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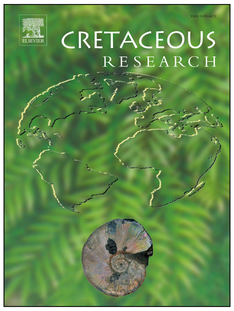

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Xenodens calminechari gen. et sp. nov., a bizarre mosasaurid (Mosasauridae, Squamata) with shark-like cutting teeth from the upper Maastrichtian of Morocco, North Africa

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ABSTRACT

The mosasaurids (Mosasauridae) were a group of lizards that became highly specialized for marine life in the mid-Cretaceous. By the end of the Cretaceous, they had undergone an adaptive radiation, and showed a wide range of body sizes, locomotor styles, and diets. Their ranks included piscivores, apex predators, and durophages. Here, we report a new taxon, *Xenodens calminechari* gen. et sp. nov., from the upper Maastrichtian phosphates of Morocco, with dental specializations unlike those of any known reptile. Teeth form a unique dental battery in which short, laterally compressed and hooked teeth formed a saw-like blade. Unique features of tooth structure and implantation suggest affinities with the durophagous *Carinodens*. The tooth arrangement seen in *Xenodens* not only expands known disparity of mosasaurids, but is unique among Squamata, or even Tetrapoda. The specialized dentition implies a previously unknown feeding strategy, likely involving a cutting motion used to carve pieces out of large prey, or in scavenging. This novel dental specialization adds to the already considerable disparity and functional diversity of the late Maastrichtian mosasaurids and marine reptiles. This provides further evidence for a diverse marine fauna just prior to the K-Pg extinction.

Keywords: Mosasauridae, Squamata, Cretaceous, Maastrichtian, Africa

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1. Introduction

Mosasaurids were a highly specialized group of marine reptiles that first appeared in the early Late Cretaceous, then radiated and dispersed during the latest Cretaceous to occupy a wide range of ecological niches (Russell, 1967; Polcyn et al., 2013; Bardet et al., 2014). Mosasaurids ranged in size from a few meters in length to over 15 meters long (Polcyn et al., 2013); in mass they would have spanned over two orders of magnitude. They were characterized by flipper-like limbs and a shark-like tail (Lindgren et al., 2011; Lindgren et al., 2013) that let them exploit open ocean habitats. Mosasaurids were also specialized divers. Some species show avascular necrosis (“the bends”) suggesting they were capable of deep diving (Rothschild and Martin, 1987), perhaps to kilometers below the surface, as in modern deep-diving elephant seals and sperm whales (Watwood et al., 2006).

In their diets and feeding strategies, mosasaurids were similarly diverse. They evolved a range of dental morphotypes (Massare, 1987; Schulp et al., 2013; Bardet et al., 2015): many had numerous small, conical teeth suitable for spearing and holding small prey items such as fish and cephalopods; others had robust, crushing teeth to crack open shelled prey such as mollusks and turtles; still others had bladelike teeth, suitable for cutting apart large prey items, or massive, conical teeth suitable for tearing apart large vertebrates. Stable isotopes confirm that these diverse tooth structures reflect diverse diets (Polcyn et al., 2013; Schulp et al., 2013). Tooth wear similarly implies diverse feeding strategies (Holwerda et al., 2013).

The best known mosasaurid faunas are from the Santonian-Campanian Niobrara Chalks, in Kansas (Everhart, 2001). These have been extensively studied for over 100 years. However, peak mosasaurid diversity was seen in the Maastrichtian, when mosasaurids showed maximum disparity in terms of size (Polcyn et al., 2013) and tooth morphology (Schulp et al., 2013; Bardet et al., 2015).

During the Maastrichtian, the most diverse mosasaurid fauna known is from Morocco (Bardet et al., 2004; Bardet et al., 2005a; Bardet et al., 2005b; Schulp et al., 2009; Bardet et al., 2010; LeBlanc et al., 2012; Cappetta et al., 2014; Bardet et al., 2017; LeBlanc et al., 2019; Strong et al., 2020). Here, a diverse assemblage has been described based on teeth and skeletal remains from phosphatic deposits. These are located in the Oulad Abdoun Basin, near Khouribga, and the Ganntour Basin, near Ben Guerir (Cappetta et al., 2014; Bardet et al., 2017). This assemblage has produced taxa and tooth morphologies showing diverse feeding strategies (Bardet et al., 2015). Despite extensive study, new species continue to emerge from these deposits, meaning that diversity is still undersampled.

Recently, a strange new mosasaurid fossil was recovered from the Sidi Chennane phosphate mine, in the Oulad Abdoun Basin (Fig 1), from beds of late Maastrichtian age (Fig.2). The new mosasaurid exhibits a dental battery with numerous small, short, bladelike teeth packed together to form a saw-like cutting edge. Features of the jaws and teeth suggest affinities with the mosasaurid *Carinodens*, a taxon with crushing teeth (Bardet et al., 2008; Schulp et al., 2009; Holwerda et al., 2013; Mulder et al., 2013; Milàn et al., 2018).

2. Geological Setting

The new mosasaurid remains come from the Sidi Chennane phosphate mine in the Oulad Abdoun Basin of Khouribga Province, Morocco (Fig. 1). Strata exposed here by mining span the Cretaceous-Paleocene boundary, extending in time from the mid?-late Maastrichtian (Kocsis et al., 2014) into the early and middle Eocene (Fig. 2). The phosphatic deposits are divided into a series of beds or ‘couches’ for the purposes of mining.

From the top down, these are Couche 0, Couche I, Couche II, and Couche III. The boundary between Couche I and II corresponds to the Paleocene-Eocene boundary and Paleocene-Eocene Thermal Maximum. The boundary between Couche II and III corresponds to the Cretaceous-Paleogene transition, but the K-Pg boundary itself and the Lower Paleocene are not preserved (Bardet et al., 2017). Couche III lacks either calcareous fossils, such as ammonites, bivalves, and foraminifera, or organic microfossils, to constrain its age. However, shark teeth correlate Couche III to the late Maastrichtian (Arambourg, 1935; Cappetta, 1987). Oxygen and carbon isotope stratigraphy corroborate this assignment (Kocsis et al., 2014).

The fossil described here was collected by locals working in the mines, rather than by paleontologists, complicating attempts to constrain stratigraphy and provenance. However, the pale white bone, and coarse grey matrix are typical of fossils from upper Couche III at Sidi Chennane.

Couche III contains an exceptional assemblage of fossil marine vertebrates. Marine reptiles, including diverse mosasaurid squamates (Bardet et al., 2004; Bardet et al., 2005a; Bardet et al., 2005b; Bardet et al., 2008; Schulp et al., 2009; LeBlanc et al., 2012; Bardet et al., 2015), elasmosaurid (Vincent et al., 2011; Vincent et al., 2013), and chelonioid turtles (Bardet et al., 2013; Lapparent de Broin et al., 2013) dominate the community. Bony fishes and selachians (Arambourg, 1952) were diverse and abundant (see Bardet et al., 2017 for faunal list and references). Above, diverse pterosaurs exploited the seas (Pereda-Suberbiola et al., 2003; Longrich et al., 2018). Rare dinosaurs suggest a nearby terrestrial community (Pereda-Suberbiola et al., 2004; Longrich et al., 2017; Longrich et al., 2020).

The epicontinental sea where fossils deposited, at the edge of the West African Craton, was characterized by upwelling (Martin et al., 2017). Upwelling could explain the high abundance, diversity and disparity of marine predators here (Martin et al., 2017). The

Couche III assemblage may sample not just a diverse time in mosasaurid history, but a uniquely diverse habitat — a biodiversity hot spot.

Abbreviations. MHNM Muséum d'Histoire naturelle de Marrakech, Université Cadi Ayyad, Morocco; OCP, Office Chérifien des Phosphates, Morocco.

3. Results

3.1 Systematic paleontology

SQUAMATA Oppel (1811)
MOSASAURIDAE Gervais (1852)
MOSASAURINAE Gervais (1852)

Xenodens calminechari gen. et sp. nov.

Etymology. The genus name is derived from the Greek *xenos*, 'strange', and Latin *dens*, 'tooth'. The species name derives from the Arabic *calminechari* (كالمنشار), 'like a saw'.

Holotype. MHNM.KH.333 (Figs. 3-5)

Horizon and locality. Upper Maastrichtian of Sidi Chennane phosphate mines, Khouribga Province, Morocco. Matrix and preservation are typical of Sidi Chennane, with a bleached white bone and pale, grey matrix characteristic of Couche III at Sidi Chennane (Fig. 3). The matrix is coarse, with a small fraction of fine particles, and contains teleost fragments. This coarse matrix is typical of fossils from upper Couche III at Sidi Chennane.

Diagnosis. Small mosasaurid (Figs. 6, 7). Anterior end of maxilla long and tapered in lateral view, with premaxilla-maxilla suture forming an angle of 15º with the dentigerous margin. Premaxillary-maxillary suture extends posteriorly 6, perhaps 7, tooth positions. At least thirteen maxillary teeth. Marginal tooth crowns low, strongly laterally compressed, up to twice as long anteroposteriorly as broad labiolingually. Crowns with strongly convex anterior surface bearing a cutting carina. Low apicobasal ridge along the anterior half of the crown defining a shallow groove or gutter on lingual and labial surfaces. Tooth apex strongly hooked posteriorly, behind the base of the crown, and posteriorly concave edge with an unserrated carina. Completely smooth enamel. Bases of crowns oriented obliquely relative to dentigerous margin of jaw in lateral view. Teeth closely packed to form a saw-like cutting edge. Roots of adjacent teeth expanded, fusing into a continuous ridge of dental bone. Anteroposteriorly elongated replacement pits.

3.2 Description

Maxilla (Figs. 3, 4). The maxilla is small, measuring 100 mm in length. It is broken posteriorly; the jugal process may have extended another centimeter or two. At its apex it measures 26 mm and posteriorly it measures 20 mm tall.

The anterior end of the maxilla forms a concave groove for the premaxilla, such that flanges of the maxilla clasped the premaxilla laterally and medially. The medial flange is larger than the lateral flange.

In lateral view, the maxilla's tip has an obtuse 'v' shape where it contacted the premaxilla, so that the premaxilla underlapped the maxilla ventrally and overlapped it dorsally. Anterodorsally the premaxillary contact is broadly convex, a feature shared with *Clidastes* and Mosasaurinae (Schulp et al., 2008). The suture continues posteriorly to form a long, straight contact with the premaxilla. This dorsal margin has a thin, sharp edge that would have contacted the premaxilla in a loose suture. The suture extends posteriorly to the sixth or perhaps seventh alveolus. A posteriorly extended suture is derived within mosasaurids. The suture extends as far as the third tooth position in *Prognathodon* spp. (Schulp et al., 2008) and *Globidens* cf. *phosphaticus* (Polcyn et al., 2010), as far as the fourth tooth in *Globidens alabamensis* (Gilmore, 1912) and *Mosasaurus hoffmanni* (Lingham-Soliar, 1995), to the fifth or sixth tooth in *Clidastes* (Russell, 1967), and the sixth or seventh tooth in *Halisaurus arambourgi* (Bardet et al., 2005b). The suture lies at a low angle, about 15 degrees, relative to the maxilla's ventral margin. Posteriorly there is a large, concave embayment for the retracted external naris.

Ventral and posterior to the naris, the sutural contact for the prefrontal is preserved with its typical zigzag shape. Given the shape of this suture and its wide dorsal extension, the prefrontal probably participates in the naris.

The lateral surface of the maxilla, just dorsal to the gum line, is covered by neurovascular foramina corresponding to the terminal branches of the maxillary nerve, as is typical of mosasaurids (Fig. 4A) (Russell, 1967). These foramina are very small and numerous anteriorly, then become larger posteriorly and form a distinct line. The line is distinctly elevated above the maxilla's ventral margin, an unusual condition shared with *Globidens alabamaensis* (Gilmore, 1912) but not other *Globidens* (Polcyn et al., 2010), or other Mosasaurini. The elaboration of these foramina may be associated with the development of nerves for mechanoreptors (Martill et al., 2021), which similar to modern sea snakes (Crowe-Riddell et al., 2016; Crowe-Riddell et al., 2019), may have been used to sense water pressure.

In medial view, the dental parapet is deep posteriorly then strongly tapers anteriorly, being reduced to a low ridge at the anterior end (Fig. 4). It is sharp and distinctly separated from the body of the maxilla by a groove. Anteriorly, a low, thin, mediodorsally directed flange of bone lies just above the dental parapet. Just above this flange a large, oval foramen. The medial dental parapet appears slightly less developed ventrally than the lateral one. This character is seen in primitive mosasaurids such as *Russellosaurus coheni* (Polcyn and Bell, 2005) and *Halisaurus arambourgi* but also in *Globidens* spp. (Gilmore, 1912; Polcyn et al., 2010).

Positions for 13 teeth are preserved. Two or three more were probably present posteriorly where the maxilla is broken away.

Dentition. Tooth crowns (Fig. 5) are bladelike and labiolingually flattened to a degree not seen in other Mosasauridae, although this condition is approached in *Carinodens* (Schulp et al., 2009). Here the teeth are more like those of varanids or theropods than other mosasaurids, where teeth have a more conical shape. Crowns are low and trapezoidal in lateral view. There is a strongly convex, crescentic anterior margin with a sharp carina, a hooked apex, and a weakly concave posterior margin with an unserrated carina. Again, teeth are like those of *Carinodens* (Schulp et al., 2009) in being low and broad, with convex anterior edges. Enamel is totally smooth, and lacks the ornamentation seen in *Carinodens* (Schulp et al., 2009), *Globidens* (Bardet et al., 2005a; Polcyn et al., 2010), and some *Prognathodon* species (Konishi et al., 2011), where a rugose texture of coarse bumps and wrinkles extends down from the tooth apex.

The enameled crowns are borne on a pedicel formed of bone of attachment (Rieppel and Kearney, 2005) as in other Mosasauridae (Russell, 1967; Caldwell, 2007). In most Mosasauridae, e.g. *Mosasaurus* (Rieppel and Kearney, 2005) this pedicel is tall, but in *Xenodens* it is short, as in *Carinodens* and *Globidens*. Crowns do not sit perpendicular to the pedicel, as typical of Mosasauridae, and instead are slightly inclined backwards. The line formed by the base of the enamel therefore lies at an oblique angle to the jaw. This is another unusual feature shared with *Carinodens* (Schulp et al., 2009).

Tooth roots insert into thecae, formed laterally by the lingual margin of the maxilla, medially by a ventrally extended, bony parapet of the maxilla, and anteriorly and posteriorly by septa formed of interdental bone (Rieppel and Kearney, 2005; Caldwell, 2007). Tooth roots are mediolaterally compressed and expanded anteroposteriorly so that adjacent roots contact each other and fuse to create a wall of bone supporting the teeth. This configuration is unique among squamates, with the exception of *Carinodens*, which shares these fused tooth bases (Schulp et al., 2009).

Tooth roots bear large replacement pits, as in most mosasaurids (Bell Jr, 1997; Rieppel and Kearney, 2005). These pits extend deep into the pedicel forming interdental crypts. The openings for these crypts are developed as anteroposteriorly elongate and narrow slots. A similar morphology is seen in *Carinodens* (LeBlanc et al., 2012), and to a much lesser degree, in *Eremiasaurus* (LeBlanc et al., 2012). These openings are displaced posteriorly relative to the crown, which seems to result from anterior displacement of the crown relative to the tooth root.

Teeth are closely packed, with a slight gap between the anterior carina of one tooth and the posterior carina of the other. A similar arrangement is seen in *C. minalmamar* (Schulp et al., 2009). The effect is to create a single, serrated cutting edge, like a sawblade.

4. Discussion

4.1 Affinities of Xenodens

Despite the unusual morphology of the teeth of *Xenodens*, multiple characters allow confident referral to the Mosasauridae. These include a long, low, triangular maxilla, elongate premaxilla-maxilla contact, such that the naris would be posteriorly retracted; tooth crowns being borne on bony pedicels, tooth bases implanting into distinct thecae, and deep replacement pits developing as crypts.

The unique dental morphology and arrangement in *Xenodens* warrants recognition of a distinct genus and species. Several features suggest affinities with *Carinodens*, a specialized, durophagous mosasaurid. Three species of *Carinodens* have been described: *Carinodens belgicus*, from the upper Maastrichtian of Belgium and the Netherlands, C. *minalmamar*, from the upper Maastrichtian of Morocco, and *C. palistinicus* from Jordan (Kaddumi, 2009). Isolated teeth of *Carinodens* have been described from elsewhere (Schulp et al., 2009; Mulder et al., 2013; Milàn et al., 2018).

Teeth of *Xenodens* resemble *Carinodens* in many respects. These include (i) low, anteroposteriorly broad crowns, (ii) the strongly convex anterior carina, (iii) labiolingual compression of the crown. The teeth however differ from those of *Carinodens* in being posteriorly hooked, with sharp apices, and in being much more laterally compressed. The enamel is also completely smooth, unlike the sculpturing and sulci seen in both *Carinodens* species and particularly in *C. belgicus*, which in this feature is like that of *Globidens*.

Teeth of *Xenodens* also resemble *Carinodens* in terms of implantation and arrangement. Unlike other mosasaurids, (v) tooth crowns are obliquely oriented relative to the dental parapet in lateral view, (vi) tooth pedicels are anteroposteriorly expanded and contacting, forming a continuous ridge of bone, and (vii) alveolar crypts are anteroposteriorly expanded in both genera.

Finally, (viii) the small reconstructed size of *Xenodens* and *Carinodens* and (xi) the relatively long, straight and low maxilla and high tooth count (mirroring the dentary of *Carinodens*) suggest affinities between the two.

Given that *Carinodens* is known from lower jaws and *Xenodens* from the upper, this poses the question of whether the two could come from one, heterodont animal. However, the shape, arrangement and ornamentation of the teeth in *Xenodens* being so distinct from *Carinodens*, it is unlikely they are the same species. Moreover, in mosasaurids as a whole, upper and lower teeth are so similar that it is difficult to determine whether teeth come from the upper or lower jaw (e.g. Russell, 1967, p 56-57). From a functional standpoint, pairing *Xenodens*-like upper teeth and *Carinodens*-like lower teeth is implausible since it would imply that upper and lower teeth functioned in radically different ways- one cutting soft-bodied prey, the other crushing armor. Different tooth functions are seen along the tooth row in squamates, and some species combine cutting and crushing teeth (e.g. *Varanus niloticus*). However, such variation is between anterior and posterior teeth, never (to our knowledge) uppers and lowers.

Apomorphies therefore identify *Xenodens* and *Carinodens* as a clade, exclusive of other mosasaurids. Beyond this, their relationships are unclear.

Carinodens has been allied with *Globidens*, in Globidensini (Schulp et al., 2004; Mulder et al., 2013; Milàn et al., 2018). The two genera share several adaptations, including a blunt tooth apex. *C. belgicus* also shares with *Globidens* rugose, ornate enamel (possibly absent in *C. minalmamar*) and both *Carinodens* species share the characteristic sulci present in some *Globidens* (Schulp et al., 2009). Blunt crowns and rugose, anastomosing enamel texture are also seen in some species of *Prognathodon* including *P. currii* where it is pronounced (Schulp, 2006). *Carinodens* and *Globidens* also share extreme heterodonty, with anterior teeth reduced, and middle teeth greatly enlarged. Blunt, inflated tooth crowns and rugose enamel are adaptations for durophagy (Schulp et al., 2004).

However, such characters are highly homoplastic. Blunt teeth and heterodonty evolved repeatedly in durophagous squamates. Molariform teeth are found in the caiman lizard *Dracaena* (Teiidae) (Dalrymple, 1979), the Nile monitor, *Varanus niloticus* (Varanidae) (D'Amore, 2015), the scincid *Tiliqua scincoides* (Scincidae) (Estes and Williams, 1984), the anguid *Diploglossus crusculus* (Anguidae) (Estes and Williams, 1984). It also evolved independently in the amphisbaenians *Trogonophis* (Trogonophidae) (Westphal et al., 2019) and *Amphisbaena ridleyi* (Amphisbaenidae) (Pregill, 1984). Molariform teeth are also found in extinct lizards such as *Odaxosaurus piger* (Anguidae) (Pregill, 1984) and *Chromatogenys tiliqoides* (Scincidae) (Makádi and Nydam, 2015).

Ridged enamel is also seen in taxa with molariform teeth, including *Tiliqua*, *Diploglossus*, and *Odaxosaurus*. These features –molariform teeth, heterodonty, and enamel ridges– form a suite of functionally correlated characters that evolved repeatedly in durophagous lizards. Even within Mosasauroidea, durophagy likely evolved multiple times – once in the lineage leading to *Globidens*, again within *Prognathodon*, and in the basal mosasauroid *Coniasaurus* (Caldwell and Cooper, 1999).

This does not prove that these features are convergent but suggests caution in using homoplastic characters. The absence of durophagous adaptations in *Xenodens* shows these characters are homoplastic even in *Carinodens*-like mosasaurids. If *Xenodens* and *Carinodens* are related, then durophagous adaptations were either lost in *Xenodens* (and absence of durophagy is a reversal) or independently gained in *Carinodens* from a nondurophagous common ancestor (and durophagy in *Carinodens* and *Globidens* are convergent).

Last, there are differences between the jaws of *Carinodens*-like mosasaurids and Globidensini. *Carinodens* has a longer, more slender, straighter mandible than *Globidens* and *Prognathodon*, where it is short, deep, and bowed (Lingham-Soliar and Nolf, 1989; Polcyn et al., 2010; Konishi et al., 2011). The low, triangular maxilla of *Xenodens* and *Carinodens* also differs from *Globidens* and *Prognathodon* (ibid). Instead, the long, low profile of the maxilla and elongate premaxilla-maxilla suture are like Mosasaurini. Strikingly, postcrania described for *Carinodens* (Kaddumi, 2009) show the short, broad first metacarpal and phalanges of digit I with anterior processes on their proximal and distal ends, giving them a 'butterfly' appearance. Such processes are well-developed on the first manus and pes digits in *Mosasaurus* and *Plotosaurus* (Russell, 1967; Lingham-Soliar, 1995; Lindgren et al., 2008) but not in other Mosasauridae, suggesting that *Carinodens* (and by extension, *Xenodens*) are part of Mosasaurini.

Only the swollen tooth crown seems to connect *Xenodens* to the Globidensini, though this character is weakly developed compared to *Globidens*, *Carinodens* and *Prognathodon* (Schulp et al., 2004).

The elevated medial parapet of the dentary and the well-developed tooth crypts are both derived features, shared with Mosasaurinae and Tylosaurinae and absent in Halisaurinae (Schulp et al., 2004). Beyond this, few features are available to resolve the higher-level affinities of the *Carinodens*-*Xenodens* group.

4.2 Function and Ecology

The unusual dental battery of *Xenodens* indicates a specialized feeding mode. Mosasaurid teeth as a whole present a common Bauplan, generally being conical in cross-section, homodont to weakly heterodont, and widely spaced (Russell, 1967). The "standard" or default plesiomorphic mosasaurid teeth are small, acutely conical hooks, like those of *Tethysaurus,* (Bardet et al., 2003), *Russellosaurus* (Polcyn and Bell, 2005), and *Halisaurus* (Bardet et al., 2005b). Such teeth are suitable for piercing small prey, indicating a diet of small prey like fish and soft-bodied invertebrates such as cephalopods.

However, over the course of the Late Cretaceous, mosasaurid teeth evolved a wide range of morphologies, suitable for piercing and holding (*Halisaurus*, *Plioplatecarpus*, *Clidastes*, etc.), piercing and cutting (*Mosasaurus*, *Tylosaurus*, etc.) or crushing (*Globidens*, *Prognathodon currii*, *Carinodens*, etc.), following the morphoguilds defined by Massare (Massare, 1987).

In some species, such as *Eremiasaurus heterodontus* (LeBlanc et al., 2012) and *Mosasaurus hoffmanni* (Lingham-Soliar, 1995) (Lingham-Soliar and Nolf, 1989), marginal teeth are large, laterally compressed, and serrated. This morphology is likely effective for seizing and tearing apart large prey. A similar morphology is seen in some varanids, such as *Varanus acanthurus*.

In others, like *Globidens* (Gilmore, 1912), *Carinodens* (Schulp et al., 2009), and to a lesser degree, *Prognathodon currii* (Christiansen and Bonde, 2002) lateral teeth are large, straight, with blunt apices, and low, bulbous crowns. These adaptations facilitate crushing of hard prey, either shelled invertebrates or bony vertebrates. Ornament in the form of bumps and ridges is well-developed on the enamel.

Tooth form and arrangement in *Xenodens* are different from any previously described morphology. Teeth are laterally compressed and bladelike to a degree unlike any other mosasaurid or squamate. Crowns are low and rectangular, the apex is hooked, and carinae are sharp but unserrated. Crowns are closely packed, leaving narrow slots between adjacent crowns. The tooth arrangement creates a slotted saw blade, similar to a circular saw. There is no similar arrangement in any other mosasaurid or lizard, or to our knowledge, any other tetrapod.

Surprisingly, a similar arrangement is seen in sharks, specifically dogfish (Squaliformes) (Fig. 8). Here, low, hooked, bladelike teeth are packed in a row to form a cutting blade (Underwood et al., 2016). This arrangement is seen in upper and lower jaws of most dogfish (Squalidae) and in the lower jaws of gulper sharks (Centrophoridae), sleeper sharks (Somniosidae) and lantern sharks (Etmophoridae) (Underwood et al., 2016). A sawblade is also seen in piranhas, the pycnodont *Serrasalmimus* (Vullo et al., 2017), and the squalimorph *Isistius* (cookiecutter shark) (Underwood et al., 2016) but these fishes differ in that they have fewer and larger teeth, and the crowns are taller and more triangular.

In dogfish sharks, the jaws apparently function as cutting blades. Long-axis roll of the jaws, a ‘head shake’ (Wilga and Motta, 1998) is used to saw prey in half. The bladelike lower teeth of Pacific sleeper sharks (*Somniosus pacificus*) allow them to gouge huge, hemispherical bolts of flesh from prey, as seen in large halibut caught on long line gear (NRL pers. obs.). The specialized cutting blades seen in Squaliformes therefore seem to be an adaptation allowing for relatively small predators to feed on proportionately large prey.

Despite these specializations, Squaliformes have broad diets, and take a range of food. *Squalus acanthias* feeds on fish, crustaceans, mollusks, nematodes and sea anemones (Jones and Geen, 1977; Avsar, 2001). Dogfish also scavenge on marine mammals (Bigelow, 1994). Rather than limiting the diet, specialized jaws and teeth seem to expand the range of prey, and may allow small sharks to feed on larger prey items than would otherwise be possible. Similarly, the piranha’s bladelike teeth are effective for eating meat but piranhas also take fruit and nuts (Prudente et al., 2016).

By analogy, the bladelike teeth in *Xenodens* may have allowed it to take a range of prey. Given the animal's small estimated size, prey likely included small invertebrates such as crustaceans and cephalopods, fish, and potentially, larger prey items, including large fish and cephalopods, or scavenging of large mosasaurids and plesiosaurs (Fig. 9).

So far, *Xenodens* appears to be rare in the fauna, but given the abundance of isolated mosasaur teeth in the phosphates, it is likely that teeth are present in the assemblage but misidentified as shark teeth. *Xenodens* teeth can be distinguished from other mosasaurids by their distinctive shape. Shed *Xenodens* teeth could readily be distinguished from shark's teeth by the absence of a root, and a basal resorption pit, which are characteristic of shed mosasaurid teeth.

5. Conclusions.

A new mosasaurid, *Xenodens calminechari* gen. et sp. nov., is represented by a small upper jaw from the upper Maastrichtian phosphates of Morocco. The new mosasaurid exhibits a dentition that is not just unique among mosasaurids, but among tetrapods, with bladelike teeth closely packed to form a serrated cutting surface. Some sharks convergently evolved similar dentition (Underwood et al., 2016), suggesting that the jaws of *Xenodens* were used to carve apart large prey items. Regardless of the jaw's precise function, the unusual dental morphology of *Xenodens* suggests a feeding strategy that was unique among mosasaurids or other marine tetrapods. Along with other specialized morphologies in mosasaurids – the button-shaped, crushing teeth of *Carinodens* and *Globidens*, the peg-like teeth of *Prognathodon currii*, bladelike teeth in *Eremiasaurus*, or the conical, orca-like teeth in large *Prognathodon* sp. – the teeth of *Xenodens* expand the remarkable functional and ecological diversity of late Maastrichtian mosasaurids, especially in the African Tethys (Bardet et al., 2015; Bardet et al., 2017). Insofar as predator diversity is driven by abundance and diversity of prey, high mosasaurid diversity prior to the K-Pg extinction suggests a diverse, stable marine ecosystem, cut down in its prime by the Chicxulub impact.

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Table 1

List of Mosasauridae from the Phosphates of the Oulad Abdoun Basin, Morocco, upper Couche III, latest Maastrichtian. Modified from Bardet et al. (2017)

Mosasaurinae

- *Mosasaurus beaugei* Arambourg, 1952
- *Eremiasaurus heterodontus* LeBlanc et al., 2012
- *Prognathdon* aff. *currii* Christiansen & Bonde, 2002
- *Prognathodon* aff. *saturator*
- *Globidens* cf. *phosphaticus* Bardet & Pereda Suberbiola, 2005
- *Carinodens minalmamar* Schulp et al., 2009
- *Carinodens belgicus* (Woodward, 1891)
- ***Xenodens calminechari new genus and species***

Plioplatecarpinae

- *Gavialimimus almaghribensis*, Strong et al. 2020

Halisaurinae

- *Halisaurus arambourgi* Bardet & Pereda Suberbiola, 2005a

FIGURE CAPTIONS

Fig. 1. Map of Northern Morocco showing the location of the Sidi Chennane phosphate mines in the Khouribga region.

Fig. 2. Stratigraphic column of Sidi Chennane, Khouribga Province, showing the stratigraphic occurrence of *Xenodens*. Stratigraphic column after Kocsis et al. (2014).

Fig. 3. MHNM.KH.331, *Xenodens calminechari* new genus and species, holotype left maxilla in matrix. Maastrichtian, Sidi Chennane, Oulad Abdoun Basin, Khouribga province, Morocco.

Fig. 4. MHNM.KH.331, *Xenodens calminechari* new genus and species. Maastrichtian, Sidi Chennane, Oulad Abdoun Basin, Khouribga Province, Morocco. Holotype left maxilla, in lateral (A), ventral (B), medial (C), and dorsal (D) views.

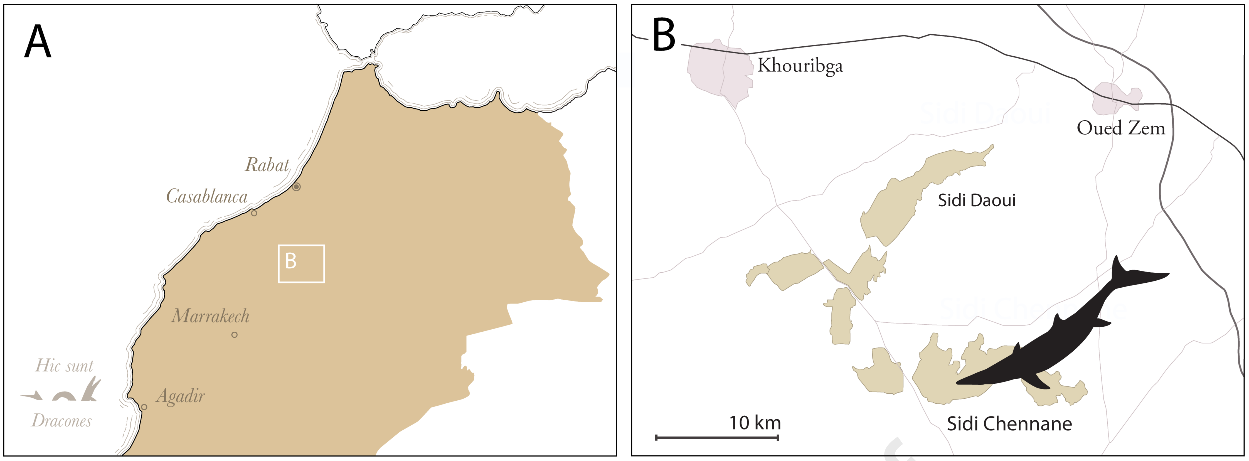
Fig. 5. MHNM.KH.331, dentition of *Xenodens calminechari* new genus and species. Maastrichtian, Sidi Chennane, Oulad Abdoun Basin, Khouribga Province, Morocco. In medial (A), lateral (B) and occlusal (C) views.

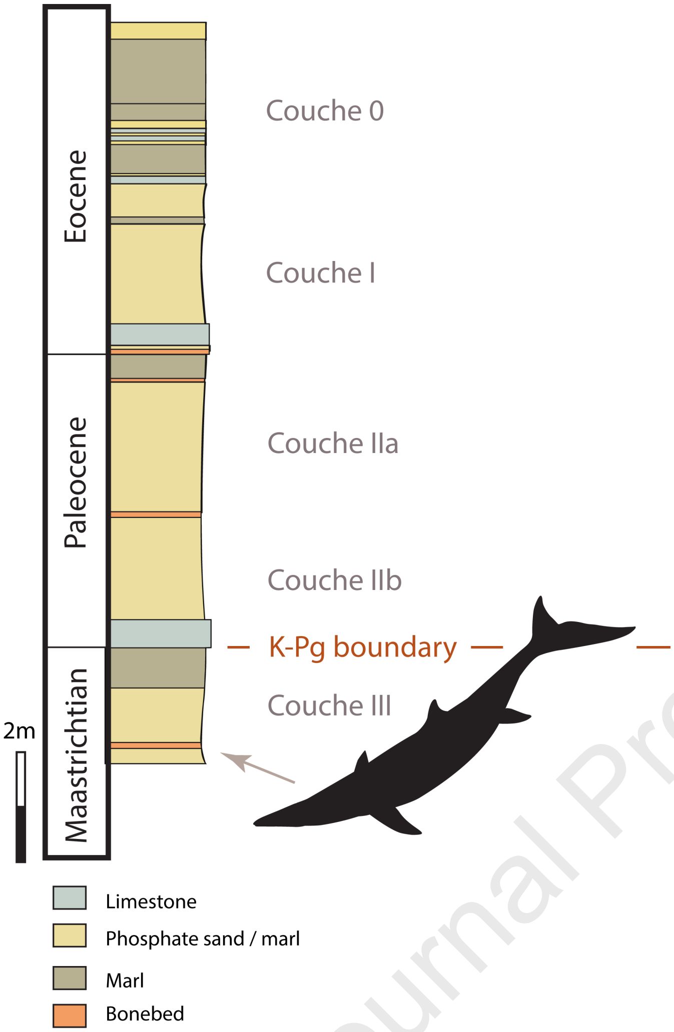
Fig. 6. Reconstruction of the skull of *Xenodens calminechari*, after *Mosasaurus hoffmanni* (Lingham-Soliar, 1995).

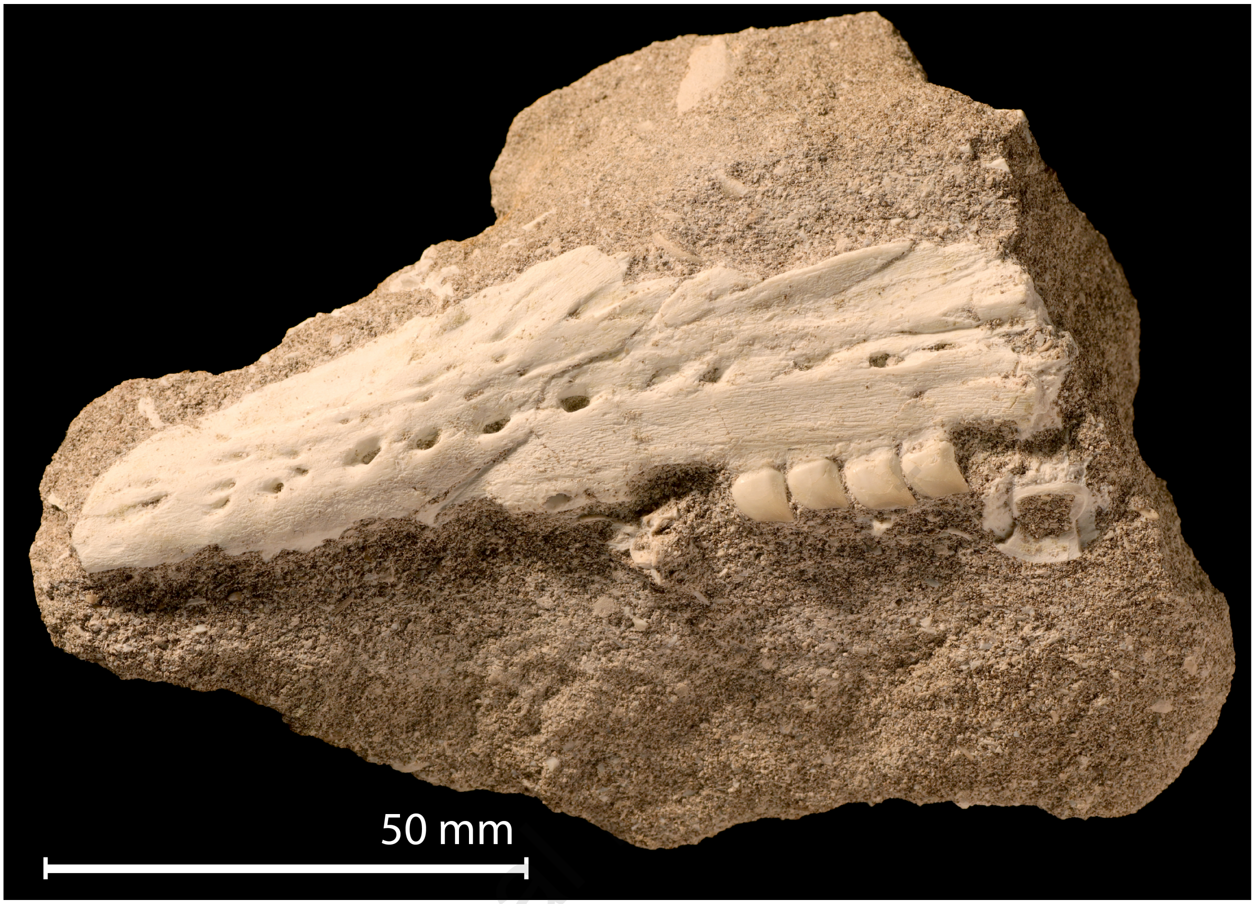
Fig. 7. Silhouette showing approximate size of *Xenodens calminechari*, with *Homo sapiens* for scale. Scale bar = 1 meter.

Fig. 8. Dogfish shark, *Squalus acanthias*, upper and lower teeth. Note teeth arranged in serrated cutting blades. Courtesy Ross Robertson, Smithsonian Tropical Research Institute.

Figure 9. Reconstruction of *Xenodens calminechari* scavenging a carcass of the elasmosaurid *Zarafasaura oceanis*. Artwork by Andrey Atuchin, 2020.


A
Rabat
Casablanca
B
Marrakech
Hic sunt
Dracones
Agadir
B
Khouribga
Oued Zem
Sidi Daoui
Sidi Chennane
10 km


Eocene
Paleocene
Maastrichtian
2m
Couche 0
Couche I
Couche IIa
Couche IIb
K-Pg boundary
Couche III
Limestone
Phosphate sand / marl
Marl
Bonebed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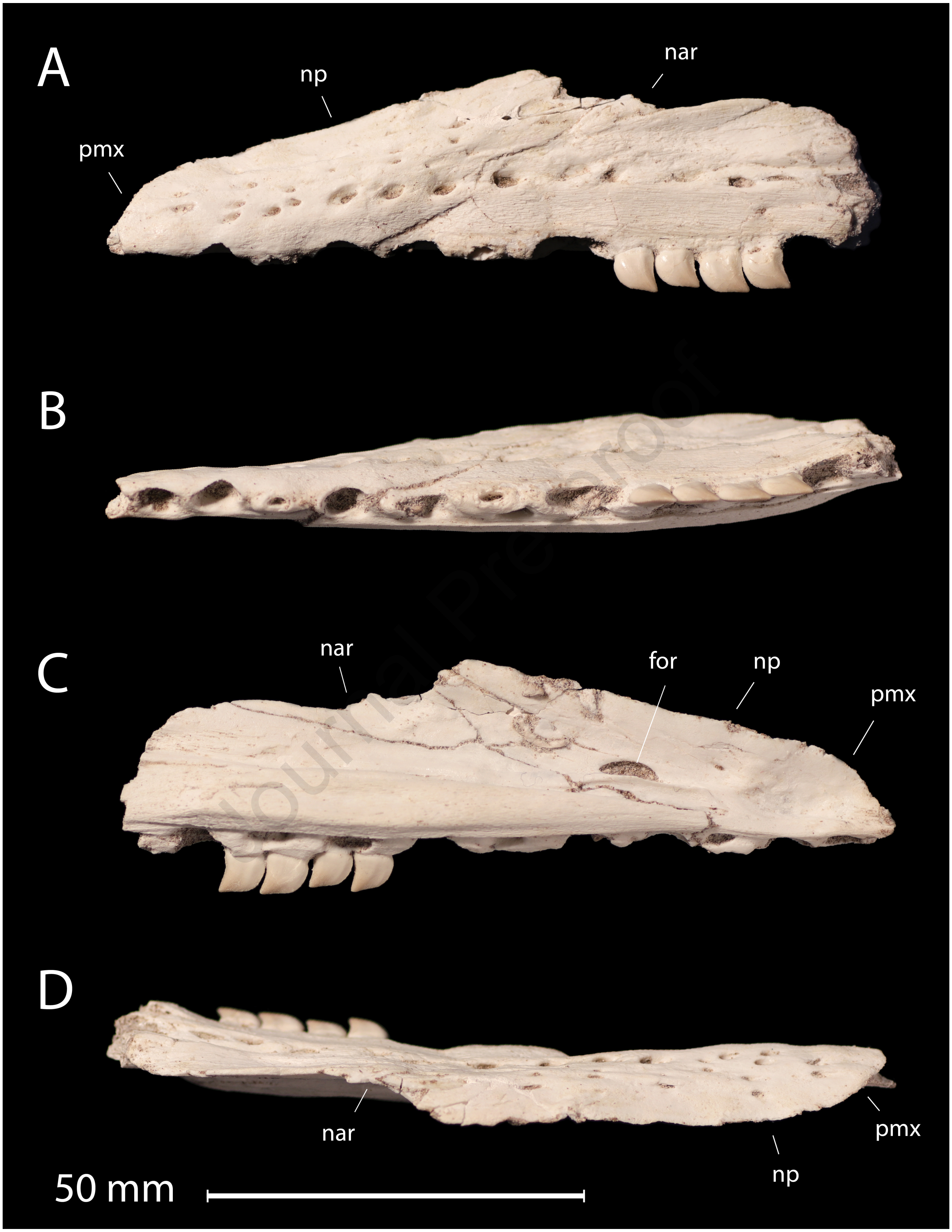
A
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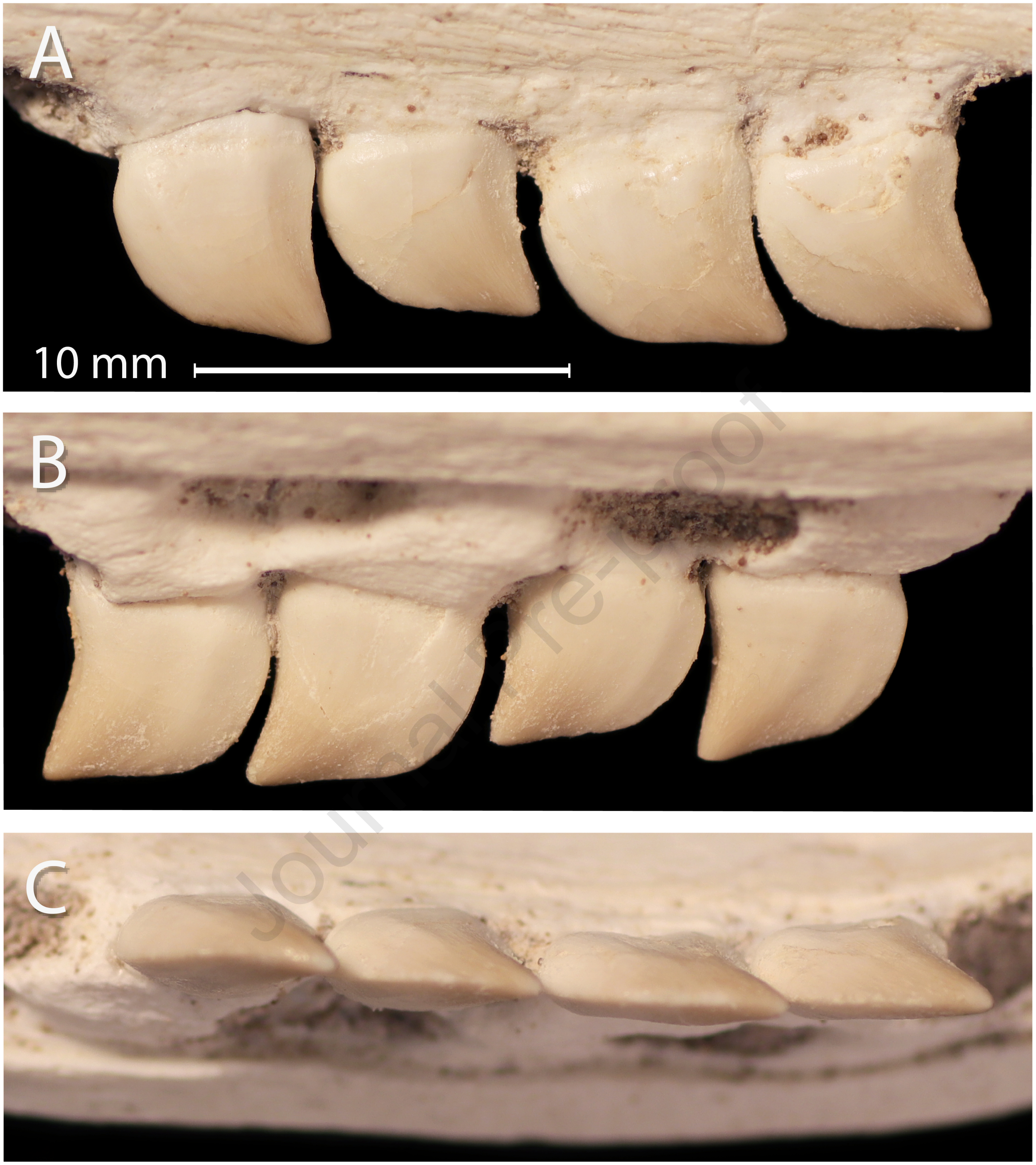
A
10 mm
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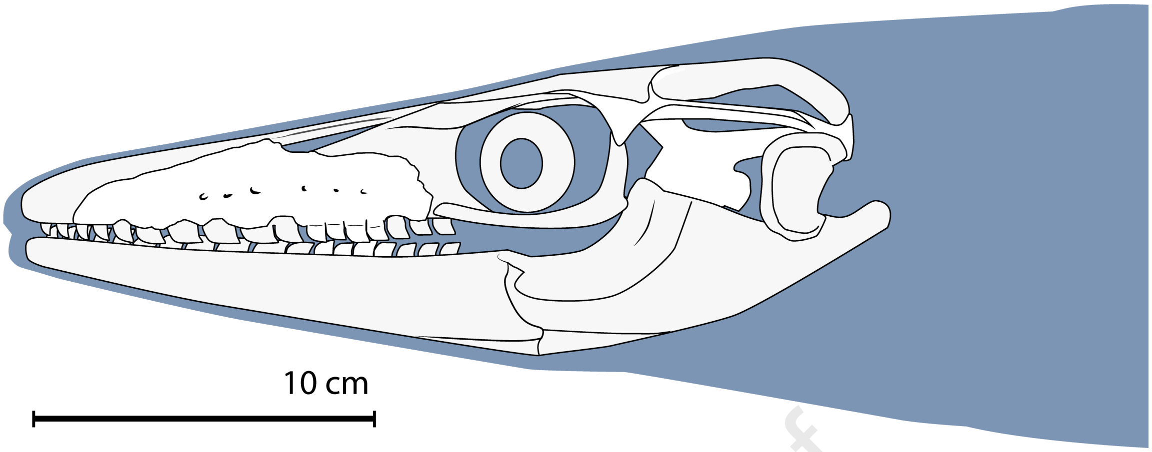
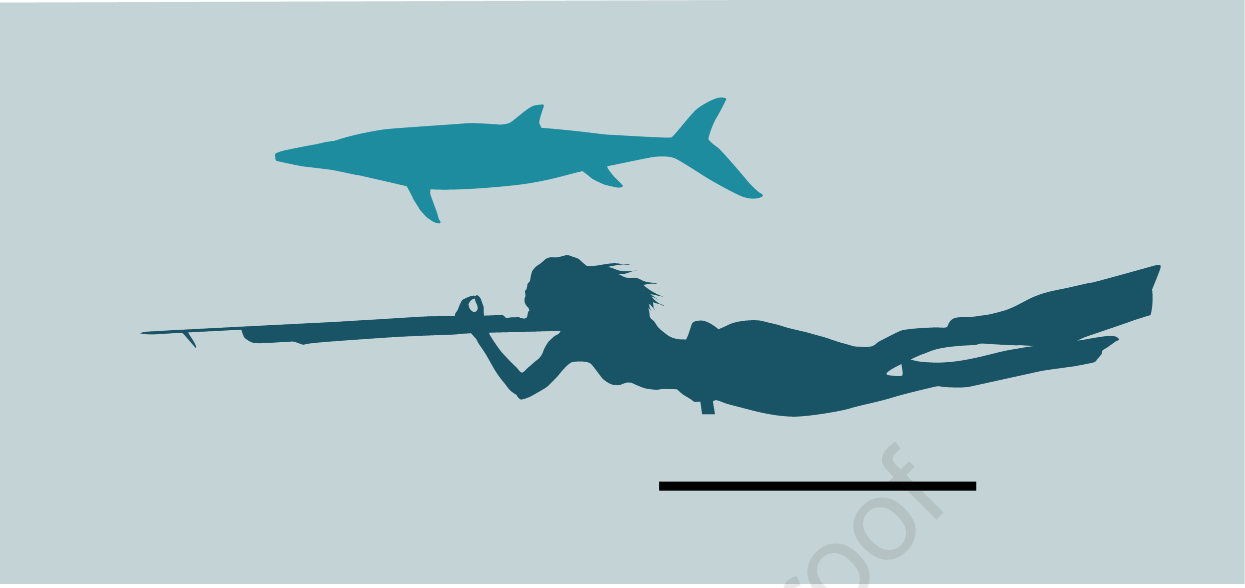
C


10 cm



Declaration of interests

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

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