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April 7, 2020

Assessing species diversity in a community of insects from the Cretaceous (Campanian) Two
Medicine Formation, Choteau, Montana

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Abstract

Assessing species diversity from insect trace fossils from the Cretaceous (Campanian) Two Medicine Formation, Choteau, Montana
By Maya Yamei Bradford

This study follows two previous studies (Martin and Varricchio 2010; Freimuth and Varricchio 2019) that described insect trace fossil assemblages dominated by *Rebuffoichnus sciuttoi* and associated with dinosaur nesting sites from Two Medicine Formation calcareous paleosols. The paleosols are located in the paleontologically classic Willow Creek Anticline near Choteau, Montana, which is known for its abundant dinosaur nesting traces and body fossils. This study reviews 1,010 new cocoons collected from eight different localities within the Willow Creek Anticline area. A few cocoons display evidence of parasitoid behavior in the form of bore holes (*Tombownichnus* isp.), attached thin burrows, and smaller cocoons within cocoons. The most abundant cocoon is assignable to *Fictovichnus sciuttoi* and its size class and morphology are consistent across all three studies. The community of insect tracemakers represented by the trace fossils reviewed by this study, Martin and Varricchio (2010), and Freimuth and Varricchio (2019) likely comprised of at least three discrete species.

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I. Introduction

The Willow Creek Anticline, west of Choteau, Montana, exposes outcrops of the Late Cretaceous (Campanian) Two Medicine Formation containing a remarkable history of dinosaur nesting. Many paleontological and geological studies focusing on dinosaur skeletal remains, eggs, and trace fossils at the Willow Creek Anticline have resulted in a well-known understanding of the stratigraphy and paleoenvironment of the area (Horner and Makela 1979; Horner 1984; Chin and Gill 1996; Rogers 1998; Varricchio et al. 1999; Shelton et al. 2006; Chin et al. 2009; Varricchio et al. 2015). However, insect trace fossils, which are also uniquely abundant at the Willow Creek Anticline, remain relatively less explored.

Insect trace fossils are valuable indicators of depositional environments but are apparently rare in continental sedimentary rocks. However, these trace fossils may be more under-recognized and under-diagnosed, rather than actually rare. Such trace fossils and their associated calcareous paleosols provide important paleoecological insights into local paleohydrology, vegetative cover, trophic relationships, and seasonality in ancient ecosystems (e.g. Genise 2016; Chin and Gill 1996). Additionally, the Cretaceous is a critical period for understanding the evolution of insect behavior, as key clades, including phytophagan beetles and aculeate hymenopterans, evolved during this time alongside flowering plants (Genise et al. 2007; Genise et al. 2020). Thus insect traces at the Willow Creek Anticline may yield critical information on Campanian paleoenvironment as well as the ecological and evolutionary relationships of insects and Cretaceous dinosaurs (e.g., Chin and Gill 1996).

Insect fossil cocoon-containing rock assemblages are particularly rare in the Cretaceous fossil record, with only nine known examples so far (Johnston et al. 1996; Genise et al. 2002;

Genise et al. 2007; Martin and Varricchio 2010; Genise and Sarzetti 2011; Lee 2018; Freimuth and Varricchio 2019; Genise et al. 2020). Of these reported occurrences, two are from localities within the WCA, nicknamed “Pete’s Pupa Peninsula” (Martin and Varricchio 2010) and “Egg Mountain” (Freimuth and Varricchio 2019).

This study follows previous reports of insect trace fossils from the middle subfacies of the Willow Creek Anticline (Martin and Varricchio 2011; Martin and Varricchio 2015; Freimuth and Varricchio 2019). As mentioned before, in-depth studies of insect trace fossils in the Willow Creek Anticline were limited to two localities: Pete’s Pupa Peninsula (Martin and Varricchio 2011; Martin and Varricchio 2015) and Egg Mountain (Freimuth and Varricchio 2019). In this study, I documented 1,010 insect trace fossils from eight different localities in the Willow Creek Anticline, including those from seven previously unreported localities.

For this study, I examined fossil cocoons and burrows that had been collected from eight discrete localities within the Willow Creek Anticline during the 2019 field season (June-July). In my analysis, I recorded their morphology and size, with the intention of testing whether this information could reveal the number and variety of insect species represented across the eight localities. Before beginning, I anticipated that I might not be able to discern between species using these data and that my finding would be similar to those of Martin and Varricchio (2011) and Freimuth and Varricchio (2019). Regardless, the data and other information gained from this study supply a more complete picture of the insect community represented in these Cretaceous paleosols.

II. Geologic setting

The Two Medicine Formation is comprised primarily of terrestrial molasse deposits that accumulated in the Western Interior foreland basin east of the Sevier thrust belt 82-72 *mya*, in the Campanian stage of the Late Cretaceous (Rogers et al. 2016). Low-sinuosity, shallow anastomosing streams draining the Cordilleran highlands flowed transversely across this upland alluvial plain towards the Western Interior Cretaceous Seaway (Shelton et al. 2006).

The Two Medicine Formation has two laterally traceable discontinuities at its Cut Bank type area. The uppermost was correlated by Shelton (2006) to the Willow Creek Anticline area, which records the time of transition between the Claggett Regression and Bearpaw Transgression (Shelton 2006). During the Claggett Regression, the Judith River shoreline of the Western Interior Cretaceous Seaway (WIKS) migrated ~300 km eastward (Gill and Cobban 1973). During the Bearpaw Transgression, the shoreline of the WIKS was ~330 km westward of present-day northern Montana and southern Alberta (Gill and Cobban, 1973).

The Campanian climate was hot and dry. Throughout the Late Cretaceous, global climate went through three distinct greenhouse periods, with the Campanian spanning the transition from the second greenhouse phase (“hot greenhouse”) to the final greenhouse phase (“cool greenhouse”) (Shelton 2006). Using climate proxies, global mean annual surface temperatures of the Campanian were ~10° C higher than today (Shelton 2006). Volcanic activity was one of several complicated and interrelated factors that increased atmospheric carbon dioxide during the Campanian (Shelton 2006).

Analyses of paleosols from the WCA reveal a semi-arid climate (rainfall <500 mm/year) for the entire interval of Two Medicine deposition (Shelton et al. 2006). Interrupted intra-annual growth patterns are in Late Cretaceous fossil trees of the Two Medicine and across a broad

latitudinal belt in the US Western Interior, indicating an erratically humid environment struck by repeated phases of droughts comparable to present-day east Africa (Falcon-Lang 2003). Shelton and others (2006) interpreted two distinct depositional environments at the WCA: an ephemeral, anastomosing river system, and a system of shallow, fluctuating freshwater lakes. The river system dominated at the beginning and end of deposition, whereas the lacustrine interval was in the middle.

The trace fossils examined in this study, and by Martin and Varricchio (2010), and Freimuth and Varricchio (2019), are from the middle lacustrine interval, when the anastomosing river systems were punctuated by ephemeral freshwater lakes. This lacustrine subfacies is carbonate rich and just younger than 75.5 *mya* (Varricchio et al. 2010). All trace fossils were found in irregularly bedded, micritic limestone and mudrocks. Abundant insect nesting traces in this lithofacies strongly suggest well-drained paleosols from a formerly fluvial deposit (Martin and Varricchio 2010; Genise 2017). Facies characterized by abundant cocoons in calcareous paleosols have been described from the Cretaceous of Argentina, Uruguay, and Mongolia and are characteristic of the *Celliforma* ichnofacies (Johnston et al. 1996; Genise et al. 2002; Genise et al. 2007; Alonso-Zarza et al. 2011; Genise and Sarzetti 2011).

The *Celliforma* ichnofacies (Genise et al. 2010) is a continental ichnofacies with abundant insect nesting traces, such as calichnia, within well-drained calcareous paleosols developed under low plant cover. Calichnia are brooding traces, biogenic structures used to protect eggs and juveniles, such as bee cells or dung beetle balls. The generalized characteristic morphology for trace fossils in this category is described as simple-to-complex burrows, usually consisting of one or more chambers that may be connected to adult-sized burrows (Rindsberg 2012). Along with ichnotaxa such as *Rebuffoichnus. sciuttoi* and *Tombownichnus isp.*, other

ichnospecies associated with insect pupation, e.g., *Celliforma isp.*, *Fictovichnus isp.*, *Rosellichnus isp.*, and *Teisseirei isp.*, may also be included in a *Celliforma* trace fossil assemblage (Cardonatto et al. 2016; Genise 2017). At the Willow Creek Anticline, the *Celliforma* ichnofacies occurs in association with *Troodon* nesting sites and the ootaxon *Continuoolithus* (Martin and Varricchio 2010).

The cocoons examined in this study represent eight discrete localities within the WCA. The localities are: TM-164 (nicknamed “Pupa Rex”, n=200), TM-159 (“Pupa Pass”, n = 177), TM-154 (“Pete’s Pupa Peninsula”, n=95), TM-153 (“Pupa Prank”, n=30), TM-223 (“Pupa Party”, n=200), TM-225 (“Pupa Penthouse”, n=200), TM-167 & TM-174 (“Pupa Pileup”, n=68), and TM-177 (“Pupa Paradise”, n=40).



Figure 1. Aerial imagery map of the WCA, with pins at each locality included in this study

Pete’s Pupa Peninsula (TM-154) is a peninsula-like outcrop of interbedded mudstones and sandy limestones that projects three meters above the surrounding topography. Rocks at Pete’s Pupa Peninsula are from the carbonate-rich middle subfacies of the WCA. Alternating micritic limestones and massive mudstones of varying thickness are interbedded with nodular to

thick, poorly sorted, matrix-supported limestones. These strata fluvial overbank deposits reworked by soil-forming processes and bioturbation (Martin and Varricchio 2010, Shelton 2006).

Pupa Pass (TM-159) is a 3.5m tall knoll made of alternating mudstones and micritic limestones which similarly suggest overbank deposits within the middle lacustrine interval of the WCA. Pupa Rex (TM-164) is a 2.6 m tall outcrop made up primarily of a fining-upward sequence of trough and planar-bedded calcareous sandstone and capped by a ~0.2 m thick cocoon-rich paleosol.

Although I did not have access to field descriptions of the other five outcrops, the host lithology for trace fossils is likely similar, described by Shelton's 2006 definition of "Lithofacies Sw". Many of the sandstones at the WCA are cemented with calcium carbonate, and Shelton (2006) distinguishes this facies of carbonate cemented sandstone for "its extensive preservation of molds and casts of ellipsoidal-shaped pupal cases." Beds of this lithofacies range from 24 cm to 2.12 m thick, and were deposited on either the channel levees of those anastomosing streams or on the shorelines of those ephemeral freshwater lakes (Shelton 2006). The accumulating sediment would have been initially dry, sandy, and above the water table, enabling insects to make their reproductive traces. Carbonate cementation occurred later, during a rise in the water table.

III. Methods and Results

Beginning January 2019 and ending January 2020, I examined these trace fossils at Emory University using Mitotuyo electronic calipers with a resolution of 0.01 mm and accuracy to 0.02 mm. I measured the x, y, and z axes (length, maximum diameter, and diameter perpendicular to maximum) of each ellipsoid to quantify differences in trace fossil morphology, duplicating methods used by Martin and Varricchio (2010). Possible evidence of parasitoid behavior was recorded by noting the occurrences of *Tombowichnus* isp., adjoining burrows of significantly smaller diameter to that of the host cocoon, and (rarely) a smaller cocoon within another cocoon. The trace fossils are currently housed at the Emory University Department of Environmental Sciences and will be deposited at the Museum of the Rockies at the conclusion of the study. Collection bias may have influenced abundance and diversity data, and I only measured specimens deemed at least 90% complete. Another major limitation of this study is that I had no access to the original field site.

The specimens are prolate ellipsoidal cocoons with a mean length of 23.35 ± 7 mm ($n=1010$). Because I measured complete specimens from the sample, the following numbers reflect the complete specimens. The cocoons have a wide size range, expressing a left-skewed distribution of both length (major axis) and circumference (minor axis). The cocoons have a spherical equatorial region, with almost equal means for mutually perpendicular widths. The mean width of the cocoons is 12.0 ± 3 mm and the length to width ratio is 0.4.

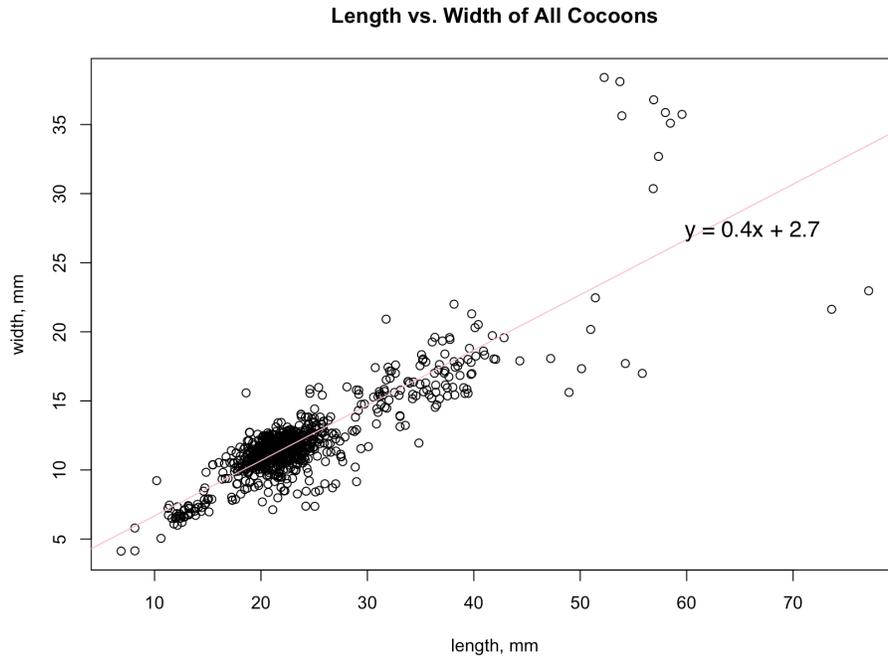


Figure 2. Length vs. width (mm) of all cocoons

Volume was calculated using the ellipsoid volume equation $V = \frac{4}{3}\pi abc$; length and width data were normalized to fit this equation. The minimum volume is 61.25 mm^3 and the maximum volume is $40,840.9 \text{ mm}^3$, with a mean volume of $2,244.4 \text{ mm}^3$ and median of $1,535.40 \text{ mm}^3$; the standard deviation is $3,709 \text{ mm}^3$.

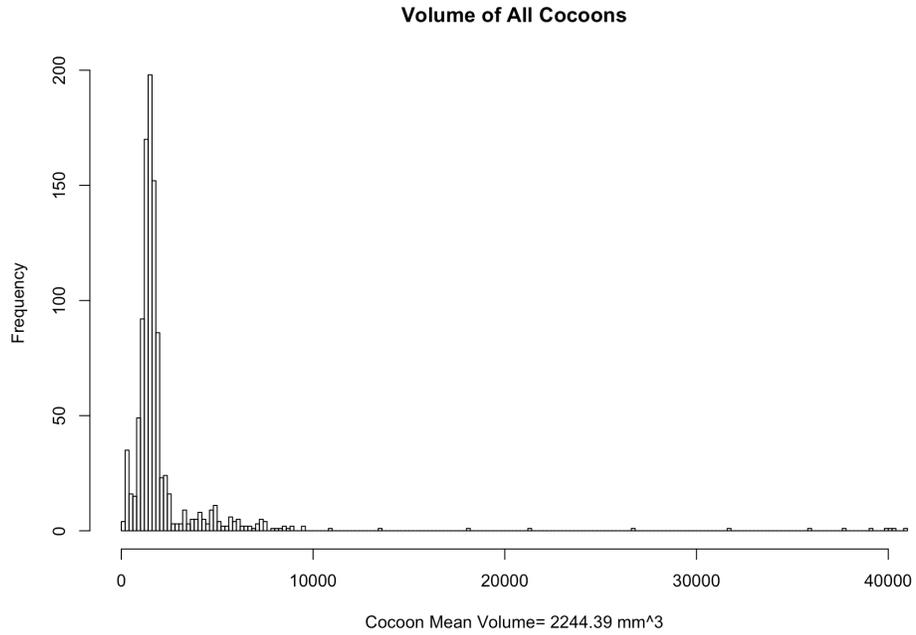


Figure 3. Frequency histogram of all cocoon volumes

Table 1. Summary of descriptive statistics of insect trace fossils from the Two Medicine Formation, Willow Creek Anticline area, Choteau, Montana:

Locality (n=)	Minimum (mm ³)	Mean (mm ³)	Median (mm ³)	Maximum (mm ³)	Standard deviation
Pupa Paradise (n=40)	1,938	4,055	3,777	7,577	1,282.2
Pupa Party (n=200)	141.7	2,354	1,528	21,270	2,833.1
Pupa Pass (n=177)	61.25	1,418	1,373	7,310	804
Pupa Penthouse (n=200)	273.6	1,990	1,450	7,477	1,491

Pupa Pileup (n=68)	943	1,536	1,651	2,724	376
Pete's Pupa Peninsula (n=95)	487.6	5,145	1,651	40,840	10,476.76
Pupa Prank (n=30)	760	2,194	1,595	5,919	1,469
Pupa Rex (n=200)	329.6	1,632	1,541	8,592	778

The median volume is lower than the mean volume from assemblages for most localities, reflecting the left-skewed distributions (Figure 3). The only exception is at Pupa Pileup, which also had the lowest standard deviation. The volume data is considerably skewed, further noted by the high standard deviations. Because the mean reflects skewing the most in this distribution, the median value may be more useful here.

Most of the cocoons have an external texture of raised, helical ridges. The most complete specimens are rounded on both ends, with no flat surfaces near one end, or with an attached burrow of appropriate diameter on one end. Those burrows may be emergence or entrance tunnels (e.g. Alonzo-Zarza et al. 2014). Some specimens have at least one flat, rounded, irregular surface, usually on one end, that is interpreted as a rupture produced by the emergence of an adult (Genise et al. 2007).

Three additional structures are associated with the cocoons. The first are sediment-filled burrows characterized by markedly thinner-diameters compared to their conjoined cocoons.

These burrows may be attached to the burrow not just at the extremes, but also along the meridian. The second type of structure are small, spherical pits in the surfaces of the cocoons, also with smaller diameters than the cocoons. The third is a cocoon within a cocoon. All three structures were described in Martin and Varricchio's (2010) study of fossil insect cocoons from Pete's Pupa Peninsula. These narrow tunnels, pits, and cocoons within cocoons were interpreted as evidence of parasitoid behavior (e.g. Martin and Varricchio 2015).

Morphology is the most critical feature for defining ichnotaxa (Rindsberg and Martin 2007; Genise 2017). Based on morphology, the ellipsoidal cocoons are most comparable to those of *Fictovichnus sciuttoi* (Appendix I), which are interpreted as chambered insect trace fossils excavated by chafer beetles, weevils, or solitary wasps (Alonso-Zarza et al. 2014; Lee 2018; Genise 2004). Associated tunnels are also comparable to burrows associated with *Rebuffoichnus* and those excavated by chafer beetles, weevils, or solitary wasps (Alonso-Zarza et al. 2014; Lee 2018). The small pits on the surface of the cocoons are comparable to those of *Tombownichnus* *isp.*, interpreted as borings by parasitic wasps, ants, or flies (Maikuláš and Genise 2003; Genise 2017).

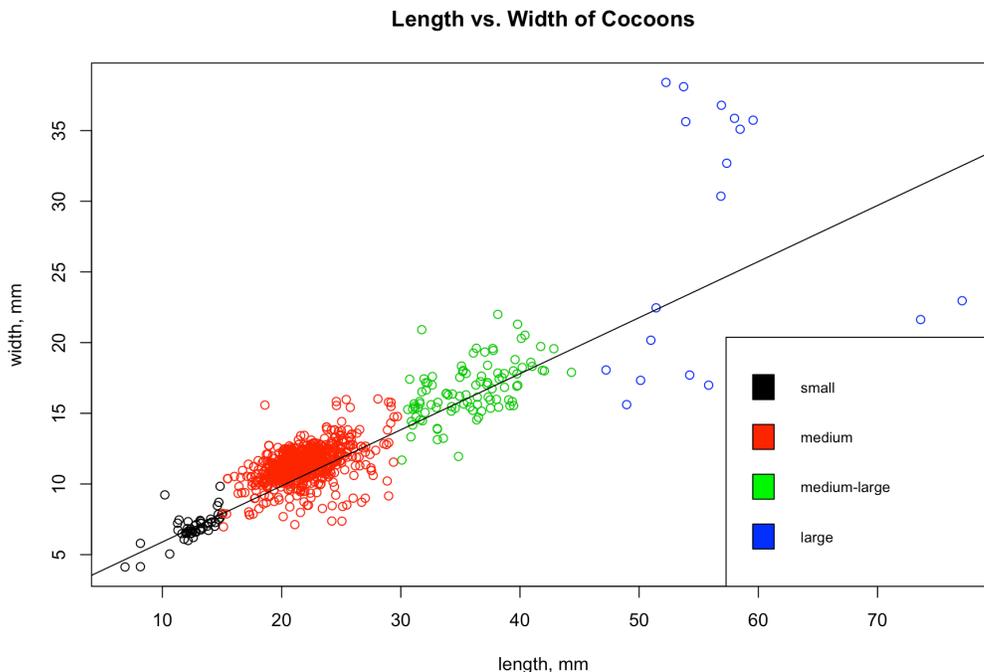


Figure 4. Length vs. width scatterplot, showing four discrete size classes

Table 2. Size classes of insect trace fossils from the Two Medicine Formation in the Willow Creek Anticline area, Choteau, Montana.

Size class	N	Mean volume (mm ³)	Mean length (mm)	Length range (mm)	Mean width (mm)	Width range (mm)
Small	47	333	12.6	6.9 – 14.9	6.9	4.1 – 9.8
Medium	846	1,518	21.8	15.1 – 29.7	11.4	6.9 – 16
Medium-large	101	5,304	35	30 – 44	16	11.7 – 22
Large	18	24,170	56	47 – 77	27	15.6 – 38

The cocoons may be categorized into four distinct size classes based on length and width. The size classes are small, medium, medium-large, and large, a classification also used by Freimuth and Varricchio (2019). The smallest size class (n=47) have average volumes of $333 \pm 120 \text{ mm}^3$, and are $12.6 \pm 1.75 \text{ mm}$ long and $6.9 \pm 1 \text{ mm}$ wide, with a length) diameter ratio of 1.82. The smallest cocoons are sourced from Pupa Party (n=25), Pupa Pass (n=13), Pupa Penthouse (n=6) and Pupa Rex (n=3). Only 4% of the smallest cocoons showed evidence of parasitoid behavior. with thin burrows recorded on two specimens.

The medium size class (n=846) have average volumes of $1,518 \pm 435 \text{ mm}^3$, and are $21.8 \pm 2 \text{ mm}$ long and $11.4 \pm 1 \text{ mm}$ wide, with a length:diameter ratio of 1.9. The medium cocoons are at every locality and have the most diverse evidence of parasitoid behavior, with 27 *Tombownichnus* isp., 109 thin burrows, and 2 cocoons within cocoons.

The medium-large size class (n=101) contains cocoons between 30 and 45 mm length. The medium-large cocoons average $5,304 \pm 1,548 \text{ mm}^3$ in volume, $35 \pm 3 \text{ mm}$ long, and $16 \pm 2 \text{ mm}$ wide. This size class is in every locality and also has evidence of parasitoid behavior, with 2 *Tombownichnus* isp., 12 thin burrows, and one cocoon within a cocoon.

The largest size class (n=18) contains cocoons over 45 mm in length. The largest cocoons are $24,170 \pm 13,926 \text{ mm}^3$, with a notably large standard deviation possibly explaining the lower mean value. The cocoons average $56 \pm 7 \text{ mm}$ long and $27 \pm 8 \text{ mm}$ wide. The largest size class contain no evidence of parasitoid behavior and are represented from Pupa Party (n=9) and Pete's Pupa Peninsula (n=9) only.

The cocoons at Pupa Paradise (n=40) contain one instance of a thin burrow and one instance of a cocoon within a cocoon. The cocoons at Pupa Party (n=200) contain 14 instances of thin burrows and 8 instances of *Tombownichnus* isp. The cocoons at Pupa Pass (n=177) contain 17 thin burrows, 2 *Tombownichnus* isp., and one cocoon within a cocoon. The cocoons at Pupa Penthouse contain one instance of a cocoon within a cocoon, 40 thin burrows, and 7 *Tombownichnus* isp. The cocoons at Pupa Pileup (n=68) contain six thin burrows and one instance of *Tombownichnus* isp. The cocoons at Pete's Pupa Peninsula (n=95) contain 14 thin burrows. The cocoons at Pupa Prank (n=30) include two instances of *Tombownichnus* isp. The cocoons at Pupa Rex (n=200) contain 31 thin burrows and nine *Tombownichnus* isp.

IV. Discussion

This study reviews 1,010 insect fossil traces sampled from eight different outcrops throughout the Willow Creek Anticline. The trace fossils were deposited near ephemeral freshwater lakes during the middle lacustrine interval of the Two Medicine Formation represented at the WCA. The traces were made in a dry, sandy substrate above the water table, but many of the insects drowned and sediment calcified in and around their trace fossils with the rise of the local water table. Thus stratigraphically correlatable cocoon-rich beds in the mid-section of the Two Medicine Formation at the WCA probably represent pulses of dry season deposition during an interval of drought and ephemeral freshwater lakes (Rogers 1998; Shelton 2006; Rogers et al 2016). This is consistent with evidence from other climate proxies indicating a drought- and desert-prone Campanian in this region (Nadon 1992; Falcon-Lang 2003).

Following Martin and Varricchio (2010) and Freimuth and Varricchio (2011), this study adds seven new localities and 1,010 additional unique specimens to their bodies of work on these insect trace fossils from the WCA. The results in this study are strikingly consistent with those previous works on these ichnofossils, while expanding on them geographically.

Three distinct ichnotaxon are identified in the sample:

(1) *Fictovichmus sciuttoi* (Genise et al. 2007; Alonso-Zarza et al. 2014)

F. sciuttoi are ellipsoidal, helically textured structures often showing flattened surfaces or truncation near an apex (Genise et al. 2007). *F. sciuttoi* The Argentinian *F. sciuttoi* holotypes (n=27) are between 26 to 33 mm long and 12 to 16 mm wide. Genise and others interpreted these as cocoons of aculeate wasps (Genise et al. 2007). The best preserved specimens from this study have fine lobed textures with helically arranged ridges and truncation near one extreme.

Freimuth and Varricchio also identified their study's primary trace fossil as *F. sciuttoi* (Freimuth

and Varricchio 2019). Martin and Varricchio named their ellipsoids *Rebuffoichnus sciuttoi* (Martin and Varricchio 2010). In the Genise et al. 2007 paper, the holotype material for *F. sciuttoi* is identified as *R. sciuttoi*, but a later revision from Alonso-Zarza et al. 2014 renamed that material *F. sciuttoi*.

(2) *Tombownichnus* isp. (Mikulás and Genise 2003)

Tombownichnus are elliptical pits near the meridian of insect pupal chambers, interpreted as borings of parasitic insects attacking the host insect in its pupal stage of development (Mikulás and Genise 2003). Mikulás and Genise (2003) and Genise (2016) have identified parasitic wasps, wasp larvae, blister beetles, and flies as tracemakers of *Tombownichnus*. *Tombownichnus* was found on 29 *F. sciuttoi* specimens in this study. *Tombownichnus* was found on two *F. sciuttoi* specimens in Freimuth and Varricchio's 2019 study. The thin burrows, while treated as a discrete and unassignable structure, may share a common tracemaker with *Tombownichnus*.

(3) *Tesserei barattinia* (Genise et al. 2013)

Teisseirei are sub-cylindrical chambers with an elliptical cross section and a smaller width/height ratio than those of *Fictovichnus* (Genise 2017). In geologically younger specimens, *Teisseirei* shows a multilayered wall; in older specimens, the wall is not as discrete. I identified two specimens identifiable as *Teisseirei* rather than *Fictovichnus* in my sample, on the basis of the long, horizontal, sub-cylindrical chambers. *Teisseirei* is interpreted by Genise (2017) as products of sphinx moth pupation.

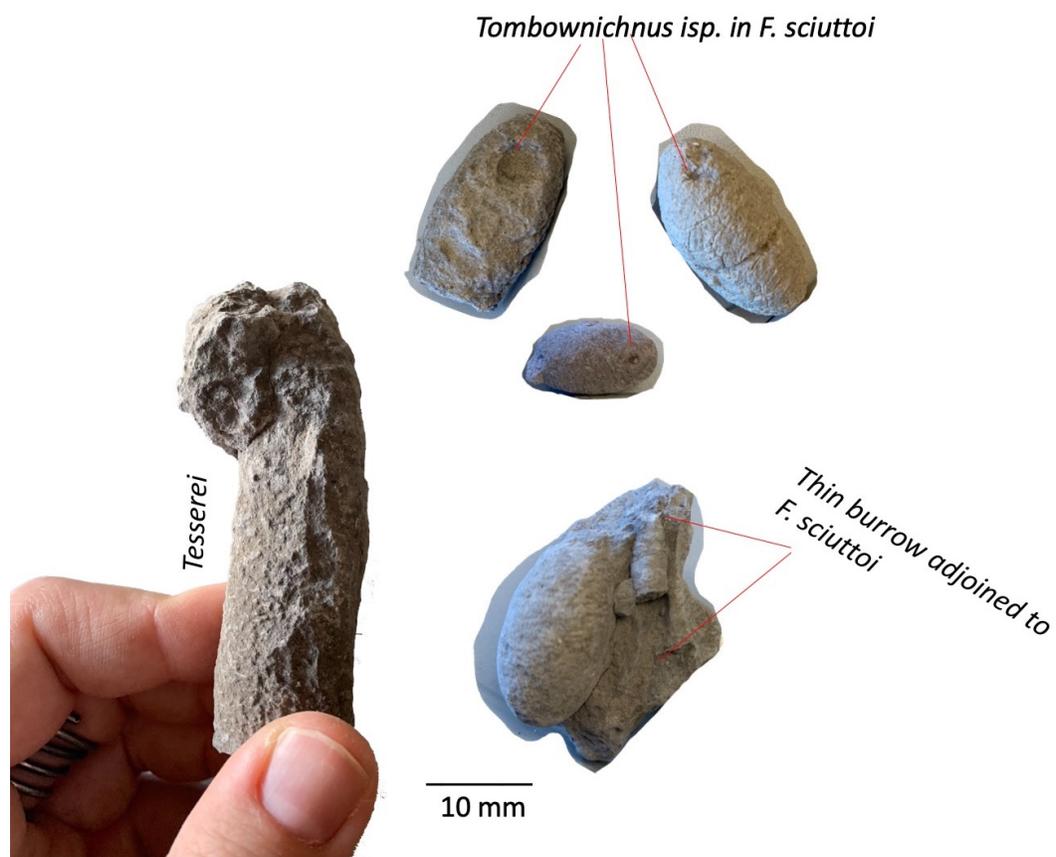


Figure 5. Representative samples of the three ichnotaxon (*F. sciuttoi*, *Tesserei*, and *Tombownichnus*) identified in this study

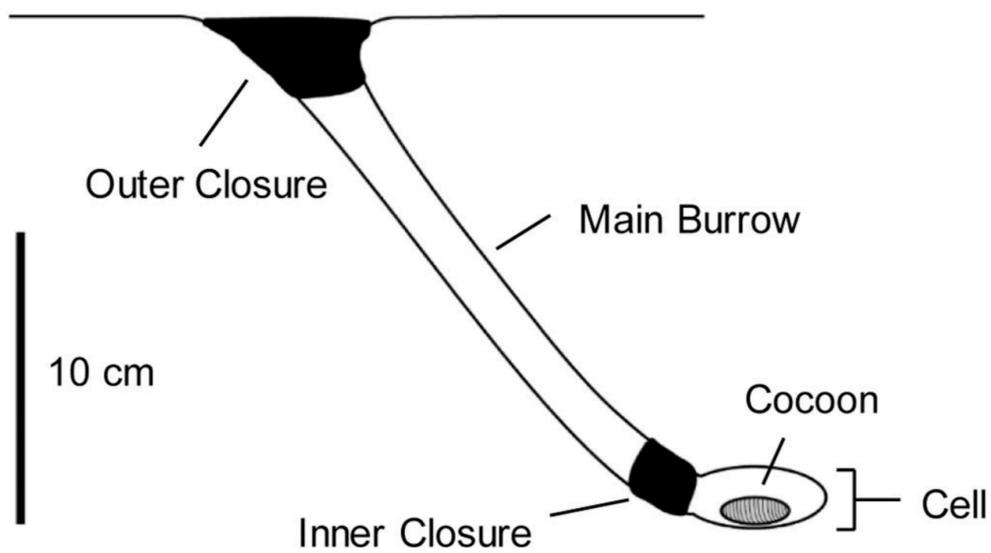


Figure 6. Generalized burrow of a solitary wasp. From Freimuth and Varricchio (2019)

F. sciuttoi is associated with ground wasps, and *Tombownichnus* is associated with parasitic wasps, ants, or flies (Genise 2017). Many modern wasps parasitize other wasps (e.g., King et al. 2018; Paukkunen et al. 2018). For example, King and others (2018) observed three extant species of burrowing wasps parasitizing pupal cases of other wasps. Female wasps often burrow below the ground to parasitize hosts in the pupal stage, while the males of the same species stay above ground looking for mates. When a wasp finds a pupal case, the female drills through its puparium with her ovipositor and lays an egg, which hatches; the offspring then eats the host and later emerges from the puparium (King et al. 2018). Because the trace fossil evidence reflects a similar behavior, the insect tracemakers are responsible for the cocoons, burrows, and borings in the Two Medicine paleosols are likely wasps. However, although *F. sciuttoi* is specifically associated with ground wasps, *Tombownichnus*' tracemaker association is more ambiguous and will not be defined in this paper.

As mentioned above, pupal cases most comparable to those of *F. sciuttoi* have been described from the Willow Creek Anticline by Martin and Varricchio (2011, 2015) and Freimuth and Varricchio (2019). In each case, the authors proposed four size classes within the ellipsoidal morphologies of *F. sciuttoi*. In each case, the second size class, or the “medium” size class, had an overwhelmingly high frequency in the total sample, making up 83% of Martin and Varricchio's (2011) sample and 53% of Freimuth and Varricchio's (2019) sample. My sample, sourced from multiple localities across the Willow Creek Anticline, likewise has these four size classes. Again, the highest frequency was the second or “medium” size class, making up 91% of my total sample. The qualitative statistics for the medium-size cocoons is thus consistent across all three studies:

Table 3. Comparison of most frequent size class from previous studies

Study	Frequency of size class	Mean volume (cm ³)	Mean length (mm)	Mean width (mm)
Martin and Varricchio (2010)	83%	1.47	22.1	11.2
Freimuth and Varricchio (2019)	53%	1.29	21.6	12.5
This study	83%	1.52	21.8	11.4

In addition to *F. sciuttoi*, *Tombownichnus* was observed at both Pete’s Pupa Peninsula and Egg Mountain (Martin and Varricchio 2011; Freimuth and Varricchio, 2019). *Tesserei* was mentioned by Martin and Varricchio (2010) but notably absent from Freimuth and Varricchio’s 2019 study, leading those authors to speculate that the *Celliforma* ichnofacies at Egg Mountain is depauperate compared to the assemblage described at Pete’s Pupa Peninsula. In all three studies, one ichnotaxon dominates: *F. sciuttoi*, with varying secondary components including *Tombownichnus*, thin burrows, cocoons within cocoons, and *Tesserei*.

Martin and Varricchio (2010) classified the ichnoassemblage at Pete’s Pupa Peninsula as representing the *Celliforma* ichnofacies. Freimuth and Varricchio (2019) were more hesitant to label the assemblage at Egg Mountain as that of the *Celliforma* ichnofacies because it was so monospecific. Like other deposits of the Two Medicine Formation with the *Celliforma* ichnofacies, the beds at Egg Mountain had “a distinct absence of traces definitively referable to bees” (Freimuth and Varricchio 2019). However, no bee trace fossils have been interpreted from the Two Medicine Formation, so this conclusion is not surprising, yet the ichnofacies still applies without bee traces.

Given this new analysis of ichnoassemblages from eight different outcrops in the WCA, we can make an even more informed estimation of the species diversity represented in this cocoon-rich subfacies. The suite of insect trace fossils featured in midsection paleosols of the

WCA represents the interaction between at minimum three species: at least one wasp species responsible for the four size classes of *F. sciuttoi*, at least one unidentified insect species responsible for the *Tombownichnus* and thin burrows associated with the *F. sciuttoi* chambers (probably wasp), and at least one lepidopteran species responsible for *Tesserei*. These trace fossils collectively indicate the *Celliforma* ichnofacies made by perhaps only a few species of insects, but with overwhelming abundance of at least one species.

The presence of *Celliforma* in the middle lacustrine interval of the Willow Creek Anticline is consistent with inferred semi-arid climates and distal floodplain environments, within which sediments of the Two Medicine Formation were deposited (Shelton 2006). Interrupted intra-annual growth patterns occur in Late Cretaceous fossil trees in the Two Medicine and across a broad latitudinal belt in the US Western Interior. These tree line growth patterns indicate an erratically humid environment struck by repeated phases of droughts comparable to present-day east Africa (Falcon-Lang 2003). Modern ground wasps likewise prefer dry soils and high densities of fossil cocoons, reflecting periods of dry season deposition (Martin and Varricchio 2010; Genise 2017). Within the middle lacustrine interval, subfacies containing *Celliforma* ichnofacies may also represent times when the Sevier foreland was especially dry and its system of ephemeral freshwater lakes was depleted.

Using modern analogues as a guide, abundant wasp cocoons suggest an abundance of edible invertebrates such as spiders, ants, and flies, as most wasps are dependent on high availability of such prey (O'Neill 2001). It is easy to imagine to imagine this scenario alongside the abundance of dinosaur coprolites also at the site (e.g. Chin and Gill 1996; Chin et al. 2009). Perhaps wasps were originally attracted to the site because of the abundant prey availability, or they and their prey were drawn to the same soil conditions: above the water table and with close

access to food. Both Martin and Varricchio (2010) and Freimuth and Varricchio (2019) described assemblages at the WCA defining an association of the *Celliforma* ichnofacies with dinosaur nesting traces. An association of *Celliforma* ichnofacies and vertebrate nesting has only been recorded from one other location, in the Mercedes Formation (Late Cretaceous, Campanian-Maastrichtian) of Uruguay (Alonso-Zarza et al. 2011).

Nadon (1993) proposed that large ornithopod dinosaurs, such as hadrosaurs, used seasonal floodplains as breeding grounds safe from predators, and compared the dry, savanna-like environments represented in the Two Medicine Formation to modern savannas, which are also habitats suitable for large herbivores. Seasonal flooding in these dry environments may have provided protection to the hadrosaurs; Nadon (1993) suggest that ornithopods used these sites during seasonal flooding as nesting grounds and migrated during the dry season. Within the middle subfacies of the WCA, Martin and Varricchio (2010) inferred that *Troodon* nesting sites and the fossil egg ootaxon *Continuoolithus* co-occur with the *Celliforma* ichnofacies, whereas nests of the hadrosaur *Maiasaura* are absent from these horizons. *Celliforma* indicates dry, well-drained environments, hence its horizons may have hosted nests of the small theropod *Troodon* but excluded the large ornithopod *Maiasaura*, supporting Nadon's 1993 hypothesis. More research should be done to test if these ichnofacies represent periods of flooding, and whether or not these ichnofacies are associated with *Maiasaura* nesting sites and those of the ootaxon *Spheroolithus*.

Conclusions

1. Two Medicine Formation (Campanian) trace fossil assemblages from eight different localities within the Willow Creek Anticline (WCA) area (Choteau, Montana) contain

- evidence for an abundance of ground-nesting insects, and at least three species of insect tracemakers that lived in well-drained soils under semi-arid conditions.
2. The trace fossils demonstrate a paleoecological relationship between ground-wasp hosts and an unknown parasitoid.
 3. These interpretations are consistent with previous studies of the Two Medicine Formation and contribute to a more comprehensive understanding of the biodiversity and paleoclimates represented by paleosols in the WCA.

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VI. Appendix

Flora and Fauna of the Two Medicine Formation at the Willow Creek Anticline

Dinosauria:

Maiasaura peeblesorum (Ornithischia: Hadrosauridae) (Horner 1983)

Acristavus gagslarsoni (Ornithischia: Hadrosauridae) (Gates et al. 2011)

Troodon formosus (Saurischia: Theropoda: Troodontidae) (Varricchio et al. 1999)

Fragments of a nodosaur (Chin and Gill 1996 citing Horner pers. comm)

Pterosauria:

Montanazhdarcho isp. (Pterodactyloidea: Azhdarchidae) (Padian et al. 1995)

Insecta:

dung beetles (Scarabaeoidea) (Chin and Gill 1996)

ground wasps (Hymenoptera) (Martin and Varricchio 2011; Freimuth and Varricchio 2019; this study)

moths (Lepidoptera) (Martin and Varricchio 2011; Freimuth and Varricchio 2019)

Gastropoda:

Megomphix sp. and *Polygyrella* sp. (Stylommatophora: Megomphicidae) (Chin et al. 2009)

Lioplacodes (Architaenioglossa: Pleuroceridae) (Chin et al. 2009)

Viviparus sp. (Architaenioglossa: Viviparidae) (Chin et al. 2009)

Prograngerella sp. and *Hendersonia* sp. (Neritopsina: Hendersoniidae) (Chin et al. 2009)

Unidentified physid (Basommatophora: Physidae) (Chin et al. 2009)

Malacostraca:

crayfish (Decapoda: Astacidea: Parastacoidea) (Martin, pers. comm)

decapod crustaceans associated with *Thalassinoides* (Martin, pers. comm)

Plantae:

Juniper and Sequoia (Pinophyta: Cupressaceae) (Chin and Gill 1996)

Comparative analysis of characteristic morphologies of *F. gobiensis*, *F. sciuttoi*, and the Willow Creek Anticline cocoons

	<i>Fictovichnus gobiensis</i> (Alonso-Zarza et al. 2014)	<i>Rebuffoichnus sciuttoi</i> (Genise et al. 2007) → <i>Fictovichnus sciuttoi</i> (Alonso-Zarza et al. 2014)
Morphologic similarities to study cocoons	<p>Rounded on both ends: “<i>Fictovichnus</i> showing both extremes rounded and smooth surface in casts detached from matrix. There is no flat surface near one extreme.”</p> <p>“<i>F. gobiensis</i> lacks the flat, oval, smoothed area near the end opposite to the scar or truncated end, which was interpreted as the attachment area of the cocoon to the floor.”</p>	<p>Discrete wall (required for original Genise et al. 2007 <i>R. sciuttoi</i> definition, Alonso-Zarza et al. 2014 dismissed this criterion when lumping into <i>F. sciuttoi</i> definition)</p> <p>“The wall displays a helical pattern of fine ridges, tightly grouped, faintly impressed over wide and flattened lobes that are also helically arranged, observable in the best-preserved specimens.”</p> <p>“In some specimens remains of the wall can be seen with the naked eye; this appears as a smooth outer layer with a helical surface texture composed of lobes and fine ridges.”</p> <p>Truncation: Some specimens are “completely ovoid” and “considered to be the closed ones from which the trace makers never emerged... Other specimens are truncated at one end, showing a flat, irregular, rounded surface.”</p>
Morphologic differences to study cocoons	<p>Smooth exterior: “Specimens show smooth surfaces overprinted by nets, which in the case of Orera Village are mostly minute channels and pits carved on the surface and in the case of Orera Quarry are mostly ridges or strings. In some specimens the external surface shows a lamellar texture as if it were composed of several overlapping layers.”</p>	<p>Slightly depressed cross section: “In cross-section, many specimens have a slightly depressed outline.”</p> <p>Flattened end: “[In truncated specimens] opposite the scar or truncation, and at the other end of the chamber, there is a sub-terminal, flat, smooth, oval area.”</p>
Descriptive statistics	<p>Length: 15-22 mm Width: 7-11 mm (n=140) Mean length: 15-13 mm Mean width: 8-9 mm</p>	<p>Length: 26-33 mm (n=11) Width: 13-16 mm (n=16) Width 2: 11-13 mm (n=13)</p>
Associated tracemaker	<p>Fillings of coleopteran pupation chambers (i.e., beetles).</p>	<p>Wasps. Characteristics shown by extant wasp cocoons should be recognized as well, such as “nipple like protuberances” at one end, equatorial protuberances or pores, a tapering end or an elongated, and surface morphologies comparable to extant cocoons (Genise 2017).</p>



From left to right: Specimen 33 showing perfect roundedness on each extreme. Specimen 70 showing surface texture resembling that of *F. sciuttoi*. Specimen 77 showing nipple like protuberance indicative of wasp tracemaker.

Re-examination of the surface textures and documentation of “nipple-like protuberances” of the cocoon chamber confirms that the surface morphologies of the chambers are comparable to extant wasp cocoons. Thus the chambers most closely resemble those of *F. sciuttoi* despite having a morphology consistent with *F. gobiensis*.