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First record of Polycotylidae (Sauropterygia, plesiosauria) from the Upper Cretaceous of Antarctica

Fernando E. Novas [a, b], Julia S. D'Angelo [a, *], José P. O'Gorman [b, c], Federico L. Agnolín [a, d], Juan M. Lirio [e], Marcelo P. Isasi [a, b]

[a] Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470 (C1405DJR), Buenos Aires, Argentina
[b] Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)
[c] División Paleontología Vertebrados, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s/n., B1900FWA, La Plata, Argentina
[d] Fundación de Historia Natural "Félix de Azara", Universidad Maimónides, Hidalgo 775 (C1405BDB), Buenos Aires, Argentina
[e] Dirección Nacional del Antártico - Instituto Antártico Argentino, Cerrito 1248, Buenos Aires 1010, Argentina

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ABSTRACT

In the present paper we report the incomplete skeleton of an indeterminate polycotylid that includes the articulated pelvic girdle. The material was collected from the Alpha Member of the Santa Marta Formation (upper Coniacian–lower Campanian) on James Ross Island, Antarctic Peninsula. The specimen is referred to the Polycotylidae on the basis of its very elongate ischia and rimmed anterior and posterior articular surfaces of the dorsal vertebrae. Additionally, the caudal vertebrae show confluent parapophyses and neural arch facets. The present report constitutes the first record for polycotylids in Antarctica, being an important addition to the fossil marine reptile diversity. Polycotylids are a scarce component of the Weddellian herpetofauna, which are dominated by aristonectine and non–aristonectine elasmosaurids. In contrast, in Northern Hemisphere assemblages, polycotylids are an important component of the plesiosaur diversity. The scarcity of polycotylids may constitute another distinctive feature of Weddellian plesiosaur faunas.

1. Introduction

Plesiosaurs are a diverse cosmopolitan group of Mesozoic marine reptiles (Carpenter, 1996; O'Keefe, 2004; Benson and Druckenmiller, 2014). During the Late Cretaceous the long–necked elasmosaurids and the short–necked polycotylids where the most diverse and abundant plesiosaurs (O'Keefe, 2004; Vincent et al., 2011; Benson and Druckenmiller, 2014; Otero et al., 2015).

Polycotylids were small to medium sized short–necked longirostrine plesiosaurs interpreted as viviparous fast–swimming predators (Carpenter, 1996; Adams, 1997; O'Keefe and Chiappe, 2011). The biochron of polycotylids spans from Aptian (Kear, 2003; Druckenmiller and Russell, 2009) to Maastrichtian times (Gasparini and de la Fuente, 2000; Sato et al., 2005; Salgado et al., 2007; O'Gorman and Gasparini, 2013). Most species come from the Western Interior Seaway of North America (Carpenter, 1996; Sato, 2005; Schmeisser McKean, 2012). In contrast, the Southern Hemisphere record is scarce (Welles and Gregg, 1971; Kear, 2003). In South America polycotylids are only represented by the latest Cretaceous genus *Sulcusuchus* Gasparini and Spalletti, 1990 and indeterminate taxa (Gasparini and de la Fuente, 2000; Salgado et al., 2007; O'Gorman and Gasparini, 2013).

In Antarctica, the plesiosaur record is, to date present, restricted to elasmosaurids (Del Valle et al., 1977; Gasparini et al., 1984; Chatterjee and Small, 1989; Kellner et al., 2011; O'Gorman, 2012; O'Gorman et al., 2013; Otero et al., 2012; O'Gorman et al., 2015). However, a recent finding of isolated vertebrae described as belonging to an indeterminate plesiosaur by Kellner et al. (2011), and later as possible related to Polycotylidae by O'Gorman (2012).

Recent exploration in Antarctica resulted in the discovery of the incomplete skeleton of a plesiosaur that includes the articulated pelvic girdle and which may be referred to the Polycotylidae clade mentioned by D'Angelo et al. (2008). The goal of the present paper is to describe and discuss the palaeobiogeographical implications of this specimen, which represents the first non-elasmosaurid plesiosaur from the entire continent.

Institutional abbreviations– **KUVP**, University of Kansas, Natural History Museum and Biodiversity Research Center, Kansas,

* Corresponding author.
E-mail address: juliasdangelo@gmail.com.ar (J.S. D'Angelo).

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USA; **MACN Pv**, Paleontología de Vertebrados Collection, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; **MNA**, Museum, of Northern Arizona, USA; **SM**, Strecker Museum, Baylor University, Waco, Texas, USA; **YPM**, Yale Peabody Museum, New Haven, Connecticut, USA.

Anatomical abbreviations— **cap**, capitulum; **cr**, crest; **d**, dorsal; **fo**, foramen; **hf**, hemal facet; **il**, iliac facet; **ilf**, facet for the ilium; **is**, ischium; **na**, neural arch; **pa**, parapophysis; **pf**, pedicellar facet; **pu**, pubis; **tro**, trochanter; **v**, ventral.

2. Geological setting

The James Ross sub–Basin (Del Valle et al., 1992) is located at the northeastern margin of the Antarctic Peninsula (Fig. 1). The Marambio Group comprises the Santa Marta, Snow Hill Island, and López de Bertodano formations (Olivero, 2012). The Santa Marta Formation is divided into the Alpha and Beta Members (Olivero, 1986, 2012). MACN Pv 19.781 was collected in Alpha Member of Santa Marta Formation, in levels of fine to medium-grained greenish sandstones located 25 m above the boundary between the Hidden Lake and Santa Marta formations. The fauna of this Formation recorded in the stratigraphic unit includes chondrichthians, teleosts (Kriwet et al., 2006; Otero et al., 2014a,b), turtles (de la Fuente et al., 2010), the mosasaur *Taniwhasaurus antarcticus* (Novas et al., 2002; Fernández and Martin, 2007), and plesiosaurs (D'Angelo et al., 2008; Kellner et al., 2011; O'Gorman, 2012).

3. Systematic paleontology

PLESIOSAURIA Owen, 1860.
PLESIOSAURIA de Blainville, 1835.
POLYCOTYLIDAE Cope, 1869.
Polycotylidae gen. et sp. indet.

Referred Material—MACN Pv 19.781, postcranial skeleton composed of four dorsal vertebral centra, nine caudal centra, both pubes, ischia and femora, numerous isolated ribs and gastroliths.

Locality and Horizon—Brandy Bay (63° 49′S; 57° 53′W), James Ross Island, N.E. Antarctic Peninsula. Lower part of Lachman Crags (Alpha) Member of the Santa Marta Formation (upper Coniacian, Upper Cretaceous; Mc Arthur et al., 2000).

4. Description

The neural arches of dorsal vertebrae are fused to the centrum, whereas neural arches of caudal vertebrae are unfused. Because plesiosaurians had a cranio-caudal pattern of neurocentral fusion, the condition observed along the vertebrae of the MACN Pv 19.781 is indicative of a young subadult individual (Brown, 1981).

Dorsal Vertebrae—The dorsal vertebrae are slightly weathered (Fig. 2). The vertebral centra are strongly amphicoelous, as in *Dolichorhynchops* and *Polycotylus* (Carpenter, 1996), being different from the Elasmosauridae, in which these are only gently concave to nearly flat (Salgado et al., 2007). The dorsoventral height of the centra is greater than their craniocaudal length (Table 1). The lateral side of the vertebral centra are craniocaudally concave. The cranial and caudal articular surfaces are bounded by rims of bone like in other polycotylids (Salgado et al., 2007). A variable amount of nutritive foramina are located at half–length of each vertebral body, as occurs in *Thililua* and *Trinacromerum* (Bardet et al., 2003; Carpenter, 1996).

Caudal Vertebrae—Nine caudals are preserved. The caudal centra are higher than long (Table 1). The pedicellar facets are large and occupy most of the dorsal surface of the vertebra in the dorsal vertebrae (Fig. 2F, H). The parapophyses are subcircular in shape

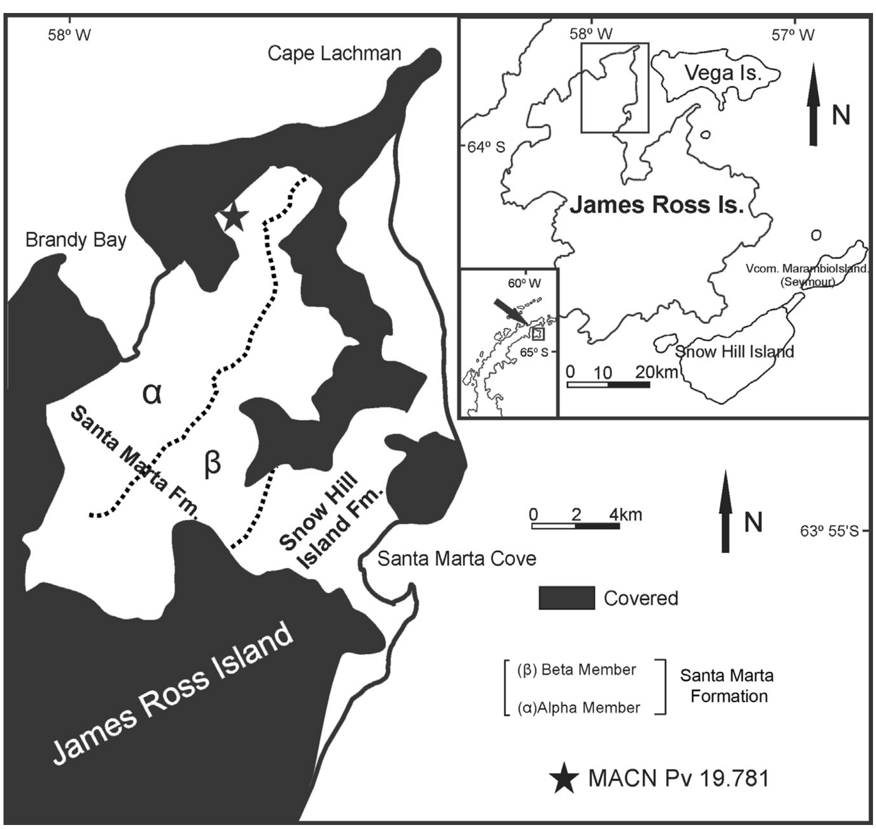

Fig. 1. Map showing the locality were MACN Pv 19.781 was collected. (Illustration modified from Olivero, 1992; Mc Arthur et al., 2000; O'Gorman, 2013).

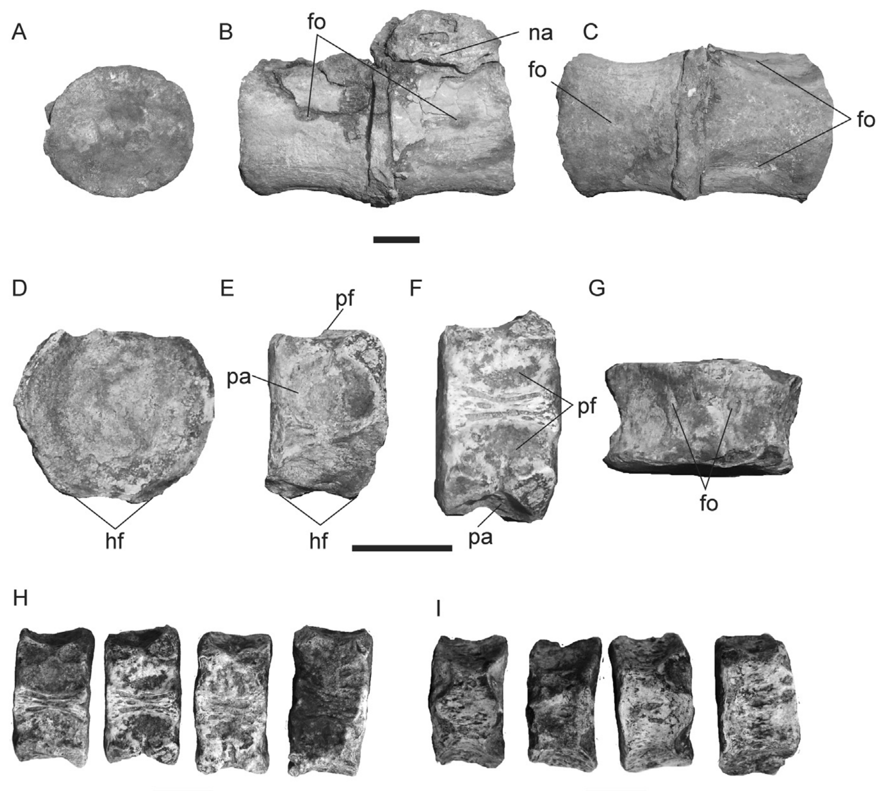

Fig. 2. MACN Pv 19.781 Polycotylidae indet. **A**–**C**, dorsal vertebrae in: **A** cranial; **B**, left lateral; and **C**, ventral views. **D**–**G**, caudal vertebral centrum in: **D**, cranial; **E**, left lateral; **F**, dorsal; and **G**, ventral views. **H**–**I** caudal centra in: **H**, dorsal, and **I**, ventral views. Scale bar equals 60 mm.

and they are dorsally confluent with the neural facet (Fig. 2E, H), a condition unknown in elasmosaurids. In the latter, the parapophyses are more ventrally located and do not contact the neural arches (Carpenter, 1996). The hemal facets are located both on the anterior and posterior sides of the centra (Fig. 2I) differing from the condition of *Dolichorhynchops osborni* and *Palmulasaurus quadratus*, in which the chevrons are located almost exclusively on the posterior margin of the centra (Carpenter, 1996; Albright et al., 2007; O'Keefe, 2008). Ventrally, there are one or two nutritive foramina (Fig. 2I). Additional smaller foramina are present on the lateral surface of the centrum ventral to the parapophysis.

Pubes—The pubes are strongly craniocaudally elongate (Fig. 3A) as in other polycotylids, with the exception of *Palmulasaurus* and *Eopolycotylus* (Fig. 4 E–I) (Albrigth et al., 2007). The cranial margin of the bone is damaged and it is impossible to determine its true outline. The caudal margin is strongly concave and forms the anterior margin of the pelvic fenestra (Fig. 3A). There is a sharp, but low crest along the median pubic symphysis, and the symphysis protrudes into the pelvic fenestra forming a caudomedial process. This process lacks contact with the ischium, therefore a pelvic bar is absent (Fig. 3B).

Table 1
Selected measurements of dorsal and caudal vertebrae of MACN Pv 19.781. Measurement taken in millimeters.

Vertebra	Length	Height	Breadth
Dorsal 1	43.27	51.17	54.05
Dorsal 2	41.03	49.60	55.25
Dorsal 3	43.65	49.76	49.05
Dorsal 4	42.19	41.20	50.50
Caudal 1	33.02	38.10	19.36
Caudal 2	33.56	33.50	19.24
Caudal 3	30.24	35.78	19.33
Caudal 4	33.51	43.23	19.20
Caudal 5	32.45	39.15	20.03
Caudal 6	31.32	34.2	19.47
Caudal 7	31.58	36.23	20.14

Ischia—As is other polycotylids the ischia are anteroposteriorly elongated (length/width equals 2.4) and even longer than the pubis (Williston, 1908; O'Keefe, 2001, 2004, Fig. 4). Its anteroposterior length is 34 cm, being 13% longer than the pubic length. The ischia of MACN Pv 19.781 are gracile as in *Polycotylus* and *Trinacromerum* but differ from the more robust condition of *Palmulasaurus* and *Eopolycotylus* (Carpenter, 1996 Albrigth et al., 2007). The acetabular ramus has a small iliac facet on its caudolateral margin (Fig. 3D). In symphysial view the ischia are dorsally convex, at the level of the acetabular ramus, but becomes caudally concave (Fig. 3C, D). Additionally, the dorsal surface of the posterior ramus is transversely concave, and conforms a long longitudinal canal along the ischiatic symphysis (Fig. 3E). This results in a V–shaped ischiadic symphysis when viewed in cross–section.

Femur—Femora are elongate, being more gracile than other polycotylids (Fig. 5). The width/length ratio is 0.48 while in other polycotylids this value is lower (e.g., *Dolichorhynchops bonneri*, *Dolichorhynchops tropicensis*; *Eopolycotylus rankini, Palmulasaurus quadratus*; Adams, 1997; following O'Keefe, 2008; Albright et al., 2007: Figs. 5 and 13; Schmeisser, 2012: Fig. 4G–I; Fig. 10). The capitulum is strongly convex and is separated from the femoral shaft by a constricted neck (Fig. 5, A–C). It lacks the hemispherical proximal head present in aristonectines and other derived xenopsarians (Otero et al., 2015). The trochanter is almost flat and proximally confluent with the capitulum, whereas in aristonectines both are separated by a deep concavity (Otero et al., 2015). The cranial margin of the femoral diaphysis is almost straight while the caudal one is markedly concave. The distal end of the femur is

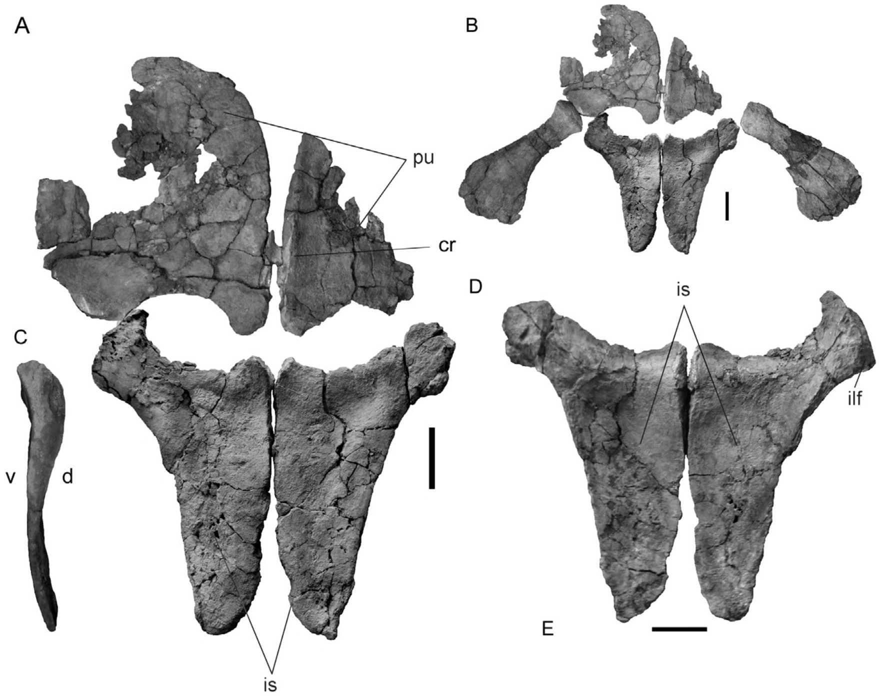

Fig. 3. MACN Pv 19.781 Polycotylidae indet. **A**, pelvic girdle in ventral view; **B** pelvic girdle showing the articulation with both femora; **C**, symphyseal view; **D** ischia in dorsal view; **E**, cross section of distal ischial rami. Scale bar equals 20 mm.

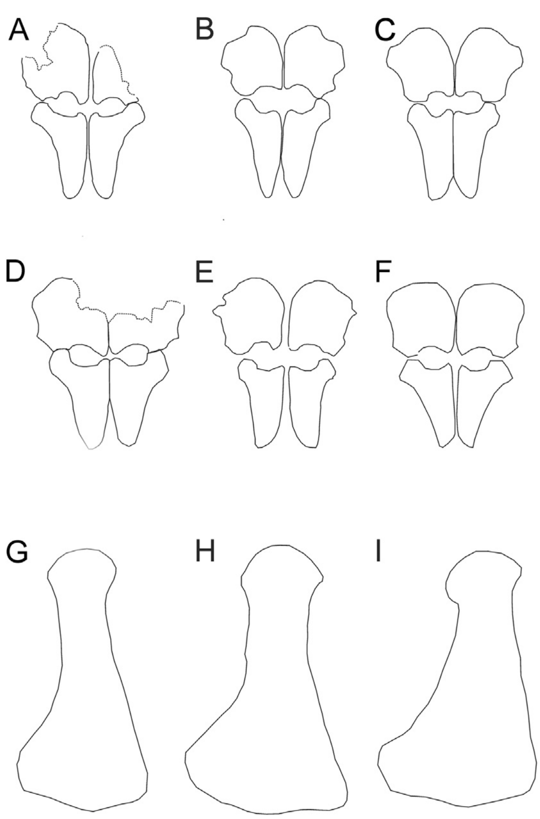

Fig. 4. **A**–**F**, polycotylid pubes and ischia in ventral view: **A**, MACN Pv 19.781; **B**, *Polycotylus latippinis*; **C**, *Trinacromerum bentonianum*; **D,** *Palmulasaurus quadratus***; E,** *Eopolycotylus rankini*; **F,** *Eopolycotylus rankini*; **F**, *Dolichorhynchops bonneri*; **G**–**I**, femora: **G**, MACN Pv 19.781; **H**, *Dolichorhynchops bonneri*; **I**, *Palmulasaurus quadratus* (modified from Carpenter, 1996; Adams, 1997; Albright et al., 2007). Not to scale.

lateromedially compressed and craniocaudally expanded. The posterodistal corner of the femur is not well preserved and the number of facets for accessory elements is not certain.

Gastroliths—15 gastroliths were collected within ventral surface of the pelvic girdle (Fig. 5). This is a low number when compared with previously reported elasmosaurids (Cinimurri and Everhart, 2001; Cerda and Salgado, 2008; O'Gorman et al., 2012, 2013) and polycotylids (Schmeisser and Gillette, 2009). However, because the specimen is incompletely preserved, it is possible that a high number of gastroliths were lost due to taphonomical biases. The long axis of the gastroliths is between 15 mm and 40 mm. The pebbles are well rounded with smooth polished surfaces (Fig. 5D).

5. Discussion

MACN Pv 19.781 shows diagnostic features of the Polycotylidae such as elongated ischia that are craniocaudally longer than the pubes (Williston, 1908; O' Keefe, 2001; Ketchum and Benson, 2010), and dorsal vertebrae with strongly concave articular surfaces surrounded by a thick rim of bone (Salgado et al., 2007). Additionally, the presence of caudal vertebrae with parapophyses confluent with pedicellar facets is a feature absent in Late Cretaceous elasmosaurids, but present in some polycotylids, such as *Dolichorhynchops* (Sato, 2005). Regrettably, the incomplete nature of MACN Pv 19.781 precludes its referral beyond the family level.

The occurrence of gastroliths associated with MACN Pv 19.781 is relevant because this association has been recorded only a few times among polycotylids (Cicimurri and Everhart, 2001; Schmeisser and Gillette, 2009). However, taphonomical bias does not allow analysis of the gastrolith cluster of MACN Pv 19.781 using sedimentological indexes, as employed by other authors (Schmeisser and Gillette, 2009).

The Weddellian Biogeographic Province included the seas of Antarctica, New Zealand, and South America and was characterized by plants and animals with ecological affinities in common, developed mainly from the Late Cretaceous to late Eocene

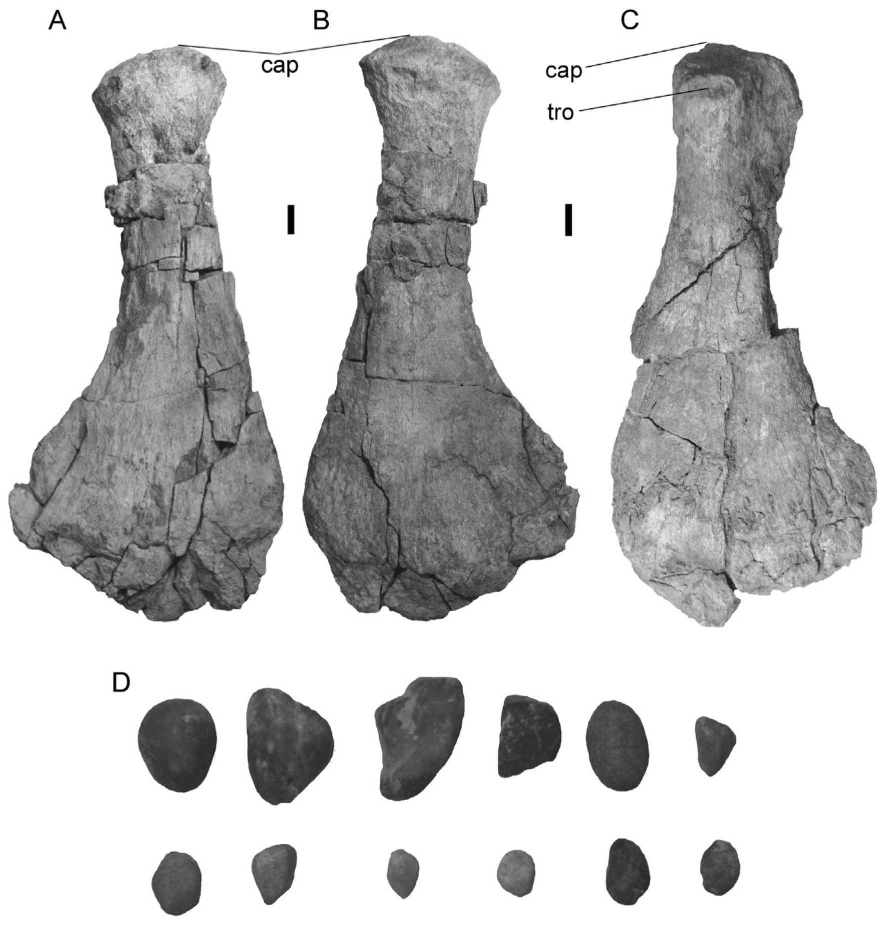

Fig. 5. MACN Pv 19.781 Polycotylidae indet. **A**–**C**, right femur in: **A**, dorsal and **B**, ventral views; **C**, left femur in dorsal view; **D**, gastroliths. Scale bar equals 20 mm.

(Zinsmeister, 1979; Novas et al., 2002; Gasparini et al., 2003b; Martin and Fernández, 2007; O'Gorman et al., 2013a,b; Otero et al., 2015).

The Weddellian record of polycotylids remains meagre, in contrast with abundant elasmosaurid reports (Welles and Gregg, 1971; O'Gorman, 2012, 2013; Otero et al., 2014a,b). In Argentina only four polycotylid specimens have been collected (Gasparini and Spalletti, 1990; Gasparini and de la Fuente, 2000; Gasparini et al., 2003a; Salgado et al., 2007; O'Gorman et al., 2011; O'Gorman and Gasparini, 2013), and scarce fragmentary remains have been reported from New Zealand (Welles and Gregg, 1971; Wiffen and Moisley, 1986). MACN Pv 19.781 represents the first representative of the clade in the Cretaceous of Antarctica, and constitutes an important addition to the known distribution of Southern Hemisphere polycotylids. The scarcity of polycotylids from the Weddellian Biogeographic Province is, together with the abundance of aristonectine elasmosaurids (Gasparini et al., 2003b; O'Gorman et al., 2013a,b; Otero et al., 2014a,b; Otero et al., 2015), one of the most distinctive features of the Late Cretaceous plesiosaur record from the Weddellian Province, contrasting with the Northern Hemisphere record (Carpenter, 1996). The present report greatly improves our knowledge of Weddellian plesiosaur faunas and constitutes an important addition to the still poorly known Late Cretaceous plesiosaur assemblages of the Southern Hemisphere.

6. Conclusions

The specimen here described is referred to the plesiosaurian clade Polycotylidae. This report constitutes the first record for the group in Antarctica and the oldest plesiosaur known so far, coming from Coniacian levels of the Santa Marta Formation. Polycotylids are a scarce component of the Weddellian herpetofauna, which contrast with abundant record in Northern Hemisphere assemblages. Its scarcity may represent another distinctive feature of Weddellian plesiosaur faunas.

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