

Experimental Neoichnology of Burrowing Arthropods
From Eolian Environments

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ABSTRACT

In desert dune settings, body fossils are rare, leaving the bulk of interpretations of ancient eolian ecosystems to be based on ichnofossils preserved in a variety of lithofacies. While many ichnofossils are simple to interpret, there are many ambiguous biogenic structures that are not well understood. Among animals that occur in modern eolian environments, arthropods are the most common bioturbators and are the likely producers of these structures. Recent studies utilizing laboratory-based neoichnological experiments have been able to bridge the gap of understanding between observed behaviors, environmental conditions, and the three-dimensional burrows produced by different continental animals. However, most eolian ichnofossils are only expressed in two dimensions and were likely produced in loose substrates that do not conform to such an experimental approach. This study examined the activities, behaviors, and two-dimensional biogenic structures produced by six arthropod species, *Hogna lenta*, *Orthoporus ornatus*, *Paragaleodes sericeus*, *Smeringurus mesaensis*, *Ammopelmatus* cf. *fuscus*, and *Eleodes armata*, in loose sandy sediment of varying composition and moisture levels. Sediment composition varied in the proportion and distribution of sand, silt, clay, and organic matter. Sediment moisture varied in ranges of 0-5%, 8-12%, and 15-25%. Active substrate disturbance activities were observed and recorded as well as behaviors associated with biogenic structures. Biogenic structures produced by individual species were compared between the different moisture levels and substrate compositions to evaluate the effect of substrate on trace morphology. Biogenic structures produced by all species in layered trials were compared to each other to evaluate the control of

tracemaker on trace morphology. The highest depth and total amount of bioturbation were compared between each species. Biogenic structures produced in these experiments were compared to identified ichnofossils and ichnofabrics found in eolianites from the Mesozoic found around the world. There were significant differences among biofabrics produced in different substrate conditions and several key controls were identified in produced distinct trace morphologies among the arthropod species. This study has helped to identify new potential behaviors and tracemakers in eolianite ichnofabrics and ichnofossils. Continual refinement of interpretation of ichnofossils will aid in the understanding of environmental conditions and the paleoecology of ancient eolian environments.

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CHAPTER ONE

INTRODUCTION

Eolian environments are well represented in the global geologic record from the Archean to the Recent and are interpreted based on a variety of preserved sedimentological and architectural features (Cosgrove et al., 2022). It is often challenging to interpret the ecology of these environments because body fossils in eolianites are rare (Ekdale and Bromley, 2012). By comparison, ichnofossils, the record of past organisms' behavioral interactions with substrates, are common (Good and Ekdale, 2014; Krapovickas et al., 2016). Issues remain, however, in interpreting many of the ichnofossils and ichnofabrics found in eolianites. The study of extant animals from similar modern environments can help aid in the interpretation of these ichnofossils (Hembree, 2016).

In this study, the sediment disturbance activities and structures of six semi-fossorial desert arthropod species were documented including *Smeringurus mesaensis*, a desert scorpion from the southwestern United States, *Paragaleodes sericeus*, a solifuge from the deserts of Egypt, *Hogna lenta*, a wolf spider known to inhabit a range of habitats across the United States, *Eleodes armata*, a darkling beetle inhabiting the western United States and Mexico, *Orthoporus ornatus*, a desert millipede from the southwestern United States, and *Ammopelmatus* cf. *fuscus*, a large orthopteran from the western United States and Mexico. All study animals were observed in a controlled laboratory setting to identify specific activities and behaviors associated with sediment disturbance and the resulting structures they produce viewed in two dimensions. The experiments were

focused on differences in structures produced under varying sediment moisture levels and sediment compositions. The resulting structures were described qualitatively and quantitatively and compared between substrate conditions and species.

This study addressed three hypotheses: 1) arthropod body plans will have a greater control on the morphology of the biogenic fabrics than phylogenetic relationships; 2) arthropod predators and detritivores will produce morphologically distinct biogenic fabrics; 3) different substrate compositions and moisture levels will result in the production of morphologically distinct biogenic fabrics among the same arthropods.

The results of this study can be used to provide additional context to the ichnofossils that occur through much of the eolianite record. Through comparative analysis of structures produced by different arthropod species under varying conditions, this study identifies and interprets the ecological and environmental significance of ichnofossils described from Mesozoic eolian deposits across the world (Tanner et al., 2006; Seike et al., 2010; Good and Ekdale, 2014; Buatois and Echevarría, 2019a; Melchor et al., 2024). The rarity of body fossils in eolian deposits makes the study of biogenic structures essential to understanding the paleoecology of ancient dune fields (Good and Ekdale, 2014). The most common inhabitants of modern dune fields are arthropods which lack biomineralized hard parts, leading to little direct representation in the fossil record of these environments (Ahlbrandt et al., 1978). Consequently, the understanding of biofabrics produced by arthropods an indispensable tool for interpreting ancient eolian ecosystems.

CHAPTER TWO

BACKGROUND

Inland Eolian Environments

Eolian (windswept) environments are known from the geologic record as far back as the Archean, with successions primarily dominated by siliciclastic inland sand seas, otherwise known as ergs (Rodriguez-Lopez et al., 2014). Modern eolian environments can be broken down into several sub-environments: dunes (divided into lee and stoss sides), dry interdunes, moist interdunes, wet interdunes, sand sheets and sabkhas (Ahlbrandt and Fryberger, 1982; Krapovickas et al., 2016; Cosgrove et al., 2021a). Dunes are the active portion an eolian environments, moving with the winds, although they can stabilize for a period of time. Interdunes are the low points between dunes that can be most affected by the water table in an eolian environment. Thus, many studies focusing on eolian environments divide interdune environments in the modern or in the past based on substrate moisture level (Cosgrove et al., 2021a). Sand sheets are the stabilized portion of eolian environments which plant-life can colonize and soils can form (Hminna et al., 2020). Sabkhas are low-relief flats in which evaporites accumulate, often associated with playa lakes. Other, less common sub-environments associated with the peripheries of eolian environments include lakes, ephemeral streams, and alluvial fans (Krapovickas et al., 2016; Cosgrove et al., 2021a). The complexity of eolian environments present unique challenges and opportunities that shape the distribution and behaviors of the organisms that inhabit each sub-environment.

An abundance of eolian deposits have been recorded in the geologic record, though they are distributed unevenly in time and space since their first appearance in the Archean (Cosgrove et al., 2021a, 2021b). In accordance with climate conditions and the innovations of life (particularly terrestrial plants), eolian deposits have been recorded in thicker and thinner successions that represent the different eolian sub-environments with varying frequency (Cosgrove et al., 2021a). Some of the thickest examples of eolianites were formed under greenhouse conditions that prevailed throughout much of the Mesozoic (Cosgrove et al., 2021b). Among these, some of the largest and most famous examples include the immense deposits from the Navajo, Aztec, and Nugget sandstones in the western portion of North America from the Late Triassic and Early Jurassic (Blakey et al., 1988; Rahl et al., 2003; Britt and Chure, 2016; Parrish et al., 2019). Other well studied eolianites from the Mesozoic include several units from the Lower and Upper Cretaceous of Argentina as well as the Upper Cretaceous Djadokhta Formation of Mongolia (Hasegawa et al., 2009; Seike et al., 2010; Buatois and Echevarría, 2019b; Melchor et al., 2024). Fewer eolianites are known from after the Mesozoic and are generally thinner (Cosgrove et al., 2021a, 2021b).

Modern Eolian Ecology and Bioturbation

Desert dune environments often are incorrectly assumed to support little diversity of life. In fact, many eolian ecosystems support a great diversity of life that has evolved convergently to survive in harsh conditions (Loope, 2008; Buatois and Echevarría, 2019b). Among organisms studied in modern eolian environments, arthropods are the most ubiquitous across sub-environments (Ahlbrandt et al., 1978; Renan et al., 2020). In

addition to being some of the most common animals on Earth (constituting more than 75 percent of Animalia), various arthropods have physiological, morphological, and behavioral adaptations that make them well-suited for eolian environments (Ahlbrandt et al., 1978; Zhang, 2013). Some of these adaptations include a tendency to avoid times of environmental extremes (such as through nocturnality), lower body-mass-to-surface-area ratios, the ability to quickly colonize ephemeral water sources, and fossorial life habits (Cloudsley-Thompson, 1991). In contrast with larger animals inhabiting deserts, arthropods tend to spend the majority of their lifespan within a single sub-environment, allowing for specialized adaptations (Cloudsley-Thompson, 1991; Punzo, 1998; Krapovickas et al., 2016).

In the modern, bioturbation is common across many disparate dune field settings (Ahlbrandt et al., 1978). Within dune fields, however, varying conditions of each sub-environment that dictate the types and quantity of bioturbation are not evenly distributed (Ahlbrandt et al., 1978, Renan et al., 2020). Controls such as aridity, landscape stability, moisture, and temperature all play a factor in trace-associated behaviors displayed as well as potential preservation of biofabrics (Hasiotis, 2002; Krapovickas et al., 2016; Buatois and Echevarría, 2019b).

Common burrowing arthropods in modern eolian settings include wasps, ants, dipterans, termites, orthopterans, beetles, scorpions, and spiders (Ahlbrandt et al., 1978; Cloudsley-Thompson, 1991). Many of these arthropods are bradytelic (conservative in morphology over time) temporally long-ranging and, many dating back to the Pennsylvanian or further (300+ million years ago) (Selden and Dunlop, 1998; Shear and

Edgecombe, 2010; Du et al., 2017; Harms and Dunlop, 2017). This makes the study of these groups in the modern useful for interpreting biogenic structures found in the geologic record (Ahlbrandt et al., 1978; Davis et al., 2007; Hembree et al., 2012).

It is a basic principle of ichnology that different species can create similar biogenic structures if engaged in similar behaviors (Frey, 1975). Even among phylogenetically disparate groups, similar biogenic structures can be produced, particularly within sub-environments. For example, tiger beetle larvae and wolf spiders can produce a similar vertical burrow, differing in size and the presence of webbing at the entrance (Ahlbrandt et al., 1978). Conversely, within the same species, morphologically distinct structures can be made with changes in substrate or behavior (Frey, 1975). For example, one modern shrimp species has been documented to construct both a structure resembling *Thalassinoides* and *Ophiomorpha* within the same burrow system (Frey, 1975). Similar examples found in continental neoichnological studies of desert animals include multiple, differing structures created by individual specimens of *Hadrurus arizonensis* (scorpion), *Scolopendra polymorpha* (centipede), and *Eryx colubrinus* (snake) (Hembree and Hasiotis, 2007; Hembree et al., 2012; Hembree, 2019). Given that ichnofossils are both convergent at times and can also differ significantly within a single species with a range of possible behaviors, experimental neoichnology is vital to their proper interpretation.

Ancient Eolian Ichnofossils and Biofabrics

Body fossils in eolianites are exceptionally rare, leaving little record to understand the paleoecology of ancient dune fields (Ekdale and Bromley, 2012; Good and Ekdale,

2014; Britt and Chure, 2016). Fortunately, ichnofossils in eolianites have been abundant at a global scale as early as the Permian (Krapovickas et al., 2016). Characteristic ichnofossils found in eolianites commonly include the four- and five-toed tracks *Brasilichnium* and *Chelichnus*, respectively, interpreted to be produced by therapsids (Krapovickas et al., 2016). Since the middle Mesozoic, trackways have also commonly included three-toed theropod dinosaur tracks of varying size, such as *Grallator*, *Eubrontes*, and *Megalosauropus* (Loope, 2006; Lockley et al., 2007; Krapovickas et al., 2016; Rowland and Caputo, 2016). Arthropod trackways such as *Paleohelcura* (interpreted as scorpion tracks), *Octopodichnus* (interpreted as spider tracks), and *Diplopodichnus* (interpreted myriapod tracks) are commonly found on bedding plane surfaces from various dune sub-environments (Brady, 1947; Krapovickas et al., 2016). Numerous fossil burrows have been attributed to arthropods in eolian settings, including the vertical burrow, *Skolithos*, the lined, sub-horizontal to sub-vertical burrow, *Palaeophycus*, mensiccate backfilled burrows such as *Taenidium* and *Entradichnus*, and non-meniscate backfilled burrows such as *Planolites* (Ekdale et al., 2007; Krapovickas et al., 2016). Some of the documented traces produced by modern arthropods are similar to those found in eolianites from the Permian to the Neogene (Ahlbrandt et al., 1978; Loope and Rowe, 2003; Ekdale et al., 2007; Seike et al., 2010; Krapovickas et al., 2016).

One of the most useful ways in which assemblages of ichnofossils are used is in the interpretation of paleoenvironmental conditions (Frey, 1975; Ekdale et al., 2007; Krapovickas et al., 2016; Buatois and Echevarría, 2019b). The framework for identifying sub-environments based on interpretations of ichnofossil assemblages is the ichnofacies

model. Several iterations of the ichnofacies model have been proposed for eolian environments in the past, including the *Laoporus* ichnofacies, *Chelichnus* ichnofacies, *Brasilichnium* ichnofacies, *Octopodichnus* ichnofacies and *Entradichnus* ichnofacies (Lockley and Hunt, 1994; Ekdale et al., 2007; Hunt and Lucas, 2007). After several revisions, two ichnofacies models have now been proposed for eolianites, the *Chelichnus* and *Octopodichnus-Entradichnus* ichnofacies (Buatois and Mangano, 2011; Krapovickas et al., 2016). *Chelichnus* ichnofacies is characterized by the presence of vertebrate trackways typically attributed to various therapsids and theropods (i.e., *Chelichnus*, *Brasilichnium*, *Grallator*, *Eubrontopus*). The *Octopodichnus* and *Entradichnus* ichnofacies is characterized by the presence of invertebrate traces, both trackways (i.e., *Octopodichnus*, *Paleohelcura*) and burrows (i.e., *Entradichnus*, *Planolites*, *Taenidium*, *Skolithos*) (Buatois and Mangano, 2011; Krapovickas et al., 2016).

Based on this framework, a recent study of ichnofabrics from core samples and their associations with eolian sub-environments has helped to refine the understanding of the spatial and ecological evolution of an eolian system over time (Buatois and Echevarría, 2019). For example, high levels of preserved bioturbation are often associated with wet or moist interdune environments that reduce eolian erosion and indicate a relatively high water table (Loope and Rowe, 2003; Ekdale et al., 2007; Buatois and Echevarría, 2019b). Cores from facies interpreted to be near the water table were associated with ichnofabrics identified as *Planolites* isp.-*Palaeophycus* isp. ichnofabric and *Taenidium* ichnofabric (Buatois and Echevarría, 2019b). These ichnofabrics were characterized by low ichnodiversity and ichnodisparity, high levels of

bioturbation, and ichnofossil morphologies suggestive of deposit feeding behaviors (Buatois and Echevarría, 2019). Cores displaying low bioturbation, identified as *Digitichnus* isp. ichnofabric, *Arenicolites* isp. ichnofabric, *Skolithos linearis* ichnofabric, and “dwelling burrow” ichnofabric, were associated with eolian dune environments (Buatois and Echevarría, 2019). These ichnofabrics were characterized by moderate ichnodiversity, low levels of bioturbation, and ichnofossil morphologies interpreted to be associated with the colonization of a limited number of dietary generalists, such as arachnid ambush predators that have been found to make *Skolithos*-style burrows (Ahlbrandt et al., 1978; Uchman et al., 2018; Buatois and Echevarría, 2019b; Hembree, 2023). The interpretation of these ichnofabrics was further supported by other forms of sedimentologic evidence, largely related to the angles of cross-cutting (in dune settings) and presence or absence of adhesion structures (in interdune associations) (Buatois and Echevarría, 2019). Thus, combining the sedimentologic and stratigraphic interpretations of eolian deposits with ichnofabric interpretations can lead to a comprehensive understanding of the evolution of eolian environments over time and space.

Though the study of desert ichnofossils and ichnofabric has yielded some understanding of the paleoecology of ancient eolian environments, there is still much work to be done with unrecognized or misinterpreted structures (Ekdale et al., 2007; Bordy, 2008; Good and Ekdale, 2014). One example is the interpretation and reinterpretation of structures in the Entrada Sandstone as either vertebrate burrows or as wells produced by heavy rainfall (i.e., entirely abiotic) (Loope, 2006; Odier, 2007). Many other examples of relatively indistinct, unlined and/or otherwise amorphous traces from

bioturbated eolian deposits in the western United States including the Moenave Formation, Navajo Sandstone, Aztec Sandstone, and Nugget Sandstone commonly remain unassigned (Tanner et al., 2006; Ekdale et al., 2007; Engelmann et al., 2014; Britt and Chure, 2016; Rowland and Caputo, 2016). As shown in previous neoichnological experiments, using study species within clades that are temporally long-ranging can mitigate this knowledge gap of eolian paleoecology (Hembree et al., 2012; Hsieh et al., 2023).

Study Species

The species investigated in this project were selected for their availability from animal suppliers and their occurrence in soils of eolian environments. In addition, their relatively disparate evolutionary relationships, several distinct body plans, and two key feeding styles (carnivore and detritivore/herbivore) were critical in observing the variability of arthropod behaviors observed in modern eolian environments. Studied species included three carnivores (*Smeringurus mesaensis*, *Hogna lenta*, and *Paragaleodes sericeus*) and three detritivores/herbivores (*Orthoporus ornatus*, *Eleodes armata* and *Ammopelmatus* cf. *fuscus*) (**Figure 1**).

Smeringurus mesaensis is a medium-to-large-sized (up to 8 cm long) scorpion restricted to sandy, open deserts in California and Arizona in the United States and Baja California and Sonora in Mexico (Haradon, 1983). Hunting at night, this scorpion typically preys on small arthropods such as crickets, beetles, and other scorpions (Polis and Farley, 1980). *Paragaleodes sericeus* is a medium-sized (5-10 cm long) species of solifuge, or camel spider, known from deserts of Egypt (Kraeplin, 1899). Like most

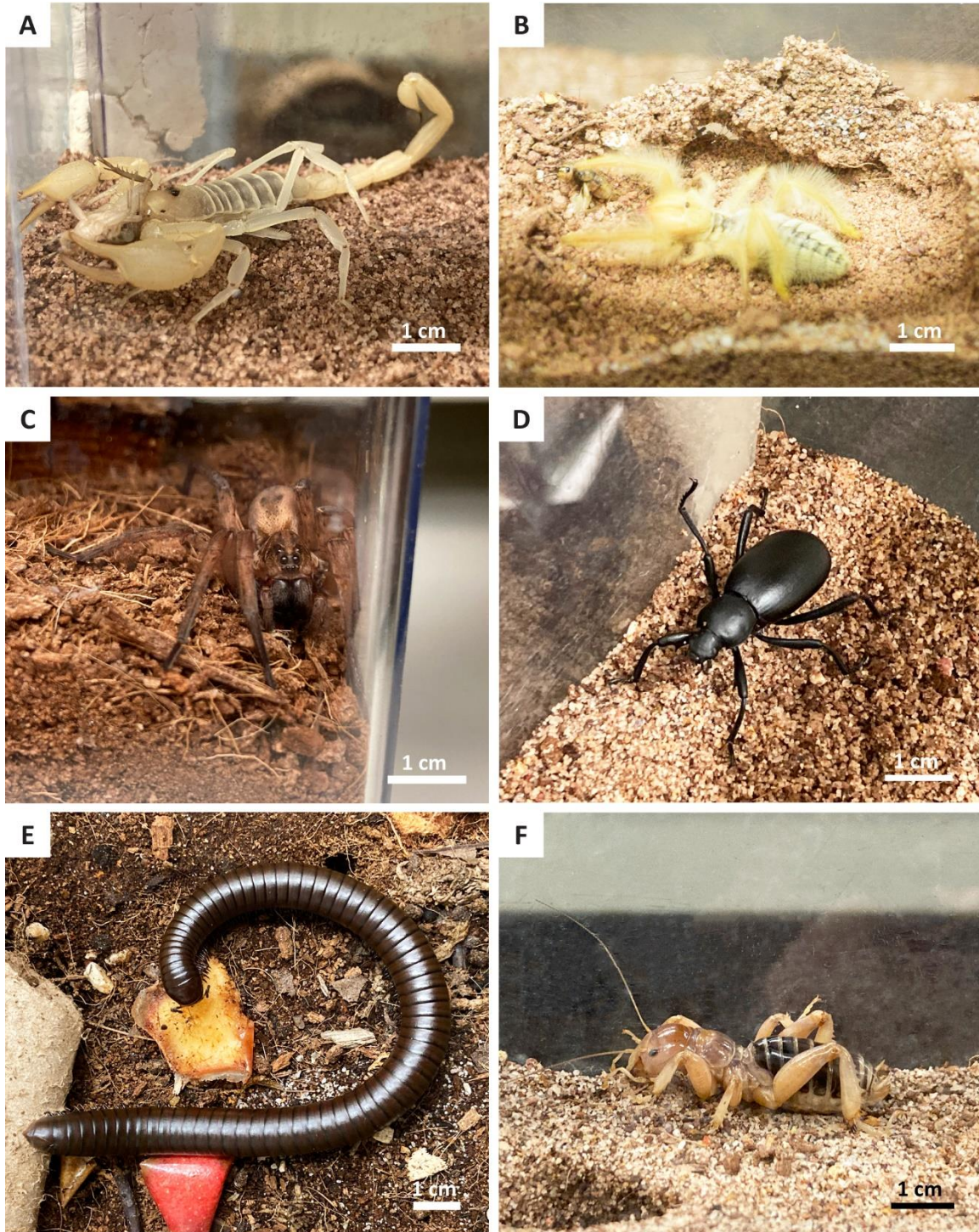


Figure 1. Arthropod species used in this study. A) *Smeringurus mesaensis* (carnivore). B) *Paragaleodes sericeus* (carnivore). C) *Hogna lenta* (carnivore). D) *Eleodes armata* (detritivore). E) *Orthoporus ornatus* (detritivore). F) *Ammopelmatus* cf. *fuscus* (detritivore).

solifuges, it is a nocturnal predator, feeding primarily on insects and other arachnids (Punzo, 1998). Solifuges are known to have a variety of adaptations to particularly harsh environments with high temperatures, like the dunes of eolian environments (Cloudsley-Thompson, 1977; Hebets et al., 2023). *Hogna lenta* is a common species of wolf spider, roughly 1-2 cm in body length, ranging across the southeastern United States (Wallace, 1942). These non-web building spiders are most frequently found on and in sandy substrates (Punzo, 1991; Eiseman and Charney, 2010). They typically inhabit burrows, oftentimes with a sealed silk-lined trapdoor, leaving at night to hunt small insects and smaller arachnids that make up most of their diet (Wallace, 1942; Punzo, 1991; Eiseman and Charney, 2010).

Orthoporus ornatus is a medium-sized (up to 10 cm long) millipede ranging from western Texas to Arizona and south into the deserts of northwestern Mexico, particularly in the deeper soils of the Sonoran Desert (Crawford et al., 1987). This millipede is a nocturnal species, spending the majority of time in burrows to avoid water loss (Wooten and Crawford, 1975). Their diet consists of detritus, superficial tissues of shrubs, and some soil (Wooten and Crawford, 1975). *Eleodes armata* is a moderate-sized (2-3 cm long) tenebrionid beetle, inhabiting much of the western United States and northwestern Mexico, particularly the Mojave and Sonoran Deserts (Thomas, 1984). During the warmer months, this species is nocturnal, coming out during the day only in cooler temperatures. It is primarily a scavenging species, feeding on decaying animal or plant matter as well as fresh plant material (Thomas, 1984). *Ammopelmatus* sp. cf. *fuscus*, commonly known as the “Jerusalem cricket”, is a robust, large (up to 7.5 cm long) insect

belonging to a relatively understudied clade of orthopterans (Stenopelmatidae) that specializes in a fossorial habit (Weissman, 2001; Weissman et al., 2021). Though much of the taxonomy of this group is still unclear, there are two specialist groups of Jerusalem crickets identifiable by distinct morphology: sand dune specialists and cloud forest specialists (Weissman, 2001). Some Jerusalem crickets, including *Ammopelmatius fuscus*, are generalists, although they may be sympatric with these two specialist groups. The range of Jerusalem crickets is from Panama to British Columbia and from the majority of the west coast of the United States east to Oklahoma, though more recently the group that lives in North America has been separated out into the genus *Ammopelmatius* (Weissman, 2001; Weissman et al., 2021). The specimens used in this study are from the deserts of southeastern California, an area which is currently under taxonomic revision (Weissman et al., 2021). This geographic area suggests that they are native to sandy habitats, in an area where dune specialists and generalists are known to be microsympatric (Weissman, 2001). Jerusalem crickets are generally known as dietary generalists (omnivores, herbivores, detritivores), and have been raised in laboratory settings on a combination of lettuce, dry cat food, rabbit food, and uncooked oats (Weissman and Bazelet, 2013).

CHAPTER THREE

MATERIALS AND METHODS

Experimental Setup and Data Collection

Specimens of six arthropod species, *Smeringurus mesaensis* (scorpion), *Pargaleodes sericeus* (solifuge), *Hogna lenta* (wolf spider), *Eleodes armata* (darkling beetle), *Orthoporus ornatus* (millipede), and *Ammopelmatus fuscus* (Jerusalem cricket) were acquired from animal suppliers and pet dealers (**Figure 1**). These species were chosen for their variability in body plans and trophic types, relatively distant phylogenetic relationships, fossorial habits, and their recorded observations in desert dune settings. Multiple specimens of each species were used to account for individual variation of behavior. Five specimens of *S. mesaensis*, *H. lenta*, *O. ornatus* and *A. cf. fuscus* (20 total specimens) were used. Four specimens of *E. armata* and two specimens of *P. sericeus* were used throughout as many trials as they could continue through (all five for *E. armata* and the low moisture, moderate moisture mixed homogenized for *P. sericeus*).

Each study animal was housed in an experimental terrarium, either 22 or 38 L, depending on the full-grown size of the species (**Table 1**) (**Figure 2**). The terrariums were sectioned off with plexiglass dividers to produce a space approximately 6 cm by 41 cm (22-liter tanks), and 6 cm by 50 cm (38-liter tanks). The front 6 cm of the terrarium was filled with sediment to a depth of 20 cm. Predatory study animals (*P. sericeus*, *S. mesaensis*, and *H. lenta*) were fed live crickets once a week. *Orthoporus ornatus*, *A. cf. fuscus*, and *E. armata* were fed plant material (apples and carrots), as needed. To

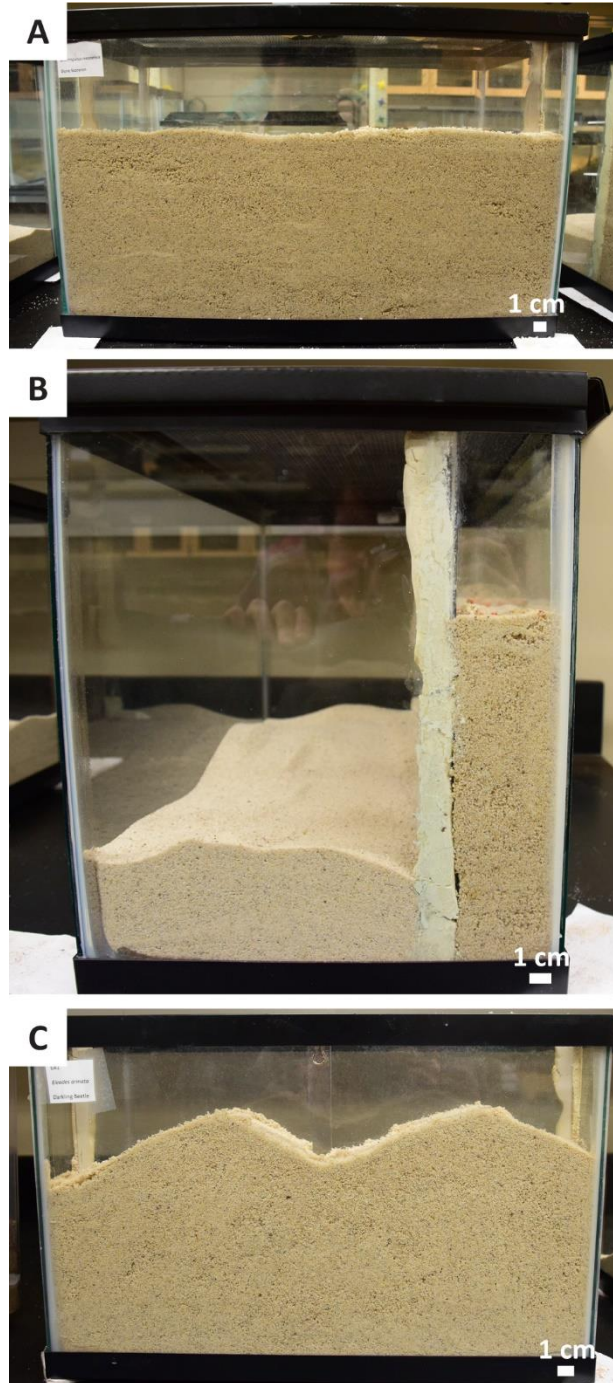


Figure 2. Enclosure set up for study with sand substrate. A) Front side of 38 L tank at start of an experiment. B) Side view of a 38 L tank during an experiment, showing plexiglass partition 6 cm back from front side of enclosure. C) Simulated wind ripple from the front side of a 22 L tank at the beginning of an experiment.

Table 1. Experimental setup for *S. mesaensis*, *P. sericeus*, *H. lenta*, *E. armata*, *O. ornatus*, and *A. cf. fuscus*. C = clay/silt, O = organics (coconut fiber), S = quartz sand.

Experiment 1. Moderate Moisture Environment

Species	# of specimens	Moisture%	Substrate Composition (Homogenized)	Tank Size (L)	Sediment Depth (cm)	Enclosure Dimensions L x W x H (cm)	Duration
<i>S. mesaensis</i>	5	8-12%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>P. sericeus</i>	2	8-12%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>H. lenta</i>	5	8-12%	25/25/50 (C/O/S)	22	20	41 x 6 x 27	14 days
<i>E. armata</i>	4	8-12%	25/25/50 (C/O/S)	22	20	41 x 6 x 27	14 days
<i>O. ornatus</i>	5	8-12%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>A. cf. fuscus</i>	5	8-12%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days

Experiment 2. Low Moisture Conditions

Species	# of specimens	Moisture%	Substrate Composition (Homogenized)	Tank Size (L)	Sediment Depth (cm)	Enclosure Dimensions L x W x H (cm)	Duration
<i>S. mesaensis</i>	5	0-5%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>P. sericeus</i>	2	0-5%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>H. lenta</i>	5	0-5%	25/25/50 (C/O/S)	22	20	41 x 6 x 27	14 days
<i>E. armata</i>	4	0-5%	25/25/50 (C/O/S)	22	20	41 x 6 x 27	14 days
<i>O. ornatus</i>	5	0-5%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>A. cf. fuscus</i>	5	0-5%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days

Experiment 3. High Moisture Conditions

Species	# of specimens	Moisture%	Substrate Composition (Homogenized)	Tank Size (L)	Sediment Depth (cm)	Enclosure Dimensions L x W x H (cm)	Duration
<i>S. mesaensis</i>	5	15-25%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>H. lenta</i>	5	15-25%	25/25/50 (C/O/S)	22	20	41 x 6 x 27	14 days
<i>E. armata</i>	4	15-25%	25/25/50 (C/O/S)	22	20	41 x 6 x 27	14 days
<i>O. ornatus</i>	5	15-25%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>A. cf. fuscus</i>	5	15-25%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days

Experiment 4. Layered Mixed Soil Substrate

Species	# of specimens	Moisture%	Substrate Composition (Layered)	Tank Size (L)	Sediment Depth (cm)	Enclosure Dimensions L x W x H (cm)	Duration
<i>S. mesaensis</i>	5	8-12%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>P. sericeus</i>	2	8-12%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>H. lenta</i>	5	8-12%	25/25/50 (C/O/S)	22	20	41 x 6 x 27	14 days
<i>E. armata</i>	4	8-12%	25/25/50 (C/O/S)	22	20	41 x 6 x 27	14 days
<i>O. ornatus</i>	5	8-12%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>A. cf. fuscus</i>	5	8-12%	25/25/50 (C/O/S)	38	23	50 x 6 x 32	14 days

Table 1. Continued
Experiment 5. Sand Substrate

Species	# of specimens	Moisture%	Substrate Composition	Tank Size (L)	Sediment Depth (cm)	Enclosure Dimensions L x W x H (cm)	Duration
<i>S. mesaensis</i>	5	8-12%	0/0/100 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>P. sericeus</i>	2	8-12%	0/0/100 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>H. lenta</i>	5	8-12%	0/0/100 (C/O/S)	22	20	41 x 6 x 27	14 days
<i>E. armata</i>	4	8-12%	0/0/100 (C/O/S)	22	20	41 x 6 x 27	14 days
<i>O. ornatus</i>	5	8-12%	0/0/100 (C/O/S)	38	23	50 x 6 x 32	14 days
<i>A. cf. fuscus</i>	5	8-12%	0/0/100 (C/O/S)	38	23	50 x 6 x 32	14 days

facilitate burrowing behavior of *E. armata*, two small (3 cm tall, ~15° slope on lee side, 30° on stoss side) mounds of sediment mimicking the architecture of large wind ripples were added at the substrate surface. When not being utilized for experiments, animals were housed in small enclosures with other members of their own species (*E. armata*, *O. orthoporus*) or individually (*H. lenta*, *P. sericeus*, *A. cf. fuscus*, *S. mesaensis*).

Five experimental trials were run with each species, focusing on two independent variables: sediment composition and sediment moisture (**Table 1**) (**Figure 3**). Three of the trials tested the independent variable of sediment composition, keeping moisture within a range of 8-12%, measured at the beginning and end of trials with a soil moisture meter (EXTECH Model MO750). Substrate disturbance behaviors were studied first with a homogenized mixture of 25% organics (coconut fiber), 25% silt/clay, and 50% quartz sand. A second trial utilized an identical proportion of organics, silt/clay, and sand set down in the enclosure in separate, 1.25-cm (organics and clay) and 2.5-cm (sand) thick layers. A third trial utilized layered 100% quartz sand. In the final two trials, substrate disturbance behavior was studied as a reflection of soil moisture change. The homogenized mixture of organic, silt/clay, and sand was used as a substrate for these two trials. The sediment had moisture ranges of 0-5% and 15-25%. Maintenance of moisture was conducted by misting the surface area of enclosures every three to six days to reach desired moisture ranges. All trials were kept at temperatures ranging between 20-25° C. To induce activity, additional heat was added to *P. sericeus* enclosures with heat lamps suspended 3 cm above enclosure lids. Each trial was run for two weeks during which

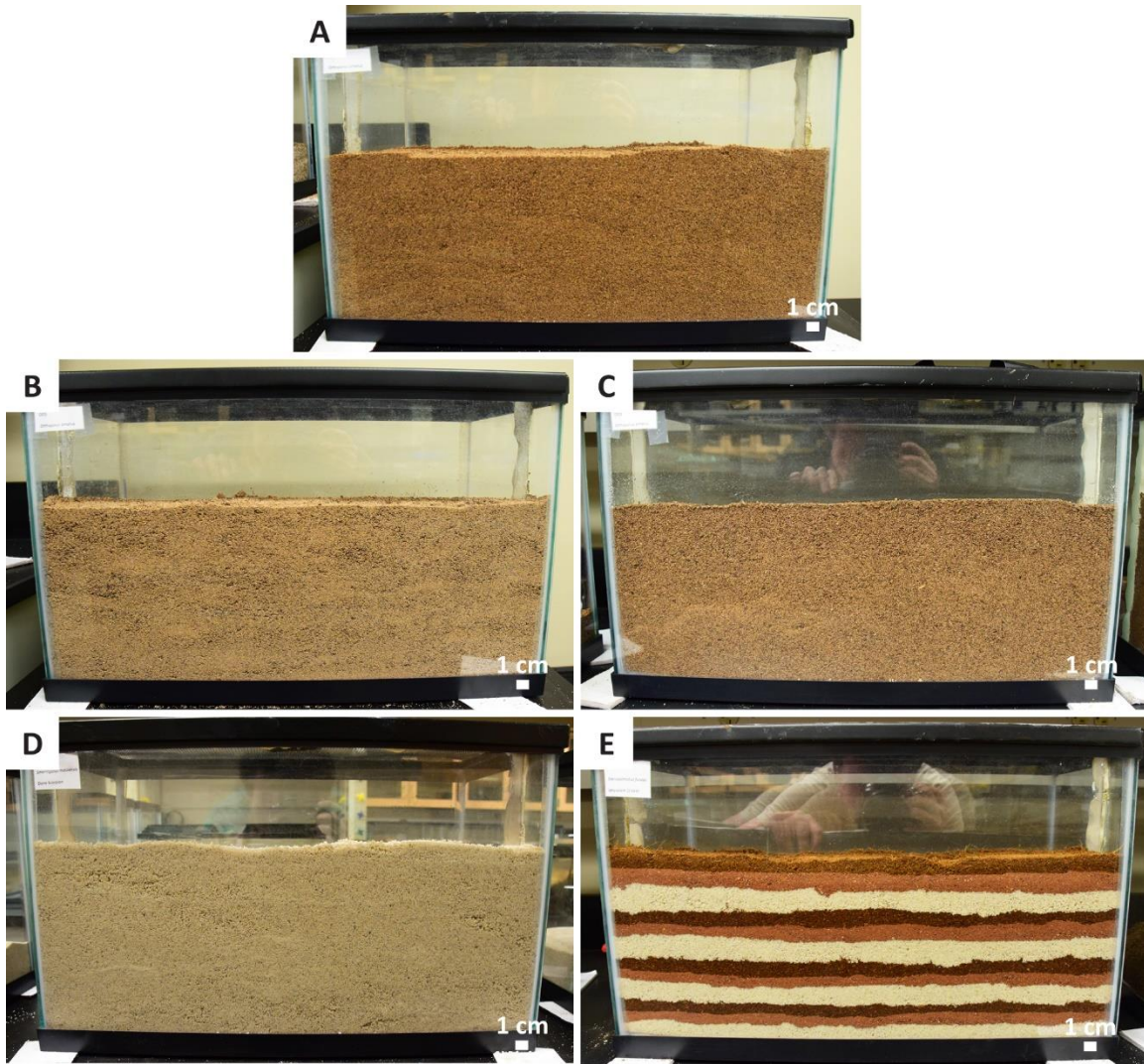


Figure 3. 38 L tanks set up at the beginning of experiments in five conditions. A) Moderate moisture (8-12%) homogenized substrate. B) Low moisture (0-5%) homogenized substrate. C) High moisture (15-25%) homogenized substrate. D) Moderate moisture (8-12%) sand substrate. E) Moderate moisture (8-12%) layered substrate with four repeated patterns of sand layers (2.5 cm), silt/clay layers (1.25 cm) and organic layers (1.25 cm).

substrate disturbance activities and structures were observed, photographed, and digitally recorded. Notes, sketches, and measurements were made of two-dimensional structures produced by substrate disturbance behavior each day.

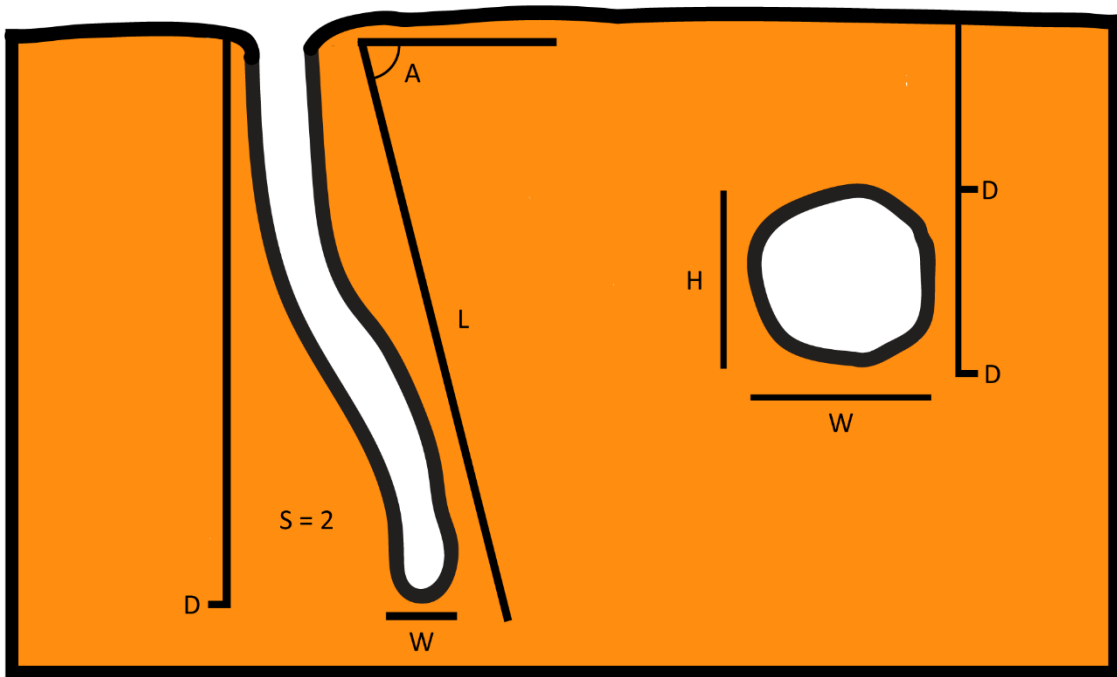
Analysis of Biogenic Fabrics

Biogenic fabrics were described in two dimensions as presented by the front, back, and side surfaces of the enclosed space, both qualitatively and quantitatively each day. Recognizable individual structures (such as shafts, tunnels, or chambers) were described in terms of their orientation, general form, branching, overall configuration, the presence or absence of walls/linings, and type of fill if present (active or passive). Quantifiable aspects of morphology recorded for each burrow included width (if possible), height, length, depth, and slope (**Figure 4**). Qualitative aspects of bioturbation were compared based on presence or absence of specific features, distinct orientations, and variation in general form. At the end of each trial, all four sides of enclosures were evaluated according to the Ichnofabric Index (II). Mean II and the highest recorded depths of disturbances from each trial were also recorded.

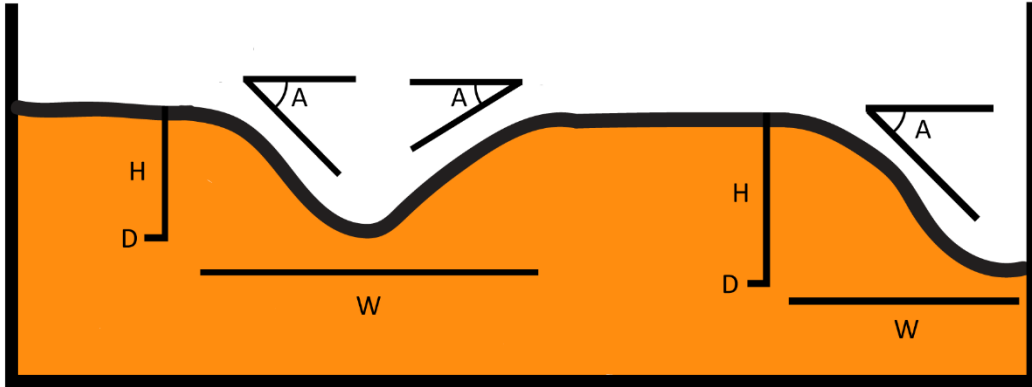
Biogenic fabrics from each trial were compared: 1) between the six species, 2) among individuals within each species, and 3) between different sediment conditions (moisture and sediment composition). Quantitative properties of individual traces were compared using cluster analyses with a Bray-Curtis similarity index used as a measure of distance, as described in Hembree (2016). Ward's method for cluster joining was used for its ability to produce discrete clusters (Legendre and Legendre, 1998). It is notable that although Ward's method is based on Euclidean distance, it is still can be used with non-

Figure 4. (next page) Examples of measured properties of two-dimensional substrate disturbances in two tanks. A) An example tank with open, sinuous burrow and a chamber with example measurements taken. B) An example tank with a full divot alongside the front of an enclosure and a divot that goes into the corner of the enclosure. A= Angle or average angle when multiple could be measured. D= minimum (if zero not shown) and maximum depth of substrate disturbance beneath substrate profile. H= Height of substrate disturbance, equivalent to L. L= Length of burrow, measured across different angles of a burrow. W= Width of disturbance. S= Sinuosity of burrows. Sinuosity was measured as the average number of turns or bends that a burrow displays.

A



B



Euclidean distance to produce meaningful results (Borcard et al., 2011). Measurements were normalized along columns to account for differences in the scale of different measured substrate disturbance properties. Cluster analyses were then performed using an agglomerative nesting method to facilitate the building of individual clusters that were most alike until a full dendrogram was constructed.

Structures made by each species under the range of moisture conditions were compared against each other using cluster analyses. A second set of cluster analyses was performed to compare structures made by the same species in the different substrate compositions. A final cluster analysis was performed to compare structures produced by all of the study animals in the layered substrate trials. Clusters defined biogenic structures that shared similar quantitative properties. Previous studies have demonstrated that clusters may be composed of structures only produced by a single species when they are distinct from those of other species (Hembree, 2016). Clusters may also define distinct changes in morphology of biogenic structures due to differences in substrate conditions, particularly if these divisions are among structures produced by the same species.

Ichnofabric index in layered substrate and the depth of bioturbation in every substrate condition were evaluated for significance first with a Kruskal-Wallis Test (Davis and Sampson, 1986). A pairwise Wilcoxon signed rank test was performed to demonstrate which results were significantly different from each other as in Rodríguez-Tovar et al. (2014). All statistical analyses were conducted using R studio (version 2024.04.2).

Biogenic structures produced in these experiments were compared qualitatively to those described from the fossil record of eolianites, including burrows and ichnofabrics displaying similar morphologies from a variety of Mesozoic sites across the world. The Early Jurassic Aztec, Navajo and Nugget sandstones, the Mid Jurassic Entrada Sandstone, the Lower Cretaceous Três Barras Formation, the Lower Cretaceous Mulichinco Formation, the Upper Cretaceous Allen Formation, and the Upper Cretaceous Djodokhta Formation all bear documented traces that are useful to compare with the substrate disturbances identified from this study.

CHAPTER FOUR

RESULTS

Burrowing Techniques

The scorpion, *Smeringurus mesaensis*, excavated sediment by utilizing one side of its body's legs and then the other side sequentially to kick sediment backwards with some velocity (**Figure 5A**). This occurred fastest in dry substrates, with low angle excavation. In more moist substrates, scorpions are more methodical in excavation, sometimes planting one or two pairs of their hind legs while excavating with their front pairs on each side, sequentially.

The solifuge, *Paragaleodes sericeus*, excavated sediment with its front two pairs of legs in tandem, keeping the back pairs of legs planted (**Figure 5B**). This resulted in a slow excavation process. When sediment was compact at the surface or dried after being wet, solifuges used their powerful chelicerae to break up the surface before using their typical excavation techniques. Occasionally, some specimens produced enclosed chambers beneath pieces of bark using their pedipalps to push sediment out from under bark and create low mounds around the edges of the bark.

The wolf spider, *Hogna lenta*, was observed excavating sediment methodically, using its pedipalps to carry individual packets of sediment from the point of excavation to the surface of a burrow or divot. Individuals deposited large numbers of these sediment packets around the burrow openings or divots to produce low mounds (**Figure 5C**). Over time, the burrows would often be lined with thin layers of silk and sediment, producing a stabilized form for the burrow regardless of any substrate displacement around it. At the

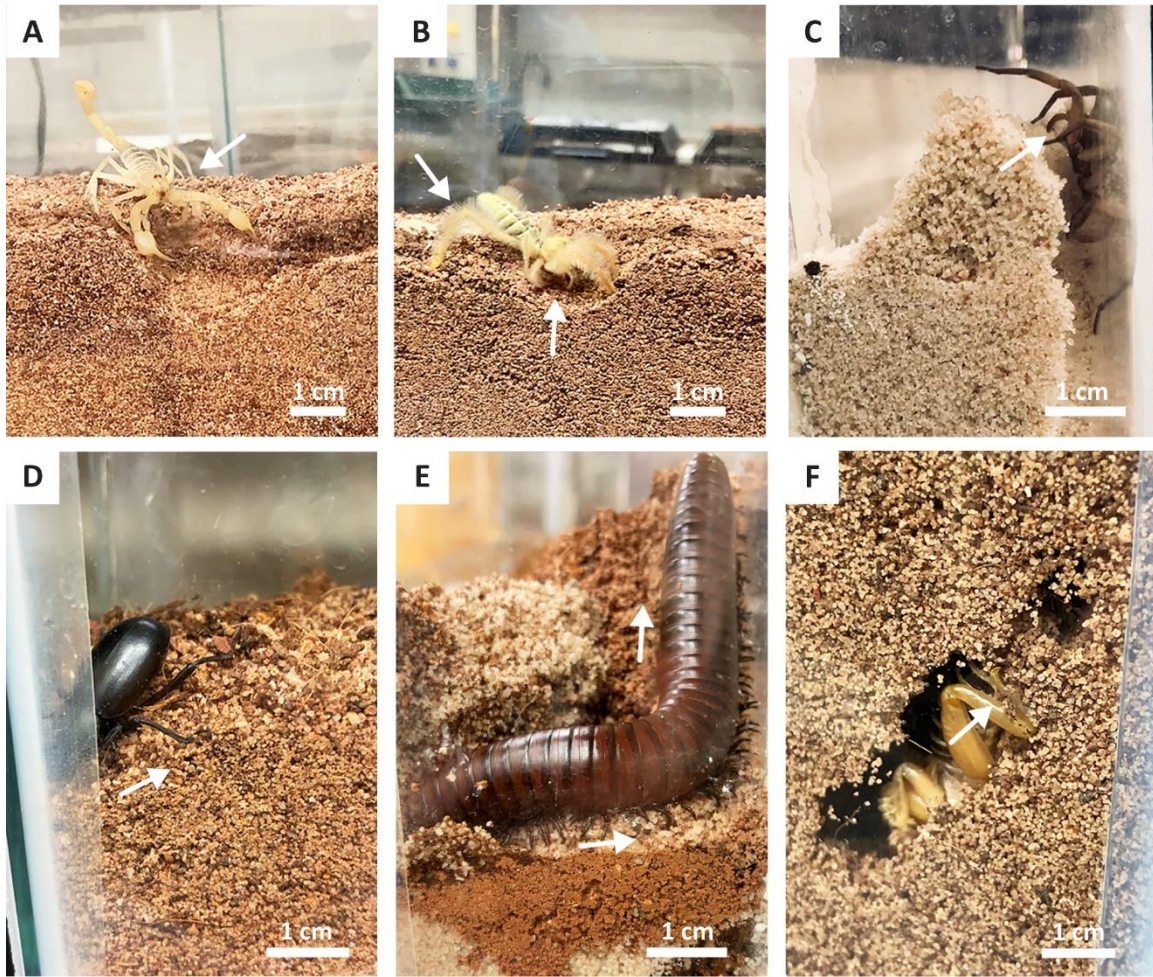


Figure 5. Burrowing techniques of the six study species. A) Excavation by *S. mesaensis*, showing one side of its body's legs actively kicking back sediment while the other is held in place. B) Excavation by *P. sericeus*, with its rear legs planted and front two pairs of legs actively grabbing and pushing back packets of sediment (at arrows). C) Excavation by *H. lenta*, with an individual packet of sand being carried to the entrance of the burrow by its pedipalps (at arrow). D) Excavation by *E. armata* in a corner of an enclosure, using its legs to push sediment slowly in the direction of the arrow. E) Excavation by *O. ornatus*, using successive pairs of legs to push sediment back in the direction of the arrows to its posterior. F) Backfilling by *A. cf. fuscus*, using its posterior legs to push a packet of sediment behind it into a space and stabilizing it.

openings of burrows, silk linings were utilized to produce a trap door that could be opened and closed as needed.

The beetle, *Eleodes armata*, was rarely seen excavating sediment. It used its front and back pairs of legs to slowly move sediment behind its body (**Figure 5D**). This had minimal effect on the substrate surface when observed, so it is difficult to attribute this activity to the few deeper divots and one very large substrate disturbance produced by *E. armata*. It is likely responsible, however, for the large amount of sediment that was redistributed to change the simulated wind rippled surfaces into flatter surfaces.

The millipede, *Orthoporus ornatus*, was observed excavating sediment by first forcing their heads into the sediment surface to create an impression. They then used their legs to repeatedly push grains and packets of sediment from the front of their body to the back, resulting in the largest observed sediment piles both near the entrance of burrows and oftentimes further away (6-8 cm from the entrance) (**Figure 5E**).

The Jerusalem cricket, *Ammopelmatus* cf. *fuscus*, was observed using a backfilling technique as it moved a chamber continuously through the subsurface while feeding. It started digging first by excavating sediment with its head, then moving the sediment backwards with its front two pairs of legs. The new chamber's position was then stabilized with a back pair of legs compacting newly excavated, loose sediment on the back end of the chamber (**Figure 5F**).

Morphology of Biogenic Structures

Smeringurus mesaensis.— The most typical substrate disturbance produced by *S. mesaensis* involved the reorganization of sediment at the surface in association with the

production and movement of 2-10 cm wide, 1-4 cm deep divots, most evident in the dry, layered, and sand substrates. Reorganization of sediment resulted in 20–40-degree parallel laminae commonly preserved shortly after misting the enclosure and most visible in layered substrates (**Figure 6A**).

In corners of the enclosures, *S. mesaensis* would excavate and maintain a stable divot that could be subhorizontal or subvertical (20-60°) (**Figure 6C-D**). The angle of these divots and their stability depended largely on the moisture conditions. Divots were most commonly produced and steepest under moderate moisture conditions. In low moisture conditions they were the shallowest and least steep, whereas in high moisture conditions they were shallow with varying steepness.

Smeringurus mesaensis produced burrows most commonly (n=25) in moderate moisture conditions, levelling out no more than 3 cm below the surface (**Figure 6D**). The burrows consisted of shallow ramps that were subhorizontal (30-45°) at their entrance and leveled off to near horizontal after several centimeters. The horizontal portion of these burrows was 3-7 cm in length, following the size of the scorpion, though many curved away from the sides of the enclosure out of view.

Paragaleodes sericeus.—*Paragaleodes sericeus* produced common (n=3) shallow, subhorizontal, open burrows that leveled out beneath bark or against glass in homogenized substrates. Angled entrances continued for 1.0-1.5 cm before levelling out and extending roughly 1 cm beyond the length of the animal (a total of 5-8 cm) in a horizontal, flask shape (**Figure 7A-C**).

When not producing a burrow, *P. sericeus* most commonly (n=8) created a

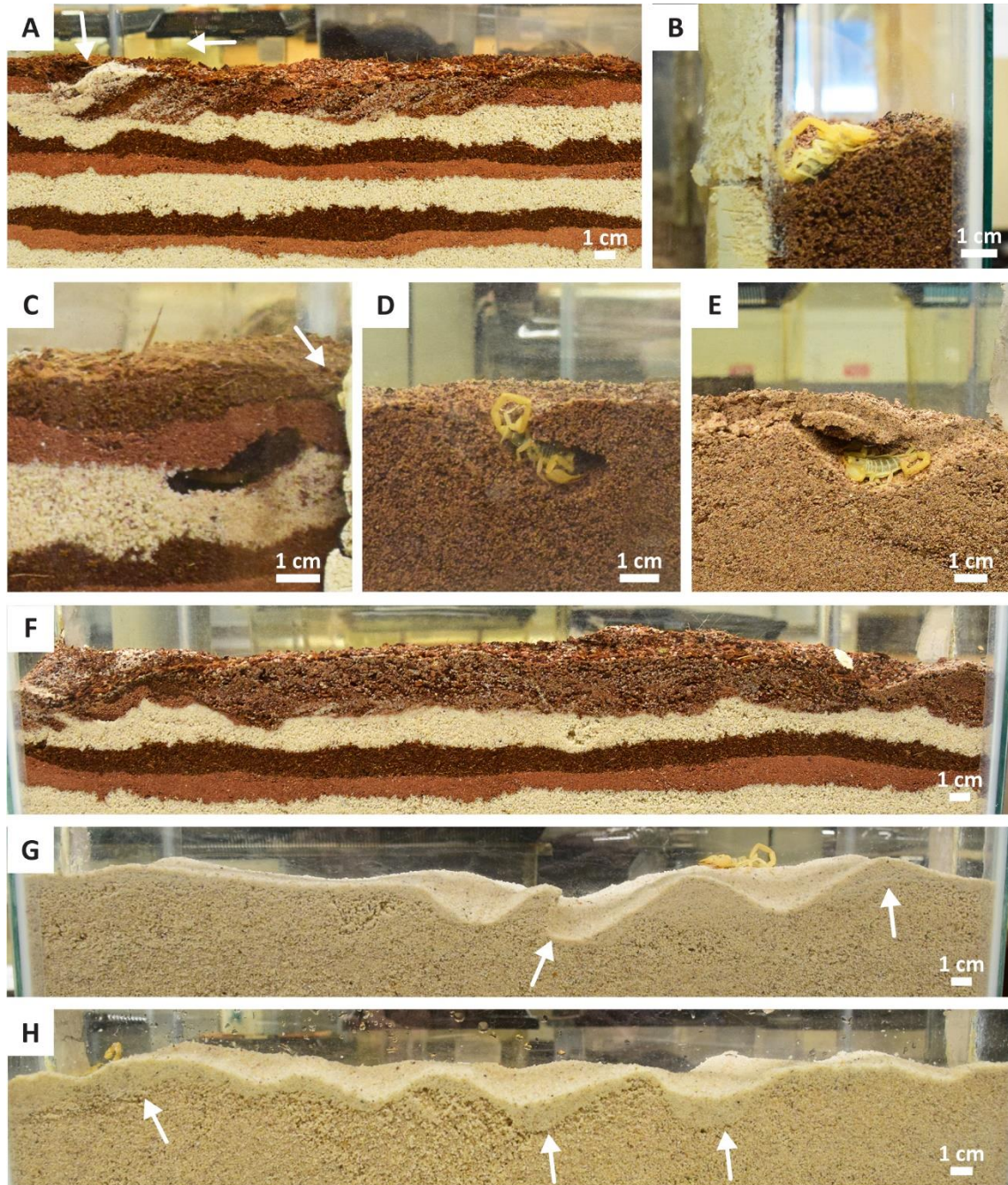


Figure 6. Biogenic structures of *S. mesaensis*. A) Parallel and subparallel laminae resulting from lateral movement of a surface divot (in direction of right arrow) to a final divot (left arrow). The final divot is located at the black arrow. B) Shallow divot created at the corner of the enclosure in a high moisture trial. C) Cross sectional view of a chamber that curves back from the glass (arrow indicates entrance). D) Burrow under active excavation in a moderate moisture trial. E) *S. mesaensis* resting in a shallow burrow before its collapse in a low moisture trial. F) ~3 cm deep homogenized surface horizon at the end of a layered substrate trial. G) Shifting divots across sand showing an attempted burrow (left arrow) and excavated sand that is highlighted when moisture is added (right arrow). H) Small deposits of excavated sand that fill in former divots (at arrows).

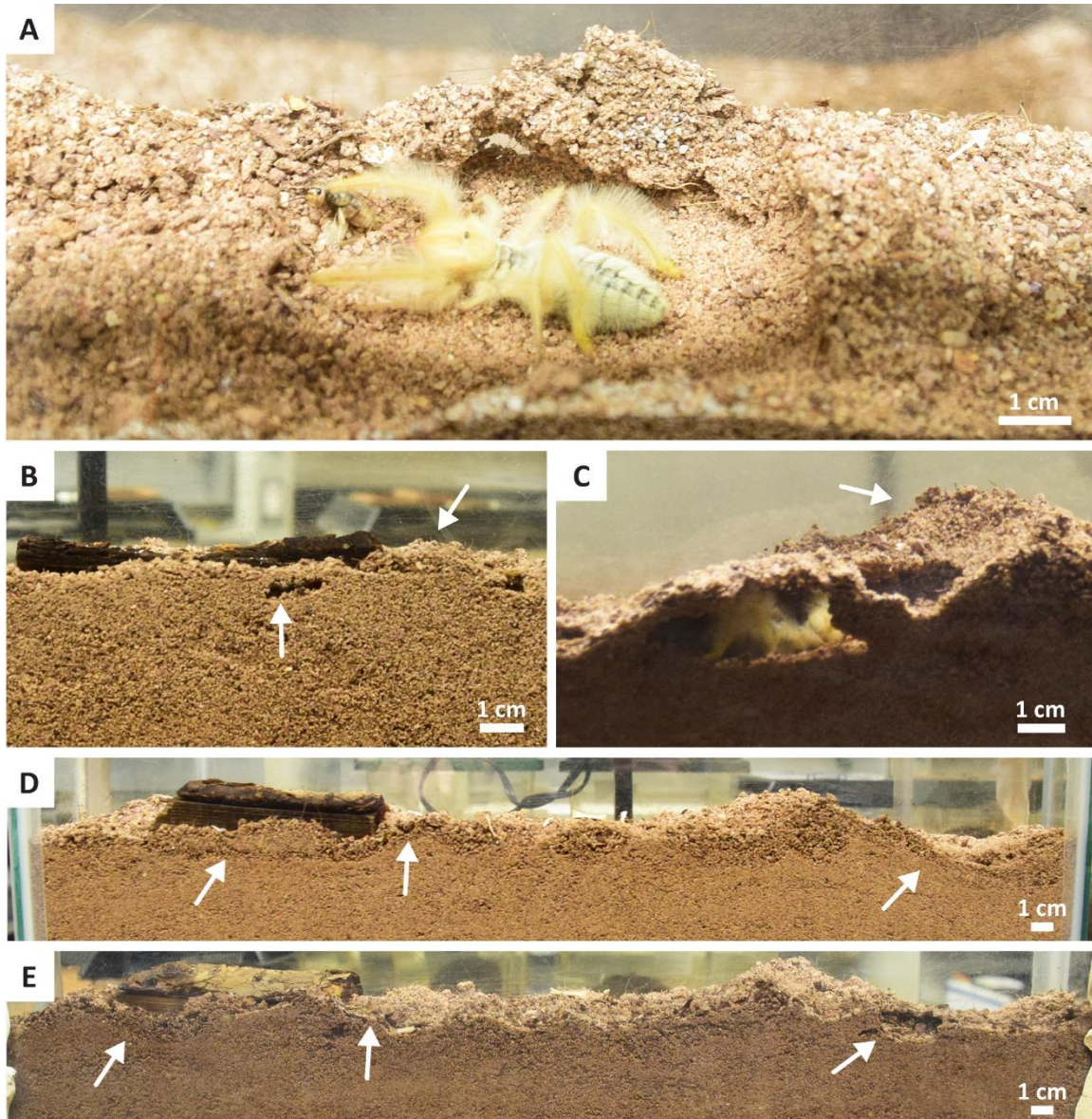


Figure 7. Biogenic structures of *P. sericeus*. A) Chamber in moderate moisture substrate produced beneath wood at surface (removed). B) Cross-sectional view of chamber (left arrow) produced beneath wood at the surface. Excavated sediment is mounded at the edge of the chamber (right arrow). C) Shallow chamber without a surface feature produced in a low moisture trial. Excavated sediment (at arrow) is deposited near the opening. D) Front view of biogenic structures produced in low moisture conditions, characterized by reworking of the upper layer of sediment across the enclosure, a chamber beneath the wood (left two arrows), and laminae produced during excavation of a large divot (right arrow). E) Back view of the same enclosure, showing the burrow under the wood (left two arrows) and a collapsed burrow from C.

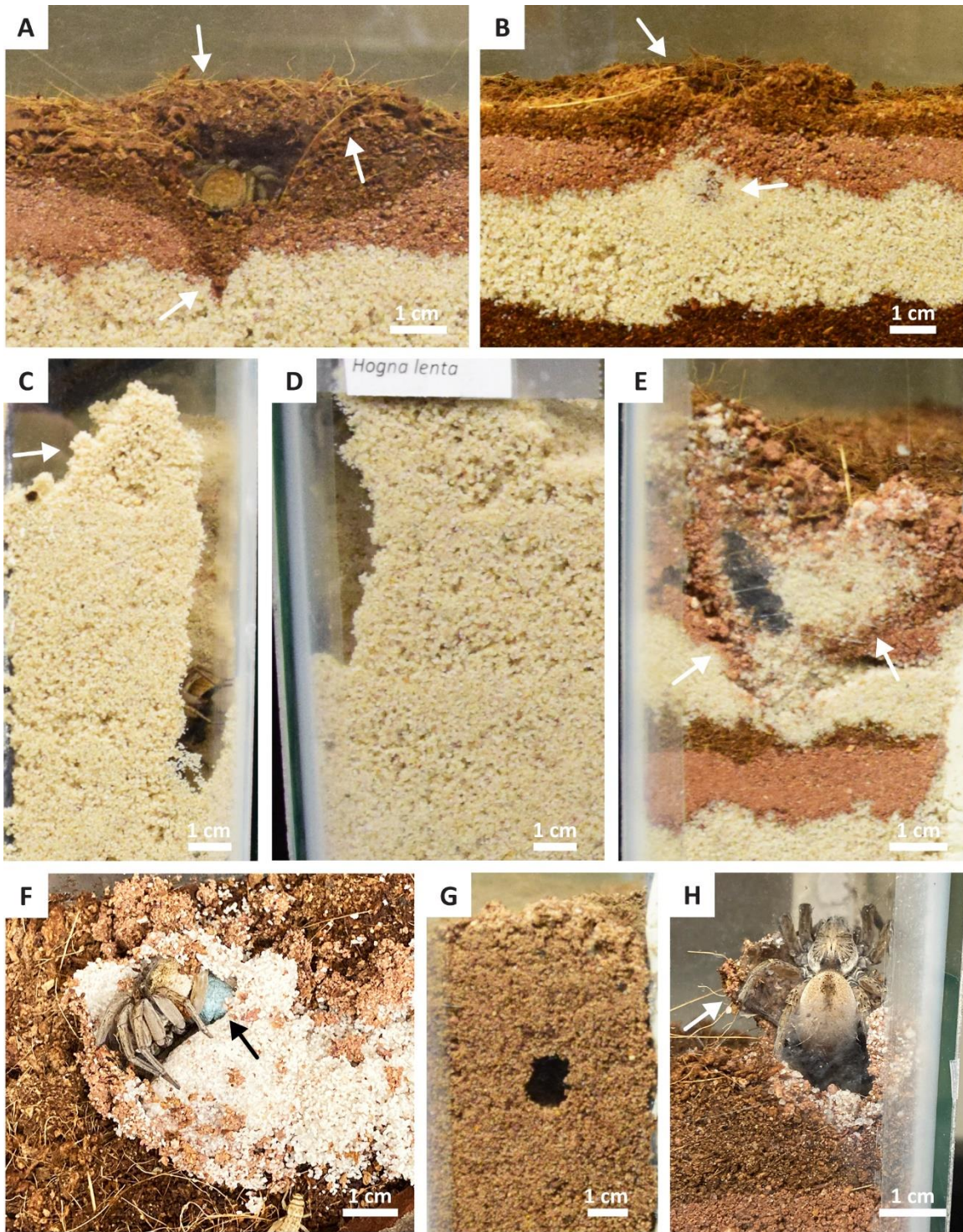
shallow (2-3 cm), semicircular divot, wide enough (3-6 cm) to fit the entire animal (**Figure 7D-E**). These divots were created in all conditions and generally in the corners of enclosures.

Hogna lenta.—One type of *H. lenta* sediment disturbance documented from all conditions (n=22) except sand was a simple circular to semi-circular divot with steep-sided (70-90°) walls, reinforced with a silk-lining around the edges. Divots ranged from 1-3 cm in width and depth with some associated substrate disturbances occurring 1-2 cm deeper than the surficial feature (**Figure 8A**).

Hogna lenta burrows observed (n=5) from layered experiments and one sand experiment included a subhorizontal to subvertical silk-lined burrow ranging in depth from just under the surface to 3 cm (**Figure 8B, 8G**). These burrows ranged in form from relatively amorphous to circular or ovular. The burrow was completed first, before silk lining was added which acted to stabilize the open burrow in the presence of additional moisture or upheaval. If near the surface, linings of entrances were opened and closed continuously over a period of days.

Two other burrows observed from sand and layered substrates were a vertical and a subvertical shaft, respectively, each 1-2 cm in width, and 5-9 cm in length and depth (**Figure 8C-E**). The shafts were produced against a corner of the enclosure. The upper portion of the shafts was lined with silk. The burrow produced in sand substrate was left open to the surface, whereas the burrow in layered substrate had a trapdoor of silk and sediment that was opened and closed in the top layer of organic matter.

Figure 8. (next page) Biogenic structures of *H. lenta*. A) Divot with silk lining (upper two arrows) produced in layered substrate showing displacement of layers below the active surface (at lower arrow). B) Cross section of a sealed off burrow chamber, characterized by mounded substrate at the sediment surface (top arrow) and displacement of layers in the subsurface (lower arrow). C) Cross-sectional view of a 10 cm vertical burrow produced in a sand substrate trial (arrow indicates mound of deposited sediment). D) Front view of the same vertical burrow, appearing shallower from this view. E) Cross-sectional view of a subvertical burrow with a homogenized, silk-lined wall surrounding the chamber (left arrow) and displaced layers far from the chamber (right arrow). F) Opened brooding chamber with a silk and sediment lining after an experiment ended, showing the egg sac (at black arrow) still being guarded. G) Cross section of a chamber in moderate moisture trial. H) A silk-lined burrow covering (at arrow) that was opened and closed several times.



Eleodes armata.—*Eleodes armata* most commonly (n=21) produced shallow (1-2 cm deep), 2-3 cm wide divots in the corners of enclosures with 30-50° slopes (**Figure 9B**). These were made across different environmental conditions, always shortly after misting. They were typically associated with moderate moisture homogenized sediments. In enclosures in which artificial wind ripples were created, specimens of *E. armata* engaged in reworking of sediment near the surface that leveled out the ripples (**Figure 9A-D**). This activity often left crusts on clay-rich substrates and lamination in all substrate compositions (**Figure 9E**).

The only observed burrow produced by *E. armata* occurred in sand substrate which cut through a simulated wind ripple, producing a shallow U-shaped burrow away from the glass. The burrow was started as a divot against the base of a wind ripple and dipped gently from horizontal to subhorizontal orientation before reaching the surface on the other side 7 cm away (**Figure 9C**).

Orthoporus ornatus.—The most common burrow (n=40) produced by *O. ornatus* under all environmental conditions was a single vertical shaft, with widths from 1.0-1.5 cm and lengths from 4-18 cm (**Figure 10B**). While burrow length had a high range of variation, more commonly vertical burrows were just long enough to accommodate the body length of the millipede (5-12 cm). Generally, as length exceeded 7-8 cm, burrows were more sinuous (**Figure 10A**).

One relatively rare (n=6) burrow morphology that was consistent across environmental conditions was a subhorizontal to subvertical ramp. These ramps (40-60° orientation) were 1-1.5 cm in diameter, 5-10 cm in length, and terminated at an enlarged

Figure 9. (next page) Biogenic structures of *E. armata*. A) The start of a sand substrate trial showing simulated wind ripples. B) The substrate surface after one day, displaying divots constructed in the corners of the enclosure (at arrows). C) Substrate surface after 13 days, showing a burrow/divot cutting through a simulated wind ripple (at arrows). D) Sediment surface at the end of a trial with the transport of sand from the crests to the troughs (arrows pointing at redeposited sand). E) The shortened entrance to a burrow (left, lower arrow) cutting into the base of a simulated wind ripple (right arrow). F) Levelled sediment surface at the end of a low moisture trial. G) Cross section of an infilled divot at the end of layered substrate trial. H) Surficial marks from the movement of *E. armata* in sand.

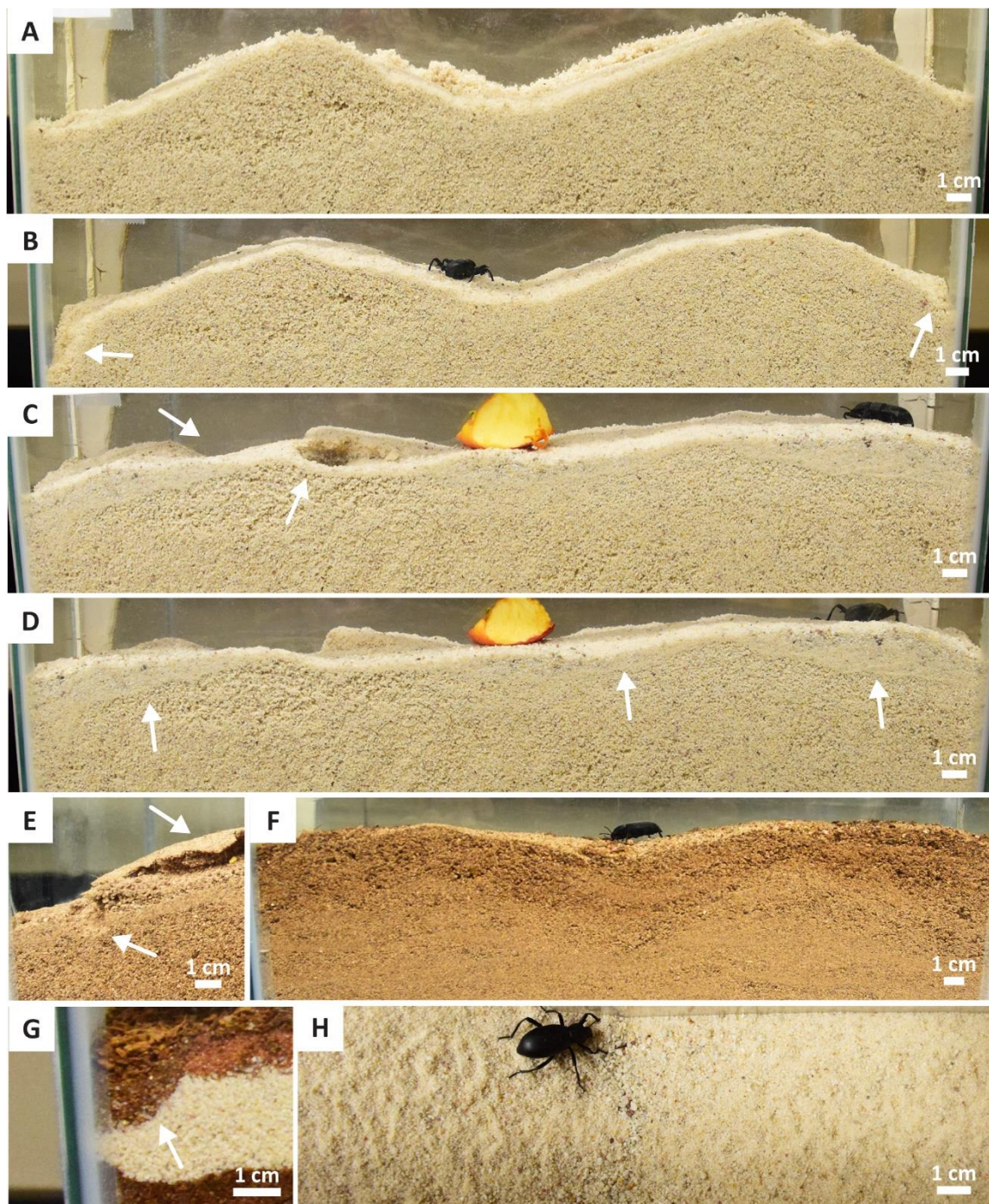
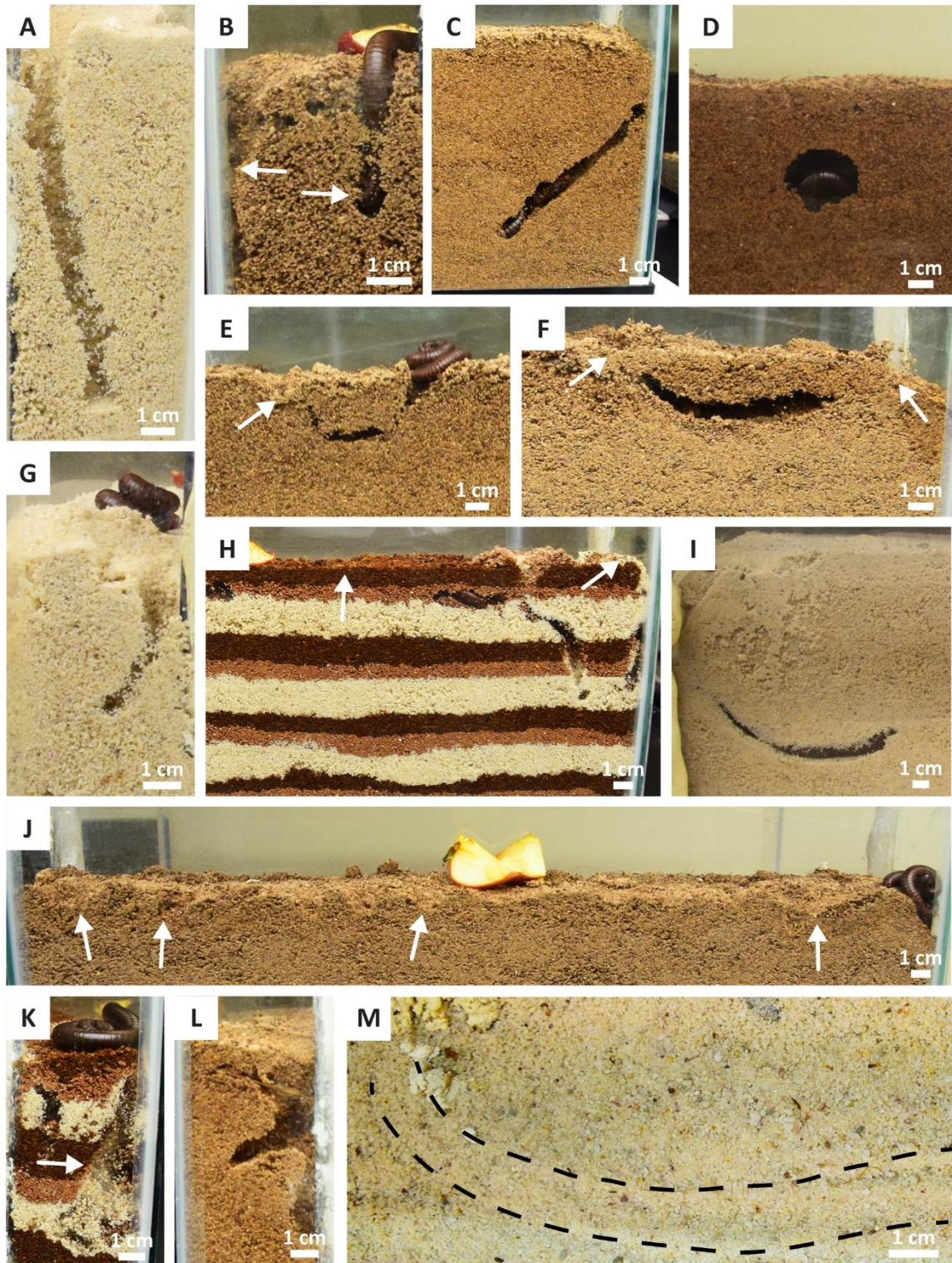


Figure 10. (next page) Biogenic structures of *O. ornatus*. A) Deep, sinuous shaft in sand substrate trial. B) Shallow, straight subvertical shaft in moderate moisture homogenized substrate indicated by arrows. C) Subvertical ramp down to a chamber where millipede remained inactive in homogenized substrate. D) Nearly complete cross-sectional view of a chamber at the end of a ramp (not visible). E) U-shaped burrow in moderate moisture homogenized substrate with one surface opening set back from glass (at arrow). F) Shallower, low-angled U-shaped burrow with two surface openings (at arrows) in low moisture substrate. G) Shallow J-shaped burrow in sand substrate. H) Complex burrow structure produced in layered substrate (arrows indicate entrances set back from side). I) Deep J-shaped burrow in sand substrate. J) Multiple shallow divots (examples at arrows) across the surface of low moisture homogenized substrate. K) Rounded, amorphous chamber (at arrow) in layered substrate. L) Amorphous chamber (at arrow) in moderate moisture homogenized substrate. M) Trackway produced in sand (inside dashed lines).



chamber (**Figure 10C-D**). The visible portion of chambers were 3-7 cm wide and 3-5 cm high and occupied by millipedes for long durations (i.e., more than 10 days). An uncommon burrow (n=2) made by *O. ornatus* in moderate moisture conditions was a subvertical to vertical, deep, highly vertical (40-70°), U-shaped burrow, with two shafts, 1-2 cm in width and 4-6 cm in length, that leveled out and connected in the last 1-2 cm of length (**Figure 10E**). In drier conditions and layered substrates, *O. ornatus* more commonly (n=6) produced shallower U-shaped burrows, generally associated with smaller specimens. The two burrow shafts were 1 cm in width, typically 4-9 cm in length, with a shallow angle of entry (30-50°) and levelling off and connecting after 1-2 cm (**Figure 10F**).

Another uncommon morphology was a shallow, simple J-shaped burrow, sometimes connected to other vertical burrows. These shafts had orientations up to 90° before levelling out to nearly horizontal after 2-4 cm and connecting within 1-2 cm (**Figure 10G, 10L**). These burrows were almost exclusively observed along the small side of enclosures in layered and homogenized substrates, and so may not have been fully representative of the form.

In sand substrates, *O. ornatus* uncommonly (n=2) produced long (16-20 cm), J-shaped burrows that extended deep (8-16 cm) beneath the surface before leveling out and curving upwards for 1-3 cm (**Figure 10I**). Sometimes these were repeated multiple times with the same entry point but with a different position for levelling out in the substrate.

Some complex structures (n=3) by *O. ornatus* were made in moderate moisture homogenized and layered substrates that combine multiple aspects of the previously

described forms (**Figure 10H, 10L**). These burrows were often partially infilled as only one to two aspects of this structure were maintained over time, with reworking occurring in the one to two days after moisture was added.

Across all conditions (n=20), but most commonly under low moisture conditions, *O. ornatus* produced relatively large, 1-3 cm wide, semi-circular divots in the corners of the enclosure which were commonly associated with 1-2 cm high and 3-8 cm wide piles of discarded sediment at the entrances of burrows, particularly those with chambers (**Figure 10H, 10J**).

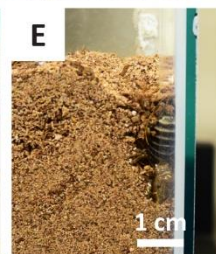
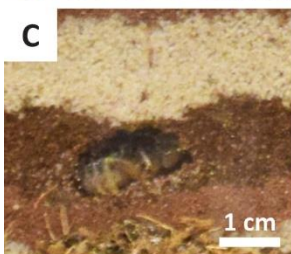
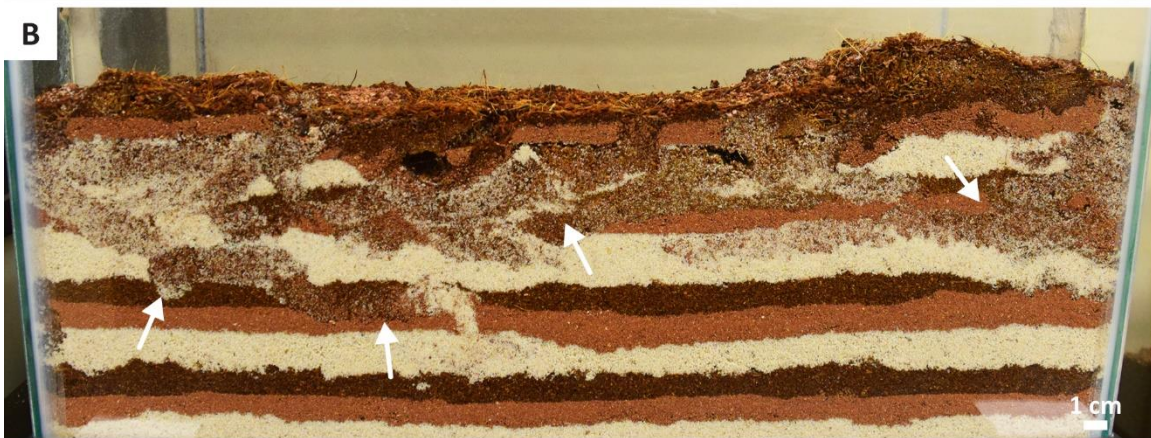
Ammopelmatus cf. *fuscus*.—The most easily observed trace produced by *A. cf. fuscus* within all substrates was a simple, 1-2 cm high and 4-6 cm wide, ovoid chamber that was moved vertically and horizontally through the substrate (**Figure 11A, 11C, 11E**).

In layered substrates, *A. cf. fuscus* produced abundant sinuous, subhorizontal to subvertical, 1-2 cm wide, backfilled burrows, infilled with homogenized substrate (**Figure 11B**). The burrow infill occasionally displayed thin (0.1-0.5 cm), unevenly spaced laminae (**Figure 11D**). These backfilled burrows were produced as a result of the movement of the open chamber, which was present at the end of the burrow. The same backfilled path was present in other substrates but was indistinct.

In layered substrates, *A. cf. fuscus* uncommonly produced amorphous, massive homogenization of the sediment layers reaching depths of up to 12 cm and typically piling excavated sediment from below up onto the surface (**Figure 11B**).

Across substrate conditions, one common substrate disturbance of *A. cf. fuscus* was

Figure 11. (next page) Biogenic structures of *A. cf. fuscus*. A) Cross-sectional view of a chamber (at arrow) produced in homogenized substrate. B) Cross-sectional view of multiple structures visible in layered substrate (after 13 days), including many homogenized trails from movement of chambers, some with light meniscate backfill patterns, as well as amorphous masses of homogenized substrate. C) Cross-sectional view of a chamber in an organic layer that was not moved for 12 days. D) Close up of meniscate backfill pattern in a sand layer. E) Shallow vertical chamber typically associated with divots produced in low moisture trials. F) Many divots and infilled divots in the upper substrate profile in low moisture substrate. G) Surface openings to burrows in sand substrate.



a vertical to subvertical 1 cm wide burrow. These ranged from 1-5 cm in length, sometimes widening to 2-3 cm at the surface of the burrow (**Figure 11E-F**).

Behaviors

Two main behaviors were displayed across species studied in these experiments, dwelling and detritivore feeding. Among these behaviors, carnivores (*Hogna lenta*, *Smeringurus mesaensis*, and *Paragaleodes sericeus*) only displayed dwelling behaviors associated with burrows. Divots and burrow chambers near the surface were created in accordance with these uses, particularly by *S. mesaensis* and *P. sericeus* (**Figure 6C-E**, **Figure 7A-C**). *Hogna lenta* created deeper burrows that were vertical to subvertical, though they were observed staying near the entrance to burrows commonly, likely engaged in ambush predation activity (**Figure 8D-E**, **8H**).

Among the three detritivore species, *Ammopelmatus* cf. *fuscus* and *Orthoporus ornatus* displayed affinities for creating dwelling chambers beneath the surface of substrates. *Orthoporus ornatus* was observed to create dwelling chambers of various morphologies. The most common dwelling chambers were wide (2-6 cm diameter), circular chambers at the ends of subhorizontal to subvertical ramps, that could remain open or naturally close, where they would subsequently often spend the duration of the trial inactive (**Figure 10D**). Millipedes were also observed creating rather large, amorphous chambers near the surface of the substrate (**Figure 10K**). A final dwelling structure produced by *O. ornatus* were simply sinuous burrows of varying orientation with no chamber where the millipede stayed in place at or near the end of the burrow (**Figure 10C**, **10I**). *Ammopelmatus fuscus* was consistent in creating a chamber roughly 1

cm longer and 0.25-0.5 cm taller than its body in which to dwell. These could be moved along with continued feeding or remain in place for up to 13 days throughout the duration of a trial (**Figure 11B-C**).

The same two of three detritivores produced structures in order to search for organics in the substrate profile. *Orthoporus ornatus* created a variety of elongate, sinuous, and narrow burrows matching their body profile to probe for organics (**Figure 10A, 10G-I**). *Ammopelmatus* cf. *fuscus* produced sinuous, lightly meniscate burrows from their continued feeding activity in the sediment profile (**Figure 11B**). Burrows from both *A. cf. fuscus* and *O. ornatus* tended to level out or end in organic layers when they encountered them in layered trials.

Eleodes armata was more ambiguous in its purpose for creating observed sediment disturbances. The largest amount of observed sediment disturbance activity occurred when *E. armata* leveled out the simulated wind ripples (**Figure 9A-D**). The large disturbance produced beneath one of the ripples was also enigmatic, though both could possibly be attributed to the search for near-surface organic matter. Simple divots that were commonly observed after the addition of moisture could possibly be for dwelling or for detritivore feeding, though beetles were not seen to stay in divots consistently like *S. mesaensis* or *P. sericeus* and they did not go deep into substrate profiles or have obvious correlations to the presence of organic matter in layered experiments like structures produced by *A. cf. fuscus* and *O. ornatus* (**Figure 9B, 9E, 9G**). This makes it difficult to assign any biogenic structures of *E. armata* to specific behaviors.

Hogna lenta was the only species that displayed brooding behavior. One 3 cm silk-lined burrow, closed to the surface, was created when the spider produced an egg sac during a layered trial (**Figure 8F**). This burrow did not display any significant morphological differences from any chambers produced by *H. lenta* previously aside from staying closed off from the surface.

Environmental Conditions

Moisture and substrate composition had varying effects on behaviors, morphologies and burrowing techniques observed from all species. However, there were some morphologies that were consistent across all conditions. *Ammopelmatus* cf. *fuscus* displayed similar burrowing techniques across all conditions, producing chambers of the same size that were repositioned over time. *Orthoporus ornatus* made the same vertical to subvertical entrance burrows across all conditions at varying rates. *Eleodes armata* made the same divots in all conditions where wind ripples were simulated. *Smeringurus mesaenis* made more divots than burrows under all conditions.

Low moisture (0-5% by volume) homogenized substrates had the most noticeable effects on the depth, number, and preservation potential of sediment disturbances across different species. *Ammopelmatus* cf. *fuscus* and *O. ornatus* were observed to make low angled burrows that would quickly get overprinted by subsequent collapse and recreation of similar burrows (**Figure 10J, Figure 11F**). Entry points for both of these species were commonly abandoned, as well, leading to divots or shallow, truncated vertical burrows the width of the tracemaker (**Figure 10J, Figure 11F**). *Eleodes armata* was observed making few discrete structures (only a few divots) during low moisture trials, though

consistent levelling of simulated wind ripples resulted in a much flatter sediment surface by the end of trials (**Figure 9F**). *Smeringurus mesaensis* and *P. sericeus* were observed to make and continuously remake and move the most divots in these settings, resulting in a largely mixed layer at the sediment surface, though few structures were made of any significant depth (**Figure 6E, Figure 7E-F**). Both species were also observed making shallow, short-lived burrows that collapsed with addition of moisture, if not before (**Figure 6E, Figure 7D**). *Hogna lenta* was not observed making any sediment disturbances during low moisture trials.

In moderate moisture homogenized substrate trials, more structures of considerable depth were made in comparison to low moisture trials. *Ammopelmatus* cf. *fuscus* and *O. ornatus* made deeper burrows, primarily after moisture was added to enclosures (**Figure 10C, 10L, Figure 11A**). Although both *S. mesaensis* and *P. sericeus* were observed to make similar numbers of burrows in moderate moisture and lower moisture trials, *S. mesaensis* was observed making more stable and deeper burrows in moderate moisture experiments (**Figure 6D**). *Eleodes armata* made relatively few divots in moderate moisture conditions, although one individual also produced a shallow entrance to what appeared to be a burrow (**Figure 9E**). *Hogna lenta* was observed to make several divots and one burrow in moderate moisture conditions (**Figure 8G**).

In high moisture homogenized substrate trials, varying effects were observed among species. Among *A. cf. fuscus* and *O. ornatus*, little effect was observed from adding moisture compared to the moderate moisture mixed homogenized substrate trials. *Eleodes armata* most consistently produced divots under these conditions, directly after

misting, though less levelling of sediment occurred. *Smeringurus mesaensis* produced fewer burrows and fewer, shallower divots in these settings compared to moderate moisture homogenized substrate conditions (**Figure 6B**). *Hogna lenta* made the most structures under moist conditions compared to all other trials in homogenized substrate, producing multiple burrows and several divots as well.

Different substrate compositions made both large behavioral differences as well as significant differences in the ability to observe the morphologies of sediment disturbances produced by the arthropods. Sandy substrates lost cohesion near the sediment surface, sometimes resulting in more collapse than other moderate moisture conditions (**Figure 6G-H, Figure 9C-D, Figure 10I**). The lack of organic matter in the substrate profile resulted in differences in the number of resurfacing events observed of *A. cf. fuscus* and *O. ornatus* (**Figure 11G**). The surfaces of the sand trials were the only substrates that preserved clear tracks and trackways. *Eleodes armata* and *O. ornatus* had preserved trackways, although only *O. ornatus* had distinct tracks (**Figure 9H, Figure 10M**). Otherwise, traces made by *O. ornatus*, and *A. cf. fuscus* were largely the same as those observed in homogenized substrates under the same moisture conditions.

Smeringurus mesaensis made a similar number of burrows and divots in sand compared to homogenized substrates with similar morphologies, although the movement of sand by the repositioning of divots over time produced a visibly distinct layer of disturbed sand after the addition of moisture (**Figure 6H**). *Eleodes armata* mostly produced divots similar to those in homogenized substrates in the sand substrates but produced a lone structure that cut under and through a simulated wind ripple in the sand (**Figure 9C**).

Hogna lenta produced multiple burrows similar to those in homogenized substrates, but also produced a lone structure that was deeper (10 cm) than any others and was kept open (**Figure 8C-D**).

Layered substrates made many biogenic structures visible that were not observed in other substrates largely due to the contrast of sediment size and color. The homogenization or inclined laminae created in the upper 4 cm of substrate by *S. mesaensis* were only easily observed in layered substrate (**Figure 6A, 6F**). In trials with *A. cf. fuscus*, the homogenization of sediment, both near the surface and in backfilled burrows leading to chambers was only apparent in layered substrates (**Figure 10B, 10D**). The backfill patterns produced by *A. cf. fuscus* were observed by the vertical and lateral displacement of the different substrate types as they moved through layers (**Figure 10B**). *Eleodes armata* produced homogenized substrates from the excavated sediment layers when creating divots (**Figure 9G**). The excavation process and production of silk linings by *H. lenta* resulted in a ~0.5-1.0 cm halo of loose, homogenized sediment around burrows (**Figure 8E**). In addition to the reorganization of sediment layers, the substrate preference of each species affected the depths of their bioturbation as well as the most commonly disturbed layers. *Orthoporus ornatus* and *A. cf. fuscus*, for example, spent considerable amounts of time in organic layers or substrates that they had homogenized previously and included significant organic components (**Figure 10H, 11B-C**). In contrast, *S. mesaensis* and *H. lenta* consistently stopped burrowing and set up dwelling chambers in the first sand layer they encountered in the subsurface (**Figure 6C, Figure 8B, 8E**).

Quantitative Analysis

Smeringurus mesaensis produced 158 biogenic structures across all environmental conditions (**Table 2**). Among the range of moisture conditions, *S. mesaensis* produced 88 structures, although the majority (n=61, 69%) were produced in low moisture conditions. The 88 structures could be grouped into three main clusters (**Figure 12A**). The first major split in the dendrogram was among various divots that comprise clusters A and B and burrows within cluster C. Cluster C (17% of structures) included burrows constructed in low moisture (n=9) and moderate moisture conditions (n=6). No burrows were produced in high moisture conditions and so were not represented. Cluster A (19%) was composed of very shallow divots (1 cm or less in depth) produced primarily in low moisture conditions (n=12 of 17). Cluster B (64%) was composed of deeper divots produced in all conditions (n= 40 in low moisture, n= 9 in moderate moisture, n= 7 in high moisture).

Among the three different substrate compositions, the 88 structures produced by *S. mesaensis* could be grouped into five main clusters (**Figure 12B**). The first major split in the dendrogram was between clusters A and B and clusters C, D and E, representing the difference between actively used divots (A, B) and burrows or infilled divots (C, D, E). Cluster A (53%) consisted of low angle divots produced most commonly in sand substrate (n=26 of 47), but also in layered (n=14) and homogenized (n=7) substrates. Cluster B (25%) was composed of divots that were deeper than 3 cm and produced in all conditions. The second major split among the remaining three clusters was between cluster E and clusters C and D. Cluster E (6%) was composed of shorter chambers that were visible only where they were horizontal, produced in layered (n=4) and sand

Table 2. The mean ichnofabric index from the end of each set of trials, the deepest observed point of bioturbation in each set of trials, and the number of discrete structures produced from all trials in each condition.

Species	Environmental Condition	Mean Ichnofabric Index	Deepest Point of Bioturbation (cm)	# of discrete structures
<i>S. mesaensis</i>	Homogenized dry	2.0	4.0	61
<i>S. mesaensis</i>	Homogenized moderate	1.2	4.5	18
<i>S. mesaensis</i>	Homogenized wet	1.0	3.0	9
<i>S. mesaensis</i>	Sand	1.8	5.0	38
<i>S. mesaensis</i>	Layered	1.8	4.0	31
<i>P. sericeus</i>	Homogenized dry	2.0	2.8	4
<i>P. sericeus</i>	Homogenized moderate	1.0	2.0	4
<i>P. sericeus</i>	Sand	0.5	1.5	2
<i>P. sericeus</i>	Layered	0.5	0.8	1
<i>H. lenta</i>	Homogenized dry	0.0	0.0	0
<i>H. lenta</i>	Homogenized moderate	0.6	4.5	5
<i>H. lenta</i>	Homogenized wet	0.8	2.0	10
<i>H. lenta</i>	Sand	1.0	10.0	6
<i>H. lenta</i>	Layered	0.8	4.3	15
<i>E. armata</i>	Homogenized dry	2.0	2.3	3
<i>E. armata</i>	Homogenized moderate	1.3	2.5	3
<i>E. armata</i>	Homogenized wet	0.6	2.5	6
<i>E. armata</i>	Sand	1.8	2.5	7
<i>E. armata</i>	Layered	0.8	2.3	8
<i>O. ornatus</i>	Homogenized dry	1.6	4.5	42
<i>O. ornatus</i>	Homogenized moderate	1.4	17.0	20
<i>O. ornatus</i>	Homogenized wet	1.2	13.3	14
<i>O. ornatus</i>	Sand	1.2	18.0	16
<i>O. ornatus</i>	Layered	1.8	15.0	26
<i>A. cf. fuscus</i>	Homogenized dry	2.0	12.0	51
<i>A. cf. fuscus</i>	Homogenized moderate	1.0	20.0	16
<i>A. cf. fuscus</i>	Homogenized wet	1.4	14.5	23
<i>A. cf. fuscus</i>	Sand	1.2	20.0	16
<i>A. cf. fuscus</i>	Layered	2.8	15.0	37

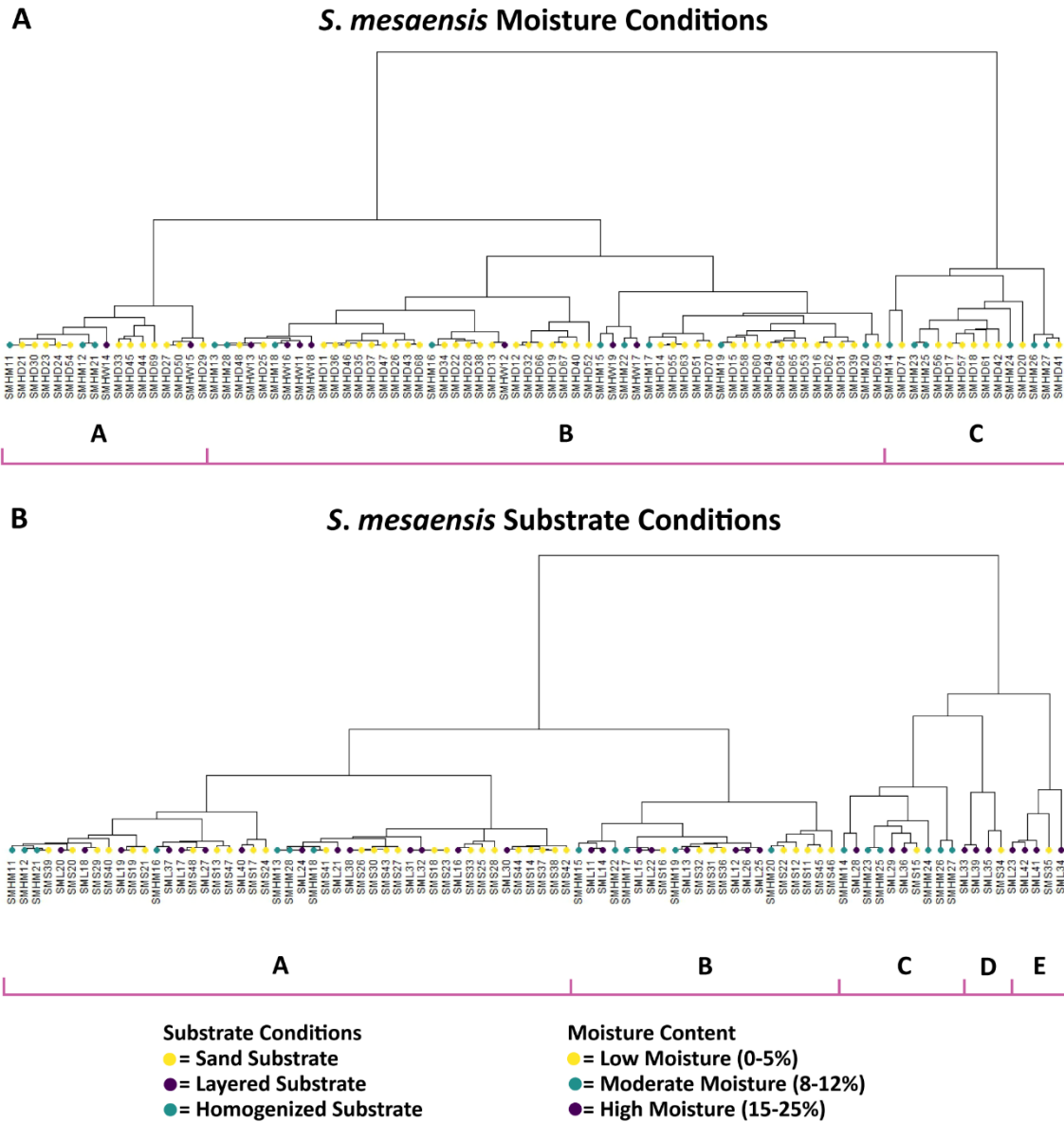


Figure 12. Dendrograms comparing biogenic structures produced by *S. mesaensis*. A) Dendrogram produced for all structures recorded across different moisture levels. B) Dendrogram produced for all structures recorded in the different substrate compositions. Clusters described in the text are demarcated by the labeled brackets.

substrate (n=1). Cluster C (11%) was composed of burrows found mostly in homogenized substrate (n=6 of 10). Cluster D (5%) consisted of two infilled structures produced from the continuous movement of divots in layered substrates and one infilled burrow each from the layered and sand substrates. The structures shared the property of a high length compared to the others.

Paragaleodes sericeus produced seven biogenic structures in the three different substrate conditions (**Table 2**). Structures produced by *P. sericeus* were subdivided into three main clusters (**Figure 13**). Cluster A (14%) plotted far from clusters B and C, consisting of a single shallow chamber underneath a piece of bark produced in homogenized substrate. Cluster B (43%) consisted of shorter divots produced in homogenized (n=2) and sand substrate (n=1). Cluster C (43%) consisted of shallow and/or wide divots, produced in each of the three conditions (n=1 each). Experiments could not be conducted under different moisture conditions with this species.

Hogna lenta produced 37 biogenic structures across all conditions (**Table 2**). Among the moisture conditions, the 15 structures produced by *H. lenta* could be grouped into two main clusters (**Figure 14A**). Cluster A (67%) consisted of 10 divots produced in both moderate moisture (n=4) and high moisture conditions (n=6). Cluster B (33%) consisted of five burrows produced in high moisture (n=4) and moderate moisture (n=1) conditions.

Among the three different substrate compositions, the 27 structures produced by *H. lenta* could be grouped into three clusters (**Figure 14B**). The first major split in the dendrogram was between divots and burrows, both recorded across all substrate

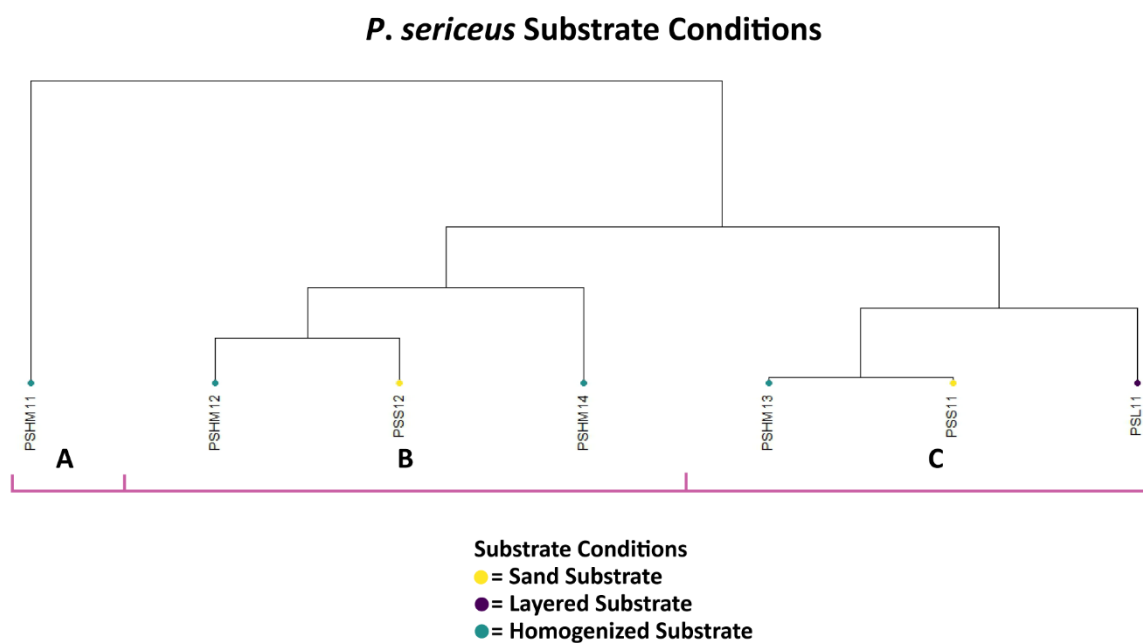


Figure 13. Dendrogram comparing biogenic structures produced by *P. sericeus*, in the different substrate compositions. Clusters described in the text are demarcated by the labeled brackets.

compositions. Cluster A (59%) consisted of 16 divots produced in all conditions, but the majority (n=10) were constructed in layered substrates. Cluster B and C consisted of burrows with a split between those that were closed and open, respectively. Cluster B (22%) included closed burrows that were constructed in layered substrates (n=5) and homogenized substrate (n=1). Cluster C (19%) included open, vertical to subvertical burrows produced in sand (n=4) and layered substrate (n=1). One exception to the open burrow grouping was that of a vertical burrow that was temporarily closed off in sand substrate.

Eleodes armata produced 27 biogenic structures across all conditions (**Table 2**). Among moisture conditions, the 12 structures produced by *E. armata* could be grouped into three clusters (**Figure 15A**). The first major split was between clusters A and B and cluster C. Cluster C (8%) consisted of a single, short J-shaped burrow produced in homogenized substrate, the only burrow produced by *E. armata* in these experiments. Cluster A (58%) consisted of low angle divots, primarily produced in high moisture conditions (n=5 of 7). Cluster B (33%) consisted of high angled divots produced in moderate (n=1) and high moisture (n=1) conditions and two large (3 cm x 2.25 cm) divots produced in low moisture conditions.

Among the three different substrate compositions, the 18 structures produced by *E. armata* could be grouped into three clusters (**Figure 15B**). The first major split in the dendrogram shows a large level of difference between clusters A and B and cluster C. Cluster C (11%) consisted of a short J-shaped burrow produced in homogenized substrate and a large burrow in the rippled sand substrate. Clusters A and B also displayed a high

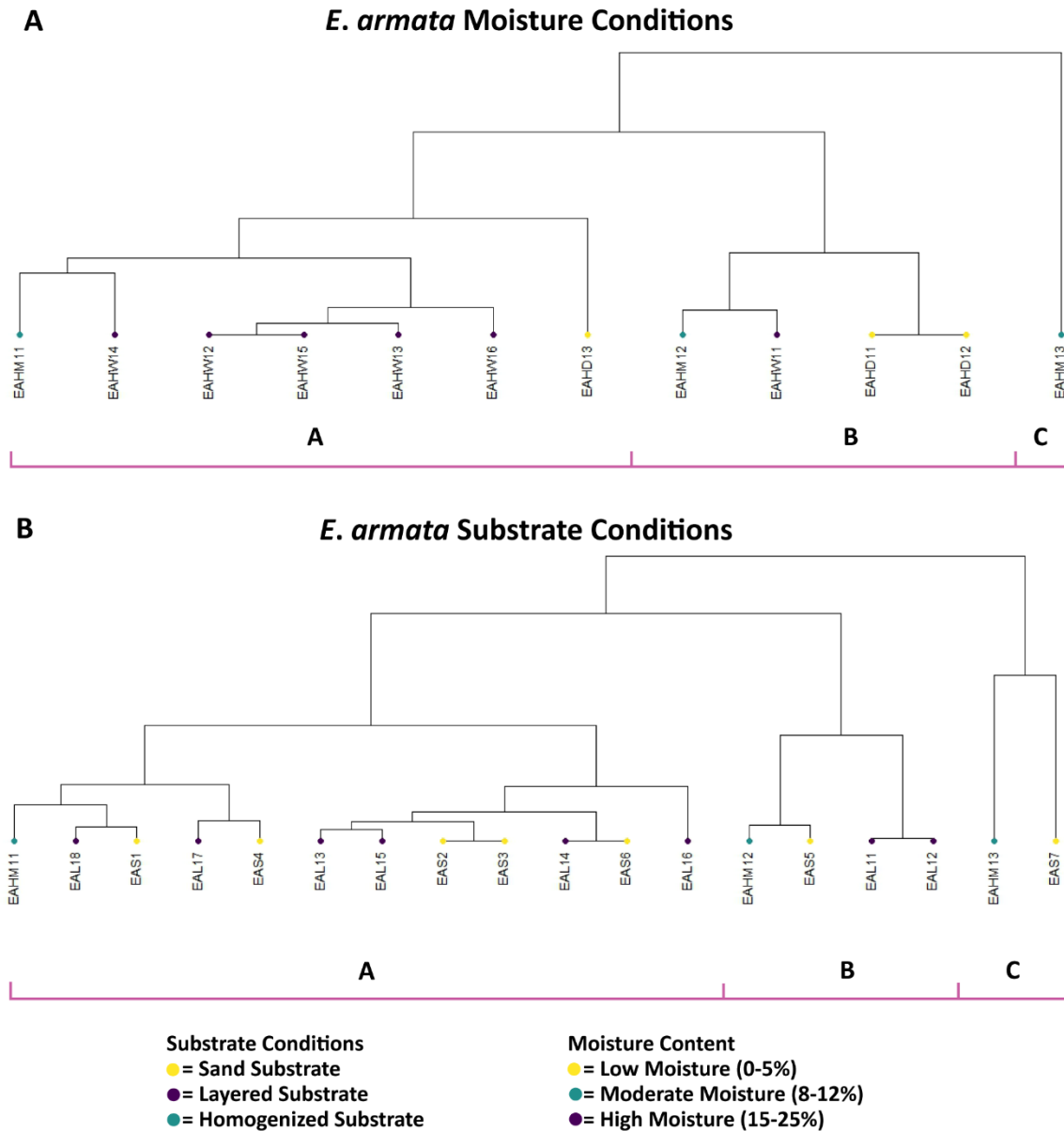


Figure 15. Dendrograms comparing biogenic structures produced by *E. armata*. A) Dendrogram produced for all structures recorded across different moisture levels. B) Dendrogram produced for all structures recorded in the different substrate compositions. Clusters described in the text are demarcated by the labeled brackets.

level of difference from each other. Cluster B (22%) consisted of high angle divots produced in homogenized (n=1) and sand (n=1) substrates and infilled divots produced in layered substrates (n=2). Cluster A (66.6%) consisted of low-angle divots that were produced in homogenized (n=1), sand (n=5) and layered (n=6) substrates.

Orthoporus ornatus produced 118 biogenic structures across all conditions (**Table 2**). Among moisture conditions, the 76 structures produced by *O. ornatus* could be grouped into four main clusters (**Figure 16A**). The first major split occurred between clusters A, B and C which included various burrows and cluster D which included divots. Cluster D (25%) consisted of 19 divots produced in low (n=18) and moderate (n=1) moisture conditions. Cluster C separated from clusters A and B, largely as a result of lower sinuosity. Cluster C (40%) included non-sinuuous burrows with a variety of burrow lengths and angles produced in all substrate compositions. Cluster A and B were separated primarily by depth. Cluster A (24%) was composed of shallow, sinuous, elongate burrows produced in all conditions, but with a large number (n=10 of 18) produced in low moisture conditions. Cluster B (12%) was composed of various burrow forms with a high maximum depth produced in moderate (n=5) and high (n=4) moisture conditions.

Among the three different substrate compositions, the 62 structures produced by *O. ornatus* could be grouped into four main clusters (**Figure 16B**). The primary split in the dendrogram was between cluster E and the rest of the clusters. Cluster D (19%) consisted of isolated, deep parts of burrows that were visible in cross section but did not represent the full length of the burrow. These occurred in layered (n=7), sand (n=3), and

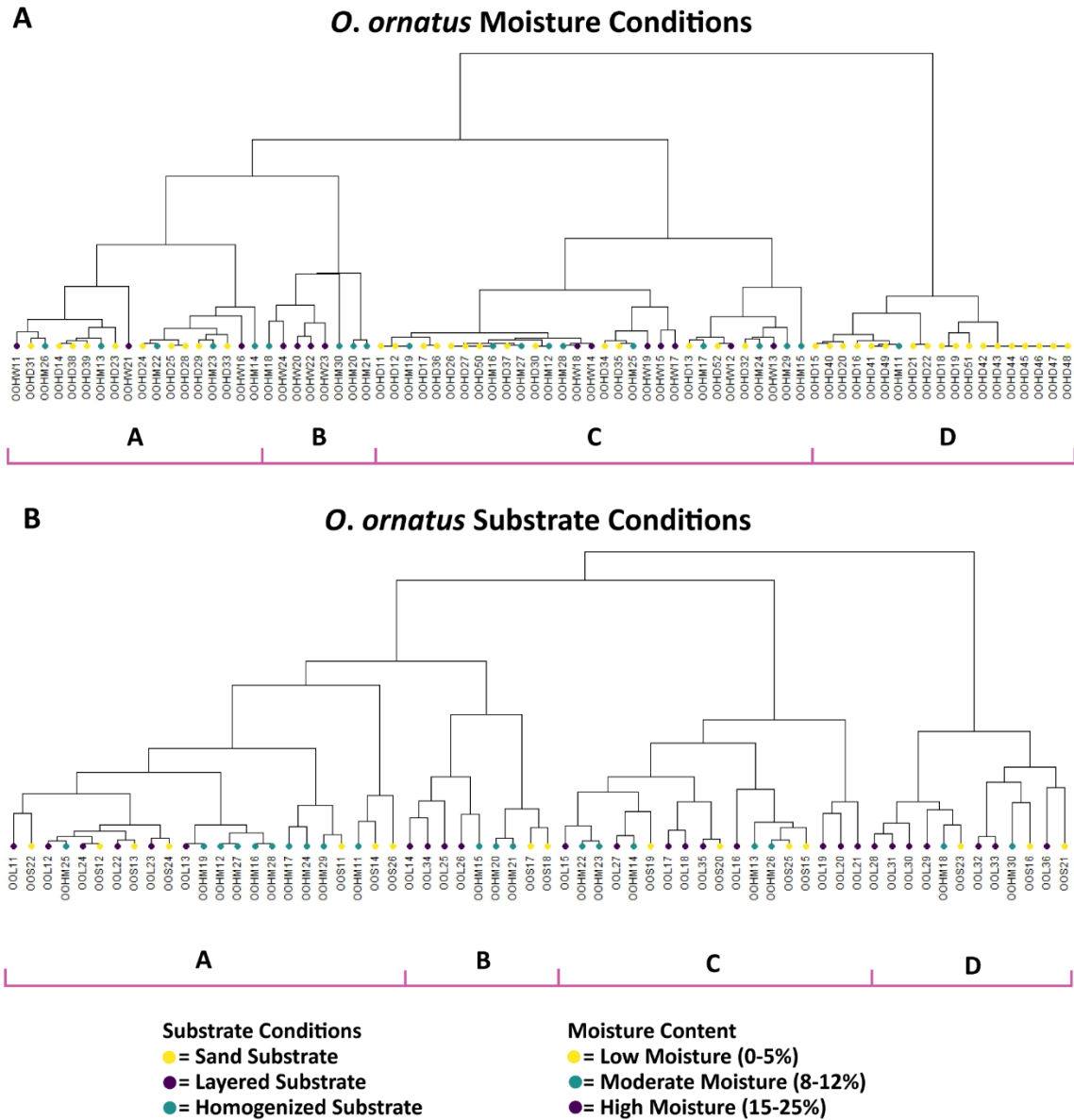


Figure 16. Dendrograms comparing biogenic structures produced by *O. ornatus*. A) Dendrogram produced for all structures recorded across different moisture levels. B) Dendrogram produced for all structures recorded in the different substrate compositions. Clusters described in the text are demarcated by the labeled brackets.

homogenized (n=2) substrates. The second major split among clusters separated cluster C from clusters A and B. Cluster C (29%) consisted of burrows with some level of sinuosity, oftentimes accompanied by multiple entrances associated with an interconnected burrow complex in layered (n=9), sand (n=4), and homogenized (n=5) substrates. The third split was between clusters A and B. Cluster B (15%) was composed of elongate, narrow burrows produced layered (n=4), sand (n=2), and homogenized (n=3) substrates. Cluster A (37%) was composed of three divots, a variety of straight, vertical to subvertical burrows, and burrow entrances of varying lengths produced in layered (n=6), sand (n=7), and homogenized (n=10) substrates.

Ammopelmatus cf. *fuscus* produced 152 biogenic structures with measurable properties across all conditions (**Table 2**). Among the moisture conditions, the 90 structures produced by *A. cf. fuscus* could be grouped into four main clusters (**Figure 17A**). The major split in the dendrogram was between clusters A and B and clusters C and D. Cluster A (17%) was composed of burrow entrances and chambers produced just beneath the surface with no backfilling which occurred in low (n=5), moderate (n=2), and high (n=7) moisture conditions. Cluster B (38%) was composed entirely of divots produced in low moisture conditions. Cluster C (17%) was composed of deep chambers produced mostly in shallow, distinctly backfilled structures produced in low (n=11), moderate (n=4), and high (n=11) moisture conditions.

Among the three different substrate compositions, the 69 structures produced by *A. cf. fuscus* could be grouped into five main clusters (**Figure 17B**). The first split was between cluster F and the rest of the clusters. Cluster F (14%) consisted of divots

produced in sand (n= 4) and layered (n= 6) substrates. The next split between clusters was between cluster E and the rest of the remaining clusters. Cluster E (19%) consisted of fully visible chambers that were deep (7 cm+) in the substrate profile, produced in sand (n= 4) and homogenized (n= 9) substrates. The next split was between clusters A and B and clusters C and D. Cluster A (7%) consisted of short burrow entrances in layered (n= 1), sand (n= 3), and homogenized (n= 2) substrates. Cluster B (6%) was composed of long burrows that were open to the surface produced in layered substrates. Cluster C (29%) consisted of chambers that were not fully visible through the enclosure at varying depths in layered (n= 10), sand (n= 5), and homogenized (n= 5) substrates. Cluster D (23%) was entirely composed of homogenized to meniscate backfilled structures produced from the movement of chambers in layered substrates.

A dendrogram was also produced to compare the structures produced by different species within the same substrate. The most visible biogenic structures with distinct measurable properties were observed during trials that utilized layered substrates. This made layered substrates the ideal condition under which to compare the structures made by different species. One hundred and twenty biogenic structures were observed in layered substrate trials from all species (**Table 2**). Biogenic structures produced by the different species in layered substrates showed more differences than those made by any single species across different environmental conditions (**Figure 18**). Structures produced in layered substrates were split into seven main clusters. The first major split among all of the observed structures was that of the difference between divots (clusters A-B) and burrows (clusters C-G). Divots were primarily the work of carnivores as well as *E*.

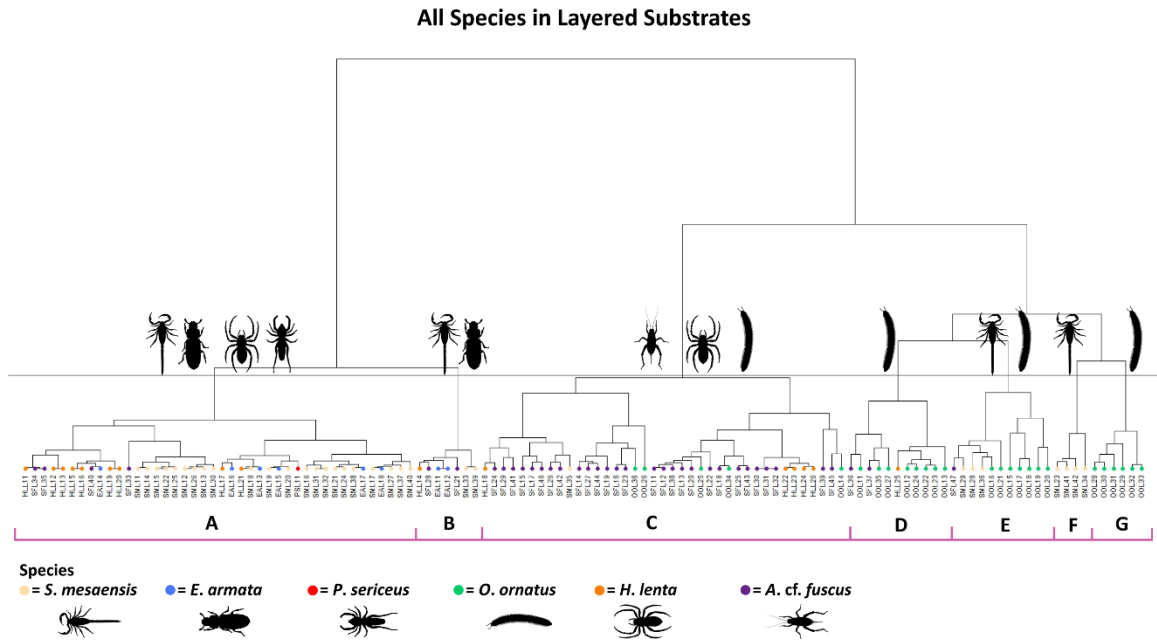


Figure 18. Dendrogram comparing biogenic structures produced by all species in layered substrate. Clusters described in the text are demarcated by the labeled brackets.

armata. Cluster A (34%) consisted of open divots produced by *S. mesaensis* (n=22), *H. lenta* (n=9), *E. armata* (n=6), *A. cf. fuscus* (n=4), and *P. sericeus* (n=1). Cluster B (6%) contained infilled divots produced by *A. cf. fuscus*, *E. armata*, and *S. mesaensis* (n=2 each) as well as *H. lenta* (n=1). Cluster C (31%) was the most dissimilar set of burrows, composed of infilled or closed off burrows made mostly by *A. cf. fuscus* (n=28 of 39). Clusters F and G plotted separately from the remaining burrows. Clusters F (3%) and G (5%) were each assemblages of chambers produced by a single species, *S. mesaensis* (n=4) and *O. ornatus* (n=6), respectively. Burrows of Clusters D and E were more similar to each other than to the others. Cluster D (9%) included deep open shafts made primarily by *O. ornatus* (n=8 of 11). Cluster E included open, sinuous burrows produced primarily by *O. ornatus* (n=7 out of 11).

Median Ichnofabric Index values differed significantly among species in layered trials (Kruskal-Wallis Test $Z=3.64$ d.f.=3 $p<0.005$). A pairwise Wilcoxon Signed Rank Test indicated that biofabrics produced by *H. lenta* differed significantly from those by *S. mesaensis*, *O. ornatus* and *A. cf. fuscus* ($p<0.05$). Ichnofabric index values did not produce significant differences from any other species' trials compared to each other.

Comparison of maximum depth of bioturbation yielded significant results among bioturbation differed significantly (Kruskal-Wallis Test $Z=3.81$ d.f.=3 $p<0.005$) between trials with *H. lenta* and *S. mesaensis* and trials with *O. ornatus* and *A. cf. fuscus* (Wilcoxon Sign Rank Test $p<0.05$). In homogenized moderate moisture substrates, the maximum depth of bioturbation differed significantly (Kruskal-Wallis Test $Z=3.76$ d.f.=3 $p<0.005$) between trials with *A. cf. fuscus* and trials that had *S. mesaensis*, *H. lenta*, and

O. ornatus (Wilcoxon Sign Rank Test $p < 0.05$). In homogenized low moisture substrates, the maximum depth of bioturbation differed significantly (Kruskal-Wallis Test $Z = 3.89$ d.f.=3 $p < 0.005$) between trials with *H. lenta* and trials with *S. mesaensis*, *O. ornatus*, and *A. cf. fuscus* and between trials with *S. mesaensis* and trials with *A. cf. fuscus* (Wilcoxon Sign Rank Test $p < 0.05$). In homogenized high moisture substrates, the maximum depth of bioturbation differed significantly (Kruskal-Wallis Test $Z = 3.30$ d.f.=3 $p < 0.005$) between trials with *A. cf. fuscus* and trials with *H. lenta* and *S. mesaensis* (Wilcoxon Sign Rank Test $p < 0.05$). In sand substrates, there were no significant differences among the maximum depths of bioturbation ($p > 0.05$).

CHAPTER FIVE

DISCUSSION

Interactions of Trace Morphology, Body Morphology and Behavior

The morphology of traces documented in this study was largely dictated by the morphology of the producer and the behavioral function that drove the disturbance of the substrate. Similar controls on trace morphology have been documented by numerous neoichnological studies with both vertebrates and invertebrates. For example, the elliptical cross section and width-to-height ratio of the body plans of multiple scorpion species in Houser and Hembree (2024) were reflected in their burrow cross sections. Other studies have shown that animals with similar body plans may also produce very different burrow morphologies based on the associated behavior, such as detritivore feeding (Hembree, 2009) and ambush predation (Hembree, 2023).

The body plan of each arthropod species was critical to the morphology of their traces. *Smeringurus mesaensis* and *P. sericeus* are both characterized by a long side profile that is relatively short vertically. From an anterior view, *S. mesaensis* is relatively flat whereas *P. sericeus* is more rounded. By comparison, *H. lenta* has an overall round body plan. *Eleodes armata* presents a more compact body plan, most like the form of *P. sericeus*. *Orthoporus ornatus* has an elongate and sinuous form that is rounded from an anterior view. *Ammopelmatus* cf. *fuscus* is similar in form to both *E. armata* and *P. sericeus* from both profiles but is closer in size to *P. sericeus*.

This variability of body plans was reflected in burrow architecture in several ways. The long and sinuous burrows produced by millipedes were nearly identical to

their tracemaker in size and shape (**Figure 10**). Chambers produced by *A. cf. fuscus* were slightly longer than tall, closely fitting their stout body form (**Figure 11A, 11C, 11F**). The slim burrows produced by *S. mesaensis* levelled out into a chamber that also fit their bodies tightly (**Figure 6C-D**). Thus, the burrows produced by *S. mesaensis*, *O. ornatus* and *A. cf. fuscus* were often placed into monotypic and nearly monotypic clusters in the dendrograms (**Figure 18**). The body plans of *P. sericeus* and *S. mesaensis* shared many qualities, particularly in their length and height along their sides. As a result, the shallow, subhorizontal burrows and divots they both produced were very similar (**Figures 6, 7**). By contrast, burrows that served the same behavioral purpose for *H. lenta* (with a different body plan) had a very different form (**Figure 8**). The vertical, subvertical, and rounded forms of *H. lenta* burrows plotted far from those of other carnivores. While rounded, fully silk-lined chambers of *H. lenta* matched their rounded body plan, their vertical and subvertical burrows were rounded in cross section, constructed just wide enough to allow the spiders to move up and down from the silk-lined entrance.

Previous neoichnological studies have shown that similar morphological characteristics within a clade have been reflected in similar burrow morphologies (e.g., Dzenowski and Hembree, 2014; Hembree, 2019). More specifically, neichnological trials that utilized scorpions show that their uniform body morphology produced burrows with a distinct width-to-height proportions that was corroborated by trials in this study (Houser and Hembree, 2024). The burrows of thelyphonids, arachnids with a body plan similar to scorpions, were similar in cross sectional shape and in width-to-height ratio (Hembree, 2013). The burrows of myriapods, generally fitting their elongate body plan, differed in

their width (Hembree, 2009, 2019). *Hogna lenta* and *Gorgyrella inermis*, spiders with similar body plans created burrows that occurred closer to each other in dendrograms than to those of other arthropods (Hils and Hembree, 2015).

The distribution of traces produced by arthropods with different morphologies within the same clusters indicates that behavior was also critical to the resulting trace morphology. For instance, divots produced by *S. mesaensis* and *P. sericeus* while engaged in resting (or temporary dwelling) behavior were placed closer to each other than to any subsurface burrows produced by *S. mesaensis* (**Figure 18**). Many morphologically similar near-surface burrows and deeper divots produced by *S. mesaensis* and *P. sericeus* were also suggestive of ambush predation as a driving behavior because of the arachnid's presence near the sediment surface (**Figures 6B, 6E, 7C**). Such behavior has been documented in other neoichnological experiments with many arachnid species (Hembree, 2013; Hils and Hembree, 2015; Hembree et al., 2017; Houser and Hembree, 2024). Although quantitative analyses were not performed to compare structures produced by all of the animals in sand and homogenized substrates, near-surface ambush predation structures were qualitatively extremely similar, indicating a distinct category of morphology (**Figures 6, 7**).

Subsurface burrows produced by *S. mesaensis* were consistently placed closer to those produced by *O. ornatus* than to other species (**Figure 18**). The behavior of hiding deeper below the surface necessitated a structure that was different in form as well as in use. These dwelling burrows were similar in sinuosity and overall form to J-shaped burrows produced by *O. ornatus* (**Figures 6D, 10F-G**). Isolated chambers used for

dwelling by *O. ornatus*, *S. mesaensis*, *A. cf. fuscus* and *H. lenta* were also placed closer to each other than to near-surface chambers or chambers that were visibly connected to complex burrows.

The long and sinuous structures produced by both *A. cf. fuscus* and *O. ornatus* were generally similar and clustered together, particularly when actively infilled with sediment. Burrows of high depth and sinuosity were always associated with their detritivore activity. Although *A. cf. fuscus* and *O. ornatus* display markedly different body plans, the similarity of these structures demonstrates the control of feeding activity on burrow morphology.

Burrowing generally continues until the behavioral need has been satiated (Hsieh et al., 2023). Detritivores and other sediment ingesting animals have a continuous need to find food, when not dormant, resulting in extensive, crisscrossed burrows such as that of callianassid shrimp (Frey, 1975). Thus, it should be expected that the long and sinuous structures of greater depth would be made by detritivores, as observed in these trials. Relatively shallow chambers for ambush predation and general shelter can be constructed quite quickly, as found in earwigs by Hsieh et al. (2023). This disparity of time invested in bioturbation for a more easily satiated behavioral need results in relatively simple burrow morphologies.

Comparisons between Detritivores and Carnivores

The most notable differences in bioturbation patterns across various environmental conditions were between carnivores and detritivores. Ichnofabrics produced by *S. mesaensis*, *P. sericeus* and *H. lenta* rarely had mean Ichofabric Index (II)

values that reached 2.0 (Table 2). Mean II values from trials of *O. ornatus* and *A. cf. fuscus* never fell below 1.0. Additionally, the depth of *S. mesaensis*, *P. sericeus*, and *H. lenta* structures rarely exceeded 4.5 cm. Lone exceptions to this trend were vertical and subvertical burrows produced by *H. lenta*, which were up to 10 cm deep. In contrast, maximum depths of burrows of *O. ornatus* and *A. cf. fuscus* were never less than 5 cm and often closer to 10 or 20 cm. These differences were related to the feeding style of these two groups of arthropods. Whereas carnivores oftentimes need only produce a single structure to shelter themselves from harsh conditions or to hide from predators or potential prey, detritivores need to continuously search for food in the substrate profile. For example, the detritivores were observed focusing on moving to and through multiple organic layers in layered substrate experiments on multiple occasions (**Figures 10H, 11B-C**). Additionally, detritivores burrowing in sand resurfaced more often than other substrate compositions, perhaps in search of an entry point with more organics (**Figure 11G**).

An exception to these observed differences was in experiments with *E. armata*, utilizing simulated wind ripples in sand substrates. Relatively few discrete structures were produced by *E. armata*, compared to other detritivores, and their depths were generally shallow (Table 2). Levelling of simulated wind ripples was the most notable change between the starting and ending conditions in the substrate (**Figure 9D, 9F**). This disparity between *E. armata* and other detritivores is likely explained by a lack of subsurface feeding activity. Other studies have documented that feeding activity of larval stage tenebrionids results in structures that more closely resemble those produced by the

other detritivores in this study (Eiseman and Charney, 2010; Thacker and Hembree, 2021). Adult tenebrionids are thought to be among the most common producers of linear and irregularly wandering trails in dunes of the western US (Eiseman and Charney, 2010). They are not known to produce many subsurface structures outside of coastal dune settings; instead, opting to utilize the burrows of other animals (Kramm and Kramm, 1972). Many of the structures produced in the corners of enclosures (20 out of 27) may have been produced as the beetles moved against the walls of the enclosure, failing to move upwards effectively and, instead, moving substrate beneath them away from corners.

Substrate Effects

Several correlations were observed in the production of traces in different substrate conditions. A greater number of structures were produced by *S. mesaensis*, *O. ornatus*, *P. sericeus*, and *A. cf. fuscus* in low moisture conditions than in any other moisture conditions. One result of the low moisture conditions was a loss of sediment cohesion, resulting in constant burrow collapse, as found in Hembree (2009). This constant burrow collapse instigated further burrowing and overprinting of substrate disturbances, producing a shallow mixed layer across the length of the enclosure. In general, shallower structures were produced in dry conditions by all species except for *S. mesaensis* and *P. sericeus*. The burrows produced by *S. mesaensis* and *P. sericeus* in other moisture conditions were also shallow, so the relative reduction in burrow depth associated with low moisture conditions was less pronounced or reversed for these species (Table 2). As a result, their trials were characterized by a similar or higher

Ichnofabric Index in low moisture conditions compared to moderate or high moisture conditions. Some substrate disturbances produced by *P. sericeus* and *S. mesaensis* in low moisture conditions also displayed cross lamination, a structure suggested to be indicative of dry substrates (**Figure 7D**) (Hembree et al., 2012).

In moderate and high moisture homogenized substrates, similar morphologies, depths, and bioturbation rates were observed among all detritivore species (Table 2). Above a minimum moisture content threshold, searching for buried organic matter may become the ideal mode of feeding, following the seasonality of arid environments (Wooten and Crawford, 1975; Crawford and Taylor, 1984; Chakravarthy and Sridhara, 2016). Temperature variation may also play a role, and this could be accounted for in future experiments (Crawford and Taylor, 1984). These similarities in bioturbation could also be related to substrate cohesion, which was significantly enhanced past the critical threshold at which burrows could be stabilized, as found in natural settings and other neoichnological experiments (Cloudsley-Thompson, 1991; Hembree, 2009, 2019).

In moderate and high moisture homogenized substrates carnivores produced a higher number of discrete, long-lasting structures than in low moisture substrates (Table 2). As with other burrowers, increased substrate cohesion was likely the controlling factor in an increased durability of burrows (Cloudsley-Thompson, 1991; Hembree, 2009). *Smeringurus mesaensis* produced the most discrete burrows in moderate moisture homogenized substrates. Divots produced by *S. mesaensis* in high moisture substrate were significantly reduced in depth as well. The adaptation of *S. mesaensis* to sandy environments, including its burrowing technique, may have made these substrates less

ideal to excavate with their relatively high cohesion and clay content. This result is similar to observations of *Hadrurus arizonensis* in experiments from Hembree (2012). The consistent tendency of *S. mesaensis* toward burrowing down into sand in the layered substrate trials provides further support for this preference.

Hogna lenta produced more structures in high moisture substrates than in any other condition, but all were shallow. *Hogna lenta* is known from wetter conditions than the other arthropods selected for this study, so this may be expected (Wallace, 1942). However, they are also known for their affinity to sandy substrates, where they produced the deepest and largest structures in these experiments (Eiseman and Charney, 2010). It is possible *H. lenta* experienced a problem similar to *S. mesaensis*, in which the high substrate cohesion made it difficult to excavate the sediment with their pedipalps resulting in shallower burrows in high moisture conditions.

Layered substrates had two primary effects on the behavior and resulting traces of the arthropods, making infilled structures more visible and revealing substrate preferences. The high number of biogenic structures observed in the layered trials, especially those produced by *O. ornatus* and *A. cf. fuscus*, largely resulted from the ability to see them with the transport of different sediment types into under- and overlying layers. In natural settings, sediment composition is seldom uniform across soil horizons (Retallack, 1991; Mack et al., 1993). Where there is incipient soil formation and preserved primary sedimentary structures in stabilized eolian environments, therefore, layered substrates are a more accurate depiction of the effects of fossorial activity, particularly of detritivores (Mescolotti et al., 2019; Uchman et al., 2024). Given that

sediment disruption and backfilled biogenic structures are commonly described in eolianites (Ekdale et al., 2007; Seike et al., 2010; Ekdale and Bromley, 2012; Krapovickas et al., 2016), the layered trials provide the best analog for these settings and associated trace-making behaviors.

Layered substrates also revealed the preferred substrate of each species. *Smeringurus mesaensis* and *H. lenta* consistently burrowed to the first layer of sand and no farther. This is consistent with observations of both species in the wild (Eiseman and Charney, 2010). In contrast, *O. ornatus* and *A. cf. fuscus* spent less time in sand layers and more in silt and organic layers. It should be expected that detritivores would focus on feeding on organics when burrowing, so this is an expected result. The uneven distribution of sand and organic matter in soil profiles means that preferential bioturbation of layers with organic matter should be represented in the ichnofossil record, as observed in Uchman et al. (2024).

Sand substrates are most representative of unstabilized dune and interdune sub-environments. The enhanced visibility of disturbed substrate in the upper wetted portions of sand experiments was critical to recognizing near-surface, infilled biogenic structures (**Figures 6G-H, 9A-D**). Previous studies have suggested that many near-surface ichnofossils, particularly trackways, found in eolianites are preserved by recognizable deformation of dune surfaces when wetted, although other controls such as clay content have been shown to have a greater effect (Loope, 1986; McKeever, 1991; Sadler, 1993; Davis et al., 2007; Rowland and Caputo, 2016). There were no recognizable surficial

trackways produced in substrates with clay, perhaps due to differing methods from previous studies concerned with trackway preservation.

An observed increase in resurfacing by detritivore species in sand substrate may have little meaning in the ichnofossil record, as they may otherwise be driven towards organic matter in the subsurface that was only present on the substrate surface in these trials. It is possible, however, that they would probe for organics in the substrate profile, not find any, and reposition for a new burrow entrance at the surface. Similar to low moisture substrates, *S. mesaensis* had many burrows in the sand substrates collapse in a short span of time due to a lack of sediment cohesion, leading to more overall activity and constant overprinting of biogenic structures. *Hogna lenta* was better equipped than other arachnids to deal with the loss of cohesion associated with sand substrate because of its ability to line burrows with silk (Eiseman and Charney, 2010; Hils and Hembree, 2015; Uchman et al., 2018; Belmontes et al., 2018), resulting in deep, well-defined burrows that lasted the duration of the experiments.

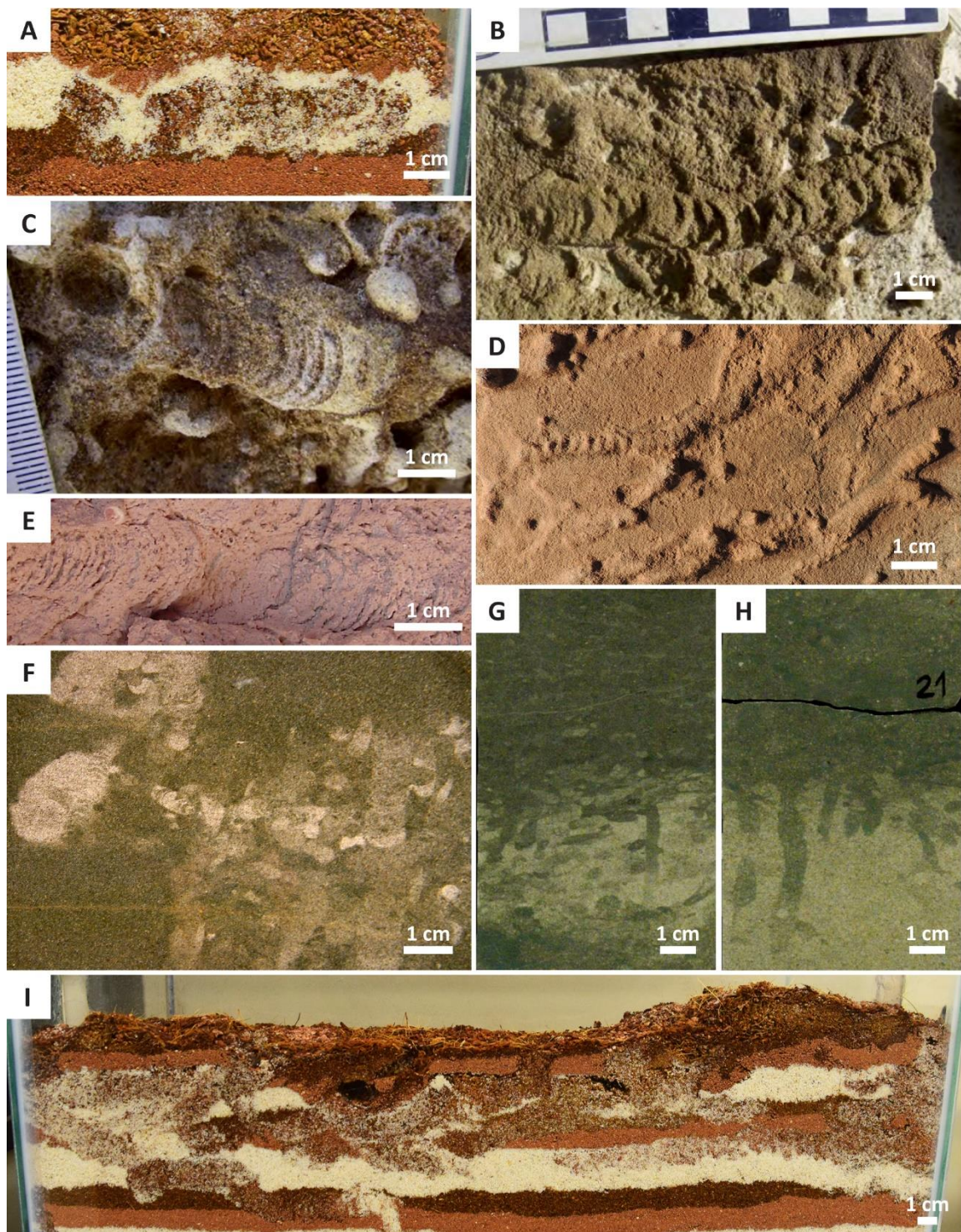
Comparisons with Ichnofossils from Eolianites

Many of the biogenic structures produced by the arthropods in this study bear resemblance to ichnofossils from Mesozoic eolianites. The most common structures produced in the experiments were the lightly meniscate backfilled burrows of *A. cf. fuscus*. Depending on substrate properties and associated variations in burrowing techniques, this structure was similar to either *Taenidium barretti* or its junior synonym, *Entradichnus meniscus*, both of which have been observed in multiple eolianites (Melchor et al., 2024). *Entradichnus meniscus* is defined as a long, unlined, unbranched,

positive epirelief burrow filled with meniscate laminae, commonly 1 cm in width (Seike et al., 2010). Seike et al. (2010) interpreted *E. meniscus* to be the product of “plowing trails” as crane fly larvae use backfill techniques to burrow move downward beneath eolian dunes, parallel to the slipface, based on inferences from Albrant et al. (1978). It is a typical ichnofossil of eolian facies, and a major component of the *Octopodichnus-Entradichnus* ichnofacies (Krapovickas et al., 2016). It has been found in eolianites globally, including the Upper Triassic-Lower Jurassic Nugget Sandstone, the Lower Jurassic Navajo Sandstone, the Lower Jurassic Aztec Sandstone, the Middle Jurassic Entrada Sandstone, and the Upper Cretaceous Djadokhta Formation (**Figure 19B-D**) (Ekdale and Picard, 1985; Sanders and Picard, 1999; Ekdale et al., 2007; Seike et al., 2010; Good and Ekdale, 2014; Rowland and Caputo, 2016). The orientation of many backfill structures made by *A. cf. fuscus* did not have the preferential downward orientation that characterizes *E. meniscus*, however.

Taenidium barreti, argued by some to be the equivalent of *E. meniscus*, is very similar to the other backfilled structures produced by *A. cf. fuscus*. It is described as an unlined, unbranching, meniscate burrow. In modern eolian environments, similar trace morphologies have been observed being produced by desert roaches (Ekdale and Bromley, 2012). *Taenidium barreti* has been found in what is interpreted to be interdune and post-sheet flood deposits in the Lower Cretaceous Mulichinco Formation in Argentina (**Figure 19F-H**) (Buatois and Echevarría, 2019b). *Taenidium barreti* is also found in poorly developed paleosols from the Lower Cretaceous Três Barras Formation in Minas Gerais in Brazil, interpreted to have formed in wet interdunes

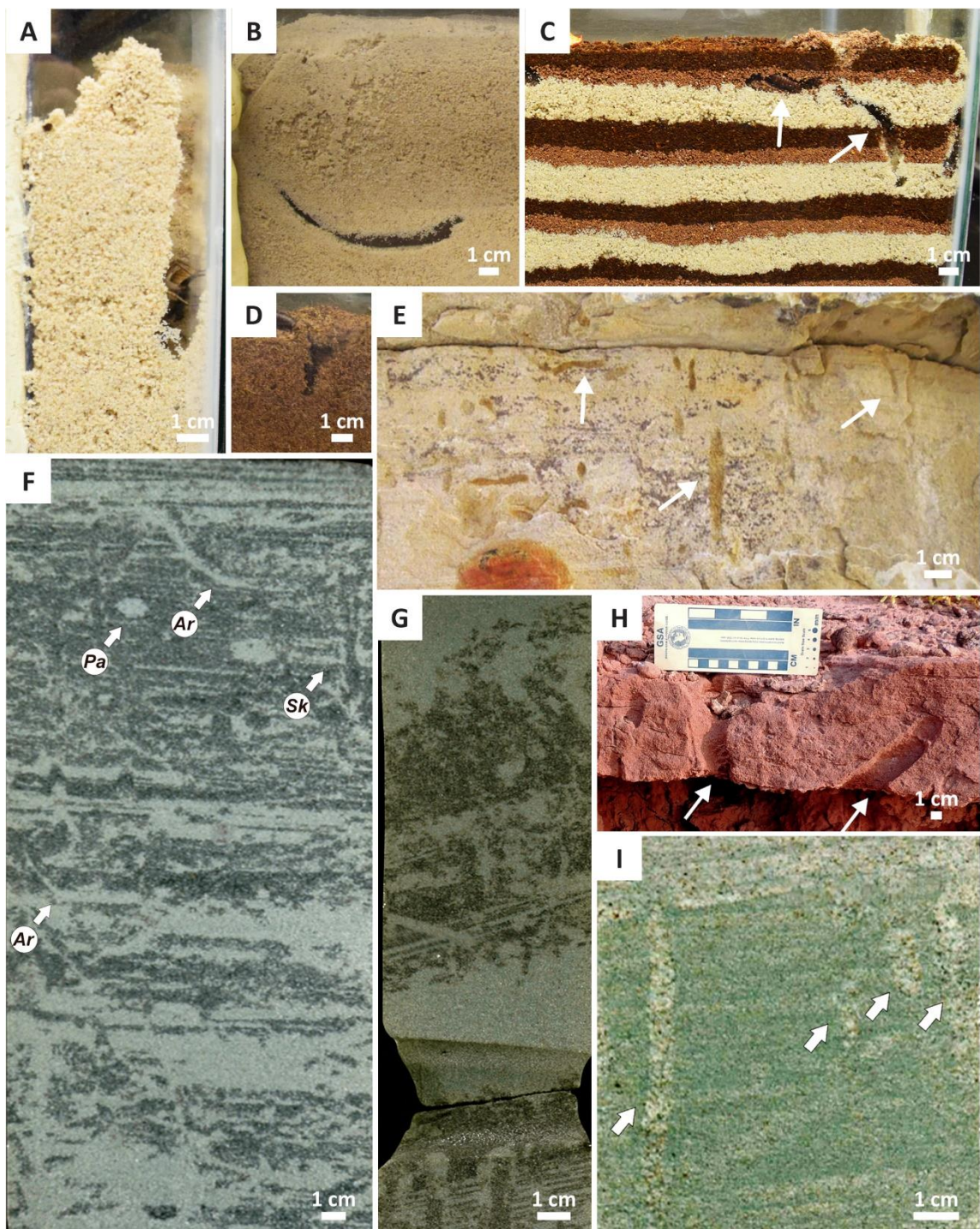
Figure 19. (next page) Biogenic structures of *A. cf. fuscus* compared with *Entradichnus meniscus* and *Taenidium barreti*. A) Backfilled burrow of *A. cf. fuscus* with light menisci. B and C) An example of *Entradichnus meniscus* from the Upper Cretaceous Djadokhta Formation in Mongolia, modified from Seike et al., (2010). D) Topotype slab of *Entradichnus meniscus* from the Middle Jurassic Entrada Formation, modified from Melchor et al. (2024). E) Sample of *Taenidium barreti* from the Upper Cretaceous Allen Formation in Argentina, modified from Melchor et al. (2024). F-H) Core samples with “*Taenidium* isp. ichnofabrics” from the Lower Cretaceous Mulichinco Formation of Argentina, modified from Buatois and Echevarría (2019). I) Sedimentary disruptions created by *A. cf. fuscus* in a layered experiment.



(Mescolotti et al., 2019). Melchor et al. (2024) documented another set of sites spanning the Cretaceous in Patagonia that contained *Taenidium barreti* in dune, dry and wet interdune, and extradune settings (**Figure 19E**). *Etradichnus meniscus* and *Taenidium barreti* both bear great resemblance to the backfilled structures produced by *A. cf. fuscus*, representing what could be an important expansion of Mesozoic eolianite paleoecology.

Vertical burrows are among the most ubiquitous ichnofossils observed in eolianites. While some vertical burrows were produced by *O. ornatus* and *A. cf. fuscus*, they were often surrounded by other burrows with different morphologies (**Figure 20A, 20D**). Burrows of *H. lenta* were exclusively vertical or nearly vertical and included no elements of sinuosity or subhorizontality (**Figures 10C-E, 20A**). Cores from the Mulichinco Formation, interpreted to originate from dunes and sandsheets, were dominated by the simple vertical structure, *Skolithos linearis* (Buatois and Echevarría, 2019b). *Skolithos linearis*, defined as a simple vertical tube often associated with high energy settings, is described from eolianites from as early as the Permian and across the Mesozoic to the modern day (Ahlbrandt et al., 1978; Eiseman and Charney, 2010; Good and Ekdale, 2014; Krapovickas et al., 2016; Melchor et al., 2024). Several other notable occurrences of *Skolithos linearis* in eolianites include moist interdunes of the upper Triassic/Lower Jurassic Nugget Sandstone, various aspects of the Lower Jurassic Navajo Sandstone, the dry interdunes of the Upper Cretaceous Cerra Barcino Formation, and the Upper Cretaceous Djadokhta Formation (Ekdale et al., 2007; Seike et al., 2010; Britt and Chure, 2016; Melchor et al., 2024). In these eolianites, *Skolithos linearis* is typically interpreted to be the dwelling structures of insects and spiders

Figure 20. (next page) Biogenic structures of *H. lenta* and *O. ornatus* compared with ichnofossils and ichnofabrics from eolianites. A) Vertical burrow produced by *H. lenta*. B) Deep J-shaped burrow produced by *O. ornatus*. C) Complex structure produced by *O. ornatus* (left arrow indicates a shallow horizontal burrow with a vertical entrance; right arrow indicates two subvertical shafts that connect just behind the glass). D) Shallow vertical burrow produced by *O. ornatus*. E) Several burrows produced in the Lower Jurassic Nugget Sandstone of Utah, modified from Good's 2013 Thesis; (Left arrow indicates shallow horizontal burrow with a vertical entrance, middle arrow indicates vertical burrow, right arrow indicates separate vertical burrows or a cross section of a U-shaped burrow with the middle set back). F-G) "Arenicolites ichnofabrics" from the Lower Cretaceous Mulichinco Formation of Argentina (arrows point to *Arenicolites*, *Skolithos*, and *Paleophycus*), modified from Buatois and Echevarría (2019). H) *Digitichnus laminatus* (at arrows) from the Upper Cretaceous Allen Formation of Argentina, modified from Melchor et al. (2024). I) "Skolithos linearis ichnofabric" from the Lower Cretaceous Mulichinco Formation of Argentina (arrows point to *Skolithos linearis*), modified from Buatois and Echevarría (2019).



(Ekdale and Bromley, 2012). These trials provide further support for the interpretation of these burrows as spider dwelling structures in eolianites.

Another common eolianite ichnofossil that is similar to structures produced in the experiments is *Digitichnus* isp. *Digitichnus* isp. is defined as a short shaft with a plug shape (~1 cm wide, 3 cm deep), angled vertically or subvertically against dune foreset laminae (Ekdale et al., 2007). *Digitichnus* isp. has been documented from eolianite Mulichinco Formation, and the Upper Cretaceous Allen Formation, as well as being generally listed as a common component of eolianites (**Figure 21F-H, 20H**) (Ekdale et al., 2007; Krapovickas et al., 2016; Buatois and Echevarría, 2019b; Melchor et al., 2024). *Digitichnus* isp. is often interpreted to represent shallow dwelling structures with passive fill (Ekdale and Picard, 1985). The creators of such dwelling structures have been hypothesized to be beetles or spiders that inhabit eolian environments (Ekdale et al., 2007; Buatois and Echevarría, 2019b). The observed dimensions and morphology of *Digitichnus* isp. resemble the abandoned entrances of burrows observed from *O. ornatus* and *A. cf. fuscus* as well as the divots produced by *S. mesaensis*, *H. lenta*, and *E. armata* (**Figure 21A-E**).

Open infilled burrows produced by *A. cf. fuscus*, *O. ornatus*, and *S. mesaensis* were qualitatively similar to several sets of burrows from a variety of studies. *Orthoporus ornatus* produced several forms of U-shaped burrows that are similar to *Arenicolites* isp., with well documented examples from the Lower Triassic Tumlin Sandstone of Poland, the Lower Jurassic Navajo Sandstone, the Lower Cretaceous Mulichinco Formation of Argentina, and the Upper Cretaceous Allen Formation of Argentina (**Figure 20F-G**)

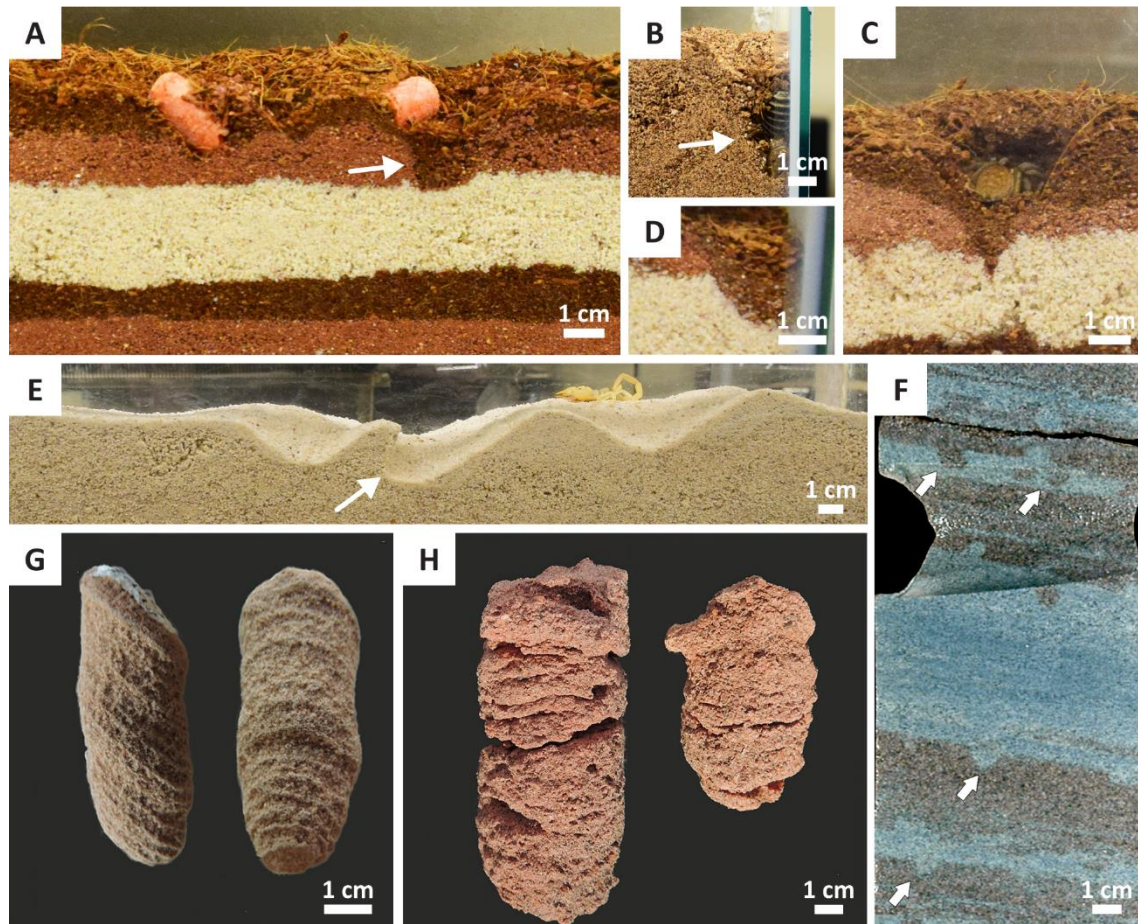


Figure 21. Biogenic structures of several arthropods compared with *Digitichnus* from eolianites. A) Disrupted substrate where *A. cf. fuscus* carried carrots to fill the entrances of burrows (arrow points to plug-shaped divot). B-E) Plug-shaped divots in the substrate made by *A. cf. fuscus*, *E. armata*, *H. lenta*, and *S. mesaensis* respectively (arrows point to plug-shaped divot). F and G) *Digitichnus laminatus* from the Upper Cretaceous Allen Formation of Argentina, modified from Melchor et al. (2024). H) “*Digitichnus* isp. ichnofabric” from the Lower Cretaceous Mulichinco Formation in Argentina (arrow points to plug-shaped divot), modified from Buatois and Echevarría (2019).

(Buatois and Echevarría, 2019b; Melchor et al., 2024). *Arenocolites* isp. in interdune settings has previously been interpreted as the product of various insect larvae or myriapods (Gradziński and Uchman, 1994; Ekdale et al., 2007; Buatois and Echevarría, 2019b). The results here reconfirm myriapods, specifically millipedes, as a possible producer.

In Buatois and Echevarría (2019), many of the cores bearing an “*Arenicolites* isp. ichnofabric” present a relatively high ichnodiversity. Interpreted to be from both dune and sandsheet sub-environments, these cores contain ichnofossils that share morphologies with scorpion, millipede, and orthopteran open, infilled burrows (**Figure 20F-G**). There are observable layers that are cross-cut by burrows that also display near-surface homogenization similar to that observed in experiments that included *S. mesaensis* and *A. cf. fuscus* (**Figure 20G**). Other vertical burrows in this same core seem to mimic the morphology of dwelling burrows produced by *H. lenta* (**Figure 20F**). The ichnodiversity presented in eolianites such as this one, with a noted similar ichnotaxa to those of North American Jurassic eolian deposits, may display a great variety of the activities of arthropods, given the implications of this study’s results (Buatois and Echevarría, 2019b). In **Figure 20F-G**, there may be represented the dwelling structures of arachnids, the feeding and dwelling structures of myriapods or orthopterans, and a homogenization of near the surface of dune deposits associated with the reshuffling of sediment observed from scorpions and orthopterans. This assemblage of traces may represent a relatively underappreciated diversity of arthropod behaviors in ancient eolian environments.

CHAPTER FIVE

CONCLUSIONS

Basic burrowing techniques, behaviors, and substrate disturbance morphologies from six extant species of desert arthropods, *Smeringurus mesaensis*, *Paragaleodes sericeus*, *Hogna lenta*, *Eleodes armata*, *Orthoporus ornatus*, and *Ammopelmatus* cf. *fuscus*, were documented for comparison to ichnofossils associated with eolianites to better interpret their paleoecosystems. It was found that variations in the body plans, behaviors, and feeding habits of the study animals produced distinct differences among their biogenic structures. The body plan of the trace-making animals was often directly reflected in the morphology of their biogenic structures, like the elongate, sinuous burrows produced by *O. ornatus* or the elongate and relatively flat burrows produced by *S. mesaensis* and *P. sericeus*. Some burrowing techniques, however, like the backfilling technique of *A. cf. fuscus*, could obscure the effect that the animal's body plan had on their trace morphology. The behavioral purpose in creating substrate disturbances also had a large control on the resulting trace morphology. For example, different arthropod species produced isolated, ovoid subsurface chambers which served to provide a safe space for inactivity, which were quite distinct from other burrows produced by the same tracemaker. The drive to either search for food within the substrate profile or waiting in ambush for prey near the surface were key factors in producing distinct ichnofabrics. In many environmental conditions, the detritivores *O. ornatus* and *A. cf. fuscus* displayed significantly more intense and deeper bioturbation than predators, resulting in deeper, more abundant burrows and higher ichnofabric indices among individuals of these

species. In contrast, predatory arthropods produced mainly shallow, near-surface structures which largely served the need for basic shelter.

Moisture content (dry, moist, wet) and substrate composition (sand, layered, homogenized) were varied across several experiments to document the effects of these environmental conditions on the behaviors and biogenic structures of each species. In dry substrates, burrows were often shallower and more easily overprinted. Only activities by *S. mesaensis* and *P. sericeus* resulting in surficial modification of the substrate were more prevalent. In moderate moisture conditions, burrows were more stable and, as a product, deeper across the range of species. In high moisture conditions, similar burrows were produced by most species, while surficial and subsurface modifications among scorpions were repressed. In sand substrate, near-surface modifications were more common among all species except *O. ornatus* and *A. cf. fuscus*, likely because of a loss of cohesion and easier visibility of disturbed substrate. In layered substrates, increased visibility of backfilled and passively infilled structures both revealed the substrate composition preferences of each species and greatly enhanced the visibility of the resulting biogenic structures.

The study of modern burrowing animals is essential to interpreting tracemakers and behaviors associated with ichnofossils. Modern eolian environments are biodiverse, especially with respect to arthropods, represented primarily by fossorial inhabitants to deal with harsh surface conditions. While eolianites provide few body fossils, ichnofossils from eolianites are common and provide a wealth of information with which to interpret past life. Therefore, documentation of biogenic structures produced by

modern eolian arthropods such as those produced in this study, observed in the two dimensions in which eolianite ichnofossils typically occur, is essential to interpreting the paleoecology of ancient eolian environments. Structures comparable to *Taenidium barreti* and *Entradichnus meniscus* were found to be produced by *A. cf. fuscus*. Other disturbances that resemble *Arenicolites* isp. were found to be produced by *O. ornatus*. Structures produced by *O. ornatus*, *A. cf. fuscus*, *E. armata*, and *H. lenta* all resemble *Digitichnus* isp. Finally, structures, produced by *H. lenta* and *O. ornatus* resembled *Skolithos linearis*. Various, more ambiguous structures, like near-surface homogenization produced by *S. mesaensis*, *P. sericeus*, *E. armata* and *A. cf. fuscus* and parallel laminae produced by *S. mesaensis* and *P. sericeus*, were also documented in these trials that reconfirms that previously documented cryptic bioturbation may be the product of the activity of desert arthropods.

Comparisons like those with the “*Arenicolites* isp. ichnofabric” reveal a surprising behavioral diversity within a single eolian sub-environment. Likely subsurface detritivore feeding and homogenization near the surface of a dune indicate that there may have been an abundance of organic material buried within the substrate profile. The presence of likely arachnid dwelling structures like *Skolithos linearis* indicate there may have been multiple trophic levels represented by traces preserved within this dune.

In this study, it was found that the traces produced by modern arthropods are useful in the interpretation of both specific substrate conditions and possible tracemakers in eolian environments. The specific conditions and the behaviors suggested by ichnofossils with modern comparisons help with the interpretation of ecological

complexity in ancient eolian ecosystems. While many eolianite ichnofossils remain ambiguous, this study represents a starting point from which to resolve the many remaining questions regarding the paleoecology of eolianite units. Results suggest there may be richer ecosystems than previously thought, driven by the behavioral adaptations to these unique environments that are reflected in the ichnofossil record.

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APPENDICES

File A1. R code for dendrogram dots.

```
clusterDots <- function(clusters, groups, groupColor, groupMembership, cex=0.5, hang=-
0.2) {
  numSamples <- length(clusters$order)
  numGroups <- length(groups)
  sampleColor <- rep("white", numSamples)
  for (i in 1:numGroups) {
    sampleColor[which(groupMembership == groups[i])] <- groupColor[i]
  }
  sampleColor <- sampleColor[clusters$order]
  points(1:numSamples, rep(0, numSamples), pch=16, col=sampleColor, cex=cex)
}
```

File A2. R code for dendrograms.

```
setwd("/Users/andre/OneDrive/Desktop/Directory")
getwd()

library(vegan)
library(cluster)
library(sparcl)

source("clusterDots.R")

#Smeringurus substrate#
smburrows <- read.table("smquants.csv", header=TRUE, row.names=1, sep=",")
head(smburrows)
smburrowproperties <- read.table("smmetas.csv", header=TRUE, row.names=1, sep=",")

smburrowsStand <- decostand(smburrows, "max", na.rm=TRUE)
smburrowsBray <- vegdist(smburrowsStand, method="bray", diag=TRUE,
na.rm=TRUE)
smburrowsCluster <- agnes(smburrowsBray, method="ward")
plot(smburrowsCluster, which.plots=2, cex=0.4, hang=-0.2, main='Smeringurus
Substrates')

smsuniquePS <- unique(smburrowproperties$Conditions)
smsuniquePS
smspsColor <- c("#21908cff", "#440154ff", "#fde725ff")
clusterDots(smburrowsCluster, groups=smsuniquePS, groupColor=smspsColor,
groupMembership=smburrowproperties$Conditions)

#Smeringurus moisture#
smburrowm <- read.table("smquantm.csv", header=TRUE, row.names=1, sep=",")
head(smburrowm)
smburrowproptiem <- read.table("smmetam.csv", header=TRUE, row.names=1,
sep=",")

smburrowmStand <- decostand(smburrowm, "max", na.rm=TRUE)
smburrowmBray <- vegdist(smburrowmStand, method="bray", diag=TRUE,
na.rm=TRUE)
smburrowmCluster <- agnes(smburrowmBray, method="ward")
plot(smburrowmCluster, which.plots=2, cex=0.4, hang=-0.2, main='Smeringurus
Moisture')

smmuniquePS <- unique(smburrowproptiem$Conditions)
smmuniquePS
```

```

smmpsColor <- c("#21908cff", "#fde725ff", "#440154ff")
clusterDots(smburrowmCluster, groups=smmuniquePS, groupColor=smmpsColor,
groupMembership=smburrowpropertyiem$Conditions)

#Ammopelmatus fuscus substrate#
sfburrowss <- read.table("afquants.csv", header=TRUE, row.names=1, sep=",")
head(sfburrowss)
sfburrowpropertyiess <- read.table("afmetas.csv", header=TRUE, row.names=1, sep=",")

sfburrowsStands <- decostand(sfburrowss, "max", na.rm=TRUE)
sfburrowsBrays <- vegdist(sfburrowsStands, method="bray", diag=TRUE, na.rm=TRUE)
sfburrowsClusters <- agnes(sfburrowsBrays, method="ward")
plot(sfburrowsClusters, which.plots=2, cex=0.4, hang=-0.1, main='Ammopelmatus
Substrate')

sfuniquePS <- unique(sfburrowpropertyiess$Conditions)
sfuniquePS
sfspColor <- c("#21908cff", "#440154ff", "#fde725ff")
clusterDots(sfburrowsClusters, groups=sfuniquePS, groupColor=sfspColor,
groupMembership=sfburrowpropertyiess$Conditions)

#Ammopelmatus moisture#
sfburrowsm <- read.table("afquantm.csv", header=TRUE, row.names=1, sep=",")
head(sfburrowsm)
sfburrowpropertiesm <- read.table("afmetam.csv", header=TRUE, row.names=1, sep=",")

sfburrowsStandm <- decostand(sfburrowsm, "max", na.rm=TRUE)
sfburrowsBraym <- vegdist(sfburrowsStandm, method="bray", diag=TRUE,
na.rm=TRUE)
sfburrowsClusterm <- agnes(sfburrowsBraym, method="ward")
plot(sfburrowsClusterm, which.plots=2, cex=0.4, hang=-0.1, main='Ammopelmatus
Moisture')

sfmuniquePS <- unique(sfburrowpropertiesm$Conditions)
sfmuniquePS
sfmpsColor <- c("#21908cff", "#fde725ff", "#440154ff")
clusterDots(sfburrowsClusterm, groups=sfmuniquePS, groupColor=sfmpsColor,
groupMembership=sfburrowpropertiesm$Conditions)

#Orthoporus Moisture#
Orthom <- read.table("Oquantm.csv", header=TRUE, row.names=1, sep=",")
head(Orthom)
orthopropertiesm <- read.table("Ometam.csv", header=TRUE, row.names=1, sep=",")

```

```

orthoStandm <- decostand(Orthom, "max", na.rm=TRUE)
orthoBraym <- vegdist(orthoStandm, method="bray", diag=TRUE, na.rm=TRUE)
orthoClusterm <- agnes(orthoBraym, method="ward")
plot(orthoClusterm, which.plots=2, cex=0.4, hang=-0.2, main='Orthoporus Moisture')

omcuniquePS <- unique(orthopropertiesm$Conditions)
omcuniquePS
ocpmColor <- c("#440154ff", "#fde725ff", "#21908cff")
clusterDots(orthoClusterm, groups=omcuniquePS, groupColor=ocpmColor,
groupMembership=orthopropertiesm$Conditions)

#Orthoporus Substrates#
Orthos <- read.table("Oquants.csv", header=TRUE, row.names=1, sep=",")
head(Orthos)
orthoproperties <- read.table("Ometas.csv", header=TRUE, row.names=1, sep=",")

orthoStands <- decostand(Orthos, "max", na.rm=TRUE)
orthoBrays <- vegdist(orthoStands, method="bray", diag=TRUE, na.rm=TRUE)
orthoClusters <- agnes(orthoBrays, method="ward")
plot(orthoClusters, which.plots=2, cex=0.4, hang=-0.2, main='Orthoporus Substrate')

oscuniquePS <- unique(orthoproperties$Conditions)
oscuniquePS
ocpmColor <- c("#440154ff", "#21908cff", "#fde725ff")
clusterDots(orthoClusters, groups=oscuniquePS, groupColor=ocpmColor,
groupMembership=orthoproperties$Conditions)

#Hogna substrates#
hls <- read.table("hlquants.csv", header=TRUE, row.names=1, sep=",")
head(hls)
hlsproperties <- read.table("hlmetas.csv", header=TRUE, row.names=1, sep=",")

hlsStand <- decostand(hls, "max", na.rm=TRUE)
hlsBray <- vegdist(hlsStand, method="bray", diag=TRUE, na.rm=TRUE)
hlsCluster <- agnes(hlsBray, method="ward")
plot(hlsCluster, which.plots=2, cex=0.4, hang=-0.2, main='Hogna Substrate')

hlsuniquePS <- unique(hlsproperties$Conditions)
hlsuniquePS
hlspsColor <- c("#21908cff", "#440154ff", "#fde725ff")
clusterDots(hlsCluster, groups=hlsuniquePS, groupColor=hlspsColor,
groupMembership=hlsproperties$Conditions)

#Hogna moisture#

```

```

hlm <- read.table("hlquantm.csv", header=TRUE, row.names=1, sep=",")
head(hlm)
hlmproperties <- read.table("hlmetam.csv", header=TRUE, row.names=1, sep=",")

hlmStand <- decostand(hlm, "max", na.rm=TRUE)
hlmBray <- vegdist(hlmStand, method="bray", diag=TRUE, na.rm=TRUE)
hlmCluster <- agnes(hlmBray, method="ward")
plot(hlmCluster, which.plots=2, cex=0.4, hang=-0.2, main='Hogna Moisture')

hlmuniquePS <- unique(hlmproperties$Conditions)
hlmuniquePS
hlmpsColor <- c("#21908cff", "#440154ff")
clusterDots(hlmCluster, groups=hlmuniquePS, groupColor=hlmpsColor,
groupMembership=hlmproperties$Conditions)

#Eleodes substrates#
eas <- read.table("eaquants.csv", header=TRUE, row.names=1, sep=",")
head(eas)
easproperties <- read.table("eametas.csv", header=TRUE, row.names=1, sep=",")

easStand <- decostand(eas, "max", na.rm=TRUE)
easBray <- vegdist(easStand, method="bray", diag=TRUE, na.rm=TRUE)
easCluster <- agnes(easBray, method="ward")
plot(easCluster, which.plots=2, cex=0.5, hang=-0.2, main='Eleodes Substrates')

easuniquePS <- unique(easproperties$Conditions)
easuniquePS
easpsColor <- c("#21908cff", "#440154ff", "#fde725ff")
clusterDots(easCluster, groups=easuniquePS, groupColor=easpsColor,
groupMembership=easproperties$Conditions)

#Eleodes Moisture#
eam <- read.table("eaquantm.csv", header=TRUE, row.names=1, sep=",")
head(eam)
eamproperties <- read.table("eametam.csv", header=TRUE, row.names=1, sep=",")

eamStand <- decostand(eam, "max", na.rm=TRUE)
eamBray <- vegdist(eamStand, method="bray", diag=TRUE, na.rm=TRUE)
eamCluster <- agnes(eamBray, method="ward")
plot(eamCluster, which.plots=2, cex=0.5, hang=-0.2, main='Eleodes Moisture')

eamuniquePS <- unique(eamproperties$Conditions)
eamuniquePS
eampsColor <- c("#21908cff", "#fde725ff", "#440154ff")

```

```

clusterDots(eamCluster, groups=eamuniquePS, groupColor=eampsColor,
groupMembership=eamproperties$Conditions)

#Paragaleodes all#
pss <- read.table("psquant.csv", header=TRUE, row.names=1, sep=",")
head(pss)
pssproperties <- read.table("psmeta.csv", header=TRUE, row.names=1, sep=",")

pssStand <- decostand(pss, "max", na.rm=TRUE)
pssBray <- vegdist(pssStand, method="bray", diag=TRUE, na.rm=TRUE)
pssCluster <- agnes(pssBray, method="ward")
plot(pssCluster, which.plots=2, cex=0.5, hang=-0.8, main='Paragaleodes Substrate')

pssuniquePS <- unique(pssproperties$Conditions)
pssuniquePS
psspsColor <- c("#21908cff", "#440154ff", "#fde725ff")
clusterDots(pssCluster, groups=pssuniquePS, groupColor=psspsColor,
groupMembership=pssproperties$Conditions)

#Layered By Species#
layer <- read.table("layerquant.csv", header=TRUE, row.names=1, sep=",")
head(layer)
layerproperties <- read.table("layermeta.csv", header=TRUE, row.names=1, sep=",")

layerStand <- decostand(layer, "max", na.rm=TRUE)
layerBray <- vegdist(layerStand, method="bray", diag=TRUE, na.rm=TRUE)
layerCluster <- agnes(layerBray, method="ward")
plot(layerCluster, which.plots=2, cex=0.4, hang=-0.2, main='Species in Layered Trials')

abline(h = .81, col="#4b4b4b")

layeruniquePS <- unique(layerproperties$Species)
layeruniquePS
layerpsColor <- c("#ff8200", "darkorchid4", "navajowhite",
"red", "royalblue1", "springgreen3" )
clusterDots(layerCluster, groups=layeruniquePS, groupColor=layerpsColor,
groupMembership=layerproperties$Species)

```

File A3. R code for statistical analyses.

```
setwd("/Users/andre/OneDrive/Desktop/Neoichnology/Data")
getwd()
library(dplyr)

Ichno1 = read.csv("Last.csv")
Ichno1$Conditions <- ordered(Ichno1$Conditions,
                             levels = c("Smeringurus", "Hogna", "Orthoporus", "Ammopelmatus"))
kruskal.test(II ~ Conditions, data = Ichno1)
pairwise.wilcox.test(Ichno1$II, Ichno1$Conditions,
                     p.adjust.method = "BH")

Depthl = read.csv("Depthl.csv")
Depthl$Condition <- ordered(Depthl$Condition,
                             levels = c("SML", "HLL", "OOL", "AFL"))
kruskal.test(Depth.max ~ Condition, data = Depthl)
pairwise.wilcox.test(Depthl$Depth.max, Depthl$Condition,
                     p.adjust.method = "BH")

Depthm = read.csv("Depthm.csv")
Depthm$Condition <- ordered(Depthm$Condition,
                             levels = c("SMHM", "HLHM", "OOHM", "AFHM"))
kruskal.test(Depth.max ~ Condition, data = Depthm)
pairwise.wilcox.test(Depthm$Depth.max, Depthm$Condition,
                     p.adjust.method = "BH")

Depthd = read.csv("Depthd.csv")
Depthd$Condition <- ordered(Depthd$Condition,
                             levels = c("SMHD", "HLHD", "OOHD", "AFHD"))
kruskal.test(Depth.max ~ Condition, data = Depthd)
pairwise.wilcox.test(Depthd$Depth.max, Depthd$Condition,
                     p.adjust.method = "BH")

Depthw = read.csv("Depthw.csv")
Depthw$Condition <- ordered(Depthw$Condition,
                             levels = c("SMHW", "HLHW", "OOHW", "AFHW"))
kruskal.test(Depth.max ~ Condition, data = Depthw)
pairwise.wilcox.test(Depthw$Depth.max, Depthw$Condition,
                     p.adjust.method = "BH")

Depths = read.csv("Depths.csv")
Depths$Condition <- ordered(Depths$Condition,
                             levels = c("SMS", "HLS", "OOS", "AFS"))
kruskal.test(Depth.max ~ Condition, data = Depths)
```

```
pairwise.wilcox.test(Depths$Depth.max, Depths$Condition,  
  p.adjust.method = "BH")
```

Table A 1. Measurement Data from substrate disturbances of *S. mesaensis*.

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
SMHM11	SM1	3	1	0	1	0	20	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM12	SM1	2.5	1	0	1	0	25	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM13	SM1	3	2	0	2	0	35	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM14	SM1	4.5	1.5	2	4	0	20	1	0	Homogenized Medium	<i>Smeringurus mesaensis</i>	1
SMHM15	SM1	1.5	2.5	0	2.5	0	60	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM16	SM2	4	1.5	0	1.5	0	20	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM17	SM2	2.5	3	0	3	0	50	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM18	SM2	2.5	2	0	2	0	40	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM19	SM3	5	3	0	3	0	30	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM20	SM3	4.5	4.5	0	4.5	0	45	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM21	SM3	2	1	0	1	0	25	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM22	SM3	2	3	0	3	0	80	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHM23	SM3	4	2	0	3.5	0	25	1	0	Homogenized Medium	<i>Smeringurus mesaensis</i>	1
SMHM24	SM4	1.5	2.5	0	2	0	40	1	0	Homogenized Medium	<i>Smeringurus mesaensis</i>	1
SMHM25	SM4	4.5	2	0	3.5	0	30	1	0	Homogenized Medium	<i>Smeringurus mesaensis</i>	1
SMHM26	SM4	7	2	0	4	0	40	2	0	Homogenized Medium	<i>Smeringurus mesaensis</i>	2
SMHM27	SM4	5	2	0	3	0	25	2	0	Homogenized Medium	<i>Smeringurus mesaensis</i>	2
SMHM28	SM5	3	2	0	2	0	35	1	1	Homogenized Medium	<i>Smeringurus mesaensis</i>	0
SMHD11	SM1	5.5	2	0	2	0	40	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD12	SM1	7	2	0	2	0	30	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD13	SM1	2.5	1.5	0	1.5	0	40	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD14	SM1	4	3	0	3	0	40	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD15	SM1	6	3	0	3	0	30	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD16	SM1	6.5	2.5	0	2.5	0	20	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD17	SM1	6	1.5	0	3	0	30	1	0	Homogenized Dry	<i>Smeringurus mesaensis</i>	1
SMHD18	SM1	7.5	1.5	0	2.5	0	20	1	0	Homogenized Dry	<i>Smeringurus mesaensis</i>	1
SMHD19	SM1	8	1.5	0	1.5	0	20	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD20	SM1	5	2	0	2.5	0	10	1	0	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD21	SM2	3	1	0	1	0	20	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD22	SM2	3	1.5	0	1.5	0	30	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD23	SM2	3.5	1	0	1	0	15	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD24	SM2	3.5	1	0	1	0	15	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD25	SM2	3	2	0	2	0	30	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD26	SM2	4	2	0	2	0	45	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD27	SM2	2	1	0	1	0	45	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD28	SM2	4	1.5	0	1.5	0	30	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD29	SM2	1.5	1	0	1	0	60	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD30	SM2	3	1	0	1	0	20	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD31	SM2	6	2.5	0	2.5	0	50	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0

Table A1. Continued

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
SMHD32	SM2	7	2	0	2	0	30	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD33	SM2	4.5	1	0	1	0	30	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD34	SM2	4	1.5	0	1.5	0	20	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD35	SM2	6	2	0	2	0	35	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD36	SM2	5.5	2	0	2	0	35	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD37	SM2	5	2	0	2	0	40	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD38	SM2	4	1.5	0	1.5	0	35	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD39	SM2	6.5	2.5	0	2.5	0	40	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD40	SM2	6	1.5	0	1.5	0	30	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD41	SM2	6	2	0	2.5	0	40	2	0	Homogenized Dry	<i>Smeringurus mesaensis</i>	2
SMHD42	SM2	6.5	2.25	0	3	0	50	1	0	Homogenized Dry	<i>Smeringurus mesaensis</i>	1
SMHD43	SM3	4	2	0	2	0	25	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD44	SM3	6	1	0	1	0	20	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD45	SM3	4.5	0.75	0	0.75	0	20	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD46	SM3	5.5	2	0	2	0	35	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD47	SM3	5	2	0	2	0	40	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD48	SM3	3	2	0	2	0	35	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD49	SM3	7.5	3	0	3	0	20	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD50	SM3	2	1	0	1	0	45	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD51	SM4	4	2.5	0	2.5	0	50	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD52	SM4	7	1.5	0	1.5	0	90	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD53	SM4	9	3	0	3	0	35	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD54	SM4	3.5	1	0	1	0	15	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD55	SM4	4	3	0	3	0	40	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD56	SM4	6	3	0	4	0	25	1	0	Homogenized Dry	<i>Smeringurus mesaensis</i>	1
SMHD57	SM4	6	1.5	0	3	0	25	1	0	Homogenized Dry	<i>Smeringurus mesaensis</i>	1
SMHD58	SM4	5.5	3.5	0	3.5	0	35	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD59	SM4	8	4	0	4	0	45	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD60	SM4	6	3	0	3	0	60	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD61	SM4	5.5	2	0	2	0	30	1	0	Homogenized Dry	<i>Smeringurus mesaensis</i>	1
SMHD62	SM4	6	2.5	0	2.5	0	25	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD63	SM4	4	3	0	3	0	35	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD64	SM4	7	3	0	3	0	25	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD65	SM4	7	3	0	3	0	40	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD66	SM4	7	2	0	2	0	20	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD67	SM4	7	1.5	0	1.5	0	20	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD68	SM5	4	2	0	2	0	30	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD69	SM5	9	1	0	1	0	15	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SMHD70	SM5	3.5	2.5	0	2.5	0	35	1	1	Homogenized Dry	<i>Smeringurus mesaensis</i>	0

Table A1. Continued

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
SMHD71	SM5	4	1	1	3	0	20	1	0	Homogenized Dry	<i>Smeringurus mesaensis</i>	0
SML11	SM1	2	3	0	3	0	55	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML12	SM1	4	3	0	3	0	35	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML13	SM1	4.5	3	0	3	0	30	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML14	SM1	1.5	3	0	3	0	60	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML15	SM2	3	3	0	3	0	45	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML16	SM2	6.5	2	0	2	0	30	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML17	SM2	5	1.5	0	1.5	0	30	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML18	SM2	3	1	0	1	0	35	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML19	SM2	5	1	0	1	0	20	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML20	SM2	4	1	0	1	0	25	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML21	SM2	3	2	0	3	0	35	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML22	SM2	3	3	0	3	0	45	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML23	SM2	6	1	2	3	0	0	1	0	Layered	<i>Smeringurus mesaensis</i>	0
SML24	SM3	3	2	0	2	0	35	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML25	SM3	3.5	3	0	3	0	40	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML26	SM3	4	3	0	3	0	35	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML27	SM3	4.5	1.5	0	1.5	0	35	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML28	SM3	7	1.5	1	4	0	30	1	0	Layered	<i>Smeringurus mesaensis</i>	1
SML29	SM3	3.5	1	0	3	0	55	1	0	Layered	<i>Smeringurus mesaensis</i>	1
SML30	SM3	4	2.5	0	2.5	0	30	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML31	SM4	4	2	0	2	0	25	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML32	SM4	4	2	0	2	0	25	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML33	SM4	16	3	0	3	1	35	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML34	SM4	3	0.75	0.5	1.25	0	15	1	0	Layered	<i>Smeringurus mesaensis</i>	0
SML35	SM4	7	3	0	3.5	1	20	1	0	Layered	<i>Smeringurus mesaensis</i>	1
SML36	SM4	5	0.75	0	3	0	25	1	0	Layered	<i>Smeringurus mesaensis</i>	1
SML37	SM5	3	1.5	0	1.5	0	25	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML38	SM5	5	2	0	2	0	40	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML39	SM5	11	3	0	3	1	35	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML40	SM5	8	1.5	0	1.5	0	20	1	1	Layered	<i>Smeringurus mesaensis</i>	0
SML41	SM5	3.5	0.75	2.25	3	0	0	1	0	Layered	<i>Smeringurus mesaensis</i>	0
SML42	SM5	3.5	1	2	3	0	10	1	0	Layered	<i>Smeringurus mesaensis</i>	0
SMS11	SM1	3	4	0	4	0	55	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS12	SM1	3	4.5	0	4.5	0	60	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS13	SM2	2	1.5	0	1.5	0	35	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS14	SM2	3.5	2.5	0	2.5	0	35	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS15	SM2	5	0.75	0	2.5	0	35	1	0	Sand	<i>Smeringurus mesaensis</i>	1
SMS16	SM2	3	3	0	3	0	45	1	1	Sand	<i>Smeringurus mesaensis</i>	0

Table A1. Continued

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
SMS17	SM2	10	1.5	0	1.5	0	15	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS18	SM3	4	2	0	2	0	25	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS19	SM3	5	1	0	1	0	20	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS20	SM3	4	1	0	1	0	25	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS21	SM3	4.5	1	0	1	0	15	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS22	SM3	6	4.5	0	4.5	0	35	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS23	SM3	4	2	0	2	0	25	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS24	SM3	10.5	1	0	1	0	15	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS25	SM3	8	2	0	2	0	25	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS26	SM3	5	2	0	2	0	40	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS27	SM3	4	2	0	2	0	45	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS28	SM3	8	2.5	0	2.5	0	30	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS29	SM4	3.5	1	0	1	0	30	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS30	SM4	5	2	0	2	0	40	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS31	SM4	6	3	0	3	0	45	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS32	SM4	6	3	0	3	0	25	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS33	SM4	6	2	0	2	0	35	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS34	SM4	9	0.75	0	2.25	1	30	1	0	Sand	<i>Smeringurus mesaensis</i>	1
SMS35	SM4	2	2	1	3	0	0	1	0	Sand	<i>Smeringurus mesaensis</i>	0
SMS36	SM4	6	3	0	3	0	35	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS37	SM5	4	2.5	0	2.5	0	35	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS38	SM5	4	2.5	0	2.5	0	35	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS39	SM5	2	1	0	1	0	25	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS40	SM5	2	1	0	1	0	45	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS41	SM5	2.5	2	0	2	0	40	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS42	SM5	3	2.5	0	2.5	0	40	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS43	SM5	4.5	2	0	2	0	40	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS44	SM5	4.5	2.5	0	2.5	0	30	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS45	SM5	2.5	3.5	0	3.5	0	55	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS46	SM5	2	5	0	5	0	90	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS47	SM5	3.5	1.5	0	1.5	0	40	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMS48	SM5	5	1.5	0	1.5	0	30	1	1	Sand	<i>Smeringurus mesaensis</i>	0
SMHW11	SM1	2	2	0	2	0	45	1	1	Homogenized Moist	<i>Smeringurus mesaensis</i>	0
SMHW12	SM1	2	1.5	0	1.5	0	35	1	1	Homogenized Moist	<i>Smeringurus mesaensis</i>	0
SMHW13	SM2	3	2	0	2	0	35	1	1	Homogenized Moist	<i>Smeringurus mesaensis</i>	0
SMHW14	SM2	2	0.5	0	0.5	0	15	1	1	Homogenized Moist	<i>Smeringurus mesaensis</i>	0
SMHW15	SM3	1.5	1	0	1	0	40	1	1	Homogenized Moist	<i>Smeringurus mesaensis</i>	0
SMHW16	SM3	2.5	2	0	2	0	35	1	1	Homogenized Moist	<i>Smeringurus mesaensis</i>	0
SMHW17	SM3	3.5	3	0	3	0	100	1	1	Homogenized Moist	<i>Smeringurus mesaensis</i>	0
SMHW18	SM5	3	2	0	2	0	60	1	1	Homogenized Moist	<i>Smeringurus mesaensis</i>	0
SMHW19	SM5	1.5	2	0	2	0	85	1	1	Homogenized Moist	<i>Smeringurus mesaensis</i>	0

Table A 2. Measurement data from substrate disturbances of *P. sericeus*.

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
PSHM11	PS1	7	2	0	2	1	10	1	0	Homogenized Medium	<i>Paragaleodes sericeus</i>	0
PSHM12	PS2	6	1.5	0	1.5	0	20	1	1	Homogenized Medium	<i>Paragaleodes sericeus</i>	0
PSHM13	PS2	7.5	1	0	1	0	15	1	1	Homogenized Medium	<i>Paragaleodes sericeus</i>	0
PSHM14	PS2	5.5	2	0	2	0	10	1	1	Homogenized Medium	<i>Paragaleodes sericeus</i>	0
PSL11	PS1	5	0.75	0	0.75	0	10	1	1	Layered	<i>Paragaleodes sericeus</i>	0
PSS11	PS1	7	1	0	1	0	15	1	1	Sand	<i>Paragaleodes sericeus</i>	0
PSS12	PS1	4	1.5	0	1.5	0	30	1	1	Sand	<i>Paragaleodes sericeus</i>	0
PSHD11	PS1	10	2	0	2	0	25	1	1	Homogenized Dry	<i>Paragaleodes sericeus</i>	0
PSHD12	PS1	7.5	2.5	0	2.75	0	20	1	0	Homogenized Dry	<i>Paragaleodes sericeus</i>	1
PSHD13	PS1	7.5	2.5	0	2.5	1	10	1	0	Homogenized Dry	<i>Paragaleodes sericeus</i>	0
PSHD14	PS3	3.5	1	0	1	0	20	1	1	Homogenized Dry	<i>Paragaleodes sericeus</i>	0

Table A 3. Measurement data from substrate disturbances of *H. lenta*.

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
HLHM11	HL2	2	0.5	0	0.5	0	45	1	1	Homogenized Medium	<i>Hogna lenta</i>	0
HLHM12	HL2	2	1.5	0	1.5	0	80	1	1	Homogenized Medium	<i>Hogna lenta</i>	0
HLHM13	HL5	1	0.75	0	0.75	0	40	1	1	Homogenized Medium	<i>Hogna lenta</i>	0
HLHM14	HL5	2	2	0	1.5	0	70	1	1	Homogenized Medium	<i>Hogna lenta</i>	0
HLHW11	HL1	1	0.5	0	0.5	1	45	1	1	Homogenized Moist	<i>Hogna lenta</i>	0
HLHW12	HL2	0.75	0.75	0	0.5	1	30	1	0	Homogenized Moist	<i>Hogna lenta</i>	0
HLHW13	HL3	2	2	0	2	1	45	1	0	Homogenized Moist	<i>Hogna lenta</i>	0
HLHW14	HL3	1	1	0	1	0	45	1	1	Homogenized Moist	<i>Hogna lenta</i>	0
HLHW15	HL4	0.75	1.5	0	1	1	90	1	0	Homogenized Moist	<i>Hogna lenta</i>	0
HLHW16	HL4	1	1.5	0	1	0	45	1	1	Homogenized Moist	<i>Hogna lenta</i>	0
HLHW17	HL4	2.5	2	0	1.5	0	45	1	1	Homogenized Moist	<i>Hogna lenta</i>	0
HLHW18	HL4	1	0.5	0	0.5	0	45	1	1	Homogenized Moist	<i>Hogna lenta</i>	0
HLHW19	HL4	1	0.5	0	0.5	0	45	1	1	Homogenized Moist	<i>Hogna lenta</i>	0
HLHW20	HL4	2.5	2.5	0	1.5	1	90	1	0	Homogenized Moist	<i>Hogna lenta</i>	0
HLL11	HL1	1	1	0	1	0	65	1	1	Layered	<i>Hogna lenta</i>	0
HLL12	HL1	3	2	0	3	0	65	1	1	Layered	<i>Hogna lenta</i>	0
HLL13	HL1	3	2	0	3	0	65	1	1	Layered	<i>Hogna lenta</i>	0
HLL14	HL1	1	1	0	1	1	45	1	1	Layered	<i>Hogna lenta</i>	0
HLL15	HL3	1.5	1	0	1	0	55	1	1	Layered	<i>Hogna lenta</i>	0
HLL16	HL3	1.5	1	0	1	0	55	1	1	Layered	<i>Hogna lenta</i>	0
HLL17	HL3	1.5	0.5	0	0.5	0	35	1	1	Layered	<i>Hogna lenta</i>	0
HLL18	HL3	4	4	0	4	1	0	1	0	Layered	<i>Hogna lenta</i>	0
HLL19	HL4	1.5	1.5	0	1.5	0	45	1	1	Layered	<i>Hogna lenta</i>	0
HLL20	HL4	1.5	1.5	0	1.5	0	45	1	1	Layered	<i>Hogna lenta</i>	0
HLL21	HL4	3	1	0	1	0	35	1	1	Layered	<i>Hogna lenta</i>	0
HLS11	HL1	10	1.75	0	10	0	90	1	0	Sand	<i>Hogna lenta</i>	0
HLS12	HL2	2	1	0	1	0	25	1	1	Sand	<i>Hogna lenta</i>	0
HLS13	HL3	1	3	1	4	1	90	1	0	Sand	<i>Hogna lenta</i>	0
HLS14	HL3	1	4	0	4	0	90	1	0	Sand	<i>Hogna lenta</i>	0
HLS15	HL4	1.5	1	0	1	0	50	1	1	Sand	<i>Hogna lenta</i>	0
HLL22	HL5	2	1	0.75	2.25	1	65	1	0	Layered	<i>Hogna lenta</i>	0
HLL23	HL5	2.5	1	0.25	2.25	1	65	1	0	Layered	<i>Hogna lenta</i>	0
HLL24	HL5	3.5	1	0.25	3	1	65	1	0	Layered	<i>Hogna lenta</i>	0
HLL25	HL5	3.75	1	0	3	0	65	1	0	Layered	<i>Hogna lenta</i>	0
HLL26	HL5	5	1	0.25	4.25	1	65	1	0	Layered	<i>Hogna lenta</i>	0
HLHM15	HL1	1	1	3.5	4.5	1	0	1	0	Homogenized Medium	<i>Hogna lenta</i>	0
HLS16	HL5	3	1.25	0	3	0	50	1	0	Sand	<i>Hogna lenta</i>	0

Table A 4. Measurement data from substrate disturbances of *E. armata*.

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
EAHM11	EA2	4	1.25	0	1.25	0	25	1	1	Homogenized Medium	<i>Eleodes armata</i>	0
EAHM12	EA2	1.5	2.5	0	2.5	0	90	1	1	Homogenized Medium	<i>Eleodes armata</i>	0
EAHM13	EA4	3	1	0	2	0	25	1	0	Homogenized Medium	<i>Eleodes armata</i>	1
EAL11	EA1	2.5	2.25	0	2.25	1	45	1	1	Layered	<i>Eleodes armata</i>	0
EAL12	EA1	3	2.25	0	2.25	1	45	1	1	Layered	<i>Eleodes armata</i>	0
EAL13	EA2	3	1	0	1	0	30	1	1	Layered	<i>Eleodes armata</i>	0
EAL14	EA2	2	1	0	1	0	40	1	1	Layered	<i>Eleodes armata</i>	0
EAL15	EA2	3.5	1	0	1	0	20	1	1	Layered	<i>Eleodes armata</i>	0
EAL16	EA3	2.5	0.5	0	0.5	0	20	1	1	Layered	<i>Eleodes armata</i>	0
EAL17	EA3	2.75	2	0	2	0	40	1	1	Layered	<i>Eleodes armata</i>	0
EAL18	EA3	3	1.5	0	1.5	0	30	1	1	Layered	<i>Eleodes armata</i>	0
EAHD11	EA1	3	2.25	0	2.25	0	40	1	1	Homogenized Dry	<i>Eleodes armata</i>	0
EAHD12	EA1	3	2.25	0	2.25	0	40	1	1	Homogenized Dry	<i>Eleodes armata</i>	0
EAHD13	EA3	3	0.5	0	0.5	0	20	1	1	Homogenized Dry	<i>Eleodes armata</i>	0
EAHW11	EA2	2	2.5	0	2.5	0	65	1	1	Homogenized Moist	<i>Eleodes armata</i>	0
EAHW12	EA3	2.5	1.5	0	1.5	0	40	1	1	Homogenized Moist	<i>Eleodes armata</i>	0
EAHW13	EA3	2	1.5	0	1.5	0	40	1	1	Homogenized Moist	<i>Eleodes armata</i>	0
EAHW14	EA3	2	1	0	1	0	30	1	1	Homogenized Moist	<i>Eleodes armata</i>	0
EAHW15	EA5	2.5	1.5	0	1.5	0	40	1	1	Homogenized Moist	<i>Eleodes armata</i>	0
EAHW16	EA5	2.5	1.75	0	1.75	0	35	1	1	Homogenized Moist	<i>Eleodes armata</i>	0
EAS1	EA1	2	1.5	0	1.5	0	40	1	1	Sand	<i>Eleodes armata</i>	0
EAS2	EA2	2	1	0	1	0	20	1	1	Sand	<i>Eleodes armata</i>	0
EAS3	EA2	2	1	0	1	0	20	1	1	Sand	<i>Eleodes armata</i>	0
EAS4	EA2	4	2	0	2	0	20	1	1	Sand	<i>Eleodes armata</i>	0
EAS5	EA4	2.5	2.5	0	2.5	0	70	1	1	Sand	<i>Eleodes armata</i>	0
EAS6	EA4	2	1	0	1	0	40	1	1	Sand	<i>Eleodes armata</i>	0
EAS7	EA4	8	2.5	0	2.5	0	0	1	0	Sand	<i>Eleodes armata</i>	0

Table A 5. Measurement data from substrate disturbances of *O. ornatus*.

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
OOHW11	OO1	4	1	0	3	0	90	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	1
OOL11	OO1	9	3	0	9	0	90	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL12	OO1	4.5	0.75	0	4.5	0	80	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL13	OO1	1	2	0	2	0	90	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL14	OO1	15	1.5	0	15	1	90	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL15	OO1	9	1	0	3	0.5	45	2	0	Layered	<i>Orthopterus ornatus</i>	2
OOL16	OO2	9.5	1	0	3	0	10	1	0	Layered	<i>Orthopterus ornatus</i>	1
OOL17	OO2	12	1	0	9	0	75	3	0	Layered	<i>Orthopterus ornatus</i>	1
OOL18	OO2	10.5	1	0	8.5	0	70	3	0	Layered	<i>Orthopterus ornatus</i>	2
OOL19	OO2	5	0.75	1.25	2	0	0	3	0	Layered	<i>Orthopterus ornatus</i>	1
OOL20	OO2	7.5	0.75	0	2	0.5	15	3	0	Layered	<i>Orthopterus ornatus</i>	1
OOL21	OO2	3.5	0.75	0	2	0	30	2	0	Layered	<i>Orthopterus ornatus</i>	1
OOL22	OO2	5	1	0	5	0	90	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL23	OO2	6.5	1	0	6.5	0	90	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL24	OO2	6	1	0	5.5	0	80	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL25	OO2	2.5	2	1.5	4	1	90	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL26	OO3	7	1	2	6	0.5	30	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL27	OO4	9.5	1	0	8	0	65	1	0	Layered	<i>Orthopterus ornatus</i>	2
OOL28	OO4	3	0.5	7	9	0	45	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL29	OO4	2	0.75	9	11	0	90	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL30	OO4	1	0.5	8.5	9.25	0	40	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL31	OO4	3	0.5	5	7	0	45	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL32	OO4	2.5	1.5	7.5	9	0	0	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL33	OO4	2	1	8	9	0	0	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOL34	OO5	11	1	0	10	1	75	1	0	Layered	<i>Orthopterus ornatus</i>	1
OOL35	OO5	14	1	0	11	0	60	1	0	Layered	<i>Orthopterus ornatus</i>	1
OOL36	OO5	4.5	2	10	12	1	0	1	0	Layered	<i>Orthopterus ornatus</i>	0
OOHD11	OO1	2	2	0	2	0	90	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD12	OO1	2	2	0	2	0	90	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD13	OO1	6	1	0	2	0	45	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD14	OO1	5.5	1	0	3	0	45	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	1
OOHD15	OO1	3	1.5	0	1.5	0	45	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD16	OO1	4	1	0	1	0	40	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD17	OO1	1	1.5	0	1	0	90	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD18	OO1	2	2	0	2	0	90	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD19	OO1	2	2	0	2	0	90	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD20	OO1	2	1	0	1	0	45	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD21	OO1	3	1	0	1	0	35	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	1

Table A 5. Continued

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
OOHD22	OO1	3.5	1	0	1	0	30	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	1
OOHD23	OO1	8.5	1	0	3.5	0	30	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	1
OOHD24	OO1	8	1	0	4	0	60	2	0	Homogenized Dry	<i>Orthopterus ornatus</i>	2
OOHD25	OO1	8	1.5	0	3	0	60	2	0	Homogenized Dry	<i>Orthopterus ornatus</i>	2
OOHD26	OO2	2.5	1.5	0	2.5	0	90	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD27	OO2	2.5	1.5	0	2.5	0	90	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD28	OO2	7	1.5	0	3	0	60	2	0	Homogenized Dry	<i>Orthopterus ornatus</i>	2
OOHD29	OO2	12	1	0	3	0	30	2	0	Homogenized Dry	<i>Orthopterus ornatus</i>	2
OOHD30	OO2	2	1	0	2	0	90	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD31	OO2	7	1.25	0	3	0	60	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	1
OOHD32	OO2	4	1.5	0	3	0	40	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD33	OO2	5	1	0	3	0	30	2	0	Homogenized Dry	<i>Orthopterus ornatus</i>	2
OOHD34	OO2	4.5	1	0	4.5	0	90	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD35	OO2	5	1	0	4.5	0	80	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD36	OO3	1	1.5	0	1.5	0	90	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD37	OO3	2.5	1.25	0	2.5	0	90	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD38	OO3	5	1.25	0	2.5	0	45	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	1
OOHD39	OO4	5	1	0	2	0	40	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	1
OOHD40	OO5	1.5	1.5	0	1.5	0	45	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD41	OO5	3	1	0	1	0	35	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD42	OO5	1	1	0	1	0	65	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD43	OO5	1	1	0	1	0	65	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD44	OO5	1	1	0	1	0	65	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD45	OO5	1	1	0	1	0	65	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD46	OO5	1	1	0	1	0	65	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD47	OO5	1	1	0	1	0	65	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD48	OO5	1	1	0	1	0	65	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD49	OO5	3	1	0	1	0	35	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD50	OO5	2.5	1.5	0	2.5	0	90	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD51	OO5	2	3	0	3	0	65	1	1	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHD52	OO5	6.5	1	0	3	0	40	1	0	Homogenized Dry	<i>Orthopterus ornatus</i>	0
OOHM1	OO1	2	1	0	1	0	35	1	1	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM1 2	OO1	2	1	0	2	0	90	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM1 3	OO1	5	1.75	0	3	0	50	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	1
OOHM1 4	OO1	12.5	1.5	0	8	0	75	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	2
OOHM1 5	OO2	7	1	0	4.5	1	40	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM1 6	OO2	2.5	1.5	0	2.5	0	90	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM1 7	OO2	6	1	0	4.25	0	45	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0

Table A 5. Continued

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
OOHM18	OO2	7	1.5	6	11	0	45	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM19	OO2	2	2	0	2	0	90	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM20	OO2	16	1.5	2	14.5	0	50	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM21	OO2	18.5	1.5	2	17	0	50	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM22	OO3	9	1	0	4	0	55	2	0	Homogenized Medium	<i>Orthopterus ornatus</i>	2
OOHM23	OO3	10.5	1	0	4	0	45	2	0	Homogenized Medium	<i>Orthopterus ornatus</i>	2
OOHM24	OO3	3.5	1	0	2	0	40	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM25	OO3	4.25	1	0	4	0	80	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM26	OO3	5	1.25	0	4	0	70	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	1
OOHM27	OO4	2.5	1	0	2.5	0	90	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM28	OO4	3	1.5	0	3	0	90	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM29	OO4	1.5	1.5	0	1	0	50	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHM30	OO5	3.5	3.5	3	6.5	0	0	1	0	Homogenized Medium	<i>Orthopterus ornatus</i>	0
OOHW1 2	OO2	6.5	1.25	0	3.5	0	40	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	0
OOHW1 3	OO2	2.75	1.5	0	2	0	45	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	0
OOHW1 4	OO2	3.5	1.25	0	3.5	0	90	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	0
OOHW1 5	OO2	8	1.5	0	8	0	90	2	0	Homogenized Moist	<i>Orthopterus ornatus</i>	0
OOHW1 6	OO2	4	1	0	2.25	0	55	2	0	Homogenized Moist	<i>Orthopterus ornatus</i>	1
OOHW1 7	OO2	4.5	1.25	0	4.25	0	75	2	0	Homogenized Moist	<i>Orthopterus ornatus</i>	0
OOHW1 8	OO3	3	1.25	0	3	0	90	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	0
OOHW1 9	OO4	5.5	1.5	0	5	0	65	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	0
OOHW2 0	OO4	2.5	1.5	9.5	12	0	90	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	1
OOHW2 1	OO4	1.5	8.5	0	8.5	0	90	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	1
OOHW2 2	OO4	4.25	3.5	8.5	12.5	0	80	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	1
OOHW2 3	OO4	5.5	1	8.5	11.25	0	30	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	1
OOHW2 4	OO4	3	1	11	13.25	0	35	1	0	Homogenized Moist	<i>Orthopterus ornatus</i>	0
OOS11	OO1	1.75	1.75	0	1.75	0	45	1	0	Sand	<i>Orthopterus ornatus</i>	0
OOS12	OO1	5.25	1	0	5	0	80	1	0	Sand	<i>Orthopterus ornatus</i>	0
OOS13	OO1	3.75	1	0	3.75	0	90	1	0	Sand	<i>Orthopterus ornatus</i>	0
OOS14	OO2	2	1	0	2	0	90	1	1	Sand	<i>Orthopterus ornatus</i>	0
OOS15	OO2	3	1.5	0	3	0	90	1	0	Sand	<i>Orthopterus ornatus</i>	1
OOS16	OO2	3	3	7	10	0	0	1	0	Sand	<i>Orthopterus ornatus</i>	1
OOS17	OO3	16	1.75	0	16	0	90	1	0	Sand	<i>Orthopterus ornatus</i>	0
OOS18	OO3	18.5	1.75	0	18	0	85	1	0	Sand	<i>Orthopterus ornatus</i>	1
OOS19	OO3	10	0.75	5	8	0	30	1	0	Sand	<i>Orthopterus ornatus</i>	2
OOS20	OO3	11.5	1	0	11	0	70	1	0	Sand	<i>Orthopterus ornatus</i>	1
OOS21	OO3	11	1.5	11	13.5	0	20	1	0	Sand	<i>Orthopterus ornatus</i>	1
OOS22	OO3	9.5	0.5	0	9	0	70	1	0	Sand	<i>Orthopterus ornatus</i>	0

Table A 5. Continued

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
OOS23	OO3	5.5	1	9	13.25	0	50	1	0	Sand	<i>Orthopterus ornatus</i>	0
OOS24	OO4	7.5	1	0	7.25	0	80	1	0	Sand	<i>Orthopterus ornatus</i>	0
OOS25	OO4	4.5	1	0	4	0	75	1	0	Sand	<i>Orthopterus ornatus</i>	1
OOS26	OO5	14	2	0	2	0	25	1	1	Sand	<i>Orthopterus ornatus</i>	0

Table A 6. Measurement data from substrate disturbances of *A. cf. fuscus*.

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
SFHM1 1	SF1	1.5	1.5	0	1.5	0	80	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM1 2	SF1	4	1	19	20	1	25	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM1 3	SF1	1	1	0	1	1	80	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM1 4	SF1	4.5	1	0	4	0	90	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM1 5	SF1	1	1	19	20	1	0	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM1 6	SF1	5	1.5	16	20	1	45	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM1 7	SF1	3	1.5	14	16	1	30	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM1 8	SF2	4.5	1	12	15	1	45	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM1 9	SF2	4	1.5	9	11	1	20	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM2 0	SF3	4	1	19	20	1	0	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM2 1	SF3	2.5	0.5	8	9	1	30	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM2 2	SF3	10.5	1	6	9	1	30	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM2 3	SF3	1	1	6	7	1	30	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM2 4	SF4	4	1	19	20	1	0	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM2 5	SF4	1	1	17	19	1	30	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHM2 6	SF5	3	1	19	20	1	0	1	0	Homogenize d Medium	<i>Ammopelmatus cf. fuscus</i>	0
SFHD11	SF1	4	1	0	2	0	20	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD12	SF1	4	1	0	1	0	80	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD13	SF1	2	0.5	0	1.5	0	40	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD14	SF1	4	1	0	3	1	30	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD15	SF1	1.5	1	0	1	0	NA	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD16	SF1	1	1	3.5	4.5	1	0	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD17	SF1	5	1	0	2	1	35	2	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD18	SF1	2.5	1.5	0	1.5	0	NA	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD19	SF1	1.5	2.5	0	2.5	0	90	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD20	SF2	2.5	1	0	2.5	1	90	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD21	SF2	3.5	3	0	3.5	0	70	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD22	SF2	2	3.5	0	2	0	40	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD23	SF2	3	3	0	3	0	45	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD24	SF2	3.5	2	0	2	0	30	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD25	SF2	4	3	0	3	0	45	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD26	SF2	5	4	0	3	0	20	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD27	SF2	4	1.5	0	0.5	0	45	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD28	SF2	4	2	0	3	1	20	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD29	SF3	2	1	0	1	0	30	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD30	SF3	3	2	0	2	0	40	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD31	SF3	3	2	0	2	0	40	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD32	SF3	4	1	1	4	1	30	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD33	SF3	5	2	0	2	0	20	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0

Table A 6. Continued

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
SFHD3 4	SF3	2.5	1	0	1	0	30	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD3 5	SF3	4	3	0	3	0	70	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD3 6	SF3	6	2	0	2	0	30	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD3 7	SF3	4	2	0	2	0	30	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD3 8	SF3	5	1	2.5	5	1	40	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD3 9	SF3	6	3.5	0	3.5	0	30	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD4 0	SF3	4.5	2.5	0	2.5	0	30	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD4 1	SF4	3	2	0	2	0	50	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD4 2	SF4	2	1	0	1	0	50	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD4 3	SF4	1	4.5	0	5	1	90	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD4 4	SF4	2	1.5	0	1.5	0	50	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD4 5	SF4	3	3	0	3	0	50	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD4 6	SF4	1	2	0	2	0	80	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD4 7	SF4	2	4	0	4	0	70	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD4 8	SF4	1.5	1.5	0	1.5	0	45	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD4 9	SF4	4	1	0	1.5	0	45	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD5 0	SF4	1.5	2.5	0	2.5	0	60	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD5 1	SF4	2.5	2.5	0	2.5	0	45	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD5 2	SF4	1	3.5	0	4	1	90	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD5 3	SF4	3	2	0	2	0	40	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD5 4	SF5	2	1	11	12	1	NA	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD5 5	SF5	2	1	0	1	0	30	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD5 6	SF5	4	1	1	3	0	30	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD5 7	SF5	2	1	0	2	0	90	2	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD5 8	SF5	2	2	0	2	0	45	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD5 9	SF5	2.5	1	0	1	0	30	1	1	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD6 0	SF5	3	1	0.5	3.5	1	90	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFHD6 1	SF5	6.5	1	1	2	1	10	1	0	Homogenize d Dry	<i>Ammopelmatus cf. fuscus</i>	0
SFL11	SF1	7	2.5	0	7	2	90	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL12	SF1	6	2.5	0	6	2	90	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL13	SF1	9	2.5	0	9	2	90	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL14	SF1	5	1	6	9	2	30	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL15	SF1	4	1	3	6	2	35	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL16	SF1	0.75	0.75	7	7.75	1	NA	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL17	SF1	3.5	2.5	2.5	5	2	35	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL18	SF2	11.5	1.5	0	9	2	75	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL19	SF2	2.5	1	9	10	1	30	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL20	SF3	6	1	0	6	2	90	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL21	SF3	3	4	0	4	2	55	1	1	Layered	<i>Ammopelmatus cf. fuscus</i>	0

Table A 6 Continued

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	Sinuosity
SFL22	SF3	2	6	0	6	2	90	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL23	SF3	0.5	1	6	7	1	0	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL24	SF3	3.5	3	0	3	2	NA	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL25	SF3	7	1.5	0	6	2	65	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL26	SF3	4	2	0	3	2	55	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL27	SF3	6.5	1	5	10.5	2	40	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL28	SF3	3	1	0	4	2	55	1	1	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL29	SF3	4.5	1.25	1	2.5	1	10	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL30	SF4	4.5	1	1	5	2	NA	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL31	SF4	4.5	1	1	5	2	NA	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL32	SF4	4.5	1	1	5	2	NA	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL33	SF4	2	2	0	2	0	45	1	1	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL34	SF4	1	1	0	1	0	70	1	1	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL35	SF4	1	1	0	1	0	70	1	1	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL36	SF4	15	2	0	14	0	85	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL37	SF4	15	1.5	0	11	0	40	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL38	SF5	3	3	0	6	1	90	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL39	SF5	38	3	0	7	1	30	3	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL40	SF5	1	1	0	1	0	45	1	1	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL41	SF5	7	2	1.5	3.5	1	0	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL42	SF5	5	2.5	0	3.5	1	40	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL43	SF5	8	1.5	0	7	1	60	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL44	SF5	4	1.5	5	8	1	40	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL45	SF5	21	1.5	2.5	15	1	35	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL46	SF5	4.5	2.5	2.5	5	1	10	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFL47	SF5	5.5	1	0	3.5	0	40	1	0	Layered	<i>Ammopelmatus cf. fuscus</i>	0
SFS11	SF1	2.5	1	0	1	0	40	1	1	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS12	SF1	0.75	0.75	7	7.75	1	0	1	0	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS13	SF2	3.5	1	1	3.25	1	40	1	0	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS14	SF2	1.75	1	3.5	5	1	75	1	0	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS15	SF2	3.5	1	0	3.5	0	90	1	0	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS16	SF2	6	1	0	6	0	90	1	0	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS17	SF2	2	1	0	1	0	45	1	1	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS18	SF3	3	1	19	20	1	0	1	0	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS19	SF4	2	1	1	2.5	1	50	1	0	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS20	SF4	2	1.5	0	1.5	0	55	1	1	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS21	SF4	2	1.5	0	1.5	0	55	1	1	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS22	SF4	0.75	0.75	1	1.75	1	0	1	0	Sand	<i>Ammopelmatus cf. fuscus</i>	0
SFS23	SF4	2	1	0	1	0	90	1	0	Sand	<i>Ammopelmatus cf. fuscus</i>	0

Table A 6. Continued

Name of Burrow	Specimen	Length	Height	Depth Min	Depth Max	Infill	Angle	Entrances	Burrow or Divot	Conditions	Species	σ
SFS24	SF5	5	3	17	20	1	0	1	0	Sand	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFS25	SF5	4.5	2	16	19.5	1	35	1	0	Sand	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFS26	SF5	5	1.5	15	19	1	40	1	0	Sand	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW11	SF1	3.5	2	12.5	14.5	1	20	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW12	SF2	4.5	1.5	9.5	12.5	1	45	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW13	SF2	4	1.5	8.5	11.5	1	45	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW14	SF3	1.5	1	6	7	1	10	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW15	SF3	3.5	1	3	5	1	40	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW16	SF3	4	1.25	8.5	11	0	35	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW17	SF3	2.5	1.5	4.5	6.5	1	70	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW18	SF3	3	1	0	2	0	20	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW19	SF3	5	1	0	4	0	50	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW20	SF3	3	1	2	4.5	0	30	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW21	SF3	4	1	3	4	0	10	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW22	SF3	7	1	0	6	0	75	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW23	SF3	3.5	2	3	5	1	5	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW24	SF3	3	1	0	2.5	0	70	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW25	SF3	4	1	0	2	0	45	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW26	SF3	2	1.75	2.25	4	1	0	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW27	SF4	1	1	2	3	1	0	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW28	SF4	4	1	0	2.5	0	50	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW29	SF4	2	1	1	3	1	90	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW30	SF4	1	1	2	3	1	0	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW31	SF4	1	1	0.5	1.5	1	0	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW32	SF4	1.5	1	4	5.25	1	30	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0
SFHW33	SF5	1	1	2	3	1	0	1	0	Homogenized Moist	<i>Ammopelmatus</i> cf. <i>fuscus</i>	0

VITA

Drew White was born in Knoxville, Tennessee. After graduating from High School, he was admitted to the University of Tennessee as a student in Biological Sciences. Inspired by his mother and grandmother's degrees in biology, he spent the first few years at UT switching majors to figure out how to use his passion for biology to feel more useful in critical times to cement positive change for the world. He graduated with a degree in Sustainability and a minor in Plant Sciences at the outbreak of COVID. Ultimately, he came back to biology with a job that focused surveys of aquatic fauna and terrestrial gastropod populations across the southeastern US, collecting scorpions for genetic study at the AMNH as a side project. A passion since his youth for paleontology and a new passion for understanding arachnids culminated in a master's degree that combined both studies in the Spring of 2023 when he joined Daniel Hembree's lab group to study the burrowing behavior of modern arthropods. During his two years in the department of Earth, Environmental and Planetary Sciences, Drew presented his work at the 2023 annual GSA meeting in Pittsburgh, Pennsylvania and also the 12th North American Paleontological Convention in Ann Arbor, Michigan. Drew also worked with undergraduate students in the department, teaching Earth, Life, and Time (GEOL/EEPS 102), The Earth's Environments (GEOL 103), and Paleobiology (GEOL 320). Drew will continue his journey at a different department of geology next fall for a PhD focusing on trace fossils and paleosols.