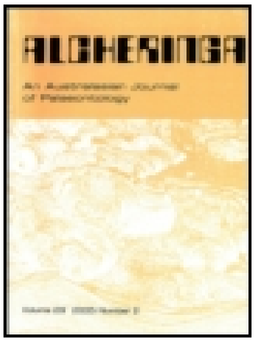

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A new elasmosaurid from the upper Maastrichtian López de Bertodano Formation: new data on weddellonectian diversity

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Elasmosaurids are one of the most frequently recorded marine reptiles from the Weddellian Province (Patagonia, Western Antarctica and New Zealand). Improvements in our knowledge of elasmosaurid diversity have been problematic because of their conservative postcranial morphology. However, recent studies have helped to improved our understanding of the diversity of this group. Here, a new elasmosaurid specimen from the upper Maatrichtian horizons of the López de Bertodano Formation, Antarctica, MLP 14-I-20-16, is described. MLP 14-I-20-16 is one of the youngest non-aristonectine weddellonectian elasmosaurids from Antarctica. We confirm the coexistence of aristonectine and non-aristonectine elasmosaurids in Antarctica until the end of the Cretaceous. MLP 14-I-20-16 shows distinctive short and broad posterior cervical vertebrae, a feature only shared among the weddellonectian elasmosaurids by the Maastrichtian *Morenosaurus stocki*, although the same vertebral proportions are also recorded for the giant Cenomanian elasmosaurids *Thalassomedon haningtoni*. Comparison between MLP 14-I-20-16 and other elasmosaurids from the Maastrichtian of Antarctica indicates that at least two different non-aristonectine elasmosaurids were present in Antarctica during the late Maastrichtian.

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Key words: Elasmosauridae, López de Bertodano, weddellonectia, Plesiosauria, marine reptiles.

ELASMOSAURIDS are a clade of long-necked plesiosaurs that achieved a worldwide distribution (Brown 1913, Carpenter 1999, Sato *et al*. 2006, Vincent *et al*. 2011, O'Gorman 2012, Sachs *et al*. 2013, Araújo *et al*. 2015a, 2015b, Sachs & Kear 2015). Elasmosaurids are the most frequently recorded plesiosaurs in the Campanian–Maastrichtian horizons of the Weddellian Province *sensu* Zinsmeister 1979 (i.e. Patagonia; Western Antarctica and New Zealand). This abundance of records during the Campanian–Maastrichtian is also observed in other localities around the world (Welles 1943, Carpenter 1999, Vincent *et al*. 2013).

The Weddellia elasmosaurids include not only the distinctive aristonectine elasmosaurids but also non-aristonectine elasmosaurids. Aristonectines (*Aristonectes* spp., '*Morturneria seymourensis*', *Kaiwhekea katiki* and *Alexandronectes zealandiensis*) have an increased number of premaxillary, maxillary and dentary teeth, a squared posterior extension of the pterygoid, extremely short mandibular symphysis, and short and broad cervical centrum (Cruickshank & Fordyce 2002, Gasparini *et al*. 2003, Otero *et al*. 2014, Otero *et al*. 2015b, O'Gorman 2016b). The non-aristonectine elasmosaurids show the typical small skull and anterior and middle cervical centra longer than high. (Otero *et al*. 2014, O'Gorman *et al*. 2015). The latter are represented by *Tuarangisaurus keyesi*; *Vegasaurus molyi* and *Kawanectes lafquenianum* (Wiffen & Moisley 1986 O'Gorman *et al.* 2015, O'Gorman 2016a). The historical *Mauisaurus haasti* is currently considered a *nomen dubium* (Hiller *et al.* 2017) as the classical autapomorphy of *Mauisaurus haasti*, the presence of a femoral hemispherical head, was also observed in *Aristonectes* (O'Gorman 2013, Otero *et al.* 2015a).

The non-aristonectine elasmosaurids from Antarctica comprise only one valid species, the lower Maastrichtian *Vegasaurus molyi.* However, the records of elasmosaurids from the James Ross Archipelago range from the lower Campanian to the upper Maastrichtian,

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and therefore the diversity was probably greater, but it remains poorly known (O'Gorman 2012, O'Gorman *et al*. 2015). Recent phylogenetic analysis recovered a Weddellian clade of elasmosaurids, called Weddellonectia, which comprises the aristonectine, the Weddellian non-aristonectine upper Campanian–lower Maastrichtian *Kawanectes lafquenianum*, the lower Maastrichtian *Vegasaurus molyi* and the Maastrichtian *Morenosaurus stocki* (O'Gorman & Coria 2016).

These new results and the detailed study of the non-aristonectine members of the Weddellonectia allow us to take the first steps in order to infer the sequence of changes that generated the aristonectine anatomy, characterized by highly derived skull morphology, relatively large body size and relatively short cervical centra (Cruickshank & Fordyce 2002, Gasparini *et al*. 2003, Otero *et al*. 2014, O'Gorman 2016a).

The main goals of this study are: to describe a new elasmosaurid specimen (MLP 14-I-20-16) from the upper Maastrichtian Klb 9 of the Allomember B, López de Bertodano Formation, Marambio Island (Antarctica, Fig. 1), to infer its phylogenetic position, to compare it with other Weddellian elasmosaurids including the other two non-aristonectine elasmosaurids from the unite Klb 9: MLP 82-I-8-1 and SGO.PV.6523 and to discuss the implications of the new data on the diversity of the Antarctic elasmosaurids.

Anatomical abbreviations

cap, capitulum; cr, caudal rib; vn, ventral notch; ad, dorsal doramina; hf, haemal facets; in, intermedium; isf, ischiadic facet; vf, ventral foramina; mvp, mid ventral process; ventral foramina; par; parapophyses; pez, prezygapophyses, poz, postzygapophyses; ps, periferic step; scr, scapular ridge; sr, sacral rib; ti, tibia; fi, fibula; tp, transverse process; tdI, distal tarsal I; tro, trochanter.

Institutional abbreviations

ANSP, Academy of Natural History, New York, USA; DM, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; DMNH, Denver Museum of Natural History, Denver, USA; LACM, Natural History Museum of Los Angeles County, Los Angeles County, USA (previously housed in the CIT, California Institute of Technology, California); MCS Pv, Museo de Cinco Saltos, Río Negro Province, Argentina; MIWG, 'Dinosaur Isle' Museum of Isle of Wight Geology, Sandown, UK; MLP, Museo de la Plata, Buenos Aires Province, Argentina; QM, Queensland Museum, Brisbane, Australia SGO.PV, Museo Nacional de Historia Natural, Santiago, Chile.

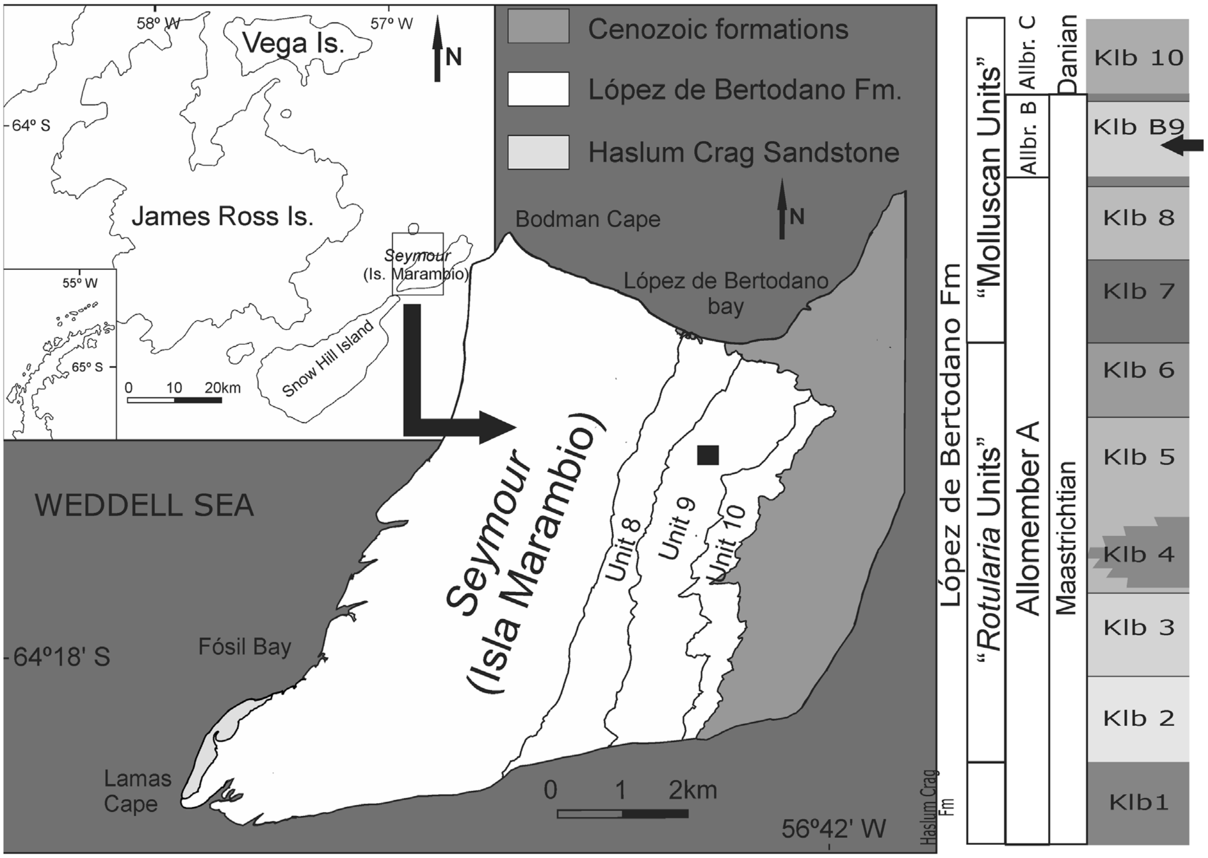

Fig. 1. **A**, Locality where the MLP 14-I-20-16 plesiosaur specimen was collected. **B**, Stratigraphic position of the MLP 14-I-20-16 (modified from Montes *et al*. 2013).

Geological setting

The López de Bertodano Formation, the uppermost formation of the Marambio Group, crops out in Seymour Island (*Is. Marambio*) and Vega Island, James Ross Archipelago (Fig. 1A). The López de Bertodano Formation comprises about 1150 m of silicoclastic sediments (sandy shales and sandstones) with less abundant carbonate horizons (Macellari 1988). Within this formation, two informal parts can be recognized: the lower one '*Rotularia* units', and the upper one 'Molluscan units'. The López de Bertodano was deposited in two different environments. A shallow marine environment near to an estuary was inferred for the '*Rotularia* units' and middle to outer platform settings for the 'Molluscan units' (Macellari 1988, Olivero *et al*. 2008). The López de Bertodano is Maastrichtian/Danian in age (Macellari 1986, 1988, Olivero & Medina 2000, Crame *et al*. 2004, Olivero 2012). MLP 14-I-20-16 was collected from the unit Klb 9 of the Allomember B, the López de Bertodano Formation (Montes *et al*. 2013), where other plesiosaurs were previously collected (Chatterjee & Small 1989, Otero *et al*. 2014, O'Gorman *et al*. 2016).

Methods

The fossil (MLP 14-I-20-16) was prepared mainly by the authors (J.P.O'G and K.P.) using MicroJack and ME 9100 jackhammers. The ilium was reconstructed by filling the cast left in the matrix with polyester resin. A mechanical caliper (accuracy of 0.5 mm) was used to calculate the indices proposed by Welles (1952), which express the proportions between the height and the length [HI = 100 × (H / L)], and between the width and the length [BI = 100 × (B / L)] of the vertebral centra. The BH [BH = 100 × (B / H)] was also considered.

The MLP 14-I-20-16 was compared with the two Weddellian non-aristonectine elasmosaurids with well-known postcranium: *Vegasaurus molyi* (MLP 93-I-5-1, holotype) and *Kawanectes lafquenianum* (MLP 71-II-13-1, holotype; MCS PV 4, referred specimen). Additionally, two indeterminate elasmosaurids from the Klb 9, Allomember B, López de Bertodano Formation, MLP 82-I-8-1 and SGO.PV.6523, were considered for comparisons. The MLP 82-I-8-1 was personally reviewed while SGO.PV.6523 was compared based on Otero *et al*. (2014). A phylogenetic analysis was performed to determine the phylogenetic position of MLP 14-I-20-16. The data-set used was compiled based on Benson & Druckenmiller (2014) and modified by O'Gorman & Coria (2016). The data-set was modified, deleting *Gronausaurus wegneri* based on a recent result that indicates its synonymy with *Brancausaurs brancai* (Sachs *et al.* 2016). The new data-set comprises 92 OTUs and 278 characters, including one new characters (see supplementary data I) and the addition of two new OTUs coded based on pers. obs. (J.P.O'G): *Aphrosaurus furlongi* (LACM 2748, holotype) from the Maastrichtian of California, USA and an indeterminate aristonectine MLP 99-XII-1-5 from the upper Maastrichtian of Sandwich Bluff Member of the López de Bertodano Formation, Vega Island Antarctica. The data-set was compiled using Mesquite Software (Maddison & Maddison 2011). The final data-set (supplementary data II) was analysed using TNT 1.5 software (Goloboff & Catalano 2016) performing a heuristic search (TBR, tree bisection reconnection, with 1000 random-addition-sequence replicates). Initial exploration for shortest trees islands was conducted using three random seeds. The resulting subset of most parsimonious trees (MPTs) was used as initial group of trees for TBR (tree bisection and reconnection). Additionally, the consistency index (CI) and retention index (RI) (Farris 1989) were calculated, and the Bremer Support (Bremer 1994) was evaluated for some of the nodes. The InterPCR scipt (Pol & Escapa 2009) was used in order to detect unstable taxa.

Systematic palaeontology

Superorder SAUROPTERYGIA Owen, 1860
Order PLESIOSAURIA de Blainville, 1835
Family ELASMOSAURIDAE Cope, 1869
WEDDELLONECTIA O'Gorman & Coria, 2016
Weddellonectia indet.
Figs 2–4, 5C

Material. MLP 14-I-20-16, 12 cervical vertebrae, three pectoral vertebrae, 11 dorsal vertebrae, one sacral vertebra, 11 caudal vertebrae, right femur, tibia, fibula and mesopodial elements, fragments of pectoral and pelvic girdles and gastroliths.

Locality and horizon. Seymour Island (*Is. Marambio*), James Ross Archipelago, Antarctic Peninsula (Fig. 1). López de Bertodano Formation. Klb 9 of the Allomember B. Upper Maastrichtian (Macellari 1988, Olivero 2012, Montes *et al*. 2013).

Description

Axial skeleton

Cervical region. There are only 12 preserved cervical vertebrae, mostly represented by fragments of vertebral centra. The cervical vertebrae show a slightly concave articular face. Almost all of the preserved cervical vertebrae have their cervical ribs fused with the centra (Fig. 2A–D). In the articular face of some vertebral centra, a periferic 'step' is observed, which is more marked in the anterior face than in the posterior one (Fig. 2E). In all the preserved centra, the lateral surface is anteroposteriorly concave and shows a ventral notch that is more pronounced in the anterior cervical vertebrae giving the typical dumbbell shape articular face of Late Cretaceous elasmosaurids (Hiller *et al*. 2005, Benson & Druckenmiller 2014, Fig. 2A, E). There are

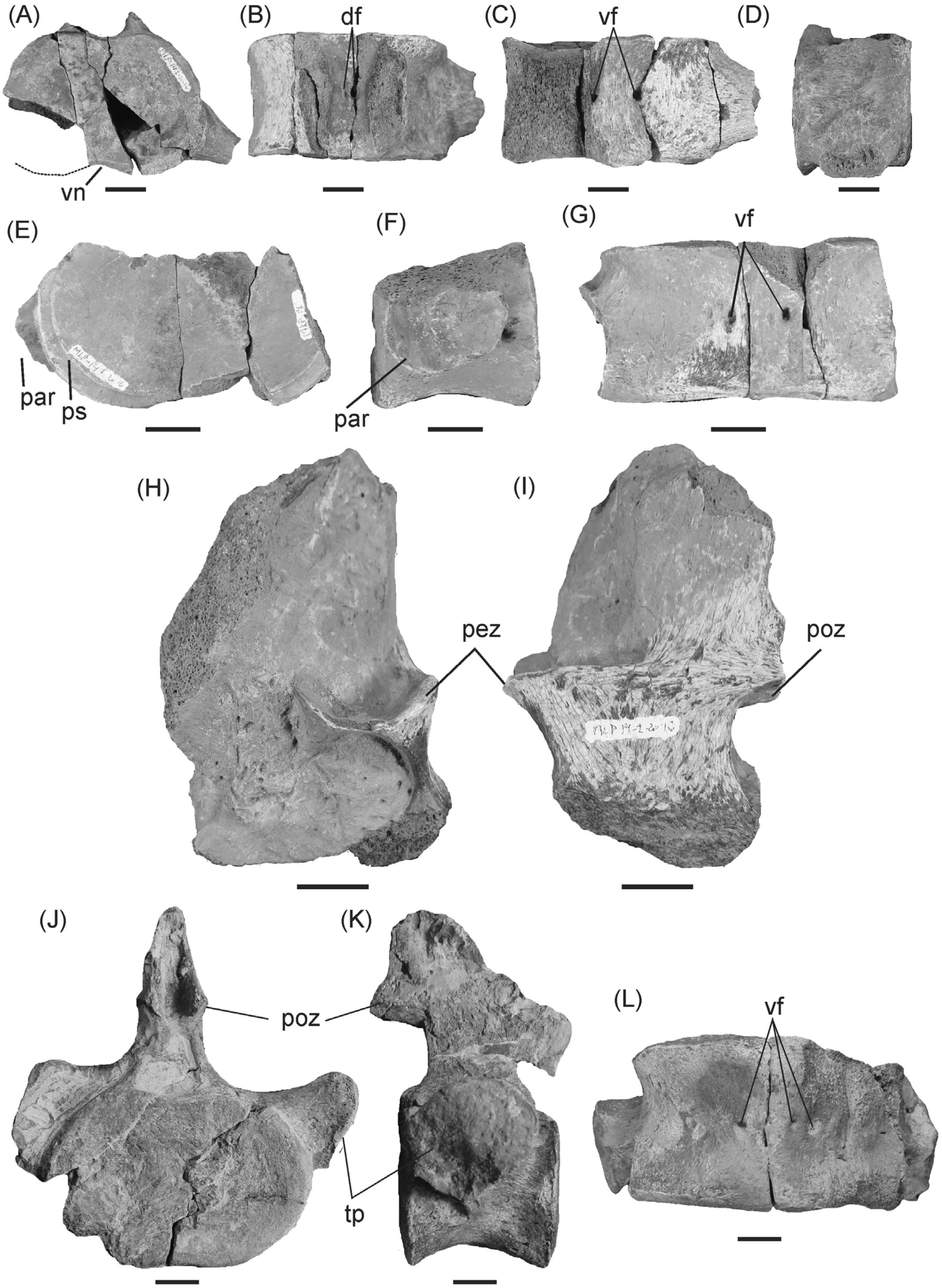

Fig. 2. Elasmosauridae indet (MLP 14-I-20-16). **A**–**D**, Cervical vertebrae in **A**, anterior, **B**, dorsal, **C**, ventral and **D**, left lateral view. **E**–**G**, Posterior cervical vertebrae in **E**, anterior, **F**, right lateral and **G**, ventral views. **H**–**I**, Cervical neural arch in **H**, anterior and **I**, left lateral view. **J**–**L**, Pectoral vertebra in **J**, posterior, **K**, right lateral and **L**, ventral views. Scale bar = 20 mm.

no vertebrae longer than high (Table 1) or with preserved lateral keel. However, as this feature is usually absent in the posterior cervical centra of elasmosaurids (Welles 1943, Hiller *et al*. 2005, O'Gorman *et al*. 2015), its absence in MLP 14-I-20-16 could be due to the lack of mid and anterior cervical centra. Ventrally, the cervical centra show two main foramina, and additionally a pair of smaller foramina piercing the floor of the neural canal (Fig. 2B, C, G). Only one posterior vertebral centrum is well preserved (Fig. 2E–G). Their vertebral centra are broader than high and higher than long. The parapophyses are free and latero-ventrally positioned, concave and subeliptically shaped (Fig. 2F).

The neural archs are fused to the vertebral centra in all the preserved vertebrae. Only one neural arch is complete and shows the medial inclination between left

Region	*L*	*H*	*B*	*H*/*L*	*B*/*L*	*B*/*H*	VLI
Cervical							
	58		102				
	58	66	97	114	167	147	71
	54	64	86	119	159	134	72
	57						
	56						
	57						
	57						
	57						
	48						
	52						
	58						
Pectoral							
	59						
	54						
	59	71	105	120	178	148	67
Dorsal							
	57	77		135			
	62	73		118			
Caudal							
	45	88	65	196	144	74	59
		86					
		85	72			85	
	45	81	67	180	149	83	61
	46	83	65	180	141	78	62
	45	77	66	171	146,	86	63
	43	73	63	170	146	86	63
	45	72	64	160	142	89	66
		70	69			98	
	46						
	41		55		134		
	37		57		154		

Table 1. Measurements and indexes of vertebral centra of MLP 14-I-20-16. L, length; H, height; B, breadth (in millimetres), HI, height (*H*)/length (*L*) ratio (HI = 100 × *H*/*L*), BI, breadth (B)/length (*L*) ratio (BI = 100 × *B*/*L*), BHI, breadth/height ratio (BHI = 100 × *B*/*H*) and VLI, Vertebral Length Index [VLI = 100 × *L*/(0.5 × (*H* + *B*))].

and right zygapophyses. Additionally, medial fusion between left and right prezygapophysis (Fig. 2H) and the medial fusion between left and right postzygapophysis is observed.

Pectoral region. Three pectoral vertebrae are preserved. They are ordered as first, second and third, based on the relative contribution of the diapophysis and parapophysis to the transverse process. The third pectoral vertebra is almost completely preserved, with the vertebral centrum being broader than high and higher than long (Table 1). As in the cervical vertebrae, the 'step' of the articular face is more marked on the anterior articular face than on the posterior face. Ventrally, it shows two main ventral foramina and a smaller one (Fig. 2L).

The prezygapophyses and postzygapophyses are not fused in the midline. The first and second pectoral vertebrae show a transverse process with concave elliptical articular facets, with its major axis caudally inclined. The third pectoral vertebra shows the articular facet of the transverse process also elliptical in shape but with convex dorsal and concave ventral sectors (Fig. 2K). Caudally to the transverse process, all the pectoral vertebrae show a circular depression, which is deeper in the anterior vertebrae and decreases in size towards the posterior ones (Fig. 2K).

Dorsal region. There are 11 preserved dorsal vertebrae, most preserving only fragments of the vertebral centra and isolated diapophysis. In ventral view, the vertebral centra are pierced by three to four ventral foramina (Fig. 3B). The only well-preserved diapophysis shows a convex articular facet of subelliptical shape and a slightly dorsoventrally compressed body, with a marked anterior crest and a less pronounced posterior one (Fig. 3C, D).

Sacral region. Only one sacral vertebra is preserved (Fig. 3E, F). The vertebral centrum is wider than high and higher than long (Table 1). It has the sacral ribs articulated with the vertebral centrum but not fused with the transverse process. The ribs are laterally directed and somewhat flattened dorsoventrally, and have a convex and subelliptical articular facet (Fig. 3E).

Caudal region. The caudal vertebral centra are broader than high and higher than long (Table 1). All caudal vertebrae preserved show the caudal ribs fused to the vertebral centra, lateral in position and dorsoventrally compressed (Fig. 3I). Towards the posterior caudal vertebrae, the caudal ribs are more dorsal in position and are reduced in size to small protuberances (Fig. 3G, H). The neural arches are fused to the vertebral centra. The ventral surface is pierced by one, two, or three foramina located in a concavity delimited by two ridges that connect the anterior hemal facets with the posterior ones (Fig. 3I). The anterior hemal facets are usually more developed than the posterior ones.

Appendicular skeleton

Pectoral girdle. Two fragments of the left scapula are preserved: the glenoid ramus and a part of the ventral ramus. The proximal part of the glenoid ramus is divided into the glenoid and coracoid facets. The first former shows a concave and subelliptical articular face of rugose texture, whereas the coracoid facet is narrower and elongated. The most conspicuous feature of the ventral ramus of the left scapula is the presence of a rounded ridge (scapular ridge) on its dorsal surface (Fig. 4A, B).

Two fragments of the coracoid have been preserved, one of which is a part of the glenoid ramus of the coracoid and bears the scapular facet. The remaining fragment belongs to the symphyseal margin of the coracoids (Fig. 4C). The medial part of the coracoid possesses the dorsal convex margin, whereas the ventral side forms the mid ventral process (Fig. 4C).

Pelvic girdle. The preserved parts of the pelvic girdle include the fragments of the pubis, partial ischium and incomplete right ilium.The right pubis is preserved in

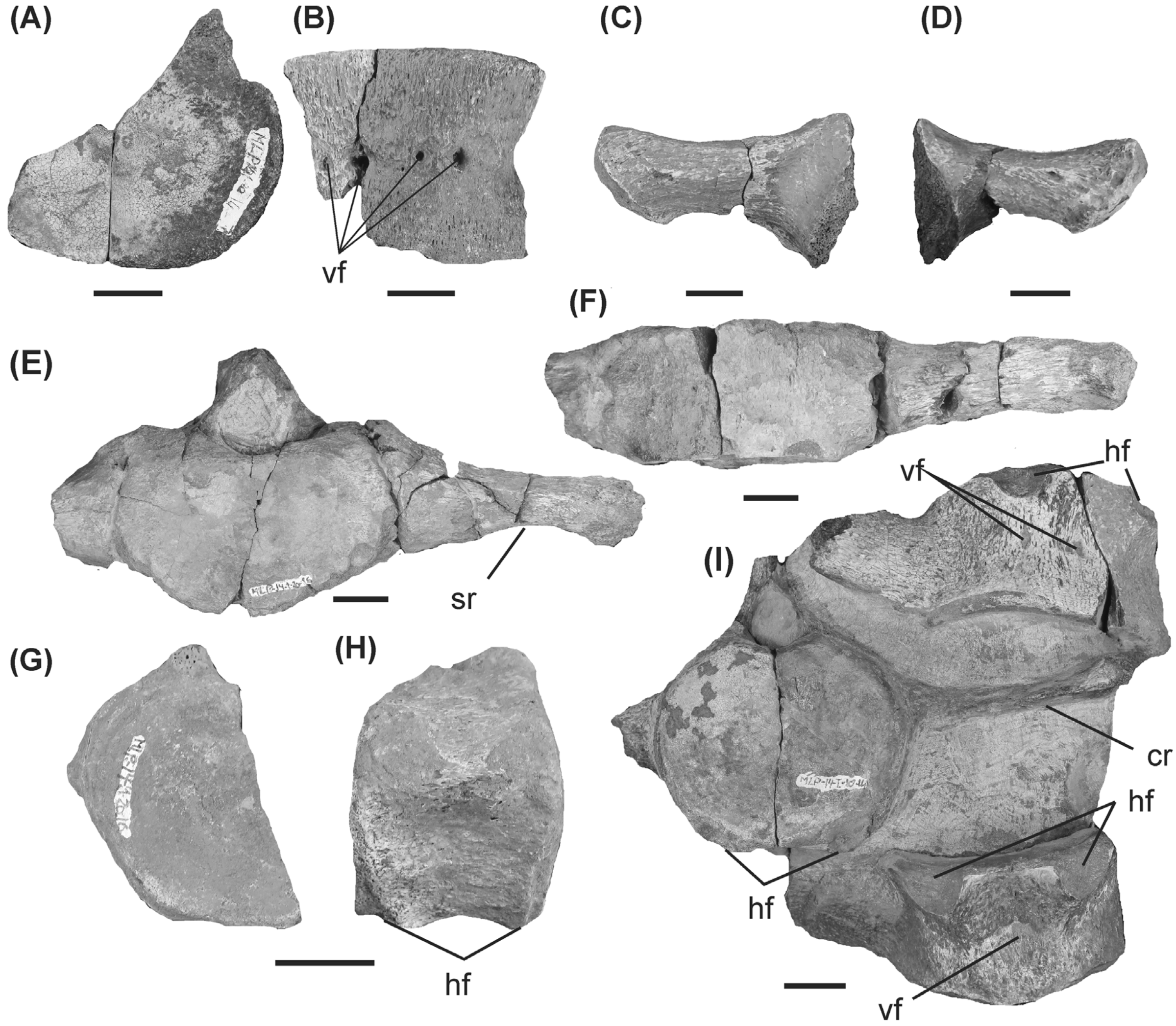

Fig. 3. Elasmosauridae indet (MLP 14-I-20-16). **A**–**B**, Dorsal centrum in **A**, anterior and **B**, ventral views. **C**–**D** diapophysis in **C**, anterior and **D**, posterior views. E–F, sacral vertebra and sacral rib in E, anterior and F, ventral views. **G**–**H**, Posterior caudal vertebrae in **G**, anterior and **H**, right lateral views. **I**, Three caudal vertebrae in ventral (top and bottom) and anterior (middle) views. Scale bar = 20 mm.

several fragments, but only its acetabular portion could be unambiguously identified. The left ischium preserves a fragment of the acetabular ramus and the left posterior ramus, which shows a concave dorsal surface and a slightly convex to flat ventral one (Fig. 4D).

The right ilium is preserved (Fig. 4E, F, G), and the ventral part is broader than the dorsal, which is laterally compressed and anteroposteriorly expanded. Ventral expansion of the ilium forms the ischiadic facet and a part of the acetabulum, with both surfaces located almost in the same plane (Fig. 4G). The dorsal end of the ilium shows a slightly concave medial side and a convex lateral one (Fig. 4E, F).

Posterior limb. The right femur was recovered, preserving its proximal and distal parts (Fig. 4H, J). The capitulum is partially confluent with the trochanter, convex and covered by transphyseal foramina (Fig. 4I).

Towards the distal part, the femur expands anteroposteriorly and flattens dorsoventrally (Fig. 4J). The ventral surface has a roughened texture with numerous slightly marked grooves directed proximo-distally and continued by a series of foramina towards the distal portion (Fig. 6J). The other elements of the limb are partially preserved (Fig. 4K). The tibia is incomplete, preserving its posterior half, showing the facet for the intermedium distally (Fig. 4J). The epipodial foramen (= spatium interosseum), which is located between the fibula and the tibia in almost all other elasmosaurids, with the exception of *Aphrosaurus furlogi* (Welles, 1943), is absent in MLP 14-I-20-16. The fibula shows a convex proximal articular facet. There is an accessory articular facet in the posterior margin of the fibula (Fig. 4L). The intermedium is hexagonally shaped, with its longer axis anteroproximally to posterior-distally directed (Fig. 4J). The distal tarsal I is short and rectangular (Fig. 4J).

Phylogenetic results

The phylogenetic analysis resulted in >20 000 MPTs with lengths of 1436 steps (consistency index = 0.287;

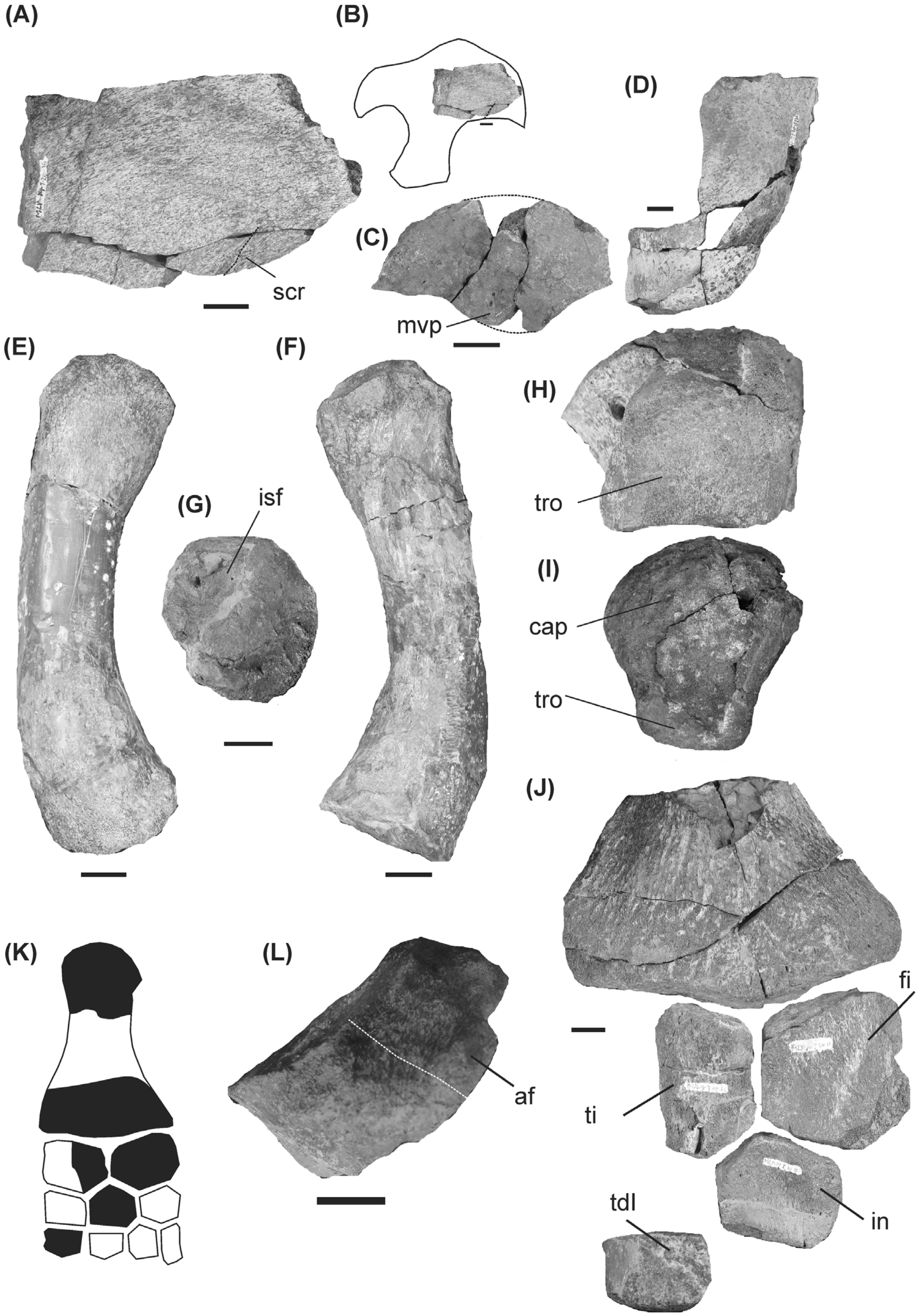

Fig. 4. Elasmosauridae indet (MLP 14-I-20-16). **A**–**B**, Ventral ramus of left scapula in **A**, dorsal view and **B**, Diagram showing relative position. **C**, Coracoid symphysis. **D**, Ischium in dorsal view. **E**–**G**, Right Ilium in **E**, lateral, **F**, medial and **G**, proximal view. **H**–**J**, Left femur in **H**, dorsal, **I**, proximal views and **J**, ventral views. **K**, Diagram indicating the limb elements preserved. **L**, Fibula in postero-distal view indicating accessory facet. Scale bar = 20 mm.

retention index = 0.672). The strict consensus tree is shown in Fig. 6. Bremer support is indicated below some nodes. MLP 14-I-20-16 was recovered deeply nested within the Elasmosauridae and forming a clade: *Aphrosaurus furlongi*, MLP 14-I-20-16, *Kawanectes lafquenianum, Morenosaurus stocki*, *Vegasaurus molyi*, MLP 15-I-7-48, *Morenosaurus stocki* (MLP 99-XII-1-5, *Aristonectes parvidens*, *Aristonectes quiriquinensis*, *Kaiwhekea katiki*). This clade is supported by 159 (2→1), posterior cervical neural spines as higth as centrum; 233

(0→1), accessory ossicle articulating with (humerus); 248 (0→1), angle between long axes of epipodial facets close to 180 degrees. This is the Weddellonectia clade sensu O'Gorman & Coria (2016) with the inclusion of *Aphrosaurus furlongi*, a taxon not considered in the data-set of O'Gorman & Coria (2016). The iterPCR script detected several wild card taxa along the entire tree but only *Vegasaurus molyi*, *Kawanectes lafquenianum* and MLP_15-I-7-48 affect the issues discussed in this contribution. The result of pruning alternatively *Vegasaurus molyi* and *Kawanectes lafquenianum* did not resolve the polytomy.

Discussion

MLP 14-I-20-16 preserves several key features that allow some comments about its growth stages, systematic identity and relationships. The specimen MLP 14-I-20-16 is considered an adult sensu Brown (1981), because the neural arches are fused to the centra, without a visible suture line.

Although several elasmosaurids have been collected from the López de Bertodano Formation, the specimens recorded from the uppermost horizons are mostly aristonectines (Chatterjee & Small 1989, Gasparini *et al.* 2003, O'Gorman 2013, O'Gorman *et al.* 2016), and therefore knowledge about the uppermost Maastrichtian non-aristonectine elasmosaurids from Antarctica is scarce. However, the previously described non- aristonectine elasmosaurids from New Zealand and the recently described non-aristonectine *Vegasaurus molyi* (Antarctica) and *Kawanectes lafquenianum* (Patagonia) provide new background information on the postcranial morphology of Weddellian elasmosaurids, allowing a detailed comparison (Hiller *et al.* 2005, O'Gorman *et al.* 2015, O'Gorman 2016a).

The general morphology of the cervical vertebrae of MLP 14-I-20-16 (medially inclined prezygapophyses and postzygapophyses; zygapophyses fused in the midline and narrower than the centra in the dorsal view) is shared by all elasmosaurids (Benson & Druckenmiller 2014), and it is also shared with SGO.PV.6523. However, two features recorded in MLP 14-I-20-16, the HI and BI values of the posteriormost cervical centra, seem to be quite distinctive. Figure 5A shows the plot of the HI and BI values of the Weddellonectia: the non-aristonectine *Morenosaurus stocki* (LACM 2802); *Vegasaurus molyi* (MLP 93-I-5-1); *Kawanectes lafquenianum* (MC PV 4) and the aristonectine: *Aristonectes* sp. (MLP 89-III-3-1) and MLP 14-I-20-16 and other elasmosaurids such as *Tuarangisaurus* sp. (CM Zfr 115); *Elasmosaurus platyurus* (ANSP 10081); *Thalassomedon haningtoni* (DMNH 1588) and the Elasmosauridae indet. (MLP 82-I-8-1). The plots of the HI and BI values of MLP 14-I-20-16 are within those of *Morenosaurus stocki* among the Weddellonectia but also are within those of the giant *Thalassomedon haningtoni*. It is also interesting that the MLP 14-I-20-16 plot differs from that of MLP 82-I-8-1, the other non-aristonectine described from the upper horizons of the López de Bertodano Formation, indicating at least two types of non-aristonectine elasmosaurids in the same horizons.

The scapula of *Vegasaurus molyi* bears a ridge on the dorsal surface of the ventral ramus (O'Gorman *et al.* 2015 fig. 8B, C). A similar ridge, although slightly more rounded, is observed in MLP 14-I-20-16, but this feature is absent in other elasmosaurids such as *Callawayasaurus colombiensis*, *Styxosaurus snowii* and *Aphrosaurus furlongi* (J.P.O'G pers. obs., Otero 2016). The scapula of SGO.PV.6523 shows a high, slender and anteriorly curved dorsal process and a short ventral ramus (Otero *et al.* 2014). Unfortunately, the scapula of SGO.PV.6523 could not be compared with the scapula of MLP 14-I-20-16, because only the ventral ramus is preserved in the latter.

The ilium of MLP 14-I-20-16 differed from that of *Morenosaurus stocki*, which shows an anterior convexity, in that it seems to have a posterior knob as a result of its bended condition. The presence of a strongly bended iliac shaft is shared by *Kawanectes lafquenianum* and *Vegasaurus molyi*. However, the ilium of MLP 14-I-20-16 appears to be more gracile than that of *Vegasaurus molyi*, and additionally, the ischiadic facet and the main part of the acetabular facet are located in two distinct planes in *Vegasaurus molyi,* while this division is not observed in the ilium of *Kawanectes lafquenianum* or of MLP 14-I-20-16. The dorsal end of the ilium is slightly cranio-caudally expanded and mediolaterally compressed in MLP 14-I-20-16, in *Morenosaurus stocki* and in *Vegasaurus molyi* (Welles 1943, O'Gorman *et al.* 2015), but lateral compression and distal expansion are observed in *Kawanectes lafquenianum* (O'Gorman 2016a).

The morphology of the femora of the Weddellian elasmosaurids has been discussed previously due to the distinctive hemispherical head classically associated with '*Mauisaurus haasti*' (Welles & Greeg, 1971, Hiller *et al.* 2005, Otero *et al.* 2010). However, it has been recently stated that a hemispherical femur head is also present in *Aristonectes* (O'Gorman 2013, Otero *et al.* 2014) and this feature also seems to be present in the Maastrichtian *Morenosarus stocki* (J.P.O'G pers obs). The femoral head of MLP 14-I-20-16 is convex as in *Vegasaurus molyi* (O'Gorman *et al.* 2015) but not hemispherical as in *Aristonectes* sp. (MLP 89-III-3-1), *Aristonectes quiriquinensis* and *Kaiwhekea katiki* (O'Gorman 2013, Otero *et al.*, 2015a, J.P.O'G pers. obs.). The distal breadth/proximal breadth ratio of MLP 14-I-20-16 (~1.8) is higher than that of *Vegasaurus molyi* (~1.6), and *Kawanectes lafquenianum* (~1.6) and the MLP 82-I-8-1 (~1.5, Fig. 5B, C, D; O'Gorman *et al.* 2015, O'Gorman 2016a).

The fibula of MLP 14-I-20-16 shows a partially preserved facet for an accessory element. This type of facet is not recorded in *Kawanectes lafquenianum*, and this

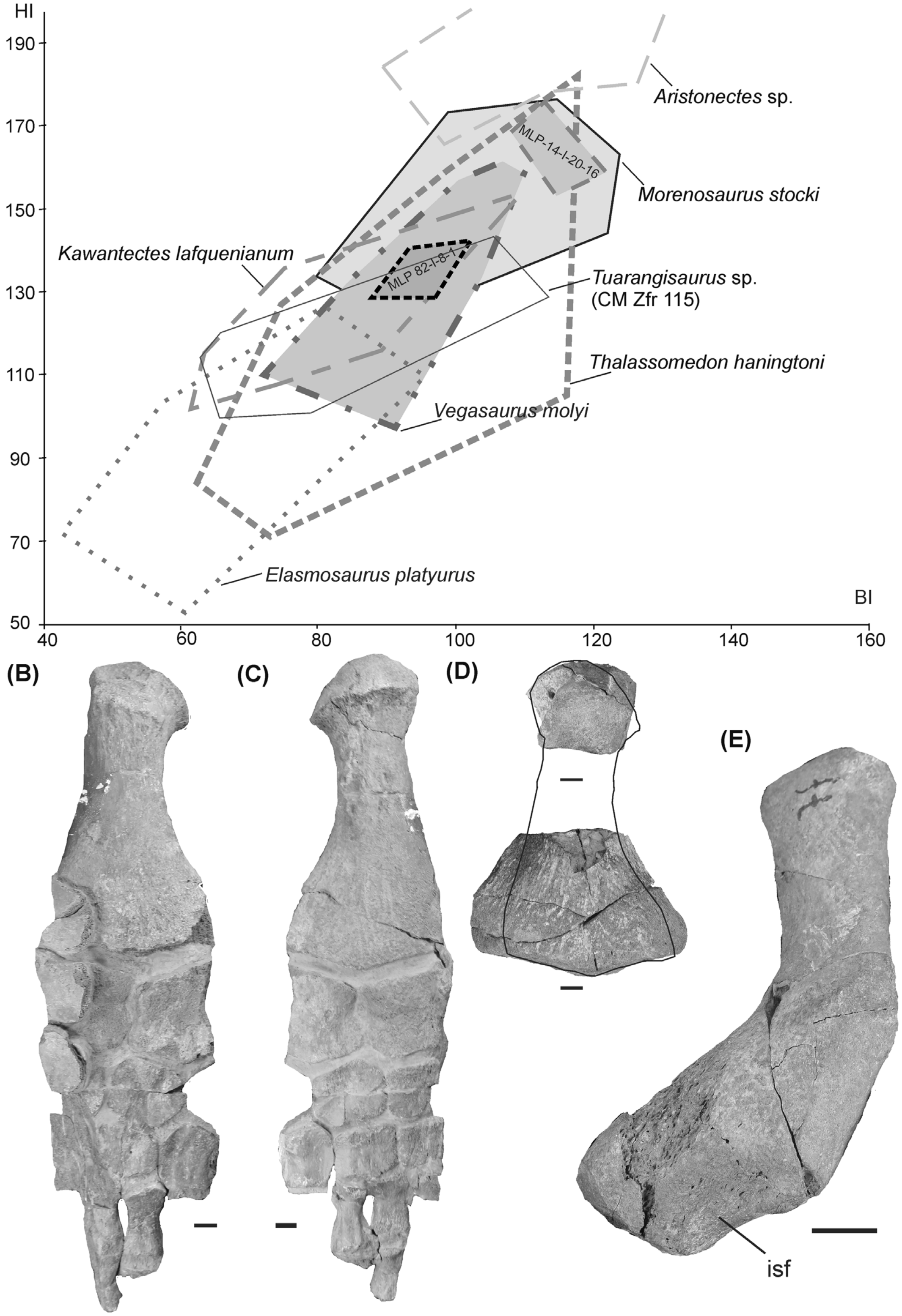

Fig. 5. Comparisons. **A**, HI (*x* values) and BI (*y* values) plot of cervical centra of MLP 14-I-20-16; *Kawanectes lafquenianum* (MCS PV 4); *Vegasaurus molyi* (MLP 93-I-5-1); *Morenosaurus stocki* (LACM 2802,); *Tuarangisaurus* sp. (CM Zfr 115); *Thalassomedon haningtoni* (DMNH 1588); *Elasmosaurus platyurus* (ANSP 10081); Elasmosauridae indet. (MLP 82-I-8-1) and *Aristonectes* sp. (MLP 89-III-3-1). B–D, Comparison of femora. B–C (MLP 82-I-8-1) on B, Dorsal and C, Ventral views; D, Comparison of MLP 82-I-8-1 silhouette and MLP 14-I-20-16 proportions; E, Right ilium of Vegasaurus molyi (MLP 93-I-5-1) in ventro medial view. Scale bar = 20 mm.

area of *Vegasaurus molyi* is not well preserved. A similar feature is clearly observed in the (DM R1529) lectotype of '*Mauisaurus haasti*', *Aristonectes quiriquinensis* and *Styxosaurus* sp. (Hiller *et al.* 2005: fig. 3, Otero *et al.* 2014: fig. 16, Otero, 2016: fig. 6F). At least one other specimen from the López de Bertodano Formation, but collected from lower Maastrichtian horizons, shows the same feature (Chatterjee & Small 1989:

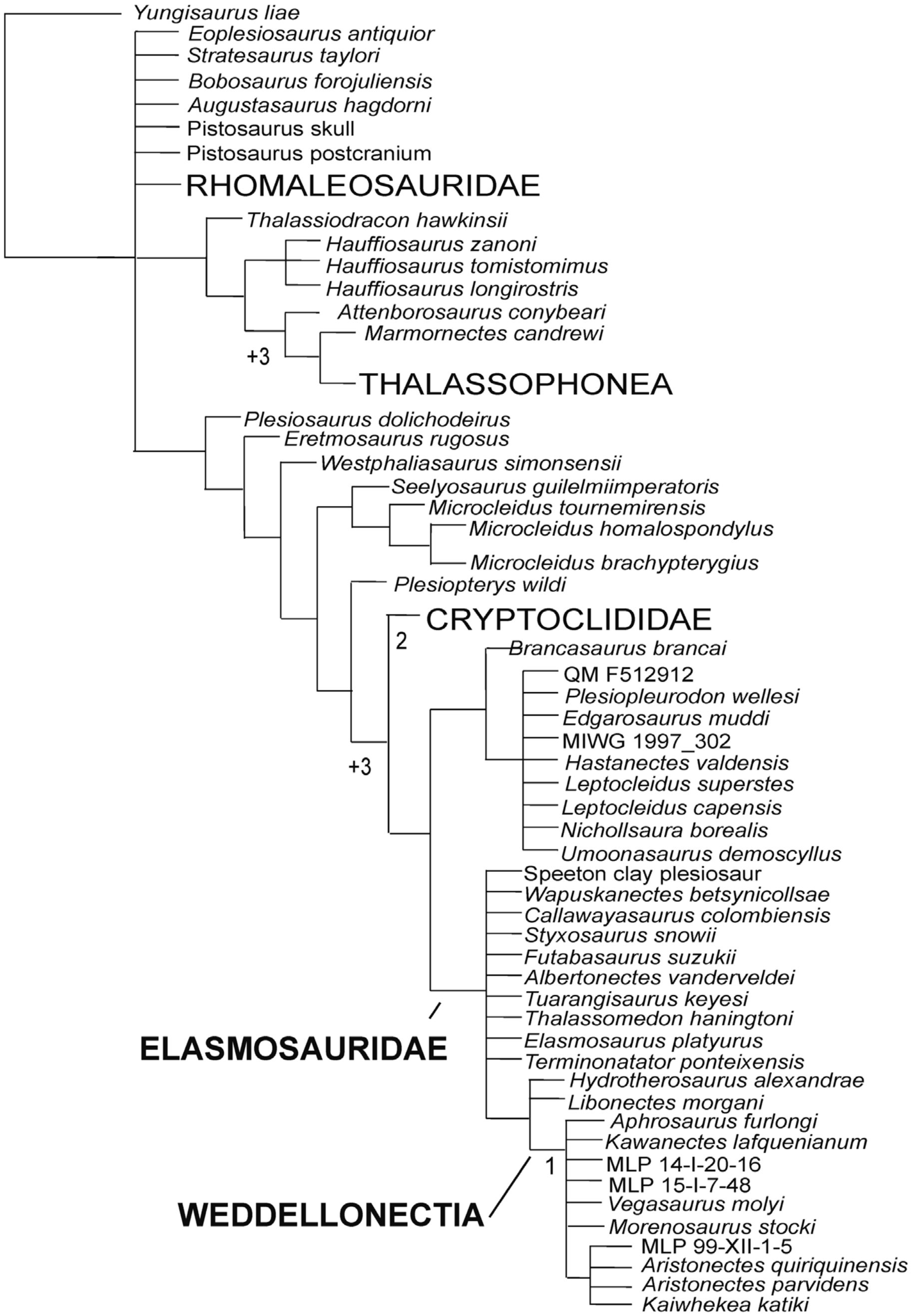

Fig. 6. Cladogram of consensus indicating the phylogenetic relationships of MLP 14-I-20-16. Bremer support is shown below selected nodes.

fig.11B). Additionally, MLP 14-I-20-16 lacks the epipodial foramen, unlike *Vegasaurus molyi*, *Morenosaurus stocki* and *Kawanectes lafquenianum* (Welles 1943, O'Gorman *et al.* 2015, O'Gorman, 2016a).

The comparison shows that MLP 14-I-20-16 differs from the lower Maastrichtian *Vegasaurus molyi* and from MLP 82-I-8-1 in the proportion of posterior cervical vertebrae, the presence of a less gracile femur and the absence of an epipodial foramen. These features indicate the presence of at least three species of non-aristonectine elasmosaurids during the Maastrichtian in the James Ross Basin area and particularly of two species recorded in the upper Maastrichtian horizons of the López de Bertodano Formation represented by MLP 14-I-20-16 and MLP 82-I-8-1. This shows a greater diversity of elasmosaurids at high latitudes prior to the massive extinction at the end of the Cretaceous.

The phylogenetic analysis recovered MLP 14-I-20-16 within the Weddellonectia clade. This is the second specimen representing non-aristonectine weddellonectian from the Upper Maastrichtian, collected from Antarctica, and the most complete one (O'Gorman & Coria 2016). An interesting result of this analysis is the inclusion of *Aphrosaurus furlongi* (Moreno Formation, California) within the Weddellonectia. However, *Morenosaurus stocki* also from the Moreno Formation was previously recovered as a Weddellonetia. Therefore, the result regarding the position of *Aphrosarus furlongi* strengthens the inferred paleobiogeographical relation between the Weddellian Province and the West coast of North America. The Weddellonectia clade is recovered with a relatively low Bremmer Support (1), probably because the unstable condition of MLP 14-I-20-16, but also indicating the conclusion must be taken with care. The results of previous phylogenetic analyses show an extremely unstable relationship within the Elasmosauridae. However, the monophyly of the aristonectine seems to be a recurrent result among the more recent analysis (Otero 2016, Sachs & Kear 2017). However, none of these include *Vegasaurus molyi* or *Kawanectes lafquenianum*, and therefore the monopyly of Weddellonectia was not tested.

Conclusions

MLP 14-I-20-16 is one of the youngest weddellonectian non-ristonectine elasmosaurids from Antarctica, and it confirms the coexistence of the aristonectines and non-aristonectines in Antarctica until the end of the Cretaceous. At least two different non-aristonectine elasmosaurids seem to be present in the upper Maastrichtian of Antarctica based on cervical proportions and posterior limbs features. *Aphrosaurus furlongi* is recovered within the Weddellonectia, reinforcing previous hypotheses about the paleobiogeographical relationship between the Weddellian Province and the west coast of North America.

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Supplemental data

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