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Comparison of water vapor conductance in a titanosaur egg from the Upper Cretaceous of Argentina and a *Megaloolithus siruguei* egg from Spain

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Abstract.—We calculated water vapor conductance (a product of eggshell porosity) from the first definitively identified sauropod egg (*Megaloolithus patagonicus*) from the Auca Mahuevo locality in Argentina. We then compared the results with those from *M. siruguei* (an egg type long associated with sauropod dinosaurs) from the Pinyes locality in Spain. The 14-cm Auca Mahuevo egg has a thinner eggshell and 47 times fewer pores than the 22-cm *M. siruguei* specimen. The resulting water vapor conductance (G_{H_2O}) of the titanosaur and *M. siruguei* eggs is 341 and 3979 mg H_2O day^{-1} $Torr^{-1}$, respectively; these values are two and ten times greater than in avian eggs of comparable size, but lower than in eggs of most modern reptiles. Clutches from Auca Mahuevo typically contain 20–40 eggs; in contrast, *M. siruguei* clutches from the Pinyes site average nine eggs. The G_{H_2O} of *M. siruguei* exceeds that of the Argentine egg by an order of magnitude, supporting previous inferences of egg burial. The G_{H_2O} of the Argentine titanosaur egg closely approximates that of *Troodon* and some oviraptorid eggs, previously calculated as equal to or two times greater than, respectively, the G_{H_2O} of avian eggs of similar size. Higher embryonic growth rates (relative to modern reptiles), especially in some dinosaurs with large clutch mass, may have required incubation in a more open environment, where water conservation represented a more critical factor than in a buried clutch. The lower G_{H_2O} calculated for the two megaloolithid eggs is consistent with previous interpretations of nesting mode that are based on site taphonomy and nesting traces. This study indicates that at least some dinosaurs did not fully bury their eggs.

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Introduction

In the last 20 years, a growing interest in understanding extinct animals as living organisms has produced considerable discourse in the scientific literature regarding dinosaur reproductive behaviors. Inferences of egg brooding (Norell et al. 1995; Dong and Currie 1996; Varricchio et al. 1997), life-history strategy (Weishampel and Horner 1994; Sander et al. in press), parental care, and neonatal development mode (Horner and Makela 1979; Horner 1984) continue to generate controversy (Geist and Jones 1996; Carpenter 1999; Ruben et al. 1996; Deeming 2002, 2006; Jackson and Varricchio 2003; Jackson et al. 2004; Grellet-Tinner et al. 2006). Although fossil eggs and nesting horizons provide potentially valuable evidence about a given egg-laying taxon, reproductive behaviors are often difficult to interpret from the fossil record (Hirsch 2001; Mueller-Töwe et al. 2002; Jackson and Varricchio 2003; Jackson et al. 2004; Grellet-Tinner et al. 2006; Sander et al. in press).

In his seminal paper on gas conductance of dinosaur eggs, Seymour (1979) argued that, in searching for evidence of dinosaur reproductive behavior and physiology, it is desirable to form conclusions that depend directly on measurements available from the fossil material. In modern taxa, the conductance of an egg closely corresponds to the type of incubation environment, thereby providing important insights into the nesting strategy (Ar et al. 1974; Seymour 1979; Deeming 2006). The amount of theoretical and empirical information available on shell conductance and water loss in bird eggs provides a model for comparing fossil specimens (Seymour 1979). For example, most avian eggs are exposed to the atmo-

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sphere during incubation and exhibit low water vapor conductance (G_{H_2O}) in order to conserve water that would potentially be lost to evaporation (Seymour 1979). In contrast, reptiles typically incubate their eggs in high humidity and low oxygen conditions such as underground burial or in vegetation mounds. The eggs generally exhibit higher gas conductance values than avian eggs. These differences between avian and reptilian egg G_{H_2O} are often used to interpret the egg incubation environment of extinct taxa (Seymour 1979; Williams et al. 1984; Sabath 1991; Grigorescu et al. 1994; Deeming 2002, 2006; Grellet-Tinner and Chiappe 2004; Grellet-Tinner et al. 2006; Sander et al. in press).

Eggs of the oofamily Megaloolithidae occur nearly worldwide and are often assigned to sauropod dinosaurs, on the basis of bones in the same stratum or formation. Mikhailov (1997) argued that the Megaloolithidae represents a single dinosaur clade, the Sauropoda. However, Kohring (1989) identified *Megaloolithus* eggs from Spain as those of hadrosaurs, and Grigorescu et al. (1994), on the basis of a hadrosaur embryo that occurred 0.5 m from an egg, assigned similar eggs from Romania to *Telmatosaurus*. However, the abundance of sauropod bones and *Megaloolithus* eggs in the Late Cretaceous of India (Mohabey 1996, 1999, 2001; Sahni et al. 1994) provides a striking contrast to the absence of hadrosaur osteological remains during the same time period (Weishampel et al. 2004), thus assignment of *Megaloolithus* eggs to hadrosaurs remains controversial.

All analyses of *Megaloolithus* eggs to date reveal a significantly higher water vapor conductance than in modern avian eggs of comparable size. Previous studies, therefore, concluded that sauropods buried their eggs underground or in incubation mounds (Seymour 1979; Williams et al. 1984; Sabath 1991; Grigorescu et al. 1994; Deeming 2002, 2006; Sander et al. in press). Furthermore, two studies (Seymour 1979; Seymour and Ackerman 1980) suggested that sauropods might have been forced to limit their clutch size to 13 eggs. Theoretically, this would have prevented unacceptably high levels of carbon dioxide and depletion of oxygen in the nest during the latter part of the incubation period when embryonic metabolic activity reached a maximum. However, eggs containing identifiable sauropod embryonic remains were unknown at the time of most previous analyses (Seymour 1979; Seymour and Ackerman 1980; Williams et al. 1984; Sabath 1991; Sahni et al. 1994) and, therefore, taxonomic identification of the eggs in these studies remains uncertain.

The 1997 discovery of the Auca Mahuevo locality in the Anacleto Formation, Neuquén Province, Argentina, allowed the first definitive correlation of a *Megaloolithus* egg (*M. patagonicus*) to a sauropod dinosaur, based on osteological remains within an egg (Chiappe et al. 1998). Detailed taphonomic studies conducted at the Auca Mahuevo locality indicate that the number of eggs in these South American titanosaur clutches far exceeds the proposed limit on sauropod clutch size. Whereas European and Indian clutches typically contain fewer than 15 eggs (Kerourio 1981; Cousin et al. 1994; Cousin and Breton 1999; Mohabey 1996, 1999, 2001; Sahni and Khosla 1994; Sander et al. 1998; Peitz 1999, 2000; López-Martínez et al. 2000; Garcia et al. 2003; Sander et al. in press), the Argentine titanosaur clutches commonly contain 20–40 eggs (Chiappe et al. 1999, 2005; Jackson et al. 2004). Furthermore, six trace fossil nests that are preserved in sandstone at the Auca Mahuevo locality indicate that the nests were open and the eggs were not buried underground (Chiappe et al. 2004). However, two papers (Grellet-Tinner and Chiappe 2004; Grellet-Tinner et al. 2006) now suggest that Auca Mahuevo titanosaur eggs were incubated in high-humidity conditions consistent with vegetation in the nest, a conclusion that appears contradictory to the open-nest hypothesis.

To examine these contrasting interpretations of incubation environment, we calculated the water vapor conductance for an Auca Mahuevo titanosaur egg, *Megaloolithus patagonicus* (Calvo et al. 1997). To address potential problems of extrapolation from modern avian egg data to masses equivalent to those of dinosaur eggs (see Carpenter 1999), we added an *Aepyornis* (the extinct elephant bird) egg to the extensive data set compiled by Ar and Rahn (1985). *Aepyornis* eggs dwarf all other avian eggs and are larger than most, if not all, dinosaur eggs (Carpenter 1999). The *Aepyornis* egg therefore, is valuable for extending the range of data and improving the regression analysis, to allow interpolation, rather than extrapolation from the data.

The unique combination of definitive egg identification, trace fossil nests, and calculated water vapor conductance allows a more rigorous evaluation of previous hypotheses regarding egg incubation and possible limits on sauropod clutch size. If Auca Mahuevo eggs were incubated in open nests (Chiappe et al. 2004), the eggs should show significantly lower conductance values than eggs incubated in high-humidity environments where substrate burial or a vegetation mound is characteristic. Comparison of the Auca Mahuevo eggs to previous European studies of *Megaloolithus* eggs, however, is difficult due to previous calculation errors and differences in field methods (i.e., lack of taphonomic and sedimentologic data, three dimensional mapping). Therefore, the techniques used at Auca Mahuevo were also applied to a new *Megaloolithus siruguei* locality in Spain (Jackson 2007). Use of similar field and laboratory procedures allows the first direct comparison of water vapor conductance rates of South American and European eggs, in order to assess potential differences in reproductive biology.

Nesting Localities

Auca Mahuevo Site

Most eggs at the Auca Mahuevo locality occur in uniform, fine-grained overbank deposits. Deposition of these sediments on the floodplain occurred at some distance from an active stream channel, and the muddy deposits exhibit no evidence of sedimentary structures (Chiappe et al. 1999). In contrast, six titanosaur clutches at Auca Mahuevo are preserved in sandstone: five occur in the upper surface of a channel deposit, and a sixth clutch is preserved in a crevasse splay sand lobe (Chiappe et al. 2004). The depressions containing the six egg clutches truncate primary sedimentary structures of the host strata, and a massive sandstone rim encircles portions of each nest (Fig. 1). The eggs within all six depressions are surrounded by mudstone, deposited from suspension settling of fine-grained sediment during one or more flood events. The lithological difference between the sandstone trace fossil nests and the mudstone that surrounds the eggs and fills the depressions indicates that the nests were open and that Auca Mahuevo eggs were *not* incubated underground (Chiappe et al. 2004).

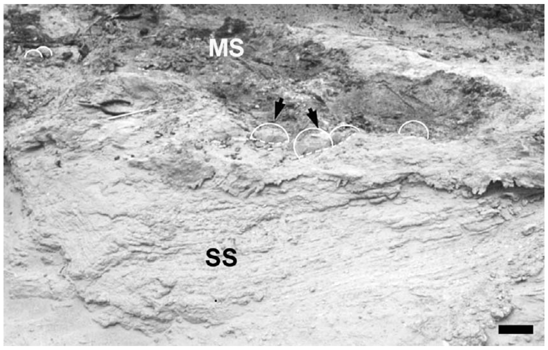

FIGURE 1. Auca Mahuevo trace fossil nest (NE05). White circles and two black arrows indicate eggs preserved within a depression that truncates cross-bedded sandstone (SS). Portions of massive sandstone rim occur in front of the eggs on the right. Darker mudstone (MS) surrounds the eggs. Scale bar, 10 cm.

Pinyes Site

The south-central Pyrenean mountain range of northern Spain contains excellent outcrop exposures of Upper Cretaceous terrestrial strata and a rich fossil record of dinosaur faunas (Galbrun et al. 1993; López-Martínez 1999; Ardèvol et al. 2000; López-Martínez et al. 2001; Jackson 2007). Numerous fossil egg localities are present within the Tremp Formation, and in situ eggs and clutches were previously mapped from at least five localities: Basturs and Coll de Nargó (Sanz and Moratalla 1997; Peitz 1999, 2000), Suterranya (Ardèvol et al. 1999), Biscarri (Martínez-López et al. 2000), and Faidella (Bravo et al. 1999). In 2003, a new megaloolithid nesting locality was discovered in outcrops approximately 20 km west of the village of Coll de Nargó, in Lleida Province, Spain (Jackson 2007).

The Pinyes locality, named for an abandoned farmstead near the site, occurs within a heavily forested tributary drainage that flows southeast from the mountains and joins

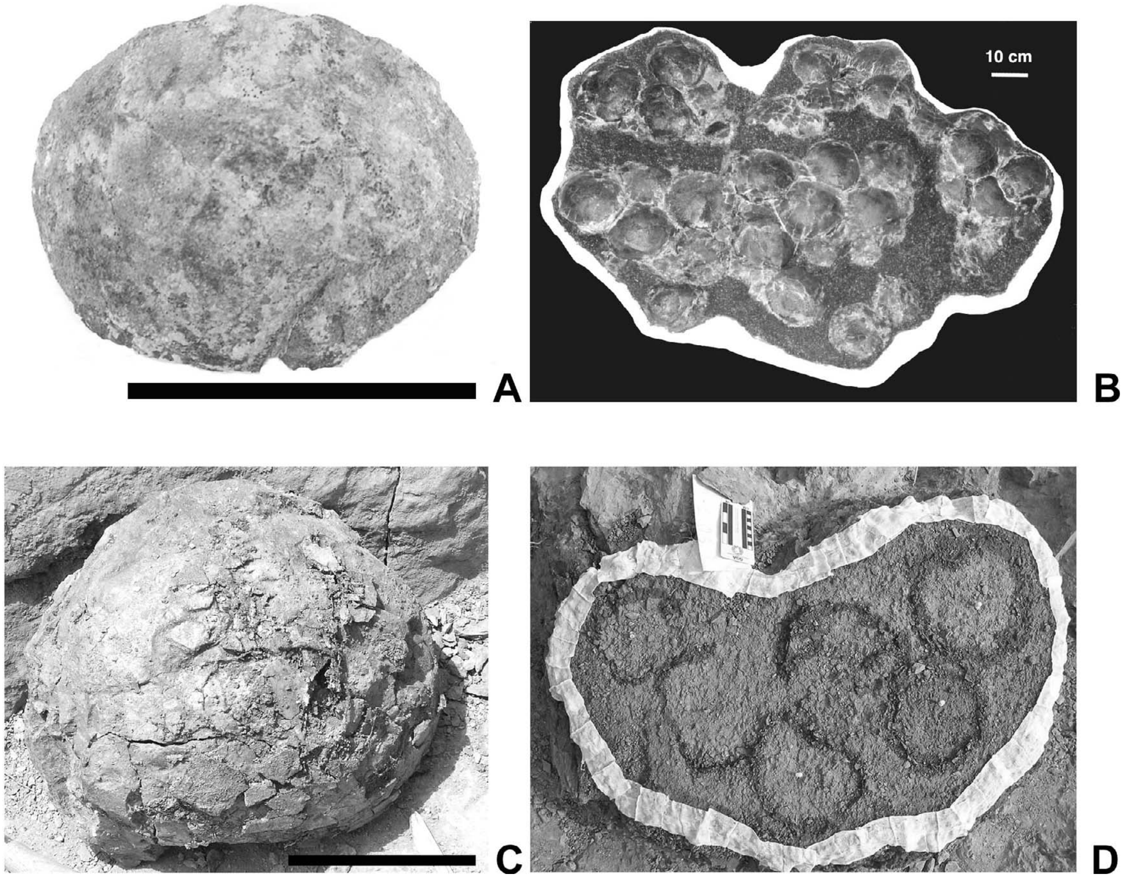

FIGURE 2. Two *Megaloolithus* eggs and clutches. A, Auca Mahuevo titanosaur egg (MCF-PVPH-775) showing the intact, lower egg hemisphere. B, Auca Mahuevo titanosaur clutch (MCF-PVPH-258) containing approximately 40 eggs, many with embryonic remains. C, Pinyes *Megaloolithus siruguei* egg (18E02-E). D, Field jacket with *M. siruguei* clutch (17E05) containing six eggs. Scale bars, 10 cm.

the Riu Sallent. Egg clutches at the Pinyes site occur within uniform, fine-grained overbank sediments, deposited distal to an active stream channel (Jackson 2007). The massive mudstone displays evidence of extensive pedogenesis and bioturbation, including sediment reworking by arthropods such as crustaceans, spiders, beetles, or other insects (Mayoral and Calzada 1998). These processes resulted in an absence of primary sedimentary structures associated with the egg clutches. Unlike at Auca Mahuevo, trace fossil nests have not been documented at the Pinyes locality.

Specimens

The prefixes used in the text and accompanying figures below denote specimens housed in the following facilities: ES, Department of Earth Sciences, Montana State University, Bozeman, Montana; MCD, Museu de la Conca Dellà, Isona i Conca Dellà, Lleida, Spain; MCF-MVPH, Museo Carmen Funes, Plaza Huincul, Argentina; and MOR, Museum of the Rockies, Bozeman, Montana.

Titanosaur Egg

MCF-MVPH-775 comes from the egg bed 3 quarry at the Auca Mahuevo locality; this stratum yields abundant eggs containing embryonic remains (Chiappe et al. 1998; Chiappe et al. 1999, 2001; Grellet-Tinner et al. 2004). The *Megaloolithus patagonicus* egg selected for this study, however, does not contain visible embryonic bones or skin. The egg exhibits an intact lower surface (Fig. 2A), whereas the upper surface is compressed downward. Because of the variation that occurs among Auca Mahuevo specimens, average values for some attributes are used in this study. For example, Auca Mahuevo clutches range from 15 to over 40 eggs (Fig. 2B), therefore, we use 25 eggs as an average clutch size for calculating total clutch G_{H_2O} (Chiappe et al. 1999; Jackson et al. 2004; Grellet-Tinner et al. 2004). Similarly, the egg dimensions (15 × 14 cm) are estimated from measurements of MCF-MVPH-775 and other eggs from the same locality (Chiappe et al. 1999, 2003, 2005; Jackson et al. 2004; Grellet-Tinner et al. 2004).

Megaloolithus siruguei

For comparison, we removed an egg (designated as ''E'') from clutch 18E02 (MCD 4885) in egg layer 2 at the Pinyes locality in northern Spain (Fig. 2C). Eggs from the Pinyes site are assigned to *Megaloolithus siruguei*, on the basis of comparison to the holotype from southern France (Vianey-Liaud et al. 1994). However, it should be noted that *M. siruguei* is also considered a junior synonym of *M. mammillare* (Peitz 1999, 2000; Sander et al. in press). Nevertheless, this egg type is commonly assigned to sauropod dinosaurs, on the basis of sauropod bones in the same horizon or formation. However, eggs from the Pinyes site (and all *M. siruguei* localities) lack embryonic remains and, therefore, taxonomic identification of the egg remains uncertain. In addition, it should be noted that the 20 × 22 cm size of the analyzed egg compares favorably with other *M. siruguei* specimens (Vianey-Liaud et al. 2003), but falls at the upper size limit for well-preserved eggs excavated at the Pinyes locality (Jackson 2007).

Aepyornis Egg

Aepyornis, the largest known bird, has been extinct since about 1650 (Davies 2002). Its eggs are larger than most, if not all dinosaur eggs (Carpenter 1999). Because a complete egg was unavailable for the study, radial and tangential thin sections of eggshell (MOR 88-51) were examined for diagenesis, and calculations performed on a tangential thin section (Fig. 3). Additional egg attributes (e.g., size, volume) were obtained from the literature (Long et al. 1998). These data were added to the extensive tables of Ar and Rahn (1978, 1985) and regression analyses performed.

Eggshell Preparation

Megaloolithus patagonicus eggshells from the Auca Mahuevo locality often exhibit diagenetic dissolution between adjacent nucleation sites at the inner shell surface; this dissolution often affects one-fourth to one-third of the shell thickness (Fig. 4A). Eggshells were therefore examined under a dissecting microscope, and ten specimens displaying minimal dissolution were then embedded in polyester resin. Tangential sections were cut mid-way between the inner and outer eggshell surfaces (Fig. 4B). Five eggshells removed from the Spanish *M. siruguei* egg are thicker and do not exhibit extensive dissolution at the interior surface of the shell (Fig. 4C). Unlike the Auca Mahuevo eggshells, the tangential sections were unlikely to intersect areas of dissolution and therefore thin sections were obtained from a commercial laboratory (Fig. 4D). All thin sections measure 30 μm thick. Additional eggshells were removed from the Auca Mahuevo and Pinyes eggs, coated with gold (10 nm), and mounted on aluminum stubs. The specimens were imaged as radial sections under a J. R. Lee Instrument Personal SEM and/or JEOL 6100 Scanning electron microscope (SEM) with Backscattered Electron Imaging (BEI) capabilities, coupled to a Noran Voyager Energy Dispersive X-ray (EDX) system.

Determining Pore Characteristics

The tangential thin sections were viewed under a Nikon Eclipse E600 petrographic microscope equipped with a digital camera. Approximately ten nonoverlapping images were photographed during systematic transects of each slide, in order to obtain maximum sample coverage. The images ($n = 247$) were imported into Adobe Photoshop. After examining several thin sections from each specimen, we determined criteria for including or excluding pores, determining original pore size, and distinguishing pores from diagenetic features. For example, some pores are filled with opaque fine-grained sediments; enhancement of brightness and contrast in Photoshop often revealed the true diameter. Other pores are en-

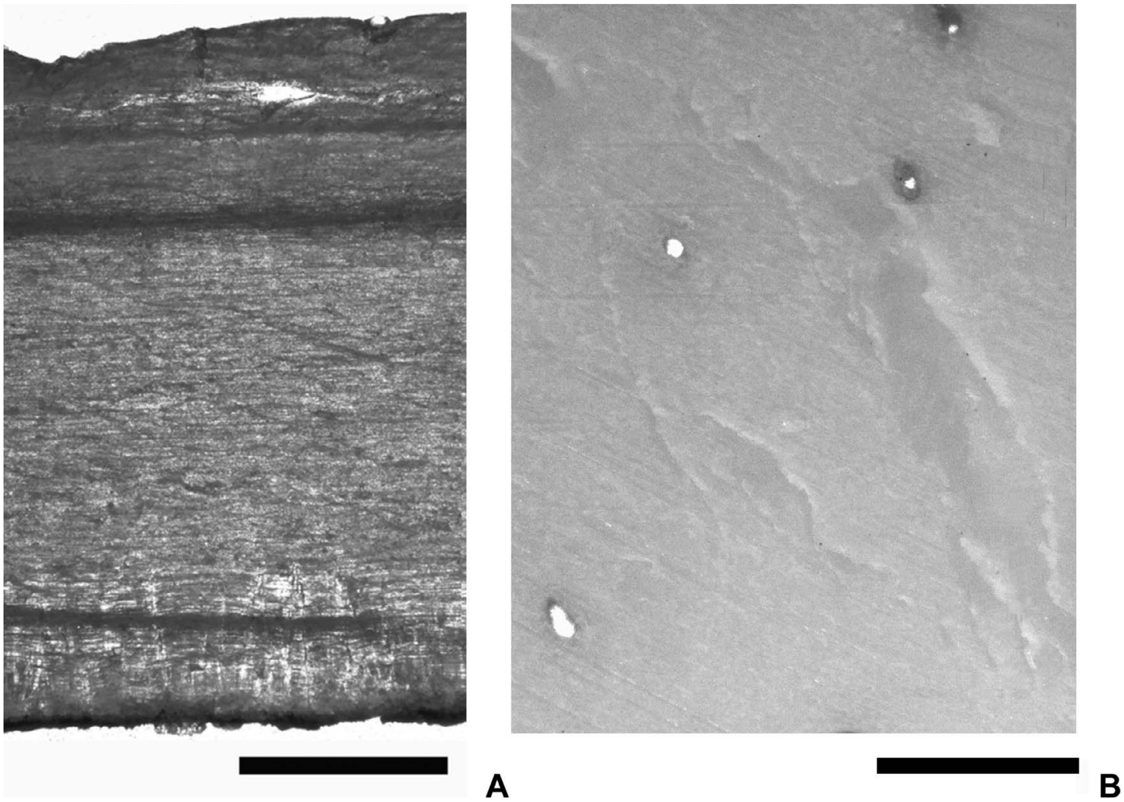

FIGURE 3. *Aepyornis* eggshell (MOR 88-51). A, Radial thin section of eggshell. B, Tangential thin section showing four pores.

larged by diagenetic dissolution, so we estimated original pore size from mean pore diameters. This may result in a slightly higher estimated eggshell porosity. In some cases the shell appears extremely thin as a result of the egg curvature and the thin-sectioning process, rendering that portion of the shell area unusable. We therefore excluded this unusable region from the calculations. Using these established criteria is likely to mean that any subjectivity and human error in accurately determining exact pore circumference will be consistent throughout the study and therefore compensatory.

The image was then imported into an image analysis program. Each pore was numbered on the image, the area calculated, and total area computed. Shell thickness was measured from additional specimens with SEM or from digital images with the image analysis software. Shell thickness, pore area, pore number, pore percentage, and pore radius values were determined for all specimens.

Variables and Equations

Conductance, as defined by Ar et al. (1974), is a measure of an egg's ability to permit gas diffusion under standard atmospheric conditions. This widely used variable represents a quantitative assessment of egg porosity or permeability and is proportional to total pore area and inversely proportional to pore length. The diffusion rate is equal to the product of eggshell conductance and the difference in partial pressure between the internal egg and external environment (Ar et al. 1974; Seymour 1979).

Calculation of water vapor conductance in this study is similar to methods used in previous studies (e.g., Ar et al. 1974; Seymour 1979; Williams et al. 1984; Deeming 2006), with minor variations noted below. Table 1 lists the variables, with units, and constants used in calculations in this study, and the middle two columns of Table 2 provide the formulae, sources, and reference of data. Water

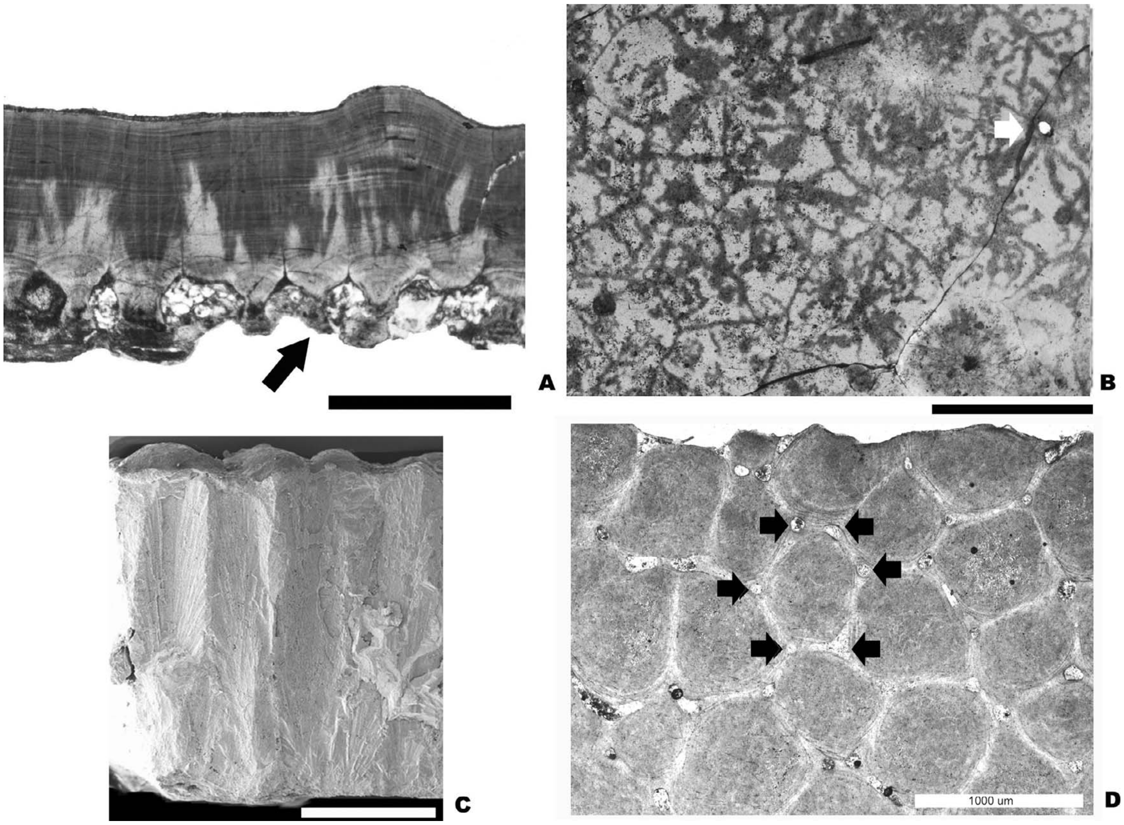

FIGURE 4. *Megaloolithus* eggshells from the Auca Mahuevo and Pinyes localities. A, Radial thin section from an Argentine egg (MCF-PVPH-112) that contains a titanosaur embryo. Outer surface of the egg is at the top of the image. Note the calcite dissolution (arrow) that occurs between nucleation sites at the inner shell surface. B, Tangential thin section of Auca Mahuevo eggshell (MCF-MVPH-775); arrow indicates a single pore filled with diagenetic spary calcite at upper right. C, SEM in radial view of a Pinyes eggshell (ES 131). D, Tangential thin section of Pinyes eggshell (ES 131) showing abundant and even distribution of calcite-filled pores. Black arrows indicate five or possibly six pores that surround a shell unit. Scale bars, 1 mm.

vapor conductance was determined for the three specimens from calculated data and direct measurements of egg attributes as discussed below. For determining the effective pore radius and subsequent water vapor conductance, we assume that the pore canals are circular in cross-section and of uniform radius throughout their lengths. This assumption is common to all previous studies. Branched pores, however, could potentially alter effective radius and gas conductance. Although some branching occurs in both *M. patagonicus* (Grellet-Tinner et al. 2006) and *M. siruguei*, this pore morphology appears to be rare in *M. patagonicus*. Finally, we consider the ''lateral pore system'' reported in an Auca Mahuevo eggshell (Grellet-Tinner et al. 2004, 2006) the result of diagenetic dissolution, a common feature at the base of *M. patagonicus* eggshell (Jackson et al. 2004).

Results

Megaloolithus Eggs

Table 2 provides the results summarized here. *Megaloolithus patagonicus* clutches from Auca Mahuevo typically contain 20 to 40 eggs, whereas *M. siruguei* clutches from the Pinyes locality average nine eggs (Chiappe et al. 1999; Jackson 2007). Both eggs share similar overall shape. However, the smaller, 15-cm Argentine egg has an estimated volume of 1500 cm^3, compared with 4488 cm^3 of the Pinyes egg. It should also be noted that the volume of the Auca Mahuevo egg significantly exceeds the incorrect volume (800 cm^3) re-

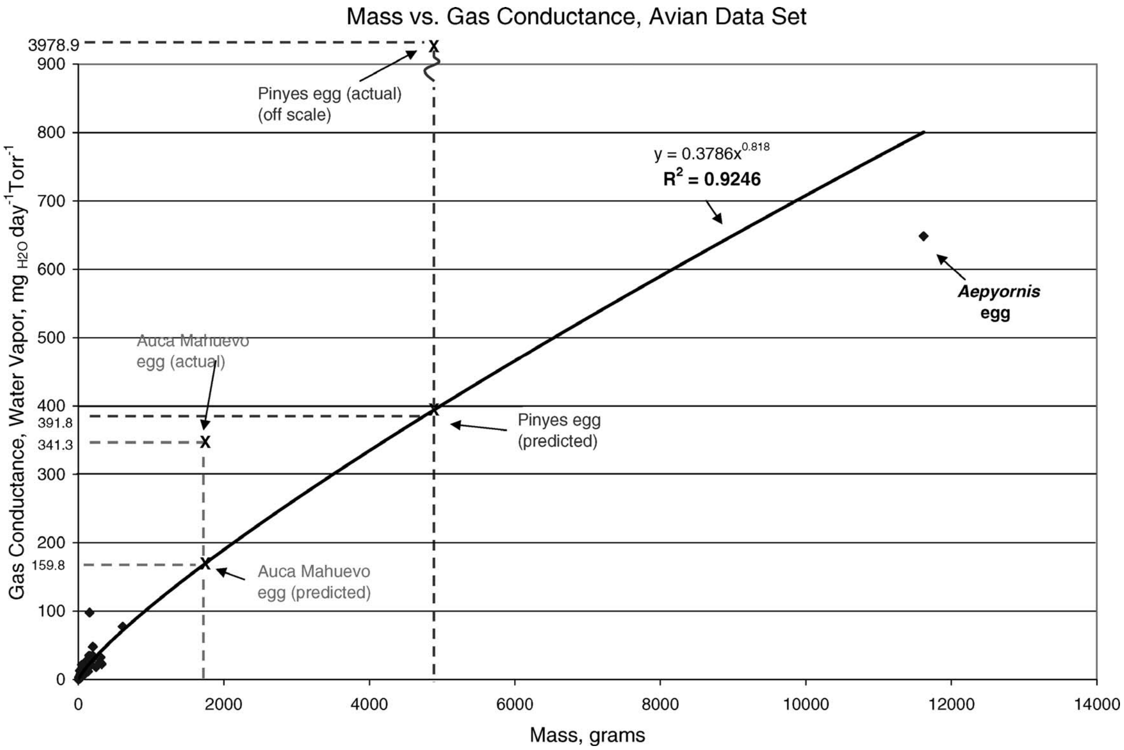

FIGURE 5. Regression analysis of eggshell water vapor conductance data sets (Ar et al. 1974; Ar and Rahn 1985) with addition of *Aepyornis*. Includes actual and predicted conductance for *Megaloolithus patagonicus* and *M. siruguei* eggs compared with avian eggs of comparable size. Note that *M. siruguei* value of 3878.9 extends far beyond the graph.

TABLE 1. Variables and constants applicable to the study.

	Definition	Units
Variable		
L	Maximum egg length	mm
W	Maximum egg width	mm
M	Egg mass	g
L_s	Shell thickness	mm
A_s	Surface area	mm^2
N	Total no. of pores	per egg
D	Pore density	No. pores/mm^2
r	Pore radius	μm
A_p	Total pore area	mm^2
A	Mean individual pore area	μm^2
G_{H2O}	Water vapor conductance	mg H_2O/(day Torr)
${}_{sp}G_{H2O}$	Mass-specific water vapor conductance	mg H_2O/(day Torr g)
${}_{p}G_{H2O}$	Water vapor conductance per pore	μg H_2O/(day Torr pore)
E	Mean eggs per clutch	
${}_{c}G_{H2O}$	Total gas conductance per clutch	mg H_2O/(day Torr clutch)
Constant		
c	Constant from empirical avian data	$c = 1.56 \times 10^{9}$ sec mg day^{-1}mol^{-1}
R	Universal gas constant	6.24×10^{4} cm^3 Torr mol^{-1} °K^{-1}
T	Temperature	T = 303°K (= assumed 30°C)
d_{H2O}	Diffusion coefficient for water vapor	0.292 cm^2 sec^{-1}

TABLE 2. Results of measurements and calculations on the Auca Mahuevo titanosaur, unidentified Pinyes, and extinct *Aepyornis* (elephant bird) eggs.

Variable	Description	Units	Formula and source	Aepyornis	Auca Mahuevo, Argentina	Pinyes, Spain
L	Egg length	cm	Data	31.7	15	22
B	Egg breadth	cm	Data	25.8	14	20
V	Egg volume	cm^3	$V = 0.51(L \times B^2)$	10,760	1500	4488
M	Egg mass	grams	$M = \rho \times V$	11,620	1620	4850
ρ	Egg density	$g\ cm^{-3}$	Assumed from avian egg data	1.08	1.08	1.08
L_s	Shell thickness	mm	Data	3.25	1.48	2.4
A_s	Surface area	cm^2	$A_s = 4.928\ V^{0.668}$	2432	652	1356
D	Pore density	no. mm^{-2}	Data	0.831	0.195	4.41
N	No. pores/egg	no.	$N = D \times A_s$	202,000	12,714	598,000
r	Pore radius	μm	Data	41.1	61.62	49.25
% Pore area	%	—	Data	0.441	0.370	3.36
A_p	Total pore area	$cm^2\ egg^{-1}$	$A_p = A_s \times$ % pore area	10.72	2.41	45.56
A	Mean individual. pore area	μm^2	$A = \pi r^2$	5307	11,929	7620
G_{H2O}	Water vapor conductance	$mgH_2O\ day^{-1}\ Torr^{-1}$	$G_{H2O} = c \cdot d_{H2O} \cdot A_p/(R \cdot T \cdot L_s)$	691.4	341.3	3978.9
Predicted G_{H2O}	For bird egg of equivalent size	$mgH_2O\ day^{-1}\ Torr^{-1}$	Regression formula (see Table 3)	800.8	159.8	391.8
Ratio	Calculated G_{H2O} to predicted	—		0.9:1	2.1:1	10.2:1
$_pG_{H2O}$	G_{H2O} per pore	$\mu g\ day^{-1}\ Torr^{-1}\ pore^{-1}$	$_pG_{H2O} = G_{H2O}\ N^{-1}$	3.42	26.84	6.65
E	Number of eggs/clutch	—	Data	Unknown	~25	~9
M_c	Clutch weight	grams $clutch^{-1}$	$M_c = M \cdot E$	Unknown	40,500	43,650
$_cG_{H2O}$	Per clutch	$mg_{H2O}\ day^{-1}\ Torr^{-1}$	$_cG_{H2O} = G_{H2O} \cdot E$	Unknown	8532	35,810
$_{spc}G_{H2O}$	Gas conductance per gram clutch weight	$mg_{H2O}\ day^{-1}\ Torr^{-1}\ gram^{-1}$	$_{spc}G_{H2O} = {}_cG_{H2O} \cdot (M \cdot E)^{-1}$	Unknown	0.211	0.820

TABLE 3. Avian data set regression formulas with inclusion of *Aepyornis*.

Egg Attributes	With *Aepyornis*	Correlation coefficient
L_s	$L_s = 0.057839\ M^{0.4248}$	$r^2 = 0.92$
N	$N = 373.54\ M^{0.7457}$	$r^2 = 0.86$
A_p	$A_p = 0.0106\ M^{1.2337}$	$r^2 = 0.95$
G_{H2O}	$G_{H2O} = 0.3786\ M^{0.818}$	$r^2 = 0.92$

ported by Chiappe et al. (1998) and recently used to calculate titanosaur egg mass (Varricchio and Jackson 2004). As typical for smaller egg size (Ar and Rahn 1985), the Auca Mahuevo eggshell is thinner than that of the larger Pinyes egg (Table 2). The Auca Mahuevo egg has 47 times fewer pores, but the individual pores are each 1.57 times larger than those of the Pinyes egg. The Argentine egg also exhibits a more irregular pore distribution. For example, pores are very abundant in all tangential thin sections from the Pinyes egg, whereas 20% of the analyzed images from all quadrants of the Auca Mahuevo egg are completely devoid of pores. The G_{H_2O} of the *M. patagonicus* and *M. siruguei* eggs is 341 and 3979 mg H_2O day^{-1} Torr^{-1} (2560 and 29,845 mg H_2O day^{-1} kPa^{-1}), respectively.

Aepyornis Egg

The 11.6-kg *Aepyornis* egg exceeds both *Megaloolithus* specimens in diameter, mass, volume, and eggshell thickness (Table 2) (Long et al. 1998). In addition, the egg is far larger than the largest known extant avian egg, which is the 1.4-kg ostrich egg (Vleck and Hoyt 1991). If representative of the entire egg, the number of pores mm^{-2} calculated for the *Aepyornis* eggshell yields approximately 202,000 pores per egg, with a water vapor conductance of 691.4 mg H_2O Torr^{-1} day^{-1} (5186 mg H_2O day^{-1} kPa^{-1}). These data, added to the avian data set of Ar and Rahn (1985) in order to extend the regression analysis range, produced only minor changes in the regression formula (Tables 3, 4, Fig. 5). The values calculated for the *Aepyornis* egg fall very close to the avian values predicted by previous regression formulas (Ar and Rahn 1985), thereby validating the original methodology.

Discussion

Megaloolithus exhibits a wide range of egg morphology and of temporal and paleogeographic distribution (Carpenter 1999). In the current study, significant variation in reproductive attributes (e.g., egg and clutch size, shell thickness, microstructure) distinguishes the South American titanosaurs from the European egg-laying taxon. (Table 2). In addition, the Auca Mahuevo titanosaur egg displays substantially lower G_{H_2O}, even after consideration of the relatively smaller surface area/volume ratio of the larger Pinyes egg

TABLE 4. Calculated and predicted $G_{H}2_{O}$ in rigid-shelled reptile eggs, compared with avian eggs of comparable size. Four additional avian eggs are also included in the table for comparison.

Taxon	Species	Ref.	Nest mode	G_{H2O} (mg H_2O day^{-1}Torr^{-1})	Predicted G_{H2O}	Difference
Gecko	*Sphaerodactylus*	3	O	1.1	5.5	0.2 ×
	Lepidodactylus lugrubris	5	O	1.7	3.4	0.5 ×
	Hemidactylus garnoti	5	O	2.6	4.4	0.6 ×
Crocodilian	*C. porosus* (infertile)	2	M	622	810	0.77 ×
	C. porosus (fertile)	2	M	2812	810	3.4 ×
	C. acutus	4	B	1185	825	1.4 ×
	Alligator mississippiensis	1	M	2902	685	4.2 ×
Turtle	*Emydura macquarii*	6, 7	B	1268	150	8.3 ×
	Trionyx spiniferus	1	B	810	150	5.46 ×
Bird	*Gallus gallus*	8	O	14	9.19	1.57 ×
	Rhea americana	8	O	78	58.04	1.34 ×
	Gavia immer (loon)	9	O/WH	98	23.3	4.2 ×
	Podilymbus podiceps (grebe)	9	O/WH	13.02	4.51	2.9 ×
	Alectura lathami (megapode)	9	M	48.15	28.75	1.7 ×

References: (1) Packard et al. 1979; (2) Grigg and Beard 1985; (3) Dunson and Bramham 1981; (4) Lutz et al. 1980; (5) Dunson 1982; (6) Thompson 1985; (7) Harrison et al. 1978; (8) Ar et al. 1974; (9) Ar and Rahn 1985; (10) Deeming 2006. Nest mode: O = open; M = mound, B = buried; O/WH = open/wet or humid.

(Table 2). For example, a 1.5 times greater G_{H_2O} would be predicted for the Pinyes egg, on the basis of egg surface area/volume ratio alone; however, the actual value is 11 times greater. The water vapor conductance of *M. patagonicus* and *M. siruguei* is 2.1 and 10.2 times greater, respectively, than for avian eggs of comparable size.

Water vapor conductance values calculated for modern avian eggs are often used to interpret the incubation environment for extinct taxa (Deeming 2006); however, such comparisons are often complicated. For example, the G_{H_2O} of the Auca Mahuevo egg is similar to that of the extant megapode *Alectura lathami*, which incubates eggs in vegetation mounds (Table 4). In most avian species the conductance of the eggshell remains relatively constant throughout incubation (Ar and Rahn 1985). In megapode eggs, however, dissolution of the inner surface occurs late in embryonic development. Significant eggshell thinning (12–21%) greatly increases G_{H_2O} in response to decreasing oxygen availability in the vegetation mound (Booth and Thompson 1991). Furthermore, the male bird continually turns over the mound material, thus mitigating the severity of the hypoxic gaseous environment (Seymour and Ackerman 1980). This behavior and the complex branching pore system of megapode eggs contribute to the difficulty of accurately comparing the conductance of these eggs with that of the titanosaur specimen.

The G_{H_2O} of the Auca Mahuevo egg, however, is lower than that of the pied-billed grebe (*Podilymbus podiceps*) and the common loon (*Gavia immer*), which exhibit G_{H_2O} values that are three and four times higher than predicted for bird eggs of similar size (Table 4). These birds incubate their eggs in humid or even wet conditions (Ar and Rahn 1985), thereby accounting for higher conductance, necessary for adequate oxygenation of the embryo.

Although water vapor conductance values are available for over 161 avian species (Ar et al. 1974; Ar and Rahn 1985), only a few studies report a calculated G_{H_2O} for rigid-shelled reptile eggs (Table 4). The paucity of studies and the broad range of values reported for reptiles, along with the questionable use of constants from the avian data for calculations, contribute to the difficulty of comparing the eggs with the titanosaur specimen. For example, *Crocodylus acutus* exhibits a G_{H_2O} only 1.4 times greater than an avian egg of comparable mass (Lutz et al. 1980), whereas *Alligator mississippiensis* measures 4.2 times greater (Packard et al. 1979; Deeming and Thompson 1991). In addition, variation in G_{H_2O} among modern reptiles results from several factors, including the stage of embryonic development (Kern and Ferguson 1997), intrinsic and extrinsic degradation of the eggshell, which increases porosity during incubation (Ferguson 1982; Wink et al. 1990), and whether the egg is fertile or infertile (Grigg and Beard 1985). For example, the G_{H_2O} of an infertile *C. porosus* egg is less than that of a bird egg of comparable size, whereas for fertile eggs it is 3.4 times higher (Table 4). Presumably, metabolism would also play a role. Some geckos incubate rigid-shelled eggs in atmospheric conditions like birds, yet their eggs exhibit lower conductance rates than equivalent-sized avian eggs (Dunson and Bramham 1981; Dunson 1982); the lower G_{H_2O} most likely results from the lower metabolic rate of geckos compared to birds (Richlefs and Stark 1998). Nevertheless, comparison of the Auca Mahuevo and Pinyes specimens provides important information on egg incubation when considered within the sedimentological and taphonomic context of the two localities. Factors that might influence variation in water vapor conductance between eggs from the two localities include (1) incubation strategy, (2) total clutch metabolism and embryonic growth rates, and (3) climate regime.

Incubation Strategy

Auca Mahuevo Locality.—Presumably the Argentine titanosaurs used a consistent strategy when constructing their nests in sandy or finer-grained areas of the floodplain. The specimen in this study comes from the mudstone facies of egg bed 3, and the low G_{H_2O} independently supports the previous interpretation (based on nesting traces from the sandstone facies) that the eggs were not buried in the substrate (see Chiappe et al. 2004). The limited soil oxygen diffusion capacity of the clay-rich vertisols (Loope et al. 2000) would amplify an already limited oxygen uptake potential that results from the egg morphology and pore structure. Substrate egg burial can be ruled out on the basis of sedimentological evidence (Chiappe et al. 2004) and calculated water vapor conductance rates reported here. Previous suggestions that the Auca Mahuevo titanosaurs incubated eggs in high humidity conditions, consistent with vegetation in the nest (Grellet-Tinner and Chiappe 2004; Grellet-Tinner et al. 2006), are misleading and warrant further discussion.

The hypothesized incubation environment (Grellet-Tinner and Chiappe 2004; Grellet-Tinner et al. 2006) was based on comparison of the Auca Mahuevo titanosaur eggs with megaloolithid eggs studied by Williams et al. (1984) from southern France. These French eggs (identified as Type 3.1 Sample B) exhibit a water vapor conductance value calculated to be 24 times greater than for modern avian eggs of equivalent size. The Auca Mahuevo eggs were thought to be similar to the French eggs in pore size, shape, and geometry; therefore, the authors assumed that the Argentine eggs must have a similar gas diffusion rate (Grellet-Tinner and Chiappe 2004; Grellet-Tinner et al. 2006).

The French eggs, 21 cm × 21 cm in diameter, are considerably larger than the 12 cm × 14 cm Auca Mahuevo specimens, however, and also have a greater volume and lower surface area-to-volume ratio. The shells of the French eggs are also thicker, which reduces G_{H_2O}; however, their much denser pore distribution, relative to the Argentine titanosaur egg (cf. Fig. 6.4B and Williams et al. 1984: Fig. 2B) more than compensates for the increased shell thickness, resulting in a much higher G_{H_2O}. Although Deeming (2006) corrected errors in the original calculations and reported G_{H_2O} for the French egg as 2322 mg H_2O $Torr^{-1}$ day^{-1} (17,417 mg H_2O day^{-1} kPa^{-1}), this value remains seven times higher than that of the Auca Mahuevo egg. The French eggs, therefore, are not an appropriate comparison for inferences about incubation environment at the Auca Mahuevo locality.

In addition, the implications of egg ornamentation for incubation strategy are unclear. According to Grellet-Tinner and Chiappe (2004) and Grellet-Tinner et al. (2006), surface ornamentation indicated the presence of vegetation in a trace fossil nest described by Chiappe et al. (2004). They suggested, ''the grain size of the siliciclastic sediment at the Auca Mahuevo site is overall smaller than the minimum internodal distance necessary for the pore to be functional''; vegetation, therefore, was considered necessary to prevent occlusion of the pores (Grellet-Tinner et al. 2006: p. 299). However, several modern turtle species (including living tortoises nesting at the Auca Mahuevo locality) bury their eggs in fine-grained sediments with high clay content (Burbidge and Kuchling 2004; Horne et al. 2003; Epperson and Heis 2005). These eggs do not exhibit surface ornamentation, nor are they incubated in vegetation. Given the lack of modern analogs for megaloolithid ornamentation, its possible influence on gas diffusion represents an untested hypothesis.

Finally, the presence of organic matter may be misleading. Organic material reported by Chiappe et al. (2004) from a trace fossil nest allegedly supported the presence of vegetation in the nest (Grellet-Tinner and Chiappe 2004; Grellet-Tinner et al. 2006). However, these minute and macerated particles are identical to organic matter present on the bedding plane of the stratum that underlies this clutch (unpublished data). The most parsimonious interpretation is that these organic materials, in both the nest and the underlying stratum, represent transported debris, rather than in situ nesting material.

Pinyes Locality.—In contrast to the Auca Mahuevo titanosaur clutches, which contain small eggs that are unburied during incubation, *Megaloolithus siruguei* clutches have larger, but substantially fewer, eggs (Table 2). The G_{H_2O} calculated for the Pinyes egg is more than an order of magnitude greater than that of the Auca Mahuevo egg. If the eggs were incubated above ground, the abundance of pores would have resulted in substantial water loss from evaporation. In a buried clutch, however, the high G_{H_2O} of *M. siruguei* would have compensated for elevated carbon dioxide and lower oxygen levels present in soils surrounding the clutch (discussed below). Although sedimentological evidence of a trace fossil nest is lacking at the Pinyes locality (Jackson 2007), the calculated G_{H_2O} supports previous interpretations of underground burial for this megaloolithid egg type (see also Deeming 2006; Mueller-Töwe et al. 2002; Sander et al. in press).

Total Clutch Metabolism

The oxygen consumption rate of the reptilian embryo increases throughout incubation, with the highest consumption rate coinciding with hatching (Ackerman 1980; Lutz et al. 1980). The high eggshell porosity in a buried clutch facilitates the transport of oxygen and carbon dioxide through the shell. This is of critical importance when air trapped inside the nest chamber becomes hypoxic and hypercapneic in the latter stages of incubation (Seymour 1979; Ackerman 1980; Deeming 2006). In addition, the physical characteristics of the substrate (e.g., soil type, permeability, water content, and aerobic microbial content) also place an upper constraint on the metabolic activity of the buried egg clutch (Ackerman 1980). In modern taxa that bury their eggs, and presumably extinct amniotes as well, this constraint is expressed as limitations on the clutch size and on incubation time (Ackerman 1980).

On the basis of the allometric relationship between egg weight and maximum egg metabolism in reptiles, Seymour (1979) and Seymour and Ackerman (1980) proposed that sauropods might have been forced to limit their clutch size to 13 eggs. The Pinyes clutches and those reported from Europe and India generally support this hypothesis: the eggs exhibit high water vapor and respiratory gas conductance, and clutches generally contain fewer than the predicted number of eggs per clutch (Kerourio 1981; Cousin et al. 1994; Cousin and Breton 1999; Mohabey 1996, 1999, 2001; Sahni and Khosla 1994; Sander et al. 1998; Peitz 1999, 2000; López-Martínez et al. 2000; Garcia et al. 2003; Jackson 2007; Sander et al. in press).

In contrast, Auca Mahuevo titanosaur clutches typically contain 20 to 40 eggs, but the eggs were not buried underground. Adequate O_2 and CO_2 exchange is much less problematic with greater exposure to the atmosphere, compared to a buried clutch. Specifically, CO_2 in soil air is often several hundred times more concentrated than in the atmosphere; oxygen concentration decreases accordingly and in some cases may be 5–10%, compared to 20% for atmospheric air (Brady and Weil 2002). Greater exposure to atmospheric gases compensated for the larger clutch size, but with a greater risk of excessive water loss due to evaporation.

Previous studies of water vapor conductance in dinosaur eggs calculated G_{H_2O} for a single egg (Seymour 1979; Williams et al. 1984; Sabath 1991; Grigorescu et al. 1994; Deeming 2006). However, total clutch conductance represents a more important factor, because embryos mature as part of the total clutch environment. For example, the G_{H_2O} of the Auca Mahuevo egg is 10.2 times lower than that of the Pinyes egg, but the total G_{H_2O} per gram of clutch weight is only about four times lower. The titanosaur and *Megaloolithus siruguei* clutches exhibit approximately equivalent clutch mass (Table 2). This suggests that water conservation was more important at Auca Mahuevo than at the Pinyes locality and that respiratory gas exchange was a less significant factor.

In contrast to atmospheric incubation conditions, the hypercapneic and hypoxic environment of a buried clutch represents the selective pressure for increased shell conductance so that tissue gas concentrations remain tolerable during incubation (Seymour and Ackerman 1980). At the Pinyes locality, this was accomplished with a greatly enhanced total pore area.

Embryonic Growth Rates

Seymour (1979) and Seymour and Ackerman (1980), when calculating clutch limit, also assumed that sauropod metabolic rates were comparable to those of modern reptiles. However, osteological characteristics indicate that growth rates in all sauropods studied thus far are closer to those of modern birds than to those of reptiles, particularly in younger individuals (Ricqlès 1983; Ricqlès et al. 1991; Sander 2000; Castanet et al. 1996, 2000; Horner et al. 2000; Sander et al. 2004; Erickson 2005;

Curry-Rogers and Erickson 2005). Because large animals grow at faster rates than small animals at all ontogenetic stages (Case 1978; Padian et al. 2004), a metabolic rate closer to that of a modern bird would most likely produce even more rapid growth in a sauropod embryo, thus requiring a higher rate of oxygen consumption. The increased oxygen demands of a faster growth rate for both the Auca Mahuevo and Pinyes embryos would represent a more significant problem in the buried Pinyes clutches than in the unburied eggs of the Auca Mahuevo locality. Because other physiological factors such as tolerance to hypoxia, length of incubation, presence of unpreserved soft tissues such as pore plugs, and influence of ornamentation on G_{H_2O} are unknown, further assessment remains difficult. Nevertheless, the functional attributes that characterize both egg types represent a successful balance between water conservation and adequate oxygen and CO_2 exchange.

Climate Regimes

The differences in egg attributes and reproductive biology at the two localities may represent adaptations to climatic regimes that were fundamentally different. Paleovertisols at the Auca Mahuevo locality in Argentina indicate a semiarid to arid climate regime, with wet and dry seasons (Chiappe et al. 1999; Loope et al. 2000). These ancient soils differed markedly from those at the Spanish nesting site, whose highly bioturbated Pinyes soil profile contains primarily kaolinite and other weathering-resistant minerals such as quartz, hematite, and magnetite (Jackson 2007). Although this mineralogy is typical of wet/warm regions with extensive leaching (Retallack 1990; Birkeland 1999), this interpretation is confounded by the red oxidized color of the mudrock at the Pinyes site. This results from hematite and may indicate well-drained soils of a drier region. Paleoclimate reconstructions by Scotese (2000), however, corroborate the interpretation of a semiarid to arid climate in northern Patagonia during the Late Cretaceous and a warm/wet regime for Spain during this same time interval. If these differences in climatic regime are correct, then in the more arid environment at Auca Mahuevo, the low porosity of the titanosaur eggshell would have limited water loss to evaporation in large clutches when the eggs were not buried by sediment. In contrast, incubation underground in a warm and wet climate most likely necessitated the higher porosity for respiratory gas exchange, as found in the Pinyes specimen.

Egg Incubation in Other Saurischian Dinosaurs

Deeming (2006) reported the water vapor conductance of a variety of fossil eggs, including those of two Late Cretaceous saurischian dinosaurs known from embryonic remains: oviraptorids and *Troodon*. The G_{H_2O} calculated for both the oviraptorid egg (Deeming 2006: p. 174) and the Auca Mahuevo titanosaur specimen reported here is 2.1 times greater than that of an equivalent-sized bird egg (Table 2). Furthermore, Deeming (2006) reported the G_{H_2O} of a *Troodon* egg as equal to that of an avian egg of comparable size. Interestingly, all three Late Cretaceous saurischian dinosaurs are known from semiarid or arid paleoenvironments. Despite these significantly lower G_{H_2O} values relative to other fossil eggs, Deeming (2006) concluded that all dinosaurs buried their eggs in the substrate. If the G_{H_2O} of *Troodon* eggs is equal to that of an avian egg, and the oviraptorid and titanosaur eggs are both 2.1 times greater, the question arises as to what water vapor conductance value in dinosaur eggs provides evidence for interpretation of partial egg burial or incubation in open nests. Stated another way, when interpreting G_{H_2O} for fossil material, what is the margin of error for eggs that are millions of years old?

Although previous studies do not address this theoretical threshold value, we suggest that water vapor conductance of modern amniotic eggs provides a ''first estimate'' for fossil eggs, rather than proof for the incubation environment. Many factors contribute to the difficulty of comparing modern and fossil specimens, such as diagenetic alteration, different analytical methodology (dyes versus thin sections), and taphonomic processes that affect egg size, shape, and determination of original pore size. Therefore, calculated conductance values of fossil eggs that differ by at least an order of magnitude from an avian egg of equivalent size (e.g., *Megaloolithus siruguei*) allow a reasonable interpretation of substrate egg burial. Conversely, when the conductance value of a dinosaur egg is equal to that of an avian egg (e.g., *Troodon*), the incubation environment most likely differed from the underground burial used by modern reptiles (contrary to Deeming 2006). However, when rates fall between these extremes of the fossil spectrum (e.g., oviraptorid and titanosaur eggs), interpretations based on G_{H_2O} require supporting evidence. For example, an adult oviraptorid, preserved in a brooding position, occurs on top of a clutch of unhatched eggs (Clark et al. 1999: p. 16). Detailed taphonomic study of the site shows that the adult sternal elements, ribs, and gastralia rest directly on eggs (Clark et al. 1999), thereby precluding complete substrate egg burial as proposed by Deeming (2002, 2006). Similarly, *Troodon* and Auca Mahuevo titanosaur nesting traces also provide sedimentological evidence that the eggs were not fully buried underground (Varricchio et al. 1997, 1999; Chiappe et al. 2004). Independent analysis of the sedimentologic and taphonomic evidence, therefore, may substantially strengthen or refute inferences that are based solely on calculated water vapor conductance.

Conclusions

This study represents the first assessment of the water vapor conductance of a *Megaloolithus* egg definitively identified as that of a titanosaur sauropod dinosaur. In addition, this study allows the first direct comparison of water vapor conductance rates between *Megaloolithus* specimens from Europe and South America. *Megaloolithus patagonicus* clutches from Argentina typically contain 20–40 eggs, whereas *M. siruguei* clutches from the Pinyes locality in Spain comprise an average of nine eggs. The 22-cm *M. siruguei* eggs are significantly larger than the 15-cm titanosaur eggs and have a volume three times greater. The *M. patagonicus* egg has a thinner eggshell, with 47 times fewer pores than *M. siruguei*; however, individual pores are 1.57 times larger, with a more irregular distribution. The water vapor conductance of the *M. patagonicus* and *M. siruguei* eggs is 341 and 3979 mg H_2O day^{-1} Torr^{-1} (2560 and 29,846 mg H_2O day^{-1} kPa^{-1}). The G_{H_2O} of the Auca Mahuevo and Pinyes eggs is 2.1 and 10.2 times greater than for avian eggs of comparable size. The total G_{H_2O} of a 25-egg Auca Mahuevo clutch is four times lower than the nine-egg Pinyes clutch. Water vapor conductance data from the Auca Mahuevo site, in conjunction with the six trace fossil nests, indicate that eggs were not buried in sediment, and the presence of vegetation cannot be substantiated by physical evidence of organic remains in any Auca Mahuevo nest. In contrast, the G_{H_2O} of *Megaloolithus siruguei* is more than an order of magnitude greater than that of the Auca Mahuevo egg, thereby allowing reasonable inference of substrate burial in the absence of sedimentological evidence of a nesting trace.

Differences in reproductive biology that characterize the two sites may result from several factors: variation in nesting strategy, total clutch metabolism, climatic regime, or life-history strategies. Large clutch size and potentially higher metabolic and growth rates may have prohibited underground incubation in some Late Cretaceous dinosaurs, including the Auca Mahuevo titanosaurs and some theropod dinosaurs. Egg water vapor conductance rates provide a first approximation of nesting environment in extinct taxa. However, detailed sedimentologic and taphonomic data provide essential information that may support or refute hypotheses based on water vapor conductance in fossil eggs.

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