

1 **A quantitative approach for identifying plant ecogroups in the Romanian Early Jurassic**
2 **terrestrial vegetation**

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22

23 **Abstract**

24 Community level ecology is considered to support significantly the recognition of the
25 ecological status of plant taxa and the identification of plant ecogroups, thus it generally

26 provides extended data sets on the spatial and temporal changes of ecological factors. Since
27 research based exclusively on plant structure and their supposed adaptation to the
28 environment is now considered inadequate, statistical methods can be used. Assuming that co-
29 occurrence of plant fossils on a single hand specimen in the case of autochthonous or
30 paraautochthonous floras is the result of their growth in the same phytocenosis, quantitative
31 ecological analysis on Mesozoic materials would yield significant insights. In this paper
32 statistical and multivariate quantitative analyses of Early Jurassic plant fossil records from the
33 Steierdorf Formation in Anina (South Carpathians, Romania) are presented. Four
34 palaeoecological groups of taxa were distinguished by Principal Component Analysis (PCA)
35 and interpreted as plant assemblages of various palaeobiotopes associated with the
36 sedimentary facies of the enclosing formation. A group of samples was analyzed using the
37 Principal Coordinate (PCO) method and the statistical significance ($p \leq 0.05$) of individual binary responses of taxa along the first two PCO ordination axes
38 was tested by General Linear Model (GLM). They revealed putative palaeoecological
39 gradients: axis 1 – disturbance caused by water level fluctuations, axis 2 – temperature,
40 corresponding with the already assumed environmental and climatic change at the
41 Hettangian/Sinemurian boundary. Multivariate analyses enabled the identification of
42 palaeoecological groups and thus inferring palaeogeographical conditions based on Mesozoic
43 materials.

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46 Keywords: Palaeoecology; plant ecogroups; Principle Component Analysis; multivariate
47 analysis; Jurassic; Romania

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51 **1 Introduction**

52 Apart from the classical interpretation (Thorn, 2001; van Konijnenburg-van Cittert,
53 2002; Wang, 2002; Gordenko, 2008; Kustatscher et al., 2010) of fossil plant structures as a
54 reaction to changing palaeoecological conditions, co-occurrence of taxa in the case of
55 autochthonous or paraautochthonous floras can be very informative.

56 Numerous palaeoecological reconstructions were based on different proxies like
57 evidence of fossil palynomorphs (e. g. Abbink, 1998; Abbink et al., 2001, 2004; Bonis et al.,
58 2010) and megaflora (e. g. Spicer & Hill, 1979; Spicer & Parrish, 1990; Spicer et al., 1992;
59 Thorn, 2001; Spicer et al., 2002; Bercovici et al., 2009; Barbacka, 2011). Also complex
60 geological data can be used like palaeosols (Sheldon & Tabor, 2009; Botfalvai et al., 2016),
61 peat forming environments (Phillips & Peppers, 1984; DiMichele & Phillips, 1994; Gastaldo
62 et al., 2004; Hámor-Vidó, 2004; DiMichele et al., 2007), complex sedimentology,
63 palaeozoological and palaeobotanical data (DiMichele & Beall, 1990; DiMichele et al., 2008;
64 Falcon-Lang et al., 2009; Libertin et al., 2009; Barbacka et al., 2015). Furthermore, analytical
65 methods were used in palaeovegetational reconstructions e.g. basic statistical methods like co-
66 occurrences, diversity (McElwain et al., 2007; Pálffy & Kocsis, 2014) and multivariate
67 methods (Spicer & Hill, 1979; Barbacka, 2011; Barbacka et al., 2015).

68 Assuming that co-occurrence of plant fossils on the same hand specimen is the result
69 of their growth in the same phytocenosis (Wing & DiMichele, 1995) plant ecogroups can be
70 distinguished, and the range of environmental tolerance of individual taxa can be determined.
71 Thus, with a verified multivariate statistical method at hand, the quantitative community level
72 ecological approach could have an impact on the interpretation of the response of plants to
73 environmental changes in the past, and this has been the subject of increased interest recently
74 (DiMichele & Gastaldo, 2008).

75 The first such study focusing on Early Jurassic flora from the Mecsek Mountains,
76 South Hungary dominated by paralic environments, identified five ecogroups containing taxa
77 that changed in accordance with moisture and disturbance (Barbacka, 2011). In the current
78 study, we test a multivariate statistical method for Romanian Early Jurassic deposits in Anina
79 in order to extend the palaeoecological hypothesis and improve the effectiveness of the
80 approach. Besides other methods PCA was performed in the community level ecological
81 study of Spicer & Hill (1979) related to the Middle Jurassic of Yorkshire, however, they
82 sampled the investigated plant bed quantitatively.

83 The ecological gradients in Anina linked with the ordination axes were inferred
84 indirectly and based on plant morphology/ecological profile as well as sedimentary data
85 (Popa, 1998). Thus, they were heuristic working hypotheses that were supported by plant joint
86 occurrences and proxy data to support conclusions.

87

88 **2 Geological and palaeobotanical background**

89 The Reșița Basin, also known in the geological literature as the Reșița-Moldova Nouă
90 sedimentary zone, is a major sedimentary basin of the Getic Nappe in the South Carpathians,
91 Romania (Fig. 1). It is composed of Palaeozoic (Upper Carboniferous and Lower Permian)
92 and Mesozoic terrestrial formations (Lower Jurassic, Hettangian – Sinemurian in age) which
93 yield fossil flora and fauna (Popa, 2009). The Lower Jurassic terrestrial sequence of this basin
94 is assigned to the Steierdorf Formation (Bucur, 1991, 1997; Popa & Kędzior, 2008; Kędzior
95 & Popa, 2013), a coal bearing formation which includes eight coal seams exploited through
96 extensive underground mining works since 1792 in Anina (formerly known as Steierdorf),
97 Caraș-Severin County (Fig. 2). The coal mining complex was one of the largest in Europe, as
98 it encompassed several coalfields (Anina North, Zona Nouă, Brădet, Uteriș, Kübeck, etc.), a
99 high number of pits (Pits I, II, IV, David, etc.), blind pits (underground shafts), and open cast

100 mines (quarries) such as Ponor, Colonia Cehă and Hildegard (Popa, 2009). This coal mining
101 complex was closed in 2006, and it included at the time 42 km of active galleries reaching a
102 depth of 1300 m, making Anina one of the deepest coal mines in Europe at the time. A high
103 number of sterile dumps fill various valleys in the Anina area, and they are also very rich in
104 fossils. Today, Ponor and Colonia Cehă Quarries and Pit I (Schlucht) in Anina are considered
105 Sites of Special Scientific Interest (SSSIs) for their rich and well preserved fossil content.

106 The extensive underground coal mining works in Anina followed the local,
107 complicated geological structures represented by various synclines (in Brădet Coalfield) and
108 anticlines (in Anina and Zona Nouă Coalfields) through directional and transversal galleries,
109 blind pits and extraction chambers. Such extensive works permitted unique sampling of fossil
110 plants, with three dimensional control of stratigraphic and lateral distribution of the
111 palaeoflora within the Steierdorf Formation. Such exceptional conditions for precise fossil
112 sampling enabled one of the authors (MEP) to build a large collection of fossil plants during
113 16 years of continuous geological activity in the mining complex of Anina area, between
114 1990 and 2006 (Popa, 2009, 2011). These fossils were collected along all types of
115 underground works in Anina area, especially from extraction chambers and from directional
116 galleries, within the roof shales, from the base of coal seams, as well as from all stratigraphic
117 intervals between coal seams. Detailed fossil sampling, sedimentological and petrographical
118 studies in underground mining works made it possible to clarify the precise stratigraphic
119 succession of the Hettangian – Sinemurian palaeoflora of the Steierdorf Formation (Popa,
120 1992, 2000b) and enabled the identification of the stratigraphic level of samples collected
121 from sterile dumps or of hand specimens studied in historical collections curated in Bucharest,
122 Cluj-Napoca, Timișoara, Budapest, Vienna, etc. (Popa, 1992, 2000b, 2009; Popa & Meller,
123 2009). To the underground fossils was added material collected from open-cast mines, road
124 cuts, natural outcrops and sterile dumps (Popa, 2009) in Anina area.

125 As shown in Fig. 2 the Steierdorf Formation includes two members, the Dealul
126 Budinic Member, Lower to Middle Hettangian in age, and the Valea Tereziei Member, Upper
127 Hettangian – Sinemurian in age (Bucur, 1991, 1997; Popa & Kędzior, 2008). The Steierdorf
128 Formation unconformably overlays the Lower Permian Ciudanovița Formation (red beds),
129 and it is conformably overlain by the Pliensbachian – Middle Toarcian Uteriș Formation
130 (black shales). The Dealul Budinic Member is a coarser, basal sedimentary unit dominated by
131 conglomerates and micro-conglomerates, indicating alluvial fan depositional environments.
132 The Valea Tereziei Member is dominated by sandstones, clays, fireclays and coal seams,
133 indicating fluvial, flood plain, crevasse splay and lacustrine depositional environments,
134 with mire (coal generating swamp or marsh) episodes. The conglomerates and micro-
135 conglomerates of the Valea Tereziei Member are included in channel fill successions, as parts
136 of a large braided river complex (Kędzior & Popa, 2013). The eight coal seams are composed
137 of bituminous, coking coals, with thicknesses reaching 2.5 m in the western flank of Anina
138 Anticline. The Steierdorf Formation was generated in a mountainous depression, bordered by
139 metamorphosed promontories of the Sebeș-Lotru Group or of Upper Palaeozoic formations.
140 Between coal seams 4 and 5, a well developed lateral fireclay seam was identified,
141 representing a large lacustrine system and a lithological marker which also coincides with the
142 Hettangian – Sinemurian boundary within the Valea Tereziei Member (Popa, 2000a, b, Popa
143 2009; Kędzior & Popa, 2013).

144 The Steierdorf Formation includes two separate floral assemblages, the Hettangian
145 *Thaumatopteris brauniana* range Zone and the Sinemurian *Nilssonia cf. orientalis* acme Zone
146 (Popa, 2000a, b; Popa & van Konijnenburg-van Cittert, 2006), each with characteristic taxa.
147 The boundary between the two floras as well as the Hettangian – Sinemurian boundary is
148 represented by the fireclay seam.

149 During the Hettangian – Sinemurian interval, the Reșița Basin was located on the
150 northern frame of the Tethys Ocean, on the southern part of the boreal (Eurosianian)
151 continental mass (Pieńkowski et al., 2009). The climate was subtropical and monsoonal
152 proved by pseudo-annual rings observed in silicified woods from Holbav (near Brașov,
153 central Romania). During the Hettangian and Sinemurian times below and above the fireclay
154 level, the climate was subtropical, wet, monsoonal. The occurrence of *Pterophyllum*,
155 *Phoenicopsis*, as well as sporadic *Sphenobaiera* and *Czekanowskia* (higher latitude groups,
156 Siberian influences) suggest not very hot climate in the Hettangian. The presence of
157 bennettitaleans like *Zamites* or *Ptilophyllum*, and other warm indicators imply hotter climate
158 in the Sinemurian above the fireclay level up to the top of coal seam 8.

159 The palaeoflora of the Steierdorf Formation in Anina is a key European Early Jurassic
160 flora. It is typically compressive and coal generating (coal flora), and also highly diverse (the
161 most representative taxa are shown in Fig. 3 a-e) and well preserved (Popa, 1998, 2000a, b,
162 2005, 2009, 2014; Popa & van Konijnenburg-van Cittert, 2006), making Anina, together with
163 its palaeozoological ichnospecies, a plant fossil Lagerstätte locality considering both diversity
164 and conservation (Popa, 1997, 2014). The palaeoflora of Anina was studied since the 19th
165 Century (Foetterle, 1850; Ettingshausen, 1852; Andrae, 1855), followed by modern studies of
166 Semaka (1962), Givulescu (1998), Popa (1992, 1998, 2000a, b, 2009, 2014), Popa & van
167 Konijnenburg-van Cittert (2006) and Popa & Meller (2009). It includes bryophytes
168 (Hepaticae), pteridophytes (lycopsids, sphenopsids, filicopsids) and gymnosperms
169 (pteridospermopsids, cycadaleans, bennettitaleans, ginkgopsids, coniferopsids), well
170 preserved with abundant cuticles and *in situ* spores (Popa, 2000a, 2009; Popa & van
171 Konijnenburg-van Cittert, 1999). The microflora of the fireclay seam of the Valea Tereziei
172 Member was studied by Antonescu (1973), and it records Early and Middle Jurassic
173 palynomorphs.

174 The Hettangian – Sinemurian ecogroups of the Steierdorf Formation were
175 characterized by Popa (1997, 1998, 2000a, 2009, 2014) in relation to their depositional
176 environments, with their age and with their coal generating character. These ecogroups were
177 identified in the field at various stratigraphic levels, in roof shales or within sandstone and
178 mudstone levels between coal seams, corresponding to mire, mire borders, levees and flood
179 plain areas. The following assemblages were identified:

180 a. mire (marsh) dwellers, such as the sphenopsid *Neocalamites (Schizoneura) carcinoides*,
181 which has a long stratigraphic range, crossing the Hettangian – Sinemurian boundary due to
182 the persistence of its aquatic habitat and to the preservation of its ecological niche;

183 b. dwellers of mire borders in flooded areas, such as the pteridosperm *Pachypteris speciosa* or
184 the conifer *Podozamites paucinervis*, often competing for their habitat, as this competition
185 was reflected in the thickness of the coal seams generated (Popa, 1997b);

186 c. dry land dwellers, in areas of flood plains or levees, represented by ferns (*Cladophlebis*
187 *denticulata*, *Dictyophyllum nilssonii*), cycadaleans (*Nilssonia* cf. *orientalis*, *N. undulata*),
188 bennettitaleans (*Zamites schmiedelii*, *Z. andraeanus*) and ginkgoaleans (*Ginkgoites*
189 *marginatus*).

190 d. possible upland flora representatives, such as the ginkgoal *Phoenicopsis potonieii*, that was
191 considered a Siberian influence indicator by Givulescu (1998).

192 Regarding the coal generating processes, Popa (1997b, 1998, 2000a, 2014) considered mire
193 dwellers such as sphenopsids and mire border dwellers such as pteridosperms and conifers as
194 primary (main) coal generators. Drier land area dwellers (floodplains, levees) such as the
195 association of ferns, bennettitaleans and ginkgoaleans were considered as secondary coal
196 generators. This association enters the mire area in its final stages, while the marsh was being
197 filled with sediments, therefore contributing to coal genesis and being continuously recorded
198 in the roof shales, especially in the roof shales of coal seams 5-8 (Sinemurian) in Anina. The

199 ternary assemblage of a fern, a bennettitalean and a ginkgoalean as secondary coal generators
200 is considered by Popa (2014) as a rule for coal genesis and having a much wider occurrence
201 in Europe and Greenland during Mesozoic times, although these taxa were not strictly mire or
202 mire border dwellers but only opportunistic species.

203

204 **3 Material and methods**

205 *3.1 Sampling*

206 The studied material includes samples with at least two species occurring on the same surface
207 of hand specimens. The material belongs to the M. E. Popa Collection, curated at the
208 University of Bucharest, Faculty of Geology and Geophysics, Laboratory of Palaeontology
209 and at the Geological Museum (Geological Institute of Romania) in Bucharest as well as to
210 various historical collections (A. Semaka, I. Z. Barbu Collections) curated at the same
211 institutions. Except for hand specimens of the M. E. Popa Collection, all other samples were
212 collected previously from sterile dumps by several scientists. The stratigraphic position of the
213 samples, however, was identified later, following a detailed sampling in the underground
214 mining works in Anina revealing plant species ranges (Popa, 2000b). The samples considered
215 for this study have a precise stratigraphic position within the Steierdorf Formation, their
216 petrographical and sedimentological context is also well characterized (Popa, 2011), and they
217 yield at least two plant fossils co-occurring on the same surface of the hand specimen. Most
218 of these samples are associated with palaeosols level and with roof shales, indicating the in
219 situ (autochthonous) character of the leaf material. The size of samples varies between 100-
220 500 mm in length and width, while the plant fragments such as fronds or large leaves have
221 large sizes on large hand specimens, indicating also an autochthonous character of the fossils.
222 Samples yielding less than two species (singletons) are far more numerous in the Popa
223 Collection or in other collections surveyed for this study.

224 3.2 *Statistic approach*

225 Altogether, 670 records of 68 taxa distributed in 263 samples were coded as a
226 presence-absence data in a binary 0-1 matrix. They represent a set of a total of 1384 samples
227 gathered in the study area and each of them contains at least two taxa, and each taxon
228 occurred repeatedly at least five times. The joint occurrence of taxa in samples was revealed
229 by a Principal Component Analysis (PCA). PCA is a multivariate method, applied on
230 numerous and variable palynological and palaeontological data (Peyrot et al., 2011). It
231 reduces multi-dimensional hyperspace of species and samples by projection onto three or less
232 principal axes, i.e. the major components of variation (Spicer & Hill, 1979). The projection of
233 samples was calculated with Principal Coordinate (PCO) analysis on a dissimilarity matrix 1 -
234 squared Jaccard binary distances. The goal of PCO is to preserve the distance relationships
235 among objects in a space of reduced dimensionality as well as possible. PCO yielded better
236 polarity for the samples, than PCA, because the arch effect was removed effectively (Alroy,
237 2015). A logistic regression model, General Linear Model (GLM) that uses the logit link
238 (Agresti, 2007) was applied to relate the binary response of variables (species) to a predictor,
239 i.e. sample loadings along PCO Axes 1 and 2. The binomial distribution of response variables
240 was assumed. A forward (stepwise) selection started from a null model was applied to find
241 best fit model for particular species based on F-test criterion and corresponding I-type error
242 based on 499 runs. The significance level of the tests was established at $p \leq 0.05$. Calculations
243 were performed with a CANOCO 5 software (ter Braak & Šmilauer, 2012).

244

245 **4 Results**

246 *4.1 Statistical multivariate analysis*

247 The first two axes of PCA species ordination explained 18.69% of the total variance,
248 i.e. 11.15% and 7.54%, respectively (Fig. 4a). The first two axes of PCO sample ordination

249 explained 12.84% of the total variance, i.e. 7.34% and 5.50%, respectively (Fig. 4b). PCA
250 analysis showed four groups of species (Fig. 4a); one group is represented by one taxon,
251 *Nilssonia* sp.1. These groups show specific patterns of distribution along the first two PCO
252 axes (Fig. 4b).

253 *Nilssonia undulata* (Group 4) occupies the extreme left side of the diagram (Fig. 4c).
254 Group 1 is termed *Podozamites* group and composed of 3 species. It is best characterized by
255 *Podozamites paucinervis* (Figs. 4d, 5a) with statistically significant response in GLM analysis
256 ($p \leq 0.05$) only along PCO 1 (Table 1). Group 2 is termed *Dictyophyllum* group, consisting of
257 7 species. *Dictyophyllum nilssonii* and *Cladophlebis nebbensis* can be found in the upper right
258 segment of the diagram, with high positive loadings in PCO 2 (Figs. 4e, 5c, d). *Dictyophyllum*
259 *nervulosum* and *Neocalamites (Schizoneura) carcinoides* are statistically insignificant ($p >$
260 0.05) along PCO 1. *Coniopteris murrayana* and *Matonia braunii* are also sub-dominant along
261 PCO 2. Group 3 is termed *Ginkgoites* group and has high negative loadings in PCO 2. It is
262 characterized by the presence of *Cladophlebis denticulata* and *Zamites schmiedelii* (Figs. 4f,
263 5e, f). *Baiera* sp. is marginally significant along PCO 2 ($p = 0.072$), *Ptilophyllum* sp. along
264 PCO 1 and *Geinitzia* sp. has insignificant response along PCO 2 ($p = 0.159$ and 0.676 ,
265 respectively) (Table 1).

266 Based on the statistical analyses, the ecologically most important taxon (mainly
267 responsible for the total variance) is *Nilssonia undulata*, shifting to the left side of PCO 1
268 (Table 1, Fig. 4b-c). Species in Group 1 are placed between *Nilssonia undulata* (Group 4),
269 and Group 2 and 3, along PCO 1 (Fig. 4b), suggesting the ecological transitory character of
270 Group 1. Groups 2 and 3 form the end-points of PCO 2 (Fig. 4a, e-f), and can be interpreted
271 as having a different ecological profile in relation to *Nilssonia undulata* and Group 1. Here
272 the most representative species ($0.0001 < p < 0.05016$), placed in the opposite ends of a
273 hypothetical ecological gradient, are distributed along PCO 2, i.e. *Schizoneura carcinoides* -

274 *Dictyophyllum nervulosum* vs. *Ptilophyllum* sp. and the marginally significant ($p=0.0072$)
275 *Baiera* sp. (Table 1).

276 The remote position of *Nilssonia undulata* may be a sign of its specific character. It
277 could have formed pure stands at the edge of a hypothetical ecological gradient imposed on
278 PCO 1. The ecological counterbalance for Group 1 and *Nilssonia undulata* formed Groups 2
279 and 3, otherwise they are well discriminated along PCO 2 (Fig. 4b, e-f).

280 GLMs visualize trends in response functions of particular groups and show the
281 statistical significance of particular taxa (Fig. 5b-f, Table 1). *Nilssonia undulata* seems to
282 have a well defined ecological extension. It is separated the most and placed in a remote
283 position along PCO 1 (Figs. 4c, 5b). It had a statistically significant response only along PCO
284 1 (Table 1), meaning that it could be influenced solely by the ecological gradient imposed on
285 this axis.

286 Group 1 is plotted in a central position, hence it could be interpreted as having a wider,
287 and unspecific ecological profile. However, it could be linked with an ecological gradient
288 represented by the axis PCO 1 but towards the centre (Figs. 4d, 5a). In Group 2 *Neocalamites*
289 (*Schizoneura*) *carcinoides* and *Dictyophyllum nervulosum* yielded statistically insignificant (p
290 > 0.10) responses along PCO 1 and statistically significant along PCO 2, while *Coniopteris*
291 *murrayana* and *Matonia braunii* gave significant responses only along PCO 1 (Table 1, Fig.
292 5c, d). In Group 3 *Ptilophyllum* sp. was statistically (marginally) significant only along PCO
293 2, and *Geinitzia* sp. along PCO 1 (Table 1, Fig. 5e-f).

294 The numerical analysis of palaeobotanical data shows the special ecological position of
295 *Nilssonia undulata* (Group 4). Ecological profile of Group 1 is less characteristic, and can be
296 associated probably to the same ecological factor as that of *Nilssonia undulata*, however, in
297 less extreme position. Group 2 and Group 3 occupy the opposite location along PCO 2
298 representing a given ecological gradient. In Group 2 the species of the most limited ecological

299 tolerance, *Dictyophyllum nervulosum* and *Neocalamites (Schizoneura) carcinoides* fitted
300 exclusively to the hypothetical ecological gradient imposed on PCO 2. They yielded
301 significant GLM responses ($p \leq 0.05$) only along PCO 2. *Matonia braunii* and *Coniopteris*
302 *murrayana* responded significantly ($p < 0.009$) only along PCO 1. They may represent an
303 ecological subset of the group. The remaining species of the group: *Cladophlebis*
304 *haiburnensis*, *C. nebbensis*, and *Dictyophyllum nilssonii* yielded significant responses
305 ($0.00001 < p < 0.00057$) both along PCO 1 and PCO 2. This could be the sign of their wide
306 ecological tolerance. In Group 3 *Cladophlebis denticulata*, *Ginkgoites* sp. and *Zamites*
307 *schmiedelii* gave significant ($0.0001 < p < 0.013$) responses along both axes, while *Geinitzia*
308 sp. and *Ptilophyllum* sp. gave significant responses along PCO 1, and PCO 2 respectively
309 (Table 1).

310

311 4.2 Palaeoecological interpretation

312 Ecogroups and their place within ecosystems as well as the mechanisms of their
313 dynamics were discussed in detail by DiMichele & Gastaldo (2008).

314 In the present study based on the known environmental requirements of particular taxa
315 (leaf morphology, cuticle structure, analogies with corresponding localities) as well as on
316 sedimentary proxies for Anina (Table 2) PCO axis 1 can be interpreted as disturbance
317 gradient caused by water level fluctuations and axis 2 as temperature gradient which
318 corresponds exactly with the Hettangian/Sinemurian transition. In fact, the assemblages are
319 influenced by several environmental factors but they can be floristically overlapped
320 (DiMichele et al., 2004). According to these gradients *Nilssonia undulata* (the upper left
321 quarter of the plot, towards lower values of disturbance) can be supposed to prefer relatively
322 undisturbed, not influenced by water stressed conditions corresponding well with the

323 requirements of *N. obtusa* and *N. revoluta* from the Mecsek Mts. in Hungary (Barbacka,
324 2011).

325 Group 1 can be characterized by affected by none of the factors mentioned a rather
326 wide ecological tolerance affected by none of the factors mentioned above. This group is very
327 characteristic in the shale topping coal seams 1-4 (late Hettangian) in Anina. The composition
328 of the taxa of the group suggests a more advanced succession (mainly trees). Their habitat
329 was less disturbed by floods. Considering palaeoenvironments at Anina, the area of this
330 ecogroup may correspond with levees representing the highest relief in the basin characterized
331 probably by tunnel-forests. One of the group members, *Podozamites paucinervis*, could also
332 have lived in the swamp or very close to it, however, on a levee.

333 In Group 2 almost all taxa belong to ferns and some are horsetails (Table 1). Horsetails
334 are represented mostly by *Schizoneura*, which is the least significant along PCO 1, suggesting
335 its independency from water level fluctuations, however, they prefer somewhat lower
336 temperature. Since the upper right quarter of the plot refers to lower temperature and higher
337 disturbance, this assemblage could be considered as a typical floodplain association.
338 influenced by seasonal changes, thus it may be inferred as a colonizer vegetation. A scattered
339 occurrence in the central and left part of the diagram could have reflected its ability to inhabit
340 the sites in a type of habitat of *Podozamites paucinervis* (Table 2).

341 Group 3 is a developed succession with ginkgoaleans and bennettitaleans and a small
342 number of ferns. It is opportunistic to all other groups along the gradient of temperature and
343 placed in the lower part of the plot reflecting higher temperature and higher disturbance.
344 Plants of this group are secondary coal generators and their fossils are constantly found in the
345 topping shale of coal seams 6, 7 and 8 (Sinemurian in age) although they are not hydrophilous
346 ones. This group may be associated with the swampy areas in its last, closing moments, when

347 they were being filled with sediments, occupying the new habitat. It is a ubiquitous, ternary
348 association in Anina (Popa, 2014).

349 The investigated plants could dwell in the following circumstances: a) in the water (in
350 lakes, in mires) along the shores, not in the middle of these water bodies where only
351 planktonic algae occurred, such as *Botryococcus*; b) on the shores of stagnant water bodies,
352 on dry land; c) in dry habitats characterized by seasonal floods washing periodically the
353 whole area. Geomorphologically considering the facies model relevant for Anina Basin a)
354 represents active channels, oxbow lakes of the meander belts and stagnant lakes of the
355 floodplain, b) represents levees and crevasse splays and c) represents the floodplain basins.

356

357 **5 Discussion**

358 Plant ecogroups and their connection with different gradients of environmental
359 changes were studied using various statistical methods. DiMichelle et al. (2007) used Non-
360 metric multidimensional scaling (NMDS) to find similarities and differences among
361 predetermined groups of species in Pennsylvanian forests. The main grouping factor was
362 facies (landward and seaward communities). Detrended correspondence analysis (DCA)
363 based ecogroup models related to the Jurassic of Mecsek Mts. (Hungary) were established by
364 Barbacka (2011) for delta environments. The main factors influencing the composition of the
365 obtained five ecogroups were disturbance and moisture. The same statistical method (DCA)
366 was applied to estimate long-term climatic change at the Tr/J boundary (McElwain et al.,
367 2007). The Jurassic Yorkshire Hasty Bank locality was sampled layer by layer and the
368 quadrat data was analyzed using PCA and Correspondence analysis (CA) (Spicer & Hill,
369 1979). Group differentiation was based on lithological data.

370 Ecological plant grouping was the subject of several other studies, as well. Wing et al.
371 (2012) used DCA, CCA and NMDS for determining plant assemblages and their

372 environmental preferences in Late Cretaceous wetlands. The major influencing factors in his
373 study were nutrient, stress and disturbance. Based on the sedimentary conditions and taxa co-
374 occurrences, wetter and drier conditions as well as substrate based succession stages were
375 distinguished in floodplain, wetland and partly marine sedimentary environments (Spicer et
376 al., 2002).

377 Usually, when ecological background factors can be interpreted water and disturbance
378 are decisive which is not surprising in wetland communities. Generally, wetland communities
379 are overrepresented because of taphonomic reasons (DiMichelle & Gastaldo, 2008). In this
380 study the temperature gradient was already known from different proxies (see chapter 2,
381 Geological and palaeobotanical background) and multivariate analyses indicated that this
382 factor really had high impact on ecogroup differentiation.

383 Ecogroups show no stable characters, they change in space and time and their
384 composition can also change according to competition between taxa (Di Michele & Gastaldo,
385 2008). Using statistical analyses we obtain a hypothetic model reflecting rather potential
386 composition of assemblages and their relation to local circumstances and not to strictly
387 determined units.

388 A statistical approach does not change general plant grouping on the basis of field
389 observations and known environmental requirements of certain taxa. However, this method
390 can provide new insights. Field experience enables broader interpretation of tendencies in
391 plant-environment relationships and makes possible preliminary assemblage reconstruction.
392 However, the multivariate approach can deal with high number of data or hardly detected, but
393 important information and refine the results, providing at the same time objective and
394 independent support.

395 There are some improvements regarding preliminary established ecogroups from
396 Anina. The temperature based ecogroups of Hettangian and Sinemurian are distinguished

397 clearly. Hettangian taxa (over axis 1 on Fig. 5) appear to represent a wider spectrum of
398 adaptation forming three ecogroups based on the tolerance for water table fluctuations, while
399 Sinemurian taxa form one group hardly influenced by disturbance. *Nilssonia undulata*, which
400 was interpreted as a dry land dweller, in areas of floodplains or levees, and associated with
401 ferns, based on the present study forms a separate group with stronger defined requirements
402 than assumed before. The ferns from the same ecogroup appeared to have opposite trends
403 being much more tolerant for disturbance. Although *Cladophlebis denticulata* and
404 *Dictyophyllum nilssonii* belong to similar habitats they show different temperature
405 preferences. Although *Neocalamites (Schizoneura) carcinoides*, was placed in the same
406 ecogroup as ferns, appears in extreme positions (a plant growing always in water).

407 This study helped also the classification of some taxa into defined ecogroups which
408 have not been classified yet. Thus their environmental preferences were identified as well.
409 The use of GLM illustrated well and supported the environmental trends of individual taxa
410 making them robust and reliable.

411 The disadvantage of the applied method is that it could not deal with singletons
412 (specimens with only one taxon), therefore some taxa could not be analyzed (e.g. some of the
413 analyzed ones co-occurred with others only during Hettangian (*Dictyophyllum nilssonii* and
414 *Neocalamites (Schizoneura) carcinoides*) or Sinemurian (*Cladophlebis denticulata*)).
415 Although such hand specimens with singletons were collected, often from underground
416 galleries and extraction chambers in which roof shale, coal beds or palaeosols were sampled
417 in difficult field conditions, they were not included in this statistical approach. In underground
418 conditions, in galleries the outcrop surfaces are only a few square metres and the surface of
419 the collected samples is generally rather small therefore singletons occur more often in such
420 samples. Although they were recorded from underground sites with their entire taxonomical

421 associations (Popa, 1992, 2000a, 2009) their transitional character was not indicated in the
422 plots.

423

424 **6 Conclusions**

425 The numerical analysis of palaeobotanical data presented here gives deeper insight
426 into the ecological context of the described ancient taxa. The joint distribution of species
427 along the orthogonal axes of PCA analysis enables the estimation of their putative ecological
428 profiles. The joint occurrence of a group of species in a group of samples (displayed along
429 PCO axes) indicates their similar environmental requirements. The mathematical
430 orthogonality (non-correlation) of the axes ensures no redundancy (independence) of the
431 inferred ecological gradients. Independent data, like morphological similarities, seen mostly
432 in the structure of macro- and micro-morphology (cuticle), can confirm the results of the
433 community level ecological approach.

434

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446 **References**

- 447 Alroy, J., 2015. A simple way to improve multivariate analyses of paleoecological data sets.
448 *Paleobiology* 41, 377–386.
- 449 Abbink, O., 1998. Palynological investigations in the Jurassic of the North Sea region. LPP
450 Contributions Series 8. LPP Foundation, Utrecht.
- 451 Abbink, O., Targarona J., Brinkhuis H., Visscher H., 2001. Late Jurassic to earliest
452 Cretaceous palaeoclimatic evolution of the southern North Sea. *Global and Planetary*
453 *Change* 30, 231–256.
- 454 Abbink, O., van Konijnenburg-van Cittert, J.H.A., Visscher, H., 2004. A sporomorph ecogroup
455 model of the Northwest European Jurassic Lower Cretaceous: concepts and framework.
456 *Geologie en Mijnbouw* 83, 17–38.
- 457 Antonescu, E., 1973. Quelques donnees sur la palynologie du Lias sous facies de Gresten de
458 Roumanie, 3rd International Palynological Conference. Moscow, 13–17.
- 459 Agresti, A., 2007. *An Introduction to Categorical Data Analysis*. John Wiley & Sons Inc.,
460 Hoboken, New Jersey.
- 461 Andrae, C., 1855. Beitrage zur kenntniss der fossilen Flora Siebenburgens und des Banates.
462 *Abhandlungen der kaiserlich-koniglich geologischen Reichsanstalt* III, 1–48.
- 463 Barbacka, M., 2011. Biodiversity and the reconstruction of Early Jurassic flora from the
464 Mecsek Mountains (Southern Hungary). *Acta Palaeobotanica* 51 (2), 127–179.
- 465 Barbacka, M., Popa, M., Mitka, J., Bodor, E., Pacyna, G., 2015: Relationships between
466 ecosystems and plant assemblages as responses to environmental conditions in the
467 Lower Jurassic of Hungary and Romania. *Acta Palaeobotanica*, 55 (1), 3–17.
- 468 Bercovici, A., Diez, J.B., Broutin, J., Bourquin, S., Linol, B., Villanueva-Amadoz, E.U.,
469 López-Gómez, J., Durand, M., 2009. A palaeoenvironmental analysis of Permian

470 sediments in Minorca (Balearic Islands, Spain) with new palynological and megafloral
471 data. *Rev. Palaeobot. Palynol.*, 158, 14–28.

472 Bonis, N.R., van Konijnenburg-van Cittert, J.H.A., Kürschner, W.M., 2010. Changing CO₂
473 conditions during the end-Triassic inferred from stomatal frequency analysis on
474 *Lepidopteris ottonis* (Goeppert) Schimper and *Ginkgoites taeniatus* (Braun) Harris.
475 *Palaeogeogr. Palaeoclimat. Palaeoecol.*, 295, 146–161.

476 Botfalvai, G., Haas, J., Bodor, E.R., Mindszenty, A., Ósi, A., 2016. Facies architecture and
477 palaeoenvironmental implications of the Upper Cretaceous (Santonian) Csehánya
478 Formation at the Iharkút vertebrate locality (Bakony Mts., Northwestern Hungary).
479 *Palaeogeography Palaeoclimatology Palaeoecology*, 441, 659–678.

480 Bucur, I.I., 1991. Proposition pour une nomenclature formelle des depots paleozoiques et
481 mesozoiques de la zone de Reșița-Moldova Nouă (Carpathes Meridionales, Roumanie).
482 *Studia Universitatis Babeș-Bolyai, Geologie XXXVI*, 3–14.

483 Bucur, I.I., 1997. Formațiunile mesozoice din zona Reșița-Moldova Nouă. Cluj-Napoca:
484 Presa Universitară Clujeană. DiMichele, W.A., Beal, S.B., 1990. Flora, fauna,
485 paleoecology of the Brazil Formation of Indiana. *Rocks Miner.*, 65, 244–250.

486 DiMichele, W.A., Beall, B.S., 1990. Flora, fauna and paleoecology of the Brazil Formation of
487 Indiana. *Rocks & Minerals*, 65, 244–250.

488 DiMichele, W.A., Gastaldo, R.A., 2008. Plant paleoecology in deep time. *Ann. Missouri Bot.*
489 *Gard.*, 95, 144–198.

490 DiMichele, W.A., Phillips, T.L., 1994. Paleobotanical and paleoecological constraints on
491 models of peat formation in the Late Carboniferous of Euramerica *Palaeogeogr.*
492 *Palaeoclimat. Palaeoecol.*, 106, 39–90.

493 DiMichele, W.A., Behrensmeyer, A. K., Olszewski, T. D., Labandeira, C. C., Pandolfi, J. M.,
494 Wing S. L., Bobe, R., 2004. Long-term stasis in ecological assemblages: Evidence from
495 the fossil record. *Ann. Rev. Ecol. Evol. Syst.*, 35, 285–322.

496 DiMichele, W.A., Falcon-Lang, H.J., Nelson, W.J., Elrick, S.D., Ames, P.R., 2007.
497 Ecological gradients within a Pennsylvanian mire forest. *Geology* 35, 415–418.

498 DiMichele, W.A., Kerp, H., Tabor, N.J., Looy, C.V., 2008. The so-called “Paleophytic–
499 Mesophytic” transition in equatorial Pangea – Multiple biomes and vegetational
500 tracking of climate change through geological time. *Palaeogeogr. Palaeoclimat.*
501 *Palaeoecol.* 268, 152–163.

502 Ettingshausen, C., 1852. *Über die fossilen Pflanzen von Steierdorf in Banat.* Jahrbuch der
503 Kaiserlich–Königlichen Geologische Reichsanstalt.

504 Falcon-Lang, H.J., Nelson, W.J., Elrick, S., Looy, C.V., Ames, P.R., DiMichele, W.A., 2009.
505 Incised channel fills containing conifers indicate that seasonally dry vegetation
506 dominated Pennsylvanian tropical lowlands. *Geology* 37(10), 923–926.

507 Foetterle, F., 1850. Verzeichniss der an die K.K. geologische Reichsanstalt gelangten
508 Eisendungen von Mineralien, Petrefacten Gebirgsarten u.s.w. Jahrbuch der Kaiserlich-
509 Königlichen Geologische Reichsanstalt 1, 350–358.

510 Francis, J.E., Ashworth, A., Cantrill, D.J., Crame, J.A., Howe, J., Stephens, R., Tosolini, A.-
511 M., Thorn, V., 2008. 100 Million Years of Antarctic Climate Evolution: Evidence from
512 Fossil Plants: 19–28. In: Cooper A.K., Barrett P.J., Stagg H., Storey B., Stump E., Wise
513 W., and the 10th ISAES editorial team (eds), *Antarctica: A Keystone in a Changing*
514 *World. Proceedings of the 10th International Symposium on Antarctic Earth Sciences.*
515 Washington, DC: The National Academies Press.

516 Gastaldo, R.A., Stevanovic-Walls, I., Ware, W.N., Greb, S.F., 2004. Community
517 heterogeneity of Early Pennsylvanian peat mires. *Geology* 32, 693–696.

- 518 Givulescu, R., 1998. Flora fosilă a Jurasicului inferior de la Anina, 1 ed. București: Editura
519 Academiei Române.
- 520 Gordenko, N.V., 2008. Middle Jurassic Flora of the Peski Locality (Moscow Region).
521 Systematics, Paleoecology, and Phytogeography. *Paleont. Jour.*, 42 (12): 1285–1382.
- 522 Hámor-Vidó, M., 2004. Coal facies studies in Hungary: a historical review. *International*
523 *Journal of Coal Geology* 58, 91–97.
- 524 Harris, T.M., 1937. The fossil flora of Scoresby Sound East Greenland. Part 5: Stratigraphic
525 relations of the plant bed. *Medd. Grønland*, 112(2): 1–114.
- 526 Harris, T.M., 1961. The Yorkshire Jurassic Flora. I: Thallophyta – Pteridophyta. Trustees of
527 the British Museum, London.
- 528 Harris, T.M., 1964. The Yorkshire Jurassic Flora. II: Caytoniales, Cycadales &
529 Pteridosperms. Trustees of the British Museum (Natural History), London.
- 530 Harris, T.M., 1969. The Yorkshire Jurassic Flora. III. Bennettitales. Trustees of the British
531 Museum (Natural History), London.
- 532 Harris, T.M., Millington, W., 1974. The Yorkshire Jurassic flora IV. Ginkgoales. Trustees of
533 the British Museum (Natural History), London.
- 534 Hesselbo, S.P., Morgans-Bell, H.S., McElwain, J.J., Rees, P.McA., Robinson, S.A., Ross,
535 C.E., 2003. Carbon-cycle perturbation in the Middle Jurassic and accompanying
536 changes in the terrestrial paleoenvironment. *The Journal of Geology* 111, 259–27.
- 537 Kędzior, A., Popa, M.E., 2013. Sedimentology of the Early Jurassic terrestrial Steierdorf
538 Formation in Anina, Colonia Cehă Quarry, South Carpathians, Romania. *Acta*
539 *Geologica Polonica* 63, 175–199.
- 540 van Konijnenburg-van Cittert, J.H.A., van der Burgh, J., 1996. Review of the Kimmeridgian
541 flora of Sutherland, Scotland, with reference to the ecology and in situ pollen and
542 spores. *Proceedings of the Geologists' Association* 107, 97–105.

543 van Konijnenburg-van Cittert, J.H.A., 2002. Ecology of some Late Triassic to Early
544 Cretaceous ferns in Eurasia. *Rev. Palaeobot. Palynol.*, 119, 113–124.

545 Kustatscher, E., van Konijnenburg-van Cittert, J.H.A., Roghi, G., 2010. Macrofloras and
546 palynomorphs as possible proxies for palaeoclimatic and palaeological studies: A case
547 study from the Pelsonian (Middle Triassic) of Kuhwiesenkopf/Monte Pra della Vacca
548 (Olang Dolomites, N-Italy). *Palaeogeography Palaeoclimatology Palaeoecology* 290,
549 71–80.

550 Libertin, M., Dašková, J., Opluštil, S., Bek, J., Edress, N., 2009. A Palaeoecological model
551 for a vegetated early Westphalian intramontane valley (Intra- Sudetic basin, Czech
552 Republic). *Rev. Palaeobot. Palynol.*, 155, 175–203.

553 McElwain, J.C., Popa, M.E., Hesselbo, S.P., Haworth, M., Surlyk, F., 2007. Macroecological
554 responses of terrestrial vegetation to climatic and atmospheric change across the
555 Triassic/Jurassic boundary in East Greenland. *Paleobiology* 33, 547–573.

556 Pálfy, J., Kocsis, Á.T., 2014. Volcanism of the Central Atlantic magmatic province as the
557 trigger of environmental and biotic changes around the Triassic-Jurassic boundary. The
558 Geological Society of America, Special Paper 505, 245–261.

559 Peyrot, D., Barosso-Barcenilla, F., Barrón, E., Comas-Rengifo, M.J. 2011.
560 Palaeoenvironmental analysis of Cenomanian–Turonian dinocyst assemblages from the
561 Castilian Platform (Northern-Central Spain). *Cretaceous Research* 32, 504–526.

562 Phillips, T.L., Peppers, R.A., 1984. Changing patterns of Pennsylvanian coal-swamp
563 vegetation and implications of climatic control on coal occurrence. *Int. J. Coal Geol.* 3,
564 205–255.

565 Pieńkowski, G., Popa, M.E., Kędzior A., 2009. Early Jurassic sauropod footprints of the
566 Southern Carpathians, Romania: palaeobiological and palaeogeographical significance.
567 *Geological Quarterly* 53, 461–470.

- 568 Popa, M.E., 1992. The Early Liassic of Anina: New Paleobotanical Aspects. *Documenta*
569 *Naturae* 1-3, 1-9.
- 570 Popa, M.E., 1997a. Liassic ferns from the Steierdorf Formation, Anina, Romania, 4th
571 European Palaeobotanical and Palynological Conference. Heerlen: Mededelingen
572 Nederlands Instituut voor Toegepaste Geowetenschappen TNO, 139-148.
- 573 Popa, M.E., 1997b. Crystospermale pteridosperms in the Liassic continental deposits of
574 Romania. *Acta Palaeontologica Romaniae*, 1, 81–87.
- 575 Popa, M.E., 1998. The Liassic continental flora of Romania: Systematics, Stratigraphy and
576 Paleocology. *Acta Botanica Horti Bucurestensis* 1, 177–184.
- 577 Popa, M.E., 2000a. Early Jurassic Land Flora of the Getic Nappe. PhD thesis, Faculty of
578 Geology and Geophysics, Bucharest
- 579 Popa, M.E., 2000b. Aspects of Romanian Early Jurassic palaeobotany and palynology. Part
580 III. Phytostratigraphy of the Getic Nappe. *Acta Palaeontologica Romaniae* 2, 377–386.
- 581 Popa, M.E., 2005. Aspects of Romanian Early Jurassic Palaeobotany and Palynology. Part VI.
582 Anina, an exceptional locality. *Acta Palaeontologica Romaniae* 5, 375-378.
- 583 Popa, M.E., 2009. Late Palaeozoic and Early Mesozoic Continental Formations of the Reșița
584 Basin. Editura Universității din București, Bucharest
- 585 Popa, M.E., 2011. Field and laboratory techniques in plant compressions: an integrated
586 approach. *Acta Palaeontologica Romaniae* 7, 279-283.
- 587 Popa, M.E., 2014. Early Jurassic bennettitalean reproductive structures of Romania.
588 *Palaeobiodiversity and Palaeoenvironments* 94, 327–362.
- 589 Popa, M.E., Kędzior, A., 2008. High resolution paleobotany and sedimentology of the
590 Steierdorf Formation, Reșița Basin, in: Bucur, I.I., Filipescu, S. (Eds.), Annual scientific
591 session "Ion Popescu Voitești". Cluj-Napoca: Cluj University Press, 57-59.

- 592 Popa, M.E., van Konijnenburg-van Cittert, J.H.A., 1999. Aspects of Romanian Early Jurassic
593 palaeobotany and palynology. Part I. In situ spores from the Getic Nappe, Banat,
594 Romania. 5th EPPC, W. Szafer Institute of Botany, Krakow, 181–195.
- 595 Popa, M.E., van Konijnenburg-van Cittert, J.H.A., 2006. Aspects of Romanian Early - Middle
596 Jurassic palaeobotany and palynology. Part VII. Successions and floras. Progress in
597 Natural Sciences 16, 203–212.
- 598 Popa, M.E., Meller, B., 2009. Review of Jurassic plants from the Anina (Steierdorf) coal
599 mining area, South Carpathians, in the collections of the Geological Survey of Austria.
600 Jahrbuch der Geologischen Bundesanstalt, 149(4), 487–498.
- 601 Schweitzer, H.J., Van Konijnenburg-van Cittert, J.H.A., Van der Burgh, J., 1997. The Rhaeto-
602 Jurassic flora of Iran and Afganistan. 10. Bryophyta, Lycophyta, Sphenophyta.
603 Pterophyta – Eusporangiatae and Protoleptosporangiatae. Palaeontographica B 243 (4–
604 6), 103–192.
- 605 Semaka, A., 1962. Asupra Reticului de la Bigăr. Dări de Seamă ale Ședințelor Comitetului
606 Geologic, XLV: 173-176.
- 607 Sheldon, N.D., Tabor, N.J., 2009. Quantitative paleoenvironmental and paleoclimatic
608 reconstruction using paleosols. Earth Sci. Rev., 95(1–2): 1–52.
- 609 Spicer, R., Hill, C.R., 1979. Principal components and correspondence analyses of
610 quantitative data a Jurassic plant bed. Review of Palaeobotany and Palynology 28, 273–
611 299.
- 612 Spicer, R.A., Parrish J.T., 1990. Late Cretaceous-early Tertiary palaeoclimates of northern
613 high latitudes: a quantitative view. Journal of the Geological Society, London, 147, 329-
614 341.

- 615 Spicer, R.A., Parrish, J.T., Grant, P.R., 1992. Evolution of vegetation and coal-forming
616 environments in the Late Cretaceous of North Slope of Alaska, GSA Special Paper,
617 267, 177–192.
- 618 Spicer, R.A., Ahlberg, A., Herman, A.B., Kelley, S.P., Raikevich, M.I., Rees, P.M., 2002.
619 Palaeoenvironment and ecology of the Middle Cretaceous Grebenka Flora of
620 northeastern Asia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 184, 65–105.
- 621 ter Braak, C.J.F., Šmilauer, P., 2012. *Canoco Reference Manual and User's Guide. Software*
622 *for Ordination (version 5.0)*, Microcomputer Power, Ithaca, USA
- 623 Thorn, V., 2001. Vegetation communities of a high palaeolatitude Middle Jurassic forest in
624 New Zealand. *Palaeogeography Palaeoclimatology Palaeoecology* 168, 273–289.
- 625 Wang, Y., 2002. Fern ecological implications from the Lower Jurassic in Western Hubei,
626 China. *Rev. Palaeobot. Palynol.*, 119: 125–141.
- 627 Wing, S. L., DiMichele W.A., 1995. Conflict between local and global changes in plant
628 diversity through geological time. *Palaios* 10, 551–564.
- 629 Wing, S.L., Strömberg, C.A.E., Hickey, L.J., Tiver, F., Willis, B., Burnham, R.J.,
630 Behrensmeyer A.K. 2012. Floral and environmental gradients on a Late Cretaceous
631 landscape. *Ecological Monographs*, 82(1), 23–47.
- 632 Zhou Z.Y., 2009. Review: An overview of fossil Ginkgoales. *Palaeoworld* 18, 1–22.

633

634 **Figure captions**

635 **Fig. 1.** Location of Anina (Steierdorf) fossil Lagerstätte locality, Caraș-Severin County,
636 central area of the Reșița Basin, Getic Nappe, South Carpathians, Romania.

637 **Fig. 2.** Synthetic stratigraphic log of the Hettangian – Sinemurian Steierdorf Formation, with
638 its eight coal seams and main fossiliferous plant levels.

639 **Fig. 3.** Examples of fossil plant species of the Steierdorf Formation in Anina. a. *Zamites*
640 *schmiedelii* (Sternberg in Presl) Andrae 1855 (Bennettitales, Williamsoniaceae),
641 Sinemurian, leaf fragments IB29/Fn, I. Z. Barbu Collection; b. *Cladophlebis denticulata*
642 (Brongniart) Fontaine 1889 (Filicales, Incertae sedis), leaf fragment P41/C2/S6/14E/F1,
643 Hettangian, Ponor Quarry; c. *Dictyophyllum nilssonii* (Brongniart) Goeppert 1846
644 (Filicales, Dipteridaceae), leaf fragment P109/C1/1/F1, indicated in the figure with (1),
645 *Cladophlebis nebbensis* (Brongniart) Nathorst 1876 (Filicales, Incertae sedis), leaf
646 fragments P109/C1/1/Fn, indicated in the figure with (2), and *Cladophlebis* sp.,
647 indicated in the figure with (3), roof shale of the Coal seam no. 2, Zona Nouă Coalfield,
648 8th Underground Horizon, Gallery 442 South, Hettangian, M. E. Popa Collection.
649 Supplementary hand drawings of leaf fragments occurring on sample P109/C1/1 were
650 given by Popa (1997a); d. *Podozamites paucinervis* (Coniferales, Incertae sedis),
651 Hettangian, Ponor Quarry, leaf fragment P40/C2/22/Fn, M. E. Popa Collection; e.
652 *Nilssonia undulata* (Cycadales, Nilssoniaceae), Hettangian, Ponor Quarry, leaf fragment
653 P40/C2/22/Fn, M. E. Popa Collection. Hand specimens curated at the University of
654 Bucharest, Laboratory of Palaeontology and Museum of Geology (Geological Institute
655 of Romania). Collecting, labeling, recording and photographing methods detailed in
656 Popa (2011). All scale bars: 10 mm.

657 **Fig. 4 a** – Principal Component Analysis of species data (arrows), only species with
658 statistically significant responses (≤ 0.072) are marked; **b** - Biplot of Principal
659 Coordinate projection of the samples (circles) based on 1 – squared Jaccard binary
660 distances (dissimilarity) and four groups of species (marked with colours) distinguished;
661 **c** – *Nilssonia* sp1; **d** – Group 1 (*Pinites* sp., *Podozamites paucinervis*, *Sphenobaiera*
662 sp.); **e** – Group 2 (*Cladophlebis haiburnensis*, *Cladophlebis nebbensis*, *Coniopteris*
663 *murrayana*, *Dictyophyllum nervulosum*, *Dictyophyllum nilssonii*, *Matonia braunii*,

664 *Neocalamites (Schizoneura) carcinoides*); **f** – Group 3 (*Baiera sp.*, *Cladophlebis*
665 *denticulata*, *Geinitzia sp.*, *Ginkgoites sp.*, *Ptilophyllum sp.*, *Zamites schmiedelii*). The
666 same pattern of response (decreasing or increasing) in a group of species means their
667 similar ecological profile. Differences in shapes of response curves depend on the
668 distribution and abundance of species along a putative environmental gradient.

669 **Fig. 5** Logistic regressions of GLM for response variables (species) in four palaeoecological
670 species groups along PCO 1 and PCO 2. **a** - Group 1, PCO 1; **b** - *Nilssonina* sp.1; **c** -
671 Group 2, PCO 1; **d** – Group 2, PCO 2; **e** - Group 3, PCO 1; **f** - Group 3, PCO 2

672

673 **Table caption**

674 **Table 1** Stepwise selection of response variables in three groups of species discriminated in
675 PCA analysis, according to logistic regression model with logit link function and
676 binomial response assumed. R^2 – coefficient of determination, F – a partial F test, p – I-
677 type error.

678 **Table 2** Environmental requirements of the most important species forming ecogroups in
679 Anina.

Figure 1

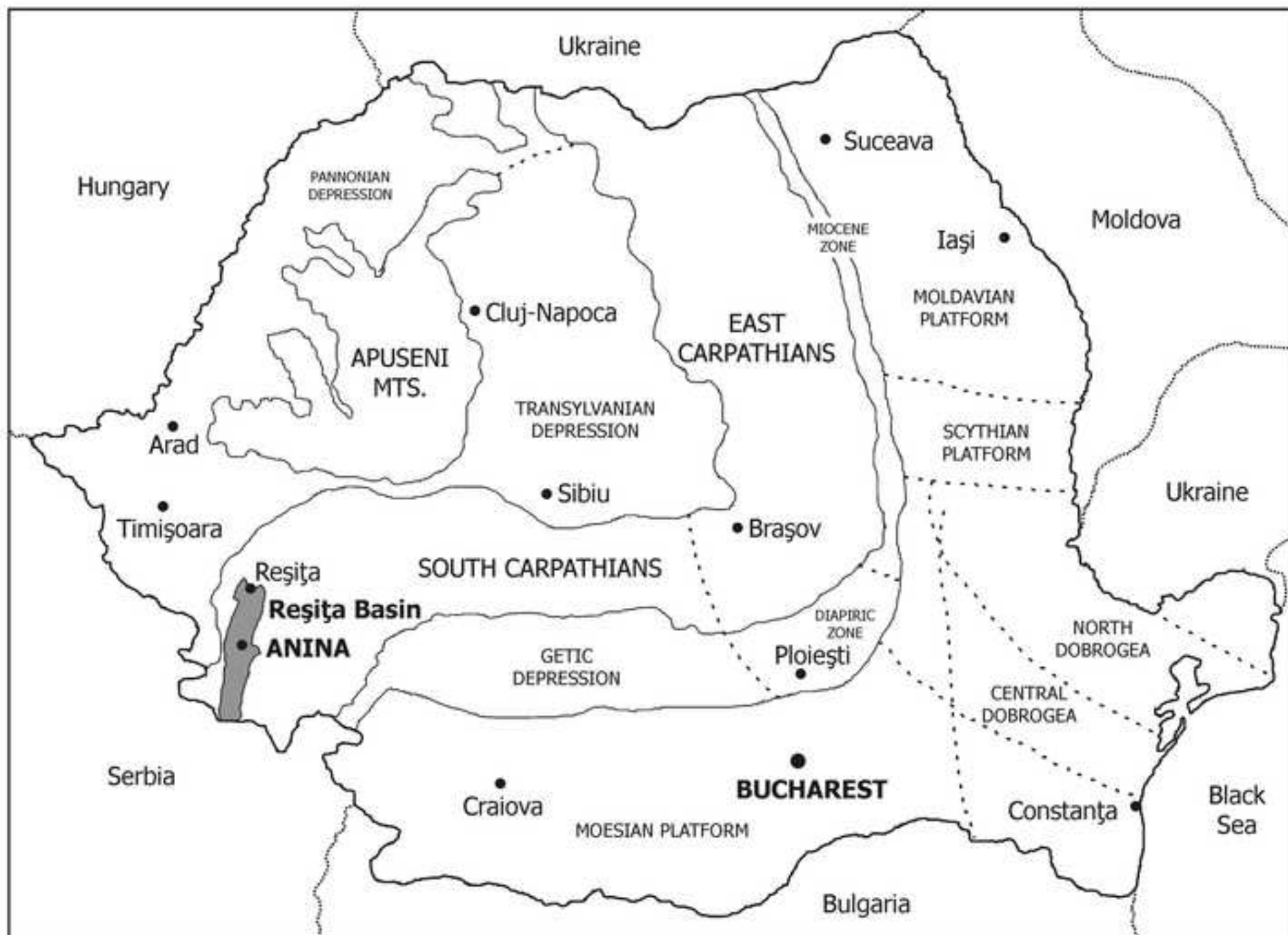


Figure 2

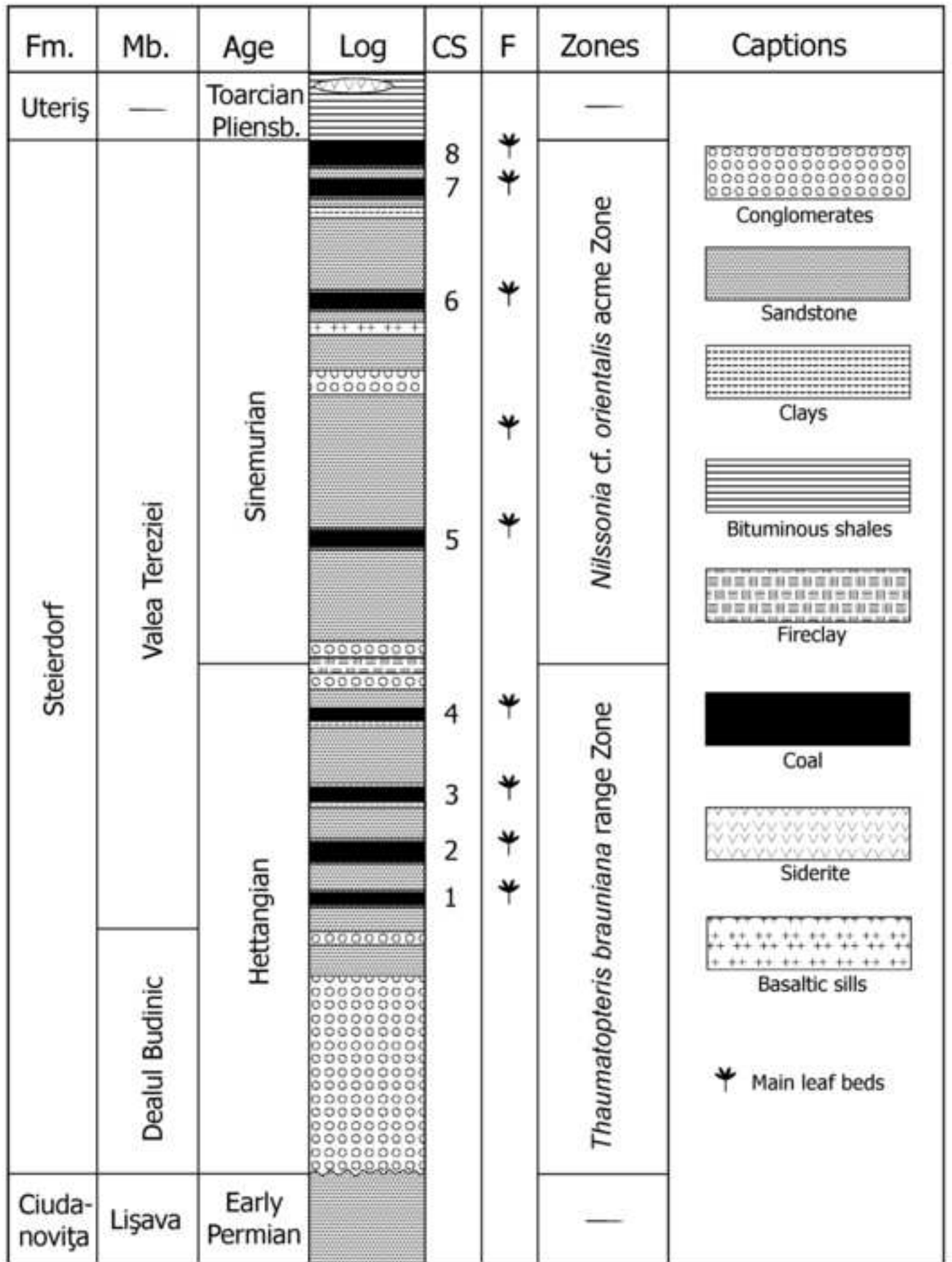


Figure 3

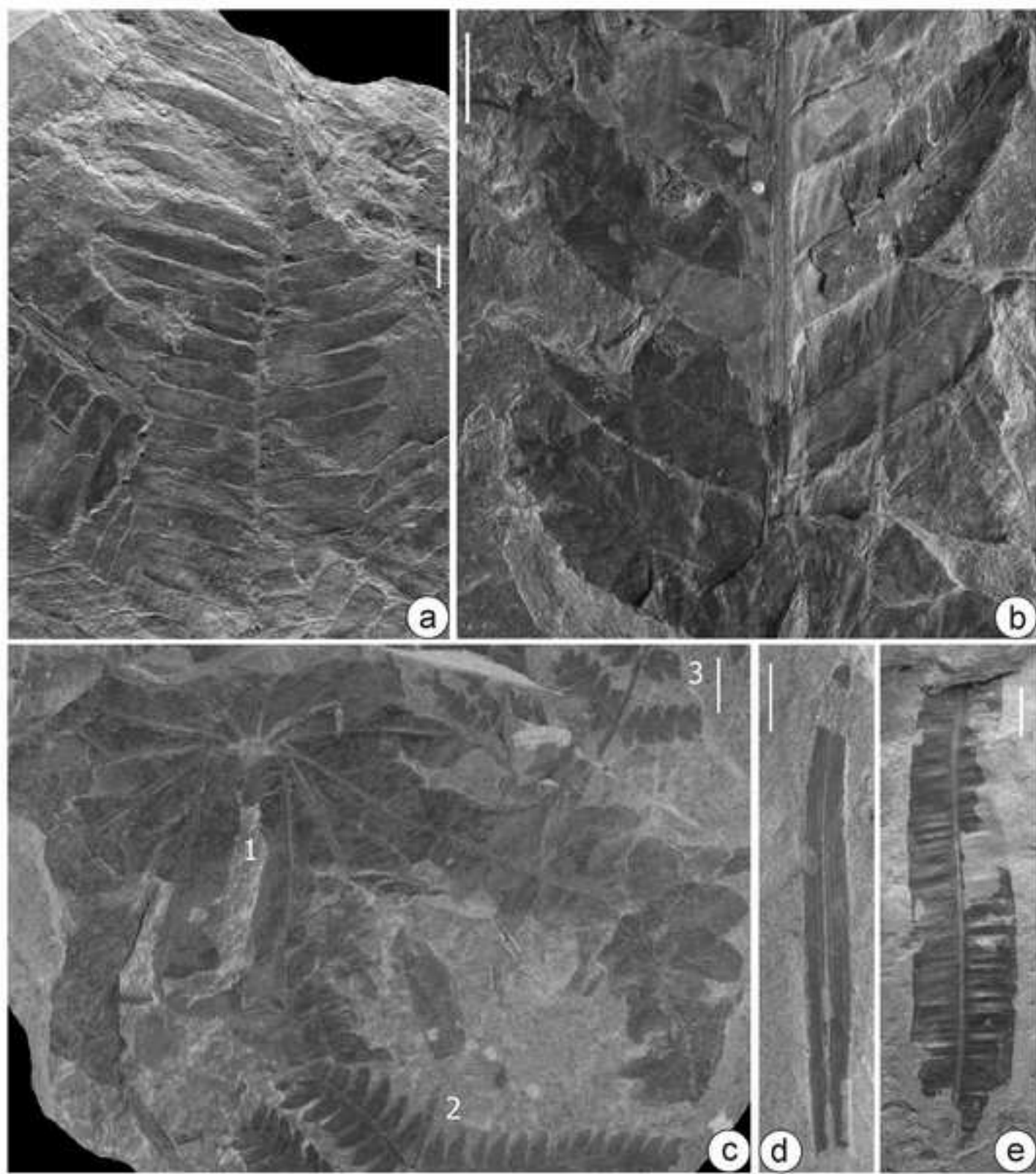


Figure 4

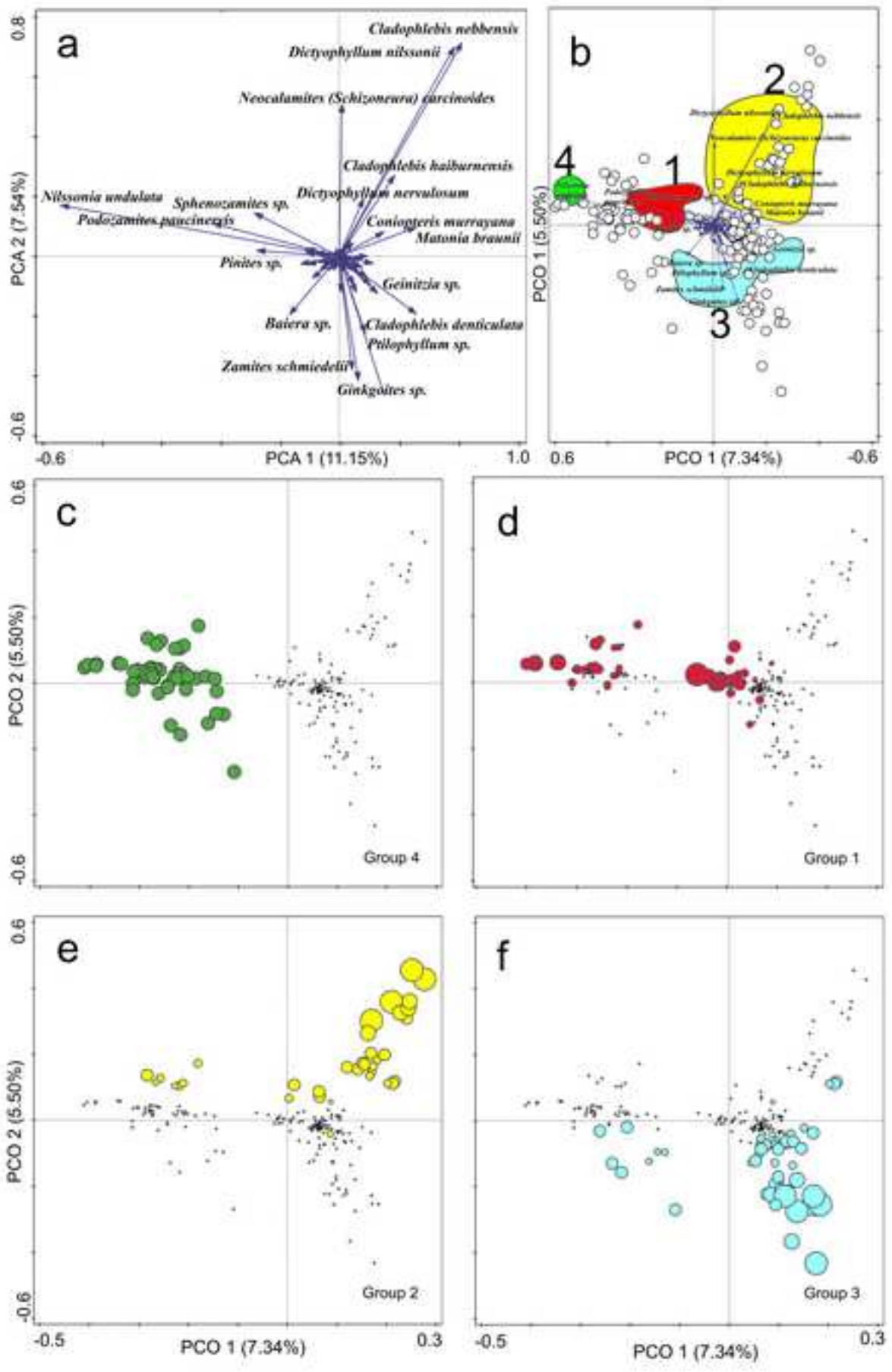


Figure 5

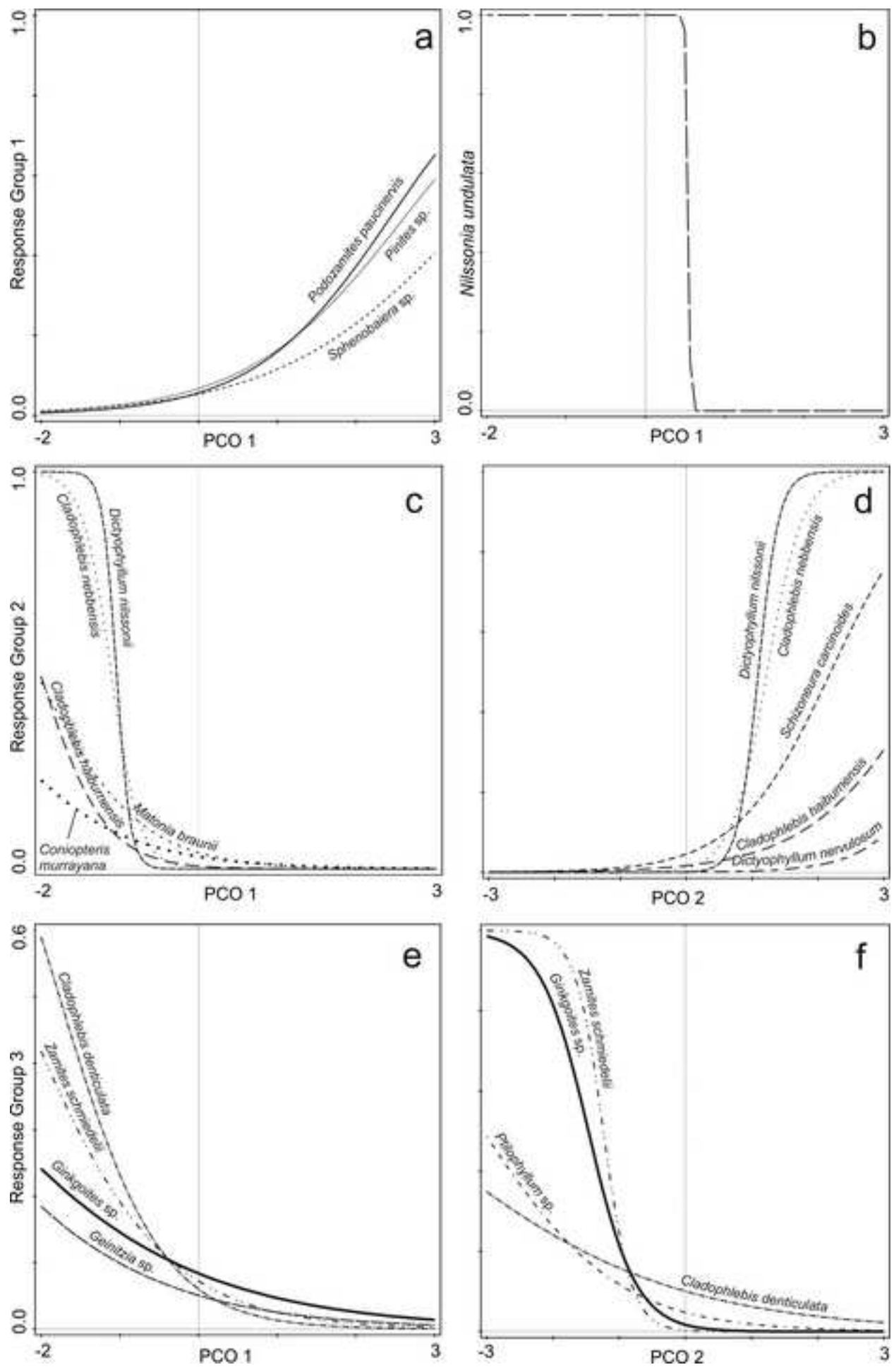


Table 1

Response	R2[%]	F	p	R2[%]	F	p
Axis	PCO1			PCO2		
Nilssonia						
<i>Nilssonia</i> sp. 1	100	312.6	<0.00001	0.8	2.50	0.11453
Group 1						
<i>Pinites</i> sp.	14.9	25.2	<0.00001	0.5	0.82	0.63366
<i>Podozamites paucinervis</i>	18.7	30.8	<0.00001	0.6	0.97	0.67445
<i>Sphenobaiera</i> sp.	10.1	13.7	0.00026	1.5	2.10	0.14949
Group 2						
<i>Cladophlebis haiburnensis</i>	17.1	12.2	0.00056	17	12.20	0.00057
<i>Cladophlebis nebbensis</i>	48.9	85.1	<0.00001	69.1	120.20	<0.00001
<i>Coniopteris murrayana</i>	7.2	7	0.00861	2.9	2.80	0.09389
<i>Dictyophyllum nervulosum</i>	20	2.6	0.10604	29.5	3.90	0.05016
<i>Dictyophyllum nilssonii</i>	73.9	125.5	<0.00001	83.7	142.10	<0.00001
<i>Matonia braunii</i>	12	17	0.00005	2.2	3.10	0.08072
<i>Schizoneura carcinoides</i>	0.1	0.2077	0.64899	27	42.10	<0.00001
Group 3						
<i>Baiera</i> sp.	4.6	1.1	0.29921	13.9	3.30	0.07212
<i>Cladophlebis denticulata</i>	13.5	24.7	<0.00001	3.6	6.60	0.01054
<i>Geinitzia</i> sp.	4.2	5.1	0.02486	0.8	0.98	0.67644
<i>Ginkgoites</i> sp.	3.8	6.2	0.01323	52.9	87.40	<0.00001
<i>Ptilophyllum</i> sp.	1.5	2	0.15892	12	15.70	0.00009
<i>Zamites schmiedelii</i>	8.9	15.4	0.00011	74.7	130.0	<0.00001

Table 1 Stepwise selection of response variables in three groups of species discriminated in

PCA analysis, 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.

Table 2

taxon	group number	sedimentary environment (Anina)	Proxies for environmental requirements
<i>Nilssonia</i> sp. 1 with entire margin	1	Finely laminated sandstones and paleosoils	upland forest or moist lush (depending on species) (van Konijnenburg-van Cittert & van der Burgh, 1996 p. 8.). Moderately disturbed, relatively dry to moderately wet (non-flooded) inland areas (Barbacka, 2011)
<i>Podozamites paucinervis</i>	2	Roof shales and fine sandstones	mire borders in flooded areas (Popa, 1997)
<i>Cladophlebis nebbensis</i>	2	Paleosoils and roof shales	Schweitzer et al. (1997), Popa (1997, 1998) Floodplain areas
<i>Dictyophyllum nilssonii</i>	2	Paleosoils and roof shales	Weakly disturbed, moderately wet canopy (Barbacka, 2011) moist marsh (van Konijnenburg-van Cittert, 2002)
<i>Neocalamites (Schizoneura) carcinoides</i>	2	Roof shales	Weakly disturbed, moderately wet canopy (Barbacka, 2011) marsh (van Konijnenburg-van Cittert 2002)
<i>Ginkgoites</i> sp.	3	Roof shales and paleosoils	Coastal, warm, humid (Harris, 1937,1961, 1964, 1969; Harris & Millington, 1974), stable and ecologically saturated (Zhou, 2009) wetland (Abbink et al., 2004) stable wetland (Francis et al., 2008) wet (Hesselbo et al., 2003) upland (Popa & van Konijnenburg-van Cittert, 2006)
<i>Cladophlebis denticulata</i>	3	Roof shales and paleosoils	Highly disturbed short-lived, moderately wet territories formed by alluvial deposits (islands, peninsulas, forelands), fully damaged by river flood, occupied by coloniser plants (Barbacka, 2011) riverbanks, or in freshwater marshes (van Konijnenburg-van Cittert, 2002) floodplains and lowlands (Gordenko, 2008)
<i>Zamites schmidelii</i>	3	Roof shales	flood plains or levees (Givulescu, 1998; Popa, 1998, 2014)

Table 2 Environmental requirements of the most important species forming ecogroups in Anina.