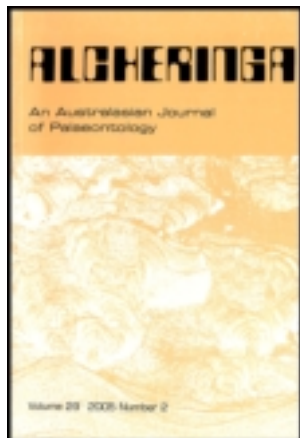


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Elasmosaurs (Sauropterygia, Plesiosauria) from the La Colonia Formation (Campanian–Maastrichtian), Argentina

JOSÉ P. O'GORMAN, LEONARDO, SALGADO, JULIO VARELA and ANA PARRAS

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Elasmosaur postcranial remains from the La Colonia Formation (Campanian–Maastrichtian), Chubut Province, Patagonia, Argentina, are described. The new material has small dimensions and caudal vertebrae with parapophyses strongly projected laterally—characters shared with some Elasmosauridae indet. from the coeval Allen Formation, Río Negro Province, Argentina. These features reinforce the similarities between the plesiosaur faunas to the north and south of the Somún Curá Plateau. The small size of these elasmosaurs may be palaeoecologically related to the marginal marine depositional environment of the sedimentary host rocks.

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Key words: Allen Formation, Upper Cretaceous, Elasmosauridae, Patagonia, palaeoecology.

PLESIOSAURS, one of the most successful groups of Mesozoic marine reptiles, are a clade of diapsid reptiles with adaptations to the marine environment. Plesiosaurs have been recorded in strata ranging from the Upper Triassic to the uppermost Cretaceous and they have been recorded on all continents including Antarctica (Welles 1952, 1962, Persson 1963, del Valle *et al.* 1977, Brown 1981, Carpenter 1996, 1999, Bardet *et al.* 1999, O'Keefe 2001, 2004, Kear 2003, Ketchum & Benson 2010). Although within this group, the Elasmosauridae constitute a major and widespread clade, the systematic relationships within the family are still disputed (Brown 1993, Storrs 1999, Sato 2002, O'Keefe 2001, 2004, Ketchum & Benson 2010). Nevertheless, all authors agree that the Late Cretaceous Elasmosauridae were cosmopolitan in distribution (Welles 1962, Gasparini *et al.* 1984, Wiffen & Moisley 1986, Chatterjee & Small 1989, Bardet *et al.* 1999, Carpenter 1999, Kear 2003, Hiller *et al.* 2005, Gasparini *et al.* 2007, Vincent *et al.* 2011, Kubo *et al.* 2012).

Typical elasmosaurs are characterized by a unique, extremely long cervical region that consists of: (1) a large number of vertebrae, (2) elongate vertebral centra, especially in the middle of the cervical region, (3) lateral ridges on the vertebral centra, and (4) dumbbell-

shaped articular faces in Late Cretaceous genera (Welles 1962, Brown 1981, 1993, Bardet *et al.* 1999, Carpenter 1999, O'Keefe 2001, 2004, Gasparini & Salgado 2000). These features allow the identification of elasmosaurs at the family level, even when the preserved material represents isolated cervical vertebrae (Wiffen & Moisley 1986, Werner & Bardet 1996, Gasparini & Salgado 2000).

Plesiosaurs from brackish or non-marine deposits have been reported by several authors (Cruikshank & Long 1997, Kear 2003, Sato *et al.* 2003, 2005, O'Gorman *et al.* 2011, Kear 2012). However, it is not certain whether these environments were their usual habitat.

Previous records of Late Cretaceous elasmosaurs in Patagonia, Argentina, derive from the lower levels of the Mata Amarilla Formation (Cenomanian), Allen and Loncoche formations (upper Campanian–lower Maastrichtian), La Colonia Formation (Campanian–Maastrichtian), Dorotea and Quiriquina formations (Maastrichtian), and Lefipán and Jagüel formations (upper Maastrichtian–Danian). Despite this abundant record, the systematics of the South American Late Cretaceous elasmosaurs is poorly resolved (Gasparini & Salgado 2000, Gasparini *et al.* 2001, 2003a, b, 2007, Previtera & González Riga 2008, Otero *et al.* 2009, O'Gorman & Varela 2010, O'Gorman *et al.* 2011, Varela *et al.* 2012).

Isolated plesiosaur remains from the La Colonia Formation were briefly reported by Ardolino & Delpino (1987), Page *et al.* (1999) and Pascual *et al.* (2000). Gasparini and de La Fuente (2000) described the polyotyloid plesiosaur *Sulcusuchus erraini* and mentioned the occurrence of elasmosaurs in the same stratigraphic levels. Later, Gasparini *et al.* (2001) described a single vertebra from the La Colonia Formation referred to Elasmosauridae.

In November 2011, a joint team formed by Z. Gasparini and J.P. O'Gorman (Museo de La Plata), L. Salgado (Universidad del Comahue), A. Parras and J. Varela (Universidad de La Pampa) and J. Sterli and P. Puerta (Museo Paleontológico 'Egidio Feruglio') collected a diverse vertebrate assemblage from the La

Colonia Formation, Chubut, Argentina (Fig. 1A, B), including three specimens referred to Elasmosauridae and described here. The aims of this paper are: (1) to describe the new elasmosaur material from the La Colonia Formation, (2) to compare these remains to other elasmosaurs from the Late Cretaceous of Patagonia, and (3) to discuss the possible link between small body size and a specific depositional environment.

Geological setting and studied section

The La Colonia Formation (Pesce 1979, Ardolino & Delpino 1987) crops out along the southeastern margin of the Somún Curá Plateau, Chubut Province, Argentina (Fig. 1A, B). In the Sierra de La Colonia area, a low

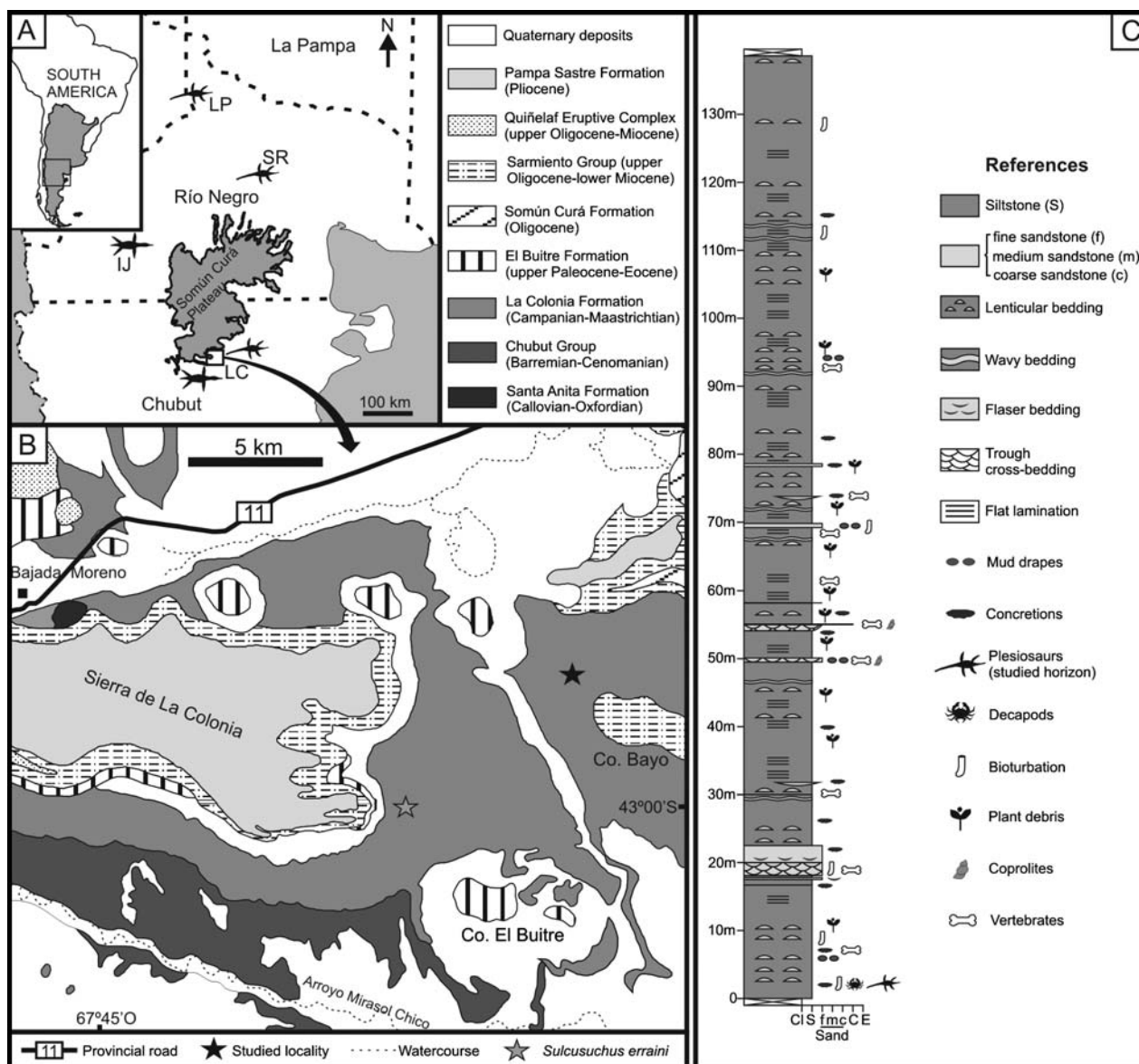


Fig. 1. A, General map showing the main localities hosting plesiosaurs in North Patagonia (LP, Lago Pellegrini; SR, Salitral de Santa Rosa; IJ, Ingeniero Jacobacci; LC, La Colonia, ★, elasmosaurs; ★, *Sulcusuchus erraini*). B, Detailed geological map of Sierra de La Colonia area showing the locality from which MPEF-PV 10601, MPEF-PV 10602 and MPEF-PV 10603 were collected, and the locality where *S. herraini* was found (modified from Anselmi *et al.* 2004 and Ardolino *et al.* 2011). C, Generalized stratigraphic section of the La Colonia Formation, north of Cerro Bayo.

angle unconformity (Pascual *et al.* 2000) separates the sedimentary rocks of this unit from the underlying rocks of the Chubut Group (Barremian–Cenomanian; Codignoto *et al.* 1979, Lapido and Page 1979). The top of the succession is covered by the basalts of the El Buitre Formation (Paleocene–Eocene) or by pyroclastic rocks of the Sarmiento Group (upper Oligocene–lower Miocene).

Pascual *et al.* (2000) recognized three facies associations within the La Colonia Formation in the Sierra de la Colonia area. The lowermost facies association is characterized by cross-bedded sandstones and conglomerates deposited in a moderate- to low-sinuosity fluvial environment. Sedimentary rocks of this facies association are considered by some authors (e.g., Pesce 1979), to be a separate lithostratigraphic unit, named the Puntudo Chico Formation. The second facies association is the thickest and most representative of the La Colonia Formation. It contains most of the vertebrate remains collected so far from this formation. It is mostly composed of laminated mudstones, fine pelitic sandstones, and banded siltstones and claystones deposited in an estuarine, tidal flat or coastal plain environment, influenced by sporadic high freshwater streamflow from the continent and tidal currents from the sea (Pascual *et al.* 2000, Cione and Gouiric-Cavalli 2012). This facies association was deposited under a seasonal climate with alternating wet and dry periods (Ardolino & Delpino 1987, Ardolino *et al.* 1995). The uppermost facies association is composed of laminated pelites containing bivalve remains and was interpreted to have been deposited in the upper part of an intertidal flat environment (Pascual *et al.* 2000).

Most of the vertebrate fauna recorded from the La Colonia Formation derives from the second facies association and includes freshwater fishes (such as dipnoans), turtles, snakes, plesiosaurs, dinosaurs and mammals (Bonaparte 1985, Albino 2000, Gasparini & de La Fuente 2000, Pascual *et al.* 2000, Rougier *et al.* 2009, Sterli & de la Fuente 2011, Clone and Gouiric-Cavalli 2012). This facies association also contains many levels with plant remains (Gandolfo & Cúneo 2005).

The age of the La Colonia Formation is not yet well established. The base is marked by an unconformity that separates this unit from the underlying rocks of the Cerro Barcino Formation of the Chubut Group, which may reach a Cenomanian age (Codignoto *et al.* 1979). Therefore, the age of the base of the La Colonia Formation depends on the time span represented by the unconformity below, but could not be older than Cenomanian. On the other hand, Ardolino & Franchi (1996) favoured a Campanian–Maastrichtian age for the upper part of this unit. These authors indicated that the top of this formation in some localities is covered by pelites with microfossils of Danian age that are probably attributable to the Salamanca Formation. Subsequently, Pascual *et al.* (2000) proposed that the uppermost part of

the La Colonia Formation might represent the lowermost Paleocene based on stratigraphic relations. In summary, and as suggested by Pascual *et al.* (2000), the La Colonia Formation spans the Campanian to Maastrichtian but sedimentation probably initiated somewhat earlier in some areas and possibly extended into the earliest Paleocene locally. Page *et al.* (1999) considered that the lower and middle parts of La Colonia Formation could be correlated, at least in part, with the Allen Formation of the Neuquén Basin, whereas its upper part was correlative with the Jagüel Formation of the same basin.

The specimens studied here were found at the base of the section exposed to the north of Cerro Bayo (Fig. 1A, B). The composite stratigraphic section at this locality (Fig. 1C) consists of 138 m of siltstones and subordinate fine-grained sandstones. The lowermost 80 m of the section are composed of massive, laminated or heterolithic siltstones alternating with sparse cross-bedded sandstones that rarely exceed 1 m thick. The vertebrate fossil content is concentrated in discrete layers or in ellipsoidal concretions. The presence of thin plant debris-bearing layers is very common. The remaining 58 m are composed mainly of heterolithic siltstones and reveal a decrease in fossil and concretion abundance.

Institutional abbreviations

CIT, California Institute of Technology, California, USA; CM, Canterbury Museum, Christchurch, New Zealand; DMNH, Denver Museum of Natural History, USA; MCS, Museo de Cinco Saltos, Río Negro Province, Argentina; MLP, Museo de la Plata, Buenos Aires Province, Argentina; MML, Museo Municipal de Lamarque, Río Negro Province, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Chubut Province, Argentina; MUC, Museo de la Universidad del Comahue, Neuquén Province, Argentina; NSM, National Science Museum, Tokyo, Japan; UC. MUS. PAL., University of California Museum of Paleontology, California, USA; USNM, National Museum of Natural History, Washington, USA.

Anatomical abbreviations

hf, haemal facets; lr, lateral ridge; na, neural arch; pa, parapophysis; pf, pedicelular facets; vf, ventral foramina; vn, ventral notch.

Methods

Linear measurements were taken using an electronic calliper, with an accuracy of 0.1 mm. The indices considered are those proposed by Welles (1952), which take into account the ratio between the centrum length (L) and height (H) ($HI = 100 * H/L$); the ratio between centrum breadth (B) and length ($BI = 100 * B/L$); and the ratio between the centrum breadth and height

($BHI = 100 * B/H$). Both breadth and height were measured on the posterior articular face. The Vertebral Length Index ($VLI = 100 * L / (0.5 * (H + B))$) proposed by Brown (1981) was also used. The ontogenetic stages proposed by Brown (1981), based on the fusion of the neural arch to the vertebral centrum, were employed to differentiate 'adult' from 'juvenile' stages.

During fieldwork, stratigraphic sections were measured using a Jacob's staff (1:10 scale). The lithology, sedimentary structures and geometry of the rock layers were documented and the fossiliferous levels were identified within this context (Fig. 1C).

Systematic palaeontology

Subclass SAUROPTERYGIA Owen, 1860
Order PLESIOSAURIA de Blainville, 1835
Superfamily PLESIOSAUROIDEA Welles, 1943
Family ELASMOSAURIDAE Cope, 1869

Gen. and sp. indet. (Fig. 2)

Materials

Three specimens are available. MPEF-PV 10601, five cervical, five dorsal, three caudal vertebrae, indeterminate vertebral fragments and ribs. MPEF-PV 10602, three cervical vertebrae and one caudal vertebra, and indeterminate fragments of vertebrae, ribs and gastroliths. MPEF-PV 10603, three cervical, one dorsal, and three caudal vertebrae, indeterminate vertebral fragments and ribs.

Locality and stratigraphic unit

All material is from the 'North Cerro Bayo' locality (42°57'S, 67°33'W39"S, 17"W), northeastern Chubut Province, Argentina (Fig. 1A, B); lower beds of the second facies association (*sensu* Pascual *et al.* 2000) of the La Colonia Formation (Fig. 1C).

Description and comparison

General features

The vertebrae described and measured are the better preserved ones but each specimen preserves vertebrae and rib fragments affected by modern weathering. Moreover, each specimen was collected in a small area, about 2 m², and separated from any other vertebrate remains. For this reason, specimens MPEF-PV 10601, MPEF-PV 10602 and MPEF-PV 10603 are considered to constitute three individuals. The specimens MPEF-PV 10601 and MPEF-PV 10602 have the neural arches fused with the vertebral centra and, therefore, are considered to be 'adults'; whereas in the MPEF-PV 10603 the neural arches are free, hence, it must be considered a 'juvenile' *sensu* Brown (1981). However, specimen MPEF-PV 10603 has the same dimensions as MPEF-

PV 10601 and MPEF-PV 10602, which are not juveniles. Moreover, the surfaces of the pedicellar facets of MPEF-PV 10603 have a complex texture (Fig. 2H), similar to that recorded in the crocodile *Alligator mississippiensis*, where it is produced by inconsistency in the vertical thickness of the chondroid cartilaginous layers (Ikejiri 2011). This inconsistency generates a complex articular surface between the neural arches and centra. In *Alligator*, this complex texture of the pedicellar facets is evident only in stages immediately prior to the closure of the neuro-central suture (Ikejiri 2011). For this reason, and due to its similar size, MPEF-PV 10603 is considered to be a subadult. All specimens have a common general morphology, and in particular, they share the presence of caudal vertebrae with strong laterally projecting parapophyses; hence, all these specimens are described together.

Axial skeleton

Cervical region. The anterior cervical centra (Fig. 2A–C) are longer than high and broader than long, and have dumbbell-shaped articular faces (Table 1, Fig. 2A–C). The lateral surface exhibits a lateral ridge (Fig. 2B). The cervical ribs are fused to the anterior cervical centra (Fig. 2A) in MPEF-PV 10601 and MPEF-PV 10602 but not in MPEF-PV 10603. The ventral surface bears paired foramina (Fig. 2C).

The posterior cervical vertebrae have centra that are higher than long and broader than high (Table 1) with elliptical articular faces lacking lateral ridges. In these vertebrae, the cervical ribs are not fused with the centra and the parapophyses are laterally and dorsally expanded.

Dorsal region. The dorsal vertebral centra are approximately spool-shaped (Fig. 2D–F), higher than long, and broader than high (Table 1). The articular faces are sub-circular (Fig. 2D). There are 3–5 ventral foramina.

Caudal region. The caudal centra are broader than high and higher than long (Table 1, Fig. 2J–M). The neural arches are not fused with the centra (Fig. 2J). The pedicellar facets are triangular (Fig. 2J). There are strong laterally projecting parapophyses on the lateral surface (Fig. 2K–L). The caudal ribs are not fused to the centra (Fig. 2L). There are haemal facets on the anterior and posterior margin of the ventral surface, and from one to six ventral foramina (Fig. 2M).

Gastroliths

One hundred and ninety-seven gastroliths were found associated with MPEF-PV 10602. The gastroliths are 35.5–8.2mm in maximum dimension and consist of hard quartzose well-rounded pebbles with a polished surface that differ from the surrounding pelitic sediment (O'Gorman *et al.* 2013).

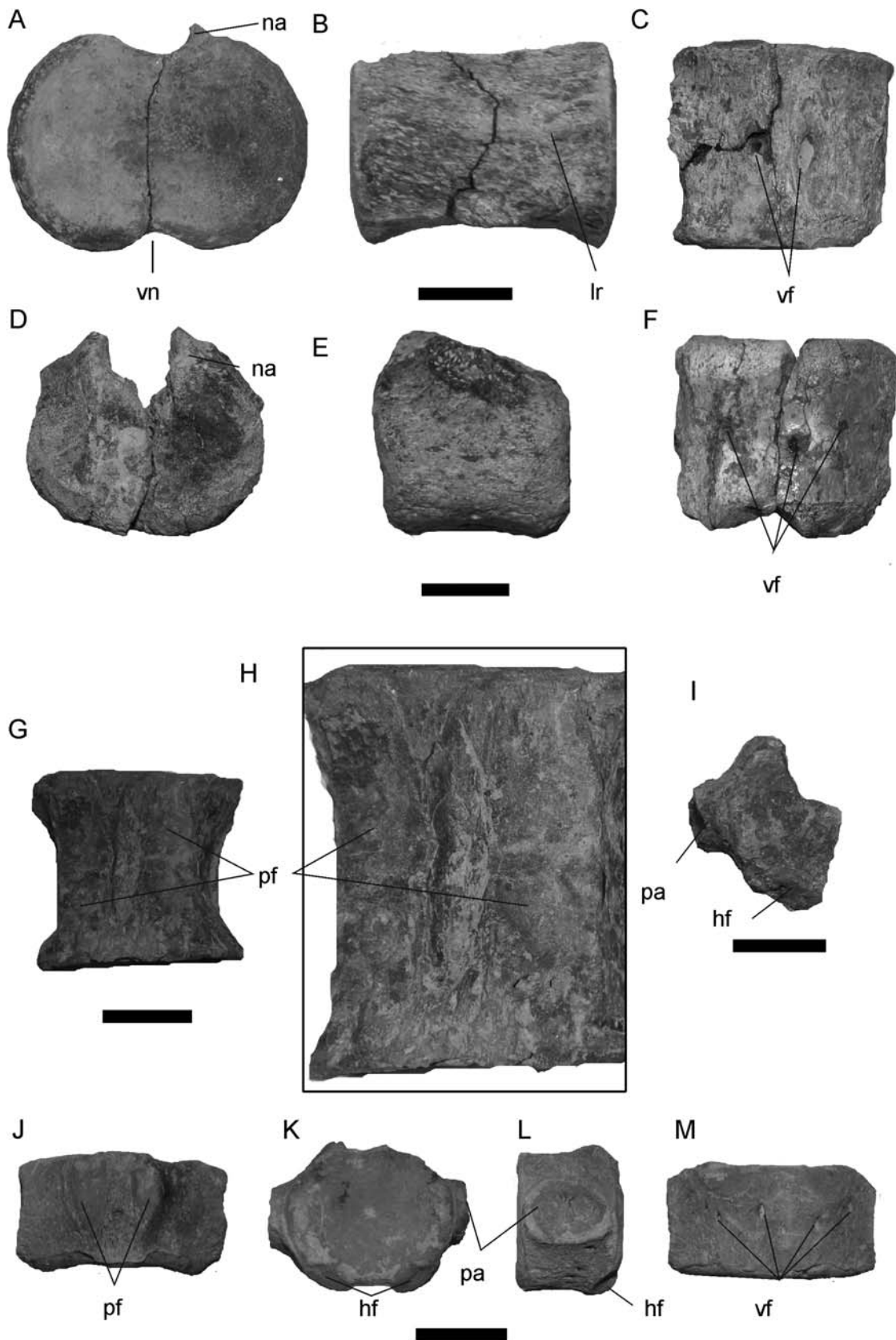


Fig. 2. MPEF-PV 10601, A–C, cervical vertebra in A, anterior, B, right lateral and C, ventral view; D–F, dorsal vertebra in D, anterior, E, left lateral and F, ventral views; MPEF-PV 10603 dorsal vertebra in G, dorsal view, H, detail of pedicellar facets; MPEF-PV 10602, I, caudal vertebrae in anterior view; MPEF-PV 10603 caudal vertebrae in J, dorsal, K, anterior, L, left lateral and M, ventral views. Scale bars = 20 mm.

	L	H	B	HI	BI	BHI	VLI
MPEF-PV 10601							
Cervical	56	46	63	112.50	112.50	136.96	102.75
Dorsal	46	52	44		95.65	84.62	95.83
Dorsal	52						
Dorsal	46	43	54	93.48	117.39	125.58	94.85
MPEF-PV 10602							
Cervical	31	24	44	77.42	141.94	183.33	91.18
Cervical	45						
Cervical	44						
MPEF-PV 10603							
Cervical	35	22	40	62.86	114.29	181.82	112.90
Cervical	42		58		138.10		
Cervical	40	41	63		157.50	153.66	76.92
Dorsal	44	43	49		111.36	113.95	95.65
Caudal	26						
Caudal	26	31	40		153.85	129.03	73.24
Caudal	25	33	41		164.00	124.24	67.57

Table 1. Measures L, H and B, and indexes HI, BI, BHI and VLI of the vertebrae MPEF-PV 10601, MPEF-PV 10602 and MPEF-PV 10603 (approximate values in italics). Lineal measurements in mm.

Discussion

Systematic affinities

Cervical centra, being longer than high with lateral ridges and dumbbell-shaped articular faces, allow referral of these specimens to Elasmosauridae (Werner & Bardet 1996, Gasparini & Salgado 2000, Ketchum & Benson 2011). However, given the current state of knowledge, specimens represented only by vertebral material can not be taxonomically determined below the family level (O'Keefe & Hiller 2006).

The specimens described here are similar to those referred to Elasmosauridae indet. by Gasparini & Salgado (2000) and Gasparini *et al.* (2007) from the Allen Formation (upper Campanian–lower Maastrichtian) of the Lago Pellegrini area, Río Negro Province, Argentina. All the specimens described here and those reported by Gasparini & Salgado (2000), share features that are not present in all Elasmosauridae: (1) cervical vertebrae that are not extremely elongated (VLI<130); (2) vertebral centra that are broader than high and long vertebral centra; and (3) caudal vertebrae with parapophyses that are strongly projected laterally. Similar caudal centra with strongly projected parapophyses have been recorded in specimens from the Allen Formation, Salitral de Santa Rosa area, Río Negro Province (O'Gorman *et al.* 2011, Fig. 3). These shared features suggest close affinities between the elasmosaurs recorded from the northern and southern slopes of the Somún Curá Plateau (Fig. 1A), which is consistent with the shared presence of the polycotyloid species *Sulcusuchus erraini* in both areas (Gasparini & Spalletti 1990, Gasparini & de La Fuente 2000).

Body size and ontogenetic stage

Adult elasmosaurs from the late Maastrichtian levels of the Jagüel Formation are poorly known, but the main

difference from the specimens described here is the disparity in body size. The adult elasmosaurs from the Jagüel Formation are twice as large as those from the Allen and La Colonia formations (Gasparini *et al.* 2003a). This difference is significant because MPEF-PV 10601 and MPEF-PV 10602 are likely 'adults', whereas MPEF-PV 10603 is considered a subadult, which suggests the distinctive size difference observed in these elasmosaurs may have systematic value (Table 1, Fig. 2). In order to test the hypothesis of small adult body size of the La Colonia and Allen formations elasmosaurs, their dorsal vertebrae were compared with those of adult individuals of other Late Cretaceous elasmosaurs. Dorsal vertebrae were used as an indicator of body size because the variation in size of dorsal vertebrae in a single specimen is lower than that observed in cervical and caudal vertebrae (Welles 1943, 1952). The elasmosaurs from the La Colonia and Allen formations (Table 1) are smaller than other Late Cretaceous adult elasmosaurs but both have similar dorsal centrum proportions (Fig. 3A).

A niche partition, where the juvenile elasmosaurs inhabited restricted environments near the coast while the adult forms lived in open marine environments, has been proposed for elasmosaurs (Wiffen & Moisley 1986). For this reason, and because of the particular palaeoenvironment of the La Colonia and Allen formations, it is important to discuss the ontogenetic stage of the specimens MPEF-PV 10601, MPEF-PV 10602 and MPEF-PV 10603 (La Colonia Formation); MLP 71-II-13-1, MCS PV 4 and MUC Pv 92 (Allen Formation). The ontogenetic variations of cervical centrum proportions of plesiosauroids, particularly progressive centrum elongation, are well known (Welles 1943, Brown 1981, O'Keefe & Hiller 2006). Therefore, the relative elongation of the cervical centra could be used to estimate the ontogenetic stage of the individual, independently of the

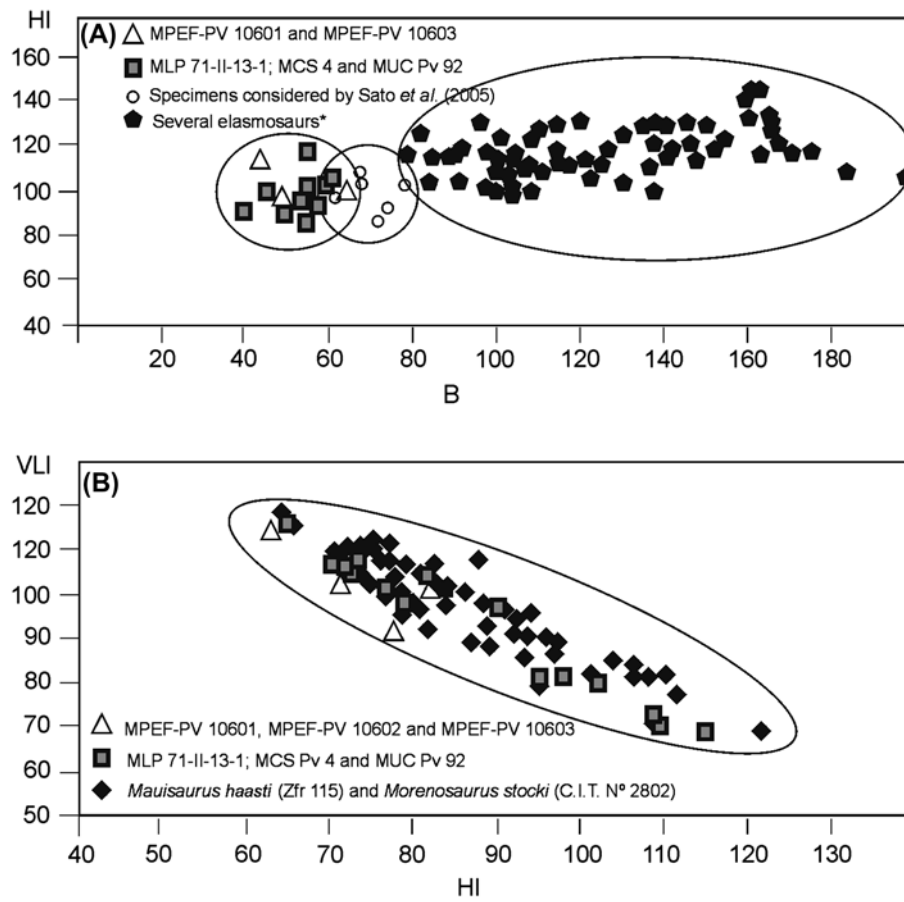


Fig. 3. A, Plot of B and HI of dorsal vertebrae modified from Sato *et al.* 2005, Δ , MPEF-PV 10601 and MPEF-PV 10603; \blacksquare MLP 71-II-13-1, MCS PV 4 and MUC Pv 92 (elasmosaurs from the Allen Formation, O’Gorman *pers. obs.*); \circ , elasmosaurs described by Sato *et al.* 2005; \blacklozenge , Several elasmosaurs: *Morenosaurus stocki* (CIT 2802); *Thalassomedon haningtoni* (DMNH 1588); *Hydrotherosaurus* sp. (UC. MUS. PAL. 33912); *Styxosaurus snowii* (USNM 11910); *Furabasaurus suzukii* (NSM PV15025); Elasmosauridae indet. (MLP 93-I-5-1). Data taken from (Welles 1943, 1952, 1962, O’Keefe and Hiller 2006, Sato *et al.* 2005, O’Gorman *pers. obs.*). B, Plot of HI and VLI of cervical vertebrae. Δ , MPEF-PV 10601, MPEF-PV 10602 and MPEF-PV 10603; \blacksquare , MLP 71-II-13-1, MCS PV 4 and MUC Pv 92 (elasmosaurs from the Allen Formation, O’Gorman *pers. obs.*); \blacklozenge , *Mauisaurus haasti* (CM Zfr 115) and *Morenosaurus stocki* (CIT 2802).

fusion of the neural arch with the vertebral centrum. The HI and VLI values of the cervical vertebrae recorded for MPEF-PV 10601, MPEF-PV 10602, MPEF-PV 10603 (La Colonia Formation) and MLP 71-II-13-1, MCS PV 4 and MUC Pv 92 (Allen Formation), have cervical centrum proportions similar to those of adult *Mauisaurus haasti* and *Morenosaurus stocki*, two elasmosaurs that are not in the ‘elongate group’ (*sensu* O’Keefe & Hiller 2006; Fig. 3B).

In summary, the elasmosaurs from the La Colonia and Allen formations are smaller than other Late Cretaceous elasmosaurs. Analysis of vertebral elongation reinforces the interpretation that the described specimens are adults or at least subadults, as was initially inferred using the growth stages of Brown (1981).

Palaeohistological analysis carried out by Salgado *et al.* (2007) indicates that specimen MUCPv 92 is probably a ‘subadult’ but it is an adult *sensu* Brown (1981). This discrepancy emerges because the palaeohistologic stages do not necessarily coincide with the growth stages recognized by Brown (1981). Similarly, MML PV4 of Salgado *et al.* (2007) is an adult, based on its histology, but it is an ‘old adult’ *sensu* Brown (1981) due to the fusion of the haemal arches to the caudal vertebrae (O’Gorman *pers. obs.*).

Small elasmosaurs preserved in marginal marine to non-marine environments were described by Sato *et al.*

(2005) from the Dinosaur Park Formation (upper Campanian). They recorded sub-adult specimens that were smaller than those recorded in nearby marine formations (Fig. 3A), and they stated that the size difference might be explained by two hypotheses: (1) the small elasmosaur specimens retained a small size throughout their life, or (2) these specimens were juveniles that had not reached their adult body size Sato *et al.* (2005). Similarly, elasmosaurs from the La Colonia Formation have a smaller body size compared with those from the marine Jagüel Formation and the evidence indicates that MPEF-PV 10601, MPEF-PV 10602, MPEF-PV 10603 described here, together with MLP 71-II-13-1, MCS PV 4 and MUC Pv 92 described by Gasparini & Salgado (2000) are adults or subadults. However, the question about their final body size remains open. There are other similarities between the La Colonia Formation and the Dinosaur Park Formation. Both units are clastic packages deposited during the initial stages of a marine transgression. They comprise a lower sandy section and an upper muddy section representing a vertical transition from fluvial to marginal marine (coastal plain to estuarine) environments (Pascual *et al.* 2000, Sato *et al.* 2005). The fine-grained beds of both units have abundant tidal-influenced sedimentary structures. Other features in common are the presence of fossiliferous lags and carbonaceous (plant-rich) layers (Pascual *et al.* 2000; Sato *et al.* 2005).

At the site from which MPEF-PV 10601, MPEF-PV 10602 and MPEF-PV 10603 were collected, the La Colonia Formation has not produced additional vertebrates with marine affinities other than the polycotyloid *Sulcusuchus erraini*. However, a great quantity of material referable to Dipnoii, Chelidae, ophidians and dinosaurs has been collected (Bonaparte 1985, Albino 2000, Pascual *et al.* 2000, Gasparini and de La Fuente 2000, Rougier *et al.* 2009, Sterli and de la Fuente 2011). This evidence, together with the sedimentologic data, reinforces the hypothesis that at least some elasmosaurs had colonized marginal marine, estuarine or even freshwater fluvial environments by the end of the Late Cretaceous, although additional data are needed to confirm this idea.

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