THE LATE CRETACEOUS NESTING SITE OF AUCA MAHUEVO (PATAGONIA, ARGENTINA): EGGS, NESTS, AND EMBRYOS OF TITANOSAURIAN SAUROPODS

by

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SUMMARY

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ABSTRACT

The late Cretaceous Auca Mahuevo nesting site (Neuquén Province, Argentina) has produced a large number of sauropod eggs, many of them containing the remains of embryos. Research at this site has generated important information about the development of the embryos, the morphology and eggshell microstructure of the eggs, and the reproductive behavior of sauropod dinosaurs. Cranial features present in the embryos have allowed their identification as those of titanosaurian sauropods. Differences in the texture of the sediments that contain some of the egg-clutches have illuminated their nest architecture. Microstructural studies of eggshells have expanded our knowledge of their variability and the incidence of pathologies within a reproductive titanosaurian population. Maps showing the spatial distribution of eggs and clutches, the stratigraphic distribution of the egg-beds, and the sedimentological context in which they are contained, have provided the basis for several inferences about the nesting behavior of these dinosaurs.

RESUME

Le site de nidification du Crétacé supérieur (Province de Neuquén, Argentine) a livré un grand nombre d'oeufs de sauropodes, beaucoup d'entre eux renfermant des restes d'embryons. Les recherches sur ce site ont généré d'importantes informations sur le développement des embryons, la morphologie et la microstructure des coquilles d'oeufs, et le comportement reproductif des dinosaures sauropodes. Les caractères crâniens présents chez les embryons ont permis leur identification comme ceux de sauropodes titanosauriens. Les différences dans la texture des sédiments qui contiennent certaines pontes ont apporté des éclaicissements sur l'architecture des nids. Les études microstructurales des coquilles d'oeufs ont élargi nos connaissances sur leur variabilité et sur l'incidence des pathologies au sein d'une population reproductrice de titanosaures. Des cartes montrant la distribution spatiale des oeufs et des pontes, la distribution stratigraphique dse niveaux à oeufs et le contexte sédimentologique qui les renferme ont apporté les bases de plusieurs inférences sur le comportement de nidification de ces dinosaures.

INTRODUCTION

Since its discovery in 1997, the late Cretaceous (early Campanian; Dingus *et al.*, 2000) nesting site of Auca Mahuevo and its adjacent localities (Barreales Norte and Barreales Escondido) have continued to illuminate aspects of the developmental biology of sauropods. The discovery of thousands of clutches of megaloolithid-type eggs, many preserving *in ovo* remains of embryos (Chiappe *et al.*, 1998, 2001), has furnished unprecedented information on the pre-hatching ontogeny (Chiappe *et al.*, 2001; Salgado *et al.*, in press), nesting architecture (Chiappe *et al.*, in press), egg morphology (Grellet-Tinner *et al.*, in press) and malformation (Jackson *et al.*, in press), and reproductive behavior (Chiappe *et al.*, 2000) of these dinosaurs. Cranial characters of the embryos have permitted the identification of the eggs as of those of titanosaurians (Chiappe *et al.*, 1998, 2001) and a series of discoveries of adult remains (Coria *et al.*, 2002; Coria and Arcucci, in press) have provided a clearer picture of the faunal composition of this nesting site. In this paper, we briefly summarize the major developments of this research program and discuss their significance for understanding the reproductive biology of these colossal dinosaurs.

Auca Mahuevo lies roughly 120 km northwest of Neuquén City, Argentina (Fig. 1). Its adjacent localities, Barreales Norte and Barreales Escondido, are approximately 15 km and 22 km to the south, respectively. All these localities occur within the red beds of the Anacleto Formation, which age is estimated to be between 83.5 and 79.5 million years old (Dingus *et al.*, 2000), in the early Campanian.

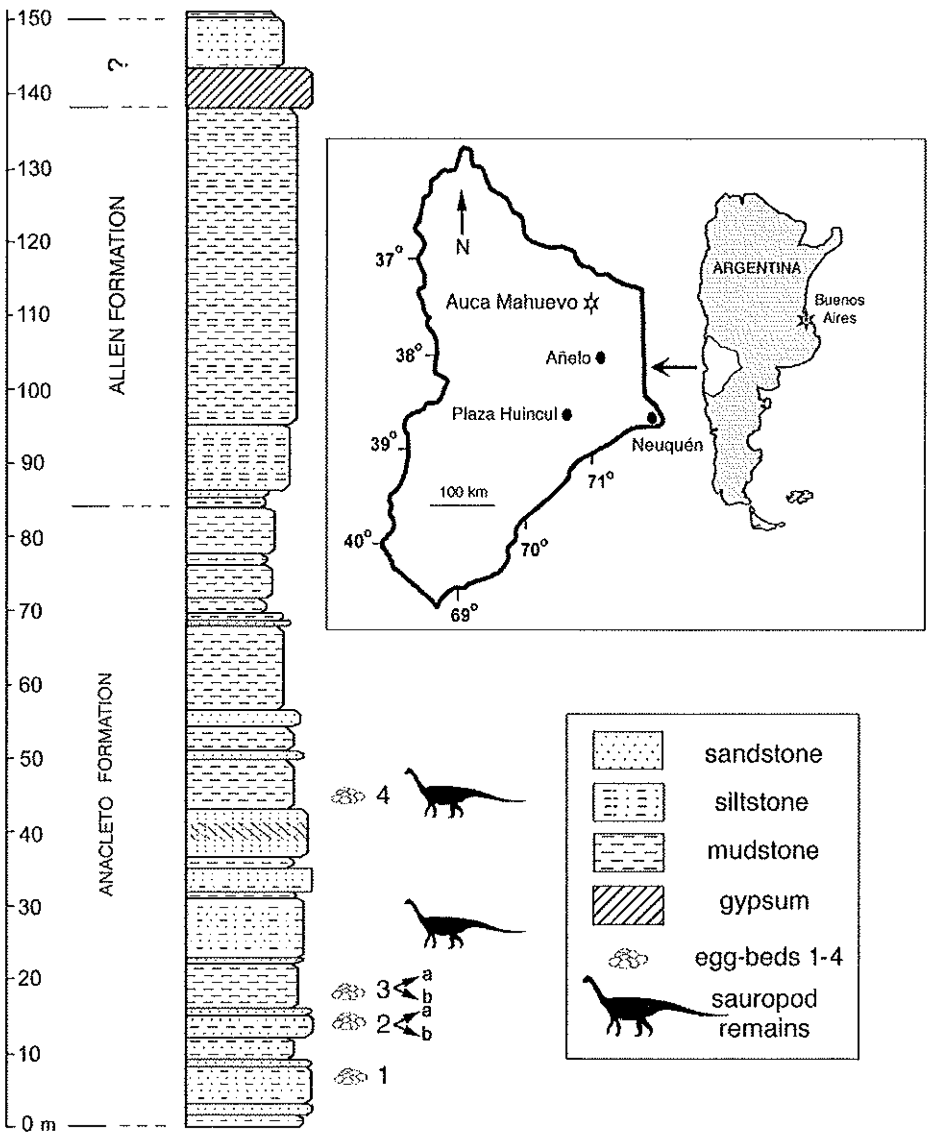

Figure 1.— Geographic location (inset map highlights the Argentine Province of Neuquén) and stratigraphic section of the Late Cretaceous locality of Auca Mahuevo.

Six different egg-beds, some of which are laterally continuous for several kilometers, are contained within the 85-meter-thick stratigraphic section of Auca Mahuevo (Fig. 1). These egg-beds occur in uniform mudstones representing overbank deposits on an alluvial plain (Dingus *et al.*, 2000). Clutches from egg-bed 3 occur in paleovertisols, a type of soil common in areas that experience wet-dry climatic cycles under semi-arid to sub-humid conditions. A network of slickensides affecting the integrity of the eggs and egg-clutches suggests these were laid prior to the complete formation of the soil.

Several remains of adult dinosaurs have also been collected from the Auca Mahuevo section, including titanosaurian sauropods and theropods. Among the latter is the nearly complete skeleton of *Aucasaurus garridoi* (Coria *et al.*, 2002), isolated teeth comparable in morphology with those of dromeosaurids, and a much larger form, which size approaches that of carcharodontosaurids (Coria and Arcucci, in press).

EGG MORPHOLOGY, CLUTCH DISTRIBUTION, AND NEST ARCHITECTURE

The morphological variation (size, ornamentation, shape, and eggshell microstructure) of the eggs from these localities is comparable to that of eggs containing *in ovo* remains of titanosaurians and unlike some other late Cretaceous nesting sites with megaloolithid-type eggs (e.g., Vianey-Liaud and Crochet, 1993; Vianey-Liaud *et al.*, 2003; Garcia *et al.*, 2003), no definitive evidence of more than one dinosaur egg-type has yet been found. This and the fact that the *in ovo* embryos are indistinguishable from each other (Chiappe *et al.*, 2001), provides evidence for only a single titanosaurian species nesting in this area.

The eggs are subspherical, approximately 12-15 cm in diameter depending on their degree of post-burial compaction, and with a surface ornamentation consisting of rounded tubercles. The eggshell consists of a single structural layer of calcite (Chiappe *et al.*, 1998) crossed by a network of vertical and horizontal pore canals intersecting at base of the eggshell units (Grellet-Tinner *et al.*, in press). This type of eggshell is indistinguishable from that of *Megaloolithus patagonicus* (Calvo *et al.*, 1997), an oospecies described from the Anacleto Formation at Neuquén City that was recently regarded as a possible junior synonym of *Megaloolithus jabalpurensis* from the late Cretaceous (Maastrichtian) of India (Vianey-Liaud *et al.*, 2003).

Regardless the possible synonymy of these two oospecies, *Megaloolithus patagonicus* is clearly a titanosaurian. This evidence, however, should not be interpreted as indicative that all megaloolithid-type eggs were laid by titanosaurian sauropods. In fact, the discovery of neonate remains of the hadrosaurid *Telmatosaurus transylvanicus* in the proximity of clutches of megaloolithid-type eggs from the late Cretaceous of Romania (Grigorescu *et al.*, 1994; 2003) has hinted at the possibility of this egg category (i.e., Megaloolithidae) being paraphyletic, highlighting once again the problematization of the traditional egg parataxonomy (e.g., Grellet-Tinner, 2000; Zelenitsky *et al.*, 2002; Zelenitsky and Vianey-Liaud, 2003). Nonetheless, the hypothesis that the hadrosaurid *Telmatosaurus* laid eggs of megaloolithid-type microstructure needs to be confirmed because neonates of this taxon were not found *in ovo*.

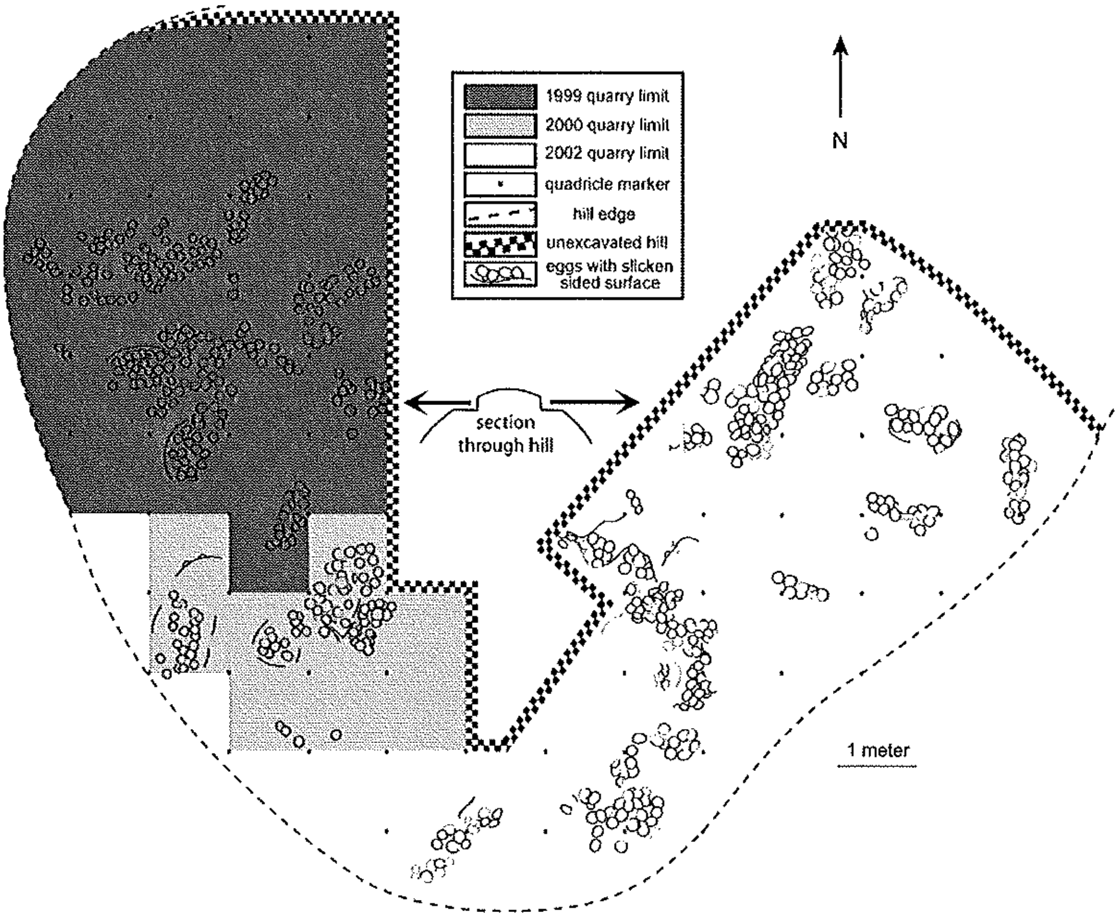

Figure 2.— Map in plan view of eggs exposed at a quarry in Auca Mahuevo's egg-bed 3. The total surface area excavated in this quarry is approximately 50 m^2. At this quarry, postburial disturbance due to soil displacement has affected the original composition of most egg-clutches.

The *in situ* clutches from Auca Mahuevo range in size from 15 to nearly 40 eggs, staked one on top of the other and lacking any spatial arrangement. The number of eggs within a clutch is typically much greater than that of other megaloolithid-type eggs (e.g., Moratalla and Powell, 1994; Peitz, 2000; Mohabey, 2001; Garcia *et al*., 2003). More than 500 whole eggs were quarried over a 50 m^2 surface of egg-bed 3 during the 1999, 2000, and 2002 field seasons. The distribution of the eggs at this quarry and on several erosional surfaces of egg-beds 2, 3, and 4 reveals a remarkable concentration of egg-clutches. An erosional surface of egg-bed 3 contained approximately 4-6 egg-clutches/100 m^2 (Chiappe *et al*., 2000). The careful inspection of many of these egg-clutches indicated that the incidence of egg malformation was very low. A survey of nearly 400 *in situ* clutches in egg-beds 2 and 3 revealed only six clutches containing abnormal, multilayered eggs (Jackson *et al.*, in press).

Several egg-clutches laid on the surface of an abandoned channel are contained within egg-bed 4. These egg-clutches provide the only reliable evidence of nest architecture in sauropod dinosaurs (Chiappe *et al.*, in press) (Table 1). These egg-clutches are contained in large, rimmed depressions in sandstone, although the eggs are entombed by mudstone. These clutches are thus preserved at the contact between sandstone and overlying mudstone. The structureless rim surrounding each of these egg-filled depressions has been interpreted as the debris produced during the excavation of the nest, and the mudstone encasing the eggs as the result of flooding (Chiappe *et al.*, in press). The fact that in none of these depressions are the eggs entombed by sandstone indicates that the eggs were laid on the surface of the substrate.

(1) Depression truncating stratification within the host substrate.

(2) Significant portions of eggs and (or) articulated juvenile skeletons with no evidence of transport within the depression.

(3) Elevated ridge of massive sediment surrounding the depression containing the eggs and (or) articulated juvenile skeletons that is lithologically different from adjacent and overlying sediment.

(4) Sediment within the depression differing in grain size, shape, sorting, fabric, sedimentary structures, and (or) mineralogic and chemical composition from the host substrate.

Table 1.— Criteria for recognizing excavated dinosaur nest structures; the criteria are listed in order of decreasing significance (Chiappe *et al.*, in press).

Although it is reasonable to infer that such a nest architecture is representative of the nesting behavior of the entire reproductive population, egg-clutches preserved at Auca Mahuevo typically lack any evidence of their surrounding nest structure. Channel sands comparable to those containing the nest structures of egg-bed 4 are not preserved in any other egg-bed and the vast majority of the Auca Mahuevo egg-clutches are preserved entirely in mudstone.

EMBRYONIC REMAINS

Dozens of *in ovo* embryos—skeletal remains and skin impressions—have been collected from egg-bed 3. No other egg-bed in Auca Mahuevo has produced definitive evidence of embryos but a handful of these have been found at Barreales Norte and Barreales Escondido. Embryos from all these localities constitute the only known *in ovo* remains of sauropods (Table 2). In these embryos, the skull exhibits a greater degree of ossification than the appendicular skeleton (no identifiable vertebral elements have ever been discovered), although it is difficult to determine how close they were from hatching.

Several cranial synapomorphies support the identification of these embryos as neosauropods and within these dinosaurs, as titanosaurians (Chiappe *et al.*, 1998, 2001; Salgado *et al.*, in press). Some of the neosauropod synapomorphies include the absence of denticles in the crowns of the teeth and the presence of a postorbital bar that is broader transversely than rostrocaudally. Within neosauropods, the embryos exhibit the prominent notch of the ventral margin of the snout, the low rostral portion of the dentary, very broad skull roof, and large mandibular fenestra of some late Cretaceous titanosaurians (Chiappe *et al.*, 2001). Despite the fact that titanosaurian skull material is extremely rare, the pencil-like shape of the embryonic teeth supports their placement within a subgroup of titanosaurians that excludes the most primitively toothed *Malawisaurus dixeyi* (Jacobs *et al.*, 1993). However, this interpretation becomes more complex in light of recent studies arguing for the multiple origin of this dental specialization within titanosaurians (Curry-Rogers and Forster, 2001).

Ornithischia
- Ornithopoda
  - Hadrosauridae
    - *Hypacrosaurus*, Late Cretaceous, USA
    - *Maiasaura*, Late Cretaceous, USA

Saurischia
- Theropoda
  - Maniraptora
  - Therizinosauridae indet., Late Cretaceous, China
  - Oviraptoridae indet., Late Cretaceous, Mongolia
  - Oviraptoridae
    - *Citipati*, Late Cretaceous, Mongolia
  - Troodontidae
    - *Troodon*, Late Cretaceous, Montana
    - *Byronosaurus*, Late Cretaceous, Mongolia
- Sauropodomorpha
  - Prosauropoda
    - Plateosauridae
      - *Mussaurus*, Late Triassic, Argentina
      - *Massospondylus*, Late Triassic, South Africa
  - Sauropoda
    - Titanosauria indet., Late Cretaceous, Argentina

Table 2.— Published occurrences of *in ovo* embryos and clutch-neonate associations of non-avian dinosaurs.

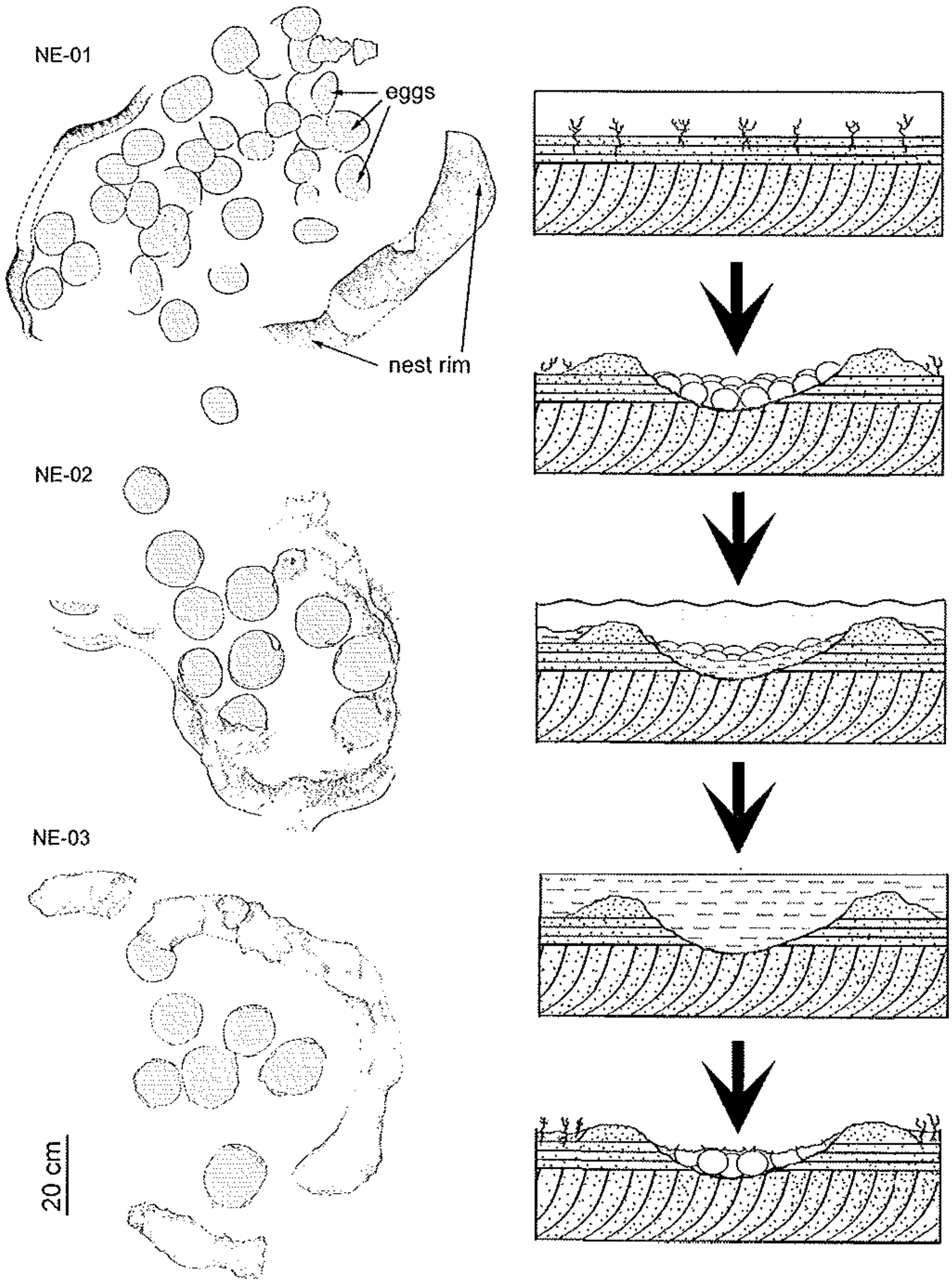

Figure 3.— Titanosaurian nest traces from the Late Cretaceous of Auca Mahuevo and diagrams depicting the interpreted sequence of events leading to their preservation.

Despite the limited cranial information of adult titanosaurians, comparisons with the embryos suggest that dramatic transformations occurred during the early ontogeny of these dinosaurs. The frontals and parietals greatly reduced their size and they became restricted to the caudal region of the orbit. The latter became constricted ventrally and developed an inverted tear-like shape. The rostrum became considerably longer and the enlarged maxilla developed a connection with the quadratojugal that excluded the jugal from the skull's ventral border. Furthermore, the external nares grew in size and migrated backwards, to be emplaced above the orbit.

NESTING BEHAVIOR

The *in situ* eggs of Auca Mahuevo and adjacent localities are the only known definitive evidence of the egg-laying behavior of titanosaurian sauropods. The research conducted at these sites allows several behavioral inferences. The remarkable concentration of egg-clutches contained within a relatively narrow stratigraphic horizon suggests a gregarious nesting behavior. The six distinct egg-beds of identical morphology supports site fidelity; one sauropod species appears to have nested at this site at least six separate times. Each egg-bed could preserve eggs laid during more than one closely occurring nesting season but stratigraphic resolution to discriminate among these possible nesting events is lacking. The well-preserved nest traces indicate that contrary to most modern reptiles, titanosaurians laid eggs in excavated depressions without burying them. Finally, although nest attendance may be inferred by phylogenetic bracketing (all living archosaurs attend their nests), the large size of adult titanosaurians and the proximity between egg-clutches suggests little or no parental care, an inference consistent with the absence of evidence of trampling.

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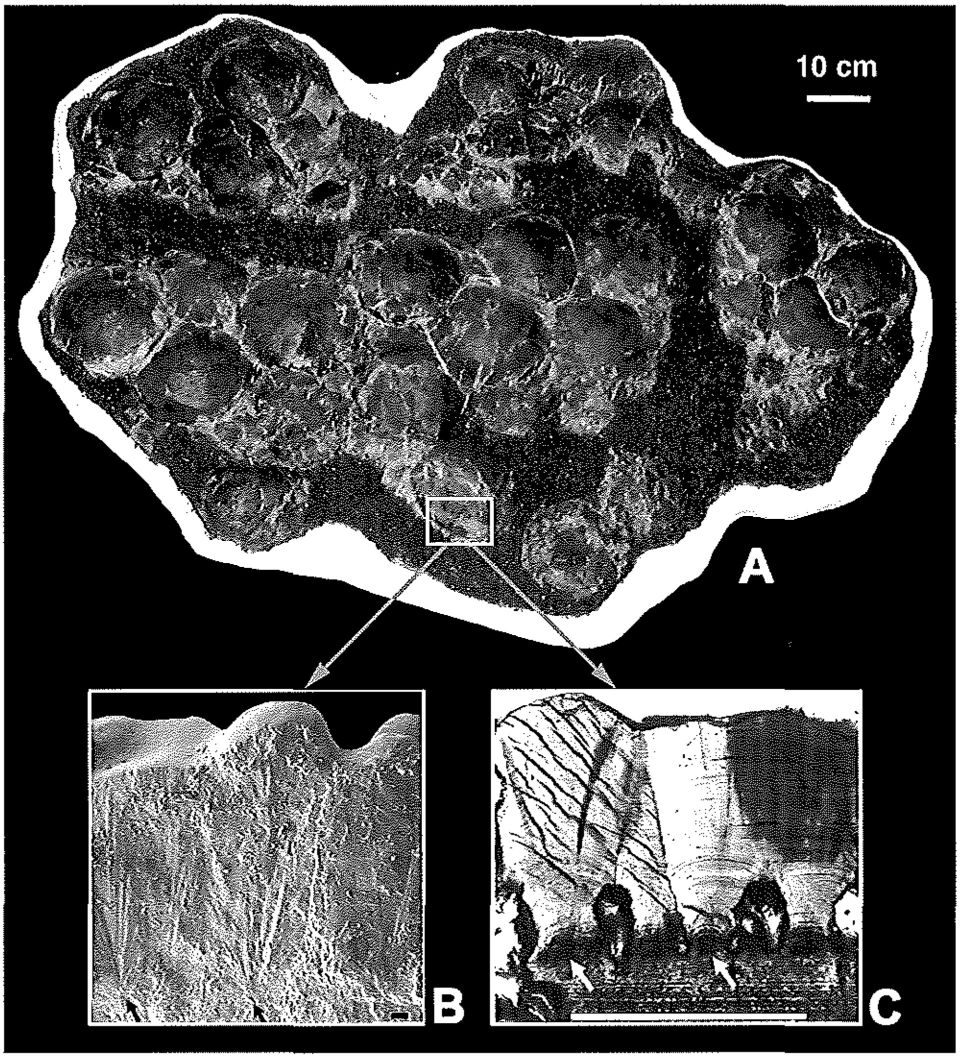
PLATE 1

Figure 1.— A, Auca Mahuevo clutch (Museo Carmen Funes, Plaza Huicul, Argentina: MCF-PVPH-258; quarry of egg-bed 3) containing nearly 40 eggs. B, C, SEM and thin section of the Auca Mahuevo eggshell. Arrows point at the position of organic cores. Scale bars in B and C equal 10 μm and 1 mm, respectively.

Figure 2.— Embryonic titanosaurian skulls from Auca Mahuevo (egg-bed 3) in left lateral view (photograph and interpretive drawing). A, MCF-PVPH-272. B, MCF-PVPH-263. Abbreviations: af: antorbital fenestra, an: angular, d: dentary, f: frontal, itf: infratemporal fenestra, j: jugal, la: lacrimal, m: maxilla, mf: mandibular fenestra, orb: orbit, p: parietal, pmx: premaxilla, po: postorbital, prf: prefrontal, pt: pterygoid, q: quadrate, qj: quadratojugal, scp: scleral plates, sq: squamosal, stf: supratemporal fenestra.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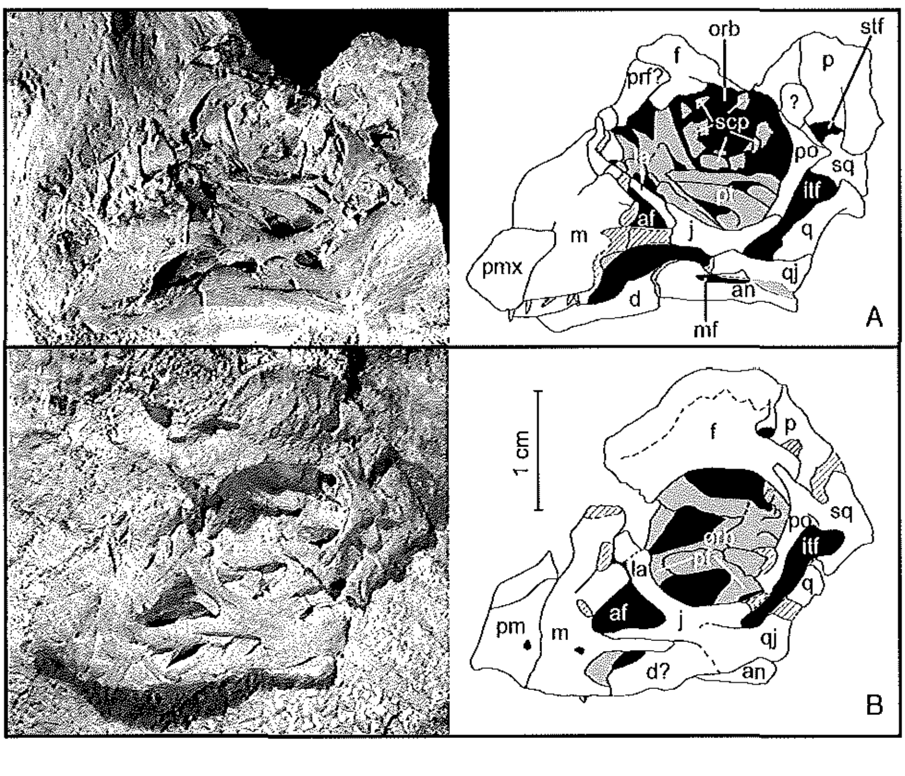
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