A new species of halisaurine mosasaurid from the Upper Cretaceous of Egypt

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Halisaurinae are an extinct subfamily of small- to medium-sized mosasaurids that diversified in the latest Cretaceous. Halisaurines were particularly abundant and diverse in the Tethys Sea and Atlantic Ocean surrounding North Africa. Here we report a new species of *Halisaurus* from the lower Maastrichtian of the Dakhla Shale from the Dakhla Oasis, in the Western Desert of Egypt. The new species is characterized by very long and slender maxillae and dentaries, a high tooth count, with 20+ maxillary and dentary teeth, a long and narrow frontal, and a highly modified quadrate in which the stapedial notch is expanded and the suprastapedial and infrastapedial processes form a thin ring of bone surrounding it. Phylogenetic analysis suggests that the new species is sister to a clade including the late Maastrichtian *Halisaurus platyspondylus* and *Halisaurus arambourgi*. The long, slender jaws and posteriorly placed coronoid process suggest a fast but relatively weak bite compared to other species of *Halisaurus*; along with the specialized ears they suggest a niche distinct from the contemporary *Halisaurus hebae* or other Halisaurinae. The existence of two morphologically distinct species in the Dakhla Shale suggests that halisaurines engaged in niche partitioning.

Key words: Mosasauridae, Halisaurinae, Late Cretaceous, Maastrichtian, Tethys, Egypt.

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Introduction

The Halisaurinae are a subfamily of Mosasauridae characterized by relatively small size, and primitive jaw and tooth morphology. Halisaurines have historically been one of the rarest and least known groups of mosasaurs (Baird 1986). Recent finds, especially from North Africa, suggest the group was far more diverse than previously thought.

Currently, Halisaurinae comprises eleven species, assigned to the genera *Eonatator*, *Halisaurus*, *Phosphorosaurus*, and *Pluridens*, and range stratigraphically from the Santonian to the uppermost Maastrichtian. Fossils of Halisaurinae are now known around the world in North and South America, Africa, Asia, and Europe, particularly in the low latitude seas surrounding Africa (Table 1). Discoveries of this group became important in understanding the diversity and evolution of mosasaurs, showcasing adaptations that helped these reptiles flourish in the oceans of the Cretaceous period.

In the summer of 2024, a field trip by members of the New Valley Vertebrate Paleontology Center, New Valley University, Egypt, discovered the disarticulated but well-preserved elements of a skull and postcranial elements of a halisaurine. These remains were found in the lower Maastrichtian of the Dakhla Shale, near the village of Teneida in the Dakhla Oasis, Western Desert of Egypt. The specimen was associated with scattered elements of bony fishes, turtle shell fragments, and plesiosaur vertebrae. It has been cleaned, restored, and is presently housed in the New Valley Vertebrate

Table 1. Described species of Halisaurinae.

Taxon	Synonymy	Stratigraphy	Location	Stage	References
Eonatator sternbergi	*Clidastes sternbergii*, *Halisaurus sternbergii*	Smoky Hill Member, Niobrara Chalk Formation and Eutaw Formation	Kansas and western Alabama, USA	Santonian	Wiman 1920; Bardet and Pereda-Suberbiola 2001; Kiernan 2002
Halisaurus coellensis	*Eonatator coellensis*	Nivel de Lutitas y Arenas	Tolima, Colombia	upper Campanian	Páramo-Fonseca 2013
Halisaurus ponpetelegans	*Phosphorosaurus ponpetelegans*	Hakobuchi Formation	Hokkaido, Japan	lowermost Maastrichtian	Konishi et al. 2016
Halisaurus platyspondylus		New Egypt Formation	New Jersey, USA	upper Maastrichtian	Marsh 1869; Polcyn and Lamb 2012
Halisaurus arambourgi		Upper Couche III	Khouribga Province, Morocco	uppermost Maastrichtian	Bardet et al. 2005; Bardet 2012; Polcyn et al. 2012
Halisaurus hebae		Dakhla Shale	Western Desert, Egypt	lower Maastrichtian	Shaker et al. 2023
Halisaurus auriculatus sp. nov		Dakhla Shale	Western Desert, Egypt	lower Maastrichtian	this paper
Phosphorosaurus ortliebi	*Halisaurus ortliebi*	Ciply Phosphatic Chalk	Belgium	upper Maastrichtian	Dollo 1889; Lingham-Soliar 1996
Pluridens walkeri		Farin-Doutchi Formation	Niger	lower? Maastrichtian	Lingham-Soliar 1998
Pluridens calabaria	*Pluridens walkeri*	Nkporo Shale	Nigeria	upper Campanian	Lingham-Soliar 1998; Longrich 2016
Pluridens serpentis		Upper Couche III	Khouribga Province, Morocco	uppermost Maastrichtian	Longrich et al. 2021
Pluridens imelaki		Upper Couche III	Khouribga Province, Morocco	uppermost Maastrichtian	Longrich and Jalil (2026)

Paleontology Center (NVP) in Kharga City, New Valley Governorate, Egypt, under number NVP040.

The unique anatomical features of the specimen indicate it represents a new species of *Halisaurus*, representing the third record of the genus *Halisaurus* in Egypt, following the report of *Halisaurus arambourgi* and description of *Halisaurus hebae* (Shaker et al. 2023).

Institutional abbreviations.—NVP, New Valley Vertebrate Paleontology Center, Kharga City, Egypt.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank, the official registry of zoological nomenclature. The LSID for this publication is: urn:lsid:zoobank.org:pub:E00D881A-7234-40BA-8D04-FDDC9AFB35A1.

Geological setting

The study area lies to the northeast of the village of Teneida, at the eastern edge of the oasis. It exposes four successive formations ranging in age from Campanian to upper Paleocene. From base to top, these formations are the Quseir Variegated Shales (lower? Campanian), the Duwi Formation (upper Campanian), the Dakhla Shale (Maastrichtian–upper Paleocene), and the Tarawan Chalk (upper Paleocene; Fig. 1A, B).

Dakhla Oasis forms a depression of the Western Desert, lying about 150 km to the west of the Kharga Oasis and 750 km southwest of Cairo. It has an east-west extension for approximately 120 km from Teneida in the east to West Mawhoob in the west (Fig. 1A).

Dakhla depression and the surrounding areas exhibit well exposed and widely distributed Upper Cretaceous and Paleocene deposits of terrestrial, fluvio-lacustrine, lagoonal and shallow marine facies, starting with the Nubia Sandstone Group in the south to the Tarawan Chalk at the top of the high plateau bordering the depression to the north (Said 1962; Hermina 1990).

The Quseir Variegated Shales (improperly called Quseir Formation by many authors) was first named by Youssef (1960). It lies exposed at the southern part of the study area. It is predominantly made up of variegated clay, ferruginous and glauconitic, alternating in its upper part with siltstones and very fine-grained sandstones indicating a fluvio-lacustrine environment grading to a shallow shelf (Hermina 1990; Mahmoud 2003). The maximum thickness of the Quseir is about 55 m, of which the upper 35 m are exposed in the Teneida area. Apart from some fragmented bones of dinosaurs and small logs of petrified wood observed in the upper part, the Quseir Variegated Shales of the Teneida area is generally unfossiliferous and so its age is somewhat uncertain. However, based on other outcrops in the Dakhla Basin and its surroundings, it is typically

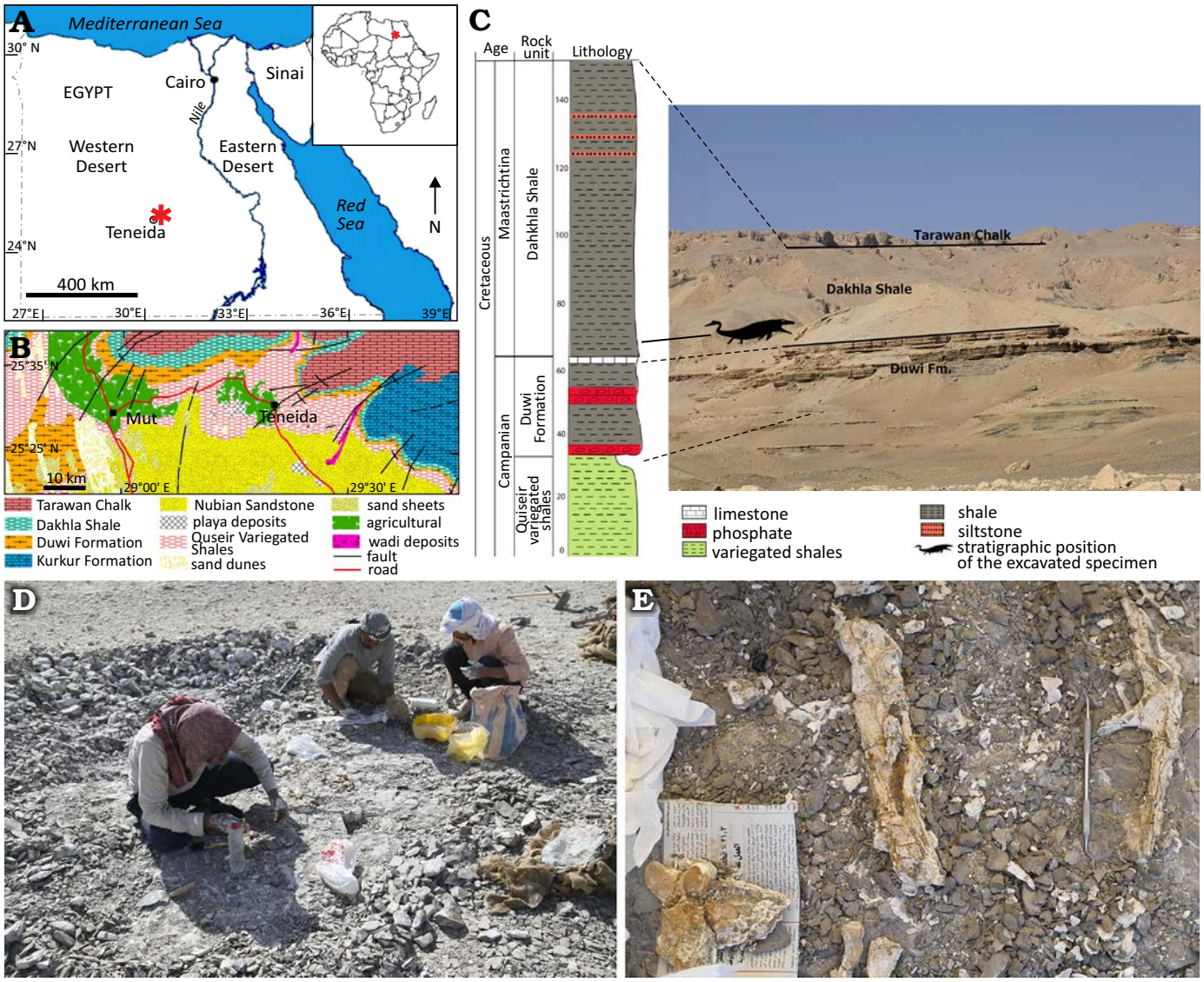

Fig. 1. Locality and stratigraphic context of *Halisaurus auriculatus* sp. nov. from the Dakhla Oasis, Western Desert, Egypt. **A**. Location of the studied area in Egypt. **B**. Geological map of the central and eastern parts of the Dakhla area (after Conoco 1987), showing the position of Gebel Teneida and the fossil locality area. **C**. Stratigraphic column showing the position of the holotype within the Dakhla Shale, with a general view of Gebel Teneida locality. **D**. Field photograph showing excavation of the holotype at Teneida locality. **E**. Close-up of the holotype remains exposed in the mudstone prior to excavation.

assigned to the Campanian (Barthel and Hermann-Degen 1981; Luger and Schrank 1987; Sallam et al. 2016, 2018). Well-preserved terrestrial palynomorphs, described from two boreholes from the Bulaq area, Kharga Oasis, suggest a Campanian, probably lower Campanian, for the base of the unit (Mahmoud 2003; Zahran et al. 2025).

The Duwi Formation, about 30 m thick, comprises several phosphatic layers separated by dark beds of shale. It was first noted in the Dakhla and Kharga oases by Zittel (1883). The phosphatic layers are highly bioturbated. The Duwi Formation is assigned to the upper Campanian due to macroinvertebrates, mainly ammonites, e.g., *Bostrychoceras polyplocum* Römer, 1941 (El Naggar 1966; Dominik and Schaal 1984) and planktic foraminifera (Tantawy et al. 2001). Its contact with the overlying Dakhla Shale coincides with the Campanian/Maastrichtian boundary (Tantawy et al. 2001). The Duwi Formation is capped by a phosphatic limestone layer, 1.5 m thick, marking its contact with the Dakhla Shale.

The Dakhla Shale consists predominantly of hard, dark gray shales and mudstones, intercalated by thin- to thick-bedded light gray and brown sandstones. It constitutes almost the entirety of the scarp face to the north of the Dakhla Oasis, being approximately 200 m in thickness throughout the area. The Dakhla Shale is dated as Maastrichtian to upper Paleocene based on planktic foraminifera and calcareous nannofossils (Tantawy et al. 2001; Hewaidy et al. 2017).

The uppermost formation in the Teneida area is the Tarawan Chalk. It forms the top of the plateau that bounds the Dakhla Oasis to the north (Fig. 1B). It varies in thickness, but typically is about 20 m thick. It has not been examined in detail in the present study. The age of the Tarawan

Chalk is upper Paleocene based on planktic foraminifera (Hewaidy et al. 2017).

The specimen described here was found embedded in compacted grey mudstone at the base of the Dakhla Shale (Mawhoob Member of some authors), just above the contact with the Duwi Formation (Fig. 1B). It is associated with other fish bones, and fragmented marine turtle remains.

Tantawy et al. (2001) identified, in the lower 3 m of the Dakhla Shale, a planktic foraminiferal assemblage indicative of Zone CF8b, hence the lowermost Maastrichtian. Since the specimen studied in this work comes from the very base of the Dakhla Shale, it can safely be assigned to the lower Maastrichtian.

Material and methods

The studied specimen NVP040 is housed in the New Valley Vertebrate Paleontology Centre of the New Valley University, Kharga City, New Valley Governorate, Egypt. It includes disarticulated elements of the skull (maxilla, frontal, jugal, pterygoid and quadrate) and of the mandible (dentary, splenial, coronoid and fused surangular-articular). Associated postcranial bones include cervical and dorsal vertebrae. All bones are preserved three-dimensionally (Figs. 2–10).

Fossils were cleaned with air scribes and consolidated with Paraloid B-72 in acetone. Photographs were taken using a digital camera (Af-S Nikkor 24–120 mm 1:4 G ED VR; Nikon) and lens (Af-S Nikkor 70–200 mm 1:28E FL ED VR; Nikon) in norm al light.

Phylogenetic analysis was conducted using the character-taxon matrix of Longrich and Jalil (2026), with the addition of the new material. The analysis was performed under equal-weights parsimony using PAUP* 4.0b10 (Swofford 2003) and using implied weighting. Chronostratigraphic units used throughout the text follow the International Stratigraphic Chart (Cohen et al. 2025).

Systematic palaeontology

Squamata Oppel, 1811

Mosasauridae Gervais, 1852

Halisaurinae Bardet & Pereda-Suberbiola in Bardet et al., 2005

Halisaurini Longrich et al., 2021

Genus *Halisaurus* Marsh, 1869

Type species: *Halisaurus platyspondylus* Marsh, 1869, Maastrichtian of New Jersey, USA (Holmes & Sues, 2000).

Halisaurus auriculatus sp. nov.

Fig. 2.

Zoobank LSID: urn:lsid:zoobank.org:act:4EE47AE5-8315-41EA-A08D-37F58BF7B1E5.

Etymology: From the Latin *auriculatus*, eared, having prominent ears; referring to the unusually large tympanic meatus in this species.

Holotype: NVP040, incomplete disarticulated skull, mandible, associated cervical, dorsal and caudal vertebrae, tibia, fibula, metapodial and phalanx.

Type locality: North of Teneida village, northeast of Mut city, Dakhla Oasis, Western Desert, Egypt.

Type horizon: Basal part of the Dakhla Shale, lower Maastrichtian, Upper Cretaceous.

Diagnosis.—The new species is diagnosed by the following combination of characters (autapomorphic characters are indicated by an asterisk): 21 maxillary teeth, 20+ dentary teeth, 8 pterygoid teeth. *Maxilla very long and low. *The ventral margin of the maxilla is convex. Premaxilla-maxilla suture extending 9 tooth positions. Frontal with a smooth and high triangular eminence with depressions on either side. The frontal is ornamented in the central part by subtle ridges and grooves. *The pterygoid tooth row is arched. The jugal bears a low, triangular posteroventral process. *The quadrate has a hypertrophied tympanic meatus. The suprastapedial process is large, robust, wide and concave. *The quadrate pterygoid articulation is wide and has a

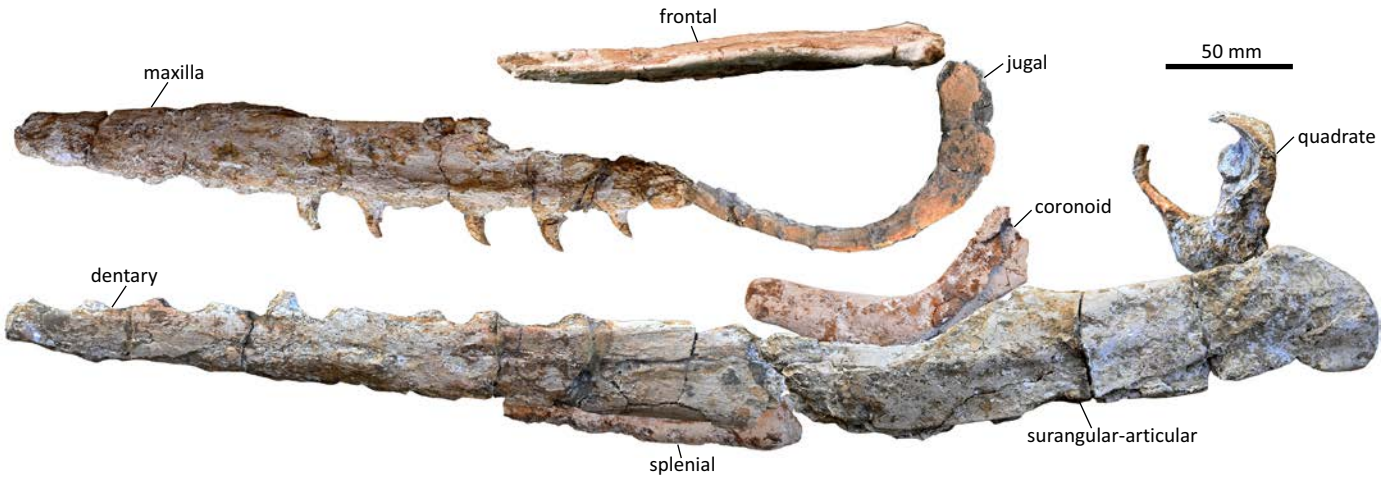

Fig. 2. Halisaurine mosasaurid *Halisaurus auriculatus* sp. nov., holotype (NVP040), Teneida, Dakhla Oasis, Western Desert, Egypt, lower Maastrichtian. Skull restoration (composite using bones from left and right sides of the skull, only right maxilla shown reversed).

rectangular outline. The mandibular condyle of the quadrate is narrow and has a triangular shape. *The coronoid is long with an ascending process shorter than the descending process. The ventral margin of the surangular-articular is emarginated with the retroarticular process broad, rounded and protruding ventrally. Surangular with a deep concave coronoid articulation.

Material.—Holotype only.

Description.—*Skull*: The skull preserves the right and left maxillae, frontal, jugals, right pterygoid and right quadrate.

Maxilla: The left and right maxillae are well preserved (Fig. 3). The left maxilla is missing the anterior tip. The complete right maxilla measures about 30 cm long. It is long and low as in other Halisaurinae. The proportions of the

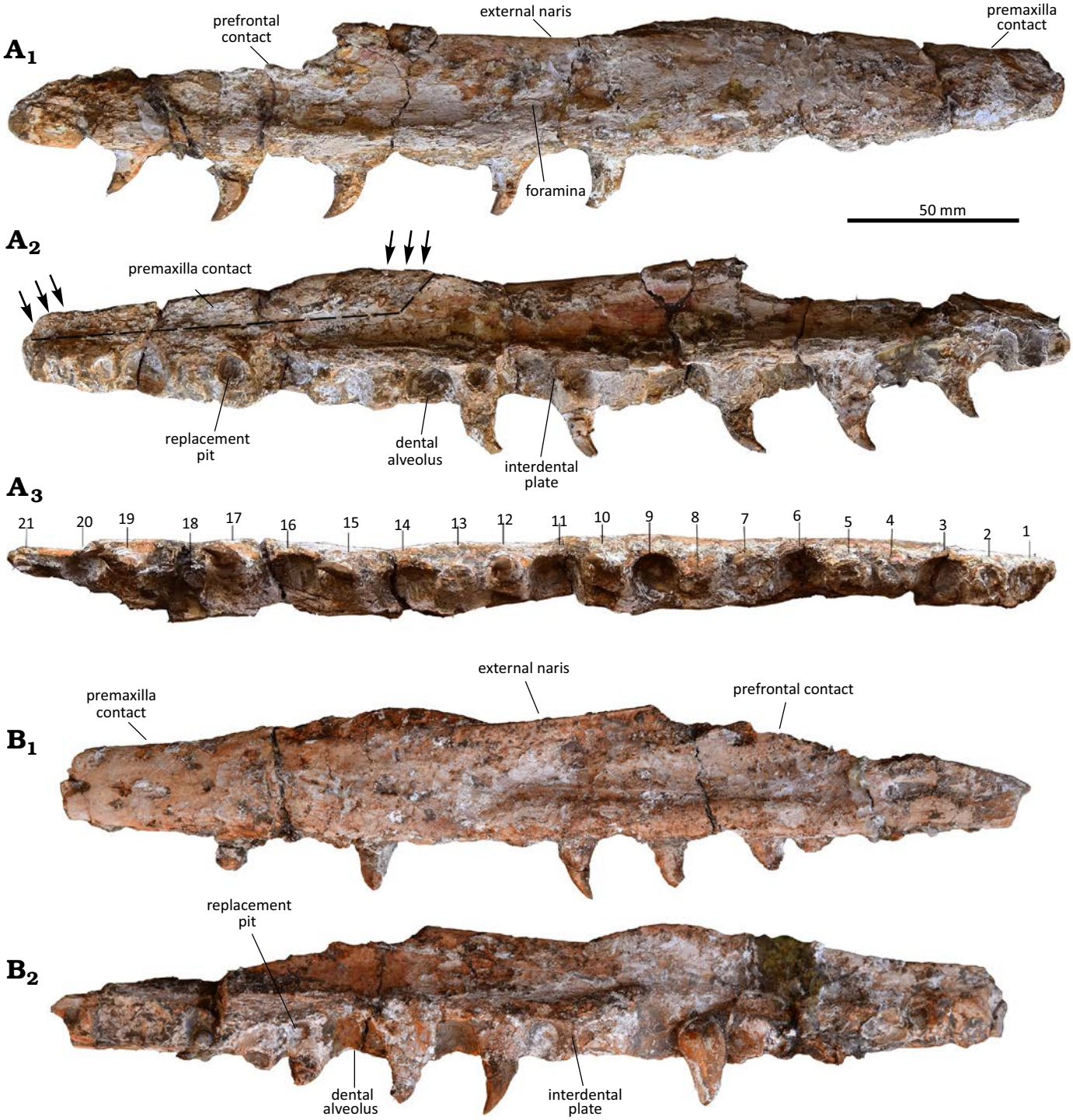

Fig. 3. Halisaurine mosasaurid *Halisaurus auriculatus* sp. nov., holotype (NVP040), Teneida, Dakhla Oasis, Western Desert, Egypt, lower Maastrichtian. **A**. Right maxilla in lateral (A_1), medial (A_2), and dorsal (A_3) views. **B**. Left maxilla in lateral (B_1) and medial (B_2) views. 1–21, dental alveoli. Arrows indicate the anterior and posterior limits of the sutural contact between the maxilla and premaxilla, whereas the dashed line outlines the extent of this contact.

maxilla approach those of *Eonatator sternbergi* (Wiman, 1920) (Bardet and Suberbiola 2001) and *Halisaurus coellensis* (Páramo-Fonseca, 2013); the maxilla in *Halisaurus arambourgi* Bardet & Pereda-Suberbiola in Bardet et al., 2005, and *Halisaurus platyspondylus* Marsh, 1869, is comparatively deeper than that of *Halisaurus auriculatus* sp. nov. (Holmes and Sues 2000; Bardet et al. 2005). In contrast to other halisaurines, the ventral margin of the maxilla is convex, an autapomorphy of this species.

The right maxilla bears 21 tooth positions (Fig. $3A_3$), with all teeth found in alternate alveolar positions except one tooth. This same tooth implantation pattern is found in *Halisaurus ponpetelegans* (Konishi et al., 2016) and is common among Halisaurinae (Bardet et al. 2005: fig. 4A; Polcyn and Lamb 2012; Konishi et al. 2016). The tooth count is higher compared to *H. arambourgi*, with 16 maxillary teeth (Bardet et al. 2005) and approaches the tooth count in *H. coellensis*, with 20 teeth (Páramo-Fonseca 2013). The teeth show variable interalveolar spacing along the jaw, with closely spaced alveoli in the anterior region, more widely spaced alveoli in the mid-jaw, and closely spaced alveoli again in the posterior region. As in other Halisaurinae, the lingual parapet is much lower than the labial parapet, leaving the tooth roots broadly exposed in lingual view.

The anterodorsal margin of the right maxilla shows a diagnostic feature of Halisaurinae; the premaxilla-maxilla contact is vertical anteriorly, oblique at midpoint and horizontal posteriorly (Bardet et al. 2005). The suture with the premaxilla runs to the ninth tooth (Fig. $3A_2$), as in *Pluridens serpentis* Longrich et al., 2021, whereas in *H. arambourgi* the suture extends only six or seven tooth positions. An elongate premaxilla-maxilla suture is a derived feature of Halisaurinae (Bardet et al. 2005; Longrich et al. 2021). The suture is developed medially as a broad, flat, dorsoventrally expanded surface, which contacts the dorsoventrally expanded narial process of the premaxilla. Again this represents a derived feature shared with other Halisaurinae, although an expanded premaxilla suture is also seen in Tylosaurinae.

The lateral surface of the maxilla is dorsally elevated such that the nares open dorsally rather than dorsolaterally. This condition is present in Halisaurinae and also oc-

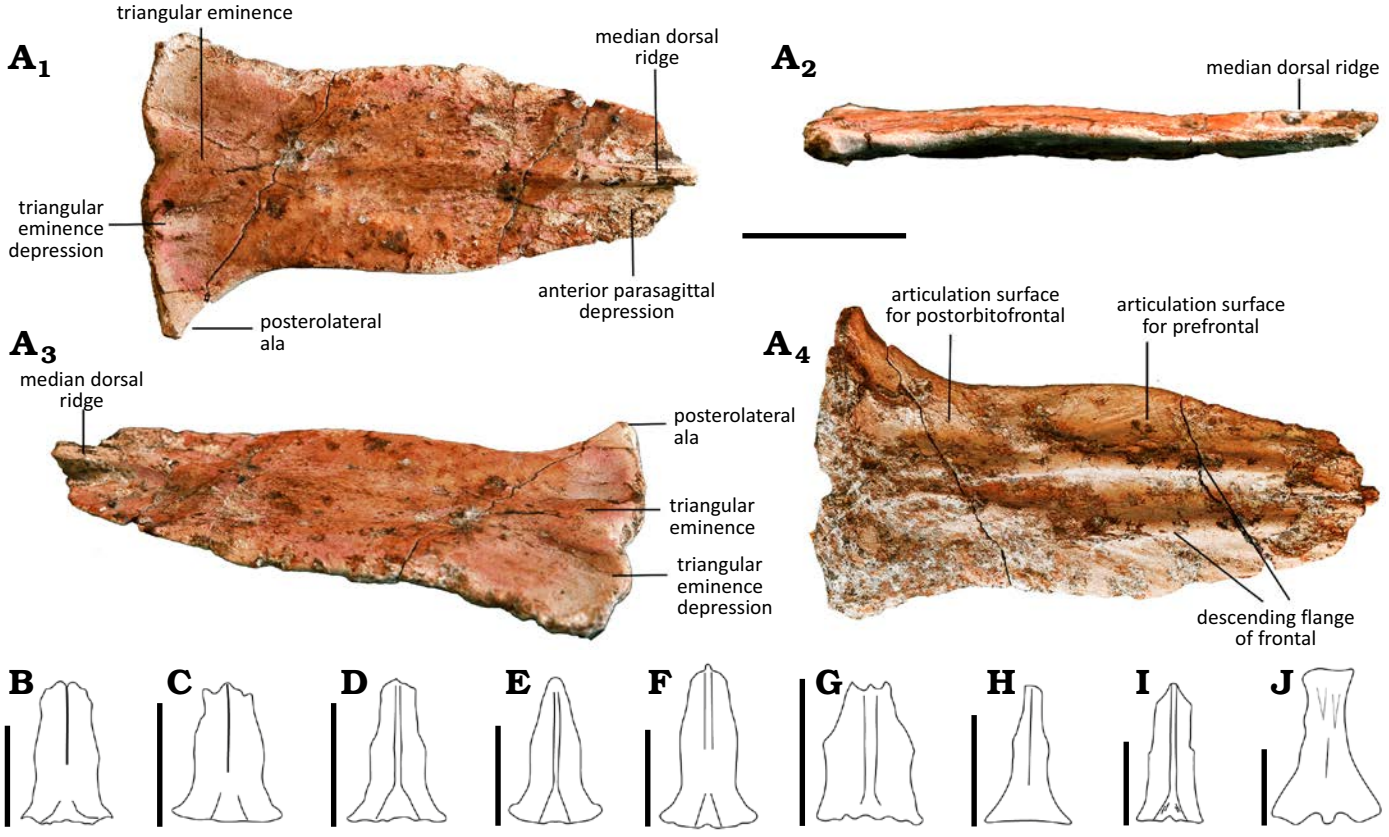

Fig. 4. Halisaurine mosasaurid *Halisaurus auriculatus* sp. nov. and comparative halisaurine frontals. **A**. *Halisaurus auriculatus* sp. nov., holotype (NVP040), Teneida, Dakhla Oasis, Western Desert, Egypt, lower Maastrichtian. Frontal in dorsal (A_1), ventral (A_2), left lateral (A_3), and oblique (A_4) views. **B**–**J**. Comparative line drawings of halisaurine frontals. **B**. *Halisaurus platyspondylus* Marsh, 1869 (redrawn from Holmes and Sues 2000: fig. 1). **C**. *Halisaurus arambourgi* Bardet & Pereda-Suberbiola in Bardet et al., 2005 (redrawn from Polcyn et al. 2012: fig. 1A). **D**. *Halisaurus ponpetelegans* Konishi et al., 2016 (redrawn from Konishi et al. 2016: fig. 7A). **E** *Halisaurus hebae* Shaker et al., 2023 (redrawn from Shaker et al. 2023: fig. 7B). **F**. *Halisaurus auriculatus* sp. nov. **G**. *Halisaurus coellensis* (Páramo-Fonseca, 2013) (redrawn from Páramo-Fonseca 2013: fig. 7B). **H**. *Eonatator sternbergi* (Wiman, 1920) (redrawn from Bardet and Pereda Suberbiola 2001: fig. 2A). **I**. *Phosphorosaurus ortliebi* (Dollo, 1889) (redrawn from Lingham-Soliar 1996: fig. 1B). **J**. *Pluridens serpentis* Longrich et al., 2021 (redrawn from Longrich et al. 2021: fig. 5). Scale bars A, 50 mm; B–J, 100 mm.

curs convergently in Tylosaurinae (Russell 1967; Lingham-Soliar 1992) and some Mosasaurinae (Lingham-Soliar 1995; LeBlanc et al. 2013; Street and Caldwell 2017). A short posterodorsal process is present on the left maxilla. It was recorded for the first time in *H. ponpetelegans* (Konishi et al. 2016) and this is the second record. The posterior end of the maxilla is very low, barely taller than the anterior end, a derived feature of Halisaurinae.

On the lateral surface of the maxilla, just above the gumline, lies a row of slit-like foramina (Fig. 3A_1, B_1). Ventrally there is a longitudinally flattened ridge supporting the tooth bases and housing the maxillary artery and the maxillary division of the fifth nerve (Russell 1967). The dorsal maxillary border is emarginated for the external naris as typical of other mosasaurs, in contrast with *H. ponpetelegans* which has a straight dorsal border.

Frontal: The frontal (Fig. 4A) generally resembles *H. arambourgi* (Bardet et al. 2005) and *H. hebae* Shaker et al., 2023, but there are also marked differences. The frontal is more elongate and has a roughly triangular form, narrowing and tapering anteriorly (Fig. 4A_1). This suggests that the contribution of the frontals to the nares is very small. In *H. arambourgi*, the frontal has a rounded, wide emargination for the nares, with concave posterolateral margins, sharp lateral corners.

The parietal suture contact is undulated (Fig. 4A_1) similar to that of *H. hebae* and *Phosphorosaurus ortliebi* Dollo, 1889 (Lingham-Soliar 1996; Shaker et al. 2023). In contrast to these taxa, *H. arambourgi* and *Eonatator sternbergi* (Bardet and Suberbiola 2001; Polcyn et al. 2012) possess a straight parietal suture contact.

The supraorbital process is broadly convex, similar

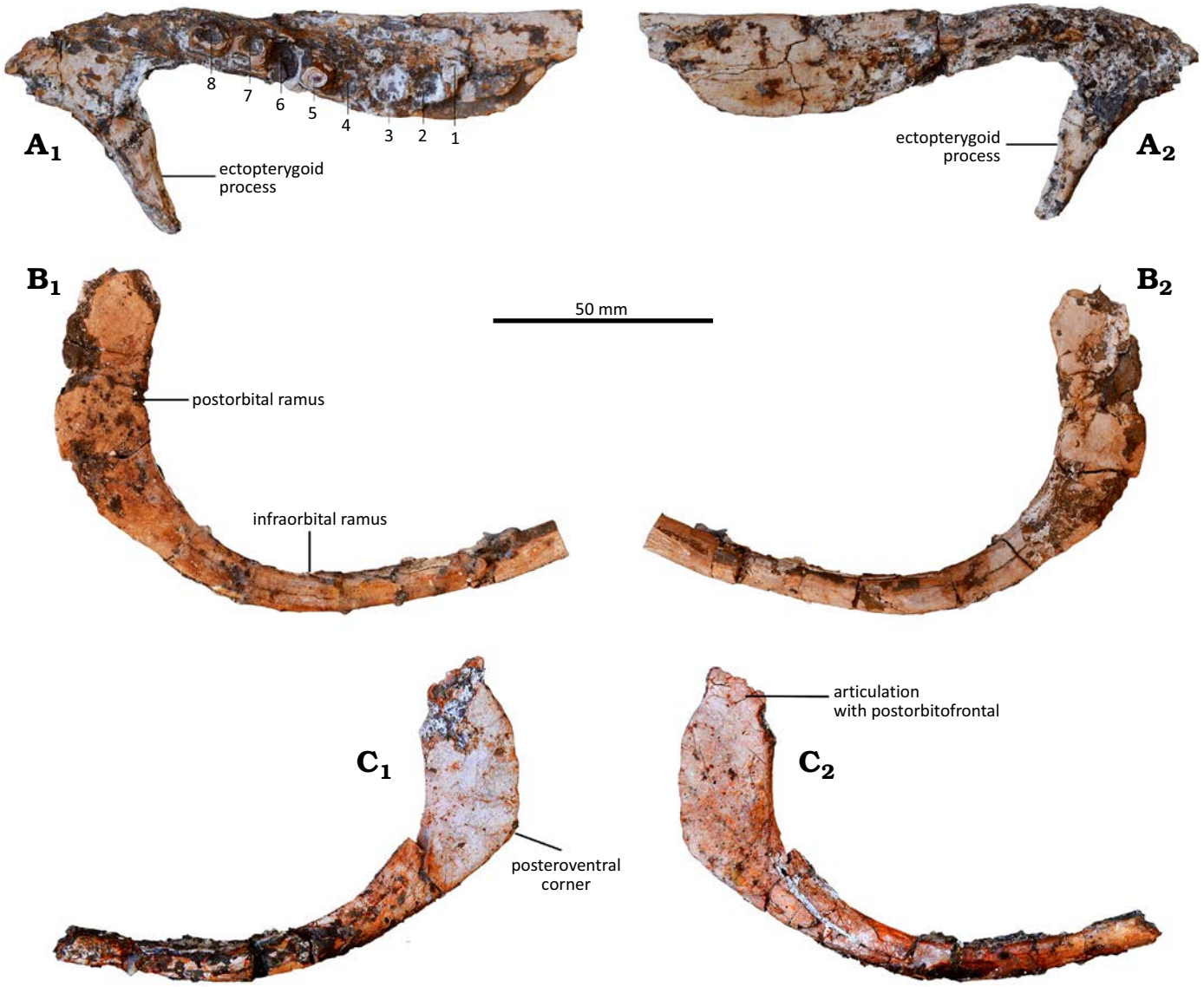

Fig. 5. Halisaurine mosasaurid *Halisaurus auriculatus* sp. nov., holotype (NVP040), Teneida, Dakhla Oasis, Western Desert, Egypt, lower Maastrichtian. **A**. Right pterygoid in dorsal (A_1) and ventral (A_2) views. **B**. Left jugal in lateral (B_1) and medial (B_2) views. **C**. Right jugal in lateral (C_1) and medial (C_2) views. 1–8, dental alveoli.

to *H. platyspondylus* (Holmes and Sues 2000), *H. arambourgi*, and *H. hebae*. It is different from *Eonatator sternbergi* (Bardet and Suberbiola 2001) and *H. ponpetelegans* (Konishi et al. 2016) which have smaller supraorbital processes and also from *Phosphorosaurus ortliebi* (Lingham-Soliar 1996) which has a rectangular supraorbital process.

The orbital margins are weakly concave as in *H. hebae*. A primitive condition is seen here, with the frontals forming the dorsal margin of the orbits like in other Halisaurinae except species of *Pluridens*, in which the frontal is excluded from the orbit by a prefrontal-postorbitofrontal contact (Longrich et al. 2021). The dorsal surface is slightly convex dorsally in lateral view (Fig. $4A_2$) as in *Eonatator sternbergi* (Bardet and Suberbiola 2001) and *H. ponpetelegans* (Konishi et al. 2016) which have a gently curved frontal profile.

The dorsal surface bears three clearly visible features: (i) a median longitudinal ridge on the anterior half of the bone; this is tall anteriorly and low posteriorly, as in *H. ponpetelegans* and *H. hebae*; (ii) a prominent, high, smooth and narrow posteromedian triangular eminence in the form of an isosceles triangle; in *H. arambourgi* it is finely ornamented by ridges and in *H. hebae* it is low or shallow (Bardet et al. 2005; Shaker et al. 2023); (iii) two depressions on both sides of the triangular eminence (Fig. $4A_3$).

The ventral surface of the frontal bears a wide and deep median groove for the olfactory stalks (Fig. $4A_4$). Facets for reception of the prefrontal and postorbitofrontal on the ventral surface are large and shallow in contrast with *H. platyspondylus*, *H. arambourgi*, and *H. ponpetelegans* which have deep facets and separated from each other (did not make contact).

Pterygoid: The right pterygoid is complete except for the palatine process (Fig. $5A_1$, A_2). The tooth row is arched unlike *H. platyspondylus* and *H. ponpetelegans* (Holmes and Sues 2000: fig. 3 and Konishi et al. 2016: fig. 11B) which have a straight row. The pterygoid bears eight alveoli versus nine in *H. platyspondylus* and *H. ponpetelegans* (Holmes and Sues 2000; Konishi et al. 2016); *H. arambourgi* possesses at least 12 (Bardet et al. 2005). The same number of teeth is found in *Mosasaurus hoffmanni* (Lingham-Soliar 1995). None of the tooth crowns are preserved.

Ectopterygoid: The ectopterygoid process (Fig. $5A_1$, A_2) is straight, slender and tapers distally. The angle between the ectopterygoid process and the dentigerous body is more than 60°.

Jugal: The left and right jugal are preserved (Fig. 5B, C). The jugal is comma-shaped as is typical of Halisaurini (Longrich et al. 2021). It resembles that of *H. arambourgi* and *H. ponpetelegans* (Bardet et al. 2005; Konishi et al. 2016). It is generally narrow and long with a relatively broad ascending (postorbital) ramus forming the posterior boundary of the orbit and a narrower anterior horizontal (infraorbital) ramus forming the ventral boundary. Although small, the posteroventral corner appears in the well-preserved left jugal. The horizontal ramus is twice as long as the vertical ramus. It differs in shape from *H. hebae* which has a broader ascending ramus.

On the medial side of the infraorbital ramus, the articular facets for ectopterygoid and maxilla are absent or reduced, suggesting weak articulation with these bones. This is unlike *H. ponpetelegans* and *H. hebae*, which have a prominent articulation on the medial side of the infraorbital ramus. The angle between the horizontal and the ascending rami is more than 120 degrees, as in *H. arambourgi* (Bardet et al. 2005) and *H. hebae* (Shaker et al. 2023). The large, broadly arched jugal seen here is associated with increased orbit size in Halisaurini (e.g., Konishi et al. 2016; Shaker et al. 2023).

Quadrate: The right quadrate is undistorted and missing only a part of the tympanic ala (Fig. 6). It is a distinctive, ring-shaped element unlike that of all other Halisaurinae or Mosasauridae. The quadrate is robust but not to the same degree as in *H. hebae* and *H. platyspondylus*. It has a ques-

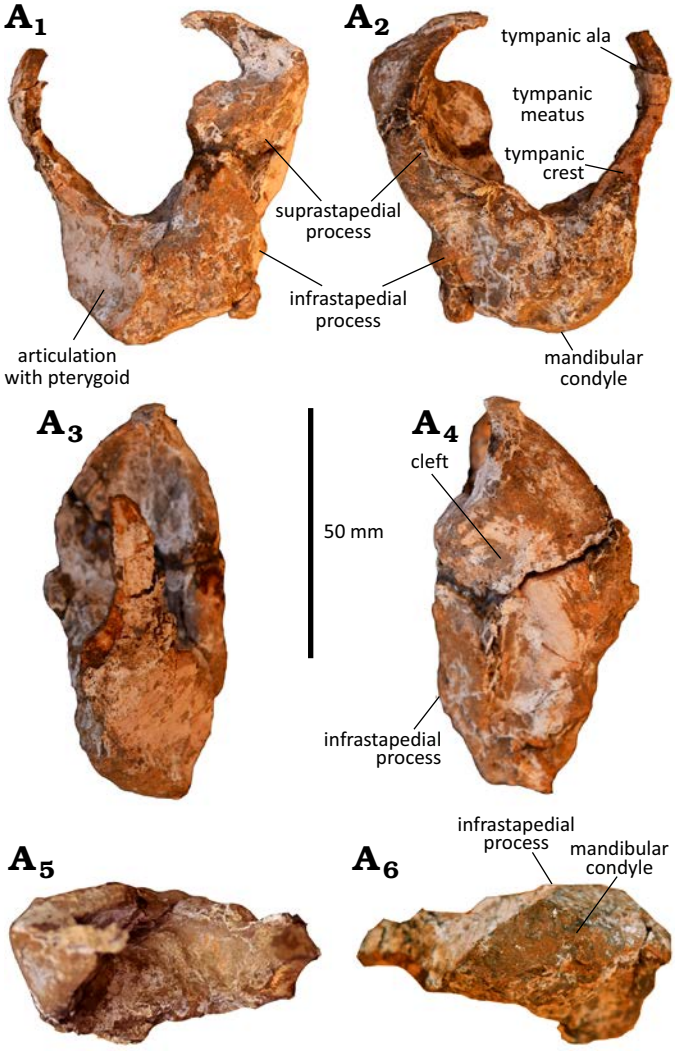

Fig. 6. Halisaurine mosasaurid *Halisaurus auriculatus* sp. nov., holotype (NVP040), Teneida, Dakhla Oasis, Western Desert, Egypt, lower Maastrichtian. Right quadrate in medial (A_1), lateral (A_2), anterior (A_3), posterior (A_4), dorsal (A_5), and ventral (A_6) views.

tion-mark shape, as in *H. arambourgi*, *H. hebae*, and *H. platyspondylus* (Holmes and Sues 2000; Bardet et al. 2005; Shaker et al. 2023).

The suprastapedial and infrastapedial processes are completely fused as in other Halisaurinae. The suprastapedial process is large, robust, wide and concave. As in *H. hebae* and *H. ponpetelegans* there is a distinct cleft or shallow depression found on the posterior face of the distal end of the suprastapedial process. Above the cleft, the suprastapedial process is reduced to half its distal width. While in *H. platyspondylus* and *Eonatator sternbergi* it remains wide (e.g., Holmes and Sues 2000: fig. 4, view 2) in *H. arambourgi* and *H. ponpetelegans* the suprastapedial process is reduced to one-third the distal width (Bardet et al. 2005: fig. 8H; Konishi et al. 2016: fig. 14A). The face for the pterygoid articulation is large and rectangular (Fig. $6A_3$).

The infrastapedial process is also well developed. There is a basin-like alar concavity formed above the mandibular condyle as in *H. platyspondylus*, *H. ponpetelegans*, and *H. hebae*. Part of the tympanic ala may be missing considering that the quadrate bone is a heavy, powerfully constructed bone (Russell 1967); accordingly the tympanic meatus is very large. The tympanic meatus differs in outline from other Halisaurinae. The mandibular condyle is narrow and has a triangular shape, unlike *H. arambourgi* and *H. hebae* which have a crescent-shaped condyle (Bardet et al. 2005: fig. 8D; Shaker et al. 2023: fig. 9F).

Mandible: Most elements of the right and left mandibular rami are preserved, including the left dentary, left splenial, right and left coronoid, and the left and right fused surangular-articular compound element. These bones broadly resemble those of other *Halisaurus* species (Figs. 7, 8).

Dentary: The left dentary is nearly complete except the broken anterior tip (Fig. 7A), which may have contained an additional alveolus. The dentary is long, narrow and robust, and measures 32 cm in length. The dorsal and ventral margins of the dentary are straight (Fig. $7A_1$, A_2). The lateral surface is gently convex. The slit-like foramina marking the exit of the terminal branches of the 5th mandibular nerve are reduced except a trace of one foramen present in the middle part of the lateral surface.

The dentary bears 20+ tooth positions, versus *H. arambourgi* which possesses 19 dentary teeth, and *H. hebae* with approximately 15 alveoli (Bardet et al. 2005; Shaker et al. 2023). As in other *Halisaurus* and *Pluridens* species the dentary's labial parapet is taller than the lingual one, so that the dental alveoli are visible in lingual view (Longrich et al. 2021; Shaker et al. 2023).

The dentary's medial surface is concave, with a deep Meckelian canal (Bardet et al. 2005) beginning near the anterior tip of the bone and widening posteriorly to form the mandibular channel. The dentary forms a prominent lip of bone below the Meckelian canal, as is typical of Halisaurinae.

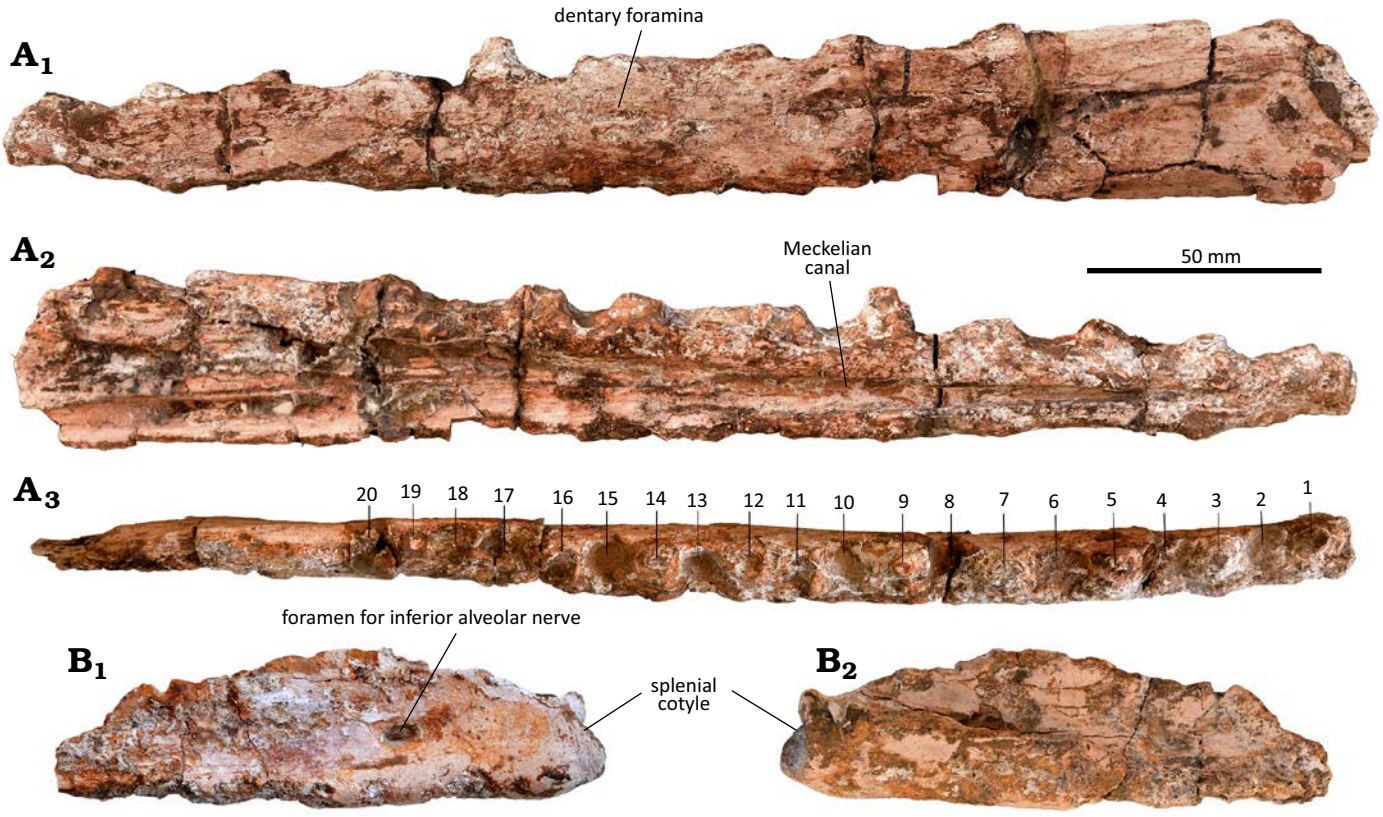

Fig. 7. Halisaurine mosasaurid *Halisaurus auriculatus* sp. nov., holotype (NVP040), Teneida, Dakhla Oasis, Western Desert, Egypt, lower Maastrichtian. **A**, **B**. Left mandibular ramus. **A**. Dentary in lateral (A_1), medial (A_2), and dorsal (A_3) views. **B**. Splenial in lateral (B_1) and ventral (B_2) views. 1–20, dental alveoli.

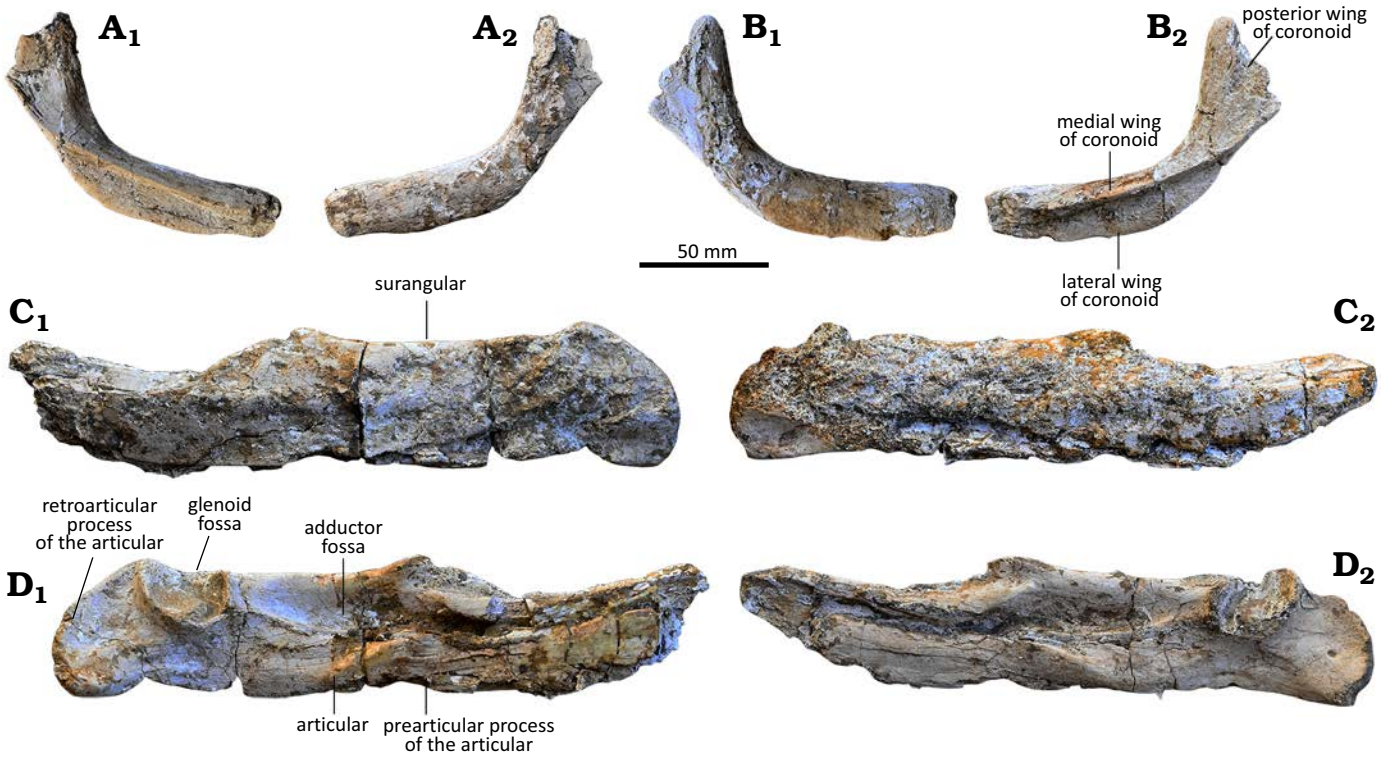

Fig. 8. Halisaurine mosasaurid *Halisaurus auriculatus* sp. nov., holotype (NVP040), Teneida, Dakhla Oasis, Western Desert Egypt, lower Maastrichtian. **A**–**D**. Left and right mandibular ramus. **A**. Left coronoid in lateral (A_1) and medial (A_2) views. **B**. Right coronoid in lateral (B_1) and medial (B_2) views. **C**. Left surangular in lateral (C_1) and medial (C_2) views. **D**. Right surangular in lateral (D_1) and medial (D_2) views. 1–20, dental alveoli.

Splenial: The left splenial preserves the posterior end and part of the lateral wing; the medial wing is broken (Fig. 7B). It forms the posterior-most extent of the anterior half of the lower jaw, and terminates in a concave cotyle that receives the angular (Street and Caldwell 2017). The bone's main body is a robust and laterally compressed rod with medial and lateral wings. It is V-shaped in cross section. The lateral wing is formed by a depressed fossa that serves as the articular facet for the dentary.

Coronoid: The left and right coronoid are well-preserved (Fig. 8A, B). The coronoid is a large, elongate bone, measuring 110 mm, comparatively larger than in the other species of *Halisaurus*, like *H. arambourgi*, *H. hebae*, *H. ponpetelegans*, and *H. coellensis* (Bardet et al. 2005; Páramo-Fonseca 2013; Konishi et al. 2016; Shaker et al. 2023). The coronoid has the typical saddle-shape of mosasaurs (Russell 1967). It is not regularly curved as in *H. hebae* and *H. arambourgi*; instead it is curved from the highest point posteriorly to a specific point at the end of the ascending process, then gently curved or nearly horizontal in the descending process. It is excavated along the midline. The lateral and medial wings are narrow but prominent; the posterior wing is well developed. The ascending process is shorter than the descending process unlike other species of *Halisaurus* (Bardet et al. 2005; Konishi et al. 2016; Shaker et al. 2023) and *Pluridens* (Longrich et al. 2021). The ascending process is also smaller and lower in plioplatecarpines and tylosaurines (Russell 1967).

Surangular-articular: Both the left and right surangular-articular are preserved (Fig. 8C, D). They fuse to form a compound bone, as in some Mosasauridae (Lingham-Soliar 1995; Christiansen and Bonde 2002; Konishi et al. 2011). The left one is nearly complete and the right one is weathered, but complete. The surangular-articular measures 265 mm. It is a long, robust and narrow bone with a rectangular shape. It occupies a large part of the posterior surface of the mandible. In lateral view, between the glenoid cavity and the coronoid process, there is a long and gently concave margin as in *H. hebae* and *H. arambourgi*. The ventral margin is emarginated, unlike other *Halisaurus* species, including *H. arambourgi*, *H. ponpetelegans*, *H. hebae*, and *H. platyspondylus*, which all have a straight ventral margin (Bardet et al. 2005: fig. 4A; Holmes and Sues 2000: fig. 6-1; Konishi et al. 2016: fig. 16A; Shaker et al. 2023: fig. 11H). The lateral surface of the surangular-articular is gently convex, and lacks the sharp crest that is found in *H. arambourgi* (Bardet et al. 2005: figs. 4A, 5A). The coronoid articulation is large and concave, sloping down from the posterior process, and rises again at the anterior end of the bone. The coronoid articulation is weakly concave in *H. hebae*, *H. arambourgi*, and *H. platyspondylus*. The coronoid buttress is high and triangular. In medial view, the surangular is covered by the long, broad prearticular process of the articular. Dorsal to its posterior part, the adductor fossa is deep, large and concave. The retroarticular process is broad, rounded and protruding ventrally. In *H. platyspondylus*, *H. arambourgi*, and *Eonatator sternbergi* (Holmes and Sues 2000; Bardet et al. 2005) the retroarticular process is rounded but narrower than our specimen. The contribution

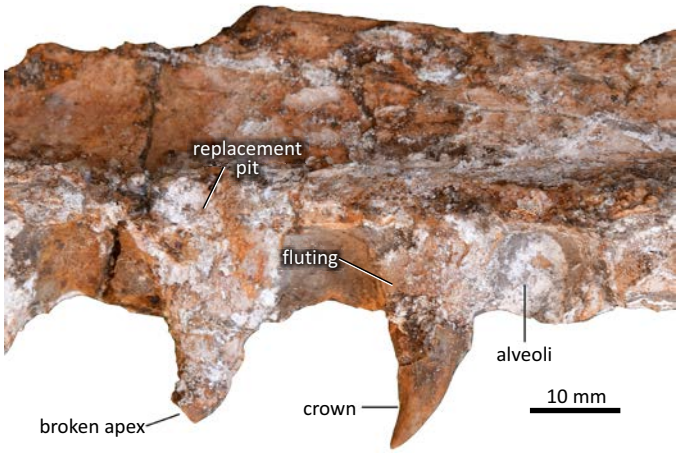

Fig. 9. Halisaurine mosasaurid *Halisaurus auriculatus* sp. nov., holotype (NVP040), Teneida, Dakhla Oasis, Western Desert, Egypt, lower Maastrichtian. Close up showing teeth of the maxilla.

of the articular to glenoid is larger than the surangular as in *H. platyspondylus*.

Dentition: One well-preserved tooth is ankylosed to the left maxilla and two are preserved in the right maxilla. Several broken teeth are also ankylosed to the dentary (Figs. 2, 3, 9). Tooth crowns are relatively large (maximum length 23 mm) when compared to teeth of other species of *Halisaurus*. They have a sharp, pointed apex. The basal part of the crown is slanted slightly anteriorly, and then curves abruptly posteriorly at midpoint as in other halisaurines (however the preserved tooth in the left maxilla is slightly curved). Strong hooking of the teeth is typical of Halisaurinae (Bardet et al. 2005; Longrich et al. 2021). The base of the crown is inflated; in cross-section it is circular, with the labial and lingual surfaces being equally convex. The enamel is smooth except for very faint striations, and the crown bears only a weak, unserrated, anterior carina, as in other Halisaurinae (Bardet et al. 2005; Longrich 2016; Shaker et al. 2023). The crown lacks fluting or striae.

The root is a massive pillar-like structure made of cementum, as is typical of mosasaurids, but in contrast to the typical squamate condition where the tooth is supported by a dentine root (LeBlanc et al. 2017). It implants in a shallow theca formed by the lateral parapet of the maxilla and dentary and interdental ridges, but the lingual parapet of the maxilla and dentary is weakly developed so that in contrast to Mosasaurinae, Tylosaurinae and Plioplatecarpinae (Konishi and Caldwell 2011; Jiménez-Huidobro and Caldwell 2016; Street and Caldwell 2017; Longrich et al. 2024a, b), the theca does not fully enclose the tooth root. This is a plesiomorphic condition shared with other Halisaurinae (Bardet et al. 2005; Konishi et al. 2016; Shaker et al. 2023). As in other halisaurines, the teeth bear deep replacement pits on the medial surface of the root (Lingham-Soliar 1998; Konishi et al. 2016; Longrich et al. 2021), but lack deep tooth replacement crypts excavating the tooth root that characterize derived mosasaurs (Welles and Gregg 1971; Lingham-Soliar and Nolf 1989; Schulp et al. 2008; LeBlanc et al. 2012; Street and Caldwell 2017).

Axial skeleton: Most of the vertebrae are poorly preserved but several cervical, dorsal and caudal vertebrae are preserved (Fig. 10A, C). These preserve diagnostic features of *Halisaurus* such as the subrectangular shape of the artic-

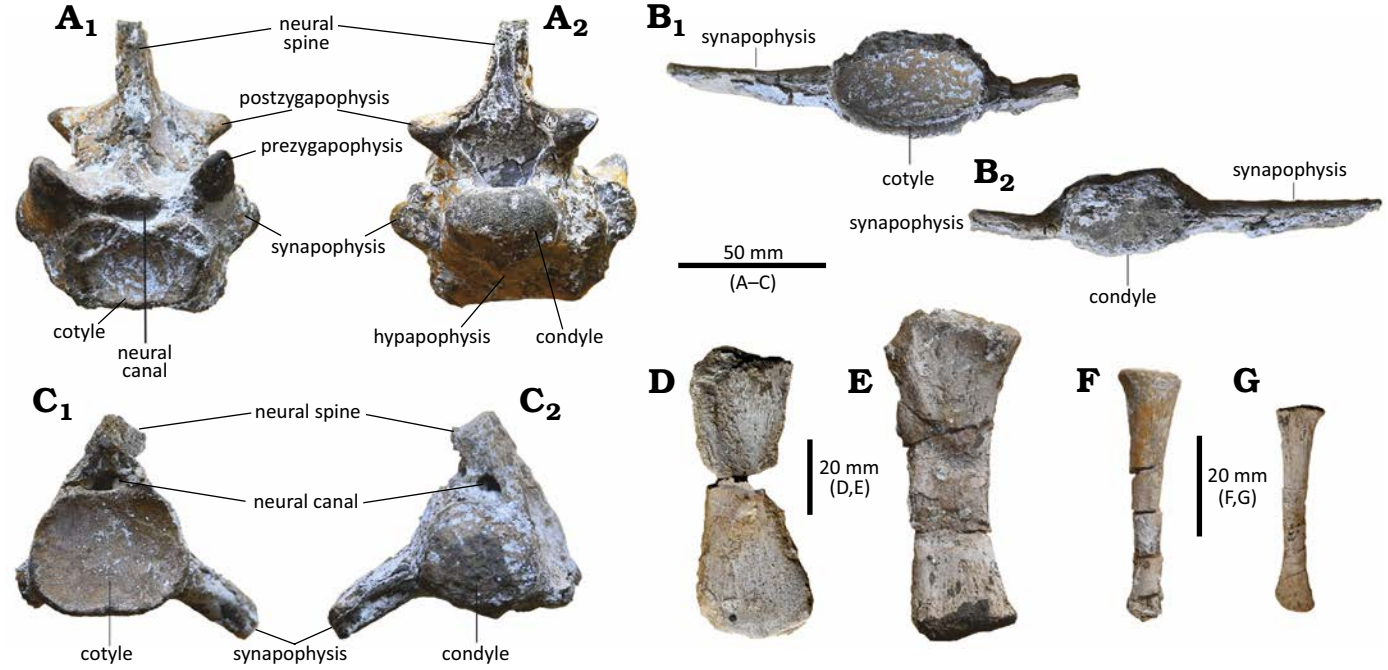

Fig. 10. Halisaurine mosasaurid *Halisaurus auriculatus* sp. nov., holotype (NVP040), Teneida, Dakhla Oasis, Western Desert, Egypt, lower Maastrichtian. Selected vertebrae and hindlimb elements. **A**. Cervical vertebra in anterior (A_1) and posterior (A_2) views. **B**. Dorsal vertebra in anterior (B_1) and posterior (B_2) views. **C**. Caudal vertebra in anterior (C_1) and posterior (C_2) views. **D**. Fibula. **E**. Tibia. **F**. Metapodial. **G**. Phalanx.

ulations in the cervical vertebrae (Fig. 10A) (Russell 1967; Caldwell and Bell 1995).

The well-preserved cervical vertebra is dorsoventrally compressed. It bears a small hypapophyseal peduncle; suggesting that it is one of the last cervical vertebrae. The pre- and postzygapophyses and synapophyses are large. The zygosphene-zygantrum complex is absent.

The dorsal vertebrae (Fig. 10B) are wide, elongated and bear very long transverse processes. The transverse processes lie anteriorly, as in *H. arambourgi* and *H. hebae* (Bardet et al. 2005; Shaker et al. 2023). The articular cotyles and condyles of the dorsal vertebrae are also strongly dorsoventrally compressed typical of Halisaurinae (Holmes and Sues 2000; Bardet et al. 2005; Konishi et al. 2016). The preserved caudal vertebra (Fig. 10C) has a circular articular surface without a fused haemal arch.

Appendicular skeleton: Scattered elements of the appendicular skeleton are preserved, including the tibia, fibula, a metapodial and phalanx (Fig. 10D–G).

The left fibula (Fig. 10D) is weathered and much of its ventral surface is eroded. It is typical of *Halisaurus* (Bardet et al. 2005) in being about three times as long as wide, with an angular proximal end, a slight constriction at midshaft, and a spatulate and rounded distal end.

The tibia is a subrectangular element, about 250% as long as wide (Fig. 10E). The proximal end is subrectangular and below this the shaft tapers and the anterior and posterior margins are slightly concave. The distal end is slightly rounded. Again the element closely resembles the corresponding bone in *H. arambourgi* (Bardet et al. 2005).

The metapodial is about 350% as long as wide, strongly flared proximally and narrow distally (Fig. 10F). The phalanx is about 400% as long as wide, triangular proximally and spatulate and rounded distally (Fig. 10G). Overall the proportions of the limb elements are similar to those of other halisaurines.

Stratigraphic and geographic range.—Lower Maastrichtian, Dakhla Shale, Dakhla Oasis, Western Desert, Egypt.

Phylogenetic analysis

Phylogenetic analysis using equal-weights parsimony produced six most-parsimonious trees (length = 73, CI = 0.5753, RI = 0.7207, RC = 0.4147). The strict consensus is shown in (Fig. 11). Implied weighting produces a broadly congruent tree topology (see SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app71-Shaker_etal_SOM.pdf).

Phylogenetic analysis recovers two main lineages within the Halisaurinae, Pluridensini (including *Pluridens* spp. and an unnamed halisaur species from the Mooreville Chalk of Alabama) and Halisaurini, which includes *Halisaurus* spp., *Phosphorosaurus ortliebi*, and *Eonatator sternbergi*.

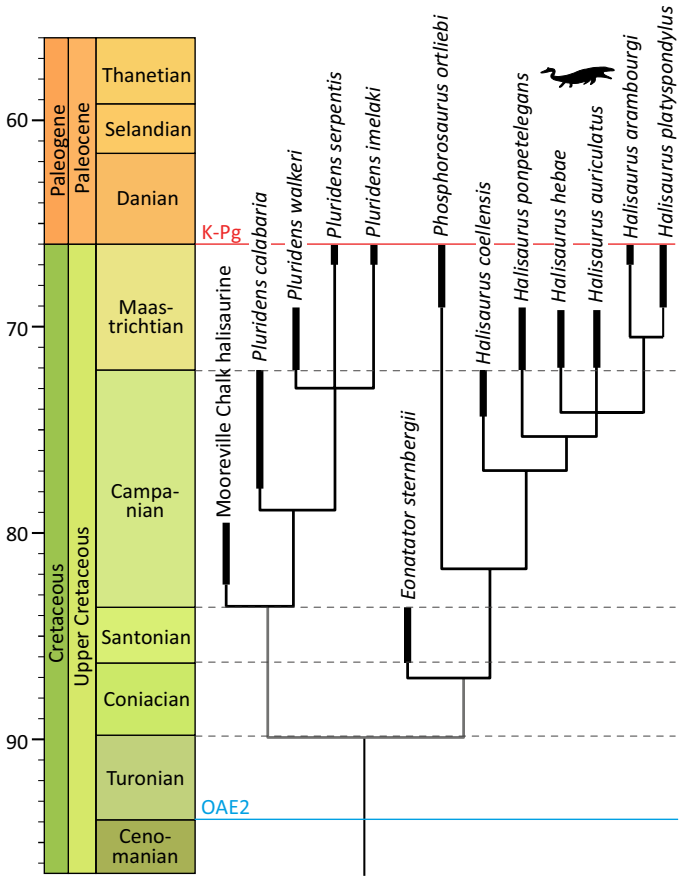

Fig. 11. Phylogeny showing the evolutionary relationships of *Halisaurus auriculatus* sp. nov. Strict consensus of 6 most-parsimonious trees.

Halisaurus auriculatus sp. nov. is recovered as sister to a clade comprising *H. arambourgi* and *H. platyspondylus*.

In the equal weights analysis, *H. auriculatus* sp. nov. forms a polytomy with *H. hebae* (Fig. 11); in the implied weights analysis, *H. auriculatus* sp. nov. is sister to the *H. arambourgi–H. platyspondylus* clade, and *H. hebae* occupies a basal position relative to these species (SOM 1).

Discussion

Affinities of *Halisaurus auriculatus* sp. nov.—*Halisaurus auriculatus* sp. nov. can be referred to Halisaurinae and to *Halisaurus* based on a combination of primitive and derived characters. The premaxilla-maxilla sutural contact is vertical anteriorly, subhorizontal posteriorly, and extends nine tooth positions, as in *Pluridens serpentis*, versus six or seven tooth positions in *H. arambourgi* (Bardet et al. 2005; Longrich et al. 2021). On the contrary, among other subfamilies within Mosasauridae this suture is noticeably shorter, extending at most 4–5 tooth positions in most Mosasaurinae (Russell 1967; Ikejiri and Lucas 2015; Street and Caldwell 2017) and 3–4 in Tylosaurinae (Russell 1967; Zietlow 2020). Prognathodontini also exhibit relatively moderate suture extension, commonly to the fourth tooth position (Lingham-

Table 2. Comparison of selected diagnostic characters among African species of *Halisaurus*.

Character	*Halisaurus arambourgi*	*Halisaurus hebae*	*Halisaurus auriculatus* sp. nov.
Maxillary tooth count	~16	–	21
Premaxilla-maxilla suture length extension	6–7 tooth positions	–	extends to 9th tooth
Frontal shape	broad with rounded narial emargination	narrower, elongate	elongate, triangular, tapering anteriorly
Parietal suture contact	straight	undulated	undulated
Posteromedian frontal eminence	finely ornamented	low/shallow	high, smooth, triangular
Pterygoid tooth count	≥12	–	8
Jugal ascending ramus	narrow	broad	narrow
Quadrate mandibular condyle shape	crescent-shaped	crescent-shaped	triangular-shaped
Quadrate tympanic meatus size	narrow	narrow	very large
Dentary tooth count	~19	~15	20+
Coronoid size	moderate	moderate	relatively large
Coronoid ascending process	longer than descending	longer than descending	shorter than descending
Surangular-articular ventral margin	straight	straight	emarginated

Soliar and Nolf 1989; Schulp et al. 2008; Lindgren et al. 2010). The maxilla also has a deep, flat contact for the subrectangular narial bar of the premaxilla, which is another derived feature of Halisaurinae (Longrich et al. 2021).

The frontal bears a tall, keel-like dorsal median ridge on its anterior part, and behind this a broad, subtriangular boss bordering the frontoparietal suture, as well as a ventral boss. The subtriangular dorsal boss is a consistent feature in all described species of *Halisaurus* (Bardet et al. 2005; Konishi et al. 2016; Shaker et al. 2023) and is absent in other mosasaurid subfamilies, including Mosasaurinae, Tylosaurinae, Prognathodontinae, and Plioplatecarpinae (Lingham-Soliar and Nolf 1989; Lingham-Soliar 1995; Konishi and Caldwell 2011; Konishi et al. 2012; Zietlow 2020). The quadrate has a large infrastapedial process, and fused infra- and suprastapedial processes as in other Halisaurinae, and convergently in prognathodontins (Lingham-Soliar and Nolf 1989; Shaker et al. 2023). The infrastapedial process is also well developed in Mosasaurinae and Plioplatecarpinae, but it is separated from the suprastapedial process (Konishi et al. 2010; Street and Caldwell 2017), in contrast with Tylosaurinae which have poorly developed or absent infrastapedial process (Zietlow 2020). Teeth are small and numerous as is typical of Halisaurinae (Bardet et al. 2005). Tooth crowns are conical and hooked, lacking raised carinae, facets or flutes. Teeth bear large but shallow replacement pits rather than crypts; labial parapet small relative to lingual parapet, as in other species of *Halisaurus* and *Pluridens* (Bardet et al. 2005; Longrich 2016; Longrich et al. 2021)

Among Halisaurinae, the specimen shares characters with Halisaurini, specifically species of *Halisaurus*. The frontal participates in the orbit margins as in other Halisaurini. The frontal has a tall and narrow dorsal median ridge on its anterior half, and a prominent triangular eminence on the posterior end. The articular bears a large buttress just posterior to the glenoid (Bardet et al. 2005). The large, comma-shaped jugal also distinguishes the Halisaurini (Longrich et al. 2021). This broadly arched jugal is associated with an increase in orbit size in the Halisaurini (e.g., Konishi et al. 2016; Shaker et al. 2023). The suprastapedial and infrastapedial processes of the quadrate are coalescent. Condylar and cotylar articulations of the cervical vertebrae are subrectangular (Russell 1967).

The new specimen can be excluded from Pluridensini (Longrich et al. 2021) which are characterized by a large number of teeth ranging from 25 to 30 (Longrich 2016; Longrich et al. 2021), and modified tooth implantation with large interdental ridges and obliquely oriented tooth roots. It can also be excluded from *Eonatator* Bardet & Pereda Suberbiola in Bardet et al., 2005, which has a completely different shaped mandible (the retroarticular process of the surangular is almost vertical and triangular in *E. sternbergi*).

The tapered anterior end of the frontal, the undulated frontal-parietal suture contact, the large and shallow facets for reception of the prefrontal and postorbitofrontal on the ventral surface, and the much elongated and narrow fused surangular-articular seen in *H. auriculatus* sp. nov. are shared with *H. hebae*.

H. auriculatus sp. nov. can be distinguished from *H. hebae* Shaker et al., 2023, by numerous characters (Table 2). The frontal median ridge extends only at the anterior half of the frontal, while in *H. hebae* it extends the whole length. The triangular boss in the posterior part of the frontal of our species is high and smooth, while in *H. hebae* it is low and bounded by two ridges. The jugal in *H. auriculatus* sp. nov. is longer and narrower than in *H. hebae*.

The shape of the quadrate is different in both taxa, and also the shape of the mandibular condyle; it is crescentric and broad in *H. hebae* while in the new specimen it is triangular and narrower. The coronoid of *H. auriculatus* sp. nov. is larger and is irregularly curved, unlike the coronoid of *H. arambourgi*, *H. hebae*, and *H. ponpetelegans* which are small and regularly curved. The retroarticular process is broad, rounded and protruding ventrally, unlike other *Halisaurus* species.

Halisaurini biology.—Like other Halisaurini, which also have small, hooked teeth, *H. auriculatus* sp. nov. is placed

into the "piercing I" guild of Massare (1987). This suggests a diet based on small and soft prey (e.g., cephalopods, fish), probably seized and captured by these conical, sharply pointed teeth, then swallowed whole (Bardet et al. 2025).

In addition, the large, anterolaterally directed orbits of *H. auriculatus* sp. nov. and binocularity suggest it relied to a large extent on vision for foraging in low-light conditions, either at night, or at depth (Konishi et al. 2016; Longrich et al. 2021; Shaker et al. 2023; Bardet et al. 2025). However, *Halisaurus* rarely exhibits the avascular necrosis of bone tissue seen in deep divers (Rothschild and Martin 2005).

Halisaurus auriculatus sp. nov. has a large coronoid bone. The coronoid bone provides attachment for the adductor muscles of the jaw, which are responsible for closing the mouth and biting. The elongated upper and lower jaws function to increase the speed with which the jaws open and close (Burnette and Gibb 2013) so the very long maxilla and dentary suggest that the jaws were adapted for fast closing. Furthermore, the position of the coronoid process relative to the condyle and jaw tip indicates low bite force.

A large tympanic meatus is a significant anatomical feature that relates to their hearing adaptations. The enlarged tympanic meatus in *H. auriculatus* sp. nov. is a derived feature. It may have improved hearing underwater and aided in the transmission of low-frequency sounds through the skull, and might aid in nocturnal or deep-water foraging in *Halisaurus*, where vision is limited and hearing is more important. The large tympanic meatus is a convergent feature seen in *Platecarpus tympaniticus* (Cope 1869; Konishi et al. 2010; Palci et al. 2020).

How mosasaurs used hearing underwater is unclear, but the diverse quadrate shapes seen in different mosasaur clades, as well as diversity of quadrate morphology within mosasaur subfamilies (Lingham-Soliar and Nolf 1989; Dortangs et al. 2002; Everhart 2005; Street and Caldwell 2017; Palci et al. 2020), suggests that they were under strong selective pressure. While mosasaurs may have lacked the active echolocation seen in odontocetes, it is possible that they had well-developed hearing for finding food and navigating, and that the specialized ears of *H. auriculatus* sp. nov. were related to a specialized hunting strategy.

Implications for mosasaur biodiversity and biogeography.—Geographically, *Halisaurus* is one of the most widely distributed mosasaur genera. Despite its comparatively small adult size when compared to other mosasaurs (Lindgren and Siverson 2005) it occurred over a large geographic area. But with the discovery of three species in Africa, this raises questions about the affiliation of this group to a specific geographical region. The discovery of a new taxon of halisaurines from Egypt suggests a degree of endemism in halisaurines.

Although several species have been discovered at relatively high latitudes in North America (Holmes and Sues 2000), Japan (Konishi et al. 2016), and Belgium (Lingham-Soliar 1996), consistent with the broadly warm Late Cretaceous greenhouse climate (O'Connor et al. 2019), published records of *Halisaurus* primarily come from the southern Tethyan and South Atlantic margins of Africa and South America (Lingham-Soliar 1998; Bardet et al. 2005; Polcyn et al. 2012; Bardet 2012; Páramo-Fonseca 2013; Fernández and Talevi 2015; Longrich 2016; Jiménez-Huidobro et al. 2019; Shaker et al. 2023). This apparent clustering suggests the paleodistribution of halisaurines might be linked to favorable climate and ecologic conditions rather than a specific concentration within tropical or subtropical latitudinal belts.

Conclusions

A new species of *Halisaurus*, *Halisaurus auriculatus* sp. nov., is reported from the lower Maastrichtian Dakhla Shale of the Western Desert of Egypt. It is distinguished from the coeval *H. hebae* by long, slender jaws, a high tooth count and unique specialization of the quadrate. These suggest adaptation for a fast bite but low bite force, and perhaps specializations of the auditory apparatus for underwater hearing. These features suggest specialization on small prey and niche partitioning between halisaurines in the fauna. Halisaurines were a diverse component of the Tethys and Atlantic in the Maastrichtian, highlighting their ecological significance within Late Cretaceous marine ecosystems.

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References

Baird, D. 1986. *Halisaurus* and *Prognathodon*, two uncommon mosasaurs from the Upper Cretaceous of New Jersey. *The Mosasaur* 3: 37–45.

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. and Suberbiola, X.P. 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'Académie des Sciences-Series IIA-Earth and Planetary Science* 332: 395–402.

Bardet, N., Fischer, V., Jalil, N.-E., Khaldoune, F., Yazami, O.K., Pereda-Suberbiola, X., and Longrich, N. 2025. Mosasaurids Bare the Teeth: An Extraordinary Ecological Disparity in the Phosphates of Morocco Just Prior to the K/Pg Crisis. *Diversity* 17 (2): 114.

Bardet, N., Pereda Suberbiola, X., Iarochene, M., Bouya, B., and Amaghzaz, M. 2005. 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.

Barthel, K.W. and Hermann-Degen, W. 1981. Late Cretaceous and Early Tertiary stratigraphy in the Great Sand Sea and its SE Margins (Farafra and Dakhla Oases), SW Desert, Egypt. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Histor. Geologie* 21: 141–182.

Burnette, M.F. and Gibb, A.C. 2013. Do changes in morphology and prey-capture movements facilitate a dietary transition in juvenile Colorado pikeminnow, *Ptychocheilus lucius*? *Evolutionary Biology* 40: 261–275.

Caldwell, M.W. and Bell, G.L. Jr 1995. *Halisaurus* sp. (Mosasauridae) from the Upper Cretaceous (? Santonian) of East-central Peru, and the taxonomic utility of mosasaur cervical vertebrae. *Journal of Vertebrate Paleontology* 15: 532–544.

Christiansen, P. and Bonde, N. 2002. A new species of gigantic mosasaur from the Late Cretaceous of Israel. *Journal of Vertebrate Paleontology* 22: 629–644.

Cohen, K., Harper, D., Gibbard, P., and Car, N. 2025. The ICS international chronostratigraphic chart this decade. *Episodes Journal of International Geoscience* 48: 105–115.

Conoco, C. 1987. *Geological Map of Egypt. Scale 1:500,000*. The Egyptian General Petroleum Corporation, Cairo.

Cope, E. 1869. On the reptilian orders Pythonomorpha and Streptosauria. *Proceedings of the Boston Society of natural History* 12: 250–266.

Dollo, L. 1889. Note sur les vertébrés récemment offerts au Musée de Bruxelles par M. Alfred Lemonnier. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie* 3: 181–182.

Dominik, W. and Schaal, S. 1984. Notes on the stratigraphy of the Upper Cretaceous phosphates (Campanian) of the Western Desert (Egypt). *Berliner geowissenschaftliche Abhandlungen A* 50: 153–175.

Dortangs, R.W., Schulp, A.S., Mulder, E.W., Jagt, J.W., Peeters, H.H., and De Graaf, D.T. 2002. A large new mosasaur from the Upper Cretaceous of The Netherlands. *Netherlands Journal of Geosciences* 81: 1–8.

El Naggar, Z. 1966. Stratigraphy and planktonic foraminifera in the Upper Cretaceous–Lower Tertiary succession in the Esna-Idfu region. *Nile Valley, Egypt, UAR: British Museum of Natural History Bulletin* 2: 291.

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

Fernández, M.S. and 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.

Gervais, P. 1853. Observations relatives aux reptiles fossiles de France. *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences* 36: 470.

Hermina, M. 1990. The surroundings of Kharga, Dakhla and Farafra oases. *In*: R. Said (ed.), *The Geology of Egypt*, 259–292. A.A. Balkema, Rotterdam.

Hewaidy, A.G.A., Farouk, S., and Bazeen, Y.S. 2017. Sequence stratigraphy of the Maastrichtian–Paleocene succession at the Dakhla Oasis, Western Desert, Egypt. *Journal of African Earth Sciences* 136: 22–43.

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

Ikejiri, T. and Lucas, S. 2015. Osteology and taxonomy of *Mosasaurus conodon* Cope, 1881 from the Late Cretaceous of North America. *Netherlands Journal of Geosciences* 94: 39–54.

Jiménez-Huidobro, P. and Caldwell, M.W. 2016. Reassessment and reassignment of the early Maastrichtian mosasaur *Hainosaurus bernardi* Dollo, 1885, to *Tylosaurus* Marsh, 1872. *Journal of Vertebrate Paleontology* 36 (3): e1096275.

Jiménez-Huidobro, P., Otero, R.A., Soto-Acuna, S., and 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.

Kiernan, C.R. 2002. Stratigraphic distribution and habitat segregation of mosasaurs in the Upper Cretaceous of western and central Alabama, with an historical review of Alabama mosasaur discoveries. *Journal of Vertebrate Paleontology* 22 (1): 91–103.

Konishi, T. and 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., Brinkman, D., Massare, J.A., and 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., and Bell Jr, G.L. 2010. Redescription of the holotype of *Platecarpus tympaniticus* Cope, 1869 (Mosasauridae: Plioplatecarpinae), and its implications for the alpha taxonomy of the genus. *Journal of Vertebrate Paleontology* 30: 1410–1421.

Konishi, T., Caldwell, M.W., Nishimura, T., Sakurai, K., and 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., and 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.

LeBlanc, A.R., Caldwell, M., and Bardet, N. 2012. A new mosasaurine from the Maastrichtian (Upper Cretaceous) phosphates of Morocco and the implications for the systematics of the Mosasaurinae. *Journal of Vertebrate Paleontology* 32: 1–23.

LeBlanc, A.R., Caldwell, M.W., and Lindgren, J. 2013. Aquatic adaptation, cranial kinesis, and the skull of the mosasaurine mosasaur *Plotosaurus bennisoni*. *Journal of Vertebrate Paleontology* 33: 349–362.

LeBlanc, A.R., Lamoureux, D.O., and 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.

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

Lindgren, J., Caldwell, M.W., Konishi, T., and Chiappe, L.M. 2010. Convergent evolution in aquatic tetrapods: insights from an exceptional fossil mosasaur. *PloS one* 5 (8): e11998.

Lingham-Soliar, T. 1992. The tylosaurine mosasaurs (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe and Africa. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 62: 171–194.

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. Biological Sciences* 347 (1320): 155–180.

Lingham-Soliar, T. 1996. The first description of *Halisaurus* (Reptilia Mosasauridae) from Europe, from the Upper Cretaceous of Belgium. *Bul-*

letin 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. and Nolf, D. 1989. The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium. *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen. Aardwetenschappen = Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre* 59: 137–190.

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. and Jalil, N.-E. 2026. A Giant Halisaurine from the Late Maastrichtian of Morocco. *Diversity* 18 (3): 159.

Longrich, N.R., Bardet, N., Khaldoune, F., Yazami, O.K., and Jalil, N.-E. 2021. *Pluridens serpentis,* a new mosasaurid (Mosasauridae: Halisaurinae) from the Maastrichtian of Morocco and implications for mosasaur diversity. *Cretaceous Research* 126: 104882.

Longrich, N.R., Pereda-Suberbiola, X., Jalil, N.-E., and Bardet, N. 2024a. A new species of the durophagous mosasaurid *Carinodens* from the Late Maastrichtian phosphates of Morocco and implications for Maastrichtian mosasaurid diversity. *Diversity* 17 (1): 25.

Longrich, N.R., Polcyn, M.J., Jalil, N.-E., Pereda-Suberbiola, X., and Bardet, N. 2024b. A bizarre new plioplatecarpine mosasaurid from the Maastrichtian of Morocco. *Cretaceous Research* 160: 105870.

Luger, P. and Schrank, E. 1987. Mesozoic to Paleogene transgressions in middle and southern Egypt. Summary of paleontological evidence. *In*: G. Matheis and H. Schandelmeier (eds.), *Current Research in African Earth Sciences*, 199–202. A.A. Balkema, Rotterdam.

Mahmoud, M.S. 2003. Palynology and palaeoenvironment of the Quseir Formation (Campanian) from central Egypt. *Journal of African Earth Sciences* 36: 135–148.

Marsh, O.C. 1869. Notice of some new mosasauroid reptiles from the Greensand of New Jersey. *American Journal of Science and Arts (1820–1879)* 48 (144): 392.

Massare, J.A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* 7: 121–137.

O'Connor, L.K., Robinson, S.A., Naafs, B.D.A., Jenkyns, H.C., Henson, S., Clarke, M., and Pancost, R.D. 2019. Late Cretaceous temperature evolution of the southern high latitudes: A TEX86 perspective. *Paleoceanography and Paleoclimatology* 34: 436–454.

Oppel, M. 1811. *Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben*. xii + 87 pp. J. Lindauer, München.

Palci, A., Konishi, T., and Caldwell, M.W. 2020. A comprehensive review of the morphological diversity of the quadrate bone in mosasauroids (Squamata: Mosasauroidea), with comments on the homology of the infrastapedial process. *Journal of Vertebrate Paleontology* 40 (6): e1879101.

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 (145): 499–518.

Polcyn, M.J. and Lamb, J. 2012. The snout of *Halisaurus platyspondylus*: phylogenetic and functional implications. *Bulletin de la Société géologique de France* 183: 137–143.

Polcyn, M.J., Lindgren, J., Bardet, N., Cornelissen, D., Verding, L., and 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.

Rothschild, B. and Martin, L. 2005. Mosasaur ascending: the phylogeny of bends. *Netherlands Journal of Geosciences* 84: 341–344.

Russell, D. 1967. Systematics and morphology of american mosasaurs (Reptilia, Sauria). *Bulletin of the Peabody Museum of Natural History* 23: 1.

Said, R. 1962. *The Geology of Egypt*. 377 pp. Elsevier, Amsterdam.

Sallam, H.M., Gorscak, E., O'Connor, P.M., El-Dawoudi, I.A., El-Sayed, S., Saber, S., Kora, M.A., Sertich, J.J., Seiffert, E.R., and Lamanna, M.C. 2018. New Egyptian sauropod reveals Late Cretaceous dinosaur dispersal between Europe and Africa. *Nature Ecology & Evolution* 2: 445–451.

Sallam, H.M., O'Connor, P.M., Kora, M., Sertich, J.J., Seiffert, E.R., Faris, M., Ouda, K., El-Dawoudi, I., Saber, S., and El-Sayed, S. 2016. Vertebrate paleontological exploration of the Upper Cretaceous succession in the Dakhla and Kharga Oases, Western Desert, Egypt. *Journal of African Earth Sciences* 117: 223–234.

Schulp, A., Polcyn, M.J., Mateus, O., Jacobs, L.L., and Morais, M.L. 2008. A new species of *Prognathodon* (Squamata, Mosasauridae) from the Maastrichtian of Angola, and the affinities of the mosasaur genus *Liodon*. *In*: M.J. Everhart (ed.), *Proceedings of the Second Mosasaur Meeting*, 1–12. Fort Hays State University, Hays.

Shaker, A.A., Longrich, N.R., Strougo, A., Asan, A., Bardet, N., Mousa, M.K., Tantawy, A.A., and El-Kheir, G.A.A. 2023. A new species of *Halisaurus* (Mosasauridae: Halisaurinae) from the lower Maastrichtian (Upper Cretaceous) of the Western Desert, Egypt. *Cretaceous Research* 2024: 105719.

Street, H.P. and 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.

Swofford, D.L. 2003. *PAUP*: Phylogenetic Analysis Using Parsimony (* and Other Methods), Version 4*. Sinauer Associates, Sunderland.

Tantawy, A., Keller, G., Adatte, T., Stinnesbeck, W., Kassab, A., and Schulte, P. 2001. Maastrichtian to Paleocene depositional environment of the Dakhla Formation, Western Desert, Egypt: Sedimentology, mineralogy, and integrated micro- and macrofossil biostratigraphies. *Cretaceous Research* 22: 795–827.

Welles, S.P. and Gregg, D.R. 1971. Late Cretaceous marine reptiles of New Zealand. *Records of the Canterbury Museum* 9: 1–111.

Wiman, C. 1920. Some reptiles from the Niobrara Group in Kansas. *Bulletin of the Geological Institution of the University of Uppsala* 18: 9–18.

Youssef, M. 1960. Upper Cretaceous rocks in Quesir area. *Bulletin de L'Institute de Egypt* 7: 35–53.

Zahran, S., El Hedeny, M., El-Sabbagh, A., Rashwan, M., El-Refaiy, A., and El-Kheir, G.A. 2025. A palaeoenvironmental reconstruction of the Campanian–lower Palaeocene succession of the Dakhla Oasis (Western Desert, Egypt): Insights from integrated sequence stratigraphy, macrobenthos, and trace fossil analyses. *Journal of African Earth Sciences* 227: 105629.

Zietlow, A.R. 2020. Craniofacial ontogeny in Tylosaurinae. *PeerJ* 8: e10145.

Zittel, K.A. 1883. Beiträge zur Geologie und Paläontologie der Libyschen Wüste und der angrenzenden Gebiete von Ägypten. *Palaeontographica* 30 (3): 1–147.