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Insect trace fossils elucidate depositional environments and sedimentation at a dinosaur nesting site from the Cretaceous (Campanian) Two Medicine Formation of Montana

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Abstract

We describe the diversity and abundance of insect (specifically hymenopterans and coleopterans) pupation structures in the Upper Cretaceous (Campanian) Two Medicine Formation at the Egg Mountain locality, western Montana, U.S.A., an important dinosaur nesting site. The study interval comprises a massive calcareous siltstone and indurated silty limestone horizons interpreted as the product of cumulative paleosols. A 7 m by 11 m area was quarried with a jackhammer at intervals of 12.5 cm thickness for a 1.5 m thick stratigraphic section. The ichnoassemblage comprises four morphotypes (small, medium, large, and wide) assigned to *Fictovichnus sciuttoi*, of which three represent wasp (hymenopteran) cocoons while the fourth (wide) type potentially was produced by a coleopteran. Medium and small *F. sciuttoi* are dominant while large and wide *Fictovichnus* are less common and absent in some sample intervals. Other probable insect traces include partial perforations in cocoons (*Tombownichnus*), isolated burrows, and an enigmatic hemispherical trace. Material is representative of a depauperate *Celliforma* ichnofacies. Pervasive cocoons and other traces throughout the sequence suggest persistent soil conditions suitable for insect nesting and pupation, and suggest an

absence of sediment pulses of sufficient thickness to prohibit thorough colonization. Peaks in pupation chamber abundance may reflect episodes of reduced sedimentation rates otherwise unseen in the absence of primary bedding structures. Well-drained and friable soil conditions favorable for insect nesting also may help explain the abundance of dinosaur nests and other vertebrate nesting events in associated strata as well as the presence of small terrestrial forms.

Keywords: ichnology; hymenopterans; coleopterans; Egg Mountain; Pupichnia

1. Introduction

Historically, ichnological studies have primarily focused on marine settings (e.g., Howard, 1975). More recently, studies have shifted to the terrestrial realm, integrating the ichnofacies paradigm and exploring ichnological implications in pedogenesis and depositional processes, paleoecology, and evolutionary trends (e.g., Hasiotis and Bown, 1992; Genise et al., 2000; Hasiotis, 2003; Melchor et al., 2012). Specifically, insect trace fossils have been recognized as valuable paleoenvironmental indicators (Genise, 2016). While insect trace fossils commonly occur in leaves and wood (e.g., Labaneira, 2006; Falcon-Lang et al. 2015), their associations in paleosols are useful indicators of paleoenvironments, as nesting insects are typically constrained by different environmental parameters (e.g., Genise et al., 2000).

The oldest records of insect-dominated ichnofacies occur in the Cretaceous with the *Celliforma* ichnofacies. Alonso-Zarza et al. (2011) describe an example of the *Celliforma* ichnofacies comprised of bee cells (*Celliforma* ispp.) and beetle pupation structures (*Fictovichnus gobiensis*) from the Campanian-Maastrichtian Mercedes Formation of Uruguay. In a second Cretaceous example of the *Celliforma* ichnofacies, Martin and Varricchio (2010) describe wasp cocoons (*Fictovichnus sciuttoi*) and

potentially bee (*Rebuffoichnus*) and moth (*Teisseirei*) pupation chambers from the Cretaceous (Campanian) Two Medicine Formation. In both instances, the presence of the *Celliforma* ichnofacies implies semi-arid environments with bare and well-drained soil conditions favored by soil-dwelling insects (Genise et al, 2010).

Here, we describe an assemblage of insect trace fossils at Egg Mountain, a dinosaur nesting locality from the Upper Cretaceous (Campanian) Two Medicine Formation of Montana (Horner, 1984; Horner, 1987). Along with abundant dinosaur eggshell and small vertebrates, this locality preserves a rich assemblage of insect traces first recognized and interpreted as carrion beetle cocoons (Horner, 1984; Horner, 1987). The locality is marked by a distinct absence of primary sedimentary structures and bedding markers, making interpretation of its depositional history difficult. Despite the paucity of stratigraphic contacts, Horner (1987) describes three distinct nesting horizons based on subtle lithologic differences and concentrations of eggshell and skeletal remains. Insect cocoons occur throughout surrounding strata and have been useful in paleoenvironmental interpretations of the area (Martin and Varricchio, 2011). Specifically, we examine the stratigraphic abundance and diversity of insect traces through a section at the Egg Mountain, and apply an approach that others have used for marine strata (Gingras et al., 1999; Dashtgard et al., 2011; Gingras et al., 2011), to assess environmental conditions and general patterns of deposition and erosion (e.g., Sánchez et al., 2010).

2. Geological Setting

The geology of the Two Medicine Formation (Upper Cretaceous) is well known, largely due to extensive studies related to abundant dinosaur eggs, trace fossils, and skeletal remains (e.g., Horner, 1979; Horner, 1982; Varricchio and Horner, 1993; Chin, 2007). $^{40}Ar/^{39}Ar$ dates near the base and top of the Two Medicine Formation indicate a Campanian age of between 74.076 ± 0.095 and 80.044 ± 0.190

Ma (Rogers et al., 1993). Two Medicine Formation deposition occurred at a paleolatitude of 56°N (Fricke et al., 2010), and a semi-arid to subhumid climate and seasonality are inferred throughout the deposition of the formation, as indicated by the abundance of caliche nodules, taphonomic data supporting episodic drought, growth interruptions in conifer fossils, and herbivorous dinosaur coprolites (Lorenz and Gavin, 1984; Rogers, 1990; Falcon-Lang, 2003; Chin, 2007). Facies are interpreted as intergrading fluvial and lacustrine systems in a volcanically active area (Lorenz and Gavin, 1984; Rogers et al., 1993).

2.1. Egg Mountain locality

The Egg Mountain locality, which forms the focus of this study, occurs at the Willow Creek Anticline near Choteau, Montana (47° 48.370' N, 112° 25.850' W) (Fig. 1). It consists of a small hill that rises around 15 meters above the surrounding topography. $^{40}Ar/^{39}Ar$ dating of a bentonite horizon of the Willow Creek Anticline suggests strata equivalent to or just stratigraphically lower than Egg Mountain are 75.53 ± 0.32 Ma (Varricchio et al., 2010). During this time, the area was positioned in geographically proximal to the emerging Rocky Mountains to the west, and distal to the Interior Seaway (Lorenz and Gavin, 1984; Horner, 1987).

The Egg Mountain site is famous for producing dinosaur egg clutches of *Troodon formosus* and the oogenus *Continuoolithus* (Horner, 1984; Horner, 1987; Hirsch and Quinn, 1990; Varricchio et al., 1999). Isolated eggshell including some attributable to *Maiasaura peeblesorum* (Oser, 2014) is common throughout the section. Recent excavations from 2010-2016 have produced an abundance of associated to articulated skeletons of the metatherian *Alphadon halleyi*, the multituberculate *Cimexomys judithae*, both previously described from the site (Montellano, 1988; Montellano et al., 2000), and an iguanomorph lizard, *Magnuviator ovimonsensis* (DeMar et al., 2017). Concentrations of unknown thin

eggshell have been excavated at different horizons, representing nesting events. Isolated and associated elements of the small ornithopod *Orodromeus* occur throughout the section. Isolated hadrosaur teeth are common, and dromaeosaurid, *Troodon*, and tyrannosaurid teeth are less common. In addition to the abundant pupal cases, rare isolated planispiral terrestrial snails have been found. An *Adocus* turtle shell fragment and an isolated frog frontal are the only aquatic vertebrate forms known.

2.2. Paleoenvironments

Deposition at the Egg Mountain locality has been interpreted as the product of crevasse splays in a fluvial upland facies (Horner, 1984; Lorenz and Gavin, 1984) or an up-dip alluvial plain (Fricke et al., 2010) and Horner (1987) interpreted the locality as a lakeside dinosaur nesting ground. The stratigraphy ~100 meters to the north is marked by lacustrine limestone and interbedded mudstone and siltstone at a similar or slightly lower stratigraphic level. Similar lacustrine sediments are present to the south of the locality. These sediments, which contain charophytes and well-preserved pterodactyloid pterosaur (Padian, 1984), are interpreted to represent a low energy alkaline lake (Lorenz and Gavin, 1984). Lorenz and Gavin (1984) suggest the lake may have been seasonal, as evidenced by subaerial mud cracks; this is parsimonious with other inferences of seasonality throughout Two Medicine deposition (e.g., Rogers, 1990; Falcon-Lang, 2003). 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 lake and braided stream lithofacies (Horner, 1987).

Paleozoic limestones to the west of the locality are the likely source of the calcareous sediments (Lorenz and Gavin, 1984). Large amounts of calcite are present in both primary features (sediment) and secondary features (infill of tectonic fractures, diagenetic crystalline infill of some fossil cocoons and eggshell). High levels of calcium limestone favor the preservation of eggshell and egg material.

Varricchio et al. (1999) argued for a pedogenic origin for the limestones based on the presence of root traces, burrows, nodules, and low rare earth element concentrations, but distinct paleosol horizons are lacking. However, isotopic analysis favors groundwater cementation (Moore et al., pers. comm., 2016). A fluctuating water table is parsimonious with inferred seasonality throughout Egg Mountain deposition and may explain the irregularity of the limestone horizons at the locality (Lorenz and Gavin, 1984).

2.3. Sedimentary facies of study section

Three lithologic units comprise the top 1.5 meters of the studied section in an artificial quarry (Fig. 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 (Fig. 3a). Some medium- to coarse-grained sand, pebbles, and small, centimeter-scale mud rip up clasts are present in the thickest portion of this unit. It is massive with no distinct internal structure. The limestone has a very irregular upper surface with decimeter scale relief that extends into the siltstone unit above (Fig. 3b). Where exposed, it is characterized by a surficial rust color. The upper contact of the limestone and siltstone is usually sharp. The dominant lithology of Unit 2 is a ~1 m thick grey calcareous siltstone. The siltstone weathers brittlely and blocky with an irregular pattern. 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 (Fig. 3c). These limestones are similar in composition to those in Unit 1 but lack larger pebbles and mud rip up clasts. Unit 3 comprises a relatively thin irregular micritic limestone 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). The unit preserves infrequent root traces, particularly within the nest structure (Varricchio et al., 1999). Overall, the sedimentary succession is homogenous and displays no

distinct bedding markers or paleosol horizons. The only marked difference between the lithologic units is the varying limestone induration.

3. Material and methods

Horner (1987) described three nest-bearing horizons at Egg Mountain in a vertical section of roughly three meters. A new 7x11 meter main quarry was opened in 2010 to the east of and adjacent to Horner's quarry and was worked each year through 2016. Excavations worked through the upper 1.5 meters of Horner's (1987) section. Another adjacent upper quarry was opened in 2015 (Fig. 4a). The trace fossil data used here have been collected from the main quarry from 2010 to 2016. 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 12.5 cm for each pass (Fig. 2). Quarry depths were measured for each pass using a sight level. In the absence of primary bedding structures, evenly spaced jackhammer passes act as artificial markers with which trace fossil abundance and diversity can be measured. Rubble created in the wake of the jackhammer was picked through and specimens were collected and sorted into bags, their abundances recorded for each jackhammer pass and used quantitatively to describe sedimentation rate and general depositional processes. Lateral location of specimens was recorded throughout the section using a meter by meter grid system (Fig. 4b). In total, 3661 fossil cocoons were collected throughout the section. An additional 1031 cocoons were collected but unassignable to any JHP in the main quarry.

Abundances and diversity data may be influenced by collection bias. Some samples are badly fractured, making identification based on size nearly impossible. Data from the 2010 field season are incomplete; only a sample of traces were collected. Thus, although the two jackhammer passes from

2010 are included in sedimentation analyses, total abundances for the two passes are underrepresented. Trace fossil data used to infer general sedimentation rates were restricted to the main quarry.

We measured the *x*, *y*, and *z* axes (i.e. length, maximum diameter, and diameter perpendicular to maximum) of all complete specimens at the Egg Mountain locality (N=1155) to quantifiably distinguish trace morphologies. Specimens were measured and included in morphological analysis only if all three dimensions accessible for measurements. The remaining traces (N=3537) were assigned to a size morphology based on measurements of accessible dimensions (i.e. measurement of one or two identifiable axes) and qualitative features such as surface texture. Minimum or maximum dimensions of traces included in length and diameter ranges overlap size categories, but those outlier specimens were qualitatively assigned to a group based on the best-preserved dimensional characteristics and observations of surface texture. The few traces that were poorly preserved, fractured, or encased in sediment and unable to be measured were not assigned to a morphology and not used in abundance counts.

All specimens are deposited in the Invertebrate Collections of Museum of the Rockies (MOR-IV) under the catalog MOR-IV-2804. Individual field bags retain their field identification numbers. Figured specimens were separated from their individual bag and given their own unique specimen identification number in addition to the field identification number.

4. Trace fossil types

4.1 Ichnofamily Pallichnidae Genise 2004

Ichnogenus *Fictovichnus* Johnston et al., 1996

Fictovichnus sciuttoi (Genise et al., 2007)

Figure 7

Material. – MOR-IV-2804; 1155 specimens.

Occurrence. – Massive grey calcareous siltstone and micritic limestone at the Egg Mountain locality (TM-006), Two Medicine Formation, Montana, USA.

Description. – *Fictovichnus sciuttoi* is an ovoid, capsule-shaped structure showing fine lobed textures with helically arranged ridges, unlike the more gracile and tapered *F. aragon* and the externally smooth *F. gobiensis* (Genise et al., 2007; Genise, 2016). Original material is described as *Rebuffoichnus sciuttoi* by Genise et al. (2007) from the Upper Cretaceous (Coniacian-Santonian) Bajo Barreal Formation of Argentina, but the original description was amended to exclude interpretive and micromorphological characteristics (Alonso-Zarza et al., 2014). From the Argentinian material, 27 specimens range from 26—33 millimeters long and 12—16 millimeters wide and were interpreted as cocoons of aculeate wasps (Genise et al., 2007). The best-preserved Egg Mountain specimens display helical ornamentation and some show scarring, a flattened surface oriented obliquely to the long axis of the structure, and/or truncation, a flat surface at one extreme of the structure with perpendicular orientation to the long axis.

Four distinct morphologies are displayed (Fig. 5, Table 1). Three ellipsoidal to ovoidal morphologies of *F. sciuttoi*—large, medium, and small—are present throughout the section at Egg Mountain (Fig. 6). Specimens of the large morphology are on average 31.5—37.7 mm x 13.0—16.0 mm in diameter (N=62) (Fig. 6A-C). They display a greater length to diameter ratio (2.4), average volume (3.02 cm^3), and average length (34.6 mm) than small and medium classes, though they display an average diameter comparable to medium morphology (14.5 mm and 12.5 mm, respectively). Medium-sized *F. sciuttoi* average 19.7—23.4 mm in length and 11.5—13.6 mm in diameter (N=674) (Fig. 6D-G). They can be distinguished from the large, more elongate morphology by a lower length to diameter ratio (1.7). *F. sciuttoi* of the small morphology also display a lower length to diameter ratio equivalent to

that of the medium morphology (1.7). Small specimens average 10.9—13.0 mm in length and 6.4—7.5 mm in diameter (N=364) (Fig. 6H-K). Despite dimensional differences, examples in each of the three size classes preserve a helical ridge ornamentation that resembles modern hymenopteran cocoons (Fig. 7). Very infrequently, some specimens display dark, dendritic markings on their exterior, interpreted as rootlet traces (Fig. 6I). This is common in extant and fossil insect traces (Johnston et al., 1996; Alonso-Zarza et al., 2014).

We analyzed the micromorphology of three specimens (MOR-IV-2804-B1.14.small, -B11.13.small, -B7.12.large). In all specimens, the differences between the inner filling and outer matrix are negligible; both consist of a tan and grey micrite with sparse calcite and plagioclase clasts and clay material. The boundary between the outer matrix and the inner filling is largely discontinuous. MOR-IV-2804-B11.13.small, a small *F. sciuttoi* specimen, exhibits a thin (20 µm) discrete calcite wall (Fig. 8A, 8B). Along the outer edge of the micritic wall (external to the cast) is a discontinuous, poorly defined layer consisting of packed grey clay material with scattered larger clasts (Fig. 8A). This layer varies in thickness from 300 µm to 600 µm. The same clay-rich zone occurs in MOR-IV-2804-B1.14.small, a small morphology of *F. sciuttoi* (Fig. 8C). This specimen does not preserve the discrete micritic wall, and is instead detached from the surrounding matrix, separated by a gap. MOR-IV-2804-B7.12.large, a specimen of large morphology isolated from the matrix, preserves a thin, discontinuous dark clay rim along the outer edge of the cast (Fig. 8D).

An additional morphology of *F. sciuttoi* displays a characteristically wider morphology than other representatives at the Egg Mountain locality and elsewhere. These specimens are designated here by the wide category (Table 1, Fig. 5). Average length is typically 25.6-33.8 mm, and average diameter is 20.0-24.3 mm (N=55). They are characterized by a low length to diameter ratio (1.3) and have the largest average volume (7.26 cm^3) and average diameter (22.1 mm) amongst pupation structures of the

locality. Some specimens preserve a bumpy linear to oblique helical texture, similar to but coarser and more irregular than that observed on other more elongate ellipsoidal cocoons of *F. sciuttoi* (Fig. 9A). Four specimens were found *in situ*, sitting vertically with the long axis perpendicular with respect to bedding (Fig. 9B). This differs from the oblique to horizontal orientation typical of *F. sciuttoi*.

The micromorphology of one wide specimen (MOR-IV-2804-B16.11.FB) was analyzed. An undulating calcite boundary is present and consistent along the outer edge of the trace, separating outer and inner matrices. The outer matrix (i.e., grey indurated limestone of unit 1) and inner matrix are similar in composition and grain size; however, the outer matrix is a greyish color, while the inner matrix is tan to brown. The boundary is composed primarily of tan crystalline calcite, 500-700 μm in thickness. The clasts do not show any alignment, as in *Rebuffoichnus casamiquelai* (Genise et al., 2007). Intermittent sections of the boundary display a fine-grained matrix with sparse calcite crystals. These matrix-supported sections interrupt the coarse-grained, crystalline sections of the boundary and occasionally interfinger.

While an outer structure provided rigidity and texture to the trace and allows it to be easily distinguished from the surrounding matrix, the boundary cannot be seen with the unaided eye, a characteristic of *Fictovichnus*. Combined with the apparent absence of *Rebuffoichnus* from the locality, this confirms that these specimens are true *Fictovichnus* and not internal casts of *Rebuffoichnus* (Genise, 2016). Despite the consistently stouter morphology compared to other material at the locality, some wide specimens preserve an external helical ornamentation. This character is diagnostic of *F. sciuttoi*; as such, we treat these specimens as an additional morph of *F. sciuttoi*. The lower aspect ratio of the wide morphology of *F. sciuttoi* is aberrant from other *F. sciuttoi* here and elsewhere, though differences in size and aspect ratio do not justify resurrecting a new ichnospecies (Bertling et al., 2006).

4.2 Ichnofamily Lazaichnidae Genise, 2016

Ichnogenus *Tombownichnus* Mikuláš and Genise, 2003

Tombownichnus cf. *parabolicus* Mikuláš and Genise, 2003

Figure 11a

Material. – MOR-IV-2804; Two specimens (MOR-IV-2804-B7.13-1, MOR-IV-2804-B7.14-1) from the Egg Mountain locality of the Upper Cretaceous Two Medicine Formation.

Occurrence. – Massive grey calcareous siltstone and micritic limestone at the Egg Mountain locality (TM-006), Two Medicine Formation, Montana, USA.

Description. – *Tombownichnus* is represented by an elliptical or sub-cylindrical pit in the midsection of insect chambers. In *T. parabolicus*, the singular pit does not breach the external surface, leaving a distinctive depression. This differs from *T. plenus*, which is represented by multiple complete borings through the interior of the chamber. These traces are also not assignable to *T. pepei*, which occur in the internal face of the discrete wall of *Coprinisphaera* specimens.

Tombownichnus cf. *parabolicus* is interpreted based on 5-7 mm long indents in the midsection of two medium-sized specimens of *F. sciuttoi* from Egg Mountain (Fig. 10A). In both specimens, the depression occurs about one third of the way along the total length of the host cocoon. The shape and size of the depressions in *F. sciuttoi* described here matches that described and figured by Martin and Varricchio (2011, Fig. 5D). Specimens are recovered from JHPs 6 and 9.

4.3 Unassignable trace fossils

Several instances of associated or cross-cutting cocoons occur throughout the measured section (Fig. 10B, 10C). Two specimens of small morphology cocoons intersecting, fused, or embedded with large morph cocoons are noted (Fig. 10B). Both the large and small morphologies are assignable to *F. sciuttoi* based on the presence of an external raised helical texture (Fig. 10B). Specimens are recovered

from JHPs 1 and 7, respectively. *Fictovichnus* of similar sizes are also preserved intersecting or cross-cutting one another. At least four instances of similarly sized intersecting cocoons are observed throughout the section, and all instances are represented by the large morphology. They intersect one another at angles ranging from 90-150° (Fig. 10C). Specimens are recovered from JHPs 6, 7, and 10.

4.4 Cylindrical burrows

Burrows collected throughout the section vary in size, but most are 1.0–2.6 cm diameter, 10–15 cm long (N=138). They are rarely associated directly with pupation chambers and are often truncated and highly fractured, in part due to the excavation process. Similar sized burrows are associated with pupation chambers in a nearby outcrop (Martin and Varricchio, 2011). Smaller burrows (3-5 mm diameter) are less common. Most are badly fractured and have been described out of geologic context, making ichnological identification difficult. However, small burrows here resemble those seen in nearby outcrop tentatively assigned to *Skolithos* by Martin and Varricchio (2011). Distinguishing burrows from root traces is difficult due to truncation and fracture in most specimens. Those specimens that are better preserved do not display tapering or branching characteristic of root traces. Other rhizoliths are present but scarce at the locality; some root traces occur on fossil pupation structures (Fig. 6I). Burrow morphologies are consistent with those of extant sand wasp species (Bembicinae). Smaller species, such as *Microbembix*, construct burrows with a diameter of 5 mm, while burrows of larger species such as *Stictia carolina* can be up to 2 cm in diameter (Evans, 1966). Wasps typically do not line the burrow and only some species backfill selected portions; this may contribute to the lack of preservation.

4.5 Pallichnidae indet.

Members of this unknown ichnotaxon are identified as small half-spherical structures with a distinctive brown coating, colloquially dubbed “Brownies” by Egg Mountain field crew. Specimens are mostly found emplaced in the sediment with the half-spherical structure extending down into the substrate. This preservation resembles that of *Feoichnus* (Krause et al., 2008), though the discrete wall is not observable macroscopically and the characteristic root notch is absent, among other differences. The defining characteristic of these traces is a brown outer rind. Specimens are not used in sedimentation rate analysis. A detailed description is in preparation (Panascí et al., 2016; Panascí, pers. comm., 2019).

5. Trace abundance and diversity

The overall cocoon abundance per JHP is presented in Figure 12. Abundances from JHP 1 and JHP 2 were not fully sampled and are therefore underrepresented and not useful in comparing JHP abundances. Traces are present throughout all jackhammer passes; there are no passes without traces (Fig. 11). Trace abundance is relatively low in the top 60 cm of the section, representing 21% of all traces. The remaining 79% of all traces are concentrated in the bottom 90 cm of the section. JHP 9 records the highest abundance of all passes with 628 traces representing 17.2% of all traces in the section. In JHP 9, 288 medium pupae were found in one 2x8 m section. Similarly, 224 medium pupae were collected from the same area of the quarry, but stratigraphically higher in JHP 8. These horizons are contained in a lateral area of 4x8 m with a vertical section of 0.6 m. In this section, a total of 1228 cocoons occur, or 34% of all traces from the main quarry.

The abundance of each cocoon morphology throughout the section is presented in Figure 12 and Table 2. Medium *F. sciuttoi* are the most common, with specimens present in all passes and comprising 53% of all traces. They are the dominant trace in all passes with the exception of JHP 1 and JHP 5 where small *F. sciuttoi* are most abundant. The medium morphology ranges in abundance from N=22 in JHP 5

to N=467 in JHP 9 (Table 2). The minimum relative abundance of the medium morphology is 20% in JHP 1, the maximum 76% in JHP 8. Small *F. sciuttoi* are consistently the second most common trace except in JHP 2. The small morphology is present in all passes, making up 32% of all traces. Their minimum abundance is in JHP 4 (N=29) and maximum abundance is in JHP 12 (N=203). Minimum relative abundance is in JHP 2 (20%) and maximum is in JHP 1 (55%). Large, elongate *F. sciuttoi* are present in all passes and are consistently less abundant than medium and small morphologies, representing 8% of the total traces in the section. The wide morphology shows the most sporadic trend in abundance. They are concentrated towards the top half of the section, with their greatest abundance in JHP 5 (N=54) and a maximum relative abundance of 21% (JHP 4). They are noticeably absent in JHPs 8 through 11, until the very bottom of the measured section where they constitute just 3% of traces (Table 2).

Trace diversity generally decreases down section (Fig. 13). From the top of the section through JHP 6, all size categories are represented. JHPs 2, 5, and 6 record the most equal distribution of trace categories (Fig. 13). Beginning at JHP 7, there is a noticeable decline in abundance of the two largest traces, the elongate and wide morphologies of *F. sciuttoi* with a corresponding increase in the relative abundance of medium *F. sciuttoi*. JHPs 8 and 9 display the highest abundances of medium *F. sciuttoi* which correspond to passes of lowest diversity (Table 2).

6. Discussion

6.1. Background on burrowing wasps

Modern sand wasps (Hymenoptera: Bembicinae) provide model organisms for equating ethological inferences of the insect traces at Egg Mountain. Sand wasps are holometabolous, meaning they undergo full metamorphosis. A larva hatches from an egg, feeds on provisions in the cell, and

undergoes an inactive pupal stage in a cocoon, typically woven from silk and occasionally constructed with sand grains (some Bembiciniae and Dryinidae) before emerging as an adult. Most species of sand wasps overwinter—they undergo the seasonal pupal stage and are univoltine (have one brood per year) (Evans, 1966). Females construct burrows and lay their eggs on flies, weevils, or other prey items. A cell is created for the prey item at the terminus of a burrow, typically at depths of 10-30 cm (Evans, 1966). However, cells have been found as shallow as 0.8 cm and as deep as 60 cm (Evans and Evans, 2007). Cells are often constructed horizontally, and burrows are typically oriented obliquely with respect to the ground surface but can vary from sub-horizontal to sub-vertical (Evans, 1966) (Fig. 14). Some species close off the cell from the main burrow or cap the burrow entrance. In general, larger wasp species tend to construct larger pupation structures and, amongst sand wasps, burrow at greater depths (Evans, 1966). However, additional environmental factors also play a role in cocoon size and burrow depth.

Most sand wasps prefer bare, dry, friable soils in open habitats often devoid of extensive vegetation cover (Genise, 2000; Evans and O'Neill, 2009), but burrows have been found in a variety of substrates (Evans and Evans, 2007). While substrate preference varies widely between different species, suitable substrate with ample prey or food sources is probably a limiting factor in the distribution of many fossorial wasps (O'Neill, 2001, p. 160). Nesting site selection is key for offspring ability to thermoregulate and control water balance (O'Neill 2001, p. 167). Burrow depth is a factor of the compactness and moisture in the soil; loose, dry soil enables deeper burrowing (Kurczweski, 2003; Evans and Evans, 2007). Additionally, burrow depth likely reflects the subsurface temperature and moisture; moist (but not saturated) horizons at depth probably provide a temperature buffer on the order of 25-30°C for wasp offspring (Willmer, 1982; O'Neill, 2001). Pupa size varies amongst species and may also be related to sexual dimorphism of the same species. Female larvae of some taxa receive several prey items in the cell while males receive fewer; this dimorphism is reflected in both cell size

and cocoon size, where longer and larger larvae receive more provisions and produce females (Evans et al., 1980; Kurczweski, 2003; Evans and Evans, 2007; Martin, 2013), though size may also simply reflect different sized prey items in provisioning the nest (e.g., Evans, 1966; Evans and O'Neill, 2009). A single species of sand wasp (e.g., *Bembix*) may prey on insects of up to 28 different orders (Evans and O'Neill, 2009).

Of the structures in a typical sand wasp nest (Fig. 14), cocoons constructed with silk and soil materials have the most potential for preservation, while simple, unlined excavations such as burrows and cells are usually not preserved (Genise and Bown, 1994; Genise and Cladera, 2004). This trend is reflected in the Egg Mountain assemblage, as internal casts of cocoons are most abundant.

6.2 Fictovichnus *trace-makers*

The size, shape, surface texture, and micromorphology of *F. sciuttoi* specimens found at Egg Mountain are comparable to those found elsewhere, and as such are interpreted as the cocoons of burrowing sphechid, pompilid, or crabronid wasps (Genise et al., 2007; Genise, 2016). They are most similar to those described by Genise et al. (2007) from the Upper Cretaceous Bajo Barreal Formation (Cenomanian; Suárez et al., 2014) and Allen Formation (Campanian-Maastrichtian; e.g., Leanza and Hugo, 2001) of Argentina and the Paleocene-Eocene Claron Formation of the United States (Bown et al., 1997). Argentinian specimens similar to the large morphology described here were associated directly with sauropod dinosaur eggs (Genise and Sarzetti, 2011). *F. sciuttoi* have also been described from the Eocene of France, where three different size morphologies are described alongside reptilian eggs (Kuntz, 2012). Fossil cocoons bearing similar external ornamentation (i.e., helical ridges and lobes) are described from the Eocene of England (Edwards et al., 1998) and the Cretaceous-Paleogene of Uruguay (Alonso-Zarza et al., 2011). Two of the morphologies described by Edwards et al. (1998)

match the proportions of medium and large *F. sciuttoi* from Egg Mountain. Scarring is interpreted as the constricted area that connects the chamber to other chambers or tunnels, as seen in *F. gobiensis* (Alonso-Zarza et al., 2014). Truncation is interpreted here and by others (Genise et al., 2007) as an adult emergence trace, where the cap, typical of an enclosed cocoon, is not preserved.

The thin, discrete external boundary observed in thin section of some *F. sciuttoi* here is similar to that of the best-preserved specimens from the Cretaceous of Argentina (Genise et al., 2007, Fig. 6A; Genise and Sarzetti, 2011, Fig. 3B) (Fig. 8A, 8B, 8D). However, unlike the Argentinian material, this structure is not continuous through the entirety of the cross section (Fig. 8D). The clay-rich zone observed in some specimens is analogous to that described by Johnston et al. (1996) in the original description of *Fictovichnus* and interpreted as mechanical artifact of the pupation chamber, formed by the trace-maker as clay and silt became densely packed into open pore spaces in the sediment (Fig 9a, 9c). Additionally, some specimens here are detached from the host matrix, a mode of preservation seen in some specimens of *F. gobiensis* from the Miocene of Spain (Alonso-Zarza et al., 2014, Fig. 3B) (Fig. 8C).

While the more elongate morphologies (i.e., small, medium, large) more closely resemble wasp cocoons, the trace-maker of the wide morphology cocoons is less certain, and interpretations here are speculative. The helical ornamentation on some specimens is strongly suggestive of wasp cocoons. However, most hymenopteran cocoons are slender and tapering, though some exhibit wider dimensions (Genise, pers. comm., 2018). Some soil-dwelling coleopteran pupation chambers may be stout, particularly those of some Scarabaeids. The thickness of the boundary casts doubt on a hymenopterous trace-maker, as the wall of wasp cocoons is typically much thinner (e.g., Genise et al., 2007). The morphology of some *Fictovichnus gobiensis* from Laetoli described by Genise and Harrison (2018) is similar to *Fictovichnus* described here, and the authors tentatively assign the trace-makers to

Tenebrionid, Curculionid and/or Scarabaeid beetles (Genise and Harrison, 2018, Fig. 1E, K). Some members of these groups, including some weevils and chafers, favor similar environments as burrowing wasps, as their trace fossils (*Rebuffoichnus, F. gobiensis*) are consistently associated with *F. sciuttoi* as components of the *Celliforma* ichnofacies (Genise, 2016). If the wide morphology *Fictovichnus* represents one of these, they still may suggest similar broad paleonenvironmental interpretations (Genise, 2016). Back-filled burrows in herbivorous dinosaur coprolites from nearby deposits of the Willow Creek Anticline are attributable to coleopterans (Chin and Gill, 1996; Chin, 2007) and offer another line of evidence for the presence of coleopteran trace-makers.

6.3 Tombownichnus *and unassignable traces*

The ichnogenus *Tombownichnus* (represented by two ichnospecies, *T. parabolicus* and *T. plenus*) is interpreted as borings of cleptoparasitic insects occurring in the walls of another chambered insect trace fossil. *T. parabolicus* shares a similar interpretation as *T. plenus*; the latter is a complete boring through the external surface of the host chamber, while the former is a failed perforation attempt (Mikuláš and Genise, 2003). Trace-makers have been attributed to parasitic wasps or wasp larvae (Mutillidae, Sapygidae, Chrysididae, Scoliidae, or Tiphiidae), blister beetles (Meloidea), or flies (Bombyliidae) (Mikuláš and Genise, 2003; Genise, 2016, p. 372-375). *Tombownichnus* occurs in several insect trace fossils, including *Rebuffoichnus* (pupation chambers of chafers and weevils), *Coprinisphaera* (dung beetle brood balls), and *Teisseirei* (moth pupation chambers). Most notably, *T. parabolicus* occurs in nearby outcrops in specimens of *Fictovichnus sciuttoi* and *Rebuffoichnus* (Martin and Varricchio, 2011). In the same outcrops, small diameter burrows are connected to *F. sciuttoi* and *Rebuffoichnus* specimens, which may also represent traces of cleptoparasites (Martin and Varricchio, 2011).

Along with *Tombownichnus* observed at the locality, associations and cross-cutting of small and large cocoons may represent parasitic behavior (Fig. 10B). Both cleptoparisitism (stealing of food or prey items) and parasitoid behavior (consuming of host) on burrowing wasp nests has been observed in many holometabolous insects, including flies and other parasitoid wasps. Predatory holometabolous insects attack the wasp during its larval or pupating (cocoon-bearing) stage, usually to deposit an egg. The egg will hatch into a larva that feeds on the provisions of the host wasp (Evans and O'Neil, 2009). Some parasitoids of the family Chrysididae (cuckoo wasps) lay eggs in host wasp cells; the parasitoid larvae wait until the host larvae spins a cocoon before feeding on the host (Evans and Eberhard, 1970; Genise, 2016). In other members of Chrysididae, the parasitic larva consumes the host pupa and spins a cocoon inside the cocoon of the host (Evans and Eberhard, 1970; Genise, 2016). This behavior has been observed in the parasitic sand wasp *Nysson*, where a parasitic larva will spin a cocoon virtually identical to the host but often smaller (Evans, 1966). Similarly, bee-flies of the genus *Hyperalonia* (Bombyliidae) will wait for the host larva to pupate before consuming the host and pupating within their cocoon (Evans and Eberhard, 1970, p. 230). Thus, the intersecting small and larger cocoons more likely records parasitoid behavior, where the parasitic taxon consumes the host pupa within its cocoon, rather than simply stealing provisions of the cell before the host larva has a chance to feed and spin a cocoon. Similar associations of small cocoons inside large cocoons have been documented from the Paleocene-Eocene Claron Formation (Bown et al., 1997). Cocoons ranging from 3.5 to 7.5 mm in length are found within 18 to 32 mm long cocoons. The larger morphs display a helical external pattern, which the authors cite as evidence for wasps, while the smaller cocoons show a smooth exterior. The trace-makers of the small cocoons are interpreted to be wasp parasites, which could be other wasps, hymenopterans, or dipterans (Bown et al., 1997). Additionally, Martin and Varricchio (2011) describe similar co-occurrences of small cocoons within larger cocoons from nearby outcrop in the Two Medicine

Formation, which they attribute to parasitoid insects, the oldest such behavior recorded in the fossil record.

Cross-cutting cocoons of similar size and morphology of pupal structures likely represent the same trace-maker. Therefore, this most likely implies multiple generations of pupation on the same horizon. These behaviors have been documented in extant wasps and may represent multivoltine patterns (more than one generation per year) that is observed some in extant wasps (Evans and Eberhard, 1970), though overlapping of traces more likely suggest multiple generations of nesting over extended periods (Genise et al., 2013). Alternatively, cross-cutting or closely associated cocoons of similar sizes may reflect usurpation of a nest by different females. Usurpation may be noncompetitive, as when a wasp takes over the space remaining in a nest after the original occupant vacates permanently (Krombein, 1976), or competitive and lead to fighting amongst females, as when one female takes over after the brood of the female that constructed the nest has emerged (O'Neill, 2001, p. 181 and references therein). Nest usurpation is often intraspecific (Field, 1992; O'Neill, 2001). Thus, associated cocoons of similar sizes may reflect nest usurpation. Similar specimens are described from a nearby outcrop (Martin and Varricchio, 2011).

6.4 A depauperate Celliforma *Ichnofacies?*

The Egg Mountain locality preserves an ichnoassemblage consisting of four (possibly five) morphologies of insect pupation structures, corresponding to different species of soil-nesting insects. The assemblage is dominated by *Fictovichnus sciuttoi*, interpreted to be burrowing wasp cocoons (though the wide morph may represent coleopterans). Notably, there is a distinct absence of traces definitively referable to bees (e.g., *Celliforma, Palmiraichnus*), beetles (*Rebuffoichnus*), and moths (*Teisseirei*), unlike other deposits of the Two Medicine Formation that represent the *Celliforma*

ichnofacies (Martin and Varricchio, 2011). The observed assemblage may represent a depauperate *Celliforma* ichnofacies, with only one dominant ichnotaxon and several secondary components, including burrows, rhizoliths, vertebrate coprolites, pellet masses, and evidence of vertebrate nesting consisting of partial to complete eggs and eggshell concentrations (Genise et al., 2010). Alternatively, the monospecific assemblage may not represent the *Celliforma* ichnofacies; nonetheless, potentially five different insect taxa are represented. If indeed the majority of cocoons represent those of solitary wasps, the paleoenvironmental conditions favored by wasps are the same conditions proposed for the *Celliforma* ichnofacies (Genise, et al., 2010; Genise, 2016). Further, a single trace has a variety of implications. Wasps prefer to burrow in well-drained, friable soils with little vegetation cover. Cell emplacement is largely controlled by subsurface conditions, independent of size of the wasp, though larger wasp species tend to construct larger cocoons, and in Bembicinae, larger taxa tend to burrow deeper (Evans, 1966).

Some specimens here assigned to *F. sciuttoi* do not show the characteristic external helical weave or lobed pattern (Fig. 6K). The lack of helical ornamentation on some Egg Mountain specimens may reflect differences related to preservation (e.g., adhering matrix). However, these specimens may represent the ichnospecies *F. gobiensis*, where the only definitive distinguishing characteristic is a smooth external texture compared to the helically ridged pattern of *F. sciuttoi*. A similar taxonomical issue is encountered at the Pliocene hominid site, Laetoli; Genise and Harrison (2018) describe thousands of *F. gobiensis*, identifying a select few specimens with helical texture, normally a characteristic of *F. sciuttoi*. Based on the scarcity of these textured specimens, the authors conserve the *F. gobiensis* designation. Similarly, we do not disregard the importance of surface texture, but instead elect not to formally treat a small subset of traces that do not display texture, which could have been altered by taphonomic processes. Regardless, designating these traces as *F. sciuttoi* (wasps) or *F.*

gobiensis (beetles, chafers, or weevils) yield broadly the same paleoenvironmental implications and are found within the *Celliforma* ichnofacies (Genise, 2016).

6.5 Paleoenvironment

The suite of trace fossils at Egg Mountain suggests the presence of three or four wasp species and potentially a fifth unknown insect species. The abundance of fossorial wasp pupation structures prescribes the nature of the local environment: friable substrate well above the water table with suitable exposure to the substrate surface. The abundance of traces in all jackhammer passes also indicates that a suitable environment for insect nesting persisted throughout the time of deposition. The environment persisted through at least the measured 1.5 meters (and likely more) of stratigraphy fairly continuously. Higher concentration of stout and large pupation structures may reflect subtle changes in substrate, water table depth, or other environmental nuances. The absence of the stout and elongate *F. sciuttoi* from particular horizons (e.g., JHP 7 through 11) may reflect unfavorable conditions for larger insect species, as exemplified in Bembicinae, where larger wasps tend to burrow deeper (Evans, 1966). Subtle changes in relative pupae abundance may thus be due to local environmental changes favoring different taxa over others. High nest density in a localized area, such as the 2x8 meter extent in JHP 8 and 9, has been documented in extant wasp populations, where the number of cells exceeds 30 per square meter (Evans, 1966). Other nest aggregations exceed 300 cells in 0.75 x 1.5-meter area (O'Neill, 2001). Evans (1970) documented several species occupying the same area in Jackson Hole, Wyoming, with up to four different species in the same 10-meter plot (O'Neill, 2001, Fig. 6-7). Similar nesting densities have been observed in other apocritans; alkali bees (of the genus *Nomia*) are native to deserts and semiarid environments with well-drained soils and have been observed nesting in aggregations of 400 nests per square meter (Linsley, 1958; Cane, 2007). High abundances in certain passes (e.g., JHP 9) may suggest

multiple brooding seasons or high population densities during one short span, such as during the dry season (Martin and Varricchio, 2011; Genise, 2016, p. 581).

Abundant insect (primarily wasp) cocoons and nesting traces suggests abundant insect prey items for nest provisions, as modern wasps seem to be limited to nesting locales based on prey availability (in addition to abiotic factors) (O'Neill, 2001). In this sense, the abundance of dinosaur nesting events and eggshell material may explain the abundance of wasp cocoons; insects feeding on decaying eggs and other organic material (first posited by Horner, 1987) would have attracted wasps that provision their nests with insects (Genise and Sarzetti, 2011). Another possibility is that both fossorial wasps and oviparous organisms were drawn to similar soil conditions. A relatively stable depositional environment with friable soil conditions that allow for reworking would be conducive not only to nest construction, but also for rearing of vertebrate eggs. Most insects prefer to construct burrows and brooding chambers in well-drained soils that are perennially or seasonally above the water table (Genise, 2000; Genise, 2004; Genise et al., 2010). These environmental parameters would be favorable to egg-laying organisms, especially those that partially bury eggs in sediment such as *Troodon formosus* (Varricchio et al., 1999) or with fully buried clutches as in crocodilians, squamates, and most dinosaurs (Deeming, 2006). The suitability of the environment for wasps and potentially other species of burrowing insects may help explain the presence of the potentially insectivorous iguanamorph lizard *Magnuviator ovimonsensis* (DeMar et al., 2017), and the small metatherian *Alphadon*, and multituberculate *Cimexomys* (Montellano, 1988; Montellano et al., 2000), which may have preyed upon the wasps, their larvae, or other insect prey items the wasps would have used in provisioning their nests. The abundance of insect nests may also explain the presence of dinosaur nesting structures and abundant eggshell material.

The assemblage at Egg Mountain records a possible association of the *Celliforma* ichnofacies with vertebrate nesting events. Additional associations of vertebrate eggs and single or associated ichnotaxa common to the *Celliforma* ichnofacies include the Campanian-Maastrichtian Allen Formation (Genise and Sarzetti, 2011), the Campanian-Maastrichtian Djakhota Formation (Johnston et al., 1996), and Eocene deposits of France (Kuntz, 2012). Aside from the Two Medicine Formation, the only additional association of the *Celliforma* ichnofacies and vertebrate eggs are recorded from the Campanian-Maastrichtian Mercedes Formation of Uruguay where bee traces (*Celliforma spirifer*, *C. germanica*) dominate (Faccio, 1994; Alonso-Zarza et al., 2011). In the Two Medicine Formation, the ichnoassemblage is dominated by traces attributed to wasps (*Fictovichnus sciuttoi*), while bee traces are notably absent (though bee traces may occur in nearby strata; see Martin and Varricchio, 2011). The differences in trace fossil and vertebrate egg assemblages between the Two Medicine Formation and the Mercedes Formation may suggest different climatic factors or environmental preferences for nesting between maniraptoran and sauropod dinosaurs, respectively. Associations of vertebrate nesting and insect trace fossils (which may represent the *Celliforma* ichnofacies) are represented elsewhere. These include *Fictovichnus sciuttoi* and sauropod eggs from the Campanian-Maastrichtian of South America (Genise and Sarzetti, 2011), *F. gobiensis* and dinosaur eggs from the Campanian-Maastrichtian of Asia (Mikhanilov et al., 1994; Johnston et al., 1996), and cf. *Fictovichnus* and reptilian eggs from the Eocene of France (Kuntz, 2012). These examples provide a framework for future work that may enlighten environmental context of the evolution of vertebrate reproductive strategies.

6.6. Depositional processes

Egg Mountain stratigraphy is devoid of primary sedimentary structures (e.g., bedding, depositional contacts). Limestone horizons generally are lenticular and not laterally continuous, display

sharp upper contacts and decimeter-scale relief on the upper surface, all characteristics of pedogenic carbonates (Retallack, 1988). Peds, cutans, and other hallmarks of developed paleosols are lacking while root traces and nodules are rare, suggesting incipient paleosol development (Retallack, 1988; Varricchio et al., 1999). However, abundant insect pupation structures and burrows attest unequivocally to the presence of a paleosol (Genise, 2016). The absence of distinct, continuous soil horizons suggests paleosol development was weak, representing an inceptisol (Retallack, 1988). Additionally, the interfingering of pedogenic carbonates with detrital siltstones suggests deposition was frequent enough to disrupt paleosol development (Alonso-Zarza, 1998; Kraus, 1999). The abundance of calcite and infrequent nodules suggests well-drained, alkaline conditions (Retallack, 1988) and corroborates previous interpretations of the paleoenvironment of the area (Lorenz and Gavin, 1984; Horner, 1987; Retallack, 1997; Martin and Varricchio, 2011). While the presence of paleosols is unequivocal, isotopic evidence suggests phreatic processes were involved in limestone formation and in overprinting original structures in the form of crystalline calcite infill of some sediment pore space, ichnofossils, root traces, and eggshell (Moore et al., pers. comm., 2016).

In the absence of well-developed paleosols, it is likely that bioturbation is the primary factor in the destruction of original bedding. Traces and burrows occur throughout the measured section consistently and as discrete structures, and overlap is infrequent (Bioturbation Index 3, or moderate; Taylor and Goldring, 1993; Genise et al., 2004). Abundant traces suggest an absence of major sediment pulses sufficiently large enough to prohibit thorough colonization. With no distinct omission in trace abundance, deposition events were certainly less than burrows lengths (10-30 cm on average for extant wasps, maximum 14 cm based on preserved burrows), and less than the 12.5 cm jackhammer passes. If deposition events were greater than the jackhammer pass depth and burrow depth, a sediment band absent of traces would be expected throughout the section. Additionally, we observe cocoons of similar

sizes (probably of the same producer) at very different depths. This variation in cocoon emplacement is not expected in extant wasps, as the same species at the same site emplaces its cells at approximately the same depth; there are no cases at the same site where cocoons would be separated by 1.5 meters, since soil conditions vary at depth clines (Retallack, 2001; Genise, 2016). Wasps place cells at approximately the same depth relative to the soil surface and the water table, so cocoons at different horizons track the accumulation of sediments over time. Thus, abundant traces throughout the section and lack of erosional contacts are indicative of relatively slow, consistent deposition and cumulative paleosols (Kraus, 1999). This relationship is seen more classically in marine settings, where low sedimentation enables thorough bioturbation of a substrate, and lack of bedding planes suggests continuous deposition (e.g., Howard, 1975). Particularly high abundances on a single horizon (e.g., JHP 9) may reflect otherwise unrecognizable hiatuses or periods of low sedimentation. Conversely, a relatively low abundance of traces in a JHP (e.g., JHP 4 and 5) may reflect a relatively higher rate of sedimentation during that interval. Three examples of cross-cutting cocoons occur in passes with relatively high abundance of traces (JHP 6, JHP 7). It is likely those passes represent extended periods of little deposition, thus increasing the potential for multiple brooding seasons on the same horizon and possibly explaining the examples of cross-cutting traces in these passes.

The preservation of cylindrical burrows and pupation structures as internal casts suggests passive filling. Additionally, the presence and abundance of fragile insect pupation chambers, particularly with minute ornamentation, reflects a largely autochthonous or parautochthonous assemblage. This is supported by the presence of nesting horizons and egg clutches (Horner, 1987; Varricchio et al., 1999), unabraded eggshell (Oser and Jackson, 2014), angularity of volcanoclastic sediments (Varricchio et al., 1999), and the extreme representation of terrestrial organisms and paucity of aquatic forms. Egg Mountain deposition and infilling of insect nests may have been brought on by seasonal flooding of the

area. Destruction of nests caused by flooding has been documented in extant burrowing apocritan populations (Fellendorf et al., 2004).

7. Conclusions

1) The trace fossil assemblage at Egg Mountain is comprised of small, medium, large, and wide morphologies of *Fictovichnus sciuttoi*, interpreted as the cocoons of fossorial wasps and potentially beetles, and represent a depauperate *Celliforma* ichnofacies. Associated and cross-cutting cocoons of different sizes along with *Tombownichnus* may further represent the oldest record of insect parasitism.
2) Hymenopteran trace fossils support a semi-arid climate and seasonality inferred during Egg Mountain deposition. Abundant wasp trace fossils indicate a sparsely vegetated subaerial environment with workable, well-drained soil conditions favorable for both fossorial insect pupation and oviparous vertebrate nesting. Pervasive insect traces suggest ample prey opportunities for abundant mammals and lizards at the locality.
3) In the absence of primary sedimentary structures and definitive paleosol horizons, trace fossil abundance and emplacement reflect sedimentological processes; pervasive insect nesting structures in bioturbated floodplain overbank deposits suggest the cumulative development of paleosols and relatively slow, continuous deposition. The continuous record of insect traces represents an absence of major depositional events, while horizons with greater abundances of traces may suggest more extended periods of subaerial exposure.
4) The continued and abundant presence of insect trace fossils together with mammals, articulated lizards, and a variety of vertebrate nesting events through the section highlight Egg Mountain as an exceptional window into terrestrial ecosystems of the Late Cretaceous of North America.

5) Components of the *Celliforma* ichnofacies here and elsewhere occur in association with vertebrate nesting events. Differences in the taxonomic diversity of the *Celliforma* ichnofacies representing different trace-makers in different egg-bearing localities may reflect subtle environmental preferences and provide environmental context to the evolution of reproductive behaviors in different oviparous groups.

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Data Availability

Supplementary Information 1 – Measurements used size distribution of traces and descriptive statistics.

Supplementary Information 2 – Distribution of trace fossils from field collections assigned to jackhammer passes.

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Figure 1. Locality map of field area at the Willow Creek Anticline, Two Medicine Formation near Choteau, Montana, U.S.A. The Egg Mountain locality (EM) is indicated with arrow. Figure modified from Rogers et al. (2010).

Figure 2. Stylized stratigraphic section for the Egg Mountain locality (left) with inset of the measured section (right). Measured section is marked by a massive calcareous siltstone and interbedded micritic limestone horizons. Schematic jackhammer passes (JHPs) are superimposed and specimens are assigned to JHPs to track stratigraphic position. Passes average 12.5 cm in thickness. The level at which fossil elements occur is approximate. *Fictovichnus sciuttoi* represents small, medium, and large size classes, and wide *Fictovichnus* represents the consistently stout morphology. Other fossils not described in the key but found throughout the section include *Orodromeus* isolated and associated elements, isolated eggshell, indeterminate bone fragments, hadrosaur teeth, tyrannosaurid teeth, rare *Troodon* teeth, and dromaeosaurid teeth.

Figure 3. Photos of the study site. (a) Unit 1 defined by 50+ cm thick limestone. Photo taken from the north end showing the thickest area of the unit. Lower contact of of Unit 1 is not visible in this photo. (b) Irregular relief of limestone layer in Unit 1 protruding through siltstone. Topography in photo represents the top of JHP 12. Note the competency contrast between the top of the limestone horizon and the siltstone. (c) Discontinuous limestone of Unit 2 visible in the east wall of main quarry. Abbreviations: Ls, micritic limestone; Sltst, calcareous siltstone.

Figure 4. Photographs of the quarry at the Egg Mountain locality. (A) Photograph of quarry from the north. Note the thick rusty limestones in the foreground, which poke through the siltstone in the main

quarry towards the southern quarry wall. A smaller discontinuous limestone lens is visible in the east wall of the main quarry (see Figure 4c). (B) Grid system of the main quarry set up 11 m north by 7 m west (N1-11/W6-12). Specimens were collected and their lateral position was measured using this system. Each quadrant is one square meter. Abbreviations: MQ, main quarry; UQ, upper quarry; Ls, micritic limestone; Sltst, calcareous siltstone.

Figure 5. Fossil pupation structure size distribution. Traces sort into four categories based on length and diameter measurements.

Figure 6. Exemplar *Fictovichnus sciuttoi* from the Egg Mountain locality. (A) MOR-IV-2804-B1.10-1, Large morphology with ridged ornamentation and subtle curvature. (B) MOR-IV-2804-B1.10-2, Large morphology with ornamented texture. Top arrow points to scar, bottom arrow denotes flattened, oval, smooth area. (C) MOR-IV-2804-B1.10-3, Large morphology with lobate texture. (D) MOR-IV-2804-B5.15-1, Medium morphology in top view (left) to show truncation (arrow). Same specimen in lateral view (right). Note asymmetry, tapered extreme, and flattened, oval, smooth area (arrow). (E) MOR-IV-2804-B5.15-2, Medium morphology with subtle helical ornamentation. Arrow denotes truncation, interpreted adult emergence trace. (F) MOR-IV-2804-B5.15-3, Medium morphology showing asymmetry and tapered end. (G) MOR-IV-2804-B5.15-4, Medium morphology with defined helically arranged ridged ornamentation. (H) MOR-IV-2804-B3.12-1, Small morphology with subtle ornamentation and crystalline preservation. (I) MOR-IV-2804-B9.12-1, Small morphology with root traces. Arrow denotes truncation. (J) MOR-IV-2804-B3.12-2, Small morphology with fine helical ornamentation. (K) MOR-IV-2804-B13.16-1, Small morphology cocoon with smooth texture and crystalline preservation. A-K all to same scale: 1 cm.

Figure 7. MOR-IV-2804-B16.15-1, a medium *Fictovichnus sciuttoi* (left) showing helically arranged ornamentation comparable to a modern insect cocoon (right, Hymenoptera indet.) from the open grasslands Willow Creek Anticline near Choteau, MT, USA. Scale 1 cm.

Figure 8. Photomicrographs of *Fictovichnus sciuttoi*. (A) Cross-polarized image of a small morphotype cocoon (MOR-IV-2804-B11.13.small). Dotted line marks the outer extent of the outer micritic boundary. Arrows point to the thin external wall. (B) Magnified image of inset box in (A) displaying discontinuous thin external wall (arrows). Discontinuity may reflect oblique section of external helical ridges. Image under plane-polarized light. (C) Small morph *F. sciuttoi* (MOR-IV-2804-B1.14.small) that is detached from the host matrix. As in (A), dotted line marks the outer extent of the outer micritic boundary. Image under cross-polarized light. (D) Large cocoon (MOR-IV-2804-B7.12.large) with discontinuous external wall (arrows). Image under plane-polarized light. Scale in (A), (C), and (D) 1 mm. Scale in (B) 100 µm.

Figure 9. Specimens of the wide morph *Fictovichnus* from the Egg Mountain locality. (A) MOR-IV-2804-B1.14-1 with irregular bumpy texture. (B) MOR-IV-2804-B9.11-1 showing coarse ridged ornamentation. (C) MOR-IV-2804-B3.12-3, a complete specimen with smooth surface and exemplary stout morphology. (D) Wide *Fictovichnus* display vertical orientation (top of photo is younging direction). Structures are outlined in black for emphasis. (E) Photomicrograph of one wide *Fictovichnus* specimen (MOR-IV-2804-B.16.11.FB) under cross-polarized light showing calcite boundary between light brown micritic inner matrix (left) and darker outer matrix. Scale 1 cm in (A), (B), (C), and (D), 1 mm in (E).

Figure 10. Traces within traces from Egg Mountain. (A) Two specimens of *Tombownichnus* cf. *parabolicus* characterized by an ovoid indentation in a medium *Fictovichnus sciuttoi* (left, MOR-IV-2804-B7.13-1; right, MOR-IV-2804-B7.14-1). (B) Two examples of small cocoons cross-cutting medium morph cocoons (left, MOR-IV-B3.12-4; right, MOR-IV-2804-B1.10-4). Note the helical ornamentation on both the small and medium cocoons (arrows). (C) Two large cocoons in close association (MOR-IV-B1.10-5). Scale 1 cm.

Figure 11. Trace fossil abundance throughout the main quarry at the Egg Mountain locality. The abundances represent the number of all four morphs of *Fictovichnus sciuttoi* recorded for each JHP. Passes 4 and 5 are markedly low, while JHP 9 displays the single highest density of traces of all passes. Data labels are presented as number of pupation structures per jackhammer pass, represented by a number and the corresponding percentage relative to total traces throughout the section. Note that JHP 1 and 2 may not reflect actual abundance as those horizons were not fully sampled.

Figure 12. Relative abundance of different fossil cocoon morphologies throughout the main quarry. Medium and small *Fictovichnus sciuttoi* are consistently the most abundant throughout the section and are present in all jackhammer passes. Large and wide *F. sciuttoi* display a notably lower abundance or a completely absent from JHP 7 through JHP 11. Note that JHP 1 and 2 may not reflect actual abundance as those horizons were not fully sampled.

Figure 13. Relative trace abundance as percentage per jackhammer pass throughout the main quarry. Trace diversity generally decreases down the measured section. Medium and small *Fictovichnus sciuttoi*

are consistently dominant in all JHPs. Large and wide *F. sciuttoi* are consistently less common and are concentrated in the top half of the measured section. Note that JHP 1 and 2 may not reflect actual abundance as those horizons were not fully sampled.

Figure 14. Generalized burrow of a solitary wasp. Cell depth and presence of inner and outer closures varies by species and substrate conditions. Terminology and burrow scheme based off Evans (1966) for sand wasps.

Table 1. Descriptive statistics of fossil cocoon categories at Egg Mountain. Average diameter is calculated from measurements of both *b* and *c* axes. Volume is calculated using all three dimensions (=4/3πabc).

Table 2. Abundance of trace morphologies per jackhammer pass at Egg Mountain. First number represents number of specimens. Percentage in parentheses represents the proportion of each trace in the jackhammer pass. Italicized numbers correspond to lowest abundance or percentage for each morphology, while bold reflects highest. *Abundances in JHP 1 and 2 should not be compared due to underrepresented data.