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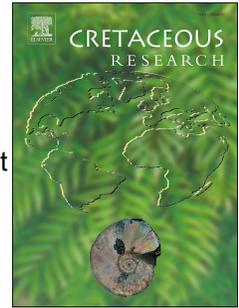
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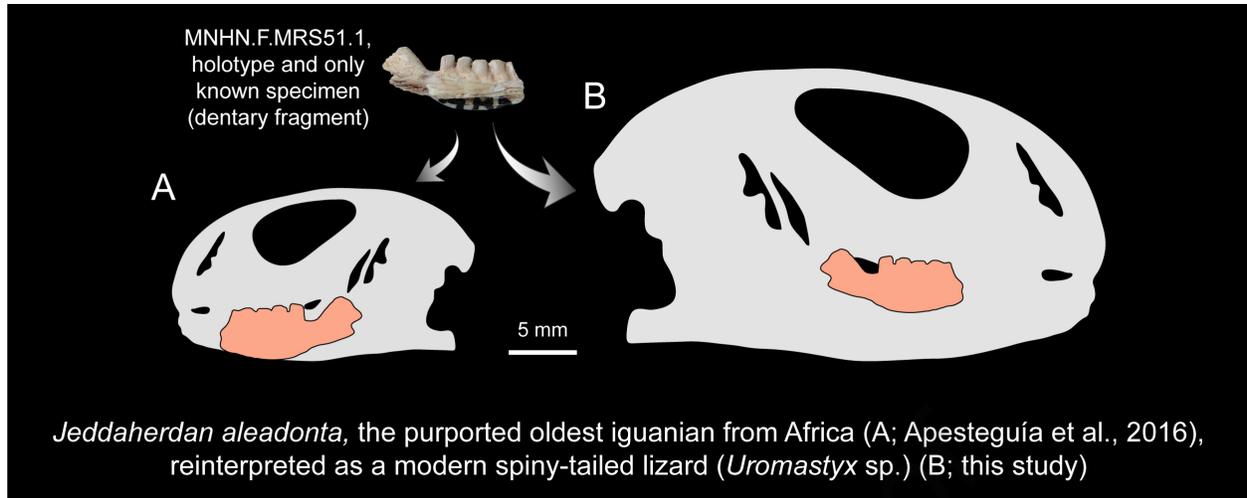
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### **Credit Author Statement**

**Authors' contribution.** R.V. conceived the study. R.V. and S.B. determined and assessed morphological traits. Y.D. performed spectroscopic analyses. R.V. drafted the manuscript. All authors discussed the results, edited the manuscript, approved the final version and agree to be held accountable for the content.

Journal Pre-proof



1 **A reappraisal of *Jeddaherdan aleadonta* (Squamata: Acrodonta), the purported oldest**  
2 **iguanian lizard from Africa**

3

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22

**23 ABSTRACT**

24 *Jeddaherdan aleadonta* Apesteguía et al., 2016 is currently known as the first and single  
25 Mesozoic iguanian lizard from Africa. The original description and age of the holotype and  
26 only known specimen (i.e. a dentary fragment bearing five teeth) are revised here. We show  
27 that this fragmentary specimen was misinterpreted anatomically, does not come from  
28 Cretaceous beds but is instead Quaternary in age, and must be assigned to an indeterminate  
29 species of *Uromastyx* (spiny-tailed lizards). Therefore, the genus *Jeddaherdan* is considered a  
30 junior synonym of *Uromastyx*, and the species *J. aleadonta* (= *Uromastyx* sp.) is considered a  
31 nomen dubium. Our results refute the presence of iguanian lizards in the Mesozoic of Africa  
32 and have major implications for reconstructing the evolution and palaeobiogeography of this  
33 group.

**34**  
**35 Keywords:**

36 Lepidosauria; *Uromastyx*; Morocco; Cretaceous; Quaternary; Raman spectroscopy  
37

**38 1. Introduction**

39  
40 Apesteguía et al. (2016) described *Jeddaherdan aleadonta* as a mid-Cretaceous  
41 acrodontan representing the oldest iguanian lizard from Africa and a biogeographic link  
42 between Cretaceous forms from Asia and South America. This species, based on a single  
43 fragmentary dentary bone (MNHN.F.MRS51.1) from southeastern Morocco, was recovered in  
44 Apesteguía et al.'s (2016) phylogenetic analysis as an uromastycine agamid sister to  
45 *Gueragama sulamericana* from the Cretaceous of Brazil. Based on a detailed redescription

46 and Raman spectroscopic analyses, our study challenges this interpretation and aims to test  
47 the hypothesis that MNHN.F.MRS51.1 is a recent (or subfossil) specimen belonging to the  
48 genus *Uromastyx*, a group of uromastycine lizards currently widespread throughout the  
49 Saharo-Arabian region (Wilms et al., 2009; Tamar et al., 2018).

50

## 51 **2. Material and methods**

52

53 MNHN.F.MRS51.1 was surface collected by René Lavocat at Gara Tabroumit  
54 (southeastern Morocco) together with vertebrate fossils derived from the Cretaceous Kem  
55 Kem beds (Lavocat, 1954a, b; Apesteguía et al., 2016). The material used for anatomical  
56 comparison consists of a series of isolated dentaries (including SHC YAM K17-SD4 S 414.1)  
57 of the Arabian spiny-tailed lizard (*Uromastyx aegyptia*) coming from the archaeological site  
58 of Al-Yamâma in Saudi Arabia (Monchot et al., 2014). In addition, a lower jaw of a recent  
59 *Uromastyx acanthinura sensu lato* (MNHN-ZA-AC-1928-242) was also examined (Table 1).

60 MNHN.F.MRS51.1 is a holotype and thus cannot be used for destructive analyses,  
61 such as DNA analysis and radiometric dating. We used Raman spectroscopy (a non-  
62 destructive and non-invasive technique that requires no sampling or alteration of the  
63 specimen) to investigate and evaluate the taphonomic and diagenetic signature of six  
64 specimens from Gara Tabroumit (i.e. MNHN.F.MRS51.2, a fish vertebra; MNHN.F.MRS51.3  
65 to MNHN.F.MRS51.6, four archosaur teeth; MNHN.F.MRS51.1, the holotype of  
66 *Jeddaherdan aleadonta*). For comparison, two modern lizard specimens (i.e. the above-  
67 mentioned specimen SHC YAM K17-SD4 S 414.1, and the humerus of the above-mentioned  
68 specimen MNHN-ZA-AC-1928-242) were also analyzed by Raman spectroscopy (for details  
69 see electronic supplementary material) (Table 1).

70 Non-biogenic geological samples, i.e. hydroxylapatite and fluorapatite, were selected  
71 as references for Raman analyses. Hydroxylapatite comes from Holly Spring (Georgia, USA),  
72 and is available in the RRUF database (reference R06180). Fluorapatite (reference RRUF  
73 R050340) was collected at Buckingham (Quebec, Canada). In addition to the humerus of  
74 MNHN-ZA-AC-1928-242, modern biogenic apatites (bone, enamel, and dentine) used as  
75 references were a small dried fragment of a long bone of *Sus scrofa* (Mammalia: Suidae) and  
76 a tooth fragment of *Hippopotamus amphibius* (Mammalia: Hippopotamidae). A small rodent  
77 (Mammalia: Rodentia indet.) bone from the Pleistocene of Olduvai (Tanzania) was used as  
78 reference for fossil bones rich in rare earth elements (REE) (for details see electronic  
79 supplementary material).

80 Abbreviations: MNHN, Muséum national d'Histoire naturelle, Paris; SHC, Saudi  
81 Heritage Commission, al-Shimaysi store, Riyadh.

82

### 83 **3. Results**

84

#### 85 *3.1. Anatomy*

86 Revised description of MNHN.F.MRS51.1 (Fig. 1): fragmentary right dentary  
87 restricted to the posteriormost portion of the dental row (five teeth preserved) and anterior  
88 portion of the coronoid process. The anterior, posterior and ventral portions of the bone are  
89 missing. The estimated original length of the dentary is about 25 mm. The specimen is broken  
90 ventral to the tooth row, thus exposing the Meckelian groove in lateral view. No mental  
91 foramina are preserved due to the fragmentary nature of the specimen. Medially, the subdental  
92 lamina (sensu Takesh et al., 2020) is partially preserved ventrally to the dental groove (sensu  
93 Čerňanský, 2010). The medial face of the specimen is heavily abraded, as indicated by the

94 exposed pulp cavity of the last tooth. The ledge ventral to the tooth bases (sensu Rage and  
95 Augé, 2015) and the dental groove are worn and poorly distinct. The incomplete coronoid  
96 process rises obliquely above the level of the tooth row. The anterior ridge of the coronoid  
97 originates posterior to the distolingual portion of the last tooth. Laterally, the coronoid process  
98 is convex due to the presence of the posterodorsally ascending crest (sensu Simões et al.,  
99 2015); medially, the coronoid process is flat due to the presence of the coronoid facet. The  
100 acrodont dentition consists of oblique, mesiolingually oriented teeth; the teeth become  
101 gradually more oblique from anterior to posterior positions. The tooth crowns are higher and  
102 more abrupt labially than lingually. The lingual faces bear a bulbous cingulum, partially  
103 covered by tooth ankylosis. In occlusal view, the anterior and posterior carinae originating  
104 from a blunt apex form a distolingually concave crest.

105

### 106 3.2. *Taphonomy and Raman spectroscopic analyses*

107 As MNHN.F.MRS51.1 was surface collected and is completely free of matrix, there is  
108 no direct evidence that this specimen originates from the mid-Cretaceous Kem Kem beds. The  
109 polished aspect and breaks displayed by MNHN.F.MRS51.1 may be due to predation (e.g.  
110 bites, digestive process) and/or weathering, as observed in many squamate remains from  
111 archaeological sites (Stoetzel et al. 2012; Smith et al., 2013, 2021; Lev et al. 2020). All the  
112 confirmed Cretaceous specimens (e.g. ganoid fish scales, theropod and pterosaur teeth)  
113 collected at the Gara Tabroumit site by Lavocat are brown to dark reddish brown, unlike  
114 MNHN.F.MRS51.1 which can be easily distinguished by its whitish pink color (see Fig. 2).

115 Raman spectra of fossil (Cretaceous) specimens from Gara Tabroumit are similar  
116 between each other (Fig. 2A), but clearly differ from those of the holotype of *Jeddaherdan*  
117 *aleadonta* and modern *Uromastyx* bones (Fig. 2B, C). The main band of apatite ( $\nu_1$  PO<sub>4</sub>) at

118 about 960 cm<sup>-1</sup> is not detected in Cretaceous specimens. In the latter, the main bands are  
119 between 1100 and 1700 cm<sup>-1</sup>, and they have no counterparts in modern specimens. Spectra of  
120 *U. acanthinura* s.l. (Recent) and *U. aegyptia* (Holocene) show the preservation of organic  
121 components (amide bands) (Fig. 2C). *U. aegyptia* and *J. aleadonta* have strong bands  
122 assigned to ν<sub>4</sub> PO<sub>4</sub>, whereas that of *U. acanthinura* s.l. is weaker (Fig. 2B, C). This suggests  
123 that the bones of *J. aleadonta* and the archaeological *U. aegyptia* were somewhat  
124 recrystallized, whereas the modern humerus of *U. acanthinura* s.l. was not modified. The  
125 values of the Full Width at Half Maximum (FWHM) confirm the low crystallinity of *U.*  
126 *acanthinura* s.l. (Fig. S3). Moreover, coefficient correlations between *J. aleadonta* and *U.*  
127 *aegyptia* on one hand, and *J. aleadonta* and a *U. acanthinura* s.l. on the other hand, are the  
128 highest (Table S1).

129

#### 130 4. Discussion

131

132 Apesteguía et al. (2016) described MNHN.F.MRS51.1 as an “incomplete left dentary  
133 missing the symphyseal and posteriormost portions” and estimated the skull length as 22.3  
134 mm (Apesteguía et al., 2016: fig. 1). Consequently, they noted that *Jeddaherdan aleadonta*  
135 was characterized by a low number of relatively large teeth compared with modern  
136 uromastycines, and that its teeth were mesiolabially oriented (instead of mesiolingually  
137 oriented in *Uromastyx*; Cooper and Poole, 1973; Holmes et al., 2010). However, our  
138 redescription shows that the size, proportions and orientation of the specimen were  
139 misinterpreted by Apesteguía et al. (2016) (Fig. 1F–H); therefore, some anatomical structures  
140 shown in their fig. 3 were also misidentified (Table 2). It clearly appears that  
141 MNHN.F.MRS51.1 actually represents a small portion of a larger right dentary (Fig. 1B). The

142 combination of features on which Apesteguía et al. (2016) based the diagnosis of *J. aleadonta*  
143 becomes inaccurate. *Jeddaherdan* is indistinguishable from *Uromastyx*, and the former is here  
144 synonymized with the latter (i.e. *Jeddaherdan* being a junior synonym of *Uromastyx*). Due to  
145 the incompleteness and poor preservation of the specimen, the species *J. aleadonta* should be  
146 considered a nomen dubium and we therefore refer MNHN.F.MRS51.1 to *Uromastyx* sp. It  
147 should be noted that as *U. nigriventris* (formerly *U. acanthinura nigriventris*) is the only  
148 species present in the Kem Kem region today (Wilms et al., 2009; Tamar et al., 2018),  
149 MNHN.F.MRS51.1 might belong to this species; however, as we cannot be sure about the  
150 past (Quaternary) distribution of other North African species of the genus, it is preferable to  
151 treat this specimen as an indeterminate species of *Uromastyx*.

152 Data obtained from Raman spectroscopy strongly suggest two distinct taphonomic and  
153 diagenetic histories between MNHN.F.MRS51.1 and other specimens from Gara Tabroumit  
154 originating unambiguously from the mid-Cretaceous Kem Kem beds (MNHN.F.MRS51.2 to  
155 MNHN.F.MRS51.6). Unlike MNHN.F.MRS51.1, these mid-Cretaceous fossils may be rich in  
156 rare earth elements as suggested by their Raman spectra similar to that of the REE-rich fossil  
157 bone from Olduvai (see electronic supplementary material; Fig. S4). Interestingly, REE  
158 enrichment was also reported in vertebrate fossils from other mid-Cretaceous Kem Kem  
159 localities (Hassler et al., 2018). The fact that MNHN.F.MRS51.1 shows no REE enrichment  
160 would indicate that this specimen does not originate from the mid-Cretaceous Kem Kem beds  
161 (Trueman, 1999). On the other hand, MNHN.F.MRS51.1 shows a similar spectrum to those  
162 of the bones of modern lizards (*Uromastyx* spp.). Therefore, it is considered here as late  
163 Quaternary in age, which is consistent with our conclusions based on anatomical evidence.

164 *Jeddaherdan aleadonta*, widely accepted as a mid-Cretaceous acrodontan since its  
165 original description (e.g. Ibrahim et al., 2020; Evans, 2022; Ijouher, 2022), has been  
166 considered in various studies as a key taxon critical for understanding the origin and

167 evolutionary history of iguanian lizards, with important implications for both  
168 palaeobiogeographic reconstructions (Simoes et al., 2017; Bittencourt et al., 2020; Rage and  
169 Gheerbrant, 2020) and node calibrations (Lafuma et al., 2021; Marjanović, 2021; Paparella,  
170 2021; although Marjanović (2021) cautiously “preferred not to use *Jeddaherdan* to date the  
171 origin of Iguania as long as further material has not been discovered”). However, our study  
172 shows that the holotype and only known specimen of *J. aleadonta* is a dentary fragment of a  
173 recent (or subfossil) subadult of *Uromastyx* sp., which is a common lizard in the Kem Kem  
174 area today (represented by the species *U. nigriventris*; Wilms et al., 2009; Tamar et al., 2018).  
175 Therefore, *J. aleadonta* can no longer be considered as the oldest known iguanian lizard from  
176 Africa, removing the only evidence for the presence of iguanians in the Mesozoic of that  
177 continent. Consequently, apart from a doubtful record from the late Palaeocene of Morocco  
178 (Augé and Rage, 2006), the earliest confirmed acrodontan from Africa to date is an  
179 indeterminate agamid from the late early–early middle Eocene from Algeria (Rage et al.,  
180 2021). Regarding uromastycines, the material referred to cf. *Uromastyx* from the early  
181 Oligocene of Egypt represents the oldest known record from Africa (Holmes et al., 2010). On  
182 the other hand, molecular studies suggest that uromastycines (*Uromastyx* spp.) colonized  
183 Africa from Asia no earlier than the middle Miocene (Amer and Kumazawa, 2005; Tamar et  
184 al., 2018).

185         Similarly to *Jeddaherdan*, *Tikiguania* is an Indian squamate taxon that was originally  
186 erroneously thought to be Late Triassic in age and therefore misinterpreted as the oldest  
187 known lizard (Datta and Ray, 2006). Subsequently, Hutchinson et al. (2012) demonstrated  
188 that this taxon is actually a late Cenozoic agamid indistinguishable from living draconines  
189 present in India (e.g. *Calotes*). The cases of *Tikiguania* and *Jeddaherdan* show that caution  
190 needs to be exercised when studying surface collected or screen washed vertebrate  
191 microremains that are completely free of matrix. Recent or subfossil elements can

192 contaminate much older fossil assemblages, potentially leading to serious misinterpretations  
193 and false evolutionary and palaeobiogeographic implications.

194

## 195 **5. Conclusions**

196

197 According to our observations, there is so far no evidence for the presence of Iguania  
198 in the Mesozoic of Africa. We reached the conclusion that the jaw fragment from southeastern  
199 Morocco recently interpreted as belonging to a new mid-Cretaceous acrodontan taxon  
200 (*Jeddaherdan aleadonta*) is actually a Quaternary specimen that comes from a modern spiny-  
201 tailed lizard (*Uromastyx* sp.). This new taxonomic assignment, primarily based on the  
202 anatomical revision and reinterpretation of the specimen, is also supported by taphonomic  
203 arguments. The present study shows that Raman spectroscopy is a non-destructive and non-  
204 invasive method that can help to discriminate contaminating (i.e. much older or younger)  
205 elements within a given vertebrate fossil assemblage.

206

## 207 **Declaration of Competing Interests**

208 The authors declare no competing interests.

209

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215

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305

#### 306 **Appendix A. Supplementary data**

307 Supplementary data to this article can be found online at

308

#### 309 **Figures captions**

310

311 **Fig. 1.** Skull reconstructions (based on *Uromastix aegyptia*) in left (A) and right (B) lateral  
312 views showing the position and relative size of MNHN.F.MRS51.1 as interpreted by  
313 Apesteguía et al. (2016: fig. 1) and in the present study, respectively. Holotype of  
314 *Jeddaherdan aleadonta* (MNHN.F.MRS51.1), fragmentary right dentary (C–E), and  
315 *Uromastix aegyptia* (SHC YAM K17-SD4 S 414.1), complete right dentary (F–H), in lateral  
316 (C, F), medial (D, G) and dorsal (E, H) views. The red silhouette in F–H shows the position of  
317 MNHN.F.MRS51.1 as interpreted here.

318

319 **Fig. 2.** Raman spectra of five fossil (mid-Cretaceous) specimens from Gara Tabroumit (from  
320 top to bottom: pterosaur tooth in black, theropod tooth in red, crocodylomorph tooth in green,

321 spinosaurid tooth in blue, fish vertebra in brown) (A), the holotype specimen of *Jeddaherdan*  
 322 *aleadonta* (B), and two modern *Uromastyx* bones (from top to bottom: *U. aegyptia* dentary in  
 323 blue, *U. acanthinura* s.l. humerus in pink) (C) (see text and Table 1 for details). Specimens  
 324 not to scale.

325

326 **Tables**

327

328 **Table 1.** Material studied, including the holotype of *Jeddaherdan aleadonta*, mid-Cretaceous  
 329 vertebrate remains from the type locality (Gara Tabroumit), and skeletal elements of modern  
 330 spiny-tailed lizards (*Uromastyx* spp.).

Collection number	Taxon	Element(s)	Age, provenance
MNHN.F.MRS51.1	<i>Jeddaherdan aleadonta</i>	Dentary fragment	Holocene (this study); previously Cenomanian (Apesteguía et al., 2016), Gara Tabroumit, Morocco
MNHN.F.MRS51.2	Actinopterygii indet. (Amiidae?)	Vertebra	Cenomanian, Gara Tabroumit, Morocco
MNHN.F.MRS51.3	Crocodylomorpha indet.	Tooth	Cenomanian, Gara Tabroumit, Morocco
MNHN.F.MRS51.4	Ornithocheiridae indet.	Tooth	Cenomanian, Gara Tabroumit, Morocco
MNHN.F.MRS51.5	cf. Spinosauridae	Tooth fragment	Cenomanian, Gara Tabroumit, Morocco
MNHN.F.MRS51.6	Theropoda indet.	Tooth	Cenomanian, Gara Tabroumit, Morocco
SHC YAM K17-SD4 S 414.1	<i>Uromastyx aegyptia</i>	Dentary	Holocene, al-Yamâma, Saudi Arabia
MNHN-ZA-AC-1928-242	<i>Uromastyx acanthinura</i> s.l.	Lower jaw and humerus (from a single individual)	Recent, Northwest Africa (precise locality unknown)

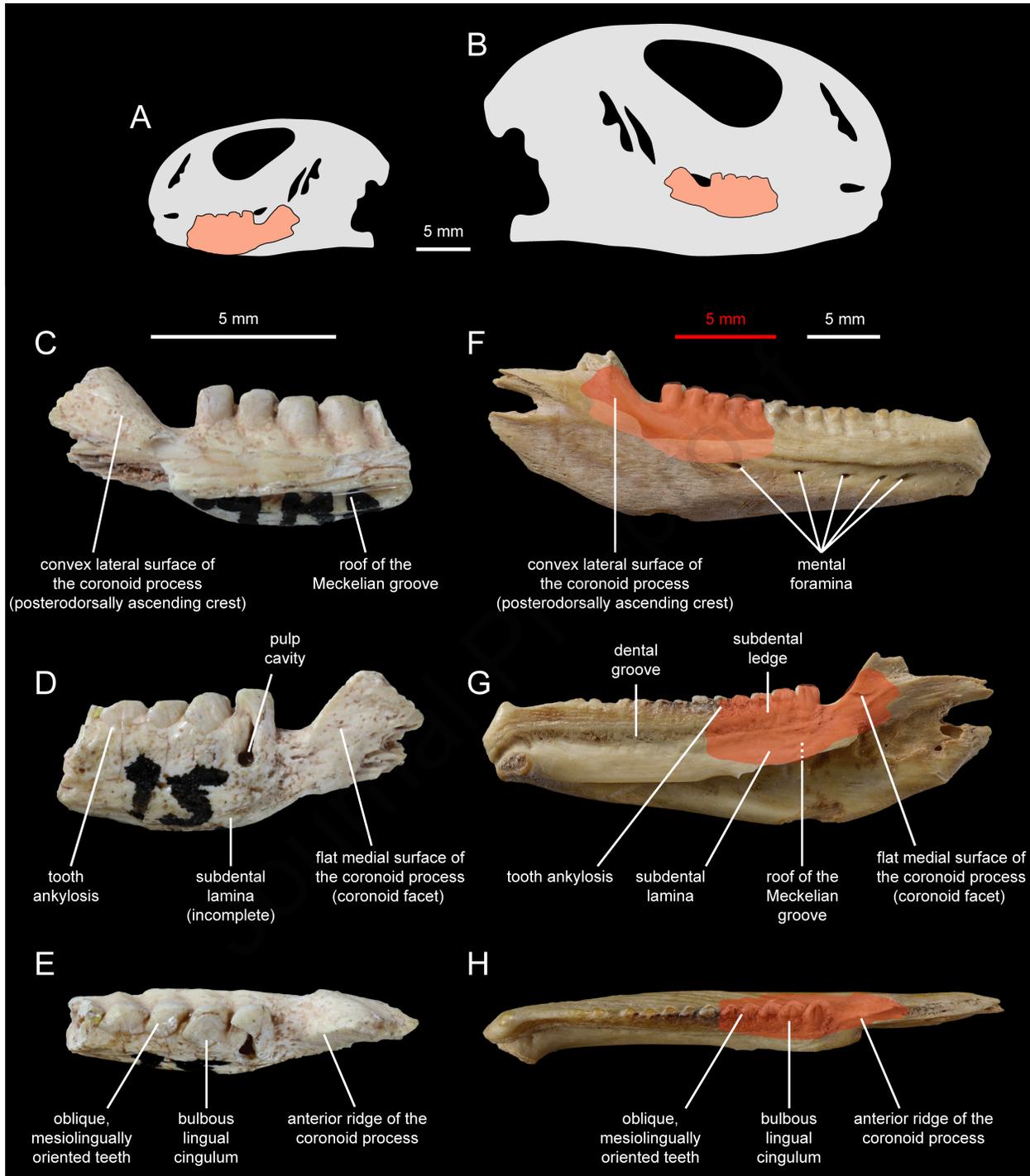
331

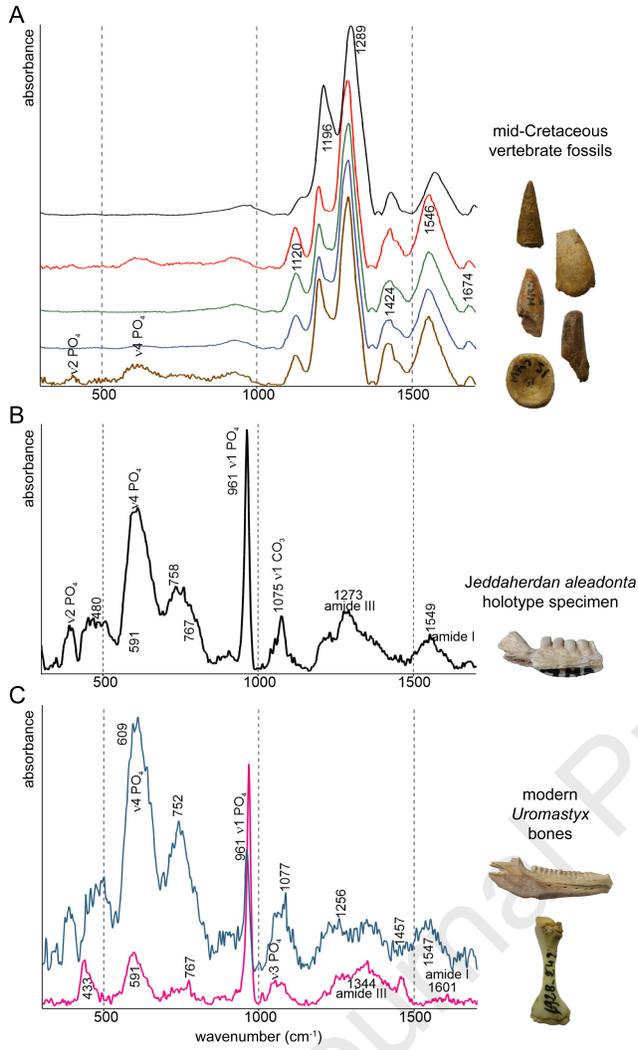
332

333 **Table 2.** Reinterpretation of some anatomical structures identified in the original description  
 334 of *Jeddaherdan aleadonta*.

Structures in Apesteguía et al.'s <b>(2016)</b> <b>fig. 3</b>	Reinterpretation (this study)
Surangular and angular facets (San.ft and An.ft, respectively)	Impression surface of the anteromedial process of the coronoid
Angular facet (An.ft) in fig. 3c	Ventral edge of the partially broken subdental lamina
Mental foramen (m.f)	Foramina located in the dental groove
Tooth wear (tt.w)	Subdental ledge forming the dorsal border of the dental groove
Dentary sulcus (D.su), coronoid facet (Co.ft), prearticular facet (Part.ft) and subdental crest (sd.cr)	Area where the lateral surface of the dentary is broken with loss of bone material.
Subdental shelf (sd.sh)	Roof of the Meckelian groove
Posteroventral process (pv.pr)	Fracture of the lateral wall of the dentary

335





The acrodontan lizard *Jeddaherdan aleadonta* from Morocco is reexamined.

Both anatomical and taphonomic arguments show that the material was misinterpreted.

It does not originate from the mid-Cretaceous Kem Kem beds as previously thought.

The single known specimen, a jaw fragment, comes from a modern spiny-tailed lizard.

Our study removes the only fossil evidence for Iguania in the Mesozoic of Africa.

**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:

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