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Exceptional preservation of a Late Cretaceous dinosaur nesting site from Mongolia reveals colonial nesting behavior in a non-avian theropod

Kohei Tanaka[1]*, Yoshitsugu Kobayashi[2]*, Darla K. Zelenitsky[3]*, François Therrien[4]*, Yuong-Nam Lee[5], Rinchen Barsbold[6], Katsuhiro Kubota[7], Hang-Jae Lee[8], Tsogtbaatar Chinzorig[6], and Damdinsuren Idersaikhan[6]

[1]Graduate School of Life and Environmental Sciences, University of Tsukuba, Tennodai 1-1-1, Tsukuba, Ibaraki 305-8572, Japan
[2]Hokkaido University Museum, Kita 10, Nishi 8, Kita-Ku, Sapporo, Hokkaido 060-0801, Japan
[3]Department of Geoscience, University of Calgary, 2500 University Drive Northwest, Calgary, Alberta T2N 1N4, Canada
[4]Royal Tyrrell Museum of Palaeontology, PO Box 7500, Drumheller, Alberta T0J 0Y0, Canada
[5]School of Earth and Environmental Sciences, Seoul National University, 1 Gwanak-ro, Gwanak-gu, Seoul 08826, South Korea
[6]Institute of Paleontology and Geology, Mongolian Academy of Sciences, PO Box-46/650, Ulaanbaatar 15160, Mongolia
[7]Museum of Nature and Human Activities, Hyogo, Yayoigaoka 6, Sanda, Hyogo, 669-1546, Japan
[8]Korea Institute of Geoscience and Mineral Resources, Daejeon 34132, South Korea

ABSTRACT

Colonial nesting behavior has been inferred in a variety of non-avian dinosaurs based on high concentrations of nests preserved in an area, but sedimentologic and taphonomic evidence demonstrating the contemporaneity of the nests is often lacking. A new nesting site discovered in the Upper Cretaceous Javkhlant Formation of the eastern Gobi Desert, Mongolia, preserves at least 15 egg clutches laid by a probable non-avian theropod, and provides strong evidence for colonial nesting in a non-avian dinosaur. The occurrence of the clutches at the top of a common paleosurface, the distribution of eggshell fragments within clutches, the presence of a consistent two-layer sediment infill within eggs, and a thin marker lithologic unit blanketing all the clutches indicate the clutches were laid and hatched in a single nesting season. Despite the absence of sedimentologic evidence indicative of nest structure, statistical analyses of egg characteristics and facies association reveal the clutches were likely incubated in covered or buried nests. Based on the number of hatched clutches, the hatching success rate of the colony was high (60%), similar to that of extant crocodylian populations and bird species that attend and/or protect their nests during the incubation period, which indicates nest attendance behavior in the Javkhlant theropods. Thus, colonial nesting with parental attendance, widespread in extant birds, likely evolved initially among non-brooding, non-avian dinosaurs to increase nesting success.

INTRODUCTION

Colonial nesting is a behavior commonly observed among living archosaurs (i.e., crocodylians and birds), where a few to thousands of individuals nest communally in an area during a single nesting season (Welty, 1982). This behavior has also been inferred in some dinosaurs, such as hadrosaurs (Horner, 1982), sauropodomorphs (Chiappe et al., 2001, 2004; Reisz et al., 2012, 2013) and non-avian theropods (Horner, 1982), based on the occurrence of numerous nests preserved within an individual lithologic unit or horizon in a local area (Table DR1 in the GSA Data Repository[1]). However, unless sedimentological evidence revealing the precise stratigraphic relations among nests is preserved or documented, it is impossible to demonstrate if these nests represent contemporaneous clutches laid during a single nesting season or simply a temporal accumulation of nests laid and buried over years, centuries, or millennia. Likely due, in part, to the nature and vagaries of the geologic record, previous studies have rarely been able to document the occurrence of more than one nest along a single paleosurface (e.g., Cousin et al., 1989).

Here we report the discovery of a high concentration of dinosaur nests, likely belonging to a non-avian theropod, preserved along a single paleosurface. The nesting site, discovered in the eastern Gobi Desert of Mongolia, is stratigraphically located within the "middle unit" of the Upper Cretaceous (?Santonian–Campanian) Javkhlant Formation (Figs. 1A and 1B), which was deposited in a proximal alluvial plain setting under a seasonally arid climate (Eberth et al., 2009). Excavations at the nest site conducted over the course of five field seasons (summers 2012–2015 and 2018) allowed detailed documentation of the sedimentology, stratigraphy, and distribution and arrangement of clutches and eggshell fragments. Taphonomic and sedimentologic data collected provide strong evidence for nest contemporaneity and true colonial nesting behavior in a non-avian theropod.

JAVKHLANT NESTING SITE

A minimum of 15 *in situ* clutches are preserved at the Javkhlant nesting site (44°23.525′N, 109°21.352′E; Figs. 1 and 2). The clutches consist of single-layered clusters of 3–30 spherical eggs, with no discernible egg arrangement. The eggs have a mean diameter of 13 cm, with a range from 10 to 15 cm (Fig. 2A).

*These authors contributed equally to the work.

[1]GSA Data Repository item 2019307, summary of materials and methods and supplementary results with tables and figures, is available online at http://www.geosociety.org/datarepository/2019/, or on request from editing@geosociety.org.

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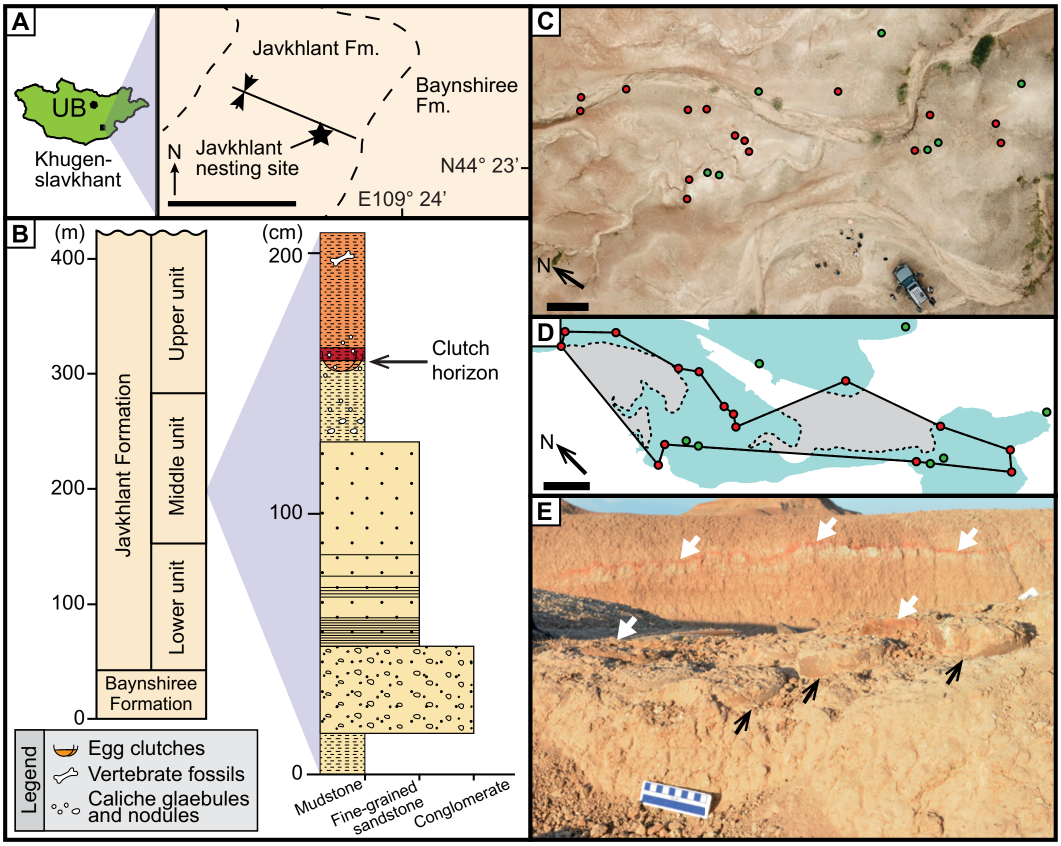

Figure 1. Javkhlant nesting site in the eastern Gobi Desert, Mongolia. (A) Geographical location of the study site in southeastern Mongolia (44°23.525′N, 109°21.352′E). Modified from Eberth et al. (2009). UB—Ulaanbaatar. Scale bar = 5 km. (B) Stratigraphic section of the nesting site. The egg-bearing horizon is situated ~156 m above the boundary between the Javkhlant Formation and the underlying Baynshiree Formation (see Eberth et al., 2009). (C) Aerial photograph of the nesting site, indicating positions of 15 *in situ* clutches (red circles) and clusters of two eggs or eggshell concentrations (green circles). Scale bar = 5 m. (D) Surficial extent (solid line) of the Javkhlant nesting site based on the distribution of egg clutches (red circles) and two-egg clusters or eggshell concentrations (green circles). The surface area of the exposed egg-bearing bed (blue) has been locally eroded by creeks (gray), resulting in the loss of nearly 50% of the nesting site. Scale bar = 5 m. (E) Field photograph of egg clutch in the foreground (black arrows) and thin red marker bed (white arrows) overlying clutches throughout the nesting site (background). Scale bar = 10 cm.

The eggs are characterized by a smooth to slightly textured outer surface, with a mean eggshell thickness of 1.55 mm. Radial thin sections of the eggshell show the inner portion of the shell units consist of irregular branches, with the outer portion forming an unbranched and more compact layer, and the presence of abundant, irregular-shaped pore canals (Fig. 2D; Fig. DR4). Based on these characteristics, the eggs are identified as belonging to the oofamily (a taxon, equivalent to a family, used to classify fossilized eggs) Dendroolithidae (see the Data Repository). Dendroolithid eggs have been previously attributed to the non-avian theropods Megalosauroidea and Therizinosauroidea, based on in-ovo embryonic remains (Manning et al., 1997; Kundrát et al., 2008; Araújo et al., 2013; Ribeiro et al., 2014). Thus, the Javkhlant eggs likely belong to therizinosauroids, as these theropods are known from the underlying Baynshiree Formation and other Upper Cretaceous

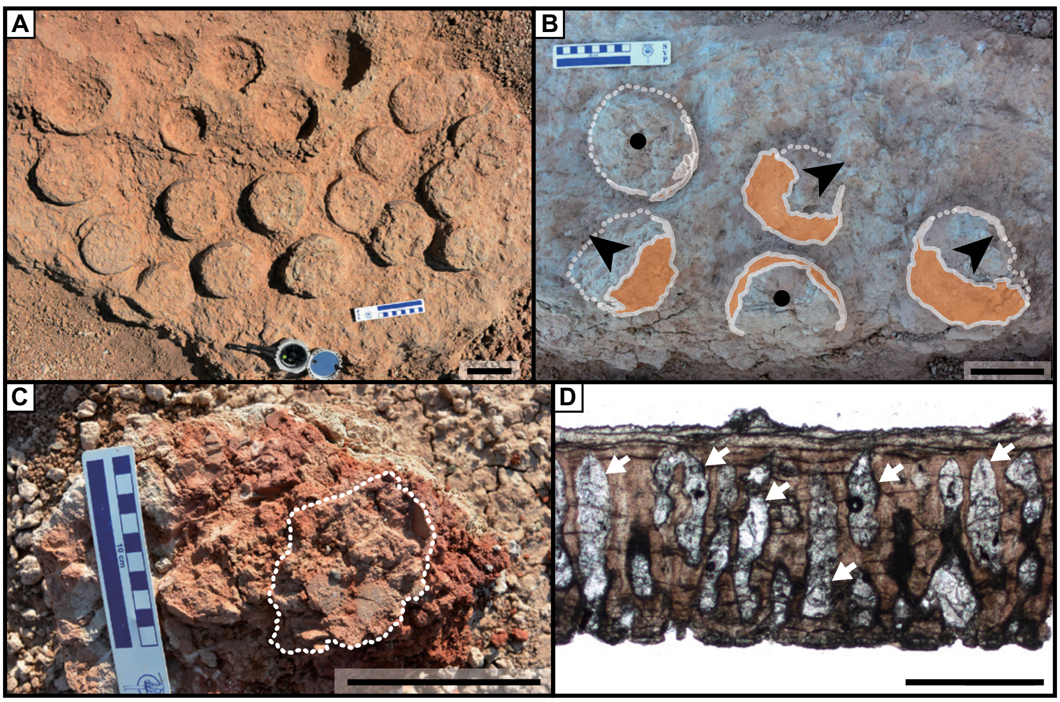

Figure 2. Dendroolithid eggs at Javkhlant nesting site in the eastern Gobi Desert, Mongolia. (A) The most complete clutch discovered at the site, preserving 30 partial eggs (21 eggs are visible), reposited at the Institute of Paleontology and Geology (MPC-D), Mongolian Academy of Sciences, Ulaanbaatar, Mongolia (specimen MPC-D 100/1030). Scale bar = 10 cm. (B) Planar view of egg clutch, preserving randomly oriented openings in the upper half of the eggs. Arrows and dots indicate the direction of the openings (clutch specimen MPC-D 100/1031). Scale bar = 10 cm. (C) Large eggshell fragment (outlined by broken line), corresponding to the size of the hatching window, scattered around egg clutch MPC-D 100/1031. Scale bar = 10 cm. (D) Photomicrograph of radial thin section of an eggshell from clutch MPC-D 100/1031, with arrows indicating location of pore canals. Photo in plane light. Scale bar = 1 mm.

deposits of Mongolia (Currie, 2000), whereas megalosauroids are absent.

The Javkhlant clutches are primarily exposed in a gently rolling area of badlands ~286 m^2 in surface area (Figs. 1C and 1D; see the Data Repository). The clutches are unevenly distributed in the area, some clutches occurring in close proximity to one another, with the shortest distance between clutches being <1.5 m and an instance where three large clutches are found within a 9 m^2 equidimensional horizontal surface area. Small, modern washes have dissected and eroded through ~150 m^2 of the egg-bearing layer (Fig. 1; Fig. DR1), suggesting that ~50% of the nesting horizon has been lost to erosion. Based on the horizontal distribution of preserved clutches, a nest density of 0.11 nests/m^2 (or ~1 nest per 10 m^2) is estimated, indicating that up to 32 nests may have been present at the site prior to erosion.

All clutches occur at the top of a laterally traceable light-gray (varying from 5YR 7/3 to 7.5YR 8/1 in the Revised Standard Soil Color Charts of Oyama and Takehara [2014]) sandy mudstone (Fig. 3; see the Data Repository for details). Because the upper part of many eggs has been lost to modern erosion, detailed excavation of the inside of 27 eggs from eight separate clutches (Fig. DR2; see the Data Repository), along with examination of one clutch exposed in cross section (Figs. 2B and 3), allows for documentation of the internal sedimentology of the eggs. The Javkhlant eggs contain two lithologically distinct layers of sediment: (1) a lower, dull orange (5YR 6/4; Oyama and Takehara, 2014), fining-upward sandy mudstone (3–5 cm thick) containing mudclasts and small scattered eggshell fragments (~0.5 cm in length), where coarser clasts and sand grains are concentrated at the base and become rare at the top (Fig. 3D); and (2) an overlying, red (10R 4/8; Oyama and Takehara, 2014), very sandy mudstone (1–6 cm thick) containing mudclasts and pebbles, which displays a faint fining-upward trend where coarser particles are located in the lower half of the unit and finer particles in the upper half (Fig. 3E; see the Data Repository for details). The red sandy mudstone is more poorly sorted, sandier, and contains coarser sand grains and more volcanic fragments than the underlying dull orange sediment filling the base of the eggs. The upper red sandy mudstone extends beyond the confines of the eggs and forms a continuous layer that extends laterally in outcrop, forming a distinct marker bed across all excavated clutches in the nesting site (Fig. 1D). The red marker bed varies little in topography (<0.4 m) throughout the area. This marker bed is overlain by a thick layer of the dull orange (5YR 6/4; Oyama and Takehara, 2014) sandy mudstone. Although the transition between the red marker bed and overlying dull orange sediment is abrupt with respect to density and

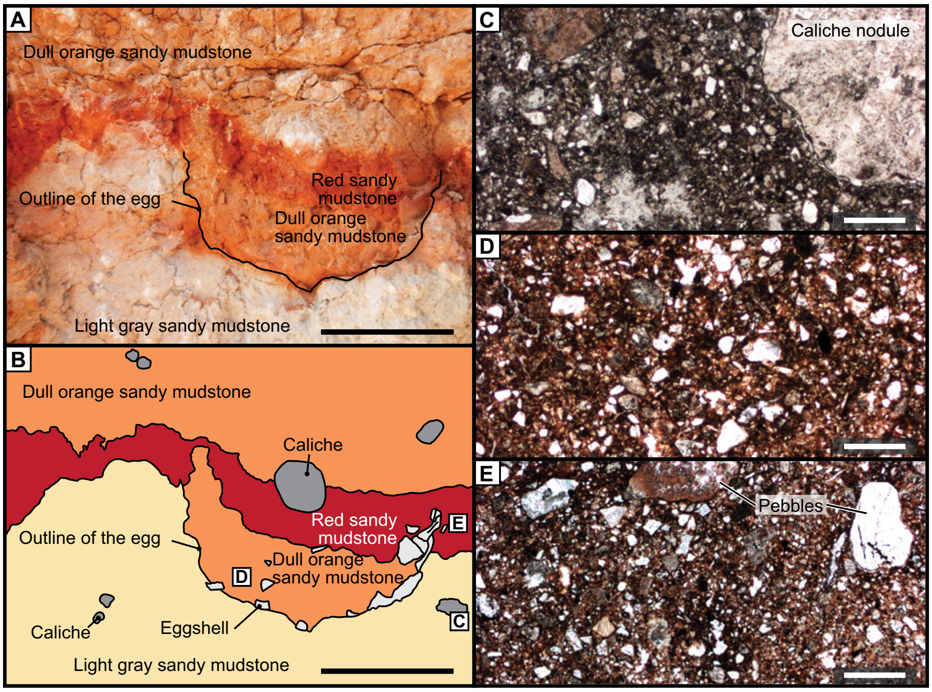

Figure 3. Sedimentology and microstratigraphy of Javkhlant (eastern Gobi Desert, Mongolia) egg clutch specimen MPC-D 100/1040 (Institute of Paleontology and Geology [MPC-D], Mongolian Academy of Sciences, Ulaanbaatar, Mongolia). (A) Natural cross section through an egg showing paleosurface on which clutches were laid, and distinct sandy mudstone layers that infill and overlay the eggs. Scale bar = 5 cm. (B) Interpretive illustration of sedimentary units recognized in A. Boxed letters represent approximate positions where rock samples were taken for the thin sections in panels C–E. Scale bar = 5 cm. (C) Photomicrograph of light-gray mudstone that forms the paleosurface on which eggs were laid. Photo in plane light. Scale bar = 0.5 mm. (D) Photomicrograph of dull orange, sandy mudstone infilling the base of the egg. Photo in plane light. Scale bar = 0.5 mm. (E) Photomicrograph of the red sandy mudstone that forms a marker bed covering the egg clutches at the Javkhlant nesting site. Photo in plane light. Scale bar = 0.5 mm.

abundance of sand grains, the color change is more gradual, occurring over 5–10 mm (see the Data Repository for details). The occurrence of both pedogenic carbonate nodules (Fig. 3; Fig. DR3) and birefringent groundmass (see Bullock et al., 1985) reflecting illuvial clay coatings in these four sedimentary units indicate they were subjected to pedogenic processes after burial.

Although no sedimentological evidence indicative of nest structure was found associated with the Javkhlant clutches, statistical methods were used to infer nest type (i.e., covered versus open). Based on a linear discriminant analysis between egg mass and eggshell porosity in extant archosaurs (Tanaka et al., 2015), the high porosity of the Javkhlant eggs (646 mm porosity for an egg mass of 1204 g; see the Data Repository) indicates they were incubated in fully covered nests (posterior probability of 1.00). Furthermore, a previously documented statistical correlation between pedogenic lithofacies and covered nest type (Tanaka et al., 2018) suggests that the Javkhlant clutches were incubated in a soil or organic-rich substrate (see the Data Repository), similar to the mound nests of living crocodylians and megapode birds (Coombs, 1989).

The taphonomy of the eggs and associated eggshell fragments indicates that many clutches at the Javkhlant site had hatched before the site was buried by flooding. Ten uneroded eggs, found in four separate clutches, are preserved with their shells complete except for a relatively large, randomly oriented opening in their upper half (Fig. 2B). The opening is reminiscent of a hatching window, an opening made by the hatchling to escape the egg (Cousin et al., 1994). Large eggshell fragments (up to 6 cm in diameter), similar in size to the openings in the eggs, are found scattered around two of these clutches (Fig. 2C), supporting the interpretation that the openings are hatching windows. Based on the number of Javkhlant clutches in which hatching windows are preserved ($n = 4$) and in which the distinct red marker bed is visible inside the eggs (indicating the eggs were open at the time of marker bed deposition; $n = 5$), at least nine clutches were determined to have successfully hatched, representing a nesting success (i.e., percentage of nests that produce at least one hatchling or one egg hatched; Mazzotti, 1989) of at least 60% for the Javkhlant nest site.

DISCUSSION

For the first time, to our knowledge, strong evidence for a dinosaur nesting colony laid and hatched in a single nesting season is presented on the basis of a detailed sedimentologic, paleontologic, and taphonomic investigation. Our study shows that all clutches were originally laid at the top of a common paleosurface, and lithofacies association indicates they were likely incubated in organic-rich covered nests. A lack of embryonic remains, the presence of hatching windows in many eggs, and the distribution of eggshell fragments indicate that many clutches successfully hatched. During or soon after hatching (i.e., prior to the eggs being damaged from exposure to the environment), the eggs were partly infilled with a dull orange, sandy mudstone that likely represents sediment and eggshell fragments that fell inside after hatching. Subsequently, the clutches were completely buried during a small flood event that deposited a thin red marker bed. The presence of the laterally traceable marker bed and the consistency of sediment infill among eggs indicate, in all likelihood, that the Javkhlant clutches were laid and would have hatched within a single season, as expected for true colonial nesting grounds. A later flood event covered the area under a thick sandy mudstone, and a calcic paleosol profile developed in the units under a semi-arid climate.

Until now, nest attendance and/or protection behaviors in non-avian dinosaurs could only reasonably be hypothesized based on a few isolated occurrences of an oviraptorosaur skeleton preserved sitting on an egg clutch (Norell et al., 1995, 2018; Dong and Currie, 1996; Fanti et al., 2012). The Javkhlant site, as a fossilized nesting colony with a high nesting success rate, reveals that nest attendance/protection by adults likely existed for non-avian dinosaur nesting colonies, not unlike that seen in colonial-nesting brooding birds. With a nesting success rate of at least 60%, the Javkhlant nesting site is comparable to that of living archosaur individuals that attend and/or protect their nests (e.g., *Alligator mississippiensis*, *Caiman yacare*, *Melanosuchus niger*, and various living neognath birds; see Table DR2 in the GSA Data Repository), but is significantly higher than those of crocodylian and megapode bird populations that abandon or rarely attend their nests (≤50%; Fig. 4A; Table DR2), due to an increase in nest predation rate (Metzen, 1977; Hunt and Ogden, 1991). Because high concentrations of clutches can attract predators (Webb et al., 1983), colonial nesting is beneficial for living archosaur species that attend/protect their nests, as it tends to reduce predation rates (Coombs, 1989; Siegel-Causey and Kharitonov, 1990). However, the absence of adults at nesting colonies is much more deleterious than their absence at solitary nests, as it results in increased nest predation rates (i.e., predation rates of 71% and 42%, respectively; Webb et al., 1983) and presumably in lower nesting success rates. Within the Late Cretaceous Javkhlant ecosystem, eggs were likely at risk of depredation, as several potential predatory species, such as turtles, lizards, non-avian theropods, and eutherian mammals, were present (Eberth et al., 2009; Nesbitt et al., 2011). As such, nest attendance/protection associated with colonial nesting could have increased the nesting success of these Javkhlant theropods.

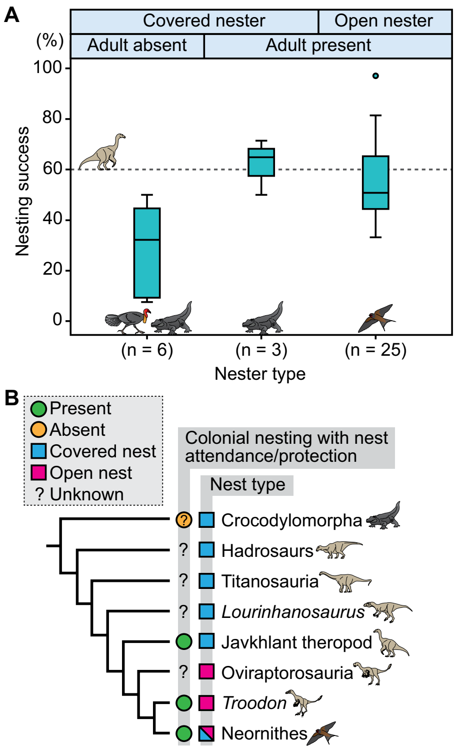

Figure 4. Comparison of nesting attributes in archosaurs. (A) Boxplot of nesting success, showing a high percentage in populations that attend and/or protect their nests during incubation (crocodylians: mean = 62.1%, range = 50.0%–71.4%; birds: mean = 55.6%, range = 32.9%–97.0%), and a lower percentage in crocodylian and megapode populations that abandon or rarely attend their nests (mean = 29.3%, range = 7.5%–50.0%). Dashed line indicates the estimated nesting success (60%) of the Javkhlant (eastern Gobi Desert, Mongolia) non-avian theropod. (B) Evolution of nesting traits in archosaurs, showing the Javkhlant non-avian theropod fills a gap in nesting behavior between derived theropods (e.g., oviraptorosaurs and troodontids) and more primitive dinosaurs (modified from Tanaka et al., 2015).

When considered in an evolutionary context, this study supports the idea of a gradual acquisition of avian reproductive traits through theropod evolution (Fig. 4B; see Varricchio and Jackson, 2016). Although widespread among living birds, nest attendance/protection behavior among colonial nesters appears to have first evolved in non-brooding non-avian dinosaur species. Open nesting style and brooding behaviors were acquired subsequently in more derived maniraptorans, and some species maintained colonial nesting likely to improve reproductive success.

CONCLUSIONS

Colonial nesting behavior in dinosaurs is difficult to demonstrate due to the nature of the geologic record. Only under rare depositional circumstances, and via detailed sedimentologic and taphonomic investigation, can evidence supporting this behavior be demonstrated. The Javkhlant nesting site is unique in preserving various lines of evidence, both sedimentologic and taphonomic, indicating colonial nesting associated with nest attendance/protection behaviors in a non-brooding non-avian dinosaur. Although widespread in birds, these behaviors may have first evolved in non-avian dinosaur species to increase hatching success in ecosystems subject to high nest predation pressure.

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