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 (Squama : Mosasauridae) du Crétacé supérieur de Patagonie, à disque tympanique conservé : un aperçu de l’oreille moyenne des mosasaures

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A R T I C L E   I N F O

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

Handled by Nathalie Bardet

Keywords:
Halisaurus
Patagonia
Late Maastrichtian
Cretaceous
Tympanic disc
Mosasauroida

A B S T R A C T

Halisaurinae is a subfamily of enigmatic, small- to medium-sized mosasauroïds, 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 mosasauroïds. 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 mosasauroïds for underwater hearing, in a manner similar to that observed in aquatic turtles.

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R É S U M É

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

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http://dx.doi.org/10.1016/j.crpv.2015.05.005
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1. Introduction

Mosasauroïds 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 mosasauroïds) rapidly radiated during the Late Turonian reaching a cosmopolitan distribution until their extinction at the K/Pg boundary (Bardet et al., 2015). Knowledge on mosasauroïd 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; Housaye and Bardet, 2012; Konishi et al., 2012; Lindgren et al., 2009, 2010, 2013). Within mosasauroïds, 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 mosasauroïds 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 mosasauroïds. 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 Russellosaurinae (= 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 (Mosasaurinae + Tylosaurinae + Plioplatecarpinae) (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 Iullemmeden 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 (Jiménez Huidobro et al., 2014).

Recent field trips carried out in the area of Los Bajos de Trapalco and Santa Rosa (Río Negro province, Argentina) resulted in the recovery of mosasauroïd 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 mosasauroïd, herein indetified 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
group worldwide; and the preservation of a tympanic disc permits exploration and discussion of the middle ear morphology in these mosasaurs.

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'), Rio 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 mosasaurs also characterized by condylar compression. The selected taxa were: H. platyponslyus, E. sternbergii, Platecarpus tympaniticus, Pliopletecarpus 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, Rio Negro province, Argentina.

3. Systematic paleontology

SQUAMATA Oppel, 1811
MOSASUROIDAE 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 rising 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: infrastapedial 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 infrastéidal ; me : méat ; sp : fosse stapédienn e ; ssp : processus suprastapédiel. Échelle = 1 cm.
et al. (2012) in *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.

**Vertebral morphology.** 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 hypapophyses. In three of the hypapophysis-bearing centra, the peduncles are stout and located posteriorly on the ventral surface of its external surfaces, probably resulting from the activity of bioerosive agents. The ventral quadrate condyle is convex in all other aspects and, as in *Halisaurus* sp. (Bardet et al., 2005a) it is perpendicular to the proximal head.

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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 quadrates 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 quadrates 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 quadrates differs from the quadrates 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

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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 arambourgii (private collection). E. Eonatator sternbergii. Scale bar = 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 expansion 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 synapophysies 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 mosasaurids also characterized bycondyle 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 Peru (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.

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). Paleoecologic 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 Pliopletecarpus, Mosasaurus and Prognathodon (Fernández et al., 2008); specimen MLMP 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 extracolumella (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 thin 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.
compared to that of Varanus or even Tupinambis. A phylogenetic tree including the relative development of the supratemporal process reveals that the most extreme bony closure of the tympanic conch — whether by fusion or confluence of the supra- and infratemporal 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 Carri (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’Corman (Universidad de La Plata), Magali 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.

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