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**Dinosaur eggshells from the lower Maastrichtian St. Mary River Formation of southern
Alberta, Canada**

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Abstract—North America is known for its rich uppermost Cretaceous record of dinosaur egg remains, although a notable fossil gap exists during the lower Maastrichtian. Here we describe a diverse dinosaur eggshell assemblage from the St. Mary River Formation of southern Alberta that, in conjunction with recently described eggs from the same formation in Montana, helps fill this gap and sheds light on the dinosaur diversity in this poorly-fossiliferous formation. Three theropod types (*Continuoolithus* cf. *C. canadensis*, *Montanoolithus* cf. *M. strongorum*, and *Prismatoolithus* cf. *P. levis*) and one ornithopod (*Spheroolithus* cf. *S. albertensis*), are reported from Albertan exposures of the St. Mary River Formation, increasing the ootaxonomic diversity of the formation from two to five ootaxa. The taxonomic composition of the eggshell assemblage is consistent with the dinosaurian fauna known from the St. Mary River Formation based on skeletal remains. *Spheroolithus* eggshells constitute the majority of identifiable eggshells in our assemblage, a trend also observed in several other Upper Cretaceous formations from North America. *Continuoolithus*, is shown to be synonymous with *Spongioolithus*, thus expanding the Maastrichtian geographic range of the ootaxon to include Utah. The St. Mary River eggshell assemblage supports a general trend of increase in eggshell thickness among theropod ootaxa from the uppermost Santonian through the Maastrichtian, which is inferred to reflect an increase in body size among some clades of small theropods through the Upper Cretaceous. Eggshell preservation in the St. Mary River Formation may be related to the semi-arid climatic and environmental conditions that prevailed.

Keywords: eggshell, dinosaur, Cretaceous, Maastrichtian, Alberta

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Introduction

Abundant dinosaur egg remains have been discovered in Upper Cretaceous formations of North America, the vast majority of which are known from Campanian deposits (Horner and Makela 1979; Hirsch and Quinn 1990; Zelenitsky and Hills 1996, 1997; Zelenitsky et al. 1996; Varricchio et al. 2002; Zelenitsky and Sloboda 2005; Welsh and Sankey 2007; Zelenitsky and Therrien 2008a; Jackson and Varricchio 2010; Tanaka et al. 2011). Comparatively limited egg material is known from the Maastrichtian, with most specimens described from upper Maastrichtian formations, including the Hell Creek Formation of Montana (Jackson and Varricchio 2016), North Horn Formation of Utah (Bray 1999; Cifelli et al. 1999; Difley 2007), and Willow Creek Formation of Alberta (Zelenitsky et al. 2017a). The recent report of two egg types from the St. Mary River Formation of northern Montana represents the first record of lower Maastrichtian-aged eggshell in North America (Jackson and Varricchio 2017). Nevertheless, with only two ootaxa reported, the lower Maastrichtian represents one of the most poorly understood intervals in the uppermost Cretaceous oological record of North America.

Here we describe a dinosaur eggshell assemblage from the lower Maastrichtian St. Mary River Formation of southwestern Alberta, Canada. Well known for its preservation of dinosaur tracks (Currie et al. 1991; Nadon 1993), this formation has produced relatively few skeletal fossils compared to the contemporaneous Horseshoe Canyon Formation of central Alberta (see Brown et al. 2015). The discovery of dinosaur eggshells in the St. Mary River Formation adds to our understanding of dinosaur diversity in this rock formation and augments the fossil record of dinosaur eggshells in North America.

Geologic Setting

The Upper Cretaceous St. Mary River Formation is a non-marine clastic unit exposed in southernmost Alberta and northwestern Montana (e.g., Nadon 1993; Hamblin 1998). Although reported thickness for the formation is highly variable, ranging from as much as 950 m (Rahmani and Schmidt 1975) to as little as 240 m (Young and Reinson 1975), these discrepancies are presumably due to the presence of thrust faults in the Monarch Fault Zone and a total thickness of 200–300 m is more likely (Nadon 1993; Hamblin 1998). The St. Mary River Formation is overlain by the Willow Creek Formation throughout its geographic extent and is locally underlain by the Blood Reserve and Bearpaw formations in southern Alberta (Jerzykiewicz and Sweet 1988; Mack and Jerzykiewicz 1989; Hamblin 1998) and by the Two Medicine Formation and Horsethief Sandstone in Montana (Hunter et al. 2010). The formation is dominated by sequences of interbedded mudstones, siltstone, and multi- and single-storied sandstones interpreted to have been deposited in river channels, crevasse splays, marshes, and lacustrine environments within an anastomosing river system (Nadon 1991, 1993, 1994).

The stratigraphic setting of the St. Mary River Formation is well established (see Hamblin, 2004:fig. 4). The formation is correlative with the upper part of the Horseshoe Canyon Formation of south-central Alberta (Nadon 1988; Hamblin 1998; Hamblin 2004; Eberth and Braman 2012), the upper Brazeau Formation of the central Alberta Foothills (Gunther and Hills 1972; Hamblin 2004), the Red Willow and Cutbank coal zones of the upper Wapiti Formation of northwestern Alberta (Glass 1990; Hamblin 2004; Fanti and Catuneanu 2009), the Eastend Formation of Saskatchewan, and the Fox Hills Formation of the U.S. Great Plains (see Glass

1990; Hamblin 2004). In their study of rock exposures in southernmost Alberta, Lerbekmo and Lehtola (2011) determined that the base of the St. Mary River Formation was deposited near the onset of magnetochron 32n•1r, a magnetochron situated at the base of the Maastrichtian (Ogg and Hinnov 2012). The presence of the Kneehill Tuff above the St. Mary River Formation in some outcrops (Tozer 1952; Irish and Havard 1968), as well as various palynological, magnetostratigraphic, and biostratigraphic studies, place the top of the formation as roughly contemporaneous with the top of the Horseshoe Canyon Formation, near the base of magnetochron 30n (Lerbekmo and Braman 2002; Eberth and Braman 2012; Eberth et al. 2013; Srivastava and Braman 2013; see also Lehman 2001). As a result, following the geologic timescale of Ogg and Hinnov (2012), deposition of the St. Mary River Formation began during the lower Maastrichtian and continued into the upper Maastrichtian, spanning a time interval between ~71.8 Ma and 67 Ma.

Well known for the preservation of dinosaur tracks (Currie et al. 1991; Nadon 1993), the St. Mary River Formation has yielded limited skeletal remains. Previous faunal diversity reports for the formation (e.g., Weishampel et al. 2004; Brown et al. 2015) were based primarily on the fossiliferous Scabby Butte locality, initially assigned to the St. Mary River Formation by Langston (1965). However, numerous other researchers recognized the locality as part of the Horseshoe Canyon Formation on the basis of stratigraphic, sedimentologic, and paleontologic evidence (Williams and Dyer 1930; Carrigy 1971; Russell 1975; Nadon, 1991). Consequently, because the faunal assemblage found at the Scabby Butte fossil locality is attributable to a different formation (i.e., the Horseshoe Canyon Formation), we provide a more accurate faunal list based on fossil discoveries made at various St. Mary River Formation exposures in southern Alberta and Montana (Table 1).

Fossil eggshell fragments ($n=81$) have been discovered at six localities in the St. Mary River Formation of southernmost Alberta. Most specimens ($n=51$) were recovered from the Whiskey Gap area, approximately 15 km west of the town of Del Bonita, whereas the others ($n=30$) were discovered along the St. Mary River west of the town of Magrath and from a microsite northeast of the town of Barons (Fig. 1). As the majority of eggshell localities occur in roadcuts, their exact stratigraphic position within the formation could not be determined; however, the eggshells are inferred to come from the middle part of the St. Mary River Formation based on their position relative to the geographic location of contacts with adjacent formations (Prior et al. 2013).

Materials and Methods

Well-preserved eggshell fragments ($n=39$) were initially categorized into different morphotypes based on characteristics of the eggshell (e.g., outer surface, microstructure, and mammillae) observed using a Leica MDG33 binocular light microscope. Select eggshell fragments of each morphotype were analyzed using scanning electron microscopy (SEM) and petrographic light microscopy, and photomicrographs of various eggshell features (e.g., nodes, ridges, mammillae, crystalline structures, etc.) were captured. For SEM, fragments were cleaned in a sonic bath and dried using compressed air, then mounted on aluminum stubs with carbon tape. At least three fragments of each morphotype (when possible) were analyzed to document the outer, radial, and inner surfaces using a FEI Quanta FEG 250 field emission scanning electron microscope at 10 kV. Thin sections for each morphotype were produced for examination under both plane and cross-polarized light with a Leica DM 2500P petrographic microscope.

Various features of the eggshells were measured. The total thickness of individual eggshell fragments (with and without ornamentation, where applicable) was measured using digital calipers. Shell unit width, mammillary layer thickness, and continuous layer thickness were measured from photomicrographs of radial sections/views of the eggshell using the software ImageJ 1.51n. Pore aperture diameter, pore spacing, minimum node diameter, minimum ridge width, maximum width of mammillae, and inter-mammillary spacing were measured from photomicrographs of plan view of the inner or outer eggshell surfaces also using the software ImageJ 1.51n.

We use the parataxonomic system devised by Zhao (1975) to classify the eggshell types from the St. Mary River Formation. Shell fragments were classified based on the features of the external surface, shell units, and pore structures. Comparisons were made with previously described ootaxa from Upper Cretaceous North American strata.

Detailed locality information for the St. Mary River eggshell sites can be accessed through collections at the Royal Tyrrell Museum of Palaeontology in Drumheller, Alberta, Canada.

Abbreviations

TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

Systematic Paleontology

Oofamily	Montanoolithidae Zelenitsky and Therrien 2008a
Oogenus	<i>Montanoolithus</i> Zelenitsky and Therrien 2008a

Montanoolithus cf. *M. strongorum* Zelenitsky and Therrien 2008a

LOCALITY: Roadcut in the Whiskey Gap area, Municipal district of Cardston, southern Alberta.

MATERIAL: Eggshell fragments from TMP 1998.52.1 (n=2).

DESCRIPTION: Both fragments are 0.64 mm thick and are coated with an external layer of diagenetic calcite (not included in measurement). Compared to other specimens of *M. strongorum*, the shell thickness is slightly thinner than those from the Two Medicine Formation (0.7–0.85 mm; Zelenitsky and Therrien 2008a) and slightly thicker than those from the Willow Creek Formation (0.58 mm; Zelenitsky et al. 2017a). Based on observation where the diagenetic calcite layer is thinnest, the outer surface of the eggshell appears to have a series of undulating ridges. The eggshell fragments show a low number of pores in tangential section. A gradational boundary is present between the continuous and mammillary layers, and the thickness ratio between the two layers is ~2:1 (Fig. 2), consistent with other reported specimens of *M. strongorum* (CL:ML ratios between 1.5:1 and 2:1, Zelenitsky and Therrien 2008a; Zelenitsky et al. 2017a), but lower than the 3:1 reported for *M. labadousensis* from southwestern Europe (Vila et al. 2017).

TAXONOMIC AFFINITY: Phylogenetic analyses of *Montanoolithus strongorum* by Zelenitsky and Therrien (2008a, b) revealed a close affinity with eggshell ascribed to *Deinonychus*

antirrhopus (Grellet-Tinner and Makovicky 2006), suggesting that the ootaxon belongs to Dromaeosauridae (Zelenitsky and Therrien 2008a, b; Vila et al. 2017)

Oofamily Prismatoolithidae Hirsch 1994
Oogenus *Prismatoolithus* Zhao and Li 1993

Prismatoolithus cf. *P. levis* Zelenitsky and Hills 1996

LOCALITY: Roadcuts in the Whiskey Gap area, Municipal District of Cardston, southern Alberta. Exposures along the bank of the Milk River, west of the town of Magrath, Municipal District of Cardston, southern Alberta.

MATERIAL: Eggshell fragments from TMP 1998.52.1 (n=2) and TMP 2016.48.3 (n=1).

DESCRIPTION: Specimens of this ootaxon have an average eggshell thickness of 0.79 mm, with a range of 0.69–0.85 mm. These measurements are consistent with those of *P. levis* from the Two Medicine Formation (0.78–1.2 mm; Varricchio et al. 2002) and Oldman Formation (0.70–1.0 mm; Zelenitsky and Hills 1996), thicker than *Prismatoolithus hirschi* from the lower Two Medicine Formation (0.50–0.56 mm; Jackson and Varricchio 2010), and thinner than the *Prismatoolithus* cf. *P. levis* fragment from the Willow Creek Formation (1.56 mm; Zelenitsky et al. 2017a). The outer surface is smooth with oval pores that are mostly isolated, although some appear to be paired (Fig. 3a). The longest diameters of the pore apertures are roughly parallel to each other, and average 0.11 mm in length with a range of 0.06 to 0.15 mm (n=25). In radial

view, the individual shell units are most distinct close to the mammillary layer, but individual units are still visible throughout the prismatic layer (Fig. 3b). The boundary between the mammillary layer and prismatic layer (PL) is usually gradational. In areas where the boundary is more distinct, the PL:ML ratio is nearly 6:1, which is comparable to specimens of *P. levis* and *Prismatoolithus* sp. from the Two Medicine and Willow Creek formations (6:1–8:1 in Varricchio et al. 2002; 5:1 in Zelenitsky et al. 2017a). No evidence of the external layer was observed, although it simply may not be preserved (Fig. 3a). The mammillae on the inner surface of the fragments tend to be poorly preserved.

TAXONOMIC AFFINITY: Eggs found with *Troodon* embryos and associated with an adult individual have been assigned to the ootaxon *Prismatoolithus levis* (Zhao and Li 1993; Varricchio et al. 1997; Varricchio et al. 2002). As such, this ootaxon is referred to Troodontidae.

Oofamily Spheroolithidae Zhao, 1979

Oogenus *Spheroolithus* Zhao, 1979

Spheroolithus cf. *S. albertensis* Zelenitsky and Hills 1997

LOCALITY: Roadcuts in the Whiskey Gap area, Municipal District of Cardston, southern Alberta. Exposure along the bank of the Milk River, west of the town of Del Bonita, Municipal District of Cardston, southern Alberta.

MATERIAL: Eggshell fragments from TMP 1987.65.7 (n=18) and TMP 2016.48.4 (n=1).

DESCRIPTION: *Spheroolithus* cf. *S. albertensis* is the most abundant ootaxon (n=19) identified in the St. Mary River eggshell assemblage. Eggshell thickness ranges from 0.75–1.30 mm, with an average of 1.08 mm. Compared with other occurrences of *S. albertensis*, the St. Mary River eggshell has a lower range of thickness than the same ootaxon from the Oldman Formation (0.96–1.46 mm; Zelenitsky and Hills 1997), but has an overall thicker range than specimens from the Willow Creek Formation (0.53–1.20 mm; Zelenitsky et al. 2017a). The outer surface ornamentation generally consists of a series of parallel- to subparallel anastomosing ridges, with pores located between the ridges (Fig. 4a). Pores on the external surface are elongated, typical of spheroolithid eggshells (Fig. 4a). Radial histological sections reveal distinct boundaries between adjacent shell units in plane light and cross-polarized light, with a shell unit height-to-width ratio of approximately 1.5:1 (Fig. 4b). A sweeping extinction pattern is observed within individual shell units when viewed radially under cross-polarized light. Radiating crystallites, originating from the area associated with the organic core, extend through the shell units. Large gaps are present on the inner surface between mammillae, which range from 0.20–0.38 mm in diameter (n=15; mean = 0.28 mm).

REMARKS: *Spheroolithus* cf. *S. albertensis* fragments from Albertan exposures of the St. Mary River Formation possess a larger range of eggshell thickness than the ?*Spheroolithus* eggs reported from exposures of the same formation in Montana (0.85–0.92 mm; Jackson and Varricchio 2017).

TAXONOMIC AFFINITY: Eggshells from the Two Medicine Formation of Montana, also assigned to *Spheroolithus albertensis* (Zelenitsky 2000), were ascribed to the hadrosaur *Maiasaura peeblesorum* due to their association with juvenile material (Horner and Makela 1979; Hirsch and Quinn 1990; Zelenitsky and Hills 1997). Although eggshells of this ootaxon from the St. Mary River Formation probably do not belong to *Maiasaura* because this taxon is known only from the older upper Two Medicine Formation (Horner and Makela 1979; Weishampel et al. 2004), these eggshells may belong to another species within Hadrosauroidea.

Oofamily indet.

Oogenus *Continuoolithus* Zelenitsky et al. 1996

SYNONYM: *Spongioolithus*: Bray 1999, p. 368–369, fig. 5.

Continuoolithus cf. *C. canadensis* Zelenitsky et al. 1996

LOCALITY: Roadcuts in the Whiskey Gap area, Municipal District of Cardston, southern Alberta. Exposures along the bank of the St. Mary River, west of the town of Magrath, Municipal District of Cardston, southern Alberta.

MATERIAL: Eggshell fragments from TMP 1987.65.7 (n=2), TMP 1987.76.4 (n=3), TMP 1987.76.8 (n = 4), TMP 2010.74.37 (n=1), TMP 2016.48.1 (n=1), and TMP 2016.48.2 (n=1).

EMENDED DIAGNOSIS: Eggs are elongated and occur in pairs. External surface ornamented primarily by isolated and coalesced nodes, with occasional ridges. Eggshell thickness ranges from 0.61–1.60 mm with ornamentation and 0.43–1.19 mm without ornamentation. Pores are usually located between or at the base of nodes/ridges, and the pore system is angusticanalicate. Two structural layers are present with a continuous to mammillary layer ratio of ~6.5:1–7:1 (including ornamentation) and of 4:1–5:1 (excluding ornamentation).

DESCRIPTION: *Continuoolithus* cf. *C. canadensis* is the most abundant theropod ootaxon (n=12) recognized in the St. Mary River eggshell assemblage. Eggshell thickness ranges between 0.88 and 1.19 mm excluding nodes, with an average thickness of 1.02 mm (1.03 mm to 1.73 mm, average of 1.37 mm including ornamentation). These measurements are comparable with the type material of *C. canadensis* from the Oldman Formation (0.84–1.04 mm; J.V. pers. obs.), but slightly thinner than fragments from the Willow Creek Formation (1.05–1.35 mm; Zelenitsky et al. 2017a). The external surface is ornamented with randomly spaced nodes (Fig. 5a) or ridges (Fig. 5b) that constitute approximately one-quarter of the total thickness of the eggshell (average node height = 0.35 mm; n=13). Nodes are circular to elongate in plan view. Circular nodes have an average diameter of 0.58 mm (n=6), whereas elongate nodes average 0.78 mm (n=8) and 1.11 mm (n=8) along the shortest and longest diameters, respectively. Pore apertures are circular to oval, with an average 0.16 mm (n=8) on the longest diameter. Radial thin sections reveal the presence of an abrupt boundary between the continuous and mammillary layers, with a CL:ML ratio of approximately 5:1 (excluding ornamentation) (Fig. 6). On the inner surface, the mammillae are relatively large, with adjacent mammillae tightly abutting one another. Only two

1 fragments possess measurable mammillae, which average 0.21 mm (n=67) along their longest
2 diameter.

3
4 REMARKS: With respect to other ootaxa in North America, *Continuoolithus canadensis* is most
5 similar morphologically to *Spongioolithus hirschi* from the North Horn Formation of Utah.

6 *Spongioolithus* is reported to range from 1.20–1.55 mm in thickness and to have a CL:ML ratio
7 of 7:1 (Bray, 1999). Although the original description does not mention if these measurements
8 include ornamentation, we suspect they do based on measurement of eggshell thickness from
9 figures in Bray (1999: fig. 5e): we measured an eggshell thickness of 1.06 mm without
10 ornamentation and 1.32 mm with ornamentation, and calculated a CL:ML ratio of ~6.5:1 with
11 ornamentation and 5:1 without ornamentation. These dimensions overlap with the St. Mary River
12 *Continuoolithus* eggshell when ornamentation is considered. Furthermore, the arrangement and
13 morphology of the ornamentation on the outer surface of *Spongioolithus* is nearly identical to
14 that of *Continuoolithus*. Given the similarities between these two oogenera, we suggest that they
15 be synonymized, designating *Spongioolithus* as the junior synonym of *Continuoolithus*. The
16 synonymization of these two ootaxa extends the Maastrichtian geographic range of
17 *Continuoolithus* from the northern Western Interior down to Utah.

18
19 TAXONOMIC AFFINITY: Although taxonomically identifiable skeletal material has yet to be
20 found in association with *Continuoolithus* eggs, the eggshell morphology of this ootaxon
21 indicates an affinity with Theropoda (Horner 1997; Zelenitsky et al. 1996; Zelenitsky and Hills
22 1997; Zelenitsky and Therrien 2008b). More specific identification is hindered by the absence of
23 diagnostic skeletal material, but the similarities between *Continuoolithus* and elongatoolithid

eggshells may further indicate an association with oviraptorosaurs (Zelenitsky 2000; Zelenitsky et al. 2017a).

Discussion

The discovery of eggshells in the St. Mary River Formation of Alberta offers an opportunity to compare oodiversity in exposures of the same formation in Montana. Our findings reveal the presence of one ornithopod ootaxon (*Spheroolithus*) and three small-bodied theropod ootaxa (*Prismatoolithus*, *Continuoolithus*, and *Montanoolithus*) in the Alberta portion of the formation. The Albertan eggshell assemblage is more diverse than the one recently reported from the Montana portion of the formation (Jackson and Varricchio 2017), which consists of only two ootaxa, a new theropod ootaxon (*Tetonoolithus nelsoni*) and a probable ornithopod ootaxon (*?Spheroolithus*). Thus, the St. Mary River eggshell assemblages from Alberta and Montana possibly share only one ootaxon, *Spheroolithus*. Determination of whether these differences in eggshell assemblage represent regional ootaxonomic differences or are the consequence of small sample size requires additional fossil discoveries. Although limited diagnostic skeletal material has been recovered from the St. Mary River Formation in Alberta and Montana, these ootaxa are consistent with dinosaur biodiversity previously established based on skeletal remains (Table 1).

Comparison with other Upper Cretaceous eggshell assemblages from North America reveals that the St. Mary River eggshell assemblage is of high diversity (Table 2). In Alberta, ornithopod eggshells (*Spheroolithus*) are the most abundant ootaxon recovered from the formation, despite the higher diversity of theropod ootaxa. This abundance of ornithopod eggshells is also observed in several other formations, including the Milk River (Zelenitsky et al.

2017b), lower Two Medicine (Jackson and Varricchio 2010), and Willow Creek formations (Zelenitsky et al. 2017a), whereas theropod ootaxa dominate eggshell assemblages in other formations, including the Dinosaur Park (Zelenitsky and Sloboda 2005), Fruitland (Tanaka et al. 2011), and Hell Creek formations (Jackson and Varricchio 2016). The ootaxonomic composition of the St. Mary River Formation is most similar to those of the Willow Creek (Zelenitsky et al. 2017a), Two Medicine (Hirsch and Quinn 1990; Zelenitsky and Hills 1996, 1997; Zelenitsky et al. 1996; Zelenitsky and Therrien 2008a), and Oldman formations (Hirsch and Quinn 1990; Zelenitsky and Hills 1996, 1997; Zelenitsky et al. 1997; Zelenitsky and Therrien 2008a, b), where all ootaxa are also present.

The St. Mary River eggshell assemblage helps establish a more continuous eggshell record between the upper Santonian and the upper Maastrichtian, and thus permits the evaluation of oological trends through the uppermost Cretaceous of North America. Based on the study of eggshell assemblages from six different rock formations (where the Two Medicine Formation is subdivided into lower and upper sections), Zelenitsky et al. (2017b) reported a trend of overall eggshell thickening of some theropod ootaxa through the uppermost Cretaceous (Table 3), which they interpreted as related to an increase in body mass in small theropod clades. Although theropods exhibit an overall phylogenetic decrease in body size toward the origin of birds (Turner et al. 2007; also see Carrano et al. 2006; Benson et al. 2014), several clades of theropods and ornithischians show trends of increase in body size in the Late Cretaceous (e.g., ceratopsids, oviraptorosaurs, dromaeosaurs, etc.; Turner et al. 2007; Zanno et al. 2012; Benson et al. 2014; also see Funston et al. 2015). Among small theropods, occurrences of unusually large taxa during the upper Maastrichtian of North America are known for ornithomimosaurs, dromaeosaurids, and oviraptorosaurs (Longrich 2008; Zanno et al. 2012; Lamanna et al. 2014;

DePalma et al. 2015). The St. Mary River eggshell provides support to the previously noted trend of increase in eggshell thickness of theropod ootaxa, particularly in *Continuoolithus* and *Prismatoolithus*, which may document an increase in body size among oviraptorosaurs and troodontids, respectively, from the upper Santonian to upper Maastrichtian of North America (Fig. 7; Table 3).

Finally, the recovery of dinosaur eggshells from the St. Mary River Formation of southernmost Alberta emphasizes the differences in fossil preservational styles between this formation and the contemporaneous Horseshoe Canyon Formation of central Alberta. Although the St. Mary River Formation preserves abundant tracks, sparse skeletal material, and eggshell fragments, the Horseshoe Canyon Formation preserves abundant skeletal material, rare tracks, and no eggshell fragments. Whereas the differential preservation of tracks and bones may be related to differences in depositional environments (e.g., Lockley 1991; Lockley and Hunt, 1995), the differences in eggshell preservation potential may be related to paleoclimatic and paleoenvironmental conditions. Paleoclimatic reconstructions indicate that the St. Mary River Formation was deposited under a semi-arid climate (Nadon 1988; Hamblin 1988; Hamblin 2004), whereas the more northerly Horseshoe Canyon Formation was deposited under more humid conditions (Hamblin 1998; Hamblin 2004; Eberth and Braman 2012; Quinney et al., 2013). Other formations known to preserve abundant eggshells, such as the North Horn Formation (Bray 1999; Difley and Ekdale 1999), Oldman Formation (Currie 1988; Zelenitsky et al. 2017a), Two Medicine Formation (Rogers 1990; Varricchio and Horner 1993), and Willow Creek Formation (Zelenitsky et al. 2017a), all bear pedogenic caliches, an indicator of semi-arid environments (e.g. Dregne 1976; Reeves 1976). Several studies have noted a correlation between the presence of pedogenic caliche and the preservational potential of dinosaur eggshells

(Carpenter 1987; Currie 1988; Tanke and Brett-Surman 2001; Zelenitsky et al. 2017a; see also Carpenter 1982), suggesting that semiarid/arid environments are more conducive to the preservation of eggshells than humid environments. Ultimately, future investigation of rock formations preserving pedogenic carbonate nodules may produce dinosaur eggshell at locations and ages from which they are unknown.

Conclusions

The discovery of eggshells from the lower Maastrichtian St. Mary River Formation expands our knowledge of eggshell distribution for the uppermost Cretaceous of North America. We recognize the presence of three theropod ootaxa (*Continuoolithus* cf. *C. canadensis*, *Montanoolithus* cf. *M. strongorum*, and *Prismatoolithus* cf. *P. levis*) and one ornithomimid ootaxon (*Spheroolithus* cf. *S. albertensis*) in the middle part of the formation, a taxonomic composition consistent with a newly-revised faunal list based on skeletal remains. The St. Mary River eggshell assemblage is largely similar to those previously reported from other uppermost Cretaceous formations in terms of ootaxonomic composition, although varies somewhat in terms of ornamentation and shell thickness. The eggshell assemblage corroborates the general trend of increase in eggshell thickness observed among theropod ootaxa (Zelenitsky et al. 2017b), particularly in *Prismatoolithus* cf. *P. levis* and *Continuoolithus canadensis*, during the uppermost Santonian to the upper Maastrichtian, which may reflect an increased body size in certain theropod clades. Based on similarity of ornamentation, eggshell microstructure and shell thickness, we synonymize the oogenus, *Spongioolithus* Bray 1999 with *Continuoolithus* Zelenitsky et al. 1996, thus expanding the Maastrichtian geographic range of the latter taxon farther south to Utah.

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TABLES

Table 1. Dinosaur taxa known from the lower Maastrichtian St. Mary River Formation of Alberta and Montana. 1, Brown and Schlaikjer 1942; 2, Weishampel and Horner 1987; 3, Witmer and Weishampel 1993; 4, Coombs 1995; 5, Chinnery and Weishampel 1998; 6, Makovicky 2010.

Table 2. Comparison of oodiversity of dinosaur eggshell assemblages from the Upper Cretaceous of North American. **Bold indicates oogenera identified in this study;** *Reassigned in this study; **Oospecies not identified. 1, Horner and Makela, 1979; 2, Horner, 1982; 3, Hirsch and Quinn, 1990; 4, Horner and Currie, 1994; 5, Zelenitsky and Hills, 1996; 6, Zelenitsky et al., 1996; 7, Zelenitsky and Hills, 1997; 8, Bray, 1999; 9, Clouse, 2001; 10, Varricchio et al., 2002; 11, Zelenitsky and Sloboda, 2005; 12, Grellet-Tinner et al., 2006; 13, Welsh and Sankey, 2008; 14, Zelenitsky and Therrien, 2008a; 15, Jackson and Varricchio, 2010; 16, Jackson et al., 2010; 17, Tanaka et al., 2011; 18, Jackson and Varricchio, 2016; 19 Jackson and Varricchio, 2017; 20, Zelenitsky et al., 2017a; 21, Zelenitsky et al., 2017b.

Table 3. Comparison of eggshell thickness of dinosaur ootaxa among Upper Cretaceous rock units in Alberta and Montana. Thickness values are recorded in millimeters. 1, Hirsch and Quinn, 1990; 2, Zelenitsky and Hills, 1996; 3, Zelenitsky et al., 1996; 4, Zelenitsky and Hills, 1997; 5, Zelenitsky and Sloboda, 2005; 6, Zelenitsky and Therrien, 2008a; 7, Jackson and Varricchio, 2010; 8, Jackson et al., 2010; 9, Zelenitsky et al., 2017a; 10, Zelenitsky et al., 2017b. *Refers to “cf.” species.

FIGURES

Fig. 1. Map of eggshell localities within the St. Mary River Formation of southern Alberta. 1, Exposures along the bank of the St. Mary River, Municipal District of Cardston, southern Alberta. 2, Roadcuts in Whiskey Gap area, Municipal District of Cardston, southern Alberta.

Fig. 2. Radial thin section photomicrograph of *Montanoolithus* cf. *M. strongorum*, TMP 1998.52.1. Note gradational boundary between continuous and mammillary layers (region located between arrows). Scale is 0.5 mm.

Fig. 3. Photographs of *Prismatoolithus* cf. *P. levis*, TMP 1998.52.1. (A) Smooth external surface showing elongated pore openings (indicated by arrows). Scale bar is 1 mm. (B) Radial thin section in cross-polarized light showing distinct prismatic structure. Prismatic-mammillary layer boundary indicated by arrow. Scale bar is 0.5 mm.

Fig. 4. Photographs of *Spheroolithus* cf. *S. albertensis*, TMP 1987.65.7. (A) External surface with parallel to subparallel anastomosing ridges and elongate pores (marked by arrows). (B) Radial thin section in plane polarized light. Width of shell unit marked by bracket. Scale bars are 0.5 mm.

Fig. 5. SEM photomicrographs of *Continuoolithus* cf. *C. canadensis*. (A) TMP 2016.48.1, a node-dominated fragment (nodes marked by white arrows) and a ridge of coalesced nodes (marked by black arrow). (B) TMP 2016.48.2, a ridge-dominated fragment with no pores (ridges marked by black arrows). Scale bars are 1 mm.

Fig. 6. Radial thin section photomicrograph of *Continuoolithus* cf. *C. canadensis*, TMP 1987.76.4 in plane polarized light showing boundary between continuous and mammillary layers (indicated by arrow). Scale bar is 0.5 mm.

Fig. 7. Variation in eggshell thicknesses of ootaxa between the upper Santonian and the upper Maastrichtian. Findings indicate an overall increase in eggshell thickness through time for theropod ootaxa *Prismatoolithus* cf. *P. levis* and *Continuoolithus* cf. *C. canadensis*. An increase in eggshell thickness was also observed in *Porituberoolithus warnerensis*, a type not recovered in the St. Mary River Formation (Zelenitsky et al. 2017a). Upper Santonian: Milk River Formation (Zelenitsky et al. 2017b); lower Campanian: lower Two Medicine Formation (Jackson and Varricchio 2010); upper Campanian: Oldman

Formation (Zelenitsky and Hills 1996; Zelenitsky et al. 1996; Zelenitsky and Hills 1997), Dinosaur Park Formation (Zelenitsky and Sloboda 2005), Upper Two Medicine Formation (Hirsch and Quinn 1990; Varricchio et al. 2002; Zelenitsky and Therrien 2008a); lower Maastrichtian: St. Mary River Formation (this study; Jackson and Varricchio 2017); upper Maastrichtian: Willow Creek Formation (Zelenitsky et al. 2017).

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Table 1. Taxonomic list of material known from the St. Mary River Formation. 1, Brown and Schlaikjer 1942; 2, Weishampel and Horner 1987; 3, Witmer and Weishampel 1993; 4, Coombs 1995; 5, Chinnery and Weishampel 1998; 6, Makovicky 2010.

Taxon	Location	Voucher specimen	Reference
Hadrosauridae			
Indet. hadrosauridae	Alberta	TMP 1997.66.1 (incomplete skeleton)	2
Indet. hadrosaurine	Montana	(not referenced)	
Ceratopsia			
cf. <i>Anchiceratops</i> sp.	Alberta	TMP 2005.55.5 (partial skull)	1, 5, 6
<i>Montanoceratops cerorhynchus</i>	Montana	AMNH 5464 (partial skeleton)	
Ankylosauridae			
Indet. ankylosaurid	Montana	AMNH 5471 (partial tail club)	4
Tyrannosauridae			
<i>Albertosaurus</i> sp.	Alberta	TMP 2014.6.248 (tooth)	
Troodontidae			
<i>Troodon</i> sp.	Alberta	TMP 2014.6.249 (tooth)	
<i>Paronychodon</i> sp.	Alberta	TMP 2014.6.250 (tooth)	
<i>Pectinodon</i> sp.	Alberta	TMP 2014.6.82 (tooth)	
Dromaeosauridae			
Indet. Saurornitholestine	Alberta	TMP 1998.52.2 (tooth)	
Ornithomimidae			
? <i>Dromiceiomimus</i>	Montana	MOR-609-88-31 (frontal)	3
Maniraptora			
Indet. taxon	Montana	MOR-609-88-56 (partial braincase)	3

Table 2. Comparison of oogenera diversity of Uppermost Cretaceous North American dinosaur eggshell assemblages. **Bold indicates oogenera identified in this study**; *Reassigned here; **Oospecies not identified. 1, Horner and Makela, 1979; 2, Horner, 1982; 3, Hirsch and Quinn, 1990; 4, Horner and Currie, 1994; 5, Zelenitsky and Hills, 1996; 6, Zelenitsky et al., 1996; 7, Zelenitsky and Hills, 1997; 8, Bray, 1999; 9, Clouse, 2001; 10, Varricchio et al., 2002; 11, Zelenitsky and Sloboda, 2005; 12, Grellet-Tinner et al., 2006; 13, Welsh and Sankey, 2008; 14, Zelenitsky and Therrien, 2008a; 15, Jackson and Varricchio, 2010; 16, Jackson et al., 2010; 17, Tanaka et al., 2011; 18, Jackson and Varricchio, 2016; 19 Jackson and Varricchio, 2017; 20, Zelenitsky et al., 2017a; 21, Zelenitsky et al., 2017b.

Oogenera	Formation	Age	Location	Reference
<i>Continuoolithus</i> , <i>Montanoolithus</i> , <i>Porituberoolithus</i> , <i>Prismatoolithus</i> (2 sp.), <i>Spheroolithus</i> (2 sp.)	Willow Creek	Upper Maastrichtian	Alberta	20
<i>Continuoolithus</i> *, <i>Ovaloolithus</i> (2 sp.), <i>Spheruprismatoolithus</i> , <i>Spheroolithus</i>	North Horn	Upper Maastrichtian	Utah	8; *reassigned here
<i>Belonoolithus</i> , <i>Dimorphoolithus</i> , <i>Spheroolithus</i> (2 sp.)	Hell Creek	Maastrichtian	Montana	18
<i>Continuoolithus</i>, <i>Montanoolithus</i>, <i>Prismatoolithus</i>, <i>Spheroolithus</i>, <i>Tetonoolithus</i>, <i>Spheroolithus</i>?	St. Mary River	Lower Maastrichtian	Alberta, Montana	this study, 19
<i>Continuoolithus</i> , <i>Montanoolithus</i> , <i>Prismatoolithus</i> , <i>Spheroolithus</i> , ** <i>Hypacrosaurus</i>	Upper Two Medicine	Upper Campanian	Montana	1-6, 10, 12, 14
<i>Continuoolithus</i> , <i>Porituberoolithus</i> , <i>Prismatoolithus</i> , <i>Reticuloolithus</i> , <i>Spheroolithus</i>	Dinosaur Park	Upper Campanian	Alberta	11
<i>Continuoolithus</i> , <i>Dispersituberoolithus</i> , <i>Porituberoolithus</i> , <i>Prismatoolithus</i> , <i>Spheroolithus</i> , <i>Tristaguloolithus</i>	Oldman	Upper Campanian	Alberta	5-7
<i>Spheruprismatoolithus</i> , <i>Prismatoolithus</i> , ** <i>Hypacrosaurus</i>	Judith River	Upper Campanian	Montana	5, 8-9, 16
<i>Continuoolithus</i> , <i>Porituberoolithus</i> , <i>Prismatoolithus</i>	Fruitland	Upper Campanian	New Mexico	17
<i>Continuoolithus</i> , <i>Porituberoolithus</i> , **dinosauroid-spherulitic, **dinosauroid-prismatic, **ornithoid-prismatic	Aguja	Upper Campanian	Texas	13
<i>Prismatoolithus</i> , <i>Spheroolithus</i> , <i>Triprismatoolithus</i> , <i>Tubercuolithus</i> , <i>Spheruprismatoolithus</i>	Lower Two Medicine	Lower Campanian	Montana	8, 15

<i>Continuoolithus, Porituberoolithus, Prismatoolithus, Spheroolithus, Trisprismatoolithus</i>	Milk River	Upper Santonian	Alberta	21
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Table 3. Eggshell thickness comparisons of dinosaur ootaxa present in the St. Mary River Formation to other Upper Cretaceous units in Alberta and Montana. Thickness values are recorded in millimeters. 1, Hirsch and Quinn, 1990; 2, Zelenitsky and Hills, 1996; 3, Zelenitsky et al., 1996; 4, Zelenitsky and Hills, 1997; 5, Zelenitsky and Sloboda, 2005; 6, Zelenitsky and Therrien, 2008a; 7, Jackson and Varricchio, 2010; 8, Jackson et al., 2010; 9, Zelenitsky et al., 2017a; 10, Zelenitsky et al., 2017b.
*Refers to “cf.” species

Age		Upper Santonian	Lower Campanian	Upper Campanian				Lower Maastrichtian	Upper Maastrichtian
Formation		Milk River	Lower Two Medicine	Judith River	Oldman	Dinosaur Park	Upper Two Medicine	St Mary River	Willow Creek
Eggshell thickness	<i>Spheroolithus albertensis</i> *				0.98–1.22	1.00	1.00–1.20	0.75–1.3 (1.07)	0.53–1.20
	<i>Prismatoolithus levis</i> *			0.80– 1.01	0.70–1.00		0.80–0.90	0.69–1.0 (0.85)	1.56
	<i>Continuoolithus canadensis</i> *	0.43	0.69–0.86		0.84–1.04		1.00–1.08	0.84–1.19 (1.01)	0.86–0.94 (0.91)
	<i>Montanoolithus strongorum</i> *				0.70–0.85		0.70–0.85	0.64	0.58
References		10	7	8	2-4, 6	5	1, 6	This study	9

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85x39mm (300 x 300 DPI)

Fig. 2. Radial thin section photomicrograph of *Montanolithus* cf. *M. strongorum*, TMP 1998.52.1. Note gradational boundary between continuous and mammillary layers (region located between arrows). Scale is 0.5 mm. [Intended for column width]

46x25mm (300 x 300 DPI)

Fig. 3. Photographs of *Prisma toolithus* cf. *P. levis*, TMP 1998.52.1. (A) Smooth external surface showing elongated pore openings (indicated by arrows). Scale bar is 1 mm. (B) Radial thin section in cross-polarized light showing distinct prismatic structure. Prismatic-mammillary layer boundary indicated by arrow. Scale bar is 0.5 mm. [Intended for column width]

118x161mm (300 x 300 DPI)

Fig. 4. Photographs of *Spheroolithus* cf. *S. albertensis*, TMP 1987.65.7. (A) External surface with parallel to subparallel anastomosing ridges and elongate pores (marked by arrows). (B) Radial thin section in plane polarized light. Width of shell unit marked by bracket. Scale bars are 0.5 mm. [Intended for column width]

139x224mm (300 x 300 DPI)

Fig. 5. SEM photomicrographs of *Continuoolithus* cf. *C. canadensis*. (A) TMP 2016.48.1, a node-dominated fragment (nodes marked by white arrows) and a ridge of coalesced nodes (marked by black arrow). (B) TMP 2016.48.2, a ridge-dominated fragment with no pores (ridges marked by black arrows). Scale bars are 1 mm. [Intended for page width]

79x34mm (300 x 300 DPI)

Fig. 6. Radial thin section photomicrograph of *Continuoolithus* cf. *C. canadensis*, TMP 1987.76.4 in plane polarized light showing boundary between continuous and mammillary layers (indicated by arrow). Scale bar is 0.5 mm. [intended for column width]

64x48mm (300 x 300 DPI)

Fig. 7. Variation in eggshell thicknesses of ootaxa between the upper Santonian and the upper Maastrichtian. Findings indicate an overall increase in eggshell thickness through time for theropod ootaxa *Prismatoolithus* cf. *P. levis* and *Continuoolithus* cf. *C. canadensis*. An increase in eggshell thickness was also observed in *Porituberoolithus warnerensis*, a type not recovered in the St. Mary River Formation (Zelenitsky et al. 2017a). Upper Santonian: Milk River Formation (Zelenitsky et al. 2017b); lower Campanian: lower Two Medicine Formation (Jackson and Varricchio 2010); upper Campanian: Oldman Formation (Zelenitsky and Hills 1996; Zelenitsky et al. 1996; Zelenitsky and Hills 1997), Dinosaur Park Formation (Zelenitsky and Sloboda 2005), Upper Two Medicine Formation (Hirsch and Quinn 1990; Varricchio et al. 2002; Zelenitsky and Therrien 2008a); lower Maastrichtian: St. Mary River Formation (this study; Jackson and Varricchio 2017); upper Maastrichtian: Willow Creek Formation (Zelenitsky et al. 2017). [Intended for column width]

137x219mm (300 x 300 DPI)

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