Nest Structure for Sauropods: Sedimentary Criteria for Recognition of Dinosaur Nesting Traces

LUIS M. CHIAPPE

Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007; Email: chiappe@nhm.org

JAMES G. SCHMITT and FRANKIE D. JACKSON

Department of Earth Sciences, Montana State University, Bozeman MT 59717

ALBERTO GARRIDO

Museo Municipal Carmen Funes, Plaza Huincul 8318, Neuquén, Argentina

LOWELL DINGUS

Infoquest Foundation, 160 Cabrini Blvd. # 48, New York, NY 10033

GERALD GRELLET-TINNER

Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007

PALAIOS, 2004, V. 19, p. 89–95

Six egg-filled depressions discovered in the Upper Cretaceous Anacleto Formation (Campanian) of Patagonia, Argentina, and interpreted as dinosaur nests, provide the only known evidence of titanosaurid sauropod nest construction. These nest trace fossils show truncation of sedimentary structures as well as differences in texture between the host substrate and in-filling sediment. Titanosaurid sauropods excavated and laid eggs in open nests rather than burying clutches in sediment. In addition, this paper establishes criteria for definitive recognition of excavated nests in the stratigraphic record.

INTRODUCTION

Despite the relative abundance of dinosaur eggs in the fossil record (Carpenter et al., 1994; Carpenter, 1999), trace-fossil evidence of dinosaur nest construction is extremely rare. The existence of a nest is typically inferred by the presence of an egg clutch and usually it is not accompanied by physical evidence of nest architecture (Erben et al., 1979; Kerourio, 1981; Coombs 1989; Sabath, 1991; Powell, 1992; Cousin et al., 1994; Mikhailov et al., 1994; Mohabey, 1996). Additionally, specific properties of the eggs themselves, such as ornamentation and pore system, are sometimes used to infer an underground or surface mode of nest construction (Seymour, 1980; Combs 1989; Sabath 1991).

While fossil egg clutches or remains of juveniles may sometimes provide circumstantial evidence of dinosaur nesting behavior, only preservation of a nest structure renders definitive evidence of nest construction. Examples of physical sedimentologic evidence previously used to infer nest construction include zones of contrasting sediment color surrounding eggs and remains of juveniles (Horner and Makela, 1979), or color attributes of egg-bearing horizons (López-Martínez et al., 2000). Given the many ways in which color is produced during pedogenesis and diagenesis, however, the use of color criteria for inferring nest structure, even in the presence of eggs and remains of juveniles, is unreliable. Primary lithologic attributes of the host sediment are rarely used for identifying fossil nest architecture. In fact, only one example of nest architecture, the rimmed nest of the Late Cretaceous theropod *Troodon*, has been described using these criteria (Varricchio et al., 1997).

This paper uses detailed analysis of lithologic characteristics and sedimentary structures to document the only known trace fossils produced by the nesting behavior of sauropod dinosaurs. In addition, it establishes criteria for recognition of excavated dinosaur nests in the fossil record. This study involves strata of the Upper Cretaceous nesting site of Auca Mahuevo, Patagonia, Argentina, where thousands of titanosaurid sauropod egg clutches, some containing exquisitely preserved fetal bone and integument, are preserved (Chiappe et al., 1998, 2000, 2001). This research also documents that titanosaurid sauropod dinosaurs did not bury their eggs in the substrate, rather, they laid them in excavated depressions that remained open on an alluvial floodplain.

STRATIGRAPHIC CONTEXT

Sauropod eggs and embryos from Auca Mahuevo occur within the Anacleto Formation of the Neuquén Group (Ramos, 1981; Ardolino and Franchi, 1996; Chiappe et al., 1998, 2000; Dingus et al., 2000). At this site, egg clutches are present within at least four stratigraphic layers in an 85-m-thick sequence of sandstones, siltstones, and mudstones. The upper two egg-bearing layers, 3 and 4, are traceable laterally for several kilometers (Chiappe et al., 2000) (Fig. 1). Paleomagnetic data suggest that egg-bearing layers 1–3 occur in an interval of reverse polarity tentatively correlated with C33R of the early to middle Campanian (Dingus et al., 2000).

Clutches previously excavated at Auca Mahuevo typically contain 15 to 35 eggs that range in diameter from 13 to 15 cm, stacked in multiple layers with no particular arrangement in silty, reddish-brown, mottled mudstone with numerous slickensided surfaces indicative of paleosol development (Chiappe et al., 2000). In some places in the egg-bearing intervals, thin channel and crevasse-splay sandstone lenses laterally interfinger with the mudstone. Therefore, egg beds are laterally continuous, but vary from mudstone to sandstone in substrate composition.

Egg bed 4 contains hundreds of clutches preserved primarily in mudstone. No indication of nest structure is discernible due to the homogeneous character of the mudstone surrounding most of the clutches. This egg-bearing layer, however, also contains six partial clutches (NE-01 through NE-06) preserved in sandstone that are the focus of this study. Five clutches occur less than one meter below a stratum containing platter-shaped, carbonate-filled depressions interpreted as sauropod footprints (Loope et al., 2000). The lateral continuity of this footprint layer (Fig. 1: Ftprint layer A) provides an index horizon for es-

0883-1351/04/0019-0089/$3.00

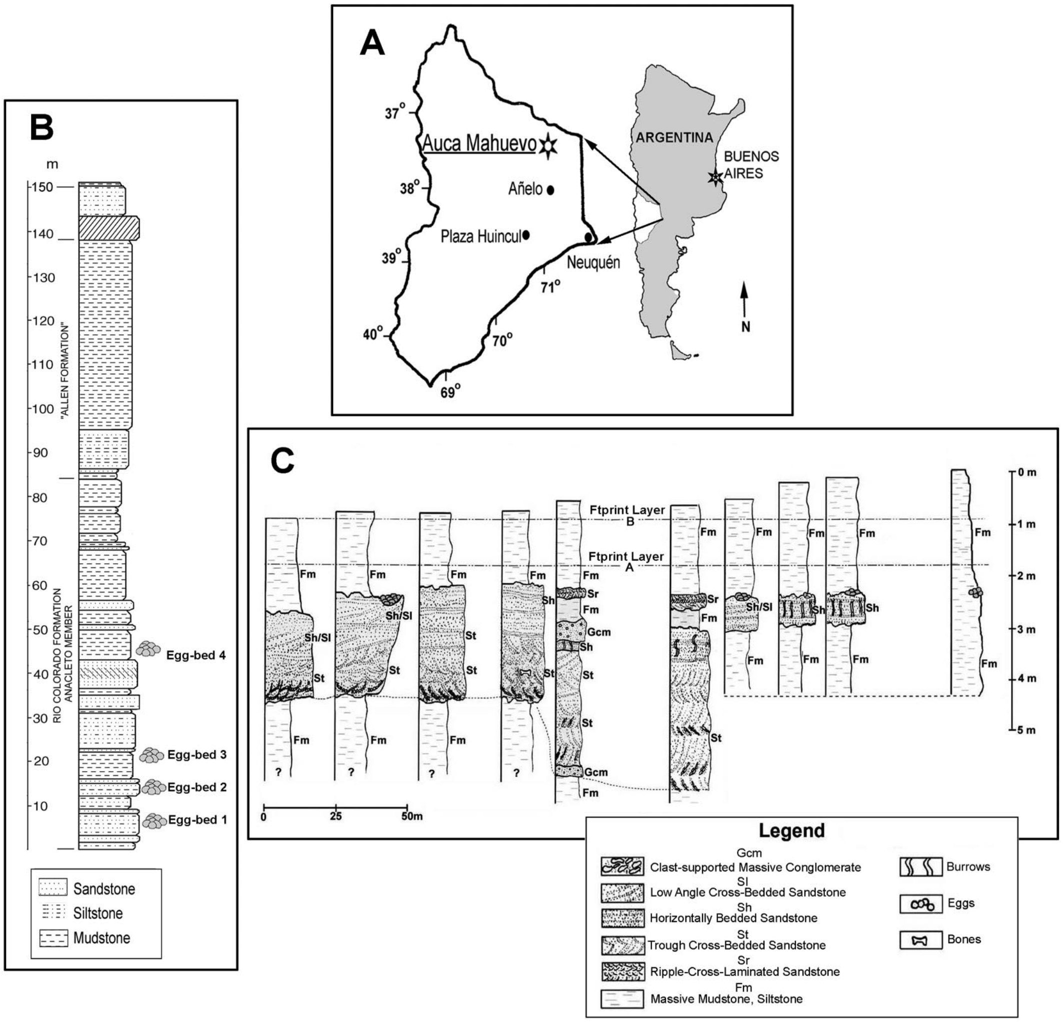


FIGURE 1—Schematic map and stratigraphic sections of the study area. (A) Regional map. (B) Stratigraphic section of Auca Mahuevo highlighting the four recognized egg beds. (C) Stratigraphic section showing locations of NE-01 to NE-05 (NE-06 was discovered in stratigraphically equivalent beds approximately 2 km from these specimens).

tablishing that the five nests (NE-01 to NE-05) all were constructed at the upper surface of a sandstone body (Fig. 1). Another partial clutch, NE-06, located approximately 2 km from the other clutches, also occurs in a sandstone unit within egg bed 4, which is traceable between the two areas.

DESCRIPTION OF THE NESTS

Clutches of eggs are present in sub-circular to sub-elliptical to kidney-shaped depressions (Figs. 2, 3) in well-cemented, medium- to fine-grained, pinkish-gray to gray sandstone. All of the depressions truncate primary stratification of the host substrate and are encircled by a rim of massive sandstone. Red mudstone laps onto the exterior rim surface, while texturally similar green mottled mudstone surrounds the eggs and typically fills the interior of most depressions. The depressions vary in size from approximately 100 to 140 cm across their maximum plan-view axes (Table 1), with depths from approximately 10 to 18 cm. These structures contain randomly distributed eggs that vary in condition from crushed to minimally deformed. In all six locations, sediment that fills the depressions and surrounds the eggs differed from the substrate in texture and/or organic content (Table 1). The sedimentary structure of the host sandstone is best discerned in the four depressions (NE-01, NE-03, NE-05, and NE-06) described below.

NE-01

The lowermost portions of the depression wall contain an approximately 11-cm-thick, fine- to medium-grained, ripple cross-laminated basal sandstone overlain by a 4-cm-thick, medium-grained, trough cross-bedded sandstone. An abrupt contact separates these two cross-stratified units (~15 cm thick) from an overlying 3–8 cm-thick massive sandstone that forms a rim around the depression's periphery. No significant grain size difference is discernible between the stratified and massive units. The maximum distance from the upper surface of the sandstone unit to the base of the depression is approximately 18 cm. Reddish brown calcareous mudstone exterior to the sandstone rim shows textural attributes similar to the

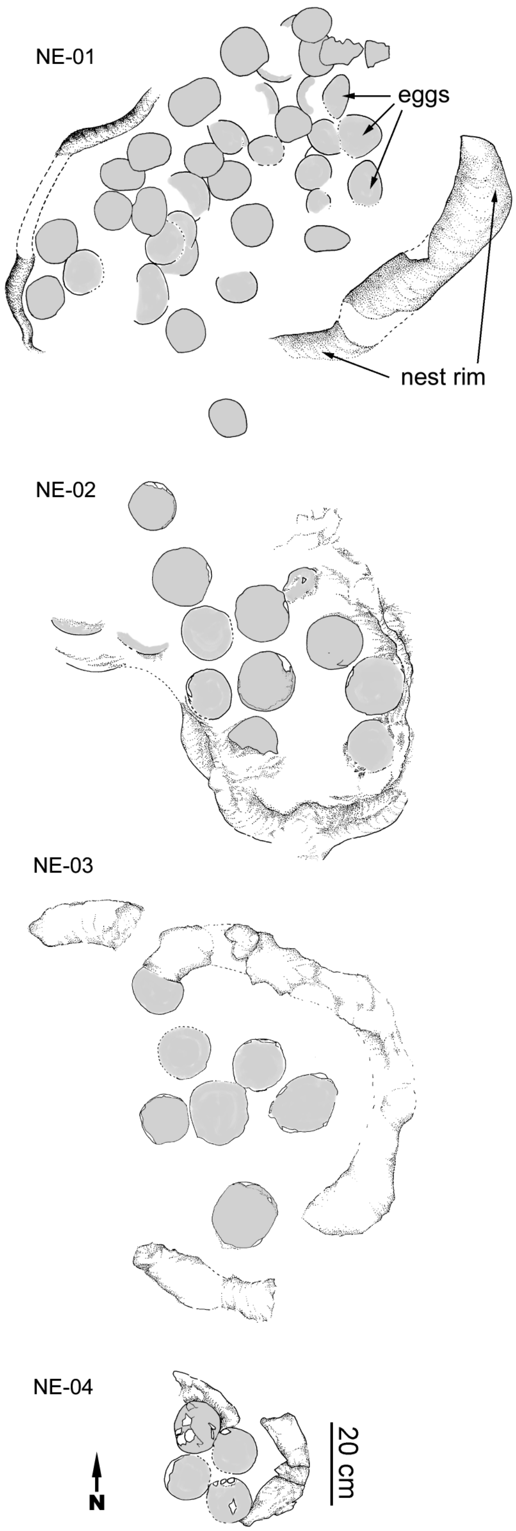


FIGURE 2—Field sketches of depressions NE-01 through NE-04 showing arrangement of eggs (gray) with respect to surrounding massive sandstone rims (shaded).

green mudstone that fills the depression. Removal of the eggs and mudstone from the depression revealed the external mold of several eggs pressed into the underlying sandstone.

NE-03

The depression occurs in a 10-cm-thick trough cross-bedded, medium- to fine-grained, well-cemented sandstone overlain by an 8-cm-thick interval of horizontally bedded, poorly cemented sandstone of similar textural properties and mineral composition. A distinct but irregular contact separates these units from massive, well-cemented sandstone (Fig. 4) that forms a sloping ridge around the depression. The outer surface of this ridge commonly slopes away from the depression; the inner surface slopes toward the depression center. Green mudstone fills the interstitial space between the eggs in the depression and becomes sandier toward the outer perimeter of the clutch. Removal of seven eggs from the depression revealed uncrushed lower hemispheres, each representing approximately one half of the original egg.

NE-05

The depression truncates a sequence composed of fine- to medium-grained, horizontally bedded sandstone, capped by a massive sandstone with scattered green mudstone intraclasts (<3 mm). The contact between the two units is distinct but irregular and, with the exception of the mudstone intraclasts, the units exhibit comparable textural properties and mineralogical compositions. The mudstone fill contains small (<5 mm), white, well-rounded intraformational mudstone clasts and possesses a strong petroliferous odor not present in the surrounding strata. The overlying massive sandstone rim encircles nearly the entire depression, but more closely outlines the perimeter of the eggs on the north side of the clutch (Fig. 3). The rim surrounding the eggs varies from 4–18 cm in width.

NE-06

The depression occurs in two stratified layers that are separated by a gradational contact. The basal layer is comprised of a poorly cemented fine- to medium-grained, faintly trough cross-bedded gray to greenish-gray sandstone with small (< 3 mm) mudstone intraclasts aligned along the foresets. This friable sandstone unit is higher in clay content and plant material than the overlying calcite-cemented, fine- to medium-grained, reddish-gray trough cross-bedded sandstone of similar mineralogy. An abrupt contact separates these stratified units from an overlying massive, sandstone rim of similar composition (Fig. 3). Aggregate thickness of the three units is 30 to 35 cm.

INTERPRETATION

These six egg-filled depressions are interpreted as nests (Fig. 5). The eggs contained in these depressions are identical in shape, size, ornamentation, and eggshell microstructure to other eggs from the same locality that contain *in ovo* fetal remains of titanosaurid sauropods (Chiappe et

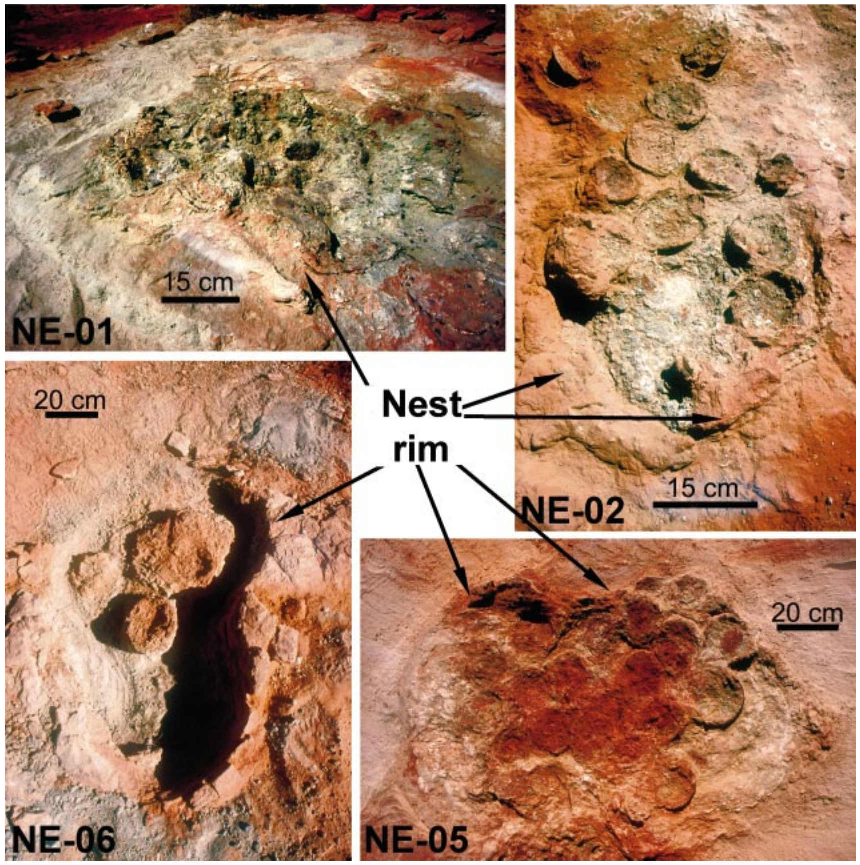


FIGURE 3—Field photographs of depressions NE-01, NE-02, NE-05, and NE-06 showing egg clutches surrounded by elevated sandstone rims. Molds of the two most complete nests (NE-01 and NE-02) were made in the field and casts are housed at the Museo Carmen Funes (Plaza Huincul, Argentina) and Natural History Museum of Los Angeles County (LACM 7324/148396).

al., 2001). These similarities support referral of the nests to the Titanosauridae.

Sedimentological evidence indicates that nesting depressions NE-01 to NE-05 were excavated into the upper surface of a channel-sand body. This lenticular sandstone fines upward from coarse- to medium-grained sand and contains a basal intraformational mudstone rip-up lag that rests upon a scoured basal contact. Such a sandstone unit contains trough cross-bedding and ripple cross-lamination in its lower and upper portions, respectively (Fig. 5). These features suggest deposition in a relatively shallow (<3 m deep), low-energy (lower flow regime) sand-bed channel with point bar development that was abandoned relatively quickly. Nest excavation occurred on top of this sand body after channel abandonment.

Nest NE-06 was excavated in a crevasse-splay sand lobe

TABLE 1—Egg and nest characteristics. Dimensions in centimeters.

	EGGS					NESTS		
	Number	Size	Arrangement	Layers	Condition	Size	Substrate	Fill
NE-01	35	14–15	random	2	possibly unhatched	90 × 109	channel sandstone	green fissile mudstone, sandier towards periphery
NE-02	13	14–15	random	1	?	60 × 100	channel sandstone	green fissile mudstone, sandier towards periphery
NE-03	7	15	random	1	unhatched	100 × 100	channel sandstone	green fissile mudstone, sandier towards periphery
NE-04	4	?	random	1	?	?	channel sandstone	green fissile mudstone, sandier towards periphery
NE-05	22	14–16	random	2	possibly hatched	94 × 140	channel sandstone	green clayey sandstone
NE-06	4	?	random	2	?	75 × 125	crevasse-splay sandstone	organic-rich sandstone

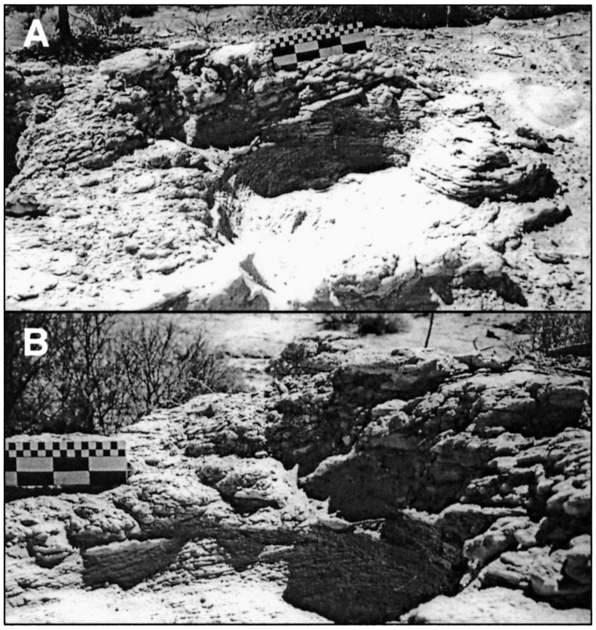
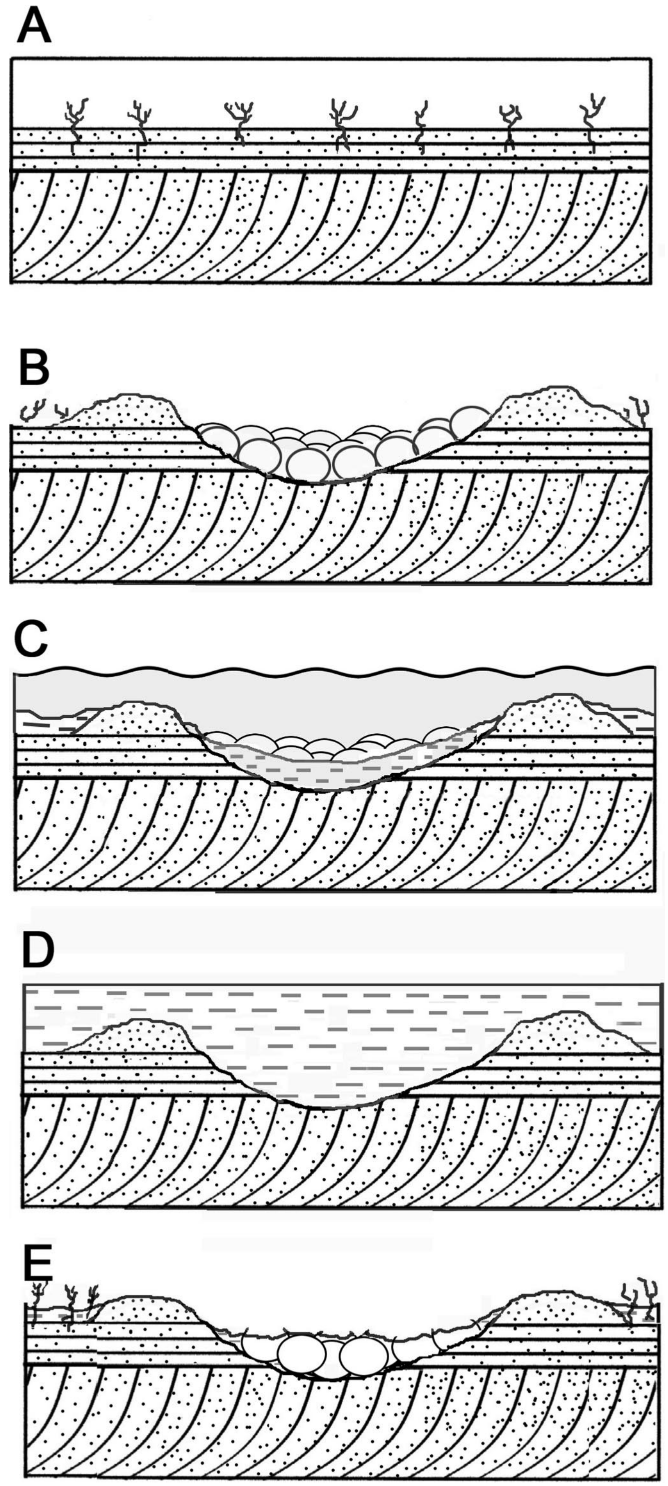


FIGURE 4—Field photograph of vertical strata exposed in the wall of NE-03 after removal of egg-clutch. Note stratification in the host substrate and absence of sedimentary structures in the elevated ridge. (A) Scale rests upon elevated massive sandstone rim; note stratification in upper right portion of wall of circular depression. (B) Scale rests upon massive sandstone rim; note contact between trough cross-bedded sandstone and overlying massive sandstone exposed just beneath the scale.

(Fig. 5). This thin (< 0.6 m) sand lobe can be traced continuously more than 50 m laterally away from the thicker channel sandstone described above. It contains coarsening-upward (fine- to medium-grained sand) ripple cross-laminated, horizontally stratified, and massive sandstone facies with abundant vertical Skolithos-like burrows. These features, combined with the decrease in sand-lobe thickness away from the thicker channel sandstone, suggest deposition of sand on the adjacent floodplain in association with breaching of channel levees during flood events.

Truncation of primary stratification observed in both the channel-sand and crevasse-splay deposits occurred during nest excavation by the adult titanosaurid. Material excavated from the nest formed the massive sandstone rim that surrounds portions of all six depressions. After the eggs were laid, the upper surface of the substrate was then buried by suspension settling of fine-grained muddy sediments resulting from one or more flooding events on the alluvial plain. Differential weathering of the mudstone and the well-cemented, more resistant sandstone facilitates recognition of the rim as a topographic high surrounding the depressions. These lithologic relations show that the egg clutches were deposited in open nests and the adults did not bury the eggs within sediment.



→

FIGURE 5 Schematic diagram depicting interpreted sequence of events leading to preservation of sauropod nesting traces. (A) Undisturbed sandstone unit (channel sandstone or crevasse-splay) containing internal stratification. (B) Undisturbed sandstone unit is truncated by excavation of a depression by an adult titanosaurid dinosaur, with concomitant formation of a massive rim composed of removed sediment, followed by filling of the depression with eggs. (C) Subsequent overbank flooding results in progressive deposition of muddy sediment by vertical accretion processes that fills the depression and surrounds the eggs. (D) Entire underlying sandstone unit is buried by muddy sediments. (E) Subsequent exposure and outcrop weathering results in differential erosion of overlying mudstone layer, exhuming the elevated sandstone rims and removing upper portions of the egg clutches contained within the depressions.

CRITERIA FOR RECOGNIZING EXCAVATED DINOSAUR NEST STRUCTURES

The following criteria, listed in the order of decreasing significance, are used for recognition of a nesting trace fossil excavated by an adult dinosaur.

(1) Presence of a depression that truncates stratification within the host substrate. The truncated strata may include either lithologic contacts or primary sedimentary structures, or both.

(2) Presence within the aforementioned depression of complete or significant portions of eggs or articulated juvenile skeletons with no evidence of transport. Caution must be exercised here because fragmentary eggshell debris and disarticulated skeletal elements commonly are concentrated by hydraulic processes (e.g., Rogers, 1993).

(3) Evidence of an elevated ridge of massive sediment surrounding the perimeter of the depression containing the eggs that is distinct lithologically (i.e., grain size, shape, sorting, fabric, and sedimentary structures) from laterally adjacent and overlying sediment.

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

DISCUSSION

A fossilized egg clutch alone provides no architectural evidence for the existence of a nest (Sander et al., 1998). Therefore, the most reliable evidence in support of an excavated nest trace is provided by primary lithologic characteristics (e.g., truncation of sedimentary structures and primary stratification) and differences in sedimentary texture between the substrate and in-filling sediment. However, because dinosaur footprints also may possess some or all of these primary lithologic criteria (Nadon, 2001), it is imperative that traces interpreted as the result of nest excavation contain either recognizable eggs or articulated skeletons of juveniles. The more independent criteria present in a particular structure, the greater the confidence in the interpretation that an egg-filled depression actually represents an excavated nest.

With the exception of Varricchio et al. (1997), previous reports (Erben et al., 1979; Horner and Makela, 1979; Kérourio, 1981; Coombs 1989; Sabath, 1991; Powell, 1992; Cousin et al., 1994; Mikhailov et al., 1994; Mohabey, 1996) have not used criteria of primary lithologic attributes for purposes of nest identification; therefore, they fail to provide definitive evidence for nest excavation. Although egg clutches are common in the fossil record (Carpenter et al., 1994), recognition of associated nesting traces using lithologic criteria is possible only at boundaries between texturally contrasting sedimentary facies. The majority of egg clutches described in the literature, however, are not preserved at lithologic boundaries. This is also the case at Auca Mahuevo. Therefore, an inherent depositional bias exists against the preservation of dinosaur nest structures for most egg clutches. Of the hundreds of egg clutches examined at Auca Mahuevo, most are preserved entirely in mudstone. Only the six reported here are preserved at contacts between sandstone and overlying mudstone. Thus, only these six nest traces provide definitive evidence of nest excavation in sauropod dinosaurs.

ACKNOWLEDGEMENTS

We are grateful to crew members of the 2000 and 2001 LACM/MCF joint expeditions, especially to N. Rufenacht who carefully helped mold NE-01 and NE-02 during the 2000 expedition. We thank B. Evans and L. Rhoads for preparing the illustrations, and J. Farlow, S. Hasiotis, J. A. Lillegraven, and D. Varricchio for their reviews and editorial comments. Field and laboratory research for this project was supported by the Ann and Gordon Getty Foundation, the Charlotte and Walter Kohler Charitable Trust, the Dirección General de Cultura de Neuquén, the Fundación Antorchas, the Infoquest Foundation, the Municipalidad de Plaza Huincul, and the National Geographic Society. Finally, we thank very especially Rodolfo Coria for his scientific and logistical contributions that made our work possible.

REFERENCES

ARDOLINO, A.A., and FRANCHI, M.R., 1996, Geología y Recursos Minerales del Departamento Añelo. Provincia del Neuquén, Rep. Argentina: Publicación Conjunta de la Dirección Provincial de Minería de la Provincia del Neuquén y Dirección Nacional del Servicio Geológico, Anales (Geología) v. 25, p. 9–106.

CARPENTER, K., HIRSCH, K.F., and HORNER, J.R., eds., 1994, Dinosaur Eggs and Babies: Cambridge University Press, Cambridge, 372 p.

CARPENTER, K., 1999, Eggs, Nests, and Baby Dinosaurs: Indiana University Press, Bloomington, 336 p.

CHIAPPE, L.M., CORIA, R.A., DINGUS, L., JACKSON, F., CHINSAMY, A., and FOX, M., 1998, Sauropod dinosaur embryos from the Late Cretaceous of Patagonia: Nature, v. 396, p. 258–261.

CHIAPPE, L.M., DINGUS, L., JACKSON, F., GRELLET-TINNER, G., ASPINALL, R., CLARKE, J., CORIA, R.A., GARRIDO, A., and LOOPE, D., 2000, Sauropod eggs and embryos from the Upper Cretaceous of Patagonia: I Symposium of Dinosaur Eggs and Embryos, Isona, Spain, p. 23–29.

CHIAPPE, L.M., SALGADO, L., and CORIA, R.A., 2001, Embryonic skulls of titanosaur sauropod dinosaurs: Science, v. 293, p. 2444–2446.

COOMBS, W.P., 1989, Modern analogs for dinosaur nesting and parental behavior: *in* Farlow, J.O., ed., Paleobiology of the Dinosaurs: Geological Society of America Special Paper 238, Geological Society of America, Boulder, Colorado, p. 21–53.

COUSIN, R., BRETON, G., FOURNIER, R., and WATTÉ, J-P., 1994, Dinosaur egg laying and nesting in France: *in* Carpenter, K., Hirsch, K.F., and Horner, J.R., eds., Dinosaur Eggs and Babies: Cambridge University Press, Cambridge, p. 56–74.

DINGUS, L., CLARKE, J., SCOTT, G.R., SWISHER, C.C. III, CHIAPPE, L.M., and CORIA, R., 2000, First magnetostratigraphic/faunal constraints for the age of sauropod embryo-bearing rocks in the Neuquén Group (Late Cretaceous, Neuquén Province, Argentina): American Museum Novitates 3290, p. 1–11.

ERBEN, H.K., HOEFS, J., and WEDEPOHL, K.H., 1979, Paleobiological and isotopic studies of eggshells from a declining dinosaur species: Paleobiology, v. 5, p. 380–414.

HORNER J.R., and MAKELA, R., 1979, Nest of juveniles provides evidence of family structure among dinosaurs: Nature, v. 282, p. 296–298.

KÉROURIO, P., 1981, Nouvelles observations sur le mode de nidification et de ponte chez les dinosauriens du Crétacé terminal du Midi de la France: Compte Rendu Sommaire des Séances de la Société Géologique de France 1, p. 25–28.

LOOPE, D., SCHMITT, J.G., and JACKSON, F., 2000, Thunder platters: thin discontinuous limestones in Late Cretaceous continental mudstones of Argentina may represent chemically-infilled sauropod tracks: Geological Society of America, Abstracts with Programs, p. A-450.

López-Martínez, N., Moratalla, J.J., and Sanz, J.L., 2000, Dinosaurs nesting on tidal flats: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 160, p. 153–163.
Mikhailov, K., Sabath, K., and Kurzanov, S. 1994, Eggs and nests from the Cretaceous of Mongolia: *in* Carpenter, K., Hirsch, K.F., and Horner, J.R., eds., Dinosaur Eggs and Babies: Cambridge University Press, Cambridge, p. 88–115.
Mohabey, D.M., 1996, A new oospecies, *Megaloolithus matleyi*, from the Lameta Formation (Upper Cretaceous) of Chandrapur district, Maharashtra, India, and general remarks on the palaeoenvironment and nesting behavior of dinosaurs: Cretaceous Research, v. 17, p. 183–196.
Nadon, G.C., 2001, The impact of sedimentology on vertebrate track studies: *in* Tanke, D.H., and Carpenter, K., eds., Mesozoic Vertebrate Life: Indiana University Press, Bloomington, p. 395–407.
Powell, J., 1992, Hallazgo de huevos asignables a dinosaurios titanosáuridos (Saurischia, Sauropoda) de la Provincia de Río Negro, Argentina: Acta Zoologica Lilloana, v. 41, p. 381–389.
Ramos, V.A., 1981, Descripción geológica de la hoja 33c, Los Chihuidos Norte, Provincia del Neuquén: Boletín del Servicio Nacional de Minería y Geología, Buenos Aires, 182 p.
Rogers, R.R., 1993, Systematic patterns of time-averaging in the terrestrial vertebrate record: a Cretaceous case study: *in* Kidwell, S.M., and Behrensmeyer, A.K., eds., Taphonomic Approaches to Time Resolution in Fossil Assemblages: Short Course in Paleontology, The Paleontological Society, Knoxville, p. 228–249.
Sabath, K., 1991, Upper Cretaceous amniotic eggs from the Gobi Desert: Acta Paleontologica Polonica, v. 36, p. 151–192.
Sander, P.M., Peitz, C., Gallemi, J., and Cousin, R., 1998, Dinosaurs nesting on a red beach?: Compte Rendu de la Academie des Séances de Paris, v. 327, p. 67–74.
Seymour, R.S., 1980, Dinosaur eggs: the relationships between gas conductance through the shell, water loss during incubation and clutch size: Memoirs de la Société Géologique de France, v. 139, p. 177–184.
Varricchio, D.J., Jackson, F., Borkowski, J.J., and Horner, J.R., 1997, Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits: Nature, v. 385, p. 247–250.

ACCEPTED AUGUST 6, 2003