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Gastroliths associated with a juvenile elasmosaur (Plesiosauria, Elasmosauridae) from the Snow Hill Island Formation (upper Campanian-lower Maastrichtian), Vega Island, Antarctica

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Gastroliths associated with a juvenile elasmosaur (Plesiosauria, Elasmosauridae) from the Snow Hill Island Formation (upper Campanian–lower Maastrichtian), Vega Island, Antarctica

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One of the unresolved problems concerning the palaeobiology of plesiosaurs is the function of gastroliths. A new juvenile specimen referred to *Elasmosauridae* indet., collected from the Cape Lamb Member of the Snow Hill Island Formation (upper Campanian–lower Maastrichtian) from Cape Lamb, Vega Island, Antarctic Peninsula with gastroliths, provides the opportunity to add information about this issue. The specimen consists of approximately 20% of a partially articulated skeleton including 333 gastroliths. Taphonomic evidence indicates rapid burial and possibly different taphonomic pathways for the dorsal (articulated) and caudal (disarticulated) regions. Analysis of the 333 gastroliths determined the mean major axis to be 14.32 mm, the mean maximum projection sphericity to be 0.7 and the standard deviation to be 1.1. Following Krumbein classification, most of the gastroliths are disk-shaped (35.4%), spheroid (34%) and cylindrical (21.3%). According to Powers's categories, most of the gastroliths are rounded (71.2%). Petrographically, the gastroliths that are larger than 15 mm (major axis) are mostly volcanic rhyolites (78.3%) and fine-grained quartz aggregates (11.6%); together with minor granitic rocks (3.1%), mudstones (3.1%) and aphanitic volcanics (3.9%); similar percentages were present among the smaller clasts. The acidic volcanic clasts likely derive from the volcanic Antarctic Peninsula Group (GPVA; Middle–Upper Jurassic). The mean values for sphericity and oblate-prolate index (OP index) indicate a fluvial origin for the gastroliths. The method of estimation of the maximum prey-size using gastroliths is discussed. The available data provides evidence against the hydrostatic function of the gastroliths because the total weight of the gastroliths is insufficient to modify the hydrostatic balance of the juvenile plesiosaur.

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LITHOPHAGIA or ingestion of rocks is recorded in various groups of aquatic tetrapods, although there are differences in this behaviour between the various groups (Taylor 1993, Whittle & Everhart 2000). Rock fragments, as any hard substance without caloric value that are or were held in the digestive system of an animal, are termed gastroliths (Wings 2007) and, in the case of fossil vertebrates, there are special taphonomic criteria that can be used to identify gastroliths (Wings 2004). The detailed study of gastroliths in fossils is important because their characteristics, such as shape, roundness, texture and lithology, are related to the gastrolith's source deposit, time spent in the digestive system, rate of abrasion and their function (Darby & Ojakangas 1980, Everhart 2000, Cicimurri & Everhart 2001, Wings 2007, Cerda & Salgado 2008, Schmeisser & Gillette 2009). Several hypotheses concerning the

specific function of gastroliths in aquatic vertebrates have been raised (Taylor 1993, Wings 2007). Since gastroliths were first reported in association with plesiosaurs in the nineteenth century, their record has increased steadily to dozens of well-documented cases (Williston 1893, 1894, 1904, Brown 1904, Welles & Bump 1949, Taylor 1993, Everhart 2000, 2005, Gasparini & Salgado 2000, Sato & Storrs 2000, Whittle & Everhart 2000, Cicimurri & Everhart 2001, Hiller *et al.* 2005, McHenry *et al.* 2005, Cerda & Salgado 2008, O'Keefe *et al.* 2009, Schmeisser & Gillette 2009, Shimada *et al.* 2010). Two functional hypotheses have been proposed to justify the presence of gastroliths in plesiosaurs. On the one hand, the hydrostatic balance hypothesis explains lithophagia as a method to adjust the hydrostatic balance and to assist diving (Taylor 1993). Several authors have rejected this hypothesis based on the lack of correlation between the gastroliths recorded in well-documented cases and the gastrolith mass predicted to be necessary using computational models (Everhart 2000, Henderson 2006, Cerda & Salgado 2008,

Schmeisser & Gillette 2009). On the other hand, the digestive hypothesis suggests that the gastroliths were used to macerate food. Some data, such as broken gastroliths, broken bones of prey associated with the gastroliths and conchoidal fractures on the gastroliths' surfaces have been mentioned as evidence in support of this idea (Everhart 2000, Cerda & Salgado 2008, Schmeisser & Gillette 2009).

Differentiation between juvenile and adult individuals in fossil vertebrates is not always easy. However, some progress has been achieved for plesiosaurs on the basis of morphological studies (Brown 1981, Carpenter 1999) and palaeohistology (Wiffen *et al.* 1995, Gasparini & Salgado 2000, Wahl 2006, Salgado *et al.* 2007). The ability to differentiate ontogenetic stages allows the investigation of palaeobiological differences between juveniles and adults; and this has been done for some Elasmosauridae (Wiffen & Moisley 1986, Wiffen *et al.* 1995). In this context, some authors have proposed the partition of foraging niches, in which juvenile elasmosaurs were restricted to more protected habitats, near the coast, whereas adults were more wide-ranging (Wiffen *et al.* 1995, Wahl 2006).

Plesiosaurs in the Antarctic Peninsula are known only from the Marambio Group, upper Coniacian–Danian (McArthur *et al.* 2000, Crame *et al.* 2004), or Santonian–Danian (Olivero & Medina 2000, Olivero 2012), and are represented by the families Elasmosauridae and Polycotyliidae. With the exception of *Aristonectes*, the elasmosaurids from the Snow Hill Island and López de Bertodano formations have not been identified to genera, although the possible presence of *Mausisaurus* has been reported (Gasparini *et al.* 1984, Chatterjee & Small 1989, Gasparini *et al.* 2003, Hiller *et al.* 2005, Martin *et al.* 2007, O'Gorman *et al.* 2008, 2010). The Polycotyliidae are represented by a single specimen referred to Polycotyliidae indet. collected from the Santa Marta Formation (D'Angelo *et al.* 2008).

Gastroliths have been recorded in Antarctic plesiosaurs since the 1980s (Chatterjee & Small 1989; Thompson *et al.* 2007). Martin *et al.* (2007) noted gastroliths associated with a juvenile elasmosaur, but neither the gastroliths nor the taphonomic characteristics of the specimen were described in detail.

During the joint Argentinian–North American 1998 Antarctic field trip, a semi-articulated postcranial skeleton of a juvenile plesiosaur referable to Elasmosauridae was collected (MLP 98-I-10-20). It was associated with gastroliths. The specimen derived from the Cape Lamb Member of the Snow Hill Island Formation (upper Campanian–lower Maastrichtian) on Vega Island, Antarctica (Fig. 1). Here, we describe the taphonomic features of MLP 98-I-10-20 and analyse the characteristics of the associated set of gastroliths by means of a detailed description and petrographic analyses. The gastroliths are compared

with examples from other plesiosaurs, and the possible source area and palaeobiological implications are discussed. Moreover, additional taphonomic features of the skeleton are described.

Geological Setting

A thick succession of sedimentary rocks is preserved in the James Ross Basin. This succession includes two major Cretaceous units, the Gustav Group of Barremian–Coniacian age and the Marambio Group of Coniacian–Danian age (Ineson 1989, Macellari 1988, McArthur *et al.* 2000, Crame *et al.* 2004) or Santonian–Danian age (Olivero & Medina 2000). Following Olivero *et al.* (2008) and Olivero (2012) the Marambio Group includes the Santa Marta, Rabot, Snow Hill Island, Haslum Crag and López de Bertodano formations.

The Cape Lamb Member of the Snow Hill Island Formation (Fig. 1) consists of 319 m of heavily bioturbated silty mudstones to silty sandstones with abundant diagenetic concretions. This formation is interpreted as a shallowing, thickening and coarsening-upward succession characterized by basal silty sandstone and mudstone strata that pass gradually into mature sandstones beds. The lower levels of the Cape Lamb Member were deposited in an offshore environment and the upper levels in a proximal

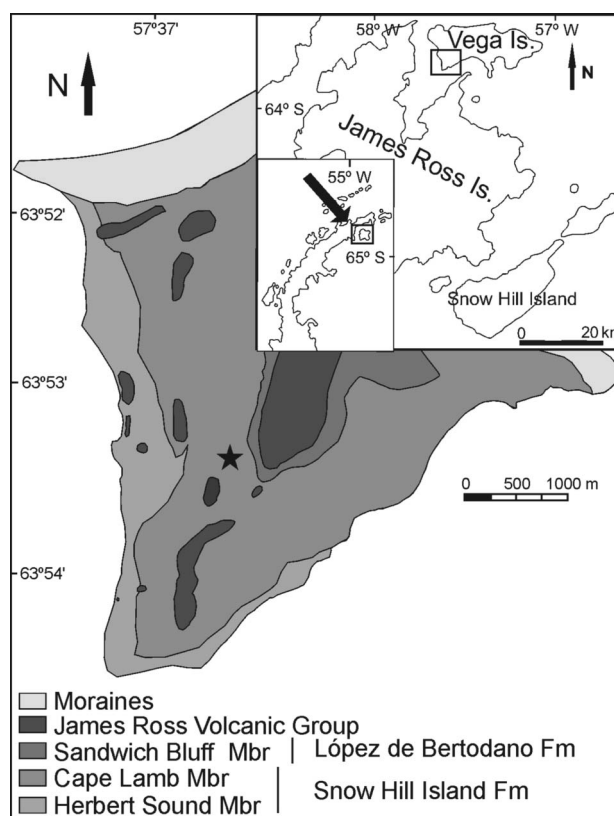


Fig. 1. Map of the locality from which MLP 98-I-10-20 was collected (modified from Marensi *et al.* 2001 and Olivero *et al.* 2008).

nearshore marine environment (Pirrie *et al.* 1991, Marensi *et al.* 2001, Olivero *et al.* 2008). The Cape Lamb Member is late Campanian–early Maastrichtian in age (Crame *et al.* 2004).

Methods

The preparation of MLP 98-I-10-20 was carried out in the División Paleontología Vertebrados (La Plata Museum). Owing to the critical importance of the taphonomic information, the fossil preparation was done by the authors using Micro jack and ME 9100 jack hammers. The preparation process was recorded, taking photographs from the abdominal area and noting the position of gastroliths in relation to the skeleton (Fig. 2). Although a few gastroliths were lost prior to the collection of the specimen (denoted by their moulds in the matrix) and others could not be recovered due to the difficulty in separating them from the matrix, the main part of the gastrolith cluster was recovered intact, and the gastroliths included in it were prepared.

The parameters usually considered in descriptions of gastroliths of plesiosaurs (Darby & Ojakangas 1980, Cicimurri & Everhart 2001, Cerda & Salgado 2008) were used to draw comparisons between MLP 98-I-10-20 and previously described examples. Specifically, we considered the number of elements in the cluster, the dimensions of the three main axes: long (a), intermediate (b) and short (c) of each gastrolith, together with the total volume and mass. The linear measurements were obtained using a digital calliper with precision of about 0.01 mm, and the volume was measured using the method of displacement of liquid in a graduated container. Size was described following the granulometric scale proposed by Wentworth (1922).

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 used (Dobkins & Folk 1970), in particular, the means and standard deviations of these indexes. The roundness of the gastroliths was also assessed following the categories proposed by Powers (1953). Shape was described using the ratios b/a and c/b , according to Krumbein (1941). Finally, thin-sections of representative gastrolith samples were used to determine the petrographic composition.

The ontogenetic categories defined by Brown (1981), based on the fusion of the neural arch to the vertebral centrum, were used to differentiate ‘adult’ from ‘juvenile’ stages. Taphonomic description follows Schäfer (1972), Martill (1985), Holz & Simões (2002) and Barnes & Hiller (2010). Body-mass estimation follows Everhart (2000).

Institutional abbreviation. MLP, Museo de La Plata, La Plata, Buenos Aires Province, Argentina.

Materials

Specimen MLP 98-I-10-20 is an incomplete postcranial skeleton consisting of posterior dorsal, sacral and caudal vertebrae, left pubis, both ilia, both ischia, left posterior limb, ribs, gastralta, indeterminate elements (Fig. 2) and 333 gastroliths (Fig. 3) located in the abdominal zone in the space between the gastralta and the dorsal ribs.

Locality and horizon

The material derives from Cape Lamb, Vega Island, James Ross Archipelago, Antarctic Peninsula (Fig. 1). Cape Lamb Member of the Snow Hill Island Formation (upper Campanian–lower Maastrichtian; Crame *et al.* 2004) and specifically within the Sequence NG (*Neograhamites-Gunnarites*) Assemblage 10 (Olivero & Medina 2000, Olivero 2012) of early Maastrichtian age.

Systematic remarks and ontogenetic stage

The skeletal anatomy of MLP 98-I-10-20 will be described in detail elsewhere. However, some comments on the features used to refer the specimen to a juvenile Elasmosauridae indet. are necessary. Because of the incomplete preservation, the specimen can only be identified to family-level. The epipodials are broader than long, a typical characteristic of the Late Cretaceous elasmosaurs (O’Keefe 2001, 2004), and the ischium is not elongated, a condition different from Polycotyliidae.

The absence of neuro-central closure in the preserved vertebrae indicates a juvenile condition (*sensu* Brown 1981). In addition, the femur does not have a differentiated tubercle and capitulum, nor are the distal articular faces traits typical of juvenile plesiosaurs.

Results

Taphonomic features

Specimen MLP 98-I-10-20 lies with its ventral side upwards and is slightly rotated to the left side of the body (Fig. 2). It is a partially articulated skeleton, of which the left pubis, the left ilium, left ischium, ribs, gastralta, the last dorsal vertebrae and the sacral vertebrae are complete and articulated (Fig. 2). The right and left ischia are in articulation, but the right one is fragmented due to surficial weathering (Fig. 2). The right hind limb could be represented only by a single metapodial element located near the right side of the body. The left femur is slightly displaced, whereas the epipodal, mesopodial and phalanges and caudal vertebrae are disarticulated but associated. In

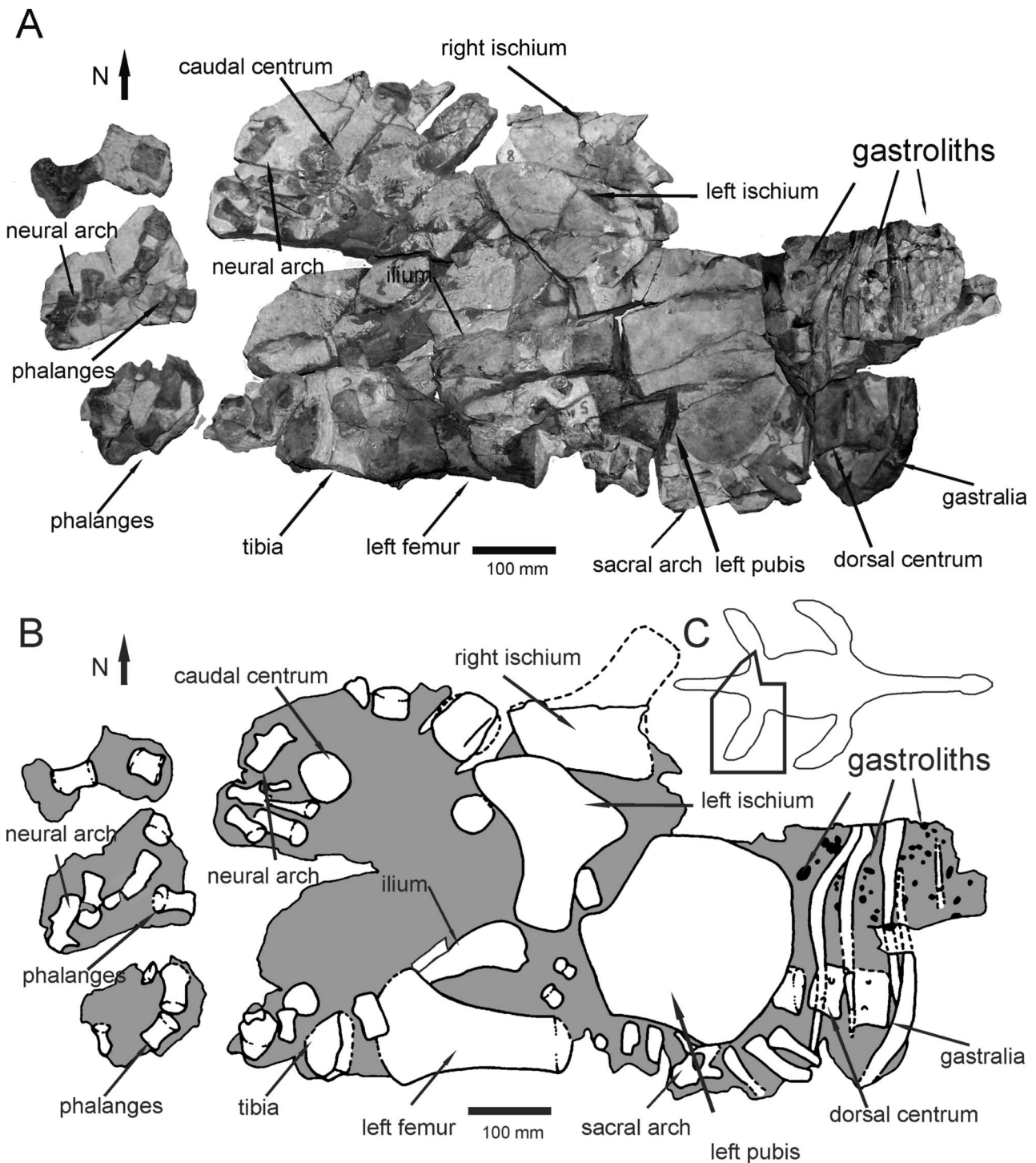


Fig. 2. MLP 98-I-10-20; A, photograph; B, interpretative drawing of the MLP 98-I-10-20 showing the position of gastroliths and C, schematic diagram showing the preserved portion. (Scale bar = 100 mm).

some cases, the caudal vertebrae lie with the articular face parallel to the substrate. The neural arches are not fused to the vertebral centra due to their juvenile condition and, therefore, the neural arches of the dorsal and sacral regions are slightly displaced but in proximity to the vertebral centra, whereas the caudal arches are dispersed. Gastroliths were preserved *in situ* between the gastralia and dorsal ribs but did not include any other stomach contents. None of the

preserved bones have any evidence indicative of predatory or scavenging activity.

Gastroliths

A set of 333 gastroliths was recovered intact associated with specimen MLP 98-I-10-20 (Fig. 3). The matrix hosting the gastroliths consists of very fine-grained, clean sandstones with carbonate cement. The

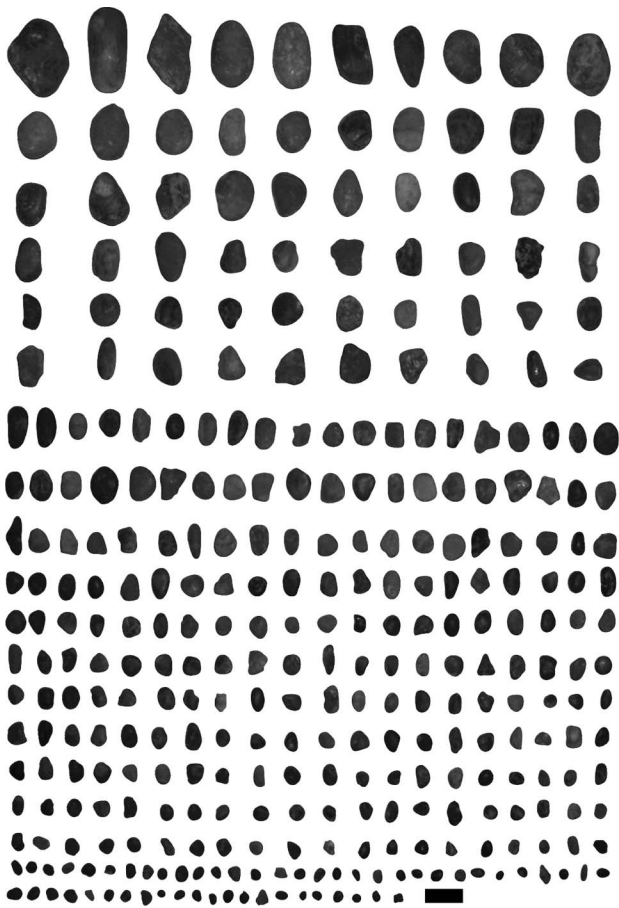


Fig. 3. MLP 98-I-10-20; Gastrolith silhouettes. Scale bar = 20 mm.

total volume of the gastroliths is 275 cm³, with a weight of 725 g; the largest gastrolith weighing 35 g. The means of the principal axes are 14.32 mm (a), 10.2 mm (b) and 6.9 mm (c), which equates to pebble size *sensu* Wentworth (1922) as is shown in Fig. 4A. The mean value of the Maximum Projection Sphericity Index (ψ) is 0.7 and the standard deviation is 0.11, with a slightly skewed frequency distribution (Fig. 4B). The OP index mean value is 0.8, the standard deviation is 4.8. According to the classification of Krumbein (1941), 34% are spheroid, 21.3% are cylindrical, 35.4% are disk-shaped and 9.3% are bladed (Fig. 5). Following the categories established by Powers (1953), 19.2% of the gastroliths are well rounded, 71.2% are rounded and 9.6% are subangular. The surface of the gastroliths is very smooth. However, some gastroliths bear a surface covered by several conchoidal fractures and a great number of pits.

The set of gastroliths that are larger than 15 mm (axis a) consists mainly of rhyolitic rocks (78.3%; Fig. 6A, B) and aggregates of quartz (11.6%); with lesser granitic rocks (3.1%), mudstones (3.1%; Fig. 6C) and aphanitic volcanic rocks (3.9%). Rhyolitic rocks include mainly (1) microporphyric rhyolites with ideomorphic crystals of quartz and feldspar immersed

in a fluid mass of devitrified felsite with marked banding and (2) very fine grained aphanitic aggregates, with a banded texture, which consist of a few microcrystals of quartz and alkali-feldspar immersed in an abundant devitrified felsitic mass. The aggregated quartz crystals are fine grained and homogeneous, and they probably correspond to quartz veins or replacements of original acidic volcanic rocks. The mudstones are black or dark grey, very homogeneous, indurated and compact rocks, locally with bioturbation (Fig. 6C).

Discussion

Taphonomy

MLP 98-I-10-20 represents approximately 20% of the original skeleton, corresponding to the posterior dorsal, sacral and anterior caudal regions. Observing the material in detail, it can be concluded that the incompleteness of the skeleton is likely due to loss by modern erosion of the host strata (right and anterior part) and by incomplete collecting due to adverse climatic conditions during fieldwork (caudal zone).

Usually, decay processes have greater intensity in the abdominal cavity after death, as a product of bacterial activity present in the viscera (Schäfer 1972). The gases produced during the decomposition of soft tissues are accumulated in the body cavity making the body float in the water column, leaving the carcass drifting and susceptible to attack by scavengers. When the gas pressure within the abdominal cavity is high enough, tissues of the body wall rupture resulting in the dispersal of the gastroliths. The preservation of the gastralia and gastroliths *in situ* indicates lack of buoyancy due to gas accumulation in the abdominal cavity (Long *et al.* 2006). However, the fact that the skeleton was found with its ventral side up suggests that some gases accumulated during decomposition, but these were insufficient to make the body float; therefore, the carcass sank gently to the sea bottom (Everhart 2000).

The articulation of the sacral and dorsal vertebrae, and the fact that the ribs, gastralia and gastroliths are in their original positions suggest that rapid burial occurred once the body reached the sea bed and that it was protected from destructive biostratinomic processes. However, the dislocation of bones of the caudal region and autopodial elements suggest a moderate residence time on the substrate (Schäfer 1972). Displacement of bones can be caused by several factors, e.g., the action of scavengers, reworking, bioturbation or dispersal by currents (Martill 1985). There is no sedimentological or taphonomic evidence suggesting bioturbation or scavenging. However, the presence of the latter cannot be ruled out. One possible scenario is that partial burial left the tail

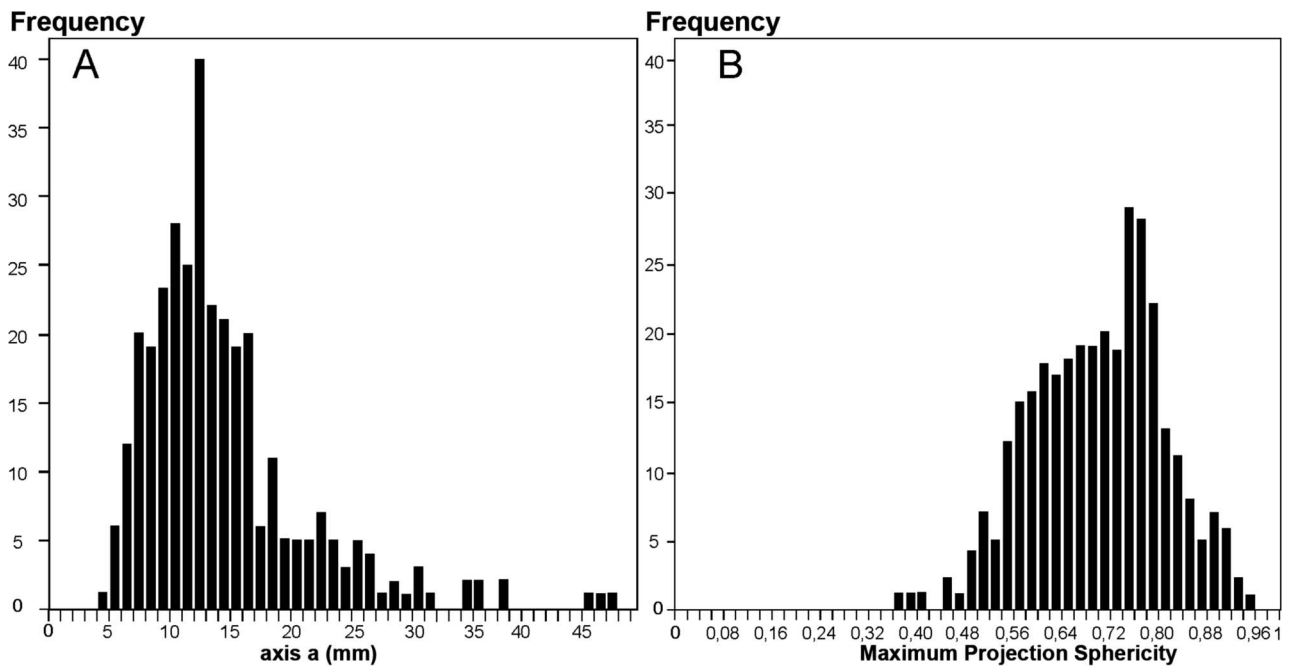


Fig. 4. Histograms showing: A, frequency of measures of axis a; B, Maximum Projection Sphericity (ψ).

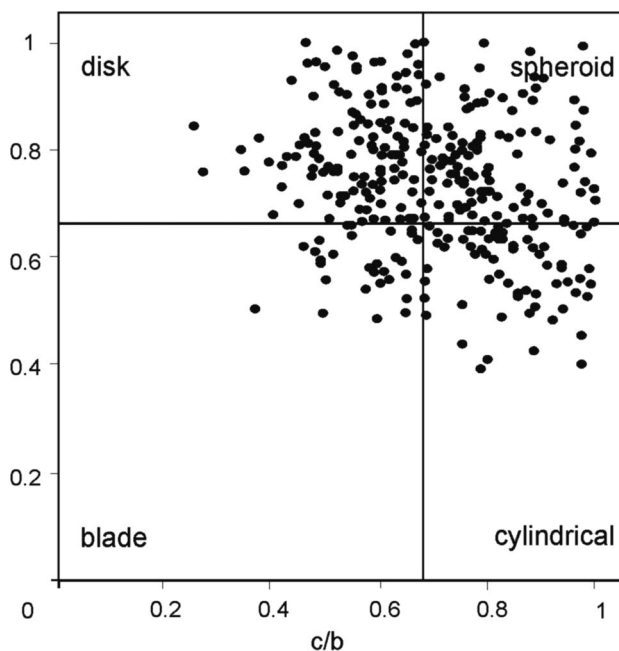


Fig. 5. Gastrolith shape distribution after Krumbein (1941).

and part of the limb exposed. The phalanges and caudal vertebrae are vulnerable to hydrodynamic transport, and their dispersal could be due to weak currents (Barnes & Hiller 2010). Another plausible hypothesis is that after burial of the carcass, the sediment that covered part of the skeleton (the caudal region and limbs) was removed by currents, resulting in the disarticulation and re-orientation of skeletal elements due to taphonomic reworking (e.g., vertebrae with articular face upward).

Recently, Martin *et al.* (2007) reported a juvenile elasmosaur, and Martin (2002) described numerous

juvenile mosasaurs and plesiosaurs excellently preserved in rocks of similar age from Cape Lamb. As in MLP 98-I-10-20, gastroliths, gastralia and ribs of the juvenile elasmosaur are preserved in their original positions, with no evidence of scavenging. The occurrence of MLP 98-I-10-20 adds another record of juvenile marine reptiles from this area.

Gastroliths

General discussion. Several taphonomic and sedimentological criteria have been proposed for the identification of gastroliths. According to Wings (2004), a set of clasts may be considered gastroliths when they are found *in situ* and located in the abdominal area of a relatively complete articulated skeleton. Moreover, the lithological composition of the clasts must be different from the surrounding sediment. Thus, according to these criteria, the clasts associated with MLP 98-I-10-20 that were located between the gastralia and the dorsal ribs (abdominal area) can be identified as gastroliths.

The number of gastroliths associated with plesiosaurs is extremely variable. The number of gastroliths recovered intact (333) from MLP 98-I-10-20, plus those assumed to have been present according to their moulds in the matrix, and the recovered fragments constitute 350 gastroliths. This number is one of the largest recorded (Table 1), only after those cases reported by Cerda & Salgado (2008; 389 gastroliths associated with *Elasmosauridae* indet.) and Thompson *et al.* (2007; 2626 gastroliths associated with an *Elasmosauridae* indet.)

The small number of gastroliths reported in some previous cases may be due to loss, before or after

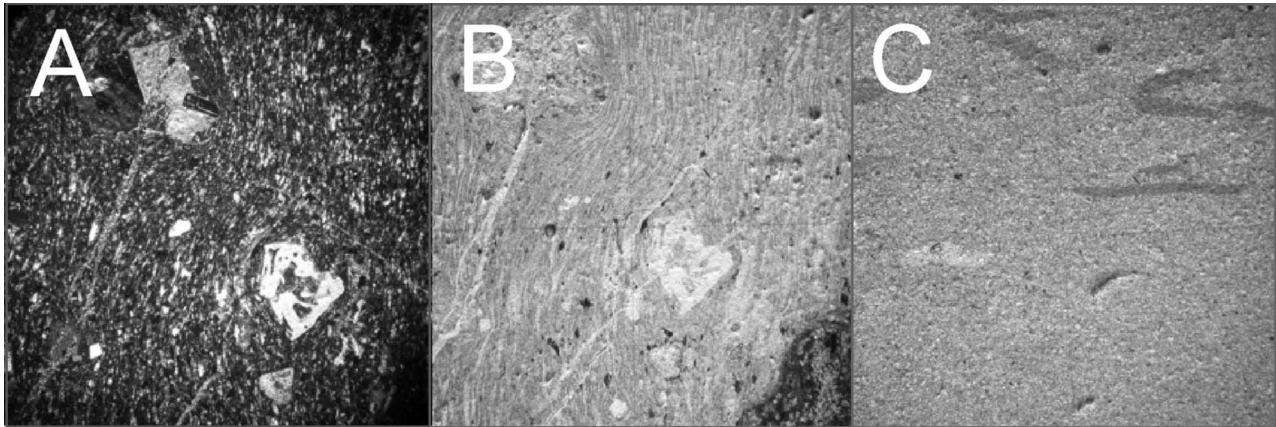


Fig. 6. MLP 98-I-10-20: A, B, thin-sections of rhyolites and C, bioturbated mudstone.

death, via various taphonomic processes (Taylor 1993), and that may be the reason why, in some cases, gastroliths were totally absent, e.g., as in the type specimen of *Elasmosaurus platyurus* reported by Cope (1869). In general, the most numerous gastroliths are associated with elasmosaurs. Relatively few gastroliths have been found associated with polycotyliids, with the exception of the record of the 289 gastroliths reported associated with a specimen referred to *Dolichorhynchops tropicensis* (Schmeisser & Gillette 2009, Schmeisser-McKean 2012), and polycotyliid remains as gastric contents of a mosasaur (Sternberg 1922, Everhart 2004b). In any case, the number of gastroliths is not the most relevant parameter in the study of lithophagous forms, since it varies considerably within the same species and even within the same individual during its life (Taylor 1993, Wings 2004).

Gastrolith physical parameters. The size of the largest gastroliths (considering axis b: 31.2 mm and 22.9 mm) is small compared with other records associated with elasmosaurs (Everhart 2000, Cicimurri & Everhart 2001, Cerda & Salgado 2008). This difference may be related to the juvenile stage of MLP 98-I-10-20 or other factors such as the availability of clasts in the source environment.

The mean value of the Maximum Projection Sphericity Index (ψ) is similar to previously reported gastroliths of plesiosaurs (Darby & Ojakangas 1980, Everhart 2000, Cerda & Salgado 2008, Schmeisser & Gillette 2009; Table 2). The similar values could indicate that the clasts were obtained in similar environments.

Dobkins & Folk (1970) recorded the mean value of sphericity (ψ) and the OP index in clasts (16 to 256 mm size) from river and beach environments. The mean sphericity value recorded for the MLP 98-I-10-20 gastroliths is 0.7 and, therefore, it is more similar to those values recorded by Dobkins & Folk (1970) for clasts from fluvial environments (mean $\psi = 0.684$) than from low-energy beaches (mean $\psi = 0.64$) and

high-energy beaches (mean $\psi = 0.584$). The standard deviation (0.11) is similar to those recorded by Dobkins & Folk (1970) from fluvial environments (0.108) but is also similar to the values recorded for low- and high-energy beaches (0.15 and 0.14). The similarity of the mean sphericity (ψ) of gastroliths in MLP 98-I-10-20 with those recorded in fluvial environments suggests that the gastroliths were obtained in a river, deltaic or estuarine environment. The mean value of the OP index (0.8) is also more similar to that recorded for clasts between 16 and 32 mm in fluvial environments (0.71) compared with those recorded for generalized beach environments (-3.15 ; Dobkins & Folk 1970). However, according to these authors, it is better to use the mean values of both indices (sphericity (ψ) and OP) to discriminate river from beach environments. Combining these indices (Fig. 7) the MLP 98-I-10-20 gastroliths cluster with the fluvial samples analysed by Dobkins & Folk (1970; Fig. 7). The position of the shoreline during deposition of the Cape Lamb Member could be roughly estimated as located within a few tens of kilometres to the west of Vega Island on the basis of sedimentary facies, palaeocurrent vectors and stratal architectures (Olivero, 2012). As a consequence, shoreline and near coastal fluvial deposits coeval with the Cape Lamb Member would be the logical candidates for the source of the gastroliths.

The roundness observed in the MLP 98-I-10-20 gastroliths is similar to that previously reported for other plesiosaurs, including very rounded, rounded and subrounded gastroliths (Everhart 2000, Cerda & Salgado 2008).

Sedimentary provenance of the gastroliths. The rhyolitic clasts among the gastrolith association were probably derived from the Antarctic Peninsula Volcanic Group (Middle–Upper Jurassic; see Hathway 2000 and references cited therein). Geographically, the closest outcrops of the felsic Jurassic volcanics are located on the northern Antarctic Peninsula near Hope Bay and Longing Gap, approxi-

Identification	Location and age	Number of gastroliths	References
Elasmosauridae			
<i>Elasmosaurus platyurus</i>	Eastern Kansas, Late Cretaceous	1	Everhart (2005)
<i>Styxosaurus snowii</i>	South Dakota, Late Cretaceous	253	Welles & Bump (1949)
<i>Styxosaurus</i> sp.	Montana, Late Cretaceous	197	Darby & Ojakangas (1980)
<i>Thalassomedon haningtoni</i>	South Montana, Cretaceous	206	Riggs (1939)
<i>Futabasaurus suzukii</i>	Japan, Early Santonian	~40	Sato <i>et al.</i> (2006)
Elasmosauridae indet.	Antarctica, Late Cretaceous	–	Chatterjee & Small (1989)
Elasmosauridae indet.	Kansas, Late Cretaceous	47	Everhart (2000)
Elasmosauridae indet.	Kansas, Late Cretaceous	95	Cicumurri & Everhart (2001)
Elasmosauridae indet.	Antarctica, Late Cretaceous	2626	Thompson <i>et al.</i> (2007)
Elasmosauridae indet.	Argentina, Campanian–Maastrichtian	389	Cerda & Salgado (2008)
Elasmosauridae indet.	Antarctic Peninsula, early Maastrichtian	333	This work
Polycotylidae			
<i>Dolichorhynchops</i> sp.	Utah, Early Turonian	289	Schmeisser & Gillette (2009)
Polycotylidae indet.	Japan, Late Cretaceous	2	Sato & Storrs (2000)
<i>Pahasapasaurus haasi</i>	South Dakota, Late Cretaceous	3	Schumacher (2007)

Table 1. Records of gastroliths associated with plesiosaurs.

Identification	Sphericity (ψ) mean	Standard deviation	Reference
Elasmosauridae indet.	0.71	0.1	Darby & Ojakangas (1980)
Elasmosauridae indet.	0.74		Everhart (2000, 2005)
Elasmosauridae indet.	0.69	0.11	Cerda & Salgado (2008)
Elasmosauridae indet	0.7	0.11	This work
<i>Dolichorhynchops</i> sp.	0.73		Schmeisser & Gillette (2009)
Fluvial	0.68	0.108	Dobkins & Folk (1970)
Low energy beach	0.64	0.115	Dobkins & Folk (1970)
High energy beach	0.58	0.114	Dobkins & Folk (1970)

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

mately 50 km to the NW and 80 km to the SSW of Vega Island, respectively. Rhyolitic clasts of the Jurassic volcanics are also relatively abundant in the Lower Cretaceous conglomerates of the Gustav Group and in the Santonian–Campanian conglomerates of the Beta Member of the Santa Marta Formation, both of which are exposed on western James Ross Island, approximately 20–30 km WSW of Vega Island (Fig. 1). All these areas, and others that may have sourced acidic volcanic clasts but are presently hidden by ice on the eastern Antarctic Peninsula, were probably exposed to subaerial erosion during deposition of the upper strata of the Cape Lamb Member.

The mudstone clasts lack metamorphic features, such as mineral recrystallization and foliation structure and, thus, were probably not derived from the low-grade metamorphic basement rocks exposed extensively around the Antarctic Peninsula. Instead, they are quite similar to the black mudstones of the Monte Flora Formation (Lower Jurassic) and the black shales of the Lower Cretaceous Gustav Group (see Hathway 2000) that are exposed on the Antarctic Peninsula and James Ross Island, near Cape Lamb

(Fig. 1). Perhaps the fact that these mudstones are very compact and indurated (with no calcareous cement) helps to explain their preservation within the gut of the marine reptiles. In addition, it is possible that the gut environment, at least in this case, was not as abrasive as that of the extant ostrich (*Struthio camelus*) studied by Wings (2007) who recorded a short persistence of mudstones in the gut. This would explain why some plesiosaur gastroliths have smooth surfaces (Everhart 2000, Cerda & Salgado 2008) in contrast to the coarse texture developed in ostrich gastroliths.

The stratigraphical provenance of the quartzose gastroliths is most difficult to infer, and their presence is not unlikely, since this type of gastrolith is common among the gastroliths of plesiosaurs in general (Darby & Ojakangas 1980, Cerda & Salgado 2008).

Since there are many additional rock types exposed in the Antarctic Peninsula, the selectivity of the preserved gastroliths is striking. It is likely that the small grain size, the hardness of the component minerals and the density or structure of these rocks were important factors in preferential ingestion or

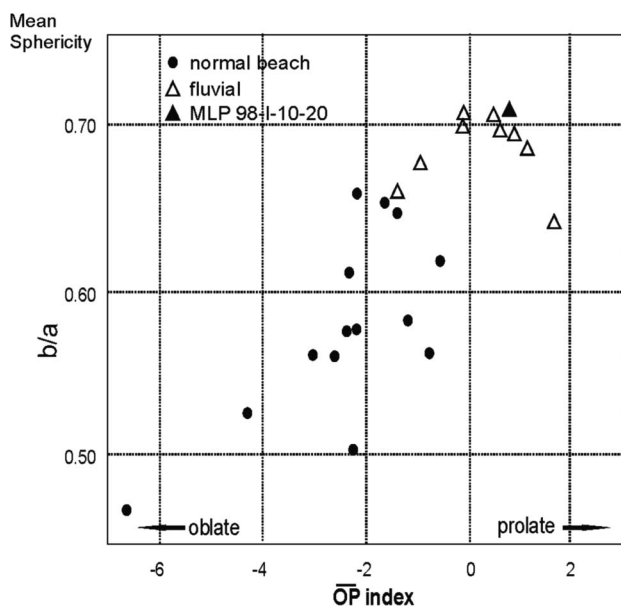


Fig. 7. Plot of mean Maximum Projection Sphericity (ψ) values vs. mean Oblate-Prolate Index (OP index). \blacktriangle , MLP 98-I-10-20 gastroliths; \triangle , fluvial samples; \bullet , normal beach samples (modified from Dobkins & Folk 1970).

retention. This result is congruent with observations made on other sets of plesiosaur gastroliths (Cerde & Salgado 2008, Darby & Ojakangas 1980).

Palaeobiology and function

According to Cicimurri & Everhart (2001) the maximum value $b \times c$ may indicate the maximum prey cross-section. In the case of MLP 98-I-10-20, the maximum prey cross-section estimated by this method is 7.46 cm². This value is lower than the one (9.54 cm²) obtained by Cerde & Salgado (2008) for a smaller Elasmosauridae indet. (J.P. O'Gorman *obs. pers.*). This suggests that the maximum prey-size was similar in both cases. However, it is also possible that the method yielded consistent results in small plesiosaurs, but underestimated the maximum prey-size in larger specimens. The consistency of the estimation could also have been influenced by the availability of clast sizes in the environment that actually correspond to the maximum prey-size usually consumed.

Niche partitioning has been proposed for plesiosaurs, particularly elasmosaurs (Wiffen *et al.* 1995). According to this hypothesis, the juveniles would have lived in protected environments, near the coast. Inference about the environment of origin of the Vega Island gastroliths indicates that they were obtained in a nearshore or fluvial environment, the expected environment for a juvenile according to this hypothesis. Significantly, Kear & Godthelp (2008) and Vajda & Raine (2010) have also proposed riverine habitats for other austral Cretaceous plesiosaurs based on feeding mode and palynological evidence. However, given the small number of analysed cases,

the evidence is too weak to support generalizations. With regard to the relationship between the source environment of the gastroliths and the final depositional environment, all that can be concluded is that the case analysed in this paper is similar to that reported by Cerde & Salgado (2008), in which the environment where the gastroliths were obtained and the sediments in which the specimen was finally preserved both have fluvial influence.

Several hypotheses have been proposed to explain the presence of gastroliths associated with plesiosaurs. One is the hypothesis of hydrostatic control (Taylor 1993), in which the function of gastroliths was to allow buoyancy control with increasing total body mass. The whole mass of gastroliths associated with MLP 98-I-10-20 that was recovered intact (725 g) plus recovered fragments weigh less than 1000 g. This mass is small compared with the total body mass estimated for the specimen MLP 98-I-10-20. Considering the reference table for elasmosaurid body mass compiled by Everhart (2000), a specimen of approximately 4.5 m in length has an estimated body mass of 350 kg. Thus, the relationship between the gastroliths' mass and body mass is less than $1/350 = 0.0028$ or 0.28%. According to computer models made for plesiosaurs (Henderson 2006), this ratio would not significantly affect the buoyancy of the animal. The impossibility of the gastrolith mass associated with the specimen MLP 98-I-10-20 to produce a significant change in buoyancy is in accord with the results obtained by other authors, who rejected the buoyancy control hypothesis for the same reason (Everhart 2000, Cerde & Salgado 2008, Schmeisser & Gillette 2009).

However, using this method to test the buoyancy control hypothesis is problematic due to the negative bias in determining the gastroliths' mass. The mass of gastroliths varies continuously through life and many gastroliths may be lost due to taphonomic processes or incomplete collection (Taylor 1993). Nonetheless, a mass of gastroliths larger than the 5% required to significantly influence buoyancy (Henderson 2006) has not been recorded. Even considering the sources of error, if gastroliths indeed had a hydrostatic function, the mass required should have been found in at least some cases. MLP 98-I-10-20 provides independent information to test the buoyancy control hypothesis. Pachyosteo sclerosis, i.e., the development of hyperplastic solid periosteal cortical and compact medullary region has been reported in juvenile elasmosaurs (Wiffen *et al.* 1995). This condition has been associated with an adaptation to slow locomotion and limited mobility, but it also correlates with diving, increasing the total body mass (Wiffen *et al.* 1995). Therefore, it can be expected that if the function of gastroliths were buoyancy control, their presence should be of less importance in juvenile specimens. MLP 98-I-10-20, a juvenile with gastroliths, does not support this inference. The presence of gastroliths in

juveniles such as MLP 98-1-10-20 and the specimen reported by Martin *et al.* (2007) from the same formation provides evidence against the buoyancy control hypothesis, but further studies are required.

The other most commonly cited hypothesis is that gastroliths aided digestion. Among the features usually cited supporting this hypothesis are conchoidal fractures (Everhart 2004a, Cerda & Salgado 2008) and the presence of broken gastroliths, of which both parts are recovered (Cerda & Salgado 2008). Both features seem to be associated with interaction among the gastroliths inside the digestive system. In MLP 98-1-10-20 only a few gastroliths with conchoidal fractures were detected that reveal a low grade of abrasion. Moreover, this does not confirm that these marks were produced after being ingested. In summary, MLP 98-1-10-20 lacks definitive information to evaluate the digestive aid hypothesis.

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