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

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

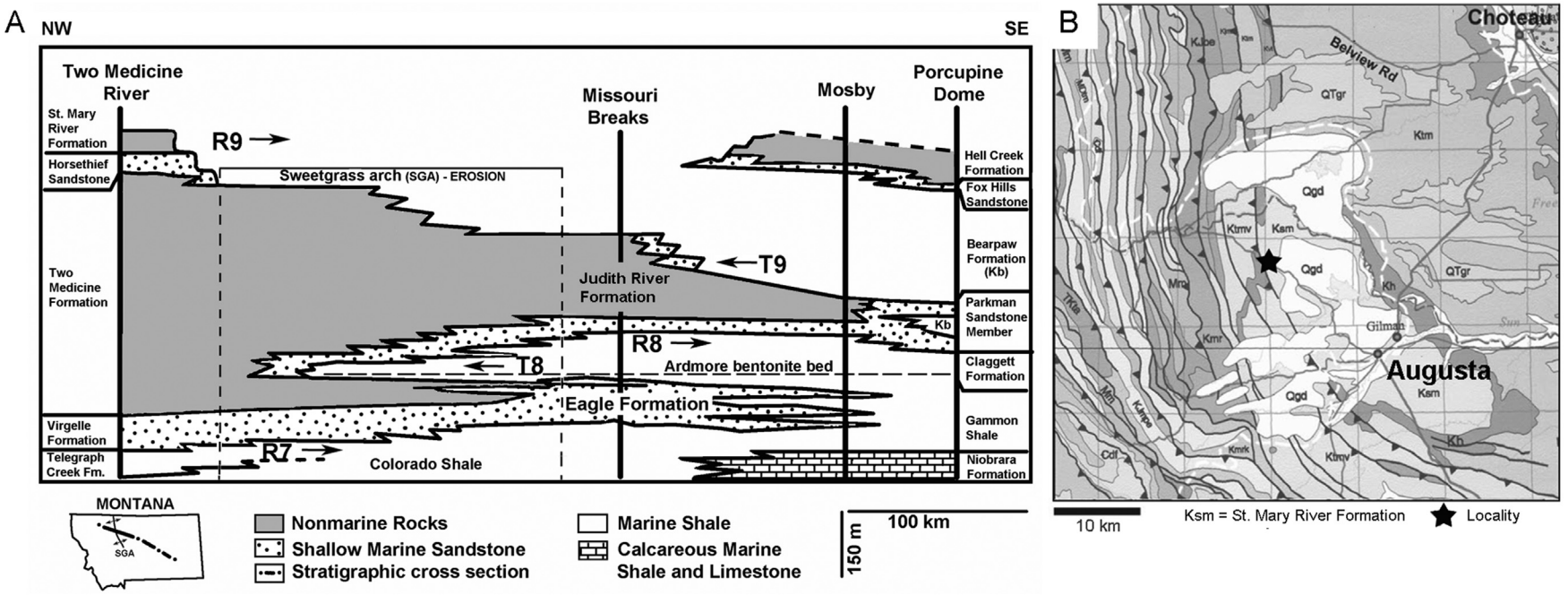

Fig. 1. Geologic setting and nesting locality. **A,** Schematic cross section of Montana Group with restoration across the Sweetgrass arch. Modified from Rogers (1998: fig. 2); T and R represent marine transgressions and regressions, respectively. **B,** geologic map of the fold and thrust belt of Montana with black star to indicate the fossil egg locality in the St. Mary River Formation (Ksm).

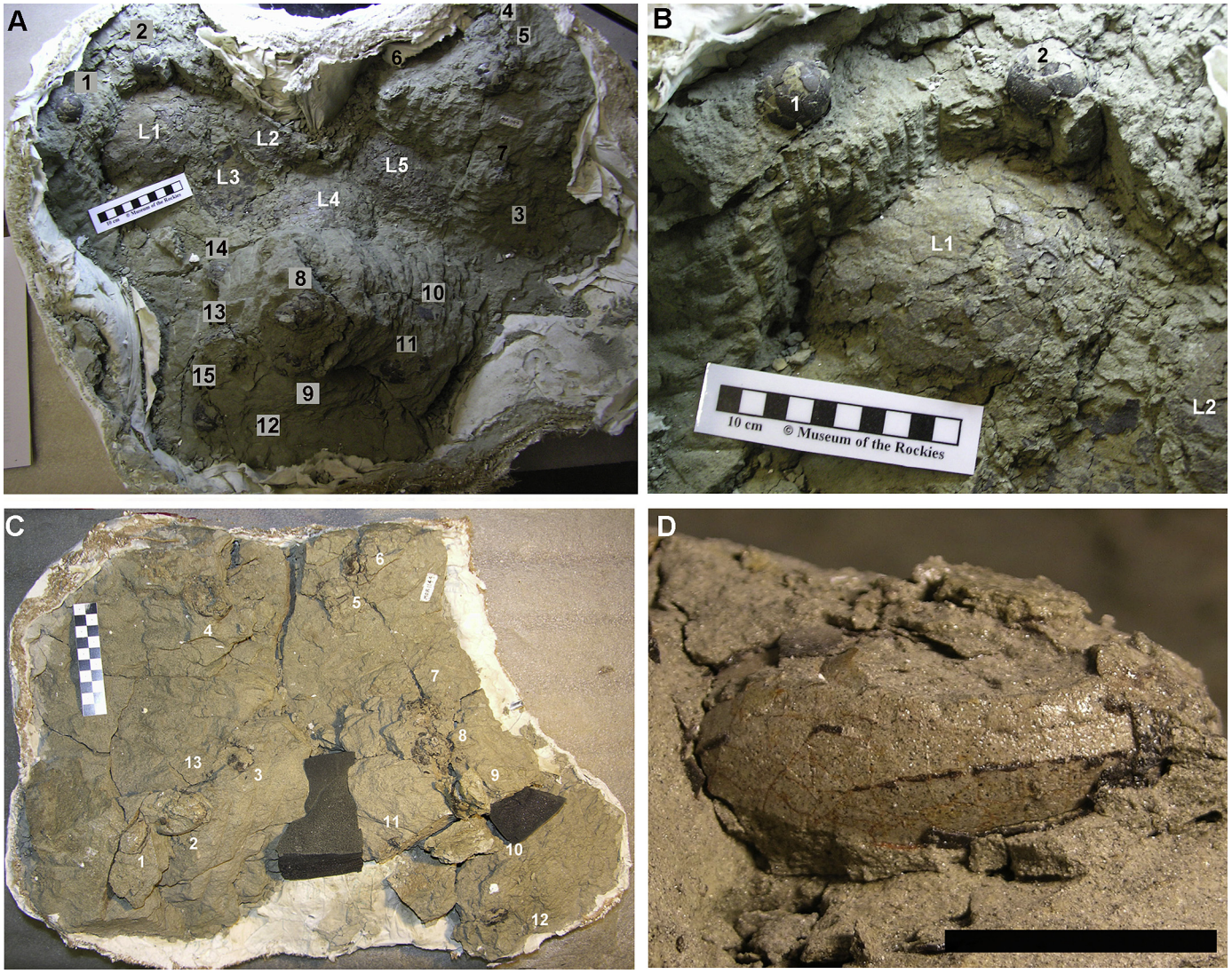

Fig. 2. Associated egg types. **A,** Specimen MOR 1044-2 containing prismatic theropod eggs (1–15) and larger eggs (L1–L5); the latter likely belonged to a hadrosaur; **B,** enlargement of upper left corner of A. Eggs were prepared upside down and therefore the small prismatic eggs are stratigraphically lower than the large eggs; **C,** MOR 1044 containing portions of 13 prismatic eggs. Gray-green sediment color appears tan due to artificial lighting. **D,** enlargement of egg 2 in C. Scale bars in A–C equal 10 cm; scale bar in D equals 2 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and 15) vary from about 10°–20°. Some eggs are incompletely exposed and therefore prohibit assessment of egg trend and, consequently, possible egg pairing.

Five large, round, brown to dark rusty colored eggs overlie the small eggs (Fig. 2A, B). These larger eggs show substantially greater lithostatic compaction than the small eggs and measure about 130 mm in diameter. They occur on a single bedding plane and lie in close contact with one or more adjacent eggs of the same type. Four of these large egg portions are concave up, whereas a fourth egg portion (L3) lies concave down. The latter may represent an extremely flatten egg bottom or the top of an adjacent, possibly hatched egg.

MOR 1144. The 43 cm by 56 cm block contains at least 12 and possibly 13 small, black eggs in approximately 10 cm–thick, green-gray very fine silty sandstone (Fig. 2C). The quality of preservation and exposure of the eggs vary and two eggshell concentrations (eggs 10, 11) may represent crushed eggs. One well-exposed and largely intact egg (egg 2) would likely have measured about 33 mm by 56 mm; it displays a smooth surface and ovoid shape (Fig. 2D). Seven eggs (eggs 1, 2, 4, 6, 8, 9, and 11) occur at or near the same level, whereas three (eggs 3, 5, and 7), and the possible 13th egg, are slightly higher. These eggs lie about 2–3 cm horizontally from the nearest adjacent egg. Two additional egg portions (eggs 10 and 12) are a further 5–6 cm above this level. This vertical distance was measured without correction for the dip of the bed. Where the axes of the eggs are discernable, the estimated orientation varies from horizontal to about 45°. Trends are inconsistent, with eggs neither parallel to one another nor centered about a given focal point. The poor preservation and incomplete exposure of the eggs prohibits definitive assessment of possible egg pairing.

Eggshell structure. The eggshells from the small eggs in both MOR 1144-2 and MOR 1144 are 530–550 μm thick, and exhibit moderate alteration (Fig. 3A, B). The eggshell consists of two structural layers: a 110 μm mammillary layer (ML) and 418 μm continuous layer (CL), with a ML:CL ratio of about 1:3.8 (Fig. 3A, B). Nucleation sites at the inner eggshell surface are absent, likely due to recent weathering. The blocky, barrel-shaped and tightly packed mammillary cones

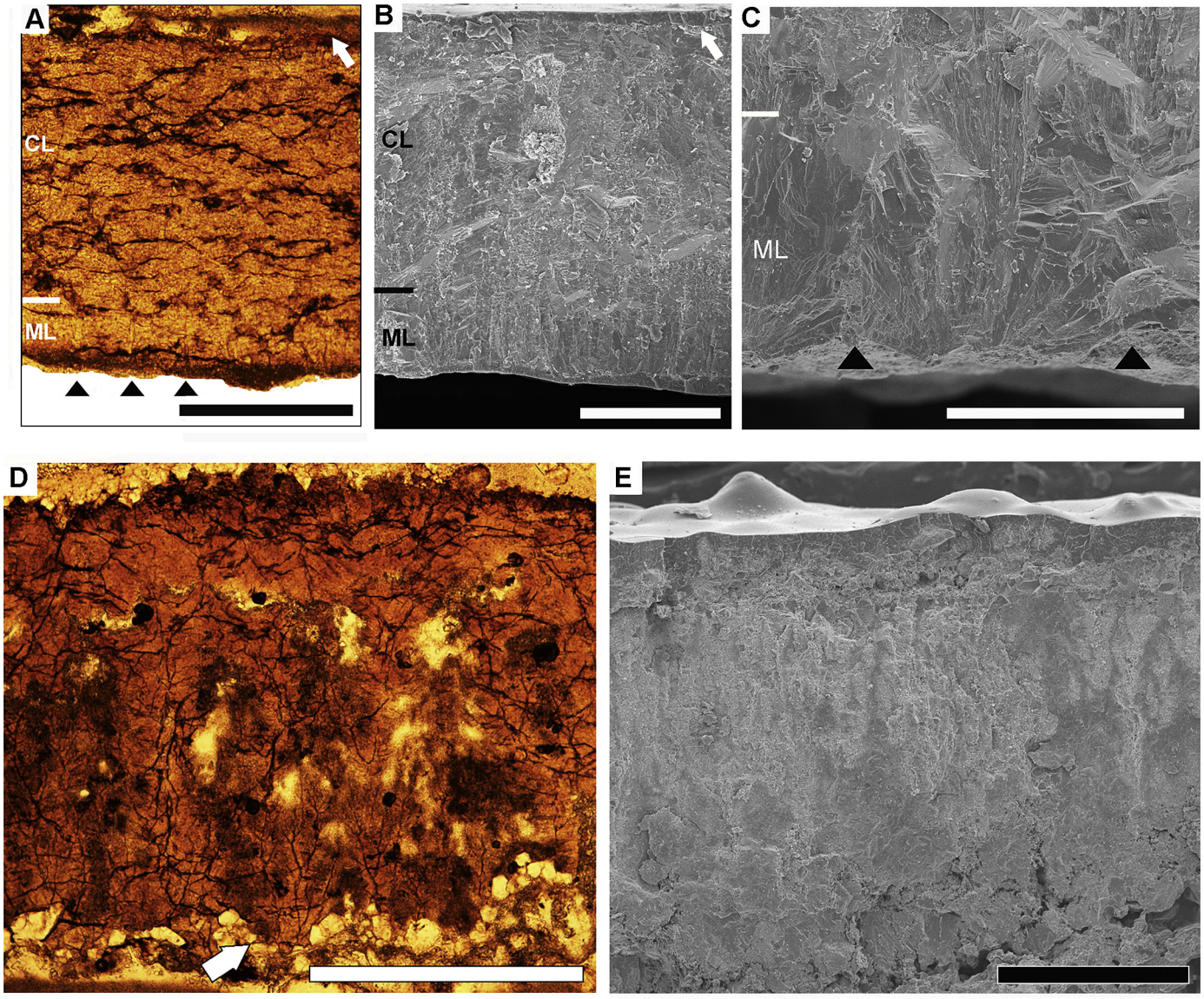

Fig. 3. Eggshell from two egg types. **A,** Thin section of eggshell under plain polarized light from small egg in MOR 1044-2; outer shell surface is at top of image. Triangles show widths of two adjacent blocky mammillary cones and white arrow points to the outer shell surface. Secondary calcite overlies the eggshell. White bar shows approximate transition between the mammillary (ML) and continuous layers (CL); **B,** same as A under SEM. Black bar indicates ML and CL transition; note prisms in the continuous layer. White arrow indicates outer shell surface; **C,** enlargement of a mammillary cone; triangles indicate cone width and white bar show marks upper boundary of the ML; **D,** eggshell from large egg (L1) in thin section showing highly altered structure; outer surface is at top of the image. Arrow points to eroded inner eggshell surface; **D,** SEM image of eggshell from L1 showing substantial alteration of calcite structure. Ornamentation on the outer shell surface consists of ridges. Scale bar in A equals 250 μm, B equals 200 μm, and C equals 100 μm; D and E equal 1000 μm.

exhibit tabular structure and measure about 100–130 μm in diameter (Fig. 3C). A gradual transition occurs from the mammillary to the continuous layer (Fig. 3B, C). The latter exhibits tightly interlocking prisms with faint margins (Fig. 3B); irregular squamatic texture and 2–4 μm-wide vesicles are recognizable in some but not all SEM images, in the latter case due to alteration of the calcite eggshell. Secondary calcite deposits cover some portions of inner and outer surface of the eggshell (Fig. 3A, B).

Eggshells from the large eggs measure about 850–920 μm thick and sometimes display irregular ridges on the outer surface (Fig. 3D, E). Diagenetic alteration almost completely obliterated the eggshell structure. Some irregular calcite-filled spaces midway through the eggshell may represent obliquely oriented pores but alteration prohibits definitive identification.

4.1. Comparisons

Small eggs. Eggs with prismatic structure in the second layer are represented by two oofamilies, Arriagadoolithidae Agnolin et al., 2012 and Prismatoolithidae Hirsch, 1994, whereas expression of this feature appears less distinct in a third oofamily, Montanoolithidae Zelenitsky and Therrien, 2008 (Table 1). The lack of a complex third layer and absence of anastomosing ridges excludes the small eggs from MOR 1044-2 and MOR 1044 from the oofamilies Arriagadoolithidae and Montanoolithidae, respectively. However, the eggs conform to the emended diagnosis of the Prismatoolithidae (Moreno-Azanza et al., 2014) in possessing a two layered eggshell structure, tabular structure of inner layer, and gradual transition between layers. The smooth surface differs from *Prismatoolithus* eggs with ornamentation, namely, *P. caboti* Garcia et al., 2000; *P. tenuis* Vianey-Liaud and

Table 1
Comparison of ootaxa with prismatic eggshell structure.

Oofamily	Oogenus	Ootaxa	Eggshell thickness	Egg size	Eggshell surface	Reference
Arriagadoolithidae	*Arriagadoolithus*	*A. patagoniensis*	900–1200	70 × ?	Nodes and ridges	Agnolin et al., 2012
	Triprismatoolithus	*T. stephensi*	525–850	30 × 75	Nodes	Jackson and Varricchio, 2010
Montanoolithidae	*Montanoolithus*	*M. labadousensis*	600–700	–	Anastomosing ridges	Vila et al., 2017
		M. strongorum	700–850	60 × 125	Anastomosing ridges	Zelenitsky and Therrien, 2008
Prismatoolithidae	*Preprismatoolithus*	*P. coloradoensis*	700–1000	60 × 110	Smooth	Hirsch, 1994
	Prismatoolithus	*P. caboti*	500–600	30 × 70	Dispersituberculate	Garcia et al., 2000
		P. gebiensis	700–900	40–70 × 120	Smooth	Zhao and Li, 1993
		P. hanshuiensis	1000–1200	140–150	Weathered	Zhou et al., 1998
		P. heyuanensis	600 (520)	48.6 × ?115	Smooth	Lü et al., 2006
		P. hirschi	500–560	–	Smooth	Jackson and Varricchio, 2010
		P. hukouensis	700–1000	56 × 140	Smooth	Zhao, 2000
		P. jenseni	830–1160	75 × 140	Smooth	Bray, 1999
		P. levis	700–1000	50–57 × 130–150	Smooth	Zelenitsky and Hills, 1996
		P. matellensis	1060–1220	–	Smooth	Vianey-Liaud and Crochet, 1993
		P. tenuous	240–600	–	Dispersituberculate	Vianey-Liaud and Crochet, 1993
		P. trempii	250–530	–	Flat nodes	Sellés et al., 2014
	Protoceratopsidovum	*P. fluxuosum*	600–700 1400	130–150 × 50–57	Smooth	Mikhailov, 1994
		P. minimum	300–700	40–?60 × 100–110	Smooth	Mikhailov, 1994
		P. sincerum	300–1200	40–50 × 110–120	Smooth	Mikhailov, 1994
	Sankofa	*S. pirenaica*	190–340	40 × 70	Smooth	López-Martínez and Vicens, 2012
	Spheruprismatoolithus[a]	*S. condensus*	660–940	–	Ridges and nodes	Bray, 1999
	Tetonoolithus	*T. nelsoni*	530–550	33 × 53, 35 × 62	Smooth	This paper
	Trigonoolithus	*T. amoae*	330–1040	–	Round-triangular	Moreno-Azanza et al., 2014
Unnamed	*Pseudogeckoolithus*	*P. nodosus*	330–350	–	Nodes	Vianey-Liaud and López-Martinez, 1997

[a] Prismatic eggshells (Jackson and Varricchio, 2010).

Crochet, 1993; and *P. trempii* Sellés et al., 2014 (Table 1). *Prismatoolithus levis* Zelenitsky and Hills, 1996 and *P. gebiensis* Zhao and Li, 1993 differ in their larger size and strongly asymmetrical egg shape. *Prismatoolithus hirschi* Jackson and Varricchio, 2010 also differ in their slender elongate mammillary cones, distinct transition between the mammillary and continuous layers, and evenly distributed squamatic texture. Lü et al. (2006) describe a possible external layer in *P. heyuanensis* and their size exceeds that of *Tetonoolithus nelsoni.* Further, the new eggs are smaller than all *Prismatoolithus* oospecies known from intact eggs (Table 1).

Other oogenera. Two additional oogenera in the Prismatoolithidae exhibit ornamentation and therefore differ from *Tetonoolithus nelsoni*: *Trigonoolithus* Moreno-Azanza et al., 2014 and *Spheruprismatoolithus* Bray, 1999 (Table 1). Jackson and Varricchio (2010) suggest that the latter may represent spherulitic, rather than prismatic eggshells. The oogenus *Pseudogeckoolithus* Vianey-Liaud and López-Martinez, 1997 is unassigned to an oofamily and possesses ornamentation (Table 1). The eggs described here also differ from *Sankofa pirenaica* López-Martínez and Vicens, 2012 and *Protoceratopsidovum* Mikhailov, 1994 in their absence of unusual texture in the continuous layer in the former and the strongly elongate and asymmetric shape of the latter. *Preprismatoolithus coloradonensis* (sensu Zelenitsky and Hills, 1996) are larger, with thicker eggshell and oblique pores. Because of the differences discussed above, we assign the small prismatic eggs as a new oogenus and oospecies, *Tetonoolithus nelsoni,* within the oofamily Prismatoolithidae.

Large eggs. The large eggs are similar in size, shape, ornamentation and eggshell thickness to eggs of the oofamily Spheroolithidae (Zhao, 1979) and, more specifically, those of the hadrosaurine *Maiasaura peeblesorum* Horner and Makela, 1979 from the stratigraphically lower Two Medicine Formation. However, the highly altered condition of the eggshell prohibits positive identification of the eggshell structure.

5. Discussion

5.1. Nesting ecology

Aggregation of extant reptilian taxa often occurs for the purpose of oviposition (Doody et al., 2009 and references therein). Two terms are used to describe this behavior: communal and colonial nesting. Espinoza and Lobo (1996) define communal nesting as eggs laid with those of conspecifics under or within structures such as rocks, logs, and vegetation. In contrast, colonial nesting refers to use of common nesting areas where buried eggs are typically not visible to other animals. This represents an important distinction because colonial nesting females often inadvertently disrupt or dig up the eggs of conspecifics. A review of the literature by Doody et al. (2009) reveals that descriptions of conspecific aggregations among extant reptiles are relatively common, whereas reports of interspecific nesting are rare.

Recognition of either type of egg-laying strategy in the fossil record presents a challenge for paleontologists. As with most reproductive behaviors (e.g., site fidelity, colonial nesting, egg brooding), paleontological definitions may differ from those of biologists, and time resolution in the rock record poses a difficult problem (Varricchio et al., 2015). For example, Horner (1982) hypothesized colonial nesting for hadrosaurs belonging to the genus *Maiasaura* at the Willow Creek anticline in Montana; he noted that the nests occurred at approximately equal vertical distances from a paleosol horizon, with absence of nest overlap. However, this and subsequent articles (e.g., Horner and Gorman, 1988; Horner, 2000) lack a stratigraphic section, taphonomic study, and detailed description of the paleosol horizon, which are essential for supporting interpretations. Further, the formation of carbonate nodules (caliche) requires hundreds to thousands of years (Chen and Pollach, 1986; Küçükuysal et al., 2011) and, thus, the *Maiasaura* nests may represent a time-averaged assemblage.

The homogeneous nature of sedimentary rock at fossil egg localities often prohibits precise determination of the stratigraphic position of clutches (Jackson, 2007). Many if not most of these nesting sites occurred in overbank deposits on the flood plain (Jackson et al., 2013 and references therein). Sediment accumulation rates in these environments are typically low, resulting primarily from vertical accretion by suspension settling of fine grained sediment (Walling et al., 1992; Aalto et al., 2003; Pizzuto et al., 2008). Estimating the amount of time represented by the few centimeters of rock separating eggs at the fossil egg localities remains problematic. Alterations to biological patterns of egg-laying

by other adults during subsequent nest construction may further contribute to the difficulty of interpreting the reproductive behavior of extinct animals (Jackson et al., 2013).

Despite these difficulties some conclusions are possible regarding the nesting site in the St. Mary River Formation. The eggs clearly represent the nesting activities of two species of dinosaurs. The small prismatic eggs represent those of theropods, whereas the size, shape, shell thickness and ornamentation of the large eggs strongly resemble *Maiasaura* eggs, suggesting that the eggs likely belonged to a hadrosaur. The size disparity between the two egg types also suggests that the theropods were substantially smaller. These small theropod eggs are widely dispersed and occur on three or possibly four levels, ranging in depth from a few to 25 cm below the larger eggs. In contrast, the five large eggs form a tight cluster on a single stratum. The scattered arrangement and inconsistent angles of the small theropod eggs suggest disruption by the same species and/or other animals as they prepared the soil and excavated their nests. Alternatively, nest predation reported at some extant nesting localities (e.g., Jackson et al., 2015) may offer a plausible explanation for the scattered distribution of the small eggs at this site.

We propose the following sequence of events to explain the egg distribution as this locality: 1) one or more small theropods excavated nests and laid the lowermost *Tetonoolithus nelsoni* eggs; 2) at least some of the eggs failed to hatch for unknown reasons; 3) during the same and/or subsequent nesting seasons other theropods of the same species excavated nests, disrupting these deeper eggs; and finally 4) a larger animal such as a hadrosaur also selected this nesting site, producing the stratigraphically higher egg clutch. Because of the large number of eggs in other hadrosaur nest sites (e.g., 16 eggs; Horner, 1999), the specimen may preserved only part of this original clutch.

Nesting site selection in modern taxa exerts a profound influence on environmental conditions critical to the developing embryo and impacts the probability of egg predation (Howard, 1978; Deeming and Ferguson, 1991). The choice of an egg-laying locality represents an important component of fitness, especially in animals without parental care (Doody et al., 2009). A number of hypotheses attempt to explain communal and colonial nesting in extant taxa: inadequate nesting sites, social behavior, mediation of predation risk, environmental conditions (e.g., shade, food, soils), and previous reproductive success as evidenced by eggshell accumulations (Doody et al., 2009). Aggression and interspecific competition may also lead to late comers driving out earlier-nesting females, thereby providing a nest, as well as eggs for adult consumption.

The aggregation of eggs at the St. Mary River Formation locality in Montana likely reflects factors such as those reported for extant taxa. Further, the multiple egg levels indicate that favorable conditions persisted over an extended period of time, and the desirability of this site was not limited to one dinosaur species. However, it remains beyond the resolution of the rock record to determine if this locality meets the biological definitions of interspecific colonial nesting or if nesting events were separated by years, decades, or possibly even centuries.

5.2. St. Mary River Formation vertebrate fauna

Although Dawson (1884) mapped the St. Mary River Formation more than a century ago, reports of vertebrate fossils from exposures in Montana are rare. Barnum Brown collected a ceratopsian dinosaur, *Montanoceratops cerorhynchus* (Brown and Schlaikjer, 1942), from a locality near Buffalo Lake in Glacier County, Montana and subsequent work yielded additional specimens (Weishampel and Horner, 1987; Chinnery and Weishampel, 1998). Witmer and Weishampel (1993) describe the frontal of an ornithomimid (cf. *Dromiceiomimus*) and the basicranium of an intermediate maniraptora from the Glacier County;Martineau (2014) also mentions four undescribed dinosaur bonebeds in Lewis and Clark County near Augusta, Montana, and Hunter et al. (2010) describe mammal remains from Shell Hell (MOR Locality 703), which lies along the Two Medicine River in Glacier County south of Browning, Montana. The Buffalo Lake site and Shell Hell localities

Table 2
Fossil eggs and eggshells from four formations in Montana.

Lower Two Medicine Formation	Mid to Upper Two Medicine Formation	Judith River Formation	Hell Creek Formation	St. Mary River Formation
				Tetonoolithus nelsoni/theropod (this paper)
Spheroolithus choteauensis/hadrosaur (10)	*Spheroolithus albertensis Maiasaura peeblesorum*/hadrosaur; (2,7)	[a]*Spheruprismatoolithus condensus*/theropod (6)	*Spheroolithus* sp., Types I and II (12)/hadrosaur	*?Spheroolithus*/hadrosaur (this paper)
[a]*Spheruprismatoolithus condensus*/theropod (6)	Oospecies unknown/Lambeosaurine *Hypacrosaurus stebingeri*/(8)	Oospecies unknown/Lambeosaurine *Hypacrosaurus stebingeri*/(9)		
Continuoolithus canadensis/theropod (10)	*Montanoolithus strongorum*/theropod (14)	*Prismatoolithus levis/Troodon* (5, 11)		
	Prismatoolithus levis/Troodon (1–4, 11)			
Triprismatoolithus stephensi/theropod (10)	*Continuoolithus canadensis*/theropod (2,13)			
Prismatoolithus hirschi/theropod (10)				
Tubercuoolithus tetonensis/theropod (10)				
			Belonoolithus garbani/theropod (12)	
			Dimorphoolithus bennetti/theropod (12)	
Krokolithes oosp./crocodilian (10)	*?Krokolithes wilsoni*/crocodilian (2)		*Krokolithes* sp./crocodilian *(12)*	
		Testudoolithus sp./turtle (9,15,16, 17)	*Testudoolithus* sp./turtle (12)	

References: 1, Horner (1982); 2, Hirsch and Quinn (1990); 3, Varricchio et al. (2002); 4, Grellet-Tinner et al. (2006); 5, Jackson et al. (2010); 6, Bray (1999); 7, Horner and Makela (1979); 8, Horner and Currie (1994); 9, Clouse (2001); 10, Jackson and Varricchio (2010); 11, Zelenitsky and Hills (1996); 12, Jackson and Varricchio (2016); 13, Zelenitsky et al. (1996); 14, Zelenitsky and Therrien (2008); 15, Jackson and Schmitt (2008); 16, Lawver and Jackson (2014); Lawver and Jackson (2017).

[a] *Spheroolithus choteauensis* and *Spheruprismatoolithus condensis* are likely the same oospecies and belonged to a hadrosaur rather than a theropod (Jackson and Varricchio, 2010).

produced lizard, turtle, champsosaurid, crocodilian, and mammalian remains (Weishampel and Horner, 1987; Hunter et al., 2010). More importantly for our study, Weishampel and Horner (1987) mention hadrosaurine and ceratopsian embryos, three types of eggshell, as well as fragmentary dinosaur eggs at the Buffalo Lake locality. Hunter et al. (2010) also report a large eggshell concentration at Shell Hell, whereby the site derived its name. However, the eggs and eggshell fragments at both localities have not been studied. The eggs reported here, therefore, represent the first fossil eggs described from the St. Mary River Formation, further contributing to our understanding of taxonomic diversity of this formation, as well as the Montana portion of the Upper Cretaceous foreland basin.

Transgressive/regressive cycles of the Western Interior Cretaceous Seaway have long been considered responsible, at least in part, for distinct biozones within the Upper Cretaceous formations of central and western Montana (Horner, 1982, 1984; Weishampel and Horner, 1987; Horner et al., 2001). Each formation is said to have its own distinct dinosaur fauna that are not present in preceding or succeeding formations (Weishampel and Horner, 1987). Differences also occur within the same formation. For example, Jackson and Varricchio (2010) describe five new ootaxa from the lowermost Two Medicine Formation that are unreported from the middle to upper portion of the same formation. Comparison of ootaxa described here to those of the Two Medicine, Judith River, and Hell Creek formations in Montana also seem to support the biozone hypothesis to some extent (Table 2; Jackson and Varricchio, 2010, 2016). The small theropod eggs *Tetonoolithus nelsoni* are unique to the St. Mary River Formation. However, the presumed hadrosaur eggs (*Spheroolithus*) also occur in the Two Medicine, Judith River, and Hell Creek formations. Generally, these *Spheroolithus* eggs share similar morphology. In contrast, the theropod eggs and eggshells from these formations show a wider range of ornamentation, number and ratios of eggshell layers, degree of squamatic textural development, complexity of the external layer, and eggshell thickness and porosity. Although Weishampel and Horner (1987) report hadrosaurine and ceratopsian embryonic remains from the Buffalo Lake site, they provide no indication of whether the osteological remains occurred inside an egg nor did they identify the type of eggshell. Although definitively identified ceratopsian eggs are unknown, the two layered structure of *Tetonoolithus nelsoni* rules out that the eggs belonged to this taxon or a hadrosaurine. Finally, *T. nelsoni* also differs from the eggs and eggshells reported from other Maastrichtian localities in the Western Interior of North America (Zelenitsky et al., 2017: Table 1). Whether the differences reflect taphonomic, ecological, or evolutionary factors requires additional specimens and further study.

6. Conclusions

Nesting site selection represents an important factor in reproductive success and sometimes leads to aggregation of animals for the purpose of oviposition. The first eggs reported from the St. Mary River Formation reflect the nesting activities of small theropods (ootaxon *Tetonoolithus nelsoni*) and a larger dinosaur, likely a hadrosaur. The multiple stratigraphic levels at which the *T. nelsoni* eggs occur suggest repeated use of the site, whereas predation or disruption resulting from subsequent nesting activity may account for their scattered distribution and inconsistent orientations. The presence of eggs belonging to a larger dinosaur immediately above the theropod eggs indicates that conditions favorable to both animals persisted over an extended, yet indeterminate amount of time, possibly years, decades, or longer. It remains beyond the resolution of the rock record to determine if this locality meets the biological definition of interspecific colonial nesting; therefore, application of such terms to fossil localities requires caution. Finally, *T. nelsoni* are unique to the St. Mary River Formation, when compared to other Upper Cretaceous formations of the Montana foreland basin.

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