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

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Elasmosauridae; Antarctica; Late Cretaceous.

Abstract
Elasmosaurs are recorded for the first time in the Lachman Crags Member (Beta Member) of the Santa Marta Formation (lower Campanian) and in the Herbert Sound Member of the Snow Hill Island Formation (upper Campanian). These are the first elasmosaurs from James Ross Island, Antarctic Peninsula. These records greatly improve our knowledge of the taxonomic diversity of plesiosaurs of the Santa Marta Formation and Herbert Sound Member of the Snow Hill Island Formation, and extend the lower limit of the record of Elasmosauridae in Antarctica to the lower Campanian, making this the oldest record of an Antarctic elasmosaur.

Plesiosaurs are a clade of reptiles adapted to the marine environment. Their record extends from the Upper Triassic to the Upper Cretaceous and their geographical distribution is cosmopolitan, having been recorded in all continents, including Antarctica (Welles 1952, 1962; Persson 1963; del Valle et al. 1977; Brown 1981; Carpenter 1996, 1999; Bardet et al. 1999; Fostowicz-Frelik & Gazdicki 2001; O’Keefe 2001, 2004; Kear 2003; Ketchum & Benson 2010; Vincent et al. 2011).

The stratigraphic range of the Elasmosauridae, one of the best represented plesiosaur groups, is under debate because it depends largely on which genera are considered as belonging to this family (Ketchum & Benson 2010). According to different authors, their stratigraphic range could be Toarcian–Maastrichtian (Brown 1993), Valanginian–Maastrichtian (O’Keefe 2001) or Aptian–Maastrichtian (Ketchum & Benson 2010). However, all authors agree that Elasmosauridae became cosmopolitan during Late Cretaceous times. In the present article, the Elasmosauridae family is understood in a general way in the sense used by Ketchum & Benson (2010).

Elasmosaurs are characterized by the development of a cervical region with (1) a high number of cervical vertebrae (reaching 72 in Elasmosaurus platyurus); (2) an elongated vertebral centra; (3) vertebral centra with lateral ridges; and (4) dumbbell-shaped articular faces in Late Cretaceous genera, for example, Hydrotherosaurus alexandrae, Morenosaurus stocky and Terminonatator ponteicensis (Welles 1943, 1962; Brown 1981, 1993; Bardet et al. 1999; Carpenter 1999; Gasparini & Salgado 2000; O’Keefe 2001, 2004; Sato 2003). The combination of these characters allows the identification at family level, even when the material consists only of cervical vertebrae. Note that only (3) is considered a synapomorphy of Elasmosauridae sensu Ketchum & Benson (2010; see Wiffen & Moisley 1986; Werner & Bardet 1996; Gasparini & Salgado 2000; O’Gorman et al. 2011).

Antarctic plesiosaurs were recorded for the first time in the 1970s (del Valle et al. 1977). Mostly elasmosaurs, they were discovered in James Ross Basin. However, elasmosaurs have never been recorded in Campanian levels in Antarctica (Table 1). During fieldwork organized by the Instituto Antártico Argentino and undertaken in the summer of 1986, Dr. E. Olivero collected two juvenile plesiosaurs referable to Elasmosauridae in the Herbert Sound Member of the Snow Hill Island Formation of James Ross Island (Figs. 1, 2). Currently housed at the Museo de La Plata (with identification numbers preceded by MDP 1986–... and others).
by “MLP”), these specimens are important because they are the first records of plesiosaurs in the Herbert Sound Member. More recently, during fieldwork in 2011, organized by the Instituto Antártico Argentino and with the participation of scientists from the MLP, the Universidad Nacional del Comahue and the Museo Municipal Carmen Funes in Plaza Huincul, Elasmosauridae remains were collected from the Lachman Crags Member of the Santa Marta Formation. The aim of this article is to describe the material collected in 1986 and in 2011, discuss their elasmosaurid affinity and highlight the implications of these records for our knowledge of Antarctic plesiosaurs.

**Geological setting**

The Marambio Group, which crops out mostly in the James Ross Archipelago, was deposited during the upper Coniacian–Danian interval (Macellari 1988; Ineson 1989; McArthur et al. 2000; Crame et al. 2004) or Santonian–Danian (Olivero & Medina 2000). This article follows the stratigraphy proposed by Olivero et al. (2008) in which

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**Table 1** Plesiosaur records from Antarctica. The stratigraphy follows Olivero et al. (2008).

| Assignment | Locality | Stratigraphy | Age | Reference |
|------------|----------|--------------|-----|-----------|
| Aristonectes parvidens (Mortuneria) | Marambio Island (Seymour) | López de Bertodano Fm. ("molluscan units") | late Maastrichtian | Chatterjee & Small 1989 |
| Aristonectes sp. | Vega Island (Cape Lamb) | López de Bertodano Fm. (Sandwich Bluff Member) | late Maastrichtian | O’Gorman et al. 2010 |
| Aristonectes cf. parvidens | Vicecomodoro Marambio Island (Seymour) | López de Bertodano Fm. ("molluscan units") | late Maastrichtian | O’Gorman, Olivero et al. 2012 |
| Mauisaurus sp. | Vega Island (Cape Lamb) | Snow Hill Island Fm. (Cape Lamb Member) | late Campanian-early Maastrichtian | Martin et al. 2007 |
| Elasmosauridae indet. | Marambio Island (Seymour) | López de Bertodano Fm. ("molluscan units") | late Maastrichtian | Chatterjee & Small 1989 |
| Elasmosauridae indet. | Marambio Island (Seymour) | López de Bertodano Fm. ("molluscan units") | late Maastrichtian | Martin & Crame 2006 |
| Elasmosauridae indet. | Marambio Island (Seymour) | López de Bertodano Fm. ("Rotularia units") | late Maastrichtian | Gasparini et al. 1984 |
| Elasmosauridae indet. | Marambio Island (Seymour) | López de Bertodano Fm. ("Rotularia units") | late Maastrichtian | Chatterjee & Small 1989 |
| Elasmosauridae indet. | Marambio Island (Seymour) | López de Bertodano Fm. ("Rotularia units") | late Maastrichtian | Fostowicz-Frelic & Gazdzicki 2001 |
| Elasmosauridae indet. | James Ross Island (Santa Marta Cove) | Snow Hill Island Fm. (Herbert Sound Member) | late Campanian | this article |
| Elasmosauridae indet. | James Ross Island (Monolitic Lake) | Santa Marta Fm. (Beta Member) (upper part of the Lachman Crags Member) | early Campanian | this article |
| Elasmosauridae indet. | Vega Island (Cape Lamb) | Snow Hill Island Fm. (Cape Lamb Member) | late Campanian–early Maastrichtian | O’Gorman et al. 2008 |
| Elasmosauridae indet. | Vega Island (Cape Lamb) | Snow Hill Island Fm. (Cape Lamb Member) | late Campanian–early Maastrichtian | O’Gorman, Gasparini et al. 2012 |
| Cf. Elasmosauridae | Marambio Island (Seymour) | López de Bertodano Fm. ("molluscan units") | late Maastrichtian | Martin & Crame 2006 |
| Polycotylidae indet. | James Ross Island (The Naze) | Snow Hill Island Fm. (Cape Lamb Member) | late Campanian–early Maastrichtian | D’Angelo et al. 2008 |
| Elasmosauridae indet. | Vega Island (Cape Lamb) | Snow Hill Island Fm. (Cape Lamb Member) | late Campanian–early Maastrichtian | del Valle et al. 1977 |
| Polycotylidae indet. | James Ross Island (The Naze) | Snow Hill Island Fm. (Cape Lamb Member) | late Campanian–early Maastrichtian | del Valle et al. 1977 |
| Plesiosauria indet. | James Ross Island (The Naze) | Snow Hill Island Fm. (Cape Lamb Member) | early Maastrichtian | Martin & Crame 2006 |
| Plesiosauria indet. | Marambio Island (Seymour) | López de Bertodano Fm. ("molluscan units") | late Maastrichtian | Martin & Crame 2006 |
| Plesiosauria indet. | James Ross Island (Branday Bay) | Santa Marta Fm. (Alpha Member) (Lachman Crags Member) | late Coniacian? | Santonian–early Campanian |

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the Marambio Group is divided into the Santa Marta, Snow Hill Island, Haslum Crag and López de Bertodano formations, and the Herbert Sound Member is considered to be the lower part of the Snow Hill Island Formation. The Santa Marta Formation, which roughly corresponds to the Lachman Crags Member proposed by Crame et al. (1991) (Figs. 1, 2), is divided into the Alpha and Beta members (Olivero et al. 1986; Olivero et al. 2008). The Alpha member is characterized by the abundance of tuffaceous sandstones and mudstones, whereas the Beta member includes interbedded conglomerates and carbonatic bioclastic layers (Olivero 1992). The Herbert Sound Member, now included in the Snow Hill Island Formation (Olivero et al. 2008), is composed of quartz sandstone and mudstone and a mudstone-dominated upper section (Olivero 1992).

The Santa Marta Formation (Alpha and Beta members) was deposited in a mid-to-outer shelf environment and the Herbert Sound Member of the Snow Hill Island Formation was deposited in a shallow marine environment (Crame et al. 1991; Olivero et al. 2008). The Santa Marta Formation represents (Alpha and Beta members) the late Coniacian–early Campanian interval (McArthur et al. 2000). Olivero & Medina (2000) interpreted that the Santonian–Campanian boundary is located in the lower to middle levels of the Alpha Member and the lower Campanian–upper Campanian boundary in the upper levels of the Beta Member (Olivero 1992; Olivero et al. 2008) and, therefore, the Herbert Sound Member is late Campanian in age (Olivero & Medina 2000).

Bivalves, ammonites (Olivero & Medina 2000), chondrichthyes, teleosts (Kriwet et al. 2006), turtles (de La Fuente et al. 2010) and plesiosaurs (D’Angelo et al. 2008; Kellner et al. 2011) have been recorded in the Santa Marta Formation. In the Herbert Sound Member of the Snow Hill Island Formation, bivalves, ammonites (Olivero & Medina 2000), chondrichthyes and teleosts (Kriwet et al. 2006) have also been recorded, as well as mosasaurs (Novas et al. 2002; Martin & Fernandez 2007; Fernandez & Gasparini 2012) and dinosaurs (Gasparini et al. 1987; Gasparini et al. 1996; Salgado & Gasparini 2006).
Material and methods

Fossils were prepared using Micro Jack and ME 9100 model jackhammers (Paleotool; Brigham City, UT, USA). The linear measurements were taken using an electronic caliper accurate to 0.01 mm. The vertebral indices used are those proposed by Welles (1952), which take into account the centrum length (L), the ratio between height (H) and length of the centrum (100*H/L), and the ratio between breadth (B) and length of the centrum (100*B/L). In addition, the ratio between the breadth and height (100*B/H) was considered. In this work, both breadth and height were measured on the posterior articular face of the centrum. The vertebral length index (VLI = L/[0.5*(H+B)]) (Brown 1981) was also used. Furthermore, the categories of ontogenetic development proposed by Brown (1981), based on the fusion of the neural arch to the vertebral centrum (neural closure), were employed to distinguish between “adult” and “juvenile” conditions.

Systematic paleontology

1. Sauropterygia Owen 1860
2. Plesiosauria de Blainville 1835
3. Plesiosauroidea Welles 1943
4. Elasmosauridae Cope 1869
5. Gen. and spp. indet.

Materials

MLP 11-II-20-4, one cervical vertebra preserving a partial rib; MLP 86-X-28-3, two cervical vertebrae; MLP 86-X-28-(2-6), 10 posterior cervical vertebrae articulated with three pectoral vertebrae, part of two dorsal vertebrae, ribs and indeterminate fragments.

Locality and horizon

MLP 11-II-20-4, Monolithic Lake (S 63° 52’ 38.4”, W 57° 54’ 36”), James Ross Island, James Ross Archipelago, Antarctica. Santa Marta Formation, lower part of Beta Member (middle levels of Lachman Crags Member), lower Campanian (McArthur et al. 2000; Olivero & Medina 2000) (Figs. 1, 2).

MLP 86-X-28-3 and MLP 86-X-28-(2-6), Santa Marta Cove, locality of QF stratigraphic section of Olivero (1992) (S 63° 55’ 36.4”, W 57° 51’ 0.8”), James Ross Island, James Ross Archipelago, Snow Hill Island Formation, Herbert Sound Member, upper Campanian (McArthur et al. 2000; Olivero & Medina 2000) (Figs. 1, 2).

Description

MLP 11-II-20-4

The vertebral centrum is longer than it is high and broader than it is long (Table 2). The articular faces are slightly concave, but their exact shape cannot be determined because they are damaged (Fig. 3b). The lateral surface has a conspicuous lateral ridge (Fig. 3a). There are two slightly anteroposteriorly elongated foramina in the ventral surface of the vertebral centrum and, in all likelihood, there was at least another one, but this cannot be determined because the ventral surface is not...
The vertebral centra are slightly longer than high and broader than long (Table 2). The articular faces are slightly dumbbell-shaped (Fig. 3d). One vertebral centrum has lateral ridges (Fig. 3c). The parapophyses are formed by a ventrolateral depression (Fig. 3c). On the ventral surface, there are two elongated ventral foramina separated by a blunt keel (Fig. 3e). The neurocentral suture of this specimen is open, so it is a juvenile sensu Brown (1981).

**MLP 86-X-28-3**

The MLP 86-X-28-3 vertebrae have slightly elongated lateral surfaces with respect to the lateral surface of the second pre-pectoral vertebra (the ventral surface of the second pre-pectoral vertebra is damaged) there are one or two extra smaller foramina in addition to the second and third pre-pectoral vertebrae (the ventral surface of the second pre-pectoral vertebra is damaged) there are one or two extra smaller foramina in addition to the two main ones (Fig. 3g). The neural spines in the most anterior cervical vertebrae are anteroposteriorly expanded and posteriorly displaced with respect to the centroid. The pectoral region consists of three vertebrae in which the passage of the rib facet from the vertebral centrum to the neural arch can be observed (Fig. 3f). The dorsal region is represented only by two fragments of vertebral centra. This specimen is considered a juvenile because the neurocentral suture is open in all vertebrae.

**MLP 86-X-28-(2-6)**

This specimen includes 10 cervical and 3 pectoral vertebrae, which were originally articulated (Fig. 3e). In addition, there are two dorsal vertebrae not articulated with the sequence. However, since all the material was collected together, they probably belong to the same individual. All of the vertebral centra are as long as high and both measurements are exceeded by breadth (Table 2). The VLI of the cervical vertebrae decreases cranio-caudally in the vertebral sequence (Table 2; Fig. 4). The articular faces are flat and suboval (Fig. 3i). The lateral surfaces of the centra are anteroposteriorly slightly concave. The parapophyses are suboval and cranio-caudally elongated in the most anterior cervical vertebrae. From the sixth pre-pectoral vertebra, the parapophyses drift dorsally towards the lateral surface and are more dorsoventrally elongated (Fig. 3f). Ventrally, there are two foramina separated by a blunt keel in the most anterior vertebrae (Fig. 3h), but in the first and third pre-pectoral vertebrae (the ventral surface of the second pre-pectoral vertebra is damaged) there are one or two extra smaller foramina in addition to the two main ones (Fig. 3g). The neural spines in the most anterior cervical vertebrae are anteroposteriorly expanded and posteriorly displaced with respect to the centroid. The pectoral region consists of three vertebrae in which the passage of the rib facet from the vertebral centrum to the neural arch can be observed (Fig. 3f). The dorsal region is represented only by two fragments of vertebral centra. This specimen is considered a juvenile because the neurocentral suture is open in all vertebrae.

**Discussion**

In the MLP 11-II-20-4 vertebra, the neurocentral suture is closed and not visible (Fig. 3a, b), so it is considered to be an adult individual. Because MLP 86-X-28-3 and MLP 86-X-28-(2-6) show open neurocentral sutures, they are considered juveniles. Therefore, among the described specimens, there are individuals of different ontogenetic stages.

The specimen MLP 11-II-20-4 possesses a vertebral centrum longer than it is high and lateral ridges and is therefore referred to Elasmosauridae. Because the articular surfaces are badly damaged, it cannot be determined whether the articular faces were originally dumbbell-shaped. However, the elongation of the vertebral centrum and the lateral ridge is a combination of characters that has not been reported in any other families of Upper Cretaceous plesiosaurs and is exclusive to Elasmosauridae (Werner & Bardet 1996; Gasparini & Salgado 2000).

The MLP 86-X-28-3 vertebrae have slightly elongated centrum, dumbbell-shaped articular faces and lateral ridges. This exclusive combination of characters allows us to refer MLP 86-X-28-3 to Elasmosauridae also.

The vertebral centra of MLP 86-X-28-(2-6) are as long as high and do not have dumbbell-shaped articular faces or lateral ridges. The absence of elongation of the vertebral centra, lateral ridge and dumbbell-shaped articular faces in MLP 86-X-28-(2-6) may be due to the

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**Table 2** Measurements of specimens MLP 11-II-20-4, MLP 86-X-28-3 and MLP 86-X-28-(2-6). Measurements of vertebral centra (in mm): length (L); height (H); breadth (B); height index (HI) 100*H/L; breadth index (BI) 100*B/L; breadth-height index (BHI) 100*B/H; and vertebral length index (VLI) L/0.5*(H+B).

| Specimen       | L     | H     | B     | HI    | BI    | BHI   | VLI  |
|----------------|-------|-------|-------|-------|-------|-------|------|
| MLP 11-II-20-4 | 104   | 80    | 118   | 77    | 113   | 148   | 1.05 |
| MLP 86-X-28-3  | 40    | 38    | 56    | 95    | 140   | 147   | 0.85 |
| MLP 86-X-28-(2-6) | 45    | 46    | 62    | 102   | 138   | 135   | 0.83 |

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ontogenetic stage and their position in the cervical region. This interpretation receives support from the posterior part of the cervical series of some elasmosaurs, which lacks certain characteristics, such as the centrum elongation, the lateral ridge and the dumbbell-shaped articular faces, although these characteristics are present in the anterior and middle cervical vertebrae (for example, in *Mauisaurus haastii*, *Morenosaurus stocki*; Welles 1943, 1952, 1962; Hiller et al. 2005). Therefore, the absence of typical characters of the Elasmosauridae in MLP 86-X-28-(2-6) does not necessarily exclude this specimen from this group because the sequence of MLP 86-X-28-(2-6)
corresponds to the 10 first pre-pectoral vertebrae (the last 10 cervical vertebrae). Moreover, the limited elongation of MLP 86-X-28-(2-6) may be due to its juvenile condition (Welles 1952, 1962; O’Keefe & Hiller 2006). Another element to take into account is that the genus Aristonectes has been recorded in the James Ross Basin, López de Bertodano Formation, upper Maastrichtian (Chatterjee & Small 1989; Gasparini et al. 2003; O’Gorman et al. 2010). The phylogenetic relationships of Aristonectes parvidens have been debated recently and it has been located within the Elasmosauridae (Ketchum & Benson 2010) or Aristonectidae (O’Keefe & Street 2009). Although the revision of the phylogenetic relationships of Aristonectes is not the aim of this article, it is still necessary to determine whether the material described here could be referred to A. parvidens. The anterior cervical vertebrae of A. parvidens (Cabrera 1941) are dumbbell-shaped (middle and posterior cervical vertebrae are not known) and their centra are only moderately elongated with ventral foramina separated by a ventral keel (Gasparini et al. 2003). Figure 4 shows a plot of the VLI of the cervical vertebrae of four Upper Cretaceous plesiosaurid adults, including the holotype of Aristonectes parvidens (Cabrera 1941), and three elasmosaur species: M. haasti (Hector 1874); Campanian–Maastrichtian of New Zealand and Chile (Hiller et al. 2005; Otero et al. 2010); M. stocki (Welles 1943); Maastrichtian of California (Welles 1962); and MLP 93-I-5-1, an Elasmosauridae represented by a complete postcranial skeleton currently under study by the author from the Cape Lamb Member of the Snow Hill Island Formation (lower Maastrichtian levels). Figure 4 shows that in M. haasti, M. stocki and MLP 93-I-5-1 the last 10 cervical vertebrae have VLI values similar to those of the cervical vertebrae of MLP 86-X-28-(2-6). This similarity is not surprising since ontological changes in the VLI are less marked in the posterior cervical vertebrae than in the anterior vertebrae (O’Keefe & Hiller 2006). In contrast, in A. parvidens the VLI decreases in the first 19 anterior cervical vertebrae (Fig. 4). Assuming that the cervical region of A. parvidens has a structure similar to that observed in other plesiosaurids (maximum VLI in the middle and anterior cervical vertebrae, and a marked decrease at the posterior cervical region; Brown 1981; O’Keefe & Hiller 2006), the VLI of the posterior cervical vertebrae of A. parvidens would be substantially less than 0.8 and therefore it would be considerably less elongated than MLP 86-X-28-(2-6). Furthermore, MLP 86-X-28-(2-6) is a juvenile and its vertebral centra may have not yet reached their maximum elongation and, therefore, maximum VLI values at the time of death. Consequently, the vertebrae of MLP 86-X-28-(2-6) cannot be referred to as A. parvidens.

The morphology of MLP 86-X-28-(2-6) does not correspond to the morphology observed in Polycotylidae, in which the vertebral centra are not elongated and the articular surfaces are subcircular and strongly depressed (Williston 1908; Storrs 1999; Sato & Storrs 2000; Salgado et al. 2007). Therefore, the specimen MLP 86-X-28-(2-6) can be reasonably assigned to Elasmosauridae.

On the basis of our present knowledge, the morphology of isolated cervical vertebrae cannot be used for taxonomic assignment below the family level in Elasmosauridae (O’Keefe & Hiller 2006). Hence, a generic determination of the described material is currently impossible.

Previous records of plesiosaurs in the Santa Marta Formation come from the Alpha Member (lower levels of the Lachman Crags Member) and include materials referred to Polycotylidae (MACN 19.781, Museo Nacional de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; D’Angelo et al. 2008) and Plesiosauria indet (MN 7163-V at The Museu Nacional de la Universidade Federal de Rio de Janeiro; Kellner et al. 2011). The vertebrae reported by Kellner et al. (2011) differ from the specimen MLP 11-II-20-4 (described in this article) in that the vertebral centrum of specimen MLP 11-II-20-4 is subequal in length and height and its articular faces are flat and dumbbell-shaped or elliptical, whereas the vertebrae described by Kellner et al. (2011) (MN 7163-V) show the vertebral centrum to be higher than long (the length of the vertebral centrum is inferred because the vertebrae are poorly preserved, although each vertebra has preserved its anterior or posterior half), with strongly concave circular articular faces. The presence of short cervical vertebrae together with strongly concave articular faces that are subcircular in shape is a combination characteristic of Polycotylidae (Williston 1908; Storrs 1999; Sato & Storrs 2000; Salgado et al. 2007). Therefore, specimen MN 7163-V may be referred to as Polycotylidae in accordance with the possibility stated by Kellner et al. (2011), making this specimen the second record of Polycotylidae in the Santa Marta Formation (D’Angelo et al. 2008).

These new records of Elasmosauridae increase our knowledge of the Plesiosauria diversity in the Santa Marta Formation. The Elasmosauridae are now recorded in three of the four formations of the Marambio Group: Santa Marta (upper Coniacian–Santonian–lower Campanian), Snow Hill Island (upper Campanian–lower Maastrichtian) and López de Bertodano (upper Maastrichtian). In contrast, the Polycotylidae are only recorded in the Santa Marta Formation (D’Angelo et al. 2008) (Table 1). Extending the record of Elasmosauridae from Antarctica to the lower Campanian, the new material...
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described in this article constitutes the oldest record of this group in Antarctica.

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