

New elasmosaurids (Sauropterygia, Plesiosauria) from the Late Cretaceous of the Magallanes Basin, Chilean Patagonia: Evidence of a faunal turnover during the Maastrichtian along the Weddellian Biogeographic Province

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ABSTRACT. Several Upper Cretaceous plesiosaur specimens recovered from southernmost Chile are described here. These were collected from upper levels of the Dorotea Formation exposed on three different localities (Sierra Baguales, Cerro Castillo, and Dumestre). The new material includes the first record of *Aristonectes* (Plesiosauria, Elasmosauridae), previously recorded from Argentina, central Chile, and Antarctica. Additional specimens include associated postcranial skeletons as well as isolated elements. Among these, we recognize the presence of aristonectines in the three studied localities, while non-aristonectine elasmosaurids were only collected from Cerro Castillo. The specimen from Dumestre is remarkable by being a small-sized adult, indeterminate aristonectine, and could be related to known representatives from Antarctica. These new finds prove the abundance of aristonectines as well as intermediate elasmosaurids along the Magallanes Basin during the uppermost Cretaceous, while extreme long-necked elasmosaurids as well as polycotyliids seems to be completely absent during this time span. This key record from southernmost Chile and its strategic placement in the middle part of the Weddellian Province gives the chance for complementing the paleobiogeography of Upper Cretaceous plesiosaurs from the Southern Hemisphere. As a first result, a faunal turnover is observed during the early Maastrichtian, when extreme (very-long necked) elasmosaurids and polycotyliids disappeared from the austral record. Since the early Maastrichtian and towards the late Maastrichtian, aristonectines became differentially abundant along the southeastern Pacific and Antarctica, but moderately represented in the southwestern Atlantic. On contrary, intermediate elasmosaurids were scarce in the Antarctic-Pacific realm, but abundant in the Atlantic. The updated record of austral plesiosaurs suggest a first stage of interchange from the Northern into the Southern Hemisphere, and through the Atlantic seaway, at least since the Coniacian to the late Campanian-early Maastrichtian. During the early Maastrichtian, aristonectines were relatively frequent in the New Zealand-Antarctica archipelago, becoming abundant along southern South America during the late Maastrichtian.

Keywords: Austral plesiosaurs, Biogeography, Weddellian Province.

RESUMEN. Nuevos elasmosáuridos (*Sauropterygia*, *Plesiosauria*) del Cretácico Superior de la Cuenca de Magallanes, Patagonia Chilena: Evidencia de recambio faunístico durante el Maastrichtiano a lo largo de la Provincia Biogeográfica Weddelliana. Varios especímenes de plesiosaurio del Cretácico Superior recuperados en el sur de Chile son descritos en este trabajo. Estos fueron colectados desde niveles superiores de la Formación Dorotea, expuestos en tres localidades diferentes (Sierra Baguales, Cerro Castillo y Dumestre). El nuevo material incluye el primer registro de género *Aristonectes* (*Plesiosauria*, *Elasmosauridae*), previamente reconocido en Argentina, Chile central y la Antártica. Ejemplares adicionales incluyen esqueletos poscraneos asociados, así como elementos aislados. Entre ellos, se reconoce la presencia de aristonectinos en las tres localidades estudiadas, mientras que elasmosáuridos no aristonectinos solo fueron hallados en Cerro Castillo. El espécimen de Dumestre resulta notable por ser un aristonectino indeterminado de tamaño adulto, sin embargo, enano, y podría estar relacionado con representantes conocidos hallados en la Antártica. Estos nuevos hallazgos demuestran la abundancia de aristonectinos así como de elasmosáuridos intermedios a lo largo de la cuenca de Magallanes durante el Cretácico Superior, mientras que los elasmosáuridos de cuello extremo y los polycotílidos parecen estar totalmente ausentes durante este lapso. Este registro clave del sur de Chile, y su ubicación estratégica en la parte media de la Provincia Weddelliana, da la oportunidad de complementar la paleobiogeografía de los plesiosaurios del Cretácico Superior del Hemisferio Sur. Como primer resultado, se observa un cambio de fauna durante el Maastrichtiano temprano, cuando los elasmosáuridos extremos y polycotílidos desaparecieron del registro austral. Desde el Maastrichtiano temprano y hasta el Maastrichtiano tardío, los aristonectinos se volvieron diferencialmente abundantes a lo largo del Pacífico suroriental y de la Antártica, pero moderadamente representados en el Atlántico sudoccidental. Al contrario, los elasmosáuridos intermedios eran escasos en el ámbito de la Antártica y el Pacífico, pero abundantes en el Atlántico. Esta actualización en el registro de plesiosaurios australes sugiere una primera etapa de intercambio desde el norte hacia el Hemisferio Sur y a través del Atlántico, por lo menos desde el Coniaciano. Esta condición pudo durar hasta el Campaniano tardío-Maastrichtiano temprano. Durante el Maastrichtiano temprano, los aristonectinos fueron relativamente frecuentes en el archipiélago de Nueva Zelanda-Antártica, volviéndose abundantes a lo largo del sur de Sudamérica durante el Maastrichtiano tardío.

Palabras clave: Plesiosaurios australes, Biogeografía, Provincia Weddelliana.

1. Introduction

Plesiosaur records from the Magallanes (=Austral) Basin have been relatively frequent but poorly informative. The first report is due to Cecioni (1955) who mentioned an articulated extremity collected near Cerro Castillo in Magallanes Region, southernmost Chile, then identified by J. Reeside Jr. as '*Coelospondylus* (*Plesiosaurus*) *chilensis* (Gay)' (*nomen dubium*), after emended as *Plesiosaurus chilensis* Gay (Cecioni and Charrier, 1974). The material of Cecioni (SGO.PV.123) was later identified by Gasparini (1979) as *Plesiosauria* indet. In addition to this record, Gasparini commented the find of indeterminate plesiosaur remains from Lago Parrillar, ca. 50 km south from Punta Arenas. Otero *et al.* (2009) reported the first material referable to an indeterminate elasmosaurid collected from uppermost levels of the Dorotea Formation exposed near Puerto Natales, having a late Maastrichtian age. Also, Otero and Rubilar-Rogers (2010) reviewed the specimen of Cecioni (SGO.PV.123), being identified as an indeterminate elasmosaurid and regarding its stratigraphic provenance from levels of the Dorotea Formation, thus, being late Maastrichtian instead late

Campanian in age as it was originally proposed by Cecioni (1955). Otero and Rubilar-Rogers (2010) also presented the first elasmosaurid remains from middle levels of the Dorotea Formation exposed in Dumestre (20 km south from Puerto Natales, Fig. 1). In addition to these records, Ortiz *et al.* (2012, 2013) reviewed a partially articulated extremity from Lago Parrillar, likely collected from Maastrichtian levels of the Rocillosa or Fuentes Formation. The specimen was first referred to an indeterminate plesiosaur and later, determined to an elasmosaurid. Additionally, Otero *et al.* (2013a) reviewed the material firstly commented by Gasparini (1979), identifying it as an indeterminate elasmosaurid from the Fuentes Formation, assigning it a tentatively early Maastrichtian age. Lastly, another regular elasmosaurid specimen was recovered from Argentina from levels of late Maastrichtian age exposed in Lago Argentino (Novas *et al.*, 2011), which represents a coeval record found in the same basin.

Even when the record of austral plesiosaurs from the Magallanes Basin is relatively abundant, the taxonomical status of most specimens remained unsolved beyond family or even ordinal level. In consequence, paleobiogeographic relationships could

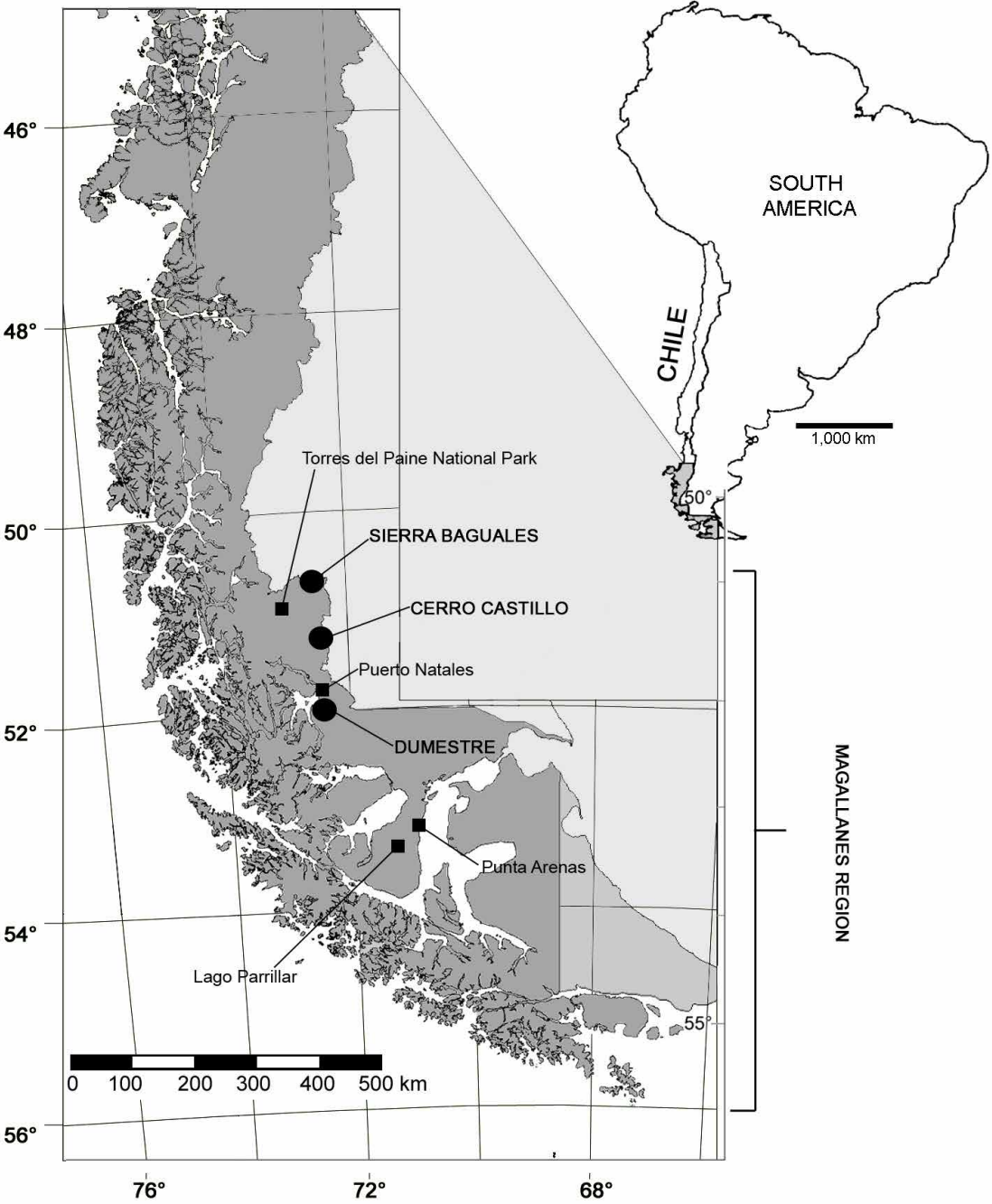


FIG. 1. Map showing the location of the three studied localities in the Magallanes Region, southernmost Chile.

not be established at this point. This paper presents new records from Chilean Patagonia recovered from three different localities distributed from north to south along the Magallanes Region, all of them

recovered from upper Maastrichtian levels. These localities are separated more than 150 km in N-S direction. In addition, the new material studied here, together with the previous plesiosaur records from

the Magallanes Region, gives the opportunity for evaluating a latitudinal sampling of near 300 km N-S along the Magallanes Basin.

2. Localities and Geological Setting

2.1. Localities

Three localities were studied (Fig. 1). The northernmost, Sierra Baguales, is settled near the northern international boundary of the Magallanes Region, and about 40 km northeast of the Torres del Paine National Park. The locality of Cerro Castillo is located *ca.* 55 km south from the first and *ca.* 55 km north from Puerto Natales. Lastly, the locality of Dumestre is placed near 20 km south from Puerto Natales. Lago Parrillar, which is relevant for this research, is settled *ca.* 35 km south from Punta Arenas, and 190 km SE from Puerto Natales.

2.2. Geologic Setting

All the specimens studied here were collected from outcrops of the Dorotea Formation (Katz, 1963). The Dorotea Formation comprises sandstones variable in color from green, gray, yellowish, brown and reddish, commonly with lenticular conglomerates and intercalations of clay levels, while upper calcareous levels contains concretionary nodules hosting a rich fossil diversity with abundant invertebrates (Katz, 1963) and vertebrates (Otero *et al.*, 2009; 2013b). The general strike has a N-S direction in the northern part of the Magallanes Region, while in the Brunswick Peninsula, this changes to a NW-SE direction. General dip of the sedimentary units falls into the E with angles lower than 45° (Hoffstetter *et al.*, 1957). The thickness of the unit is laterally variable. In Sierra Baguales, the section exposed at the studied site reaches near *ca.* 100 m, being much thicker in the northern part of the Sierra. For those outcrops exposed near Cerro Castillo, the combined thickness of the underlying Tres Pasos Formation together with the Dorotea Formation reaches 1,000 m, with *ca.* 300 m belonging to the latter unit. In the Southern end of the Sierra Dorotea near Puerto Natales, the exposed section reaches *ca.* 350 m, having its base partially covered by Pleistocene and recent deposits, reappearing in the coast of Dumestre due to the removal of recent sediments by effect of the tides. The relative position of the sections exposed

on each locality is included in a general stratigraphic column of the main units exposed in the northern Magallanes Region (Fig. 2). The age of the Dorotea Formation was first assigned to the undifferentiated Maastrichtian based on marine invertebrates (Katz, 1963). Later, it was emended to the late Campanian-Maastrichtian mostly based on trigonoid bivalves (Pérez and Reyes, 1978), but additional evidence based on microfossils (Martínez-Pardo, 1965) as well radioisotopic dates (Hervé *et al.*, 2004) supports a late Maastrichtian age (Fig. 2). Vertebrates recovered from this unit in Sierra Baguales includes the taxa *Carcharias* sp., *Ischyrrhiza chilensis*, *Serratolamna serrata* (Agassiz), *Centrophoroides* sp. and *Dasyatidae* indet., which are typical Maastrichtian fauna with affinities to those of the Quiriquina Formation (Otero *et al.*, 2013b). Teeth of *Carcharias* sp. were also been found in equivalent levels of Cerro Castillo during the fieldwork on 2014. Also, the upper slopes of the Sierra Dorotea in front of Puerto Natales have yielded remains of a juvenile, intermediate elasmosaurid (Otero *et al.*, 2009), while remains of another indeterminate elasmosaurid were previously reported by Otero and Rubilar-Rogers (2010) from Dumestre (SGO. PV.6580, re-studied here).

The fossil-bearing levels of the Dorotea Formation cropping out in Dumestre are topographically exposed near 1 m a.s.l. The previously described indeterminate elasmosaurid SGO.PV.6648 from Cerro Dorotea near Puerto Natales (Fig. 2) (which is the closest geographical record in the region) was recovered in a transported block found 243 m a.s.l. correlated with uppermost levels of the same unit (Otero *et al.*, 2009). The age of the latter outcrops was constrained through radioisotopic dates with detrital zircons from the base of the Cerro Dorotea (*i.e.*, *ca.* 200 m below the occurrence of SGO.PV.6648). These returned a maximum of 67.4 ± 1.5 Ma (Hervé *et al.*, 2004), thus, indicating a late Maastrichtian age for the lower part of the Cerro Dorotea section, and in consequence, conferring a maximum late Maastrichtian age to the SGO.PV.6648 (Otero *et al.*, 2009). In consequence, it is possible to assure that the fossil-bearing levels of Dumestre are older than 67.4 ± 1.5 Ma, and therefore, we propose an early late Maastrichtian age for them.

3. Material and Methods

Specimens from Cerro Castillo were collected by the authors during fieldwork in January, 2014.

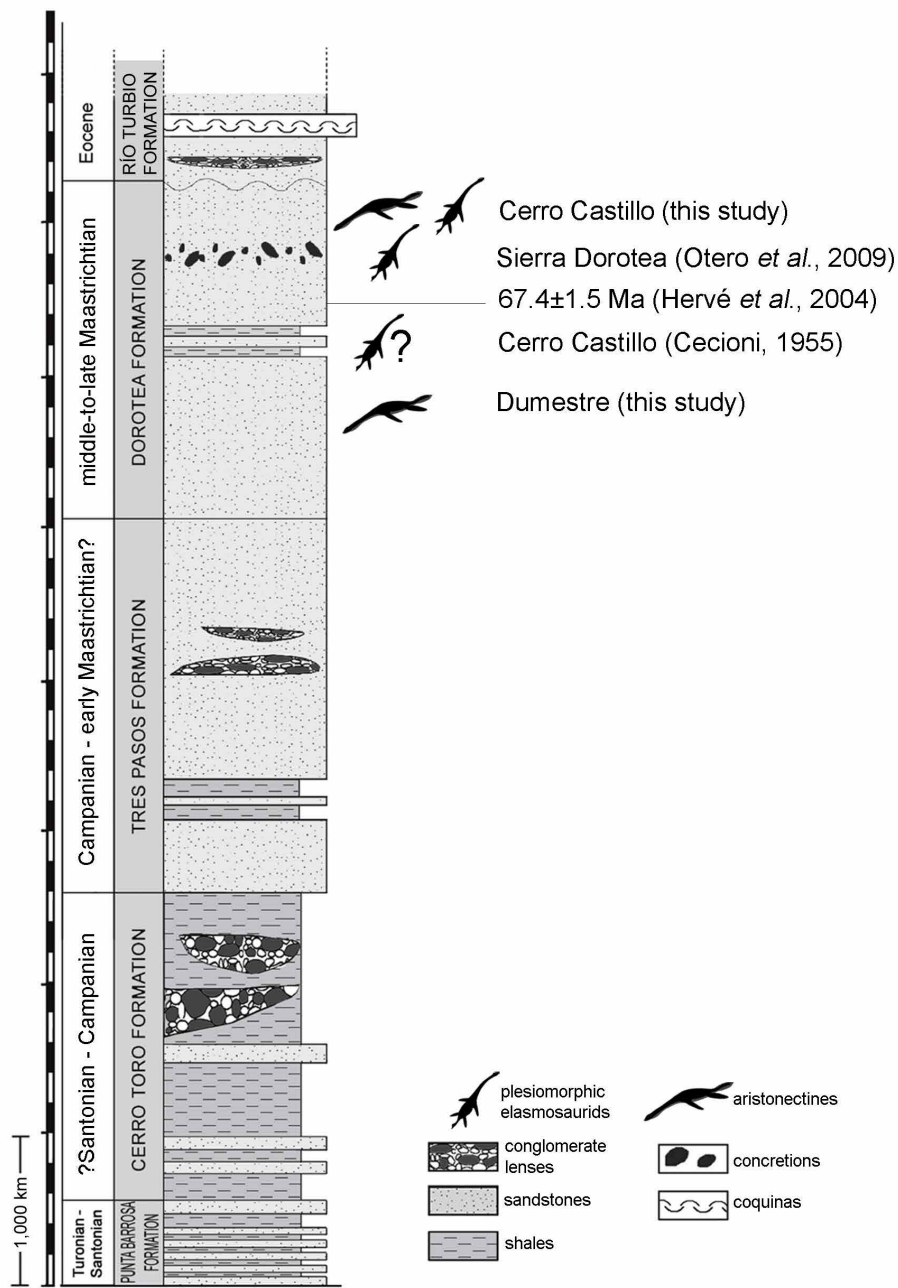


FIG. 2. General stratigraphic column indicating the relative placement of the respective sections exposed on the studied localities. Thickness measurements as given by Katz (1963).

Associated postcranial skeleton SGO.PV.6558 was found *in situ* and subsequently excavated. This was recovered through 16 main blocks of a large concretion, few of them naturally divided by erosion and by action of recent roots. The largest block (16)

is a concretion of 45x35 cm which was naturally divided in five parts, subsequently numbered 16-1 to 16-5. Other remains from different individuals were collected from surface, founded as scattered but concentrated in a radius of few meters. Their

stratigraphic provenance is consistent with a single level, likely, the same that hosted SGO.PV.6558, although its lateral continuity is not evident over the surface because of the recent soil and vegetation. Preliminary analyses performed in the field indicate that they belong to several individuals, based on repeated elements. Even more, among the collected material there are remains referable to mosasaurs (under study by the authors). The vertebra from Sierra Baguales was collected by S.S.A. during fieldwork of the same project on January 2012. Thus, it was found as an element isolated from the sediment, although its stratigraphic provenance could be traced from the massive, yellowish sandstone level of the Dorotea Formation that crops out few tenths of meters near the 'Tetas de Las Chinas' Hill, the latter settled in the upper slopes of the western Sierra Baguales. Finally, the material from Dumestre was collected *in situ* by R.A. Otero and J.L. Oyarzún during May 2009.

Bivariate graphic analysis was performed for cervical centra, using the indices proposed by Welles (1952), taking into consideration the ratios between height (H) and length (L) ($100 \times H/L$), breadth (B) and length ($100 \times B/L$), and breadth and height ($100 \times B/H$) of vertebral centra. Breadth and height were measured on the posterior articular faces. The Vertebral Length Index [$VLI = L / (0.5 \times (H + B))$] of Brown (1981) was also used. Estimation of measurements for the incomplete cervical centra was obtained using photographic mirroring of the available portions.

The chronostratigraphic nomenclature and formal divisions used here follows the scheme of the International Stratigraphic Chart of Cohen *et al.* (2013).

Institutional Abbreviations: SGO.PV.: Paleontología de Vertebrados, Museo Nacional de Historia Natural, Santiago, Chile; CM: Canterbury Museum, Christchurch, New Zealand; ZPAL: Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland; MCS: Museo de Cinco Saltos, Río Negro, Argentina; MML: Museo Municipal de Lamarque, Río Negro, Argentina; MUC: Museo de Geología y Paleontología, Universidad Nacional de Comahue, Neuquén, Argentina; DM: Te Papa Tongarewa Museum, Wellington, New Zealand (former Dominion Museum); TMP: Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; ANSP: Academy of Natural Sciences of Philadelphia; BM: British Museum of Natural History, London, UK.

Anatomical Abbreviations: 16-1 to 16-5, Block 16, part 1 to 5; c: centrum; c1-c8: cervical centra from 1 to 8, hosted in block 16; car: caudal rib; cr: cervical rib; dfp: deep fossa for the postzygapophysis; fh: femoral head; fna: facets for the neural arch; ah: articular head; na: neural arch; ic: indeterminate centrum; igf: indeterminate girdle fragment; lk: lateral keel; mp: mesopodial; nc: neural canal; ns: neural spine; ns-c5: neural spine of the cervical 5 of block 16; pna: pedicels of the neural arch; poz: postzygapophysis; pr: propodial; prz: prezygapophysis; px: phalanges; rf: rib facet; sc?: scapula?; tp: transverse process; tr/tb: trochanter/tuberosity of the propodial; vf: ventral foramina; vk: ventral keel; vn: ventral notch.

4. Systematic Paleontology

Sauropterygia Owen, 1860

Plesiosauria de Blainville, 1835

Plesiosauroidea Welles, 1943

Elasmosauridae Cope, 1869 (*sensu* Ketchum and Benson, 2010)

Elasmosauridae gen. et sp. indet.

Fig. 3

Material: SGO.PV.6560a, a lateral half of an anterior caudal centrum; SGO.PV.6560b, dorsolateral half of a posterior caudal centrum; SGO.PV.6560c, an almost complete mid caudal centrum lacking its ventral portion.

Locality and Horizon: Cerro Castillo, Magallanes Region, southernmost Chile. Uppermost levels of the Dorotea Formation, upper Maastrichtian.

Description: SGO.PV.6560a (Fig. 3D-F) preserves the lateral half of the centrum. This is higher than long, and based in the expectable size by mirroring, it is broader than high. Its articular contour is likely to be hexagonal. The preserved part of the articular facet is slightly concave. In lateral view, the centrum shows the facet for its respective caudal rib, which is oval and axially extended. This facet overlies a projection that raises from the centrum in the same way of a transverse process, and is placed in the upper half of the centrum. Because of this, it is identified as an anterior caudal element. On ventral view, the centrum has a ventrolateral keel that connects anterior and posterior haemal facets. SGO.PV.6560b (Fig. 3A-C) preserves its

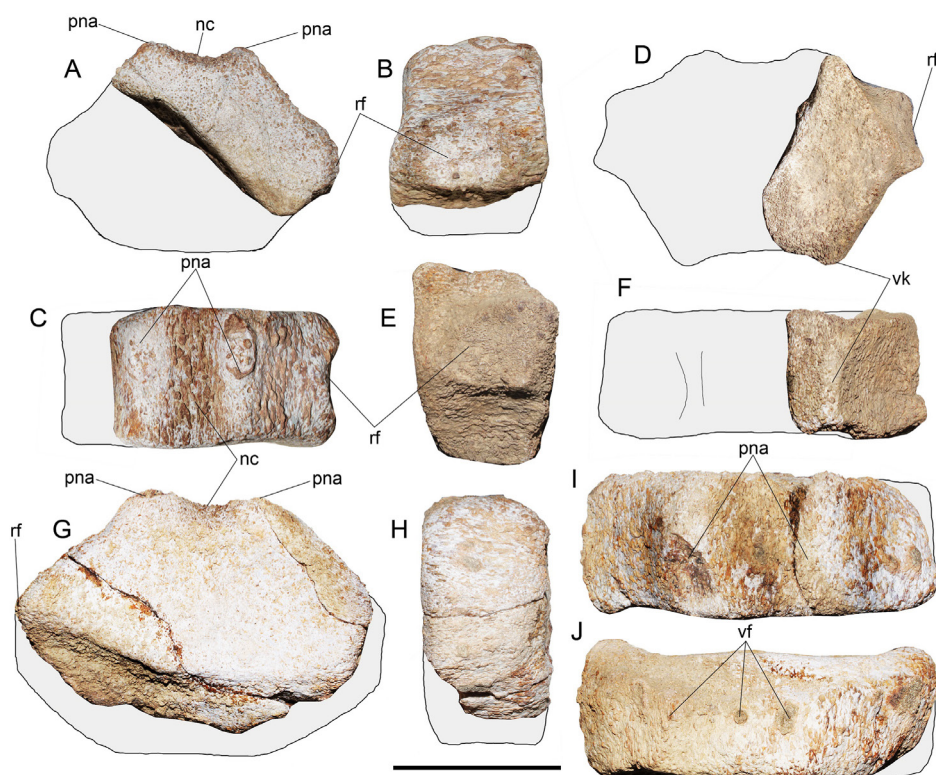


FIG. 3. Elasmosauridae gen. et sp. indet. SGO.PV.6560b. A-C. dosolateral half of anterior caudal centrum in A) articular view, B) lateral view and C) dorsal view. SGO.PV.6560a; D-F. a fragment of an anterior caudal centrum in D) articular view, E) lateral view, and F) ventral view. SGO.PV.6560c; G-J. partial anterior caudal centrum in G) articular view, H) lateral view, I) dorsal view and J) cross-section, ventral view. Grey areas represent missing portions. Scale bar equals 100 mm.

dorsolateral part, which allows observing the neural canal and the pedicels of the neural arch. These are fused, without any visible suture line. The pedicels are thin and elongated over the whole dorsal surface, leaving a broad neural canal. The articular facet shows a partial hexagonal outline based on its flat dorsal surface and by the presence of two well-marked surfaces over its lateral side, these being separated by the rib facet. The articular facets are both slightly concave. The rib facet is oval and slightly expanded axially. SGO.PV.6560c (Fig. 3G-J) is a third centrum with similar features. This is clearly broader than high and higher than long. Despite having its ventral portion broken, the exposed section of three ventral foramina can be observed.

Ontogenetic Observations: SGO.PV.6560b and SGO.PV.6550c have fragments of neural pedicels strongly attached to each centra. On the other hand,

SGO.PV.6560a and SGO.PV.6560b have visible facets for their respective caudal ribs. Following the criteria of Brown (1981) for the neurocentral fusion, we can refer these specimens as adults, while the lack of fusion between ribs and each centra reflects a juvenile feature that could occur even in adult individuals with strong neurocentral fusion (Gasparini and Salgado, 2000; Otero *et al.*, 2014a). Because of these facts, we refer the SGO.PV.6560a-c to a likely a single adult individual.

Remarks: the three specimens were collected scattered over the soil in an area of *ca.* 30 m². All of them show the same kind and degree of erosion by weathering, which indicate a similar time of exposure from the fossil-bearing level. Finally, morphological features and similar size of the vertebrae are consistent in all the three specimens. Because of these facts, we consider this material as likely belonging to a single individual. Also no redundant elements were found.

Elasmosauridae gen. et sp. indet.**Fig. 4**

Material: SGO.PV.6561, SGO.PV.6562, two fragmentary propodials; SGO.PV.6563, an isolated, indeterminate preaxial mesopodial; SGO.PV.6564, an isolated distal carpal/tarsal IV; SGO.PV.6565a-c, isolated phalanges; SGO.PV.6566, a fragmentary ischium.

Locality and Horizon: Cerro Castillo, Magallanes Region, southernmost Chile. Upper levels of the Dorotea Formation, upper Maastrichtian.

Description: SGO.PV.6561 (Fig. 4A, B) comprises fragmentary but associated remains of a single propodial. It preserves most of the distal and proximal part. The articular head is flattened and has a trochanter/tuberosity which is low and has a slight post-axial displacement. The distal end is

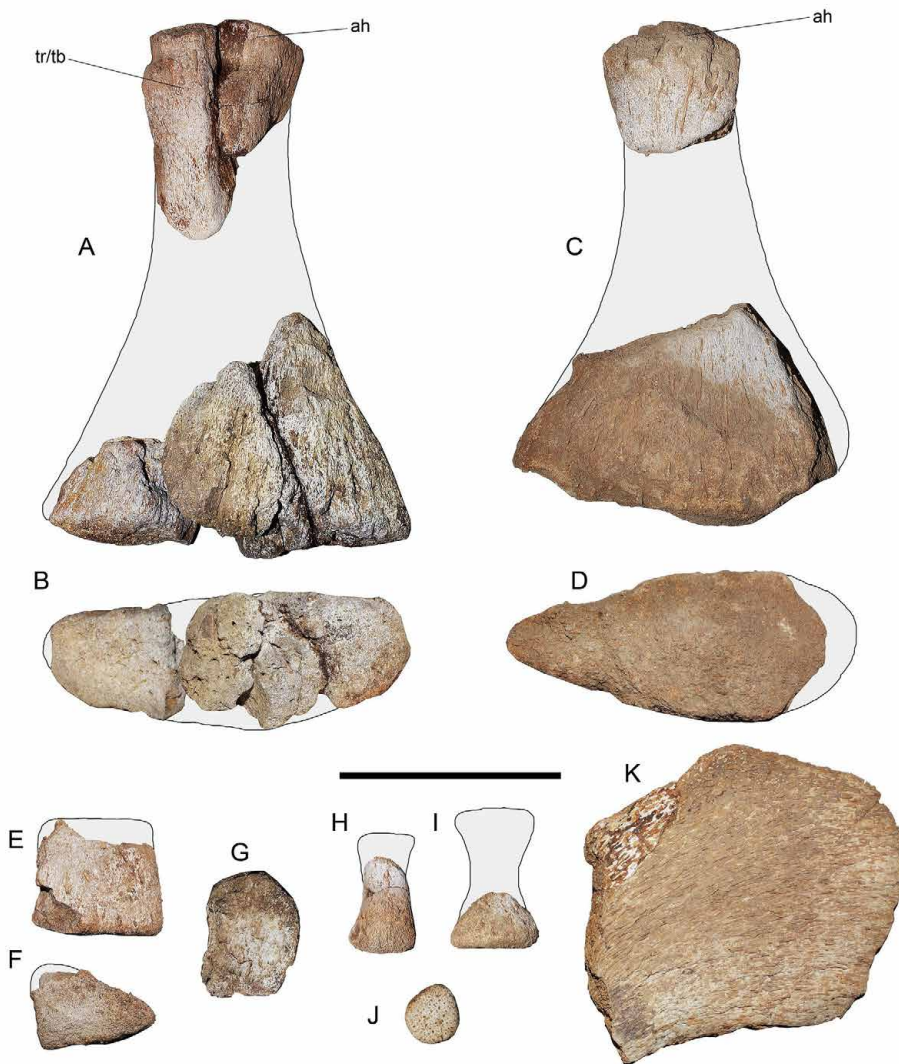


FIG. 4. Elasmosauridae gen. et sp. indet. A-B SGO.PV.6561. Isolated, fragmentary propodial in A) dorsal view; and B) distal view. SGO.PV.6562 Isolated, fragmentary propodial. In C) dorsal view and D) distal view. SGO.PV.6563. Isolated radiale/tibiale or distal carpal/tarsal I in E) dorsoventral view and F) axial view. SGO.PV.6564. G) isolated distal carpal/tarsal IV in dorsoventral view. SGO.PV.6565a, SGO.PV.6565b. H, I) isolated phalanges in dorsoventral view. SGO.PV.6565c. J) a fragmentary phalanx in axial view. SGO.PV.6566. K) A fragmentary ischium. Grey areas represent missing portions. Scale bar equals 100 mm.

incomplete and eroded, but still allows observing the typical bi-convex distal outline with the dorsal surface comparatively flatter. The propodium SGO.PV.6562 (Fig. 4C, D) also preserves its proximal and distal end. The latter is thick and has three well-defined articular facets, two for the epipodials, and a third for a probable pisiform or another post-axial ossification. The proximal portion is heavily eroded and does not preserve the tuberosity/trochanter. Despite of this, SGO.PV.6562 represents a different propodial morphology. SGO.PV.6563 (Fig. 4E, F) is an isolated bone of dubious anatomic identity, which has a sharp lateral board and a thick medial margin, giving it a triangular outline in articular view (not clear if this is proximal or distal). In paraxial (dorsal or ventral) view, it shows a squared outline, slightly broader than long. SGO.PV.6564 (Fig. 4G) is a polygonal distal carpal or tarsal, larger than broad, with two proximal facets forming an angle of *ca.* 120°, and a single distal facet which is flat. SGO.PV.6565a,b (Fig. 4H, I) comprises two isolated phalanges which are dorsoventrally depressed, with laterally expanded facets. On the other hand, SGO.PV.6565c (Fig. 4J) is an articular portion of a phalanx which has a nearly circular articular facet. SGO.PV.6566 (Fig. 4K) is a large and flattened portion of bone. One surface is concave, and therefore is here interpreted as the ventral area that faces to the girdle musculature. **Remarks:** SGO.PV.6561 and SGO.PV.6562 although fragmentary, these represent two different types of propodials. It is not possible with the available material to determinate if each propodial belong to a humerus or to a femur. SGO.PV.6563 is identified as preaxial mesopodial or metacarpal/tarsal I based on the sharp exterior board and the thick medial margin that matches with preaxial elements distally located from the epipodials, such the radiale/tibiale or the distal carpal or tarsal I. The lack of other articulated bones preclude an accurate identification. SGO.PV.6564 can be easily recognized among the other elements of the extremity by its distinctive elongated outline and by the presence of two proximal and one distal articular facet. The position of this element is constrained by the two facets for the mid and post-axial mesopodials, and distally, for the rest of the digit IV. Even more, the flat distal articular facet as well as the general outline are remarkably similar to those of *Aristonectes quiriquinensis* Otero

et al. (2014c: fig. 15), from the late Maastrichtian of the Quiriquina Formation in central Chile, but the lack of additional articulated extremities of regional plesiosaurs for comparison preclude any assignation beyond family level.

Ontogenetic Observations: SGO.PV.6561 has an articular head which is well-differentiated from the trochanter/tuberosity. This is indicative of a young adult or adult stage, since juvenile individuals often show articular heads with poorly differentiated morphology (Welles and Gregg, 1971; Otero *et al.*, 2012b). SGO.PV.6562, SGO.PV.6563, SGO.PV.6564, SGO.PV.6565A-C, and SGO.PV.6566 are difficult to evaluate because of their incompleteness.

Elasmosauridae gen. et sp. indet.

Figs. 5-8

Material: SGO.PV.6558: associated postcranial skeleton preserved in 16 fragments of a large concretion. The block 16, the largest one, includes 8 cervical vertebrae associated with few phalanges and a mesopodial; one isolated cervical vertebra; other block includes at least 4 additional vertebrae, a propodial cast, girdle fragments and phalanges.

Locality and Horizon: Cerro Castillo, Magallanes Region, southernmost Chile. Upper levels of the Dorotea Formation, upper Maastrichtian.

Description: this partial postcranial skeleton (Figs. 5-8) was included in a large concretion. The bones are not articulated but associated. Cervical vertebrae are not correlative; they are randomly arranged with posterior and middle centra mixed and few other elements such phalanges. Most of the vertebrae were broken by the natural fracture of the concretion; however, most of the cervical centra can be measured. Two types of cervical vertebrae are observed, one of them having a comparatively smaller size and lateral keels, such as the vertebra identified as 'c6' (Figs. 5B, 7A). The other type is a larger type of centrum with a well-marked ventral notch and bilobed articular shape, without evidence of a lateral keel. Such are the cases of the centra identified as 'c1' (Figs. 5A, B; 6A, B) and 'c2' (Fig. 6C). In all cases, the cervical neural spines are high, near twice the centrum height. These have slightly expanded dorsal ends and their respective neural channels are oval and dorsoventrally expanded, with delicate neural

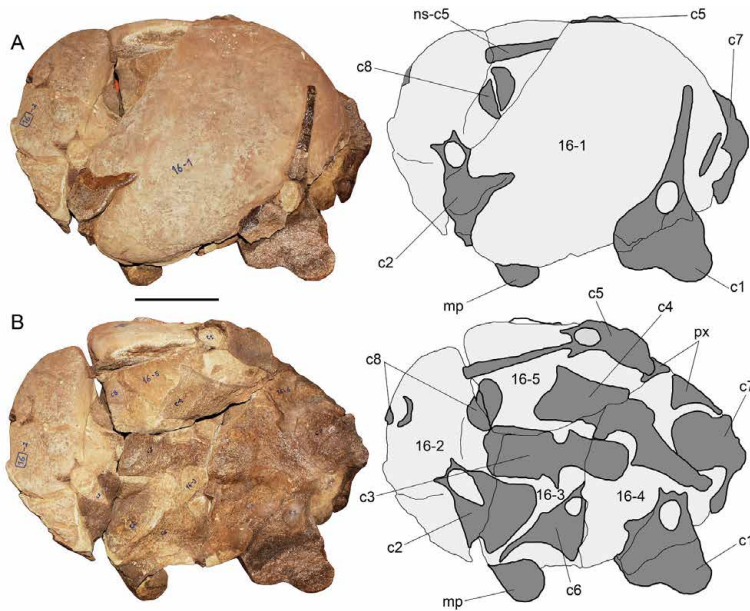


FIG. 5. Elasmosauridae gen. et sp. indet. SGO.PV.6558. Larger concretionary block No. 16 containing a portion of the neck. Anatomical interpretation of the elements are indicated in the outline diagrams on the right. **A**, external view of the block; **B**, internal view of the same block by removing the upper fragment. Scale bar equals 100 mm.

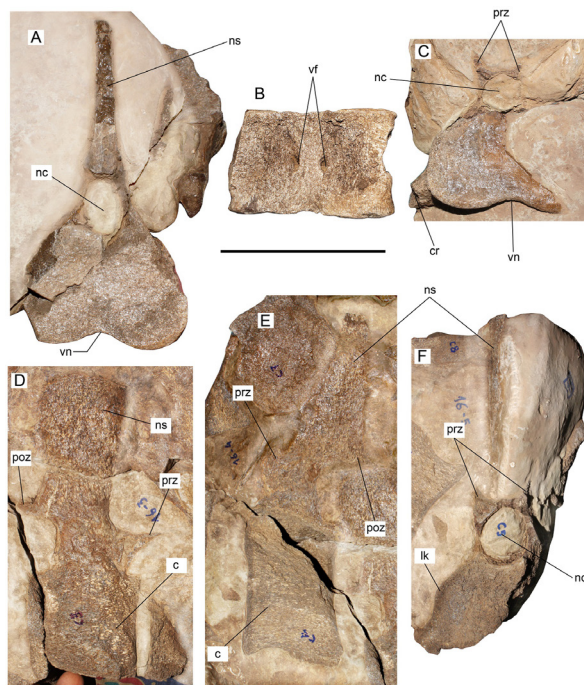


FIG. 6. Elasmosauridae gen. et sp. indet. SGO.PV.6558. Detail of the cervical vertebrae. **A-B**. Cervical vertebra 'c1' in A) anterior articular view and B) ventral view of the same vertebra; **C**, cervical vertebra 'c2' in anterior articular view; **D**, cervical vertebra 'c3' in right lateral view; **E**, cervical vertebra 'c4' in left lateral view; **F**, cervical vertebra 'c5' in anterior articular view. Scale bar equals 100 mm.

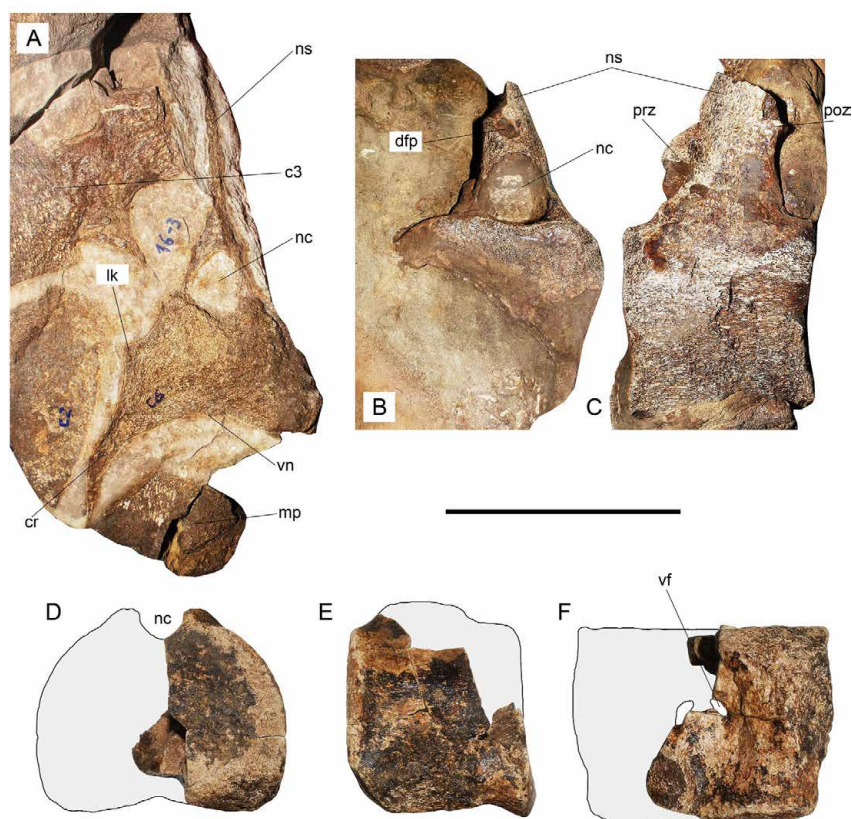


FIG. 7. Elasmosauridae gen. et sp. indet. **A-C.** SGO.PV.6558. Detail of the cervical vertebrae in A) cervical vertebra 'c6' in axial cross-section: B) cervical vertebra 'c7' in anterior articular view and C) same in left lateral view; **D-F.** cervical vertebra 'c8' in D) articular view, E) lateral view and F) ventral view. Grey areas represent missing portions. Scale bar equals 100 mm.

pedicels surrounding it. On ventral view, cervicals have one pair of oval, relatively large foramina, each one aside the ventral midline. These are separated by a broad bony bridge instead a ventral keel. On those cervicals visible on lateral view, the prezygapophysis and postzygapophysis are axially sharp. Every observed neural spine is vertically settled with respect to the centrum. A single pectoral vertebra is preserved in the block 06. This has the same dorsoventrally extended, oval neural canal with massive transverse processes on each side, the latter settled in a low position with respect to the neural canal, which is consistent with its transitional position between the neck and the trunk. A cast of one propodial diaphysis is preserved on the block 01. This lacks the proximal and distal end, making impossible to identify its anatomical position. The same block also preserves one centrum and few broken neural spines embedded in the sandstone.

Block 5 preserves part of a girdle element, likely a pubis, based on its large, in the dished visible surface (consistent with the ventral surface of this element) and in the rounded contour preserved in the bone. Together with this lies an isolated phalanx which is thick and massive. Similar phalanges are present in part of the block 16-4 and in other scattered blocks separated from the concretion.

Ontogenetic observations: This specimen has fused neurocentral sutures. Available lateral views of few cervical vertebrae do not show any evidence of the neurocentral sutures. Additionally, broken vertebrae show centra and their respective neural arches strongly fused. Under these observations and following the criteria of Brown (1981), the SGO. PV.6558 is here considered as an adult specimen.

Remarks: The size of the vertebrae of this specimen shows that it belonged to a large adult individual. To date, this is the most complete specimen recovered

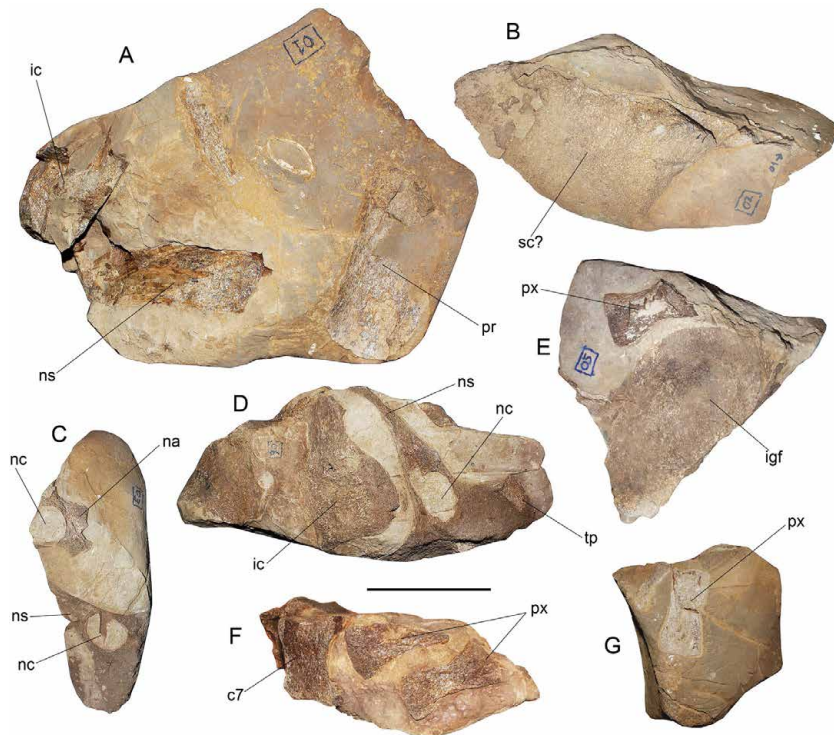


FIG. 8. Elasmosauridae gen. et sp. indet. SGO.PV.6558. Assorted blocks. **A.** Block 01 containing fragmentary neural spines and one propodial cast?; **B.** Block 02 containing a fragment of a girdle element, likely a scapula; **C.** Block 03 containing fragmentary neural arches and centra; **D.** Block 06 containing part of one 'pectoral' vertebra (right side); **E.** Block 05 containing a fragment of a girdle element and a phalanx; **F.** One of the fragments of Block 16 containing the 'c7' and few phalanges; **G.** isolated block containing a phalanx. Scale bar equals 100 mm.

from Magallanes Region. Morphological features of the cervical vertebrae are almost identical to those of the juvenile, indeterminate elasmosaurid SGO.PV.6648 recovered from upper levels of the Sierra Dorotea near Puerto Natales (Otero *et al.*, 2009).

**Aristonectinae O'Keefe and Street, 2009;
sensu Otero *et al.*, 2012b.**

**Aristonectinae gen. et sp. indet.
Fig. 9**

Material: SGO.PV.6569: a half of a small cervical centrum of a juvenile individual.

Locality and Horizon: Sierra Baguales, Magallanes Region, southernmost Chile. Upper levels of the Dorotea Formation, upper Maastrichtian.

Description: A fragment of a centrum (Fig. 9) which preserves most of their lateral surface. The best preserved articular facet is slightly concave. In

axial view, the centrum is dorsoventrally depressed and laterally expanded, without ventral notch. On dorsal view, nearly circular neural facets are observed. Ventrally, the centrum preserves one ventral foramen and part of the bony bridge that separate the latter from its paired ventral foramen. This allows estimating the complete measurements of this centrum by mirroring of the preserved portion. On lateral view a nearly circular, soft surface is interpreted as the facet for cervical rib. Both facets (*i.e.*, those for the neural arch and those for the cervical ribs) are clearly visible since erosion mostly affected the non-articular surfaces. This indicates that articular surfaces possess a more compact, better ossified tissue, compared with the rest of the centrum.

Ontogenetic observations: The available articular facets are soft without signs of fusion neither evidence of partial contact neither with the neural arches nor the cervical ribs. Together with this, the very small size indicates that this was a very young specimen.

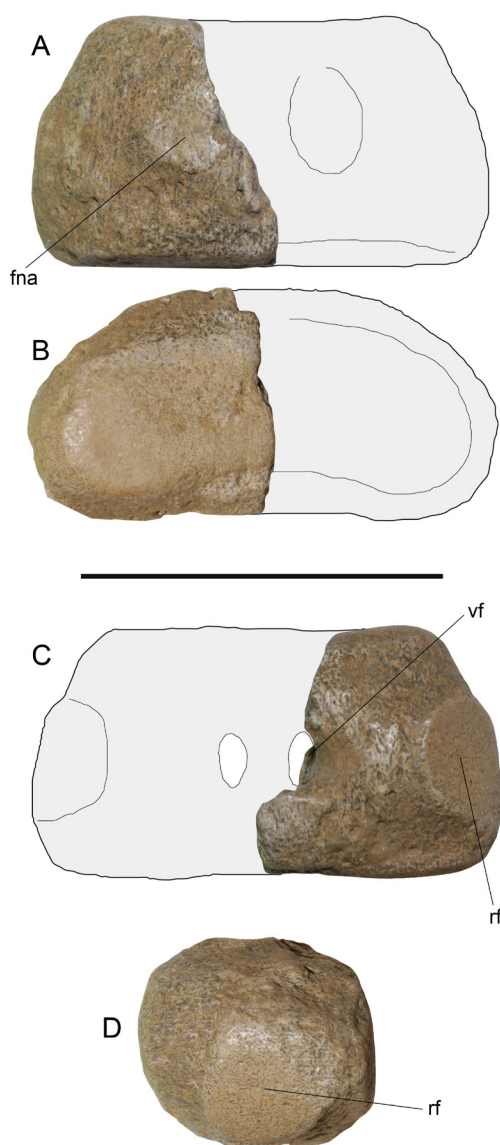


FIG. 9. *Aristonectinae* gen. et sp. indet. **A-D**. SGO.PV.6569. Fragment of a very juvenile mid cervical centrum in **A**. dorsal; **B**. articular; **C**. ventral and **D**. lateral views. Grey areas represent missing portions. Scale bar equals 50 mm.

Remarks: This specimen represents the northernmost occurrence of *aristonectines* in the Magallanes Basin. It was collected from surface in the same place where other vertebral remains referred to an indeterminate non-hadrosauroid ornithopod dinosaur were recovered (Rubilar-Rogers *et al.*, 2013), thus, indicating very shallow waters.

Aristonectinae gen. et sp. indet.

Fig. 10

Elasmosauridae indet.: Otero and Rubilar-Rogers (2010).

Material: SGO.PV.6580. Associated remains of a single small individual comprising an almost complete femur, the proximal end of the other femur, two caudal vertebrae, two dorsal vertebrae, few ribs and gastralia. **Locality and Horizon:** Dumestre, south of Puerto Natales, Magallanes Region, southernmost Chile. Middle to upper levels of the Dorotea Formation, lower upper Maastrichtian.

Description: Dorsal centra (Fig. 10A-D) with a medial constriction and being dorsoventrally depressed. The neural pedicels of dorsal vertebrae are thick and their respective transverse processes, although broken, they show a nearly oval section. The neural arches are well-fused to each centra. The articular facets (Fig. 10E) of caudal centra change from octagonal in mid caudals to hexagonal in posterior centra. Caudal centra are strongly fused to their respective ribs, neural arches and haemal arches. The femur (Fig. 10F, G) has an elongated and slender diaphysis with a distal end without well-marked articular facets, while its proximal end with has a prominent, hemispherical articular head.

Ontogenetic Observations: the presence of neuro-central fusion in the dorsal centra and even in the caudal-most centra, the erased suture lines, and the well defined, prominent hemispherical head of the femur, are all indicative of an adult stage (Brown, 1981).

Remarks: The presence of dorsoventrally compressed dorsal centra with thick neural arches are common features of the *aristonectines* (Otero *et al.*, 2012b; O’Gorman *et al.*, 2014a, b). Even more, the mid caudal centrum with octagonal outline is consistent with the presence of a likely octagonal anterior centrum such those diagnostic of the genus *Aristonectes* (see further text), although in the SGO.PV.6580, these are less expanded laterally. In addition, the propodial has an expanded, hemispherical articular head which depends on the ontogeny. Based on the specimen SGO.PV.260 from the upper Maastrichtian of central Chile (juvenile individual referred to *A. quiriquinensis*, Otero *et al.*, 2014c), during the ontogeny the femur passes from a shallowly convex proximal end to a very hemispherical articular head in the adult (SGO. PV.135, referred). Therefore, the condition observed in the SGO.PV.6580 is consistent with an adult individual. Based on these facts, the SGO.PV.6580 is here identified

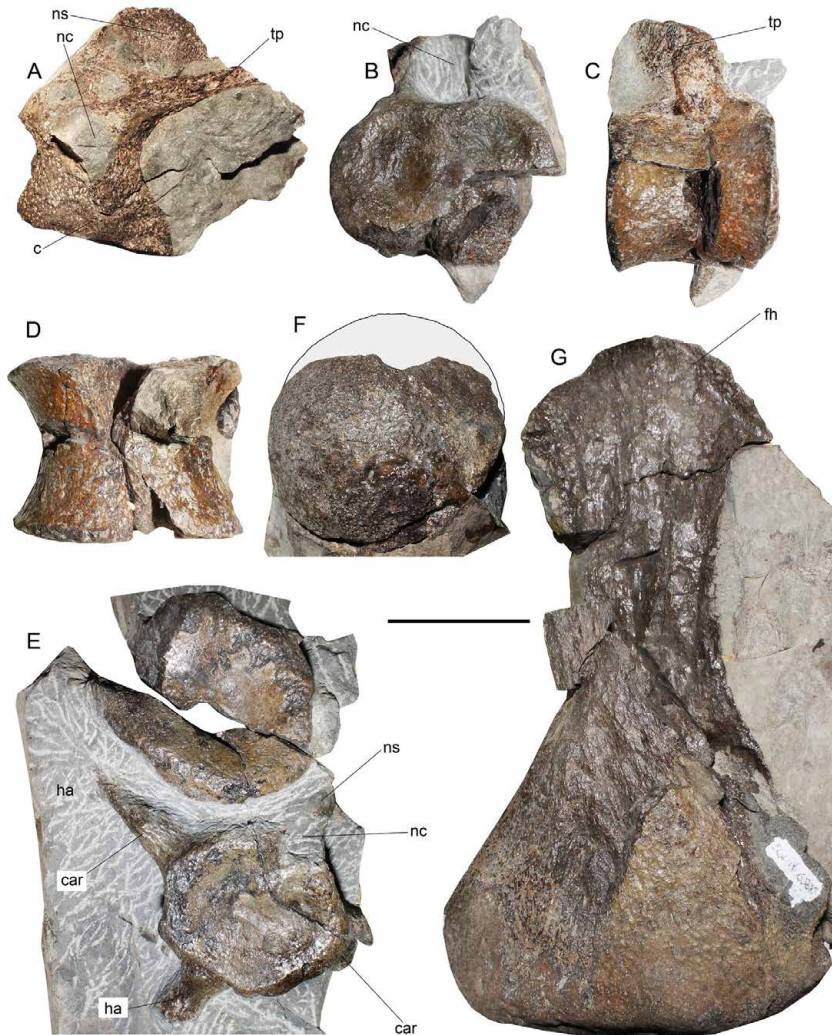


FIG. 10. *Aristonectinae* gen et sp. indet. SGO.PV.6580. **A**, mid-dorsal vertebra in anterior articular view; **B-C**, anterior dorsal vertebra in **B**, anterior articular and **C**, right lateral and **D**, ventral view; **E**, two mid-caudal vertebrae in articular vie; **F-G**, femur; **F**, detail of the hemispherical articular head; **G**, dorsal view. Grey areas represent missing portions. Scale bar equals 100 mm.

as an indeterminate aristonectine. Interestingly, even in its adult stage, this specimen represents a very small aristonectine compared with other well-known skeletons such those of *A. quiriquinensis* and *Kaiwhekea katiki* Cruickshank and Fordyce, 2002, from the early Maastrichtian of New Zealand.

Genus *Aristonectes* Cabrera, 1941

Type Species: *Aristonectes parvidens* Cabrera, 1941. Chubut, Argentina. Lefipán Formation, upper Maastrichtian.

Aristonectes sp.

Fig. 11

Material: SGO.PV.6559. One isolated, incomplete anterior caudal centrum.

Locality and Horizon: Cerro Castillo, Magallanes Region, southernmost Chile. Upper levels of the Dorotea Formation, upper Maastrichtian.

Description: Only a left half of a centrum is preserved (Fig. 11A-D). By mirroring of the articular facet we can recognize a distinctive octagonal outline. The centrum is broader than high and higher than long.

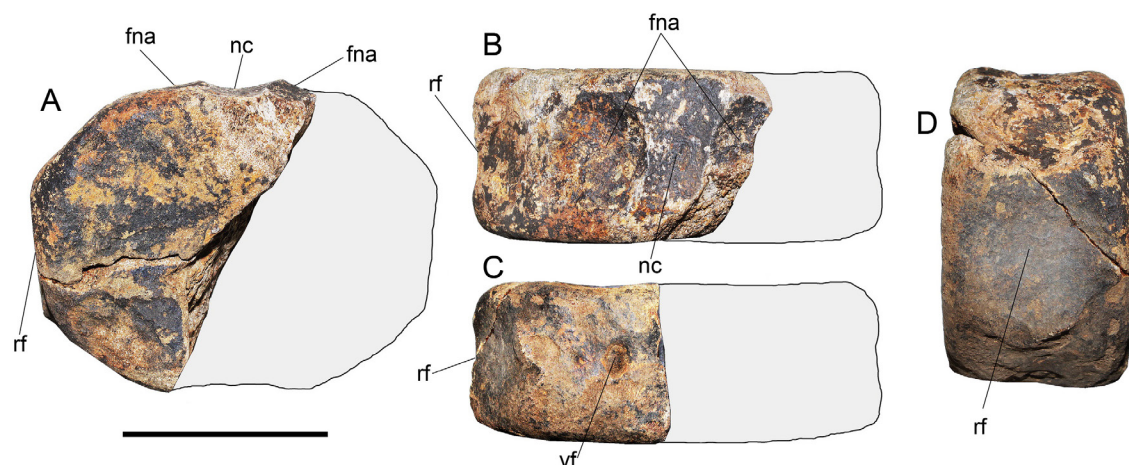


FIG. 11. *Aristonectes* sp. A-D. SGO.PV.6559. Isolated anterior caudal centrum in A. Anterior articular; B. dorsal; C. ventral and D. right lateral views. Grey areas represent missing portions. Scale bar equals 100 mm.

In dorsal view, oval and axially extended neural facets are observed, leaving a brief anterior space before each axial facet. The neural canal is narrower than each neural facet and one its posterior margin is broader, which allow orientation of the vertebra (based on specimen SGO.PV.94 under study). On ventral view can be observed one large foramen and a small lateral foramen. The left lateral view allows observing a rib facet which is oval and extended dorsoventrally.

Ontogenetic Observations: The clearly visible facets for the neural arches and the cervical ribs indicate that this could belong to a juvenile specimen. The comparative size of the centrum is similar to the respective centra of the juvenile SGO.PV.260 of *A. quiriquirensis*. More recent data shows that neurocentral fusion of the axial skeleton in plesiosaurs occurs from cranial to caudal direction (Gasparini and Salgado, 2000; O’Gorman et al., 2013; Otero et al., 2014a), it is difficult to assign an ontogenetic stage for this specimen; nevertheless, the well-defined octagonal articular outline and its relatively large size support a young adult stage.

Remarks: The octagonal articular outline of the anterior caudal vertebrae has been regarded as unusual even in their first description by Gay (1848: *Erpetología fósil* No. 1, figs. 1, 2). Such vertebrae, originally considered to be cervicals, were included in the hypodigm of ‘*Plesiosaurus chilensis*’ Gay (*nomen dubium*), based on several specimens from the upper Maastichtian Quiriquina Formation

in central Chile. These unusually short centra, their large rib facets, and the octagonal outline were later referred by Deecke (in Steinmann et al., 1895) to a ‘plesiosaur’ *sensu lato*, and therefore, Deecke reassigned the species of Gay to ‘*Plesiosaurus chilensis*’ Gay (*nomen dubium*). Remarkably similar vertebrae were later described for the holotype of *Aristonectes parvidens* Cabrera, 1941 from the upper Maastrichtian of Chubut, Argentina, and also regarded as cervicals in its original description. After, Welles (1962: 70-73) reviewed these records and noted these unusual vertebrae, commenting that these were not diagnostic to species level. Based on their proportions, Welles referred the octagonal centra as belonging to an indeterminate ‘plesiosaur’. This latter author mixed in his taxonomical opinion a specimen from Broili (1930) which actually belong to a non-aristonectine elasmosaurid (Otero et al., 2014a) and proposed to refer all them as *Dolychorhynchopidae* indet. Gasparini et al. (2003b) recognized these elements as belonging to the caudal centra of *A. parvidens*. Later Otero et al. (2012b) and O’Gorman et al. (2013) confirmed the anatomical position of the octagonal centra, based on several articulated skeletons from Chile and Antarctica. In the particular case of the SGO.PV.260 which has octagonal anterior caudal centra, this specimen was first identified as *Aristonectes* sp. through a bivariate graphic analysis of their cervical centra (Otero and O’Gorman, 2013), and later referred to *A. quiriquirensis* by Otero et al. (2014c) based on

diagnostic morphological features. These records allow recognizing the anterior caudal centra with octagonal articular outline as diagnostic of the genus *Aristonectes*. Such feature is present both in *A. quiriquinensis* and in *A. parvidens*.

5. Discussion

5.1. Bivariate Graphic Analysis

Cervical measurements of the studied specimens are summarized on Table 1. These were compared with other uppermost Cretaceous adult specimens from the Weddellian Biogeographic Province (Zinsmeister, 1979; WBP hereafter) and from North America (O’Gorman *et al.*, 2013; Otero *et al.*, 2014b). Plotting of the SGO.PV.6558 shows a low dispersion pattern (Fig. 12A). This plot is distributed within the dispersion of known adult aristonectines in all the three graphics (HI *versus* BI, VLI *versus* BI and VLI *versus* HI), but part of the plot of aristonectines is intersected with the plot of non-aristonectine elasmosaurids. Because of this, the adult SGO.PV.6558 can only be discarded as an extreme, very-long necked form such *Elasmosaurus platyrus* Cope, 1869, from the uppermost Cretaceous of North America, but

its taxonomical identification cannot be precised beyond family level. SGO.PV.6558 has cervical proportions which are coincident with adult aristonectines, but they are also narrowly similar to intermediate adult forms such the specimen CM Zfr 115 from the upper Campanian Conway Formation in New Zealand (Hiller *et al.*, 2005), the SGO.PV.6506 from early late Maastrichtian levels of the Quiriquina formation exposed in Pelluhue (Otero *et al.*, 2014a), and is also coincident with the indeterminate elasmosaurid SGO.PV.6523 from upper levels of the López de Bertodano Formation (upper Maastrichtian) exposed in Seymour Island, Antarctica (Otero *et al.*, 2014b). Because CM Zfr 115 is a juvenile, near adult specimen, we include its plot among the graphic analysis of adults, as well as in that of the juveniles.

On the other hand, SGO.PV.6569 from Sierra Baguales was compared with coeval juvenile specimens from the WBP and North America. In all the three graphics, this was returned within the *Aristonectinae* (Fig. 12B), the latter being clearly dissociated from regular elasmosaurids. Therefore, SGO.PV.6569 is confidently referred to an indeterminate aristonectine, being the northernmost record of the subfamily along the Magallanes Basin.

TABLE 1. MEASUREMENTS OF VERTEBRAL CENTRA OF THE STUDIED SPECIMENS.

COLLECTION NUMBER	IDENTIFICATION WITHIN THE FOSSIL	LENGTH	HEIGHT	BREADTH
SGO.PV.6558	C1	63.93	77.47	108.88
	C2	58.29	62.92	98.25
	C3	60.95	68.63	-
	C4	61.83	95.84	-
	C5	68.61	-	123*
	C6	57.05	62.58	87.83
	C7	65.76	70.81	99.5*
	C8	61.09	-	106.17
	C9	67.98	79.52	84.3*
SGO.PV.6569	C1	33.8*	32*	65.5*

Absence of measurements is denoted with a line, while those measures estimated by mirroring of the available portions are denoted by an asterisk. Vertebral Length Index (VLI)= $L/(0.5*(H+B))$ from Welles (1952) and Brown (1981); index of ratio between height and length (HI)=($100*H/L$) and index of ratio between breadth and length (BI)=($100*B/L$) from Welles (1952).

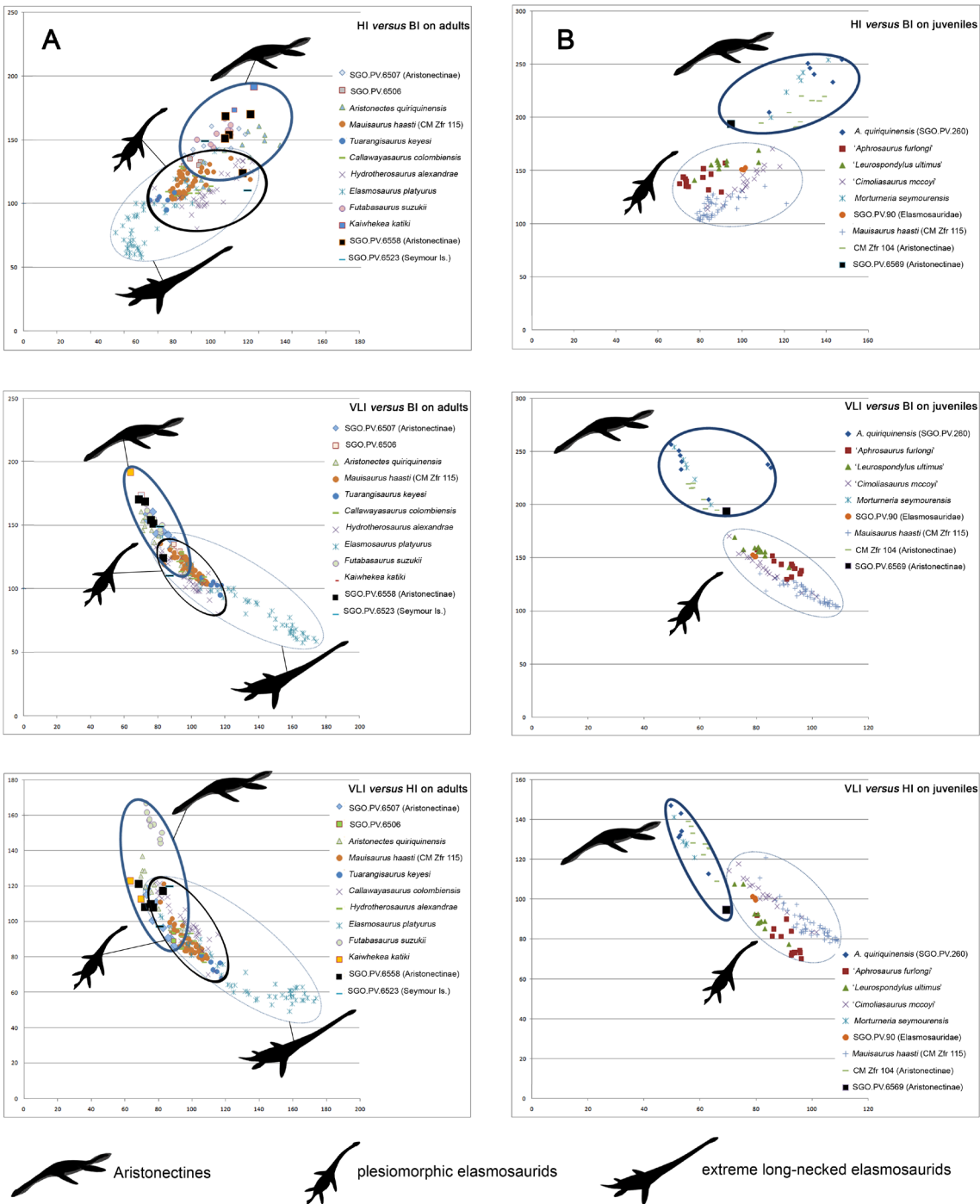


FIG. 12. Plots obtained with the bivariate graphic analysis: HI versus BI, VLI versus BI, and VLI versus HI. **A.** From up to down, plots for adult specimens; **B.** From up to down, plots for juvenile specimens. Data taken from O’Gorman et al. (2013), Otero and O’Gorman (2013), Otero et al. (2014a, b).

5.2. Establishing three major groups within Elasmosauridae

Elasmosaurus platyurus from the lower Campanian of United States, which is the family-type species of the Elasmosauridae, has a remarkable number of 72 cervical vertebrae, only overpassed by *Albertonectes vanderveldei* Kubo *et al.*, 2012, from the middle upper Campanian of Canada, with 76 cervicals. Both taxa represent the longest necked animals known to date (Sachs *et al.*, 2013). On the other hand, the global record of elasmosaurids includes several lower Aptian-Maastrichtian, fairly complete axial skeletons, most of them having a cervical count between 60 to 66. This condition is observed in North American taxa such *Thalassomedon haningtoni* Welles, 1943 (62 cervicals), *Styxosaurus snowii* (Welles, 1952) (62 cervicals), *Hydrotherosaurus alexandrae* Welles, 1943 (60 cervicals), as well as the CM Zfr 115 from New Zealand, referred to *Mauisaurus haasti* (Hiller *et al.*, 2005) (66 cervicals). Interestingly, oldest elasmosaurids from the Aptian-Cenomanian such *Callawayasaurus colombiensis* (Welles, 1962) and *T. haningtoni*, possess 23 to 25 dorsal centra (Welles, 1943, 1962). This dorsal count also happens on leptocleidids (*i.e.*, *Nichollssaura borealis* (Druckenmiller and Russell, 2008)) and cryptocleidids (*i.e.*, *Cryptocleidus eurymerus* Phillips, 1871), supporting that 23 to 25 dorsals is the plesiomorphic condition among elasmosaurids. On the other hand, the extreme-necked species *E. platyurus* and *A. vanderveldei* have 18 and 19 dorsals, respectively. This shows the shifting of few dorsal centra into the neck, as well as an increasing on the number of cervical centra, finally reflected in a very long neck with even 10 additional centra with respect to the common plesiomorphic elasmosaurids.

At this point it is not clear how (and how many times) the extreme long-necked forms evolved within elasmosaurids. So far, we can identify a plesiomorphic condition of the neck, having *ca.* 60 cervicals (linked to 23-25 dorsal centra), while the appearance of disparate neck types at least occurred twice. One could happened during the Campanian in North America, represented by the extreme long-necked taxa such *E. platyurus* and *A. vanderveldei*, with up to 72 cervicals (linked to 18-19 dorsals); a second evolutionary stage is represented by the appearance of the shortened and robust necks of aristonectines (43 cervicals linked to 23-24 dorsals).

Based on this, we propose three morphotypes within the Elasmosauridae: **i.** plesiomorphic elasmosaurids (60 cervicals); **ii.** extreme long-necked elasmosaurids (72-76 cervicals); **iii.** the Aristonectinae, characterized among other features by *ca.* 43 cervicals.

5.3. Cervical changes during ontogeny and their consequences on the Bivariate Graphic Analysis

The indeterminate aristonectine SGO.PV.6569 shows that in early stages of the growth, aristonectines have an axial skeleton dorsoventrally depressed with respect to adult specimens. During the growth, cervical vertebrae change their juvenile flattened proportions by increasing the height of each centrum. This is particularly evident in *A. quiriquinensis* comparing the cervicals of the juvenile specimen SGO.PV.260 with those of the adult holotype SGO.PV.957. This situation is evident on the bivariate graphic analysis. While in juveniles we can split aristonectines from other elasmosaurids, on adults they have a partial intersection of the plots. As a consequence, bivariate graphic analysis is here proved to be useful among juveniles, but it is inaccurate when applying it to adult elasmosaurids (Fig. 12). Despite of this, the analysis of adult proportions is indeed useful for separate aristonectines from extreme forms (*e.g.*, *E. platyurus*), but leaves an uncertain situation between adult aristonectines and adult plesiomorphic-necked elasmosaurids like CM Zfr 115 (65 cervicals).

5.4. Comparisons with other plesiosaurs from the WBP

5.4.1. SGO.PV.6558, Elasmosauridae indet. from Cerro Castillo

Neural spine features of the indeterminate elasmosaurid SGO.PV.6558 are remarkably similar to those observed in the upper Maastrichtian adult specimen from Antarctica SGO.PV.6523 (Elasmosauridae indet.: Otero *et al.*, 2014b). Both specimens bear an identical deep fossa for articulation of the postzygapophysis of the following anterior vertebra (Otero *et al.*, 2014b: fig. 3). This can be observed especially on the neural spine of the cervical vertebra 'c7' of the SGO.PV.6558 (Fig. 7B). SGO.PV.6558 also has cervical vertebrae with deep fossae for articulation of the postzygapophysis, which are

very similar to those of the specimen CM Zfr 115 from lower Maastrichtian levels of the Conway Formation in New Zealand. This specimen was referred by Hiller *et al.* (2005) to *Mauisaurus haasti* Hector, 1874. It preserves the complete neck with 63 cervicals plus the atlas-axis (missing), thus, it can be excluded from the aristonectines which have less than 45 cervicals (*e.g.*, *K. katiki*, *A. quiriquinensis*) (Otero, 2014).

On the other hand, the outline of the mid and posterior cervical vertebrae of the SGO.PV.6558 are remarkably coincident with those of the juvenile specimen SGO.PV.6648 found in upper levels of the Dorotea Formation exposed in Cerro Dorotea near Puerto Natales (Otero *et al.*, 2009: fig. 4c). Both specimens have a very similar stratigraphic provenance and were found in the same basin, which suggest they belong to the same taxon.

5.4.2. SGO.PV.6560a-c, *Elasmosauridae* indet. from Cerro Castillo

These vertebrae have hexagonal articular contour, and also a lateral surface between the neural arch and each caudal rib which is comparatively larger than the surface between the rib facet and the ventral surface. This gives to the centra triangle-like aspect in articular view. Another remarkable feature is the presence of a sharp ventral keel that defines the articulation for the haemal arches in posterior caudal centra. Finally, these centra have slightly amphicoelous articular surfaces. All these features are also present in the indeterminate elasmosaurid SGO.PV.6506 from lower upper Maastrichtian levels of the Quiriquina Formation exposed at Pelluhue, Maule Region (Otero *et al.*, 2014a), and these have been reported in other late Maastrichtian specimens from central Chile (Broili, 1930).

5.4.3. SGO.PV.6580, *Aristonectinae* indet. from Dumestre

This specimen has caudal vertebrae which are almost identical to the ZPAL R.8/1-4 described by Fostowicz-Frelik and Gaździcki (2001) from a small individual from the Klb2 unit (early upper Maastrichtian) of the López de Bertodano Formation exposed in Seymour Island, Antarctica. Interestingly, the femur SGO.PV.6580 is similar to the ZPAL R.8/6 (Fostowicz-Frelik and Gaździcki, 2001: pl 3, 4). Both specimens have slender diaphysis and hemispherical articular heads. The specimen from

Antarctica (ZPAL R.8) have been described as a sub-adult based in the absence of neurocentral fusion on the available caudal centra, while the SGO.PV.6580 has strong fusion between the caudal centra and their respective neural arches, caudal ribs, and even their haemal arches, indicating that this is an adult individual. Both specimens also share a similar size, considering the sub-adult stage of the first and the adult stage of the second, being both small compared with other aristonectines such *K. katiki* of *Aristonectes* spp. Another specimen from the same locality of the ZPAL R.8, and also from the López de Bertodano Formation (MLP 82-I-28-1) was identified as an indeterminate elasmosaurid (Gasparini and Del Valle, 1984). The specimen is an adult and has a remarkably similar femur with hemispherical head, slender diaphysis, and small size. Finally, the same set of morphological features described for the SGO.PV.6580 are partially present in associated remains of likely a single individual (SGO.PV.6579) recovered from upper Campanian levels of the Santa Marta Formation exposed in the James Ross Island, Antarctica (Otero *et al.*, 2014b: fig. 6). This share similar caudal centra and a propodial head which is indeed hemispherical, and likely referable to a femur.

6. Paleoenvironment

6.1. Sierra Baguales

The fragmentary cervical SGO.PV.6569 was found as transported in the surface together with other vertebrates, among them teeth of the chondrichthyan *Carcharias* sp. and a fragmentary caudal centrum of an indeterminate ornithomimid dinosaur (Rubilar-Rogers *et al.*, 2013). Together with these, bivalvians of the genus *Lahillia* were also found, while in lower levels, incomplete leaf prints were observed. These fossils indicate the proximity to the coast and a local shallow transgression that caused the deposition of marine vertebrates and invertebrates.

6.2. Cerro Castillo

Among the specimens collected, SGO.PV.6558 is clearly a large adult. The specimens SGO.PV.6560a-c, SGO.PV.6561, SGO.PV.6562, SGO.PV.6563, SGO.PV.6564, SGO.PV.6565a-c, and SGO.PV.6566, although very fragmentary, these show

the presence of mid-sized to large elasmosaurids. The fossil diversity observed in lower levels of the section includes associated banks of *Pterotrionia cazadoriana* Wilckens, the bivalves *Lahillia luisa* Wilckens, and indeterminate oysters. The presence of trioniids indicates shallow-water habitats, no deeper than 10-15 m (Stanley, 1977).

6.3. Dumestre

The fauna associated with the aristonectine SGO.PV.6580 includes indeterminate trioniids, as well as kossmaticeratids, gaudryceratids and nautiloids. The fossil-bearing sediment of the associated fauna corresponds to fine to medium-coarse sandstone, and could belong to a shoreface environment.

7. Paleobiogeography of Upper Cretaceous plesiosaurs along the WBP

Among elasmosaurids, aristonectines have necks with less than 45 cervical vertebrae, and centra which are comparatively reduced in length compared to the proportions observed in other elasmosaurids (Otero, 2014). Despite of this, representatives of the genus *Aristonectes* could reach an adult size over 10 m, not implying an actual adult shorter neck than other elasmosaurids, but instead, different body proportions (Otero *et al.*, 2014c). As explained in the Material and Methods, their VLI cervical indices have commonly an average of 80 in adults (O’Gorman *et al.*, 2013), falling to 59 in juvenile specimens (based on TTU P 9219 and SGO.PV.260). The other opposite dispersion are the extreme long-necked forms such *E. platyurus*. Calculation of average VLI indices based on the measurements provided by Welles (1952) indicate for adult extreme long-necked forms a value of 135, while juvenile individuals have average VLI of 85.

Among the specimens discussed here, those elasmosaurid postcranial skeletons which preserve the neck (*i.e.*, CM Zfr 115, SGO.PV.260, SGO.PV.957, and the holotype of *K. katiki*, among others), show a clear trend for increasing the mid cervical VLI values (O’Keefe and Hiller, 2006: fig. 3). Thus, mid cervical centra are, comparatively, the most flattened cervicals along the neck of a single individual (average of height plus breadth is the lowest along the neck). Anterior cervicals are smaller, but they are commonly less expanded laterally (or

else, more rounded in articular view), while posterior cervicals tend to be more oval to circular, but larger in size. Such considerations could help to explain the presence of intermediate cervicals with average VLI values of 98, which cannot be placed neither among extreme long-necked, neither among aristonectines. Summarizing these considerations, intermediate elasmosaurids are characterized by having a number of cervical vertebrae ranging near 56 to 65, together with an adult average VLI of 99 (juvenile average VLI=85). Examples of these are distributed widespread during the Cretaceous and are the most common elasmosaurids, among them, *Callawayasaurus colombiensis* (Welles, 1962; Carpenter, 1999) from the Aptian of Colombia (VLI: 92-107), CM Zfr 115 referred to *M. haasti* (Hiller *et al.*, 2005) from New Zealand (VLI: 83-109), and *Hydrotherosaurus alexandrae* Welles, 1943 from the Maastrichtian of Colorado, USA (VLI: 79-117). Opposed to these are two extremes; the aristonectines, with less than 45 cervicals and adult average of 80 (juvenile average VLI=55, based on the specimen SGO.PV.260), and the extreme long-necked forms with more than 70 cervicals and average adult VLI of 135 (juvenile average VLI=85), the latter based on *E. platyurus* (72 cervicals) and *Albertonectes vanderveldei* Kubo, Mitchell and Henderson, 2012 from the upper Campanian of Canada (although the cervical elements of the latter cannot be measured in all the three dimensions).

Following these three different morphotypes, the plesiomorphic elasmosaurids, the subfamily Aristonectinae (dwarf and very large representatives), and the extreme long-necked elasmosaurids, we review their respective known occurrences along the WBP.

7.1. Aristonectines

Upper Campanian: So far, the oldest records of indeterminate aristonectines were recovered from upper Campanian levels of the Santa Marta Formation in James Ross Island, Antarctica (Otero *et al.*, 2014b: fig. 6), and from the coeval Allen Formation in Argentinean Patagonia (MUC Pv 131, O’Gorman *et al.*, 2013).

Lower Maastrichtian: An articulated juvenile specimen recovered from Sandwich Bluff on Vega Island (upper Snow Hill Island Formation, lower Maastrichtian) was described by Martin *et al.* (2007) and can be referred to an aristonectine based on the distinctive anterior caudal centra. The record from

New Zealand comprises the holotype of *K. katiki*, one of the most complete aristonectine skeletons known to date, recovered from lower Maastrichtian levels exposed at Shag Point, north of Dunedin, New Zealand (Cruikshank and Fordyce, 2002). A fragmentary skull (CM Zfr 73 and 91) described by Hiller and Mannering (2004) from lower Maastrichtian levels of the Conway Formation in New Zealand is also referable to an aristonectine under the light of the morphologies of the posterior skull of *A. quiriquinensis*. Interestingly, this skull has a smaller size than those of *K. katiki*, *A. parvidens*, and *A. quiriquinensis*. In addition, other records of early upper Maastrichtian age from Seymour Island, Antarctica (Klb2 unit of the López de Bertodano Formation) shows the presence of morphotypes which are closely related to the aristonectine SGO.PV.6580 from Dumestre (Gasparini et al., 1984: fig. 6; Fostowicz-Frelik and Gaździcki, 2001: plates 1, 3 and 4), suggesting the presence in Antarctica of aristonectines with adult size smaller than those from upper Maastrichtian units of South America (i.e., *A. parvidens* and *A. quiriquinensis*).

Upper Maastrichtian: The holotype of *A. parvidens* (MLP 40-XI-14-6) was recovered from upper Maastrichtian levels of the Lefipán Formation, Chubut, Argentina (Cabrera, 1941; Gasparini et al., 2003b). Other Atlantic records include the specimen MML PV 5 from upper Maastrichtian beds of the Jagüel Formation in Salinas de Trapalcó, Argentina, which was first referred to *Tuarangisaurus? cabazai* by Gasparini et al. (2003a) and later reassigned to *Aristonectinae* indet. by O’Gorman et al. (2014a). Previous to this research, south Pacific records were only known from the upper Maastrichtian Quiriquina Formation of central Chile, including the holotype of *A. quiriquinensis*. (SGO.PV.957). In this unit, aristonectines are abundant and they are the most common marine reptile remains, followed by indeterminate, non-aristonectine elasmosaurids (Steinmann et al., 1895; Broili, 1930; Otero et al., 2014a), turtles (Gasparini and Biró, 1986; Karl and Tichy, 2002; Parham et al., 2014), and scarce mosasaurs (Jiménez-Huidobro et al., 2010, 2014). Upper Maastrichtian records from Antarctica include several aristonectines (Martin et al., 2007; O’Gorman et al., 2013), among them, the genus *Aristonectes* from Vega Island (O’Gorman et al., 2010) and the species *M. seymourensis* (considered Jr. synonym of *Aristonectes parvidens* by Gasparini et al., 2003b) from Seymour Island (Chatterjee and Small, 1989).

The specimen from Sierra Baguales, the SGO.PV.6559 from Cerro Castillo, and the SGO.PV.6580 from Dumestre which have been described here, verifies the presence of aristonectines in southernmost Chile during this time span. The records of *Aristonectes* spp. from central Chile and Argentinean Patagonia show the presence of very large aristonectines towards the end of the Maastrichtian (Gasparini et al., 2003b; Otero et al., 2014c; Suazo and Otero, 2014).

7.2. Non-aristonectine elasmosaurids, intermediate morphotypes

Coniacian-Santonian: A single elasmosaurid specimen of this age closely related to plesiomorphic forms instead to extreme long-necked representatives have been reported from middle Cenomanian levels of the Mata Amarilla Formation of the Argentinean Patagonia (O’Gorman and Varela, 2010: fig. 4.1, 2; Varela et al., 2012).

Lower Campanian: A single cervical vertebra of an adult individual (MLP 11-II-20-4) from the Santa Marta Formation, Monolithic Lake, James Ross Island, Antarctica, has VLI of 105 (O’Gorman, 2012: fig 3a,b). Therefore, it can be regarded as a plesiomorphic elasmosaurid.

Upper Campanian: The species *Mauisaurus haasti* Hector, 1874, was based in several upper Campanian specimens from New Zealand. One of them (DM R1529) is currently considered as the lectotype of this species while the remaining specimens were referred to *Elasmosauridae* indet. (Welles, 1962; Welles and Gregg, 1971; Hiller et al., 2005). Later, a fairly complete skeleton (CM Zfr 115) also from New Zealand and late Campanian in age was referred to *Mauisaurus haasti* Hector by Hiller et al. (2005). This specimen has a cervical average VLI of 101 (measurements from Hiller et al., 2005: table 1). It can be referred to an intermediate form also based on their ca. 68 cervical vertebrae.

Lower Maastrichtian: The lower Maastrichtian Estratos de Quebrada Municipalidad on Algarrobo, central Chile, have provided frequent remains on non-aristonectine elasmosaurids (Otero et al., 2012a), while remains referable to aristonectines from the same unit remain unknown until now. Cervical proportions of the best axial skeleton recovered from this locality (SGO.PV.90) have indices with plots far from extreme long-necked forms (this study). Additionally on southernmost Chile, associated

remains of a fragmentary elasmosaurid recovered through several field campaigns (SGO.PV.158-161, SGO.PV.221-225, 227-230) collected from Lago Parrillar (Otero *et al.*, 2013a) has cervical indices in the range of plesiomorphic forms, with a VLI value of 91. The fossil-bearing levels are part of the Fuentes Formation and are tentatively assigned to the early Maastrichtian waiting more stratigraphic precision and/or radioisotopic dates. Also, an enigmatic specimen of indeterminate elasmosaurid (CM Zfr 145) from early-to-middle Maastrichtian levels of the Conway Formation in New Zealand was described by Hiller and Mannering (2005). Because of the lack of the skull and the entire neck, it is difficult to evaluate their taxonomic affinities.

Upper Maastrichtian: Specimens described to date from the Quiriquina Formation of central Chile include few intermediate elasmosaurids. Steinmann *et al.* (1895) included within the hypodigm of '*Cimoliasaurus andium*' Deecke several caudal series. All of them have been correlated with an additional specimen (SGO.PV.6506) which preserves few cervical vertebrae. The SGO.PV.6506 shows adult proportions that resulted in indices plotted far from extreme long-necked forms, but partially overlapped with adult aristonectines (Fig. 12A; Otero *et al.*, 2014a). SGO.PV.6506 also correlates with the specimen described by Broili (1930) which also belong to a plesiomorphic elasmosaurid. These are the only few representatives of the latter group recovered from the Quiriquina Formation in more than 160 years of prospection and collection of plesiosaur remains, beginning with Gay (1848). On the other hand, records from Argentina include an isolated, bilobed cervical vertebra (MML Pv 3) from the Jagüel Formation (Gasparini *et al.*, 2003a). This is an adult with a VLI=105 (measurements provided by Gasparini *et al.*, 2003a). Specimens SGO.PV.6560a-c described here (referred to an aristonectine based on the femoral and caudal features) adds the presence of these forms during the upper Maastrichtian of southernmost Chile.

7.3. Extreme long-necked elasmosaurids (e.g., *E. platyurus*).

Middle Campanian: Gasparini and Salgado (2000) and Gasparini *et al.* (2001) described cervical vertebrae of two juvenile specimens (MUC Pv 92 and MCS 4) and a partial, juvenile postcranial skeleton

(MLP 71-II-13-1) from Lago Pellegrini, Argentinean Patagonia. Based on the figured material (Gasparini *et al.*, 2001: fig. 3-4) it is possible to estimate a VLI of ca. 110, placing these specimens among extreme long-necked forms.

Upper Campanian: a single cervical vertebra (SGO.PV.6508) of an juvenile, extreme long-necked elasmosaur was collected from upper Campanian levels of the Santa Marta Formation, James Ross Island, Antarctica. The proportions of this specimen were tested through a bivariate graphic analysis that returned it among extreme morphotypes with representatives such *E. platyurus* (Otero *et al.*, 2014b: fig. 8). O'Gorman (2012) described two juvenile specimens (MLP 86-X-28-3 and MLP 86-X-28-(2, 6) from levels of the Snow Island Formation in Santa Marta Cove, James Ross Island, Antarctica. MLP 86-X-28-3 has a single VLI value of 85, while MLP 86-X-28-(2, 6) has an average VLI=81. These values put them among the expectable values for juvenile, extreme long-necked elasmosaurids.

Lower Maastrichtian: among elasmosaurids from New Zealand described to date, there is no clear evidence of extreme long-necked elasmosaurids. Most records can be referred to plesiomorphic elasmosaurids or to aristonectines (Welles and Gregg, 1971; Hiller *et al.*, 2005; O'Gorman *et al.*, 2014b). The Argentinean records from the Allen Formation could include lower Maastrichtian remains referable to extreme long-necked elasmosaurids (Gasparini *et al.*, 2001: fig. 3, 3-4; 2007). To date there is no evidence of these forms from the southeastern Pacific during this time span.

Upper Maastrichtian: Interestingly, despite remains of plesiosaurs are abundant in the Quiriquina Formation of central Chile, to date there is no evidence of extreme long-necked forms, while most of the known records belong to aristonectines (Otero *et al.*, 2014c) and secondarily, to plesiomorphic elasmosaurids (Otero *et al.*, 2014a).

7.4. Polycotyliids

Upper Coniacian-lower Campanian: D'Angelo *et al.* (2008) described an articulated pelvic girdle and femora of a polycotyliid from the Alpha Member of the Santa Marta Formation, James Ross Island, Antarctica. This is the oldest record of a polycotyliid from the WBP. Additionally, Kellner *et al.* (2011) described fragmentary specimens from Santonian

beds of James Ross Island. As O’Gorman (2012) pointed out, one cervical vertebra (Kellner *et al.*, 2011: fig. 2) shows a nearly circular articular facet and thickening of the bone in the articular contour which are distinctive features of polycotylids (Salgado, 2007).

Upper Campanian-lower Maastrichtian: Several cervical vertebrae from the Allen Formation in Argentina were referred to indeterminate polycotylids by Salgado *et al.* (2007) and O’Gorman *et al.* (2011). In addition, an endemic species, *Sulcusuchus erraini* Gasparini and Spalletti, 1990 was recovered from Los Alamitos Formation, Río Negro Province, Argentinean Patagonia, and from La Colonia Formation, Chubut Province (O’Gorman and Gasparini, 2013). Several additional localities of the same age have yielded additional remains referable to polycotylids (O’Gorman and Gasparini, 2013). Hector (1874: plate 27) described an isolated propodial (B.M. R838) and a cervical centrum from Haumuri Bluff, New Zealand, erecting the species *Polycotylus tenuis*. The former was later reviewed by Welles and Gregg (1971: p. 44). These authors recognized the juvenile stage of the propodial, and the lack of enough diagnostic features for genus or species identification. Because of this, it was left as Polycotylidae indet. Slender propodials could also occur among elasmosaurids (Hiller *et al.*, 2014), reason why the diagnosis based on an isolated propodial is uncertain. Additionally, the propodials CM Zfr 99 and 125 referred to indeterminate polycotylids by Welles and Gregg (1971: p. 46) have been personally reviewed by one of the authors (R.A.Otero). One of them (CM Zfr 99) is the proximal end of a large elasmosaurid propodial with hemispherical articular head, while the other specimen of Welles and Gregg, CM Zfr 125, is a propodial with similar proportions of the elasmosaurid CM Zfr 159 described by Hiller *et al.* (2014). A single cervical vertebra, a cervical series and isolated teeth from Mangahouanga Stream and described by Wiffen and Moisley (1986) represents the best evidence (although scarce) of polycotylids from New Zealand. Finally, polycotylids remain unreported from early Maastrichtian units of central Chile.

Upper Maastrichtian: To date, there are no records of polycotylids from central Chile, southernmost Chile, Antarctica, Argentina, neither from New Zealand.

7.5. Biogeographical interpretation of the known plesiosaur record from the WBP

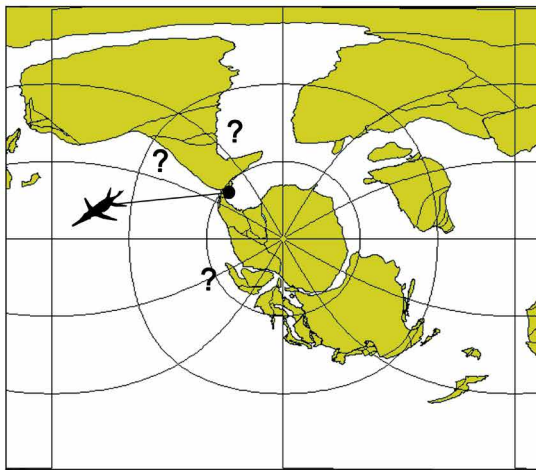
Besides the record of upper Coniacian polycotylids from Antarctica (D’Angelo *et al.*, 2008), no other clade was recognized to date in coeval units. Indeterminate plesiosaurs of Santonian age from the James Ross Island have been reported (Kellner *et al.*, 2011) but these are not enough informative even for familial level (although part of the material shows affinities to polycotylids). During the middle-to-upper Campanian, polycotylids appear on the southwestern Atlantic (Argentina) (Salgado *et al.*, 2007; O’Gorman and Gasparini, 2013). Together with this, the presence of small aristonectines, extreme long-necked, as well as plesiomorphic elasmosaurids, occurs together in the James Ross Island, Antarctica (Otero *et al.*, 2014b). The middle-to-upper Campanian plesiosaur record from New Zealand so far includes plesiomorphic elasmosaurids (Welles and Gregg, 1971; Wiffen and Moisley, 1986), while aristonectines as well as extreme long-necked elasmosaurids are still unknown during this lapse. During the same time span, there are no known plesiosaur records from the southeastern Pacific (central and southernmost Chile), being impossible, by the moment, to evaluate the eventual diversity. During the lower Maastrichtian, aristonectines became relatively frequent in New Zealand (Cruickshank and Fordyce, 2002; O’Gorman *et al.*, 2014b). The same happened with plesiomorphic elasmosaurids (Hiller, 2014), although polycotylids seem to be scarce (Welles and Gregg, 1971) and extreme long-necked elasmosaurids seems to be absent. Finally, during the upper Maastrichtian, aristonectines became very abundant in Antarctica and southern South America, distributed in both the southeastern Pacific and the southwestern Atlantic, while coeval polycotylids and extreme long-necked elasmosaurids are unknown in the entire WBP. To date, the mid-to-upper Maastrichtian records of plesiosaurs from New Zealand only include indeterminate elasmosaurids which are fragmentary (Consoli and Stillwell, 2009), making impossible any analysis of the cervical proportions. Another gap is present in the northern margin of the Quiriquina Basin. The lower Maastrichtian elasmosaurids from Algarrobo in central Chile are the northernmost occurrence of the group in the WBP (Otero *et al.*, 2012a), but these cannot be contrasted with any information because

of the lack of younger fossil-bearing levels at the same latitude. A synthesis of all these records along the WBP is provided on figure 13.

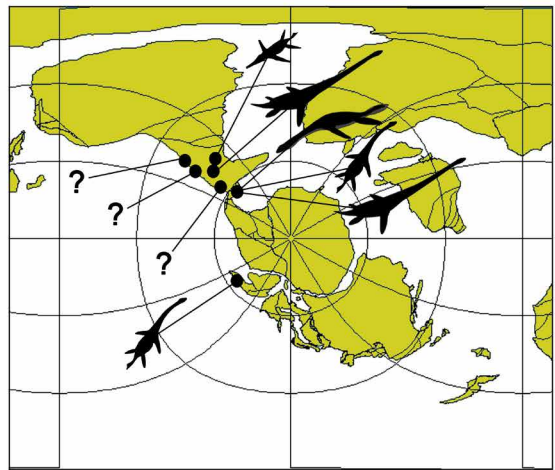
7.6. Faunal Turnover

Summarizing, polycotyliids were present at least since the Coniacian in Antarctica, and until the late Campanian-early Maastrichtian in the southwestern

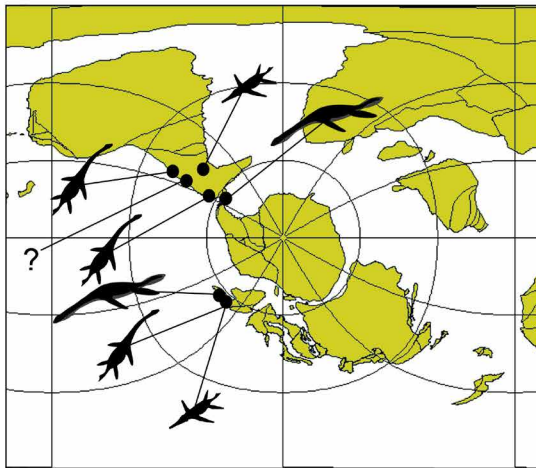
Atlantic (D'Angelo *et al.*, 2008; Salgado *et al.*, 2007; O'Gorman and Gasparini, 2013). After the lower Maastrichtian, there are no records of this group from main uppermost Cretaceous units of the WBP, supporting a probable extinction of the group prior to the upper Maastrichtian. The group seems to be diversified along the southwestern Atlantic before disappearing from the Weddellian record (Fig. 14).



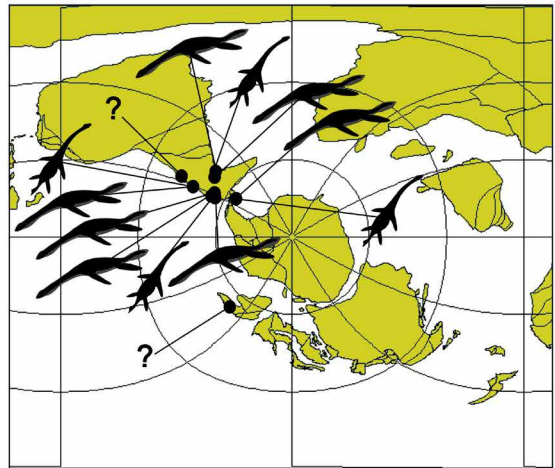
Coniacian-Santonian boundary, 86.3 Ma



middle-to-late Campanian, 77 to 72.1 Ma



early Maastrichtian, 72.1 to 70 Ma



middle to late Maastrichtian, 69 to 66 Ma



FIG. 13. Plate tectonic maps showing the evolution between the Coniacian-late Maastrichtian, associated to the known records of plesiosaurs along the WBP. Plate tectonic maps were obtained through the free online software of ODSN Plate Tectonic Reconstruction Service, University of Bremen, Germany (<http://www.odsn.de/odsn/services/paleomap/paleomap.html>) Last visit on March 25, 2015.

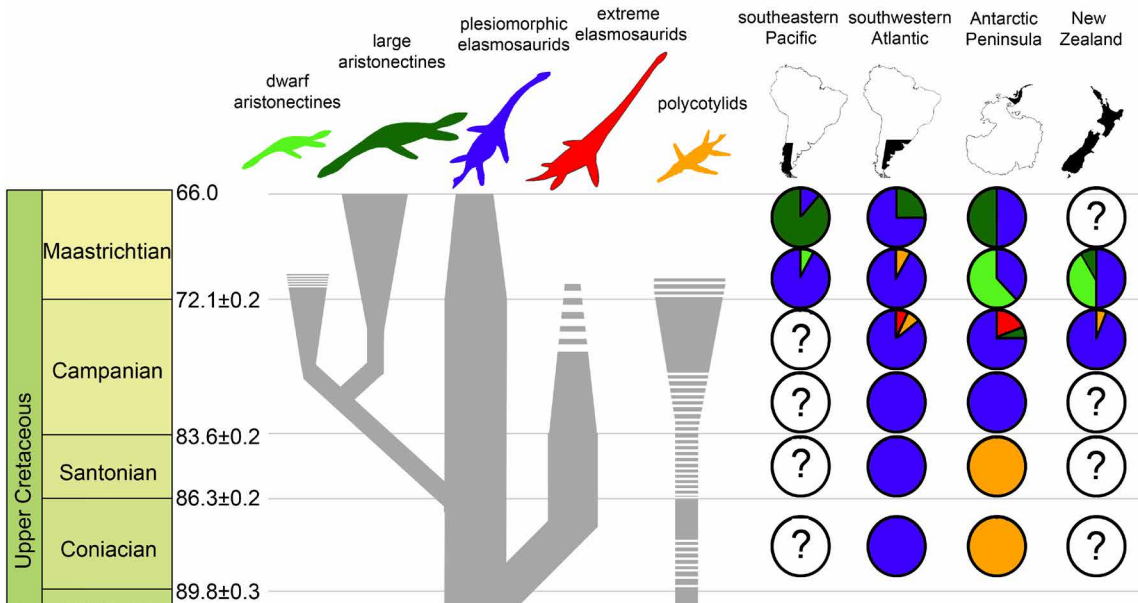


FIG. 14. Graphic relationship showing the relative abundance of the different plesiosaur groups recognized along the WBP. Grey lines reflect the relative abundance of each group in the WBP. Pie graphics reflect the relative abundance of the records known to date on each subdivision of the Province. Colors are consistent with each plesiosaur group.

During the upper Campanian, extreme long-necked elasmosaurids have been recognized in Antarctica and the southwestern Atlantic, without known younger records. These occurrences are coincident with the known Weddellian record of polycotyliids. Both suggest that a direct pattern of influence from the Northern Hemisphere could occur along the Atlantic into the Southern Hemisphere, as was proposed by Gasparini and De la Fuente (2000). The early occurrence of polycotyliids and intermediate elasmosaurids in Antarctica and Argentinean Patagonia, respectively, suggest a similar pattern during the Coniacian-lower Campanian. Polycotyliids and extreme long-necked elasmosaurids appear as locally extinct during the lower Maastrichtian. During the same lapse, aristonektines became relatively abundant in New Zealand and Antarctica, so far represented by small-sized individuals and by a mid-sized exception which is *K. katiki*. During the upper Maastrichtian, there is a clear pattern of expansion of aristonektines into the southeastern Pacific, where these reached a high abundance and became the main herpetofaunal component. Aristonektines are also recorded in the southwestern Atlantic during the same time-span, although

these are not such abundant and represent a minor proportion of the elasmosaurid diversity (O’Gorman *et al.*, 2014a). The largest known aristonektines have been reported from upper Maastrichtian beds along South America (*e.g.*, *A. parvidens*, *A. quiriquinensis*) and Antarctica (O’Gorman *et al.*, 2013), while similar large individuals remain unreported in older beds along the WBP, suggesting that very large aristonektines were exclusively restricted to the upper part of the Maastrichtian. Both, the aristonektines and the plesiomorphic elasmosaurids, reached the uppermost part of the Maastrichtian and were common forms in Antarctica and South America (Otero *et al.*, 2014b). Thus, this research propose the existence of a faunal turnover starting in the lower Maastrichtian, passing from polycotyliids + extreme long-necked elasmosaurids + small aristonektines, to large aristonektines + plesiomorphic elasmosaurids during the upper Maastrichtian. The mechanisms of such turnover are still obscure. By the moment, partial evidence derived from the skull adaptations and the specialized teeth suggest that polycotyliids and aristonektines had a very different diet, and therefore, hypotheses regarding faunal replacement on similar ecologic niches are difficult to support.

7.7. Consistence between the upper Campanian-lower Maastrichtian plesiosaur turnover and the coeval paleogeography of the WBP

The upper Maastrichtian radiation of aristonectines along the southeastern Pacific quantitatively differs from their distribution on Argentinean Patagonia, where these are less abundant. This research proved the frequent presence of this group in the Magallanes Basin, including the first local record of the genus *Aristonectes*, previously recognized in Argentina, central Chile, and Antarctica. Also, previous records of Maastrichtian chondrichthyans in the Magallanes Basin show clear affinities to similar fauna from the Quiriquina Formation, instead to known chondrichthyan diversity from Argentinean Patagonia (Otero *et al.*, 2013b). A remarkably similar situation is now verified for aristonectines and plesiomorphic elasmosaurids. Such biogeographical changes suggest the existence of a direct (and maybe brief) seaway between the southeastern Pacific and the Magallanes Basin during the upper Maastrichtian, which allowed the interchange of shelf marine vertebrates. This corridor was previously proposed by Cecioni (1970), but no enough faunal evidence was available at that time for reinforcing such hypothesis.

During the lower Maastrichtian, known records of aristonectines are constrained to New Zealand and Antarctica. Seaway models of Zinsmeister (1982), Huber and Watkins (1992) and Stillwell (1997) support the existence of a western boundary current flowing between Antarctica and the southeastern Pacific with a counterclockwise circulation. Since the upper Campanian-lower Maastrichtian, microfossil evidence (Huber, 1992) points to circum-Antarctic flow of shallow surface waters and the presence of a trans-Antarctic seaway. Such changes in the main seaways are consistent with the lower Maastrichtian distribution of aristonectines restricted to New Zealand-Antarctica, and their posterior upper Maastrichtian, differential abundance in the southeastern Pacific and southwestern Atlantic, respectively.

On the other hand, a geographic barrier in the northern margin of the Magallanes Basin is inferred from the austral plesiosaur record. Such barrier should avoid a direct interchange between the Magallanes Basin and the open Atlantic, based on the less frequent record of aristonectines along the latter. Ciesielski *et al.* (1977) obtained Campanian-

Maastrichtian cores drilled 60 west from the Malvinas Islands containing a foraminifer and palynomorph assemblage reflecting mixed water temperatures. These authors considered that the sharp faunal and floral changes observed are believed to have resulted not from changes across a normal surface temperature gradient but rather from a steepened gradient produced at the confluence of two separate water masses. Subsequently, they postulated the existence of a topographic barrier separating the major water masses of the Austral Basin and the rest of the Atlantic.

8. Conclusions

This contribution describes new plesiosaur finds from southernmost Chile, including a remarkable concentration of several individuals from Cerro Castillo, an associated individual from Dumestre, and one isolated, juvenile vertebra from Sierra Baguales. All the studied material came from the uppermost levels of the Dorotea Formation of late Maastrichtian age, giving a good chance of latitudinal sampling (*ca.* 300 km north-south) along the Magallanes Basin and providing informative specimens that add relevant taxonomical data about the previously unknown diversity of plesiosaurs of this region, as well as about their distribution.

Among the taxa recognized, we present the first confirmed record of *Aristonectes* Cabrera, 1941 from upper Maastrichtian levels of the Magallanes Basin, proving that this genus was a widespread taxon along Antarctica and southern South America, with known representatives on both the Atlantic and the Pacific Ocean. In addition, two indeterminate aristonectines are here described, also recovered from upper levels of the Dorotea Formation, being these collected from Sierra Baguales in the northern part of Magallanes Region, and from Dumestre, south of Puerto Natales, respectively. The specimen from Dumestre (SGO.PV.6580) represents a novel form among aristonectines, based on its evident adult size, noticeably smaller than *Aristonectes parvidens* from Argentinean Patagonia, or *Aristonectes quiriquinensis* from central Chile. Additionally, we describe an associated postcranial skeleton of an elasmosaurid which represents a morphotype different from aristonectines and from extreme long-necked elasmosaurids such *Elasmosaurus platyurus* Cope. Based on the cervical

proportions, we propose an informal segregation of the latter specimen, as well as any elasmosaurid clearly separable from the two extreme types (aristonectines and very long-necked elasmosaurs), therefore, identifying them as plesiomorphic elasmosaurids. This morphologic criterium is useful for paleobiogeographic interpretations since extreme long-necked elasmosaurids are not frequent along the WBP. On contrary, plesiomorphic elasmosaurids are one of the most abundant marine reptiles in the WBP at least since the middle Campanian.

Regarding the biogeography of Weddellian plesiosaurs, based on their known record from the province, this research proposes the occurrence of a faunal turnover during the latest Cretaceous and prior to the extinction of the group. Lower Maastrichtian diversity from the WBP included polycotylids, extreme long-necked elasmosaurids, and small aristonectines. Polycotylids as well as extreme long-necked elasmosaurids seem to dissappear from the WBP during the upper Maastrichtian, while large aristonectines as well as plesiomorphic elasmosaurids became the most frequent marine reptiles.

Finally, the evaluation of the plesiosaur record from the WBP under the light of the new material described here is consistent with previous models of paleogeographic settings for the Austral Basin, the Antarctic Peninsula and even more, the Malvinas Islands. The new records support the hypotheses of a direct contact between the Magallanes and Quiriquina Basin, as well as the existence of a topographic barrier in the northeastern part of the Magallanes Basin driven by a temporal upwelling of the Malvinas Plateau. This could cause a separation of water masses from the Magallanes Basin and the rest of the Atlantic, precluding a major faunal interchange. Else, a lack of enough depth caused by this upwelling could lead to selective interchange of shallow-shelf marine vertebrates.

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References

- Broili, F. 1930. Plesiosaurierreste von der Insel Quiriquina. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie Beilage-Band (B)* 63: 497-514.
- Brown, D.S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum (Natural History), Geology* 4: 225-234.
- Cabrera, A. 1941. Un Plesiosaurio nuevo del Cretáceo del Chubut. *Revista del Museo de La Plata* 2: 113-130.
- Carpenter, K. 1999. Revision of North American elasmosaurs from the Cretaceous of the Western Interior. *Paludicola* 2: 148-173.
- Cecioni, G. 1955. Distribuzione verticale di alcune Kossmaticeratidae della Patagonia cilena. *Società Geológica Italiana, Bolettino* 74: 141-148.
- Cecioni, G. 1970. Esquema de paleogeografía chilena. *Editorial Universitaria*: 144 p. Santiago, Chile.
- Cecioni, G.; Charrier, R. 1974. Relaciones entre la Cuenca Patagónica, la Cuenca Andina y el Canal de Mozambique. *Ameghiniana* 11: 1-38.
- Ciesielski, P.F.; Sliter, W.V.; Wind, F.H.; Wise, Jr. S.W. 1977. A Cretaceous Islas Orcadas core from the Falkland (Malvinas) Plateau, southwest Atlantic. *Antarctic Journal of the United States* 12: 65-67.
- Chatterjee, S.; Small, B.J. 1989. New plesiosaurs from the Upper Cretaceous of Antarctica. *In* *Origins and Evolution of the Antarctic Biota* (Crame, J.; editor). Geological Society of London, Special Publication 47: 197-215.
- Cohen, K.M.; Finney, S.M.; Gibbard, P.L.; Fan, J.X. 2013. The ICS International Chronostratigraphic Chart. *Episodes* 36 (3): 199-204.

- Consoli, C.P.; Stillwell, J.D. 2009. Late Cretaceous marine reptiles (Elasmosauridae and Mosasauridae) of the Chatham Islands, New Zealand. *Cretaceous Research* 30: 991-999.
- 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 cryptocleidid plesiosaurs. *Palaeontology* 45: 557-575.
- D'Angelo, J.; Novas, F.; Lirio, J.; Isasi, M. 2008. Primer registro de Polycotylidae (Sauropterygia, Plesiosauroidea) del Cretácico Superior de Antártida. In Congreso Latinoamericano de Paleontología de Vertebrados, No. 3, Libro de Resúmenes: p. 72. Neuquén.
- De Blainville, H.M.D. 1835. Description de quelques espèces de reptiles de la Californie precede de l'analyse d'un système general d'erpétologie et d'amphibiologie. *Nouvelles Annales du Muséum d'Histoire Naturelle de Paris*, Serie 3-4: 233-296.
- Druckenmiller, P.S.; Russell, A.P. 2008. Skeletal anatomy of an exceptionally complete specimen of a new genus of plesiosaur from the Early Cretaceous (Early Albian) of northeastern Alberta, Canada. *Palaeontographica Abteilung A* 283: 1-33.
- Fostowicz-Frelik, Ł.; Gaździcki, A. 2001. Anatomy and histology of plesiosaur bones from the Upper Cretaceous of Seymour Island, Antarctic Peninsula. In *Palaeontological Results of the Polish Antarctic Expeditions. Part III* (Gaździcki, A.; editor). *Palaeontologia Polonica* 60: 7-32.
- Gasparini, Z. 1979. Comentarios críticos sobre los vertebrados mesozoicos de Chile. In Congreso Geológico Chileno, No. 2, Actas 3: H15-H32. Arica.
- Gasparini, Z.; Biró-Bagoczky, L. 1986. *Osteopygis* sp. (Reptilia, Testudines, Toxochelyidae). Tortuga Fósil de la Formación Quiriquina, Cretácico Superior, Sur de Chile. *Revista Geológica de Chile* 27: 85-90. doi: 10.5027/andgeoV13n1-a07.
- Gasparini, Z.; Spalletti, L.A. 1990. Un nuevo cocodrilo en los depósitos mareales mastrichtianos de la Patagonia noroccidental. *Ameghiniana* 27: 141-150.
- 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. Elasmosauridos (Plesiosauria) del Cretácico Tardío del Norte de Patagonia. *Revista Española de Paleontología* 15: 13-21.
- Gasparini, Z.; Del Valle, R.; Goñi, R. 1984. An *Elasmosaurus* (Reptilia, Plesiosauria) of the Upper Cretaceous in the Antarctic. *Boletín del Instituto Antártico Argentino* 305: 1-24.
- Gasparini, Z.; Casadio, S.; Fernández, M.; Salgado, L. 2001. Marine reptiles from the Late Cretaceous of northern Patagonia. *Journal of South American Earth Sciences* 14: 51-60.
- Gasparini, Z.; Salgado, L.; Casadio, S. 2003a. Maastrichtian plesiosaurs from northern Patagonia. *Cretaceous Research* 24: 157-170.
- Gasparini, Z.; Bardet, N.; Martin, J.E.; Fernández, M. 2003b. 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.; Parras, A. 2007. Late Cretaceous plesiosaurs from northern Patagonia, Argentina. *Geological Journal* 42: 185-202.
- Gay, C. 1848. Historia Física y Política de Chile. Zoología, Tomo Segundo. Imprenta Maulde y Renou: 371 p. París.
- Hector, J. 1874. On the fossil reptiles of New Zealand. *Transactions of the New Zealand Institute* 6: 333-358.
- Hervé, F.; Godoy, E.; Mpodozis, C.; Fanning, M. 2004. Monitoring magmatism of the Patagonian batholith through the U-Pb SHRIMP dating of detrital zircons in sedimentary units of the Magallanes Basin. In GEOSUR, International Symposium on the Geology and Geophysics of the Southernmost Andes, the Scotia Arc and the Antarctic Peninsula (Carcione, J.; Donda, F.; Lodolo, E.; editors), Actas: 4-06. *Bolletino di Geofisica Teorica ed Applicata* 45 (2): 113-117. Buenos Aires.
- Hiller, N.; Mannering, A. 2004. Elasmosaur (Reptilia: Plesiosauria) skull remains from the Upper Cretaceous of North Canterbury. *New Zealand. Records of the Canterbury Museum* 18: 1-7.
- Hiller, N.; Mannering, A. 2005. An unusual new elasmosaurid plesiosaur (Sauropterygia) from the Upper Haumurian (Maastrichtian) of the South Island, New Zealand. *Memoirs of the Queensland Museum* 51: 27-37.
- Hiller, N.; Mannering, A.; Jones, C.; Cruickshank, A. 2005. The nature of *Mauisaurus haasti* Hector, 1874 (Reptilia: Plesiosauria). *Journal of Vertebrate Paleontology* 25: 588-601.
- Hiller, N.; O'Gorman, J.P.; Otero, R.A. 2014. A new elasmosaurid plesiosaur from the lower Maastrichtian of North Canterbury, New Zealand. *Cretaceous Research* 50: 27-37.

- Hoffstetter, R.; Fuenzalida, H.; Cecioni, G. 1957. Chile-Chili. In *Lexique Stratigraphique International. Amérique Latine*, Centre National de la Recherche Scientifique 5 (7): 444 p. Paris.
- Huber, B.T. 1992. Paleobiogeography of Campanian-Maastrichtian foraminifera in the southern high latitudes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 92: 325-360.
- Huber, B.T.; Watkins, D.K. 1992. Biogeography of Campanian-Maastrichtian calcareous plankton in the region of the Southern Ocean: paleogeographic and paleoclimatic implications. In *A Perspective on Global Change* (Kennett, J.P.; Warnke, D.A.; editors). Antarctic Research Series, American Geophysical Union 56: 31-60.
- Jiménez-Huidobro, P.; Otero, R.A.; Rubilar-Rogers, D. 2010. First Evidence of a tylosaurine mosasaur from Chile. *Journal of Vertebrate Paleontology*, Program and Abstracts: p. 112A. Pittsburgh.
- Jiménez-Huidobro, P.; Otero, R.A.; Soto-Acuña, S.; Caldwell, M. 2014. Mosasaur record (Squamata: Mosasauridae) from the Upper Cretaceous of Chile. In *Meeting of the Society of Vertebrate Paleontology*, No. 74, Abstracts: p. 155. Berlin.
- Karl, H.V.; Tichy, G. 2002. *Australobaena chilensis* n. gen. n. sp., and the homology of secondary palatines in marine turtles (Anapsida: Testudines). *Studia Geologica Salmanticensia* 38: 11-19.
- Katz, H. 1963. Revision of Cretaceous stratigraphy in Patagonian Cordillera of Última Esperanza, Magallanes province, Chile. *American Association of Petroleum Geologists Bulletin* 47: 506-524.
- Kellner, A.W.A.; Rodrigues-Simões, T.; Riff, D.; Grillo, O.; Romano, P.; de Paula, H.; Ramos, R.; Carvalho, M.; Sayão, J.; Oliveira, G.; Rodrigues, T. 2011. The oldest plesiosaur (Reptilia, Sauropterygia) from Antarctica. *Polar Research* 30: 1-6.
- Ketchum, H.F.; Benson, R.B.J. 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.
- 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.
- Martin, J.; Sawyer, F.; Reguero, M.; Case, J. 2007. Occurrence of a young elasmosaurid plesiosaur skeleton from the Late Cretaceous (Maastrichtian) of Antarctica. In *Antarctica: A Keystone in a Changing World*, Online Proceedings of the 10th International Symposium of Antarctic Earth Sciences, United States Geological Survey, Open-File Report 2007-1047 (Cooper, A.K.; Raymond, C.; Anderson, J.; Barrett, P.; Barron, J.; Bart, P.; Blankenship, D.; Cooper, A.; Davey, F.; Diggles, M.; Finn, C.; Fitzgerald, P.; Florindo, F.; Francis, J.; Futterer, D.; Gamble, J.; Goodge, J.; Hammer, W.; Helton, P.; Ivins, E.; Kyle, P.; LeMasurier, W.; Mayewski, P.; Naish, T.; Passchier, S.; Pekar, S.; Raymond, C.; Ricci, C.; Stagg, H.; Storey, B.; Stump, E.; Studinger, M.; Sugden, D.; Thorn, V.; Wilson, T.; Wise, W.; editors). Short Research Paper 066: 1-4. doi: 10.3133/of2007-1047.srp066.
- Martínez-Pardo, R. 1965. The presence of *Bolivina* *draco dorreeni* Finlay from the Magellan basin, Chile. *Micropaleontology* 11 (3): 360-364.
- Novas, F.E.; Isasi, M.P.; D'Angelo, J.S.; Busker, F.; Damato, M.; Bogan, S.; Ibiricu, L.; Lacovara, K. 2011. Hallazgo de un esqueleto de plesiosaurio asociado con dientes de seláceos en la Formación El Calafate (Cretácico Superior) de la Provincia de Santa Cruz. In *Resúmenes del Congreso Latinoamericano de Paleontología de Vertebrados*, No. 4. Ameghiniana 48 (suplemento): R247.
- O'Gorman, J.P. 2012. The oldest elasmosaurs (Sauropterygia, Plesiosauria) from Antarctica, Santa Marta Formation (upper Coniacian? Santonian-upper Campanian) and Snow Hill Island Formation (upper Campanian-lower Maastrichtian), James Ross Island. *Polar Research* 31: 1-10.
- O'Gorman, J.P.; Varela, A.N. 2010. The oldest lower Upper Cretaceous plesiosaurs (Reptilia, Sauropterygia) from southern Patagonia, Argentina. *Ameghiniana* 47: 447-459.
- O'Gorman, J.P.; Gasparini, Z. 2013. Revision of *Sulcusuchus erraini* (Sauropterygia, Polycotylidae) from the Upper Cretaceous of Patagonia, Argentina. *Alcheringa: An Australasian Journal of Palaeontology* 37 (2): 163-176.
- O'Gorman, J.P.; Gasparini, Z.; Reguero, M. 2010. *Aristonectes parvidens* Cabrera (Sauropterygia, Plesiosauria) from Cape Lamb, Vega Island (Upper Cretaceous), Antarctica. In *Scientific Committee on Antarctic Research (SCAR) Open Science Conference*, No. 31, Abstract 557: 1 p. Buenos Aires.
- O'Gorman, J.P.; Salgado, L.; Gasparini, Z. 2011. Plesiosauros de la Formación Allen (Campaniano-Maastrichtiano) en el área del Salitral de Santa Rosa (Provincia de Río Negro, Argentina). *Ameghiniana* 48: 129-135.
- O'Gorman, J.P.; Gasparini, Z.; Salgado, L. 2013. Postcranial morphology of *Aristonectes* Cabrera, 1941 (Plesiosauria,

- Elasmosauridae) from the Upper Cretaceous of Patagonia and Antarctica. *Antarctic Science* 25: 71-82.
- O’Gorman, J.P.; Gasparini, Z.; Salgado, L. 2014a. Reappraisal of *Tuarangisaurus? cabazai* (Elasmosauridae, Plesiosauria) from the Upper Maastrichtian of northern Patagonia, Argentina. *Cretaceous Research* 47: 39-47.
- O’Gorman, J.P.; Otero, R.A.; Hiller, N. 2014b. First record of a juvenile aristonectine (Plesiosauria, Elasmosauridae) from the Upper Cretaceous Conway Formation of New Zealand, and the nature of the *Mauisaurus haasti* hypodigm. *Alcheringa* 38: 1-8.
- 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 taxonomic status of the Cimoliasauridae. *Journal of Vertebrate Paleontology* 29: 48-57.
- Ortiz, H.; Mansilla, H.; Monecino, D.; Jujihara, T.; Leppe, M. 2012. Primer reporte de Plesiosauria (Reptilia: Sauropterygia) en estratos del Cretácico Superior en la Reserva Nacional Laguna Parrillar, Península Brunswick, Región de Magallanes y Antártica Chilena. In *Abriendo ventanas al pasado* (Leppe, M.; Aravena, J.C.; Villa-Martínez, R.; editors), Libro de Resúmenes. Simposio Paleontología en Chile, No. 3: 135-138. Punta Arenas.
- Ortiz, H.; Mansilla, H.; Manríquez, L.; Leppe, M. 2013. Registro de los plesiosaurios más australes de América. Sistemática, paleoambiente y estratigrafía. In *Congreso Latinoamericano de Ciencia Antártica*, No. 7, Libro de resúmenes: 183-186. La Serena.
- Otero, R.A. 2014. The axial formula of *Aristonectes quiriquinensis* and its diagnostic value for aristonectines. In *Meeting of the Society of Vertebrate Paleontology* No. 74: p. 200. Berlin.
- Otero, R.A.; Rubilar-Rogers, D. 2010. Nuevos restos de plesiosaurios elasmosáuridos del Cretácico Superior (Maastrichtiano) de Puerto Natales, Region de Magallanes, con comentarios sobre la procedencia estratigráfica de los registros previos en el área. In *Simposio Paleontología en Chile*, No. 2, Libro de Actas: p. 56. Concepción.
- 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 method. *Cretaceous Research* 41: 86-89.
- Otero, R.A.; Suárez, M.E.; Le Roux, J.P. 2009. First record of elasmosaurid plesiosaurs (Sauropterygia: Plesiosauria) in upper levels of the Dorotea Formation, Late Cretaceous (Maastrichtian), Puerto Natales, Chilean Patagonia. *Andean Geology* 36 (2): 342-350. doi: 10.5027/andgeoV36n2-a08.
- Otero, R.A.; Parham, J.F.; Soto-Acuña, S.; Jiménez-Huidobro, P.; Rubilar-Rogers, D. 2012a. Marine reptiles from the Late Cretaceous (early Maastrichtian) of Algarrobo, central Chile. *Cretaceous Research* 35: 124-132.
- Otero, R.A.; Soto-Acuña, S.; Rubilar-Rogers, D. 2012b. A postcranial skeleton of an elasmosaurid plesiosaur from the Maastrichtian of central Chile, with comments on the affinities of Upper Cretaceous plesiosauroids from the Weddellian Biogeographic Province. *Cretaceous Research* 37: 89-99.
- Otero, R.A.; Soto-Acuña, S.; Yury-Yáñez, R.; Rubilar-Rogers, D. 2013a. Southernmost occurrence of an elasmosaurid plesiosaur in the Late Cretaceous of South America (Magallanes Basin). In *Geosur 2013*, Bollettino di Geofisica teorica ed applicata (Supplement B) 54: 334-336.
- Otero, R.A.; Oyarzún, J.L.; Soto-Acuña, S.; Yury-Yáñez, R.; Gutiérrez, N.; Le Roux, J.; Torres, T.; Hervé, F. 2013b. Neoselachians and Chimaeriformes (Chondrichthyes) from the Upper Cretaceous-Paleogene of Sierra Baguales, southernmost Chile. Chronostratigraphic, paleobiogeographic and paleoenvironmental implications. *Journal of South American Earth Sciences* 48: 13-30.
- Otero, R.A.; Soto-Acuña, S.; Vargas, A.O.; Rubilar-Rogers, D. 2014a. A new postcranial skeleton of an elasmosaurid plesiosaur from the Upper Cretaceous of central Chile and reassessment of the historic species *Cimoliasaurus andium* Deecke. *Cretaceous Research* 50: 318-331.
- Otero, R.A.; Soto-Acuña, S.; Vargas, A.O.; Rubilar-Rogers, D.; Yury-Yáñez, R.; Gutstein, C.S. 2014b. Additions to the diversity of elasmosaurid plesiosaurs from the Upper Cretaceous of Antarctica. *Gondwana Research* 26: 772-784.
- 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, L.A. 2014c. *Aristonectes quiriquinensis* sp. nov., a new highly derived elasmosaurid from the upper Maastrichtian of central Chile. *Journal of Vertebrate Paleontology* 34: 100-125.
- Owen, R. 1860. On the orders of fossil and recent Reptilia and their distribution in time. *Report of the British Association for the Advancement of Science* 29: 153-166.
- Parham, J.F.; Otero, R.A.; Suárez, M.E. 2014. A Sea Turtle Skull from the Late Cretaceous of Chile with Comments

- on the Taxonomy and Biogeography of *Euclastes* (formerly *Osteopygis*). *Cretaceous Research* 49: 181-189.
- Pérez, E.; Reyes, R. 1978. Las trigonias del Cretácico Superior de Chile y su valor cronoestratigráfico. Instituto de Investigaciones Geológicas (Chile), Boletín 34: 71 p. Santiago.
- Phillips, J. 1871. *Geology of Oxford and the valley of the Thames*. Oxford: 523 p.
- Rubilar-Rogers, D.; Soto-Acuña, S.; Otero, R.A.; Yury-Yáñez, R. 2013. First evidence of a dinosaur from Upper Cretaceous levels of the Dorotea Formation, Sierra Baguales, southernmost Chile. *In* Geosur 2013, Bollettino di Geofisica teorica ed applicata (Supplement B) 54: 345-348.
- Sachs, S.; Kear, B.P.; Everhart, M.J. 2013. Revised Vertebral Count in the 'Longest-Necked Vertebrate' *Elasmosaurus platyurus* Cope 1868, and Clarification of the Cervical-Dorsal Transition in Plesiosauria. *Plos One* 8: e70877.
- 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.
- Stanley, S.M. 1977. Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves. *Palaeontology* 20: 869-899.
- Steinmann, G.; Deecke, W.; Möricke, W. 1895. Das Alter und die Fauna der Quiriquina-Schichten in Chile. *Neues Jahrbuch für Mineralogie Geologie und Palaeontologie* 14: 1-118.
- Stillwell, J. 1997. Tectonic and palaeobiogeographic significance of the Chatham Islands, South Pacific, Late Cretaceous fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* 136: 97-119.
- Suazo, F.; Otero, R.A. 2014. Análisis gráfico bivariado de proporciones vertebrales dorsales en plesiosaurios elasmosáuridos del Cretácico Superior de Chile y Norteamérica: su valor diagnóstico para la identificación de aristonectinos adultos de gran tamaño. *In* Simposio Paleontología en Chile, No. 4, Libro de Resúmenes: p. 39. Valdivia.
- Varela, A.N.; Poiré, D.G.; Martin, T.; Gerdes, A.; Goin, F.J.; Gelfo, J.N.; Hoffmann, S. 2012. U-Pb zircon constraints on the age of the Cretaceous Mata Amarilla Formation, Southern Patagonia, Argentina: its relationship with the evolution of the Austral Basin. *Andean Geology* 39 (3): 359-379. doi: 10.5027/andgeoV39n3-a01.
- 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: 1-96.
- Welles, S.P.; Gregg, D.R. 1971. Late Cretaceous marine reptiles from New Zealand. *Records of the Canterbury Museum* 9: 1-111.
- Wiffen, J.; Molesley, W. 1986. Upper Cretaceous reptiles (families Elasmosauridae, Pliosauridae) from the Mangahouanga Stream, North Island, New Zealand. *New Zealand Journal of Geology and Geophysics* 29: 205-252.
- Zinsmeister, W.J. 1979. Biogeographic significance of the Upper Mesozoic and early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final break-up of Gondwanaland. *In* *Historical Biogeography, Plate Tectonics and the Changing Environment* (Gray, J.; Boucot, A.J.; editors). Oregon State University Press: 349-355. Oregon.
- Zinsmeister, W.J. 1982. Late Cretaceous-early Tertiary molluscan biogeography of the southern circum-Pacific. *Journal of Paleontology* 55: 1083-1102.