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Upper Cretaceous dinosaur nesting sites of Río Negro (Salitral Ojo de Agua and Salinas de Trapalcó-Salitral de Santa Rosa), northern Patagonia, Argentina

Leonardo Salgado [a,1,*], Rodolfo A. Coria [b,1], Claudia M. Magalhaes Ribeiro [c], Alberto Garrido [b], Raymond Rogers [d], María E. Simón [e], Andrea B. Arcucci [f], Kristina Curry Rogers [g], Ariana Paulina Carabajal [b,1], Sebastián Apesteguía [h], Mariela Fernández [a], Rodolfo A. García [a,1], Marianella Talevi [i,1]

[a] *Universidad Nacional del Comahue, Museo de Geología y Paleontología, Buenos Aires 1400, 8300 Neuquén, Argentina*
[b] *Museo ''Carmen Funes'', 8318 Plaza Huincul, Neuquén, Argentina*
[c] *Universidade Federal do Rio de Janeiro, Instituto de Geociências, Departamento de Geologia, Av. Brigadeiro Trompowski, Cidade Universitaria, 21949-900, Ilha do Fundão, Rio de Janeiro, RJ, Brazil*
[d] *Macalester College, Geology Department, 1600 Grand Avenue, Saint Paul, Minnesota 55105, USA*
[e] *COPADE, Área de Programas y Proyectos, Rivadavia 42, 5to. Piso, 8300 Neuquén, Argentina*
[f] *Universidad Nacional de San Luis, Facultad de Química, Bioquímica y Farmacia, Chacabuco y Pedernera, 5700 San Luis, Argentina*
[g] *Science Museum of Minnesota, 120 West Kellogg Blvd., Saint Paul, Minnesota 55102, USA*
[h] *Museo Argentino de Ciencias Naturales ''Bernardino Rivadavia'', Av. Ángel Gallardo 470, 1405 Buenos Aires, Argentina*
[i] *Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Buenos Aires, Argentina*

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Abstract

Twenty three different sites in two areas of Río Negro Province (Salitral Ojo de Agua and Salitral de Santa Rosa-Salinas de Trapalcó), preserving eggs and eggshells from the Allen Formation (Upper Cretaceous) were studied, and five egg levels were identified. Three different types of eggshell were recognized. Eggs possessing thick eggshells of Type 1 are abundant in both areas, sometimes associated with eggs having thinner shells. Eggs of eggshell Type 1 are included in the oofamily Faveoloolithidae of the parataxonomic classification. Eggshell Type 2 is subdivided into two groups (Types 2A and 2B), mostly based on the mean thickness of the eggshells and other parameters. Eggs of eggshell Type 2 are assigned to the oofamily Megaloolithidae of the parataxonomic classification, and ascribed to titanosaurs. A third type of eggshell (Type 3) is only recorded at one of the localities (Salitral Ojo de Agua, egg level 2). This type is intimately associated with theropod bones, and its microstructure agrees with an assignation to the Theropoda. It is assigned to the oofamily Elongatoolithidae.

Keywords: Dinosaur eggs; sauropods; titanosaurs; Upper Cretaceous; Río Negro Province; Patagonia; Argentina

1. Introduction

Dinosaur eggs in Río Negro Province were first reported by J.E. Powell in Los Alamitos and Salitral Moreno-Salitral Ojo de Agua (Powell, 1987, 1992), and by R. Andreis and collaborators, and C.M. Magalhães-Ribeiro in Salitral de Santa Rosa (Andreis et al., 1991; Magalhães-Ribeiro, 1997). The

Abbreviations: MEGyP, Museo Educativo de Geología y Paleontología del Instituto de Formación Docente Continua, Gral. Roca, Río Negro, Argentina; MML-Pv, Museo Municipal de Lamarque, Vertebrate Paleontology, Río Negro, Argentina; MPCA, Museo Provincial "Carlos Ameghino", Cipolletti, Río Negro, Argentina.

* Corresponding author.
E-mail address: lsalgado@uncoma.edu.ar (L. Salgado).
[1] CONICET.

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egg-bearing units are the Los Alamitos Formation (Campanian–Maastrichtian; Bonaparte et al., 1984) and the Allen Formation (Campanian–Maastrichtian, Uliana and Dellapé, 1981), respectively.

The works cited above described eggshells, complete eggs, and clutches of various types. Powell (1987, 1992) focused on a type of spherical, thick-shelled egg that he taxonomically associated with titanosaurian sauropods. Other thin-shelled egg-types, supposedly non-titanosaurian, were mentioned but not described in comparable detail (Powell, 1992).

Magalhães-Ribeiro (1997), in turn, studied eggshells collected in the ‘‘Bajo de Santa Rosa’’. She recognized two types of thick-shelled eggs, and provided basic data on microstructure and taphonomy. Unlike Powell (1987, 1992), she did not speculate on the identity of the egg producers.

Recently, Chiappe and colleagues (Chiappe et al., 1998; Grellet-Tinner et al., 2004) confirmed that the thin-shelled megaloolithid eggs first reported by Calvo et al. (1997) from the Neuquén Basin were produced by titanosaurs. The discovery of thousands of these eggs preserving embryos in Upper Cretaceous sediments of neighbouring Neuquén Province has made it possible to link with confidence an eggshell morphology (according to the parataxonomic classification, the megaloolithid type of Zhao, 1979) to a specific group of sauropod dinosaurs, the titanosaurs (Chiappe et al., 1998, 2001; Salgado et al., 2005).

In this paper we present the preliminary results of field studies carried out between October and December 2003 in the Salinas de Trapalcó-Salitral de Santa Rosa (ST-SSR) and Salitral Ojo de Agua (SOA) areas in the north-central part of the Argentine Río Negro Province, North Patagonia (Fig. 1). Our goal is to contribute to the knowledge of the dinosaur nesting sites in northern Patagonia by reporting new egg types, and by supplying precise information on the stratigraphic occurrence of the eggshells and eggs, as well as many associated vertebrate bony remains.

2. Geology

The central region of the Río Negro province is characterized by a series of ‘‘bajos’’ (shallow continental basins) that originated by the combined action of structural and eolian process (deflation played a major role; González Díaz and Malagnino, 1984). The ‘‘bajos’’ often preserve ‘‘salinas’’ (salt deposits) or ‘‘salitrales’’ (saltpetre deposits). The sites mentioned in this contribution are on the slopes of two of these ‘‘bajos’’ (Fig. 1; Tables 1–3). As previously mentioned, the Allen Formation contains some of the main egg-bearing deposits of the Rio Negro Province, including those studied in this report.

Based on foraminifera (Ballent, 1980) and palynomorphs (Papú, pers. comm. 1999), the Allen Formation is middle Campanian–early Maastrichtian in age. It is composed of a thick succession of sandstones and mudstones, with intercalations of carbonate and evaporitic rocks in its upper part. In the past, these deposits were referred to by different names, such as the ‘‘Capas Dinosaurianas’’ (Wichmann, 1916), the ‘‘Base del Piso Rocanense’’ (Windhausen, 1914; Wichmann, 1919), ‘‘Pehuenchiano’’ (Windhausen, 1922), the ‘‘Margas con Ostrácodos’’ (Wichmann, 1922), the ‘‘Senoniano Superior’’ (Wichmann, 1922, 1924), the ‘‘Facies Lacustre Senoniana’’ (Wichmann, 1927), and the ‘‘Senoniano Lacustre y Salobre’’ (Groeber, 1931).

In the area of Lago Pellegrini, 60 km northeast of Salitral Ojo de Agua, Andreis et al. (1974) recognized three members of the Allen Formation, which he interpreted as a sand flat environment close to the shoreline (lower member), followed by mixed flat deposits of an intertidal environment (middle member), which in turn are capped by sediments that accumulated in a restricted and hypersaline marginal sabka environment (upper member). Barrio (1990) established four lithotypes in the same area, which presumably represent the following environments in ascending order: (1) subtidal to intertidal with the development of barriers; (2) subtidal to intertidal estuarine; (3) lagoonal; and (4) upper intertidal to supratidal deposits reflecting a sabka environment. Leanza and Hugo (2001) suggested that the Allen Formation is a continental package with a lower member characterized by fluvial deposits of moderate energy followed by lacustrine and lower energy fluvial deposits (middle member) and, finally, shallow lacustrine deposits with evaporitic facies (upper member).

The Allen Formation is widely exposed in the areas of SOA and ST-SSR, which contain the sites discussed herein (Table 1). In neither area is the base visible, while the top can only be observed in the ST-SSR area, where the formation passes conformably into marine fine-grained muddy deposits of the overlying Jagüel Formation (Concheyro et al., 2002; Gasparini et al., 2003).

Our observations have led to the recognition of two subunits in the Allen Formation: (1) a lower subunit comprising fine-grained sandy deposits with subordinate muddy layers and two thin evaporitic levels; and (2) a thick succession of siltstone and mudstone deposits with thin intercalations of ostracod-rich limestones and sandy levels. The latter subunit is present only in the ST-SSR section (Fig. 2).

On the basis of sedimentological and lithofacies characters, the lower subunit, which yields vertebrate fossils, is interpreted as reflecting brackish lagoonal and supratidal environments, associated with aeolian sands (dunes) and deposits of ephemeral rivers. Abundant rhizoturbation, termite structures, and caliches in the egg-bearing deposits indicate the presence of palaeosols, which presumably developed in a supratidal environment in close proximity to the coast. An intertidal to supratidal environment is inferred for the upper subunit, which to date has not yielded vertebrate remains.

The passage between both subunits is marked by an extensive and continuous sandy layer that yields vertebrate fossils. This marker bed (within which is preserved the uppermost egg level) has been used to correlate lithological sections (Fig. 2). Moreover, it is exposed at Cerro de Guerra in the SOA area, and at García I and II, Cerro Laguna Trapalcó, and, principally, Cerro Tortugas in the ST-SSR area (Tables 2, 3).

Five egg-bearing levels have been recognized in the middle and upper parts of the lower subunit (it should be noted that

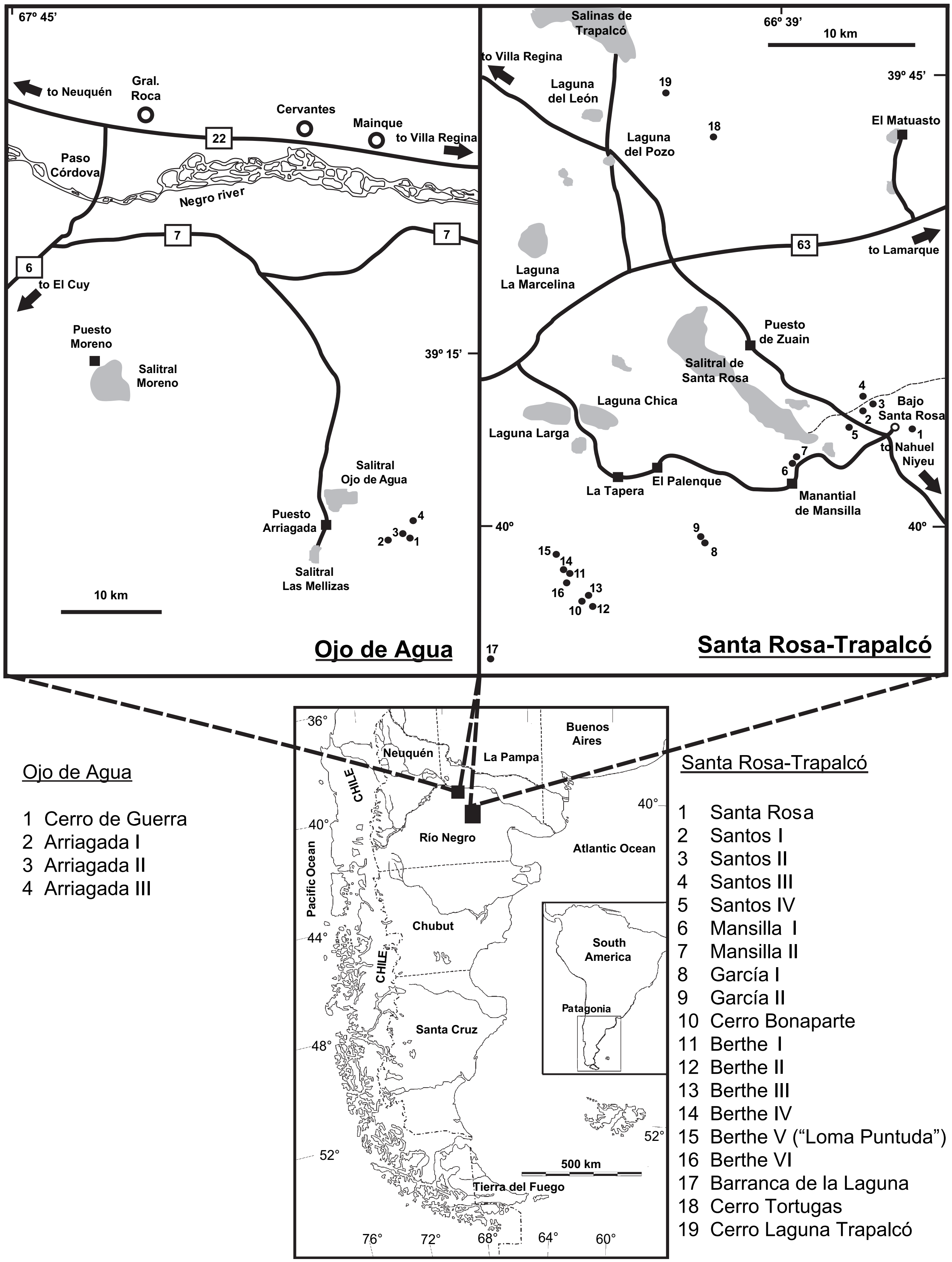

Fig. 1. Map showing the location of the egg sites in the Salitral Ojo de Agua (left) and Salinas de Trapalcó-Salitral de Santa Rosa areas (right).

Table 1
GPS coordinates for the 23 sites with dinosaur eggs and eggshells included in this study

SALITRAL OJO DE AGUA		
1	CERRO DE GUERRA	39° 27′ 47″ S, 67° 20′ 36″ W
2	ARRIAGADA I	39° 26′ 55″ S, 67° 19′ 21.6″ W
3	ARRIAGADA II	39° 26′ 34″ S, 67° 18′ 56″ W
4	ARRIAGADA III	39° 25′ 55″ S, 67° 17′ 40″ W
SALINAS DE TRAPALCÓ-SALITRAL DE SANTA ROSA		
1	SANTA ROSA	39° 57′ 7″ S, 66° 34′ W
2	SANTOS I	39° 56′ 22″ S, 66° 35′ 35″ W
3	SANTOS II	39° 56′ 21.6″ S, 66° 35′ 24.4″ W
4	SANTOS III	39° 55′ 55″ S, 66° 35′ 30.8″ W
5	SANTOS IV	39° 57′ 1.8″ S, 66° 35′ 53.8″ W
6	MANSILLA I	39° 58′ 53.7″ S, 66° 38′ 45.4″ W
7	MANSILLA II	39° 58′ 33.9″ S, 66° 38′ 13.2″ W
8	GARCÍA I	40° 1′ 19″ S, 66° 42′ 41″ W
9	GARCÍA II	40° 1′ 13.9″ S, 66° 43′ 10.9″ W
10	Co. BONAPARTE	40° 3′ 31.9″ S, 66° 48′ 5″ W
11	BERTHE I	40° 2′ 27″ S, 66° 48′ 37″ W
12	BERTHE II	40° 3′ 33″ S, 66° 48′ 1.3″ W
13	BERTHE III	40° 3′ 30.2″ S, 66° 48′ 4.8″ W
14	BERTHE IV	40° 2′ 27″ S, 66° 48′ 37.7″ W
15	BERTHE V	40° 1′ 44″ S, 66° 49′ 24.4″ W
16	BERTHE VI	40° 3′ 2.5″ S, 66° 49′ 0.7″ W
17	Bca. LA LAGUNA	40° 6′ 3″ S, 66° 52′ 6″ W
18	Co. TORTUGAS	39° 47′ 2.7″ S, 66° 42′ 16.5″ W
19	Co. LAGUNA TRAPALCÓ	39° 45′ 13.2″ S, 66° 44′ 54.6″ W

the fifth egg level contains only a few reworked eggshells). In the ST-SSR area, the lowermost egg-bearing level (level I), clearly exposed at Berthe II, is continuous towards Cerro Bonaparte (Fig. 3A), where the remains of saltasaurine sauropods (Martinelli and Forasiepi, 2004), and probable dromaeosaurid theropods (Novas et al., 2003), were found. In the SOA area, at levels probably equivalent to egg-bearing level I, remains of the theropod *Quilmesaurus curriei* (Coria, 2001) were found.

Except for these records, and for other bones found in egg level 2 at Arriagada III (SOA, see below), the other localities studied only rarely yielded osseous remains from the egg-bearing layers. In Cerro Tortugas, as well as in other localities where layers equivalent to egg level 5 are exposed (in the ST-SSR area: García I and II and Cerro Laguna Trapalcó), the few eggshells recorded were associated with gastropods of the genus *Paleoanculosa*, the bivalve *Diplodon* aff. *Diplodon bodenbenderi*, numerous fragments of hadrosaur dinosaurs, worn plesiosaur vertebrae, and the scattered remains of fishes, turtles, and snakes. In Cerro de Guerra (SOA), just a few reworked eggshells were found, but in Salitral Moreno, in levels correlated with the only fossil-bearing layer at Cerro Tortugas, Powell (1992, fig. 2) reported numerous eggshells.

Although Powell (1992) correlated the egg-bearing deposits exposed in Salitral Moreno and the SOA area with the lower member of the Allen Formation (Powell, 1992, p. 382), the facies and environmental conditions of these deposits suggest that the egg-layers of the SOA and ST-SSR (the lower subunit) areas are, instead, best linked to the middle member of the Allen Formation (sensu Andreis et al., 1974). Supporting this idea is the fact that 20 km west of SOA, fluvial deposits equivalent to the lower member of the Allen formation lie under the egg-bearing deposits.

3. Material and methods

Collected eggshells were observed with a binocular loupe "Stemi SV6 Zeiss", at magnifications of ×1.0 and ×3.2 (for macrocharacters). Microcharacters were observed in transverse thin section using a polarizing microscope ("Zeiss Axioplan") at magnifications of ×0.4 and ×10. The eggshells were photographed using this polarizing microscope equipped with a digital camera. Prior to analysis, the eggshells were submitted to a process of cleaning using ultrasound.

In the SOA area, three different structural types of eggshell were identified: Type 1 (assignable to the oofamily Faveoloolithidae), Types 2A and 2B (Megaloolithidae) and Type 3 (Elongatoolithidae). In the ST-SSR area, Types 1, 2A and 2B were recorded.

3.1. Eggshell Type 1 (oofamily Faveoloolithidae, Zhao and Ding, 1976) (Figs. 3B, C, 4A, B, 5A). SOA: MEGyP-120–123, 136, MPCA-501 (Arriagada I, egg level 3); MEGyP-119, 141, 144 (Arriagada II, egg level I). ST-SSR: MML-Pv-6, 10, 14–16, 31, 33, 36, 40 (Santos II, egg level 3); MML-Pv-7, 9, 38 (Cerro Bonaparte, egg level 2); MML-Pv-27 (Cerro Bonaparte, egg level 3); MML-Pv-11–13, 39 (Berthe II, egg level 1); MML-Pv-18 (Berthe VI, egg level 4); MML-Pv-20, 23 (Berthe III, egg level 2); MML-Pv-22 (Berthe IV, egg level 3); MML-Pv-24 (Santos I, egg level 2); MML-Pv-28 (Santos III, egg level 3); MML-Pv-29, 34 (Berthe V egg level 4); MML-Pv-32 (Santa Rosa, egg level 3); MML-Pv-35/6-34 (García I, egg level 5).

3.2. Eggshell Type 2A (oofamily Megaloolithidae, Zhao, 1979) (Fig. 4C, D, 5B). SOA: MEGyP-124, 125, 134, 142 (Arriagada I, egg level 4). ST-SSR: MML-Pv-8 (Cerro Bonaparte, egg level 2); MML-Pv-11 (Berthe II, egg level 1); MML-Pv-21, 41 (Berthe IV, egg level 3).

3.3 Eggshell Type 2B (oofamily Megaloolithidae, Zhao, 1979) (Fig. 4E, F). SOA: MEGyP-126–129, 133, 135, 138–140, 143 (Arriagada III, egg level 2). ST-SSR: MML-Pv-17 (Berthe VI, egg level 4); MML-Pv-19 (Berthe III, egg level 2); MML-Pv-25 (Mansilla I, egg level 3); MML-Pv-37 (Mansilla II, egg level 3); MML-Pv-26 (Mansilla I, egg level 3); MML-Pv-30 (Berthe V, egg level 4); MML-Pv-35/1-5 (García I, egg level 5).

3.4. Eggshell Type 3 (oofamily Elongatoolithidae, Zhao, 1975) (Fig. 4G, H). SOA: MEGyP-130–132, 137 (Arriagada III, egg level 2).

4. Description

Eggs of Type 1 are spherical and 18–21 cm in diameter (Fig. 3B, C). The thickness of the eggshell varies from 4 to 6 mm. The outer surface is sculptured by nodular, subpolygonal to rounded, non-coalescent structures (Fig. 4A). The diameter of the nodules varies between 0.32 and 0.8 mm, but more frequently within 0.48 and 0.8 mm. The pore apertures are subrounded and visible on the outer surface, having

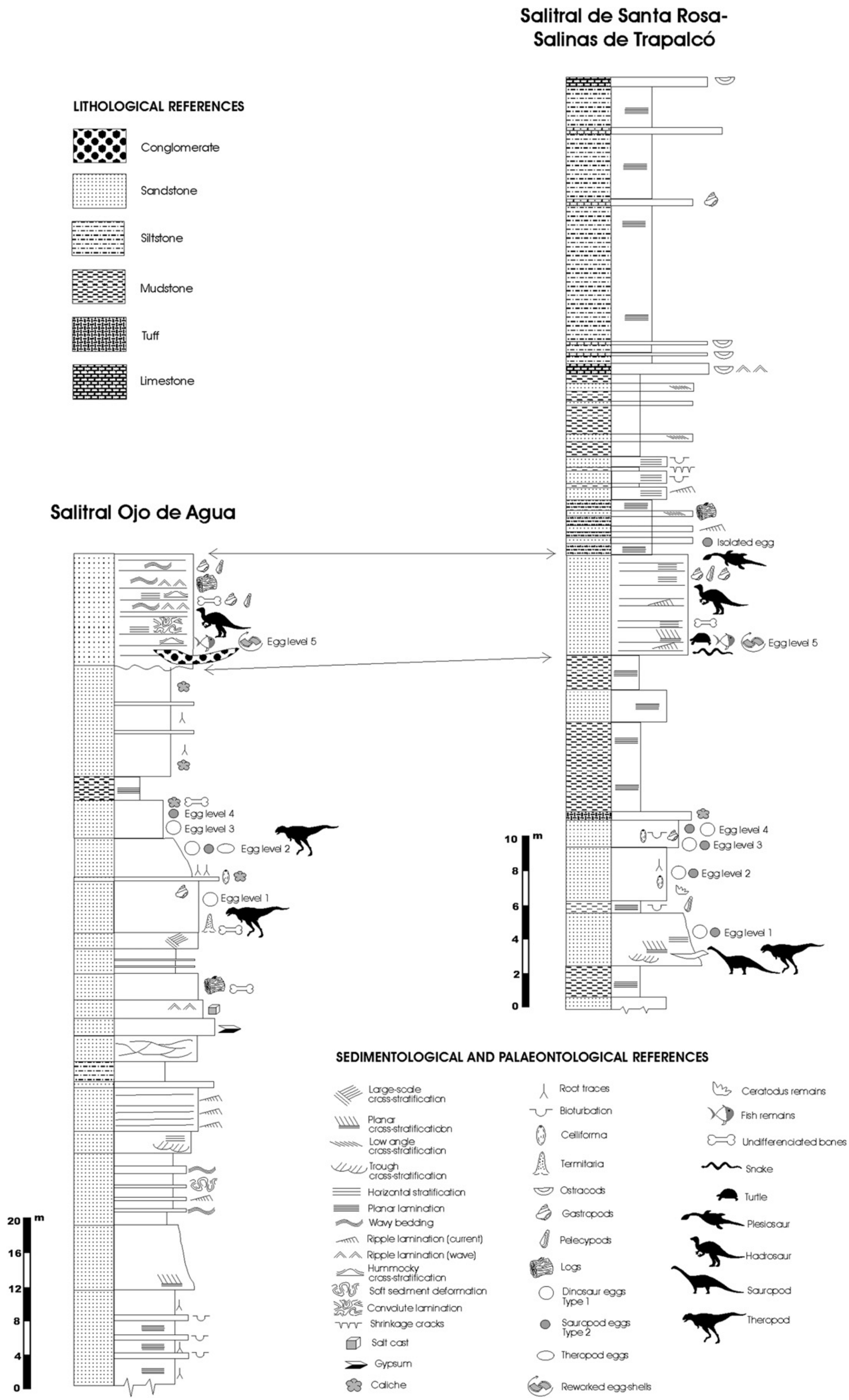

Fig. 2. Correlation of stratigraphic sections of the Salitral Ojo de Agua (left) and Salinas de Trapalcó-Salitral de Santa Rosa areas (right).

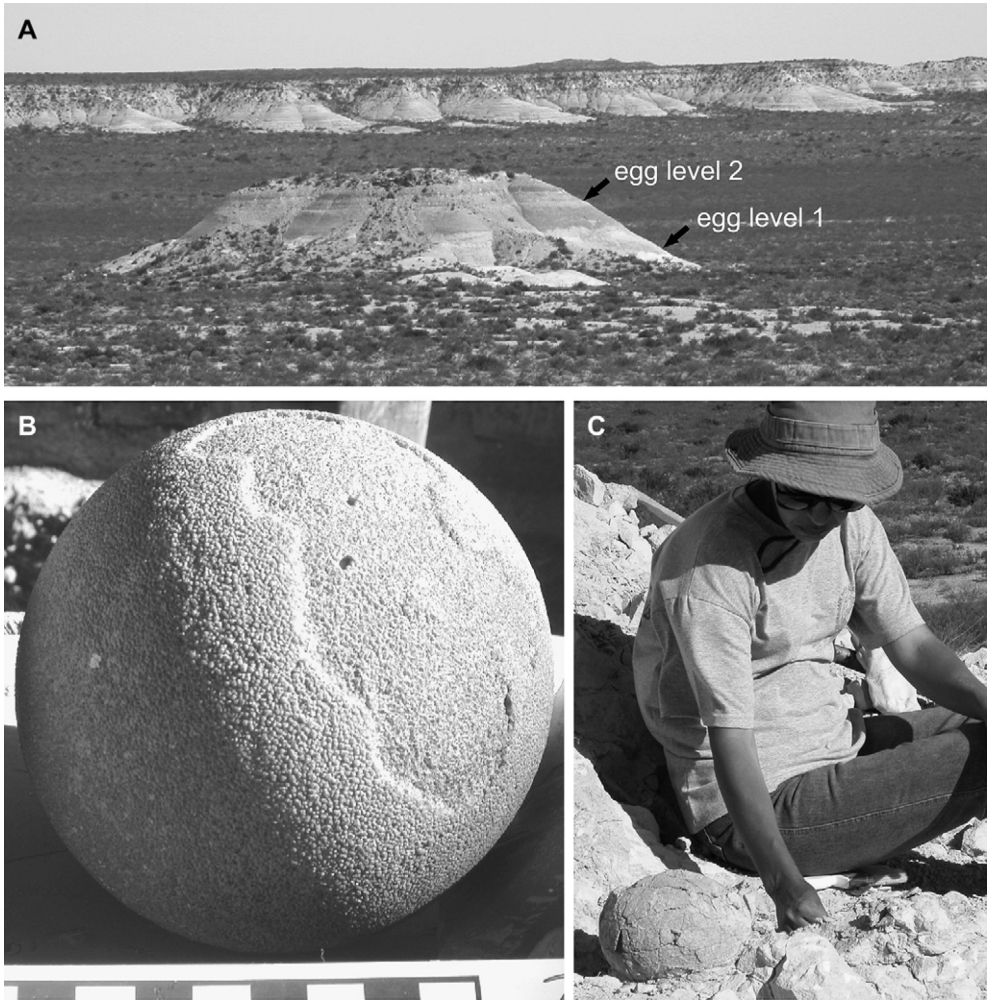

Fig. 3. A, an overview of Cerro Bonaparte (ST-SSR) from the northeast, showing egg levels 2 and 3. B, C, complete Type 1 eggs.

diameters of 0.16 mm. On the inner surface, the mammillary structures are irregular, with diameters varying between 0.32 and 0.8 mm, and coalescent in groups of two, three or more. The eggshell units are, in most cases, biramificated (Fig. 4B), having minimum diameters of 0.32 mm, and maximum diameters of 0.8 mm, reaching occasionally 1.0–1.2 mm in some eggshells from the SOA area. The height of the eggshell units varies between 4.0 and 4.8 mm. The accretionary lines are arched. The pore system is multicanaliculate.

The eggs of Type 2A are subspherical, averaging 12–14 cm in diameter (Fig. 5B). The eggshells are thin, with a mean thickness of 1.05 mm at Arriagada I (egg level 4) (Fig. 6). However, they attain a thickness of 1.23 mm at the Berthe IV locality (egg level 4). The ornamentation of the outer surface is composed of rounded nodules ranging in diameter from 0.32 to 0.8 mm, which coalesce in twos or threes, forming low crests and hence a compactituberculate surface morphology (Fig. 4C). Pore openings are subrounded, with diameters averaging 0.16 mm (the pore system is tubocanaliculate). The coalescent mammillary structures have diameters that vary between 0.48 and 0.8 mm. The eggshells have a fan format (Fig. 4D), with measurements varying between a maximum of 0.64–0.8 mm and a minimum of 0.32 mm. The height of the eggshell unit varies from 0.8 to 1.12 mm. The accretionary lines are arched.

The eggs of Type 2B are spherical and estimated to range from 12–14 cm in diameter. The eggshell is somewhat thicker than in the previous types. At Arriagada III (SOA), the mean thickness of the eggshells is 1.81 mm (Fig. 6). At Mansilla I and II (ST-SSR), the mean diameters are 1.8 and 2 mm respectively. These dimensions match well the megaloolithid eggshells recorded from Neuquén City (Calvo et al., 1997). The outer surface is compactituberculate, ornamented with rounded nodular structures that average 0.8 mm in diameter, but which can be as small as 0.64 mm (Fig. 4E). Occasionally, the nodules are coalescent, forming irregular crests. The pore openings in the outer surface are subrounded, and have diameters ranging from 0.1 to 0.32 mm. This variation in pore diameter may reflect the effects of diagenesis. The well-compacted mammillary structures have diameters that mainly range from 0.32 to 0.48 mm, but some reach 0.64 mm. The eggshell units are fan-shaped, and have diameters averaging 1.6 mm (maximum 1.7 mm) (Fig. 4F). The maximum

Table 2
Egg level and eggshell type distribution in the sites included in the study, 1: Salitral Ojo de Agua

	Egg level 1	Egg level 2	Egg level 3	Egg level 4	Egg level 5
CERRO DE GUERRA					T1 EGGSHELLS
ARRIAGADA I			T1 EGGS	T2A EGGS	
ARRIAGADA II	T1 EGGS				
ARRIAGADA III		T1 EGGSHELLS, T2B EGGS and T3 EGGSHELLS			

T1, Type 1; T2A, Type 2A; T2B, Type 2B; T3, Type 3.

diameter of these units ranges from 0.7 to 0.8 mm, and the minimum averages 0.32 mm. The accretion lines are in an arch pattern. The pore system is tubocanaliculate.

The thickness of Type 3 eggshells ranges from 1.1 to 1.2 mm. The outer surface is composed of crests about 0.8 mm high but sometimes reaching 2.4 mm, exhibiting a typical linearituberculate ornamentation (Fig. 4G). There are also some isolated nodules of about. 0.48 mm diameter. On the inner surface, the mammillary cones are compacted, and the subrounded pore openings are 0.16 mm in diameter. The microstructure reveals a well-developed mammillary layer composed of well-defined wedges of radial calcite crystals, with organic cores at their base (Fig. 4H, black star). This layer occupies one-half to one-quarter of the lower portion of the eggshell. Above the mammillary layer there is a continuous prismatic layer of squamatic ultrastructure, with undulating accretionary lines (Fig. 4H, white star). The pore system is angusticanaliculate.

5. Discussion

Eggshells of Type 1 include those assigned by Powell (1992, p. 385) to titanosaurian sauropods. These are, as previously mentioned, the only eggs/eggshells described in some detail in his account. Eggshells of this type have also been reported by Simón (1999, 2006) from the neighbouring locality of Salitral Moreno, and by Manera de Bianco (1996) from other localities in Río Negro Province.

Similar eggshells, also assignable to the oofamily Faveoloolithidae, have been formerly attributed to sauropod dinosaurs (Mikhailov et al., 1996), although this should be reconsidered in light of new evidence from Auca Mahuevo. At present, we do not dwell on which group of dinosaurs laid this type of egg. There are two main possibilities: (1) The eggs are of sauropod origin; if it is this case, we should accept that members of this group produced more than one type of egg (at least the types here named as Types 1 and 2). (2) Type 1 eggs belong not to sauropods but to another dinosaur clade; we regard this as more plausible. Besides sauropods, hadrosaurs and theropods have also been recorded in the areas studied, and thus these groups are also potential producers of the eggs.

In the SOA area, eggshells and complete eggs of Type 1 were recorded in egg levels 1–3. Two clutches of seven (39° 26′ 51″ S, 67° 19′ 23″ W) (MPCA-501), and four (39° 26′ 51″ S, 67° 19′ 24″ W) eggs, and a complete egg (39° 26′ 53″ S, 67° 19′ 24″ W), were recorded at Arriagada I (egg level 3). The clutches documented at this site do not comprise more than eight eggs, although Powell (1992) reported groups of up to 12 eggs from the same level (though possibly from other sites).

As can be seen in MPCA-501, the eggs comprising each clutch are in close proximity (nearly touching). Coupled with the fact that, apparently, the deepest eggs seem to be those in the centre of the clutch, this may indicate that the dinosaurs deposited their eggs in shallow depressions. Interestingly, at this site we observed two contiguous, subcircular depressions in the sandstone that were ca. 1.2 m in diameter, encircled by a more or less continuous rim of massive sandstone 3–5 cm high (Fig. 5A). One of these depressions preserved the remains of at least five Type 1 eggs. The other contained fragmentary eggshells of the same type. Both structures are in a well-defined palaeosol horizon composed of fine to medium quartzitic, buff-coloured sandstone with a high concentration of cineritic matrix and carbonate cement.

Table 3
Egg level and eggshell type distribution in the sites included in the study, 2: Salitral de Santa Rosa-Salinas de Trapalcó

	Egg level 1	Egg level 2	Egg level 3	Egg level 4	Egg level 5
SANTA ROSA			T1 EGGS		
SANTOS I		T1 EGGS			
SANTOS II			T1 EGGS		
SANTOS III			T1 EGGS		
SANTOS IV		T1 EGGSHELLS			
MANSILLA I			T2B EGGSHELLS		
MANSILLA II			T2B EGGSHELLS		
GARCÍA I					T1 and T2B EGGSHELLS
GARCÍA II					T1 EGGSHELLS
Co. BONAPARTE		T1 and T2A EGGSHELLS	T1 EGGSHELLS		
BERTHE I		T1 EGGSHELLS			
BERTHE II	T1 and T2A EGGSHELLS				
BERTHE III		T1 and T2B EGGSHELLS			
BERTHE IV			T1 and T2A EGGS	T2A EGGS and T1 EGGSHELLS	
BERTHE V				T1 and T2B EGGSHELLS	
BERTHE VI				T1 and T2B EGGSHELLS	
Bca. LA LAGUNA				T1 EGGSHELLS	
Co. TORTUGAS					T1 and T2A EGGSHELLS
Co. L. TRAPALCÓ					T2A EGGS

T1, Type 1; T2A, Type 2A; T2B, Type 2B; T3, Type 3.

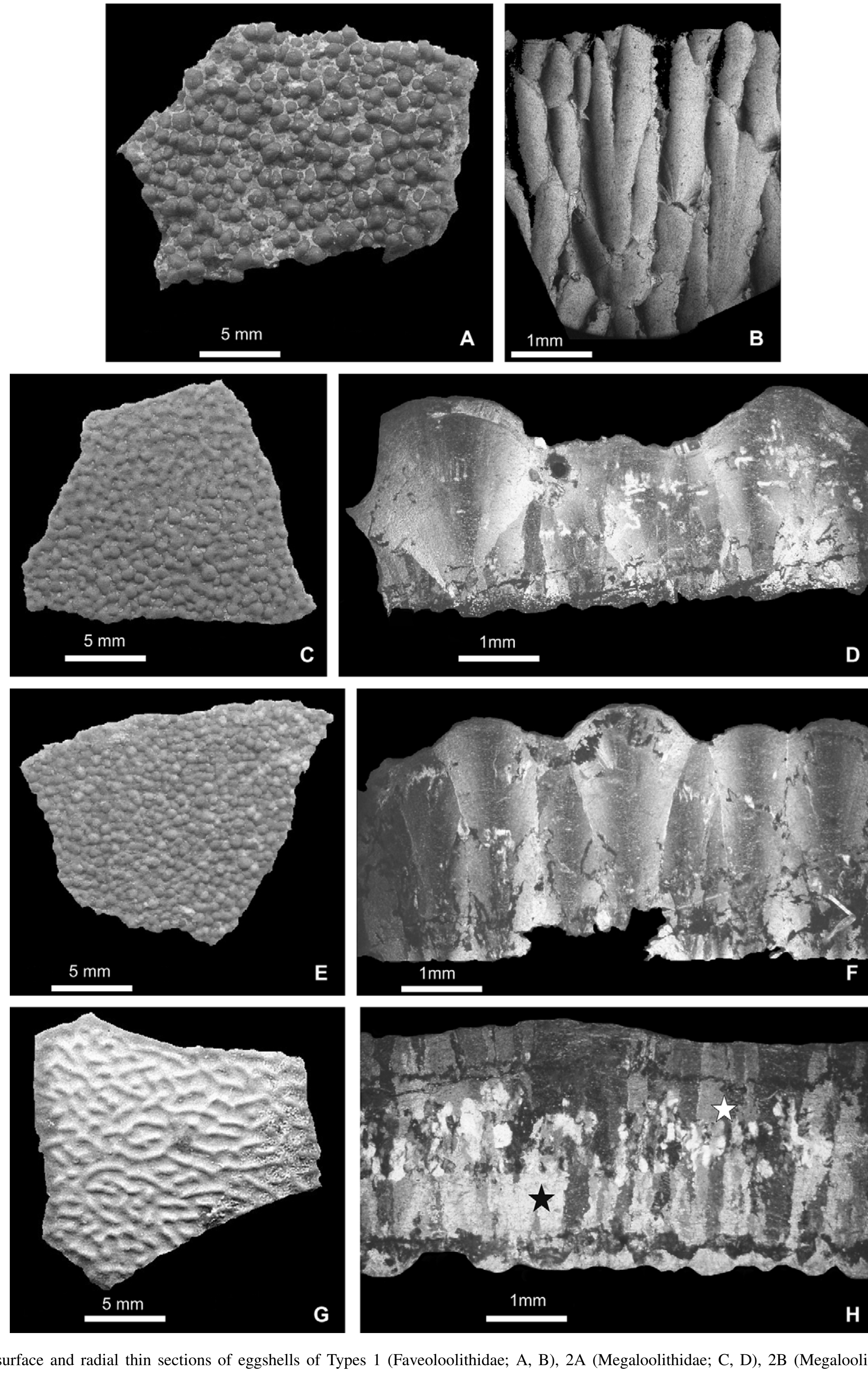

Fig. 4. Outer surface and radial thin sections of eggshells of Types 1 (Faveoloolithidae; A, B), 2A (Megaloolithidae; C, D), 2B (Megaloolithidae; E, F) and 3 (Elongatoolithidae; G, H).

Abundant rhizoliths and bioturbation typifies this horizon. These depressions are filled by unconsolidated silty sandstone, showing a clear compositional difference from the substrate (palaeosol). Based on previous studies (Garrido et al., 2001; Chiappe et al., 2004), we interpret this structure as a dinosaur nest.

In the ST-SSR area, eggshells, eggs, and clutches of Type 1 are present in all the localities and levels apart from Mansilla I, II, and Cerro Laguna Trapalcó (Table 3).

A clutch with at least ten eggs from Santos I (39° 56′ 22″ S, 66° 35′ 35″ W), and another from Santos II preserving seven eggs (39° 56′ 22″ S, 66° 35′ 34″ W), were recorded. At Berthe IV, a clutch with three partial eggs was found 1.5 m from a clutch of Type 2A eggs (Fig. 5B). Isolated eggs or pairs of eggs were found at 40° 02′ 27″ S, 66° 48′ 39″ W and 40° 02′ 24″ S, 66° 48′ 37″ W (Fig. 3C).

The eggs of Type 2A are morphologically and microstructurally identical to those assigned to titanosaurs by Chiappe et al. (1998), and Grellet-Tinner et al. (2004). For this reason, they are assigned to the same sauropod clade. In the SOA area, eggshells of Type 2A are exclusively present at Arriagada I (egg level 4). In the ST-SSR area, eggshells of Type 2A are present at Cerro Bonaparte (egg level 2; Fig. 3A), Berthe II (egg level 1), and Berthe IV (egg levels 3 and 4) (Table 3). At the last site and level an ovoid clutch containing 14 eggs, each having a diameter of 12–14 cm was encountered (Fig. 5B). As mentioned earlier, this clutch was located 1.5 m from a series of three collapsed Type 1 eggs. At the same site, but at egg level 4, a complete egg of Type 2A was found, as were a few eggshells of Type 1.

Arriagada III (level 2) is the only site in the SOA area where eggs of Type 2B were collected (Table 2). At this locality, a clutch of at least 25 eggs of this type was discovered, associated with a few eroded eggshells of Type 1, and abundant eggshells of Type 3. Unfortunately, this clutch could not be collected, but it seemed to have an oval shape with eggs occurring at different depths within the clutch. In the ST-SSR area, eggshells of Type 2B were recorded at numerous sites, but are particularly abundant at Mansilla I and II (Table 3).

Eggshells of Type 3 (possibly belonging to theropods) were only recorded in the SOA area, at Arriagada III (egg level 2), and are associated here with a few isolated eggshells of Types 1 and 2B as well as with numerous osseous remains of coelurosaurian theropods (Coria et al., in prep.) and basal iguanodontians (Coria et al., 2004, in manuscript). To date, no entire eggs of this kind are known, although Powell (1992) reported two complete eggs that possibly belong to Type 3. Interestingly, he noted that the eggs and eggshells in question were also associated with theropod remains. We tentatively suggest that the eggshells mentioned by Powell (1992) belong to Type 3, and that the theropod remains he reported were probably coelurosaurian.

In general, the eggshells analyzed herein are well preserved, although diagenetic alteration observed in many fragments was linked to dissolution and later precipitation of the calcite, mainly in the middle portion of the eggshell units and in the accretionary lines (Fig. 4D, F). In other samples, diagenesis is evidenced by recrystalization of the eggshell units, obliteration of the pore canals (Fig. 4H), or substitution by secondary carbonate along the accretionary lines. In some cases, carbonate substitution affected the whole of the eggshell units and the mammillary structures (Magalhães-Ribeiro, 2002; Grellet-Tinner et al., 2004). However, this alteration does not seem to affect the morphostructure of the fossilized eggshells.

Type 1 eggs show considerable variation in many characters. The thickest eggshells were reported at Santos III (up to 6 mm), whereas the thinnest were collected from Santos IV (4 mm). Type 1 single eggshells (MEGyP 119, 120, 123) also exhibit considerable variation in their nodular diameters. These are normally between 0.48 and 0.64 mm, but reach a minimum of 0.32 mm and a maximum of 0.8 mm (Fig. 4A). The degree of variation recorded in these eggshells is thus greater than in other eggshell types. While the diameter of the pore opening is similar in eggshells of Types 1 and 2 (0.1 mm), the shape of the openings is different, being

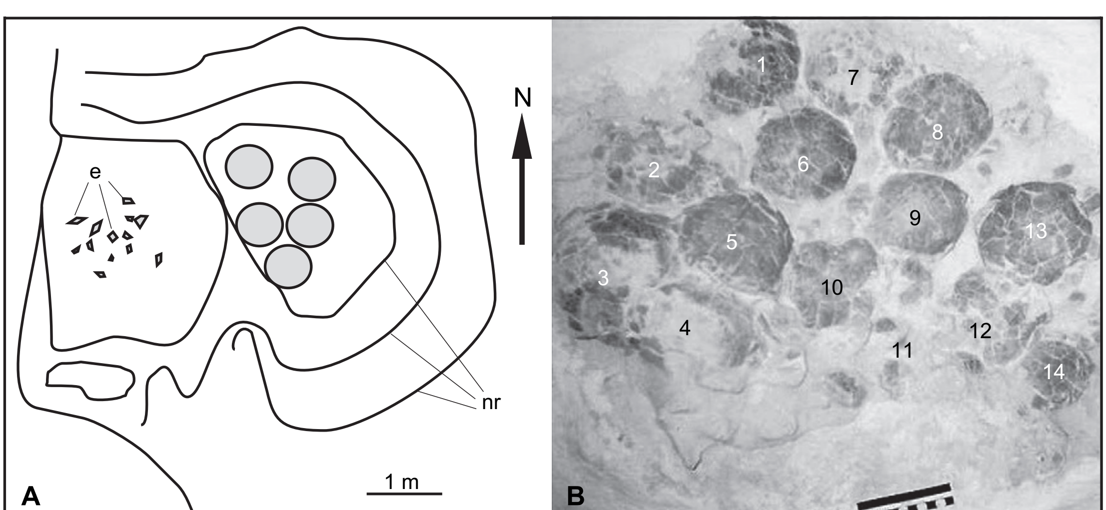

Fig. 5. A, sketch of a nest structure recorded at Arriagada I (SOA), containing partial eggs of eggshell Type 1 (Faveoloolithidae). B, clutch of 14 eggs (MML-Pv 41) of eggshell Type 2A (Megaloolithidae), at Berthe IV (ST-SSR). e, eggshells; nr, nest rim.

subrounded in Type 1 and rounded in Type 2. In some of the samples analyzed, the covering of sandstone with carbonate cementing of the surfaces impedes observation of the pore openings (Fig. 4A, C, E).

Type 3 eggshells do not show significant morphometric variations because their dimensions remain relatively constant (Fig. 4G, H).

The most intriguing issue relates to the variation observed within the megaloolithids. At present we cannot determine whether they were produced by two different titanosaurian species, or if they merely represent two ‘‘classes’’ within the same eggshell type. At Mansilla I, two clusters are apparently present (Fig. 6), a situation that could lead to the recognition of two different types, masked by what we labelled as Type 2B. In fact, similar differences in the eggshell thickness allowed Vianey-Liaud et al. (1994) to differentiate two oospecies of the genus *Megaloolithus* at the French locality of Roquehautes Grand Creux (*M. aureliensis* and *M. petralta*). However, other factors may explain the marked variation in thickness present in the megaloolithid eggshells described here. Horner (1999), for example, proposed that most variation in eggshell thickness occurs in embryo-bearing eggs, whereas eggs that lack embryos show minimal variation. The great deviation in eggshell thickness could, therefore, be a result of the fact that some of the eggshells belonged to hatched eggs. However, there is no clear correspondence between eggshell thickness and presence/absence of resorption craters. The interpretation of this fact (a considerable variation in eggshell thickness) is obstructed by a series of basic doubts: Were all reproducing titanosaurs of the same age? Did titanosaurs of different ages lay eggs of similar size and eggshell thickness? To what extent does the normal variation in eggshell thickness affect other structural parameters, traditionally considered of parataxonomical value? Future studies on these nesting sites or on others could shed new light on these issues.

The dinosaur nesting sites of the Allen Formation are widely distributed in Rio Negro Province. Although less spectacular than those of Auca Mahuevo, they preserve a greater diversity of eggshell types, including: (1) the same type of eggs found at Auca Mahuevo (Type 2A); (2) a second variety of megaloolithid (Type 2B, also assignable to titanosaurs); (3) Type 1 eggs (faveoloolithids); and (4) Type 3 eggs (elongatoolithids).

Our observations suggest that these sauropods shared their nesting areas with other dinosaurs. This is particularly evident at Berthe IV, level 3. However, the coexistence of titanosaurian eggs and eggs of other groups of dinosaurs is not regular; rather, it varies from locality to locality. The differences recorded between sites and/or levels are herein interpreted as potentially reflecting the differential occupation of available nesting spaces through time.

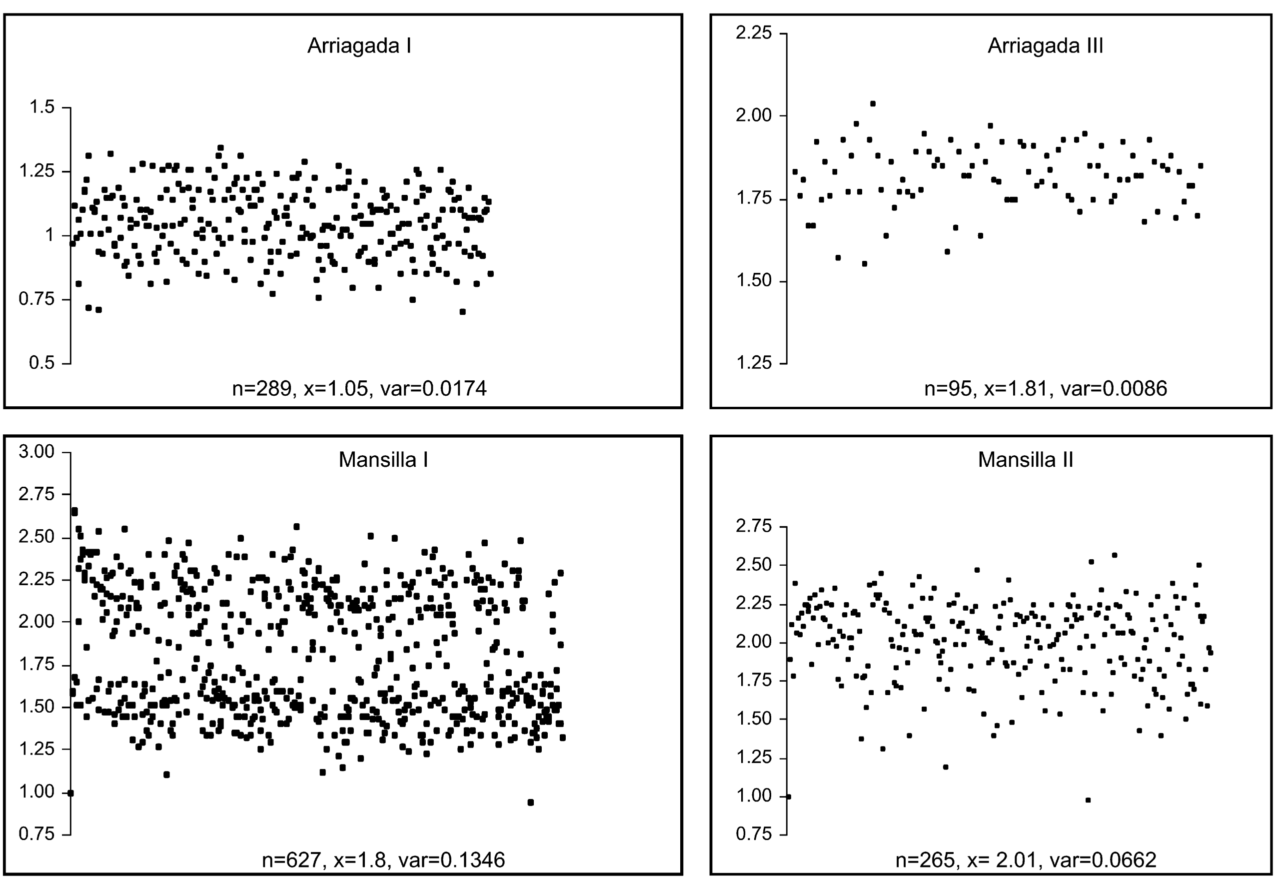

Fig. 6. Eggshell thickness in mm (including ornamentation) of samples collected from Arriagada I (MEGyP-134), Arriagada III (MEGyP-133), Mansilla I (MML-Pv 25), and Mansilla II (MML-Pv 37). n, number of eggshells; var, variance; x, mean thickness.

Another aspect worthy of note is the extent of the nesting areas. The minimal rectangular area comprising all localities of level 3 in the ST-SSR area (undoubtedly the best represented of all levels: Santa Rosa, Santos II, Mansilla I and II, Cerro Bonaparte, and Berthe IV; Table 2), encompasses nearly 250 km^2. Of course, we do not know if these sites were all part of a single colony, but they at least suggest that the area used by these dinosaurs for nesting extended across a wide region.

At some sites, always in egg level 3, eggs/eggshells of Type 1 are preserved in isolation (in SOA, Arriagada I; in ST-SSR, Santa Rosa, Santos II, Santos III and Cerro Bonaparte); in others, faveoloolithids and megaloolithids of Type 2A are associated (in ST-SSR, Berthe IV). Finally, at Mansilla I and II, only megaloolithids of Type 2B are recorded. At Santos II and III, in egg level 3, in situ eggs (faveoloolithids) were found.

In egg level 3 of Berthe IV, faveoloolithid and megaloolithid eggs (Type 2A) are closely associated. The clutch MML-Pv 41, consisting of megaloolithid eggs of Type 2A 12−14 cm of diameter (Fig. 5B), was found 1.5 m from a clutch of three collapsed faveoloolithids. While the proximity of the clutches is certainly interesting, it is impossible to know if they were incubating at the same time.

Our data suggest that the same area was occupied differentially throughout time. This could be a result of microenvironmental changes that operated within the nesting area (e.g., a fluctuating shoreline or shifting rivers). In this regard, an area occupied mostly by titanosaurs could have been occupied in successive reproductive seasons, mostly by non-titanosaurian dinosaurs.

The eggs and eggshells found at Cerro Tortugas (Type 1) and Salinas de Trapalcó (a partial egg of Type 2A), were collected from a level immediately above level 4. These findings in levels immediately above level 4 (our egg level 5), shows that the dinosaur producer of Type 1 eggs and titanosaurs (Types 2A and 2B) reproduced in the same area until the precise moment that the environment came under marine influence.

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