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A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the Halisaurinae (Squamata: Mosasauridae)

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A new species of the basal mosasaurid *Halisaurus* from the Late Cretaceous (Late Maastrichtian) of the Oulad Abdoun Phosphate Basin of Morocco is described on the basis of both cranial and postcranial remains. ***H. arambourgi* sp. nov.** is characterized by unique features of the nares, frontal, parietal, girdle and limb bones. A phylogenetical analysis supports the monophyletic status of *Halisaurus*; *H. platyspondylus* (Maastrichtian, New Jersey), *H. ortliebi* (Maastrichtian, Belgium) and *H. arambourgi* form an unresolved polytomy. This study does not support the attribution of '*Halisaurus*' *sternbergii* (Santonian, Kansas) to *Halisaurus* nor to any known genus. A new genus, ***Eonatator***, is proposed for the reception of this species, *Eonatator sternbergii* comb. nov. The new taxon Halisaurinae (*Halisaurus* + *Eonatator*) is the sister-group of more advanced mosasaurids (Natantia). Halisaurines are defined by the shape of the lateral premaxilla–maxilla suture; an oblique contact plane between the parietal and the supratemporal; a preaxial ridge present on the distal two-thirds of the radius length; and tibia and fibula long and slender with slightly expanded extremities.

ADDITIONAL KEYWORDS: ***Eonatator* gen. nov.** – ***Halisaurus arambourgi* sp. nov.** – Maastrichtian – phylogeny – systematics.

INTRODUCTION

As a result of an active collaboration between the 'Office Chérifien des Phosphates' (OCP, Morocco), the 'Ministère de l'Energie et des Mines' (Morocco) and the 'Centre National de la Recherche Scientifique' (CNRS, France), new palaeontological fieldwork has been undertaken in the Oulad Abdoun phosphatic Basin of Morocco in recent years. This work resulted in the discovery of a great number of marine vertebrate remains, especially mosasaurids from the Maastrichtian strata, crocodilians from the Palaeogene levels and turtles from both deposits. These new discoveries have significantly improved our knowledge of these marine reptiles, which were previously known mainly from fragmentary and isolated remains (Arambourg, 1952).

Halisaurus is a key taxon in mosasauroid phylogeny as it has been considered the sister-group of all other mosasaurids (DeBraga & Carroll, 1993; Bell, 1997). This taxon has always been problematic because it was represented only by fragmentary specimens from the Santonian to Maastrichtian formations of the Americas and Europe (see Caldwell & Bell, 1995; Holmes & Sues, 2000). Recently, new attention has been devoted to *Halisaurus* with the description of

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more complete specimens of the type species *H. platyspondylus* (Wright, 1988; Holmes & Sues, 2000), the assignment of '*Phosphorosaurus*' *ortliebi* Dollo, 1889 to *Halisaurus* (Lingham-Soliar, 1996), and the revision of *Halisaurus sternbergii* (Wiman, 1920) (Bardet & Pereda Suberbiola, 2001). A new species of *Halisaurus* from Alabama has also been mentioned (Bell, 1997), but remains undescribed. The aim of this paper is to describe a new species of *Halisaurus* from the Late Maastrichtian of Morocco and to discuss the status of the Halisaurinae mosasaurids on the basis of a new cladistic analysis.

Abbreviations: BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie (München, Germany); IRSNB/KBIN, Institut Royal des Sciences Naturelles de Belgique (Bruxelles, Belgium); MNHN, Muséum National d'Histoire Naturelle (Paris, France); NHMM, Natuurhistorisch Museum Maastricht (Maastricht, The Netherlands); NJSM, New Jersey State Museum (Trenton, USA); OCP, Office Chérifien des Phosphates (Khouribga, Morocco); UPI, Uppsala University Palaeontological Institute (Uppsala, Sweden); USNM, United States National Museum (Washington, USA); YPM, Yale University Peabody Museum of Natural History (New Haven, USA).

GEOGRAPHICAL AND STRATIGRAPHICAL OCCURRENCES

The phosphatic deposits of Morocco, known since 1908, have been exploited as an economical resource since the 1920s (Office Chérifien des Phosphates, 1989). They are part of the Mediterranean Tethyan phosphogenic province, which extends from North Africa to the Middle-East (Lucas & Prévôt-Lucas, 1996). The phosphatic deposits of Morocco outcrop in four main basins, which are from north-east to south-west: Oulad Abdoun, Ganntour, Meskala and Bu-Craa in the Sahara (Fig. 1A). Stratigraphically, they extend from the Late Cretaceous (Maastrichtian) to the middle Eocene (Lutetian), spanning the largest interval of time of all Tethyan phosphates (Lucas & Prévôt-Lucas, 1996).

The phosphates of Morocco are very rich in marine vertebrate remains, especially selachians, bony fishes and reptiles (Arambourg, 1952; Noubhani & Cappetta, 1997; Cavin *et al.*, 2000). In recent years, the Palaeogene deposits have yielded land mammals (see Gheerbrant *et al.*, 2001, 2003, and references therein), and pterosaur and dinosaur remains have been unearthed from the Maastrichtian levels (Pereda Suberbiola *et al.*, 2003, 2004).

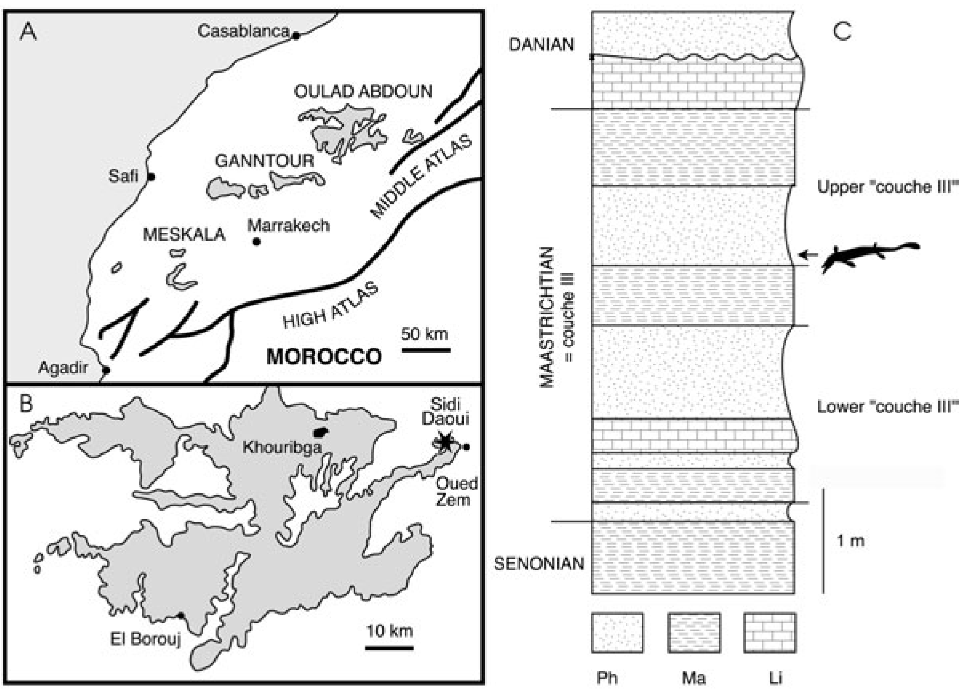

Figure 1. A, map showing the main phosphatic basins of Morocco; B, geographical occurrence of ***Halisaurus arambourgi* sp. nov.** in the Sidi Daoui zone of the Oulad Abdoun Basin; C, stratigraphical occurrence of the new species into the synthetic Maastrichtian phosphatic series of the Oulad Abdoun Basin. *Abbreviations:* Li, limestones; Ma, marls; Ph, phosphates.

The Maastrichtian marine reptiles include plesiosaurs (elasmosaurids), squamates (mosasaurids and varanoids), turtles (bothremydids and chelonioids) and very rarely crocodilians. Mosasaurid remains are the most abundant, with at least six taxa represented (Bardet *et al*., 2004a, b), including species of *Mosasaurus*, *Prognathodon*, *Platecarpus*, *Globidens* and *Halisaurus*. Some of them were described by Arambourg (1952) on the basis of isolated teeth but with different generic attribution. *Halisaurus* is known from numerous fossils in the eastern part of the Oulad Abdoun Basin, near Khouribga, mainly from the Sidi Daoui zone of Grand Daoui, an actively quarried area for phosphate (Fig. 1B). Sidi Daoui is by far the richest zone in Maastrichtian marine vertebrates of the basin.

The Maastrichtian phosphatic series of the Oulad Abdoun Basin ('Couche III' of the miners, or bed III) is very condensed, being only about 2–5 m thick. It consists of two units: a basal unit of grey limestone rich in fish remains overlaid by yellow, soft phosphates (lower Couche III); a second unit consists of grey and brown-striped, soft phosphates overlaid by marls (upper Couche III). These two units are separated by a thin yellow marly layer (Fig. 1C). Stratigraphically, the mosasaurid remains described occur in the upper Couche III, which is Late Maastrichtian in age on the basis of selachian teeth (Cappetta, 1987).

SYSTEMATIC PALAEONTOLOGY

SQUAMATA OPPEL, 1811
MOSASAURIDAE GERVAIS, 1853
HALISAURINAE BARDET & PEREDA SUBERBIOLA, **NEW TAXON**
HALISAURUS MARSH, 1869

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

Referred species: *Halisaurus ortliebi* (Dollo, 1889), Maastrichtian of Belgium (Lingham-Soliar, 1996).

Emended diagnosis: See Discussion.

HALISAURUS ARAMBOURGI BARDET & PEREDA SUBERBIOLA, SP. NOV.

Etymology: In honour of the late Prof. Camille Arambourg, for his pioneering work on fossil vertebrates from the phosphates of North Africa and the Middle East.

Holotype: MNHN PMC 14, incomplete skeleton including a disarticulated skull and 27 associated articulated vertebrae (seven cervicals, 18 dorsals, two distal caudals) (Figs 2, 3).

Type locality and horizon: Grand Daoui area, near Khouribga, central Morocco; phosphates of the Oulad Abdoun Basin, upper Couche III, Late Cretaceous, Late Maastrichtian (Cappetta, 1987).

Referred specimens from the same locality and horizon: MNHN PMC 15, disarticulated cranium with three cervical vertebrae (Figs 4A, 5A); MNHN PMC 16, disarticulated incomplete cranium; OCP-DEK/GE 100, incomplete disarticulated skeleton with cranial remains, vertebrae, girdle and limb bones (Figs 4B, 5B, 8A, 9A, 10A, 11A, 12B, 13B); OCP DEK/GE 101, incomplete skeleton including caudal vertebrae, pelvic girdle and hindlimb bones (Figs 6, 7, 10B, 11B); OCP DEK/GE 102, incomplete disarticulated skeleton with cranial remains, vertebrae and forelimb bones (Figs 8B, 9B, 12C, 13C); OCP DEK/GE 103, incomplete skeleton with vertebrae and forelimb bones (Figs 12A, 13A). Other incomplete specimens are kept in the OCP collections (OCP DEK/GE 12, 23, 39, 53, 73, 73 bi, 104–108, 150, 176, 185, 244, 272–277) as well as in private collections (Figs 8C–H, 9C–H, 14C).

Remarks: Isolated teeth from the Maastrichtian Phosphates of the Ganntour Basin of Morocco (N. Bardet, pers. observ.), the Early Maastrichtian phosphates of Syria (Plioplatecarpinae indet. in Bardet *et al*., 2000) and Jordan (Bardet & Pereda Suberbiola, 2002) and, tentatively, the Maastrichtian of Negev (as *Platecarpus* (?) sp. in Raab, 1963: pl. 3, figs 17–19) and Angola (as Mosasauridae indet. in Telles Antunes, 1964: pl. 26, fig. 5-5a) could also belong to this taxon.

Diagnosis: Small mosasaurid (adult total length 3–4 m). External nares extend from 6th to 12th maxillary teeth, V-shaped anteriorly and U-shaped posteriorly; prefrontal contributes moderately to margin of naris and possesses small anterior supraorbital ridge; frontal with median dorsal ridge extending on two-thirds of the bone length, and two anterior oblique ridges; parietal with triangular table ornamented by transverse undulated ridges and a lenticular foramen, the anterior end of which is located half its length from the frontal suture; quadrate with a vertical oval stapedial notch; pterygoid with short palatine process at about 45° relative to the ectopterygoid process; dental formula: 2 premaxillary, at least 16 maxillary and 12 pterygoid teeth, 19 dentary teeth; teeth very fine and sharp, abruptly posteriorly recurved, with a circular basal cross-section, two carinae and enamel ornamented by minute ridges; estimated vertebral formula: 7 cervicals, at least 20 dorsals and pygals, more than 29 median and 45 distal caudals; humerus length approximately 1.6 times distal width; femur length approximately 1.5 times distal width.

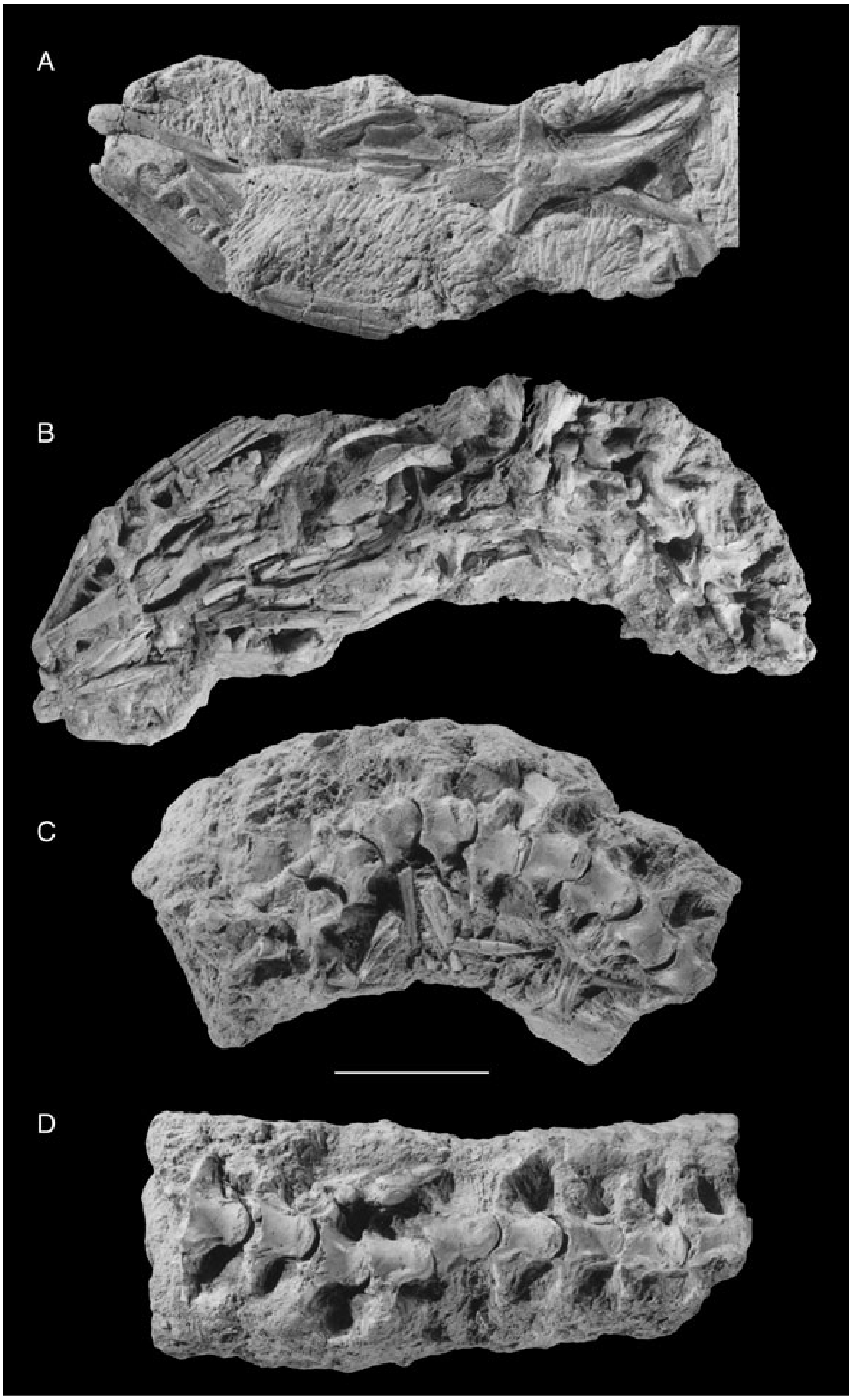

Figure 2. ***Halisaurus arambourgi* sp. nov.**, MNHN PMC 14, holotype, disarticulated cranium and associated vertebrae, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco. A, cranium in dorsal view; B, cranium in ventral view; C, cervical and dorsal vertebrae in ventral view; D, dorsal and isolated caudal vertebrae in ventral view. Scale bar = 10 cm.

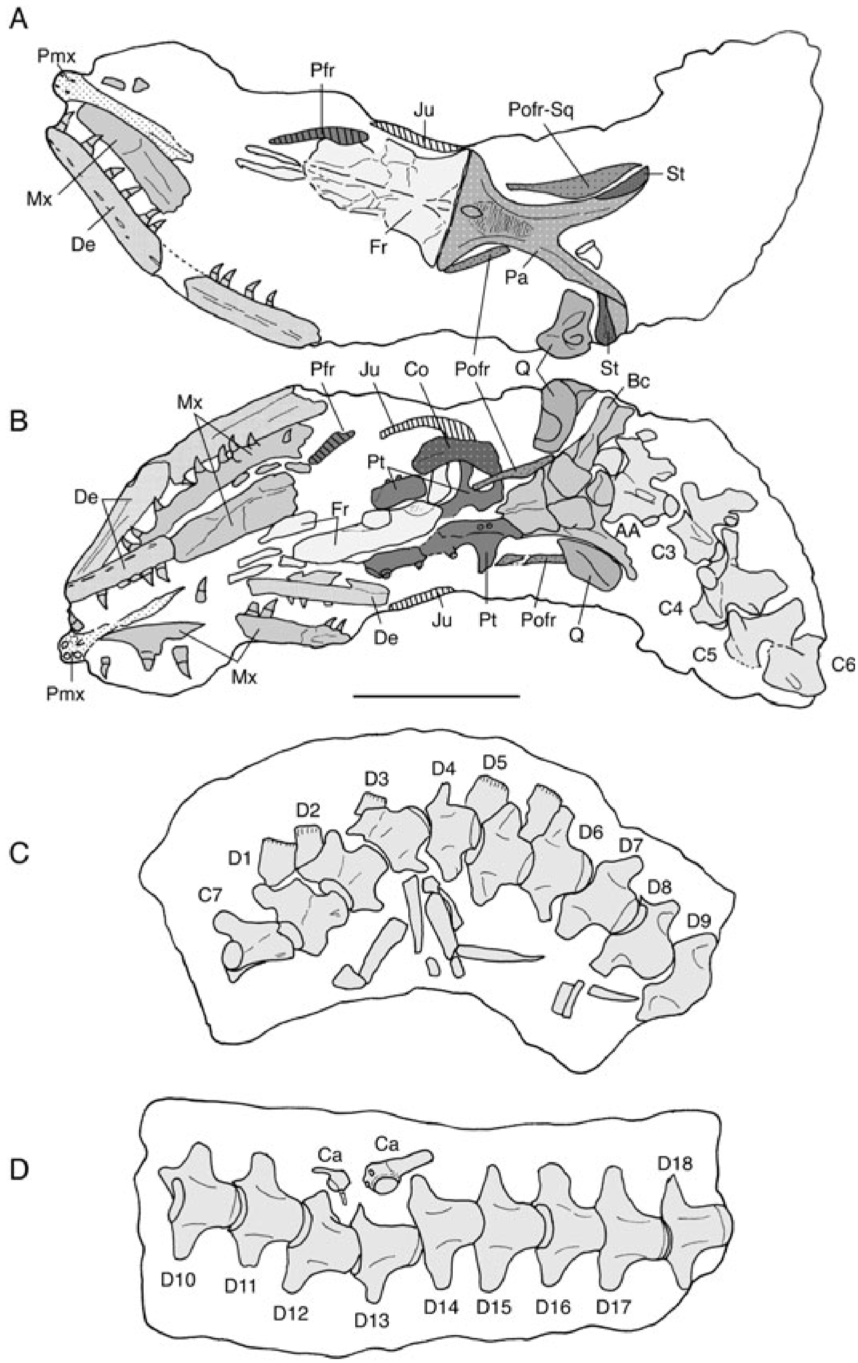

Figure 3. ***Halisaurus arambourgi* sp. nov.**, MNHN PMC 14, holotype, disarticulated cranium and associated vertebrae, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco, interpretative drawings. A, cranium in dorsal view; B, cranium in ventral view; C, cervical and dorsal vertebrae in ventral view; D, dorsal and isolated caudal vertebrae in ventral view. *Abbreviations* (and for Figs 5, 7): AA, atlas-axis; An, angular; Ar, articular; As, astragalum; Bc, basicranium; C, cervical vertebrae; Ca, caudal vertebrae; Co, coronoid; Cr, coracoid; D, dorsal vertebrae; De, dentary; F, fibula; Fe, femur; Fr, frontal; Hu, humerus; Il, ilium; Is, ischium; Ju, jugal; M, metapods; Mx, maxilla; P, pygal vertebrae; Pa, parietal; Pfr, prefrontal; Ph, phalanx; Pl, palatine; Pmx, premaxilla; Pofr, postorbitofrontal; Pt, pterygoid; Pu, pubis; Q, quadrate; Ra, radius; Sa, surangular; Sc, scapula; Sp, splenial; Sq, squamosal; St, supratemporal; T, tibia; V, indeterminated vertebrae. Scale bar = 10 cm.

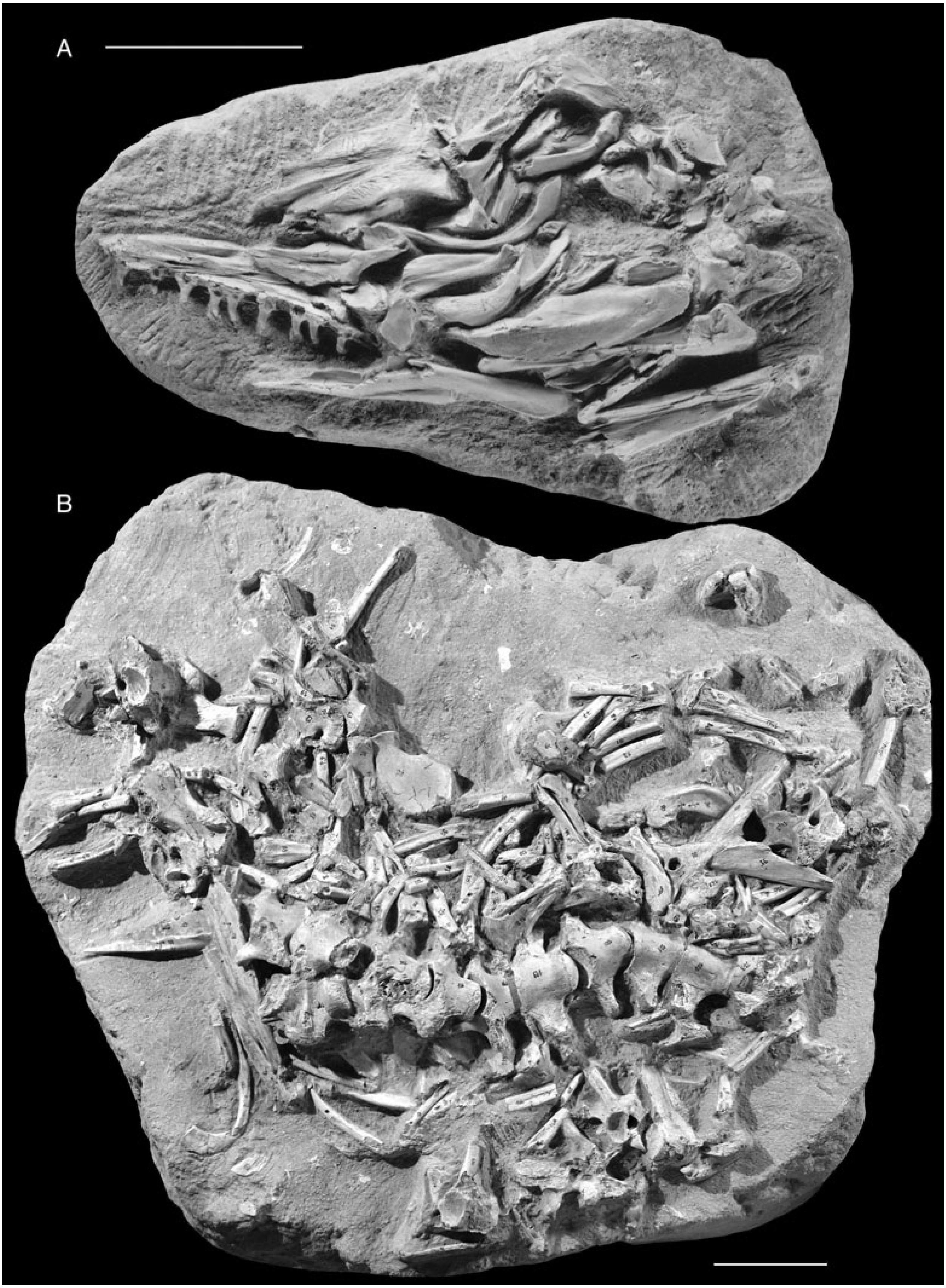
A
B

Figure 4. ***Halisaurus arambourgi*** **sp. nov.** A, MNHN PMC 15, referred specimen, disarticulated cranium, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco; B, OCP DEK/GE 100, referred specimen, incomplete disarticulated skeleton, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco. Scale bars = 10 cm.

DESCRIPTION

General preservation

Several incomplete but complementary specimens are known (see list of material above); reconstructions of skull and mandible have been attempted (Fig. 15). Most skulls are disarticulated and range from 30 to 45 cm in length (Fig. 15). The total body length is estimated as approximately 3–4 m in adults. Although most of the skull and mandibular bones remain unfused, indicating a high degree of cranial kinetism, the studied specimens are regarded as belonging to subadult or to adult individuals.

Skull (Fig. 15)

The premaxilla is short anteriorly, U-shaped and without a rostrum (Figs 2A, B, 3A, B). It bears two pairs of teeth and two rows of large foramina (3–5) for the dorsal ophthalmic ramus of the cranial nerve V. The suture with the maxilla is long and reaches the level of the 6th or 7th maxillary tooth. In lateral view, the suture is vertical, then oblique and becomes horizontal posteriorly. The internarial bar is slender, triangular in cross-section and bears a prominent dorsal longitudinal crest.

The long and narrow maxilla (Figs 2A, B, 3A, B, 4A, 5A) bears at least 16 teeth, exhibits a lateral row of large foramina located above the entire length of the gum line and has a posterodorsal process. The lingual parapet is slightly shorter than the labial one.

The nares are located between the 6th or 7th and the 12th maxillary teeth. They are V-shaped anteriorly and U-shaped posteriorly (Fig. 16C). There is no evidence of the septomaxilla or nasal bones.

The prefrontal is a large triangular bone that contributes moderately to the margin of the external naris (Figs 4A, 5A). Its posterior ramus extends far posteriorly along the lateral margin of the frontal and bears a small, anteriorly located supraorbital process.

The frontal is long and narrow, with concave posterolateral margins, sharp lateral corners and straight parietal suture (Figs 2A, 3A, 4A, 5A, 16C). Facets for reception of the prefrontal and postorbitofrontal on its ventral surface indicate that these two bones did not made contact. Anteriorly, the emarginations for the nares are rounded. The lateral borders are slightly sinusoidal. The dorsal surface bears three distinctive features: a median longitudinal ridge on the anterior two-thirds of the bone; a prominent, finely ridged, posteromedian triangular area; and two anterior oblique ridges, less marked on larger specimens. The ventral surface of the frontal bears a wide median groove for the olfactory stalks and a triangular posteromedian roof for the cerebral hemispheres. The ventral sutural surface for the prefrontal is larger than that for the postorbitofrontal. The frontal orbital margin is reduced.

The postorbitofrontal is not well known in any specimen. It overlaps the frontal and parietal and has a larger contact with the frontal (Figs 4A, 5A). The short posterior squamosal ramus does not reach the posterior margin of the supratemporal fenestra.

The long and slender jugal lacks posteroventral process (Figs 2B, 3B, 4, 5). The horizontal ramus is very long compared with the vertical ramus. The ascending ramus, forming an angle of more than 90° with the horizontal one, is mediolaterally compressed and expands distally.

The parietal is long and broad, occupying more than one-quarter of the skull length (Fig. 16C). The parietal table is roughly triangular and bears a median surface ornamented by transversal undulated ridges (Figs 2A, 3A, 4, 5, 10B, 11B). The margin of the large, lenticular parietal foramen is elevated with respect to the dorsal surface of the parietal table. Its anterior margin is located half way from the frontal suture. The foramen opens ventrally on a triangular boss. It is obliquely orientated, so that its ventral opening is located more posteriorly than the dorsal one. The suspensorial rami are long and mediolaterally compressed, and the surface of articulation for the supratemporal is obliquely orientated.

The supratemporal is a narrow lamina of bone located between the parietal, squamosal and the paroccipital process of the opisthotic-exoccipital (Figs 2A, 3A).

The squamosal is a comma-shaped, slender bone (Figs 4A, 5A).

The quadrate has a question-mark shape in lateral view (Figs 2A, B, 3A, B, 8C–H, 9C–H, 14C). The suprastapedial process is very large and strongly swollen distally, so that it seems divided into two parts that include a circular depression, probably for the origination of m. depressor mandibulae (Russell, 1967: 48). The infrastapedial process is also well developed medially, forming a very large oblique process. Both are coalescent but not fused. The stapedial

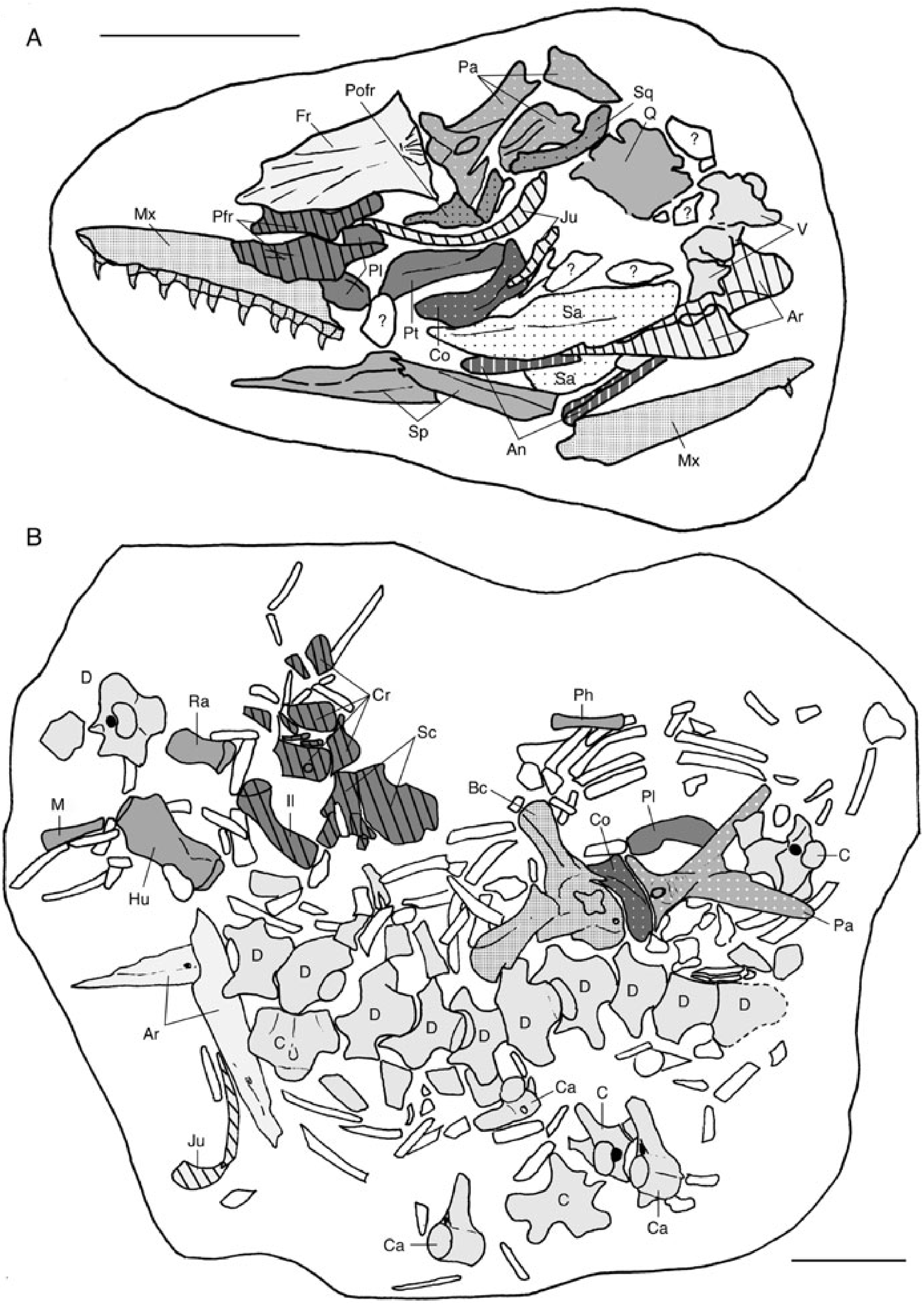

Figure 5. ***Halisaurus arambourgi* sp. nov.** A, MNHN PMC 15, referred specimen, disarticulated cranium, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco; B, OCP DEK/GE 100, referred specimen, incomplete disarticulated skeleton, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco, interpretative drawings. Abbreviations as in Fig. 3. Scale bars = 10 cm.

Figure 6. ***Halisaurus arambourgi* sp. nov.** OCP DEK/GE 101, incomplete disarticulated skeleton, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco. Scale bar = 10 cm.

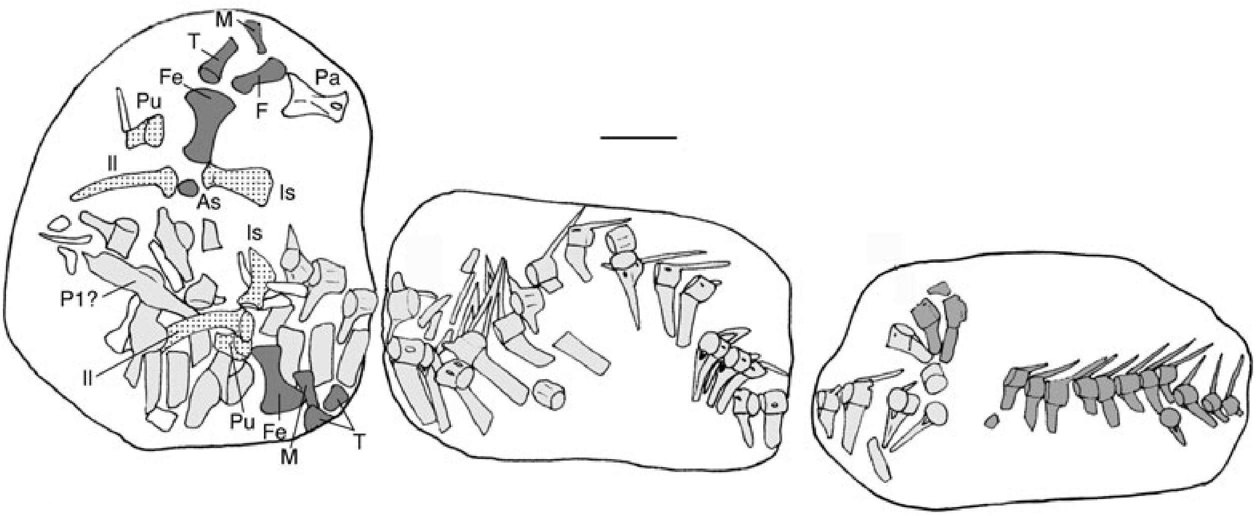

Figure 7. ***Halisaurus arambourgi* sp. nov.** OCP DEK/GE 101, incomplete disarticulated skeleton, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco, interpretative drawings. Abbreviations as in Fig. 3. Scale bar = 10 cm.

notch (tympanic meatus) is oval, vertical and located in the dorsal portion of the bone. The stapedial pit is small, narrow and oval. The broken tympanic ala was probably thin. The distal condyle is convex from side to side and orientated perpendicular to the proximal head.

The braincase unit preserved only parts of the basioccipital (Figs 8B, 9B), basisphenoid, prootic, opisthotic-exoccipital and supraoccipital (Figs 4B, 5B, 8A, 9A). The basioccipital has a typically crescentic condyle. The basal tubera (sphenoccipital tubercles) are of medium size and anterolaterally directed. The suture between the basioccipital and the basisphenoid is transverse. The square basipterygoid bears short, small processes that are not fan-shaped. The prootic preserves only the posterior ascending branch (suspensorial process) for the supratemporal. It is long, narrow and widens distally and dorsally. The

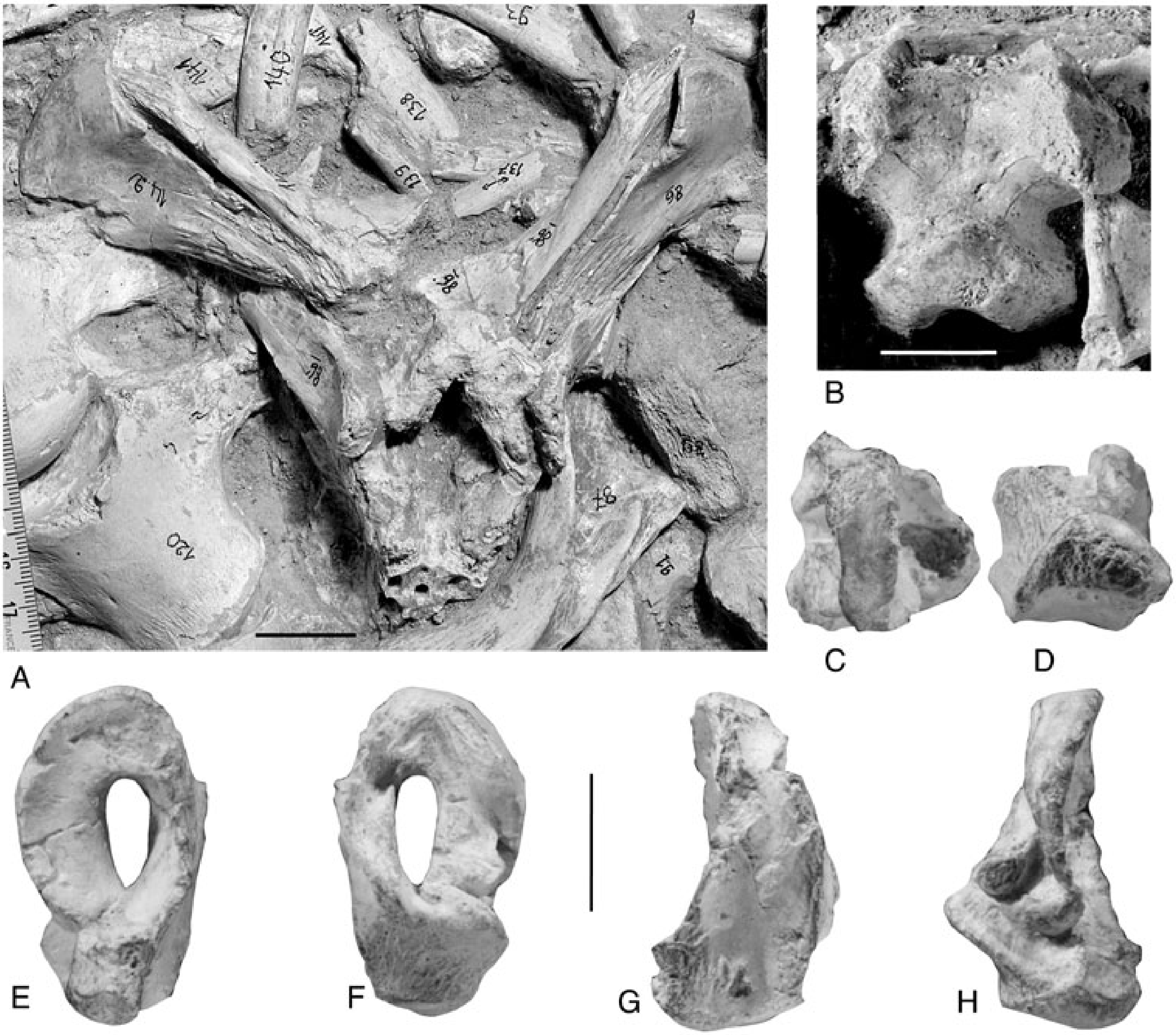

Figure 8. ***Halisaurus arambourgi* sp. nov.** A, OCP DEK/GE 100, basicranium in anterodorsal view; B, OCP DEK/GE 102, basioccipital in ventral view; C–H, private collection, right quadrate in dorsal (C), ventral (D), lateral (E), medial (F), anterior (G) and posterior (H) views, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco. Scale bars = 2 cm.

prootic covers the opisthotic anterolaterally. The large opening for the internal auditory meatus is located beneath a sulcus near the base of the suspensorial process of the prootic. There is a small otosphenoidal crest obscuring the foramen for cranial nerve VII (internal jugular vein). The paroccipital process of the opisthotic-exoccipital is long, narrow and expands distally. It bears longitudinal ridges on its medial surface, probably for the insertion of the m. obliquus capitis magnus. There are two oblique lenticular foramina separated by a thin sheet of bone for the exits of cranial nerves X–XI (jugular foramen, the largest) and XII (condylar foramen, the smallest). The supraoccipital is a rectangular, roof-shaped bone firmly attached to the parietal. The foramen magnum is large and dorsally elongated.

The pterygoid is poorly preserved in all specimens (Figs 2B, 3B, 4A, 5A). It bears at least 12 teeth on specimen OCP DEK/GE 23. The teeth are delicate, strongly posteriorly recurved, without carinae and only slightly smaller than the marginal ones. The short palatine process is broad anteriorly and tapers posteriorly. The ectopterygoid process projects from the main body of the bone at an angle of about 45° to the palatine process. The basisphenoid process is long, narrow and rounded at its extremity.

Some palatine fragments are available (Figs 4, 5) and resemble those of *Platecarpus ictericus* (Russell,

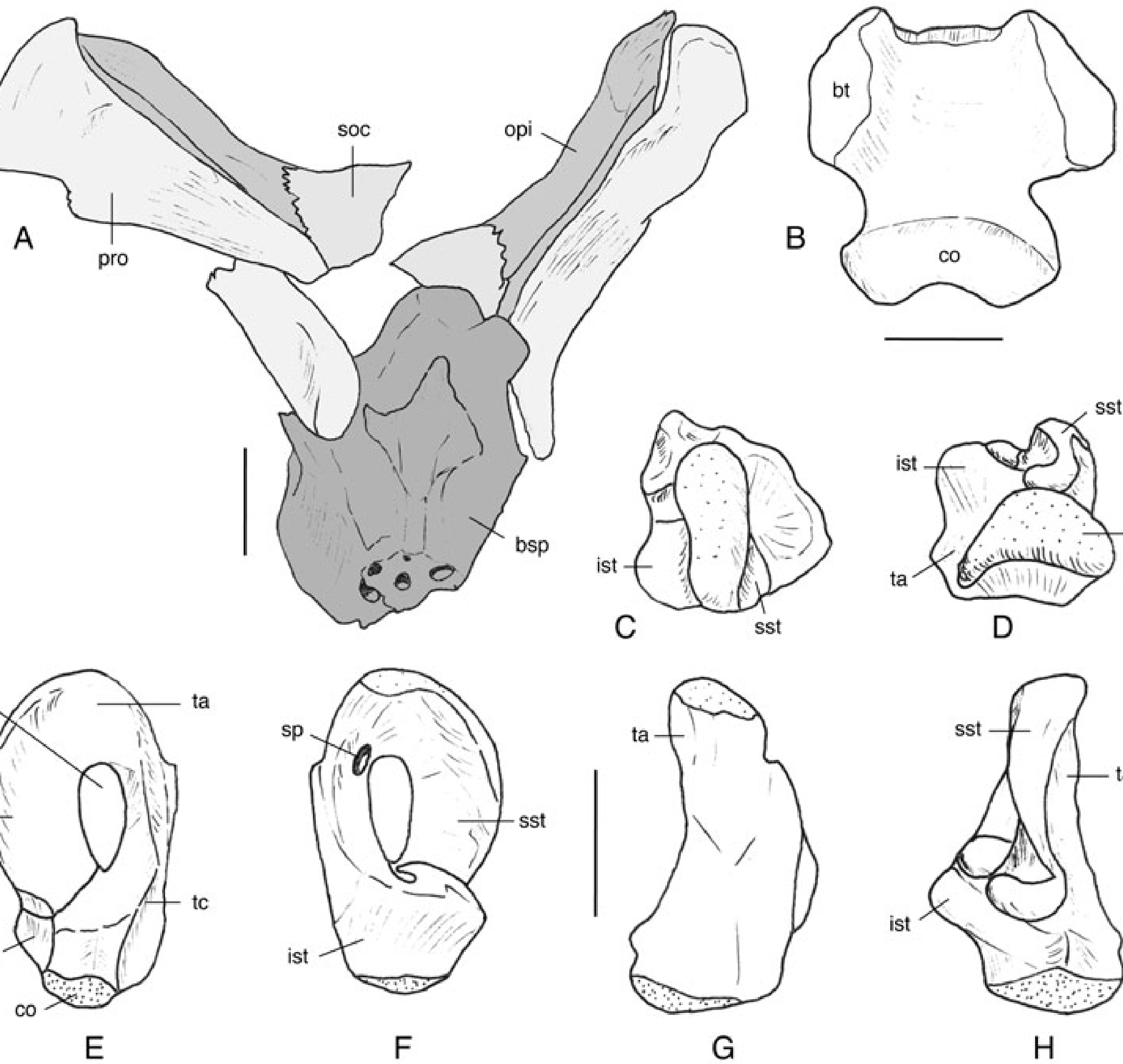

Figure 9. ***Halisaurus arambourgi* sp. nov.** A, OCP DEK/GE 100, basicranium in anterodorsal view; B, OCP DEK/GE 102, basioccipital in ventral view; C–H, private collection, right quadrate in dorsal (C), ventral (D), lateral (E), medial (F), anterior (G) and posterior (H) views, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco, interpretative drawings. *Abbreviations:* co, condyle; bsp, basisphenoid; bt, basal tubera; ist, infrastapedial process; opi, opisthotic; pro, prootic; soc, supraoccipital; sp, stapedial pit; sst, suprastapedial process; ta, tympanic ala; tc, tympanic crest; tm, tympanic meatus. Scale bars = 2 cm.

1967: fig. 6). It is a subrectangular bone with a curvilinear medial margin.

Mandible (Fig. 15)

This is the only species of *Halisaurus* that preserves the complete mandible. In general terms, its resembles that of *H. platyspondylus*.

The dentary is long and narrow, without rostrum (Figs 2A, B, 3A, B). It bears 19 teeth. There is a large edentulous process posterior to the last tooth. The dorsal and ventral margins are almost straight. The medial parapet is lower than the lateral one. The lateral surface is gently convex with a dorsal row of foramina for the mandibular terminal branch of the cranial nerve V. Anteriorly, there is a ventral second row of foramina. The medial surface is concave with a deep Meckelian canal beginning near the anterior tip of the bone and widening posteriorly to form the mandibular channel. The posterior margin of the dentary is posteroventrally oblique, strongly striated and bears a median groove.

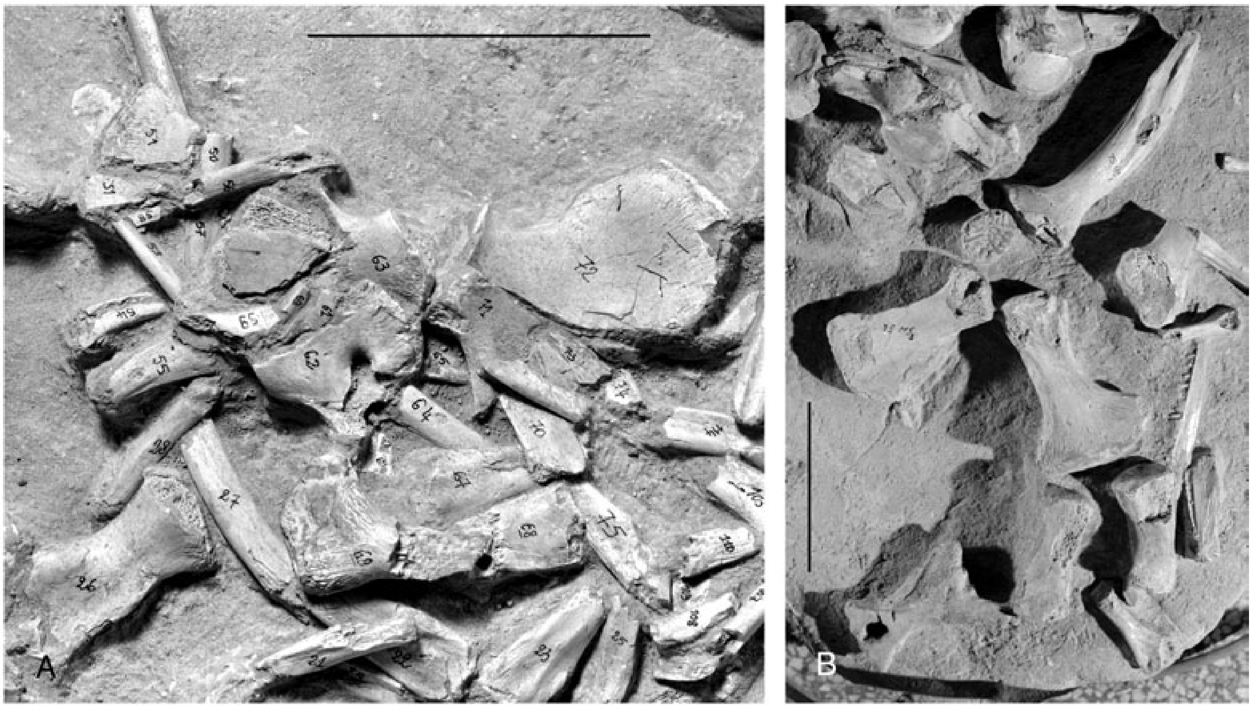

Figure 10. ***Halisaurus arambourgi* sp. nov.** A, OCP DEK/GE 100, pectoral girdle; B, OCP DEK/GE 101, pelvic girdle, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco. Scale bar = 10 cm.

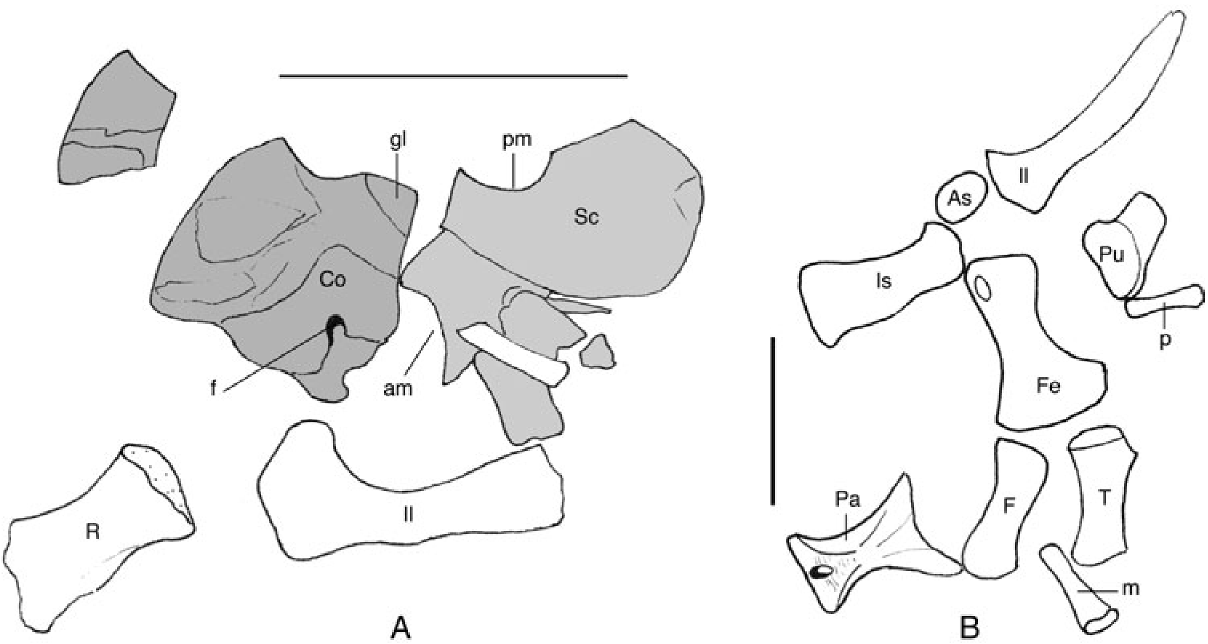

Figure 11. ***Halisaurus arambourgi* sp. nov.** A, OCP DEK/GE 100, pectoral girdle; B, OCP DEK/GE 101, pelvic girdle, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco, interpretative drawings. Abbreviations: am, anterior margin; As, astragalus; Co, coracoid; F, fibula; f, foramen; Fe, femur; gl, glenoid; Il, ilium; m, metapod; p, phalanx; Pa, parietal; pm, posterior margin; Pu, pubis; R, radius; Sc, scapula; T, tibia. Scale bar = 10 cm.

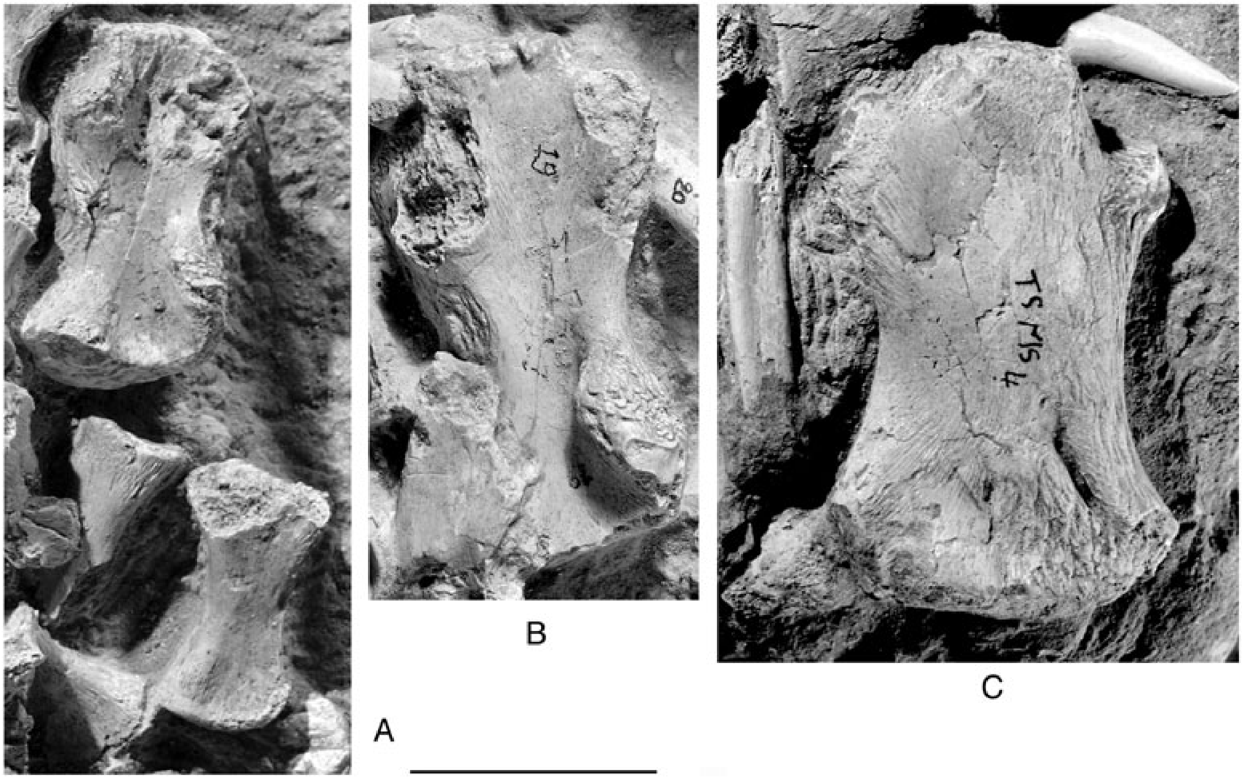

Figure 12. ***Halisaurus arambourgi* sp. nov.** A, OCP DEK/GE 103, right humerus, radius and ulna in flexor view; B, OCP DEK/GE 100, right humerus in flexor view; C, OCP DEK/GE 102, right humerus in extensor view, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco. Scale bar = 5 cm.

The long, triangular splenial (Figs 4A, 5A) extends far anteriorly spanning more than half the length of the dentary. The lateral wing is oblique posteriorly but rotated to be horizontal anteriorly. The medial wing is poorly preserved but is higher than the lateral one. Ventroposteriorly, it bears a large foramen for the inferior alveolar nerve. The well-developed concave articulation for the angular is elliptical and bears an oblique comma-shaped groove located lateral to the centre of the articulation. There is no anteromedial contact with the coronoid.

The long and narrow angular tapers posteriorly (Figs 4A, 5A). The lateral wing is low and largely exposed below the surangular. The medial wing is triangular and very well developed. Near its articulation with the splenial it bears a large foramen for the angular branch of the mandibular nerve.

The large, rectangular surangular is widely exposed in lateral view and occupies most of the surface of the posterior part of the mandible (Figs 4A, 5A). The lateral surface bears a nearly horizontal sharp crest for the insertion for the m. adductor mandibulae externus. The coronoid buttress is low and rounded. The coronoid suture extends onto the anterior half of the bone. The anterior margin of the surangular is oblique. The posterior lateral suture with the articular is posteriorly convex. The surface for the glenoid fossa is smaller than that of the articular.

The coronoid is long, narrow and regularly curved, forming a saddle-shaped bone (Figs 4, 5). There is no posteromedial process and the lateral and medial wings are poorly developed. The posterior ascending process is large.

As in other mosasauroids, the prearticular and articular are fused to form a unique bone (DeBraga & Carroll, 1993) (Figs 4, 5). The prearticular process extends anteriorly through the mandibular joint. The contribution of the articular to the glenoid surface is greater than that of the surangular. The glenoid fossa is surrounded posterolaterally by a large conical buttress process. The square retroarticular process is nearly vertical.

Marginal dentition

The teeth of *Halisaurus arambourgi* resemble those of *Plioplatecarpus*, suggesting a diet probably based on soft and small prey (Massare, 1987). They are poorly

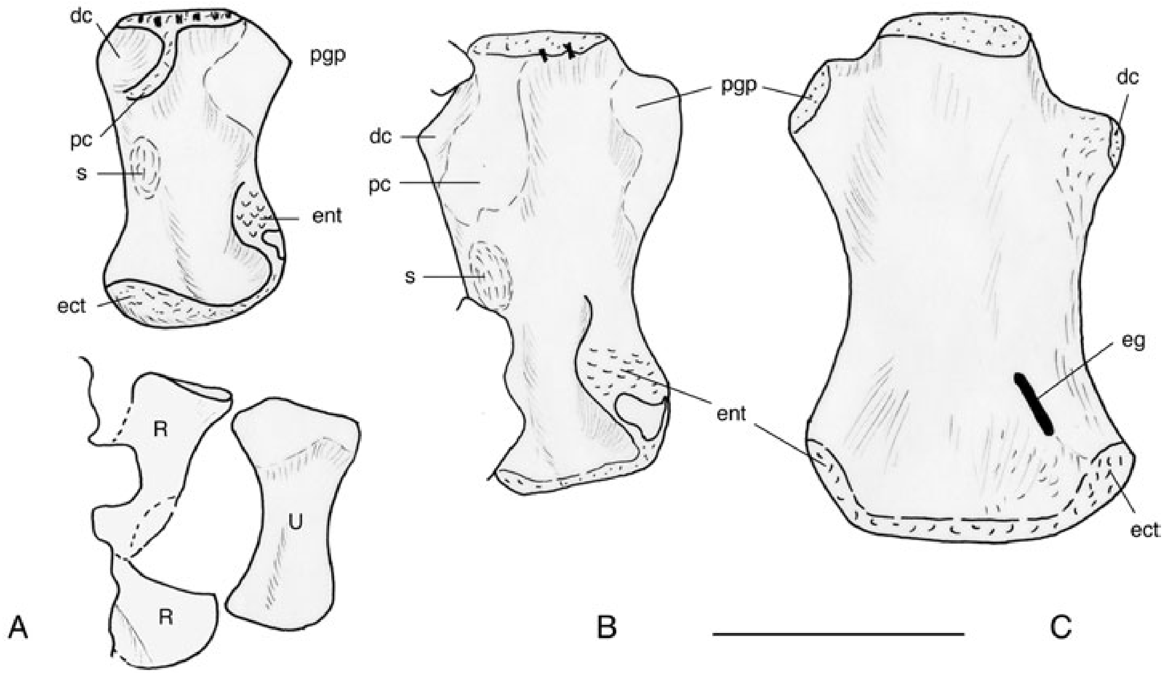

Figure 13. ***Halisaurus arambourgi*** **sp. nov.** A, OCP DEK/GE 103, right humerus, radius and ulna in flexor view; B, OCP DEK/GE 100, right humerus in flexor view; C, OCP DEK/GE 102, right humerus in extensor view, Late Cretaceous (Maastrichtian), Oulad Abdoun Basin, Morocco, interpretative drawings. Abbreviations: dc, deltoid crest; ect, ectepicondylar process; eg, ectepicondylar groove; ent, entepicondylar process; pc, pectoral crest; pgp, postglenoid process; R, radius; s, scar; U, ulna. Scale bar = 5 cm.

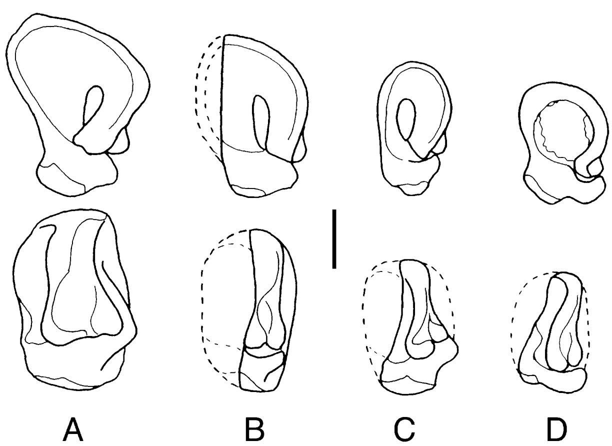

Figure 14. Comparisons of halisaurine quadrates in lateral (above) and posterior (below) views. A, *Halisaurus platyspondylus* (USNM 442450; from Holmes & Sues, 2000); B, *Halisaurus ortliebi* (IRSNB R 34; N.B. pers. observ.); C, ***Halisaurus arambourgi*** **sp. nov.** (private collection); D, *Eonatator sternbergii* (UPI R 163; N.B. pers. observ.). Scale bar = 2 cm.

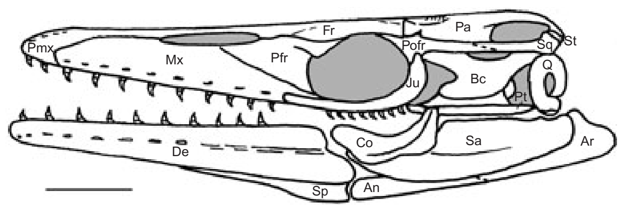

Figure 15. Reconstruction of the skull and mandible of *Halisaurus arambourgi* in left lateral view. Scale bar = 10 cm.

differentiated both in shape and in size along the jaw margins (Figs 2A, B, 3A, B, 4A, 5A). The crowns are delicate and small, approximately 1 cm high (the largest ones can reach 2 cm in height). They bear a pointed apex and are abruptly posteriorly recurved from about the midpoint of the crown, as in *Plioplatecarpus*. The basal cross-section is circular and both lingual and labial surfaces are convex. On the largest specimens, the base of the root exhibits a slight fluting. The enamel crown bears anterior and posterior carinae and is ornamented by minute ridges, more marked at the base of the crown, giving it a silky aspect. The crowns of the teeth are generally shorter,

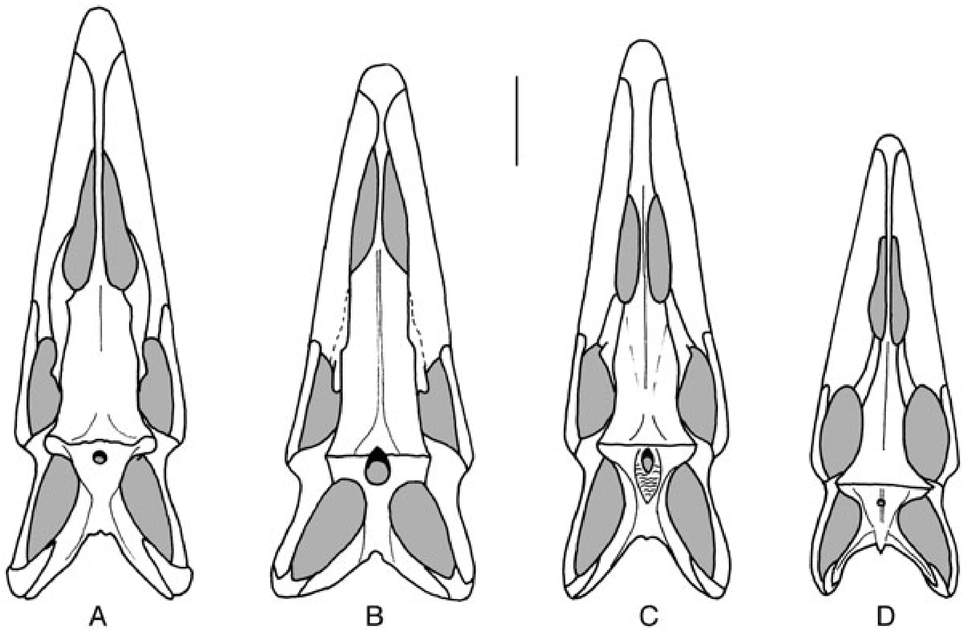

Figure 16. Halisaurine skull reconstructions in dorsal view. A, *Halisaurus platyspondylus* (from Holmes & Sues, 2000); B, *Halisaurus ortliebi* (from Lingham-Soliar, 1996); C, ***Halisaurus arambourgi* sp. nov.**; D, *Eonatator sternbergii* (from Bardet & Pereda Suberbiola, 2001). Scale bar = 10 cm.

with a more delicate ornamentation, than those of *Plioplatecarpus*.

Axial skeleton

No specimen has a complete vertebral column. Based on complementary specimens, the vertebral formula could be estimated as follows: seven cervicals, at least 20 dorsals and pygal caudals (with transverse processes), more than 29 median caudals (both transverse processes and haemal arches) and more than 45 distal caudals (only haemal arches). There is no zygosphene–zygantrum complex and the zygapophyses extend on the cervical and dorsal vertebrae as in most mosasaurids. There are no sacral vertebrae.

The atlas consists of paired arches, centrum and intercentrum. The axis comprises a centrum with a fused neural spine and bears a facet for hypapophysis and small synapophyses. In addition to the atlas-axis, there are five cervical vertebrae bearing a hypapophyseal peduncle (Figs 2B, C, 3B, C). The articulation surfaces are roughly subrectangular, strongly dorsoventrally compressed (height/width ratio approximately 0.5) and slightly obliquely orientated. The condyle is slightly constricted from the main body of the centrum. The peduncle for the hypapophysis is located posteriorly on the ventral surface of the centrum. It is large, elliptical and slightly obliquely orientated. The pre- and postzygapophyses are very large and almost horizontal. The synapophyses are large, located anteriorly on the centrum and are connected to the prezygapophyses by a sharp crest. Their ventral border extends well below the ventral surface of the centra.

The dorsal vertebrae are wide and short and bear anteriorly located transverse processes. As in the cervicals, the articulating surfaces are strongly dorsoventrally compressed and slightly obliquely orientated (Figs 2C, D, 3C, D, 4B, 5B).

As no specimen preserves a complete vertebral series, it is difficult to estimate the number of dorsal and pygal vertebrae. There is no evidence of a direct contact between the vertebrae of the sacral region and the pelvic girdle. The pygal caudals bear a large and stout transverse process (Figs 6, 7). The median caudals have vertical elliptical articular surfaces, transverse processes and fused haemal arches (Figs 6, 7). The distal caudal centra are as high as long. They have circular articular surfaces, no synapophyses and fused haemal arches (Figs 6, 7).

Appendicular skeleton

All girdle elements are ossified separately, as typically in mosasaurids (DeBraga & Carroll, 1993). The limb bones remain plesiomorphic but are more derived than those of *Varanus* and *Aigialosaurus* in the following characters: the propodial and mesopodial bones are flat and have reduced length relative to width; propodial diaphyses and epiphyses lay in the same plan; and antebrachial and crurial foramina are lenticular (see DeBraga & Carroll, 1993).

Shoulder girdle: The scapula appears to be larger than the coracoid (Figs 4B, 5B, 10A, 11A), although it could be an artefact of poor preservation of the coracoid. The scapula is fan-shaped and overall resembles that of *Platecarpus ictericus*. The anterior margin is slightly shorter than the posterior one. The posterior margin is deeply concave just dorsal to the glenoid and then straight, as in *Platecarpus*, *Plioplatecarpus*, *Ectenosaurus* and *Tylosaurus*. The dorsal margin is regularly convex. The coracoid bears a short neck ventral to the glenoid. It is difficult to say whether the anterior margin is longer or shorter than the posterior one. The posterior margin is concave just ventral to the glenoid. The coracoid foramen is large.

Forelimb. The humerus is longer than wide (length approximately 1.6× distal width) and slightly expanded at both extremities (Figs 4B, 5B, 12, 13). The proximal articular end is almost flat, elliptical in shape and strongly grooved and pitted. It is well separated from both the deltoid crest and the postglenoid process. The postglenoid process is expanded. The deltoid and pectoral crests are separated. The deltoid crest is located more distally from the condyle than the postglenoid process. The pectoral crest is developed on the anteroventral portion of the humerus. A large oval scar is present on the anteromedian ventral part of the shaft. The distal end of the humerus is flat, without well-defined articular facets for radius and ulna. The ectepicondylar and entepicondylar tuberosities are moderately developed. The ectepicondylar foramen for the radial nerve is an oblique and narrow groove on the anteromedian dorsal part of the shaft. The radius is long, and its distal extremity is wider than the proximal one (Figs 4B, 5B, 10A, 11A, 12A, 13A). The proximal articular surface is nearly straight whereas the distal one is gently convex. The radius bears a well-developed preaxial ridge extending on the distal two-thirds of its length. The ulna is long and hourglass-shaped (Figs 12A, 13A). The proximal end is wider than the distal one. The olecranon is prominent. The distal extremity is slightly convex and undifferentiated.

Pelvic girdle: The slender club-shaped ilium (Figs 6, 7, 10, 11) expands ventrally to include the articular facets for pubis and ischium and the lateral acetabular facet, which is broad and well defined. The proximal shaft is elliptical in cross-section and anteriorly inclined, as in other mosasaurids. The distal part of the shaft tapers and does not articulate with vertebrae. Both pubes are preserved in OCP DEK/GE 101 but are broken at about their anterior third (Figs 6, 7, 10B, 11B). The size, shape and orientation of the pubic tubercle are unknown. The obturator foramen is not visible. Ventral to the rounded acetabular facet, the pubes become very narrow. The ischium is long and slender (Figs 6, 7, 10B, 11B), particularly distally. The ischiadic tubercle is small and located very close to the acetabular face.

Hindlimb: The femur is long and slender (length approximately 1.5× distal width) (Figs 6, 7, 10B, 11B). The proximal and distal ends are gently convex and undifferentiated. The shaft is slender and straight. The anterior surface is less concave than the posterior one. The internal trochanter is well developed and located anteriorly and proximally on the ventral surface of the bone. The tibia is slightly wider and shorter than the fibula (Figs 6, 7, 10B, 11B). The proximal end of the tibia is wider than the distal one and bears an anterior flange. The anterior margin is more concave than the posterior one. There is a distinct astragalar facet on the posterior part of the distal articular surface. The fibula has a distal extremity wider than the proximal one. Both are regularly convex. A possible astragalus, roughly elliptical, is preserved in OCP DEK/GE 101 (Figs 6, 7, 10B, 11B). Only a few metapodials and phalanges are known (Figs 4B, 5B, 6, 7, 10B, 11B). They are long and hourglass-shaped. The proximal ends of the metapodial bones are larger than the distal ones. The phalanges of both extremities are similar in size.

DISCUSSION

Phylogenetic analysis

To understand the phylogenetic affinities of the new taxon from Morocco, a cladistic analysis has been performed using PAUP* 4.0 (Swofford, 1998). The data matrix (Appendix 3), comprising 111 characters and 12 ingroup taxa, was analysed using the 'Branch and Bound' and 'Heuristic' algorithms. *Varanus varius* and *Aigialosaurus dalmaticus* were chosen as successive outgroups (Appendix 1). The ingroup taxa include the new taxon from Morocco and a selection of mosasaurid species known from well-preserved material, recently reviewed and/or personally inspected (Appendix 1). Characters have either been taken and/or modified from Bell (1997) and DeBraga & Carroll (1993) or newly developed based on personal examination of some taxa (Appendix 2). All characters have been treated as unordered and unweighted. Autapomorphies have not been included into the matrix. Characters state transformations were DELTRAN optimized. Six most parsimonious trees were generated (270 steps, CI = 0.678, HI = 0.322, RI = 0.675) (Fig. 17).

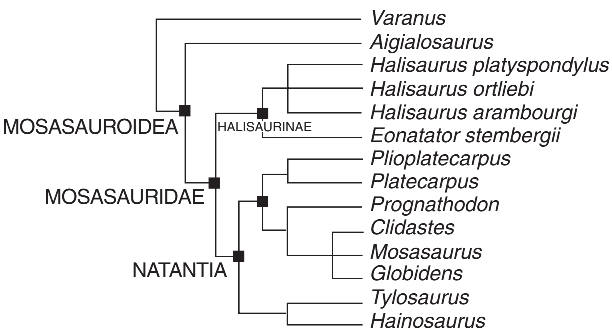

Figure 17. Strict consensus tree of six most parsimonious trees (270 steps) showing the phylogenetic relationships of ***Halisaurus arambourgi* sp. nov.** and Halisaurinae among Mosasauridae.

The topology of the strict consensus tree supports the Mosasauridae as a monophyletic group defined by a large number of synapomorphies (Bremer index = 5; Fig. 17, Appendix 4). This analysis does not support the monophyly of the Russellosaurinae (= Plioplatecarpinae + *Tylosaurus*) of Bell (1997), and the main difference from previous phylogenetic analyses (DeBraga & Carroll, 1993; Bell, 1997; Christiansen & Bond, 2002) is that the Plioplatecarpinae and Mosasaurinae form a monophyletic clade (unnamed in Appendix 4; see Fig. 17), which is the sister-group to the Tylosaurinae (Fig. 17, Appendix 4). Finally, the analysis also confirms the inclusion of *Prognathodon* in the clade Mosasaurinae (Fig. 17), as already suggested by Bell (1997) and Christiansen & Bond (2002).

The new species from Morocco is referred to *Halisaurus* on the basis of the following unambiguous synapomorphies: frontal with a posteromedial dorsal triangular area [character 14]; articular with a large conical buttress just posterior to glenoid [character 58]; cervical vertebrae articular surfaces subrectangular (width approximately twice the height) [character 67(1)].

The clade comprising *Halisaurus arambourgi* sp. nov., *H. platyspondylus* from the Maastrichtian of New Jersey (Holmes & Sues, 2000) and *H. ortliebi* from the Maastrichtian of Belgium (Lingham-Soliar, 1996; N.B., pers. observ.) forms an unresolved polytomy (Fig. 17). When autapomorphies are considered, *H. arambourgi* can be differentiated from the other species on the basis of the following features (Figs 14, 16): external nares V-shaped anteriorly and U-shaped posteriorly (strongly inflated posteriorly in *H. platyspondylus*; regularly oval in *H. ortliebi*); prefrontal with moderate participation in the naris and bearing a small, anteriorly located supraorbital ridge (large narial participation and posteriorly located supraorbital ridge in *H. platyspondylus*; small narial participation and anteriorly located supraorbital ridge in *H. ortliebi*); frontal with a median dorsal ridge extending for two-thirds of the bone length and having two anterior oblique ridges (no anterior ridges in *H. platyspondylus*; median dorsal ridge extending the entire length of prefrontal in *H. ortliebi*); parietal with a triangular table ornamented by transversal undulated ridges and a lenticular foramen with its anterior margin located half its length from the suture [smooth triangular table with circular foramen located its length from the suture in *H. platyspondylus*; smooth triangular table with very large circular foramen invading the frontal and bordered posteriorly by teardrop-shaped depression (incorrectly identified as the ventral surface by Lingham-Soliar, 1996) in *H. ortliebi*]; quadrate with oval vertical stapedial notch (narrow and oblique in *H. platyspondylus*; very narrow and vertical in *H. ortliebi*); pterygoid with at least 12 teeth (nine teeth in *H. platyspondylus*; eight teeth in *H. ortliebi*) and short palatine process at approximately 45° relative to the ectopterygoid process (long palatine process at approximately 65° in *H. platyspondylus*; short palatine process at about 45° in *H. ortliebi*).

Additional characters present in *H. arambourgi* remain undescribed or are missing in the two other species of *Halisaurus*. They comprise: at least 16 maxillary and 19 dentary teeth; very fine and sharp teeth that are abruptly recurved posteriorly; crowns with circular basal cross-sections, two carinae, and enamel ornamented by minute ridges; external nares extending from the 6th to the 12th maxillary tooth; estimated vertebral formula: seven cervicals, at least 20 dorsals and pygals, more than 29 median and 45 distal caudals; humerus length approximately 1.6× distal width; femur length approximately 1.5× distal width. Pending the discovery of more complete material of *H. platyspondylus* and *H. ortliebi*, the listed features are here provisionally considered autapomorphies of *H. arambourgi*.

Our phylogenetic analysis does not support the referral of the species '*Halisaurus*' *sternbergii* to *Halisaurus* nor to *Clidastes* or any other known genus. Indeed, the six most parsimonious trees all show this species as the sister-group of the clade including *H. platyspondylus*, *H. ortliebi* and *H. arambourgi* (Fig. 17). *Clidastes sternbergii* Wiman, 1920 is based on a nearly complete skeleton (UPI R 163) from the Santonian of Kansas (Wiman, 1920). Since its original description, the generic status of this species has been subject to discussion. Dollo (1924: 198) was the first who cast doubts about the systematic attribution of this species to *Clidastes*. Later, Russell (1967: 127) suggested that *C. sternbergii* could belong to a new genus distinct from *Clidastes*, but finally referred it to *Halisaurus*, arguing from similarities between the type specimen and new halisaurine material from Alabama (Russell, 1970). More recently, DeBraga & Carroll (1993: 273) agreed with the removal of this species from *Clidastes* but also questioned its referral to *Halisaurus*. By contrast, Lingham-Soliar (1996) referred the Uppsala specimen (UPI R 163) to *Clidastes*, as originally proposed by Wiman (1920). Subsequently, Caldwell & Bell (1995), Caldwell (1996), Bell (1997), Holmes & Sues (2000) and Bardet & Pereda Suberbiola (2001) regarded this species as belonging to *Halisaurus*.

On the basis of the results of the phylogenetical analysis, we suggest restricting the genus *Halisaurus* to the species *H. platyspondylus* (type species), *H. ortliebi* and *H. arambourgi* sp. nov. and referring '*Halisaurus*' *sternbergii* to a new genus, for which the name *Eonatator* is proposed (see below).

Eonatator can be differentiated from *Halisaurus* on the basis of the following features: parietal with a smooth triangular table extending far posteriorly, bearing a medium-sized, circular foramen, located at a distance twice its diameter from the frontal–parietal suture, and surrounded anteriorly and posteriorly by two parallel ridges; rounded quadrate with a regularly convex tympanic ala; vertebral formula: seven cervicals, 24 dorsals, four pygals, 28 median caudals and at least 41 terminal caudals; humerus length approximately 2.5× distal width. It is also characterized by the following ambiguous characters: premaxilla–maxilla lateral suture ending posterior to the 9th maxillary tooth; tail about 40% of the head and trunk length (convergent in mosasaurines); caudal vertebrae longer than wide; fewer than four pygal vertebrae; femur length about twice distal width (convergent in *Clidastes*). In addition to the systematic aspects, the stratigraphical distribution of these taxa (Santonian for *Eonatator*, Maastrichtian for *Halisaurus*) is consistent with this hypothesis.

Halisaurus and *Eonatator* are here regarded as representatives of the Halisaurinae (Bremer index = 2; Fig. 17, Appendix 4). This new taxon is mainly defined by the shape of the lateral premaxilla–maxilla suture [character 5(1)]; an oblique contact plane between the parietal and the supratemporal [character 24(1)]; a preaxial ridge extending on the distal two-thirds of the radius length [character 101(3)]; and tibia and fibula long and slender with slightly expanded extremities [character 105(1)]. The Halisaurinae are the sister-group of more advanced mosasaurids (Natantia of Bell, 1997), as previously suggested (see DeBraga & Carroll, 1993; Bell, 1997).

The classification of the Halisaurinae is proposed below, with emended diagnosis and data regarding the types and referred species of each taxon.

SYSTEMATICS OF HALISAURINAE

MOSASAURIDAE GERVAIS, 1853
HALISAURINAE BARDET & PEREDA SUBERBIOLA, **NEW TAXON**

Definition: Mosasauridae more closely related to *Halisaurus* than to *Mosasaurus*.

Diagnosis: Unambiguous characters: premaxilla–maxilla sutural contact vertical anteriorly, oblique at midpoint and horizontal posteriorly; contact plane between the parietal and the supratemporal oblique; preaxial ridge extending on two-thirds of the length of the radius; tibia and fibula long and slender with slightly expanded extremities. Ambiguous characters: dorsal median ridge borne on the anterior two-thirds of the frontal; frontal with ventral boss; parietal foramen surrounded by a ventral boss; quadrate with large infrastapedial process; coalescent infra- and suprastapedial processes of quadrate; zygosphene–zygantrum complex absent; synapophyses of the cervical vertebrae extending ventrally to the ventral surface of the centrum; fused haemal spines.

HALISAURUS MARSH, 1869

1869 *Macrosaurus* Marsh, oral communication (in Marsh, 1869: 395).
1869 *Halisaurus* Marsh, p. 395.
1870 *Baptosaurus* Marsh, p. 3.
1889 *Phosphorosaurus* Dollo, p. 68.

Type species: *Halisaurus platyspondylus* Marsh, 1869.

Geographical and stratigraphical occurrences: Late Cretaceous (Maastrichtian) of eastern North America (Baird, 1986), Europe (Lingham-Soliar, 1996), Africa (this work) and, probably, the Middle East (Bardet & Pereda Suberbiola, 2002; this work).

Emended diagnosis: Unambiguous characters: frontal with posteromedial dorsal triangular area; articular with large conical buttress just posterior to glenoid; cervical vertebral articulations subrectangular (height : width = 1 : 2). Ambiguous characters: premaxilla–maxilla suture located between the 4th and 9th maxillary teeth (convergent in *Tylosaurus* and Mosasaurinae); prefrontal with small supraorbital ridge (convergent in *Platecarpus* and *Plioplatecarpus*); frontal with sinusoidal lateral margins (convergent in *Plioplatecarpus*, *Platecarpus*, *Clidastes*); large parietal foramen (convergent in *Platecarpus*) located close to the frontal–parietal suture (convergent in *Platecarpus*, *Prognathodon* and Mosasaurinae); supraoccipital fused to the parietal; prootic with small otosphenoidal crest (convergent in *Platecarpus*, *Prognathodon*, *Clidastes*); posteriorly convex surangular–articular lateral suture (convergent in *Aigialosaurus*); teeth delicate, abruptly posteriorly recurved and finely striated (convergent with *Plioplatecarpus*, *Platecarpus*, *Clidastes*).

HALISAURUS PLATYSPONDYLUS MARSH, 1869

Holotype: YPM 444, two vertebrae, an angular bone (originally described as a splenial) and a basicranium fragment described by Marsh (1869: 395) and figured by Baird (1986).

Type locality and horizon. New Egypt Formation, Late Maastrichtian (Late Cretaceous), near Hornestown, Monmouth County, New Jersey (USA).

Main referred specimens: NJSM 12146, incomplete cranium, Navesink Formation, Late Maastrichtian (Late Cretaceous), New Jersey (USA) (Wright, 1988); USNM 442450, incomplete skeleton, Severn Formation, middle Maastrichtian (Late Cretaceous), Maryland (USA) (Holmes & Sues, 2000).

Emended diagnosis: Autapomorphies: external naris strongly posteriorly inflated; prefrontal with large narial participation and posteriorly located supraorbital ridge; frontal with no anterior ridges; parietal with a smooth triangular table bearing circular foramen located at a distance its length from the suture; quadrate with a narrow and oblique stapedial notch; pterygoid with nine teeth and long palatine process at about 65° relative to the ectopterygoid process.

HALISAURUS ORTLIEBI (DOLLO, 1889)

Holotype: IRSNB R34, incomplete skull described by Dollo (1889: 181–182).

Type locality and horizon: Ciply Phosphatic Chalk (Early Maastrichtian), near Mesvin, Hainault, Belgium.

Emended diagnosis: Autapomorphies: regularly oval external naris; prefrontal with small narial participation and anteriorly located supraorbital ridge; frontal with median dorsal ridge extending on the whole length of the bone; parietal with smooth triangular table with very large circular foramen invading the frontal and bordered posteriorly by a teardrop-shaped depression; quadrate with a very narrow and vertical stapedial notch; pterygoid with eight teeth and short palatine process at about 45° relative to the ectopterygoid process.

HALISAURUS ARAMBOURGI BARDET & PEREDA SUBERBIOLA, **SP. NOV.**

See Systematic palaeontology section.

EONATATOR BARDET & PEREDA SUBERBIOLA, **GEN. NOV.**

1920 *Clidastes*, Wiman, p. 13
1967 *Clidastes*, Russell p. 126
1970 *Halisaurus*, Russell, p. 369
1993 *Halisaurus*, DeBraga & Carroll, p. 273
1995 *Halisaurus*, Caldwell & Bell, p.536
1996 *Clidastes*, Lingham-Soliar, p. 134
1996 *Halisaurus*, Caldwell, p.415
1997 *Halisaurus*, Bell, p. 300
2000 *Halisaurus*, Holmes & Sues, p. 309
2001 *Halisaurus*, Bardet & Pereda Suberbiola, p. 395

Etymology: from *Eos* (Greek), dawn and *natator* (Latin), swimmer.

Type species: *Clidastes sternbergii* Wiman, 1920.

Geographical and stratigraphical occurrences. Late Cretaceous (Santonian) of central North America.

Emended diagnosis: As for the type and only species known, *Eonatator sternbergii*.

EONATATOR STERNBERGII (WIMAN, 1920) **COMB. NOV.**

Holotype: UPI R 163, a nearly complete skeleton described by Wiman (1920).

Type locality and horizon: Smoky Hill Member, Niobrara Chalk, Santonian (Late Cretaceous), Kansas (USA).

Referred specimen: USNM 3777, incomplete skeleton, Smoky Hill Member, Niobrara Chalk, Santonian (Late Cretaceous), Beaver Creek, Logan County, Kansas (USA) (Russell, 1967: 126).

Emended diagnosis: Ambiguous characters: premaxilla–maxilla lateral suture ending posterior to the 9th maxillary teeth; tail about 40% of the head and trunk length (convergent in mosasaurines); caudal vertebra length greater than width; fewer than four pygal vertebrae; femur length about twice distal width (convergent in *Clidastes*). Autapomorphies: parietal with smooth triangular table extending very far posteriorly, bearing medium-sized circular foramen, located at distance twice its diameter from the frontal–parietal suture, and surrounded anteriorly and posteriorly by two parallel ridges; rounded quadrate with regularly convex tympanic ala; vertebral formula: seven cervicals, 24 dorsals, four pygals, 28 median caudals and at least 41 terminal caudals; humerus length approximately 2.5× distal width.

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APPENDIX 1

Two outgroup and 12 ingroup taxa were used for the cladistic analysis. For each taxon, the references used and/or the collection number of the specimens inspected are indicated. Asterisks indicate species personally reviewed.

Outgroup taxa: **Varanus varius*, recent, Australia (MNHN AC-1910-2); **Aigialosaurus dalmaticus* Kramberger, 1892, Cenomanian–Turonian transition, Croatia (DeBraga & Carroll, 1993; Bell, 1997; BSP 1902II501). Ingroup taxa: *Halisaurus platyspondylus* Marsh, 1869, Maastrichtian, USA (Wright, 1988; Bell, 1997; Holmes & Sues, 2000); **Halisaurus ortliebi* (Dollo, 1889), Maastrichtian, Belgium (Lingham-Soliar, 1996; ISRNB R34); **Halisaurus arambourgi* Bardet & Pereda Suberbiola sp. nov., Maastrichtian, Morocco (this work); **Eonatator sternbergii* (Wiman, 1920), Santonian, USA (DeBraga & Carroll, 1993; Bell, 1997; Bardet & Pereda Suberbiola, 2001; UPI R 163); *Plioplatecarpus primaevus* Russell, 1967, Campanian, North America (Holmes, 1996) (specimens of *P. marshi* and *P. houzeaui* from the Maastrichtian of Europe kept in the IRSNB collections were used for comparisons); *Platecarpus ictericus* (Cope, 1871), Santonian–Campanian, USA (Russell, 1967; Bell, 1997); *Prognathodon overtoni* (Williston, 1897), Maastrichtian, USA (Russell, 1967; Bell, 1997) (specimens of *P. solvayi* and *P. giganteus* from the Maastrichtian of Europe kept in the IRSNB collections were used for comparisons); *Tylosaurus proriger* (Cope, 1869b), Santonian–Campanian, USA (Russell, 1967; Bell, 1997); **Hainosaurus bernardi* Dollo, 1885, Maastrichtian, Belgium (Bardet, 1990; Lingham-Soliar, 1992; IRSNB R23); *Clidastes propython* Cope, 1869a, Santonian–Campanian, USA (Russell, 1967; Bell, 1997); **Mosasaurus hoffmanni* Mantell, 1829, Maastrichtian, Europe (Lingham-Soliar, 1995; MNHN AC 9648; IRSNB R12, 26-27, NHMM 1993024); *Globidens dakotaensis* Russell, 1975, Campanian, USA and Belgium (Russell, 1975).

APPENDIX 2

Character state distribution among mosasauroids are either taken and/or modified from Bell (1997) (designated B below) and DeBraga & Carroll (1993) (designated DC below), or newly developed based on personal study of some taxa. The original bibliographical source of each character is indicated, followed by the number of the character in the mentioned work.

1. Premaxilla number of tooth pairs: more than two = 0; two = 1 (DC-3).
2. Premaxillary rostrum: absent = 0; short = 1; long = 2 (B-1+2 modified; DC-4).
3. Premaxillary rostral shape: broadly arcuate = 0; narrowly arcuate = 1; long and cylindrical = 2; sharp and conical = 3 (B-3 and DC-4 modified).
4. Premaxilla–maxilla suture posterior termination: anterior to fourth maxillary tooth = 0; between fourth and ninth tooth = 1; posterior to ninth tooth = 2 (B-36).
5. Premaxilla–maxilla suture lateral shape: regularly arcuated = 0; arcuated but with straight lines (first vertical, then oblique and then horizontal) = 1; anteriorly arcuated first = 2. Commonly, the premaxilla–maxilla suture is regularly arcuated in lateral view. In halisaurines, this suture is straight vertical first, then oblique and finally horizontal. In tylosaurines, the suture, instead of being vertical, arcuates first anteriorly, then turns obliquely posteriorly to become finally horizontal.
6. Prefrontal–naris contact: present = 0; absent = 1 (contact maxilla–frontal) (DC-8 modified).
7. Prefrontal supraorbital ridge: absent = 0; small = 1; large = 2 (B-29 modified; DC-13).
8. Septomaxilla: present = 0; absent = 1.
9. Nasal: present = 0; vestigial or absent = 1 (B-8; DC = 12).
10. Postorbitofrontal–frontal and parietal area of contact: parietal contact larger = 0; frontal contact larger = 1 (DC-15 modified).
11. Postorbitofrontal squamosal ramus: does reach posterior margin of temporal fenestra = 0; does not reach posterior margin of temporal fenestra = 1 (B-34).
12. Prefrontal–postorbitofrontal contact above orbit: absent = 0; present = 1 (B-30; DC-16 modified).
13. Frontal dorsal median ridge: absent = 0; present on two-thirds of dorsal surface = 1; present on three-quarters of dorsal surface = 2; present on entire length of dorsal surface = 3 (B-12 modified).
14. Frontal dorsal posteromedian triangular area: absent = 0; present = 1. In *Halisaurus*, there is a distinct median deltaic relief formed by irregular ridges on the posterodorsal surface of the frontal.
15. Frontal general shape: short and narrow = 0; long and narrow = 1; short and broad = 2 (B-10 and DC-17 modified).
16. Frontal lateral margins: concave = 0; sinusoidal = 1; straight or slightly convex = 2 (B-9 and DC-23–25 modified).
17. Frontal–parietal suture: straight = 0; presence of small flanges = 1; presence of large flanges = 2 (B-17–20 and DC-20 modified).
18. Frontal olfactory canal embrasure: descending processes poorly developed = 0; descending processes well developed = 1 (B-14; DC-18).
19. Frontal ventral posteromedian boss: absent = 0; present = 1 (B-16).
20. Parietal table shape: triangular with sides converging but not meeting = 0; narrow medially = 1; swollen medially = 2; triangular with sides converging and meeting = 3 (B-22 and DC-26 modified).
21. Parietal foramen size: small = 0; large = 1; enormous = 2 (B-23 modified).
22. Parietal foramen position: distance from frontal suture equal to twice its diameter = 0; distance equal to its diameter = 1; anterior margin of foramen near or in contact with suture = 2; foramen invading suture = 3 (B-24 modified).
23. Parietal foramen ventral opening: at level of the main surface = 0; on a ventral boss surrounded by a ridge (B-25 modified).
24. Parietal suspensorial rami orientation: vertical = 0; oblique = 1; horizontal = 2 (DC-27 modified).
25. Jugal shape: curvilinear = 0; 'L'-shaped = 1 (B-39).
26. Jugal posteroventral process: absent = 0; present = 1 (B-40).
27. Pterygoid teeth: absent = 0; present = 1 (DC-51).
28. Pterygoid tooth size compared with marginal ones: smaller = 0; equal = 1 (B-43).

29. Supraoccipital–parietal contact: loose contact = 0; weak articulation = 1; fused = 2 (DC-31 modified).
30. Prootic otosphenoidal crest: large = 0; small = 1; absent = 2.
31. Prootic exit for nerves X, XI and XII: paired = 0; single = 1 (DC-33).
32. Basioccipital canal: absent = 0; small foramen or groove = 1; large canal = 2 (B-67 and DC-34 modified).
33. Basioccipital basal tubera: short and small = 0; long and large = 1 (B-65+66 modified).
34. Basisphenoid basipterygoid process: long and narrow = 0; short and broad (fan-shaped) = 1 (B-64; DC-36).
35. Quadrate general shape: narrow, almost vertical with poor tympanic crest = 0; massive, with expanded tympanic crest = 1; massive, almost circular with very expanded tympanic crest (conch-shaped) = 2 (B-50 and DC-39 modified).
36. Quadrate suprastapedial process: absent or short (located in the upper half of the bone shaft) = 0; medium (extends halfway down the shaft) = 1; long (reaches lower half of the shaft) = 2 (B-44; DC-40 modified).
37. Quadrate suprastapedial process distal shape: narrow = 0; swollen = 1; tapered = 2. In posterior view, the suprastapedial process is distally narrow (as wide as in the dorsal part) or tapers into a narrow tip. In halisaurines and plioplatecarpines, the distal part of the suprastapedial process is greatly swollen (wider that the dorsal part). Moreover, in halisaurines, it seems divided into two oval balls enclosing a deep depression.
38. Quadrate infrastapedial process: absent = 0; small = 1; large = 2 (B-49 modified; DC-43).
39. Quadrate supra- and infrastapedial processes contact: no = 0; coalescent = 1; fused = 2 (B-47 modified; DC-43).
40. Quadrate distal condyle: saddle-shaped = 0; flat = 1; convex in any view = 2 (B-61 modified).
41. Intramandibular joint: absent = 0; present = 1 (DC-63).
42. Dentary rostrum: absent = 0; short = 1; long = 2 (B-69+70 modified).
43. Dentary medial parapet development: at the base of tooth roots = 0; half the height of the lateral parapet = 1; same level as the lateral parapet = 2 (B-71).
44. Dentary ventral margin: convex = 0; almost straight or straight = 1 (DC-67).
45. Dentary posterior edentulous process: present (the dentary ends up a distance from the last tooth) = 0; absent (the dentary ends up just posterior to the last tooth) = 1. The primitive condition present in *Varanus* is retained in *Plioplatecarpus* and *H. arambourgi*.
46. Splenial contact with anteromedial margin of coronoid: bones fused = 0; bones in contact = 1; bones separated = 2 (DC-65).
47. Splenial anterior extension: extends no more than half the dentary length = 0; extends more than half the dentary length = 1 (DC-66 modified).
48. Angular lateral exposition: large = 0; weak = 1.
49. Angular dorsomedial wing: absent = 0; present = 1 (DC-59 modified).
50. Surangular coronoid buttress: confluent with long axis of jaw, without coronoid buttress = 0; rises steeply anterodorsally, developing a coronoid buttress = 1 (B-78; DC-57).
51. Surangular coronoid suture extension: half the dorsal surface of the surangular = 0; reduced surface = 1.
52. Surangular–articular lateral suture: descends and angles regularly = 0; curves first posteriorly, then descends = 1 (B-80 modified).
53. Coronoid general shape: saddle-shaped (slight dorsal curvature) = 0; 'L'-shaped (very concave above) = 1 (B-74).
54. Coronoid posteromedial process: strong = 0; small = 1; absent = 2 (B-75 and DC-62 modified).
55. Coronoid medial wing: does not reach angular = 0; reach angular = 1 (B-76; DC-60 modified).
56. Articular participation in glenoid: articular forming glenoid = 0; articular participation larger than surangular = 1; equal articular and surangular participations = 2 (DC-54 modified).
57. Articular retroarticular process inflection: less than 60° = 0; almost 90° = 1 (B-81).
58. Articular posterolateral margin of the glenoid: almost flat = 0; surrounded by a stout process of bone = 1. In *Halisaurus*, the posterolateral margin of the glenoid surface is surrounded by a stout process.
59. Marginal teeth general shape: fine and sharp recurved fangs = 0; strong and robust fangs = 1; low and bulbous fangs = 2 (B-83+88 and DC-52 modified).
60. Marginal teeth ornamentation: smooth = 0; small minute ridges = 1; facets = 2; anastomosed enamel = 3 (B-83+88 and DC-52 modified).
61. Marginal teeth carinae: absent = 0; weak = 1; strong = 2 (B-83+88 and DC-52 modified).
62. Marginal teeth basal cross-section: flat = 0; rounded = 1; swollen = 2; 'U'-shaped = 3 (B-83+88 and DC-52 modified).
63. Presacral vertebra number: less than 33 = 0; between 33 and 40 = 1; more than 40 = 2 (B-105+106; DC-71 modified).

64. Cervical and dorsal articulation orientation: strong oblique = 0; weak oblique = 1; vertical = 2 (B-100 and DC-74 modified).
65. Functional zygapophyses: on entire column = 0; vestigial in caudals = 1; lost in first dorsals = 2 (B-99 and DC-78 modified).
66. Zygosphene–zygantrum complex: well developed = 0; rudimentary = 1; absent = 2 (B-93+94 modified; DC-79).
67. Cervical articulation shape: broad oval (height/width about one-third) = 0; oval – subrectangular (height/width about one-half) = 1; elliptical – heart-shaped (height/width about three-quarters) = 2; circular (height approximately equal to width) = 3 (B-101 and DC-75 modified).
68. Cervical number: seven = 0; more than seven = 1 (DC-70).
69. Cervical hypapophysal peduncle shape in cross-section: subrectangular = 0; triangular = 1; ovoid = 2; lenticular = 3 (DC-77).
70. Cervical hypapophysal peduncle fusion: present = 0; absent = 1.
71. Cervical synapophyse location: anteriorly on the centrum = 0; middle of the centrum = 1.
72. Cervical synapophyse ventral extension relative to centrum ventral surface: above = 0; approaching = 1; below = 2 (B-98 modified).
73. Tail length: head and trunk shorter than or equal to tail length = 0; head and trunk longer than tail = 1 (B-112; DC-84).
74. Caudal length/height: length greater than height = 0; length equal to height = 1 (DC-87).
75. Caudal sacral number: two = 0; less than two or lost = 1 (B-107; DC-72)
76. Caudal pygal number: four = 0; more than four = 1; more than 10 = 2 (DC-73 modified).
77. Caudal transverse processes: present on all caudals = 0; on anterior caudals only = 1 (DC-85).
78. Caudal haemal spines: not fused to centrum = 0; fused = 1 (B-110; DC-89).
79. Girdle element ossification: present = 0; absent = 1 (B-117; DC-94 +123).
80. Scapula/coracoid size: scapula smaller than coracoid = 0; scapula and coracoid nearly equal in size = 1; scapula larger than coracoid = 2 (B-113 and DC-95 modified).
81. Scapula general shape: narrow = 0; fan = 1; strong fan = 2 (B-114).
82. Scapula anterior margin: shorter than posterior one, slight emargination = 0; half the posterior one, strong emargination = 1; horizontal with weak emargination = 2 (DC-96).
83. Scapula posterior margin: gently concave = 0; deeply concave = 1 (B-116; DC-97).
84. Coracoid anterior neck: absent = 0; present and short = 1; present and long = 2 (B-119 modified; DC-98).
85. Coracoid anterior margin: shorter than posterior one = 0; longer than posterior one = 1 (DC-99).
86. Coracoid anterior emargination: two = 0; one = 1; absent = 2 (B-120 modified).
87. Ilium sacral rib contact: present = 0; absent = 1 (DC-121).
88. Ilium direction: dorsal and posterior = 0; dorsal and anterior = 1 (DC-122).
89. Pubis distal part: perpendicular to body long axis = 0; parallel to body long axis = 1 (DC-124).
90. Pubis distal expansion: fan = 0; slender = 1 (DC-125).
91. Pubis tubercle location/acetabulum: large, ventrolateral, far = 0; large, anterior, close = 1; large, fan-shaped, close = 2; reduced or absent = 3 (B-138 modified; DC-126).
92. Ischium distal part: fan = 0; slender fan = 1; slender = 2 (DC-128 modified).
93. Ischium tubercle/acetabulum: large, distal = 0; large, proximal = 1; reduced, proximal = 2 (B-139 modified; DC-127).
94. Propodial condyle: spherical = 0; flat and smooth = 1; flat with grooves and pits = 2 (B-123 modified; DC-105+131).
95. Humerus general shape: shaft long and narrow (length 4× distal width) with perpendicular extremities = 0; shaft long and compressed (length 3.4× distal width) = 1; shaft reduced (length 1.5–2× distal width) with moderately expanded extremities = 2; shaft reduced (length slightly larger than distal width) with expanded extremities = 3; shaft strongly reduced (length lower or equal to distal width) with strongly expanded extremities = 4 (B-121 and DC-104 modified).
96. Humerus postglenoid process/glenoid: absent = 0; small and continuous = 1; large and continuous = 2; large and separate = 3 (B-122 and DC-104 modified).
97. Humerus deltopectoral crest: processes anterior and undivided = 0; anterior and separate = 1; separate with anterior deltoid crest and medial pectoral one = 2 (B-124 and DC-107 modified).
98. Humerus ectepicondyle groove: present = 0; absent = 1 (B-126).
99. Humerus ectepi- and endepicondyles development: moderate = 0; very large = 1 (B-127 +128 and DC-109 modified).
100. Radius shape: long, slender, not expanded distally = 0; slightly expanded distally and medially = 1; short, strongly expanded at both extremities = 2 (B-129; DC-113 modified).

101. Radius preaxial ridge: absent = 0; developed on distal third = 1; developed on distal half = 2; developed on distal two-thirds = 3 (DC-113 modified).
102. Ulna shape: long and slender = 0; slightly expanded medially = 1; hour-glass shaped = 2 (DC-110 modified).
103. Femur shape: sigmoidal, distal width about one-quarter length = 0; straight, distal width about one-half length = 1; straight, distal width about two-thirds length = 2; straight, distal width about three-quarters length = 3 (DC-130+134 modified).
104. Femur distal facets: separate = 0; confluent = 1.
105. Tibia and fibula shape: long, slender, extremities not expanded = 0; shorter and flat, extremities slightly expanded = 1; shorter and flat, extremities strongly expanded = 2 (DC-136 +137 modified).
106. Tibia cnemial crest: present = 0; absent = 1 (DC-135).
107. Fibula posterodistal process: absent = 0; small = 1; large = 2 (DC-138).
108. Carpus and tarsus composition: nine carpals and four tarsals = 0; seven carpals and three tarsals = 1 (B-132 and DC-114 modified).
109. Metapode shape: long and slender = 0; shorter = 1; short and broad = 2 (B-134 and DC-116 modified).
110. Phalange number: 2–3–4–5–3/4 = 0; hyperphalangy = 1 (B-135 modified; DC-117+142).
111. Phalange ungual: clawed = 0; unclawed = 1 (DC-120).

APPENDIX 3

Matrix of characters

Varanus varius
```
0000000000 0000000000 0000000010 1000000000 0000000000 0000000000
0000000000 0000000000 0000000000 0000000000 0000000000 0
```
Aigialosaurus dalmaticus
```
101?000?10 0000100??0 00?000??0? ??0012???1 1?11?11000 1101?10000
0?0110?011 000101100? ??????00?? ???0100000 0001000000 0
```
Halisaurus platyspondylus
```
1011?01??? ?011110110 1111??1021 ??1?121211 1????2?000 0102010111
1101121 0?1 02?????1?? ?????????? ?????????? ?????????? ?
```
Halisaurus ortliebi
```
?????01?11 0031110110 2311101 0?? ????121211 1????????? ??020???11
?????????? ?????????? ?????????? ?????????? ?????????? ?
```
Halisaurus arambourgi
```
1011101111 0011110110 1111001021 0011121211 1011021010 0102010111
1101121021 02?1111112 1011??11?? ?222211001 3121110?0? ?
```
Eonatator sternbergii
```
10121????? ??10100?10 0011??10?? ????121211 1?11???0?0 000??100??
??0?12?0?1 0210101110 0011111011 ???021?001 311111010? ?
```
Plioplatecarpus primaevus
```
1010001011 1010112103 2302101002 1211221212 1021021100 1002020011
2102222021 1101121012 2212111111 2222322002 2231211111 1
```
Platecarpus ictericus
```
1010001111 1120212113 1102111001 1211121102 1021121100 1002020011
2102112011 1101111011 2212111111 2122322002 2221211111 1
```
Prognathodon overtoni
```
1010002111 1100222101 01?2101111 1211111221 1020121011 0012121023
2112112011 00011?111? ?????????? ???2322102 2??1?????? ?
```
Tylosaurus proriger
```
1221210001 1100221112 02?2111000 1011102101 1221121000 0002020021
1302112031 1001111010 0011121111 3202212001 1121211101 1
```
Hainosaurus bernardi
```
1220210111 1100221102 02?2101000 1010102101 122112?000 0002020021
1122112131 1001121010 0011211?? ???2212001 1121211111 1
```
Clidastes propython
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1131002111 1010111101 0112101001 0010110101 1121121111 0012020010
2022103021 0111111110 2101111111 1211431112 2210212121 1
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Mosasaurus hoffmanni
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1131002011 1130222101 0112111010 0010100102 1121121101 0012121022
2322103121 0011111111 2101121111 1211431112 2230212121 1
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Globidens dakotaensis
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1131002111 1120222111 01?210000? ?01?110221 1??1?21??1 ?012?20033
02?2?03?21 01?1??111? ?????????? ???143111? ?????????? ?
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APPENDIX 4

Synapomorphies of high-clade categories, *Halisaurus* and *Eonatator*.

Mosasauridae. *Unambiguous*: 10(0–>1), 18(0–>1), 33(0–>1), 46(0–>2), 54(0–>2), 75(0–>1), 79(0–>1), 84(0–>1), 85(0–>1), 87(0–>1), 89(0–>1), 90(0–>1), 92(0–>2), 95(0–>2), 96(0–>1), 100(0–>1), 102(0–>1), 106(0–>1), 108(0–>1). *Ambiguous*: 8(0–>1), 27(0–>1), 34(0–>1), 37(0–>1), 38(0–>2), 60(0–>1), 61(0–>1), 62(0–>1), 69(0–>2), 83(0–>1), 86(0–>1), 103(0–>2).

Halisaurinae. *Unambiguous*: 5(0–>1), 24(0–>1), 101(0–>3), 105(0–>1). *Ambiguous*: 13(0–>1), 19(0–>1), 23(0–>1), 38(0–>2), 39(0–>1), 66(0–>2), 72(0–>2), 78(0–>1).

Halisaurus. *Unambiguous*: 14(0–>1), 58(0–>1), 67(0–>1). *Ambiguous*: 4(0–>1), 7(0–>1), 16(0–>1), 21(0–>1), 22(0–>1), 29(0–>2), 30(0–>1), 52(0–>1), 59(0–>1).

Eonatator. *Ambiguous*: 4(0–>2), 73(0–>1), 74(1–>0), 76(1–>0), 103(2–>1).

Natantia. *Unambiguous*: 11(0–>1), 24(0–>2), 43(1–>2), 56(1–>2), 64(1–>2), 67(0–>2), 105(0–>2), 107(0–>1), 110(0–>1), 111(0–>1). *Ambiguous*: 12(0–>1), 15(1–>2), 16(0–>2), 25(0–>1), 45(0–>1), 59(0–>2), 66(0–>1), 88(0–>1), 94(0–>2), 97(0–>2).

Unnamed. *Unambiguous*: 81(0–>2), 95(2–>3), 96(1–>2), 100(1–>2), 101(0–>2), 102(1–>2). *Ambiguous*: 17(0–>2), 22(0–>1), 30(0–>1), 61(1–>2).

Plioplatecarpinae. *Unambiguous*: 20(0–>3), 82(0–>2), 84(1–>2), 91(0–>2). *Ambiguous*: 7(0–>1), 16(2–>1), 32(0–>2), 40(1–>2), 48(0–>1), 51(0–>1), 59(2–>1), 71(0–>1), 72(0–>1), 93(0–>2), 109(0–>1).

Mosasaurinae. *Unambiguous*: 20(0–>1), 50(0–>1), 53(0–>1), 98(0–>1). *Ambiguous*: 7(0–>2), 36(2–>1), 60(1–>3), 78(0–>1).

Tylosaurinae. *Unambiguous*: 2(0–>2), 3(1–>2), 5(0–>2), 6(0–>1), 20(0–>2), 42(0–>2), 101(0–>1). *Ambiguous*: 17(0–>1), 22(0–>2), 36(2–>0), 37(1–>2), 38(2–>1), 69(2–>3), 71(0–>1), 86 (1–>2).