



**HAL**  
open science

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

Layla El Hajj, François Baudin, Raymond Gèze, Lionel Cavin, Jean Dejax,  
Géraldine Garcia, David Horne, Sibelle Maksoud, Olga Otero, Dany Azar

### ► To cite this version:

Layla El Hajj, François Baudin, Raymond Gèze, Lionel Cavin, Jean Dejax, et al.. Dysodiles from the lower Barremian of Lebanon: Insights on the fossil assemblages and the depositional environment reconstruction. *Cretaceous Research*, 2021, 120, pp.104732. 10.1016/j.cretres.2020.104732 . hal-03136990

**HAL Id: hal-03136990**

**<https://hal.science/hal-03136990>**

Submitted on 3 Feb 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

4 Layla EL HAJJ<sup>1,2,3\*</sup>, François BAUDIN<sup>2</sup>, Raymond GÈZE<sup>1</sup>, Lionel CAVIN<sup>4</sup>, Jean DEJAX<sup>5</sup>,  
5 Géraldine GARCIA<sup>6</sup>, David J. HORNE<sup>7</sup>, Sibelle MAKSOUD<sup>1</sup>, Olga OTERO<sup>6</sup>, Dany AZAR<sup>1\*</sup>

6 <sup>1</sup>Lebanese University, Faculty of Sciences II, Fanar-Matn, P.O.box 90656 Jdeideh, Lebanon

7 <sup>2</sup>Sorbonne Université, Institut des Sciences de la Terre Paris, IStEP, UMR 7193, CNRS, 4 Place  
8 Jussieu, 75005 Paris, France

9 <sup>3</sup>Centre de Recherche en Paléontologie - Paris, CR2P, UMR 7207, CNRS, Sorbonne Université,  
10 4 Place Jussieu, 75005 Paris, France

11 <sup>4</sup>Secteur des Sciences de la Terre, Muséum d'Histoire Naturelle, CP6434, 1211 Genève 6, Suisse

12 <sup>5</sup>Centre de Recherche en Paléontologie - Paris, CR2P, UMR 7207, CNRS, Muséum National  
13 d'Histoire Naturelle, 57 rue Cuvier, CP 38, 75005 Paris, France

14 <sup>6</sup>PalEvoPrim, UMR CNRS 7262, Université de Poitiers, UFR SFA, Bât. B35, 6 rue M. Brunet,  
15 TSA 51106, 86073 Poitiers cedex 9, France

16 <sup>7</sup>School of Geography, Queen Mary University of London, Mile End Road, London E1 4NS, UK

17

18 \* Corresponding authors: [layla.el\\_hajj@sorbonne-universite.fr](mailto:layla.el_hajj@sorbonne-universite.fr); [danyazar@ul.edu.lb](mailto:danyazar@ul.edu.lb)

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**

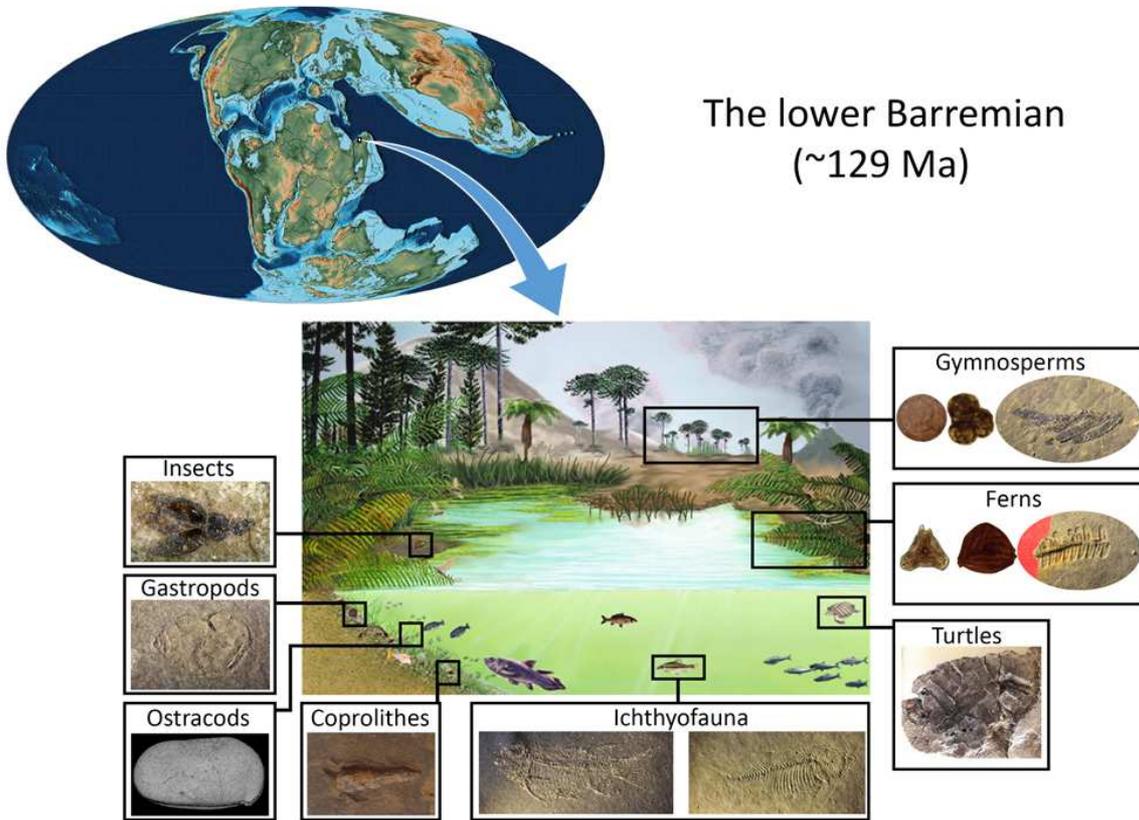
27 The Recent re-/discovery of unusual Lower Cretaceous continental sediments (dysodiles) brings  
28 important and exceptional paleontological assets. Dysodile beds are found in many localities  
29 across Lebanon and are characterized by their high organic matter content and their richness in  
30 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 m<sup>2</sup>. 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 m<sup>2</sup> 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 $\mu$ 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  $\mu\text{m}$ ), 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), Staphylinidae (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 Cittert, 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

#### 446 **Acknowledgments**

447 The authors would like to thank the “Société Murex”, Mr. Salim EDDE and the Lebanese  
448 University for their scholarship grant to L. EL HAJJ. The authors express their gratitude to  
449 Florence SAVIGNAC for her assistance during the palynofacies analysis, Fred DELBES for the  
450 preparation of the thin sections (ISTeP laboratory Paris), Frank SENEGAS for the extraction of  
451 the ostracods using the hot acetolysis method (CR2P laboratory Paris) and Florian WITZMANN  
452 (Museum für Naturkunde Berlin) for information. GG also thanks Renaud BOISTEL, Xavier  
453 VALENTIN (PalEvoPrim, Université de Poitiers) and Arnaud MAZURIERS (IC2MP,  
454 Université de Poitiers) for their technical support. This paper is a contribution to the project  
455 “Dysodiles of the Lower Cretaceous of Lebanon: stratigraphical, paleontological and  
456 geochemical characterization” financed by the Lebanese University. We thank Eduardo  
457 KOUTSOUKOS, Elena YAZYKOVA and the anonymous reviewers for their valuable  
458 comments and suggestions allowing us to improve the manuscript.

459

#### 460 **References**

461 Alvin, K.L., 1974. Leaf anatomy of *Weichselia* based on fusainized material. *Palaeontology* 17  
462 (3), 587 – 598.

463 Alvin, K.L., 1982. Cheirolepidiaceae: Biology, structure and palaeoecology. Review of  
464 Palaeobotany and Palynology 37, 71 – 98.

465 Anderson, F.W., Bazley, R.A.B., Shephard-Thorn, E.R., 1967. The sedimentary and faunal  
466 sequence of the Wadhurst Clay (Wealden) in boreholes at Wadhurst Park, Sussex. Bulletin of the  
467 Geological Survey of Great Britain 27, 171 – 235.

468 Azar, D., 2007. Preservation and accumulation of biological inclusions in Lebanese amber and  
469 their significance. Comptes rendus Palevol 6, 5 – 56.

470 Azar, D., 2012. Lebanese amber: a “Guinness Book of Records”. Annales Universitatis  
471 Paedagogicae Cracoviensis 111, 44 – 60.

472 Azar, D., Gèze, R., Acra, F., 2010. Lebanese Amber (Chapter 14). In: Penney, D. (Ed.),  
473 Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press, Manchester,  
474 304, pp. 271 – 298.

475 Azar, D., De La Ferté, C., El Hajj, L., Nel, A., Maksoud, S., 2019. An exceptional  
476 ephemeropteran larva from the Lower Cretaceous dysodiles of Lebanon. Palaeoentomology 2  
477 (2), 192 – 198.

478 Bischoff, G., 1963. Ostracoden-Studien im Libanon 2, Die Gattung Cypridea im Aptien  
479 inferieur. Senckenbergiana Lethaea 44 (4), 301 – 319.

480 Boomer, I., Horne, D.J., Slipper, I.J., 2003. The use of ostracods in palaeoenvironmental studies,  
481 or what can you do with an ostracod shell? In: Park, L.E. & Smith, A.J. (Eds.), Bridging the gap:  
482 Trends in the Ostracode Biological and Geological Sciences. The Paleontological Society Papers  
483 9, 290, pp. 153 – 179.

484 Botta, P., 1831. Sur la structure géognostique du Liban et de l'Anti-Liban. Bulletin de la Société  
485 Géologique de France 10, 234 – 239.

486 Brew, G., Barazangi, M., Al-Maleh, A.K., Sawaf, T., 2001. Tectonic and geologic evolution of  
487 Syria. *GeoArabia* 6 (4), 573 – 616.

488 Briggs, D.E.G., 2003. The role of decay and mineralization in the preservation of soft-bodied  
489 fossils. *Annual Review of Earth and Planetary Sciences* 31, 275 – 301.

490 Combaz, A., 1964. Les palynofaciès. *Revue de Micropaléontologie* 7, 205 – 218.

491 Conway, B.H., 1996. A palynological investigation across the Jurassic-Cretaceous boundary on  
492 the south-east flanks of Mount Hermon, Israel. *Cretaceous Research* 17, 197 – 214.

493 Cordier, L., 1808. Sur le dysodile, nouvelle espèce minérale. *Journal des Mines* 23, 271 – 274.

494 Danilov, I.G., Vitek, N.S., 2012. Cretaceous trionychids of Asia: an expanded review of their  
495 record and biogeography. In: Brinkman, D.B., Holroyd, P.A., Gander, J.D. (Eds.), *Morphology  
496 and Evolution of Turtles*. Springer Science + Business Media, Dordrecht, Netherlands. DOI:  
497 10.1007/978-94-007-4309-0-12.

498 De la Fuente, M., Zetter, R., 2016. Palynomorphs. In: Poyato-Ariza, F.J., Buscalioni, A.D.  
499 (Eds.), *Las Hoyas: A Cretaceous Wetland. A multidisciplinary synthesis after 25 years of  
500 research on an exceptional fossil Lagerstätte from Spain*. Verlag Dr. Friedrich Pfeil, München  
501 Germany, 262, pp. 31 – 42.

502 Dubertret, L., 1955. Notice explicative de la carte géologique du Liban (200000°). Ministère des  
503 travaux publics, Beyrouth, Liban. 74 pp, 30 fig.

504 Durand, B., Nicaise, G., 1980. Procedures for kerogen isolation. In: Durand, B. (Ed.), Kerogen:  
505 Insoluble organic matter from sedimentary rocks. Technip, Paris, 519, pp. 35 – 54.

506 Edwards, W., 1929. Lower Cretaceous plants from Syria and Transjordan. The annals and  
507 magazine of Natural History 5 (10), 394 – 405.

508 El Hajj, L., Baudin, F., Littke, R., Nader, F.H., Gèze, R., Maksoud, S., Azar, D., 2019.  
509 Geochemical and petrographic analyses of new petroleum source rocks from the onshore Upper  
510 Jurassic and Lower Cretaceous of Lebanon. International Journal of Coal Geology 204, 70 – 84.

511 El Hajj, L., Horne, D.J., Baudin, F., Gèze, R., Azar, D., 2020. The first non-marine ostracod  
512 fauna from the Lower Barremian dysodiles of Lebanon. Lethaia, DOI: 10.1111/let.12393 vol.  
513 000, pp. 1 – 13.

514 Ferreira, G.S., Langer, M.C., 2013. A pelomedusoid (Testudines, pleurodira) plastron from the  
515 Lower Cretaceous of Alagoas, Brazil. Cretaceous Research 46, 267 – 271.

516 Forey, P.L., Yi, L., Patterson, C., Davies, C.E., 2003. Fossil fishes from the Cenomanian (Upper  
517 Cretaceous) of Namoura, Lebanon. Journal of Systematic palaeontology 1 (4), 227.

518 Fraas, O., 1878. Geologisches aus dem Libanon. Jahreshefte des Vereins für vaterländische  
519 Naturkunde, Württemberg, 34, 257 – 391.

520 Fregenal-Martínez, M., Meléndez, N., 2016. Environmental reconstruction : a historical review.  
521 In: Poyato-Ariza, F.J., Buscalioni, A.D. (Eds.), Las Hoyas: A Cretaceous Wetland. A  
522 multidisciplinary synthesis after 25 years of research on an exceptional fossil Lagerstätte from  
523 Spain. Verlag Dr. Friedrich Pfeil, München Germany, 262, pp. 14 – 28.

- 524 Gayet, M., Belouze, A., Abi Saad, P., 2003. Liban Mémoire du temps. Les poissons fossiles.  
525 Editions Desiris. 158 pp.
- 526 Grande, L., Hilton, E.J., 2006. An exquisitely preserved skeleton representing a primitive  
527 sturgeon from the Upper Cretaceous Judith River Formation of Montana (Acipenseriformes:  
528 Acipenseridae: n. gen. and sp.). *Journal of Paleontology* 80, 1 – 39.
- 529 Granier, B., Azar, D., Maksoud, S., Gèze, R., Habchi, R., 2015. New fossiliferous sites with  
530 Barremian Charophyta in the “Grès du Liban” auct. (Lebanon), with a critical perspective  
531 regarding the nature of *Munieria* Deecke, 1883. *Carnets de Géologie* 15 (15), 199 – 229.
- 532 Granier, B., Toland, C., Gèze, R., Azar, D., Maksoud, S., 2016. Some steps toward a new story  
533 of the Jurassic-Cretaceous transition in Mount Lebanon. *Carnets de Géologie* 16 (8), 247 – 269.
- 534 Guernet, C., Lethiers, F., 1989. Ostracodes et recherche des milieux anciens: possibilités et  
535 limites. *Bulletin de la Société Géologique de France* 3, 577 – 588.
- 536 Hirayama, R., Brinkman, D.B., Danilov, I.G., 2000. Distribution and biogeography of non-  
537 marine cretaceous turtles. *Russian Journal of Herpetology* 7 (3), 181 – 198.
- 538 Horne, D.J., Colin, J.-P., 2005. The affinities of the ostracod genus *Cypridea* Bosquet, 1852, and  
539 its allies, with consideration of implications for the phylogeny of nonmarine cypridoidean  
540 ostracods. *Revue de micropaléontologie* 48, 25 – 35.
- 541 Janensch, W., 1925. Fische aus dem Dysodil des Wealden vom Libanon. *Zeitschrift der*  
542 *Deutschen Geologischen Gesellschaft (Abhandlungen und Monatsberichte)* 76, 54 – 59.
- 543 Jin, F., 1999. Middle and Late Mesozoic acipenseriformes from northern Hebei and western  
544 Liaoning, China. *Palaeoworld (in Chinese)* 11, 188 – 280.

545 Kachacha, G., Cuny, G., Azar, D., Abi Saad, P., 2017. Revision of the fossil batomorphs from  
546 the Cretaceous of Lebanon and their impact on our understanding of the early stage of evolution  
547 of the clade. *Research & Knowledge* 3 (2), 33 – 37.

548 Kunzmann, L., 2007. Araucariaceae (Pinopsida): Aspects in palaeobiogeography and  
549 palaeobiodiversity in the Mesozoic. *Zoologischer Anzeiger* 246 (4), 257 – 277.

550 Lethiers, F., Crasquin-Soleau, S., 1988. Comment extraire les microfossiles à tests calcitiques  
551 des roches calcaires dures. *Revue de Micropaleontologie* 311, 56 – 61.

552 Lichtig, A.J., Luxas, S.G., 2016. Cretaceous non-marine turtle biostratigraphy and evolutionary  
553 events. *Cretaceous period: Biotic diversity and biogeography: New Mexico Museum of Natural  
554 History and Science Bulletin* 71, 185 – 194.

555 Maksoud, S., Azar, D., 2020. Lebanese amber: latest updates. *Palaeoentomology* 3 (2), 125 –  
556 155.

557 Meisch, C., 2000. *Freshwater Ostracoda of Western and Central Europe*. Spektrum  
558 Akademischer Verlag GmbH, Heidelberg, Berlin. 522 pp.

559 Nader, F.H., 2014. *The geology of Lebanon*. Scientific Press Ltd., Beaconsfield, UK. 108 pp.

560 Nesson, L.A., 1995. On some Mesozoic turtles of the Fergana Depression (Kyrgyzstan) and  
561 Dzhungar Alatau Ridge (Kazakhstan). *Russian Journal of Herpetology* 2, 134 – 141.

562 Neumann, V.H., Borrego, A.G., Cabrera, L., Dino, R., 2003. Organic matter composition and  
563 distribution through the Aptian – Albian lacustrine sequences of the Araripe Basin, northeastern  
564 Brazil. *International Journal of Coal Geology* 54, 21 – 40.

565 Peters, K.E., Walters, C.C., Moldowan, J.M., 2005. The biomarker guide. In: Biomarkers and  
566 isotopes in petroleum exploration and Earth history, second ed., vol. 2, Cambridge University  
567 Press, Cambridge, 475 – 1155.

568 Poropat, S.F., Martin, S.K., Tosolini, A-M. P., Wagstaff, B.E., Bean, L.B., Kear, B.P., Vickers-  
569 Rich, P., Rich, T.H., 2018. Early Cretaceous polar biotas of Victoria, southeastern Australia – an  
570 overview of research to date. *Alcheringa: An Australian Journal of Palaeontology*. DOI:  
571 10.1080/03115518.2018.1453085.

572 Poyato-Ariza, F.J., Martín-Abad, H., 2016. Osteichthyan fishes. In: Poyato-Ariza, F.J.,  
573 Buscalioni, A.D. (Eds.), *Las Hoyas: A Cretaceous Wetland. A multidisciplinary synthesis after*  
574 *25 years of research on an exceptional fossil Lagerstätte from Spain*. Verlag Dr. Friedrich Pfeil,  
575 München Germany, 262, pp.114 – 132.

576 Romano, C., Koot, M.B., Kogan, I., Brayard, A., Minikh, A.V., Brinkmann, W., Bucher, H.,  
577 Kriwet, J., 2016. Permian – Triassic Osteichthyes (bony fishes): Diversity dynamics and body size  
578 evolution. *Biological reviews* 91, 106 – 147.

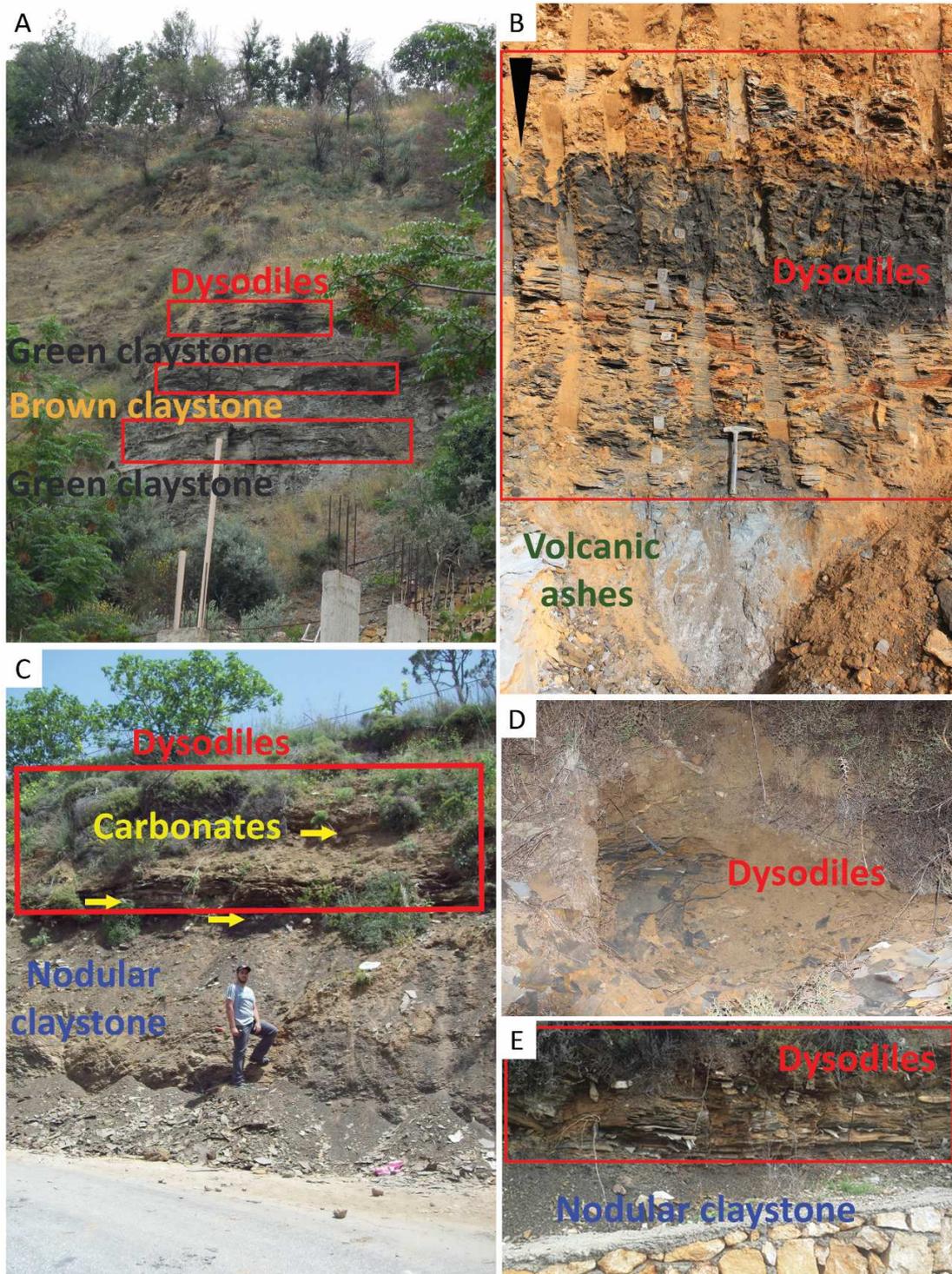
579 Rosenfeld, A., Hirsch, F., Honingstein, A., 1995. Early Cretaceous ostracodes from the Levant.  
580 In: Riha, J. (Ed.), *Ostracoda in Biostratigraphy*. Balkema, Rotterdam, 464, pp. 111 – 121.

581 Scotese, C.R., 2014. Atlas of Early Cretaceous Paleogeographic Maps, PALEOMAP Atlas for  
582 ArcGIS, volume 2, The Cretaceous, Maps 23 – 31, Mollweide Projection, PALEOMAP Project,  
583 Evanston, IL.

584 Srivastava, S.K., 1968. Ephedralean pollen from the Upper Cretaceous Edmonton Formation of  
585 Alberta (Canada) and their paleoecological significance. *Canadian Journal of Earth Sciences* 5,  
586 211 – 221.

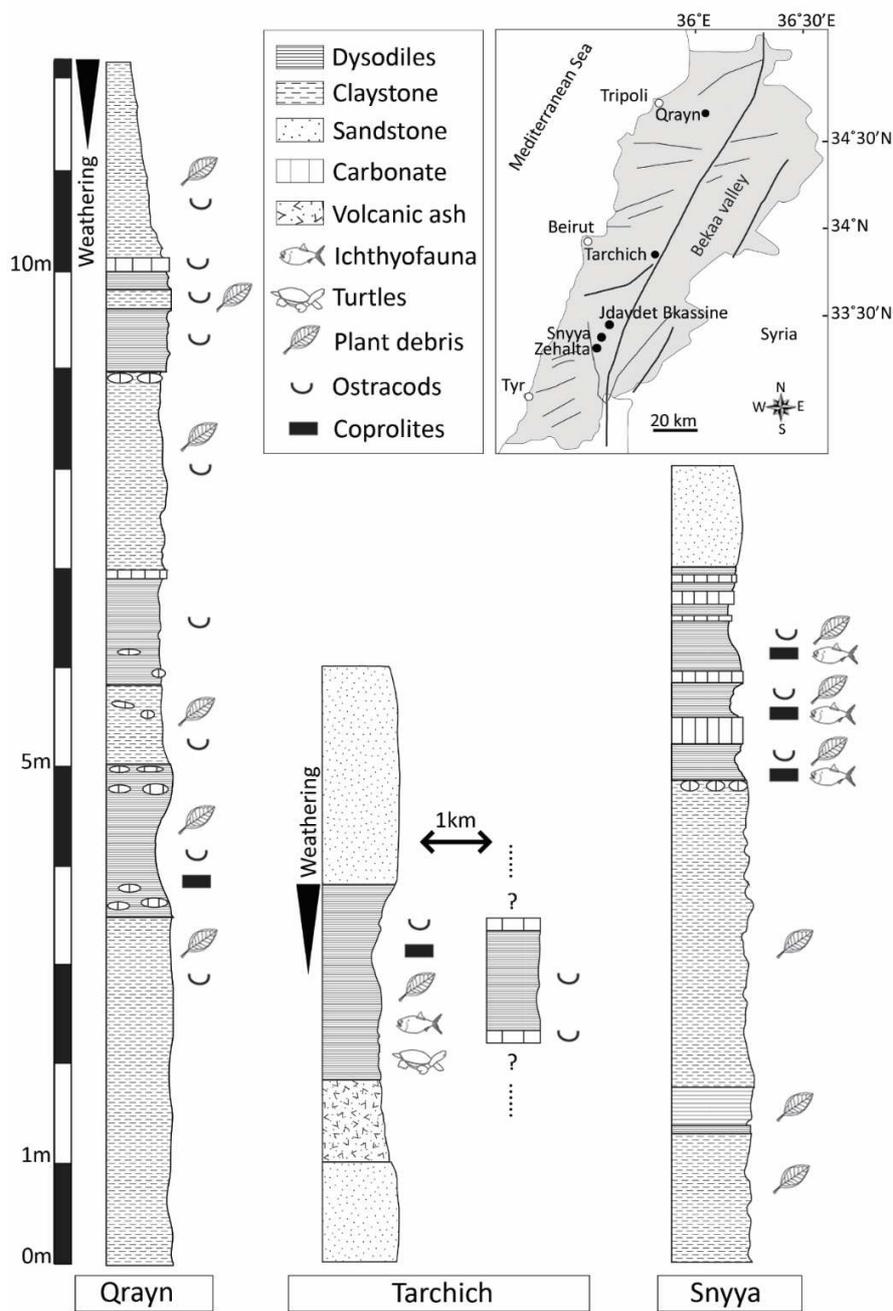
- 587 Talbot, M., Allen, P., 1996. Lakes. In: Reading, H.G. (Ed.), Sedimentary environments,  
588 processes, facies and stratigraphy. Blackwell publishing, UK, 704, pp. 83 – 124.
- 589 Tintori, A., Sun, Z.Y., Lombardo, C., Jiang, D.Y., Sun, Y.L., Hao, W.C., 2010. A new basal  
590 neopterygian from the Middle Triassic of Luoping County (South China). *Rivista Italiana di*  
591 *Paleontologia e Stratigrafia* 116 (2), 161 – 172. Traverse, A., 2007. *Paleopalynology: Second*  
592 *Edition*. Springer Science & Business Media, Netherlands 813 pp.
- 593 Tyson, R., 1995. *Sedimentary organic matter: Organic facies and palynofacies*. Chapman and  
594 Hall, London, 615 pp.
- 595 Van Konijnenburg-Van Cittert, J.H.A., 2002. Ecology of some late Triassic to Early Cretaceous  
596 ferns in Eurasia. *Review of Palaeobotany and Palynology* 119, 113 – 124.
- 597 Veltz, I., 2008. *Le Passage Jurassique Crétacé au Liban*. Thèse de doctorat, Université de Reims  
598 Champagne-Ardenne, Reims, France, 279 pp.
- 599 Vitek, N.S., Joyce, W.G., 2015. A review of the fossil record of New World turtles of the clade  
600 Pan-Trionychidae. *Bulletin of the Peabody Museum of Natural History* 56, 185 – 244.
- 601 Watson, J., Alvin, K., 1996. An English Wealden floral list, with comments on possible  
602 environmental indicators. *Cretaceous Research* 17, 5 – 26.
- 603 Zhou, Z., 2014. The Jehol Biota, an Early Cretaceous terrestrial Lagerstätte: new discoveries and  
604 implications. *National Science Review* 1 (4), 543 – 559.

605



606

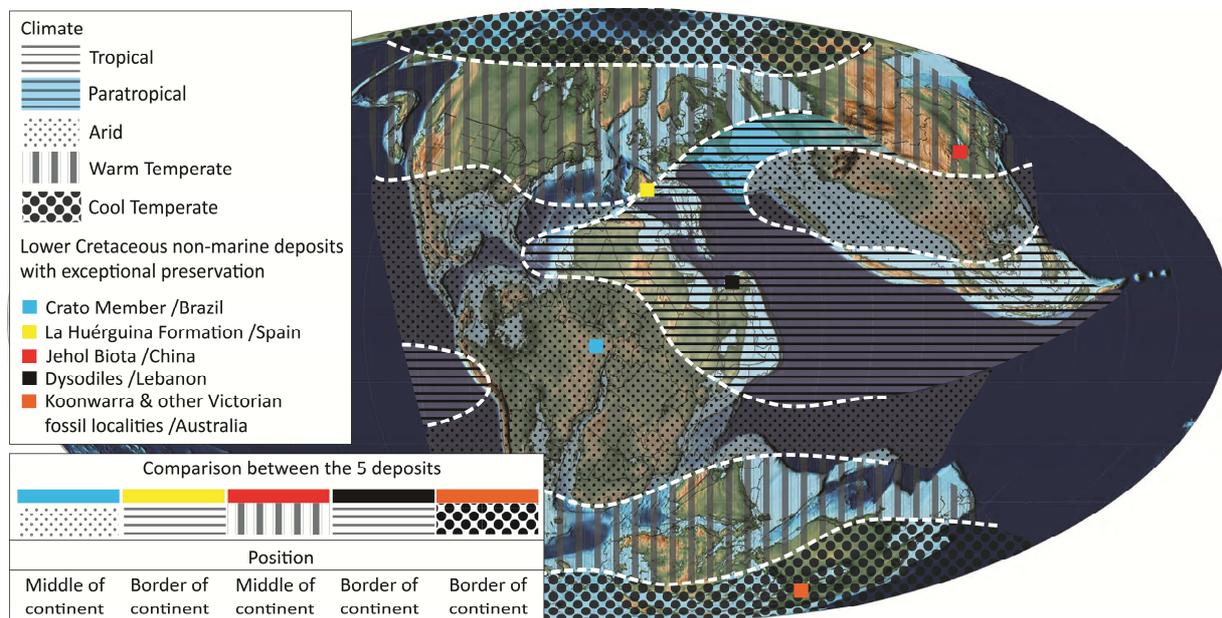
607 Figure 1. General view of the five sampling localities: A. Qrayn, B. Tarchich, the black arrow  
 608 indicates the decreasing weathering effect, C. Snyya, D. Jdaydet Bkassine, E. Zehalta



609

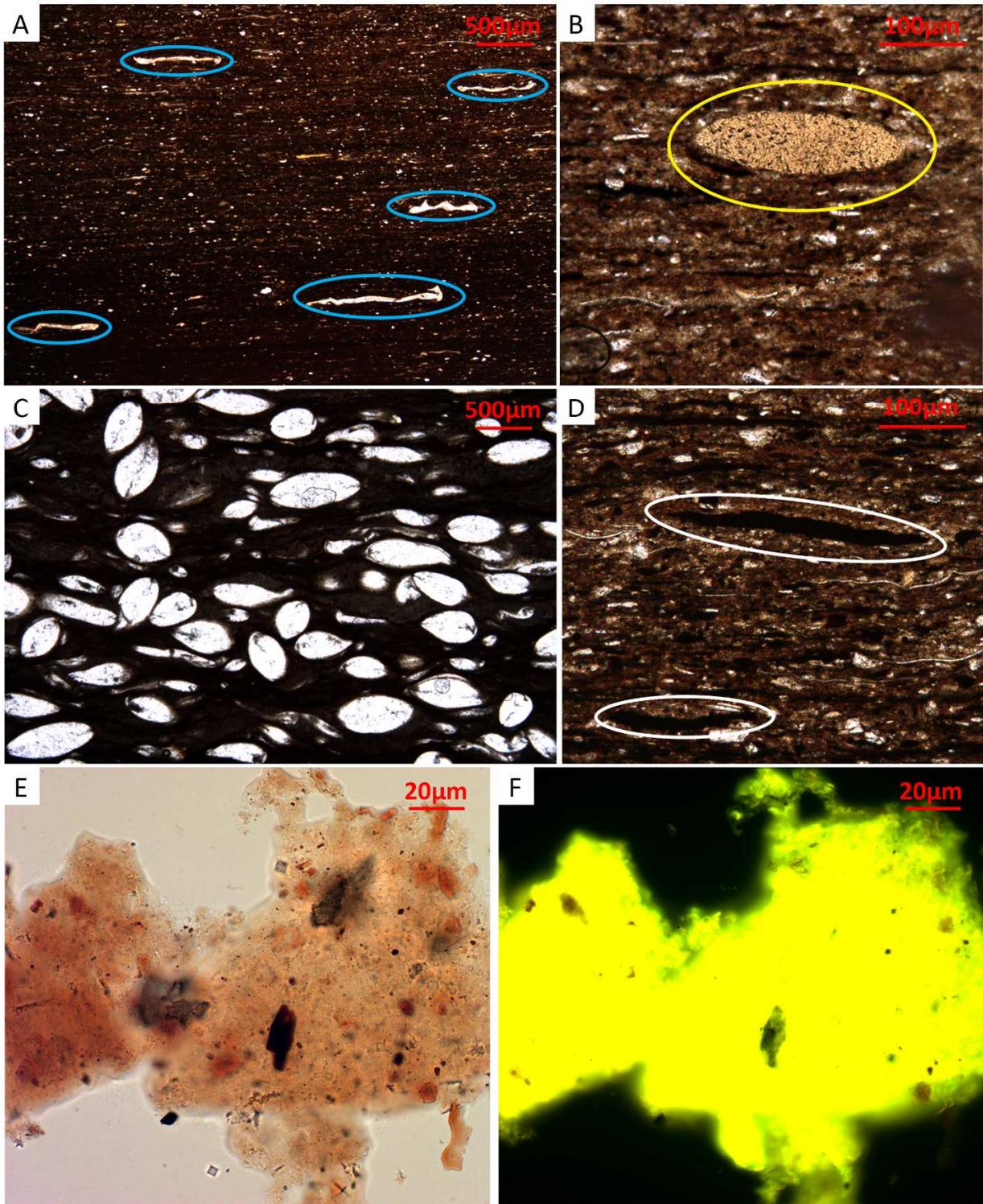
610 Figure 2. Location of the five sampling localities on the simplified map of Lebanon (Nader,  
 611 2014) & detailed stratigraphic logs of the three main sampling localities, showing the facies and  
 612 the different fossils; Qrayn in the North of Lebanon, Tarchich in the Center of Lebanon, and  
 613 Snyya in the South of Lebanon

614



615

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

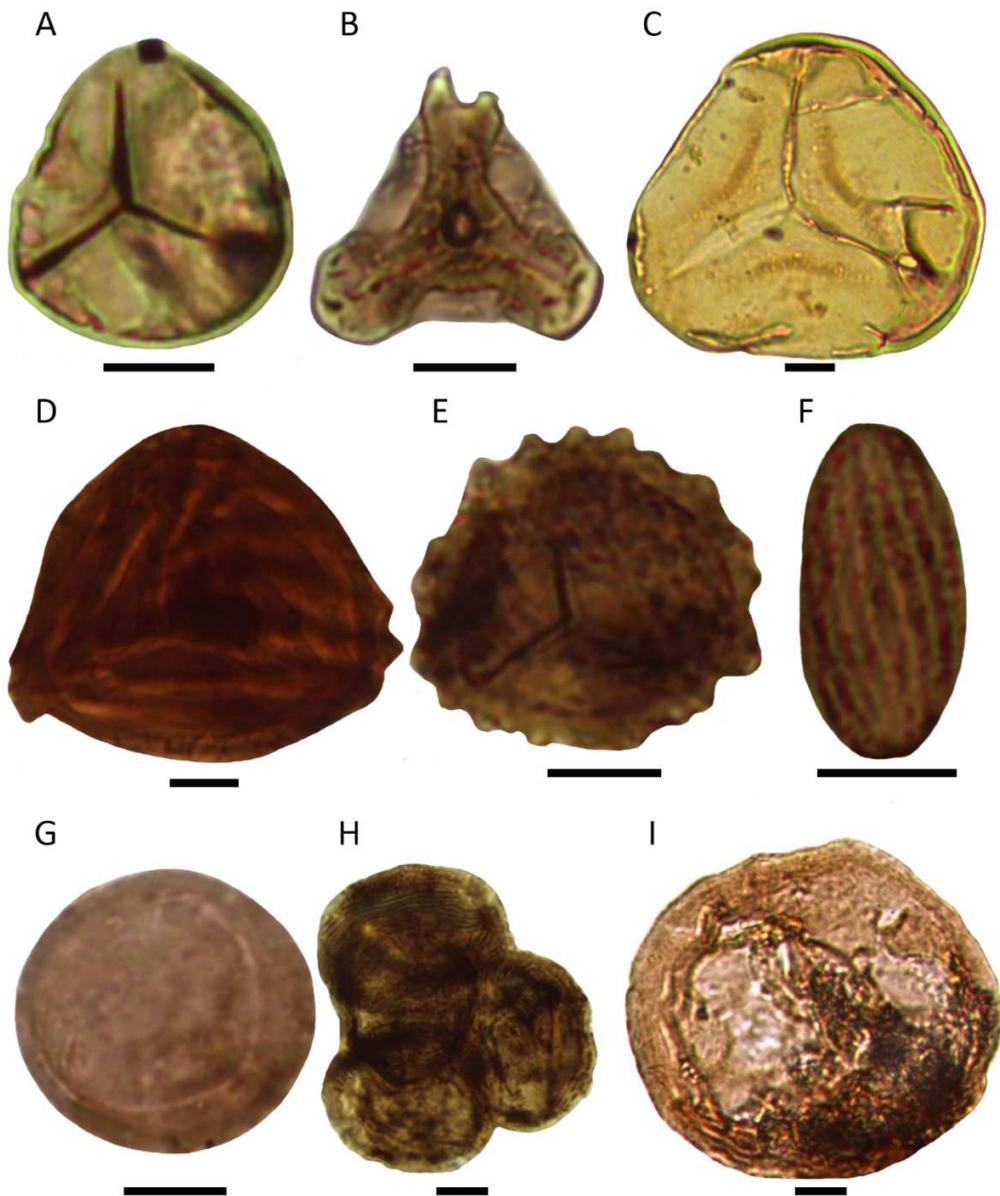


626

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

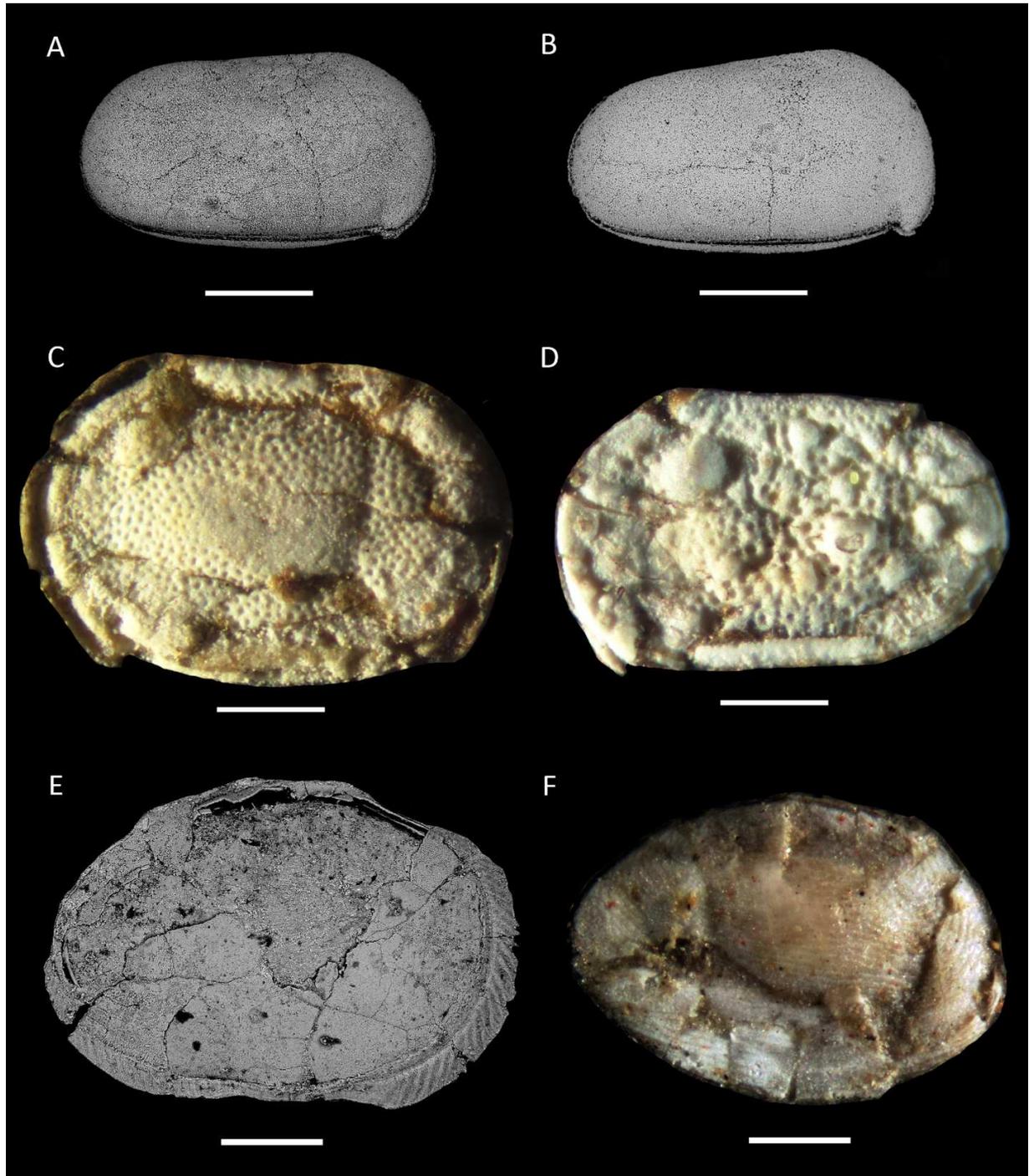


630

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-

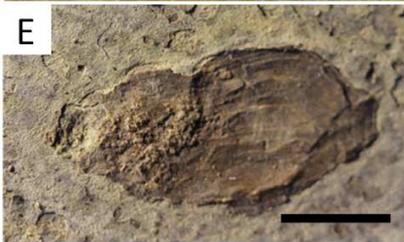
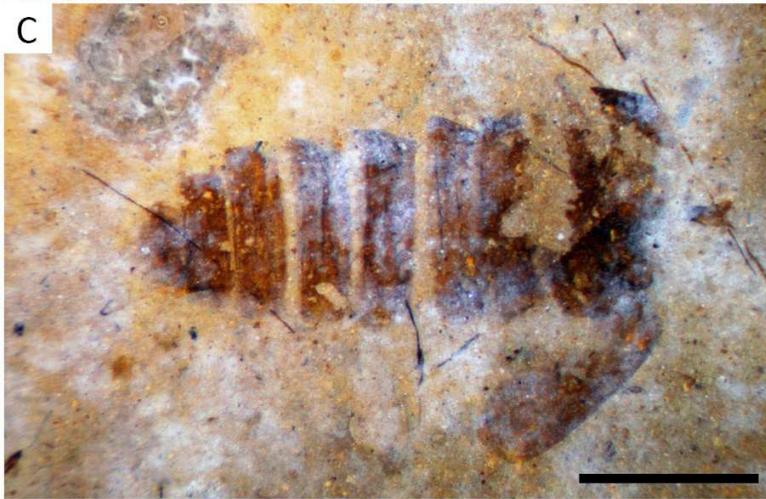
636 PALY-37353/6-11, H: F-PALY-37353/5-5, I. *Araucariacites* sp. from Qrayn: F-PALY-37353/5-

637 48. Scale bar = 10  $\mu$ m



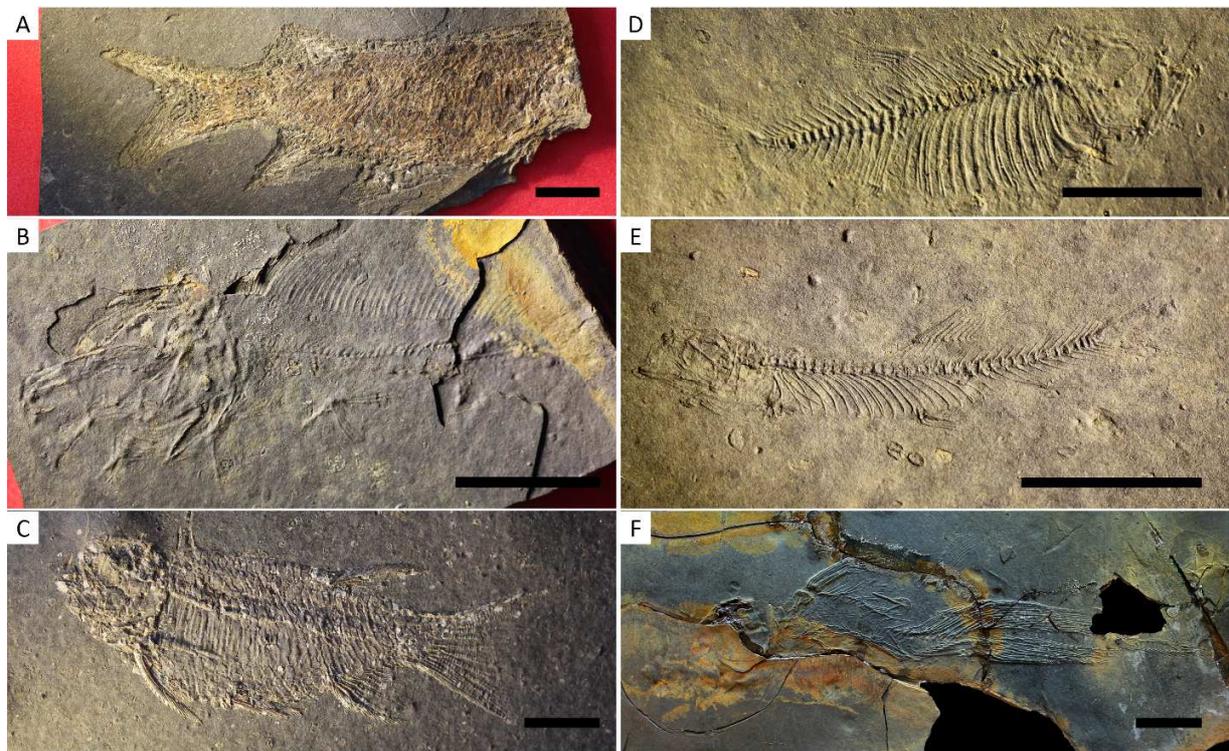
638

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  $\mu$ m



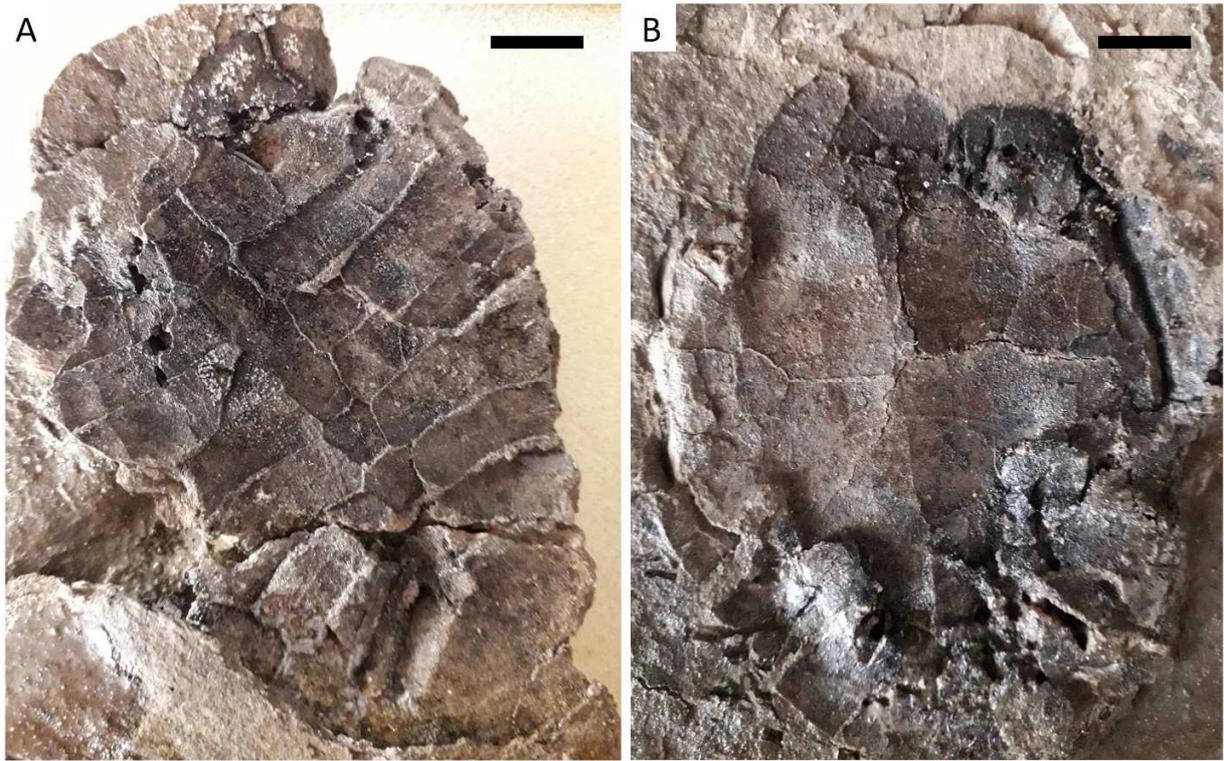
645 Figure 8. A-D. Fossil insects found in the dysodiles of Jdaydet Bkassine: A. Coleoptera  
 646 (Anthicidae): F-INS-63124/2, B. Ephemeroptera represented by the newly described species  
 647 *Libanoephemera inopinatabranchia* (Azar *et al.*, 2019): F-INS-63124/1, C. Coleoptera  
 648 (Staphylinioidea): 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

651



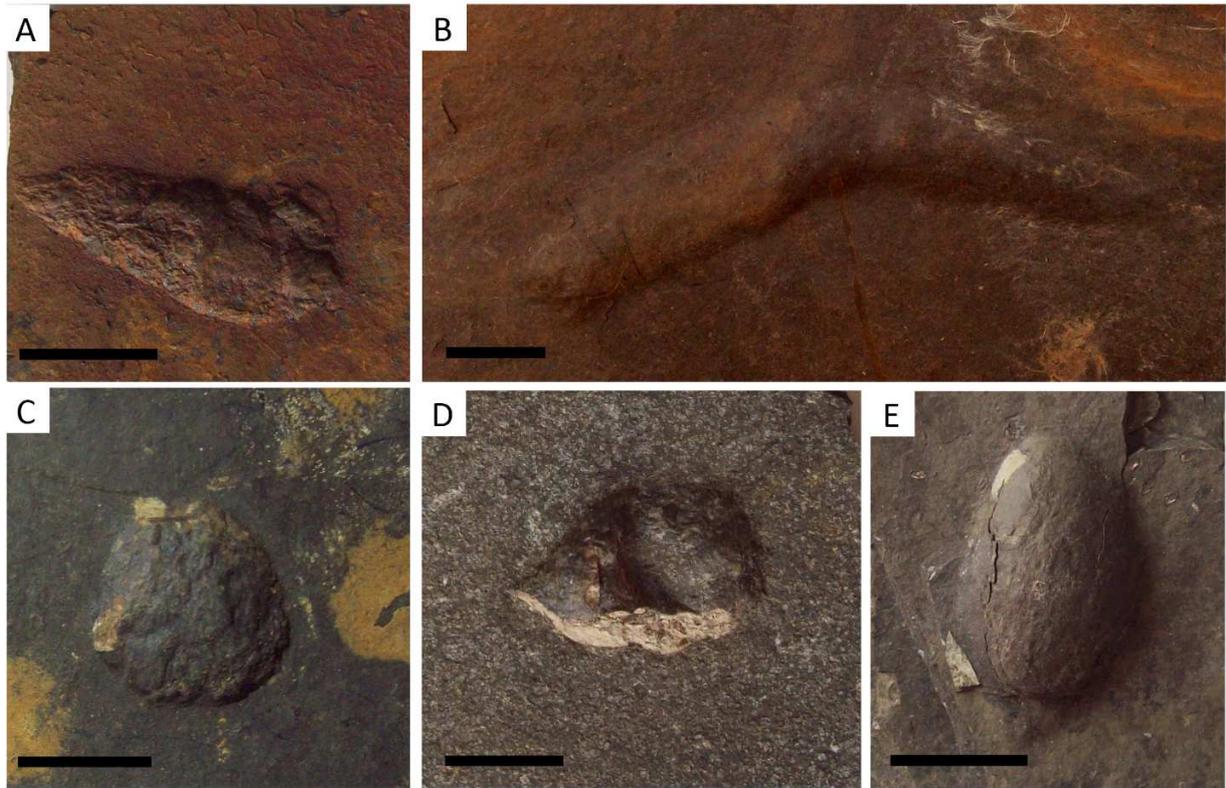
652

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



657

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



660

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



664

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

667

668

669

670

671

672

673

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					
<b>Facies</b>	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
<b>Plant debris</b>	1	?	-	1	-	1-2-3-4	1-4	?	?	1-4
<b>Fern spores</b>	-	-	-	1-2-4-5	1	-	1-2-4	2-3	1-2-3	-
<b>Pollen grains</b>	1-2	2	1-2	1-2	-	-	1-2	1	1-2-3	1
<b>Ostracods</b>	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
<b>Insects</b>	-	-	-	-	-	+	+	-	-	-
<b>Gastropods</b>	-	-	-	-	-	+	+	-	-	+
<b>Ichthyofauna</b>	-	-	-	4	-	1-2-3-4-5	3-4	-	-	4
<b>Turtles</b>	-	-	-	+	-	-	-	-	-	-

683

684

685

686

687

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.

698

699

700

701

702

703

704

705

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

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

707