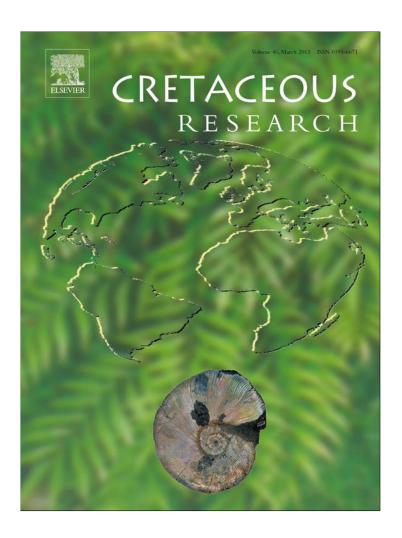
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First record of gastroliths associated with elasmosaur remains from La Colonia Formation (Campanian—Maastrichtian), Chubut, Patagonia Argentina, with comments on the probable depositional palaeoenvironment of the source of the gastroliths

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ABSTRACT

A gastrolith set, comprising 197 elements, associated with an indeterminate elasmosaurid plesiosaur collected from the Campanian—Maastrichtian La Colonia Formation, Chubut, Argentina, is described. Most of the gastroliths are discoidal (41.9%) or spheroidal (34.8%), with a mean Maximum Projection Sphericity Index value of 0.69 and a mean OP Index value of -0.74. The values of these indices are compared with those recorded for gastroliths associated with other Upper Cretaceous elasmosaurids to see if patterns with palaeobiological relevance are evident. The mean values of the Maximum Projection Sphericity Index and the Oblate-Prolate Index allow us to infer a fluvial or estuarine origin for all the elasmosaurid gastroliths for which these indices have been calculated. This inference is palaeobiologically informative because it indicates that at least some Upper Cretaceous elasmosaurs entered into estuarine (or fluvial) environments. It also helps explain the interesting vertebrate assemblage of the Allen and La Colonia formations where a rich continental fauna is recorded but elasmosaurids and polycotylids are the only well represented vertebrates with marine affinities.

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1. Introduction

Lithophagia, defined as the ingestion of rocky fragments called gastroliths or, more specifically, geo-gastroliths (Wings, 2007), is well documented in elasmosaurid plesiosaurs (Welles and Bump, 1949; Taylor, 1993; Everhart, 2000, 2005; Gasparini and Salgado, 2000; Whittle and Everhart, 2000; Cicimurri and Everhart, 2001; Hiller et al., 2005; McHenry et al., 2005; Cerda and Salgado, 2008; Kubo et al., 2012; O'Gorman et al., in press). Even though the function of gastroliths in these marine reptiles has been under debate since they were first recorded (see Wings, 2007 and bibliography therein), it is clear that the parameters of gastroliths are palaeobiologically informative (Darby and Ojakangas, 1980; Everhart, 2000, 2005; Cerda and Salgado, 2008; Schmeisser and

Gillette, 2009; O'Gorman et al., in press). Cerda and Salgado (2008) described a well-preserved gastrolith cluster associated with an Elasmosauridae indet. (MCS Pv 4) from Río Negro, which was collected from the upper Campanian—lower Maastrichtian levels of the Allen Formation, and they inferred a fluvial or estuarine environment as the original gastrolith source. In November 2011, a joint team from the Museo de La Plata, the Universidad de La Pampa and the Museo Paleontológico "Egidio Feruglio", led by Z. Gasparini, collected an elasmosaur specimen with associated gastroliths from the Campanian—Maastrichtian La Colonia Formation. The aim of this paper is to describe the new set of gastroliths, to compare them with other sets associated with coetaneous elasmosaurid specimens, especially with that described by Cerda and Salgado (2008), and to discuss their original source environment and the palaeobiological significance.

2. Geological setting

The La Colonia Formation crops out on the south-western margin of the Somún Curá Massif, Chubut Province, Argentina

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(Ardolino and Delpino, 1987) (Fig. 1). Pascual et al. (2000) recognized three facies associations in the formation. The lowermost facies is characterized by cross-bedded sandstones and conglomerates deposited in a fluvial environment. The middle facies, from which the material described in this work was collected, is composed mostly of laminated mudstones, pelitic fine sandstones, and banded siltstones and claystones that represent deposition in an estuarine environment or tidal flat, influenced by occasional high freshwater streamflows from the continent and tidal currents from the sea (Pascual et al., 2000). This facies association was deposited under a seasonal climate with alternating periods of humidity and aridity (Ardolino and Delpino, 1987). The uppermost facies association is composed of laminated pelites deposited in a tidal flat setting (Pascual et al., 2000).

The vertebrate fauna recorded in the La Colonia Formation includes freshwater fishes (such as dipnoans), turtles, snakes, plesiosaurs, dinosaurs and mammals (Bonaparte, 1985; Albino, 2000; Gasparini and de La Fuente, 2000; Pascual et al., 2000; Apesteguía et al., 2007; Rougier et al., 2009; Sterli and de la Fuente, 2011).

The La Colonia Formation is Campanian—Maastrichtian in age, based on records of foraminiferans and ostracods (Page et al., 1999). The lower and middle parts of the formation can be correlated with the upper Campanian—lower Maastrichtian Allen Formation, whereas the upper part is correlative with the upper Maastrichtian—Danian Jagüel Formation, which crops out in the Neuquén Basin (Page et al., 1999).

3. Material and methods

3.1. Material

Specimen MPEF-PV 10602 is an incomplete postcranial skeleton consisting of cervical, dorsal and caudal vertebrae, ribs, a carpal/tarsal element, indeterminate fragments and 197 gastroliths (Fig. 2).

Locality and horizon. MPEF-PV 10602 was collected in Cerro Bayo (43°00′S, 67°37′W), north-east Chubut Province, Argentina (Fig. 1), from the middle facies association of the La Colonia Formation, upper Campanian—lower Maastrichtian (Page et al., 1999; Pascual et al., 2000).

Systematic remarks and ontogenetic stage. One fragment of a cervical vertebra shows an elongated centrum with lateral ridges and

bilobed articular faces, three features typical of Upper Cretaceous elasmosaurs (O'Keefe, 2001, 2004).

Caudal vertebrae with strongly projected parapophyses, similar to those of MPEF-PV 10602, are also found in the elasmosaurid specimens MCS Pv 4, MLP 71-II-13-1 and MUC Pv 92 (Lago Pellegrini) and MML PV 420 (Salitral de Santa Rosa area), collected from the upper Campanian—lower Maastrichtian Allen Formation (Gasparini and Salgado, 2000; O'Gorman et al., 2011). Although this character could have systematic value, at the current state of knowledge we cannot go beyond a familial assignation; thus, we assign the MPEF-PV 10602 to Elasmosauridae indet.

The presence of the neuro-central closure in the preserved vertebrae of MPEF-PV 10602 indicates that it is an adult (sensu Brown, 1981).

3.2. Methods

The parameters considered in this study are those usually employed in descriptions of plesiosaur gastroliths (Darby and Ojakangas, 1980; Cicimurri and Everhart, 2001; Cerda and Salgado, 2008), and they were specifically applied to draw comparisons between MPEF-PV 10602 and previously described gastrolith samples. In order to do that, we took into account the number of gastroliths in the cluster, the dimensions of the three main axes of each gastrolith: long (a), intermediate (b) and short (c), together with the total volume and mass of the set. The linear measurements were obtained using callipers with a precision of about 0.1 mm. The volume was measured using the method of displacement of liquid in a graduated container. Size was described following the scale proposed by Wentworth (1922).

The Maximum Projection Sphericity Index ($\psi = (c^2/b * a)^{1/3}$) and the Oblate-Prolate Index [OP = (10/(c/a)) * ((a - b)/(a - c) - 0.5)] (Dobkins and Folk, 1970), in particular the means and standard deviations of these indices, were used in this work. 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).

Several gastroliths were found broken by recent fractures and were not considered in order to avoid the introduction of errors related to changes in shape, sphericity and roundness.

Institutional abbreviations. MCS Pv, Museo de Cinco Saltos, Río Negro Province, Argentina; MLP, Museo de La Plata, Buenos Aires Province, Argentina; MML, Museo Municipal de Lamarque, Río

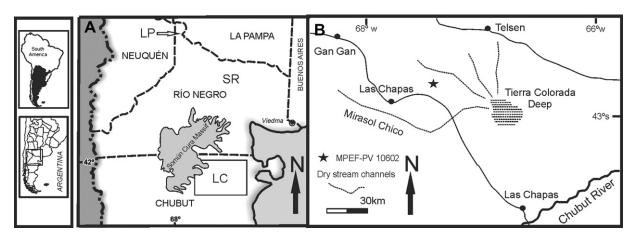


Fig. 1. A, general map of North Patagonia: LC, La Colonia area; LP, Lago Pellegrini locality; SR, Salitral de Santa Rosa area. B, map of the La Colonia area where the MPEF-PV 10602 was collected (modified from Pascual et al., 2000; Gasparini et al., 2007).

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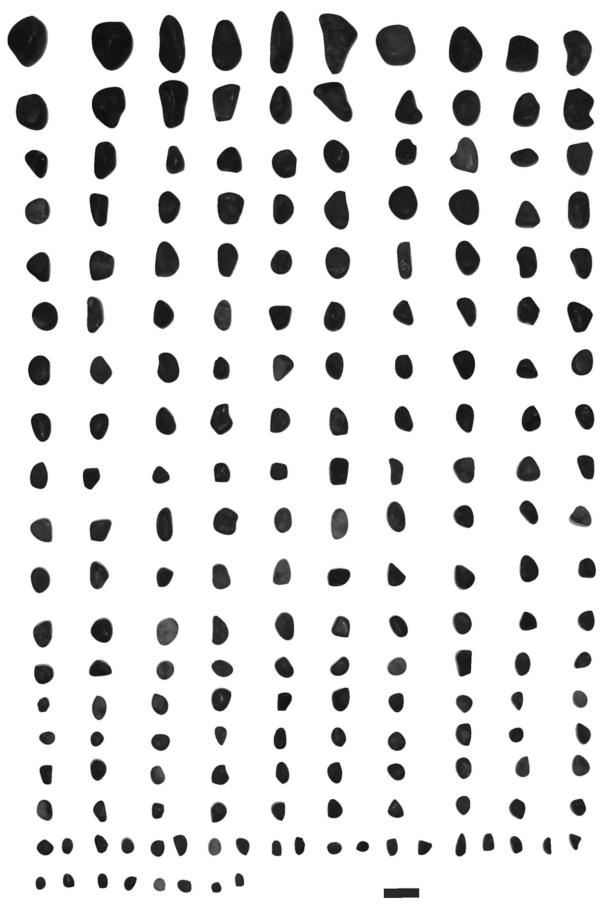


Fig. 2. MPEF-PV 10602; gastroliths. Scale bar represents 20 mm.

Negro Province, Argentina; MPEF, Museo Paleontológico "Egidio Feruglio", Chubut Province, Argentina.

4. Results

The gastrolith set has 197 elements (Fig. 2). The total volume occupied by the gastrolith set is 250 cm³, with a weight of 441 g and with the largest gastrolith weighting 18.6 g. The means of the principal axes are 15.19 mm (a), 11.64 mm (b), and 7.94 mm (c), which equate to pebble size sensu Wentworth (1922).

The mean value of the Maximum Projection Sphericity Index (ψ) is 0.69, and the standard deviation is 0.11. The OP index mean value is -0.74, and the standard deviation is 4.85. According to the classification of Krumbein (1941), 34.8% are spheroidal, 16.8% are cylindrical, 41.9% are discoidal, and 6.5% are blade-shaped (Fig. 3). Following the categories established by Powers (1953), 9.9% of the gastroliths are well rounded, 61.3% are rounded and 28.8% are subangular. The surface of the gastroliths is very smooth and evenly polished. Only a few gastroliths bear a surface covered by several conchoidal fractures; most of the gastroliths have parts of the surface covered by pits (Fig. 4). All the gastroliths are hard siliceous rocks of black, dark or light grey colour.

5. Discussion

Specimen MPEF-PV 10602 was collected from a surface of about 2 m²: 197 small stones were spread among the associated bones of this single specimen. Because of the absence of similar stones in the surrounding area, we interpret these elements as gastroliths. Although 197 gastroliths were recovered more stones may have been lost by erosion. Bone breakage produced by erosion is very pronounced but most of the gastroliths are intact, probably as a result of their siliceous composition.

The number of gastroliths collected is in the range known in other elasmosaurs: 253, *Styxosaurus snowii* (Welles and Bump, 1949); 197, *Styxosaurus* sp. (Darby and Ojakangas, 1980); 389, Elasmosauridae indet. (Cerda and Salgado, 2008); 333, Elasmosauridae indet. (O'Gorman et al., in press), with the only exception being the 2626 gastroliths recorded by Thompson et al. (2007). The shape proportions are similar to other records, being mostly

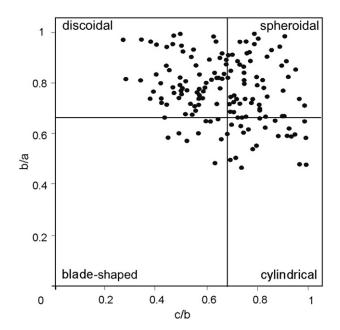


Fig. 3. MPEF-PV 10602; gastrolith shape distribution after Krumbein (1941).



Fig. 4. MPEF-PV 10602; detail of the surface of one gastrolith. Scale bar represents 20 mm.

spheroidal or discoidal (Darby and Ojakangas, 1980; Cerda and Salgado, 2008; O'Gorman et al., in press). The roundness and features of the surface are also similar to those previously recorded for plesiosaur gastroliths (Everhart, 2000, 2005; Schmeisser and Gillette, 2009; Cerda and Salgado, 2008; O'Gorman et al., in press).

The most important parameters in gastrolith studies are the Maximum Projection Sphericity Index (ψ) and the Oblate-Prolate Index (OP), because they provide information about the original depositional environment from which the gastroliths were sourced. Hence, they may say something about the palaeobiology of the animal that ingested them. The mean Maximum Projection Sphericity Index recorded for MPEF-PV 10602 (0.69) is comparable to other values recorded for elasmosaurid gastrolith sets (0.71, Darby and Ojakangas, 1980; 0.74, Everhart, 2000, 2005; 0.69, Cerda and Salgado, 2008; 0.7, O'Gorman et al., in press) and a polycotylid set ($\psi = 0.73$, Schmeisser and Gillette, 2009), which indicates a similar depositional environmental origin. Dobkins and Folk (1970) recorded similar Maximum Projection Sphericity mean values from fluvial samples (0.68). These values are greater than those they recorded for beach environments (0.64, low energy beaches; 0.58, high energy beaches). Therefore, the Maximum Projection Sphericity mean values of the gastroliths of MPEF-PV 10602 and other Upper Cretaceous elasmosaurs and polycotylids are more similar to those recorded for fluvial samples than the values recorded for beach samples (Darby and Ojakangas, 1980; Everhart, 2000, 2005; Cerda and Salgado, 2008; Schmeisser and Gillette, 2009; O'Gorman et al., in press; this paper).

The OP Index has been less used than the Maximum Projection Sphericity in descriptions of gastroliths; in particular, Cerda and Salgado (2008) did not record the OP Index of the MCS Pv 4 set. For comparative purposes, the OP Index of the MCS Pv 4 set was calculated in this work based on the original data used by Cerda and Salgado (2008). The OP Index recorded in MPEF-PV 10602 is -0.74, and that of MCS Pv 4 is 0.15; these values fall approximately within the range of OP mean values recorded for fluvial environments (Dobkins and Folk, 1970). Fig. 5 shows the values of the main sphericity (ψ) and OP indices, of the sets from MPEF-PV 10602, MCS Pv 4 and MLP 98-I-10-20 (lower Maastrichtian of Vega Island, Antarctica). The values of these sets are closer to the normal fluvial examples, and differ from the beach samples.

Thus, the mean values of the Maximum Projection Sphericity and OP indices calculated for different Upper Cretaceous elasmosaurid and polycotylid gastrolith sets are similar to those recorded

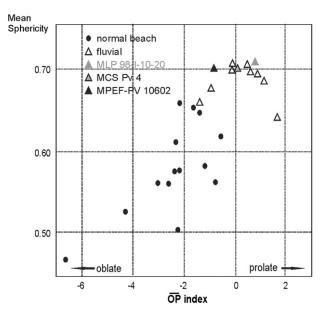


Fig. 5. Plot of mean Maximum Projection Sphericity (ψ) values vs. mean Oblate-Prolate Index (OP Index). \blacktriangle , MPEF-PV 10602 (Elasmosauridae indet.); \vartriangle , MCS Pv 4 (Elasmosauridae indet.); \blacktriangle , MILP 98-I-10-20 (Elasmosauridae indet.); 战, fluvial samples; \blacksquare , normal beach samples (modified from Dobkins and Folk, 1970). Elasmosauridae data taken from Cerda and Salgado (2008) and O'Gorman et al. (in press).

for clasts of fluvial environments or estuaries. It is important to note that fluvial clasts could be deposited at the distal ends of fluvial systems in estuaries, but still retain the fluvial values of the indices (Dobkins and Folk, 1970).

Therefore, the inference about the fluvial or estuarine source of gastroliths (FESG) is a subject that needs to be discussed in greater depth. Interestingly, the FESG seems to be independent of the ontogenetic stage and taxonomy of the specimen, because it has been recorded in both adults and juveniles of different genera of elasmosaurs (Everhart, 2000, 2005; Cerda and Salgado, 2008; O'Gorman et al., in press) and even in polycotylids (Schmeisser and Gillette, 2009). The FESG inferred for Upper Cretaceous Elasmosauridae and Polycotylidae (although the latter needs to be confirmed by well-documented cases) indicates that these reptiles ingested pebbles in fluvial or estuarine environments, where they also would have looked for food. The locality from which MPEF-PV 10602 was collected has not yielded any vertebrates with marine affinities other than plesiosaurs, but a great deal of material referred to Dipnoii, Chelidae, ophidians and dinosaurs has been recovered (Bonaparte, 1985; Albino, 2000; Gasparini and de La Fuente, 2000; Pascual et al., 2000; Apesteguía et al., 2007; Rougier et al., 2009; Sterli and de la Fuente, 2011). The inference about the FESG and therefore of the entry of elasmosaurs into estuarine environments could be related to the vertebrate assemblage recorded for the Campanian-Maastrichtian La Colonia Formation, which embraces vertebrates with marine affinities (represented only by Elasmosauridae and Polycotylidae) and a rich continental fauna. A similar case can be seen in specimen MCS Pv 4, since the Allen Formation is very rich in continental vertebrates, with plesiosaurs being the only marine vertebrates (Martinelli and Forasiepi, 2004).

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