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Samir Zouhri, Philip Gingerich, Bouziane Khalloufi, Estelle Bourdon, Sylvain Adnet, et al.. Middle Eocene vertebrate fauna from the Aridal Formation, Sabkha of Gueran, southwestern Morocco. Geodiversitas, 2021, 43 (5), 10.5252/geodiversitas2021v43a5 . hal-03432986

HAL Id: hal-03432986

https://hal.umontpellier.fr/hal-03432986v1

Submitted on 23 Nov 2021

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La faune des vertébrés du Bartonien (Eocène moyen) de la Formation d'Aridal dans la Sabkha de Gueran au sud-ouest du Maroc.

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Abstract

In the Sahara Desert of southwestern Morocco, the Aridal Formation of Gueran is known for the world's richest Bartonian-age archaic whale assemblage, which includes both protocetids and basilosaurids. Gueran has also yielded another rich and diverse vertebrate fauna described in detail herein —The chondrichthyan assemblage of twelve species is quite similar to that of the Midawara Formation (Egypt). Actinopterygians include siluriformes, perciformes and *Cylindracanthus*Leidy, 1856. Turtles are attributed to at least three indetermined species: two marine cryptodires— a cheloniid and a dermochelyid, and a possible littoral pleurodire, as found in Ad-Dakhla (Morocco) and Fayum (Egypt). The crocodylians comprise at least two longirostrine taxa, including a gavialoid that resembles the Late Eocene-Early Oligocene *Eogavialis africanum* Andrews, 1901 from Egypt. The second form is too fragmentary to be identifyied more precisely than Crocodyliformes indet. Two snake vertebrae belong to *Pterosphenus* cf. *schweinfurthi* Andrews, 1901. Two other incomplete snake vertebrae probably belong to Paleophiidae as well. Seabird remains belong to a gigantic soaring pseudo-toothed bird (*Pelagornis* sp. Lartet, 1857) constituting the earliest occurrence of this genus and extending its fossil record back in time by at least 10 million years. Based on their size and enamel microstructure, mammal dental fragments are attributed to the proboscidean ?*Barytherium* sp.. The Bartonian age of the fauna, initially based on an archaeocete cetacean assemblage, is also supported by chondrichthyans. Affinities of the Gueran faunal assemblage are analyzed in comparison with those from other middle and upper Eocene deposits of North Africa and elsewhere.

Key words: Aridal Formation, Sabkha of Gueran, Moroccan Sahara, Vertebrates, middle Eocene.

Résumé

La Formation Aridal de la Sabkha de Gueran, au sud du Maroc, a livré le plus riche assemblage de cétacés archéocètes bartoniens, comprenant à la fois des protocétidés et des basilosauridés. Gueran a également produit une autre faune de vertébrés que nous décrivons ici en détaillée. L'assemblage des douze espèces de chondrichtyens ressemble à celui de la Formation de Midawara (Égypte). Les actinoptérygiens incluent des siluriformes, des perciformes et *Cylindracanthus* Leidy, 1856. Les tortues sont rapportées à au moins trois taxons indéterminés : deux cryptodires marins, un chéloniidé et un dermochélyidé, et un possible pleurodire littoral, comme à Ad-Dakhla (Maroc) et au Fayum (Égypte). Le matériel de crocodyliens permet de reconnaître au moins deux formes longirostrines, dont un gavialoïde ressemblant à *Eogavialis africanum* Andrews, 1901 de l'Éocène supérieur-Oligocène inférieur d'Egypte**.** Les fossiles de la deuxième forme sont très fragmentaires et sont considérés comme Crocodyliformes indet. Certaines vertèbres de serpent appartiennent au Palaeophiidae *Pterosphenus* cf. *schweinfurthi* Andrews, 1901. D'autres, incomplètes, appartiennent vraisemblablement aussi à un palaeophiidé. Les restes d'oiseaux marins appartiennent à un gigantesque oiseau planeur, un Pelagornithidae, constituant la première occurrence du genre *Pelagornis* Lartet, 1857, ce qui recule son apparition d'au moins 10 millions d'années. À partie de leur microstructure d'émail, des fragments dentaires de proboscidien sont attribuésau genre ?*Barytherium* sp.. D'après l'assemblage d'Archaeoceti, l'âge de cette faune est bartonien, ce qui est confirmé par les chondrichtyens. Les affinités de la faune de Gueran avec celles d'autres gisements, notamment celles de l'Éocène d'Afrique du Nord, sont analysées.

Mots clés: Formation d'Aridal, Sabkha de Gueran, Vertébrés, Éocène moyen, Sahara, Maroc.

1. Introduction

The Sabkha (a flat-bottomed depression, sometimes inundable, where salty soils limit vegetation) of Gueran is located 125 km southeast of Boujdour in the Sahara Desert of southwestern Morocco (Fig.1). The Gueran depression is known to have yielded a rich and diverse middle Eocene marine vertebrate fauna, including the world's richest Bartonian-age Archaeoceti cetacean assemblage (Gingerich & Zouhri 2015). Three species of Protocetidae and three species of Basilosauridae have been described from Gueran (Gingerich & Zouhri 2015, Tabl.1). The complete vertebrate assemblage from Gueran was summarized in Zouhri (2018). Marine vertebrates of the middle and upper Eocene age are relatively well documented in the eastern part of Tethys (the Indo-Pakistani subcontinent) and the Middle East (Egypt). However, much less is known for the western part of Tethys, including the current Maghreb (Tunisia, Algeria and Morocco), andfor the Atlantic coast of West Africa. The middle Eocene-Oligocene faunas discovered near Ad-Dakhla area (Adnet 2010; Zouhri *et al*. 2014, 2017; Marivaux *et al*. 2017a,b and 2018; Elboudali *et al*. 2018) and the Bartonian middle Eocene fauna discovered thereafter at Gueran (Gingerich & Zouhri 2015; Zouhri *et al*. 2018) and described here help to fill this gap. Here we provide a comprehensive description of the various non-cetacean vertebrate taxa in the fauna from Gueran, with an exhaustive comparison with contemporaneous faunas of the Fayum Depression in Egypt, Dur At-Talah in Libya, and other Eocene localities on the Atlantic coast of North and Western Africa (Nigeria, Togo, Senegal and Morocco) and up to the Anglo-Franco-Belgian Eocene basin of western Europe. Finally, we consider the biostratigraphical, paleobiogeographical and paleoenvironmental significances of this diverse marine upper middle Eocene fauna from northwestern Africa.

Figure 1

2. Geological setting

The vertebrate fauna described here comes from the Aridal Formation of the Gueran depression in the Sahara Desert of southwestern Morocco. Geologically, this formation belongs to the Atlantic basin of Tarfaya-La'Youn-Ad-Dakhla (Ranke *et al*. 1982; Davison & Dailly 2010). This basin is the onshore, proximal part of the Atlantic passive margin; the oldest, Triassic-Liassic deposits of the margin are lacking here beneath the continental lower Cretaceous sandstones and overlying upper Cretaceous-Cenozoic marine beds (Hafid *et al*. 2008). Gingerich & Zouhri (2015) summarized the geological context of the Gueran deposits based on previous works on the geology of the study area (Ratschiller 1967, 1970; Lindner & Querol 1971; Hollard *et al*. 1985; Rjimati *et al*. 2008). The bone bed that yielded vertebrate fossil remains is some 11 meters abovethe base of the section located at the northeast wall of the depression. The stratigraphic sequence is illustrated in detailes *in* Zouhri *et al*. (2018: fig. 2).

3. Material and Methods

The fossil remains described hereinwere collected during several seasons fieldwork of one to two weeks each in the Sabkha of Gueran in southwestern Morocco. These fossils came from several fossiliferous localities weathering out from the same stratigraphic level. While the fossils of Archaeoceti and chondrichthyan teeth are very abundant, remains of other taxa are much less common. Similarly, while Archaeoceti are represented by both isolated elements and articulated skeletons, the non-cetacean vertebrate taxa are represented mainly by isolated and fragmentary specimens. The overall composition of the vertebrate assemblage of the sabkha of Gueran has been specified previously by Zouhri *et al*. (2018: fig.3). Excluding chondrichthyans, taxa studied here represent about 22% of the Gueran fossils assemblage, while cetaceans represent about 78%. All specimens described here are permanently stored in the Paleontological Collections of the Department of Geology, Faculty of Sciences Aïn Chock, Hassan II University of Casablanca, Morocco.

Stratigraphic abbreviations: Faunal comparisons are often made to fossils from Middle-Late Eocene localities of Wadi al Hitan in Egypt, and Ad-Dakhla in southwestern Morocco, and Dur At-Talah in Libya. We use the following abbreviations in the whole text: Midawara Fm. (MI) Wadi el Rayan, Egypt dated to latest Lutetian and possibly earliest Bartonian according to Strougo *et al*. (2013); Gehannam Fm. (GE), Wadi al Hitan, Egypt dated to latest Bartonian – early Priabonian in Strougo et al. (2013); Birket Qarum Fm. (BQ) Fayum, Egypt dated as early Priabonian in Peters *et al*. (2009);

Qasr el-Sagha Fm. (QS), Fayum, Egypt dated as late Priabonian in Peters *et al*. (2009); Samlat Fm. (SA) southwestern Morocco dated as Bartonian-Priabonian (Adnet *et al*. 2010; Zouhri *et al*. 2014; Gingerich & Zouhri 2017; Bennami *et al*. 2017).

Institutional abbreviations: FSAC Bouj, Faculty of Sciences Aïn Chock, Boujdour collection, Casablanca (Morocco); MNHNF, Muséum national d'Histoire naturelle, Paris, collection of Paleontology.

4. Systematic paleontology

4.1. Elasmobranchii Bonaparte, 1838

Fossils were collected only by surface picking around the archaeocete whale carcasses (protocetids and basilosaurids, see Gingerich & Zouhri 2015), and thus the majority of small to medium-sized sharks and rays remain currently unknown. Thousands of specimens were collected from several localities around Gueran Depression (Locality I, Garouaz, Iddir and Laazri, see Gingerich & Zouhri 2015: Fig.2). The majority of the fossil material consists of isolated teeth, rare barbs of myliobatid rays, and indeterminate vertebrae representing at least 12 species of sharks and rays.

Figure 2.

The chondrichthyan fauna currently consists of 12 species of elasmobranchs belonging to orders: Lamniformes, Carcharhiniformes and Rhinopristiformes. Most unnamed species are in course of study, awaiting careful comparisons with those from subcontemporaneous deposits (e.g. MI, GE) in Waddi el-Rayyan and Wadi Hitan (Whale Valley) in Egypt.

Lamniformes Berg, 1937

Lamnidae Müller and Henle, 1838

Macrorhizodus (*Cosmopolitodus* = *Isurus*) Glikman, 1964

Macrorhizodus praecursor (Leriche, 1905)

Material: Hundreds of isolated teeth, figured material includes FSAC Bouj–327, 328, 329 and 330

Description: The more abundant complete and well-preserved teeth (Fig. 2H-K) recovered in both localities (Locality I, Garouaz, Iddir and Laazri) belong to the lamnid *Macrorhizodus praecursor*. Central cusp is especially triangular in anterolateral files (e.g., Fig. 2J) with a flat labial face and a little convex lingual face.

Remarks: This species, representing an extinct pelagic mako shark, is very abundant in all middle and late Eocene localities and distributed worldwide in the marine realm.

Otodontidae Glückman, 1964

Otodus Jordan and Hannibal, 1923

Otodus (*Carcharocles)* cf. *sokolowi* (Jaekel, 1895).

Material: Around twenty broken isolated teeth, figured material includes FSAC Bouj–320, 321 and 322.

Description: Teeth can reach up to 10 cm in height, displaying a large triangular cusp with well-marked and regular serrations on the cutting edges and a pair of lateral cusplets (Fig. 2A). Cusplets are not very high when conserved and often divergent in lateral teeth (Fig. 2A) to less developed in anterior teeth (Fig. 2B).

Remarks: Teeth of *Otodus* (*Carcharocles)* cf. *sokolowi* are relatively common around the archaeocete carcasses (Fig. 2A-C). Case & Cappetta (1990) have discussed about the taxonomic distinctness of *Otodus* (*Carcharocles) sokolowi* compared to the other Eocene species of subgenus, and in particularly with the smaller and coeval species *Otodus* (*Carcharocles) auriculatus* (Blainville 1818). *Otodus* (*Carcharocles) sokolowi* appears widely distributed and relatively common in the tropical marine realm since the GEA–C (uppermost Bartonian - lowermost Priabonian) and throughout the Priabonian successions (GE D-G, BQ, QS) according to Underwood *et al*. (2011), southwestern Morocco included (Adnet *et al*. 2010). However this species seems relatively discrete in older deposits, as in the MI (Underwood *et al*., 2011). Its occurrence in Bartonian of Gueran, Morocco, testify of its spatial expansion along the Tethysian coasts during the Bartonian.

Otodus (*Carcharocles*) sp.

Material*:* A dozen isolated teeth, figured material includes FSAC Bouj–323

Description*:* Teeth are some smaller than those of previous species and up to 5 cm in height (Fig. 2D-E). Compared to *Otodus* (*Carcharocles)* cf. *sokolowi*, teeth of this second species display a flatter root with subrectangular basal extremities of lobes, a more slender cusp with finer serrations and two cusplets which are smaller and lower than in other coeval species.

Remarks: These characters are different from the coeval small megatoothed shark species *Otodus* (*Carcharocles) auriculatus,* commonly reported in worldwide Middle Eocene deposits (e.g., Ward &Wiest 1990; Dutheil 1991; Long 1992; Cappetta & Stringer 2002, Cappetta & Case 2016). Similar otodontid morphology is observed in the Lutetian material of Togo (Pers. Observ.) where co-occurrence of two representatives of megatoothed sharks is also noticed.

Odontaspididae Müller and Henle, 1839

Carcharias Rafinesque, 1810

'Carcharias' koerti (Stromer, 1910)

Material: Thirty broken isolated teeth, figured material included FSAC Bouj–325 and 326

Description: Occurrence of the Middle Eocene *'Carcharias' koerti* is confirmed in Gueran (Fig. 2F-G). Interestingly, the majority of recovered teeth (e.g., Fig. 2G) are relatively small compared to the usual Lutetian representatives.

Remarks: The generic affinity of this large pelagic shark to ''*Carcharias*" or "*Brachycarcharias*" still remains unclear (e.g., Strougo *et al*. 2007, Underwood *et al*. 2011), this large pelagic shark is preferentially known in the Lutetian deposits and is widely distributed around the North and Western African coasts (Stromer 1910; White 1955; Dartevelle & Casier 1959; Cappetta & Traverse 1988; Cappetta *et al*. 2000; Noubhani & Cappetta 1997; Strougo *et al*. 2007). Rarely recovered in MI (Uppermost Lutetian – Lowermost Bartonian), GA (Lutetian-Bartonian) and lacking in GE A–C (uppermost Bartonian) and the remainder of the succession of Wadi al Hitan, Egypt (see Underwood *et al*. 2011), its occurrence in Boujdour area seems to indicate that the age of the deposits is likely older than latest Bartonian.

Tethylamna (Case, 1981)

Tethylamna cf. *twiggsensis* (Case, 1981)

Material: Fifty isolated teeth, figured material includes FSAC Bouj–331, 332, 333, 334, 335 and 336.

Description: Numerous teeth are attributed to odontaspidid *Tethylamna* cf. *twiggsensis*. This species is easily recognizable by a pair of double flat cusplets on anterior (Fig. 3A, F) and lateral teeth (Fig. 3 C-E).

Remarks: The range of this species is currently restricted to the Latest Lutetian-Late Priabonian and its geographic distribution extends to paleotropical seas between tropical eastern Pacific, Caribbean and oriental Neotethys (Casier 1971; Case 1981; Case & Borodin 2000; Case & Cappetta 1990; Ward & Weist 1990; Adnet *et al*. 2007; Underwood *et al*. 2011; Cappetta & Case 2016). Originally described from the late Eocene of Georgia, USA (Case 1981), distinction between the middle and the late Eocene representatives are sometimes controversial. The Bartonian teeth have lateral cusplets less pronounced compared to those from Priabonian (Underwood *et al*. 2011) explaining why they are often referred to confer *twigssensis*. These Bartonian samples could corresponds to intergradual change from the possible ancestor *T. dunni* of Cappetta & Case (2016) recovered from the Lutetian of Alabama, USA toward those of Priabonian, including type of species (Case, 1981).

Figure 3

Carcharhiniformes Compagno 1973

Carcharhinidae Jordan & Evermann, 1896

Galeocerdo Müller & Henle, 1838

Galeocerdo eaglesomi (White, 1955)

Material: Thirty isolated teeth, figured material includes FSAC Bouj–337, 338 and 339.

Description: The African *Galeocerdo eaglesomei* is unfrequent compared to the contemporaneous and worldwide species *G. latidens* Agassiz, 1843. However, *G. eaglesomei* differs from it by teeth with a higher crown, a longer and abrupt distal heel without distinct notch with main cusp, with more numerous and larger denticles and with a deeper basal medial concavity of the root deeper. Our teeth (Fig. 3G-I), as those from the Lower Priabonian of SA, southwestern Morocco (Adnet *et al*. 2010), are relatively larger and display a much higher crown compared to the Lutetian specimens,,which makes it possible to provisionally assign these to *G. eaglesomei*, to which the youngest specimens from Southwestern Morocco are likely affiliated.

Remarks: Relatively scarce teeth of *Galeocerdo* cf. *eaglesomi* are quite similar in shape to *G. eaglesomi* from the late Lutetian of Nigeria (Andrews 1920), the Lutetian-Bartonian of GA (Strougo *et al*. 2007), the middle to late Eocene of Madagascar (Samonds *et al*. 2019) and to those recovered in MI, Egypt, where it is one of the most conspicuous elements of the uppermost Lutetian – lowermost Bartonian assemblage (Underwood *et al*. 2011).

Physogaleus Cappetta, 1980

Physogaleus sp.

Material: Forty isolated teeth, figured material includes FSAC Bouj–340, 341, 342 and 343.

Description & Remarks: Among the smaller carcharhinids, teeth of *Physogaleus* sp. (Fig. 3A-C) are relatively frequent in both localities. Two coeval species of *Physogaleus* are redundant in the middle Eocene deposits. It concerns the larger *P. secundus* (Winkler 1876) widespread in most middle Eocene deposits of North Atlantic (see Cappetta & Case 2016) and Neotethys, and the smaller *P. tertius* (Winkler 1876) recorded in the same areas (Cappetta 2012). With very tenuous differences, both species may enter in the morphological variability of the other. Our material is well conserved, and teeth appear larger (up to 1.5cm) than those of northern representatives.

Hemipristis AGASSIZ, 1835

Hemipristis curvatus (Dames, 1883)

Material: Five broken isolated teeth, figured material includes FSAC Bouj–343.

Description: An upper tooth (Fig. 4D) belonging to the snuggle tooth shark *Hemipristis curvatus* was recovered from the Locality 1. The crown is compressed labio-lingually, slanted distally with unserrated mesial cutting edge.

Remarks: The snuggle tooth shark, *Hemipristis curvatus* is known in all the tropical seas during the late Eocene, from Western Neotethys (e.g., Case & Cappetta 1990; Mustafa & Zalmout 2002; Underwood *et al*. 2011) to western central Atlantic (e.g., Case & Borodin 2000). Its occurrence in the middle Eocene is less usual (Underwood *et al*. 2011). Only two teeth were recorded in MI (Underwood *et al*. 2011), it becomes common from the GE A–C (around the Bartonian/Priabonian boundary) and within the rest of the BQ (Priabonian).

Abdounia Cappetta, 1980

Abdounia sp.

Material*:* A dozen isolated teeth, figured material includes FSAC Bouj–344.

Description and Remarks*:* Some rare medium-sized shark teeth (Fig. 3E-F) with low or incipient cusplets correspond to a large unnamed *Abdounia* species previously observed in the middle to late Eocene of Egypt (included in *C. frequens* in Case & Cappetta 1990: pl.7, fig. 147; Underwood et al. 2011: fig. 2F). Occasional in MI, this unnamed species becomes common in GE A–C and younger series (Underwood *et al*. 2011).

Carcharhinus Blainville, 1816

Carcharhinus sp.

Material: A dozen isolated teeth, figured material includes FSAC Bouj–345, 346 and 347.

Description and Remarks: some rare medium-sized sharks (Fig. 3G-I) are provisionally attributed to *Carcharhinus* sp. The upper tooth (Fig. 4G) reminds those of *Negaprion* sp. (unserrated cutting edges, main cusp separated from heels by notches) associated with erect and gracile lower teeth (Fig. 3H-I) usually observed in *Carcharhinus,* and especially in Priabonian species *C. frequens* (Dames, 1883). Assignement of middle Eocene carcharhinid teeth to genera *Carcharhinus* or *Negaprion* remains debatable and uncertain (see also Sweydan *et al.*, 2019 for discussion) but its attribution to *Carcharhinus* seemly more appropriate in regard to the dignathic heterodonty. Underwood et al. (2011) only reported a Carcharhinidae nov.gen. with smooth cutting edges in the Middle Eocene MI, which is easily distinguishable from our material. No other medium-sized carcharhinid was collected within the studied area, particularly no representative of the "bull-shark" group among the Requiem sharks (see Adnet *et al*. 2007) that displays upper teeth with a modern morphology (e.g., serrated cutting edges). However, such representative was possibly reported in MI by Underwood *et al*. (2011: *Carcharhinus* sp. 1) but the rare specimens are often poorly preserved and were provisionally referred to taxa only well-identified in Priabonian levels. Underwood & Gunter (2012) illustrated a large and unique upper tooth probably representing one of the oldest evidences of "Bull-shark" from Jamaica (Underwood & Gunter 2012: fig. 2); postulated to have been from the Yellow Limestone Group exposed at Broomwell and dated as middle Eocene. However, the age of this unique evidence in still uncertain and no other middle Eocene record was verified. Uncertainty about the age of *Carcharhinus underwoodi* Samonds *et al*. (2019), the other oldest representative of "Bull-shark" group, is quite similar; being currently reported from middle to late Eocene of Madagascar.The lack of large modern *Carcharhinus* species in Boujdour area seems to indicate an early Bartonian age of the deposits, at least their absence is paleoenvironmentally controlled.

Batoidea Compagno, 1973

Besides the undeterminable broken caudal sting of Myliobatiformes (unfigured), only rostral teeth of two fossil sawfishes (Rhinopristiformes) were identified.

Rhinopristiformes Naylor *et al*. 2012

Pristidae Bonaparte, 1838

Propristis Dames, 1883

Propristis schweinfurthi Dames, 1883

Material: Five rostral denticles, figured material includes FSAC Bouj–348

Description & Remarks: *Propristis schweinfurthi* (Fig. 4J) is a rare but widespread sawfish, and is easily distinguishable from all the other fossil or living Pristidae, *Pristis* cf. *lathami* included, by short and rounded rostral teeth without posterior barbs (Fig. 4J). This species is known in the middle to late Eocene of the Neotethysian realm from Caribbean (Case 1981; Case & Borodin 2000; Cappetta & Stringer 2002) to Egypt (Case & Cappetta 1990; Strougo *et al*. 2007; Underwood *et al*. 2011) and Atlantic coasts (e.g., White 1926; Dartevelle & Casier 1959; Cappetta & Traverse 1988).

Pristis Latham, 1794

Pristis cf. *lathami* Galeotti, 1837

Material*:* A dozen of broken rostral teeth.

Description and Remarks: The second sawfish (unfigured here) is a common worldwide sawfish recovered from many Tethyan middle-late Eocene deposits (Cappetta 2012).

Figure 4

4.2 Actinopterygii Cope, 1887 (Fig 5A-G)

Actinopterygii *incertae sedis*

Cylindracanthus Leidy, 1856

Cylindracanthus sp.

Material: FSAC Bouj-141, 356 (Fig. 5A)**,** 357, 358, 359, 360, 361, 362, fragments of rostra.

Description. The rostra are incomplete and cylindrical. The external surface is crossed by sub-parallel longitudinal ridges, sometimes convergent. The cross-section is circular, with a notched circumference owing to the longitudinal ridges. A unique median canal lies in the center of the cross-section.

Remarks. These remains are very common in Boujdour. The notched circular cross-section showing a canal and the fluted external surface correspond to the rostrum of *Cylindracanthus*. This genus is only known by these peculiar rostra, sometimes showing two rows of minute teeth. They are retrieved in various localities from the Cretaceous to Eocene (and possibly Miocene and Pliocene, see Schultz 1987) in Africa, Asia, Europe, and North and South America (Schultz 1987; Gallo *et al*. 2012; Averianov 2014; Grandstaff *et al*. 2017). Putative isolated vertebrae have also been reported but without anatomical connection with the rostra, (Leriche, 1910; White 1926). The phylogenetic relationships of *Cylindracanthus* are still discussed and affinities with chimaeroids, billfishes, dercetids, acipenseriforms and beloniforms have been proposed (Schultz 1987; Weems 1999; Parris *et al*. 2001; Monsch 2004; Friedman 2012; Bonde & Leal 2017) while Grandstaff *et al*. (2017) excluded structural resemblances with the billfish *Makaira* and the paddlefish *Polyodon* by analysing thin sections. In North Africa, *Cylindracanthus* occurs in the Ypresian beds of the Phosphate basins of Morocco and Algeria (Arambourg 1952; Khalloufi *et al*. 2017), and in the Priabonian beds of Ad-Dakhla (Adnet *et al*. 2010).

Acanthomorpha Rosen, 1973

Perciformes *sensu* Johnson & Patterson, 1993

Gen. sp. indet.

Material: FSAC Bouj-141, 363 (Fig.5C), 364, 365, 366, 367, 368, 369, isolated centra.

Description. The centra are amphicoelous and their height is greater than their anterioposterior length (Figs. 5B-C). The cross-section is circular to slightly ovoid, with distinct growth rings. The surface of the centrum is ornamented by several longitudinal ridges of various sizes, separated by a thinner trabecular structure. In some centra, one or two weakly marked lateral fossae are present. Broken dorsal expansions indicate that neural arches were fused to the centrum. Bouj-363 is slightly different than other centra in having more marked longitudinal ridges of irregular size and orientation, well-marked small lateral pits and an irregularly circular cross-section.

Remarks. Except Bouj-363, all centra show comparable ornamentation and size and probably correspond to the same taxon. The cylindrical shape, higher than long, and the ornamentation, formed by narrow longitudinal ridges of various sizes and trabeculae, is reminiscent of the abdominal centra of various perciforms like serranids, latids or scorpaenids. However, in these families, the ornamentation is formed by ridges of almost the same size, whereas the centra studied herein show an irregular alternation of narrow and larger ridges. Moreover, in latids and serranids the last abdominal centra show more marked lateral fossae (Otero 2004; B.K. pers. obs.). In some Eocene scombrids (e.g., *Scomberomodon*, *Paleocybium*, *Neocybium* and *Sphyraenodus* from Belgium and England), the anteriormost abdominal centra are higher than long, ornamented with longitudinal ridges of irregular size and with reduced or absent lateral fossae (Leriche 1910; Monsch 2004; B.K. pers. obs.). The material from Gueran is considered as undetermined perciforms. Bouj-363 is interpreted as an anterior abdominal vertebra of the same taxon.

Material: FSAC Bouj-370, (Fig. 5D), incomplete basioccipital.

Description. The bone is ornamented by thin ridges. The insertions for the Baudelot's ligament are ovoid and lateroventrally located.

Remarks. The basioccipital supporting the Baudelot's ligament insertions is a feature encountered in many beryciforms and percomorphs (Johnson & Patterson 1993; Patterson & Johnson 1995). The bone shows superficial resemblances in the ornamentation with those of serranids and latids. The insertions for the Baudelot's ligament are located more laterally in latids, and lateroventrally in serranids or *Semlikiichthys* (Otero *et al*. 2008), like in Bouj-370. The size, vermiculated ornamentation and circular articulation for the first vertebrae suggest that the basioccipital and the isolated centra described above belong to the same taxon.

Material: FSAC Bouj-371, (Fig. 5E), incomplete fin spine.

Description. This proximal fragment of fin spine includes articular processes and a proximal portion of the shaft. The shaft is smooth and shows a lentoid cross-section. The anterior surface is dissymmetrical, the right half showing a depression. The posterior surface is crossed by a thin posterior sulcus. The lumen is well-marked but the basal bar, which extends from the two lateral articular processes, is broken. The anterior and posterior articular processes are not very developed, but they were probably smoothed by erosion.

Remarks. Based on the absence of ornamentation and the morphology of the articular processes, the spine Bouj-371 is comparable to unpaired fin spines of extant perciforms, like serranids or latids.

Scombridae Rafinesque, 1815

Gen. sp. indet.

Material. FSAC-Bouj-358 (Fig. 5F), fragment of toothed bone.

Description. The bone supports two subcomplete and four broken teeth, with very reduced interspace. Teeth are labiolingually compressed, with sharp and convex edges and acute apex. The base of the external surface of the tooth shows a small median depression. The pulpar cavity is full. The lingual surface of the bone is smooth. The labial side is concave but less preserved.

Remarks. The tooth morphology and its position in the bone are very similar to scombroid remains found in the Priabonian beds of Ad-Dakhla (Zouhri *et al*. 2017). Comparable teeth are retrieved in the extant *Acanthocybium* ¸and in the fossils *Aramichthys* from the Eocene of Syria and *Scomberodon*, *Neocybium* and *Palaeocybium* from the Eocene of Belgium and England (Leriche 1905, 1910; Signeux 1959; Monsch 2004). Comparable isolated teeth were reported as '*Cybium*' (=*Scomberodon*) *dumonti* from the Ypresian Phosphate basins of Morocco by Arambourg (1952).

Ostariophysi Sagemehl, 1885

Siluriformes Cuvier, 1817

Gen. sp. indet.

Material. FSAC-Bouj-372 (Fig. 5G), proximal fragment of a right pectoral spine.

Description. Only the left part of the proximal portion of the spine is preserved. The cleithral process is short with a thick and smooth external surface. The ornamentation of the base of the shaft is formed by ridges and thin tubercles.

Remarks. The spine is too fragmentary to be attributed to a siluriform family, but the ornamentation pattern of the spine body is reminiscent of ariid pectoral spines.

Figure 5

Testudines Linnaeus, 1758 (Fig. 5)

Cryptodira Cope, 1868

Chelonioidea Oppel, 1811

Cheloniidae Oppel, 1811

Genus and species indeterminata.

Material: FSAC Bouj-109 (Fig. 5H), costal fragment; 352 (Fig. 5I), fragmentary hyoplastral process; 351 (Fig. 5J) fragmenttary hypoplastron; 353 (Fig. 5K) and 354 (Fig. 5L), dermal plate fragments.

Description. FSAC Bouj-109 (Fig. 5H) is a fragment of costal of a large-sized turtle, covered by three scute parts. The thoracic rib is visible, included in the dermal bone, lentoid in cross-section and roundly protruding along the ventral costal face. The direction of the rib and scutes indicate a medial fragment of costal, not far from the neural, covered by two successive vertebrals (medially) and the corresponding pleural scute (laterally). The ornamentation of the plate is formed by irregular dichotomic sulci on a rough and granulous surface, which are features found in the basic ornamentation of Cheloniidae (Lapparent de Broin 2014).

FSAC Bouj-352 (Fig 5I), a fragmentary lateral process of right hyoplastron, and Bouj-351 (Fig. 5J) a subcomplete right hypoplastron, probably belong to the same individual. Both fragments show a granulous surface with protruding elongated polygones and dichotomic sulci, representing ornamentation features known in cheloniids. Digitations of hyoplastral and hypoplastral lateral processes are broken close to their base. However, they are much enveloped in the dermal callosity and seem to have shortly overtaken the callosity border. Between both lateral processes lies an important lateral fontanelle that was originally rectangular or square. The medial part of the hypoplastron, along with its counterpart, indicates a very short and narrow central fontanelle with a triangular posteromedial border, and posteriorly both hypoplatra were close and lacked digitations on their medial border. The main body of the hypoplastron is posteriorly broken anterior to the contact with the xiphiplastron, close to the area of the abdominofemoral sulcus. Anterior to the inguinal notch on the lateral hypoplastral process, an inguinal scute sulcus (i.e. the posterior inframarginal of the complete series that is present in cheloniids) joins the area of the femoroabdominal sulcus medially. The lateral hyo-hypoplastral processes are narrower than the main medial body of each hypoplastron, and consequently the lateral fontanelles are narrower than the main hypoplastral bodies and they are narrower than high. The base of each lateral, hyoplastral and hypoplastral process is also shorter than the length of the lateral fontanelles.

FSAC Bouj-353 (Fig. 5K) and Bouj-354 (Fig. 5L) are fragments of dermal plate which are not located on the shell. Bouj-354 shows a granulous surface, not clearly polygonous, and probably corresponds to the same individual as Bouj-352 (Fig. 5I) and Bouj-351(Fig. 5J). Bouj-353 shows a comparable ornamentation.

Remarks. FSAC Bouj-352 (Fig. 5I), Bouj-351 (Fig. 5J) and possibly Bouj-354 (Fig. 5L) are parts of the same cheloniid individual, being found lying together in one piece (Fig. 5P), which also contained Bouj-350 (Fig. 5M), a dermochelyid remain**.** Bouj-353 (Fig. 5K) was probably collected near this piece and corresponds to the same cheloniid and possibly to the same individual.

The combination of the nearly flat bridge (not an obliquely elevated bridge), surface ornamentation, and fenestration of the plastron matches the cheloniid pattern. Only few middle to late Eocene cheloniids are known from their plastron in the Old World. Among the various cheloniid clades, some cheloniid genera were grouped in the western-European "Eochelyinae Moody, 1968", now considered as a paraphyletic taxon representing an evolutionary grade (Lapparent de Broin *et al.* 2014, 2018). The Gueran species, represented by Bouj-351 and Bouj-352, represents this grade. It differs from the defined species included in the group in the relative proportions of the hyo-hypoplastral main body, in relation to the lateral and central fontanelles. There are several species in the early Eocene of the London Clay basin (Ypresian of the Isle of Sheppey (Kent) and Harwich (Essex) (UK), described by Owen & Bell (1849) and Owen (1849-1884). Boujdour species is similar to "*Chelone breviceps* Owen, 1842" (see Owen & Bell, 1849, pl. 2), i.e. a junior synonym of *Argillochelys antiqua* (König, 1825), in the shape of the quadrangular lateral fontanelles, but it differs in the wider proportions of these lateral fontanelles correlated with a narrower hypoplastral main body, and it differs in the robustness of the plates. However, the central fontanelle was narrow and short in both species. By contrast and as *A. antiqua*, the Gueran species differs from "*Chelone convexa*" (undefined taxon, perhaps a junior synonym of *Argillochelys cuneiceps* (Owen, 1849 *in* Owen & Bell 1849), the shell of which is not defined), *Eochelone brabantica* Dollo, 1903 (Lutetian, middle Eocene of Brabant, Belgium) and *Eochelone voltregana* Lapparent de Broin *et al.*, 2018 (Priabonian of Osona county, Spain) in the much narrower central fontanelle, the main body of each hypoplastron being wider, but it is similar in the quadrangular lateral fontanelle general proportions. And in the robustness of the plastral elements, it is similar to *E. voltregana*. The Gueran species also differs from *Puppigerus camperi* (Gray, 1831) (Ypresian of London Clay and Lutetian of Brabant) in the lateral fontanelle size and shape, this structure being much smaller and triangular in *Puppigerus* adults with much wider hypoplastra, in a much wider plastron as a whole (due to the more developed shell ossification characteristic of this taxon) (Moody 1974; Lapparent de Broin *et al.* 2018).

Dermochelyoidea Fitzinger, 1843

Dermochelyidae Fitzinger, 1843

Gen. et sp. indet.

Material. FSAC Bouj-350 (Fig. 5M), pelvis fragment.

Description. FSAC Bouj-350 (Fig. 5M) is the lateral pubic process of a right pelvis. Its distal extremity is robust and shows an irregularly lentoid epiphysis.

Remarks. The morphology of this elongate process corresponds to that of the pubic process of the extant *Dermochelys*, in which this struture is longer than the median main body of pubis, while the pubic process is shorter and wider at its base in cheloniids. Compared with *Dermochelys*, in Bouj-350 the process is slightly shorter than its basal width, the epiphysis is anterolaterally shorter and the lateroexternal border is slightly curved. The presence of a dermochelyid associated with a cheloniid in Gueran is not strange, since the same association occurs in the Priabonian of Ad-Dakhla (Morocco) and Fayum (Qasr-el-Sagha) (Egypt) (Andrews 1906; Zouhri *et al*. 2017). Scarce remains of these two taxa in the three localities, and absence of preserved pubic processes in Ad-Dakhla and Fayum do not provide further information.

?Pleurodira Cope, 1864

?Podocnemidoidea Cope, 1868

Gen. et sp. indet.

Material. FSAC Bouj-196, fragmentary hypoplastron (Fig. 5N).

Description. FSAC Bouj-196 (Fig. 5N) is a fragment of right hypoplastron, in the inguinal notch corner, and it bears the lateral end of the abdominofemoral sulcus. The surface is rather smooth, bright, not granulous and ornamented by not protruding polygons.

Remarks. The lateral curve of the plate in the inguinal buttress area shows an obliquely elevated bridge. This is not the case in marine cryptodiran turtles: the bridge is flat in Cheloniidae and the plastron is so much reduced that there is no more bridge in Dermochelyidae (Gervais 1872, figs. 7-8). The decoration indicates an aquatic form and probably a pleurodire. In the African context at that time, this specimen ought to be a podocnemidoid turtle (Podocnemididae or Bothremydidae). The position of the femoroabdominal sulcus matches these families. By comparison with turtle distribution at Ad-Dakhla and Fayum localities, it might be a member of the littoral Stereogenyina (Zouhri *et al*. 2017).

Testudines indeterminata

?Podocnemidoidea Cope, 1868

Gen. et sp. indet.

Material. FSAC Bouj-95, **a** fragment of carapace plate.

Description. FSAC Bouj-95 (Fig. 5O) is a fragment of dermal plate of a carapace, covered dorsally by parts of three meeting scutes. A natural border that makes an acute angle for a ventral scute lip is present, but it is not possible to locate and orientate the plate based on this information.

Remarks. The smooth ornamentation of the surface and the presence of a lip preclude assignment to cheloniids. This plate and Bouj-196 might belong to the same pleurodiran taxon.

4.4. Serpentes (Fig 6A-F)

Ophidia Brongniart, 1800 sensu Caldwell & Lee, 1997

Palaeophiidae Lydekker, 1888

Palaeophiinae Lydekker, 1888

Pterosphenus Lucas, 1899

Pterosphenus cf. *schweinfurthi* (Andrews, 1901)

Material: Four vertebrae recovered from the Garouaze Locality in Gueran Depression. Two of the specimens (FSAC Bouj -300 and 317**)** clearly belong to the Palaeophiidae. The two other vertebrae (FSAC Bouj -316 and 318) are very incomplete, but they also likely belong to palaeophiids.

Description. The description is mainly based on FSAC Bouj-317 (Fig. 6A-E) but more information is drawn from FSAC Bouj-300 (Fig. 6F). These vertebrae belong to a large snake. In FSAC Bouj-317, measurements are as follows: centrum length, from the cotyle rim to the tip of condyle = 21.7 mm; horizontal diameter of cotyle = 13.1 mm; zygosphene width = 13.7 mm. FSAC Bouj-300 is larger, but its centrum length cannot be measured; the horizontal diameter of its condyle is approximately 19.9 mm and the width of its zygosphene is 21.6 mm. Both vertebrae are tall, short and compressed laterally. FSAC Bouj-317 preserves incomplete pterapophyses above the postzygapophyses.

In anterior view, FSAC Bouj-317 is clearly compressed laterally, and is very narrow. The cotyle is broad and approximately circular but somewhat truncated dorsally. The size of the preserved prezygapophysis, on the right side, appears much reduced compared to the cotyle. The neural canal is small. The articular facet of the prezygapophysis lies approximately at the level of the floor of the neural canal. The width of the zygosphene is nearly similar to that of the cotyle. The zygosphene is relatively thick and arches dorsally. The top of the zygosphene forms the base of the anterior border of the neural spine. FSAC Bouj -300 differs from FSAC Bouj-317 in being slightly less compressed laterally and in having a markedly thicker zygosphene.

In dorsal view, FSAC Bouj-317 appears narrow and comparatively elongate. The interzygapophyseal constriction is so shallow that it is almost not expressed. The axis of the small prezygapophyseal facet is directed anterolaterally. The anterior border of the zygosphene forms an obtuse notch. The neural spine extends through the whole preserved length of the neural arch; anteriorly, it reaches the anterior border of the zygosphene. FSAC Bouj-300 was likely less narrow and less elongate.

In lateral aspect, the neural spine is long anteroposteriorly; unfortunately, its dorsal part is broken away and its height cannot be estimated. Its anterior border comprises a vertical portion that rises from the zygosphene and a longer, posteriorly inclined dorsal portion. The vertebra does not preserve the tips of both prezygapophyses, so that the length of the latter remains unknown. The anterior edge of the pterapophyses is inclined posterodorsally at an angle of approximately 45°. The interzygapophyseal ridge is very prominent but blunt. The prezygapophyseal buttress forms an anterolateral sharp ridge. Unfortunately, the two paradiapophyses are completely eroded and hypapophyses are not preserved. The axis of the condyle is horizontal. FSAC Bouj-300 only provides one additional information: it bears the basis of a vertical hypapophysis. It is not possible to determine whether or not an anterior hypapophysis was present.

The ventral face of the centrum of FSAC Bouj-317 is narrow and elongate, not limited by subcentral ridges. The sagittal area is damaged. The bases of the paradiapophyses are markedly separated from each other. The ventral face of FSAC Bouj-300 is poorly preserved. However, its sagittal area forms a carina. The hypapophysis originates from the posterior portion of this carina. Apparently, there is no room for an anterior hypapophysis.

The posterior aspect of FSAC Bouj-317 is striking. Above the neural canal, the neural arch is extremely thick and bounded laterally by vertical borders. The dorsolateral parts of the neural arch form the bases of the broken pterapophyses. The posterior face of FSAC Bouj-300 does not display observable characters.

FSAC Bouj-316 and 318 are two centra whose morphology is consistent with those of FSAC Bouj-300 and 317. Although very incomplete, both specimens bear an entirely preserved hypapophysis. In both vertebrae, the short, laterally compressed hypapophysis shows a vertical posterior border that contacts the condyle and a weakly (in FSAC Bouj-318) or strongly (in FSAC Bouj-316) inclined anterior border. It is not possible to determine whether an anterior hypapophysis was present in these two vertebrae.

Comparison and Remarks: The lateral compression, reduced prezygapophyses, prezygapophyseal buttresses forming an anterolateral edge, presence of pterapophyses and horizontal axis of condyle constitute a combination of characters that occur only in Palaeophiidae. In addition, the shortness and height of the vertebrae, as well as low position of the zygapophyseal plane, make it possible to discard the Archaeophiinae and to refer the specimens to the Palaeophiinae (Rage *et al*. 2003).

Two genera, *Palaeophis* and *Pterosphenus*, are assigned to the Palaeophiinae of Palaeophiidae, a family including species of various sizes, slightly adapted to strongly specialized for aquatic life, and widely distributed from America to Asia. The species from Gueran is large and marine, and it was first identified in Fayum (Andrews 1901). The vertebrae of the species referred to these two genera form a morphological cline (Rage 1983a). Compared with the generalized snake vertebrae, *Palaeophis* species have vertebrae displaying the more conservative morphology. In *Pterosphenus*, vertebrae are more laterally compressed, the prezygapophyses are more reduced, and the pterapophyses are taller than in *Palaeophis*. However, in the morphocline, there is a blurred transition between species that may be referred to either *Palaeophis* or *Pterosphenus*; the distinction between the two genera is phenotypic and artificial (Rage 1983a).

Fortunately, the morphology of the vertebrae from Gueran is consistent with that of the more derived species. Consequently, the specimens are assigned to *Pterosphenus*. This assignment based on the degree of lateral compression and height of the vertebrae is confirmed by the continuity between the top of the zygosphene and the anterior border of the neural spine; this feature is known only in *Pterosphenus* (Rage 1983b). This character unquestionably occurs in FSAC Bouj-300 and FSAC Bouj-317 (it cannot be checked in FSAC Bouj-316 and FSAC Bouj-318). The zygosphene of FSAC Bouj-300 is markedly thicker and narrower than that of FSAC Bouj-317, which corresponds to intracolumnar variation. FSAC Bouj-300 is a vertebra from the mid-trunk portion whereas FSAC Bouj-317 comes from the posterior trunk region. The smaller size of FSAC Bouj-317 likely also reflects intracolumnar variation; the anterior and posterior trunk regions of palaeophiids appear to have been slenderer than the mid-trunk portion. FSAC Bouj-300 and 317 likely belong to the same species (but no conclusion can be made about 316 and 318).

Five recognized species belong to *Pterosphenus* (Rage *et al*. 2003; McCartney & Seiffert 2016): *P. schucherti*, the type species, middle (Bartonian and ?Lutetian) and late (Priabonian) Eocene of the U.S.A.; *P. schweinfurthi*, late Eocene (Bartonian) of Libya and late Eocene (Priabonian) of Egypt: note that McCartney & Seiffert (2016) assigned an Eocene/Oligocene age to the fossils from Libya; however, we follow Abouassa *et al*. (2012) who referred the Libyan locality to the late Bartonian. *P. sheppardi*, late Eocene of Ecuador; *P. kutchensis* and *P. biswasi*, both from the lower Eocene (Ypresian) of India. The fact that paradiapophyses are clearly separated from each other and that the anterior border of the neural spine reaches the anterior border of the zygosphene allows to exclude *P. kutchensis*. The morphology of FSAC Bouj-300 and 317 is close to that of *P. biswasi*. However, the latter species differs from FSAC Bouj-300 and 317 in having a less concave anterior border of the zygosphene. Another possible difference is that, on the centrum, the base of each paradiapophysis is less extended dorsoventrally in FSAC Bouj-317 (not observable in FSAC Bouj-300) than in *P. biswasi*. Comparison with *P. sheppardi* is difficult because this species is only represented by five articulated vertebrae. If the vertebrae were articulated, several significant characters would have been concealed. However, the pterapophyses of *P. sheppardi* are smaller and shorter than those of FSAC Bouj-317 (no possible comparison with FSAC Bouj-300). If this difference is not an intracolumnar variation, then it is significant at the species level variations. Distinction between *P. schucherti* and *P. schweinfurthi* is not clear. Specific differences that were put forward are perhaps only intracolumnar variation (Rage *et al*. 2003; Parmley & DeVore 2005; McCartney & Seiffert 2016). *P. schweinfurthi* may be a junior synonym of *P. schucherti* but this cannot be demonstrated. FSAC Bouj-300 and 317 do not show significant differences with the known vertebrae of both *P. schucherti* and *P. schweinfurthi* (Lucas 1899; Janensch 1906; Westgate & Ward, 1981; McCartney & Seiffert 2016). However, in view of the limited material and its incomplete nature and taking into account the uncertainty that remains about the possible synonymization of *P. schweinfurthi* with *P. schucherti*, we assign the material from Gueran to *Pterosphenus* cf. *schweinfurthi*.

It is worth noting that the geographically close locality of Ad-Dakhla yielded some palaeophiid vertebrae. Bedbone 1 from which the palaeophiid fossils in Ad-Dakhla area came from is slightly younger than the fossiliferous level of Gueran. Zouhri *et al*. (2014) assigned a Priabonian age to Bedbone 1. In the vertebrae from Ad-Dakhla, the junction between the anterior borders of the zygosphene and neural spine clearly belongs to the *Pterosphenus* type. In addition, one (unnumbered) incomplete vertebra displays proportions that are similar to those of the known vertebrae of the *P. schweinfurthi- P. schucherti* assemblage and may be referred to *P*. cf. *schweinfurthi*. However, one vertebra from Ad-Dakhla (Dak-349) is less compressed laterally and its proportions resemble those of species belonging to the transition between *Palaeophis* and *Pterosphenus*. It is not possible to state whether Dak-349 belongs to a species distinct from the *P. schweinfurthi- P. schucherti* assemblage or if it represents an intracolumnar variation of the later assemblage that was hitherto unknown. Whatever the case may be, *Pterosphenus* cf. *schweinfurthi* is present in Gueran (Bartonian) as in Ad-Dakhla.

Figure 6.

4.5. Crocodyliformes Hay, 1930 (*sensu* Benton and Clark, 1988) (Fig. 7)

Crocodyliformes indet.

Material. FSAC BOUJ-355, fragment of a right dentary; 406, posterior fragment of left mandibular ramus.

Description. FSAC BOUJ-355 is a fragment of a left dentary (Fig. 7I). The best preserved alveolus is large and seems slightly compressed lateromedially. The lateral and medial margins of the dentary are parallel, suggesting that it was included in a long mandibular symphysis, and that the specimen was a longirostrine form. The alveolar margins are slightly offset, and the symphysis was slightly wider than high.

FSAC Bouj-406 is a posterior portion of a left dentary (Fig. 7J), and preserves four circular alveoli, probably the posteriormost. The portion is low in lateral view. It is not possible to determine if it can be related to the one of the species described above and below.

Eusuchia Huxley, 1875 (*sensu* Brochu, 2003)

Eusuchia indet.

Material. FSAC Bouj-410, could be the (?) ninth cervical vertebra; FSAC Bouj-1b, anterior? cervical vertebra; 400, posterior dorsal vertebra; 1a, first caudal vertebra; 124, caudal vertebra; 96, two fragments of large dorsal osteoderms; 94, fragment of osteoderm.

Description. Numerous postcranial remains have been found in Gueran. These include five procoelous vertebrae and several fragments of osteoderms. FSAC Bouj-410 is a posterior cervical vertebra (Fig. 7A). It bears a long hypapophysis, and the location of the diapophysis and parapophysis suggests that it could be the ninth cervical vertebra. Bouj-1b is a more anterior cervical (Fig. 7B), but it is not possible to determine its exact location in the vertebral column. FSAC Bouj-400 is an isolated procoelous centrum lacking most of the neural arch (Fig. 7C). The transverse process is high on the centrum, which indicates that it is a dorsal vertebra. A first caudal vertebra with a biconvex centrum is preserved (Fig. 7D). The osteoderm fragments have their dorsal surfaces densely ornamented with deep pits (Fig. 7F-H). Bouj-96 is a fragment of large and thick osteoderm with a smooth anterior articular surface.

Gavialoidea Hay, 1930

Gavialoidea indet.

Material. FSACBouj-401, 403 and 404, anterior and posterior portion of left maxilla; 407, posterior portion of a left maxilla; 402, mid-portion of a right maxilla. All these specimens are from the same individual. Also 405, portion of a left dentary.

Description. The reconstruction of the maxillae shows a slender snouted form with 16 preserved teeth but more teeth were probably present (Fig. 7L-N). The snout is wider than highand the palate is lower than the tooth row, so that the tooth row is underlined. The diameter of the alveoli is nearly constant along the tooth row and the interalveolus distances are equal or slightly longer than the alveolus diameter. The lateral margin of the maxilla is marked with shallow grooves visible in dorsal view for the occlusion of dentary teeth. FSAC Bouj-405 consists of a left portion of dentary, (Fig. 7K). Its lateral margin is marked by deep natural notches that indicate occlusal grooves for the maxillary teeth. The mandible was more than twice wider than high, and the symphysis was probably very long. Its morphology suggests than it is probably from the same species as the maxillary fragments. FSAC Bouj-407 is a fragment of the posterior portion of the left maxilla and with two complete teeth.

Teeth are preserved. They are moderately long, circular in cross section (posteriormost being slightly compressed lateromedially) and their surfaces are smooth and bear anterior and posterior carinae.

Comparison and Discussion. All recovered vertebrae are procoelous, suggesting eusuchian affinity. The material belongs to at least two species, and both are longirostrine forms. FSAC Bouj-355 has a different morphology from other mandibular and maxillary fragments (Fig. 7I). It has large alveoli and its symphysis is slightly wider than high. The second form, represented by maxillae and portions of left and right dentaries (Fig. 7 K-P), has its symphysis much wider than high with smaller alveoli than the first species. Two groups of longirostrine eusuchians have been described from the late Eocene: the gavialoids and the tomistomines (Brochu 2003). FSAC Bouj-355 is too fragmentary to be attributed with certainty to any group, but its symphysis slightly wider than high with a straight lateral margin, the short distance between the left and right alveoli and their offset margins clearly differs from what is found in gavialoids and tomistomines. Even if no amphycoelous vertebra has been found, it cannot be excluded that this mandible pertains to a dyrosaurid, a group of non-eusuchian crocodyliformes, in which previously cited characters are present (Jouve *et al*. 2019). These neosuchians survived to the Lutetian in Africa and Burma (Buffetaut 1978). Awaiting more diagnostic material, FSAC Bouj-355 is thus considered as Crocodyliformes indet. The second mandible has laterally opened alveoli and its alveolar margin is not leveled with the palate, characters that are found in gavialoids (Hua & Jouve 2004; Jouve *et al*. 2006, 2014). Gavialoids are particularly scarce in the Eocene and Oligocene of the Peri-Tethys deposits, and only three gavialoids are known: "*Gavialis*" *dixoni* Owen, 1849, from the early-middle Eocene of England and now considered as a *nomen dubium* (Brochu 2007), unidentified Bartonian gavialoid remains from Dur-El-Talha (Southern Libya) (Llinas Agrasar 2004), and *Eogavialis africanum* (Andrews, 1901) from the Priabonian and Rupelian of Fayum Egypt, (Müller 1927). The remains from Gueran strongly resemble *Eogavialis africanum*, but they are too poorly preserved for an in-depth comparison. Therefore, the Gueran gavialoid is here considered as Gavialoidea indet. (Jouve *et al.* 2019).

Figure 7

4.6. Aves (Fig. 6 G–K)

Odontopterygiformes Howard, 1957

Pelagornithidae Fürbringer, 1888

Pelagornis Lartet, 1857

Pelagornis sp.

Material: FSAC Bouj-373, distal portion of maxillary rostrum bearing pseudo-teeth (two fragments).

Measurements in mm (pseudo-teeth are numbered consecutively from the most proximal to the most distal). Preserved length of proximal portion of maxillary rostrum = 163.0; preserved length of distal portion of maxillary rostrum = 86.0; minimum length of maxillary rostrum anterior to narial openings = 243.0; length between transverse furrow and tip of maxillary rostrum = 44.0; distance between rostral end of longitudinal sulcus (left side) and tip of maxillary rostrum = 19.2; distance between distalmost rank 1 pseudo-tooth (PT6) and tip of maxillary rostrum = 32.6; length between TPT2 (left side) and tip of maxillary rostrum = 14.0; height of maxillary rostrum (apex to culmen) at the level of PT6 = 23.4; maximal width of bill tip = 18.6; PT1, anteroposterior length at base = 6.0; PT1, height = 4.5; PT2, anteroposterior length at base = 3.7; PT2, height = 1.3; PT4, anteroposterior length at base = 13.6; PT4, height = 10.6; PT6, anteroposterior length at base = 10.3; PT6, height = 8.8; TPT1, anteroposterior length at base = 4.2; TPT1, height = 2.4; distance between PT1 and PT4 = 47.4; distance between PT1 and PT2 = 19.2; distance between PT2 and PT3 = 12.2; distance between PT3 and PT4 = 16.0; distance between PT5 and PT6 = 10.7; distance between PT6 and TPT1 = 10.2.

Description. Anatomical terminology follows Baumel and Witmer (1993), with English equivalents of the Latin nomenclature. FSAC Bouj-373 consists of two fragments of maxillary rostrum that are almost contiguous (Fig. 6G-K). The posterior fragment consists of a large portion of maxillary rostrum located anterior to the narial openings (Fig. 6G, K). It is mediolaterally crushed and only preserves part of the right side of the maxillary rostrum. The poorly distorted anterior fragment mainly preserves the right side of the maxillary rostrum and the tip of the beak (Fig. 6H-J).

As in other pseudo-toothed birds (Pelagornithidae), spike-like projections called pseudo-teeth are present along the tomial crest of the beak (Louchart *et al*. 2018). The tips of preserved pseudo-teeth are eroded. In spite of the bad preservation, pseudo-teeth seem to be arranged in a regular pattern similar to that found in other species of *Pelagornis* (Howard 1957; Stidham 2004; Mourer-Chauviré & Geraads 2008; Mayr & Rubilar-Rogers 2010; Ksepka 2014), with large rank 1 pseudo-teeth being separated by three smaller ones, the central rank 2 pseudo-tooth being larger than the adjacent rank 3 pseudo-teeth. In addition, rudimentary rank 4 pseudo-teeth occur in the middle of the space between rank 3 and rank 1-2 pseudo-teeth. In the Gueran specimen, the right tomial crest of the posterior fragment preserves four pseudo-teeth (Fig. 6G), including one medium-sized pseudo-tooth (PT1, rank 2) and one large pseudo-tooth (PT4, rank 1). A small pseudo-tooth (PT2, rank 3) and a tiny knob-like pseudo-tooth (PT3, rank 4) are located in the space between the larger pseudo-teeth (PT1 and PT4). The anterior portion of the maxillary rostrum preserves two pseudo-teeth on the right side (Fig. 6H), including one rudimentary knob-like pseudo-tooth (PT5, rank 4) and one large pseudo-tooth (PT6, rank 1). Rank 1 to rank 3 pseudo-teeth are conical in shape and stand vertically. On the left side (Fig. 6J), two tomial pseudo-teeth (TT1 and TT2) are located between the anterior tip of the rostrum and the first rank 1 pseudo-tooth. These tomial pseudo-teeth are sub-equal in size and more rounded than the other pseudo-teeth. Only one tomial pseudo-tooth (TT1) is preserved on the right side, the anterior one (TT2) being broken.

Neurovascular foramina are visible on the bone surface. As in other pseudo-toothed birds, the lateral surface of the maxillary rostrum exhibits a deep longitudinal sulcus (Fig. 6G, H), which roughly parallels the culmen just above mid-height of the maxillary rostrum, and curves down at the level of the first rank 1 pseudo-tooth. The anterior end of the longitudinal sulcus lies between the two tomial pseudo-teeth. The anterior tip of the bill is downturned and broadly rounded. It is set apart from the rest of the maxillary rostrum by a transverse furrow (Fig. 6H), which is positioned just posterior to the first large pseudo-tooth, as in other species of *Pelagornis* (Stidham 2004; Mayr & Rubilar-Rogers 2010; Ksepka 2014; Solórzano & Rincón 2015). The transverse furrow was originally complete across the dorsal surface of the rostrum. However, the specimen only preserves the right side of this structure. The transverse furrow turns anteroventrally near the point where it joins the longitudinal sulcus. As in other pseudo-toothed birds, the ventral surface of the maxillary rostrum bears two longitudinal sulci for reception of mandibular tomial crests and deep fossae for reception of mandibular pseudo-teeth (Fig. 6I). A palatal ridge runs along the midline of the ventral surface and extends to the anterior tip of the beak. This palatal ridge is strongly convex and devoid of median sulcus, as in several fossils referable to *Pelagornis* (Spulski 1910; Mayr & Rubilar-Rogers 2010; Solórzano & Rincón 2015).

The pseudo-toothed birds (Pelagornithidae) are an extinct group of large seabirds that included gigantic forms with wingspans above 5 m (Mayr & Rubilar-Rogers 2010; Ksepka 2014). Phylogenetic studies have shown that these highly specialized soaring birds are not part of the neoavian radiation (Bourdon 2005; Mayr 2011). Pelagornithids had a worldwide distribution and occur in late Paleocene to late Pliocene marine deposits (Harrison 1985; Averianov *et al.* 1991; Mourer-Chauviré & Geraads 2008; Bourdon *et al.* 2010; Mayr & Rubilar-Rogers 2010; Boessenecker & Smith 2011; Fitzgerald e*t al*. 2012; Cenizo *et al.* 2015). Pseudo-toothed birds have an extensive stratigraphic range in Africa. Abundant pelagornithid remains assigned to the genus *Dasornis* Owen, 1870 are known from the late Paleocene (Thanetian) - early Eocene (Ypresian) phosphate deposits of the Oulad Abdoun Basin in Morocco (Bourdon *et al.* 2010). A sternum assigned to *Gigantornis* Andrews, 1916 is known from the middle Eocene (Lutetian) Ameki Formation of Nigeria (Andrews 1916). Fragmentary wing bones tentatively assigned to *Gigantornis* have been described from the middle Eocene (Lutetian) deposits of Kpogamé-Hahotoé, Togo (Bourdon & Cappetta 2012). Indeterminate mandibular remains of pseudo-toothed birds are known from the Late Eocene (Priabonian) deposits of the Samlat Formation in Morocco (Zouhri *et al.* 2017). Cranial and postcranial remains assigned to *Pelagornis* Lartet, 1857 have been discovered in the late Pliocene deposits of Ahl Al Oughlam, Morocco (Mourer-Chauviré & Geraads 2008).

The Gueran specimen exhibits several diagnostic features of the Pelagornithidae: tomial crest bearing pseudo-teeth arranged in a regular pattern; presence of longitudinal sulcus on the lateral surface of the maxillary rostrum; ventral surface of maxillary rostrum bearing deep fossae for reception of mandibular pseudo-teeth and median palatal ridge (e.g., Bourdon *et al*. 2010; Mayr & Rubilar-Rogers 2010; Mayr & Zvonok 2012; Cenizo *et al*. 2015; Solórzano & Rincón 2015). The partial rostrum described here is from the upper middle Eocene (Bartonian), and constitute the second oldest record of the pseudo-toothed birds in North Africa.

The first appearance of *Pelagornis* comes from the late Oligocene of North America (Mayr *et al*. 2013; Ksepka 2014), and its latest record is in the late Pliocene of North America and Africa (Mourer-Chauviré & Geraads 2008; Boessenecker & Smith 2011). With the exception of Antarctica, *Pelagornis* achieved a global distribution during the Neogene (Lartet 1857; Howard & Warter 1969; Olson 1985; Ono 1989; Matsuoka *et al*. 1998; Stidham 2004; Mourer-Chauviré & Geraads 2008; Mayr & Rubilar-Rogers 2010; Boessenecker & Smith 2011; Fitzgerald *et al*. 2012; Mayr *et al*. 2013; Solórzano & Rincón 2015).

The taxonomic assignment of the Gueran specimen to *Pelagornis* is based on the presence of a transverse furrow positioned just posterior to the first large pseudo-tooth, which is a diagnostic feature of the genus (Mayr & Rubilar-Rogers 2010). Such a transverse furrow is absent in the late Paleocene / early Eocene *Dasornis toliapicus* (Bourdon *et al*. 2010) and in the middle Eocene *Lutetodontopteryx tethyensis* (Mayr & Zvonok 2012). In addition, in FSAC Bouj-373, several features including pseudo-tooth pattern, presence of tomial pseudo-teeth, down-curved bill and convex median palatal ridge, match well with species of *Pelagornis* (Stidham 2004; Mourer-Chauviré & Geraads 2008; Mayr & Rubilar-Rogers 2010; Spulski 1910; Ksepka 2014; Solórzano & Rincón 2015). The earliest ascertained record of the genus *Pelagornis* is late Oligocene (Chattian) in age (Ksepka 2014). The specimen from

Gueran is upper middle Eocene (Bartonian) in age and extends the fossil record of *Pelagornis* back by at least 10 million years.

The anterior hook of the beak is longer in FSAC Bouj-373 than in *Pelagornis orri* (Howard 1957; Stidham 2004) and *Pelagornis sandersi* (Ksepka 2014). Moreover, the presence of two tomial pseudo-teeth on either side of the anterior end of the longitudinal sulcus is similar to the condition found in *P. orri* (Stidham 2004) and *Pelagornis chilensis* (Mayr & Rubilar-Rogers 2010). In contrast, in *P. sandersi*, there is only one tomial pseudo-tooth between the tip of the beak and the first large pseudo-tooth (Ksepka 2014). However, the fragmentary nature of FSAC Bouj-373 precludes assignment to the species level.

4.7 Proboscidea Illiger, 1811 (Fig. 8)

Barytherioidea Andrews, 1906

Barytheriidae Andrews, 1906

***Barytherium* Andrews, 1901**

?*Barytherium* sp.

Material: FSAC Bouj-380a, 380b, and 380c, dental fragments.

Zouhri *et al*. (2018) mentioned fragmentary dental remains of undetermined proboscideans in Gueran fauna (Laazri locality). Combining light and SEM microscopy, we here studied these dental fragments (FSAC Bouj-380a, 380b, and 380c) to describe the enamel microstructure and propose a systematic assignment. Following the protocol detailed in Tabuce *et al*. (2017), we realized and analyzed a vertical section for the three specimens, which reveal a similar enamel microstructure. From the enamel dentine junction (EDJ) to the outer enamel surface (OES), the specimens present a one-layered Schmelzmuster [‘enamel pattern,’ the spatial distribution of enamel prisms and prism types within the enamel covering a tooth crown surface (Koenigswald & Sander, 1997)] formed by thick bundles of prisms that decussate in all directions; this enamel type is the so-called 3D enamel, a structure known only in proboscideans. In some zones of the outer part of the enamel layer, the vertical component of the decussation is attenuated, evoking Hunter-Schreger bands (HSB).

Three-dimensional enamel is documented in several Paleogene proboscidean species: *Numidotherium koholense* (sampled from the early Eocene of El Kohol, Algeria, Bertrand 1988 and Tabuce *et al*. 2007), *Numidotherium* sp. (sampled from the late Eocene of Ad-Dakhla, Morocco, Adnet et al. 2010), *Arcanotherium savagei* (sampled from the ?late Eocene of Dur At-Talah Escarpment, Libya, Tabuce *et al*. 2007), *Barytherium grave* (sampled from Dur At-Talah Escarpment, Libya, Bertrand 1988), and *Omanitherium dhofarensis* (sampled from the earliest Oligocene of Thaytiniti 2, Oman; Tabuce unpublished data).

Among these five species, only *Arcanotherium savagei* differs from the proboscidean from Laazri by a three-layered Schmelzmuster with 3D enamel only limited to the inner zone, overlain by HSB then radial enamel in the outer zone. Such a complex Schmelzmuster also characterizes all Neogene elephantoids (mammutids, gomphotheres, stegodonts, and elephants) and in a lesser degree *Palaeomastodon beadnelli* which developed slightly irregular HSB in the inner zone, evoking 3D enamel (Koenigswald *et al*. 1993). As a result, similar to the proboscidean from Laazri, only *Numidotherium koholense*, *Numidotherium* sp. from Ad-Dakhla, *Barytherium grave*, and *Omanitherium dhofarensis* present a one-layered Schmelzmuster formed by 3D enamel.

In addition, the HSB-like structures that occur in places in the outer part of the enamel the proboscidean from Laazri were only mentioned in *Numidotherium koholense* and *Numidotherium* sp. from Ad-Dakhla (Tabuce 2007, Adnet *et al*. 2010). However, the supposed lack of such HSB-like structures in *Barytheriumgrave* must be taken with caution due to the unique published macroscopic analysis (no SEM data available) for this species (Bertrand 1988). Interestingly, in his unpublished Ph.D. thesis, Bertrand (1989 plate 18D) figured a view of the outer part of the enamel of *Barytheriumgrave* in which HSB-like structures are clearly visible. To conclude, *Barytherium* and *Numidotherium* present the same enamel microstructure as the proboscidean from Laazri.

To complete the observations, we measured the molar enamel thickness in *Barytherium*, *Numidotherium*, and *Omanitherium*. Comparison with the proboscidean remains from Laazri reveals interesting results. The great enamel thickness of FSAC Bouj-380a (±3.4 to 4.6mm), Bouj-380b (±2.6 to 2.9 mm) and Bouj-380c (±3.1 to 4.2 mm) approaches the rare available data for *Barytherium grave* (±2 mm, ±3.1 mm, ±2.5 mm; plate 18A-C in Bertrand 1989). Conversely, molars of *Numidotherium* sp. from Ad-Dakhla and *Omanitherium dhofarensis* have thinner enamel thickness (±1 mm and ±0.7 mm, respectively). Molars of *Numidotherium koholense* have also thinner enamel thickness (± 2.4 to 3.1 mm for the M3, the largest molar).

To conclude, enamel microstructure and thickness strongly favor an assignment to *Barytherium* for the proboscidean from Laazri. The presence of *Barytherium* in the Aridal Formationat of Gueran, if confirmed, this would indicate that this genus occurred as early as the Bartonian. So far, this genus was only known by its type species, *Barytherium grave,* originally described from the late Eocene (Priabonian) of the Fayum depression and then from the Dur At-Talah Escarpment, a locality which is still poorly constrained in age between Bartonian to Priabonian (Tabuce *et al*. 2012; Sallam & Seiffert 2016; Longrich 2017). Interestingly also, Gingerich & Cappetta (2014) mentioned a possible *Barytherium*-sized proboscidean from the early middle (Lutetian) of Togo.

Figure 8

5. Results

5.1 Gueran fauna (Tabl. 1)

The Gueran fauna is composed of selachians, actinopterygians, turtles, palaeophiid snakes, crocodylians and pelagornithid seabirds, and mammals including archaeocete whales and proboscideans, (sirenians are not represented).

The Gueran selachian fauna consists of twelve fossil species (cf.Tabl. 1) belonging to Lamniformes, Carcharhiniformes and Rhinopristiformes. Its shows great similarity to the selachian faunas of the Midawara Formation, Wadi el Rayan, of Egypt.

The actinopterygian fauna is only known from fragmentary or isolated remains belonging to at least three or four forms referred to perciforms (including scombrids), siluriforms and the genus *Cylindracanthus* sp. These taxa are common in African and European Eocene-Oligocene localities

The two marine families of the Gueran tutles, the cheloniid and the dermochelyid, have a wide distribution, being Laurasiatic in origin. Similar turtle elements are represented in African localities: Cheloniidae and Dermochelyidae in the Priabonian of Morocco (Ad-Dakhla, Zouhri *et al*. 2017) and of Egypt (Fayum, Qasr-el-Sagha, Andrews 1906) and a dermochelyid is known from the Eocene of Ombialla District, Nigeria (Andrews 1920). The indeterminate taxon is very probably a pleurodiran littoral form, representing the Gondwanan element of the faunas, i.e. a Seteogenyina as known in Ad Dakhla, Fayum, and also as represented at Dur-Al-Talhah (upper Eocene of Libya) by undescribed material (MNHNF. 1952, Lefranc collection).

The Nigerian dermochelyid form, based on epithecal shell plates, is different from those known from Ad-Dakhla and Fayum. The Gueran material, based on an appendicular pubic bone, and the Fayum form being known by a humerus and plates, decisive comparisons are not possible. The Gueran cheloniid carapace element does not allow recognizing cheloniid forms of the Fayum and of Moroccan Phosphate and Tunisian phosphate basins (Ypresian). In these localities, the cheloniid group is represented by skulls and not by carapaces (Bardet *et al*. 2017). At least it is possible, among all the cheloniid groups, to relate the Gueran cheloniid to the taxa of the cheloniid taxa of Anglo-Franco-Belgian Basin Eocene (Ypresian-Priabonian), which were previously united in the “Eochelyinae subfamily” (Moody 1968, 1974) and which follow their evolution in the extant cheloniids (Lapparent de Broin *et al*. 2018).

The hypothetical possible pleurodiran element ought to be a possible littoral element belonging to the *Shweboemys* subgroup of Stereogenyina, known in Ad-Dakhla and Fayum (Qasr-el-Sagha) and possibly as early as the Lutetian of Europe and Somalia (Zouhri *et al*. 2017; Lapparent de Broin *et al*. 2018). It is not complete enough to be usefully compared with the poorly defined Paleogene Pelomedusoides of the Ouarzazate basin (Thanetian) at Ilimzi and Adrar Mgorn 1 in Morocco (Gheerbrant *et al*. 2017). Nothing allows attributing it to Bothremydidae, the only pleurodira present in marine Moroccan and Tunisian phosphates. No continental (terrestrial or freshwater) turtle element is preserved in Gueran, contrary to the mixed terrestrial-marine faunas of Priabonian of Ad-Dakhla and Fayum (Birket-el-Qurun) where the fauna is mixed, terrestrial-marine, and also contrary to the more continental Paleogene Ouarzazate basin fauna (Gheerbrant *et al*. 2017).

As preserved, the Gueran turtle fauna appears as open marine and littoral, for which there are no frontiers: the forms might have followed the African Eocene coasts without problem, the Atlantic opening on the Tethys having also given way from Europe to Africa, America and Asia. Gueran is however important, showing a new and rare step in this faunistic progression around the northern African coast through time.

Sharing the same habitats of turtles, the Bartonian snakes of Gueran are marine dewellers. Unlike the Ouarzazate basin (Thanetian Adrar Mgorn 1, and Ypresian N'Tagourt 2) where the known snakes are continental (Gheerbrant *et al*. 2017). The only Gueran snake identified down to the species level is *Pterosphenus* cf. *P. schweinfurthi*, also known in Ad-Dakhla, Dur At-Talah and Fayum (Zouhri *et al*. 2017).This is a condition where contemporaneous marine shore-face and adjacent continental habitas are inhabited with a wide range of vertebrate fauna. In Moroccan marine phosphates, the family is represented by one other marine large form of the same family, *Palaeophis maghrebianus* of Arambourg (1952) in the Ypresian level. The Eocene *Pterosphenus* genus has a wide paleogeographical repartition from Ecuador to Uzbekistan and India, including the Eocene of North America but the Gueran species is only known from Africa, showing the similarity between the African localities. *Pterosphenus* lived in marine, brackish, and fresh-water areas close to the coasts (Rage *et al*. 2003; Houssaye *et al*. 2013; Zouhri *et al*. 2017), and in its spread around African coasts, the Bartonian-Priabonian *P*. cf. *schweinfurthi* accompanied other marine vertebrates of Gueran such as marine turtles.

The Crocodyliforms preserved in Gueran consist of at least two longirostrine species. One is too fragmentary to be more precisely identified with certainty than Crocodyliformes indet., but the second is clearly a gavialoid. Gavialoids are particularly scarce in the Peri-Tethys area during the Eocene–Oligocene epoch, found in North Africa such as in Libya (Barthonian, Dur-El-Talha), and Egypt (Priabonian-Rupelian, Fayum). Although the remains from Gueran are poor, their similarities with *Eogavialis africanum* from Egypt are interesting, compared with its geographical location, as gavialoids seem to reach South America during the late Eocene to Oligocene (Salas-Gismondi *et al*. 2016). Moreover, older species of gavialoids are also present in Morocco with the Maastrichtian *Ocepesuchus eoafricanus* of Jouve et al. (2008), and the Danian *Argochampsa krebsi* Hua and Jouve, 2004, both from the Oulad Abdoun Basin. The presence of a late Eocene gavialoid on the African Atlantic coast bearing affinities with a more western form could be pivotal for the interpretation of the gavialoid dispersal to South America, but more complete material is required to clearly state the phylogenetic relationships of this species with both South American and African forms.

Two morphotypes are recognized within the Pelagornithidae (Bourdon *et al*. 2010). The first morphotype corresponds to the genus *Dasornis*, which includes small, medium-sized and large birds showing plesiomorphic skeletal morphology (Bourdon *et al*. 2010). *Dasornis* is restricted to late Paleocene/early Eocene deposits of Morocco (Bourdon *et al*. 2010) and early Eocene deposits of England (Harrison & Walker 1976; Mayr 2008). In contrast, the widespread genus *Pelagornis* includes only gigantic forms that were exceedingly specialized for soaring flight (e.g., Lartet 1857; Howard 1957; Mourer-Chauviré & Geraads 2008; Mayr & Rubilar-Rogers 2010; Boessenecker & Smith 2011; Ksepka 2014; Solórzano & Rincón 2015). With a skull length of 569 mm and an estimated humeral length of 940 mm, the holotype of *P. sandersi* provides evidence for a wingspan over 6 m, representing the largest wingspan among birds (Ksepka 2014). With a skull length of 450 mm and a humeral length of 821 mm, the smaller species *P. chilensis* had a wingspan over 5 m (Mayr & Rubilar-Rogers 2010). The specimen from Gueran lacks postcranial elements that would make it possible to estimate precisely its wingspan. However, in FSAC Bouj-373, the distance between the transverse furrow and the anterior tip of the maxillary rostrum is 44 mm. This distance is estimated to 45 mm in

P. sandersi and 40 mm that of *P. chilensis* (Solórzano & Rincón 2015).Moreover, the estimated length of maxillary rostrum anterior to narial openings is 220 mm for *P. chilensis* (estimation based on Mayr & Rubilar-Rogers 2010: fig. 1). In the Gueran specimen, the minimum length of the maxillary rostrum anterior to narial openings is 243 mm, which is larger than in *P. chilensis*. Based on these measurements, we suggest that the Gueran specimen belonged to a gigantic pseudo-toothed bird with an estimated wingspan between 5 and 6 m. The Gueran specimen provides evidence that the *Pelagornis* morphotype appears in the fossil record more than 10 million years earlier than previously thought. It also indicates that giant species of *Pelagornis* (present study) and less specialized pelagornithids (e.g., Mayr & Smith 2010; Bourdon & Cappetta 2012; Mayr & Zvonok 2012; Cenizo *et al*. 2015) coexisted during the middle Eocene.

?*Barytherium* sp.evokes *Barytherium grave* of Andrews (1901), a species originally described from the Priabonian of the Fayum depression and then from the Dur At-Talah escarpment, a locality which is poorly constrained in age between Bartonian to Priabonian.

Archaeocete whales were previously studied (Gingerich & Zouhri 2010, cf. Table 1) and the whole fauna was reported briefly in Zouhri *et al*. (2018). The Gueran fauna is interesting in having a combination of protocetid and basilosaurid species.

Table 1. Faunal list of the vertebrate taxa the Aridal Formation from Sabkha of Gueran locality, Bartonian, Sahara Desert, Morocco.

Elasmobranchii Bonaparte, 1838

Lamniformes:

- Lamnidae
  - *Macrorhizodus praecursor* (Leriche, 1905)
  - *Otodus*(*Carcharocles*) cf. *sokolowi* (Jaekel, 1895)
  - *Otodus* (*Carcharocles*) sp.
  - *'Carcharias' koerti* (Stromer, 1910)
- Odontaspididae
- *Tethylamna* cf. *twiggsensis* (Case, 1981)

Carcharhiniformes:

- Carcharhinidae
  - *Galeocerdo* cf. *eaglesomi* (White, 1955)
  - *Physogaleus* sp.
  - *Hemipristis curvatus* (Dames, 1883)
  - *Abdounia* sp.
  - Cf. *Carcharhinus* sp.

Rhinopristiformes:

- Pristidae
  - *Propristis schweinfurthi* (Dames, 1883)
  - *Pristis* cf. *lathami* (Galeotti, 1837)

Actinopterygii Cope, 1887

Cylindracanthus sp.

Acanthomorpha Rosen, 1973

Perciformes *sensu* Johnson & Patterson, 1993

Gen. et sp. indet.

Scombridae Rafinesque, 1815

Gen. et sp. indet.

Siluriformes Cuvier, 1817

Gen. et sp. indet.

Sauropsida Huxley, 1864

Testudines Linnæus, 1758

Cryptodira Cope, 1868

Chelonioidea Oppel, 1811

Cheloniidae Oppel, 1811

Gen.et sp. indet.

Dermochelyoidea Fitzinger, 1843

Dermochelyidae Fitzinger, 1843

Gen. et sp. indet.

?Pleurodira Cope, 1864

?Podocnemidoidea Cope, 1868

Gen. et sp. indet.

Indeterminata

?Podocnemidoidea Cope, 1868

Gen. et sp. indet.

Testudines Linnaeus, 1758

Cryptodira Cope, 1868

Chelonioidea Oppel, 1811

Cheloniidae Oppel, 1811

Gen.et sp. indet.

Dermochelyoidea Fitzinger, 1843

Dermochelyidae Fitzinger, 1843

Gen. et sp. indet.

?Pleurodira Cope, 1864

?Podocnemidoidea Cope, 1868

Gen. et sp. indet.

Indeterminata

?Podocnemidoidea Cope, 1868

Gen. et sp. indet.

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

Crocodyliformes indet.

Eusuchia Huxley, 1875 (*sensu* Brochu, 2003)

Gavialoidea Hay 1930 (*sensu* Brochu, 2003)

Gen. and sp. indet.

Eusuchia indet.

Squamata Oppel, 1811

Ophidia Brongniart, 1800 sensu Caldwell & Lee, 1997

Palaeophiidae Lydekker, 1888

Pterosphenus cf. *schweinfurthi* (Andrews, 1901)

Palaeophiidae indet.

Aves Linnaeus, 1758

Odontopterygiformes Howard, 1957

Pelagornithidae Fürbringer, 1888

Pelagornis sp.

Mammalia Linnaeus, 1758

Cetacea Brisson, 1762

Archaeoceti Flower, 1883

Protocetidae Stromer, 1908

Protocetid species A (small)

Protocetid species B (medium)

Pappocetus lugardi Andrews, 1920

Basilosauridae Cope, 1868

Chrysocetus fouadassii Gingerich & Zouhri, 2015

Platyosphys aithai Gingerich & Zouhri, 2015

Eocetus schweinfurthi (Fraas, 1904)

Proboscidea Illiger, 1811

Barytheriidae Andrews, 1906

Barytherium Andrews, 1901

?*Barytherium* sp.

5.2 Precision on the age of Gueran fauna

After the Samlat Formation of Ad-Dakhla, the Aridal Formation of Gueran is the second formation in the Moroccan Sahara to produce Eocene vertebrate remains. Slightly older faunas from the Paleocene-Eocene transition to Lutetian are known farther to the north in the Oulad Abdoun phosphate basinand in the Ouarzazate basin.

A Bartonian age was assigned to the Gueran fauna based on the mixed assemblage of protocetid and basilosaurid archaeocetes, which characterise this period (Gingerich & Zouhri 2015). This age was reinforced by the assemblage of selacians of Gueran, which is partially similar to that of the Midawara Formation of Egypt dated to late Lutetian according to Strougo *et al.* (2008).

The Gueran fauna would be slightly older than those from Bonebeds 1 and 2 of Unit 2 of the stratigraphic section of the Gueran Member of the Samlat Formation at the locality of Garitas south of Ad-Dakhla. On the other hand, Gueran could be the same Bartonian age as the lower fossileferous level A1 about 40 m below B1 in the sequence at Garitas that yielded remains of a small protocetid and tooth and bone of the large protocetid *Pappocetus lugardi* (Gingerich & Zouhri 2017).

6. Conclusions

The Moroccan Sahara is a key region for studying Eocene-Oligocene marine faunas. It is similar in importance to the Indo-Pakistan subcontinent, to Wadi Al-Hitan and Wadi El-Rayyan in Egypt, and to Dur-Al-Talah in Libya as shown by numerous discoveries of middle to upper Eocene marine vertebrate remains in this area (Adnet *et al*. 2010; Zouhri *et al*. 2014; Gingerich & Zouhri 2015, 2017; Zouhri *et al*. 2017, 2018; Jouve *et al*. 2019).

The Bartonian (middle Eocene) fauna from Gueran and the Bartonian-Priabonian (middle to upper Eocene) marine faunas from Ad-Dakhla area as well as the faunas from others localities in the adjacent West African Atlantic margin of the Atlantic (Togo, Senegal, Nigeria), constitute an interesting connection between the middle to upper Eocene marine faunas from the eastern part of the Tethys (Indian and Pakistan Subcontinent) and the Middle East (Egypt) and the contemporaneous faunas from the American continent. New information from the Moroccan Sahara provides deeper insights into faunal exchanges between Asia, Africa and America through the seaway that links Tethys Ocean and Atlantic Ocean.

Even though many taxa from Gueran are not identified to the species level, the fauna shows biogeographic affinities with middle Eocene levels of Egypt and Libya. This supports a close biogeographical relationship between Tethyan Bartonian faunas from southeastern and southwestern coasts of the Mediterranean Sea (north and northwest Africa). The taxonomic groups of the Gueran fauna were represented earlier on African coasts and widely spread elsewhere in the world before the Bartonian, thanks to theTethys and Atlantic connections across the middle to late Eocene and and early Oligocene for allowing such distribution and dispersion.

Acknowledgements

We are grateful to the reviewers Kishor Kumar and Iyad Zalmout who contributed to the improvement of this work. We thank Annelise Folie, Cécilia Cousin (Institut royal des Sciences naturelles de Belgique, Brussels), Philippe Béarez (UMR 7209, Muséum national d'Histoire naturelle, Paris), Gaël Clément (UMR 7207, MNHN), Patrice Pruvost and Zora Gabsi (UMR 7208, MNHN) who provided access to comparative material and collections. We are grateful to Philippe Béarez and François Meunier (UMR 7208, MNHN) for fruitful discussions, Hélène Bourget (UMR 7207, MNHN) for preparation of the material, and Philippe Loubry (UMR 7207, MNHN) for taking photographs. Fieldwork research was supported by a grant from the National Geographic Society (9765-15) to senior author, to the the Museum of Paleontology at the University of Michigan (Ann Arbor, U.S.A.), and by Hassan II University (Casablanca, Morocco).

Captions of the figures

Figure 1. Geological map showing the desert in southwestern Morocco and the location of the Sabkha of Gueran relative to Boujdour city. Red symbols mark sites yielding the vertebrates remains described here and in Gingerich and Zouhri (2015), Zouhri et al. (2018) and Jouve et al. (in press). The geology is from Hollard et al. (1985) and map modified from Gingerich and Zouhri (2015). Inset shows the geographic distribution of Eocene marine faunal localities on the African continent. The principal African localities of interest are numbered from 1 to 8. **1**, **Gueran** locality in southwestern Morocco, Bartonian (Ginerich & Zouhri 2015; Zouhri et al. 2018**). 2, Garitas** and nearby sites south of **Ad-Dakhla** in southwestern Morocco Bartonian-Priabonian (Zouhri et al. 2014, 2018; Gingerich & Zouhri 2017**). 3, Ndomor Diop** site near Taïba Ndiaye in Senegal, Lutetian (Hautier et al. 2014). **4, Tiavandou** in Senegal, Priabonian (Elouard, 1981**). 5, Kpogame** in Togo, Lutetian (Gingerich & Cappetta 2014). **6**, **Ameke** in southern Nigeria, Bartonian (Andrews, 1920; Halstead & Middleton 1974, 1976).**7, Fayum Depression** in Egypt, which yielded a rich vertebrae faunas of Eocene-Oligocene age. **8, Dur at-Talah** in Sirt Basin in Libya, Eocene–Oligocene (Abouessa et al. 2012).

Figure 2. **Elasmobranchii Lamniformes teeth remains** from Sabkha of Gueran collected around Archaeocete whale carcasses. (A-C) *Otodus* (*Carcharocles*) cf. *sokolowi*: (A) FSAC Bouj–320 lateral upper tooth in (A1) labial and (A2) lingual views; (B) FSAC Bouj–321 anterior lower tooth in labial view; (C) FSAC Bouj–322 lateral lower tooth in labial view. (D-E) *Otodus* (*Carcharocles*) sp.: (D) FSAC Bouj–323 antero-lateral tooth in (D1) labial and (D2) lingual views; (E) FSAC Bouj–324 lateral tooth (E1) labial and (E2) lingual views. (F-G) *"Carcharias" koerti*; (F) FSAC Bouj–325 anterolateral upper tooth in (F1) labial and (F2) lingual views; (G) FSAC Bouj–326 anterior tooth of juvenile (G1) labial and (G2) lingual views. (H-K) *Macrorhizodus praecursor*: (H) FSAC Bouj–327 anterior lower tooth (H1) labial and (H2) lingual views; (I) FSAC Bouj–328 anterior upper tooth in (I1) labial and (I2) lingual views; (J) FSAC Bouj–329 lateral upper tooth in (J1) labial and (J2) lingual views; (K) FSAC Bouj–330 lateral lower tooth (K1) labial and (K2) lingual views. Scale bar equals 10 mm.

Figure 3. Elasmobranchs from Sabkha of Gueran collected around the Archaeocete whale carcasses. (A-F) *Tethylamna* cf. *twiggsensis*: (A) FSAC Bouj–331 anterior lower tooth in labial view; (B) FSAC Bouj–332 anterolateral lower tooth in labial view; (C) FSAC Bouj–333 lateral lower tooth in (C1) labial and (C2) lingual views; (D) FSAC Bouj–334 posterior lower tooth in labial view; (E) FSAC Bouj–335 lateral lower tooth in (E1) labial and (E2) lingual views; (F) FSAC Bouj–336 anterior upper tooth in (F1) labial and (F2) lingual views. (G-I) *Galeocerdo* cf. *eaglesomei*; (G) FSAC Bouj–337 anterior tooth in (G1) labial and (G2) lingual views; (H) FSAC Bouj–338 anterolateral tooth in lingual view; (I) FSAC Bouj–339 lateral tooth in (I1) labial and (I2) lingual views. Scale bar equals 10 mm.

Figure 4. **Elasmobranchs** from Sabkha of Gueran collected around the Archaeocete whale carcasses. (A-C) *Physogaleus* sp.: (A) FSAC Bouj–340 anterolateral tooth (A1) labial and (A2) lingual views; (B) FSAC Bouj–341 more anterolateral tooth in (B1) labial and (B2) lingual views; (C) FSAC Bouj–342 lateral tooth in (C1) labial and (C2) lingual views. (D) FSAC Bouj–343 *Hemipristis curvatus* lateral upper tooth in (D1) labial and (D2) lingual views. (E-F) FSAC Bouj–344 *Abdounia* sp. lateral teeth in (E1, F1) labial and (E2, F2) lingual views. (G-I) Cf. *Carcharhinus* sp.: (G) FSAC Bouj–345 lateral upper tooth in (G1) labial and (G2) lingual views; (H) FSAC Bouj–346 lateral lower tooth (H1) labial and (H2) lingual views; (I) FSAC Bouj–347 anterior lower tooth in (I1) labial and (I2) lingual views. (J) *Propristis schweinfurthi* FSAC Bouj–348 rostral “tooth” in (J1) dorsal and (J2) lateral views. Scale bar equals 10 mm.

Figure 5. Actinopterygii and **Testudines** from the Sabkha of Gueran. **(A-G) Actinopterygii:** *Cylindracanthus* sp., FSAC Bouj-356, rostral spine in (A1) lateral and (A2) transversal views. (B-E) Perciformes indet.; (B) FSAC Bouj-369, vertebra in (B1) lateral and (B2) transversal views; (C) FSAC Bouj-363, vertebra in (C1) lateral and (C2) transversal views; (D) FSAC Bouj-370, basioccipital in left lateral view; (E) FSAC Bouj-371, fin spine in anterior view. (F) Scombridae indet., FSAC Bouj-358, incomplete jawbone in labial view. (G) Siluriformes indet. FSAC Bouj-372, right pectoral spine in

anterior view. **(H-P) Testudines**: (H-L) Cheloniidae indet., FSAC Bouj-109, fragmentary costal in (H1) lateral transection, (H2) ventral, (H3) dorsal and (H4) medial transection views; (I) FSAC Bouj-352,fragmentary lateral process of right hyoplastron in (I1) ventral and (I2) dorsal views; (J) FSAC Bouj-351, subcomplete right hypoplastron in (J1) ventral and (J2) dorsal views; (K), FSAC Bouj-353, fragment of dermal plate, unlocated on the carapace, in dorsal view; (L) FSAC Bouj-354, fragment of dermal plate, unlocated on the shell in (L1, L2) both faces. (M) Dermochelyidae indet., FSAC Bouj-350, lateral pubic process of right pubis in (M1) ventral and (M2) dorsal views. (N) ? Podocnemidoidea indet., FSAC Bouj-196, fragment of right hypoplastron in (N1) dorsal and (N2) ventral views. (O) Indeterminata (? Podocnemidoidea indet.), FSAC Bouj-95, fragment of dermal plate of carapace in (O1) dorsal and (O2) ventral views. (P) Gueran turtles, pieces of the four fragments of figs. I, J, L and M, as preserved in view of conjunction in situ. Scale bar equals 20 mm.

Figure 6. **Serpentes** and **Aves** from Sabkha of Gueran. (A–F) **Serpentes**, vertebrae: (A–E) FSAC Bouj-317, in (A) anterior, (B) right lateral, (C) dorsal, (D) posterior and (E) ventral views; (F) FSAC Bouj-300 in anterior view. (G–K) **Aves** from Sabkha of Gueran, *Pelagornis* sp. (Pelagornithidae), FSAC Bouj-373, two fragments of maxillary rostrum: (G, K) posterior fragment in (G) right lateral and (K) left lateral views; (H–J) tip of maxillary rostrum in (H) right lateral, (I) ventral and (J) left lateral views. Abbreviations: c, culmen; fos, fossae for reception of mandibular pseudo-teeth; ls, longitudinal sulcus; plr, palatal ridge; r1–r4, rank 1–rank 4 pseudo-teeth; tc, tomial crest; tf, transverse furrow. Pseudo-teeth (PT1–PT6) and tomial pseudo-teeth (TT1–TT2) are numbered consecutively from the most proximal to the most distal. Scale bar equals 10 mm.

Figure 7: **Crocodyliformes** remains from Gueran. **Eusuchia indet**. (A-J), A, FSAC BOUJ-410, last cervical (ninth) vertebra in left lateral view; B, FSAC BOUJ-1b, anterior cervical vertebra in left lateral view; C, FSAC BOUJ-400, posterior dorsal vertebra in left lateral view; D, FSAC BOUJ-1a, first caudal vertebra in left lateral view; E, FSAC BOUJ-124, caudal vertebra in left lateral view; F, FSAC BOUJ-94, osteoderm in dorsal view; G, FSAC BOUJ-96, posterior portion of a dorsal

osteoderm, and H, FSAC BOUJ-96, lateral portion of a dorsal osteoderm in dorsal views; **Crocodyliformesindet**. (I-J), I, FSAC BOUJ-355, mid portion of a dentary in dorsal view; J, FSAC BOUJ-406, posterior fragment of a left mandibular ramus in dorsal view. **Gavialoidea indet**. (K-P), K, FSAC BOUJ-405, portion of a left dentary in dorsal view; L, FSAC BOUJ-402, mid portion of a right maxilla in ventral view; M, N, FSAC BOUJ-404, FSAC BOUJ-403 and FSAC BOUJ-401, anterior (M) and mid portion (N) of left maxilla in ventral views; O, P, FSAC BOUJ-407, posterior portion of a left maxilla in lateral (O) and ventral (P) views. Scale bar: 1 cm.

Figure 8: Bartonian? *Barytherium* sp. partial tooth fragment from the Gueran fauna (Laazri locality), FSAC Bouj-380b, vertical enamel section. From the enamel dentine junction (EDJ) to the outer enamel surface (OES), the specimen presents a one-layered Schmelzmuster formed by 3D enamel (thick bundles of prisms that decussate in all directions).

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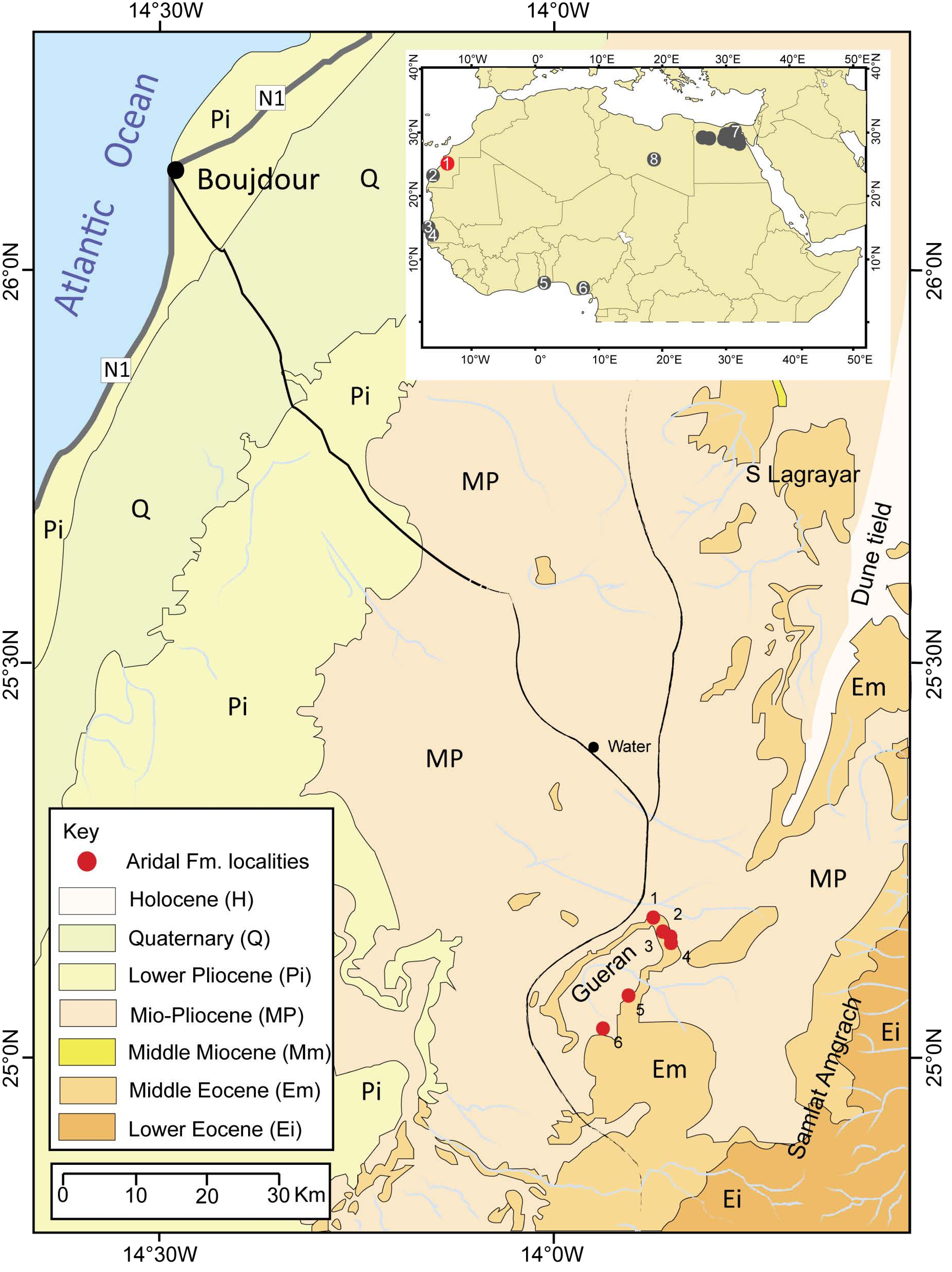
TABLE 1. — Faunal list of the vertebrate taxa from the Aridal Formation, Sabkha of Gueran locality, Bartonian, Sahara Desert, Morocco.

- **Elasmobranchii** Bonaparte, 1838
  - Lamniformes
    - Lamnidae Bonaparte, 1835
      - *Macrorhizodus praecursor* (Leriche, 1905)
      - *Otodus*(*Carcharocles*) cf. *sokolowi* (Jaekel, 1895)
      - *Otodus* (*Carcharocles*) sp.
    - Odontaspididae Müller & Henle, 1839
      - '*Carcharias*' *koerti* (Stromer, 1910)
      - *Tethylamna* cf. *twiggsensis* (Case, 1981)
  - Carcharhiniformes
    - Carcharhinidae Jordan & Evermann, 1896
      - *Galeocerdo eaglesomei* (White, 1955)
      - *Physogaleus* sp.
      - *Hemipristis curvatus* (Dames, 1883)
      - *Abdounia* sp.
      - *Carcharhinus* sp.
- **Batoidea** Compagno, 1973
  - Rhinopristiformes
    - Pristidae Bonaparte, 1835
      - *Propristis schweinfurthi* Dames, 1883
      - *Pristis* cf. *lathami* Galeotti, 1837
- **Actinopterygii** Cope, 1887
  - Actinopterygii *incertae sedis*
    - *Cylindracanthus* sp.
  - Acanthomorpha Rosen, 1973
    - Percomorpha Rosen, 1973
      - Gen. et sp. indet.
      - Gen. et sp. indet.
      - Gen. et sp. indet.
    - Scombridae Rafinesque, 1815
      - Gen. et sp. indet.
  - Ostariophysi Sagemehl, 1885
    - Siluriformes Cuvier, 1817
      - Gen. et sp. indet.
- **Sauropsida** Huxley, 1864
- **Testudines** Linnaeus, 1758
  - Cryptodira Cope, 1868
    - Chelonioidea Oppel, 1811
      - Cheloniidae Oppel, 1811
        - Gen. et sp. indet.
    - Dermochelyoidea Fitzinger, 1843
      - Dermochelyidae Fitzinger, 1843
        - Gen. et sp. indet.
  - Pleurodira Cope, 1864
    - ?Podocnemidoidea Cope, 1868
      - Gen. et sp. indet. A.
      - Gen. et sp. indet. B.
- **Squamata** Oppel, 1811
  - Serpentes Linnaeus, 1758
    - Palaeophiidae Lydekker, 1888
      - Palaeophiinae Lydekker, 1888
        - *Pterosphenus* cf. *schweinfurthi* (Andrews, 1901)
- **Crocodyliformes** Hay, 1930 *sensu* Benton & Clark (1988)
  - Crocodyliformes indet.
  - Eusuchia Huxley, 1875 (*sensu* Brochu 2003)
    - Eusuchia indet.
  - Gavialoidea Hay, 1930 (*sensu* Brochu 2003)
    - Gavialoidea indet.
- **Aves** Linnaeus, 1758
  - Odontopterygiformes Howard, 1957
    - Pelagornithidae Fürbringer, 1888
      - *Pelagornis* sp.
- **Mammalia** Linnaeus, 1758
  - Cetacea Brisson, 1762
    - Archaeoceti Flower, 1883
      - Protocetidae Stromer, 1908
        - Protocetid species A (small)
        - Protocetid species B (medium)
        - *Pappocetus lugardi* Andrews, 1920
  - Basilosauridae Cope, 1868
    - *Chrysocetus fouadassii* Gingerich & Zouhri, 2015
    - *Platyosphys aithai* Gingerich & Zouhri, 2015
    - *Eocetus schweinfurthi* (Fraas, 1904)
  - Proboscidea Illiger, 1811
    - Barytherioidea Andrews, 1906
      - Barytheriidae Andrews, 1906
        - *Barytherium* Andrews, 1901
        - ?*Barytherium* sp.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Middle Miocene (Mm)
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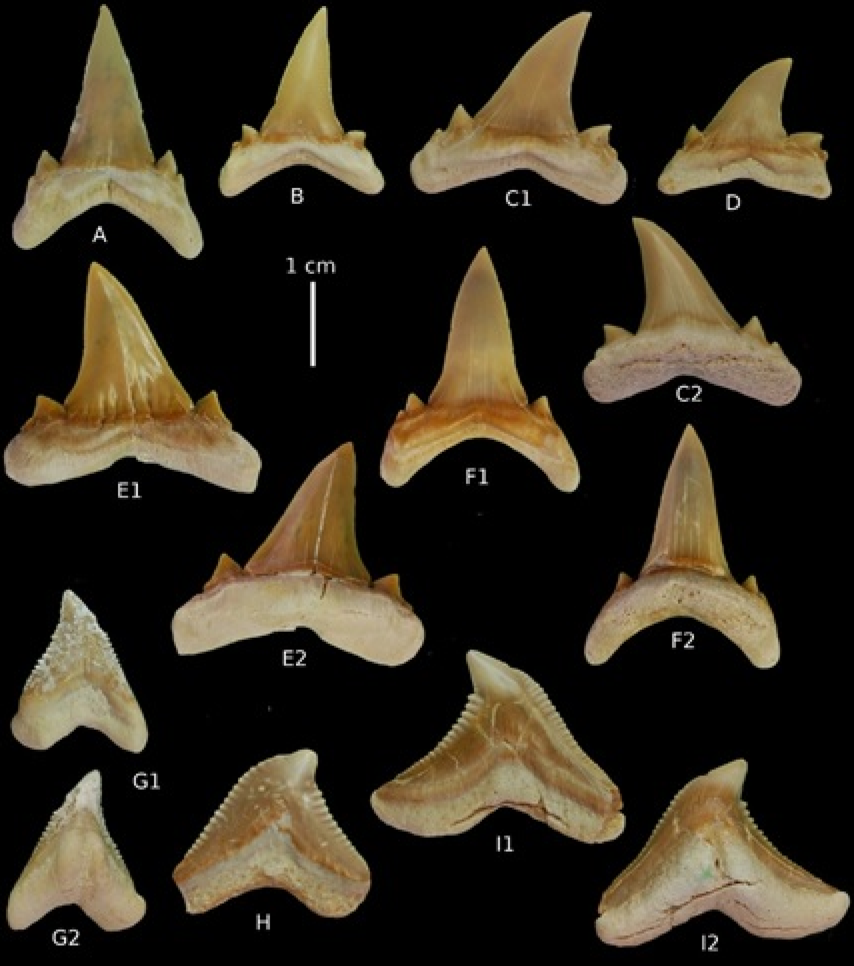
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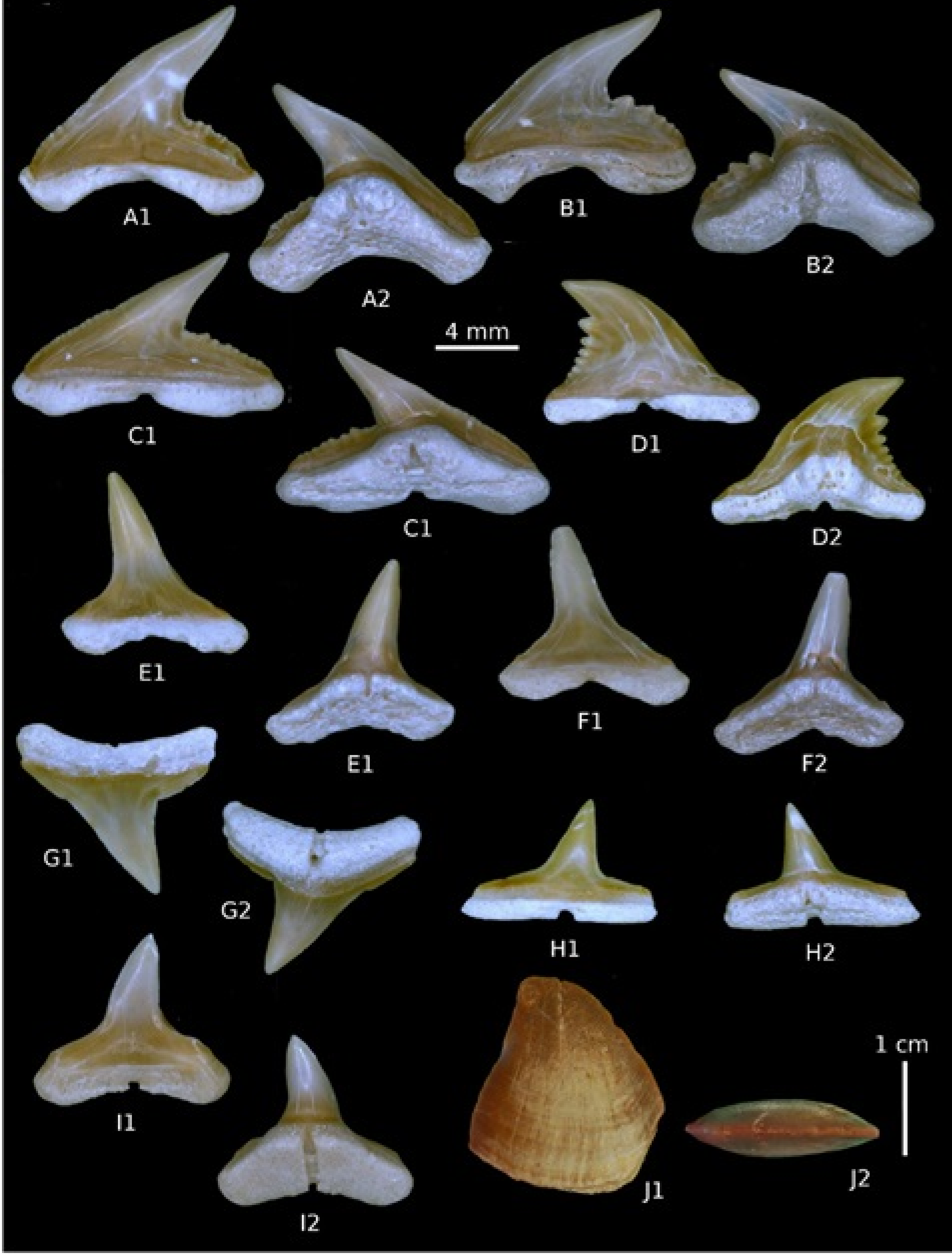
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A1
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H3
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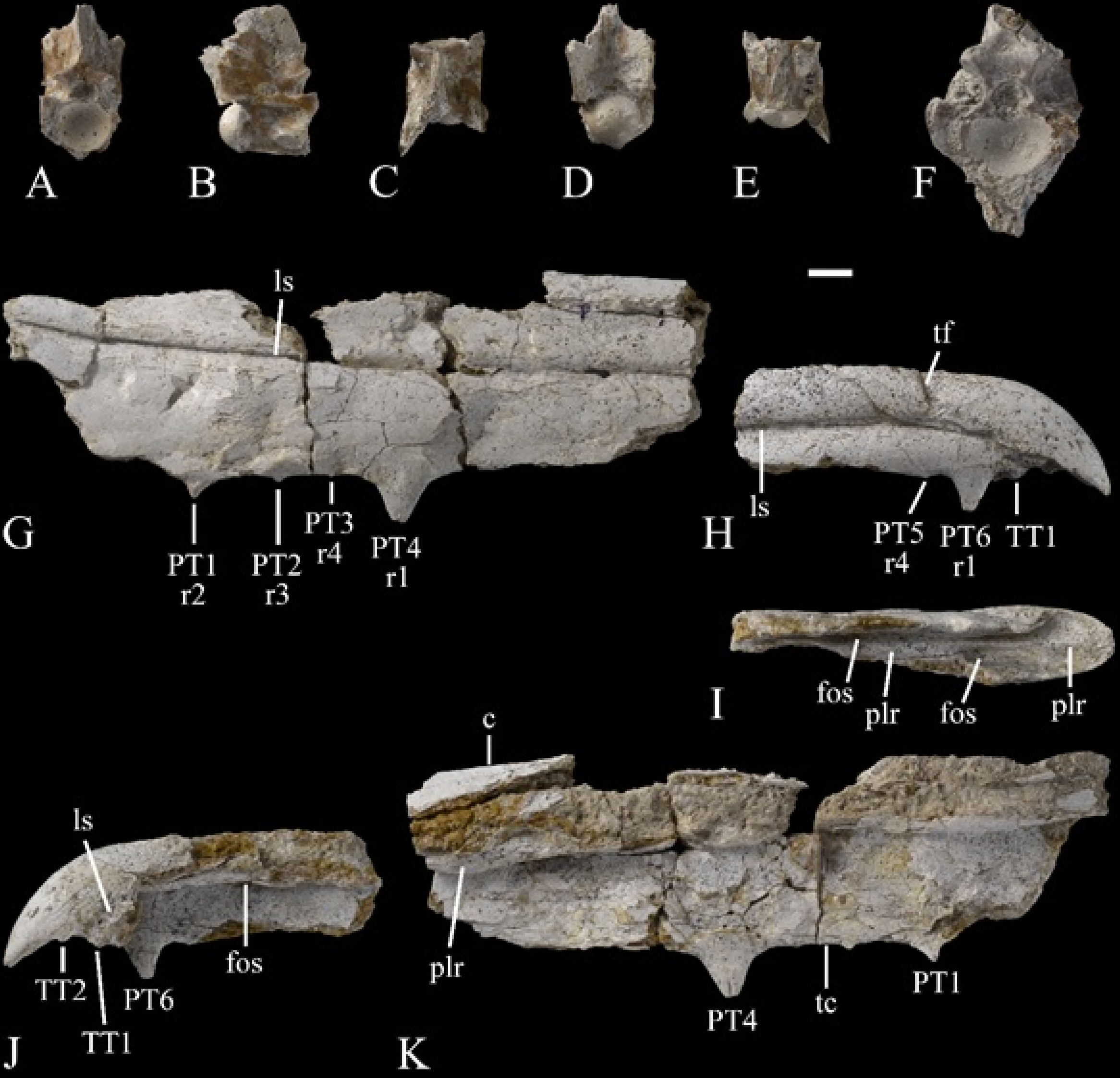
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