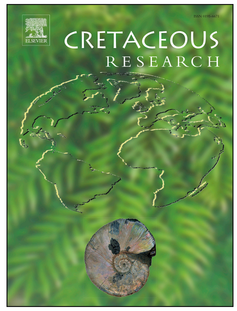

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Darla K. Zelenitsky, François Therrien, Kohei Tanaka, Yoshitsugu Kobayashi, Christopher L. DeBuhr

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Dinosaur eggshells from the Santonian Milk River Formation of Alberta, Canada

Darla K. Zelenitsky[a], François Therrien[b], Kohei Tanaka[a,c], Yoshitsugu Kobayashi[d], and Christopher L. DeBuhr[a]

[a] Department of Geoscience, University of Calgary, 2500 University Dr. NW, Calgary, Alberta T2N 1N4 Canada

[b] Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0 Canada

[c] Nagoya University Museum, Nagoya University, Furocho, Chikusa-Ku, Nagoya, 464-8601 Japan

[d] Hokkaido University Museum, Hokkaido University, N10 W8 Kita-Ku, Sapporo, Hokkaido, 060-0810 Japan

E-mail: dkzeleni@ucalgary.ca (DKZ); ktanaka@ucalgary.ca (KT); francois.therrien@gov.ab.ca (FT); ykobayashi@museum.hokudai.ac.jp (YK); cdebuhr@ucalgary.ca (CLD).

*Corresponding author: Darla K. Zelenitsky

Department of Geoscience, University of Calgary, 2500 University Dr. NW, Calgary, Alberta T2N 1N4 Canada

Tel: +1 (403) 210-6082

Abstract

The North American fossil record of dinosaur eggshells for the Cretaceous is primarily restricted to formations of the middle (Albian–Cenomanian) and uppermost (Campanian–Maastrichtian) stages, with a large gap in the record for intermediate stages. Here we describe a dinosaur eggshell assemblage from a formation that represents an intermediate and poorly fossiliferous stage of the Upper Cretaceous, the Santonian Milk River Formation of southern Alberta, Canada. The Milk River eggshell assemblage contains five eggshell taxa: *Continuoolithus*, *Porituberoolithus*, *Prismatoolithus*, *Spheroolithus*, and *Triprismatoolithus*. These ootaxa are most similar to those reported from younger Campanian–Maastrichtian formations of the northern Western Interior than they are to ootaxa reported from older middle Cretaceous formations (i.e., predominantly *Macroelongatoolithus*). Characteristics of the Milk River ootaxa indicate that they are ascribable to at least one ornithopod and four small theropod species. The taxonomic affinity of the eggshell assemblage is consistent with the dinosaur fauna known based on isolated teeth and fragmentary skeletal remains from the formation, although most ornithischians and large theropods are not represented by eggshell. Relative to the Milk River Formation eggshell, similar oospecies occurring in younger Cretaceous deposits tend to be somewhat thicker, which may reflect an increase in body size of various dinosaur lineages during the Late Cretaceous.

Key words: Alberta, dinosaurs, eggshells, Milk River Formation, Santonian, theropod.

1. Introduction

Dinosaur eggshells are useful indicators of taxonomic diversity and faunal composition, particularly in formations or paleogeographic regions where skeletal remains are sparse (Tanaka et al., 2016; Zelenitsky et al., 2017). Cretaceous dinosaur egg remains from North America are reported primarily from formations of the middle (Albian–Cenomanian) and uppermost (Campanian–Maastrichtian) stages. Uppermost Cretaceous formations (e.g., Oldman, Dinosaur Park, Two Medicine, Fruitland, Aguja, Hell Creek, North Horn, and Willow Creek formations) have yielded several dinosaur ootaxa , which have been ascribed primarily to ornithopods (e.g., *Spheroolithus*) and small theropods (e.g., *Continuoolithus*, *Prismatoolithus*) (Zelenitsky and Hills, 1996, 1997; Zelenitsky et al., 1996, 2017; Bray, 1999; Zelenitsky and Sloboda, 2005; Welsh and Sankey, 2008; Jackson and Varricchio, 2010, 2016; Tanaka et al., 2011). Only one ootaxon, *Macroelongatoolithus*, has been described from middle Cretaceous formations (e.g., Dakota, Wayan, and uppermost Cedar Mountain formations), and has been assigned to giant oviraptorosaurs (Zelenitsky et al., 2000; Huh et al., 2014; Simon, 2014; Krumenacker et al., 2017). The differences in eggshell taxonomic composition between middle and uppermost Cretaceous formations reflect some of the changes indicated by skeletal remains that occurred in dinosaur faunas during the Late Cretaceous in North America (Weishampel et al., 2004). There is, however, a dearth of dinosaur fossils from intervening Upper Cretaceous stages, specifically from the Turonian through the Santonian. Here we provide the description of a dinosaur eggshell assemblage from the Santonian Milk River Formation of southern Alberta, Canada, which has bearing on our understanding of the Late Cretaceous dinosaur faunas of North America.

2. Geological Setting and Locality

The Milk River Formation is widespread in the subsurface of southern Alberta, although exposures are limited to coulees and river valleys east of the town of Milk River. This formation is the first of several regressive-transgressive clastic wedges deposited during the Late Cretaceous in the Western Canada Basin in response to Cordilleran orogenic pulses. It overlies the calcareous marine shales of the Colorado/Alberta Group and is overlain by the marine Pakowki Formation, making it stratigraphically equivalent to the Telegraph Creek and Eagle formations of Montana (Payenberg et al., 2002). The Milk River Formation is subdivided into three members. In ascending stratigraphic order, they are: 1) the Telegraph Creek member, dominated by offshore shales; 2) the Virgelle member, composed of storm-dominated shoreface sandstones at the base and tidal channel or estuarine sandstones at the top; and 3) the Deadhorse Coulee member, consisting of mudstones, sandstones, and coal beds of alluvial origin (for a review, see Meyer et al., 1998; Braman, 2001; and Payenberg et al., 2002). The age of the formation has been constrained to the late Santonian (~84.5–83.5 Ma) on the basis of bio-, palyno-, and magnetostratigraphy as well as radiometrically-dated volcanic deposits (Payenberg et al., 2002).

The Deadhorse Coulee Member is considered to be latest Santonian in age (Braman, 2001; Payenberg et al., 2002) and is the only member of the Milk River Formation known to preserve fossil remains of terrestrial organisms. Macrofloral remains suggest that the Santonian was characterized by a warm and humid climate (Bell, 1963; Wolfe and Upchurch, 1987; Upchurch and Wolfe, 1993), while microfloral assemblages indicate a landscape of open forests with shallow ponds (Braman, 2001; Kalgutkar and Braman, 2008). The Deadhorse Coulee

Member has produced a diverse fauna composed of amphibians, bony fishes, chondrichthyans, crocodylomorphs, dinosaurs, mammals, squamates, and turtles, although most are represented by microvertebrate remains and isolated or partial skeletal remains (for a recent review, see Larson, 2010; Ryan et al., 2012; Evans et al., 2013; Larson et al., 2014). This faunal assemblage documents a transitional phase in Late Cretaceous ecosystems that preserves the last occurrences of archaic taxa and the earliest representatives of faunas typical of the latest Cretaceous (e.g., Fox, 1968; Larson, 2010).

While bones and teeth are known from the Deadhorse Coulee Member, fossil eggshells have yet to be reported. Here we describe fossil eggshell fragments (n ≈ 400) recovered from a single locality over several field seasons between 2009 and 2015 in outcrops of the member exposed along Verdigris Coulee (Fig. 1). The fossil locality is inferred to be situated in the upper half of the member, based on correlation with regional stratigraphic sections (see Larson, 2010). The eggshells were found on a small hill where the exposures consist of channel sandstones interbedded with pedogenically modified mudstones, and appear to have weathered out of a cross-stratified channel sandstone near the top of the butte (Fig. 2).

3. Materials and Methods

Eggshell fragments were classified into various morphotypes based on macro- and microstructures using a stereomicroscope, and their thicknesses (with and without ornamentation) were measured with digital calipers and a micrometer. The microstructure and ultrastructure of each eggshell morphotype were studied using stereoscopic (Leica M80), petrographic (Leica DM 2500P), and scanning electron (FEI Quanta FEG 250 SEM) microscopes. Radial thin sections for each eggshell morphotype were produced for examination with a petrographic microscope, particularly for polarized light microscopy (PLM). For scanning electron microscopy (SEM), eggshell fragments were ultrasonically cleaned, dried with compressed gas, and were affixed to aluminum stubs with double-sided carbon tape. The fragments were then examined on the inner and outer surfaces, as well as on freshly-fractured radial surfaces.

The description of the eggshell focuses on morphological features that differ from similar ootaxa found in other formations. The eggshells are classified using a parataxonomic scheme previously established for fossil eggs (Zhao, 1975; Hirsch, 1994).

The eggshells are accessioned in the collections of the Royal Tyrrell Museum of Palaeontology (TMP), Drumheller, Alberta, Canada, and in the Zelenitsky Egg Catalogue (ZEC) at the University of Calgary, Calgary, Alberta, Canada. Although all eggshells are from the same locality and horizon, they have been assigned different catalogue numbers as they have been collected by different individuals and over several years.

4. Systematic Description

Oofamily Prismatoolithidae Hirsch, 1994 emend. Moreno-Azanza et al., 2014

Oogenus Prismatoolithus Zhao and Li, 1993 emend. Zelenitsky and Hills, 1996

Oospecies Prismatoolithus sp.

Material. Isolated eggshell fragments (n = 6) (TMP2009.151.1, n = 4; ZEC-449, n = 2).

Description and Comparison. This eggshell morphotype is thin, ranging from 0.21–0.27 mm, with an average of 0.24 mm. The smooth outer surface (Fig. 3A) and microstructure are comparable to *Prismatoolithus* sp. and *Prismatoolithus hirschi* reported from the lower Willow Creek Formation and lowermost Two Medicine Formation (Jackson and Varricchio, 2010; Zelenitsky et al., 2017), respectively, although it is thinner (Table 1).

Taxonomic affinity. Theropoda (see Zelenitsky et al., 2017).

Oofamily Spheroolithidae Zhao, 1979

Oogenus Spheroolithus Zhao, 1979 emend. Mikhailov, 1994a

Oospecies Spheroolithus cf. *S choteauensis*

Material. Isolated eggshell fragments (n = 313) (TMP2009.151.1, n = 202; ZEC-448, n = 24; ZEC-449 n = 87).

Description. *Spheroolithus* cf. *S. choteauensis* is the dominant eggshell morphotype recovered from the locality, representing approximately 82% of all eggshell fragments recovered. The eggshell thickness ranges from 0.40 to 0.70 mm (mean 0.57 mm), which is slightly thinner than *Spheroolithus choteauensis* reported from the lowermost Two Medicine Formation and from the lower Willow Creek Formation (Table 1). The outer surface of most fragments is relatively smooth, although some show weakly ornamented or undulating surface textures (Fig. 3B) as reported for *Spheroolithus choteauensis* (Jackson and Varricchio, 2010). The eggshell consists of individual shell units that have parallel to slightly divergent lateral boundaries in radial thin section. The inner part of the shell units consist primarily of acicular crystals that grade into coarser wedges in the remainder of the shell unit. The shell units show an overall sweeping extinction pattern in PLM, although sometimes appear blocky presumably due to recrystallization. The base of the shell units in many fragments preserve basal plate groups that would have been anchored in the shell membrane in life.

Taxonomic affinity. Ornithopoda (see Jackson and Varricchio, 2010; Zelenitsky et al., 2017).

Oofamily Incertae sedis
Oogenus Continuoolithus Zelenitsky et al., 1996
Oospecies Continuoolithus cf. *C. canadensis*.

Material. One eggshell fragment (ZEC-448).

Description and Comparison. The eggshell thickness is 0.43 mm and 0.61 mm, without and with ornamentation, respectively. The outer surface ornamentation (Fig. 3C) and microstructure of this fragment are comparable to those of other egg remains ascribed to *Continuoolithus*, although it is slightly thinner than known *Continuoolithus* eggshells reported from Campanian and Maastrichtian localities in the northern Western Interior (Table 1).

Taxonomic affinity. Theropoda (see Zelenitsky et al., 2017).

Oogenus Porituberoolithus Zelenitsky et al., 1996

Oospecies Porituberoolithus cf. *P. warnerensis* Zelenitsky et al., 1996

Material. One eggshell fragment (ZEC-448).

Description and Comparison. The eggshell thickness is 0.37 mm and 0.71 mm, without and with ornamentation, respectively. The eggshell fragment is comparable in morphology (Fig. 3D) and microstructure to *Porituberoolithus warnerensis* from the Oldman and Willow Creek formations (Zelenitsky et al., 1996, 2017), although it is slightly thinner (Table 1).

Taxonomic affinity. Theropoda (see Zelenitsky et al., 2017).

Oogenus Triprismatoolithus Jackson and Varricchio, 2010

Oospecies Triprismatoolithus sp.

Material. Isolated eggshell fragments (n = 60) (TMP2009.151.1, n = 39; ZEC-448, n = 6; ZEC-449, n = 15).

Description and Comparison. This ootaxon is the second most abundant from the locality, representing approximately 16% of all eggshell fragments recovered. The eggshell thickness ranges from 0.40 to 0.60 mm (mean 0.50 mm) without ornamentation, and the nodes are up to half of the eggshell thickness in height. The outer surface ornamentation consists of circular to oval nodes (in plan view) that are interconnected by a network of narrow ridges that give the outer surface a pitted appearance (Fig. 4A). The ornamentation differs from *Triprismatoolithus stephensi*, which has nodes but lacks the network of ridges (Jackson and Varricchio, 2010). Pore openings, located between the nodes and ridges, are circular to oval in plan view and connect to narrow, straight canals. The microstructure consists of narrow columnar shell units that reveal an overall prismatic extinction in PLM. At least two structural layers, an outer prismatic layer and an inner mammillary layer, are present (Fig. 4B). In SEM, the uppermost part of the prismatic layer (about 100 µm in thickness) appear to consist of more blocky crystals than the remainder of the prismatic layer, and may be analogous to the third structural layer (i.e., external layer) as described for *Triprismatoolithus stephensi* (Fig. 4C). Of the fragments examined with SEM, the prismatic layer appears more coarsely crystalline and does not show squamatic ultrastructure as described for *Triprismatoolithus stephensi*. This is presumably due to obliteration of the squamatic textures as a result of recrystallization. The boundaries between structural layers of the shell units are gradual, and tabular ultrastructure can be found to varying degrees throughout the shell units. The mammillae are formed of wedge-like crystals and are tightly packed on the inner surface (Fig. 4D).

Taxonomic affinity. Theropoda/Aves (see Jackson and Varricchio, 2010).

5. Discussion

The Milk River Formation preserves one of the most diverse pre-Campanian dinosaur eggshell assemblages reported from North America. The eggshells described here reveal the presence of at least one ornithopod (*Spheroolithus*) and four theropod species (*Continuoolithus*, *Porituberoolithus*, *Prismatoolithus*, *Triprismatoolithus*) in the Santonian of the northern Western Interior. The thinness of the theropod ootaxa indicates that the eggshells belong to animals of small body size (<100 kg; Tanaka et al., 2016), potentially species of caenagnathids, dromaeosaurids, troodontids, or birds. The taxonomic composition of the eggshell assemblage is consistent with that known from skeletal remains (Brown et al., 2015), although most ornithischian and large theropod taxa known are not represented by eggshell. A diversity of small theropod ootaxa is also typical of the Dinosaur Park and lower Willow Creek formations of Alberta (Zelenitsky and Sloboda, 2005; Zelenitsky et al., 2017), the Fruitland Formation of New Mexico (Tanaka et al., 2011), and the Sasayama Group of Japan (Tanaka et al., 2016).

The ootaxa of the Milk River eggshell assemblage are thinner, on average, than the same ootaxa reported from younger formations (i.e., Dinosaur Park, Oldman, Two Medicine, and Willow Creek formations) of the northern Western Interior (Table 1). Since eggshell thickness is related to egg mass and presumably body mass in theropods (Tanaka et al., 2016), perhaps the increase in eggshell thickness in stratigraphically younger formations represents an increase in body size of various theropod lineages (e.g., caenagnathids, dromaeosaurids, troodontids) toward the end of the Cretaceous. Unfortunately, the fragmentary nature of skeletal remains from the Milk River Formation (as well as from other Santonian formations in North America) precludes accurate assessment of the body size of most dinosaur species during that stratigraphic interval. Nevertheless, a general trend of increase in tooth size among various theropod lineages observed between the Milk River Formation and terminal Cretaceous formations (see Larson and Currie, 2013: fig. 3) supports such an inference of increase in body size during the Late Cretaceous.

The Milk River eggshell assemblage contains ootaxa similar to those previously described from Campanian and Maastrichtian deposits of Alberta and Montana. This research extends the stratigraphic range of several ootaxa, such as *Continuoolithus canadensis*, *Porituberoolithus warnerensis*, *Prismatoolithus* sp., and *Spheroolithus choteauensis*, from the Campanian–Maastrichtian into the Santonian, and *Triprismatoolithus* from the lowermost Campanian into the Santonian. Overall, dinosaur ootaxonomic diversity appears to have remained relatively consistent from the latest Santonian through the Maastrichtian (see also Jackson and Varricchio, 2010).

The composition of the Milk River eggshell assemblage differs from that of the next oldest, middle Cretaceous (Albian–Cenomanian) eggshell assemblages known from North America, namely those from the Mussentuchit Member of the Cedar Mountain Formation (Zelenitsky et al., 2000), Dakota Formation (Zelenitsky et al., 2000; referred to as Naturita Formation by Carpenter, 2014), and Wayan Formation (Simon, 2014; Krumenacker et al., 2017). Many dinosaur eggshell fragments have been collected from these formations and nearly all eggshell described is assignable to *Macroelongatoolithus*, an oogenus attributable to giant oviraptorosaurs (Zelenitsky et al., 2000; Huh et al., 2014; Simon, 2014; Krumenacker et al., 2017; Pu et al., in press). Skeletal remains of these animals are as yet undescribed from North America, but such remains and *Macroelongatoolithus* eggs/eggshells have been reported from the Cenomanian through lower Campanian of Asia (Wang and Zhou, 1995; Fang et al., 2000; Jin et al., 2007; Xu et al., 2007; Wang et al., 2010; Huh et al., 2014; Tsuihiji et al., 2015; Pu et al., in press). Nevertheless, the abundance of *Macroelongatoolithus* eggshell reveals that giant oviraptorosaurs were relatively common in North America during the middle Cretaceous. The absence of *Macroelongatoolithus* eggshell in the Milk River and younger formations suggests that giant oviraptorosaurs disappeared in North America prior to the latest Santonian (~83.5 Ma), while they purportedly persisted in Asia through the early Campanian (Kim et al., 2011; Huh et al., 2014). Thus, the eggshell taxa observed between middle and Upper Cretaceous formations may reflect the extinction of giant oviraptorosaurs prior to the late Santonian and the radiation of smaller-bodied maniraptorans during the latest Cretaceous in North America.

Ootaxa from the Late Cretaceous of North America reflect some of the faunal changes that occurred between the middle and later part of this time period, an interval that saw the decline of allosauroids, sauropods and tenontosaurs, and the rise of ceratopsids, hadrosauroids, maniraptorans and tyrannosaurids (Weishampel et al., 2004). Although faunal changes should result in changes in the taxonomic composition of eggshell assemblages, this is complicated by the limited preservation potential of egg fossils (i.e., there are few pre-Campanian Cretaceous egg sites known) and the limitations of our understanding of the taxonomic affinity of many ootaxa, as the egg remains of many dinosaur clades known from the middle or Upper Cretaceous of North America have yet to be identified (e.g., ankylosaurs, basal neoceratopsians, ceratopsids, iguanodontids, pachycephalosaurs, therizinosaurs, tyrannosaurids). Nevertheless, the eggshell and fragmentary skeletal remains from the Milk River Formation indicates that the dinosaur fauna that characterizes the latest Cretaceous in North America was already present by the late Santonian, albeit potentially represented by less massive species.

Conclusions

An eggshell assemblage from the Santonian Milk River Formation of Alberta represents the oldest fossil eggshells reported to date from Canada. Because Santonian eggshells are exceedingly rare in North America, this new assemblage fills an important gap in the fossil record of Late Cretaceous eggshells. The Milk River eggshell assemblage, representing ornithopods and small theropods, reflects the establishment of typical latest Cretaceous dinosaurian faunas in North America by the latest Santonian (~83.5 Ma). The Milk River ootaxa are unreported in the next oldest eggshell assemblages known from the middle Cretaceous (Albian–Cenomanian), which are dominated by eggshell of giant oviraptorosaurs (*Macroelongatoolithus*). As such, the Milk River eggshell assemblage suggests that the extinction of giant oviraptorosaurs in North America occurred prior to the latest Santonian. Finally, Milk River theropod ootaxa tend to be thinner than similar ootaxa found in younger Cretaceous formations, indicating that a trend toward increased body size may have occurred in maniraptorans during the Late Cretaceous.

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Figure captions

Figure 1. Map showing the location of the Milk River Formation eggshell locality in Verdigris Coulee, southern Alberta, Canada.

Figure 2. Stratigraphic section of the rock exposure at the Milk River eggshell locality, Verdigris Coulee, southern Alberta, Canada.

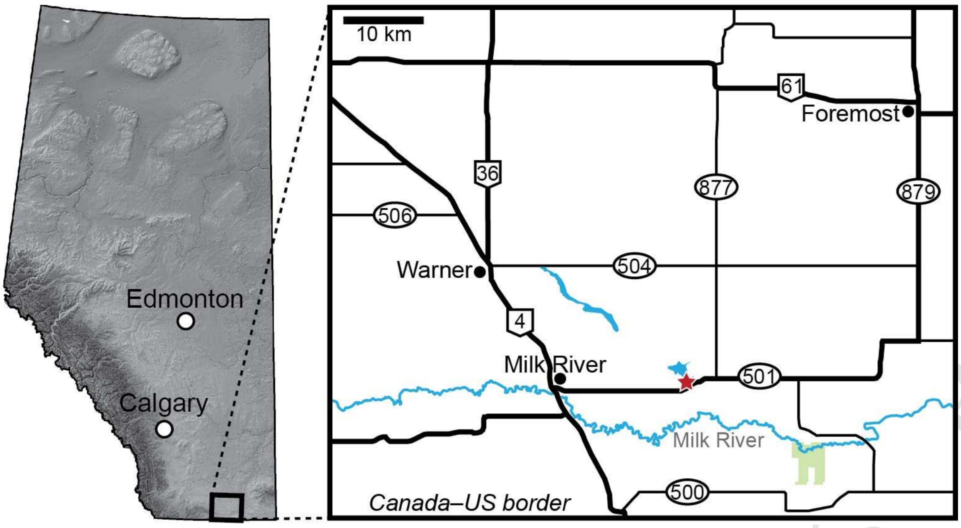
Figure 3. Photographs of the outer surface of Milk River ootaxa. (a) *Prismatoolithus* (TMP2009.151.1). (b) *Spheroolithus* (TMP2009.151.1). (c) *Continuoolithus* (ZEC-448). (d) *Porituberoolithus* (ZEC-448). Scale bars are 1 mm.

Figure 4. SEM micrographs of eggshell of *Triprismatoolithus* sp. (TMP2009.151.1) from the Milk River Formation, southern Alberta. (a) Outer surface showing nodes and network of ridges. Pore openings indicated by arrows. (b) Radial view showing mammillary layer (ML) and prismatic layer (PL). (c) Possible external layer (arrow) near the outer surface of the eggshell. (d) Mammillary layer (radial view) with tablular ultrastructure (arrow).

Table 1

Comparison of eggshell thickness of Milk River Formation oospecies with comparable ooospecies in the northern Western Interior. Eggshell thicknesses of *Triprismatoolithus*, *Porituberoolithus*, and *Continuoolithus* exclude height of ornamentation. Parentheses indicate mean thickness values if available. * and † indicate ootaxa including "cf." and "sp.", respectively. References: a, this study; b, Jackson and Varricchio (2010); c, Jackson et al. (2010); d, Zelenitsky and Hills (1996); e, Zelenitsky and Hills (1997); f, Zelenitsky et al. (1996); g, Zelenitsky and Therrien (2008); h, Zelenitsky and Sloboda (2005); i, Hirsch and Quinn (1990); j, Zelenitsky et al. (2017). Abbreviations: C, Campanian; M, Maastrichtian; S, Santonian.

Formation	Milk River[a]	Lower Two Medicine[b]	Judith River[c]	Oldman[d–g]	Dinosaur Park[h]	Upper Two Medicine[g,i]	Willow Creek[j]
Age	S	C	C	C	C	C	M
*Continuoolithus**	0.43	0.69–0.86		0.84–1.04		1.00–1.08	0.86–0.94 (0.91)
Porituberoolithus	0.37			0.50–0.65			0.45–0.78
*Prismatoolithus hirschi**/sp.	0.21–0.27 (0.24)	0.50–0.56					0.31–0.63
*S. choteauensis**	0.40–0.70 (0.57)	0.80–0.85					0.40–0.93
Triprismatoolithus†	0.40–0.60 (0.50)	0.53–0.85					


Edmonton
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Foremost
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877
879
506
Warner
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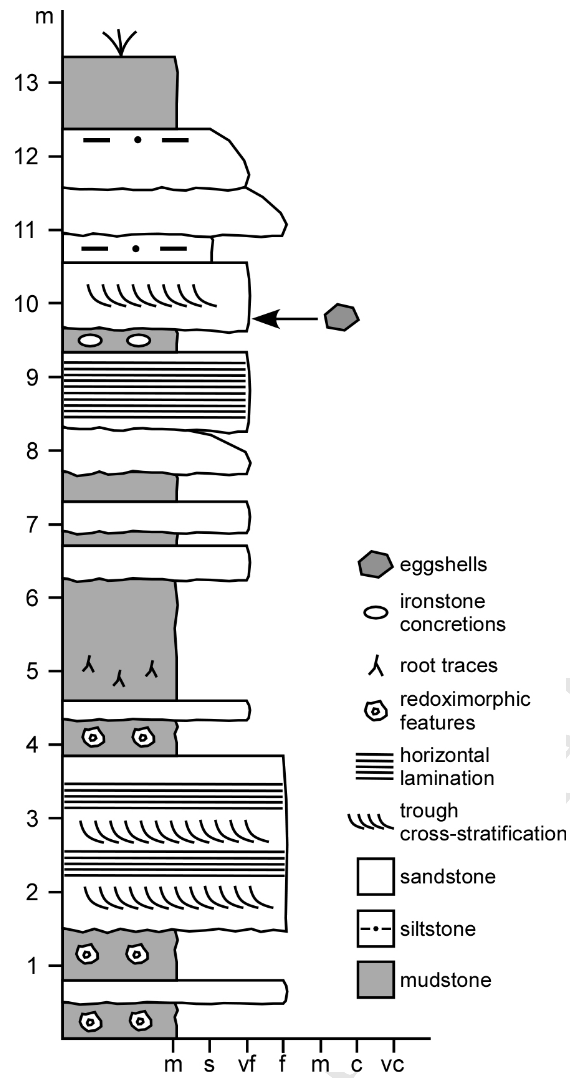
4
Milk River
501
Milk River
500
Canada–US border


m
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12
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4
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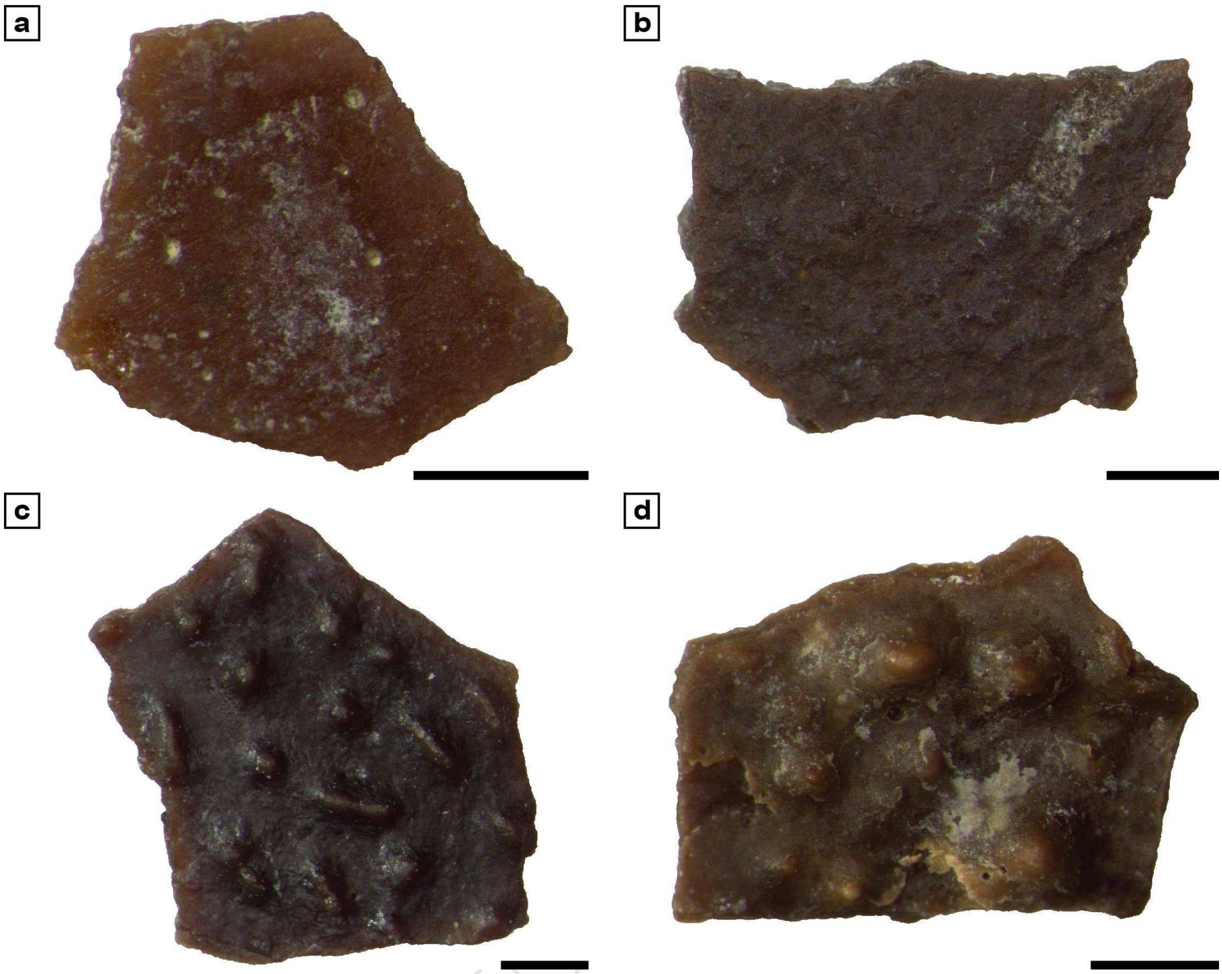
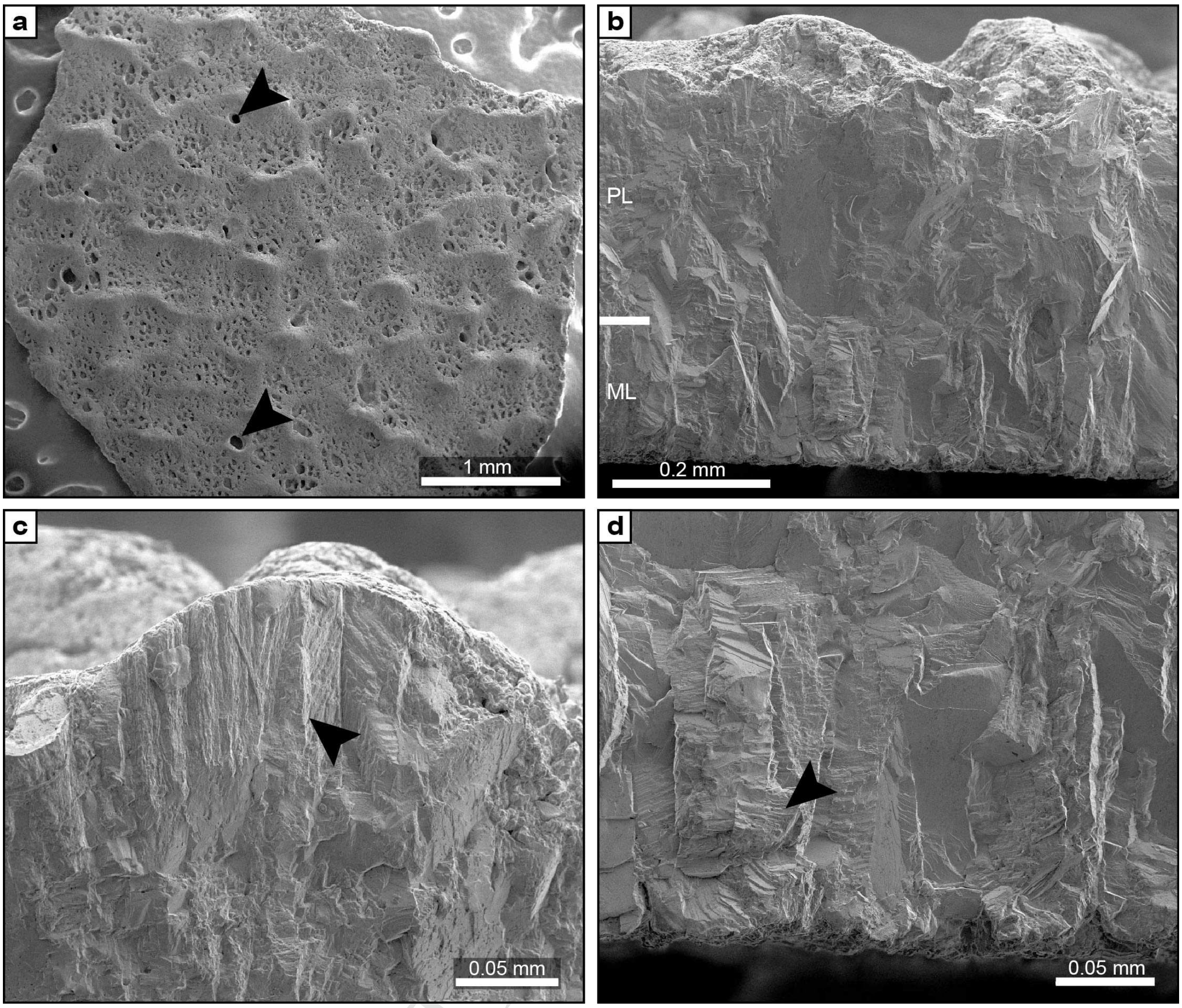
2
1
m s vf f m c vc
eggshells
ironstone concretions
root traces
redoximorphic features
horizontal lamination
trough cross-stratification
sandstone
siltstone
mudstone


a
b
c
d



a
1 mm
b
PL
ML
0.2 mm
c
0.05 mm
d
0.05 mm