

WATER VAPOR CONDUCTANCE OF THE LOWER CRETACEOUS DINOSAURIAN EGGS FROM SANAGASTA, LA RIOJA, ARGENTINA: PALEOBIOLOGICAL AND PALEOECOLOGICAL IMPLICATIONS FOR SOUTH AMERICAN FAVEOLOOLITHID AND MEGALOOLITHID EGGS

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ABSTRACT

The water vapor conductance (G_{H_2O}) of the neosauropod eggs from the Lower Cretaceous Sanagasta nesting site in La Rioja Province, Argentina, was examined and compared with other Cretaceous Argentinean oological material. The 2900 $\text{mgH}_2\text{O}/\text{day}\cdot\text{Torr}$ G_{H_2O} of the Sanagasta eggshells confirms an extremely moist nesting environment and supports field observations of dug-out nests in a geothermal setting. The observed thinning of the outer eggshell surface during incubation increases gas conductance and concomitantly decreases eggshell mechanical resistance during the late ontogenetic stages, thus facilitating embryonic development and hatching. The Sanagasta and Entre Ríos Province faveoololithid eggs display the highest and comparable G_{H_2O} values and share several morphological and diagenetic characters, indicating comparable nesting strategy in geothermal settings. However, the faveoololithid Yaminué and La Pampa Province specimens cluster together with lower G_{H_2O} values closer to the megaloolithid eggs. The G_{H_2O} of the megaloolithid egg *Megaloolithus patagonicus* was reconsidered and new results are now congruent with other reported megaloolithid G_{H_2O} values. Additionally, we hypothesize that Y-shaped pore canals of *M. patagonicus*, which upper sections reach only the top third or half eggshell thickness and, a wider section in the middle would not compromise the overall egg mechanical resistance like vertical pores connecting directly the outer to the inner eggshell surfaces. Such pore spatial arrangement and geometry would enhance, as the eggshell thins during incubation, a greater G_{H_2O} , G_{O_2} and G_{CO_2} and facilitate embryonic development in high moisture nesting contents. Overall, data suggests that neosauropod nesting and brooding behaviors were dependent on elevated moisture nesting environments.

INTRODUCTION

The recent discovery of a neosauropod dinosaur nesting site (Grellet-Tinner and Fiorelli, 2010) in an Early Cretaceous geothermal environment in the Los Llanos Formation exposures of the Sanagasta Geologic Park (Sanagasta valley), La Rioja Province (Argentina), yielded several egg clutches with complete eggs. The excessive 7.9 mm eggshell thickness of these eggs combined with an observed variation from 7.9 mm to <1.3 mm on single eggs and an extensive pore network that gives a spongy appearance to the material raise questions about eggshell functional morphology and its properties with respect to the nesting environment. Eggshell structural and functional properties are paramount for the incubating and hatching success of reptile and bird embryos (Board, 1982). Eggshell thickness determines the amount of mechanical protection against extrinsic forces and, together with pore density and size, regulates the amount of gas exchange during incubation (Board, 1982; Burton and Tullett, 1985). Gas diffusion

through the pores occurs according to the laws of diffusion and can be quantified as the eggshell conductance to water vapor or G_{H_2O} .

Water vapor conductance is commonly obtained for modern birds and reptiles by measuring water loss with a known gradient of water vapor pressure across the shell (Ar et al., 1974). In fossil dinosaur eggs, G_{H_2O} can be estimated from eggshell and pore system observations, which are a valuable proxy for assessing the moisture content in dinosaur nests and their environments (Seymour, 1979; Seymour and Ackerman, 1980) and nesting strategies (Ar et al., 1974; Seymour, 1979; Birchard and Kilgore, 1980; Seymour et al., 1987; Deeming, 2006).

The purpose of this study is to estimate the G_{H_2O} of the newly discovered Sanagasta eggs and compare the results with other Argentinean neosauropod eggshells and extant reptiles to present ensuing reproductive strategies and nesting behavior hypotheses.

Institutional Abbreviations

CICyTTP R: Museo de Diamante, Diamante, Entre Ríos, Argentina. CRILAR: Centro Regional de Investigaciones Científicas y Transferencia Tecnológica, Anillaco, La Rioja, Argentina. MACN-RN: Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Rio Negro Collection), Buenos Aires, Buenos Aires, Argentina. MCF: Museo Carmen Funes, Plaza Huincul, Neuquén, Argentina. MML: Museo Municipal Paleontológico de Lamarque, Río Negro, Argentina. MPA: Museo Municipal de Ciencias Naturales Carlos Darwin, Punta Alta, Buenos Aires, Argentina.

MATERIAL AND METHODS

Material

The material consists of eggs previously discovered in La Rioja, Entre Ríos, Río Negro, and La Pampa Argentinean Provinces (Fig. 1, Table 1) that were classified as *Sphaerovum erbeni* Mones, 1980 (Faveoololithidae) and assigned to titanosaur dinosaurs (Powell, 1987, 1992; Manera de Bianco, 1996; Casadio et al., 2002; de Valais et al., 2003; Simón, 2006; Salgado et al., 2007; Tauber, 2007), although this taxonomic assignment has never been positively supported by embryos *in ovo*. Additionally, specimens previously classified as megaloolithid from two Argentinean provinces, Río Negro and Neuquén, were also included in this study for comparative purposes.

1. Complete eggs and eggshells (Figs. 2–4) from the Lower Cretaceous of La Rioja Province, Los Llanos Formation, were recovered at the Sanagasta Geological Park (SGP); CRILAR-Pv 400 to 409 (for more information on the Sanagasta materials see Grellet-Tinner and Fiorelli, 2010). Forty-seven well-preserved eggshell fragments, referred to in the text as Sanagasta (Table 1) were used and 76 thin sections were prepared for this study.

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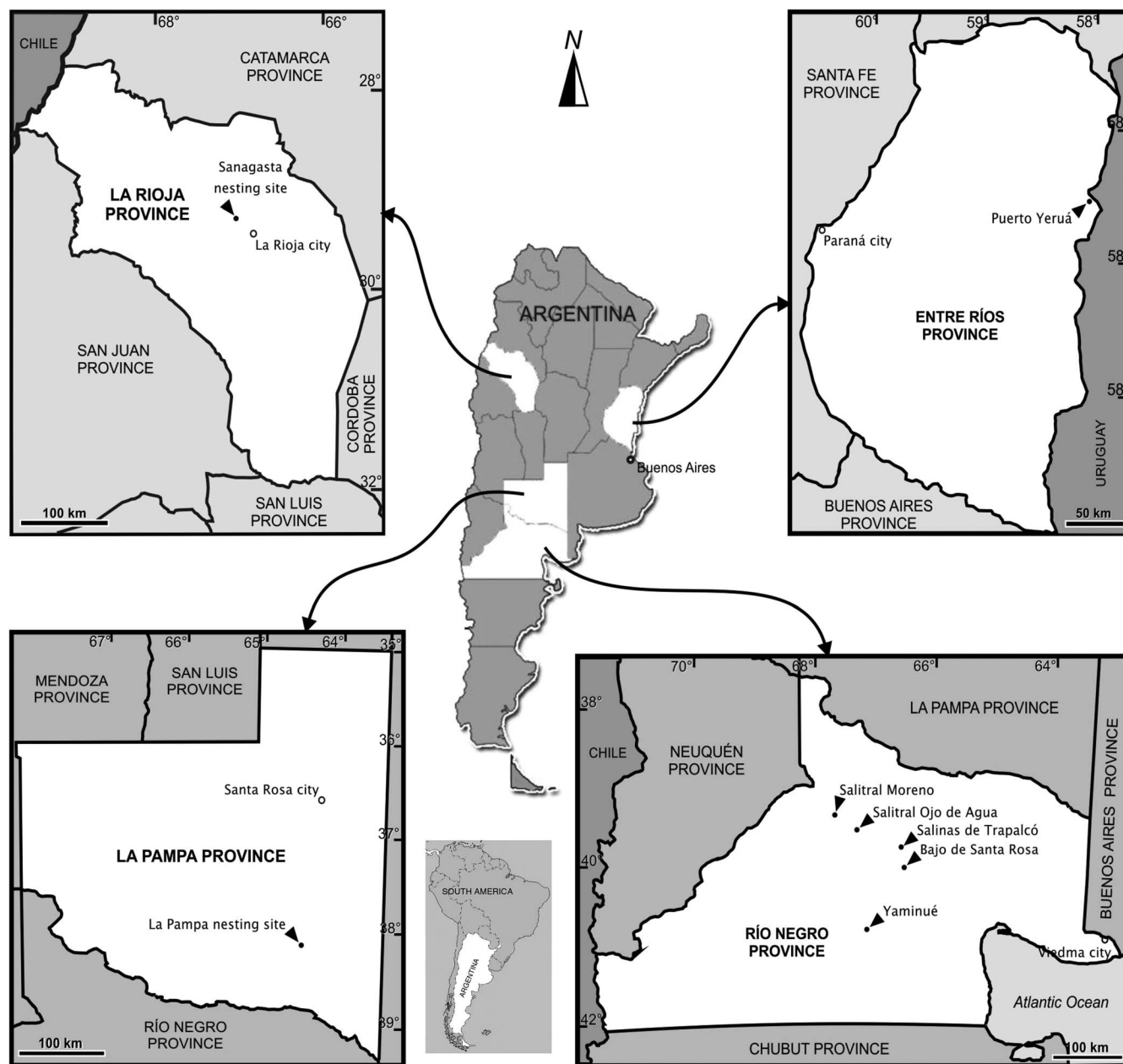


FIGURE 1—Eggshell specimen localities in Argentina.

2. The only existing eggshell fragment from the Upper Cretaceous Puerto Yerúa Formation (Tofalo and Pazos, 2002; Aceñolaza, 2004), Entre Ríos Province (Fig. 1) referred to as Entre Ríos in the text (Table 1), was described previously by de Valais et al. (2003) and loaned for this study by the Museo de Diamante: CICyTTP R-1-1 (Fig. 5A).

3. The eggshell fragments from Upper Cretaceous Allen Formation (Uliana and Dellapé, 1981), Río Negro Province, are from the following sites (Fig. 1): (A) the eggshells from Bajo de Santa Rosa-Salinas de Trapalcó, MML-Pv 11 to 13 and MACN-PV RN 1088 (Fig. 5B), which were provided by the Museo Municipal Paleontológico de Lamarque and the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, respectively; (B) the information and data for the eggshell from Salitral Ojo de Agua and Salitral Moreno (Fig. 5C) nesting sites are from Simón (2006) and Salgado et al. (2007); (C) the Yaminué samples loaned by Dr. Manera de Bianco consist of two eggshell fragments (Fig. 5D) from the MPA 85 to 93 collections (see

also Manera de Bianco, 1996). The A and B samples are considered the same eggshell type and, hence, are treated together here as a single entity referred as Río Negro 1 in the text (Table 1). The C samples are very different and, thus, referred to in the text as Yaminué (Table 1).

4. Information and data for the only known La Pampa Province nesting site (Colorado Formation, Upper Cretaceous; Figs. 5E and F) are from Casadío et al. (2002). This material is referred to in the text as La Pampa (Table 1).

5. Megaloolithid specimens (Megaloolithid Type 2B *sensu* Salgado et al., 2007, 2009) from Bajo de Santa Rosa-Salinas de Trapalcó, Allen Formation, Upper Cretaceous (Uliana and Dellapé, 1981), Río Negro Province: MML-Pv-25, 26 and 37. These samples are referred as Río Negro 2 (Table 1) in the text.

6. Megaloolithid specimens from Auca Mahuevo's egg bed 4 (*sensu* Grellet-Tinner et al., 2004), Anacleto Formation, lower Campanian, Upper Cretaceous (Garrido, 2010a), Neuquén Province: MCF-PVPH 444. Titanosaur eggs parataxonically classified as *Megaloolithus*

TABLE 1—Eggs and eggshell material as named throughout this work, alongside their locality, formation, age, and parataxonomic groups.

Material	Parataxonomy	Locality	Province	Formation	Age	Samples	References
Sanagasta	Faveoololithidae	Sanagasta Geological Park	La Rioja	Los Llanos	Lower Cretaceous	CRILAR-Pv 400–409	Grellet-Tinner and Fiorelli, 2010
Entre Ríos	Faveoololithidae	Ita-i-cora	Entre Ríos	Puerto Yeruá	Cretaceous	CICyTTP R-1-1	de Valais et al. (2003)
Río Negro 1	Faveoololithidae	Bajo de Santa Rosa–Salinas de Trapalcó, Salitral Ojo de Agua, Salitral Moreno	Río Negro	Allen	Upper Cretaceous	MML-Pv 11–13	Martinelli and Forasiepi, 2004
Yaminué	Faveoololithidae	Yaminué	Río Negro	Allen	Upper Cretaceous	MPA 85–93	Manera de Bianco, 1996
La Pampa	Faveoololithidae	Hucal Department	La Pampa	Colorado	Upper Cretaceous	—	Casadio et al., 2002
Río Negro 2	Megaloolithidae	Bajo de Santa Rosa–Salinas de Trapalcó	Río Negro	Allen	Upper Cretaceous	MML-Pv 25, 26, 37	Salgado et al., 2007
Auca Mahuevo	Megaloolithidae	Auca Mahuevo	Neuquén	Anacleto	Upper Cretaceous	MCF-PVPH 442	Grellet-Tinner et al., 2004

patagonicus. Eggs from Auca Mahuevo were used by Jackson et al. (2008) to calculate their water vapor conductance and, thus, are appropriate for comparative purposes. These samples are referred as Auca Mahuevo (Table 1) throughout the text.

Methods

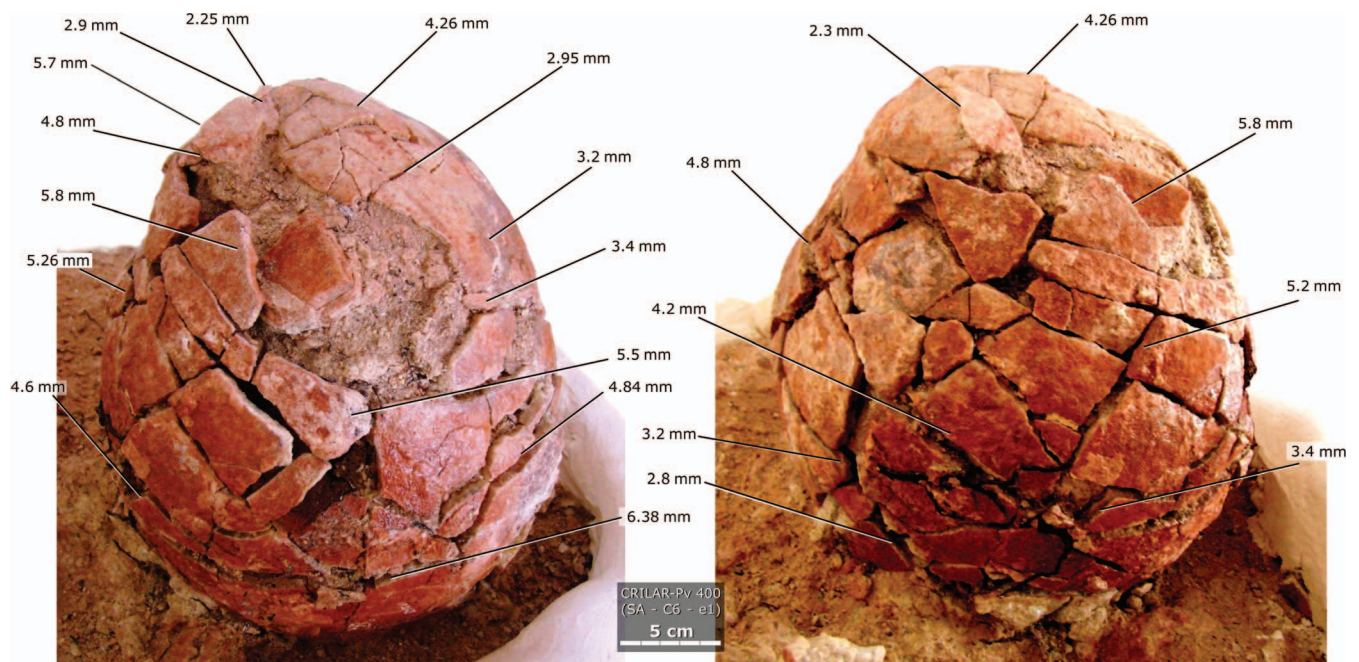
The following oological parameters are required to obtain water vapor conductance (G_{H_2O}), and are obtained by simple measurement: egg radius (r), eggshell thickness (L_s), pore density (D), and pore diameter (dp). All the other parameters can be obtained by simple equations (Table 2): egg surface area ($A_s = 4\pi r^2$), number of pores per egg ($N = D \cdot A_s$), pore area [$ap = \pi(dp/2)^2$], and total pore area per egg ($Ap = N \cdot ap$).

In order to properly compare the eggs with prior eggshell G_{H_2O} investigations, the water vapor conductance was calculated with the most commonly used formula:

$$G_{H_2O} = Ap / (0.478 \cdot L_s)$$

where Ap is the total pore area of the egg (mm^2) and L_s the pore length (mm). This equation was originally proposed by Paganelli (1980), who derived it from Fick's first law of gas diffusion across a porous barrier. This equation was also used by Ar and Rahn (1985) and Deeming (2006). The constant in the formula is linked to a 25 °C nesting temperature, a temperature commonly noted in extant crocodilians and turtles (Seymour and Ackerman, 1980). For simplicity and to facilitate comparison of our results with previous authors, pore canals are considered cylindrical and pore length (L_s) is considered equal to eggshell thickness.

Sanagasta Eggs and Eggshell Analyses.—Forty-seven Sanagasta eggshell fragments and 76 thin sections were selected and observed with a stereoscopic microscope (Leica® MZ12) and a petrographic microscope (Leica® DM2500P), and recorded with a digital camera (Leica® DFC295) attached to the microscopes. Pore density (pores/ mm^2) was acquired with CorelDRAW® X4, and pore dimensions were

**FIGURE 2**—Two views of a Sanagasta egg with typical eggshell thickness variation; label describes repository and number (SA–C6–e1 = subsite A, Clutch 6, egg 1).

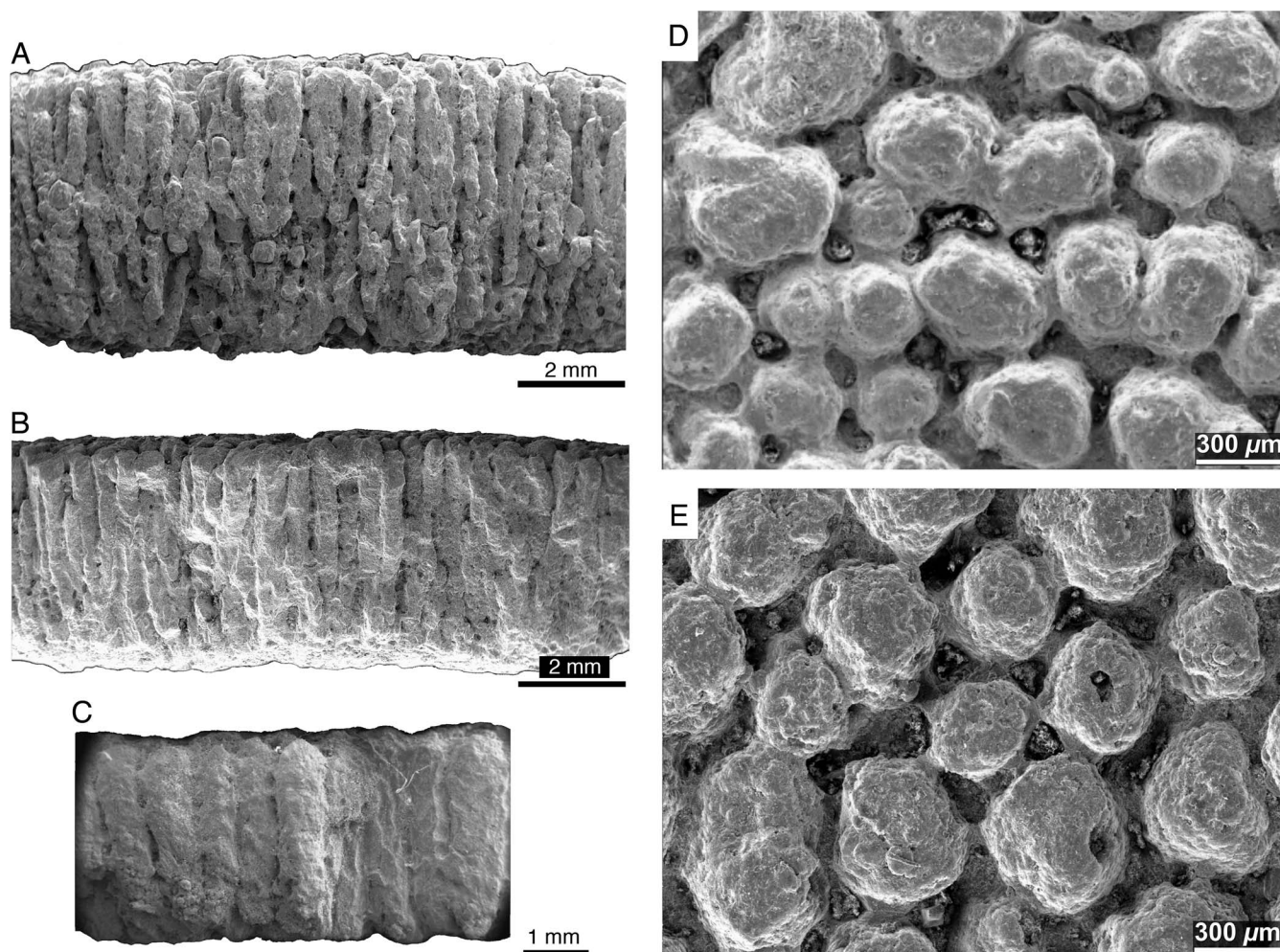


FIGURE 3—SEM images of eggshell fragments from Sanagasta. A–C) Morphological changes as the eggshell thins through ontogenetic growth; note the two pseudostructural layers in A. D–E) Eggshell outer surface showing the morphology of nodes and pore apertures.

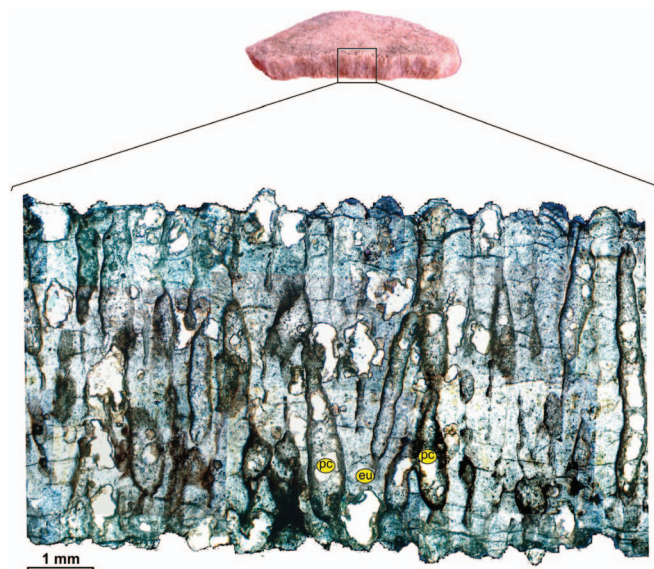


FIGURE 4—Radial thin section of a Sanagasta eggshell fragment with identification of the main eggshell units and pore-canals; eu = eggshell unit; pc = vertical pore canals.

measured using the software Leica® QWin. The values of pore diameter used are the mean of all measures of pore canals (without pore aperture) from each fragment. Eggshell thickness was measured from digital images using Leica® QWin and CorelDRAW® X4 and with a digital caliper for macrospecimens.

Entre Rios Eggshell and Río Negro, La Pampa, and Auca Mahuevo Eggs Analyses.—Pore density and pore diameter were assessed by observing, respectively, six fragments and five thin sections from Bajo de Santa Rosa-Salinas de Trapalcó (Río Negro 1), and one for Yaminué and Entre Ríos sites. The observations of the megaloolithid eggshells rest on 3 samples and one thin section from Río Negro (Río Negro 2), and 1 sample from Auca Mahuevo. Average egg diameter and shell thickness were obtained from previous reports: Salgado et al. (2007) for Bajo de Santa Rosa-Salinas de Trapalcó and Salitral Ojo de Agua, Martinelli and Forasiepi (2004) for Bajo de Santa Rosa, Simón (2006) for Salitral Moreno, Manera de Bianco (1996) for Yaminué, Casadio et al. (2002) for La Pampa, and Grellet-Tinner et al. (2004) for Auca Mahuevo.

Eggshell fragments were measured with a digital caliper to obtain both the fragment length (L) and the length of the sagitta (s). The radius (r) was obtained by the formula $r = (s / 2) + [L^2 / (8 \cdot s)]$ derived from the Pythagorean theorem, when complete eggs were not available.

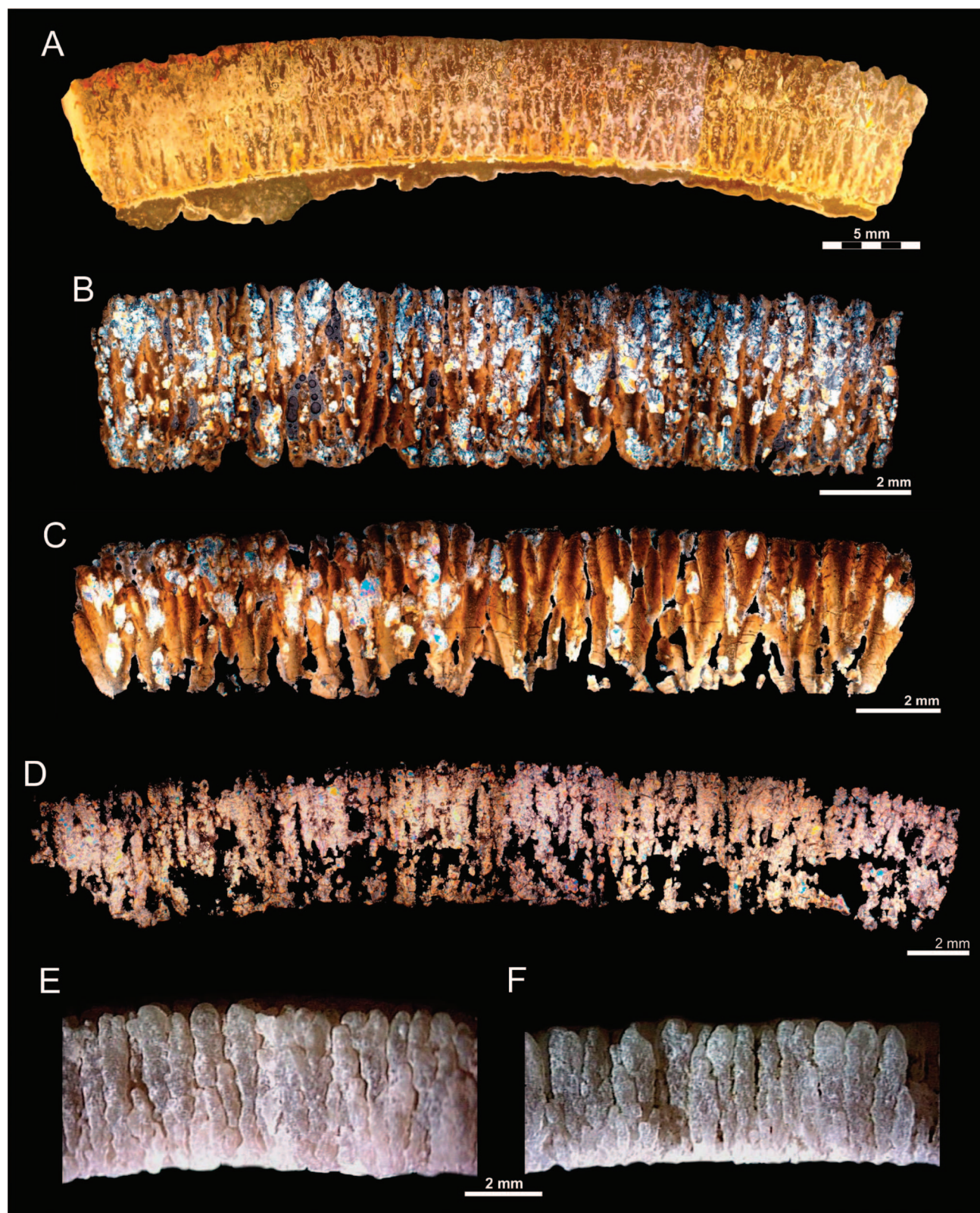


FIGURE 5—Radial thin section: comparison of specimens from A) Entre Ríos (CICyTTP R-1-1). B) Río Negro (Bajo de Santa Rosa-Salinas de Trapalcó). C) Río Negro (Salitral Moreno). D) Yaminué. E) and F) La Pampa.

TABLE 2—Egg and eggshell morphological characters for the faveoololithid eggs from Sanagasta, Entre Ríos, Río Negro 1 (Bajo de Santa Rosa/Salinas de Trapalcó, Salitral Ojo de Agua, Salitral Moreno), Yaminué, La Pampa, Río Negro 2 (Bajo de Santa Rosa/Salinas de Trapalcó), and Auca Mahuevo.

Parameters		Unit	Formula/Method	Sanagasta	Entre Ríos	Río Negro 1	Yaminué	La Pampa	Río Negro 2	Auca Mahuevo
r	Egg radius	cm	data from observation	10.5	10	9.75	9.4	9	6.5	6.1
d	Egg diameter	cm	data from observation	21	20	19.5	18.8	18	13	12.2
As	Egg surface area	cm ²	$As = 4\pi r^2$	1385	1270	1195	1105	1018	531	471
V	Egg volume	cm ³	$V = (4/3) \cdot \pi r^3$	4849	4257	3882	3451	3054	1150	963
Ls	Eggshell thickness	mm	data from observation	4.0	7.2	5.0	4.7	4.9	1.8	1.3
D	Pore density	pores/mm ²	data from observation	3.48	2.96	2.99	2.98	2.90	2.22	1.67
N	Number of pores per egg	pores/egg	$N = D \cdot As$	482133	375993	3571863	329131	295184	117866	78730
dp	Pore diameter	mm	data from observation	0.12	0.18	0.15	0.12	0.13	0.07	0.14
ap	Pore area	mm ²	$ap = \pi \cdot (dp/2)^2$	0.0113	0.0254	0.0177	0.0133	0.0133	0.0044	0.0154
Ap	Total pore area	cm ² /egg	$Ap = N \cdot ap$	55	96	63	37	39	5	12
GH2O	Water vapor conductance	mgH2O/day·Torr	$GH2O = Ap / (0.478 \cdot Ls)$	2852	2796	2641	1675	1676	602	1935
pGH2O	GH2O per pore	μgH2O/day·Torr·pore	$pGH2O = GH2O/N$	6.47	7.44	7.39	5.09	5.68	5.11	24.58
GO2	O2 conductance	mgO2/day·Torr	$GO2 = GH2O \cdot 0.85 \cdot (22.414/18.02)$	3289	2956	2792	1771	1772	636	2046
GCO2	CO2 conductance	mgCO2/day·Torr	$GCO2 = GH2O \cdot 0.67 \cdot (22.414/18.02)$	2592	2330	2201	1396	1397	502	1613

DESCRIPTION

Sanagasta Eggs and Eggshells

This section recapitulates the highlights of the description and discussion by Grellet-Tinner and Fiorelli (2010) that are significant for this research. The Sanagasta nesting site represents a single ootaxon, as there are no true or notable specific differences in egg size and eggshell morphologies within or between the clutches. The slightly ovoid eggs average 21 cm in diameter (min. 20 cm and max. 23 cm), 61–63 cm in circumference, and their average volume is 4850 cm³. A regular and notable variation in thickness occurs within single specimens from 7.54 to 1.29 mm. The mean eggshell thickness is 3.84 mm, the median 4.19 mm with high values of variance and standard deviation ($\sigma^2 = 1.173$; $n = 3077$). The thick eggshell specimens display notable nodular structures on their outer surfaces. The nodes are scaly and generally rounded or subpolygonal (see Grellet-Tinner and Fiorelli, 2010). Their average diameter, excluding the coalescent nodular structures, is 0.63 mm ($n = 476$) with highest values of 1.52 mm and smallest of 0.30 mm. The average node concentration per mm² is $X = 2.94$ (min = 1; max = 5.2; $Me = 3$; $\sigma^2 = 0.751$; $n = 105$).

Eggshell cross sections indicate the presence of a single structural layer, typical of non-theropod saurischian dinosaurs. No alleged pathological eggshell fragments with two or more structural layers were recovered at Sanagasta, although the sampling for this study is extremely high; more than 70 clutches and thousands of eggshell fragments. The eggshell unit nuclei are only observed in very few cases and are generally preserved poorly. In eggshells thicker than ~2.5 mm, the eggshell units display secondary dichotomic or polytomic ramifications as they grow outward. The main units, as well as each secondary ramification, terminate in nodes at the eggshell outer surface. In addition, the eggshell units, with slender concentric and convex growth lines, appear wider at their bases due to the union of several ramifications in a unique basal trunk as displayed in thin section and SEM observations. The overly abundant pore canals are notably straight in thin eggshells with a greater diameter toward the innermost eggshell surface in thin eggshells, giving them an overall megaloolithid aspect. Conversely in thick eggshells, pores begin to meander and branch between the main eggshell units and display several dichotomous ramifications toward the outermost eggshell surface. Furthermore,

several pore canals coalesce together commonly near to the external eggshell surface. Irrespective of the eggs, the internal pore channel diameter is highly variable ($X = 0.194$ mm; min. = 0.01 mm and max. = 0.85 mm; $Me = 0.14$ mm; $\sigma^2 = 0.0206$; $n = 433$). Conversely, the size of the external pore apertures is narrower with a constant diameter ($X = 0.1854$ mm; min. = 0.05 mm; max. = 0.49 mm; $Me = 0.17$ mm; $\sigma^2 = 0.0078$; $n = 63$). The concentration of pores per mm² varies according to the pore canal patterns ($X = 5.86$ p/mm²; min. = 1; max. = 14; $Me = 5$; $\sigma^2 = 7.622$; $n = 122$). Well-preserved specimens display a network of horizontal pore canals at their base as observed in the Auca Mahuevo eggshells (Grellet-Tinner et al., 2004, p. 954).

All the egg clutches were recovered within 1–3 m of such geothermal structures as mounds, terraces, and geysers. Although the regularly distributed eggs easily identify the clutches, no nest structures (e.g., sedimentary rims), as described previously at Auca Mahuevo by Chiappe et al. (2004), were identified. Egg clutches exhumed from the outcrop display up to 35 eggs per clutch. Such clutches average 1.8 m² surface with a maximum clutch axis of 220 cm where the eggs are arranged in a maximum of 2 superposed rows. The upper egg row contains more specimens than the lower one, a spatial distribution indicating a dug-out hole rather than eggs having been deposited on the surface as a nesting behavior (Grellet-Tinner and Fiorelli, 2010). The eggs were complete and not fractured at burial but exposed to compression after burial when the matrix solidified, as the majority of the eggs are superficially fractured in multiple eggshell fragments (Mueller-Töwe et al., 2002). The sandstone cement at the nesting site consists mostly of carbonates and silicates that originated from the geothermal activities that took place at Sanagasta and regionally in the Sierras Pampeanas during the late Early Cretaceous (Mutti et al., 2005; Grellet-Tinner and Fiorelli, 2010).

From a parataxonomic perspective and according their morphological characters, the eggs from Sanagasta correspond generally to Faveoololithidae with a filispherulitic morphotype and multicanalliculate pore system. Some thinner eggshells, however, would be assigned mostly to Megaloolithidae with a discretispherulitic eggshell structure morphotype, compactituberculate surface morphology, and tubocanalliculate pore system (Grellet-Tinner and Fiorelli, 2010). The monospecific assertion for the eggs of the nesting site rests on the fact that oological remains are identical throughout the entire stratigraphic section, despite the noted eggshell thickness variations. The Sanagasta

TABLE 3—Sauropod fossil recorded between 110 and 130 Ma in South America.

Species	Taxonomic groups	Locality	Age	References
<i>Chubutisaurus insignis</i>	Macronaria, Titanosauria	Argentina	Albian–Cenomanian	del Corro, 1974
<i>Ligabuesaurus leanzai</i>	Macronaria, Titanosauria	Argentina	Aptian–Albian	Bonaparte et al., 2006
<i>Agustinia ligabuei</i>	Macronaria, Titanosauria	Argentina	Aptian	Bonaparte, 1999
<i>Amargatitanis macni</i>	Macronaria	Argentina	Barremian	Apesteguía, 2007
<i>Zapalasaurus bonapartei</i>	Diplodocoidea	Argentina	upper Barremian–lower Aptian	Salgado et al., 2006
<i>Limaysaurus tessonei</i>	Diplodocoidea, Rebbachisauridae	Argentina	Albian–Turonian	Calvo and Salgado, 1995
<i>Rayososaurus agriensis</i>	Diplodocoidea, Rebbachisauridae	Argentina	Apitan–Cenomanian	Bonaparte, 1996; Carballido et al., 2010
<i>Amargasaurus cazaui</i>	Diplodocoidea, Dicraeosauridae	Argentina	Berriasian–Barremian	Salgado and Bonaparte, 1991
<i>Nopcsaspondylus alarconensis</i>	Diplodocoidea	Argentina	Aptian–Albian	Apesteguía, 2007
<i>Amazonsaurus maranhensis</i>	Diplodocoidea, Rebbachisauridae	Brazil	Aptian–Albian	Carvalho et al., 2003

oological material is, therefore, considered as a single ootaxon, regardless of the vagaries of the parataxonomic classification. This single ootaxon assemblage, however, still remains elusive in terms of its true dinosaurian taxonomic identity, but could be narrowed down to Neosauropoda based on its eggshell phylogenetic characters. An exhaustive search of the sauropod fossil record between 110 and 130 Ma in Argentina and neighboring countries reveals an equal presence of macronarian and diplodocoid sauropods (Table 3). Even considering large body size as a possible determinant factor, the South American macronarians (*Amargatitanis macni*, *Chubutisaurus insignis* and *Ligabuesaurus leanzai*) and diplodocoids (*Amargasaurus cazaui*, *Zapalasaurus bonapartei* and *Limaysaurus tessonei*) both represent valid clades for parenting the Sanagasta eggs. As such, Grellet-Tinner and Fiorelli (2010) referred the Sanagasta and similar Argentinean material to Neosauropoda until more supportive skeletal evidence comes forth. This taxonomic identification is followed in this study.

Entre Ríos Eggshell Fragment.—The eggshell fragment (CICyTTP R-1-1) is reexamined here, expanding and revising the previous description by de Valais et al. (2003). The curved triangular piece of eggshell (Figs. 5A, 6) measures $42 \times 43 \times 56$ mm and shows variable thickness with an average of 7.2 mm (min = 6.96 mm; max = 7.53 mm). As with the Sanagasta material, the outer surface of this fragment is sculptured with rounded nodes that display clear signs of acid dissolution (Figs. 6A–D). Pore canals exhibit various morphologies giving the eggshells an overall spongy appearance. In addition, the pores meander between the eggshell units and display several dichotomous ramifications toward the outermost eggshell surface and sometimes coalesce together near to the external eggshell surface. The average pore diameter is 0.18 mm ($n = 533$; min = 0.05 mm; max = 0.68 mm) with an average external pore density of 2.96 pores/mm².

Description of the Other Specimens.—For detailed descriptions of the Bajo de Santa Rosa-Salinas de Trapalcó and the Salitral Ojo de Agua eggs and shells, see Salgado et al. (2007, 2009); Martinelli and Forasiepi (2004) for the Bajo de Santa Rosa eggshells; Simón (2006) for Salitral Moreno; Manera de Bianco (1996) for Yaminué; Casadío et al. (2002) for La Pampa; and Grellet-Tinner et al. (2004) for Auca Mahuevo.

RESULTS

Overall, the Sanagasta G_{H_2O} values are the highest of all (Table 2) and cluster with the Entre Ríos and Río Negro 1 specimens. Interestingly, the Yaminué-La Pampa group values are close to the megaloolithid eggs (Table 4), which overall tend to have lower G_{H_2O} values than faveoolithid eggs. The values for Río Negro 2 (megaloolithid eggs Type 2B *sensu* Salgado et al., 2007) are among the lowest for this egg group (Table 4) and the recalculated Auca Mahuevo value falls well within the range of other known megaloolithid eggs (Table 4). The new 1934 mgH₂O/day·Torr value for *M. patagonicus*, however, contrasts sharply with the 341 mgH₂O/day·Torr obtained by Jackson et al. (2008) for the same eggs (Table 4). Such a difference seems biologically incongruous for the same egg species. This

inconsistency could be either related to the use of different parameters (such as temperature) by previous authors, the paraphyletic nature of the megaloolithid parataxonomic group, or the oviposition of the same egg type in extremely different ecosystems, although the latter seems unlikely in view of the patterns observed in other extinct and extant archosaurs (Brazaitis and Watanabe, 2011).

DISCUSSION

The choice of a judicious nesting site is critical in oviparous species, as the parents cannot compensate post-hatching for a poor choice of nesting environment (Shine and Harlow, 1996; Kolbe and Janzen, 2002; Kamel and Mrosovsky, 2005). Such maternal selectivity will affect hatching success and developmental rate, even to the precise location of the nests within preferential sites (Shine, 2005; Göth and Vogel, 1997). Nest moisture content and heat are the two extrinsic parameters that are vital for hatching success. Water vapor conductance is related to moisture content and, thus, becomes a valid proxy for moisture content and a source for hypotheses to infer optimum nesting sites for a given species.

Faveoolithid Eggs

The Sanagasta, Entre Ríos, Río Negro 1, Yaminué and La Pampa eggs were previously identified as *Sphaerovum erbeni* Mones, 1980, a subset of the faveoolithid parataxonomic egg group characterized by a filispherulitic morphotype and a multicanalicular pore system (Zhao and Ding, 1976; Mikhailov, 1991, 1997). However *Sphaerovum erbeni* was recently placed within the megaloolithid eggs, another parataxonomic group (Mikhailov, 1997; Sander et al., 2008). Grellet-Tinner and Fiorelli (2010) questioned this affiliation, as the *Sphaerovum erbeni* holotype lacks apomorphic characters and is considered parataxonically a *nomen dubium*. Regardless of their faveoolithid or megaloolithid parataxonomic classification, these eggs have been hypothesized to belong to titanosaurs (Mones, 1980; Faccio, 1994; Manera de Bianco, 1996; Casadío et al., 2002; Huh and Zelenitsky, 2002; Paik et al., 2004; Simón, 2006; Tauber, 2007), a taxonomic association not yet supported positively by any skeletal evidence. As such, the titanosaurian assignment for these eggs is considered doubtful in this study and a less inclusive neosauropod affiliation (see Grellet-Tinner and Fiorelli, 2010) is recommended until a positive identification comes forth (Grellet-Tinner et al., 2006).

The Sanagasta, Entre Ríos, and Río Negro 1 eggs group at nearly the same G_{H_2O} , whereas the Yaminué sample clusters with La Pampa specimens. The distribution pattern of the three first specimens is interesting as they share very similar estimated water vapor conductances, with negligible differences that would express only minor variations in their nesting environments. Geological evidence suggests that the Sanagasta neosauropods chose a geothermal paleoenvironment for nesting ground (Grellet-Tinner and Fiorelli, 2010), and an examination of this biological adaptation is warranted in the context of this study.

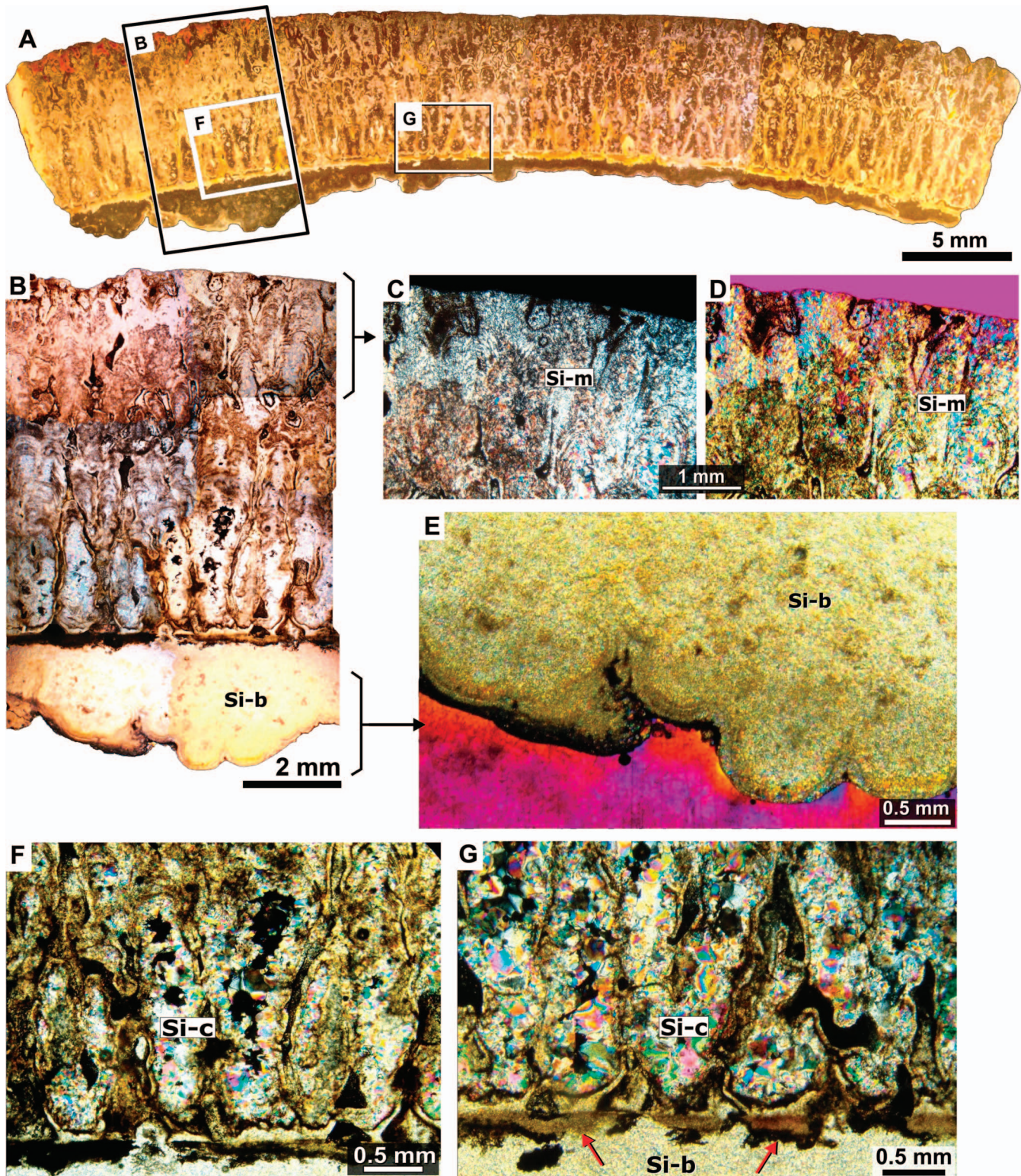


FIGURE 6—Entre Rios specimen. A) Entire fragment section viewed on a stereomicroscope. B) Radial thin section viewed on a biological microscope (MML-13). C) to G) Same section viewed on a petrographic microscope under cross-polarized light. C) and D) Replacement of original calcite by microchert. E) Botryoidal silica covering fragment's inner surface. F) and G) Replacement of original calcite by chalcedony (red arrows point to remnants of the fossilized membrana testacea). Si-b = botryoidal quartz; Si-m = microchert quartz; Si-c = chalcedony.

The geothermal nesting strategy is not an isolated event in extant reptiles; Pacific island megapodes and Galapagos iguanas utilize geothermal energy for incubation (Werner, 1983; Göth and Vogel, 1997). This interesting adaptive reproductive strategy avoids thermally

heterogeneous nesting environments and helps maintain constant temperature and moisture content in egg clutches. Geothermal solutions and vapors may have released acidic vapors, however, that likely affected the eggs during their incubation, as described for the

TABLE 4— G_{H_2O} values (in $\text{mgH}_2\text{O}/\text{day}\cdot\text{Torr}$) from this work compared with those from previous studies. G_{H_2O} values for modern reptiles were experimentally measured.

Source	Locality	Egg	G_{H_2O}
This study	Sanagasta, ARG	<i>Sphaerovum</i> (?) <i>erbeni</i> (neosauropod)	2852
	Entre Rios, ARG	<i>Sphaerovum</i> (?) <i>erbeni</i> (neosauropod)	2796
	Río Negro 1, ARG	<i>Sphaerovum</i> (?) <i>erbeni</i> (sauropod)	2641
	Yaminué, ARG	<i>Sphaerovum</i> (?) <i>erbeni</i> (sauropod)	1675
	La Pampa, ARG	<i>Sphaerovum</i> (?) <i>erbeni</i> (sauropod)	1676
	Río Negro 2, ARG	Megaloolithid eggs Type 2B (titanosaur)	602
	Auca Mahuevo, ARG	<i>Megaloolithus patagonicus</i> (lithostrotian)	1935
	Bouches-du-Rhône, FRA	<i>Hypselosaurus</i> (?) <i>priscus</i> (sauropod)	1203
Seymour (1979)	FRA	<i>Cairanoolithus roussetensis</i> (sauropod)	1305
Deeming (2006)	FRA	<i>Megaloolithus microtuberculata</i> (sauropod)	906
	FRA	<i>Megaloolithus petralta</i> (sauropod)	1388
	FRA	<i>Megaloolithus pseudomamillare</i> (sauropod)	1629
	FRA	<i>Megaloolithus mamillare</i> (titanosaur)	2175
Jackson et al.(2008)	Auca Mahuevo, ARG	<i>Megaloolithus patagonicus</i> (lithostrotian)	341
	Pinyes, ESP	<i>Megaloolithus siruguei</i> (sauropod)	3979
	Hateg Basin, ROM	<i>Megaloolithus</i> cf. <i>siruguei</i> (nemegtosaur?)	~2000
Grigorescu et al. (1994, 2010)	Asia	<i>Crocodylus porosus</i> (saltwater crocodile)	2800
Grigg and Baird (1985)	USA	<i>Alligator mississippiensis</i> (american alligator)	2900
Packard et al. (1979)			

Sanagasta nesting site (Grellet-Tinner and Fiorelli, 2010). The outer eggshell surfaces of the thick eggshells were thinned (Fig. 7) through dissolution and acidification (Clayburn et al., 2004; see also Grellet-Tinner and Fiorelli, 2010). As this process occurred, the G_{H_2O} consequently increased, as per the formula $G_{H_2O} = A_p/(0.478 \cdot L_s)$. Concomitantly to this external erosion, developing embryos also contributed to this thinning process by absorbing the innermost eggshell surface (Figs. 7C and C'), thus further increasing G_{H_2O} (Seymour et al., 1987; Deeming and Ferguson, 1991), as documented in dinosaur eggs with embryos (Sabath, 1991; Grellet-Tinner et al., 2004; Grellet-Tinner, 2006; Martin, 2006). As such, the internal biologically induced eggshell resorption combined with the outer chemical erosion

in Sanagasta eggshell resulted in thinning of the shell (the extreme values of eggshell thickness being 7.9 and 1.4 mm). Such a process was beneficial for the embryonic growth by maintaining an optimal gas exchange and water loss and concurrently facilitated the hatching process by allowing the hatching embryos to easily break through a thinner and more fragile material. Moreover, as lungs develop (Burton and Tullett, 1985), the need for O_2 increases but concomitantly becomes increasingly depleted in dug-out nests. A thinner shell with increased conductance values, as observed at Sanagasta, would have compensated and facilitated gas exchange during the late developmental ontogenetic stages. As such we regard the presence of extremely thick eggshells in geothermal environments as a natural reproductive

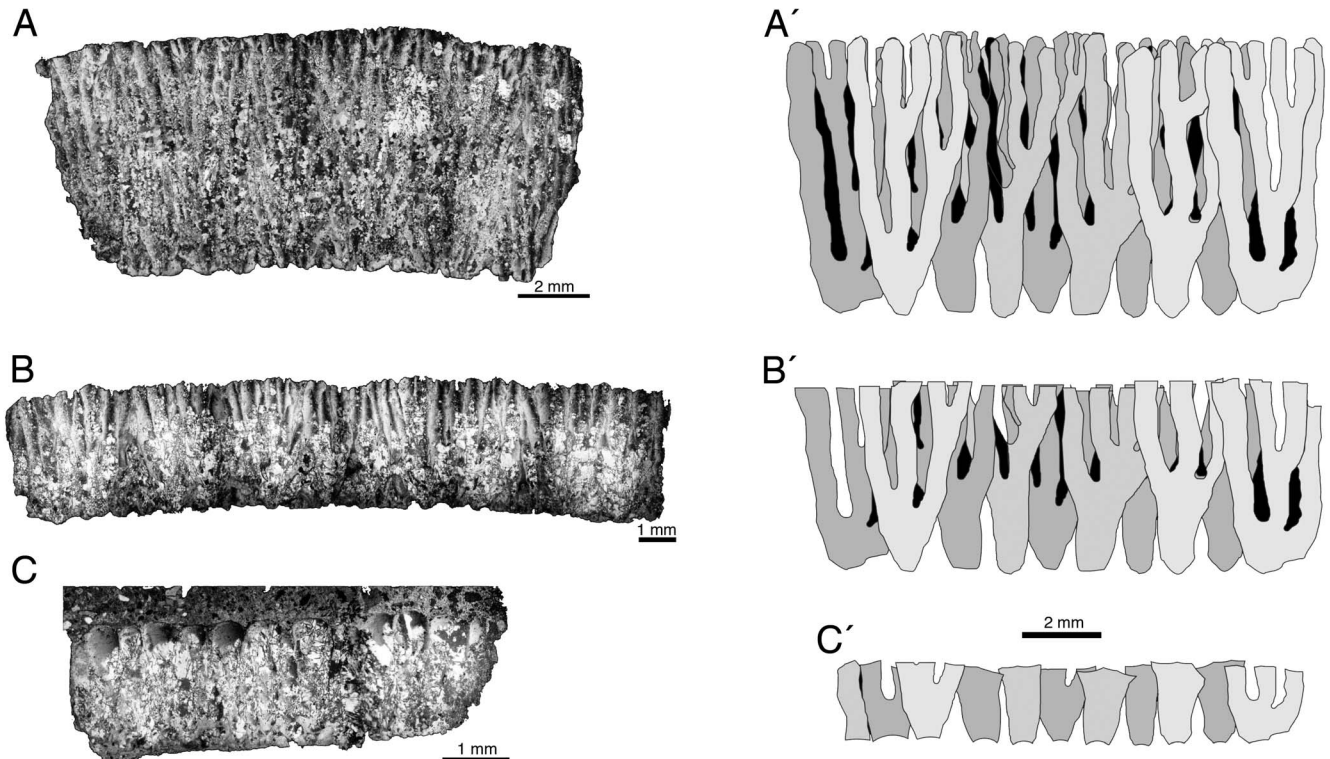


FIGURE 7—Sanagasta eggshells showing erosion and shell thinning. A, B, C) Eggshell sections. A', B', C') Schematics of pore canals for A, B, and C, respectively. A, A') A thick eggshell, showing limited erosion. B, B') Slightly eroded and thinner eggshell; note the pore arrangement in B' corresponds to the lower section of A'. C, C') Thinnest eggshell; only the base of the pores remained.

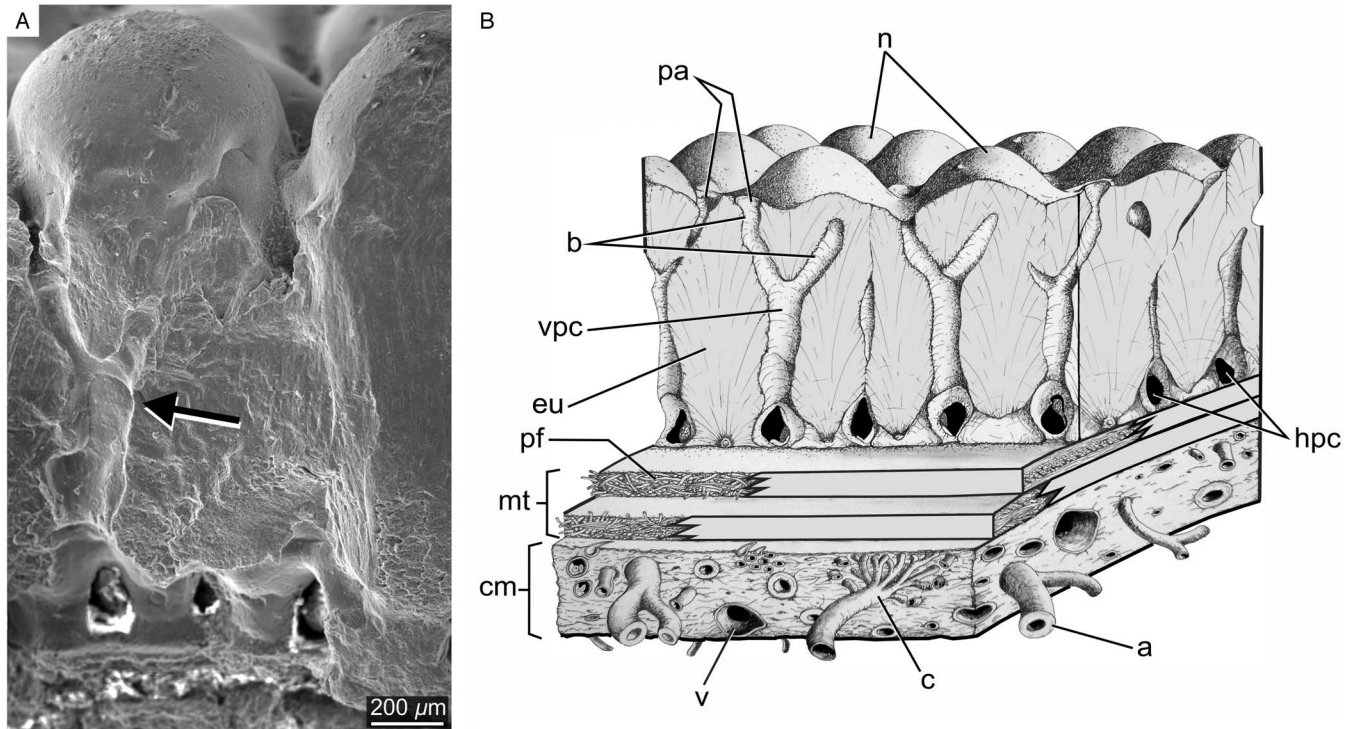


FIGURE 8—A) Eggshell fragment from Auca Mahuevo, Neuquén, Argentina showing the total view of the radial section of the eggshell and a Y vertical pore canal with an arrow where it widens B) Schematic interpretation of Auca Mahuevo eggshells. Note the transverse Y vertical pore canals and the corresponding horizontal network system according to Grellet-Tinner et al. (2004) SEM observations. (Restoration by L.E. Fiorelli based on Kardong, 2001, and Grellet-Tinner et al., 2004). This pore canal system suggests an adaptation to moist environments to favor efficient gas exchanges. a = arteries; b = branches of pore canal; c = capillaries; cm = corioallantoid membrane; eu = eggshell unit; hpc = horizontal pore canals; mt = membrana testacea; n = node on outer eggshell surface; pa = pore aperture; pf = protein fibers of the membrana testacea; r = root of a recent plant; v = veins; vpc = vertical pore canals.

adaptation and a symbiotic relationship between the dinosaur parent lineage and this specific environment.

In respect to incubation constraints, hydrothermal and geothermal settings are characterized by the presence of sediments with high permeability increasing groundwater percolation (Pirajno, 2009). As such, eggs are not drowned in pore fluids but contained in extremely water-saturated soils with moderate to low pHs due to acidic vapors, which create a thermally and moisture homogeneous nesting environment. The loss of eggshell thickness during the incubation process is precisely one of the particular reproductive adaptations to such specialized environments (Grellet-Tinner and Fiorelli, 2010).

The Entre Ríos eggshell fragment (Figs. 5A, 6) is morphologically similar to the Sanagasta specimens (Figs. 4–6): it also appears to display two pseudostructural layers, as described previously by de Valais et al. (2003) (Figs. 6A–B). The appearance of two structural layers stems, however, from the abrupt termination of several eggshell units and their branching in the shell mid-section (Fig. 6B), a feature also shared with specimens from Río Negro 1 (i.e., MML-13; Salgado et al., 2007). In addition, the Entre Ríos fragment's original calcium carbonate has been replaced by epidote aggregates (Figs. 6F–G) and other silicates (chalcedony, botryoidal, and microchert; Figs. 6C–G), similar to the Sanagasta eggshells, and suggestive of geothermal environments (Grellet-Tinner and Fiorelli, 2010). This mineral alteration coupled with the above-mentioned egg morphological features and comparable G_{H_2O} values implies similar nesting conditions in geothermal environments at Sanagasta and Entre Ríos. To date, however, no such geological evidence has yet been reported at the Río Negro 1 nesting site.

The G_{H_2O} of the Sanagasta, Entre Ríos, and Río Negro 1 eggs matches that of modern crocodilians and exceeds the values of the Yaminué and La Pampa specimens (Tables 2, 4). The dissimilarities between these two groups likely reflect different nesting conditions with

lower moisture contents for Yaminué and La Pampa. Overall, these results suggest that closely related neosauropod clades may have adopted various nesting strategies, where some groups would have sought thermally homogenous nesting environments when and where available.

Megaloolithid Eggs

Although the faveoololithid eggs of Yaminué and La Pampa show G_{H_2O} values are very similar to megaloolithid eggs, megaloolithid eggshells display overall lower G_{H_2O} values, ranging from 600 to 2000 $\text{mgH}_2\text{O}/\text{day}\cdot\text{Torr}$ with a mean of 1300 $\text{mgH}_2\text{O}/\text{day}\cdot\text{Torr}$ (Table 4), than the faveoololithid specimens. Curiously, the recalculated 1935 $\text{mgH}_2\text{O}/\text{day}\cdot\text{Torr}$ value for *M. patagonicus* matches Grigorescu et al.'s (1994, 2010) values for *M. siruguei* but contrasts sharply with that obtained by Jackson et al. (2008) for the Auca Mahuevo eggs (Table 4). The previous value not only departs from the presently calculated value but also stands greatly outside the established range by others, which is quite intriguing and warrants further discussion. Jackson et al.'s (2008) low value of 341 $\text{mgH}_2\text{O}/\text{day}\cdot\text{Torr}$ likely results from a pore density underevaluation (0.195 pores/ mm^2), which is 8 times lower (Table 2) than our present observations and illustrated in Grellet-Tinner et al.'s (2004) description; also see Figure 4 herein.

In addition to the pore concentration underestimation, Jackson et al. (2008) refutes the presence of Y-shaped pore canals and a complex pore canal system located apposed to the membrana testacea. Contrary to these claims, well-preserved Auca Mahuevo eggshells, illustrated in Grellet-Tinner et al. (2004), display neatly formed Y-shaped pore canals (Fig. 8), where the diameter of the common section greatly widens in respect to each branch of the Y (Fig. 8). In addition, the lateral pore canal system located at the innermost level of the eggshells is most obvious when the underlying membrana testacea is fossilized (Grellet-

Tinner et al., 2004) and, thus, is not an erosional artifact but a biological feature observable mostly in well-preserved specimens (Fig. 8). Such oversight of these observations will dramatically bias interpretations of the material. We, therefore, propose the following hypothesis based on a positive correlation between egg mass and eggshell thickness, where egg mass is directly correlated to egg size (Ar et al., 1974, 1979; Rahn et al., 1975; Anderson et al., 1979; Ar and Rahn, 1985; Rahn and Paganelli, 1989; Birchard and Deeming, 2009; Donaire and López-Martínez, 2009): Eggshell characters are genetically dictated (Grellet-Tinner, 2006; Gautron et al., 2007; Nys and Gautron, 2007; Hincke et al., 2008; Rose and Hincke, 2009). The number and concentration of straight pore canals for G_{H_2O} and gas exchanges are adaptations that reflect a range of nesting environments. Given a determined egg mass and eggshell thickness, an overly excessive concentration of pore canals that connect directly the outer with the inner eggshell surfaces would negatively affect the mechanical resistance of a relatively thin monolayered eggshell structure. Y-shaped pore canals (Fig. 8), the upper sections of which reach only the top third of the eggshell thickness, with the common section nearly widening twice as much as each branch, however, compromise the overall mechanical resistance less than pores connecting directly the outer to the inner eggshell surfaces.

As witnessed in crocodilians, birds and extinct dinosaurs (Clayburn et al., 2004), and Sanagasta eggs (Grellet-Tinner and Fiorelli, 2010), the outer eggshell surface becomes progressively eroded during incubation (see figures in Grellet-Tinner et al., 2004). As a consequence, when thinning occurs, the upper branches of the Y-shaped pore canals are lost and the wider section of the canals is exposed. This, in turn, would increase gas conductance during later ontogenetic stages, when more gas exchanges are required by the growing embryo. Furthermore, the lower sections of the Y-shaped pore canals, well documented in the Auca Mahuevo eggs (Grellet-Tinner et al., 2004), abut in a secondary pore canal system that is located at and above the level of the membrana testacea and surrounds the embryo (Grellet-Tinner et al., 2004). Hence, the whole system enhances gas exchanges with the highly vascularized chorioallantoic membrane and becomes a specialized network that facilitates O_2 and CO_2 exchange (Fig. 8), like the specialized trachea and lungs of the respiratory system (West, 1990; Kardong, 2001). As such, this internal pore network and its geometry would enhance a greater G_{H_2O} , G_{O_2} , and G_{CO_2} through the shell to facilitate embryonic development in completely or semi-buried nests with high moisture content, as hypothesized by Deeming (2006). Considering our hypothesis and reexamination of the values expressed in Table 4, our interpretation is that the Auca Mahuevo clutches were incubated in substantially higher moisture conditions (Garrido, 2010b) than previously indicated.

The reproduction of oviparous vertebrates are more constrained by environmental factors than their viviparous counterparts. Therefore, judicious nesting site selection becomes critical for successful reproduction. Deeming (2006) concluded that dinosaur eggs were incubated in buried nests. However, whether the megaloolithid eggs were incubated in dug-out holes, semi-buried under vegetal mounds, or rimmed nests is still debated. This brings to light the interesting case of the five Auca Mahuevo trace fossils that were interpreted as rimmed nests (Chiappe et al., 2004), perhaps a questionable interpretation and one that could have profound biological, ecological, and phylogenetic implications. One of the authors (GGT) examined the rimmed nests made in the Auca Mahuevo paleoriver silty sediments (Garrido, 2010b) and recognized them as dinosaur manus and pes prints with associated lateral sediment displacements similar to those reported in Spain (Bates et al., 2008). Observations of modern archosaurs demonstrate that dug-out nests are not pes or manus-shaped depressions. The presence of a few eggs in some of these tracks is easily explained by the floating property of eggs (Tokaryk and Storer, 1991), combined with the fact that the Auca Mahuevo nesting site results from multiple and successive flooding events (Garrido, 2010b).

Regardless, whether titanosaur eggs were buried in dug-out holes or covered with a vegetal covering as proposed by Grellet-Tinner et al. (2004) is still unresolved, but the rimmed-nest hypothesis seems the least parsimonious considering modern analogues, sedimentary evidence, and the pes and manus shapes of the Auca Mahuevo trace fossils. Nevertheless, it is quite plausible that the neosauropod dinosaurs, as a family that laid megaloolithid eggs, could have adopted several nesting strategies adapted to very moist nesting environments like the modern crocodilians (Singh and Bustard, 1977; Verdade and Lavorenti, 1990; Whitehead et al., 1990; Hunt and Ogden, 1991; Piña et al., 2007; Stevenson and Whitaker, 2010; Brazaitis and Watanabe, 2011).

CONCLUSIONS

This study demonstrates that the Sanagasta, Entre Ríos, and Río Negro 1 eggs group at the highest G_{H_2O} (above 2600 mgH₂O/day·Torr), like modern crocodilians, suggesting a saturated nesting moisture content, while the Yaminué sample clusters with La Pampa specimens at lower values closer to megaloolithid eggs. Geological evidence suggests that the Sanagasta neosauropods deliberately chose a geothermal paleoenvironment for their nesting ground (Grellet-Tinner and Fiorelli, 2010). The Cretaceous Entre Ríos' eggshell fragments show morphological characters and diagenetic inclusions that are congruent with those observed at Sanagasta, suggesting that the neosauropods at these nesting sites adopted a similar reproductive strategy by ovidepositing their egg clutches in geothermal settings to avoid thermally heterogeneous nesting environments, thus optimizing hatching success.

The thinning of the Sanagasta outer eggshell surfaces by erosive geothermal fluids—coupled with an internal calcium resorption by the developing embryos—reduced the eggshell thickness, increasing gas conductance, and concomitantly decreasing eggshell mechanical resistance during the late ontogenetic stages and facilitating hatching. G_{H_2O} values for Río Negro 1 eggs are similar to those of Sanagasta and Entre Ríos (albeit a little smaller), but presently there is no evidence of a geothermal setting. The G_{H_2O} values for the faveoolithid Yaminué and La Pampa specimens, which overlap with the highest known values for megaloolithid eggs, suggests the existence of several nesting strategies for these dinosaurs in relatively elevated moisture content nesting environments. Among all the megaloolithids, the previously calculated *M. patagonicus* G_{H_2O} value has been found to be much lower than the rest of the G_{H_2O} values of this parataxonomic egg group. However, a revised G_{H_2O} value for *M. patagonicus* suggests the eggs were laid in a nesting environment with high moisture content. Moreover, this investigation puts forth a novel hypothesis that considers the mechanical structure of relatively thin eggshells in respect to egg mass, pore canal concentration, and the Y-shaped pores, which optimize gas diffusion. Neosauropod brooding and nesting behaviors, based on observations presented herein, relied on elevated moisture levels in nesting environments, and some groups were opportunistic nesters by using geothermal settings to avoid thermally heterogeneous nesting environments.

ACKNOWLEDGMENTS

We acknowledge the CRILAR technicians (Sergio de la Vega, Roxana Brizuela, and Carlos Bustamante), and our colleagues B.M. Tomotani, I. Amelotti, J. Torrén, P. Alasino, M. Larrovere, D. Pol, and R. Tomassini for their help and support. We are especially thankful to Drs. L. Salgado (INIBIOMA-CONICET), T. Manera de Bianco (UNS), J. Noriega (CICYTTP-CONICET), S. Casadio (UNRN), A. Kramarz (MACN), and Biol. E. Simón for accessing fossil egg material under their care. We acknowledge the Secretaría de Cultura de La Rioja and the Consejo Federal de Ciencia y Tecnología (COFECYT) for its funding (SCTIP N°1198/06 – Proyecto LR02/06). We also thank Dr. Beder Herrera, Valeria Soriano, and Beba de Soria for their support. GGT is particularly grateful for financial support from Valeria Soriano, Beder Herrera, the

AMMRF TAP GRANT# 1016, Drs. A. Jones and S. Ringer (University of Sydney, AUS) and for scientific and technical assistance from Drs. Jones, Ratnac, and Trimby. We thank M. Vianey-Liaud, another anonymous reviewer, and S. Hasiotis for suggestions and constructive comments that helped improve this manuscript.

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