

PALEOECOLOGICAL UTILITY OF FEEDING TRACES AT EGG MOUNTAIN, A
RICH TERRESTRIAL VERTEBRATE LOCALITY OF THE UPPER CRETACEOUS
TWO MEDICINE FORMATION, MONTANA, U.S.A.

by

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ABSTRACT

The Egg Mountain locality is a rich terrestrial vertebrate site from the Upper Cretaceous Two Medicine Formation of Montana. Numerous skeletal remains and nesting and dwelling traces of insects and other invertebrates, mammals, lizards, and carnivorous and herbivorous dinosaurs are known from the locality. Despite the diversity of different taxa and behaviors represented, little is known about their respective ecologies. To address this, I investigate a series of feeding traces, including regurgitalites (fossil gastric pellets) and invertebrate fecal pellets, and assess their potential trace-makers and paleoecological and paleoenvironmental implications for the site.

Two amalgams of the metatherian *Alphadon halleyi* are identified as regurgitalites based on the presence of multiple individuals in a confined area, an abundance of paired and indigestible tooth-bearing cranial elements, extensive breakage and disarticulation, and periosteal corrosion patterns attributable to digestion. These are the first mammal-bearing regurgitalites from the Mesozoic. A third amalgam is composed of the multituberculate *Filikomys primaevus* and is represented by crushed skulls and abundant articulated postcrania, suggestive of a non-predatory origin. The available evidence favors *Troodon formosus* as the regurgitalite producer. The similar taphonomic features of these regurgitalites and the prey in regurgitates of diurnal raptors suggest *Troodon* may have manipulated prey during feeding. The ability to egest pellets in a large-bodied, non-volant troodontid supports previous hypotheses that avian-style pellet egestion may have evolved to accommodate increased physiological processes leading to modern birds.

A series of unusual peloidal structures are interpreted as invertebrate fecal pellets and resemble the pellet-filled burrow trace *Edaphichnium* isp. Three morphotypes are identified, including linearly-arranged pellets, pellets in condensed masses, and pellets in dispersed masses. Potential trace-makers include coleopterans, millipedes, and possibly earthworms. The abundance of *Edaphichnium* isp. and other traces at specific horizons throughout the locality suggest buildup of organic material in the substrate, likely induced by depositional hiatuses. Some *Edaphichnium* isp. are associated with *Maiasaura* egg clutches, suggesting invertebrate communities scavenged the decaying nest materials.

Taken together, these studies provide ecological and depositional context to the abundance of dinosaur nesting and the diversity of taxa and behaviors represented at the Egg Mountain locality.

CHAPTER ONE

INTRODUCTION

Feeding traces (“digestichnia” sensu Vialov, 1972) are trace fossils that originate from the digestive processes of organisms and include coprolites, gut contents, gastroliths, and regurgitalites. They are often useful in inferring paleoecological interactions and depositional environments, and, when a specific producer can be identified, a wealth of paleobiological information, including trophic interactions, digestive anatomy and processes, and the evolution of feeding behavior (Chin et al., 1998; Varricchio, 2001; Chin, 2007; Wings, 2007).

This thesis assesses a series of feeding traces from Egg Mountain, an Upper Cretaceous terrestrial vertebrate locality from the Two Medicine Formation of north-central Montana, U.S.A. The locality consists of stacked calcareous siltstones and calcretes, interpreted as bioturbated, well-drained paleosols (Lorenz and Gavin, 1984; Freimuth and Varricchio, 2019). Egg Mountain famously produced multiple egg clutches and a nesting structure of the non-avian theropod *Troodon formosus* (Horner, 1982, 1987; Varricchio et al., 1997, 1999, 2002). Additional evidence of nesting includes eggs and isolated eggshell attributable to *Maiasaura peeblesorum* (Oser, 2014), clutches and eggshell of the theropod oogenus *Continuoolithus* (Hirsch and Quinn, 1990), and concentrations of unknown thin eggshell. Several well-preserved metatherian (Montellano, 1988) and multituberculate mammals (Montellano et al., 2000) and lizards (DeMar et al., 2017) have been collected from the locality. Skeletal remains of the small ornithopod *Orodromeus makelai* and shed teeth assignable to *Troodon*, dromaeosaurids,

hadrosaurs, and tyrannosaurids are also recovered throughout the stratigraphic section (Scofield, 2018). Invertebrate trace fossils are abundant and represent the *Celliforma* ichnofacies, including the cocoons of wasps and/or beetles (*Fictovichnus sciuttoi*) and feeding chambers attributable to cicadas or other invertebrates (*Feoichnus martini*) (Freimuth and Varricchio, 2019; Panasci and Varricchio, 2020). The abundance and diversity of biological activity recorded in Egg Mountain paleosols is rare for Late Cretaceous deposits, yet little is known about specific trophic interactions and ecological processes amongst the taxa at the locality. Feeding traces assessed in this thesis provide environmental and ecological context to the plethora of skeletal and nesting remains at the Egg Mountain locality.

The first manuscript (chapter two) investigates the taphonomy and depositional origin of three unusual multi-individual accumulations of mammal skeletons. Two consist primarily of the metatherian *Alphadon halleyi* and are interpreted as regurgitalites based on an absence of a mineralized ground mass, an overwhelming representation by indigestible cranial remains, extensive breakage and disarticulation of skeletal elements, and corrosion patterns congruent with partial digestion. These represent the first known mammal-bearing regurgitalites from the Mesozoic. A third amalgam comprises two individual multituberculates and is characterized by greater degrees of articulated and complete elements, likely of non-predatory origin. The difference in taphonomic features between the metatherian and multituberculate assemblages may reflect ecological separation between the mammalian taxa at the locality. The available evidence at the locality suggests the non-avian theropod *Troodon formosus* is the regurgitalite producer,

corroborating past inferences of a small prey diet and potentially indicating nocturnal feeding behavior. The similarities between the Egg Mountain regurgitalites and prey in diurnal raptor gastric pellets may suggest manipulation of prey during feeding. The ability to egest pellets in a large-bodied, non-volant troodontid supports previous hypotheses that avian-style pellet egestion may have evolved to increase digestive efficiency and accommodate heightened physiological processes in groups leading to modern birds.

The second manuscript (chapter three) addresses a series of enigmatic, small peloidal structures from the locality. Morphological and geochemical analyses reveal these structures represent fecal pellets of deposit-feeding organisms and are referred to the ichnotaxon *Edaphichnium*, a component of paleosol trace fossil assemblages throughout Mesozoic to recent deposits. Potential trace-makers of *Edaphichnium* at Egg Mountain include earthworms, chafers, and millipedes. Regardless of the specific trace-maker, *Edaphichnium* occur at specific horizons throughout the measured section, reflecting increased organics in the subsurface likely connected to depositional hiatuses. Additionally, some *Edaphichnium* specimens occur alongside *Fictovichnus* wasp cocoons and *Maiasaura* eggs and perinatal skeletal remains, likely reflecting invertebrate communities attracted to the organics associated with the *Maiasaura* nest. Invertebrates may have helped rid nesting areas of pathogenic microorganisms, potentially facilitating dinosaur nest site fidelity. It is also likely that dinosaur nests elsewhere in the fossil record, with large eggs, egg clutches, and colonial nesting, provided substantial ecological resources for invertebrate and vertebrate predators and scavengers.

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CHAPTER TWO

MAMMAL-BEARING REGURGITALITES POTENTIALLY ATTRIBUTABLE TO
TROODON FORMOSUS AT THE EGG MOUNTAIN LOCALITY, UPPER
CRETACEOUS TWO MEDICINE FORMATION, MONTANA, U.S.A.

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TROODON FORMOSUS AT THE EGG MOUNTAIN LOCALITY, UPPER
CRETACEOUS TWO MEDICINE FORMATION, MONTANA, U.S.A.

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Abstract

Though rare, fossil gastric pellets (regurgitalites) have distinct taphonomic characteristics that allow for inferences of behavioral ecology and, when a specific predator can be identified, rare insight into dietary processes, physiology, and the evolution of behaviors in deep time. In more recent deposits, the taphonomic patterns of small mammals in different predator-derived assemblages have received significant attention. We use these guidelines to assess the taphonomy of three unusual multi-individual aggregates of mammal skeletons from paleosol deposits at Egg Mountain, a dinosaur nesting locality from the Upper Cretaceous Two Medicine Formation, Montana, USA. Two amalgams are comprised of three and eleven individuals, respectively, primarily of the marsupialiform *Alphadon halleyi*. High proportions of crania and indigestible elements, prevalent disarticulation, extensive breakage, periosteal corrosion patterns, and the absence of a phosphatic ground mass are indicative of regurgitalites and align with features of prey in gastric pellets of modern diurnal raptors. These are the first known mammal-bearing regurgitalites from the Mesozoic. A third aggregate consists of two individual multituberculates, *Filikomys primaevus*, characterized by high breakage of crania but greater representation of articulated and complete postcrania and a distinct absence of corrosion and traces attributable to feeding, suggestive of a non-predatory origin. The discrepancy of taphonomic features may suggest ecological or behavioral separation between the two mammalian taxa at the locality. The available evidence suggests *Troodon formosus* is the predator responsible, corroborating previous inferences of a small prey diet. The parallels between prey in regurgitalites here and those in diurnal

raptors pellets suggests manipulation of prey during feeding. The ability to egest pellets in a large-bodied non-volant troodontid corroborates previous inferences that avian-style pellet egestion may have evolved to enhance digestive efficiency and accommodate increased physiological processes in groups leading to modern birds.

Introduction

Direct evidence of dietary processes and predator-prey relationships are particularly rare in the fossil record. The most convincing evidence is found in preserved gut contents, which provide direct evidence of predator-prey interactions (Varricchio, 2001; Kriwet et al., 2008; O'Connor et al., 2011; O'Connor et al., 2019). Occasionally, coprolites and tooth marks on bone are diagnostic to family- or species-level predator-prey interactions (Erickson and Olson, 1996; Chin et al., 1998; Chin et al., 2003; Njau and Blumenschine, 2005). Modern regurgitated gastric pellets and fossil regurgitalites are also useful in interpreting ecological relationships (Andrews, 1990; Terry, 2010; Mayr and Schaal, 2016).

The record of fossil gastric pellets (regurgitalites) is sparse despite their preservation potential and suggested ubiquity across extant vertebrate groups (Myhrvold, 2012). The sparsity of regurgitalites is in part due to the difficulty in recognizing these structures, though several efforts have been made providing taphonomic criteria for the identification of these fossils (Myhrvold, 2012; Thies and Hauff, 2012; Gordon et al., 2020). Prey items in modern gastric pellets have a unique combination of taphonomic characteristics that also serve in identification of gastric pellets in the fossil record

(Andrews, 1990). These include representation of multiple individuals that typically show high proportions of indigestible remains (e.g., teeth, feathers, hair), characteristic breakage patterns of skulls and postcrania, and evidence of corrosion by digestion (e.g., Andrews, 1990; Myhrvold, 2012). The most effective criterion in both identifying remains as regurgitated prey and assessing their predator is modification to the bone and tooth surface caused by digestive acids (Andrews, 1990; Fernandez-Jalvo and Andrews, 1992). The effects of digestion on surface bone are distinct from those produced by abrasion and inorganic (e.g., soil) corrosion, as digestive acids and enzymes tend to preferentially affect articular surfaces and epiphyses before shafts and other bone surfaces (Andrews, 1990; Fernandez-Jalvo et al., 2014; Fernandez-Jalvo and Andrews, 2016). Taphonomic patterns on prey items are unique to certain predator groups, reflecting the dietary processes of predators and elucidating depositional history of prey assemblages (Duke, 1975; Andrews, 1990; Czaplewski, 2011; Mayr and Schaal, 2016).

Few regurgitalites are identified from Mesozoic terrestrial deposits. Sanz et al. (2001) report an isolated regurgitalite of four juvenile bird skeletons from the Lower Cretaceous of Spain. Compared to numerous vertebrate specimens from that locality, the amalgamation of four individuals is anomalous, and skeletal elements display corroded aspects of articular ends and surface pitting, hallmarks of modification by digestion (Sanz et al., 2001). The identity of the predator responsible is reduced to a small theropod or pterosaur (Sanz et al., 2001). Gordon et al. (2020) describe a regurgitalite from the Upper Triassic of Arizona, U.S.A., containing the remains of the pseudosuchian *Revueltosaurus*. The assignment of the specimen as a regurgitalite (as opposed to a coprolite) is based on

a dearth of acid etching by digestion and an absence of a phosphatic ground mass. The producer is tentatively linked to a phytosaur, rauisuchid, or temnospondyl (Gordon et al., 2020).

Even rarer are regurgitalites that can be attributed to specific producers. The Early Cretaceous ornithuromorph bird *Yanornis* is preserved with a mass of disarticulated fish bones within the cervical region, interpreted as a gastric pellet (Zheng et al., 2014), and another ornithuromorph *Iteravis* preserves a disarticulated bone mass adjacent to the rostrum (Zhou et al., 2014) that has since been interpreted as regurgitated remains (O'Connor and Zhou, 2019). Zheng et al. (2018) report four specimens of the probable basal troodontid *Anchiornis huxleyi* from the Upper Jurassic of China, each associated with what is interpreted as a regurgitalite. One regurgitalite is preserved within the esophageal region and consists of three individual lizards represented by partly disarticulated skeletons all contained within a discrete matrix. These are the first reports of associated pellets with non-avian theropod dinosaurs and suggest avian-style digestion and that antiperistalsis was present in paravians (Zheng et al., 2018). Gastric pellets in the fossil record conform to the general taphonomic characteristics of gastric pellets typified by modern predators (Myrhvold, 2012; Thies and Hauff, 2012).

Here, we assess and interpret the taphonomic characteristics of three separate multi-individual aggregates of mammals from Egg Mountain, a dinosaur nesting locality of the Upper Cretaceous Two Medicine Formation, USA. The locality famously produced the first dinosaur eggs from North America (Horner, 1982; Horner, 1987) and several egg clutches and a nesting structure for the theropod *Troodon formosus*

(Varricchio et al., 1997; Varricchio et al., 1999). We describe these aggregates and assess their taphonomic characteristics, probable origins, and ecological implications for the site.

Geological Setting

Two Medicine Formation and Willow Creek Anticline

All referred specimens are recovered from the Egg Mountain locality (TM-006) of the Upper Cretaceous Two Medicine Formation, Montana, U.S.A. (Fig 2.1). The Two Medicine Formation is a siliciclastic sequence spanning the Campanian age between 74.076 ± 0.095 and 80.044 ± 0.190 Ma (Rogers et al., 1993; though see Fowler, 2017). Deposition occurred proximal to the North American Cordilleran fold and thrust belt on an up-dip alluvial plain, contemporaneous with the eastward Judith River Formation and the Foremost, Oldman, and Dinosaur Park Formations of Alberta, Canada (Lorenz and Gavin, 1984; Rogers, 1998; Fowler, 2017). The Two Medicine Formation overlies regressive nearshore facies of the Virgelle Sandstone (Lorenz and Gavin, 1984). The Horsethief Sandstone and Bearpaw Shale overlie the Two Medicine Formation and represent the subsequent transgression of the Bearpaw Sea (Lorenz and Gavin, 1984). Climate and floral models suggest semiarid to subhumid conditions at roughly 48°N paleolatitude (Wolfe and Upchurch, 1987; Golonka et al., 1994). Additionally, seasonality is inferred throughout the deposition of the formation, indicated by the abundance of caliche nodules, drought-derived dinosaur bonebeds, growth interruptions in conifer tree fossils, herbivorous dinosaur coprolites, and integrated climate modelling

and oxygen isotope evidence (Lorenz and Gavin, 1984; Rogers, 1990; Falcon-Lang, 2003; Chin, 2007; Fricke et al., 2010). Sedimentary facies are represented by intergrading fluvial and lacustrine systems in a volcanically active area, evidenced by bentonite horizons and volcanogenic deposits (Lorenz and Gavin, 1984; Rogers et al., 1993; Roberts and Hendrix, 2000).

Egg Mountain occurs in the Lake Subfacies of the Willow Creek Anticline, a NE–SW dipping, SE–plunging tectonic folds within the upper lithofacies of the Two Medicine Formation exposed west of Choteau, Montana (Fig 2.1A) (Lorenz and Gavin, 1984). The Willow Creek Anticline has produced a wealth of information related to dinosaur paleobiology, including studies of eggs, ontogeny, and diet (Horner and Makela, 1979; Horner, 1982; Varricchio and Horner, 1993; Chin, 2007; Woodward et al., 2015). Well-drained soil conditions and seasonality are inferred based on abundant insect trace fossils (Martin and Varricchio, 2011; Freimuth and Varricchio, 2019).

Egg Mountain locality

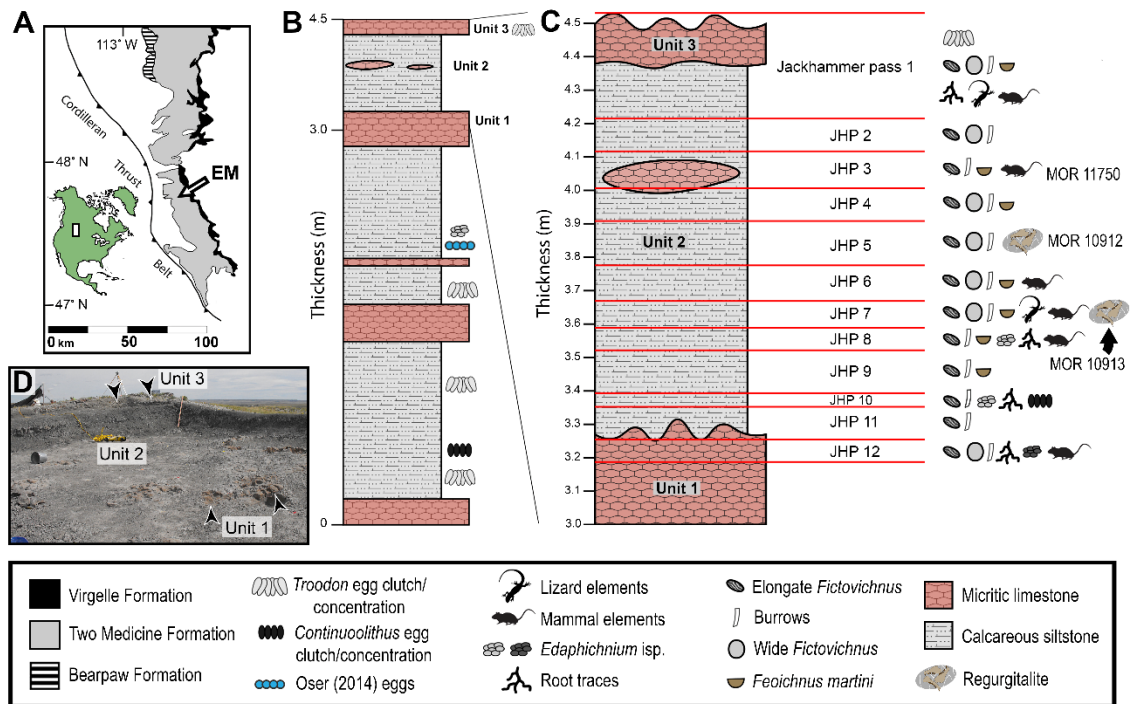
The Egg Mountain locality is 16.5 m above a bentonite dated to 75.53 ± 0.32 Ma (Shelton, 2007; Varricchio et al., 2010). Its three major lithologic units consist of calcareous-cemented detrital siltstones that are distinct from irregular micritic limestone horizons (Fig 2.1B–D). The limestones and siltstones are massive, and primary sedimentary structures and discernible paleosol horizons are absent. Fossil insect cocoons and dwelling traces are recovered throughout the measured section and suggest incipient, cumulative pedogenesis and slow, relatively continuous distal floodplain deposition

(Bown and Kraus, 1987; Freimuth and Varricchio, 2019; Panasci and Varricchio, 2020).

The occurrence of invertebrate traces throughout the measured section suggests a lack of large (> 10 cm) depositional events (Freimuth and Varricchio, 2019). Insect traces also suggest well-drained and workable soils with extended periods of subaerial exposure (Genise, 2016; Freimuth and Varricchio, 2019). Limestones were interpreted as lacustrine by Horner (1987), but the abundance of insect traces precludes an aquatic origin; limestones instead likely represent calcretes, cemented by infiltrating subsurface waters (Alonso-Zarza, 2003; Freimuth and Varricchio, 2019; Panasci and Varricchio, 2020). Other ichnofossil-bearing calcretes are also reported from the Willow Creek Anticline (Martin and Varricchio, 2011).

The locality has famously produced 12 egg clutches and a nesting structure of the non-avian theropod *Troodon formosus* and several clutches of the probable theropod oogenus *Continuoolithus* (Horner, 1984; Horner, 1987; Hirsch and Quinn, 1990; Varricchio et al., 1997, 1999). Isolated eggshell is also common and distributed throughout the section, with some attributable *Maiasaura peeblesorum* (Oser, 2014; Oser and Jackson, 2014). Recent excavations from 2010-2016 have yielded several associated to articulated remains of the marsupialiform *A. halleyi* (Montellanno, 1988), the multituberculate *F. primaevus*, and an iguanomorph lizard, *Magnuviator ovimonsensis* (DeMar et al., 2017). Formerly, multituberculate specimens from the locality had been referred to *Cimexomys judithae* (Montellano et al., 2000). Recent taxonomic revision identifies them as *Filikomys primaevus* (Weaver et al., in review). Associated to articulated elements of the small ornithopod *Orodromeus* occur throughout the section.

Shed hadrosaur teeth are common, and shed dromaeosaurid (including *Saurornitholestes*), *Troodon*, and tyrannosaurid teeth are less common (Scofield, 2018). Insect trace fossils referable to *Fictovichnus sciuttoii* likely representative of wasps and/or beetles and are pervasive at the locality (Freimuth and Varricchio, 2019), and other invertebrate traces, including *Feoichnus martini* (Panasci and Varricchio, 2020), *Edaphichnium* isp., and isolated planispiral terrestrial snails are less abundant. An *Adocus* turtle shell fragment and an isolated frog frontal are the only aquatic vertebrate remains known to date.



Materials and Methods

Institutional abbreviations: MOR, Museum of the Rockies, Bozeman, Montana, U.S.A.

Collection and field area

Referred specimens were recovered from the Egg Mountain locality (TM-006), Two Medicine Formation, U.S.A. A 7 x 11 meter main quarry was opened in 2010 and was worked each year through 2016. Excavations worked down through the upper 1.5 meters of calcareous siltstones and micritic limestones. The 1.5 meters of vertical section through the main quarry was lowered systematically in a series of 12 jackhammer passes (JHPs), with an average thickness of ~11 cm for each pass, in order to track precise stratigraphic associations (Fig 2.1C). The stratigraphic level for each specimen was measured using a sight level and standardized to a fixed origin point in the quarry. The lateral location of specimens was mapped using a grid system with 1 x 1 meter square increments, and specimen location and orientation (when possible) was then measured within a single grid unit using a tape measure.

Specimens were manually prepared at the Burke Museum of Natural History and the University of Washington with air scribes. Images were captured at the Burke Museum of Natural History and Culture paleontology collections with a Canon EOS 7D and EOS 5DS, and Capture One and Zerene Stacker software. Figures were created using Adobe Photoshop and Illustrator.

Taphonomic analysis

We analyzed several taphonomic attributes using methodology proposed by Andrews (1990) and Fernandez-Jalvo and Andrews (1992) for small mammals. To assess the anatomical completeness and element abundance of each specimen, we calculated the total number of bones in each assemblage, including unidentifiable fragments (n), number of identifiable elements (NISP), minimum number of elements (MNE), and minimum number of individuals (MNI) (Table 2.1). Relative abundance (RA) of different skeletal elements was calculated using the following equation after Andrews (1990):

$$RA = N_{\text{observed}} / (MNI \times N_{\text{expected}})$$

Relative abundance of elements in Egg Mountain specimens are compared to prey remains in gastric pellet and scat assemblages for known predator groups. Limb elements of MOR 11750, MOR 10912, and MOR 10913 are primarily represented by unidentifiable shafts with missing epiphyses. When assessing the relative abundance of skeletal elements, we combined all possible appendicular elements for *Alphadon* and *Filikomys* (humerus, radius, ulna, femur, tibia, fibula) into a single “limb elements” category. To standardize comparisons, we combined published data for limb elements into a single category based on five elements (humerus, radius, ulna, femur, tibia) (Andrews, 1990; Montalvo and Fernández, 2019) (Appendix A). Rodents, the most common prey taxon, have a single hindlimb autopodial element (tibia), while *Alphadon* and *Filikomys* have both a tibia and fibula. This discrepancy between the number of limb elements may cause artificially lower limb element abundances for Egg Mountain material compared to modern data. Additionally, published data represent average prey

contents across large samples in pellet and scat assemblages (Andrews, 1990; Montalvo and Fernández, 2019), whereas MOR 11750, 10912, and 10913 are isolated examples.

We performed a Pearson's chi-squared analysis to compare skeletal relative abundance of Egg Mountain specimens to prey skeletal relative abundance for known predator groups (Appendix B). The total observed maxillae, mandibles (or dentaries), and limb elements were included separately for MOR 11750 and averaged between MOR 10912 and MOR 10913. These values were multiplied by published average relative abundances for select predator groups. This provides expected element counts for each modern predator group given the number of elements in each MOR specimen. A separate analysis was performed to compare Egg Mountain material for each selected predator group.

We assessed the degree of articulation (Behrensmeyer, 1991), the degree of completeness, and breakage patterns of crania and postcrania using methodology for small mammals (Andrews, 1990). Categories of skull breakage ranging from complete skulls (low modification) to isolated maxillae (high modification) were assessed using methodology of Andrews (1990). Similarly, we assessed breakage of mandibles after Andrews (1990), ranging from complete (low modification) to missing ascending ramus and inferior (lingual) border (high modification). Postcrania breakage was based on the condition of distal and/or proximal ends of long bones (Andrews, 1990), and the type of fracture was assessed and interpreted after methodology of Shipman (1981). Some elements show post-fossilization breaks attributable to collection or preparation

processes. Breaks that cannot be determined if they occurred pre- or post-fossilization were noted but not used in the assessment in overall pre-fossilization breakage patterns.

Surface texture of bones was assessed using a standard observation microscope at 50x magnification. Referred specimens here were compared to other *Alphadon* specimens from Egg Mountain of different taphonomic status (two isolated dentaries, MOR 250 and MOR 310; Montellano, 1988).

Body mass estimates

Body mass estimates for Egg Mountain taxa were gathered from published estimates when accessible (Gordon, 2003; Wilson et al., 2012). Estimates for *Troodon* specimens were calculated using the minimum femur circumference and regression equation given by Campione et al. (2014) for bipeds. *Anchiornis* mass is derived from published femur lengths (Zheng et al., 2018) using the equation from O’Gorman and Hone (2012). Though femur length has been suggested as a poor predictor for body mass (Campione and Evans, 2012; Campione et al., 2014), femur length is the only available datum for associated *Anchiornis* specimens with pellets. Modern predator mass for a single taxon is calculated from an average of male and female masses using data from Andrews (1990, appendix 15) (Appendix C).

Pellet statistics and size comparisons

Pellet sizes, prey masses, and maximum ingestion capacities are compiled from published data for modern raptors. Pellet volume is assumed to be an ellipsoid ($\frac{4}{3}\pi lwb$)

calculated from length, width, and breadth measurements of Andrews (1990, appendix 14). The data point for *Anchiornis* was added after the regression equation was calculated from modern taxa. Dimensions provided for *Anchiornis* pellets are only long and short axes; third axis was estimated using the same dimensions as the short axis. Maximum ingestion capacities for each taxon are taken from Hiraldo et al., (1991), and predator masses for these taxa are averages of male and females given by del Hoyo et al. (1994) (Appendix C).

Results

The mammal aggregates include accumulations comprised predominantly of the marsupialiform *Alphadon halleyi* (MOR 10912 and MOR 10913) and the multituberculate *Filikomys primaevus* (MOR 11750). All specimens were recovered from different intervals in the calcareous siltstone of Unit 2 (Fig. 2). Element representation is summarized in Table 2.1, breakage patterns are summarized in Table 2.2, and digestive corrosion patterns are summarized in Table 2.3.

MOR 10912

MOR 10912 consists of three disarticulated individuals of the marsupialiform *Alphadon halleyi*, all recovered from a ~0.01 m² area. In total, 33 bones and unidentifiable fragments are present, including three pairs of associated maxillae, an isolated ulna, an isolated dentary, and four associated long bone shafts lacking epiphyses.

A minimum of three individuals is based on three preserved right maxillae (Fig 2.2A–C). MOR 10912 was collected and prepared in five primary pieces. Pieces 2 and 3 fit together indicating *in situ* arrangement, but remaining pieces cannot be assessed in relation to each other. The host matrix is an indurated calcareous siltstone that is massive and lacking any primary sedimentary structures. Few fine-grained clasts of micas, chert, and other volcanoclastics are observable in the calcareous matrix. There is no discernible difference in color, composition, grain size, or sedimentary fabric between the matrix immediately adjacent to the bony elements of MOR 10912 and that comprising the rest of the quarry.

Piece 1 consists of right and left paired maxillae folded onto one another with *in situ* canines and all premolars and molars (Fig 2.2A). The last molar (M₄) was broken posteriorly after fossilization. Two associated long bone shafts are broken without epiphyses. The anterior border of the orbit is preserved, but the posterior portion of the orbit and posterior portions of the skull are missing; these breaks are sharp and truncated by matrix. Small, matrix-filled fractures dominate the lateral surface of the maxillae. Other than breaks, the surface bone of both maxillae is intact with no indication of corrosion. The left canine is broken, but it and the molars appear unmodified with enamel intact across all surfaces.

Piece 2 includes a right maxilla and partial left maxilla embedded in matrix (Fig 2.2B). The posterior portion of the right maxilla is lost, as well as M₄, and only the anterior and ventral border of the orbit is preserved. Similar to piece 1, these edges are sharp and truncated by matrix, and the lateral surface has many pre-fossil breaks. Surface

bone and teeth show no signs of corrosion. The maxilla in piece 2 sits 2.0 cm from the elements in piece 3, putting these elements in a 12.5 cm² area.

Piece 3 consists of right and left paired maxillae, a left dentary, and two associated long bone shafts with missing epiphyses (Fig 2.2C). The paired maxillae in piece 3 are folded similar to those of piece 1 but are more fragmentary; the contribution to the orbit is not preserved in either maxilla, and the lateral surface of each displays many matrix-filled breaks (Fig 2.2C). All teeth are preserved *in situ* and unmodified in the right maxilla, but P₂ is missing. The left maxilla is highly fragmentary, with the anterior (including canine, P₁, and P₂) and posterior portions missing prior to fossilization. These truncations are sharp and abutted by matrix. All molars are present and lack modifications to enamel surfaces. The left dentary is truncated posteriorly, with the broad ascending ramus (Montellano, 1988) missing. The anterior part of the masseteric fossa and angular process are preserved but broken. These breaks are sharp with jagged edges and truncated by matrix. Part of M₂ is present and M₃ and M₄ are present. M₂ and the anterior portion of the dentary were broken post-fossilization. The enamel surface of M₃, M₄, and the preserved portion of M₂ appear unaffected. The two associated shafts lack epiphyses, and loss of periosteum is apparent at different points along the shafts. The surface is particularly modified at the broken ends, with more concentrated loss of surface bone (Fig 2.2D).

Piece 4 consists of a mass of highly disarticulated and broken bone fragments that spans an area of 1.0 cm by 1.5 cm (Fig 2.2E). The number, type, and taxonomic affinity of bone fragments in this piece are difficult to determine because of the extensive

breakage. Loss of periosteum is apparent on many fragments, reflected in changes from dark brown, smooth texture to light brown and tan porous or gritty texture. Discernible epiphyses and other morphology are absent.

Piece 5 is an isolated right ulna (Fig 2.2F). Proximally, the surface bone on the olecranon process and the trochlear notch is patchy and pitted. The posterior portion of the olecranon is broken, and the jagged, uneven edge is truncated by matrix (Fig 2.2G). The shaft is largely intact with minute transverse and stepped fractures. The shaft is generally smooth, but patches of irregular texture are visible on the ventral surface abutting matrix. The distal end of the ulna is obscured by matrix and broken pre-fossilization. The surface texture of one broken fragment appears unaltered, but texture in the remaining fragments is obscured by matrix and difficult to discern.

In total, 7 of 12 identifiable elements are cranial (58%). Maxillae are most prevalent ($n = 6$), yielding a minimum of three individuals. Maxillae occur in pairs folded onto one another, broken and isolated from other portions of the skull, and rarely associated with other cranial elements. No posterior skull portions are associated or present in the assemblage. Corrosion and periosteal modification are observable on the isolated ulna, indeterminate bone shafts, and highly broken fragments (Fig 2.2D– E, G), but apparently lacking on crania and teeth.

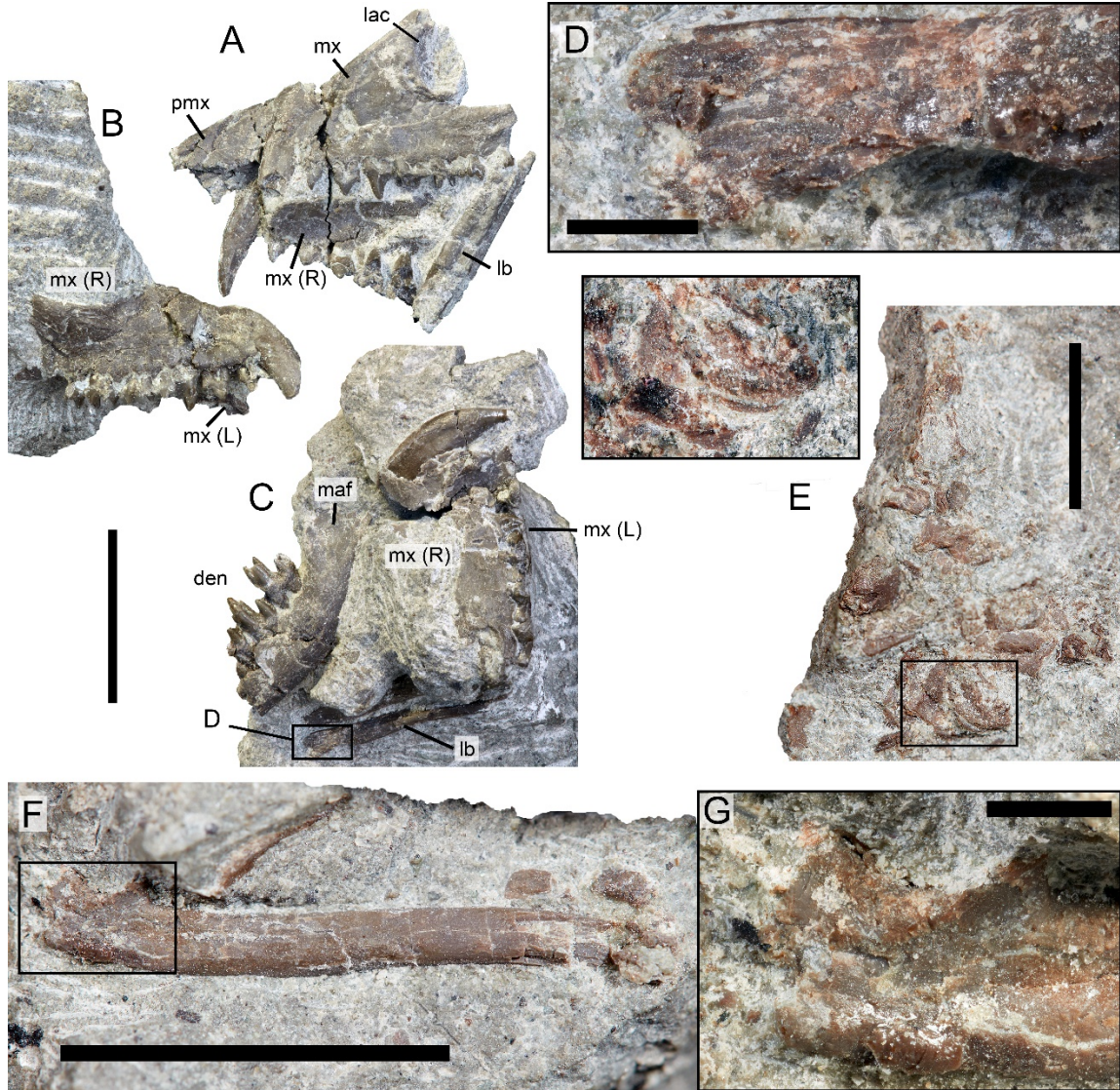


Fig 2.2. Representative elements of MOR 10912. (A) Piece 1, *Alphadon halleyi* paired and folded maxillae with indeterminate long bone shafts; note matrix-terminated breaks. (B) Piece 2, paired and folded maxillae of *A. halleyi*; note matrix-terminated breaks. (C) Piece 3, *A. halleyi* associated maxillae, dentary, and indeterminate shafts. (D) Inset in (C) showing corroded end of long bone shaft. (E) Piece 4, unidentifiable bone fragments with inset showing irregular loss of periosteum. (F) Piece 5, right ulna with corroded proximal end and broken distal end. (G), Inset of (F) highlighting corroded, patchy periosteal bone of the trochlear notch and olecranon process. Scale bars, 1 cm (A–C, E, F), 1 mm (D, G). Abbreviations: den, dentary; lac, lacrimal; lb, indeterminate long bone shaft; maf, masseteric fossa; mx, maxilla; pmx, premaxilla; (L), left; (R), right.

MOR 10913

There are two components to MOR 10913. The first is an assortment of elements collected in the rubble generated by the jackhammer in an area of $\sim 0.03 \text{ m}^2$. Because of this, several pieces are broken post-fossilization; these are noted in assessing skeletal statistics and overall breakage patterns. The second component consists of *in situ* material that was jacketed and collected from directly underneath the first assemblage; the distribution of skeletal elements here may be more reflective of the true assemblage. Their association is interpreted as occurring via the same depositional processes and is assessed as such. All elements are referable to *A. halleyi* unless otherwise specified. A calcareous siltstone encases the boney elements of MOR 10913. The matrix containing the boney elements is indistinguishable from the matrix throughout the quarry in terms of color, grain size, composition, and sedimentary texture.

The taphonomic statistics for both components of MOR 10913 is summarized in Table 2.1. In total, 114 total bone fragments are present, 85 of which are identifiable. 64 total elements are tooth-bearing; 16 are maxillae, 33 are dentaries, and 15 are unidentifiable. Of the 16 maxillae fragments, eight represent lefts, five rights, and three cannot be identified to a side. Ten left and ten right dentaries are present, and 13 cannot be sided. Other elements include two partial braincases, seven skull fragments, nine indeterminate long bone shafts, and a partial lizard skull. An MNI of ten for *Alphadon* is based on dentaries, and an additional lizard skull yield an MNI of 11 for the deposit.

Because of destruction during excavation, we assessed breakage patterns on elements that remain in matrix and were careful in assessing isolated fragments. Like

MOR 10912, maxillae are broken dorsally and posteriorly and occur isolated from the posterior of the skull. One larger block (~5 x 4 cm) contains a pair of maxillae and other fragments that show matrix-truncated breaks. This likely represents the distribution of most elements prior to excavation (Fig 2.3A). Ten maxillae occur in pairs folded onto one another where observable (10 of 16, or five pairs). Of the five pairs of folded maxillae, three pairs occur isolated, one pair is associated with fragmentary long bones, and one pair is associated with another maxilla (with additional matrix-bound fragments that may represent a paired maxilla). Four maxillae are isolated, and one maxilla is associated with a dentary. Where observable, breaks on maxillae are sharp and truncated by matrix. Overall, all periosteal surfaces of maxillae and associated fragments and enamel surfaces of teeth appear intact and uncorroded.

Two *A. halleyi* braincases are preserved (Fig 2.3B). Because of excavation processes, the *in situ* orientation of braincases cannot be established. μ CT scans of one specimen yield an associated but disarticulated left maxilla and dentary. The second braincase is embedded in and truncated by matrix. Surface bone is thin or removed on parts of one braincase, likely lost in excavation. Neither braincase displays evidence of corrosion or surface bone modification prior to excavation processes.

An indeterminate lizard is represented by a maxilla with teeth, possible frontals, and other indeterminate skull elements (Fig 2.3C). Where exposed, natural and broken edges are clean and truncated by matrix. Most of the probable frontal is missing, leaving an impression of the bone morphology; this was likely lost in excavation. *In situ* bone surface and enamel surfaces on teeth appear regular and uncorroded.

Ten total dentaries are represented in matrix, of which five are isolated; one of these is associated with an indeterminate bone fragment. One pair is isolated, and one pair is associated with a maxilla. An additional 19 dentary fragments are excavated or prepared out of matrix. No pre-fossil breaks are observed, so breakage patterns of dentaries remain ambiguous. Of the 33 dentary fragments, 19 were assessable for surface modifications. Eight pieces have some surface modification; six have longitudinal linear markings and sub-millimeter scale scours, and two fragments show millimeter scale pits that break the periosteal surface (Fig 2.3D). These markings are present on all surfaces of the dentary leading up to the alveolar cavities. One dentary definitively displays loss of teeth prior to fossilization, where several alveoli are empty, but the canine remains intact. Remaining dentaries show varying degrees of edentulism, but it is likely tooth breaks and loss occurred in excavation.

The portion of MOR 10913 preserved *in situ* and undamaged in the field consists of a partial *Alphadon* skull, including left and right dentaries and maxillae close to occlusion, as well as an isolated right dentary and three unidentifiable fragments (Fig 2.3E). The posterior portion of the skull is missing. Both maxillae are broken dorsally, leaving only the teeth-bearing portions. Some of the breaks likely occurred during excavation, but breaks anteriorly and posteriorly are truncated by matrix, suggesting those breaks occurred prior to fossilization. All teeth appear unmodified except for the left canine, which is displaced and rotated anteriorly. Both dentaries are truncated posteriorly, with only the anterior portion of the masseteric fossa preserved on the right dentary. Some breaks on the dorsal aspect are sharp and truncated by matrix, while others

appear rounded and are likely products of excavation. Teeth appear *in situ* and enamel is uniform and complete. The anterior portion of the isolated dentary is preserved. Matrix covers the broken end posteriorly. Of the three unidentifiable fragments, one is clearly broken post-fossilization, while the other two are truncated by matrix.

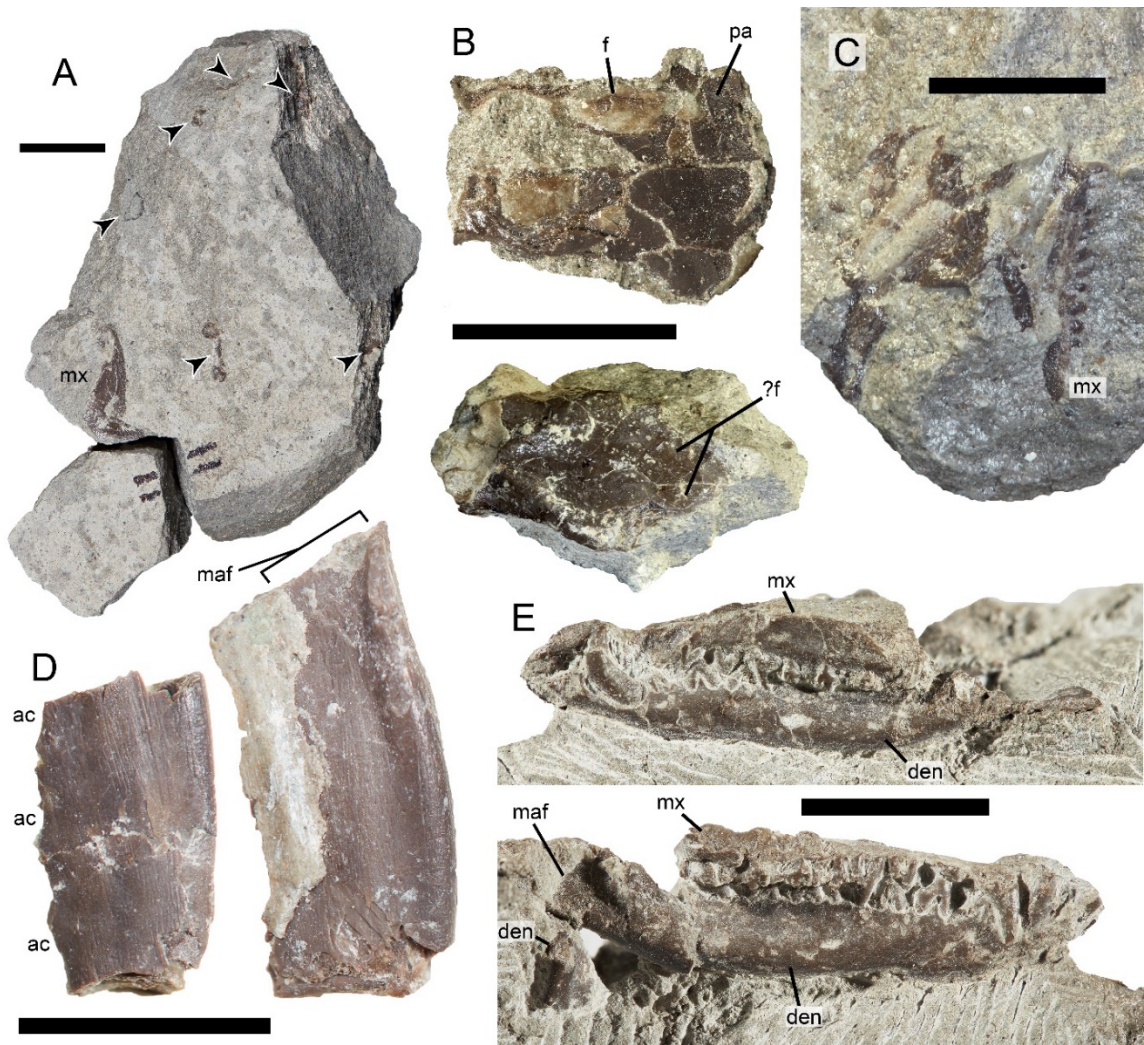


Fig 2.3. Representative elements of MOR 10913. (A) Probable distribution of elements in matrix prior to excavation. Note lack of a ground mass and unidentifiable bone fragments (arrows). (B) Two *A. halleyi* braincases, dorsal view. (C) Disarticulated lizard skull (D) *A. halleyi* dentary fragments with irregular linear cracks and pitting. (E) *A. halleyi* occluded jaws in right lateral (top) and left lateral (bottom) views. Scale bars, 1 cm (A, B, E), 0.5 cm (C, D). Abbreviations: ac, alveolar cavity; den, dentary; f, frontal; maf, masseteric fossa; mx, maxilla; pa, parietal.

MOR 11750

An additional multi-individual amalgamation of mammal elements was collected at Egg Mountain in 2010. This specimen, MOR 11750, was collected in several parts from an area $\sim 0.05 \text{ cm}^2$. The *in situ* orientation and arrangements of blocks was lost during collection. As in MOR 10912 and 10913, the calcareous host matrix encasing the skeletal elements of MOR 11750 is very similar to that throughout the locality. Few fine-grained clasts are present in the massive calcareous matrix, and no primary sedimentary structures are observable.

Element representation of MOR 11750 are summarized in Table 2.1. In total, there are at least 29 bone fragments, 24 of which are identifiable. Ten of these elements are cranial, including two dentaries, two maxillae, and six isolated teeth. The remaining 14 identifiable elements are represented by five vertebrae, two humeri, one radius, one ulna, two femora, one tibia, two fibulae, and four indeterminate long bone shafts. All elements represent lefts except a single right maxilla and right hindlimb; no elements occur in pairs. An MNI of two is based on left dentaries of the multituberculate *Filikomys primaevus*.

Parts of two skulls are contained within three blocks. Molding putty holds two blocks together. The most prominent feature of these blocks is a mass of bone contained in an area $\sim 25 \times 13 \times 20 \text{ mm}$. Identifiable elements include a right squamosal articulated with a fragmentary right maxilla (Fig 2.4A). The dorsal and anterior portion of the skull is crushed and considerably deformed, represented by a fragmented petrosal (Fig 2.4A). Broken edges are interrupted by matrix, indicating pre-fossil occurrence. On the opposite

side of this block is an isolated right upper M2 (Fig 2.4B). Surrounding the tooth is a patch of small brecciated bone fragments, likely representing elements of the basicranium. Matrix isolates the fragments from one another, indicating breaks occurred syn- or post-burial. Dark brown surface bone appears to be retained on all fragments (Fig 2.4B). Along the edge of the block is a right maxilla with an upper I2 and I3, both of which may be erupting, and an upper P1 in lingual view (Fig 2.4C). Abutting this maxilla is a right dentary with a preserved lower p3 (Fig 2.4C). These teeth are retained in alveolar cavities, but the surrounding bone is missing with jagged breaks. An additional block contains parts of other cranial elements, including a right upper M1, a left upper P4, and a lower left m1 and m2 (Fig 2.4D). These teeth are associated with brecciated cranial material. It is likely brecciation of boney elements occurred after deposition and during or after burial.

An isolated left dentary preserves the first incisor and blade-like p4 (Fig 2.4E). Some bone loss is apparent at the base of the alveolar cavity of the incisor, and small pits occur on the lingual surface of the mandible. However, enamel surfaces on all teeth appear unmodified. This block is prepared out of original orientation, and the direct association with other elements is unclear.

A block with a partial left dentary and left maxilla in occlusion is visible in lingual view. The dentary is incomplete so that only p4 and m1 are present. The m2 alveolus is present, but the tooth is missing. The dentary is truncated anteriorly as well as posterior to the m2 socket. Edges of the breaks are matrix-truncated and irregular. The lingual face of the dentary is irregular and broken bone marks the periphery ventrally.

The p4 is broken parasagittally on the lingual surface and matrix fills the broken surface. Four maxillary teeth appear to be present, but bone on the lingual surface of the maxilla is heavily fractured and displaced, with no coherent borders. Additional fragments surround the area dorsal to the maxilla, and it is unclear if these represent continuation of the crumbled maxilla or separate elements. Though this block does not fit with any other skull blocks, the preservation of brecciated bone is similar to that in Fig 2.4B.

A partial fibula and articulated left humerus, radius, and ulna occur in a ~2.5 x 1.5 cm area (Fig 2.4F, G). Along the edge of the block spanning the distance from the articulated limb to the isolated fibula is a section of minute indeterminate bone fragments, suggesting association with similar brecciated bone of other skull parts. An additional small fragment ~1.5 cm from the articulated limb may be a distal rib. The humerus is broken proximally and transversely, perpendicular to the shaft. Surface bone of the humeral shaft splinters longitudinally, with portions missing on the ventral surface; this damage is likely related to preparation or excavation. Both the radius and ulna are broken with some displacement so that only the proximal portions are preserved. It is difficult to discern the origin of these breaks. Bone on the articular surface and epiphyses is intact and unmodified (Fig 2.4F, G). The isolated fibula has much of the shaft removed longitudinally due to excavation; however, the proximal end appears crushed with portions shattered into minute fragments, still contained within the border of the fibular head. This modification is more consistent with compaction rather than corrosion.

An articulated right femur, tibia, and partial fibula occur in an isolated block (Fig 2.4H, I). The tibia and fibula are flexed so that they form an acute angle with the femur.

The femur shaft is broken longitudinally on the lateral and anterior surface, and the large greater trochanter is missing, likely due to excavation. Molding putty fills in the fractures of the femoral shaft. The tibia is complete but offset by a transverse fracture at the midshaft. The fibula is also broken transversely midshaft and only the distal portion is preserved. This break is abutted by matrix, suggesting a pre-fossil origin. The articular surfaces of all bones are in good condition and show no signs of corrosion or other modification.

Another block contains a partial left femur visible in posterior view. The entire element is flattened antero-posteriorly, and the femoral head is crushed. A transverse fracture occurs midshaft, and matrix abuts the breaks, suggesting it occurred pre-burial. The femur is associated with a jumble of skull fragments, including partial indeterminate teeth, and an additional indeterminate long bone shaft. Elements here display matrix-truncated breaks, suggesting pre-fossilization breakage. Across all preserved elements in this block, including unidentifiable fragments, surface bone appears in-tact and complete.

Several elements were isolated during preparation; their direct association with other elements is unknown. Two lumbar vertebrae are present and show irregularity in surface bone texture, possibly indicative of corrosion. Two isolated, elongate caudal centra are present and slightly crushed. An additional fragment is crushed and may be vertebral. A distal humerus is preserved with the surface bone on the ulnar condyle crumbly and ratty. This appears to be related to crushing rather than corrosion. A partial right maxilla retains a complete P1 and partial P2 *in situ*. Posteriorly, the maxilla is broken and covered by matrix, suggesting pre-fossil occurrence. The maxilla is broken

anteriorly and dorsally; it is unclear if these breaks occurred pre- or post-fossilization. An isolated indeterminate molar is present with one broken cusp; this may have occurred during preparation. Two shaft fragments (12 and 25 mm long) and three additional indeterminate fragments are present. Their size and shape resemble carpals, tarsals, or phalanges, but they are incomplete and cannot be confidently identified. Broken edges of these elements are jagged, but indeterminately pre- or post-fossilization.

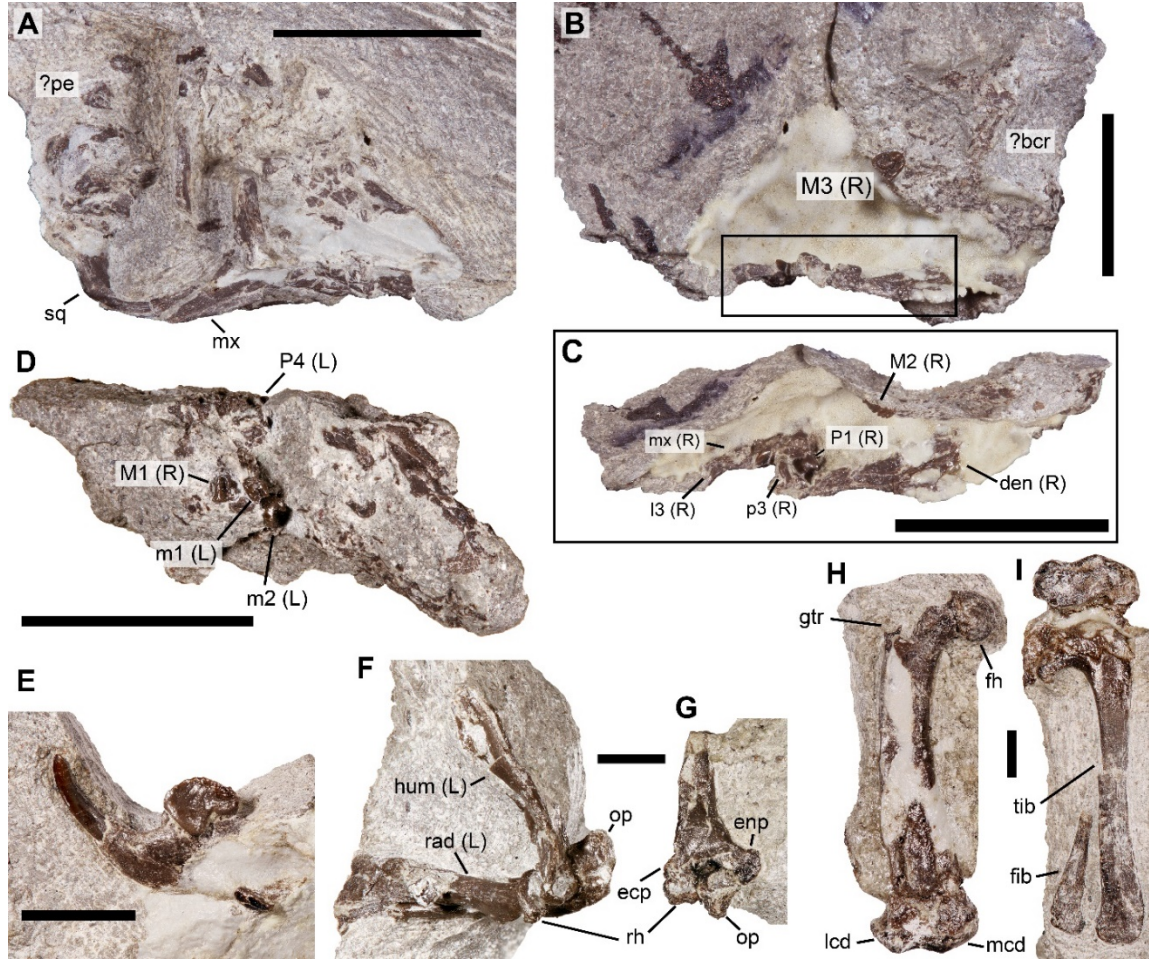


Fig 2.4. Representative elements of MOR 11750. (A) Skull of *F. primaevus* in dorsal view. Squamosal and partial maxilla are in-tact, but the skull roof is highly fragmentary. Note matrix-truncated breaks on fragments, indicating *in situ* breakage. (B) Same skull block in (A), ventral view. Note small, highly fragmentary indeterminate bone fragments. (C) Inset of (B) rotated to view dentary and maxilla in lingual view. Bone edges are broken and jagged. (D) Associated cranial fragments and teeth of *F. primaevus*. (E) Left dentary in labial view. (F) Articulated left forelimb in lateral view. (G) Articulated left forelimb in posterior view. (H), Articulated right femur in anterior view. (I) Articulated right tibia and partial fibula in anterior view. Scale bars, 1 cm (A–D), 5 mm (E), 2 mm (F–I). Abbreviations: ?bcr, ?basicranium; ecp, ectepicondyle of humerus; enp, entepicondyle of humerus; fib, fibula; fh, femoral head; gtr, greater trochanter; hum, humerus; lcd, lateral condyle; mcd, medial condyle; mx, maxilla; op, olecranon process; ?pe, petrosal; rad, radius; rh, radial head; sq, squamosal; tib, tibia; (L), left; (R), right.

Table 2.1. Element representation of MOR 10912, MOR 10913, and MOR 11750.

	<i>n</i>	NISP	MNE	No. pc	No. c	Paired jaw elements	MNI
MOR 10912	33+	12 6 maxillae 1 dentary 1 ulna 4 long bone shafts	8 6 maxillae 3 L, 3 R 1 ulna (R) 1 dentary (L)	5	7	6 of 6 maxillae	3 <i>Alphadon</i> (right maxillae)
MOR 10913	114	85 16 maxillae 33 dentaries 15 indet. tooth- bearing frags 7 skull frags 2 braincases 9 long bone shafts 1 lizard skull 2 indet. lizard teeth	38 13 maxillae 8 L, 5 R 20 dentaries 10 L, 10 R 2 braincases 1 lizard skull 2 indet. lizard teeth	9	33	10 of 13 maxillae 8 of 20 dentaries	10 <i>Alphadon</i> (right dentaries) 1 lizard (partial skull) = 11 total
MOR 11750	29+	25 3 dentaries 2 maxillae 5 vertebrae 2 humeri 1 ulna 1 radius 2 femurs 1 tibia 2 fibulae 1 indet. molar 1 indet. tooth 4 long bone shafts	17 3 dentaries 2 L, 1 R 2 maxillae 1 L, 1 R 5 vertebrae 2 lumbar 2 caudal 1 indet. 2 humeri (L) 1 ulna (L) 1 radius (L) 2 femurs 1 L, 1 R 1 tibia (R) 2 fibulae 1 L, 1 R	13	5	0 of 2 maxillae 0 of 3 dentaries	2 <i>Filikomys</i> (left dentaries)

n, number of fragments, including unidentifiable ones (*n*+ accounts for bone hash or breccia); NISP, number of identifiable elements; MNE, minimum number of elements; No. pc, number of postcranial elements (limb elements); No. c, number of cranial elements; MNI, minimum number of individuals; L, left; R, right.

Table 2.2. Breakage patterns of MOR 10912, MOR 10913, and MOR 11750.

	% crania broken	Notes on crania breakage	% postcrania broken	Notes on postcrania breakage
MOR 10912	100% (7 of 7 observable)	Breaks truncated by matrix (pre-burial); Isolated maxillae and dentaries broken posteriorly; teeth intact or broken by excavation	100% (5 of 5 observable)	Isolated ulna broken proximally and distally; other limb elements lack identifiable ends; highly disarticulated jumble of indeterminate bones
MOR 10913	100% (33 of 33 observable)	Breaks truncated by matrix (pre-burial); several indeterminate skull fragments; Isolated maxillae and dentaries broken posteriorly; Teeth broken by excavation; one edentulous dentary	100% (9 of 9 observable)	All limb elements lack identifiable ends
MOR 11750	100% (5 of 5 observable)	Skulls are brecciated but near anatomical position, with sediment separating breaks; teeth intact, some jaws occur near occlusion, where teeth are intact but bone is heavily broken	77% (7 of 9 limb elements)	Transverse fractures on limbs (post-fossil); limbs predominantly articulated with some broken ends

Table 2.3. Digestive corrosion on MOR 10912, MOR 10913, and MOR 11750.

	% teeth digestion	Notes on teeth digestion	% bone digested	Notes on bone digestion
MOR 10912	0% (0 of 7 observable)	Enamel intact across all surfaces	30% (3 of 10 observable)	Isolated ulna corroded, broken; loss of periosteum on mass of indeterminate fragments
MOR 10913	0% (0 of 19 observable)	Enamel intact across all surfaces	42% (8 of 19 observable)	Surface of dentaries display irregular pitting and linear markings; broken bone ends on indeterminate long bones may represent digestion
MOR 11750	0% (0 of 5 observable)	Enamel intact across all surfaces	0% (0 of 9 limb elements, 0 of 5 jaws)	Highly broken and brecciated crania display regular surface bone texture

Discussion

Microvertebrate skeletal assemblages can be concentrated by abiotic (hydraulic, aeolian sorting) and biotic (predators, scavengers, burrows/bioturbation) processes. These different mechanisms may result in different taphonomic characteristics and different biases inherent to paleoecological and paleoenvironmental interpretation (e.g., Behrensmeyer and Hook, 1992; Lyman, 2004; Rogers and Brady, 2010). The Egg Mountain locality is marked by a distinct absence in bedding, attributed in large part to bioturbation (Lorenz and Gavin, 1984; Freimuth and Varricchio, 2019). As noted previously, invertebrate pupation structures and dwelling traces record pervasive *in situ* soil activity and suggest incipient pedogenesis with an apparent absence of large depositional episodes (Freimuth and Varricchio, 2019; Panasci and Varricchio, 2020). Egg clutches, eggshell concentrations, and a nesting structure throughout the section additionally indicate *in situ* terrestrial activity (Horner, 1982; Horner, 1987; Varricchio et al., 1999). Nearly all recovered vertebrate remains are of terrestrial taxa; a single turtle shell fragment and an isolated frog frontal are the only aquatic or semiaquatic vertebrates represented to date, an anomaly for Cretaceous microvertebrate sites (Rogers and Brady, 2010). The only evidence for allochthonous fossil material is weathered shed hadrosaur and tyrannosaurid teeth (Scofield, 2018). Taken together, this suite of characteristics represents the taphonomic mode of well-drained floodplains, where organic remains are incorporated into soils by bioturbation and slow burial under accumulating sediment (Bown and Kraus, 1981; Behrensmeyer and Hook, 1992). The abundance and variety of eggshell at the locality suggests frequent nesting; prey item accumulation (whether

discarded and uneaten or regurgitated remains) is common proximal to avian nesting and roosting sites (Andrews, 1990; Emslie and Messenger, 1991; Hayward et al., 2000; Ferguson et al., 2018; McGrath et al., 2020). This is analogous to the taphonomic mode of caves and traps where skeletal accumulation is driven by predators and scavengers (Brain, 1981; Andrews, 1990; Behrensmeyer and Hook, 1992). The abundance of observed paleobiological activity makes Egg Mountain an exceptional setting to potentially preserve gastric pellets or other traces of predation.

Additional evidence for abiotic accumulation mechanisms is lacking. The accumulation of multiple individual mammals in a confined area is anomalous at the locality, and the prevalence of associated maxillae, dentaries, and skull parts contrasts with independently derived hydraulic (Dodson, 1973; Korth, 1979) and aeolian (Arriaga et al., 2012) sorting groups (Table 2.4). Elements also display sharp, matrix-filled breaks and no evidence of edge rounding by transport. Elements of MOR 11750 show high degrees of completeness and articulation, also unexpected for assemblages dominated by fluvial transport (though see Coard and Dennell, 1995).

Table 2.4. Sorting groups (sensu Voohries, 1969) for small vertebrate remains.

Immediate removal Light/high surface area		Gradual removal		Lag deposit “heavy”/low surface area
I	I/II	II	II/III	III
A, Generalized sequence based on settling velocity (Korth, 1979)				
Rib	Atlas Radius Ulna Pelvis	Calcaneum Astragalus Humerus Scapula Femur Molars Maxilla	Molars (small mammals)	Mandible Tibia
B, Transport sequence of <i>Mus</i> (Dodson, 1973)				
Thoracic vertebrae Maxilla	Pelvis Vertebrae	Skull Tibia Femur Humerus	Calcaneum Radius Ulna	Mandible
C, Wind dispersal of rodent bones (Arriaga et al., 2012)				
Vertebrae Skull Scapula	Metapodials Molars Astragalus Calcaneum		Femur Humerus Radius Ulna Tibia Pelvis	Maxillae Incisors Mandibles

Elements in bold are the most prevalent in Egg Mountain specimens and occur in disparate sorting groups. (A) Hydraulic sorting groups from Korth (1979). (B) Hydraulic sorting groups from Dodson (1973). (C) Aeolian sorting groups from Arriaga et al. (2012).

While it is unlikely that the Egg Mountain specimens described here are derived strictly from abiotic depositional processes, characteristics of MOR 10912 and MOR 10913 are different from MOR 11750 and likely indicate different origins. MOR 11750 displays more abundant postcrania relative to cranial remains and better representation of an entire individual, high degrees of completeness and articulation of postcrania and limbs, presence of more distal limb elements, lack of corrosion by digestion on epiphyses and articular surfaces, and a lack of contralateral pairs (Table 2.1–2.3, Fig 2.4). These

features are atypical of regurgitalites and other predator-derived deposits, which tend to include more abundant disarticulated and fragmentary indigestible prey elements (e.g., Andrews, 1990). The absence of corrosion by digestion precludes the identification of MOR 11750 as a partially digested then regurgitated gastric pellet, and other feeding traces (e.g., “leftover” prey remains) tend to show more breakage, disarticulation and very high proportions of crania and indigestible elements (Montalvo and Tallade, 2009; Montalvo et al., 2016). For these reasons, we exclude MOR 11750 as a feeding trace.

The multiple associated individuals, degree of articulation, and absence of abrasion in MOR 11750 is not expected for an allochthonous origin, and the rapid burial required for such preservation is unlikely given the inferred depositional processes at the site (Freimuth and Varricchio, 2019). *Filikomys primaevus* shares morphological features with modern fossorial mammals, and the taphonomy of other aggregates suggest preservation in the subsurface, likely within a burrow or subsurface shelter (MOR 10908; Weaver et al., in review). The brecciated crania and transverse fractures on long bones (Fig 2.4F, I) are more reminiscent of *in situ* weathering and post-burial abiotic processes, such as lithostatic compaction (Behrensmeyer, 1978; Shipman, 1981; Tomassini et al., 2017). Hadrosaur elements on the same horizon display similar weathering patterns. MOR 11750 is taphonomically similar to MOR 10908 in preserving multiple individuals with high proportions of articulated postcrania and an absence of acid etching or other predation traces. However, MOR 11750 does not preserve many contralateral pairs of elements (8 left vs. 4 right; Table 2.1) and displays markedly greater breakage of cranial remains (Fig 2.4A–C). The more incomplete nature of MOR 11750 may reflect

preservation in the taphonomically active zone closer to the sediment-air interface (e.g., Lyman and Lyman, 1994). Taken together, the features of MOR 11750 align more closely with intrinsic biotic accumulation and post-burial taphonomic processes than a predatory trace.

In contrast, MOR 10912 and MOR 10913 are characterized by a disproportionate element relative abundance (58% crania in MOR 10912, 83% crania in MOR 10913), loss of elements, high breakage with sharp, matrix-truncated edges, an absence of abrasion, significant disarticulation, and corrosion of epiphyses and articular surfaces. This is not expected for other taphonomic settings that could accumulate multi-individual, predominantly monospecific deposits (e.g., burrows; Behrensmeyer and Hook, 1992; Caledo, 2016; Tomassini et al., 2017). Instead, these features closely resemble pellet and scat assemblages of diurnal raptors and mammalian carnivores (see below under **Taphonomic patterns of predator groups**; Andrews, 1990; Souttou et al., 2012; Montalvo and Fernández, 2019). Additionally, the common occurrence of jaw elements in associated pairs (16 of 19 total maxillae) and little discrepancy among the frequency of paired elements (total 11 left, 8 right maxillae; 11 left, 10 right dentaries) is unexpected for an assemblage that has experienced a significant level of transport but is observed in some owl pellet assemblages (Kusmer, 1990).

In both MOR 10912 and MOR 10913, the absence of an observable phosphatic or mineralized ground mass but the abundance of identifiable bone indicates these specimens are not coprolites (Myhrvold, 2012; Thies and Hauff, 2012; Vallon, 2012; Gordon et al., 2020; Hoffman et al., 2020). In contrast, regurgitalites tend to have less

organically-derived matrix surrounding boney elements (Myhrvold, 2012; Gordon et al., 2020). Regurgitalites of the probable troodontid *Anchiornis* preserve a definitive matrix encasing skeletal elements (Zheng et al., 2018), but these are either preserved within or are closely associated with the articulated skeletons of their presumed producer and likely were buried and/or lithified rapidly in a lacustrine environment (O'Connor and Zhou, 2019). This setting is different from the subaerially exposed terrestrial environment of Egg Mountain, and a discrete ground mass is not observed in MOR 10912 and MOR 10913. Hair and mucus that typically binds pellets would likely decay and are unlikely to be preserved under extended periods of subaerial exposure at Egg Mountain, leading to spatially definable assemblages (~ 0.01 and ~ 0.03 m²) of bones that likely represent dispersed or partially dispersed pellets (Terry, 2004). Other organic materials likely present in Egg Mountain soils were likely oxidized through soil processes or diagenesis and not preserved, an alternative explanation for a lack of an organic ground mass in MOR 10912 and 10913. Similar amalgamations of fossil skeletal elements lacking a discrete, observable ground mass are often interpreted as gastric pellets (Sanz et al., 2001, Fig 1; Czaplewski, 2011, Fig 4; Cadele, 2016, Fig 8B; Montalvo et al., 2017, Fig 1g; Garcia-Morato et al., 2019, Fig 2; Gordon et al., 2020).

We interpret MOR 10912 and MOR 10913 as regurgitated gastric pellets based on the following observations: 1) absence of phosphatic or mineralized ground mass, indicative of coprolites; 2) multiple disarticulated individuals (of different taxa) amalgamated in a small (~ 0.01 m² and ~ 0.03 m²) area; 3) skewed proportions of cranial remains relative to postcrania; 4) associated elements representative of contrasting

hydraulic sorting groups for small vertebrates (Dodson, 1973; Korth, 1979); 5) sharp pre-fossilization breaks on crania and postcrania consistent with breakage patterns of small mammal prey items in pellets; 6) no evidence abrasion or rounding, indicative of transport; 7) loss of surface bone on articular surfaces and epiphyses of some postcrania and other skeletal elements that is consistent with corrosion by digestion; and 8) frequent retention of contralateral maxillae and dentaries. Thus, we can make several comparisons to modern gastric pellets and assess the predator responsible for these assemblages and the ecological implications.

Comparison to modern gastric pellets

No definitive pellet size or shape can be discerned for Egg Mountain regurgitalites; however, gastric pellet shape and size can be similar for a variety of predators and may be less informative than other taphonomic characteristics. The number of prey individuals per pellet depends largely on relative prey to predator size, where a higher ratio of predator to prey size can yield more individuals per pellet (Lyman et al., 2003; Lyman, 2012). An average of 3.61 prey items per pellet was observed for barn owl (*Tyto alba*) samples consisting of adult voles (45 g), whereas different barn owl samples containing primarily juvenile deer mice (21 g) averaged 4.38 prey per pellet (Lyman, 2012). Additionally, larger pellets contain the remains of more individuals than smaller pellets (given the same size prey; Lyman et al., 2003), and larger predator taxa produce larger pellets (Andrews, 1990). Single pellets from larger taxa like the European Eagle Owl (*Bubo bubo*, mass 1.62–4.00 kg; Andrews, 1990, appendix 15) regularly contain up

to six or seven individual mammals (Andrews, 1990). However, smaller taxa are also capable of producing high numbers of prey per pellet; study of Tawny owl (*Strix aluco*, mass 0.41–0.80 kg; Andrews, 1990, appendix 15) pellets from Lithuania averaged 2.84 prey per pellet, but a single pellet contained 10 individuals, including mammal, bird, and amphibian prey items (Balėiauskienė et al., 2006). It is not out of the realm of possibility that MOR 10913 represents a single regurgitated pellet with 11 individuals, especially given the close proximity ($\sim 0.03 \text{ m}^2$) of skeletal elements. That only some elements (8 of 19 in MOR 10913) show signs of digestive corrosion may be attributed to different gastric retention time of different meals prior to regurgitation. Alternatively, MOR 10913 may also represent multiple egested pellets in a single regurgitation event, which results from the need to eliminate large quantities of indigestible material (Balgooyen, 1971). In this case, multiple pellets in a single regurgitation event are on average ~ 3.5 times more voluminous than single pellets ($5.86 \pm 2.10 \text{ cm}^3$ compared to $1.59 \pm 1.18 \text{ cm}^3$, respectively; Balgooyen, 1971). This may explain the similar taphonomic characteristics observed between MOR 10912 and MOR 10913 but the disparate MNI.

Taphonomic patterns of predator groups

Different groups of predators can be broadly distinguished based on categories of modification to prey items, largely because of their differing food processing habits (outlined by Andrews, 1990; Terry, 2007). Little to moderate modification is characterized by relatively even representation of skeletal elements, low incidences of breakage on skulls and postcrania, and light digestion on teeth and postcrania, among

other characteristics. Owls swallow prey whole, allowing for better skeletal representation with fewer breaks, and comprise little to moderate modification categories. Heavy modification is characterized by skewed crania to postcrania ratios, breakage of anterior portions of skulls and epiphyses of long bones, and corrosion on teeth and epiphyses of postcrania. Diurnal raptors encompass heavy modification categories, as they dismember prey with beaks and claws, resulting in more breakage and increased surface area for digestion. Extreme modification is characteristic of mammalian carnivores, who greatly process food by chewing; this is reflected in very skewed crania to postcrania representation, only isolated maxillae and high skull breakage, and extreme digestive corrosion on teeth and postcrania. Light to moderate, heavy, and extreme modification categories are consistent for North American and Eurasian (Andrews, 1990), and South American (Montalvo and Fernández, 2019) owls, diurnal raptors, and mammalian carnivores, respectively, and are useful in assessing patterns in MOR 10912 and MOR 10913.

The relative abundance of skeletal elements for Egg Mountain specimens is compared to average element abundance of prey remains from regurgitates and scat of representative predator groups (Fig 2.5). Chi-squared analyses were performed under the null hypothesis that MOR 11750, MOR 10912 and 10913 are equivalent to prey element abundance in modern predator groups. The element relative abundance of MOR 10912 and 10913 is significantly different than that of MOR 11750 ($p = 0.001$). While MOR 11750 retains greater identifiable postcrania ($n = 13$) than cranial remains ($n = 5$), the relative abundance of elements cannot be distinguished statistically from any of the

predator groups of Figure 5 (Appendix B). However, element relative abundance alone is not enough to determine depositional origin; the relative abundance of small mammal skeletal elements can appear similar in a variety of taphonomic settings, including predator-derived (Andrews, 1990), buried or surficial assemblages (Rafuse et al., 2019), and preservation within burrows (Weissbrod and Zaidner, 2014; Tomassini et al., 2017). The other features of MOR 11750—lack of contralateral pairs, high degrees of completeness and articulation, lack of digestion or predatory traces—are suggestive of a non-predatory origin.

Both MOR 10912 and MOR 10913 display abundant crania relative to postcrania, with 58% (7 of 12) of MOR 10912 and 83% (43 of 52) of MOR 10913 represented by crania. Chi-squared analyses yield significant differences between prey element relative abundance in MOR 10912 and 10913 and average owl regurgitates ($p = 0.0003$), barn owl regurgitates ($p = 0.0006$), and average mammalian carnivore scat ($p = 0.01$). In contrast, prey remains in regurgitates of diurnal raptors ($p = 0.058$), specifically the long-winged harrier (*Circus buffoni*; $p = 0.526$), as well as the scat from pumas ($p = 0.392$) cannot be statistically distinguished from (i.e., they are more similar to) element abundance in MOR 10912 and 10913. The extreme representation of crania and the near complete absence of some more robust elements that would be expected to survive egestion (femora, humeri) may be a product of winnowing elements post-egestion (Korth, 1979; Terry, 2004). Indeterminate long bone shafts and fragments may represent some of these elements that were damaged by digestive processes and/or post-egestion taphonomic agents. Abiotic processes acting on pellets after egestion can produce

modifications (breaks, element loss) similar to those produced by feeding, potentially obscuring distinct taphonomic signals of predators (Terry, 2004). Given the dispersed nature MOR 10912 and 10913, it is likely that abiotic post-egestion and post-burial processes had some effect on the assemblages, but quantifying these effects is difficult.

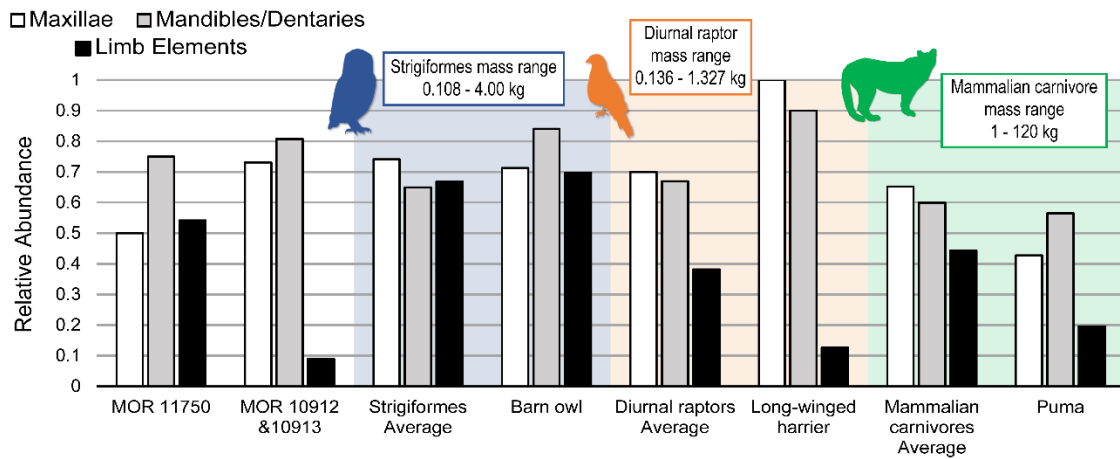


Fig 2.5. Relative abundance of selected crania and postcrania of Egg Mountain specimens compared with small prey from regurgitates and scat of modern predator groups. Element abundance of MOR 11750 does not differ significantly from any modern predator taxa (see text). Element abundance in MOR 10912 and 10913 most closely resemble (i.e., are not statistically different than) patterns of diurnal raptor pellets ($\chi^2 = 5.71$, $p = 0.058$), pellets of the long-winged harrier (*Circus buffoni*) ($\chi^2 = 1.29$, $p = 0.526$), and prey in puma scat (*Puma concolor*) ($\chi^2 = 1.87$, $p = 0.392$). Averages for Strigiformes, diurnal raptors, and mammals are compiled from North American and Eurasian (Andrews, 1990) and South American species (Montalvo and Fernández, 2019). Average relative abundances for barn owl from Andrews (1990), long-winged harrier from Gómez (2007), and puma from Montalvo et al. (2007). Faunal outlines modified from PhyloPic (<http://phylopic.org>).

Most crania are represented by paired or isolated tooth-bearing maxillae and dentaries that are broken posteriorly and folded onto one another. Paired and folded maxillae are frequent (16 of 22 total maxillae represented) and could be a product of prey processing during feeding, pellet formation, or post-deposition processes (e.g., sediment

compaction). Only two braincases are present. The degree of skull breakage is also reminiscent of heavy to extreme modification, typical for diurnal raptors and mammalian carnivores (Andrews, 1990; Montalvo and Fernández, 2019). Preserved maxillae of MOR 10912 and 10913 closely resemble break patterns on isolated marsupial maxillae in Late Pleistocene raptor pellets from Patagonia (Fernández et al., 2012, Fig 4f). All dentaries of MOR 10912 and 10913 lack the large ascending ramus, similar to heavy modification categories on rodent mandibles seen in diurnal raptor and mammalian carnivore prey assemblages (Andrews, 1990). Postcranial breakage is extensive, with remains largely represented by fragmentary long bone shafts with missing epiphyses. Similar patterns of postcranial breakage are observed in long-winged harrier pellets, with all postcrania broken (Gómez, 2007), as well as caracara pellets, with all but two humeri incomplete (Montalvo and Tallade, 2009). Breaks exacerbate digestive processes, exposing more surface bone and medullary cavities to gastric acids that progressively degrade and fragment bone further (Yalden and Yalden, 1985; Dauphin, 2003; Czaplewski, 2011; Fernandez-Jalvo and Andrews, 2016). This process could explain the mass of corroded fragments in MOR 10912 (Fig 1E).

Some postcrania and unidentified fragments show loss of periosteum on epiphyses and articular surfaces, while shafts appear relatively unaltered. This pattern is consistent with corrosion by digestion, which is directional and progressive, acting on ends and salient edges before shafts (Fernandez-Jalvo et al., 2014; Fernandez-Jalvo and Andrews, 2016). This is distinct from other corrosive agents, such as soil or water, which affect all bone surfaces indiscriminately (see Fernandez-Jalvo and Andrews, 2016 for

review). Digestion is observed particularly clearly on an ulna of MOR 10912, where the olecranon and trochlear notch appear corroded, the shaft is largely intact, and the distal end is broken with possible corrosion (Fig 2.2G). Similar patterns are seen on mice ulnae from the pellets of kites (*Elanus caeruleus*) (Souttou et al., 2012, Fig 3e).

Linear markings and sub-millimeter pitting are visible on 8 of 19 observable dentaries in MOR 10913. These markings are present on all surfaces of the dentary up to the base of the alveolar cavities (Fig 2.3D). Similar modifications are seen on mice mandibles in kite pellets (Souttou et al., 2012, Fig 2e–f). Linear markings are visible on isolated *A. halleyi* dentaries that are presumed of different taphonomic status (MOR 250, MOR 318; Montellano, 1988), but these markings are more regular and restricted to the ventral surface of the dentary, concentrated between m3 and m4, and do not extend dorsally to the tooth row.

Teeth in both MOR 10912 and MOR 10913 are unaltered by digestion, with enamel intact and no signs of corrosion. In some instances, similar assemblages of skewed crania relative to postcrania with a notable lack of digestion on some elements have been interpreted as a combination of pellets and discarded prey remains, and uneaten remains can accumulate in association with digested remains from pellets (Montalvo and Tallade, 2009; Montalvo et al., 2016). However, these data come from large, time-averaged pellet accumulations. Here, the close, spatially definable ($\sim 0.01 \text{ m}^2$ and $\sim 0.03 \text{ m}^2$) association of partially digested postcrania and seemingly undigested craniodental elements in what may represent single pellets (or multiple egested pellets) is anomalous. The long-winged harrier (*Circus buffoni*) shows heavy to extreme

modification based on relative abundance and element breakage, but only moderate digestion degrees on teeth (Gómez, 2007; Montalvo and Fernández, 2019); this may offer an explanation for similar patterns observed in MOR 10912 and MOR 10913. Modern monodelphine marsupial molars have characteristically thicker and more uniform enamel structure than rodents, which delays evidence of digestion until typical heavy or extreme modification characteristics by predators (Fernández et al., 2017; Montalvo and Fernández, 2019). Thus, the same predator would show more evidence of digestive corrosion on rodent molars than it would show on marsupial molars under the same conditions. This may also explain the observed digestion on *Alphadon* postcrania and lack of digestion on teeth in closely associated elements. *Alphadon* molar enamel thickness averages $\sim 250\ \mu\text{m}$, comparable to $140\text{--}250\ \mu\text{m}$ (average $163\ \mu\text{m}$) in molars of American opossum *Didelphis virginiana* and much thicker than $110\ \mu\text{m}$ in mouse molars (Stern et al., 1989; Lyngstadaas et al., 1998). The observed postcrania digestion of MOR 10912 and MOR 10913 is consistent with other observed characteristics of heavy modification, but digestion on marsupial molars is not observable until heavy and extreme categories of modification (Fernández et al., 2017).

Assessment of predator

Despite variable MNI between MOR 10912 and MOR 10913, both display similar taphonomic characteristics on the same prey taxon, *Alphadon halleyi*—skewed crania relative to postcrania, high degree of cranial and postcranial breakage, isolated maxillae,

and observable digestion. We tentatively regard both specimens as the product of the same predator taxon.

In modern terrestrial ecosystems, large carnivores tend to take proportionally larger prey compared to small carnivores (Vézina, 1985), and carnivores weighing 21.5 kg or less feed mostly on prey that is 45% or less their own mass (Carbone et al., 1999). A similar threshold (~16 to 32 kg) seems to equate to models of dinosaurian communities (Codron et al., 2013) and provides a framework to assess the predator responsible for the pellets at Egg Mountain.

The relationship between predator and prey size, regurgitate size, and taphonomic modification is complex and variable, but we attempt to generalize some patterns useful in assessing the predator responsible for the Egg Mountain specimens. Lyman et al. (2003) provide several basic quantitative taphonomic indices from an extensive collection of barn owl (*Tyto alba*) pellets; to the best of our knowledge, similar data for diurnal raptors currently do not exist. Larger pellets by volume tend to yield higher average MNI per pellet (given the same size prey item) (Lyman et al., 2003); however, as the size of the most abundant prey item increases, the average MNI per pellet decreases (Lyman et al., 2003). Larger meals (a single large prey item or multiple small prey items) or multiple meals prior to egestion result in larger pellets (Duke et al., 1976). Pellet volume tends to scale linearly with predator body mass, where larger taxa produce larger pellets on average (Fig 2.6A). *Anchiornis* fits this model based on body mass estimates from published femur lengths and pellet sizes (Zheng et al., 2018) (Fig 2.6A). At Egg Mountain, however, the pellets are dispersed or partially dispersed and an accurate pellet

volume cannot be determined. The maximum ingestion capacity of a predator also forms a linear relationship with body mass of the predator, where larger taxa are capable of ingesting greater quantities (Fig 2.6B). With ten ~ 45 g *Alphadon halleyi* (Gordon, 2003) and an additional lizard in MOR 10913, this yields a biomass of at least 450 g for the deposit, scaling to a 2.1 kg predator (Fig 2.6B). Several factors suggest this may be a minimum estimation of the hypothetical predator body mass. The sample of predator taxa used here is largely skewed to lightweight, volant, carnivorous birds; other larger carnivores consume small mammals as a regular part of their diet, including various felids and canids (4–15 kg; Andrews, 1990; Mukherjee et al., 2004), maned wolves (30 kg; Aragona and Setz, 2001), Komodo dragons (35–59 kg; Auffenburg, 1981), and pumas (29–120 kg; Montalvo et al., 2007). Pellets during formation tend to occupy a volume similar to the dorsal half of the ventriculus prior to egestion (Duke et al., 1976). Assuming both MOR 10912 and MOR 10913 represent typical pellets, they may also reflect an underestimate of the predator's mass based on maximum ingestion capacity (Fig 2.6B). Relatively small pellets (< 5.5 cm long) from the Miocene of Argentina are attributed to the 10 kg phorusrhacid *Procariama* (Alvarenga and Höfling, 2003; Nasif et al., 2009).

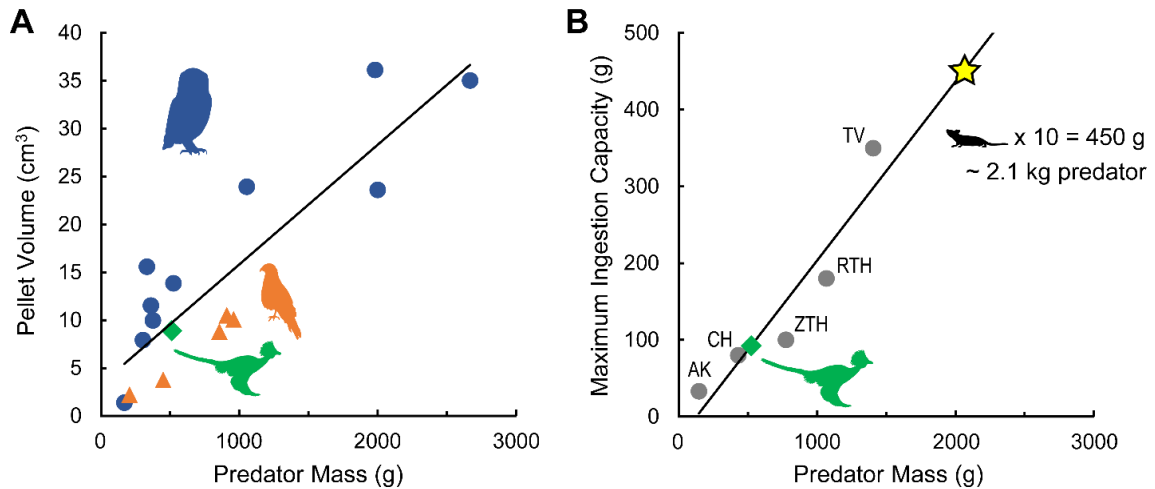


Fig 2.6. Regressions of pellet volume (A) and maximum ingestion capacity (B) with predator mass. Pellet volume ($R^2 = 0.77$) and ingestion capacity ($R^2 = 0.88$) scale linearly with predator size. Predator mass for a single taxon represents an average of male and female masses from Andrews (1990, appendix 15) (A) and del Hoyo et al. (1994) (B); see text for *Anchiornis* body mass estimate. Pellet volume is assumed to be an ellipsoid ($4/3\pi lwb$) calculated from length, width, and breadth measurements of Andrews (1990, appendix 14). Blue circles represent Strigiformes, orange triangles diurnal raptors, green diamond *Anchiornis huxleyi*. Estimated ingestion capacity for *A. huxleyi* equates to ~93 g. A minimum of 10 individual *Alphadon halleyi* in MOR 10913 at 45 g each (Gordon, 2003) is equivalent to ingested prey of 450 g (yellow star). This predicts a minimum predator mass of ~2.1 kg. Maximum ingestion capacities for each taxon from Hiraldo et al., (1991). AK, American kestrel; CH, Cooper's hawk; ZTH, Zone-tailed hawk; RTH, Red-tailed hawk; TV, Turkey Vulture.

The ability to regurgitate indigestible prey remains is apparently ubiquitous across many extant vertebrate clades and likely their extinct relatives (Myhrvold, 2012). Thus, it is reasonable to assess the possible pellet producers based on the representative faunal assemblage at Egg Mountain (Fig 2.7) as well as other potential producers not represented at the locality. Carnivores represented at the locality include tyrannosaurids, dromaeosaurids, *Troodon formosus*, and a large carnivorous varanoid lizard comparable to *Labrodioctes* (Gao & Fox, 1996). Pterosaurs and birds are also known from the Two Medicine Formation and are assessed as well.

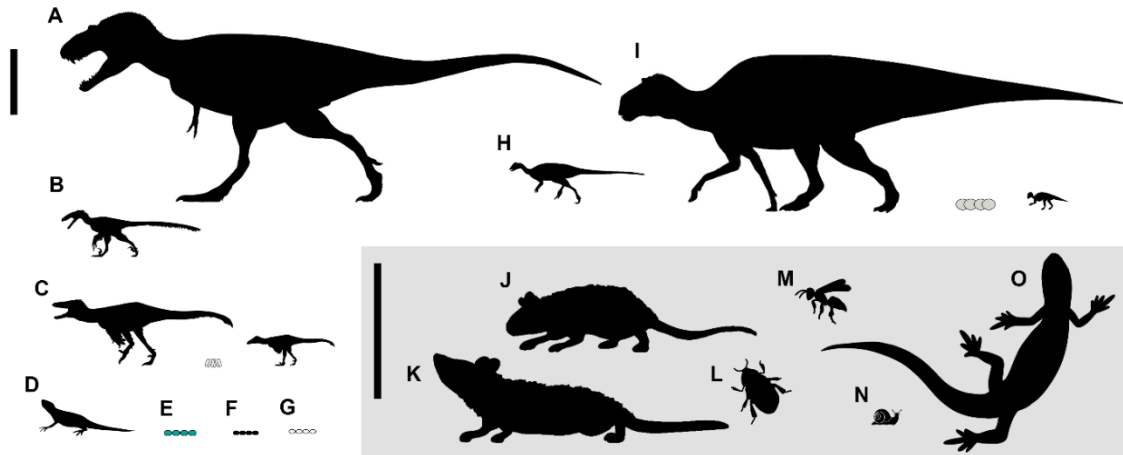


Fig 2.7. Representative fauna at Egg Mountain. (A) Tyrannosauridae indet. shed teeth. (B) Dromaeosauridae indet. and *Saurornitholestes* sp. shed teeth. (C) *Troodon formosus* juvenile skeleton, shed teeth, eggshell and egg clutches. (D) cf. *Labrodioctes*, isolated dentary. (E) *Continuoolithus* oosp. eggshell. (F, G) indeterminate thin eggshell. (H) *Orodromeus makelai* articulated, associated and isolated skeletal elements. (I) cf. *Maiasaura* skeletal elements, nestlings, eggs and eggshell. (J) *Filikomys primaevus* skeletons. (K) *Alphadon halleyi* skeletons. (L) possible coleopteran trace fossils. (M) hymenopteran trace fossils. (N) Gastropoda indet. (O) *Magnuviator ovimonsensis* skeletons. The only semi-aquatic or aquatic vertebrates are represented by one *Adocus* turtle shell fragment, one frog bone, and one crocodilian tooth. Dinosaur reconstructions (except *Troodon*) modified from originals by Scott Hartman. *Troodon*, small vertebrates, and invertebrates by Jason Hogan. Scale bar 1 m (A–I), 10 cm (J–O).

While shed tyrannosaurid teeth comprise nearly half of observed theropod teeth throughout the section at Egg Mountain ($n = 51$; Scofield, 2018), it is likely that large tyrannosaurids would not be sustained by consistently feeding upon small mammals. Additionally, large tyrannosaurids appear to readily ingest bone of large prey items based on preserved gut contents (Varricchio, 2001) and coprolites (Chin et al., 1998; Chin et al., 2003), retaining the plesiomorphic coelurosaurian digestive condition (Varricchio, 2001; O'Connor and Zhou, 2019). While small juvenile tyrannosaurids seem capable of feeding on small mammals and differences in diet through ontogeny cannot be ruled out, there is no evidence of extended activity by tyrannosaurids at the locality.

Snakes and lizards typically digest most bone. However, some taxa, particularly varanids, are capable of egesting gastric pellets that usually contain primarily hair, but sometimes teeth, claws, feathers, and bone, resembling the pellets of raptors (Gans, 1952; Auffenberg, 1981, 1988, 1994). Egestion typically occurs because of overconsumption of meals too large to digest or an environmental perturbation (e.g., too warm or cold, high stress, or the need to evade a predator) and does not appear to be a habitual process as it is in birds (Duke et al., 1976; Fisher, 1981; Naulleau, 1983; Andrews et al., 2000; Bartlett and Bartlett, 2003; Fathinia et al., 2009). The only carnivorous squamate representative from the locality is a single dentary tentatively referable to *Labrodioctes*, a monstersaurian (i.e., Gila monsters and kin, including Varanidae; Gao and Fox, 1996). While modern Gila monsters are capable of regurgitation (Hensley, 1949; Durham, 1951), little is known about their predatory taphonomic signatures. Hensley (1949) reports a captive Gila monster regurgitating three juvenile cottontail rabbits in varying condition but largely intact with articulated limbs and postcrania. This pattern is also seen in a putative squamate gastric pellet from the Eocene of Germany (Mayr and Schaal, 2016). This is in contrast to the crania-dominated, disarticulated and broken elements of MOR 10912 and 10913, and we consider it unlikely that carnivorous squamates are the predators responsible.

Other potential predators not represented at the locality include pterosaurs and birds. Pterosaur gut contents and coprolites are reported (Hone et al., 2015; Qvarnström et al., 2019; see Witton, 2018 for review), and putative regurgitates associated with skeletons are known but sparse (Brown, 1943; Bennett, 2001; Bennett, 2014). The

disarticulated vertebrae of two fish occur in a mass wedged between the mandibular rami of a *Pteranodon* specimen (Brown, 1943; Bennett, 2001). The fish remains are relatively small compared to the inferred size of the *Pteranodon* individual, and they are interpreted as ejected gut contents during death throes (Bennett, 2001). The small rhamphorhynchoid *Scaphognathus crassirostris* is preserved with an articulated vertebral column of an unidentified fish near its skull, interpreted as regurgitated gut contents during death and decomposition (Bennett, 2014). The pellet described by Sanz et al. (2001) is suggested to have been produced by a pterosaur but cannot be conclusively demonstrated. The dietary habits of Mesozoic birds have received considerable attention (e.g., O'Connor, 2019), as has the evolution of the unique avian digestive system, including the ability to produce pellets (Zheng et al., 2018; O'Connor and Zhou, 2019). The Early Cretaceous ornithuromorph bird *Yanornis* preserves associated regurgitalites (Zheng et al., 2014), and a specimen of *Iteravis* (Zhou et al., 2014) preserves a mass of disarticulated and corroded bones reassessed as a regurgitalite by O'Connor and Zhou (2019). While both ornithuromorph birds and apparently pterosaurs are capable pellet producers, little information is available on the taphonomic features of prey remains. Both groups are poorly represented in the Two Medicine Formation (Padian, 1984; Varricchio and Chiappe, 1995; Agnolin and Varricchio, 2012), and absent at the locality. While a transient pterosaur or bird cannot be excluded with certainty, there is no evidence for either group from the Egg Mountain locality.

With other potential candidates deemed unlikely in the context of the locality, it is useful to discuss dromaeosaurids and troodontids together, as they often group together

as the sister clade to Avialae and share abundant morphological and behavioral similarities. However, recent analyses recover troodontids as the sister taxa to Avialae (e.g., Foth and Rauhut, 2017; Cau, 2018; Gianechini et al., 2018), though the affinities of several clades within paravians is far from concrete (Agnolin et al., 2019).

Dromaeosaurid remains are infrequent from Egg Mountain and the Willow Creek Anticline. Of the 96 theropod teeth from the locality, ten are referable to dromaeosaurids and four referable to *Saurornitholestes* (Scofield, 2018). Body mass estimates for *Saurornitholestes* sp. from the Two Medicine Formation (MOR 721 and MOR 660) are 10.5 and 19.5 kg, respectively, and other similarly sized dromaeosaurids range from 13–24 kg (Campione et al., 2014). These are under or near the proposed 21.5 kg threshold of preference for small prey (Carbone et al., 1999; Codron et al., 2013) and are comparable to other carnivores that are frequent predators of small mammals (Andrews, 1990; Mukherjee et al., 2004). However, dromaeosaurids show traits that suggest hypercarnivory (Zanno and Mackovicky, 2011), and exceptional associations of dromaeosaurids and ornithischians (Maxwell and Ostrom, 1995; Carpenter, 1998), biomechanical analyses of teeth (Torices et al., 2018) and metatarsal and pedal morphology (Fowler et al., 2011) suggest dromaeosaurids may have been adapted for feeding on relatively larger prey items.

The dromaeosaur *Microraptor* is known from over 200 specimens, with the only evidence of diet represented by stomach contents of often articulated prey remains (O'Connor et al., 2011), suggesting an inability to formulate and egest gastric pellets (O'Connor et al., 2019; O'Connor and Zhou, 2019). Similarly, other more basal

coelurosaurs with preserved stomach contents suggest the ability to readily ingest bone (e.g., Varricchio, 2001; Currie and Chen, 2001; Hurum et al., 2006; Xing et al., 2012). In contrast, a similar sample size of the probable basal troodontid *Anchiornis* ($n = 230$) recovers four specimens associated with gastric pellets, with one example preserving disarticulated remains of three lizards (Zheng et al., 2018). No specimens of *Anchiornis* currently known preserve stomach contents (O'Connor and Zhou, 2019). The disparity of digestive processes between *Microraptor* and *Anchiornis* suggests avian-style pellet egestion evolved at the base of Troodontidae, an ability unique to troodontids and birds and that excludes dromaeosaurs (O'Connor et al., 2019, O'Connor and Zhou, 2019).

If avian-style pellet production does unite troodontids with birds and exclude dromaeosaurids (O'Connor et al., 2019, O'Connor and Zhou, 2019), the most likely candidate as the regurgitalite producer here is *Troodon formosus*. *Troodon* teeth are second-most abundant at the locality after tyrannosaurids ($n = 24$; Scofield, 2018), and several eggs, egg clutches, and a nesting structure suggest frequent activity at the locality (Horner, 1982, 1987; Varricchio et al., 1997, 1999). It is common for pellets and prey items to accrue at nesting sites of predatory birds (e.g., Andrews, 1990; Laudet and Selva, 2005; Lloveras et al., 2012; Lloveras et al., 2014; Ferguson et al., 2018; McGrath et al., 2020) and proximal to favorable denning and thermoregulatory locales of carnivorous mammals and varanids (Auffenberg, 1981; Brain, 1981). Additionally, morphology of tarsal and pedal elements (Fowler et al., 2011), tooth morphology and denticle morphometrics (Holtz et al., 1998; Hendrickx et al., 2019), analysis of correlated herbivorous traits (Zanno and Mackovicky, 2011), and tooth biomechanics (Torices et al.,

2018) suggest *Troodon* may have been omnivorous or favored smaller or softer prey items compared to hypercarnivorous dromaeosaurids and tyrannosaurids. Abundant *Troodon* teeth at a hadrosaur nesting site (Ryan et al., 1998) and possible troodontid predatory digging traces associated with mammal burrows (Simpson et al., 2010) offer additional evidence for preferential predation on small prey items.

The body mass of an adult *Troodon* is ~50 kg (Varricchio, 1993; 48.5 kg based on Campione et al., 2014), presumably too large to consistently feed on a ~45 g *Alphadon* (Carbone et al., 1999; Gordon, 2003). However, minimum prey mass is demonstrated to be independent of predator mass, and large carnivores will exploit a wider range of prey sizes, occasionally consuming much smaller prey (Radloff and duToit, 2004) and more regularly consuming smaller prey when larger predators are present (Dickman, 1988). A pertinent comparison is the maned wolf (*Chrysocyon brachyurus*), an omnivorous canid that feeds on small rodents, insects, and fruit (Aragona and Setz, 2001). A 30-kg adult will eat 374–584 g per day in captivity (Barboza, et al., 1994), equivalent to the represented biomass (~ 450 g) in MOR 10913. A small juvenile *Troodon* recovered from the locality (MOR 430) has an estimated body mass of 2.4 kg, and a larger juvenile (MOR 563) has an estimated mass of 12.9 kg (after Campione et al., 2014). These match closely with the body masses of some modern Strigiformes and mammalian carnivores, respectively, both frequent predators of small mammals (Andrews, 1990, appendix 15). Given the abundance of nesting evidence at the locality, immature *Troodon* may be good candidates for the pellet producers at Egg Mountain.

In summary, *Troodon* is considered the most likely producer of Egg Mountain regurgitalites based on the following: 1) pervasive activity at the locality supported by abundant nesting; 2) abundant shed teeth indicative of active feeding behavior; 3) teeth morphologically and biomechanically suited for omnivory or small prey; 4) tarsal and pedal morphology suitable for small prey; and 5) an inferred derived ability found in troodontids and Aves to egest gastric pellets. Birds and small pterosaurs, both seemingly capable pellet-producers, cannot be ruled out definitively, but their complete absence at the locality compared to the abundance of *Troodon* material favors the latter as the producer. Though the large size of adult *Troodon* seems inconsistent with regular predation of small mammals, there are several examples of modern medium- and large-sized carnivores that regularly prey upon small mammals (Andrews, 1990; Aragona and Setz, 2000; Montalvo et al., 2007). As such, we consider *Troodon* the likely producer of regurgitalites at Egg Mountain and assess the implications for the ecology of the site.

Ecological and evolutionary implications

Regurgitalites from Egg Mountain are the oldest known mammal-bearing gastric pellets, allowing for unique comparison to modern gastric pellets. Some raptor pellet assemblages tend to reliably track small mammal community structure, even amongst fossil time-averaged assemblages (Terry 2010; Andrade et al., 2016), and have been used to infer ecological interactions from the Holocene to the Eocene (Andrews, 1990; Czaplewski, 2011; Mayr and Schaal, 2016). At Egg Mountain, the abundance of *Alphadon* in regurgitalites may reflect a greater abundance relative to other small prey

taxa in the paleocommunity. In turn, the observed paucity of lizard (DeMar et al., 2017) and multituberculate (Montellano et al., 2000; Weaver et al., in review) remains in regurgitalites may reflect a lower overall abundance in community structure.

Alternatively, multituberculate remains from the locality exhibit different taphonomic and morphological characteristics potentially indicative of a fossorial lifestyle and communal sheltering behavior (Weaver et al., in review), which may have made them less susceptible to predation compared to *Alphadon*. Taken together, the discrepancies in taphonomic characteristics of Egg Mountain mammals likely reflect differences in their respective ecological roles, offering rare insight into Late Cretaceous mammal community structure.

The available evidence favors *Troodon* as the predator responsible for the Egg Mountain regurgitalites, a rare instance of linking a trace to a likely specific trace-maker. Accordingly, several inferences can be made about *Troodon* ecology and behavior in the context of the Egg Mountain locality and the evolution of gastric pellet production and dietary processes along the avian lineage.

The taphonomic characteristics of modern prey in regurgitated gastric pellets reflect the feeding style of specific predators, and the same is likely true for regurgitalites at Egg Mountain. Owls tend to swallow prey items whole, which preserves better overall element representation, few breaks, and less digestive etching of prey remains in pellets. In contrast, diurnal raptors tend to manipulate prey during feeding, dismembering prey while using the feet for stabilization, resulting in pellets proportionally higher in crania than postcrania, more frequent breakage of all elements, and greater effects of digestion.

These features are similar to prey in the scat of mammalian carnivores that greatly modify prey through mastication. MOR 10912 and 10913 share several features with prey from diurnal raptor pellet assemblages, including proportionally higher representation of craniodental elements, high degree of breakage of crania and postcrania, and observable corrosion by digestion. Given these taphonomic similarities, it stands to reason that *Troodon* fed in a similar manner to diurnal raptors, significantly processing prey during feeding. Such behavior has also been inferred for deinonychosaurs, where the feet and hypertrophied digit II are hypothesized to grasp and pin prey (Fowler et al., 2011). Differences between dromaeosaurid and troodontid metatarsi and pedal morphology suggest ecological separation; dromaeosaurid metatarsi are stouter and pedal phalanges are ginglymous, adaptations for grip strength, torsion resistance, and larger prey, whereas *Troodon* possesses a proximally pinched mt-III (the arctometarsalian condition), an adaptation for cursoriality, in addition to a ball-like articular facet of mt-I, suggestive of a weaker but more opposable and uniform grasping arrangement suitable for smaller prey (Holtz, 1994; Fowler et al., 2011). Additionally, a relatively robust manus and forelimb are suggestive of grasping capabilities (Russell, 1969; Russell and Séguin, 1982; Holtz et al., 1998). The observed taphonomic patterns are consistent with manipulation of prey during feeding, a rare instance of observable prey processing by a derived maniraptoran theropod (Currie and Jacobsen, 1995; Hone and Rauhut, 2010).

Troodon was first posited as a hunter of crepuscular small mammals by Russell (1969). Anteriorly directed and large diameter orbits indicate stereoscopic vision analogous to modern raptors and suggest possible adaptations for low light conditions

(Russell and Séguin, 1982; Fiorillo and Gangloff, 2000; Stevens, 2006). Other small bodied carnivorous dinosaurs have been interpreted as nocturnal based on sclerotic ring and orbit dimensions (Schmitz and Motani, 2011; but see Hall et al., 2011). Given the prevailing hypothesis that most Mesozoic mammals were nocturnal (e.g., Kielan-Jaworowska et al., 2004; Heesy and Hall, 2010), it is possible that the presumed *Alphadon*–*Troodon* relationship represents nocturnal feeding interaction, as has been suggested for other exceptional instances of dinosaur predator–prey interactions (Schmitz and Motani, 2011).

A modified alimentary canal and the ability to egest pellets in birds is thought to have arisen as an adaptation to reduce weight for flight (Zheng et al., 2014). However, several disparate non-volant vertebrate groups are capable of producing pellets (Bowen et al., 2002; Myrhvold, 2012), albeit by different digestive mechanisms than modern birds (Fisher, 1981; Duke, 1997; Andrews et al., 2000). Additionally, the apparent inability of the volant *Microraptor* to egest pellets casts doubt on this hypothesis (O'Connor et al., 2019). *Troodon* and *Anchiornis* are unique examples, as they seemingly possess more avian-style pellet egestion yet are non-volant, with *Troodon* approaching body masses one to two orders of magnitude larger than most modern raptorial birds (~50 kg vs. ~0.5–5 kg). The potential *Troodon* regurgitalites here support the hypothesis that avian-style pellet egestion likely evolved to increase digestive efficiency, accommodating increased physiological processes associated with the dinosaur-bird transition instead of being directly related to decreasing weight for flight (O'Connor et al., 2019). The ability to egest pellets also adds to the array of evidence suggesting *Troodon* and troodontids were

highly active, possessing an avian-like metabolism and physiological processes (e.g., Russell, 1969; Russell and Séguin, 1982; Russell and Dong, 1993; Varricchio, 1993; Xu and Norell, 2004; Varricchio and Jackson, 2004). This study provides another example of derived non-avian theropod and mammal feeding interactions (Currie and Chen, 2001; Hurum et al., 2006; Larsson et al., 2010).

Conclusions

Egg Mountain paleosols yield two specimens of multi-individual, crania-skewed, partially digested remains of the marsupialiform *Alphadon halleyi* that are the earliest known mammal-bearing gastric pellets. An additional multi-individual specimen of the multituberculate *Filikomys primaevus* likely originated by a different depositional mechanism, and allows for comparison of taphonomic characteristics between feeding traces and non-feeding traces at the locality. Together, these specimens allow for unique comparison to the extensive literature on mammal remains in modern gastric pellets. The relative abundance of crania and postcrania, breakage patterns, and observed digestive corrosion of MOR 10912 and 10913 align with predatory modification observed in diurnal raptors and mammalian carnivores. The abundance of *Alphadon* in pellets may reflect the microvertebrate community and possible ecological or behavioral segregation between multituberculates and metatherians at the locality. While other small predators (e.g., pterosaurs, birds, other small theropods) cannot be definitively ruled out, available evidence favors *Troodon* as the producer of the regurgitalites, corroborating past

inferences of a small or soft prey diet. The parallels with Egg Mountain regurgitalites and gastric pellets of diurnal raptors suggest significant manipulation of prey during feeding. *Troodon* is a large-bodied troodontid and this study further suggests that avian-style pellet production evolved to increase digestive efficiency to accommodate enhanced metabolic processes in paravians.

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CHAPTER THREE

PALEOECOLOGICAL IMPLICATIONS OF INVERTEBRATE FECAL PELLETS
(*EDAPHICHNIUM*) AT A RICH TERRESTRIAL VERTEBRATE LOCALITY, UPPER
CRETACEOUS TWO MEDICINE FORMATION, MONTANA, USA.

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PALEOECOLOGICAL IMPLICATIONS OF INVERTEBRATE FECAL PELLETS
(*EDAPHICHNIUM*) AT A ICHNOFOSSIL-RICH DINOSAUR NESTING LOCALITY,
UPPER CRETACEOUS (CAMPANIAN) TWO MEDICINE FORMATION,
MONTANA, USA

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Running Header: *Edaphichnium* at a rich terrestrial vertebrate locality

Abstract.—The terrestrial feeding trace *Edaphichnium lubricatum* Bown and Kraus 1983 is known from the Triassic to recent and is indicative of substrate feeding by invertebrates, typically earthworms. We describe 11 specimens attributable to *Edaphichnium* isp. from Egg Mountain, a diverse Upper Cretaceous vertebrate locality from Montana, USA, and assess possible trace-makers and ecological and environmental implications at the locality. A 1.5-meter stratigraphic succession comprises calcareous siltstones and micritic calcretes with abundant fossil insect cocoons (*Fictovichnus sciuttoi*), representing well-drained paleosols. Three morphotypes of *Edaphichnium* are

identified, including linearly arranged pellets, pellets in condensed masses, and pellets in dispersed masses. Maximum pellet lengths range from 1.87–6.70 mm (mean 4.13 mm) and maximum diameters range from 1.01–4.06 mm (mean 2.62 mm). Pellets are consistently ellipsoidal in shape and characteristically fine-grained and compositionally homogenous relative to the sedimentary host matrix. Possible trace-makers include chafer or other coleopteran larvae and millipedes along with earthworms, suggesting a range of capable trace-makers of *Edaphichnium*. The presence of *Edaphichnium* at specific horizons throughout the locality suggests increased organic content in the subsurface, potentially connected to depositional hiatuses. Notably, fecal pellets are associated with *Maiasaura* eggs and hatchlings and *Fictovichnus sciuttoii* wasp cocoons, suggesting decaying dinosaur nests hosted communities of invertebrate decomposers that rid the soil of pathogens, potentially facilitating nest site fidelity. *Edaphichnium* adds a secondary component to the *Celliforma* ichnofacies known from Egg Mountain and surrounding strata, and adds to the array of nesting, feeding, and dwelling traces of wasps, beetles, other invertebrates, mammals, and dinosaurs from the locality.

Introduction

In modern terrestrial ecosystems, the interactions of biota—including those of plants, microbes, invertebrates, vertebrates, and carrion—act as important drivers to shape the formation, structure, composition, and maintenance of soils and cycling of nutrients (Lee and Foster, 1991; Jenny, 1994). Several organisms exploit organic matter

in soils for food, ingesting detritus and particulate organic material within the substrate or on the surface and depositing sediment-rich fecal pellets (Rusek, 1985; Kooistra and Pulleman, 2010). Trace fossils can record this behavior in paleosols, such as *Edaphichnium lubricatum* Bown and Kraus 1983, which is characterized by tubular burrows filled and lined with ellipsoidal fecal pellets. *E. lubricatum* is recorded from paleosols from the Triassic to the Pleistocene and are commonly attributed to burrows of earthworms, though a wealth of other invertebrates also feed and deposit fecal pellets in soils (Table 3.1).

The advent and diversification of flowering plants in the Early Cretaceous sparked innovations in soil ecosystems, including novel nesting behaviors and the first paleosol ichnofacies dominated by insects, the *Celliforma* ichnofacies (Genise et al., 2010; Genise, 2016; Genise et al., 2020). Additionally, the record of dinosaur nesting is best known from the Cretaceous, and certain dinosaur reproductive traits—e.g., large eggs and clutch sizes, colonial nesting, site fidelity—suggest nesting sites hosted substantial accumulations of organic material and acted as an important ecological resource for predatory and scavenging vertebrates and invertebrates (e.g., Horner, 1982; Chiappe et al., 2005; Varricchio, 2011; Bois and Mullin, 2017). Indeed, dinosaur nest predation by vertebrates is supported by an associated nest and snake skeleton from the Late Cretaceous of India (Wilson et al., 2010). Nest predation is also a proposed ecology for various Late Cretaceous mammalian taxa (e.g., Wilson et al., 2016; Bois and Mullin, 2017; Brannick and Wilson, 2020). However, there is little evidence of invertebrate activity at dinosaur nests. Genise and Sarzetti (2011) report several wasp cocoons

(*Fictovichnus sciuttoii*) within a sauropod egg, suggesting wasps would have preyed upon insects and other invertebrates attracted to the dry and decaying eggs. Other associations of insects and dinosaur nests have been noted (Horner, 1984; Martin and Varricchio, 2011; Freimuth and Varricchio, 2019), but direct evidence of invertebrates feeding on nest material remains elusive.

Here, we describe 11 specimens of *Edaphichnium* isp. from Egg Mountain, a dinosaur nesting locality from the Two Medicine Formation (Campanian) of north-central Montana, U.S.A. We identify three morphotypes—fecal pellets arranged linearly, pellets in condensed masses, and pellets in dispersed masses—and describe their morphology, microstructure, and geochemical and mineralogic features to assess possible trace-makers. *Edaphichnium* at the locality occur at specific stratigraphic and geographic locales, and their implications for depositional environments are also assessed. Notably, some *Edaphichnium* fecal pellets are associated with *Maiasaura* eggs and perinatal remains and shed light on the role of invertebrates in carrion communities surrounding nesting dinosaurs.

Table 3.1. Occurrences of *Edaphichnium* and other fecal pellet trace fossils from paleosols and terrestrial settings.

Geography	Formation	Age	Depositional Setting	Additional Trace Associations	<i>Edaphichnium</i> or pellet trace-maker	References
Uruguay	Sopas	Late Pleistocene	Pedogenized silty and muddy fluvial facies; seasonal climate and well-aerated soils	<i>Castrichnus incolumis</i> , <i>Taenidium serpentinum</i> , rhizoliths	Earthworms	Verde et al. (2007)
Oregon, USA	John Day	Late Oligocene–Early Miocene	Wooded grassland paleosols, seasonally wet alluvial lowland; subhumid–semiarid and seasonally wet climate	<i>Pallichnus dakotensis</i> , <i>Taenidium</i> , <i>Scaphichnium</i> , <i>Termitichnus</i> , root traces	Earthworms	Retallack et al. (2000); Retallack (2004)
Colorado, USA	White River	Early Oligocene	Silty mudstone, composite and cumulative inceptisols; savannah–woodland environments, well-drained but moist soils	<i>Cellicalichnus ficioides</i> , <i>Fictovichnus</i> isp., <i>Macanopsis</i> , <i>Pallichnus dakotensis</i> , <i>Parowanichnus</i> , <i>Planolites</i> , backfilled burrows, rhizoliths, “wasp cocoons”	Earthworms	Hembree and Hasiotis (2007)
Fayum Province, Egypt	Jebel Qatrani	Oligocene	Medium sand, point bar deposits; nearshore fluvial environment, tropical–subtropical monsoonal rainforest and open unvegetated areas	<i>Ophiomorpha</i> , <i>Masrichnus</i> , <i>Termitichnus</i> , solitary wasps, rhizoliths, vertebrate burrows	Earthworms	Bown (1982)

Patagonia, Argentina	Sarmiento	Middle Eocene– Early Miocene	Poorly to moderately pedogenized volcanic ash deposits; subhumid–arid climate *Pellets occur within <i>Coprinisphaera</i> brood balls	<i>Coprinisphaera</i> , <i>Tombornichnus pepei</i> , <i>Lazaichnus fistulosus</i>	Rhizophagous beetles or Earthworms	Sánchez and Genise (2009)
Utah, USA	Uinta	Eocene	Lacustrine and fluvial deposits	Ant nests, meniscate burrows, wasp cocoons	Earthworms	Sandau (2005)
Wyoming, USA	Willwood	Late Paleocene– Early Eocene	Red, purple, yellow- brown paleosols, gleyed paleosol (spodosols) horizons; well- to poorly-drained soils	<i>Camborygma lironomos</i> , <i>Cylindricum</i> , <i>Ichnogyrus</i> , <i>Macanopsis</i> , <i>Naktodemasis</i> <i>bowni</i> , <i>Planolites</i> , <i>Scaphichnium hamatum</i> , <i>Steinichnus</i> , wasp cocoons, bee cells, meniscate burrows, rhizoliths	Earthworms	Bown and Kraus (1983, 1987); Hasiotis et al. (1993); Smith et al. (2008, 2009)
North Dakota, USA	Mud Buttes, K- Pg boundary	Earliest Paleocene	Lignite overlaid by silty sandstone; aquatic, saturated substrate	<i>Planolites</i> isp.	Earthworms	Chin et al. (2013)

Montana, USA	Two Medicine	Late Cretaceous (Campanian)	Siltstones and micritic calcretes; incipient, well-drained paleosols under semiarid, seasonal environments	<i>Fictovichnus sciuttoi</i> , <i>Fictovichnus</i> isp., <i>Feoichnus martini</i> , rhizoliths, unlined burrows (cf. <i>Skolithos</i>)	Earthworms, beetle larvae, and/or millipedes	Martin and Varricchio (2011); Freimuth and Varricchio, (2019) Panasci and Varricchio (2020); this study
Chubut, Argentina	Laguna Palacios	Late Cretaceous	Ashfall deposits, fluvially and pedogenetically altered; seasonality	<i>Beaconites</i> , <i>Cellicalichnus</i> <i>meniscatus</i> , <i>Cellicalichnus</i> <i>chubutensis</i> , <i>Loloichnus</i> <i>baqueroensis</i> , <i>Rebuffoichnus</i> <i>casamiquelai</i> , <i>Skolithos</i> , <i>Taenidium</i> , <i>Tombownichnus plenius</i> , earthworm diffuse boxworks, root traces	Earthworms	Genise (2016, Fig. 3.11e, 15.20)
Argentina	Laguna Manantiales (= La Matilde)	Jurassic	Volcaniclastic sediments, tuffs, sandstones; lowland setting with associated volcanics	<i>Ameghinichnus</i> , dinosaur tracks, invertebrate traces, root traces	Earthworms	Melchor et al. (2004); De Valias (2009); Genise (2016, Fig. 15.20)
New South Wales, Australia	Narrabeen Group	Triassic	Red, massive, clay- rich strata, well- developed paleosols	Variety of “insect traces”, <i>Subglockeria</i> , <i>Glockeria</i> , vertebrate burrows, abundant rhizoliths	Earthworms	Retallack (1976)

Geological Setting

Two Medicine Formation and Willow Creek Anticline.—The Two Medicine Formation is a 600-meter thick terrestrial siliciclastic sequence spanning the Campanian age between 74.076 ± 0.095 and 80.044 ± 0.190 Ma and is contemporaneous with the Judith River Formation of eastern Montana, and the Foremost, Oldman, and Dinosaur Park Formations of Alberta, Canada (Rogers et al., 1993; though see Fowler, 2017 for modified dates). Facies represent varying floodplain deposition proximal to the source on an up-dip alluvial plain. The Two Medicine Formation overlies regressive shore facies of the Virgelle Sandstone (Lorenz and Gavin, 1984). The Horsethief Sandstone and Bearpaw Shale overlie the Two Medicine Formation and represent the subsequent transgression of the Bearpaw Sea (Horner et al., 2001). Two Medicine Formation deposition occurred at a paleolatitude of 48°N (Golonka et al., 1994), where climate and floral models suggest semiarid to subhumid conditions with a mean annual temperature of $16^{\circ}\text{C} \pm 8^{\circ}\text{C}$ (Wolfe and Upchurch, 1987). Seasonality is inferred throughout the deposition of the formation, as indicated by the abundance of caliche nodules, taphonomic data supporting episodic drought, growth interruptions in fossil conifers, herbivorous dinosaur coprolites, and integrated climate modelling and oxygen isotope evidence (Lorenz and Gavin, 1984; Rogers, 1990; Falcon-Lang, 2003; Chin, 2007; Fricke et al., 2010). Facies are interpreted as intergrading fluvial and lacustrine systems in a volcanically active area, indicated by abundant bentonite horizons and volcanogenic deposits (Lorenz and Gavin, 1984; Rogers et al., 1993; Roberts and Hendrix, 2000).

The Willow Creek Anticline is a series of NE–SW dipping, SE-plunging tectonic folds within the upper lithofacies of the Two Medicine Formation exposed west of Choteau, Montana (Lorenz and Gavin, 1984). The geology of the Willow Creek Anticline is well known (Lorenz and Gavin, 1984; Shelton, 2007), largely due to extensive studies related to abundant dinosaur eggs, trace fossils, and skeletal remains (e.g., Horner and Makela, 1979; Horner, 1982; Varricchio and Horner, 1993; Chin, 2007; Woodward et al., 2015). Well-drained soil conditions through the Willow Creek Anticline are inferred from oxidized paleosols associated with abundant hadrosaur nesting and pupichnia (Retallack, 1997; Martin and Varricchio, 2011).

Egg Mountain locality.—The Egg Mountain locality (TM-006) occurs at the Willow Creek Anticline near Choteau, Montana (Fig. 3.1). $^{40}\text{Ar}/^{39}\text{Ar}$ dating of a bentonite 16.5 m stratigraphically below Egg Mountain yield dates of 75.53 ± 0.32 Ma (Shelton, 2007; Varricchio et al., 2010; but see Fowler, 2017). During this time, the area was positioned geographically proximal to the Sevier thrust belt to the west, and distal to the Interior Seaway at peak Claggett regression (Lorenz and Gavin, 1984; Horner, 1987).

Egg Mountain is known for producing egg clutches of the non-avian theropod dinosaur *Troodon formosus* and the oogenus *Continuoolithus* (Horner, 1984, 1987; Hirsch and Quinn, 1990; Varricchio et al., 1997, 1999). Isolated eggshell is common throughout the section, including some attributable to *Maiasaura peeblesorum*. Recent excavations from 2010-2016 have yielded several associated to articulated skeletons of the marsupialiform *Alphadon halleyi* (Montellano, 1988), the multituberculate *Filikomys*

primaevus (Montellano et al., 2000; Weaver et al., in review), and an iguanomorph lizard, *Magnuviator ovimonsensis* (DeMar et al., 2017). Isolated and associated articulated elements of the small ornithopod *Orodromeus makelai* occur throughout the section. Isolated shed hadrosaur teeth are common, and shed dromaeosaurid (including *Saurornitholestes*), *Troodon*, and tyrannosaurid teeth are less common (Scofield, 2018). Insect trace fossils such as *Fictovichnus*, likely representative of wasps and/or beetles, are pervasive at the locality (Freimuth and Varricchio, 2019), and other invertebrate traces (*Feoichnus*; Panasci and Varricchio, 2020) and isolated planispiral terrestrial snails are subordinate. An *Adocus* turtle shell fragment, an isolated frog frontal, and an isolated crocodilian tooth are the only aquatic vertebrate remains known to date.

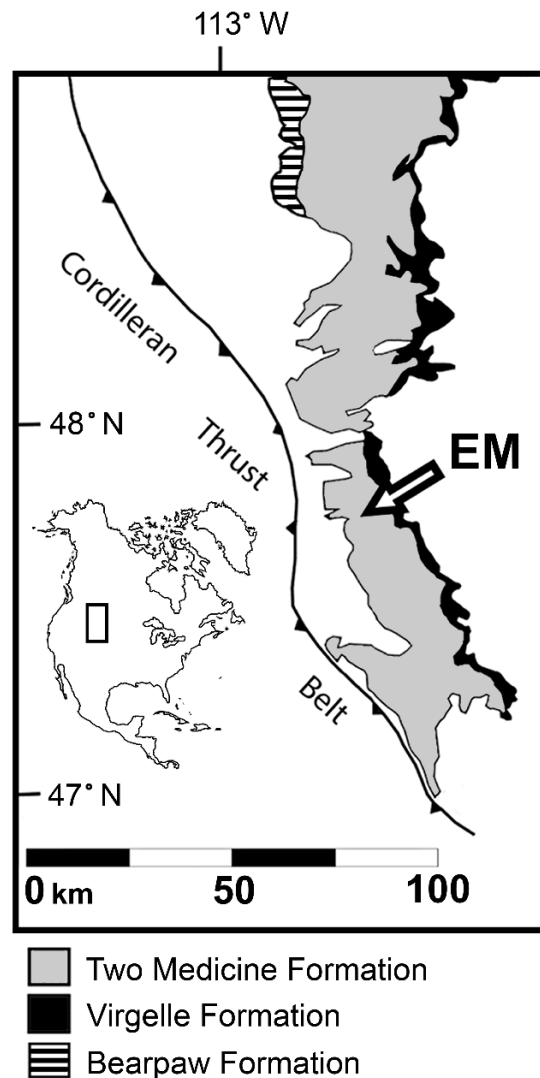


Figure 3.1. Schematic geologic map of the Two Medicine Formation in north-central Montana, U.S.A. EM, Egg Mountain locality.

Sedimentary facies of study section.—Three lithologic units comprise the top 1.5 meters of the studied section at Egg Mountain in an artificial quarry (Fig. 3.2). The lowermost interval (Unit 1) is defined by a >50 cm thick micritic limestone that is laterally continuous across the 7 m by 11 m quarry. The unit is thickest at the north end of the quarry and thins to the south. Some medium- to coarse-grained clastic material is present,

though the micritic matrix is predominant. Centimeter-scale mud rip up clasts are present in the thickest portion of this unit. This unit is massive with no distinct internal structure. Combined, these characteristics are suggestive of a calcrete, as seen in other ichnofossil-bearing deposits of the Willow Creek Anticline (Martin and Varricchio, 2011). The upper surface of the calcrete of Unit 1 is very irregular with decimeter scale relief that extends into the siltstone unit above. Where exposed, the top of Unit 1 is characterized by a surficial rust color. The contact of this limestone unit and the overlying siltstone is usually discrete. The dominant lithology of Unit 2 is a ~1 m thick grey calcareous muddy siltstone. The siltstone weathers in an irregular, blocky pattern. Irregular mudstone nodules (diameters 4.6–17.4 mm) occur infrequently in the siltstone units. Indurated, irregular micritic limestones inter-finger with the siltstone to form irregular discontinuous beds. These limestones are similar in composition to the calcrete of Unit 1 but lack larger clasts and mud rip-ups. Unit 3 comprises a relatively thin irregular micritic limestone likely representing a calcrete similar to those in Unit 2. The limestone is variable in thickness and topographic relief of the upper surface. Unit 3 preserved a *Troodon* nest structure and egg clutch (Varricchio et al., 1999). Infrequent root traces occur within the nest structure (Varricchio et al., 1999). Overall, the sedimentary succession is compositionally homogenous and displays no distinct bedding markers or definitive paleosol horizons. The only marked difference between the lithologic units is the surficial rust color and marked induration of the limestone units.

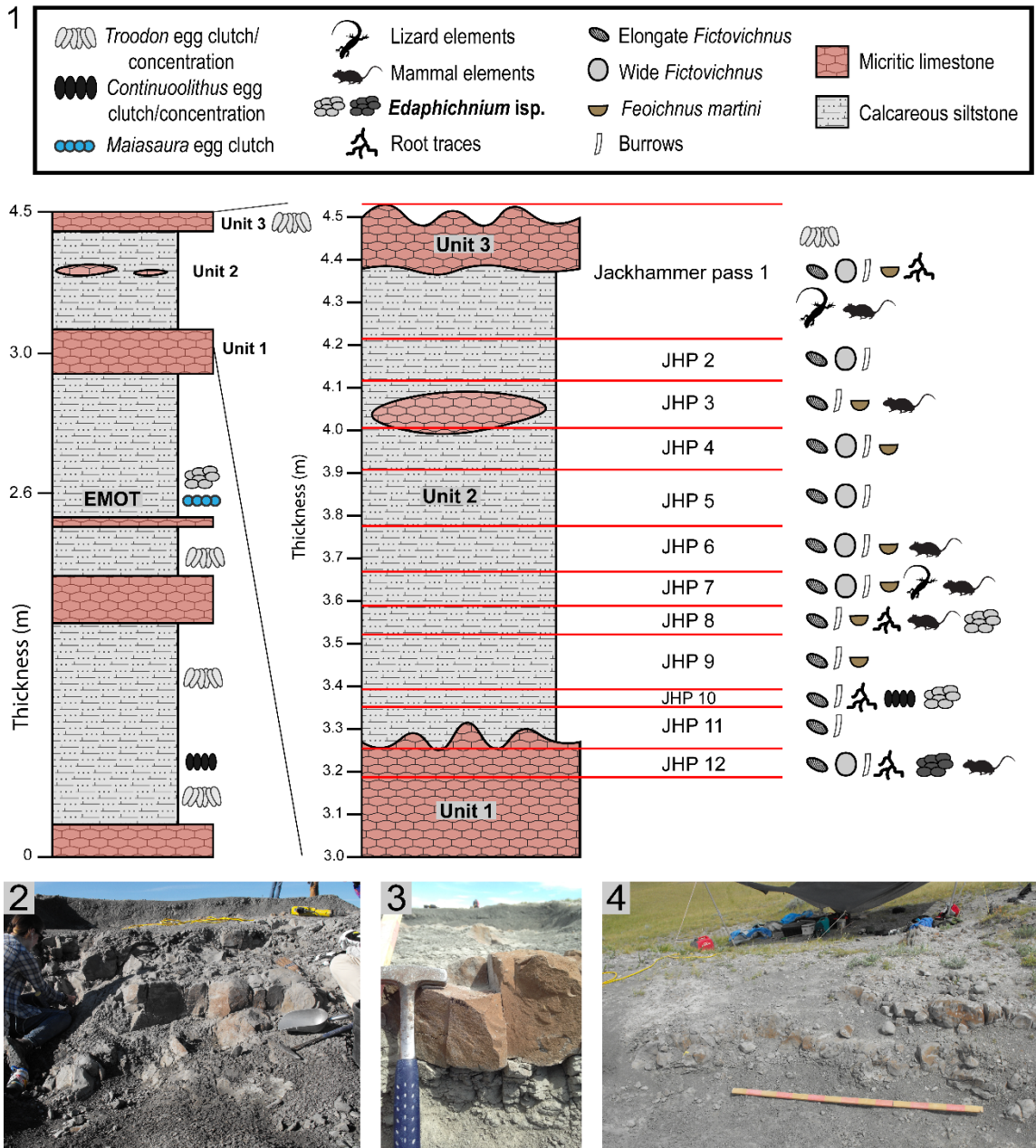


Figure 3.2. Stratigraphy and fossil remains from Egg Mountain. (1), stylized stratigraphic section through Egg Mountain (left) and the top 1.5 meters of the measured section (right). Schematic jackhammer passes (JHPs) are superimposed over stratigraphy, and specimens are assigned to JHPs to track their stratigraphic position. The level at which specimens occur within a JHP is approximate. Passes average ~11 cm in thickness. EMOT refers to Egg Mountain Oser Thesis quarry; (2), thick micritic limestone of Unit 1; (3), sharp contact between rusty micritic limestone and calcareous siltstone of Unit 2; (4), thin and irregular micritic limestone of Unit 1.

Paleoenvironments and depositional processes.—Deposition at Egg Mountain has been interpreted as crevasse splay deposits in upland fluvial facies (Horner, 1984; Lorenz and Gavin, 1984) or an up-dip alluvial plain (Fricke et al., 2010). To the north and east, facies change to interbedded sandstones deposited in shallow braided streams (Lorenz and Gavin, 1984). The Egg Mountain locality lies at the interface of the lacustrine and braided stream lithofacies (Horner, 1987). Incipient pedogenesis is apparent at the locality based on the presence of insect and invertebrate trace fossils (Freimuth and Varricchio, 2019; Panasci and Varricchio, 2020), root traces, and proportions of rare earth elements (Varricchio et al., 1999).

Paleozoic marine limestones along the thrust belt to the west of the locality are the likely source of the calcareous sediments (Lorenz and Gavin, 1984). Angular volcanoclastics are present in both siltstones and limestones at the locality, attributable to the contemporaneous Elkhorn Mountain volcanics (Lorenz and Gavin, 1984; Rogers, 1998); however, these are sparse compared to other channel sandstones in the Willow Creek Anticline, likely due to the more distal position of the locality from primary channels and more extensive soil processes and bioturbation (Bown and Kraus, 1981; Needham et al., 2004). Calcite is pervasive in both primary features (lithology) and secondary features (infill of tectonic fractures, diagenetic crystalline infill of some fossil insect cocoons, eggshell, and root traces). High levels of calcium carbonate favor the preservation of eggshell, teeth, bone, and other mineralized hard parts (Retallack, 1984). Horner (1987) interpreted the locality as a lakeside dinosaur nesting ground based on intermittent limestone units. However, the presence of insect pupation chambers in

indurated limestone horizons precludes a lacustrine origin, as most insects require subaerial exposure and well-drained substrates for pupation (Genise, 2000; Genise, 2016). Varricchio et al. (1999) suggested a pedogenic origin for the limestones based on the presence of root traces, burrows, nodules, and low rare earth element concentrations. Incipient pedogenesis is apparent based on the presence of insect trace fossils (Genise, 2016) and rhizoliths, but definitive paleosol horizons are lacking (Freimuth and Varricchio, 2019). However, sharp basal and upper contacts and massive horizons lacking internal structure or laminations are suggestive of groundwater calcretes rather than pedogenic calcretes (Mack et al., 2000; Alonso-Zarza and Wright, 2010).

A lack of peds, cutans, and persistent paleosol horizons represent inceptisols (Retallack, 1988), and laterally continuous units of detrital siltstones and mudstones truncating micritic horizons suggest deposition was frequent enough to disrupt paleosol development (Alonso-Zarza et al., 1998; Kraus, 1999). In the absence of well-developed paleosols, bioturbation is likely the primary factor in the destruction of original sedimentary structures and bedding (Lorenz and Gavin, 1984; Freimuth and Varricchio, 2019). Abundant insect traces throughout the measured section and a lack of erosional contacts suggest relatively slow, continuous deposition and cumulative paleosol development (Alonso-Zarza et al., 1998; Kraus, 1999; Freimuth and Varricchio, 2019). Depositional events were likely less than invertebrate burrow lengths (10-30 cm, 14 cm maximum based on preserved burrows; Freimuth and Varricchio, 2019) and less than ~11 cm jackhammer passes. The abundance of insect nesting traces is indicative of well-drained, workable soils (Genise, 2000), and extended subaerial exposure and their

occurrence throughout the section suggest suitable conditions persisted throughout the time of deposition (Freimuth and Varricchio, 2019).

Egg Mountain Oser Thesis (EMOT) quarry.—Four *Edaphichnium* isp. specimens are associated with *Maiasaura* (Hadrosauridae) eggs and perinatal remains that are recovered from a satellite quarry ~30 m south of and 2.41 m below the main quarry datum (Fig. 3.2). Eggs and associated fossil remains occur within a ~12 m² area on the same ~7–10 cm thick mudstone horizon (Oser, 2014). The mudstone is weakly calcareous and comprised of quartz, plagioclase, and the clay mineral montmorillonite (Oser, 2014). Twenty-two eggs are present, and the most complete are 12 cm in diameter and lithostatically compressed to 1.0–2.0 cm thick (Oser, 2014). A thin (0.04–0.1 mm) mineral rind occurs on the eggs, consistent with the cryptocrystalline apatitic mineral collophane (Oser, 2014). Associated with the eggs are 55 *Spheroolithus* eggshell fragments, a perinatal *Maiasaura* metatarsal and fibula, *Edaphichnium* fecal pellets, and *Fictovichnus sciuttoii* wasp cocoons. An additional 6–7 eggs occur 0.25 m above the mudstone horizon, and collophane occurs within these eggs (Oser, 2014). Eggshell shows moderate to heavy diagenetic modification, but no evidence of transport or fluvial reworking (Oser, 2014; Oser and Jackson, 2014).

Materials and Methods

Field collection.—A 7 x 11 m main quarry was opened in 2010 and worked through 2016. A grid system with 1 x 1 m units was emplaced spanning the area of the quarry

relative to the original datum to track the lateral location of fossil specimens. The top 1.5 meters of vertical section through this main quarry were lowered in 12 systematic jackhammer passes (JHPs) that average ~11 cm in thickness (Fig. 3.2). Quarry depths were measured in the center of meter grid units for each pass using a sight level. Specimens were collected from the blocks created in the wake of the jackhammer. Because of this, the original stratigraphic orientation of some specimens is not known, while it is specified with others. Additionally, specimens may be truncated due to excavation and not representative of their full extent. Specimens were collected and designated a field number, and field numbers were assigned to a given jackhammer pass to track the stratigraphic position of all specimens.

Morphological analysis.—Pellet length and greatest diameter were measured where accessible ($n = 62$). Pellets were only considered for dimensional comparisons if both length and width were accessible on the same sample. Pellets were examined without magnification and under a stereo microscope, and measurements were performed using a digital caliper. Specimens were photographed using a Nikon D800 and SWM VRED IF Micro lens. Petrographic thin sections were made at Spectrum Petrographics (Vancouver, WA). Thin sections were observed using Leica DM750P and Leica DMR petrographic microscopes and images were captured with a Leica EC3 camera mount and a Canon 5D Mark II digital SLR camera. Figures were created in Adobe Photoshop and Illustrator.

Chemical analysis.— Bulk mineralogic and trace element composition of four specimens (MOR 10878 EMOT 91B and associated matrix, and MOR 10878 2016-29 and associated matrix) were analyzed using x-ray diffraction (XRD) and portable x-ray fluorescence (pXRF) spectroscopy at the Imaging and Chemical Analysis Laboratory (ICAL) at Montana State University, Bozeman. Samples were ground into powder using a mortar and pestle. A standard scan was performed from 2–72 degrees two theta at two degrees per minute scan rate. Quantitative analyses were performed to provide a relative abundance of major minerals for each sample (Supp. Info). The pXRF samples are reported as the average of three trials for enhanced precision. The complete dataset is available in appendix D.

Repository and institutional abbreviations.—All specimens are deposited in the Museum of the Rockies (MOR) in Bozeman, Montana, U.S.A., under the catalog MOR 10878. Individual specimens are designated by their field identification number, comprising a year and given number (e.g., MOR 10878 YEAR-##). EMOT specimens were collected in 2011 and have this designation before the given field number (e.g., MOR 10878 EMOT-##). Eleven specimens are referred to in this study: MOR 10878 2012-10; MOR 10878 2012-49; MOR 10878 B11.12-1; MOR 10878 2013-57; MOR 10878 2015-40; MOR 10878 2016-29; MOR 10878 2016-31; MOR 10878 EMOT-43; MOR 10878 EMOT-91A; MOR 10878 EMOT-91B; MOR 10878 EMOT-115.

Results

Descriptive overview.—Fecal pellets at Egg Mountain match closely in size in shape to fecal pellets of the trace *Edaphichnium lubricatum* known from terrestrial deposits from the Triassic to the Pleistocene (Table 3.1). However, Egg Mountain fecal pellets lack the characteristic horizontal tubular and verrucose burrows of *E. lubricatum*, and as such are tentatively referred to *Edaphichnium* isp. Fecal pellets here match dimensions of millimeter sized ellipsoidal fecal pellets of *Edaphichnium* elsewhere (e.g., Bown and Kraus, 1983; Hembree and Hasiotis, 2007; Smith et al., 2011).

Edaphichnium isp. here occur at different horizons within the calcareous siltstones of Unit 2 and the micritic carbonate of Unit 1 in the main quarry, as well as in calcareous mudstone of the EMOT quarry (Fig. 3.2). Three specimens (MOR 10878 2012-49, MOR 10878 2012-10, MOR 10878 B11.12-1) occur 0.9–1.0 m below the datum (JHP 8) in the calcareous siltstone of Unit 2, one specimen (MOR 10878 2013-57) occurs 1.1–1.15 m below the datum (JHP 10) in calcareous siltstone of Unit 2, three specimens (MOR 10878 2015-40, MOR 10878 2016-29, MOR 10878 2016-31) occur 1.2–1.3 m below the datum in the micritic carbonate of Unit 1, and four specimens (MOR 10878 EMOT-43, MOR 10878 EMOT-91A, MOR 10878 EMOT-91B, MOR 10878 EMOT-115) occur 2.4 m below the datum and are directly associated with *Maiasaura* eggs and perinatal skeletal elements (Oser, 2014).

Three morphotypes of *Edaphichnium* isp. are qualitatively distinguished based on a recurring arrangement of fecal pellets. Type A *Edaphichnium* are characterized by

pellets exhibiting a general linear arrangement. Some specimens also display a mottled or granular texture, distinct from the sedimentary host, that contains fecal pellets in a linear arrangement and interpreted as burrows. Type A *Edaphichnium* here resemble *E. lubricatum* (Bown and Kraus, 1983) and Type A *Edaphichnium* isp. described by Hembree and Hasiotis (2007) in the linear arrangement of fecal pellets, but lack defining burrow structures ubiquitously infilled and lined with fecal pellets. Representative Type A specimens include MOR 10878 2012-10, MOR 10878 2013-57, MOR 10878 EMOT-91A, MOR 10878 EMOT-91B, and MOR 10878 EMOT-115. Type B *Edaphichnium* are characterized by an amorphous condensed mass of pellets that occur on a single horizon but without a linear pattern or burrow structure. Pellets are in contact with one another or occur in localized mm- to cm-scale areas. Type B specimens include MOR 10878 2012-49, MOR 10878 2016-29 and MOR 10878 2016-31. Type C *Edaphichnium* consist of dispersed or diffuse masses of pellets throughout the matrix, occasionally both vertically and horizontally. No burrow structure or definitive arrangement of pellets is observed. Pellets may be in contact or adjacent to other pellets, but usually have ≥ 5 mm of matrix separating one another. Type C specimens include MOR 10878 2015-40 and MOR 10878 EMOT-43. Types B and C *Edaphichnium* isp. here are comparable to Type B *Edaphichnium* isp. described by Hembree and Hasiotis (2007), characterized by diffuse masses of fecal pellets in mudstone nodules from the Oligocene White River Formation, Wyoming, USA.

Generally, fecal pellets are ellipsoidal in shape (sensu Knaust, 2020) and distinctly fine-grained and homogenous relative to the host matrix. Pellets typically

appear slightly darker grey than the surrounding matrix, and they lack (or infrequently contain) medium-grained and larger clastic material that is found throughout the host matrix. The external pellet surface is unornamented and bears no characteristic smooth or textured patterning, as in some pupichnia (e.g., Genise et al., 2007). Fecal pellet sizes range from 1.87–6.70 mm in maximum length (mean 4.13 mm; $n = 62$) and 1.01–4.06 mm in maximum diameter (mean 2.63 mm; $n = 62$) (Fig. 3.3). This yields an average length to diameter ratio of 1.57 ($n = 62$). Pellet shape (i.e., length:diameter) is consistent across specimens ($R^2 = 0.873$) (Fig. 3.3 1). Descriptions and measurements are summarized in Table 3.2.

Table 3.2. Descriptive and quantitative summary of *Edaphichnium* isp. specimens from Egg Mountain. Lithology for EMOT specimens summarized from Oser (2014). Quad represents the 1 x 1 m quadrant in the main quarry from which specimens were recovered. EMOT specimens are not designated by a quadrant in the main quarry. See text for full descriptions.

Specimen	Lithology	Quad	Average maximum length (mm)	Average maximum diameter (mm)	Summary Description	Other Associations
MOR 10878 EMOT-115	Calcareous mudstone	-	2.49 mm, 2.58 mm (n = 2)	1.72 mm, 1.73 mm (n = 2)	10 pellets linearly arranged, potentially in pairs; no definitive burrow structure	<i>Maiasaura</i> eggs and perinatal remains, <i>Fictovichnus</i> cocoons
MOR 10878 2012-49	Unit 2, grey calcareous siltstone	N5/W5	3.30 mm (n = 5)	2.24 mm (n = 7)	≥ 10 ellipsoidal pellets, linear arrangement; J-shaped mottled sedimentary texture	Same horizon as multituberculate skeletons, root traces, <i>Fictovichnus</i> cocoons, <i>Feoichnus</i>
MOR 10878 2013-57	Unit 2, grey calcareous siltstone	N2/W10	2.29 mm (n = 4)	1.37 mm (n = 7)	≥ 37 ellipsoidal pellets; loosely composing linear structure; pellets occur in mottled burrow structure cemented with micrite	Rootlet traces, <i>Fictovichnus</i> cocoons
MOR 10878 EMOT-91A	Calcareous mudstone	-	None available	None available	≥ 10 ellipsoid pellets, similar features as 91B; no definitive burrow structure	<i>Maiasaura</i> eggs and perinatal remains, <i>Fictovichnus</i> cocoons

Type A – linearly arranged pellets

Type A (cont.)

MOR 10878 EMOT-91B	Calcareous mudstone	-	4.23 mm (n = 35)	2.75 mm (n = 39)	≥ 70 ellipsoidal pellets, most prepared from matrix	<i>Maiaasaura</i> eggs and perinatal remains, <i>Fictovivchnus</i> cocoons
MOR 10878 2012-10	Unit 2, grey calcareous siltstone	N4/W5	3.30 mm, 3.65 mm (n = 2)	1.62 mm, 2.53 mm (n = 2)	≥ 12 pellets in dense mass; fine-grained, homogenous relative to host matrix, epirelief	Same horizon as multituberculate skeletons, root traces, <i>Fictovivchnus</i> cocoons, <i>Feoichnus</i>
MOR 10878 2016-31	Unit 1, micritic limestone	N9/W12	6.34 mm, 6.7 mm (n = 2)	4.19 mm (n = 7)	≥ 33 pellets in cross section; occur in mass; dark grey; probably associated with 2016-29	Root traces, <i>Fictovivchnus</i> cocoons
MOR 10878 2016-29	Unit 1, micritic limestone	N9/W12	5.69 mm (n = 8)	3.51 mm (n = 0)	≥ 164 pellets; occur in mass; dark grey; probably associated with 2016-31	Root traces, <i>Fictovivchnus</i> cocoons
MOR 10878 B11.12-1	Unit 2, grey calcareous siltstone	N3-5/W5	3.53 mm, 3.57 mm (n = 2)	2.07 mm, 2.00 mm (n = 2)	≥ 21 ellipsoidal pellets in a condensed mass; mottled sedimentary texture;; small accessory “burrow” with small pellets	Same horizon as multituberculate skeletons, root traces, <i>Fictovivchnus</i> cocoons, <i>Feoichnus</i>

Type B – pellets in condensed mass

Type C – dispersed pellets

MOR 10878 2015-40	Unit 1, micritic limestone	N10/W14	3.36 mm (n = 7)	2.26 mm (n = 14)	≥ 108 dispersed ellipsoid pellets; dark grey; homogenous, distinct from host matrix	Root traces, <i>Fictovichnus</i> cocoons
MOR 10878 EMOT-43	Calcareous mudstone	-	1.81 mm (n = 1)	1.08 mm (n = 3)	≥ 10 dispersed ellipsoid pellets; light grey; fine- grained; homogenous, calcareous composition	<i>Maiaasaura</i> eggs and perinatal remains, <i>Fictovichnus</i> cocoons

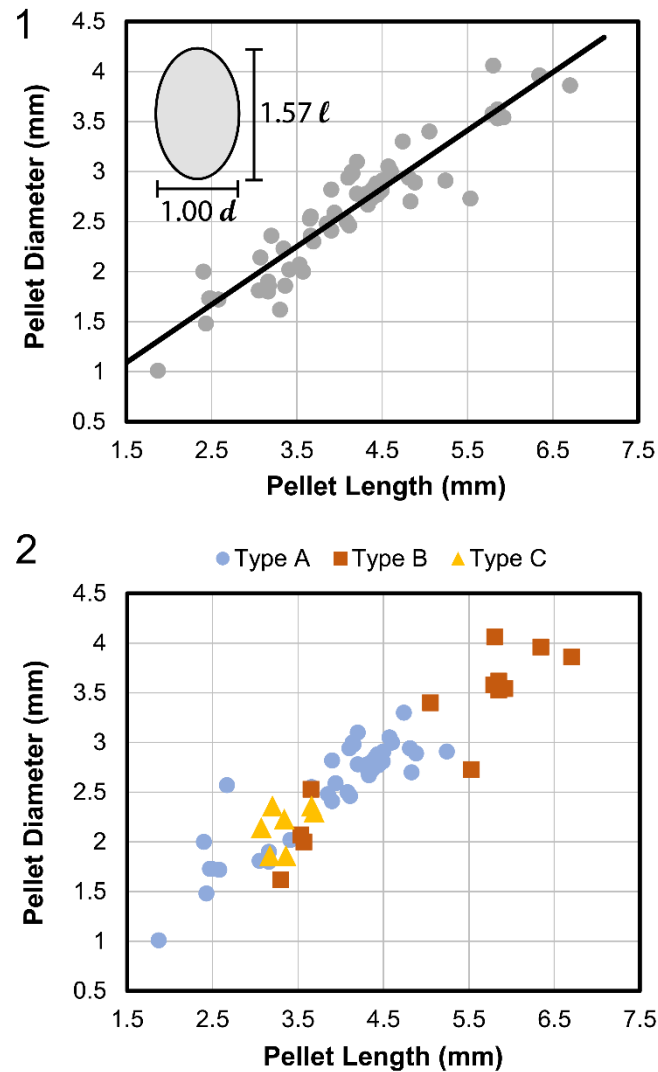


Figure 3.3. Egg Mountain fecal pellet dimensions. (1), Fecal pellet maximum length (mm) and maximum diameter (mm) for all measurable fecal pellets and (2) distinguished by morphotypes. Pellets are only included if both maximum length and maximum diameter were measurable on the same specimen. Pellet average maximum length is 4.13 mm, and average maximum diameter is 2.63 mm, yielding an average length:diameter of 1.57 ($n = 62$). Pellet shape is consistent across specimens ($R^2 = 0.873$). See Table 2 for average dimensions of individual specimens.

Type A.—Type A *Edaphichnium* comprise specimens MOR 10878 EMOT-91A, MOR 10878 EMOT-91B, MOR 10878 2012-49, MOR 10878 2013-57, and MOR 10878

EMOT-115 and consist of ellipsoidal pellets that occur in a general linear arrangement. Some fecal pellets occur within mottled host sediment and burrows, resembling *E. lubricatum*. Others do not preserve a definitive burrow structure. These specimens are described below.

MOR 10878 EMOT-91A and 91B.—MOR 10878 EMOT-91A and -91B occur associated with *Maiasaura* eggs and perinatal skeletal remains of the EMOT quarry (Fig. 3.2). Pellets occur in a general linear pattern ~2 cm wide, 1–2 cm beneath one partial egg (Fig. 3.4 1–2). No definitive burrow structure is present, and pellets occur in patches at random orientations in epirelief within the calcareous mudstone and siltstone host matrix (Fig. 3.4 2). Pellets were also recovered adjacent to a perinatal *Maiasaura* fibula MOR 6629-3.

Fecal pellets of MOR 10878 EMOT-91A and -91B were removed from their original orientation during preparation of the eggs and perinatal remains. Both specimens are recovered from an area 1–2 cm below a *Maiasaura* egg and are directly associated with perinatal skeletal remains (Oser, 2014). Overall, ≥ 70 pellets are present, with average length of 4.23 mm ($n = 35$), average maximum diameter of 2.75 mm ($n = 39$), and average minimum diameter of 1.73 mm ($n = 31$) (Table 3.2). This flattened ellipsoid shape of the pellets likely is representative of other specimens described here where measurable dimensions are inaccessible. Three small blocks contain pellets that remain *in situ*; one block shows superficial linear arrangement of pellets, but the fragmentary nature precludes further interpretation (Fig. 3.4 3). Most ($n = 36$) pellets are prepared out of the

host matrix (Fig. 3.4 4). The surface texture is amorphous, and crystalline calcite and infrequent fine-grained clastic material is visible on the external surface (Fig. 3.4 4).

MOR 10878 EMOT-91A is a 5.0 x 2.6 cm block of matrix-supported calcareous siltstone and fine-grained sandstone that contains ≥ 10 *in situ* pellets visible on one face (Fig. 3.4 5). Sedimentary structures are not visible, and the siltstone weathers in flakes. Pellets are inaccessible for quantitative measurements, but they appear ellipsoidal with the wider diameter perpendicular to the preserved orientation (i.e., pellets are compressed perpendicular to bedding). The long axes of the pellets extend into the matrix. Pellets are distinctly fine-grained and homogeneous compared to the surrounding matrix. Silt and larger sized clasts are not visible on the exposed external surfaces. Coarser matrix separates pellets from one another.

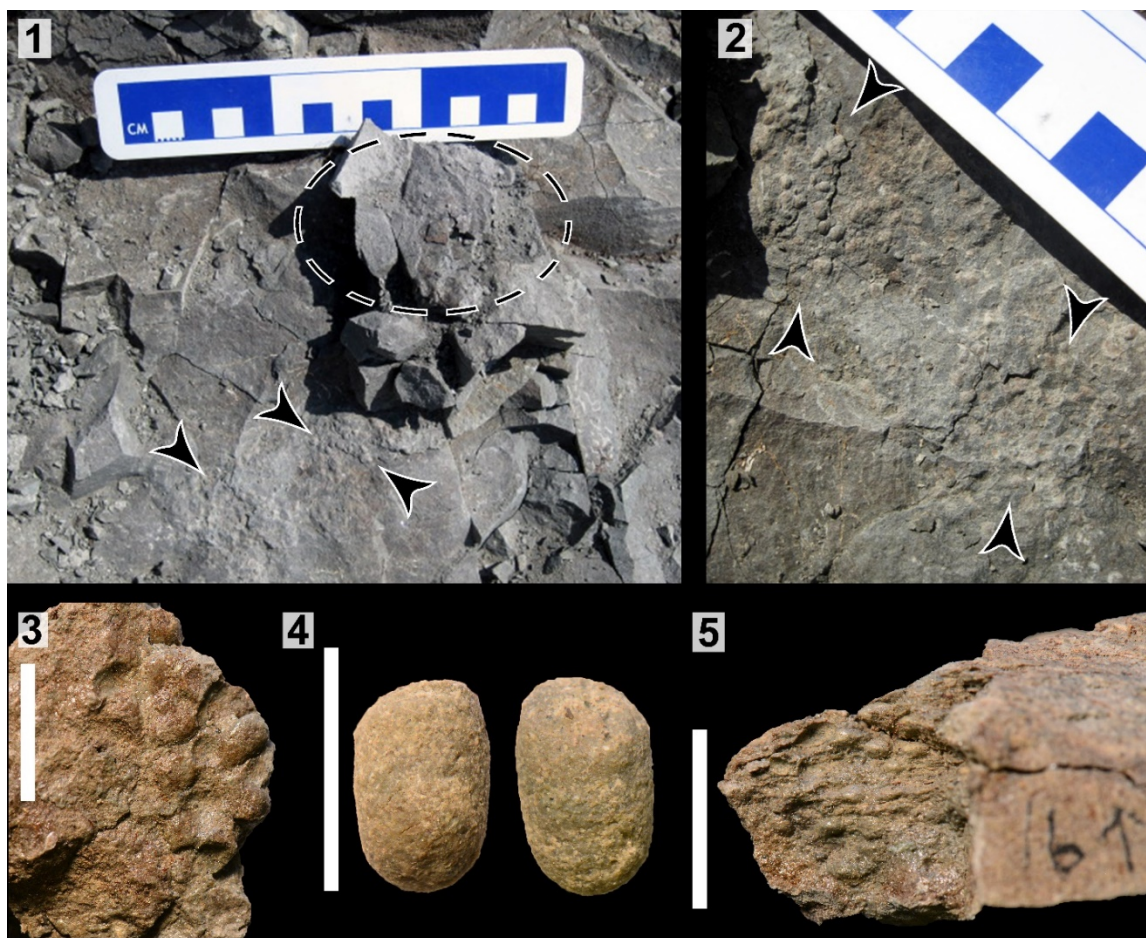


Figure 3.4. Type A *Edaphichnium* isp. associated with *Maiasaura* egg; (1), *in situ* partial egg (dashed circle) and fecal pellets in a linear arrangement (arrows); (2), Same pellets (arrows) as in (1). Note the scattered orientation of individual pellets and lack of a definitive burrow structure; (3), MOR 10878 EMOT-91B, *in situ* pellets, probably part of a linear alignment in (1) and (2); (4), Isolated pellet from MOR 10878 EMOT-91B with views of both sides. Note the fine-grained, homogenous composition, general lack of clastic inclusions, and lack of surface pattern or texture. This likely represents the morphology of most *Edaphichnium* pellets at the locality; (5), MOR 10878 EMOT-91A. The long axis of ellipsoidal pellets extends into the sediment. (1–3, 5) Scale bar = 1 cm; (4) scale bar = 0.5 cm.

MOR 10878 2012-49.—MOR 10878 2012-49 consists of ≥ 12 ellipsoidal pellets in a single block matrix-supported muddy siltstone (Fig. 3.5 1–2). The original orientation of the block is not preserved. Pellets are arranged in a linear configuration that

has a diameter of 0.9–1.0 cm and observable length of 2.3 cm (Fig. 3.5 1). The sedimentary texture immediately adjacent to the pellets is mottled and granular, distinct from the regular texture of the sedimentary host matrix (Fig. 3.5 1). The orientation of individual pellets is random. Pellets are fine-grained and homogenous relative to the host matrix, with no discernible clastics visible on the external surface. Most pellets here are preserved in negative epirelief. Those pellets preserved in positive epirelief exhibit a uniform exterior texture. Two pellets can be reliably measured, with maximum lengths of 3.30 mm and 3.65 mm and maximum diameters of 1.62 mm and 2.53 mm, respectively (Table 3.2).

On the opposite face of this block is a putative burrow structure (Fig. 3.5 2). The structure is characterized by a mottled texture with coarser grainy material relative to the fine-grained, regular texture of the surrounding matrix. The burrow structure forms an L-shape, and the mottled, granular texture continues to the adjacent face, where it can be clearly seen and differentiated from the host matrix (Fig. 3.5 2). The mottled patterns appear to lead to the face that contains the larger, linearly arranged pellets (Fig. 3.5 1), but the texture is not present on this face. However, the larger pellets are arranged linearly along the same horizon as the mottled texture, perhaps suggesting a single continuous structure.

MOR 10878 EMOT-115.—MOR 10878 EMOT-115 consists of ≥ 10 linearly arranged pellets on a 4.2 x 2.2 cm block of calcareous siltstone (Fig. 3.5 3–4). The sedimentary fabric is uniform and fine-grained adjacent to the row of pellets and weathers in flakes. Pellets are distinctly light tan in color and fine-grained relative to the

surrounding matrix. They are arranged linearly and superficially in pairs, with a maximum extent of 1.8 cm and diameter of 0.5 cm (Fig. 3.5 3). No burrow structure is present (Fig. 3.5 4).

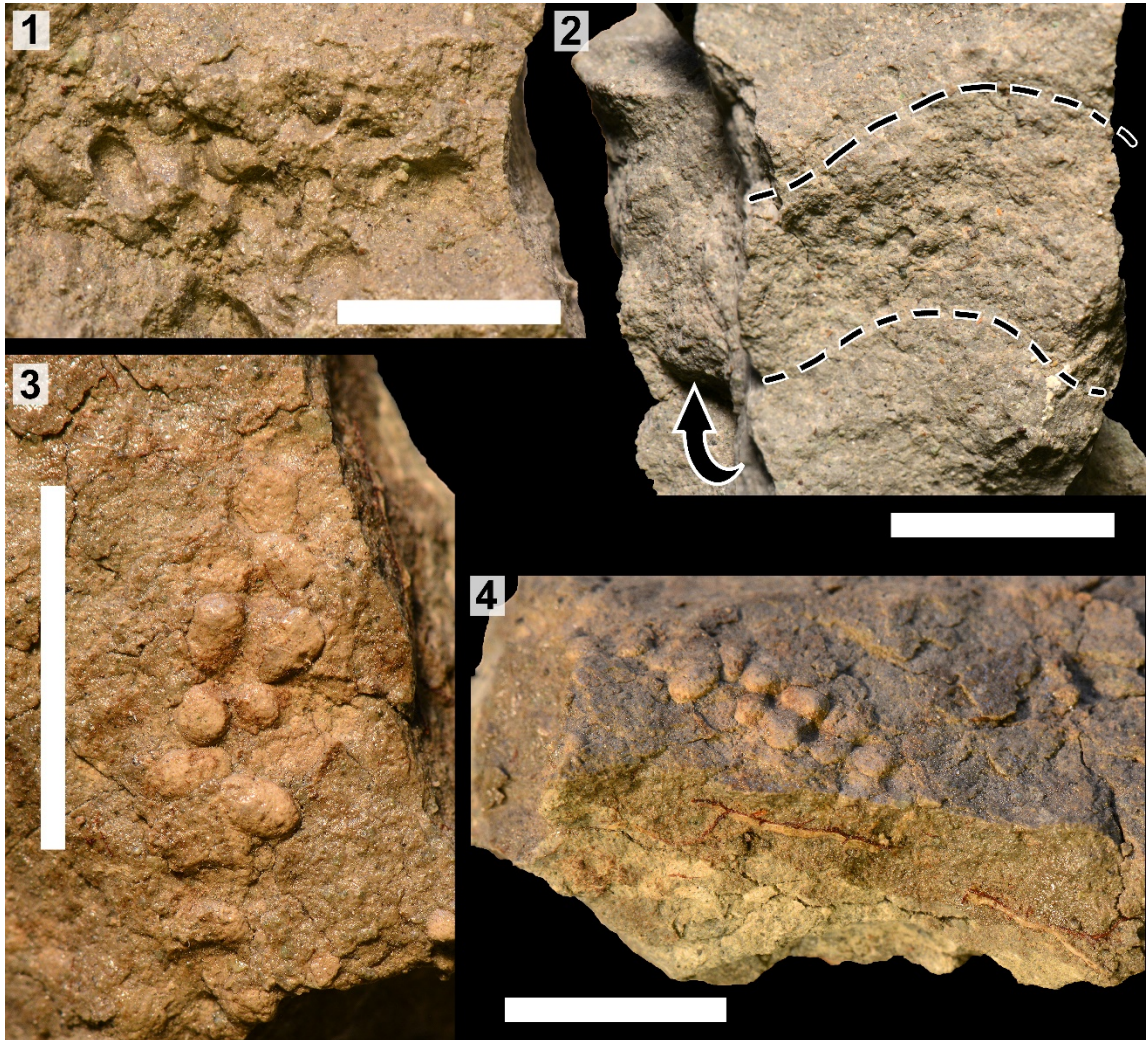


Figure 3.5. Linearly arranged (Type A) *Edaphichnium* from Egg Mountain; (1), MOR 10878 2012-49 showing discrete pellets with a linear arrangement and mottled texture distinct from the host matrix; (2), Adjacent and opposite face of MOR 10878 2012-49 that shows mottled texture at the same horizon as the pellets in (1) (within dashed lines) compared to uniform texture of the host matrix. The mottled texture continues in an L-shape upward (arrow), potentially representing a burrow; (3), MOR 10878 EMOT-115, linearly arranged pellets occur in pairs; (4), side view of MOR 10878 EMOT-115. Scale bars = 1 cm.

MOR 10878 2013-57.—MOR 10878 2013-57 comprise ≥ 59 pellets across two blocks. 11 pellets occur in an area 1.0 x 0.5 cm. Measurable pellets are among the smallest from the locality, with observable lengths ranging from 1.87–2.47 mm ($n = 4$) and maximum diameters from 1.01–2.00 mm ($n = 7$) (Fig. 3.6). Apart from the smaller dimensions, pellets of MOR 10878 2013-57 are similar to others: fine-grained and homogenous relative to the host matrix, lack of clastic inclusions, slightly darker grey than the surrounding matrix.

In one block, pellets occur throughout a confined area, approximately 1.0 cm wide and 2.4 cm long (Fig. 3.6 1). The block is broken so that the true length of the pelletal arrangement is unknown. The confined area is roughly linear and interpreted as a burrow (Fig. 3.6 1). The burrow displays a coarser mottled to granular texture that is distinct from the fine-grained host matrix (Fig. 3.6 1). Pellets are dispersed throughout this mottled area, but they are not ubiquitous and do not form or line the peripheries as in *E. lubricatum*. In thin section, the burrow infill is cemented with micrite, and distinct pellets float within the calcite infill (Fig. 3.6 2). The crystalline infill of the burrow is distinct from sedimentary host matrix, and the contact of the burrow and host matrix varies from relatively discrete and regular to irregular and poorly defined (Fig. 3.6 2). Pellets show no preferred orientation and variable exposure on two faces of the block (Fig. 3.6 1, 3). The mottled area is not as clearly defined on the adjacent face, but ≥ 11 pellets occur in a 2.0 by 1.2 cm area (Fig. 3.6 3). Some pellets on this face have calcareous rootlet traces on their exterior surface that also extend across the surface of the matrix (Fig. 3.6 4).

The second block is fragmentary, and while it is associated with the first block, the two do not fit together. Pellets are concentrated in a 1.5 x 1.2 cm area along one edge. The same mottled texture is apparent in the pelletal concentration, but a definitive arrangement of pellets cannot be determined. Qualitatively, pellets are of similar dimensions to those of the first block, but no single pellet is accessible for confident measurements.

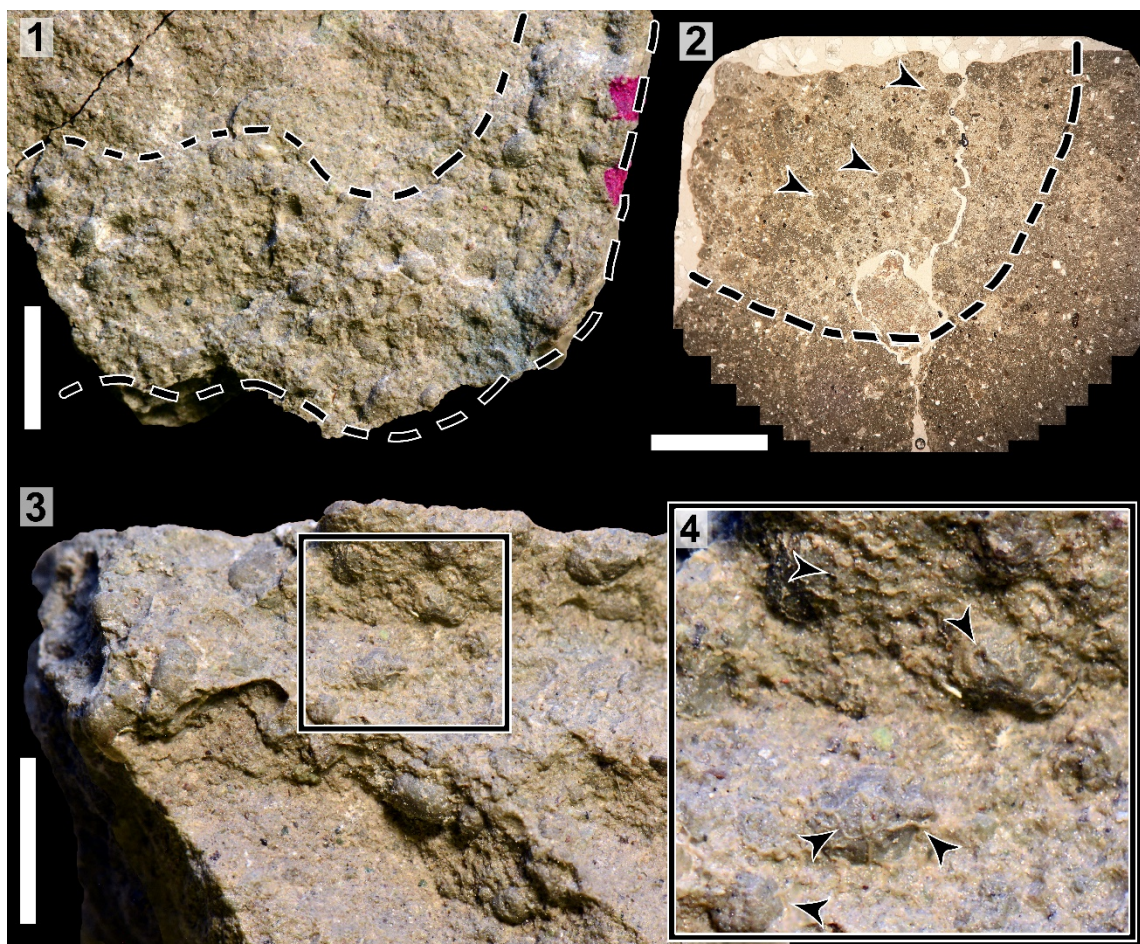


Figure 3.6. MOR 10878 2013-57, Type A *Edaphichnium*. (1), Mottled texture of burrow with interspersed fecal pellets (outlined with dashed lines). Mottled, granular texture is distinct from uniform sedimentary fabric (outside dashed lines); (2), Petrographic section showing burrow in cross section with pellets (arrows) and calcite cement infill that is distinct from the darker grey host matrix. Burrow border is relatively well defined at the bottom contact and diffuse and irregular on the side; (3), side view of same block with pellets interspersed throughout the host matrix; (4), inset of (3) highlighting calcareous rootlet traces on exterior of pellets and meshwork on matrix (arrows). (1, 3) Scale bar = 1 cm; (2) scale bar = 0.5 cm.

Type B.—Type B *Edaphichnium* are represented by specimens MOR 10878 2012-10, MOR 10878 B11.12-1, MOR 10878 2016-31, and MOR 10878 2016-29, and consist of

ellipsoidal pellets that occur in dense masses on a single horizon. Type B *Edaphichnium* here resemble Type B *Edaphichnium* described Hembree and Hasiotis (2007).

MOR 10878 2012-10.—MOR 10878 2012-10 consists of ≥ 10 pellets across three small blocks. The host matrix is predominantly silt-sized grains, though some larger clasts are infrequent and scattered throughout all blocks. No relict sedimentary structures are present, and the fabric is largely amorphous and unorganized. Pellets here display similar characteristics of other specimens from the locality: fine-grained and compositionally homogenous relative to the matrix, lack of larger clasts, unornamented surface texture, and no preferred orientation of individual pellets (Fig. 3.7 1). Pellets are concentrated on a single horizon and in a 1.9 x 2.3 cm area, but do not occur in any particular arrangement, and no burrow structure is evident (Fig. 3.7 1). The mottled texture of the matrix observed in other specimens is not present in MOR 10878 2012-10. Few pellets can be measured in all dimensions with confidence. Maximum observable lengths range from 3.05–3.70 mm ($n = 6$), and maximum diameters range from 1.80–2.88 mm ($n = 7$). Some pellets show light tan sinuous markings on their exterior, interpreted as rootlet traces.

MOR 10878 B11.12-1.—MOR 10878 B11.12-1 is a single block that hosts ≥ 21 pellets condensed in a $\sim 2 \times 2$ cm area on a single horizon (Fig. 3.7 2). Pellets are only visible on one surface (Fig. 3.7 2). Pellets are ellipsoidal and generally are oriented with the long axis perpendicular to the exposed surface but are show no preferred alignment or orientation with respect to one another. Pellets are fine-grained and homogenous relative to the matrix and share the same ellipsoidal dimensions as other specimens here. Some

pellets are preserved as negative casts or broken to expose a homogenous mud-grade interior devoid of clastic material. Only two individual pellets can be measured reliably, yielding maximum diameters of 3.53 mm and 3.57 mm, and maximum diameters of 2.07 mm and 2.00 mm, respectively. Adjacent to the primary mass of pellets are at least six smaller pellets arranged quasi-linearly (Fig. 3.7 2). No definitive burrow structure is present, but pellets occur across a consistent diameter of 3.80 mm. One of these pellets has a diameter of 0.79 mm; others are inaccessible for measurement but possess similar dimensions. The sedimentary texture across the entirety of the face and surrounding the pellet mass is generally mottled and granular, but with no distinct pattern and not arranged linearly as in MOR 10878 2013-57.

MOR 10878 2016-31.—MOR 10878 2016-31 comprises ≥ 33 pellets across a larger block and two small pieces. This specimen was recovered from the calcrete of Unit 1 and are associated with pellets of MOR 10878 2016-29. Both specimens display similar characteristics: pellets are relatively darker grey compared to the surrounding matrix, fine-grained, lack medium-grained and larger clastic material, possess diffuse, poorly defined borders, and the majority are preserved in cross section. The most notable concentration consists of 22 pellets on a $\sim 4 \times 4$ cm area (Fig. 3.7 3). Medium-grained clastic material is scattered throughout the calcareous matrix. Clasts are poorly sorted and overall matrix supported. Coarser clasts are notably less frequent within pellets. Pellets show random orientation and display different cross-sectional angles on the exposed face. Pellets primarily occur as discrete entities, though some specimens are packed together and their borders touch (Fig. 3.7 3). Definitive measurements are difficult to obtain, but

pellets viewed in cross section perpendicular to the inferred long axis are 6.34 and 6.70 mm long, longer than other pellets described here. Inferred maximum diameters are 4.45 and 4.76 mm, also larger than other pellets from the locality (Table 3.2).

MOR 10878 2016-29.—MOR 10878 2016-29 consists of three large blocks from the thick calcrete of Unit 1. These blocks are broken in several smaller pieces, making quantitative measurements of pellets difficult. 164 total pellets are observable. Average length of pellets is 5.70 mm ($n = 8$), and average maximum diameter is 3.50 mm ($n = 8$). Pellets here are similar both quantitatively and qualitatively to those of MOR 10878 2016-31 (Fig. 3.7 3, 3.7 4). They are ellipsoidal, relatively darker in color, fine-grained, homogenous compared to the surrounding matrix, and occur predominantly in cross section of varying orientation.

Block one consists of ≥ 22 pellets observable on two faces that occur on a single horizon spanning $\sim 10 \times 7$ cm. This horizon occurs ~ 2 cm below the top of the block with respect to original bedding. It is likely more pellets occur on this horizon but are obscured by matrix. No burrow structure or modification of sedimentary texture is apparent. The calcareous host matrix is well-indurated, fine-grained, massive and amorphous, and no relict sedimentary structures are preserved. Pellets occur at random orientations, and besides occurring on a single horizon do not display any preferred arrangement.

Blocks two and three consists of ≥ 142 pellets in a roughly 16×5 cm area all on the same horizon (Fig. 3.7 4). Blocks two and three fit together, but do not fit with block one. The original orientation of blocks two and three with respect to bedding is unclear, but pellets likely occur at the top of the block, as in block one. Pellets are preserved in

cross section and at random orientations. No burrow structure or mottled texture is present around the pellets, and the sedimentary texture is massive and lacks structure. Pellets occur in patches in varying densities on the same horizon, but in no particular preferred arrangement (Fig. 3.7 4). Few pellets are visible in cross section throughout the block on a different horizon than the primary pellet mass. A sparry crystalline calcite root trace (4 cm length, 0.2 cm width) is visible on the underside of block three.

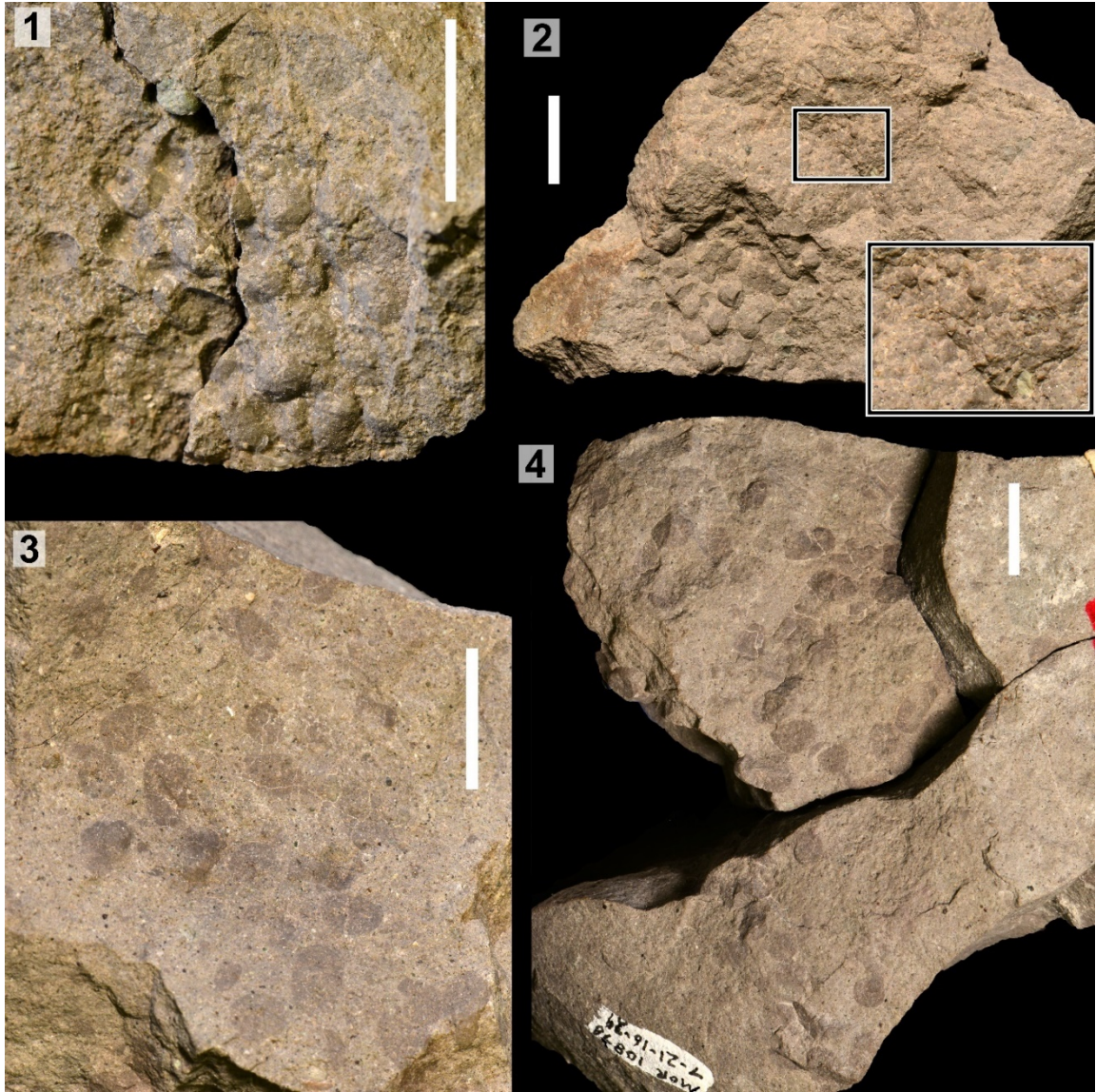


Figure 3.7. Type B *Edaphichnium* from Egg Mountain, condensed masses of pellets. (1), MOR 10878 2012-10, condensed pellet mass; (2), MOR 10878 B11.12-1, top view of pellet mass. Pellets occur in a discrete area and on a single horizon. Inset box showing smaller, linearly arranged pellets; (3), Larger block of MOR 10878 2016-31, dark pellet mass viewed in cross section. Pellets are devoid of larger clastic material compared to the host matrix; (4), Part of block two of MOR 10878 2016-29, dark pellet mass of block two, top view. Pellets are oriented randomly and viewed in cross section. Scale bars = 1 cm.

Type C.—Type C *Edaphichnium* isp. are represented by specimens MOR 10878 2015-40 and MOR 10878 EMOT-43 and consist of ellipsoidal pellets that occur in a diffuse or dispersed masses where individual pellets rarely contact one another. Pellets occur horizontally and vertically throughout host matrix and are not confined to a single horizon. Type C *Edaphichnium* isp. here resemble dispersed fecal pellet masses of Type B *Edaphichnium* isp. described by Hembree and Hasiotis (2007), but with a distinct horizontal and vertical component to the distribution of pellets through the matrix.

MOR 10878 EMOT-43.—MOR 10878 EMOT-43 consists of a single 4.2 x 3.6 cm block of matrix-supported calcareous siltstone. The texture of the matrix is regular; no mottling nor sedimentary structures are observed. Very few fine- to medium-grain clasts are present. Pellets (≥ 10) are notably dispersed across one face (Fig. 3.8 1). This differs from other specimens that are linearly arranged or occur in discrete masses. Some pellets are broken, revealing a muddy and homogenous internal matrix, devoid of fine-grained or larger clastic material. Few pellets are lost and preserved in negative relief. On the edge of the pellet-bearing face is a putative burrow in cross section (Fig. 3.8 1). The putative burrow is unlined and small (greatest diameter 0.5 mm, greatest length 1.2 cm) and discontinuous. This structure is compositionally similar to the surrounding matrix but has a characteristic mottled texture. Only one pellet has an accessible length measurement (1.81 mm), and three have reliable diameter measurements (0.95 mm, 1.11 mm, 1.17 mm). Other observable pellets appear to fall within these dimensions.

MOR 10878 2015-40.—MOR 10878 2015-40 consists of three blocks of indurated calcareous siltstone with ≥ 108 pellets. Pellets of MOR 10878 2015-40 are

generally more dispersed throughout the matrix, unlike other specimens in linear arrangements or in concentrated masses. Pellets show similar features of others described here: ellipsoidal shape, fine-grained and homogenous composition relative to the host matrix, and a lack of clastic inclusions. Few pellets can be confidently measured; observable maximum lengths average 3.36 mm ($n = 7$), and observable maximum diameters average 2.26 mm ($n = 14$). Pellets of MOR 10878 2015-40 are noticeably darker grey than other specimens. Block one shows an amorphous sedimentary texture and radial to conchoidal fracturing (Fig. 3.8 2). This block contains ≥ 21 pellets over a 9 x 6 x 5 cm area. On one face of this block, seven pellets are scattered across the visible surface (Fig. 3.8 2–3). A calcite-filled root trace and a fossil cocoon (*Fictovichnus sciuttoii*) are visible on this surface (Fig. 3.8 3–4). On the opposite face of this block, ~ 14 dispersed pellets are distinguishable, but they are obscured by matrix or represented as negative casts and unable to be measured. Calcite-filled root traces are apparent on this face as well.

The second block has a similarly amorphous texture and exhibits radial fracturing patterns. On one face, ≥ 17 pellets are concentrated in a $\sim 1 \times 2$ cm cluster. Some pellets are broken or preserved as negative relief. Broken pellets exhibit a fine-grained, dark, amorphous internal structure. Sedimentary texture around the cluster is amorphous, and no mottling is apparent. Pellets here are not accessible for dimensional analyses, but appear ellipsoidal, fine-grained, and homogenous compared to the surrounding matrix. Larger clasts are absent from pellets. Notably, pellets here are much darker than the

matrix. On the opposite face, ≥ 13 similar pellets are dispersed across a $\sim 4 \times 6$ cm area.

The sedimentary texture is similarly structureless.

Like the first two blocks, the third block consists of structureless indurated calcareous siltstone. Few larger clasts are visible throughout the siltstone matrix. Across these two blocks, ≥ 51 total pellets are countable in a $\sim 3.5 \times 2.5 \times 2$ cm area. Most pellets occur in cross section, making length and diameter measurements difficult. No burrow structure is present, and the sedimentary texture is uniform throughout the blocks.

Between the fracture of the two blocks, pellets form a poorly defined arc, though the fragmentary nature and unknown original orientation of the specimen impedes further observations and interpretations of pellet arrangement.

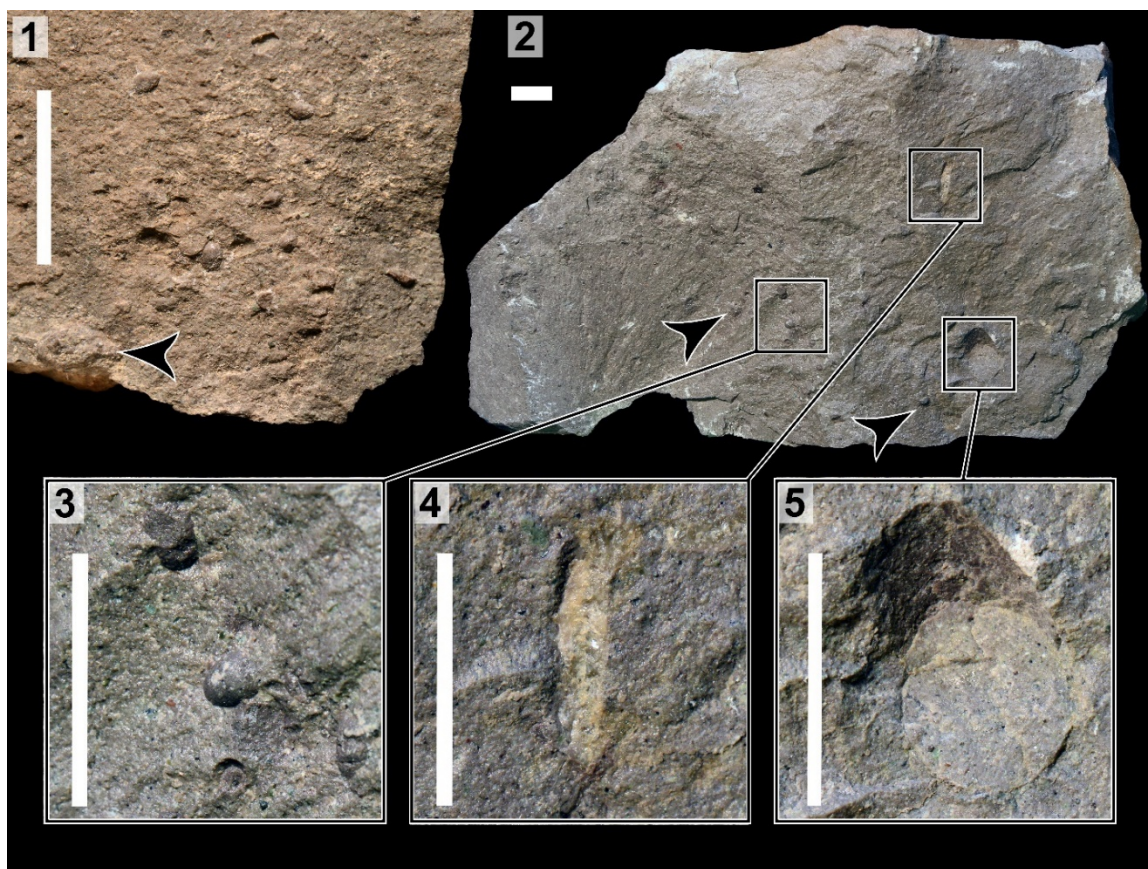


Figure 3.8. Dispersed (Type C) *Edaphichnium* isp. at Egg Mountain. (1), MOR 10878 EMOT-43, small diffuse mass of pellets with putative burrow structure in cross section (arrow); (2), Block one of MOR 10878 2015-40 consists of indurated, amorphous calcareous siltstone containing (3) fecal pellets (also arrows), (4) a root trace with sparry crystalline calcite infill, and (5) cf. *Fictovichnus sciuttoi* in cross section. Note similar internal and external matrix of *F. sciuttoi* compared to distinct internal matrix of *Edaphichnium* fecal pellets (3). Scale bars = 1 cm.

Micromorphology.—We assessed the micromorphology of two *Edaphichnium* isp.

specimens. MOR 10878 2012-49a (Type B) was recovered from the calcareous siltstone of Unit 2. Three pellets are visible in MOR 10878 2012-49a and are distinct from sparry calcitic host matrix (Fig. 3.9 1). Dark clasts (< 0.5 mm), possibly organic or volcanoclastic in origin, are infrequent throughout the host matrix (Fig. 3.9 1). Pellets appear ovoid in cross section, with maximum diameters of 1.5–1.8 mm, though this likely

does not represent the true maximum diameter (Table 3.2). Pellets consist predominantly of a clay- and silt-sized ground mass and infrequent larger (> 0.25 mm) clastic material. There is no distinct fabric or grain alignment within pellets. These characteristics have previously been noted in *Edaphichnium* and other fecal pellets from the Oligocene of Colorado, the early Paleogene of North Dakota, and the Cretaceous of Argentina (Hembree and Hasiotis, 2007; Chin et al., 2013; Genise, 2016, fig. 3.11). A thin, discontinuous micritic rind surrounds some pellets (Fig. 3.9 2). This rind is a maximum of 10 μm thick, but thickness is variable and irregular, with occasional fingering projections outward into the host matrix (Fig. 3.9 2). Similar rinds are reported from *Edaphichnium* specimens from the Oligocene of Colorado, USA (Hembree and Hasiotis, 2007).

MOR 10878 2016-31a (Type B) represents a darker pellet from the micritic carbonate of Unit 1 (Fig. 3.9 3). The pellet is strongly ovoid in shape and likely represents an oblique cross section with respect to the maximum length and diameter. Few tiny (~ 10 μm) dark clasts, possibly amorphous organics or volcanoclastics, occur within the pellet, and few larger (60–100 μm) dark clasts occur scattered in the host matrix. The internal fabric of the pellet is amorphous; no preferential grain alignment is observed (Fig. 3.9 3). The pellet is primarily composed of very fine silt and mud particles (< 5 μm) that are distinctly smaller from the fine sand-sized grains of the host matrix (Fig. 3.9 3). Grains larger than 0.1 mm are infrequent within the pellet. Individual grains within the pellet are randomly oriented; no distinct fabric or texture is present (Fig. 3.9 2). A portion of the pellet border is detached from the host matrix (Fig. 3.9 3). A similar

preservation style is seen in some *Fictovichnus* cocoons and is likely due to differential compaction or grain size of sediments between the pellet and host matrix (Alonso-Zarza et al., 2014; Freimuth and Varricchio, 2019).

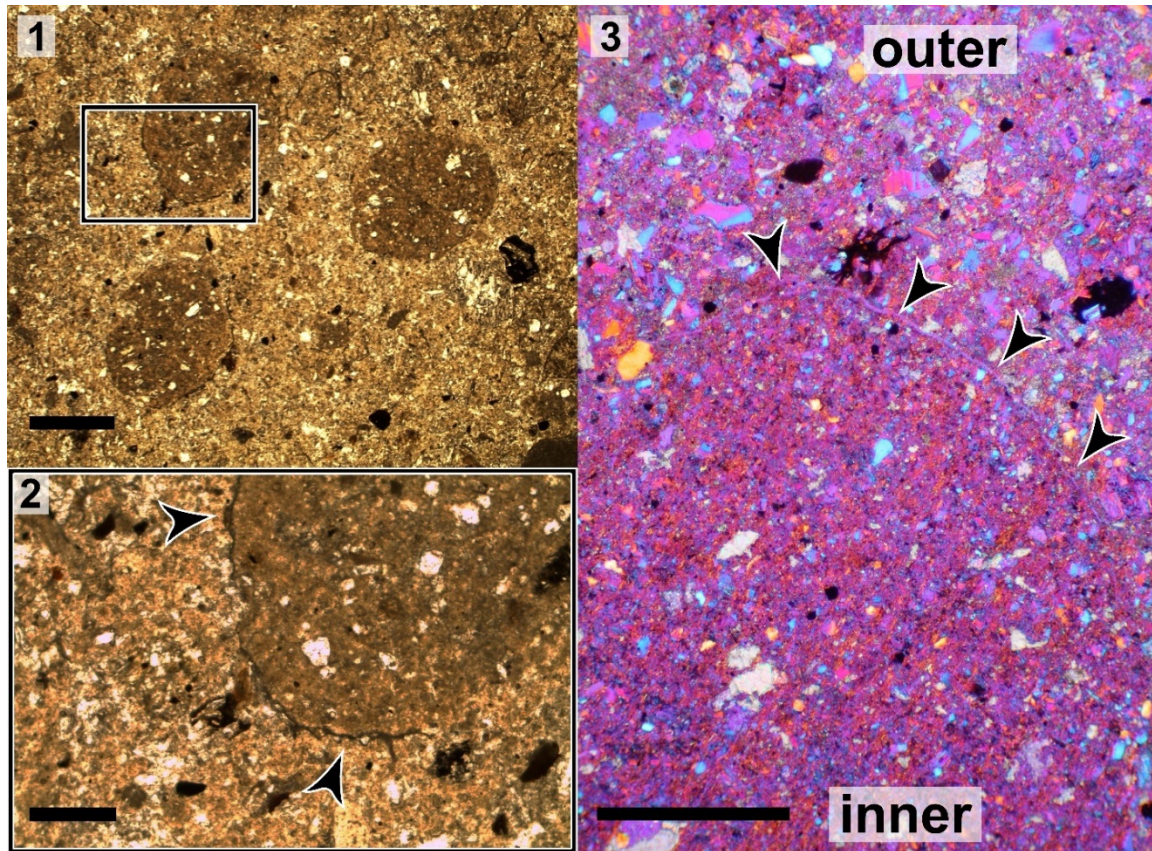


Figure 3.9. Micromorphology of *Edaphichnium* isp. fecal pellets from Egg Mountain. (1), MOR 10878 2012-49a under plane polarized light, three pellets with micritic inner matrix and infrequent clastic material; (2), Inset of (1) under plane polarized light showing fine-grained matrix and discontinuous, irregular micritic rind (arrows); (3), MOR 10878 2016-31a under cross polarized light with lambda plate, single pellet with distinct fine-grained, irregular inner texture compared to coarser outer matrix. Arrows denote partial detachment of pellet from host matrix, likely due to difference in compaction. (1) Scale bar = 1 mm; (2) scale bar = 0.1 mm; (3) scale bar = 0.3 mm.

XRD and pXRF analyses.—Two *Edaphichnium* specimens and samples of associated host matrix (MOR 10878 EMOT-91B, 2016-29) were subjected to x-ray diffraction and partial x-ray fluorescence analyses (Fig. 3.10, Table 3.3). MOR 10878 EMOT-91B (Type A) are representative lighter colored pellets from the calcareous siltstone of Unit 2, and MOR 10878 2016-29 (Type B) are darker colored pellets from the calcrete of Unit 1. All samples display prominent peaks corresponding to quartz, plagioclase feldspar, and calcite; clay minerals (expected from around 3–12 degrees 2θ) are notably absent (Fig. 3.10). Quantitative analyses of the XRD data reveal MOR 10878 EMOT-91B is composed of lower proportions of quartz and calcite, but higher proportions of plagioclase than the host matrix (Table 3.3). Similarly, MOR 10878 2016-29 is also enriched in plagioclase relative to the host matrix; however, quartz is proportionally higher compared to the matrix, and calcite is much less abundant compared to the host matrix (Fig. 3.10 2, Table 3.3). The pXRF analysis reveals the presence of aluminum and trace amounts of phosphorus and potassium present in the host rock, with increased abundances of each in both light and dark pellets (Table 3.3).

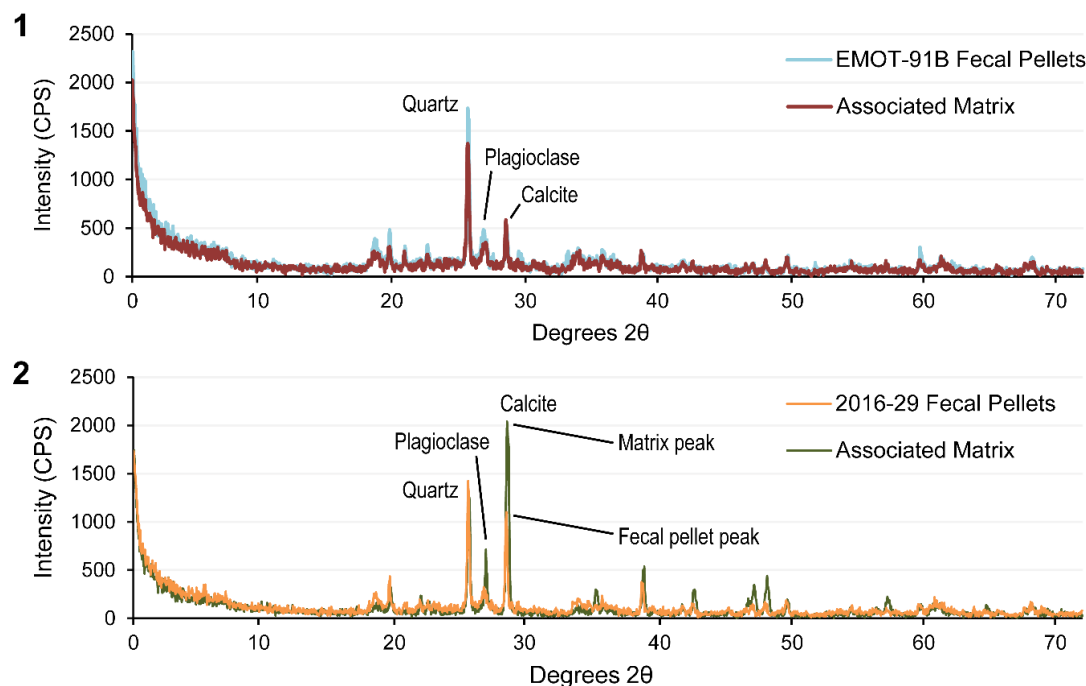


Figure 3.10. XRD results of *Edaphichnium* specimens and associated matrix at Egg Mountain. (1) MOR 10878 EMOT-91B (Type A, light colored pellets) shows prominent peaks for quartz, plagioclase, and calcite, all comparable to the associated host matrix. (2) MOR 10878 2016-29 (Type B, dark colored pellets) shows similar peaks for quartz, plagioclase, and calcite. Note the weak intensity calcite peak of the fecal pellets relative to the host matrix. Clay minerals are notably absent in both light and dark pellets.

Table 3.3. Select XRD and pXRF results for MOR 10878 *Edaphichnium* isp. and associated host matrix. XRD data are reported as relative abundances (%), and pXRF data as parts per million (ppm).

Specimen	XRD			pXRF		
	Quartz	Plagioclase	Calcite	K (ppm)	P (ppm)	Al (ppm)
EMOT-91B	40.5%	48.5%	11.3%	37066	8801	51243
Matrix	47.3%	33.1%	19.6%	18963	5514	19714
2016-29	41.4%	24.5%	34.1%	24627	5980	29074
Matrix	26.5%	17.0%	56.5%	10595	2454	11411

Discussion

Origin of pellets.—Though ellipsoidal pelletal structures here resemble the fecal pellet feeding trace *Edaphichnium*, most specimens are fragmentary or lack the characteristic pellet-filled horizontal burrows of *E. lubricatum*, so a brief discussion of other possible origins is warranted. Inorganic peloids are common in calcrete deposits (e.g., Alonso-Zarza, 2003), but are unlike the Egg Mountain specimens described here. In thin section, inorganic calcrete peloids are fine-grained and often display alternating dark and light micritic laminae (Hay and Wiggins, 1980; Alonso-Zarza, 2003). In contrast, Egg Mountain peloids appear fine-grained relative to the host matrix, but are structureless with no distinct fabric or laminae (Fig. 3.9 1–3). Peloids here do not display any laminar patterning, as is characteristic of inorganic calcrete peloids (Hay and Wiggins, 1980; Alonso-Zarza, 2003). Ooids can also be excluded, as they display a distinct clastic or micritic nucleus separate from an external concentric coating (Hay and Wiggins, 1980). The consistent recurring morphology of peloids here are suggestive of an organic origin (Genise, 2016), but are likely too large to be produced by micro- or mesofauna (< 10.4 mm body length; Swift et al., 1979; Rusek, 1985; Hasiotis, 2000). The symmetrical, ellipsoidal morphology of peloids devoid of a pointed or pinched extreme combined with the absence of identifiable organic inclusions is inconsistent with the interpretation of these structures as vertebrate fecal pellets (Chame, 2003; Macphail and Goldberg, 2010; Mychajiliw et al., 2020). It is also unlikely that peloids represent invertebrate pupal cases,

given the difference amongst grain size between infill from the host matrix (Fig. 3.8 3, 5, 3.9 1–3).

The most parsimonious interpretation of peloidal structures at Egg Mountain are fecal pellets of deposit feeding invertebrates. Several observations lead to this interpretation: 1) consistent and recurring size and shape; 2) relatively homogenous composition and amorphous texture compared to host matrix; 3) higher proportions of mud- and silt-sized grains and fewer larger clastic grains than the surrounding matrix; 4) occasional presence of pellets in burrows; and 5) increased abundance of phosphorus and potassium relative to the host matrix, common in feces of soil macrofauna (e.g., Lunt and Jacobsen, 1944; Pawluk, 1987; Lavelle and Spain, 2005; Li et al., 2006). Similar morphological features are observed in modern and fossil invertebrate fecal pellets (Rusek, 1985; Hembree and Hasiotis, 2007; Kooistra and Pulleman, 2010; Chin et al., 2013; Genise, 2016).

The consistent shape of fecal pellets from the locality may suggest a single trace-making taxon, where larger pellets were produced by larger individuals (Fig. 3.3) (Smith et al., 2011). However, while certain groups can be distinguished based on unique fecal pellet shape and size, several groups produce pellets of indistinguishable morphologies (Rusek, 1985; Kooistra and Pulleman, 2010; Knaust, 2020). Fecal pellets of MOR 10878 2015-40, 2016-29, and 2016-31 are noticeably darker in color and typically larger than other *Edaphichnium* pellets at the locality (Table 3.2). These specimens occur in the indurated calcrete of Unit 1, while other lighter-colored and smaller *Edaphichnium* occur in the calcareous siltstone of Unit 2 and the mudstone of the EMOT quarry (Fig. 3.2).

Both pellet size and color differences may indicate a different trace-maker or feeding behavior, perhaps related to substrate conditions (e.g., depth or organic content within the soil profile). Alternatively, different diagenetic conditions within the calcrete horizons may also be reflected in color differences of these pellets. Nonetheless, the characteristics of both small, light-colored pellets and darker, larger pellets—consistently ellipsoidal shape, fine-grained, homogenous in composition, dearth of large clastic materials, elevated phosphorus and potassium—are consistent with fecal pellets of geophagous or detritivorous invertebrate organisms.

The linear arrangement of fecal pellets that characterize Type A *Edaphichnium* isp. likely reflect preferential feeding as the organism moves through the substrate, the behavior also recorded by *E. lubricatum* (Bown and Kraus, 1983). On the other hand, Type B and C *Edaphichnium* isp., characterized by condensed and dispersed pellet masses, respectively, may represent feeding and pellet deposition on the substrate surface where a burrow or discernible direction of movement would not be apparent (Hembree and Hasiotis, 2007). Alternatively, Type B and C *Edaphichnium* may represent feeding on a single horizon in the subsurface and preferential preservation of the compacted fecal pellets. Dispersed fecal pellets may also be a product of bioturbation, where burrow structures are lost and pellets distributed throughout the matrix. These behaviors are investigated further in conjunction with possible trace-makers, and the paleoecological implications are assessed in the context of the locality.

Assessment of trace-maker.—Fecal pellet morphology combined with inferred paleoenvironmental parameters at the locality help to narrow the field of potential *Edaphichnium* trace-makers. The ichnoassemblage at Egg Mountain is dominated by *Fictovichnus sciuttoi*, interpreted as wasp cocoons, suggesting well-drained, subaerially-exposed substrates well above the water table (Genise et al., 2010; Genise, 2016; Freimuth and Varricchio, 2019). For this reason, strictly aquatic organisms (e.g., bivalves) can be excluded as pellet-producers. We also exclude crustaceans, which are generally constrained to soils with high moisture conditions, close to the level of the water table, and/or proximal to bodies of water (Maitland and Maitland, 1985; Hasiotis and Mitchell, 1993; Vannini et al., 2003; Melchor et al., 2010; Genise, 2016). No other evidence of crustacean activity is present at the locality. We use these parameters to assess several terrestrial invertebrate groups as possible trace-makers of *Edaphichnium* isp.; this is discussed below and summarized in Table 3.4.

The trace-maker of *Edaphichnium* (known from a single ichnospecies, *E. lubricatum*) was originally assigned to earthworms based on ubiquitous fecal pellets, 4.5–6.0 mm long and 2.5–3.0 mm wide, that infill and form the periphery of sinuous horizontal burrows from gleyed (waterlogged) paleosols (Bown and Kraus, 1983). Other occurrences of *Edaphichnium* in terrestrial deposits and paleosols are often attributed to earthworms based on these features (Table 3.1). Earthworm fecal pellets can be scattered throughout or occur in segments in some burrows as the animal feeds and moves (Lee, 1985). Type B and C fecal pellets at Egg Mountain (Fig. 3.7–3.8) resemble *Edaphichnium* Type B described by Hembree and Hasiotis (2007) from the Oligocene

White River Formation. They are interpreted as surface casts, where earthworms emerge from the soil to feed at the surface and deposit irregular masses of pellets (Lee, 1985; Hembree and Hasiotis, 2007). These specimens co-occur with “wasp cocoons” and *Fictovichnus* “*parvus*” (= *gobiensis*) (Hembree and Hasiotis, 2007).

Earthworms are particularly sensitive to soil characteristics. Of paramount importance are adequate moisture (for respiration through the body wall), fine-grained substrates, and abundant organic material in soils for foraging (Lee, 1985). Well-drained substrate conditions inferred throughout the deposition of Egg Mountain sediments may not be preferential for earthworms, especially if dispersed and condensed masses of pellets on a single horizon are representative of surface feeding (Lee, 1985; Hembree and Hasiotis, 2007; Freimuth and Varricchio, 2019). However, some modern earthworms inhabit semiarid areas (Suthar, 2009), and *Edaphichnium* attributable to earthworms co-occur with wasp cocoons in several instances, suggesting occasional overlap of environmental preferences for pupating wasps and feeding earthworms (Bown, 1982; Sandau, 2005; Hembree and Hasiotis, 2007; Smith et al., 2008) (Table 3.1). Earthworms have been documented to invade subterranean nests and brood balls of dung beetles, and pellets tend to scatter on a single horizon, similar to Type B *Edaphichnium* here (Cantil et al., 2015, fig. 2k; Genise, 2016, fig. 14.5). While it may be unlikely that earthworms frequented the presumably dry upper portions of well-drained Egg Mountain soils, pore space in soils or space created by burrows and chambers of invertebrates and vertebrates may offer a suitable subsurface horizon for deposition and preservation of horizontal and dispersed pellet masses, characteristic of Type B and Type C *Edaphichnium* here. The

association of rootlet traces with some specimens further suggests deposition of fecal pellets below the soil surface. Other evidence of earthworm activity—aestivation chambers, boxworks, and back-filled burrows—is absent at the locality (Verde et al., 2007; Bedatou et al., 2009).

Bown and Kraus (1983) connected *Edaphichnium lubricatum* to earthworms in part based on the high (85–93%) calcium carbonate content of fecal pellets and burrows, even higher than associated calcrete glaebules (62–90%), a product of the calciferous glands in some taxa that rid of excess harmful calcium carbonate (Lunt and Jacobsen, 1944). As such, some earthworms may avoid alkaline and calcic substrates or excrete greater amounts of calcium carbonate under alkaline conditions (Lee, 1985; Lambkin et al., 2011). *Edaphichnium* fecal pellets here exhibit proportionally low calcium carbonate compositions (11.3%, 31.4%) that are depleted compared to the associated host matrix (19.6%, 56.5%) (Fig. 3.10, Table 3.3). This may suggest earthworm taxa without calciferous glands as potential trace-makers. Earthworms are also noted to weather minerals in their guts and on some occasions produce fecal pellets enriched in clay minerals (Needham et al., 2004; Chin et al., 2013). Clay minerals are noticeably absent in Egg Mountain fecal pellets despite high proportions of aluminum (Fig. 3.10; Table 3.3). High proportions of aluminum may be attributed to the presence of plagioclase feldspar in fecal pellets and the matrix. The absence clay minerals combined with well-drained, calcic conditions inferred at the locality may not be favorable for earthworms; however, the morphology and arrangement of Type B and C *Edaphichnium* resemble fecal pellets

of earthworms, and thus cannot be definitively ruled out as producers of *Edaphichnium* isp. at Egg Mountain (Table 3.4).

Millipedes (Class Diplopoda) also produce fecal pellets through feeding, but their ichnological identification and significance is less well-recognized compared to that of earthworms (Hembree, 2009; Bowen and Hembree, 2014). Most millipedes are detritivores that feed on organic material on the surface or within the soil subsurface (Lavelle and Spain, 2005). In the absence of earthworms, millipedes take on a larger role as decomposers, consuming ~25% of leaf litter (Hopkin and Read, 1992). Millipedes tend to construct burrows for short term occupation to prevent evaporative water loss (Hopkin and Read, 1992), but will avoid saturated sediment in favor of moist to dry conditions (Hembree, 2009). Saprophagous millipedes tend to favor humid and moist environs amongst leaf litter or dead plant material but are also found inhabiting desert climes (Hopkin and Read, 1992). In addition to dwelling purposes, millipedes also burrow to forage and feed on organic material within the soil, producing fecal pellets as a byproduct (Rusek, 1985; Hembree, 2009; Bowen and Hembree, 2014). Fecal pellets can be ellipsoidal, spherical, or elongate, and tend to be between 0.5–4 mm in length, but larger taxa such as the Giant African millipede (*Archispirostreptus gigas*) and the Sonoran Desert millipede (*Orthopus ornatus*) apparently produce ellipsoidal fecal pellets up to 1 cm long (Babel, 1975; Rusek, 1985; Hembree, 2009, fig. 3). Millipede fecal pellets can contain large soil litter fragments, but also large quantities of substrate and mineral particles, often greater than 60% (Rusek, 1985; Hembree, 2009). Fecal pellets can be deposited at the surface or within L- or U-shaped burrow sections that partially fill

tunnels or are incorporated into the walls and floors of burrows (Hembree, 2009; Bowen and Hembree, 2014). This resembles the morphology of some Type A *Edaphichnium* here (Fig. 3.5 1–2), as well as Type B and Type C pellet masses. Some millipede taxa construct simple, unlined, cylindrical burrows 1–1.5 cm in diameter (Hembree, 2009). This matches some Type A *Edaphichnium* with 0.9–1.0 cm diameter burrows and other fragmentary unlined burrows at Egg Mountain (Hembree, 2009; Freimuth and Varricchio, 2019). The Giant African millipede constructs burrows 2.5–3.6 cm in diameter and will deposit sediment-rich fecal pellets on the soil surface (Hembree, 2009); a 2.5 cm L-shaped diameter cylindrical, unlined burrow is recovered from the same JHP as the large, horizontally arranged (Type B) fecal pellets MOR 10878 2016-29 and 2016-31 (Fig. 3.7 3–4). However, no apparent diagnostic features are present, such as body or leg impressions (Hembree, 2009). Many millipedes have calcite-impregnated chitinous exoskeletons, and consequently favor substrates rich in calcium (Kime and Golovatch, 2000; Bowen and Hembree, 2014). The abundance of calcium carbonate in Egg Mountain sediments, particularly in the calcrete of Unit 1, would have been favorable for millipedes. *Edaphichnium* fecal pellets from this unit are depleted in calcium carbonate relative to the surrounding matrix, perhaps indicative of preferential uptake and ingestion of calcium (Fig. 3.10 2). This geochemical evidence combined with associated burrows, pellet morphologies, and inferred substrate conditions suggest millipedes are possible producers of some *Edaphichnium* isp. at the locality (Table 3.4).

Rhizophagous beetle larvae and chafer larvae are members of the Scarabaeidae family (Coleoptera) that feed on soil detritus and produce fecal pellets in burrows similar

to some Egg Mountain specimens. Counts and Hasiotis (2009) describe burrows of adult and larval masked chafers (Coleoptera: Scarabaeidae) consisting of meniscated to granular-textured infill with higher porosity than the surrounding sediment. Though no fecal pellets were observed in artificial enclosures, chafer larvae would leave behind pellets in burrows in natural settings (Sánchez and Genise, 2009; Counts and Hasiotis, 2009). A thin, discontinuous lining is present at burrow margins, though may be easily destroyed and not identifiable or preserved in fossil chafer burrows (Counts and Hasiotis, 2009). Two Type A *Edaphichnium*, MOR 10878 2013-57 (Fig. 3.6 1–4) and MOR 10878 2012-10 (Fig. 3.5 1–2), closely resemble feeding traces of chafer larvae and rhizophagous coleopteran larvae. The mottled, granular texture and ellipsoidal fecal pellets scattered throughout a burrow match characteristics and dimensions of chafer and rhizophagous larvae burrows (Counts and Hasiotis, 2009; Sánchez and Genise, 2009, pl. 2; Eisman et al., 2010, p. 160; Genise, 2016, fig. 15.21). In MOR 10878 2013-57, the calcite-cemented infill of the burrow (and absence of sparry cement in the surrounding host matrix) likely reflects preferential cementation due to increased porosity within the burrow (Fig. 3.6 2) (Counts and Hasiotis, 2009). Calcite is the predominant diagenetic, void-filling mineral, observed in fractures in the rock and infilling pedotubules, *Fictovichnus* cocoons, and some fossil vertebrate bones at the locality and elsewhere in the Two Medicine Formation (Rogers et al., 2020). The co-occurrence of associated fecal pellets and rhizoliths in some specimens also supports chafer larvae or other rhizophagous beetles as *Edaphichnium* producers. This may also explain the dispersed nature of some fecal pellets, where larvae preferentially feed (and deposit pellets) where roots occur (e.g.,

MOR 10878 2015-40). Some rhizophagous scarab beetles (subfamily Dynastinae) have the ability to change their feeding habits as larvae depending on their environment (i.e., facultative rhizophagy) (Oliviera and Salvadori, 2012). If eggs are laid in soils rich in organic matter, larvae will develop as saprophagous, feeding on organic particulates in the soil and depositing fecal pellets; if larvae develop in root-rich, organic-poor soil, they will employ rhizophagy through development (Oliviera and Salvadori, 2012). Feces of scarab beetle larvae are documented to be enriched in phosphorus and other nutrients, a pattern observed in *Edaphichnium* here (Table 3.3) (Li et al., 2006). The well-drained, workable subsurface conditions inferred at the locality are also favored by coleopterans that burrow and pupate in soils (Genise et al., 2000; Genise, 2016). Some pupation chambers at the locality (wide *Fictovichnus* and cf. *F. gobiensis*) might also be attributable to chafers or other coleopterans (Genise, 2016; Freimuth and Varricchio, 2019). Based on burrow and pellet morphology, preservation, and associated root traces and pupation chambers, it is likely that some *Edaphichnium* specimens at Egg Mountain are attributable to chafers or other coleopterans (Table 3.4).

The observed morphology and composition of *Edaphichnium* specimens here combined with inferred well-drained substrates suggest trace-makers can be attributed to millipedes and coleopterans, and are less likely representative of earthworm burrows and fecal casts (Table 3.2). While earthworms are often soundly attributed as the *Edaphichnium* trace-makers (Table 3.1), a holistic approach to interpreting fecal pellet trace-makers in paleosols is needed given the abundance of deposit feeders that leave fecal pellets in soils (e.g., Rusek, 1985). While *Edaphichnium* isp. at Egg Mountain are

likely distinct from *E. lubricatum*, both in morphology and probable trace-makers, the limited material is insufficient to confidently establish novel ichnotaxonomic assignment. Nonetheless, the material is useful in assessing paleoecological and paleoenvironmental conditions at the locality.

Table 3.4. Summary of trace-makers and their characteristics with potential Egg Mountain *Edaphichnium* specimens.

Trace-maker	Characteristics	Potential Egg Mountain specimens
Earthworms	- mm-sized ellipsoidal fecal pellets, typically ubiquitously infilling and lining burrows (Bown and Kraus, 1983) - masses of pellets when feeding at surface (Hembree and Hasiotis, 2007) - prefer moist substrate (Lee, 1985) - some taxa produce pellets enriched in CaCO_3 (Bown and Kraus, 1983) and clay minerals (Chin et al., 2013)	Type B and Type C MOR 10878 2012-10 MOR 10878 EMOT 43 MOR 10878 B11.12-1
Millipedes	- mm-sized ellipsoidal fecal pellets in burrows and at surface (Hembree, 2009; Bowen and Hembree, 2014) - cylindrical 1–3.6 cm diameter unlined burrows (Hembree, 2009) - may favor alkaline substrates (Bowen and Hembree, 2014) - favor moist to well-drained substrate (Hembree, 2009; Bowen and Hembree, 2014)	Some Type A, B, and C MOR 10878 2016-29 MOR 10878 2016-31 MOR 10878 2015-40 MOR 10878 2012-49
Chafer larvae	- mm-sized ellipsoidal fecal pellets scattered in unlined burrows (Sánchez and Genise, 2009; Genise, 2016) - high porosity in burrows (Counts and Hasiotis, 2009) - nest in well-drained substrates (Genise, 2016)	Type A MOR 10878 2013-57 MOR 10878 2012-49 MOR 10878 EMOT 91A MOR 10878 EMOT 91B MOR 10878 EMOT 115

Paleoenvironmental and paleoecological implications.—Regardless of the specific identity of the trace-maker, *Edaphichnium* isp. here represents feeding and processing of the substrate by invertebrates, suggesting at least localized accumulations of organic material in the subsurface not otherwise preserved or recognized based on sedimentological evidence alone. Increased abundance of phosphorus and potassium within fecal pellets demonstrates recycling of nutrients and likely sources for a variety of microbes and soil bacteria (Table 3.3) (Lunt and Jacobsen, 1944; Pawluk, 1987; Li et al., 2006). *Edaphichnium* are only recovered from particular stratigraphic and geographic locales throughout the measured section and suggest higher proportions of organics may have been concentrated at these horizons (Fig. 3.2, Table 3.2). Notably, fecal pellets are also associated with hadrosaurid *Maiasaura* eggs and perinatal remains (Oser, 2014) and are interpreted as invertebrates scavenging the decaying nest material.

Egg Mountain Edaphichnium associated with dinosaur eggs.—Four *Edaphichnium* specimens (MOR 10878 EMOT-43, EMOT-91A, EMOT-91B, EMOT-115) occur outside the main quarry in the EMOT quarry (Fig. 3.2). These specimens occur in association with burrows, wasp cocoons (*Fictovichnus sciuttoi*), and several eggs and perinatal remains attributable to *Maiasaura peeblesorum* (Oser, 2014) (Fig. 3.11). A single field jacket (EMOT 11-07E) has yielded five partial eggs, associated perinatal skeletal remains, abundant scattered eggshell, and the four *Edaphichnium* specimens (Fig. 3.11 2). The cryptocrystalline apatitic mineral collophane is present on the exterior of and within several of the *Maiasaura* eggs and eggshell and is likely the product of

decaying organic material inside the enclosed space of the egg (Oser, 2014). Similar localized phosphatization is reported in the stomachs of fossil frogs from Miocene lacustrine deposits and is connected to early stage organic decay within an enclosed space of the stomach and body cavity (McNamara et al., 2009). Microbes and bacteria are also known to precipitate authigenic phosphates connected to organic material, as exemplified in coprolites (e.g., Qvarnström et al., 2016). This may explain the trace amounts of phosphorus detected in the associated matrix (Table 3.3). Given the preservation of the eggs and connection to decay, we hypothesize that invertebrates, represented by *Edaphichnium* fecal pellets, were attracted to the decaying material and/or microbial activity concentrated around the nest.

Invertebrates may have also been attracted to the eggs themselves. Some fecal pellets are abutted by eggshell and show irregular large inclusions amongst the fine-grained matrix (Fig. 3.11 8). These inclusions display birefringence and optical properties similar to the associated eggshell, but lack diagnostic morphology seen in other cross-sectionally or tangentially oriented eggshell pieces (Fig. 3.11 8–9). Invertebrates are known to predate modern reptile eggs (Maros et al., 2003), and eggshell can act as a source of calcium and other nutrients (as well as microbes) favored by invertebrates.

The precise succession of different invertebrate fauna at carrion sites is well documented and powerful tool in forensic entomology (e.g., Smith, 1986; Benbow et al., 2015). Several of the trace-makers outlined above, including millipedes and scarab beetles, are known to feed on organic material or microbes at carrion sites during later stages of decay, after flies have colonized and liquid organic matter has dried (Merritt

and De Jong, 2015; Strickland and Wickings, 2015). Invertebrates could have been attracted to the eggs during incubation, as hadrosaurs may have used vegetated cover or mound nesting facilitated by microbial decay (Tanaka et al., 2018). High eggshell porosity of *Maiasaura* eggs suggests a humid nesting environment (Deeming, 2006; Oser, 2014), conditions that also may have been favorable for detritus feeding invertebrates (Lee, 1985; Hopkin and Read, 1992; Oliveira and Salvadori, 2012). However, it is more likely that deposit feeders were attracted to decomposing material of the eggs and perinatal remains, or to the microbes that were attracted to the decaying material, both of which are substantial resources for invertebrates at carrion sites (Merritt and De Jong, 2015). Some modern scarab beetles are found near carcasses of large herbivorous mammals and feed on the plant material in the gastrointestinal tract as it is exposed through decomposition, a potential analog for decaying vegetated nests and eggs (Merritt and De Jong, 2015).

Edaphichnium also provide evidence of likely prey items for crabronid or pompilid wasps, which are represented by abundant ellipsoidal to sub-cylindrical shaped *Fictovichnus sciuttoi* cocoons at the locality (Genise et al, 2007; Freimuth and Varricchio, 2019; Sarzetti et al., 2019). Similar *Fictovichnus sciuttoi* also occur in associated strata with the *Maiasaura* eggs (Fig. 3.11 6) (Oser, 2014). Wasps are known as predators and late arrivals to modern carrion sites (Smith, 1986; Genise and Sarzetti, 2011). Communities of invertebrate scavengers exploit the nests and eggs of various organisms, such as lizards, turtles, crocodiles, and birds; several members of these scavenging communities are known producers of fecal pellets, including coleopterans and

millipedes (Hicks, 1959; Hayward et al., 1989; Maros et al. 2003; Bell et al. 2004; Pfrommer and Krell 2004; Katilmiş and Urhan, 2007).

The *Maiasaura* eggs and perinatal remains here occur in association with *Edaphichnium*, likely representative of beetles or millipedes feeding at later stages of decay, and *Fictovichnus sciuttoi*, representative of wasps, predators and late arrivers to carrion sites (Dadour and Harvey, 2008; Merritt and De Jong, 2015). Decomposers in modern carrion communities serve to rid carcasses of harmful microorganisms and pathogens (Benbow et al., 2015). The same is likely true for *Edaphichnium* associated with the *Maiasaura* nest, where invertebrates rid the soil of pathogens and microorganisms and allow for continual reuse of the same nesting area (site fidelity), a behavior previously inferred at the locality (Horner, 1982). A similar relationship is also inferred for insect traces associated with sauropod eggs (Genise and Sarzetti, 2011).

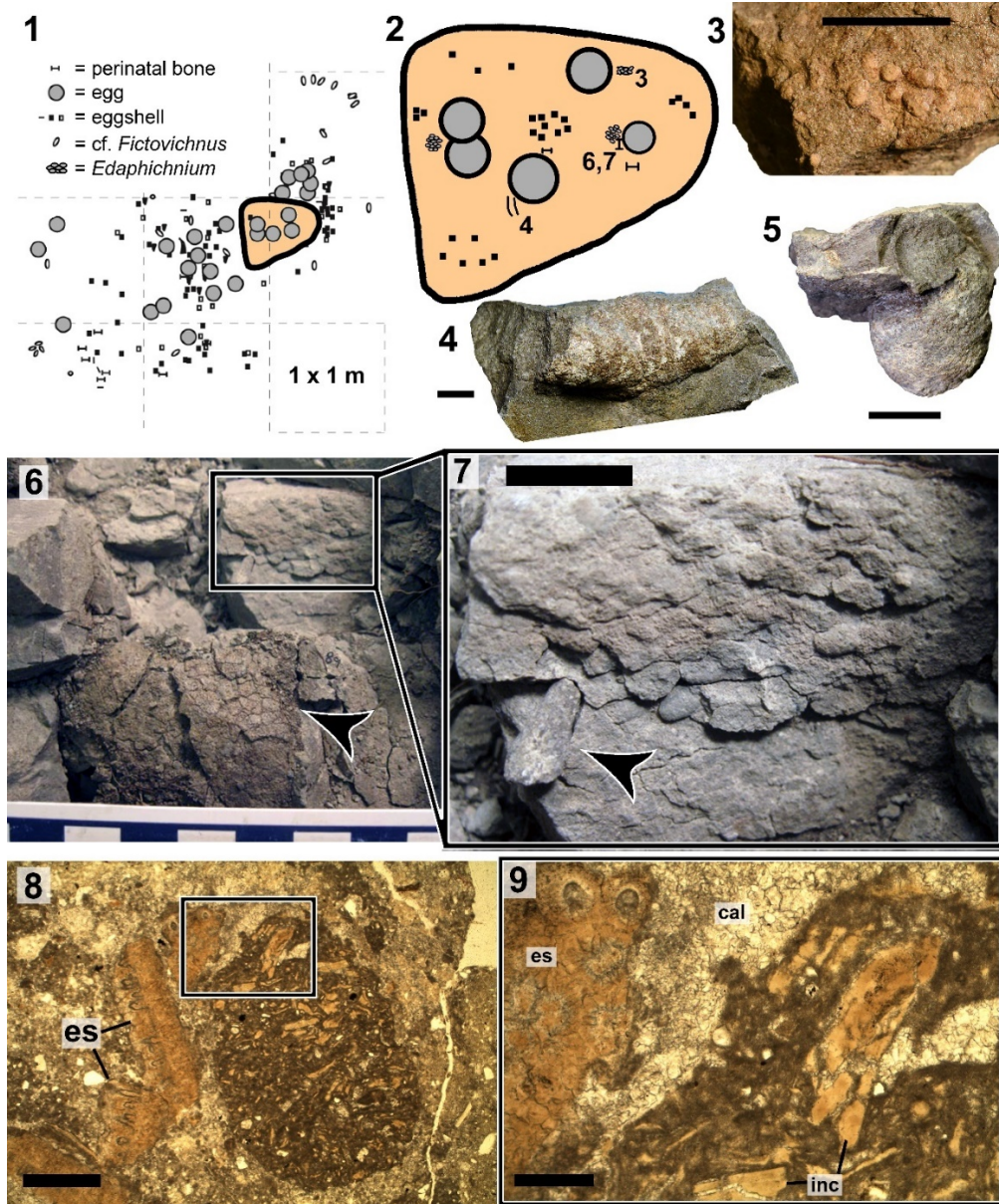


Figure 3.11. Invertebrate trace fossils associated with *Maiasaura* nest from the EMOT quarry. (1), Schematic map in plan view of the nest and distribution of fossil materials (adapted from Oser, 2014); (2), inset of nest in (1) highlighting EMOT 11-07E jacket, including eggs, eggshell, perinatal bones, and *Edaphichnium* fecal pellets. Numbers correspond to figured specimens; (3), MOR 10878 EMOT-115, Type A *Edaphichnium* adjacent to one egg; (4), fragmentary burrow associated with an egg; (5), exemplar *Fictovichnus sciuttoii* cocoon from the EMOT quarry; (6), partial *Maiasaura* egg (arrow, same specimen in Fig. 3.4 1) resides 1-2 cm above pellets of MOR 10878 EMOT-91A and 91-B; (7), inset of pellets in (6) showing ellipsoidal pellets adjacent to perinatal *Maiasaura* fibula (arrow); (8), fecal pellet associated with eggshell (es) fragments; (9) inset of pellet and eggshell (es) within calcareous matrix (cal) in (8) showing large irregular inclusions (inc) similar to eggshell. (1–7) scale bar 1 cm, (8) scale bar 1 mm, (9) scale bar 0.1 mm.

Invertebrate traces and dinosaur nesting in the fossil record.—Invertebrate trace fossils are useful in interpreting environmental and substrate conditions, and their association with dinosaur eggs and nests suggest shared environmental preferences for nesting (Martin and Varricchio, 2011; Freimuth and Varricchio, 2019). Direct association of invertebrate fecal pellets and *Maiasaura* nest and eggs here additionally suggest a trophic relationship, with invertebrates scavenging the nest material.

Another record of insect traces occurring in association with dinosaur eggs is reported from paleosols of the Campanian-Maastrichtian Allen Formation of Argentina (Genise and Sarzetti, 2011). Several wasp cocoons (*Fictovichnus sciuttoii*) are preserved within the upper portion of a probable titanosaur egg and were likely attracted to the plethora of insect prey items feeding on the decaying dinosaur eggs (Genise and Sarzetti, 2011). Wasps represent the top of carrion food webs (Payne and Mason, 1971; Smith, 1986), but no direct evidence of lower trophic levels are observed (Genise and Sarzetti, 2011).

A bird egg from the Pliocene of Laetoli, Tanzania contains several dipteran pupal cases and burrows attributed to the hatched larvae within the sediment infilling the egg (Harrison, 2005). It is likely that an adult fly laid eggs which then pupated within the decaying bird egg, with the larvae feeding on the egg contents (Harrison, 2005). Flies represent early colonizers within carrion communities (Dadour and Harvey, 2008; Merritt and De Jong, 2015). No other evidence of additional invertebrate trophic interaction is reported (Harrison, 2005).

These associations suggest that archosaur nests occasionally offer concentrations of nutrients for invertebrate communities. At Egg Mountain, representation of different invertebrate trophic levels suggest *Maiasaura* nests and eggs provided a resource for scavenging communities, corroborating inferences by Genise and Sarzetti (2011) on insect traces associated with sauropod eggs. The record of invertebrate scavenging here and that described by Genise and Sarzetti (2011) may be extended to other dinosaurian taxa, where large clutch sizes and extensive nesting colonies are known in both hadrosaurs and sauropods and likely provided ample resources for invertebrate and vertebrate predators and scavengers alike (Bois and Mullin, 2017).

Sedimentological and ichnological context.— The presence of *Edaphichnium* may also reflect sedimentological processes at the locality overall. Bedding planes and other primary sedimentary structures are absent, as are well-developed paleosol horizons (Lorenz and Gavin, 1984; Freimuth and Varricchio, 2019); however, geophagous invertebrate fecal pellets suggests the presence of organic material, likely at the soil surface and in the upper portions of the subsurface (Kooistra and Pulleman, 2010). Deposit feeding organisms are significant agents of soil homogenization, corroborating previous interpretations that bioturbation was likely the predominant factor in the destruction of bedding planes and primary sedimentary structures (Lorenz and Gavin, 1984; Freimuth and Varricchio, 2019). Bioturbation is known to accelerate mineral weathering, a probable explanation for the dearth of micas throughout the host matrix (Needham et al., 2004). The occurrence of *Edaphichnium* feeding traces and rootlet

traces along with abundant *Fictovichnus sciuttoii* and other invertebrate traces on particular horizons (e.g., JHPs 8, 10, 12; Fig. 3.2) suggest more extended soil development and colonization by invertebrates and vegetation in between sedimentation events (Bown and Kraus, 1987; Freimuth and Varricchio, 2019). Depositional hiatuses also would allow time for organic materials to be incorporated into the subsurface, perhaps explaining the increased relative abundance of deposit feeding traces on these horizons. *Edaphichnium* together with possible cicada nymph feeding traces *Feoichnus martini* may suggest relatively moist and/or organic-rich soil conditions, perhaps seasonally, seemingly in contrast to well-drained conditions inferred from abundant *Fictovichnus* (Freimuth and Varricchio, 2019; Panasci and Varricchio, 2020). The infrequent occurrence of *Edaphichnium* and *F. martini* in comparison to abundant *Fictovichnus* may suggest drier soil conditions were predominant (and moist conditions subordinate) throughout the time of deposition. Alternatively, deposition may have been prolonged enough such that wasps were able to colonize the substrate, but frequent enough to prohibit thorough build-up of organic material and thorough colonization by deposit feeding organisms (Genise, 2016).

Concentrations of *Edaphichnium* (specimens MOR 10878 2012-10, 2012-49, B11.12-1) occur within the same ~10 cm thick horizon as several multi-individual aggregates of multituberculate skeletons (JHP 8; Fig. 3.2). *Edaphichnium* specimens on this horizon occur in quads N3–5/W5, less than 2 meters away from an aggregate of five individual multituberculates MOR 10908 (Weaver et al., in review). At least 13 individuals occur on this horizon in a 32 m² area (Weaver et al., in review).

Morphological evidence suggests these were fossorial taxa, and taphonomic evidence suggests these aggregates represent social groups that accumulated beneath the surface, possibly within burrows (Weaver et al., in review). Ichnological evidence also suggests abundant subsurface activity on this horizon. In addition to relatively abundant mammals and *Edaphichnium*, *Fictovichnus sciuttoi*, *Feoichnus martini*, and root traces display particularly high abundances on this horizon as well (Freimuth and Varricchio, 2019; Panasci and Varricchio, 2020) (Fig. 3.2). The abundance of insect traces and lack of sedimentary structures suggests bioturbation was especially prevalent on these horizons, a factor known to disarticulate and disperse vertebrate hard parts within soils (Armour-Chelu and Andrews, 1994).

Suitable environmental conditions supporting a variety of behaviors and organisms is recorded in Egg Mountain paleosols, including fodichnia of invertebrates represented by *Edaphichnium* isp., pupichnia of crabronid or pompilid wasps and/or beetles represented by four morphs of *Fictovichnus sciuttoi*, probable cicada or other invertebrate traces represented by *Feoichnus martini*, social aggregations of multituberculate mammals, and buried and partially buried dinosaur eggs (Varricchio et al., 1999; Deeming, 2006; Oser, 2014; Freimuth and Varricchio, 2019; Panasci and Varricchio, 2020; Weaver et al., in review). The co-occurrence and abundance of these organisms not only reflect suitable substrates and preservation conditions, but likely ample resources supporting communities of invertebrates and vertebrates at the locality, including wasps, beetles, mammals, lizards, and herbivorous and carnivorous dinosaurs. More broadly, *Edaphichnium* and pelletal traces are noted as a secondary component in

the initial description of the *Celliforma* ichnofacies (Genise et al., 2010), and specimens here add another component to the impoverished *Celliforma* ichnofacies documented at Egg Mountain (Freimuth and Varricchio, 2019) and other occurrences of the Willow Creek Anticline (Martin and Varricchio, 2011).

Conclusions

- 1) Three morphotypes of the pellet-containing burrow trace *Edaphichnium* isp. occur in Egg Mountain paleosols, including linearly arranged fecal pellets, pellets in condensed masses, and dispersed pellet masses.
- 2) *Edaphichnium* isp. at Egg Mountain represents deposit feeding by invertebrates, including millipedes, rhizophagous beetle and chafer larvae, and possibly earthworms, suggesting a variety of taxa are capable *Edaphichnium* producers in addition to earthworms. Regardless of the specific trace-maker, fecal pellets likely reflect increased organic content in the subsurface that is otherwise undetectable and was likely lost through diagenesis or soil processes. *Edaphichnium* also adds credence to previous inferences that bioturbation is significant in sediment homogenization at the locality.
- 3) Invertebrate fecal pellets (*Edaphichnium* isp.) and wasp cocoons (*Fictovichnus sciuttoi*) are associated with *Maiasaura* eggs and perinatal remains and represent different trophic levels of invertebrate carrion communities, suggesting decaying dinosaur eggs and other remains supported complex invertebrate communities in the

Late Cretaceous. By ridding the soil of detritus and potentially pathogenic microbes, these communities may have facilitated dinosaur nest site fidelity inferred at the locality.

- 4) *Edaphichnium* together with *Fictovichnus sciuttoi* and *Feoichnus martini* represent the *Celliforma* ichnofacies previously described from the locality and the Willow Creek Anticline. The variety of trace fossils indicating soil activity and trophic interactions by invertebrates and vertebrates make Egg Mountain a unique fossil site that presents a rare window into a terrestrial ecosystem in the Late Cretaceous of North America.

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CHAPTER FOUR

CONCLUSIONS

This thesis includes two manuscripts that offer novel paleobiological information surrounding invertebrates, mammals, and dinosaurs at the Egg Mountain locality. The first manuscript (chapter two) investigates the taphonomy and origin of three multi-individual accumulations of mammals. Two amalgamations consist primarily of the metatherian *Alphadon halleyi* are characterized by multiple individuals in a small area, an absence of a mineralized or phosphatic ground mass, an abundance of indigestible paired craniodental elements relative to postcrania, extensive breakage and disarticulation of all elements, and periosteal corrosion congruent with digestion. These taphonomic features are common to prey in gastric pellets of modern diurnal raptors. As such, these represent the oldest mammal-bearing regurgitalites known in the fossil record, the first from the Mesozoic. An additional accumulation of multiple multituberculates display greater representation of postcrania, along with complete and articulated elements and an absence of digestion or predation traces. This suggests a non-predatory origin for the deposit, and possible burial in the subsurface, but a definitive depositional origin is difficult to surmise. Nonetheless, the assemblages allow for comparison of taphonomic features of the small mammalian taxa at the locality. Modern pellet assemblages tend to reliably track the population structure of small mammal communities (Terry, 2010; Andrade, 2016). If the same is true at Egg Mountain, *Alphadon* may be more abundant than lizards or multituberculates. The latter may have engaged in communal, fossorial

behavior, potentially an advantageous life mode compared to other prey taxa (Weaver et al., in review). The available evidence favors *Troodon formosus* as the most likely producer of the regurgitalites and supports previous inferences of a small or soft prey diet (Russell, 1969; Fowler et al., 2011; Torices et al., 2018). Given the similarities between Egg Mountain regurgitalites and gastric pellets of diurnal raptors, we hypothesize *Troodon* manipulated prey during feeding, a behavior suggested previously for deinonychosaurs (Fowler et al., 2011). If the large-bodied, non-volant *Troodon* is the producer of the regurgitalites, this further corroborates inferences that pellet egestion evolved to enhance digestive efficiency and accommodate increased metabolism and physiological processes along the avian lineage, rather than (but perhaps was exapted to) decrease weight for powered flight in Aves (Zheng et al., 2014; O'Connor et al., 2019; O'Connor and Zhou, 2019).

The second manuscript identifies three morphotypes of the terrestrial feeding trace *Edaphichnium* isp., characterized by ellipsoidal fecal pellets. Maximum pellet lengths range from 1.87–6.70 mm (mean 4.13 mm) and maximum diameters range from 1.01–4.06 mm (mean 2.62 mm). Pellets lack larger clastic or organic inclusions and are distinctly fine-grained compared to the host matrix, characteristic of fecal pellets from deposit feeding invertebrates. Possible trace-makers include chafers, coleopteran larvae, and millipedes, along with the often-attributed earthworms, suggesting several taxa are capable *Edaphichnium* producers. Four *Edaphichnium* specimens along with several *Fictovichnus sciuttoi* wasp cocoons occur associated with eggs and perinatal remains of the hadrosaur *Maiasaura peeblesorum*, representing invertebrate communities

scavenging the decaying nest. This corroborates other inferences that dinosaur nests and eggs would have provided abundant resources to invertebrate and vertebrate predators and scavengers alike (Genise and Sarzetti, 2011; Bois and Mullin, 2017). *Edaphichnium* are subordinate in the ichnoassemblage at Egg Mountain and occur at specific horizons that may have been subjected to extended depositional hiatuses and buildup of organic material in the soil. The presence of deposit feeders also offers additional evidence that bioturbation is the primary contributor to the homogenization of horizons and destruction of primary sedimentary structures at the locality. Invertebrate communities represented by *F. sciuttoii*, *Edaphichnium* isp., and *Feoichnus martini* represent the *Celliforma* ichnofacies and likely offered abundant resources for lizards, mammals, and dinosaurs at the locality.

Taken together, these studies offer two novel instances of trophic interactions at the Egg Mountain locality, spanning decomposers through carnivores, and begin to place the fauna at the locality in an ecological context. Additionally, these findings add to previously documented ecosystem interactions from the Willow Creek Anticline and the Two Medicine Formation (Chin and Gill, 1996; Varricchio, 2001; Chin, 2007; Chin et al., 2009). Future studies, such as stable isotope analyses, may clarify inferences made here and provide additional quantitative context to the ecosystem at Egg Mountain and the Two Medicine Formation.

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APPENDICES

APPENDIX A

RELATIVE ABUNDANCE OF MAMMAL ELEMENTS AT EGG MOUNTAIN AND
FOR MODERN PREDATOR GROUPS

RELATIVE ABUNDANCE FOR FIG 5

	Maxillae	Mandibles/Dentaries	Limb Elements	REF
MOR 11750		0.5	0.75	0.541666666 n/a
MOR 10912 & 10913	0.73077	0.80769	0.80769	0.08974 n/a
Strigiformes Average	0.741011235	0.650005689	0.650005689	0.668983664 Andrews (1990) and Montalvo and Fernández (2019)
Barn owl	0.713	0.841	0.841	0.6976 Andrews (1990)
Diurnal raptors Average	0.699471256	0.669100845	0.669100845	0.381942899 Andrews (1990) and Montalvo and Fernández (2019)
Long-winged harrier	1	0.9	0.9	0.127 Gómez (2007)
Mammalian carnivores Average	0.652147479	0.599524293	0.599524293	0.443763537 Andrews (1990) and Montalvo and Fernández (2019)
Puma	0.4275	0.5652	0.5652	0.1956 Montalvo et al. (2007)

AVERAGE STRIGIFORMES

	avg Limb Elements Montalvo and Fernández (2019)	avg Limb Elements Andrews (1990)	averages all Strigiformes
maxillae	61.36649829	86.83574879	74.1011235
mandibles	71.42625856	58.57487923	65.0005689
humeri	64.93643836	66.30434783	66.8983664
radii	63.29571062	61.352657	
ulnae	56.60733333	66.90821256	
femora	72.19970034	69.20289855	
tibiae	72.08940925	76.08695652	

AVERAGE DIURNAL RAPTORS

	avg Limb Elements Montalvo and Fernández (2019)	avg Limb Elements Andrews (1990)	averages all diurnal raptors
maxillae	62.06333333	77.83091787	69.9471256
mandibles	59.49166667	74.32850242	66.9100845
humeri	31.99333333	60.22222222	38.1942899
radii	18.59666667	24.30193237	
ulnae	27.63166667	47.85507246	
femora	39.24333333	56.46859903	
tibiae	26.60833333	49.02173913	

AVERAGE MAMMALIAN CARNIVORES

	avg Limb Elements Montalvo and Fernández (2019)	avg Limb Elements Andrews (1990)	averages all mammalian carnivores
maxillae	47.98222222	82.44727358	65.2147479
mandibles	59.17777778	60.7270808	59.9524293
humeri	39.72222222	81.20815966	44.3763537
radii	22.06444444	26.15565879	
ulnae	30.63333333	41.58159164	
femora	53.91666667	69.12799844	
tibiae	37.29111111	42.06235062	

APPENDIX B

CHI SQUARED ANALYSES FOR MOR 10912, 10913, MOR 11750, AND
SELECT MODERN PREDATORS RELATIVE ABUNDANCE

	maxillae	dentaries	limbs	total		chi sq value	p value					
MOR 10912 & 10913	19	21	13	53	14.3484552	14.2111646	24.4403802	1.50795806	3.243104096	5.3551662	16.169016	0.0003
Owl avg	19.26629212	16.9001479	52.1807258	88.347166	23.9178369	23.6889833	40.7403457	0.90463317	1.945557794	3.2125967		
	38.26629212	37.9001479	65.1807258	141.34717								
	max	den	limb									
MOR 10912 & 10913	19	21	13	53	21.2366214	20.9534664	10.8099122	0.2355589	0.000103342	0.4437117	1.28651014	0.5256
long-winged harrier	26	23.4	9.906	59.306	23.7633786	23.4465336	12.0960878	0.21051195	9.23537E-05	0.3965319		
	45	44.4	22.906	112.306								
	max	den	limb									
MOR 10912 & 10913	19	21	13	53	13.4593226	15.3696873	24.17099	2.28088045	2.062528659	5.1628427	14.8199867	0.0006
barn owl	18.538	21.866	54.4128	94.8168	24.0786774	27.4963127	43.24181	1.27494984	1.152897154	2.885888		
	37.538	42.866	67.4128	147.8168								
	max	den	limb									
MOR 10912 & 10913	19	21	13	53	16.6494702	17.1913911	19.1591387	0.33184181	0.843765436	1.9799945	5.71389428	0.05747
diurnal raptor avg	18.18625266	17.396622	29.7915461	65.374421	20.5367825	21.2052309	23.6324074	0.26902901	0.684052992	1.6052105		
	37.18625266	38.396622	42.7915461	118.37442								
	max	den	limb									
MOR 10912 & 10913	19	21	13	53	15.8597408	16.1384199	21.0018393	0.62177736	1.464515181	3.0487535	9.18759982	0.01011
mam avg	16.95583445	15.5876316	34.6135559	67.157022	20.0960936	20.4492117	26.6117166	0.49070371	1.155788365	2.4060617		
	35.95583445	36.5876316	47.6135559	120.15702								
	max	den	limb									
MOR 10912 & 10913	19	21	13	53	16.9676401	20.1116821	15.9206778	0.24343319	0.039236335	0.5358038	1.87477357	0.3916
puma	11.115	14.6952	15.2568	41.067	13.1473599	15.5835179	12.3361222	0.31416854	0.050637391	0.6914944		
	30.115	35.6952	28.2568	94.067								

	max	den	limb							chi sq value	p value
MOR 11750	2	3	13	18	2.25526351	2.54420078	13.2005357	0.02889217	0.081657443	0.0030464	0.20817327
Owl avg	2.964044942	2.60002276	16.0556079	21.619676	2.70878143	3.05582198	15.8550722	0.0240549	0.06798594	0.0025364	0.9011
	4.964044942	5.60002276	29.0556079	39.619676							
MOR 11750	2	3	13	18	3.76989668	4.14688634	10.083217	0.83093371	0.317189375	0.843741	5.35902717
long-winged harrier	4	3.6	3.048	10.648	2.23010332	2.45311366	5.96478302	1.4046588	0.536195412	1.4263089	0.0686
	6	6.6	16.048	28.648							
MOR 11750	2	3	13	18	2.13230986	2.79678894	13.0709012	0.00820983	0.014765053	0.0003846	0.04167393
barn owl	2.852	3.364	16.7424	22.9584	2.71969014	3.56721106	16.6714988	0.00643673	0.011576196	0.0003015	0.9794
	4.852	6.364	29.7424	40.9584							
MOR 11750	2	3	13	18	2.64581807	3.13028148	12.2239005	0.15763781	0.005422228	0.0492748	0.47338606
diurnal raptor avg	2.797885024	2.67640338	9.16662957	14.640918	2.15206696	2.54612191	9.94272911	0.19380483	0.00666632	0.06058	0.7892
	4.797885024	5.67640338	22.1666296	32.640918							
MOR 11750	2	3	13	18	2.46470538	2.88693926	12.6483554	0.08761741	0.00442778	0.0097763	0.21887998
mam avg	2.608589916	2.39809717	10.6503249	15.657012	2.14388454	2.51115792	11.0019695	0.10072888	0.005090374	0.0112393	0.8963
	4.608589916	5.39809717	23.6503249	33.657012							
MOR 11750	2	3	13	18	2.50438774	3.55123532	11.9443769	0.10158451	0.085564698	0.0932941	0.8630011
puma	1.71	2.2608	4.6944	8.6652	1.20561226	1.70856468	5.75002306	0.21101892	0.177741374	0.1937975	0.6495
	3.71	5.2608	17.6944	26.6652							

APPENDIX C

PELLET VOLUME, BODY MASS, AND MAXIMUM INGESTION CAPACITY
DATA

Taxon	length (mm)	breadth (mm)	width (mm)	Pellet volume (cm3)	REF	
European eagle owl		78	34	26	35.0	Andrews (1990), Appendix 14
Verreaux eagle owl		77	31	28	23.6	Andrews (1990), Appendix 14
snowy owl		63	29	25	36.2	Andrews (1990), Appendix 14
Great grey owl		60	30	25	23.9	Andrews (1990), Appendix 14
Red kite		50	27	22	10.1	Andrews (1990), Appendix 14
Common buzzard		55	24	20	10.5	Andrews (1990), Appendix 14
Peregrine		50	22	20	8.8	Andrews (1990), Appendix 14
Tawny owl		50	20	20	13.8	Andrews (1990), Appendix 14
Hen harrier		48	20	20	3.8	Andrews (1990), Appendix 14
short-eared owl		48	22	18	10.0	Andrews (1990), Appendix 14
Spotted eagle owl		42	20	20	11.5	Andrews (1990), Appendix 14
Barn owl		40	21	18	15.6	Andrews (1990), Appendix 14
Long-eared owl		32	16	14	7.9	Andrews (1990), Appendix 14
Kestrel		23	14	13	2.2	Andrews (1990), Appendix 14
Little owl		22	12	10	1.4	Andrews (1990), Appendix 14
<i>Anchiornis</i>		53	20	20*	8.9	Zheng et al. (2018)
Sparrow Hawk single	N/A	N/A	N/A		1.6	Balgooyen (1971)
Sparrow Hawk multiple	N/A	N/A	N/A		5.9	Balgooyen (1971)
Taxon	Body Mass (g)	REF				
European eagle owl	2666	Andrews (1990), Appendix 15				
Verreaux eagle owl	2000	Andrews (1990), Appendix 15				
Snowy owl	1983	Andrews (1990), Appendix 15				
Great grey owl	1057	Andrews (1990), Appendix 15				
Red kite	963	Andrews (1990), Appendix 15				
Common buzzard	913	Andrews (1990), Appendix 15				
Peregrine	859	Andrews (1990), Appendix 15				
Tawny owl	529	Andrews (1990), Appendix 15				
Hen harrier	455	Andrews (1990), Appendix 15				
Short-eared owl	381	Andrews (1990), Appendix 15				
spotted eagle owl	365	Andrews (1990), Appendix 15				
Barn owl	337	Andrews (1990), Appendix 15				
Long-eared owl	308	Andrews (1990), Appendix 15				
Kestrel	213	Andrews (1990), Appendix 15				
Little owl	174	Andrews (1990), Appendix 15				
<i>Anchiornis</i>	516	Zheng et al. (2018) after O'Gordon and Hone (2013)				
Sparrow Hawk single	220	del Hoyo et al. (1994)				
Sparrow Hawk multiple	220	del Hoyo et al. (1994)				
Taxon	Body Mass (g)	Mass REF	Maximum ingestion capacity (g) (Hiraldo et al., 1991)			
Red-tailed hawk	1075	del Hoyo et al. (1994)	180			
Zone-tailed hawk	772	del Hoyo et al. (1994)	100			
Cooper's hawk	416.5	del Hoyo et al. (1994)	80			
American kestrel	122.5	del Hoyo et al. (1994)	33			
Turkey vulture	1425	del Hoyo et al. (1994)	350			
MOR 10913	2098	del Hoyo et al. (1994)	450 equivalent to min. 10 x 45 g Alphadon in MOR 10913			
Anchiornis	516	Zheng et al. (2018),	93			
O'Gordon and Hone (2013)						

APPENDIX D

pXRF DATASET

Index	Reading No	Time	Type	Duration	Units	Sigma Value	Sequence	Flags	specimen	Mo	Mo Error
1	472	4/20/2020 19:13	TestAll Geo	120 ppm	2 Final	-8mm	EWOT 91B	-8mm	sample a 1	10.82	4.32
2	473	4/20/2020 19:17	TestAll Geo	120 ppm	2 Final	-8mm		-8mm	sample a 2	12.98	2.47
3	474	4/20/2020 19:20	TestAll Geo	120 ppm	2 Final	-8mm		-8mm	sample a 3	11.4	2.43
4	475	4/20/2020 19:26	TestAll Geo	120 ppm	2 Final	-8mm		-8mm	sample b 1	6.97	2.59
5	476	4/20/2020 19:29	TestAll Geo	120 ppm	2 Final	-8mm	EWOT matrix	-8mm	sample b 2	7.14	2.57
6	477	4/20/2020 19:33	TestAll Geo	120 ppm	2 Final	-8mm		-8mm	sample b 3	5.82	2.6
7	478	4/20/2020 19:38	TestAll Geo	120 ppm	2 Final	-8mm		-8mm	sample c 1	11.55	2.54
8	479	4/20/2020 19:41	TestAll Geo	120 ppm	2 Final	-8mm	2016-29 dark pellets	-8mm	sample c 2	11.59	2.61
9	480	4/20/2020 19:44	TestAll Geo	120 ppm	2 Final	-8mm		-8mm	sample c 3	7.91	2.56
10	481	4/20/2020 19:47	TestAll Geo	120 ppm	2 Final	-8mm		-8mm	sample d 1	4.61	2.57
11	482	4/20/2020 19:49	TestAll Geo	120 ppm	2 Final	-8mm	dark pellets - matrix	-8mm	sample d 2	< LOD	3.79
12	483	4/20/2020 19:52	TestAll Geo	120 ppm	2 Final	-8mm		-8mm	sample d 3	3.79	2.51

K	K error	P	P error
91B	37085.48667	617.5166667	8800.723333
91B m	18963.08333	321.72	5514.1
2016-29	24626.69	455.87	5879.82
2016-29 m	10594.97667	216.47	2453.836667

*all values are parts per million

Zr	Zr Error	Sr	Sr Error	U	U Error	Rb	Rb Error	Th	Th Error	Pb	Pb Error	Au	Au Error	Se	Se Error	As	As Error	Hg
185.59	10.41	704.6	20.23	< LOD	300000	116.62	7.19	< LOD	300000	< LOD	300000	< LOD	300000	< LOD	300000	15.74	9.43	< LOD
174.39	5.75	676.84	11.23	< LOD	300000	115.95	4.08	< LOD	300000	12.69	6.11	< LOD	300000	< LOD	300000	13.75	5.48	< LOD
183.42	5.8	681.24	11.16	< LOD	300000	108.18	3.9	< LOD	300000	20.65	6.36	< LOD	300000	< LOD	300000	< LOD	8.19	< LOD
175.02	5.01	538.13	7.06	< LOD	7.73	67.01	2.56	5.51	2.98	27.58	5.12	< LOD	5.55	< LOD	3.2	< LOD	5.27	< LOD
173.47	4.97	534.39	7	< LOD	7.52	66.39	2.54	5.3	2.94	24.2	4.92	< LOD	5.66	< LOD	3.13	< LOD	5.12	< LOD
170.51	5.02	535.14	7.11	< LOD	7.98	67.99	2.6	< LOD	4.37	23.72	4.99	< LOD	5.55	< LOD	3.27	7.18	4.52	< LOD
140.8	5.37	510.86	9.87	< LOD	300000	82.58	3.61	< LOD	300000	13.63	6.28	< LOD	300000	< LOD	300000	< LOD	8.22	< LOD
141.45	5.54	517.24	10.22	< LOD	300000	80.8	3.68	< LOD	300000	11.15	6.33	< LOD	300000	< LOD	300000	< LOD	8.27	< LOD
142.94	5.61	521.24	10.35	< LOD	300000	82.59	3.74	< LOD	300000	15.98	6.57	< LOD	300000	< LOD	300000	10.85	5.89	< LOD
100.59	4.18	327.41	5.83	< LOD	6.5	28.8	1.88	< LOD	4.01	7.32	4.15	< LOD	6.24	< LOD	3.36	< LOD	4.29	< LOD
98.9	4.14	325.49	5.79	< LOD	6.49	30.06	1.89	< LOD	3.88	< LOD	5.73	< LOD	5.99	< LOD	3.32	< LOD	5.45	< LOD
101.02	4.1	323.65	5.68	< LOD	6.3	29.21	1.85	< LOD	3.82	< LOD	5.81	< LOD	6.26	< LOD	3.4	< LOD	4.03	< LOD

Hg Error	Zn	Zn Error	W	W Error	Cu	Cu Error	Ni	Ni Error	Co	Co Error	Fe	Fe Error	Mn	Mn Error	Cr	Cr Error	V
300000	247.06	34.76	182.72	106.52	105.74	41.73	< LOD	300000	< LOD	300000	74908.75	1128.3	373.91	149.81	61.83	11.03	136.56
300000	222.33	19.17	191.9	62.52	100.21	23.97	< LOD	300000	< LOD	300000	75575.14	649.04	413.95	86.28	76.15	10.92	93.29
300000	236.99	19.25	130.18	61.85	68.59	22.69	< LOD	300000	< LOD	300000	73193.26	629.2	314.09	82.9	70.35	10.87	132.78
8.68	101.63	9.63	< LOD	37.72	53.27	13.77	< LOD	23.17	< LOD	123.77	32672.85	315.1	242.1	45.63	111.8	26.9	95.22
8.6	91.91	9.28	< LOD	37.28	48.43	13.55	< LOD	23.06	< LOD	122.92	32458.75	313.69	235.22	45.06	116.26	26.06	215.03
9.02	88.31	9.37	< LOD	38.64	57.49	13.96	< LOD	22.75	< LOD	125.14	32408.81	317.6	239.71	45.9	120.14	26.75	101.47
300000	89.14	16.22	170.93	67	236.64	30.01	< LOD	300000	< LOD	300000	51709.6	547.93	1971.58	133.66	43.8	7.22	62.08
300000	97.57	17.11	224.7	68.97	235.39	30.86	< LOD	300000	< LOD	300000	51885.54	564.37	1971.71	137.43	39.52	7.13	67.99
300000	86.74	16.85	222.42	69.16	247.07	31.49	< LOD	300000	< LOD	300000	52267.46	571.65	1990.09	138.78	42.92	7.15	52.14
9.14	39.45	8.03	< LOD	40.93	36.48	14.24	< LOD	24.29	< LOD	98.93	18921.64	252	3961.44	115.78	21.17	7.25	40.3
9.44	37.99	7.92	< LOD	65.16	26.92	13.9	< LOD	24.54	< LOD	99.35	18806.3	250.19	4045.41	116.28	14.84	7.17	40.74
9.18	34.7	7.69	< LOD	39.72	49.13	14.28	< LOD	23.37	< LOD	95.82	18954.07	247.34	3855.46	112.06	74.78	29.55	50.36

V Error	Ti	Ti Error	Sc	Sc Error	Ca	Ca Error	K	K Error	S	S Error	Ba	Ba Error	Cs	Cs Error	Te	Te Error	Sb
26.05	3394.27	85.83	67.66	39.35	64631.9	1328.39	36736.35	650.4	413.41	125.8	< LOD	33.6	< LOD	7.72	< LOD	21.04	< LOD
25.16	3154.51	83.98	< LOD	56.91	67571.05	1257.02	37668.86	608.65	< LOD	332.94	< LOD	34.14	< LOD	7.92	< LOD	21.73	< LOD
25.09	3126.62	82.3	91.31	38.34	65953.83	1236.08	36791.25	595.5	< LOD	320.56	< LOD	34.67	< LOD	7.9	< LOD	21.65	< LOD
18.17	2113.63	59.15	99.78	33.94	53133.82	817.17	18858.22	323.84	< LOD	245.05	362.28	38.82	< LOD	8.75	< LOD	26.35	< LOD
38.85	2133.79	57.97	84.44	33.21	53027.32	805.96	18984.57	319.62	169.5	89.11	387.97	37.5	< LOD	8.59	< LOD	25.5	< LOD
18.25	2117.63	59.08	93.09	33.48	52955.68	808.65	19046.46	321.7	184.08	85.08	363.52	38.21	< LOD	8.61	< LOD	25.85	< LOD
15.43	1517.24	51.03	89.45	42.04	141342.45	1583.84	24539.31	453.85	< LOD	204.85	< LOD	44.5	< LOD	10.13	< LOD	28.79	< LOD
15.51	1477.99	50.87	115.8	42.18	142519.69	1607.38	24464.79	454.82	< LOD	236.81	< LOD	44.15	< LOD	10.08	< LOD	29.1	< LOD
15.37	1516.19	51.28	88.06	41.95	142495.58	1611.63	24875.97	458.94	< LOD	251.01	< LOD	43.77	< LOD	10.08	< LOD	29.23	< LOD
14.52	1147.2	49.95	131.85	64.75	172772.73	1391.54	10521.8	216.34	< LOD	327.91	211.54	28.88	< LOD	9.62	< LOD	29.05	< LOD
14.53	1104.45	49.8	144.89	65.02	172642.39	1389.18	10592.4	217.56	374.59	236.13	186.56	28.71	< LOD	9.6	< LOD	28.84	< LOD
14.22	1153.26	48.66	159.73	64.2	171690.73	1367.47	10670.73	215.51	< LOD	325.87	200.19	28.87	< LOD	9.61	< LOD	29.35	< LOD

Sb Error	Sn	Sn Error	Cd	Cd Error	Ag	Ag Error	Pd	Pd Error	Bal	Bal Error	Nb	Nb Error	Bi	Bi Error	Re	Re Error	Ta
10.19 < LOD		6.69 < LOD		7.79 < LOD		5.08 < LOD		7.08	487024.19	4809.17	30.63		5.19 < LOD		18.1 < LOD		1.5 < LOD
10.44 < LOD		6.75 < LOD		7.88 < LOD		5.26 < LOD		7.56	484059.97	2631.9	26.35		2.86	12.54	7.43 < LOD		1.5 < LOD
10.62 < LOD		6.75 < LOD		7.94 < LOD		5.49 < LOD		7.43	490377.19	2588.67	25.6		2.82 < LOD		16.43 < LOD		1.5 < LOD
12.96 < LOD		8.44	10.35	6.02	6.34	3.36 < LOD		8.38	712727	1417.91	13.54		2.11 < LOD		9.12 < LOD		1.5 < LOD
12.83 < LOD		8.18	9.94	5.76	6.76	3.24 < LOD		8.38	712864.56	1417.04	11.54		2.07 < LOD		8.98 < LOD		1.5 < LOD
12.81 < LOD		8.3	14.04	6.03 < LOD		6.35 < LOD		8.38	713227.38	1439.21	11.81		2.1 < LOD		7.93 < LOD		1.5 < LOD
14.21 < LOD		9.15 < LOD		10.4 < LOD		7.11 < LOD		9.99	545533.63	2524.69	21.8		2.92 < LOD		9.32 < LOD		1.5 < LOD
14.01 < LOD		9.15 < LOD		10.99 < LOD		7.36 < LOD		9.55	543573.69	2589.84	22.33		3.01 < LOD		10.7 < LOD		1.5 < LOD
13.92 < LOD		9.17 < LOD		10.39 < LOD		7.49 < LOD		9.48	542642.38	2624.51	20.78		3 < LOD		9.26 < LOD		1.5 < LOD
14.29	20.43	11.21	13.38	7.14 < LOD		7.21 < LOD		9.56	654399.31	1681.53	5.01		2.05 < LOD		5.82 < LOD		1.5 < LOD
14.31 < LOD		9.08 < LOD		10.4	5.54	3.52 < LOD		9.37	658440.69	1651.25	7.29		2.08 < LOD		5.58 < LOD		1.5 < LOD
14.18 < LOD		9.34 < LOD		10.46 < LOD		5.25 < LOD		9.61	655296.19	1648.9	5.41		2.01 < LOD		5.62 < LOD		1.5 < LOD

Ta Error	Hf	Hf Error	Al	Al Error	P	P Error	Si	Si Error	Cl	Cl Error	Mg	Mg Error
1.5 < LOD		1.5	52729.84	2095.98	8603.03	417.86	266369.03	2490.52	< LOD	85.31	< LOD	3767.65
1.5 < LOD		1.5	50712.89	1991.82	9006.73	416.22	266308.66	1977.18	< LOD	87.48	< LOD	4010.01
1.5 < LOD		1.5	50283.91	2031.53	8792.41	419.32	265620.78	1992.83	< LOD	88.57	< LOD	5715.2
1.5 < LOD		1.5	19128.69	944.17	5522.49	259.68	153228.88	1381.33	< LOD	58.9	< LOD	3243.38
1.5 < LOD		1.5	20153.11	982.55	5640.89	266.5	152277.05	1401.03	< LOD	60.64	< LOD	2955.37
1.5 < LOD		1.5	19859.79	929.47	5378.92	251.86	152516.48	1361.05	< LOD	57.74	< LOD	2124.78
1.5 < LOD		1.5	29291.68	1681.99	5642.68	374.26	194006.61	1830.65	< LOD	95.69	< LOD	4418.22
1.5 < LOD		1.5	28992.52	1720.31	5994.03	387.62	194705.55	1873.43	< LOD	98.47	< LOD	4851.39
1.5 < LOD		1.5	28939.24	1735.95	6303.05	392.05	194548.19	1877.93	< LOD	125.16	< LOD	5918.09
1.5 < LOD		1.5	11441.68	1020.12	2317.44	257.46	119501.23	1361.97	75.85	43.63	< LOD	3516.08
1.5 < LOD		1.5	11716.39	1024.19	2515.82	260.61	118184.17	1361.15	< LOD	83.84	< LOD	2943.56
1.5 < LOD		1.5	11075.71	1012.42	2528.25	259.78	118857.29	1356.36	75.43	43.56	3965.68	2398.29