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Paleoecological implications of two closely associated egg types from the Upper Cretaceous St. Mary River Formation, Montana

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A B S T R A C T

Two closely associated egg types occur at the same locality in the Upper Cretaceous (Maastrichtian) St. Mary River Formation in north central Montana. These specimens represent the first fossil eggs described from this formation. At least fifteen small ovoid eggs or egg portions are scattered through a 25 cm interval of rock. Five significantly larger, round eggs overlie these smaller eggs and are in close proximity to one another on a single bedding plane. The best preserved egg of the smaller size measures 36 mm × 62 mm and exhibits the prismatic, two-layered eggshell structure of a theropod egg. The dispersed distribution and inconsistent angles of these small eggs likely resulted from disturbance by subsequent nesting activity and/or possibly nest predation. At least twelve additional small prismatic eggs also occur at this site. We assign the small eggs as a new oogenus and oospecies, *Tetonoolithus nelsoni*, within the Prismatoolithidae. The large round eggs measure 130 mm in diameter and the eggshell displays substantial diagenetic alteration. These eggs likely belonged to a hadrosaur due to their similarity in egg size, shape, and eggshell thickness to *Maiasaura* eggs from the stratigraphically lower Two Medicine Formation. Eggs at different stratigraphic levels at this site indicate that conditions favorable to both dinosaur species persisted for an extended period of time. However, determining whether these dinosaurs occupied the nesting site at the same or different years remains beyond the resolution of the rock record.

1. Introduction

Mesozoic nesting localities occasionally preserve two or more ootaxa at the same stratigraphic level or at the same general nesting locality (Salgado et al., 2007; Selles et al., 2013). Russo et al. (2014), for example, report crushed eggs belonging to the oofamily Krokolithidae collected from a theropod nesting site in the Upper Jurassic Lourinhã Formation of Portugal. Horner (1984) also reports two egg types that occurred together at three stratigraphic levels at the Egg Mountain locality in Montana; these were later assigned as *Prismatoolithus levis* Zelenitsky and Hills, 1996 (i.e., *Troodon*) and *Continuoolithus canadensis* Zelenitsky et al., 1996 (an unidentified theropod). However, closely associated egg types that are separated by a few centimeters or occur in the same nest are rare. Varricchio et al. (1999) describe a hatched or destroyed clutch of *C. canadensis* next to a nesting trace containing *Troodon* eggs at the Egg Mountain locality. Jackson and Varricchio (2010) report prismatic and spherulitic eggs immediately adjacent to one another from the lowermost Two Medicine Formation in Montana, and Fernández and Garcia (2013) report clutches of faveoloolithid and filispherulithid eggs from the Allen Formation of northern Patagonia. The filispherulithid clutch also contains a single megaloolithid egg that Fernández and Garcia (2013) suggest may represent nest parasitism.

Documentation of nesting sites facilitates a better understanding of possible association of dinosaur nests to specific lithologies in the rock record; permits recognition of past surfaces of subaerial exposure; and allows assessment of environments favored by various dinosaur species and other reproductive behaviors (Varricchio et al., 2015). However, some descriptions that mention the occurrence of different egg types at the same locality fail to discuss their spatial relationship and possible significance (e.g., Horner, 1982; Hirsch and Quinn, 1990; Jackson and Varricchio, 2010). These multiple egg occurrences provide additional information about paleoecology and nesting behavior beyond that obtainable from the eggs of either taxon alone. Here, we describe

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the occurrence of two closely associated egg types from the St. Mary River Formation, Teton County, Montana. We assign the eggs to ootaxonomy and discuss potential inferences of reproductive behavior at this site. Below, we provide the geologic setting in order to compare ootaxonomic diversity within four Upper Cretaceous formations exposed in north central and eastern Montana.

2. Geologic setting

During Late Cretaceous time an Andean-style plate collision resulted in subduction of the oceanic Farallon plate beneath the western margin of North America. The resulting foreland basin experienced marine incursions from the north and south that eventually joined to form the Western Interior Cretaceous Seaway (Kauffman, 1977). Terrigenous clastic sediments resulting from erosion of older sedimentary rocks in the Cordilleran thrust belt were delivered eastward by fluvial systems to the western margin of the Cretaceous seaway (Horner et al., 2001). Together, the Two Medicine and Judith River formations represent an eastward thinning clastic wedge of terrestrial sediments that accumulated primarily during regression of the Claggett Sea and subsequent transgression of the Bearpaw Sea (Fig. 1A: R8 and T9, respectively). The Sweetgrass arch truncates this formerly intact lithosome (Horner et al., 2001). Regression of the Bearpaw Sea (Fig. 1A: R9) produced the shoreline deposits of the Horsethief Sandstone and/or marine Bearpaw Shale over the Two Medicine Formation, whereas only the latter covers the Judith River Formation (Lorenz, 1981; Rogers et al., 2016). The clastic deposits of the St. Mary River and Hell Creek formations, respectively, overlie the Horsethief Sandstone to the west, and the transitional marine-to-brackish Fox Hills Sandstone to the east (Fig. 1; Rogers et al., 1993; Fastovsky and Bercovici, 2016).

Dawson (1884) reported the non-marine deposits of the St. Mary River Formation as Maastrichtian in age, whereas Cobban and Reeside (1952) further refined the age as early Maastrichtian. More recent work based on mammalian fossils from the St. Mary River Formation in Montana provides support for an “Edmontonian” land mammal age (approximately 74 to 67 Ma; Hunter et al., 2010). The St. Mary River Formation crops out in a relatively small area of northwestern Montana. The study area lies north and east of Augusta, Montana on the edge of the fold and thrust belt (Fig. 1B). The St. Mary River Formation varies from 300 to 400 m thick and records deposits of upland fluvial environments similar to the underlying Two Medicine Formation (Cobban, 1955; Weishampel and Horner, 1987). In contrast, lowland habitats characterize the Hell Creek Formation to the east (Weishampel and Horner, 1987). The non-marine Willow Creek Formation overlies the St. Mary River Formation, and the K–P boundary lies within this formation. The Willow Creek Formation is thought to correlate with the upper parts of the Lance and Hell Creek formations and lower part of the Fort Union Formation (Russell, 1975). All four formations yield fossil dinosaur eggs.

3. Materials and methods

Museum of the Rockies specimens MOR 1144-2 and MOR 1144 were collected from the same locality in 1991 by David Weishampel and his crew from Johns Hopkins University. The Museum of the Rockies' Saint Mary River Formation locality, SM 110, lies approximately 24 km west of Augusta, Montana in Lewis and Clark County, USA (Fig. 1B). MOR 1144-2 includes small prismatoolithid eggs and substantially larger eggs with altered eggshell, whereas the second specimen, MOR 1144, contains only the former. The lack of a measured section at the time of excavation limits stratigraphic information to data discernable from the rock surrounding the eggs in the two plaster jackets. Preparation of the specimens included removal of matrix with small hand tools and stabilizing loose eggshell fragments with glue. Egg orientations were measured with a Brunton compass. Eggshells fragments were removed from both egg types and half of each fragment was prepared as a standard petrographic thin section (30 μm thick) and studied by transmitted and polarized light microscopy. The other half of each eggshell was coated with gold (10 nm), mounted on an aluminum stub, and imaged at 15 kV under a JEOL 6100 scanning electron microscope (SEM) with backscattered electron imaging (BEI). Structural attributes (shell thickness, pore width) were measured with ImageJ analysis software (http://imagej.nih.gov/ij/).

4. Systematic paleontology

Oofamily Prismatoolithidae Hirsch, 1994
Oogenus *Tetonoolithus* oogen. nov.

Diagnosis. As for type and only oospecies.
Oospecies. *Tetonoolithus nelsoni* oosp. nov.
Figs. 2–3

Holotype. Prismatic eggs from MOR 1144-2, a specimen that also includes larger eggs with highly altered eggshell structure.
Derivation of name. Tetonoolithus for the nearby Teton River and “oolithus” from the Greek word meaning “egg stone”. The specific name “nelsoni” honors Joel Nelson, in recognition of his discovery of the specimen and many contributions to the MOR field camp at Egg Mountain.
Type locality and age. MOR locality SM 110; Teton County, north central Montana, U.S.A., Saint Mary River Formation, Upper Cretaceous (Maastrichtian).
Referred specimens. MOR 1144, a cluster of 12–13 prismatoolithid eggs.
Diagnosis (as combined characters). Smooth, ovoid eggs approximately 33 mm by 62 mm with Elongation Index (EL) of approximately 1.7. Eggshell 530–550 μm; two structural layers of calcite, with gradual transition from mammillary to prismatic layer; ML:CL = 1:3.8; unevenly distributed squamatic texture within discernable prisms.
Description. The original field sketch gave the strike and dip of the sandstones beneath the eggs as N20°W and 45°W, respectively. The sketch shows that most eggs were concentrated in an area of about 500 cm^2; however, the total number of eggs excavated from this site remains unclear. Nevertheless, MOR 1144-2 and MOR 1144 represent two jackets removed from this denser concentration of eggs. Although both jackets were prepared upside down, the following description depicts the eggs in their original orientations within the stratum.
MOR 1144-2. The 51 cm by 58 cm block preserves 15 small smooth, black egg or egg portions dispersed within 25 cm green-gray, very fine sandstone to siltstone (Fig. 2A, B). These eggs occur at three or possibly four levels and lie stratigraphically lower than the second egg type (described below). Only a few of the small eggs are in contact with one another (Fig. 2A, B). Additional eggs may occur within the matrix that supports the specimen. Eggshell debris on the edge of the plaster jacket near egg 4 suggests loss of an egg during excavation. Some of the small eggs exhibit continuity of eggshell that curves into the surrounding rock, suggesting they may represent complete, unhatched eggs. A few specimens appear more fragmentary and disturbed. For example, eggs 3, 6, 12, and 10 appear badly crushed, and egg 10 may represent large fragments from three nearby eggs. The most completely preserved egg bottoms (eggs 5 and 8) measure approximately 36 mm × 61 mm and 35 mm × 62 mm, indicating an ovoid egg shape. Most eggs lie nearly horizontal within the rock, whereas others (eggs 1, 2, 4, 14