C. R. Palevol 14 (2015) 483–493

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

An halisaurine (Squamata: Mosasauridae) from the Late Cretaceous of Patagonia, with a preserved tympanic disc: Insights into the mosasaur middle ear

Un halisauriné (Squamata : Mosasauridae) du Crétacé supérieur de Patagonie, à disque tympanique conservé : un aperçu de l'oreille moyenne des mosasaures

Marta S. Fernández[a,*], Marianella Talevi[b]

[a] *CONICET - División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina*
[b] *CONICET - Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Isidro Lobo y Belgrano, 8332 General Roca, Río Negro, Argentina*

ARTICLE INFO

Article history:
Received 15 September 2014
Accepted after revision 13 May 2015

Handled by Nathalie Bardet

Keywords:
Halisaurus
Patagonia
Late Maastrichtian
Cretaceous
Tympanic disc
Mosasauroidea

Mots clés :
Halisaurus
Patagonie
Maastrichtien supérieur
Crétacé
Disque tympanique
Mosasauroidea

ABSTRACT

Halisaurinae is a subfamily of enigmatic, small- to medium-sized mosasauroids, which retain a mosaic of primitive and derived features. The first record of a South American *Halisaurus* with precise stratigraphic information includes a quadrate carrying a tympanic disc together with twelve vertebrae, collected in the Late Maastrichtian of Jagüel Formation in northern Patagonia (Argentina). The preservation of a tympanic disc allows exploring and discussing the mechanisms of sound transmission in these mosasauroids. The location of the tympanic disc resembles that one formed by the extracolumella of aquatic turtles and at least one extant lizard. Based on morphological comparison of the middle ear we discuss previous hypotheses on the modification of the tympanic middle ear system of mosasauroids for underwater hearing, in a manner similar to that observed in aquatic turtles.

RÉSUMÉ

Les Halisaurinae représentent un clade énigmatique de mosasauroïdés de taille petite à moyenne. Un os carré avec un disque tympanique conservé et des vertèbres, découverts dans la Formation Jagüel d'âge Maastrichtien supérieur, Nord de la Patagonie (Argentine), représentent la première occurrence à provenance stratigraphique précise d'*Halisaurus* d'Amérique du Sud. La préservation d'un disque tympanique permet d'explorer et de discuter le mécanisme de transmission des sons chez ces mosasauroïdés. L'emplacement du

---

* Corresponding author.
E-mail addresses: martafer@fcnym.unlp.edu.ar (M.S. Fernández), mtalevi@unrn.edu.ar (M. Talevi).

http://dx.doi.org/10.1016/j.crpv.2015.05.005
1631-0683/

disque tympanique ressemble à ceux formés par les extracolumella des tortues aquatiques. Sur la base de la comparaison morphologique, nous émettons l'hypothèse que, comme proposé précédemment, le système de l'oreille moyenne tympanique des mosasauroïdés a été modifié pour une audition subaquatique, d'une manière similaire à celle des tortues aquatiques.

1. Introduction

Mosasauroids were squamates that invaded marine environments during the Late Cretaceous. The earliest record is from the Cenomanian of Israel (Polcyn et al., 1999) while the youngest records have been recovered from Late Maastrichtian deposits from numerous localities in both hemispheres, including Antarctica (Bardet et al., 2014; Fernández and Gasparini, 2012; Gallagher, 2005; Kiernan, 2002; Martin, 2006; Mulder et al., 1998). The fossil records indicate that they rapidly radiated within the marine realm to achieve an almost worldwide distribution (Polcyn and Everhart, 2008). Their extinction has been associated with the K/Pg crisis brought about by the collapse of the marine food web driven by the Chicxulub asteroid impact (Gallagher et al., 2012; Jouve et al., 2008; Polcyn et al., 2014). Disparity in craniodental anatomy and body size, among and within major clades, suggests foraging niche partitions (Polcyn et al., 2014). Advanced forms (i.e. hydropedal and hydroplevic mosasauroids) rapidly radiated during the Late Turonian reaching a cosmopolitan distribution until their extinction at the K/Pg boundary (Bardet et al., 2015). Knowledge on mosasauroid biology has increased significantly in recent years. This was triggered by new findings, re-examination of historical collections, and re-analysis of fossils by means of new tools and/or within new conceptual frameworks. Growing consensus considers them as obligatory aquatic, viviparous, probably endotherm, and fast sustained swimmers (e.g., Bell et al., 1996; Bernard et al., 2010; Caldwell and Lee, 2001; Houssaye and Bardet, 2012; Konishi et al., 2012; Lindgren et al., 2009, 2010, 2013). Within mosasauroids, most of the phylogenetic analyses recovered four major clades formally named as subfamilies Halisaurinae, Mosasaurinae, Plioplatecarpinae, and Tylosaurinae (Bell, 1997; Bell and Polcyn, 2005; Polcyn and Bell, 2005; Polcyn et al., 2014) (Fig. 1A). Palci et al. (2013) recognized two other clades, formally named Tethysaurinae and Yaguarasaurinae. The subfamily Halisaurinae represents an enigmatic and still poorly known group of small- to medium-sized mosasauroids which range from the Santonian to the Maastrichtian. Although they are consistently found as a monophyletic group, formally defined by Bardet et al. (2005a) as a subfamily, there is no generalized agreement on the phylogenetic relationships of halisaurines with the rest of the mosasauroids. Thus, some phylogenetic analyses recover them as basal members of Plioplatecarpines (Lingham-Soliar, 1988), or as the sister taxon of Mosasaurinae (Palci et al., 2013) (Fig. 1B); or as the sister taxon to Russellosaurina (= Tylosaurinae + Plioplatecarpinae) (Bell and Polcyn, 2005; Caldwell and Palci, 2007; Makádi et al., 2012), or even in a more basal position as the sister taxon to Natantia (Mosasaurines + Tylosaurines + Plioplatecarpines) (Bardet et al., 2003, 2005a; Polcyn et al., 2012). The taxonomic diversity of the clade is low, not only in comparison with the other clades but also in absolute terms: four generally accepted nominal species are known, included in two or three genera according to different authors. These are *Eonatator sternbergii* (Wiman, 1920) Bardet and Pereda Suberbiola in Bardet et al., 2005a; *Halisaurus platyspondylus* Marsh, 1869; *Halisaurus arambourgi* Bardet and Pereda Suberbiola in Bardet et al., 2005a; and *Phosphorosaurus ortliebi* Dollo, 1889. A fifth species – *Halisaurus walkeri* (Lingham-Soliar, 1998) from the Maastrichtian of Niger – could be recognized as valid according to Lindgren and Siverson (2005) and Bardet (2012). Most recently, a new species, *Eonatator coellensis*, was described from Columbia on the basis of a mostly articulated skeleton (Páramo-Fonseca, 2013). In spite of the comparatively scarce record, their geographic distribution reveals that halisaurines were widely distributed, at least during the Maastrichtian. They have been documented from both paleogeographic provinces of the Mediterranean Tethys, from the Western Interior seaway, Gulf Coast and East Pacific of North America, from the Iullemmenden basin (Niger-Nigeria), and from the Kristianstad Basin in southern Sweden (Bardet, 2012; Lindgren and Siverson, 2005; Lindgren, 2007). A new halisaurine has been recently reported from the Lowest Maastrichtian of northern Japan (Konishi et al., 2013) extending their spatial distribution to the northwestern Pacific. The South American records of halisaurines has been until now restricted to an isolated Late Cretaceous (probably Santonian) vertebra from Peru (Caldwell and Bell, 1995), and to a fragmentary jaw with teeth from the Maastrichtian central Chile tentatively identified as a Halisaurinae (Jimenez Huidobro et al., 2014).

Recent field trips carried out in the area of Los Bajos de Trapalcó and Santa Rosa (Río Negro province, Argentina) resulted in the recovery of mosasauroid remains from Late Maastrichtian rocks assigned to the Jagüel Formation (Fernández et al., 2008; Gasparini et al., 2003). Among them there are a quadrate preserving a tympanic disc, and 12 vertebrae of a small mosasaur. The same bed yielded remains of *Plioplatecarpus, Mosasaurus* and *Prognathodon* previously reported by Fernández et al. (2008). The main purpose of this contribution is to describe this newly discovered mosasauroid, herein indentified as *Halisaurus* sp., and to discuss the meaning of a tympanic disc in its middle ear.

The finding reported herein is significant for the following reasons: it documents the first stratigraphically and taxonomically precise occurrence of a halisaurine in South America; it represents the southernmost occurrence of the

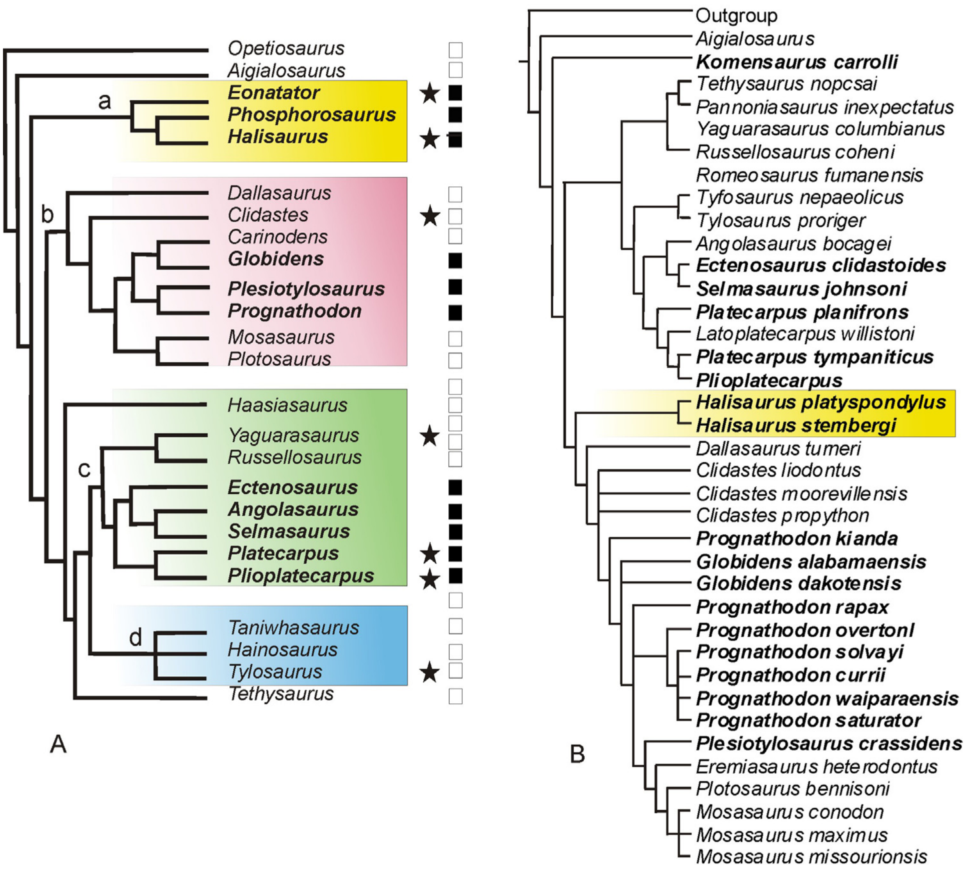

Fig. 1. (Color online). Mosasauroids phylogenetic trees simplified and modified from Polcyn et al., 2014 (A) and Palci et al., 2013 (B). A. Letters above the nodes indicate the clades Halisaurinae (a), Mosasaurinae (b), Plioplatecarpinae (c), and Tylosaurinae (d). Black square, genera with extreme bony enclosure of middle ear by means of elongation, confluence and/or fusion of the suprastapedial and infrastapedial processes. Stars indicate taxa in which a tympanic disc has been reported. B. The shadow box indicates the phylogenetic position of Halisaurinae.

Fig. 1. (Couleur en ligne). Arbre phylogénétique des mosasauroïdés, simplifié et modifié d'après Polcyn et al., 2014 (A) et Palci et al., 2013 (B). A. Les lettres au-dessus des nœuds indiquent les clades des Halisaurinae (a), Mosasaurinae (b), Plioplatecarpinae (c), et Tylosaurinae (d). Les carrés noirs indiquent les genres avec encerclement osseux extrême de l'oreille moyenne par l'intermédiaire d'allongement, confluence et/ou fusion des processus suprastapédial et infrastapédial. Les étoiles indiquent les taxons chez lesquels un disque tympanique a été mentionné. B. La zone ombrée indique la position phylogénétique des Halisaurinae.

group worldwide; and the preservation of a tympanic disc permits exploration and discussion of the middle ear morphology in these mosasauroids.

2. Material and methods

Mosasauroid specimen MML 1243 was collected from the upper part of the Jagüel Formation (Late Maastrichtian, Cretaceous) (Fernández et al., 2008; Gasparini et al., 2003), exposed at Los Bajos de Trapalcó and Santa Rosa (S 39 44′; W 66 40′), Río Negro Province, northern Patagonia, Argentina. It consists of an almost complete right quadrate and 12 vertebrae.

The centrum and both articulating surfaces are completely preserved in one of the cervical vertebrae (Fig. 3E–H). Following Caldwell and Bell (1995), in order to quantify the degree of the condyle compression, the absolute values of condyle width and height relative to overall centrum length of this vertebra were converted to ratios. The values obtained were plotted with those of other mosasauroids also characterized by condylar compression. The selected taxa were: *H. platyspondylus*, *E. sternbergii*, *Platecarpus tympaniticus*, *Plioplatecarpus primaevus*, and the specimen identified as *Halisaurus* sp. from Perú (Caldwell and Bell, 1995). Values of condyle compression ratios of these materials were taken from Caldwell and Bell (1995, Appendix 1).

Terminology.- To avoid confusions and simplify comparison, the term "*lizards*" is used in the Discussion section to refer to extant non-ophidian squamates.

Institutional abbreviations.- IAA: Instituto Antártico Argentino; IRSNB: Institut royal des Sciences naturelles de Belgique; MLP R: Museo de La Plata, Argentina; MML: Museo Municipal de Lamarque, Río Negro province, Argentina.

3. Systematic paleontology

SQUAMATA Oppel, 1811
MOSASAURIDAE Gervais, 1853

HALISAURINAE Bardet et al., 2005a
Halisaurus Marsh, 1869
Halisaurus sp.
(Figs. 2–4)

Material. Specimen MML 1243, a right quadrate and 5 cervicals and 7 anterior dorsal vertebrae of a single specimen.

3.1. Description

General accounts. The quadrate and vertebrae of specimen MML 1234 were found associated – although not articulated – in the same bed and within an area of approximately two square meters. The location of the elements recovered suggest that they were preserved articulated and that dislocation occurred as a consequence of recent weathering.

Quadrate (Fig. 2). The right quadrate is almost complete except for a portion of the anterolateral tympanic rim. Its maximum height is 56 mm. The suprastapedial process is long and contacts ventrally with a low and stout infrastapedial process. The oval and elongated tympanic meatus is completely enclosed by the suprastapedial process. The suprastapedial process is parallel-sided for most of its length and flares slightly in a ventral direction, ending in two distinctive lateral and medial blunt and swollen crests as in *H. arambourgi* (Bardet et al., 2005a). In lateral view, the lateral crest is deflected anteriorly, and together with the medial crest, encloses a triangular depression. The suprastapedial process is ventrally confluent, but not fused, with a short and stout infrastapedial process. The stapedial pit for the reception of the internal process of the extrastapes is relatively small and oval, and its margins are poorly defined. There is a well-defined ventromedial articulation area for the pterygoid ramus (Fig. 2A, D, F). The median ridge is single, sharp and raising vertically. As it was described by Polcyn et al. (2012) in *H. arambourgi*, the median ridge turns posterodorsally at about the level of the stapedial pit. The median ridge turns sharply in a dorsal direction, separating the median surface of the quadrate from the swollen cephalic head. The median ridge and the anterior edge of the tympanic meatus enclose an elongated depression ending at about the level of the dorsal edge of the meatus. The stapedial pit is located on the dorsal portion of this depression (Fig. 2A). The posteroventral edge, as described by Polcyn

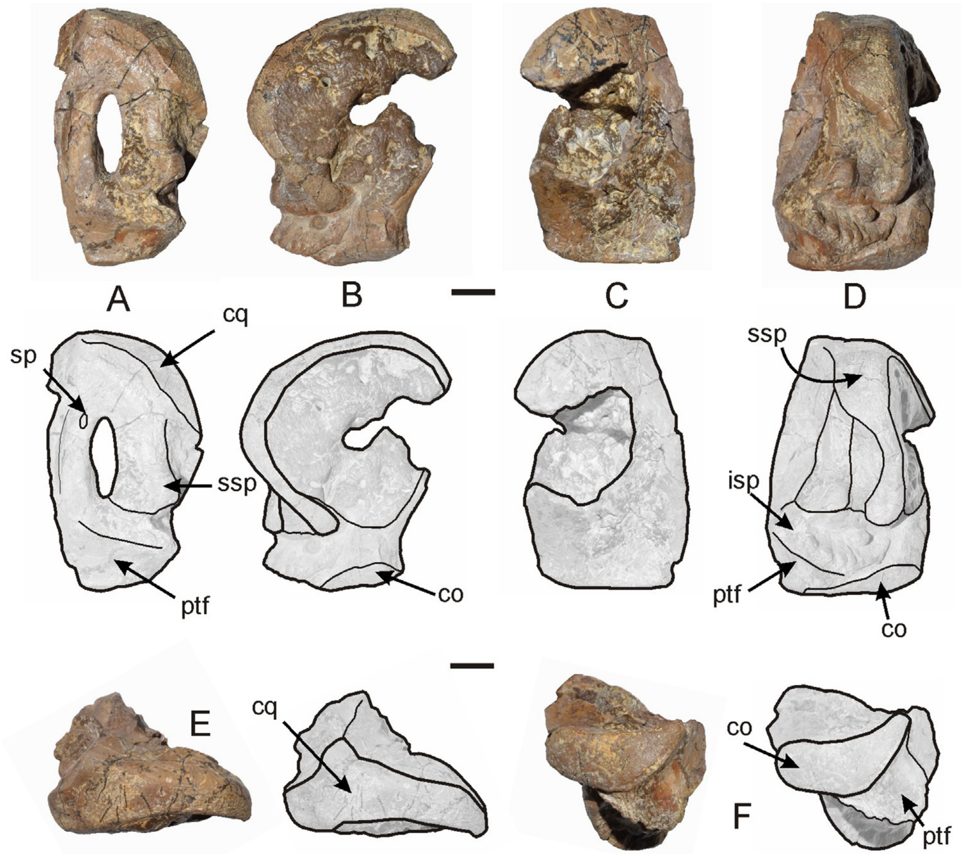

Fig. 2. (Color online). *Halisaurus* sp. MML 1243. Quadrate in medial (A), lateral (B), anterior (C), posterior (D), dorsal (E), and ventral (F) views. Anatomical abbreviations: co: condyle; cq: cephalic head; ptf: ventromedial articulation for pterygoid ramus; isp: infrastedial process; sp: stapedial pit; ssp: suprastapedial process. Scale bar = 1 cm.

Fig. 2. (Couleur en ligne). *Halisaurus* sp. MML 1243. Os carré en vues médiane (A), latérale (B), antérieure (C), postérieure (D), dorsale (E) et ventrale (F). Abréviations anatomiques : co : condyle ; cq : tête céphalique ; ptf : facette pour le ptérygoïde ; isp : processus infrastédial ; me : méat ; sp : fosse stapédienne ; ssp : processus suprastapédial. Échelle = 1 cm.

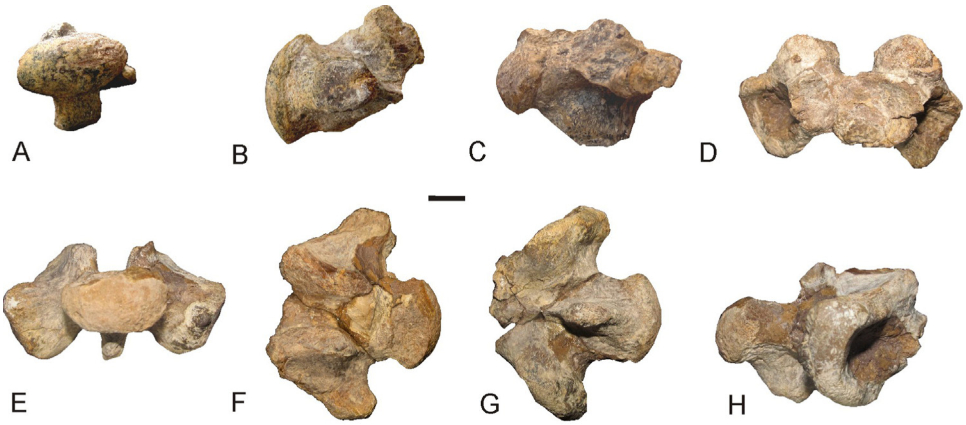

Fig. 3. (Color online). *Halisaurus* sp. MML 124. Cervical vertebrae. A–B. Posterior (A) and ventral views of an anterior cervical centrum. C–D. Lateral (C) and anterior (D) views of another cervical vertebra. E–H. The most complete cervical vertebra recovered in posterior (E), dorsal (F), ventral (G), and right lateral (H) views. Scale bar = 1 cm.

Fig. 3. (Couleur en ligne). *Halisaurus* sp. MML 124. Vertèbres cervicales. A–B. Centrum cervical antérieur en vue postérieure (A) et ventrale (B). C–D. Autre vertèbre cervicale en vue latérale (C) et antérieure (D). E–H. Vertèbre cervicale la plus complète récoltée, en vues postérieure (E), dorsale (C), ventrale (G) et latérale droite (H). Échelle = 1 cm.

et al. (2012) in *H. arambourgi*, is sculpted by a series of vertical grooves interpreted as the osteological correlates of a strong ligamentous attachment with the posterior rim of the mandibular glenoid. The tympanic ala is almost complete except for a small anterodorsal portion. The dorsal portion of its rim is uniformly curved to define a large tympanic area in such a way that the dorsal articular surface of the quadrate is not exposed in lateral view. A tympanic disc is almost complete except for its anterodorsal portion, which is broken. Its rugose texture and color make it clearly distinguishable from the bony tympanic rim. The most conspicuous feature of this disc is the presence of a perforation in its center and other minor pits and shallow furrows on its external surfaces, probably resulting from the activity of bioerosive agents. The ventral quadrate condyle is convex in all other aspects and, as in *H. arambourgi* (Bardet et al., 2005a) it is perpendicular to the proximal head.

Vertebrae. Twelve vertebrae were preserved, five cervicals and seven dorsals. However, the neural arches were not preserved on any of them. Although not articulated, they were found in close proximity. Four vertebrae bear hypapophyses. A fifth vertebra lacking most of its centrum could correspond to a posterior cervical, or an anterior dorsal, based on the location and morphology of the synapophyses. In three of the hypapophysis-bearing centra, the peduncles are stout and located posteriorly on the ventral surface of

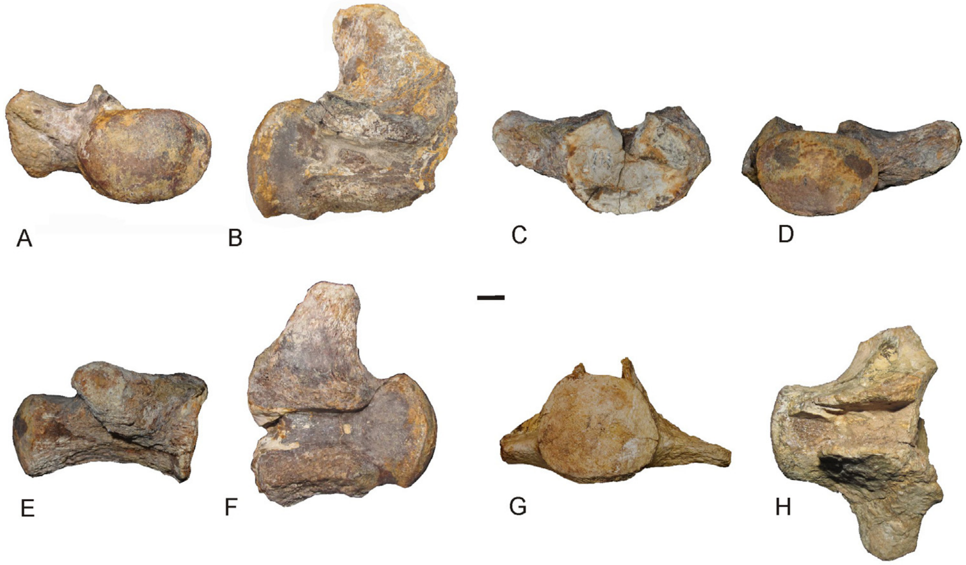

Fig. 4. (Color online). *Halisaurus* sp. MML 124. Four selected dorsal vertebrae: A–B; C–D; E–F; and G–H. A, D, and G. Posterior views. B, F, H. Dorsal views. C. Anterior view. E. Right lateral views. Scale bar = 1 cm.

Fig. 4. (Couleur en ligne). *Halisaurus* sp. MML 124. Quatre vertèbres dorsales sélectionnées : A–B ; C–D ; E–F ; et G–H. A, D et G. Vues postérieures. B, F, H. Vues dorsales. C. Vue antérieure. E. Vue latérale droite. Échelle = 1 cm.

the centra (Fig. 3A–C), while in the remaining it is notably less developed suggesting that this vertebra corresponds to one of the last of the cervical series (Fig. 3E–H). As this is the most completely preserved centrum and the only one in which the total length could be measured, description of the cervical vertebrae is mainly based upon it. This centrum measures 59.02 mm long. The two articulating surfaces are dorsoventrally compressed. The cotyle is roughly rectangular, with a height/width ratio of 0.54. The synapophyses are large, stout, located close to the cotyle and posteroventrally projected. In dorsal view, the posterior projections of the synapophyses produce an angle of approximately 92° between the main axis of both synapophyses. Their anterior surfaces bear an anterodorsal and a posteroventral blunt crest forming a deep embayment. The anterodorsal crest curves slightly upward, continuing as a blunt ridge to merge with the robust bases of the prezygapophyses (Fig. 3H). In posterior view, the distal edges of the synapophyses are well below the ventral rim of the centrum (Fig. 3E). The condyle is roughly rectangular in outline (width = 31.07; height = 19.41 mm), and slightly obliquely orientated. This articulating surface is separated from the main body of the centrum by a slight constriction. In lateral view, the central articulations are obliquely inclined relative to the vertical vertebral axis (Fig. 3H).

Seven vertebrae from the dorsal series are preserved. Five of them, identified as anterior dorsals, bear robust synapophyses located on the anterior part of the centrum (Fig. 4A–F). In posterior view their ventral edges do not reach below the ventral surface of the centra. Their articulating surfaces are, as in the cervicals, dorsoventrally compressed with an average height/width ratio of 0.67. Another vertebra lacks synapophyses so its relative position in the dorsal series is difficult to determine. However, based on the centrum length, the location of the bases of the missing synapophyses, and the condyle compression, it could also correspond to the anterior dorsal series. One dorsal vertebra has dorsoventrally compressed transverse processes, located at half of the centrum height; the distal facets for the rib articulations are roughly elliptical in outline. The articulating surfaces are deep with a height/width ratio of 0.90 (Fig. 4G and H). This vertebra probably corresponds to the posterior dorsal series.

3.2. Comparison and systematical determination

The quadrate of specimen MML 1234 is characterized by the following combination of character states: extremely elongate, ventrally flaring suprastapedial process that meets a low, broad and shelf-like infrastapedial process below; small and weakly emarginated stapedial pit; well-defined ventromedial articulation for the pterygoid ramus; posterior enclosure of an elongated tympanic meatus formed by the elongated suprastapedial process. This unique combination of quadrate features (Bardet et al., 2005a; Polcyn and Everhart, 2008; Polcyn et al., 2012) allows referring specimen MML 1234 to Halisaurinae.

Within halisaurines, the MML 1234 quadrate differs from the quadrate of *E. sternbergii* by the general shape of the tympanic rim. In *E. sternbergii* the quadrate is rounded, with a regularly convex tympanic rim (cf. Bardet and Pereda Suberbiola, 2001, Fig. 2; Bardet et al., 2005a, Fig. 5E; Wiman, 1920, Fig. 5) whereas in MML 1234 the tympanic rim is roughly triangular. In *E. sternbergii* the infrastapedial

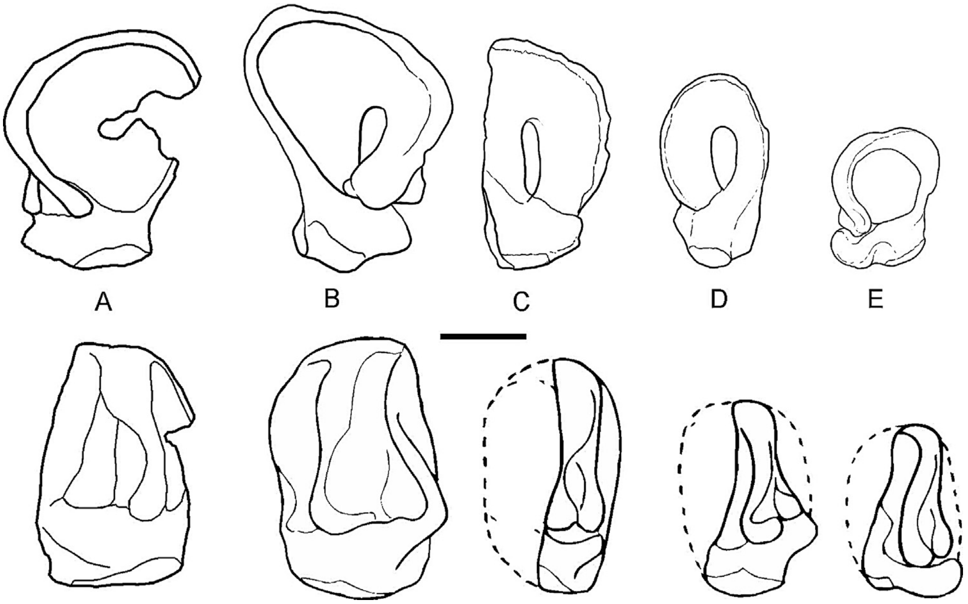

Fig. 5. Comparison of halisaurinae quadrates in lateral (top) and posterior (bottom) views. B, D–E. Modified from Bardet et al. (2005a). A. *Halisaurus* sp. MML1234. B. *Halisaurus platyspondylus*. C. *Halisaurus ortliebi* (IRSNB R 34). D. *Halisaurus arambourgi* (private collection). E. *Eonatator sternbergii*. Scale bar = 2 cm.

Fig. 5. Comparaison des carrés d'halisaurinés en vues latérale (en haut) et postérieure (en bas). B, D–E. Modifié d'après Bardet et al. (2005a). A. *Halisaurus* sp. MML1234. B. *Halisaurus platyspondylus*. C. *Halisaurus ortliebi* (IRSNB R 34). D. *Halisaurus arambourgi*. E. *Eonatator sternbergii*. Échelle = 2 cm.

process is strongly projected medially and relatively low in posterior view (cf. Bardet and Pereda Suberbiola, 2001; Wiman, 1920, Fig. 5) when compared to that of MML 1234, *H. platyspondylus* (cf. Holmes and Sues, 2000, Fig. 4), *H. arambourgi* (cf. Polcyn et al., 2012, Fig. 2) and *P. ortliebi* (Lingham-Soliar, 1996, Fig. 5; MSF personal observations). Specimen MML 1234 differs from *P. ortliebi* by the shape and extension of the tympanic meatus and the shape of the suprastapedial process. In *P. ortliebi* the tympanic meatus is extremely long and narrow, with its anterior and posterior edges almost straight and parallel (MSF personal observations) while in MML 1243 the anterior edge of the tympanic meatus is slightly convex and the meatus outline is roughly oval (Fig. 5). The suprastapedial process of MML 1243 is distally less swollen than in *P. ortliebi*. The medial crest on the ventral ending of the suprastapedial process is anteromedially projected in *P. ortliebi* in such a way that it remains exposed in a medial view of the quadrate. Contrarily, in MML 1234 the medial projection of the crest is less pronounced and almost hidden in medial view.

In posterior view, the dorsal portion of the suprastapedial process of MML 1234 resembles that of *H. platyspondylus* (cf. Holmes and Sues, 2000, Fig. 5) and differs by its robustness from those of *H. arambourgi* (cf. Bardet et al., 2005a, fig. 8H; Polcyn et al., 2012, Fig. 2E), *E. sternbergii* (cf. Bardet and Pereda Suberbiola, 2001, Fig. 2; Wiman, 1920, Fig. 5) and *P. ortliebi* (MF pers. observ). Thus, in the MML 1234 quadrate the width of the dorsal portion of this process is more than half the width of its ventral ending, whereas in *H. arambourgi*, *P. ortliebi* and *E. sternbergii* the dorsal portion of the suprastapedial process is mediolaterally compressed (Fig. 5). The quadrate morphology of MML 1234 also resembles that of *H. platyspondylus* (Fig. 5B) in the outline of the tympanic rim. Thus, in both forms the anterodorsal tympanic rim is more tightly curved than the rest of the rim.

The cervical and anterior dorsal vertebral morphologies, characterized by dorsoventrally compressed vertebral centra, subrectangular outline of the articulating surfaces, and synapophyses flaring distally and projecting below the ventral rim of centra, also confirm the halisaurine affinities of specimen MML 1243. When relative values of the condyle compression of MML 1234 are plotted with those of other mosasauroids also characterized by condyle compression, they fall within the range of other halisaurines reported in literature (Bardet et al., 2005a; Caldwell and Bell, 1995), and also close to the isolated cervical vertebra of *Halisaurus* sp. from Perú (Fig. 6). The remaining cervical vertebrae lack most of their centra and condyle compression could only be estimated by means of the height/width ratios. The values of this ratio range from 0.5 to 0.63.

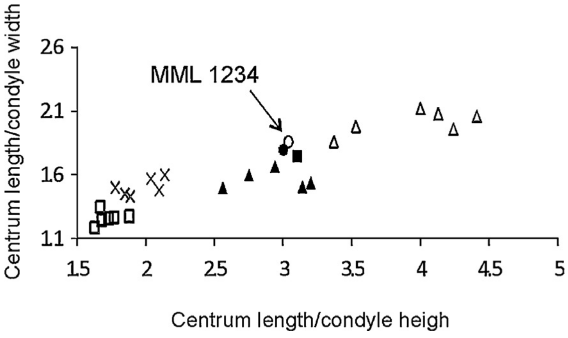

Fig. 6. Comparison of condyle compression of the MML 1234 and cervical vertebra series provided by Caldwell and Bell (1995, Appendix 1) in *Platecarpus tympaniticus* AMNH 1559 (open square), *Plioplatecarpus primaevus* NMC 11035 (cross), *Halisaurus platyspondylus* USNMH 442450 (black triangle), "*Halisaurus*" *sternbergii* PR195 (open triangle) with the addition of data points of two-single cervical vertebrae: *Halisaurus* sp. MCZ 2607 (black square) and *H. platyspondylus* YPM 412 (black circle). Institutional abbreviations: AMNH: Museum of Natural History, New York, US; MCZ: Harvard University, Cambridge, US; NMC: National Museum of Canada; PR: Field Museum of Natural History, Chicago, US; USNMNH: United States National Museum of Natural History, Washington, US; YMP: Yale University, New Haven, US.

Fig. 6. Comparaison de la compression du condyle entre la MML 1234 et la série de vertèbres cervicales fournie par Caldwell and Bell (1995, Annexe 1) dans *Platecarpus tympaniticus* AMNH 1559 (carrés blancs), *Plioplatecarpus primaevus* NMC 11035 (croix), *Halisaurus platyspondylus* USNMH 442450 (triangles noirs), « *Halisaurus* » *sternbergii* PR195 (triangle blanc) avec l'ajout de points de deux vertèbres cervicales simples : *Halisaurus* sp. MCZ 2607 (carré noir) et *H. platyspondylus* YPM 412 (cercle noir). Abréviations institutionnelles : AMNH : Museum of Natural History, New York, États-Unis ; MCZ : Harvard University, Cambridge, États-Unis ; NMC : National Museum of Canada ; PR : Field Museum of Natural History, Chicago, États-Unis ; USNMNH : United States National Museum of Natural History, Washington, États-Unis ; YMP : Yale University, New Haven, États-Unis.

4. Discussion

4.1. A halisaurine in northern Patagonia

The discovery of a halisaurine in northern Patagonia is significant as it documents the widespread distribution of halisaurines during the Late Maastrichtian, and also the southernmost certain occurrence of the group. As a consequence of Atlantic transgressions during the Maastrichtian, northern Patagonia was flooded and transformed into an archipelago in a sea named the Kawas Sea by Casamiquela (1973). Paleobiogeographic analysis of the Maastrichtian marine faunas from this area, based mainly on mollusk and decapod crustaceans, revealed affinities with southern high latitude faunas (Weddellian Province, Zinsmeister, 1982). However, near the K/Pg boundary the Danian, Weddellian forms were replaced by others typical from low latitudes such as northern Brazil, the Caribbean and northern Africa (Aguirre-Urreta et al., 2008). Although fragmentary, Maastrichtian mosasaur evidences recovered up to now show no evidences of the endemism, at least at a genus level, that characterized the Weddellian Province. Thus, Late Maastrichtian rocks deposited in the Kawas Sea yielded the same mosasaur taxa known to occur worldwide such as *Plioplatecarpus*, *Mosasaurus* and *Prognathodon* (Fernández et al., 2008); specimen MMLP 1234 confirms the presence of *Halisaurus*. Up to now, no evidence of durophagous forms such as *Globidens* and *Carinodens*, which seem to have been widespread during the Latest Cretaceous (Bardet et al., 2005b; Polcyn et al., 2010), has been found. Further exploration of the Jagüel Formation, and more complete materials are needed to test whether Late Maastrichtian mosasaur faunas are cosmopolitan or if endemism are represented at species levels.

4.2. A tympanic disc in the middle ear of mosasauroids

The presence of a tympanic disc seems to be a widespread feature among mosasauroids as it has been recorded in phylogenetically distant taxa (Fig. 1). The tympanic disc has been mentioned and described as a calcified tympanic membrane (e.g., Lingham-Soliar, 1994, p. 200; Russell, 1967, p. 58; Vaughn and Dawson, 1956). However, other authors identified the tympanic disk as an expanded portion of the calcified extracollumella (Caldwell et al., 2007; McDowell, 1967; Polcyn, 2010, 2011). Polcyn (2011) interpreted the tympanic disc as a calcified extracolumellar cartilage forming a relatively stiff and functional pseudo-tympanum suspended by the true tympanum. The tympanic disc of specimen MML 1234, as others described in the literature, is restricted and fills the tympanic conch. Of the two main mechanisms for sound transmission, i.e. tympanic middle ear pathway and bone conduction, the morphology of the bony middle ear elements of mosasauroids is consistent with the typical tympanic middle ear configuration (Clack and Allin, 2004; Nummela and Thewissen, 2008). The non-mammalian tympanic middle ear, which arose independently several times during tetrapod evolution (Christensen-Dalsgaard and Carr, 2008; Clack and Allin, 2004), is a highly adaptable system (Hetherington, 2008) and consists of a tympanic membrane, supported by bones and ligaments, and an extracolumella and stapes that cross an air filled cavity towards the inner ear.

The general pattern of the middle ear of mosasauroids resembles that of most lizards but there are some striking differences particularly in the location and pattern of the sound-receiving elements. In lizards, except in the forms in which the tympanic membrane was secondarily lost or reduced (e.g., Chamaeleonids and the earless monitor lizard *Lanthanotus*, McDowell, 1967; Clack and Allin, 2004), key elements of the sound conducting apparatus include the inner bony stapes and the outer slim cartilaginous extracolumella attached to the tympanic membrane. The tympanic membrane is partially enclosed by the quadrate. It is attached by means of ligaments to the posterior margin of the quadrate anteriorly, and to the retroarticular process of the lower jaw ventrally (Rieppel, 2002; Rieppel and Zaher, 2000) (Fig. 7C). Contrarily, in mosasauroids and as a result of the bony enclosure the middle ear is conspicuously more massive. Although in some lizards, such as *Varanus* or *Tupinambis* (Fig. 7A and B), the quadrate suprastapedial process projects posteriorly above the stapes, this ventral projection is not as pronounced as in mosasauroids. It should be noted that even the mosasauroids with a short suprastapedial process (e.g., tylosaurines, Fig. 7D), it is still relatively long

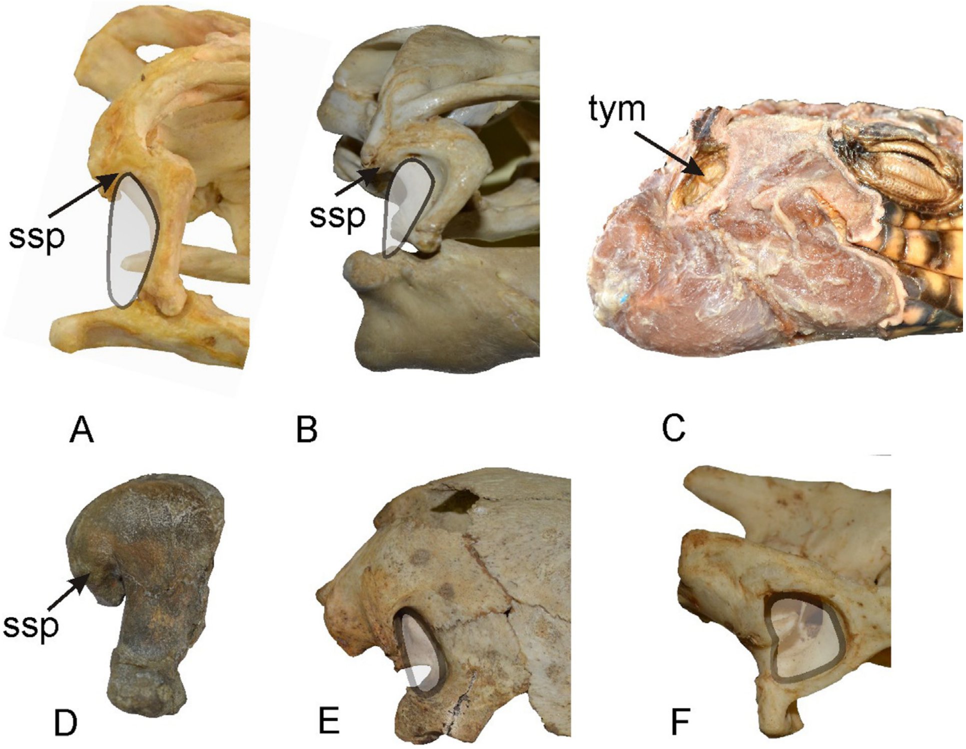

Fig. 7. (Color online). A, B, E, F. Posterior part of the skull showing the area of attachment of the tympanic membrane in *Varanus niloticus* MLP.R. 5209 (A); *Tupinambis teguixin* MLP R. 6250 (B); *Caretta caretta* MLP.R. 6243 (E); *Chelonoidis carbonaria* MLP R. s/n (F). C. Posterior portion of the head of *T. teguixin* (skin removed) showing the location of the tympanic membrane. D. Right quadrate of the tylosaurine *Taniwhasaurus antarcticus* (IAA 2000-JR-PSM-1). tym: tympanum; ssp: suprastapedial process. Not to scale.

Fig. 7. (Couleur en ligne). A, B, E, F. Partie arrière du crâne, montrant la zone d'insertion de la membrane tympanique chez *Varanus niloticus* MLP.R. 5209 (A) ; *Tupinambis teguixin* MLP R. 6250 (B) ; *Caretta caretta* MLP.R. 6243 (E) ; *Chelonoidis carbonaria* MLP R. s/n (F). C. Partie arrière du la tête de *T. teguixin* (avec la peau enlevée), montrant l'emplacement du la membrane tympanique. D. Carré droit en vue latérale de *Taniwhasaurus antarcticus* (IAA 2000-JR-PSM-1). tym : tympanum ; ssp : processus suprastapédial. Pas à l'échelle.

compared to that of *Varanus* or even *Tupinambis*. A phylogenetic tree including the relative development of the suprastapedial process reveals that the most extreme bony closure of the tympanic conch – whether by fusion or confluence of the supra- and infrastapedial processes evolved independently several times during the evolutionary history of mosasauroids (Fig. 1). This extreme enclosure suggests a general trend towards an acoustic isolation of tympanic cavities. Another difference between the middle ear of most lizards and mosasauroids is the lateral expansion of the extracolumella to form a tympanic disc in the latter. A similar tympanic disc has been described in the middle ear of *Lanthanotus borneensis*, which lacks the tympanic membrane (McDowell, 1967).

On the other hand, the middle ear of mosasauroids resembles that of turtles. As reported by McDowell (1967), Russell (1967), and Hetherington (2008), in both lineages the middle ears are enclosed by bone and separated from the mandible (Fig. 7E and F). Recently, Christensen-Dalsgaard and Carr (2008) and Christensen-Dalsgaard et al. (2012) demonstrated that the middle ear of the aquatic turtle *Trachemys scripta* is most sensitive to sound underwater and that their sensitivity depends on the large middle ear, which has a cartilaginous tympanic disc, and not on the tympanic membrane as the key sound receiver. Willis et al. (2013) increased taxon sampling to non-aquatic turtles and demonstrated that the pattern of the middle ear is similar in extant turtles regardless their ecological niche or phylogenetic position. They proposed that enlarged and isolated middle ear cavities acting as resonator enhanced hearing in both underwater and air hearing conditions.

Based on the morphological similarity between the middle ear among turtles (i.e. enlarged and bony enclosed middle ear, laterally expanded extracolumella forming a disc, and tympanic area separated from the lower jaw), it appears likely that the middle ear of mosasauroids functioned as that of extant turtles. In other words, that the key sound receiver was the tympanic disc (= expansion of the extracolumella), the bony tympanic conch acting as a resonator.

5. Conclusions

Specimen MML 1243, collected in the Late Maastrichtian of Jagüel Formation is the first record of a halisaurine in Patagonia and the southernmost occurrence of the group worldwide. Previous reports of South American halisaurines are stratigraphically or taxonomically uncertain. Within halisaurines, specimen MML 1234 is identified as *Halisaurus* sp. The most outstanding feature of this quadrate is the preservation of a tympanic disc that is an expanded part of the extracolumella, completely enclosed by the tympanic conch. The extension and location of mosasauroid tympanic discs resemble those of turtles. Contrary to the condition in lizards, but similar to the turtle condition, the extension of the tympanic rim indicates that the sound receiver was restricted to the "tympanic area" of the quadrate, and therefore more free than in lizards from the influence of mandibular movements. Based on morphological similarities, it is likely that the tympanic middle ear system of mosasauroids was modified for underwater hearing in a way parallel to that described for turtles, in which the bony tympanic conch could act as a resonator, and the expanded distal portion of the extracolumella was the key sound-receiving element. It is still unclear whether a tympanic membrane was secondarily lost in mosasauroids or remained as support of the tympanic disc.

Acknowledgements

We acknowledge Daniel Cabaza (Museo Municipal de Lamarque) for access to collections under his care and for his continuous support to Patagonian Mesozoic marine reptiles program during the last decade. MF thanks Dr. Pascal Godefroit (IRSNB) for access to collections under his care and his help during her visit to Belgium. We thank José O'Gorman (Universidad de La Plata), Magalí Cardenas, Santiago Gonzalez, Juan Ignacio Ison (Universidad de Río Negro) for help in fieldtrip and assistance in numerous ways. We thank Yanina Herrera for comments on the draft of the manuscript, Miguel Griffin for English corrections, and Laura Zampatti for French translation. We thank Johan Lindgren for providing photographs of the PMU R 163. Comments of reviewers, Nathalie Bardet and Michael Polcyn, greatly improve the quality of the manuscript. This research was financially supported by ANCyT- PICT 0748, CONICET- PIP433 and UNLP-N479 grants to MF; and by ANCyT-PICT 2013-0663 to MT.

References

Aguirre-Urreta, M.B., Casadío, S., Cichowolski, M., Lazo, D.G., Rodríguez, D.L., 2008. Afinidades paleobiogeográficas de los invertebrados cretácicos de la Cuenca Neuquina. Ameghiniana 45, 591–611.

Bardet, N., 2012. Maastrichtian marine reptiles of the Mediterranean Tethys: a palaeobiogeographical approach. Bull. Soc. geol. France 183, 573–596.

Bardet, N., Pereda Suberbiola, X., 2001. The basal mosasaurid Halisaurus sternbergii from the Late Cretaceous of Kansas (North America): a review of the Uppsala type specimen. C. R. Acad. Sci. Paris, Ser. IIa 332, 395–402.

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

Bardet, N., Pereda Suberbiola, X., Iarochene, M., Bouya, B., Amaghzaz, M., 2005a. A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the Halisaurinae (Squamata: Mosasauridae). Zool. J. Linn. Soc. 143, 447–472.

Bardet, N., Pereda Suberbiola, X., Iarochène, M., Amalik, M., Bouya, B., 2005b. Durophagous Mosasauridae (Squamata) from the Upper Cretaceous phosphates of Morocco, with the description of a new species of Globidens. Neth. J. Geosci. 84, 167–175.

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

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

Bell Jr., G.L., 1997. A phylogenetic revision of North American and Adriatic Mosasauroidea. In: Callaway, J.M., Nicholls, E.L. (Eds.), Ancient Marine Reptiles. Academic Press, San Diego, pp. 293–332.

Bell, G.L., Polcyn, M.J., 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the phylogeny of Mosasauridae (Squamata). Neth. J. Geosci. 84, 177–194.

Bell Jr., G.L., Sheldom, M.A., Lamb Jr., J.P., Martin, J.F., 1996. The first direct evidence of live birth in Mosasauridae (Squamata): exceptional preservation in the Cretaceous Pierre Shale of North Dakota. J. Vertebr. Paleontol. Suppl. 16, 21A–22A.

Bernard, A., Lécuyer, C., Vincent, P., Amiot, R., Bardet, N., Buffetaut, E., Prieur, A., 2010. Regulation of body temperature by some Mesozoic marine reptiles. Science 328, 1379–1382.

Caldwell, M.W., 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. J. Vertebr. Paleontol. 15, 532–544.

Caldwell, M.W., Lee, M.S., 2001. Live birth in Cretaceous marine lizards (mosasauroids). Proc. R. Soc. B-Biol. Sci. 1484, 2397–2401.

Caldwell, M.W., Palci, A., 2007. A new basal mosasauroid from the Cenomanian (U. Cretaceous) of Slovenia with a review of mosasauroid phylogeny and evolution. J. Vertebr. Paleontol. 27, 863–880.

Caldwell, M.W., Konishi, T., Dutchak, A., Bell Jr., G.B., Lamb, J., 2007. Osteology of the middle ear in mosasaurs (Squamata): from impedance matching to underwater hearing. In: Everhart, M.J. (Ed.), Second Mosasaur Meeting Abstract Booklet. Fort Hays State University – Sternberg Museum of Natural History, Hays, p. 10.

Casamiquela, R.M., 1973. La zona litoral de la transgresión maastrichtense en el norte de la Patagonia. Aspectos ecológicos. Ameghiniana 15, 137–148.

Clack, J.A., Allin, E., 2004. The evolution of single- and multiple-ossicle ears in fishes and tetrapods. In: Manley, G.A., Popper, A.N., Fay, R.R. (Eds.), Evolution of the Vertebrate Auditory System. Springer, New York, pp. 128–163.

Christensen-Dalsgaard, J., Carr, C.E., 2008. Evolution of a sensory novelty: tympanic ears and the associated neural processing. Brain Res. Bull. 75, 365–370.

Christensen-Dalsgaard, J., Brandt, C., Willis, K.L., Christensen, C.B., Ketten, D., Edds-Walton, P., Fay, R.R., Madsen, P.T., Carr, C.E., 2012. Specialization for underwater hearing by the tympanic middle ear of the turtle, *Trachemys scripta elegans*. Proc. R. Soc. B: Biol. Sci. 279, 2816–2824.

Dollo, L., 1889. Première note sur les mosasauriens de Mesvin. Bull. Soc. Belge Geol. Paleontol. Hydrol. 3, 271–304.

Fernández, M.S., Gasparini, Z., 2012. Campanian and Maastrichtian mosasaurs from Antarctic Peninsula and Patagonia, Argentina. Bull. Soc. geol. France 183, 93–102.

Fernández, M., Martin, J., Casadío, S., 2008. Mosasaurs (Reptilia) from the late Maastrichtian (Late Cretaceous) of northern Patagonia (Río Negro, Argentina). J. South Am. Earth Sci. 25, 176–186.

Gallagher, W., 2005. Recent mosasaur discoveries from New Jersey and Delaware, USA: stratigraphy, taphonomy, and implications for mosasaur extinction. Neth. J. Geosci. 84, 241–245.

Gallagher, W.B., Miller, K.G., Sherrell, R.M., Browning, J.V., Field, M.P., Olsson, R.K., Wahyudi, H., 2012. On the last mosasaurs: Late Maastrichtian mosasaurs and the Cretaceous-Paleogene boundary in New Jersey. Bull. Soc. geol. France 183, 145–150.

Gasparini, Z., Salgado, L., Casadío, S., 2003. Maastrichtian plesiosaurs from northern Patagonia. Cretaceous Res. 24, 157–170.

Gervais, P., 1853. Observations relatives aux reptiles fossils de France. C. R. Acad. Sci. Paris 36, 374–377.

Hetherington, T., 2008. Comparative anatomy and function of hearing in aquatic amphibians, reptiles, and birds. In: Thewissen, J.G.M., Nummela, S. (Eds.), Sensory Evolution on the Threshold: Adaptations in Secondarily Aquatic Vertebrates. University of California Press, Berkeley, pp. 183–209.

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

Houssaye, A., Bardet, N., 2012. Rib and vertebral microanatomical characteristics of hydropelvic mosasauroids. Lethaia 45, 200–209.

Jimenez Huidobro, P., Otero, R., Soto-Acuña, S., Caldwell, M., 2014. Mosasaur record (Squamata: Mosasauroidea) from the Upper Cretaceous of Chile. In: 74th Society of Vertebrate Paleontology Meeting, Abstract 94.

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

Kiernan, C.R., 2002. Stratigraphic distribution and habitat segregation of mosasaurs in the Upper Cretaceous of western and central Alabama, with an [sic] historical review of Alabama mosasaur discoveries. J. Vertebr. Paleontol. 22, 9–103.

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

Konishi, T., Caldwell, M.W., Nishimura, T., Sakurai, K., Tanoue, K., 2013. A new halisaurine (mosasauridae: halisaurinae) material from northern Japan. In: 4th Triennial International Mosasaur Meeting, Texas, Abstract Book, 26.

Lindgren, J., 2007. First *Halisaurus* (Squamata: Mosasauridae) from the Pacific Coast of North America. Paleobios 27, 40–47.

Lindgren, J., Siverson, M., 2005. *Halisaurus sternbergi*, a small mosasaur with an intercontinental distribution. J. Paleontol. 79, 763–773.

Lindgren, J., Alwmark, C., Caldwell, M.W., Fiorillo, A.R., 2009. Skin of the Cretaceous mosasaur *Plotosaurus*: implications for aquatic adaptations in giant marine reptiles. Biol. Lett. 5, 528–531.

Lindgren, J., Caldwell, M.W., Konishi, T., Chiappe, L.M., 2010. Convergent evolution in aquatic tetrapods: insights from an exceptional fossil mosasaur. PLoS One 5, e11998.

Lindgren, J., Kaddumi, H.F., Polcyn, M.J., 2013. Soft tissue preservation in a fossil marine lizard with a bilobed tail fin. Nat. Commun. 4, 2423.

Lingham-Soliar, T., 1988. The mosasaur *Goronyosaurus* from the Upper Cretaceous of Sokoto State, Nigeria. Palaeontology 31, 747–762.

Lingham-Soliar, T., 1994. The mosasaur *Plioplatecarpus* (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe. Bull. Inst. R. Sci. Nat. Belg. 64, 177–211.

Lingham-Soliar, T., 1996. The first description of *Halisaurus* (Reptilia, Mosasauridae) from Europe, from the Upper Cretaceous of Belgium. Bull. Inst. R. Sci. Nat. Belg. 66, 129–136.

Lingham-Soliar, T., 1998. A new mosasaur *Pluridens walkeri* from the Upper Cretaceous, Maastrichtian of the Iullemmeden Basin, Southwest Niger. J. Vertebr. Paleontol. 18, 709–717.

McDowell, S.B., 1967. The extracolumella and tympanic cavity of the “earless” monitor lizard *Lantanothus borneensis*. Copeia 1, 154–159.

Makádi, L., Caldwell, M.W., Ősi, A., 2012. The first freshwater mosasauroid (Upper Cretaceous, Hungary) and a new clade of basal mosasauroids. PloS One 7, e51781.

Martin, J.E., 2006. Biostratigraphy of the Mosasauridae (Reptilia) from the Cretaceous of Antarctica. In: Francis, J.E., Pirrie, D., Crame, J.A. (Eds.). Cretaceous-Tertiary High Latitude Paleoenvironments, James Ross Basin, Antarctica. Geol. Soc. London, Spec. Publ. 258, 101–108.

Marsh, O.C., 1869. Notice of some new mosasauroid reptiles from the Greensand of New Jersey. Am. J. Sci. Arts. 48, 392–397.

Mulder, E.W.A., Jagt, J.W.M., Kuypers, M.M.M., Peeters, H.H.G., Rompen, P., 1998. Preliminary observations on the stratigraphic distribution of Late Cretaceous marine and terrestrial reptiles from the Maastrichtian type area (SE Netherlands, NE Belgium). Oryctos 1, 55–64.

Nummela, S., Thewissen, J.G.M., 2008. The physics of sound in air and water. In: Thewissen, J.G.M., Nummela, S. (Eds.), Sensory Biology on the Threshold: Adaptations in Secondarily Aquatic Vertebrates. University of California Press, Berkeley, pp. 175–182.

Oppel, M., 1811. Die Ordnung, Familien und Gattung der reptilien als Prodrom einer Naturgeschichte derselben. Joseph Lindauer, Munich, 86 p.

Palci, A., Caldwell, M.W., Papazzoni, C.A., 2013. A new genus and subfamily of mosasaurs from the Upper Cretaceous of northern Italy. J. Vertebr. Paleontol. 33, 599–612.

Páramo-Fonseca, M.E., 2013. *Eonatator coellensis* nov. sp. (Squamata: Mosasauridae), a new species from the Upper Cretaceous of Colombia. Rev. Acad. Colomb. Cienc. 37, 499–518.

Polcyn, M., 2010. Sensory adaptations in mosasaurs. J. Vertebr. Paleontol. 30 (3, supplement), 128A.

Polcyn, M., 2011. Sensory adaptations in mosasaurs. In: 6th Conference on Secondary Adaptation of Tetrapods to Life in Water, San Diego, California.

Polcyn, M.J., Bell Jr., G.L., 2005. *Russellosaurus cohenin*. gen., n. sp., a 92 million-year-old mosasaur from Texas (USA), and the definition of the parafamily Russellosaurina. Neth. J. Geosci. 84, 321–333.

Polcyn, M.J., Everhart, M.J., 2008. Description and phylogenetic analysis of a new species of *Selmasaurus* (Mosasauridae: Plioplatecarpinae) from the Niobrara Chalk of western Kansas. In: Proceedings of Second Mosasaur Meeting. Fort Hays Stud. Spec. Issue 3, 13–28.

Polcyn, M.J., Tchernov, E., Jacobs, L.L., 1999. The Cretaceous biogeography of the eastern Mediterranean with a description of a new basal mosasauroid from Ein Yabrud, Israel. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), Proceedings of Second Gondwanan Dinosaur Symposium. Natl. Sci. Mus. Monogr. Tokyo 15, 259–290.

Polcyn, M.J., Jacobs, L.L., Schulp, A.S., Mateus, O., 2010. The North African Mosasaur *Globidens phosphaticus* from the Maastrichtian of Angola. Hist. Biol. 22, 175–185.

Polcyn, M.J., Lindgren, J., Bardet, N., Cornelissen, D., Verding, L., Schulp, A.S., 2012. Description of new specimens of *Halisaurus arambourgi* Bardet

& Pereda Suberbiola, 2005 and the relationships of Halisaurinae. Bull. Soc. geol. France 183, 123–136.

Polcyn, M.J., Jacobs, L.L., Araújo, R., Schulp, A.S., Mateus, O., 2014. Physical drivers of mosasaur evolution. Palaeogeogr. Palaeoclimatol. Palaeoecol. 400, 17–27.

Rieppel, O., 2002. Feeding mechanics in Triassic stem-group sauropterygians: the anatomy of a successful invasion of Mesozoic seas. Zool. J. Linnean Soc. 135, 33–63.

Rieppel, O., Zaher, H., 2000. The braincases of mosasaurs and *Varanus*, and the relationships of snakes. Zool. J. Linnean Soc. 129, 489–514.

Russell, D.A., 1967. Systematics and morphology of American mosasaurs (Reptilia, Sauria). Bull. Peabody Mus. Nat. Hist. 23, 1–241.

Vaughn, P.P., Dawson, M.R., 1956. On the occurrence of calcified tympanic membranes in the mosasaur Platecarpus. Trans. Kansas Acad. Sci. 1903, 382–384.

Willis, K.L., Christensen-Dalsgaard, J., Ketten, D.R., Carr, C.E., 2013. Middle ear cavity morphology is consistent with an aquatic origin for testudines. PloS One 8, e54086.

Wiman, C.J., 1920. Some reptiles from the Niobrara group in Kansas. Bull. Geol. Inst. Uppsala 18, 9–18.

Zinsmeister, W.J., 1982. Late Cretaceous-Early Tertiary molluscan biogeography of the southern Circum-Pacific. J. Paleontol. 56, 84–102.