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Postcranial elements of *Maledictosuchus riclaensis* (Thalattosuchia) from the Middle Jurassic of Spain

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Abstract

Maledictosuchus riclaensis is a metriorhynchid crocodylomorph from the Callovian (Middle Jurassic) of Ricla (Spain). It is the most basal member of the Rhacheosaurini Tribe; it has recently been described and defined by its cranial elements (an almost complete skull and part of the lower jaw), but there were no data on the postcranial elements. Associated with the skull three vertebrae were collected. These vertebrae were preserved in black calcite nodules, and they have recently been prepared. The postcranial elements of the metriorhynchids are poorly documented, and usually badly preserved or included in the matrix. Herein we describe the three vertebrae (part of the holotype) of *M. riclaensis*. These comprise one cervical, one dorsal and one caudal vertebra, which, like the skull, are well preserved and lack post-mortem distortion or deformation.

Keywords: Metriorhynchidae, crocodylomorph, Callovian, vertebrae, Teruel, Iberian Peninsula

Resumen

Maledictosuchus riclaensis es un crocodilomorfo metriorrínquido del Calloviense (Jurásico medio) de Ricla (España). Es el miembro más basal de la tribu de los raqueosaurinos, y ha sido definido a partir de sus elementos craneales (un cráneo prácticamente completo y parte de la mandíbula inferior). Sin embargo no había datos de los elementos poscraneales. Durante la campaña de prospección en la que se recuperó el holotipo, se recuperaron tres vértebras asociadas al cráneo. Las vértebras estaban preservadas en nódulos de calcita, y han sido preparadas recientemente. Los elementos poscraneales de los metriorrínquidos están poco documentados, y normalmente, mal preservados o incluidos en la matriz. En este trabajo se hace descripción de tres vértebras, cervical, dorsal y caudal, del ejemplar tipo de *M. riclaensis*.

Palabras clave: Metriorhynchidae, crocodilomorfo, Calloviense, vértebras, Teruel, Península Ibérica

1. Introduction

The metriorhynchids are a group of Mesozoic marine crocodylomorphs, the only archosaurian group to return secondarily to a pelagic lifestyle. Recent works have led to a better understanding of this group, but while cranial elements are relatively abundant in the fossil record, postcranial elements are scarce and poorly described, often incomplete, deformed, or embedded in the matrix (e.g. *Cricosaurus saltillensis*, Buchy *et al.*, 2013; *Cricosaurus lithographicus*, Herrera *et al.*, 2013a; *Neptunidraco ammoniticus*, Cau and Fanti, 2011;

Tyrannoneustes lythrodectikos, Young *et al.*, 2013; *Torvoneustes carpenteri,* Wilkinson *et al.,* 2008; Thalattosuchia, Gea *et al.*, 2001; *Cricosaurus vignaudi*, Frey *et al.*, 2002).

Teleosaurid and metriorhynchid thalattosuchians are represented in Jurassic deposits from the Iberian Peninsula (Martínez *et al.*, 1995; Quesada *et al.*, 1998; Ruiz-Omeñaca *et al.*, 2007; Bardet *et al.*, 2008), but few can be identified at the generic level. Among the metriorhynchid remains, only two are diagnostic: an isolated tooth described as *Dakosaurus* sp. (Ruiz-Omeñaca *et al.*, 2010) and lately reassigned to cf. *Plesiosuchus manselii* (Young *et al.*, 2012), and a skull and ver-

tebrae described as *Maledictosuchus riclaensis* (Parrilla-Bel *et al.*, 2013). This taxon comes from the Ágreda Formation (Middle Callovian) in Ricla (Zaragoza). It is the basal-most known member of Rhacheosaurini, a lineage of increasingly mesopelagic piscivores, and the species was erected on the basis of the cranial elements. Some of the main characters that define *M. riclaensis* are: large amount of teeth, heterodont dentition and occlusion mechanism adapted for impaling and securely holding small prey items; hydrodynamic skull, with an acute angle between the medial and lateral processes of the frontal, and external nares divided by a septum and posterodorsally retracted, among others.

Three vertebrae associated with the skull were also collected. These were discovered by C. Gonzalvo, C. Laplana and M. Soria in 1994 during a prospecting campaign undertaken prior to the construction of the AVE railway line in this area. The vertebrae were preserved in black calcite nodules, and they have recently been prepared by chemical and mechanical methods. Like the skull, these vertebrae, though incomplete, are very well preserved, lacking post-mortem deformation. The postcranial elements of the metriorhynchids are described only briefly in the literature (in contrast to the abundance of skulls), and the fossil remains are usually poorly preserved or included in the matrix. Vertebrae from other specimens show that there is a general morphology shared by all metriorhynchids, with very few differences among species and genera.

The aim of this paper is to describe the vertebrae that form part of the holotype of *M. riclaensis*, which, although not diagnostic elements, increase our knowledge of this rhacheosaurin species. In addition, we complete the character matrix with some new data provided by these postcranial elements, and undertake a new phylogenetic analysis.

Institutional abbreviations: Institutional abbreviations: BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; MHBR, Museum d'Histoire Naturelle du Havre, Brun Collection, Le Havre, France; MLP, Museo de La Plata, La Plata, Argentina; MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, Spain; NHMUK, Natural History Museum, London, UK; PMO, Natural History Museum, University of Oslo, Paleontological collections, Oslo, Norway; USNM, Smithsonian Institution.

2. Material and methods

The holotype of *Maledictosuchus riclaensis* (MPZ 2001/130) consists of a nearly complete skull and mandible (MPZ 2001/130 a) and three vertebrae (MPZ 2001/130 b, c, d) assigned to a cervical vertebra, dorsal vertebra and caudal vertebra. The material is housed at the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ-2001/130).

We undertook a phylogenetic analysis to establish whether the data from the vertebrae modified the phylogenetic position of *M. riclaensis*. The analysis was based on the matrix of Parrilla-Bel *et al.* (2013), only adding the vertebrae data (5 characters were recoded). It included 74 taxa coded for 240 characters, with the non-crocodylomorph pseudosuchian archosaur *Postosuchus kirkpatricki* used as the outgroup taxon. The same methodology was also used for the analyses in TNT v 1.1 (Willi Hennig Society Edition; Goloboff *et al.*, 2008); tree-space was searched using new technology search methods: sectorial search, tree fusion, ratchet and drift, for 1,000 random addition replicates. The default settings for the advanced search methods were changed to increase the iterations of each method per replicate: 100 sectorial search drifting cycles, 100 ratchet iterations, 100 drift cycles and 100 rounds of tree fusion per replicate. This tree-space search procedure was repeated for five different random start seeds. Bremer supports and bootstrap frequencies (1000 bootstrap replicates) were used to assess the robustness of the nodes. An additional round of TBR (Tree Bisection Reconnection) branch swapping was carried on the 143 MPTs obtained in the new technology search.

The analysis was carried out with the following characters ordered: 1, 7, 8, 10, 13, 25, 38, 39, 42, 43, 47, 50, 56, 58, 69, 86, 87, 96, 126, 132, 133, 151, 152, 154, 156, 166, 179, 181, 182, 183, 184, 198, 202, 214, 218, 225, 228, 230, 231 and 237. All characters were equally weighted.

The data matrix and the list of characters are provided as supplementary material.

Note that character 186 has been emended. The apomorphy of metriorhynchids is state (1) instead of state (0) as was said in Young *et al.* (2012) and Parrilla-Bel *et al.* (2013).

3. Results

3.1 Description and comparison.

Cervical vertebra (MPZ 2001/130b)

The vertebra, although incomplete, is very well preserved, and lacks post-mortem deformation (Fig. 1). Part of the neural spine and the left diapophysis are missing. MPZ 2001/130 b is interpreted as a cervical vertebra, cervical vertebrae *sensu* Andrews (1913) being the vertebrae in which the parapophyseal process is located on the centrum and not associated with the neural arch.

The anterior articular face is nearly circular and the posterior is oval, being slightly higher than wide (Figs. 1a-c). Both faces are moderately concave (i.e. amphicoelous vertebra), the posterior face more so. The vertebral centrum is 40 mm in length and hourglass-shaped in ventral view, highly depressed in the midpoint, a common character among metriorhynchids (Andrews, 1913; Young *et al.*, 2013). Ventrally there is a longitudinal median keel. The anterior and posterior borders of the centrum are raised into a series of fine rugosities for the attachment of ligaments (Andrews, 1913; Schwarz-Wings, 2013).
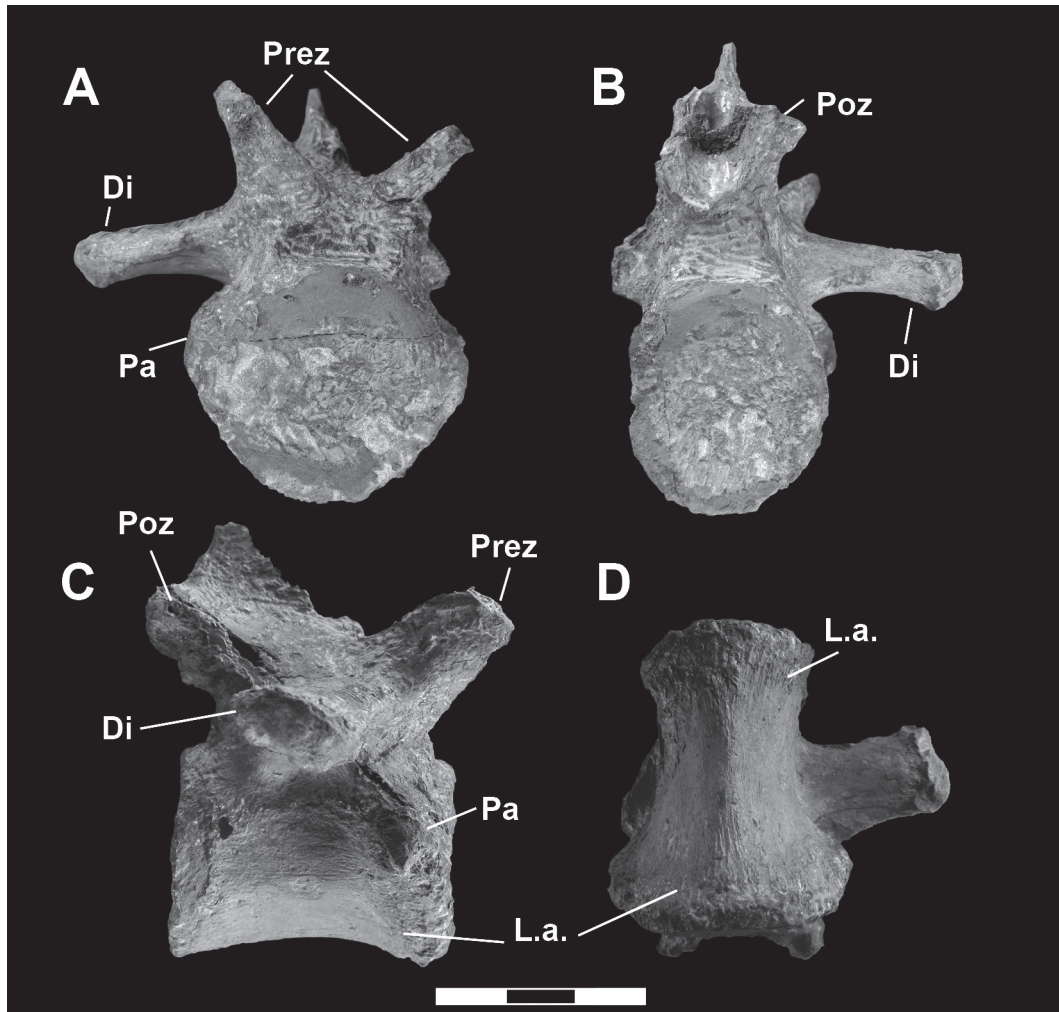
Fig. 1.- Cervical vertebra of *Maledictosuchus riclaensis* holotype (MPZ 2001/130 b). A, anterior view. B, posterior view. C, right lateral view. D, ventral view. Scale bar = 3 cm. Abbreviations: Di, diapophysis; L.a., ligament attachment; Pa, parapophysis; Poz, postzygapophysis; Prez, prezygapophysis.

The diapophyseal processes are associated with the neural arch, located on the base of the neural spine. The left diapophysis is lower than the prezygapophyses and is elongated, forming the transverse process. The transverse process has an overall length of ca. 25 mm and an oval cross-section, dorsoventrally flattened, with a maximum diameter of 14 mm. It is horizontal and slightly caudolaterally directed. The parapophyses, which are very short, are situated anteriorly, on both sides of the anterior articular face, and up on the centrum. They are anteroventrally to dorsocaudally oval in outline, forming a strong prominence immediately beneath the neurocentral suture, as described in Andrews (1913).

The prezygapophyses are large and strongly developed, projecting considerably beyond the centrum, each with a flat articulation surface, as in *Torvoneustes carpenteri* (Wilkinson *et al.*, 2008). The angle between the articulation surface and the sagittal plane is approximately 40 degrees. The postzygapophyses are worse preserved and closer together than the prezygapophyses. They also project beyond the centrum, but not as far as the prezygapophyses. Only the base of the neural

spine is preserved, and it is located on the posterior two thirds of the vertebral centrum. The neurocentral suture is closed.

Metriorhynchids have five post-axial cervical vertebrae (Fraas, 1902; Andrews, 1913; Steel, 1973). Herrera *et al.* (2013b) describe a variation in the cervical vertebrae of *Cricosaurus araucanensis*, with an increase in the length and width of the centra and the size of the parapophyses and diapophyses, and movement of the parapophyses from a lateroventral position in the centrum to a laterodorsal position. Wilkinson *et al.* (2008) also describe differences for *Torvoneustes carpenteri* between the first cervical vertebrae and the last one, which is at the boundary between the cervicals and the dorsals. The first four cervical vertebrae have the parapophyses in an anterior position and towards the base of the centrum, while in the fifth cervical vertebra, both the diapophyses and parapophyses have moved up the centrum (Wilkinson *et al.*, 2008), and the diapophyses are horizontal, and not directed downwards as in the more anterior cervical vertebrae. MPZ 2001/130 b closely resembles the fifth cervical vertebra of *Torvoneustes carpenteri* referred in Wilkinson *et al.* (2008). However, this

vertebra in *T. carpenteri* is much shorter than high and wide, while MPZ 2001/130b is longer (Fig. 2).

Dorsal vertebra MPZ 2001/130 c

MPZ 2001/130 c is practically complete and very well preserved (Fig. 3). It has been identified as a dorsal vertebra on the basis of the position of the parapophyses and diapophyses, both of which join to form the transverse processes and are born from the neural arch (Andrews, 1913; Young *et al.*, 2013).

The vertebra is amphicoelous, with the posterior articular face markedly concave. Other metriorhynchids, such as *Tyrannoneustes lythrodectikos*, have the anterior articular face more concave than the posterior one (Young *et al.*, 2013). Both articular faces are rounded and slightly higher than wide. The vertebral centrum is approximately 40 mm in length and hourglass-shaped in ventral view, concave ventrally and laterally, and highly constricted in the middle, with a minimum width of 14 mm. The ventral surface is very narrow, but rounded (i.e., it lacks a small keel like the cervical vertebra has). The neural spine is vertical, and its base is placed posteriorly on the centrum. The dorsal margin of the neural spine is slightly mediolaterally broadened.

The parapophyses are located entirely on the neural arch, together with the diapophyses, forming a step-like prominence on the anterior edge of the transverse process, as in other metriorhynchids (Andrews, 1913; Wilkinson *et al.*, 2008) (Fig. 4). The parapophyses are 15 mm in length, and the diapophyses, 45 mm. The transverse process is born on the base of the neural spine and is ventrally bent.

The prezygapophyses and postzygapophyses are less developed than the zygapophyses of the cervical vertebra, with a smaller articulation surface. Both the pre- and the postzygapophyses project slightly beyond the centrum.

In the first dorsal vertebra the parapophyses pass partially onto the neural arch, and the diapophyses and parapophyses are still separated (Andrews, 1913; Wilkinson *et al.*, 2008; Herrera *et al.*, 2013b). MPZ 2001/130 c would be at least the second dorsal vertebra: the parapophyses and diapophyses together form the transverse process and are wholly on the neural arch.

Caudal vertebra MPZ 2001/130d

This vertebra is also amphicoelous, but with the anterior articular face more concave than the posterior. The face is rounded and a bit wider than high (approximately 32 mm wide and 26 mm high). The length of the centrum, 40 mm, is greater than the width (Fig. 5).

The left transverse process has been preserved. It is much flattened dorsoventrally. The transverse process is born from the anteroventral region of the centrum and is ventrally deflected, projecting slightly below the centrum. It is 23 mm long.
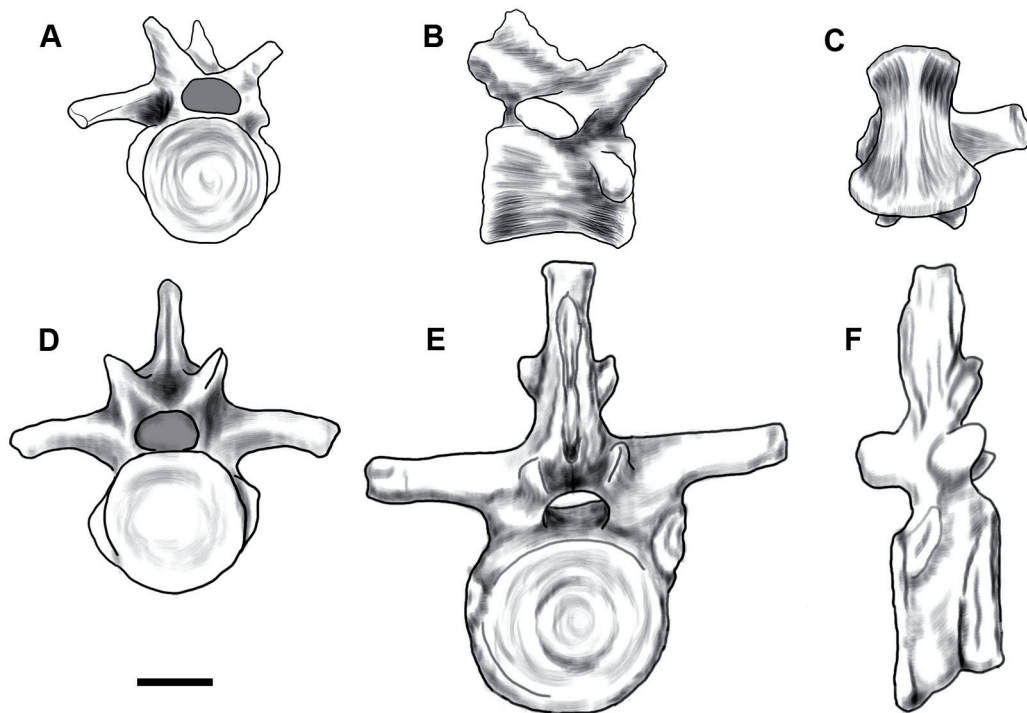

Fig 2.- Comparative plate of metriorhynchid fifth cervical vertebra. A-C, *Maledictosuchus riclaensis* (MPZ 2001/130 b). A, anterior view. B, right lateral view. C, ventral view. D, *Metriorhynchus* sp. (MHBR 1020), anterior view (redrawn from Hua, 1993: pls. 1-3; referred there as dorsal vertebra). E-F, *Torvoneustes carpenteri* (BRSMG Cd7203; from Wilkinson *et al.*, 2008). E, anterior view. F, left lateral view. Scale bar = 2 cm.
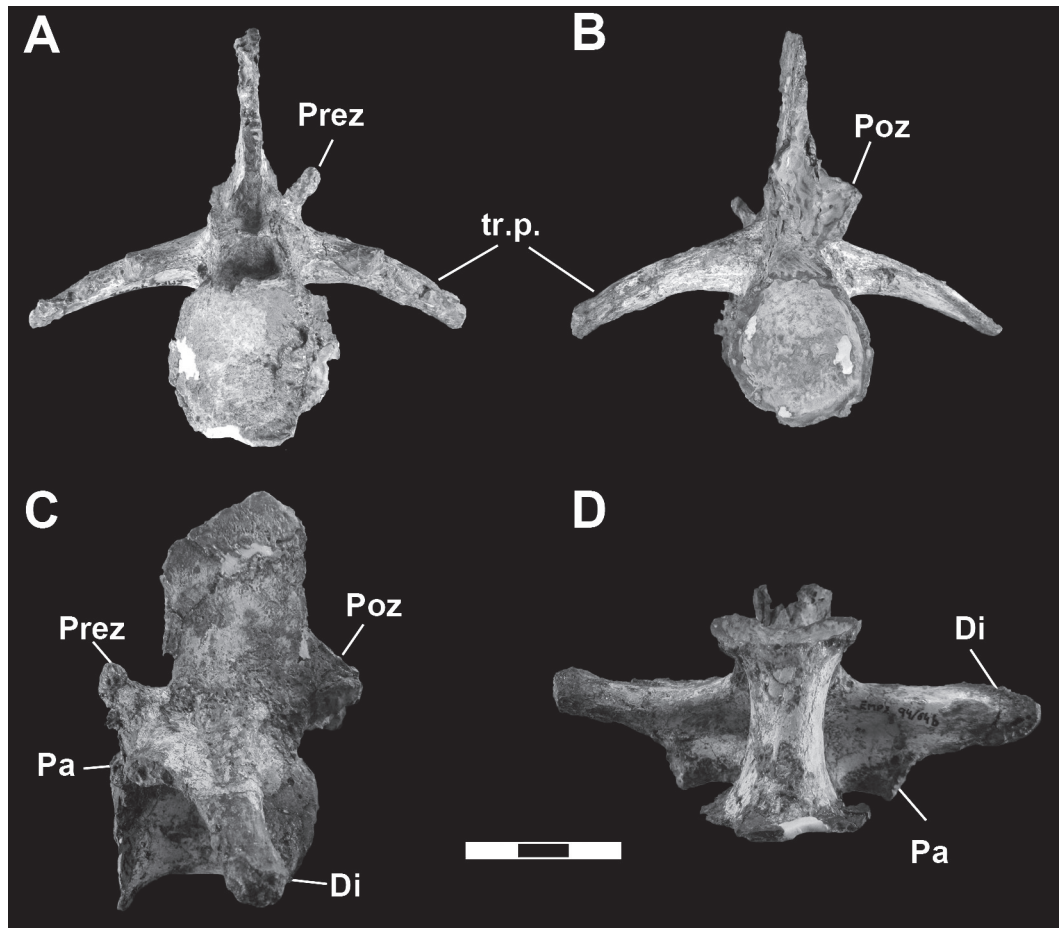
Fig 3.- Dorsal vertebra of *Maledictosuchus riclaensis* holotype (MPZ 2001/130 c). A, anterior view. B, posterior view. C, left lateral view. D, ventral view. Scale bar = 3 cm. Abbreviations: Di, diapophysis; Pa, parapophysis; Poz, postzygapophysis; Prez, prezygapophysis; tr.p. transverse process.

Ventrally the centrum is hourglass-shaped, but the constriction is not as noticeable as in the cervical and dorsal vertebrae. There are two anteroposteriorly directed crests in the ventral region and a marked longitudinal ventral groove in the middle. One of the articular faces for the haemal arch (chevron) has been preserved in the left posterior region, which obliquely truncates the ventral ridge, as described by Andrews (1913).

The neural spine is tall and vertically oriented. It is thicker at the base than the spine of the dorsal vertebra MPZ 2001/130c. It is poorly preserved, and it is not possible to see if it had an anterior notch on the anterodorsal portion, as described by Fraas (1902) for *Rhacheosaurus* and also seen in *C. araucanensis* and *C. suevicus* (Herrera *et al.*, 2013b) (Fig. 6). The neurocentral suture is closed.

The prezygapophyses are small and very close together. They project slightly beyond the articular face. Only the left postzygapophysis is partially preserved.

MPZ 2001/130d is a caudal vertebra. It has transverse processes that are dorsoventrally flattened and ventrally deflected, fused to the centrum, and a tall and vertically oriented neural spine. Transverse processes (caudal ribs) are described for the first vertebrae in *Cricosaurus araucanensis* (at least 12 vertebrae), the first 17 in *Metriorhynchus superciliosus*, the

first 11 in *C. suevicus* (Herrera *et al.*, 2013b) and for the first 13-14 in Oxford Clay metriorhynchids (Andrews, 1913).

3.2 Phylogenetic analysis

Five characters associated with the vertebrae have been re-coded. The results of the analysis maintain the phylogenetic position of *Maledictosuchus riclaensis*, and the strict consensus is identical to that of Parrilla-Bel *et al.* (2013) (Fig. 7).

The phylogenetic analysis (with forty ordered characters) returned 143 trees and the additional TBR round raises this number (best score hit once per replication) to 390 most parsimonious cladograms (length = 680, CI = 0.472, RI = 0.860, RC = 0.406). The number of most parsimonious cladograms has increased with respect to Parrilla-Bel *et al.* (2013) due to the additional TBR round performed, and the length of the tree has grown by one step. Bremer support and bootstrap values are also very similar to the values obtained in Parrilla-Bel *et al.* (2013), but the thalattosuchian node is better supported (Bremer = 8).

Among the characters associated with the vertebrae, character 181 should be highlighted. This character describes the relationship between the centrum length *versus* the centrum width of the cervical vertebrae. The geosaurini (*Me-*
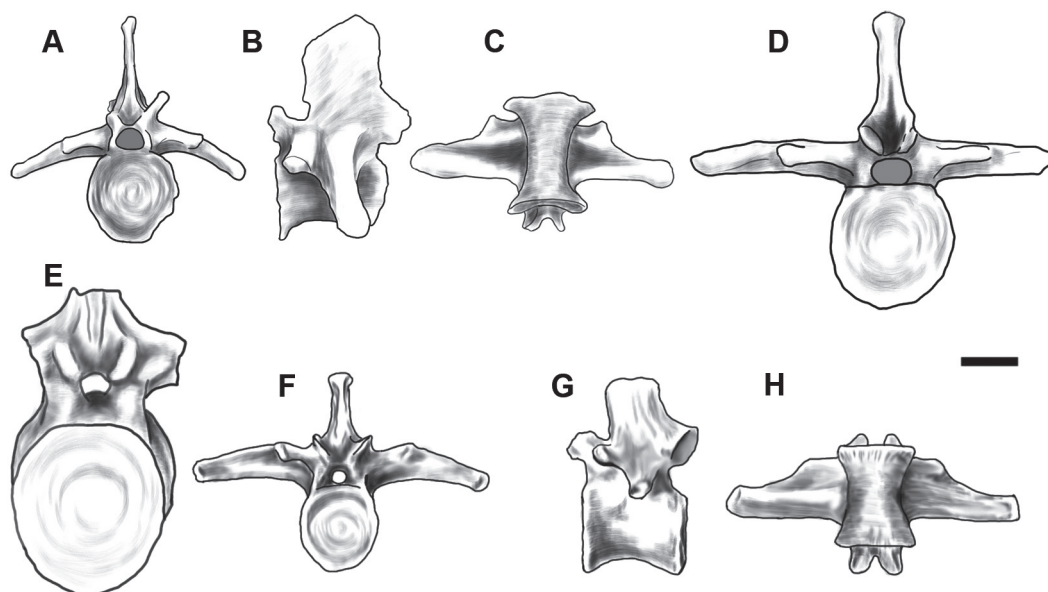
Fig 4.- Comparative plate of metriorhynchid dorsal vertebra. A-C, *Maledictosuchus riclaensis* (MPZ 2001/130 c). A, anterior view. B, left lateral view. C, ventral view. D, *Metriorhynchus* sp. (MHBR 1020), anterior view (redrawn from Hua, 1993: pls. 1-9). E, *Torvoneustes carpenteri* (BRSMG Cd7203; from Wilkinson *et al.*, 2008), anterior view. F-H *Metriorhynchus superciliosus* (NHMUK R. 2054; from Andrews, 1913: fig. 62; scale unavailable). F, Anterior view. G, Left lateral view. H, Ventral view. Scale bar = 2 cm.
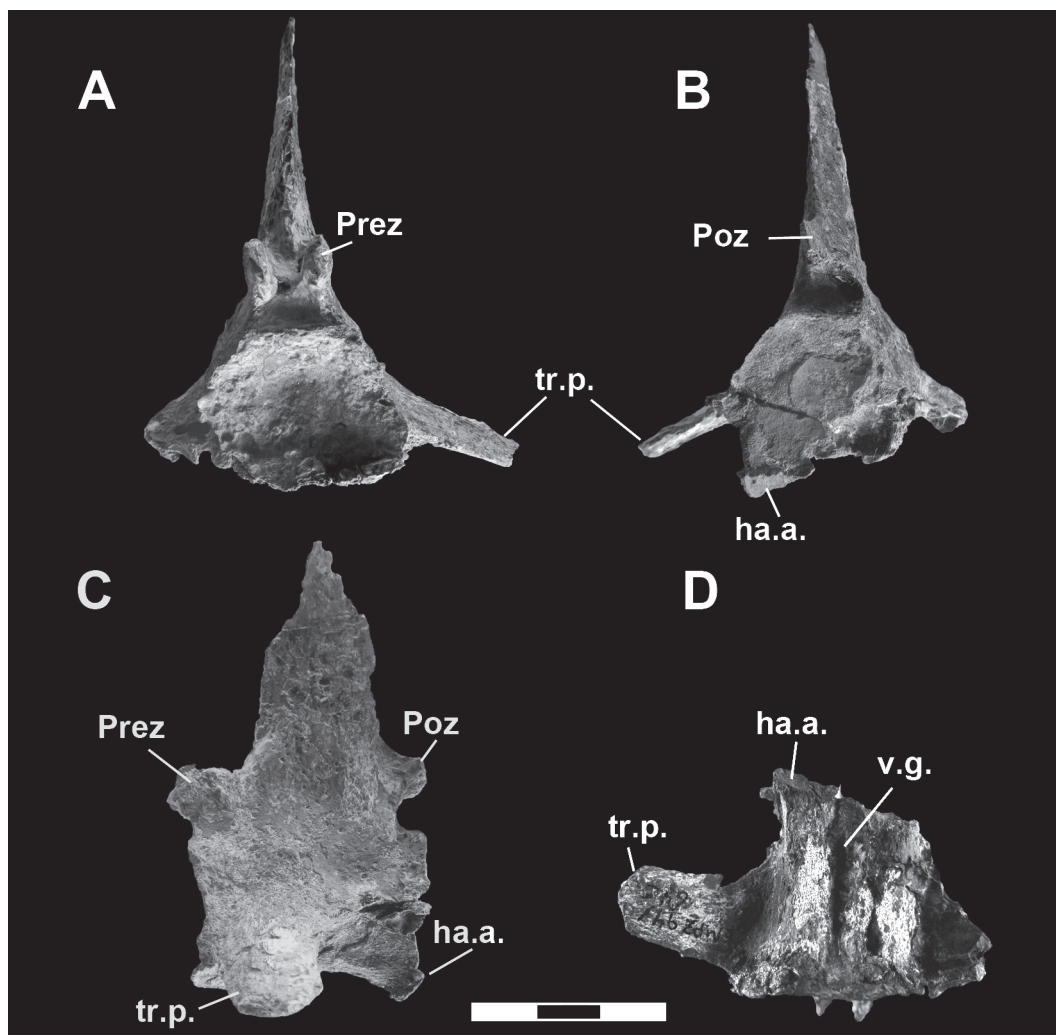

Fig. 5.- Caudal vertebra of *Maledictosuchus riclaensis* holotype (MPZ 2001/130 d). A, anterior view. B, posterior view. C, left lateral view. D, ventral view. Scale bar = 3 cm. Abbreviations: ha.a, haemal arch articulation; Poz, postzygapophysis; Prez, prezygapophysis; tr.p. transverse process; v.g., ventral groove.

triorhynchus brachyrhynchus, Neptunidraco ammoniticus, Tyrannoneustes lythrodectikos, Torvoneustes carpenteri, Geosaurus lapparenti and *Dakosaurus maximus*) are coded [1] (centrum length and width subequal), whereas the metriorhynchines (*Cricosaurus suevicus, Cricosaurus gracilis, Rhacheosaurus gracilis* and *Metriorhynchus superciliosus*) are coded [2] (centrum length less than centrum width). *M. riclaensis* is coded [0] (centrum longer than wide), as are

other non-metriorhynchid thalattosuchians and other non-thalattosuchian crocodylomorphs.

4. Discussion

As has been said above, the vertebrae among thalattosuchians are not very diagnostic at generic or specific level. As with all other thalattosuchians the vertebrae of *M. riclaen-*
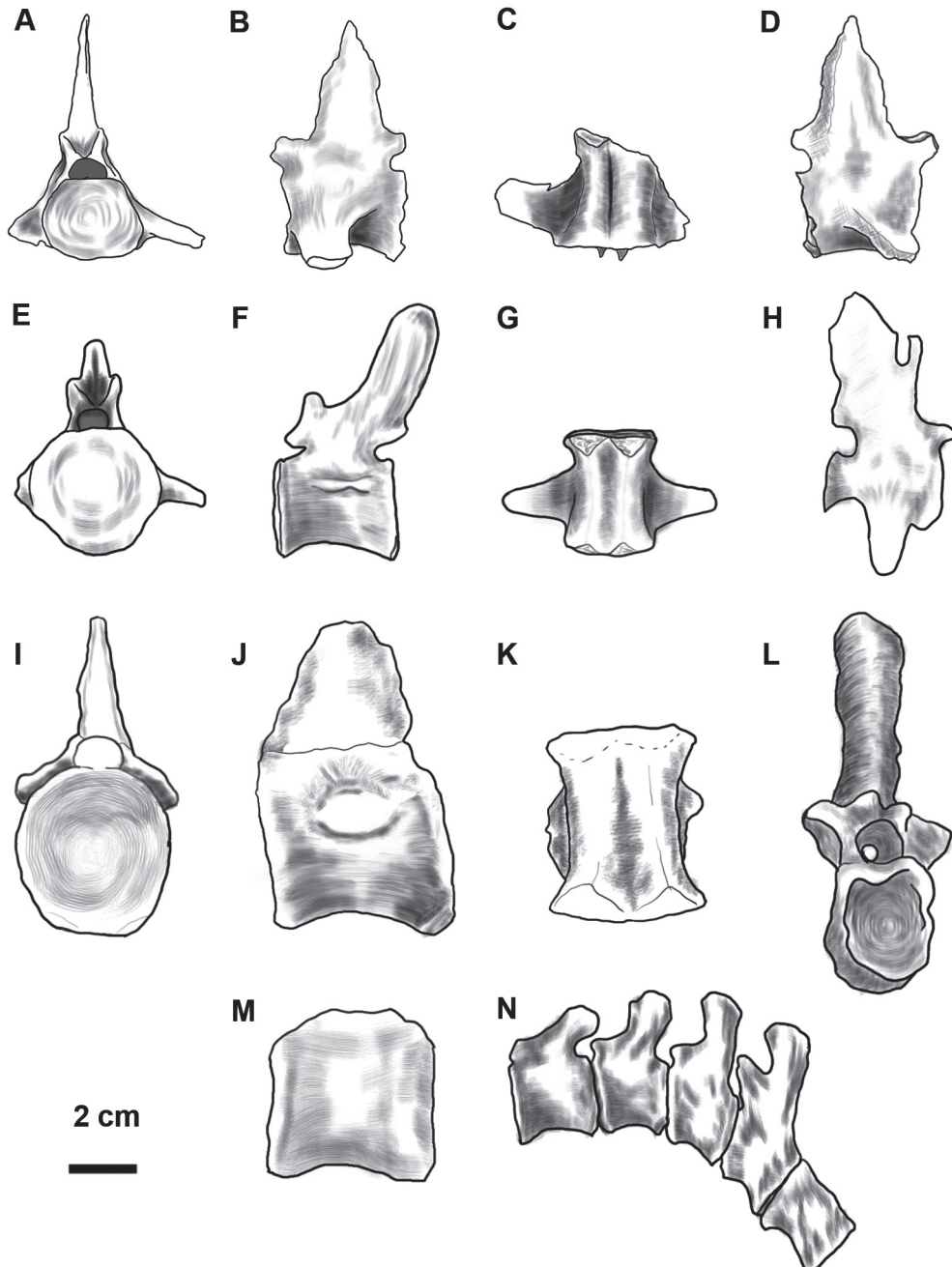

Fig 6.- Comparative plate of metriorhynchid caudal vertebra. A-D, *Maledictosuchus riclaensis* (MPZ 2001/130 d). A, anterior view. B, left lateral view. C, ventral view. D, right lateral view. E, *Metriorhynchus* sp. (MHBR 1020), anterior view (redrawn from Hua, 1993: pls. 1-12). F, Anterior caudal of *Metriorhynchus laeve* (NHMUK R. 3014), left lateral view (redrawn from Andrews, 1913: fig. 65A; scale unavailable). G-H, *Cricosaurus araucanensis* (MLP 72-IV-7-1), G, ventral view. H, left lateral view (redrawn from Herrera *et al.*, 2013b). I-K, Thalattosuchia indet. I, posterior view. J, left lateral view. K, ventral view (redrawn from Buffetaut and Thierry, 1977: pl. 9-3, pl. 8-4). L, Metriorhynchidae indet. (EII-II-6(749), anterior view (redrawn from Hua *et al.*, 1998). M, *Torvoneustes carpenteri* (BRSMG Cd7203), lateral view (redrawn from Wilkinson *et al.*, 2008). N, vertebrae at bend of tail of *Metriorhynchus laeve* (NHMUK R. 3014), left lateral view (redrawn from Andrews, 1913: fig. 65D; scale unavailable). Scale bar = 2 cm.
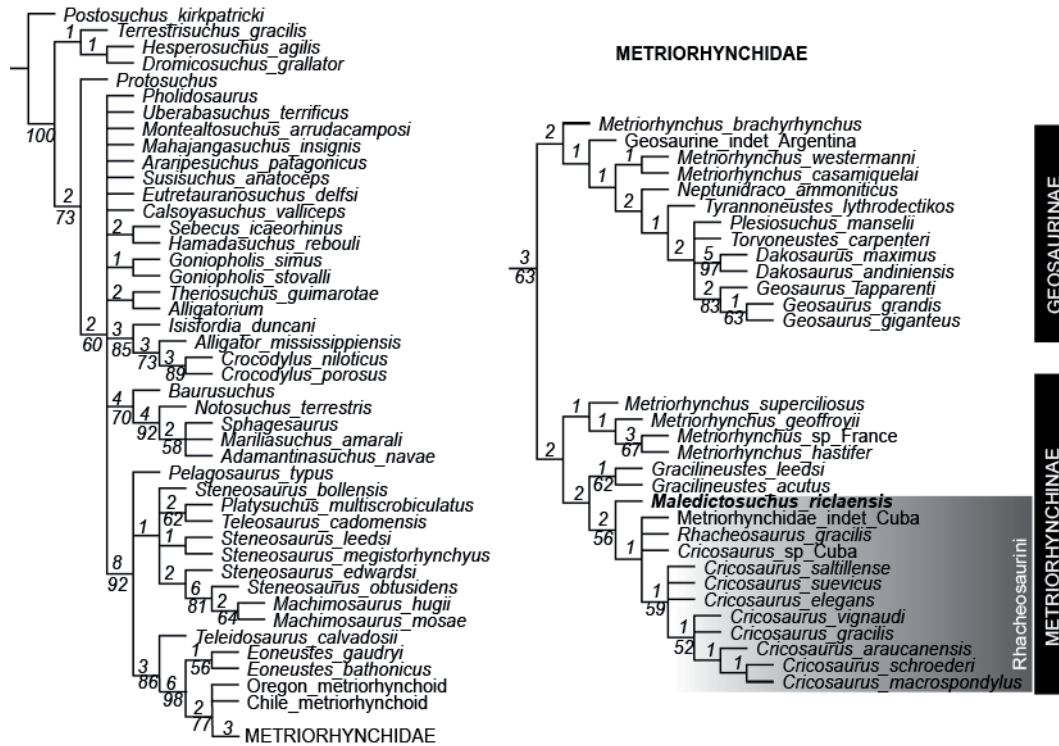
Fig. 7.- Strict consensus of 143 most parsimonious cladograms of 680 steps, showing the phylogenetic relationships of *Maledictosu-chus riclaensis* within Metriorhynchidae with forty ordered characters. Ensemble consistency index, CI = 0.412; ensemble retention index, RI = 0.860; rescaled consistency index, RC = 0.406. Numbers over lines represent Bremer support values. Numbers under lines represent bootstrap values (only values over 50% represented).

sis present the following apomorphies: amphicoelous centra, diapophyseal and parapophyseal processes well developed, lack of hypapophyses (Young *et al.*, 2012). The dimensions and shape of the vertebrae of *M. riclaensis* closely resemble those described for *C. araucanensis* (Herrera *et al.*, 2013b). The three vertebrae (MPZ 2001/130 b, c, d) have articular faces that are circular to oval in shape, and the vertebral bodies are hourglass-shaped in ventral view, with the lateral and ventral faces concave, especially markedly in the dorsal vertebra. This hourglass-shape is observed e.g. in *Tyrannoneustes* (Young *et al.*, 2013), *Metriorhynchus* (Andrews, 1913) and *Torvoneustes carpenteri* (Wilkinson *et al.*, 2008), and also in other thalattosuchians such as *Machimosaurus* (Buffetaut, 1982; Martin & Vincent, 2013) and *Pelagosaurus typus* (Mueller-Töwe, 2006).

Interestingly, the cervical vertebra of *M. riclaensis* is long (longer than wide). The centrum length is slightly less than 1.5 times the centrum width (see character 181), but the difference is relatively small and it has been coded [0]. Maybe the description of this character should be redefined, or a new state between [0] and [1] included. Either way, this would be an autapomorphy of *M. riclaensis*. However, more specimens with well-preserved vertebral series should be analysed to confirm the matter.

MPZ 2001/130 c shares the typical metriorhynchid morphology. However, referral of MPZ 2001/130 d, significantly different from other metriorhynchid vertebra, is more difficult. It has a chevron facet, which indicates that it is a caudal

vertebra. Metriorhynchid material from the posterior axial column is scarce. Caudal series have a very large number of vertebrae which differ greatly from one another in different parts of the tail (Andrews, 1913) (see Fig. 6) and there are few specimens with a complete axial skeleton to compare it.

The proportions of the centrum (length is greater than width and height), the absence of foramina for nutritive vessels, and the morphology and position of the transverse processes rejects its assignation to other Jurassic marine reptiles such as ichthyosaurs or plesiosaurs (Fig. 8).

MPZ 2001/130 d shares some characters with the anterior caudal vertebrae of *Cricosaurus* (Herrera *et al.*, 2013b) and Oxford Clay metriorhynchids (Andrews, 1913). The vertebrae are longer than wide, constricted in the middle (hourglass-shaped), with caudal ribs strongly compressed from above downward and ventrally deflected, and small zygapophyses. They also have two ventral ridges, which are obliquely truncated by the chevron facets in the posterior region (Andrews, 1913), or in the anterior and posterior (Herrera *et al*., 2013b). However, while in Oxford Clay metriorhinchids the ventral surface between these lateral ridges is flat, MPZ 2001/130 d has a median groove that divides the ventral surface in the two longitudinal rounded crests (Fig 6). The detailed description of the *M. riclaensis* vertebrae provides new information about this species, and helps to increase our knowledge of thalattosuchian crocodylomorphs. In addition, the neurocentral sutures are completely obliterated, as in mature crocodylians (Brochu, 1996; Herrera *et al.,* 2013b),
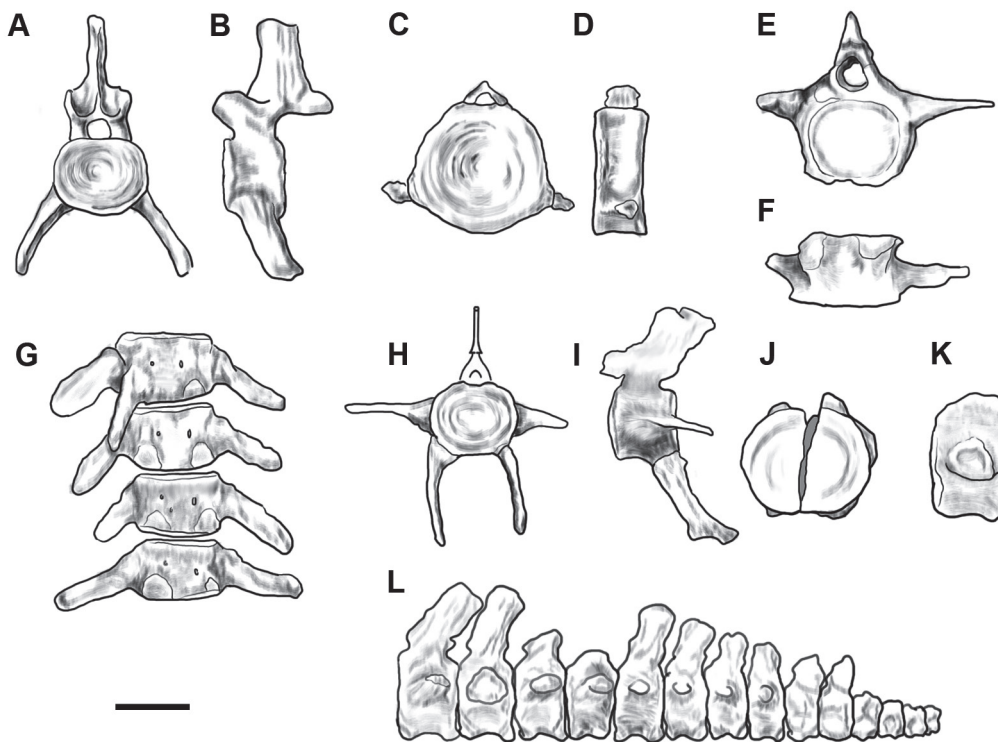
Fig 8.- Comparative plate of Jurassic marine reptile vertebrae. A-B, Anterior cervical vertebra of *Cryptoclidus oxoniensis* (NHMUK R. 2412). A, anterior view. B, left lateral view. C-D, Anterior caudal vertebra of *Ophthalmosaurus* (NHMUK R. 3534). C, anterior view. D, lateral view (A-D redrawn from Andrews, 1910: figs. 79A-B; 27 A-B respectively; scale unavailable). E-F, Caudal vertebra of *Colymbosaurus svalbardensis* (PMO 216.838) (redrawn from Knutsen *et al*., 2012: figs. 4 A, D). E, posterior view. F, ventral view. G-I, Caudal vertebrae of *Pantosaurus striatus* (USNM 536965) (redrawn from Wilhelm and O'Keefe, 2010: figs. 4 and 5, bottom row). G, 5th to 8th caudal vertebrae in ventral view. H, 7th caudal vertebra in posterior view. I, 7th caudal vertebra in left lateral view. J-K, 13th caudal vertebra of *Colymbosaurus svalbardensis* (PMO A 27745) (redrawn from Andreassen, 2004). J, anterior view. K, lateral view. L, Posterior caudal vertebrae of *Cryptoclidus oxoniensis* (R 3705) from left lateral view (redrawn from Andrews, 1910: fig. 85A). Scale bar = 5 cm.

confirming that the *Maledictosuchus riclaensis* holotype was an adult specimen, as suggested in Parrilla-Bel *et al.* (2013).

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