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Paleocene resurrection of a crocodylomorph taxon: Biotic crises, climatic and sea level fluctuations

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► To cite this version:

Stéphane Jouve, Nour-Eddine Jalil. Paleocene resurrection of a crocodylomorph taxon: Biotic crises, climatic and sea level fluctuations. *Gondwana Research*, 2020, 85, pp.1-18. 10.1016/j.gr.2020.03.010 . hal-02933167

HAL Id: hal-02933167

<https://hal.sorbonne-universite.fr/hal-02933167>

Submitted on 8 Sep 2020

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1 **Paleocene resurrection of a crocodylomorph taxon: biotic crises,**
2 **climatic and sea level fluctuations**

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16 Running title: A Paleocene pholidosaurid from Morocco.

17

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21

22 Postcranial material of a crocodylomorph from the Danian of Oulad
23 Abdoun Basin (Morocco) is described. Several characters, in particular the
24 shape of its dorsal osteoderms, allows its attribution to Pholidosauridae.
25 Up till now, the latest known pholidosaurid was *Terminonaris*, from the
26 Early Turonian of North America, so, the Moroccan pholidosaurid extends
27 the stratigraphic range of the group to more than 20 million years
28 younger, and shows that the pholidosaurids survived the K-Pg crisis. The
29 reevaluation and the phylogenetic analysis of *Dakotasuchus kingi*,
30 *Woodbinesuchus byersmauricei*, and *Sabinosuchus coahuilensis*,
31 previously considered as goniopholidids and dyrosaurid, respectively,
32 revealed rather that they are pholidosaurids. This analysis also suggests
33 that at least two independent pholidosaurid lineages reached the
34 Maastrichtian, among which one crossed the K-Pg boundary. This study
35 proposes the first analysis of tethysuchian diversity from the Late Jurassic
36 to the Early Paleogene. Two diversity peaks are observed during the
37 Oxfordian and Cenomanian, two stages of high paleotemperatures
38 evaluated with the $\delta^{18}\text{O}$. The tethysuchian diversity strongly decreases
39 after the Cenomanian, a decline that may be correlated with the "Ocean
40 Anoxic Event" (OAE 2), which caused the strong marine faunal turnover
41 during the Cenomanian-Turonian time interval. The large Turonian-
42 Coniacian oceanic regression could also be a factor in the tethysuchian
43 decline. After that, tethysuchian diversity remains low until the
44 Maastrichtian-lower Paleocene marine tethysuchian dyrosaurid
45 diversification, correlated with the Late Cretaceous-Paleocene

46 transgression. At least one pholidosaurid lineage crossed the K-Pg
47 boundary, confirming the weak impact of this crisis on the
48 crocodylomorphs. Pholidosaurids seem to go extinct at the beginning of
49 the Paleocene, possibly due to the strong radiation of dyrosaurids in
50 marine environments and crocodylians in fresh-water during this time
51 period.

52

53 *Keywords:* Crocodylomorpha – Pholidosauridae – Danian – Morocco –
54 Oulad Abdoun Basin – KT crisis.

55

56 **1. Introduction**

57

58 A collaborative work between the OCP, MEM, CNRS, and FSSM, led
59 to the discovery of a great number of well-preserved crocodylomorph
60 specimens in the phosphatic Oulad Abdoun Basin of Morocco (Fig.
61 1)(Jouve, 2004; Hua and Jouve, 2004; Jouve et al., 2005a, b, 2006a, b,
62 2008a, b, 2014; Bardet et al., 2010, 2014, 2017), contrasting with the
63 isolated and fragmentary remains previously known (Arambourg, 1952).
64 Most of the crocodylomorphs described from the Oulad Abdoun Basin are
65 marine dyrosaurids (Jouve et al., 2005a, 2005b, 2006a, 2008b),
66 nevertheless remains of crocodylians have also been described (Hua and
67 Jouve, 2004; Jouve et al., 2006b, 2008a, 2014). Both groups are common
68 in the Moroccan Maastrichtian and Paleogene levels. The crocodylomorph

69 described herein highlights the possible presence of a third group, the
70 pholidosaurids.

71 Tethysuchians are known from the Late Jurassic to the Middle
72 Eocene. They are formed by pholidosaurids and dyrosaurids. Up to now,
73 pholidosaurids were known from Late Jurassic to Early Turonian (Meyer,
74 1841; Koken, 1887; Andrews, 1913; Sereno et al., 2001; Wu et al., 2001;
75 Billon-Bruyat and Mazin, 2002), while dyrosaurids are documented from
76 Maastrichtian to middle Eocene, but possible dyrosaurid remains have
77 been described in the Cenomanian (Buffetaut and Lauvergat, 1978). The
78 origin of the dyrosaurids is particularly obscure, and a long ghost lineage
79 exists between the divergence between the pholidosaurids and
80 dyrosaurids and the oldest known dyrosaurid.

81 The Moroccan specimen described from the Danian is, then, more
82 than 20 millions years younger than the youngest known pholidosaurid
83 (*Terminonaris* spp.). So, the Moroccan pholidosaurid is particularly
84 significant since it proves that the pholidosaurids spanned all the Late
85 Cretaceous, and also survived the K-Pg crisis. The studied remains are
86 fragmentary, and to evaluate its phylogenetic relationships, we included
87 the Moroccan pholidosaurid in a matrix focused on tethysuchians, and
88 thus including most known pholidosaurids and dyrosaurids (see below).
89 This also offers the opportunity to reevaluate several Late Cretaceous
90 crocodylomorphs of uncertain phylogenetic affinities.

91 *Sabinosuchus coahuilensis* Shiller et al., 2016 from the Maastrichtian
92 of Mexico has been recently described as a dyrosaurid, but this attribution

93 has been questioned (Jouve et al., submitted). *Dakotasuchus kingi* Mehl,
94 1941 and *Woodbinesuchus byersmauricei* Lee, 1997, both from the
95 Cenomanian of North America, have been described as goniopholidids
96 (Lee, 1997; Frederickson et al., 2017), and are the youngest members of
97 this group. Nevertheless, several characters make these attributions
98 doubtful. The relationships of these species will be tested herein.

99

100 **2. Material and Method**

101

102 *2.1. MHNM-Kh01a*

103

104 The specimen described herein comes from local collectors, so its
105 precise origin is unknown. Nevertheless, associated typical selachian fauna
106 found in embedded sediment (*Dasyatis tetraedra*, *Squalus* sp.,
107 *Palaeogaleus* aff. *brivesi*; Cappetta, pers. com., 2007), indicates that it is
108 from the 'couche 2b' stratum, which is lower Palaeocene (Danian) in age
109 (H. Cappetta, Pers. Com., 2007).

110 All bones were on the same and unprepared block. The bones were
111 partially embedded in the natural matrix without glue and clearly this
112 bone association is not a fake built by sellers as is often the case for
113 phosphate fossils. Indeed, the fossil dealers provide reconstruction of
114 skulls with high economic value, and never on postcranial remains, except
115 for alignment of articulated vertebrae, but it is not the case for the studied
116 specimens. The specimens have been prepared by one of the authors

117 (S.J.)(Figs. 1, 2). The small specimens are particularly scarce in Moroccan
118 phosphates and, among the hundreds of crocodylomorph bones collected,
119 those presented herein are by far the smallest ever found. At least 7
120 dorsal osteoderms were present on the block, and all are from the left
121 side (Fig. 3A-C). The orientation of the lateral margin preserved on some
122 of them suggests that they come from the anterior portion of the dorsal
123 shield, one being the third or fourth (Fig. 3B). The shape and anterior
124 articular surface seen in most of the ventral osteoderms also suggest the
125 anterior portion of the ventral shield, probably from the neck. All
126 preserved bones also come from the anterior part of trunk, and most are
127 from the left side: anteriormost dorsal vertebra, left scapula, left
128 humerus, a left anterior thoracic rib, and numerous left anterior dorsal
129 osteoderms (Figs. 2, 3). A reviewer of an older version of the present
130 paper asserted that the sample is an accumulation of three different taxa:
131 a dyrosaurid vertebra and scapula, an ornithopod (dryosaurid) humerus,
132 and pholidosaurid osteoderms. Such taphonomic assemblage is highly
133 improbable. Indeed, the probability of finding on the same block remains
134 matching in size, no duplicate, from the same left anterior anatomical
135 region of three distinct species, two marine crocodylomorphs, and one
136 dinosaur is almost nill. In addition, the Danian age clearly excludes the
137 presence of an ornithopod.

138 The taphonomic data strongly argues against an artificially
139 association or the results of a reworking (as indicated by the quality of the

140 preservation). On the contrary, they suggest that these remains can be
141 attributed to a single individual.

142 The present specimen is unique among the hundreds of remains of
143 crocodyliforms found in the same layer, so it is possible that this species
144 did not live in the sea in which the sediments were deposited, but rather
145 on the continent. The remains could have been brought by a river, as it
146 was suggested for the only known specimen of *Ocepesuchus eoafricanus*
147 Jouve et al., 2008a from the Maastrichtin of the Oulad Abdoun (Bardet et
148 al., 2017), as is the case for several mammal remains founds in the same
149 field (Bardet et al., 2017).

150

151 2.2. Phylogenetic analyses

152

153 In order to assess the phylogenetic position of MHNM-Kh01, we
154 performed a phylogenetic analysis including goniopholidids, and
155 tethysuchians (pholidosaurids and dyrosaurids) (list of characters and
156 data matrices available at Mendeley datasets: <http://dx.doi.org/>). It was
157 based on several previous analyses (e.g. Jouve et al., 2005a, b, 2008b;
158 Hastings et al., 2014; Young et al., 2016), and includes 224 characters,
159 with 69 new ones.

160 *Fortignathus felixi* (Lapparent de Broin, 2002) considered as a
161 tethysuchian by Young et al. (2014, 2016), has not been considered
162 herein as we suspect that this species is not related to this group. The
163 specimen is known by mandibular fragments, and several characters

164 suggest that it is a peirosaurid (S.J. pers. obs.). In the analysis proposed
165 by Young et al. (2016), the 'gladius'-shape of the anterior extremity is not
166 considered as homologous in peirosaurids / sebecids with basal
167 dyrosaurids / *F. felixi* mainly due to the shape of their symphyses.
168 Consequently the character has been divided into two (157, 158; Young et
169 al., 2016), but the shape of the anterior extremity of the mandible is
170 similar in all of these groups. The shape of the symphysis is already
171 considered in another character and should not be considered in the
172 coding of the anterior extremity shape. So, when character 157 and 158
173 are fused (Appendices 1, 2 of Supplementary Information), and
174 considered as a single character, *Fortignathus felixi* is not a tethysuchian,
175 but a peirosaurid (Appendix 3). Several other characters suggest these
176 affinities, but the phylogenetic affinities of this species will be tested in
177 detail in a future paper.

178 On the other hand, *Sabinosuchus coahuilensis* Shiller et al., 2016
179 considered as a dyrosaurid tethysuchian (Shiller et al., 2016; Ristevski et
180 al., 2018), is included in the analysis. Two other species, until now
181 considered as gonipholidids, have also been introduced: *Dakotasuchus*
182 *kingi* and *Woodbinesuchus byersmauricei*. Their age is incongruent
183 compared to the age usually recognised for goniopholidids.
184 *Denazinosuchus kirtlandicus* (Wiman, 1932), another putative
185 goniopholidid, is known from the Campanian of North America. Its
186 phylogenetic relationships are unstable, being found as a goniopholidid
187 (Andrade et al., 2011) or outside of this group (Allen, 2012). As our aim is

188 not to test the species belonging to goniopholidids or their monophyly, we
189 did not include this unstable taxon.

190 The maximum parsimony analysis is conducted using TNT version
191 1.5 (Goloboff et al. 2003, 2008; Goloboff and Catalano, 2016). Tree-space
192 is searched by using the advanced search methods in TNT for 5,000
193 random addition replicates. The default settings for the advanced search
194 methods are changed to increase the iterations of each method per
195 replicate, which now comprises of 100 sectorial search drifting cycles, 100
196 ratchet iterations, 100 drift cycles, and 100 rounds of tree fusion per
197 replicate. This tree-space search procedure is repeated for five different
198 random start seeds. Nodal support is evaluated using Bremer support
199 index using the TNT script BREMER.RUN included in the TNT software
200 package (Goloboff et al. 2008a,b), and the trees are manipulated with
201 Mesquite (Maddison and Maddison, 2011). Three continuous characters
202 (1, 2, and 3; list of characters available as Appendix 1 at Mendeley
203 datasets: <http://dx.doi.org/>) were included, as TNT allows the use of
204 continuous characters (matrix available as Appendix 2 at Mendeley
205 datasets: <http://dx.doi.org/>). The same characters have been discretized
206 (1', 2', and 3'; list of characters available as Appendix 1 at Mendeley
207 datasets: <http://dx.doi.org/>), and used alternatively with their continuous
208 versions (matrix available as Appendix 3 at Mendeley datasets:
209 <http://dx.doi.org/>). The result does not vary between the two versions.

210

211 *2.3. Diversity curves*

212

213 We compared the evolution of tethysuchian diversity with environmental
214 proxies (Appendix 4-8 of Supplementary data). The diversity data were
215 corrected with the new phylogenetic analysis. The phylogenetic
216 relationships are thus superimposed on the stratigraphy, and ghost
217 lineages of species are filled (Appendix 9) following the method proposed
218 by Cavin and Forey (2007).

219 In order to limit the impact of ghost lineages and poor sampling, we
220 considered the unidentified species in the count of species. For several
221 stages, only indeterminate crocodylomorph remains are present
222 (Appendices 4, 6), therefore, using only the clearly identified species could
223 strongly biases the analyses. As the distribution of each observed species
224 is restricted to a unique continent, we have considered these
225 indeterminate remains as a different species in our diversity counts. This
226 allows to consider in the analysis, the presence of tethysuchians on a
227 continent where no identifiable remains at specific or generic levels have
228 been found so far. On the contrary, when identifiable species were present
229 on one given continent, the indeterminate remains observed on the same
230 continent were not considered as a different species, even if they were
231 from a different formation. This procedure was considered independently
232 on each continent: unidentified remains present on two different
233 continents have been considered as different species. Several lithologic
234 units have uncertain and contiguous age assignments. The diversity

235 counts of these units have been counted for the stages included in the
236 uncertainty range.

237 The sampling is particularly poor in some continents, and numerous
238 data must be improved and completed to provide a clearer pattern in the
239 stratigraphic distribution of the tethysuchians, in particular for
240 pholidosaurids, through Late Jurassic to Early Paleogene. To complete and
241 support the comparisons, we conducted correlation analyses of raw and
242 corrected data (Appendices 10, 11). Such an analysis is strongly biased by
243 the quality of the original data and fossil record (e.g. Alroy 2010; Lloyd et
244 al. 2012; Benton et al. 2013; Rook et al. 2013; Jouve et al. 2017). So, as
245 a result, we conducted simple analyses in the present preliminary work,
246 pending stronger data to conduct more complex statistical analyses. We
247 calculated the correlation between the various diversity data sets and $\delta_{18}\text{O}$
248 paleotemperature proxy from the compendium provided by Prokoph et al.
249 (2008) (Appendix 8 of Supplementary data). We calculated the mean of
250 $\delta_{18}\text{O}$ for each time interval, using only the $\delta_{18}\text{O}$ data from tropical,
251 subtropical, and temperate climate. As tethysuchians are not found in cold
252 climates, we excluded the data from deep sea, Arctic, and Antarctic
253 climates. Spearman's rho values and Spearman rank correlations have
254 been calculated (Table 1; Appendix 10) using Past 3.10 (Hammer et al.,
255 2001). Correlations with the sea level (Miller et al., 2005) have also been
256 calculated (Table 2; Appendix 11).

257 The diversity curve analyses suffer from numerous biases (e.g. Alroy
258 2010; Lloyd et al. 2012; Benton et al. 2013; Rook et al. 2013), and a

259 clear taxonomic background is required to have the best reliable statistical
260 support (Jouve et al., 2017). The pholidosaurids received little attention
261 for decades, and several species should be reviewed such as *Terminonaris*
262 sp. (*Teleorhinus* sp.) from Germany (Buffetaut and Wellnhofer, 1980), and
263 the Berriasian remains from Cherves-Cognac, France, attributed to the
264 English species *Pholidosaurus purbeckensis* which could be a new species.
265 Nevertheless, contrary to that which is observed with teleosauroids (Jouve
266 et al., 2017), as pholidosaurid remains are particularly infrequent, few
267 species have been erected on fragmentary remains, and diversity does not
268 seem to be overestimated as in the thalattosuchian taxa. Nevertheless, as
269 the number of species is particularly low, the present diversity analysis
270 should thus be considered with caution, but we think that it reflects the
271 general trend of tethysuchian evolution.

272 Abbreviations

273 CNRS: Centre National de la Recherche Scientifique, Paris, France.

274 FSSM: Faculté des Sciences Semlalia, Marrakech, Morocco.

275 MEM: Ministère de l'énergie et des Mines, Rabat, Morocco.

276 MHNM: Muséum d'Histoire Naturelle de Marrakech, Morocco.

277 OCP: Office Chérifien des Phosphates, Khouribga, Morocco.

278

279 **3. Systematic paleontology**

280

281 Crocodyliformes Hay, 1930 (sensu Clark, in Benton and Clark, 1988)

282 Neosuchia Benton and Clark, 1988

283 Tethysuchia Buffetaut, 1982

284 Pholidosauridae Zittel and Eastman, 1902

285 Pholidosauridae indet.

286

287 *Locality and age*

288 Sidi Chenane, "couche 2b", Danian, Oulad Abdoun Basin, Morocco.

289

290 *Referred specimen*

291 MHNM-Kh01a, an anterior dorsal vertebra (Fig. 2A, B), a left
292 humerus (Fig. 2D-F), a left scapula (Fig. 2C), a left dorsal rib (Fig. 2G),
293 left dorsal (Fig. 3A-C) and ventral (Fig. 3D-K) osteoderms. All these
294 remains are from the same individual, and housed in the Muséum
295 d'Histoire Naturelle de Marrakech, Marrakech, Morocco.

296

297 **4. Description and comparison**

298

299 *4.1. Vertebra*

300

301 A single vertebra has been found (MHNM-Kh01a; Fig. 2A, B). It is
302 amphicoelous, with long and laterally projected diapophyses. The latter is
303 high, nearly at the same level as the zygapophyses, and in the posterior
304 mid-portion of the vertebra. The parapophysis is much shorter, lower in
305 position and located at mid-height of the centrum, and slightly in the
306 anterior mid-portion. The zygapophyses are almost horizontally oriented,
307 and the prezygapophysis is slightly ahead of the anterior margin of the

308 centrum. The postzygapophysis is beyond the posterior margin of the
309 centrum. The neural spine is high, strongly inclined posteriorly, and thin
310 lateromedially on all its height. Its anterior margin is posterior to the
311 anterior margin of the centrum (Fig. 2A), and its length progressively
312 decreases dorsally, such that, its dorsalmost portion is less than half the
313 length of the ventral part. The anterior and posteroventral margins of the
314 neural spine are thinner than the median part. The amphicoelous centrum
315 bears a high hypapophysis, and is located on its anterior two-thirds. The
316 anterior margin of this hypapophysis is slightly posteroventrally inclined,
317 while its posterior margin seems to have been more vertical. It is difficult
318 to define the exact location of the vertebra along the vertebral series, in
319 particular between posteriormost cervicals and anteriormost dorsals.
320 Contrary to Souza et al. (2019), even in tethysuchian dyrosaurid species
321 in which almost complete vertebral columns are known, only a
322 combination of neural spine and centrum characters can distinguish their
323 precise location. Intraspecific variability in the shape, length, and height of
324 the hypapophysis exists in *Dyrosaurus maghribensis* Jouve et al., 2006a
325 the only dyrosaurid species for which postcranial remains are known
326 from several individuals (Appendix 12). It precludes the differentiation of
327 the last cervicals and first dorsals based uniquely on the morphology of
328 this anatomical structure, and so, it is not possible to determine the
329 precise location in the column of the holotype vertebrae of *Hyposaurus*
330 *rogersii* Owen 1849, as Souza et al. (2019) did. In particular, the
331 hypapophysis characters these authors provided to distinguish last

332 cervical from first dorsal, their height, length, posterior extent and
333 centralization on the centrum, strongly vary intraspecifically, and cannot
334 help to differentiate the last cervical from the first dorsal (see Appendix
335 12). The parapophysis of the crocodyliform cervical vertebra is
336 anteroventral to the centrum/arch suture, whereas on the dorsal
337 vertebrae, it is anterodorsal to this suture (Wu et al., 2001), but this
338 difference is not clearly marked in *D. maghribensis* (Jouve et al., 2006a).
339 No doubt that postcranial remains probably bear diagnostic characters,
340 but it is precisely known in only two species (*D. maghribensis* and *C.*
341 *bequaerti*), and it bears particularly high intraspecific variability (Appendix
342 12). Consequently, it is not possible to provide any confident conclusions
343 on the location of isolated vertebrae, and the characters suggested as
344 possibly diagnostic by Souza et al. (2019) should be regarded as
345 irrelevant at the moment. MHNM-Kh01a has a broad neural spine, long
346 diapophysis, and a centrum/neural arch suture that crosses the dorsal
347 margin of the parapophysis (Fig. 2A, B). The dorsal margin of the neural
348 spine of the dorsal vertebrae is linear in dyrosaurids whereas it is more
349 rounded in cervicals and its anterior margin is more arched (Jouve et al.,
350 2006a; Callahan et al., 2015), but intraspecific variability also exists in
351 these characters (Appendix 12). So, compared with the vertebrae known
352 in *D. maghribensis*, the vertebra could be the last cervical, but more
353 probably the first or second dorsal. Among the pholidosaurids, posterior
354 cervical or anterior dorsal vertebrae are known in *Sarcosuchus imperator*
355 Broin and Taquet, 1966 (Sereno et al., 2001; pers. obs.) and

356 *Terminonaris robusta* Mook, 1934 (Wu et al., 2001). *S. imperator* is
357 distinguished from MHNM-Kh01a, by the dorsal neural spines that are
358 lower, and much wider, with a flat dorsal surface for strong attachment of
359 the ligaments of the osteoderms. Even poorly known, the neural spines in
360 *Terminonaris* seem to have been less wide than in *Sarcosuchus*, and the
361 anterior margin is posteriorly inclined, as in the Moroccan specimens and
362 in dyrosaurids. The hypapophyses, absent in *Sarcosuchus*, are present
363 and high on the posterior cervicals and anterior dorsals of *Terminonaris*
364 (Wu et al., 2001), as it is in MHNM-Kh01a (Fig. 2A), but it is knob-like,
365 not blade-like as in the Moroccan specimen. The Moroccan vertebra
366 resembles the dorsals of dyrosaurids, a taxon closely related to the
367 pholidosaurids (e.g. Clark, 1994; Wu et al., 2001; Sereno et al., 2001;
368 Jouve et al., 2006a; Fortier et al., 2011; Meunier and Larsson, 2017;
369 Young et al., 2017), in having high hypapophyses, and tall neural spines
370 that narrow dorsally.

371

372 4.2. Humerus

373

374 A left humerus is preserved without its distal portion (MHNM Kh01b;
375 Fig. 2D-F). The distal and proximal ends are not twisted in relation to each
376 other, with the medial margin of the proximal head being only slightly
377 curved. The proximal head ends with a slightly concave articular surface
378 that bears a wide anterior bulge (Fig. 2E). Ventral to this bulge, the
379 anterior surface bears a shallow triangular depression (Fig. 2E). The

380 deltopectoral crest extends on the lateral margin of the humerus, parallel
381 to the lateral margin of the proximal extremity (Fig. 2D). It extends to
382 more than one-third of the length of the humerus, and appears as a
383 moderately developed rounded crest, that begins gently slightly posterior
384 to the proximal head. The humeral shaft is circular in cross-section. The
385 proximal head is distinctive in that it is concave (Fig. 2D, E), instead of
386 being convex, as in *T. robusta* and the dyrosaurid *Congosaurus bequaerti*
387 Dollo, 1914 (Jouve and Schwarz, 2004), or straight, as in *T. browni*,
388 *Pholidosaurus purbeckensis* (Mansel-Pleydell, 1888) (S.J., pers. obs.), and
389 the dyrosaurids *Rhabdognathus* sp. (Langston, 1995), *Hyposaurus rogersii*
390 Owen, 1849 (Troxell, 1925), and *Dyrosaurus maghribensis* (pers. obs.).
391 This character can vary within the same genus, and even in the same
392 species, as it is in *Dyrosaurus* where the margin is straight in *D.*
393 *phosphaticus*, (Bergougnieux, 1956), or convex in *D. maghribensis* (S.J.,
394 pers. obs.), but it never has a concave margin. A similar concave shape is
395 present in an undescribed isolated humerus from the Kem-kem beds
396 preserved in the MNHN collections, the size of which suggests a possible
397 attribution to *Elosuchus* sp., a genus herein closely related to
398 dyrosaurids (Jouve, 2009; Andrade et al., 2011; Fortier et al., 2011;
399 Young et al., 2017; Meunier and Larsson, 2017). In MHNM-Kh01a, the
400 deltopectoral crest is more rounded anteriorly than in *T. robusta*, *T.*
401 *browni*, the humerus attributed to *Elosuchus* sp., where the anterior
402 margin is more abrupt. It looks more like that of the dyrosaurids *C.*

403 *bequaerti* (Jouve and Schwarz, 2004), *H. rogersii* (Troxell, 1925), and
404 *Dyrosaurus* sp. (Bergougnieux, 1956).

405

406 4.3 Scapula

407

408 A left scapula is preserved, and exposed in lateral view (MHNM-
409 Kh01c; Fig. 2C). Its anterior margin is strongly concave, with a straighter
410 medial portion, between the scapular head and the blade. The anterior
411 margin of the head bears a laterally deflected crest. The ventral portion of
412 the posterior margin is as concave as the anterior margin, but the dorsal
413 portion is nearly straight, and vertical. Even if the posterior part of the
414 dorsal margin of the scapular wing is not preserved, it is dorsally convex.
415 The glenoid fossa is caudoventrally directed and strongly concave. The
416 scapula is also strongly dorsally expanded with a strongly concave anterior
417 margin, as in the dyrosaurids *D. maghribensis*, *C. bequaerti*, and
418 *Hyposaurus natator*. It has a typical dyrosaurid-like shape, but this shape
419 is also found in *D. kingi* (Mehl, 1941), until now considered as a
420 goniopholidid, but recognised herein as a probable pholidosaurid. In
421 pholidosaurids, the scapula is known in *Terminonaris robusta* (Wu et al.,
422 2001; S. J., pers. obs.), *Sarcosuchus imperator* (Serenó et al., 2001;
423 Larsson pers. com.), and *P. purbeckensis* (MHNUK R3956), but the shape
424 of the anterior margin cannot be evaluated in the later species. They differ
425 from MHNM-Kh01c in having a less concave anterior margin and a less
426 expanded dorsal wing, but resembles that which is seen in goniopholidids,

427 where the scapula is poorly known. It has been described in
428 *Anteophthalmosuchus hooleyi* (Martin et al., 2016a) as having parallel
429 sides of its blade, but direct observation of the specimen shows that the
430 anterior margin of the blade was curved (see below).

431

432 *4.4. Thoracic rib*

433

434 The thoracic rib is bow-shaped with a convex anterior margin (Fig.
435 2G). The tuberculum head is long, but the capitulum being less than twice
436 longer suggests a second left prothoracic rib. The orientation of the
437 tuberculum and capitulum, as well as the shape of the costal body,
438 suggest that the rib was bowed laterally, and oriented less vertically than
439 the ribs of *C. bequaerti* (Schwarz-Wing et al., 2009).

440

441 *4.5. Dorsal osteoderms*

442

443 Several pitted dorsal osteoderms are preserved (MHNM-Kh01d to f;
444 Fig. 3A-C). They are rectangular in shape, and nearly three times wider
445 than long. Their dorsal surface is densely ornamented with small pits, with
446 a smooth anterior portion for the articulation with the preceding
447 osteoderm. These two areas are separated by a deep lateromedial groove,
448 itself ornamented with deep pits. The lateral part, less ornamented, bends
449 downward forming a corner with the dorsal surface. A small rounded
450 process is present on the anteriormost part of this corner (Fig. 3A-C). The

451 smooth portion narrows laterally, so that the osteoderms are shorter
452 medially than laterally (except in the bent lateral portion). The anterior
453 margins of the osteoderms are gently convex in their mid-length (Fig. 3A).
454 In one osteoderm (Fig. 3C), the smooth anterior area of the bent lateral
455 portion progressively shortens ventrally in lateral view, so that the
456 anterior margin is ventroposteriorly directed. In another one, the anterior
457 margin is vertical, and the smooth area has the same length on all of its
458 height. These characters are probably related to the location of the
459 osteoderms along the dorsal shield. The lack of a sutural zones on both
460 lateral margins suggests that the dorsal osteoderms form two longitudinal
461 rows parallel to the midline, with many transverse rows. Their anterior
462 margins were overlapped by their preceding neighbours. The width of the
463 largest dorsal osteoderms, three times wider than long, is a highly
464 diagnostic character-state only known in the pholidosaurids (see below).
465 As in the Moroccan specimen (Fig. 3A-C), the anterolateral process is
466 reduced to a small anterolateral lobe in trunk osteoderms in *T robustus*,
467 *Pholidosaurus* spp., *W. byersmauricei*, and *D. kingi* (Koken, 1887;
468 Salisbury and Frey., 2001; Wu et al., 2001; S. J. pers. obs.). In
469 *Sarcosuchus* this process is more robust and longer. The lateral margin of
470 the dorsal osteoderm is nearly vertical in *Sarcosuchus*, *Terminonaris*, *W.*
471 *byersmauricei*, and the Moroccan specimen, but not in *Pholidosaurus* and
472 *D. kingi*, where the bend is much less marked, being gently inclined. In
473 goniopholidids, a dorsal shield arranged in two parallel rows with a bent
474 lateral margin and an anterolateral process is also present, but the

475 width/length ratio is lower (see below). Moreover, the dorsal surface of
476 the osteoderms is densely ornamented with small pits in MHNM-Kh01 as
477 in most pholidosaurids such as *Pholidosaurus* sp. (Martin et al., 2016b),
478 *Sarcosuchus imperator* (Sereno et al., 2001), *Woodbinesuchus*
479 *byersmauricei* (Lee, 1997), and *Oceanosuchus boecensis* Hua et al., 2007.
480 In goniopholidids, the ornamentation is formed by larger pits as in
481 *Anteophthalmosuchus* spp. (Salisbury and Naish, 2011; Puértolas-Pascual
482 et al., 2015; Martin et al., 2016a; Ristevski et al., 2018), *Goniopholis* spp.
483 (Schwarz, 2002; Hups et al., 2006), and *Sunosuchus* spp. (Wu et al.,
484 1996). In dyrosaurids, there are four longitudinal rows, the anterolateral
485 process is absent, and the lateral margin is not bent (Langston, 1995;
486 Jouve and Schwarz, 2004; Jouve et al., 2006a).

487 The lateral margin of one of the dorsal osteoderm is anteromedially
488 oriented (Fig. 3C), suggesting that it was an anterior osteoderm.
489 Compared with the shield of *Pholidosaurus* sp. (Martin et al., 2016b), it
490 could be the third or fourth.

491

492 4.6. Ventral osteoderms

493

494 Ventral armour is represented by thinner and smaller dermal scutes
495 (MHNM-Kh01e to l, Fig. 3D-K). Some of these osteoderms are rectangular
496 in outline, with two kinds of ornamentation: well-marked ornamentation
497 with deep pits on the posteriormost part, and a less ornamented strip on
498 less than one third of the length, ornamented with shallow grooves and

499 ridges. These two areas are separated by a groove with pits deeper than
500 in the two other parts. As in the dorsal osteoderms, the lack of a suture
501 on the anterior and posterior sides, suggests that each osteoderm
502 overlapped the anterior margins of its succeeding neighbours. The
503 presence of lateral and medial sutures suggests that the ventral
504 osteoderms form a plastron-like structure, consisting of many longitudinal
505 parallel rows. Two osteoderms have rounded anterior and lateral margins
506 (Fig. 3G, H). If the general characteristics are the same as in previous
507 osteoderms, the deep groove that delimits the strongly and the smoothly
508 ornamented area, is curved anteriorly. The absence of lateral suture
509 suggests that they formed lateral margin of the ventral armour. A ventral
510 osteoderm, probably from the neck region, differs from previously
511 described osteoderms (Fig. 3D). It is wider than long, faintly ornamented
512 and thinner (Fig. 3D). A rhombic osteoderm has been also recovered (Fig.
513 3E). Its entire dorsal surface is ornamented with similar pattern to those
514 of the dorsal osteoderms, with a corner faintly sculptured in comparison
515 with the rest of the body. There is no groove separating two areas, and all
516 its outlines seem to have been sutured to the neighbouring osteoderms.
517 Polygonal ventral osteoderms are known in goniopholidids, pholidosaurids,
518 and dyrosaurids (Martin et al., 2016a; Wu et al., 1996, 2001; Schwarz,
519 2003; Jouve et al., submitted), and form most of the ventral shield.
520 Osteoderms with anterior articular facet are known in some goniopholidids
521 (Wu et al., 1996) and dyrosaurids (Schwarz, 2003; Jouve et al.,
522 submitted), but their exact location is only known in the goniopholidid

523 *Sunosuchus junggarensis* Wu et al., 1996, in which they form the articular
524 area between the neck and the ventral shield. These osteoderms thus
525 likely come from the neck region.

526

527 **5. Discussion**

528

529 *5.1. Late Cretaceous tethysuchians*

530

531 The number of characters scored in the matrices is low for all newly
532 added species in the matrix used in this study (8.85% for the Moroccan
533 specimen, 16.81% for *S. coahuilensis*, 6.19% for *D. kingi*, and 16.37% for
534 *W. byersmauricei*). Nevertheless, the phylogenetic analysis provides 24
535 equally parsimonious trees (784.243 steps), and the consensus tree is
536 relatively well resolved (Fig. 4). It recovers *S. coahuilensis*, *D. kingi*, *W.*
537 *byersmauricei*, and the Moroccan specimen as pholidosaurid
538 tethysuchians. Even if all these species are known from fragmentary
539 material, the result is strongly supported with high Bremer indices, except
540 for *Dakotasuchus kingi*.

541 In the analysis the pholidosaurids form a monophyletic group (Fig.
542 4). They are grouped with the longirostrine dyrosaurids to form the
543 tethysuchians (Fig. 4). This contrasts with some recent results. Meunier
544 and Larsson (2017) and Young et al., 2017 recovered the genus
545 *Pholidosaurus* as the sister taxon to the clade

546 Pholidosauridae+Dyrosauridae with at least one of the matrices they used,
547 suggesting a paraphyly of the pholidosaurids.

548 Souza et al. (2019) also found the pholidosaurids as paraphyletic,
549 with *M. valliparadisi*, *Sarcosuchus* spp., and *T. robusta* more closely
550 related to the dyrosaurids than to other pholidosaurids and form a new
551 clade, Tethysuchoidea. Unfortunately, numerous mistakes are present in
552 this paper. The characters described as supporting the new clade and
553 included in the diagnosis are those supporting the clade including *V.*
554 *letognathus*, *E. cherifiensis*, and Dyrosauridae. The correct characters
555 supporting the tethysuchoids are the presence of paramedian depressions
556 on the palatal surface of the premaxilla (character 57), the posterior
557 premaxillary teeth that are larger than anterior ones (character 250), and
558 the anterior premaxillary teeth are aligned (character 254). All these
559 characters are reversed in dyrosaurids, and on the other hand, numerous
560 codings are erroneous or questionable (Appendix 13). The reliability of
561 this phylogenetic analysis is thus strongly doubtful.

562 Our phylogenetic analysis suggests that MHNM-Kh01 is a
563 pholidosaurid closely related to *T. robusta* (Fig. 4). This clade is supported
564 by the anterior margin of the neural spine of the posterior cervical or
565 anterior dorsal that is arched posteriorly (character 200) and by several
566 characters of dorsal osteoderms: the absence of a longitudinal dorsal keel
567 (character 219), the lateral margin of the posterior margin of the anterior
568 dorsal osteoderms that curves (character 223), their anterolateral process
569 is short (character 221), and its lateral margin is smooth (character 218).

570 Several other characters support the Moroccan specimen as a
571 pholidosaurid: the largest dorsal osteoderms are more than 2.5 times
572 wider than long (character 216) and ornamented with small and deep pits
573 (character 217), and the humeral deltopectoral crest is low (character
574 204) and extends on more than a quarter and less than a third the length
575 of the humerus (character 205) as in many dyrosaurids. The width/length
576 ratio of the dorsal osteoderms (width from medial margin of the
577 osteoderm to lateral margin of the anterolateral process compared to
578 minimal length medial to the anterolateral process) of the Moroccan
579 specimen (2.88) is close to that seen in *Pholidosaurus* (3; NHMUK R3956;
580 pers. obs.), *S. imperator* (2.79; S. J. pers. obs.), *D. kingi* (2.77), *O.*
581 *boecensis* (2.77; S. J. pers. obs.), and higher than that of
582 *Woodbinesuchus byersmauricei* Lee, 1997 (2.44) and *Terminonaris* (2.28;
583 Wu et al., 2001)(Fig. 5). Nevertheless, it is not excluded that this ratio
584 could be higher in *T. robusta* and *W. byersmauricei*, since this ratio varies
585 along the dorsal shield, and only two or three dorsal osteoderms have
586 been figured for both species (Lee, 1997; Wu et al., 2001). It is possible
587 that the osteoderms described for these species were not the largest. The
588 ratio is lower in goniopholidids, such as in *Anteophthalmosuchus hooleyi*
589 (2.43), *Amphicotylus lucasii* (1.83)(a complete dorsal shield is known for
590 both species), *A. epikrator* (2.47) and *Sunosuchus junggarensis* (1.77)
591 (Wu et al., 1996) (Fig. 5). The shape of the scapula previously considered
592 as a typical dyrosaurid character with the extreme concave anterior
593 margin is convergent between MHNM-Kh01, *D. kingi* and dyrosaurids (Fig.

594 6). It has been described in the goniopholidid *Anteophthalmosuchus*
595 *hooleyi* (Martin et al., 2016a) as having parallel sides, but the blade is
596 strongly damaged, precluding any confident evaluation of its shape. The
597 second scapula of the same specimen (the left one), is slightly better
598 preserved and demonstrates that the anterior margin of its blade was
599 curved (Fig. 6G). Moreover, a scapula preserved in the NHMUK and
600 attributed to *Goniopholis* (NHMUK.R3553), successively labelled as pubis
601 and ischium, also shows a curved anterior margin (Fig. 6H), less than in
602 dyrosaurids, the Moroccan specimen, and *D. kingi*, but not different from
603 that is observed in *Terminonaris* and *S. imperator*. The curvature is
604 stronger than in *Theriosuchus pusillus* (Fig. 6).

605 Nevertheless, this result should be considered with caution since it is
606 supported by postcranial characters while postcranial anatomy is unknown
607 in numerous tethysuchians, in particular in pholidosaurids. New
608 discoveries could change this interpretation, but the dorsal end of the
609 scapula is long in pholidosaurids such as *S. imperator*, *T. robusta*, and
610 goniopholidids (Fig. 6), less different than previously supposed.

611 *S. coahuilensis*, previously considered as a dyrosaurid (Shiller et al.,
612 2016; Ristevski et al., 2018), forms a clade with *Woodbinesuchus*
613 *byersmauricei* and *Oceanosuchus boecensis* and is a pholidosaurid (Fig.
614 4). This species has been described on the basis of poor material, and
615 numerous characters make its attribution to the tethysuchian dyrosaurids
616 particularly doubtful. The mandibular teeth described as the first and
617 second are more probably the third and fourth. The first preserved tooth

618 is far from the tip of the mandible, and both left and right teeth have a
619 lateral position on the mandible and are well separated from each other
620 (Appendix 14). The interalveolar distance separating the first and second
621 preserved alveoli is very short and they are almost confluent and larger in
622 size than any other tooth. All these characters are observed on the third
623 and fourth teeth of many neosuchians such as the pholidosaurids
624 (Appendix 14)(Mawson and Woodward, 1907; Mook, 1934; Buffetaut and
625 Ingavat, 1984; Martin et al., 2016b), goniopholidids (Owen, 1879;
626 Buffetaut and Ingavat, 1983; Schwarz, 2002; Martin et al., 2016a), but
627 not in dyrosaurids (Jouve et al., 2006a). As such, the tooth described as
628 the seventh dentary tooth is actually the ninth. Contrary to that which is
629 observed in dyrosaurids (Jouve et al., 2006a), this tooth is not really
630 smaller than the other teeth. Its anteroposterior length is equal to that
631 observed in the teeth described as d5 (and d7 herein) and d6 (d8) in the
632 left side, 1mm smaller than d2 (d4) and d5 (d7) in the right side. The
633 linguo-labial diameter is 2mm smaller than in d6 (d8) and d8 (d10) in the
634 left side, equal to d6 (d8), and 1mm smaller than d1 (d3), d4 (d6), d5
635 (d7), and d10 (d12) in right side (Shiller, 2012). So, the difference in size
636 of the teeth described as the 7th by Shiller (2012), is not significant
637 compared to neighbouring ones, only the estimated circumference
638 artificially increase it. Several other characters also confirm that this
639 attribution was erroneous. The medial wing of the retroarticular process is
640 dorsally located as in many neosuchians, and in particular pholidosaurids
641 (Koken, 1887; Mook, 1934; Buffetaut and Ingavat, 1984; Martin et al.,

642 2016b) and goniopholidids (Owen, 1879; Buffetaut and Ingavat, 1983;
643 Schwarz, 2002; Martin et al., 2016a). The retroarticular process is
644 extremely short and posteriorly oriented, an apomorphy of the clade
645 uniting *S. coahuilensis* with *O. boecensis* (character 179; list of characters
646 available as Appendix 1 at Mendeley datasets: <http://dx.doi.org/>). The
647 retroarticular process is long and posteriorly directed in most of the
648 pholidosaurids, and extremely long and strongly curved dorsally in all
649 dyrosaurids, particularly in long snouted forms, and its medial wing is
650 strongly deflected ventrally, a strong dyrosaurid apomorphy (Jouve et al.,
651 2006a). *Vectisuchus leptognathus* Buffetaut and hutt, 1980, has a long
652 retroarticular process with a low medial wing retroarticular process, while
653 *Elosuchus* has a long retroarticular process that curves posterodorsally,
654 and its medial wing resembles that which is observed in dyrosaurids
655 (MNHN uncatalogued specimens; S.J. per. obs.). The participation of the
656 splenial in the symphysis is very short in *S. coahuilensis*, stretching the
657 length of three teeth, whereas the complete symphysis is particularly
658 long, and exceeds the level of the 17th tooth. The splenial participates
659 deeply in the long symphysis in all dyrosaurids, reaching the length of five
660 to seven teeth in all long snouted forms (Jouve et al., 2006a), and being
661 the length of three teeth only in the short snouted *Cerrejonisuchus*
662 *improcerus* Hasting et al., 2010. The splenial forms more than a third of
663 the symphysis length in all dyrosaurids and close relatives. The symphysis
664 is also proportionally shorter compared to the symphysis length in
665 pholidosaurids (Buffetaut and Ingavat, 1984; Martin et al., 2016b), and in

666 particular in *Oceanosuchus boecensis* and *Woodbinesuchus*
667 *byersmauricei* (Hua et al., 2007; Lee, 1997), where it is less than a third
668 the length of the symphysis (character 168). The absence of a mandibular
669 fenestra is also an apomorphy (character 181) supporting the clade *S.*
670 *coahuilensis*, *O. boecensis* and *W. byersmauricei*. All these characters
671 confirm the affinities of *Sabinosuchus coahuilensis* with pholidosaurids.
672 *Woodbinesuchus byersmauricei* and *Dakotasuchus kingi*, previously
673 described as goniopholidids (Lee, 1997; Mehl, 1941; Frederickson et al.,
674 2017), are found as pholidosaurids in our analysis. Unlike the
675 goniopholidids, and as in many pholidosaurids, *W. byersmauricei* has a
676 long and narrow dentary symphysis, suggesting a slender snouted animal.
677 The mandibular symphysis is more than half the length of the mandibular
678 tooth row (character 164), the dorsal edge of the dentary shows a single
679 concavity posterior to the caniniform (character 166), and the teeth are
680 equal in size posterior to it (character 185), as found in pholidosaurids and
681 *Sunosuchus*, and contrary to most goniopholidids. The splenial that is less
682 than a third the length of the symphysis (character 168), as in
683 *Sunosuchus*, *S. coahuilensis* and *O. boecensis*, and does not participate
684 in the medial wall of the posterior alveoli (character 171), as found in *S.*
685 *coahuilensis* and *O. boecensis*. The anterior portion of its mandible is
686 spatulate and at least 25% wider than the minimal width of the mandible,
687 as in pholidosaurids (character 163) and its retroarticular process is
688 elongated (character 179). The ventral hypapophysis in the preserved
689 cervical of *W. byersmauricei* differs from that of goniopholidids (Martin et

690 al., 2016a) in being longer, and resembles that of *Terminonaris robusta*
691 (Wu et al., 2001), but it is not possible to know if it is knob-like as found
692 in this species and goniopholidids. The osteoderms are particularly wide,
693 and densely ornamented with small pits (character 217), as in
694 pholidosaurids (Martin et al., 2016b; Sereno et al., 2001; Hua et al.,
695 2007). This differs from what is observed in most of the goniopholidids
696 (Wu et al., 1996; Schwarz, 2002; Hups et al., 2006; Salisbury and Naish,
697 2011; Puértolas-Pascual et al., 2015; Martin et al., 2016a; Ristevski et al.,
698 2018). On the contrary, *W. byersmauricei* has a scapula with a narrow
699 distal portion with parallel sides (Fig. 6D), resembling to that which is
700 found in alligators (Brochu, 1999), and differs from that which is found in
701 Tethysuchians and known goniopholidids (Fig. 6). Could this suggest that
702 the scapular blade is incomplete? Direct re-examination of the holotype
703 and new material are thus required.

704 *Dakotasuchus kingi* is exclusively known from postcranial material.
705 Alternatively, it is closely related to *Terminonaris* and the Moroccan
706 pholidosaurids or *Pholidosaurus*, relationships supported by four
707 apomorphies: the osteoderm has no longitudinal keel (character 219), as
708 in *Terminonaris* and Moroccan specimen, its lateral margin is slightly bent
709 (character 215), its posterolateral margin curves (character 223), and its
710 anterolateral process is short and rounded (221) as in *Terminonaris* and
711 *Pholidosaurus*. It also shares with pholidosaurids very wide dorsal
712 osteoderms (character 216) ornamented with small and deep pits
713 (character 217). Its scapula is strongly expanded dorsally (Fig. 6C), as in

714 dyrosaurids and MHNM-Kh01 (Character 210), with an anterior margin
715 that is more concave than in other pholidosaurids and goniopholidids (Fig.
716 6).

717 These attributions provide new information on the evolution of the
718 pholidosaurids. Four more species are now considered as belonging to this
719 group. They were previously considered as extinct since the Turonian, but
720 the reattribution of *Sabinosuchus coahuilensis* and the Moroccan specimen
721 suggest that pholidosaurids survived later than previously thought, 28My
722 later (Fig. 7). Thus, the pholidosaurids crossed the KT crisis.

723 These results, mainly based on postcranial characters, should be
724 considered with caution, but the pholidosaurid osteoderms are different
725 enough from those of all other crocodylomorphs to confidently support
726 affinities of MHNM-Kh01 with pholidosaurids.

727

728 *5.2. Basal dyrosaurid history*

729

730 The phylogenetic analysis provides a relatively well resolved result
731 (Figs. 4, 8), with significant differences compared to previous works.
732 *Elosuchus cherifiensis* has been described as a pholidosaurid (e.g. Jouve
733 et al., 2006; Jouve, 2009; Andrade et al., 2011; Fortier et al., 2011;
734 Martin et al., 2013; Meunier et al., 2016; Young et al., 2016; Adams et
735 al., 2017; Noto et al., 2019), or closely related to the clade formed by the
736 pholidosaurids and dyrosaurids (Jouve, 2009; Wilberg, 2015; Ristevski et
737 al., 2018; Wilberg et al., 2019).

738 *Vectisuchus leptognathus* was first described as a goniopholidid
739 (Buffetaut and hutt, 1980; Jouve et al., 2006; Jouve, 2009; Wilberg,
740 2015), but later as a pholidosaurid (Young et al., 2016; Meunier et al.,
741 2016; Ristevski et al., 2018), and sometimes closely related to *E.*
742 *cherifiensis* (Andrade et al., 2011; Ristevski et al., 2018; Wilberg et al.,
743 2019; Souza et al., 2019). In the present work, *Elosuchus* and
744 *Vectisuchus* are more closely related to dyrosaurids than to
745 pholidosaurids, *Elosuchus* being the sister taxon to Dyrosauridae (Fig. 4).

746 *V. leptognathus* and *Elosuchus* spp. are from the Barremian and
747 Albian-Cenomanian respectively, and their phylogenetic relationships at
748 the base of the dyrosaurids partly fill the stratigraphic gap between the
749 oldest known dyrosaurids, dated possibly from the Cenomanian but more
750 confidently from the Maastrichtian, and the divergence between
751 pholidosaurids and dyrosaurids dated from the Late Jurassic (Fig. 7). The
752 phylogenetic relationships will be more deeply discussed in a paper
753 dedicated to the description of 3 new dyrosaurid species (Jouve et al.,
754 submitted). *Vectisuchus leptognathus* and *Elosuchus* spp. are known from
755 fresh water environment, contrary to most of the later known dyrosaurids.
756 As noted by Salas-Gismondi et al. (2016) in gavialoids, one must
757 emphasize that several fresh-water tethysuchians have strongly
758 telescoped orbits (*Elosuchus* spp., *Sarcosuchus imperator*, *Vectisuchus*
759 *leptognathus*), while marine forms have not (*Oceanosuchus boecensis*,
760 *Terminonaris robusta*). This environmental adaptation has strong impact
761 on the gavialoid phylogenetic analysis in which the fresh-water forms with

762 telescoped orbits are grouped in the same clade. This should be
763 considered in future phylogenetic analyses focused on tethysuchian
764 relationships.

765

766 *5.2. Tethysuchian diversity and abiotic factors*

767

768 The pholidosaurids were previously considered as an extinct group
769 since the Turonian and as a poorly diversified crocodylomorph group with
770 only nine species. The present work identifies four more pholidosaurid
771 species, increasing their diversity by 44%. This diversity with 13
772 recognised species remains lower than that of the closely related
773 dyrosaurids, known by at least 21 recognised species, 24 considering the
774 dyrosaurs and species more closely related to them than to
775 pholidosaurids, and 3 additional species currently under study (Jouve et
776 al., submitted). Pholidosaurid diversity stretches for more than 95 My, and
777 our phylogenetic analysis suggests that dyrosaurs and close relatives lived
778 during nearly 119My (from Kimmeridgian to Bartonian), but all recognized
779 dyrosaurids are known in a time interval of less than 35 My. The early
780 history of the dyrosaurid lineage is poorly known with only three species
781 from the Late Jurassic (Kimmeridgian) to the middle Late Cretaceous
782 (Campanian). So, most of the dyrosaurid diversification occurred during
783 the latest Cretaceous and the beginning of the Paleocene.

784 The reevaluation of the possible pholidosaurid species and the
785 phylogenetic analysis considering most of them creates the opportunity to

786 formulate hypotheses on the evolution of the tethysuchian diversity (Fig.
787 8). The oldest known pholidosaurid tethysuchians, *Anglosuchus geoffroyi*
788 (Owen, 1884) and *Anglosuchus laticeps* (Owen, 1884), have been
789 described from the Bathonian. Both species strongly resemble the
790 Berriasian *Pholidosaurus purbeckensis*, and this early age is thus doubtful.
791 These species are not considered herein.

792 The first confirmed tethysuchian appears during the Late Jurassic
793 (Kimmeridgian), and their diversity increases up to the lowermost
794 Cretaceous (Berriasian) (Fig. 8). The second and higher diversity peak is
795 observed during the Cenomanian. Both diversity peaks coincide with two
796 periods of high temperatures established from the oxygen isotope (Fig. 8).
797 The second time interval of highest temperature continues up to the
798 Santonian, and the temperatures decrease during the Campanian
799 continuously to the Paleocene (Fig. 8). The fall of the tethysuchian
800 diversity during the Turonian does not correspond with the temperature
801 variations as the latter remain high to the Santonian. No global statistical
802 correlation is found between the paleotemperature proxies from $\delta^{18}\text{O}$
803 (Prokoph et al., 2008) and tethysuchian diversity (Table 1), but
804 considering only the Late Jurassic-Earliest Cretaceous (Cenomanian)
805 interval, the correlation is high (Table 1). A weak correlation is found
806 between sea level and tethysuchian diversity, but no correlation if only the
807 Oxfordian-Cenomanian time interval is considered (Table 2). Even if
808 correlation does not mean causality, this correlation suggests that the
809 temperature during the Late Jurassic-Early Cretaceous interval could have

810 been a driver to the general evolution of tethysuchians Such correlation as
811 also been suggested for polycotylid plesiosaurians and ichthyosaurs during
812 the same period of time (Fischer et al., 2016, 2018). This relationship is
813 not surprising as crocodyliforms are known to be strongly dependent on
814 climatic variations (Markwick, 1998a, 1998b; Carvalho et al., 2010; Martin
815 et al., 2014; Mannion et al., 2015).

816 The late Cenomanian is marked by a strong “Ocean Anoxic Event”
817 (OAE 2), characterized by the record of a rising CO₂ (Arthur et al., 1987;
818 Friedrich et al., 2006; Jenkyns, 2010; Jenkyns et al., 2017). An important
819 impact on marine fauna with a biotic turnover has been documented
820 (Kauffman, 1995; Eaton and Kirkland, 2001; Caron et al., 2006; Monnet,
821 2009; Sepkoski, 1989, 1996; Wan et al., 2003), and this destabilization of
822 marine food web related to OAE 2 corresponds to the strong decrease of
823 marine tethysuchian diversity between the Cenomanian and Turonian
824 (Figs. 7, 8).

825 Several Cenomanian tethysuchians lived in fresh-water
826 environments (Fig. 7), and works on the effect of the Cenomanian-
827 Turonian boundary crisis on this environment are particularly scarce. A
828 major faunal turnover has been noted in North American fresh-water fish
829 and turtle taxa (Eaton et al., 1997; Redman, 2012; Brinkman et al., 2013;
830 Frederickson and Cifelli, 2017). The reason for this faunal turnover has
831 not been clearly identified. No anoxia has been found in tested fresh-
832 water layers (Rustad, 2013), but Eaton et al. (1997) suggested that the
833 large Turonian regression could have reduced the brackish environments

834 and the riverine-brackish-water contacts, and excluded from the riverine
835 environments the species that required some contacts with marine or
836 brackish water during their life cycles. This regression is clearly visible in
837 sea level curves, and extends from the Turonian to the Santonian, the
838 time interval to which the tethysuchian diversity coincides less with the
839 temperatures (Fig. 8).

840 In contrast to what is found for the Oxfordian-Cenomanian interval
841 of time, the tethysuchian diversity is strongly correlated to the sea level
842 during the Turonian-Thanelian and strongly inversely correlated with the
843 temperature (Table 2). A strong Turonian-Thanelian inverse correlation is
844 also observed between temperatures and sea level (Table3). The number
845 of marine tethysuchian forms is higher during this time interval compared
846 to the higher proportion of fresh water forms during the Early Cretaceous.
847 Could the destabilisation of the fresh-water fauna caused by the
848 regression have impacted the piscivorous tethysuchians in fresh-water
849 during the middle Late Cretaceous, as the regression and OAE 2 could
850 have impacted the near shore forms? These should be considered in
851 future investigations.

852 Contrary to the pholidosaurids, the dyrosaur lineage diversity
853 strongly increases during the Maastrichtian. Their diversity from Turonian-
854 Thanelian is strongly inversely correlated with the temperature, but also
855 positively with sea level. This diversity rise despite the fall of the
856 temperature, is surprising as the crocodyliforms are considered as a
857 climate sensitive group (Markwick, 1998a, 1998b; Carvalho et al., 2010;

858 Martin et al., 2014; Mannion et al., 2015). Was there a differential
859 tolerance between both tethysuchian lineages as suggested between some
860 eusuchians lineages (Martin, 2010; Lance, 2003; Jouve et al., 2019)?
861 Competition between both tethysuchian groups, as with the emerging
862 crocodylians and with other large marine reptiles such as mosasaurs, and
863 regional factors form also a complex set of factors not tested here.

864

865 *5.3. Late Cretaceous tethysuchian evolution and K-Pg crisis survivorship*

866

867 The presence of Maastrichtian and Danian pholidosaurid species
868 proves that the group survived more than 28 million years later than
869 previously thought, and that it crossed the K-Pg crisis. Moreover, the
870 distant phylogenetic relationships of the Maastrichtian *S. coahuilensis* and
871 the Danian Moroccan specimen obtained in the phylogenetic analysis
872 performed herein, suggests that two independent lineages survived to the
873 Late Maastrichtian, but only one crossed the K-Pg boundary (Fig. 7).

874 The number of crocodylomorph taxa that survived the K-Pg crisis is
875 relatively low, the terrestrial sebecids (notosuchians), two tethysuchian
876 lineages (pholidosaurids and dyrosaurids), and several marine and fresh
877 water crocodylian groups (gavialoids, alligatoroids, crocodyloids,
878 planocraniids, and *Borealosuchus*) (Fig. 9). The diversity of terrestrial
879 forms (notosuchians) decreases prior to the K-Pg mass extinction events
880 (Mannion et al., 2015), and is not related to the K-Pg crisis, but probably
881 to the fall of temperatures through the second half of the Late Cretaceous

882 (Fig .8; Linnert et al., 2014). The effect of the K-Pg crisis on marine and
883 fresh-water crocodylomorphs has been considered as minor, however,
884 their marine diversity strongly increases after the K-Pg boundary,
885 benefiting from the extinction of large marine reptiles such as
886 mosasauroid squamates (Jouve, 2004; Jouve et al., 2008a, submitted;
887 Barbosa et al., 2008). The survivorship of the pholidosaurids through the
888 K-Pg boundary confirms its weak impact on crocodylomorphs, even on a
889 group poorly diversified at the end of the Cretaceous. If we consider that
890 *S. coahuilensis* and the Moroccan pholidosaurid are from two independent
891 lineages, two pholidosaurid lineages reached the K-Pg boundary, and one
892 survived the crisis.

893 Two groups of longirostrine crocodylomorphs radiated during the
894 end of the Cretaceous: the gavialoids and the tethysuchian dyrosaurids.
895 The first diversifies constantly from the Late Cretaceous to the beginning
896 of the Paleocene, while the second strongly benefited from the crisis to
897 greatly increase its number of species. Both gavialoids and dyrosaurids
898 emerged during the Campanian, but diversified during the Maastrichtian,
899 the period during which the pholidosaurids “resurrected” after 20 My of
900 apparent absence from middle Turonian to the Maastrichtian. The
901 longirostrine dyrosaurids radiated at the end of the Cretaceous, but their
902 diversity clearly shot up during the Paleocene (Jouve et al., submitted;
903 Fig. 8). This competition in marine environments, as well as the
904 emergence of the first fresh-water crocodylians, could have contributed to

905 the extinction of a particularly fragile group, the pholidosaurids, restricted
906 to tropical areas maybe due to the low Late Cretaceous temperatures.

907

908 **6. Conclusions**

909

910 New material from Morocco shows that the pholidosaurids,
911 previously thought to have gone extinct during the Turonian, survived
912 through the Late Cretaceous, crossed the K-Pg Crisis and persisted to the
913 Early Paleocene. Late Cretaceous crocodylomorphs (*Dakotasuchus kingi*,
914 *Woodbinesuchus byersmauricei* and *Sabinosuchus coahuilensis*), formerly
915 attributed to Goniopholididae and Dyrosauridae, are reviewed and
916 reattributed to the pholidosaurids. *Dakotasuchus kingi* and
917 *Woodbinesuchus byersmauricei* were mainly described on the basis of
918 postcranial material that strongly resembles both goniopholidids and
919 pholidosaurids. Nevertheless, we highlight significant differences in the
920 shape of the dorsal osteoderms, particularly in most derived
921 pholidosaurids, that could help future determination of isolated remains.

922 These new species considered as pholidosaurs make possible a first
923 analysis of the evolution of tethysuchian diversity through the Late
924 Jurassic to the Lower Paleocene. A strong global correlation with the
925 temperature change exists considering the Oxfordian-Cenomanian time
926 interval. The strong decline of tethysuchian diversity coincides with the
927 "Oceanic Anoxic Event 2", considered as the origin of a strong marine
928 biotic event at the Cenomanian-Turonian boundary. The large oceanic

929 regression could also have heavily impacted on the tethysuchian diversity
930 during this time interval, It is hard to evaluate which of these factors was
931 the main driver, but OAE 2 is a punctual event that occurred at the end of
932 the Cenomanian and the beginning of the Turonian, while the oceanic
933 regression occurred from the Turonian-Santonian interval, corresponding
934 to the pholidosaurid and dyrosaur lineage diversity fall. The later Late
935 Cretaceous sea level rise event could have benefited the diversification of
936 the dyrosaurs.

937 While the impact of the OAE 2 on marine invertebrate faunas has
938 been largely investigated, its effect on the marine reptiles has not been
939 deeply studied, seeing the demise of several marine reptile groups during
940 the Cenomanian-Turonian interval such as pliosaurs and ichthyosaurs
941 (Fischer et al., 2016, 2018). The OAE 2 and the large Turonian regression
942 have probably weakened the diversity of the near shore and fresh-water
943 tethysuchians, their effect on other marine reptiles such as pliosaurs and
944 ichthyosaurs should also be investigated. Several other marine reptiles
945 survived the Cenomanian-Turonian crisis (polycotylids, marine turtles),
946 and others have begun their diversification during this time interval
947 (mosasaurs). Future investigations should consider and compare the
948 evolution of all these marine groups, as well as the evolution of fresh-
949 water reptiles, to determine the reason why some survived while other
950 became extinct. They should also evaluate the more precise stratigraphic
951 distribution of the tethysuchian species, to provide a clearer pattern in the

952 relationships of their evolution with the sea level, OAE 2 phases, and
953 paleotemperature variations.

954

955 **Acknowledgements**

956

957 This work benefits from the support of the “Agence Universitaire de
958 la Francophonie”. Many thanks to the OCP team for their help and the
959 precious logistical support with fieldwork. This work has been made in the
960 framework of the Convention between the Ministry of Energy and Mines
961 (Morocco), the Office Chérifiens des Phosphates (Morocco), the
962 Universities Cadi Ayyad and Chouaib Doukali (Morocco) and the National
963 Museum of Natural History (Paris). S. J. thanks the staff of the Université
964 Cadi Ayyad, and the Natural History Museum of Marrakech for their
965 welcome, especially M. Ghamizi and A. Faskaoune. The pictures were
966 realised by Mr. P. Loubry. Many thanks to Henri Cappetta for the
967 identification of the shark fauna found associated with the specimen
968 studied herein. The authors thank Mark Young and an anonymous
969 reviewer for their particularly constructive comments. This research
970 received support from the SYNTHESYS Project
971 (<http://www.synthesys.info/>), which is financed by the European
972 Community Research Infrastructure Action under the FP7 ‘Capacities’
973 Program (GB-TAF-3366). We also thank John Jones for reviewing the
974 English grammar in the paper.

975

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1393 **Fig. 1.** Geographical location of the marine phosphatic basins of Central
1394 Morocco.

1395 1.5 column fitting page image

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1397 **Fig. 2.** Pholidosauridae indet. MHNM-kh01, postcranial remains, Oulad
1398 Abdoun Basin, Morocco, Danian. Photographs (A-G): A-B, MNHN-Kh01a,
1399 cervical 9 or dorsal 1 or 2 vertebra in left lateral (A) and anterior (B)
1400 views; C, MHNM-kh01 left scapula in lateral view; D-F, MHNM-kh01b, left
1401 humerus in anterior (D), posterior (E) and lateral (F) views; G, left
1402 thoracic rib in lateral view.

1403 2 columns fitting page image

1404

1405 **Fig. 3.** Pholidosauridae indet. MHNM-kh01, postcranial remains, Oulad
1406 Abdoun Basin, Morocco, Danian. Photographs (A-K): A, dorsal osteoderm
1407 in dorsal view; B, dorsal and ventral osteoderms in dorsal view; C, detail
1408 of a dorsal osteoderm in antero-lateral view; D, ventral osteoderm from
1409 neck region in ventral view; E, ventral osteoderm in ventral view; F and
1410 G, lateroventral osteoderms in ventral view; H, I, J and K, medioventral
1411 osteoderms in ventral view.

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1414 **Fig. 4.** Strict consensus cladograms from 24 most parsimonious trees
1415 obtained from a matrix including 224 characters (list of characters and
1416 data matrix available as Appendix 1 and 2 at Mendeley datasets:
1417 <http://dx.doi.org/>). Taxa in bold are added for the present study.

1418 2 columns fitting page image

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1420 **Fig. 5.** Comparison of the dorsal osteoderms of various
1421 pholidosaurids and goniopholidids. A, *Pholidosaurus purbeckensis*, NHMUK
1422 R3956, dorsal osteoderm in dorsal view; B, *Oceanosuchus boecensis*,
1423 MHNH.9036, dorsal osteoderm in dorsal view; C, *Sarcosuchus imperator*,
1424 from Sereno et al. (2001), dorsal osteoderm in dorsal view; D,
1425 *Dakotasuchus kingi*, from Frederickson et al. (2017), dorsal osteoderm in
1426 dorsal view; E, *Terminonaris robusta*, from Wu et al. (2001), dorsal
1427 osteoderm in dorsal view; F, MHNM-Kh01a, dorsal osteoderm in dorsal
1428 view; G, *Goniopholis* sp., from Puértolas-Pascual et al. (2015), dorsal
1429 osteoderm in dorsal view; H, *Anteophthalmosuchus hooleyi*, IRSNB 1537,
1430 dorsal osteoderm in dorsal view; I, cf. *Amphicotylus lucasii*, from Erickson
1431 (2016), dorsal osteoderm in dorsal view; J, *Sunosuchus junggarensis*,
1432 from Wu et al., 1996, dorsal osteoderm in dorsal view; J,
1433 *Anteophthalmosuchus epikrator*, from Ristevski et al. (2018), dorsal
1434 osteoderm in dorsal view. All figures are fit to the same size and are not
1435 to scale. W, width of the osteoderm from the medial margin to the lateral
1436 margin of the anterolateral process; L, length of the osteoderm medial to
1437 the anterolateral process. W/L, width length ratio. Arrows indicate the
1438 curvatures of the lateral posterior margin of the osteoderms.

1439 1.5 columns fitting page image

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1441 **Fig. 6.** Comparison of the scapula of various crocodyliforms. A,
1442 *Sarcosuchus imperator*, MNHN.F.326.1, left scapula in lateral view; B,

1443 *Terminonaris robusta*, from Wu et al. (2001), left scapula in lateral view;
1444 C, *Dakotasuchus kingi*, from Mehl (1941), right scapula in lateral view; D,
1445 *Woodbinesuchus byersmauricei*, from Lee (1997), right scapula in lateral
1446 view; E, MHNM-Kh01a, left scapula in lateral view; F, *Congosaurus*
1447 *bequaerti*, MRAC 1809, right scapula in medial view; G,
1448 *Anteophthalmosuchus hooleyi*, IRSNB R47, left scapula in medial view; H,
1449 *Goniopholis* sp., NHMUK R3553, left scapula in medial view; I,
1450 *Theriosuchus pusillus*, NHMUK 48216, right scapula in medial view. All
1451 specimens are fit to same size and are not to scale. Dashed lines:
1452 reconstructed parts.

1453 1.5 columns fitting page image

1454

1455 **Fig. 7.** Strict consensus cladogram of tethysuchians obtained in the
1456 phylogenetic analysis conducted in the present work, placed in
1457 stratigraphic context (Appendices 4, 6 of Supplementary data). Taxa
1458 figured are those used in the diversity curve (Fig. 8). The relationships of
1459 *Dakotasuchus kingi* used in the figure is the stratigraphically most
1460 congruent. Blue color is used to figure the marine forms, and pink area
1461 figures the extension of the Oceanic Anoxic Event 2 (OAE2).

1462 2 columns fitting page image

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1464 **Fig. 8.** Comparison of the pholidosaurids diversity from the Late Jurassic
1465 to the end of the Paleocene, with sea level and paleotemperature proxies
1466 from $\delta^{18}\text{O}$. The diversity count is corrected with the phylogenetic

1467 relationships obtained in the present work, and considers several
1468 specimens and species not included in the phylogenetic analysis (see Fig.
1469 7; Appendices 4-7). $\delta^{18}\text{O}$ is from Prokoph et al. (2008) and sea level is
1470 from Miller et al. (2005) (Appendices 8, 9).

1471 2 columns fitting page image

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1473 **Fig. 9.** Biochronology of the Crocodylomorpha simplified from the strict
1474 consensus tree obtained by Wilberg et al. (2019).

1475 1.5 columns fitting page image

1476

| | | |
|---|---------------------|-------------------|
| Tethysuchia diversity | | |
| | Spearman's <i>r</i> | <i>p</i> |
| | 0.14382 | 0.56912 |
| Tethysuchia diversity, Oxfordian-Cenomanian | | |
| | Spearman's <i>r</i> | <i>p</i> |
| | -0.75314 | 0.011911 |
| Pholidosauridae diversity | | |
| | Spearman's <i>r</i> | <i>p</i> |
| | -0.19656 | 0.43437 |
| Pholidosauridae diversity, Oxfordian-Cenomanian | | |
| | Spearman's <i>r</i> | <i>p</i> |
| | -0.4211 | 0.22554 |
| "Dyrosaur lineage" diversity | | |
| | Spearman's <i>r</i> | <i>p</i> |
| | 0.032521 | 0.89807 |
| Dyrosauroidea diversity, Turonian-Thanelian | | |
| | Spearman's <i>r</i> | <i>p</i> |
| | 0.96978 | 0.00059524 |

1478

1479 **Table 1**

1480 Correlation between $\delta^{18}\text{O}$ and various tethysuchian diversity datasets. The
1481 diversity counts used are the corrected phylogenetically. The significant
1482 correlations are in bold. See Appendix 10 for complete results.

1483

1484

| | |
|---|-------------------|
| Tethysuchia diversity | |
| Spearman's r | p |
| 0.47615 | 0.045771 |
| Tethysuchia diversity, Oxfordian-Cenomanian | |
| Spearman's r | p |
| 0.60504 | 0.063838 |
| Tethysuchia diversity, Turonian-Thantetian | |
| Spearman's r | p |
| 0.77846 | 0.03006 |
| "Dyrosaur lineage" diversity | |
| Spearman's r | p |
| 0.73855 | 0.00046445 |
| "Dyrosaur lineage" diversity, Turonian-Thantetian | |
| Spearman's r | p |
| 0.84702 | 0.014881 |
| Pholidosauridae diversity | |
| Spearman's r | p |
| -0.40216 | 0.098037 |
| Pholidosauridae diversity, Oxfordian-Cenomanian | |
| Spearman's r | p |
| 0.074087 | 0.83882 |

1486

1487 **Table 2**

1488 Correlation between sea level and various tethysuchian diversity

1489 datasets. The diversity counts used are the corrected phylogenetically.

1490 The significant correlations are in bold. See Appendix 11 for complete
1491 results.

1492

| Mean $\delta^{18}\text{O}$ / Sea level | |
|--|----------|
| Spearman's r | p |
| -0.41736 | 0.084846 |

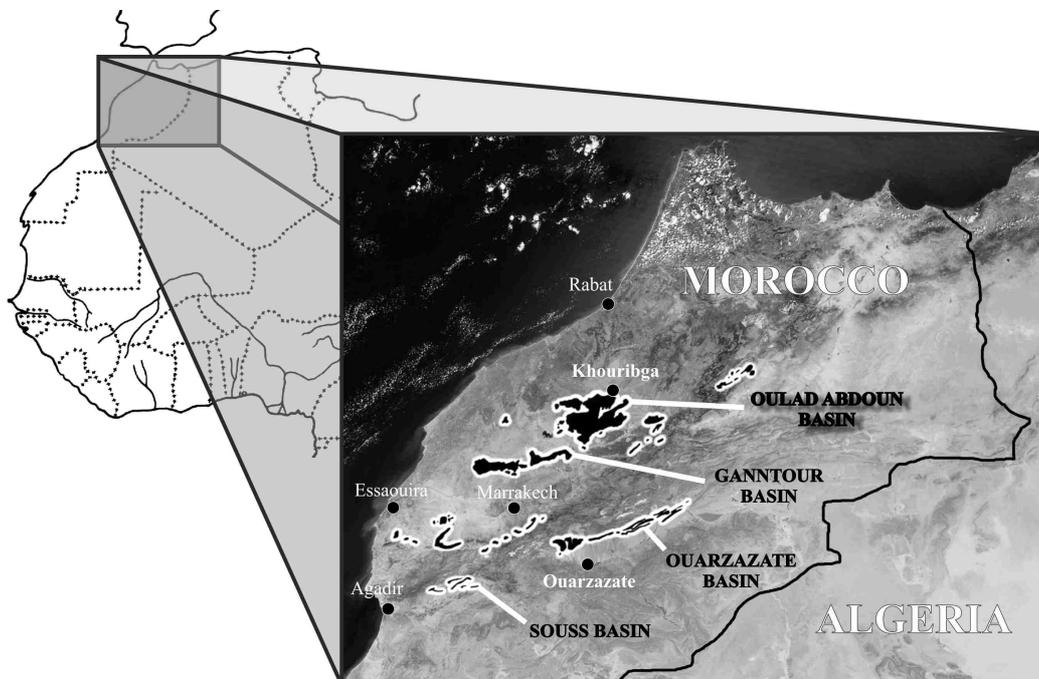
| Mean $\delta^{18}\text{O}$ / Sea level Oxfordian-Cenomanian | |
|--|-----------------|
| Spearman's r | p |
| -0.70517 | 0.022738 |

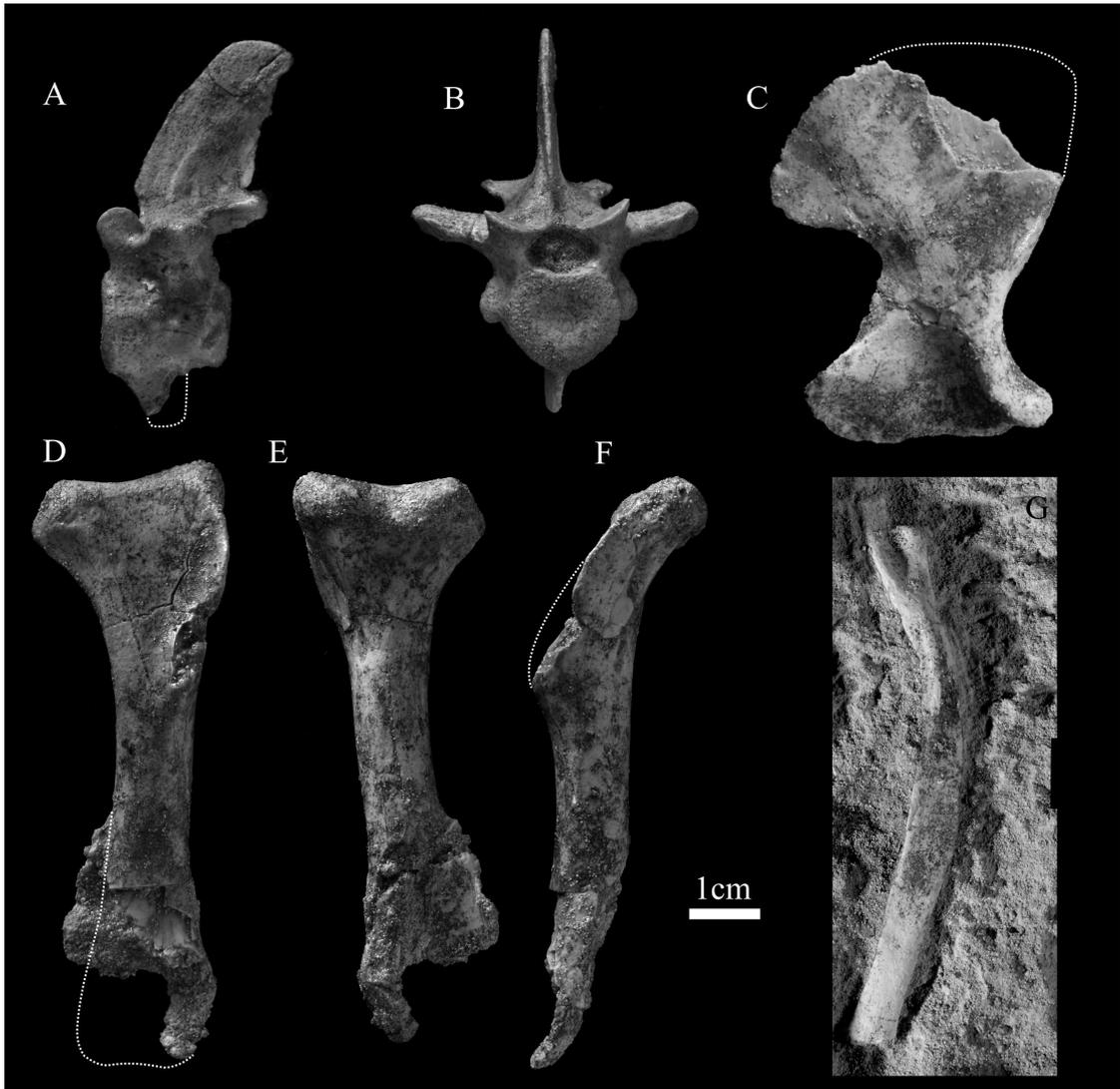
| Mean $\delta^{18}\text{O}$ / Sea level Turonian-Thantetian | |
|---|-----------------|
| Spearman's r | p |
| 0.83333 | 0.010714 |

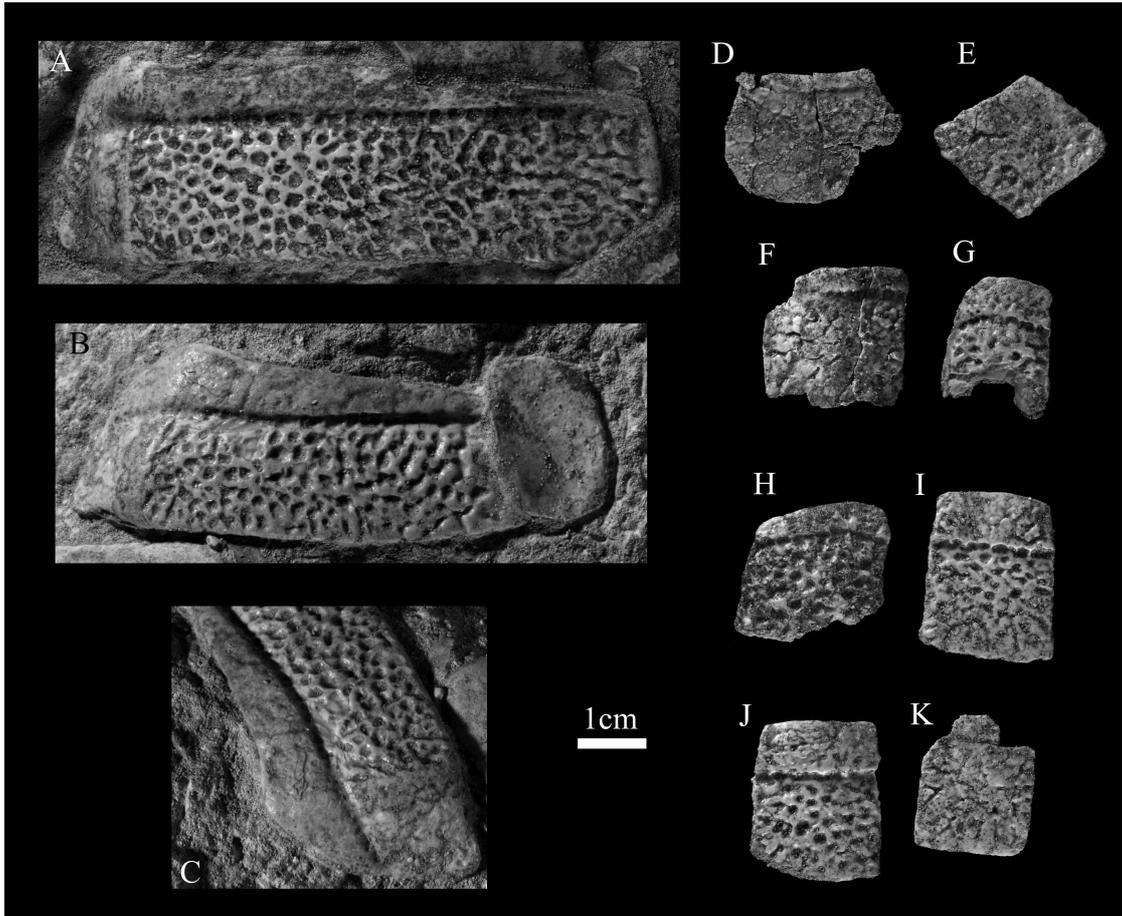
1493

1494 **Table 3**

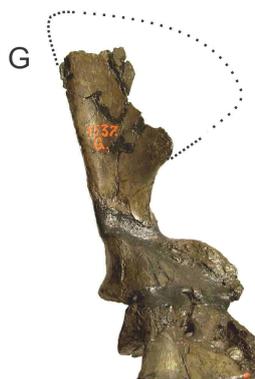
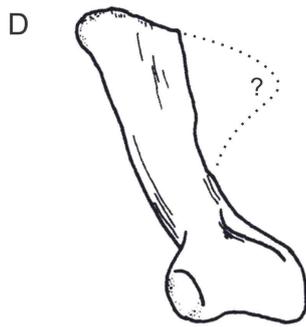
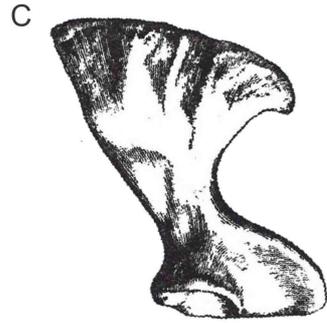
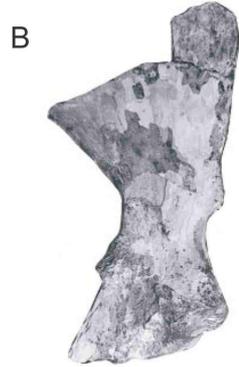
1495 Correlation between $\delta^{18}\text{O}$ and sea level for several time intervals.











H



I



