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A Giant Halisaurine from the Late Maastrichtian of Morocco

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Abstract

The Late Cretaceous deposits of Morocco have yielded one of the richest and most diverse assemblages of marine reptiles in the world, with the mosasaurids representing the dominant group. Among the most common mosasaurs are members of the subfamily Halisaurinae. Halisaurines ranged in size from the relatively small *Halisaurus*, which reached 4–5 m in length, to the larger *Pluridens serpentis*, which may have reached 7.5 m in length. Here we report a new, giant species of *Pluridens*, *Pluridens imelaki*. The new *Pluridens* is characterized by a slender, rectangular snout, a T-shaped premaxilla–maxilla junction, interlocking premaxilla–maxilla joint, a prominent dorsal ridge on the premaxilla, an exceptionally long and slender mandible, a tooth count of ~25 dentary teeth, straight, triangular tooth crowns that are strongly bent back just above the tooth–root junction, a low coronoid process and a tall and slender retroarticular process. The skull is 1.25 m long, suggesting a body length of ~9 m or more, comparable in size to large predators such as *Thalassotitan*. Differences between *P. imaleki* and *P. serpentis* in the jaw and tooth structure, eye size and innervation of the rostrum, as well as overall size, suggest they had different foraging strategies and occupied distinct ecological niches. *Pluridens imelaki* reveals that Halisaurinae were not only more species-rich than previously recognized, but also exhibited greater diversity in tooth morphology, jaw shape, and body size than previously thought. Rather than simply being outcompeted by Mosasaurinae, the Halisaurinae staged a minor adaptive radiation in the Late Cretaceous and were important members of the ecosystem in low latitudes. *Pluridens imelaki* appears to have been exceptionally rare in the phosphates, being documented by only a single specimen among the many hundreds of mosasaur remains recovered over many years. This underscores how the species richness of the phosphates and other diverse assemblages is driven by rare taxa that are only revealed through extensive sampling.

Keywords: Squamata; Mosasauridae; Halisaurinae; Late Cretaceous; Maastrichtian

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1. Introduction

The late Cretaceous witnessed a major radiation of the Mosasauridae, a specialized clade of large marine squamates, which became the dominant marine predators during the final 25 million years of the period [1–3]. The most diverse known mosasaurid assemblage, and possibly the most diverse marine reptile fauna in the world, comes from the late Maastrichtian phosphatic beds of Morocco [3,4] (Figures 1 and 2). Many new species have been described in recent years [5–8], and more than 16 species have now been reported [7]. All four major mosasaurid subfamilies are represented in the phosphates—Mosasaurinae [5–7], Plioplatecarpini [8], Tylosaurinae, and Halisaurinae [9,10], and the basal mosasauroid *Pachyvaranus* [11]. Although Mosasaurinae contribute most of the species diversity, Halisaurinae are particularly abundant in the phosphates and were also common across Africa [12] during the Cretaceous.

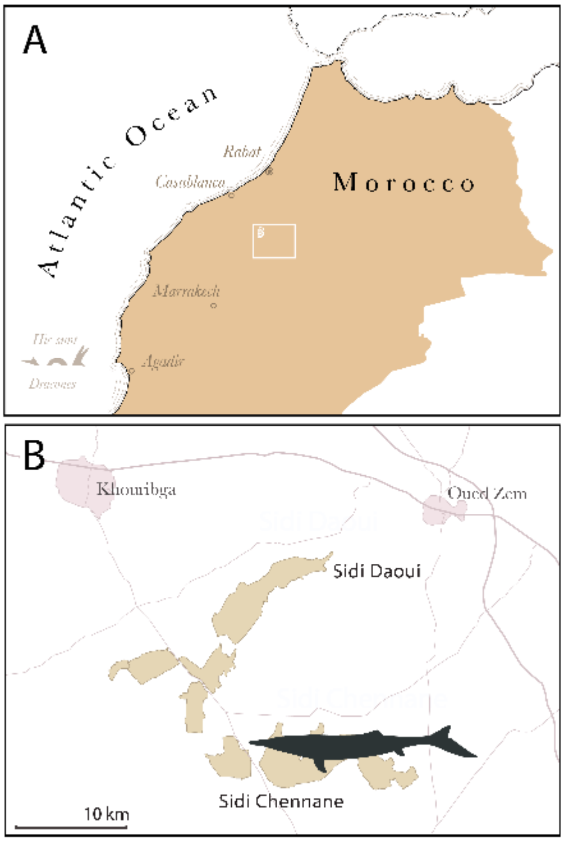

Figure 1. Map of the central part of Morocco showing the Sidi Chennane locality where *Pluridens imelaki* was discovered (**A**) and closeup showing the location of the phosphates mines (**B**).

The most common halisaurine in the phosphates is *Halisaurus*, represented by *Halisaurus arambourgi* [10,13]. *Halisaurus* is characterized by small, numerous, and hooked teeth and a relatively small body size, estimated at 4–5 m in length, suggesting a diet of small fish and squid. *Halisaurus* is also unusual in having large orbits [12,14] and a degree of binocular vision [14], implying adaptation for visual foraging in low-light conditions, either at depth or, given the relative lack of evidence for deep-diving in the genus [15] as well as isotopic evidence suggesting it exploited shallow, nearshore environments [16], at night.

The other halisaurine in the phosphates is *Pluridens* [9]. The genus is characterized by its relatively long, slender jaws and a high tooth count ranging from around 25 to as many as 30 [9,17,18]. Three species of *Pluridens* have previously been described. *Pluridens walkeri*, from the Maastrichtian of Niger [17], is characterized by a long, straight dentary with around 30 small teeth, the highest tooth count known for a mosasaur. *P. calabaria*, from the Campanian of Nigeria [18], is more primitive with fewer and larger teeth. The *Pluridens* species previously reported from the phosphates, *P. serpentis* [9], is slightly younger than *P. walkeri* but appears to have been more primitive in terms of having a lower tooth count. It is characterized by a broad snout, a powerful coronoid process of the mandible, and relatively small orbits [9], features not known for the other *Pluridens* species, which are known only by jaw material.

Recently, a new *Pluridens* skull was discovered in the uppermost Maastrichtian beds of upper Couche III at Sidi Chennane, in Khouribga Province. This new specimen is larger than any previously known specimen of *Pluridens*, with a skull approximately 1.25 m in length, and exhibits peculiarities of the premaxilla–maxilla articulations and unusually long and slender jaws that proclude assignment to *P. serpentis*, and it is here described as a new species.

2. Materials and Methods

The studied material is accessioned at the Museum of Natural History of Marrakech (Cadi Ayyad University), Marrakech, Morocco.

Phylogenetic analysis is based on a revised version of a previously published halisaurine dataset [12]. A number of codings were revised, and *Pluridens imelaki* was added. Analyses were run in PAUP* 4.10 b10 [19].

3. Geological Setting

The new mosasaurid comes from the uppermost Maastrichtian phosphate beds of Sidi Chennane, in Khouribga Province, Morocco (Figure 1).

The phosphate beds represent a marine upwelling zone, which was laid down in a shallow marine embayment along the eastern margin of the Atlantic between the late Maastrichtian and the early Eocene. They are part of a large series of phosphate beds that accumulated along the margin of the Tethys and the eastern Atlantic during the Late Cretaceous and early Paleogene [20]. The phosphate beds of the nearby Ganntour Basin of Morocco have been interpreted as a high-productivity marine upwelling zone [21] where the food chain is supported by a high biomass of small prey.

No formal geological formations have been named; instead, the phosphates are divided into a series of beds or 'couches' by the mining industry (Figure 2) [22]. Couche III is late Cretaceous (late Maastrichtian) in age, Couche II is Paleocene, and the top spans the Paleocene–Eocene boundary interval and the PETM; the uppermost beds, Couche 0 and 1, are early Eocene (Ypresian) in age [22].

Couche III is divided into upper and lower levels. Upper Couche III is the latest Maastrichtian in age, 66–67 Mya, based on the vertebrate fauna [23] and chemostratigraphy [22]. Lower Couche III preserves a broadly similar fauna but seems to be somewhat older; based on shark fossils, it is likely late but not latest Maastrichtian in age.

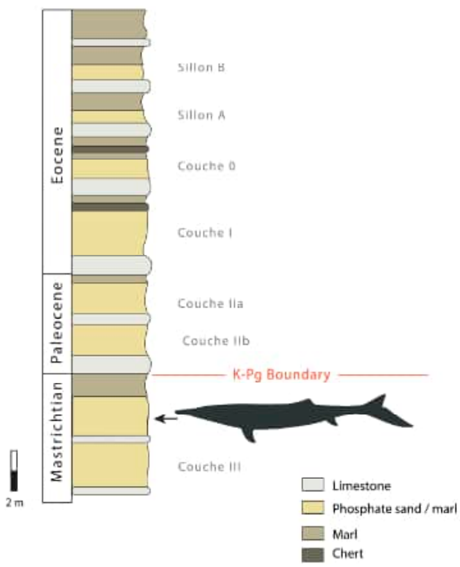

Figure 2. Synthetic stratigraphic column of the Oulad Abdoun Basin showing the stratigraphic placement of *Pluridens imelaki*. After [22].

Vertebrate remains are exceptionally abundant in the phosphates [24,25]. There are abundant marine reptiles, including mosasaurs [4–10,26–34], plesiosaurs [35,36], and marine turtles [37,38]; crocodilians are present but rare, and may represent animals from freshwater habitats [39]. Fish and sharks are both exceptionally diverse and abundant [23,24]. Marine pterosaurs are common [40]; rare dinosaur remains are also found [41–45].

4. Results

4.1. Systematic Paleontology

Squamata Oppel, 1811 [46].

Mosasauridae Gervais, 1852 [47].

Halisaurinae Bardet and Pereda-Suberbiola, 2005 [10].

Pluridensini Longrich et al., 2021 [9].

Pluridens Lingham-Soliar, 1998 [17].

Pluridens imelaki n. sp.

Holotype. MHNM.KHG.1525, articulated skull, associated lower jaws, and associated dentition (Figure 3).

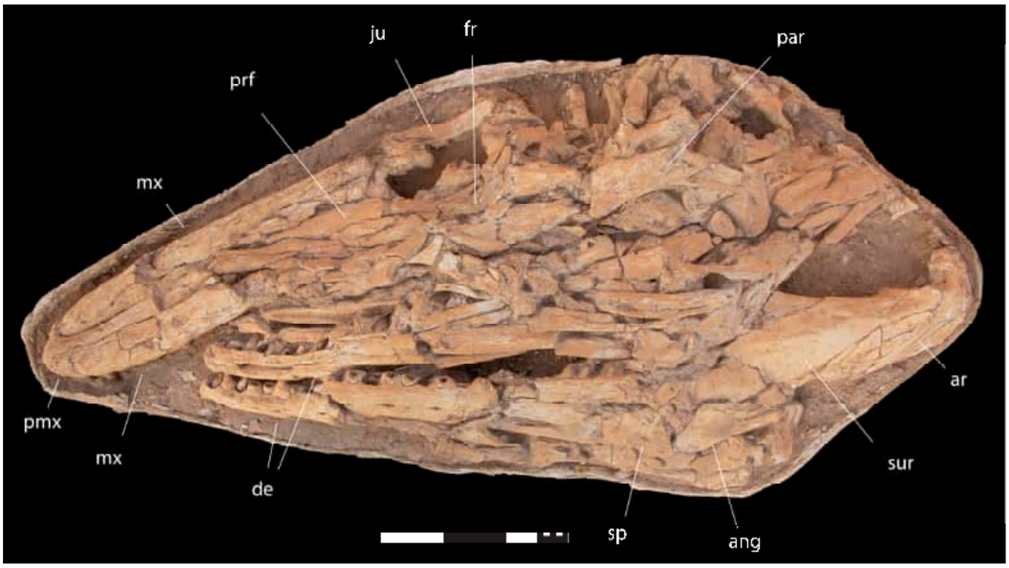

Figure 3. *Pluridens imelaki* n. sp. MHNM.KHG.1525, holotype, skull and associated mandibles. Sidi Chennane, Oulad Abdoun Basin, Morocco, upper Couche III, uppermost Maastrichtian. Abbreviations: ang, angular; ar, articular; de, dentary; fr, frontal; ju, jugal; mx, maxilla; par, parietal; pmx, premaxilla; prf, prefrontal; sp, splenial; sur, surangular. Scalebar = 30 cm.

Locality and Horizon. Sidi Chennane, Khouribga Province, Morocco (Figure 1), Upper Couche III, uppermost Maastrichtian (Figure 2).

Diagnosis. Large halisaurine, skull length up to 125 cm (Figure 3), and total length of >9 m, characterized by the following features (* = autapomorphy): premaxilla with a pointed apex and a broad, rounded dorsal ridge between maxillae; premaxilla body forming a T-shaped contact with the maxillae anteriorly*; premaxilla–maxillae contact with a small process of the premaxilla inserting into a notch in the anterior margin of the maxillae*, and a long finger-like process underlapping the maxillae*; neurovascular foramina of premaxillae few in number; extremely long maxillae, slender and straplike in shape*; extremely elongated premaxilla–maxilla suture, extending over 10–12 tooth positions; very long and slender dentaries, weakly bowed; ~25 dentary tooth positions; recurved and claw-like anterior teeth; and posterior teeth with short, wide crowns (crown height 150% basal diameter), being strongly hooked backwards at the base and with a straight, triangular apex*.

4.2. Description

MHNM.KHG.1525 consists of a complete skull preserved with the lower jaws in articulation, and associated dentition (Figure 3). The skull has undergone extensive post-mortem crushing and breakage following burial, as is typical of many specimens from the phosphates. As a result, the sutures between many bones are difficult to discern, and direct comparison of several elements with *Pluridens serpentis* is limited. Nevertheless, parts of the rostrum and the lower jaws are well-preserved, along with a number of the teeth, allowing comparison between the two species.

Skull. The skull is crushed, but it was very long and narrow, probably about four times longer than wide. The tip of the rostrum (Figures 4 and 5) is bluntly pointed and flattened, giving it a shoe-shaped appearance similar to that of *P. serpentis* [9], though with a slightly more pointed nose. Behind the premaxilla, the snout is long, slender, and rectangular, whereas in *P. serpentis* is broader and the lateral margins diverge posteriorly, giving it a more subtriangular shape. The posterior of the skull is poorly preserved, but the parietal is almost complete, except for the distal half of the posterolateral ramus, which is preserved, showing that the temporal region is elongate and narrow, as in *P. serpentis*, and unlike in *Halisaurus,* where the parietal and temporal region are shorter and wider. The orbits appear to have been larger than those of *P. serpentis*, but not as enlarged as in *Halisaurus* spp. The jaws are remarkably long and slender, especially for such a large animal (Figure 6).

Figure 4. *Pluridens imelaki* n. sp. MHNM.KHG.1525, holotype, Sidi Chennane, upper Couche III, uppermost Maastrichtian, close-up of the rostrum in dorsal view. Abbreviations: de, dentary; mx, maxilla; nas, nasal; pmx, premaxilla; pre, prefrontal. Scale = 10 cm.

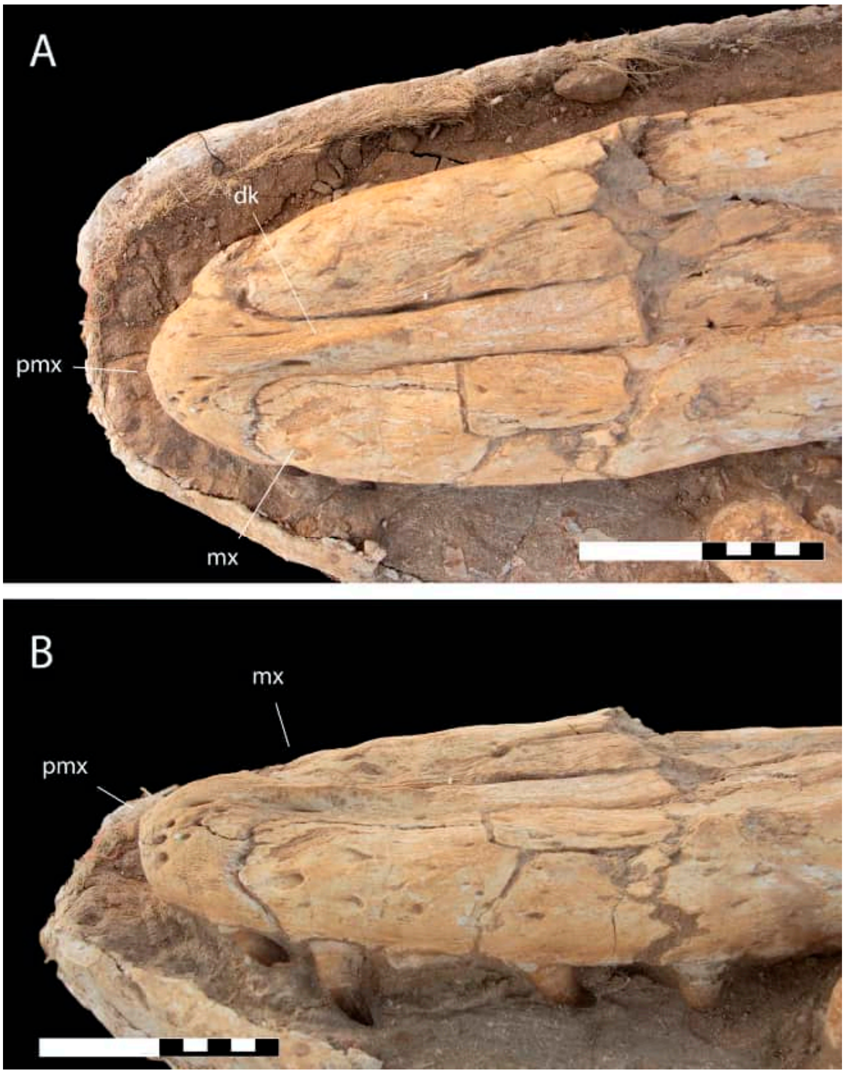

Figure 5. *Pluridens imelaki* n. sp. MHNM.KHG.1525, holotype, close-up of the premaxilla and anterior rostrum, in (**A**), dorsal and (**B**), left lateral views. Sidi Chennane, Oulad Abdoun Basin, Morocco, upper Couche III, uppermost Maastrichtian. Abbreviations: dk, dorsal keel; mx, maxilla; pmx, premaxilla. Scale = 10 cm.

Figure 6. *Pluridens imelaki* n. sp. MHNM.KHG.1525, holotype, close-up of the dentaries. Sidi Chennane, Oulad Abdoun Basin, Morocco, upper Couche III, uppermost Maastrichtian. Abbreviations: ds, dentary symphysis; ld, left dentary; rd, right dentary; meg, Meckelian groove; sdr, subdental ridge; sp, splenial; vl, ventral lip of dentary. Scalebar = 10 cm.

Premaxilla. The premaxilla (Figures 4 and 5) is overall similar to that of *Pluridens serpentis* [9]. The main body of the premaxilla is short and broad (Figure 5A), being more than twice as wide as long; it is strongly dorsoventrally depressed (Figure 5B), being about three times as wide as high. This morphology contributes to a low, broad 'shoe-shaped' rostrum that is shared with *P. serpentis* [9], and which differentiates the genus from *Halisaurus* [10,48] and other mosasaurids. The dorsal surface of the rostrum bears a series of large neurovascular foramina (Figure 5A). These are smaller and fewer in number than in *P. serpentis* [9] and are arranged in two rows on either side of the premaxilla, rather than being scattered over its surface as in *P. serpentis*. The dorsal surface of the premaxilla bears a low, robust dorsal keel (Figure 5A), which starts just anterior to the maxillae and extends back onto the anterior end of the narial process; this keel is absent in *P. serpentis* and *Halisaurus*.

The tip of the premaxilla (Figure 5A) is slightly pointed, in contrast to the blunt and rounded rostrum of *P. serpentis* [9]. As in other halisaurines, the premaxilla lacks a prominent predental rostrum; instead, it exhibits a very slight conical protuberance.

The main body of the premaxilla contacts the tip of the maxillae with an almost transverse suture (Figure 5). Behind this, a long, broad narial process extends posteriorly and contacts the dorsal margins of the maxillae, forming a sort of T-shaped contact with the maxillae. In *P. serpentis*, by contrast, the main body of the premaxilla obliquely contacts the tip of the maxillae, forming a Y-shaped contact with the maxillae and wedging between them; a similar Y-shaped arrangement is seen in *Halisaurus coellensis*.

The suture between the premaxilla and the anterior edge of the maxilla is not straight; instead, two small tabs from the premaxilla project back and interlock with the sinuous anterior margin of the maxilla, producing an interdigitating suture (Figure 5). In *P. serpentis* [9], by contrast, this suture is straight. Laterally, the premaxilla has a long and posteriorly directed process that hooks back underneath the ventral margin of the maxilla (Figure 5B); in *P. serpentis* [9] and *Halisaurus* [48], this posteroventral process is shorter and does not extend as far beneath the maxilla.

The narial process is a robust bar, as in other halisaurines (Figures 4 and 5). It is about one-third the width of the premaxillae anteriorly. It narrows just behind the premaxillary body, where it is clasped by the maxillae, then gradually becomes wider posteriorly, similar to the condition in *P. serpentis* [9].

Maxilla. The maxilla (Figure 4) of *P. imelaki* is an elongated, strap-like element similar to that of *P. serpentis* [9] and some halisaurini, such as *H. coellensis* [49] and *Eonatator sternbergii* [50]; advanced *Halisaurus* such as *H. ponpetelegans* [14] and *H. platyspondylus* [48] have a more triangular maxilla. The maxilla is almost straight, giving the snout a long, rectangular shape, whereas the maxilla is bowed in *P. serpentis* [9] and *H. coellensis* [49]. There are an estimated 18 tooth positions, similar to *P. serpentis* [9], but the posterior end of the maxilla is damaged, and so the actual tooth count may have been higher.

The anterior end of the maxilla (Figure 5) is broadly U-shaped with a squared-off apex, as discussed above, and it forms a complex interdigitating suture with the premaxilla. There is a long articulation between the anterodorsal margin of the maxilla and the premaxilla. Although crushing obscures the precise extent of the suture, it appears to extend back 9 tooth positions; in *P. serpentis*, the suture extends back 8 or 9 tooth positions [9]. A comparably elongate premaxilla–maxilla suture is present in *H. coellensis*, spanning perhaps 8–9 tooth positions [49]; in *H. platyspondylus*, the suture extends only 5 tooth positions [48].

The dorsal margin of the maxilla (Figure 4) forms the lateral margin of the external naris, and as in other Halisaurinae [9], it is elevated so that the nares open entirely dorsally.

Nasal. An element contacting the nasal process of the premaxilla (Figure 4) may represent the nasal. It is very narrow anteriorly and becomes a broad, strap-like element posteriorly. Large nasals are also seen in *P. serpentis* [9]; the nasals tend to be highly reduced in many mosasaurids [2].

Prefrontal. A broad, ovoid element represents the prefrontal (Figure 4), although poor preservation makes it difficult to say much about the shape. It has a very long anterior process abutting the posterodorsal margin of the maxilla, as in *P. serpentis* [9] and *Halisaurus* [48]. As in other halisaurines, it has a prominent lateral ridge, but not the wing-like lateral process seen in Mosasaurinae.

Frontal. The frontal is damaged (Figure 4), making its shape and contacts difficult to determine. However, it appears broadly comparable in shape to that of *P. serpentis* [9], being relatively small and triangular, narrow anteriorly and wider posteriorly where it contacts the parietals; the frontals of *Halisaurus arambourgi* [13] and *H. platyspondylus* [51] are large and subrectangular elements.

Parietal. The parietal is heavily crushed (Figure 4) but appears to be a large and elongate element, similar to that of *P. serpentis* [9]; the parietal is shorter and broader in *Halisaurus* [51].

Postorbitofrontal. The postorbitofrontal is damaged, and its contacts are difficult to discern (Figure 4). It is unclear whether it contacted the prefrontal as it does in *P. serpentis* [9].

Jugal. The ventral body of the jugal is preserved (Figure 4). It is a long, deep, bowed element, suggesting a larger orbit than in *P. serpentis* [9]. In *Halisaurus*, the jugal is strongly bowed and slender, a morphology linked to the enlargement of the orbits [14].

Dentary. The dentary (Figure 6) is an extremely long, slender element, even more so than in *P. serpentis* [9] or *P. walkeri* [17,18]. The dentary is slightly bowed along its entire length, similar to *P. serpentis*; that of *P. walkeri*, by contrast, is straight anteriorly. The dentary has an estimated 25 tooth positions, similar to *P. serpentis* [9]; *P. walkeri* has ~30 tooth positions [17,18].

The lateral surface of the dentary is strongly convex at the tip, and the side of the dentary projects laterally beyond the toothrow, giving the anterior dentary a cylindrical cross-section, as in *P. serpentis* [9] and especially *P. walkeri* [17,18]. In *P. calabaria,* this rounded shape appears to be weakly developed or absent [18]. The dentary as a whole in Pluridensini is transversely expanded relative to Halisaurini or other mosasaurs, which is associated with transverse expansion of the alveoli and reorientation of the replacement pits onto the lingual surface of the tooth roots [18] and the wide jaw may have evolved in part to help accommodate these wider alveoli.

The dentary is relatively shallow posteriorly, unlike in *P. serpentis* [9], *P. walkeri* [17,18] and *P. calabaria* [18], in which the dentary is deep posteriorly.

In the medial view, there is a large and rugose symphysis that extends above and below the Meckelian groove. A long ventral lip is present below the Meckelian groove, as in other *Pluridens* [17,18] and Halisaurinae [10]. The subdental ridge is relatively narrow.

As in other *Pluridens*, the subdental ridge lies well below the lateral parapet of the dentary, resulting in a broad medial exposure of the tooth roots [9,17,18]. The alveoli are well-developed, with a prominent interdental ridge that is expanded ventrally to form a sort of interdental plate similar to those seen in theropod dinosaurs, a feature shared with *P. walkeri* [17,18]; interdental plates are weakly developed in *P. serpentis* [9] and *P. calabaria* [18]. The interdental ridges are obliquely inclined relative to the jaw such that the tooth socket and tooth roots are inclined obliquely backwards relative to the jaw; this feature is well-developed in *P. serpentis* and particularly *P. walkeri*, but is only weakly expressed in *P. calabaria* [18] and the Demopolis chalk pluridensin [52].

Splenial (Figure 7). As in other mosasaurids, the splenial is a triangular element that broadly covers the medial surface of the dentary. It projects ventral to the dentary to form a concave joint to receive the angular, contributing to the intramandibular joint, as in other mosasaurids [2].

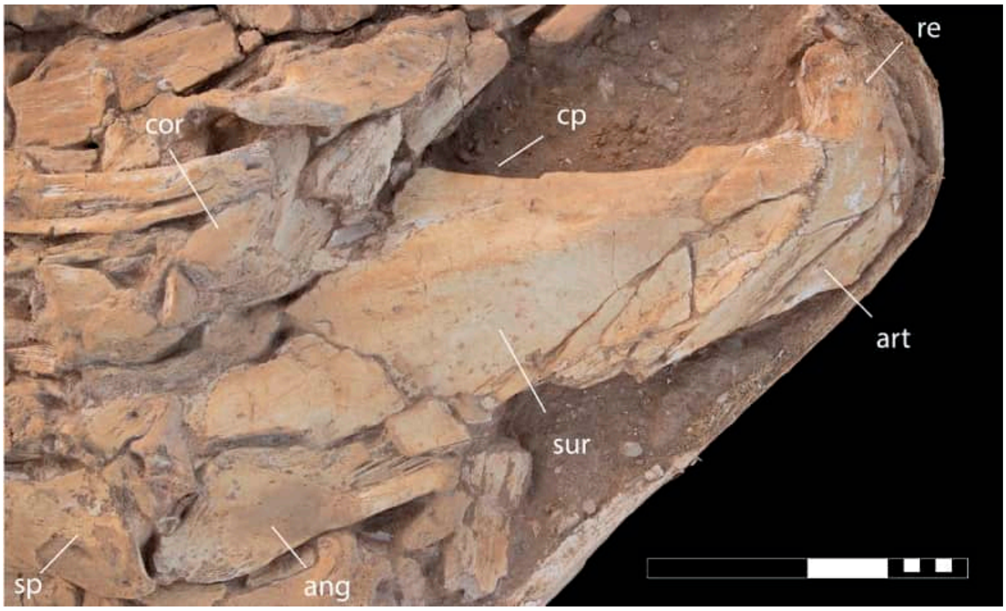

Figure 7. *Pluridens imelaki* n. sp. MHNM.KHG.1525, holotype, close-up of the posterior end of the left mandible in lateral view. Sidi Chennane, Oulad Abdoun Basin, Morocco, upper Couche III, uppermost Maastrichtian. Abbreviations: ang, angular; art, articular; cor, coronoid; cp, coronoid process of surangular; re, retroarticular process; sp, splenial; sur, surangular. Scale = 20 cm.

Surangular (Figure 7). The surangular is a triangular element. Unlike *Halisaurus*, but similar to *Pluridens serpentis* [9], it has a prominent, triangular coronoid process, although this process is less developed than in *P. serpentis*. As in *P. serpentis,* the dorsal margin of the coronoid process is concave. Its posterior end contributes to the glenoid of the lower jaw.

Coronoid. There is a crescent-shaped coronoid (Figure 7) with a strong lateral ridge delimiting the adductor fossa of the jaw. It is poorly preserved and generally resembles that of *P. serpentis* [9].

Angular. The angular (Figure 7) projects far ventral to the surangular, where it articulates with the splenial to contribute to the intramandibular joint.

Articular. The articular (Figure 7) contacts the surangular dorsally and the angular anteriorly. Posteriorly, it contributes to the glenoid and the retroarticular process. The retroarticular process differs from that of *P. serpentis* [9] in having a tall, narrow, rectangular dorsal extension of the retroarticular process. In contrast, the retroarticular process of *P. serpentis* is short and roughly triangular in shape. *P. imelaki* also lacks the pronounced posteroventral extension of the retroarticular process seen in *P. serpentis*.

Dentition. Premaxillary teeth are not exposed. The maxillary dentition appears to consist of at least 18 teeth; there were ~25 dentary teeth, but crushing of the lower jaws prevents a precise count. The teeth are relatively small for a large-sized animal, and short but stoutly constructed. Anterior maxillary teeth are recurved and claw-shaped.

Posterior dentary teeth (Figure 8) have straight, triangular crowns about 150% taller than wide mesiodistally at their bases. Just above the crown-root junction, the crown hooks strongly posteriorly, then is straight distally (Figure 8). This morphology differs markedly from *P. serpentis*, in which the teeth are erect at the base, then the crown hooks posteriorly at mid-height [9], and from *P. walkeri,* where the teeth are more strongly curved and claw-like in the back of the jaw [17,18].

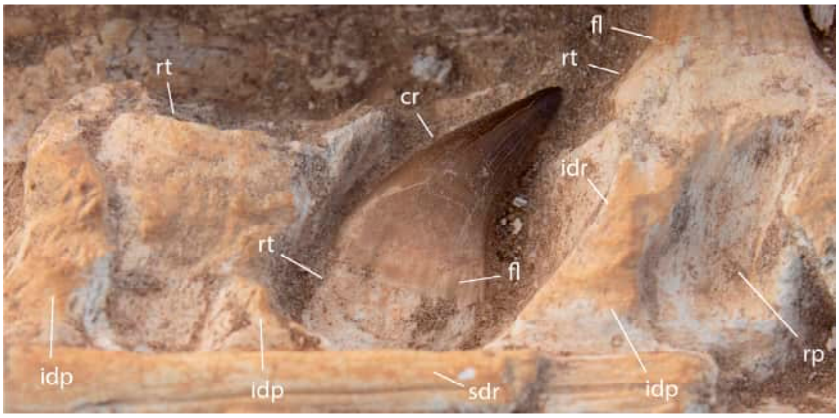

Figure 8. Posterior dentary teeth of MHNM.KHG.1525, holotype of *Pluridens imelaki*. Abbreviations: cr, crown; fl, fluting; idp, interdental plate; idr, interdental ridge; rp, replacement pit; rt, root; sdr, subdental ridge. Scale missing.

The basal part of the crown bears fluting, with weak but numerous ridges and sulci, similar to the condition in *P. serpentis* [9]; the state of this character is unknown in *P. walkeri* [17,18] or *P. calabaria* [18]. Carinae are relatively well-developed compared to *Halisaurus* [48], but are less prominent than in, e.g., Mosasaurinae [53]; serrations appear to be absent. The crown surface bears a very fine texture of anastomosing ridges, as in other Halisaurinae [9,18].

4.3. Phylogenetic Analysis

The phylogenetic analysis is well-resolved, producing 6 most-parsimonious trees; the strict consensus is shown in Figure 9. As found previously [9,12], Halisaurinae form two distinct clades, Pluridensini and Halisaurini. The Maastrichtian *Pluridens imelaki*, *P. serpentis*, and *P. walkeri* form a clade successively sister group to the Campanian *Pluridens calabaria* and an unnamed species from the Mooreville Chalk Formation of Alabama (Figure 9). Phylogenetic analysis using implied weights (K = 2, K = 10) produces identical results for Pluridensini but slightly different topologies for Halisaurini.

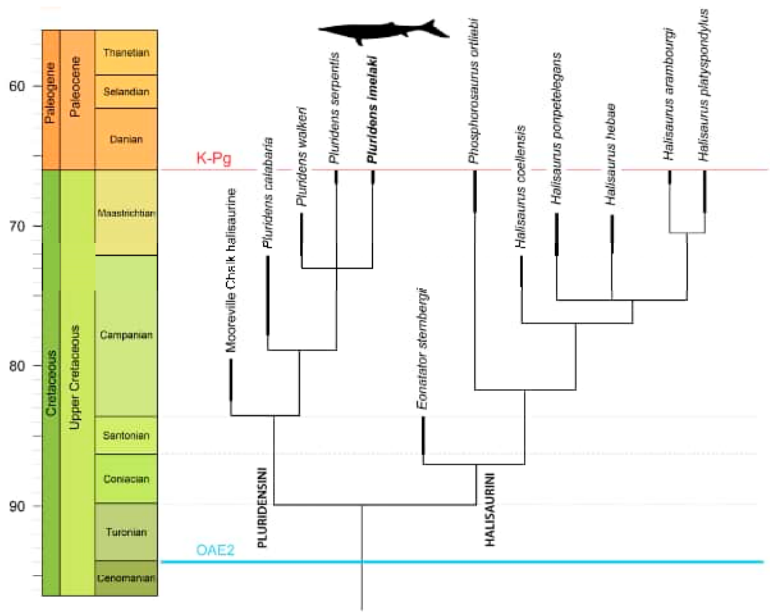

Figure 9. Phylogenetic relationships and stratigraphic distribution of Halisaurinae, showing the phylogenetic position of *P imelaki* n. sp. Strict consensus of six most parsimonious trees, treelength = 71 CI = 0.5915, RI = 0.7264.

5. Discussion

5.1. Affinities of Pluridens imelaki

Phylogenetic analysis supports the placement of MHNM.KHG.1525 within the genus *Pluridens*. Numerous features are shared by *Pluridens imelaki* and other *Pluridens* with *Halisaurus*, supporting the placement of *Pluridens* in Halisaurinae as originally proposed by Lingham-Soliar [17]. These include an elongated premaxilla–maxilla contact [48]; a broad narial bar [10], the absence of a well-developed predental or dentary rostrum [9,10,48], and a tall dorsal margin of the maxilla [9,48], which directs the nares dorsally (a feature occurring convergently in other groups, including Mosasaurinae and Tylosaurinae); a relatively high tooth count [9,10,17]; and hooked crowns, with weak carinae and fine, anastomosing surface ornament [9,18]. Tooth implantation and replacement are also typical of Halisaurinae: the lingual parapet of the jaws fails to obscure the tooth roots, and the tooth roots are broadly exposed.

Within Halisaurinae, *Pluridens imelaki* shares numerous features with Pluridensini. These include a high tooth count (at least 25 teeth) [9,17,18]; a short and very broad premaxilla [9]; strap-shaped maxillae [9]: and a well-developed coronoid process of the mandible [9]. The teeth share basal fluting with *P. serpentis* [9]; tooth roots are separated by large interdental ridges with interdental plates [9,17,18]. Replacement teeth are positioned medially, rather than posteromedially, relative to the tooth root, and the alveoli are transversely expanded to accommodate this shift in replacement tooth position [9,18].

Within *Pluridens*, the oblique orientation of the tooth roots of the dentary is shared with *P. serpentis* and *P. walkeri* [18], but is only weakly expressed in *P. calabaria* [18] and this character appears to be absent in the Mooreville Chalk pluridensin [52]. Likewise, the strongly convex lateral surface of the dentary, creating a cylindrical jaw structure, is more similar to *P. serpentis* and *P. walkeri*, being weakly developed in *P. calabaria* [18] and the Mooreville Chalk pluridensin [52]. Together, these features suggest *P. imelaki*, *P. serpentis*, and *P. walkeri* form a clade of derived, relatively large Pluridensini.

Despite the similarities, *P. imelaki* is distinguished from the co-occurring *P. serpentis* by numerous characters, both plesiomorphic and derived (Table 1, Figure 10). These include a longer and more rectangular rostrum, a more pointed premaxilla, a specialized premaxilla–maxilla articulation, more elongate and slender lower jaws, and differences in the coronoid and retroarticular processes of the lower jaws (Table 1). Although the features differentiating the two are in some cases small, in extant lizards, closely related species are typically distinguished by numerous minor differences in features such as the proportions of the rostrum and temporal region, the shape of skull bones, and the sutures between them [54–58]]. Individual variation in lizards tends to be much more subtle and involves minor differences in suture shape, the position of vascular foramina, etc. [59,60].

Ontogenetic changes are unlikely to explain the differences seen here. Lizards do undergo significant ontogenetic changes, and many skull bones, particularly the frontals and parietals, can undergo changes in their shapes and proportions [60,61]. Juvenile lizards can therefore differ as much from their parents as different species do.

However, in the case of *Pluridens*, large numbers of *P. serpentis* have been recovered from Morocco, including relatively small juveniles and subadults, and large adults [9]. The patterns seen here are inconsistent with the referral of *P. imelaki* to *P. serpentis*. First, tooth morphology is remarkably consistent in *P. serpentis* across a range of sizes, with juveniles and larger individuals exhibiting the same slender, strongly hooked crowns [9]; none approach the condition seen in *P. imaleki*. Second, although jaw morphology does change, in *P. serpentis*, the jaw becomes more robust in larger individuals [9]. Thus, the ontogenetic trends are the opposite expected if MHNM.KHG.1525 was simply a very large *P. serpentis*.

Third, differences in the number of neurovascular foramina cannot be ontogenetic, since the blood vessels and branches of the trigeminal nerve (nerve V) form in the embryo.

Table 1. Characters differentiating *P. serpentis* and *P. imelaki*.

Character	*Pluridens serpentis*	*Pluridens imelaki*
Size	Moderately large, 107 cm skull est. length; est. 7.5 m total length	Very large, 125 cm skull; est. 9 m total length
Premaxilla	Rounded tip	Pointed tip
Premaxillary neurovascular foramina	Large and numerous, 10–12 per side	Small and few in number, 6–8 per side
Premaxilla articulation between maxillae	Y-shaped	T-shaped
Premaxilla contact with the end of the maxilla	Straight contact	Tab inserting into the maxilla
Premaxilla underlap of the maxilla	short	elongate
Maxilla shape	Long and straplike, curved laterally	Extremely long and straplike, straight
Dentary shape	Moderately elongate	Extremely long and slender
Crown shape	slender	Short and robust
Crown curvature	Lateral teeth are strongly hooked at the mid-height of the crown	Lateral teeth are strongly hooked at the base of the crown
Coronoid process	Very tall and triangular	Moderately developed
Retroarticular process	Short, with a strong posterior wing	Tall and rectangular, with a small posterior wing

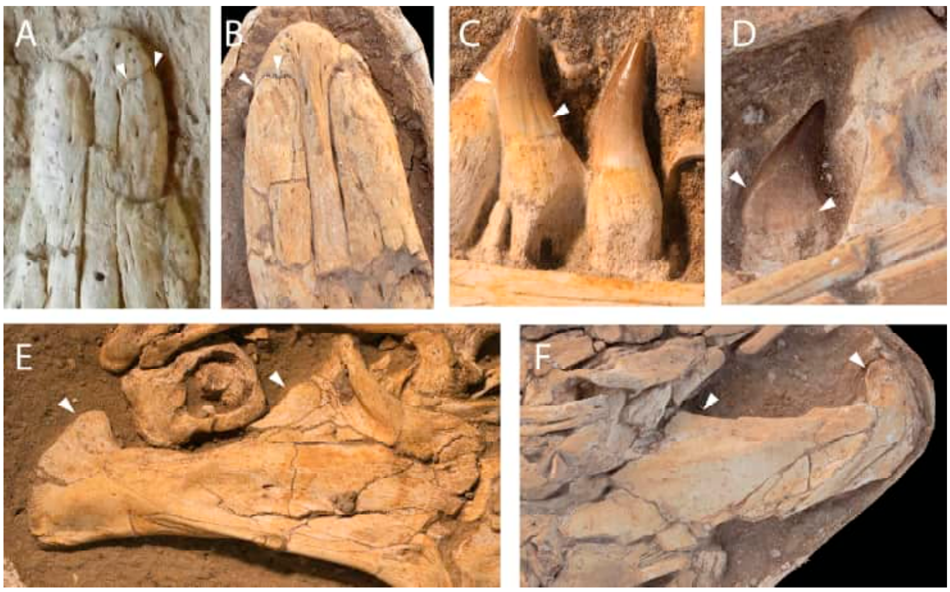

Figure 10. Comparisons of *P. serpentis* (**A**,**C**,**F**) with *P. imelaki* (**B**,**D**,**E**). Premaxilla/maxilla with oblique and simple suture in *P. serpentis* (**A**) versus transverse interlocking suture with premaxilla underlapping maxilla in *P. imelaki*; teeth slender, with few ridges and hooked at midheight in *P. serpentis* (**C**) versus teeth broad-based, with numerous ridges and hooked just above base in *P. imelaki* (**D**); tall coronoid process and broad, triangular retroarticular process in *P.* serpentis (**E**) versus lower coronoid process and narrow, rectangular retroarticular process in *P. imelaki*.

This demonstrates that *P. imelaki* is not a large and mature *P. serpentis*. Neither would ontogeny be expected to produce such large changes in the premaxilla–maxilla articulation, coronoid process, or retroarticular process over the range of sizes seen in *Pluridens*.

Although several studies have argued that mosasaurs show extensive ontogenetic and/or individual variation, in particular based on the large series available for *Tylosaurus* [62,63]. These studies include specimens from different localities and horizons, which span several million years of time [64] and whose stratigraphic horizon and ages are often poorly constrained. These studies assume rather than prove extensive variation, in that it is unclear that these specimens actually belong to a single species. By contrast, the mosasaurs from Khouribga provide large numbers of specimens [5,9,10,13] that are stratigraphically well-constrained and which sample a narrow window of time [22]. These specimens [5,9,10,13] and ongoing work suggest that although significant ontogenetic changes and individual variation are seen in the sample, they are less extreme than previously proposed for mosasaurs [62,63]. Mosasaurs may be overlumped, with at least some of the variation previously attributed to ontogeny and individual variation in mosasaurs instead resulting from species-level differences.

5.2. Ecology

Even within *Pluridens*, the jaw proportions differ, tooth size and shape differ [9,17,18], and overall body size shows variation (Figure 11). This morphological variation suggests substantial variation in ecology and in feeding strategy and diet. *Pluridens imelaki* differs from *P. serpentis* and *P. walkeri* in jaw morphology, dentition, and its large size, suggesting the occupation of a distinct ecological niche. Its most striking feature is the slenderness of the jaws, implying a relatively weak bite force; despite its large size, it apparently consumed relatively small and soft-bodied prey.

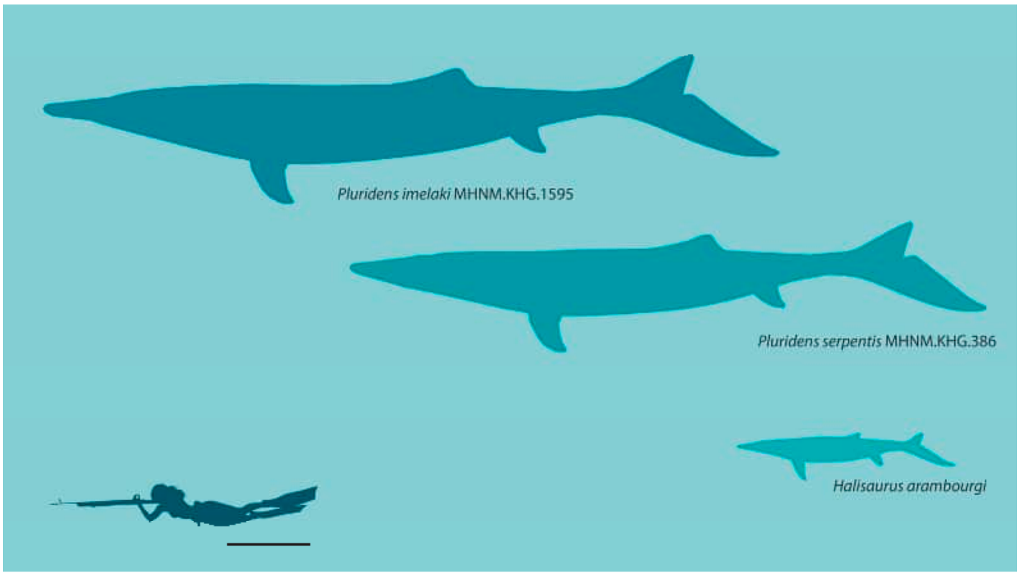

Figure 11. Relative size of *P. imelaki*, *P. serpentis*, and *Halisaurus arambourgi*, all from the latest Maastrichtian-aged phosphates, upper Couche III, Khouribga, Morocco. Scale = 1 m.

It is unclear whether *Pluridens* was a deep diver or not. A wide range of mosasaurs were deep divers, as evidenced by the presence of avascular necrosis in the skeleton [15,65]. *Halisaurus* does not show evidence of deep diving [15]. They apparently favoured more nearshore habitats based on both stable isotopes [16] and are highly abundant in the shallow water settings of the Ouled Abdoun Basin [22]. As discussed, *Halisaurus* clearly had a specialized ecology, and it is unclear whether the absence of deep diving in the genus

Halisaurus itself can be generalized to Halisaurinae as a whole, but *Pluridens*' occurrence in environments like the Farin-Doutchi Formation of Niger [17], a shallow coastal-to-littoral environment [66], the Nkporo Formation of Nigeria [17] (representing deltaic, brackish, and shallow shelf facies [66]), and *Pluridens'* relatively frequent occurrence in the phosphates of the Ouled Abdoun Basin in Morocco, which represent a shallow marine environment [22], suggests that it was more likely a predator of shallow water, nearshore environments than deep water or offshore settings.

It has previously been proposed that *Pluridens* was ichthyosaur-like in its feeding habits [17]; ichthyosaur diets varied but included fish [67] and especially cephalopods such as coleoids [67–70]. *Pluridens* may have occupied a broadly similar niche, perhaps specializing in cephalopods such as belemnites, but it differs conspicuously from ichthyosaurs in that extreme enlargement of the eyes is seen in Ichthyosauria [71] whereas the eyes are moderate in size or reduced in *Pluridens* [9], suggesting ichthyosaurs are not directly analogous.

Another possible analogue might be dolphins, which have relatively long, slender jaws and high tooth counts [72]. Certain species, such as bottlenose dolphins, are broadly similar in their jaw shape, but *P. imelaki* grew much larger; other dolphins, such as the common dolphin, have much smaller teeth and higher tooth counts. In general, dolphins and porpoises have smaller teeth and may feed on smaller prey than mosasaurs, perhaps aided by their ability to hunt using sonar.

In general, while there are probably broad similarities between mosasaurs and other marine tetrapods such as ichthyosaurs and extant cetaceans, there were probably significant differences—cetaceans have active echolocation, ichthyosaurs had exceptionally large eyes [71], whereas mosasaurs may have relied more heavily on senses like chemoreception with the tongue and mechanoreception [9,73]. The available prey may also have been different between the Cretaceous and the Jurassic or Cenozoic. Mosasaurs were perhaps broadly similar to cetaceans, pinnipeds, and ichthyosaurs in niche occupation, but they had distinct anatomy and physiology and occupied a different ecosystem, and so their ecological niches may have lacked precise analogues to earlier or later marine tetrapod faunas.

5.3. Diversity

Halisaurines appear to have been more diverse than previously appreciated. In addition to *Halisaurus arambourgi*, at least two species of *Pluridens* inhabited the phosphates, and recently, a new halisaur has been described from the Early Maastrichtian of Egypt [12]. Halisaurines are relatively uncommon in Campanian and older strata, but are widespread in the Maastrichtian, being known from the Maastrichtian of West Africa [17,18] South America [74–76] Europe [77], eastern North America [48,51,78,79] and Japan [14], suggesting a major radiation at the end of the Cretaceous.

Although Mosasaurinae were the most species-rich clade of mosasaurs, halisaurs were highly abundant and achieved high diversity alongside them. Similarly, plioplatecarpines seem to have maintained relatively high diversity throughout the Maastrichtian [8,28,80]. While competition likely occurred, the radiation of Mosasaurinae [1,5,6,32] did not necessarily outcompete other mosasaurs. Instead, the various mosasaur subfamilies staged radiations contemporaneously, occupying distinct ecological niches and continuing to explore new niches and diversify until the end of the Maastrichtian. Whereas mosasaurinae appear to have been especially successful as apex predators [5,81,82] and durophages [7,29,83], Halisaurinae appear to have exploited small prey, as indicated by their relatively small size [10] or, in the case of *Pluridens*, proportionately small teeth [9,17].

Pluridens imelaki is also noteworthy in that decades of research on the Moroccan phosphate deposits have not previously yielded specimens of this mosasaur, not even isolated jaws or teeth. Although it is possible that specimens have been overlooked or misidentified, the evidence suggests that *P. imelaki* was an extremely rare component of the phosphate fauna. This pattern is common in modern marine ecosystems: within whale communities, a handful of species are common, other species are uncommon, and some are rare, occurring as vagrants or migrants [84]. *P. imelaki* seems to have been such a rare taxon, possibly a migrant or even a stray individual.

The phosphates also span a considerable period of time, with upper Couche III spanning perhaps a million years [22], during which changes in climate and water temperature, particularly late Maastrichtian cooling [85], doubtless resulted in ecosystem changes; species may have shifted their ranges in response to these environmental changes and changes in food availability. Thus, time-averaging across a million years or so might result in capturing species that appeared briefly during this interval, but which were not present throughout the entire period. This pattern could also explain the existence of rare mosasaurids, such as *P. imelaki*.

The discovery of rare mosasaurids, such as *P. imelaki*, *Xenodens* [31,32], and *Khinjaria* [8] is striking and emphasizes the extent to which rare species contribute to species richness and morphological disparity in an assemblage. It is only the extraordinary productivity of the phosphates that has made it possible to recognize such rare species. This pattern suggests that if we had similarly extensive samples of other highly diverse assemblages of Mesozoic marine reptiles or dinosaurs, we might recognize rare species in them, and that we are systematically underestimating the diversity of Mesozoic faunas.

6. Conclusions

A mosasaur skull from the uppermost Maastrichtian of Morocco represents a new, giant halisaurine species, *Pluridens imelaki*. This species is characterized by an unusual premaxilla–maxilla articulation, long and slender jaws, straight posterior teeth, a weak coronoid process, and a tall retroarticular process. Halisaurines seem to have been more diverse than previously thought, and show a wide variety in their jaw shapes, eye size, and body size, indicating diverse feeding strategies. *P. imelaki* also appears to have been one of a number of very rare mosasaurid species in the phosphates, emphasizing the contribution of rare species to the diversity of fossil communities.

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