

# Bird-like characteristics of troodontid theropod eggshell



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Revised manuscript accepted 8 March 2002

Description of well-preserved fossil eggshell (oospecies *Prismatoolithus levis*), recently assigned to the theropod dinosaur *Troodon formosus*, reveals traits that are shared with the eggshell of both fossil and Recent avians. Bird-like characteristics of troodontid eggshell include: fibres associated with eisospherites that are attached to the bases of the mammillae, fine radiating crystals that form the spherulites and grade into blocky wedges of the mammillae, and prisms in the outer layer that exhibit squamatic ultrastructure. The presence of two layers (mammillary and squamatic) within the eggshell is either a theropod apomorphy or it arose within Theropoda; the external eggshell layer of crown-group avians is apomorphic with respect to other theropod eggshell. Despite disagreement on the putative sister taxon of birds, recent theropod phylogenies suggest strongly that prismatic ultrastructure evolved independently in Troodontidae and Neognathae. Our identification of squamatic ultrastructure in troodontid eggshell, which was previously thought to lack this structure, reveals problems with the previous assignment of this eggshell to the dinosauroid-prismatic morphotype and with the concept of eggshell morphotype in the current eggshell parataxonomy. We conclude that the dinosauroid-prismatic morphotype should be abandoned.

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KEY WORDS: fossil eggshell parataxonomy; dinosaur eggs; theropods; bird origins; eggshell morphotype; Upper Cretaceous; Alberta.

## 1. Introduction

The origin of birds from non-avian theropod dinosaurs has been firmly established by evidence from both the skeleton and the integument (Gauthier, 1986; Forster *et al.*, 1998; Ji *et al.*, 1998, 2001; Xu *et al.*, 2001). In recent years, the preservation of adult troodontid and oviraptorid theropods atop egg clutches suggests that some behaviour (e.g., brooding) is also shared by birds and non-avian theropods (Varricchio *et al.*, 1997; Clark *et al.*, 1999; but see Geist and Jones, 1996; Horner, 2000). The association of adults with eggs and of eggs with embryos among non-avian, Cretaceous theropods allows a definitive correlation between the eggs (ootaxa) and the egg layers (skeletal taxa). The associated eggs and eggshells also reveal additional shared characteristics among the eggs of birds and those of non-avian theropods.

Prior to the discovery of associated adult or embryonic theropod skeletons and eggs, Mikhailov (1992) recognised that the eggshell of birds and non-avian theropods share the presence of two structural layers or zones (mammillary and squamatic). This was based on the assumption that eggs of the oofamily Elongatoolithidae, which showed these features, belonged to non-avian theropods. Following the discovery of eggs containing embryos and of eggs associated with adult skeletons, elongatoolithid eggs were confirmed to have been laid by oviraptorid theropods (Norell *et al.*, 1994, 1995; Dong & Currie, 1996).

Other dinosaur eggs known in the early 1990s also shared characteristics of avian eggs, although they were not initially recognised as theropod. For example, eggs and eggshells from the Upper Cretaceous of Montana were initially attributed to the hypsilophodontid *Orodromeus makelai*, based on their

association with embryonic remains (Horner & Weishampel, 1988). Hirsch & Quinn (1990, p. 496) described the eggshell as exhibiting “typical avian-like eggshell structure similar to those found in neognathean fossil eggs”. They discussed the two-layered nature of this eggshell, although squamatic ultrastructure was not apparent in the outer layer. It was therefore thought that hypsilophodontid eggshell did not exhibit the squamatic ultrastructure found in the second eggshell layer of theropods (i.e., birds and oviraptorids; Mikhailov, 1992, 1994). In 1996, however, the hypsilophodontid (*Orodromeus makelai*) embryos were re-identified as the theropod *Troodon formosus* (Horner & Weishampel, 1996). Thus, the two layers within this eggshell should represent the squamatic and mammillary zones present in the eggshells of other non-avian (i.e., oviraptorid) theropods. Although squamatic ultrastructure has not yet been recognised in all of their eggs, two structural layers are shared among those eggs closely associated with theropod skeletal remains (Norell *et al.*, 1994; Dong & Currie, 1996; Varricchio *et al.* 1997; Makovicky & Grellet-Tinner, 2000).

Eggs and eggshells identical to those of *Troodon formosus* from Montana were discovered in coeval deposits in 1994 in neighbouring Alberta and were assigned to the oospecies *Prismatoolithus levis* (Zelenitsky & Hills, 1996). They share several characteristics with *Troodon* eggs from Montana, including: upright orientation of elongate eggs in a subcircular clutch, shell thickness of approximately 1 mm, alignment of double and single pore apertures, smooth outer surface, and two-layered eggshell with a gradational boundary. The eggs from Montana were also assigned to *Prismatoolithus levis* (Zelenitsky, 2000) and join a growing list of egg fossils that are ascribed to non-avian theropod taxa, one that also includes oviraptorids, dromaeosaurids (Makovicky & Grellet-Tinner, 2000), and possibly allosauroids (Mateus *et al.*, 1997). *Prismatoolithus levis* is, however, the only North American ootaxon that, because of identifiable embryonic remains (Varricchio, 2001), is confidently attributable to a specific non-avian theropod, i.e., *Troodon formosus*.

The original misunderstanding that *Troodon* (*Prismatoolithus*) eggs belonged to ornithischians created problems, particularly relating to the parataxonomy and the parentage of other fossil eggs. Firstly, eggs similar to *Prismatoolithus* were attributed to ornithischians rather than to theropods (e.g., Zhao & Li, 1993; Mikhailov, 1994). This, in turn, prompted Mikhailov (1994) to erect the oogenus *Protoceratopsidovum* for Mongolian eggs that were similar to, but did not share all the characteristics of

*Elongatoolithus* eggs. Because protoceratopsians and theropods were found in the same beds as both types of eggs, Mikhailov assigned *Protoceratopsidovum* to protoceratopsians and *Elongatoolithus* (because of the squamatic zone) to theropods. Secondly, the prismatic structure in the eggshell of *Prismatoolithus* and *Protoceratopsidovum* eggs was the basis for the establishment of the dinosauroid-prismatic morphotype (Hirsch & Quinn, 1990; Mikhailov, 1991). These purported ornithischian (now troodontid) eggs were classified as belonging to the dinosauroid-prismatic morphotype, whereas the elongatoolithid (now oviraptorid) eggs of assumed (correctly) theropod origin were classified as the ornithoid-ratite morphotype. Both morphotypes were characterized by two structural layers, but they were thought to differ in the absence of squamatic ultrastructure in the outer eggshell layer of the dinosauroid-prismatic morphotype (Mikhailov, 1991, 1994). The apparent schism between these two morphotypes and the misconception that eggshell of the dinosauroid-prismatic morphotype was attributable to ornithischians has permeated the literature (Mikhailov 1991, 1997a; Hirsch, 1994). As revealed by embryonic theropod remains however, it is now known that at least certain egg taxa (i.e., *Prismatoolithus* and *Elongatoolithus*) that are assigned to separate morphotypes (i.e., dinosauroid-prismatic and ornithoid-ratite, respectively) belong to non-avian theropods (i.e., troodontids and oviraptorids, respectively).

Troodontid (*Prismatoolithus*) eggshell from the Upper Cretaceous of Alberta is superbly preserved, and provides a unique and timely opportunity to examine, in detail, eggshell from a theropod dinosaur that is closely related to birds. The microstructural characteristics of troodontid eggshell is described and compared to those of other fossil and modern theropod eggshell. The purpose of this paper is not to draw parallels between non-avian theropods and particular avian taxa. Instead, it is intended to document details of the microstructure neither recognised nor illustrated previously in eggshell attributable to a non-avian, Cretaceous theropod. It is evident that the initial misidentification of the troodontid embryos, misinterpretation of structures due to preservational state of fossil material, and the authoritarian nature of the evolutionary systematic methodology inherent in the practice of eggshell parataxonomy, have led to the obfuscation of eggs assigned to both the dinosauroid-prismatic and ornithoid-ratite morphotypes. The new material permits a detailed investigation into the ultrastructure of troodontid eggshell and allows an assessment of the validity of the dinosauroid-prismatic morphotype.

## 2. Material and methods

The eggs and eggshells were collected from the Devil's Coulee locality, southern Alberta, in the Upper Cretaceous (Campanian) Oldman Formation (Zelenitsky *et al.*, 1996). Eggs of *Prismatoolithus levis* were excavated from one site at Devil's Coulee and eggshell fragments were collected from several other sites. Although adult and embryonic troodontid remains have been collected from Devil's Coulee (pers. obs.), there is no direct association between the eggshells and the skeletal remains as in the Montana specimens.

The best-preserved fragments were utilized from Devil's Coulee, including 32 fragments from Royal Tyrrell Museum of Palaeontology specimens TMP 94.157.1, 94.157.2, 94.157.4, and 94.157.5. Eggs and eggshells of both paleognathes (*Dromaius*, *Rhea*, *Casuarius*, moa, *Apteryx*, *Struthio*, *Aepyornis*) and neognathes (*Gallus*, *Numida*, *Anser*, *Alectura*), together with eggshell of indeterminate avian taxa of Oligocene, Eocene, and Cretaceous age, were used for comparative purposes from the HEC (Hirsch Egg Catalogue) and the ZEC (Zelenitsky Egg Catalogue). Eggshell fragments were examined using binocular and scanning electron (SEM) microscopes. Characteristics of the eggshell microstructure were measured digitally using the Image Processing Tool Kit v3.0 for Adobe Photoshop. Descriptive terminology follows Mikhailov (1987a, b).

## 3. Description

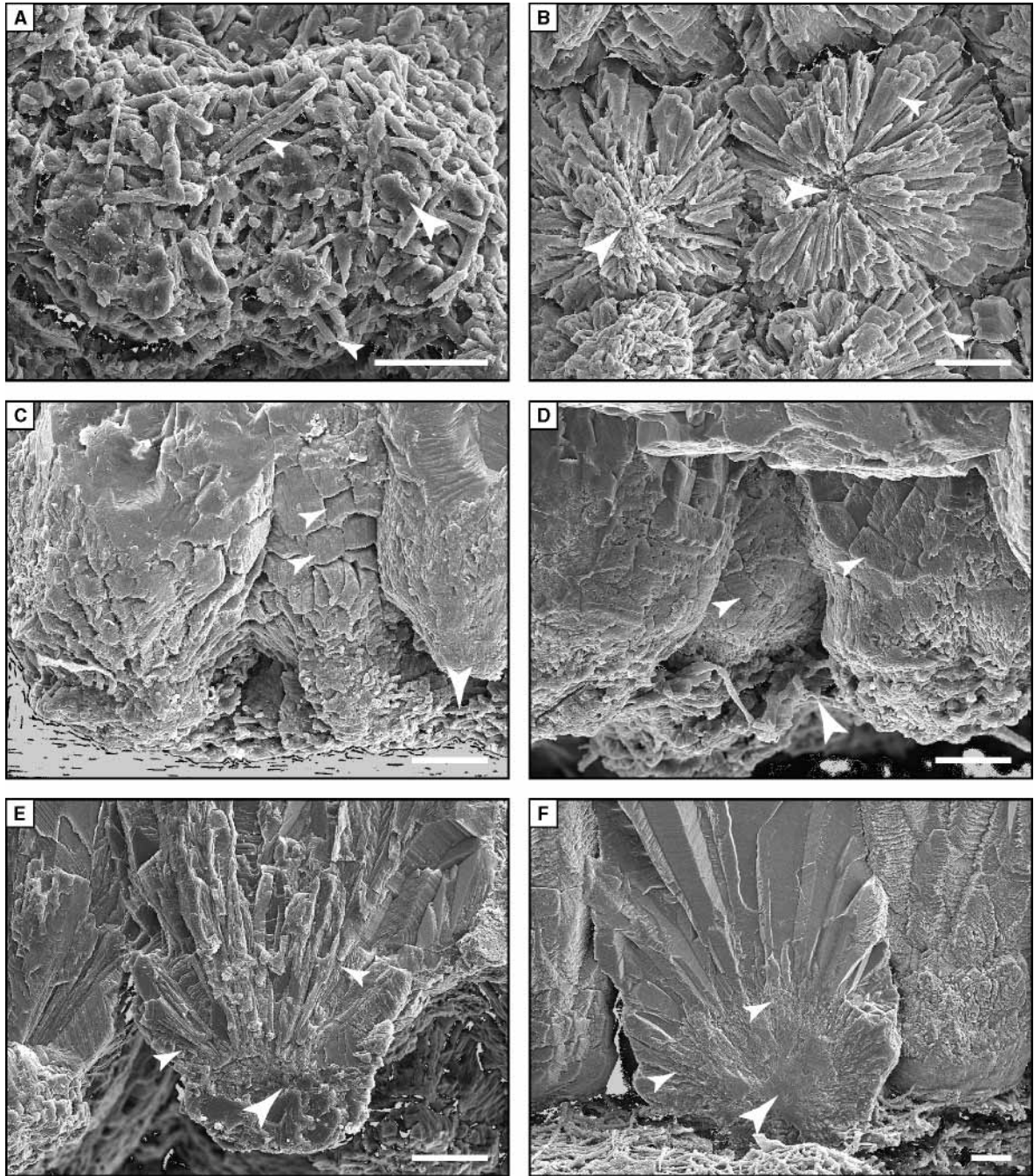
The egg and clutch morphology of *Prismatoolithus levis* has been described elsewhere (Hirsch & Quinn, 1990; Zelenitsky & Hills, 1996; Varricchio *et al.*, 1999). The well-preserved nature of this eggshell is revealed in the presence of abundant calcite-replaced, organic fibres on the bases of the mammillae, which represent remnants of the outermost part of the organic shell membrane. The fibres form dense, multi-layered concentrations that are mixed with calcite crystals of the eisospherites at the bases of the mammillae (Figure 1A). These concentrations represent portions of fibres that adhered to the inner surface after the membrane had been torn away. The preserved portion of the shell membrane is approximately 29  $\mu\text{m}$  at its thickest and, judging from other theropod eggshell with shell membrane attached (pers. obs.), this probably represents only a fraction of the original thickness. Single fibres are rod-shaped or flattened rods with their long axes oriented randomly, subparallel to the inner surface of the eggshell. Some fibres were observed in bundles of two to seven and run parallel to or twist around each other (Figure 1A); other fibres bifurcate or branch.

Within one fragment, the fibres range in diameter from 0.70–3.30  $\mu\text{m}$ , with an average diameter of 1.79  $\mu\text{m}$  ( $N=343$ ). Some fibres interconnect adjacent mammillae; the longest measured fibre is 55.6  $\mu\text{m}$ . The arrangement, morphology, and diameter (Table 1) of the fibres are comparable to those of birds in general.

In four fragments where the fibres and eisospherites do not obscure the mammillae, the average diameter of the mammillae (measured as mammilla centre to adjacent mammilla centre) ranges from 67.5 to 78.6  $\mu\text{m}$  ( $N=1079$  measurements), which is comparable to that of ratite eggs (Table 1). Some of the fragments also preserve the fine details of the bases of the mammillae and show fine radiating calcite crystals emanating from central cores and broadening towards their distal ends (Figure 1B). As in ratite eggshell, these radiating crystals aggregate to form blade-like crystals that diverge from the central core toward the exterior of the shell and collectively form the spherulite or secondary spherite at the base of the mammilla (Figure 1C, D). These radiating crystals also grade into elongate wedges that form the bulk of the mammillae (Figure 1E, F). These wedges are characterized by parallel striations (tabular ultrastructure) and a blocky habit, similar to those of galloanserine and ratite birds.

The eggshell consists of two structural layers, an inner mammillary layer and an outer prismatic layer (Figure 2A). The boundary between these two layers is not abrupt as in modern ratite eggshell, and thus is more comparable to that of neognathes (e.g., *Alectura* and *Gallus*). Several well-preserved fragments show a difference in colour between the mammillary and prismatic layers that also corresponds with structural differences in the eggshell. Under the SEM, these fragments show that the elongate wedges of the individual mammillae (mammillary layer) are divergent and more numerous than the broad, vertical prisms of the prismatic layer (Figure 2A, B). Although the thickness ratio of the mammillary to prismatic layers was initially described as 1:8 to 1:6 (Hirsch & Quinn, 1990; Zelenitsky & Hills, 1996), it is apparent from well-preserved specimens that the average ratio is actually 1:1.77 to 1:2.35 ( $N=60$  measurements, 8 fragments), a ratio that is close to that of various birds (Table 1). The previous thickness ratios were probably derived from the thickness of the spherulites (consisting of radiating crystals) at the bases of the mammillae and, due to preservation, did not include the elongate wedges that comprise the bulk of the mammillary layer. The entire thickness of the mammillary layer was, therefore, not considered in previous descriptions.





**Figure 1.** A–F, SEM micrographs of mammillae (inner layer) of theropod eggshell. A, B, tangential views of troodontid eggshell. A, TMP 94.157.5, dense concentrations of randomly oriented, replaced fibres (small arrows) of the shell membrane are intermixed with calcite crystals (large arrow) of the eisospherite. Upper arrow shows bundle of three fibres. B, TMP 94.157.2, fine radiating crystals (small arrows) of the mammillae broaden distally and emanate from a central core (large arrows). C–F, radial views. C, D, unbroken mammillae show blade-like crystals (arrows) at the base of the mammillae, which form the spherulite in C, troodontid (TMP 94.157.5) and D, *Dromaius* (Emu) eggshell. E, F, broken surfaces, showing fine radiating crystals (small arrows) emanating from a central point (large arrows), which form blade-like crystals of the spherulite and grade into the long wedges of the mammillae in E, troodontid (TMP 94.157.5) and F, *Struthio* eggshell. Scale bars represent 20  $\mu\text{m}$ .

**Table 1.** Eggshell characteristics of modern birds (from ZEC) and *Troodon* (*Prismatoolithus*). Modern bird values represent the average of several fragments from single eggs, whereas each entry for *Troodon* represents a single eggshell fragment. All measurements in  $\mu\text{m}$ .

Taxon	FD	MW	MH	MH/MW	Th	(Th-MH)/MH
<i>Aepyornis</i>	—	99.8	915	9.16	3471	2.79
<i>Anser</i>	1.79	—	181	—	480	1.64
<i>Apteryx</i>	1.76	78.0	133	1.72	461	2.44
<i>Dinornis</i>	—	73.3	297	4.06	775	1.90
<i>Dromaius</i>	1.63	56.8	188	3.32	775	3.12
<i>Struthio</i>	1.61	93.7	521	5.57	1881	2.61
<i>Troodon</i>	—	74.4	311	4.19	863	1.77
<i>Troodon</i>	1.79	—	259	—	867	2.35
<i>Troodon</i>	—	72.6	351	4.84	1030	1.93

Abbreviations: FD, fibre diameter; MH, mammilla height; MW, mammilla width; Th, eggshell thickness.

In the original description of material from Montana, the troodontid (dinosauroid-prismatic) eggshell was described as sharing the prismatic structure in the second layer with neognathe bird eggshell, although the details of the ultrastructure of this layer were not discussed by Hirsch & Quinn (1990). It was later determined that the eggshell from Montana and that from Alberta exhibited tabular ultrastructure in the outer layer (Mikhailov, 1991; Zelenitsky & Hills, 1996), rather than the squamatic ultrastructure present in avian eggshell. The indisputable nature of the tabular structure is illustrated by Zelenitsky and Hills (1996, fig. 2e), who described it as being within the prisms of the outer layer. At that time however, the inner mammillary layer, which typically shows wedges with tabular ultrastructure, was recognised as comprising only one-eighth to one-sixth of the shell thickness. Therefore, the long wedges of the inner layer, which are now known to comprise approximately one-third of the shell thickness, were erroneously identified as prisms of the outer layer.

The ultrastructure of the second layer is similar to that of Oligocene and Eocene bird eggshell, in which the squamatic structure is usually not well preserved. The newly examined materials from Alberta, however, locally preserve vesicles and squamatic ultrastructure similar to those of avian eggshells (Figure 2C-F; Mikhailov, 1997b). Squamatic structure was observed in all the modern bird eggshells that were examined (including moas and *Aepyornis*), as well as in an unidentified Cretaceous bird egg. The nature of the squamatic ultrastructure, however, varies among the different bird eggshells, which may be related to the orientation of calcite crystals (Silyn-Roberts &

Sharp, 1985) in the second layer. Of the modern bird eggshells examined, the squamatic structure in troodontids appears most similar to that of the galliformes (e.g., *Gallus*, *Alectura*).

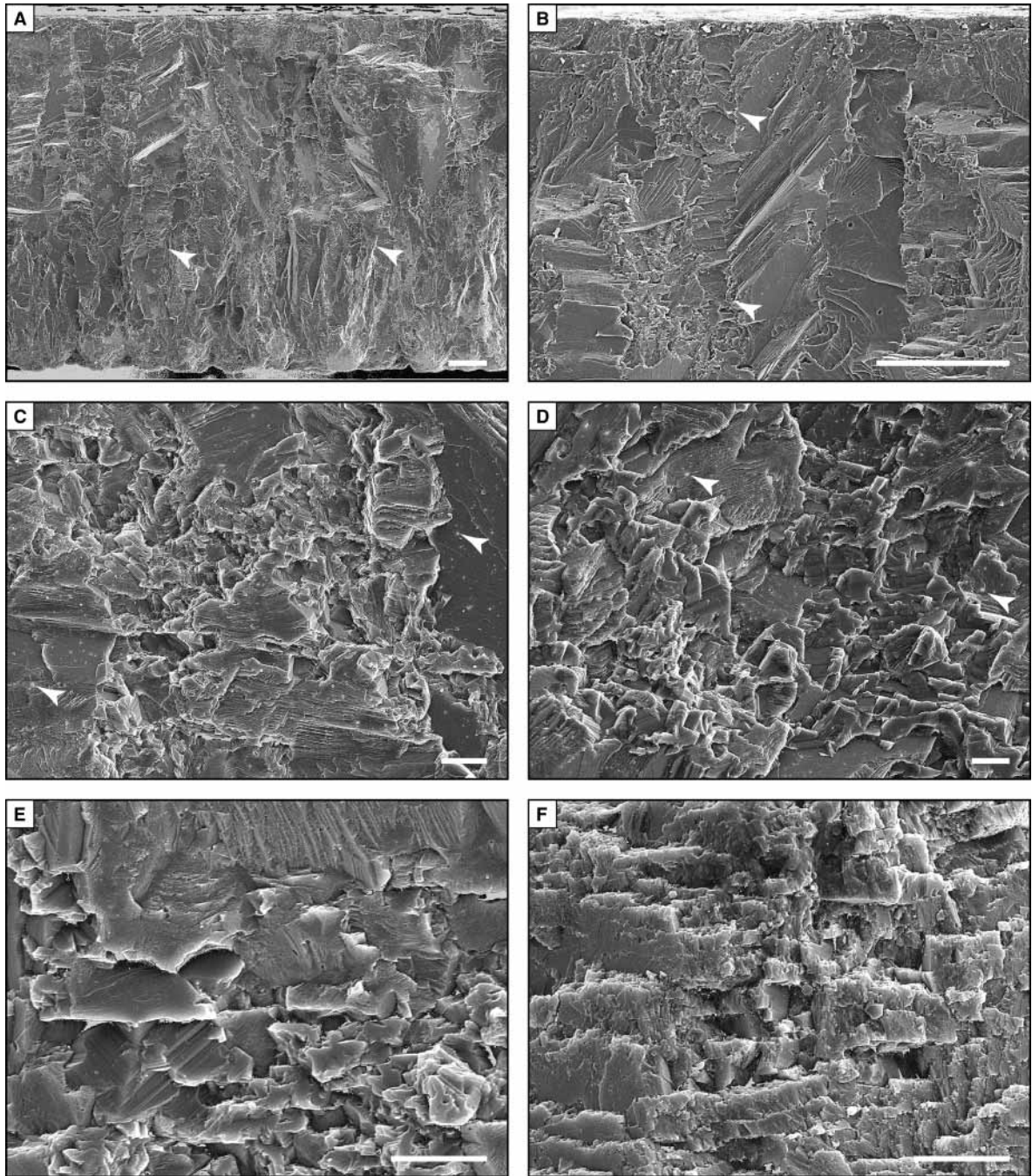
The outer layer consists of vertical prisms that are structurally continuous from the mammillary layer boundary to the exterior surface of the eggshell (Figure 2A). Unlike most modern bird eggshell, there does not appear to be a structural change approaching the outer surface of the eggshell that would correspond to the external zone of the eggshell of Recent avians (Figure 2B). However, it may not be readily visible where the squamatic structure is not consistently well-defined or preserved throughout prisms of the squamatic zone. In this respect, troodontid theropod eggshell closely resembles that of laevisoolithid, gobioolithid, and elongatoolithid eggs in the preservation of only the mammillary and squamatic zones.

#### 4. Discussion

The microstructural features of fossil eggshell, like those of fossil skeletal material, may be altered or obliterated by weathering and diagenesis. This may, in turn, lead to the misinterpretation or misidentification of some features. Previously described troodontid eggshells from Alberta (Zelenitsky & Hills, 1996) and Montana (Hirsch & Quinn, 1990) do not exhibit the microstructural characteristics present in the specimens described herein. These eggshells permit the recognition of microstructural characteristics shared with the eggshell of modern birds. In addition to the presence of the two structural layers (mammillary and squamatic), bird-like characteristics of the eggshell of troodontids include: (1) fibres associated with eisospherites attached to the bases of the mammillae; (2) fine radiating crystals emanating from a central core that form the spherulite and grade into coarse, blocky wedges of the mammilla; and (3) the presence of prisms in the second layer showing squamatic ultrastructure. With respect to the fibre and mammillae diameters, those of troodontids are comparable to those of various modern birds, as is the ratio of the shell thickness to the inner layer thickness (Table 1). The volume-to-shell-thickness ratio of troodontid eggs is lower than that of ratites, but comparable to that of neognathes (Table 2). Finally, the breadth-to-width ratio of the eggs is lower than that of both paleognathes and neognathes, and is comparable to that of elongatoolithids (Table 2).

The eggshell of troodontid theropods appears to be plesiomorphic compared to that of extant birds in the absence of an external layer. This distinction may be valid, or alternatively, it may be attributable to a





**Figure 2.** Radial SEM micrographs of theropod eggshell. A, B, TMP 94.157.5, troodontid eggshell. A, boundary (arrows) between wedges of inner layer and prisms of outer layer is gradational. B, prism boundaries (arrows) of outer layer are vertical and prisms show no structural change near the shell surface. C, D, outer layer of C, troodontid (TMP 94.157.5) and D, Eocene bird eggshell (HEC 107) appears similar with vesicles (arrows) in the squamatic zone. E, F, remnant particles of squamatic structure (lower half of photograph) in E, troodontid (TMP 94.157.2) and squamatic structure in F, *Anser* eggshell. Scale bars represent 100  $\mu\text{m}$  in A–B and 10  $\mu\text{m}$  in C–F.

taphonomic phenomenon. The observation that the external layer is rare in the eggshell of Cretaceous birds may have an important bearing on these two possibilities. An external layer has been reported in

bird eggshells from the Upper Cretaceous of Alberta, although their precise taxonomic affinities are unknown (Zelenitsky *et al.*, 1996). It is apparently absent in laevisoolithids, an ootaxonomic group that may be

**Table 2.** Egg and eggshell characteristics of modern birds and non-avian dinosaurs. Egg volumes were calculated using the (ellipse) formula in [Sabath \(1991\)](#), except for those of *Protoceratopsidovum* and the unidentified elongatoolithid, which are from [Sabath \(1991\)](#).

Taxon	LD (cm)	SD (cm)	Vol (cc)	Th (cm)	Vol/Th	SD/LD
<i>Aepyornis</i> *	31.2	22.8	8488	0.350	24 300	0.73
<i>Apteryx</i> *	11.6	7.0	297	0.042	7080	0.60
<i>Dinornis</i> **	24.0	17.8	3979	0.210	18 900	0.74
<i>Dromaius</i> †	12.3	8.8	498	0.086	5790	0.72
<i>Gallus</i> †	5.9	4.4	60	0.030	2000	0.75
<i>Numida</i> †	5.0	3.5	32	0.051	630	0.70
<i>Rhea</i> †	12.5	8.5	475	0.082	5800	0.68
<i>Struthio</i> †	15.3	12.9	1331	0.204	6530	0.84
<i>Protocerato</i> ‡	15.0	5.4	230	0.100	2300	0.36
Elongatoolithid‡	17.0	6.8	420	0.130	3230	0.40
<i>Troodon</i> *	15.0	7	385	0.100	3850	0.47

Abbreviations as in [Table 1](#), plus: LD, long diameter; *Protocerato*., *Protoceratopsidovum*; SD, short diameter of egg; Vol, egg volume. Source: \*HEC, \*\*Gill (2000), †ZEC, ‡Sabath (1991).

attributable to enantiornithine birds, and it may be absent in gobiolithids, an ootaxon that may be attributable to *Gobipteryx* (an enantiornithine) or to an unidentified paleognathe ([Mikhailov, 1991, 1997a](#)). If the absence of the external layer in the eggshell of stem-birds (i.e., birds that fall outside the avian crown-group) is genuine (i.e., unaffected by diagenesis), then this suggests that the external layer evolved subsequent to the origin of birds. However, if the absence of an external layer is due to non-preservation, then the same interpretation might apply to troodontids (and possibly a few other non-avian theropod groups) in order to account for the presence of only two structural layers. Unless material is extremely well preserved, it may be difficult to determine the presence or absence of an external layer because it may be thin, eroded, or indistinguishable from the prisms of the squamatic layer in recrystallised material. An example of such a possibility is moa eggshell, which has been described several times since the late 1800s, yet the presence of an external layer was not identified until recently ([Grellet-Tinner, 2000; Gill & Zelenitsky, 2001](#)). Thus, it is possible that the discovery of pristine troodontid or other non-avian theropod eggshell might allow the recognition of an external layer as an apomorphy of a more inclusive group within Theropoda.

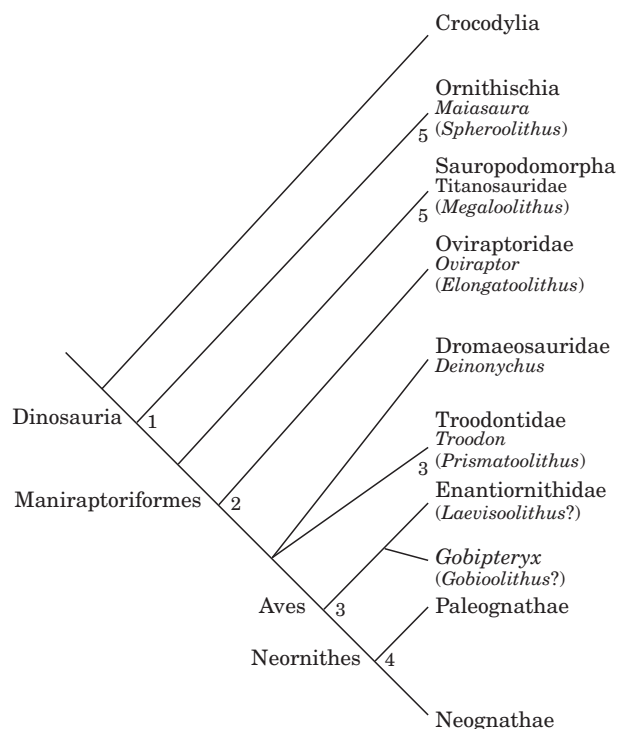
The identification of squamatic ultrastructure in the outer layer of troodontid (*Prismatoolithus*) eggshell is perhaps the most significant finding of this study. In the first description of the eggshell material from

the Two Medicine Formation, troodontid eggshell (regarded at that time to be of hypsilophodontid parentage) was the basis for the creation of the dinosauroid-prismatic morphotype ([Hirsch & Quinn, 1990; Mikhailov, 1991](#)). This initial classification was based on the identity of the eggs as dinosaurian, in addition to the observation that they exhibited the prismatic structure ([Hirsch & Quinn, 1990](#)). [Mikhailov \(1991, 1994\)](#) determined, based mainly on Mongolian material he assumed to be protoceratopsian, that the structure of the dinosauroid-prismatic eggshell should be segregated from bird eggshell because of the absence of squamatic structure (present in bird eggshell) and the presence of tabular structure (absent in bird eggshell) in the outer prismatic layer. Subsequently, [Zelenitsky & Hills \(1996\)](#) erroneously described troodontid eggshell from Alberta as displaying tabular structure in prisms of the outer layer, which are now known to represent the tabular wedges of the inner (mamillary) layer. The present description of the exceptionally well-preserved eggshell from the same locality permits the recognition of squamatic ultrastructure in the outer, prismatic layer.

Our identification of squamatic ultrastructure in the same type of dinosaur eggshell that was the basis for the establishment of the dinosauroid-prismatic morphotype now permits a consideration of the evolution of prismatic structure in dinosaur eggshell. Prior to the corrected identification of troodontid embryos, prismatic structure was thought to be convergent in the eggshells of neognathous birds, two ornithischians (hypsilophodontids, protoceratopsians), and possibly allosauroids (based on *Preprismatoolithus*). Currently, prismatic ultrastructure can be confirmed only in Troodontidae and Neognathae. Despite competing hypotheses of theropod phylogeny and the lack of consensus on the relative positions of Dromaeosauridae, Troodontidae, and Aves (e.g., [Forster \*et al.\*, 1998; Makovicky & Sues, 1998; Sereno, 1999](#)), optimization of the distribution of prismatic ultrastructure reveals that it arose independently in Troodontidae and Neognathae ([Figure 3](#)). This reconstruction, of course, assumes that the eggshell described by [Makovicky & Grellet-Tinner \(2000\)](#) is truly dromaeosaurid in origin, and that gobiolithid and laevisolithid are correctly attributed to enantiornithine birds.

The eggshell parataxonomy that developed around the description and study of fossil eggs and eggshell was a natural and necessary avenue of research in the absence of closely associated skeletal materials. However, as more specimens of associated adult and embryonic materials are now coming to light problems with this parataxonomy are becoming more





**Figure 3.** Consensus of archosaurian phylogeny from Forster *et al.* (1998), Makovicky & Sues (1998), and Sereno (1999), showing selected skeletal taxa with both known and possible egg-layers (indicated by '?'). Alternative character placements are indicated under the accelerated transformation (ACCTRAN) or delayed transformation (DELTRAN) options. Characters diagnose nodes and/or branches as follows: 1, organic cores in eggshell units (Mikhailov, 1991); ornamentation present; spherical to subspherical eggs (ACCTRAN). 2, squamatic zone present; increase in egg volume with respect to adult body size (Varricchio *et al.*, 1999); eggshell porosity reduced; eggs elongate (ACCTRAN). 3, potential for asymmetric eggs (Varricchio *et al.*, 1999); reduction of fine radiating calcite structure to basal part of mammillary layer. 4, external zone present. 5, eggs subspherical (DELTRAN).

apparent. Our opinion is that the establishment of the dinosauroid-prismatic morphotype was counter-productive because the concept of the morphotype was held in higher importance than characters of potential phylogenetic usefulness. The usage of morphotypes in eggshell taxonomy constrains workers to assign new egg taxa to established groupings (i.e., morphotypes) that may or may not represent natural taxa. Although the number of characters from eggshell is limited, it has been demonstrated that they do display phylogenetic usefulness (Mikhailov, 1992; Grellet-Tinner, 2000). It would be more worthwhile for eggshell specialists to discuss their work in a cladistic context and, if feasible, allow eggshell data to

complement that obtained from skeletons. Finally, the concept and application of egg morphotypes should be abandoned, just as most systematists now eschew the use of Linnean ranks in cladistic studies of skeletal taxa.

### Acknowledgements

We thank Ms Mimi Reichenbach and Mr Alan Gordon of GR Petrology Consultants Inc., Calgary, Alberta, whose company provided many hours on their scanning electron, petrographic, and binocular microscopes. We also thank Dr Christopher DeBuhr (of GR Petrology) for his assistance with the scanning electron microscope, Mr Woo Jong Oh for sample preparation, Ms Wendy Sloboda for assistance in the collection of material, and Dr Hans-Dieter Sues for his comments on an early version of the manuscript. This work was supported by the University of Calgary and by research grants from the Natural Sciences and Engineering Research Council of Canada to Dr Philip J. Currie (University of Calgary) and Dr Hans-Dieter Sues (University of Toronto).

### References

- Clark, J. M., Norell, M. A. & Chiappe, L. M. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avian-like brooding position over an oviraptorid nest. *American Museum Novitates* **3265**, 1–36.
- Dong, Z. & Currie, P. J. 1996. On the discovery of an oviraptorid skeleton on a nest of eggs at Bayan Mandahu, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* **30**, 631–636.
- Forster, C. A., Sampson, S. D., Chiappe, L. M. & Krause, D. W. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* **279**, 1915–1919.
- Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. In *The origin of birds and the evolution of flight* (ed. Padian, K.), pp. 1–55 (Memoirs of the California Academy of Sciences, Volume 8; Towne and Bacon, San Francisco).
- Geist, N. R. & Jones, T. 1996. Juvenile skeletal structure and the reproductive habits of dinosaurs. *Science* **272**, 712–714.
- Gill, B. J. 2000. Morphometrics of moa eggshell fragments (Aves: Dinornithiformes) from Late Holocene dune-sands of the Karikari Peninsula, New Zealand. *Journal of The Royal Society of New Zealand* **30**, 131–145.
- Gill, B. J. & Zelenitsky, D. K. 2001. Preliminary analysis of moa eggshells (Aves: Dinornithiformes) from northern New Zealand. *Journal of Vertebrate Paleontology* **21** (Supplement to No. 3), 54A.
- Grellet-Tinner, G. 2000. Phylogenetic interpretation of eggs and eggshells of Paleognathae. In *First international symposium on dinosaur eggs and babies* (eds Bravo, A. M. & Reyes, T.), pp. 61–73 (Isona I Conca Dellà Catalonia, Spain).
- Hirsch, K. F. 1994. Upper Jurassic eggshells from the Western Interior of North America. In *Dinosaur eggs and babies* (eds Carpenter, K., Hirsch, K. F. & Horner, J. R.), pp. 137–150 (Cambridge University Press, Cambridge).
- Hirsch, K. F. & Quinn, B. 1990. Eggs and eggshell fragments from the Upper Cretaceous Two Medicine Formation of Montana. *Journal of Vertebrate Paleontology* **10**, 491–511.
- Horner, J. R. 2000. Dinosaur reproduction and parenting. *Annual Review of Earth and Planetary Sciences* **28**, 19–45.



- Horner, J. R. & Weishampel, D. B. 1988. A comparative embryological study of two ornithischian dinosaurs. *Nature* **332**, 256–257.
- Horner, J. R. & Weishampel, D. B. 1996. A comparative embryological study of two ornithischian dinosaurs—a correction. *Nature* **383**, 103.
- Ji, Q., Currie, P. J., Norell, M. A. & Ji, S. 1998. Two feathered dinosaurs from northeastern China. *Nature* **393**, 753–761.
- Ji, Q., Norell, M. A., Gao, K., Ji, S. & Ren, D. 2001. The distribution of integumentary structures in a feathered dinosaur. *Nature* **410**, 1084–1088.
- Makovicky, P. J. & Grellet-Tinner, G. 2000. Association between a specimen of *Deinonychus antirrhopus* and theropod eggshell. In *First international symposium on dinosaur eggs and babies* (eds Bravo, A. M. & Reyes, T.), pp. 123–128 (Isona I Conca Dellà Catalonia, Spain).
- Makovicky, P. J. & Sues, H.-D. 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. *American Museum Novitates* **3240**, 1–27.
- Mateus, I., Mateus, H., Telles, A. M., Mateus, O., Taquet, P., Ribeiro, V. & Manuppella, G. 1997. Couvée, oeufs et embryons d'un dinosaure théropode du Jurassique supérieur de Lourinhã (Portugal). *Comptes Rendus de l'Académie des Sciences de Paris, Série 2* **53**, 71–78.
- Mikhailov, K. E. 1987a. The principal structure of the avian egg-shell: data of SEM studies. *Acta Zoologica Cracoviensia, Krakow* **30**, 53–710.
- Mikhailov, K. E. 1987b. Some aspects of the structure of the shell of the egg. *Paleontological Journal* **21**, 54–61.
- Mikhailov, K. E. 1991. Classification of fossil eggshells of amniotic vertebrates. *Acta Palaeontologica Polonica* **36**, 361–373.
- Mikhailov, K. E. 1992. The microstructure of avian and dinosaurian eggshell: phylogenetic implications. In *Papers in avian paleontology honoring Pierce Brodkorb* (ed. Campbell, K.), pp. 361–373 (Contributions in Science, Natural History Museum, Los Angeles County).
- Mikhailov, K. E. 1994. Theropod and protoceratopsian dinosaur eggs from the Cretaceous of Mongolia and Kazakhstan. *Paleontological Journal* **28**, 101–120.
- Mikhailov, K. E. 1997a. Fossil and Recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification. *Special Papers in Palaeontology* **56**, 1–80.
- Mikhailov, K. E. 1997b. Avian eggshells: an atlas of scanning electron micrographs. *The British Ornithologists' Club, Occasional Publications* **3**, 1–88.
- Norell, M. A., Clark, J. M., Dashzeveg, D., Barsbold, R., Chiappe, L. M., Davidson, A. R., McKenna, M. C., Perle, A. & Novacek, M. J. 1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science* **266**, 779–782.
- Norell, M. A., Clark, J. M., Chiappe, L. M. & Dashzeveg, D. 1995. A nesting dinosaur. *Nature* **378**, 774–776.
- Sabath, K. 1991. Upper Cretaceous amniotic eggs from the Gobi Desert. *Acta Palaeontologica Polonica* **36**, 151–192.
- Sereno, P. C. 1999. The evolution of dinosaurs. *Science* **284**, 2137–2147.
- Silyn-Roberts, H. & Sharp, R. M. 1985. Preferred orientation of calcite in the ratite and tinamou eggshells. *Journal of Zoology, London, A* **205**, 39–52.
- Varricchio, D. J. 2001. “Beautiful wounding tooth”: ontogeny and osteology in the theropod *Troodon formosus*. *Journal of Vertebrate Paleontology* **21** (Supplement to No. 3), 110A.
- Varricchio, D. J., Jackson, F., Borkowski, J. J. & Horner, J. R. 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* **385**, 247–250.
- Varricchio, D. J., Jackson, F. & Horner, J. R. 1999. A nesting trace with eggs for the Cretaceous dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology* **19**, 91–100.
- Xu, X., Zhou, Z.-H. & Prum, R. O. 2001. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature* **410**, 200–204.
- Zelenitsky, D. K. 2000. Dinosaur eggs from Asia and North America. *Journal of the Paleontological Society of Korea, Special Publication* **4**, 13–26.
- Zelenitsky, D. K. & Hills, L. V. 1996. An egg clutch of *Prismatolithus levis* oosp. nov. from the Oldman Formation (Upper Cretaceous), Devil's Coulee, southern Alberta. *Canadian Journal of Earth Sciences* **33**, 1127–1131.
- Zelenitsky, D. K., Hills, L. V. & Currie, P. J. 1996. Parataxonomic classification of ornithoid eggshell fragments from the Oldman Formation (Judith River Group; Upper Cretaceous), southern Alberta. *Canadian Journal of Earth Sciences* **33**, 1655–1667.
- Zhao, Z. & Li, R. 1993. First record of Late Cretaceous hypsilophodontid eggs from Bayan Mandahu, Inner Mongolia. *Vertebrata Palasiatica* **31**, 77–84.