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

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ABSTRACT

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

Keywords:

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

1. Introduction

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

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

2. Material and methods

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

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

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

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

3. Results

3.1. Anatomy

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

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

3.2. Taphonomy and Raman spectroscopic analyses

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

Raman spectra of fossil (Cretaceous) specimens from Gara Tabroumit are similar between each other (Fig. 2A), but clearly differ from those of the holotype of *Jeddaherdan aleadonta* and modern *Uromastyx* bones (Fig. 2B, C). The main band of apatite ($\nu_1 \text{PO}_4$) at

about 960 cm^{-1} is not detected in Cretaceous specimens. In the latter, the main bands are between 1100 and 1700 cm^{-1} , and they have no counterparts in modern specimens. Spectra of *U. acanthinura* s.l. (Recent) and *U. aegyptia* (Holocene) show the preservation of organic components (amide bands) (Fig. 2C). *U. aegyptia* and *J. aleadonta* have strong bands assigned to $\nu_4\text{ PO}_4$, whereas that of *U. acanthinura* s.l. is weaker (Fig. 2B, C). This suggests that the bones of *J. aleadonta* and the archaeological *U. aegyptia* were somewhat recrystallized, whereas the modern humerus of *U. acanthinura* s.l. was not modified. The values of the Full Width at Half Maximum (FWHM) confirm the low crystallinity of *U. acanthinura* s.l. (Fig. S3). Moreover, coefficient correlations between *J. aleadonta* and *U. aegyptia* on one hand, and *J. aleadonta* and a *U. acanthinura* s.l. on the other hand, are the highest (Table S1).

4. Discussion

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

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

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

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

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

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

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

5. Conclusions

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

Declaration of Competing Interests

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at

Figures captions

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

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

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

Tables

Table 1. Material studied, including the holotype of *Jeddaherdan aleadonta*, mid-Cretaceous vertebrate remains from the type locality (Gara Tabroumit), and skeletal elements of modern spiny-tailed lizards (*Uromastix* 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>Uromastix aegyptia</i>	Dentary	Holocene, al-Yamâma, Saudi Arabia
MNHN-ZA-AC-1928-242	<i>Uromastix acanthinura</i> s.l.	Lower jaw and humerus (from a single individual)	Recent, Northwest Africa (precise locality unknown)

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

Structures in Apesteguía et al.'s (2016) fig. 3	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

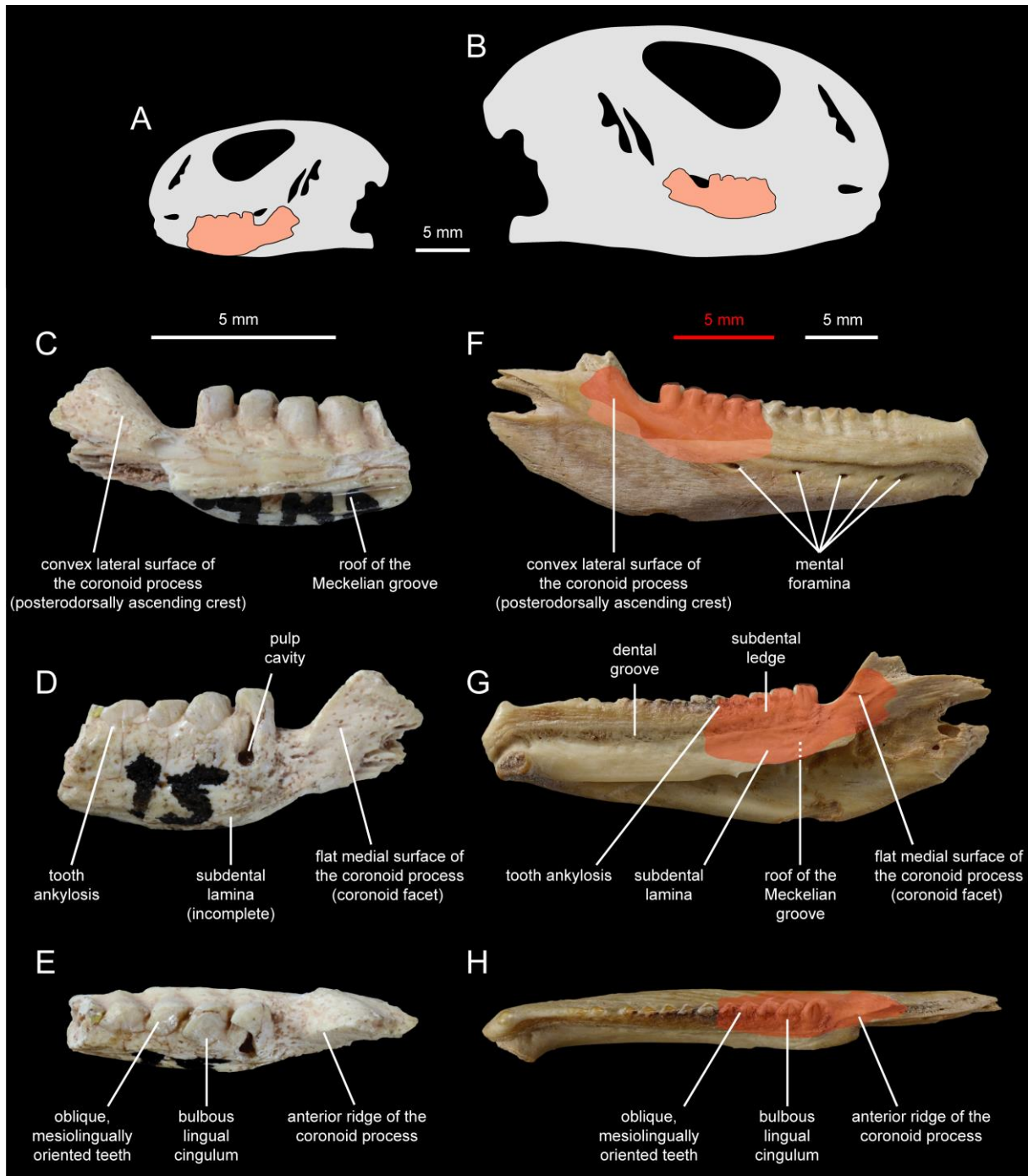


Figure 1

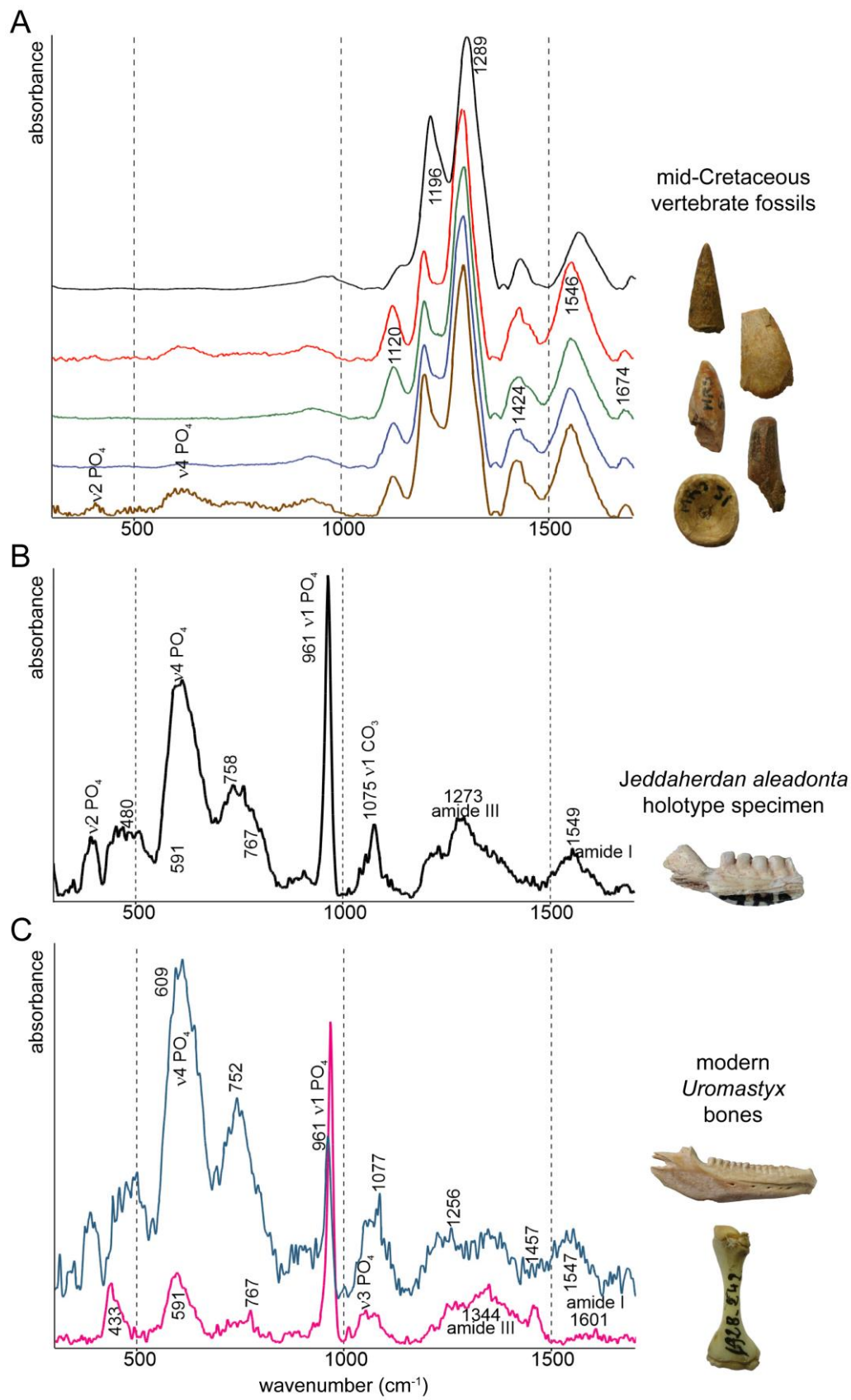


Figure 2