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Hassan Aouraghe, Rachid Chennouf, Hamid Haddoumi, Maxime Lasseron, Hicham Mhamdi, et al.. A new Gondwanan perspective on the Jurassic-Cretaceous transition from the Tithonian-Berriasian interval of southeastern Morocco. *Cretaceous Research*, 2024, 162, pp.105932. <10.1016/j.cretres.2024.105932>. <mnhn-04712422>

HAL Id: mnhn-04712422

<https://mnhn.hal.science/mnhn-04712422v1>

Submitted on 27 Sep 2024

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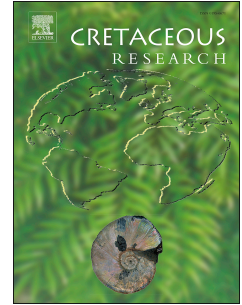


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PII: S0195-6671(24)00105-8

DOI: <https://doi.org/10.1016/j.cretres.2024.105932>

Reference: YCRES 105932

To appear in: *Cretaceous Research*

Received Date: 8 December 2023

Revised Date: 18 May 2024

Accepted Date: 19 May 2024

Please cite this article as: Aouraghe, H., Chennouf, R., Haddoumi, H., Lasseron, M., Mhamdi, H., Gheerbrant, E., Martin, J.E., A new Gondwanan perspective on the Jurassic-Cretaceous transition from the Tithonian-Berriasian interval of southeastern Morocco, *Cretaceous Research*, <https://doi.org/10.1016/j.cretres.2024.105932>.

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1 **A new Gondwanan perspective on the Jurassic-Cretaceous transition from the**
2 **Tithonian-Berriasian interval of southeastern Morocco**

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10 **Abstract.** Knowledge of continental faunas and floras from the Jurassic–Cretaceous
11 transition in Gondwana, and especially in Africa, is limited. Here, we report the
12 discovery of a rare assemblage of plants and aquatic reptiles from the Tithonian–
13 Berriasian interval of the Anoual syncline in southeastern Morocco. Our preliminary
14 field investigations led to the discovery of a disarticulated skeleton of a goniopholidid
15 crocodylomorph, of a single fragment of a turtle plate, and of abundant plant
16 remains, inviting further exploitation of the fossiliferous horizon. This assemblage
17 indicates a freshwater habitat bordered by a lush moist conifer forest. Its taxonomic
18 composition shows a strong similarity with better known contemporaneous Laurasian
19 assemblages and stresses the paucity of coeval Gondwanan assemblages. Our
20 discovery highlights that peri-Tethys continental assemblages may have shared
21 common taxa and raises the question whether Laurasian and Gondwanan taxa from
22 the Jurassic-Cretaceous transition were cosmopolitan, before they diverged later
23 during the Cretaceous.

24 Keywords: Continental assemblage, Gondwana, Tithonian–Berriasian, Morocco

25 **1. Introduction**

26 Morocco is an important source of fossiliferous continental deposits of the Jurassic
27 and Cretaceous. More specifically, the Jurassic Red Beds (Haddoumi et al., 1998,
28 2010) and the so-called “continental intercalaire” with the Cretaceous Kem Kem
29 beds (Lavocat, 1948; Lapparent, 1951; 1960) significantly contributed to our
30 knowledge of dinosaur assemblages (see reviews in Cavin et al., 2010; Ibrahim et
31 al., 2020). However, faunal and floral assemblages of the Jurassic–Cretaceous
32 transition remain poorly known, making it difficult to assess their evolution over this
33 period. On the other hand, the much more abundant Mesozoic Laurasian continental
34 assemblages (Tennant et al., 2017; Allain et al., 2022) provide fossil data that make
35 it possible to discuss the hypothesis of a major extinction event on continents at the
36 Jurassic/Cretaceous boundary, albeit with the problem of a still poorly defined
37 stratigraphic boundary between the Tithonian and Berriasian (Granier, 2020). Until
38 now, the contribution of Gondwanan assemblages to the extinction event debate
39 around the indiscriminate Tithonian/Berriasian boundary was virtually absent. Here,
40 our preliminary report aims to fill this gap and to encourage further field efforts to
41 elucidate this question.

42 Regionally, previous studies have focused on fossiliferous localities from the
43 Jurassic-Cretaceous transition of the Anoual Syncline (eastern High Atlas, Morocco),
44 with the Bathonian site of Guelb el Ahmar (Haddoumi et al., 2016; Lasseron et al.,
45 2020) and the indiscriminate Tithonian-Berriasian site of Ksar Metlili, which have
46 produced rich microvertebrate faunas (Monbaron, 1980; Haddoumi et al., 2016;
47 Lasseron 2019; Lasseron et al., 2020, 2022). Here, we report in the Anoual Syncline

48 the fossil discoveries from a new locality from the Jurassic-Cretaceous, which
49 provides new important data, in particular: 1) macro-remains of a single
50 crocodylomorph individual, highlighting the presence of large tetrapods; 2) an
51 abundant and exceptional Jurassic-Cretaceous floral assemblage that allows
52 comparisons with other coeval localities worldwide. This preliminary report aims to
53 present the geological context of this new and additional Anoual Syncline site and to
54 discuss on its significance and perspectives as compared to other localities from
55 Gondwana.

56 **2. Geological settings**

57 The new fossiliferous locality, herein named Guelb Rzoug (GR), crops out on the
58 northern margin of the eastern High Atlas in the region of Anoual (Figure 1A, B) at
59 about thirty kilometers to the northeast of the town of Talsint. In this region, Jurassic
60 and Cretaceous deposits make up most of the sedimentary successions of two
61 synclines, namely the Anoual and Ksar Jilali synclines. In the Anoual syncline
62 (Figure 1B), the Red Beds, which are mostly of continental origin, have produced
63 fossil remains in the new locality GR (Figures 1B–C; Figure 2A), which adds to the
64 Guelb el Ahmar (GEA) and Ksar Metlili (KM) sites. These Red Beds are intercalated
65 between the Middle Jurassic marine deposits known as « Formation des Marno-
66 calcaires à Pholadomyes » and the Cretaceous marine deposits of the Cenomanian-
67 Turonian limestones (Figure 1C). In the Anoual syncline, Haddoumi et al. (2008)
68 differentiated three lithostratigraphic units in the Red Beds (Figure 1B), which are
69 from base to top: the Anoual Formation (lower Bathonian), the Ksar Metlili Formation
70 (indiscriminate Tithonian- Berriasian), and the Dekkar Group (?Barremian to
71 Cenomanian). The Ksar Metlili Formation (~80 m thick) is delimited by two

72 unconformities D1 and D2 (Figure 1B). The lithology and sedimentary structures of
73 the Ksar Metlili Formation and of the lower member of the Anoual Formation (Fig.
74 2B-C) suggest a flooding plain and/or deltaic depositional environment. This is
75 consistent with the large fossil tree trunks that are common in these units.
76 The GR fossil assemblage (Fig. 1B-C), as is the case of KM assemblages
77 (Haddoumi et al., 2016; Lasseron et al., 2020), is stratigraphically located within the
78 lower part of the Ksar Metlili Formation, above the D2 unconformity (Fig. 1B-C) and a
79 marine incursion (Marine or upper Member, Haddoumi et al., 1998, 2008) of the
80 Anoual Formation. The GEA locality and fossil assemblage are located below this
81 marine member (Figure 1B, C; Haddoumi et al., 2016; Lasseron et al., 2020). The
82 GR assemblage is probably of the same age as the KM microvertebrate fauna
83 (Sigogneau-Russell et al., 1988, 1990; formerly known as “the Anoual fauna” in
84 Sigogneau-Russell et al., 1998), which has yielded the most diversified African and
85 Gondwanan Mesozoic mammal assemblage and one of the richest vertebrate
86 faunas of the Gondwanan Mesozoic (Lasseron, 2019; Lasseron et al., 2020; 2022).
87 The Ksar Metlili Formation is dated as Berriasian on the basis of calcareous
88 nanofossils (coccolithophores) (Sigogneau-Russell et al., 1990), or late Tithonian-
89 early Berriasian based on charophytes (Haddoumi et al., 2008; Mojon et al., 2009)
90 and its microvertebrate association that is the most reminiscent of those known in
91 the Purbeckian facies (Lasseron et al. 2020, 2022). As a summary, the new GR
92 locality is identified as part of the Ksar Metlili Formation on the basis of its position
93 above the D1 and below the D2 unconformities (Figure 1B–C) and a Berriasian or
94 Tithonian age for the GR locality is proposed on the basis of biostratigraphic
95 evidence from other co-eval localities of the Anoual Basin. It is expected that in the
96 near future, the GR assemblage will provide more significant new fossil data to test

97 the Tithonian or Berriasian age of the Ksar Metlili Formation and represent a key
98 new continental locality in the Gondwana (Fig. 1D).

99 **3. Material and methods**

100 Bone fragments and plant remains were discovered at GR by one of us (HA) during
101 a geological survey in July 2020. Among the first bone fragments to be collected,
102 some were later identified in May 2022 by JEM and ML as belonging to a
103 crocodylomorph. In May 2023, a field team including HA, HH, RC and JEM
104 undertook a geological investigation and a preliminary excavation at GR in order to
105 retrieve more fossil material in situ and to position the fossiliferous level in a precise
106 stratigraphic context. The 2020 excavating trench in the fossiliferous level was
107 refreshed and expanded. The excavation surface was about two square meters.
108 Cranial and postcranial elements of a single disarticulated crocodylomorph individual
109 were uncovered. Bones are extremely fragile and needed to be consolidated
110 immediately using cyanoacrylate. All these remains were carefully excavated and
111 entrapped in three plaster jackets that will undergo mechanical laboratory
112 preparation. Plant remains were discovered at different levels in the excavation
113 trench and several samples were taken just above and just below the fossiliferous
114 horizon yielding the crocodylomorph remains. All fossiliferous horizons seen in the
115 trench section were sampled for laboratory processing for microremains extraction.
116 All the paleontological material recovered from GR is curated at Université
117 Mohammed I^{er} Oujda, Morocco (Musée de l'Université d'Oujda) under the acronym
118 Mo-GR.23. In order to help prevent pillaging, GPS locality information is stored with
119 the curated material and is available on demand to qualified researchers pending
120 they provide a valid field permit from the Ministère des Mines of Morocco.

121 **4. Preliminary description and comparisons**

122 4.1. *Crocodylomorph skeleton*

123 Disarticulated postcranial elements are associated with a damaged skull and
124 mandibles, suggesting that all elements belong to a single individual (Figs. 2B, C, E).
125 Although heavily damaged, the posterior portion of the skull preserves a connection
126 with elements of the left mandibular branch, showing a contact between the quadrate
127 and the articular. In this area, the quadratojugal dorsal surface bears an
128 ornamentation of deep ovoid cupules, as is often the case in semi-aquatic tetrapods.
129 An estimation of the skull length is only tentative because further study must await
130 preparation of the plaster jackets, but according to our field observation, the skull
131 length exceeds 30 cm in total length. Several vertebral centra were recovered and
132 the absence of apophyses indicates that they come from the trunk series. All centra
133 are amphicoelous indicating they belong to a non-eusuchian neosuchian. Several
134 osteoderms have been collected; they are rectangular in outline, being wider than
135 long and showing a process or spine on their anterolateral corner (Fig 2C). These
136 features combined, indicate a goniopholidid or a pholidosaurid affinity for the GR
137 crocodylomorph. The ornamentation pattern on the external surface of the
138 osteoderms highly resembles those of goniopholidids but are unlike the
139 ornamentation made of smaller pits typical of pholidosaurids (Martin et al., 2016c).
140 For the reasons above, we provisionally assign the GR crocodylomorph to a
141 goniopholidid, i.e., a group of neosuchian crocodylomorphs with semi-aquatic
142 adaptations and known from the Jurassic to the Early Cretaceous (e.g., Buffetaut,
143 1982; Salisbury et al., 1999; Andrade et al., 2011; Martin et al., 2016b).

144 4.2. *Indeterminate turtle bone fragment*

145 A single bone fragment (Fig. 2D) was discovered in the trench and was likely broken
146 off during the initial excavation. It is plate-like and slightly concave with smooth
147 dorsal and ventral surfaces. The preserved piece is too small to preserve sutures. Its
148 broken edges reveal a compact diploe-structure typical of turtle shell bones with the
149 cancellous zone sandwiched between a thick external cortex and a thinner internal
150 cortex (e.g., Scheyer and Sander, 2007).

151 4.3. *Plant remains*

152 The plant association from the GR locality (Fig. 2 F-K) is represented by macrofossil
153 remains composed of parts of fern fronds and small branches of conifers associated
154 with indeterminate petrified wood. Despite the poor preservation of most of the floral
155 assemblage, some morphological details can be observed in some black mineralized
156 cuticles or imprints. The fern remains belong to Matoniaceae (Fig. 2 F-G) and
157 Schizaeaceae (Fig. 2H-I). The Matoniaceae remains display an affinity with
158 *Phlebopteris* or to the similar genus *Piazopteris* (Hu and Winship, 2014). Sterile (Fig.
159 2F) and fertile pinnae (Fig. 2G) are observed. Sori of fertile pinnae are positioned in
160 single rows on either side of the pinnule midrib and contain approximately 14
161 sporangia. Pinnules are broadly attached, opposite to sub-opposite, elongated, with
162 rounded apices and an entire margin. Schizaeaceae (Fig. 2H-I) are represented by
163 digitate fronds consisting of repeatedly dichotomizing narrow lanceolate segments.
164 Each segment is branching in its terminal part into narrow strips. These fern remains
165 are usually associated with small branches of undetermined conifers. Figure 2 (J-K)
166 shows two samples of compressed leafy terminal branches.

167 5. Discussion

168 5.1. *Lithology, sedimentology and paleoenvironnement*

169 During the deposition of the Ksar Metlili Formation (Tithonian-Berriasian), the Anoual
170 region was a distal alluvial plain located between the African craton to the South and
171 the Tethys Ocean to the North, in which a diverse continental vertebrate assemblage
172 was present (Haddoumi et al., 2016; Lasseron et al., 2020, 2022).

173 The fossiliferous level of the GR locality occurs within greenish or brownish to
174 purple argillites bearing yellow ochres stains within a network of tectonic fractures.
175 These argillites form inframillimeter to millimeter-sized layers with intercalated thin
176 layers of lignites that sometimes form decimetric lenses rich in fossil wood or other
177 oxidized plant debris.

178 The argillites result from the deposit of a very fine, soft mud at the bottom of a
179 water body in-between river channels of the flood plain. Occasionally, the
180 depositional environment was weakly agitated with limited hydrodynamism. This is
181 illustrated by the limited disarticulation and fragmentation of the crocodile skeleton
182 and the mixing and concentration of plant remains in the same level. These
183 sedimentological data indicate that the fossiliferous remains are sub-autochthonous in
184 this horizon. This is in agreement with the association of sterile and fertile parts of
185 the fern fronds and of the conifer branches that corroborate this interpretation. The
186 muddy sediment was probably poorly oxygenated or even anoxic as evidenced by
187 the preservation of finely detailed carbonized plant imprints. The conifer fossil
188 remains and the abundance of centimeter-sized to pluri-decimeter-sized fossil wood
189 suggest the proximity of a conifer forest that thrived near local water bodies and river
190 channels of the flood plain. Fossil wood of metric size, plant remains and scattered
191 vertebrate fragments have been identified in channelized sandstones that laterally
192 limit or cover the fossiliferous argillites of the GR locality.

193 This forest was home to an understory with ferns that probably thrived under a
194 hot and humid climate. The majority of the Jurassic-Cretaceous ferns are considered
195 to be elements of moist lush vegetation (Harris, 1961) often occurring near river
196 banks (Pelzer et al., 1992). Only a few taxa (e.g., *Gleichenia* [Gleicheniaceae],
197 *Phlebopteris*, and *Weichselia* [Matoniaceae]) can tolerate full sunlight and are able to
198 adapt to the water-stress related conditions (Konijnenburg-Cittert, 2002; Abbink et
199 al., 2004; Schrank, 2010). During the Tithonian-Berriasian period, the Anoual region
200 belonged to an arid climatic zone (Chumakov, 1995; Hay and Floegel, 2012). These
201 climatic inferences seem to differ from the hot and humid conditions suggested by
202 the newly reported plant at GR but are partly similar, depending on the resolution,
203 when compared to recent models of Köppen zones indicating a temperate, humid
204 subtropical zone but close to the hot steppe during the Berriasian-Valanginian
205 interval (Burgener et al., 2023). The ferns of GR probably tolerated sunlight and are
206 able to adapt to the water-stress related conditions (Konijnenburg-Cittert, 2002;
207 Abbink et al., 2004; Schrank, 2010).

208 5.2. Paleobiogeographic context of the flora and fauna

209 The new fern-conifer assemblage from GR locality is the first reported in Morocco.
210 Only petrified wood (Haddoumi, 1998; Haddoumi et al., 2008) and palynomorphs
211 and wood fragments (microflora of GEA, Haddoumi et al., 2016) have previously
212 been reported in the eastern High Atlas. An assemblage of ferns and microphyllous
213 conifers such as *Sphenopteris* cf. *fittoni* and *Onychiopsis* have been reported from
214 the sub-unit 1b of the ?Callovian-Barremian in the Dadès Valley (Benvenuti et al.,
215 2017). At the regional scale of North Africa, some fern-conifer assemblages were
216 reported in Jurassic and Cretaceous strata (Barale, 2007; Barale et al., 2007; Ouaja

217 et al., 2002) but floral macroremains from the Jurassic-Cretaceous transition are
218 virtually unknown, the floral elements of that age range at the Tendaguru site in
219 Tanzania being known from palynomorphs, cuticles, or seeds (Aberhan et al., 2002).

220 The latest Jurassic–earliest Cretaceous fossil record of freshwater
221 crocodylomorphs in Africa is indeed very poor, being restricted to rare atoposaurid
222 and teleosaurid remains found in the nearby KM site (see references below). In this
223 regard, and independently from its taxonomic attribution, the new find from the GR
224 locality is highly important to understand neosuchian evolution in Gondwana. Despite
225 its unprepared condition, the new crocodile specimen can be preliminary assigned to
226 the Goniopholididae on the basis of shared features such as amphicoelous
227 vertebrae, deep-sculptured external ornamentation, and osteoderm morphology.
228 This will have to be confirmed with further preparation of the collected material
229 presently encased in plaster jackets. Freshwater crocodylomorphs from the Jurassic
230 of Africa are virtually unknown despite the presence of continental formations
231 yielding dinosaurs in the Lower Jurassic Red Beds of Morocco (e.g., Allain and
232 Aquesbi, 2008). Limited evidence for the presence of crocodylomorphs comes from
233 the Jurassic-Cretaceous transition of the KM microvertebrate sites near Anoual that
234 have produced isolated atoposaurid and freshwater teleosaurid teeth as well as
235 fused premaxillae of cf. *Theriosuchus* (Lasseron et al., 2020). At a wider continental
236 scale, the only other mention of Late Jurassic to Early Cretaceous freshwater
237 neosuchians is from the Saurian beds of Tendaguru in Tanzania (Heinrich et al.,
238 2001). Fossil discoveries in African lowermost Cretaceous strata (Berriasian) are
239 equally limited and the earliest record known from Lower Cretaceous strata comes
240 from much younger, Barremian–Aptian deposits, with the derived neosuchian
241 *Brillanceausuchus babouriensis* from Cameroon (Michard et al., 1990). The Upper

242 Cretaceous continental record of Africa is restricted to that from Egypt (Saber et al.
243 2019). Older African deposits have yielded a much higher diversity of freshwater
244 crocodylomorphs from the Aptian–Cenomanian interval in Morocco, Algeria, Libya,
245 Niger, and Tanzania (e.g., Broin and Taquet, 1961; Larsson and Gado, 2000;
246 Sereno and Larson, 2009; Martin and Lapparent de Broin, 2016; Nicholl et al., 2022;
247 Pochat-Cottilloux et al., 2023).

248 During the Jurassic–Cretaceous transition, the apex predatory niche in
249 freshwater ecosystems was occupied by generalist forms of neosuchian
250 crocodylomorphs. While goniopholidids dominate the Laurasian landscape in Europe
251 (Andrade et al., 2011; Martin et al., 2016b), North America (Yoshida et al., 2021) and
252 Asia (Wu et al., 1996; Lauprasert et al., 2007), the crocodylomorph diversity in
253 Gondwana from coeval formations remains notoriously poor. Notably, the
254 Gondwanan fossil record from the Jurassic–Cretaceous transition consists solely of
255 South American forms such as *Batrachomimus pastosbonensis* from the Upper
256 Jurassic of Brazil (Montefeltro et al., 2013) and *Burkesuchus mallingrandensis* from
257 the Tithonian of Chile (Novas et al., 2021). Thus, the evolutionary history of
258 continental crocodylomorphs at this time in Africa remains largely unknown.

259 This paucity in the fossil record of African vertebrates (Rage and Gheerbrant,
260 2020) may be attributed to a sampling bias but also to the scarce availability of
261 freshwater deposits for that time interval. Fossil discoveries from the Jurassic–
262 Cretaceous transition of Africa, such as those from the GR sites, may considerably
263 renew our understanding of the biogeographic affinities of latest Jurassic–earliest
264 Cretaceous faunas (e.g., Lasseron et al., 2020). They make it possible to extend the
265 analysis of the Jurassic-Cretaceous faunal transition to a global level, well beyond
266 Laurasia to which current discussions are restricted, being based on Purbeckian-

267 type deposits from Western European assemblages (Tennant et al., 2017; Allain et
268 al., 2022). Continental Africa has yielded several neosuchians of younger age
269 (Aptian-Albian), such as *Kaprosuchus saharicus* or *Stolokrosuchus lapparenti*
270 (Larsson and Gado, 2000; Sereno and Larsson, 2009), although of poorly resolved
271 phylogenetic affinities. The phylogenetic relationships of the new Moroccan
272 crocodylomorph reported here, either with these African Aptian-Albian taxa or as a
273 distant lineage of Laurasian goniopholidids, will be clarified after the new found GR
274 fossils have been prepared and compared in detail.

275

276 5.3. Implications for the Jurassic/Cretaceous boundary

277 The Jurassic/Cretaceous boundary awaits a clear definition (see review in Granier,
278 2020). There are currently two opposing views: the Jurassic/Cretaceous boundary
279 corresponds either to the Tithonian/Berriasian boundary (Wimbledon et al., 2020a,
280 2020b) or to the Berriasian/Valanginian boundary (Granier, 2019; Enay, 2020;
281 Granier et al., 2020). The GSSP definition on this boundary has yet to be discussed
282 (Granier, 2020).

283 Recent study on the composition of vertebrate assemblages from Western
284 Europe did not conclude in support of a biological turnover at the
285 Tithonian/Berriasian boundary (Allain et al., 2022). In fact, the Berriasian continental
286 vertebrate faunas of Angeac-Charente and Cherves-de-Cognac show strong affinities
287 with Late Jurassic vertebrate assemblages but differ in composition from post-
288 Berriasian vertebrate assemblages (Allain et al., 2022; Mazin et al., 2008). Thus, at
289 least in Western Europe, the continental vertebrate fossil record from the
290 Jurassic/Cretaceous transition is in favour of the hypothesis placing the
291 Jurassic/Cretaceous boundary at the Berriasian/Valanginian boundary (Allain et al.,

292 2022; contra Tennant et al., 2017). This would mean a latest Jurassic age for the
293 Ksar Metlili Formation faunas such as KM and GR. This would be in agreement with
294 a Jurassic rather than a Cretaceous affinity of the KM microvertebrate fauna
295 (Lasseron et al., 2020).

296 The future paleontological exploitation of the new GR locality from Anoual
297 holds interesting perspectives to further test this question, with a new viewpoint from
298 Gondwanan continental assemblages. The present preliminary study is too
299 premature to draw definitive conclusions as one will need to assess the composition
300 of the whole faunal assemblage. In particular, the presence of goniopholidid
301 crocodylomorphs at the GR site cannot help to place it in relation to Jurassic or
302 Cretaceous boundary, as the group has been recovered throughout the wide
303 Kimmeridgian-Albian interval (see Table 1 in Martin et al., 2016).

304

305 **6. Conclusions and perspectives**

306 The Jurassic-Cretaceous transition has been interpreted as corresponding to a
307 dramatic faunal change, either as a possible extinction event (i.e., one of the eight
308 mass extinctions), or as a more gradual environmental change in a cooling world
309 (see review in Tennant et al., 2017). Yet, the core of the available fossil data for this
310 discussion comes from Laurasia. Understanding the evolution of continental biotas
311 and their paleoenvironment at a global scale during the Jurassic-Cretaceous
312 transition requires fossil data from the Gondwanan continents. Here, the discovery in
313 the northern part of Africa of the GR locality, which seems to correspond to this
314 indiscriminate Tithonian-Berriasian interval, opens for the first time tangible
315 perspectives for answering these questions on a wide paleogeographical scale.

316 Acknowledgements

317 We thank the Ministère de la Transition Énergétique et du Développement Durable
318 (MEMDD) in Rabat, Morocco for providing us the authorization to conduct fieldwork
319 in the Anoual area « Ministère de la Transition Énergétique et du Développement
320 Durable, Direction de la Géologie N°1201/DG). Several persons helped us including
321 Abderrahman Aniba. We thank Faculté des Sciences de l'Université Mohammed 1er
322 for providing the field vehicle. The 2023 field campaign was supported by the
323 Agence Nationale de la Recherche (SEBEK project no. ANR-19-CE31- 0006-01 to
324 JEM). JEM thanks R. Allain, L. Boudchiche, N.E. Jalil, M. Pujol, and R. Vullo for
325 various advices and discussions on Moroccan geosciences. We thank B. Granier
326 and one anonymous reviewer for their comments that helped improve the initial
327 version of this work.

328 Declaration of competing interests

329 The authors declare no competing interests.

330 Author contributions

331 Conceptualization: HA, HH; Funding acquisition: JEM, HA; Investigation: HA, RC,
332 HH, ML, EG, JEM; Methodology: HA, RC, HH, HM, JEM; Project administration: HA,
333 JEM; Resources: HA, JEM; Roles/Writing - original draft: JEM, RC, HH; and Writing -
334 review & editing: HA, RC, HH, ML, HM, EG, JEM.

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554 **Figure Captions**

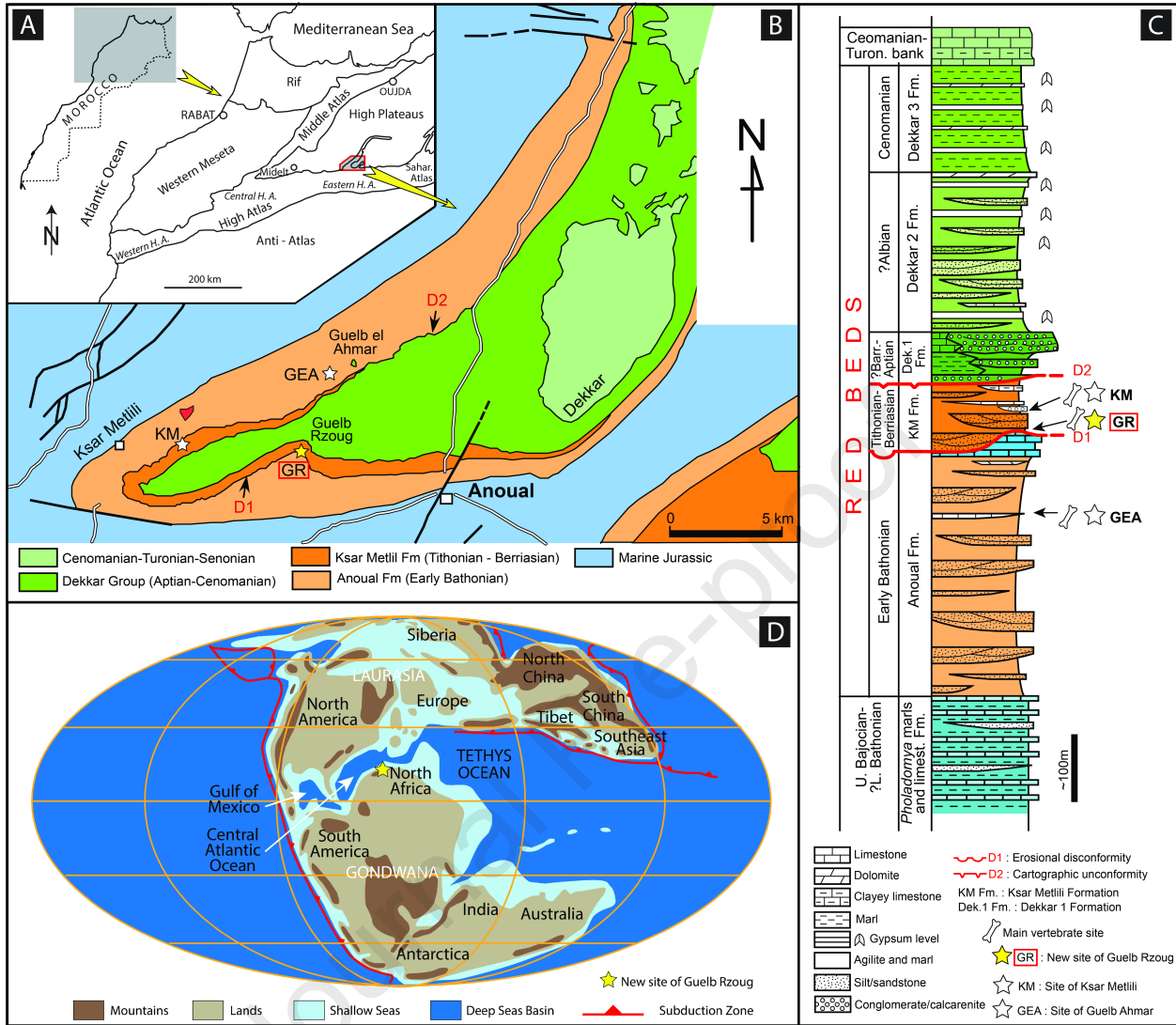
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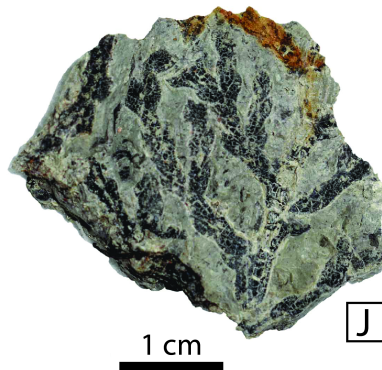
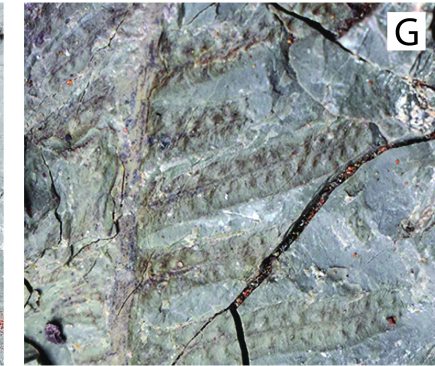
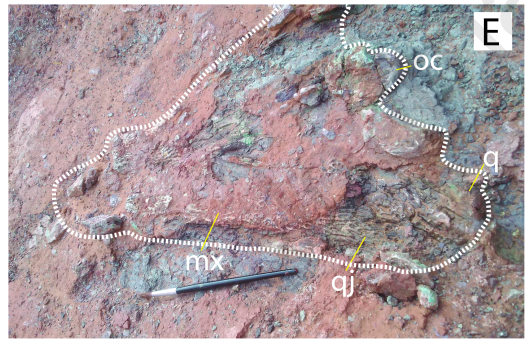
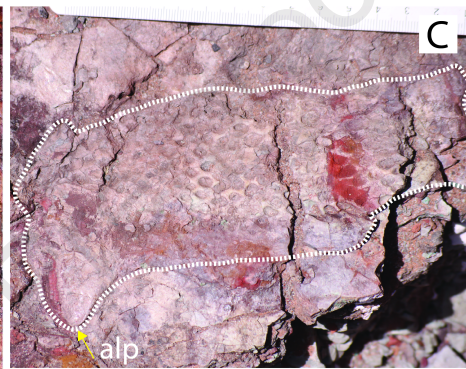
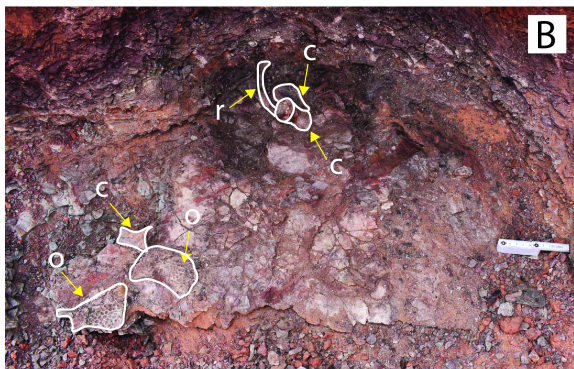
556 **Figure 1.** General context of the new Guelb Rzoug (GR) locality from the
557 indeterminate Tithonian-Berriasian interval. A, Geographic situation in northeastern
558 Morocco showing its localization in the eastern High Atlas; B, regional geological
559 map of the Anoual syncline showing the GR locality together with previously
560 identified fossiliferous localities of Ksar Metlili (KM) and Guelb el Ahmar (GEA). D1
561 and D2 refer to the Bathonian–Tithonian discontinuity and the
562 Berriasian–?Barremian discontinuity, respectively; C, stratigraphic log of the
563 Jurassic-Cretaceous Red Bed series showing the horizon corresponding to the GR
564 locality; D, Global paleogeographic map showing the position of the new GR locality
565 as part of northern Gondwana. Map after Scotese (2001). [The print version will be in
566 black and white].

567

568 **Figure 2.** Presentation of the new indiscriminate Tithonian-Berriasian locality of
569 Guelb Rzoug (GR) and selected photographs of discovered fossils. A, general view
570 in the field showing the locality at the base of the Ksar Metlili Fm; B, detail of the
571 excavation surface showing scattered postcranial elements of the crocodylomorph in
572 situ; C, detail of one osteoderm in dorsal view (Mo-GR.23-001); D, a sectioned turtle
573 bone fragment (Mo-GR.23-002); E, a goniopholidid skull (Mo-GR.23-001) in dorsal
574 view during the excavation - the brush is 15 cm in length; F, sterile pinna of
575 Matoniaceae (Mo-GR.23-003); G, fertile pinna of Matoniaceae (Mo-GR.23-004); H,
576 frond of Schizaeaceae (Mo-GR.23-005); I, frond of Schizaeaceae (Mo-GR.23-006);
577 J, ultimate branch of indeterminate conifer (Mo-GR.23-007); K, ultimate branch of
578 indeterminate conifer (Mo-GR.23-008). Scale bar for F–K equals 1 cm.

579 Abbreviations: alp, anterolateral process; c, centrum; mx, maxilla; o, osteoderm; oc,
580 occipital condyle; q, quadrate; qj, quadratojugal; r, rib [The print version will be in
581 black and white].





Highlights

-We report on a new fossiliferous locality from the Tithonian-Berriasian interval of Morocco

-This continental assemblage preserves semi-aquatic reptiles and macro-floras

-this discovery represents a rare addition to the late Jurassic-early Cretaceous continental assemblages of Gondwana

-perspectives on the evolution of continental ecosystems during the Jurassic-Cretaceous transition are presented

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Journal Pre-proof