Parataxonomic classification of ornithoid eggshell fragments from the Oldman Formation (Judith River Group; Upper Cretaceous), southern Alberta

Darla K. Zelenitsky, L.V. Hills, and Philip J. Currie

Abstract: Examination of a large number of eggshell fragments collected from the Oldman Formation of southern Alberta reveals a greater ootaxonomic diversity than is known from complete eggs or clutches. Three new oogenera and oospecies of the ornithoid-ratite morphotype and one of the ornithoid-prismatic morphotype are established, based on the eggshell fragments. ***Porituberoolithus warnerensis*** oogen. et oosp. nov. and ***Continuoolithus canadensis*** oogen. et oosp. nov. have a microstructure similar to that of elongatoolithid eggs of theropod dinosaurs. ***Tristraguloolithus cracioides*** oogen. et oosp. nov. and ***Dispersituberoolithus exilis*** oogen. et oosp. nov. possess an external zone and thus have a microstructure like modern avian eggshell. *Tristraguloolithus* has a shell thickness, microstructure, and surface sculpture similar to those of recent bird eggshell of the family Cracidae (order Galliformes). *Dispersituberoolithus* exhibits the primitive or normal eggshell condition of some recent neognathous avian taxa. The ootaxa described indicate a diversity of both avian and theropod dinosaur egg layers within Devil's Coulee and Knight's Ranch, southern Alberta, during the Late Cretaceous.

Résumé : L'examen de très nombreux fragments de coquilles d'oeuf livrés par la Formation d'Oldman, dans le sud de l'Alberta, révèle une plus grande diversité ootaxonomique que celle qui a été divulguée par les oeufs complets ou les couvées. L'étude de fragments de coquilles d'oeuf a permis d'établir trois nouveaux oogenres et ooespèces du morphotype ornithoïde-ratite et un autre du morphotype ornithoïde-prismatique. ***Porituberoolithus warnerensis*** n. oogen. et oosp. et ***Continuoolithus canadensis*** n. oogen. et oosp. ont une microstructure similaire aux oeufs élongatoolithides des dinosaures théropodes. ***Tristraguloolithus cracioides*** n. oogen. et oosp. et ***Dispersituberoolithus exilis*** n. oogen. et oosp. possèdent une zone externe, par conséquent leur microstructure est identique à celle de la coquille des oiseaux actuels. L'épaisseur, la microstructure et les motifs à la surface de la coquille de *Tristraguloolithus* sont analogues aux coquilles d'oiseaux récents de la famille des Cracidés (ordre Galliformes). *Dispersituberoolithus* présente l'aspect de la coquille primitive ou normale de certains taxons aviaires néognatheux. Les descriptions présentées ici indiquent une diversité ootaxonomique dans les couches à oeufs d'oiseaux et aussi à oeufs de dinosaures théropodes, dans les dépôts de Devil's Coulee et de Knight's Ranch, du sud de l'Alberta, au Cretacé tardif.
[Traduit par la rédaction]

Introduction

In the past two decades, numerous discoveries of fossil eggs and eggshells worldwide have increased interest in these trace fossils. Many descriptive papers have been published and several different approaches to eggshell classification have been taken (Hirsch 1989). A binominal nomenclature was used for many years to classify fossil eggs from China (Zhao and Jiang 1974; Zhao 1975), prior to being adopted elsewhere. Hirsch and Quinn (1990) and Mikhailov (1991, 1992) established a structural classification that defines eggshells according to basic types, morphotypes, ornamentation, and pore systems. The integration of this structural classification with a binominal nomenclature has resulted in a viable parataxonomic system that has been applied on specimens from China (Zhao 1994), France (Vianey-Liaud et al. 1994), India (Khosla and Sahni 1995), Mongolia (Mikhailov 1991), and the United States (Hirsch 1994). This parataxonomy has facilitated the comparison and correlation of fossil eggshells worldwide and made it possible to unravel some of their taxonomic affinities (Mikhailov 1994*a*, 1995*a*), thereby increasing our knowledge of the paleoecology and paleobiology of extinct egg layers.

The discovery of nesting sites from the Late Cretaceous of northern Montana and southern Alberta has raised interest in fossil egg remains from North America (Hirsch 1994; Hirsch and Quinn 1990; Zelenitsky and Hills 1996). In southern Alberta, several localities within the Oldman Formation have produced isolated eggshell fragments, including Devil's Coulee, Knight's Ranch, and Wann's Hill (Zelenitsky 1995). Of these, Devil's Coulee has yielded the greatest abundance of eggs, embryos, and eggshell fragments. Several egg clutches of *Hypacrosaurus stebingeri* Horner and Currie, 1994 and approximately 20 000 isolated eggshell fragments have been collected from this site.

Zelenitsky (1995) identified seven oospecies from Devil's Coulee, based on the isolated eggshell fragments. This diversity of ootaxa indicates that several egg-laying taxa are represented by the eggshell fragments in addition to those known

Received February 13, 1996. Accepted July 29, 1996.

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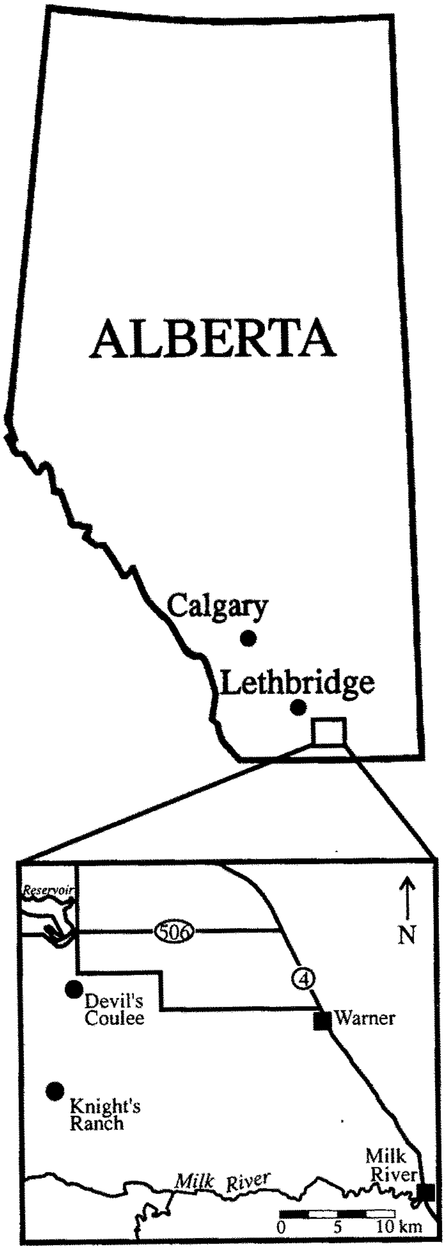
Fig. 1. Map of Alberta, showing Devil's Coulee and Knight's Ranch localities.



from the egg clutches. The purpose of this paper is to systematically describe the eggshell fragments that are referable to the ornithoid-ratite and ornithoid-prismatic morphotypes.

Abbreviations: cl, continuous layer; DMNH, Denver Museum of Natural History, Denver, Colo.; ez, external zone; HEC, Hirsch's Egg Catalogue, University of Colorado Museum, Boulder, Colo.; ml, mammillary layer; PLM, polarizing light microscopy; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alta.; SEM, scanning electron microscopy; USNM, United States National Museum, Washington, D.C.

Locality and stratigraphic setting

The ornithoid-type eggshells were collected from four sites (Faye Walker's Coulee, North Baby Butte, Little Diablo's Hill, Juvie Camp) within Devil's Coulee and a single site on the Knight's Ranch, southern Alberta (Fig. 1). Precise location data for these sites are on file at RTMP. The eggshells were recovered from mudstones of the Oldman Formation (Dawson et al. 1994; Eberth and Hamblin 1993; Russell and Landes 1940). Eberth and Deino (1992) obtained radiometric Ar^{40}/Ar^{39} dates of 74.94 $\pm$ 0.08 and ?75.6 Ma from bentonites located at the base of the Devil's Coulee section, confirming a late Campanian age (Obradovich 1993).

Materials and methods

Eggshell fragments were recovered through surface collecting and screenwashing by RTMP field crews from 1987 to 1995. One hundred and forty-seven eggshells were identified as belonging to the ornithoid basic type. No complete eggs with an ornithoid shell structure were discovered and the shell fragments are too small to estimate the original size and shape of the eggs. Eggshells of two modern avian species, *Crax rubra* (USNM 18854) and *Ortalis vetula* (DMNH 3136/HEC-843), of the family Cracidae (order Galliformes), were examined for comparison.

The shell fragments were cleaned ultrasonically and their thicknesses were measured using a micrometer. Fifty-five thin sections and 82 eggshell fragments were examined in radial view with PLM and SEM, respectively. The inner and outer surfaces were studied using SEM and a dissecting microscope. Preparation techniques for SEM and thin sectioning follow Hirsch (1983).

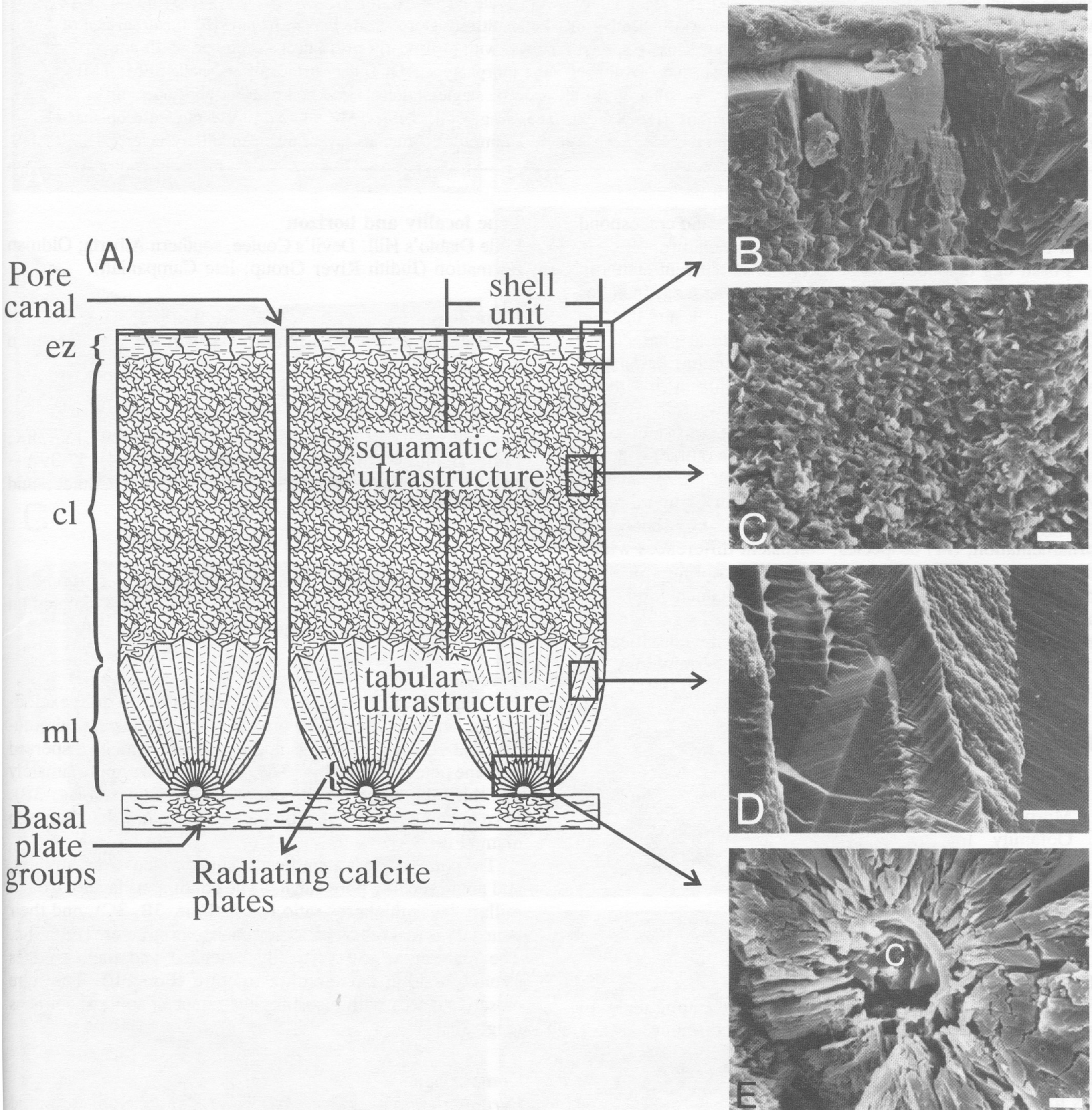
Eggshell structure and classification

Modern eggshell of the rigid type is structurally stable among certain taxonomic groups at the higher systematic levels. This eggshell displays a particular sequence of horizontal ultrastructural zones referred to as the basic type of eggshell organization (Mikhailov 1991, 1992). Four basic types have been established on modern rigid eggshell, including ornithoid (avians), crocodiloid (crocodilians), testudoid (testudinates), and geckonoid (geckonids). Two additional basic types (dinosauroid-spherulitic and dinosauroid-prismatic) have been described for dinosaur eggshell. A third group of dinosaurian eggshells, belonging to theropods, are of the ornithoid basic type.

An understanding of modern avian eggshell (Erben 1970; Mikhailov 1987*a*, 1987*b*) has provided a good basis for the study of fossil eggshell, particularly for those of the ornithoid basic type. Avian eggshell is composed of three to five crystalline ultrastructural zones (Fig. 2). Fossil eggshell of the ornithoid basic type generally shows three ultrastructural zones: the basal plate groups (eisospherites), an inner mammillary layer of tabular ultrastructure, and an outer continuous layer of squamatic ultrastructure. The external zone and the zone of radiating calcite crystals (calcite radial ultrastructure) evident in some modern avian eggshell are rarely described in fossil eggshells. Additionally, in fossil eggshell the continuous layer is usually recrystallized and therefore the squamatic ultrastructure is often obliterated.

The ornithoid basic type is expressed in two morphotypes, ratite and prismatic. It should be clarified, however, that these morphotypes are strictly structural categories because some neognathous birds (e.g., Cuculiformes, Piciformes) exhibit an ornithoid-ratite structure like those of thin-shelled

Fig. 2. (A) Schematic of avian eggshell showing shell units, pore canal, and structural components (radial view). (B–D), SEM photomicrographs (radial view). Ultrastructure of recent avian eggshell. (B) External zone of vertically oriented calcite crystals. Scale bar = 10 μm. (C) Squamatic ultrastructure of continuous layer. Scale bar = 10 μm. (D) Tabular ultrastructure of mammillary layer. Scale bar = 10 μm. (E) SEM photomicrograph (tangential view). Radiating calcite plates (calcite radial ultrastructure) emanating from the central core (c) at the base of the mammilla. Scale bar = 4 μm. cl, continuous layer; ez, external zone; ml, mammillary layer.



paleognathes (e.g., *Apteryx*, *Tinamou*). Others (e.g., Anseriformes, Galliformes) have an eggshell structure more or less expressed in the ratite morphotype like that of modern *Struthio* eggshell (Mikhailov 1994*b*). The ornithoid-ratite morphotype is characterized by a pronounced, distinctly structured mammillary layer that changes abruptly into the continuous layer of weakly developed prismatic structure. The ornithoid-ratite morphotype is shared by both birds and theropod dinosaurs. In the ornithoid-prismatic morphotype, shell units are generally distinct and are composed of mammillae and prisms. The change in structure between the continuous layer and mammillary layer is gradational. These morphotypes are

Fig. 3. (A–F), *Porituberoolithus warnerensis* oogen. et oosp. nov. Ornithoid-ratite morphotype. (A) Outer surface of eggshell; SEM; TMP 94.157.39C. Dispersituberculate ornamentation consisting of single nodes with pore openings (arrows) located on nodes. Scale bar = 200 μm. (B–E), Radial view, outer surface of eggshell is up. (B) SEM; TMP 94.157.60 (holotype). Node height is approximately one third of entire shell thickness. Note two distinct structural layers (mammillary layer and continuous layer) without any indication of shell units. Scale bar = 200 μm. (C) PLM, not polarized; TMP 94.157.38B. Two structural layers are visible as in (B). Scale bar = 200 μm. (D) Boundary between the continuous layer and mammillary layer; SEM; TMP 94.157.38B. Note change in structure between the continuous layer and mammillary layer. Scale bar = 20 μm. (E) SEM; TMP 94.157.60 (holotype). Wedges of mammilla with distinct striations (arrows) indicative of tabular ultrastructure. Scale bar = 10 μm. (F) Inner surface of eggshell; SEM; TMP 94.157.38F. Mammillae are closely spaced (arrows) with eisospherites (e) intact. Scale bar = 20 μm. (G, H) *Continuoolithus canadensis* oogen. et oosp. nov. Ornithoid-ratite morphotype. (G) Outer surface of eggshell; SEM; TMP 94.157.11A. Dispersituberculate ornamentation consisting of closely spaced, single and coalesced nodes. Note pore openings (arrows) near the base of nodes. Scale bar = 1 mm. (H) Outer surface of eggshell; SEM; TMP 94.157.10A. Note teardrop-shaped nodes with pore openings located between them (arrows). Scale bar = 1 mm. cl, continuous layer; ml, mammillary layer.

used to describe and classify fossil eggshells and correspond with the hierarchical parataxonomic nomenclature.

Fossil egg taxonomy has evolved to its current status in which the hierarchical ranking of ootaxa (egg taxa) includes oofamilies, oogenera, and oospecies. It is suggested that the following macrostructural and microstructural characteristics be used in defining ootaxa of the ornithoid basic type at the following systematic levels (Mikhailov et al. 1996): (*i*) oofamily: morphotype, types of pore system, types of ornamentation, and egg shapes; (*ii*) oogenus: consistent variation within the microstructure (i.e., thickness ratio of continuous layer to mammillary layer or thickness ratio of external zone to continuous layer to mammillary layer), general range of egg size and shell thickness, pore system, egg shape, and ornamentation; (*iii*) oospecies: consistent differences within the oogenus including pore pattern, precise range of shell thickness and egg size, and details of ornamentation. The above characteristics, with the exception of egg size and shape, have been considered for the systematic classification of the ootaxa described herein. Descriptive terminology follows Hirsch and Quinn (1990) and Mikhailov (1991).

Systematic paleontology

Basic type Ornithoid
Morphotype Ratite
Oofamily Incertae sedis
Oogenus ***Porituberoolithus*** oogen.nov.

Type oospecies
Porituberoolithus warnerensis oosp.nov.

Etymology
Porus, Latin meaning porous; tuber, Latin meaning node, in reference to the location of pore openings on nodes.

Diagnosis
As for type and only known oospecies.

Porituberoolithus warnerensis oogen. et oosp. nov.
(Figs. 3A–3F)

Holotype
TMP 94.157.60, single eggshell fragment (Figs. 3B, 3E).

Type locality and horizon
Little Diablo's Hill, Devil's Coulee, southern Alberta; Oldman Formation (Judith River Group; late Campanian).

Etymology
In reference to Warner County, in which the type specimen was collected.

Referred specimens
Eggshell fragments including TMP 94.157.38B–94.157.38K, Little Diablo's Hill, Devil's Coulee; TMP 94.157.39A–94.157.39C, Faye Walker's Coulee, Devil's Coulee; and TMP 95.17.4A, 95.17.4B, Knight's Ranch.

Diagnosis
Eggshell thickness 0.50–0.65 mm; cl:ml thickness ratio 2:1; ornamentation dispersituberculate; pore openings situated on nodes; and pore system angusticanaliculate.

Description
The eggshell thickness ranges from 0.50 to 0.65 mm, excluding the ornamentation. The ornamentation is dispersituberculate and consists of single nodes that are widely dispersed over the outer surface (Fig. 3A). The nodes are approximately one third the height of the entire shell thickness (Fig. 3B). Pore openings are located on the nodes, rather than between them (Fig. 3A).

The pore system is angusticanaliculate with narrow, straight, and nonbranching pore canals. The continuous layer to mammillary layer thickness ratio is 2:1 (Figs. 3B, 3C), and their boundary is marked by an abrupt change in structure (Fig. 3D). The mammillae are vertically extended and their wedges strongly exhibit tabular ultrastructure (Fig. 3E). They are closely spaced, with eisospherites intact in some specimens (Fig. 3F).

Comparison
Porituberoolithus warnerensis is similar to elongatoolithid eggshells in microstructure, but differs from them in ornamentation, pore patterns, and shell thickness (Table 1). *Porituberoolithus* exhibits a dispersituberculate ornamentation, and the pore openings are situated on the nodes. Elongatoolithid oogenera typically do not show this pore pattern and their ornamentation is linearituberculate in the equatorial

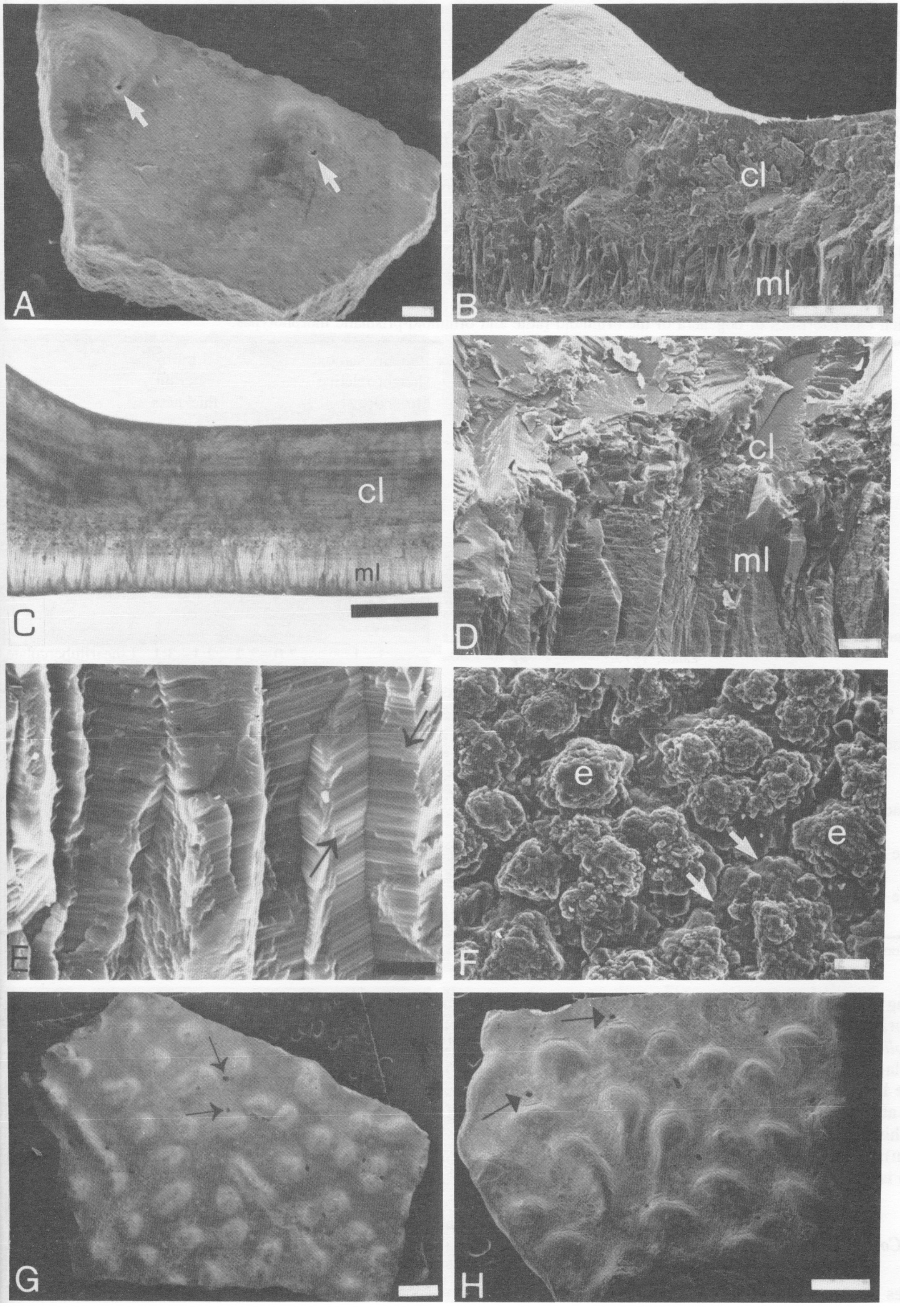

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Fig. 4. (A–D) *Continuoolithus canadensis* oogen. et oosp. nov. Ornithoid-ratite morphotype. (A) Outer surface of eggshell; SEM; TMP 94.157.15C. Note numerous pore openings (arrows) surrounding a single node. Scale bar = 200 μm. (B–D) Radial view, outer surface of eggshell is up. (B) PLM, not polarized; TMP 94.157.61 (holotype). Note two structural layers (continuous layer and mammillary layer) without any indication of shell units. Scale bar = 400 μm. (C) SEM; TMP 94.157.17A. Two structural layers are visible as in (B). Scale bar = 400 μm. (D) Boundary between continuous layer and mammillary layer; SEM; TMP 94.157.61 (holotype). Note tabular ultrastructure (arrows) of mammillary layer and recrystallized continuous layer. Scale bar = 40 μm. (E–H) *Tristraguloolithus cracioides* oogen. et oosp. nov. Ornithoid-ratite morphotype. TMP 95.17.6 (holotype). (E) Outer surface of eggshell; SEM. Dispersituberculate ornamentation consisting of widely dispersed, single nodes. Scale bar = 400 μm. (F–H) Radial view, SEM; outer surface of eggshell is up. (F) Three structural layers (external zone, continuous layer, and mammillary layer) without any indication of shell units. Scale bar = 100 μm. (G) Three structural layers as in (F). Note shell unit boundaries (arrows) are visible. Scale bar = 100 μm. (H) Note change in structure between external zone and recrystallized continuous layer. Scale bar = 40 μm. cl, continuous layer; ez, external zone; ml, mammillary layer.

Table 1. Eggshell characteristics of oogenera of the ornithoid-ratite and ornithoid-prismatic morphotypes.

Oofamily	Morphotype	Oogenus	Shell thickness excluding ornamentation (mm)	Ornamentation height relative to entire shell thickness	EL[a]	cl:ml or ez:cl:ml thickness ratio	Ornamentation
Incertae sedis	Ornithoid-ratite	*Porituberoolithus* oogen. nov.	0.50–0.65	$\frac{1}{3}$	Unknown	2:1	Dispersituberculate
Incertae sedis	Ornithoid-ratite	*Tristraguloothus* oogen. nov.	0.32–0.36	$\frac{1}{4}$	Unknown	0.5:1:1	Dispersituberculate
Incertae sedis	Ornithoid-ratite	*Continuoolithus* oogen. nov.	0.84–1.04	$\frac{1}{5}$	Unknown	4:1–5:1	Dispersituberculate
Incertae sedis	Ornithoid-prismatic	*Dispersituberoolithus* oogen. nov.	0.26–0.28	$\frac{1}{3}-\frac{1}{2}$	Unknown	0.5:2:1	Dispersituberculafe
Elongatoolithidae	Ornithoid-ratite	*Elongatoolithus* Zhao, 1975 emend. Mikhailov, 1994*a*	Up to 1.50	$\frac{1}{4}-\frac{1}{5}$	2.0–2.2	2:1–3:1	Linearituberculate
Elongatoolithidae	Ornithoid-ratite	*Macroolithus* Zhao, 1975 emend. Mikhailov, 1994*a*	Up to 2.0	$\frac{1}{4}-\frac{1}{5}$	2.0–2.4	2:1–3:1	Linearituberculate
Elongatoolithidae	Ornithoid-ratite	*Trachoolithus* Mikhailov, 1994*a*	0.3–0.5	$\frac{1}{2}-\frac{1}{3}$	Unknown	3:1–4:1	Linearituberculate
Laevisoolithidae	Ornithoid-ratite	*Laevisoolithus* Mikhailov, 1991	<1.0	Not applicable	1.9	2:1.5	Smooth surface
Laevisoolithidae	Ornithoid-ratite	*Subtiliolithus* Mikhailov, 1991	0.3–0.4	?	Unknown	1:1–1:2	Smooth or microtubercles

[a]EL (elongation index): ratio of the long diameter of an egg to its short diameter.

regions, grading to ramotuberculate towards the polar regions, and only dispersituberculate at the poles.

Porituberoolithus is very similar to *Subtiliolithus Kachchhensis* Khosla and Sahni, 1995 of the ornithoid-ratite eggshells from the Late Cretaceous of India (Sahni et al. 1994). This oospecies also exhibits dispersituberculate ornamentation, but is slightly thinner (0.35–0.45 mm) than *Porituberoolithus* (0.5–0.65 mm). The continuous layer to mammillary layer thickness ratio is 2:1 in both *Porituberoolithus* and *S. Kachchhensis*.

Oogenus ***Continuoolithus*** oogen.nov.

Type oospecies
Continuoolithus canadensis oosp.nov.

Etymology
Continuoo-, Latin meaning continuous, in reference to the thickest layer (continuous layer) of the eggshell.

Diagnosis
As for type and only known oospecies.

Continuoolithus canadensis oogen. et oosp. nov. (Figs. 3G, 3H, 4A–4D)

Holotype
TMP 94.157.61, single eggshell fragment (Figs. 4B, 4D).

Type locality and horizon
Little Diablo's Hill, Devil's Coulee, southern Alberta; Oldman

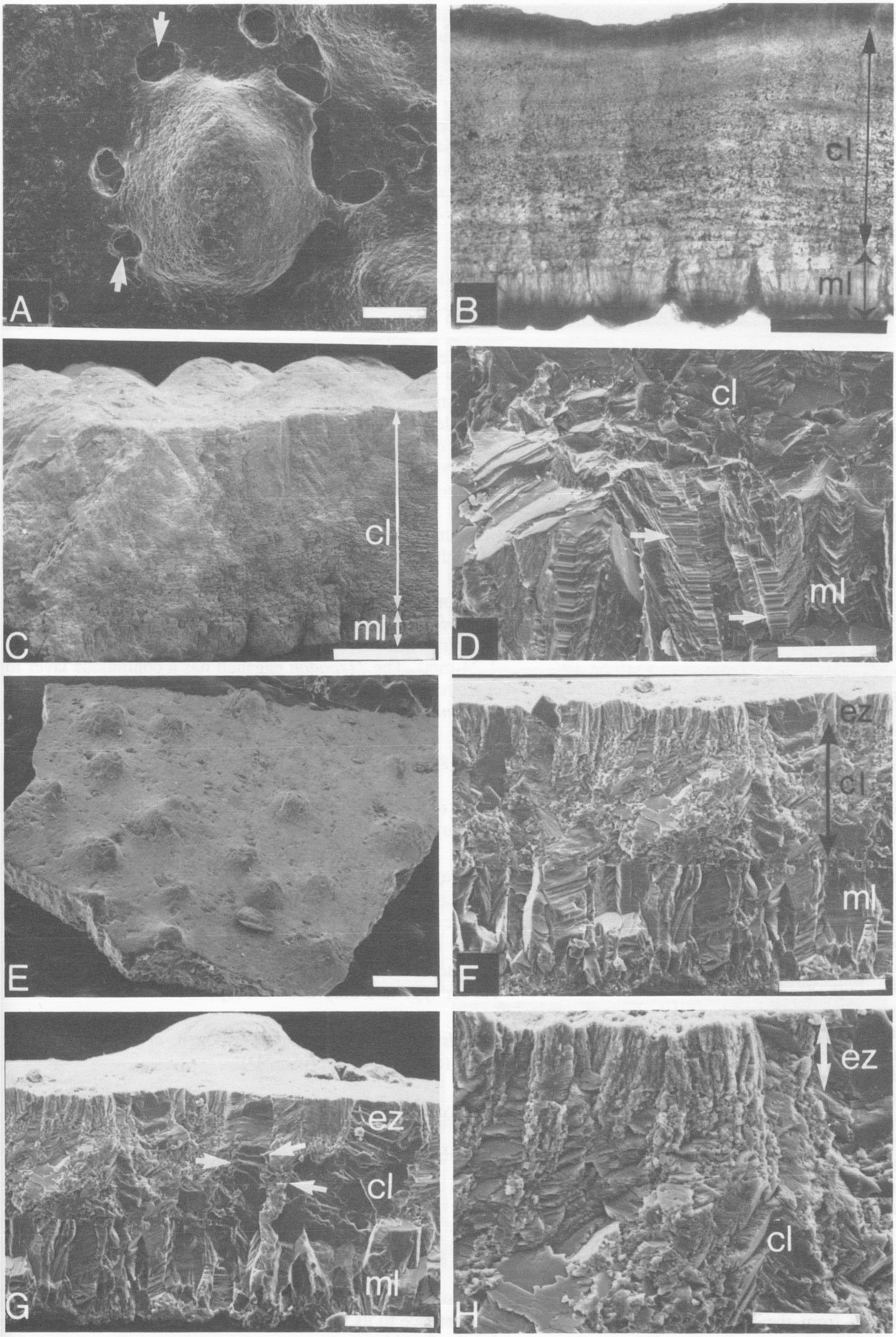
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Fig. 5. (A–D) *Tristraguloolithus cracioides* oogen. et oosp. nov. (A, B) Radial view, SEM; TMP 95.17.6 (holotype). (A) Boundary between continuous layer and mammillary layer. Note distinct change in structure between these two layers. Scale bar = 40 μm. (B) Mammilla are vertically extended and wedges (w) display tabular ultrastructure (arrows). Scale bar = 40 μm. (C, D) Inner surface of eggshell, SEM; TMP 94.157.55C. (C) Note radiating crystallites (calcite radial ultrastructure) (arrows) of an individual mammilla. Scale bar = 10 μm. (D) Mammilla are closely spaced. Scale bar = 100 μm. (E) Recent avian eggshell of *Ortalis vetula* (family Cracidae). Radial view, SEM; DMNH 3136/HEC-843. Note three structural layers: external zone, continuous layer, and mammillary layer. Compare with microstructure of *Tristraguloolithus* in Figs. 4F–4G. Scale bar = 100 μm.
(F–H) *Dispersituberoolithus exilis* oogen. et oosp. nov. Ornithoid-prismatic morphotype. (F) Outer surface of eggshell; SEM; TMP 94.157.62 (holotype). Note dispersituberculate ornamentation showing prominent, single nodes. Scale bar = 400 μm. (G) Radial view, outer surface of eggshell is up; PLM, not polarized; TMP 94.157.62 (holotype). Note prisms and boundaries (arrows) of shell units visible but discrete. Scale bar = 100 μm. (H) Radial view, outer surface of eggshell is up; SEM; TMP 94.157.58A. Three structural layers: an external zone, continuous layer, and mammillary layer are present, and show a gradational change in structure. Scale bar = 100 μm. cl, continuous layer; ez, external zone; ml, mammillary layer.

Formation (Judith River Group; late Campanian).

Etymology
In reference to the country in which the type specimen was collected.

Referred specimens
Eggshell fragments including TMP 94.157.10A, 94.157.10B, 94.157.10E–94.157.10K, 94.157.11A–94.157.11D, Little Diablo's Hill, Devil's Coulee; TMP 94.157.15A–94.157.-15C, 94.157.15E–94.157.15R, 94.157.17A–94.157.17D, 94.157.17F–94.157.17H, North Baby Butte, Devil's Coulee; TMP 94.157.18A–94.157.18C, 94.157.18E–94.157.18T, Faye Walker's Coulee, Devil's Coulee; TMP 94.157.21A–94.157.21D, Juvie Camp, Devil's Coulee; and TMP 95.17.-5A, 95.17.5B, Knight's Ranch.

Diagnosis
Eggshell thickness 0.94–1.24 mm; cl:ml thickness ratio of 4:1–5:1; ornamentation dispersituberculate; and pore system angusticanaliculate.

Description
The eggshell thickness ranges from 0.94 to 1.24 mm, including ornamentation. The dispersituberculate ornamentation is composed of closely spaced, single nodes. Some nodes coalesce to form short ridges (Fig. 3G). Single nodes are usually isomorphic, although teardrop-shaped nodes are visible on some specimens (Fig. 3H). Pore openings are isolated and situated between the nodes and ridges (Figs. 3G–3H). Two specimens have unusual pore patterns in which pore openings completely surround the individual nodes (Fig. 4A).

The pore system is of the angusticanaliculate type. The continuous layer to mammillary layer thickness ratio ranges from 4:1 to 5:1 (Figs. 4B, 4C). Tabular ultrastructure of the mammillae is distinguished from the recrystallized, superjacent continuous layer at the boundary between the continuous layer and mammillary layer (Fig. 4D). The mammillae are as high as they are wide and closely spaced.

Comparison
Data on egg size and shape are not available for the Alberta material because only isolated shell fragments were recovered. *Continuoolithus* differs from the elongatoolithid oogenera mainly in the ornamentation (Table 1). *Continuoolithus* displays a dispersituberculate ornamentation, whereas the elongatoolithid oogenera have an ornamentation that is linearituberculate traversing the equator, ramotuberculate grading towards the poles, and dispersituberculate at the poles. *Continuoolithus* and *Trachoolithus* Mikhailov, 1994*a* have similar continuous layer to mammillary layer thickness ratios. However, *Trachoolithus* exhibits a prominent linearituberculate ornamentation and is much thinner than *Continuoolithus* (Table 1).

Complete, elongate–ovoidal eggs (123 mm × 77 mm) from the Two Medicine Formation of Montana (Hirsch and Quinn 1990) are also of the ornithoid-ratite morphotype and were provisionally assigned to the theropod *Troodon* sp. The ?*Troodon* eggshell has a similar ornamentation, but is slightly thicker (1.20–1.28 mm) than *Continuoolithus* (0.94–1.24 mm). The ?*Troodon* eggshell has a continuous layer to mammillary layer thickness ratio of 8:1 or greater, whereas in *Continuoolithus* it ranges from 4:1 to 5:1.

Oogenus ***Tristraguloolithus*** oogen.nov.

Type oospecies
Tristraguloolithus cracioides oosp.nov.

Etymology
Tri, Latin meaning three; stragulus, Latin meaning layered, in reference to the presence of three structural layers.

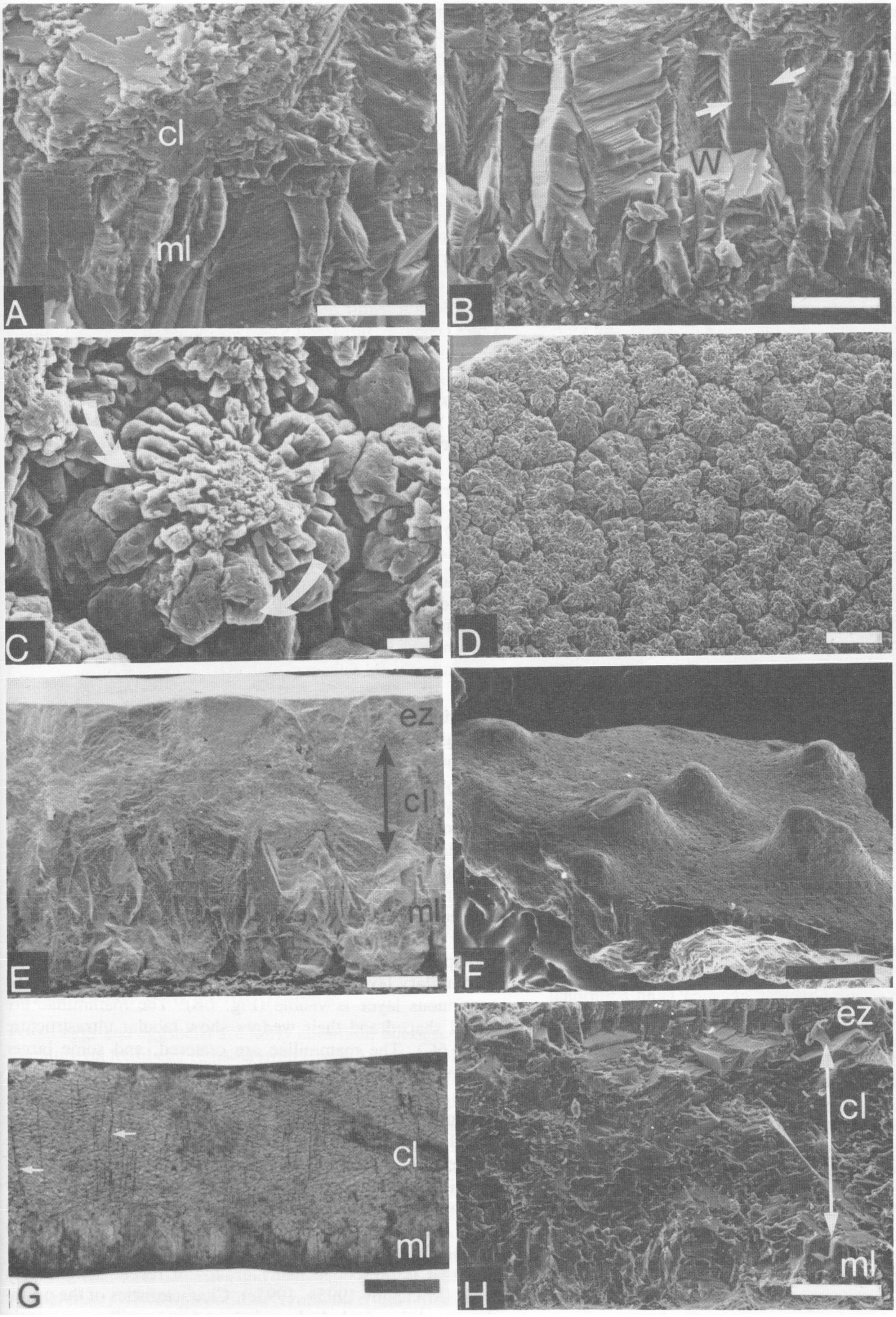
Diagnosis
As for type and only known oospecies.

Tristraguloolithus cracioides oogen. et oosp. nov.
(Figs. 4E–4H, 5A–5D)

Holotype
TMP 95.17.6, single eggshell fragment (Figs. 4E–4H, 5A, 5B).

Type locality and horizon
Knight's Ranch, southern Alberta; Oldman Formation (Judith River Group; late Campanian).

Etymology
In reference to its similarity to modern avian eggshell of the family Cracidae.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Referred specimens
Eggshell fragments including TMP 94.157.55A–94.157.55E, Little Diablo's Hill, Devil's Coulee; TMP 94.157.56A, 94.157.56B, Faye Walker's Coulee, Devil's Coulee; and TMP 95.17.1A, Knight's Ranch.

Diagnosis
Eggshell thickness 0.32–0.36 mm; three structural layers (external zone, continuous layer, and mammillary layer); ez:cl:ml thickness ratio of 0.5:1:1; ornamentation dispersituberculate; and pore system angusticanaliculate.

Description
The eggshell thickness measures 0.32–0.36 mm, excluding ornamentation. The ornamentation is low in relief and consists of irregularly spaced, isomorphic nodes (Fig. 4E) that are approximately one quarter the height of the entire shell thickness.

The pore system is angusticanaliculate. Three structural layers are visible in radial view: an external zone, a continuous layer, and a mammillary layer (Figs. 4F, 4G). The external zone to continuous layer to mammillary layer thickness ratio is 0.5:1:1 (Figs. 4F, 4G). The external zone is composed of vertically oriented calcite crystals that are clearly discernible from the subjacent, recrystallized continuous layer (Fig. 4H). The boundary between the continuous layer and mammillary layer is evidenced by a sharp change in structure (Fig. 5A). The mammillae are laterally compressed and vertically extended, and their height is twice their width (Fig. 5B). The mammillae display two structural zones: (*i*) individual wedges with prominent tabular ultrastructure (Fig. 5B), and (*ii*) a zone of radiating calcite plates (calcite radial ultrastructure) at the base of the mammillae (Fig. 5C). The mammillae are closely spaced (Fig. 5D).

Comparison
The presence of an external zone distinguishes *Tristraguloolithus* from the other known oogenera of the ornithoid-ratite morphotype (Table 1). *Tristraguloolithus* compares well with modern bird eggshell, in particular those of the family Cracidae (order Galliformes). The eggshell of *O. vetula* (family Cracidae) (Fig. 5E) is very similar in microstructure and shell thickness to that of *Tristraguloolithus*. Modern bird eggshell does not generally exhibit an outer surface sculpture pattern, but its presence in recent Cracidae eggshell is an additional similarity to *Tristraguloolithus*. Furthermore, eggshell of modern ratite, galliform, and anseriform birds generally have elongated mammillae with a two-zonal structure (Mikhailov 1987*b*). These characteristics of the mammillae were also described for *Tristraguloolithus*.

Morphotype Prismatic
Oofamily Incertae sedis
Oogenus ***Dispersituberoolithus*** oogen.nov.

Type oospecies
Dispersituberoolithus exilis oosp.nov.

Etymology
Dispersus, Latin meaning dispersed; tuber, Latin meaning node, in reference to the numerous nodes dispersed over the outer surface.

Diagnosis
As for type and only known oospecies.

Dispersituberoolithus exilis oogen. et oosp. nov.
(Figs. 5F–5H, 6A–6D)

Holotype
TMP 94.157.62, single eggshell fragment (Figs. 5F, 5G, 6B–6D).

Type locality and horizon
Little Diablo's Hill, Devil's Coulee, southern Alberta; Oldman Formation (Judith River Group; late Campanian).

Etymology
Exilis, Latin meaning thin, in reference to the eggshell thickness.

Referred specimens
Eggshell fragments including TMP 94.157.58A, 94.157.58B, 94.157.58D, 94.157.58E, Little Diablo's Hill, Devil's Coulee.

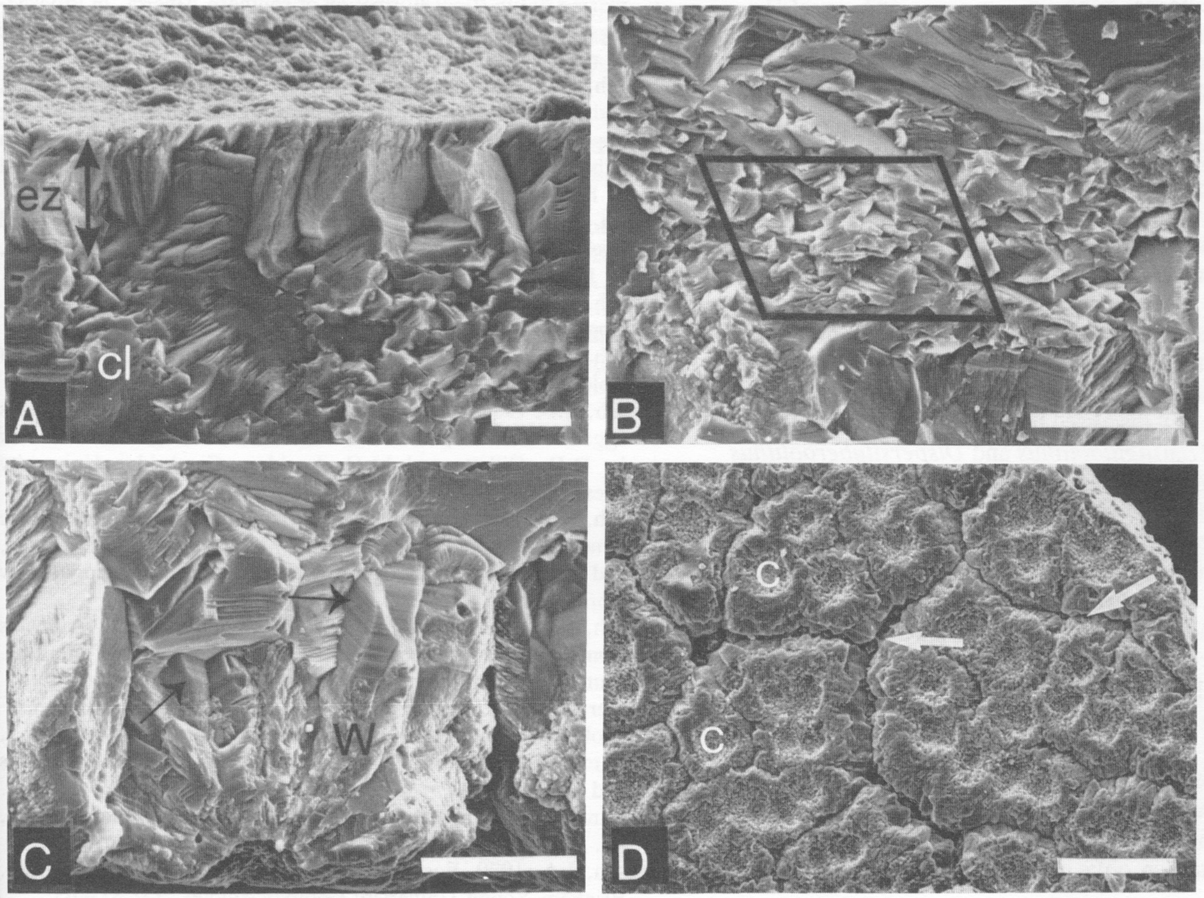
Diagnosis
Eggshell thickness 0.26–0.28 mm; three structural layers (external zone, continuous layer, and mammillary layer); ez:cl:ml thickness ratio of 0.5:2:1; ornamentation dispersituberculate; and angusticanaliculate pore system.

Description
The eggshell thickness measures 0.26–0.28 mm, excluding ornamentation. The ornamentation consists of irregularly and widely dispersed, single nodes (Fig. 5F) that are approximately one third to one half the entire shell thickness.

The pore system is angusticanaliculate and faint shell unit boundaries are visible in radial thin section (Fig. 5G). The external zone to continuous layer to mammillary layer thickness ratio is 0.5:2:1 (Fig. 5H). The change in structure between these three layers appears more or less gradational under SEM (Fig. 5H). The external zone is not well defined and appears blocky (Fig. 6A). Near the continuous layer – mammillary layer boundary, squamatic ultrastructure of the continuous layer is visible (Fig. 6B). The mammillae are barrel shaped and their wedges show tabular ultrastructure (Fig. 6C). The mammillae are cratered, and some larger spaces exist between them (Fig. 6D).

Comparison
Fossil eggshells of the ornithoid-prismatic morphotype have not been described in detail and therefore compare best with descriptions of modern avian eggshells. *Dispersituberoolithus* cannot be linked to any particular taxonomic group of modern birds based on the shell structure. However, it appears to exhibit the primitive or normal condition of eggshell structure that is present in many groups of recent neognathous birds (Mikhailov 1995*b*, 1995*c*). Characteristics of the primitive condition include barrel-shaped mammillae, a poorly defined external zone that appears blocky, and a continuous

Fig. 6. *Dispersituberoolithus exilis* oogen. et oosp. nov. Ornithoid-prismatic morphotype. (A) Boundary between the external zone and continuous layer. Radial view, SEM; TMP 94.157.58D. External zone appears blocky with a gradational change in structure between these layers. Scale bar = 20 μm. (B–D) Radial view, SEM; TMP 94.157.62 (holotype). (B) Boundary between the continuous layer and mammillary layer. Note squamatic ultrastructure (outlined) of continuous layer. Scale bar = 40 μm. (C) Mammillae are barrel-shaped and composed of divergent wedges (w) that exhibit tabular ultrastructure (arrows). Scale bar = 40 μm. (D) Inner surface of eggshell. Mammillae are cratered (c) and some larger spaces exist between the individual mammilla (arrows). Scale bar = 100 μm. cl, continuous layer; ez, external zone.



layer to mammillary layer thickness ratio of 2:4. *Dispersituberoolithus* shows these features of the primitive eggshell condition.

Discussion and conclusions

Fossil eggs and eggshells are fairly common, but descriptive literature on fossil egg remains from North America is limited (Hirsch 1985, 1994; Jensen 1970; Zelenitsky and Hills 1996). To facilitate comparisons with material from other regions it is important that these eggs and eggshells be described and, if feasible, parataxonomically assigned. Eggshells of neither the ornithoid-prismatic nor the ornithoid-ratite morphotype have previously been parataxonomically assigned from the Late Cretaceous of North America. However, the exceptional preservation and uniqueness of the eggshells from Alberta justify their parataxonomic assignment. Thus, in this paper we establish four new oogenera and oospecies: *Porituberoolithus warnerensis*, *Tristraguloolithus cracioides*, and *Continuoolithus canadensis*, which are referable to the ornithoid-ratite morphotype, and *Dispersituberoolithus exilis*, which is referable to the ornithoid-prismatic morphotype. Oofamilies were not established, because only shell fragments were recovered.

A positive correlation between an egg and its egg layer is only possible if an identifiable embryo exists within the egg. In modern eggshell, a structural stability is evident among certain taxonomic groups at the higher systematic levels. Limitations on suggesting the taxonomic position of fossil eggshells exist because eggs containing identifiable embryos are rare and taphonomic processes (i.e., diagenesis, dissolution, and weathering) can alter the original eggshell structure. However, comparison of fossil eggshells of the ornithoid basic type with avian and theropod dinosaur eggshell may help determine the egg layers at the higher systematic levels.

The basic type of eggshell organization provides a firm basis for assigning egg layers at the higher systematic levels, although the taxonomic implications of the morphotype (i.e., ratite vs. prismatic) are less clear. The ornithoid-ratite morphotype is common to modern paleognathous and some neognathous birds, and theropod dinosaur eggshell. The ornithoid-prismatic morphotype is found in most modern neognathous bird eggshell, but has never been positively correlated with an extinct egg-laying taxon. With regard to eggshell ultrastructure, the external zone appears to be a unique character of bird eggshell. However, this zone is not present in the eggshell of all avian taxa. To date, only one ootaxon referable to the ornithoid basic type has been correlated with birds. The Laevisoolithidae Mikhailov, 1991 from the Late Cretaceous of Mongolia are suggested as belonging to enantiornithid birds, and have ornithoid-ratite eggshell structure, which lacks an external zone.

The four ootaxa described from Alberta can be divided into two groups based on the presence or absence of an external zone. The thicker eggshells of *Porituberoolithus* and *Continuoolithus* lack an external zone and have a microstructure like that of the elongatoolithid eggshells that have been attributed to theropod dinosaurs (Norell et al. 1994; Mikhailov 1994*a*). The thinner eggshells of *Tristraguloolithus* and *Dispersituberoolithus* have the greatest similarity to modern bird eggshell, because they both possess an outermost external zone of vertically oriented calcite crystals. *Tristraguloolithus* is very similar in shell thickness and microstructure to modern bird eggshell of the family Cracidae. *Dispersituberoolithus* shows the primitive or normal condition of modern neognathous bird eggshell discussed by Mikhailov (1995*b*, 1995*c*). Therefore, both *Tristraguloolithus* and *Dispersituberoolithus* were probably laid by birds.

It is evident that a comprehensive study of eggshell fragments within a nesting site provides a more complete understanding of the taxonomic diversity of the egg layers. Eggs containing embryonic remains of *Hypacrosaurus stebingeri* have indicated the nesting of hadrosaurs at Devil's Coulee (Horner and Currie 1994), but the morphological diversity of eggs and eggshell fragments suggests that several additional taxa were laying eggs at this site (Zelenitsky 1995). The ootaxa described in this paper suggest a diversity of both avian and theropod dinosaur egg layers. Our examination of the eggshell from Alberta also documents the occurrence of avian eggshell from the Cretaceous of North America, which was previously known only in Mongolia.

Acknowledgments

We would sincerely like to thank Drs. Karl Hirsch and Rolf Kohring for their review of this paper. Karl devoted much time and effort in preparing this paper prior to its official review. We are very appreciative of his constructive comments, as they greatly improved the paper. Karl passed away on June 1, 1996, and his dedication to the study of fossil eggs has considerably advanced the understanding of this subject. We would also like to thank Dr. Konstantin Mikhailov of the Russian Academy of Sciences for his suggestions and for providing information on the eggshell of modern birds. We are also grateful to Mr. M. Horvath and Mr. J. Resultay for their help in thin section preparation and Mrs. D. Glatiotis for her assistance with the scanning electron microscope. Mr. K. Aulenback of the Royal Tyrrell Museum of Palaeontology offered information on the sites and material. Financial assistance was provided by Research Services and a Thesis Research Grant through The University of Calgary. Fieldwork was supported by the Royal Tyrrell Museum of Palaeontology. The first author would especially like to thank her parents for all their support throughout this project.

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