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ABNORMAL, MULTILAYERED TITANOSAUR (DINOSAURIA: SAUROPODA) EGGS FROM IN SITU CLUTCHES AT THE AUCA MAHUEVO LOCALITY, NEUQUÉN PROVINCE, ARGENTINA

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ABSTRACT—Abnormal, multilayered eggshells are frequently reported in fossil specimens. However, previous reports of this pathological condition pertain to taxonomically unidentified fossil eggs or eggshell fragments rather than in situ clutches. A survey of 393 in situ clutches, referable to titanosaur sauropod dinosaurs, from Upper Cretaceous rocks in northwestern Patagonia, Argentina, revealed that six of these clutches contain both normal eggs and abnormal, multilayered eggs within the same clutch. Excavation of one clutch exposed 30 eggs, distributed in three levels, including 27 normal eggs and 3 multilayered eggs. The three abnormal eggs occupied the highest level within the clutch and represent the last eggs laid by the female sauropod. The innermost eggshell layer in multilayered eggs from all six clutches exhibits typical megaloolithid calcite structure. The structure of the overlying, abnormal shell layer(s), however, varies among the clutches and within a single egg. Three types of abnormal eggshell morphology are documented. All previous studies that link abnormal eggshells to dinosaur physiology and the terminal Cretaceous extinction event are incomplete in terms of taphonomy, taxonomic identification, and lack rigorous statistical methods.

INTRODUCTION

The 1997 discovery of the extensive dinosaur nesting site of Auca Mahuevo in Upper Cretaceous (Campanian) (Dingus et al., 2000) strata in southwestern Argentina (Fig.1A) allowed the first definitive assignment of megaloolithid eggshell structure to titanosaur sauropod dinosaurs based on embryonic remains inside the eggs (Chiappe et al., 1998, 2000, 2001). At least four egg-bearing layers (egg beds 1–4, in ascending stratigraphic order) are now identified within the Auca Mahuevo section (Fig. 1B) (Dingus et al., 2000; Chiappe et al., 2000). Excavation of a quarry in egg bed 3 showed the arrangement of in situ eggs, while mapping of over a hundred clutches at a nearby locality documented clutch distribution (Chiappe et al., 2000). This latter locality, a low-relief erosional surface exposing egg beds 2 and 3, recently produced the first sauropod egg clutches containing abnormal, multilayered eggs.

Multilayered eggshell occurs occasionally in the hard-shelled aragonite or calcite eggs of some extant amniotes due to prolonged egg retention, often resulting from environmental or physiological stress (Romanoff and Romanoff, 1949; Erben, 1970; Erben et al., 1979; Ewert et al., 1984; Hirsch, 2001; Solomon, 1997; Jackson and Varricchio, 2003). Although pathological conditions are occasionally reported in dinosaur eggshells, most descriptions pertain to isolated fragments rather than eggs from in situ clutches (Sochava, 1971; Erben et al., 1979; Kerourio, 1981; Mohabey, 1984; Vianey-Liaud et al., 1994; Zelenitsky and Hills, 1997; Hirsch, 2001) and none are taxonomically identified on the basis of embryonic remains.

Despite the paucity of taxonomically referable in situ material, several studies have nonetheless endeavored to link climate change and abnormal fossil eggshell to dinosaur extinction (Erben et al., 1979; Yang et al., 2001; Zhao et al., 2002). Inferences of dinosaur physiology and reproductive anatomy are also based on comparisons of fossil eggshell abnormalities with those occasionally found in eggs of living taxa (Erben, 1970; Erben et al., 1979; Ewert et al., 1984; Hirsch et al., 1989; Hirsch, 1994b; Zelenitsky and Hills, 1997; Carpenter, 1999). However, assessment of dinosaur physiology or reproductive anatomy based on multilayered eggshells remains problematic.

We present the first systematic study of eggshell abnormalities from clutches of a known taxon within Dinosauria, titanosaur sauropods. More specifically, our objectives are to determine the incidence of these abnormalities by assessing the abundance of clutches possessing abnormal eggs, the number of abnormal eggs in each of these clutches, and by documenting the microstructural differences of normal and abnormal eggs. We describe the methodology employed in conducting this survey, the taphonomy of clutches containing abnormal eggs, and three distinct forms of eggshell abnormality present in the eggs. Finally, we discuss previous hypotheses that relate multilayered eggshell to the terminal Cretaceous extinction event and interpretations of dinosaur reproductive anatomy and physiology.

Institutional Abbreviations—MCF-PVPH, Museo Carmen Funes, Paleontología de Vertebrados, Plaza Huincul, Argentina.

GEOLOGY

The Auca Mahuevo fossil egg locality is located 87 km southeast of Rincón de los Sauces City, Neuquén Province, Argentina (Fig. 1A). Extensive outcrops of Upper Cretaceous strata at this site include the uppermost units of the Neuquén Group and overlying lowermost units of the Malargüe Group. Approximately 1,300 meters thick, the Neuquén Group (Cenomanian—early to middle Campanian age) consists of siliclastic terrestrial deposits characterized by braided and meandering fluvial sediments that accumulated during the terminal back-arc stage of the Neuquén basin (Cazau and Uliana, 1973; Gazzera and Spalletti, 1990; Dingus et al., 2000).

Auca Mahuevo is contained within the Anacleto Formation,

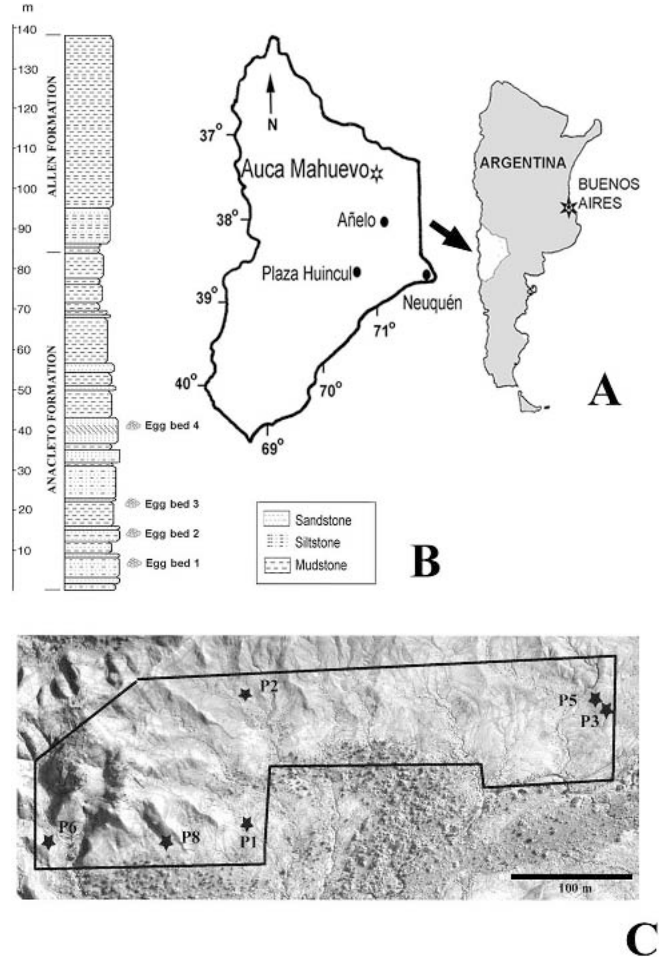

FIGURE 1. The Auca Mahuevo locality. **A**, geographic location. **B**, detailed stratigraphic column for the Anacleto Formation and overlying unit showing positions of egg beds 1–4. **C**, air photograph of the study area showing location of the 6 clutches containing abnormal eggs (P1, P2, P3, P5, P6, P8).

which conformably overlies the Bajo de la Carpa Formation. A low-angle disconformity (Ardolino and Franchi, 1996) occurs at the contact between the Anacleto Formation and overlying Allen Formation (Malargüe Group). In the study area, the Anacleto Formation is 85 meters thick (Fig. 1B) and characterized by reddish and reddish-brown mudstones and interbedded gray-green, thin sandstone bodies. The age of the Anacleto is early to middle Campanian (Legarretta and Gulisano, 1989), an age recently confirmed from paleomagnetic data (Dingus et al., 2000). Four egg-bearing levels occur within the mudstone and fine-grained sandstone facies interpreted as overbank deposits of a distal fluvial plain (Dingus et al., 2000). Two egg layers, egg beds 3 and 4, extend laterally for up to eight kilometers. Small root traces, caliche nodules, and abundant slickensided surfaces indicate paleosol development and relatively abundant vegetation on the floodplain. Arid climatic conditions, with pronounced seasonal alteration of wet and dry conditions, characterize deposition of the Neuquén Group (Garrido, 2000).

METHODS AND MATERIALS

A randomly selected site (~38,000 m^2) was chosen within the larger Auca Mahuevo study area after field reconnaissance (Fig. 1C). Criteria used for site selection included the presence of hundreds of exposed in situ egg clutches and the ability to assign these clutches to their proper stratigraphic unit (egg bed 2 or 3) (Chiappe et al., 2000; Dingus et al., 2000). Clutches on this relatively flat surface typically contain eroded eggs exposed in plan view (Fig. 2A). However, dense concentrations of fragmented eggshells are also present, representing more extensively weathered clutches (Chiappe et al., 2000). The weathered condition of most fossil material within the study area necessitates an explanation of the terms and criteria used in this survey.

Terms and Criteria Used for Clutch Investigation

Intact clutches previously quarried from egg bed 3 contain up to 35 eggs; each clutch covers an area of approximately one square meter (Chiappe et al., 2000). In the study area, differential weathering often exposes eggs in different areas of the same clutch. Therefore, eggs that are less than one meter apart and separated by abundant eggshells are considered to belong to the same clutch. Eggs within these clutches occur in close proximity to one another and the eggshell is oriented vertically in the sediment, preserving a significant portion (>⅓) of the original egg perimeter in cross section (Fig. 2A). Normal eggs from this locality (some containing sauropod embryonic remains) are approximately 15 cm in diameter, with 1.00 to 1.78 mm-thick megaloolithid eggshell structure (Fig. 2B) (Chiappe et al., 1998). The surface ornamentation consists of tubercles (<1 mm diameter) that occasionally coalesce to form ridges (Figs. 2C). An abnormal egg, therefore, is defined as an egg with an unusually thick eggshell (>2.5 mm) comprised of two or more superimposed eggshell layers, with rugose, prominent tubercles that are typically greater than 1 mm in diameter (Figs. 2D, 3A–C). Petrographic thin sections and scanning electron microscopy provide verification of initial field identification of abnormal eggs.

The Survey

Systematically spaced, parallel transects approximately one meter apart were conducted within the ~38,000 m^2 study site. Each clutch was examined for characteristics described above and then marked in order to avoid duplication. Sedimentological and taxonomic attributes were documented for each site that exposed a clutch containing abnormal eggs. These clutches were photographed and eggshell samples from normal and abnormal eggs were removed for laboratory analysis. To calculate the area of the study site, five-meter long cross marks were spray painted on the ground and the area was photographed from a small airplane. Each clutch was located on the aerial photograph and assigned to the appropriate stratigraphic layer (Fig. 1B, C). To conserve the fossil material, only one clutch containing abnormal eggs was excavated. This clutch was mapped using a 1 m^2 grid and graph paper and the trend and plunge of slickenlines were measured with a Brunton compass and noted on the map.

Laboratory Analysis

Eggshell fragments from normal and multilayered eggs from all six clutches were ultrasonically cleaned and half of the specimens were prepared as standard petrographic thin sections (30 μm thick) and studied by transmitted and polarized light microscope. The remaining specimens were gold coated (10 nm), mounted on aluminum stubs, and imaged under a J. R. Lee Instrument Personal SEM and/or JEOL 6100 SEM with Backscattered Electron Imaging (BEI) capabilities, coupled to a Noran Voyager Energy Dispersive X-ray (EDX) system. Structural attributes (shell thickness, pore width) were measured with Buhler Omnimet Enterprise image analysis software. Two partial eggs collected from clutch P-6 (MCF-PVPH-514) and all eggshell

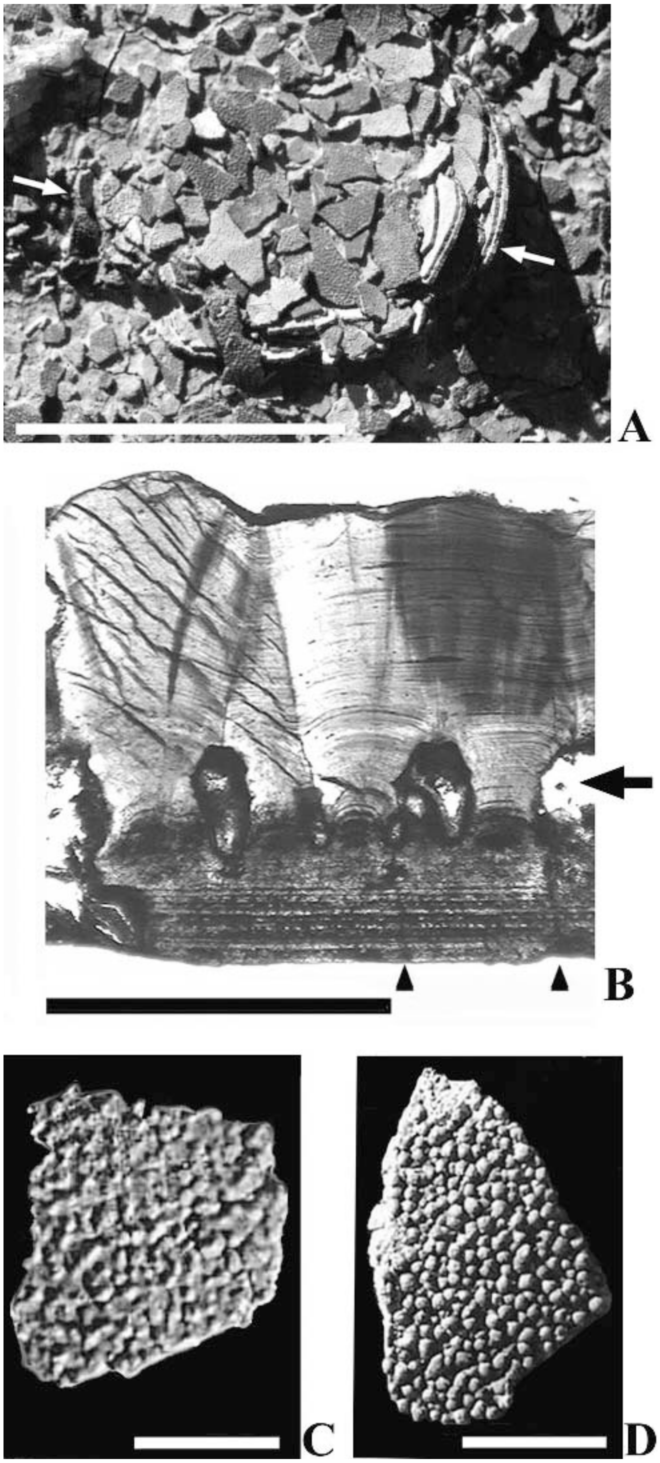

FIGURE 2. Abnormal and normal egg and eggshells. **A**, weathered abnormal, multilayered egg from clutch P1 (MCF-PVPH-251) exposed in cross section. Arrows show double eggshell and maximum egg diameter. Scale bar equals 10 cm. **B**, petrographic thin section of eggshell from an egg with normal megaloolithid calcite structure from P-5 (MCF-PVPH-254) showing preserved stratified membrane beneath the interior shell surface. Note membrane thickness and nucleation sites at the outer membrane surface. Triangles denote pores that traverse the membrane; arrow marks eggshell dissolution and replacement by calcite. Scale bar equals 1 mm. **C**, **D**, surface of normal and multilayered eggshell, respectively, from clutch P-5 (MCF-PVPH-254). Note the more rugose surface ornamentation in D. Eggs are adjacent to one another and subject to similar weathering. Scale bars equal 1 cm.

fragments are catalogued in the Museo Carmen Funes, Plaza Huincul, Province of Neuquén, Argentina.

RESULTS

Taphonomy

Exposures of egg bed 3 produced 329 in situ egg clutches within the 35,000 m^2 study area; five of these clutches contain both normal and abnormal eggs. Fourteen clutches, one of which contains a multilayered egg, are present in the more limited exposures of egg bed 2 (3,000 m^2). Since other clutches are unexcavated, the total computed number of eggs (normal and abnormal) (Table 1) represents a minimum number present and additional eggs may remain undetected in the substrate. The following general description applies to all clutches present within the study area, followed by a more detailed description of a nearly complete clutch (P-6) excavated from egg bed 3.

General Clutch Description—The weathered clutches from egg beds 2 and 3 preserve normal and abnormal eggs exposed in plan view (Fig. 2A) and occur in similar sandy, reddish brown mudstone. The sediments surrounding these clutches exhibit no lithologic evidence of nest structure (see Chiappe et al., 2004), and the condition of the eggs prior to burial (intact or hatched) remains uncertain in all clutches except P-6, discussed below. In clutches containing more than one multilayered egg (P-3, P-6, P-8), the eggs are adjacent to each other, rather than separated by normal eggs. A narrow (1–2 cm) blue-green "halo" outlines the exposed eggs, indicating chemical reduction of the sediment immediately surrounding the egg, possibly the result of decomposition of the contents after burial. Occasionally, small (<3 mm) calcium carbonate nodules are aligned along the egg perimeter, replacing portions of missing eggshell. Clutch P-5 represents the only clutch with associated bone: immediately down slope from a normal egg, an unidentified bone fragment adheres to a small (<1.5 cm) piece of normal eggshell. No additional bone was present in the vicinity.

Clutch P-6—In the steeper terrain of the southwest portion of the study area, egg bed 3 crops out 3.3 meters above the base of a slope and approximately one meter below a horizon containing small (~1.0 cm) caliche nodules. The laterally continuous exposures of egg bed 3 produce dense concentrations of eggshell one to three meters apart along the contour of the hill. Most of these concentrations exhibit eggshells with normal surface ornamentation. However, abundant multilayered eggshells with rugose surface morphology cover the slope immediately below two partially eroded, abnormal eggs (Fig. 3A–D). Surface collection on the slope beneath these two eggs produced 382 fragments of multilayered eggshell and only 14 single-layer fragments. One egg (P-6-2) exhibits missing portions of the outer abnormal shell, exposing normal eggshell beneath the abnormal layer (Fig. 3A, C). These 14 normal specimens, therefore, most likely represent eggshell that separated from the abnormal, multilayered egg during recent weathering.

Excavation of the clutch revealed a total of 30 eggs, 27 normal eggs and 3 multilayered eggs with rugose surface ornamentation (Fig. 3D). The eggs are distributed in three levels within the clutch; the three abnormal eggs occur at the highest level, in close proximity to one another (Fig. 3D). Both normal and abnormal eggs in P-6 contain concave-down eggshell fragments, indicating that whole eggs were crushed by lithostatic compression. The narrow blue-green "halos" surrounding the eggs resemble those present in the other five clutches and elsewhere in egg bed 3. Diagenetic growth of gypsum crystals within this zone facilitates rapid weathering of the fossil material. Mudstone surrounding and filling the eggs shows relatively abundant parallel striations (slickenlines), with varying orientations (Fig. 3D) and one to several centimeters of vertical offset, as determined by

TABLE 1. Summary of taphonomic and structural information for six clutches containing abnormal, multilayered eggs. Where more than one abnormal egg occurs in a clutch, the eggs are distinguished by sequential numbering.

Clutch	Egg bed	Total no. of eggs	Abnormal eggs	Egg size range	Surface morphology	Structural type	Comments
P-1	2	3	1	13–15 cm	normal	I	—
P-2	3	3	1	13 cm	rugose	I, II, III	—
P-3	3	5	2	12–15 cm	rugose	II, III	P-3-1 & P-3-2 exhibit III & II, respectively
P-5	3	4	1	12–17 cm	rugose	II, III	—
P-6	3	30	3	8–15 cm	rugose	II	present in all 3 eggs
P-8	3	5	2	10–12 cm	rugose	II, III	present in both eggs

field measurements using a Brunton compass and a centimeter ruler, respectively.

Discussion of P-6 Taphonomy—The absence of nearly any normal eggshell on the slope below this clutch suggests that recent erosion was limited to the abnormal eggs occupying the highest level within the clutch. The number (30) and distribution of eggs in P-6 typifies other intact clutches previously excavated from egg bed 3 (Chiappe et al., 2000), and the three egg levels represent the maximum number of superimposed eggs yet documented at this locality (unpublished data). Clutch P-6, therefore, most likely represents a complete, in situ clutch. Burial and preservation of the eggs, like other clutches from egg bed 3, resulted from suspension settling of fine-grained material during a flood event (Chiappe et al., 2000).

The highly variable orientation of slickenlines on the surface of the mudstone results from vertisol development within the nesting horizon (Chiappe et al., 2000). In a seasonally wet and dry climate, repeated shrinking and swelling occurs in high clay-content soils. During the rainy season the clay expands and blocks of soil shear off and slide past each other under pressure, producing striated surfaces (Brady and Weil, 2002). The presence of slickensides inside some eggs indicates that vertisol development occurred (or continued) after burial and subsequent infilling of the eggs by sediment. Pedogenesis undoubtedly produced compaction and displacement of some eggs within this clutch. However, movement was typically no more than a few centimeters, based on field measurements of offset rock surfaces, suggesting minimal change in the original egg orientation and distribution.

The level at which the abnormal eggs occur and their close proximity to each other in clutch P-6 is significant. Some extant turtles produce more than one clutch in a season. Occasionally, one or more eggs are retained in the oviduct and additional eggshell layers are deposited over the eggs with shelling of the next clutch. These retained eggs represent the first eggs laid with subsequent oviposition. Ewert et al. (1984) suggested that if dinosaurs produced multiple clutches in a single season, one might expect to find retained eggs at the bottom of the clutch. Although a reasonable hypothesis, the presence of the three abnormal eggs at the highest level in clutch P-6 indicates that they are the last eggs laid by the female sauropod. Although multilayered eggs also occur adjacent to each other in unexcavated clutches (P-3 and P-8), no assessment is possible of the level at which they occur.

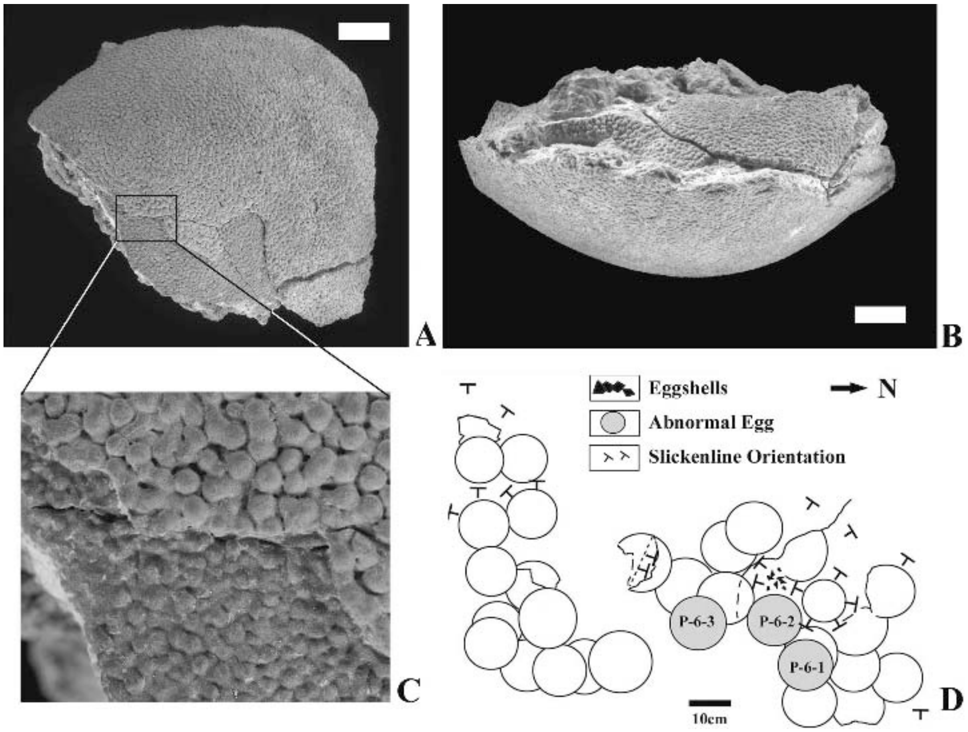

FIGURE 3. An excavated clutch, P6 (MCF-PVPH-514). **A**, **B**, eggs P-6-2 and P-6-3, respectively, two eroded abnormal eggs that occupied the highest level in the clutch. Scale bars equal 1 cm. **C**, enlargement of double eggshell layers indicated by box in A. Note difference in diameter in tubercles of the inner and outer eggshell layers. **D**, field map of clutch P6 showing location of three multilayered eggs. Dip symbols indicate direction of slickenlines on egg and rock surfaces.

Microscopic Analysis of Eggshell

Diagenesis—Scanning electron microscopic (SEM) images and petrographic thin sections of eggshells from the six clutches often show soft tissue preservation in the form of eggshell membrane. Embryonic integument (Chiappe et al., 1998) and eggshell membrane (Grellet-Tinner, 2002) previously reported from other eggs in this study area further support this interpretation. In the six clutches containing abnormal eggs, permineralized eggshell membrane is present at the base of some eggshells (Fig. 2B) and occasionally separates the multiple layers in abnormal eggs (Figs. 4A, B). In addition, freshly broken eggshell from the multilayered egg in clutch P-5 exhibits an 860 μm-long feature (9 μm thick) that consists of two intertwined strands that appear to flatten before entering an opening in the calcite eggshell (Fig. 4C–E). Elemental analysis shows no quantitative difference in composition between the calcite eggshell and the permineralized strand. This structure may represent permineralized protein matrix, an organic latticework on which the calcite mineral is deposited during eggshell formation. However, differentiating fossilized contaminants such as bacteria or fungi from the protein matrix of the original eggshell remains problematic because of their similar morphology (Jackson et al., 2002).

In all specimens, diagenetic dissolution of eggshell calcite took place primarily between individual shell units at the interior eggshell surface and, less frequently, within the upper portion of the shell (Figs. 2B, 4C, 5A, B). Reprecipitation of sparry calcite accompanied this diagenetic alteration in most specimens. Authigenic analcime replacement often occurs in association with the protein membrane (Figs. 5A–E, 6A), suggesting that the membrane was preferentially susceptible to analcime replacement. Identification of the zeolite mineral is based on crystal morphology in thin section and SEM images (Fig. 5C) and energy dispersive xray (EDX) analysis of individual crystals.

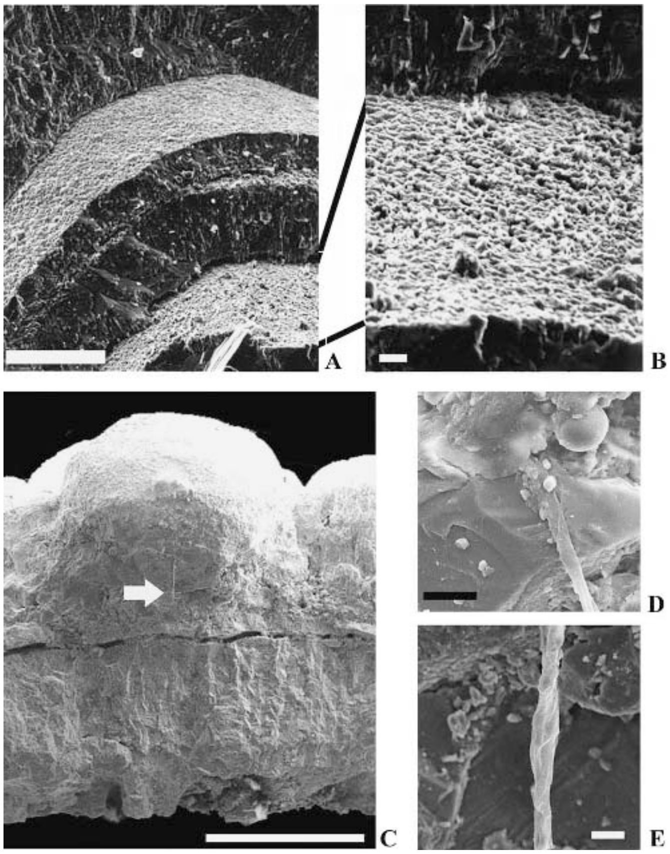

FIGURE 4. Soft tissue preservation. **A**, **B**, SEM image of multiple shell layers and preserved membrane in P-8–2 (MCF-PVPH-255). **C**, SEM image of multilayered eggshell (MCF-PVPH-254). Arrow marks the location of permineralized strand shown in D and E. Scale bar equals 1 mm. **D**, upper portion of strand shown in C as it enters an opening in the eggshell calcite. Scale bar equals 10 μm. **E**, enlargement of fibrous twisted structure shown in C. Scale bar equals 10 μm.

Eggshell Microstructure—All normal, single-shelled eggs from the six clutches exhibit megaloolithid eggshell structure (Fig. 2B) identical to eggs from egg bed 3 that contain titanosaur sauropod embryos (Chiappe et al., 1998, 2001). Abnormal eggs from all six clutches display an unusually thick shell comprised of superimposed eggshell layers (Figs. 3A–C, 4A–C, 5A, 6A–C). The inner eggshell shows similar thickness, calcite microstructure, and surface ornamentation to normal sauropod eggs from this site. However, the additional abnormal layers vary in number and structure (Fig. 6A–C). This variation occurs within and among the six clutches and even within a single egg. The outer surface of all multilayered eggs displays rugose ornamentation, except for the abnormal egg in clutch P-1 that exhibits normal ornamentation. Table 1 summarizes three types of abnormal morphology (Types I–III) documented in the multilayered eggs and provides additional data from the six clutches. When more than one abnormal egg is present in a clutch (e.g. P-8), the eggs are sequentially numbered: P-8-1, P-8-2.

Type I Morphology—This type of abnormal eggshell morphology exhibits two superimposed eggshell layers, both with normal megaloolithid structure and thickness (Fig. 6A) (Chiappe et al., 1998). Occasionally, remnants of permineralized membrane that separates the superimposed eggshell layers exhibit nucleation sites comprised of radiating calcite spherulites. Under crossed polars in petrographic thin sections, these spherulites exhibit pseudouniaxial crosses and extinction occurs simultaneously in both eggshell layers when the microscope stage is turned (Fig. 6A). Where more extensive diagenetic replacement occurs, these nuclei comprised of radiating crystals "float" within authigenic analcime crystals between the eggshell layers (Fig. 5D, E). These calcite nucleation sites are lateral to one another, at a consistent distance above the unweathered surface of the underlying eggshell (Fig. 5D).

Type II Morphology—The inner eggshell exhibits normal structure, while the outer eggshell is typically thinner and lacks calcite nuclei (Figs. 4C, 5A, 6B, 7A, B). Calcite crystals are "seeded" to the underlying eggshell, with or without visible membrane separation. The base of the abnormal layer closely conforms to the tuberculate surface ornamentation of the underlying egg (Figs. 5A, 6B) and the calcite structure of the abnormal eggshell maintains the established crystal orientation. Under crossed nicols in thin sections, a sweeping extinction pattern extends through both the inner and outer eggshell layers simultaneously in some areas, indicating optical continuity between the two eggshells (Fig. 7B). However, where multiple shell units of the inner eggshell correspond to a single shell unit in the outer eggshell layer, the extinction pattern may be disrupted.

Type III Morphology—This structure consists of three or more superimposed eggshell layers (Figs. 4A, B, 6C, 7C, D). The innermost eggshell exhibits normal calcite structure and ornamentation. The abnormal layers follow the contour of the underlying shell, displaying a smooth basal contact, and an absence of calcite nucleation sites. In some areas of the abnormal egg in clutch P-2, the second and third abnormal layers display small tubercles on the outer shell surface (Fig. 7C, D). Remnants of mesh-like permineralized membrane often separate the calcite layers (Figs. 4A, B, 6C). Occasionally, the additional shell layers block pores that traverse the inner eggshell, thereby restricting gas exchange to the embryo (Fig. 6C). Shell units comprising the outermost eggshell terminate in broad (>1.0 mm), rounded tubercles, producing rugose surface ornamentation compared to normal eggs exposed within the same clutch (compare Fig. 2C to D).

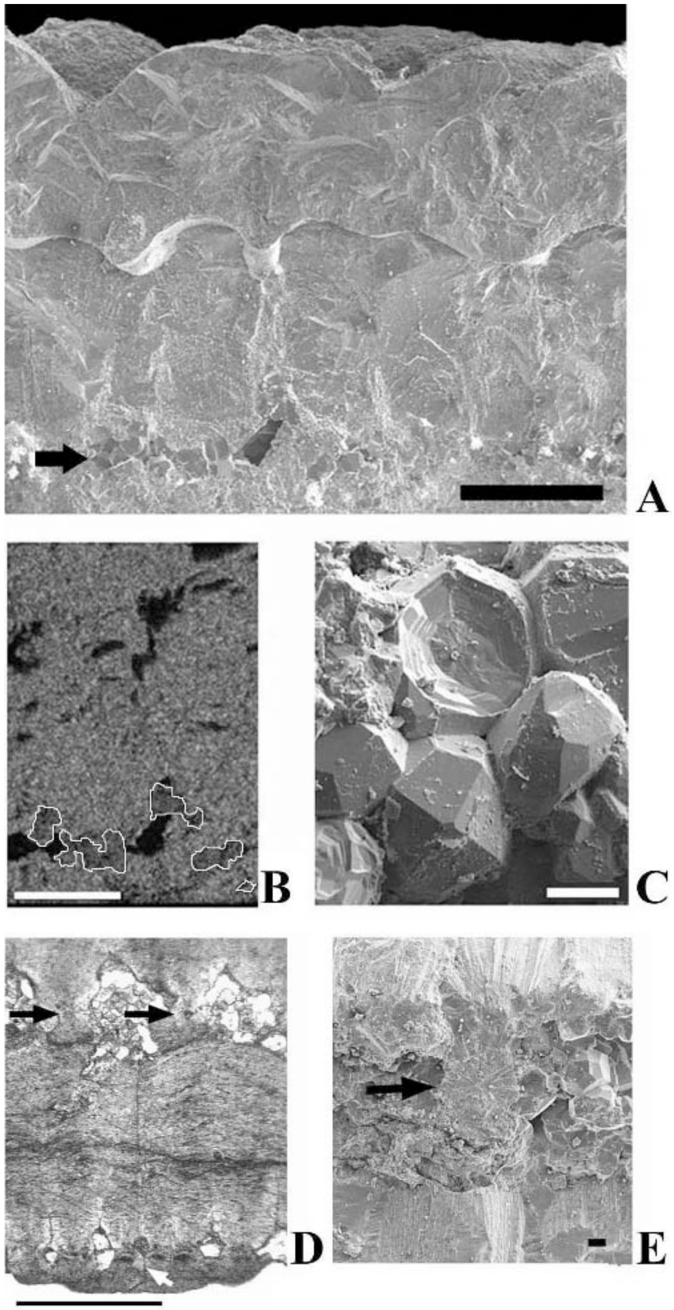

FIGURE 5. Diagenetic eggshell alteration. **A**, SEM image of abnormal eggshell from P-8–2 (MCF-PVPH-255). Arrow indicates area of membrane replacement by analcime. Scale bar equals 1 mm. **B**, elemental map of inner eggshell of same egg with outlined areas indicating analcime replacement in the membrane area of the inner eggshell. Scale bar equals 1 mm. **C**, close up of analcime crystal morphology. Scale bar equals 10 μm. **D**, **E**, black arrows point to calcite nucleation sites surrounded by authigenic analcime in laterally adjacent sites in P-1 (MCF-PVPH-251) and between the inner and outer eggshell in P-2 (MCF-PVPH-252), respectively. Note the distance from the surface of the inner eggshell to the nucleation site, denoting approximate thickness of the former membrane. White arrow in D indicates closely spaced nucleation sites at base of inner eggshell, compared to more widely spaced nucleation sites at the base of the overlying outer eggshell. Scale bars in D and E equal 1 mm and 100 μm, respectively.

DISCUSSION

Occurrence of Eggshell Abnormalities

Modern amniotes that lay hard-shelled eggs include some geckos and turtles and all crocodilians and birds. Egg abnormalities in these taxa occasionally result from egg retention, often in response to physiological or environmental "stress." Such stress may result from absence of appropriate nesting substrate or material (Ewert et al., 1984; Hughes et al., 1986), handling, oviduct obstruction (Asmundson, 1933), disease or injury (Romanoff and Romanoff, 1949), diet (Grau and Kamei, 1949), and high population density (Ferguson, 1985; Solomon, 1997). With prolonged egg retention, additional eggshell layer(s) may be deposited over the first eggshell (Romanoff and Romanoff, 1949; Erben et al., 1979; Kérourio, 1981; Ewert et al., 1984; Jackson and Varricchio, 2003).

With the exception of turtles, documentation of abnormal, multilayered eggshell in extant amniotes is very limited. Erben et al. (1979) reported this multilayered condition in an unidentified crocodilian egg; however, the paper lacks citation, photographs, and description of the egg or eggshell microstructure. Some birds occasionally produce abnormal, superimposed eggshell layers that are similar in structure to abnormal dinosaur eggshells (Solomon, 1997; Jackson and Varricchio, 2003). However, reports of multilayered avian eggs are rare. In contrast, multilayered eggs are relatively common in some hard-shelled turtle eggs, currently reported in at least nine extant species (Cagle and Tihen, 1948; Erben, 1970; Erben et al., 1979; Ewert et al., 1984; Schleich and Kästle, 1988).

Multilayered dinosaur eggshells are reported from Upper Cretaceous rocks of Asia, Europe, and North and South America (Dughi and Sirugue, 1958; Thaler, 1965; Erben, 1970; Sochava, 1971, Mohabey, 1984; Zhao et al., 1991; Vianey-Liaud et al., 1994; Powell, 1987; Zelenitsky and Hills, 1997; Ribeiro, 1999; Zhao et al., 2002). Reports of intact, multilayered eggs include only three isolated eggs from different localities in Maastrichtian rocks of southern France (Kérourio, 1981) and a single egg from the Jurassic Morrison Formation in Utah (Hirsch et al., 1989). Jackson et al. (2002) reported a multilayered fossil turtle egg from the Judith River Formation of Montana, and Schleich and Kästle (1988) reported multilayered gecko eggs from the Oligocene of Germany. Although present in a variety of fossil eggshell types, the multilayered condition is most frequently reported in the megaloolithid eggshell structure (Hirsch, 2001).

Abnormalities in Titanosaur Eggs

In extant taxa, eggshell abnormalities provide information on the timing of stress (Tyler and Simkiss, 1959; Hughes et al., 1986; Solomon et al., 1987; Solomon, 1997; Jackson and Varricchio, 2003). Fossil eggshells provide similar information: in all abnormal eggs from the six sauropod clutches, the inner eggshell is comparable in thickness, microstructure, and surface ornamentation to normal titanosaur eggs from the Auca Mahuevo locality. Therefore, the adverse stimuli that resulted in egg retention occurred at or near the end of shell deposition, before oviposition could occur.

In Type I morphology, secretion of additional membrane followed this egg retention. Where analcime or calcite replaces the membrane between the superimposed eggshell layers, the original membrane thickness may be inferred by measuring the distance from the surface of the underlying eggshell to the calcite nuclei at the base of the overlying, abnormal eggshell layer (Fig. 5D, E). From these measurements we conclude that the additional membrane deposited over the retained egg was thinner than that present at the interior shell surface of normal eggs (compare Figs. 2B to 5D, E). In eggshell of extant birds, the organic cores are located within the upper surface of the two-

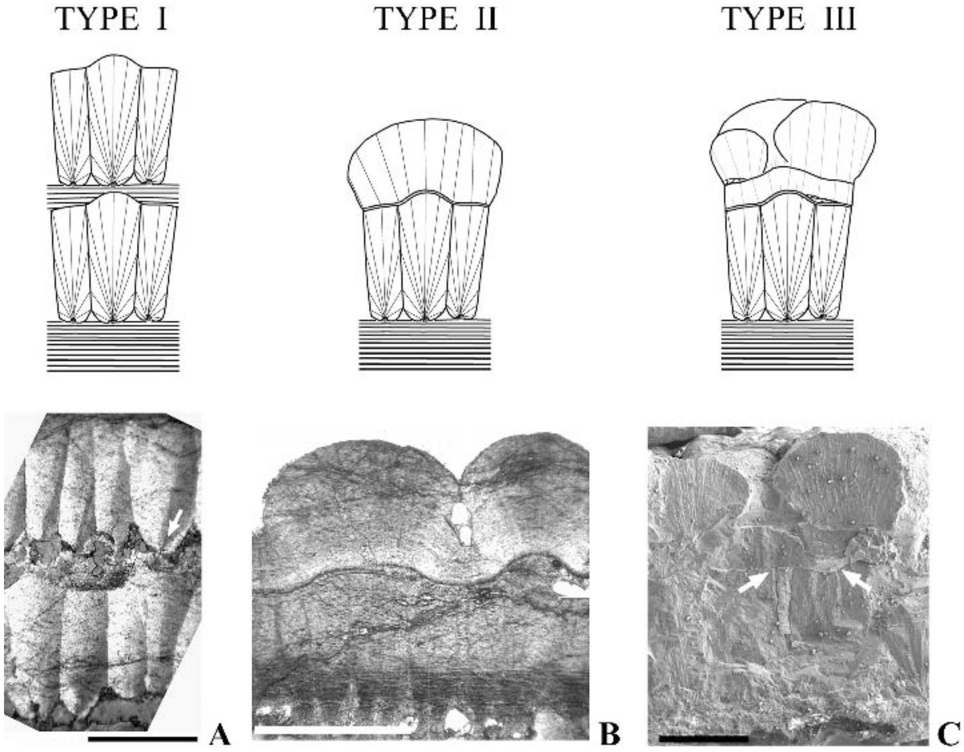

FIGURE 6. Types I-III abnormal morphology in schematic and microscopic images. **A**, Type I morphology showing a normal eggshell overlain by a structurally complete eggshell layer. Arrow in thin section indicates pseudouniaxial cross at the nucleation site in P-1 (MCF-PVPH-251). **B**, Type II morphology in eggshell thin section from P-5 (MCH-PVPH-254); note that abnormal layer closely conforms to the unweathered tuberculate surface ornamentation of the underlying egg. **C**, SEM image of Type III morphology in P-3 (MCF-PVPH-253) comprised of three eggshell layers. Left arrow points to pore truncated by second shell layer; right arrow shows membrane fragment between layers 1 and 2. Scale bars on all images equal 1 mm.

layered membrane structure, adjacent to the shell. Proteins of these organic cores are thought to initiate calcite nucleation and exert critical control over the resulting crystal morphology (Nys, et al., 1999; Dennis et al., 1996). Despite significant reduction in membrane thickness between the superimposed eggshells in P-1, calcite nucleation sites are present at the interior surface of the abnormal layer, thereby producing normal calcite structure in the overlying eggshell.

In Type II and III morphologies, nucleation sites are absent at the base of the abnormal eggshell layers and these additional eggshell layers are structurally incomplete (Figs. 4A–C, 5A, 6B, C, 7A–D). The superimposed layers are closer together than in Type I morphology, suggesting further reduction or absence of membrane and elimination of the organic cores necessary for normal eggshell structure. In these specimens, mineral deposition follows the crystallographic "template" provided by inner eggshell. Lateral expansion of the shell unit, unimpeded by competition from crystal growth of an adjacent nucleation site, produces the broad, bulbous surface ornamentation characteristic of most multilayered eggshells from this locality. In at least one multilayered egg (P-2), the eggshell exhibits highly variable morphology that includes all three types of abnormal morphology (Types I, II, III) within the same abnormal egg.

Comparison to Eggs of Extant Taxa

Morphology similar to Type I occurs in both extant turtle and bird eggs (Ewert et al., 1984; Jackson and Varricchio, 2003). In both living taxa, the abnormal shell layer exhibits organized structure. Nucleation sites at the base of the outer, abnormal layer are often farther apart than those at the base of the inner eggshell (Ewert et al., 1984:figs. 8, 9; Jackson and Varricchio, 2003), a condition also observed in the abnormal sauropod egg from clutch P-1 (Fig. 5D). In Type I sauropod morphology, however, the outer eggshell is structurally complete and of normal thickness. In contrast, multilayered bird and turtle eggs exhibit a thinner and structurally incomplete outer eggshell, compared to the underlying egg (Erben et al., 1970:fig. 2; Ewert et al., 1984:figs. 9, 10; Jackson and Varricchio, 2003).

Abnormal shell morphologies similar to Types II and III also occur in fossil and extant turtle eggs and the membrane that separates the multiple, mineralized layers varies in thickness (Erben et al., 1979; Ewert et al., 1984:figs. 7, 8; Hirsch, 2001:figs. 12, 13; Jackson et al., 2002:fig. 11). To the best of our knowledge, abnormal morphology similar to Type II and III has not been documented in birds, despite numerous studies that include a variety of abnormal eggshell conditions (Hargitt, 1897; Curtis, 1916; Asmundson, 1933; Romanoff and Romanoff, 1949; Grau and Kamei, 1949; Sykes, 1955; Tyler and Simkiss, 1959; Von Nathusius translated by Tyler, 1964; Hughes et al., 1986; Solomon et al., 1987; Solomon, 1997; Jackson and Varricchio, 2003).

PREVIOUS HYPOTHESES BASED ON ABNORMAL EGGSHELL

All previous reports of pathological dinosaur eggshells pertain to isolated, taxonomically unidentified eggs (Kérourio, 1981; Hirsch et al., 1989) or eggshell fragments (Dughi and Sirugue, 1958; Thaler, 1965; Erben, 1970; Sochava, 1971; Erben et al., 1979; Kérourio, 1981; Mohabey, 1984; Powell, 1987; Zhao et al., 1991; Vianey-Liaud et al., 1994; Zelenitsky and Hills, 1997; Ribeiro, 1999; Yang et al., 2001; Zhao et al., 2002) rather than in situ egg clutches. Thus, most literature on fossil dinosaur eggshell abnormalities is incomplete in terms of taphonomy, descriptive

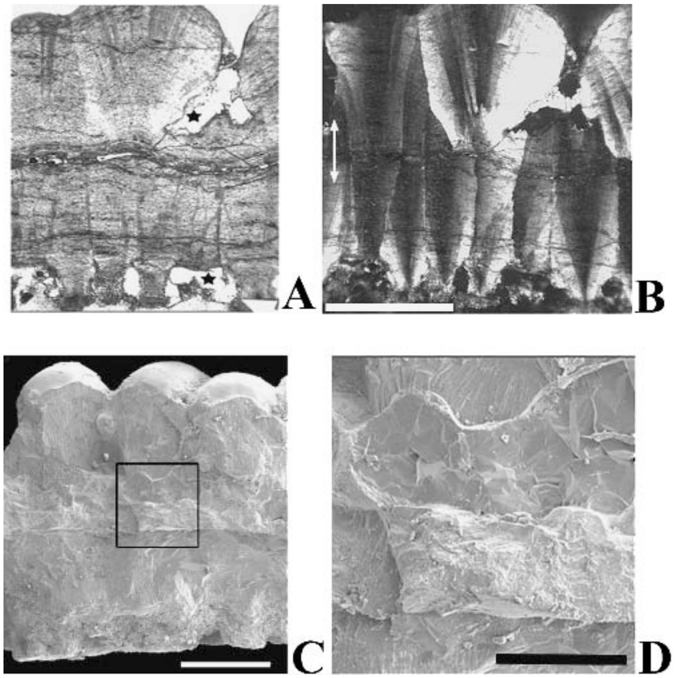

FIGURE 7. Type II and III morphology. **A**, eggshell from an abnormal egg in clutch P-2 (MCF-PVPH-252) showing Type II structure. Star symbols indicate areas of eggshell dissolution and replacement by calcite. **B**, same eggshell under crossed polars. Vertical arrow indicates extinction pattern that crosses the inner and outer eggshell in the left ¼ of the photograph; upper shell unit in the center of the photograph shows disruption of extinction pattern. **C**, four eggshell layers in the abnormal egg from clutch P-2 (MCF-PVPH-252). **D**, close up of C showing the small tuberculate ornamentation present in layers 2 and 3.

parameters, and taxonomic identification necessary for interpretation of their occurrence, formation, and phylogenetic significance. Several authors, however, have attempted to correlate eggshell abnormalities with Late Cretaceous climate change, iridium anomalies, and dinosaur extinction (Dughi and Sirugue, 1958; Thaler, 1965; Zhao et al. 1991; Yang et al., 2001; Zhao et al., 2002).

Implications for Cretaceous Extinction Scenarios

Erben et al. (1979) report that pathological conditions occur in 10% of eggshells in Upper Cretaceous rocks from France and the authors suggest a progressive, stratigraphically upward increase in these abnormalities as a result of changing climatic conditions. Similarly, Zhao et al. (2002) report a 56% and 74% frequency of pathological eggshells in the oospecies *Macroolithus yaotunensis* near the Cretaceous-Tertiary boundary in two locations in the Nanxiong Basin, South China. However, there is no indication in either report that the fossil material represents in situ eggs or clutches, nor do the authors discuss the statistical methods used for calculating abnormal eggshell abundance or the alleged increase in eggshell abnormalities over a stratigraphic interval. Furthermore, Kérourio (1981) considered at least one of the eggshell localities examined by Erben to represent material reworked from the underlying strata.

These and other attempts to link abnormal, multilayered eggshell to climate change and dinosaur extinction fail to consider the magnitude of geologic time associated with the Cretaceous-Tertiary extinction event. In extant animals, eggshell abnormalities may result from environmental stress related to overcrowding, drought, or substrate conditions (Ewert et al., 1984; Ferguson, 1985). Although acute stress may affect eggshell structure for a considerable time (Hughes et al., 1986; Solomon, 1997), this time interval (hours to weeks in birds and reptiles) is extremely short when compared to the much longer intervals of geologic time ($\geq 10^2$–10^4 years) associated with global climate change or the terminal Cretaceous extinction event (Dingus, 1984).

Without taphonomic context provided by in situ dinosaur egg clutches, multilayered eggshell fragments provide little stratigraphic resolution or information about how frequently this abnormal condition occurred in dinosaur populations. For example, sauropod clutches from Auca Mahuevo typically contain up to 35 eggs (Chiappe et al., 2000) and partial fragmentation of only two multilayered eggs within clutch P-6 resulted in nearly 400 specimens of abnormal eggshell at an early stage of clutch weathering. Subsequent transport and distribution of this material could contribute to the perception of a more frequent occurrence of eggshell abnormalities in an area. The large clutch size and laterally extensive nesting horizons characteristic of titanosaurs at this site and other megaloolithid eggshell sites worldwide undoubtedly contribute to more frequent reports of multilayering in this type of eggshell structure. Although an unprecedented number of clutches is present at the Auca Mahuevo locality, the incidence of clutches containing abnormal eggs (6 of 343 clutches examined) and number of abnormal eggs within these clutches (maximum 3 of 30 in P-6) appears very low.

Inferences of Dinosaur Physiological and Reproductive Anatomy

Aspects of dinosaur physiology and reproductive anatomy have also been inferred by purported similarities or differences in eggshell abnormalities present in fossil and extant eggs (Erben et al., 1979; Hirsch et al., 1989; Hirsch, 1994a; Carpenter et al., 1994; Zelenitsky and Hills, 1997). For example Dughi and Sirugue (1958) interpreted multilayering of eggshell as an interruption in shell deposition during brief cold periods and hypothesized dinosaur ectothermy based on this abnormal eggshell condition. The authors, however, provided no modern analog for this process. Erben et al. (1979) compared abnormalities in dinosaur eggshell to similar multilayered eggshell (ovum in ovo) of living birds. Citing stress-related hormonal changes that can affect domestic fowl, these authors speculated that environmental change and overpopulation might have produced frequent aggressive interactions that upset female estrogen levels, resulting in abnormal eggshell formation. Clearly, the fossil record is not capable of recording the information necessary to test this anthropocentric speculation. Furthermore, Erben et al. (1979) hypothesized that a genetic mutation spread rapidly through dinosaur populations near the end of the Cretaceous, increasing the frequency of pathological eggs, with a corresponding reduction of offspring. However, it is difficult to envision how a genetic change that leads to embryonic mortality can propagate through a dinosaur population.

Abnormal, multilayered eggshells have also been used to infer dinosaur reproductive anatomy (Hirsch 1989; Hirsch et al., 1989; Hirsch, 1994a; Zelenitsky and Hills, 1997; Carpenter, 1999). For example, multilayered eggshell was thought to occur exclusively in eggs of reptiles and not birds (Hirsch et al., 1989, Zelenitsky and Hills, 1997). However, superimposed eggshells occur in archosaurs (birds, possibly crocodilians) and non-archosaurian reptiles (turtles, geckos), despite significant differences in reproductive anatomy (Erben et al., 1979; Ewert et al., 1984; Schleich and Kästle, 1988; Palmer and Guillette, 1992; Jackson and Varricchio, 2003). The range of eggshell abnormalities present in sauropod eggs from Auca Mahuevo (Fig. 6A–C) encompasses that documented in both birds and turtles, suggesting that eggshell abnormalities represent a common response to physiological or environmental stress in amniotes that lay hard-shelled eggs (Jackson and Varricchio, 2003). However, the presence of both multilayered eggs and normal eggs within the same sauropod clutch raises intriguing questions regarding clutch formation and, ultimately, the evolution of reproductive mode within Archosauria.

CONCLUSIONS

Exposures of egg bed 3 (~35,000 m^2) within the study area contain 329 in situ egg clutches, while the more limited exposures of egg bed 2 (~3000 m^2) contain 14 clutches referable to titanosaur sauropod dinosaurs. Five clutches from egg bed 3 and one clutch from egg bed 2 contain both normal and multilayered eggs within the same clutch. Excavation of clutch P-6 reveals 30 eggs distributed in three levels: 27 normal eggs and three laterally adjacent, multilayered eggs that occur at the highest level in the clutch, representing the last eggs laid by the titanosaur female.

Microscopic examination shows that the structure of the innermost layer in all abnormal eggs is identical to the normal, megaloolithid calcite structure present in other Auca Mahuevo eggs containing diagnosable titanosaur embryonic remains. Permineralized eggshell membrane, often replaced by authigenic analcime, occurs at the base of some eggshell and/or separates the inner from the outer eggshell layers. Three distinctive types of abnormal morphology characterize the abnormal eggshell layers: Type I, a structurally complete eggshell with basal nucleation sites and typical megaloolithid structure, thickness, and ornamentation; Type II, a thinner than normal eggshell that lacks calcite nuclei and exhibits rugose ornamentation; and Type III, multiple shell layers that lack nucleation sites and display rugose ornamentation in the outermost eggshell layer. Variation in abnormal morphology occurs among eggs of the same clutches and within a single egg. This morphological variation encompasses abnormal shell morphology documented in both archosaurs (birds) and non-archosaurian reptiles (turtles), despite significant differences in reproductive anatomy that characterize these groups. This suggests that abnormal eggshell is a common response to environmental or physiological stress in amniotes that lay hard-shelled eggs.

Previous attempts to relate the presence of pathological eggshell in Upper Cretaceous rocks to environmental change and dinosaur extinction have relied on isolated eggs or multilayered eggshells rather than in situ egg clutches containing abnormal eggs of a known dinosaur taxon. These reports lack the rigorous statistical documentation necessary for supporting the alleged increase of egg abnormalities in the stratigraphic interval that precedes the Cretaceous-Tertiary boundary. Furthermore, although acute stress may affect eggshell structure for a considerable length of time relative to the reproductive cycle in modern amniotes, this brief interval of time is not comparable to the larger magnitude of geologic time involved in global climate change and the Cretaceous extinction event.

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