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A new elasmosaurid specimen from the upper Maastrichtian of Antarctica: new evidence of a monophyletic group of Weddellian elasmosaurids

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A new fossil elasmosaurid specimen, MLP 15-I-7-48, from the upper Maastrichtian Sandwich Bluff Member of the López de Bertodano Formation, Vega Island, Archipelago James Ross, Antarctica, is described. The fossil is a well-preserved anterior limb, which shares with *Vegasaurus molyi* from the upper Maastrichtian of Antarctica, a concave to flat anterior margin of the humeral shaft, and with *Vegasaurus molyi* and *Aphrosaurus furlongi* from the upper Maastrichtian of California, a well-defined depression on the anterior margin of the ventral surface of the humeral shaft. A phylogenetic analysis recovered MLP 15-I-7-48 as sister group of the lower Maastrichtian *Vegasaurus molyi* within a new clade nominated as Weddellonectia: *Kawanectes lasquenianum* (*Vegasaurus molyi*; MLP 15-I-7-48) (*Morenosaurus stocki* (Aristonectinae)). This indicates that the previously proposed faunal turnover between the early and late Maastrichtian Weddellian marine reptile fauna, did not severely affect the non-aristonectine elasmosaurids. Additionally, other taxa previously considered evidence of a faunal turnover are re-evaluated.

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ELASMOSAURID plesiosaurs were a group of 'long necked' plesiosauromorphs that peaked in diversity during the Late Cretaceous (Carpenter 1999, Hiller *et al.* 2005, Sato *et al.* 2006, Vincent *et al.* 2011, Otero *et al.* 2014). The elasmosaurid record from the Weddellian Biogeographic Province (*sensu* Zinsmeister 1979; i.e., Patagonia; Western Antarctica and New Zealand) includes representatives of both aristonectine and non-aristonectine elasmosaurids (Table I).

Phylogenetic analyses of the Weddellian elasmosaurids carried out by several authors (Otero *et al.* 2012, 2014, O'Gorman *et al.* 2015, 2016) support the monophyly of the aristonectines, which are distributed through the entire Weddellian Province. Additionally, close relationships between the lower Maastrichtian *Vegasaurus molyi* and the upper Campanian–lower Maastrichtian *Kawanectes* and the aristonectine were proposed recently (O'Gorman 2016). However, a close phylogenetic relationship between the lower and upper Maastrichtian Weddellian non-aristonectine elasmosaurids has not yet been inferred, nurturing the concept of a possible faunal turnover between the early and

late Maastrichtian marine reptiles in the Weddellian Province (Consoli & Stilwell 2009, Otero *et al.* 2015). Consoli & Stilwell (2009) distinguished an 'older fauna' (middle Campanian–early Maastrichtian) comprising tylosaurines, mosasaurines, the elasmosaurid *Mauisaurus haasti* and an indeterminate polycotyloid plesiosaur, from a 'younger fauna' (late Maastrichtian) that includes aristonectine *Kaiwhekea* and the mosasaurine *Prognathodon*. In turn, Otero *et al.* (2015) proposed a turnover in the plesiosaur fauna within the Weddellian Province. Thus, a lower Maastrichtian assemblage of polycotyloids, 'extreme long-necked elasmosaurids' and 'small aristonectines' was suggested to have been succeeded by a faunal association with large aristonectines and 'plesiomorphic elasmosaurids' during the late Maastrichtian.

Here we describe a new specimen, MLP 15-I-7-48, from the Sandwich Bluff Member of the López de Bertodano Formation (upper Maastrichtian), Vega Island, Antarctica, which provides new information about the anterior limb anatomy of Weddellian elasmosaurids. Additionally, we test the hypothesis of the faunal turnover between the early and late Maastrichtian plesiosaur faunas based on the phylogenetic affinities and the stratigraphic provenance of the new specimen.

Geological setting

The Sandwich Bluff Member (SBM) of the López de Bertodano Formation represents the uppermost Cretaceous unit at Cape Lamb, southwestern Vega Island in the James Ross Archipelago, Antarctic Peninsula (Fig. 1). It overlies the upper Campanian–lower Maastrichtian Cape Lamb Member of the Snow Hill Island Formation and it underlies the Sobral? or the Hobbs Glacier Formation (Roberts *et al.* 2014). The SBM is a volcanoclastic unit that includes thin conglomerates, pebbly sandstones, sandstones and mudstones. Sedimentary structures include wave ripples and hummocky cross-stratification. Roberts *et al.* (2014) provided a detailed description of the sedimentology of the SBM. This unit was divided into 15 sub-units (SBM 1–SBM 15). Although identification of the boundaries between each subunit is not easy in the field, the specimen MLP 15-I-7–48 is considered to have been collected from SBM 11.

The SBM has yielded a rich assemblage of vertebrates that includes chondrichthyans? and teleosts (Martin & Crame 2006, Roberts *et al.* 2014), plesiosaurs and mosasaurs (Martin & Crame 2006, Martin *et al.* 2007, O’Gorman *et al.* 2010), and dinosaurs including birds (Case *et al.* 2000, Clarke *et al.* 2005). The unit’s late Maastrichtian age is based on dinoflagellate biostratigraphy (Pirrie *et al.* 1991).

Material and methods

The terminology used for the limb follows Welles (1943) and Sato (2003). A data-set was compiled based on the results of Benson & Druckenmiller (2014) and modified by O’Gorman (2016). These data were supplemented with information for two new characters (see supplementary data I) and compiled using Mezquite Software (Maddison & Maddison 2011). The final data-set (supplementary data II) was analyzed using TNT 1.5 version software (Goloboff *et al.* 2008) using a heuristic search (tree bisection reconnection, with 1000 random addition sequence replicates). The Consistency (CI) and retention RI indexes (Farris 1989) were calculated and Bremer Support (Bremer 1994) values were indicated for some nodes.

Institutional abbreviations. CM, Canterbury Museum, Christchurch, New Zealand; DM, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; LACM, Natural History Museum of Los Angeles County, Los Angeles, USA (material originally housed in the CIT, California Institute of Technology, California, USA); MLP, Museo de La Plata, Buenos Aires Province, Argentina; MCS, Museo de Cinco Saltos, Río Negro Province, Argentina; MCS, Museo de Cinco Salto, Río Negro Province, Argentina; MUC, Museo de la Universidad del Comahue, Neuquén, Argentina; OU, Otago Museum, Dunedin, New Zealand; RSM, Royal Saskatchewan Museum, Regina, Saskatchewan, Canada; SDSM, South Dakota School of Mines and Technology, South Dakota, USA; SGO, Área Paleontología, Museo Nacional de Historia Natural, Santiago de Chile, Chile; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; UCMP, University of California Paleontological Museum, San Francisco, USA.

Anatomical abbreviations. Ad, anterior depression; ca, capitulum; dc I, distal carpal I; dc II+III, distal carpal II+III; fs, concave to flat surface; fo, foramen-like depression; in, intermedium; ld, longitudinal depression; tro, trochanter, u, ulna; ul, ulnare; i, intermedium, dc II+III, ms, muscle scar; ps, pisciform; pae, posterior ecessory elements.

Systematic palaeontology

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Welles, 1943
ELASMOSAURIDAE Cope, 1869
WEDDELLONECTIA new clade

Etymology. ‘Weddello’ after the Weddell Province, from which most of the taxa have been collected and ‘nectia’ for ‘nectes’ (swimmer).

Included taxa and phylogenetic definition. Weddellonectia includes *Aristonectes*, *Kaiwhekea*; *Morenosaurus*, *Vegasaurus*, *Kawanectes*, their most recent ancestor, and all descendants.

Aristonectine elasmosaurids

Aristonectines parvidens Cabrera, 1941
Aristonectines quiroquinensis Otero, Soto-Acuña, O’Keefe, O’Gorman, Stinnesbeck, Suárez, Rubilar-Rogers, Quinzio-Sinn & Salazar, 2014
Kaiwhekea katiki Cruickshank & Fordyce, 2002
Alexandronectes zealandiensis Otero, O’Gorman, Hiller, O’Keefe & Fordyce, 2016

Non-aristonectine elasmosaurids

Tuarangisaurus keyesi Wiffen & Moisley, 1986
Vegasaurus molyi O’Gorman Salgado, Olivero & Marenssi, 2015
Kawanectes lafquenianum (Gasparini & Goñi, 1985) O’Gorman, 2016

Table 1. List of elasmosaurids from the Weddellian Biogeographic Province.

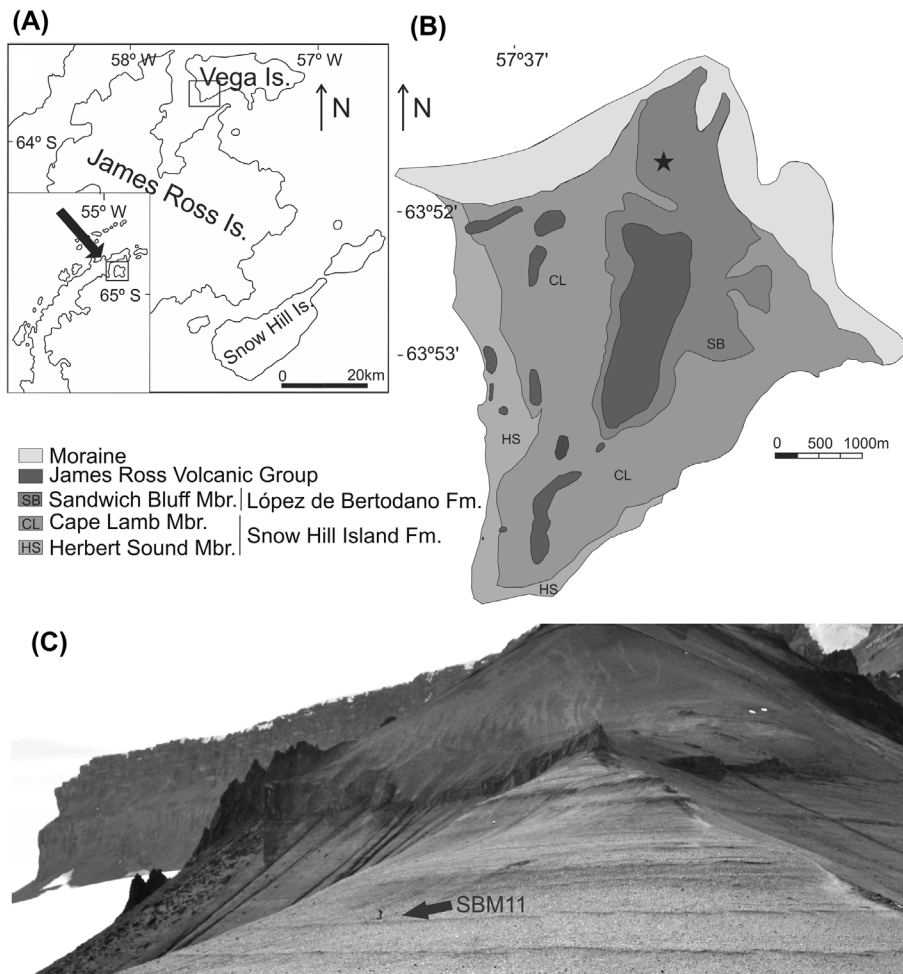


Fig. 1. Locality from which the MLP 15-I-7-48 was collected: **A**, General map; **B**, Cape Lamb geological map modified from Marensi *et al.* (2001) and **C**, panoramic photo.

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), and a 180° angle between epipodial facets in dorsal view (also shared by the poorly known lower Albian *Wapuskaneetes betsinicollae*). Additional features that characterize Weddellonectia (although convergently shared by other elasmosaurids) are: cervical vertebrae wider than long; less 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 head (absent in *K. lafquenianum* and *V. molyi*).

Weddellonectia indet. (Fig. 2)

Materials. MLP 15-I-7-48, right humerus, ulna, ulnare, intermedium, distal carpal I, distal carpal II+III, pisiform, phalanges and one rib (Fig. 2).

Locality, unit and age. Sandwich Bluff, Cape Lamb, Vega Island, Antarctica (63°51'32.6"S; 57°34'13.9"W); Sandwich Bluff Member of the López de Bertodano

Formation; approximately SBM 11 of Roberts *et al.* (2014); late Maastrichtian (Pirrie *et al.* 1991).

Description. MLP 15-I-7-48 was collected in an articulated state (Fig. 2A–J) but lacks vertebrae and, therefore, the growth stages proposed by Brown (1981) based on the fusion between the neural arches and vertebral centra could not be evaluated directly. However, other features, such as the well-defined articular faces on the limb elements indicating an advanced grade of ossification, are consistent with an adult growth stage of MLP 15-I-7-48.

The humerus is almost complete, lacking only part of the capitulum, the trochanter and part of the posterodistal projection owing to weathering (Fig. 2A–E). Although damaged, a B:L index of 75% is estimated (ca 252 mm total length; ca 183.5 mm distal breadth). The capitulum is represented by a part detached from the humeral shaft. The surface of the capitulum is convex and the articular surface is pierced by transphyseal foramina (Fig. 2B). The tuberosity is not well preserved, but the surface is completely visible in dorsal view. The entire tuberosity is slightly displaced posteriorly with respect to the axis shaft.

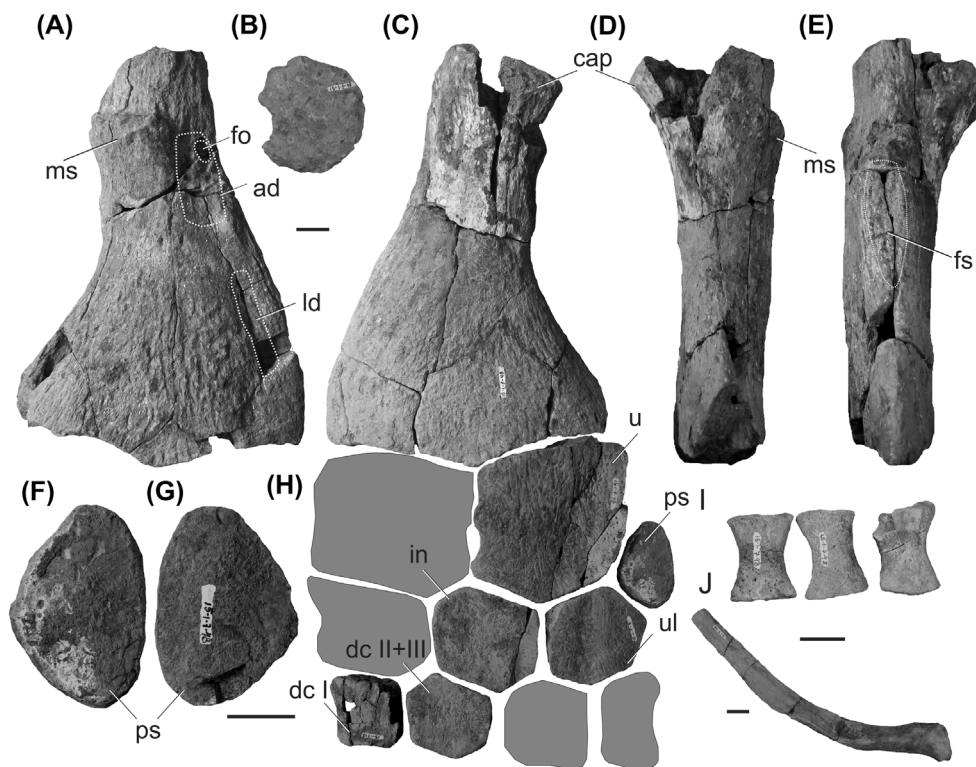


Fig. 2. Elasmosauridae indet. MLP 15-I-7-48. Right humerus in A, dorsal, B, proximal, C, ventral, D, posterior and E, anterior views. Right pisiform in F, ventral and G, dorsal views, H, epipodial mesopodia and distal carpal elements of the right forearm in ventral view. I, phalanges and J, dorsal rib. Scale bar = 20 mm.

In dorsal and ventral view, the anterior margin of the humerus is concave in its proximal half but convex in the distal one, whereas the posterior margin is concave along most of the humeral length up to the incompletely preserved posterodistal expansion (Fig. 2A, C). The dorsal surface is relatively smooth, but the ventral surface bears several muscle scars. The largest of these scars is located near the proximal end and displaced to the posterior margin. This scar is strongly convex and is limited proximally and anteriorly by a marked step (Fig. 2A). Anterior to the described scar is a large concave area pierced by a well-defined foramen-like depression (Fig. 2A). There is longitudinal depression delimited anteriorly by a convex and rugose anterior margin (Fig. 2A). In anterior view, there is a flat to slightly concave area that interrupts the general elliptical cross-section of the humeral shaft (Fig. 2E). There are irregular striae located on the ventral surface of the distal expansion (Fig. 2A). The distal end bears two well-defined and concave epipodial facets, with the radial (95 mm), only slightly longer than the ulnar (ca 92 mm).

The ulna is slightly broader than long. Distally, it is divided in two articular facets, the posterior of which is slightly shorter. The distal facets articulate with the intermedium, the ulnar and the pisiform (Fig. 2H). There is a well-defined but proximo-distally short epipodial foramen near the distal end of the anterior

margin of the ulna. The intermedium is hexagonal with its longer axis oriented anteroproximally to posterodistally. The ulnar is also hexagonal and has a well-defined posteroproximal pisiform facet (Fig. 2H). The pisiform is a subtriangular element that has two well-defined facets for articulation with both the ulna and ulnare (Fig. 2H). The distal tarsal I is rectangular. The phalanges are almost as long as wide and have a constricted middle shaft (Fig. 2I). Only a rib is preserved, probably belonging to the dorsal region (Fig. 2J).

Discussion

Comparisons

The morphology of the MLP 15-I-7-48 humerus reflects elasmosaurid affinities based on its expanded distal end (B:L ca 75%; Benson & Druckenmiller 2014, O’Gorman *et al.* 2015), whereas the broad epipodial elements suggest non-aristonectine affinities (O’Gorman *et al.* 2013, Otero *et al.* 2014). However, the incomplete state of MLP 15-I-7-48 only allows assignment to an indeterminate Weddellonectia elasmosaurid.

Previously recorded plesiosaur remains from the SBM are scarce and comprise only a juvenile referred to *Mauisaurus* (SDSM 78156, Martin *et al.* 2007, Fig. 2), currently considered non-diagnostic at the generic level (O’Gorman 2013), a caudal vertebra referred

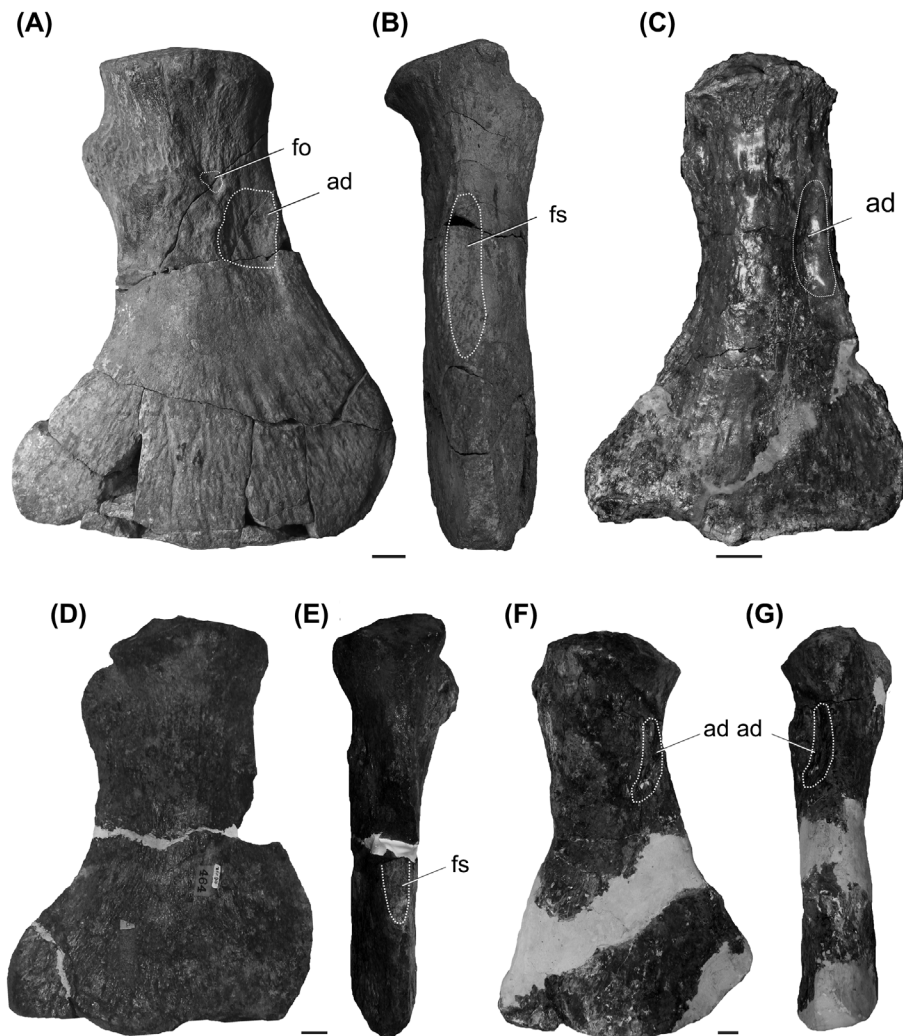


Fig. 3. Elasmosauridae humerus. A–B, *Vegasaurus molyi* (MLP 93-I-5–1) in A, ventral and B, anterior views; C, *Kawanectes lafquenianum* (MLP 71-II-13–1); D–E, CM Zfr 90 Elasmosauridae indet (CM Zfr 90) in D, ventral and E anterior views. F–G *Aphrosaurus furlongi* (LACM 2748) in F, ventral and G, anterior views. Scale bar = 20 mm.

to *Aristonectes* (O’Gorman *et al.* 2010), and an incomplete skull and a few postcranial elements referred to Plesiosauria indet. mentioned briefly by Roberts *et al.* (2014, Fig. 6F). Therefore, no direct comparison with MLP 15-I-7–48 is possible.

A recent review of elasmosaurids from the Weddellian Province revealed propodial and epipodial morphological variability (Hiller & Mannering 2005, Otero *et al.* 2014, O’Gorman *et al.* 2015, O’Gorman 2016). The tuberosity is posteriorly displaced in the humerus of *Vegasaurus molyi* and *Kawanectes lafquenianum* (O’Gorman 2016) and its posterior margin is visible even in ventral view (Fig. 3A, C), unlike MLP 15-I-7–48 where the tuberosity is less displaced posteriorly (Fig. 2A, B). The ventral surface of MLP 15-I-7–48 bears irregular striae, unlike the three well-defined sulci evident in *Vegasaurus molyi* (Fig. 3A). *Vegasaurus molyi* and MLP 15-I-7–48 share an anterior depression placed cranial to the main ventral muscle scar (Figs 2A, 3A). The anterior depression, although less marked than in MLP 15-I-7–48 and *Vegasaurus*

molyi, is also present in *Kawanectes lafquenianum* and *Aphrosaurus furlongi* (Fig. 3C, F), but absent in *Thalassomedon haningtoni*, *Callawayasaurus colombiensis*, *Wapuskaneetes betsinicollae*, *Hydrotherosaurus alexandrae* and *Albertonectes vanderveldei* (Fig. 4A, C, D, J.P. O’Gorman per. obs.). Both *Vegasaurus molyi* and MLP 15-I-7–48 share the foramen-like depression on the ventral surface. However, in the former, the foramen-like depression is located proximal to the anterior depression, whereas it is located inside its limits in MLP 15-I-7–48 (Figs 3A, 4A). *Vegasaurus molyi* and MLP 15-I-7–48 also share the anterior flat to concave surface of the humeral shaft (Figs 2E, 3B). This feature is also expressed in CM Zfr 90, an elasmosaurid humerus probably from the lower Maastrichtian of the Conway Formation (New Zealand), but it is absent in *K. lafquenianum*, *C. colombiensis*, *W. betsinicollae*, *M. stocki*, *A. furlongi*, *T. hanigtoni*, *H. alexandrae* and *A. vanderveldei* (J.P. O’Gorman pers. obs; Figs 3E, G, 4B).

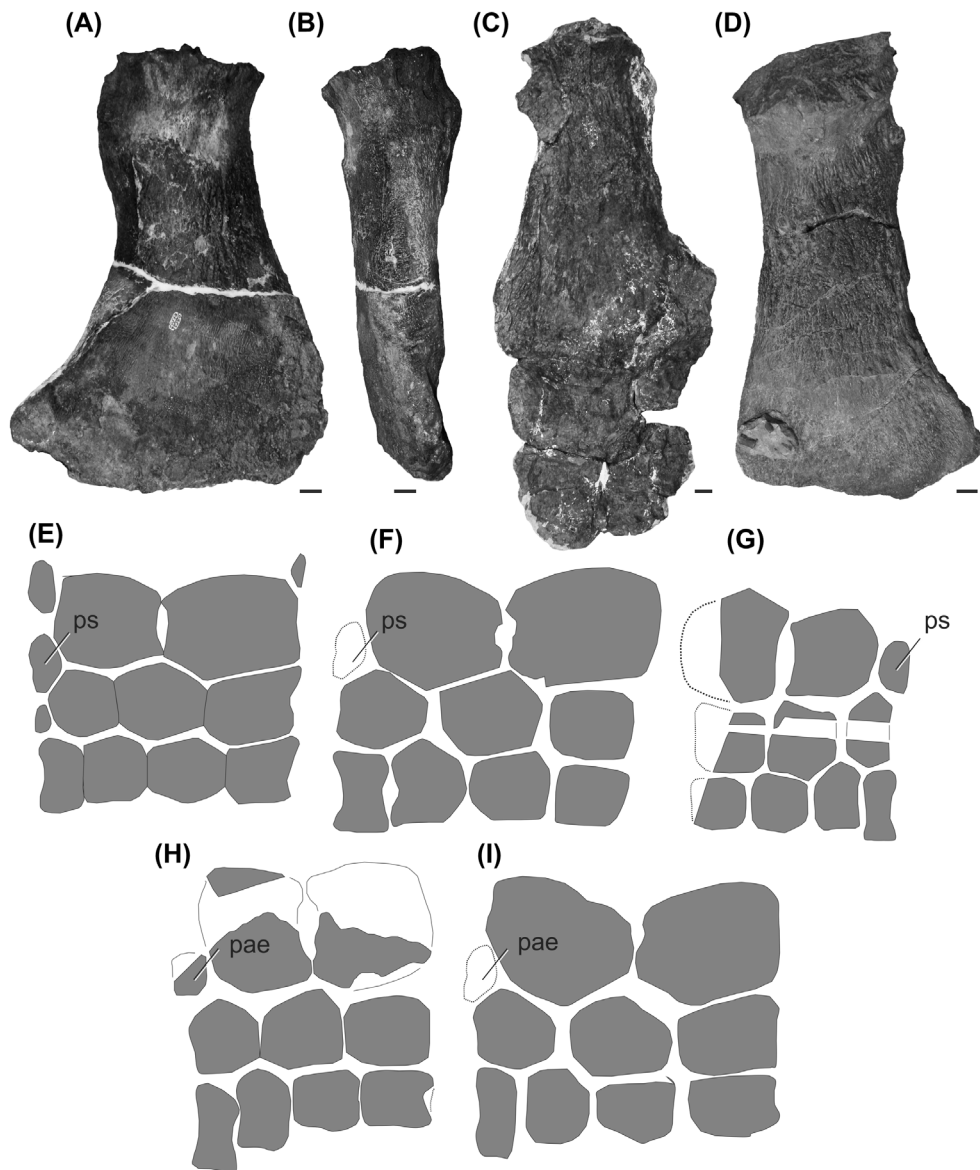


Fig. 4. **A–D**, Elasmosaurid humeri; **A–B**, left humerus of *Callawayasaurus colombiensis* (UCMP 38349) in **A**, ventral and **B**, anterior views. **C**, Right humerus of *Hydrotherosaurus alexandrae* (UCMP 33912). **D**, Right humerus of *Albertonectes vanderveldei* (TMP 2007.011.0001) Scale bar = 20 mm. **E–G**, Epipodial, mesopodial and distal carpal of Weddellian and Californian Elasmosaurids. **E**, *Morenosaurus stocki* (LACM 2802); **F**, Elasmosauridae indet (MML PV 4) from Patagonia. **G**, *Aristonectes quiriquinensis* (SGO.PV.957). **H, I**, Epipodial, mesopodial and distal tarsal of **H**, *Mauisaurus haasti* (DM R1529, lectotype) and **I** *A. quiriquinensis* (SGO.PV.957). Not to scale.

The elongated concave area, limited anteriorly by a convex and rugose anterior margin of MLP 15-I-7-48, is not evident in *Vegasaurus molyi*, in which only a slightly rugose surface is present (Fig. 3A). The humerus MLP 15-I-7-48 has a well-developed posterior expansion as represented in other non-aristonectines, such as *V. molyi*, *M. stocki*, *K. lafquenianum* and CM Zfr 90 (Welles 1943, O’Gorman *et al.* 2015). The last three have a posterior accessory facet that was possibly present in MLP 15-I-7-48 but it is impossible to be certain because of the incomplete state of that portion. The anterior knee is convex, generating a semicircular margin in *V. molyi* but only convex in MLP 15-I-7-48 because it is cut off by the radial facet (Figs 2A, 3A). Thus, the aforementioned differences indicate that MLP

15-I-7-48 can not be referred to *V. molyi* and that it represents a separate taxon.

Another feature evident in other Weddellian elasmosaurids is the large ossified pisiform, articulated in a well-developed facet that borders a deep notch between the ulna and ulnare. A similar feature has been recorded in *Aristonectes quiriquinensis* (Otero *et al.* 2014, fig. G). Other Weddellian elasmosaurids have the same features in both, the ulna and ulnare but the pisiform itself is not preserved (i.e., MML PV 4, Fig. 4F) from the upper Maastrichtian of Patagonia. Other non-Weddellian elasmosaurids do possess the pisiform element, e.g., *Morenosaurus stocki* from the upper Maastrichtian of California (Fig. 4E) and *Terminonatator ponteixensis* from the upper Campanian of Canada (Sato 2003), with the pisiform less

developed in the latter. Another interesting feature is that *A. quiriquinensis* has a postaxial accessory element in the posterior limb (Fig. 4H). It is not a pisiform, although it is an accessory ossification located in an analogous position. In turn, the *Mauisaurus haasti* lectotype (DM R1529; Fig. 4I) has a well-developed notch, probably related to the presence of a similar element. Therefore, the presence of well-developed accessory ossifications is present among the representatives of Weddellonectia but also occurs in other elasmosaurids, such as *Terminonatator ponteixensis* (Sato 2003).

Phylogenetic results and faunal turnover

The phylogenetic analysis resulted in 330 most parsimonious trees (MPTs) with lengths of 1431 steps (consistency index 0.286; retention index 0.672). The strict

consensus tree is illustrated with Bremer support below some nodes (Fig. 5). MLP 15-I-7-48 was recovered within the clade *Kawanectes lafquenianum* ((MLP 15-I-7-48, *Vegasaurus molyi*) (*Morenosaurus stocki* (Aristonectinae))). The synapomorphies of the Weddellonectia clade are 233 (0→1); postaxial accessory ossicle articulating with the humerus (indicated by a posterior accessory articular facet in the humerus) and 248 (0→1), angle between epipodial facets in dorsal view = 180°.

These phylogenetic relationships were previously observed in Aristonectinae, which are recorded at least from the early Maastrichtian up to the K/Pg boundary (O’Gorman *et al.* 2013, 2014, Otero *et al.* 2014), indicating close phylogenetic relationships between the early and late Maastrichtian Weddellian elasmosaurids of the Weddellonectia clade.

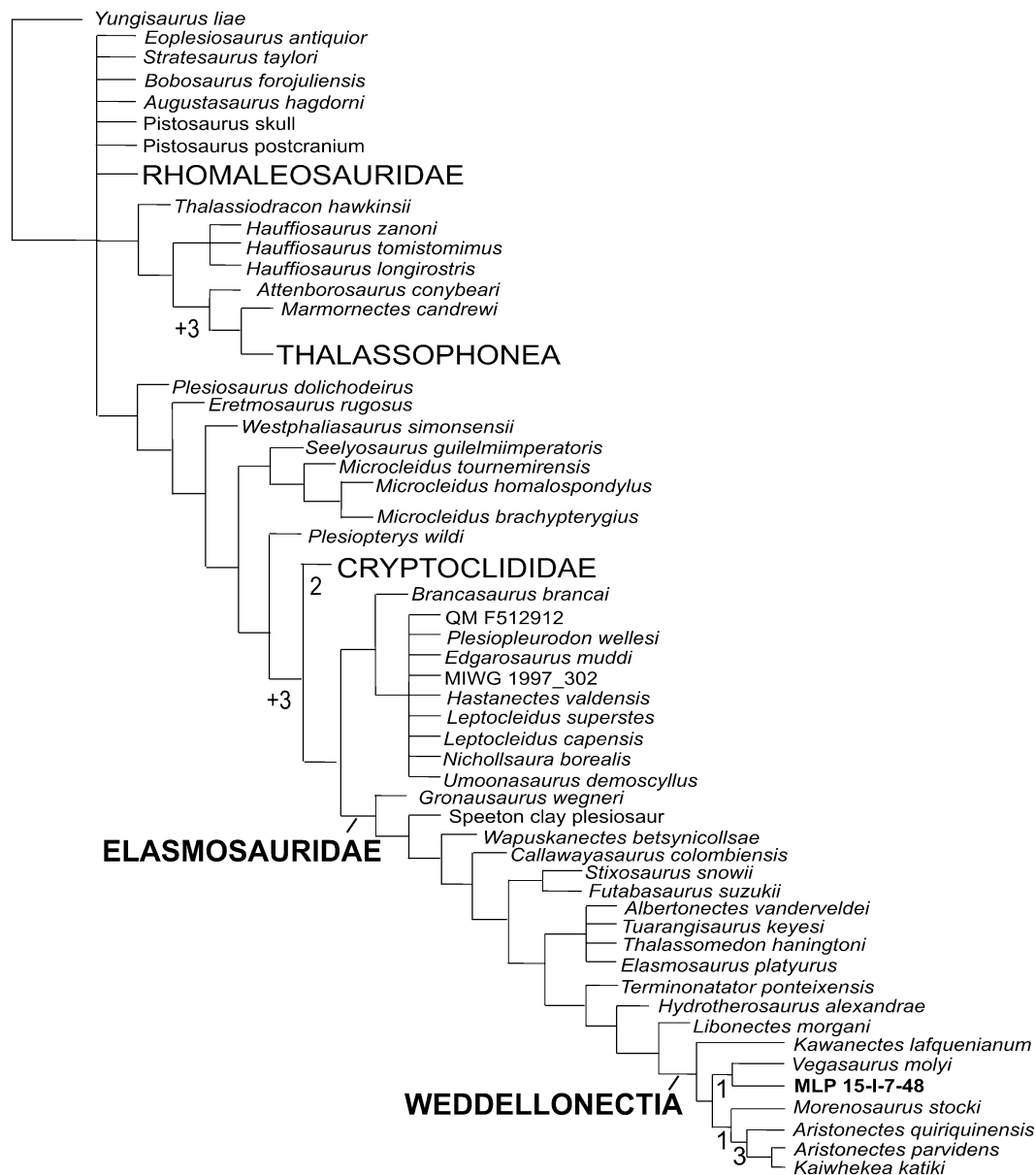


Fig. 5. Cladogram showing the phylogenetic relationships of MLP 15-I-7-48. Bremer support is shown below selected nodes.

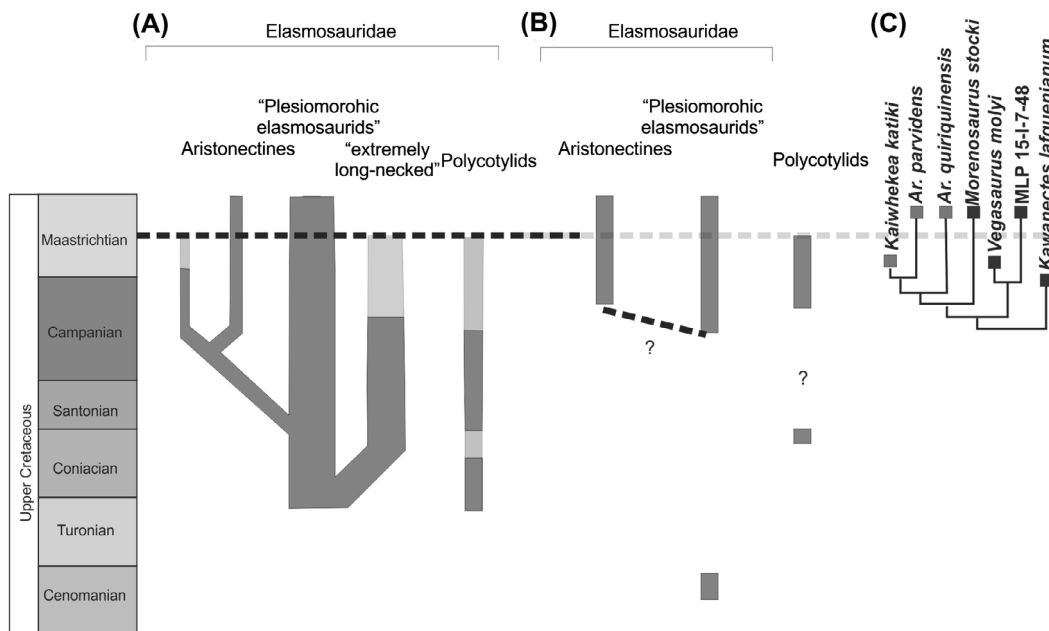


Fig. 6. Weddellian plesiosaur faunal changes during the Late Cretaceous and at the early/late Maastrichtian transition. A, Otero *et al.* (2015), B, modified from Otero *et al.* (2015) based on the phylogenetic results shown in C.

Among elasmosaurids, two types of neck elongation pattern are recorded: the ‘extreme long-necked elasmosaurids’ of Otero *et al.* 2015 (=elongate group of O’Keefe & Hiller 2006) and plesiomorphic elasmosaurids of Otero *et al.* 2015 (=non-elongate group of O’Keefe & Hiller 2006). The former are characterized by the extremely height VLI values (ranging between 60 to 100); average vertebral length index (125–138) and possession of some mid-cervical vertebrae with vertebral length index (Brown 1981) higher than 150.

The disappearance of the ‘extreme long necked’ elasmosaurids *sensu* Otero *et al.* (2015) (=‘elongate group’ *sensu* O’Keefe & Hiller 2006) is based on the interpretation that MUC Pv 92, MCS PV 4 and MLP 71-II-13-1, from Lago Pellegrini, Argentinean Patagonia (holotype of *Kawanectes lafquenianum* and referred material) are members of the ‘extreme long necked’ (Otero *et al.* 2015). However, Otero *et al.* (2016) and O’Gorman 2016 indicated that *Kawanectes lafquenianum* is not a member of the ‘extreme long necked’ and, therefore, this group was not present in Patagonia.

Another of the indicators of the faunal turnover mentioned by Otero *et al.* (2015) regarding the disappearance of polycotyliids from the Atlantic margin of Patagonia after the early Maastrichtian also needs careful consideration. The only polycotyliid from Patagonia comes from the marginal marine (lagoonal, estuarine) Allen, Los Alamitos and La Colonia formations (Gasparini & Spalletti 1990, O’Gorman *et al.* 2011, O’Gorman & Gasparini 2013, O’Gorman 2015). All the specimens from these formations probably belong to *Sulcusuchus erraini*, although some of them are not diagnostic. Thus, the disappearance of *Sulcusuchus erraini* might be related more to an environmental

change from marginal marine (e.g., estuarine) to fully marine conditions during the second stage of the late Maastrichtian Atlantic transgression (Page *et al.* 1999).

The evidence indicates that: 1, at least one late Maastrichtian elasmosaurid (MLP 15-I-7–48) from the Weddellian province has, close phylogenetic affinities with the early Maastrichtian *Vegasaurus molyi* and other weddellonectians; 2, the elasmosaurid members of the ‘extreme long necked’ elasmosaurids were not present in Patagonia at all; and 3, the disappearance of *S. erraini* might be related to a local environmental change during the late Maastrichtian. These three characteristics indicate that the plesiosaur faunal turnover between the early and late Maastrichtian, if it existed as a major faunal change, did not severely affect the elasmosaurid fauna as was previously assumed, and provides a new general view of the changes in the plesiosaur fauna of the Weddellian Province (Fig. 6B, C).

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Disclosure statement

No potential conflict of interest was reported by the authors.

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