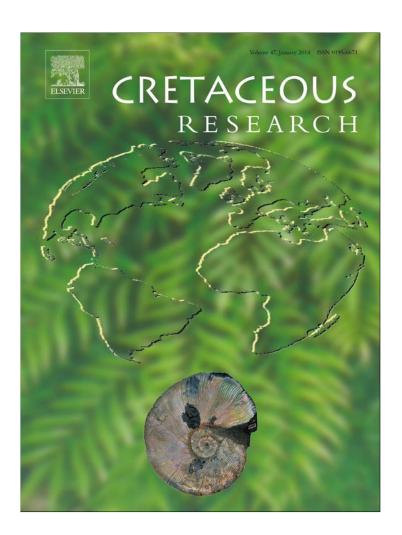
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Reappraisal of *Tuarangisaurus? cabazai* (Elasmosauridae, Plesiosauria) from the Upper Maastrichtian of northern Patagonia, Argentina



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ARTICLE INFO

Article history: Received 9 June 2013 Accepted in revised form 15 October 2013 Available online 4 December 2013

Keywords: Elasmosauridae Aristonectinae Weddellian Province

ABSTRACT

The holotype of *Tuarangisaurus*? *cabazai* Gasparini, Salgado and Casadio, 2003 (Elasmosauridae, Plesiosauria) from the Upper Maastrichtian Jagüel Formation (northern Patagonia, Argentina) is redescribed, its taxonomic status is reconsidered, and its phylogenetic relationships analysed. We conclude that it must be referred as an aristonectin elasmosaurid. The complete ilium of an Aristonectinae is described for the first time, and reveals a distinctive proximodistally elongated facet in its distal end. Aristonectins are the most commonly recorded Weddellian elasmosaurids. There is a high proportion of osteologically immature individuals ("juveniles") within the investigated sample of specimens. Most of these are larger than other juvenile elasmosaurids, and apparently retain juvenile features at larger body sizes.

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1. Introduction

The Argentinean record of elasmosaurids is mostly Campanian—Maastrichtian in age, and virtually restricted to the Río Negro and Chubut provinces, Patagonia (Gasparini and de la Fuente, 2000; Gasparini and Salgado, 2000; Gasparini et al., 2003a,b; Gasparini et al., 2007; O'Gorman et al., 2013). However, in spite of this rather abundant record, most specimens are identifiable only at familial level, in part due to the lack of well preserved cranial material (Gasparini et al., 2007).

Gasparini et al. (2003b) described a new species, *Tuarangisaurus? cabazai*, on the basis of a juvenile represented by an almost complete postcranium (MML PV 5), collected from the Upper Maastrichtian Jagüel Formation, in Bajo de Trapalcó, Río Negro Province (Fig. 1). This generic assignation was based on the similarity between the holotype (MML PV 5) and two juvenile specimens from New Zealand (NZGS CD 427, NZGS CD 428) referred to cf. *Tuarangisaurus keyesi* by Wiffen and Moisley (1986, figs 7–31). Sato et al. (2006: 479) considered these specimens to be not diagnostic of *Tuarangisaurus*. This consideration, coupled with doubts raised

on the validity of the diagnostic characters of *Tuarangisaurus? cabazai*, prompted Gasparini et al. (2007) to reassign MML PV 5 to Plesiosauroidea indet.

O'Gorman et al. (2013) stated that certain elasmosaurid juvenile specimens could be referred to Aristonectes cf. parvidens based on the proportions of the cervical centra. Specifically, these authors referred the MUC Pv 131, collected from the Upper Campanian-Lower Maastrichtian Allen Formation (Río Negro Province), and previously referred to Tuarangisaurus by Gasparini et al. (2003b), to Aristonectes cf. parvidens. Otero and O'Gorman (2013) applied the same criterion to refer the SGO 260, an almost complete juvenile specimen from the Upper Maastrichtian beds of the Quiriquina Formation (central Chile), to Aristonectes sp. Later, Otero et al. (2013), nominated Aristonectes quiriquinensis from the Upper Maastrichtian of Chile, to which SGO 260 was assigned. The presence of juvenile cervicals with the same proportions seen in material recovered in New Zealand (J.P.O'G, pers. obs. 2013), where Kaiwhekea Cruickshank and Fordyce, 2002 but not Aristonectes Cabrera, 1941 has been recorded, indicates that the distinctive proportions are probably diagnostic only at subfamilial level. Therefore, the affinities of the specimens described by O'Gorman et al. (2013) and Otero and O'Gorman (2013) probably need to be reviewed. However the assignation of MUC Pv 131 to Aristonectinae remains valid.

The Aristonectinae has a complex taxonomical and nomenclatural history. O'Keefe and Street (2009) created the family Aristonectidae

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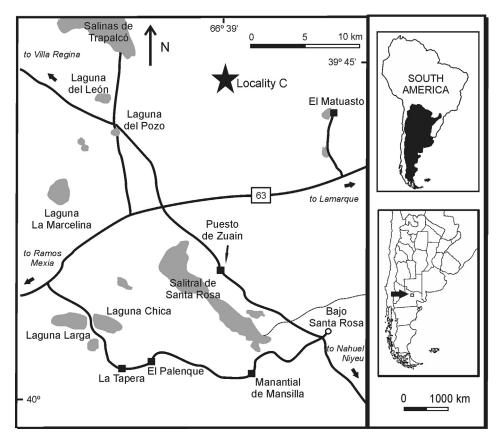


Fig. 1. Geographic position of the locality C sensu Gasparini et al. (2003b) where the investigated specimen of Aristonectinae gen. et sp. indet. was collected (modified from Salgado et al., 2007).

comprising Aristonectes parvidens, Kaiwhekea katiki, Tatenectes laramiensis and Kimmerosaurus langhami. Later phylogenetic analysis (Ketchum and Benson, 2010, 2011; Benson and Druckenmiller, 2013) do not recover the Aristonectidae sensu O'Keefe and Street (2009). Otero et al. (2012) nominated the Aristonectinae within the Elasmosauridae, which is comprised only by the Late Cretaceous elasmosaurids Kaiwhekea katiki, Aristonectes parvidens and Futabasaurus suzukii. The position of Futabasaurus suzukii grouped with Kaiwhekea katiki and Aristonectes parvidens has not been supported by recent phylogenetic analysis of Kubo et al. (2012). Therefore, we restrict here the composition of the Aristonectinae as grouping Kaiwhekea katiki and Aristonectes parvidens. These two elasmosaurids are characterised by very distinctive features among the Elasmosauridae, such as large skulls with increased number of teeth and short cervical centra in the anterior an medial zone of the neck.

Under the ICZN (1999: article 50.3.1): "The authorship of the name of a nominal taxon within the family group, genus group or species group is not affected by the rank at which it is used". Therefore, the change from "Aristonectidae" to Aristonectinae, which maintains the genus *Aristonectes* as part of it, do not change the authorship, that is O'Keefe and Street in both cases. However, the Aristonectinae are here used in a sense more similar to the expressed by Otero et al. (2012), as is indicated in the Systematic Paleontology section.

The main goals of this article are to redescribe the holotype of *Tuarangisaurus? cabazai* Gasparini, Salgado and Casadío, 2003b (MML PV 5), and to discuss its nomenclatural status and systematic affinities.

2. Geological setting

The Late Cretaceous transgression in northern Patagonia is recorded in the Malargüe Group, which in the Río Negro Province

is composed, from base to top, by the Allen, Jagüel and Roca formations (Uliana and Dellapé, 1981). The Jagüel formation covers the Allen Formation (Late Campanian—Early Maastrichtian in age) composed of sandstones, mudstones, limestones and evaporites deposited in a littoral to restricted marine environment (Uliana and Dellapé, 1981). It is covered by the shallow marine calcareous facies of the Roca Formation, assigned to the Maastrichtian—Danian on the basis of its fossil content (Casadío et al., 1998; Parras et al., 1998).

In the area of Salinas de Trapalcó, where the MML PV 5 was collected (Fig. 1), the Jagüel Formation consists of massive to laminated shales which are deposited in a shallow inner to middle shelf environment (Concheyro et al., 2002). In this area, the Jagüel Formation yielded scarce Maastrichtian marine bivalves as well as a very rich association of calcareous nannofossils that indicate a Late Maastrichtian age, CC26 Biozone (Concheyro et al., 2002).

The Jagüel Formation has produced species of Chondrichthyes such as *Serratolamna*, *Cretalamna* and *Odontaspis* and Osteichthyes as *Enchodus* (Bogan and Agnolin, 2010); elasmosaurids (Gasparini et al., 2007) and mosasaurs such as *Mosasaurus* sp. aff. *M. hoffmanni*, *Plioplatecarpus* sp., and *Prognathodon* sp. (Fernández et al., 2008; Fernández and Gasparini, 2012).

3. Material and methods

3.1. Material

The investigated material is housed in several institutions which are abbreviated as follows: AM, Australian Museum, Sydney, Australia; AMNH, American Museum Natural History, New York, USA; CIT, California Institute of Technology, California, USA; MLP, Museo de La Plata, Buenos Aires Province; MML, Museo Municipal

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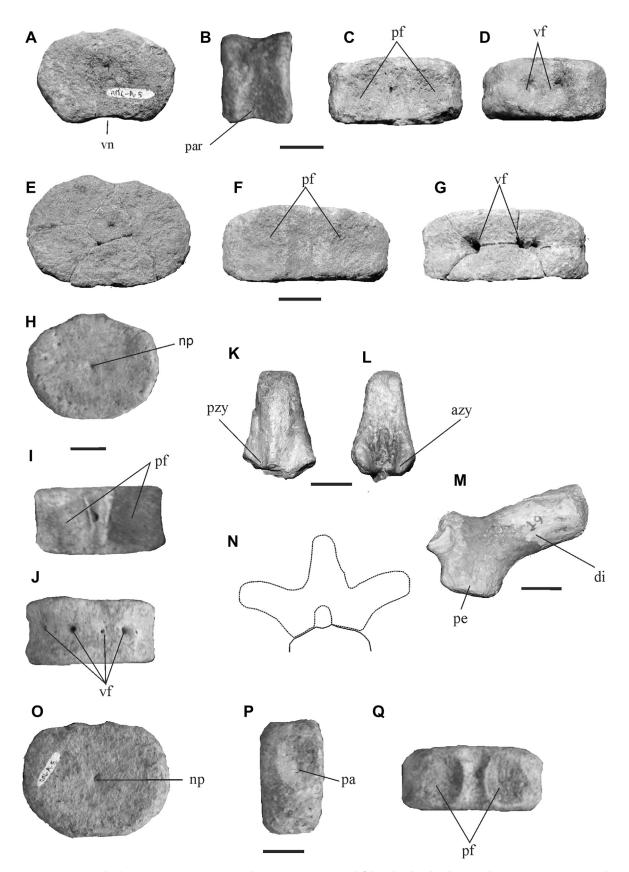


Fig. 2. Aristonectinae gen. et sp. indet. (MML PV 5). A—D, anterior cervical centrum in A, anterior, B, left lateral, C, dorsal, and D, ventral views. E—G, posterior cervical centrum in E, anterior, F, dorsal and G, ventral views. H—J, dorsal centrum in H, anterior I, dorsal and J, ventral views. K—N, dorsal neural arch, neural spine in K, posterior and L, anterior views and M, N, diapophysis and pedicel. O—Q, caudal centra in O, anterior, P, lateral and Q, dorsal views. Scale bars represent 20 mm.

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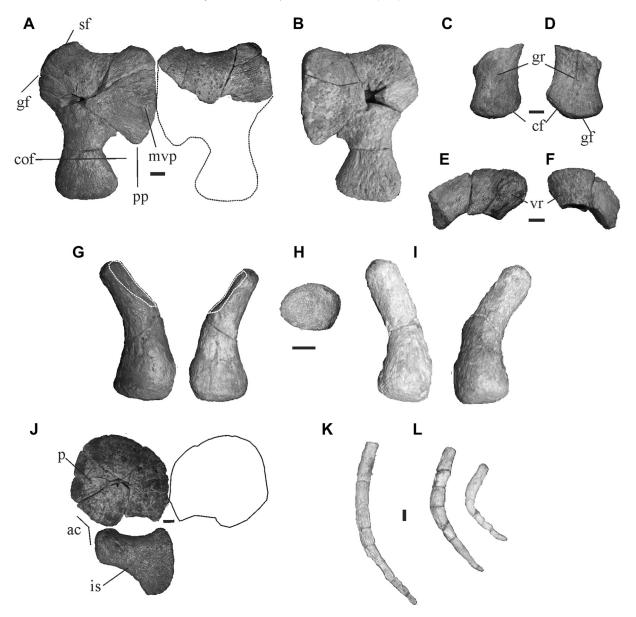


Fig. 3. Aristonectinae gen. et sp. indet. (MML PV 5). A–B, coracoids in A, ventral, and B, dorsal views. C–D, glenoid ramus of the right scapula in C, ventral and D, dorsal views. E–F, ventral ramus of left scapula in E, dorsal and F, ventral views. G–I, ilia in G, left and right ilia in medial view, H, right ilium in proximal view and I, right and left ilium in lateral view. J, pubis and ischium in dorsal view. K, dorsal rib; L, gastralia. Scale bars represent 20 mm.

de Lamarque, Río Negro Province, Argentina; MUC, Museo de la Universidad del Comahue, Neuquén Province, Argentina; NZGS, New Zealand Geological Survey, Lower Hutt, New Zealand; TTU, Museum of Texas Tech University, Texas, USA.

3.2. Methods

The vertebral indices considered in the present description are those proposed by Welles (1952), which take into account the vertebral centrum proportions, specifically height (H)/length (L) ratio (HI = 100^*H/L) and breadth (B)/length (L) ratio (BI = 100^*B/L). Moreover, the breadth/height ratio (BHI = 100^*B/H) is also recorded. Breadth and height were measured on the posterior articular face. Also, the Vertebral Length Index [VLI = $100^*\text{L/}(0.5^*(\text{H} + \text{B}))$] was used (Brown, 1981). The B:L index (Welles, 1952), which records the ratio between the distal breadth and total length of propodials, is also considered.

Bivariate graphics, used previously by O'Gorman et al. (2013) and Otero and O'Gorman (2013), were considered to further improve the description. These bivariate graphics allow making comparisons between the proportions of vertebrae independently from their position in the sequence. The ontogenetic categories proposed by Brown (1981), which are based on the fusion of the neural arch to the vertebral centrum, were also used.

Anatomical abbreviations: azy, anterior zygapophyses; ac, acetabular facets; cap, capitulum; cf, coracoid facet; cof, cordiform fenestra; gf, glenoid facet; gr, glenoid ramus; is, ischium; mvp, mid ventral process; np, notochordal pit; pa, parapophyses; pf, pedicellar facet; pp, posterior process; pzy, posterior zygapophyses; p, pubis; sf, scapular facet; vf, ventral foramina; vn, ventral notch; vr, ventral ramus.

4. Systematic paleontology

Sauropterygia Owen, 1860

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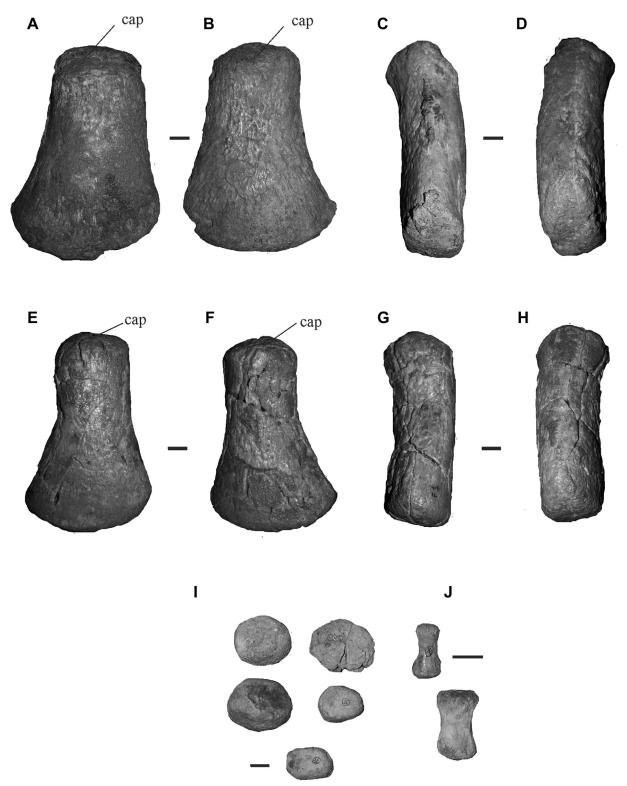


Fig. 4. Aristonectinae gen. et sp. indet. (MML PV 5). A-D, right humerus in A, dorsal, B, ventral, C, posterior and D, anterior views. E-H, right femur in E, dorsal, F, ventral, G, posterior and H, anterior views. I, four epipodials/tarsal/carpal indeterminate elements. J, phalanges. Scale bars represent 20 mm.

Plesiosauria de Blainville, 1835 Plesiosauroidea Welles, 1943 Elasmosauridae Cope, 1869 Aristonectinae O'Keefe and Street, 2009 (sensu Otero et al., 2012)

Aristonectinae gen. et sp. indet.

(Figs. 2-4)

2003b Tuarangisaurus? cabazai Gasparini et al., figs 5-7 2007 Plesiosauroidea indet. Gasparini et al., fig. 7

Material. MML PV 5. A postcranial skeleton comprising nineteen complete cervical centra, seventeen dorsal and nine caudal centra, other indeterminate vertebral remains, ribs and gastralia, a

complete right coracoid and fragments of the left coracoid, part of both scapulae, both ischia, ilia and pubis, and incomplete fore and hindlimbs.

Locality and horizon. MML PV 5. Salinas de Trapalcó, Locality C of Gasparini et al. (2003b). Upper part of the Jagüel Formation, Upper Maastrichtian (Fig. 1).

Description

Axial skeleton. Nineteen cervical centra were preserved complete. Some remains of neural arches are preserved, but since the neuro-central sutures are open, these were found separated from the cervical centra. All the cervical centra are broader than high than long (Table 1). The pedicellar facets are circular to square shaped in outline. The anteriormost preserved cervical centra have

Table 1 Aristonectinae gen. et sp. indet. (MML PV 5). Measurements of L, length; H, height and B, breadth (all in mm), indexes HI, height (H)/length (L) ratio (HI = $100^*\text{H}/\text{L}$), BI, breadth (B)/length (L) ratio (BI = $100^*\text{B}/\text{L}$), BHI, breadth/height ratio (BHI = $100^*\text{B}/\text{H}$) and VLI, Vertebral Length Index [VLI = $100^*\text{L}/(0.5^*(\text{H} + \text{B}))$] and number of ventral foramina (Num. For.) of vertebral centra. The order given is relative because the skeleton was found disarticulated, values in italics are aproximated.

	L	Н	В	HI	BI	BHI	VLI	Num. For.
Cervical	19	22	30	115.8	157.9	136.4	73.1	2
	19	22	32	115.8	168.4	145.5	70.4	?
	18	21	31	116.7	172.2	147.6	69.2	2?
	20	24	31	120.0	155.0	129.2	72.7	2
	19	22	31	115.8	163.1	140.9	71.7	2?
	20	25	34	125.0	170.0	136.0	67.8	2
	20	25	35	125.0	175.0	140.0	66.7	?
	20	26	37	130.0	185.0	142.3	63.5	?
	21	31	46	147.6	219.1	148.4	54.6	?
	24	35	50	145.8	208.3	142.9	56.5	2?
	25	37	53	148.0	212.0	143.2	55.6	2
	26	38	56	146.2	215.4	147.4	55.3	2
	26	40	58	153.9	223.1	145.0	53,1	2
	28	41	57	146.5	203.6	139.0	57.1	2?
	26	42	60	161.6	230.8	142.9	50.9	2
	27	45	65	166.7	240.7	144.5	49.1	2
	26	46	69	177.0	265.4	150.0	45.2	2
	31	_	72	_	232.3	_	_	2
_	35	58	70	165.0	200.0			?
Dorsal	31	53	70	171.0	225.9	132.1	50.4	2
	31	54	69	174.2	222.6	127.8	50.4	2?
	34	_	70	_	205.9	_	_	4
	33	59	66	178.8	200.0	111.9	52.8	?
	28	49	70	175.0	250.0	142.9	47.1	3
	31	51	69	164.6	222.6	135.3	51.7	3
	31	49	69	158.1	222.6	140.8	52.5	2
	30	51	69	170.0	230.0	135.3	50.0	2
	33	56	71	169.7	215.1	126.8	52.0	3
	33	56	67	169.70	203.0	119.6	53.7	?
	32	57	67	178.1	209.4	117.5	51.7	?
	32	55	70	171.9	218.8	127.3	51.2	3
	35	56	72	160.0	205.7	128.6	54.7	3
	33	55	70	166.7	212.1	127.3	52.8	4
	33	59	70	178.8	212.1	118.6	51.2	3
	35	55	76	157.1	217.1	138.2	53.4	4
	35	54	74	154.3	211.4	137.0	54.7	4
Caudal	24	53	69	220.4	287.5	130.2	39.3	2
	26	56	66	215.4	253.9	117.9	42.6	3
	25	55	66	220.0	264.0	120.0	41.3	1
	27	51	59	188.9	218.5	115.7	49.1	2
	27	50	63	185.2	233.3	126.0	47.8	3
	28	51	62	182.1	221.4	121.6	49.6	?
	28	50	71	178.6	253.6	142.0	46.3	2
	25	50	60	200.0	240.0	120.0	45.5	3
	26	50	42	192.3	161.5	84.0	56.5	1

articular faces with a ventral notch, which makes the articular faces dumbbell-shaped (Fig. 2A), a feature typical of Late Cretaceous elasmosaurids (Hiller et al., 2005; Ketchum and Benson, 2011). This ventral notch is absent in the posteriormost cervical centra; therefore, the articular faces are elliptical in these vertebrae (Fig. 2E). All cervical vertebrae have amphiplatyan vertebral centra. There are deeply excavated facets for the parapophyses on the ventrolateral sides of the centra (Fig. 2B). Also, there are two foramina located in a ventral depression in the anteriormost preserved cervical centra, whereas in the middle to posterior ones the ventral foramina are not located in a ventral depression (Fig. 2D, G).

Seventeen dorsal vertebrae are preserved, some of which are represented by the disarticulated neural arch and centrum. All the dorsal centra are broader than high and higher than long (Table 1). The pedicellar facets are square in outline and laterally inclined (Fig. 21). One or two foramina are observed on the floor of the neural canal (Fig. 21). The articular faces are elliptical but with their dorsal parts divided in three parts: the two laterals correspond to the pedicellar facets and the medial third to the base of the neural canal (Fig. 2H). There is a notochordal pit in the centre of the articular faces (Fig. 2H). The lateral sides of the centra are slightly concave anteroposteriorly (Fig. 2I, J). Ventrally, there are two to four foramina (Fig. 2]).

The neural arches are stocky elements with rounded pedicels and a cylindrical diapophysis (Fig. 2M, N). The neural spines are short with a posterior rounded keel (Fig. 2K, L).

There are nine preserved caudal vertebrae. Their centra are broader than high than long (Table 1). There is one foramen on the floor of the neural canal. The pedicelar facets are circular (Fig. 2Q) and the articular faces are roughly octagonal (Fig. 2O). The central zone of the lateral surface of the centrum is occupied by a rounded articular facet for the parapophysis (Fig. 2P).

The dorsal ribs have a circular or elliptical cross-section, with a slightly concave proximal end (Fig. 3K), whereas the gastralia are shorter and are strongly bent (Fig. 3L).

Appendicular skeleton. Scapulae and coracoids are partially preserved (Fig. 3A–D). The scapulae are represented only by the proximal part of the glenoid ramus of the right element and the distal margin of the ventral ramus of the left one (Fig. 3C–F). The glenoid ramus is stocky (Fig. 3C, D). It is proximally limited by the coracoid and glenoid facets which are angled approximately 130° relative to each other (Fig. 3C, D). The anterior margin of the ventral ramus is strongly convex (Fig. 3E).

The coracoid has the typical shape observed in elasmosaurids (Hiller et al., 2005; Ketchum and Benson, 2011; Welles, 1943, 1962). The glenoid ramus bears the scapular and glenoid facets, which form an angle of approximately 130° (Fig. 3A, B). The anterior margin, between the glenoid ramus and the anterior process, is concave (Fig. 3A, B). The symphysial surface (Fig. 3A) is anteroposteriorly long and exhibits a mid ventral process located in the medial margin of the ventral surface (Fig. 3A). There is a rounded posterior process (Fig. 3A). The posterior ramus limits the cordiform fenestra (Fig. 3A).

Both pubes, ischia and ilia are preserved (Fig. 3G—J). The pubis is rounded and stocky, broader than long (Fig. 3J). The anterior margin is strongly convex without an anterolateral projection (Fig. 3J). A pelvic bar is absent.

The ischia have the typical "inverted L-shape" and is anteroposteriorly not elongated (Fig. 3J). The thickest zone corresponds to the acetabulum. The acetabular and pubic facets form an angle of approximately 140° (Fig. 3J).

The ilia are rounded and stocky elements with a bent shaft (Fig. 3G–I). The proximal zone near the acetabular and ischiadic facets is thickened (Fig. 3G–I). The distal zone is laterally

Table 2Aristonectinae gen. et sp. indet. (MML PV 5). Measurements of the right humerus (in mm) and femur and B:L index (100*distal breadth/total length).

Measurements (mm)	Right humerus	Right femur	
Length	193	185	
Distal breadth	140	125	
Proximal breadth	83	69	
B:L index	73	68	

compressed, with a long proximodistal facet but with no evident anteroposterior expansion (Fig. 31).

Both humeri and femora have been preserved (Fig. 4A—H). The humerus is rounded, stocky, and dorsoventrally compressed (Fig. 4A—D, Table 2). The proximal end forms the capitulum, but the trochanter is not differentiated (Fig. 4A—D). The distal end is anteroposteriorly expanded, the posterior expansion being the largest one (Fig. 4A, B).

The femur is stocky and dorsoventrally compressed, proportionally similar to the humerus but slightly shorter and more gracile (Fig. 4E—H, Table 2). The proximal end forms the capitulum, but as in the humerus, a trochanter is not differentiated (Fig. 4E—H). The distal end of the femur is anteroposteriorly expanded, the posterior expansion being larger than the anterior one (Fig. 4E, F).

Probably, all epipodial and mesopodial elements are preserved, but since the specimen was disarticulated it is impossible to identify each one. All these elements have rounded margins without articular facets. The phalanges have the typical hour-glass morphology.

5. Discussion

In previous description of the MML PV 5, the smallest vertebral centra preserved were considered as caudals (Gasparini et al., 2003b). However, some of these centra are cervicals because their dumbbell-shaped articular faces and ventrolateral parapophyses are features recorded only in the cervical vertebrae of Elasmosauridae (i.e., Ketchum and Benson, 2011; Benson and Druckenmiller, 2013). In addition, a centrum interpreted as sacral by Gasparini et al. (2003b, fig 5D, E) is here reinterpreted as a caudal. Thus, MML PV 5 is referable to elasmosaurids due to the presence of dumbbell-shaped articular faces and a coracoid with a posterior cordiform fenestra (i.e., Ketchum and Benson, 2011).

The neural arches of the MML PV 5 are not fused to their centra, which indicates a juvenile condition sensu Brown (1981). The absence of closed suture between the ribs and vertebral centra, the rounded edges of the bones, and the poorly defined articular faces of the appendicular bones are also consistent with a juvenile condition (Brown, 1981).

Determination of juvenile elasmosaurids is very difficult because of the great ontogenetic variation observed in these reptiles (Brown, 1981; Wiffen and Moisley, 1986; Carpenter, 1999). Nonetheless, some information about the affinities of the MML PV 5 can be obtained using bivariate graphs based on cervical central proportions (O'Gorman et al., 2013; Otero and O'Gorman, 2013). The bivariate diagram of the Fig. 5 shows the plotting of the cervical vertebrae of MML PV 5. Two interesting results are noteworthy: 1) the cervical centra of MML PV 5 are split into two

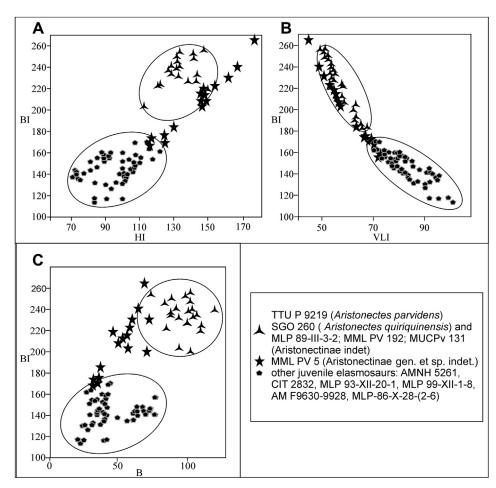


Fig. 5. Bivariate diagrams of cervical centra, values of juveniles of Aristonectinae and other elasmosaurids. A, HI-BI, B, VLI-BI, C, BI-B.

groups, and 2) differences in the HI and BI index between MML PV 5 and specimens referred to Aristonectinae (Fig. 5A). However, at the same time, the vertebral proportions of MML PV 5 show strong differences with the proportions of the cervical vertebrae of other juvenile Elasmosauridae, which indicates that MML PV 5 does not have the typical vertebral proportions of a non-Aristonectinae Elasmosauridae. The existence of two proportionally different groups of cervical centra in MML PV 5 is due to differences between the vertebrae in various regions of the neck, which, on the other hand, have already been recorded in other Elasmosauridae (Welles, 1952; O'Keefe and Hiller, 2006). We ignore whether the observed differences between the other Aristonectinae specimens (MML 89-III-3-2, MML PV 192, MUC Pv 131) and MML PV 5 are ontogenetic (the MML PV 5 is an extremely juvenile specimen), or if they have some systematic value at generic or specific level. Pending the discovery of additional more diagnostic material, we here refer all these specimens, including MML PV 5, as to indeterminate genus and species of Aristonectinae.

Until now, only two species of Aristonectinae from South America have been recorded: *A. parvidens* Cabrera, 1941 (see Gasparini et al., 2003a for a review) and a new species described by Otero et al. (2013), distinguished mostly by features of the cranium, mandible and atlas—axis complex. Consequently, postcranial features are a poor means to distinguish these two species.

The juvenile stage of the closely related species, *Kaiwhekea katiki*, from the Lower Maastrichtian of New Zealand, is unknown since the holotype and only known specimen is an adult (Cruickshank and Fordyce, 2002); hence, a direct comparison with MML PV 5 is not feasible. However, it is possible to compare MML PV 5 with SGO 260, an almost complete postcranium of juvenile Aristonectinae from Chile (Otero et al., 2012). Particularly interesting is the fact that the lateral margin of the pubis of the MML PV 5 is almost straight (Fig. 6B), while in SGO 260 it is strongly concave (Fig. 6A). Moreover, the pubis of MML PV 5 is proportionally shorter anteroposteriorly with respect to that of SGO 260. In the same way, the anterior margin of the ischium of MML PV 5 is distinctly less concave than the one of SGO 260. There is some evidence indicating

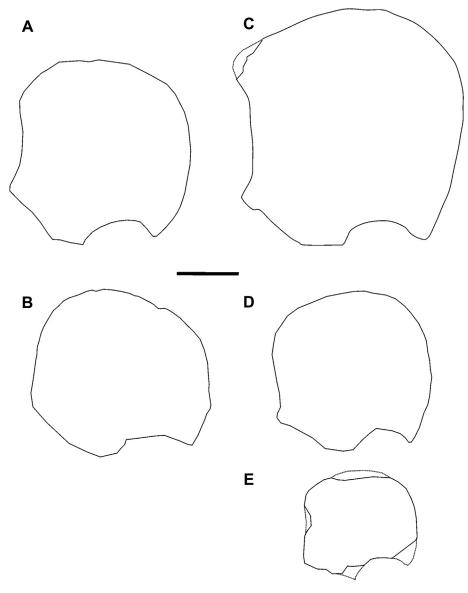


Fig. 6. Comparison of pubis of elasmosaurids. A—B, Aristonectinae, A, Aristonectes quiriquinensis (SGO 260) and B, Aristonectinae gen. et sp. indet. (MML PV 5). C—E, possible growth series of pubis referred to Elasmosauridae indet. C, CD 438, D, CD 439 and E, CD 440. Scale bar represents 100 mm.

that these differences might be ontogenetic because a similar trend: that is an anteroposterior elongation and the increased of the lateral marginal concavity correlated with an increasing size, has been recorded by Wiffen and Moisley (1986) for pubes of juvenile elasmosaurids from the Campanian—Maastrichtian interval of the Mangahouanga Stream, New Zealand (Fig. 6C—E).

Aristonectinae is the most common Weddellian Late Cretaceous plesiosaur clade. It has been recorded in the Maastrichtian of Chile, Upper Maastrichtian of the Antarctic Peninsula and Upper Campanian—Maastrichtian of Patagonia, Argentina (Gasparini et al., 2003a; O'Gorman et al., 2013; Otero and O'Gorman, 2013).

The abundance of juveniles is another interesting feature of the South American aristonectins record because seven of the nine known specimens of this clade are juveniles (sensu Brown, 1981), but most of them are not as small as other juvenile elasmosaurids (see Fig. 5C). There are two possible explanations for this pattern: first, these juvenile (sensu Brown, 1981) are actually adult but retain juvenile features; or second, adult specimens reach larger sizes (and standard "adult features") than other elasmosaurids. The only three aristonectin adult specimens (sensu Brown, 1981) known have estimated body sizes of 7–8 m in length, extremely robust necks and tails, and osteological features related with an adult condition (Cruickshank and Fordyce, 2002; Gasparini et al., 2003b; Otero et al., 2013), which indicates that the second explanation is the most probable.

Acknowledgements

We thank Daniel Cabaza, the staff of the Museo Municipal de Lamarque and the Municipality of Lamarque for technical and logistical support; Ewan Fordyce (Otago University, New Zealand); Paul Scofield (Canterbury Museum) and John Simes (National Paleontology Collection, GNS Science Avalon, New Zealand) for allowing us to review the elasmosaurids from those institutions. We also thank Dr. Norton Hiller for help during the revision of some specimens from Canterbury Museum. We thank Paula Arregui (Universidad Nacional de La Plata) and Michael J. Everhart (Sternberg Museum of Natural History, USA) for improvement of the English grammar of this article. This research was supported by PICT 2008-0261, PIP 0433, UNLP N 607, and PICT 2012-0748.

References

- Benson, R.B.J., Druckenmiller, P.S., 2013. Faunal turnover of marine tetrapods during the Jurassic—Cretaceous transition. Biological Reviews (in press). http://dx.doi. org/10.1111/brv.12038.
- Blainville de, H.D., 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'Erpétologie et d'Amphibiologie. Nouvelles Annales du Muséum (National) d'Histoire Naturelle, Paris 4, 233–296.
- Bogan, S., Agnolin, F.L., 2010. Primera ictiofauna marina del Cretácico Superior (Formación Jagüel, Maastrichtiano) de la provincial de Río Negro, Argentina. Papéis Avulsos de Zoologia 50, 175—188.
- Brown, D.S., 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauroidea. Bulletin of the British Museum of Natural History (Geology) 35, 253–347.
- Carpenter, K., 1999. Revision of North American elasmosaurs from the Cretaceous of the Western Interior. Paludicola 2, 148–173.
- Cabrera, A., 1941. Un plesiosaurio nuevo del Cretáceo del Chubut. Revista del Museo de la Plata (Nueva Serie) 2, 113–130.
- Casadío, S., Parras, A., Concheyro, A., Pires, M., 1998. El diacronismo de la sedimentación carbonática en la cuenca Neuquina durante la transición Cretácico Paleógeno. Actas del VII Congreso Argentino de Paleontología y Bioestratigrafía, Bahía Blanca, p. 125.
- Concheyro, A., Náñez, C., Casadío, S., 2002. El límite Cretácico-Paleógeno en Trapalcó, provincia de Río Negro, Argentina, ¿una localidad clave en América del Sur?. 15° Congreso Geológico Argentino (El Calafate). Actas 1, 590–595.
- Cope, E.D., 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Transactions of the American Philosophical Society (New Series) 14, 1–252.

- Cruickshank, A.R., Fordyce, R.E., 2002. A new marine reptile (Sauropterygia) from New Zealand: further evidence for a Late Cretaceous austral radiation of cryptoclidid plesiosaurs. Palaeontology 45, 557–575.
- Fernández, M., Martin, J., Casadío, A., 2008. Mosasaurs (Reptilia) from the late Maastrichtian (Late Cretaceous) of northern Patagonia (Río Negro, Argentina). Journal of South American Earth Sciences 25, 176—186.
- Fernández, M.S., Gasparini, Z., 2012. Campanian and Maastrichtian mosasaurs from Antarctic Peninsula and Patagonia, Argentina. Bulletin de la Société Géologique de France 183, 93–102.
- Gasparini, Z., de la Fuente, M., 2000. Tortugas y plesiosaurios de la Formación La Colonia (Cretácico Superior) de Patagonia, Argentina. Revista Española de Paleontología 15. 23—35.
- Gasparini, Z., Salgado, L., 2000. Elasmosáuridos (Plesiosauria) del Cretácico Tardío del norte de Patagonia. Revista Española de Paleontología 15, 13–21.
- Gasparini, Z., Bardet, N., Martin, J.E., Fernández, M., 2003a. The elasmosaurid plesiosaur Aristonectes Cabrera from the latest Cretaceous of South America and Antarctica. Journal of Vertebrate Paleontology 23, 104–115.
- Gasparini, Z., Salgado, L., Casadio, S., 2003b. Maastrichtian plesiosaur from Northern Patagonia. Cretaceous Research 24, 157–170.
- Gasparini, Z., Salgado, L., Parras, A., 2007. Late Cretaceous plesiosaurs from northern Patagonia, Argentina. Geological Journal 42, 185–202.
- Hiller, N., Mannering, A.A., Jones, C.M., Cruickshank, A.R., 2005. The nature of Mauisaurus haasti Hector, 1874 (Reptilia: Plesiosauria). Journal of Vertebrate Paleontology 25, 588–601.
- International Commission on Zoological Nomenclature, 1999. International Code of Zoological Nomenclature, fourth ed. International Trust for Zoological Nomenclature, London.
- Ketchum, H.F., Benson, R.B., 2010. Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses. Biological Reviews 85, 361–392.
- Ketchum, H.F., Benson, R.B.J., 2011. A new pliosaurid (Sauropterygia, Plesiosauria) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: evidence for a gracile, longirostrine grade of Early—Middle Jurassic pliosaurids. Special Papers in Palaeontology 86, 109—129.
- Kubo, T., Mitchell, M.T., Henderson, D.M., 2012. Albertonectes vanderveldei, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. Journal of Vertebrate Paleontology 32, 557–572.
- O'Gorman, J.P., Gasparini, Z., Salgado, L., 2013. Postcranial morphology of *Aristonectes* (Plesiosauria, Elasmosauridae) from the Upper Cretaceous of Patagonia and Antarctica. Antarctic Science 25, 71–82.
- O'Keefe, F.R., Hiller, N., 2006. Morphologic and ontogenetic patterns in elasmosaur neck length, with comments on the taxonomic utility of neck length variables. Paludicola 5, 206–229.
- O'Keefe, F.R., Street, H.P., 2009. Osteology of the cryptocleidoid plesiosaur *Tatenectes laramiensis*, with comments on the taxonomical status of the Cimoliasauridae. Journal of Vertebrate Paleontology 29, 48–57.
- Otero, R.A., O'Gorman, J.P., 2013. Identification of the first postcranial skeleton of *Aristonectes* Cabrera (Plesiosauroidea, Elasmosauridae) from the upper Maastrichtian of the south-eastern Pacific, based on a bivariate graphic analysis. Cretaceous Research 41, 86–89.
- Otero, R.A., Soto-Acuña, S., Rubilar-Rogers, D., 2012. A postcranial skeleton of an elasmosaurid plesiosaur from the Maastrichtian of central Chile, with comments on the affinities of Late Cretaceous plesiosauroids from the Weddellian Biogeographic Province. Cretaceous Research 37, 89–99.
- Otero, R.A., Soto-Acuña, S., O'Keefe, F.R., O'Gorman, J.P., Stinnesbeck, W., Suárez, M.E., Rubilar-Rogers, D., Salazar, C., Quinzio-Sinn, L.A., 2013. *Aristonectes quiriquinensis* sp. nov., a new highly derived elasmosaurid from the upper Maastrichtian of central Chile. Journal of Vertebrate Paleontology (in press).
- Owen, R., 1860. On the orders of fossil and recent Reptilia, and their distribution in time. Reports of the British Association for the Advancement of Science 29, 153–166.
- Parras, A., Casadío, S., Pires, M., 1998. Secuencias depositacionales del Grupo Malargüe y el límite Cretácico Paleógeno, en el sur de la provincia de Mendoza, Argentina. In: Casadío, S. (Ed.), Paleógeno de América del Sur y de la Península Antártica, Publicación Especial 5. Asociación Paleontológica Argentina, Buenos Aires, pp. 61–69.
- Salgado, L., Parras, A., Gasparini, Z., 2007. Un plesiosaurio de cuello corto (Plesiosauroidea, Polycotylidae) del Cretácico Superior del norte de Patagonia. Ameghiniana 44, 349–358.
- Sato, T., Hasegawa, Y., Manabe, M., 2006. A new elasmosaurid plesiosaur from the Upper Cretaceous of Fukushima, Japan. Palaeontology 49, 467–484.
- Uliana, M., Dellapé, D., 1981. Estratigrafía y evolución paleoambiental de la sucesión maastrichtiana-eoterciaria del engolfamiento neuquino (Patagonia Septentrional). Actas del 88° Congreso Geológico Argentino 3, 673–711.
- Welles, S.P., 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. Memoirs of the University of California 13, 125–254.
- Welles, S.P., 1952. A review of the North American Cretaceous elasmosaurs. University of California. Publications in Geological Sciences 29, 47–144.
- Welles, S.P., 1962. A new species of Elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. University of California Publications in Geological Sciences 44, 1–89.
- Wiffen, J., Moisley, W.L., 1986. Late Cretaceous reptiles (Families Elasmosauridae and Pliosauridae) from the Mangahouanga Stream, North Island, New Zealand. New Zealand Journal of Geology and Geophysics 29, 205–252.