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Cretaceous Antarctic plesiosaurs: stratigraphy, systematics and paleobiogeography

José Patricio O'GORMAN[1,2*], Rodrigo OTERO[3], Marcelo REGUERO[1,4] & Zulma GASPARINI[1,2]

[1] División Paleontología Vertebrados, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s/n., B1900FWA, La Plata, Argentina;
[2] Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, Godoy Cruz 2290, C1425FQB, CABA, Argentina;
[3] Red Paleontológica U-Chile, Laboratorio de Ontogenia y Filogenia, Departamento de Biología, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Santiago, Chile;
[4] Instituto Antártico Argentino, 25 de Mayo 1143, B1650HMK, San Martín, Buenos Aires, Argentina

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Abstract The last twenty million years (Maastrichtian–Santonian) of Southern Hemisphere plesiosaur history is especially well recorded in the Weddellian Province (Patagonia; Western Antarctica and New Zealand). The oldest Late Cretaceous plesiosaurs, two specimens referred to Polycotylidae indet., come from the Santonian levels of the Santa Marta Formation, while the oldest elasmosaurids come from the lower Campanian of the same formation. In the lower Maastrichtian of the Snow Hill Island Formation the non-aristonectine elasmosaurid *Vegasaurus molyi* is recorded together with other non-diagnosable elasmosaurid specimens, but no aristonectines are present. Aristonectines appears in the Antarctic record in the upper Maastrichtian of the López de Bertodano Formation and are represented by *Morturneria* and cf. *Aristonectes*. The specimens from the upper Campanian previously referred to Aristonectinae indet. are referred to Elasmosauridae indet., shortening the temporal record of Aristonectinae in Antarctica. Therefore aristonectines appears in the Antarctic record in the upper Maastrichtian of the López de Bertodano Formation and are represented by *Morturneria* and cf. *Aristonectes*. The Antarctic Cretaceous elasmosaurids show a paleobiogeographic connection with South America and New Zealand (Weddellian Province). This connection is indicated by the shared presence of the Aristonectinae *Kaiwhekea katiki* (New Zealand) and *Aristonectes* (Argentina and Chile). Recent phylogenetic analysis recovered the aristonectines within the Weddellonectia clade, which includes the aristonectines and the non-aristonectines *Vegasaurus molyi* (Isla Vega, Antarctica); *Kawanectes lafquenianum* (Argentina); *Morenosaurus stocki* and *Aphrosaurus furlongi* (California). Among the Weddellonectia, the aristonectines show a relatively large body size and extremely derived features and probably occupied a trophic niche that differed from the trophic niche of other elasmosaurids. By way of contrast *Kawanectes lafquenianum* is an extremely small body-sized elasmosaurid restricted to marginal marine (probably estuarine) environments. Therefore the Weddellonectia show high morphological and probably high ecological diversity.

Keywords **Elasmosauridae, Aristonectinae, Polycotylidae, Santa Marta Formation, Snow Hill Island Formation, López de Bertodano Formation, Weddellonectia**

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1 Introduction

Plesiosaurs are a clade of diapsid marine reptiles whose biochron extends from the Late Triassic to the K/Pg boundary (Ketchum and Benson, 2010). Plesiosaurs, thus, have one of the longest biochrons among the Mesozoic marine reptiles, and they successfully invaded the marine environment (Benson and Druckenmiller, 2014). Plesiosaurs had four limb locomotions, differing from the axial

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[*] Corresponding author, E-mail: joseogorman@fcnym.unlp.edu.ar

locomotion inferred for mosasaurs and ichthyosaurs (Massare, 1994; O'Keefe and Carrano, 2005). Recent advances in plesiosaur paleobiology indicate the possibility of viviparism and high body temperature (Bernard et al., 2011; O'Keefe and Chiappe, 2011).

Plesiosaurs were cosmopolitan; they are recorded on every continent since the Jurassic, including Antarctica (Ketchum and Benson, 2010; O'Gorman et al., 2018b). The last twenty million years of the Southern Hemisphere plesiosaur history (i.e. Santonian–Maastrichtian) is especially well-recorded in the Weddellian Province (Zinsmeister, 1979; Wiffen and Moisley, 1986; Cruickshank and Fordyce, 2002; Gasparini et al., 2003a, 2003b; Hiller et al., 2005; O'Gorman, 2012; O'Gorman and Gasparini, 2013; Figure 1). This record has been improved in the last two decades by field studies in southern South America (Argentina and Chile), the Antarctic Peninsula, and the revision of the New Zealand historic collections (O'Gorman et al., 2013, 2017a, 2017b; Otero et al., 2014b; O'Gorman, 2016a, 2016b; Hiller et al., 2017). Especially relevant has been the scientific activity in Antarctica organized by the Instituto Antárctico Argentino (IAA) which has organized annual fieldtrips spanning four decades, obtaining a continuously growing plesiosaur collection from different Antarctic localities.

The main goal of this contribution is to describe the Late Cretaceous Antarctic plesiosaur record, giving a comprehensive list of the main plesiosaur specimens (Table 1), discussing the main features of the Late Cretaceous Antarctic plesiosaurs record and their importance in the phylogeny and paleobiogeography of Weddellian plesiosaurs.

Figure 1 Weddellian Province. Modified from Zinsmeister (1982) and Cruickshank and Fordyce (2002).

Table 1 Comprehensive list of Antartic plesiosaur specimens

Specimen	Determination	Stratigraphic horizon	Reference
TTU P 9219	*Morturneria seymourensis*	López de Bertodano Fm.	Chatterjee and Small, 1989
TTU P 9217	Elasmosauridae indet.	López de Bertodano Fm.	Chatterjee and Small, 1989
TTU P 9218	Elasmosauridae indet.	López de Bertodano Fm.	Chatterjee and Small, 1989
TTU P 9220	Elasmosauridae indet.	López de Bertodano Fm.	Chatterjee and Small, 1989
TTU P 9221	Elasmosauridae indet.	López de Bertodano Fm.	Chatterjee and Small, 1989
TTU P 9238	Elasmosauridae indet.	López de Bertodano Fm.	Chatterjee and Small, 1989
TTU P 9239	Elasmosauridae indet.	López de Bertodano Fm.	Chatterjee and Small, 1989
TTU P 9240	Elasmosauridae indet.	López de Bertodano Fm.	Chatterjee and Small, 1989
ZPAL R.8	Elasmosauridae indet	López de Bertodano Fm.	Fostowick-Frelik and Gazdzicki, 2001
MLP 89-III-3-1	cf. *Aristonectes*	López de Bertodano Fm.	O'Gorman et al., 2019
MLP 89-III-3-2	Aristonectinae indet	López de Bertodano Fm.	O'Gorman et al., 2013
MLP 14-I-20-8	Aristonectinae indet	López de Bertodano Fm.	O'Gorman et al., 2017a
MLP 82-I-28-1	Elasmosauridae indet	López de Bertodano Fm.	Gasparini et al., 1984
MLP 93-I-5-1	*Vegasaurus molyi*	Snow Hill Island Fm.	O'Gorman et al., 2015
MLP 14-I-20-16	Weddellonectia indet	López de Bertodano Fm.	O'Gorman et al., 2017b
MLP 15-I-7-6	Weddellonectia indet	Snow Hill Island Fm.	O'Gorman et al., 2018a
MLP 15-I-7-48	Weddellonectia indet	Snow Hill Island Fm.	O'Gorman and Coria, 2017
MLP 82-I-28-1	Elasmosauridae indet	López de Bertodano Fm.	Gasparini et al., 1984
MLP 11-2-20-4	Elasmosauridae indet.	Santa Marta Fm.	O'Gorman, 2012
MLP 86-X-28-3	Elasmosauridae indet.	Snow Hill Island Fm.	O'Gorman, 2012
MLP 86-X-28-(2-6)	Elasmosauridae indet.	Snow Hill Island Fm.	O'Gorman, 2012

Continued

Specimen	Determination	Stratigraphic horizon	Reference
SGO.PV.6579	Elasmosauridae indet.	Snow Hill Island Fm.	Otero et al., 2014b
SGO.PV.6508	Elasmosauridae indet.	Snow Hill Island Fm.	Otero et al., 2014b
SGO.PV.6523	Elasmosauridae indet.	López de Bertodano Fm.	Otero et al., 2014b
SDSM 78156	Elasmosauridae indet.	Snow Hill Island Fm.	Martin et al., 2007
MLP 98-I-10-20	Elasmosauridae indet.	Snow Hill Island Fm.	O’Gorman et al., 2012
MN 7163-V	Polycotylidae indet.	Santa Marta Fm.	Kellner et al., 2011
MACN Pv 19.781	Polycotylidae indet.	Santa Marta Fm.	Novas et al., 2015

2 Antarctic Plesiosaurs: historical account

The first described plesiosaur material from Antarctica belongs to remains of indeterminate elasmosaurids (del Valle et al., 1977) collected from the Snow Hill Island Formation cropping on James Ross and Vega islands. Later, additional and more complete elasmosaurid material (MLP 82-I-28-1) collected from the López de Bertodano Formation, Seymour Island (= Marambio) was described by Gasparini et al. (1984), however the lack of cranial material precluded identifying the specimen beyond the family level.

After Chatterjee and Small (1989) described a new elasmosaurid *Morturneria seymourensis* also from the López de Bertodano Formation. It was initially named as *Turneria seymourensis*, but changed by Chatterjee and Creisler (1994) to *Morturneria* because *Turneria* was a preoccupied name. *Morturneria seymourensis* Chatterjee and Creisler, 1994 is a plesiosaur similar to *Aristonectes parvidens* and considered as a junior synonym of it by Gasparini et al. (2003a).

Additional material referred to *Mauisaurus* Hector, 1874 from the Snow Hill Island Formation, Vega Island, was described by Martin et al. (2007) but the genus *Mauisaurus* is currently considered as not valid (Hiller et al., 2017). New material from the lower levels of the Santa Marta Formation (MN 7163-V), is probably referable to the Polycotylidae (Kellner et al., 2011; O’Gorman, 2012; Novas et al., 2015), and new elasmosaurids from upper levels (Beta Member) of the same lithostratigraphic unit were described by O’Gorman (2012) and Otero et al. (2014b).

The first non-aristonectine elasmosaurid from Antarctica identified to species level was *Vegasaurus molyi* O’Gorman, Salgado, Olivero, Marenssi, 2015, described from the Cape Lamb Member of the Snow Hill Island Formation (O’Gorman et al., 2015; Figure 2a). A phylogenetic approach indicated a close relationship with the non-aristonectine elasmosaurids from the Weddellian Province (O’Gorman et al., 2015; O’Gorman, 2016b). An analysis was performed on the sedimentological and petrographic features of gastroliths associated with an aristonectine (O’Gorman et al., 2014) and non-aristonectine elasmosaurids (Thompson et al., 2007; O’Gorman et al., 2012). The sedimentological features indicated a fluvial (estuarine) environment, while the petrographic analyses indicated a relatively close locality as the origin of the ingested clasts (O’Gorman et al., 2012, 2014).

3 Geological setting

3.1 Santa Marta Formation

The Lachman Cragg Member of the Santa Marta Formation (Alpha and Beta members) crops out on James Ross Island (Figures 2, 3). The Santa Marta Formation comprises mudstones, fine-grained sandstones, pebbly or coarse-grained sandstones and re-sedimented conglomerates (Olivero, 2012). This unit has yielded bivalves, ammonites (Olivero and Medina, 2000), chondrichthyes, teleosts (Kriwet et al., 2006; Otero et al., 2014a), turtles (de la Fuente et al., 2010) and plesiosaurs (Kellner et al., 2011; O’Gorman, 2012; Novas et al., 2015). The depositional setting was a mid-shelf, delta slope and prodelta basin plain (Olivero, 2012). The Santa Marta Formation was deposited during the late Coniacian–middle Campanian interval (McArthur et al., 2000) or Santonian–middle Campanian interval (Olivero, 2012).

3.2 Snow Hill Island Formation

At James Ross Island, James Ross Archipelago (Figures 2, 3), the Herbert Sound Member of the Snow Hill Island Formation (= Gamma Member) comprises quartz sandstone with coquina levels (Olivero, 2012). The Herbert Sound Member has yielded a rich fauna of bivalves, ammonites (Olivero and Medina, 2000), chondrichthyes and teleosts (Kriwet et al., 2006) as well as marine reptiles such as mosasaurs and plesiosaurs (Novas et al., 2002; Fernández and Gasparini, 2012; O’Gorman et al., 2015), and continental tetrapods such as dinosaurs (Salgado and Gasparini, 2006). The Herbert Sound Member was deposited in an inner shelf environment during the late Campanian (Olivero, 2012).

At Vega Island, James Ross Archipelago, the Cape Lamb Member of the Snow Hill Island Formation is a fossiliferous sequence of sandy mudstones and muddy sandstones to medium-grained sandstones (Marenssi et al.,

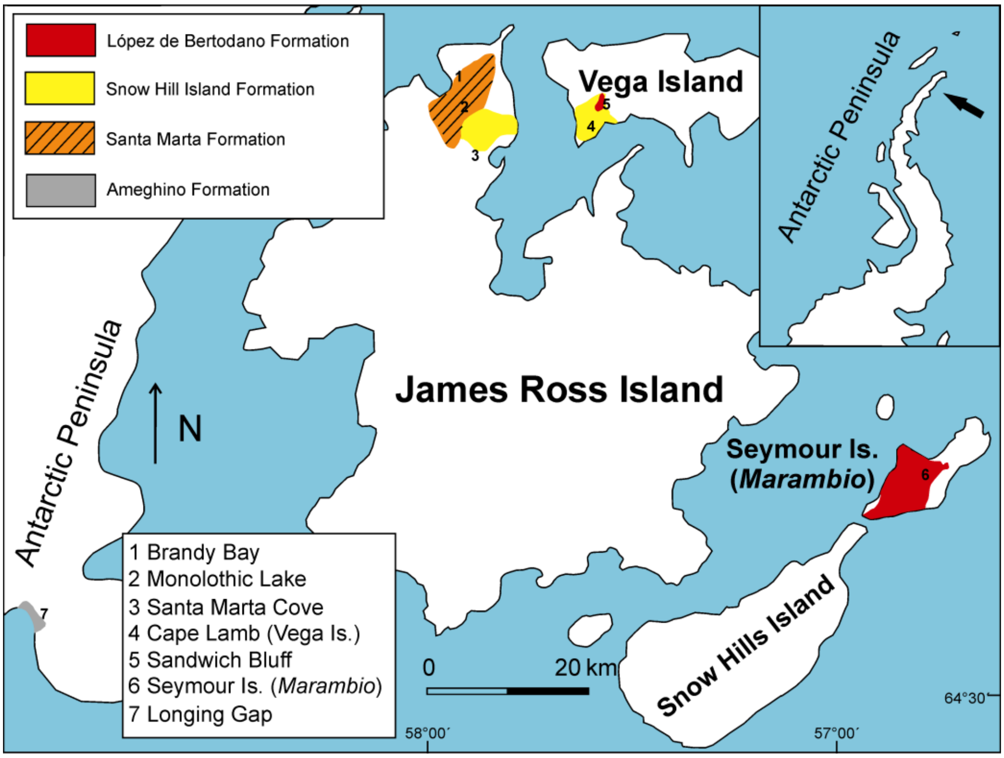

Figure 2 Maps of Antarctic localities mentioned in the text (Modified from Withman and Doyle, 1989; Olivero, 2012).

2001). The Cape Lamb Member has yielded invertebrates such as cephalopods, bivalves, annelids and decapods (Pirrie et al., 1991; Olivero et al., 1992) and vertebrates such as mosasaurs and plesiosaurs (Martin et al., 2007; Fernández and Gasparini, 2012; O'Gorman et al., 2015), and dinosaurs (Pirrie et al., 1991). This unit was deposited in an off-shore to nearshore environment (Pirrie et al., 1991; Marenssi et al., 2001; O'Gorman et al., 2012). Based on bioestratigraphy the Snow Hill Island Formation is considered late Campanian–early Maastrichtian in age (Olivero, 2012).

3.3 López de Bertodano Formation

The López de Bertodano Formation crops out in Seymour Island (=Marambio) and Vega Island, James Ross Archipelago (Figures 2, 3). At Seymour Island (=Marambio) the López de Bertodano Formation consists of about 1150 m of sandy shales and sandstones (Macellari, 1988). The fossil contents of the López de Bertodano Formation include ammonoids, bivalves, gastropods, annelids and echinoderms (Macellari, 1988; Olivero and Medina, 2000), and chondrichthyes (Cione and Medina, 1987; Otero et al., 2013, 2014a), plesiosaurs (Gasparini et al., 1984; Chatterjee and Small, 1989; O'Gorman et al., 2017a, 2017b), mosasaurs (Fernández and Gasparini, 2012) and birds (Hospitaleche and Gelfo, 2015). The lower part ("*Rotularia* units") was deposited in a shallow marine environment near an estuary (Macellari, 1988; Olivero et al., 2008), while the upper part ("molluscan units") was deposited in the middle to outer marine platform (Macellari, 1988). The López de Bertodano Formation is Maastrichtian–Danian in age (Macellari, 1988; Olivero and Medina, 2000; Crame et al., 2004), thus, including the Maastrichtian/Danian boundary approximately between informal units Klb 9 and Klb 10 of the "molluscan units" (Macellari, 1988).

The following section describes the main plesiosaur material from Antarctica (Table 1), with remarks on each specimen.

4 Systematic paleontology

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943
WEDDELLONECTIA O'Gorman and Coria, 2017

Included taxa and phylogenetic definition. Weddellonectia include *Aristonectes*, *Kaiwhekea*, *Morturneria*, *Alexandronectes*, *Morenosaurus*, *Vegasaurus*, *Kawanectes*, *Aphrosaurus* their most recent ancestor, and all descendants.

Diagnosis. Elasmosaurids with two distinctive humeral synapomorphies: a postaxial accessory ossicle articulating with the humerus (indicated by a posterior accessory articular facet in the humerus, also shared by the poorly known lower Albian *Wapuskanectes betsynichollsae*), and a 180° angle between epipodial facets in dorsal view. Additional features that characterize Weddellonectia (although convergently shared by other elasmosaurids) are:

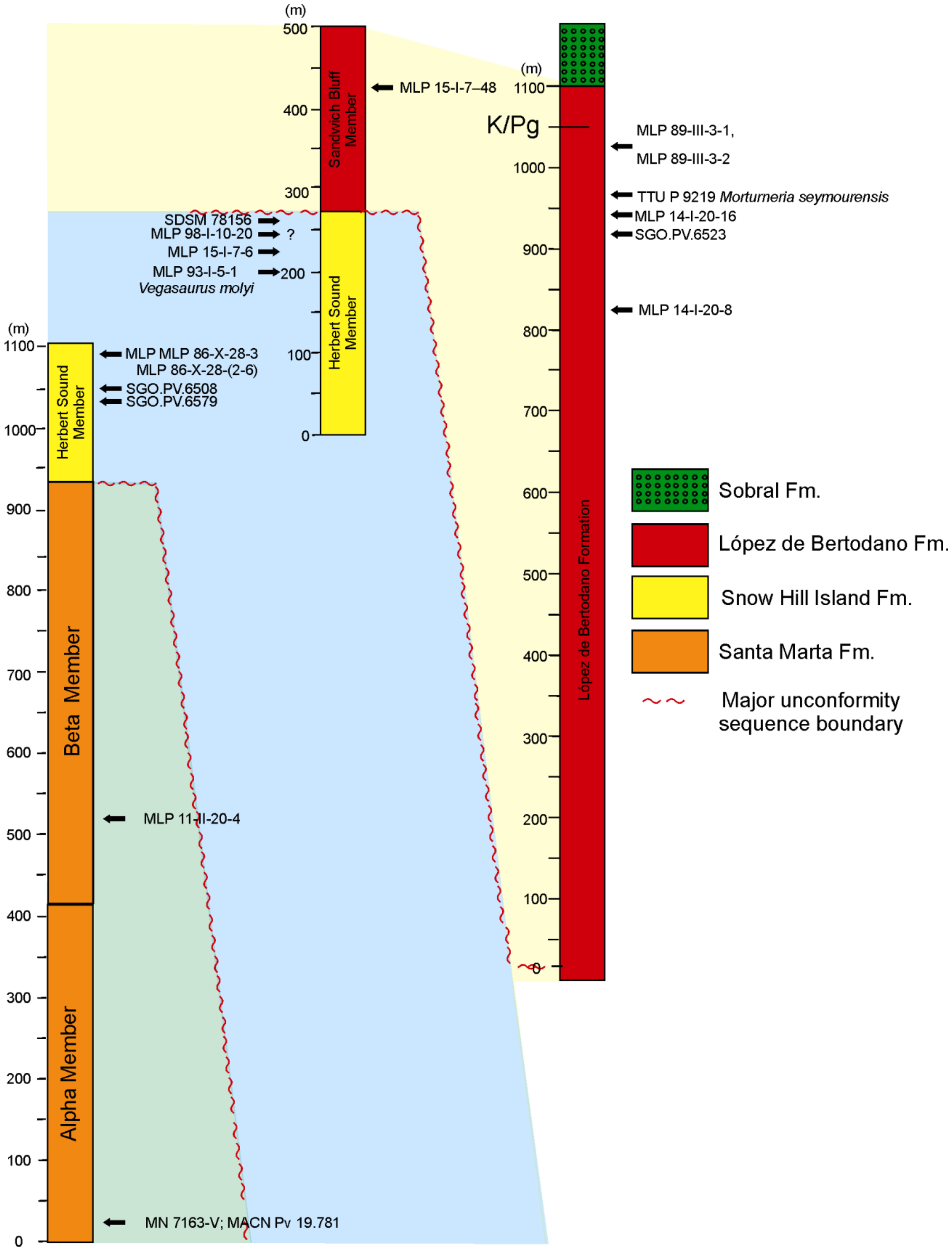

Figure 3 Simplified Cretaceous stratigraphic section of the James Ross/Vega and Seymour (= Marambio) islands and the plesiosaur specimens mentioned in the text (Modified from Olivero, 2012; see text for references to specimen bearing levels).

cervical vertebrae wider than long; fewer than 56 cervical vertebrae; pectoral bar absent; an angled ilium shaft; femora with long and dorsally expanded trochanter (absent in *K. lafquenianum*); and a hemispherical capitulum (absent in *K. lafquenianum* and *V. molyi*).

ARISTONECTINAE O'Keefe and Street, 2009 (sensu Otero et al., 2012)

Type Genus. *Aristonectes* by original designation (O'Keefe and Street, 2009).

Diagnosis (revised from Otero et al., 2012a; O'Gorman, 2016b; Otero et al., 2016). Late Cretaceous elasmosaurid with the following combination of characters: relatively small teeth with seven or more teeth on each premaxilla; 36 or more teeth on each maxilla; 42 or more teeth on each dentary; short premaxilla in lateral view; cervical centra length shorter than or equal to height.

Morturneria seymourensis (Chatterjee and Small, 1989)

Type Genus. *Morturneria* Chatterjee and Small, 1989

Type Species. *Morturneria seymourensis* (Chatterjee and Small, 1989).

Generic Diagnosis. As for the species.

Holotype. TTU P 9219, partial skull (Figure 4) including, atlas/axis complex and mid-cervical vertebrae.

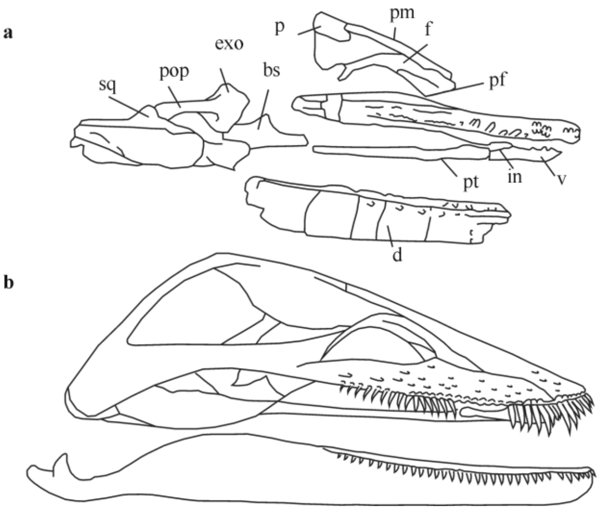

Figure 4 TTU P 9219, *Morturneria seymourensis* holotype. **a**, diagram of preserved elements of the holotype and **b**, restoration (redrawn from O'Keefe et al., 2017).

Locality and horizon. Seymour (Marambio) Island, Antarctica. Higher, 'molluscan' units (Klb 9) of the López de Bertodano Formation, upper Maastrichtian (Olivero, 2012, Figures 2, 3).

Diagnosis (Modified from O'Keefe et al, 2017). Deeply arched palate with a medial ventral keel formed anteriorly by the vomer; obliquely oriented internal naris; dentary teeth with procumbent alveoli recurving; internal naris formed by palatine; discrete, round facet for articulation of flared end of paraoccipital process on squamosal only; eight or nine teeth on premaxilla; at least 38 teeth on maxilla and at least 46 teeth on dentary; procumbent teeth.

Aristonectes Cabrera, 1941

Type species. *Aristonectes parvidens* Cabrera, 1941.

Amended diagnosis (modified from Gasparini et al., 2003a; Otero et al., 2014c). Aristonectine elasmosaurid with large, slightly flattened and broad skull without premaxillary–maxillary constriction, differing from the high skull of *Kaiwhekea katiki*; more than 50 mandibular procumbent alveoli. Anterior and middle cervical vertebrae with low average Vertebral Length Index (100×ratio between length and the average of breadth and height of vertebral centra) ~80 though slightly greater than that of *Kaiwhekea katiki*.

cf. *Aristonectes*, Figures 5a, 5c

Material. MLP 89-III-3-1, incomplete postcranial specimen, comprising vertebrae, partial pectoral girdle, and partial anterior and posterior limbs, gastroliths (Figure 5)

Locality and horizon. All from Seymour Island (=Marambio). James Ross Archipelago, Antarctic Peninsula. López de Bertodano Formation. Upper Maastrichtian (Olivero and Medina, 2000; Figures 2, 3).

Remarks. MLP 89-III-3-1 is one of the largest elasmosaurids ever found (O'Gorman, 2013) and the youngest elasmosaurid from Antarctica, having been collected a few meters below the K/Pg limit (Figure 3). The femur of MLP 89-III-3-1 (Figures 5a, 5b) shows the hemispherical head previously considered autapomorphic of *Mauisaurus* (Hiller et al., 2017).

Aristonectinae indet., Figure 6

Material. MLP 89-III-3-2, first pre-pectoral vertebra, pectoral vertebrae and dorsal vertebrae, coracoids, portion of the left scapula, and incomplete anterior limb (Figures 6e, 6f). MLP 14-I-20-8 is a postcranial skeleton comprising two cervical, one pectoral, dorsal vertebrae, coracoids, scapulae, pubes, ischia, humeri, femora dorsal ribs and gastralia (Figures 6a–6d).

Locality and horizon. All from Seymour Island (=Marambio). James Ross Archipelago, Antarctic Peninsula. López de Bertodano Formation, (MLP 14-I-20-8) boundary between Klb 8 and (MLP 89-III-3-2), Klb 9. Upper Maastrichtian (Olivero and Medina, 2000: Figs 2, 3).

WEDDELLONECTIA

Genus *Vegasaurus* O'Gorman, Salgado, Olivero and Marenssi, 2015

Type species: *Vegasaurus molyi* O'Gorman, Salgado, Olivero and Marenssi, 2015

Vegasaurus molyi O'Gorman, Salgado, Olivero and Marenssi, 2015, Figures 7a–7i

Holotype specimen. MLP 93-I-5-1, postcranial skeleton preserving an almost complete vertebral column, pectoral and pelvic girdles, forelimbs and hind limbs, ribs, and gastroliths.

Type locality and horizon. Cape Lamb, Vega Island,

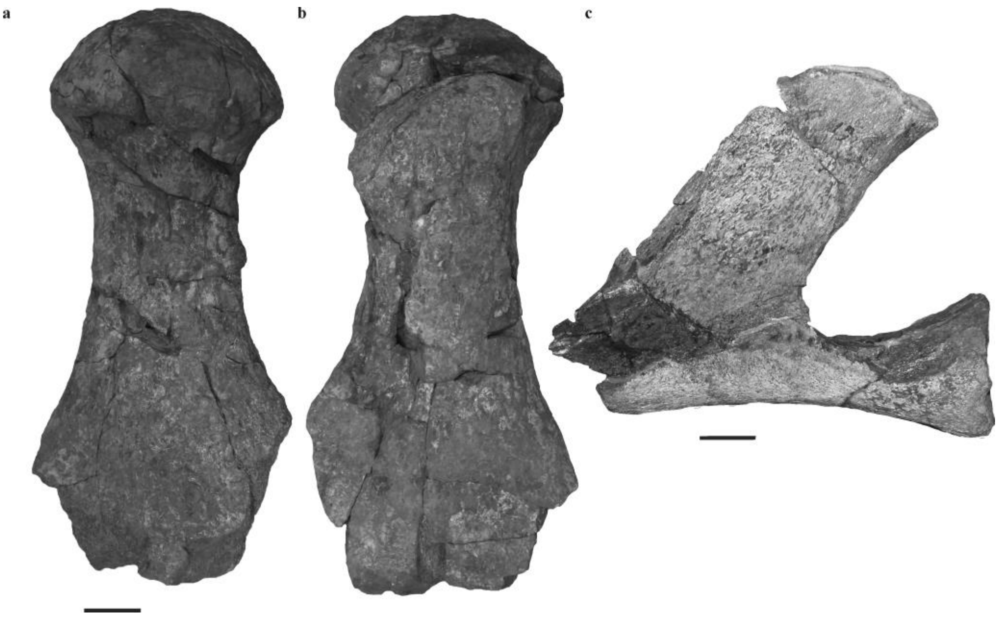

Figure 5 cf. *Aristonectes* indet. MLP 89-III-3-1. **a**–**b**, right femur in **a**, ventral and **b**, dorsal view. **c**, left scapula in lateral view. Scale bar = 20 mm.

James Ross Archipelago, Cape Lamb Member of the Snow Hill Island Formation. Lower Maastrichtian (Olivero and Medina, 2000).

Diagnosis (modified from O'Gorman et al., 2015). Elasmosaurid (sensu Ketchum and Benson, 2010, 2011) defined by the presence of 54 cervical vertebrae and the following combination of features: cervical centra with Vertebral Length Index (100 × ratio between length and the average of breadth and height of vertebral centra) = 108; atlas-axis complex with marked hypophyseal keel; lateral ridge in cervical vertebrae from the eighth to the 42nd; ventral notch well developed in cervical centra posterior to the seventh but absent in the last five vertebrae; dorsolateral process of the scapula rectangular in lateral view; ventral ramus of the scapula with a prominent ridge on the anteromedial margin of its dorsal surface; coracoids with mid-ventral process; absence of pectoral and pelvic bars; ilium shaft with two sections angled at about 140° and with a distal expansion; humerus with anterior knee and a strong posterior expansion ending in an accessory posterior facet, a feature only shared with *Morenosaurus stocki* and *Kaiwhekea katiki*; and femur with strongly convex capitulum.

Remarks. MLP 93-I-5-1, holotype of *Vegasaurus molyi*, is considered an adult specimen based on the fusion between neural arches and vertebral centra along the vertebral column but the posteriormost preserved caudal vertebrae. MLP 93-I-5-1 was collected during three Antarctic expeditions. The quarry covers approximately 3 m^2. The skeleton was collected semi articulated and lying with its right side up. The specimen is about 7 m in length; it represents the most complete non-aristonectine elasmosaurid from the Weddelian Province.

Weddellonectia indet (Figures 8, 9). Material. MLP 14-I-20-16, skeleton comprising cervical, pectoral, dorsal, sacral and caudal vertebrae, incomplete hind limb, fragments of pectoral and pelvic girdles and gastroliths (Figures 8a–8c). MLP 15-I-7-6, partial skull comprising caudal half of pterygoids, basisphenoid, basioccipital, squamosal, exoccipital-opisthotic (Figures 8d, 8e), cervical, dorsal, sacral and caudal centra; cervical and dorsal ribs, two partially preserved propodials. MLP 15-I-7-48, right humerus, ulna, ulnare, intermedium, distal carpal I, distal carpal II+III, pisiform, phalanges and one rib (Figure 9).

Locality and horizon. MLP 15-I-7-6, Cape Lamb (Figures 2, 3), Vega Island, James Ross Archipelago; Cape Lamb Member of the Snow Hill Island Formation. Lower Maastrichtian (Olivero and Medina, 2000). MLP 14-I-20-16, Seymour Island (= Marambio), James Ross Archipelago, Antarctic Peninsula (Figures 2, 3). López de Bertodano Formation. Klb 9. Upper Maastrichtian. MLP 15-I-7–48, Sandwich Bluff, Cape Lamb (Figures 2, 3), Vega Island, Antarctica; Sandwich Bluff Member of the López de Bertodano Formation; approximately SBM 11 of Roberts et al. (2014). Upper Maastrichtian (Pirrie et al., 1991).

Remarks. MLP 14-I-20-16, MLP 15-I-7-6, and MLP 15-I-7-48 were recovered within the Weddellonectia, and two of them (MLP 14-I-20-16, MLP 15-I-7-6) show features previously recorded only among aristonectines indicating a more complex process of acquisition of the aristonectine features (O'Gorman and Coria, 2017; O'Gorman et al, 2017b, 2018a).

ELASMOSAURIDAE Cope, 1969

Elasmosauridae indet., Figures 10, 11

Material. MLP 11-2-20-4, cervical vertebrae; MLP

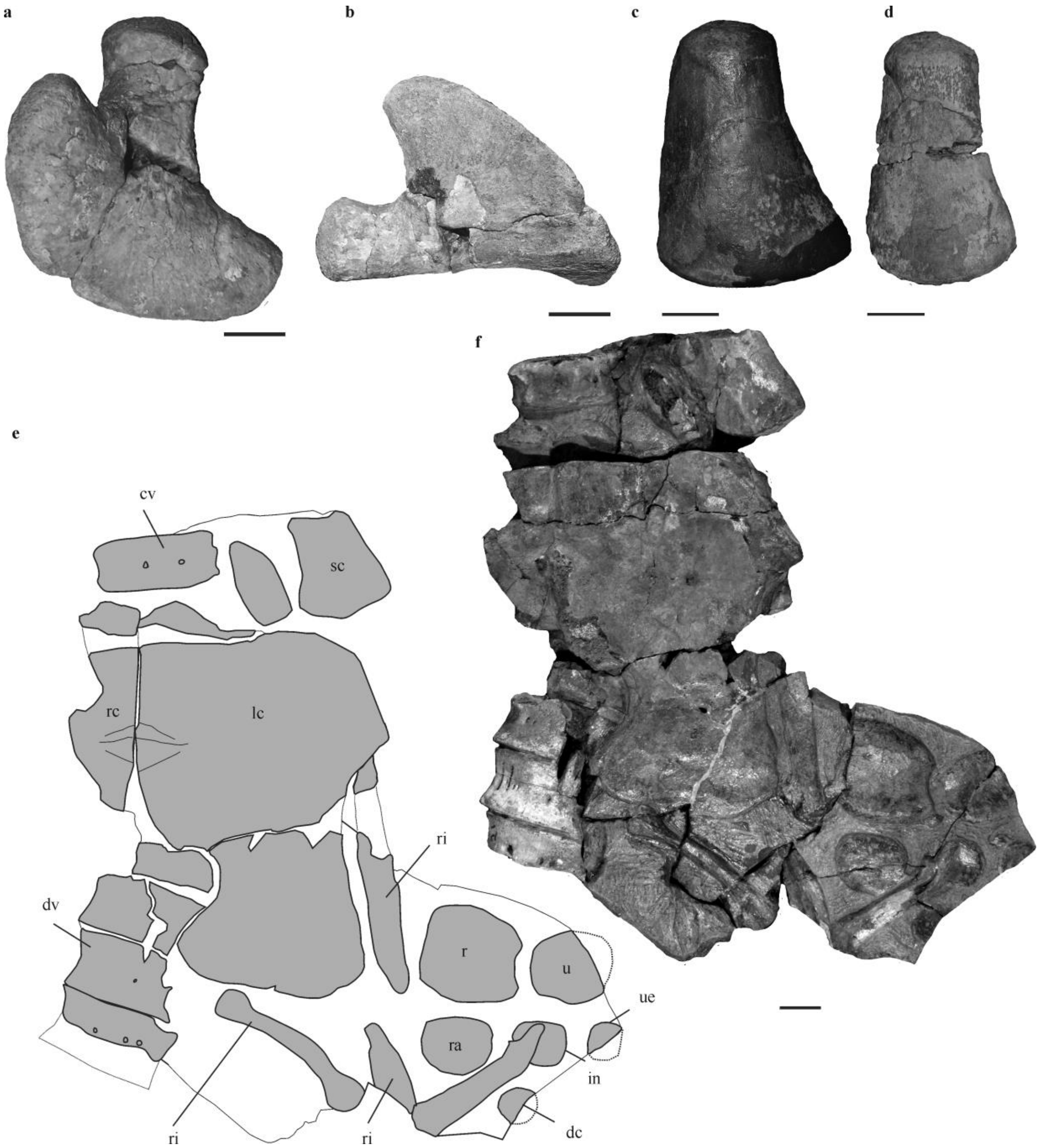

Figure 6 Juvenile individuals of Aristonectinae indet. MLP 14-I-20-8, **a**–**b**, right scapula in dorsal and lateral views. **c**, left humerus in dorsal view, **d**, left femur in ventral view. MLP 89-III-3-2, **e**–**f**, specimen in ventral view, **e**, diagram and **f**, photo. Scale bars = 20 mm.

86-X-28-3, two cervical centra; MLP 86-X-28-(2-6), ten posterior cervical vertebrae articulated with three pectoral vertebrae, part of two articulated dorsal centra (Figure 10e); SGO.PV.6579, fragmentary postcranial skeleton including caudal centra, fragmentary ilium and pubis, propodial heads (femora?), one epipodial (fibula?) and one metacarpal V (Figures 11a–e); SGO.PV.6508, fragmentary postcranial skeleton including caudal vertebrae, part of the pelvic girdle, propodial articular heads and one epipodial (Figure 11j); SGO.PV.6523, fragmentary postcranial skeleton including nine cervical vertebrae, scapula, gastralia and an isolated metacarpal V (Figures 11f–11i). SDSM 78156, posteriormost cervical, pectoral, dorsal, sacral and anteriormost caudal vertebrae, partial paddles, gastralia and gastroliths (Martin et al., 2007: Fig. 2). MLP 98-I-10-20, postcranial skeleton consisting of posterior dorsal, sacral and caudal vertebrae, left pubis, ilia, ischia, left posterior limb, ribs, gastralia and gastroliths (O’Gorman et al., 2012: Fig. 2; O’Gorman, 2013).

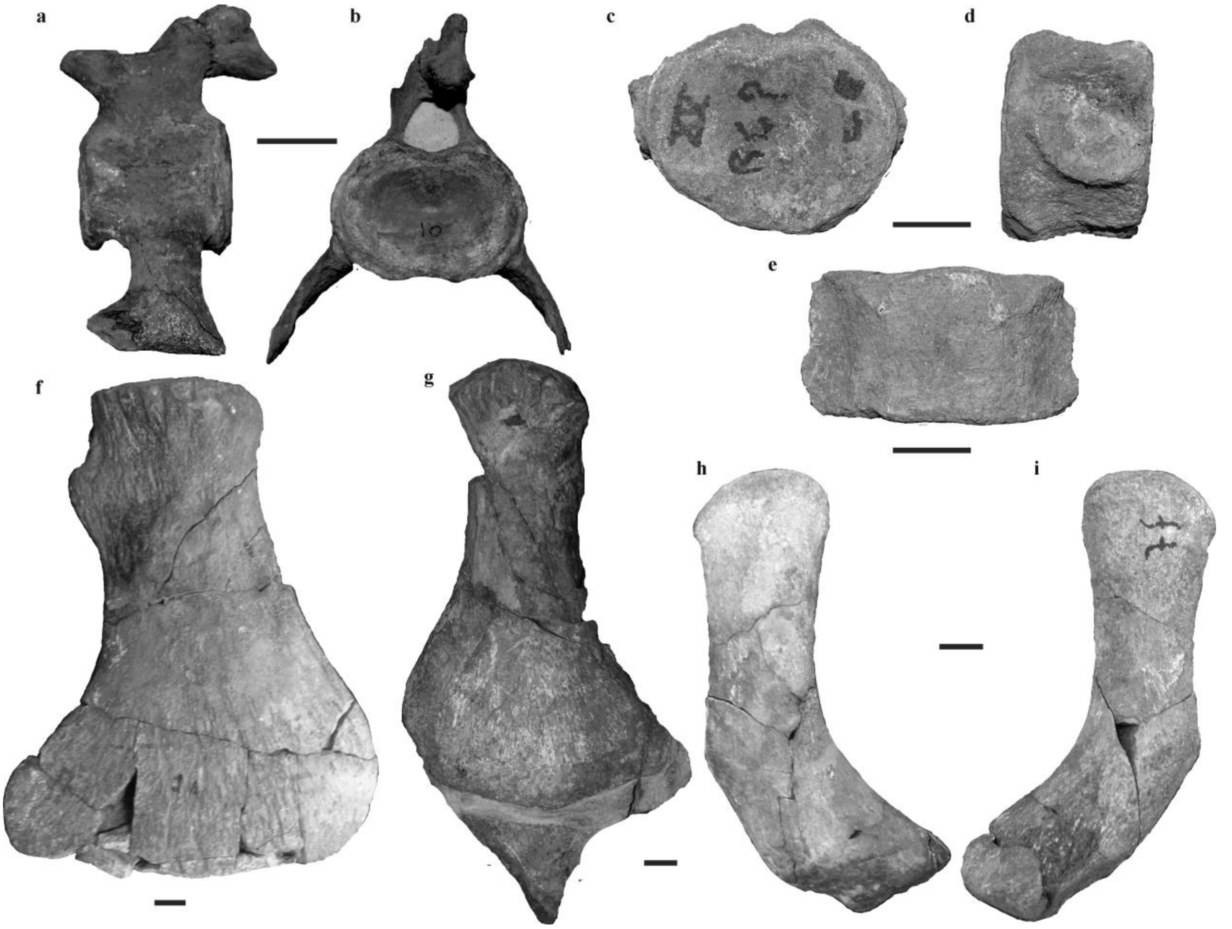

Figure 7 MLP 93-I-5-1, *Vegasaurus molyi* holotype. **a**–**b**, anterior cervical vertebrae in **a**, left lateral and **b**, posterior views. **c**–**e**, caudal vertebrae in **c**, posterior, **d**, right lateral and **e**, ventral views. **f**, left humerus in ventral view; **g**, right femur in ventral view. **h**–**i**, left ilium in **h**, lateral and **i**, medial views. Scale bar = 20 mm.

Locality and horizon. MLP 11-2-20-4, Monolithic Lake Locality (Figures 2, 3). Upper part of the Lachman Crags Member of the Santa Marta Formation. Lower Campanian. MLP 86-X-28-3, MLP 86-X-28-(2-6), SGO.PV.6579, SGO.PV.6508, Santa Marta Cove Locality (Figures 2, 3). James Ross Island. Herbert Sound Member (upper Campanian), Snow Hill Island Formation (McArthur et al., 2000; Olivero and Medina, 2000); SGO.PV.6579, inner part of Santa Marta Cove, James Ross Island, Antarctica. Herbert Sound Member, Snow Hill Island Formation, upper Campanian; SGO.PV.6508, inner part of Santa Marta Cove, James Ross Island, Antarctica. Herbert Sound Member, Snow Hill Island Formation, upper Campanian; SGO.PV.6523, Seymour Island (=Marambio), Antarctica. Klb 9 unit, López de Bertodano Formation, upper Maastrichtian (Olivero and Medina, 2000; Figures 2, 3). SDSM 78156, Cape Lamb, Vega Island, Antarctic. Cape Lamb Member (lower Maastrichtian), Snow Hill Island Formation. MLP 98-I-10-20, Cape Lamb (Figures 2, 3), Vega Island, Antarctic Peninsula. Cape Lamb Member of the Snow Hill Island Formation (upper Campanian–lower Maastrichtian).

Remarks. MLP 86-X-28-(2-6) and MLP 86-X-28-3 are clearly juvenile specimens based on the absence of fusion between the neural arches and vertebral centra. Otero et al. (2014b) considered SGO.PV.6508 and SGO.PV.6579 as juveniles. However SGO.PV.6508 lacks well-preserved pedicellar facets, and therefore the growth stage sensu Brown (1981) cannot be well defined. Additionally, the Vertebral Length Index (VLI =110) is high for a juvenile elasmosaurid (J.P.O'G. pers. obs.). SGO.PV.6579 was considered a juvenile by two features: (1) lack of fusion of the neural arches and caudal ribs with the caudal centra; and (2) ilium and pubis smaller than other known juvenile specimens of *Aristonectes quiriquinensis*. However the lack of fusion of neural arches and ribs in the caudal region has been recorded in adult specimens such as MLP 40-XI-14-6 (*Aristonectes parvidens*, holotype) and several specimens referred to *Kawanectes lafquenianum*, a small sized non-aristonectine elasmosaurid from Patagonia (MLP 71-13-3-1 and MUC Pv 92; Gasparini and Salgado, 2000: Fig 3; O'Gorman, 2016a). Otero et al. (2014b) also mentioned that the ilium and pubis of SGO.PV.6579 are smaller than the ones referred to juvenile specimens of *Aristonectes* but almost the same size as the holotype of

Kawanctes lafquenianum (Gasparini and Salgado, 2000: Fig. 5; O'Gorman, 2016a).

The affinities of the MLP 86-X-28-(2-6); MLP 86-X-28-3 and SGO.PV.6508 specimens from the Gamma Member are difficult to determine because of the absence of clear diagnostic elements and for that reason almost all them were referred to Elasmosauridae indet. by O'Gorman (2012) and Otero et al. (2014b). The only specimen determined below the family level is SGO.PV.6579, which was referred to Aristonectinae indet. by Otero et al. (2014b), by comparison with SGO.PV 260. Following Otero et al. (2013), SGO.PV.260 is undoubtedly an Aristonectinae. But as new specimens from Patagonia and Antarctica have been described recently (O'Gorman et al., 2013; O'Gorman, 2016a), SGO.PV.6579 could be reinterpreted. Otero et al. (2014b) considered this specimen as an aristonectine based on: (1) caudal vertebrae with distinctive octagonal articular outline; (2) caudal vertebrae with sub-triangular, pedicellar facets for the neural arches and (3) massive and robust ventral part of the ilium, with a shaft bent in the middle part. However the articular faces of the caudal vertebrae figured by Otero et al. (2014: Figs 6a, 6e) are not clearly octagonal shaped and additionally the triangular facets of the caudal vertebrae are present in several elasmosaurids including *Aristonectes* (MLP 40-XI-14-6, only in few caudal vertebrae); but also in *Kawanectes lafquenianum* and (MUC

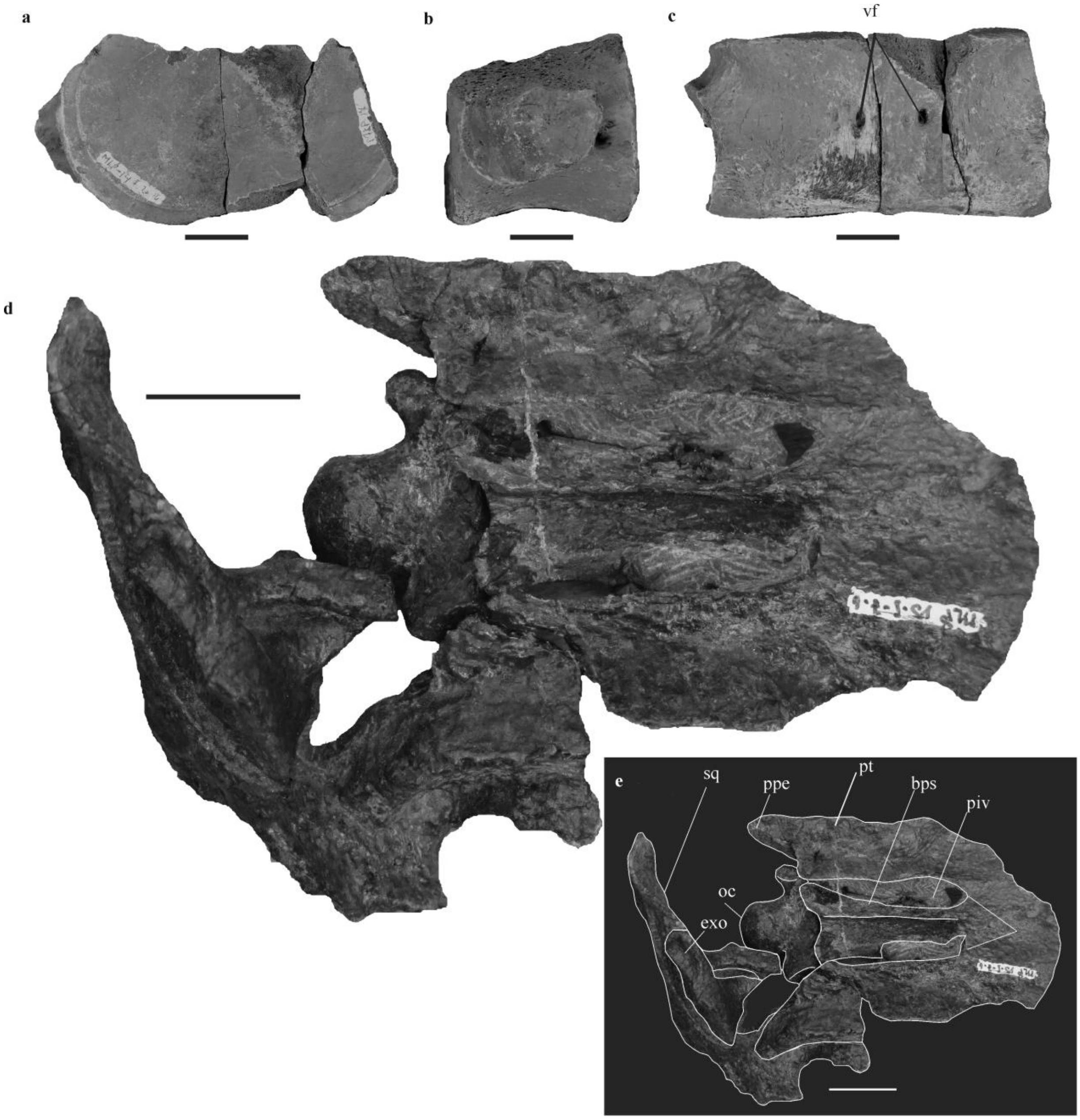

Figure 8 Weddellonectia indet. MLP 14-I-20-16, **a**–**c**, posterior cervical vertebrae in **a**, posterior, **b**, left lateral and **c**, ventral views. MLP 15-I-7-6, **d**, **e**, partial palate, occipital condyle and displaced squamosal. **d**, photo and **e**, diagram. Scale bar = 20 mm.

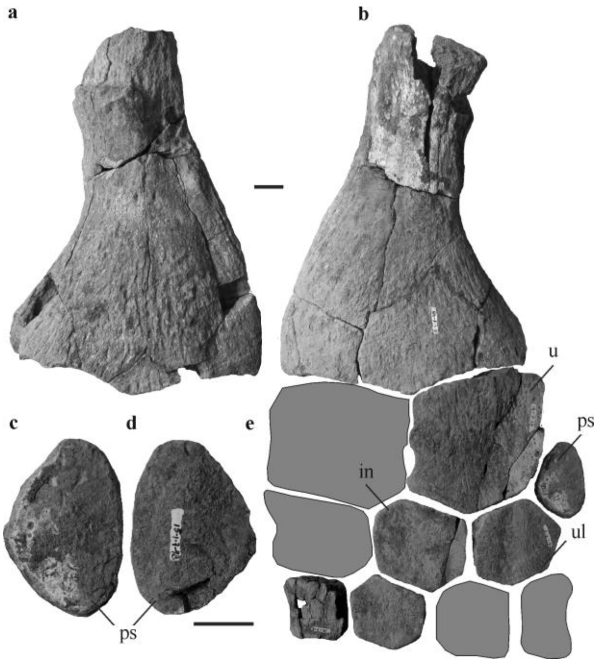

Figure 9 Weddellonectia indet. MLP 15-I-7-48. **a**–**b**, right humerus in dorsal and **b**, ventral views. **c**–**d**, pisiform in ventral and dorsal views. **e**, ulna, mesopodial and metapodials. Scale bar = 20 mm.

Pv 92 Gasparini and Salgado, 2000: Fig 3; O'Gorman et al., 2013: Fig. 2j) and *Vegasaurus molyi* (MLP 93-I-5-1; O'Gorman et al., 2015: Fig. 7r). Therefore the triangular pedicellar facets on caudal centra are not a diagnostic features of Aristonectinae. Following Otero et al. (2014b) similar caudal vertebrae were recorded by Fostowicz-Frelik and Gaździcki (2001) from the lower Maastrichtian of the Haslum Crag Sandstone of López de Bertodano that includes among other remains articulated caudal vertebrae similar to SGO.PV.6579 and to MLP 71-II-13-1, MCS PV 4 and MUC Pv 92 from the upper Campanian–lower Maastrichtian Allen Formation. These specimens were considered a small-sized non-aristonectine elasmosaurid by O'Gorman (2013). In summary SGO.PV.6579 does not shows clearly features of an aristonectinae other than the general similarity of the ilium (i.e. *Aristonectes* Cabrera, 1941, *Kaiwhekea* Cruickshank and Fordyce, 2002) and therefore it is reinterpreted here as an Elasmosauridae indet. Despite this, a possible relation with the aristonectines cannot be discarded. Additionally it is interesting to remark, following Otero et al. (2014b), that similar specimens have been collected from North Patagonia and Seymour (=Marambio) Island. More specimens are necessary to clarify its affinities.

SDSM 78156 is the most complete juvenile specimen from the Cape Lamb Member. The specimen was collected, articulated and shows an uncommon set of well-preserved gastralia. Additionally this specimen preserves gastroliths associated with the skeleton. Martin et al. (2007) referred the specimen to *Mauisaurus* based on (1) rounded end of the femur; (2) conical mid-ventral process of the coracoids, and (3) forked gastralia. The presence of femur with a hemispherical capitulum has been considered an autapomophy of *Mauisaurus* since Welles and Gregg (1971). However the femur of SDSM 78156 is just rounded, not hemispherical. Also rounded hemispherical head in femurs

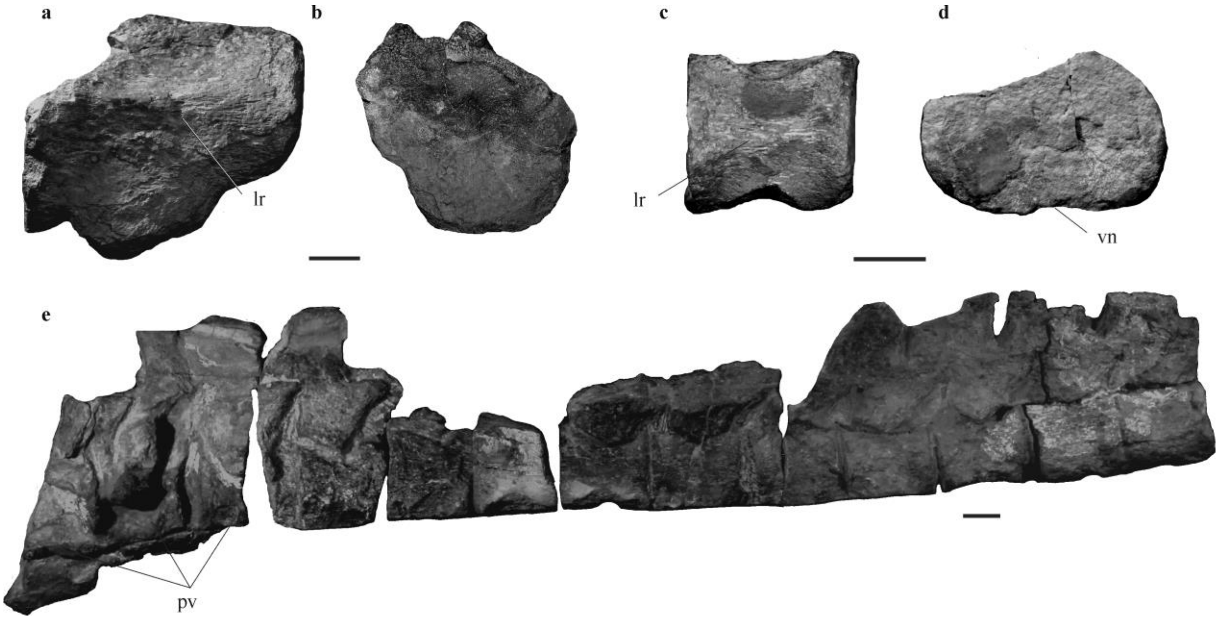

Figure 10 Elasmosauridae indet. **a**–**b**, MLP11-II-20-4, cervical vertebra in **a**, left lateral and **b**, anterior views. **c**–**d**, MLP 86-X-28-3 cervical vertebra in **c** left lateral and **d** anterior views. **e**, MLP 86-X-28-(2-6) cervical-pectoral series in right lateral view. Scale bar = 20 mm.

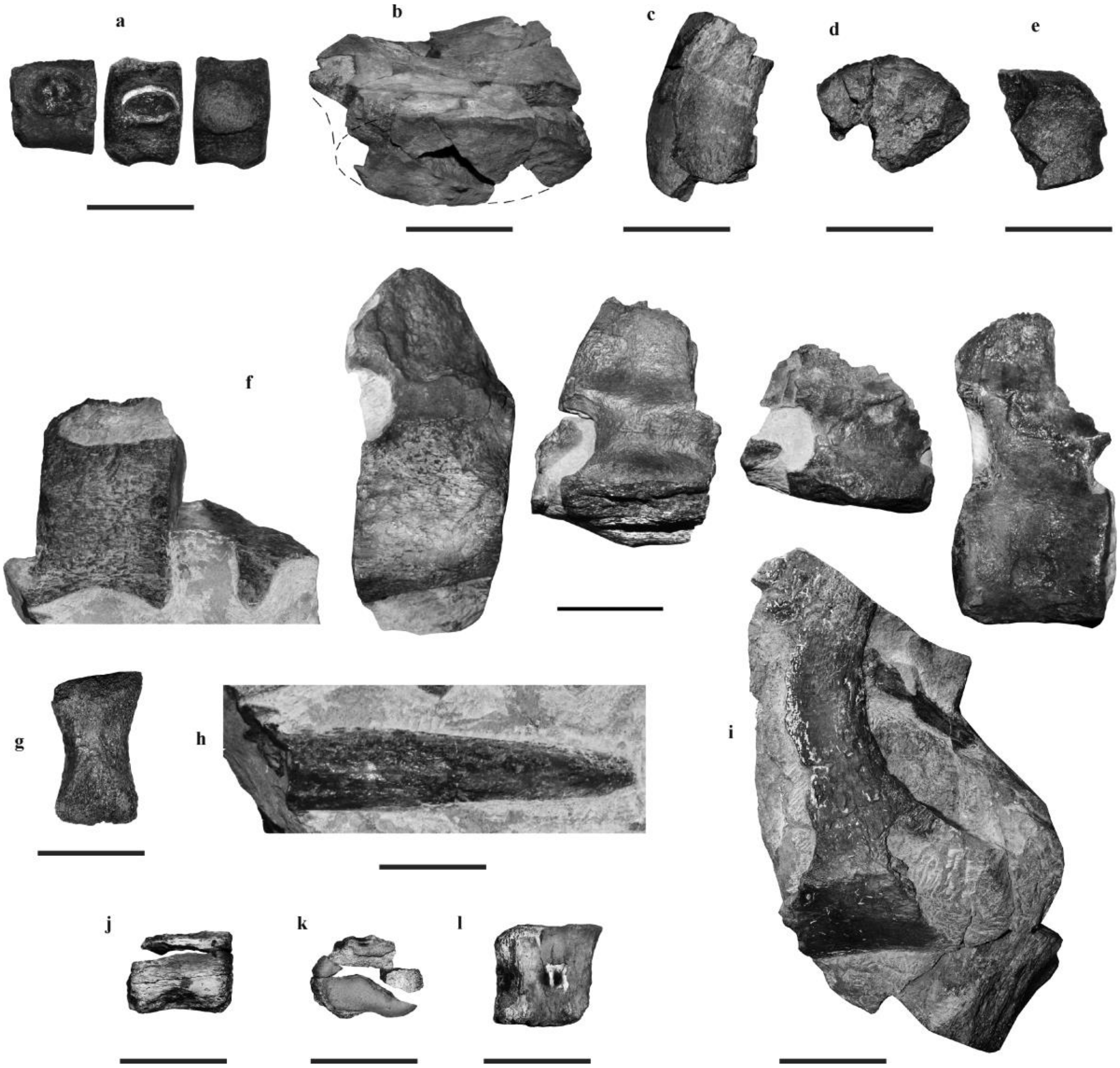

Figure 11 Elasmosauridae indet. **a**–**e**, SGO.PV.6579. **a**, three caudal vertebrae in right lateral view. **b**, pubis in lateral view. **c**, fragmentary right ilium in posterior view. **d**, articular head of an indeterminate propodial (likely femur). **e**, fragmentary epipodial (fibula?). **f**–**i**, SGO.PV.6523. **f**, five posterior cervical vertebrae in right lateral view. **g**, isolated metacarpal V. **h**, isolated gastralia. **i**, fragmentary scapula in right lateral view. **j**–**l**, SGO.PV.6508. Juvenile cervical vertebra in **j**, right lateral, **k**, articular and **l**, ventral views. Modified from Otero et al. (2014b). Scale bar = 50 mm.

is recorded in other elasmosaurids such as *Terminonatator ponteixensis*, *Vegasaurus molyi* and *Kawanectes lafquenianum* (Sato, 2003; O'Gorman et al., 2015; O'Gorman, 2016a). The mid-ventral process is present in *Mauisaurus* sensu Hiller et al. (2005), however it is also present in other elasmosaurids such as *Callawayasaurus colombiensis*; *Libonectes atlasense* and *Vegasaurus molyi* (Welles, 1943; Otero et al., 2014c; O'Gorman et al., 2015; Sachs and Kear, 2017). Finally the forked gastralia was not considered autapomorphic by Hiller et al. (2005). Also Hiller et al. (2017) revised *Mauisaurus haasti* and considered it invalid. For this reason we referred the SDSM 78156 specimen to Elasmosauridae indet. until a more detailed study becomes available, although the relatively large body size for a juvenile could indicate aristonectine affinities.

MLP 98-I-10-20 was considered a juvenile specimen sensu Brown (1981) because of the absence of fusion between the neural arches with the vertebral centra. Unfortunately no skull or cervical vertebrae were preserved and therefore its affinities are not known. A large cluster of gastroliths was located in the abdominal zone in the space between the gastralia and the dorsal ribs. O'Gorman et al. (2012), analysed this cluster using sedimentological indexes, concluding that the gastroliths were probably ingested in an estuarine environment.

POLYCOTYLIDAE Cope, 1869

Polycotylidae indet.

Material. MN 7163-V, Parts of a propodial bone, numerous autopodial elements and cervical and caudal vertebrae (Kellner et al., 2011: Figs 2, 3); MACN Pv 19.781, four dorsal vertebral centra, nine caudal centra, both pubes, ischia and femora, numerous isolated ribs and gastroliths (Novas et al., 2015: Figures 2, 3, 5).

Locality and horizon. Brandy Bay, James Ross Island, N.E. Antarctic Peninsula. Lower part of Lachman Crags(Alpha) Member of the Santa Marta Formation. Upper Coniacian? Santonian (McArthur et al., 2000; Olivero and Medina, 2000).

Remarks: These two specimens are the only ones referred to Polycotylidae from Antarctica.

5 Taphonomic remarks

The Antarctic plesiosaurs came from different formations and sedimentary environments (see Geologic Settings) and therefore different taphonomic features are observed. The articulation varies from almost complete and articulated specimens such as SDSM 78156 or MLP 98-I-10-20, to completely disarticulated and incomplete such as MLP 14-I-20-8 (Figure 12). Considering the study of the *Crocodylus porosus* decay patterns by Syme and Salisbury (2014), as an analogue for the Antarctic plesiosaurs decay, it can be inferred that preservation of articulation was a result of the inhibition of floating via early burial or damage that prevented bloat. This pattern of articulation is clear in SDSM 78156, MLP 98-I-10-20 and partially in MLP 93-I-5-1 and MLP 89-III-3-1 and MLP 89-III-3-2, but differs from that observed in MLP 14-I-20-8. Therefore following this model there is a requirement of rapid burial or strong damage in order to prevent complete disarticulation and the loss of elements during bloat. The first hypothesis opens the possibility of a detailed analysis in order to correlate the articulation with the geological setting.

6 Discussion

6.1 General features and the Santonian–Campanian marine reptile turnover.

The Upper Cretaceous Antarctic plesiosaur record is composed mainly of Santonian polycotylids and post-Santonian elasmosaurids (O’Gorman, 2012). Both aristonectines and non-aristonectines are present among elasmosaurids (Otero et al., 2014b; O’Gorman et al., 2015).

The oldest elasmosaurid from Antarctica comes from the lower Campanian of the Santa Marta Formation while the oldest Late Cretaceous plesiosaurs are two Polycotylidae specimens from Santonian levels of the Santa Marta Formation (Kellner et al., 2011; O’Gorman, 2012; Novas et al., 2015: Figs 2, 3). In both cases, these records are referred to gen. et sp. indet. Non-aristonectine elasmosaurids are recorded from the upper Campanian Herbert Sound Member of the Snow Hill Island Formation (O’Gorman, 2012; Otero et al., 2014b). Therefore plesiosaurs are recorded in the Santonian–Campanian interval but their currently known records are scarce and non-diagnostic beyond the familial level. The most relevant record during this interval is the presence of Polycotylidae during the Santonian.

Vegasaurus molyi along with some non-diagnostic specimens have been recorded from the lower Maastrichtian part of the sequence; there is an apparent absence of material clearly referable to the aristonectine from this stage (O’Gorman et al., 2015, 2018a: Fig. 3).

Aristonectines appear in the Antarctic record during the upper Maastrichtian (Chatterjee and Small, 1989; O’Gorman et al., 2017a). The group is represented by *Morturneria seymourensis* and cf. *Aristonectes* and several indeterminate juvenile specimens. Several additional non-aristonectine specimens have been collected in the same stage (Chatterjee and Small, 1989; Otero et al., 2014b; O’Gorman et al., 2017a: Fig. 3).

The Antarctic plesiosaur record summarized here and the records from the rest of the Weddellian Province indicate a certain degree of congruence. Non-aristonectine elasmosaurids are present in New Zealand at least since the middle Campanian (Wiffen and Moisley, 1986; Hiller et al., 2005), and aristonectines have been recorded in the boundary between lower and upper Maastrichtian (Cruickshank and Fordyce, 2002; O’Gorman et al, 2014; Otero et al., 2016). The main difference between the provinces is the presence of two records of Polycotylidae (Welles and Gregg, 1971; Wiffen and Moisley, 1986) from the Maastrichtian. However, elasmosaurid records prevail as the most common forms in New Zealand, while the number of Polycotylidae specimens remains low, following the same tendency observed in Antarctica.

The records of the Upper Cretaceous from the southern tip of South America shows some differences with the ones of New Zealand and Antarctica. The only valid non-aristonectine species, *Kawanectes lafquenianum* comes from upper Campanian–lower Maastrichtian levels of the Allen Formation and the middle facies association of La Colonia Formation, with similar age (O’Gorman, 2016b; 2017). Until now no, Santonian or lower Campanian plesiosaur records have been recovered from the southern tip of South America. Aristonectines are present in the South American record from the upper Campanian–lower Maastrichtian (O’Gorman et al., 2013) until the upper Maatrichtian, with two valid species *A. quiriquinensis* and *A. parvidens*, plus several indeterminate specimens (Cabrera, 1941; Gasparini et al., 2003b; Otero et al., 2014c). Polycotylids are recorded from the Upper Campanian–Maastrichtian of La Colonia Formation and from the upper Campanian–lower Maastrichtian of the Allen Formation.

The absence of post-Santonian polycotylids from the Antarctic Cretaceous plesiosaur record is remarkable as polycotylids are present in other localities until at least the lower Maastrichtian (Sato et al., 2005; Salgado et al., 2007; O’Gorman and Gasparini, 2013). Additionally, marine

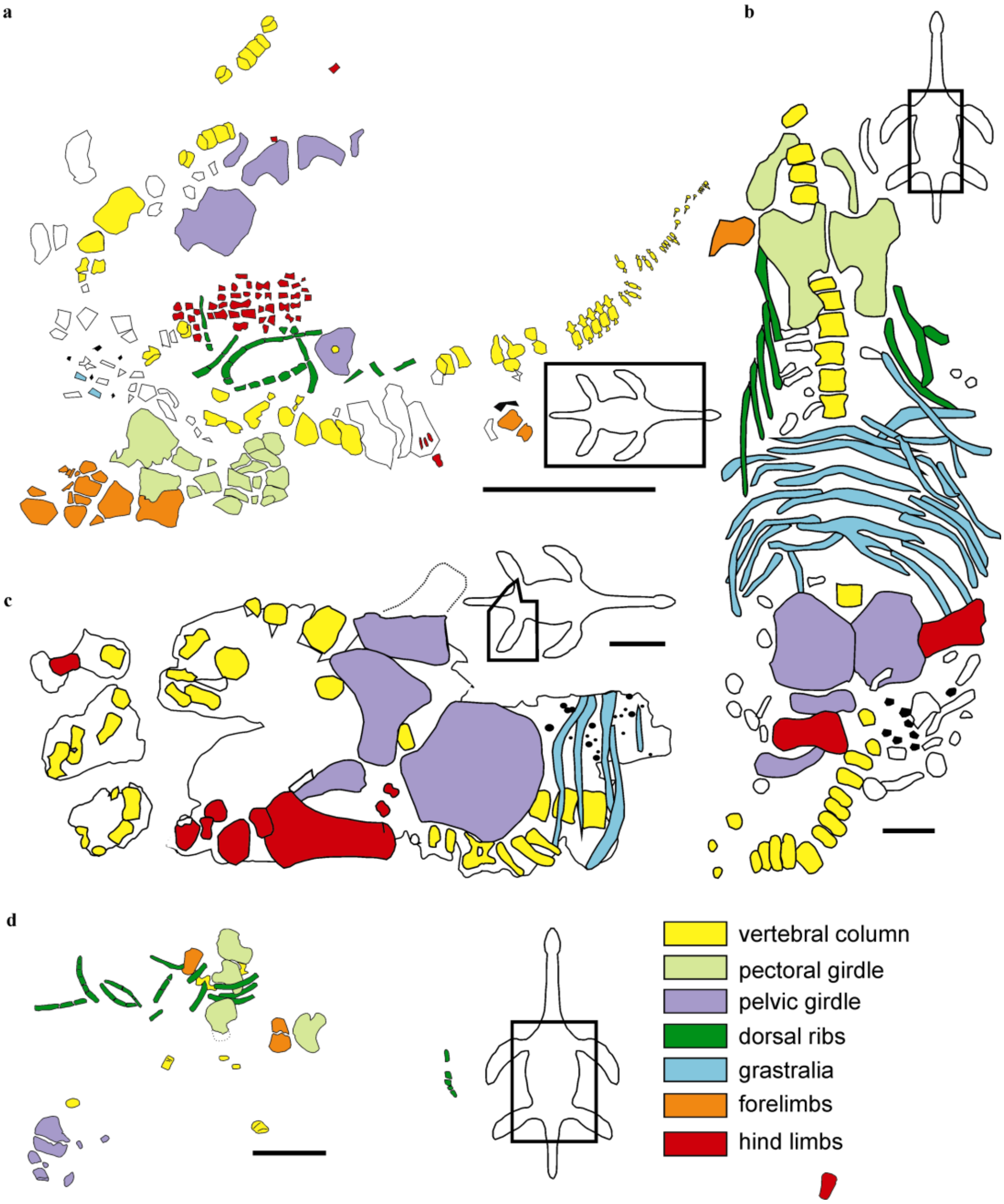

Figure 12 **a**–**d**, diagram of extraction of several Antarctic elasmosaurids. **a**, MLP 93-I-5-1; **b**, SDSM 78156; **c**, 98-I-10-20; **d**, 14-I-20-8. **a**, Scale bar = 1000 mm; **b**, **c** = 100 mm; **d** = 20 mm. (Modified from Martin et al., 2007: Fig. 2; O'Gorman et al., 2015: Fig. 3; O'Gorman et al., 2012: Fig. 2b; O'Gorman et al., 2017: Fig. 1b).

turtles, present in the Santonian of the Santa Marta Formation (de la Fuente et al., 2010) also disappear from the Post-Santonian Cretaceous levels of the James Ross Basin. This disappearance of Polycotylidae and marine turtles may indicate a major change in the Cretaceous marine reptile fauna of Antarctica. This could be related to a change in water temperatures that occurred during the Campanian–Maastrichtian (Ditchfield et al., 1994; Dingle et al., 1998; Huber et al., 2002). However, testing this hypothesis requires major efforts to collect in the Santonian–Campanian interval.

6.2 Rise of the Aristonectines and the transition to the Aristonectinae morphology

One of the main features of the Weddellian plesiosaur record is the presence of the aristonectine elasmosaurids. The aristonectines are the most distinctive group of austral elasmosaurids showing features that differ from all other known elasmosaurids, such as relatively large skull, increased number of teeth and short cervical centra (Gasparini et al., 2003b; Otero et al., 2014c, 2018; O'Gorman, 2016b). These features have been interpreted

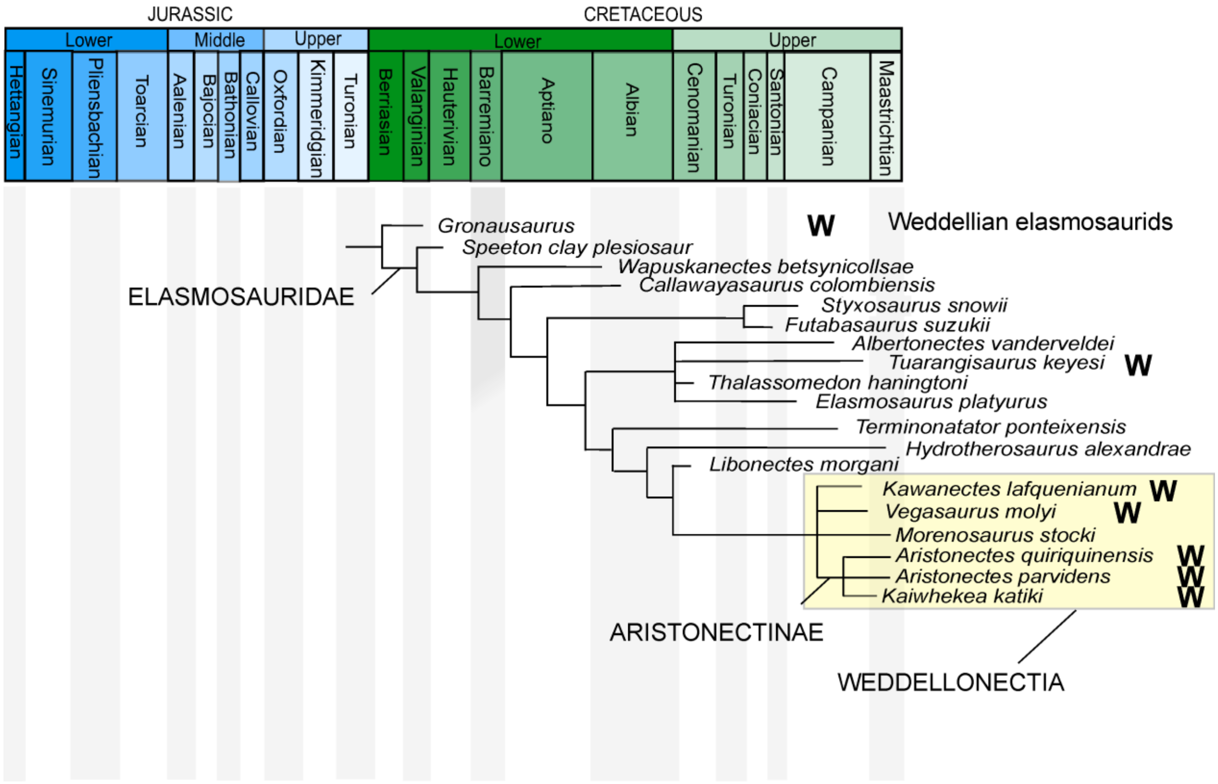

Figure 13 Time-calibrated elasmosaurid cladogram (modified from O’Gorman, 2016a).

as consistent with differences in prey capture strategy from the typical elasmosaurid strategy to sieve feeders (O’Gorman, 2016b; O’Keefe et al., 2017; Otero et al., 2018). The aristonectine Antarctic record is quite important as it comprises one of the most complete aristonectine skulls (TTU P 9219) and the most complete aristonectine perinatal specimen MLP 14-I-20-8 (Chatterjee and Small, 1989; O’Gorman et al., 2017a). Another feature of the Antarctic record related to the aristonectines is the progressive record of features previously considered exclusive of the aristonectines in non-aristonectines. Among these, the MLP 14-I-20-16 shows extremely short and wide posterior cervical centra, although slightly longer than observed among aristonectines (O’Gorman, 2016b; O’Gorman et al., 2017b). Another example is the pterygoid with posterior plate-like extension observed in MLP 15-I-7-6, although again the development of this feature is not as extreme as that observed among unambiguous aristonectines (O’Gorman et al., 2018a). These two specimens will be of major importance to determine the sequence of acquisition of the aristonectine features.

6.3 Paleobiogeography and diversification of the Weddellonectia

The Antarctic Cretaceous elasmosaurids show a paleobiogeographic connection with South America and New Zealand (Weddellian Province). This connection is indicated by the shared presence of the Aristonectinae (*Kaiwhekea katiki* and *Alexandronectes zealandiensis* from New Zealand, Cruickshank and Fordyce, 2002, Hiller and Mannering, 2005; Otero et al., 2016) and *Aristonectes* from Argentina and Chile (Gasparini et al., 2003b; Otero et al., 2014c; 2018). O’Gorman and Coria (2017) recovered the Aristonectinae nested within a clade called Weddellonectia (Figure 13). The Weddellonectia include *Vegasaurus molyi* (Isla Vega, Antarctica); *Kawanectes lafquenianum* (Argentina); *Morenosaurus stocki* and *Aphrosaurus furlongi* (California). Therefore the combination of phylogeny and geography indicate a strong connection between few Weddellian elasmosaurids and two species from California.

The Weddellonectia also shows another distinctive feature a relatively high diversity. Among them the Aristonectinae show extremely derived features and probably occupy a new trophic niche (O’Keefe et al., 2017) and also show a relatively large body size. However *Kawanectes lafquenianum* is an extremely small-sized elasmosaurid, among the smallest ever recorded and restricted to marginal marine environments (probably estuarine) where they are the only vertebrate with marine affinities (O’Gorman, 2016a; 2017). The other Weddellonectian taxa *Vegasaurus molyi*, *Morenosaurus stocki* and *Aphrosaurus furlongi* seem to be more typical elasmosaurids (Welles, 1943; O’Gorman et al., 2015). This morphological and ecological diversity shows an elasmosaurid radiation that probably started during the late Campanian, in which the Weddellian Province and probably Antarctica had an important role (Otero et al., 2014c; O’Gorman, 2016a, 2016b; O’Gorman and Coria, 2017).

Institutional abbreviations

MACN Pv–Paleontología de Vertebrados Collection, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina

MCS–Museo Cinco Saltos, Río Negro, Argentina

MLP–Museo de La Plata, Buenos Aires Province, Argentina

MN–National Museum of the Federal University of Rio de Janeiro

MUC–Museo de la Universidad del Comahue, Neuquén Province, Argentina

SDSM–South Dakota School of Mines and Technology, USA

SGO.PV–Colección de Paleontología de Vertebrados, Área de Paleontología, Museo Nacional de Historia Natural, Santiago, Chile

TTU P–Museum of Texas Tech University, Texas, USA

ZPAL–Institute of Paleobiology, Polish Academy of Sciences, Warszawa

Anatomical abbreviations

bps–basiparasphenoid; **cv**–cervical vertebrae; **d**–dentary; **dc**–distal carpal; **dv**–dorsal vertebrae; **exo**–exoccipital; **in**–intermedium; **lc**–left coracoids; **lr**–lateral ridge; **oc**–occipital condyle; **p**–parietal; **pf**–prefrontal; **piv**–posterior interpterygoid vacuity; **pm**–premaxilla; **pop**–paraoccipital process; **ppc**– posterior plate like extension of pterygoid; **ps**–pisiform; **pt**–pterygoid; **pv**–pectoral vertebrae; **r**–radius; **ra**–radiale; **rc**–right coracoid; **ri**–rib; **sc**–scapula; **sq**–squamosal; **u**–ulna; **ue**–ulnare; **v**–vomer; **vf**–ventral foramina; **vn**–ventral notch.

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References

Benson R B, Druckenmiller P S. 2014. Faunal turnover of marine tetrapods during the Jurassic–Cretaceous transition. Biol Rev, 89: 1-23.

Bernard A, Lécuyer C, Vincent P, et al. 2010. Regulation of body temperature by some Mesozoic marine reptiles. Science, 328: 1379-1382.

Brown D S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. Bulletin of British Museum of Natural History (Geology), 35: 253-347.

Cabrera A. 1941. Un Plesiosaurio nuevo de Cretáceo del Chubut. Revista del Museo de La Plata (Nueva Serie), 2: 113-130.

Chatterjee S, Creisler B S. 1994. *Alwalkeria* (Theropoda) and *Morturneria* (Plesiosauria), new names for preoccupied Walkeria Chatterjee, 1987 and *Turneria* Chatterjee and Small, 1989. J Vertebr Paleontol, 14: 142-142.

Chatterjee S, Small B J. 1989. New plesiosaurs from the Upper Cretaceous of Antarctica. Geol Soc Lond Spec Pub, 47: 197-215.

Cione A L, Medina F A. 1987. A record of *Notidanodon pectinatus* (Chondrichthyes, Hexanchiformes) in the Upper Cretaceous of the Antarctic Peninsula. Mesozoic Res, 1: 79-88.

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.

Crame J A, Francis J E, Cantrill D J, et al. 2004. Maastrichtian stratigraphy of Antarctica. Cret Res, 25: 411-423.

Cruickshank A R I, Fordyce R E. 2002. A new marine reptile (Sauropterygia) from New Zealand: further evidence for a Late Cretaceous Austral radiations of cryptoclidid plesiosaur. Palaeontology, 45: 557-575.

de Blainville H D. 1835. Description de quelques espèces de reptiles de la Californie, precédée de l'analyse d'un système général d'herpetologie et d'amphibiologie. Nouvelles Archives du Museum d'Histoire Naturelle, 4: 233-296.

de la Fuente M, Novas F E, Isasi M P, et al. 2010. First Cretaceous turtle from Antarctica. J Vertebr Paleontol, 30: 1275-1278.

del Valle R A, Medina F, Gasparini Z. 1977. Nota preliminar sobre el hallazgo de reptiles fósiles marinos del suborden Plesiosauria en las islas James Ross e Vega, Antártida (Preliminary note on the discovery of fossil marine reptiles from the suborder Plesiosauria from James Ross and Vega islands, Antarctica). Contribución del Instituto Antártico Argentino, 212: 1-13.

Dingle R V, Lavelle M. 1998. Late Cretaceous–Cenozoic climatic variations of the northern Antarctic Peninsula: new geochemical evidence and review. Palaeogeogr Palaeocl, 141, 215-232.

Ditchfield P W, Marshall J D, Pirrie D. 1994. High latitude palaeotemperature variation: new data from the Thithonian to Eocene of James Ross Island, Antarctica. Palaeogeogr Palaeocl, 107, 79-101.

Fernández M S, Gasparini Z. 2012. Campanian and Maastrichtian mosasaurs from Antarctic Peninsula and Patagonia, Argentina. Bulletin de la Société Géologique de France, 183: 93-102.

Fostowicz-Frelic L, Gazdzicki A. 2001. Anatomy and histology of plesiosaur bones from the Late Cretaceous of Seymour Island, Antarctic Peninsula. Palaeontologia Polonica, 60: 7-32.

Gasparini Z, Del Valle R A, Goñi R. 1984. An elasmosaur (Reptilia, Plesiosauria) of the Upper Cretaceous in the Antarctic. Contribución del Instituto Antártico Argentino, 305: 1-24.

Gasparini Z, Salgado L. 2000. Elasmosáuridos (Plesiosauria) del Cretácico Tardío del norte de Patagonia. Revista Española de Paleontología, 15:

13-21.

Gasparini Z, Salgado L, Casadío S. 2003a. Maastrichtian plesiosaurs from northern Patagonia. Cret Res, 24: 157-170.

Gasparini Z, Bardet N, Martin J E, et al. 2003b. The elasmosaurid plesiosaur *Aristonectes* Cabrera from the Latest Cretaceous of South America and Antarctica. J Vertebr Paleontol, 23: 104-115.

Hector J. 1874. On the fossil reptiles of New Zealand. Transactions of the New Zealand Institute, 6: 333-358.

Hiller N, Mannering A A, Jones C M, et al. 2005. The nature of *Mauiasaurus haasti* Hector, 1874 (Reptilia: Plesiosauria). J Vertebr Paleontol, 25: 588-601.

Hiller N, O'Gorman J P, Otero R A, et al. 2017. A reappraisal of the Late Cretaceous Weddellian plesiosaur genus *Mauisaurus* Hector, 1874. New Zeal J Geol Geop, 60: 112-128.

Hospitaleche C A, Gelfo J N. 2015. New Antarctic findings of Upper Cretaceous and lower Eocene loons (Aves: Gaviiformes). Annales de Paléontologie 101, 315-324.

Huber B T, Norris R D, Macleod K G. 2002. Deep-sea paleotemperature record of extreme warmth during the Cretaceous. Geology, 30: 123-126.

Kellner A W A, Rodrigues Simões T, Riff D, et al. 2011. The oldest plesiosaur (Reptilia, Sauropterygia) from Antarctica. Polar Res, 30: 1-6.

Ketchum H F, Benson R B. 2010. Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses. Biol Rev, 85: 361-392.

Ketchum H F, Benson R B. 2011. A new pliosaurid (Sauropterygia, Plesiosauria) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: evidence for a gracile, longirostrine grade of Early-Middle Jurassic pliosaurids. Spec Pap Palaeontol, 86: 109-129.

Kriwet J, Lirio J M, Nuñez H J, et al. 2006. Late Cretaceous Antarctic fish diversity. J Geol Soc London, Special Publications, 258: 83-100.

Macellari C E. 1988. Stratigraphy, sedimentology, and paleoecology of Upper Cretaceous/Paleocene shelf-deltaic sediments of Seymour Island. Geol Soc Am (Memoir), 169: 25-54.

Marenssi S A, Salani F M, Santillana S N. 2001. Geología del cabo Lamb, Isla Vega, Península Antártica. Instituto Antártico Argentino Contribución, 530: 1-43.

Martin J E, Sawyer J F, Reguero M, et al. 2007. Occurence of a young elasmosaurid plesiosaur skeleton from the Late Cretaceous (Maastrichtian) of Antartica USGS OF-2007-1047, Short Research Paper 066.

Massare J A. 1994. Swimming capabilities of Mesozoic marine reptiles: a review//Maddock L, Bone Q, Rayner J M V. Mechanics and physiology of animal swimming. Cambridge: Cambridge University Press, 133-149.

McArthur J M, Crame J A, Thirlwall M F. 2000. Definition of Late Cretaceous stages boundaries in Antarctica using strontium isotope stratigraphy. J Geol, 108: 623-640.

Novas F E, D'Angelo J S, O'Gorman J P, et al. 2015. First record of Polycotylidae (Sauropterygia, plesiosauria) from the Upper Cretaceous of Antarctica. Cret Res, 56: 563-568.

Novas F E, Fernández M, Gasparini Z, et al. 2002. *Lakumasaurus antarcticus*, n. gen. et sp., a new mosasaur (Reptilia, Squamata) from the Upper Cretaceous of Antarctica. Ameghiniana, 39: 245-249.

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 Res, 31: 1-10.

O'Gorman J P. 2013. Plesiosaurios del Cretácico Superior de Patagonia y Península Antártica. PhD thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 527, http://sedici.unlp.edu.ar/bitstream/handle/10915/26140/Tomo_I.

O'Gorman J P. 2016a. A small body sized Non-Aristonectine Elasmosaurid (Sauropterygia, Plesiosauria) from the late Cretaceous of Patagonia with comments on the relationships of the Patagonian and Antarctic Elasmosaurids. Ameghiniana, 53: 245-268.

O'Gorman J P. 2016b. New Insights on the *Aristonectes parvidens* (Plesiosauria, Elasmosauridae) Holotype: news on an old specimen. Ameghiniana, 53: 397-417.

O'Gorman J P. 2017. First record of *Kawanectes lafquenianum* (Elasmosauridae, Sauropterygia) from La Colonia Formation, Chubut. Resumenes 31 Jornadas Argentinas de Paleontología de Vertebrados. Santa Clara del Mar, Partido de Mar Chiquita, Provincia de Buenos Aires, Argentina 3 al 6 de mayo de 2017. Libro de Resumenes: 44.

O'Gorman J P, Coria R A. 2017. A new elasmosaurid specimen from the upper Maastrichtian of Antarctica: new evidence of a monophyletic group of Weddellian elasmosaurids. Alcheringa, 41: 240-249.

O'Gorman J P, Coria R A, Reguero M, et al. 2018a. The first non-aristonectine elasmosaurid (Sauropterygia; Plesiosauria) cranial material from Antarctica: New data on the evolution of the elasmosaurid basicranium and palate. Cret Res, 89: 248-263.

O'Gorman J P, Gasparini Z. 2013. Revision of *Sulcusuchus erraini* (Sauropterygia, Polycotylidae) from the Upper Cretaceous of Patagonia, Argentina. Alcheringa, 37: 163-176.

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. Antarc Sci, 25: 71-82.

O'Gorman J P, Gouiric-Cavalli S, Scasso X, et al. 2018b. New evidence on the dispersion of marine fauna through the trans-Erytraean Seaway: a Late Jurassic plesiosaur in Antarctica. C R Palevol, 17: 158-165.

O'Gorman J P, Olivero E B, Cabrera D A. 2012. Gastroliths associated with a juvenile elasmosaur (Plesiosauria, Elasmosauridae) from the Snow Hill Island Formation (upper Campanian–lower Maastrichtian), Vega Island, Antarctica. Alcheringa, 36: 531-541.

O'Gorman J P, Olivero E B, Santillana S, et al. 2014. Gastroliths associated with an Aristonectes specimen (Plesiosauria, Elasmosauridae), López de Bertodano Formation (upper Maastrichtian) Seymour Island (Is. Marambio), Antarctic Peninsula. Cret Res, 50: 228-237.

O'Gorman J P, Panzeri K M, Fernández M S, et al. 2017b. A new elasmosaurid from the upper Maastrichtian of the López de Bertodano Formation: new evidence on the Weddellonectia diversity. Alcheringa, 41: 240-249.

O'Gorman J P, Salgado L, Olivero E B, et al. 2015. *Vegasaurus molyi*, gen. et sp. nov. (Plesiosauria, Elasmosauridae), from the Cape Lamb Member (lower Maastrichtian) of the Snow Hill Island Formation, Vega Island, Antarctica, and remarks on Wedellian Elasmosauridae. J Vertebr Paleontol, 35, e931285.

O'Gorman J P, Santillana S, Otero R, et al. 2019. A giant elasmosaurid

(Sauropterygia; Plesiosauria) from Antarctica: New information on elasmosaurid body size diversity and aristonectine evolutionary scenarios. Cret Res, 102: 37-58.

O'Gorman J P, Talevi M, Fernandez M. 2017a. Osteology of a perinatal aristonectine (Plesiosauria; Elasmosauridae). Antarc Sci, 29: 61-72.

O'Keefe F R, Carrano M T. 2005. Correlated trends in the evolution of the plesiosaur locomotor system. Paleobiology, 31: 656-675.

O'Keefe F R, Chiappe L M. 2011. Viviparity and K-selected life history in a Mesozoic marine plesiosaur (Reptilia, Sauropterygia). Science, 333: 870-873.

O'Keefe F R, Otero R A, Soto-Acuña S, et al. 2017. Cranial anatomy of *Morturneria seymourensis* from Antarctica, and the evolution of filter feeding in plesiosaurs of the austral Late Cretaceous. J Vertebr Paleontol, 37: e1347570.

O'Keefe F R, Street H P. 2009. Osteology of the cryptocleidoid plesiosaur *Tatenectes laramiensis*, with comments on the taxonomic status of the Cimoliasauridae. J Vertebr Paleontol, 29: 48-57.

Olivero E. 1992. Asociaciones de amonites de la Formación Santa Marta (Cretácico Tardío), Isla James Ross. (Ammonite asociations in the Santa Marta Formation [Late Cretaceous])//Rinaldi C A. Geología de la Isla James Ross. Instituto Antartico Argentino. Buenos Aires, 47-76.

Olivero E B. 2012. Sedimentary cycles, ammonite diversity a palaeoenvironmental changes in the Upper Cretaceous Marambio Group, Antarctica. Cret Res, 34: 348-366.

Olivero E B, Medina F A. 2000. Patterns of Late Cretaceous ammonite biogeography in southern high latitudes: the family Kossmaticeratidae in Antarctica. Cret Res, 21: 269-279.

Olivero E B, Ponce J J, Martinioni D R. 2008. Sedimentology and architecture of sharp-based tidal sandstones in the upper Marambio Group, Maastrichtian of Antarctica. Sed Geol, 210: 11-26.

Otero R A, Gutstein C, Vargas A, et al. 2014a. New chondrichthyans from the Upper Cretaceous (Campanian–Maastrichtian) of Seymour and James Ross islands, Antarctica. J Paleontol, 88: 411-420.

Otero R A, O'gorman J P, Hiller N, et al. 2016. *Alexandronectes zealandiensis* gen. et sp. nov., a new aristonectine plesiosaur from the lower Maastrichtian of New Zealand. J Vertebr Paleontol, 36: e1054494.

Otero R A, Rubilar-Rogers D, Yury-Yañez R E, et al. 2013. A new species of chimaeriform (Chondrichthyes, Holocephali) from the uppermost Cretaceous of the López de Bertodano Formation, Isla Marambio (Seymour Island), Antarctica. Antarc Sci, 25: 99-106.

Otero R A, Soto-Acuña S, O'keefe F R. 2018. Osteology of *Aristonectes quiriquinensis* (Elasmosauridae, Aristonectinae) from the upper Maastrichtian of central Chile. J Vertebr Paleontol, 38(1): e1408638, doi: 10.1080/02724634.2017.1408638.

Otero R A, Soto-Acuña S, Rubilar-Rogers D. 2012. A postcranial skeleton of an elasmosaurid plesiosaur from the Maastrichtian of central Chile, with comments on the affinities of Late Cretaceous plesiosauroids from the Weddellian Biogeographic Province. Cret Res, 37: 89-99.

Otero R A, Soto-Acuña S, Vargas A O, et al. 2014b. Additions to the diversity of elasmosaurid plesiosaurs from the Upper Cretaceous of Antarctica. Gondwana Res, 26: 772-784.

Otero R A, Soto-Acuña S, O'Keefe F R, et al. 2014c. *Aristonectes quiriquinensis*, sp. nov, a new highly derived elasmosaurid from the upper Maastrichtian of central Chile. J Vertebr Paleontol, 34: 100-125.

Owen R. 1860. On the orders of fossil and recent Reptilia, and theirdistribution in time. Reports of the British Association for the Advancement of Science, 29: 153-166.

Pirrie D, Crame J A, Riding J B. 1991. Late Cretaceous stratigraphy and sedimentology of Cape Lamb, Vega Island, Antarctica. Cret Res, 12: 227-258.

Roberts E M, Lamanna M C, Clarke J A, et al. 2014. Stratigraphy and vertebrate paleoecology of Upper Cretaceous–? lowest Paleogene strata on Vega Island, Antarctica. Palaeogeogr Palaeocl, 402: 55-72.

Sachs S, Kear B P. 2017. Redescription of the elasmosaurid plesiosaurian *Libonectes atlasense* from the Upper Cretaceous of Morocco. Cret Res, 74: 205-222.

Salgado L, Gasparini Z. 2006. Reappraisal of an ankylosaurian dinosaur from the Upper Cretaceous of James Ross Island (Antarctica). Geodiversitas, 28: 119-135.

Salgado L, Parras A, Gasparini Z. 2007. Un plesiosaurio de cuello corto (Plesiosauroidea, Polycotylidae) del Cretácico Superior del norte de Patagonia. Ameghiniana, 44: 349-358.

Sato T. 2005. A new polycotylid plesiosaur (Reptilia: sauropterygia) from the Upper Cretaceous Bearpaw Formation in Saskatchewan, Canada. J Paleontol, 79: 969-980.

Syme C E, Salisbury S W. 2014. Patterns of aquatic decay and disarticulation in juvenile Indo-Pacific crocodiles (*Crocodylus porosus*), and implications for the taphonomic interpretation of fossil crocodyliform material. Palaeogeogr Palaeocl, 412: 108-123.

Thompson W A, Martin J E, Reguero M. 2007. Comparison of gastroliths within plesiosaurs (Elasmosauridae) from the Late Cretaceous marine deposits of Vega Island, Antarctic Peninsula, and the Missouri River area, South Dakota. Special Papers, Geol Soc Am, 427: 147.

Welles S, Gregg D R. 1971. Late Cretaceous marine reptiles of New Zealand. Records of the Canterbury Museum, 9: 1-111.

Welles S P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. Memoirs of the University of California, 13: 125-254.

Wiffen J, Moisley W. 1986. Late Cretaceous reptiles (families Elasmosauridae, Pliosauridae) from the Mangahouanga Stream, North Island, New Zealand. New Zeal J Geol Geop, 29: 205-252.

Zinsmeister W J. 1979. Biogeographic significance of the late Mesozoic and early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland. Ohio State University, Institute of Polar Studies, 349-355.

Zinsmeister W J. 1982. Late Cretaceous-early Tertiary molluscan biogeography of the southern circum-Pacific. J Paleontol, 56: 84-102.