

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

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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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20 Highlights

• New continental Konservat-Lagerstätte from the lower Barremian of Lebanon

Contribution to the knowledge of the lacustrine flora and fauna of north-eastern
 Gondwana

• Palaeoenvironmental reconstruction of the lacustrine Lebanese lower Barremian

25

26 Abstract

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

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.

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

47 Graphical Abstract



50 **1. Introduction**

Historically, Lebanon is paleontologically famous for its Late Cretaceous (Cenomanian) marine 51 carbonate beds yielding abundant and exquisitely preserved fishes (Forey et al., 2003; Gayet et 52 al., 2003; Kachacha et al., 2017), and its numerous Early Cretaceous amber outcrops with 53 biological inclusions (Azar, 2007; Azar et al., 2010). The recent re-/discovery of unusual Lower 54 Cretaceous continental sediments (dysodiles) brings important and exceptional paleontological 55 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 (Cordier, 1808) and well-preserved fossils (Fraas, 1878). 58

Dysodile beds are found in different lacustrine deposits in various areas of Lebanon, from the 59 lower Barremian and the Albian stages respectively. Old references mentioned their presence in 60 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 their richness in fossils including fish and plant debris, and he identified some plant species. The 63 latter were reviewed and attributed to Zamites sp. and Weichselia reticulata by Edwards (1929), 64 while Janensch (1925) identified two small actinopterygian fishes, as Pleuropholis koerti and 65 Thrissops sp. Then, since the 1930s, dysodiles were forgotten until their recent rediscovery 66 through our extensive geological fieldwork which resulted in the finding of seven localities, five 67 of them in the lower Barremian and two in the Albian. Recently, in addition to their petroleum 68 interest and source rock potential (El Hajj et al., 2019), the ostracod fauna found within the 69 dysodile layers was identified and its contribution to understanding the paleoenvironment was 70 discussed (El Hajj et al., 2020). However, these dysodiles certainly deserve multidisciplinary 71 72 approaches in order to reveal and understand their depositional conditions, their relationship with environmental regional context and their continental paleobiodiversity. Besides the ostracods
identified from five dysodile sampling localities (El Hajj et al., 2020), only fossiliferous amber
[with biological inclusions (mainly insects and other terrestrial arthropods) (Azar et al., 2010;
Azar, 2012; Maksoud & Azar, 2020)] and lignite have provided insights on the terrestrial flora
and fauna during the early Barremian of Lebanon (Azar et al., 2010; Azar, 2012; Maksoud &
Azar, 2020). Thus, the study of the fossil assemblages found in the dysodiles will significantly
increase our knowledge of these Early Cretaceous lacustrine environments and their biodiversity.

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

95 2016). The dysodile outcrops correspond to small isolated lakes and/or swamps, within this unit96 (less than 1 km in lateral extent and 2 m in thickness).

Field observations show a similarity between the southern sampling sites, where, in the three 97 localities Jdaydet Bkassine, Snyya and Zehalta, dysodiles overlie altered volcanic claystone 98 deposits and nodular carbonates. It is noteworthy that these southern outcrops are not distant 99 100 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 claystone is evident. In central Lebanon, Tarchich, a bed of volcanic ash is located just 102 underneath the dysodile beds. However, dysodiles crop out throughout the village of Tarchich, 103 and 1 km to the south of the main sampling site, dysodiles are contained between 10 cm of 104 carbonate beds. Figure 2 gives detailed stratigraphic logs of three main sampling localities, 105 106 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 Gondwana111 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 (Australia) (Fig. 3). We can notice that China was located in the middle of the continent under
temperate climate (Zhou, 2014); the Araripe Basin was also in the middle of the continent, but
under arid climate (Neumann et al., 2003), while the Iberian plate was located on the border of
the continent in a subtropical and highly seasonal climate (Fregenal-Martínez & Meléndez,
2016). The Gippsland Basin was located on the border of the continent, under humid cool
temperate climate (Poropat et al., 2018). The Lebanese dysodiles are thus unique in having
formed in a warm tropical climate on a continental border.

124

125 **2.2.2. Tectonics and Volcanism**

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

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

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

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

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

150

3. Methods

152 **3.1. Sampling**

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

157 Tarchich was sampled several times between 2014 and 2017. Dysodile layers were separated on158 the spot in the search for fossils; blocks were also taken from the sampling sites, covering the

entire section and the different outcrops in the village. However, the main sampling site locatedin 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^2 . 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^2 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

Facies preparation was performed in the ISTeP laboratory (Paris, France), by means of thin sections and palynofacies analysis. The collected fossils were cleaned and the dysodiles carefully split in order to preserve the part and the counter-part of each macrofossil. Each fossil was numbered according to the notation used by the Natural History Museum, Faculty of Sciences II of the Lebanese University. No treatment was applied to these fossils. However, in order to study 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 were175 examined under white light using a *ZEISS AXIO IMAGER* microscope.

The palynofacies and the palynomorph extraction and preparation (Combaz, 1964; Tyson, 1995) was performed using the protocol described by Durand & Nicaise (1980). It consisted of successive acid digestions of the fragmented rock, using hydrochloric acid (HCl, 33%) to eliminate the carbonates, then hydrofluoric acid (HF, 70%) to eliminate the silicates, and finally hot hydrochloric acid to eliminate the neo-formed minerals and the residual fluorides. After each acid digestion, the sample was washed with demineralized water in order to eliminate the excess
of acid and neutralize the pH. Slides (bulk and sieved using a 10µm mesh) were mounted from
this isolated organic matter using polyvinyl alcohol and UV resin (NOA61). The slides were then
observed under a *ZEISS Axioplan 2 imaging* optical microscope, by the mean of a *ZEISS Plan- NEOFLUAR 63x/1.25* oil immersion objective, using white and UV light.

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

189

4. Results

191 **4.1. Dysodiles main facies**

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

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

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

206

207 4.2. Paleontological findings

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

213

214 **4.2.1. Plant debris**

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

225 **4.2.2.** Palynomorphs

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

230

231 **4.2.3. Ostracods**

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

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

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

The ostracods could not be identified to species level because of their crushed state (Fig. 7), but all belong to the superfamily Cypridoidea, which is characterized by a "pawprint" adductor muscle scar (Horne & Colin, 2005). Among these, we could identify three genera: *Cypridea* Bosquet, 1852 represented by four putative species, *Cyprois* Zenker, 1854 and *Zonocypris* Müller, 1898. These ostracods and their paleoenvironmental implications are detailed in a separate publication (El Hajj et al., 2020).

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

255

256 **4.2.4.** Insects

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

263

264 **4.2.5.** Gastropods

Numerous aquatic gastropods were found but not yet studied (Fig. 8E–G). They are flattened, of different sizes (between 0.5 and 2 cm) and shapes (some elongated, others rounded), resembling pulmonate snails and *Lymnaea*, indicating different limnic species, living either in freshwater or on the nearby wetland. 270 **4.2.6. Ichthyofauna**

Fish fossils are the most abundant vertebrates in the dysodile beds of Lebanon. Their 271 preservation is different between the sampling sites and in the same sampling site between 272 273 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 greater sampling effort in this locality. The dysodile ichthyofauna includes diverse 278 actinopterygians (ray-finned fishes) as well as sarcopterygians (lobe-finned fishes) represented 279 solely by coelacanths. Details of the identified taxonomic groups are given below and illustrated 280 281 in Fig. 9.

282 Superclass: Osteichthyes Huxley 1880

283 Class: Actinopterygii Klein 1885

284 Grade: Palaeopterygii (Fig. 9A)

285 Genus and species indet.

A single headless specimen, 6.5 cm long, shows primitive characters including ganoid scales and

a heterocercal caudal fin. We refer it provisionally to the non-monophyletic grade Palaeopterygii

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.

A single specimen (part and counter-part), is a scale-less fish with no ossified vertebral centra, 291 but with only neural arches. The dorsal fin starts just behind the skull and apparently runs along 292 most of the back of the fish. The skull is not prepared yet and provides little information at this 293 stage. A naked body without mineralized vertebral centra is not common among 294 295 actinopterygians, but is found in acipenserifoms. These fishes usually have a short dorsal fin, 296 except in the peipiaosteid *Yanosteus* from the Lower Cretaceous of Liaoning, China (Jin, 1999) and in the acipenserid *Psammorhynchus* from the Upper Cretaceous of USA (Grande & Hilton, 297 2006). In these genera, however, the dorsal fin does not start just after the posterior limit of the 298 skull, and in *Psammorhynchus* the body is almost completely covered with thick scales. 299 Scaleless basal neopterygians, without ossified vertebral centra, are known in the Middle Triassic 300 301 (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 it could correspond to a scaled-neopterygian with an elongate dorsal fin, such as a macrosemiid 303 304 for instance, which could have lost its squamation for taphonomical reasons. For now it is regarded cautiously as a possible acipenseriform, pending the preparation of the fossils and the 305 discovery of new material. 306

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 ganoid scales slightly deeper than long along the dorsal and ventral margin of the body, and with 312 a single row of deepened scales in the mid-depth of the flank, which are ca 4 times deeper than 313 long. The dorsal and anal fins are located posteriorly, close to the caudal peduncle. These fins, as 314 well as the pelvic and caudal fins are preceded by few basal fulcra (1-2) and by a series of 315 elongated fringing fulcra extending up to the tip of fins. The pectoral fin differs from the other 316 317 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 structure. The occurrence of a single row of deepened thin ganoid scales along the flank is a 319 320 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 Naturkunde Berlin where Janensch spent his career (Florian Witzmann, personal communication 324 May 2020) and they have not been located elsewhere so far. The sketchy figure of one specimen, 325 together with the rather detailed description of the postcranial skeleton of this species (the head 326 is poorly preserved in all specimens) by Janensch stresses common characters with the 327 pleuropholid described herein, notably the occurrence of a series of deep scales running along 328 the flanks, a feature that confirms its inclusion in the family Pleuropholidae. Differences in 329 meristic features, as well as the higher position of the pectoral fins (contra a lower position in 330 our specimens), argue for distinct species. Moreover, Janensch did not mention the peculiar 331 denticulated spine in front of the pectoral fins formed by fused fulcrae, a typical and well-visible 332 feature in our material. Although the differences between the specimens described by Janensch 333

and ours could partly be explained by the difference in size of the fishes, we prefer here to consider that *P. koerti* is a *nomen nudum*. The speciesdescribed briefly here probably 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. Two339 morphotypes are easily distinguished:

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

345 Morphotype II (Fig. 9E)

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

- 350 Class: Sarcopterygii Klein 1885
- 351 Subclass: Actinistia Cope 1871
- 352 Order: Coelacanthiformes Berg 1937
- 353 Suborder: Latimerioidei Schultze 1993
- 354 Family: Mawsoniidae Schultze 1993 (Fig. 9F)

355 Genus and species indet.

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

366

367 4.2.7. Turtles

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

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

382

383 **4.2.8.** Coprolites

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

389

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.

The sedimentology, the absence of salinity biomarkers (El Hajj et al., 2019) and the lack of marine organisms, together with the presence of an ephemeropteran larva and three ostracod genera indicative of freshwater environments (Anderson et al., 1967; Meisch, 2000), indicate a depositional environment corresponding to a series of small, shallow lakes and/or swamps foundin the vicinity of volcanic edifices.

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

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

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

The morphology of the fishes indicates different feeding habits and therefore different lifestyles,
occupying various levels of the water column (Poyato-Ariza & Martín-Abad, 2016).
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. Teleosts, due to their upturned mouth with or without teeth, were probably plankton filterers or 423 fed by suction on all kind of food particles. Some of them have the fusiform body of active 424 swimmers living in the nekton, while others have an ovoid body, dorsally straight and ventrally 425 curved adapted for swimming in superficial waters. The latter is also plausible for the 426 427 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 they may have been nektobenthonic), but this does not rule out the possibility that planktonic 429 430 crustaceans were present but had no shells to be preserved. These considerations underline the importance of studying this fauna of basal actinopterygians co-existing with more derived 431 432 actinopterygians that would constitute the core of subsequent freshwater assemblages.

Based on this information, figure 12 represents a preliminary reconstruction of the depositionalenvironment of the Barremian dysodiles of Lebanon.

435

436 **3.** Conclusion

The present study provides an insight on the fossil assemblages found in the dysodiles of the Barremian of Lebanon. The assemblage comprises plants, pollen and spores, invertebrates such as gastropods, ostracods and insects, and vertebrates including turtles and a diverse fish fauna, providing evidence of a freshwater lake environment and its surrounding vegetation. Faunal and floral diversity differ between sites, however, and our preliminary reconstruction of the 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 deposition444 of dysodiles.

445

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



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



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)



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



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



Figure 6. Figure 6. Palynomorphs identified within the dysodiles: A. *Deltoidospora* sp. from
Tarchich: F-PALY-21481/1-15, B. *Dictyophyllidites harrissii* from Snyya: F-PALY-63287/6-15,
C. *Matonisporites* sp. from Tarchich: F-PALY-21481/13-21, D. *Cicatricosisporites* sp. from
Snyya: F-PALY-63287/14-4, E. *Verrucosisporites* sp. from Tarchich: F-PALY-21481/8-3, F. *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 = $10 \,\mu m$

- 639 Figure 7. Ostracods found in the dysodiles: A, B and E are SEM images, while C, D and F are
- optical images under incident light. A. Cypridea sp.1 from Tarchich: F-O-21481/1, B. Cypridea
- 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
- Equation 243 Zehalta: F-O-63177/2. Scale bar for the ostracods = $500 \,\mu m$



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





Figure 9. Fossil Ichthyofauna found in the dysodiles of Jdaydet Bkassine: A. Palaeopterygii: F-F63124/35, B. Acipenseriformes: F-F-63124/69, C. Pleuropholidae: F-F-63214/1, D. Teleostei
indet. Morphotype I: F-F-63124/33, E. Teleostei indet. Morphotype II: F-F-63124/17, F.
Mawsoniidae: F-F-63124/300. Scale bar = 1 cm except for F scale bar = 5 cm



Figure 10. Fossil turtle shell found in the dysodile of Tarchich: F-T-21481/1 A. Ventral view of

the dorsal shell, B. Visceral view of the plastron. Scale bar = 1 cm



660

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



Figure 12. Preliminary reconstruction of the depositional environment of the dysodiles of thelower Barremian of Lebanon

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

	Qrayn			Tarchich		Idaydat				
Site				Main site	1 km away	Bkassine	Snyya			Zehalta
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	-	-	-	+	-	-	-	-	-	-

689	Division	Family	Taxa of spores and pollen
690	21101011		grains
601		Cyatheaceae,	Deltoidospora sp.
091		Dicksoniaceae?	
692	Monilonhyta	Matoniaceae	Matonisporites sp.
693	Womophyta	Watomaccae	Dictyophyllidites harrissii
694		Schizaeaceae	Cicatricosisporites sp.
COL		Zygopteridaceae?	Verrucosisporites sp.
695		Cheirolepidiaceae	Classopollis sp.
696	Coniferophyta	Araucariaceae	Araucariacites australis
697		Ephedraceae	Ephedripites sp.
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Table 2. The botanical affinities of identified taxa of spores and pollen grains 688

706	Table 3. Habitat and ecological niche of the entomofauna found	in the dysodiles
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Habitat	Ecological niche	Entomofauna					
Terrestrial							
	Herbivorous/ fungivorous	Diptera					
Forest	Carnivorous	Staphylinoidea					
	Omnivorous	Anthicidae adults					
Shallow waters/ rivers	No feeding	Ephemeroptera adults					
Fully aquatic							
Plankton	Plankton inhabitants	Diptera pupae					
	Bottom burrowers	Ephemeroptera larvae					
Benthos	Detritivorous	Diptera larvae					
		Ephemeroptera larvae					