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.

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

4

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 $\delta_{18}O$

248 paleotemperature proxy from the compendium provided by Prokoph et al.

249 (2008) (Appendix 8 of Supplementary data). We calculated the mean of

250 $\delta_{18}O$ for each time interval, using only the $\delta_{18}O$ 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

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

Abbreviations

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

FSSM: Faculté des Sciences Semlalia, Marrakech, Morocco.

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

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

OCP: Office Chérifien des Phosphates, Khouribga, Morocco.

3. Systematic paleontology

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

Neosuchia Benton and Clark, 1988

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 sligthly 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 amphycoelous 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 reamains 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*, (Bergougnioux, 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 generus 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. (Bergougnioux, 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* (Sereno 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 anteriomost 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 ostoderms, three times wider than long, is a highly

464   diagnostic chatacter-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 osteorderms 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. Unfortunatelly, 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: <mark>http://dx.doi.org/</mark>). 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 ressembles 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 *Wooodbinesuchus*

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 participates

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

dyrosaurids and MHNM-Kh01 (Character 210), with an anterior margin

that is more concave than in other pholidosaurids and goniopholidids (Fig.

6).

These attributions provide new information on the evolution of the

pholidosaurids. Four more species are now considered as belonging to this

group. They were previously considered as extinct since the Turonian, but

the reattribution of *Sabinosuchus coahuilensis* and the Moroccan specimen

suggest that pholidosaurids survived later than previously thought, 28My

later (Fig. 7). Thus, the pholidosaurids crossed the KT crisis.

These results, mainly based on postcranial characters, should be

considered with caution, but the pholidosaurid osteoderms are different

enough from those of all other crocodylomorphs to confidently support

affinities of MHNM-Kh01 with pholidosaurids.

5.2. Basal dyrosaurid history

The phylogenetic analysis provides a relatively well resolved result

(Figs. 4, 8), with significant differences compared to previous works.

Elosuchus cherifiensis has been described as a pholidosaurid (e.g. Jouve

et al., 2006; Jouve, 2009; Andrade et al., 2011; Fortier et al., 2011;

Martin et al., 2013; Meunier et al., 2016; Young et al., 2016; Adams et

al., 2017; Noto et al., 2019), or closely related to the clade formed by the

pholidosaurids and dyrosaurids (Jouve, 2009; Wilberg, 2015; Ristevski et

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

formulate hypotheses on the evolution of the tethysuchian diversity (Fig.

8). The oldest known pholidosaurid tethysuchians, *Anglosuchus geoffroyi*

(Owen, 1884) and *Anglosuchus laticeps* (Owen, 1884), have been

described from the Bathonian. Both species strongly resemble the

Berriasian *Pholidosaurus purbeckensis*, and this early age is thus doubtful.

These species are not considered herein.

The first confirmed tethysuchian appears during the Late Jurassic

(Kimmeridgian), and their diversity increases up to the lowermost

Cretaceous (Berriasian) (Fig. 8). The second and higher diversity peak is

observed during the Cenomanian. Both diversity peaks coincide with two

periods of high temperatures established from the oxygen isotope (Fig. 8).

The second time interval of highest temperature continues up to the

Santonian, and the temperatures decrease during the Campanian

continuously to the Paleocene (Fig. 8). The fall of the tethysuchian

diversity during the Turonian does not correspond with the temperature

variations as the latter remain high to the Santonian. No global statistical

correlation is found between the paleotemperature proxies from $\delta^{18}O$

(Prokoph et al., 2008) and tethysuchian diversity (Table 1), but

considering only the Late Jurassic-Earliest Cretaceous (Cenomanian)

interval, the correlation is high (Table 1). A weak correlation is found

between sea level and tethysuchian diversity, but no correlation if only the

Oxfordian-Cenomanian time interval is considered (Table 2). Even if

correlation does not mean causality, this correlation suggests that the

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 ichtyosaurs 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 CO_2 (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 intervall 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-Thanetian and strongly inversely correlated with the

843   temperature (Table 2). A strong Turonian-Thanetian 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   Thanetian 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

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956

975

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976 **References**

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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

1396

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.

1412   2 columns fitting page image

1413

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

1419

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

1440

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

1463

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 $\delta^{18}O$. 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). $\delta^{18}O$ 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

1472

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

1477

Tethysuchia diversity	
Spearman's *r*	*p*
0.14382	0.56912

Tethysuchia diversity, Oxfordian-Cenomanian	
Spearman's *r*	*p*
-0.75314	**0.011911**

Pholidosauridae diversity	
Spearman's *r*	*p*
-0.19656	0.43437

Pholidosauridae diversity, Oxfordian-Cenomanian	
Spearman's *r*	*p*
-0.4211	0.22554

"Dyrosaur lineage" diversity	
Spearman's *r*	*p*
0.032521	0.89807

Dyrosauroidea diversity, Turonian-Thanetian	
Spearman's *r*	*p*
0.96978	**0.00059524**

1478

1479 **Table 1**

1480 Correlation between $\delta^{18}O$ 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-Thanetian	
Spearman's *r*	*p*
0.77846	**0.03006**

"Dyrosaur lineage" diversity	
Spearman's *r*	*p*
0.73855	**0.00046445**

"Dyrosaur lineage" diversity, Turonian-Thanetien	
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 δ18O / Sea level	
Spearman's *r*	*p*
-0.41736	0.084846

Mean δ18O / Sea level Oxfordian-Cenomanian	
Spearman's *r*	*p*
-0.70517	**0.022738**

Mean δ18O / Sea level Turonian-Thanetian	
Spearman's *r*	*p*
0.83333	**0.010714**

1493

1494   **Table 3**

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

Essaouira

Marrakech

Agadir

Ouarzazate

Rabat

Khouribga

OULAD ABDOUN BASIN

GANNTOUR BASIN

OUARZAZATE BASIN

SOUSS BASIN

MOROCCO

ALGERIA

Theriosuchus pusillus
Theriosuchus guimarotae
Sunosuchus junggarensis
Amphicotylus lucasii
Eutretauranosuchus defsi
Goniopholis baryglphaeus
Goniopholis kiplingi
Goniopholis simus
Anteophthalmosuchus hooleyi
Meridiosaurus vallisparadisi
Dakotasuchus kingi
French *Pholidosaurus*
Pholidosaurus schaumbergensis
Pholidosaurus purbeckensis
Woodbinesuchus byersmauricei
Sabinosuchus coahuilensis
Oceanosuchus boecensis
Dakotasuchus kingi
Terminonaris spp.
MHNM-kh01
Sarcosuchus hartii
Sarcosuchus imperator
Chalawan thailandicus
Vectisuchus leptognathus
Elosuchus spp.
Chenanisuchus lateroculi
Anthracosuchus balrogus
Cerrejonisuchus improcerus
Phosphatosaurus gavialoides
Sokotosuchus ianwilsoni
Bolivian sp. 1
Bolivian sp. 2
Hyposaurus derbianus
Hyposaurus natator
Arambourgisuchus khouribgaensis
Bolivian sp. 3
Dyrosaurus maghribensis
Dyrosaurus phosphaticus
Acherontisuchus guajiraensis
Atlantosuchus coupatezi
Rhabdognathus aslerensis
Congosaurus bequaerti
Rhabdognathus keiniensis

PHOLIDOSAURIDAE
TETHYSUCHIA
DYROSAURIDAE

13.202
1.471
5.007
8.011
2.883
2.883
1
9
8.976
13.007
16.312
2.471
0.471
6.509
0.471
1
1
8.976
8.976
3
3.79
2.027
3.79
5.895
10.013
2.013
1.626
2
3.279
16.382
2.932
1
0.92
0.92

A
W/L: 3

B
W/L: 2.77

C
W/L: 2.79

D
W/L: 2.77

E
W/L: 2.28

F
W/L: 2.88

G
W/L: 2.28

H
W/L: 2.43

I
W/L: 1.83

J
W/L: 1.77

K
W/L: 2.47

Figure showing phylogenetic/stratigraphic chart of Tethysuchia.

Geologic time scale (top):

LATE JURASSIC			EARLY CRETACEOUS							LATE CRETACEOUS						PALEOC.		
Oxford.	Kim.	Tithon.	Ber.	Val.	Hau.	Barr.	Aptian	Albian	Cenom.	Tur.	Co.	Sa	Campanian	Maast.	Dan.	Sel	Tha.

Marine species (legend)

Taxa labels:

Meridiosaurus vallisparadisi
Pholidosauridae (France)
Pholidosauridae (Spain)
Pholidosaurus sp. (France)
Pholidosaurus from Cherves-de-Cognac
Pholidosaurus schaumbergensis
Pholidosaurus purbeckensis
Oceanosuchus boecensis
Woodbinesuchus byersmauricei
Sabinosuchus coahuilensis
Pholidosauridae indet. (USA)
Dakotasuchus kingi
Terminonaris robusta
Terminonaris browni
Terminonaris (Germany)
MHNM-kh01
Chalawan thailandicus
Sarcosuchus imperator
Sarcosuchus hartti
Dyrosauridae indet. (India)
Dyrosauridae indet. (Pakistan)
Dyrosauroidea indet. (Egypt)
"Chenanisuchus" from Mali
Dyrosauridae indet. ("*Rhabdognathus keiniensis*")
Vectisuchus leptognathus
Elosuchus broinae
Elosuchus cherifiensis
Chenanisuchus lateroculi
Dyrosauridae indet. (Colombia, Bolivia)
Anthracosuchus balrogus
Cerrejonisuchus improcerus
Phosphatosaurus sp. (Egypt)
cf. *Phosphatosaurus* sp. (Pakistan)
Phosphatosaurus sp. (Saudi Arabia, Morocco, Mali)
Phosphatosaurus gavialoides
Sokotosuchus ianwilsoni
Bolivian species 1
Bolivian species 2
Dyrosauridae indet. (North America)
Dyrosauridae indet. (USA)
Hyposaurus natator
Hyposaurus derbianus
Hyposaurus sp. 1 (Mali, Niger)
Hyposaurus sp. 2 (Mali, Niger)
Hyposaurus paucidens
Hyposaurus sp. (Morocco)
Bolivian species 3
Arambourgisuchus khouribgaensis
Dyrosaurus phosphaticus
Dyrosaurus maghribensis
Archerontisuchus guajiraensis
Atlantosuchus coupatezi
Congosaurus bequaerti
Rhabdognathus keiniensis
Rhabdognathus aslerensis
Congosaurus compressus (Niger, Nigeria, Mali, Saudi Arabia)
Rhabdognathus sp.(Saudi Arabia)
Tethysuchia indet. (UK)
Dyrosauridae indet. (Portugal)

Group labels: TETHYSUCHIA, PHOLIDOSAURIDAE, "DYROSAUR LINEAGE", DYROSAURIDAE

A phylogenetic and stratigraphic chart of Crocodylomorpha spanning from the Triassic through the Cenozoic. Taxa and clades shown include "Sphenosuchia" (*Dibothrosuchus elaphros*, *Junggarsuchus sloani*), Thalattosuchia (Teleosauroidea, Metriorhynchoidea), Protosuchia, Notosuchia (Peirosauridae, *Araripesuchus patagonicus*, *Notosuchus terrestris*, *Mariliasuchus amarali*, *Sphagesaurus huenei*, Baurusuchidae, Sebecidae), *Theriosuchus*, Goniopholididae, Eusuchia, Hylaeochampsidae, Crocodylia (Gavialoidea, *Borealosuchus*, Planocraniidae, Crocodyloidea, Alligatoroidea), Tethysuchia ("Dyrosaur lineage", Pholidosauridae).

Time scale: MESOZOIC (TRIASSIC — Middle: Anisian, Ladinian; Upper: Carnian, Norian, Rhaetian; JURASSIC — Lower: Hettangian, Sinemurian, Pliensbachian, Toarcian; Middle: Aalenian, Bajocian, Bathonian, Callovian; Upper: Oxfordian, Kimmeridgian, Tithonian; CRETACEOUS — Lower: Berriasian, Valanginian, Hauterivian, Barremian, Aptian, Albian; Upper: Cenomanian, Turonian, Coniacian, Santonian, Campanian, Maastrichtian); CENOZOIC (PALEOGENE — Paleoc, Eocene, Oligoc; NEOGENE — Miocene, Pliocene; Q — Holoc, Pleistoc).