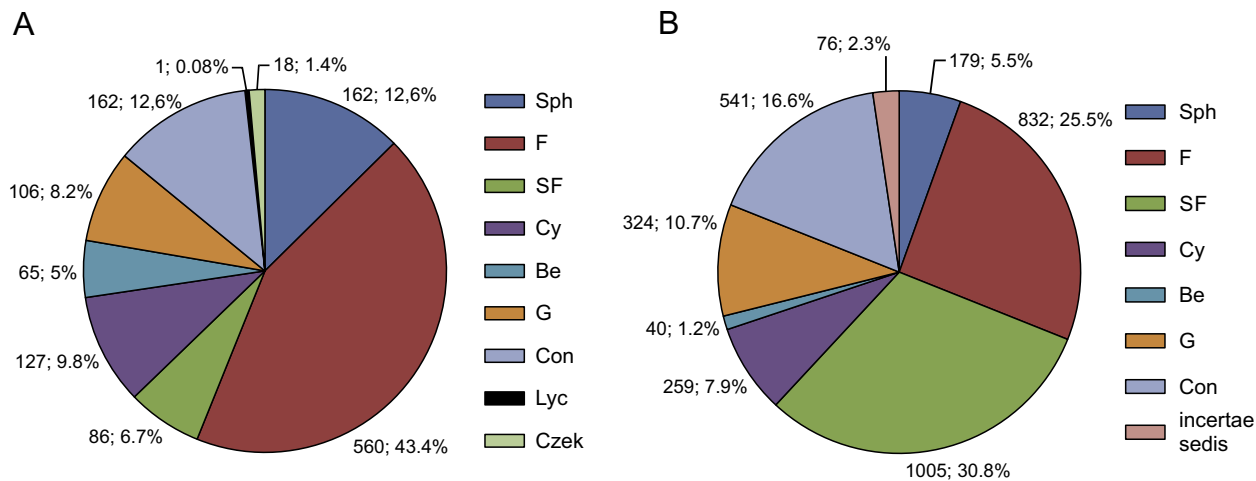


Fig. 2. Number of specimens and percentage of the major taxonomical plant groups (A) in Anina, (B) in Mecsek. Sph – sphenophytes, F – ferns, SF – seed ferns, Cy – cycads, Be – bennettitaleans, G – ginkgophytes, Con – conifers, Lyc – lycophytes, Czek – Czekanowskiales

Pachypteris is very rare (single specimen of *P. banatica*) and *Komlopteris* occurs in large numbers (54.9% of seed ferns). *Sagenopteris* sp. is also rare in Anina but in Mecsek it has a 31% share of seed ferns. *Ptilozamites cycadea* is much more frequent in Mecsek (13.9%, versus 2 specimens in Anina). This group shows the largest quantitative disproportions in the presence of a given taxon.

Cycads (Fig. 6) are present in almost the same proportions in the two localities: in Anina, 6 genera and 10 species (Popa & Van Konijnenburg-van Cittert 2006), constituting 9.8% of the total number of specimens (Fig. 2 A, B); in Mecsek, 4 genera and 6 species (Barbacka 2001), forming 7.9% of the total material.

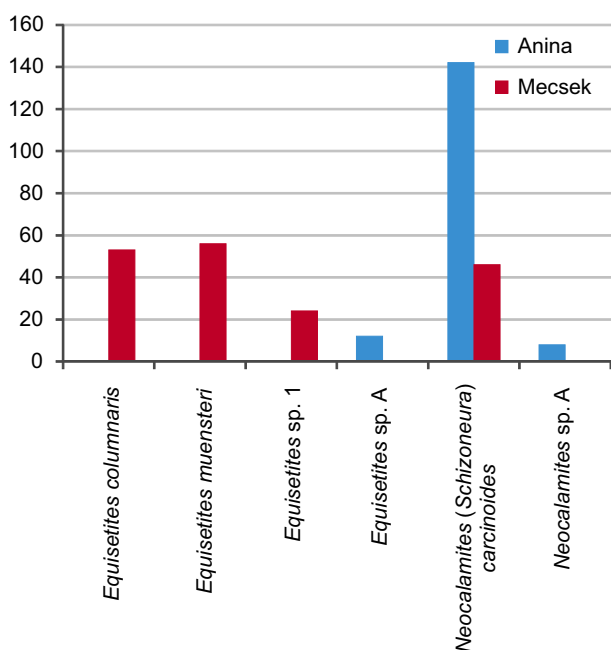


Fig. 3. Sphenophytes represented in Anina and Mecsek

Nilssonia sp. A (60% of cycads) is most numerous in Anina; *Nilssonia obtusa* represents 69.9% of the cycad material in Mecsek. *Bjuvia simplex* is more frequent in Mecsek (10.8%); *Bjuvia* sp. accounts for only 2 specimens in Anina.

Bennettitaleans (Fig. 7) are not very frequent in either locality. Although in Anina (Popa 2001b, 2014) they are quite diverse (6 genera, 12 species), their number is not high (8.4% of the whole flora). In Mecsek there are only 2 genera (one of them, *Pterophyllum*, shared with Anina) and 2 species (both different from Anina), together forming 1.2% of the entire material (Fig. 2A, B).

Ginkgophytes (Fig. 8) are less diverse: 4 genera and 7 species were recorded in Anina (Popa & Van Konijnenburg-van Cittert 2006), 7.8% of the whole flora, while in Mecsek (Barbacka 2002) there were 3 genera and 6 species noted (10%, Fig. 2A, B). All genera from Mecsek are also present in Anina, but there are no common species. In Anina the commonest is *Sphenobaiera* sp. A (50% of ginkgophytes); in Mecsek the most numerous is *Ginkgoites marginatus* (37.3%).

Conifers (Fig. 9) in Anina were represented by 9 genera and 15 species, 11.7% of the whole flora (Fig. 2A, B). In Mecsek, 4 genera and 5 species were recognised (Barbacka 2011, Thévenard & Barbacka 2000), 16.6% of the total number of specimens. In Anina the most common conifer was *Podozamites paucinervis* (26.5%), and in Mecsek *Elatocladus* sp. (67.7%).

One specimen of *Czekanowskia rigida* indicates the presence of the order Czekanowskiales

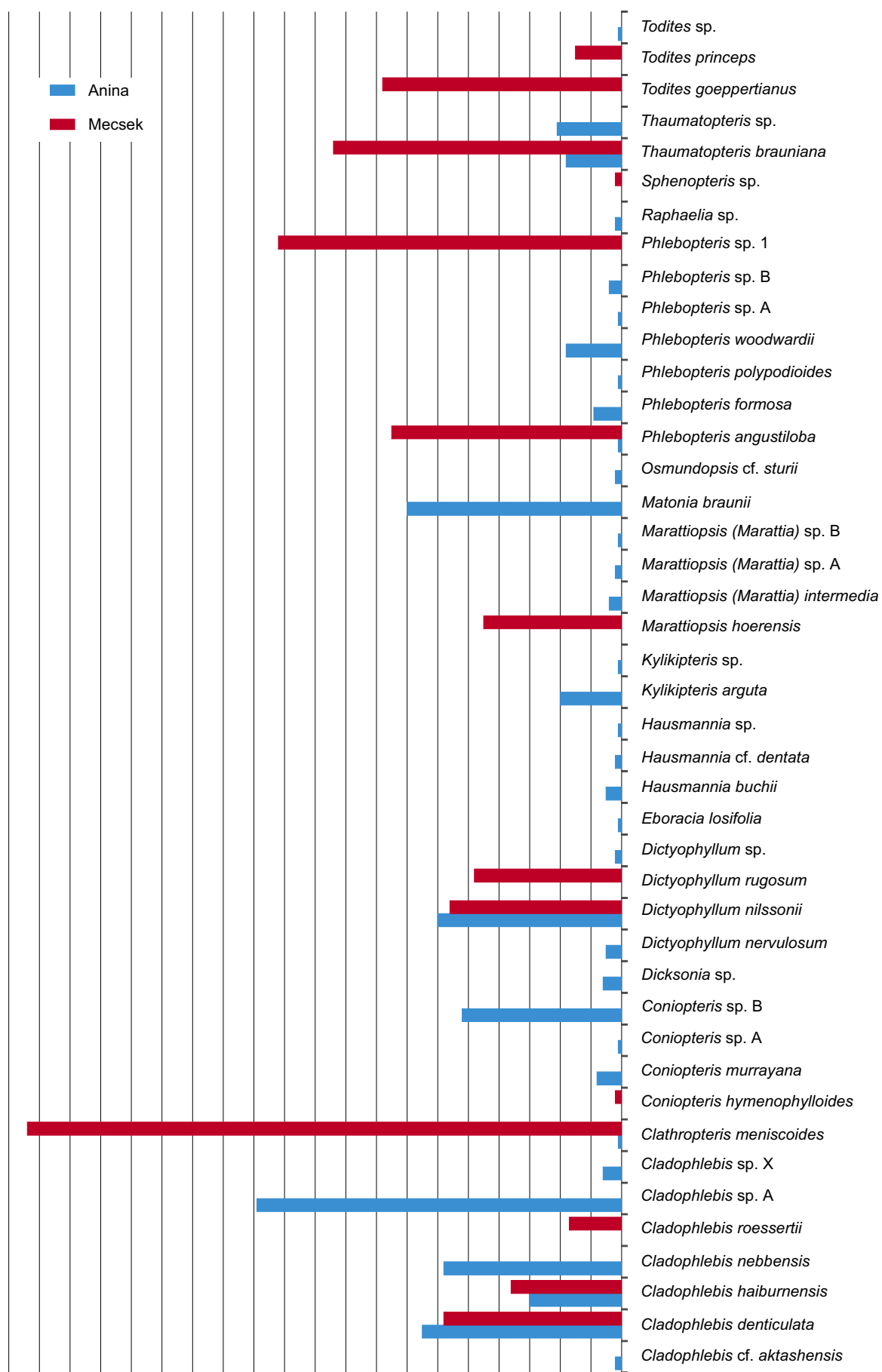


Fig. 4. Ferns represented in Anina and Mecsek

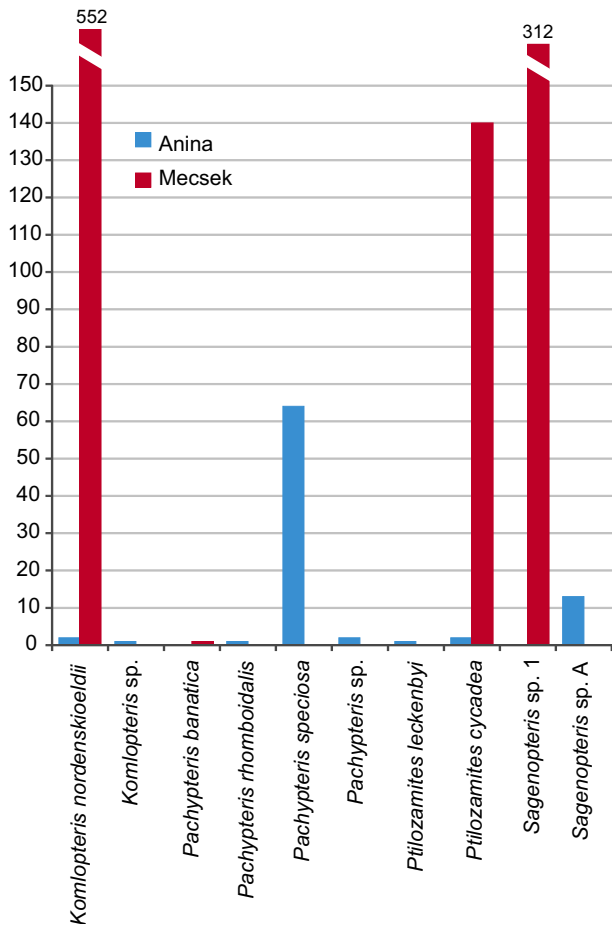


Fig. 5. Seed ferns represented in Anina and Mecsek

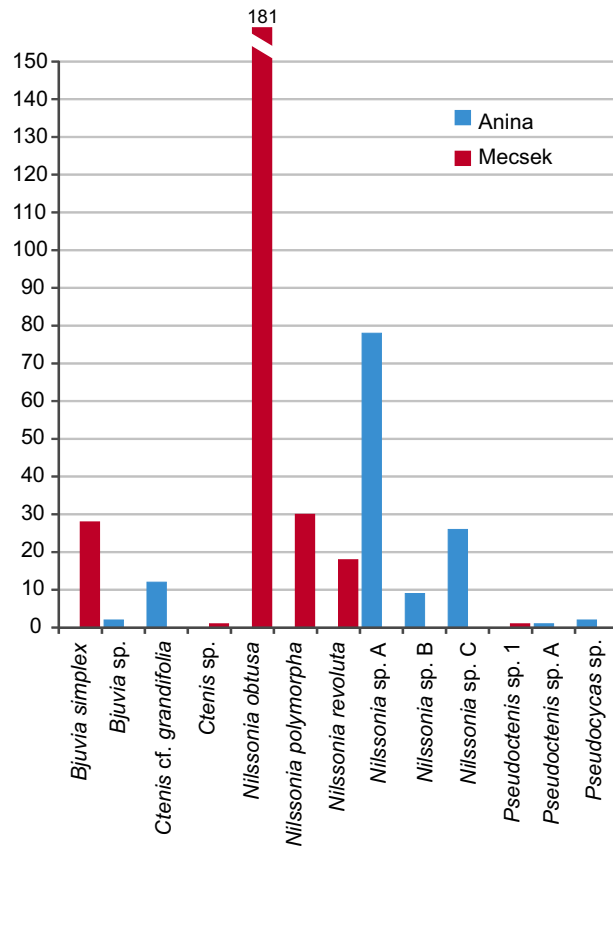


Fig. 6. Cycads represented in Anina and Mecsek

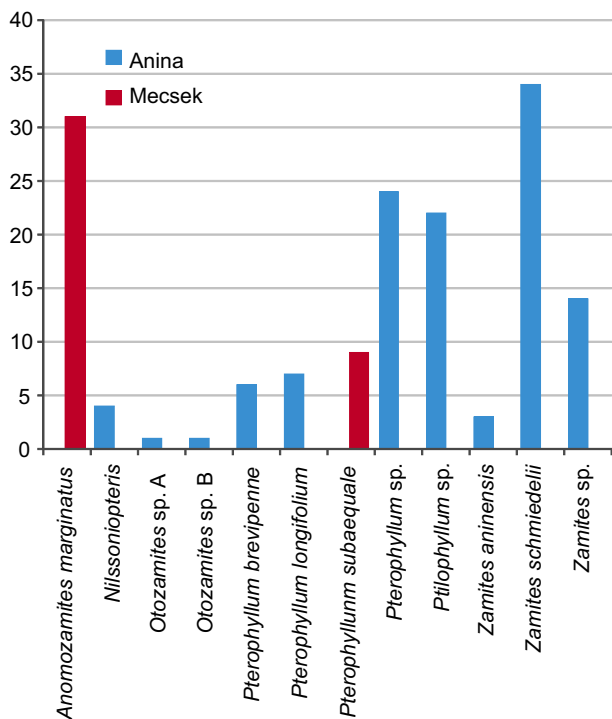


Fig. 7. Bennettitaleans represented in Anina and Mecsek

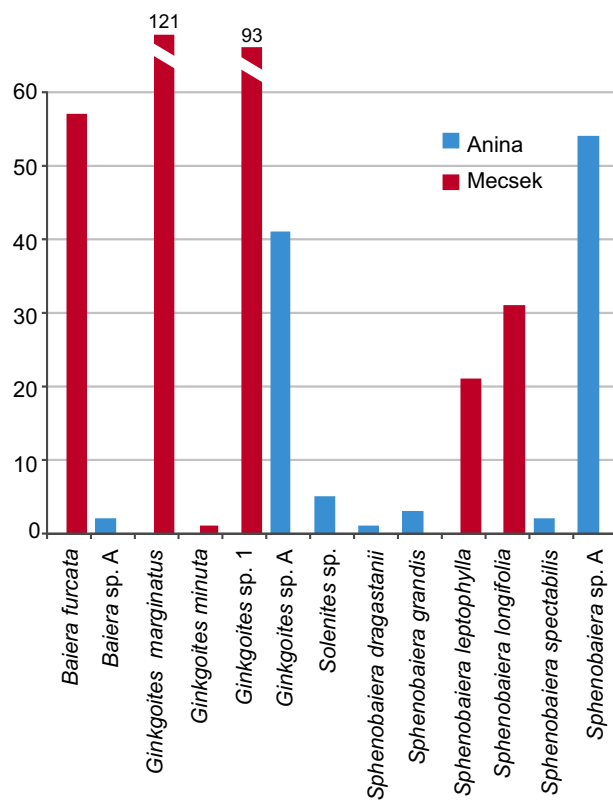


Fig. 8. Ginkgoites represented in Anina and Mecsek

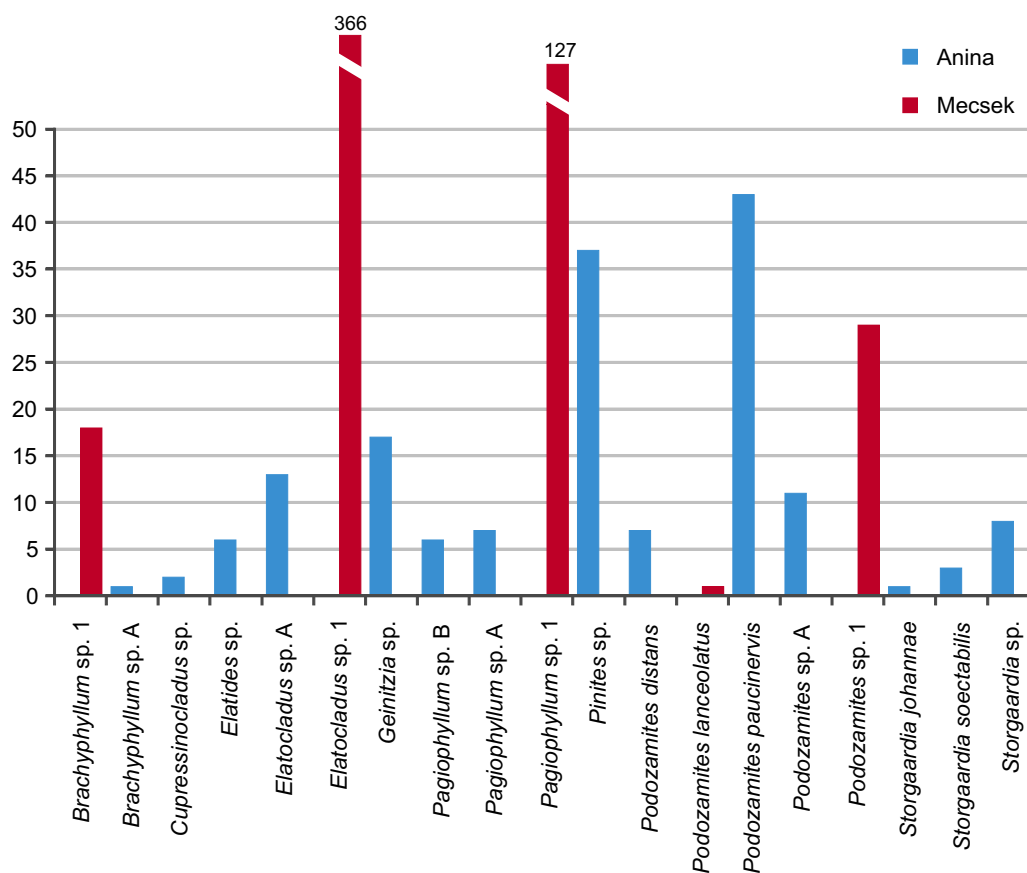


Fig. 9. Conifers represented in Anina and Mecsek

in Anina (Popa 1992), which in Mecsek is absent. *Desmiophyllum* sp. was not observed in Anina but was noted in Mecsek as *Gymnospermae incertae sedis*, forming 2.3% of the entire flora.

GLM OF COMMON SPECIES

Seven of the 9 taxa common to the two localities were used in the analyses; 2 species (*Phlebopteris angustiloba* and *Clathropteris meniscoides*) were represented by only one specimen in Anina.

In Mecsek these 7 species were distributed in four groups (according to ecogroup as defined by Barbacka 2011): *Komlopteris*, *Sagenopteris*, *Ptilozamites*, and *Thaumatopteris*. Among them, only *Ptilozamites cycadea* and *Komlopteris nordenskiöldii*, found in the common *Komlopteris* group, showed statistically significant ($p \leq 0.05$) GLM responses (Table 2). *Komlopteris nordenskiöldii* accounted for 67.0–74.06% of the total variance and *P. cycadea* only 1.3% along PCO axis 1. The species within the remaining groups had statistically non-significant ($p > 0.05$) GLM responses which accounted for <0.1–2% of the total variance.

In Anina the 7 shared species were distributed in two groups: *Podozamites* and *Schizoneura* (Table 3). In the *Podozamites* group, *Cladophlebis haiburnensis* accounted for 17.0–17.1% of the variance along both PCO axes; along PCO axis 2, *Neocalamites (Schizoneura) carcinoides* accounted for 27% and *Dictyophyllum nilssonii* for 83.7% of the total variance. These species correspond to the *Ptilozamites* and *Thaumatopteris* ecogroups from Mecsek.

In the *Schizoneura* group only *Cladophlebis denticulata* had a statistically significant GLM response, accounting for 13.5% and 3.6% of the total variance along PCO axes 1 and 2 respectively. This species corresponds to the *Sagenopteris* group from Mecsek.

The remaining species (5 from Mecsek, 3 from Anina), though concordant in their response profiles, did not have statistically significant responses ($p < 0.05$, Figs 10, 11).

DISCUSSION

Cluster analyses of European Jurassic floras (Barbacka et al. 2014) produced groupings of localities with similar taxonomical compositions. The analyses were done on both genus

Table 2. Site A. Stepwise selection of response variables (species in groups discriminated in PCA analysis) along PCO axes 1 and 2, according to logistic regression model with logit link function and binomial response assumed. R^2 – coefficient of determination, F – a partial F test, p – I-type error

Response	R^2 [%]	F	p	R^2 [%]	F	p
Ordination		PCO 1			PCO 2	
				<i>Komlopteris</i> Group		
<i>Ptilozamites cycadea</i>	1.3	5.2	0.0223	<0.1	<1	0.63854
<i>Komlopteris nordenskiöldii</i>	74.6	791.9	<0.00001	67.0	710.4	<0.00001
				<i>Sagenopteris</i> Group		
<i>Cladophlebis denticulata</i>	1.2	<1	0.26045	<0.1	<1	0.74282
				<i>Ptilozamites</i> Group		
<i>Cladophlebis haiburnensis</i>	2.0	<1	0.30447	<0.1	<1	0.88202
<i>Dictyophyllum nilssonii</i>	0.1	<1	0.60082	<0.1	<1	0.78458
				<i>Thaumatopteris</i> Group		
<i>Thaumatopteris brauniana</i>	0.2	<1	0.57259	1.0	4.0	0.04661
<i>Neocalamites (Schizoneura) carcinoides</i>	0.1	<1	0.72214	0.7	1.4	0.23091

Table 3. Site B. Stepwise selection of response variables (species in groups discriminated in PCA analysis) along PCO axes 1 and 2, according to logistic regression model with logit link function and binomial response assumed. R^2 – coefficient of determination, F – a partial F test, p – I-type error

Response	R^2 [%]	F	p	R^2 [%]	F	p
Axis		PCO 1			PCO 2	
				Group 1		
<i>Cladophlebis haiburnensis</i>	17.1	12.2	0.00056	17.0	12.2	0.00057
<i>Dictyophyllum nilssonii</i>	73.9	125.5	<0.00001	83.7	142.1	<0.00001
<i>Neocalamites (Schizoneura) carcinoides</i>	0.1	<1	0.64899	27.0	42.1	<0.00001
<i>Thaumatopteris brauniana</i>	0.5	<1	0.51394	1.1	1.0	0.31199
				Group 2		
<i>Cladophlebis denticulata</i>	13.5	24.7	<0.00001	3.6	6.60	0.01054
<i>Komlopteris nordenskiöldii</i>	1.0	<1	0.71227	1.3	<1	0.68558
<i>Ptilozamites cycadea</i>	1.4	<1	0.73992	0.8	<1	0.66795

and species levels. The genus cluster tended to separate delta and fluvial ecosystems from coastal/lagoonal ones. This suggests that the delta and fluvial environments maintained similar conditions for the corresponding genera.

Within the genus cluster, Mecsek is on the same branch with Scoresby (Lower Jurassic, Greenland), while Reșița (Anina, with some smaller localities from the same unit), together with Yorkshire (the Middle Jurassic, UK), occupies the neighbouring final branches. In the species cluster, however, the two localities are far from each other, on different primary branches.

When genera are considered without quantitative data, the two localities seem similar, but a quantitative comparison at species level shows 8 species in common; apart from them, only the ferns *Cladophlebis denticulata* and *Dictyophyllum nilssonii* occur in relatively equal numbers, and the amounts of the remaining species are very disproportionate. Both of these fern species are widespread, especially *Cladophlebis denticulata* (Barbacka et al. 2014).

Bearing in mind that 25 genera but only 9 species are shared between the two localities, we stress that for the present case the much more accurate palaeoenvironment indicator is species-level taxonomy rather than genus-level taxonomy.

A statistical study of the flora from Mecsek (Barbacka 2011) showed that species of the same genera had their maximum occurrence in different ecogroups. This suggests that fine differences in conditions led to differentiation of species composition, while the same genera appeared in similar types of ecosystems. Our comparison of the ecogroups distinguished in Anina and Mecsek, and of their taxonomical structure, supports this supposition. In both localities, ecogroups of pioneer type are present, consisting exclusively of ferns (in Anina the *Schizoneura* group, in Mecsek the *Thaumatopteris* group), but in Anina there are , species that do not occur in Mecsek: *Cladophlebis nebbensis*, *Dictyophyllum nervulosum*, *Coniopteris murrayana*, and *Matonia braunii*. Their environmental preferences tend towards open

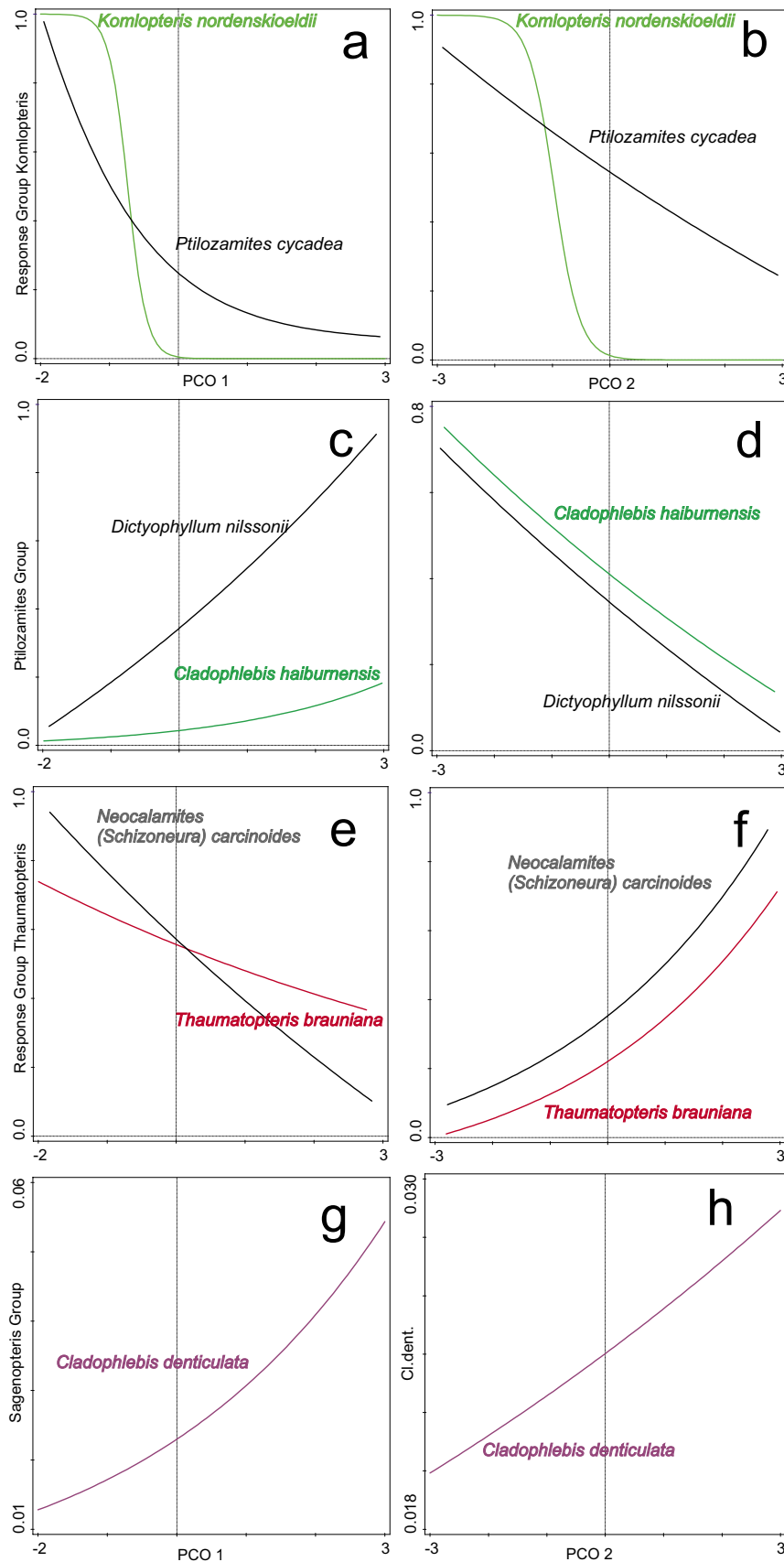


Fig. 10. Logistic regressions of GLM for response variables (species) in four palaeoecological species groups along PCO 1 and PCO 2. **a** – *Komlopteris*, *Ptilozamites* – PCO 1; **b** – *Komlopteris*, *Ptilozamites* – PCO 2; **c** – *Dictyophyllum*, *Cladophlebis* – PCO 1; **d** – *Dictyophyllum*, *Cladophlebis* – PCO 2; **e** – *Neocalamites (Schizoneura)*, *Thaumatopteris* – PCO 1; **f** – *Neocalamites*, *Thaumatopteris* – PCO 2; **g** – *Cladophlebis denticulata* – PCO 1; **h** – *Cladophlebis denticulata* – PCO 2. The same pattern of response (decreasing or increasing) in a group of species means their ecological profile are similar. Differences in shapes of response curves depend on the distribution and abundance of species along a putative environmental gradient

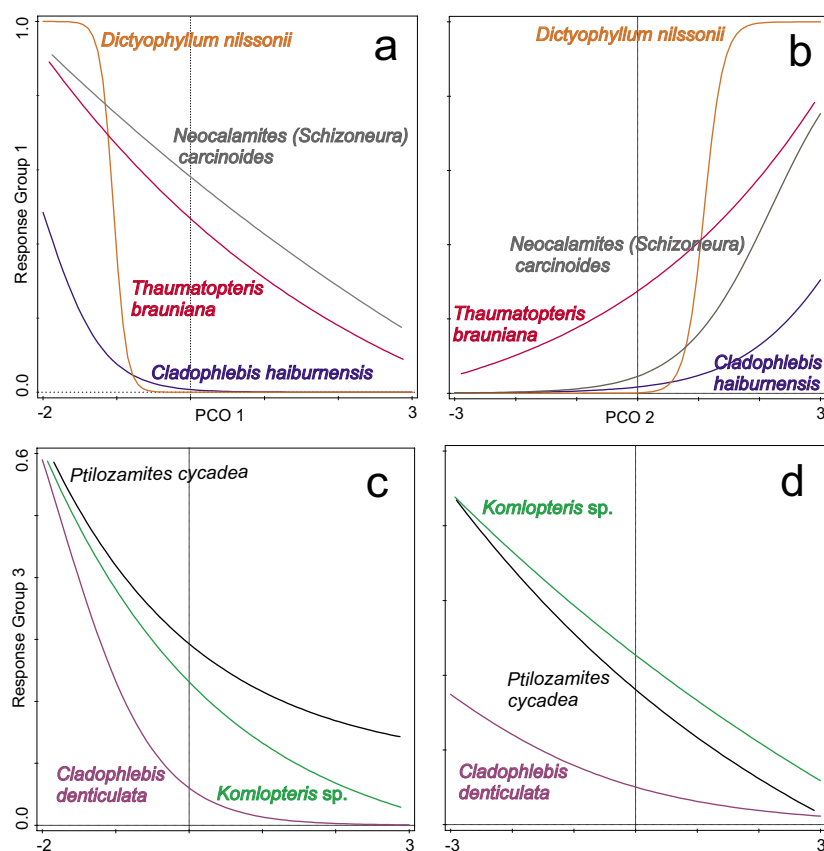


Fig. 11. Logistic regressions of GLM for response variables (species) in four palaeoecological species groups along PCO 1 and PCO 2. **a** – Species Group 1 – PCO 1; **b** – Species Group 1 – PCO 2; **c** – Species Group 3 – PCO 1; **d** – Species Group 3 – PCO 2. The same pattern of response (decreasing or increasing) in a group of species means their ecological profile are similar. Differences in shapes of response curves depend on the distribution and abundance of species along a putative environmental gradient

plains or clearings, more typical of periodically inundated flood plains, while the pioneer assemblage from Mecsek was interpreted as growing mainly on easily eroded channel banks or floating islands (Barbacka 2011).

The moderately wet and weakly disturbed habitat represented in Mecsek by the *Ptilozamites* group corresponds to the moderately wet and disturbed habitat in Anina occupied by the *Podozamites* group, but the taxonomical composition of these habitats differs completely between the two localities. The differences probably are due to differences in the climatic conditions of these localities, related mainly to mean annual temperature. This ecogroup in Mecsek was connected with calcareous river cliffs with at least periodic semi-arid conditions and high insolation (Barbacka 2011). In Anina, the Reșița Basin is bordered by crystalline heights of the Sebes-Lotru metamorphic series and partly by Variscan (Upper Carboniferous – Lower Permian) promontories, contributing to different edaphic conditions.

In Anina during the Sinemurian, the increase of temperature and relatively high

moisture provided favourable conditions for swampy habitats to develop. This increase of temperature is comparable to the Hettangian interval in Mecsek, when mires also occurred but with slightly different phytocoenoses (Popa 2000b, 2009, Popa & Van Konijnenburg-van Cittert 2006). The plant assemblages from this stage are interpreted as characteristic for the closing drier phase of mire development. Probably this phase does not correspond fully with the Hettangian swamp phase from Mecsek. This phase was manifested in taxa assemblages which in Mecsek are connected to both habitats: swampy (*Komlopteris nordenskiöldii* or possibly *Baiera* sp.; in Anina they occur in trace amounts) and slightly drier (*Cladophlebis denticulata* or *Ginkgoites* sp., *Ptilozamites cycadea*). The remaining taxa from this ecogroup (e.g. *Zamites schmiedelii*, *Geinitzia* sp., *Ptilophyllum* sp.) occur in Anina and correspond well with the described conditions.

Relatively dry, moderately warm and undisturbed levees in Anina were occupied mainly by *Nilssonia* sp. This habitat in Mecsek would correspond to the *Sagenopteris* ecogroup with

Nilssonia obtusa, *N. revoluta*, *Cladophlebis denticulata*, *Marattiopsis hoerensis*, *Sagenopteris* sp., and *Anomozamites marginatus*. In Mecsek this type of environment was inhabited by a very developed plant succession. The monospecific character of the Anina site might be due to edaphic factors.

In Mecsek the monospecific group of *Ginkgoites marginatus* is explained possibly by expansive growth, and by analogy with *Ginkgo biloba* with its moderate allelopathy (Nam et al. 1997, Barbacka 2011).

The occurrence of species shared by the localities makes it possible to compare their joint responses. While in Mecsek they represent four ecogroups of putatively different ecological profiles, in Anina they are distributed in two groups (*Schizoneura* and *Zamites* groups).

The *Schizoneura* group in Anina encompasses the *Ptilozamites* and *Thaumatopteris* ecogroups from Mecsek, both well supported statistically. This could be an effect of having similar ecological niches in Anina. The *Zamites* group also encompasses two ecogroups previously recognised in Mecsek, namely *Sagenopteris* and *Komlopteris* (Barbacka 2011). Of these, only *Sagenopteris* was supported statistically. This could mean that the *Komlopteris* group was in fact ecologically distinct from *Sagenopteris* and that its joint presence here was a chance event. This fully corresponds with our knowledge of the plant assemblages from Mecsek. *Komlopteris nordenskiöldii* was in fact a species of very wide tolerance, and its co-occurrence with taxa from different ecogroups is highly probable (Barbacka 2011).

For the statistical analyses we assumed that common GLM responses along the ordination axes denote species with the same ecological requirements. Figures 10 and 11 show the curves for shared species with the same requirements. For example, the *Komlopteris* Group (Fig. 10a, b) differs from the *Thaumatopteris* Group (Fig. 10e, f) by the difference in response along axis 2. An exact comparison is hampered by probable differences in the main environmental factors influencing the plant composition of the two localities. According to a previous interpretation (Barbacka 2011), two factors were decisive in Mecsek: the humidity gradient according to axis 1 of the plot, and the disturbance gradient according to axis 2. In Anina, humidity and disturbance were together on axis 1, and a third factor was

linked with axis 2: temperature, which did not play a role in Mecsek (in the literature, no mention of temperature change in Mecsek during the Hettangian and Sinemurian). Hence, the types of GLM responses in particular species groups are not represented by the same ecological groups. For example, *Neocalamites* (*Schizoneura*) *carcinoides* and *Thaumatopteris brauniana* reacted differently in Mecsek and in the opposite direction to *Dictyophyllum nilssonii* and *Cladophlebis haiburnensis*, while in Anina they show the same preferences. Similarly, *Cladophlebis denticulata*, which in Mecsek was opposite to *Komlopteris nordenskiöldii* and *Ptilozamites cycadea*, had the same tendencies as the latter two in Anina. Only *Komlopteris nordenskiöldii* and *Ptilozamites cycadea* showed similar trends for both localities and were similarly opposite to *Dictyophyllum nilssonii* and *Cladophlebis haiburnensis*.

For Mecsek, *Thaumatopteris brauniana* and *Neocalamites* (*Schizoneura*) *carcinoides* were interpreted as connected to the pioneer assemblage of a highly disturbed and moderately wet habitat. According to a previous analysis, *Dictyophyllum nilssonii* and *Cladophlebis haiburnensis* were in one putative ecogroup with *Thaumatopteris brauniana* (Barbacka 2011). In another analysis employing PCA ordination, pairs of species differed in their preferences in the Mecsek locality. In Anina they formed one ecogroup (*Schizoneura*) in PCA (Barbacka et al. in prep). It was associated with high moisture/high disturbance and relatively low temperature, interpreted as a flood plain association.

Ptilozamites cycadea and *Komlopteris nordenskiöldii* are numerous in Mecsek; the latter is the most numerous fossil in this locality, but in Anina they are very rare (*Zamites* group). Only *Cladophlebis denticulata* from this ecogroup occurs in almost equal amounts at both sites. In Mecsek, *Ptilozamites cycadea* indicates moderately wet and undisturbed habitat, while *Komlopteris nordenskiöldii* prefers wetter, swampy places. However, the latter's wide tolerance enables it to appear in different ecogroups. In Mecsek, *Cladophlebis denticulata* was associated with rather drier and moderately disturbed conditions; in Anina it belongs to an association of swampy habitat but in the last, not so wet, closing stage of mire development (Barbacka 2011, Popa 1998, 2014). Since both *K. nordenskiöldii* and

Ptilozamites cycadea are very rare in Anina, their real preferences in this area cannot be unambiguously interpreted.

Species from the *Zamites* group in Anina first appeared in the Sinemurian after an increase of temperature, when the climate became warmer and slightly more humid than during the Hettangian (Popa 1998, 2000b, 2009). In general, the species common to both localities show similar trends, occupying corresponding habitats within two similar though not identical environments.

CONCLUSIONS

1. The environments of Mecsek (delta – limnic – lagoonal) and Anina (fluvial) generally differ but have similar topographic elements such as river/channel banks, flooded or swampy areas, lakes, river levees, or marine barriers (Mecsek).

2. Although the generic composition of the floras seems similar, fine differences in local conditions led to significant quantitative and qualitative dissimilarity of species composition.

3. The eight common species do not occur in strictly corresponding ecogroups but their environmental preferences are similar. All of them show quite wide tolerance.

4. Differences in climate (mean annual temperature, humidity) and edaphic conditions (different provenance areas differing in petrographic composition) explain the differences between floras at species level under similar genus-level composition.

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