SAUROPOD EGGS AND EMBRYOS FROM THE LATE CRETACEOUS OF PATAGONIA

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INTRODUCTION

In November of 1997, we discovered an extensive sauropod nesting ground in Late Cretaceous rocks of northwestern Patagonia, Argentina (Chiappe *et al.*, 1998). Auca Mahuevo, as we named this site, is centered in the Argentine province of Neuquén, some 1,100 km southwest of Buenos Aires, on the southeastern slope of the extinct volcano, Auca Mahuida. In March of 1999, we organized a second expedition to Auca Mahuevo. A summary of the research conducted so far at Auca Mahuevo's nesting ground is presented here.

GEOLOGICAL SETTING OF THE EGG BEARING DEPOSITS AT AUCA MAHUEVO

Auca Mahuevo occurs within the Anacleto Member of the Río Colorado Formation, the uppermost formation of the continental Neuquén Group, one of the richest dinosaur-producing units of Patagonia (Bonaparte, 1991; Coria, 1999). The estimated age of the Río Colorado Formation has ranged from Coniacian to Campanian (Dingus *et al.*, 2000). Recent paleomagnetic data, the first such data from the Neuquén Group, indicates that the Anacleto Member represented in the Auca Mahuevo section was deposited between 83.5 and 79.5 million years ago, within the Campanian (Dingus *et al.*, 2000).

Rocks of the Anacleto Member are predominantly composed of fluvial sandstones, siltstones, and mudstones (Fig. 1). Dinosaur eggs at Auca Mahuevo occur in reddish-brown mudstones representing overbank sediments deposited away from shallow stream channels draining the floodplain (Dingus *et al.*, 2000). Chiappe *et al.* (1998) reported a single, 5-m-thick layer of egg-bearing deposits. However, new field research documents two distinct egg-layers within this horizon (here refer to as egg-layers 2 and 3; Fig. 1). In addition, two other egg-layers (egg-layers 1 and 4; Fig. 1) were recognized in 1999. While egg-layers 1 and 2 are not laterally extensive, egg-layers 3 and 4 (the two uppermost ones) extend laterally for several kilometers.

Several lines of sedimentological evidence suggest that most dinosaur eggs at Auca Mahuevo are *in situ*. Mud deposited from suspension surrounds the eggs and the surfaces upon which they rest show no evidence of scour. Bedload materials are absent and there are no reworked mud clasts, carbonate nodules, or imbricated eggshell conglomerates. We know of no mechanism by which fluid flow could generate the distinct clustering of eggs seen in layer 3 and possibly the remaining three egg-layers present within the Auca Mahuevo section.

Two microstratigraphic cross-sections of egg-layer 4 reveal that the clusters of eggs appear to be associated with ancient, small-scale paleotopographic surfaces. Relief between the highs and lows on the surfaces mapped so far varies as much as 30 cm. In at least some instances, the clusters of eggs appear to sit directly

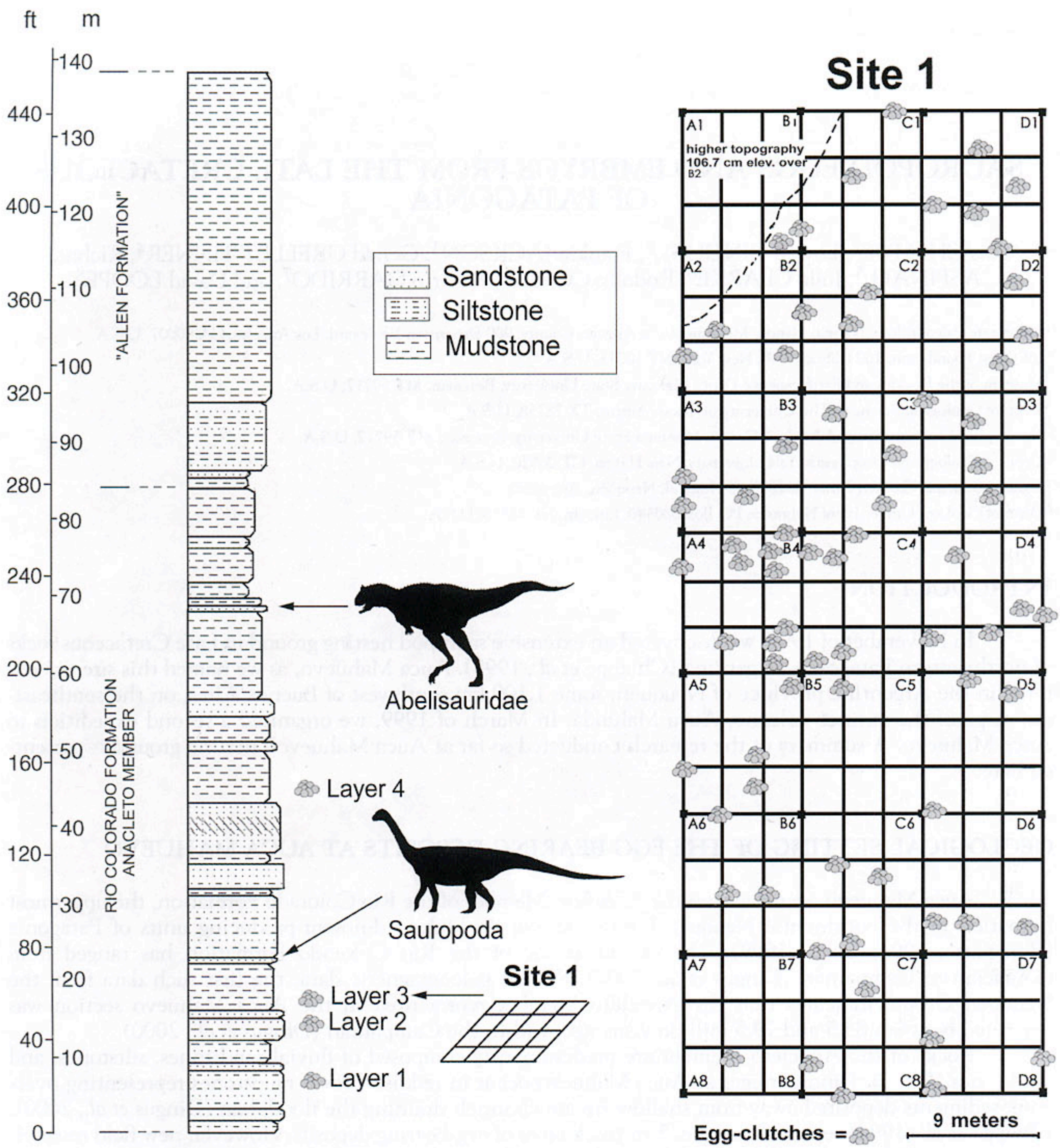

Figure1. A composite section at Auca Mahuevo reveals the presence of four stratigraphically distinct layers of sauropod eggs. A map (plan view on the right) of egg-clutches on the erosional surface of egg-layer 3 (Site 1) as well as the remains of adult abelisaur theropods and indeterminate sauropods are plotted on the section. Only *in situ* eggs with recognizable shape were mapped in order to eliminate transported material exposed on the erosional surface. Sandstone units represent paleochannel facies. Units dominated by mudstone or siltstone represent overbank facies.

on the paleotopographic surfaces. Some of the topographic relief may well have been generated by the development of vertisols. This process of soil formation results in soil slippage and heaving during alternating wet and dry periods. Numerous slickensided surfaces occur within the egg-bearing mudstones of both egg-layer 4 and 3, providing primary evidence for this tentative interpretation.

EGG MORPHOLOGY AND EMBRYONIC ANATOMY

Auca Mahuevo eggs have a diameter ranging between 12 to 15 cm. They are subspheric but somewhat compressed in one axis. Because their compressed axis is typically perpendicular to the bedding plane, it is likely that the eggs were subspherical when laid and that they have later deformed by postburial compaction. The surface ornamentation of the eggs varies widely with the degree of weathering. Typically, it consists of compact, domed tubercles that may coalesce into short ridges. The shell thickness averages 1.4 mm. There is only one inorganic layer in radial view; the eggshell microstructure is characteristic of the megaloolithid eggshell, defined under the traditional parataxonomic classification (Mikhailov, 1997). The calcitic shell has straight, well-defined shell units.

Perhaps the most remarkable feature of Auca Mahuevo is the abundance of embryonic remains. All studied embryos are from egg-layer 3. These occur both *in situ* and inside fragments of eggs exposed on erosional surfaces. Embryonic bones are usually poorly preserved, disarticulated, and flattened against the inner surface of the bottom eggshell. The degree of ossification of the skull bones exceeds that of postcranial elements. The surface of the latter exhibits a characteristic shredded texture.

It has been possible to study only certain aspects of the embryonic cranial morphology so far. The postorbital has an inverted L-shape; its depressed and tapering anterior process is much longer than the blunt squamosal process. The long and tapering jugal process displays a gentle cranial curvature. The lacrimal expands proximally but without developing into a process. The frontals form an expanded, flat bony plate that is slightly wider than long. Concave arches, corresponding to the dorsal margin of the orbits, symmetrically indent the lateral margins of this plate. Remnants of a sclerotic ring are visible in one of the studied specimens. The tiny embryonic teeth are distinctly pencil-like, approximately 2 mm in length, with margins tapering toward the crown. The enamel is smooth and devoid of denticles or primary ridges. One tooth exhibited a distinct wear facet with an approximate angle of 33º with respect to the tooth's axis. A minimum of 32 teeth were counted in one specimen, although none of these teeth (or others from different specimens) were found in articulation.

Auca Mahuevo is the only fossil site that yields unquestionable evidence of the skin of non-avian dinosaur embryos (Chiappe *et al.*, 1998). Dozens of egg fragments found on erosional surfaces of egg-layer 3 contain large patches of embryonic integument, preserved both as positive casts or negative imprints. The non-overlapping scales of the embryonic skin form a variety of distinct patterns. In some specimens, three rows of large scales cross a field of smaller, tubercle-like scales of subequal size (~ 300 μm across). The central row of this stripe is formed by subrectangular scales that are twice (~ 800 μm) as large as those of the side rows (~ 400 μm) (Chiappe *et al.*, 1998). In other instances, scales form distinct patterns that are randomly distributed over the skin. These include rosette-like and flower-like scale arrangements. Because the skin is not associated with articulated portions of the skeleton, it is impossible to determine the precise location of these scale patterns on the body. In the case of the triple row of larger scales, however, it seems likely that this symmetrical design ran along the spine of the embryos.

EGG AND EMBRYONIC SYSTEMATICS

It has become evident in the last few years that the discovery of diagnosable embryonic material contained inside an egg represents the only reliable way of identifying fossil eggs (Carpenter *et al.*, 1994; Norell *et al.*, 1994). An elongate jugal process of the postorbital bone has been interpreted as a synapomorphy of Sauropoda (Gauthier, 1986). Within sauropods, the presence of teeth with wear facets and smooth enamel, devoid of denticles, are synapomorphies of Eusauropoda and Neosauropoda, respectively (Wilson and Sereno, 1998). Further, the pencil-like teeth of the Auca Mahuevo embryos are known exclusively from diplodocid and titanosaur sauropods. The vertical wear facets of the teeth of the Auca Mahuevo embryos are more similar to those of titanosaurs than to the more horizontal wear facets of diplodocid teeth (Calvo, 1994). Given these derived characters, the placement of the Auca Mahuevo embryos within neosauropod dinosaurs (the common ancestor of Diplodocus, Brachioaurus, and Saltasaurus plus all its descendants) appears well-supported (Fig. 2). The vertical aspect of the tooth wear facets further suggests their identification as titanosaur sauropods, a conclusion consistent with the abundance of titanosaur remains found in the Río Colorado Formation. Nevertheless, the Late Cretaceous sauropod Nemegtosaurus from Mongolia also exhibits pencil-like teeth with vertical wear facets (Calvo, 1994). *Nemegtosaurus* has been considered both a titanosaur (Salgado *et al.*, 1997; Wilson and Sereno, 1998) and a diplodocoid (Upchurch, 1999). If *Nemegtosaurus* proves to be an Asian titanosaur, that would lend more support to the idea that the Auca

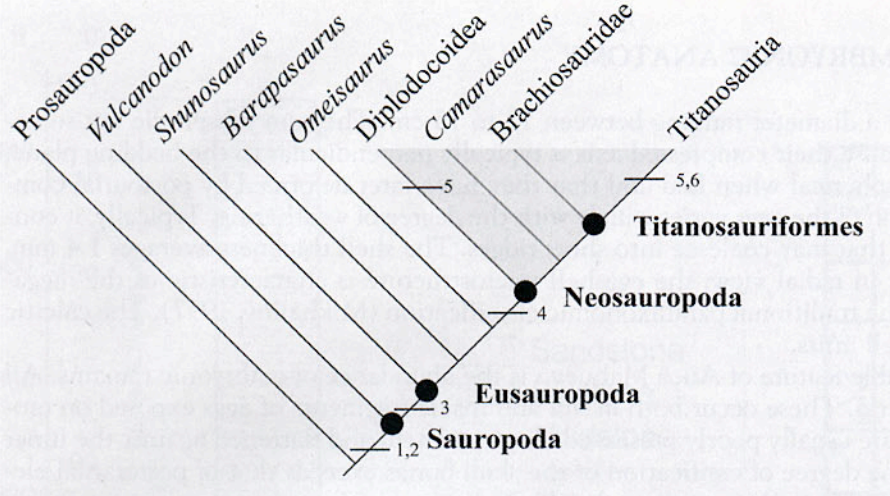

Figure 2. Phylogenetic relationships of sauropod dinosaurs (modified from Wilson and Sereno, 1998). Synapomorphies present in the Auca Mahuevo embryos are mapped on this cladogram: (1) elongate jugal process of postorbital, (2) frontals wider than long, (3) tooth wear facets, (4) tooth enamel smooth, lacking denticles, (5) pencil-like teeth,(6) vertical wear facets of teeth. These synapomorphies strongly support the inclusion of the Auca Mahuevo embryos within Neosauropoda.

Mahuevo embryos are titanosaurs. At present, however, *Nemegtosaurus* is not known from postcranial elements that would clarify its taxonomic identity. Therefore, we prefer to limit the identification of the Auca Mahuevo embryos to neosauropod dinosaurs (Fig. 2).

EGG DISTRIBUTION AT AUCA MAHUEVO

The concentration of eggs at Auca Mahuevo is so remarkable that the egg-layers can be better referred as "egg-beds," following the operational definition of Behrensmeyer (1999) for bone-beds (i.e., a minimum of 5% of bone or dental material within a particular rock layer). At a single quarry in egg-layer 3, more than 200 whole eggs were mapped in a 25-m2 area. Depths measured on individual eggs allowed construction of a three-dimensional quarry map that revealed two distinct levels of eggs, separated by several centimeters of sediment (Fig. 3). Spatial analysis showed the eggs in each level were clustered rather than randomly distributed, thus suggesting that the egg distribution represents individual egg-clutches and not fluvial transport.

Egg-clutches at Auca Mahuevo typically contain large numbers of eggs. Of the nine or more clutches identified in the quarry, seven have between 15 and 34 eggs. This number is significantly larger than the 10 eggs or less commonly reported for clutches of megaloolithid eggs (Jain, 1989; Moratalla and Powell, 1994). The large clutch size and egg density in the nesting ground (11 eggs per m2 at the quarry in egg-layer 3) would produce large quantities of eggshell fragments with each nesting season. In the low moisture, high calcium carbonate soils interpreted for this area, eggshell fragments would accumulate over time (Clayburn, 1986). However, both layers in the quarry contain predominantly whole eggs, with little or no fragmented eggshell in between the clutches. This suggests each layer represent a single egg-laying event rather than an attritional accumulation.

At a different but stratigraphically equivalent sublocality in egg-layer 3, egg-clutches exposed on a gently sloping, erosional ground surface were mapped in plan view (Fig. 1). One mapped area (Fig. 1) preserved 74 egg-clutches randomly distributed within a 1,701 m2 area. Another mapped area of this erosional surface contained 31 egg-clutches scattered at random over 486 m2. The maximum stratigraphic thickness between egg-clutches at these two sites was less than 70 cm. These mapped areas represent a small portion of the total area containing egg-clutches on this exposed, flat erosional surface of egg-layer 3. Excavation between egg-clutches at two nearby sublocalities of egg-layer 3 produced no *in situ* eggs or eggshells, again suggesting the egg-clutches are in place and not transported.

NESTING BEHAVIOR OF THE AUCA MAHUEVO SAUROPODS

Although the behavior of extinct organisms cannot be directly observed, it can be inferred when the product of an organism's conduct is preserved in the fossil record (Clark *et al.*, 1999). Because we can envision no sedimentary process operating within overbank settings that would account for the clustered distri-

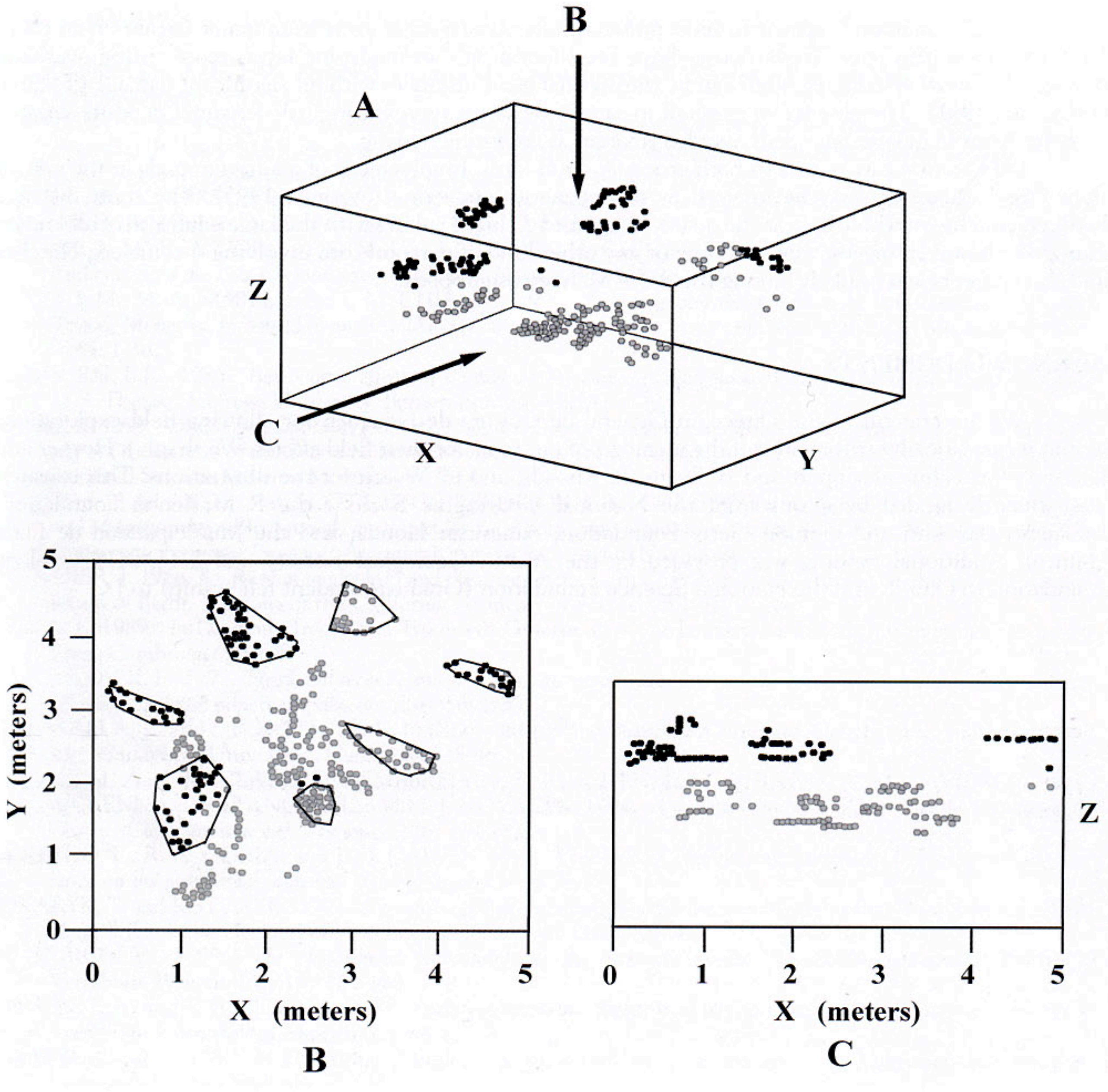

Figure 3. Map of eggs exposed at a quarry in egg-layer 3. A, three-dimensional map. B, map in plan view. C, cross-sectional view. This map was made using a decimetric grid and measuring depths of individual eggs from a fixed datum point (the bedding at this quarry is essentially flat). The total surface area excavated in this quarry is roughly 25 m2. Geographic Information Systems (GIS) spatial analysis shows a clustered distribution of the eggs (outlined in B) and two distinct levels of eggs (black and gray dots). To facilitate the visualization of these two levels in (A) and (C), a 10X vertical exaggeration has been added to the actual scales.

bution of the Auca Mahuevo eggs, the mapped eggs most likely represent *in situ* clutches: the preserved physical evidence of the sauropods' egg-laying behavior. Consequently, the distribution of eggs at Auca Mahuevo can be used to infer the following behavioral attributes for the nesting sauropods of this fossil site:

(1) Although identifying single nesting events is difficult-even in the more stratigraphically controlled section of the mapped quarry-the densely distributed egg-clutches of egg-beds 3 and 4 suggest a gregarious nesting behavior beyond any reasonable doubt. The alternative, that the hundreds of egg-clutches exposed at Auca Mahuevo were laid by solitary females, seems quite unlikely.

(2) Based on the four stratigraphically distinct layers of eggs (Fig. 1) and the two egg-levels recognized by statistical and spatial analysis within egg-bed 3 (Fig. 3), sauropods returned to this site at least five separate times to lay their eggs. However, it is not yet possible to estimate the time intervals separating these nesting occurrences.

(3) The sauropods appear to have preferentially chosen areas away from major stream channels to lay their eggs at this site. To date, eggs have been found only in mudstone layers representing overbank deposits. In fluvial systems, eggshell can be transported great distances without significant damage (Tokaryk and Storer, 1991). The absence of eggshell in sandstone layers representing paleochannel deposits suggests that the Auca Mahuevo sauropods avoided riparian areas during nesting.

(4) Parental care occurs in both crocodiles and birds. Involvement of adult sauropods in the care of their brood, therefore, may be inferred by phylogenetic bracketing (Witmer, 1995). The short distance between clutches of whole eggs at the quarry in egg-bed 3 (Fig. 3) along with the large adult size of all known sauropods, however, suggest that brooding or any other kind of parental care involving specific egg-clutches and their parents was unlikely among the Auca Mahuevo sauropods.

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