Taxonomic identification of the Megaloolithid egg and eggshells from the Cretaceous Bauru Basin (Minas Gerais, Brazil): comparison with the Auca Mahuevo (Argentina) Titanosaurid eggs

Gerald Grellet-Tinner¹,²
Hussam Zaher²

ABSTRACT

The taxonomically (Titanosaurid) identified eggs and eggshells of Auca Mahuevo (Patagonia, Argentina) provide an opportunity to compare and identify orphan megaloolithid eggs found elsewhere. Previous investigation determined that the oological material from Neuquén (Megaloolithus patagonicus) and Peru (M. pseudomamillare) are related to Titanosaurid dinosaurs. Examination of an egg and several (megaloolithid) eggshell fragments from the Upper Cretaceous Marilia Formation strongly suggests, as oological characters are at least genus specific, that the same group of Titanosaurid dinosaurs, which lived in the Neuquen Basin during the Late Campanian, were also present and reproducing in the Cretaceous Bauru Basin (Brazil). Furthermore, it has been suggested that these Titanosaurs, based on the site of Auca Mahuevo, demonstrated colonial nesting and nesting fidelity. These reproductive behaviors would advocate that similar nesting sites should exist in the Upper Cretaceous formations of the Bauru Basin and remain to be discovered, as the present Peiropolis locality represents a secondary deposit where fossils have been transported by high-energy fluvial system.

Keywords: Titanosaurid eggs, Bauru Basin, Auca Mahuevo, eggshell structure, dinosaur paleobiology.

INTRODUCTION

The parataxonomic megaloolithid oofamily regroups a significant number of eggs that have not been positively identified taxonomically (Vianey-Liaud et al., 2003). Megaloolithid eggs (Bravo et al., 2000; Mohabey, 2000; Sahni et al., 1994; Vianey-Liaud et al., 1994, 2003) have been mostly associated with sound support to sauropod dinosaurs and even on occasions to Titanosaurs (Erben, 1970; Powell, 1992; Sahni et al., 1994; Faccio, 1994; Vianey-Liaud et al., 1994, 1997; Calvo et al., 1997).

Localities that preserve Mesozoic eggs with embryonic remains inside (embryo in ovo) are unique, not only by their rarity, but also because they provide a reliable frame of reference for identification.
of isolated oological remains found in other fossil bearing layers. Furthermore, once an egg and eggshell structure has been taxonomically identified, it becomes an excellent proxy to infer the presence of the parent dinosaur lineage. This is the case for the exceptionally preserved oological material from the Patagonian locality of Auca Mahuevo (Chiappe et al., 2001a, Grellet-Tinner et al., 2004, Grellet-Tinner, 2005). A detailed description of eggs unequivocally associated with titanosaurid dinosaurs from the Late Cretaceous colonial nesting site of Auca Mahuevo (Neuquén Province, Argentina) was provided by Chiappe & Dingus (2001) and Grellet-Tinner et al. (2004). Oological remains from this Patagonian locality also suggest that titanosaurids would have come to lay their eggs season after season, thus demonstrating a nesting site fidelity (Chiappe & Dingus, 2001). In addition to the oological description, the authors provided a comparison of these titanosaur eggs, their eggshell structure, and nesting behaviors with other South American eggs and eggshells that shared a suite of common characters (Grellet-Tinner et al., 2004). However, this investigation did not include eggs or eggshells from Brazil as their availability and description at the time were extremely scanty (Magalhães Ribeiro, 1999, 2000, 2002). Presently, only one egg and associated eggshell fragments from near the city of Uberaba in the state of Minas Gerais could potentially match the Auca Mahuevo oological material. This material, classified in the Megaloolithid parataxonomic oofamily (Magalhães Ribeiro, 1999, 2000, 2002), has been recovered from the Late Cretaceous Marília Formation of the Bauru Basin (Fig 1), which deposition is approximatively coeval with the Anaclito Formation where the referred Patagonian eggs were discovered (Candeiro et al., 2006; Leanza et al., 2004). If both oological materials are similar, their presence in contemporaneous sedimentary basins is congruent with the titanosaurid fossil record based on disarticulated skeletal material (Campos & Kellner, 1999; Kellner & Campos, 2000; Santucci & Bertini, 2000, 2001, 2006). Furthermore, this would be the first paleobiological evidence that this group of sauropods would have reproduced in what is presently Brazil during the late Cretaceous, which could have been expected but had not yet documented, as it seems that evidence support these dinosaurs migrated to colonial sites they favored to lay their eggs.

Abbreviations
Institutional abbreviations: CPP, Centro de Pesquisas Paleontologicas Llewellyn Ivor Price of Peirópolis, Brazil; LACM, Natural History Museum of Los Angeles County, U.S.A.; MCF-PVPH, Museo Carmen Funes, Plaza Huincaul, Argentina; MUCPV, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina;

Technical abbreviations: MT, Membrana Testacea; PLM, polarized light microscopy; SEM, scanning electron microscope; TLM, transmitted light microscopy.

MATERIAL AND METHODS

Material examined for this study and used as a comparative framework to interpret the oological remains known from the Brazilian Cretaceous Bauru Basin are as follows: Auca Mahuevo (Patagonia): eggs: MCF-PVPH 147, 250, 262, 263, 264; eggshells: MCF-PVPH 442, 443, 444; embryos in ovo MCF-PVPH 147, 250, 262, 263, 264 (Chiappe et al. 2001). Material used as representatives of the oological remains from the Brazilian Cretaceous Bauru basin and illustrated by Magalhães Ribeiro (1999, 2000, 2002) are as follows: Peirópolis (Minas Gerais): egg: CPP457; eggshells: CPP456, 411.

Eggshells from Auca Mahuevo were treated as described in Grellet-Tinner et al. (2004). Specimens from Peirópolis were compared solely based on their three descriptions (Magalhães Ribeiro, 1999, 2000, 2002) as the author of these publications restricted access of the collection for further observations.

DESCRIPTION

The Auca Mahuevo eggs typically display a spherical to subspherical shape (Fig. 2A) and signs of fractures with various degrees of compression (Grellet-Tinner et al., 2004). Their diameters range between 125 and 140 mm. The preserved aspect of these eggs is here interpreted as the result of their original shape combined with sedimentary compaction coupled with a certain amount of plasticity due to the monolayered nature of the eggshell structure (Grellet-Tinner et al., 2004).

Eggshell fragments can show substantial diagenetic variations visible in their internal structure, their pore canals and apertures, as well as their outer surface (Grellet-Tinner, 2005). In best-preserved specimens, the outer eggshell surface displays equally distributed nodes (Figs. 2C, D) that are visible to the naked eye, with some coalescing into longer structures (Fig. 2C). The average diameter of the nodes is 0.58 mm, their
nodular height measured from the base to the apex is 0.28 mm, and recorded internodular distances range from 0.52 to 0.87 mm. The eggshell thickness ranges from 0.65 mm to 1.31 mm according to the degree of diagenetic alteration, but this higher dimension corresponds to

![Map of the Bauru Basin and surrounding areas showing stratigraphic relationships.](image)

**FIGURE 1**: A) Location of the Peirópolis titanosaurid oological material in the Bauru Basin-Brazil (after Riccomini 1997, modified): 1. Precambrian basement rocks; 2. Paraná Basin (Ordovician to Triassic); 3. Serra Geral Formation (Early Cretaceous); 4. Bauru Basin (Late Cretaceous). B) Stratigraphic relationships of the Bauru Group in the southeastern part of the Bauru Basin: 1. basaltic rocks; 2. cross-bedded sandstone; 3. massive to slightly stratified sandstone; 4. massive to slightly stratified sandstone interlayered with mudstones; 5. sandstone, siltstone and mudstone; 6. sandstone and mudstone; 7. sandstone and conglomerate with limestone cement.
FIGURE 2: Eggs and eggshells from the locality of Auca Mahuevo, Río Colorado Formation, Neuquén Basin. A: Titanosaurid egg found on the surface of stratigraphic egg layer 3. Note the sub-spherical shape of the specimen here considered either as a biological character of this saurischian family or influenced by taphonomic processes coupled with a certain eggshell plasticity due to its mono-layered structure. B: The site of Auca Mahuevo is interpreted as a flood plain with seasonally overbanking rivers where titanosaurid dinosaurs would exhibit colonial nesting and site fidelity behaviors. A large number of egg clutches are surfacing in several stratigraphic egg layers. C: Eggshell surface ornamentation displays single and coalescent nodes (two black arrows where nodes coalesce). D: SEM image of the perfect nodular ornamentation of titanosaurid eggshells with round pore apertures located in the interstices between the nodes. E: SEM detail of figure 1D. F: cross section of a titanosaurid eggshell that shows a pore canal (arrow 1) transecting the entire thickness of the mono-layered eggshell. Note the network of connecting vertical pores with a system of horizontal pore canals here only visible because of the MT preservation. G: TLM view of a thin section that contains two eggshell fragments facing each other. Note the cores of the shell units as shown by arrow 1, the shell units (arrows 2 and 3) crossed by lines that are interpreted as ex-organic structures, and the MT (arrow 4) preserved only in one section of the slab.
well-preserved specimens. Eggshell is composed of a single structural layer consisting of acicular calcitic crystals radiating from nucleation centers located in upper section of the MT (Figs. 2F, G). The regular grouping of the acicular crystals radiating out of any given core and their vertical extension define the eggshell unit and the thickness of the eggshell. From the inner eggshell surface, the units flare out at approximately 40 degrees and average 0.63 mm as they reach a third of the total eggshell thickness (Fig. 2G). Pores are ubiquitous (Fig. 2E) and form a network of horizontal canals connected to the vertical pores that open between the nodes of the outer surface with apertures ranging from 0.15 to 0.29 mm (Figs. 2D, G). When observed in PLM and TLM, the eggshell units are transversally crossed by thin and compact growth lines (Fig. 2G) that correspond to the proteinous fabric of the eggshell structure (Grellet-Tinner et al., 2004).

The ellipsoidal shape of the Peirópolis megaloolithid egg (Fig. 3A) results from lateral compaction (Magalhães Ribeiro, 2002), yet the measured diameters of 150 by 100 mm are well within the range of those from Auca Mahuevo. The nodular surficial ornamentation consists of well-distributed nodes ranging from 0.5 to 0.8 mm (Magalhães Ribeiro, 2000, 2002) with some coalescing into longer structures (Fig. 3B). According to the author, the egg suffered from several phases of diagenetic alteration resulting in manganese and calcitic depositions; nevertheless, average eggshell thickness is estimated at 1.5 mm for the egg and ranges from 1 to 1.5 mm for isolated eggshell fragments found nearby. The mono-layered eggshell consists of eggshell units radiating from nucleation centers that are irregularly spaced and separated by substantial intervals at their base. Eggshell units average 0.6 to 0.8 mm at their maximum width and are crossed throughout by arched growth lines. When observed, pores are described as tubocanaliculate (word issued from the egg parataxonomic classification used by Magalhães Ribeiro, 2002) alternatively measuring 70 to 100 mm (Magalhães Ribeiro, 2000) and 0.6 to 0.1 mm (Magalhães Ribeiro, 2002) in diameter. Besides the obvious fact that these measurements are not consistent and clearly erroneous for the former, it is not clear whether they represent the diameters of the pore openings at the surface and/or that of the pore canals only. Observation of figure 3C in Magalhães Ribeiro (2002) is not congruent with the 70 to 100 mm measurement presented in Magalhães Ribeiro (2000); this favours the interpretation that pore canals range between 0.06 and 0.1 mm.

**DISCUSSION**

In previous work of Grellet-Tinner et al. (2004) noted that several South American isolated eggshell fragments and complete eggs have been referred to the megaloolithid oofamily, which the Auca Mahuevo eggs belong to. Among those, a few were alleged to be titanosaurid eggs (e.g., Erben, 1970; Powell, 1992; Sahni et al., 1994; Faccio, 1994; Vianey-Liaud et al., 1994, 1997; Calvo et al., 1997). However, after examination only two occurrences (Grellet-Tinner et al., 2004) favorably compare with the taxonomically identified titanosaurid eggs from Auca Mahuevo (Table 1). Those are the eggs from the early Camaanian (Dingus et al. 2000) Anacleto Formation nearby Neuquén (Calvo et al., 1997), and the material from the Late Cretaceous Formation at Laguna Umayo, a site near the Peruvian town of Puno (Sigé, 1968; Kérourio & Sigé, 1984, Vianey-Liaud et al., 1994). The latter was re-evaluated by Vianey-Liaud et al. (1997) and subsequently assigned to the parataxonomic oo-species Megaloolithus pseudomamillare, an oologie species traditionally related to titanosaurids.

The Brazilian egg and eggshells from Peirópolis, also assigned to the Megaloolithidae parataxonomic family by Magalhães Ribeiro (2000, 2002), share some striking features with the Auca Mahuevo eggs (Table 1). Although altered by diagenetic and taphonomic processes, the two diameters (100 and 150 mm) of the Peirópolis egg are well within the recorded range (125 and 140 mm) of the Patagonian titanosaurid eggs. The nodular surficial ornamentation matches that of Auca Mahuevo by its shape, size, and even in the random coalescence of several nodes. In both materials, the eggshell is mono-layered and their respective thickness considering diagenetic alteration is notably similar. Magalhães Ribeiro (2000, 2002) notes wide intervals between the nucleation centers of the shell units. The same intervals are reported in Grellet-Tinner et al. (2004) and Grellet-Tinner (2005) as part of a horizontal pore network above the MT that intersects with the numerous vertical pore canals (Fig. 2F). This observation was only made possible by the presence of the underlying fossilized MT in the titanosaurid eggs (Grellet-Tinner, 2005), which is not present in the Brazilian egg and eggshells. Shell units in either specimens display identical shape and dimension. In addition, both are transversally crossed by growth lines, described as thin and compact for Auca Mahuevo and arched for Peirópolis specimens. Similarities extend also to the geometry of the pore system, although the reported measurements of Magalhães Ribeiro (2000, 2002) are inconsistent. All the
FIGURE 3: Eggs and eggshells from the locality of Peirópolis, Marília Formation, Bauru Basin (from Magalhães Ribeiro, 2002). A: Note the elongated sub-spherical shape of this titanosaurid egg. The presence of a single egg with eroded eggshell fragments combined with grain size of the siliciclastic sediments suggests that the egg was transported and the Peirópolis locality, in contrast to Auca Mahuevo (Patagonia), is not the primary nesting site of these dinosaurs. B: Similarly to the well-identified titanosaurid eggs from Auca Mahuevo, the eggshell surficial ornamentation of the Peirópolis material displays single and coalescent nodes. C: Eggshell accumulation and compaction on a single slab suggesting that the egg was subjected to taphonomic forces as it was still unbroken, a process also observed in Auca Mahuevo. D: SEM view of the radial section of a Peirópolis eggshell that displays the same eggshell structure with radiating acicular crystals and shell units arrangements as those from Auca Mahuevo. E: TLM view of a Peirópolis eggshell that shows organic lines that cross horizontally the eggshell thickness as observed in specimens from Auca Mahuevo.
above-mentioned shared-characters are synapomorphic for the titanosaurid dinosaurs (Grellet-Tinner et al., 2004). Although the material from Peirópolis does not match in quantity and quality that from Auca Mahuevo, it is sufficient to positively identify it as belonging to the family Titanosauridae, thus further supporting the presence of these sauropods in the Bauru Basin during the Campanian.

There are notable disparities between the Auca Mahuevo and Peirópolis localities. Auca Mahuevo is a site that extends over several kilometers and several stratigraphic layers interpreted as a nesting site (Fig. 2B) where titanosaur eggs would have come to reproduce seasonally (Chiappe & Dingus, 2001), thus exhibiting nesting fidelity, colonial nesting (Grellet-Tinner et al., 2004), and indirectly reproductive-related migrations to specific rookeries. The paleoenvironment of this locality has been described as a riparian setting with intermittent over-banking rivers that would deposit their suspended load during flooding periods (Dingus et al., 2000). In contrast, the Peirópolis egg and eggshells as attested by the nature of the sediments (Magalhães Ribeiro, 2000) have been transported and deposited at this site. Consequently, the Peirópolis locality unlike Auca Mahuevo cannot be considered as a rookery where titanosaur eggs would have reproduced season after season. Conversely, the presence of titanosaurid egg and eggshells at Peirópolis suggests the possibility that nesting sites with substantial numbers of eggs and egg clutches should occur in the Upper Cretaceous formations of the Brazilian Bauru Basin but are yet to be discovered.

RESUMO

Os ovos e cascas de ovos provenientes de Auca Mahuevo (Patagônia, Argentina) e identificados taxonomicamente como sendo de titanosaurídeos servem de base para comparação e identificação de ovos megaloolithídeos encontrados em outras localidades. Investigações prévias determinaram que os materiais oológicos encontrados em Neaquén (Megaloolithus patagonicus) e no Peru (M. pseudomamillare) estão na realidade relacionados à dinossauros titanosaúridos. O estudo de um ovo e diversos fragmentos de cascas de ovos (megaloolithídeos) provenientes do Cretáceo Superior da Formação Marília sugere que o mesmo grupo taxonômico de dinossauros titanosaúros que ocorria no Campaniano tardio da Bacia Neaquén também estava presente e se reproduzia durante o Cretáceo na Bacia Bauru, isto porque os caracteres oológicos estudados são reconhecíveis ao nível gênero. Além disso, foi sugerido que estes titanosaúros do sítio de Auca Mahuevo apresentavam comportamento reprodutivo colonial e fidelidade ao sítio de desova.

A presença deste tipo de comportamento reprodutivo apontaria para a existência de sítios de desova similares nas formações do Cretáceo Superior da Bacia Bauru, ainda a serem descobertos, já que a localidade de Peirópolis representa um depósito secundário onde os fósseis foram transportados através de um sistema fluvi e de alta-energia.

PALAVRAS-CHAVE: titanosaur eggs, Bauru Basin, Auca Mahuevo, eggshell structure, dinosaur paleobiology.

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REFERENCES


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