Additions to the diversity of elasmosaurid plesiosaurs from the Upper Cretaceous of Antarctica

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A B S T R A C T

Three specimens of elasmosaurid plesiosaurs (Sauropterygia, Plesiosauria) from Upper Cretaceous beds of Antarctica are described here. These include postcranial remains of a single adult individual recovered from late Maastrichtian beds of Marambio (=Seymour) Island, possessing a distinctive combination of features: cervical vertebrae having centra with a triangular outline in transverse section, a vertical groove on the rostral and caudal edge of the neural spines, and a deep articulation over the neural arch for the following postzygapophysis, while the scapula shows an unusually large and anteriorly recurved dorsal process. This combination of features is unknown in any adult, postcranial elasmosaurid genus recovered to date in the Upper Cretaceous of the Weddellian Biogeographic Province and could represent a new form. Additional specimens from James Ross Island comprise the first record of an Aristonectinae (Plesiosauria, Elasmosauridae) in late Campanian beds, being the oldest known record of this sub-family. Finally, a third specimen from the same age and locality reveals the presence of very-long necked elasmosaurids with affinities to typical representatives from the Upper Cretaceous of the Northern Hemisphere. These findings add to the known diversity of Upper Cretaceous elasmosaurids in high latitudes of the Southern Hemisphere.

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1. Introduction

Plesiosauria (Reptilia, Sauropterygia) from Antarctica are known since the seventies. The first report is due to Del Valle et al. (1977) who mentioned the presence of indeterminate plesiosaurs on James Ross and Vega Islands, east of the Antarctic Peninsula. Later, Chatterjee and Zinsmeister (1982) mentioned the first remains of these reptiles in Marambio (=Seymour) Island, also east of the Antarctic Peninsula. Gasparini et al. (1984) described associated postcranial remains of a single individual recovered from the latter island, this they regarded as a different morphotype from previously known elasmosaurids, although no genus or species was proposed. These records were discussed by Gasparini and Goñi (1985) in a regional context together with previous Upper Cretaceous records from Argentina and Chile. The first Antarctic species described was ‘Turneria seymourensis’ by Chatterjee and Small (1989) from late Maastrichtian beds of Marambio Island, based on a partial skull and associated cervicals. This was later re-named as ‘Morturneria seymourensis’ by Chatterjee and Creisler (1994) due to duplication of the genus name in another taxon. Fostowicz–Frelik and Gaździcki (2001) described new plesiosaur remains of a probable single specimen, recovered from Marambio Island. Based on histological sections and the morphology of the recovered portions, these authors indicated that the specimen was small (about 2 m in length) and probably a sub-adult individual, while several morphologic characters, especially the tibia and the femoral head, where considered similar to those of the species Mauisaurus haastii from the Campanian of New Zealand. Thereafter, Gasparini et al. (2003) re-described the holotype of Aristonectes parvidens Cabrera (1941), a very strange plesiosaur with uncertain affinities at that time, recovered from Maastrichtian beds of Chubut, Argentina. Besides the inclusion of A. parvidens among the elasmosaurids, additional materials referred to by Gasparini et al. (2003) to this species included finds in the late Maastrichtian of Chile (Casamiquela, 1969), while the holotype of ‘Morturneria seymourensis’ from Argentina (comprised by a juvenile specimen) was considered as a junior synonym of A. parvidens. Additional material of elasmosaurids from Seymour Island was described by Martin and Crame (2006) including associated vertebrae with ribs and fragments of propodials of a single individual, a second specimen comprising a partial postcranial skeleton and one last specimen comprising a partial propodial. The latter authors also mentioned an additional specimen referred to cf. Elasmosauridae as well as seven specimens referred to Plesiosauria indet., from James Ross and Seymour Islands. A pelvic girdle

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referred to Polycotylidae indet, was also recovered from Coniacian beds on James Ross Island (D’Angelo et al., 2008). Additional finds of Santonian age on James Ross Island include scattered postcranial remains referred to Plesiosaura indet. (Kellner et al., 2011). The oldest elasmosaurids from James Ross Island were described by O’Gorman (2012), having a late Coniacian to late Campanian age. On Vega Island (east of James Ross Island), other elasmosaurids have been recorded, including one articulated specimen referred to the genus *Mausaurus* Hector (1874) by Martin et al. (2007). Postcranial remains referred to *Aristopectes* were reported by O’Gorman et al. (2010), also from James Ross. Finally, O’Gorman et al. (2013) described the first postcranial skeleton of *Aristopectes* from late Maastrichtian beds of Marambio Island.

Despite the abundant records of plesiosaurs in Marambio, James Ross, and Vega Islands, only two genera have so far been discussed as being present in Antarctica, *Aristopectes* (represented by the specimens referred to *Aristopectes* cf. *parvidens* and *Morturneria seymourensis*), and a few specimens referred to *Mausaurus*. The present paper describes three new specimens: a novel morphotype based on a fragmentary postcranial skeleton from late Maastrichtian strata of Marambio Island; an indeterminate, very-long necked elasmosaurid from late Campanian beds of James Ross Island with affinities to Upper Cretaceous, North American elasmosaurids, and the first record of an aristonectine in late Campanian–early Campanian strata of the Snow Hill Island Formation, representing the oldest record of the subfamily *aristonectines*, previously known only in the Santonian and the Maastrichtian.

2.1. Santa Marta Formation (Olvero et al., 1986)

Marine volcaniclastic and epiclastic shelf sediments that reach a thickness of ca. 1200 m. It was originally divided into three informal members (Alpha, Beta, and Gamma) (Olvero et al., 1986) based on distinctive lithofacies. The age of this unit was assigned to the Santonian–early Campanian for the Alpha member based on ammonoids, while the Beta and Gamma members were assigned to the early/late Campanian, and early Campanian–early Maastrichtian, respectively.

2.2. Snow Hill Island Formation (Pirrie et al., 1997)

Poorly lithified gray sandy mudstones with well-lithified, fine-grained sandstones and very fossiliferous concretions that reach a minimum thickness of ca. 610 m. Based on the fossil content of palynomorphs and ammonoids, a late Campanian to ?late Maastrichtian age was originally assigned to the unit (Pirrie et al., 1997). Outcrops for this unit are present in the vicinity of Santa Marta Cove (Olvero et al., 1986). Subsequently, the former Gamma member of the Santa Formation was later considered as part of the Snow Hill Island Formation by Olivero (2012). Remains of a single plesiosaur individual (SGO.PV.6579) were found near Santa Marta Cove (63°55'10"S; 57°53'24"W) on January 2012 by some of the authors of this paper (A.V.M., D.R.R., R.Y.Y., R.A.O.) and excavated from siltstone beds consistent with the upper part of the Gamma member (Lithofacies Association E, sensu Scasso et al., 1991) originally referred to the Santa Marta Formation (Olvero et al., 1986), now currently included in the Snow Hill Island Formation. A second specimen (SGO.PV.6508) comprising an isolated vertebra was found by A. Llanos (Universidad de Chile) almost 2 km east of the previous locality (63°54'42"S; 57°50'55"W) being probably hosted in the same unit judging from the low dispersion of the fragments which indicate little transport.

2.3. Haslum Crag Sandstone (Olvero et al., 2008)

Originally defined by Pirrie et al. (1997) as the upper member (Haslum Crag Member) of the Snow Hill Island Formation, it comprises gray to green bioturbated muddy sandstones with sulphurous nodules as well as large concretions, intercalated with thin tuff beds. Glaucinite
beds are present in its basal half. Ammonoids and palytomorphs indicate a late Campanian–early Maastrichtian age for this unit. The Haslum Crag Member of the Snow Hill Island Formation (Pirrie et al., 1997) was elevated to formation status and differentiated as the Haslum Crag Sandstone by Olivero et al. (2008).

2.4. López de Bertodano Formation (Rinaldi et al., 1984)

This unit crops out in the southwestern half of the Marambio Island, comprising mainly friable sandy siltstones with a yellow to gray color, variable in hardness, but relatively constant in grain size and mud percentage (Macellari, 1988). The age of this formation was assigned by the latter author to the Maastrichtian–Paleocene, based on mollusks (Zinsmeister, 1979, 1982), microfossils (Huber, 1988) and palytomorphs (Askin, 1989), and thereafter constrained to the latest Maastrichtian based on different stratigraphic criteria (Crame et al., 2004). The López de Bertodano Formation was divided into 10 informal units (Macellari, 1984, 1988), named from base to roof as Klb1 to Klb9 which are late Maastrichtian in age, while the uppermost KTplb10 includes strata of Paleocene age. Specimen SGO.PV.6523 was recovered from the upper portion of the Klb9 unit, and was collected during January of 2011 by one of the authors (RAO).

3. Materials and methods

Two of the studied specimens (SGO.PV.6523 and SGO.PV.6508) include cervical centra. Their proportions were evaluated using a bivariate graphic analysis following O’Gorman et al. (2013). The indices here considered are those proposed by Welles (1952), particularly the height/length ratio (HI = 100 * H / L), the breadth/length ratio (BI = 100 * B / L), as well as the rate of vertebral elongation (VU = 100 * L / (0.5 * (H + B))). Since SGO.PV.6523 belongs to an adult individual, comparisons were carried out considering adult representatives from the Upper Cretaceous of North America, particularly Hydrotherosaurus alexandrae, and Elasmosaurus platyurus, as well as Callawayasaurus colombiensis, from the Upper Cretaceous of Colombia (of these specimens were taken from Welles, 1943, 1952, 1962). Also, adult elasmosaurids from the WBP were included, particularly the holotype of Tuarangisaurus keyesi (measurements from Wiffen and Moisley (1986)) and the holotype of Kaiwhekea katiki Cruickshank and Fordyce, 2002 (measurements taken directly from the specimen), both from the Maastrichtian of New Zealand. Futabasaurus suzukii, from the Santonian of Japan, was also included (measurements taken from Sato et al. (2006)). Phylogenetic analysis was not carried out since specimen SGO.PV.6523 is very fragmentary, thus, making it only scorable for a few characters.

For comparison of the SGO.PV.6508 belonging to a young individual from late Campanian beds of James Ross Island, juvenile representatives from the Upper Cretaceous of North America were selected including the type material of Cimoliasaurus maccoti, Leurospondylus ultimus, and ‘Aphrosaurus furlongi’ (measurements from Brown, 1913; Welles, 1943; Kear, 2005) currently considered as indeterminate elasmosaurids due to their ontogenetic stage, which allows assignments to be questioned (Kear, 2002; O’Keeffe and Hiller, 2006; Sato and Wu, 2006). In addition, young individuals from the WBP: include: 1) the type material of ‘Mortunera segoumensis’ (measurements from Chatterjee and Small, 1989)) from the late Maastrichtian of Antarctica, 2) a young indeterminate elasmosaurid from the late Campanian (Beta Member) of James Ross Island (measurements from O’Gorman, 2013), and 3) the young specimen SGO.PV.260 from the late Maastrichtian of central Chile, referred to Aristonectes sp. by Otero and G’orman (2013), and 4) the juvenile specimen CM Zfr 115 referred to Mauisaurus haasti from the late Campanian of New Zealand (measurements from Hiller et al. 2005)).

Finally, SGO.PV.6579 was directly compared with specimens of the genus Aristonectes (SGO.PV.957, adult, and SGO.PV.260, juvenile) (Suárez and Fritis, 2002; Otero et al., 2012), both recovered from late Maastrichtian beds of the Quiriquina Formation in central Chile.

**Anatomical abbreviations.** af, anterior articual facet of the vertebral; ag, anterior portion of the neural spine groove; aps, anterior process of the scapula; c2, cervical vertebra 2; c3, cervical vertebra 3; c5, cervical vertebra 5; cr, caudal rib; dfp, deep heart-shaped facet for postzygapophyses; dvs, dorsal process of the scapula; fha, facets for the haemal arches; g, gastraulium; nc, neural canal; ns, neural spine; pcf, fragment of vertebral posterior to c2; pc3, fragment of vertebra posterior to c3; pg, posterior portion of the neural spine groove; pna, facets for pedicles of the neural arch; poz, postzygopophysis; r, rib; rf, rib facet; vf, ventral foramina; vn, ventral notch.

**Institutional abbreviations.** SGO.PV., Colección de Paleontología de Vertebrados, Área de Paleontología, Museo Nacional de Historia Natural, Santiago, Chile; MLP, Museo de La Plata, Argentina; MCS, Colección del Museo de Cinco Saltos, Río Negro, Argentina; CM Zfr, Canterbury Museum, Christchurch, New Zealand; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

4. Systematic paleontology

**DIAPSIDA Osborn, 1903.**
**SAUROPTERYGIA Owen, 1860.**
**PLESIOSAURIA de Blainville, 1835.**
**ELASMOSAURIDAE Cope, 1869 (sensu Ketchum and Benson, 2010).** Elasmosauridae gen. et sp. indet. (Figs. 2–4).

4.1. Material

SGO.PV.6523: Postcranial remains of a single adult individual, including remains of 9 mid-to-posterior cervical vertebrae (6 of them preserving parts of their centra), the right scapula, several fragments of ribs and gastralia, and one phalanx.

4.2. Locality, geologic unit and age

Central part of Marambio Island, Antarctica, about 1550 m south of López de Bertodano Bay. Klb9 unit, López de Bertodano Formation (Macellari, 1984), latest Maastrichtian.

4.3. Ontogenetic observations

The studied specimen has cervical centra with tightly fused neural arches, without traces of sutures between them. This is considered as indicative of an adult stage (Brown, 1981). On the other hand, the unique recovered phalanx shows a poor ossification with a weak periosetal surface. Such a condition was described by Caldwell (1997) as a feature of adult limb morphology, because ossification is generally delayed. Based on these observations, we consider specimen SGO.PV.6523 as a near-adult individual. This allows direct comparisons with the species Aristonectes parvidens Cabrera (1941), K. katiki Cruickshank and Fordyce (2002), Mauisaurus haasti Hector (1874) (referred specimen CM Zfr 115), and T. keyesi Wiffen and Moisley (1986), all of them from the Upper Cretaceous of the WBP and described as adult or near-adult specimens. SGO.PV.6523 can be also compared with other Upper Cretaceous adult elasmosaurids from Argentina and New Zealand where the scapula is preserved.

4.4. Cervical vertebrae

Nine incomplete vertebrae are preserved, with six of them preserving the centrum or at least part of it, while two additional centra are represented by fragments of prezygopophyses that do not match any other vertebra. A fragment of a posterior cervical centrum is preserved in the block that hosts the scapula, followed by a last preserved centrum...
in the same block. An isolated portion of a centrum lacking the neural
arches and cervical ribs was also collected but not figured here since it
is not informative. The pedicels for the neural arches are thin in all
cases, indicating that no rib attachment is present in the neural arch,
thus, discarding them as pectoral or dorsal centra. Vertebrae including
both neural spines and part of the centrum have been arranged based
on their respective lengths (Table 1), being also named c1 to c5 from
the anteriormost to the posterior element. Neural spines have a vertical
groove along their anterior, and dorsal posterior borders, with a
conserved depth along each groove (Fig. 3). In the anterior groove two
lateral keels are developed on each side, with the anterior left one
being slightly more prominent than the right one. The anteriormost

Fig. 2. Elasmosauridae gen. et sp. indet. (SGO.PV.6523). Marambio Island, Antarctica. López de Bertodano Formation, Klb9, late Maastrichtian. Left view of the preserved centra. A, posterior
cervical centra hosted in the block of the scapula (c5, left). B, posterior cervical vertebra (c4). C, D, fragmentary, mid-cervical vertebrae (c2 and c3 from right to left, respectively).
E, anteriormost cervical vertebra preserved (c1). Scale bar represents 50 mm.

Fig. 3. Elasmosauridae gen. et sp. indet. (SGO.PV.6523). Anteriormost cervical vertebra c1. A, anterior view. B, dorsal view. C, posterior view showing its transverse section. D, cervical
vertebra c2 in anterior view. E, posterior view of c2 and a fragment of the immediately posterior neural arch in anatomical position. F, cervical vertebra c3 in anterior view. G, posterior view of
c3 and a fragment of the immediately posterior neural arch in anatomical position. H, cervical vertebra c4 in posterior view showing its transverse section. I, detail of the neural arch of c1.
Scale bars represent 50 mm, and 10 mm in l.

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Vertebral (c1) is the best preserved cervical (Fig. 3A–C), although the neural spine lacks its dorsal end (Fig. 3B). This centrum has the left part of its posterior articular facet absent, allowing a view of its transverse outline in posterior view (Fig. 3C), which has an obtuse angle between the vertical neural spine and the medial surface of the centrum. The latter is unusually large and reaches 157°, conferring a slightly triangular outline to the transverse section of the centrum. The anterior and posterior articular facets are larger than the rest of the centrum, and they have bilobed outlines with a ventral notch, which is typical of the Elasmosauridae (Gasparini et al., 2003). The

Table 1

Measurements of vertebral centra in the studied specimens. Absence of measurements is denoted with a line, while non-applicable indexes are denoted by 'NA'. Vertebral Length Index (VLI) = L / (0.5 * (H + B)) from 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).

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same features can be observed in the following c2 and c3 (Fig. 3D–G), reaching angles slightly over 150°, and becoming a little narrower in the last cervical c4, which has the lowest angle of 150° (Fig. 3H). No lateral keels are observed in any centra, suggesting that the preserved vertebrae can belong to posterior positions along the neck, which is also supported for the associated occurrence of trunk elements such as the scapula, several ribs and gastralia. Another striking feature is the presence in the neural spines of a deep, semi-cylindrical articulation above the neural canal, which locks with the postzygapophyses of the immediately anterior vertebra. In anterior view, this morphology is similar to most elasmosaurids, which have prominent and recurved prezygapophyses, although the articulation goes deep in the neural spine, parallel to the neural canal. Also, it is distinctively broad and causes a lateral bulk at the base of the neural spine over the neural canal, giving the base of the spine a more massive appearance compared with its dorsal portion. The inner surface of the articulation (Fig. 3I) has a heart-shaped excavation in its ventral portion that interlocks with the ventroposterior contour of the postzygapophyses. Also, the ventral end of the anterior neural groove reaches the middle portion of the heart-shaped excavation. This is especially visible on the c2 vertebra and the following posterior fragment attached in the same block. In addition, the pedicles of the neural arches are very thin, leaving a broad space for the neural canal which is subcircular in transversal section. Cervical rib facets also have interesting features, including short and sub-circular facets with a small posterior projection (Fig. 4A). An additional centrum, probably a posterior cervical, is hosted in the block of the scapula. This appears to be nearly circular in articular view, although it lacks part of its right, dorsolateral surface, making it difficult to evaluate its contour (Fig. 4B, C). Its neural canal is broad, bearing delicate and thin pedicels for the neural spine, suggesting that this is still a cervical centrum instead of a pectoral or dorsal vertebra, which normally shows a thickening of the neural arch pedicels due to the presence of transverse processes for rib attachment.

4.5. Scapula

Only the right scapula is preserved (Fig. 4D–F). Although it is incomplete, part of the ventral process can be evaluated since its cast is preserved in the sandstone matrix. The ventral process seems to be short and anteriorly rounded, but its medial features cannot be evaluated since this portion is not preserved. The most obvious feature in the scapula is the presence of a very high, slender and anteriorly angled dorsal process. Although this is incomplete, its posterior margin is delicate and thin, which indicates that the dorsal process does not extend far posteriorly, while the dorsal end preserves part of the entire contour of the scapula, allowing inference of its outline (Fig. 4E). The anterior portion of the scapula is incomplete, but its lateral outline is partially preserved in the sandstone matrix. In posterior view, the dorsal process diverges from the horizontal plane at almost 75° (Fig. 4F).

4.6. Ribs and gastralia

Four fragments of large and thin bones are recognized among the studied material. Three of them comprise bones with a medullary cavity, reason why these are interpreted as ribs, while an additional bone has a pachyostotic cross-section, being interpreted as a gastralia, following the criteria of O’Keefe et al. (2011). The ribs have a cross-section that is variable between rhomboidal to triangular, with a thin periosteal surface. On the other hand, the gastralia seems to have a distal portion that is U-shaped in cross-section, with a ventral groove (Fig. 4G, H).

4.7. Phalanges

A single phalanx was recovered directly associated with the other remains. This is elongated and massive, with a polygonal articular facet (the proximal facet being best preserved). This element is poorly ossified, with a limited periosteal surface that seems to be mostly absent, rather than being removed before burial.

4.8. Remarks

Although the specimen is a fragmentary postcranial skeleton, the combination of morphologic characters emerges as unique among any known adult plesiosaur from the WBP: features of the cervical vertebrae include a neural spine with a groove along its anterior and posterior edge, leaving two edges with the left one slightly prominent with respect to the right; presence of a deep, concave and semi-cylindrical articular facet in the neural spines over the prezygapophyses, having a heart-shaped facet in its ventral margin that interlocks with the postzygapophysis of the immediately anterior vertebra, giving a thick appearance to the basal portion of the neural spine. In addition, mid-to-posterior cervical centra have a transversal section with a triangular shape, being higher than broad, having their dorsomedial surfaces angled between 150°–160° with respect to the neural spine. The articular facets become very expanded, having a bilobed outline with a ventral notch (Fig. 3). Other distinctive characters are present in the scapula, which has an unusually high, slender and anteriorly recurved dorsal process, while the ventral process seems to be short. Additional morphologies contributing to a unique combination of characters include: neural arches with very thin and delicate pedicels; cervical ribs having oval facets and displaced into the posterior half of the centrum; the presence of trunk ribs with a triangular cross-section; pachyostotic gastralia with a U-shaped cross-section; and proximal phalanges being elongated and massive.

Elasmosauridae indet.
(Fig. 5A–D).

4.9. Material

SGO.PV.6508: one isolated cervical vertebra centrum. Santa Marta Cove, N of Shark Stream, James Ross Island. Lithofacies Association E, Gamma member, Santa Marta Formation (sensu Scasso et al., 1991), late Campanian (Olivero, 1992).

4.10. Description

A damaged centrum, which is preserved in four fragments. The centrum is broader than long and longer than high (Table 1), markedly platycoelous, having a ventral notch and bilobed contour in articular view. The bases of the neural arch pedicels are sub-triangular, leaving a space for the neural canal that is comparatively broader in the posterior margin. The base of the neural arch is conspicuously broad, representing nearly 50% of the total breadth of the centrum. The rib facet can be observed in lateral view, having an oval contour. No lateral keel can be observed. In ventral view, there are two foramina placed in a sub-central position, with an oval contour, separated by a thin bone bridge without a medial keel between them. The small size of the centrum and the evident rib facet (not fused) indicate that this belonged to a juvenile individual (Brown, 1981).

Aristonectinae Otero et al. (2012).
Aristonectinae indet.
(Fig. 6A–O, Q).

4.11. Material

SGO.PV.6579: Fragmentary postcrania! skeleton preserving eight fragmentary caudal centra, two articular propodial heads (likely femora), an epipodial (likely a fibula), ventral portion of the right ilium, partial left pubis, and several rib portions.
4.12. Ontogenetic observations

The specimen has caudal centra bearing ribs unfused to the centra. Additionally, the preserved portions of the ilium and pubis are smaller than other known juvenile specimens of Aristonectes (particularly the SGO.PV.260, described by Otero et al., 2012). Based on these facts, we consider this specimen to be a juvenile individual following the criteria of Brown (1981).

4.13. Caudal centra

Eight incomplete portions of caudal centra were recovered. The most complete centra (Fig. 6A–H) show that these are broader than high and higher than long. In lateral view the rib facets occupy almost the whole length of the centrum, leaving a small gap before the posterior articular face. Rib facets are oval and excavated into the centrum. In ventral view, one central foramen can be observed. The posteroverentral margin of the centra has two well-marked, semicircular facets for the haemal arches, confirming its caudal position. In dorsal view, these centra have large facets for the pedicles of each neural arch. These are massive, anteriorly broader and reaching the margin of the anterior articular face, while its posterior end is reduced in breadth giving a triangular outline to the pediclear facet, and does not reach the posterior articular margin of the centrum.

The anterior articular face has a distinctive octagonal outline defined by the surface of the neural canal, the surface between the neural arch pedicels and the rib facets, the rib facet itself, and the flat ventral surface of the centrum between the keels that rise from the facets for the haemal arches (Fig. 6A, E). This octagonal articular outline has been found to be diagnostic of the genus Aristonectes (Otero et al., 2012; O’Gorman et al., 2013), although the caudal vertebrae in the latter genus are notoriously broader than high, while the vertebrae of the SGO.PV.6579 are slightly broader than high. Additional materials belong to fragments of caudal centra with similar features (Fig. 6I, J).

4.14. Propodials

Two different proximal portions were recovered (Fig. 6K, L). These are fragmentary, although they do show the longitudinal section of the articular head which has a circular outline, thus indicating that the articular head was hemispherical. Each articular head has a distal constriction, indicating that the latter was prominent with respect to the diaphysis, as occurs in the lectotype of Mauisaurus haasti (Hector, 1874; Welles, 1962), in the propodials of Aristonectes sp. (Otero et al., 2012), as well as in another Antarctic specimen (ZPAL R.B.11/1) previously described by Postowicz-Freliek and Gaździcki (2001). Considering the associated pelvic portions and caudal vertebrae preserved in SGO.PV.6579, these articular heads are likely part of each femur.

4.15. Epipodial

A single fragmentary epipodial was recovered (Fig. 6M), which is broken in sagittal section and also missing its lateral half. The preserved portion (medial half) is as broad as it is long, thus indicating that the complete epipodial was broader than long. The proximal articular facet is recognized by being comparatively thicker than the distal facet. The first has a rounded border that articulates with the lateral facet of the propodial, while the internal margins have a medial concavity that separates the proximal facet from the distal one. Such a concavity is typically placed in the axial margin of the epipodials. Also, the straight distal facet is large enough for articulation with a centrale element, while in the case of radius/tibia, the facet for the centrale is more reduced (Broili, 1930; Welles, 1952). Based on this, the epipodial likely belongs to an element placed in the posterior half of the limb. Since the associated postcranial elements of the SGO.PV.6579 are caudal and pelvic portions, it is likely that the epipodial belongs to a fibula rather than an ulna.

4.16. Ilium

The ventral portion of the right ilium is preserved (Fig. 6N). This is very massive and recurved. Its ventral articular face is incomplete, but allows evaluating the ventral length of the bone. The dorsal portion is lost, but it is possible to see a medial reduction of the shaft section in the part where the bone is recurved.
4.17. Pubis

A large amount of scattered bone fragments were collected and later re-assembled (Fig. 6M). These include a very fragmentary articular face of a probable right pubis, as well as the acetabular portion of the left pubis. This latter bears an oval articular face for the femoral head. The rest of the bone is poorly preserved, lacking most of its perimeter, although it is possible to see the distinctive dorsal (internal) view of the pubis surface which is slightly concave.

5. Discussion

5.1. Comparison of SGO.PV.6523 with other elasmosaurids from the WBP

Morphological characters of SGO.PV.6523 include the presence of an anterior and posterior groove on the edge of the neural spines at least on mid-to-posterior cervical vertebrae (its presence on anterior cervicals cannot be verified since the latter are not preserved). A similar condition is observed in posterior cervicals of specimen SGO.PV.260 referred
to Aristonectes sp. (Otero and O’Gorman, 2013) from late Maastrichtian strata of the Quiriquina Formation in central Chile, where the neural groove is present in the basal portion of the neural spine, but reaches only one third of the spine’s height. Similarly, in the latter taxon, the anterior left flank that rises from the groove turns into an enlarged, flat and delicate bony layer, while its posterior right flank has a similar structure. This was originally described as ‘delicate alternate flanks’, in Otero et al. (2012: fig 3E, F) for the juvenile specimen SGO.PV.260, later referred to the genus Aristonectes by Otero and O’Gorman (2013) and therefore considered as a highly diagnostic feature. The presence of similar structures in the neural spines of SGO.PV.6523 suggests affinities with the genus Aristonectes, although it represents a different taxon than the latter, based on the cervical vertebrae, scapula and the comparatively smaller adult size.

In the case of Aristonectes parvidens, the anterior and posterior groove of the neural spines are not present, at least based on the neural spines of the anterior and middle portion of the neck (Cabrera, 1941: fig. 4A, B). Such a feature is also absent from T. keyesi (Wiffen and Moisley, 1986: figs. 4 and 5) and in specimen CM Zfr 115 referred to Mauisaurus haasti (Hiller et al. 2005: figs. 11 and 12), discounting narrow relationships with these taxa. Another interesting morphology in SGO.PV.6523 is the cervical vertebrae with a triangular outline in the transversal section of each centrum, having an angle between neural spines and the dorsolateral surface of each centrum close to 150–160°, conferring them a distinctive aspect. Although a similar angle and outline are present in anterior cervicals of the holotype of Aristonectes parvidens (RAO, pers. obs.), this becomes reduced to nearly 125° in middle cervicals, which is a distinctive aspect. Although a similar angle and outline are present in anterior cervicals of the holotype of Aristonectes parvidens (RAO, pers. obs.), this becomes reduced to nearly 125° in middle cervicals (Gasparini et al., 2003: fig. 2F). In addition, the same angle in the referred specimen CM Zfr 115 of Mauisaurus haasti shows values between 130°–140° on anterior and middle cervicals (Hiller et al., 2005: figs. 10–12), while the posterior centra show very similar values as well as similar articular outlines with those of specimen SGO.PV.6523 from Seymour Island (RAO, pers. obs.); similar values between 130°–140° can be inferred from the anterior cervicals of the holotype of T. keyesi (Wiffen and Moisley, 1986: fig. 5). Moreover, the semi-cylindrical articular facet for postzygapophyses is indeed present in other elasmosaurs (Welles, 1943), although in SGO.PV.6523 the breadth and depth of this structure are unusual, as well as the presence of a distinctive heart-shaped internal facet. Finally, the dorsal process of the scapula is one of the most remarkable characters, being unusually high and anteriorly recurved, a feature not known in any adult elasmosaurid specimen from the WBP. All the known scapulae of adult individuals recovered in this province (Fig. 7A–F) have dorsal processes angled posteriorly, except in the case of ZPAL R.B/11 from the Klbk2 unit of the López de Bertodano Formation on Marambio Island (Fostowicz–Frelik and Gażdzić, 2001). Here the dorsal process is absent, making it impossible to compare, although it matches SGO.PV.6523 in size and in the outline of the anterior process of the scapula. In addition, scapulae of adult or near-adult specimens of Aristonectes sp. (SGO.PV.957), Mauisaurus haasti, and the indeterminate elasmosaurid CM Zfr 145 from the late Maastrichtian of the Conway Formation, in New Zealand (Hiller and Mannering, 2005), are notoriously larger than the scapula of SGO.PV.6523. The scapula of the indeterminate elasmosaur MUCS-4 from late Campanian–early Maastrichtian beds of the Allen Formation, Argentina (Gasparini and Salgado, 2000) is slightly smaller than SGO.PV.6523 and has a dorsal process which is still recurved posteriorly, but comparatively more vertical than those of Aristonectes sp., Mauisaurus haasti and CM Zfr 145.

Other morphologic characters could be potentially apomorphic. The cervical ribs in SGO.PV.6523 are known from only a few fragments. Their exposed cross-section reveals a triangular outline, which differs from the oval to circular cross-section in the ribs of Aristonectes (RAO, pers. obs.). A similar oval outline was also described for the ribs of Mauisaurus haasti by Hiller et al. (2005) and K. katiki (Cruickshank and Fordyce, 2002), while in T. keyesi these are not known, although the referred specimens bear oval transverse processes suggesting an oval cross-section of the ribs (Wiffen and Moisley, 1986: fig. 17). Cervical ribs could include distinctive features. In SGO.PV.6523 these have oval facets with a thin posterior projection, being constrained to the posterior half of the centrum, contrary to the oval cervical rib facets in Mauisaurus, Tuarangisaurus, Aristonectes and Kainhovekea, all of them extended along most of the centrum length (Wiffen and Moisley, 1986: fig. 4; Cruickshank and Fordyce, 2002: fig. 6; Gasparini et al., 2003: fig. 2E; Hiller et al., 2005: figs. 11, 12).

Fig. 7. Comparison between scapulae of adult elasmosaurids from the Upper Cretaceous of the WBP. A, Aristonectes sp. (SGO.PV.957, late Maastrichtian of central Chile), right scapula in lateral view. B, Elasmosauridae gen. et sp. indet. (SGO.PV.6523, late Maastrichtian of Marambio Island, Antarctica), right scapula in lateral view. C, Elasmosauridae indet. (MCS-4, late Campanian–early Maastrichtian of Argentina), dorsal scapula in lateral view (modified from Gasparini and Salgado (2000)). D, aff. Mauisaurus sp. (ZPAL R.B/11, early Maastrichtian of Marambio Island, Antarctica), left scapula in medial view (modified from Fostowicz–Frelik and Gażdzić, 2001). E, Mauisaurus haasti (CM Zfr 115, late Campanian of New Zealand), left scapula in medial view (modified from Hiller et al. (2005)). F. Elasmosauridae indet. (CM Zfr 145, late Maastrichtian of New Zealand), left scapula in medial view (modified from Hiller and Mannering (2005)). Scale bar equals 50 mm.
Although SGO.PV.6523 bears apparently unique morphologic characters, its fragmentary condition prevents accurate comparisons, particularly with other records from Marambio Island comprising different anatomical portions, such as the skull and anterior neck of 'Morturneria seymourensis' (Chatterjee and Small, 1989).

5.2. Functional aspects on the neck of SGO.PV.6523

The presence of a groove along the anterior and posterior edge of the cervical neural spines is a feature poorly described in known plesiosaurs. Anterior grooves in neural spines are present in posterior caudal and dorsal vertebral of the Jurassic cryptoclidid Muraenosaurus (Andrews, 1910: figs. 51, 52 and 54), but the grooves fade into the dorsal portion of the spines. Other elasmosaurs have distinctive morphologies on the edges of neural spines. Dorsal pits are present in posterior cervicals of H. alexandrae (Welles, 1943: plate 27). Similar morphologies are also present in F. suzuki, which has an anterior pit and a posterior swelling in the dorsal portion of the posterior cervical neural spines (Sato et al., 2006: fig. 5C, D). This evidence suggests that the neural spines of posterior vertebrae in elasmosaurs are highly distinctive and can be taxonomically informative. Also, these portions allow inferences to be made about the rigidity of the posterior neck. Analog muscular attachments in birds and sauropods (Wedel and Sanders, 2002: fig. 2) show that neural spines can develop large interspinal muscles related to the ability of curving the neck dorsally as it occurs in the sauropod Apatosaurus. Nevertheless, in the latter, the interspinal space is large, contrary to the very reduced space between neural spines of SGO.PV.6523, which also has deep grooves in the anterior and posterior margin of the neural spines, indicating a strong muscular attachment but scarce possibilities for dorsoventral movement of the posterior neck. This is also consistent with the large semi-cylindrical facets for articulation of the postzygapophyses, which allow interlocking between successive cervicals. Based on this, it is likely that the elasmosaur SGO.PV.6523 possessed a stiff posterior portion of the neck, with reduced movement.

5.3. Associated fauna and environment of the SGO.PV.6523

This specimen was recovered completely isolated from any other vertebrate remains. The fossil-bearing unit was traced over a large area while looking for additional remains. These findings include cranial material of a large mosasaur (presently being studied by the authors), isolated teeth of odontaspid sharks, scattered but frequent dental plates of indeterminate callorhynchid fishes and dental plates of Callorhinichus torresi (Otero et al., 2013). Additional remains of elasmosaur plesiosaurs were found separated by several tens of meters, which allow a possible mixing of elements from different individuals to be discarded. The common presence of frequent dental plates of holoccephalans and odontaspid teeth suggests a shallow shelf environment (Stahl, 1999; Compagno, 2001).

5.4. Specimen SGO.PV.6508

The presence of very-long necked elasmosaurs (with cervical indices in the range of representatives from the Upper Cretaceous of North America) in the Campanian–Maastrichtian of the Southern Hemisphere is restricted to finds in New Zealand (Welles and Gregg, 1971; Wilfien and Moisley, 1986; Hiller et al., 2005) and Argentina (Gasparini et al., 2001: fig. 3), but are very scarce in Chile (RAO, pers. obs.). Also, the records from Antarctica include long-necked elasmosaurs referred to the genus Mauisaurus by Martin et al. (2007) from Maastrichtian beds of Vega Island, although the cervicals of the specimen were not recovered. O’Gorman (2012) also described the oldest elasmosaur from Coniacian–Campanian beds of James Ross Island, including a juvenile specimen with several cervical vertebrae. The studied specimen verifies the presence of very-long necked elasmosaurs during the late Campanian on the James Ross Island.

5.5. Specimen SGO.PV.6579

The presence of anterior caudal centra much broader than high and higher than large, with an octagonal articular outline, has been regarded as a diagnostic feature of the genus Aristonectes (Gasparini et al., 2003: fig. 31; J. O’Gorman et al., 2010; Otero et al., 2012: fig. 5). The studied material SGO.PV.6579 has different proportions with respect to the diagnostic anterior caudals of Aristonectes, with a breadth slightly larger than the height. Since SGO.PV.6579 has ventral facets for the haemal arches, this verifies their anatomical position in a posterior position with respect to the diagnostic anterior caudals of Aristonectes, with a breadth slightly larger than the height. Since SGO.PV.6579 has ventral facets for the haemal arches, this verifies their anatomical position in a posterior position with respect to the diagnostic anterior caudals of Aristonectes, with a breadth slightly larger than the height. Since SGO.PV.6579 has ventral facets for the haemal arches, this verifies their anatomical position in a posterior position with respect to the diagnostic anterior caudals of Aristonectes, with a breadth slightly larger than the height. Since SGO.PV.6579 has ventral facets for the haemal arches, this verifies their anatomical position in a posterior position with respect to the diagnostic anterior caudals of Aristonectes, with a breadth slightly larger than the height. Since SGO.PV.6579 has ventral facets for the haemal arches, this verifies their anatomical position in a posterior position with respect to the diagnostic anterior caudals of Aristonectes, with a breadth slightly larger than the height.
ornithopods; Salgado and Gasparini, 2006; Coria et al., 2007; Cerda et al., 2012; Coria et al., 2013), which indicate shallow water facies for the two specimens of plesiosaurs studied here.

5.7. Results of bivariate graphic analysis

Bivariate graphic analysis of the indices of SGO.PV.6523 returned a low dispersion of the points (Fig. 8). The plot occupies an intermediate position between adult aristonectines (Aristonectes sp. and F. suzukii) and a second sub-group including the adult individuals of T. keyesi, Mauisaurus haasti (referred), and Callawayasaurus colombiensis. The results are not conclusive for separating SGO.PV.6523 neither from aristonectines or from intermediate forms (Mauisaurus, Tuarangisaurus, Callawayasaurus), but allow discarding it as a representative of very-long necked elasmosaurids such as those from the Upper Cretaceous of North America.

Regarding the juvenile elasmosaurid SGO.PV.6508 from James Ross Island, this has a VLI index of 111, and has clear rib facets with the ribs not fused to the centrum, indicating that the specimen was a juvenile (Brown, 1981). Based on this, comparison was carried out with other juvenile elasmosaurids. Among aristonectines, the juvenile specimen SGO.PV.260 from central Chile has an average VLI of nearly 62 (Otero and O’Gorman, 2013), while the holotype of ‘Mortuneria seymourensis’ from Antarctica has an average VLI of nearly 56. Additionally, a juvenile specimen from James Ross Island previously described by O’Gorman (2012) was included, having an average VLI close to 81. Juvenile representatives of very-long necked elasmosaurids from North America have average VLI indices between 81–91 (measurements from Brown (1913); Welles (1943); Kear (2005)), while the closest average VLI is


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that of CM Zfr 115 referred to *Mausoasaurus haasti*, nearly 101, although the latter is a near-adult specimen. The results of bivariate graphic analysis support SGO.PV.6508 as being a juvenile individual of a very long-necked elasmosaurid.

6. Conclusions

The studied material SGO.PV.6523 represents an unusual indeterminate elasmosaurid from late Maastrichtian strata of the López de Bertodano Formation exposed on Marambio Island. Despite this being a fragmentary specimen, it represents a novel, relatively small animal with a probably rigid neck and a scapula very different from the scapula known in any Wedellian elasmosaurid. The fragmentary condition of the material prevents direct comparison with other taxa, while the cervical features and the bivariate graphic analysis suggest that this can belong to a form within Aristonectinae, based on the cervical proportions and the presence of an incipient left anterior flank in the neural spines, a feature that partially matches the cervical morphologies observed in Aristonectes sp. (SGO.PV.957) from late Maastrichtian strata of central Chile; Nevertheless, SGO.PV.6523 surely represents a different taxon based on the much smaller adult size.

In addition, the studied material from James Ross Island (SGO.PV.6508) shows the presence of very-long necked elasmosaurs during the late Campanian, to date are completely unknown in Upper Cretaceous units of the southeastern Pacific (Chile), but known in Argentinean units of the same age. Their common presence in Argentina, Antarctica, and New Zealand during the late Campanian–Maastrichtian and their posterior absence in the southeastern Pacific during the late Maastrichtian, raise questions about paleogeographic or environmental changes that could have affected their distribution during this period.

Finally, additional material from James Ross Island allows the identification of the first remains of an indeterminate aristonectine in late Campanian strata of Antarctica, while suggesting the presence of the same taxon also in early Maastrichtian strata of the López de Bertodano Formation on Marambio Island. This is the oldest known record of this sub-family, widely distributed within the WBP, but previously restricted only to late Maastrichtian beds of Antarctica, Argentina, Chile, and New Zealand. The three new specimens studied here represent new information about the diversity of Upper Cretaceous Antarctic plesiosaurs.

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