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1 **Dysodiles from the lower Barremian of Lebanon:**
2 **Insights on the fossil assemblages and the depositional environment**
3 **reconstruction**

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19

20 **Highlights**

- 21 • New continental Konservat-Lagerstätte from the lower Barremian of Lebanon
- 22 • Contribution to the knowledge of the lacustrine flora and fauna of north-eastern
23 Gondwana
- 24 • Palaeoenvironmental reconstruction of the lacustrine Lebanese lower Barremian

25

26 **Abstract**

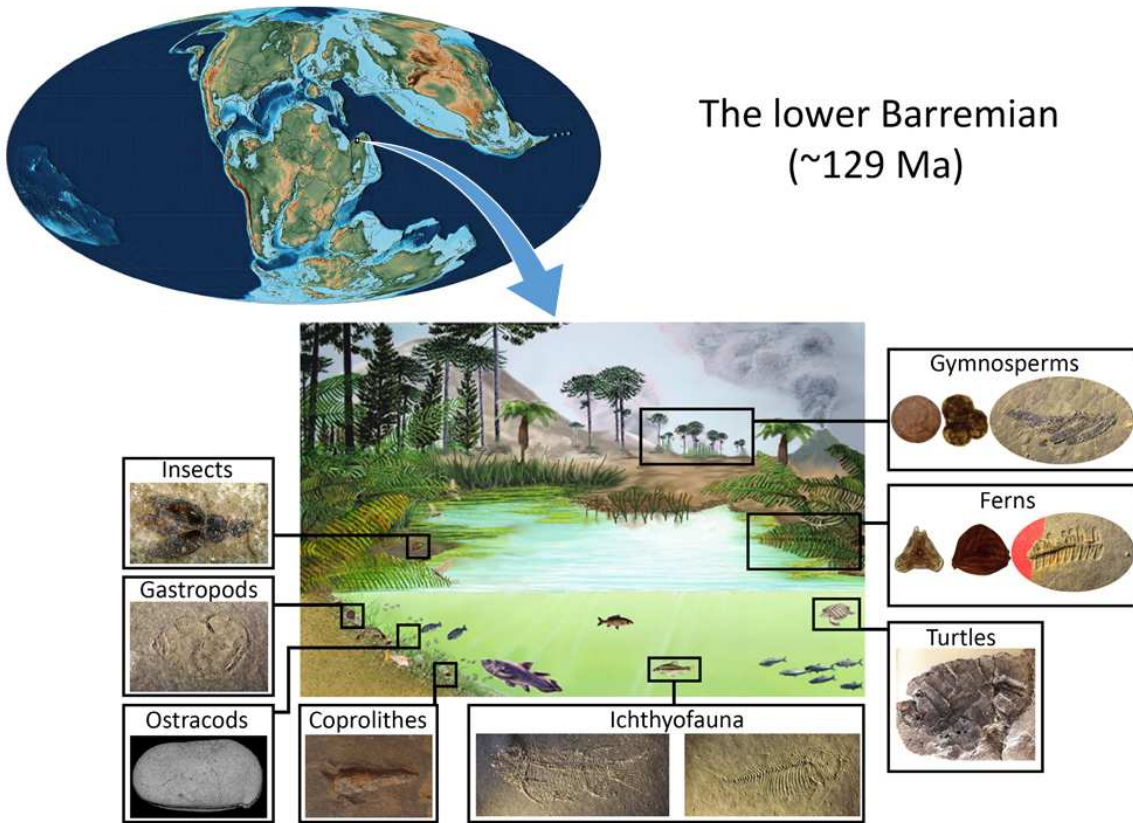
27 The Recent re-/discovery of unusual Lower Cretaceous continental sediments (dysodiles) brings
28 important and exceptional paleontological assets. Dysodile beds are found in many localities
29 across Lebanon and are characterized by their high organic matter content and their richness in
30 exceptionally well-preserved fossils. We focus our study on five sampling localities in the lower
31 Barremian sandstone beds, deposited when Lebanon was located in the north-eastern part of the
32 Gondwana supercontinent. The localities are found associated with volcanic deposits suggesting
33 a close relation between volcanism and their deposition and/or preservation. The present study
34 provides, for the first time, insights on the fossil assemblages found in the dysodiles, including
35 fishes, turtles, gastropods, insects, plant debris (macroflora and palynomorphs), ostracods and
36 coprolites. We provide a preliminary reconstruction of the depositional environment that is
37 common to the five sampling localities. It was a freshwater lake or possibly a series of
38 interconnected lakes, in the vicinity of volcanic edifices, surrounded by a typical Lower
39 Cretaceous flora (open forest environment), and inhabited by basal actinopterygian fishes and
40 teleosts that will constitute the core of subsequent freshwater assemblages. The Lebanon
41 localities have important implications for local palaeoenvironments as well as worldwide

42 biogeography. In addition, the fossil assemblages show some taxonomic and taphonomic
43 differences between the sampling sites, suggesting local differences in environmental conditions
44 during deposition.

45 **Keywords:** freshwater, paleoenvironment, taphonomy, Cretaceous, black shales.

46

47 **Graphical Abstract**



48

49

50 1. Introduction

51 Historically, Lebanon is paleontologically famous for its Late Cretaceous (Cenomanian) marine
52 carbonate beds yielding abundant and exquisitely preserved fishes (Forey et al., 2003; Gayet et
53 al., 2003; Kachacha et al., 2017), and its numerous Early Cretaceous amber outcrops with
54 biological inclusions (Azar, 2007; Azar et al., 2010). The recent re-/discovery of unusual Lower
55 Cretaceous continental sediments (dysodiles) brings important and exceptional paleontological
56 assets (El Hajj et al., 2019; Azar et al., 2019; El Hajj et al., 2020). Dysodiles are sedimentary
57 rocks characterized by finely laminated (micrometric) layers, high organic matter content
58 (Cordier, 1808) and well-preserved fossils (Fraas, 1878).

59 Dysodile beds are found in different lacustrine deposits in various areas of Lebanon, from the
60 lower Barremian and the Albian stages respectively. Old references mentioned their presence in
61 the Lower Cretaceous sandstones of Mount Lebanon (Botta, 1831), of the South (Fraas, 1878)
62 and of the Center of Lebanon (Janensch, 1925). Fraas (1878) was the first author to point out
63 their richness in fossils including fish and plant debris, and he identified some plant species. The
64 latter were reviewed and attributed to *Zamites* sp. and *Weichselia reticulata* by Edwards (1929),
65 while Janensch (1925) identified two small actinopterygian fishes, as *Pleuropholis koerti* and
66 *Thrissops* sp. Then, since the 1930s, dysodiles were forgotten until their recent rediscovery
67 through our extensive geological fieldwork which resulted in the finding of seven localities, five
68 of them in the lower Barremian and two in the Albian. Recently, in addition to their petroleum
69 interest and source rock potential (El Hajj et al., 2019), the ostracod fauna found within the
70 dysodile layers was identified and its contribution to understanding the paleoenvironment was
71 discussed (El Hajj et al., 2020). However, these dysodiles certainly deserve multidisciplinary
72 approaches in order to reveal and understand their depositional conditions, their relationship with

73 environmental regional context and their continental paleobiodiversity. Besides the ostracods
74 identified from five dysodile sampling localities (El Hajj et al., 2020), only fossiliferous amber
75 [with biological inclusions (mainly insects and other terrestrial arthropods) (Azar et al., 2010;
76 Azar, 2012; Maksoud & Azar, 2020)] and lignite have provided insights on the terrestrial flora
77 and fauna during the early Barremian of Lebanon (Azar et al., 2010; Azar, 2012; Maksoud &
78 Azar, 2020). Thus, the study of the fossil assemblages found in the dysodiles will significantly
79 increase our knowledge of these Early Cretaceous lacustrine environments and their biodiversity.
80 Here we provide a paleoenvironmental reconstruction of the depositional environments of the
81 lower Barremian dysodiles, based on the facies and fossil record.

82

83 **2. Geological setting**

84 **2.1. Regional framework and stratigraphy**

85 Lower Barremian dysodiles crop out in five localities across Lebanon, at the base of the “Grès du
86 Liban” unit; an outcrop in the North [Qrayn (N 34°23', E 36°1', 806 m)], another in the Center
87 [Tarchich (N 33°51', E 35°49', 1704 m)], and the three remaining in the South of Lebanon
88 [Jdaydet Bkassine (N 33°33', E 35°34', 713 m), Snyya (N 33°31', E 35°33', 875 m) and Zehalta
89 (N 33°30', E 35°32', 900 m)]. Figure 1 shows the general view of the five sampling locations.
90 The “Grès du Liban” unit comprises a few meters in the North and up to 300 m in the South of
91 fluvio-deltaic sandstone, locally laminated claystone and basalt (Nader, 2014), that pass laterally
92 into lacustrine carbonate rich in charophytes (Granier et al., 2015). Recent findings in
93 micropaleontology, particularly the record of the foraminifer *Balkhania balkhanica* Mamontova
94 1966, allow the attribution of an early Barremian age to the “Grès du Liban” unit (Granier et al.,

95 2016). The dysodile outcrops correspond to small isolated lakes and/or swamps, within this unit
96 (less than 1 km in lateral extent and 2 m in thickness).

97 Field observations show a similarity between the southern sampling sites, where, in the three
98 localities Jdaydet Bkassine, Snyya and Zehalta, dysodiles overlie altered volcanic claystone
99 deposits and nodular carbonates. It is noteworthy that these southern outcrops are not distant
100 from each other, suggesting that during deposition they could have been interconnected under
101 certain conditions. In the northern sampling site, Qrayn, a repetitive alternation of dysodiles and
102 claystone is evident. In central Lebanon, Tarchich, a bed of volcanic ash is located just
103 underneath the dysodile beds. However, dysodiles crop out throughout the village of Tarchich,
104 and 1 km to the south of the main sampling site, dysodiles are contained between 10 cm of
105 carbonate beds. Figure 2 gives detailed stratigraphic logs of three main sampling localities,
106 Qrayn, Tarchich and Snyya.

107

108 **2.2. Palaeogeographical framework**

109 **2.2.1. Palaeogeographical location and climatic conditions**

110 During the lower Barremian, Lebanon was located in the northeastern part of the Gondwana
111 supercontinent. Global sea level was 80 m higher than it is now.

112 On the paleomap of the Lower Cretaceous (Scotese, 2014), Lebanon is situated alongside other
113 Lower Cretaceous non-marine deposits with exceptional preservation: those containing the Jehol
114 Biota in the Eastern block of North China plate, those containing the Crato Formation in the
115 Araripe Basin (Brazil), the deposits from La Huérguina Formation on the Iberian plate (Las
116 Hoyas) and the deposits found in Koonwarra and other Victorian fossil sites in Gippsland Basin

117 (Australia) (Fig. 3). We can notice that China was located in the middle of the continent under
118 temperate climate (Zhou, 2014); the Araripe Basin was also in the middle of the continent, but
119 under arid climate (Neumann et al., 2003), while the Iberian plate was located on the border of
120 the continent in a subtropical and highly seasonal climate (Fregenal-Martínez & Meléndez,
121 2016). The Gippsland Basin was located on the border of the continent, under humid cool
122 temperate climate (Poropat et al., 2018). The Lebanese dysodiles are thus unique in having
123 formed in a warm tropical climate on a continental border.

124

125 **2.2.2. Tectonics and Volcanism**

126 Veltz (2008) studied the transition between the Jurassic and the Cretaceous of Lebanon, and
127 highlighted that the deposition of the sandstone occurred in a tectonically unstable continental
128 context. During the lower Barremian, Lebanon witnessed many volcanic episodes related to fault
129 reactivation (Brew et al., 2001), and faults might have promoted the development of small lakes
130 and/or swamps.

131 Indications of volcanism are found in all sampling sites. The dysodiles are associated with the
132 volcanic ashes; the volcanic activity occurred both prior to (Dubertret, 1955) and synchronous
133 with the dysodile deposition since ash could also be detected within the dysodile layers
134 themselves. In addition, the claystone associated with dysodiles in both locations, Qrayn and
135 Snyya, could be the result of basaltic alteration. Therefore, we envisage a close relation between
136 volcanism and dysodiles deposition and/or preservation.

137

138 **2.3. Influence of palaeogeography on deposition and preservation**

139 The paleogeographic conditions of Lebanon, mostly influenced by the tectonics and the climate
140 (warm tropical climate), may have enhanced the primary productivity and diversity of these lake
141 systems. Volcanic activity would have enriched the lakes and/or swamps with nutrients favoring
142 the proliferation of organisms (Veltz, 2008). However, volcanic activity could have also
143 rendered lake waters toxic, leading to mass mortality (Veltz, 2008).

144 The excellent preservation of the organic matter and fossils could have been facilitated by calm,
145 anoxic bottom conditions, evidenced by the absence of bioturbation and the fine parallel
146 laminations observed under the microscope as well as by the high content in total organic carbon
147 (El Hajj et al., 2019), with a Pristane/Phytane ratio lower than 1 (Peters et al., 2005; El Hajj et
148 al., 2019), and the absence of biodegradation. Rapid burial in small lakes and/or swamps could
149 also have contributed to excellent preservation by inhibiting the degradation of organic matter.

150

151 **3. Methods**

152 **3.1. Sampling**

153 Sampling was done by collecting dysodile blocks and then separating them into fine laminations
154 in the search for fossils. Sampling frequency was different between the sampling sites: Qrayn
155 was sampled only once in summer 2017 due to the topography preventing easy access to the site.
156 Blocks of 10 cm thickness were collected throughout the section.

157 Tarchich was sampled several times between 2014 and 2017. Dysodile layers were separated on
158 the spot in the search for fossils; blocks were also taken from the sampling sites, covering the

159 entire section and the different outcrops in the village. However, the main sampling site located
160 in a sand quarry is now inaccessible, covered by sediment embankments.

161 Jdaydet Bkassine has been sampled continuously since 2014 on a total area of 1 m². Snyya was
162 visited six times between 2014 and 2017, when blocks of dysodiles were sampled on the entire
163 section, but the area they cover is much less than 1 m² because of the weathering and the
164 topography preventing easy access.

165 Zehalta was sampled only twice in 2014 before the building of a wall in front of it.

166

167 **3.2. Facies and fossil preparation**

168 Facies preparation was performed in the IStEP laboratory (Paris, France), by means of thin
169 sections and palynofacies analysis. The collected fossils were cleaned and the dysodiles carefully
170 split in order to preserve the part and the counter-part of each macrofossil. Each fossil was
171 numbered according to the notation used by the Natural History Museum, Faculty of Sciences II
172 of the Lebanese University. No treatment was applied to these fossils. However, in order to study
173 some of them, special methods were used (palynomorph & ostracod extraction).

174 Cuttings perpendicular to the bedding served for the preparation of the thin sections. They were
175 examined under white light using a *ZEISS AXIO IMAGER* microscope.

176 The palynofacies and the palynomorph extraction and preparation (Combaz, 1964; Tyson, 1995)
177 was performed using the protocol described by Durand & Nicaise (1980). It consisted of
178 successive acid digestions of the fragmented rock, using hydrochloric acid (HCl, 33%) to
179 eliminate the carbonates, then hydrofluoric acid (HF, 70%) to eliminate the silicates, and finally
180 hot hydrochloric acid to eliminate the neo-formed minerals and the residual fluorides. After each

181 acid digestion, the sample was washed with demineralized water in order to eliminate the excess
182 of acid and neutralize the pH. Slides (bulk and sieved using a 10 μ m mesh) were mounted from
183 this isolated organic matter using polyvinyl alcohol and UV resin (NOA61). The slides were then
184 observed under a *ZEISS Axioplan 2 imaging* optical microscope, by the mean of a *ZEISS Plan-*
185 *NEOFLUAR 63x/1.25* oil immersion objective, using white and UV light.

186 Ostracod extraction was performed using the hot acetolysis method (Lethiers & Crasquin-Soleau,
187 1988) and, after picking, specimens were observed and imaged with a Scanning Electron
188 Microscope *HITACHI TM3000 Tabletop Microscope* (CR2P laboratory, Paris, France).

189

190 **4. Results**

191 **4.1. Dysodiles main facies**

192 In thin sections (Figs. 4A–D), dysodiles appear to be finely laminated well-compacted layers rich
193 in organic matter. Quartz grains, phosphate grains and nodules (Fig. 4B), wood debris (Fig. 4D),
194 and in some of the samples, ostracod valves (Figs. 4A & C) could also be found.

195 Palynofacies analysis shows the dominance of amorphous organic matter (El Hajj et al., 2019;
196 Figs. 4E & F) which originated from the accumulation of organic matter deriving from
197 phytoplanktonic blooms, faecal pellets of zooplankton and bacterial mats, or even degraded plant
198 debris (Tyson, 1995). However, the high fluorescence under UV light proves the planktonic and
199 bacterial origin of the organic matter forming the dysodile, as well as the organic geochemical
200 data [Type I organic matter of algal and bacterial origin (El Hajj et al., 2019)]. In addition, the
201 molecular results support a bacterial origin [presence of hopanes (Peters et al., 2005; El Hajj et
202 al., 2019)]. Thus, it is important to consider the likely role of microbial mats in the fossil

203 preservation. It is probable that these bacteria and microorganisms generated microbial mats that
204 enveloped the decaying organisms, slowing the decay mechanism and protecting the body from
205 breakage (Briggs, 2003).

206

207 **4.2. Paleontological findings**

208 A wide variety of well-preserved fossils was collected from all of the sampling sites. This
209 includes microfossils, such as palynomorphs (spores and pollen grains) and ostracods, and
210 macrofossils such as plant debris, invertebrates represented by insects and gastropods, and
211 vertebrates represented by fishes and turtles. Table 1 summarizes the paleontological findings in
212 each facies within the different localities.

213

214 **4.2.1. Plant debris**

215 Plant debris are frequent and well preserved. They include a variety of leaves, wood, stems and
216 fruits, either found as compressions or as carbonized and burnt remains. However, fern leaves
217 are the dominant fossils, among which small, rounded pinnae with reticulate venation probably
218 belonging to *Weichselia reticulata* (Fig. 5A). Nevertheless, scaly leaves and fragments of
219 coniferales attributed to *Pagyophyllum* sp. (Fig. 5B), and *Cyparissidium* sp. (Fig. 5C) are
220 present, in addition to some isolated pinnae (1.5 cm) with parallel venation, probably belonging
221 to *Zamites?*, or *Podozamites?* of the Cycadaceae family (Fig. 5D). Even though the same plants
222 were previously identified in the dysodiles of South of Lebanon by Fraas (1878) and Edwards
223 (1929), only a detailed study of the cuticle can validate our identifications.

224

225 **4.2.2. Palynomorphs**

226 Palynomorphs are very rare and poorly preserved. The identified taxa and their botanical
227 affinities are listed in Table 2 and Figure 6. They correspond to a typical Early Cretaceous flora
228 (Watson & Alvin, 1996; de la Fuente & Zetter, 2016), dominated mostly by gymnosperm pollen
229 grains and less frequent but more diverse fern spores.

230

231 **4.2.3. Ostracods**

232 Ostracods were found in all of the sampling sites. With fishes, these are the most frequent fossils
233 in the dysodiles.

234 Ostracods show a variety of preservation modes since they can be found flattened and crushed
235 (Fig. 4A), or with crystalline infilling (Fig. 4C), or as internal moulds in some of the claystone
236 layers. However, it is notable that the ostracod fossils are always articulated carapaces (i.e., two
237 articulated valves), suggesting an absence of post-mortem transport (Boomer et al., 2003). The
238 flattening of the valves is a result of rapid burial and subsequent compaction. On the other hand,
239 crystalline infilling may be the result of slow burial rate and/or ion availability coupled with
240 early diagenesis.

241 Where ostracods are so abundant as to cover the entire surface of a layer, we consider this to be
242 possible evidence of mass mortality (El Hajj et al., 2020), but no other fossils are visible in these
243 layers.

244 The ostracods could not be identified to species level because of their crushed state (Fig. 7), but
245 all belong to the superfamily Cypridoidea, which is characterized by a “pawprint” adductor
246 muscle scar (Horne & Colin, 2005). Among these, we could identify three genera: *Cypridea*

247 Bosquet, 1852 represented by four putative species, *Cyprois* Zenker, 1854 and *Zonocypris*
248 Müller, 1898. These ostracods and their paleoenvironmental implications are detailed in a
249 separate publication (El Hajj et al., 2020).

250 Size variation is obvious among *Cypridea* specimens (300 to 1200 μm), probably indicating the
251 assemblage of adults and juveniles or sexual dimorphism. If the size difference among ostracods
252 indicates adults and juveniles, this implies the absence of size-sorting induced by current or wave
253 action and such an assemblage represents a low energy thanatocoenosis (Guernet & Lethiers,
254 1989; Boomer et al., 2003)

255

256 **4.2.4. Insects**

257 Dysodiles yielded around 40 fossil insects (Fig. 8A – D) showing excellent preservation and
258 belonging to the Coleoptera [Anthicidae (Fig. 8A), Staphylinioidea (Fig. 8C)], Diptera (Fig. 8D),
259 Ephemeroptera (Fig. 8B) and Hymenoptera. Among these insects, a new family of
260 Ephemeroptera was described: Libanoephemeridae, represented by an ephemeropteran nymph
261 *Libanoephemera inopinatabranchia* (Azar et al., 2019). Table 3 summarizes the habitat and the
262 ecological niche of these insects to explore the diversity of their ecological niches.

263

264 **4.2.5. Gastropods**

265 Numerous aquatic gastropods were found but not yet studied (Fig. 8E–G). They are flattened, of
266 different sizes (between 0.5 and 2 cm) and shapes (some elongated, others rounded), resembling
267 pulmonate snails and *Lymnaea*, indicating different limnic species, living either in freshwater or
268 on the nearby wetland.

269

270 **4.2.6. Ichthyofauna**

271 Fish fossils are the most abundant vertebrates in the dysodile beds of Lebanon. Their
272 preservation is different between the sampling sites and in the same sampling site between
273 different layers. Most of the fish skeletons are complete and articulated (more than 400
274 specimens). The scales are in place, and skeleton and fin rays are fully articulated, supporting the
275 minimal transport and rapid burial hypothesis. Moreover, soft tissue is also preserved in the form
276 of eye impressions. They show taxonomic diversity and sizes ranging from 2 cm to 40 cm of
277 total length. The highest diversity derives from the Jdaydet Bkassine site, possibly due to the
278 greater sampling effort in this locality. The dysodile ichthyofauna includes diverse
279 actinopterygians (ray-finned fishes) as well as sarcopterygians (lobe-finned fishes) represented
280 solely by coelacanth. Details of the identified taxonomic groups are given below and illustrated
281 in Fig. 9.

282 Superclass: Osteichthyes Huxley 1880

283 Class: Actinopterygii Klein 1885

284 Grade: Palaeopterygii (Fig. 9A)

285 Genus and species indet.

286 A single headless specimen, 6.5 cm long, shows primitive characters including ganoid scales and
287 a heterocercal caudal fin. We refer it provisionally to the non-monophyletic grade Palaeopterygii
288 as defined by Romano et al. (2016), which gathers all non-neopterygian actinopterygians.

289 Order: Acipenseriformes Berg 1940 (Fig. 9B)

290 Genus and species indet.

291 A single specimen (part and counter-part), is a scale-less fish with no ossified vertebral centra,
292 but with only neural arches. The dorsal fin starts just behind the skull and apparently runs along
293 most of the back of the fish. The skull is not prepared yet and provides little information at this
294 stage. A naked body without mineralized vertebral centra is not common among
295 actinopterygians, but is found in acipenseriforms. These fishes usually have a short dorsal fin,
296 except in the peipiaosteid *Yanosteus* from the Lower Cretaceous of Liaoning, China (Jin, 1999)
297 and in the acipenserid *Psammorhynchus* from the Upper Cretaceous of USA (Grande & Hilton,
298 2006). In these genera, however, the dorsal fin does not start just after the posterior limit of the
299 skull, and in *Psammorhynchus* the body is almost completely covered with thick scales.
300 Scaleless basal neopterygians, without ossified vertebral centra, are known in the Middle Triassic
301 (see Tintori et al., 2010 for a discussion of naked basal neopterygians), and we cannot exclude
302 that this specimen could be a late representative of this kind of fish. Neither can we exclude that
303 it could correspond to a scaled-neopterygian with an elongate dorsal fin, such as a macrosemiid
304 for instance, which could have lost its squamation for taphonomical reasons. For now it is
305 regarded cautiously as a possible acipenseriform, pending the preparation of the fossils and the
306 discovery of new material.

307 Subclass: Neopterygii Regan 1923

308 Infraclass: Teleostei Müller 1844

309 Family: Pleuropholidae Saint-Seine 1949 (Fig. 9C)

310 Genus and species indet.

311 Five complete specimens are referred to the family Pleuropholidae. The body is covered with
312 ganoid scales slightly deeper than long along the dorsal and ventral margin of the body, and with
313 a single row of deepened scales in the mid-depth of the flank, which are *ca* 4 times deeper than
314 long. The dorsal and anal fins are located posteriorly, close to the caudal peduncle. These fins, as
315 well as the pelvic and caudal fins are preceded by few basal fulcra (1-2) and by a series of
316 elongated fringing fulcra extending up to the tip of fins. The pectoral fin differs from the other
317 fins by a series of fringing fulcra, which are fused to each other along the first proximal third of
318 the fin. This arrangement forms proximally a strong and massive denticulated spine-like
319 structure. The occurrence of a single row of deepened thin ganoid scales along the flank is a
320 feature of pleuropholids. Examination of the anatomy, in particular of the skull, will be necessary
321 to refine this identification.

322 Janensch (1925) referred three small fish specimens from the locality of Tarchich to a new
323 species of the genus *Pleuropholis*, *P. koerti*. These fossils are not housed in the Museum für
324 Naturkunde Berlin where Janensch spent his career (Florian Witzmann, personal communication
325 May 2020) and they have not been located elsewhere so far. The sketchy figure of one specimen,
326 together with the rather detailed description of the postcranial skeleton of this species (the head
327 is poorly preserved in all specimens) by Janensch stresses common characters with the
328 pleuropholid described herein, notably the occurrence of a series of deep scales running along
329 the flanks, a feature that confirms its inclusion in the family Pleuropholidae. Differences in
330 meristic features, as well as the higher position of the pectoral fins (*contra* a lower position in
331 our specimens), argue for distinct species. Moreover, Janensch did not mention the peculiar
332 denticulated spine in front of the pectoral fins formed by fused fulcrae, a typical and well-visible
333 feature in our material. Although the differences between the specimens described by Janensch

334 and ours could partly be explained by the difference in size of the fishes, we prefer here to
335 consider that *P. koerti* is a *nomen nudum*. The species described briefly here probably
336 corresponds to a new species that remains to be defined and named.

337 Teleostei indet. (Fig. 9D, E)

338 Teleostean fishes are dominant and well represented. Their size is never more than 6 cm. Two
339 morphotypes are easily distinguished:

340 Morphotype I (Fig. 9D). The skull is as deep as long and contained *ca* 3.5 times in the standard
341 length. The opercular series is narrow. The body is proportionally short and deep, with *ca* 14
342 abdominal and 14 caudal vertebrae. The general morphology is reminiscent of an
343 ellimmichthyiform, but no ventral scutes typical of these fishes are visible on the available
344 material.

345 Morphotype II (Fig. 9E)

346 The skull (with the opercular series) is about twice longer than deep and contained more than 3.5
347 times (*ca* 3.7) in the standard length. The opercular series is narrow. The body is proportionally
348 elongated, with *ca* 20 abdominal and 15 caudal vertebrae. The general morphology is
349 reminiscent of the Cretaceous clupavids.

350 Class: Sarcopterygii Klein 1885

351 Subclass: Actinistia Cope 1871

352 Order: Coelacanthiformes Berg 1937

353 Suborder: Latimerioidei Schultz 1993

354 Family: Mawsoniidae Schultz 1993 (Fig. 9F)

355 Genus and species indet.

356 An approximately 40 cm long specimen is referred to a mawsoniid coelacanth. The skull is still
357 unprepared and its identification is only provisional. The presence of an anterior ray-finned fin
358 and of a posterior lobe-finned fin supported by a basal plate with the typical anterior double
359 processes, as well as the occurrence of a supplementary medial lobe of the caudal fin, make
360 indisputable the identification of this specimen as a coelacanth. The supplementary lobe of the
361 caudal fin is very elongated and may indicate that the specimen is a juvenile. The head is still
362 covered with a thin layer of sediment, but the general outline of the braincase is visible and
363 shows that the ethmosphenoid portion is much longer than the otico-occipital portion. This
364 feature, together with the presence of abdominal ribs are evidence to refer, with caution, this
365 specimen to the mawsoniids.

366

367 **4.2.7. Turtles**

368 A nearly complete turtle carapace (Fig. 10) and several shell plate remains were found in the
369 Tarchich sampling site. The specimen which is slightly flattened with a small ovoid shape (5 x 6
370 cm: width/length for the partial dorsal shell and 6 x 8 cm: width/length for the plastron)
371 corresponds probably to a juvenile and is preliminary identified as a primitive pleurodiran turtle
372 belonging to the Pelomedusoides. One part of the dorsal shell can be observed only in ventral
373 view and composed of thin 6 neurals with incomplete costal plates. Some peripherals are
374 preserved and connected with the plastron around the posterior margin of the carapace; their
375 external surfaces bear a fibrous aspect. The plastron is embedded in the bearing rock, and only
376 three quarters of the plastron are observed in visceral view. Two short and wider than long
377 mesoplatrons are clearly distinguishable and no fontanelles are present along the median line. .

378 The material from Tarchich might provide new data for understanding the early diversification
379 and evolution of this aquatic Gondwanian group, for which the oldest fossil record is mainly
380 known in the Lower Cretaceous (Barremian and Aptian/Albian) of South America (Hirayama et
381 al., 2000; Ferreira & Langer, 2013; Lichtig & Lucas, 2016).

382

383 **4.2.8. Coprolites**

384 Coprolites are abundant within the dysodiles. Their shape and size (Fig. 11) suggest a variety of
385 organisms that most probably have not yet been found in the fossil records. The study of
386 coprolites is important in order to understand the food chain inside these small lakes and/or
387 swamps, and may provide evidence of big predators roaming around the depositional
388 environment, such as crocodiles, dinosaurs or others.

389

390 **5. Discussion**

391 **Reconstruction of the depositional environment**

392 It is clear that faunal and floral diversity differ from one sampling site to another. This could be
393 due to the difference in sampling frequency, or to the presence of specific conditions in each site.
394 Since the cause of this discrepancy is still unclear, we chose to reconstruct a preliminary
395 depositional environment, focusing on characteristics that are common to the five sampling sites.

396 The sedimentology, the absence of salinity biomarkers (El Hajj et al., 2019) and the lack of
397 marine organisms, together with the presence of an ephemeropteran larva and three ostracod
398 genera indicative of freshwater environments (Anderson et al., 1967; Meisch, 2000), indicate a

399 depositional environment corresponding to a series of small, shallow lakes and/or swamps found
400 in the vicinity of volcanic edifices.

401 According to the plant fossils, a typical Lower Cretaceous vegetation surrounded the lakes and/or
402 swamps (Watson & Alvin, 1996; Traverse 2007): ferns inhabited the swamps and lake and/or
403 swamp margins (Van Konijnenburg-van Citteret, 2002) while gymnosperms were found nearby.

404 Pteridophyte/fern spores indicate a moist, humid environment favorable for their growth and
405 reproduction (Van Konijnenburg-van Citteret, 2002). However, the possibility of aridity and a
406 stressed environment should not be ruled out: *Weichselia reticulata* is a widespread Lower
407 Cretaceous halophytic and xerophytic fern (Alvin, 1974; Watson & Alvin, 1996; Traverse,
408 2007).

409 *Classopollis* pollen grains belong to the family Cheirolepidiaceae that occupied ecologically
410 diverse habitats (Alvin, 1982; Conway, 1996), but also thrived in stressed environments (Alvin,
411 1982; Traverse, 2007). Araucariaceae tolerate moderate humidity (Kunzmann, 2007), while
412 recent Ephedraceae prefer a dry arid or semi-arid climate (Srivastava, 1968). Nevertheless, the
413 very low number of detected palynomorphs is not conclusive evidence of aridity, hence the need
414 of a detailed and quantitative palynological study.

415 The above considerations notwithstanding, it is evident that diverse invertebrate and vertebrate
416 organisms flourished within these small lakes and/or swamps, including insects, ostracods,
417 gastropods, fishes, and turtles.

418 The morphology of the fishes indicates different feeding habits and therefore different lifestyles,
419 occupying various levels of the water column (Poyato-Ariza & Martín-Abad, 2016).
420 Coelacanths, having a robust body and lobed fins, may have lived in the benthos feeding on

421 small invertebrates or small fishes. The Palaeopterygii specimen, even if headless, has a fusiform
422 body shape suggesting an active swimming locomotion and belonging to the nektonic organisms.
423 Teleosts, due to their upturned mouth with or without teeth, were probably plankton filterers or
424 fed by suction on all kind of food particles. Some of them have the fusiform body of active
425 swimmers living in the nekton, while others have an ovoid body, dorsally straight and ventrally
426 curved adapted for swimming in superficial waters. The latter is also plausible for the
427 Pleuropholidae, feeding on planktonic crustaceans. Nevertheless, it is worth mentioning that the
428 ostracods, the only crustaceans found in the dysodile assemblages, are not planktonic (although
429 they may have been nektobenthonic), but this does not rule out the possibility that planktonic
430 crustaceans were present but had no shells to be preserved. These considerations underline the
431 importance of studying this fauna of basal actinopterygians co-existing with more derived
432 actinopterygians that would constitute the core of subsequent freshwater assemblages.

433 Based on this information, figure 12 represents a preliminary reconstruction of the depositional
434 environment of the Barremian dysodiles of Lebanon.

435

436 **3. Conclusion**

437 The present study provides an insight on the fossil assemblages found in the dysodiles of the
438 Barremian of Lebanon. The assemblage comprises plants, pollen and spores, invertebrates such
439 as gastropods, ostracods and insects, and vertebrates including turtles and a diverse fish fauna,
440 providing evidence of a freshwater lake environment and its surrounding vegetation. Faunal and
441 floral diversity differ between sites, however, and our preliminary reconstruction of the
442 depositional environment can be refined and reshaped by means of further studies that will either

443 confirm or reject the possibility of different lake and/or swamp types favorable for the deposition
444 of dysodiles.

445

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459

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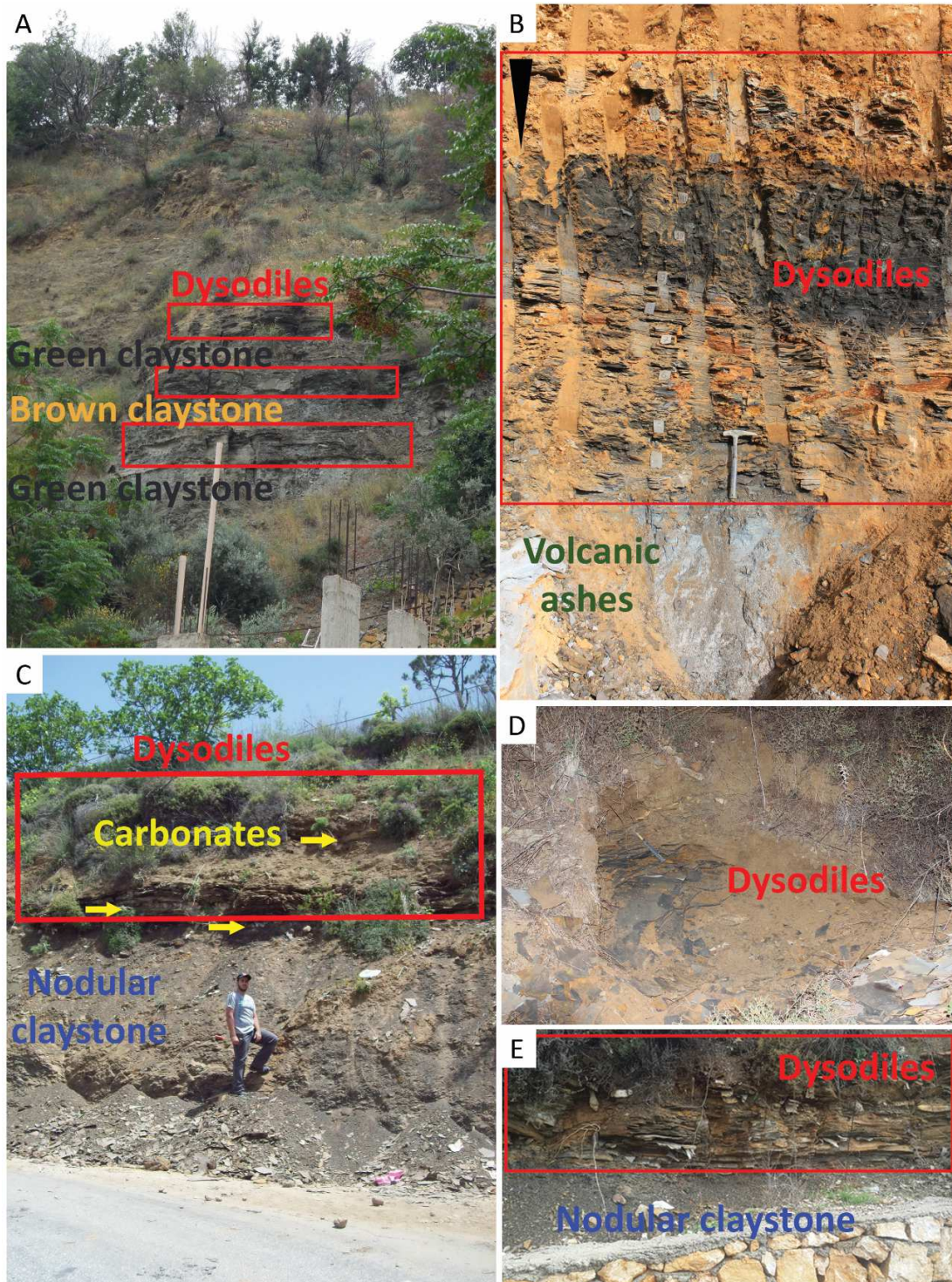
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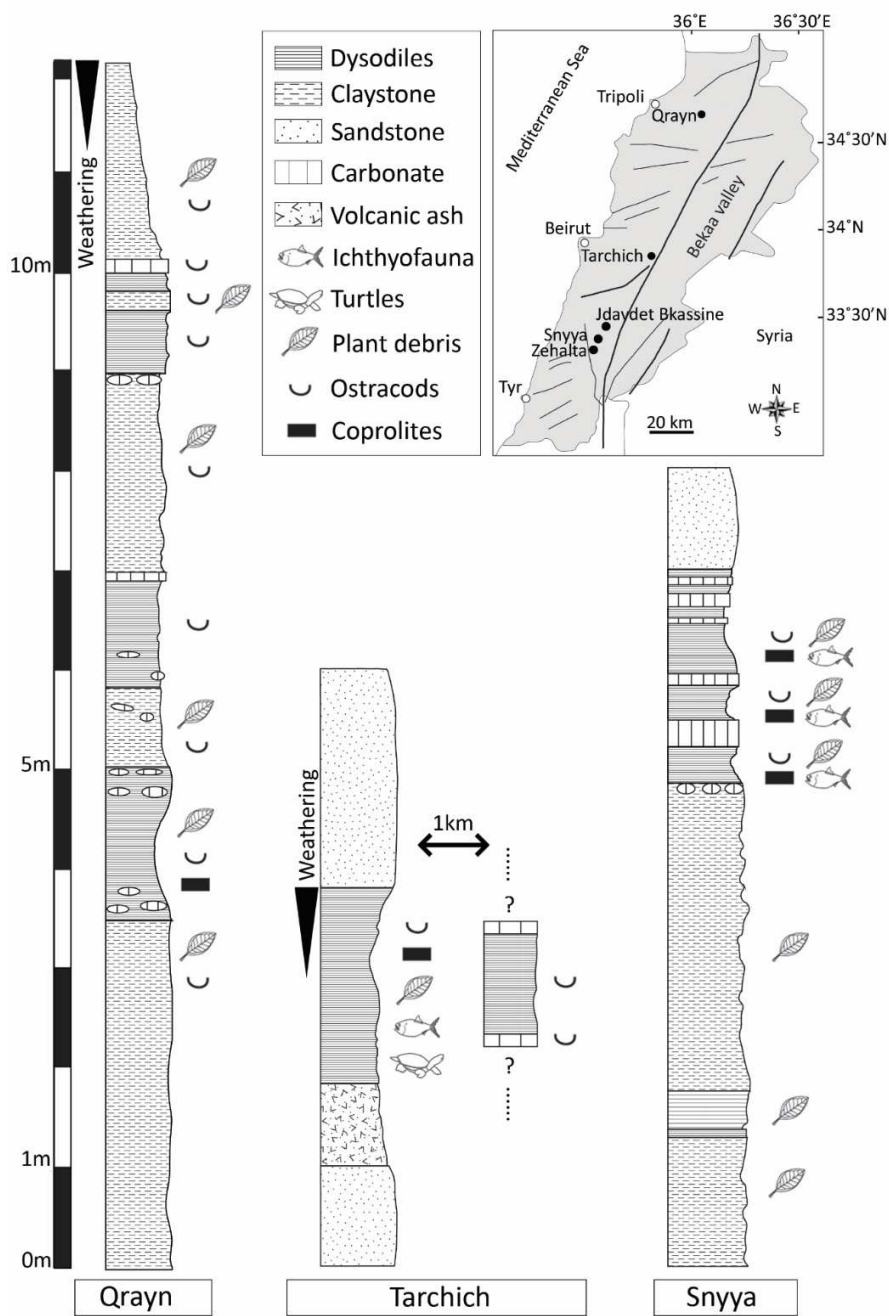
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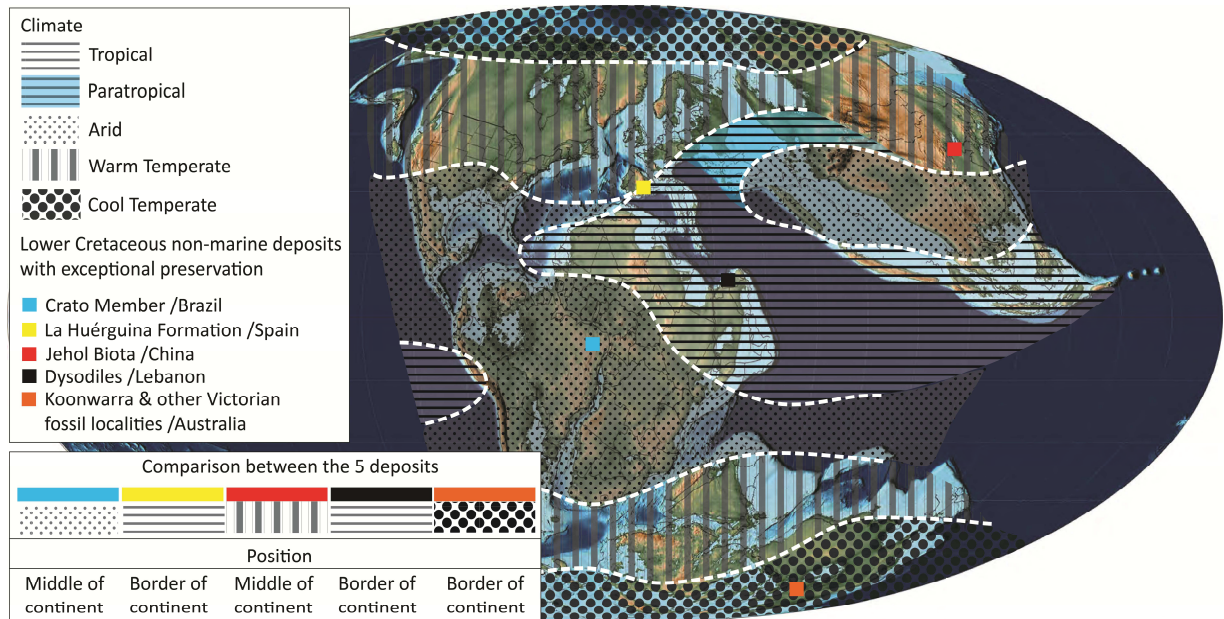


606

607 Figure 1. General view of the five sampling localities: A. Qrayn, B. Tarchich, the black arrow
 608 indicates the decreasing weathering effect, C. Snyya, D. Jdaydet Bkassine, E. Zehalta

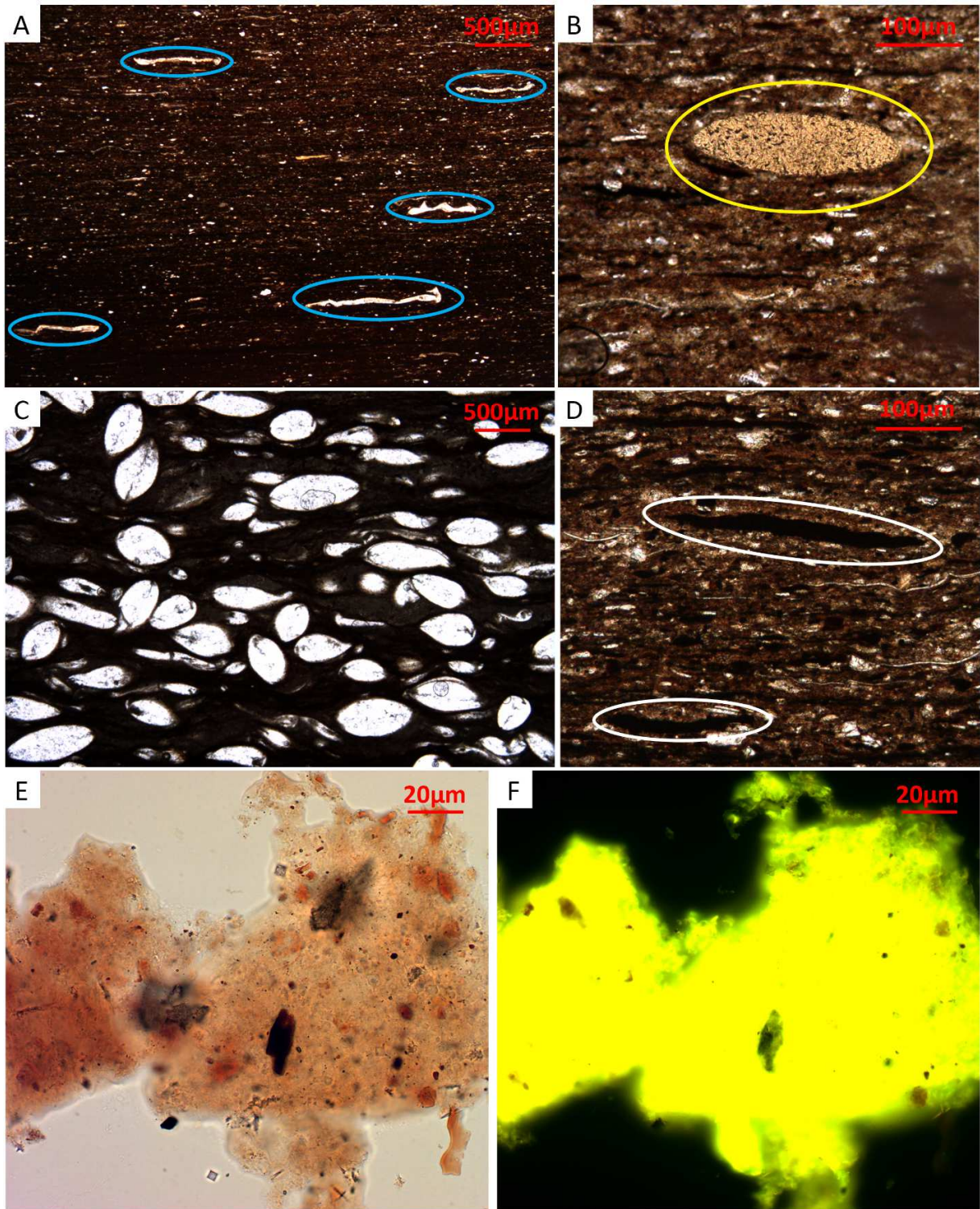


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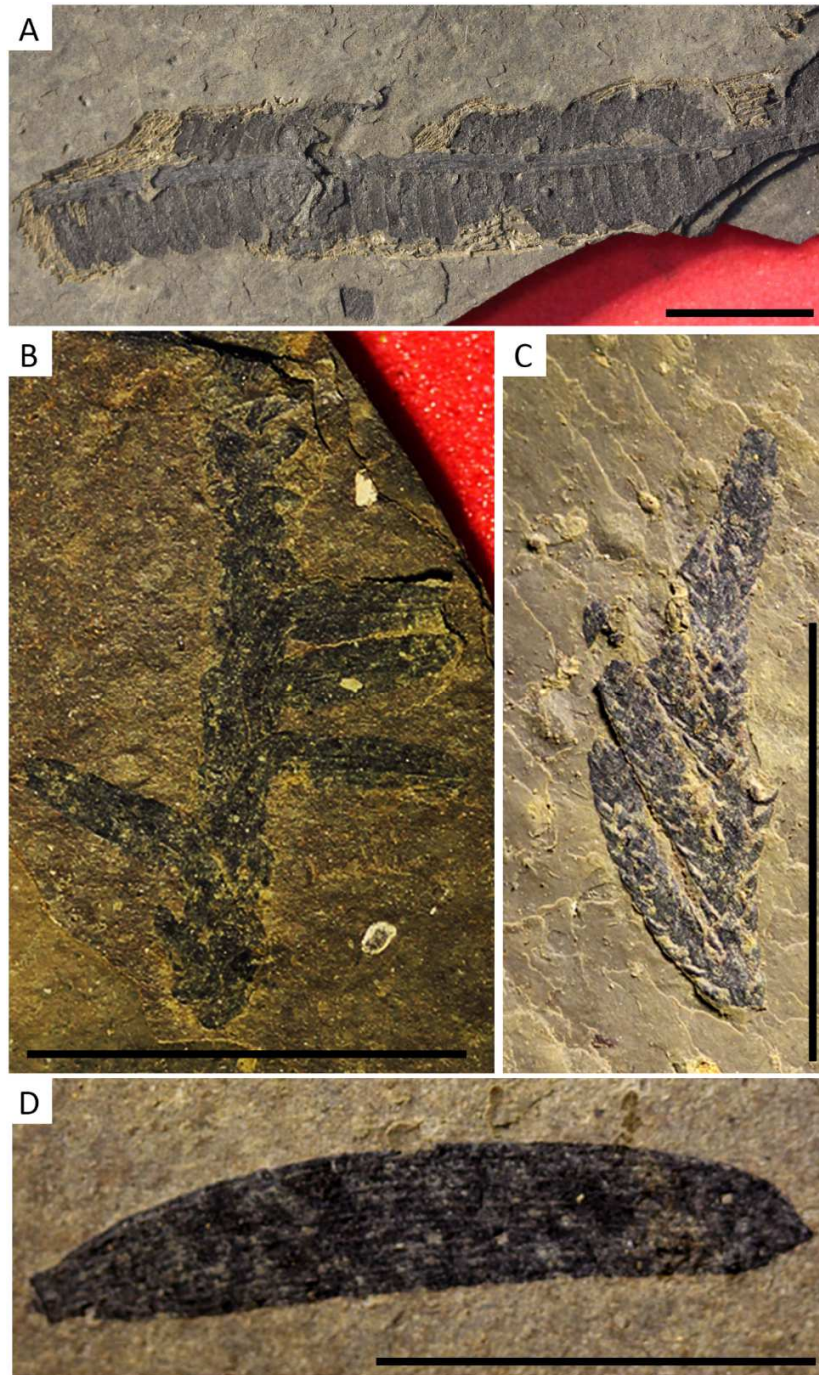
616 Figure 3. Comparison between the Lebanese dysodiles and other Lower Cretaceous non-marine
617 deposits with exceptional preservation. Paleomap modified from Scotese, 2014. The
618 paleoclimate data are extracted from Paleomap project (<http://www.scotese.com>)



619

620

621 Figure 4. Facies analysis: A-D. Thin sections of dysodiles showing the accumulation of organic
622 rich layers containing quartz minerals, some phosphate nodules (B), crushed ostracods (A,
623 encircled in blue), ostracods with crystalline infilling (C) and some dark lignite debris (D). E-F.
624 Palynofacies analysis shows the dominance of amorphous fluorescent organic matter indicating
625 algal or bacterial origin

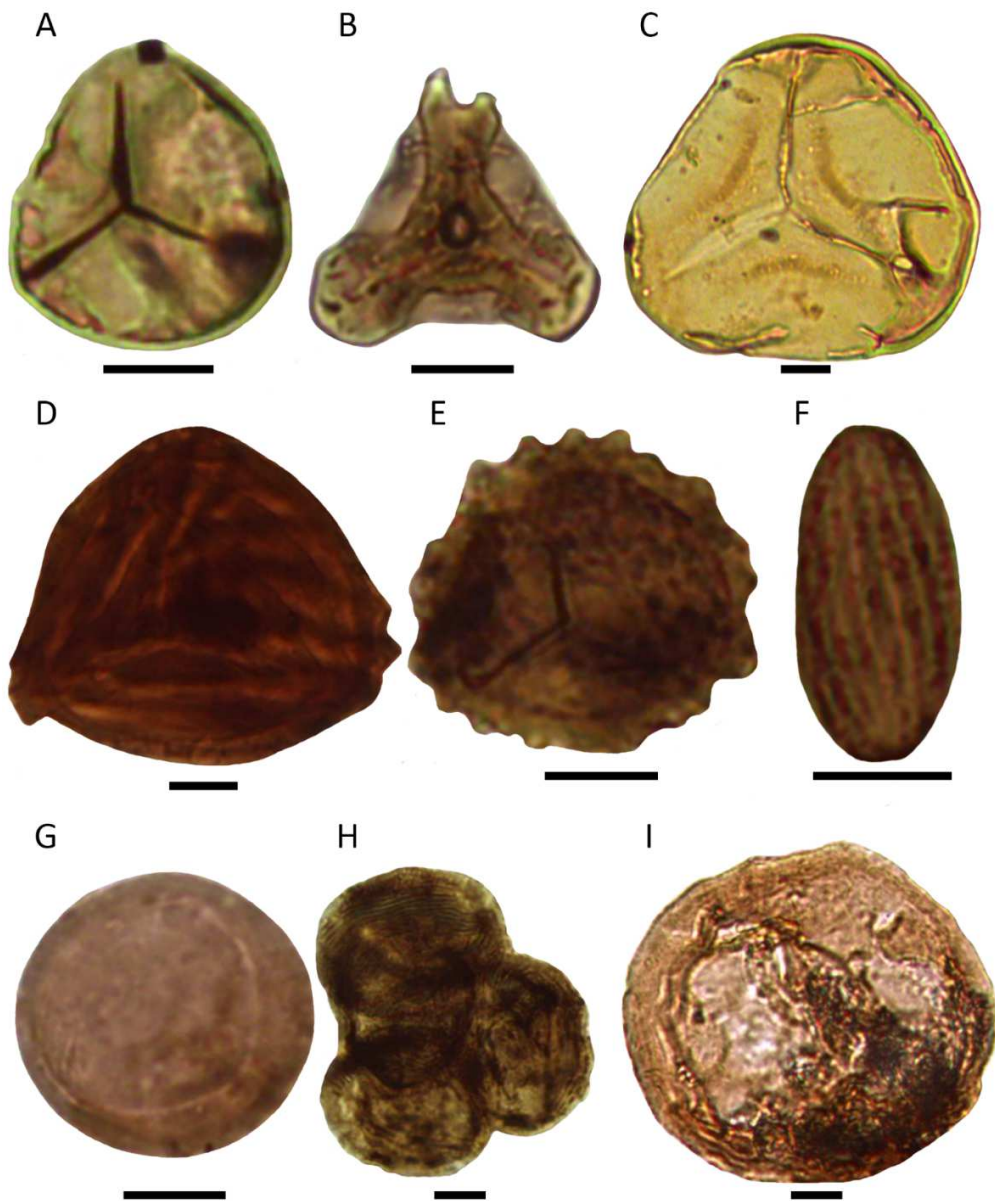


626

627 Figure 5. Main plant debris found in the dysodiles: A. *Weichselia reticulata*: F-PD-63124/4, B.

628 *Pagyophyllum* sp.: F-PD-63124/8, C. *Cyparissidium* sp.: F-PD-63124/42, D. *Zamites?* or

629 *Podozamites?*: F-PD-63124/37. Scale bar = 1cm

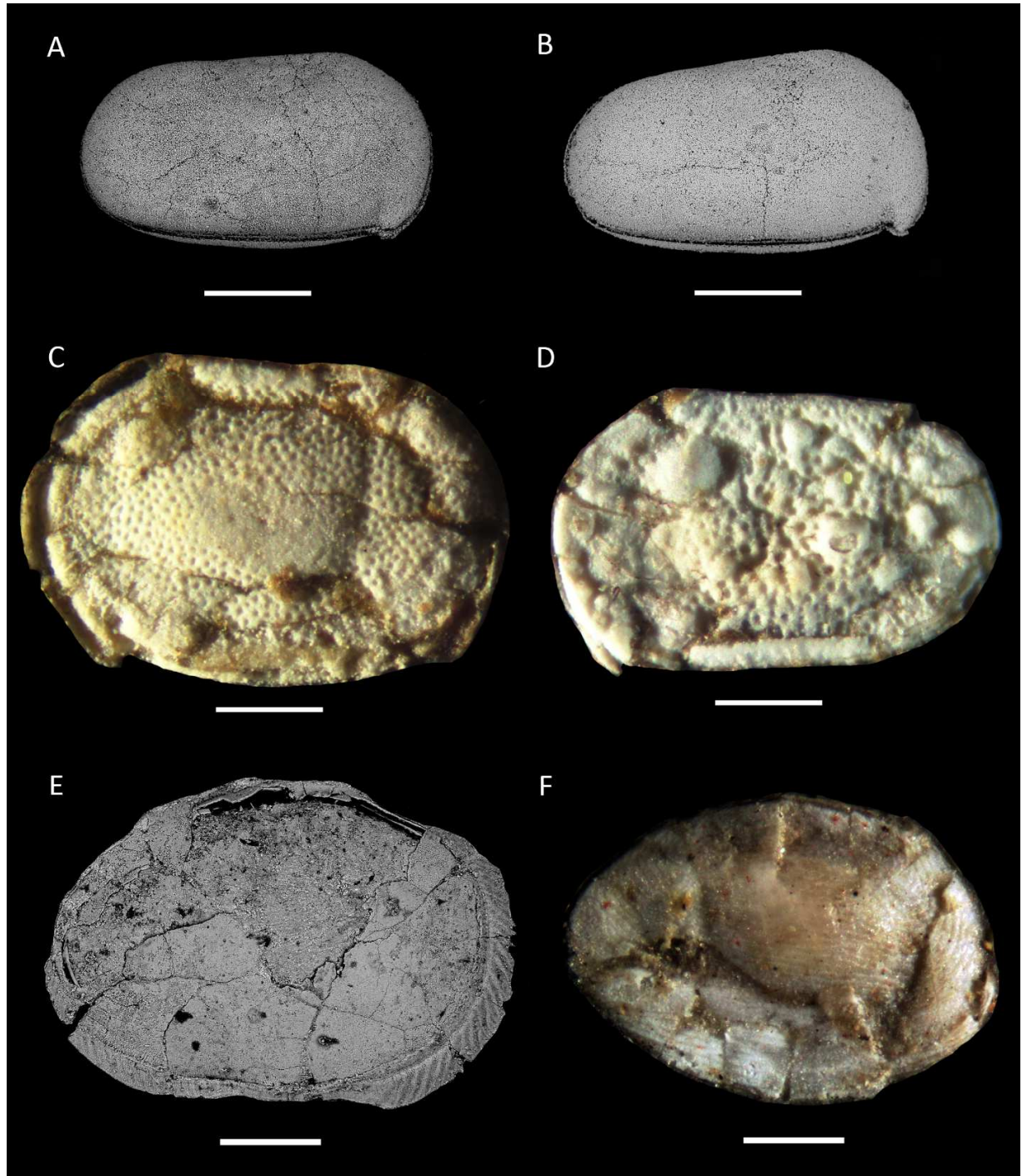


630

631 Figure 6. Figure 6. Palynomorphs identified within the dysodiles: A. *Deltoidospora* sp. from
 632 Tarchich: F-PALY-21481/1-15, B. *Dictyophyllidites harrissii* from Snyya: F-PALY-63287/6-15,
 633 C. *Matonisorites* sp. from Tarchich: F-PALY-21481/13-21, D. *Cicatricosisporites* sp. from
 634 Snyya: F-PALY-63287/14-4, E. *Verrucosisporites* sp. from Tarchich: F-PALY-21481/8-3, F.
 635 *Ephedripites* sp. from Snyya: F-PALY-63287/6-6, G-H. *Classopollis* sp. from Qrayn: G: F-

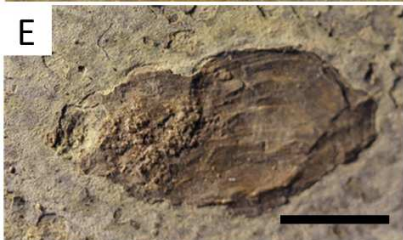
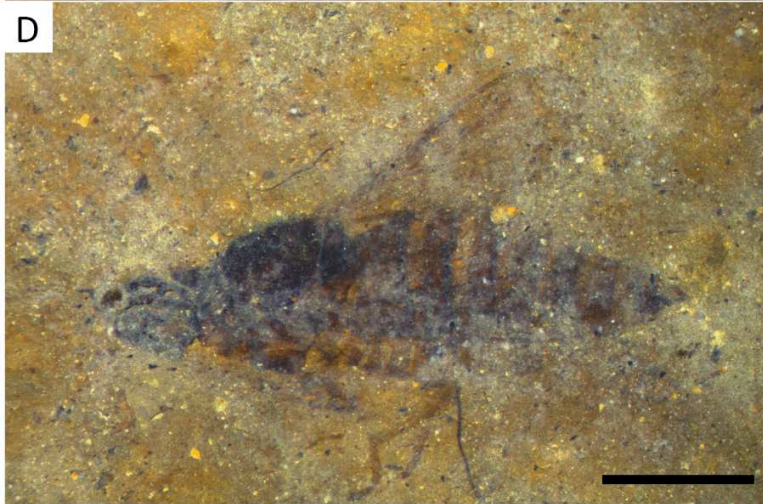
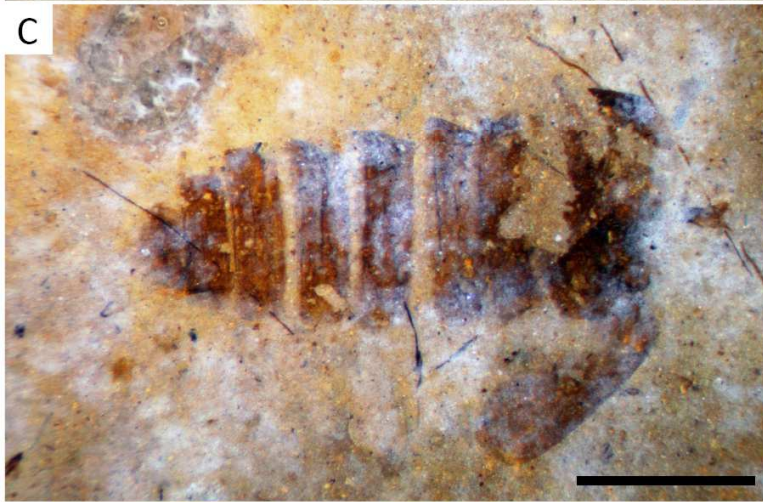
636 PALY-37353/6-11, H: F-PALY-37353/5-5, I. *Araucariacites* sp. from Qrayn: F-PALY-37353/5-

637 48. Scale bar = 10 μ m



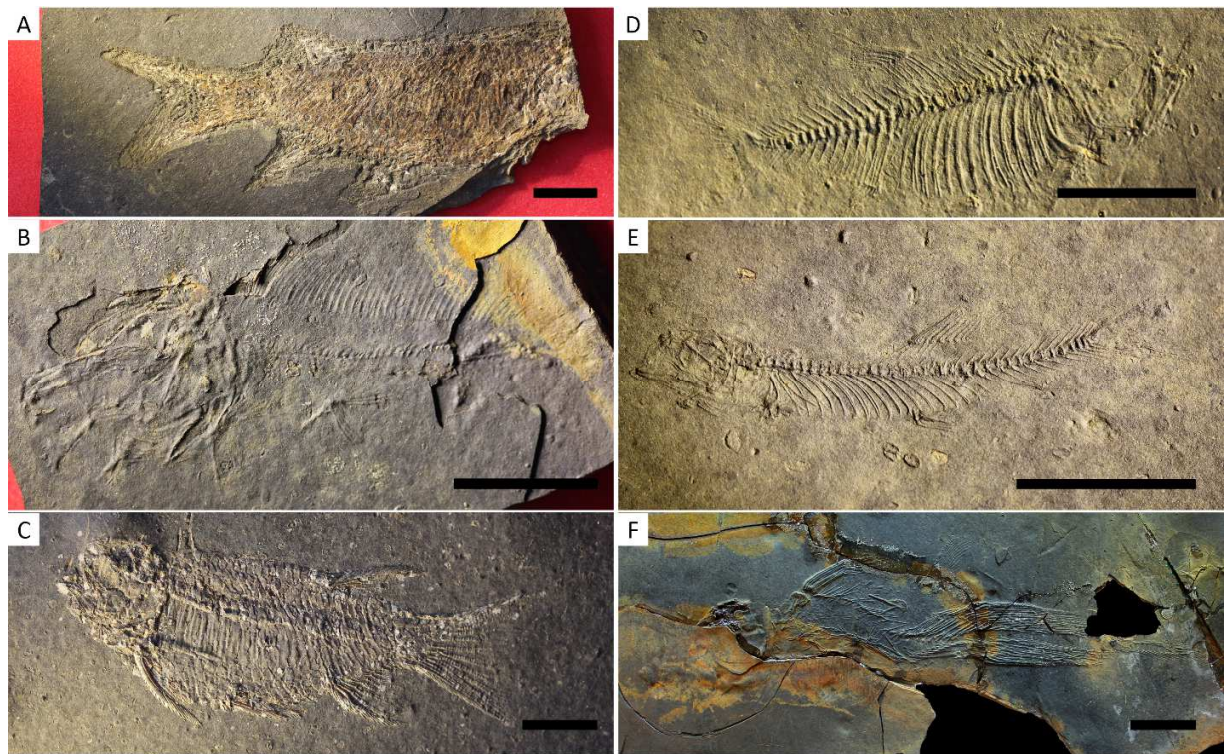
638

639 Figure 7. Ostracods found in the dysodiles: A, B and E are SEM images, while C, D and F are
640 optical images under incident light. A. *Cypridea* sp.1 from Tarchich: F-O-21481/1, B. *Cypridea*
641 sp.2 from Tarchich: F-O-21481/3, C. *Cypridea* sp.3 from Snyya: F-O-63287/1, D. *Cypridea* sp.4
642 from Zehalta: F-O-63177/1, E. *Cyprois* sp. from Qrayn: F-O-37353/2, F. *Zonocypris* sp. from
643 Zehalta: F-O-63177/2. Scale bar for the ostracods = 500 μ m



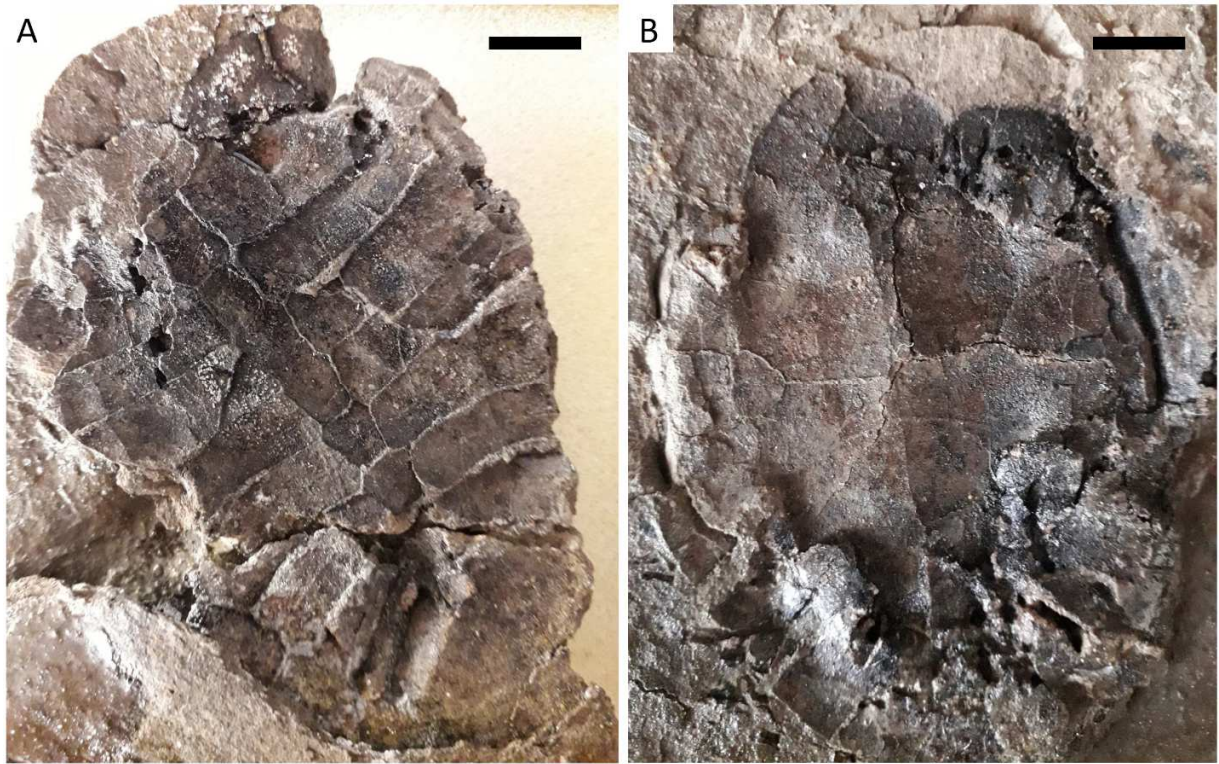
645 Figure 8. A-D. Fossil insects found in the dysodiles of Jdaydet Bkassine: A. Coleoptera
 646 (Anthicidae): F-INS-63124/2, B. Ephemeroptera represented by the newly described species
 647 *Libanoephemera inopinatabranchia* (Azar *et al.*, 2019): F-INS-63124/1, C. Coleoptera
 648 (Staphylinioidea): F-INS-63124/3, D. Diptera: F-INS-63124/4. Scale bar = 1 mm. E. – G.
 649 Gastropods found in the dysodiles: E: F-G-63124/13, F: F-G-63287/1, G: F-G-63124/1. Scale
 650 bar = 0.5 cm

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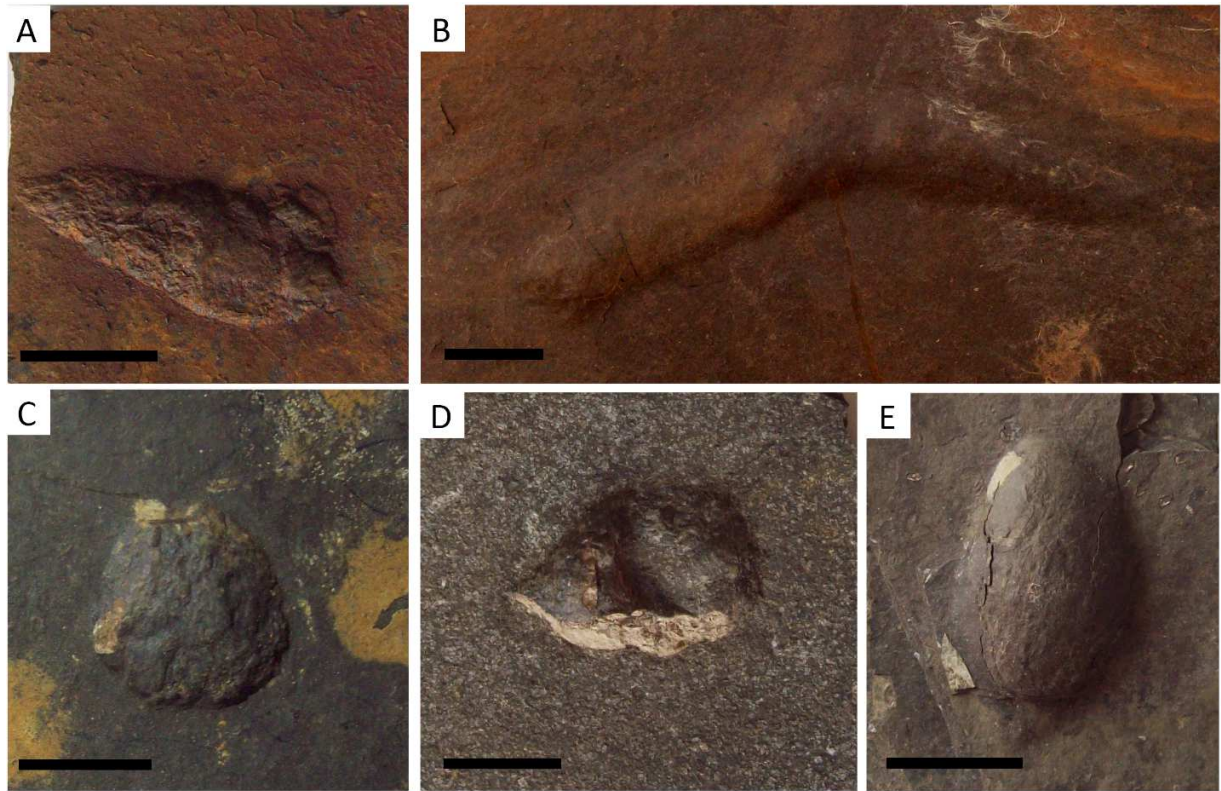
652

653 Figure 9. Fossil Ichthyofauna found in the dysodiles of Jdaydet Bkassine: A. Palaeopterygii: F-F-
 654 63124/35, B. Acipenseriformes: F-F-63124/69, C. Pleuropholidae: F-F-63214/1, D. Teleostei
 655 indet. Morphotype I: F-F-63124/33, E. Teleostei indet. Morphotype II: F-F-63124/17, F.
 656 Mawsoniidae: F-F-63124/300. Scale bar = 1 cm except for F scale bar = 5 cm



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658 Figure 10. Fossil turtle shell found in the dysodile of Tarchich: F-T-21481/1 A. Ventral view of
659 the dorsal shell, B. Visceral view of the plastron. Scale bar = 1 cm



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661 Figure 11. Coprolites found in the dysodiles showing different sizes and shapes. A. – D.
662 Coprolithes from Jdayet Bkassine: A. F-COP-63124/50, B. F-COP-63124/141, C. F-COP-
663 63124/5, D. F-COP-63124/59, E. Coprolithe from Snyya: F-COP-63287/2. Scale bar = 1 cm



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665 Figure 12. Preliminary reconstruction of the depositional environment of the dysodiles of the
666 lower Barremian of Lebanon

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674 Table 1. The fossils found in each facies in the different sampling sites: Facies 1 = organic rich
675 layers/ algal & bacterial organic matter, 2 = quartz minerals, 3 = phosphate nodules, 4 = dark
676 lignite debris; Plant debris 1 = *Weichselia reticulata*, 2 = *Pagyophyllum* sp., 3 = *Cyparissidium*
677 sp., 4 = *Zamites?* or *Podozamites?*; Fern spores 1 = *Deltoidospora* sp., 2 = *Matonisporites* sp., 3
678 = *Dictyophyllidites harrissii*, 4 = *Cicatricosisporites* sp., 5 = *Verrucosisporites* sp.; Pollen grains
679 1 = *Classopollis* sp., 2 = *Araucariacites australis*, 3 = *Ephedripites* sp.; Ostracods 1 = *Cypridea*
680 sp.1, 2 = *Cypridea* sp.2, 3 = *Cypridea* sp.3, 4 = *Cypridea* sp.4, 5 = *Cyprois* sp., 6 = *Zonocypris*
681 sp.; Ichthyofauna 1 = Palaeopterygii, 2 = Acipenseriformes, 3 = Pleuropholidae, 4 = Teleostei
682 indet., 5 = Mawsoniidae; + = present, - = absent, ? = not identifiable

Site	Qrayn			Tarchich		Jdaydet Bkassine	Snyya			Zehalta
				Main site	1 km away		Dysodiles 1-2-3-4	Dysodiles 1-2-3-4	Dysodiles 1-2-3-4	
Facies	Dysodiles 1-2-4	Claystone 1-2-4	Carbonates 1-4	Dysodiles 1-2-3-4	Dysodiles 1-2-3-4	Dysodiles 1-2-3-4	Dysodiles 1-2-3-4	Claystone 1-2-4	Dysodiles- like 1-2-4	Dysodiles 1-2-3-4
Plant debris	1	?	-	1	-	1-2-3-4	1-4	?	?	1-4
Fern spores	-	-	-	1-2-4-5	1	-	1-2-4	2-3	1-2-3	-
Pollen grains	1-2	2	1-2	1-2	-	-	1-2	1	1-2-3	1
Ostracods	Crushed & flattened 5	Cristalline infilling & internal moulds 5	-	Crushed & flattened 1-2	Cristalline infilling 1-2	Crushed & flattened 1-2-3-4-6	Crushed & flattened 1-2-3-4-6	-	-	Crushed & flattened 1-2-3-4-6
Insects	-	-	-	-	-	+	+	-	-	-
Gastropods	-	-	-	-	-	+	+	-	-	+
Ichthyofauna	-	-	-	4	-	1-2-3-4-5	3-4	-	-	4
Turtles	-	-	-	+	-	-	-	-	-	-

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688 Table 2. The botanical affinities of identified taxa of spores and pollen grains

Division	Family	Taxa of spores and pollen grains
Monilophyta	Cyatheaceae, Dicksoniaceae?	<i>Deltoidospora</i> sp.
	Matoniaceae	<i>Matonisorites</i> sp. <i>Dictyophyllidites harrissii</i>
	Schizaeaceae	<i>Cicatricosisporites</i> sp.
	Zygopteridaceae?	<i>Verrucosisporites</i> sp.
	Coniferophyta	Cheirolepidiaceae
Araucariaceae		<i>Araucariacites australis</i>
Ephedraceae		<i>Ephedripites</i> sp.

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706 Table 3. Habitat and ecological niche of the entomofauna found in the dysodiles

Habitat	Ecological niche	Entomofauna
Terrestrial		
Forest	Herbivorous/ fungivorous	Diptera
	Carnivorous	Staphylinioidea
	Omnivorous	Anthicidae adults
Shallow waters/ rivers	No feeding	Ephemeroptera adults
Fully aquatic		
Plankton	Plankton inhabitants	Diptera pupae
Benthos	Bottom burrowers	Ephemeroptera larvae
	Detritivorous	Diptera larvae Ephemeroptera larvae