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A VERTEBRATE NESTING SITE IN NORTHEASTERN ITALY REVEALS UNEXPECTEDLY COMPLEX BEHAVIOR FOR LATE CARNIAN REPTILES

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ABSTRACT

We interpret 13 large subcircular or horseshoe-shaped depressions discovered in Late Triassic peritidal carbonate rocks of the Dogna Valley in Udine Province, northeastern Italy, to be reptile nests. These trace fossils show truncation of strata, elevated ridges of massive sediment, and sediment infill within the depression differing in shape and sedimentary structures from the host sediment. The palynological assemblage of a shaly interbed close to the nest layer indicates a Tuvalian age (late Carnian). Archosaurian footprints, produced possibly by aetosaurs, are on a surface 130 cm above the nest-bearing layer. The trackmakers are considered the most probable nest makers.

INTRODUCTION

In this paper we interpret 13 large subcircular or horseshoe-shaped depressions as reptile nests in Late Triassic peritidal carbonate rocks of the Dogna Valley in Udine Province, Friuli Venezia Giulia Region, northeastern Italy. In 1994 archosaurian trackways were discovered in a layer of the Tuvalian (upper Carnian, Upper Triassic) Monticello Formation (Dalla Vecchia, 1996) cropping out along the Dogna Creek. Flooding since 1996 removed debris that covered part of the section with the footprint-bearing surface and exposed an underlying horizon with large subcircular or horseshoe-shaped depressions. Such structures were discovered in 2003 by some of us (D.P, N.P., M.R., and G.R.; see Avanzini et al., 2004).

The Dogna Valley is a narrow valley incised by Dogna Creek in the Julian Alps close to the border between Italy, Slovenia, and Austria (Fig. 1). The Late Triassic geology of the area has been well known only since the 1980s (Bianchin et al., 1980; Carulli et al., 1987). Vertebrate remains of chondrichthyans, osteichthyans, and reptilians have been reported from the area since the late 1800s (Bassani, 1892; Pinna, 1990; Sirna et al., 1994; Rieppel and Dalla Vecchia, 2001, Dalla Vecchia and Avanzini, 2002, Dalla Vecchia, 2006), where they occur in the early Carnian Rio dal Lago Formation.

STRATIGRAPHY AND SEDIMENTOLOGY

Upper Triassic strata of the Dogna Valley consist of about 1000 m of sedimentary succession dominated by marls and carbonates deposited in shallow-water marine settings (Fig. 2). This Upper Triassic succession lies on a paleosol developed on the Middle Triassic Schlern Dolostone Formation, a dolomitized carbonate platform. The overlying ~600 m contains the Rio di Terrarossa dolomites, Rio del Lago Formation, Dogna Formation, Tor Formation, and Portella dolomite deposited in a mixed carbonate-siliciclastic ramp sedimentary environment (Preto et al., 2005). The age of this succession is mostly early Carnian, except for the upper Tor Formation and the Portella dolomite, which are late Carnian. Vertebrate remains are especially abundant in the lower part of the Rio del Lago Formation (Dalla Vecchia, 2006).

Above the Portella dolomite, the Monticello Formation and the lower Dolomia Principale represent the remainder of the Late Carnian. These units were deposited landward of a bioconstructed rim in an inner platform sedimentary environment (Gianolla et al., 2003).

The large biogenic structures described here are within the Monticello Formation. This formation is well exposed along the Dogna Valley and consists of well-bedded alternations of dark gray to black shales, gray and dark gray dolostones (Carulli et al., 1987). The thickness of this unit at Dogna is ~300 m.

In 2003, a ~4-m-thick section of Monticello Formation, including the ichnofossil-bearing layer and overlying trampled layer, was measured and sampled along the riverbed of the Dogna Creek. Despite the pervasive dolomitization, the original texture of the carbonates is well preserved, allowing a facies description and interpretation.

Carbonates exhibit a variety of facies and structures. Some thick layers, up to 60 cm, are composed of bioturbated peloidal dolostones (wackestone-packstones) containing ostracodes, agglutinated and hyaline foraminifers, and less-common mollusks and green algae. These dolostones were deposited in a restricted shallow subtidal (maybe intertidal, in some cases) carbonate platform environment. Other, usually thinner, layers are dolostone (mudstone-wackestone) with algal laminae (stromatolites), mud cracks, planar fenestrae, and scattered, isolated burrows (Fig. 2B). Fossils are rare, except for occasional ostracode-rich laminae. These laminated and mud-cracked dolostones were likely deposited in a carbonate supratidal flat. A third group of dolostones includes thin mud layers with planar fenestrae and sheet cracks, flat pebbles, and vadose pisoids, the latter being indicative of pedogenesis (Fig. 2C). Some surfaces on top of intraformational breccias are also characterized by rubefaction. Dark silty shales are associated more commonly with these dolostones. The large depressions, as well as the footprint-bearing layer (Dalla Vecchia, 1996; Roghi and Dalla Vecchia, 1997) 130 cm higher in the succession, belong to this third lithofacies. The marls overlying the footprint-bearing layer show a fully continental palynological association. Thus, the intraformational breccias, and at least some of the dark silty shales, formed in a pedogenetic environment, relatively isolated from marine input. The three sedimentary environments identified here alternate in the measured section at the meter scale (Fig. 2A).

PALYNOLOGY

Palynological analysis reveals three main assemblages in the Rio del Lago and Monticello Formations of the Dogna Valley (Preto et al., 2004). According to the palynological subdivision in the neighboring Cave del Predil (former Raibl) area (Roghi, 2004), these assemblages are time constrained to the Julian and the Tuvalian, respectively.

A rich microfloral association (Table 1) was found in the sample dog13

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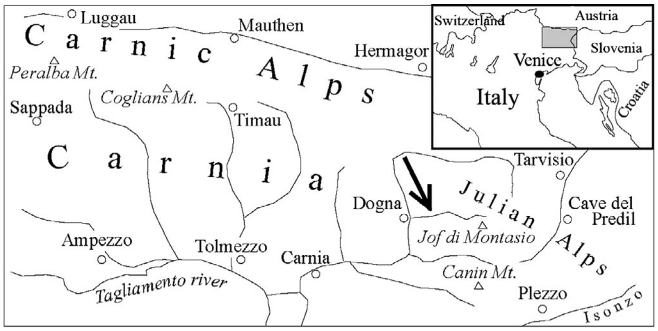

FIGURE 1—Schematic map of the study area.

(Dogna 13) of the Monticello Formation from just above the footprint-bearing layer (Roghi and Dalla Vecchia, 1997). It belongs to the upper Tuvalian *Granuloperculatipollis rudis* assemblage (Roghi, 2004). This assemblage contains *Porcellispora longdonensis*, *Camerosporites secatus*, *Paracirculina quadruplicis*, *Granuloperculatipollis rudis* and *Samaropollenites speciosus*. This assemblage is also typical of the haeteropic Carnitza Formation of Cave del Predil area, yielding ammonoids of the *Tropites subbullatus* and *Anatropites spinosus* Zones (Gallet et al., 1994, De Zanche et al., 2000, Gianolla et al., 2003). The assemblage of sample dog13 is also very rich in bisaccate and monosaccoid pollens, evidence of local xerophytic vegetation (Roghi and Dalla Vecchia, 1997).

VERTEBRATE FOOTPRINTS

A vertebrate footprint-bearing layer occurs in the same outcrop as the large depressions (Dalla Vecchia, 1996; see Fig. 3). The layer is a dark gray marly and dolomitic mudstone, with spots of wackestone at the top and deep desiccation cracks (Roghi and Dalla Vecchia, 1997). Most of the exposed bed surface was removed to avoid its destruction by flooding and rock falls and is currently exhibited in a small museum in the town of Dogna. It preserves two trackways (A and B) and few other scattered footprints described in Dalla Vecchia (1996). Part of the surface with half a dozen footprints (Dalla Vecchia, personal communication, 2003) was covered subsequently by sediments. Only a lesser portion of the footprint-bearing surface remains exposed in situ and does not reveal a useful evidence of footprints.

The footprints were impressed by quadrupeds with a tetradactyl or pentadactyl manus at least 50% smaller than the pentadactyl pes. Pedal prints are plantigrade, 17–20 cm long, have a narrow and elongate shape, and are wider anteriorly and relatively symmetrical with five short and narrow digital marks (Figs. 3B–C). Traces of the free portion of the digits are sharply pointed and represent the deepest part of the footprint. This is due to the fact that the trackmaker was moving on a dry and firm carbonate sediment, with desiccation cracks, resulting in generally shallow footprints with digital marks left mainly by claws during the foot withdrawal. Digit III is the longest, digit I is the shortest, and digits II and IV have similar lengths. The very shallow digit V mark, visible in few footprints, is short, thin, situated posteriorly, curved and anteriorly oriented. The manual prints are subcircular and are in front and slightly medial with respect to the pedal print. Their morphology is less clear than that of pedal prints. Usually four digital marks can be recognized, which are sometimes short and of irregular shape, sometimes long, narrow, and deep. The latter case is related to the claws scratching the surface during the withdrawal of the manus. Since the state of preservation is suboptimal, we cannot discount the possible presence of a small fifth digit.

The pace is about 45 cm, the stride is about 70 cm. The trackway is wide (30 cm), with a pedal pace angulation of about 100°. The pedal prints show only limited outward rotation; there is no evidence of foot dragging and also no tail, chest, or belly marks. The evidence suggests that the trackmaker was a quadruped with a relatively wide body, an erect stance, and a relatively efficient gait like those of fast-walking crocodiles.

Dalla Vecchia (1996) and Roghi and Dalla Vecchia (1997) suggested archosaurian reptiles as the tracemakers and indicated phytosaurs, primitive crocodylomorphs retaining digit V, aetosaurians, and rauisuchians as possible trackmakers. In fact, footprint morphology, the inferred pedal and manual morphology, parameters of the trackways, and the geological age indicate that the trackmaker was a crurotarsal archosaur.

The general outline of the pedal print is similar to living crocodilians (Fig. 3D5) and some early crocodylomorphs (Fig. 3D4), which, however, are tetradactyl. Furthermore, early crocodylomorphs were mainly gracile and possibly bipedal animals (Carroll, 1988), the oldest of which are Norian in age (Benton, 1994). The oldest ichnological record of crocodylomorph trackmakers is Early Jurassic in age (Olsen and Padian, 1986).

Phytosaurs (Parasuchia) are crocodile-like basal Crurotarsi with five digits in the hind limb that were common and distributed worldwide during the Late Triassic. They were aquatic, and some taxa are considered marine (Renesto and Lombardo, 1999). Thus, they appear to be good candidates for the Dogna trackways, as the passage from the shallow platform and the open sea was only few kilometers east of the site. The skeletal morphology of the phytosaurian hind foot, however, does not support this hypothesis. The pedal morphology of those reptiles is not well known, but when preserved (*Pseudopalatus pristinus*, Long and Murry, 1995; *Parasuchus hislopi* and *Rutiodon tenuis*, Parrish, 1986), digits V and I are nearly at the same height along the lateral and medial margins of the foot, respectively, and digit V is not posterior in the foot. This is evident in the hypothetical *Rutiodon* pes print by Parrish (1986; see Fig. 3D6), but not in the case of the Dogna footprints.

The pedal print in the Dogna trackways has an arrangement of five toe marks like that of chirotheroid footprints, with digit V posterior in the print (Figs. 3D1, D2, D3). The digit V print of chirotheroid pedal prints, however, is wide and characteristically points laterally, not posteriorly.

Chirotheroid footprints are attributed to aetosaurians and rauisuchians, which, unlike phytosaurs, have a pedal digit V placed slightly more posterior than digit I. As the rauisuchian body plan is generally narrower and more suited to the relatively faster gait of the predator than the body plan of the vegetarian aetosaurians, the narrow-gauged chirotheroid trackways are usually attributed to rauisuchians. Thus, the body plan of the vegetarian aetosaur fits better with Dogna trackways.

Dogna footprints do not fit well with any known ichnotaxon or foot skeletal model. We hypothesize that the peculiar shape of Dogna footprints is due to sediment properties. The trackmaker was moving on firm carbonate sediment, and consequently, the footprints were shallow and barely distinct, with the deepest mark as narrow grooves left by claws during the foot withdrawal. It can be considered a peculiar chirotheroid ichnofossil.

Thus we conclude that the trackmaker was a quadrupedal crurotarsal archosaur with a relatively wide, crocodile-like body plan and an erect stance, most probably an aetosaur according to what we know of Triassic reptiles. The trackmaker would be about 2.5 m long, based on the reconstruction of the aetosaur *Stagonolepis* (Roghi and Dalla Vecchia, 1997).

DESCRIPTION OF THE STRUCTURES

The exposed bed surface shows 13 large subcircular or horseshoe-shaped depressions (Fig. 4). Some of them are connected to form a composite figure 8–like structure. The depressions are edged with a rim made of two or more sediment flows superimposed on one another and, thus, were formed by two or more events of mud displacement. The depressions vary in size from 100 cm to 160 cm across their maximum plan-view axes, rim included. The depth varies from 5 cm to 20 cm. The depression margins sometime show a complex system of extensional, concentric, and subparallel fractures. The depressions are evenly spaced in plan view (Fig. 5).

All the structures cut a decimeter-thick layer of a bioturbated mudstone-

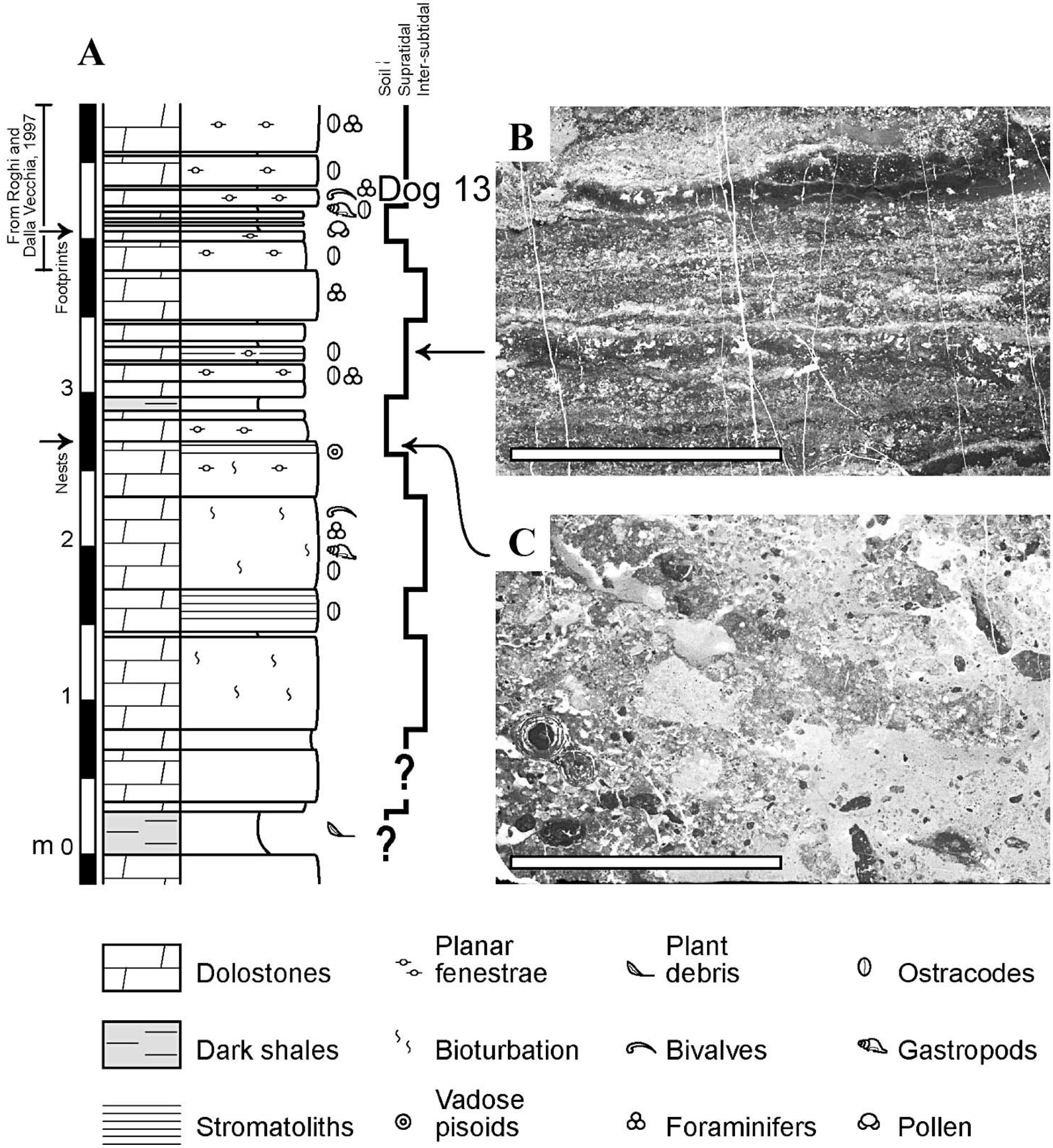

FIGURE 2—A) Stratigraphic outcrop log; scale in meters. B) Thin-section micrograph of a stromatolithic dolostone with wavy lamination and planar fenestrae, supratidal flat environment; scale bar = 1 cm. C) thin-section micrograph of the layer (intraformational breccia with flat pebbles and vadose pisoids) bearing the possible nest traces; scale bar = 1 cm.

packstone with vadose pisoids, stromatolithic laminations, and small burrows filled with geopetal micrite. The sediments that fill the depressions differ from the substrate composition in sedimentology and organic content. The infill is a massive, blackish mudstone that covers both the floor and the rim of the structures.

Nine of the 13 structures can be differentiated into 2 morphotypes and are described in detail (see Table 2); these morphotypes are type 1, which is horseshoe shaped and symmetric (N1 and N6) and type 2, which is circular (N2–N5, N7–N8, and N11).

Type 1 (N1 and N6)

Depression N1, the best-preserved structure of this morphotype, has a wide horseshoe shape. The section of the structure is irregular with a

TABLE 1—Microfloral association found in the sample dog13 (Dogna 13) from just above footprint-bearing layer, from the upper Tuvalian *Granuloperculatipollis rudis* assemblage. The assemblage is very rich in bisaccate and monosaccoid pollens, evidence of local xerophytic vegetation.

Convolutispora sp.
Enzonalasporites vigens Leschik, 1956
Patinasporites densus Leschik, 1956 emend. Scheuring, 1970
Pseudoenzonalasporites summus Scheuring, 1970
Vallasporites ignacii Leschik, 1956
Abietinaepollenites bujakii Dunay et Fisher, 1979
Alisporites opii Daugherty emend. Jansonius, 1970
Alisporites spp.
Chordasporites sp.
Falcisporites oviformis Dunay et Fisher, 1979
Klausipollenites schaubergeri (Potonié et Klaus) Jansonius, 1962
Lueckysporites cf. *L. virkiae* Potonié et Klaus 1954, emend. Klaus, 1963
Lunatisporites acutus Leschik, 1956 emend. Scheuring, 1970
Minutosaccus sp.
Ovalipollis ovalis Krutzsch, 1955
Ovalipollis pseudoalatus (Thiergart, 1949) Schuurman, 1976
Pityosporites devolvens Leschik, 1956
Pityosporites neomundanus Leschik, 1956
Pityosporites sp.
Platysaccus queenslandii de Jersey, 1962
Protodiploxypinus ujhely Dunay et Fisher, 1979
Samaropollenites speciosus Goubin, 1965
Triadispora sp.
Camerosporites secatus Leschik, 1956 emend. Scheuring, 1978
Duplicisporites verrucosus Leschik, 1956 emend. Scheuring, 1978
Paracirculina maljawkinae Klaus, 1960
Paracirculina quadruplicis Scheuring, 1970
Partitisporites novimundanus Leschik in Kräusel et Leschik, 1956
Granuloperculatipollis rudis (Venkatachala and Góczán, 1964) emend. Scheuring in Mostler et al., 1978
Cycadopites sp.
Porcellispora longdonensis (Clarke, 1965) Scheuring, 1970 emend. Morbey, 1975

floor 18 cm deep. The rim hems the entire perimeter and varies from 16 cm to 45 cm in width (Fig. 6).

Where the floor is deeper, the rim is narrow, and the walls of the structure are vertical. Where the floor is shallow, the rim is wide and slopes gently on to the floor. The rim is formed by three or four massive carbonate mud units (Fig. 6B). The inner part of the rim is locally collapsed (Figs. 6A–B). On the floor, a millimeter-thick film rich in organic matter of vegetal origin is recognizable. The collapsed rim sometimes covers this film.

Eccentric holes filled by sediment are present in the deeper part of the depressions. These structures are present also in other depressions (N5–N7). The ridge of the rim and the floor of the structures show desiccation cracks.

The shape and sedimentary features of depression N6 are the same as N1. The rim, 20–30 cm in wide, is more regular than that of N1 and shows only two distinct superimposed mud units.

Type 2 (N2–N5, N7–N8, and N11)

Depression N2 is circular, its diameter is 144 cm, and its rim ranges from 18 cm to 31 cm wide (Figs. 3, 5). The cross section of the structure is asymmetric and 20 cm deep. The inner margin of the depression cuts the substrate vertically. The rim is formed by two superimposed massive mud units. The outer part of the rim is collapsed outward (Fig. 7). A millimeter-thick layer of dark clay with plant debris covers the floor of the depression. The fill is made of a blackish mudstone. Similar well-preserved, subcircular depressions (N4, N5, N7, N8) are close to each other and partly connected. The rims of N4–N5 and N7–N8 are joined, and the floor of N5 is connected into that of N4; N7 is connected into that of N8 forming a composite figure 8–like depression (Figs. 7A–B). An elliptical (90 × 75 cm) mud mound, 20 cm high, is preserved on the same bed (see Fig. 5).

COMPARISON WITH ABIOGENIC STRUCTURES AND VERTEBRATE TRACES

Load Structures, Fluid Escape Structures, and Other Liquefaction Structures

We compare the depressions of Dogna to load structures in mud, fluid-escape structures, water-transfer cylindrical structures, artesian sand boils, and sand-blow craters induced by liquefaction. Inorganic, plastic deformation of fine sand and mud almost always occurs soon after deposition and may produce rimmed depressions.

Load structures in mud, also known as load casts, are bulbous bodies of sandy or silty material that intrude downward into underlying weaker, finer-grained muddy sediments (Allen, 1982). The severity of deformation is controlled by the differences in densities between the over- and underlying layers and the weakness of the underlying layer. The resultant planar morphology may result in a subcircular depression at the top of the intruded layer, rarely with small marginal ridges. The Dogna structures are preserved on the top of a supratidal carbonate unit with evidence of early lithification. The superimposed layers are undeformed carbonates with very similar density. Thus, the Dogna structures are not load casts.

Pillar-like water-escape structures (Lowe and Lo Piccolo, 1974) are the only water escape structures large enough to resemble the Dogna depressions, but they require liquefaction of unconsolidated sediments to form. The Dogna depressions lie on partially early lithified carbonate without any evidence of liquefaction.

In water-transfer cylindrical structures (Deynoux et al., 1990), laminae are arranged in a cone-in-cone internal organization that forms subcircular, concentric, laminated rims with a central depression at the surface. These surface features seem very close to the Dogna depressions in dimension and general outline. Water-transfer cylindrical structures, however, have extensive continuity, and boundaries are easily recognizable for each structure. At Dogna, the layers below the circular rim are undeformed, and the depression and rim is localized only in the middle to upper part of a thin, 20-cm-thick carbonate bed. Moreover, water-transfer structures occur mostly in clastic deposits.

Artesian subaerial conditions cause local sand boils (Li et al., 1996) that are cone-shaped structures with a feeding dikes below their center. Thus, these structures are clearly different from the Dogna depressions.

Sand-blow craters are induced by liquefaction triggered mostly by earthquakes, and they commonly show a marked unconformity between the sediment in the crater (infill) and preexisting soil units (Obermeier, 1996). In contrast to artesian boils, liquefaction sand blows normally develop tabular fissures in the cap. Liquefaction occurs mainly where a thin sand bed is confined between clay-rich layers, and the evidence of liquefaction is generally the development of such features as recumbent folds along the thin sand layer. This is not the case at Dogna, where only carbonate fine-grained beds are documented.

Biogenic Structures: Vertebrate Footprints and Burrows

The Dogna Valley depressions are reminiscent of very large vertebrate footprints, specifically those of graviportal sauropod dinosaurs whose digits were extremely short or embedded in a pad. The pedal print is oval to circular, and the manual print is crescentic, semicircular, or horseshoe shaped (e.g., Platt and Hasiotis, 2006). Like the latter, the Dogna structures do not show any evidence of free digit prints and claw marks, and some are somewhat semicircular or horseshoe shaped. Many observations argue against this interpretation, however.

The earliest dinosaur fossils are reported to be Tuvalian in age and are represented by primitive forms from Africa and South America (e.g., Benton, 1994); only recently have some basal taxa from Brazil been dated as Late Ladinian or Early Carnian (Langer, 2004). Remains attributed to

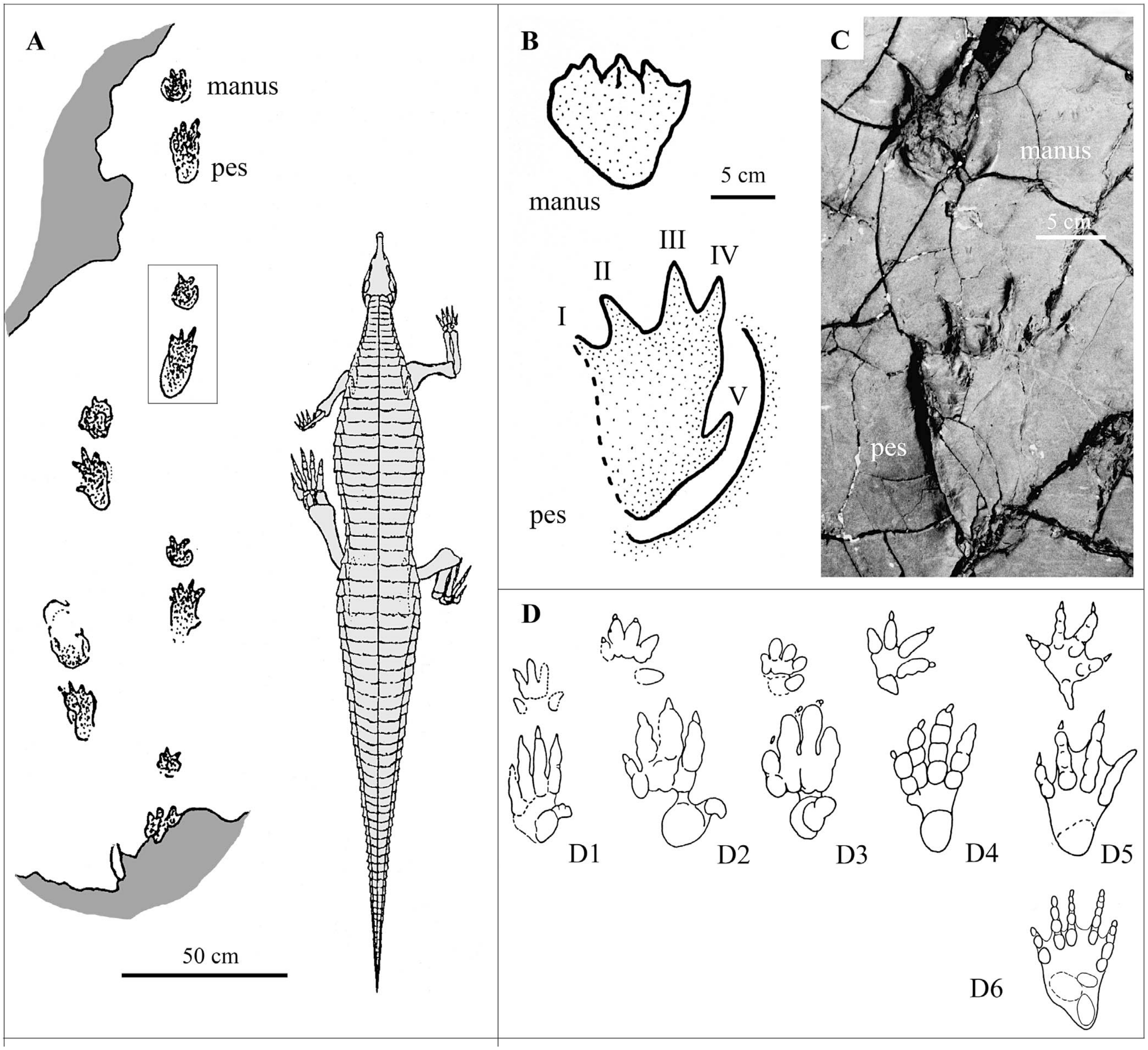

FIGURE 3—A) Trackway A and most probable trackmaker—an aetosaur. B) A right manus-pes set from trackway B. C) a right manus-pes set from trackway A (shown in Fig. 3A). D) Right manus-pes set of Triassic–Early Jurassic crurotarsal archosaurs and living *Alligator*, not drawn to scale: (D1) Late Triassic *Chirotherium lulli*; (D2) Early Triassic *Chirotherium barthi*; (D3) Late Triassic *Brachychirotherium parvum*; (D4) *Batrachopus dewey*, a Liassic ichnotaxon referred to a crocodylomorph; (D5) the living *Alligator*; (D6) an hypothetic reconstruction of a pedal print of the Norian phytosaur *Rutiodon*. The aetosaur *Stagonolepis* of Fig. 3A (after Krebs, 1976) is from the upper Tuvalian of Scotland. D1 after Haubold (1971), D2–D5 after Olsen and Padian (1986), D6 after Parrish (1986).

sauropodomorphs have been described from the Karoo Basin of South Africa (e.g., Raath et al., 1992; Yates and Kitching, 2003), the Argana Basin of Morocco (Gauffre, 1993), and the Morondava Basin of Madagascar (Flynn et al., 1999). In addition to African records, fairly complete specimens are known from South America. The Paraná Basin of southern Brazil has yielded the basal sauropodomorphs *Saturnalia* (Langer et al., 1999) and *Guaibasaurus* (Bonaparte et al., 1999).

The earliest sauropod bone record (*Blikanasaurus*, *Melanorosaurus*, and *Antetonitrus*) is Norian in age and is represented by relatively small-sized individuals, as would be expected in basal taxa (Buffetaut et al., 2000; Yates and Kitching, 2003). They are much smaller than the Dogna depressions. Furthermore, those basal taxa are reminiscent morphologically of the strictly related prosauropods—the most common Late Triassic vegetarian dinosaurs—that did not have a graviportal stance and sometimes had huge, long, free portions of the digits and claws (Yates and Kitching, 2003; Galton and Upchurch, 2004).

Triassic tracks and trackways assigned to sauropodomorph trackmakers have been mentioned from middle to the latest Triassic horizons from both northern and southern Pangea. Several tetradactyl footprints from the Late Triassic Chinle Formation, western United States, have been interpreted as sauropodomorphs (Lockley and Hunt, 1995; Lockley et al., 2001; Lucas et al., 2001; Lucas, 2003; Wilson, 2005). The Late Triassic, Gondwanan dinosaur footprint record is more restricted than that of Laurasia and is known mainly from the Karoo Basin of southern South Africa (Ellenberger, 1970, 1972, 1974; Raath et al. 1990; Lucas and Hancox, 2001) and the Cuyana Basin (Portezuelo Formation) in west-central Argentina (Marsicano and Barredo, 2004). Recently, a Late Triassic footprint assemblage with specimens suggesting the presence of middle-to-

FIGURE 4—Field photograph of depressions N1, N2, N4–N5, and N6 showing the elevated mudstone rims; scale = 2 m.

large-sized sauropodomorphs was described from west-central Argentina in the Portezuelo Formation (Marsicano and Barredo, 2004; Marsicano et al., 2004). The larger currently known Late Triassic sauropodomorph footprints, however, are only 30–50 cm long and are much smaller than the Dogna depressions.

The first very large sauropods are Early Jurassic in age (Jain et al., 1975), and the first large sauropod footprints, comparable in size and shape to the Dogna traces, are those found in the Middle-to-Late Jurassic of Spain and Portugal (Farlow et al., 1989; Thulborn, 1990; Farlow, 1992; Lockley et al., 1994, 2001; Lockley and Hunt, 1995; Lockley and Meyer, 1999; Avanzini et al., 2003). Therefore it seems unlikely that the presence of giant dinosaur footprints with the derived features of the feet of Late Jurassic neosauropods (McIntosh, 1997; Wilson and Sereno, 1998; Upchurch et al., 2004) would occur in the Late Carnian.

Furthermore, the Dogna depressions do not show a regular, trackway-like pattern. Some structures (i.e., N4 and N5) are close to each other as in a manus-pes set of a sauropod, but the rims and the floor are connected each other. In the case of footprints, the last print made, usually the pedal, disturbs the manual print and its expulsion rim.

The definitive characteristic that does not fit with an interpretation of footprints is the morphology of the supposed displacement rim, in which several discrete mud units are recognizable. These units seem to be formed by discrete and successive mud displacement events and not at once, as in the case of footprints (Figs. 6C, 7C).

The Dogna structures are not pits or holes produced by fishes (Martinell et al., 2001) or other obligatorily aquatic vertebrates, as the host bed surface is characterized by features indicative of supratidal conditions. Holes and pits are produced also by several extant terrestrial vertebrates, but trace-fossil evidence of vertebrate burrowing is exceedingly rare in the geologic record (Smith, 1987). Enigmatic small-to-large-diameter burrows occur in Triassic and Jurassic continental deposits of North America and Antarctica (Hasiotis et al., 2004), but they have shapes that differ from that of the Dogna depressions.

Interpretation of Dogna Traces as Nesting Structures

Enigmatic trace fossils interpreted as possible nests on the basis of their architectural and surfaces morphologies are reported from the Lower Triassic Fremouw Formation and from the Upper Triassic Chinle Formation of the United States (Hasiotis et al., 2004). The structures are bowl shaped, hollow pits preserved on the uppermost part of sandstone layers related to a highly sinuous meandering river (Hasiotis and Martin, 1999). The circular-to-elliptical pit openings range from 10 cm to 20 cm in diameter. A shallow, broad depression 53–65 cm long and 35–40 wide occurs under the larger pit openings. Many of those pits are on footprint-bearing surfaces and are close to each other with a density of about 1 per square meter (Hasiotis et al., 2004). The vertebrate tracks on the surface are preserved poorly, and the trackmaker is still unidentified.

Hasiotis et al. (2004) pointed out that these ichnofossils are quite similar to nest holes excavated by living crocodiles, alligators, and sea and terrestrial turtles (Zug et al., 2001); they suggest that the large shallow depressions associated with some of the pits could represent body traces made by a female excavating her nest and laying eggs. Phytosaur and aetosaur bones are among the vertebrate remains found in the same stratigraphic interval. According to Hasiotis et al. (2004), phytosaurs, aetosaurs, and rauisuchians have body plans similar to those of living crocodilians, and one of them could have excavated the nests. The nest architecture is reminiscent also of hole nests made by turtles (Cousin et al., 1994). The Dogna structures, however, differ from these pits in their

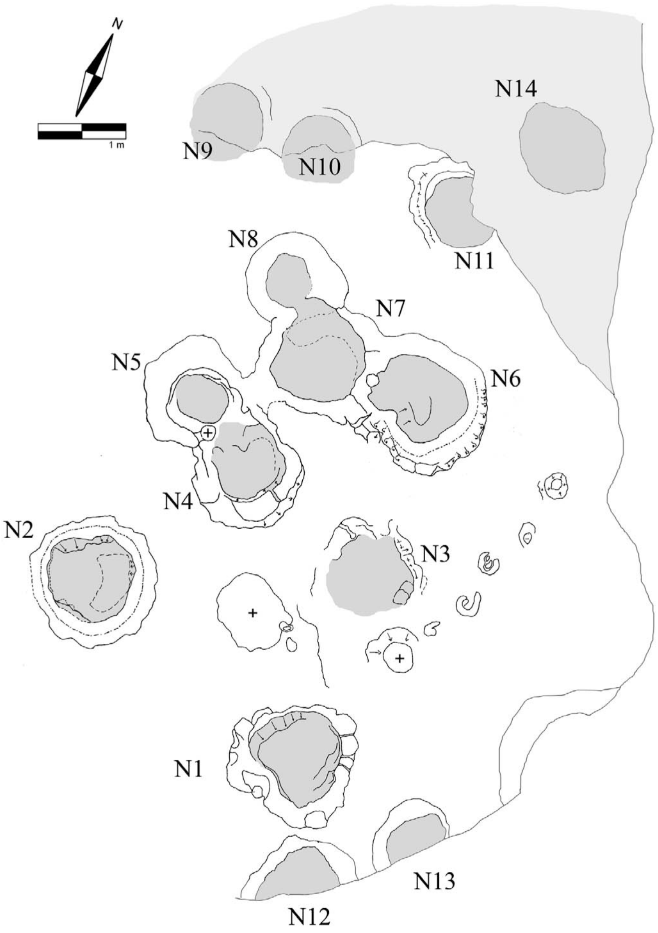

FIGURE 5—Sketch of nest-bearing surface.

much wider dimensions, shallower depth, and presence of a discrete mud rim.

Well-known examples of fossil reptile nests are those built by the theropod dinosaur *Troodon* from the Upper Cretaceous of Montana (Varricchio et al., 1997, 1999) and those referred to sauropod dinosaurs in the Upper Cretaceous of Patagonia (Chiappe et al., 2004). Those nests exhibit morphologies similar to the much older, Late Triassic nests of Dogna and are characterized by shallow bowl-like depressions with distinct rims; symmetrical and similarly sized nests on one bed surface; truncation of the host sediment; and sediment fill within depressions that differ in grain size and shape and sedimentary structures from that of the host sediment. In addition, the depressions are closely and equally spaced. For these reasons, we suggest that the Dogna depressions are nesting structures, even though fossil nests are recognized usually for the presence of eggs or egg remains, which were not found at the Dogna site.

Probable Nest Makers and Nesting Behavior in Extant and Extinct Archosaurs

The mean distance between the nests is 50 cm. If the Dogna depressions represent a nesting colony, it is possible to estimate that the nest maker was more or less 2 m long. This size is in agreement with the estimated size of the trackmakers recorded by the footprints preserved in the footprint-bearing layer above the nest-bearing layer. Thus, the nesting site may be that of the crurotarsal archosaurs that left their footprints at the same site but in a bed slightly higher than the nest-bearing unit. Although we consider crurotarsal archosaurs as the most probable nest makers, the possibility that the structures were made by other tetrapods that left no other fossil evidence of their existence cannot be excluded.

Very little is known about the nesting behavior of extinct reptiles. As different families of living crocodilians build different kinds of nests, we might expect that such Triassic archosaurs as phytosaurs, aetosaurs, rauisuchians, ornithosuchians, and prosauropods also had different nesting strategies.

When we considering living archosaurs—Crocodylia and Aves—we see that the complexity of nests increases, in a very broad sense, as parental care increases. The American alligator, *Alligator mississipiensis*, which is noted for its good parenting skills (Deitz and Hines, 1980; Woodward et al., 1984; Carpenter 1999), builds a large moundlike heap of fresh plant material, mud, and debris above the waterline on either a bank or vegetation mat. In the center of the mound, the female digs a hole with her hind feet and deposits up to 50 eggs. She then covers it using her forelimbs and jaws. As time passes, the mud hardens to encase the eggs inside. Within the nest, the eggs incubate in the warmth of the decomposing vegetation for a little over 2 months. Outside, the mother stands guard and fiercely defends the nest should a scavenger try to unearth the eggs. As the eggs hatch, she breaks the nest open and carries the chirping babies to the water, where she protects them for a year or more. The limited dexterity of alligators likely prevents them from weaving an intricate nest, yet they take great care in selecting a nest site and constructing the mound. If conditions are not those required for nesting, the female abandons the site. Caimans and other alligatorids also build this kind of nest. Caiman nest size—usually 1.5–2 m in diameter and 40–100 cm high—and composition depend more on the availability of the building material than on different species behavior.

Crocodylids (e.g., *Crocodylus niloticus*, *C. palustris*) and the gavial (*Gavialis gangeticus*), nest in simple pits excavated in sand or crumbly soil in the beach or on the banks, close to the water (Cott, 1961). After digging a hole with her hind feet—the depth corresponding to length of the hind limbs, which is usually 60 cm—the female deposits her eggs and covers them with sand, pressing it with her hind feet. This kind of nest resembles that of other, nonarchosaurian reptiles (e.g., turtles) and is

TABLE 2—Measurements (in centimeters) of the best preserved nestlike structures, differentiated into 2 morphotypes: type 1 = horeshoe shaped and symmetric; type 2 = circular.

	N1	N2	N4	N5	N6	N7	N8
External length (cm)	143	144	108	120	170	145	116
External width (cm)	160	144	115	130	155	123	103
Internal length (cm)	92	99	64	77	90	105	55
Internal width (cm)	102	90	64	70	90	93	49
Maximum width of rim (cm)	45	31	40	14	30	24	41
Minimum width of rim (cm)	16	18	24	44	18	12	16
Exterior perimeter (cm)	475	487	384	275	473	420	339
Interior perimeter (cm)	314	325	236	223	311	315	178
Exterior area (m^2)	1.65	1.69	1.06	1.3	1.71	1.34	0.85
Interior area (m^2)	0.66	0.78	0.42	0.55	0.68	0.75	0.23
Nest type	Type 1	Type 2	Type 2	Type 2	Type 1	Type 2	Type 2

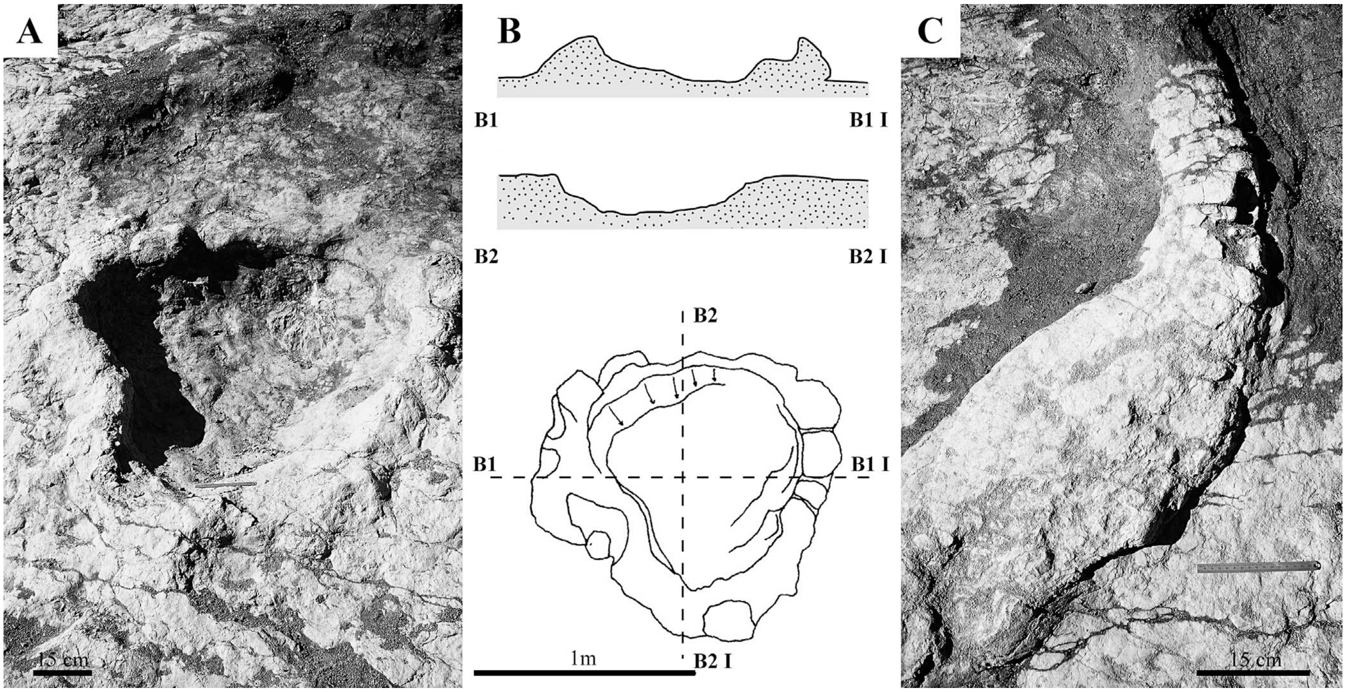

FIGURE 6—A) Close-up photography of structure N1; scale = 15 cm. B) Schematic section of the structure N1. C) Close-up of the mud rim of the structure N2; scale = 15 cm.

more primitive than that of alligatorids. In both cases, the nest type is different from that found at the Dogna site.

Among living amniotes, only birds build open, bowl-shaped nests to clutch eggs. Birds produce a variety of ground nests, not only according to species-specific behavior but also based on the characteristics of the nesting site and the material available to build them.

Complex nest-building and hatching behavior is considered one of the factors for the evolutionary success of birds; however, such behavior is not seen in all birds. The megapodes of the Australasian region incubate their eggs inside a mound of decomposing vegetation, as do alligatorids (Carpenter, 1999). Many water birds belonging to the Phoenicopteriphormes, Struthioniformes, Sphenisciformes, Pelecaniformes, and Procellariiformes build their nests in colonial nesting sites on the ground. Greater flamingos (*Phoenicopterus ruber*) make nests of mud by scooping bits of mud on top of one another with the lower jaw and then piling and smoothing this mud with their hind feet. They build small, cone-shaped mounds with scooped out tops, approximately 30 cm high. Usually a small moat is excavated around the base. Nests in a colony are built close to each other. The elevated mud prevents the eggs from being flooded by the alkaline lagoon water in which the flamingos live. The nests of flamingo colonies found on rocky islands are composed of a small circular rim of debris (del Hoyo et al., 1992).

The nest of rehid ratites (Struthioformes) is a rimmed depression about 1 m wide and 12 cm deep that the male constructs with his hind feet; the bottom is covered with dried-out vegetation. The females generally approach each nest as a group and one after another, lay their eggs in the hollow bowl, and leave the nest site as a group (del Hoyo et al., 1992).

The nest of the ostrich, *Struthio camelus*, is a shallow-rimmed depression about 3 m across that the male scratches out with his hind feet. Two to five—but as many as eighteen—other females lay their eggs in the same nest (del Hoyo et al., 1992).

Penguins (Sphenisciformes) construct nests in the open, in vegetation, in hollows, and in caves. The material used varies from place to place and with the species, but it generally consists of pebbles and old feathers. A medium-sized nest of the Gentoo penguin (*Pygoscelis papua*) is composed of some 1,700 pebbles, whereas the more modest Chinstrap penguin (*P. antarctica*) often has a rim of only 10 stones—whatever number is necessary to prevent the egg from rolling away.

Diomedeidae—the albatrosses—usually build nests with mud and grasses in the form of large truncated cones with a shallow depression on the top. A nest reaches 15 cm in height, depending on the species and location. The three North Pacific albatrosses construct more rudimental nests. The Black-footed albatross (*Diomedea nigripes*) digs out a scrape in the sand to build an elevated rim all around the depression. The Laysan albatross (*D. immutabilis*) builds a substantial rim around its nest by accumulating sand and pebbles, and the Short-tailed albatross (*D. albatrus*) builds a shallow bowl by scratching the ground (Harrison, 1990).

Pelicans (Pelecanidae) are almost always colonial ground-nesters. Nests tend to be fairly crude ground scrapes, sometimes constructed with the bill, although the American white pelican (*Pelecanus erythrorhynchos*) may produce a rimmed nest up to 90 cm wide and 50 cm high by accumulating a substantial mound of debris. The nest, however, is usually a cone with an apical depression instead of a true-rimmed nest. Nests are usually contiguous, and hatching birds may even touch each other. The nest density in a colony of the Great white pelican (*P. onocrotalus*) in the Great Rann of Kutch, India, is about 1 nest per m^2 (Ali and Ripley, 1978).

Open and rimmed nests with eggs not covered by sediment or vegetative matter imply clutching of the eggs. This is also characteristic of such advanced, nonavian theropods as *Troodon* (Moratalla and Powell, 1994; Varricchio et al., 1997, 1999). This kind of nest and nesting behavior is not found in living members of the crurotarsi clade (i.e., Crocodylia), and it should not be found in basal members of the clade (i.e., phytosaurs, aetosaurs, and rauisuchians), according to the extant phylogenetic brackets (Brochu, 2001). We, however, have found rimmed nests that possibly contained some vegetative matter, as is common in fossil nests (Horner, 1982; Sabath, 1991; Carpenter et al., 1994; Mickhailov et al., 1994; Carpenter, 1999; Chiappe et al., 2000). The Dogna depressions are therefore a new type of nesting behavior different from others described to date and more sophisticated than that of living crocodylians. The patterns seen in the Dogna depressions suggest that the female placed a bed of vegetation at the bottom, laid her eggs on it, and may have cared

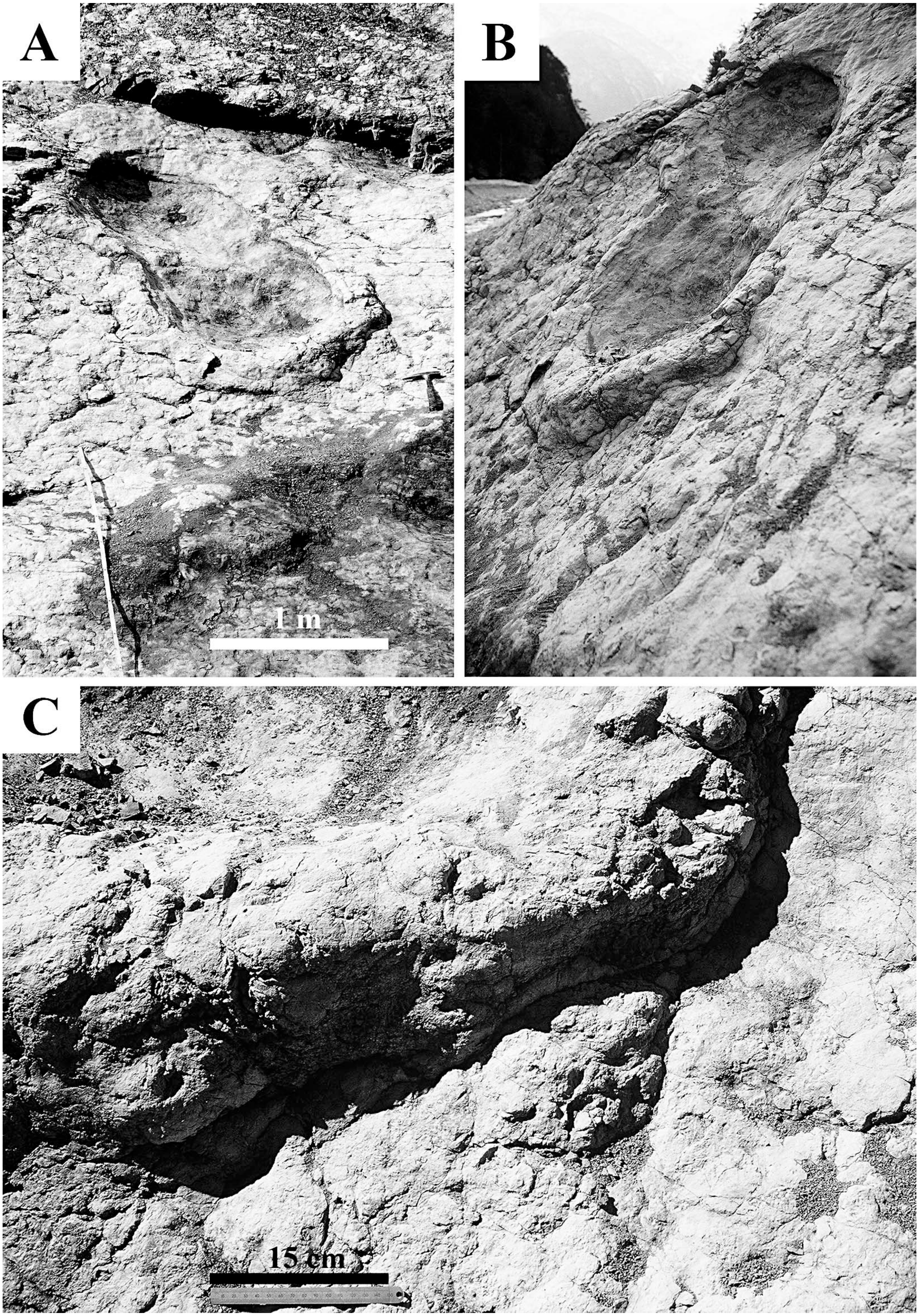

FIGURE 7—A) Close-up of structures N4 and N5 forming a composite figure 8 depression; scale = 1 m. B) Rims N4 and N5 formed by discrete and successive mud displacement events. C) Close-up of the mud rim of N4 formed, in this area, by two massive carbonate mud units; scale = 15 cm.

for the eggs; this represents unexpectedly complex behavior for Triassic reptiles.

CONCLUSION

The Dogna nesting site represents the earliest evidence for reproductive behavior of nondinosaurian archosaurs. The behavior that underlies the construction of a rimmed, open nest is relatively derived. Late Triassic reptiles were thought to build or dig more primitive nests similar to those of extant turtles and crocodylians. The architecture of and method for building a ground, rimmed nest has apparently changed very little since the Late Triassic. Primitive archosaurs used reproductive strategies similar to those of dinosaurs and birds in constructing nests to protect their eggs from flood events, predators, and cooling. This discovery provides new perspectives about the paleoecology of Late Triassic environments and biota in coastal plain settings.

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