Pluridens serpentis, a new mosasaurid (Mosasauridae: Halisaurinae) from the Maastrichtian of Morocco and implications for mosasaur diversity

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A B S T R A C T

Mosasaurids (Mosasauridae) were specialized marine lizards that evolved and radiated in the Late Cretaceous. Their diversity peaked in the Maastrichtian, with the most diverse faunas known from Morocco. Here we describe a new species of mosasaurid from this fauna. *Pluridens serpentis* sp. nov. is described based on two complete skulls and referred jaws. It is referred to *Pluridens* based on the elongate and robust jaws, small teeth, and specialized tooth implantation. *Pluridens* is referred to Halisaurinae based on the posteriorly expanded premaxilla, long premaxilla-maxilla suture, broad premaxillary facet on the maxilla, closed otic notch, and small, striated, hooked teeth. The orbits are reduced relative to other halisaurines while the snout is robust and flat with a broad, rounded tip. The jaws bear numerous small, hooked, snake-like teeth. Skulls imply lengths of 5-6 meters; referred material suggests lengths of ≥10 meters. *Pluridens'* specialized morphology – especially the contrasting large size and small teeth - suggests a distinct feeding strategy. Small orbits imply that *P. serpentis* relied on nonvisual cues including touch and chemoreception during foraging, as in modern marine snakes. Numerous neurovascular foramina on the premaxillae are consistent with this idea. The small teeth suggest proportionately small prey. The dentary becomes massive and robust in the largest individuals, suggesting sexual selection and perhaps sexual dimorphism, with the mandibles possibly functioning for combat as in modern beaked whales and lizards. The new mosasaur emphasizes how Maastrichtian mosasaurids were characterized by high species richness, functional diversity of niches occupied, and a certain degree of endemism, i.e. geographic specialization. and continued diversifying until the end of the Cretaceous, just prior to the K-Pg extinction.

1. Introduction

Mosasaurids (Mosasauridae) were a specialized group of squamates that became adapted for marine life in the mid-Cretaceous, before emerging as the dominant predators in marine ecosystems at the end of the Cretaceous (Polcyn et al., 2014). Peak mosasaurid diversity occurred in the Maastrichtian, when mosasaurs achieved high disparity in body size (Polcyn et al., 20134), tooth shape, and jaw morphology (Bardet et al., 2015). These patterns suggest that they occupied a wide range of marine niches broadly analogous to modern marine mammals, although mosasaurid biology would have differed from that of marine mammals, as did the available prey.

The most diverse known mosasaurid fauna comes from the upper Maastrichtian phosphates of the Oulad Abdoun Basin (Fig. 1) in the Khouribga Province of Morocco (Table 1) (Bardet et al., 2004; Bardet et al., 2005a; Bardet et al., 2005b; Schulp et al., 2009; LeBlanc et al., 2012) (Bardet et al., 2008; Bardet et al., 2015; Strong et al., 2020; Longrich et al., 2021). Moroccan mosasaurids ranged in size from the small *Halisaurus* to the giant *Mosasaurus* and *Prognathodon*, and their morphology shows a similar diversity. Teeth range from simple cones designed to pierce and hold, to bulbous teeth designed to crush, to cutting blades; jaw morphology is also diverse (Bardet et al., 2015). Yet despite the high known diversity, new species continue to emerge from the assemblage with forms displaying dental specialisation unlike those of any other known reptiles (Longrich et al., 2021), suggesting true diversity was substantially higher. We here report a new species of halisaurine, referred to *Pluridens*, adding to the fauna's diversity.

Halisaurines (Bardet et al., 2005b) are a deep-diverging lineage of mosasaurids. As in other mosasaurids, they had aquatic specializations, including retracted nares, flipper-like limbs, and a hypocercal tail (Bardet and Pereda-Suberbiola, 2001; Páramo-Fonseca, 2013), though the limbs are less specialized for aquatic locomotion than in other mosasaurids (Lindgren et al., 2008; Konishi et al., 2012). Unlike the giant Tylosaurinae and Mosasaurinae, which reached lengths of 15 meters or more, most Halisaurinae were small bodied, many were just 2-3 meters long (Polcyn et al., 20134). The exception is *Pluridens*, which grew larger (Lingham-Soliar, 1998).

The new material is referable to *Pluridens*, a poorly known genus previously reported from Niger and Nigeria (Lingham-Soliar, 1998; Longrich, 2016). The new material supports placement of *Pluridens* in Halisaurinae (Lindgren and Siverson, 2005; Longrich, 2016) and emphasizes the genus' highly distinct morphology and ecology. Finally, it provides further evidence that late Maastrichtian mosasaurids were characterized by remarkably high diversity.

2. Geological Setting

The phosphatic sedimentary series of Morocco were deposited in warm, shallow epicontinental seas along the western margin of the African craton (Bardet et al., 2010; Kocsis et al., 2014; Bardet et al., 2017). The environment represents a gulf or embayment open to the Atlantic Ocean in the west. The area was characterized by upwelling (Kocsis et al., 2014;

Polcyn et al., 20134) in a low-latitude environment, resulting in high primary productivity and a large biomass of small forage animals like fish and squid (Martin et al., 2017).

The phosphatic series (Fig. 2) extends almost continuously from the latest Cretaceous (Maastrichtian) to the base of the middle Eocene (Lutetian), about 25 MYR (Bardet et al., 2010; Kocsis et al., 2014) Phosphates comprise phosphatic and more or less indurated sands, marls, and limestones; vertebrates occur mostly in the sands (Kocsis et al., 2014). No formation or members are formally named, but the phosphates are divided into beds or layers termed 'couches' (Kocsis et al., 2014). Couche III is middle(?) - upper Maastrichtian (Fig. 2), Couche II is middle to upper Palaeocene, and Couches I and 0 are lower to middle Eocene. Upper Couche III is correlated to the upper Maastrichtian based on shark teeth (Cappetta, 1987). Oxygen and carbon isotope stratigraphy further constrain the age to latest Maastrichtian, ≥ 1 Ma before the K-Pg boundary (Kocsis et al., 2014). Lower Couche III is probably middle to upper Maastrichtian based on biostratigraphy (Kocsis et al., 2014). Most described mosasaurs come from Upper Couche III.

Fossils described here come from Upper Couche III at Sidi Daoui (Fig. 1). The matrix and preservation of these beds are distinctive. The matrix contains a high proportion of fine sediments with coarser sand-sized grains, sand grains mostly being fragments of bone. Matrix is yellow-orange- and blue-grey in color, and marbled suggestive of extensive bioturbation. Fish bones, teeth of sharks, mosasaurids, plesiosaurs and coprolites are abundant in the matrix. Skeletons tend to be disarticulated and scattered but bones often retain association and sometimes in articulation. Bones are three-dimensionally preserved, but often cracked and broken due to uneven settling of the matrix.

Upper Couche III has an exceptionally rich vertebrate fauna. It comprises sharks (Arambourg, 1952; Cappetta et al., 2014), fish (Arambourg, 1952; Vullo et al., 2017), mosasaurid (Bardet et al., 2005a; Bardet et al., 2005b; Bardet et al., 2008; Bardet et al., 2010; Bardet et al., 2017)(Bardet et al., 2004; Bardet et al., 2005b; Schulp et al., 2009; LeBlanc et al., 2012) (Bardet et al., 2004; Longrich et al., 2021)\(LeBlanc et al., 2019; Strong et al., 2020) and pachyvaranid (Houssaye et al., 2011) squamates, elasmosaurid plesiosaurs (Vincent et al., 2011; Vincent et al., 2013), marine turtles (Bardet et al., 2013; Lapparent de Broin et al., 2013), and rarely crocodilians (Jouve et al., 2008). Pterosaurs are diverse and abundant (Pereda-Suberbiola et al., 2003; Longrich et al., 2018), and rare dinosaurs are also present (Pereda-Suberbiola et al., 2004; Longrich et al., 2017; Longrich et al., 2020).

2.1 Institutional Abbreviations

MHNM— Muséum d'Histoire naturelle de Marrakech, Université Cadi Ayyad, Marrakech, Morocco.

OCP, Office Chérifien des Phosphates, Khouribga, Morocco.

3. Systematic Paleontology

Squamata (Oppel, 1811)
Mosasauridae (Gervais, 1852)
Halisaurinae Bardet and Pereda Suberbiola, 2005 in (Bardet et al., 2005b)

Pluridensini new taxon
Pluridens (Lingham-Soliar, 1998)
Pluridens serpentis sp. nov.

Syntypes: OCP DEK-GE 548 (Figs. 3, 4), skull; MHNM.KH.262 (Figs. 5-7), articulated skull, lower jaw, cervical vertebrae 1-4.

Referred: (Figs. 8-11) MHNM.KH.386, fragmentary skull including dentaries, maxillae, and dentition; MHNM.KH.387, left and right maxillae; MHNM.KH.388, right maxilla (Fig. 8); MHNM.KH.393, partial right dentary (Fig. 9); MHNM.KH.394, right dentary (Fig. 10), MHNM.KH.389, left and right dentaries (Fig. 11B); MHNM.KH.390, left dentary (Fig. 11C); MHNM.KH.391, left dentary (Fig. 11A); MHNM.KH.392, right dentary; MNHN.KH395a-b, left and right dentaries of the same individual.

Locality: Syntypes and referred specimens come from phosphate mines in Sidi Daoui area, Oulad Abdoun Basin, Khouribga Province, Morocco (Fig. 1).

Horizon: Upper Couche III of the phosphatic series, latest Maastrichtian (Fig. 2).

Diagnosis: Large halisaurine, skull length to ~120 cm, total length to ~10 meters. Snout short, rostrum ~50% of skull length. Snout low, broad, and bluntly rounded anteriorly, with dense neurovascular foramina. Premaxilla very broad, with premaxilla-maxilla suture extending posteriorly as far as the ninth maxillary tooth. Maxilla strap-like, with anterior end of maxilla blunt, parallel dorsal and ventral margins. Nasals large and with large, triangular tongue-like overlaps onto frontals. Prefrontals with long anterior process largely excluding the maxilla from the external naris. Prefrontal-postorbitofrontal lateral contact, excluding frontals from orbit. Parietal foramen anteroposteriorly elongate. Jugal small and L-shaped with prominent posteroventral process, orbits small relative to skull length. Dentary relatively long and tapered, becoming massive with a strongly cylindrical cross section in the largest individuals. Large contribution of surangular to coronoid process. Up to 28 dentary and ?18 maxillary teeth. Teeth small, strongly hooked cones, carinae weak and unserrated, with 4-5 rounded apicobasal ridges separated by shallow grooves. Enamel covered with microscopic anastomosing ridges. Tooth roots obliquely inclined relative to crown and separated by tall interdental septa (shared with *Pluridens walkeri* and *P. calabaria*). Weak mediolateral expansion of tooth sockets.

Pluridens serpentis can be differentiated from the closely related *Pluridens walkeri* and *P. calabaria* in that the dentary is evenly tapered along its length, similar to the condition in *Halisaurus*. By contrast, in both *P. walkeri* and *P. calabaria* the dentary is narrow anteriorly and then strongly expanded posteriorly. Teeth are larger than in *P. walkeri*, more similar to the condition in *P. calabaria*. The tooth sockets are moderately expanded mediolaterally, versus more strongly expanded in *P. calabaria* and especially *P. walkeri*.

4. Description

4.1 Skull

Premaxillae. The anterior part of the premaxilla (Figs. 3, 4A) is proportionately short and broad to a degree not seen in other mosasaurids except *Tethysaurus* (Bardet et al., 2003), being about twice as broad as long. It has a blunt, rounded tip. This contrasts with *Halisaurus arambourgi* (Bardet et al., 2005b), *Halisaurus platyspondylus* (Polcyn and Lamb, 2012), *Eonatator coellensis* (Páramo-Fonseca, 2013) and all other Mosasauridae, where the premaxilla is narrower and often acutely pointed anteriorly (Russell, 1967; Bell Jr., 1997). The main body of the premaxilla broadly contacts the tips of the maxillae. Its dorsal surface is covered with large neurovascular foramina (Fig. 4A) which represent the exits for a the ramus nasalis medialis of the trigeminal nerve (Álvarez–Herrera et al., 2020). Similar foramina are found in all mosasaurs. The foramina in *Pluridens* are more numerous than in *H. platyspondylus* or taxa such as *Platecarpus* and *Clidastes*, but neurovascular foramina are numerous in other taxa, especially tylosaurines such as *Tylosaurus* (Russell, 1967) and *Taniwhasaurus* (Álvarez–Herrera et al., 2020).

As in other mosasaurids, an elongate narial process contacts the dorso-medial margins of the maxillae anteriorly and would contact the frontals posteriorly (see nasal description below). The narial process resembles other Halisaurinae in being narrow anteriorly, then broader posteriorly, just ahead of the nares, such that where the maxillae contact the premaxilla it is distinctly pinched or constricted between them in dorsal view . This posteriorly expanded narial process is shared with *Halisaurus arambourgi* (Bardet et al., 2005b), a halisaurine from the early Campanian of Alabama (Lindgren and Siverson, 2005) and *Eonatator coellensis* (Paramo-Fonseca, 2013) and is considered here a derived feature of Halisaurinae. In other mosasaurids, the narial process is straight-sided (Tylosaurinae) or tapers in dorsal view (Plioplatecarpinae, Mosasaurinae) (Russell, 1967; Bell Jr., 1997).

The narial process forms an elongate lateral contact with the maxillae, with the premaxilla-maxilla suture extending posteriorly to at least the ninth tooth position, and about 40% the length of the maxilla. A long premaxilla-maxilla suture characterizes Halisaurinae, extending to the fifth tooth in *H. platyspondylus* (Polcyn and Lamb, 2012) and the sixth or seventh tooth in *H. arambourgi* (Bardet et al., 2005b). Primitively, and in most other mosasaurids the suture extends just to three teeth (e.g. *Platecarpus* (Konishi et al., 2012), *Prognathodon overtoni* (Konishi et al., 2011)), but an elongate suture evolves independently (e.g. *Mosasaurus hoffmanni* (Lingham-Soliar, 1995); *Clidastes* spp. (Lively, 2018)). The shape of the contact with the maxilla is vertical anteriorly, oblique behind this, then horizontal posteriorly, a derived condition shared with *Halisaurus* (Bardet et al., 2005b).

Maxilla. The maxilla (Figs. 3, 4, 5, 6, 8) resembles other Halisaurinae in being long and low, but uniquely among Mosasauridae is subrectangular and strap-like in shape in lateral view. The maxilla's anterior tip has a blunt, squared-off shape. Its anterior margin is perpendicular to the dorsal contact with the premaxillae, so that the premaxilla makes a T-shaped contact with the maxilla in dorsal view. The contacts with the premaxilla are angled or curved in other mosasaurids in general (Russell, 1967) such as, e.g., *Halisaurus platyspondylus* (Polcyn and Lamb, 2012), *Platecarpus tympaniticus* (Konishi et al., 2012), *Mosasaurus hoffmanni* (Lingham-Soliar, 1995; Street and Caldwell, 2017) and *Tylosaurus proriger* (Russell, 1967) so that the premaxilla wedges between the maxillae in dorsal view.

The tip of the maxilla is unusual in having subparallel dorsal and ventral margins, not tapering in lateral view as in other halisaurines (Bardet et al., 2005b; Polcyn and Lamb, 2012)

and other mosasaurids (Russell, 1967). It is also unusual in that the anterior end of the maxilla is as deep as the posterior end.

The concave narial emargination seen in other halisaurines and other mosasaurids in general is absent; the narial margin is straight to slightly concave. Posteriorly, the ascending process of the maxilla is low, as in other Halisaurinae (Polcyn and Lamb, 2012), but to a greater degree in *P. serpentis*. The jugal process of the maxilla is short and deep compared to other Halisaurinae (Bardet et al., 2005b; Polcyn and Lamb, 2012; Konishi et al., 2016).

Nasals. Surprisingly, large individualized nasal bones appear to be preserved on both OCP DEK-GE 548 and MHNM.KH.262 (Figs. 3, 4, 5, 6, 7). Though crushing and breakage obscure the nasal's shape and their contacts, they   contact the premaxillae anteriorly and the frontals posteriorly. They are narrow anteriorly and contribute to the narial bar, and expand posteriorly where they contact the frontals. Here the nasals form a pair of triangular tongue-shaped processes that overlap the frontals and appear separated from each other by a median sharp tongue of the frontal. In OCP DEK-GE 548 the posterior triangular portions are preserved though in MHNM.KH.262 only the sutural surface on the frontal is kept. This condition is seen in *Eonatator coellensis* though the shape and size of these nasal bones differ. However, crushing and breakage obscures the nasal's shape and their contactsThe presence and shape of the nasals is not known in other halisaurines. Nasals are highly reduced or absent in other mosasaurids (Russell, 1967).

Prefrontals. The prefrontals (Figs. 3, 4, 5, 6, 7) contact the maxillae anteriorly, the frontals medially, and the postorbitofrontals posteriorly. They resemble other mosasaurids (Russell, 1967) being platelike dorsally with a triangular descending ala. The prefrontal's anteroventral margin contacts the maxilla obliquely in a straight suture. The anteromedial margin forms the posterolateral margin of the external nares as in most mosasaurids (Russell, 1967). The medial margin of the prefrontal is regularly convex where it articulates with the frontal's concave lateral margin.

The prefrontal's dorsolateral margin bears an incipient supraorbital process, resembling the small, ridgelike one seen in other Halisaurinae (Russell, 1967; Bell Jr., 1997; Polcyn and Lamb, 2012). The large, winglike supraorbital process, as seen in Mosasaurinae (Lively, 2018)(Lingham-Soliar, 1995) is absent.

The posterior portion of the prefrontal is distinctly elongate and tapers to form a V-shaped joint with the anterior branch of the postorbitofrontal, excluding the frontals from the orbital rim. Exclusion of the frontals from the orbital rim by a prefrontal-postorbitofrontal contact is absent in other Halisaurinae (Bardet et al., 2005b; Polcyn and Lamb, 2012; Konishi et al., 2016), but resembles the condition in Mosasaurinae (Lingham-Soliar, 1995; Bell Jr., 1997).

Frontals. The frontals (Figs. 3, 4, 5, 6, 7) are fused, triangular elements as typical of Mosasauridae (Russell, 1967). They contact the premaxillae anteriorly, prefrontals anterolaterally, postorbitofrontals posterolaterally, and parietals posteriorly. They do not participate in the orbits.

The frontals are relatively short for halisaurines, the main body (excluding the narial process) being ~140% as long as wide. This contrasts with the very long and slender frontals

seen in *Eonatator sternbergii* (Bardet and Pereda-Suberbiola, 2001) and *Phosphorosaurus ortliebi* (Lingham-Soliar, 1996), and more closely resembles *"Phosphorosaurus" ponpetelegans* (Konishi et al., 2016), *Halisaurus platyspondylus* (Polcyn and Lamb, 2012), and *H. arambourgi* (Bardet et al., 2005b).

The frontals' anterior margin has two V-shaped embayments where the frontals participated in the nares. The participation in the nares is broad, about 40% the width across the postorbital processes, as in *H. arambourgi*, *H. platyspondylus*, *P. ortliebi*, and *P. ponpetelegans* (ibid.). Frontal participation in the nares is narrower in *E. sternbergii* (ibid.).

The frontal's anterolateral margins are concave where they contact the prefrontals. In contrast to *H. arambourgi*, *H. platyspondylus*, *P. ortliebi*, and *P. ponpetelegans*, where the frontals are expanded between the ends of the prefrontals, with a broad, convex supraorbital flange, the frontals are narrow here in *P. serpentis*, about 40% the width across the postorbital processes, more similar to the condition in *E. sternbergii*.

The frontals' posterolateral alae are roughly triangular. The suture for the parietal has a complex, interlocking contact. A pair of tonguelike processes of the parietal project forward, between them is a triangular median process of the frontal, and to either side are a pair of short, broad triangular lappets of the frontal that project posteriorly. A similar median projection of the frontal is seen in *Eonatator sternbergii*, and a very small median eminence is found on the frontal in *P. ponpetelegans*. That of *Halisaurus arambourgi* forms a broadly convex V-shaped contact with the parietal; the contact is shallowly concave in *H. platyspondylus*, and the parietal foramen participates in the frontal in *Phosphorosaurus ortliebi* (Lingham-Soliar, 1996).

The dorsal surface of the frontal is smooth and lacks foramina, as in other Halisaurinae. This is a primitive character, and contrasts with the presence of large foramina in tylosaurines (Everhart, 2005), plioplatecarpines (Konishi and Caldwell, 2011), and mosasaurines (Lingham-Soliar, 1995). Just behind the nares, the dorsal surface of the frontals bears the midline ridge characteristic of mosasaurids (Russell, 1967). It is weakly developed in *P. serpentis* relative to the condition observed in other halisaurines, where the median ridge forms a thick, tall dorsal keel (Lingham-Soliar, 1996; Bardet et al., 2005b; Polcyn and Lamb, 2012; Konishi et al., 2016). Just behind the nares are a pair of depressions. In other mosasaurids, there are often a pair of shallow channels or fossae here, perhaps the posterior extension of the narial fossae. The deep triangular depressions seen in *P. serpentis* may instead be articular surfaces, receiving the posterior ends of the large nasals. This feature is not seen in other halisaurines or other mosasaurids. Posteriorly, the frontal's dorsal surface is flat where it contacts the parietals. This contrasts with other Halisaurinae, where a triangular median boss lies ahead of the frontal-parietal suture (Lingham-Soliar, 1996; Polcyn and Lamb, 2012; Konishi et al., 2016). This median boss is a derived feature of Halisaurinae. The dorsal surface of the frontal of *P. serpentis* also differs significantly from that of *H. arambourgi* by lacking the two anterior oblique ridges converging posteriorly around mid-part of the bone (Bardet et al., 2005b).

Postorbitofrontals. The postorbitofrontals (Figs. 3, 4, 5, 6, 7) contact the prefrontals anteriorly, the frontals and parietals dorsomedially, the jugal ventrolaterally, and the squamosals posteriorly. The anterior end of the postorbitofrontal is elongate and broad, reaching the prefrontal in an interdigitating suture. By constrast, in *P. ponpetelegans*, the postorbitofrontal has a short and narrow anterior projection that makes a limited contribution to the dorsal

margin of the orbit, such that the frontals broadly participate in the orbits. The sutures of the frontals suggest a similar morphology in other Halisaurinae (Lingham-Soliar, 1996; Polcyn and Lamb, 2012)(Polcyn et al., 2012) (Bardet et al., 2005b). Medially, the postorbitofrontal has a process that wraps around the back of the frontal's posterolateral ala. A similar process is present in most mosasaurids, e.g. *Platecarpus* (Konishi et al., 2012) and *Mosasaurus* (Lingham-Soliar, 1995) but it is reduced in *P. ponpetelegans*; in this respect *P. serpentis* is primitive. The posterior process is straight, and more robust than in *P. ponpetelegans*, resembling that of *H. arambourgi* (Bardet et al., 2005b). It extends about 75% the length of the supratemporal fenestra. It broadly overlaps the squamosal in a long scarf joint, as in other mosasaurids. The descending process of the postorbitofrontal contacts the jugal, and together they form the posterior margin of the orbit. The descending process is relatively short and robust compared to that of *P. ponpetelegans*.

Parietals. The fused parietals (Figs. 3, 5, 7) are typically Y-shaped. As in other mosasaurids, the bone contacts the frontals and postorbitofrontals anteriorly and the squamosals posterolaterally, forming the medial and posterior margins of the large, ovoid supratemporal fenestrae.

Anteriorly, the parietal table is long but narrow, with a reduced exposure between the enlarged supratemporal fossae, with a narrow exposure between the enlarged supratemporal fossae, compared to *Halisaurus sternbergii* (Holmes and Sues, 2000), *H. arambourgi* (Bardet et al., 2005b; Polcyn et al., 2012), *P .ponpetelegans* (Konishi et al., 2016), and most other mosasaurids. The lateral margins of the parietal table are straight. They are distinctly convex in *Halisaurus platyspondylus*, *H. arambourgi* and *P. ponpetelegans*, a condition widely but variably distributed in Mosasauridae.

The parietal foramen is fully enclosed in the parietal. It is enlarged, anteroposteriorly elongate, and surrounded by a lip of bone, such that it is distinctly elevated above the parietal table. A similar striated rim around the parietal table is seen in *Halisaurus arambourgi* where it is particularly marked (Bardet et al., 2005b; Polcyn et al., 2012). Posteriorly the lateral rami of the parietal are elongate, strap shaped, and bowed posteriorly, as typical of Mosasauridae. The lateral rami are distinctly elongate relative to *H. arambourgi* (Bardet et al., 2005b; Polcyn et al., 2012), *Eonatator sternbergii* (Holmes and Sues, 2000), *P. ponpetelegans* (Konishi et al., 2016), and their tips are strongly turned outward, forming a broad obtuse angle, whereas they form a narrower angle in the other taxa.

Squamosals. As in other mosasaurids, the squamosals (Figs. 3, 5, 7) contact the postorbitofrontals anterolaterally, the parietals posteromedially, and the quadrate ventrally. They contribute medially to the supratemporal bar by a very long anteromedial tongue of bone that imbricates with the posterolateral one of the postorbitofrontal in a long oblique suture, defining the lateral margin of the long supratemporal fenestra.

Supratemporal. As in other mosasaurids (Russell, 1967) a long, flat supratemporal articulates with the underside of the squamosal lateral rami. The tip of the squamosal is exposed in dorsal view. Its end articulated with the top of the quadrate.

Jugal. The jugal (Figs. 3, 5) is a relatively small, L-shaped bone contacting the postorbitofrontal dorsally and the maxilla anteriorly. It has a short, very broad dorsal process whose posterior edge hooks backwards. Below, there is a broad, robust jugal posterior tuberosity that projects posteriorly. The ventral ramus of the jugal forms the ventral border of the orbit. It is longer and more slender than the dorsal process but far more robust than the ventral ramus in other halisaurs (Konishi et al., 2016)

The jugal's morphology differs greatly from both *Halisaurus arambourgi* (Bardet et al., 2005b) and "*Phosphorosaurus*" *ponpetelegans* (Konishi et al., 2016). In those taxa, the jugal is a large, comma-shaped element, with a tall dorsal ramus, no posterior tuberosity, and a long, slender, broadly arched ventral ramus. The enlarged, comma-shaped jugal is a derived characteristic associated with enlargement of the eyes in these taxa.

The small jugal in *P. serpentis* is associated with smaller orbits, which represents either the primitive condition, or perhaps even a reduction of the orbits relative to the primitive condition in other Mosasauridae.

Quadrate. The quadrate (Figs. 5, 7) is typical of Mosasauridae in bearing a broad lateral conch. There is a well-developed suprastapedial process that curls back and down around the stapedial notch. This suprastapedial process is fused to the infrastapedial process a derived feature shared with all other Halisaurinae (Bardet et al., 2005b; Fernández and Talevi, 2015; Konishi et al., 2016). There is no visible sutural contact between the two processes. The quadrate is proportionately short and broad. The lateral conch is about as wide as tall, with a broadly rounded dorsal margin, and a slightly triangular ventral rim. This shape is similar to *Eonatator sternbergii* (Bardet and Pereda-Suberbiola, 2001) and a halisaurine from the late Maastrichtian Jagüel Formation of Argentina (Fernández and Talevi, 2015). It differs from these taxa in having a very broad bony rim around the margin of the conch, ornamented by wrinkled ridges.

4.2. Mandible

Dentary. The dentary (Figs. 5-7, 10, 11, 12) articulates with the splenial and the articular, which is fused with the pre-articular in mosasaurids (Russell, 1967; DeBraga and Carroll, 1993) medially, and posteriorly with the surangular, and perhaps the coronoid. It resembles other Halisaurinae and *Pluridens* spp. (Fig. 12) in relatively being long and slender, but its shape varies with size, with the largest individuals having a more robust dentary with a strongly cylindrical section (Fig. 11).

The tip of the dentary forms a bluntly rounded, protruding prow that mirrors the premaxillary one. It is not preserved in either *P. walkeri* or *P. calabaria*, making comparisons impossible. However, this blunt prow is absent in *Halisaurus arambourgi* (Bardet et al., 2005b) and the Mooreville Chalk halisaurine (Lindgren and Siverson, 2005).

Anteriorly, the dentary's lateral surface is convex and rounded. The syntype MHNM.KH.262 lacks the highly convex lateral surface and distinctive circular cross-section seen in the middle Maastrichtian *P. walkeri* (Lingham-Soliar, 1998), or the strong lateral shelf of the dentary seen in that taxon; in this respect the jaw is actually more primitive and similar to the older, late Campanian *P. calabaria* (Longrich, 2016). However, a large referred specimen (MHNM.KH.386) shows this strongly convex lateral surface (Fig. 11C), suggesting that this feature is correlated to size and/or maturity.

The lateral surface of the dentary bears large foramina for exit of the terminal branches of the 5th mandibular nerve (Russell, 1967), and the anterior end of the bone bears randomly distributed round to oval foramina, as in other mosasaurids. A dorsal row of foramina parallels the dorsal margin of the dentary. These foramina are roughly circular at the tip of the dentary, and enlarge regularly to become elongated, narrow slots posteriorly. The posteriormost foramina are the largest, they reach up to 2.5 cm long x 2 mm wide.

The dentary's dorsal margin is gently concave and the ventral one gently convex. The anteroventral margin is very gently bowed; in *Halisaurus arambourgi*, the ventral margin of the dentary is slightly downturned at the tip (Bardet et al., 2005b), a derived feature absent here. The posteroventral margin is more strongly convex. The posteroventral margin of the dentary in *Pluridens walkeri* appears to be bowed (Longrich, 2016), as is that of *E. sternbergii* (Bardet and Pereda-Suberbiola, 2001). The posteroventral margin of the dentary is straight in *Halisaurus arambourgi* (Bardet et al., 2005b) and *Halisaurus* sp. from Chile (Jiménez-Huidobro et al., 2019). The bowed posteroventral margin is probably primitive, being seen in outgroups such as *Tylosaurus* (Everhart, 2005) and particularly pronounced in *Prognathodon* (e.g. (Lingham-Soliar and Nolf, 1989).

Posteriorly the dentary is relatively shallow in lateral view, similar to the condition in *Halisaurus* (Jiménez-Huidobro et al., 2019). By contrast, the posterior end of the dentary is strongly expanded in *P. walkeri* and *P. calabaria* (Longrich, 2016), a derived character uniting the two.

The posterior margin of the dentary bears a well-developed crescentic emargination, forming a mobile intramandibular joint with the surangular, a primitive condition for mosasaurids. The articulation with the coronoid appears to be a simple overlapping contact, a primitive condition shared with *Halisaurus arambourgi* (Bardet et al., 2005b; Jiménez-Huidobro et al., 2019); in Mosasaurinae a distinct notch in the dentary receives the coronoid (Lingham-Soliar, 1995).

In medial view, the Meckelian groove is broadly open posteriorly, and strongly tapers anteriorly, ending very anteriorly at the level of the 3rd-4th dentary tooth. The Meckelian groove is bounded below by a prominent ventral lip. A well-developed ventral lip of the dentary characterizes Halisaurinae (Longrich, 2016), but it is especially well-developed in *P. serpentis*, extending posteriorly about half the length of the dentary, a derived condition shared with *P.walkeri* and *P. calabaria* (Longrich, 2016).

Dorsally, there is a long edentulous process posterior to the last tooth, like in *Halisaurus* (Bardet et al., 2005b) and other *Pluridens* species. The medial dental parapet is slightly lower than the lateral one, a plesiomorphic character (Bell Jr., 1997) so that it does not extend the full height of the dentary as in derived mosasaurids such as *Mosasaurus hoffmanni* (Lingham-Soliar, 1995). Instead, the medial surface of the tooth roots is broadly exposed, as well as the tooth replacement pit. Interdental septa arise from the dentary and separate the tooth roots into almost individual dental alveolae. They are very well-developed, and project well above the medial parapet. These prominent septa are shared with *P. walkeri* and *P. calabaria* (Longrich, 2016) and also *Globidens simplex* (LeBlanc et al., 2019), but absent from *Halisaurus arambourgi* (Bardet et al., 2005b) and *Halisaurus* sp. from Chile (Jiménez-Huidobro et al., 2019). The septa extend posterodorsally rather than dorsally, in association with the oblique orientation of the tooth roots relative to the jaw (see below).

Splenial. The splenial (Fig. 5, 7) is largely obscured by the dentary in lateral view. Only its posteroventral margin being visible: it is a low triangular tongue of bone tapering anteriorly and disappearing at about the two thirds of the dentary length. On the contrary, its medial wing is widely expanded and largely covers the Meckelian groove of the dentary on its entire length. Posteroventrally it bears a large oval foramen that transmits the inferior alvaelor nerve into the Meckelian canal (Russell, 1967). Caudally the splenial contacts the angular to form a mobile intramandibular joint as in other mosasaurids (Russell, 1967).

In lateral view, the splenial hangs well below the mandible, a derived feature of Mosasauridae that is absent in the dolichosaurid *Coniasaurus* (Caldwell and Cooper, 1999) and other squamates. It forms a mobile contact with the angular, as in dolichosaurids (Caldwell and Cooper, 1999) and Mosasauridae (Russell, 1967).

The articular surface for the angular is strongly extended forward onto the lateral surface of the splenial to receive a large lateral lappet of the angular, such that the splenial-angular contact is C-shaped in lateral view. The shape of the joint remains unknown as both bones are articulated in MHNM.KH.262. A similar C-shaped contact is seen in other halisaurines (Holmes and Sues, 2000)(Bardet et al., 2005b), but appears to be more well-developed in *P. serpentis*.

Coronoid. The coronoid (Figs. 3, 5, 7) is a crescentic element forming the apex and anterior margin of the coronoid process, as in other Mosasauridae (Russell, 1967). It overlapped the dorsal and lateral surfaces of the surangular, and contacted an ascending process of the surangular posteriorly to form the coronoid process of the jaw. It may have overlapped the dentary anteriorly when the jaws were closed. It exhibits the plesiomorphic condition of a simple low saddle-shaped bone without developed lateral (nor most probably medial) wings (Bell Jr., 1997).

The anterior end of the coronoid is a flat, tongue-shaped process and may have overlapped onto the dentary when the jaw closed, but was not tightly connected to it; there may have been a ligamentous connection between the two bones contributing the intramandibular joint. Behind this, the coronoid curves up vertically to form the apex of the coronoid process. The coronoid is strongly curved in lateral view to a degree not seen in other halisaurines, e.g. "*Phosphorosaurus*" *ponpetelegans* (Konishi et al., 2016), a feature associated with the elevated coronoid process. There is a limited lateral overlap of the surangular ventrally, and a broad, convex contact with the dorsal wing of the surangular. A thick lateral ridge marks the anterior margin of the adductor fossa of the coronoid process, as in other mosasaurids (Russell, 1967).

Angular. The angular (Figs. 3, 5, 7) resembles that of other mosasaurids (Russell, 1967). It contacts the splenial anteriorly, the surangular dorsally, and the articular posteriorly. The anterior contact with the splenial is unusual in that a long lappet of the angular extends anteriorly to overlap the lateral surface of the splenial. The joint may have been developed more as a saddle joint than the typical concavo-convex joint seen in other mosasaurids. The ventral margin of the angular is straight. The lateral wing is low, exposed below the surangular, and tapers to overlap the articular in a posteroventral tongue ending roughly ventral to the glenoid articulation.

Surangular. The surangular (Figs. 5, 7) is a large, triangular plate occupying most of the lateral surface of the posterior portion of the mandible. It articulates with the dentary anteriorly in a mobile oblique joint, dorsally with the coronoid, ventrally with the angular, and posteriorly with the articular, where it forms part of the glenoid.

The anterior end is gently convex where it underlapped the dentary to form an oblique mobile intramandibular joint, as in other mosasaurids (Russell, 1967). The ventral margin is straight where it overlaps the angular. Posteriorly the surangular tapers to form a blunt, rounded end where it overlaps the articular.

The dorsal margin of the surangular is unusual in being elaborated into a tall and very robust coronoid buttress. In other Halisaurinae, the surangular has a concave dorsal margin and is elevated anteriorly to make a limited contribution to the coronoid process, e.g. *Halisaurus platyspondylus* (Holmes and Sues, 2000) and *Halisaurus arambourgi* (Bardet et al., 2005b). The surangular makes a very limited contribution to the coronoid process in Tylosaurinae and Plioplatecarpinae (Russell, 1967). The surangular does however make an extensive contribution to the coronoid process in *Clidastes* (Russell, 1967) and Mosasaurinae in general (Lingham-Soliar, 1995; Bell Jr., 1997). A large coronoid buttress appears to evolve convergently in *Pluridens* and in Mosasaurinae.

Articular. As in other mosasaurids, the articular and prearticular (Figs. 5, 7) are fused (DeBraga and Carroll, 1993). The articular contacts the angular ventrally and the surangular anteriorly. It is broad and triangular in shape, expanding posteriorly to form a large retroarticular process. The angular has a long, slender posterior spur that overlapped onto the articular; whereas the surangular has a broader, tongue-like flange that overlapped onto the articular. The posterior end of the articular is broadly expanded to form a fan-shaped retroarticular process nearly vertical as in *Halisaurus arambourgi* (Bardet et al., 2005b) but much more robust. The wide retroarticular process is derived relative to *Halisaurus platyspondylus* (Holmes and Sues, 2000) and *Phosphorosaurus ponpetelegans* (Konishi et al., 2016). The relative contribution of the surangular and articular to the glenoid cavity is not visible.

4.3. Dentition

The premaxilla is damaged in MHNM.KH.262 (Fig. 5, 6) and the teeth are not visible in OCP DEK-GE 548 (Figs. 3, 4), but it presumably bore four teeth as in other mosasaurids. There are roughly 18 maxillary teeth and around 26 to 28 dentary teeth, depending on the specimens (Figs. 5, 6, 8). The maxillary tooth count is unknown for *Pluridens*, but the estimated count of *P. serpentis* (18) is higher than that of *H. arambourgi* (16) (Bardet et al., 2005b). The dentary tooth count (Figs. 5, 10, 11, 12) is similar to that estimated for *P. calabaria* (~25, Longrich, 2016) and the Mooreville Chalk halisaurine (Lindgren and Siverson, 2005). Teeth of *Pluridens walkeri* are more numerous (~30, Longrich, 2016) and correspondingly much smaller. *Halisaurus arambourgi* has 19 dentary teeth (Bardet et al., 2005b). Exact tooth counts are unknown for other halisaurines.

Tooth crowns resemble those of other Halisaurinae and basal mosasauroids such as *Tethysaurus nopscai* (Bardet et al., 2003) in being sharp, slender, recurved cones (Figs. 5, 6, 8-11). They are around 1.5 cm height but can reach 2 cm in largest specimens. Low but discrete carinae, lacking serrations, are present anteriorly and posteriorly.

The basal cross-section is circular, and both lingual and labial surfaces are convex. In lateral view, crowns are strongly posteriorly recurved as in *Tethysaurus* (Bardet et al., 2003), other halisaurines and *Plioplatecarpus* (Lingham-Soliar, 1994). Basally, the tooth crowns bear ridges, grooves, and striations that extend halfway to two-thirds the way up the crown. The lingual surface of the tooth bears up to five, six, or even seven broad, rounded ridges extending up to one-third of the crown height, which may be separated by deep, concave grooves or fluting. The ridges and grooves are better developed on the labial surface of the crowns than on the lingual face. Development of ridges and grooves varies along the tooth row and specimens but shows no clear pattern. It is weakly developed in MHNM.KH.262, but better developed in referred specimens. Similar variation in the development of ridges is seen in other mosasaurs.

Just dorsal to the base, around midpoint, the crowns abruptly curve posteriorly. The upper part of the crown does not bear grooves and fluting, only minute ridges, giving the enamel a silky, smoother texture. Tooth apices are sharply hooked with slender tips, their shape being reminiscent of snake teeth. The teeth of the Alabama halisaurine (Lindgren and Siverson, 2005) and *Phosphorosaurus ponpetelegans* (Konishi et al., 2016) are more slender. Those of *H. platyspondylus* (Polcyn and Lamb, 2012), *H. arambourgi* (Bardet et al., 2005b) and *Halisaurus* sp. from Chile (Frey et al., 2016) are more weakly curved.

As usual in mosasaurids (Russell, 1967) teeth are short anteriorly, taller near the middle of the tooth row, then become small again posteriorly. But they are noteworthy in being only weakly heterodont in *P. serpentis*, showing very limited variation in size and shape along the toothrow. Teeth are too poorly preserved in *H. walkeri* and *H. calabaria* (Lingham-Soliar, 1998; Longrich, 2016) hindering comparisons, but a similar pattern is seen in the teeth of the Mooreville chalk halisaur (Lindgren and Siverson, 2005) as well as in *H. arambourgi* (Bardet et al., 2003) and *Phosphorosaurus ponpetelegans* (Konishi et al., 2016).

As in other Mosasauridae, the teeth are borne on a massive root that projects above the dentary, which is fused to the jaw by a mineralized periodontal ligament (Caldwell, 2007; Luan et al., 2009; Liu et al., 2016)(Russell, 1967; Rieppel and Kearney, 2005; LeBlanc et al., 2017). Implantation is thecodont, with the root deeply inserting and fusing into a socket or theca (Fig. 9). The theca is formed by the lateral parapet of the dentary, a medial parapet formed by the subdental ridge, and by interdental ridges separating adjacent alveoli (ibid.).

The roots and thecae are unusual in *P. serpentis*, however, in being obliquely oriented with respect to the long axis of the dentary (Fig. 9). Tooth roots therefore emerge posterodorsally rather than vertically. This feature is shared by *Pluridens walkeri* and *P. calabaria*, but not by other halisaurines (Frey et al., 2016; Jiménez-Huidobro et al., 2019) (Konishi et al., 2016) or other mosasaurids (Russell, 1967), and represents a unique derived character of these taxa.

Roots are deeply excavated by replacement pits (Fig. 9), as in other mosasaurids (Russell, 1967; Rieppel and Kearney, 2005; Caldwell, 2007). The replacement pits are noteworthy in being very large and located medially. Medially placed replacement pits shared with *Pluridens walkeri*, *P. calabaria*, (Longrich, 2016) and the Mooreville Chalk halisaurine (Lindgren and Siverson, 2005). In *Halisaurus arambourgi* (Bardet et al., 2005b), *Halisaurus*. sp. from Chile, and other mosasaurids (Russell, 1967; Rieppel and Kearney, 2005; Caldwell, 2007), replacement pits are located more posteromedially than medially. Medial placement of replacement pits is thus probably a unique, derived feature of *Pluridens*.

4.4 Postcranium

MHNM.KH.262 preserves the axis, atlas, and C3 in articulation, C4 is disarticulated (Fig. 5) . The cervicals are typical of Halisaurinae (Holmes and Sues, 2000). The centra are moderately elongate relative to the condition in Plioplatecarpinae (Russell, 1967) and Mosasaurinae (LeBlanc et al. 2012), and in this respect resemble *Halisaurus* and primitive mosasauroids such as *Tethysaurus nopscai* (Bardet et al., 2003) and *Dallasaurus* (Bell and Polcyn, 2005) . The atlas neural spine is triangular, moderately elongate, and raked backwards. The neural spines of C3 and C4 are moderately elongate, rectangular, and raked backwards. Synapophyses are well-developed. The hypapophysis is well-developed. Prezygapophyses are elongate and well-developed.

5. Phylogenetic analysis, *Systematics and evolution of Pluridens* and Halisaurinae.

Phylogenetic analysis was undertaken to understand the placement of *P. serpentis* within Halisaurinae. The analysis includes 10 ingroup taxa, 3 outgroups, and 26 characters (see SI). Several characters are taken from Konishi et al. (2016); most are new. Phylogenetic analysis was run using PAUP 4.0 B10 with implied weighting and K = 2.

The analysis recovers 6 most parsimonious trees (treelength = 45, CI = .6512, RI = .4881). The tree recovers two groupings within Halisaurinae, Halisaurini and Pluridensini (Fig. 13), defined below.

Numerous features of *Pluridens serpentis* support its placement in Halisaurinae. These include the premaxilla's posteriorly expanded narial process, a long premaxilla-maxilla contact, broad articulation of the maxilla and premaxillary narial process, the low dorsal wing of the maxilla, a closed otic notch of the quadrate, contribution of the surangular to the coronoid process, high tooth count, weakly heterodont dentition, tooth crowns strongly posteriorly recurved with basal ridges and grooves, weakly developed, unserrated carinae, and finely striated enamel (Bardet et al., 2005b; Longrich, 2016).

Other features are unusual among Halisaurinae. These include exclusion of the frontals from the orbits by a prefrontal-postorbitofrontal contact (shared with Mosasaurinae) and the large dorsal coronoid buttress of the surangular contributing to the coronoid process (shared with Mosasaurinae and *Clidastes*). Given other features supporting halisaurine affinities, these are likely convergent.

Within Halisaurinae, *P. serpentis* appears to be closely related to *P. walkeri* and *P. calabaria*. Features supporting this assignment include the animal's large size, a dentary that is laterally convex at its end, the high tooth count, obliquely oriented tooth bases, and large, medially positioned tooth replacement pits. Together, *P. serpentis*, *P. calabaria*, and *P. walkeri*, as well as the halisaurine from the Mooreville Chalk of Alabama, form a distinct, specialized lineage of Halisaurinae, here named Pluridensini.

Pluridensini is defined as all species closer to *Pluridens walkeri* than to *Halisaurus platyspondylus*.

Pluridensini are characterized by dental specializations including increased tooth count and obliquely oriented tooth roots; teeth are smaller anteriorly than in the middle of the toothrow, but it is unclear if this is a primitive or derived characteristic. An isolated dentary

from the Early Campanian Mooreville Chalk of Alabama shows similarities to *Pluridens* including a high tooth count and obliquely inclined tooth bases. Referred to *Halisaurus (=Eonatator) sternbergii* (Lindgren and Siverson, 2005), it is here recovered with Pluridensini.

Diagnosing various *Pluridens* species is necessarily restricted to differences in jaws and teeth. *P. serpentis* differs from *P. walkeri* and *P. calabaria* in lacking strong posterior expansion of the dentary. It has more teeth than in *P. calabaria*, but dentary tooth count (~26-28) is similar to that inferred for *P. walkeri* (~30). The shape of the mandible also differs, being more evenly tapered in *P. serpentis*, versus straight and rodlike in *P. walkeri*. The cylindrical shape of the anterior dentary in *P. walkeri* was initially assumed to be diagnostic, but this feature appears ontogenetic or even due to sexual dimorphism. The extensive variation seen here suggests some caution in diagnosing species on the basis of jaws, but we note that none of the large series of dentaries known from Morocco conform closely to either *P. walkeri* or *P. calabaria* in morphology, arguing that *P. serpentis* is distinct from either. Tooth count and tooth shape appear to vary little with size, supporting the distinction between *P. calabaria* and *P. walkeri*. Pluridensini are characterized by an increased tooth count, which suggests specialization on relatively small prey.

A new taxon, Halisaurini, is also created here and defined as all species closer to *Halisaurus platyspondylus* than *Pluridens serpentis*. It includes *Halisaurus platyspondylus*, *H. arambourgi*, *Phosphorosaurus ortliebi*, *Phosphorosaurus ponpetelegans*, *Eonatator coellensis*, and *Eonatator sternbergii* as sister group of all the former.

Halisaurini are united by a prominent frontal keel, a median frontal boss along the frontoparietal suture and in at least some taxa, very large, slender and comma-shaped jugals. Within Halisaurini, *Halisaurus platyspondylus* and *H. arambourgi* are united by broad frontals in which the preorbital part of the frontals is short and broad. *Halisaurus*, "*Phosphorosaurus*" *ponpetelegans* and "*Eonatator*" *coellensis* all share extremely large, comma-shaped jugal associated with enlarged orbits. *Phosphorosaurus ortliebi* appears to have a different jugal morphology. In contrast to *P. serpentis*, Halisaurini are characterized by enlarged orbits and a degree of binocularity, both of which increase the ability to gather light from an object to form an image. These features suggest visual detection of prey in low-light conditions, either at night or at depth.

Both the specialized morphology of Pluridensini and Halisaurini and their diversity - at least six halisaurines occur in the Maastrichtian, and at least four in the late Maastrichtian-reject previous interpretations of declining halisaurine diversity in the latest Cretaceous (Polcyn et al., 20134). Instead, Halisaurinae appear to diversify and peak in their diversity (Fig. 13), niche occupation, and large geographic range (Fig. 14) over the course of the Late Cretaceous, paralleling the adaptive radiation seen in Mosasaurinae, while presumably occupying distinct niches.

6. Discussion

6.1 Ecology of Pluridens

Pluridens is unlike other mosasaurs in terms of morphology and presumably ecology. In comparison with the other mosasaurids taxa of the Maastrichtian Phosphates of Morocco, *Pluridens serpentis* was far larger than the contemporary *Halisaurus arambourgi* and probably rivalled mosasaurines such as *Eremiasaurus* in size (Fig. 15) as well as plioplatecarpines like *Gavialomimus almaghribensis* (Strong et al., 2020). Despite the animals large size, the teeth are small, numerous and weakly heterodont, suggesting it fed on small prey such as fish and cephalopods, which stable isotopes suggest were abundant (Martin et al., 2017) .

The proportions of the orbits also suggest a very different hunting strategy than in Halisaurini. Halisaurini had proportionally large orbits and presumably correspondingly large eyes, and a degree of binocular vision, suggesting visual foraging (Konishi et al., 2016). These adaptations may have been useful for using visual cues in low-light conditions- dusk, dawn, night, and deep water, or simply for tracking small and/or fast-moving prey items.

Pluridens meanwhile had relatively small orbits, reinforced by a large prefrontal-postorbitofrontal contact above orbit forming a robust rim of bone. The small eyes suggest a distinct hunting strategy. Large eyes may have been less important during the day or at shallow depths, where light levels were high. Another possibility is that *Pluridens* hunted in dark waters, using non-visual cues (Fig. 16).

Some species of sea snakes (Hydrophiinae) (Dunson and Minton, 1978; Udyawer et al., 2015), sea kraits (*Laticauda*) (Dunson and Minton, 1978) and filesnakes (*Acrochordus*) (Shine and Lambeck, 1985) forage nocturnally. Non-visual senses appear to play a key role in foraging in these species, and many of them, including *Acrochordus* and many species of sea snake, have small eyes. In particular tongue-flicking is used by sea snakes (Kutsuma et al., 2018), sea kraits (Radcliffe and Chiszar, 1980) and filesnakes (Vincent et al., 2005) to detect chemical cues, specifically water-soluble molecules in the water, which are transported by the tongue to the vomeronasal organ (VNO). Tongue-flicking is also used by semiaquatic lizards, e.g. Varanus (Mayes et al., 2005). It has previously been suggested that mosasaurids may have had a forked tongue (Schulp et al., 2005). Given that mosasaurs appear closely related to snakes and anguimorphs (Martill et al., 2015; Reeder et al., 2015), it is likely they had a forked tongue used for chemoreception, as in these taxa. It may have played an important role where visual cues were lacking.

Sense of touch likely contributed to foraging as well. Mosasaurs in general have a large number of neurovascular foramina in the premaxilla, maxilla, and dentary, especially at the tip (Russell, 1967) suggesting extensive innervation of the face to receive tactile cues (Álvarez–Herrera et al., 2020). *Pluridens* is unusual in having more neurovascular foramina than in *Halisaurus*, suggesting elaboration of mechanoreceptors relative to other halisaurines and mosasaurids in general. A number of modern and extinct taxa have sophisticated mechanoreception allowing them to forage using tactile cues. Numerous mechanoreceptors in the scales of sea (Crowe-Riddell et al., 2016; Crowe-Riddell et al., 2019) and filesnakes (Van Der Kooij and Povel, 1996) for example, increase touch sensitivity and perhaps also sense variations in water pressure caused by prey. Similar tactile sensors also occur in crocodylians (Leitch and Catania, 2012; Di-Poï and Milinkovitch, 2013) where they are associated with elaboration of facial nerves similar to that seen in mosasaurs. Increased numbers of neurovascular foramina are also seen in tactile foraging birds such as sandpipers and kiwis (Martill et al., 2021). Among extinct taxa, the densely innervated premaxillae of pliosaurs

(Foffa et al., 2014) and certain pterosaurs (Martill et al., 2021) have been proposed to be adaptations for foraging using mechanoreception.

The different foraging strategies, visual versus nonvisual, have advantages and disadvantages. Visual foraging can detect prey at long ranges, which is effective for foraging in open habitats, or hunting fast-moving prey. Chemoreception is presumably less useful in open habitats where chemical cues quickly disperse, and the slow process of following chemical trails is of little use for tracking fast-moving prey. However, olfaction can be effective where visual cues are not. For example olfaction can be effective at night when too little light is available to hunt using vision. It is also useful for finding hidden prey, such as fish in crevices and burrows in reefs, or species concealed by camouflage. Many marine snakes therefore use chemoreception and mechanoreception to hunt at night when visual cues are less useful, and/or specialize on hidden prey such as eels in burrows and crevices (Brischoux et al., 2007, 2009) that are difficult for a visually hunting predators to find.

6.2 Variation in jaw morphology

Pluridens shows a remarkable change in jaw morphology from the smallest to the largest individuals, with the largest individual having an extremely robust, massive jaw relative to the smaller individuals (Figs. 3 to 12). It was initially assumed that two different species of *Pluridens* might exist in the assemblage. However, the jaws seem to show continuous variation and share features such as curvature, tooth size, tooth count, and arrangement of the neurovascular foramina, suggesting an ontogenetic series. Preliminary studies of other mosasaurids in the fauna (*Halisaurus arambourgi*, cf. *Prognathodon*) suggest that the jaws of mosasaurs became more robust as they grew larger, but the extremely massive jaw seen in the largest individual is striking.

It is possible that the robust jaws were in some way related to feeding and the need to generate high bite forces. This raises the question however of why large individuals would need much more robust jaws than younger ones. Also, the dentary is unusual in that it is not simply deep (which improves the jaws resistance in dorsoventral bending experienced during biting down) but expanded mediolaterally which would increase strength in mediolateral bending and torsion. Furthermore, the small, conical teeth of *Pluridens* imply that they were used to pierce and hold relatively small prey items, which raises the issue of why the jaws would be so massive.

Another possibility is that the mandibles were used for fighting. Combat is common in modern whales such as sperm whales (Carrier et al., 2002) and beaked whales (Heyning, 1984; MacLeod, 2002). Male sperm whales appear to use their enlarged melon as a battering ram in combat, and are capable of sinking ships with it, as in the infamous case of the whaleship Essex. In the beaked whale *Mesoplodon*, males bear large bladelike teeth. Scars on their flanks suggest that the teeth are used in combat (Heyning, 1984), and in some species, the bone of the rostrum is extremely dense, which is thought to be an adaptation for combat (MacLeod, 2002).

By analogy, the robust jaws of the largest individuals of *Pluridens serpentis* might be an adaptation for combat. A pathological lesion on one specimen (Fig. 10) is consistent with the idea that the jaws of *Pluridens serpentis* were used in combat, and sometimes suffered injury. Although preservation is poor, rugosity on the lateral surface of the mandible in the holotype of *Pluridens walkeri* may also indicate pathology. Evidence of traumatic injury is

also seen in other mosasaurids, including *Mosasaurus hoffmanni* (Lingham-Soliar, 2004) and *Tylosaurus kansensis* (Everhart, 2008), suggesting it may have been common in mosasaurids. Similar injuries are seen in the jaws of the lepidosaur *Gephyrosaurus* (Evans, 1983), extant lizards, and the jaws of theropod dinosaurs (Tanke and Currie, 1998).

Combat could potentially be over territory or mates. Although mosasaurids would have been able to range widely in search of food, feed is likely to have been highly localized, good 'fishing spots' would have been in demand and mosasaurs may have aggressively defended foraging territories. In whales, combat in both sperm whales (Carrier et al., 2002) and beaked whales (Heyning, 1984) is between males, over mates. By analogy, larger and more robust *Pluridens* jaws may represent males engaging in combat. Among lizards, males sometimes have larger skulls than females (Carothers, 1984) as an adaptation for combat. If so, the differences in size in the *Pluridens* in our sample may at least in part reflect differences in head size, rather than overall body size.

6.3 Paleobiodiversity and palaeobiogeography of Halisaurinae prior to the K-Pg extinction

The late Maastrichtian Phosphates of the Oulad Abdoun Basin of Morocco have the most diverse known mosasaur fauna known from this period, or any other (Bardet et al., 2015). With the addition of *Pluridens*, at least ten species of mosasaur are known (Table 1). Here, as elsewhere, Mosasaurinae dominate in terms of number of species, with other groups such as Plioplatecarpinae and Halisaurinae playing a subordinate role (Bardet et al., 2015). Some species- *Prognathodon* aff. *saturator*, *Mosasaurus beaugei*, *Halisaurus arambourgi*, *Eremiasaurus heterodon*, and *Gavialimimus almaghribensis* dominate in terms of specimens, the others being uncommon to rare. As a result, following discovery of the relatively few common species of the assemblage, uncommon and rare species such as *Pluridens* continue to be discovered. The implication is that the diversity of the fauna remains poorly known and that additional sampling will continue to produce new species. The Moroccan assemblage may therefore be far more diverse than we have appreciated. Future finds will test this hypothesis.

In addition to adding to the species richness of the fauna, *Pluridens* appears to occupy a niche distinct from previously known species in the assemblage. Moroccan mosasaurids were extremely diverse in terms of their ecology (Cappetta et al., 2014; Bardet et al., 2015). In size, the marine squamates ranged from the diminutive *Pachyvaranus* and small *Halisaurus* to the giant *Mosasaurus* and *Prognathodon*. Tooth morphology shows remarkable variation as well, teeth included simple cones, cutting blades, and blunt crushing morphologies (Bardet et al., 2015); likewise jaw and skull structures vary, suggesting distinct feeding styles.

Pluridens is distinct from other Moroccan mosasaurids in terms of combining large size (estimated 6-10 m long), relatively small piercing and poorly heterodont dentition, and small eyes. It apparently hunted in a different way than *Halisaurus* or other mosasaurids in the assemblage. *Pluridens* therefore expands not just the species richness but the ecological disparity and functional diversity of the fauna.

In addition to contributing to our understanding of diversity and disparity, mosasaurid faunas from the Maastrichtian of Morocco document the existence of a distinct fauna found in the southern Tethys Margin Province, including the Arabo-African Platform and Brazil. The fauna of this province differs from those known elsewhere at the time such as the northwest Pacific of California, the southwest Pacific of New Zealand, and especially the Northern

Tethys Margin Province of New Jersey and Europe (Bardet, 2012; Cappetta et al., 2014; Bardet et al., 2015). The faunas can be segregated into these two provinces (as defined by Bardet, 2012), respectively developed around palaeolatitudes 20°N-20°S into intertropical environments *versus* palaeolatitudes 30-40°N into warm-temperate environments. The precise reasons for these differences remain unknown, but these patterns probably reveal palaeoecological preferences linked to differences in palaeolatitudinal gradients and/or to palaeocurrents (Bardet, 2012).

Within the palaeobiogeographical framework of the Southern Tethys Margin Province, and specifically the Arabo-African Platform, the mosasaurids (and Maastrichtian marine reptiles in general) from Morocco show high affinities with those of Angola and the Middle-East. Those from the Iullemmeden intracratonic basin - one of the major Meso-Cenozoic basins of Central West Africa, cropping out mainly in Niger and Nigeria - were considered as endemic (see Bardet, 2012 for details). The most emblematic mosasaurids of the Iullemmeden Basin are *Goronyosaurus nigeriensis*, *Igdamanosaurus aegyptiacus* and *Pluridens walkeri* (see Bardet, 2012 for details). With the recent description of new species of *Pluridens* in Niger (Longrich, 2016) and now Morocco (this work), this palaeobiogeographical framework is changing: *Pluridens* no longer represents an endemic taxon from the Iullemmeden Basin but rather emphasizes a broader African distribution. It seems probable that the Trans-Saharian Seaway (and the Iullemmeden Basin, being a diverticulum of it) that connected the Tethys to the southern Atlantic ocean during the Maastrichtian transgression (Moody and Sutcliffe, 1991; Rat et al., 1991) played an important role in dispersion of these faunas and of *Pluridens* in particular (Fig. 14). *Pluridens*, being unknown in coeval Maastrichtian assemblages from the Northern Tethys Margin Province (Europe and New Jersey; Bardet, 2012), or the Moreno Formation of California (Lindgren and Schulp, 2010), underscores this pattern.

Given their high degree of aquatic specialization, mosasaurids should have dispersed readily across oceans. Some genera, such as *Mosasaurus*, *Prognathodon*, *Halisaurus*, and even *Carinodens* did so (Bardet et al., 2014) . Other lineages with more restricted distributions, such as *Pluridens* and *Plotosaurus*, apparently did not. The biogeographical distribution of some current nectonic cetaceans - able to cross oceans due to their high degree of marine specialisation like mosasaurids, shows the complexity of these patterns: whereas *Orca* and *Physeter* have worldwide distributions, the delphinid *Lagenorhynchus* exhibits narrow latitudinal distributions, with for example *L. cruciger* being tropical and *L.albirostris* being circum-Antarctic (Bardet, 2012). It is commonly thought that large taxa are more able than smaller ones to disperse across large marine expanses. The mosasaurid examples cited above – especially *Plotosaurus* versus *Carinodens* - suggest that size does not necessarily play a primary role in driving dispersal and geographic range.

The endemism seen in mosasaurs was thus likely driven not by dispersal ability, but by constraints imposed by climate, food availability, competitors, and predators. Endemism can be seen as another kind of niche specialization- geographic and habitat specialization- and in this light, agrees with the idea that many Maastrichtian mosasaurids , including *Pluridens*, were highly specialized.

Taken together, the mosasaurid fauna from the Maastrichtian Phosphates of Morocco suggests high species richness, a high diversity of niches occupied, and of endemism, i.e. geographic specialization. This last pattern also predicts that global mosasaur diversity, both

in terms of niche occupation and species richness, will increase as geographic sampling improves.

7. Conclusions

Mosasaurid fossils from the late Maastrichtian Phosphates of Morocco document a new species of halisaurine, *Pluridens serpentis*, emphasizing the high diversity of the fauna. *Pluridens* is unusual among mosasaurs in combining large size and specializations for capturing small prey. Small eyes and numerous neurovascular foramina in the rostrum imply a reliance on nonvisual foraging, perhaps at great depths, or at night. Absence of *Pluridens* from Europe and North America suggests that despite being able to disperse long distances, this taxon was rather endemic to the epicontinantal seas of western Africa (Oulad Abdoun Basin of Morocco and Iullemeden Basin of Niger-Nigeria). *Pluridens. serpentis* provides additional evidence for the existence of a highly diverse, specialized, and mosasaurid fauna with specialized distribution in the late Maastrichtian, mirroring patterns observed for other marine reptiles (Vincent et al., 2011), immediately prior to the end-Cretaceous mass extinction. These patterns support a catastrophic extinction of marine reptiles at the K-Pg boundary.

References

Álvarez–Herrera, G., Agnolin, F., Novas, F., 2020. A rostral neurovascular system in the mosasaur Taniwhasaurus antarcticus. The Science of Nature 107, 1-5.

Arambourg, C., 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). Notes et Mémoires du Service Géologique du Maroc. 92, 1-372.

Bardet, N., 2012. Maastrichtian marine reptiles of the Mediterranean Tethys: a palaeobiogeographical approach. Bulletin de la Société Géologique de France 183, 573-596.

Bardet, N., Falconnet, J., Fischer, V., Houssaye, A., Jouve, S., Pereda-Suberbiola, X., Perez-García, A., Rage, J.-C., Vincent, P., 2014. Mesozoic marine reptile palaeobiogeography in response to drifting plates. Gondwana Research 26, 869-887.

Bardet, N., Gheerbrant, E., Noubhani, A., Cappetta, H., Jouve, S., Bourdon, E., Pereda-Suberbiola, X., Jalil, N.-E., Vincent, P., Houssaye, A., Solé, F., El Houssaini Darif, K., Adnet, S., Rage, J.-C., Lapparent de Broin de, F., Sudre, J., Bouya, B., Amaghzaz, M., Meslouh, S., 2017. Les Vertébrés des phosphates crétacés-paléogènes (72, 1-47, 8 Ma) du Maroc, Mémoires de la Société Géologique de France N.S. 180, pp. 351-452.

Bardet, N., Houssaye, A., Vincent, P., Pereda-Suberbiola, X., Amaghzaz, M., Jourani, E., Meslouh, S., 2015. Mosasaurids (Squamata) from the Maastrichtian phosphates of Morocco: biodiversity, palaeobiogeography and palaeoecology based on tooth morphoguilds. Gondwana Research 27, 1068-1078.

Bardet, N., Jalil, N.-E., de Lapparent de Broin, F., Germain, D., Lambert, O., Amaghzaz, M., 2013. A Giant Chelonioid Turtle from the Late Cretaceous of Morocco with a Suction Feeding Apparatus Unique among Tetrapods. PLoS ONE 8, e63586.

Bardet, N., Pereda-Suberbiola, X., 2001. The basal mosasaurid *Halisaurus sternbergii* from the Late Cretaceous of Kansas (North America): a review of the Uppsala type specimen. Comptes Rendus de l'Academie des Sciences-Series IIA-Earth and Planetary Science 332, 395-402.

Bardet, N., Pereda-Suberbiola, X., Iarochène, M., Amalik, M., Bouya, B., 2005a. Durophagous Mosasauridae (Squamata) from the Upper Cretaceous phosphates of Morocco, with description of a new species of *Globidens*. Netherlands Journal of Geosciences 84, 167-175.

Bardet, N., Pereda-Suberbiola, X., Iarochène, M., Bouya, B., Amaghzaz, M., 2005b. A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the Halisaurinae (Squamata: Mosasauridae). Zoological Journal of the Linnean Society 143, 447-472.

Bardet, N., Pereda-Suberbiola, X., Iarochène, M., Bouyahyaoui, F., Bouya, B., Amaghzaz, M., 2004. *Mosasaurus beaugei* Arambourg, 1952 (Squamata, Mosasauridae) from the Late Cretaceous phosphates of Morocco. Geobios 37, 315-324.

Bardet, N., Pereda-Suberbiola, X., Jalil, N.-E., 2003. A new mosasauroid (Squamata) from the Late Cretaceous (Turonian) of Morocco. Comptes Rendus Palevol 2, 607-616.

Bardet, N., Pereda-Suberbiola, X., Jouve, S., Bourdon, E., Vincent, P., Houssaye, A., Rage, J.-C., Jalil, N.-E., Bouya, B., Amaghzaz, M., 2010. Reptilian assemblages from the latest Cretaceous–Palaeogene phosphates of Morocco: from Arambourg to present time. Historical Biology 22, 186-199.

Bardet, N., Pereda-Suberbiola, X., Schulp, A.S., Bouya, B., 2008. New material of *Carinodens* (Squamata, Mosasauridae) from the Maastrichtian (Late Cretaceous) phosphates of Morocco, Proceedings of the Second Mosasaur Meeting. Fort Hays Studies, Special, pp. 29-36.

Bell, G., Polcyn, M., 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). Netherlands Journal of Geosciences 84, 177.

Bell Jr., G.L., 1997. A phylogenetic revision of North American and Adriatic Mosasauroidea, Ancient marine reptiles. Elsevier, pp. 293-332.

Brischoux, F., Bonnet, X., Shine, R., 2007. Foraging ecology of sea kraits *Laticauda* spp. in the Neo-Caledonian Lagoon. Marine Ecology Progress Series 350, 145-151.

Brischoux, F., Bonnet, X., Shine, R., 2009. Determinants of dietary specialization: a comparison of two sympatric species of sea snakes. Oikos 118, 145-151.

Caldwell, M.W., 2007. Ontogeny, anatomy and attachment of the dentition in mosasaurs (Mosasauridae: Squamata). Zoological Journal of the Linnean Society 149, 687-700.

Caldwell, M.W., Cooper, J.A., 1999. Redescription, palaeobiogeography and palaeoecology of *Coniasaurus crassidens* OWEN, 1850 (Squamata) from the Lower Chalk (Cretaceous; Cenomanian) of SE England. Zoological Journal of the Linnean Society 127, 423-452.

Cappetta, H., 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. Handbook of paleoichthyology 3, 1-193.

Cappetta, H., Bardet, N., Pereda-Suberbiola, X., Adnet, S., Akkrim, D., Amalik, M., Benabdallah, A., 2014. Marine vertebrate faunas from the Maastrichtian phosphates of Benguérir (Ganntour Basin, Morocco): Biostratigraphy, palaeobiogeography and palaeoecology. Palaeogeography, Palaeoclimatology, Palaeoecology 409, 217-238.

Carothers, J.H., 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. The American Naturalist 124, 244-254.

Carrier, D.R., Deban, S.M., Otterstrom, J., 2002. The face that sank the Essex: potential function of the spermaceti organ in aggression. Journal of Experimental Biology 205, 1755-1763.

Crowe-Riddell, J.M., Snelling, E.P., Watson, A.P., Suh, A.K., Partridge, J.C., Sanders, K.L., 2016. The evolution of scale sensilla in the transition from land to sea in elapid snakes. Open biology 6, 160054.

Crowe-Riddell, J.M., Williams, R., Chapuis, L., Sanders, K.L., 2019. Ultrastructural evidence of a mechanosensory function of scale organs (sensilla) in sea snakes (Hydrophiinae). Royal Society open science 6, 182022.

DeBraga, M., Carroll, R.L., 1993. The origin of mosasaurs as a model of macroevolutionary patterns and processes, Evolutionary biology. Springer, pp. 245-322.

Di-Poï, N., Milinkovitch, M.C., 2013. Crocodylians evolved scattered multi-sensory micro-organs. EvoDevo 4, 1-16.

Dunson, W.A., Minton, S.A., 1978. Diversity, distribution, and ecology of Philippine marine snakes (Reptilia, Serpentes). Journal of Herpetology, 281-286.

Evans, S.E., 1983. Mandibular fracture and inferred behavior in a fossil reptile. Copeia 1983, 845-847.

Everhart, M., 2005. *Tylosaurus kansasensis*, a new species of tylosaurine (Squamata, Mosasauridae) from the Niobrara Chalk of western Kansas, USA. Netherlands Journal of Geosciences-Geologie en Mijnbouw 84, 231-240.

Everhart, M.J., 2008. A bitten skull of *Tylosaurus kansasensis* (Squamata: Mosasauridae) and a review of mosasaur-on-mosasaur pathology in the fossil record. Transactions of the Kansas Academy of Science 111, 251-262.

Fernández, M.S., Talevi, M., 2015. An halisaurine (Squamata: Mosasauridae) from the Late Cretaceous of Patagonia, with a preserved tympanic disc: insights into the mosasaur middle ear. Comptes Rendus Palevol 14, 483-493.

Foffa, D., Sassoon, J., Cuff, A.R., Mavrogordato, M.N., Benton, M.J., 2014. Complex rostral neurovascular system in a giant pliosaur. Naturwissenschaften 101, 453-456.

Frey, E., Mulder, E.W., Stinnesbeck, W., Salazar, C., Quinzio-Sinn, L.A.H., 2016. A mosasaur, cf. *Plotosaurus*, from the upper Maastrichtian Quiriquina Formation in Central Chile. Cretaceous Research 61, 17-25.

Gervais, P., 1852. Zoologie et paléontologie françaises (animaux vertébrés): nouvelles recherches sur les animaux vivants del la France. Arthus Bertrand.

Heyning, J.E., 1984. Functional morphology involved in intraspecific fighting of the beaked whale, Mesoplodon carlhubbsi. Canadian Journal of Zoology 62, 1645-1654.

Holmes, R.B., Sues, H.-D., 2000. A partial skeleton of the basal mosasaur *Halisaurus platyspondylus* from the Severn Formation (Upper Cretaceous: Maastrichtian) of Maryland. Journal of Vertebrate Paleontology 74, 309-316.

Houssaye, A., Bardet, N., Rage, J.-C., Pereda-Suberbiola, X., Bouya, B., Amaghzaz, M., Amalik, M., 2011. A review of *Pachyvaranus crassispondylus* Arambourg, 1952, a pachyostotic marine squamate from the latest Cretaceous phosphates of Morocco and Syria. Geological Magazine 148, 237-249.

Jiménez-Huidobro, P., Otero, R.A., Soto-Acuña, S., Caldwell, M.W., 2019. Reassessment of cf. *Plotosaurus* from the upper Maastrichtian of Chile, with comments on the South American distribution of halisaurine mosasaurs. Cretaceous Research 103, 104162.

Jouve, S., Bardet, N., Jalil, N.-E., Pereda-Suberbiola, X., Bouya, B., Amaghzaz, M., 2008. The oldest African crocodylian: phylogeny, paleobiogeography, and differential survivorship of marine reptiles through the Cretaceous-Tertiary boundary. Journal of Vertebrate Paleontology 28, 409-421.

Kocsis, L., Gheerbrant, E., Mouflih, M., Cappetta, H., Yans, J., Amaghzaz, M., 2014. Comprehensive stable isotope investigation of marine biogenic apatite from the Late Cretaceous–Early Eocene phosphate series of Morocco. Palaeogeography, Palaeoclimatology, Palaeoecology 394, 74-88.

Konishi, T., Brinkman, D., Massare, J.A., Caldwell, M.W., 2011. New exceptional specimens of *Prognathodon overtoni* (Squamata, Mosasauridae) from the upper Campanian of Alberta, Canada, and the systematics and ecology of the genus. Journal of Vertebrate Paleontology 31, 1026-1046.

Konishi, T., Caldwell, M.W., 2011. Two new plioplatecarpine (Squamata, Mosasauridae) genera from the Upper Cretaceous of North America, and a global phylogenetic analysis of plioplatecarpines. Journal of Vertebrate Paleontology 31, 754-783.

Konishi, T., Caldwell, M.W., Nishimura, T., Sakurai, K., Tanoue, K., 2016. A new halisaurine mosasaur (Squamata: Halisaurinae) from Japan: the first record in the western Pacific realm and the first documented insights into binocular vision in mosasaurs. Journal of Systematic Palaeontology 14, 809-839.

Konishi, T., Lindgren, J., Caldwell, M.W., Chiappe, L., 2012. *Platecarpus tympaniticus* (Squamata, Mosasauridae): osteology of an exceptionally preserved specimen and its insights into the acquisition of a streamlined body shape in mosasaurs. Journal of Vertebrate Paleontology 32, 1313-1327.

Kutsuma, R., Sasai, T., Kishida, T., 2018. How snakes find prey underwater: sea snakes use visual and chemical cues for foraging. Zoological science 35, 483-486.

Lapparent de Broin, F.d., Bardet, N., Amaghzaz, M., Meslouh, S., 2013. A strange new chelonioid turtle from the Latest Cretaceous phosphates of Morocco. Comptes Rendus Palevol 13, 87-95.

LeBlanc, A.R., Lamoureux, D.O., Caldwell, M.W., 2017. Mosasaurs and snakes have a periodontal ligament: timing and extent of calcification, not tissue complexity, determines tooth attachment mode in reptiles. Journal of Anatomy 231, 869-885.

LeBlanc, A.R., Mohr, S.R., Caldwell, M.W., 2019. Insights into the anatomy and functional morphology of durophagous mosasaurines (Squamata: Mosasauridae) from a new species of *Globidens* from Morocco. Zoological Journal of the Linnean Society 186, 1026-1052.

LeBlanc, A.R.H., Caldwell, M.W., Bardet, N., 2012. A new mosasaurine from the Maastrichtian (Upper Cretaceous) phosphates of Morocco and its implications for mosasaurine systematics. Journal of Vertebrate Paleontology 32, 82-104.

Leitch, D.B., Catania, K.C., 2012. Structure, innervation and response properties of integumentary sensory organs in crocodilians. Journal of Experimental Biology 215, 4217-4230.

Lindgren, J., Caldwell, M.W., Jagt, J.W., 2008. New data on the postcranial anatomy of the California mosasaur *Plotosaurus bennisoni* (Camp, 1942)(Upper Cretaceous: Maastrichtian), and the taxonomic status of P. tuckeri (Camp, 1942). Journal of Vertebrate Paleontology 28, 1043-1054.

Lindgren, J., Schulp, A.S., 2010. New material of *Prognathodon* (Squamata: Mosasauridae), and the mosasaur assemblage of the Maastrichtian of California, USA. Journal of Vertebrate Paleontology 30, 1632-1636.

Lindgren, J., Siverson, M., 2005. *Halisaurus sternbergi*, a small mosasaur with an intercontinental distribution. Journal of Paleontology 79, 763-773.

Lingham-Soliar, T., 1994. The mosasaur *Plioplatecarpus* (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe. Bulletin-Institut royal des sciences naturelles de Belgique. Sciences de la terre 64, 177-211.

Lingham-Soliar, T., 1995. Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae, Reptilia) from the Upper Cretaceous, Upper Maastrichtian of the Netherlands. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 347, 155-180.

Lingham-Soliar, T., 1996. The first description of *Halisaurus* (Reptilia Mosasauridae) from Europe, from the Upper Cretaceous of Belgium. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 66, 129-136.

Lingham-Soliar, T., 1998. A new mosasaur *Pluridens walkeri* from the Upper Cretaceous, Maastrichtian of the Iullemmeden Basin, southwest Niger. Journal of Vertebrate Paleontology 18, 709-717.

Lingham-Soliar, T., Nolf, D., 1989. The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre 59, 137-190.

Lingham-Soliar, T., 2004. Palaeopathology and injury in the extinct mosasaurs (Lepidosauromorpha, Squamata) and implications for modern reptiles. Lethaia 37, 255-262.

Liu, M., Reed, D.A., Cecchini, G.M., Lu, X., Ganjawalla, K., Gonzales, C.S., Monahan, R., Luan, X., Diekwisch, T.G., 2016. Varanoid tooth eruption and implantation modes in a late Cretaceous mosasaur. Frontiers in Physiology 7, 145.

Lively, J.R., 2018. Taxonomy and historical inertia: *Clidastes* (Squamata: Mosasauridae) as a case study of problematic paleobiological taxonomy. Alcheringa: An Australasian Journal of Palaeontology 42, 516-527.

Longrich, N.R., 2016. A new species of *Pluridens* (Mosasauridae: Halisaurinae) from the upper Campanian of Southern Nigeria. Cretaceous Research 64, 36-44.

Longrich, N.R., Bardet, N., Schulp, A.S., Jalil, N.-E., 2021. *Xenodens calminechari* gen. et sp. nov., a bizarre mosasaurid (Mosasauridae, Squamata) with shark-like cutting teeth from the upper Maastrichtian of Morocco, North Africa. Cretaceous Research, 104764.

Longrich, N.R., Martill, D.M., Andres, B., 2018. Late Maastrichtian pterosaurs from North Africa and mass extinction of Pterosauria at the Cretaceous-Paleogene boundary. PLoS Biology 16, e2001663.

Longrich, N.R., Pereda-Suberbiola, X., Jalil, N.-E., Khaldoune, F., Jourani, E., 2017. An abelisaurid from the latest Cretaceous (late Maastrichtian) of Morocco, North Africa. Cretaceous Research 76, 40-52.

Longrich, N.R., Pereda-Suberbiola, X., Pyron, R.A., Jalil, N.-E., 2020. The first duckbill dinosaur (Hadrosauridae: Lambeosaurinae) from Africa and the role of oceanic dispersal in dinosaur biogeography. Cretaceous Research, 104678.

Luan, X., Walker, C., Dangaria, S., Ito, Y., Druzinsky, R., Jarosius, K., Lesot, H., Rieppel, O., 2009. The mosasaur tooth attachment apparatus as paradigm for the evolution of the gnathostome periodontium. Evolution & development 11, 247-259.

MacLeod, C.D., 2002. Possible functions of the ultradense bone in the rostrum of Blainville's beaked whale (*Mesoplodon densirostris*). Canadian Journal of Zoology 80, 178-184.

Martill, D.M., Smith, R.E., Longrich, N., Brown, J., 2021. Evidence for tactile foraging in pterosaurs: a sensitive tip to the beak of *Lonchodraco giganteus* (Pterosauria, Lonchodectidae) from the Upper Cretaceous of southern England. Cretaceous Research 117, 104637.

Martill, D.M., Tischlinger, H., Longrich, N.R., 2015. A four-legged snake from the Early Cretaceous of Gondwana. Science 349, 416-419.

Martin, J.E., Vincent, P., Tacail, T., Khaldoune, F., Jourani, E., Bardet, N., Balter, V., 2017. Calcium isotopic evidence for vulnerable marine ecosystem structure prior to the K/Pg extinction. Current Biology 27, 1641-1644. e1642.

Mayes, P., Thompson, G., Withers, P., 2005. Diet and foraging behaviour of the semi-aquatic *Varanus mertensi* (Reptilia: Varanidae). Wildlife Research 32, 67-74.

Moody, R., Sutcliffe, P., 1991. The Cretaceous deposits of the Iullemmeden basin of Niger, central West Africa. Cretaceous Research 12, 137-157.

Oppel, M., 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben. Lindauer, München.

Páramo-Fonseca, M.E., 2013. *Eonatator coellensis* nov. sp.(Squamata: Mosasauridae), a new species from the Upper Cretaceous of Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 37, 499-518.

Pereda-Suberbiola, X., Bardet, N., Iarochène, M., Bouya, B., Amaghzaz, M., 2004. The first record of a sauropod dinosaur from the Late Cretaceous phosphates of Morocco. Journal of African Earth Sciences 40, 81-88.

Pereda-Suberbiola, X., Bardet, N., Jouve, S., Iarochène, M., Bouya, B., Amaghzaz, M., 2003. A new azhdarchid pterosaur from the Late Cretaceous phosphates of Morocco. Geological Society, London, Special Publications 217, 79-90.

Polcyn, M.J., Jacobs, L.L., Araújo, R., Schulp, A.S., Mateus, O., 20134. Physical drivers of mosasaur evolution. Palaeogeography, Palaeoclimatology, Palaeoecology 400, 17-27.

Polcyn, M.J., Lamb, J., 2012. The snout of *Halisaurus platyspondylus* Marsh 1869: phylogenetic and functional implications. Bulletin de la Societe Geologique de France 183, 137-143.

Polcyn, M.J., Lindgren, J., Bardet, N., Cornelissen, D., Verding, L., Schulp, A.S., 2012. Description of new specimens of *Halisaurus arambourgi* Bardet & Pereda Suberbiola, 2005 and the relationships of Halisaurinae. Bulletin de la Société Géologique de France 183, 123-136.

Radcliffe, C.W., Chiszar, D.A., 1980. A descriptive analysis of predatory behavior in the yellow lipped sea krait (*Laticauda colubrina*). Journal of Herpetology 14, 422-424.

Rat, P., Lang, J., Alzouma, K., Dikouma, M., Johnson, A., Laurin, B., Mathey, B., Pascal, A., 1991. Coastal marine basins as records of continental palaeoenvironments (Gulf of Guinea and Iullemmeden Cretaceous and Tertiary basins). Journal of African Earth Sciences (and the Middle East) 12, 23-30.

Reeder, T.W., Townsend, T.M., Mulcahy, D.G., Noonan, B.P., Wood Jr, P.L., Sites Jr, J.W., Wiens, J.J., 2015. Integrated Analyses Resolve Conflicts over Squamate Reptile Phylogeny and Reveal Unexpected Placements for Fossil Taxa. PloS one 10, e0118199.

Rieppel, O., Kearney, M., 2005. Tooth replacement in the Late Cretaceous mosasaur *Clidastes*. Journal of Herpetology 39, 688-692.

Russell, D.A., 1967. Systematics and morphology of American mosasaurs. Bulletin of the Peabody Museum of Natural History 23, 1-240.

Schulp, A.S., Bardet, N., Bouya, B., 2009. A new species of the durophagous mosasaur *Carinodens* (Squamata, Mosasauridae) and additional material of *Carinodens belgicus* from the Maastrichtian phosphates of Morocco. Netherlands Journal of Geosciences 88, 161-167.

Schulp, A.S., Mulder, E., Schwenk, K., 2005. Did mosasaurs have forked tongues? Netherlands Journal of Geosciences 84, 359-371.

Shine, R., Lambeck, R., 1985. A radiotelemetric study of movements, thermoregulation and habitat utilization of Arafura filesnakes (Serpentes: Acrochordidae). Herpetologica, 351-361.

Street, H.P., Caldwell, M.W., 2017. Rediagnosis and redescription of *Mosasaurus hoffmannii* (Squamata: Mosasauridae) and an assessment of species assigned to the genus Mosasaurus. Geological Magazine 154, 521-557.

Strong, C.R., Caldwell, M.W., Konishi, T., Palci, A., 2020. A new species of longirostrine plioplatecarpine mosasaur (Squamata: Mosasauridae) from the Late Cretaceous of Morocco, with a re-evaluation of the problematic taxon '*Platecarpus*' *ptychodon*. Journal of Systematic Palaeontology, 1-36.

Tanke, D.H., Currie, P.J., 1998. Head-biting behavior in the theropod dinosaurs: paleopathological evidence. Gaia 15, 167-184.

Udyawer, V., Simpfendorfer, C.A., Heupel, M.R., 2015. Diel patterns in three-dimensional use of space by sea snakes. Animal Biotelemetry 3, 29.

Van Der Kooij, J., Povel, D., 1996. Scale sensillae of the file snake (Serpentes: Acrochordidae) and some other aquatic and burrowing snakes. Netherlands Journal of Zoology 47, 443-456.

Vincent, P., Bardet, N., Houssaye, A., Amaghzaz, M., Meslouh, S., 2013. New plesiosaur specimens from the Maastrichtian Phosphates of Morocco and their implications for the ecology of the latest Cretaceous marine apex predators. Gondwana Research 24, 796-805.

Vincent, P., Bardet, N., Pereda Suberbiola, X., Bouya, B., Amaghzaz, M., Meslouh, S., 2011. *Zarafasaura oceanis*, a new elasmosaurid (Reptilia: Sauropterygia) from the Maastrichtian Phosphates of Morocco and the palaeobiogeography of latest Cretaceous plesiosaurs. Gondwana Research 19, 1062-1073.

Vincent, S.E., Shine, R., Brown, G.P., 2005. Does foraging mode influence sensory modalities for prey detection in male and female filesnakes, Acrochordus arafurae? Animal Behaviour 70, 715-721.

Vullo, R., Cavin, L., Khalloufi, B., Amaghzaz, M., Bardet, N., Jalil, N.-E., Jourani, E., Khaldoune, F., Gheerbrant, E., 2017. A unique Cretaceous–Paleogene lineage of piranha-jawed pycnodont fishes. Scientific reports 7, 1-9.

Figure Captions
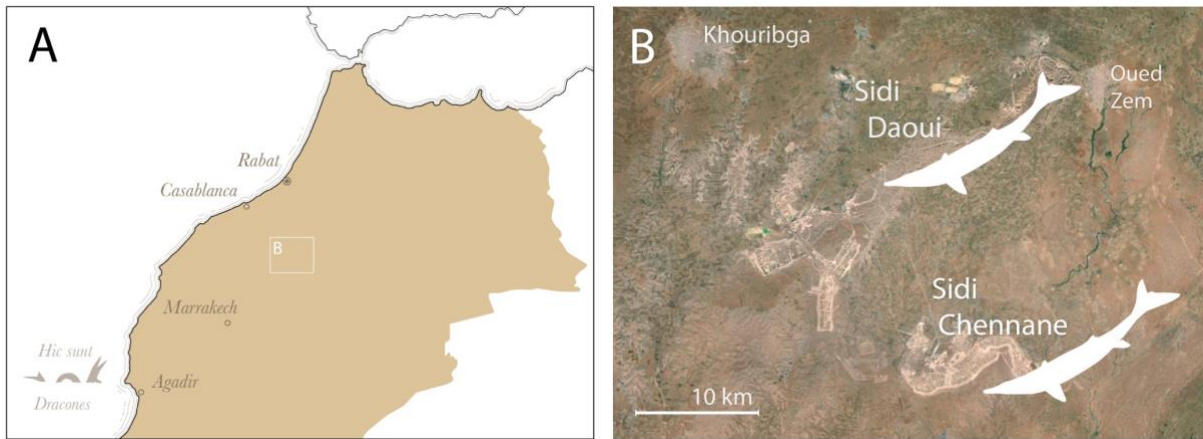
Fig. 1. Map of northern Morocco (A) showing the location of the OCP Group phosphate mines of Sidi Daoui and Sidi Chennane (B).
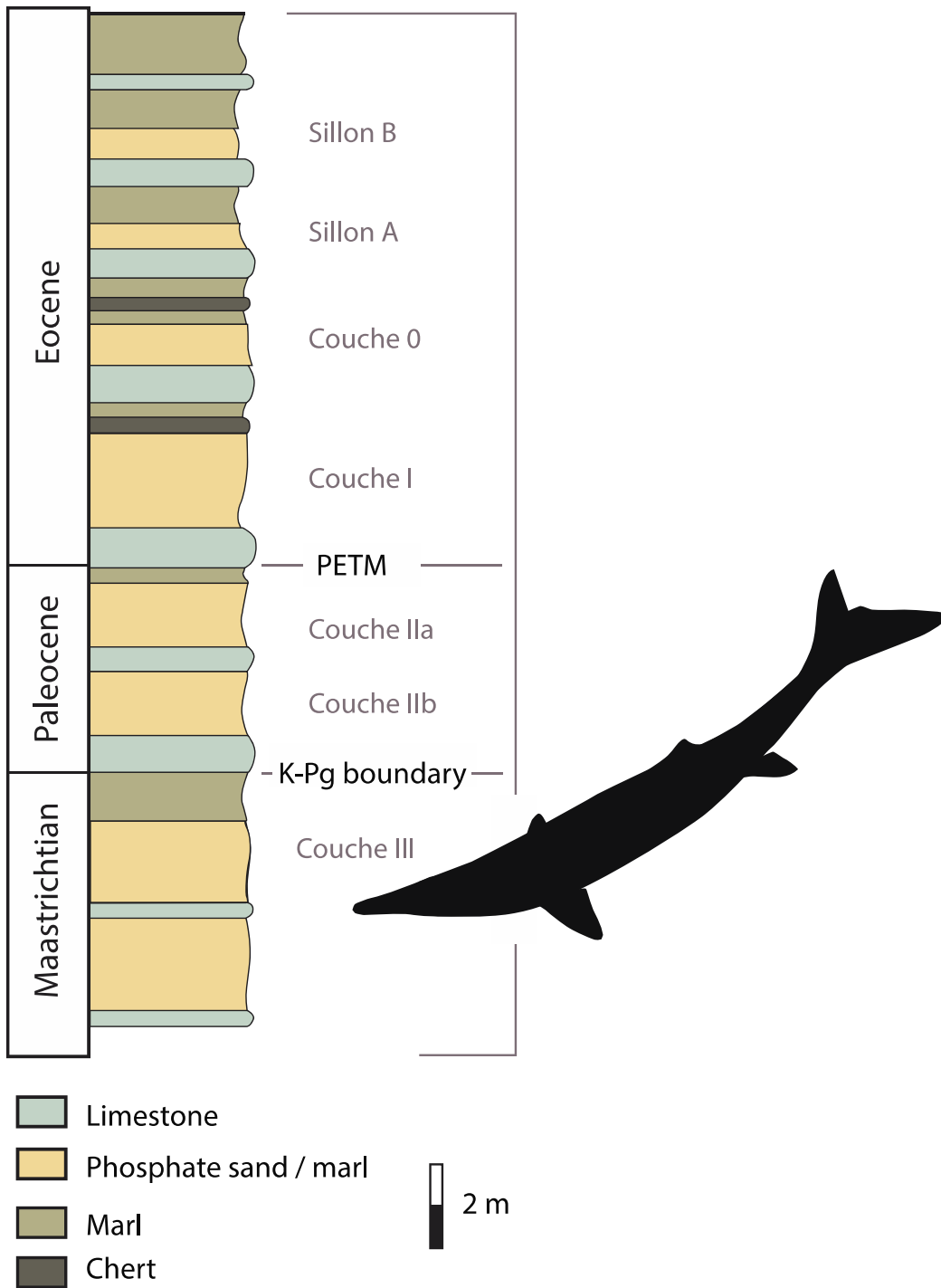
Fig. 2. Schematic stratigraphic column showing the position of *Pluridens serpentis* sp. nov. in the upper Maastrichtian strata of Couche III, Sidi Daoui, Khouribga Province, Morocco. Stratigraphic column after Kocsis et al. (2014).
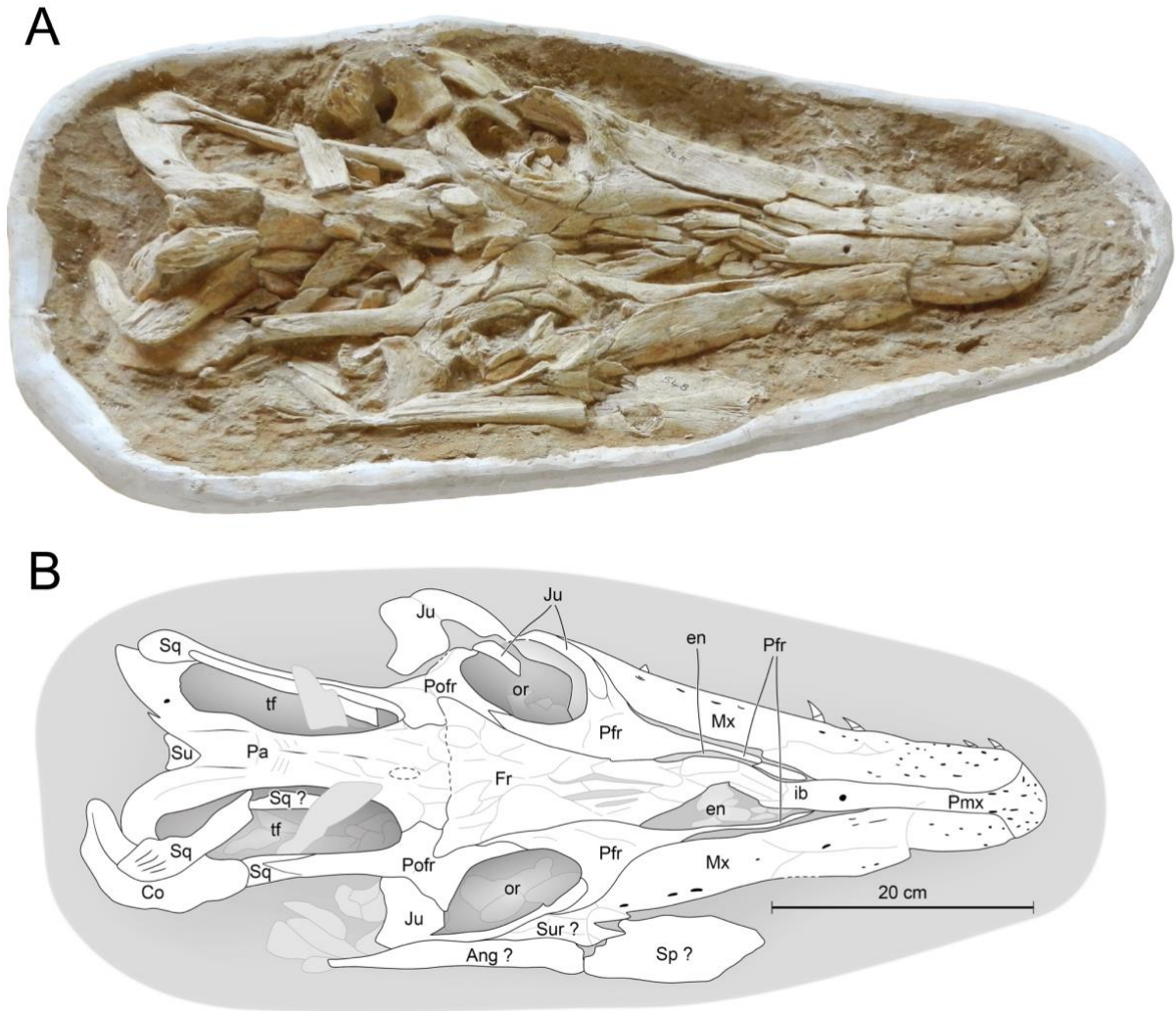
Fig. 3. *Pluridens serpentis* sp. nov, OCP DEK-GE 548, syntype skull ., Couche III, Oulad Abdoun Basin, Sidi Daoui, Morocco. A, skull in dorsal view; B, interpretive drawing. Abbreviations: Ang, angular; Co, coronoid; en, external naris; Fr, frontal; ib, internarial bar; Ju, jugal; Mx, maxilla; or, orbit; Pa, parietal, Pfr, prefrontal, Pmx, premaxilla; Pofr, postorbitofrontal; Sp, splenial; Sq, squamosal; Su, supraoccipital; Sur, surangular; tf, temporal fenestra.
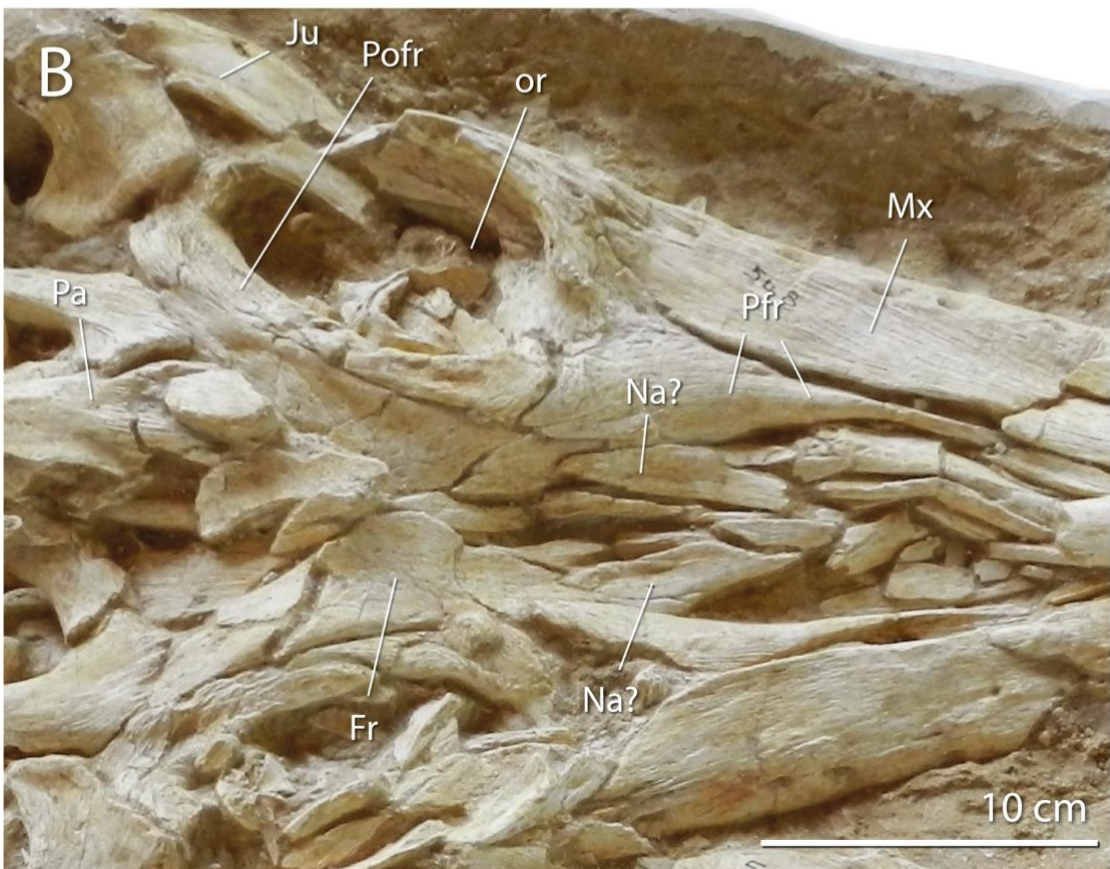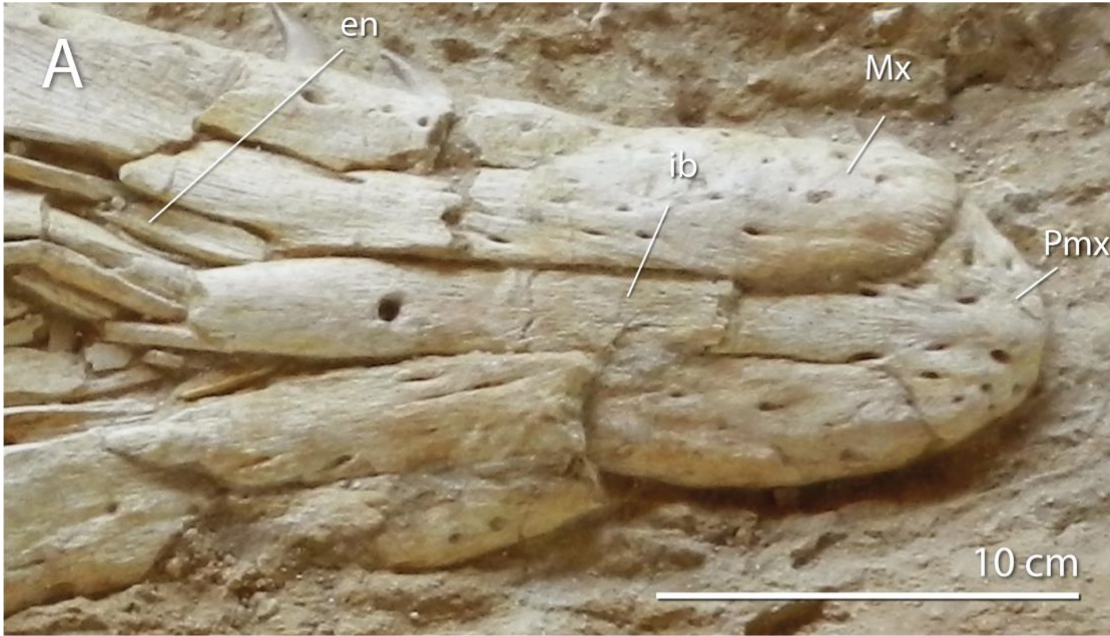
Fig. 4. *Pluridens serpentis* sp. nov.. OCP DEK-GE 548, syntype skull. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. A, closeup of rostrum; B, closeup of skull roof. Abbreviations: en, external naris; Fr, Frontal; ib, internarial bar; Ju, jugal; Mx, Maxilla; Na?, Nasal; or, orbit; Pa, Parietal; Pfr, Prefrontal; Pofr, postorbitofrontal. Scale bars = 10 cm.
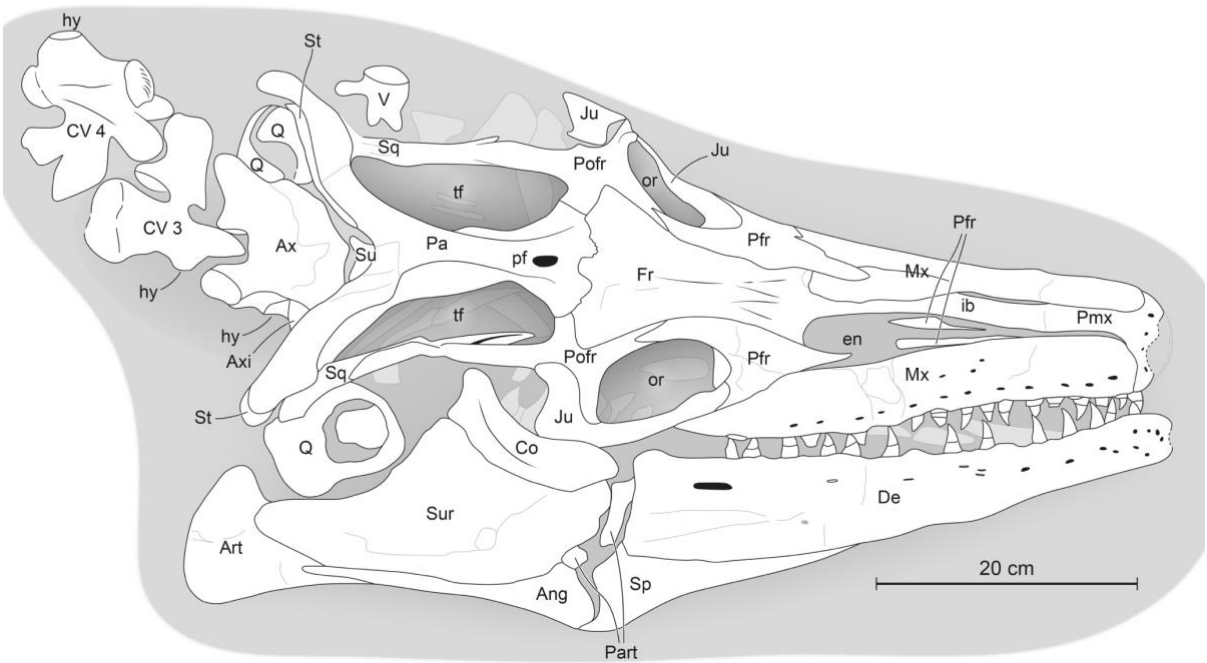
Fig 5. *Pluridens serpentis* sp. nov.. MHNM.KH.262, syntype skull and jaws. Couche III, Oulad AbBdoun Basin, Sidi Daoui , Morocco. Abbreviations: Ang, angular; Art, articular; Ax, Axis; Axi, axial intercentrum; CV, cervical vertebra; Co, coronoid; De, dentary; en, external naris; Fr, frontal; hy, hypapophysis; ib, internarial bar; Ju, jugal; Mx, maxilla; or, orbit; Op-Ex, Opisthothic-Exoccipital; Pa, parietal; Part, prearticular; pf, parietal foramen; Pfr, prefrontal, Pmx, premaxilla; Pofr, postorbitofrontal; Q, quadrate; Sp, splenial; Sq, squamosal; St, Supratemporal; Su, supraoccipital; Sur, surangular; tf, temporal fenestra; V, vertebra.
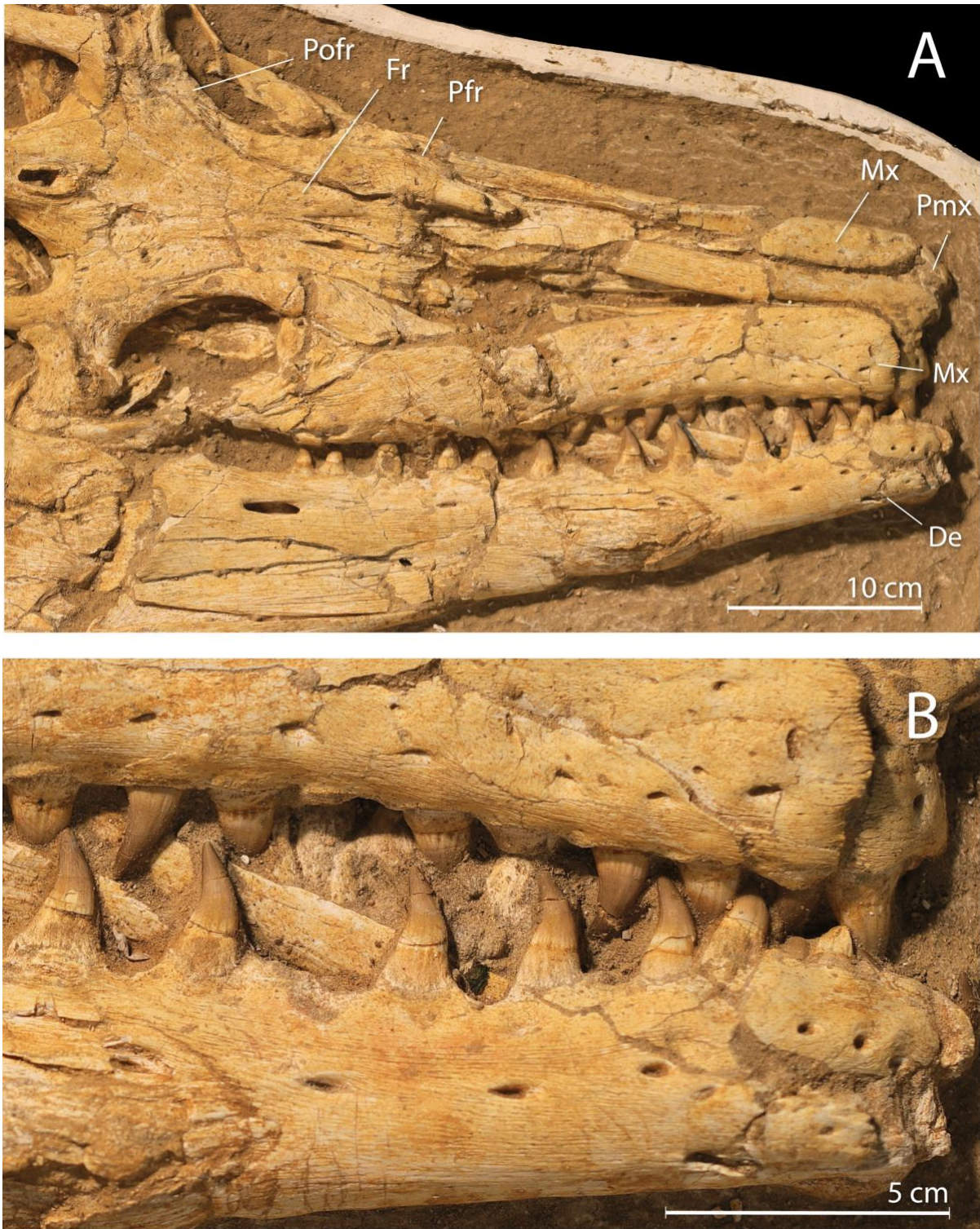
Fig. 6. *Pluridens serpentis* sp. nov., MHNM.KH.262, syntype skull and jaws. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. **A**, rostrum; **B**, anterior dentition. Abbreviations: De, dentary; Fr, frontal; Mx, maxilla, Pfr, prefrontal; Pmx, premaxilla; Pofr, postorbitofrontal.
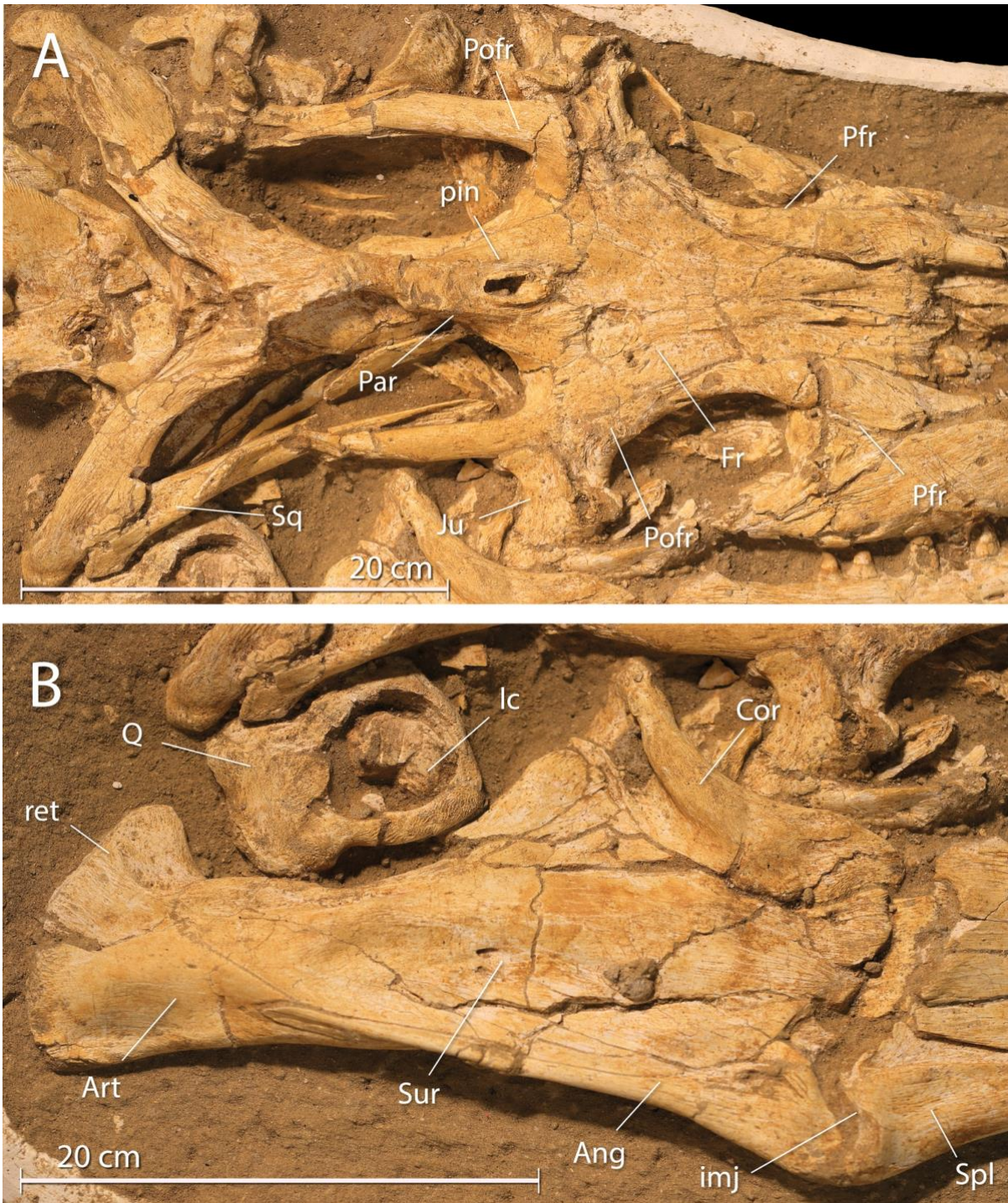
Fig. 7. *Pluridens serpentis* sp. nov., MHNM.KH.262, syntype skull and jaws. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. **A**, Closeup of cranial roof, **B**, closeup of posterior mandible and quadrate. Abbreviations: Ang, angular; Art, articular; Co, coronoid; Fr, frontal; Ju, jugal; lc, lateral conch; Pa, parietal; pf, pineal foramen; Pofr, postfrontal; Pfr, prefrontal; Q, quadrate; ret, retroarticular process; Sp, splenial; Sq, squamosal; Sur, surangular.
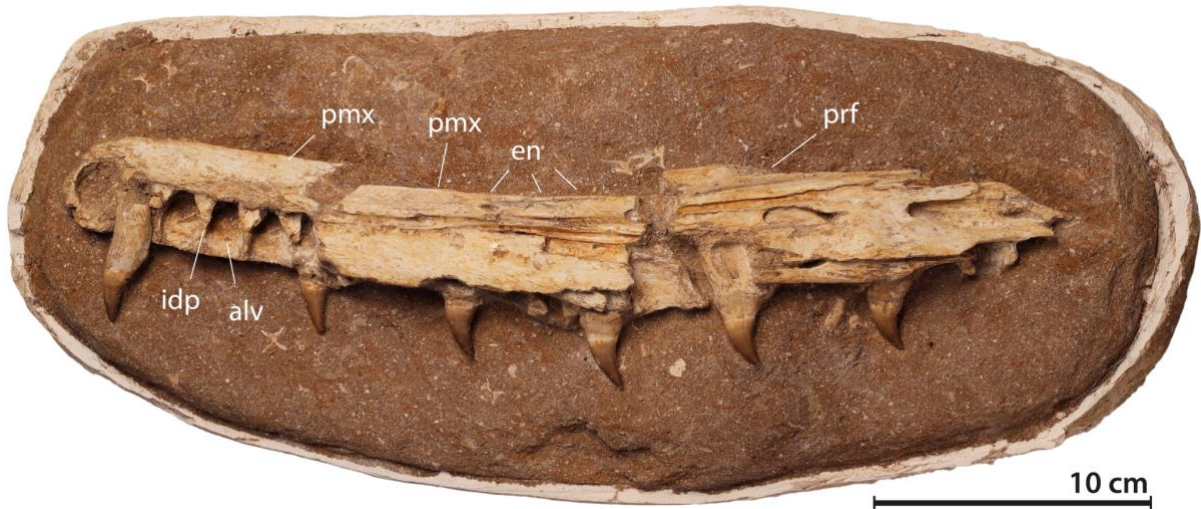
Fig. 8. *Pluridens serpentis* sp. nov., MHNM.KH.390, referred maxilla in medial view. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. Abbreviations: alv, alveolus; en, external naris; idp, interdental plate; pmx, premaxilla contact; prf, prefrontal contact.
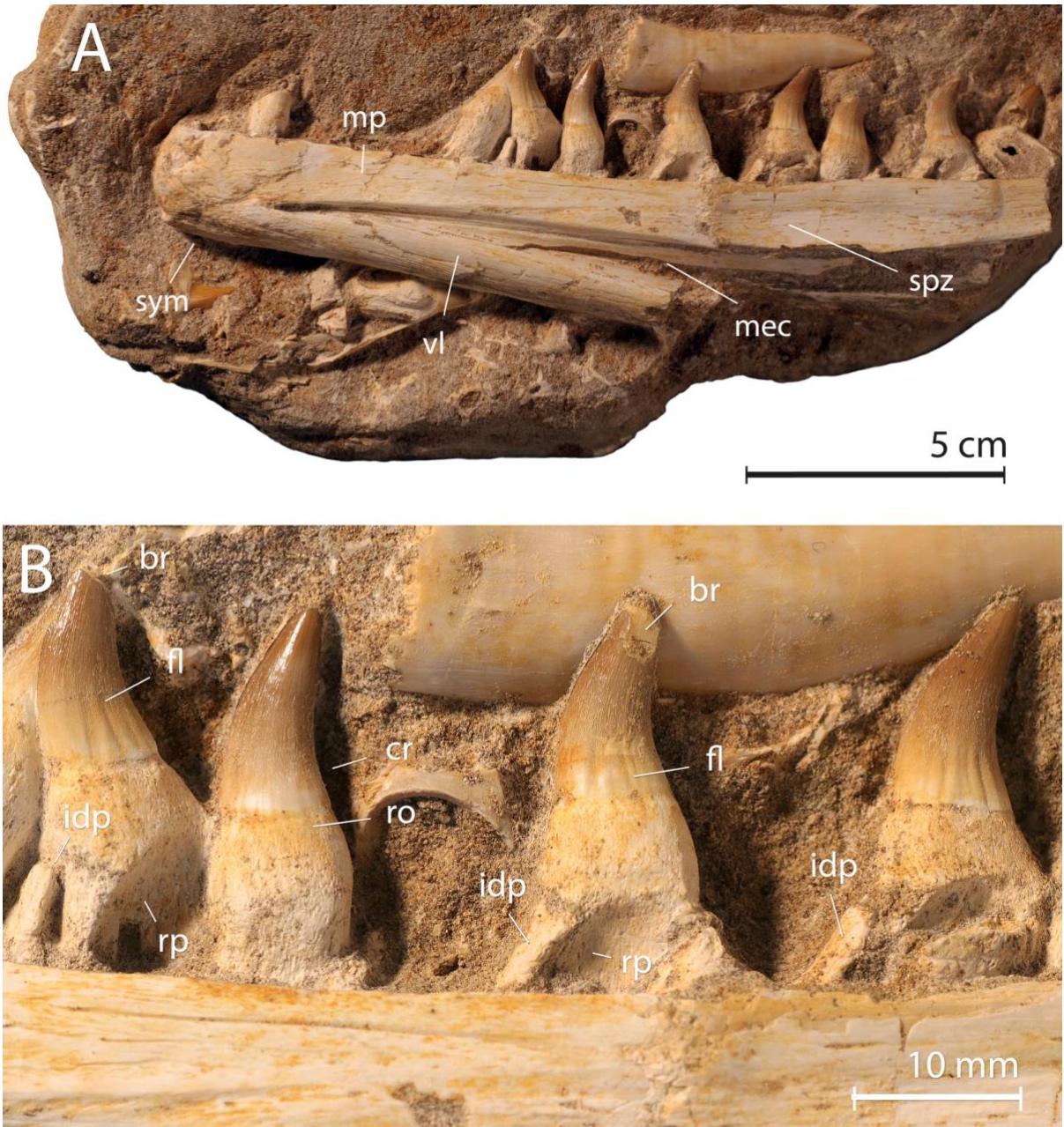
Fig. 9. *Pluridens serpentis* sp. nov., MHNM.KH.389. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. A, referred dentary in medial view; B, closeup showing teeth. Abbreviations: br, broken apex; cr, crown; fl, fluting; idp, interdental plate; mec, meckelian canal; mp, medial parapet; ro, root; rp, replacement pit; sym, symphysis; vl, ventral lip.
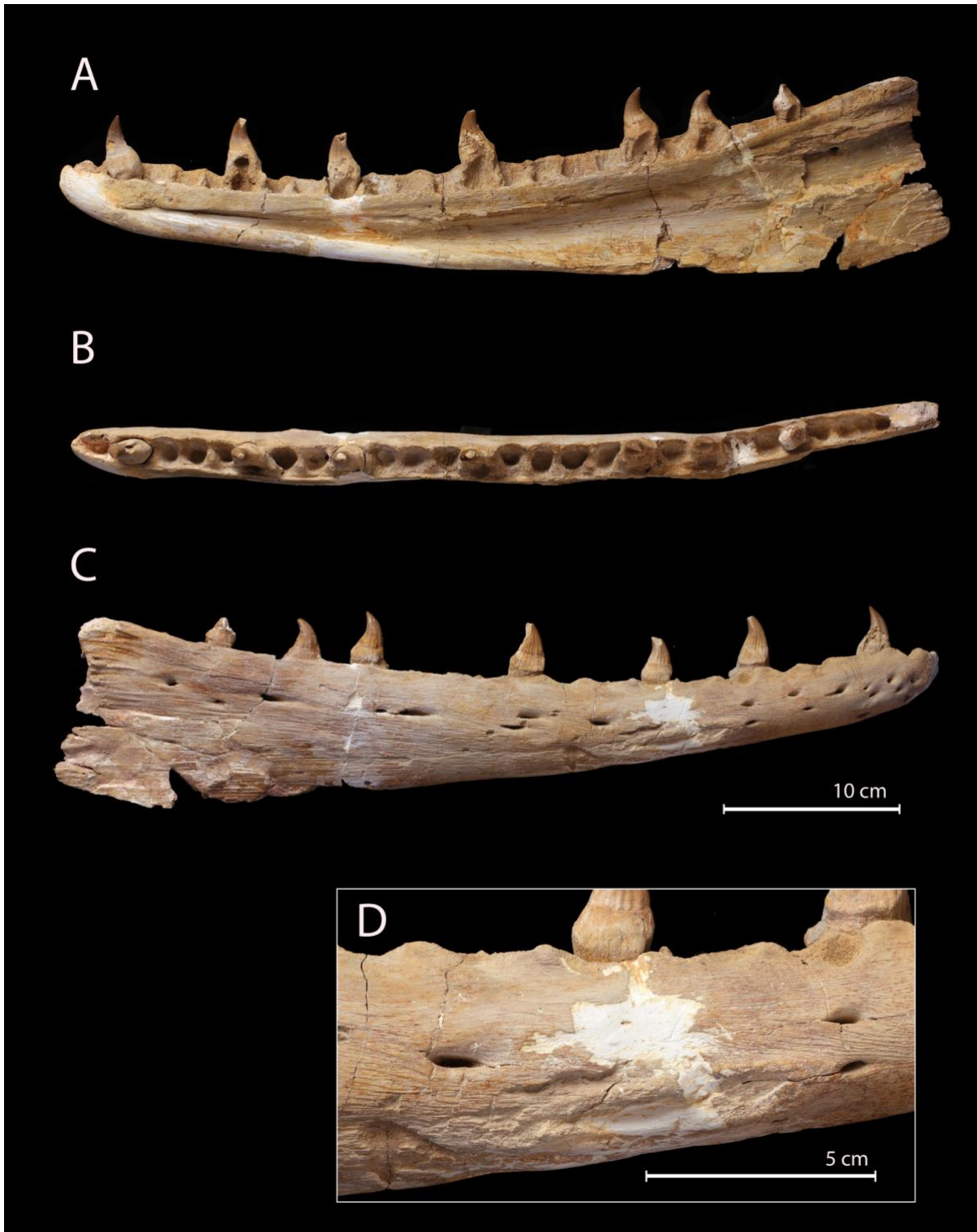
Fig. 10. *Pluridens serpentis* sp. nov., referred dentary. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. MHNM.KH.394, right dentary in A, medial, B, dorsal, C lateral views; D, closeup showing pathology.
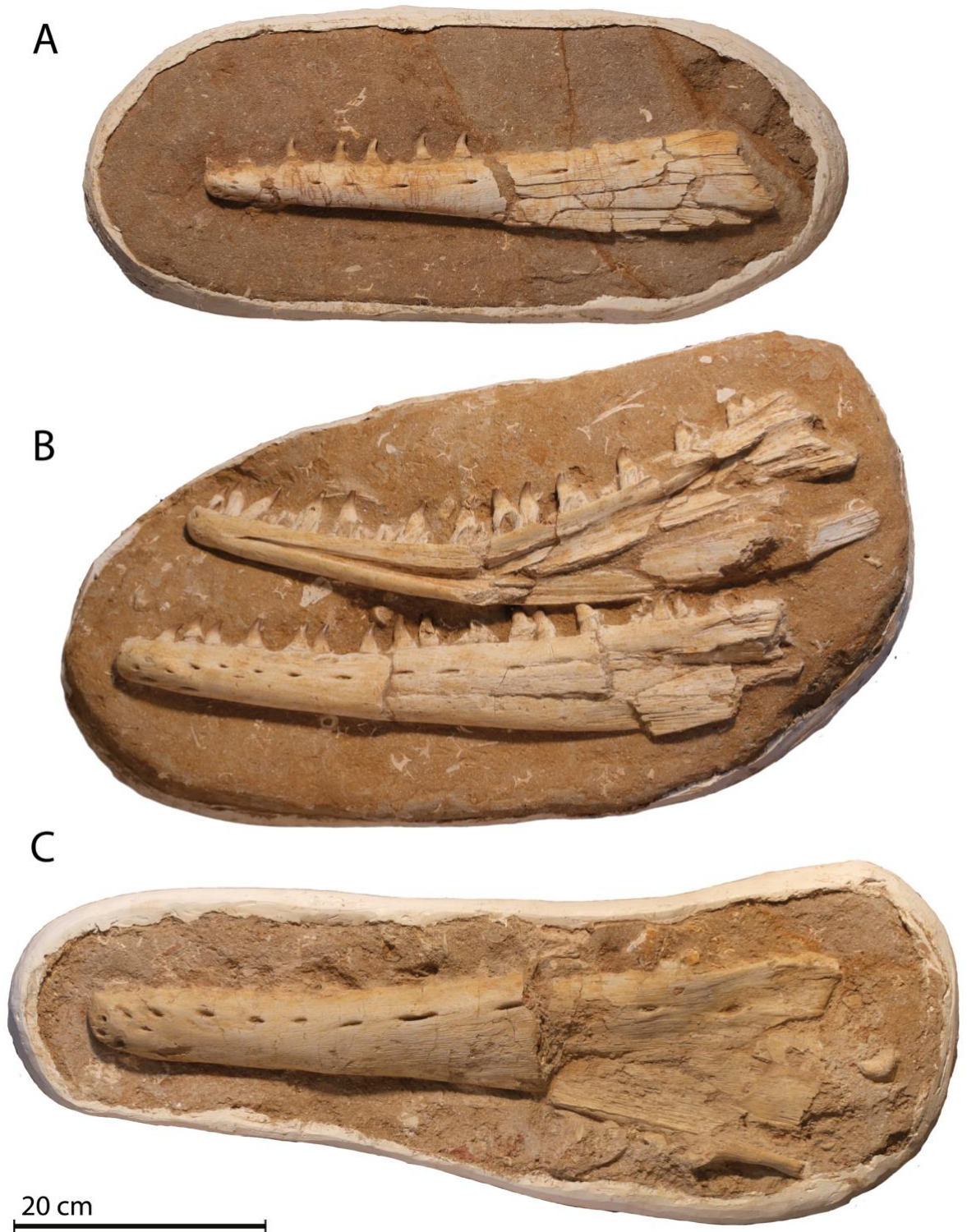
Fig. 11. *Pluridens serpentis* sp. nov., referred mandibles. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. A, MHNM.KH.387, left dentary in lateral view; B, MHNM.KH.388, left and right dentaries (reversed) in medial and lateral views respectively, C, MHNM.KH.386, left dentary in lateral view.
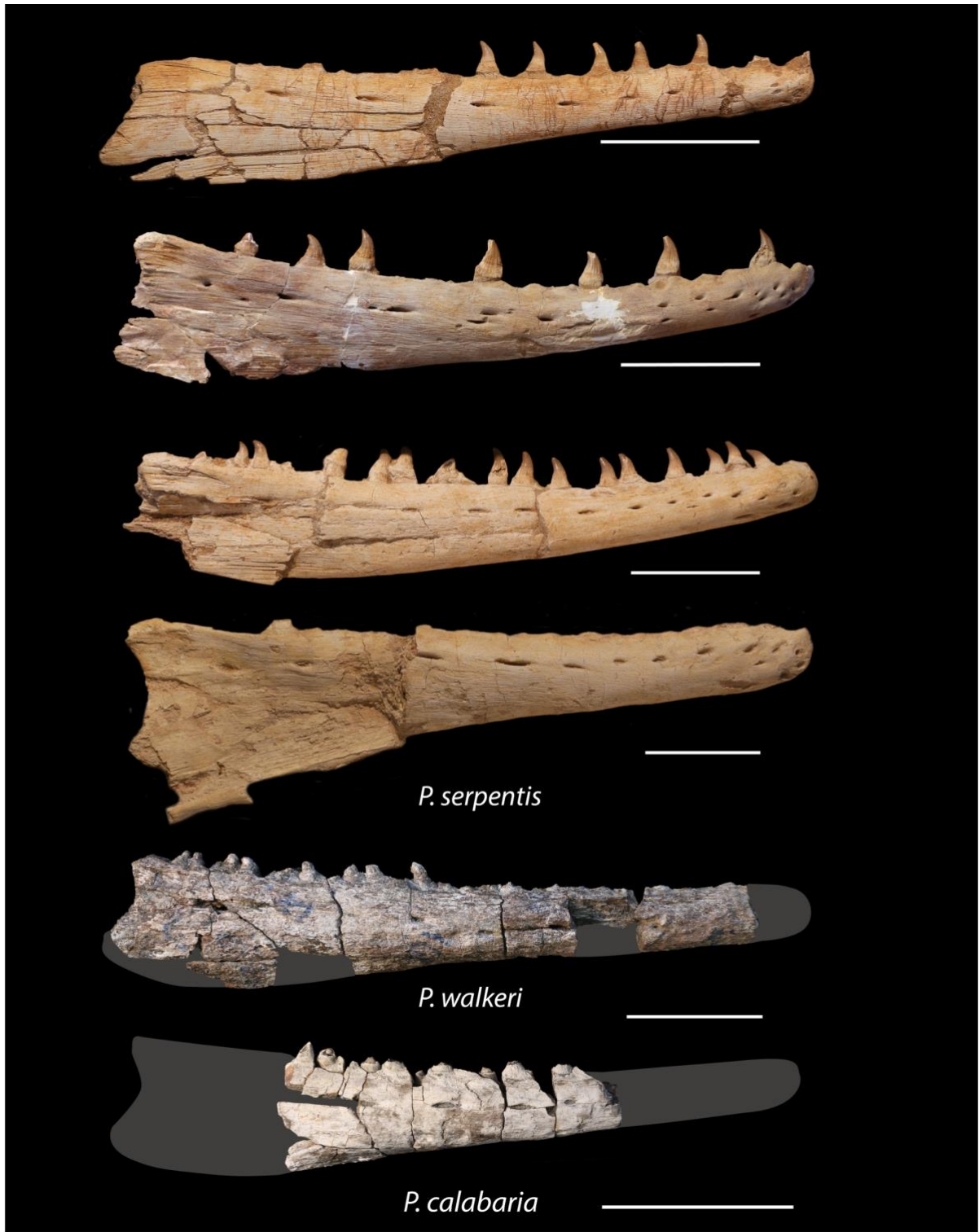
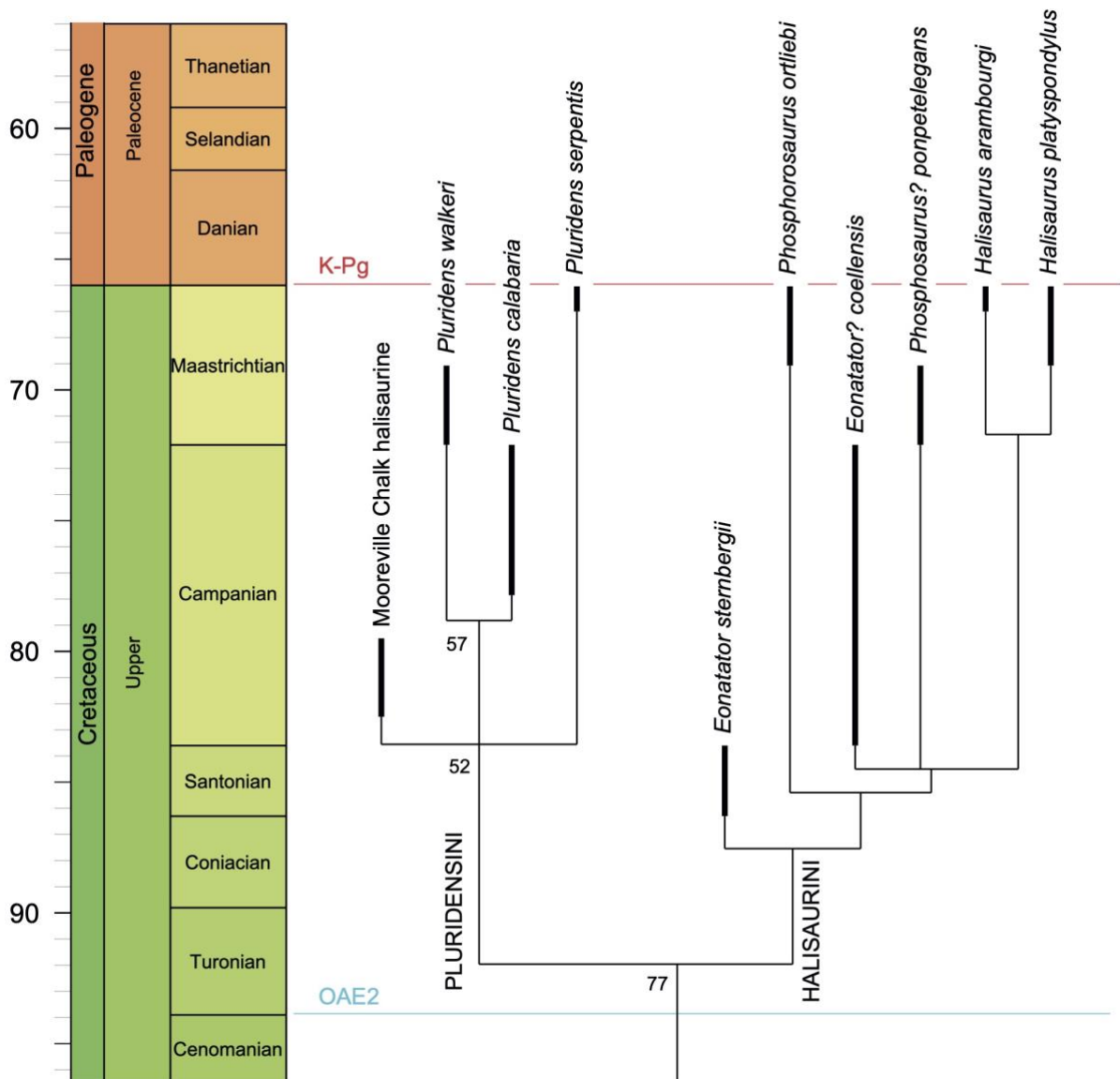**Fig. 12.** Dentaries compared for *Pluridens walkeri*, *P. calabaria*, *P. serpentis* sp. nov.

Fig 13. Phylogeny of Halisaurinae, Strict consensus of 6 most parsimonious trees (treelength = 45, CI = .6512, RI = .4881), showing placement of *P. serpentis* sp. nov. and split of Halisaurinae into the new tribes Pluridensini and Halisaurini. Numbers refer to support values for nodes with more than 50% support in bootstrap analysis (1000 replicates).
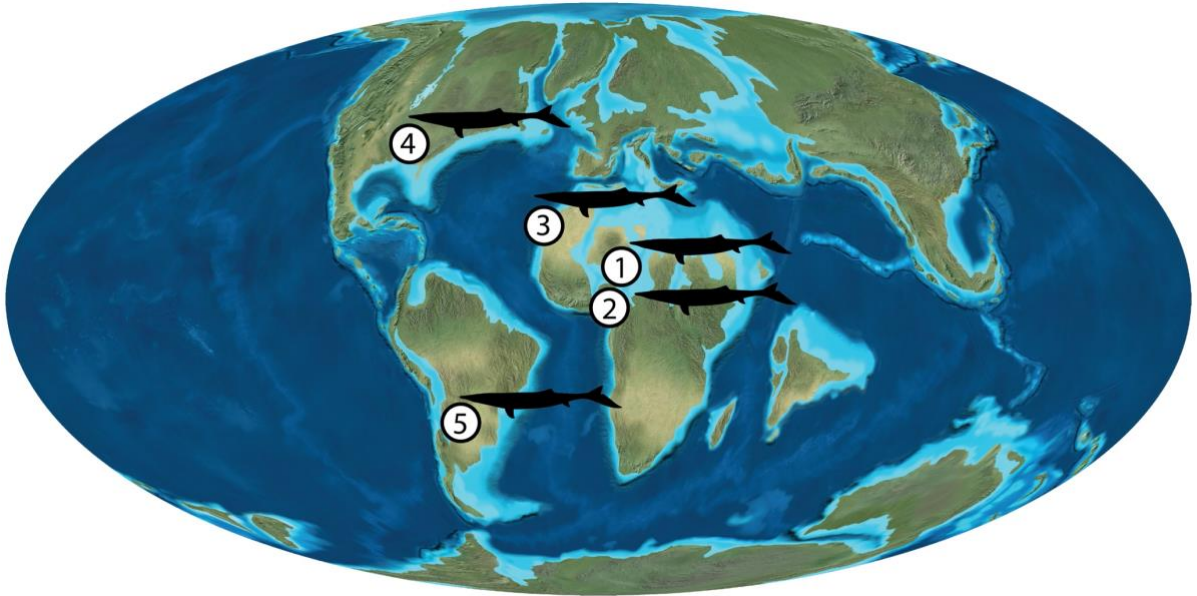
Fig. 14. Occurrences of Pluridensini. 1, *Pluridens walkeri*, early Maastrichtian, Niger; 2, *Pluridens calabaria*, late Campanian, Nigeria; 3, *Pluridens serpentis* sp. nov., late Maastrichtian, Morocco; 4, aff. *Pluridens*., early Campanian, Alabama, USA; ?Pluridensini, late Maastrichtian, Argentina.. Map by R. Blakey.
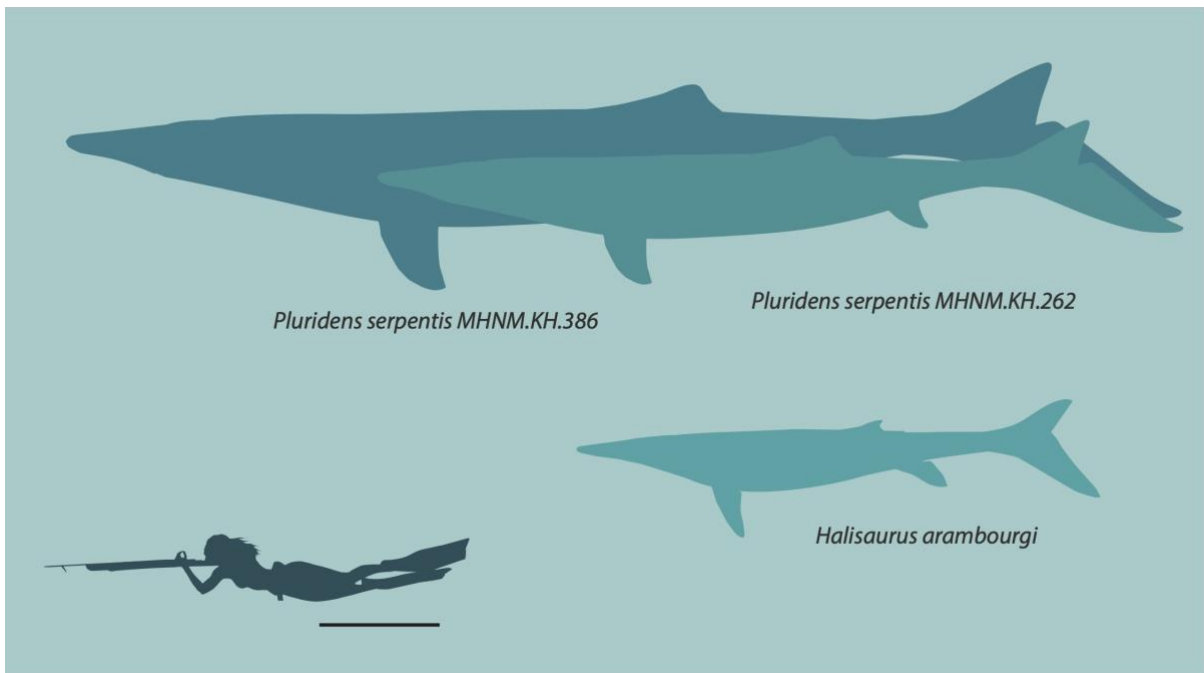

Fig. 15. Relative size of *Pluridens serpentis* sp. nov., syntypes and largest referred specimens, *Halisaurus arambourgi*. *Homo sapiens* for scale. Body shape after *Eonatator sternbergii* (*P. serpentis*) and "*Eonatator*" *coellensis* (*H. arambourgi*). Scale = 1 meter.

Fig. 16. Reconstruction of *Pluridens serpentis* from the late Maastrichtian of Morocco, shown hunting in low-light conditions. Illustration by Andrey Atuchin.