FOSSIL EGGS AND PERINATAL REMAINS FROM THE UPPER CRETACEOUS TWO MEDICINE FORMATION OF MONTANA: DESCRIPTION AND IMPLICATIONS

by

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of the requirements for the degree

of

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in

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ABSTRACT

Egg Mountain is a dinosaur nesting site located in the Upper Cretaceous, Two Medicine Formation of western Montana. The site was located on a coastal plain with seasonal variations in rainfall and was utilized as a nesting location by several taxa. Egg Mountain hosts a remarkable diversity of fossil eggshell and is a window into the reproductive behavior of multiple extinct taxa. A recent 4x6 m excavation revealed two clusters of unidentified eggs, 185 *Spheroolithus* eggshell fragments, and perinatal osteological remains within homogenous siliciclastic mudstone. Insect burrows (*Celliforma*) and cocoons (*Rebuffoichnus*) were excavated from the micritic limestone bed capping the excavation. The objectives of this thesis are to 1) describe the eggs and eggshell fragments, 2) determine nesting environment, 3) assign the osteological remains to taxon, and 4) investigate the taphonomic history of the site. Analytical methods include scanning electron microscopy, cathodoluminescence, petrographic microscopy, and ImageJ photo analysis. The lithologically compressed, unidentified 12 cm diameter eggs occur in two clusters containing 7–22 eggs. Diagenetic alteration obscures eggshell microstructure, inhibiting ootaxonomic assignment of the 0.5 mm thick eggshell. The 0.8–1.3 mm thick fragmentary eggshell is assigned to *Spheroolithus albertensis* based on microstructure, sagenotuberculate ornamentation, and prolatocanaliculate/ rimocanaliculate pores.

To assess taphonomic history of the *Spheroolithus* fragments, chicken (*Gallus gallus domesticus*) and ostrich (*Struthio camelus*) eggshells were placed in a tumbler with water and quartz sand to simulate transport. The resulting wear on these fragments was compared to unabraded eggshell. In addition, modern eggshell was compared to fossil eggshells from a fossil nesting site, crevasse splay and channel deposits, and Egg Mountain. *Spheroolithus* eggshell from Egg Mountain lack edge rounding and resemble fossil eggshell from a nesting site and unabraded modern eggshell, suggesting a parautochthonous assemblage. *Spheroolithus* and unidentified eggs from cluster 1 respectively have gas conductance values 16–32x and 4–13x higher than avian eggs of the same mass, suggesting enclosed nest environments. The morphology of the humerus and skull elements of the perinatal osteological remains is consistent with the Hadrosauridae, though the juvenile status and incomplete nature of the specimen inhibits further taxonomic assignment.

INTRODUCTION

The study of fossilized dinosaur eggs and nesting sites provides a unique window into the reproductive biology and nesting behavior of extinct taxa. For example, after a detailed taphonomic assessment, nesting behavior can sometimes be inferred from the arrangement of the eggs (Cousin, 1994; Varricchio et al., 1997; Vila et al., 2010), the physical characteristics of the eggshell such as porosity (Seymour, 1979; Sabath, 1991; Deeming, 2006; Jackson et al., 2008; Grellet-Tinner et al., 2012), and sedimentological features surrounding the eggs (Varricchio et al., 1999; Chiappe et al., 2004). Exposures of the Upper Cretaceous (Campanian) Two Medicine Formation near the Willow Creek anticline (WCA) in western Montana reveal a number of dinosaur nesting sites (Horner and Makela, 1979; Hirsch and Quinn, 1990). The material recently excavated from the Egg Mountain (TM 006) locality is the subject of this study.

Geologic and Paleoenvironmental Context

The Upper Cretaceous Two Medicine Formation is exposed in western Montana, USA. During the Late Cretaceous, numerous third order trangressive-regressive cycles of the Western Interior Cretaceous Seaway (WICS) and substantial tectonic activity associated with the Sevier Orogeny influenced depositional environments in North America (McGookey, 1972; Gill and Cobban, 1973; Kauffman, 1977; Varricchio, 1993; Rogers, 1998; Jackson and Varricchio, 2010). Terrestrial sediments derived from uplift and erosion of the Cordillera to the west of Egg Mountain were deposited in an eastward-thinning clastic wedge. Crustal loading within the overthrust belt resulted in flexural

subsidence, forming a foredeep basin where fluvial systems deposited sediment (Lorenz, 1981). The north-south trending Sweetgrass arch (SGA) truncates this clastic wedge, splitting the Two Medicine Formation in the west from the correlative Judith River Formation to the east (Rogers, 1998). The Judith River Formation is bounded by the marine Claggett and Bearpaw shales, deposited during transgressions of the WICS. The Two Medicine Formation is up to 600 meters thick and overlies the shoreface deposits of the Virgelle Sandstone (Lorenz and Gavin, 1984). The Two Medicine and Judith River formations are stratigraphically equivalent to the Dinosaur Park, Oldman, and Foremost formations in southern Alberta, Canada (Eberth, 1990; Rogers et al., 1993; Jackson and Varricchio 2010).

Bentonite horizons are common in the Two Medicine Formation, derived from contemporaneous igneous activity associated with the Elkhorn Mountains volcanic center to the south (Lorenz and Gavin, 1984; Rogers, 1998; Trexler, 2001). Radiometric dates range from 80 Ma approximately 100 m above the base of the formation south of Choteau, MT to 74 Ma 10 m below the top of the formation near Shelby, MT (Rogers et al., 1993). A bentonite horizon 16.5 m below the stratigraphic level of Egg Mountain yields a radiometric date of 75.9 Ma (Varricchio et al., 2010). Egg Mountain lies approximately 400–450 m above the Two Medicine-Virgelle contact within the lake subfacies of Lorenz and Gavin's lithofacies d, with nearby nesting sites occurring in the fluvial deposits of the lower subfacies (Lorenz, 1981; Horner, 1984; Lorenz and Gavin, 1984). Horner (1987, 1988) interpreted Egg Mountain as a lacustrine environment, where dinosaurs laid their eggs on islands within an ephemeral alkaline lake. Shelton (2007)

conducted a detailed stratigraphic analysis in the area around Egg Mountain and although she did not identify lacustrine carbonates at the quarry location, she reported lacustrine carbonates stratigraphically lower than the quarry interval at sites adjacent to Egg Mountain.

The paleolatitude of Montana during the Campanian was approximately 48° N, near its current position (Golonka et al., 1994). Climate models and floral data suggest that the North American western interior had an average temperature of 16° C, with an annual temperature range of only 8° C due to the buffering effect of the WICS (Hays and Pitman, 1973; Valdes et al., 1996; Wolfe and Upchurch, 1987). The Two Medicine-Judith River clastic wedge was deposited on a coastal plain between the ancestral Rockies to the west and the WICS to the east. Fluctuations in sea level drastically affected terrestrial habitats on the coastal plain, which was approximately 500 km wide during the maximum regression of the Claggett Sea and only 150 km wide during the maximum transgression (Horner, 1984b; Horner and Weishampel and Horner, 1987; Varricchio, 1993). The Two Medicine Formation was deposited during the Judith River regressive phase of the WICS (Lorenz and Gavin, 1984), with Egg Mountain situated on the upper coastal plain. Seasonal variation in rainfall is inferred for the region based on drought-induced bonebeds (Rogers, 1990; Varricchio and Horner, 1993; Varricchio, 1995), irregular cessations in growth rings of fossil conifers (Falcon-Lang, 2003), *Celliforma* ichnoassemblages (Genise et al., 2010; Martin and Varricchio, 2010), charcoal deposits indicative of fires (Carpenter, 1987), broad-leafed coriaceous

evergreens lacking drip tips (Crabtree, 1987), and abundant caliche deposits (Lorenz and Gavin, 1984; Varricchio, 1993).

Egg Mountain

Previous excavations at Egg Mountain revealed clutches of elongate, asymmetrical eggs (Horner, 1984, 1987; Hirsch and Quinn, 1990). One clutch containing 24 eggs was preserved within a bowl-shaped nest structure (Varricchio et al., 1997, 1999). These eggs were assigned to the oospecies *Prismatoolithus levis* (Varricchio et al., 2002) based on their similarity to eggs from the Upper Cretaceous Oldman Formation in Alberta, Canada (Zelenitsky and Hills, 1996). Although initially identified as *Orodromeus makelai* eggs (Horner and Weishampel, 1988), subsequent examination of embryonic material from eggs of the same oospecies elsewhere in the WCA revealed that they belonged to the theropod *Troodon formosus* (Horner and Weishampel, 1996; Varricchio et al., 2002). In addition, Hirsch and Quinn (1990) describe a small, isolated avian-like egg from Egg Mountain but did not assign the specimen to an ootaxon. Additional eggs described from the site include elongate and slightly asymmetrical unidentified theropod eggs (Horner 1984, 1987, 1997; Hirsch and Quinn, 1990). Similar eggs from the Upper Cretaceous Oldman Formation in Alberta, Canada were assigned as *Continuoolithus canadensis* by Zelentisky et al. (1996). Varricchio et al. (2002) referred the WCA eggs to this oospecies. Schaff (2012) investigated the incubation environment of *C. canadensis* eggs from Egg Mountain and the nearby Flaming Cliffs (TM 160) locality. Examination of gas conductance and nest structure suggest that these eggs were

buried and incubated in either sediment or vegetation (Schaff, 2012). Osteological remains previously documented at Egg Mountain include *Orodromeus makelai*, *Troodon formosus*, varanid and teiid lizards, multituberculate and marsupial mammals, as well as tyrannosaurid teeth and fragmentary remains of hadrosaurs and tyrannosaurs (Horner, 1984, 1987; Varricchio et al., 1999).

In 2011 and 2012, excavation of a new quarry on the south side of the Egg Mountain locality revealed two clusters of unidentified eggs within a 70 cm-thick interval of homogenous mudstone containing hadrosaur perinatal remains and 185 *Spheroolithus* eggshell fragments. Previous studies use ratios of concave-up to concave-down eggshell fragments to assess transport history (Kennedy and Spencer 1995; Hayward et al. 1997; Owen and Hayward 1997; Hayward et al. 2000; Hayward et al. 2011; Imai 2012); however, because the eggshell fragments do not occur on discrete horizons and have varying abundance and orientation ratios throughout the section at Egg Mountain, existing taphonomic techniques cannot be applied. *Spheroolithus* eggshell associated with *Maiasaura peeblesorum* perinatal remains has been described from nearby localities at the WCA; however, they are previously unreported from Egg Mountain (Horner and Makela, 1979; Horner, 1982, 1984; Hirsch and Quinn, 1990; Horner 1999). This study 1) describes the eggs in the clusters, *Spheroolithus* eggshell fragments, and perinatal bones; 2) interprets the nesting environment of the site using gas conductance and ichnofacies association; and 3) investigates the taphonomic history of the site using the condition of the bones and the abrasion state of the *Spheroolithus* fragments.

CHAPTER TWO

FOSSIL EGGS, EGGSHELL, AND PERINATAL OSTEOLOGICAL REMAINS FROM THE UPPER CRETACEOUS TWO MEDICINE FORMATION OF WESTERN MONTANA

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2 and 3

Author: Sara E. Oser

Contributions: Collected the majority of fossil materials, obtained funding, collected and analyzed data, wrote manuscript.

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FOSSIL EGGS, EGGSHELL, AND PERINATAL OSTEOLOGICAL REMAINS FROM THE UPPER CRETACEOUS TWO MEDICINE FORMATION OF WESTERN MONTANA

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RRH: EGGS AND EGGSHELL AT EGG MOUNTAIN

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ABSTRACT

Egg Mountain (TM 006) is one of several dinosaur nesting sites at the Willow Creek anticline in the Upper Cretaceous (Campanian) Two Medicine Formation of Montana. A recent 4x6 m excavation revealed two unidentified egg clusters, perinatal osteological remains, *Spheroolithus* eggshell, and trace fossils within siliciclastic mudstone. Ichnotaxa present at the site include insect cocoons (*Rebuffoichnus*) and burrows (*Celliforma* ichnofacies), indicative of a well-drained soil that developed on a distal paleo-floodplain. The two unidentified egg clusters respectively contain approximately 6–7 and 22 spherical eggs that are up to 12 cm in diameter and are distributed over 1 m^2 and 2.5 m^2 areas. Diagenetic alteration obscures the microstructure of the 0.3–0.5 mm-thick eggshell in both clusters,

prohibiting ootaxonomical assignment. Calculated gas conductance values of the eggs in cluster 1 and the *Spheroolithus* eggshells are, respectively, 4–13 and 16–32 times higher than avian eggs of similar mass, suggesting enclosed nest environments. Osteological remains occur within and immediately below egg cluster 1. The morphology of the humerus and skull elements, their small size, and lack of fusion between the dorsal centra and neural arches allows assignment to a perinate within Hadrosauridae. However, the juvenile status and incomplete nature of the specimens inhibit further taxonomic assignment. Close association of several elements, as well as minimal surface modification, suggests little or no transport or subaerial exposure prior to burial. Although hadrosaurid remains (eggshell, eggs, clutches, neonatal elements) are known from other sites at the Willow Creek anticline, the fossils described here represent the first hadrosaurid perinatal remains and *Spheroolithus* eggshell documented from the Egg Mountain locality.

INTRODUCTION

Egg Mountain (TM 006), located in the Upper Cretaceous (Campanian) Two Medicine Formation of western Montana, is one of several dinosaur nesting localities at the Willow Creek anticline (WCA). Over the last 30 years, this site has yielded a substantial amount of fossil material and information about dinosaur reproduction (Horner, 1982, 1984, 1988; Hirsch and Quinn, 1990; Varricchio et al., 1997, 1999, 2002, 2013).

Previous excavations at Egg Mountain revealed clutches of elongate, asymmetrical eggs (Horner, 1984, 1987; Hirsch and Quinn, 1990). One clutch comprised of 24 eggs was preserved within a bowl-shaped nest structure (Varricchio et al., 1997, 1999). These eggs are identified as the oospecies *Prismatoolithus levis* (Varricchio et al., 2002) based on their similarity to eggs from the Upper Cretaceous Oldman Formation in Alberta, Canada (Zelenitsky and Hills, 1996). Although initially identified as *Orodromeus makelai* eggs (Horner and Weishampel, 1988), subsequent examination of embryonic material within eggs of the same oospecies elsewhere in the WCA revealed that they belonged to the theropod *Troodon formosus* (Horner and Weishampel, 1996; Varricchio et al., 2002). In addition, Hirsch and Quinn (1990) describe a small, isolated avian-like egg from Egg Mountain but did not assign the specimen to an ootaxon. Additional eggs from the site include elongate and slightly asymmetrical unidentified theropod eggs (Horner 1984, 1987, 1997; Hirsch and Quinn, 1990). Similar eggs from the Upper Cretaceous Oldman Formation in Alberta, Canada were assigned as *Continuoolithus canadensis* by Zelentisky et al. (1996). Varricchio et al. (2002) referred the WCA eggs to this oospecies. Schaff (2012) investigated the incubation environment

of *C. canadensis* eggs from Egg Mountain and the nearby Flaming Cliffs (TM 160) locality. Examination of gas conductance and nest structure suggest that these eggs were buried and incubated in either sediment or vegetation (Schaff, 2012). Osteological remains previously documented at Egg Mountain include *Orodromeus makelai*, *Troodon formosus*, varanid and teiid lizards, multituberculate and marsupial mammals, as well as tyrannosaurid teeth and fragmentary remains of hadrosaurs and tyrannosaurs (Horner, 1984, 1987; Varricchio et al., 1999).

In contrast to avian and elongate theropod eggs previously reported from Egg Mountain, excavation in 2011 at a stratigraphic level 2.41 m below the main quarry revealed two clusters of spherical eggs associated with 185 *Spheroolithus* eggshell fragments and several perinatal hadrosaur bones. Whereas *Spheroolithus* eggs associated with hadrosaur hatchling bones are described from other sites at the WCA (Horner and Makela, 1979; Horner, 1982, 1984b; Hirsch and Quinn, 1990), this represents the first documentation of these fossils at the Egg Mountain locality. The objectives of this study are to (1) describe the perinatal bones, (2) describe the egg clusters, (3) investigate the taphonomic history of the site, and (4) calculate water vapor conductance in order to interpret the nesting environment.

Geologic Context

The Upper Cretaceous Two Medicine Formation is exposed in western Montana, USA (Fig. 1). During the Late Cretaceous, numerous third order trangressive-regressive cycles of the Western Interior Cretaceous Seaway (WICS) and substantial tectonic activity associated with the Sevier Orogeny influenced depositional environments in North America (McGookey, 1972; Gill and Cobban, 1973; Kauffman, 1977; Rogers, 1998). Terrestrial sediments derived from uplift and erosion of the Cordillera to the west were deposited in an eastward-thinning clastic wedge (Fig 1B). Crustal loading within the overthrust belt resulted in flexural subsidence, forming a foredeep basin where fluvial systems deposited sediment (Lorenz, 1981). The north-south trending Sweetgrass arch (SGA) truncates this clastic wedge, splitting the Two Medicine Formation in the west from the correlative Judith River Formation to the east (Rogers, 1998). The Judith River Formation is bounded by the marine Claggett and Bearpaw shales, deposited during transgressions of the WICS. The Two Medicine Formation is up to 600 m thick and overlies the shoreface deposits of the Virgelle Sandstone (Lorenz and Gavin, 1984). The Two Medicine and Judith River formations are stratigraphically equivalent to the Dinosaur Park, Oldman, and Foremost formations in southern Alberta, Canada (Eberth, 1990; Rogers et al., 1993; Jackson and Varricchio, 2010).

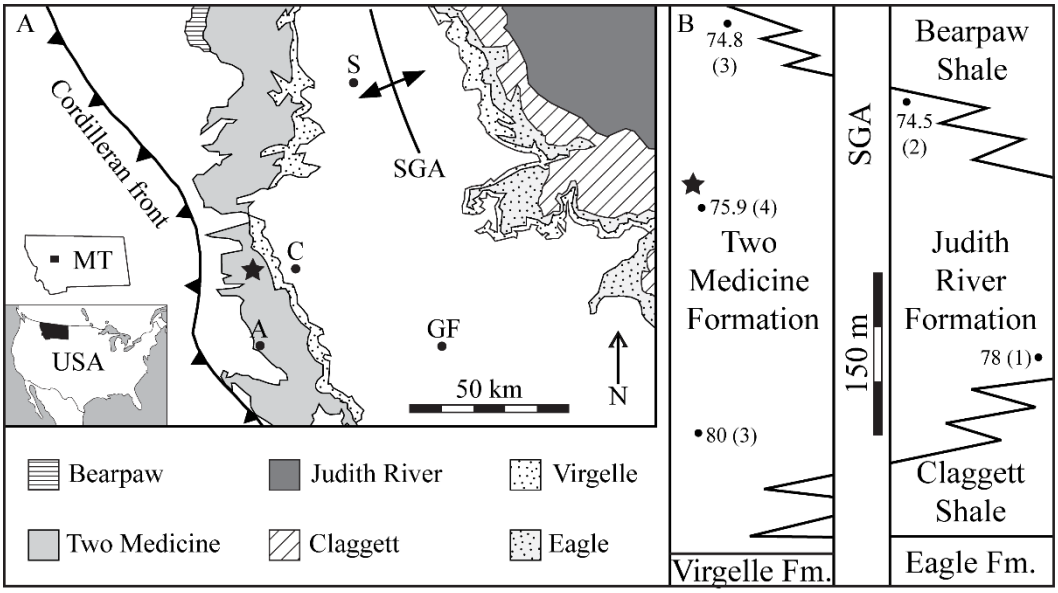

FIGURE 1— Upper Cretaceous outcrops near the field area. A) Map displaying the extent of the Two Medicine Formation and adjacent units (after Rogers, 1998). Abbreviations: Augusta (A), Choteau (C), Great Falls (GF), Shelby (S), Sweetgrass arch (SGA). B) Cross section of strata near the field area, showing formations deposited during several transgressions and regressions of the Western Interior Cretaceous Seaway (after Jackson and Varricchio, 2010) as well as radiometric dates. References in B are (1) Goodwin and Deino, 1989; (2) Eberth et al., 1992; (3) Rogers et al., 1993; (4) Varricchio et al., 2010.

Bentonite horizons are common in the Two Medicine Formation, derived from contemporaneous igneous activity associated with the Elkhorn Mountains volcanic center to the south (Lorenz and Gavin, 1984; Rogers, 1998; Trexler, 2001). Radiometric dates range from 80 Ma approximately 100 m above the base of the formation south of Choteau, MT to 74 Ma 10 m below the top of the formation near Shelby, MT (Rogers et al., 1993). Egg Mountain lies approximately 400–450 m above the Two Medicine-Virgelle contact within the lake subfacies of Lorenz and Gavin's lithofacies d, with nearby nesting sites occurring in the fluvial deposits of the lower subfacies (Lorenz, 1981; Horner, 1984; Lorenz and Gavin, 1984). A bentonite horizon 16.5 m below the

stratigraphic level of Egg Mountain yields a radiometric date of 75.9 Ma (Varricchio et al., 2010). Horner (1987, 1988) interpreted Egg Mountain as a lacustrine environment, where dinosaurs laid their eggs on islands within an ephemeral alkaline lake. Shelton (2007) conducted a detailed stratigraphic analysis at the WCA and although she did not identify lacustrine carbonates at Egg Mountain, she reported lacustrine carbonates stratigraphically lower than the quarry interval at sites adjacent to Egg Mountain.

Paleoenvironment

The paleolatitude of Montana during the Campanian was approximately 48° N, near its current position (Golonka et al., 1994). Climate models and floral data suggest that the North American western interior (proximately present-day Montana and Alberta) had an average temperature of 16° C, with an annual average temperature range of only 8° C due to the buffering effect of the WICS (Hays and Pitman, 1973; Wolfe and Upchurch, 1987; Valdes et al., 1996). The Two Medicine-Judith River clastic wedge was deposited on a coastal plain between the ancestral Rockies to the west and the WICS to the east. Fluctuations in sea level drastically affected terrestrial habitats on the coastal plain, which was approximately 500 km wide during the maximum regression of the Claggett Sea and only 150 km wide during the maximum transgression (Horner, 1984b; Weishampel and Horner, 1987; Varricchio, 1993). The Two Medicine Formation was deposited during the Judith River regressive phase of the WICS (Lorenz and Gavin, 1984), with Egg Mountain situated on the upper coastal plain. Seasonal variation in

rainfall is inferred for the region based on drought-induced bonebeds (Rogers, 1990; Varricchio and Horner, 1993; Varricchio, 1995), irregular cessations in growth rings of fossil conifers (Falcon-Lang, 2003), *Celliforma* ichnoassemblages (Genise et al., 2010; Martin and Varricchio, 2010), charcoal deposits indicative of fires (Carpenter, 1987), and abundant caliche deposits (Lorenz and Gavin, 1984; Varricchio, 1993).

MATERIALS AND METHODS

Field

The Egg Mountain (TM 006) locality west of Choteau, MT is owned by the Museum of the Rockies, Inc. The excavation described here began in 2010 on the south side of the site at a stratigraphically lower level than the main quarry. Because of outcrop interference with direct line-of-site to the original quarry, a second datum was established 30 m due south and 2.4 m below the primary datum. A grid comprised of 1 m^2 increments was constructed over the site and the surface material within each square meter was screened prior to excavation. Each *in situ* element within the quarry was mapped on graph paper and depths were recorded using a Sokkia C3-30 autolevel and stadia rod, providing three-dimensional Cartesian coordinates for each element. These coordinates were used to generate a three-dimensional map of the quarry using the MATLAB program described in Storrs et al. (2013). Trend and plunge were measured for

elongate elements using a Brunton compass. The concave-up or concave-down orientation of eggshells was also noted. Table 1 lists fossil material removed from the site and discussed in this study.

Specimen number	Element	Location
MOR 6631-1	Hadrosaurid right dentary	below cluster 1
MOR 6631-2	Hadrosaurid left dentary	below cluster 1
MOR 6631-3	Hadrosurid left premaxilla	below cluster 1
MOR 6631-4	Hadrosaurid right exoccipital/paroccipital	below cluster 1
MOR 7038	Hadrosaurid right humerus	float
MOR 7039	Hadrosaurid dorsal vertebrae and ribs	float
MOR 6629-3	Hadrosaurid fibula	in cluster 1
MOR 6629-2	Hadrosaurid metatarsal	in cluster 1
MOR 7034	Hadrosaurid sacral rib	below cluster 1
MOR 7035-1	Tyrannosaurid tooth	above cluster 2
MOR 7035-2	Tyrannosaurid tooth	above cluster 2
MOR 6628-3	Tyrannosaurid tooth	below cluster 1
MOR 7033	Tetrapod (?lizard) vertebrae and ribs	below cluster 1
MOR 6628/6629	Unidentified eggs	cluster 1
MOR 6630	Unidentified eggs	cluster 1
MOR 6629-5	*Spheroolithus* fragment	in cluster 1
MOR 7036-1	*Spheroolithus* fragment	below cluster 1
ES 228	*Spheroolithus* fragment	float
ES 228-1	Unidentified eggshell	cluster 2
ES 402	*Spheroolithus* fragment	in cluster 1
ES 404	*Spheroolithus* fragment	in cluster 1
ES 405	*Spheroolithus* fragment	in cluster 1
ES 410	Unidentified eggshell	cluster 1
ES 419	Unidentified eggshell	cluster 1
ES 420	Unidentified eggshell	cluster 1
ES 429	Unidentified eggshell	cluster 1
ES 430	Unidentified eggshell	cluster 1
ES 441	*Spheroolithus* fragment	below cluster 1
ES 442	Unidentified eggshell	cluster 1

TABLE 1— Osteological remains, eggs, and eggshell described in this study.

In addition, a stratigraphic section was measured and described from a vertical trench dug through the excavation site. Oriented samples were collected at 10 cm intervals through the quarry and from the limestone capping the excavation. Additional non-oriented specimens collected include matrix and mineral samples from the egg-bearing strata.

Laboratory

Matrix and mineral samples collected from the egg-bearing strata were crushed using a porcelain mortar and pestle and then sifted through a 63 μm standard testing sieve. The mineral associated with cluster 2 (Unidentified ootaxon; MOR 6630) was placed in an unoriented powder mount and analyzed using a SCINTAG X1 powder diffraction spectrometer. The mineral thin sections were analyzed using energy-dispersive X-ray spectroscopy (EDX). Mudstone samples were prepared according to the United States Geological Survey (USGS) filter-peel method and analyzed using X-ray diffraction (XRD) spectroscopy.

Laboratory preparation of the fossil material included removal of sediment from each element using small hand tools and stabilization with a thin solution of polyvinyl acetate. Each element recovered during preparation of the jackets was mapped and orientations (concave-up or concave-down) were noted for all eggshell fragments. The mapped elements from each jacket were then added to the quarry map.

Ten tangential thin sections were prepared from eggshell fragments collected from three eggs in cluster 1 (Unidentified ootaxon; MOR 6628/6629) and from two isolated *Spheroolithus* eggshell fragments in cluster 1. In addition, two *Spheroolithus* eggshell fragments and two unidentified eggshell fragments were collected from cluster 1. Each of these eggshell fragments were broken into two pieces: one half was prepared as a 30 micron-thick radial thin section, the other half was coated with gold using a Desk II Dentron vacuum sputter coater at 45 mA for 30 seconds. The small size prohibited breaking some samples in half and therefore separate fragments from the same egg were prepared for SEM imaging and radial thin sectioning. The specimens were imaged at 15–20 kV under an Aspex Personal scanning electron microscope (SEM) in the Gabriel Laboratory for Molecular and Cellular Biology at the Museum of the Rockies (MOR). Further, an additional 15 *Spheroolithus* eggshell fragments and 24 unidentified eggshell fragments (seventeen from cluster 2 and five from cluster 1) were prepared as 30 micron-thick radial thin sections. All thin sections were examined under a Nikon Eclipse LV100POL petrographic microscope and photographed using an attached Nikon Digital Sight DS-5Mc digital camera. Multiple overlapping images of each tangential thin section were merged using Adobe Photoshop and analyzed using ImageJ analysis software to determine pore area per square cm.

The lithologically compressed unidentified fossil eggs from cluster 1 were separated into two regions: the pole (region 1) and equator (region 2) in order to evaluate potential differences in gas conductance (G_{H2O}) across the egg, as in studies of extant eggs (Booth and Seymour, 1987; Rokitka and Rahn, 1987). The area of the pole was

defined as the region from the center of the egg out to half the radius (r = 0–0.5) and the equator was defined as the region from half the radius out to the edge (r = 0.5–1). Samples were removed from each region in a manner that minimized damage to the eggs. This resulted one sample from region 1 and two samples from region 2 in egg A (MOR 6629-6), three samples from region 1 and one sample from region 2 in egg B (MOR 6629-7), and one sample from region 1 in partial egg C.

Gas conductance was calculated using the equation from Seymour (1979); however, a temperature of 25°C and the associated diffusion coefficient value of 0.25 $cm^2 \cdot s^{-1}$ is used to facilitate comparison of the results with previous studies (Equation 1; Table 2).

$$G_{H2O} = \frac{C}{RT} \cdot D_{H2O} \cdot \frac{A_p}{L} \quad (1)$$

Term	Definition	Value/Units
G_{H2O}	water vapor conductance	mg $H_20 \cdot day^{-1} \cdot Torr^{-1}$
C	conversion factor	1.5569 x 10^9 $sec \cdot mg \cdot day^{-1} \cdot mol^{-1}$
R	universal gas constant	6.236 x 10^4 $cm^3 \cdot Torr \cdot mol^{-1} \cdot K^{-1}$
T	absolute temperature	298.15 K
D_{H2O}	diffusion coefficient of water in air	0.25 $cm^2 \cdot s^{-1}$
A_p	total pore area of the egg	cm^2
L	pore length (=L_S)	Cm

TABLE 2— Variables and constants used in Equation 1 (Seymour, 1979; Paganelli, 1980).

Calculating G_{H2O} requires measurement of egg radius (r), eggshell thickness (Ls), and pore area (Ap). Lithostatic compaction exhibited by both clusters prohibits direct measurement of egg radius. Dimensions for the unidentified eggs were inferred based on measurement of the egg circumference (c′) in cross section using a flexible tape measure.

Assuming that the eggs were initially spherical (based on the circular dimensions of the compacted eggs) the radius (r) was determined according to Equation 2.

$$r = \frac{c'}{2\pi} \tag{2}$$

Although the site included only fragmentary *Spheroolithus* eggshell, intact *Spheroolithus* eggs occur at other localities at the WCA providing an approximate radius measurement of 6 cm (Horner, 1999). Eggshell thickness, measured from radial thin sections, was used as a proxy for pore length (L_S = L) for all eggshells. For the unidentified eggshell, pores were assumed to be cylindrical in shape. Because the variation in pore diameters can be estimated for *Spheroolithus* by measuring their cross section in radial thin sections, pore geometry can be accounted for in G_{H2O} calculations by introducing the diameter variation as a source of error. Measurement error was propagated using Equation 3, which is derived in Appendix A (Taylor, 1997). See Tables 2 and 3 for the list of terms.

$$u\{G_{H2O}\} = G_{H2O} \times \sqrt{\left(\sqrt{\left(\frac{\sqrt{\left(\left(\frac{\left(\pi\frac{d_{max}}{2}^2 - \pi\frac{d_{min}}{2}^2\right)}{2}\right)^2 \times N\right) + \left(m_p{}^2 \times N\right)}}{A_{P1}}\right)^2 + \left(\frac{\frac{SA}{SA_1} \times \sqrt{\left(\frac{u(SA)}{SA}\right)^2 + \left(\frac{u(SA_1)}{SA_1}\right)^2}}{SA_1}\right)^2}\right)^2 + \left(\frac{\sqrt{\left(\frac{L_{Smax} - L_{Smin}}{2}\right)^2 + L_{SM}{}^2}}{L_S}\right)^2} \tag{3}$$

Term	Definition	Units
$u\{\text{term}\}$	uncertainty of the term	
N	number of pores measured	
D	diameter of single pore	cm
m_p	measurement error for the area of a pore	cm^2
SA_1	surface area of the measured fragment	cm^2
SA	surface area of the egg	cm^2
A_{P1}	pore area of the measured fragment	cm^2
L_S	eggshell thickness	cm
L_{SM}	measurement error of eggshell thickness	cm

TABLE 3— Variables used in Equation 3.

Gas conductance values were then plotted against a regression line describing the relationship between egg mass (m) and G_{H2O} using the equation calculated from Ar and Rahn's (1985) open-nest avian data (Equation 4; Appendix B).

$$G_{H2O} = 0.3736m^{0.8084} \quad (4)$$

RESULTS

Mapping each *in situ* element allows for two-dimensional and three-dimensional reconstructions of the quarry (Fig. 2). This revealed the relative positions of the pupa cases, burrows, perinatal hadrosaur bones, *Spheroolithus* eggshell fragments, and other osteological remains to the two clusters of unidentified eggs.

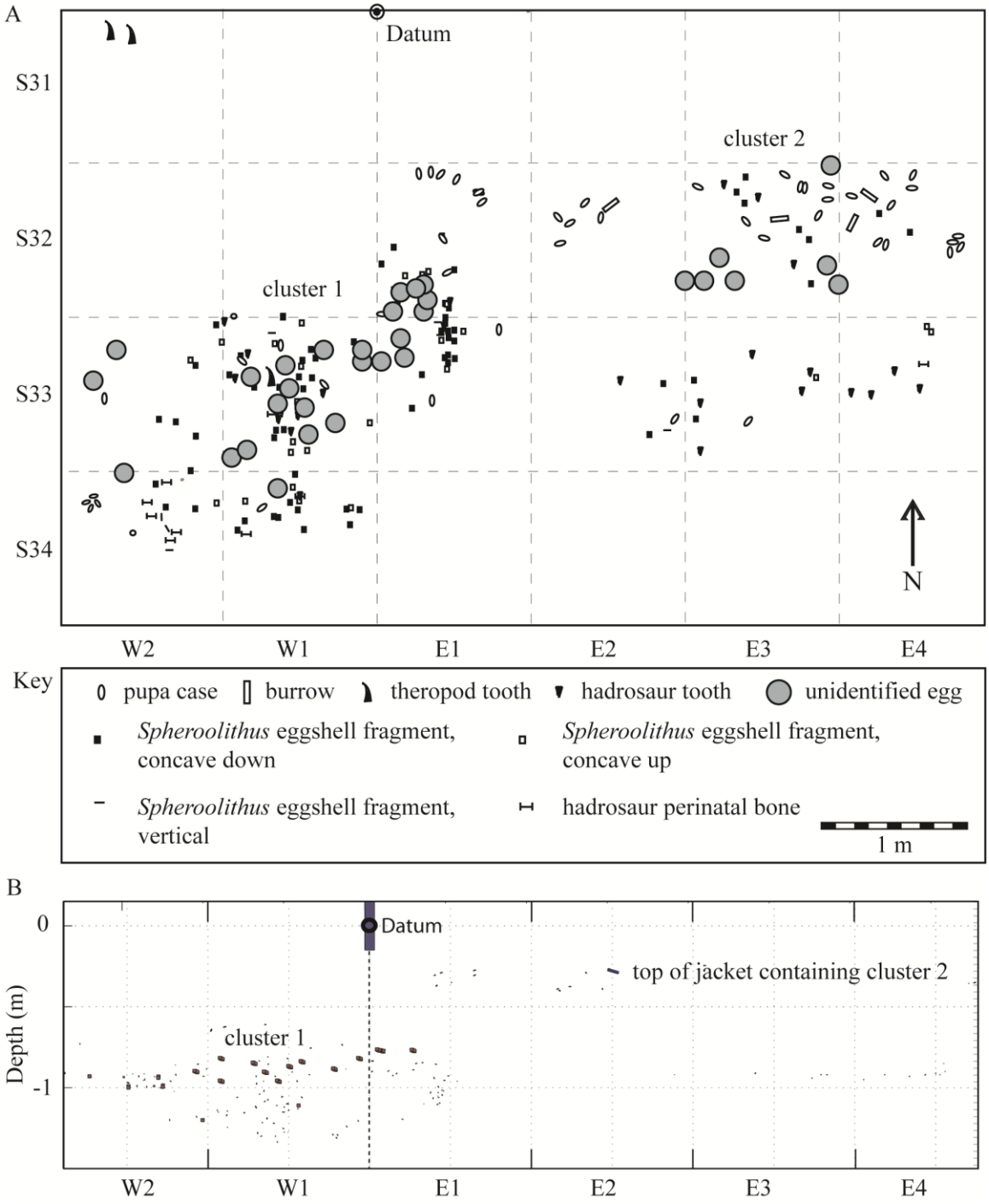

FIGURE 2—Quarry maps from the 2011–2012 field seasons. A) Quarry map in plan view. North arrow designates magnetic north. B) Three-dimensional map showing the view looking north through the quarry. Large dots represent eggs, small dots represent all other fossil material.

Stratigraphy and Lithology

The 130 cm-thick interval containing the fossil material consists of 110 cm of blocky, slightly calcareous grey mudstone capped by 20 cm of grey micritic limestone (Fig. 3). Here, the term ‘mudstone’ refers to siliciclastic mudrock whereas the term ‘micrite’ refers to fine grained limestone (Folk, 1959). Color designations are based on Munsell (1994) color index.

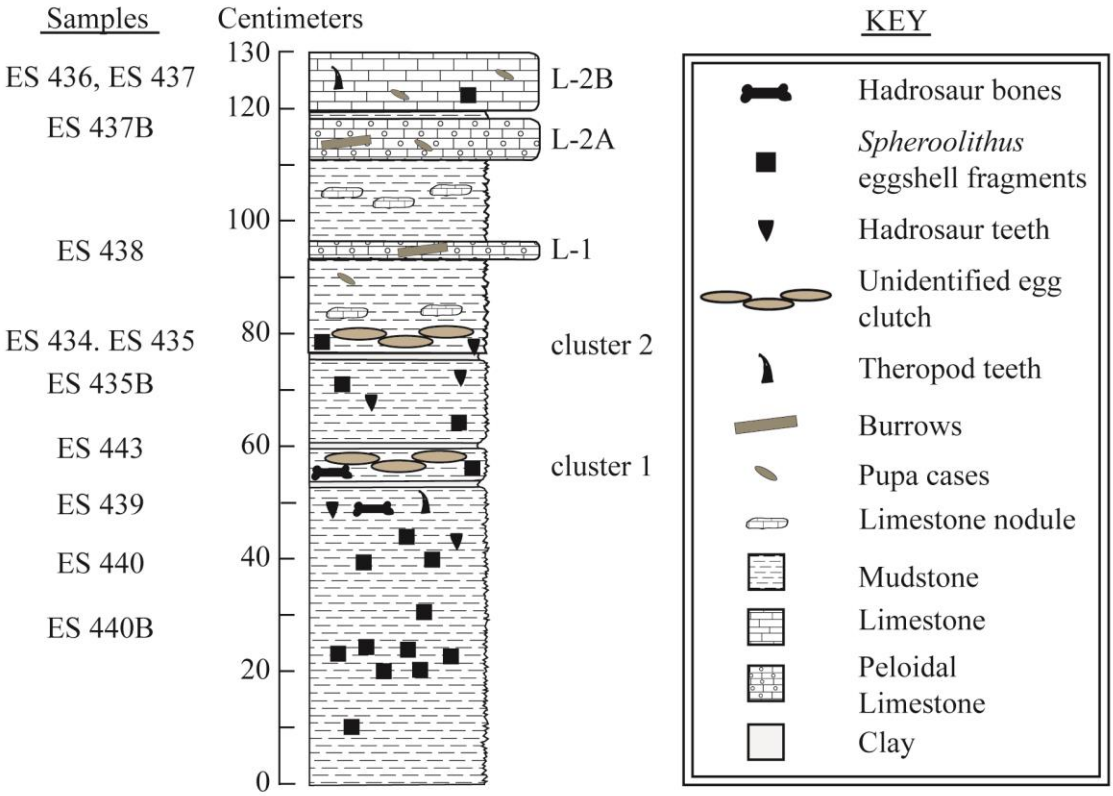

FIGURE 3—Stratigraphic section through the 2011–2012 quarry at Egg Mountain, showing fossil material and location of samples used in analyses. Horizontal axis represents weathering profile.

Mudstone.—The blocky, non-fissile mudstone within the quarry is medium-grey (6/5G) on both fresh and weathered surfaces. Exposure to hydrochloric acid results in mild effervescence, suggesting the presence of a small amount of carbonate cement. When viewed in thin section, the silt content in the mudstone surrounding the two clusters (Fig. 4D, G) is low compared to that between clusters (Fig. 4C, E). The former also exhibits moderate red-brown mottling in thin section, which is absent in the latter. Small (0.32 mm diameter), reddish rhizohalos are present in thin sections of mudstone surrounding cluster 2 (Fig. 4F, H). X-ray diffraction analyses of samples removed from cluster 1 indicate the presence of quartz and plagioclase (Fig. 5). Further, treating a sample with ethylene glycol expands the 14 Å peak to 17 Å and heating a sample collapsed the 14 Å peak to 10 Å, indicating the presence of montmorillonite (Fig. 5). Accumulations of 20–40 small (1.6 mm x 1.6 mm x 2.5 mm) micritic prolate spheroidal fecal pellets are associated with cluster 1 (Fig. 6). Pupa chambers (Pupichnia) occur in the mudstone 83–108 cm above the base of the section and consist of prolate spheroids infilled with calcareous mudstone. Sizes vary from 6.6–31.0 mm long and average 7.8 mm x 7.8 mm x 15.9 mm. These Pupichnia exhibit a high degree of lithostatic compaction with height to width ratios ranging from 0.59–0.36. All Pupichnia from mudstone were approximately parallel to bedding (0–5º plunge).

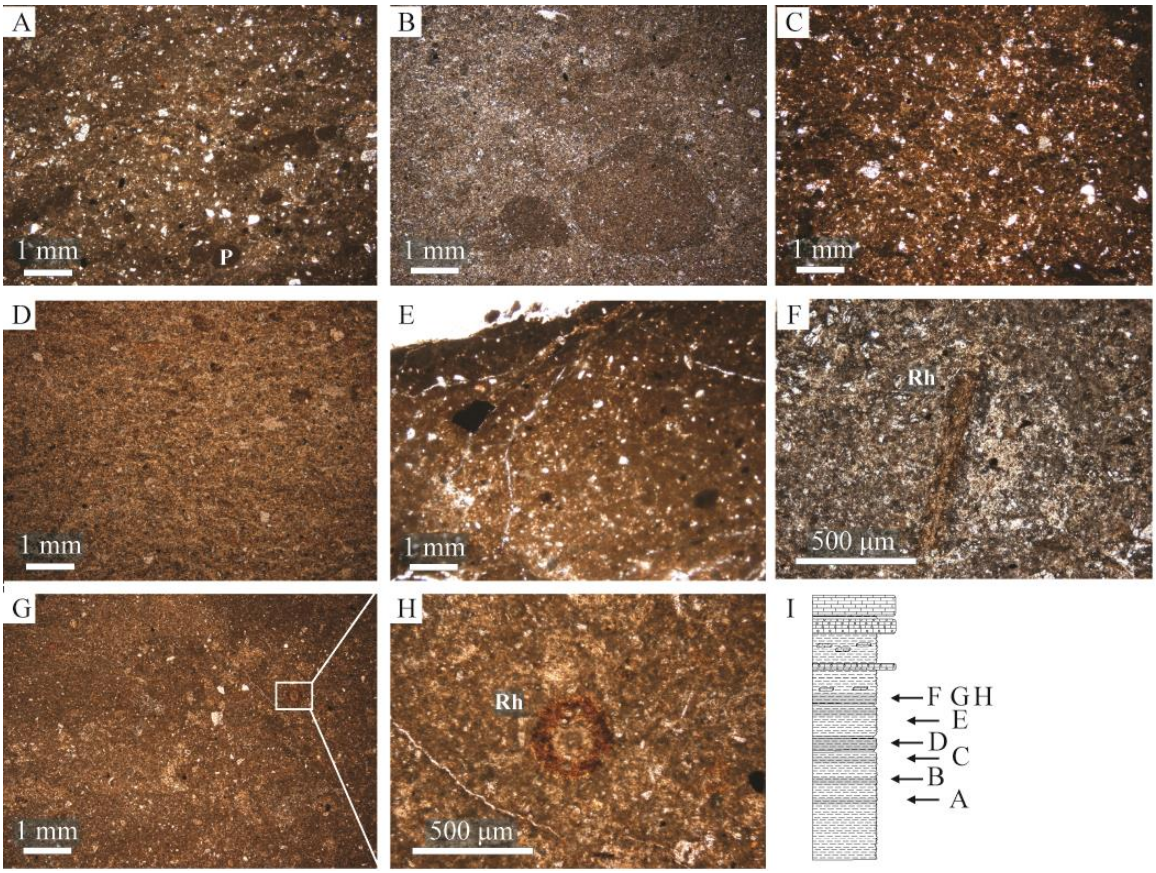

FIGURE 4—Mudstone thin sections and sample location diagram. A) Peloids (P) and angular to subrounded silt-sized quartz grains (ES 440B). B) Mudstone with low silt content (ES 440). C) Angular to subrounded silt-sized quartz grains (ES 439). D) Mudstone from cluster 1 with low silt content (ES 443). E) Angular to subrounded silt-sized quartz grains (ES 435B). F) Longitudinal section of a rhizohalo (Rh) (ES 435). G) Mudstone from cluster 2 with low silt content (ES 434). H) Cross section of a rhizohalo (Rh) (ES 434).

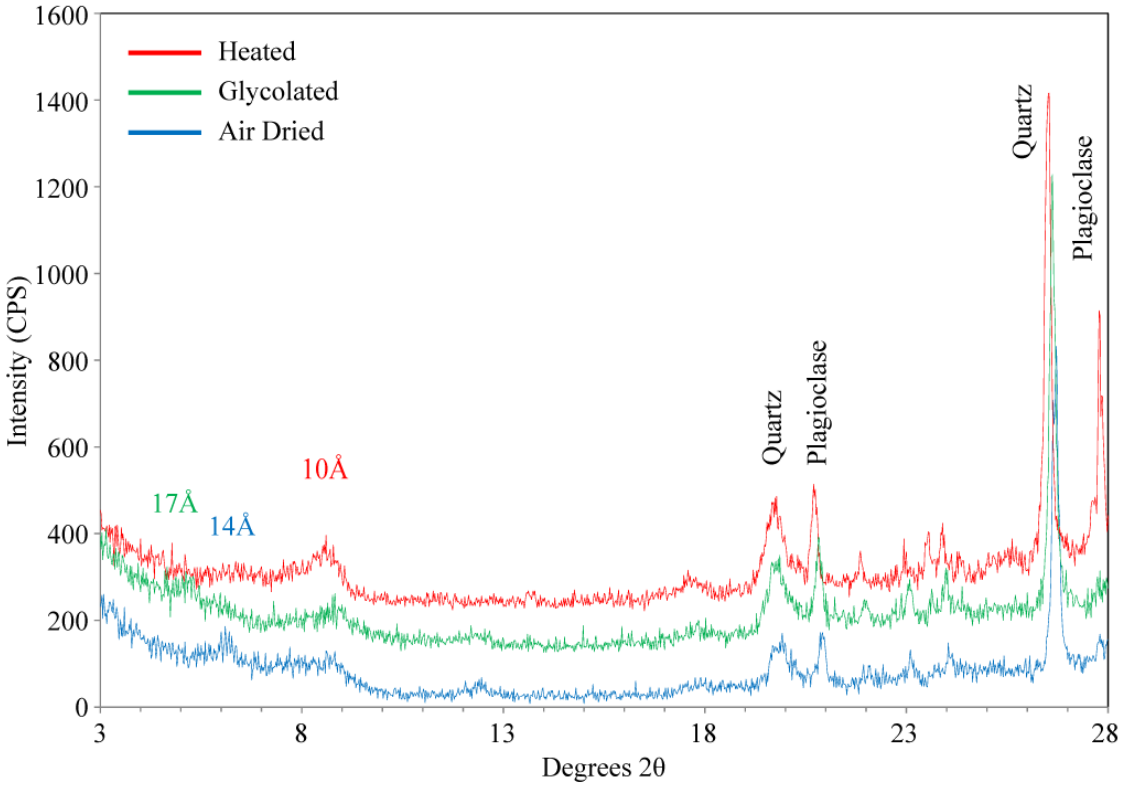

FIGURE 5—XRD profile of mudstone surrounding cluster 1. Peaks indicate the presence of quartz and plagioclase. Heating and glycolating samples allowed identification of the clay mineral montmorillonite.

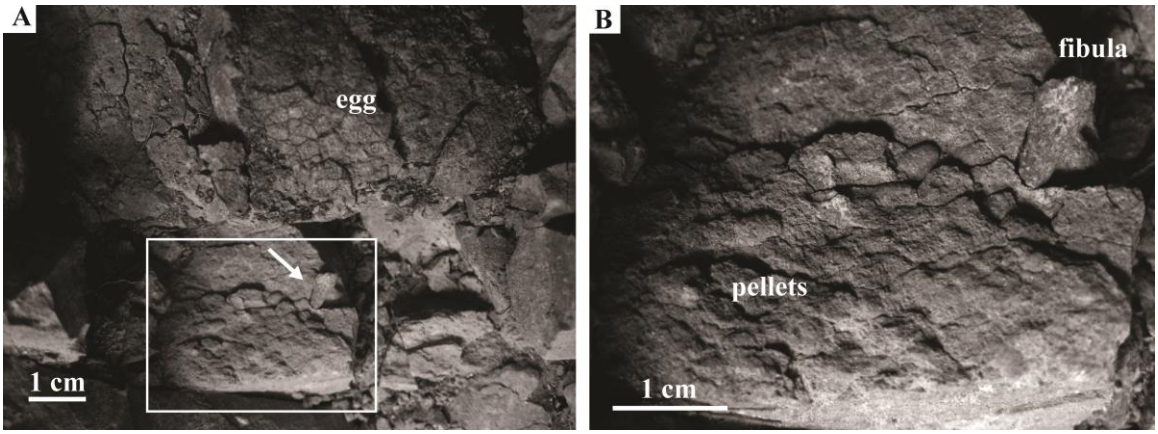

FIGURE 6—Traces and body fossils A) Fecal pellets in cluster 1 associated with an unidentified egg. Arrow points to a perinatal hadrosaur fibula. B) Inset shown in A at a higher magnification.

Limestone.—Two limestone beds overlie the quarry and are laterally traceable for at least 10 m. They are light grey (7/10 GY) on freshly broken surfaces and weather to a slightly reddish grey-brown color (5YR 6/3). A 3 cm-thick limestone (L-1) occurs 91–94 cm above the base of the section and overlies the mudstone containing the fossil material. Bed L-1 includes peloids, coated grains, *Microcodium*, small fecal pellets, and irregular, 5 mm x 0.5 mm cavities infilled by sparry calcite (Fig. 7A–D). This limestone is overlain by a 14 cm-thick mudstone that is comparable to the underlying mudstone unit. A second, 20 cm-thick limestone (L-2) occurs 108–128 cm above the base of the section and contains abundant Pupichnia infilled with micrite or sparry calcite as well as tubular structures infilled with micrite. The structures measure 10–25 mm in diameter and are often crosscut by Pupichnia. Excavation revealed that two of these tubular structures ended in horizontal, lithologically compressed terminal chambers indicative of burrows (Fig. 8A). Most of the Pupichnia are smooth, although a few display an external layer with raised helical contours (Fig. 8B). Measuring the azimuth of the long axis of the Pupichnia reveals no preferred orientation in the horizontal plane. Thirty-four percent of Pupichnia were nearly parallel to bedding (0º–5º plunge). Most Pupichnia from the limestone were oblique (> 5º) (Fig. 8D, E).

Bed L-2 splits laterally into two, 10 cm thick horizons separated by 2 cm of mudstone. The lower horizon (bed L-2A) exhibits very fine circumgranular cracking around abundant peloids (Fig. 7E) in thin section. The peloids are 0.4–1.0 mm wide, circular to oval in cross section, and are darker than the surrounding micritic matrix. Both

the peloids and matrix contain 0.05–0.19 mm wide subrounded quartz grains. The upper horizon (bed L-2B) has an irregular upper surface and displays mottling (Fig. 7F) as well as small (0.3 mm diameter) reddish rhizohalos in thin section (Fig. 7G, H).

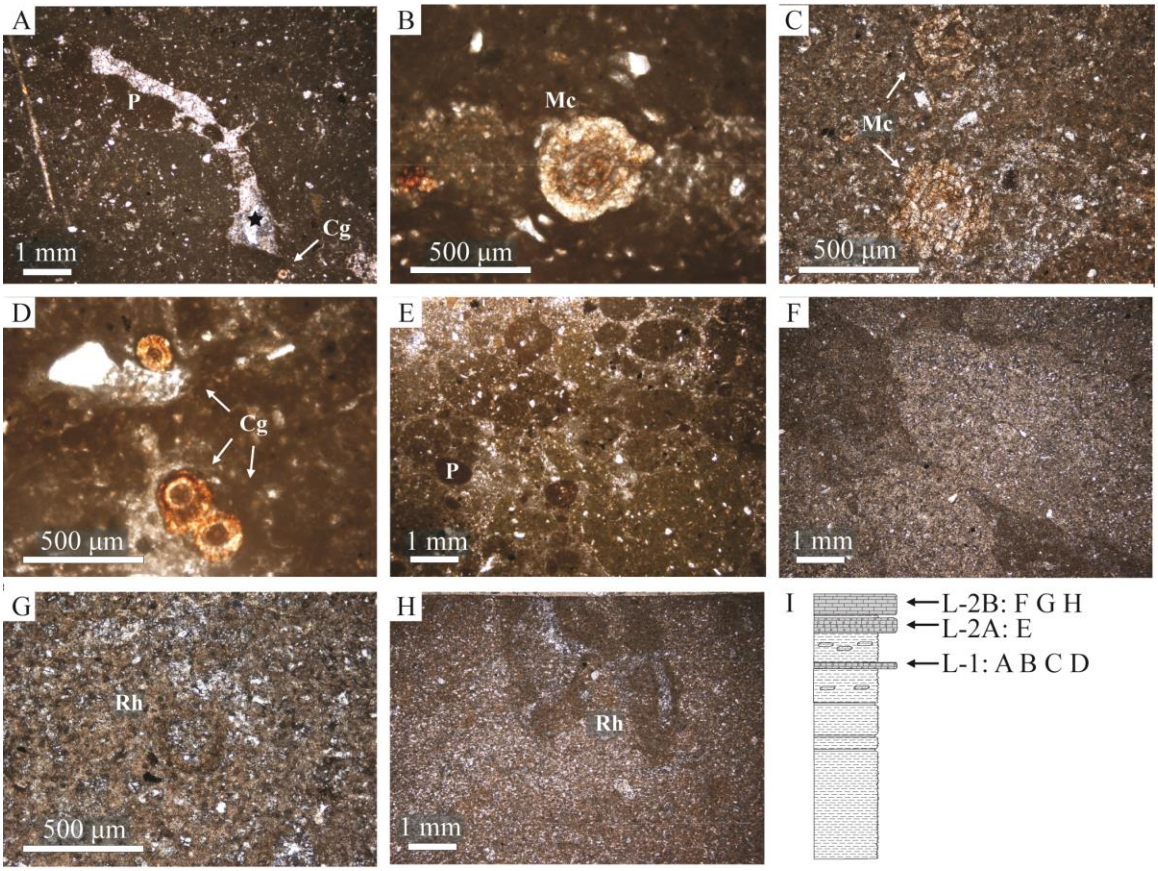

FIGURE 7—Limestone thin sections and sample location diagram. A) Peloids (P), calcite-filled root cavity or pseudomicrokarst (star), and coated grains (Cg) (ES 438). B) *Microcodium* (ES 438). C) M*icrocodium* (ES 438). D) Coated grains (ES 438). E) Peloids (P) (ES 437B). F) Micrite with a mottled fabric (ES 436). G) Cross section of a rhizohalo (Rh) (ES436). H) Rhizohalos (ES 437).

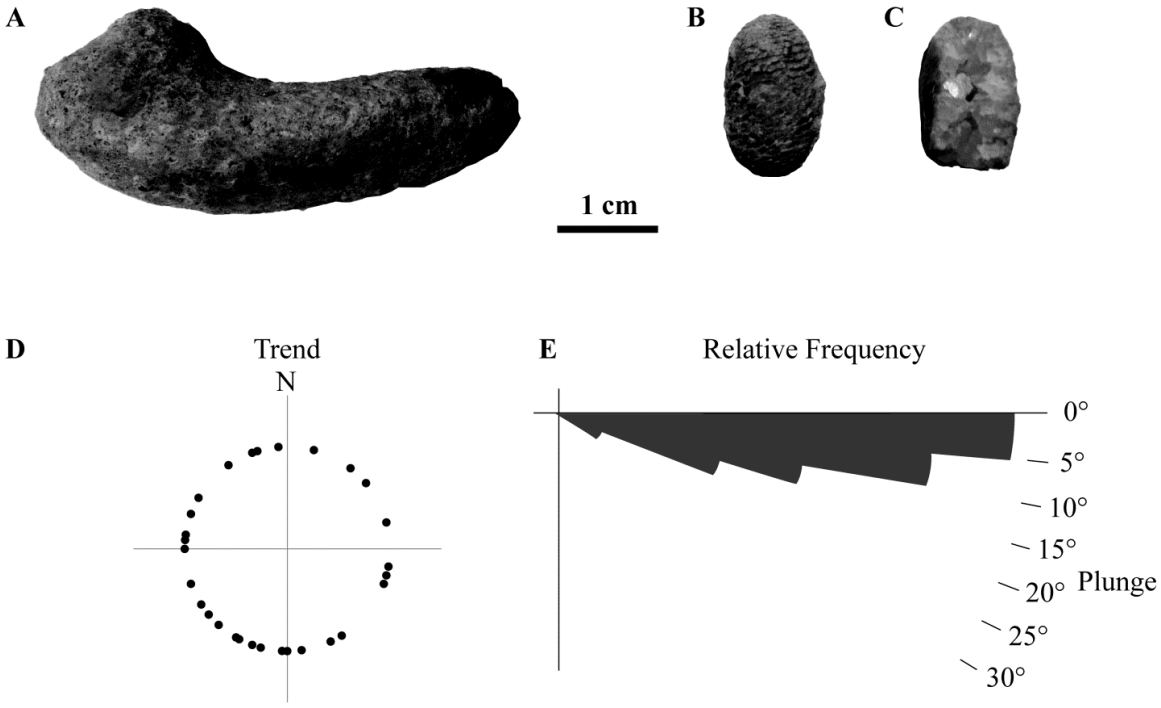

FIGURE 8—Ichnofossils from the mudstone and limestone. A) Terminal burrows (likely *Celliforma*). B) Pupichnia (*Rebuffoichnus*) displaying helical raised ridges. C) Pupichnia (*Rebuffoichnus*) infilled with sparry calcite. D) Corona dot diagram showing trend distribution of long axis of Pupichnia within the mudstone and limestone. N=31. E) Rose diagram showing the relative frequency and plunge degree of Pupichnia within the mudstone and limestone. N=31.

Osteological Material

Ten small bones occured *in situ* within the mudstone 41–56 cm above the base of the section and 0–15 cm below the level of cluster 1. Whereas the metatarsal and fibula occurred as isolated elements, the four ribs were closely associated with three dorsal vertebrae and the four disarticulated skull elements remained within 14 cm of each other (Fig. 9). Osteological remains exhibited no post-mortem surface modification (tooth marks, boring, root etching, etc.) or evidence of cracking or flaking resulting from

weathering (Behrensmeyer, 1978) (Fig. 10). The four elongate *in situ* bones (left and right dentaries, fibula, and metatarsal) lack preferred orientation in the horizontal plane; however, they are aligned parallel to bedding at 0–5º south. Table 4 lists measurements for each element described below.

Sample	Taxon	Element	Size (mm)
MOR 6631-2	Hadrosauridae	left dentary	40.5 L, 3.7-13.5 H
		dental battery	31.6 L, 12 H
MOR 6631-1	Hadrosauridae	right dentary	27.08 L, 2.88-5 H, 6.02 W
		dental battery	22.23 L, 10 H
MOR 6631-3	Hadrosauridae	left premaxilla	19.49 L, 14.46 W
MOR 6631-4	Hadrosauridae	right exoccipital / paroccipital	14.55 L
MOR 7038	Hadrosauridae	right humerus	41.08 L, 5.76 W mid-shaft
		deltopectoral crest	21.35 L, 10.33 W
MOR 7039	Hadrosauridae	dorsal vertebrae centra	5.63 L, 7.16 H, 5.94 W
		neural arch	9.0 L, 10.04 H
MOR 7039	Hadrosauridae	ribs	L = 16.2, 21.8, 20.67, 20.56
MOR 6629-3	Hadrosauridae	fibula	37.65 L, 3.1 W mid-shaft
MOR 6629-2	Hadrosauridae	metatarsal	16.06 L, 3.42 W at mid-shaft
MOR 7034	Hadrosauridae	sacral rib	12.5 L, 9 H
MOR 7035-1	Tyrannosauridae	tooth	43 L, 15 W
MOR 7035-2	Tyrannosauridae	tooth	33 L, 13 W
		denticles	0.5 W, 0.5 H
MOR 6628-3	Tyrannosauridae	tooth	64.5 L, 6-17 W
		denticles	0.3-0.4 W, 0.4 H
MOR 7033	Tetrapod (?lizard)	ribs, vertebrae, limb elements	n/a

TABLE 4—Osteological material from the Egg Mountain quarry. Abbreviations: Length (L), Width (W), Height (H).

Cranial Elements.—The right dentary occurred immediately adjacent to the left dentary and left premaxilla, with the exoccipital located 14 cm to the north (Fig. 9). It displays perpendicular breaks on the rostral and posterior ends and lacks the coronoid process (Fig. 10A). The dental battery includes two rows of four teeth that curve buccally. The teeth exhibit rectangular bases that curve upward into a flattened rhombic/lanceolate shape (with an average crown height of 5 mm), centered around a raised median carina on the lingual side. One complete tooth includes a wear facet. The caudal portion of the left dentary is missing most of the coronoid process due to a perpendicular fracture (Fig. 10B). The dental battery includes two rows of 4–5 teeth that curve buccally and lack denticles. Most teeth are broken at the tips; however, two are complete and show wear facets. The rostral end of the left premaxilla is complete, whereas the dorsal and caudolateral processes are incomplete (Fig. 10C). The right exoccipital includes a ventrally deflected paroccipital process (Fig. 10D).

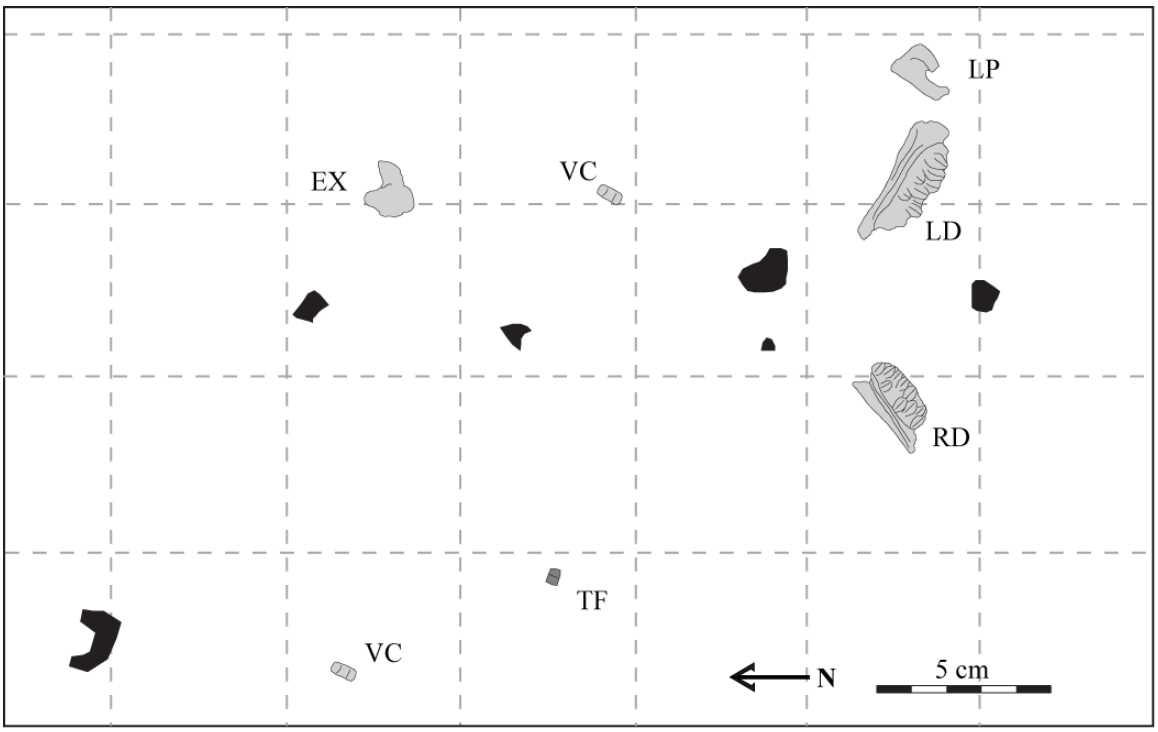

FIGURE 9—Schematic diagram of jacket MOR 6631, showing the association between cranial bones and other elements. Black polygons are fragments of *Spheroolithus* eggshell. Modified from the map drawn by Laurie Spicher. Abbreviations: EX, right exoccipital; LD, left dentary; LP, left premaxilla; RD, right dentary; TF, hadrosaur tooth fragment; VC, vertebra centrum.

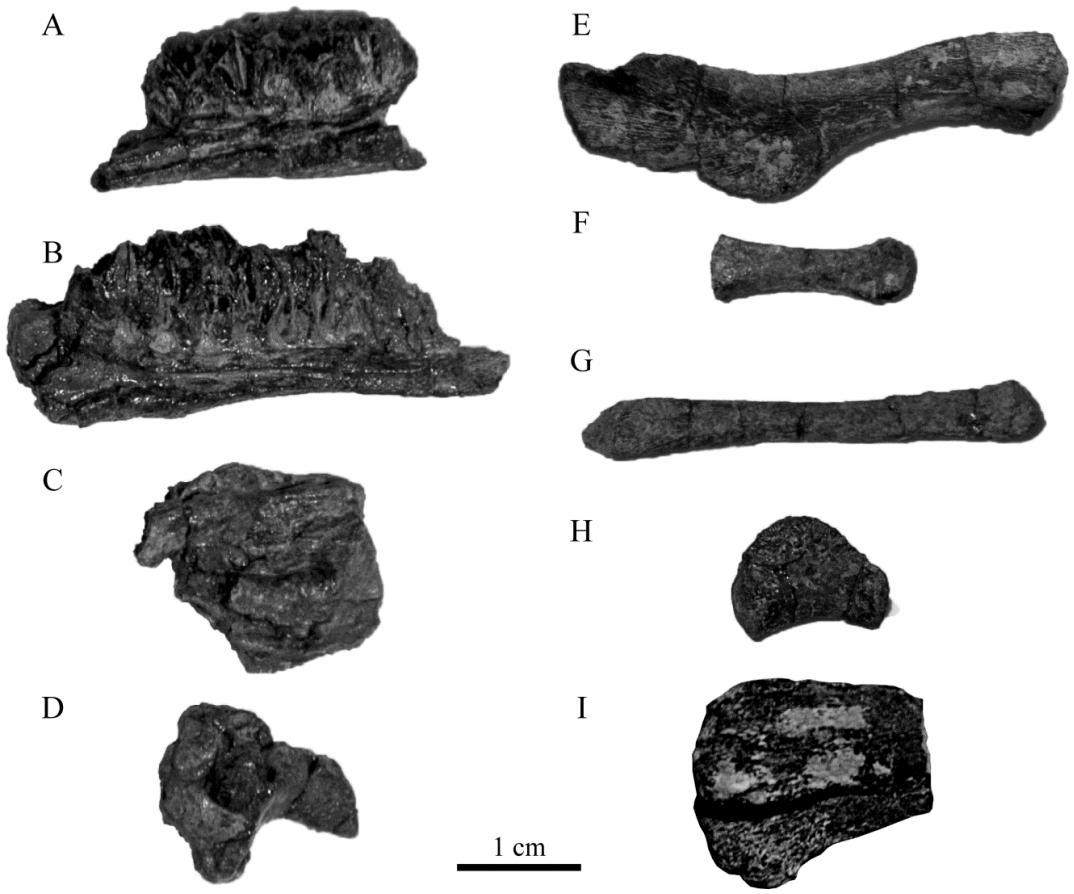

FIGURE 10— Hadrosaur perinatal bones. A) Right dentary. B) Left dentary. C) Left premaxilla. D) Right exoccipital and paroccipital. E) Right humerus. F) Metatarsal. G) Fibula. H) Sacral rib. I) Distal end of femur.

Postcranial Elements.—Portions of the right humerus were sifted from the overburden at the quarry and later assembled, resulting in a nearly complete specimen (Fig. 10E). The radial and ulnar condyles of the humerus are slightly displaced due to lithostatic compaction. Two articulated dorsal vertebrae occur in association with four dorsal ribs and other unidentified partial elements within a 40 x 20 mm carbonate nodule (Fig. 11). The anterior centrum exhibits an associated unfused neural arch, whereas the

posterior centrum lacks the neural arch. The fibula and metatarsal were adjacent to eggs in cluster 1 (Fig. 10F, G). Both elements display minor lithostatic compaction but are otherwise complete.

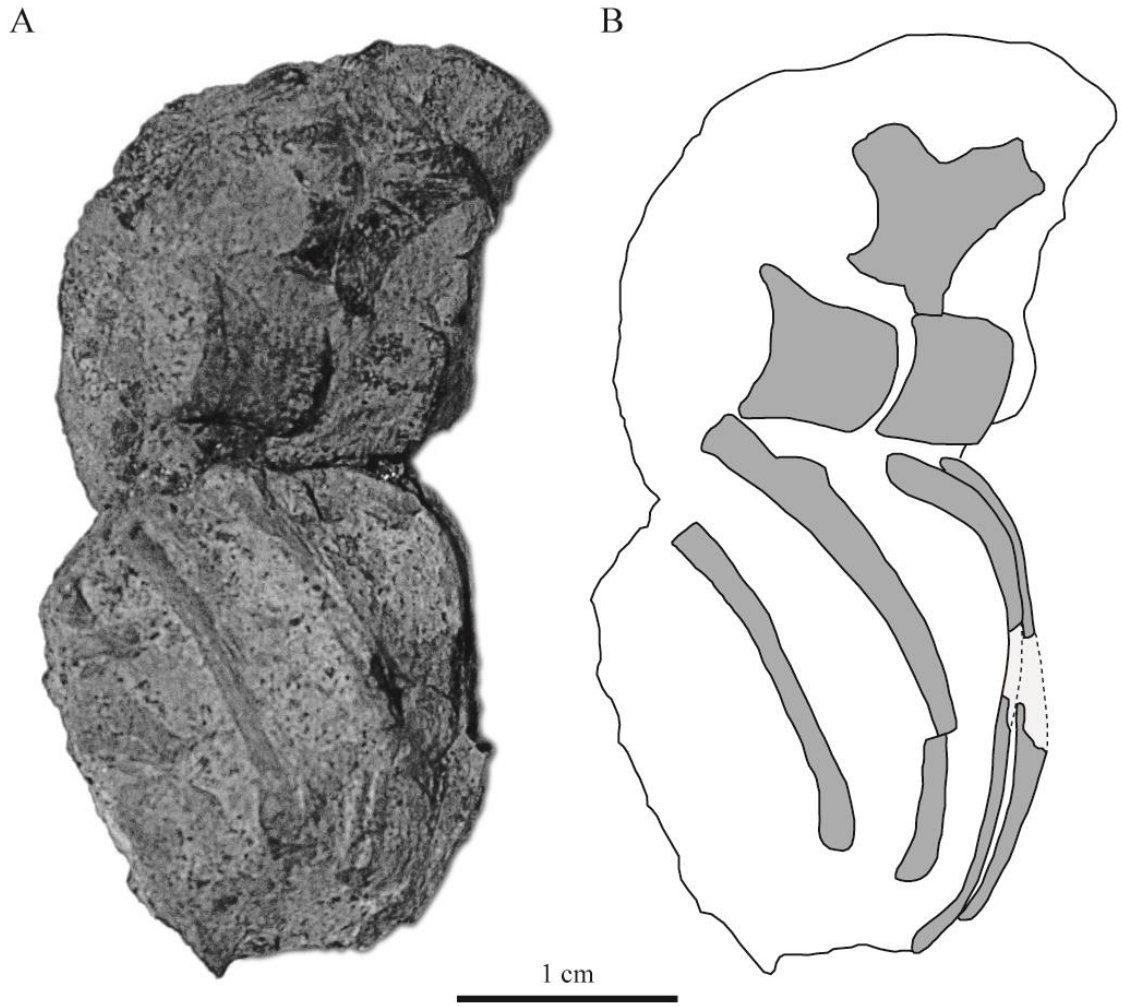

FIGURE 11—Perinatal hadrosaur bones. A) Articulated dorsal vertebrae and ribs. B) Schematic diagram of A.

Other osteological remains.—A closely associated accumulation of disarticulated ribs, vertebrae, and limb elements of an unidentified small tetrapod occurred below cluster 1 (Fig. 12). In addition, an isolated, fragmentary theropod tooth occurred less than 10 cm below cluster 1 (< 46 cm above the base of the section; Fig. 13). The tooth sliver displays two longitudinal fractures with an oblique fracture at the tip. The enamel appears highly eroded with numerous gouges and missing sections. The anterior carina has 2.5–3.0 denticles per mm and exhibits very faint blood grooves. In addition, two isolated, fragmentary theropod teeth (MOR 7035-1, MOR 7035-2) were exposed by recent weathering from limestone bed L-2B (125 cm above the base of the section). Although both are highly fragmentary, MOR 7035-2 displays a small portion of exposed carina that includes denticles and blood grooves.

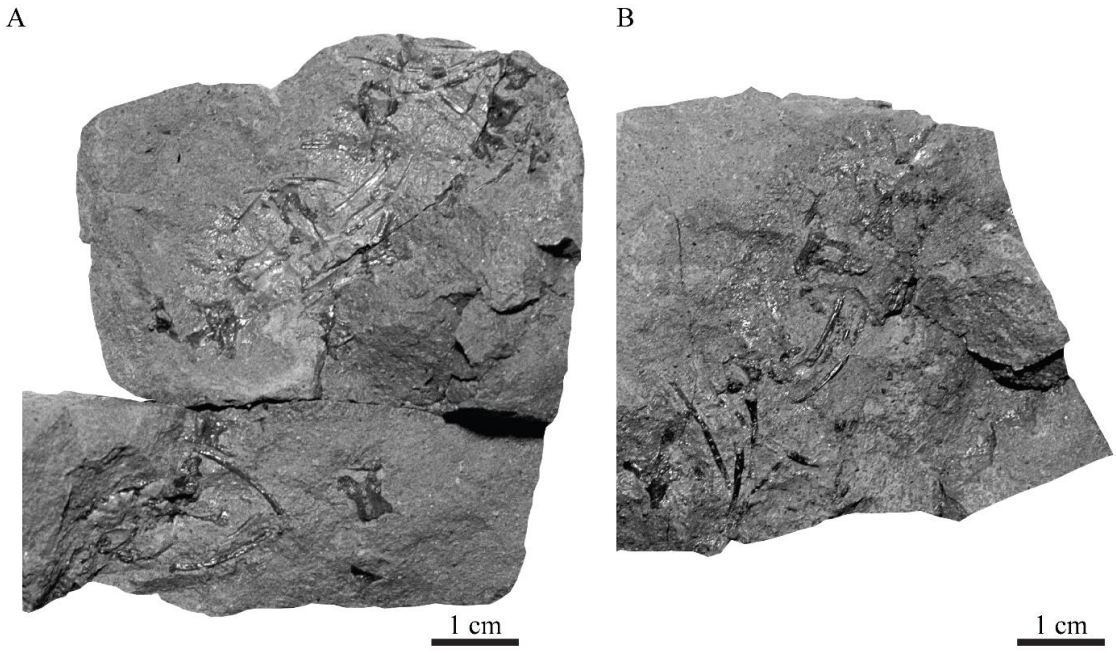

FIGURE 12—Partial skeleton of a small unidentified tetrapod (possibly lizard) below cluster 1. A) Ribs, vertebrae, and a limb element. B) Ribs and vertebrae.

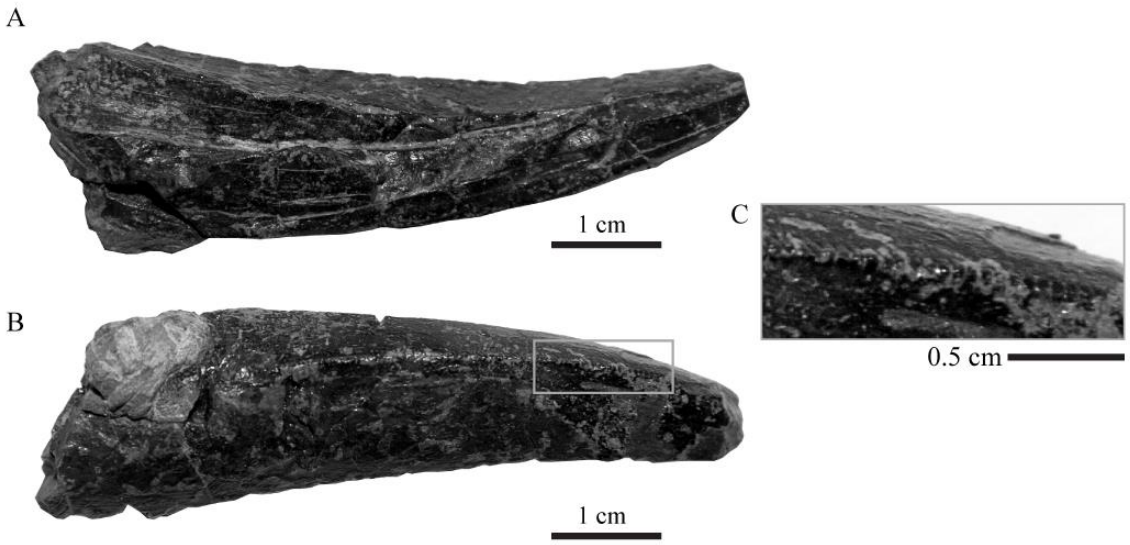

FIGURE 13—Partial tyrannosaurid tooth from below cluster 1. A) Posterior view displaying longitudinal fracture. B) Anterior view showing carina. C) Inset shown in B displays denticles with faint blood grooves.

Eggs and Eggshell

Unidentified cluster 1.—The lower cluster (cluster 1) is 56 cm above the base of the section and consists of at least 22 eggs. The most complete, well-preserved eggs are approximately 12 cm in diameter and are compressed to a thickness of 1.0–2.0 cm (Fig. 14). The eggs are stacked, with some 8.0–10 cm below others. Eggs are dispersed within a NE-SW trending cone-shaped area 2.5 m long and 1 m wide at the base. Eggs are more closely spaced within the apex at the NE potion of the cluster and are more dispersed towards the SW. Eggshell thickness varies from 0.3–0.5 mm. Microscopic examination reveals that eggshell samples exhibit substantial diagenetic alteration. Radial thin sections show possible nucleation sites that occur 0.12 mm apart. Several samples exhibit a zone

of columnar extinction that extends 0.22 mm above the inner shell surface, with the remaining eggshell exhibiting more extensive diagenetic alteration (Fig. 15). In addition, a mineral deposit forms a thin (0.04–0.1 mm) crust on the inner and outer surfaces of the eggshell (Fig. 15). Viewed in thin section, this mineral is consistent with collophane. Pore geometry is not discernible in radial thin sections; however, tangential thin sections reveal that the pores are circular in cross section and have an average diameter of 0.088 mm, with an average cross-sectional area of 0.006 mm^2 (Fig. 16). The outer surface of the eggshell is smooth and weathers to a rusty orange (7.5YR 6/8). Cluster 1 contains a small metatarsal and fibula as well as over 55 fragments of *Spheroolithus* (Mikhailov, 1994) eggshell randomly distributed at and below the egg level.

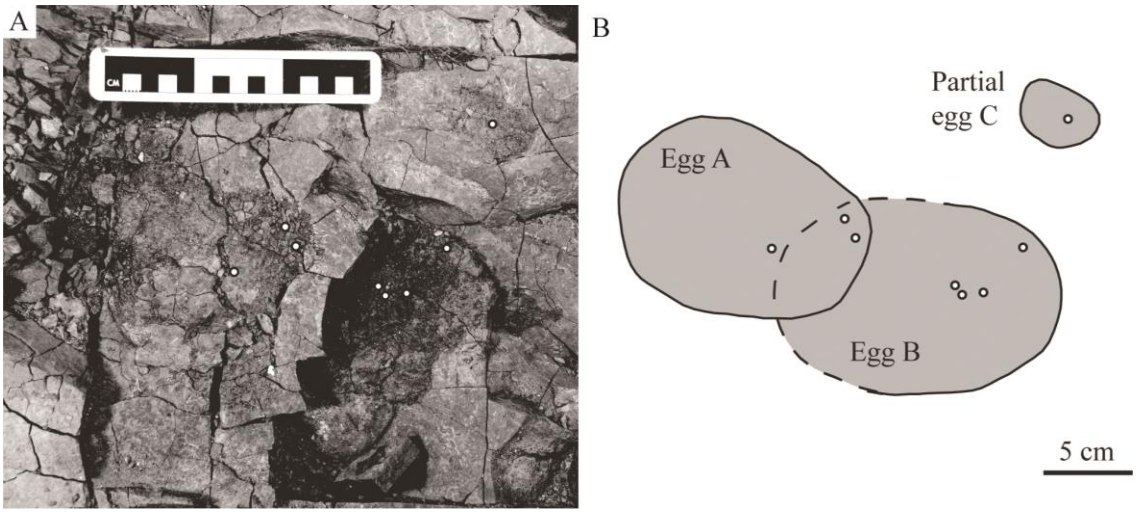

FIGURE 14—Eggs and partial eggs from cluster 1. A) Two eggs and one partial egg from the eastern half of cluster 1. B) Schematic diagram of A. White circles indicate the locations of egghshell removed for tangential thin sections.

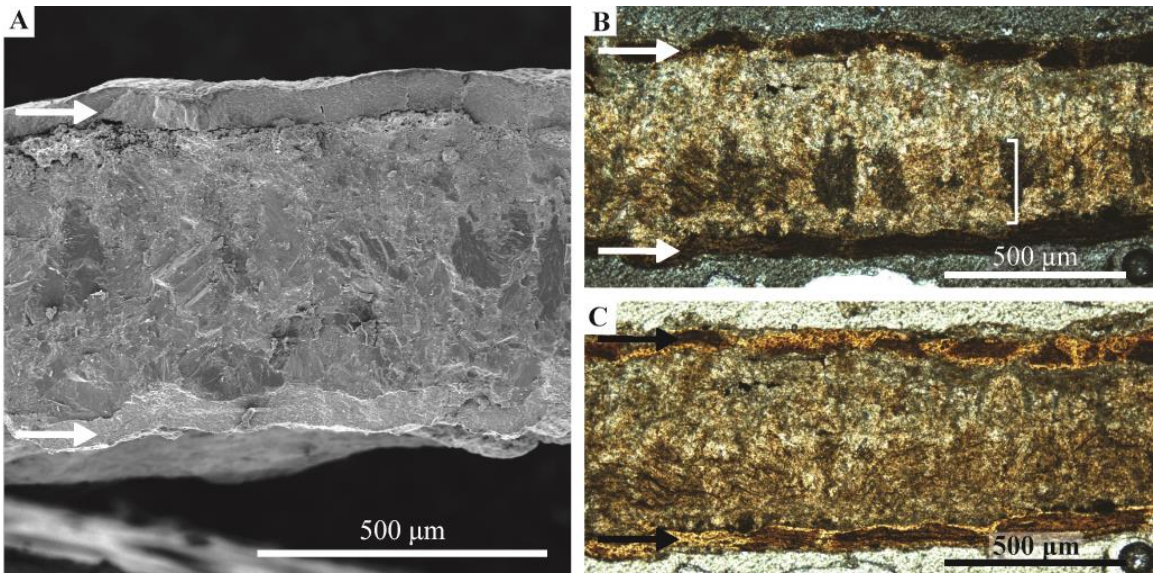

FIGURE 15—Unidentified eggshell from cluster 1. A) SEM image of a fresh break (ES 422). B) Radial thin section of ES 422 under cross-polarized light. Bracket indicates zone of columnar extinction. C) Radial thin section of ES 422 in plane polarized light. Arrows indicate mineral deposits adhering to the outer and inner surfaces.

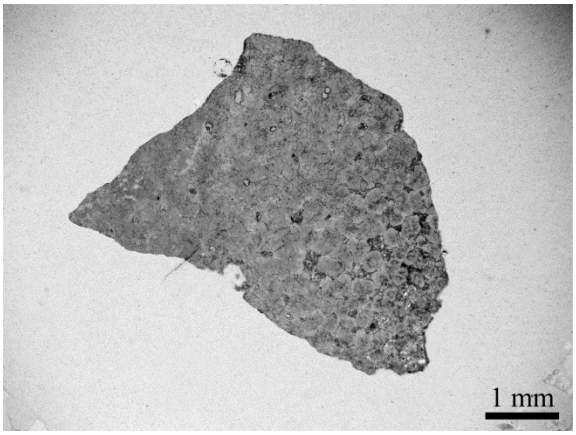

FIGURE 16—Tangential thin section of eggshell from cluster 1 (ES 410) showing the size, irregular shape, and distribution of pores.

Unidentified cluster 2.—The upper cluster (cluster 2) is 0.25 m above and 3 m northeast of cluster 1 and consists of 6–7 eggs (Fig. 17). The 10–11 cm diameter eggs are compressed to a thickness of 3.0–4.0 cm. With the exception of one specimen located 0.7

m to the NE, all the aggs are distributed in a 1 m-long E-W trending line. Egghsell thickness is comparable to that of cluster 1 (0.3–0.5 mm). Microscopic examination reveals that eggshell samples exhibit substantial diagenetic alteration similar to cluster 1. SEM imagery shows a possible radial structure near the inner surface of the eggshell. Examination of radial thin sections under an optical cathodoluminescence microscope reveals that the eggshell fluoresces, indicating diagenetic recrystallization (Fig. 18). Pore geometry is not discernible in radial thin sections and the outer surface of the eggshell is smooth and weathers to a rusty orange (7.5YR 6/8). Whereas the eggs of cluster 1 have thin mineral deposits encrusting the inner and outer surfaces of the eggshell, the eggs of cluster 2 have large (1–4 cm) blocky mineral deposits occuring within the eggs. Calcium and phosphate are present in the XRD and EDX profiles, suggesting that the mineral is in the apatite group (Klein and Dutrow, 2008; Fig. 19). The amorphous mineral is black with a brown streak, weathers light blue, and is opaque in thin section, characteristic of collophane, a cryptocrystalline form of apatite (Klein and Dutrow, 2008).

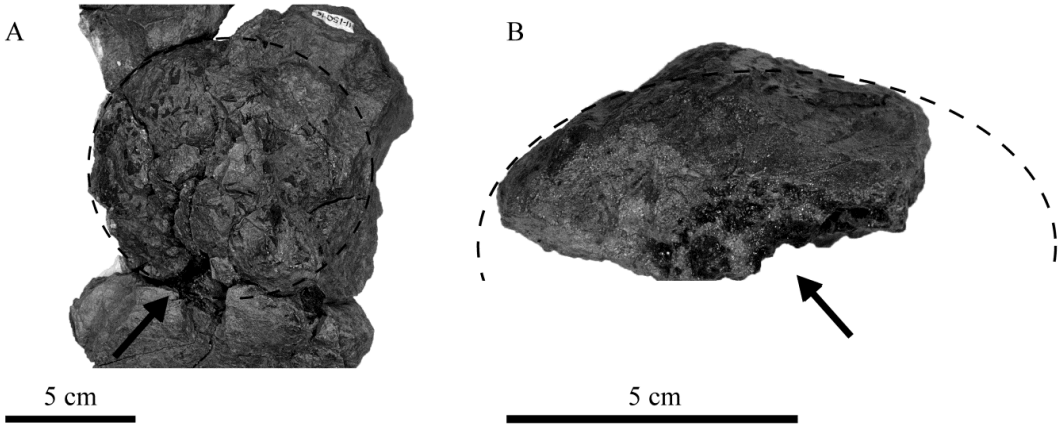

FIGURE 17—Two partially crushed eggs from cluster 2. A) Plan view of MOR 6630-1 with collophane visible (arrow) B) Lateral view of MOR 6630-3 displaying lithostatic compression and collophane deposits (arrow).

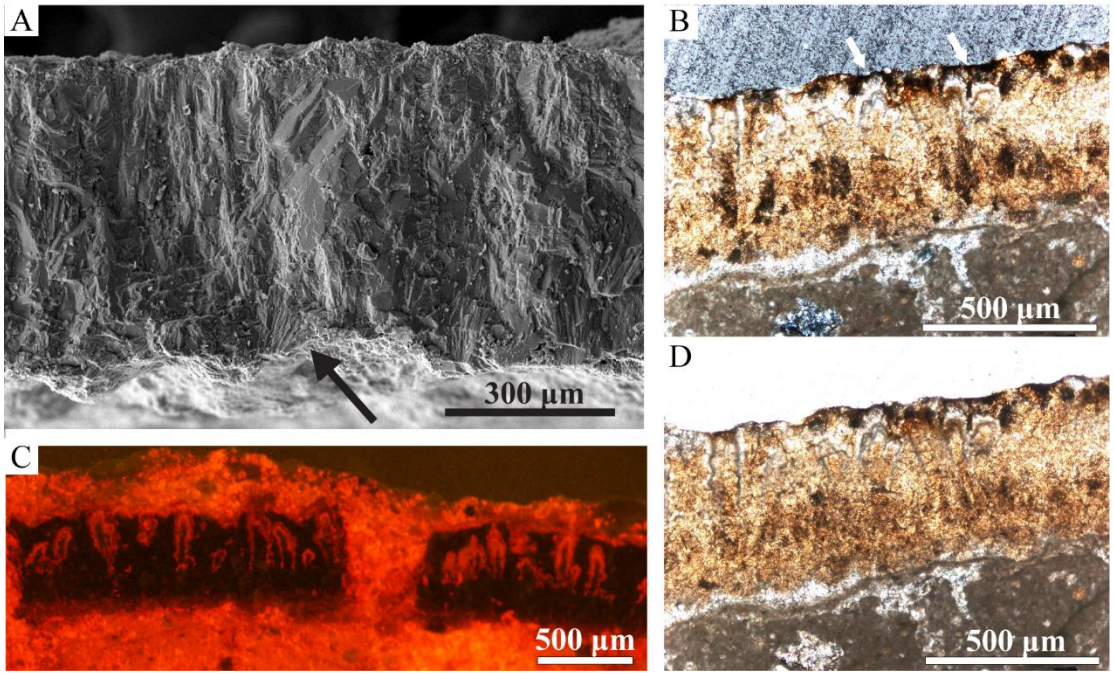

FIGURE 18—Unidentified eggshell from cluster 2. A) SEM image of a fresh break. Radial structures visible near inner shell surface (arrow). B) Radial thin section in cross-polarized light (ES 228-1). The 'lobes' visible in the upper part of the eggshell (arrows) are not typical fossil eggshell microstructures. C) Cathodoluminescence image showing that the 'lobes' fluoresce, indicating diagenetic alteration. D) Radial thin section in plane polarized light.

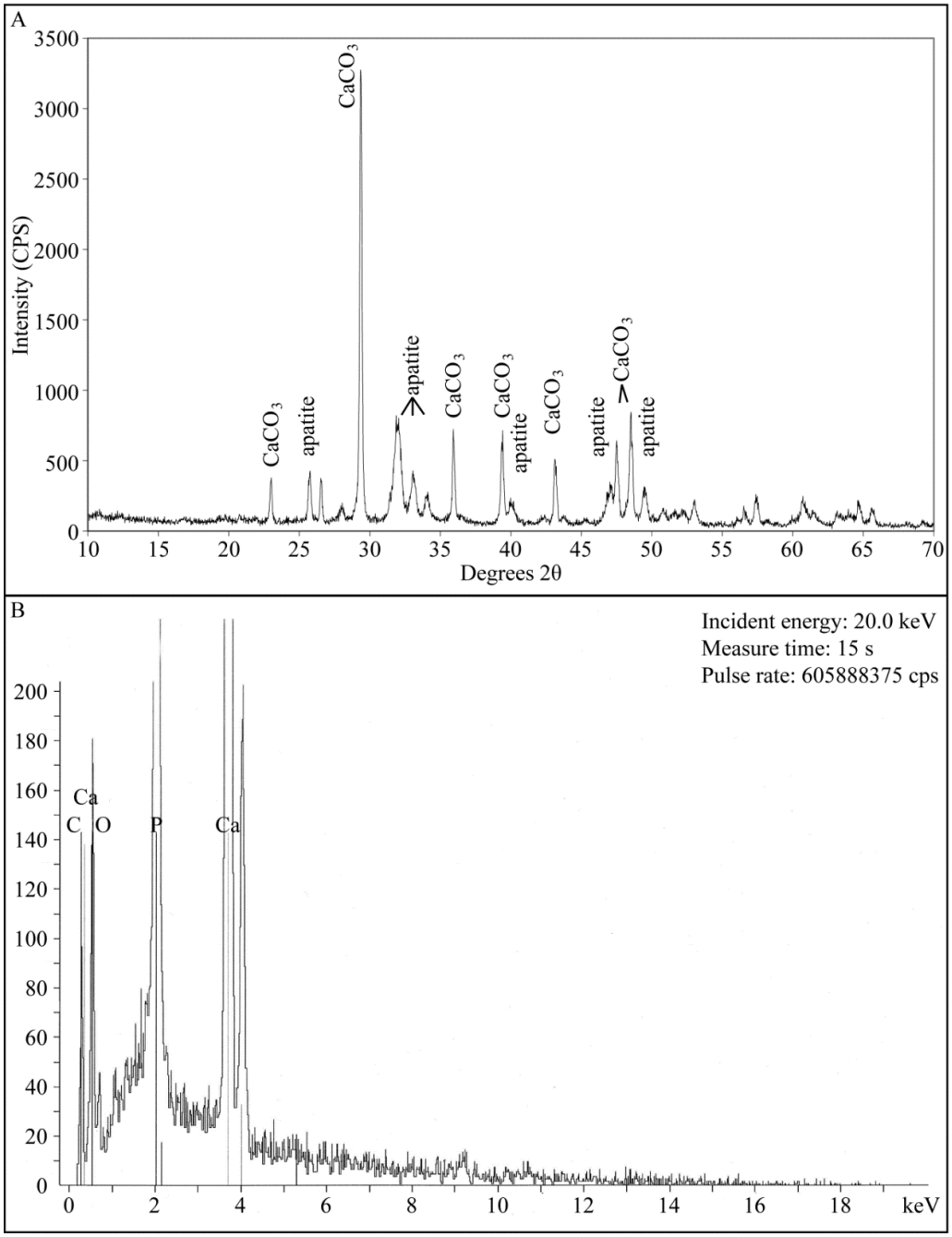

FIGURE 19—Analyses of the mineral associated with eggs of cluster 2. A) XRD profile showing peaks suggesting the presence of calcite and apatite. B) EDX profile verifying presence of C, O, P, and Ca.

Spheroolithus eggshell fragments.—A total of 185 eggshell fragments occurred at varying abundances throughout a 70 cm interval of mudstone that includes the egg clusters (Fig. 3). Rare fragments also occurred outside of this interval in limestone bed L-2. Eggshell orientations in the mudstone included 101 concave-down (CCD), 80 concave-up (CCU), and 4 vertical (Oser and Jackson, 2014). The thickness of eggshells from the mudstone varies from 0.77–1.31 mm and averages 1.08 mm. Thin sections and SEM imaging of the eggshells show shell units comprised of a single layer of radiating spherulites (Fig. 20A, B). Nucleation sites preserved at the inner shell surface average 0.17 mm apart. Large interstices between the nucleation sites are filled with secondary calcite and extend 0.5 mm upwards from the inner shell surface (Fig. 20D). The shell units lack clear delineation and are composed of thin wedges that display a sweeping extinction pattern visible in radial thin sections under cross-polarized light (Fig. 20E). Dark, undulating accretion lines are visible starting 0.16 mm above the inner surface (i.e., 1/7 the eggshell thickness). The accretion lines dip downwards at the pore margins, but are otherwise laterally continuous across the shell units.

The prolatocanaliculate pores of the *Spheroolithus* eggshell fragments have diameters that can vary by as much as 0.074 mm along their length (Fig. 21A, B). Pores are circular to oval in cross section and have an average diameter of 0.085 mm, with an average cross-sectional area of 0.0075 mm^2 (Fig. 21C). Rare fragments display rimocanaliculate pore openings (Fig 21D). The surface of the eggshell displays sagenotuberculate ornamentation consisting of low (0.17 mm) reticulate nodes and ridges

consistent with Mikhailov's (1991) 'variant 1' (Fig. 22). Pores generally open between the nodes and ridges of the ornamentation.

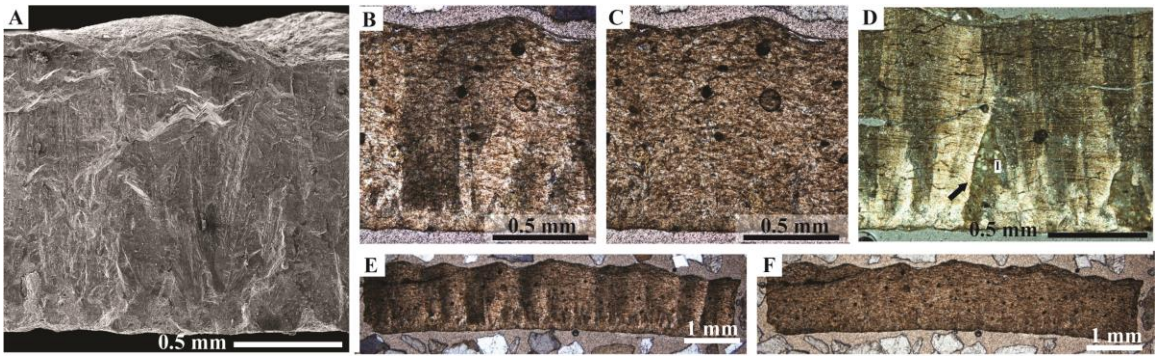

FIGURE 20—*Spheroolithus* eggshell. A) SEM image of a fresh break showing radiating spherulites and nucleation sites (ES 441). B) Radial thin section of ES 441 viewed under cross-polarized light. C) Radial thin section of ES 441 viewed under plane polarized light. D) Radial thin section of ES 402. Note the accretion lines dipping downward (arrow) and the large calcite-filled interstice (I). E) Radial thin section of ES 441 under cross-polarized light displaying sweeping extinction. F) Radial thin section of ES 441 viewed under plane polarized light.

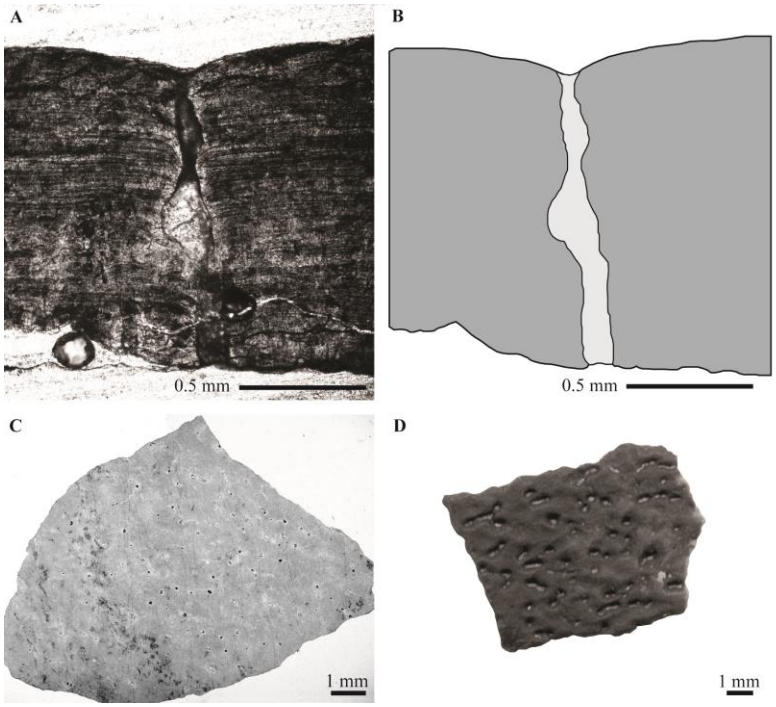

FIGURE 21— *Spheroolithus* pores. A) Thin section of ES 228 displaying prolatocanaliculate pore geometry. B) Schematic diagram of A. C) Tangential thin section of *Spheroolithus* eggshell (ES 405) showing the size and distribution of pores. D) Surface of eggshell fragment (MOR 7036-1) displaying rimocanaliculate pore openings.

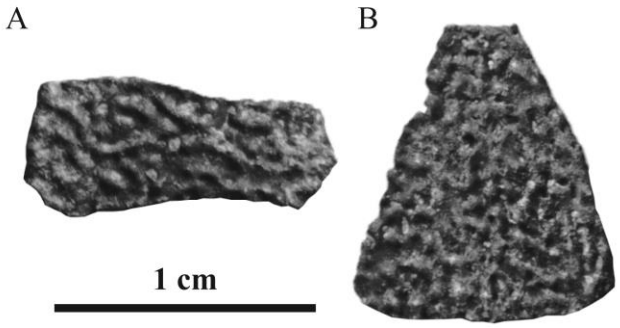

FIGURE 22—Two examples of sagenotuberculate surface ornamentation of *Spheroolithus* eggshell. A) Ornamentation composed primarily of branching ridges B) Ornamentation composed primarily of connected nodes.

Gas Conductance

The G_{H2O} of five eggshells removed from eggs in cluster 1 range from 276.89 ± 43.96 to 88.66 ± 9.77 mg $H_20 \cdot day^{-1} \cdot Torr^{-1}$ based on an inferred egg radius of 3.93 cm (Table 5). The eggshells sampled from region 1 have calculated gas conductance values from 120.09 ± 10.8 to 276.89 ± 43.96 mg $H_20 \cdot day^{-1} \cdot Torr^{-1}$, whereas eggshell from region 2 ranges from 88.66 ± 9.77 to 188.02 ± 28.16 mg $H_20 \cdot day^{-1} \cdot Torr^{-1}$. Averaging the values calculated from eggshells in egg A and B gives 138.34 ± 29.8 and 124.89 ± 20.1 mg $H_20 \cdot day^{-1} \cdot Torr^{-1}$, respectively. The gas conductance values of two *Spheroolithus* eggshell fragments (ES 404 and ES 405) are respectively 923.22 ± 291.78 and 1851.66 ± 526.28 mg $H_20 \cdot day^{-1} \cdot Torr^{-1}$. The diameter of a single pore varies by 0.074 mm, introducing 13–19% error; when combined with measurement error this results in 28– 31% total error. The average pore area per square cm for the unidentified eggshell is 8x less than that of the *Spheroolithus* eggshell from the quarry. The gas conductance of eggshell from the three unidentified eggs of cluster 1 are 6, 6.5, and 13 times higher than the predicted value for avian eggs of similar mass, whereas gas conductance values for *Spheroolithus* eggshell fragments are 16 and 32 times higher (Fig. 23).

Sample (Region)	Ootaxon	Surface area (SA) (cm^2)	Pore area (Ap) (cm^2)	L (cm)	r (cm)	G_{H2O}
ES 404 (?)	*Spheroolithus*	452.38	4.76	0.108	6.0	923.22 ± 291.78
ES 405 (?)	*Spheroolithus*	452.38	9.55	0.108	6.0	1851.66 ±526.28
ES 410 (1)	Unidentified eggshell (cluster 1, egg C)	194.09	0.661	0.05	3.93	276.89 ±43.96
ES 419 (1)	Unidentified eggshell (cluster 1, egg B)	194.09	0.309	0.05	3.93	129.69 ±16.95
ES 420 (1)	Unidentified eggshell (cluster 1, egg B)	194.09	0.287	0.05	3.93	120.09 ±10.8
ES 429 (2)	Unidentified eggshell (cluster 1, egg A)	194.09	0.449	0.05	3.93	188.02 ±28.16
ES 430 (2)	Unidentified eggshell (cluster 1, egg A)	194.09	0.212	0.05	3.93	88.66 ±9.77

TABLE 5—Measurements and calculations for cluster 1 and *Spheroolithus* eggshell. Gas conductance (G_{H2O}) is given in $mgH_20 \cdot day^{-1} \cdot Torr^{-1}$. Region 1 denotes eggshell fragments sampled from the center of the eggs, region 2 denotes fragments collected from near the edges of the egg.

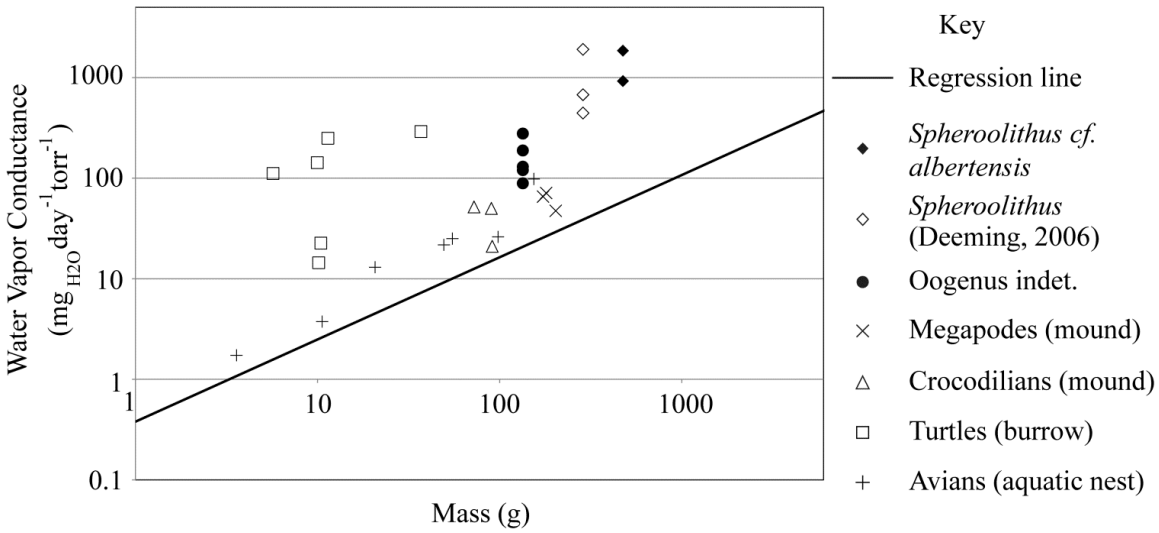

FIGURE 23— Regression analysis of modern avian values using Ar and Rahn's (1985) open-nest avian data. Values for *Spheroolithus* and unidentified eggshell from Egg Mountain are plotted against the regression line to facilitate comparisons with avian eggs of similar mass. Megapodiidae (*Alectura lathami),* Crocodylia (*Alligator mississippiensis, Crocodylus acutus, Crocodylus porosus),* Chelonia (*Chrysemys picta, Chelydra serpentina, Caretta caretta, Trionyx spiniferus, Emydura macquarii*), and avian aquatic nesters (*Podilymbus podiceps, Aechmophorus occidentalis, Dendrocygna bicolor, Oxyura leucocephala, Chlidonias niger, Agelaius phoeniceus,* and *Gavia immer*) are plotted for comparison (Packard et al., 1979; Seymour and Ackerman, 1980; Seymour et al., 1986; Vleck et al., 1984; Deeming and Thompson, 1991).

DISCUSSION

Stratigraphy and Lithology

Mudstone.—The sedimentology and ichnoassemblage at the quarry are consistent with a terrestrial environment with seasonal variation in rainfall. For example, mottling indicates iron remobilization caused by changes in groundwater redox potential as a response to a fluctuating water table (Freytet, 1973; Alonso-Zarza and Wright, 2010) and

rhizoliths form from decay around plant roots with fluctuating soil moisture levels (Kraus and Hasiotis, 2006). Additionally, the mudstone also includes accumulations of small pellets, which are consistent in size and shape with the fecal pellets of soil-dwelling invertebrates (Retallack, 1990; Hembree and Hasiotis, 2007). The presence of fecal pellets and rare pupa cases suggests that the homogenous texture of the mudstone and lack of primary laminae could have been produced by bioturbation (Potter et al., 1980). Montmorillonite (present in the mudstone XRD profile) is one of the main constituents of bentonite and indicates volcaniclastic input, likely derived from the contemporaneous igneous activity at the Elkhorn Mountains volcanic center south of the locality. Thus, the mudstone exposed at the quarry was likely deposited on a distal floodplain characterized by wet and dry seasons and soil development.

Limestone.—The sedimentology and ichnology of the micritic limestone beds at the site share features of paleocaliche as well as carbonates deposited within small, ephemeral bodies of water. Floodplain limestones with similar features (e.g., mottling, rhizoliths, peloids, "calcified root cells" (i.e., *Microcodium*), and "spar-filled pores" (i.e., either pseudomicrokarst or calcite-filled root casts)) have been previously described from the Clark's Fork basin, Wyoming (Gingerich, 1987; Kraus, 1988; and Bowen and Bloch, 2002). Carbonate was likely sourced from Paleozoic strata exposed in the Cordilleran fold and thrust belt to the west of the WCA, with some influx of CO_2 from the atmosphere (Lorenz and Gavin, 1984; Bowen and Bloch, 2002). The carbonate mud was then subject to desiccation, followed by plant colonization and pedogenic overprinting.

Siliciclastic input was limited during carbonate precipitation suggesting that the bodies of water occurred during a hiatus in clastic sedimentation.

Features supporting this interpretation include the presence of irregular cavities infilled with sparry calcite in bed L-1, consistent with pseudomicrokarst. These form from desiccation due to subaerial exposure and subsequent plant colonization of unlithified carbonate mud and are characteristic of carbonates deposited under aquatic conditions (Freytet and Plaziat, 1982; Freytet and Verrecchia, 2002; Alonso-Zarza and Wright, 2010). These cavities could also represent calcite-filled root casts which indicate plant coloization and are a common constituent of paleocaliche. *Microcodium* in bed L-1 commonly occurs in carbonate rocks and calcareous paleosols in continental settings with seasonal variation in precipitation (Košir, 2004) including floodplain, palustrine, wetland, lacustrine, and rarely, karstic paleoenvironments (Esteban, 1974; Klappa, 1978; Freytet and Plaziat, 1982; Wright and Platt, 1995; Alonso-Zarza, 2003). Micritic peloids in bed L-1 form from grainification due to subaerial exposure and desiccation of lime mudstone or biotic reworking. They are a common constituent of paleocaliche and palustrine limestone (Alonso-Zarza et al., 1992; Flügel, 2004; Stokes et al., 2007; Alonso-Zarza and Wright, 2010). Fecal pellets further indicate the presence of soil-dwelling invertebrates.

Limestone bed L-2B is a peloidal packstone with fine circumgranular cracking. Circumgranular cracking, a fabric commonly seen in both palustrine carbonates and paleocaliche, forms during repeated cycles of inundation and desiccation of the substrate (Alonso-Zarza et al., 1992; Alonso-Zarza 2003; Flügel, 2004; Aharipour et al., 2010; Alonso-Zarza and Wright, 2010). Limestone bed L-2B contains abundant Pupichnia and

burrows, which permit paleoecological inferences (Genise et al., 2000; Genise et al., 2010; Martin and Varricchio, 2010). The Pupichnia described in this study closely resemble the ichnospecies *Rebuffoichnus sciuttoi*, which is diagnosed by its ovoid shape and surface texture comprised of low, densely packed helical ridges (Genise et al., 2007). Vertical burrows ending in horizontal, lithologically compressed terminal chambers are also present at the site, which may represent a variation of the ichnogenus *Celliforma* (Genise, 2000). Martin and Varricchio (2010) report *Rebuffoichnus*, *Celliforma* and other ichnotaxa at other sites at the WCA. They note that the presence of burrows and insect cocoons within micritic limestone indicates a well-drained paleosol consistent with the *Celliforma* ichnofacies described by Genise et al. (2010), suggesting that utilization of the substrate by these invertebrate taxa likely occurred during seasonally dry conditions. The lack of preferred orientation of the Pupichnia indicates that they were not subject to fluvial transport and are likely autochthonous. Martin and Varricchio (2010) report that 79% of the Pupichnia in their study occurred oblique to bedding, whereas in this study 66% were oblique (>5º plunge). All of the Pupichnia with oblique plunges in this study occurred in limestone, whereas most of the Pupichnia parallel to bedding (0–5º plunge) occurred in mudstone, likely an artifact of lithostatic compaction.

Osteological Elements

The excavation revealed osteological remains 0–15 cm below the level of cluster 1. The small size of the elements, lack of fusion between the neural arches and dorsal

centra, and absence of a well-developed periosteum on all elements indicate these are juvenile bones. Additionally, the proximal and distal ends of the fibula are poorly preserved, possibly a result of incomplete ossification (Horner, 1997). The limited number of preserved elements, combined with the juvenile status of the individuals, contributes to the difficulty of recognizing synapomorphies necessary for taxonomic identification. However, the lateral expansion of the premaxilla is characteristic of the Hadrosauridae (Sereno, 1986; Weishampel et al., 1993; Head, 1998). In addition, hadrosaur humeri are distinctive in that they possess a robust deltopectoral crest that extends from the proximal end of the bone to midshaft (Horner et al., 2004).

Hadrosaurs previously excavated from the Two Medicine Formation include *Prosaurolophus blackfeetensis, Gryposaurus latidens, Acristavus gagslarsoni, Hypacrosaurus stebingeri,* and *Maiasaura peeblesorum* (Varricchio and Horner, 1993; Varricchio, 1995, Gates et al., 2011). Due to the difficulty in differentiating ontogenetic from morphological features, the material described here was compared to other hadrosaur perinatal remains from the Two Medicine Formation: *M. peeblesorum* (Saurolophinae; Horner and Makela, 1979) from a nearby locality at the WCA and *H. stebingeri* (Lambeosaurinae; Horner and Currie, 1994) from the uppermost 100 m of the formation in northern Montana and southern Alberta. The deltopectoral crest in *Maiasaura* is smaller than that of *Hypacrosaurus,* projecting half the diameter of the shaft (Horner and Currie, 1994; Horner, 1999); however, comparing the juvenile humerus morphology of *M. peeblesorum* and *H. stebingeri* to the humerus described here reveals no substantial difference between the three. The premaxilla described in this study

appears to have a premaxillary foramen, which is present in *Maiasaura* but not *Hypacrosaurus* (Horner, 1983; Head, 1998); however, the premaxilla is incomplete and therefore this 'foramen' may result from breakage. For these reasons the juvenile remains are referred to Hadrosauridae but not assigned to a genus.

Comparison of elements from the quarry indicates that the fibula and metatarsal are smaller than would be expected, based on the size of the humerus, ribs, vertebrae, and skull elements. This suggests that the assemblage includes at least two different sized individuals (Fig. 24). Horner et al. (2000) describe a *Maiasaura peeblesorum* growth series and identified six distinct growth stages (based on bone histology), which they categorize by femur length. The femur length of the larger individual in this study would be approximately 6.38 cm long based on the size of the distal femur fragment from the quarry and the femur to humerus length ratio figured in Horner and Makela (1979, fig. 2). This corresponds to an overall body length of approximately 40 cm, which is smaller than the "early nestling" growth stage (femur length at 7 cm; body length at 45 cm) defined by Horner et al. (2000) and thus may represent a late embryonic or hatchling stage (i.e., perinate). Comparing the fibula to femur length ratio suggests a femur length of approximately 4.21 cm for the smaller individual. This corresponds with a body size of approximately 27 cm, which is considerably smaller than the "early nestling" growth stage and likely represents an embryo (Horner et al., 2000). Given that the the two bones from the smaller individual occur adjacent to eggs in cluster 1 and the elements from the larger individual occurred 15 cm below cluster 1, it is likely that at least two separate generations are represented by the assemblage.

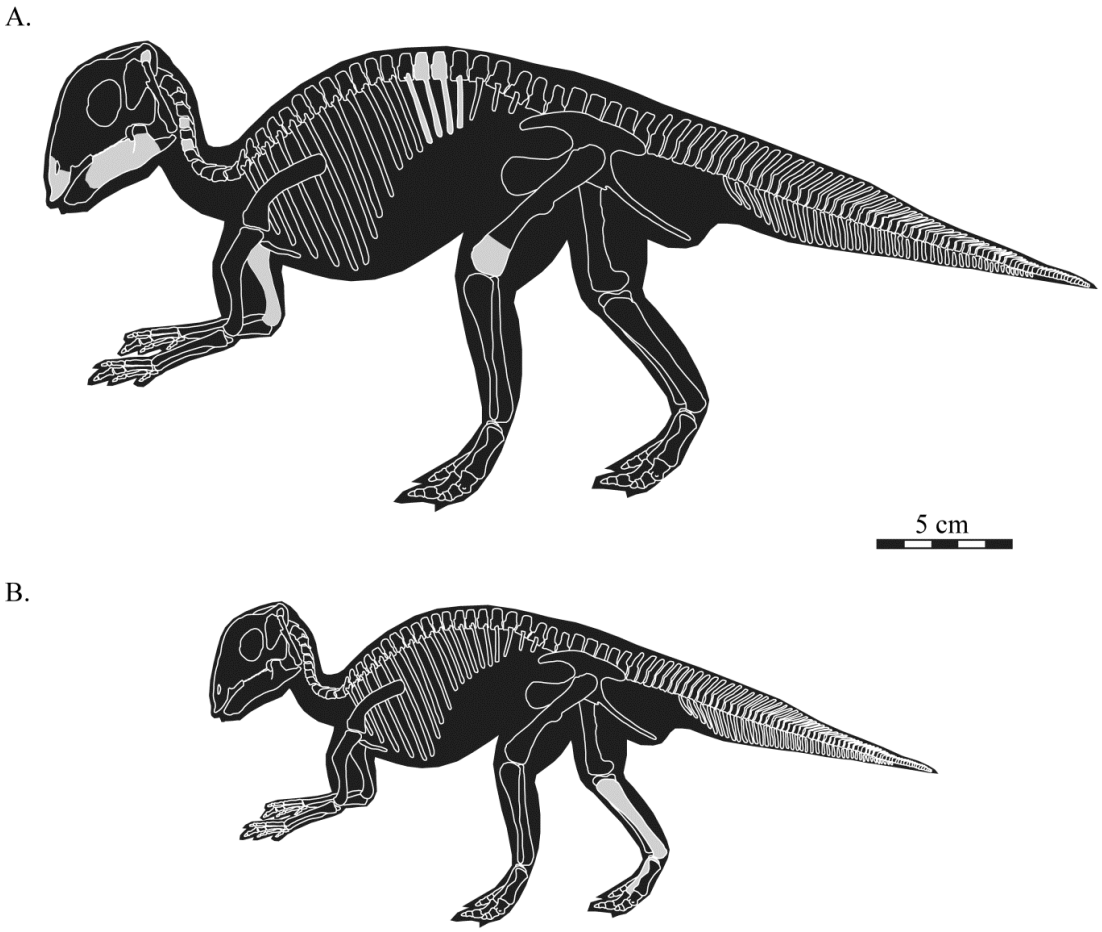

FIGURE 24—Perinatal hadrosaur skeleton with the bones described in this study highlighted. Positions of the ribs and vertebrae are estimated. A) Skull elements, ribs, vertebrae, humerus, and femur. B) Fibula and metatarsal are 28% smaller relative to elements in A, suggesting bones are from at least two individuals of different size. Image modified from a reconstructed *Maiasaura peeblesorum* nestling on display at the US National Museum (Smithsonian Institution), Washington DC.

The various elements of the skull were disarticulated but associated. The skull and limb elements are among the first elements to disarticulate from modern adult ungulate skeletons, whereas the ribs disarticulate later (Hill, 1979; Hill and Behrensmeyer, 1984).

Although the ribs were no longer articulated with the thoracic vertebrae, they were only slightly displaced, indicating that burial occurred shortly after the first stages of disarticulation and before the ribs became scattered. This was also characteristic of the small, unidentified tetrapod (likely a small lizard) below cluster 1. Additionally, the lack of preferred orientation in the long bones and Pupichnia suggests that they were not subject to fluvial transport (Voorhies, 1969). The overall lack of bone modification (breakage, tooth marks, boring, root etching, etc.) in both the hadrosaur and small tetrapod bones and the rapid degradation of juvenile bones observed in modern taxa (Behrensmeyer, 1978) further suggest limited exposure of these elements prior to burial; however, caution should be used when applying the results of taphonomic studies on modern adult large mammal bones to juvenile dinosaur and small tetrapod bones.

The three theropod teeth from the mudstone and limestone units at the quarry display blood grooves comparable to teeth referable to Tyrannosauridae from the Upper Cretaceous Judith River Formation described by Currie et al. (1990). The two tyrannosaurid teeth (MOR 7035-1 and MOR 7035-2) from bed L-2B were exposed at the surface and are highly fragmentary. The tyrannosaurid tooth below cluster 1 (MOR 6628-3) is relatively large, recurved, and exhibits longitudinal and oblique fracturing as well as enamel with gouges and missing flakes. Behrensmeyer (1978) noted that tooth weathering does not correlate well with the bone weathering stages; however, the high level of post-mortem modification displayed by the tooth suggests that it was likely exposed longer than the eggs, eggshell, and other osteological material.

Eggs and Eggshell

Unidentified cluster 1.—The unidentified eggs occur in two distinct groups (cluster 1 and cluster 2) on two discrete horizons suggesting separate nesting events. The egg shape is similar to *Maiasaura peeblesorum* from elsewhere in the WCA; however, the reconstructed egg radius is 1.5 x smaller (Horner, 1999). Thin sections, cathodoluminescence, and SEM imaging of eggshell from cluster 1 reveal that the calcite microstructure is completely recrystallized, hindering ootaxonomic assignment of the eggs. The dispersal of the eggs over a 2.5 m^2 area suggests that they are parautochthonous. The two discrete clusters of eggs suggests that the assemblage represents at least two clutches of eggs; however, the wide dispersal of eggs suggests the influence of a transport agent that spread the eggs out without moving them too far. Non-preservation of some eggs may also contribute to their current distribution.

Unidentified cluster 2.—Thin sections show that the eggshell preservation in cluster 2 is similar to cluster 1. Additionally, the eggs in cluster 2 (MOR 6630) are associated with large deposits of the mineral collophane. Klein and Dutrow (2008) note that collophane is often impure and contains calcium carbonate, which is also present in the XRD profile (Fig. 15). Terrestrial phosphate deposits are typically rare, occurring primarily in lacustrine, karst, and alluvial sand deposits (Thiry et al. 2006). Wilby and Whyte (1995) described localized phosphatization within bivalves. Because this alteration only occurred in articulated specimens, they conclude that the tightly articulated shells provided an enclosed microenvironment where phosphate, liberated by

soft tissue decay, could concentrate. Furthermore, the decay process created an acidic environment conducive to phosphate deposition (Fairbridge, 1983; Briggs and Kear, 1993; Wilby and Whyte, 1995). Additionally, McNamara et al. (2009) report localized phosphatization occurring in the stomachs of Miocene frogs preserved in lacustrine mudstone. They suggest that the enclosed, organic-rich, acidic environment of the stomach also provided an environment ideal for calcium phosphate deposition. Large deposits of apatite within the eggs of cluster 2 and thin deposits adhering to the inner and outer surfaces of the eggs of cluster 1 suggest that the eggs may also have provided an enclosed microenvironment favorable to phosphate deposition in the form of collophane, a process previously unreported for fossil eggs. The eggs in cluster 1 show a substantially greater degree of lithostatic compression than those of cluster 2. This suggests that precipitation of the collophane occurred during the early stages of diagenesis, either before or during sediment compaction. This allowed some compression of the eggs of cluster 2 but prevented the complete flattening observed in the eggs of cluster 1 (which lack substantial collophane deposits within the egg). The fact that the *Spheroolithus* eggshell fragments in and around the clusters are relatively unaltered suggests that the conditions favoring eggshell recrystallization were extremely localized around the eggs, potentially due to decay of the egg contents.

Spheroolithus eggshell fragments.—The eggshell fragments occurred 56% CCD, resembling eggshell previously documented assemblages transported by mudflows and *in situ* eggshells subject to chick trampling (Kennedy and Spencer, 1995; Hayward et al., 2011) The eggshells at Egg Mountain are dispersed over a 70 cm-thick interval of

mudstone and this ratio is not consistent at all depths (Oser and Jackson, 2014, fig. 8). The eggshell does not exhibit evidence of abrasion, indicating a parautochthonous origin (Oser and Jackson, 2014). The eggshell dispersion may be due to bioturbation; however, additional research is needed to determine whether bioturbation can induce abrasion on eggshell. In contrast to the eggs in the clusters, the eggshell fragments are not associated with collophane. The fragmentary eggshells are referable to the oofamily Spheroolithidae (Zhao, 1979; Mikhailov, 1991) and oogenus *Spheroolithus* (Zhao, 1979; Mikhailov, 1994) based on prolatospherulitic microstructure with sweeping extinction, prolatocanaliculate pores, and sagenotuberculate ornamentation. *Spheroolithus* is ascribed to the hadrosaur *Maiasaura peeblesorum* at WCA based upon eggshell association with hatchlings, although Hirsch and Quinn (1990) do not assign these eggs to an oospecies.

Spheroolithus sp. (Hirsch and Quinn, 1990) from the Two Medicine Formation is characterized by the following: (1) 1.0–1.2 mm thick eggshell; (2) widely spaced mammillary units with large interstices; (3) spherulitic shell units displaying sweeping extinction, and lack visible boundaries between units; (4) pronounced horizontal growth lines that follow the contour of the outer shell surface; (5) prolatocanaliculate pores with openings 0.08–0.12 mm in diameter; and (6) up to 0.3 mm high sagenotuberculate ornamentation. Zelenitsky and Hills (1997) established the oospecies *Spheroolithus albertensis* based on eggshell fragments from the contemporaneous Oldman Formation of Alberta, Canada. Diagnostic features included (1) 0.98–1.22 mm eggshell, (2) prolatospherulitic shell units, (3) primarily prolatocanaliculate pores, with some

rimocanaliculate pores, and (4) fine (< 0.2 mm high) sagenotuberculate ornamentation. Horizontal growth lines are also present. *Spheroolithus* sp. (Hirsch and Quinn, 1990) and *S. albertensis* (Zelenitsky and Hills, 1997) are similar in microstructure and thickness to each other and to the eggshell described here from Egg Mountain (Table 6). Zelenitsky and Hills (1997) distinguish *S. albertensis* from the eggshell described by Hirsch and Quinn (1990) based upon finer and more variable ornamentation; however, Carpenter (1999) informally assigns Hirsh and Quinn's *Spheroolithus* sp. to *S. albertensis.* While the average ornamentation height is similar, the maximum height of the *Spheroolithus* sp. eggshell ornamentation (0.3 mm) is greater than *S. albertensis* and the eggshell described here. The parautochthonous origin of the Egg Mountain *Spheroolithus* suggests that the reduced ornamentation height is not due to abrasion. The lack of pitting further indicates that the ornamentation height wasn't affected by chemical dissolution (Bravo et al., 2003; Smith and Hayward, 2010). The Egg Mountain material conforms to the diagnostic criteria of *S. albertensis* (Zelentisky and Hills, 1997); however, because the Egg Mountain material and *S. albertensis* both consist of fragmentary material, the eggshell described here is tentatively assigned to *S. albertensis*.

Interpretation of Incubation Environment

The porosity and gas conductance of the eggs of modern taxa directly reflect their incubation environment (Seymour, 1979; Deeming, 2006). Reptile eggs incubated in low oxygen environments such as vegetation mounds or burrows require a high eggshell

porosity to provide adequate oxygen to the growing embryo. In contrast, avian eggs incubated in open nests exhibit low porosity to prevent desiccation. Because fossilized archosaur eggs share many analogous features to those of modern archosaurs, calculation of gas conductance permits inferences about the nesting mode of extinct taxa (Seymour, 1979; Williams et al., 1984; Coombs, 1989; Sabath, 1991; Mikhailov, 1997; Deeming, 2006; Jackson et al., 2008; Grellet-Tinner et al., 2012; Varricchio et al., 2013).

Plotting calculated gas conductance values of extinct taxa against a regression line of modern avian egg values (Ar and Rahn, 1985) allows comparison of fossil eggs to avian eggs of similar mass. Because the vast majority of avian data included in the calculation of the regression line comes from eggs incubated in open nests (see Appendix B), values that fall above the regression line indicate a higher gas conductance than avian eggs of similar mass incubated in open nests, suggesting incubation in either an enclosed nest (e.g., vegetation mound, closed burrows) or humid nesting environment (e.g., floating nest in a lake or marsh). For example, the eggs of modern taxa that utilize vegetation mounds (e.g., some crocodilians and members of the Megapodiidae) (Packard et al., 1979; Seymour and Ackerman, 1980; Seymour et al., 1984; Vleck et al., 1984), floating nests (e.g., Western grebe, White-headed duck, Black tern, and Great northern loon) (Ar and Rahn, 1985), and burrows (e.g., some turtles and crocodilians) (Packard et al., 1979; Deeming and Thompson, 1991) for incubation exhibit gas conductance values above the regression line (Fig. 22). Taxa that nest in open burrows (e.g., Atlantic puffin, Bonin petrel) or in tree cavities (e.g., Tawny owl, Black-bellied whistling duck) have gas conductance values within the range of open nesters (Ar and Rahn, 1985). Water vapor

conductance is therefore an especially useful method to use when nesting trace criteria outlined by Chiappe et al. (2004) are lacking, as is the case with both Egg Mountain clusters.

The eggs of cluster 1 have gas conductance values 4–13 times higher than avian eggs of similar mass, suggesting an incubation strategy consistent with humid nesting environments. Although the average gas conductance of eggshell from region 1 is higher than region 2, the ranges overlap substantially. This suggests that either (1) the gas conductance does not vary significantly over the surface of the eggs; (2) some horizontal displacement occurred when the eggs were crushed such that region 1 and region 2 do not correspond to the poles and equator of the eggs, respectively; or (3) diagenesis may have altered the porosity enough to mask regional differences (Jackson et al., 2008). Because eggshell from the unidentified eggs exhibits a high degree of alteration, it is likely that the gas conductance values were also affected. For example, diagenetic eggshell thinning would artificially increase gas conductance values. Thus the calculated gas conductance and inferred nesting mode should be considered a first estimate. In contrast, the *Spheroolithus* eggshell fragments associated with the clusters do not display evidence of substantial alteration. They have gas conductance values 16–32 times higher than avian eggs of similar mass, also suggesting a humid nesting environment (Fig. 22). These values are similar to those reported by Deeming (2006) for *Spheroolithus* from Canada and Korea.

The error margins on the gas conductance values reported in this study are relatively high (9–31%). The error for each individual measurement was very low (<

1%); however, propagating multiple sources of measurement error through the gas conductance equation expands the error margin. Combining measurement error with the variability in pore shape and eggshell thickness increases the margin even more. It should be noted that previous studies have not addressed error propagation and these error margins are likely typical of other studies as well.

Finally, it should be noted that the gas conductance values for alligator (*Alligator mississippiensis*) and turtle (*Trionyx spiniferus*) originally reported by Packard et al. (1979) are misreported in subsequent literature. The actual values in the paper are 0.387 $g \cdot d^{-1} \cdot kPa^{-1}$ and 0.108 $g \cdot d^{-1} \cdot kPa^{-1}$ for *Alligator* and *Trionyx*, respectively. These values are equivalent to 51.6 mg $H_20 \cdot day^{-1} \cdot Torr^{-1}$ and 14.4 mg $H_20 \cdot day^{-1} \cdot Torr^{-1}$. Citing Packard et al. (1979), however, Garcia et al. (2008), Jackson et al. (2008), and Grellet-Tinner et al. (2012) report erroneous values of 2903 and 810 mg $H_20 \cdot day^{-1} \cdot Torr^{-1}$ for *Alligator* and *Trionyx*, respectively.

SUMMARY AND CONCLUSIONS

The Egg Mountain locality is an especially prolific dinosaur nesting site in the Upper Cretaceous Two Medicine Formation of western Montana, USA. A new quarry at a stratigraphically lower level than previous excavations reveals two clusters of unidentified eggs, hadrosaur perinatal bones, and abundant *Spheroolithus* eggshell fragments. Ichnofacies and lithology of the site support the previous interpretation of a

seasonally wet and dry environment for the upper coastal plain during the Late Cretaceous (Lorenz and Gavin, 1984; Carpenter, 1987; Rogers, 1990; Varricchio, 1995; Varricchio and Horner, 1993; Falcon-Lang, 2003; Martin and Varricchio, 2010). The mudstone likely represents deposition that occurred in a terrestrial, low energy environment with plant colonization on the distal portion of a floodplain. The limestone beds above the clusters are consistent with either paleocaliche or deposition of carbonate-rich mud in small ephemeral bodies of water. Further sampling is required to determine the origin of the limestones at the site.

Two clusters of spherical unidentified eggs up to 12 cm in diameter occur on two stratigraphic horizons. The stratigraphically lower cluster (cluster 1) contains 22 lithologically compressed eggs dispersed over a 2.5 m^2 NE-SW trending cone-shaped area, suggesting that they are likely parautochthonous. The stratigraphically higher cluster (cluster 2) contains 6–7 eggs distributed in an E-W trending line with one egg 0.7 m to the NE. The eggs in the clusters display a preservation process previously unreported in fossil eggs, in which eggs provided an enclosed microenvironment during decay that facilitated localized collophane deposition. The limited lithologic compaction of the eggs with large collophane deposits suggests that collophane deposition occurred early in diagenesis, before the eggs had a chance to be compressed. The lack of sedimentary structures associated with the clusters and *Spheroolithus* eggshell fragments prohibits the identification of a nest structure; however, the incubation environment can be inferred by calculating gas conductance. The gas conductance values for unidentified eggs and *Spheroolithus* eggshell are, respectively, 4–13 and 16–32 times higher than

avian eggs of similar mass, suggesting a high humidity and low oxygen environment consistent with burial, vegetation mounds, or similar incubation environments.

Although *Spheroolithus* eggshell and hadrosaur perinatal remains are relatively common at some localities at the WCA, this represents the first documented occurrence at Egg Mountain. The perinatal hadrosaur osteological remains at Egg Mountain are assigned to the Hadrosauridae based on morphological features of the skull and humerus. Further taxonomic assignment is hindered by the limited number of elements and the juvenile status of the individuals. The condition and articulation of the hadrosaur perinatal bones indicates limited subaerial exposure with little or no transport. It is likely that the site was utilized by hadrosaurs prior to or during egg laying of the unidentified clutches. *Spheroolithus* eggshell fragments and associated perinatal remains occurring below clutch 1 suggests that the site was first utilized by hadrosaurs. *Spheroolithus* eggshell fragments and hadrosaur embryonic remains within egg cluster 1 could be the result of contemporaneous nesting or incorporation of recently deposited eggshell and osteological remains into the clutch during nest excavation and egg-laying. The eggs of cluster 1 were then dispersed to the SW by some transport agent, though it it unlikely that they were transported more than a couple meters beyond the boundary of the clutch. The eggs of cluster 2 were laid sometime after interment of cluster 1, with similar incorporation of *Spheroolithus* eggshell fragments. The presence of *Troodon formosus* nests, *Continuoolithus* eggs and eggshell, *Spheroolithus* eggshell, and the unidentified egg clusters occurring at multiple stratigraphic levels at Egg Mountain further

demonstrates that regardless of incubation strategy, this locality provided a favorable site for nesting activity over multiple seasons (Horner, 1982).

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CHAPTER THREE

SEDIMENT AND EGGSHELL INTERACTIONS: USING ABRASION TO ASSESS TRANSPORT IN FOSSIL EGGSHELL ACCUMULATIONS

Contribution of Authors and Co-Authors

Manuscripts in Chapters 2 and 3

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Contributions: Collected the materials, conducted experiments, collected and analyzed data, wrote manuscript.

Co-Author: Frankie D. Jackson

Contributions: Provided discussion and substantial edits.

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Sediment and eggshell interactions: using abrasion to assess transport in fossil eggshell accumulations

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Recent excavation at the Late Cretaceous Egg Mountain locality in Montana revealed abundant *Spheroolithus* eggshell fragments. Determining the depositional history of the fragments is problematic due to the vertical dispersal of eggshell in homogenous mudstone. The results of previous studies assessing eggshell transport are based on thin, modern eggshell occurring on well-defined horizons. Therefore, assessment of depositional history required a different method. Chicken (*Gallus gallus domesticus*) and ostrich (*Struthio camelus*) eggshells were placed in a tumbler with water and quartz sand for 168-504 hours to simulate transport. The resulting wear on these fragments, revealed under scanning electron microscope (SEM), was compared to unabraded eggshell. In addition, the modern eggshell was compared to fossil eggshells from a nesting site, crevasse splay and channel deposits, and Egg Mountain. Fossil eggshells from high energy palaeoenvironments display similar edge rounding to modern eggshell placed in the tumbler. In contrast, eggshell from Egg Mountain lacked edge rounding and resembled fossil eggshell from a nesting site and unabraded modern eggshell, suggesting that the Egg Mountain locality represents a parautochthonous assemblage. This study indicates that sediment interaction leaves distinct patterns of abrasion on eggshell, which may be useful for assessing transport of eggshell at fossil localities.

Keywords: taphonomy; transport; eggshell; abrasion;

Sediment and eggshell interactions: using abrasion to assess transport in fossil eggshell accumulations

1. Introduction

Fossil nesting sites provide a unique opportunity to investigate the reproductive biology and nesting behavior of extinct taxa. Detailed taphonomic assessment of each locality is required prior to interpretation, especially when evaluating whether eggshell fragments at a nesting site have been transported. For example, dinosaur nesting sites at the Museum of the Rockies (MOR) Egg Mountain locality (TM 006) in the Upper Cretaceous Two Medicine Formation, Teton County, western Montana (Horner et al. 2001; Figure 1) include abundant dinosaur eggshell fragments. In 2011 and 2012, excavation of a new site on the south side of the Egg Mountain locality revealed two egg-bearing horizons within a 70 cm-thick interval of homogenous mudstone containing *Spheroolithus* eggshell fragments. Eggshells do not occur on discrete horizons and abundance and orientation ratios vary throughout the section. The transport history of these fragments is unclear based upon existing taphonomic techniques. Determining the taphonomic history of fossil assemblages represents a challenge, given the complex processes that acted upon the biological materials (e.g. bioturbation, abrasion, dissolution). For this reason, an increasing number of researchers recognize the value of documenting physical attributes of biological remains (e.g. bones, eggshell) in modern environments. In addition, actualistic experiments provide a better understanding of how taphonomic processes such as fluvial transport influence organic mineralized remains.

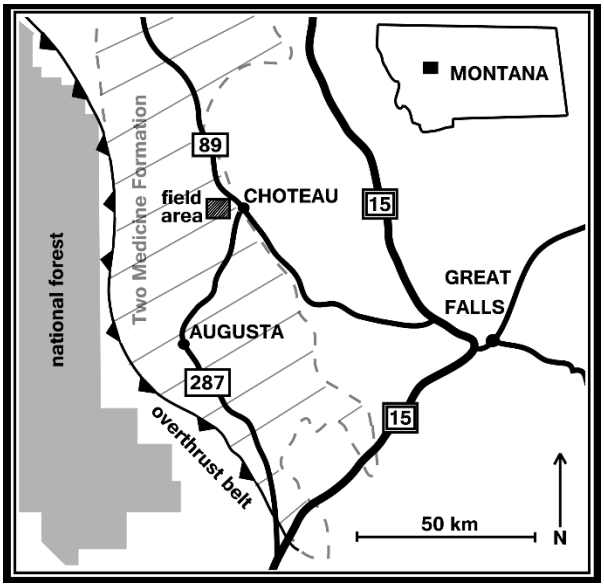

Figure 1. Egg Mountain field area and surrounding region, showing the extent of the Two Medicine Formation (modified from Lorenz 1981 and Google Maps).

The presence of abrasion and preferred orientation have been used to assess the transport history of bones and invertebrate skeletal remains (Hunt 1978; Shipman 1981; Behrensmeyer 1982, Brett and Baird 1986; Shipman and Rose 1988; Fernandez-Jalvo and Andrews 2003; Thompson et al. 2011). Similar taphonomic attributes are also applicable to studies of fossil eggshell, and several studies investigate two proxies for eggshell transport: ratios of concave-up (CCU) to concave-down (CCD) eggshells (Figure 2; Kennedy and Spencer 1995; Hayward et al. 1997; Owen and Hayward 1997; Hayward et al. 2000; Hayward et al. 2011; Imai 2012; Wang et al. forthcoming date) and eggshell fragment size (Tokaryk and Storer 1991). Additionally, environmental conditions and biotic activity can produce corrosion of eggshell surface features (Bravo et al. 2003; Clayburn et al. 2004; Smith and Hayward, 2010). It is therefore necessary to

consider as many potential causes of eggshell surface alteration as possible before interpreting a particular feature as transport-induced. A review of the literature on taphonomic features of modern and fossil eggshell demonstrates how physical and chemical processes can influence eggshell orientation and preservation.

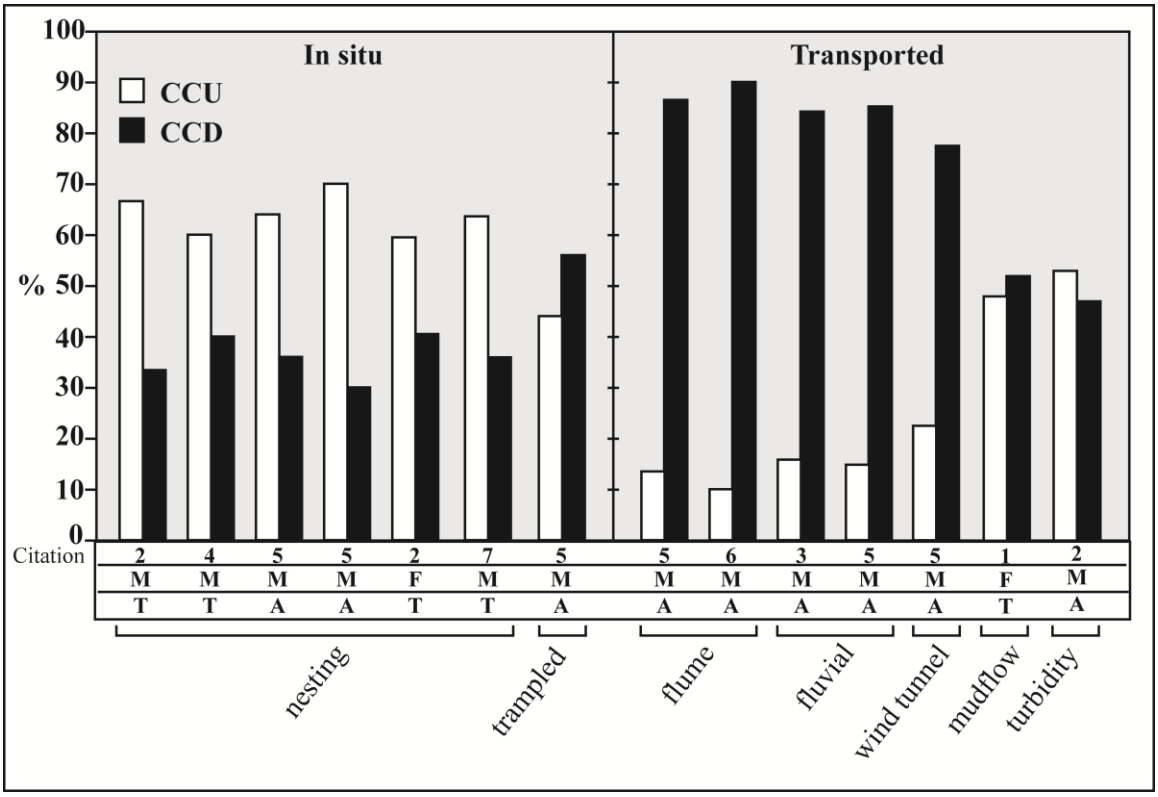

Figure 2. The ratio of concave-up (CCU) to concave-down (CCD) eggshell fragments from parautochthonous and transported environments. Reference numbers are: 1) Kennedy and Spencer 1995; 2) Hayward et al. 1997; 3) Owen and Hayward 1997; 4) Hayward et al. 2000; 5) Hayward et al. 2011 (rough substrate); and 6) Imai 2012; 7) Wang et al. (forthcoming date). Abbreviations: 'M' refers to studies conducted on modern eggshell, 'F' refers to fossil eggshell. 'A' indicates actualistic studies and 'T' indicates taphonomic studies.

Hayward et al. (2000) examined modern glaucous-winged gull (*Larus glaucescens*) colonies to determine the general characteristics of large nesting grounds

and compared the results to dinosaur nesting sites. They reported that 37–40% of eggshell occurred CCD at two gull colonies, and that these values were similar to those of a dinosaur nesting site (39.5% CCD) at Devil's Coulee in the Oldman Formation, Alberta, Canada. Hayward et al. (1997) reported similar values at an *L. glaucescens* egg cannibal midden (33% CCD) and a dinosaur nesting site in the St. Mary's Formation near Augusta, MT (40% CCD). Wang et al (forthcoming date) examined nests at a common tern (*Sterna hirundo*) colony and recorded that 36% of eggshell occurred CCD at hatching sites. In contrast, Kennedy and Spencer (1995) examined transported dinosaur eggshell from a mudflow deposit and report that 52% of the eggshell occurred CCD.

Researchers conducted actualistic experiments to simulate hatching sites as well as transport environments in order to observe the effects of organism behavior and transport on eggshell orientation. Hayward et al. (2011) constructed controlled nesting arenas and examined how hatching and trampling by chicks effected eggshell orientation. They also investigated the behavior of eggshell in a wind tunnel, flume, and natural stream. Hatching (without subsequent trampling) resulted in 38% CCD eggshells, whereas chick trampling produced 56% CCD fragments. In contrast, transport via wind tunnel, flume, and natural stream yielded 75–80%, 85–88%, and 85% CCD eggshell fragments, respectively. Imai (2012) examined eggshell in a flume and reported an even greater proportion of CCD eggshell fragments (up to 90%). Hayward et al. (1997) simulated turbidity flows, observing that 47% of eggshell was deposited CCD. Eggshell size, however, does not necessarily correlate to transport history. For example, Tokaryk and Storer (1991) placed chicken eggshells in a tumbler with sand and water for 70 hours

and observed no change in eggshell fragment size (i.e. the eggshells failed to show further fracturing or fragmentation). Finally, Owen and Hayward (1997) placed chicken eggshell in a natural stream and reported that 84% of the recovered eggshells were deposited CCD.

Several studies assess the chemical alteration of eggshell prior to interment (Bravo et al. 2003; Clayburn et al. 2004; Smith and Hayward, 2010). Clayburn et al. (2004) noted that exposure to moist acidic habitats leaves distinct traces on the eggshell compared to dry alkaline habitats. Bravo et al. (2003) reported that dissolution features occur on the inner surface of the eggshell, resembling resorption craters. In addition, Smith and Hayward (2010) observed bacterial dissolution of modern gull eggshell and noted that eggshell colonized by bacteria exhibited pitting on the surface. Recognizing dissolution features can help distinguish whether edge rounding was caused by abrasion or chemical alteration.

Taphonomic and actualistic experiments described above provide valuable information for understanding the physical and chemical processes that influence eggshell distribution and condition in fossil localities. However, these studies focus on eggshell accumulations at or near the ground surface that form discrete horizons, which may not provide comparable analogs for some fossil localities. For example, dinosaur nesting sites at the Egg Mountain locality often exhibit sparse, dispersed eggshell fragments throughout homogenous mudstone. This distribution differs significantly from modern eggshells that occur on discrete, well-defined horizons at modern colonial nesting sites. In addition, eggshell thickness may be a factor influencing how fragments are

oriented by fluvial transport. The thickness of the glaucous-winged gull (*Larus glaucescens*) eggshell used in several orientation studies (Hayward et al. 1997; Owen and Hayward 1997; Hayward et al. 2000; Hayward et al. 2011) is 0.3–0.4 mm (Speich et al. 1992), which is much thinner than the 1.2 mm-thick dinosaur eggshell at Egg Mountain. In addition, the disparate nesting strategies utilized by dinosaurs and modern birds may also affect eggshell distribution. Finally, comparing eggshell orientation ratios at Egg Mountain with data from actualistic studies is also problematic because the sample size for fossil eggshell at any one stratigraphic level is small and the eggshells may have been deposited asynchronously. Thus, taphonomic assessment required a different approach for ascertaining eggshell transport.

The purpose of this study is to: 1) document features resulting from abrasion on modern eggshell; 2) determine if similar features occur in fossil eggshell; 3) determine if the presence of abrasion corresponds to transported assemblages; and 4) use these comparisons as a baseline for recognizing potential transport of eggshell at the Egg Mountain locality. Further, this approach will be used to test the following hypotheses: H1) eggshell subjected to abrasion will consistently display signs of edge wear as a result; and H2) fossil eggshell from high energy depositional environments will display edge rounding, whereas untransported eggshell from nesting localities will not. The method described here can be used to augment existing tools for reconstructing taphonomic history and provide a broadly applicable means to identify transported eggshell.

2. Materials and methods

2.1 Definitions

Here, abrasion describes the interaction between sediment grains and the eggshell surface when: 1) entrained eggshells contact sediment grains in the bed load and/or suspended load during any type of fluid transport, or 2) moving grains contact eggshell that remains stationary on the bed. Both situations can abrade modern bone (Behrensmeyer 1982; Thompson et al. 2011) and therefore warrant consideration. The term 'edge wear' describes the result of sediment interaction with the edges of eggshell (i.e. abrasion) and includes rounded and/or chipped edges, whereas 'edge rounding' refers to rounding of eggshell edges by any agent (i.e. it can be the result of abrasion or chemical dissolution). In addition, 'parautochthonous' is used to describe eggshell fragments from nesting localities that were either untransported or transported for short distances. In the latter case eggshell may have washed out of the nest and been deposited within the nesting area without signs of abrasion.

2.2 Modern eggshell

Chicken (*Gallus gallus domesticus*) eggshell was selected due to its availability and similar thickness (~0.3 mm) to the gull eggshell examined in previous studies (Hayward et al. 1997, 2000, 2011). In contrast, the thicker (~2 mm) ostrich (*Struthio camelus*) eggshell more closely resembles dinosaur eggshell. Before tumbling, the chicken eggshell included the cuticle, shell membrane, and traces of amnion, whereas the ostrich eggshell

included the cuticle. Chicken eggshells were broken into approximately 1 cm^2 fragments and allowed to dry. Thirty fragments were divided into three, ten-fragment groups and placed in a 1600 cm^3 Thumler model A-R2, No. 115 tumbler drum with 300 mL of sand and the remaining space filled with tap water. Sand consisted of rounded quartz grains ranging from 0.5–1.0 mm in diameter. Groups A, B, and C were tumbled for one week, two weeks, and three weeks, respectively. Groups A and B also included one ostrich eggshell fragment each. The 12.7 cm diameter tumbler ran constantly at approximately 60 rpm, resulting in a tangential velocity of 0.67 cm/s at the edge of the drum. Eggshell fragments were removed from the tumbler, washed to remove residual sand grains, and placed under a lamp to dry for six hours. All samples were placed in an Emitech sputter coater for 45 seconds at 20 mA and coated with 15 nm of iridium, then grounded with colloidal graphite. Eggshells were imaged at 20 kV under a scanning electron microscope (SEM; JEOL model JSM-6100) at the Image and Chemical Analysis Laboratory (ICAL), Montana State University (MSU). Imaging of additional eggshells that were not placed in the tumbler (10 chicken and 2 ostrich) provided a control group for comparison.

2.3 Fossil eggshell

Six fossil eggshell fragments from three localities (one nesting site and two transported assemblages) provide a baseline for comparing the Egg Mountain material. Two eggshells come from the Jackknife site in the Cretaceous (Albian-Cenomanian) Wayan Formation, Caribou National Forest, Idaho. One fragment (IMNH 2428/49609) occurred in situ within a horizon containing eggshell fragments and partial eggs interpreted as a

nesting site, whereas the other (IMNH 2428/49613) was collected as surface float prior to excavation (Simon, 2012). Four eggshells (2 each: TMP-2008-051-0095 and TMP-2008-051-0046) are from two localities, interpreted as crevasse splay and fluvial channel deposits, in the Upper Cretaceous Judith River Group, Dinosaur Provincial Park, Alberta, Canada (Eberth 1990; Brinkman 1998). *Spheroolithus* eggshells (n= 178) were collected from the Egg Mountain locality with their orientation (CCU vs. CCD) noted at the time of excavation. These eggshells (MOR 7036-1) come from the vicinity of two clutches (MOR 6628–MOR 6630) and associated perinatal remains (MOR 6631) within homogenous mudstone at the quarry. Eggshells from all localities are of similar thickness (~1 mm) and size (5–10 mm). The three eggshells from Egg Mountain and one from the Jackknife locality were randomly selected for SEM imaging from a collection of eggshells set aside because they occurred in situ and separated from the matrix intact without damage. The specimen collected as float from the Jackknife locality and samples from the Judith River Group were also randomly selected. The fossil eggshells were placed in a Desk II Dentron vacuum sputter coater at 45 mA for 30 seconds and coated with 23 nm of gold, then imaged at 15–20 kV using the Aspex LLC Personal SEM in the Gabriel Laboratory for Molecular and Cellular Biology at the Museum of the Rockies.

3. Results

3.1 Modern eggshell

Scanning electron microscope images reveal that the chicken eggshell completely lost the cuticle after one week. With continued abrasion the eggshell surface became polished and the pore openings enlarged. Both chicken and ostrich eggshell displayed progressive edge wear and loss of surface detail over the course of the experiment; namely the sharp, irregular edges of freshly broken surfaces became increasingly rounded and smooth (Figures 3, 4). Edge wear appeared more uniform in chicken than ostrich eggshell, and the latter acquired a stepped appearance as sections of the cuticle cracked and separated from the specimen. In addition, the incidence of eggshell breakage was low (2 of 10 samples of chicken eggshell from Group C), consistent with observations of Tokaryk and Storer (1991).

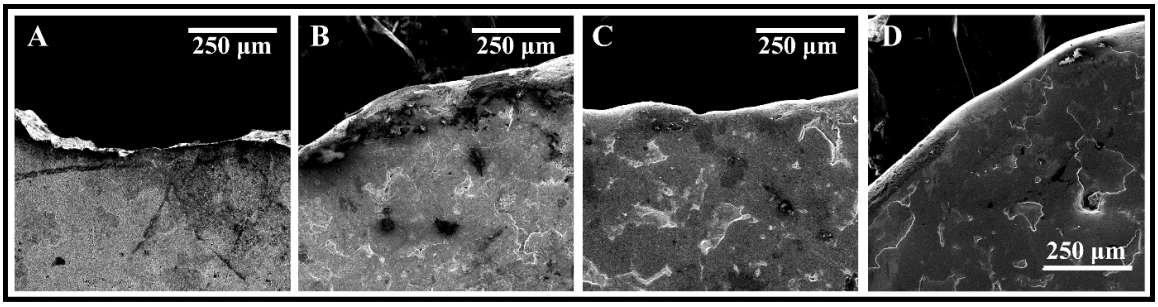

Figure 3. Substantial, progressive edge wear in chicken (*Gallus gallus domesticus*) eggshell after tumbling. (A) Fresh edge. (B) Edge wear after one week. (C) After two weeks. (D) Edge completely rounded after three weeks.

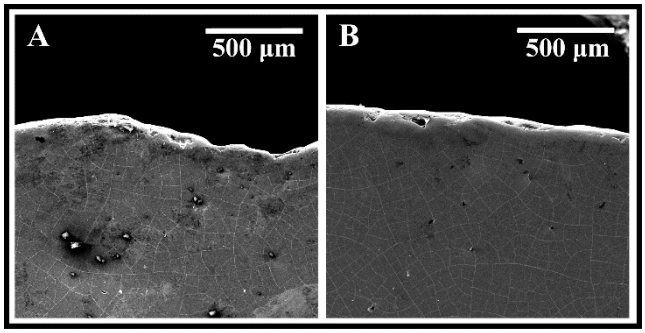

Figure 4. Edge wear present in ostrich (*Struthio camelus*) eggshell after tumbling. (A) Evident edge wear after one week. (B) After two weeks.

3.2 Fossil eggshell

Scanning electron microscope examination of both in situ fossil eggshell and eggshell collected as float from the Jackknife locality revealed sharp, irregular edges (Figure 5). In contrast, SEM imaging revealed that transported fossil eggshell from crevasse splay and channel deposits showed substantial edge rounding similar to that observed on abraded chicken eggshell (Figures 6, 7). Because the loan agreement for the transported fossil material prohibited destructive analyses (e.g., thin sectioning), it was not possible to confidently assign the eggshells to a specific ootaxon. Thus, it is not possible to assess potential changes to pore openings and ornamentation in the transported fossil eggshell at this time, hindering comparisons to untransported material of the same ootaxa.

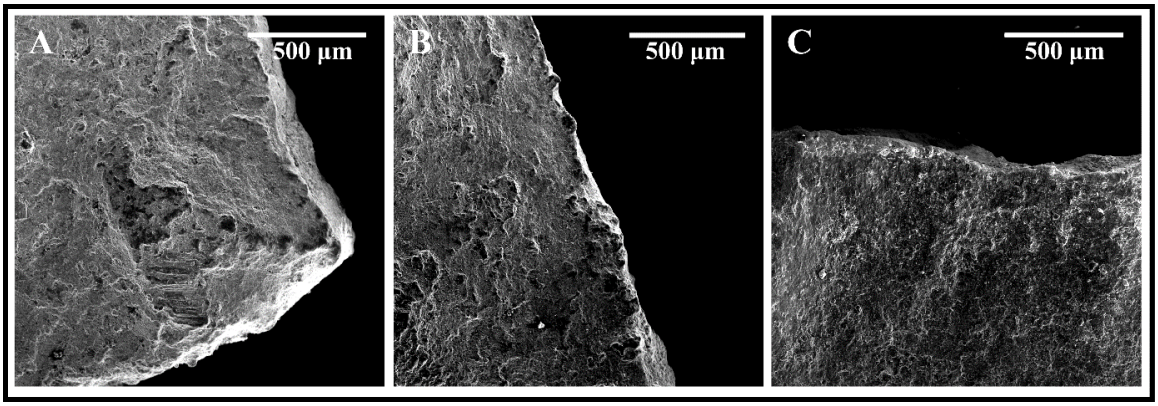

Figure 5. Eggshell fragments from the Jackknife locality, a nesting site in the Wayan Formation, Caribou National Forest, Idaho. (A, B) In situ fragment. (C) Fragment collected as float. Neither sample displays evidence of edge rounding.

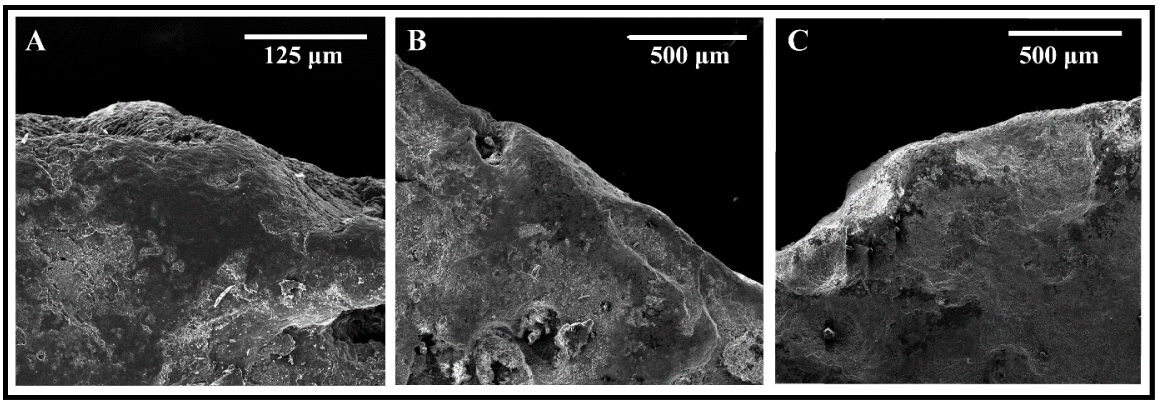

Figure 6. Eggshell fragments from a crevasse splay deposit (RTM locality BB104, TMP-2008-051-0095) in the Dinosaur Park Formation, Dinosaur Provincial Park, Alberta, Canada. All samples display edge rounding.

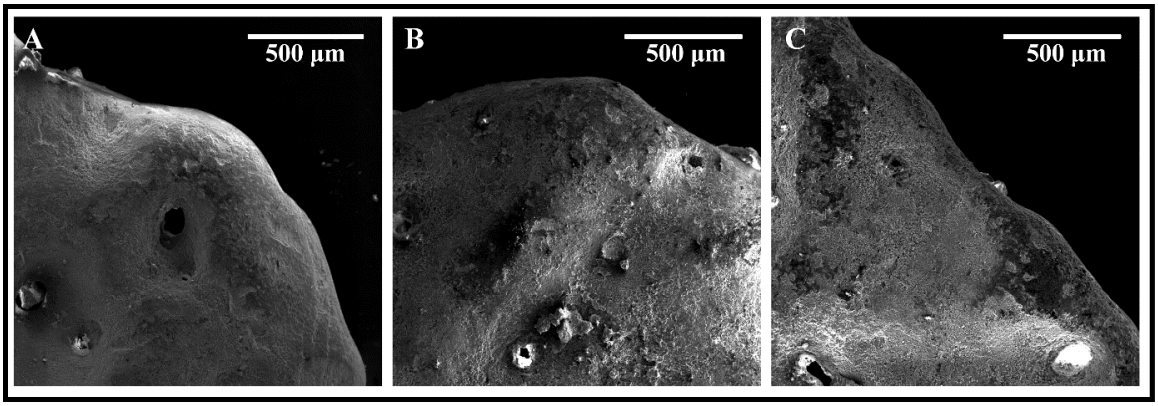

Figure 7. Eggshell fragments from a channel deposit (RTM locality BB105, TMP-2008-051-0046) in the Oldman Formation, Dinosaur Provincial Park, Alberta, Canada. All samples display a high degree of edge rounding.

Orientation data for all *Spheroolithus* eggshell fragments from the Egg Mountain quarry revealed that 56% occurred CCD. An uneven distribution of eggshell fragments characterized the 70 cm-thick interval at the site, resulting in low sample sizes at any 1 cm increment. Binning the data from 5 cm-thick increments allowed calculation of CCD percentages at different depths and revealed that the value is not consistent at all depths (Figure 8). Under SEM, the Egg Mountain material exhibited sharp edges with no evidence of edge rounding, similar to unabraded chicken eggshell and fossil eggshell from the Jackknife nesting site (Figure 9; Table 1).

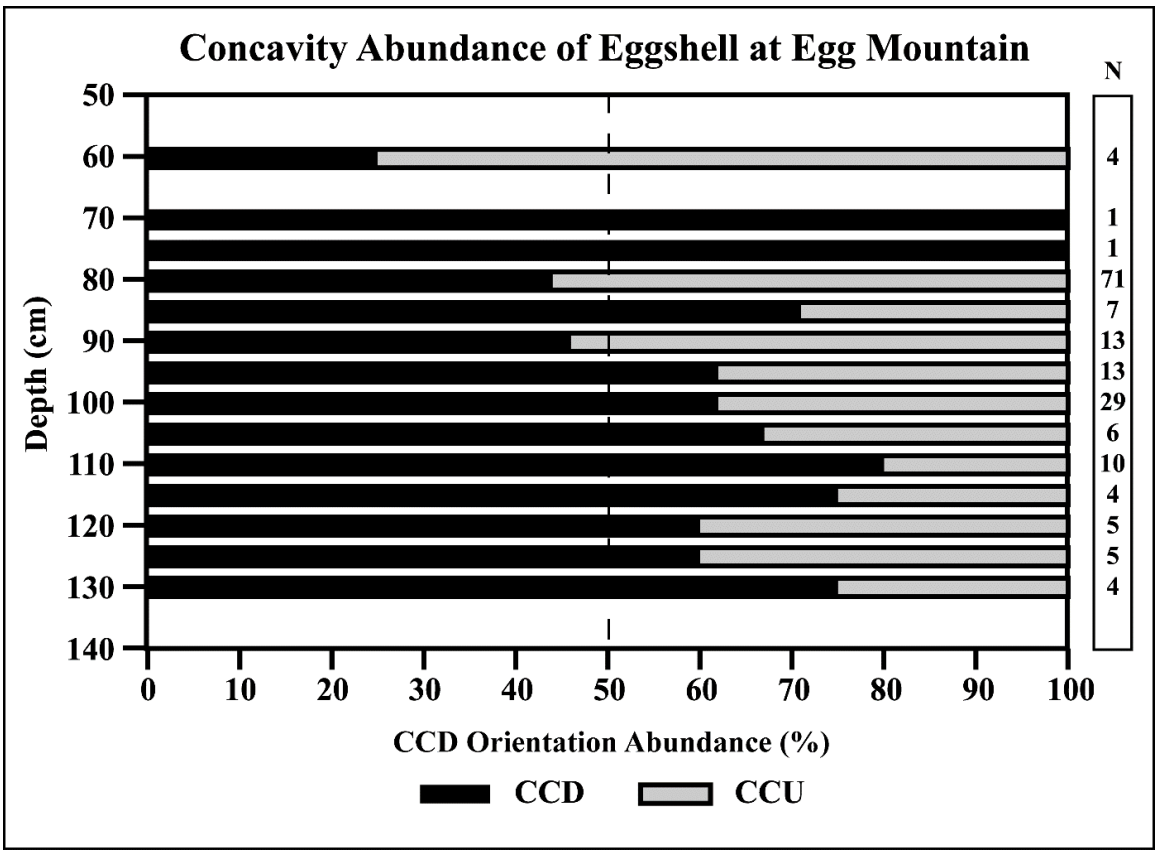

Figure 8. Distribution of concave-up (CCU) versus concave-down (CCD) *Spheroolithus* eggshell fragments from a 70 cm vertical section at the Egg Mountain (TM 006) locality.

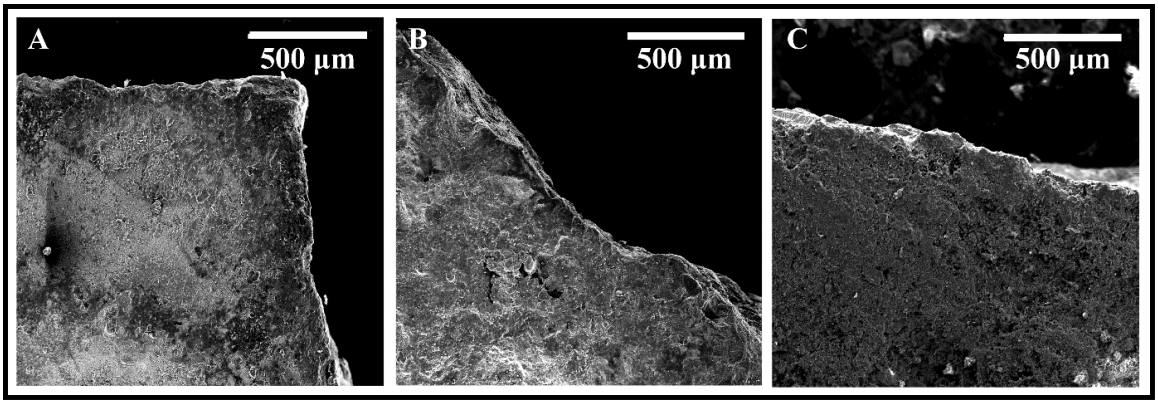

Figure 9. *Spheroolithus* eggshell fragments (A: MOR6629-1, B: MOR6629-4, and C: MOR6628-1) from Egg Mountain (TM 006). The edges are sharp, resembling unabraded modern eggshell and fossil eggshell from a nesting site (Jackknife Locality, IMNH 2428).

Table 1: Fossil eggshell from four localities.

Sample number	Locality	Formation	Depositional history	Edge rounding present?
IMNH 2428/49609	Jackknife IMNH 2428	Wayan	parautochthonous nesting site	No
IMNH 2428/49613	Jackknife IMNH 2428	Wayan	'Float' at nesting site	no
TMP-2008-051-0095	U-2 BB104	Dinosaur Park	Transported (crevasse splay)	yes
TMP-2008-051-0046	Dave's II BB105	Oldman	Transported (channel)	yes
MOR6629-1, MOR6629-4, and MOR6628-1	Egg Mountain TM 006	Two Medicine	Under study	no

4. Discussion

Based upon sedimentologic characteristics alone, it remained unclear whether the eggshell fragments from Egg Mountain represented a parautochthonous or transported assemblage. The *Spheroolithus* fragments occurred 56% CCD, similar to values reported for transported assemblages (Kennedy and Spencer 1995; Hayward et al. 1997; and Kennedy 1997). However, comparing Egg Mountain data to these and other reports is problematic for several reasons. These studies document chicken and gull eggshell, which are substantially thinner (0.3–0.4 mm) than ~1.0 mm-thick fossil eggshell. In addition, gulls and chickens incubate their eggs in open nests, whereas gas conductance values indicate that many fossil dinosaur eggs (including *Spheroolithus*) were incubated in enclosed nests (Deeming 2006). Eggshell from open nests are exposed at the surface and can be readily weathered, transported, or abraded in place. In contrast, eggshell

buried in the substrate or vegetation would be more protected. Additionally, the developmental stage of hatchlings represents an important consideration. Altricial hatchlings linger in the nest and require parental care, whereas precocial hatchlings leave the nest shortly after hatching. Both developmental strategies are present in modern avians. For example, California condors (*Gymnogyps californianus*) spend five months in the nest before leaving (Amadon 1964), whereas megapode chicks leave the nest immediately after hatching (Coombs 1989). Similar variation in nest occupation is hypothesized for dinosaurs. Evidence suggests that *Maiasaura* hatchlings were altricial, whereas *Troodon*, *Psittacosaurus*, and oviraptorids were precocial (Coombs 1980; Horner 1984; Horner and Weishampel 1988; Horner and Weishampel 1996; Weishampel et al. 2008). Altricial hatchlings may increase bioturbation and dispersal of eggshell at a nesting site.

Assessing transport history at Egg Mountain required an understanding of how sediment/eggshell interactions might modify features in modern eggshell, whether similar features occur in fossil eggshell, and if so, whether they correspond to specific depositional environments. Two hypotheses were tested in order to address these questions: H1) eggshell subjected to abrasion will consistently display edge wear; and H2) fossil eggshell from high energy depositional environments will display edge rounding, whereas untransported eggshell from nesting localities will not. The results of the current study showed that modern chicken and ostrich eggshell developed edge wear when abraded, thus supporting H1. Fossil eggshell from two transport depositional environments in Dinosaur Provincial Park revealed edge rounding similar to chicken and

ostrich eggshell that had been abraded in a tumbler. Inner and outer surfaces of the fossil eggshell did not display pitting, thus it is unlikely that edge rounding resulted from bacterial or groundwater dissolution (Bravo et al. 2003; Smith and Hayward, 2010). Flume studies show that bone abrasion can occur without transport (Behrensmeyer 1982; Thompson et al. 2011); therefore, sediment-eggshell interaction may not represent a direct indicator of transport and thus may indicate a potential limitation of this study.

In contrast to the eggshell from transport environments, those from the Jackknife nesting site exhibit sharply defined edges consistent with the absence of abrasion, thus supporting H2. Eggshell collected as surface float also has sharp, irregular edges, demonstrating that short-term subaerial exposure of untransported fossil material fails to produce observable rounding. The *Spheroolithus* eggshell fragments at Egg Mountain also have sharp edges, comparable with observations of untransported eggshell at the Jackknife nesting site.

While the first signs of edge wear in modern eggshell became apparent after one week in the tumbler, determining the minimum transport distance required to produce wear is difficult. Tumbler time cannot be equated to fluvial transport distance (Shipman and Rose 1988). Transport within fluvial systems is intermittent, occurs at varying speeds, and can include various sediment sizes and types. Thus biotic remains are subject to varying amounts of abrasion. Whereas minimal transport will cause changes in the orientation ratio in flume studies on rough substrates (Imai 2013), controlled experiments in fluvial systems are required to determine how much transport or in situ abrasion would be necessary to produce wear.

5. Conclusions

Determining whether a fossil eggshell assemblage represents a nesting site or transported accumulation significantly impacts interpretations of the reproductive biology of extinct taxa, especially when eggshells are associated with nesting traces or bones. Examination of modern eggshell placed in a tumbler revealed that sediment interaction abrades eggshell, resulting in edge wear (supporting H1). Examination of fossil eggshell under SEM revealed that edge rounding corresponded to depositional environment (supporting H2). Eggshell from crevasse splay and channel deposits displayed edge rounding, whereas eggshell from a nesting site lacked this feature. Distinguishing transport-induced abrasion from other possible causes of edge rounding requires attention to sedimentologic context and careful examination of eggshell surface features. *Spheroolithus* eggshell from the recent excavation at Egg Mountain did not display edge rounding, suggesting that they were parautochthonous and that the locality represents a nesting site. Simply inferring transport on the basis of edge rounding remains problematic given other possible causes, whereas its absence supports the interpretation of a nesting locality. Future studies focused on eggshell dissolution may be useful in differentiating transport abrasion from other potential causes of edge rounding. In addition, conducting studies in natural fluvial environments would produce more realistic conditions than tumblers in a laboratory setting.

The method proposed in this study can be used to augment existing methods and provide a more broadly applicable way of identifying transported eggshell than previous

techniques alone. This approach is particularly useful under the following circumstances: 1) the sample size is low, 2) the fossil eggshell does not occur in discrete horizons, or 3) when sedimentologic characteristics alone are insufficient for determining the depositional history of the fossil material.

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CONCLUSIONS

The fossil material from the Willow Creek anticline in western Montana is an important source of information of the reproductive behavior of multiple extinct taxa, not only in the quantity of well-preserved material but also the diversity of eggs, eggshell, and perinatal osteological remains. Situated on a coastal plain with seasonal variations in precipitation, the region provided an especially favorable nesting environment during the Cretaceous. Egg Mountain is an especially prolific nesting site at the WCA, hosting five ootaxa at multiple stratigraphic levels. The primary excavation near the uppermost limestone at the locality revealed nests of the theropod *Troodon formosus* (oospecies *Prismatoolithus levis*). Additional excavations have revealed eggs of the oospecies *Continuoolithus canadensis* as well as a small, unidentified avian-like egg. A new quarry at a lower stratigraphic level revealed two clusters of an unidentified ootaxon, *Spheroolithus* eggshell fragments, and hadrosaur perinatal osteological remains.

Ichnofacies and lithology of the site support the previous interpretation of a seasonally wet and dry environment for the upper coastal plain during the Late Cretaceous (Lorenz and Gavin, 1984; Carpenter, 1987; Crabtree, 1987; Rogers, 1990; Varricchio, 1993, 1995; Varricchio and Horner, 1993; Falcon-Lang, 2003; Martin and Varricchio, 2010). The mudstone likely represents deposition that occurred in a terrestrial, low energy environment with plant colonization on the distal portion of a floodplain. The limestone beds above the egg clusters are consistent with either paleocaliche or deposition of lime mud in small ephemeral bodies of water.

Two clusters of spherical unidentified eggs up to 12 cm in diameter occur on two stratigraphic horizons. The stratigraphically lower cluster (cluster 1) contains 22 lithologically compressed eggs dispersed over a 2.5 m^2 NE-SW trending cone-shaped area, suggesting that they are likely parautochthonous. The stratigraphically higher cluster (cluster 2) contains 6–7 eggs distributed in an E-W trending line with one egg 0.7 m to the NE. The eggs in the clusters display a preservation process previously unreported in fossil eggs, in which eggs provided an enclosed microenvironment during decay that facilitated localized collophane deposition. The fragmentary eggshell was tentatively assigned to *Spheroolithus albertensis* based on size, shell microstructure, ornamentation, and pore structure. These eggshell fragments occurred 56% CCD. Previous studies at other nesting sites use the ratio of CCU/CCD eggshell fragments to ascertain the transport history (Kennedy and Spencer 1995; Hayward et al. 1997; Owen and Hayward 1997; Hayward et al. 2000; Hayward et al. 2011; Imai 2012). The *Spheroolithus* eggshell at Egg Mountain is dispersed through a 70-cm thick section with varying ratios throughout. Instead of using the CCU/CCD ratio, abrasion of eggshell fragments was used to infer transport history. Modern chicken (*Gallus gallus domesticus*) and ostrich (*Struthio camelus*) eggshell were placed in a tumbler with quartz sand to simulate the effects of transport on eggshell. The tumbled modern eggshells and fossil eggshells recovered from high energy channel and crevasse splay deposits displayed substantial edge wear under SEM, whereas fossil eggshell from a parautochthonous nest site and *Spheroolithus* eggshell from Egg Mountain did not, suggesting that the *Spheroolithus* eggshell was parautochthonous.

The lack of sedimentary structures associated with the egg clusters and *Spheroolithus* eggshell fragments prohibits the identification of a nest structure; however, incubation environment can be inferred by calculating gas conductance. The gas conductance values for unidentified eggs and *Spheroolithus* eggshell are, respectively, 4–13 and 16–32 times higher than avian eggs of similar mass, suggesting a high humidity and low oxygen environment consistent with burial, vegetation mounds, or similar incubation environments.

Although *Spheroolithus* eggshell and hadrosaur perinatal remains are relatively common at some localities at the WCA, this represents the first documented occurrence at Egg Mountain. The perinatal hadrosaur osteological remains at Egg Mountain are assigned to the Hadrosauridae based on morphological features of the skull and humerus. Further taxonomic assignment is hindered by the limited number of elements and the juvenile status of the individuals. The condition and articulation of the hadrosaur perinatal bones indicates limited subaerial exposure with little or no transport. The presence of parautochthonous *Spheroolithus* eggshell fragments and associated hadrosaur perinatal remains suggest that the nesting site was utilized by hadrosaurs prior to or during egg laying of the unidentified egg clusters. The presence of *Troodon formosus* nests, *Continuoolithus* eggs and eggshell, *Spheroolithus* eggshell, and the unidentified clusters occurring at multiple stratigraphic levels at Egg Mountain further demonstrates that regardless of incubation strategy, this locality provided a favorable site for nesting activity over multiple seasons (Horner, 1982).

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APPENDICES

APPENDIX A

PROPAGATING ERROR IN THE GAS CONDUCTANCE EQUATION

When calculating a value based upon uncertain quantities, it is important to propagate the uncertainty in order to determine the error of the final value. The quantities used in the gas conductance (G_{H2O}) equation have two types of uncertainty: measurement and variability. Measurement uncertainty is the error associated with the tools or methods used to measure a quantity. The errors associated with ImageJ measurements were calculated using the average deviation of multiple measurements taken at each scale used. The errors associated with all other measuring instruments used in this study are the least counts (i.e., the smallest increment marked on the instrument).

Propagating the error associated with pore diameter and eggshell thickness also required incorporating variation as a source of uncertainty. The diameter of a single pore varies along its length in *Spheroolithus* eggshell. Because the area for each pore is measured at a single cross section, it is impossible to know whether the measurement represents the maximum, minimum, or an intermediate diameter of the pore. Additionally, when a tangential section is made from a curved eggshell surface with pores radiating outward, the section will crosscut pores at increasing angles further from the center of the specimen. Thus, a circular pore will appear as an ellipse and will have a larger apparent cross-sectional area (see Section 2). The error introduced in this way is negligible (< 1%) and is not accounted for in this study.

One radial thin section exposed a cross section of a pore, allowing measurement of pore diameter variation. The variation in eggshell thickness (Ls) was measured using 134 measurements of 5 *Spheroolithus* samples and 76 measurements of 7 samples of unidentified eggshell.

The equation used for propagating the error in the G_{H2O} equation is derived below. See tables A1 and A2 for the list of terms.

Term	Definition	Value/Units	Uncertain?
G_{H2O}	Water vapor conductance	mg $H_20 \cdot day^{-1} \cdot Torr^{-1}$	Yes
C	Conversion factor	1.5569×10^9 $sec \cdot mg \cdot day^{-1} \cdot mol^{-1}$	No
R	Universal gas constant	6.236×10^4 $cm^3 \cdot Torr \cdot mol^{-1} \cdot K^{-1}$	No
T	Absolute temperature	298.15 K	No
D_{H2O}	Diffusion coefficient of water in air	0.25 $cm^2 \cdot s^{-1}$	No
A_p	Total pore area of the egg	cm^2	Yes
L	Pore length (=L_S)	Cm	Yes

TABLE A1— Variables and constants used in Equation 1 (Seymour, 1979; Paganelli, 1980).

Term	Definition	Units
u{term}	uncertainty of the term	
N	Number of pores measured	
D	diameter of single pore	Cm
m_p	measurement error for the area of a pore	cm^2
SA_1	Surface area of the measured fragment	cm^2
SA	Surface area of the egg	cm^2
A_{P1}	Pore area of the measured fragment	cm^2
L_S	Eggshell thickness	Cm
L_{SM}	measurement error of eggshell thickness	Cm

TABLE A2—Variables used in Equation 6.

Equations

Gas Conductance Equation. —

$$G_{H2O} = \frac{C}{R \cdot T} \cdot D_{H2O} \cdot \frac{A_p}{L} \qquad [A1]$$

Uncertainty Equations.—

$$u\{A+B\} = u\{A-B\} = \sqrt{u\{A\}^2 + u\{B\}^2} \quad \text{[A2]}$$

$$u\left\{\frac{A}{B}\right\} = \frac{A}{B} \cdot \sqrt{\left(\frac{u\{A\}}{A}\right)^2 + \left(\frac{u\{B\}}{B}\right)^2} \quad \text{[A3]}$$

$$u\{A \cdot B\} = (A \cdot B) \cdot \sqrt{\left(\frac{u\{A\}}{A}\right)^2 + \left(\frac{u\{B\}}{B}\right)^2} \quad \text{[A4]}$$

$u\{k \cdot A\} = k \cdot u\{A\}$ where k is any constant [A5]

Derivation

Uncertainty of A_P.—

$$A_P = A_{P1} \cdot \frac{SA}{SA_1}$$

Area variability of a single pore due to pore geometry:

$$u\{A_g\} = \frac{\left(\pi\frac{d_{max}}{2}^2 - \pi\frac{d_{min}}{2}^2\right)}{2}$$

Uncertainty of A_{P1} due to pore geometry (Eq. A2):

$$u\{A_{P1G}\} = \sqrt{u\{A_g\}^2 \cdot N}$$

Uncertainty of A_{P1} due to measurement error (Eq. A2):

$$u\{A_{P1M}\} = \sqrt{{m_p}^2 \cdot N}$$

Uncertainty of A_{P1} (Eq. A2):

$$u\{A_{P1}\} = \sqrt{u\{A_{P1G}\}^2 + u\{A_{P1M}\}^2} = \sqrt{\left(u\{A_g\}^2 \cdot N\right) + \left({m_p}^2 \cdot N\right)}$$

Uncertainty of SA/SA_1 (Eq. A3):

$$u\left\{\frac{SA}{SA_1}\right\} = \frac{SA}{SA_1} \cdot \sqrt{\left(\frac{u(SA)}{SA}\right)^2 + \left(\frac{u(SA_1)}{SA_1}\right)^2}$$

Uncertainty of A_P (Eq. A4):

$$u\{A_P\} = A_P \cdot \sqrt{\left(\frac{u\{A_{P1}\}}{A_{P1}}\right)^2 + \left(\frac{u\{\frac{SA}{SA_1}\}}{\frac{SA}{SA_1}}\right)^2}$$

$$u\{A_P\} = A_P \cdot \sqrt{\left(\frac{\sqrt{\left(u\{A_g\}^2 \cdot N\right) + \left({m_p}^2 \cdot N\right)}}{A_{P1}}\right)^2 + \left(\frac{\frac{SA}{SA_1} \cdot \sqrt{\left(\frac{u(SA)}{SA}\right)^2 + \left(\frac{u(SA_1)}{SA_1}\right)^2}}{SA_1}\right)^2}$$

Uncertainty of L (L_S). —

Uncertainty of L_S due to variation in eggshell thickness:

$$u\{L_S\} = \frac{L_{Smax} - L_{Smin}}{2}$$

Uncertainty of L_S including eggshell thickness variation and measurement error (Eq. A2):

$$u\{L_S\} = \sqrt{\left(\frac{L_{Smax} - L_{Smin}}{2}\right)^2 + {L_{SM}}^2}$$

Uncertainty of A_P/L (Eq. 3).—

$$u\left\{\frac{A_P}{L}\right\} = \frac{A_P}{L} \cdot \sqrt{\left(\frac{u\{A_P\}}{A_P}\right)^2 + \left(\frac{u\{L\}}{L}\right)^2}$$

$$u\left\{\frac{A_P}{L}\right\} = \frac{A_P}{L} \cdot$$

$$\sqrt{\left(\sqrt{\left(\frac{\sqrt{\left(u\{A_g\}^2 \cdot N\right)+\left(m_p{}^2 \cdot N\right)}}{A_{P1}}\right)^2 + \left(\frac{\frac{SA}{SA_1}\cdot\sqrt{\left(\frac{u(SA)}{SA}\right)^2+\left(\frac{u(SA_1)}{SA_1}\right)^2}}{SA_1}\right)^2}\right)^2 + \left(\frac{\sqrt{\left(\frac{L_{Smax}-L_{Smin}}{2}\right)^2+L_{SM}{}^2}}{L}\right)^2}$$

Uncertainty of G_{H2O} (Eq. A1 and A5).—

$$u\{G_{H2O}\} = \left(\frac{C \cdot D_{H2O}}{R \cdot T}\right) \cdot u\left\{\frac{A_P}{L}\right\}$$

$$u\{G_{H2O}\} = \left(\frac{C \cdot D_{H2O}}{R \cdot T}\right) \cdot \frac{A_P}{L} \cdot$$

$$\sqrt{\left(\sqrt{\left(\frac{\sqrt{\left(u\{A_g\}^2 \cdot N\right)+\left(m_p{}^2 \cdot N\right)}}{A_{P1}}\right)^2 + \left(\frac{\frac{SA}{SA_1}\cdot\sqrt{\left(\frac{u(SA)}{SA}\right)^2+\left(\frac{u(SA_1)}{SA_1}\right)^2}}{SA_1}\right)^2}\right)^2 + \left(\frac{\sqrt{\left(\frac{L_{Smax}-L_{Smin}}{2}\right)^2+L_{SM}{}^2}}{L_S}\right)^2}$$

$$u\{G_{H2O}\} = G_{H2O} \cdot$$

$$\sqrt{\left(\sqrt{\left(\frac{\sqrt{\left(\left(\frac{\left(\pi\frac{d_{max}}{2}{}^2-\pi\frac{d_{min}}{2}{}^2\right)}{2}\right)^2 \cdot N\right)+\left(m_p{}^2 \cdot N\right)}}{A_{P1}}\right)^2 + \left(\frac{\frac{SA}{SA_1}\cdot\sqrt{\left(\frac{u(SA)}{SA}\right)^2+\left(\frac{u(SA_1)}{SA_1}\right)^2}}{SA_1}\right)^2}\right)^2 + \left(\frac{\sqrt{\left(\frac{L_{Smax}-L_{Smin}}{2}\right)^2+L_{SM}{}^2}}{L_S}\right)^2}$$

(6)

Section 2

Pores ideally radiate outward generally perpendicular to a line tangent to the eggshell surface. Thus, when a flat tangential section is made from the curved surface of an eggshell, the cross sections of the pores will occur at increasing angles further from the center of the specimen. Modeling the pores as simple cylinders, any angled cross section will result in an ellipse, resulting in increasing apparent pore area further from the center of the specimen (peripheral extension: i.e., $b > r$).

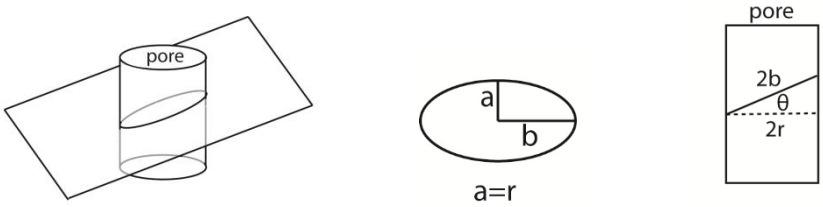

Figure A1: The angled cross section of a cylindrical pore is an ellipse, the dimensions of which are dependent on the angle (θ) of the cross section (i.e., the distance of the pore from the center of the specimen (L)).

What follows are calculations to model how much larger the apparent pore area will be and to determine the percent error expected from measuring pore area directly from tangential sections (without taking the peripheral extension into account).

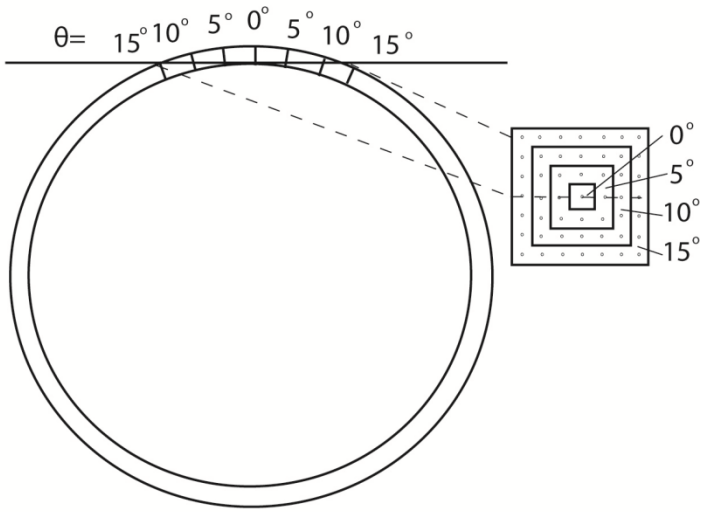

Figure A2: Hypothetical spherical egg with known θ. The angles that the pores intersect are equivalent to their angle away from the center of the specimen. Inset is the top view of the hypothetical sampled section, with an even distribution of pores.

Equations and Variables

R = radius of spherical egg (mm) (measured to center of eggshell)

r = radius of pore (mm) (i.e., smallest axis of ellipse)

L = distance of pore from center of sample (mm) (measured from center of sample)

b = half of major axis of ellipse (mm) (i.e., r + distortion)

A_P = pore area (mm^2)

$A_{P(L)}$= pore area as a function of L (includes peripheral distortion) (mm^2)

A_E = ellipse area (mm^2)

L_S = shell thickness (mm)

θ = angle of incidence (degrees)

$A_E = \pi r b$

$G_{H2O} = \frac{A_P}{0.477 L_S}$ (Ar and Rahn 1985)

$\%error = \frac{|\exp erimental - actual|}{actual} * 100$

Calculations

Area of extended pore:

$Cos\theta = \frac{2r}{2b} \quad \rightarrow \quad b = \frac{r}{Cos\theta}$

$A_E = \pi r b$

$A_E = \frac{\pi r^2}{Cos\theta}$ [A6]

Sample pore area calculation of hypothetical sample in Figure 2:

49 pores (r = 1 mm); 1 at 0 ^{o}, 8 at 5 ^{o}, 16 at 10 ^{o}, and 24 at 15^o.

$A_{P\ exp}$ = 3.14 + 25.23 + 51.04 + 78.06 = **157.47 mm^2**.

$A_{P\ act}$= 3.14 x 49 = **153.86 mm^2**.

Error = $\frac{|153.86 - 157.47|}{153.86} * 100 = 2.35\%$

The angle of incidence will not be readily measurable while looking at tangential sections, thus it must be solved for in terms of measurable variables:

Angle of incidence (higher angles = higher distortion)

$$Tan\theta = \frac{L}{R}$$

$$\theta = Tan^{-1}\left(\frac{L}{R}\right) \qquad \text{[A7]}$$

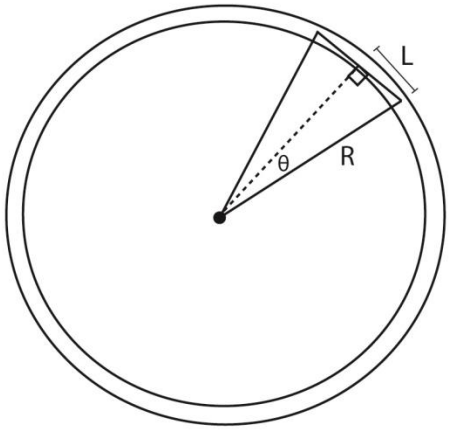

Figure A3: Hypothetical spherical egg with θ unknown. L is the distance of each pore from the center of the sample, R is the radius of the egg.

Area of the pore as a function of distance from the center of the sample (substitute equation A7 into equation A6):

$$A_{p(L)} = \frac{\pi r^2}{Cos(Tan^{-1}(L/R))} \qquad \text{[A8]}$$

Sample calculation of porosity with θ unknown, using Figure A4. Assume r = 1 mm and R = 30 mm:

Pore	L (mm)	$A_{p(L)}$
1	1.49	3.1455
2	1.58	3.1459
3	2.6	3.1534
4	0.27	3.1417
5	0.78	3.1427
6	2.53	3.1527
7	2.96	3.1568

Table A3: Values for pores pictured in the hypothetical sample in Figure A4.

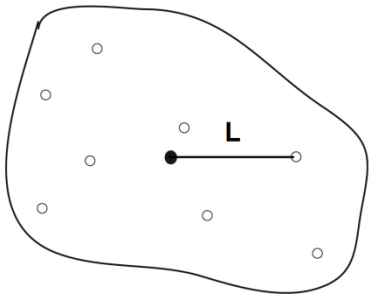

Figure A4: Hypothetical sample, with unknown θ and an uneven distribution of pores.

$A_{p(L)\exp} = 22.039\,mm^2$ (using equation A8)

$A_{p(L)act} = 3.14 * 7 = 21.991\,mm^2$ (using equation A8, L=0)

$$\%error = \frac{|22.039 - 21.991|}{21.991} * 100 = 0.22\%$$

Significantly less error when smaller angles (>6°) are used and fewer pores are measured.

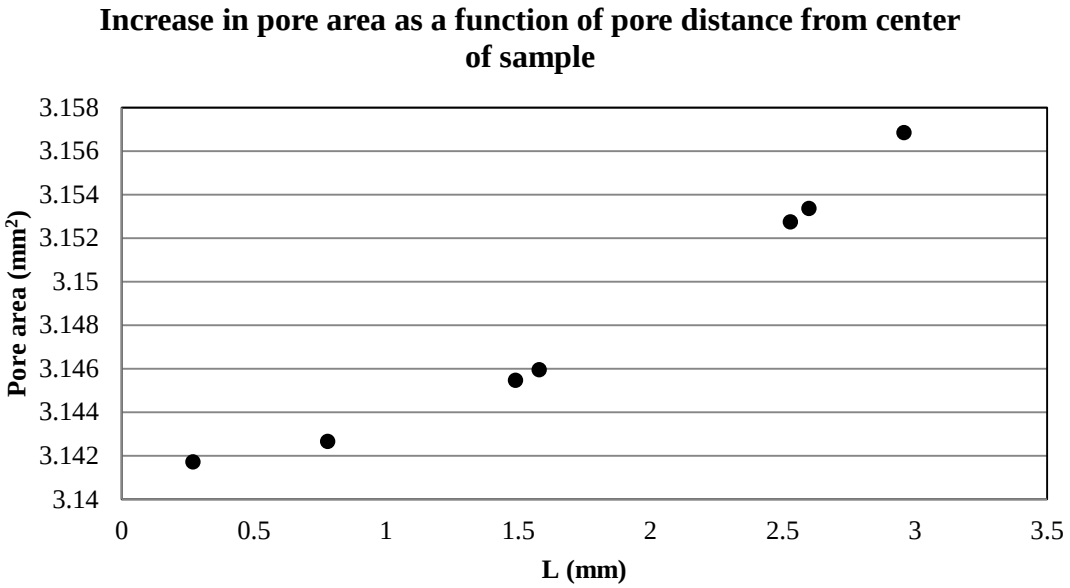

Figure A5: Chart displaying how pore area varies with distance from center of sample. The actual pore area is given where L=0. Values taken from Table A3.

The error introduced by not accounting for peripheral extension is minimal, and the assumptions of using this method may outweigh the influence of the error it's trying to correct. (i.e., spherical, undistorted egg, cylindrical pores intersecting surface perpendicular to tangent, position of sample center subject to error). If the above assumptions were to prove accurate, the simplest way to compensate is to treat the minor axis of each ellipse as the diameter (i.e., a= r). Thus, it is perhaps best not to include correction of the peripheral extension, but to note that there is a small error in the porosity.

APPENDIX B

A NOTE ON COMPARING FOSSIL EGGSHELL GAS CONDUCTANCE VALUES TO MODERN AVIAN DATASETS

It is common practice in gas conductance studies to compare the gas conductance values of fossil eggshell with the regression line of modern avian values calculated by Ar and Rahn (1985). It is assumed that values above the regression line indicate a higher gas conductance than avian eggs of similar mass incubated in open nests, suggesting incubation in a humid nesting environment; however, dataset includes a variety of nesting environments and this method only works because the vast majority of avian data included in the calculation of the regression line comes from eggs incubated in open nests (Fig. B1). Ideally, it would be best to only include data from open nests for this type of comparison.

Isolating the open nest avian data resulted in a regression just below the line for the combined data (Fig. B2). Additionally, the regression line has a slightly better fit when the open nest data is isolated (R^2 of 0.9272 vs. 0.8968 for the combined data) (Fig. B3).

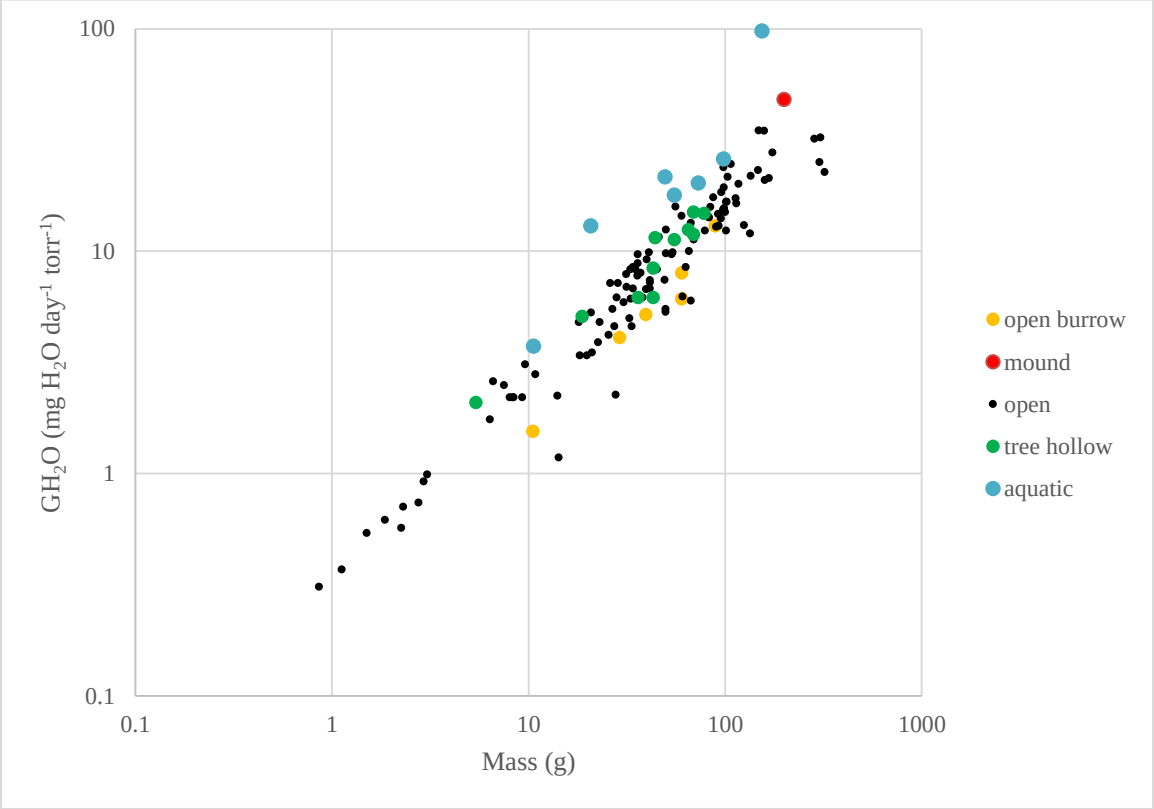

Figure B1: Chart displaying the diversity of nest types included in the modern avian dataset and the distribution of gas conductance values across each type. Aquatic nesters and the one megapode fall above the rest of the data. Birds that nest in open burrows and tree hollows are well within the 'open' neste range, presumably because these types of nests don't restrict airflow.
Open burrow = a hole dug into the ground without burying the eggs, an opening remains (e.g., Puffins)
Mound = vegetation mound (e.g., megapodes and crocadilians)
Open = an uncovered nest occurring in tree branches or upon the ground surface
Tree hollow = an open space within a tree trunk (living or dead)
Aquatic = a floating nest. Here, nests suspended immediately above the water surface on reeds are also included

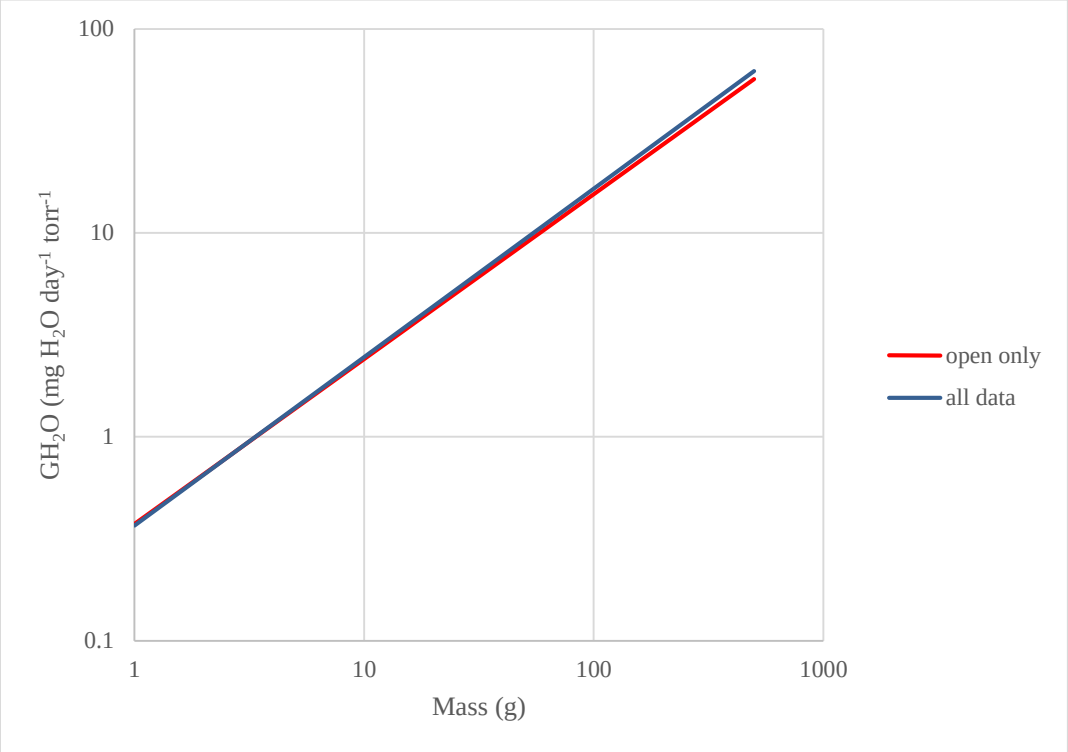

Figure B2: Isolating the open nest data resulted in a shallower regression line.

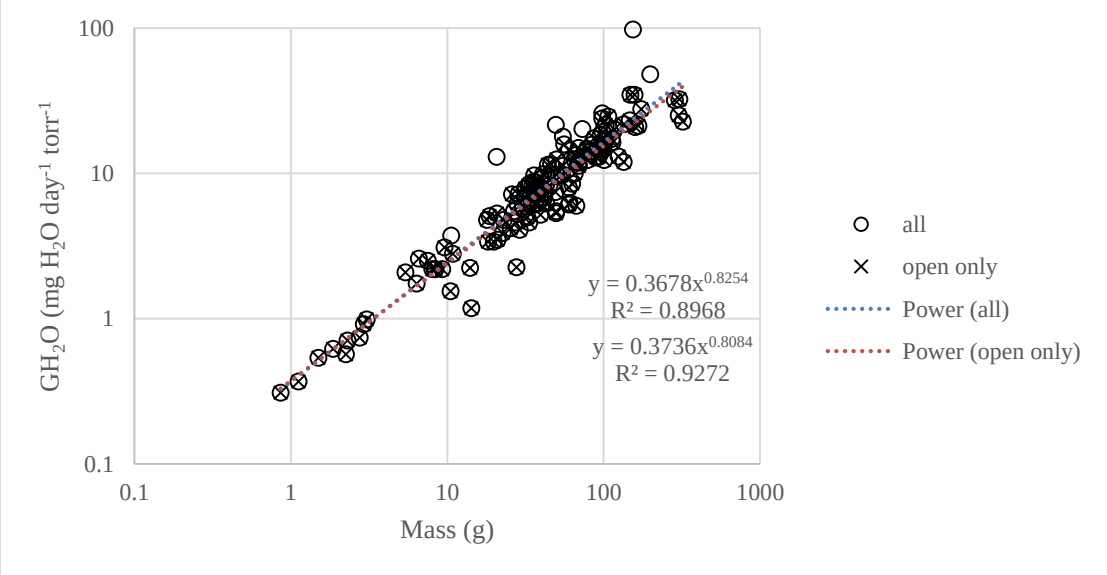

Figure B3: Isolating the open nest data resulted in a better fit for the regression line.