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An accumulation of turtle eggs with embryos from the Campanian (Upper Cretaceous) Judith River Formation of Montana

Daniel R. Lawver [a, b, *], Frankie D. Jackson [a]

[a] Department of Earth Sciences, Montana State University, Bozeman, MT, 59717, USA
[b] Museum of the Rockies, Bozeman, MT, 59717, USA

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ABSTRACT

A weathered accumulation of turtle eggs, interpreted as remnants of a single clutch composed of at least 16 turtle eggs (MOR 710) from the Campanian (Upper Cretaceous) Judith River Formation of north-central Montana, USA, represents a new oospecies *Testudoolithus zelenitskyae*. This ootaxon is diagnosed by the following unique combination of characters: spherical eggs 34–39 mm in diameter, 660–760 μm thick eggshell, shell unit height-to-width ratio of 3.15:1–5.5:1, and domed shell units. Estimated egg mass indicates that the egg-laying adult likely possessed a carapace 35.0–54.4 cm in length. Similarities between *T. zelenitskyae* oosp. nov. and *Adocus* sp. eggs, along with comparable body size, suggest that this taxon might have produced MOR 710. One egg exhibits abnormal multilayered eggshell, likely resulting from prolonged egg retention by the female turtle. At least five of these eggs, including the multilayered specimen, preserve embryonic remains that demonstrate a late stage of embryonic development. This suggests that death occurred just prior to hatching.

1. Introduction

Fossil turtle egg clutches, gravid adults, and turtle embryos are relatively rare in the rock record when compared to dinosaurian specimens (Lawver and Jackson, 2014). Jackson et al. (2008) report an in situ turtle egg clutch preserving 23 spherical eggs in three superimposed layers from the Albian (Lower Cretaceous) deposits of Tiantai basin of Zhejiang, China. Zelenitsky et al. (2008) describe a clutch of 26 eggs from the Campanian (Upper Cretaceous) Oldman Formation of Alberta, Canada and estimated that a female with carapace length of 49.5 cm produced the clutch. A possible tortoise clutch containing at least five eggs comes from the Pliocene Apolakkia Formation of Rhodes, Greece (Mueller-Töwe et al., 2011), and fossil egg clutches from the Pleistocene of Lord Howe Island, Australia are tentatively assigned to the stem turtle, *Meiolania platyceps* (Anderson, 1925; Gaffney, 1996; Lawver and Jackson, in press).

In contrast to these turtle clutches, fossil gravid turtles provide definitive assignment of eggs to a specific taxon. A gravid turtle and a turtle clutch from the Upper Cretaceous Dinosaur Park and Oldman formations, respectively, show similar eggshell microstructure. Zelenitsky et al. (2008) conclude that both are referable to *Adocus* sp. Likewise, Knell et al. (2011) report portions of two eggs within a gravid *Adocus* sp. from the Campanian (Upper Cretaceous) Kaiparowits Formation of Utah. Additionally, an undescribed gravid *Basilemys variolosa* from the Dinosaur Park Formation of Alberta, Canada preserves at least three eggs that were discovered when the specimen was inadvertently damaged (Braman and Brinkman, 2009). Finally, a eurysternid specimen from the Upper Jurassic of Solnhofen in Germany contains spherical objects that Joyce and Zelenitsky (2002) interpreted as highly altered eggs.

Fossil turtle embryos are known from North America (Zelenitsky, 1995; Clouse, 2001; Jackson and Schmitt, 2008; Zelenitsky et al., 2008; McGee, 2012), Asia (Mikhailov et al., 1994; Cohen et al., 1995; Fang et al., 2009), and Europe (Hemprich, 1932). Although, morphological analysis of these specimens could assist in determining their taxonomic affinity, only one specimen has been investigated. Using computerized tomography (micro-CT) McGee (2012) confirmed that *Adocus* sp. produced the clutch from the Oldman Formation, thereby agreeing with the previous identification of Zelenitsky et al. (2008).

Although rare, fossil turtle clutches, gravid females, and embryonic remains provide important information about the

* Corresponding author. Department of Earth Sciences, Montana State University, Bozeman, MT, 59717, USA.
E-mail addresses: danlawver@gmail.com (D.R. Lawver), frankiej@montana.edu (F.D. Jackson).

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evolution of turtle reproduction and paleoecology. Here, we describe a weathered accumulation of turtle eggs (some containing embryos), which we interpret as remnants of a single clutch. The egg accumulation is from the Campanian strata of the Judith River Formation of north-central Montana, USA. Jackson and Schmitt (2008) briefly report the microstructure of the multilayered egg from this clutch when establishing criteria for recognition of egg abnormalities in the fossil record. However, a detailed description of the clutch was beyond the scope of their paper. Jackson and Schmitt (2008) simply referred to this egg as MOR 710, whereas here it is assigned as MOR 710B. We describe this weathered clutch, assign the eggs to parataxonomy, and discuss the implications for the evolution of turtle reproductive biology.

Institutional Abbreviations: AM, Australian Museum, Sydney, New South Wales, Australia; BMNH, The Natural History Museum, London, United Kingdom; HEC, Hirsch Eggshell Catalogue, University of Colorado, Boulder, Colorado, U.S.A; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LBA, L. Barry Albright field number; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A; MOR, Museum of the Rockies, Bozeman, Montana, U.S.A; NHMU, Natural History Museum of Utah, Salt Lake City, Utah, U.S.A; TMP, Royal Tyrrell Museum of Paleontology, Alberta, Canada; UCM, University of Colorado Museum, Boulder, Colorado, U.S.A; ZMNH, Zhejiang Museum of Natural History, Hangzhou, Zhejiang Province, China.

2. Materials and methods

The fossil turtle eggs studied are housed at the Museum of the Rockies (MOR) in Bozeman, Montana. Two multilayered eggshells were removed from an egg from MOR 710. One was etched with hydrochloric acid for about five seconds in order to better reveal the fine crystalline structure. Histological radial sections were made through eggshell fragments from both normal eggs (MOR 710A, C), the multilayered specimen (MOR 710B), and an embryonic costal element labeled MOR 710:EB 3 (the exact location of the section is indeterminate). Additional eggshell thin sections (MOR 710:ES 1–3) came from unspecified eggs within the clutch. Histological procedures follow Lamm (2013). Eggshell fragments were mounted on an aluminum stub, coated with 10 nm of gold, and imaged under a JEOL JSM-6100 scanning electron microscope (SEM) at 10 kV. Images included the inner surface and radial cross sections of the eggshell. Photomicrographs of histological sections of eggshell and bone were taken with a Nikon Digital Sight DS-5Mc camera and microstructural features were measured with the image analysis software ImageJ (Rasband, 1997; http://imagej.nih.gov/ij/). Assessment of potential diagenetic alteration of the eggshell included a Nikon eclipse 50i microscope equipped with cathodoluminescence (CL). Egg mass was calculated using Hoyt's (1979) equation:

$$\text{Mass} = 0.000548 \times \text{LB}^2$$

where L is egg length in mm and B is egg breadth in mm. Carapace length for the gravid female turtle that produced MOR 710 is estimated using the positive correlation between egg mass and adult carapace length (Elgar and Heaphy, 1989) and the regression line:

$$y = 0.0568x + 1.5811$$

The latter was derived from 63 species (Elgar and Heaphy, 1989: Appendix), where y is the egg mass and x is carapace length ($r^2 = 0.666$). Note that the regression equation provided in Elgar and Heaphy (1989: Fig. 1) contains a typographical error, which results in unrealistically small carapace lengths.

3. Geology

The Campanian (Upper Cretaceous) Judith River and Two Medicine formations in north-central Montana consist of eastward thinning, non-marine clastic deposits that record regressive-progradational phases of shoreline migration of the Western Interior Cretaceous Seaway (Fig. 1A, B) (Lorenz, 1981; Rogers, 1998). The temporally and lithostratigraphically correlative formations are now separated by the Sweetgrass arch, a north-south-trending anticline (Fig. 1A, B). The Judith River Formation in eastern Montana includes deposits of a broad lowland coastal alluvial plain (Rogers, 1998). Marine rocks of the Claggett and Bearpaw formations underlie and overlie the formation, respectively (Rogers, 1998). Eberth et al. (1992) and Goodwin and Deino (1989) dated rocks of the Judith River Formation in central Montana as 74.5 and 78.0 Ma, respectively, which corresponds to the middle to late Campanian (Fig. 1B).

MOR 710 comes from a sandy siltstone in a fining-upward stratigraphic sequence representing overbank deposits at the Egg White Site (MOR locality JR-122L) in Hill County, near Havre, Montana (Clouse, 2001; Fig. 1). This specimen occurred approximately 4 m laterally from a clutch of lambeosaurine eggs preserved beneath a bentonite layer within the so-called upper nesting horizon of the lower nesting ground (Clouse, 2001). According to Clouse (2001), this nesting ground lies in the upper half of the Judith River Formation, deposited during the latter half of the Bearpaw Seaway transgression. Invertebrate fossils within the nesting horizon consist of freshwater and brackish species, including large unionid bivalves, as well as unidentified small bivalves and gastropods (Clouse, 2001). Vertebrate fossils include shed theropod and ornithopod teeth and fragmentary turtle shells referable to *Basilemys* sp., *Adocus* sp., *Aspideretoides* sp., and an undescribed large-bodied terrestrial form.

4. Systematic paleontology

Oofamily Testudoolithidae Hirsch, 1996 sensu Jackson et al., 2008

Oogenus *Testudoolithus* Hirsch, 1996 sensu Jackson et al., 2008

Oospecies ***Testudoolithus zelenitskyae*** oosp. nov.
Figs. 2–3

Holotype. MOR 710, the weathered remains of a clutch composed of at least 16 turtle eggs.
Etymology. After Darla Zelenitsky in recognition of her initial description of *Adocus* eggs from Alberta, Canada and continuing contribution to oological research.
Type locality and age. MOR locality JR-122L, Egg White Site, north-central Montana, U.S.A, Judith River Formation, Upper Cretaceous (Campanian).
Diagnosis. *Testudoolithus zelenitskyae* oosp. nov. differs from all other oospecies in the following unique combination of characters: spherical turtle eggs 34–39 mm in diameter; 660–760 μm thick eggshell; shell unit height-to-width ratio of 3.15:1–5.5:1 and domed shell units.
Distribution. Judith River Formation, Montana, U.S.A. (Jackson and Schmitt, 2008, MOR 710), Oldman and Dinosaur Park formations, Alberta, Canada (Zelenitsky et al., 2008, TMP 1999.63.2 and TMP 2008.27.1, respectively), and Kaiparowits Formation, Utah, U.S.A. (Knell et al., 2011, NHMU 16868 [LBA-06-7]). All these formations are Campanian (Late Cretaceous) in age.
Description
Eggs. Eleven beige eggs (Fig. 2) measuring 34–39 mm in diameter occurred on a weathered surface eroded into a concretionary layer (Fig. 1C). The lithostatically compressed eggs are filled by sandy