



Gastroliths associated with an *Aristonectes* specimen (Plesiosauria, Elasmosauridae), López de Bertodano Formation (upper Maastrichtian) Seymour Island (*Is. Marambio*), Antarctic Peninsula

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ABSTRACT

The occurrence of a large gastrolith set associated with a specimen referred to *Aristonectes* sp. is reported here for the first time. The specimen MLP 89-III-3-1 comes from Seymour Island (*Is. Marambio*), Antarctic Peninsula, López de Bertodano Formation (upper Maastrichtian). The gastrolith cluster is composed of 793 elements (534 in their presumed original state and about 259 that are broken). The gastroliths are described using sedimentological indices. The mean major axis of the gastroliths is 21 mm, the mean Maximum Projection Sphericity is 0.71 and the standard deviation is 0.11. According to Krumbin’s classification, 43.3% are spheroidal (equant), 14.9% are cylindrical (prolate), 34.7% are discoidal and 7.1% are bladed (laminar). Following Powers’ roundness categories, 10.1% are very rounded, 29.2% are rounded and 60.7% are subrounded. The mean Maximum Projection Sphericity value indicates a fluvial origin for the gastroliths. Petrographically, the gastroliths comprise rhyolitic volcanites (56.2%), quartz vein material (27.8%), subarkose arenites (14.5%) and laminated, radiolarian-rich mudstones and tuffs (1.5%). The potential geological sources are several formations from the Antarctic Peninsula, such as the Upper Jurassic Antarctic Peninsula Volcanic Group (rhyolitic volcanites), the Permian–Triassic Trinity Peninsula Group (subarkose arenites), and the Kimmeridgian–Berriasian Ameghino Formation (radiolarian-rich mudstones and tuffs). All these formations crop out within about 100 km of the locality where the specimen was collected. We also discuss how gastroliths were ingested, concluding that the ingestion was not done individually. Finally, this record of gastroliths provides evidence against the hypothesis of their use for buoyancy control.

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1. Introduction

Gastroliths (stomach stones) are hard objects without caloric value that were ingested by an animal. In the particular case of vertebrates, gastroliths are always rock fragments and therefore have been referred to as geo-gastroliths (Wings, 2007). The features

of gastroliths (i.e., mass, shape, roundness and texture) are related to their function and other factors such as the environment of origin, the rock type, the time of retention in the gastrointestinal tract and the wear rate (Cerdeña and Salgado, 2008; Cicimurri and Everhart, 2001; Darby and Ojakangas, 1980; Everhart, 2000; O’Gorman et al., 2012, 2013b; Schmeisser and Gillette, 2009; Wings, 2007).

The function of gastroliths in plesiosaurs is still controversial and has generated several hypotheses (see discussion in Wings, 2007). The most often cited hypotheses are those that discuss either their use in buoyancy control or in the digestive process, the latter being the most widely accepted by recent authors (Cerdeña and Salgado, 2008; Cicimurri and Everhart, 2001; Everhart, 2000).

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Gastroliths have been documented in association with several families of plesiosaurs (Brown, 1904; O’Keefe et al., 2009; Sato and Storrs, 2000; Schmeisser and Gillette, 2009; Welles and Bump, 1949; Williston, 1893, 1894, 1904). The work of Darby and Ojakangas (1980) established a method of analysing sets of gastroliths by a detailed sedimentological description. This methodology allows analysing how the physical features of gastroliths vary with the characteristics of the associated specimen, such as the systematic identity, body mass and ontogenetic stage. The relationship between the features of the original source of the gastroliths and the characters of the final depositional environment is also interesting (Cerdeña and Salgado, 2008; Cicimurri and Everhart, 2001; Darby and Ojakangas, 1980; Everhart, 2000; Schmeisser and Gillette, 2009; Thompson et al., 2007). This is the line of research followed in this work.

Gastroliths have been previously reported in several Antarctic plesiosaurs, but they have never been associated with a specimen referred to *Aristonectes* (Chatterjee and Small, 1989; Martin et al., 2007; O’Gorman et al., 2012; Thompson et al., 2007). *Aristonectes* is a Wedellian elasmosaurid genus that has only been recorded in the upper Maastrichtian of Argentina and Antarctica and the Maastrichtian of Chile (Cabrera, 1941; Chatterjee and Small, 1989; Gasparini et al., 2003; Suárez and Fritis, 2002; O’Gorman et al., 2010, 2013a).

This record of gastroliths associated with a specimen referable to *Aristonectes* is relevant for two main reasons. Firstly, the relationship between gastroliths and plesiosaur palaeobiology is a topic under discussion and, therefore, every new record adds relevant information. Secondly, the peculiar cranial morphology of *Aristonectes* characterised by a high number of teeth could be related to its palaeoecology, and the occurrence of gastroliths could provide information related to this issue (Gasparini et al., 2003; Ketchum and Benson, 2010, 2011; Taylor, 1993). The only gastroliths previously associated with a specimen referred to *Aristonectes* (Otero et al., 2014) are composed of just a few elements and, therefore, it was not possible to carry a complete analysis on the subject.

The purposes of this paper are to provide a detailed description of the cluster of gastroliths of specimen MLP 89-III-3-2, referred to *Aristonectes* sp., collected in Seymour Island (*Is. Marambio*), Antarctica (Fig. 1A), to compare this description with other clusters recorded for plesiosaurs and to infer a possible source area. Palaeobiological information such as the maximum prey size, niche partition between adults and juveniles, mode of ingestion of gastroliths and their function are also discussed.

2. Geological setting

The López de Bertodano Formation crops out in Seymour Island (*Is. Marambio*) and Vega Island, James Ross Archipelago (Fig. 1A). It consists of about 1150 m of sandy shales and sandstones with interbedded fine concretions and subordinate carbonate facies (Macellari, 1988). The López de Bertodano Formation can be divided into two informal units of approximately equal thickness. The lower unit (“Rotularia units”) was deposited in a shallow marine environment near an estuary (Macellari, 1988; Olivero et al., 2008). The upper unit (“molluscan units”) was deposited in middle to outer platform settings (Macellari, 1988). The López de Bertodano is Maastrichtian–Danian in age (Crame et al., 2004; Macellari, 1986, 1988, Olivero and Medina, 2000). It is particularly interesting to mention that the Maastrichtian/Danian boundary is located approximately between the informal units 9 and 10 (top of the “molluscan units”) (Macellari, 1988; Zinsmeister et al., 1989).

3. Material and methods

3.1. Material

Specimen MLP 89-III-3-1 is an incomplete postcranial skeleton (O’Gorman, 2013) associated with a set of 793 gastroliths (Fig. 2).

Locality and horizon. MLP 89-III-3-1 was collected in Seymour Island (*Is. Marambio*). López de Bertodano Formation, (“molluscan units”), uppermost part of the KlB unit 9, *Pachydiscus ultimus* ammonite Biozone (Macellari, 1988; Olivero and Medina, 2000) (Fig. 1A).

Systematic remarks and ontogenetic stage. The anatomy of MLP 89-III-3-1 will be described in detail elsewhere however, the feature that allows us to assign MLP 89-III-3-1 to *Aristonectes* should be mentioned here. The middle and posterior cervical vertebrae preserved are very short (VLI = 80–60) [Vertebral Length Index: $VLI = (100 \times L)/(H + B) \times 0.5$], with dumbbell-shaped articular faces and very elongated cervical ribs, a morphology recorded from the Upper Cretaceous of South America and Antarctica in adult specimens only for *Aristonectes* (Gasparini et al., 2003; Otero et al., 2014). However, the determination at specific level requires a more detailed description and therefore MLP 89-III-3-1 is conservatively referred to *Aristonectes* sp.

The presence of neural arch–centrum closure in all the vertebrae indicates an adult condition (*sensu* Brown, 1981). This specimen has an estimate body length of about 8 m following the estimation of Otero et al. (2014).

3.2. Methods

The preparation of MLP 89-III-3-1 was carried out in the División Paleontología Vertebrados (Museo de La Plata) by the authors and the entire process was recorded photographically. Micro Jack and ME 9100 jackhammers were used for the preparation of the specimen. At least some of the gastroliths had been removed by erosion prior to the field collection (these could be seen by moulds left in the surrounding matrix) and some gastroliths were lost during preparation due to the difficulty in separating them from the extremely hard concretion. Although a careful collection of the gastroliths was made, it is possible that not all the original elements were collected and, therefore, the gastrolith total must be considered to be a minimum number. The gastroliths broken by recent fractures (about 259) were included in the total count but their measurements were not taken into account in the calculation of index values.

In the description of the skeletal parts of MLP 89-III-3-1 the VLI index (Vertebral Length Index: $100 \times L/(H + B) \times 0.5$) proposed by Brown (1981) was considered. In addition, the categories of ontogenetic development proposed by Brown (1981), based on the fusion of the vertebral neural arches with the vertebral centra to differentiate the “adult” and the “juvenile” stages, were used.

In the description of the gastroliths, the parameters previously used in the description of plesiosaur gastroliths (Cerdeña and Salgado, 2008; Cicimurri and Everhart, 2001; Darby and Ojakangas, 1980; Schmeisser and Gillette, 2009) were employed. The parameters used are as follows. The number of gastroliths; the length of the three principal axes: long (a), intermediate (b) and short (c); total volume and mass. The linear measurements were taken using digital callipers to an accuracy of 0.01 mm, the mass was measured using a scale mark (LNEAM model) and the volume was determined by the method of liquid displacement in a graduated container. The granulometric scale used is that proposed by Wentworth (1922).

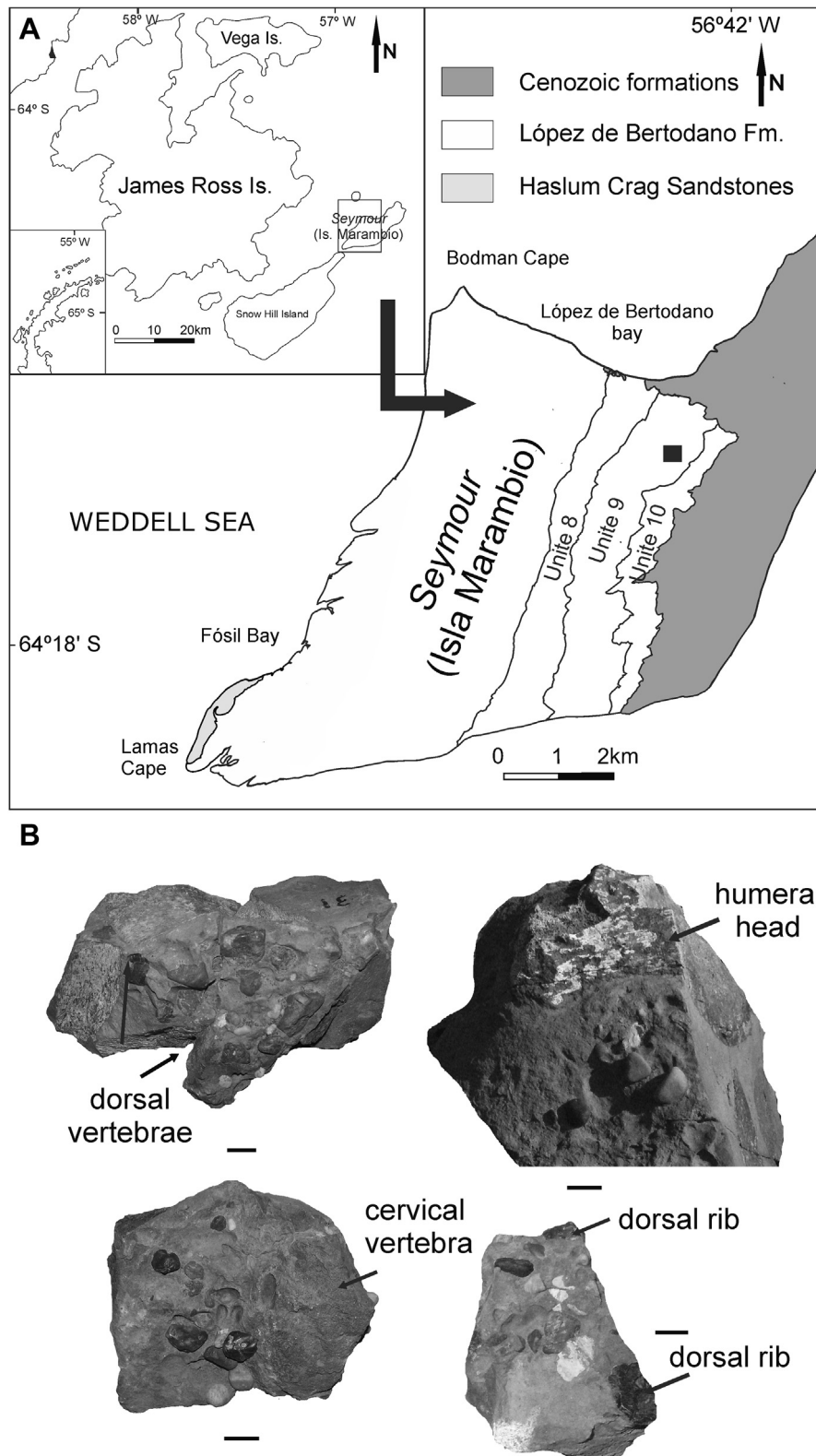


Fig. 1. A, Locality where the MLP 89-III-3-1 plesiosaur specimen was collected. B, Fragments of the concretion with gastroliths associated with skeletal elements. Scale bar = 20 mm.

The Maximum Projection Sphericity Index ($\psi = (c^2/b \times a)^{1/3}$) and the Oblate–Prolate Index ($OP = 10/(c/a) \times ((a - b)/(a - c) - 0.5)$) were calculated, considering the mean value and the standard deviation (Dobkins and Folk, 1970). In addition, the roundness categories of Powers (1953) were used. The ratios b/a and c/b were

used for the description of the shape, following Krumbein (1941). Finally, analysis of the lithology was carried out using thin-sections of representative gastrolith samples. The preliminary body mass estimation of MLP 89-III-3-1 was made using the data tabulated by Everhart (2000).

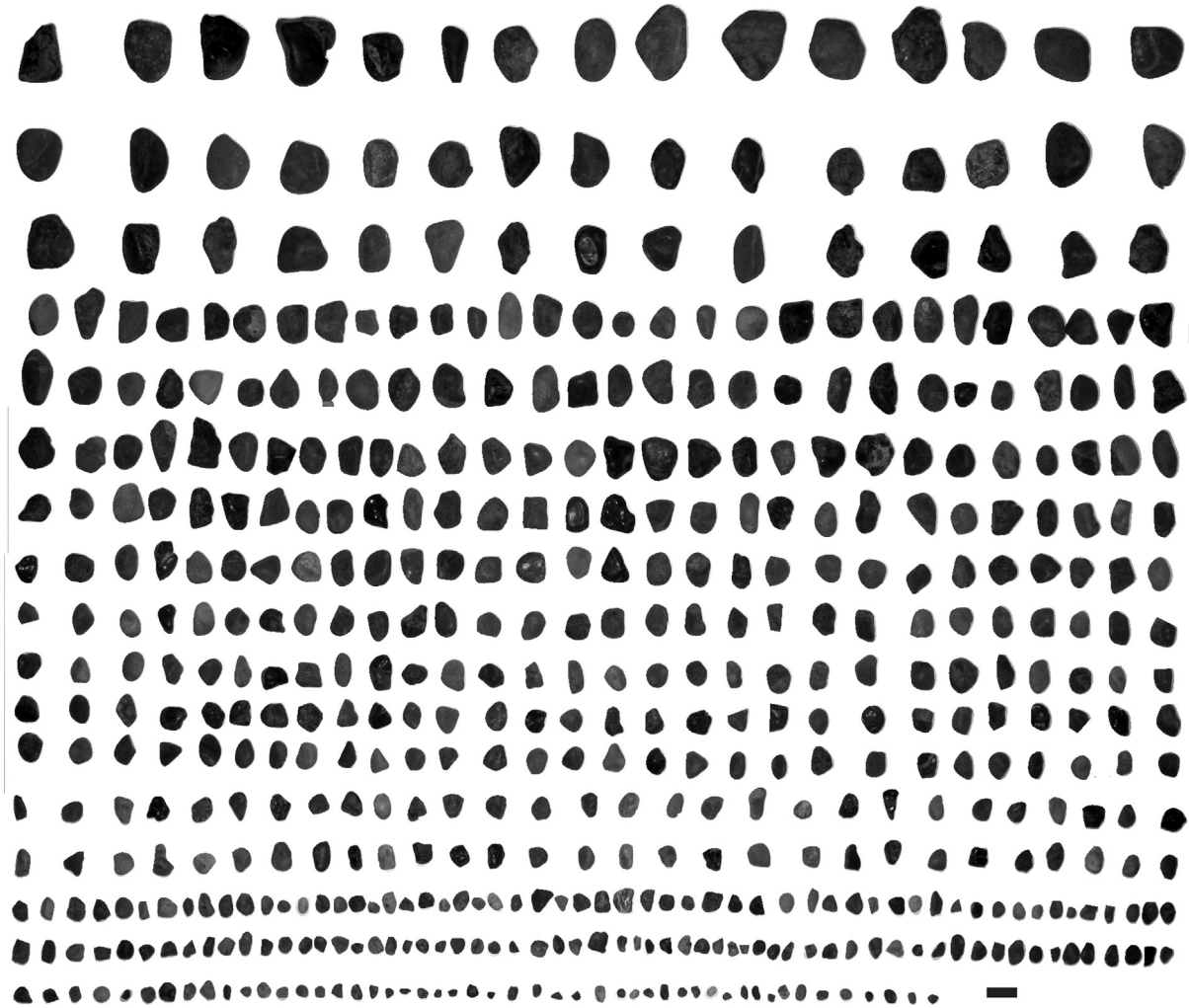


Fig. 2. Intact gastroliths (534) associated with MLP 89-III-3-1 (*Aristonectes* sp). Scale bar = 20 mm.

Institutional abbreviations. MCS, Museo de Cinco Saltos, Río Negro Province, Argentina; MLP, Museo de la Plata, Buenos Aires Province, Argentina. MPEF, Museo Paleontológico “Egidio Feruglio”, Chubut Province, Argentina.

4. Results

The set of gastroliths recovered associated with MLP 89-III-3-1 is composed of 793 gastroliths (534 in perfect state and about 259 broken gastroliths) (Fig. 2). The gastroliths are pebble size (4–64 mm). The mean lengths of the principal axes are 21 mm (a), 15.9 mm (b) and 11 mm (c). The total volume is about 2350 cm³ and the total weight is 6404 g. The largest gastrolith of the set weighs 124.6 g. The Maximum Projection Sphericity Index (ψ) values are between 0.37 and 0.99, the mean value is 0.71 and the standard deviation is 0.11. The Oblate–Prolate Index (OP) mean value is –0.06 and the standard deviation is 4.71. In relation to the shape of the clasts, the majority of the gastroliths (43.3%) are spheroidal (equant), 14.9% are cylindrical (prolate), 34.7% are discoidal (oblate) and 7.1% are bladed (laminar) (Fig. 3). Following the roundness categories of Powers (1953), 10.1% are very rounded, 29.2% are rounded and 60.7% are subrounded. Compositionally, the sample consists of rhyolitic volcanites (56.2%); quartz vein material (27.8%); subarkose arenites (14.5%); laminated, radiolarian-rich mudstones

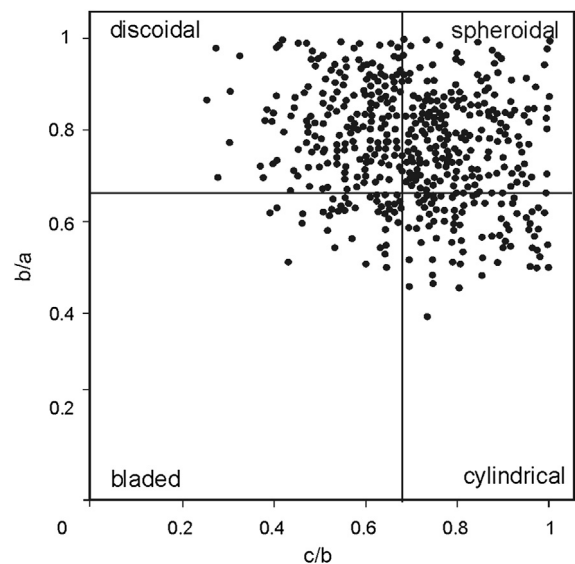


Fig. 3. MLP 89-III-3-1; gastrolith shape distribution, after Krumbein, 1941.

and tuffs (1.5%) (see Fig. 4). Some of the aphanitic rhyolitic gastroliths (about 10%) have superficial conchoidal fractures (Fig. 4f).

5. Discussion

5.1. Identification and comparison with other plesiosaur gastroliths

The clasts associated with MLP 89-III-3-1 were recovered either associated in the part of the concretion containing elements of the skeleton (Fig. 1B) or associated in the surrounding area. Furthermore, the clasts differ in size and lithology from the mostly pelitic components of the surrounding sediment. Thus, the features observed allow identification of the clasts associated with MLP 89-III-3-1 as gastroliths.

The number of gastroliths associated with plesiosaurs has proven to be highly variable, from a few clasts to 2626 gastroliths in one case (Cerdeña and Salgado, 2008; Darby and Ojakangas, 1980; Cicimurri and Everhart, 2001; Hiller et al., 2005; Everhart, 2000; Sato, 2003; Thompson et al., 2007; Druckenmiller, 2009; Whittle and Everhart, 2000; Table 1). The number of gastroliths from MLP 89-III-3-1, considering the ones that were recovered intact (534), plus the fragmentary ones, is 793 which, as indicated above, is a minimum number. This number falls in the upper part of the recorded range for plesiosaurs (Table 1). However, a high variability in the number of gastroliths per individual is seen in extant birds where individuals of the same species and ontogenetic stage exhibit a remarkable difference in the number of gastroliths present in their digestive tracts (Best and Gionfriddo, 1991).

The size of the gastroliths from MLP 89-III-3-1, (mean value: 21 mm (a), 15.9 mm (b) and 11 mm (c)) is relatively small compared to the size of the animal, especially when compared to the large cranium of *Aristonectes*: 735 mm length; 480 wide (MLP 40-XI-14-6,

Aristonectes parvidens, holotype). It would therefore appear that cranium size has no correlation with the size of the gastroliths.

5.2. Palaeoenvironment source and stratigraphical provenance of gastroliths

The mean Maximum Projection Sphericity (ψ) value of the gastroliths from MLP 89-III-3-1 (0.71) and the standard deviation (0.11) are more similar to those recorded by Dobkins and Folk (1970) in fluvial environments (0.684) than to those of low-wave-energy beach (0.64) or high-wave-energy beach (0.58) environments. Therefore, the mean sphericity of the gastroliths indicates a likely fluvial origin for these clasts. The Oblate–Prolate Index (0.06) is also more similar to that recorded by Dobkins and Folk (1970) for clasts between 16 and 32 mm in fluvial environments (0.71) than was recorded by these authors for clasts from generalised beach environments (–3.15). According to Dobkins and Folk (1970), the mean values of both indexes (ψ and OP) combined gave a better environmental discrimination. The graph of ψ versus OP (Fig. 5) shows the gastroliths of MLP 89-III-3-1 grouped with the fluvial samples considered by Dobkins and Folk (1970).

Interestingly, the mean value of the sphericity and standard deviation of the gastroliths in MLP 89-III-3-1 are similar to those recorded for other elasmosaurids and polycotylids (Table 2). This could indicate that all these plesiosaurs, in spite of the differences in their body proportions, obtained their gastroliths from the same type of environment. However, this inference implies the assumption that the overall shape of the stones changed a little after entering the animal’s digestive system. It is likely that the stones did wear down within the gastric mill as a result of their interaction (Everhart, 2004b) but it is also probable, however, that the individual replaced the stones periodically and, therefore, the

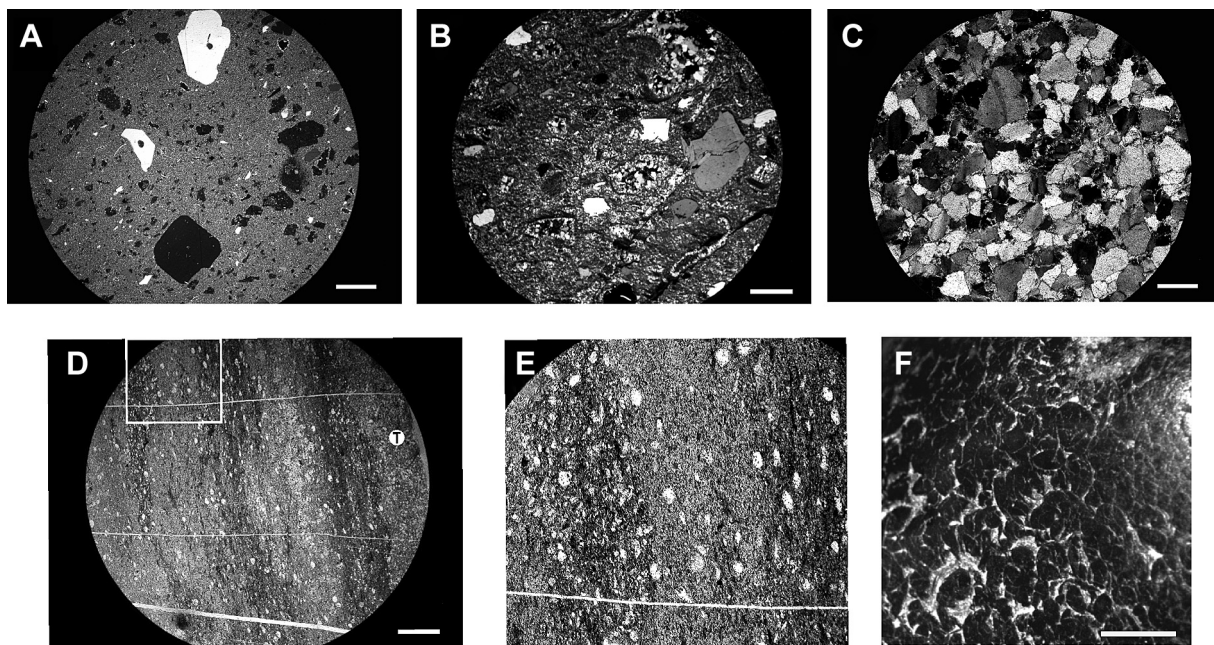


Fig. 4. Photomicrographs of selected thin sections representative of the main gastrolith lithologies. A, V1 rhyolite type, showing large, corroded bipyramidal quartz crystals, abundant felsitic groundmass showing diffuse banding in the original glass- and quartz-filled amygdules, scale bar = 1 mm, view under crossed polars. B, V2 rhyolite type, showing large, embayed bipyramidal quartz crystals immersed in a homogeneous very fine felsitic groundmass, scale bar = 1 mm, view under crossed polars. C, Very fine-grained arenite, subarkose, showing moderately sorted, angular grains of quartz and plagioclase and the very little recrystallized matrix, scale bar = 0.25 mm, view under crossed polars. D–E, D, Laminated dark grey radiolarian mudstones and tuffs (T), the square indicates the position of the close-up image in E. Scale bar = 1 mm, view in plane-polarized light. F, Superficial conchoidal fractures on a dark, aphanitic, rhyolitic gastrolith. The matrix is a very fine-grained aggregate of quartz microcrystallites, probably devitrified glass, with scarce quartz phenocrysts. Scale bar = 2 mm.

Table 1
Records of gastroliths associated with plesiosaurs.

Determination	Num. Gast.	Max. long axis (mm)	Weight (g)	References
Elasmosauridae				
<i>Aristonectes</i> sp.	793		6404	This paper
<i>Styxosaurus snowii</i> (Williston) Welles, 1943	253		8249	Welles and Bump, 1949
<i>Styxosaurus snowii</i> (Williston) Welles, 1943	95		6800	Cicimurri and Everhart, 2001
<i>Mauisaurus haasti</i> Hector, 1874	>30	40		Hiller et al., 2005
<i>Albertonectes vanderveldei</i> Kubo, Mitchell, Henderson, 2012	>97		~9005	Kubo et al., 2012
<i>Terminator ponteixensis</i> Sato, 2003	>150	60		Sato, 2003
Elasmosauridae indet.	197	114	8840	Darby and Ojakangas, 1980
Elasmosauridae indet.	47	170	13078	Everhart, 2000
Elasmosauridae indet.	2626		3002	Thompson et al., 2007
Elasmosauridae indet.	42			Thompson et al., 2007
Elasmosauridae indet.	389	79	1460	Cerda and Salgado, 2008
Elasmosauridae indet.	333		725	O’Gorman et al., 2012
Elasmosauridae indet.	197		440	O’Gorman et al., 2013b
Polycotylidae				
Polycotylidae indet.	12			Druckenmiller and Russell, 2009
Polycotylidae indet.	2			Sato and Storrs, 2000
<i>Pahasapasaurus haasi</i> Schumacher, 2007	2			Schumacher, 2007
<i>Dolichorhynchops tropicensis</i> Schmeisser McKean, 2012	289		518	Schmeisser and Gillette, 2009; Schmeisser McKean, 2012
Rhomaleosauridae				
<i>Rhomaleosaurus zetlandicus</i> Phillips, 1854	1			Taylor, 1992
Pliosauridae				
<i>Peloneustes</i> Lydekker, 1889	Many			Andrews, 1910
<i>Liopleurodon</i> Sauvage, 1873	+7			Martill, 1992

general environmental signal remains consistent. This is a point that needs to be studied in detail in the future.

MLP 89-III-3-1 was collected at the top of the López de Bertodano Formation which was deposited in a marine shelf environment (Macellari, 1988). In this case, as in many other occurrences, the original environment where the gastroliths were obtained is

not directly correlated with the depositional environment of the formation where they were collected.

As in the previously studied Antarctic plesiosaur from Vega Island (O’Gorman et al., 2012), the gastroliths of MLP 89-III-3-1 are predominantly composed of rhyolitic volcanites and fine-grained aggregates of quartz crystals. The rhyolitic gastroliths were most likely derived from the Upper Jurassic Antarctic Peninsula Volcanic Group. The quartz aggregates may have been derived either from the same source or from quartz veins, which are known to be present in the low-grade metamorphic rocks of the Permian–Triassic Trinity Peninsula Group (see Smellie, 1991). In addition, the petrographic features of the subarkose are characteristic of the arenites of the Trinity Peninsula Group, widely exposed on northeastern Antarctic Peninsula (Smellie, 1991). The laminated radiolarian mudstones and tuffs can be assigned almost certainly to the Kimmeridgian–Berriasian Ameghino Formation (also known as the Nordenksjöld Formation), widely exposed on the eastern part of the Antarctic Peninsula. In this regard, the lithological similarity between the gastrolith illustrated in Figs. 4D, E with that of the Ameghino Formation (see Scasso, 2001, figure 5) is remarkable.

MLP 89-III-3-1 was collected from the informal unit 9 (Macellari, 1988) of the López de Bertodano Formation. Unit 9, as well as the entire thickness of the López de Bertodano Formation, about 1150 m, consists exclusively of very fine-grained silty sandstones and silty mudstones. Hence, the fine-grained granulometry of these sediments ruled out the possibility that the source area of the gastroliths was the same area where MLP 89-III-3-1 was collected. The most likely source area for these gastroliths is the eastern area of the Antarctic Peninsula which, during late Maastrichtian times, was located adjacent to the western margin of the James Ross Basin. In this regard, the closest candidate area is located on the Antarctic Peninsula, covering a northeastern trending belt stretching from Sobral Peninsula and Longing Gap in the southwest to Hope Bay in the northeast, where extensive outcrops of the Permian–Triassic Trinity Peninsula Group, Late Jurassic Antarctic Peninsula Volcanic Group, and Late Jurassic–Early Cretaceous Ameghino

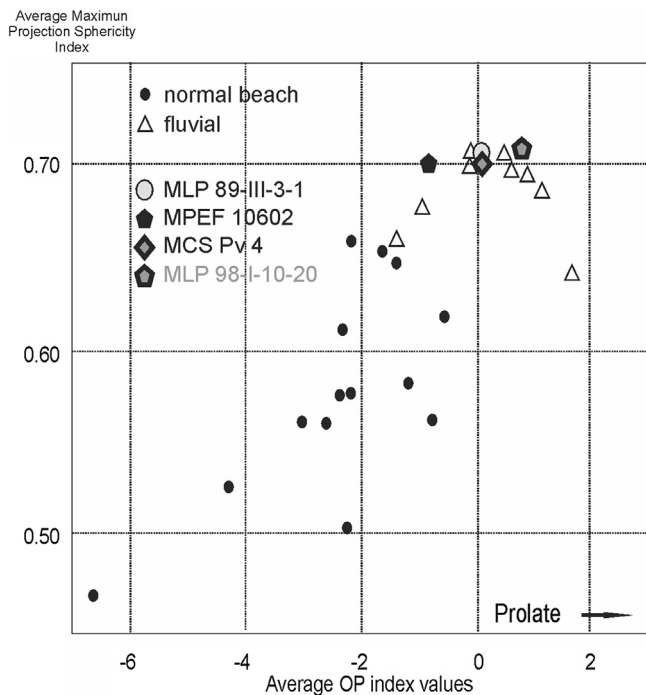


Fig. 5. Plot of average Maximum Projection Sphericity (ψ) values vs. mean Oblate–Prolate Index (OP index) values. ○, MLP 89-III-3-1, *Aristonectes* sp.; ◆, MPEF 10602, *Elasmosauridae* indet.; ◆, MCS PV 4, *Elasmosauridae* indet.; ◆, MLP 98-I-10-20, *Elasmosauridae* indet., gastroliths; ●, normal beach samples; △, fluvial samples (modified from Dobkins and Folk, 1970, data taken from O’Gorman et al., 2012, 2013a, 2013b).

Table 2
Shape features of the gastroliths associated with plesiosaurs compared with fluvial and marine clasts samples.

Determination	Average (ψ)	Standard deviation	Mean OP Index
<i>Aristonectes</i> sp. (this article)	0.71	0.11	−0.06
Elasmosauridae indet. (Darby and Ojakangas, 1980)	0.71	0.1	
Elasmosauridae indet. (Cerde and Salgado, 2008)	0.69	0.11	0.15
Elasmosauridae indet. (Everhart, 2000)	0.73		
Elasmosauridae indet. (O’Gorman et al., 2012)	0.7	0.11	0.8
Elasmosauridae indet. (O’Gorman et al., 2013b)	0.69	0.11	−0.74
<i>Panjiangsaurus</i> Chen and Cheng, 2003 (Ichthyosaur) (Long et al., 2006)	0.57	0.176	
Fluvial (Dobkins and Folk, 1970)	0.684	0.108	
Low-wave energy beach (Dobkins and Folk, 1970)	0.64	0.115	
High-wave energy beach (Dobkins and Folk, 1970)	0.58	0.114	

Formation are present (British Antarctic Survey, 2011) (Fig. 6). It is interesting to compare the case with that recorded by McHenry et al. (2005) where the nearest source of gastroliths was possibly over 300 km from the site of final deposition or with that recorded by Everhart (2000) who, based on material studied by Williston (1903), inferred a distance of over 700 km.

The shapes of the gastroliths from MLP 89-III-3-1 are similar to those previously reported in plesiosaur gastroliths (Cerde and Salgado, 2008; Darby and Ojakangas, 1980; Everhart, 2000; Schmeisser and Gillette, 2009) but, interestingly, are different from those observed in an ichthyosaur from the Triassic of China (Long et al., 2006). In that case, the dominant form is the discoidal (oblate) and bladed (laminar), and the mean sphericity value is 0.575. Therefore, there is a difference between this and the sets associated with plesiosaurs. It is likely that these differences are related to the environment from which the gastroliths were obtained (by the specimen which contains them or from prey consumed by the specimen, see Moodie, 1912 and Everhart, 2004a).

The rounding categories recorded in the gastroliths from MLP 89-III-3-1 are similar to those reported by Cerde and Salgado (2008) and O’Gorman et al., 2012, 2013a, 2013b.

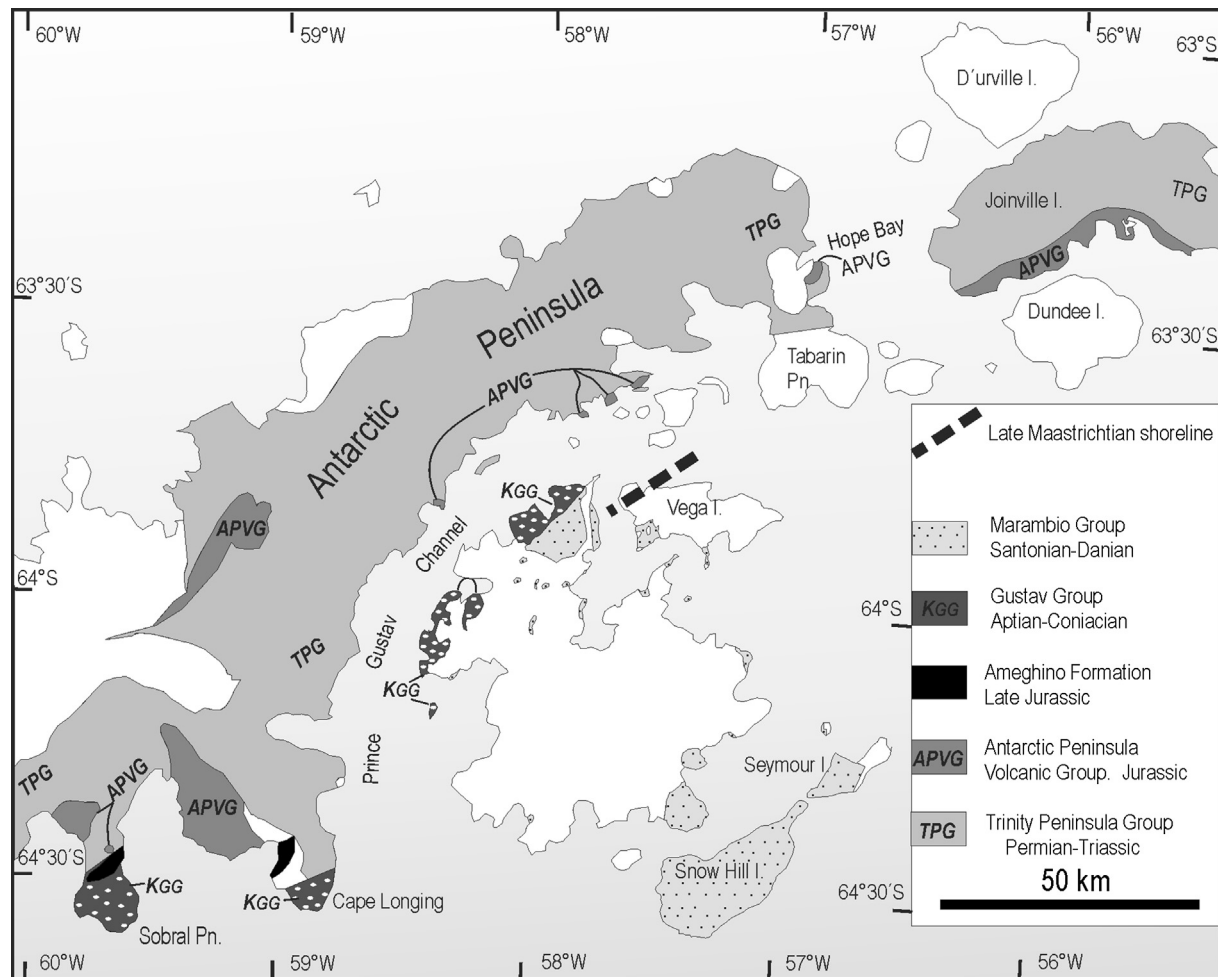


Fig. 6. Geological sketch of the northern Antarctic Peninsula showing the distribution of the possible provenance rocks of the gastroliths (Trinity Peninsula Group; Antarctic Peninsula Volcanic Group and Ameghino Formation) and the Cretaceous rocks of the James Ross Basin (Gustav Group and Marambio Group). Sketch map based on British Antarctic Survey, 2011. The inferred trend and position of the late Maastrichtian (Unit 9) shoreline is also shown (see Olivero, 2012, for details).

5.3. Palaeobiology

Cicimurri and Everhart (2001) noted that the length of the intermediate (b) and short (c) axes ($b \times c$) of the larger gastroliths could indicate the maximum prey cross section that the plesiosaur could consume. Among the gastroliths of MLP 89-III-3-1, the highest value ($b \times c$) is 13.85 cm². A value of 9.45 cm² was recorded by Cerda and Salgado (2008) for a set of gastroliths associated with MCS 4, a smaller elasmosaurid (with a femur length of about 170 mm) than the MLP 89-III-3-1 (with a femur length of 540 mm). This indicates either that both specimens consumed the same prey-size, despite the differences in body size, or that the method produces inconsistent results. The first option indicates that both specimens consumed small-sized fishes or invertebrates. The second option may indicate that the obtained value is just the maximum size of clast available in the environment where they were obtained.

It has been hypothesized that there existed a spatial niche partitioning between juvenile and adult plesiosaurs. According to this hypothesis, the juvenile or subadult individuals remained near the coast while the adults utilised a wider range of habitats (Wiffen et al., 1995; Wiffen and Moislely, 1986). However, the inference of a fluvial or estuarine origin of gastroliths in all the cases in which the sphericity has been calculated (Table 2) indicates that juveniles and adults shared these kinds of environments, at least at the time when the gastroliths were ingested.

Regarding the acquisition of gastroliths, there are several factors that suggest that the gastroliths were obtained by a method more similar to taking a random sample of sediment than to taking clasts individually, as is recorded in modern birds (Best and Gionfriddo, 1991). Some features of the gastroliths from MCS 4 (Elasmosauridae subadult-adult, Cerda and Salgado, 2008); MLP 98-I-10-20 (Elasmosauridae juvenile) O'Gorman et al., 2012 and MLP 89-III-3-1 (*Aristonectes* adult, this paper) support this hypothesis: 1) the absence of size selection, as shown by the continuity of sizes of the gastroliths; and 2) the similar mean sphericity value recorded, which seems to be independent of the ontogenetic stage, size and systematic identity. These features could be best explained by the activity of sampling the clasts without selection. Moreover, in the case of *Aristonectes*, based on the holotype of *Aristonectes parvidens*, which has a skull of about 735 mm in length, it is obvious that it would have been unable to select individual small gastroliths between 2 and 10 mm in size but more probably took random samples of sediment. Furthermore, this hypothesis of a random ingestion would explain why the mean sphericity of the sets of gastroliths is close to values observed today in random clasts samples from defined environments, specifically fluvial environments.

Another element that provides evidence of how the gastroliths were ingested is the record of sand bodies in the abdominal cavity of plesiosaurs. This type of deposit has been recorded since the early twentieth century (Andrews, 1910). More recently, Everhart (2004a) recorded a sand body associated with a mosasaur that had ingested a small polycotyloid, and O'Keefe et al. (2009) observed a similar sand body in a specimen of *Pantosaurus striatus*, a cryptocleoid from the Upper Jurassic of Wyoming, USA. The sand body was different from the surrounding sediment that included the stomach contents and 14 gastroliths. These records could indicate that sandy sediment was ingested together with the gastroliths. Wings (2007) proposed that the boundary between lithophagy (ingestion of rocks) and geophagy (ingestion of "ground") follows the limit between mud and sand grain size. Therefore the sand grains recorded as gut content in plesiosaurs are gastroliths *sensu* this definition.

The occurrence of gastroliths is known in the families Pliosauridae (Andrews, 1910), Rhomaleosauridae (Taylor, 1992),

Elasmosauridae (Cerda and Salgado, 2008; Darby and Ojakangas, 1980; Everhart, 2005; O'Gorman et al., 2012, 2013b; Welles and Bump, 1949) and Polycotyloidea (Druckenmiller and Russell, 2009; Schmeisser and Gillette, 2009). The distribution of gastroliths records in the different families shows a complex pattern that does not necessarily reflect biological differences. This is because the lack of records in one specimen does not prove that gastroliths were absent in other individuals of the same species, or that the absence is not a product of taphonomic processes (Taylor, 1993). In relation to this, it is important to note that the number of gastroliths and their roundness probably changed constantly. However, there is a dominance of gastrolith records associated with the Elasmosauridae compared to other families (Table 1). This could be related to palaeobiological differences, since there is no known taphonomic process that eliminates gastroliths selectively only from non-elasmosaurid plesiosaurs. The new record of gastroliths in *Aristonectes* sp., an elasmosaurid with special body proportion (short neck and large skull), is interesting because it extends the behaviour of lithophagia to this bizarre elasmosaurid morphotype.

5.4. Function

The function of gastroliths has been discussed several times (Taylor, 1993; Whittle and Everhart, 2000; Wings, 2007). The hydrostatic function has been raised and discussed thoroughly (Henderson, 2006; Taylor, 1993). The total mass of the gastroliths of MLP 89-III-3-1 (6404 g), which was recovered intact, seems to be too low to change the hydrostatic balance. Even considering the possible losses of mass related to the broken gastroliths, the total mass of the gastroliths is less than 7500 g.

According to the elasmosaurid body mass table of Everhart (2000), a specimen of 8 m length corresponds to an approximate body mass of 1300 kg; however, this table is based on elongated neck elasmosaurids in which much of the length corresponds to the cervical region. Therefore, using this model for an *Aristonectes* sp., which probably had a proportionally shorter neck (Gasparini et al., 2003), would tend to underestimate the mass of the animal. For the foregoing reasons, the ratio (mass of gastroliths)/(mass of the individual) is less than 7.5 kg/1300 kg = 0.58%. According to the model of Henderson (2006), this percentage of weight of gastroliths would have been unable to modify the hydrostatic balance of the animal. However, because the skeleton was not articulated, the number of gastroliths lost is unknown and therefore the weight of the gastroliths must be a minimum value. Nonetheless, this result clearly corresponds to other gastrolith weights previously recorded (Everhart, 2000; Cerda and Salgado, 2008; Schmeisser and Gillette, 2009).

Conchoidal fractures (Fig. 4F) were observed on the outer surface of some (about 10%) very fine-grained rhyolite gastroliths from MLP 89-III-3-1. Several authors have reported similar observations, suggesting that the fractures were made after ingestion of the clasts and were related to strong peristaltic contractions of the gizzard (Cerda and Salgado, 2008; Everhart, 2000; Schmeisser and Gillette, 2009). However, the only incontrovertible evidence of modification of clasts inside the gizzard is the presence of broken gastroliths from which both parts have been recovered. In MLP 89-III-3-1, this evidence was not detected. As is well-known, the texture of the material is the main factor controlling the formation of conchoidal fractures. In our case, the conchoidal fractures are restricted to very homogeneous, aphanitic rhyolitic rocks and thus it is not possible to evaluate if jostling of the clasts producing the fractures took place before or after ingestion by the animal. Therefore, the MLP 89-III-3-1 does not provide new conclusive evidence about the digestive hypothesis.

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