



FIRST RECORD OF ELONGATOOLITHID THEROPOD EGG SHELL FROM NORTH AMERICA: THE ASIAN OOGENUS *MACROELONGATOOLITHUS* FROM THE LOWER CRETACEOUS OF UTAH

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ABSTRACT—Theropod eggshell is identified for the first time from the Lower Cretaceous of North America. Eggshell microstructure and variability in ornamentation and thickness of this material is comparable to that present in elongatoolithid theropod eggs, known previously only from Asia. This identification is based on re-examination of the holotype of the putative spheroolithid *Boletuoolithus carlylensis* and description of additional eggshell fragments from the Lower Cretaceous of Utah. This oospecies is characterized by the ornithoid-ratite morphotype (i.e., of theropod parentage) and not, as recently suggested, by the dinosauroid-prolatospherulitic morphotype (i.e., of ornithoid parentage). Additionally, *Boletuoolithus carlylensis* includes a much broader range of eggshell morphologies than previously described: eggshell thickness ranges from 1.38–3.04 mm, ornamentation is remarkably variable, and sometimes the typical elongatoolithid microstructure is altered by extreme development of both the ornamentation and pore system. The thickness, ornamentation, and elongatoolithid microstructure indicate that the holotype and referred materials assigned to *Boletuoolithus carlylensis* are indistinguishable from the Asian elongatoolithid *Macroelongatoolithus xixiaensis*. Accordingly, the oogenus *Boletuoolithus* is rendered a junior subjective synonym of *Macroelongatoolithus*. In turn, *Macroelongatoolithus xixiaensis* is regarded as a junior synonym of *Macroelongatoolithus carlylei* (new combination and emendation of specific epithet) by virtue of publication priority.

INTRODUCTION

The best known non-avian theropod eggs are those of the oofamily Elongatoolithidae, a grouping that includes eggs found associated with adult and embryonic specimens of oviraptorids (Norell et al., 1994, 1995; Dong and Currie, 1996). Elongatoolithids are elongate, symmetrical eggs with linearituberculate and dispersituberculate ornamentation, and have an eggshell microstructure referable to the ornithoid-ratite morphotype. Eggs within a clutch are positioned sub-horizontally and arranged in a circular configuration. The Elongatoolithidae is represented by five oogenera, *Elongatoolithus*, *Macroolithus*, *Macroelongatoolithus*, *Nanhsiungoolithus*, and *Trachoolithus*, all of which are known from the Cretaceous of Asia (Mikhailov, 1997). The oogenera differ from one another in egg size, shell thickness, and ornamentation; the largest is *Macroelongatoolithus* with a maximum length of 600 mm, and the smallest is *Elongatoolithus* at 170 mm maximum length. Elongatoolithids have not been previously reported from other than Asian provenance.

The most commonly occurring theropod eggs in North America belong to *Troodon* cf. *T. formosus* and are known from the Upper Cretaceous Two Medicine and Oldman formations of Montana and Alberta, respectively (Hirsch and Quinn, 1990; Horner and Weishampel, 1996; Zelenitsky and Hills, 1996). These eggs, assigned to the oospecies *Prismatoolithus levis* (oofamily Prismatoolithidae), were initially thought to belong to a hypsilophodontid (Horner and Weishampel, 1988). Prismatoolithid eggs differ from elongatoolithid eggs in their eggshell microstructure (angustiprismatic morphotype), lack of ornamentation, and vertical orientation of eggs within a clutch.

Currently, the North American ootaxon with eggshell characteristics most similar to the Asian elongatoolithids is *Continuoolithus*. This oogenus is characterized by elongate, ovoid eggs with eggshell that is approximately 1.2 mm thick. The ornamentation is dispersituberculate, and the shell microstructure is of the ornithoid-ratite morphotype. Remains of *Contin-*

uoolithus are known from the Upper Cretaceous of Alberta and Montana (Hirsch and Quinn, 1990; Zelenitsky et al., 1996). Theropod eggshell fragments, which appear similar to *Continuoolithus*, were recently described from the Upper Jurassic of New Mexico (Bray and Lucas, 1997). Thus, while theropod eggshell has been described from both the Upper Jurassic and the Upper Cretaceous of North America, it has never been reported from intervening strata.

Fossil eggshell fragments were initially collected from the Lower Cretaceous of North America in the 1960s, from the Cedar Mountain and Kelvin formations of Utah. These specimens were originally described by Jensen (1970), who merely identified them as dinosaur eggshell fragments. Jensen's (1970) description of eggshell from the Castle Dale locality of the Cedar Mountain Formation focused primarily on their outer surface ornamentation. By applying the rudimentary parataxonomy used by Young (1959, 1965) to describe Asian egg material, Jensen (1970) erected the first North American oospecies, *Oolithes carlylensis*. Jensen (1970:62) characterized the ornamentation of this oospecies as having "deep meandriform channeling amidst truncated ridges," with ridge profiles varying from "moderate mushroom to aphanite chambering produced beneath radically overcast edges." Jensen's diagnosis was restricted to eggshell with this type of unusual ornamentation and collected only from his Castle Dale locality.

At the time of Jensen's (1970) description, the parataxonomy of fossil eggshell was still in its infancy; no system existed for classifying eggshell according to microstructure or morphotype. However, Jensen's (1970:text-fig. 5) illustration of the holotype fragment, which shows an inner mammillary layer and an outer continuous layer, indicates that *O. carlylensis* possesses the ornithoid-ratite morphotype. The distinctiveness of the layering in the eggshell microstructure was observed by Zhao (1975), who reassigned *O. carlylensis* to the Asian oogenus *Macroolithus* (oofamily Elongatoolithidae). At the time of Zhao's (1975) study, the large, thick-shelled eggs of *Macroelongatoolithus* Li et al., 1995 had not yet been discovered. Although his study is

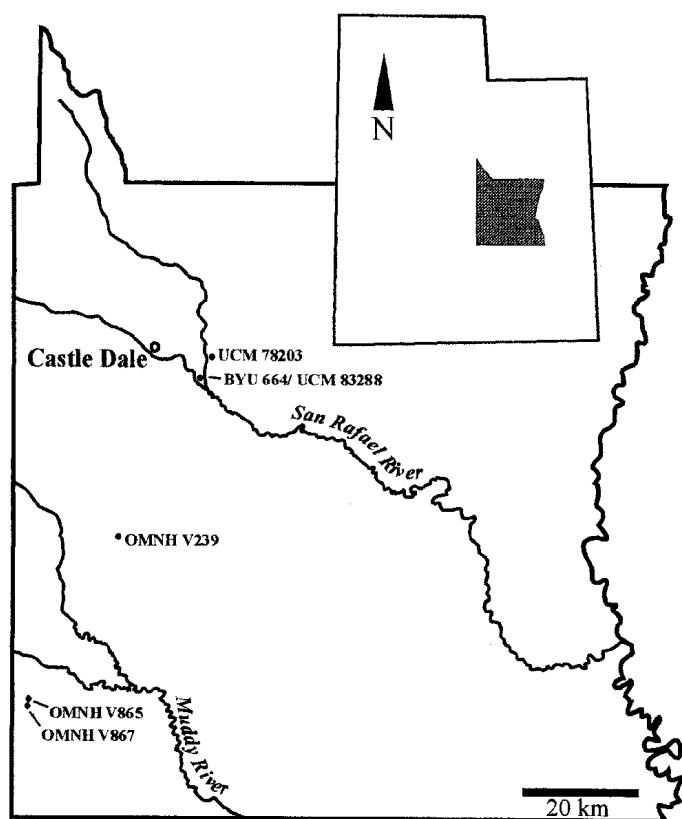


FIGURE 1. Map showing eggshell localities in Emery County, Utah. Shaded area of inset shows location of Emery County in Utah.

regarded as a seminal work in egg parataxonomy, Zhao's (1975) revision of the Castle Dale oospecies was not accepted by subsequent workers (Zelenitsky, 1995; Mikhailov et al., 1996; Bray, 1998).

More recently, Bray (1998) transferred the Castle Dale oospecies to the newly erected oogenus *Boletuoolithus* (oofamily Spheroolithidae), based on her interpretation that the shell units were of the prolatospherulitic morphotype. Furthermore, she suggested that Lower Cretaceous eggshell of the prolatospherulitic morphotype differs from that of the Upper Cretaceous in the presence of pronounced radial ultrastructure of the mammillary region of the former. Interestingly, previously described prolatospherulitic eggshell does not have a well-defined mammillary layer, a diagnostic trait of ornithoid-ratite eggshell. This apparent conflict warrants further investigation of the eggshell currently assigned to *Boletuoolithus carlylensis*.

Numerous eggshell fragments from the Castle Dale type locality of *B. carlylensis* and from four additional Lower Cretaceous localities of central Utah were examined for this review (Fig. 1). Examination of all these materials suggests previous errors in the description of the shell microstructure and unrecognized variation within *B. carlylensis*. Similar microstructure and variation in external ornamentation and shell thickness have been observed in theropod (elongatoolithid) eggs assigned to the Asian oogenus *Macroelongatoolithus*.

Institutional Abbreviations—BYU, Brigham Young University, Provo; DMNH, Denver Museum of Natural History, Denver; OMNH, Oklahoma Museum of Natural History, Norman; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller; UCM, University of Colorado Museum, Boulder.

MATERIALS AND METHODS

Eggshell fragments ($n > 225$) from Jensen's original eggshell collection, which includes the holotype and four paratype fragments of *Boletuoolithus carlylensis*, and additional materials from the Cedar Mountain Castle Dale locality were obtained from BYU for study. Although the Castle Dale locality was revisited, no further eggshell was found. However, over 1,500 fragments of eggshell were collected in 1998 by DMNH field crews from four different sites within the uppermost member of the Cedar Mountain Formation and the lowermost part of the overlying Dakota Formation of central Utah. At each site, the shell fragments were found concentrated in an area of approximately 1 m². These fragments may represent eggshell from one or more eggs of a clutch.

In this study, the aforementioned specimens have been used in a redescription of *Boletuoolithus carlylensis*. Eggshell characteristics examined include shell thickness, outer surface ornamentation, pore pattern, and microstructure (i.e., ultrastructure, pore system, thickness ratio of eggshell layers). The thickness of 364 shell fragments was taken using calipers. The average of three repeat measurements of each fragment determined its thickness. Outer surfaces of approximately 350 fragments were examined and/or photographed using a binocular microscope. Thin sections of Jensen's eggshell ($n = 42$) and of the newly collected material ($n = 49$) were prepared and examined; methods used for thin sectioning are those of Hirsch (1983). Approximately 60% of the total number of eggshell fragments were extensively weathered, eliminating the outer surface ornamentation and inner mammillary layer, and notably reducing the eggshell thickness. This description therefore concentrates on the remaining well-preserved fragments with outer and inner surface features recognizable. The aforementioned materials were compared to elongatoolithid eggshell fragments from a clutch of eggs from the Cretaceous of China and to spheroolithid eggshell fragments from the Upper Jurassic Morrison, Lower Cretaceous Cedar Mountain, and Upper Cretaceous Oldman formations of North America.

SYSTEMATIC PALEONTOLOGY

Oofamily ELONGATOLITHIDAE Zhao, 1975

Oogenus *MACROELONGATOLITHUS* Li, Yin, and Liu, 1995

Type Oospecies—*Macroelongatoolithus carlylei* (Jensen, 1970).

Revised Diagnosis—Eggs are large, exceeding 380 μ m in length; largest reported is 600 μ m. Elongation index is 2.6–3.1. Eggshell thickness averages 2 mm, primarily ranges from 1.8–2.2 mm, total range from 1.38–3.2 mm. Thickness ratio of continuous layer to mammillary layer ranges from 2:1 to 4:1. Ornamentation is variable with typical elongatoolithid pattern in some eggs and very well-developed ornamentation in others.

MACROELONGATOLITHUS CARLYLEI

(Jensen, 1970) new combination + emendation

(Figs. 2, 4A, C–G)

Oolithes carlylensis, Jensen 1970: p. 62–63, pl. 1, figs. 1, 2, 4, 6; pl. 2, figs. 3, 5, 6; pl. 3, figs. 4, 7, 8; text-fig. 5.

Macroolithes carlylei (Jensen), Zhao 1975: p. 108.

Macroelongatoolithus xixiaensis, Li et al. 1995: p. 38–40, figs. 1–4.

Boletuoolithus carlylensis (Jensen) Bray 1998: p. 221–222, figs. 1, 2.

Hypodigm—BYU-E 200 (holotype), eggshell fragment and thin section. BYU VP13699, VP13700, VP13701, and VP13702 (paratypes), four eggshell fragments. BYU-E 201,

TABLE 1. Summary statistics of eggshell thickness for elongatoolithids. **A**, *Macroelongatoolithus carlylei* eggshells from type locality (BYU Loc. #664). **B**, *Macroelongatoolithus carlylei* eggshells from OMNH Loc. #V239. **C**, *Macroelongatoolithus carlylei* eggshells from UCM Loc. #78203. **D**, *Macroelongatoolithus xixiaensis* eggshells (TMP 98.107.1) from single clutch. **E**, *Macroelongatoolithus xixiaensis* from single egg (Li et al., 1995). **F**, *Macroolithus mutabilis* eggshells from Ikh-Shunkht locality (Mikhailov, 1994). All measurements in millimeters.

	A	B	C	D	E	F
n	196	83	85	25	n/a	n/a
mean	1.97	2.00	2.02	2.05	n/a	n/a
s	0.28	0.23	0.38	0.25	n/a	n/a
min.	1.50	1.38	1.38	1.68	2.00	1.30
max.	3.00	2.76	3.04	2.56	3.20	2.30
main range	1.76–2.10*	1.85–2.14*	1.74–2.30*	1.96–2.16*	n/a	1.50–1.80†

*Main range is interquartile range.

†Main range as in Mikhailov (1994).

BYU VP13703, VP13704, VP13705, VP13706, and UCM 82008 (referred material), >225 eggshell fragments.

Type Locality and Horizon—An eggshell locality (BYU Loc. # 664/ UCM Loc. # 83288) located eight kilometers southeast of Castle Dale, Emery County, Utah (Fig. 1). The eggshell was discovered in the uppermost part of the Mussentuchit Member of the Lower Cretaceous Cedar Mountain Formation immediately below the Dakota Formation sandstones.

Referred Specimens—Eggshell fragments (>1,500): TMP 98.107.4, 98.107.15, 98.107.18, and 98.107.22 (OMNH Loc. # V239), TMP 98.107.7 (OMNH Loc. # V865), TMP 98.107.10 (OMNH Loc. # V867), Mussentuchit Member, Cedar Mountain Formation, Emery County, Utah. Eggshell fragments (n > 200): TMP 98.107.5, 98.107.16, 98.107.17, 98.107.20, 98.107.21 (UCM Loc. # 78203), Dakota Formation, Emery County, Utah. Six complete eggs: HX 9301, HX 9302, HX 9303, HWX 9301, HWX 9302, HWX 9303, Cretaceous, Xixia County, Henan Province.

Known Distribution—Lower Cretaceous Cedar Mountain and Dakota formations, Emery County, central Utah; Lower Cretaceous Kelvin Formation, Summit County, northern Utah; Cretaceous, Xixia County, Henan Province, China.

Revised Etymology—Jensen's (1970) original specific epithet "*carlyensis*" is emended to "*carlylei*" following provisions in the International Code of Zoological Nomenclature (1985), because the oospecies was intended to honor a Mr. Carlyle Jones.

Diagnosis—Same as for oogenus.

Description—Individual fragments range up to 3 cm² in size. The curvature and conspicuous thickness of the fragments suggest that the eggs were large and not spheroidal. Most eggshell fragments are curved preferentially about one axis, suggesting an elongate egg. The thickness of the fragments from the type locality ranges from 1.5–3.0 mm (mean = 1.97 mm), including ornamentation. Minor variations in the ranges of shell thickness occur between sites (Table 1). These values compare well with the thickness range of the Asian oospecies *Macroelongatoolithus xixiaensis* (1.68–3.2 mm) and extend beyond that of *Macroolithus mutabilis* (1.3–2.3 mm; Table 1).

The outer surface ornamentation is extremely variable among fragments collected from the type locality, and the type of ornamentation does not appear to be correlated with shell thickness. The variants of ornamentation and their relative proportions are relatively consistent between sites. Within a single site, 50–60% of the well-preserved fragments exhibit dispersituberculate ornamentation, having both isolated and coalesced nodes (Fig. 2A); this ornamentation appears more prominent in some fragments than in others. Fewer fragments (15–20%) have nodes coalesced and aligned on the outer surface to form linearituberculate ornamentation (Fig. 2B; Jensen, 1970:pl. 1, fig. 4). Some fragments (15–20%) have an unusual ornamentation with well-developed, sinuous ridges (Fig. 2C) or well-developed, irregularly- to regularly-shaped nodes (Fig. 2D–F; Bray,

1998:fig. 1). The nodes and ridges are separated by depressions or valleys, which generally house extensive networks of elongate pore openings. This ornamentation is hereafter referred to as "well-developed"; the holotype and paratype specimens fall within this category (Fig. 2E, F). Some fragments (<10%) exhibit little to no relief in the outer surface and are riddled with large slit-like pores distributed in deep grooves (Fig. 2G), which is typical of funnel-shaped (rimocanaliculate) pore canals. It is difficult to determine whether the slit-like pores and nearly smooth outer surface are primary biogenic features or the result of some taphonomic process. The aforementioned variation in the outer surface is also present in the Asian oospecies *Macroelongatoolithus xixiaensis* (Fig. 3A–D) and *Macroolithus mutabilis* (Mikhailov, 1994:pl. X, fig. 2).

Examination of numerous radial thin sections (n = 91) from different sites reveals that the nature of the ornamentation and pore system is closely linked to the eggshell microstructure, and hence the microstructure can appear quite variable. All fragments belong to the ornithoid-ratite morphotype, which is evidenced by the presence of two ultrastructural layers: (1) an inner mammillary layer and (2) an outer continuous layer (Fig. 4A). The majority of eggshell fragments have a typical elongatoolithid microstructure, like that of *Macroelongatoolithus xixiaensis* (Fig. 4B), in which the continuous layer/mammillary layer boundary is abrupt and growth lines are undulating (Fig. 4A, C–G). The continuous layer to mammillary layer thickness ratio ranges from 2:1 to 4:1 among fragments and varies with the nature of the ornamentation (Fig. 4A, C, D). The boundary between these two layers is not always clearly defined because the mammillae appear malformed (Fig. 4C). Similar aberration of the mammillary layer has been reported in the oogenus *Macroolithus* (Zhao, 1994:fig. 12.15).

Several fragments deviate from the "normal" elongatoolithid microstructure due to extreme development of their ornamentation and pore system. As in "normal" fragments, those with a well-developed ornamentation have a pore system that is angusticanaliculate (Fig. 4C). However, not all pore canals run perpendicular to the outer surface; some are angled otherwise and others undercut nodes and ridges at various angles (Fig. 4D). The diagnoses of *Boletuoolithus carlylensis* provided by Jensen (1970) and Bray (1998) include only those eggshell fragments with ornamentation undercut by pores and chambers. These features, however, are also found in some eggshell fragments of the Asian oospecies *Macroelongatoolithus xixiaensis* (Fig. 4B; Li et al., 1995:fig. 4b). The microstructure of fragments with a well-developed ornamentation may appear to have mushroom- or fan-shaped shell units (Fig. 4C; Bray, 1998:fig. 2), depending on the arrangement and morphology of the pore canals. The mushroom-like form is seen in the holotype, hence the name *Boletuoolithus*, in which the undercutting of nodes is extreme (Fig. 4E). This undercutting, however, may have been augmented by diagenesis. The appearance of these "shell units" results in a microstructure that superficially resembles

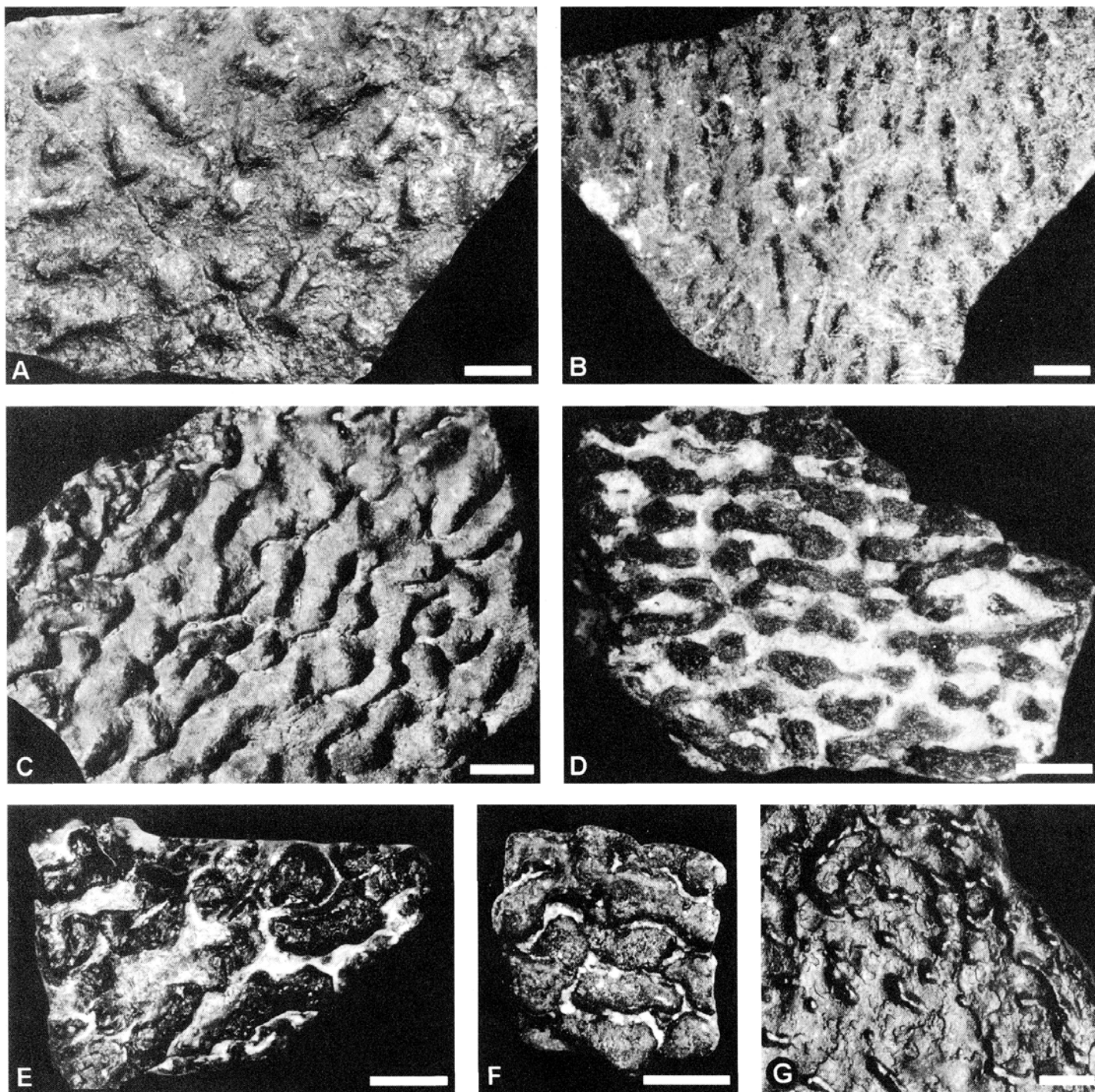


FIGURE 2. Outer surface of *Macroelongatoolithus carlylei* showing variation in ornamentation of eggshell fragments. A, TMP 98.107.15; typical dispersituberculate ornamentation with isolated nodes; B, TMP 98.107.17; linearituberculate ornamentation; note alignment of coalesced nodes; C, TMP 98.107.16; ornamentation consisting of sinuous, bulbous ridges; D–F, ornamentation consisting of bulbous, irregular- to regular-shaped nodes. D, TMP 98.107.18, referred specimen; E, BYU-E 200, holotype; F, BYU VP13699, paratype; G, TMP 98.107.22, nearly smooth outer surface with slit-like pores. Scale bars equal 2 mm.

that of the spheroolithids (prolatospherulitic morphotype). However, the presence of a mammillary layer (Fig. 4A, C–G) and columnar extinction (Fig. 4F) under crossed polars indicates that these eggshell fragments, including the holotype specimen, are clearly of the ornithoid-ratite morphotype. Additionally, several mammillae are present per “shell unit” (Fig. 4C), which does not occur in the prolatospherulitic morphotype (Mikhailov, 1997). The transition from typical ornithoid-ratite to the aberrant, prolatospherulitic-like microstructure can be seen in some individual fragments (Fig. 4G).

In a re-description of *Oolithes carlylensis*, this oospecies was

misidentified as belonging to the prolatospherulitic morphotype (Bray, 1998). Eggshell that is truly of the prolatospherulitic morphotype is known from the Cedar Mountain and Morrison formations; however, as in Upper Cretaceous prolatospherulitic eggshell (Fig. 5A, B), it has sagenotuberculate ornamentation, does not have a well-defined mammillary layer, and has a sweeping extinction pattern across shell units under crossed polars (Fig. 5C–E). Eggshell fragments referred to *B. carlylensis* by Bray (1998:fig. 2) have pronounced radial ultrastructure of the mammillae and a distinct mammillary layer/continuous layer boundary, which is diagnostic of the ornithoid-ratite mor-

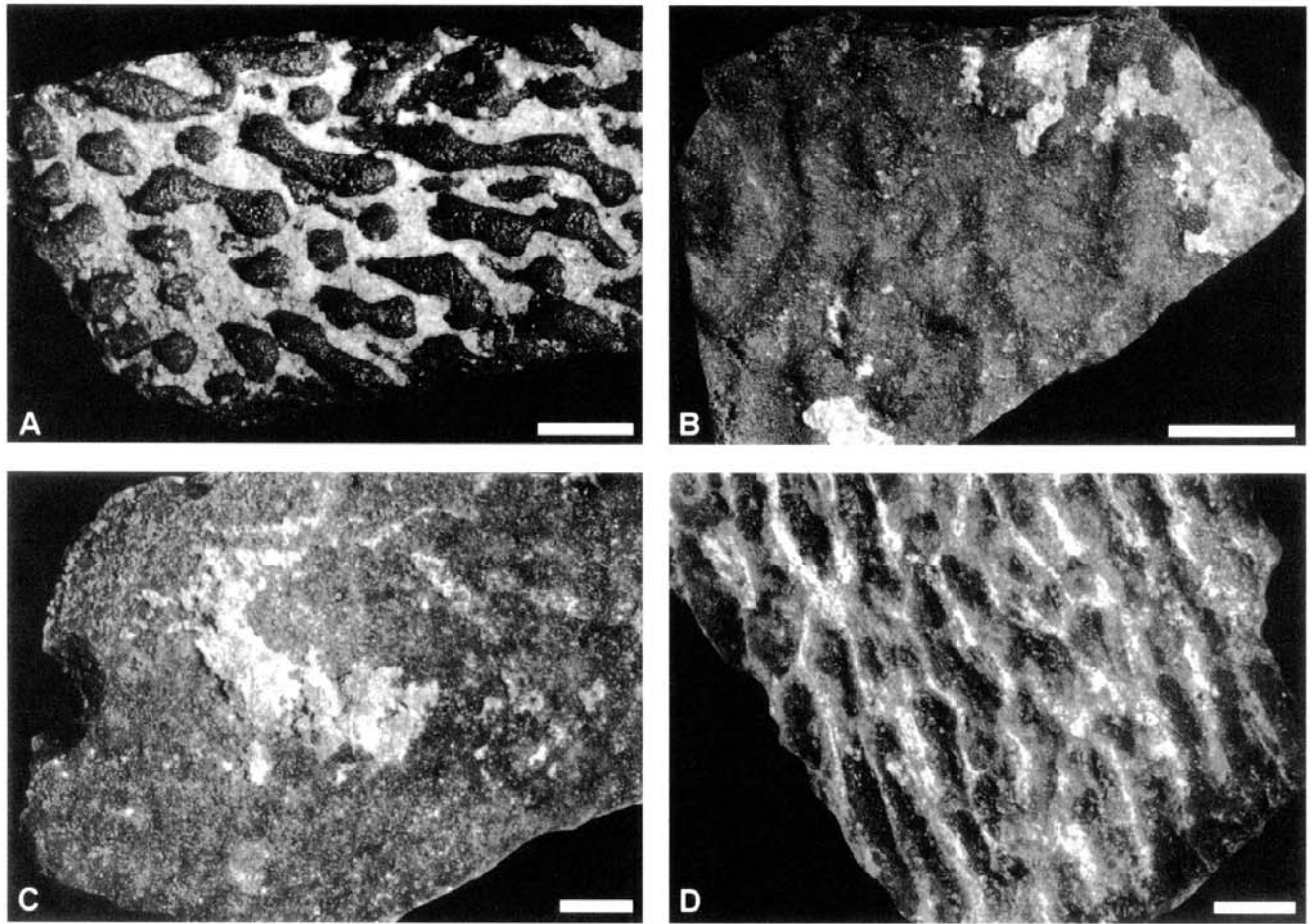


FIGURE 3. Outer surface of *Macroelongatoolithus xixiaensis* showing variation in ornamentation of eggshell fragments. **A**, TMP 98.107.23; ornamentation consisting of bulbous, irregular- to regular-shaped nodes, note similarity to 2D; **B**, TMP 98.107.25; dispersituberculate ornamentation; note similarity to 2A; **C**, TMP 98.107.26; nearly smooth outer surface; **D**, TMP 98.107.24; ornamentation consisting of sinuous ridges; note similarity to 2C. Scale bars equal 2 mm.

phototype. These characteristics are not, however, present in the prolatospherulitic morphotype.

DISCUSSION

Even though dinosaur eggshell fragments have been known from the Lower Cretaceous of North America for 30 years, they were previously unrecognized as belonging to theropods. This is surprising because we observed that theropod eggshell is by far the most common eggshell in the Lower Cretaceous of Utah, based on collections of eggshell fragments from six localities within the Dakota and Cedar Mountain formations. All eggshell fragments from five of these sites, occurring in the Mussentuchit Member (dated near the Albian–Cenomanian boundary; Kirkland et al., 1997) of the Cedar Mountain Formation and the lowermost part of the overlying Dakota Formation (middle to late Cenomanian), are attributable to the ornithoid-ratite morphotype (i.e., to theropods). This eggshell is relatively thick (ca. 2 mm) and can be assigned to a single oospecies. The similarity in ootaxa between the Dakota Formation and the Mussentuchit Member of the Cedar Mountain Formation is not surprising considering the similarities in the dinosaur fauna (Kirkland et al., 1997). All eggshell collected from the remaining locality, in the Yellow Cat Member of the Cedar Mountain Formation, is relatively thin (ca. 1 mm) and is referable to the prolatospherulitic morphotype (i.e., to ornithopods).

Jensen's oospecies, *Oolithes carlylei*, from the Cedar Moun-

tain Castle Dale locality was reassigned by Bray (1998) to her oogenus *Boletuoolithus*. Bray's (1998) oospecific diagnosis reiterates Jensen's original diagnosis, considering only those eggshells with a well-developed outer surface ornamentation that is characterized by undercut nodes and ridges. Although Bray (1998) based her study on materials from the Castle Dale locality and may have examined the holotype, she did not consider the remaining eggshell from the type locality and whether it may have had some bearing on her re-description and taxonomic revision of *Oolithes carlylei*. We agree that *O. carlylei* should be transferred to another oogenus. The nomen *Oolithes* was erected originally by Buckman (1859) for fossil eggs that are now known to be of the testudoid eggshell morphotype (Hirsch, 1996), and thus Buckman's nomen cannot be applied to the Castle Dale eggshell because it is of the ornithoid-ratite morphotype. Our study strongly suggests that the Castle Dale oospecies can be easily accommodated within an existing oogenus and thus need not be assigned to a new nomen.

Re-examination of the holotype and of additional material from the type locality reveals that the the Castle Dale eggshell was erroneously attributed to the prolatospherulitic morphotype (Bray, 1998). Furthermore, we argue that the morphology and variation of this oospecies is almost indistinguishable from that of the large elongatoolithid eggs from China. More importantly, the Castle Dale eggshell, like all elongatoolithids, is characterized by the ornithoid-ratite morphotype and not by the prola-

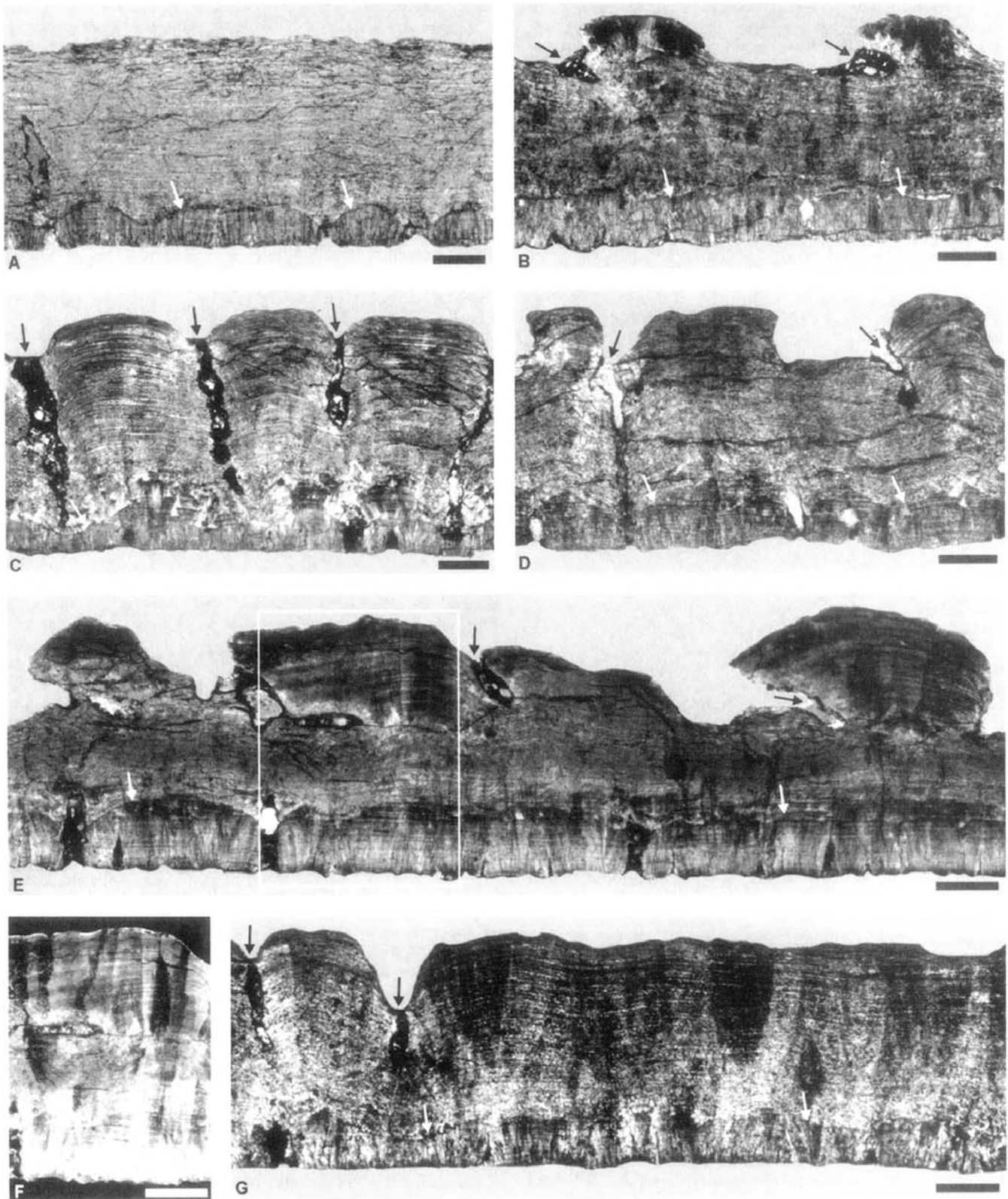


FIGURE 4. Radial thin sections showing variation in elongatoolithid microstructure. Outer surface is up, white arrows denote continuous layer/mammillary layer boundary, and black arrows denote pore canals. Two layers, separated by an undulating boundary, are present: (1) an outer continuous layer above the boundary, and (2) an inner mammillary layer below boundary. **A, C–G.** *Macroelongatoolithus carlylei*. **B.** *Macroelongatoolithus xixiaensis*. **A.** BYU VP13703; typical elongatoolithid microstructure. **B.** TMP 98.107.19; microstructure as in **A**, but with pores undercutting nodes. **C.** TMP 98.107.20; elongatoolithid microstructure appears to have fan-shaped shell units between straight (angusticanaliculate) pore canals, thus mimicking spheroolithid microstructure. Continuous layer/mammillary layer boundary not as clearly defined as in **A**. **D.** TMP 98.107.21; microstructure as in **A**, but with pores undercutting nodes (as in **B**). **E.** BYU-E 200, holotype; elongatoolithid microstructure with outer surface badly degraded: note extreme undercutting of node on right by pore canal, which produced a mushroom-like form **F** (boxed area from **E**), showing columnar extinction pattern typical of ornithoid-ratite eggshell. **G.** TMP 98.107.22; typical elongatoolithid microstructure on right with spheroolithid-like microstructure on left (between black arrows). Scale bars equal 0.5 mm.

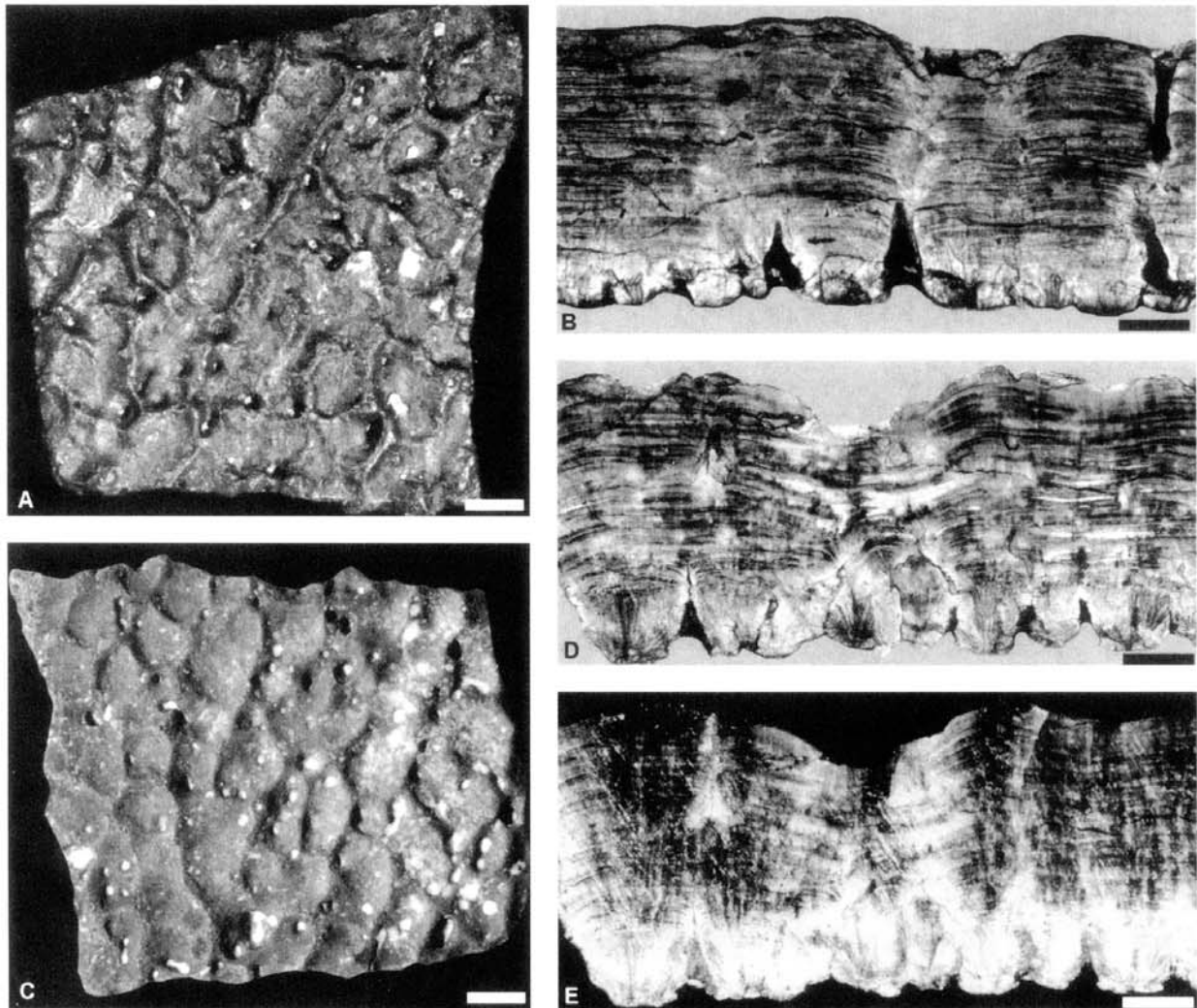


FIGURE 5. Spheroolithid eggshell of prolatospherulitic morphotype. **A, B.** *Spheroolithus albertensis*, Upper Cretaceous Oldman Formation, Alberta. **C–E.** *Spheroolithus* sp., Upper Jurassic Morrison Formation, Utah. **A, C.** outer surface; **B, D, E.** radial thin sections showing spheroolithid microstructure (outer surface is up). **A, C.** TMP 98.107.11; typical sagenotuberculate ornamentation with net-like pattern of ridges; **B.** TMP 98.107.13; typical spheroolithid microstructure with fan-shaped shell units and no distinct mammillary layer. **C.** TMP 98.107.12; **sagenotuberculate ornamentation (as in A); D.** TMP 98.107.14; typical spheroolithid microstructure (as in B); **E.** crossed polars of D, showing sweeping extinction pattern of shell units; compare with columnar extinction pattern in ornithoid-ratite eggshell in 4F. **A, C.** scale bars equal 1 mm. **B–D.** scale bars equal 0.25 mm.

tospherulitic morphotype. Depending on vagaries in ornamentation and porosity, the elongatoolithid microstructure (ornithoid-ratite morphotype) may resemble the spheroolithid microstructure (prolatospherulitic morphotype), although the true microstructure is elucidated in individual fragments in which it changes from distinctly ornithoid-ratite to the aberrant, prolatospherulitic-like variant. The latter variant has only a superficial resemblance to the prolatospherulitic morphotype and the presence of an undulating mammillary layer and a columnar extinction pattern indicates that all eggshell is of the ornithoid-ratite morphotype. Additional variation in the Castle Dale eggshell is revealed in a thickness ranging from approximately 1.4–3.0 mm and an ornamentation that varies from nearly smooth to well-developed. All of the aforementioned characteristics fall well within those described for the elongatoolithid *Macroelongatoolithus xixiaensis* (Fig. 3; Table 1; Li et al., 1995). There are no discrete features that can be used to separate the Castle Dale eggshell from the Asian eggshell that is assigned currently to *M. xixiaensis*. The subtle differences that can be detected, e.g., possible differences in the degree of ornamentation and

porosity, can be attributed to individual variation. Accordingly, the Castle Dale oospecies can be accommodated easily into the oogenus *Macroelongatoolithus* Li, Yin, and Liu 1995 as *Macroelongatoolithus carlylei* Jensen 1970 (new combination and emendation of specific epithet). Consequently, the oogenus *Bolatuoolithus* Bray 1998 can be recognized as a junior subjective synonym of *Macroelongatoolithus* Li, Yin, and Liu 1995.

Interestingly, the realization that the Castle Dale elongatoolithid is conspecific with the Asian ootaxon *Macroelongatoolithus xixiaensis* necessitates a further taxonomic revision. Because Jensen's (1970) oospecies has publication priority over the oospecies described by Li et al. (1995), *M. xixiaensis* Li, Yin, and Liu 1995 must be regarded as a junior synonym of *M. carlylei* Jensen 1970. cursory examination of complete *M. carlylei* eggs from China suggests that those from Utah may have a higher percentage of dispersituberculate ornamentation. If this can be demonstrated convincingly (i.e., if complete eggs from Utah are ever collected), it may be sufficient evidence to resurrect *M. xixiaensis* as a valid oospecies. Furthermore, the close resemblance between the Laurasian *M. carlylei* and the

endemic Asian elongatoolithid *Macrooolithus mutabilis* is striking, so much so that we are unable to differentiate between them beyond the latter's thinner eggshell and minor variations in ornamentation. A major obstacle in elucidating differences among these oospecies is that only eggshell fragments are known of the Mongolian *Macrooolithus mutabilis* and the North American *Macroelongatoolithus carlylei*, whereas complete eggs are known of the Chinese eggs of the later oospecies. Another problem, unfortunately, is the fact that the Chinese eggs have been described only briefly (Li et al., 1995). Our examination of the complete eggs reveals that, like the eggs of *Elongatoolithus*, an individual egg of *Macroelongatoolithus* has an outer surface that varies from smooth to a sculptured pattern of nodes and ridges. Additionally, ornamentation between eggs of a single clutch of *Macroelongatoolithus* can vary: some are covered with a well-developed ornamentation similar to that described herein for *M. carlylei*, whereas others have the more typical elongatoolithid pattern described by Mikhailov (1994). Furthermore, Li et al. (1995) indicate that eggshell thickness within a single egg can range from 2.0–3.2 mm and that the length of eggs within a clutch may vary by several centimeters. This degree of variation is not typical of all oological remains, but is not surprising in *Macroelongatoolithus* eggs considering their enormity. Once the complete eggs and clutches of *M. carlylei* from Xixia are described in further detail, and perhaps if complete eggs of *M. carlylei* from Utah are discovered and described, the variation within each of these oospecies and differences between them may become more apparent.

The morphological and parataxonomic problems outlined here highlight the difficulties in working with fossil eggshell materials. If oospecies have been erected on the basis of variable (i.e., non-discrete) characteristics such as shell thickness and ornamentation (Mikhailov et al., 1996), problems can be expected when dealing with fragmentary materials, especially those that appear to be characterized by extremes of the established variation for such characters. For example, the Castle Dale eggshell assigned now to *Macroelongatoolithus carlylei* includes only fragments of varying size. Not even partial eggs are known. The fragmentary nature of the only known material precludes any attempt to quantify the ornamental and microstructural variation within an egg or clutch, if only for the reason that the eggshell collected represents in all likelihood a mixture of eggshell from more than one egg of a clutch. It is also possible that the fragments represent samples from more than one clutch. We suggest, as in the case of *M. carlylei* outlined here, that specimens of complete eggs or clutches of the same morphotype from other localities can be used for inferring variation in oospecies that are represented by fragmentary materials. Similarly, when morphological and microstructural variants of the same eggshell morphotype occur in the same relative proportions from discrete, coeval localities that are geographically close, we propose that the most appropriate interpretation is that the eggshell fragments are attributable to same oospecies, as we indicated for the Castle Dale eggshell (assigned collectively by us to *M. carlylei*) and for eggshell collections made from two other Lower Cretaceous localities. Our work on *Macroelongatoolithus carlylei* is ample caution that investigators must be more circumspect when studying eggshell of apparently different characteristics when they come from the same deposit. Judicious use of clues from the degree of weathering of the materials and whether ostensibly different types of eggshell discovered at one locality are found in the same proportions from neighboring localities will be important in the rigorous identification of eggshell fragments.

The recognition of an elongatoolithid oospecies from North America has important implications for investigations into the role of Asia in the evolution of Mesozoic North American faunas (e.g., Cifelli et al., 1997; Kirkland et al., 1997; Russell,

1993). *Macroelongatoolithus carlylei* represents the earliest oological evidence of an Asian influence in the theropod component of North American dinosaur faunas during the Cretaceous. Currently, only two associations of embryonic remains with elongatoolithid eggs are known. Both of these taxa are from Asia and can be assigned to oviraptorosaurs or oviraptorosaur-like theropods (Norell et al., 1994; Zelenitsky, unpublished). The occurrence of an elongatoolithid oospecies in the Lower Cretaceous Cedar Mountain Formation of Utah is particularly interesting because it is suggestive of the presence of oviraptorosaurs in Early Cretaceous North America. This has been demonstrated recently by the reinterpretation that *Microvenator celer*, from the Lower Cretaceous Cloverly Formation of Montana, is an oviraptorosaur or oviraptorosaur-like theropod (Makovicky and Sues, 1998). The type and only known skeleton of *M. celer* is small and juvenile, and the adult size is unknown. Based on eggshell thickness and curvature, the *M. carlylei* eggs from Utah were probably similar in size to those from Xixia, which commonly exceed 380 mm in length. Therefore, judging from the size of the eggs assigned to *Oviraptor philoceratops* (ca. 170 mm in length), it is likely that *M. carlylei* belonged to a relatively large theropod. Currently, oviraptorosaurs are unknown from the Cedar Mountain, Dakota, and Kelvin formations; however, the eggshell material described in this paper suggests their presence within these formations.

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