



PLESIOSAURS (DIAPSIDA, SAUROPTERYGIA) FROM LATE CRETACEOUS (LATE CAMPANIAN–EARLY MAASTRICHTIAN) MARGINAL MARINE ENVIRONMENTS FROM NORTH PATAGONIA

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Abstract. During the late Campanian and early Maastrichtian, Northern Patagonia suffered the first stage of the Atlantic marine ingression that reached the Neuquén Basin. The Allen and La Colonia formations show the early stages of this change, and were deposited in a complex association of marginal marine environments, including coastal and marine deposits (*i.e.*, flood plains, estuaries and lagoons). The plesiosaurs from the Allen and La Colonia formations included at least three species, each with a distinctive morphotype, representing a high diversity in the Late Cretaceous. The only species that preserved cranial material, *Sulcusuchus erraini* Gasparini and Spalleti, is a strange polycotyloid characterized by the presence of deep grooves in the rostrum and mandible. The other two species correspond to aristonectine and non-aristonectine elasmosaurids. The former are distinguished by relatively large skulls and a high number of teeth compared to other elasmosaurids, whereas the non-aristonectine elasmosaurids are characterized by their relatively small body sizes, despite being adult specimens.

Key words. Elasmosauridae. Polycotyliidae. Late Cretaceous. Patagonia. *Sulcusuchus erraini*.

Resumen. PLESIOSAURIOS (DIAPSIDA, SAUROPTERYGIA) DEL CRETÁCICO TARDÍO (CAMPANIANO TARDÍO–MAASTRICHTIANO TEMPRANO) DE AMBIENTES MARINO-MARGINALES DEL NORTE DE PATAGONIA. Durante el Campaniano tardío y el Maastrichtiano temprano el norte de la Patagonia sufrió la primera etapa de la ingesión marina atlántica, que alcanzó la Cuenca Neuquina. Las formaciones Allen y La Colonia evidencian las primeras etapas de este cambio, habiéndose depositado en una asociación de ambientes irregulares que incluyen depósitos marino-marginales (es decir de llanuras mareales, estuarios y lagunas costeras). Los plesiosaurios de las formaciones Allen y La Colonia incluyen al menos tres especies, cada una con un morfotipo distintivo, lo que representa una alta diversidad hacia fines del Cretácico. La única especie con material craneano preservado es *Sulcusuchus erraini* Gasparini y Spalleti, un extraño policotílido caracterizado por la presencia de profundos surcos en el rostro y la mandíbula. Las otras dos especies corresponden a elasmosáuridos aristonectinos, caracterizados por tener cráneos relativamente grandes y elevado número de dientes comparados con otros elasmosáuridos y a elasmosáuridos no aristonectinos, que se destacan por su relativo pequeño tamaño, a pesar de tratarse de ejemplares adultos.

Palabras clave. Elasmosauridae. Polycotyliidae. Cretácico Tardío. Patagonia. *Sulcusuchus erraini*.

PLESIOSAURS are diapsid marine reptiles with a biochron extending from the Late Triassic to the final extinction at the end of the Cretaceous (Ketchum and Benson, 2010). Plesiosaur history can be divided into several stages, the last one extending over the Late Cretaceous when polycotyliids (short-necked xenopsarian plesiosaurs) and elasmosaurids (long-necked plesiosaurs) were the most diverse groups (Benson and Druckenmiller, 2014). A surprising discovery is that both polycotyliids and elasmosaurids are closely phylogenetically related (O'Keefe, 2001), demonstrating the plasticity of the body plans of plesiosaurs.

The Campanian–Maastrichtian plesiosaur diversity is well recorded not only in North America (Carpenter, 1999) but also in the Weddellian Province, which comprises Patagonia, Western Antarctica, New Zealand and Eastern Australia (Zinsmeister, 1979; Cruickshank and Fordyce, 2002; Hiller *et al.*, 2005; Gasparini *et al.*, 2007; Otero *et al.*, 2014; O'Gorman *et al.*, 2015).

One of the most striking feature of the plesiosaur record from Patagonia is the presence of abundant specimens from marginal marine levels of the Allen, Los Alamitos (“lower Coli Toro”) and La Colonia formations (Gasparini and Salgado,

2000; O’Gorman *et al.*, 2011, 2013a–c; Gasparini *et al.*, 2015). This record comprises the polycotyloid *Sulcusuchus erraini* Gasparini and Spalleti, 1990, an unnamed aristonectine elasmosaurid and a small long-necked non-aristonectine elasmosaurid.

The aim of this review is to describe the plesiosaur association of the Allen, Los Alamitos (“lower Coli Toro”) and La Colonia formations, highlighting its peculiarities and its relationship with other Weddellian plesiosaurs.

Institutional abbreviations. **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.

Anatomical abbreviations. **af**, accessory facet; **al**, alveolus; **ang**, angular; **ar**, articular; **bot**, basioccipital tuber; **cap**, capitulum; **de**, dentary; **hf**, hemal facet; **mca**, meckelian canal; **mg**, mandibular groove; **mx**, maxilla; **oc**, occipital condyle; **pa**, parietal; **par**, parapophysis; **pf**, pedicellar facet; **pipv**, posterior interpterygoid vacuity; **pmr**, premaxillar ridge; **pmx**, premaxilla; **ps**, parasphenoid; **psk**, parasphenid keel; **pt**, pterygoid; **q**, quadrate; **rap**, retroarticular; **rf**, radial facet; **rg**, rostral groove; **sq**, squamosal; **su**, surangular; **to**, tooth; **tub**, tuberculum; **uf**, ulnar facet; **vf**, ventral foramina; **vn**, ventral notch.

GEOLOGICAL BACKGROUND

Allen Formation

The Allen Formation crops out in the north of Patagonia (Fig. 1) (Río Negro, La Pampa and Neuquén provinces). This formation is a thick succession of sandstones and shales with interbedded levels of carbonate and evaporite rocks in its uppermost part (Andreis *et al.*, 1974).

The fauna recorded from the Allen Formation comprises molluscs, dipnoans teleosts, chelid turtles (de la Fuente *et al.*, 2001; Martinelli and Forasiepi, 2004; Salgado *et al.*, 2007b), snakes (Martinelli and Forasiepi, 2004), hadrosaurid dinosaurs (Coria *et al.*, 2012), sauropods (Martinelli and Forasiepi, 2004), theropods (Novas *et al.*, 2009) as well as elasmosaurid and polycotyloid plesiosaurs (Gasparini and Salgado, 2000; Salgado *et al.*, 2007a). The Allen Formation

was deposited in a marginal marine environment (Barrio, 1990) and, based on microfossils and magnetostratigraphy, was assigned to the late Campanian–early Maastrichtian (Ballent, 1980; Dingus *et al.*, 2000).

Los Alamitos Formation (“lower Coli Toro”)

Los Alamitos Formation was formally nominated by Bonaparte *et al.* (1984) to include the sediments of the Cona Niyeu zone located stratigraphically between the Chubut Group and the Roca Formation. Subsequent studies have extended this name to the sedimentary deposits from the Ingeniero Jacobacci region previously mapped as part of the Coli Toro Formation (Getino, 1995). Los Alamitos Formation can be correlated with the lower and middle continental levels of La Colonia Formation (Page *et al.*, 1999), and with part of the sequence from the Ingeniero Jacobacci area (Page *et al.*, 1999).

Los Alamitos Formation was deposited in coastal fresh-water lagoons (lower section) and tidal mudflats with marine influence (upper section) (Bonaparte *et al.*, 1984, 1987). In its type section, the lower part has provided a rich fauna

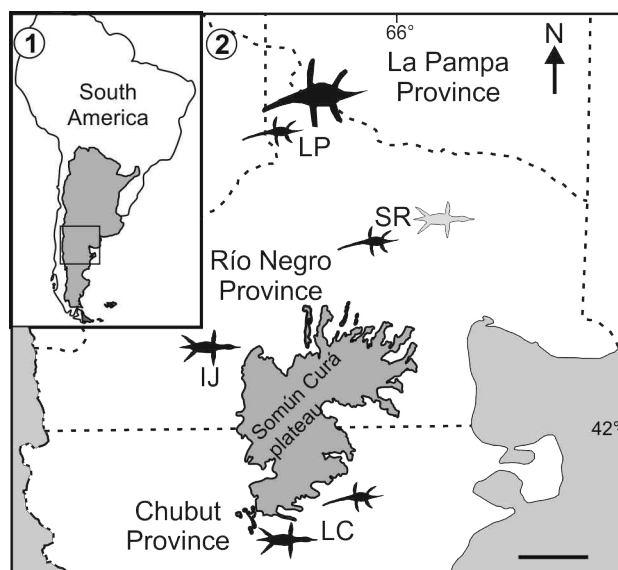


Figure 1. Map showing the localities in north Patagonia where the specimens mentioned in the text were collected. 1, General map. 2, Northern Patagonia. ★, *Sulcusuchus erraini*; ★, MML PV 43, Polycotyloidea indet; ★, MUCPV 131, Aristonectinae indet; ★, MLP 71-II-13-1, MCS PV 4, MUCPV 92, MPEF-PV 10601, MPEF-PV 10602, Elasmosauridae indet. “small-sized elasmosaurid of La Colonia and Allen formations”. LP, Lago Pellegrini; SR, Bajo Santa Rosa area; IJ, Ingeniero Jacobacci area; LC, La Colonia area. Scale bar= 100 km.

composed by molluscs (Getino, 1995), continental vertebrates such as *Lepisosteus*, siluriforms, lungfish, frogs, chelid turtles, snakes, sauropods, hadrosaurids and theropods (Bonaparte *et al.*, 1987), mammals (Bonaparte *et al.*, 1984) and the polycotyloid *Sulcusuchus erraini* (Gasparini and Spalletti, 1990). The levels where the holotype of *S. erraini* was collected were deposited during the late Campanian–early Maastrichtian (Getino, 1995; Page *et al.*, 1999).

La Colonia Formation

La Colonia Formation is exposed along the southeastern margin of the Somún Curá Massif (North Patagonic Massif), Chubut Province, Patagonia, Argentina (Fig. 1). In the Sierra de la Colonia area, La Colonia Formation comprise three facies associations, *sensu* Pascual *et al.* (2000). The second facies association, the thickest and most representative of the La Colonia Formation, contains the most diverse assemblage of vertebrates collected so far from this unit. 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 stream flow and tidal currents from the sea (Pascual *et al.*, 2000). Fossils from this facies association include freshwater fishes (such as dipnoans), turtles, snakes, plesiosaurs, dinosaurs and mammals (Bonaparte *et al.*, 1984; Albino, 2000; Gasparini and de la Fuente, 2000; Pascual *et al.*, 2000; Rougier *et al.*, 2009; Sterli and de la Fuente, 2011; O'Gorman *et al.*, 2013b,c) and many levels contain plant remains (Gandolfo and Cúneo, 2005).

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.

SYSTEMATIC PALEONTOLOGY

Subclass SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Superfamily PLESIOSAUROIDEA Welles, 1943

(*sensu* O'Keefe 2001)

Family POLYCOTYLIDAE Cope, 1869

Genus *Sulcusuchus* Gasparini and Spalletti, 1990

Type species. *Sulcusuchus erraini* Gasparini and Spalletti, 1990, Los Alamos ("lower Coli Toro") Formation, Ingeniero Jacobacci, Río Negro Province, Argentina.

Sulcusuchus erraini Gasparini and Spalletti, 1990

Figure 2

Type material. MLP 88-IV-10-1, fragment of mandibular symphysis (Fig. 2.4–5) (Gasparini and Spalletti 1990: pl. 1).

Type Locality and horizon. Northeastern margin of Laguna Cari-Laufquén Grande, 25 km north of Ingeniero Jacobacci (41° 01' 50" S; 69° 27' 78" W), Río Negro Province, Argentina (Fig. 1); Los Alamos Formation (basal levels of the "Coli Toro" Formation *sensu* Gasparini and Spalletti 1990); upper Campanian–lower Maastrichtian (Getino, 1995).

Referred material. MPEF PV 650, part of cranium and mandible (Fig. 2.1–3).

Geographic and stratigraphic occurrence. Cerro Bosta (43° 00' 21" S; 67° 37' 13" W), northeastern Chubut Province, Argentina (Fig. 1); middle levels of La Colonia Formation, upper Campanian–lower Maastrichtian (Page *et al.*, 1999).

Remarks. *Sulcusuchus erraini* was originally described as a dyrosaurid crocodyliform by Gasparini and Spalletti (1990) based on the holotype. Later, the referred specimen of *S. erraini* was assigned to a typical long-rostrum polycotyloid (Gasparini and de la Fuente, 2000; O'Gorman and Gasparini, 2013).

The most striking features of *Sulcusuchus erraini* is the presence of deep rostral and mandibular grooves. The texture of the inner surface of these grooves differs from the outer surface, indicating the presence of some special soft tissue housed inside them. O'Gorman and Gasparini (2013) discussed the possible nature of the soft tissue inside the grooves, concluding that the presence of glands or sensory organs was the most probable alternative. New better preserved specimens would allow to improve the knowledge about these distinctive structures. *Sulcusuchus erraini* is recorded in two localities (Fig. 1) of the south and north part of the Somún Curá Masif, which show similar faunas; this is also supported by the similar "small sized elasmosaurids" collected in both areas.

Polycotylidae indet.

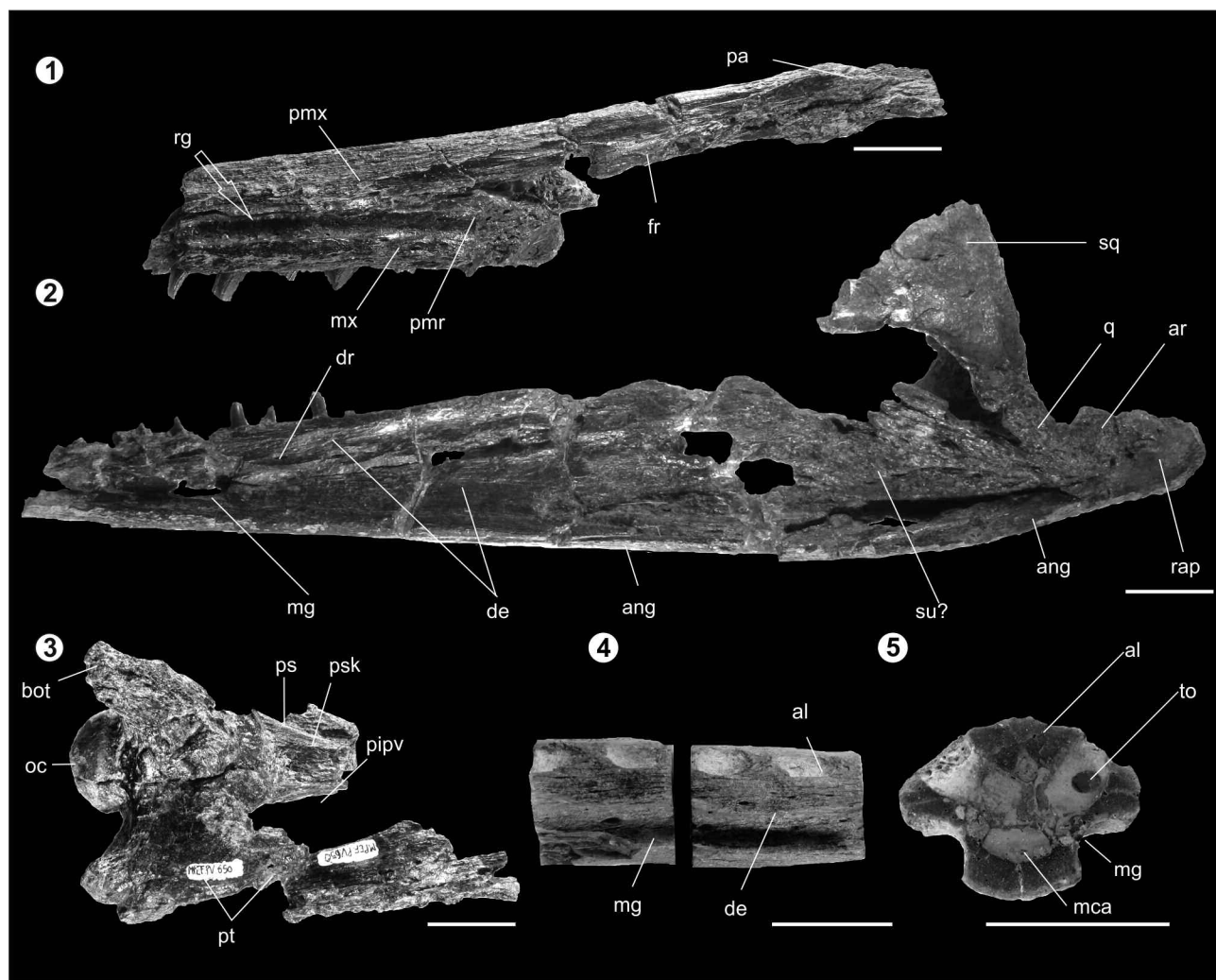


Figure 2. *Sulcusuchus erraini*. 1–3, MPEF-PV 650; 1, rostrum and skull roof in left lateral view; 2, left mandibular ramus, quadrate and squamosal in lateral view; 3, basicranium and posterior part of palate associated in ventral view. 4–5, MLP 88-IV-10-1 (holotype); mandibular symphysis in 4, right lateral view and 5, cross-sections in posterior view. Scale bars= 20 mm.

Material. MML PV 43, partial postcranial skeleton (Salgado *et al.*, 2007a: figs. 3–4).

Geographic and stratigraphic occurrence. Loma Puntuda, Río Negro Province, northern Patagonia. Middle Member? of the Allen Formation. Upper Campanian–lower Maastrichtian.

Remarks. MML PV 43 has not enough diagnostic features to allow its identification beyond a familial assignment. However, the presence of spoon-like neural spines has been mentioned as a possible diagnostic feature (O’Gorman, 2013). It is probable than this specimen belongs to *S. erraini* due to its occurrence in levels of the same age and nearby locality, but anatomical evidence is currently unavailable.

Family ELASMOSAURIDAE Cope, 1869
 Subfamily ARISTONECTINAE O’Keefe and Street, 2009
 (*sensu* Otero *et al.*, 2012)

Aristonectinae indet.

Figure 3.1–7

Material. MUCPv 131, four cervical vertebrae, two dorsal vertebrae, a fragment of scapula?, a tarsal or carpal element and four phalanges (Fig. 3.1–7).

Geographic and stratigraphic occurrence. Contralmirante Cordero (38° 46’ 42” S; 68° 04’ 85” W), Río Negro Province,

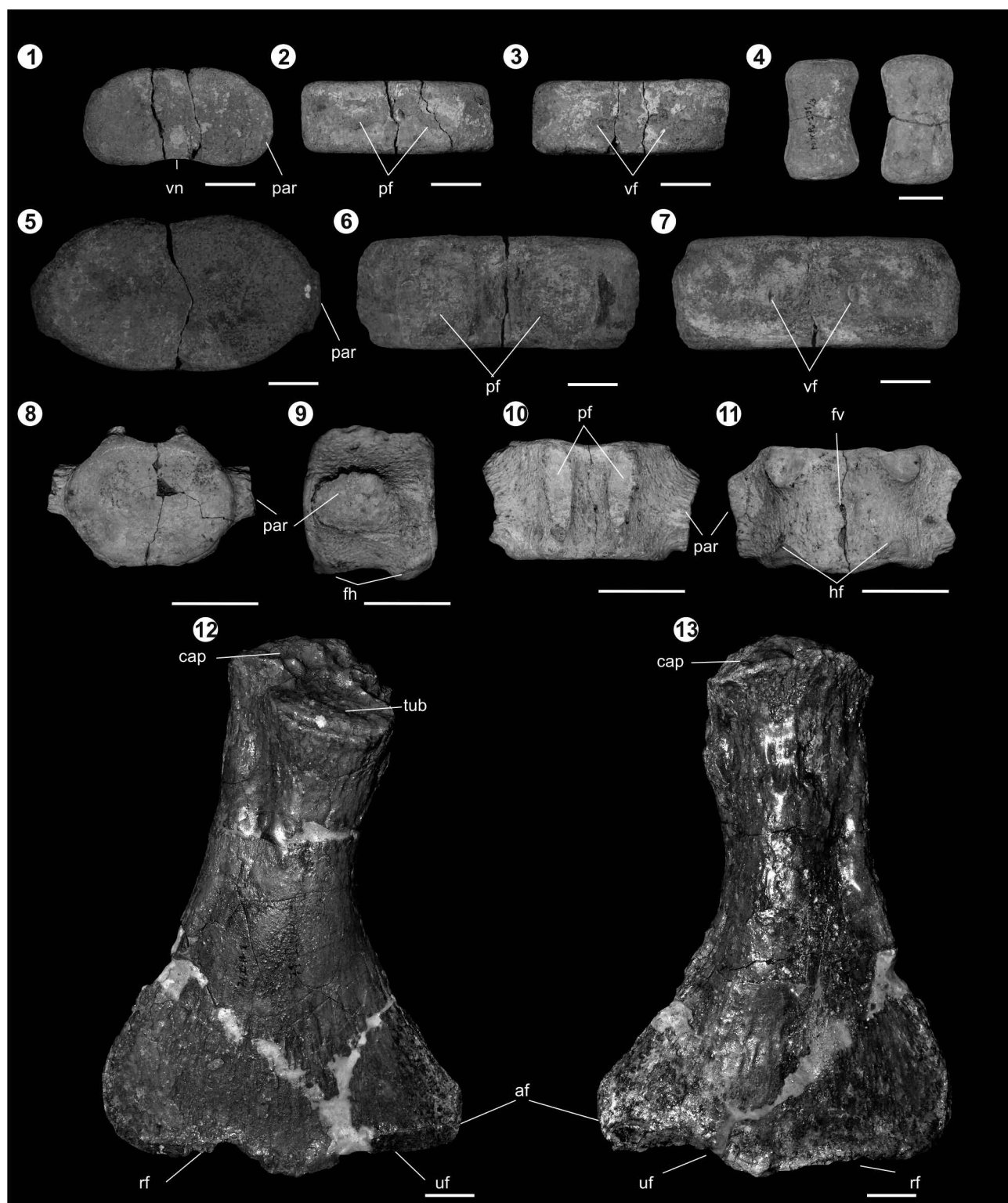


Figure 3. 1–7, *Aristonectinae* indet., MUCPv 131; 1–3, anterior cervical vertebra in 1, anterior, 2, dorsal, and 3, ventral views; 4, phalanges; 5–7, posterior cervical centrum in 5, anterior, 6, dorsal, and 7, ventral views. 8–11, *Elasmosauridae* indet., MUCPv 92, caudal vertebrae in 8, anterior, 9 right lateral, 10, dorsal, and 11, ventral views. 12–13, *Elasmosauridae* indet. MLP 71-II-13-1, left humerus in 12, dorsal and 13, ventral views. Scale bars= 20 mm.

Argentina. Middle Member of the Allen Formation, upper Campanian–lower Maastrichtian (Ballent, 1980; Dingus *et al.*, 2000).

Remarks. Gasparini *et al.* (2003a) referred MUCPv 131 to *Tuarangisaurus*, based on the similarities with MML PV 5, the holotype of *Tuarangisaurus? cabazai* Gasparini, Salgado and Casadío, 2003a from the upper Maastrichtian Jagüel Formation. More recently, Gasparini *et al.* (2007) referred both specimens MUCPv 131 and MML PV 5 to Plesiosauroidea indet. questioning the diagnostic value of the feature used to referred MML PV 5 to *Tuarangisaurus*. O’Gorman *et al.* (2013a) discussed the diagnostic value of the proportion of the cervical centra of juvenile specimens, and referred MML PV 131 to *Aristonectes cf. parvidens*. Lately, the discovery of *Aristonectes quiriquinensis* Otero *et al.*, 2014 and the presence of the same kind of cervical centra (with extremely broad cervical centra) in the Upper Cretaceous of New Zealand (O’Gorman Pers. Obs.) allowed to propose that these special proportions are diagnostic features only at subfamily level (O’Gorman *et al.*, 2014).

Elasmosauridae indet.

Figure 3.8–13

Referred material. MLP 71-II-13-1, six cervical vertebrae, three dorsal vertebrae, three sacral vertebrae, nine caudal vertebrae, left humerus, femur and an ilium, an element of the carpus or tarsus, a rib and a phalanx (Fig. 3.12–13). MCS PV 4, 15 cervical vertebrae, three pectorals vertebrae, 15 dorsals, three caudals, one right scapula, proximal part of right coracoid, two pubes, two ischia, distal end of a femur with both epipodial elements articulated, phalanges and gastroliths. MUCPv 92, two cervical vertebrae, three dorsals vertebrae, one sacral vertebra, eight caudals vertebrae, fragments of pectoral? girdle, ribs, phalanges, femur, two epipodial elements (Fig. 3.8–11). MPEF-PV 10601, five cervical, five dorsal, three caudal vertebrae, indeterminate vertebral fragments and ribs. MPEF-PV 10602, three cervical vertebrae, 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.

Geographic and stratigraphic occurrence. MLP 71-II-13-1,

MCS PV 4, MUCPv 92, Northeast of Lago Pellegrini, Río Negro Province (Fig. 1). Bentonites of the Middle Member of the Allen Formation. Upper Campanian–lower Maastrichtian (Ballent, 1980; Dingus *et al.*, 2000). MPEF-PV 10601, MPEF-PV 10602, MPEF-PV 10603, North Cerro Bayo locality (42° 57’ S; 67° 33’ W), northeastern Chubut Province, Argentina; lower beds of the second facies association (*sensu* Pascual *et al.*, 2000) of La Colonia Formation.

Remarks. The elasmosaurids recorded from the Allen and La Colonia formations seem to belong to a still unnamed species which has been informally called “the small-sized elasmosaurs” from La Colonia and Allen formations by O’Gorman *et al.* (2013c), referring to the distinctive body size.

Specimens MLP 71-II-13-1, MCS PV 4, MUCPv 92, MPEF-PV 10601, MPEF-PV 10602, MPEF-PV 10603 share features that are not present in all elasmosaurids: (1) cervical vertebrae that are not extremely elongated, similar to other elasmosaurids from the non-elongated group *sensu* O’Keefe and Hiller (2006); (2) vertebral centra that are broader than high along the cervical region; and (3) caudal vertebrae with parapophyses that are strongly projected laterally.

Another distinctive feature of these specimens is their small size. It is interesting because specimens MLP 71-II-13-1, MCS PV 4, MUCPv 92, MPEF-PV 10601 and MPEF-PV 10602 are adults *sensu* Brown (1981). Comparison with other elasmosaurids of the same age shows that this species has a distinctively small body size (O’Gorman *et al.*, 2013c).

DISCUSSION

Summarizing, the plesiosaur association recorded in the marginal marine environments (tidal flats, estuarine) from the upper Campanian–lower Maastrichtian of north Patagonia is composed by one polycotyloid (*Sulcusuchus erraini*), aristonectines and one small body-sized non-aristonectine elasmosaurid. Therefore, two families and three different morphotypes are present in these environments.

Despite the particular environment where these specimens have been collected, it seems to be close relationships with other plesiosaur faunas from the Weddellian Province. The relationships observed among invertebrates (Zins-

meister, 1979) and other marine reptiles (Martin and Fernández, 2007) of the Weddellian Province are also observed among Weddellian plesiosaurs (Gasparini *et al.*, 2003a,b; Otero *et al.*, 2012, 2014).

Aristonectines (*i.e.*, *Aristonectes*, *Kaiwhekea*) are a group of elasmosaurids characterised by short cervical centra, large skulls and high number of teeth. They are probably the most distinctive elasmosaurid group from the Weddellian Province (Gasparini *et al.*, 2003b; Otero *et al.*, 2014) and, therefore, their presence in the upper Campanian–lower Maastrichtian of north Patagonia is expectable. Unfortunately, neither adults nor well-preserved aristonectine specimens have been recovered from the Allen or La Colonia formations; consequently, the generic and specific affinities of the aristonectines that inhabit these environments are unknown.

The non-aristonectine elasmosaurid present in the assemblage is distinguished by its small body size. O'Gorman (2013) estimated a body length of 3.7 m combining measurements from MLP 71-II-13-1, MCS PV 4 and MUCPV 92, all adult specimens. This “small-sized elasmosaurid” has narrow phylogenetic relationships with *Vegasaurus molyi* O'Gorman, Salgado, Olivero and Marensi, 2015, from the lower Maastrichtian levels of the Cape Lamb Member of the Snow Hill Island Formation, Antarctica (O'Gorman *et al.*, 2015).

The only taxon far related to other lineages from the Weddellian Province is *Sulcusuchus erraini*, probably because only few polycotyloid specimens are known throughout this province (Welles and Gregg, 1971; Novas *et al.*, 2015).

The most interesting feature of this association is the presence of three morphotypes, one polycotyloid (short necked) and two elasmosaurids (long necked) including one aristonectine and one non-aristonectine, sharing a complex marginal marine environment where plesiosaurs are practically the only vertebrates with marine affinities (Martinelli and Forassiepi, 2004; Gasparini *et al.*, 2015). Noticeably missing are mosasaurs, which by the end of the Cretaceous had become diverse and the top marine predators, very common in the Weddellian Province (Fernández and Gasparini, 2012). A similar assemblage, comprising more than one plesiosaur species from an environment different to normal marine, has been reported from the freshwater

early–middle Aptian Eumeralla Formation, Australia (Benson *et al.*, 2013). Therefore the invasion of this kind of environment by several plesiosaur species has been achieved more than once during the Cretaceous.

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