Canadian Journal of Earth Sciences
Revue canadienne des sciences de la Terre

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Journal:	<i>Canadian Journal of Earth Sciences</i>
Manuscript ID	cjes-2017-0273.R1
Manuscript Type:	Article
Date Submitted by the Author:	05-Feb-2018
Complete List of Authors:	Funston, Gregory; University of Alberta, Department of Biological Sciences Currie, Philip J.; University of Alberta, Biological Sciences
Is the invited manuscript for consideration in a Special Issue? :	N/A
Keyword:	Eggshell, Horseshoe Canyon Formation, Prismatoolithidae, Troodontidae, Maastrichtian

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The first record of dinosaur eggshell from the Horseshoe Canyon Formation (Maastrichtian) of
Alberta, Canada

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Abstract—Eggs and eggshell are generally rare in the Upper Cretaceous rocks of Alberta, despite being relatively abundant nearby in Montana. Palaeontologists and other people have been prospecting the Horseshoe Canyon Formation for more than a 130 years, but eggshell fragments have only just been recovered. The fragments are unornamented with angusticanalicate pores and three structural layers. Numerous features support their referral to *Prismatoolithus levis*, and they confirm the presence of a bird-like external layer in this ootaxon. The fragments, which likely belonged to *Albertavenator curriei*, are from a site with abundant troodontid teeth and perinate material from hadrosaurs, ceratopsians, and theropods. The discovery of eggshell challenges the notion that the Horseshoe Canyon Formation is too heavily sideritized to preserve eggshell.

Keywords: Eggshell; Horseshoe Canyon Formation; Prismatoolithidae; Troodontidae; Maastrichtian

Résumé— Les œufs et la coquille d'œuf sont généralement rares dans les roches du Crétacé supérieur de l'Alberta, mais ils sont relativement abondants en Montana. Des paléontologues ont étudié la Formation de Horseshoe Canyon depuis plus de 130 ans, mais des fragments de coquilles d'œufs viennent tout juste d'être découvertes. Les surfaces des fragments sont lisses, et les pores sont angusticanaliculaires. Les coquilles sont composées de trois couches structurelles, comprenant une couche externe, ressemblant les œufs d'oiseaux. De nombreuses caractéristiques soutiennent leur référence à *Prismatoolithus levis*, et elles confirment la présence d'une couche externe dans cet ootaxon. Les fragments, qui ont probablement appartenu au troodontidé *Albertavenator curriei*, proviennent d'un site avec des dents de

34 troodontidés abondantes et des matériaux périnataux provenant d'hadrosaures, de
35 cératopsiens et de théropodes. La découverte de la coquille d'œuf remet en question l'idée que
36 la Formation de Horseshoe Canyon est trop sidérisée pour préserver la coquille d'œuf.

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Introduction:

The Upper Cretaceous sediments of Alberta are well known for their abundant fossil resources, particularly dinosaurs. In addition to exceptional skeletal material, dinosaurs are represented by footprints, skin impressions, coprolites, and relatively rare eggshell. Despite an abundance of eggs in nearby deposits in Montana (Horner 1982, 2000, Varricchio and Jackson 2004) and adjacent parts of Alberta (Currie 1988, Zelenitsky et al. 1996, Zelenitsky and Hills 1996), eggs and eggshell are relatively rare in Alberta. In contrast with its incredible density of skeletal material, the Dinosaur Park Formation has produced relatively little eggshell (Zelenitsky and Sloboda 2005). Recent work has expanded the temporal range of Albertan eggshell to the Santonian (Zelenitsky et al. 2017b) and Maastrichtian (Zelenitsky et al. 2017a, Voris et al. In Press).

The absence of eggshell in some formations, like the Campanian–Maastrichtian Horseshoe Canyon Formation, is perplexing. The Horseshoe Canyon Formation has been recognized for its fossil richness for more than 130 years. It is more than twice as thick (250–300 m; Eberth and Braman 2012) than the combined Dinosaur Park and Oldman Formations (70 m and 40 m, respectively; Eberth 2005), so it is surprising that no eggshell has yet been reported. Multiple sites are known to produce embryonic or hatchling dinosaurs, which suggests that there were nests nearby (Ryan et al. 1998). Some authors, like Ryan et al. (1998), explained the absence of eggshell in this formation as the consequence of high sideritization rates indicative of soil acidity. This may also apply to other formations, like the Dinosaur Park Formation, where eggshell is most abundant in conjunction with bivalve shells, which may

buffer soil acidity (Currie 1988). However, the Horseshoe Canyon Formation also produces extensive bivalve beds, which do not preserve eggshell. Furthermore, it records a transgression-regression cycle, with a wide array of depositional environments, soil types, and climates, not all of which are siderite-rich (Eberth and Braman 2012). Thus, although the pervasive presence of siderite likely explains the absence of eggshell in much of the Horseshoe Canyon Formation, eggshell might be expected from exceptional sites.

Here, the first fossil eggshell recovered from the Horseshoe Canyon Formation is described. The fragments were collected from a microsite that also preserves ceratopsian, hadrosaur, and theropod perinate material, plus abundant troodontid teeth. These specimens, which pertain to a troodontid theropod nester, fill a gap in the record of eggshell in Alberta, and expand the northern range of eggshell from North America.

Institutional Abbreviations: TMP, Royal Tyrrell Museum of Palaeontology; UALVP, University of Alberta Laboratory of Vertebrate Palaeontology.

Methods and Material:

UALVP 57622-A–AD. *Prismatoolithus levis*. Thirty fragments of eggshell. Felber Troodon Site 2 (FTS-2), Horsethief Member, Horseshoe Canyon Formation, Morrin, Alberta (GPS: 12U 368023, 5726540, elevation 707 masl).

82 UALVP 57622-A–UALVP 57622-AD were collected under the appropriate permits to GFF.

83 An equal number of fragments were recovered through screen washing ($n = 15$) and surface
84 collection ($n = 15$). Four fragments (UALVP 57622-A–D) of varying thickness and external pore
85 structure were histologically thin-sectioned. The fragments were stabilized using Castolite AC
86 polyester resin under a vacuum. The sections were prepared to a thickness of 230 μm using an
87 Isomet 1000 wafer blade saw and polished using CeO_2 powder until the desired contrast was
88 achieved. They were imaged on a Nikon Eclipse E600POL trinocular polarizing microscope with
89 an attached Nikon DXM 1200F digital camera using NIS Elements.

90 UALVP 57622-D–G were scanned using a Zeiss EVO Scanning Electron Microscope (SEM)
91 with a LaB6 electron source in the SEM Laboratory in the Department of Earth and Atmospheric
92 Sciences at the University of Alberta. Images were taken in Variable Pressure SEM mode using
93 the Variable Pressure Secondary Electron detector (VPSEM) and Electron Backscatter detector
94 (BSD) modes. Three of the fragments (UALVP 57622-D–F) were broken to obtain fresh edges for
95 imaging in radial view.

96 97 Geological Setting:

98 FTS-2 (Fig. 1) is one of several microsites in the Horseshoe Canyon Formation that
99 produces an abundance of troodontid material. It is similar to a previously described site in the
100 Horseshoe Canyon (L2000; Ryan et al. 1998), but FTS-2 is farther north near the Morrin Bridge.
101 Fossils at FTS-2 occur throughout a ~5 m thick, lens-shaped deposit. There is no single
102 fossiliferous layer, suggesting prolonged deposition at the site. The bed is exposed for
103 approximately 50 m close to the base of a west-facing slope, and is truncated at its northern

end by an area of extensive slumping (Fig. 1). Stratigraphically, it occurs near the top of the Horsethief Member (Eberth and Braman 2012), just below the #9 coal, essentially equivalent to L2000 (Ryan et al. 1998). Sedimentologically, the deposit is remarkably similar to L2000, occurring in an olive-coloured silty mudstone, with occasional lenses of sand. However, it lacks the mauve patches and ironstone beds of L2000, and sideritized nodules are less common. It overlies a sequence of alternating grey mudstones and white-tan channel sandstones, which suggests that it also represents an overbank deposit. Like L2000, fossil material is concentrated as a deflation lag.

Systematic Palaeontology:

Oofamily Prismatoolithidae Hirsch (1994)

Genus *Prismatoolithus* Zhao and Li (1993)

Prismatoolithus levis Zelenitsky and Hills (1996)

Description:

Thirty eggshell fragments were recovered, and all pertain to a single egg morph. Fragments range in size from $\sim 6 \text{ mm}^2$ – $\sim 100 \text{ mm}^2$. In colour, the shell fragments vary from light tan to dark brown, which contrasts with most eggshell collected from further south in Alberta and Montana. The eggshell ranges in thickness from 0.47 mm – 1.23 mm, with a mean thickness of 0.929 mm. The distribution of thickness is bimodal (Fig. 2), with peaks around 0.7 mm thick and 1.1 mm thick, probably corresponding to the sides and poles of the eggs,

respectively. The surfaces of all fragments are smooth (Fig. 3), and only four fragments show conspicuous external pores. In one of these fragments (UALVP 57622-F; Fig. 3 A, B), the pores are large and circular, whereas other fragments have small, oval pores (Fig. 3 C, D), comparable to *Prismatoolithus levis* from other formations (Zelenitsky and Hills 1996, Varricchio et al. 2002). Pores occur either singly or in pairs (Fig. 3A), and all are housed in depressions. Although most of the pieces are too small to determine curvature, the largest fragments show more curvature along one axis than the other, suggesting that the eggs were not completely spherical. The internal surfaces of almost all fragments have been weathered, which means that the bases of mammillary units cannot be discerned. The possible exceptions are UALVP 57622-A and UALVP 57622-F (Fig. 3B), where there are internal iron-stained layers that may represent mammillae.

In radial view (Fig. 4), at least two layers are visible: an internal mammillary layer, and a prismatic layer. Many of the fragments are also encrusted with a layer of calcite crystals, oriented perpendicular to the shell surface. Some better-preserved fragments (e.g. UALVP 57622-D) have a thin, bright layer towards the outer surface of the eggshell (Fig. 4). In thin section, this layer has a sharp contact (Fig. 4A)—and shows a continuous extinction pattern (Fig. 4B)—with the columns of the prismatic layer. Furthermore, this layer follows the contours of pores (Fig. 4E), indicating that it represents an eggshell structure, rather than a diagenetic feature. This suggests that it represents an external layer (Varricchio et al. 2002, Varricchio and Jackson 2004, Jackson et al. 2010). The shell units have a relatively low width to height ratio of approximately 1:5, even in UALVP 57622-A, where the bases of the mammillae seem to be intact. The transition between the mammillary and prismatic layers is gradual, rather than abrupt, and both layers have prominent laterally continuous growth lines oriented parallel to

the shell surface. The ratio of mammillary to prismatic and external layers is approximately 1:2.6:0.3, respectively, in most fragments, although this may have been modified by weathering, because the bases of the mammillae are worn. Under cross polarized light, the prismatic layer is divided into sharp-bordered columns (Fig. 4B), which taper towards the inside of the shell. The pores are relatively sparse and are angusticanaliculate (Fig. 4C). They are perpendicular to the shell surface and do not branch. Their openings on the outside surface of the shell are funnel-shaped in radial view.

SEM images only show two general layers, which are relatively poorly delimited. The mammillary layer fractures into large, angular blocks, similar to the fracture pattern described by Varricchio (Varricchio et al. 2002). These blocks have striated faces, demonstrating the tabular ultrastructure typical of mammillae in *Prismatoolithus* (Zelenitsky et al. 2002). The bases of the mammillae and the central cores from which these blocks radiate are weathered away in the fragments examined. Shell units in the prismatic layer are relatively easily discerned: where they meet, they form distinctive chevron-like patterns. The prismatic layer shows some regions of ill-defined squamatic ultrastructure, especially near the external layer. However, there are also some large, flat regions produced by cleavage planes. These facets do not show the striae present in the mammillary layer. Numerous small vesicles are visible throughout each of the structural layers. In SEM images, the transition between the external and prismatic layers is difficult to discern, but the cleavage of crystals within each layer differs (Fig. 5). In the prismatic layer, borders between crystal faces are oriented about at about 45°, whereas in the external layer (Fig. 5B) they are mostly perpendicular to the egg surface.

Discussion:

Several features of UALVP 57622 support the referral of the fragments to Prismatoolithidae and *Prismatoolithus*. The narrow, sharp-bordered columns of the prismatic layer are typical of the oofamily, as are laterally continuous growth lines (Varricchio et al. 2002, Skutschas et al. 2017). The tabular ultrastructure of the mammillary layer and the ill-defined squamatic ultrastructure of the prismatic layer are both characters of Prismatoolithidae (Zelenitsky et al. 2002). The blocky fracture of the mammillary layers is a prismatoolithid feature noted by Varricchio et al. (2002) as a difference from most other types of eggshell. Finally, the gradual transition between the mammillary and prismatic layers is considered a defining feature of Prismatoolithidae (Skutschas et al. 2017). Within Prismatoolithidae, oogenera vary in both surface ornamentation and in the number of structural layers. The combination of smooth eggshell lacking ornamentation and the presence of three structural layers are only known within a single oogenus, *Prismatoolithus*. Only two oospecies, *Prismatoolithus ilekensis* (Skutschas et al. 2017) and *Prismatoolithus levis* (Zelenitsky and Hills 1996), show both of these characters, although the presence of an external layer in the latter is controversial (Varricchio et al. 2002, Zelenitsky et al. 2002, Jackson et al. 2010). Between these oospecies, fragments of UALVP 57622 are more similar to *Prismatoolithus levis* in terms of the ratio of mammillary to prismatic layers (~1:2.5) and eggshell thickness (0.7 mm – 1.2 mm)—more than double the thickness of *Prismatoolithus ilekensis*. The ratio of mammillary to prismatic layers for *Prismatoolithus levis* was initially reported as 1:8 – 1:6 (Zelenitsky and Hills 1996), but this was revised to 1:1.77 – 1:2.35 by Zelenitsky et al. (2002). Although reported by Varricchio et al. (2002) as 1:8 – 1:6, measurement from their figures indicates the ratio of the

structural layers is closer to 1:2.5:0.2. Because the fragments of UALVP 57622 do not preserve the bases of the mammillae, it is possible these ratios would have fallen within the range of Zelenitsky et al. (2002). Regardless, their proximity of the distribution to previously reported ranges supports referral of all fragments to *Prismatoolithus levis*.

Excluding the external layer, there are still multiple characteristics of UALVP 57622 that support its referral to *Prismatoolithus levis*. Of *Prismatoolithus* oospecies, the range of thickness of UALVP 57622 is consistent with only three ootaxa: *Prismatoolithus jenseni* (Bray 1999), *Prismatoolithus levis* (Zelenitsky and Hills 1996), and *Prismatoolithus hukouensis* (Zhao 2000). UALVP 57622 differs from *Prismatoolithus jenseni* in the presence of paired pore openings (Fig. 2a), and relatively wider shell units (1:5 vs 1:7). Little information is available on *Prismatoolithus hukouensis*, but based on provenance it is unlikely that UALVP 57622 is referable to that ootaxon. There are no features reported in *Prismatoolithus levis* that UALVP 57622 lacks, nor does it possess any features that are outside the range of variation in *Prismatoolithus levis*. UALVP 57622 thus confirms the presence of an external layer in *Prismatoolithus levis*, and supports the suggestion of Zelenitsky et al. (2002) that its detection may rely on taphonomy.

The eggshell assemblage at FTS-2 is unusual in that all of the eggshell pertains to a single ootaxon. Oospecies of *Prismatoolithus* are generally regarded as corresponding to troodontids (Varricchio et al. 2002). Only one troodontid, *Albertavenator curriei* (Evans et al. 2017), is currently known from the Horseshoe Canyon Formation. However, troodontid material is rare in the formation, with the exception of two sites, L2000 (Ryan et al. 1998) and FTS-2, which preserve abundant troodontid teeth. Both frontals referred to *Albertavenator*

curriei were recovered from the Horsethief Member near the 8-9 Coal Zones, and TMP 1996.005.0008 was recovered near FTS-2 (Evans et al. 2017). It is therefore likely that the troodontid teeth and eggshells collected at L2000 and FTS-2, both just below the #9 Coal, are referable to *Albertavenator curriei*. The abundance of troodontid material at these two sites, despite their rarity throughout the rest of the formation, strongly suggests an ecological preference for this type of environment. The combination of teeth and eggshell suggests that FTS-2 represents a nesting site of *Albertavenator curriei*. Were this the case, the inference of prolonged deposition at the site would support previous hypotheses of nest-site fidelity (Varricchio et al. 2015). As suggested by Ryan et al. (1998), perinate material from other dinosaur taxa at FTS-2 and L2000 might be explained by targeted predation by *Albertavenator curriei*.

The discovery of eggshell in the Horseshoe Canyon Formation is important for future assessments of its fossil resources. The fragments collected at FTS-2 challenge the notion that the Horseshoe Canyon Formation is too sideritized to preserve eggshell. Targeted re-examination of microsites and lithologically similar sites may result in the detection of more eggshell.

Conclusions:

Thirty eggshell fragments referable to *Prismatoolithus levis* constitute the first eggshell from the Horseshoe Canyon Formation. The eggshell is composed of three structural layers and confirms the presence of the external layer in this ootaxon. Eggshell and teeth recovered from

235 this site likely pertain to *Albertavenator curriei*. The abundance of troodontid material at FTS-2
236 suggests an environmental preference, and supports hypotheses of nest-site fidelity.

237
238 Acknowledgements:

239 The specimens were collected on the 2016–2017 Horseshoe Canyon Formation Expedition,
240 made possible by the generosity of the Dinosaur Research Institute and the commitment of
241 volunteers. We thank E. Felber for discovering the site and showing us its location. We
242 especially thank G. Behuniak, S. Diesel, J. Funston, E. Kuhn, S. Mendonca, M. Powers, M. Rhodes
243 and R. Wilkinson, without whom the site would not have been screenwashed. A. Whitebone
244 screenwashed the material with help from D. Brinkman (TMP) and helped in identifying
245 material. GFF is funded by the Alberta Historical Resources Foundation, Alberta Innovates, the
246 Alberta Lottery Fund, DRI, NSERC, and Vanier Canada. PJC is funded by NSERC [grant # RGPIN-
247 2017-04715].

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- 311

Figure Captions:

Fig. 1. Location of Felber Troodontid Site 2 (FTS-2). Map of Alberta, Canada (A), highlighting Red Deer River area shown in (B). Satellite image (©Google/Landsat) of Red Deer River valley (B), showing location of FTS-2 (star). Photograph (C) of FTS-2 as seen looking North East. Fine dotted line indicates contact of Horsethief and Morrin Members, below which lies the #9 Coal (Eberth and Braman, 2012). Coarse dashed line outlines the fossiliferous bed. Solid line shows slumping to the North of the bed, arrow indicates direction of slumping. Ellipse encircles 3 people, for scale.

Fig. 2. Histogram of eggshell fragment thickness, with bins of 0.1 mm. Peaks probably correspond to sides (red line) and poles (blue line) of the eggs.

Fig. 3. Photographs (A–E) and SEM images (F–J) of eggshell fragments, showing external structure. Black boxes indicate locations of SEM images below. UALVP 57622-G (A–B, F–G) in external view (A) and VPSEM (F), showing single and paired pores (white arrows), and internal view (B) and BSD (G) showing possible iron-stained mammillary layer (white arrow). UALVP 57622-F in external view (C) and VPSEM (H), showing pores housed in a depression. UALVP 57622-D in external view (D) and VPSEM (I), showing location of thin section in Figure 4 (D, white line) and oval pore in a depression (I). UALVP 57622-E (E, J), showing calcite rind on eggshell (white arrows) in normal light (E) and BSD (J). Dashed black box highlights transition

between calcite and prismatic layer shown in J. Image J was taken from broken fragment not shown in E. Abbreviations: Ca, calcite; ML?, possible mammillae; PL, prismatic layer.

Fig. 4. Thin sections of UALVP 57622-D (A–D) and UALVP 57622-A (E) in radial view. UALVP 57622-D in radial view under normal light (A) and cross-polarized light (B), showing gradual transition of mammillary and prismatic layers, presence of external layer, and sharp-bordered columns of shell units (white arrows). White lines indicate boundaries of structural layers. Detail (C) of boundary between external layer and prismatic layer. Detail (D) of external pore (top arrow), and external layer (bottom arrow), which traces the boundaries of the pore depression. UALVP 57622-A in radial view under normal light (E), showing angusticanalicate pore (white arrows). Abbreviations: Ca, calcite; EL, external layer; ML, mammillary layer; PL, prismatic layer.

Fig. 5. SEM images of UALVP 57622-D in BSD. Radial view (A), showing structural layers. Solid box shows location of detail C. Dashed boxes show equivalent locations of images B, D, and E, which were taken from parts of UALVP 57622-D not shown. Detail (B) of exterior of eggshell, showing calcite rind, external layer, and prismatic layer. Dashed lines show approximate boundaries of external layer inferred from thin sections. Detail (C) of mammillary layer, showing blocky fracture and tabular ultrastructure of mammillae. Detail (D) of eggshell units in prismatic layer, showing chevron-shaped boundaries between eggshell units (white arrows). Close-up (E) of prismatic and external layers, showing ill-defined squamatic ultrastructure and vesicles

354 (white arrows). Abbreviations: Ca, calcite; EL, external layer; ML, mammillary layer; PL,
355 prismatic layer; sq, ill-defined squamatic ultrastructure.
356

Draft

Fig. 1. Location of Felber Troodontid Site 2 (FTS-2). Map of Alberta, Canada (A), highlighting Red Deer River area shown in (B). Satellite image (©Google/Landsat) of Red Deer River valley (B), showing location of FTS-2 (star). Photograph (C) of FTS-2 as seen looking North East. Fine dotted line indicates contact of Horsethief and Morrin Members, below which lies the #9 Coal (Eberth and Braman, 2012). Coarse dashed line outlines the fossiliferous bed. Solid line shows slumping to the North of the bed, arrow indicates direction of slumping. Ellipse encircles 3 people, for scale.

298x350mm (300 x 300 DPI)

Fig. 2. Histogram of eggshell fragment thickness, with bins of 0.1 mm. Peaks probably correspond to sides (red line) and poles (blue line) of the eggs.

135x123mm (300 x 300 DPI)

Fig. 3. Photographs (A–E) and SEM images (F–J) of eggshell fragments, showing external structure. Black boxes indicate locations of SEM images below. UALVP 57622-G (A–B, F–G) in external view (A) and VPSEM (F), showing single and paired pores (white arrows), and internal view (B) and BSD (G) showing possible iron-stained mammillary layer (white arrow). UALVP 57622-F in external view (C) and VPSEM (H), showing pores housed in a depression. UALVP 57622-D in external view (D) and VPSEM (I), showing location of thin section in Figure 4 (D, white line) and oval pore in a depression (I). UALVP 57622-E (E, J), showing calcite rind on eggshell (white arrows) in normal light (E) and BSD (J). Dashed black box highlights transition between calcite and prismatic layer shown in J. Image J was taken from broken fragment not shown in E. Abbreviations: Ca, calcite; ML?, possible mammillae; PL, prismatic layer.

363x178mm (300 x 300 DPI)

Fig. 4. Thin sections of UALVP 57622-D (A-D) and UALVP 57622-A (E) in radial view. UALVP 57622-D in radial view under normal light (A) and cross-polarized light (B), showing gradual transition of mammillary and prismatic layers, presence of external layer, and sharp-bordered columns of shell units (white arrows). White lines indicate boundaries of structural layers. Detail (C) of boundary between external layer and prismatic layer. Detail (D) of external pore (top arrow), and external layer (bottom arrow), which traces the boundaries of the pore depression. UALVP 57622-A in radial view under normal light (E), showing angusticanaliculate pore (white arrows). Abbreviations: Ca, calcite; EL, external layer; ML, mammillary layer; PL, prismatic layer.

275x451mm (300 x 300 DPI)

Fig. 5. SEM images of UALVP 57622-D in BSD. Radial view (A), showing structural layers. Solid box shows location of detail C. Dashed boxes show equivalent locations of images B, D, and E, which were taken from parts of UALVP 57622-D not shown. Detail (B) of exterior of eggshell, showing calcite rind, external layer, and prismatic layer. Dashed lines show approximate boundaries of external layer inferred from thin sections. Detail (C) of mammillary layer, showing blocky fracture and tabular ultrastructure of mammillae. Detail (D) of eggshell units in prismatic layer, showing chevron-shaped boundaries between eggshell units (white arrows). Close-up (E) of prismatic and external layers, showing ill-defined squamatic ultrastructure and vesicles (white arrows). Abbreviations: Ca, calcite; EL, external layer; ML, mammillary layer; PL, prismatic layer; sq, ill-defined squamatic ultrastructure.

151x171mm (300 x 300 DPI)