

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

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## **SUPPLEMENTARY TEXT**

### **Field Data Collection**

Excavation at the Javkhlant nesting site occurred every summer from 2012 to 2015 and during the summer of 2018 (Figs. DR1–3). Eggs were excavated carefully to observe sediments both inside and outside the eggs (Fig. DR2). Sedimentologic and taphonomic data, as well as egg/clutch morphology (e.g., clutch size and configuration, egg diameter) were recorded in the field. Egg clusters that had at least three eggs visible were considered as *in situ*; isolated pairs of eggs and localized high concentrations of eggshell fragments were not considered to represent clutches. Two partial clutches containing six and 30 eggs were collected and are repositated at the Institute of Paleontology and Geology (MPC-D), Mongolian Academy of Sciences, Ulaanbaatar, Mongolia for further preparation (MPC-D 100/1030 for the clutch of 30 eggs, although 20 eggs were collected, and MPC-D 100/1031 for the clutch of six eggs).

Aerial photography of the nest site was acquired with the use of a drone (DJI Mavic Pro) to analyze clutch distribution. The surficial extent (m<sup>2</sup>) of the nest site was estimated with photogrammetric techniques, using software Agisoft PhotoScan Standard v. 1.3.2 and Image J v.

1.51K (W. Rasband, National Institutions of Health, Bethesda, USA). The surface area of the exposed egg-bearing horizon was estimated by adding elevation contour lines on the photogrammetric image, using the software CloudCompare v. 2.9.1 ([www.cloudcompare.org](http://www.cloudcompare.org)).

### **Microscopic Analyses of eggshell fragments and rock samples**

Eggshell fragments from ten clutches (MPC-D 100/1031 through MPC-D 100/1039 and MPC-D 100/1048), five clusters of paired eggs (MPC-D 100/1041 through MPC-D 100/1044 and MPC-D 100/1049), and rock samples from one clutch (MPC-D 100/1040) were thin-sectioned and analyzed using a scanning electron microscope and petrographic light microscope at the Hokkaido University (Japan), Nagoya University (Japan), University of Tsukuba (Japan), and University of Calgary (Canada). Eggshell thickness (in mm) was measured from radial thin sections, whereas pore density ( $\text{mm}^{-2}$ ) and cross-sectional, single pore area ( $\text{mm}^2$ ) were calculated from tangential thin sections, using Adobe Photoshop v. 12.01 and Image J.

### **Petrographic analysis of sedimentary layers at Javkhlant nesting site**

Thin sections were made of the four lithologic layers present at the Javkhlant nesting site and examined with a polarizing petrographic microscope.

Light gray sediment underlying the egg clutches (Fig. 3C): Feldspathic sandy mudstone, ~25% sand particles in mudstone matrix. The rock is poorly to very poorly sorted. Sand grains range from very fine to very coarse in size, with the majority in the very fine to fine range. Pebble-sized fragments of volcanic rock are present. Sand grains range from very angular to subrounded in shape, with the majority being subangular. Mineralogical composition consists of 5% pedogenic carbonate nodules (*in situ*, not detrital), 5% calcite fragments or cement, 5% lithic

fragments (volcanic rocks, mudclasts), 10% chert, 10% plagioclase, 30% potassium feldspars, and 35% quartz. Pedogenesis is indicated by the presence of birefringent illuvial clay coatings lining infilled root traces and pores as well as b-fabric of groundmass (see Bullock et al., 1985). Pedogenic carbonate nodules can reach 2 cm in diameter or larger in outcrop.

Dull orange sediment filling bottom of eggs (Fig. 3D): Feldspathic sandy mudstone, ~35% sand particles in mudstone matrix. The rock is poorly to very poorly sorted and contains mudclasts and small scattered eggshell fragments (approximately 0.5 cm in length: Fig. DR2). Sand grains range in size from very fine sand to very coarse, with the majority in the very fine to medium range. Sand particles range from very angular to subrounded in shape, with the majority being subangular. In hand sample, the unit fines-upwards, with larger particles concentrated at the base of the unit but rare toward the top. Sand grains are more consistent in size (i.e., better sorted) near the top. Mineralogical composition consists of <5% pedogenic carbonate nodules (*in situ*, not detrital), traces of calcite fragment or cement, 5% chert, 5% plagioclase, 5% lithic fragments (primarily mudclasts), 35% potassium feldspars, and 45% quartz. Pedogenesis is indicated by the presence of birefringent clay around clasts and long pores, representing illuvial clay. Birefringent b-fabric of groundmass (see Bullock et al., 1985) is better developed than in underlying unit.

Red marker bed covering the clutches (Fig. 3E): Feldspathic very sandy mudstone, ~45% sand grains in mudstone matrix. The rock is very poorly sorted and contains reworked mudclasts, pebbles, and caliche nodules. Particles range in size from very fine sand to pebbles, with the majority in the medium sand size range. Clasts range from very angular to subrounded in shape, with the majority subrounded-to-subangular. Subtle fining-upward trend in which coarser particles are located in the lower half of the unit and finer particles in the upper half.

Mineralogical composition consists of 5% chert, 5% calcite fragments, 10% pedogenic carbonate nodules (*in situ*, not detrital), 10% lithic fragments (lots of volcanic fragments), 10% plagioclase, 30% quartz, and 30% potassium feldspars. Well-developed birefringent b-fabric (see Bullock et al., 1985) in finer, upper part of sample, some related to illuvial clay coatings. Lower part of samples is much less birefringent, and illuvial clay is less common.

Transition between red marker bed and overlying dull orange sediment is abrupt with respect to density and abundance of sand grains, but color change is more gradual, occurring over 5 to 10 mm. Pebble-sized (7–12 mm in diameter) pedogenic carbonate nodules occurring at the transition between the two lithologic units engulf surrounding sand particles, indicating that the carbonate nodules developed after deposition of the units (i.e., pedogenic in origin) and thus are not detrital in origin.

Dull orange sediment overlying red marker bed: Feldspathic sandy mudstone, ~30% sand particles in mudstone matrix. The rock is poorly sorted. Sand grains range in size from very fine sand to very coarse sand, with the majority in the fine to medium size range. Clasts range from angular to subrounded in shape, with the majority subrounded to subangular. Mineralogical composition consists of 5% chert, 5% lithic fragments (almost no volcanic fragments), 5% plagioclase, 40% potassium feldspars, and 45% quartz. Areas of high birefringence representing illuvial clay coatings around grains and along pores/root traces. Otherwise, birefringent b-fabric of groundmass is indicative of pedogenesis (see Bullock et al., 1985).

Carbonate nodules are found in the stratigraphic interval ranging from the top of the light gray unit underlying the egg clutches through the base of the dull orange unit overlying the red marker bed that covers the eggs (Fig. DR3). As these nodules have margins that engulf surrounding sand particles, they clearly formed *in situ* and are not detrital in origin (i.e., not

transported). As such, they are the result of pedogenic processes and formed subsequent to burial of the egg clutches and incorporation of the associated lithological units into the Bk horizon of a calcic soil profile.

### **Inference of Nest Type**

To infer the nest type in which the Javkhlant eggs were incubated, eggshell porosity (i.e., sum of cross-sectional surface area of all pores in an egg divided by pore length, in mm, according to Ar et al., 1974) and egg mass (in g) were estimated following Toien et al. (1988) and Tanaka et al. (2015). Eggshell porosity was calculated by multiplying pore density, by the surface area of an egg (in  $\text{mm}^2$ ) and the cross-sectional area of a single pore, divided by eggshell thickness. In the Javkhlant eggs, pore density and pore area vary throughout the thickness of the eggshell (Fig. DR4); pore density and the cross-sectional area of a single pore are both extremely high at the midpoint of the shell thickness (in average  $13.46 \text{ pores/mm}^2$  and  $0.15 \text{ mm}^2$ , respectively: Fig. DR4C), but they are significantly reduced in the outermost quarter (23.89% of the eggshell thickness) of the eggshell thickness ( $1.27 \text{ pores/mm}^2$  and  $0.004 \text{ mm}^2$ , respectively: Fig. DR4B). Thus, the total number of pores in an egg (i.e., pore density multiplied by the surface area of the egg, which is  $52,917 \text{ mm}^2$ ) can be estimated to be 712,348 pores at the midpoint of the shell thickness and 67,124 pores at the periphery of the eggshell. Although pores were assumed to have a straight tubular shape as pore shape is generally round in cross-section (Fig. DR4), the pore canals of the Javkhlant eggshell are somewhat irregularly-shaped as the cross-sectional pore area significantly decreases in the outermost part of the eggshell. The change in pore area across the eggshell was taken into consideration following the method of Toien et al. (1988), who applied both Stefan's law and Fick's law to estimate eggshell porosity.

Assuming that only 67,124 pores pierce the outer surface and that cross-sectional pore area is  $0.004 \text{ mm}^2$  at the outermost quarter (23.89%) of the eggshell thickness and  $0.15 \text{ mm}^2$  at the inner third, eggshell porosity can be estimated to be 645.88 mm. Egg mass and surface area of an egg were estimated based on the average diameter of eggs, following the methods of Paganelli et al. (1974) and Hoyt (1979). Nest type (covered vs. open nests) of the Javkhlant eggs was then inferred based on values of eggshell porosity and egg mass (Fig. DR5). A linear discriminant analysis on these values, the methods of which are outlined by Tanaka et al. (2015), was conducted with IBM SPSS Statistics v. 22.0.0 (IBM SPSS Inc.).

### **Taxonomic Identification of the Javkhlant Eggs**

Morphologically, the eggs/eggshells are all ascribable to a single egg species (i.e., oospecies) and their presence in a single horizon suggests that all clutches were likely laid by the same dinosaur species. Eggs vary between 10 and 15 cm (mean = 13 cm) in diameter and the eggshells vary between 1.32–1.91 mm (mean = 1.55 mm) in thickness. The eggshell microstructure consists of fan-shaped shell units with irregular branches emanating from the base of the individual shell units (Fig. DR4A). Pore canals are irregular in shape. These microstructures are characteristic of the oofamily Dendroolithidae, which has been attributed to non-avian theropods based on previous discoveries of association with embryos of Megalosauroidea (Araujo et al., 2013; Ribeiro et al., 2014) or Therizinosauria (Manning et al., 1997; Kundrat et al., 2008). A recent phylogenetic analysis using dinosaur egg/eggshell characters also suggests that dendroolithid eggs belong to Theropoda (Vila et al., 2017), although Dendroolithidae is morphologically dissimilar from the eggs of non-avian maniraptorans closely

related to Aves (e.g., elongated eggs with two- or three-layered eggshell of oviraptorosaurs and troodontids: Norell et al., 1994; Clark et al., 1999; Varricchio et al., 2002).

### **Inference of Incubation Style in Javkhlant Dendroolithidae**

Determination of the incubation style of the Javkhlant dendroolithid eggs, i.e., whether the eggs were incubated in mound nests using heat derived from microbial decay or in-filled hole nests using solar or geothermal heat, was based on their association with lithofacies. In extant covered nesters (i.e., crocodylians and megapode birds), nest substrates reflect incubation style; organic-rich soil is used in mound nests that relies on microbial decay whereas sand-dominated substrate is used in in-filled hole nests that relied on solar or geothermal heat for incubation (Tanaka et al., 2018). Based on this relationship, incubation style of extinct dinosaurs has been inferred; hadrosaur and some sauropod (megaloolithid) clutches that occur in fine-grained pedogenic sediments suggest mound nesting with heat derived from microbial decay for incubation, whereas other sauropod (faveoolithid) clutches that occur in sandstone or conglomerate suggest in-filled hole nesting with solar or geothermal heat. Clutches of the Javkhlant dendroolithid are found in pedogenic sandy mudstone, suggesting that the Javkhlant eggs were incubated with heat from microbial decay in organic-rich mound nests.

## SUPPLEMENTARY TABLES

Table DR1. Reported colonial nesting grounds of non-avian dinosaurs.

Taxon/oootaxon	Size of colony	Formation	Locality
Ovaloolithidae <sup>1</sup>	?	Bayanshiree (Campanian)	Mogoyin-Ulagiyn-Khaets, Mongolia
<i>Maiasaura</i> <i>peeblesorum</i> <sup>2</sup>	Eight clutches, including nests of juveniles and eggshell concentrations, from a single horizon	Two Medicine (Campanian)	Willow Creek Anticline, Montana, USA
Possible <i>Lufengosaurus</i> <sup>3</sup>	Embryonic bonebed with eggshells	Lufeng (Sinemurian)	Kunming, Yunnan Province, China
<i>Massospondylus</i> <i>carinatus</i> <sup>4</sup>	10 clutches from at least four horizons	Upper Elliot (Lower Jurassic)	Golden Gate Highlands National Park, South Africa
Sauropodomorpha ( <i>Megaloolithus</i> <i>matleyi</i> ) <sup>5</sup>	10 clutches from a single horizon (Site B: <60 m <sup>2</sup> )	Lameta (Maastrichtian)	Pavna, Chandrapur, Maharashtra, India
Titanosauridae ( <i>Megaloolithus</i> <i>patagonicus</i> ) <sup>6,7</sup>	Hundreds of clutches from at least four beds (e.g., 74 and 31 clutches from areas of 1701 and >486 m <sup>2</sup> , respectively)	Anacleto (Campanian)	Auca Mahuevo, Neuquen Province, Patagonia, Argentina
Sauropodomorpha ( <i>Megaloolithus</i> <i>rahioliensis</i> ) <sup>8</sup>	11 clutches from a single horizon (1200 m <sup>2</sup> )	Lameta (Maastrichtian)	Rahioli, Balasinor Taluka, Kheda, Gujarat, India
Sauropodomorpha ( <i>Megaloolithus</i> <i>siruguei</i> ) <sup>9</sup>	Six clutches from a single horizon (Egg Horizon 5)	Tremp (Maastrichtian)	Coll de Nargo, Lleida, Catalonia, Spain
Sauropodomorpha ( <i>Megaloolithus</i> sp.) <sup>10,11</sup>	24 clutches from a single bed (6000–8000 m <sup>2</sup> )	Aren (Maastrichtian)	Bastus, Tremp syncline, southern



			Pyrenees, Catalonia, Spain
Sauropodomorpha ("Hypselosaurus <i>priscus</i> ": Megaloolithidae) <sup>12,13</sup>	>115 eggs from at least three horizons (31 m <sup>2</sup> )	Maastrichtian marls	Rennes-le-Chateau, Aude, France
Sauropodomorpha (Megaloolithidae) <sup>14</sup>	Nine clutches from a single horizon (5000 m <sup>2</sup> )	Lameta (Maastrichtian)	Pat Baba Mandir, Madhya Pradesh, India
Sauropodomorpha (Faveoolithidae) <sup>15,16</sup>	>70 clutches from three horizons in 10 sub-sites (300,000 m <sup>2</sup> )	Los Llanos (Hauterivian- Aptian)	Sanagasta, La Rioja, Argentina
Sauropodomorpha (Faveoolithidae) <sup>17</sup>	Clutches and eggs from at least 10 horizons	Shiwha (Aptian)	Whaseong, Gyeonggi Province, South Korea
Non-avian theropod (Dendroolithidae) <sup>18</sup>	15 clutches from a single horizon (136 m <sup>2</sup> )	Javkhlant (?Santonian– Campanian)	Eastern Gobi, Mongolia
<i>Troodon formosus</i> ( <i>Prismatoolithus levis</i> ) <sup>2</sup>	10 clutches from three horizons	Two Medicine (Campanian)	Willow Creek Anticline, Montana, USA

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Sources: 1, Mikhailov et al. (1994); 2, Horner (1982); 3, Reisz et al. (2013); 4, Reisz et al. (2012); 5, Mohabey (1996); 6, Chiappe et al. (2001); 7, Chiappe et al. (2004); 8, Srivastava et al. (1986); 9, Vila et al. (2010); 10, Sanz et al. (1995); 11, Sander et al. (1998); 12, Cousin et al. (1989); 13, Cousin et al. (1994); 14, Sahni et al. (1994); 15, Grellet-Tinner and Fiorelli (2010); 16, Fiorelli et al. (2012); 17, Lee (2003); 18, this study.

Table DR 2. Nesting success in the Javkhlant non-avian theropod and living archosaurs. Values of nesting success in living birds were compiled primarily from the datasets of Hickey (1955) and Nice (1957), with additional sources cited in the table. For each case, mean nesting success was calculated. The mean nesting success rate of cases where adults are usually absent at the nests is 29.31% (n = 6) and the mean nesting success rate of cases where adults are present at the nests/protect the nests is 56.26% (n = 28). A two-independent-samples T-test (conducted with the software IBM SPSS Statistics v. 25.0.0, IBM SPSS Inc.) revealed that nesting success is significantly higher in populations where adults are usually present at the nests than those where adults are usually absent ( $T = -3.876$ ,  $df = 32$ ,  $p < 0.001$ ).

<b>Taxon</b>		<b>Number of nests</b>	<b>Nesting success (%)</b>
Dinosauria <sup>1</sup>	Javkhlant Dendroolithidae	15	60.0
<b>Covered nest type: adult usually absent</b>			
Crocodylia <sup>2-6</sup>	<i>Alligator mississippiensis</i>	485	44.7
Crocodylia <sup>7</sup>	<i>Caiman crocodilus</i>	40	7.5
Crocodylia <sup>8</sup>	<i>Caiman yacare</i>	48	20.8
Crocodylia <sup>9</sup>	<i>Crocodylus acutus</i>	46	9.4
Crocodylia <sup>10</sup>	<i>Crocodylus johnstoni</i>	88	43.4
Galliformes <sup>11</sup>	<i>Leipoa ocellata</i>	68	50.0
<b>Covered nest type: adult usually present</b>			
Crocodylia <sup>3,5,12,13</sup>	<i>Alligator mississippiensis</i>	153	64.9
Crocodylia <sup>14</sup>	<i>Caiman yacare</i>	24	50.0
Crocodylia <sup>15</sup>	<i>Melanosuchus niger</i>	7	71.4
<b>Open nest type: adult present</b>			
Anseriformes <sup>16</sup>	<i>Somateria mollissima</i>	963	37.5
Columbiformes <sup>17,18-21</sup>	<i>Zenaidura macroura</i>	5329	48.0
Galliformes <sup>22</sup>	<i>Bonasa umbellus</i>	1431	61.4
Galliformes <sup>23,24</sup>	<i>Callipepla californica</i>	155	40.2

Galliformes <sup>25-27</sup>	<i>Centrocercus urophasianus</i>	534	43.2
Galliformes <sup>28,29</sup>	<i>Colinus virginianus</i>	791	41.0
Galliformes <sup>30,31</sup>	<i>Lagopus lagopus</i>	232	71.5
Galliformes <sup>32-34</sup>	<i>Perdix perdix</i>	19468	48.0
Galliformes <sup>35-39</sup>	<i>Phasianus colchicus</i>	1991	32.9
Galliformes <sup>40</sup>	<i>Tympanuchus cupido</i>	100	47.7
Galliformes <sup>40</sup>	<i>Tympanuchus phasianellus</i>	22	50.0
Gruiformes <sup>41</sup>	<i>Fulica americana</i>	380	97.0
Passeriformes <sup>20</sup>	<i>Bombycilla cedrorum</i>	14	57.1
Passeriformes <sup>42</sup>	<i>Calcarius mccownii</i>	45	60.0
Passeriformes <sup>43</sup>	<i>Carduelis tristis</i>	24	66.7
Passeriformes <sup>20</sup>	<i>Dendroica petechia</i>	12	41.7
Passeriformes <sup>20</sup>	<i>Dumetella carolinensis</i>	22	54.5
Passeriformes <sup>44</sup>	<i>Emberiza calandra</i>	53	75.5
Passeriformes <sup>45</sup>	<i>Eremophila alpestris</i>	30	60.0
Passeriformes <sup>46</sup>	<i>Melospiza melodia</i>	223	48.0
Passeriformes <sup>20</sup>	<i>Quiscalus quiscula</i>	88	50.6
Passeriformes <sup>48</sup>	<i>Saxicola rubetra</i>	129	44.2
Passeriformes <sup>49</sup>	<i>Spizella passerina</i>	88	65.9
Passeriformes <sup>50</sup>	<i>Spizella pusilla</i>	16	81.3
Passeriformes <sup>51-53</sup>	<i>Turdus migratorius</i>	372	65.1

Sources: 1, this study; 2, Joanen (1969); 3, Metzen (1977); 4, Goodwin and Marion (1978); 5, Deitz and Hines (1980); 6, Ruckel and Steele (1984); 7, Staton and Dixon (1977); 8, Crawshaw and Schaller (1980); 9, Kushlan and Mazzotti (1989); 10, Webb et al. (1983); 11, Frith (1959); 12, Wilkinson (1984); 13, Platt et al. (1955); 14, Cintra (1988); 15, VillamarIn-Jurado and Suarez (2007); 16, Choate (1967); 17, Nice (1939); 18, Pearson and Moore (1939); 19, McClure (1946); 20, Young (1949); 21, Cowan (1952); 22, Darrow (1947); 23, Glading (1938); 24, Williams (1967); 25, Rasmussen and Griner (1938); 26, Keller et al. (1941); 27, Patterson (1949); 28, Stoddard (1931); 29, Lehmann (1946); 30, Olstad (1932); 31, Kristoffersen (1937);

32, Hickey (1955); 33, Yeatter (1934); 34, McCabe and Hawkins (1946); 35, Hamerstorm (1936); 36, Randall (1940); 37, Leedy and Hicks (1945); 38, Rasmussen and McKean (1945); 39, Baskett (1947); 40, Hamerstrom (1939); 41, Kiel (1955); 42, Mickey (1943); 43, Walkinshaw (1939); 44, Ryves and Ryves (1934); 45, Pickwell (1931); 46, Nice (1937); 47, Petersen and Young (1950); 48, Schmidt and Hantge (1954); 49, Walkinshaw (1952); 50, Walkinshaw (1945); 51, Howell (1942); 52, Koehler and Koheler (1945); 53, Young (1955).

## SUPPLEMENTARY FIGURES

Figure DR1. The Javkhlant nesting site during excavation.



Figure DR2. Sedimentology of the Javkhlant eggs. (A) *In situ* partial egg (only the lower half is preserved) after surface cover was removed, showing the in-filled dull orange sandy mudstone. (B) Line drawing of (A), showing pedogenic carbonate nodules (white) and pebbles (black) inside of the egg. (C) Same egg after excavation. Box represents the area of (E) and (F). (D) Line drawing of (C), showing the intact eggshell of the egg bottom (dark grey) and scattered eggshell fragments (light grey). (E) Close-up of the scattered eggshell fragments at the bottom. (F) Line drawing of (E), showing the intact eggshell (dark grey) and scattered eggshell fragments (light grey). Scale bars, (A–D) 2 cm, (E, F) 0.5 cm.



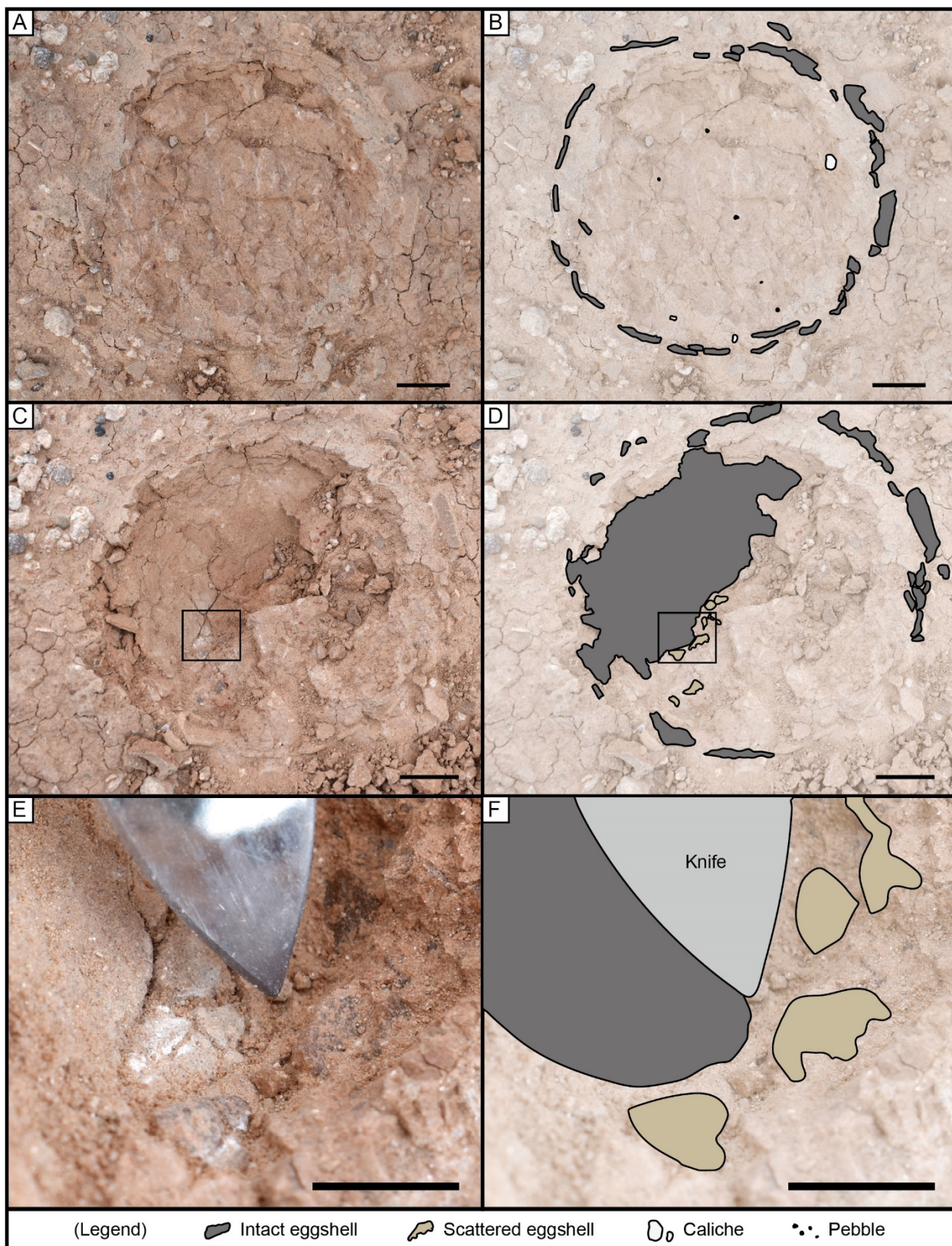




Figure DR3. Sedimentology of Javkhlant egg clutch MPC-D 100/1040. (A) Natural cross-section through same egg featured in Figure 3A but three years later. Natural weathering has emphasized the presence of pedogenic carbonate nodules. (B) Interpretive illustration of sedimentary units recognized in (A). Note that the dull orange sandy mudstone layers deposited in two different episodes.

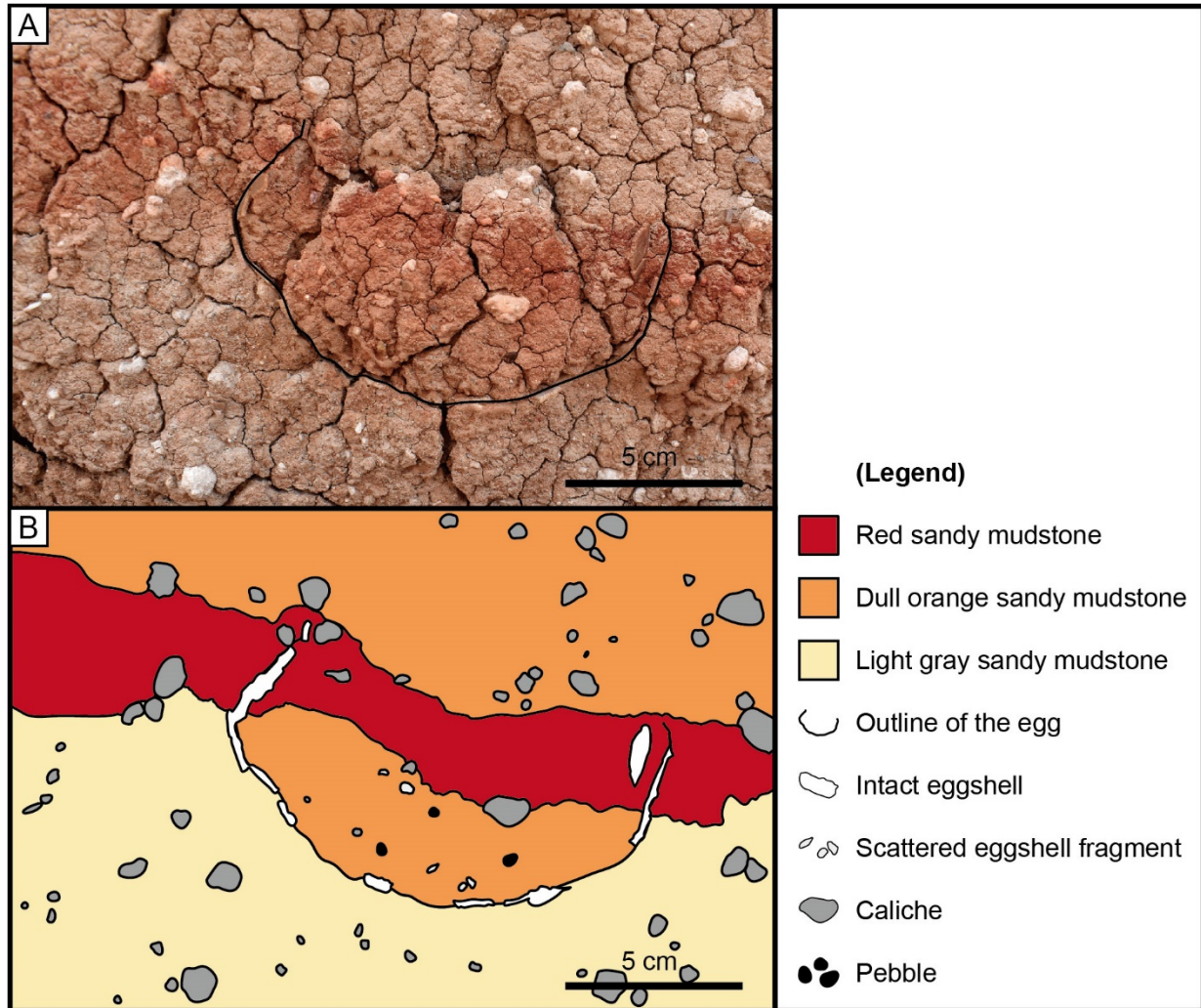




Figure DR4. Microstructure of the Javkhlant eggshell. (A) Radial view of eggshell under scanning electron microscope, revealing fan-shaped shell units with branching structures (broken lines) (MPC-D 100/1041). (B) Tangential thin section of eggshell at the uppermost part of the eggshell thickness, showing a paucity of pores (arrows) (plane light) (MPC-D 100/1044). (C) Tangential thin section of eggshell at the middle part of the eggshell thickness, showing abundant pores (plane light) (MPC-D 100/1032). All scale bars equal to 1 mm.

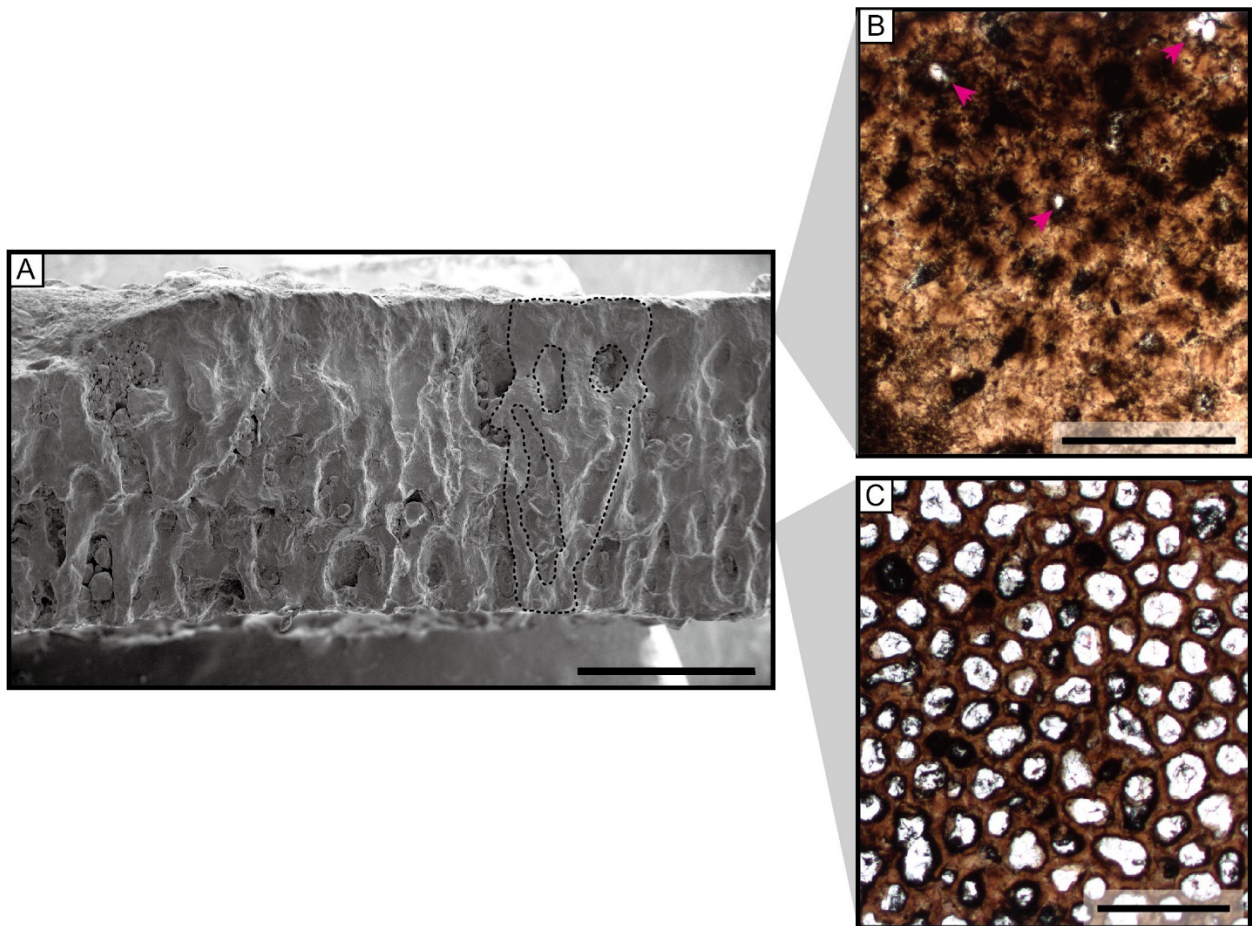
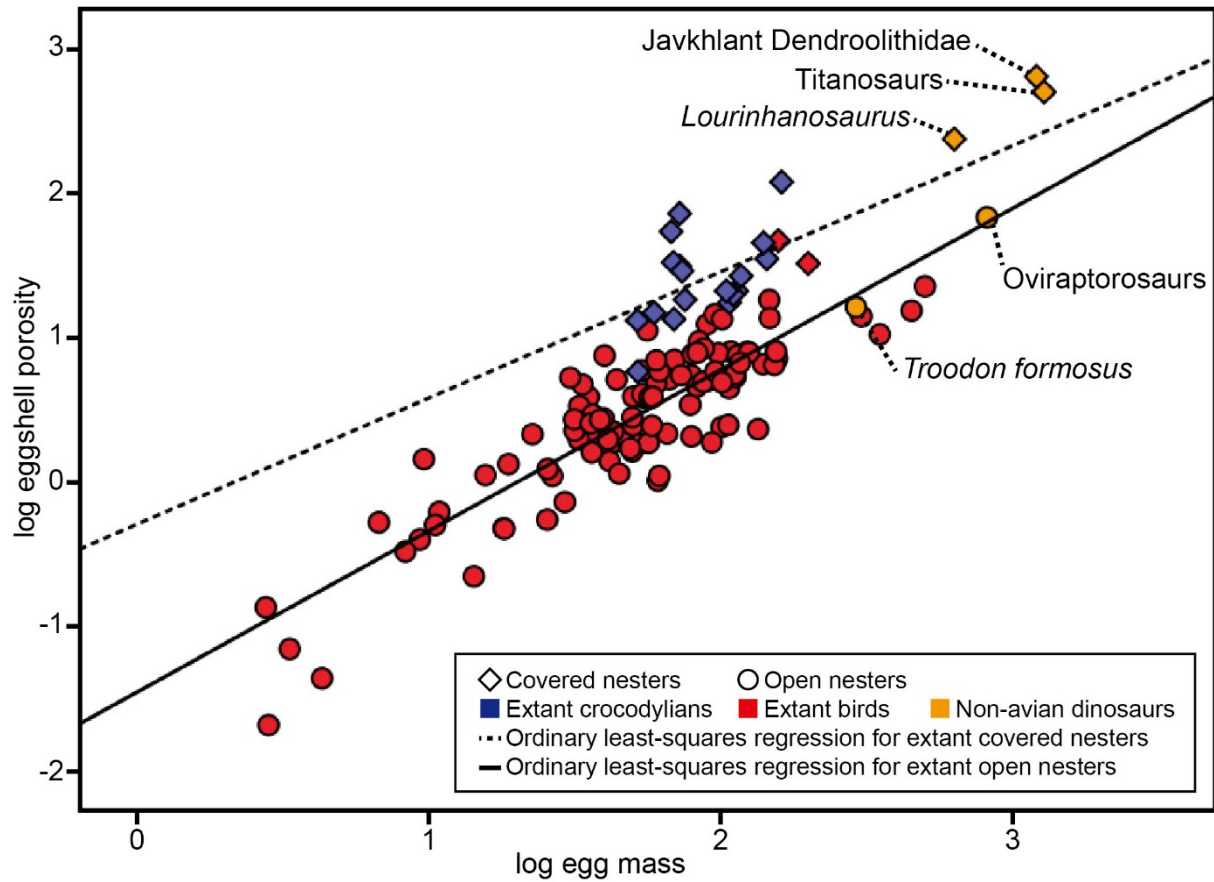


Figure DR5. Bivariate plot of eggshell porosity and egg mass in archosaurs. Note that eggshell porosity of the Javkhlant dendroolithid theropod is higher than that of open nesters, but comparable to that of covered nesters. Modified from Tanaka et al. (2015).



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