

Neoichnology of the Burrowing Spiders *Gorgyrella inermis* (Araneae: Mygalomorphae)
and *Hogna lenta* (Araneae: Araneomorphae)

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This thesis titled
Neoichnology of the Burrowing Spiders *Gorgyrella inermis* (Araneae: Mygalomorphae)
and *Hogna lenta* (Araneae: Araneomorphae)

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ABSTRACT

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Neoichnology of the Burrowing Spiders *Gorgyrella inermis* (Araneae: Mygalomorphae) and *Hogna lenta* (Araneae: Araneomorphae)

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Trace fossils are useful for interpreting the environmental conditions and ecological composition of strata. Neoichnological studies are necessary to provide informed interpretations, but few studies have examined the traces produced by continental species and how these organisms respond to changes in environmental conditions. Spiders are major predators in modern ecosystems. The fossil record of spiders extends to the Carboniferous, but few body fossils have been found earlier than the Cretaceous. Although the earliest spiders were probably burrowing species, burrows attributed to spiders are known primarily from the Pleistocene. The identification of spider burrows in the fossil record would allow for better paleoecological interpretations and provide a more complete understanding of the order's evolutionary history. This study examines the morphology of burrows produced by the mygalomorph spider *Gorgyrella inermis* and the araneomorph spider *Hogna lenta* (Arachnida: Araneae). Individuals of both species were provided sediment-filled terraria in which to produce burrows. Seven different burrow architectures were produced during this study: vertical shafts, vertical shafts with terminal chambers, subvertical shafts, subvertical shafts with terminal chambers, isolated chambers, J-shaped burrows, and Y-shaped burrows. Changes in sediment density and sediment moisture did not result in statistically

significant differences in quantitative burrow properties, although architectural diversity decreased as sediment density increased and sediment moisture was increased and decreased by 20% from the norm. The silk lining on the burrow walls increased as sediment became unstable, but was much thinner to absent when sediment became stable. The burrows of *G. inermis* and *H. lenta* are highly similar to one another, but only moderately similar to dissimilar to the burrows of other burrowing arachnids and millipedes. When compared to previously measured specimens of the trace fossils *Skolithos* and *Macanopsis*, the spider burrows are highly similar to the specimens of *Skolithos* and two specimens of *Macanopsis*. Qualitative properties of the burrows produced by *G. inermis* and *H. lenta* may be used to differentiate these burrows from the burrows of other arthropods that are statistically similar. The results of this study will aid paleoecological and paleoenvironmental interpretations. Two distantly related species of spiders produced burrows that are qualitatively and quantitatively similar. The burrows have special characteristics that differentiate them from other burrowing arthropods. Architectural diversity and thickness of silk linings can provide clues to the sediment composition and stability. Finally, the spider burrows were shown to be similar to specimens of *Skolithos* and *Macanopsis*, two ichnogenera whose potential tracemakers include spiders.

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CHAPTER 1: INTRODUCTION

Organisms produce biogenic structures by modifying a substrate in response to abiotic and biotic environmental conditions. These structures may be preserved in the geologic record as trace fossils. Trace fossils may, therefore, be used to infer the presence of organisms whose bodies are rarely fossilized (Cameron, 1969; de Giberte et al., 2000; Fernandez and Pazos, 2013; Chin et al., 2013) and to interpret the environmental conditions under which the trace was produced (Turner et al., 1981; Savrda and Bottjer, 1986; Maples and Archer, 1989; Kraus and Hasiotis, 2006; Dashtgard et al., 2008). These interpretations are possible because of studies of living tracemakers in the field and laboratory (Hasiotis, 2007). The traces produced in marine ecosystems have long been studied (Dapples, 1938; Moore, 1938; MacGinitie, 1945; Barnes and Powell, 1950; Frey, 1968; Gingras et al., 2008), but more recent studies have begun to focus on the traces found in continental ecosystems (Ahlbrandt et al. 1978; Ratcliff and Fagerstrom, 1980; O'Green and Busacca, 2001; Gingras et al., 2002; Hembree and Hasiotis, 2006; Lawfield and Pickerill, 2006; Genise et al., 2009; Hamer and Sheldon, 2010; Buynevich et al., 2011).

Trace fossils were once considered rare in continental settings, but they have been found to be quite common in many types of continental strata (Hasiotis, 2002). In fact, continental trace fossils first appear during the Cambrian (MacNaughton et al., 2002). The organisms that produced these trace fossils can be difficult to interpret. It is possible, however, to make general interpretations about the identity of a tracemaker based on the morphology of the organism and the trace fossil. This has allowed workers to interpret

the presence of continental invertebrates such as various terrestrial annelids and arthropods in otherwise unfossiliferous units. Terrestrial arthropods contribute to soil formation by burrowing through and manipulating sediment as they make shelter, find food, and create places for reproduction (Smith and Hasiotis, 2008; Counts and Hasiotis, 2009; Hembree, 2009; Halfen and Hasiotis, 2010; Melchor et al., 2010; Fairchild and Hasiotis, 2011; Mikuš and Uchman, 2013; Getty et al., 2013). Ratcliffe and Fagerstrom (1980) provided some examples of the types of biogenic structures produced by several extant, nonmarine arthropods and the purposes of these structures. Arachnids (spiders, scorpions, mites) are common burrowing arthropods with an extensive fossil record extending to the Silurian (Dunlop, 2009). Prior neoichnological studies on arachnids such as scorpions and whip scorpions have shown that modern burrowing arachnids produce unique biogenic structures and are active in soil formation and soil alteration (Sadler, 1993; Hembree et al., 2012; Schmerge et al., 2013; Hembree, 2013, Hembree, 2014). Spiders are another important group of burrowing arachnids, but few studies have documented the morphology of spider burrows or how these animals respond to environmental stresses.

The purpose of this study is to document the burrow morphology of the trapdoor spider *Gorgyrella inermis* and the wolf spider *Hogna lenta* (Arachnida: Araneae) in a controlled laboratory setting. The spiders burrowed in sediments modeled after their natural habitats as well as sediments with such stresses as varying sediment composition and moisture. The results of this study include qualitative descriptions of the different burrow architectures produced by these spiders and a quantitative comparison to burrows

produced by other burrowing soil arthropods including millipedes, scorpions, and whip scorpions as well as specimens of the ichnogenera *Macanopsis* and *Skolithos*. The results of this study will: 1) improve our understanding of the behaviors and techniques associated with burrowing by spiders; 2) aid in the interpretation of potential tracemakers and environmental conditions of fossil continental burrows; 3) facilitate the inference of spiders in strata in which body fossils are rare or absent, thereby improving paleoecological interpretations; and 4) allow for better paleoenvironmental interpretations by statistically comparing the relationship between soil conditions and burrow properties.

CHAPTER 2: SPIDER EVOLUTION AND BEHAVIOR

Spiders (Order Araneae) belong to Subphylum Chelicerata. Chelicerates first appeared during the Cambrian (Dunlop, 2010). They are defined by the presence of chelicerae, a pair of joined pincers present on the second segment of the body, pedilapalps located near the mouth, four pairs of walking legs, and the absence of antennae, mandibles, and wings (Rupert et al., 2004). Members of Class Arachnida first appear during the Silurian (Dunlop, 2010). The earliest arachnids were marine, but nearly all modern arachnids are terrestrial (Pechnik, 1991). There are approximately 97,000 described extant species of arachnids (Dunlop, 2008). Arachnid bodies are divided into two sections: the anterior cephalothorax and the posterior abdomen (Rupert et al., 2004). Arachnids use pedipalps, non-walking appendages near the chelicerae, to grab and kill prey as well as to assist in reproduction (Pechnik, 1991).

Spider bodies differ from other arachnids in that the cephalothorax and abdomen are connected by a pedicle that enables each segment to move independently (Figure 1) (Gertsch, 1949; Rupert et al., 2004). The segments composing the cephalothorax are completely fused and those of the abdomen are fused in all derived spiders (Rupert et al.,

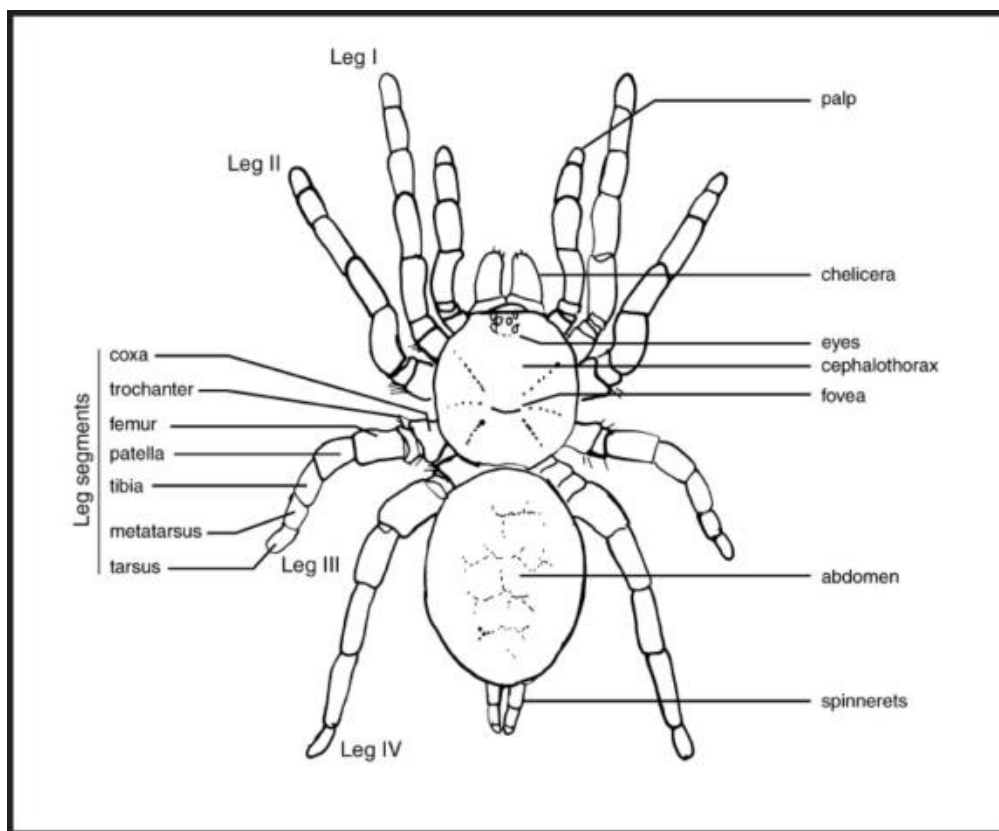


Figure 1: Basic spider morphology. Modified from Dipennar-Schoeman (2002).

2004). Nearly all spiders are carnivores that paralyze or kill prey by injecting venom using the chelicerae. The venom may also begin the digestion process (Rash and Hodgson, 2002). Spiders produce silk using spinnerets located near the end of the abdomen. The silk can vary both chemically and physically depending on its intended purpose (Pechenick, 1991).

Araneae consists of 44,032 extant species (Platnick, 2013) and is divided into two suborders: Mesothelae and Opisthothelae. Mesothelae is considered to be the most basal of the extant spiders as these spiders have a segmented abdomen and four pairs of spinnerets (Selden, 1996; Dippenarr-Schoeman, 2001). All extant mesothele spiders are

members of Family Liphistiidae, which contains 87 species in three genera (Platnick, 2013). Liphistiidae is limited to eastern Asia (Coddington, 1991). These spiders all live in burrows, and some, like the Japanese kimura-gumo (*Heptathela kumurai*), deposit lines of silk outside of their burrows to alert the spider when prey approaches (Platnick and Goloboff, 1985; Coddington, 1991). Opisthothelae contains two infraorders: Mygalomorphae and Araneomorphae. Most extant spiders are araneomorphs, with 41,748 species in 3,595 genera (Platnick, 2013). Mygalomorphae contains 2,792 species in 329 genera (Platnick, 2013). These spiders are generally slender, web-building spiders such as orb-weaver spiders and black widows. Mygalomorph spiders are generally bulky, ground-dwelling spiders that include trapdoor spiders and tarantulas. The chelicerae of araneomorphs cross each other transversely whereas the chelicerae of mesotheles and mygalomorphs move parallel against the body (Figure 2).

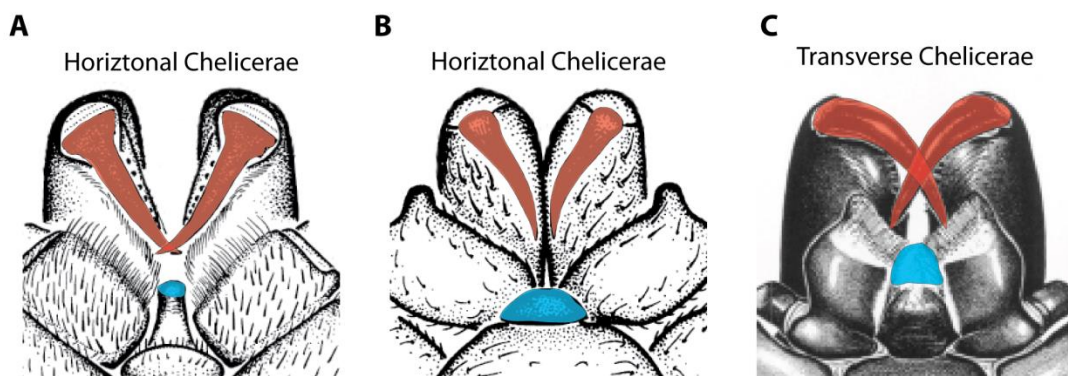


Figure 2: Ventral side of cephalothorax. Chelicerae are orange, mouth plates are blue. A) A mesothelae spider (modified from Platnick and Gertsch, 1979), B) A mygalomorph spider (modified from Platnick and Forster, 1982), C) An araneomorph spider (modified from Forster et al., 1987).

The fossil record of spiders extends to the Carboniferous and currently consists of approximately 1,185 valid species (Dunlop et al., 2013). The oldest known fossil mesothele is from the Carboniferous of France near Montceau-les-Mines (Selden, 1996; Selden, 2000). The oldest known opisthotheles appear in the Triassic consisting of a mygalomorph from the Grès à meules Formation of France (Selden and Gall, 1992) and two contemporaneous araneomorphs from the Molteno Formation of South Africa and the Cow Branch Formation of Virginia (Selden et al., 1999).

All extant mesothele spiders construct burrows (Bristowe, 1976; King, 2004) as do most mygalomorphs (Hamilton et al., 2012). The early spiders, therefore, were likely all burrowers like the ancestral arachnids (Decae, 1984). Positively identified spider burrows are rare, and occur mainly from the Cenozoic, such as the Miocene (Pickford, 2000) and the Pleistocene (Hasiotis, 2002). Spiders construct burrows as protection against predators and changes in climatic conditions as well as for brooding and obtaining prey (Gertsch, 1949; Hamilton et al., 2012). Construction of a burrow is energetically expensive and, therefore, sites are chosen carefully (Bond and Coyle, 1995; M'Rabet et al., 2007; Hamilton et al., 2012). Burrows are excavated using both chelicerae and pedipalps (Gertsch, 1949). The burrows are typically lined with silk, but the thickness of the silk lining varies between species and sediment types (Gertsch, 1949). Burrow size and complexity depends on the species and age of the individual (Gertsch, 1949).

2.1 *Gorgyrella inermis* and *Hogna lenta*

This study focuses on two species of burrowing spiders: *Gorgyrella inermis* Tucker, 1917 and *Hogna lenta* (Hentz), 1844. *Gorgyrella inermis* (Figure 3A,B) belongs to the mygalomorph family Idiopodae, which is known only from the recent (Platnick, 2013). Members of this family are typically nocturnal ambush predators that wait for prey at the opening of their burrows. *Gorgyrella inermis* is native to the grasslands of South Africa. These spiders have short legs and thick abdomens and may live up to 10 years. The burrows of *G. inermis* have been described as long, simple shafts with an oval shaped opening (Dippenaar-Schoeman, 2001). The trapdoor is D-shaped and very wide with a hinge that exceeds the width of the burrow (Dippenaar-Schoeman, 2001). *Hogna lenta* (formerly *Lycosa lenta*) (Figure 3C) belongs to the araneomorph family Lycosidae, which has a fossil record extending to the Cretaceous (Platnick, 2013). Members of this family are active hunters that use their burrows as a retreat.

Hogna lenta is native to the southeastern portion of the United States, particularly Florida (Wallace, 1942). They occupy a variety of habitats although they are often found in sandy sediments (Eisman et al., 2010). These spiders are nocturnal and emerge from

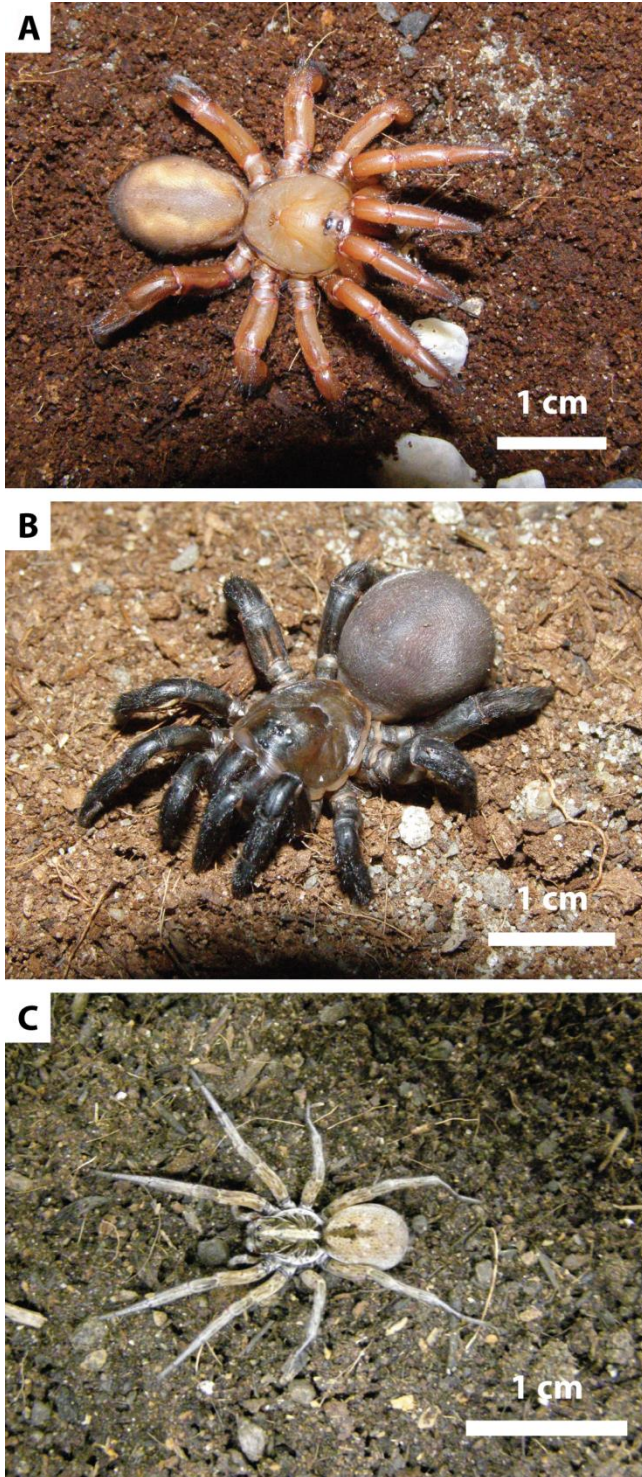


Figure 3: Representatives of spiders used in this study. A) Adult *Gorgyrella inermis*, B) Juvenile *G. inermis*, C) *Hogna lenta*.

their burrows at dusk to search for prey (Wallace, 1942). *Hogna lenta* lives for up to one year upon reaching adulthood (Anderson, 1974). The burrows produced by *H. lenta* are generally simple, vertical shafts that may have a turret (Wallace, 1942; Gertsch, 1949). The burrows are sealed with a trapdoor constructed of a thick layer of silk covered by sand or other material (Eisman et al., 2010).

2.2 Spider Burrows in the Fossil Record

Previously described spider burrows superficially resemble the ichnogenera *Skolithos* Halderman, 1984 (Figure 4) and *Macanopsis* Mascotay, 1967 (Figure 5). *Skolithos* and *Macanopsis* include a vertical to subvertical shaft with one surface opening, but *Macanopsis* also includes a chamber at the terminus of the shaft. Both ichnogenera occur in marine and continental strata (Schlirf and Uchman, 2005; Mikus and Uchman, 2013) and both have been interpreted as dwelling structures (Muñiz and Mayoral, 2001; Schlirf and Uchman, 2005). *Skolithos* is diagnosed as a straight shaft that is subcylindrical and unbranched (Häntzschel, 1975). Continental specimens are attributed to insects and spiders (Ratcliffe and Fagerstrom, 1980). *Macanopsis* is diagnosed as a straight or somewhat bent, nonbranching tunnel with a circular to elliptical cross section ending in a chamber (Häntzschel, 1975). Continental specimens have been attributed to several arthropods, but Brown and Kraus (1983), Hasiotis (2002), and Retallack et al. (2003) have suggested spiders as potential tracemakers.

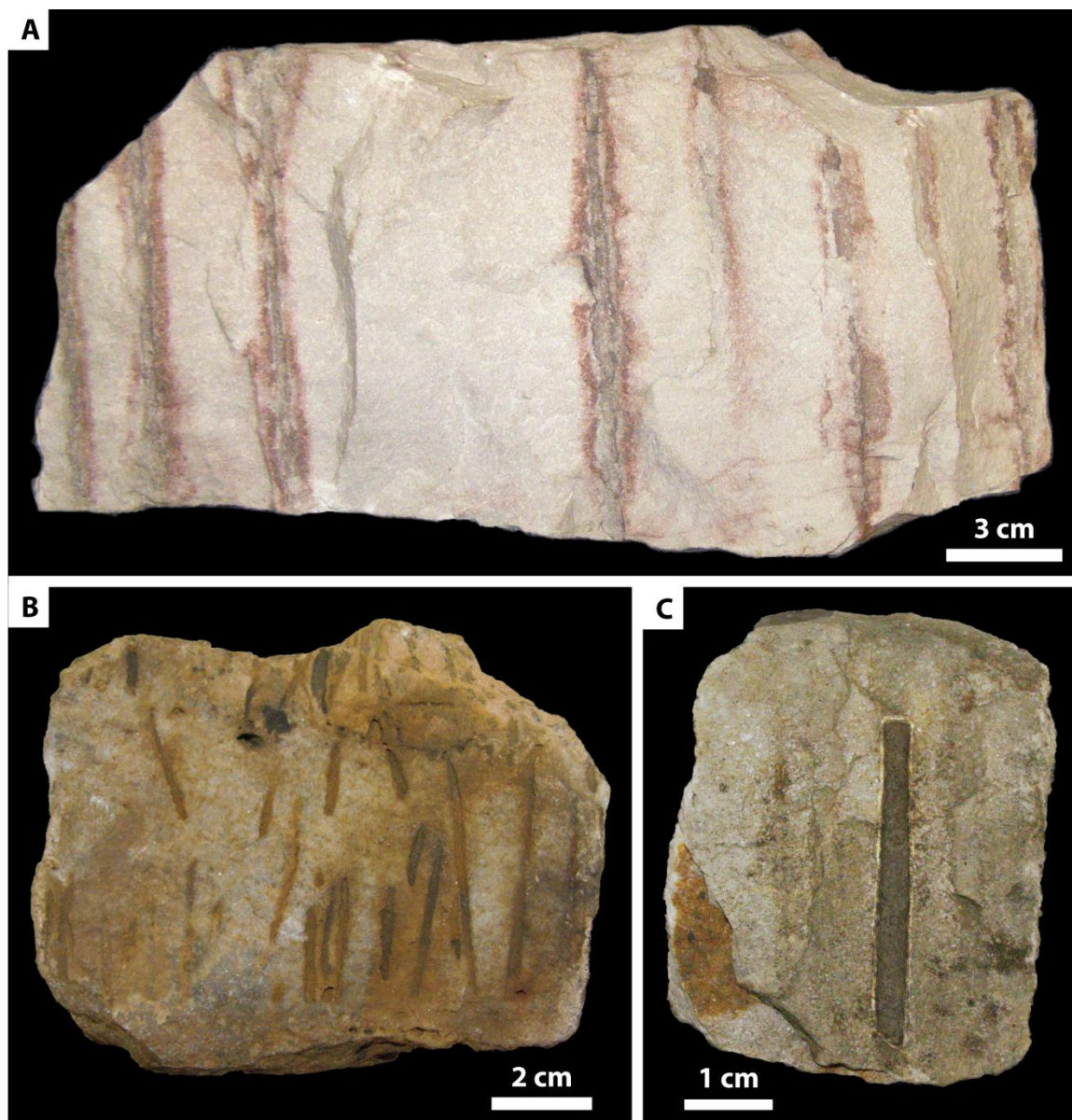


Figure 4: Specimens of *Skolithos* from the Yale Peabody Museum. A) Specimen No. 9013, B) Specimen No. 325521, C) Specimen No. 8183. The surrounding matrix has been lightened to ease identification within the rock.

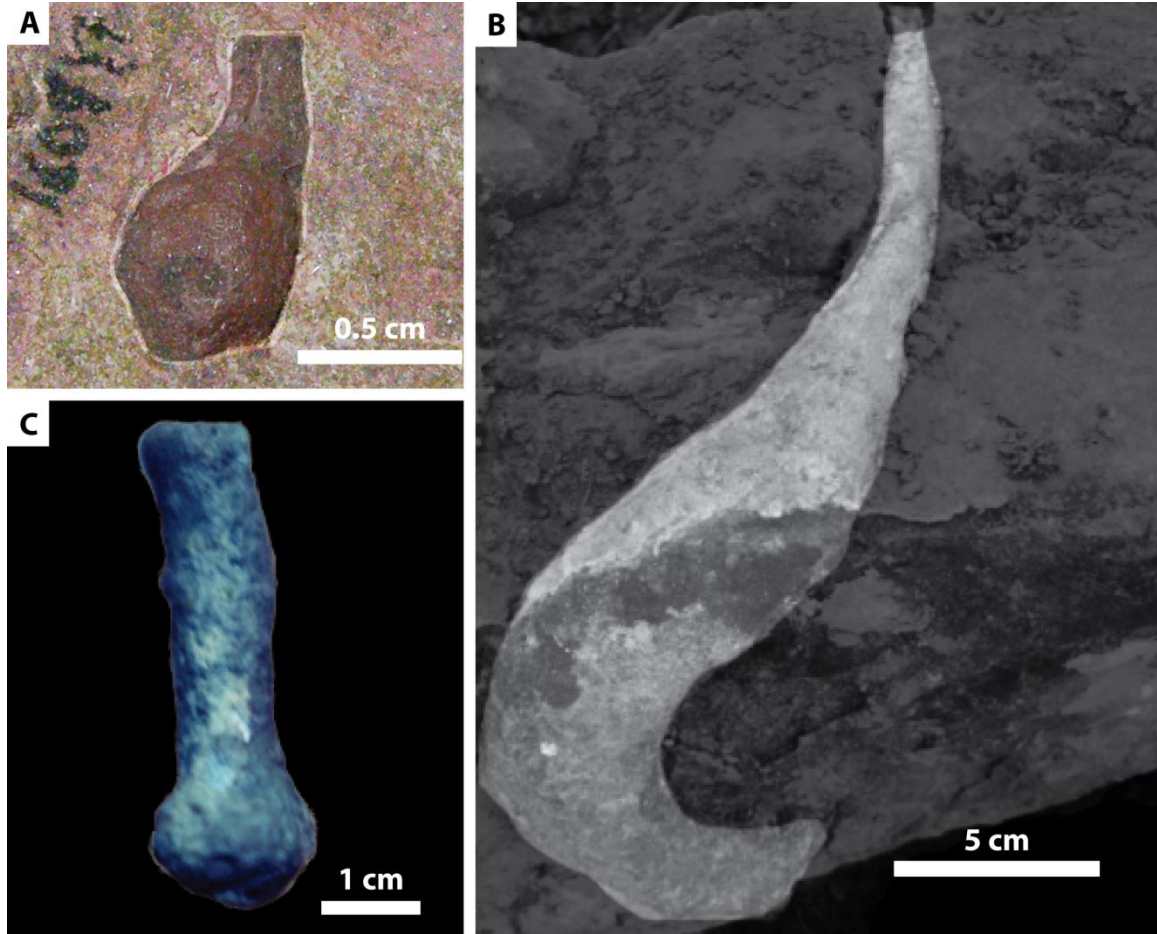


Figure 5: Specimens of *Macanopsis*. A) Specimen No. 160717 from Yale Peabody Museum. The matrix has been lightened to ease identification of the specimen B) Photo of specimen from Brown and Kraus (1983) by Hasiotis (U.S. Geological Survey 5866), C) Specimen from Carvhaolo et al. (2010). The matrix has been darkened to ease identification of the specimen.

CHAPTER 3: MATERIALS AND METHODS

Eight individuals of *G. inermis* and eleven individuals of *H. lenta* obtained from a commercial source were used in this study. All representatives of *H. lenta* were adults, whereas *G. inermis* representatives included five adults and three juveniles. The adult specimens of *G. inermis* were red and the juveniles were black. The spiders of both species were not sexed for this study, but four representatives of *H. lenta* produced eggs multiple times. Adult *G. inermis* had an average body length of 3.7 cm and a body width of 1.4 cm, whereas juveniles had an average body length of 2.6 cm and body width of 0.85 cm. *Hogna lenta* specimens had an average body length of 2.3 cm and body width of 0.85 cm.

The spiders were allowed to acclimate to laboratory conditions for at least two weeks before the experiments began. During this time, they were housed individually in 10 gal (38 L) terraria filled with 100% finely shredded coconut fiber, a medium not used for the experiments. The laboratory was kept on a 12-hour light cycle with temperatures between 25–30 °C and humidity at ~35%. Media were kept moist by daily spraying of water both during the acclimation period and the experiments. In addition, individuals of *H. lenta* were provided water dishes which were refilled when media were moistened. Both species were fed live crickets weekly; any dead crickets were removed from the terraria. Direct handling of the spiders was minimized to avoid altering their behavior and to avoid additional stress.

Three sizes of terraria were used during the experiments: 10 gal (38 L) ($50l \times 25w \times 30h$ cm), 20 gal (76 L) ($60l \times 30w \times 42h$ cm), and 30 gal (114 L) ($90l \times 42w \times 30h$ cm).

The terrarium sizes used with each species were determined by evaluating the size of the adult individuals and the potential size of the burrows as determined during the acclimation period. The tanks were filled to depths of 25, 26, and 35 cm of sediment respectively. These depths were chosen to allow enough room for the spiders to move but also to prevent escape. The terraria were covered with screens to further prevent escape of the individuals. All study specimens were kept at laboratory temperatures with no additional heat input. The sediments used were different mixtures of finely shredded coconut fiber (organic material), fine- to medium-grained quartz sand, and sifted potting soil (organic rich silt and clay). Sediment mixtures were homogenized and moistened to the correct moisture content prior to filling the terraria. The density and moisture of the sediment were measured using a Field Scout SC900 Soil Compaction Meter (Spectrum Technologies Inc.) and an Aquaterr EC-300 Salinity Multimeter, respectively.

Three experiments were conducted with different sediment compositions and moisture contents to determine if burrow morphology changed in response to changes in environment (Table 1). The point of reference for the burrow morphology of each species was established in Experiment 1. The sediment mixtures and sediment moisture levels in Experiment 1 resembled those of each species' natural habitat (Table 1A). Two additional parameters were tested in Experiment 1: the time allowed for burrowing and the size of the terrarium used. Spiders were allowed to burrow over time intervals of 14 and 30 days in order to determine if the morphology of the burrows would change over time. The spiders were housed in two terrarium sizes according to the species, one small (10 or 20 gal) and one large (20 or 30 gal), to test the effect of enclosure size on burrow

Table 1: Experimental design and burrows produced. Sediment density is given in kgf/cm². Sediment moisture values are in percent total volume. VS: vertical shaft, VC: vertical shaft with terminal chamber, SS = subvertical shaft, SC = subvertical shaft with terminal chamber, JS = J-shaped burrow, YS = Y-shaped burrow, IC = isolated chamber.

A. Experiment 1: Basic Morphology

Species	Individuals	Terrarium		Sediment Depth (cm)	Sediment Density	Sediment Moisture	Duration (day)	Resulting Burrow Architectures
		Size (gal)	Sediment Composition					
<i>G. inermis</i>	5	20	30-50-20% organic-sand-clay/silt	35	0.35	55%	14	VS (3), SS (1), IC (1)
<i>G. inermis</i>	5	20	30-50-20% organic-sand-clay/silt	35	0.35	55%	30	VS (2), VC (2)
<i>G. inermis</i>	3	30	30-50-20% organic-sand-clay/silt	25	0.35	55%	14	VS (1), VC (1), SC (1)
<i>G. inermis</i>	3	30	30-50-20% organic-sand-clay/silt	25	0.35	55%	30	VS (1), SS (1)
<i>H. lenta</i>	5	10	50-50% organic-clay/silt	25	0.35	35%	14	VS (3), YS (1)
<i>H. lenta</i>	4	10	50-50% organic-clay/silt	25	0.35	35%	30	VS (2), VC (1)
<i>H. lenta</i>	4	20	50-50% organic-clay/silt	26	0.35	35%	14	VS (1)

B. Experiment 2: Sediment Composition

Species	Individuals	Terrarium		Sediment Depth (cm)	Sediment Density	Sediment Moisture	Duration (day)	Resulting Burrow Architecture
		Size (gal)	Sediment Composition					
<i>G. inermis</i>	5	20	30-35-35% organic-sand-clay/silt	35	0.35	55%	30	VS (4)
<i>G. inermis</i>	5	20	30-20-50% organic-sand-clay/silt	35	0.70	55%	30	VS (2), VC (2)
<i>H. lenta</i>	3	20	25-75% organic-clay/silt	26	0.35	35%	30	VS (2), SS (1)
<i>H. lenta</i>	4	20	100% clay/silt	26	0.70	35%	30	VS (1), SS (3)

C. Experiment 3: Sediment Moisture

Species	Individuals	Terrarium		Sediment Depth (cm)	Sediment Density	Sediment Moisture	Duration (day)	Resulting Burrow Architecture
		Size (gal)	Sediment Composition					
<i>G. inermis</i>	4	20	30-50-20% organic-sand-clay/silt	35	0.35	35%	30	VS (2), SS (1), JS (1)
<i>G. inermis</i>	4	20	30-50-20% organic-sand-clay/silt	35	0.70	75%	30	VS (1)
<i>H. lenta</i>	4	20	50-50% organic-clay/silt	26	0.35	15%	30	VS (2)
<i>H. lenta</i>	4	20	50-50% organic-clay/silt	26	0.35–0.70	55%	30	VS (1), SS (1)

morphology in laboratory conditions. The sediment composition was altered in Experiment 2 to include two sediment types with an increased percentage of fine-grained material (Table 1B). The sediment moisture content was altered in Experiment 3 by decreasing and increasing sediment moisture content by 20% per trial (Table 1C).

The spiders were observed, photographed, and digitally recorded during the experiment. Recorded observations included time elapsed before the spiders began a burrow, silk-production related to burrow construction, and sediment surface features resulting from burrowing. Spiders were removed from the experimental set-up at the conclusion of each trial by either capturing them on the surface or direct extraction from the burrow. The latter method was used for most individuals of *G. inermis*, which do not leave their burrows, and some individuals of *H. lenta*. To accomplish this, ~1 cm sheet of thin plastic was attached to the end of a drinking straw which was inserted into the spider burrows (Figure 6). When the spiders attacked the straw, their chelicerae became stuck in the plastic and they could be gently pulled from their burrows. Some spiders fled their burrow when the straw was placed in their burrows.

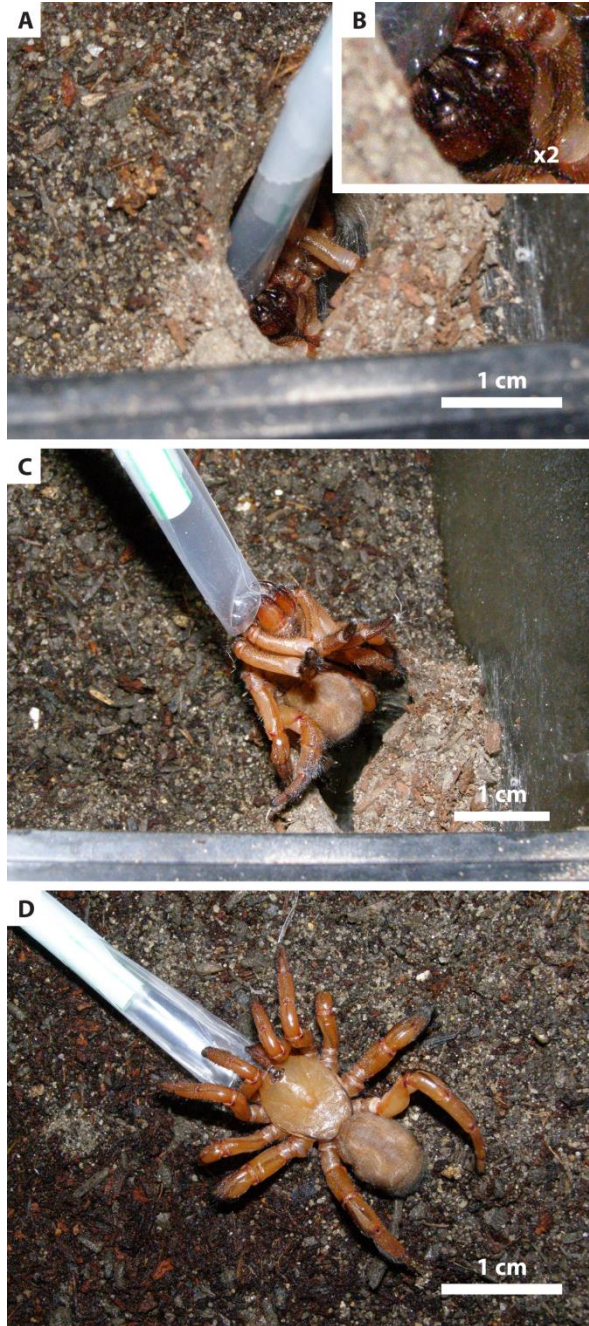


Figure 6: Extracting *G. inermis* from its burrow. A) Spider bites the plastic with chelicerae, B) Close-up of chelicerae in the plastic, C) Spider is nearly extracted, but is holding onto the silk lining of the burrow with its back legs, D) Spider is completely extracted but continues to hold on to the plastic with its chelicerae and pedipalps.

Open burrows were filled with Drystone® plaster. The trapdoors on the burrows of *G. inermis* were covered with plaster and kept attached to the burrow cast to maintain orientation of the burrow. The burrows of *H. lenta* were marked to indicate where the spider generally entered and exited the burrow. In these ways, the height and width of the burrow relative to the spider in life position were known for the measurements. The burrow casts were washed and cleaned of silk and sediment. The silk lining was discarded after the relative amount of silk and how deeply the silk lined the burrow were noted.

Qualitative data of the burrows were recorded including general shape, number of surface openings, number of burrow branches, and number of chambers. Quantitative measurements included the maximum depth, total length, burrow width, height, and circumference measured at 1 cm intervals along the cast's length, the width/height ratio, the maximum and minimum angles of the burrow with respect to the sediment surface, and the average angle of branching if present. Complexity and tortuosity were also calculated. Both are scale-independent measurements that can be used to compare burrow systems produced by animals of different sizes (Meadows, 1991). Burrow complexity is a measure of the number of segments (s), the number of openings in the sediment surface (e), and the number of chambers (h) (Figure 7A). Complexity (C) is calculated by summing these factors: $C = s + e + h$, where $C \geq 1$. Tortuosity is the measure of the deviation of a shaft or tunnel from a straight line (Figure 7B). Tortuosity is calculated by dividing the total length of a segment (u) by the straight line distance between the ends of the segment (v) (Figure 7C).

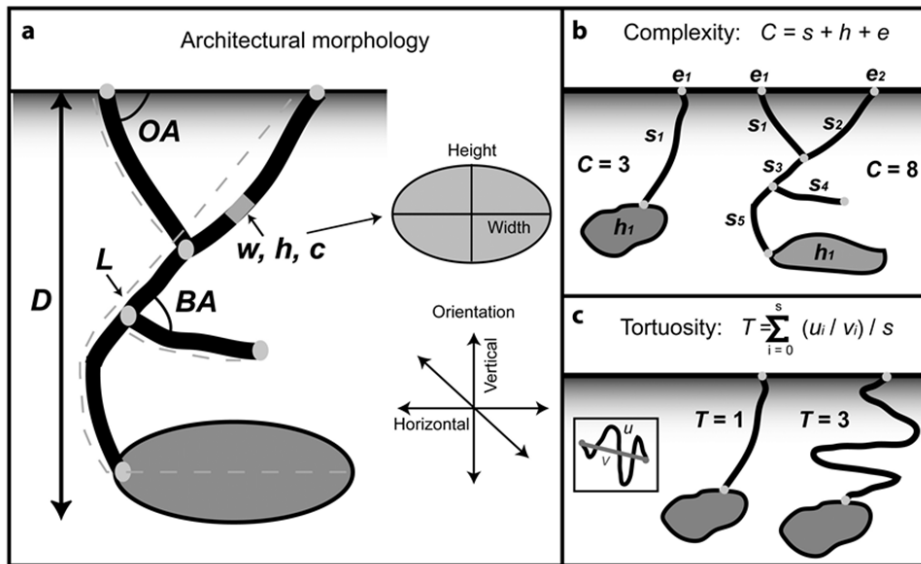


Figure 7: Quantitative properties of burrows. A) Measurements of burrows included maximum depth (D), tunnel and shaft width (w), height (h), and circumference (c), total length (L), and branching angle (BA). B) Complexity (C) is the sum of the number of segments, chambers, and surface openings (e) of a single burrow system. C) Tortuosity is a measure of the average sinuosity of all of the segments of a burrow system. The tortuosity of a single segment is found by dividing the total length (u) by the straight-line distance (v). Modified from Hembree et al., 2012.

The Bray-Curtis similarity measure was used to determine the degree of similarity of burrow morphologies within each individual species and between the two species of spiders. The Bray-Curtis similarity measure is a nonparametric statistical analysis in which the sum of the differences for each quantitative measurement is compared to the sum of the total measurements in the sample (Bray and Curtis, 1957). This number is subtracted from 1.0 to determine similarity. These analyses were performed using PAST (ver. 2.17b) (Hammer et al., 2001). The scores resulting from the analyses can be shown in a matrix. Similarity is ranked from 0.0 (completely dissimilar) to 1.0 (identical). In this study, two burrows with a rank of 1.0 were considered identical, ranks between 0.9 and

0.6 express high to moderate similarity, and ranks ≤ 0.5 are dissimilar (Hembree et al., 2012; Hembree, 2013, Hembree, 2014; Catena and Hembree, 2014; Dzenowski and Hembree, 2014; Bowen and Hembree, 2014). This analysis was used to determine if the morphologies of the spider burrows are similar, indicating a common burrow morphology produced by spider tracemakers, and to see if the morphologies changed with variations in sediment composition and moisture.

The scores resulting from the Bray-Curtis analysis were then used to construct dendrograms of similarity. The dendrogram provides a graphical representation of Bray-Curtis scores. A dendrogram is formed by grouping two burrows with the closest similarity. The score of the next similar burrow is averaged with the scores of the two previous burrows. This results in groups, or clusters, of burrows that are more similar to each other than to the other burrows. Analyses of the dendrograms reveal the amount of similarity between burrows with different qualitative architectures and those produced under different environmental conditions. The dendrograms were also used to determine if the burrows of different animals separate into specific clusters.

The burrows produced by the spiders were compared to those produced by five other burrowing arthropods from previous studies. These burrows were measured and described in the same manner as the spider burrows. The burrows of three other arachnid species were used to determine similarity of burrows within Arachnida: the Mexican blond tarantula (Figure 8A,B), *Aphonopelma chalcodes* ($n = 2$) (Araneae:

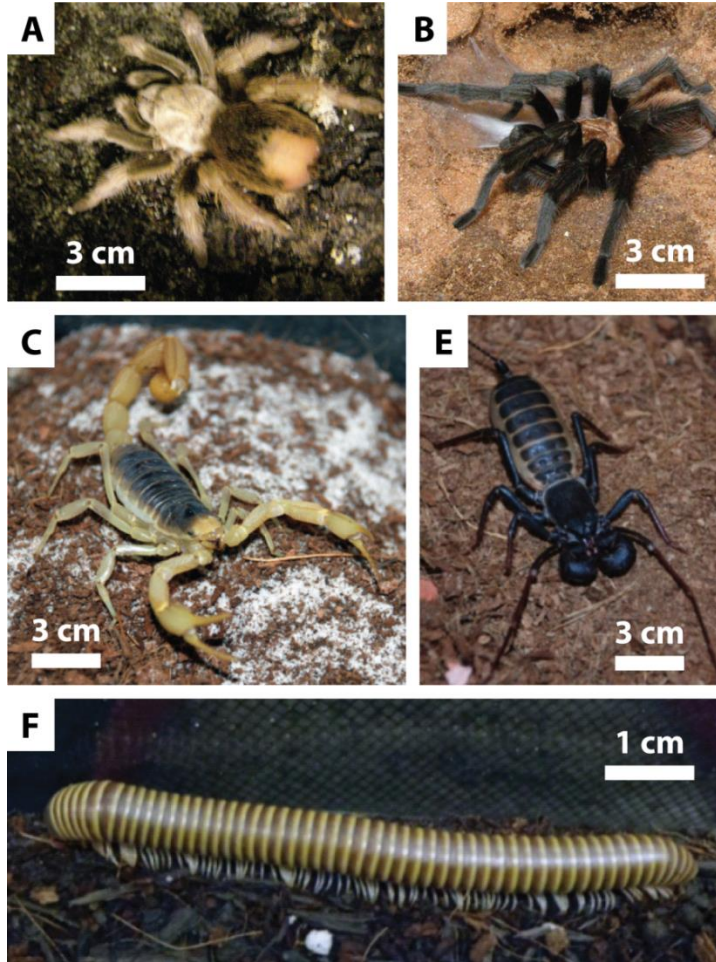


Figure 8: Representatives of other laboratory animals used for burrow comparisons within arthropods. A) A female Mexican blond tarantula (*Aphonopelma chalcodes*), B) A male *A. chalcodes*, C) The Arizona hairy desert scorpion (*Hadrurus arizonensis*), D) The whip scorpion (*Mastigoproctus giganteus*), E) The giant American centipede (*Narceus americanus*).

Theraphosidae), the Arizona desert hairy scorpion (Figure 8C), *Hadrurus arizonensis* ($n = 17$) (Scorpiones: Caraboctonidae) (Hembree et al., 2012), and the American whip scorpion (Figure 8D), *Mastigoproctus giganteus* ($n = 18$) (Thelyphonida: Thelyphonidae) (Hembree, 2013). It was expected that arachnid burrows would be similar as all five species share the same basic body plan. The burrows of the American giant millipede

(Figure 8E), *Narceus americanus* ($n = 15$) (Diploda: Spirobolida) (Bowen and Hembree, 2014), were used to determine the similarity of the spider burrows with unrelated arthropods. It was expected that the spider burrows would not be similar to the millipede burrows because the body plans and life habits of millipedes are very different than those of arachnids.

The spider burrows were also compared to specimens of *Skolithos* ($n = 6$) and *Macanopsis* ($n = 3$). Specimens were obtained from Yale Peabody Museum of Natural History. Individual specimens of *Skolithos* and *Macanopsis* were measured in the same manner as the spider burrows. All specimens of *Skolithos* and one specimen of *Macanopsis* occurred in marine strata. The measurements of four specimens of *Skolithos* were taken from multiple specimens in the same sample when specific aspects of the morphology were unable to be measured from a single specimen. Measurements of two *Macanopsis* specimens (MAC 2 and MAC3) were taken from the literature (Brown and Kraus, 1983; Carvahlo et al., 2010) and occurred in continental strata. Burrow depth was not measured as this characteristic was unable to be determined. Burrow depth of the burrows produced by *G. inermis* and *H. lenta* was excluded from Bray-Curtis analyses when compared with the trace fossils.

The nonparametric Mann-Whitney and Kolmogorov-Smirnov tests were used to evaluate the differences in individual properties between groups of burrows. The Mann-Whitney test determines if two samples are from the same population by testing the similarity of their medians. The Kolmogorov-Smirnov test compares the distribution of two samples to determine if they are similar. Properties compared for each test included:

1) total depth, 2) total length, 3) average width, 4) average height, 5) average circumference, 6) average slope, 7) complexity, and 8) tortuosity. The tests were used for two different analyses. The first was to determine if statistically significant changes occurred in burrow properties in different sediment compositions and in different sediment moisture conditions. The second was to determine if the quantitative burrow properties of *G. inermis* and *H. lenta* were similar, and then to determine if the burrow properties of both spider species were similar to those of the other arthropods and trace fossils.

CHAPTER 4: RESULTS

4.1 Behaviors

Individuals of *G. inermis* and *H. lenta* burrowed within 0–15 days after the experiments began with an average of 5 days to begin burrowing. Those spiders that did not burrow immediately moved around the enclosure and tested the sides of the glass. Some spiders climbed to the top of the terrarium and along the screen lid. The smaller individuals of *G. inermis* and *H. lenta* generally burrowed faster than larger ones. Some spiders, most commonly *H. lenta*, never produced a burrow. Burrows could be located at any place in the terraria, but the spiders often burrowed along the side of the glass wall.

Both species began constructing their burrows by manipulating the sediment with their pedipalps and chelicerae. Representatives of *H. lenta* were observed pushing the sediment against the walls of their burrows (Figure 9). Although Gertsch (1949) reported that wolf spiders removed sediment wrapped in silk from their burrows, this behavior was

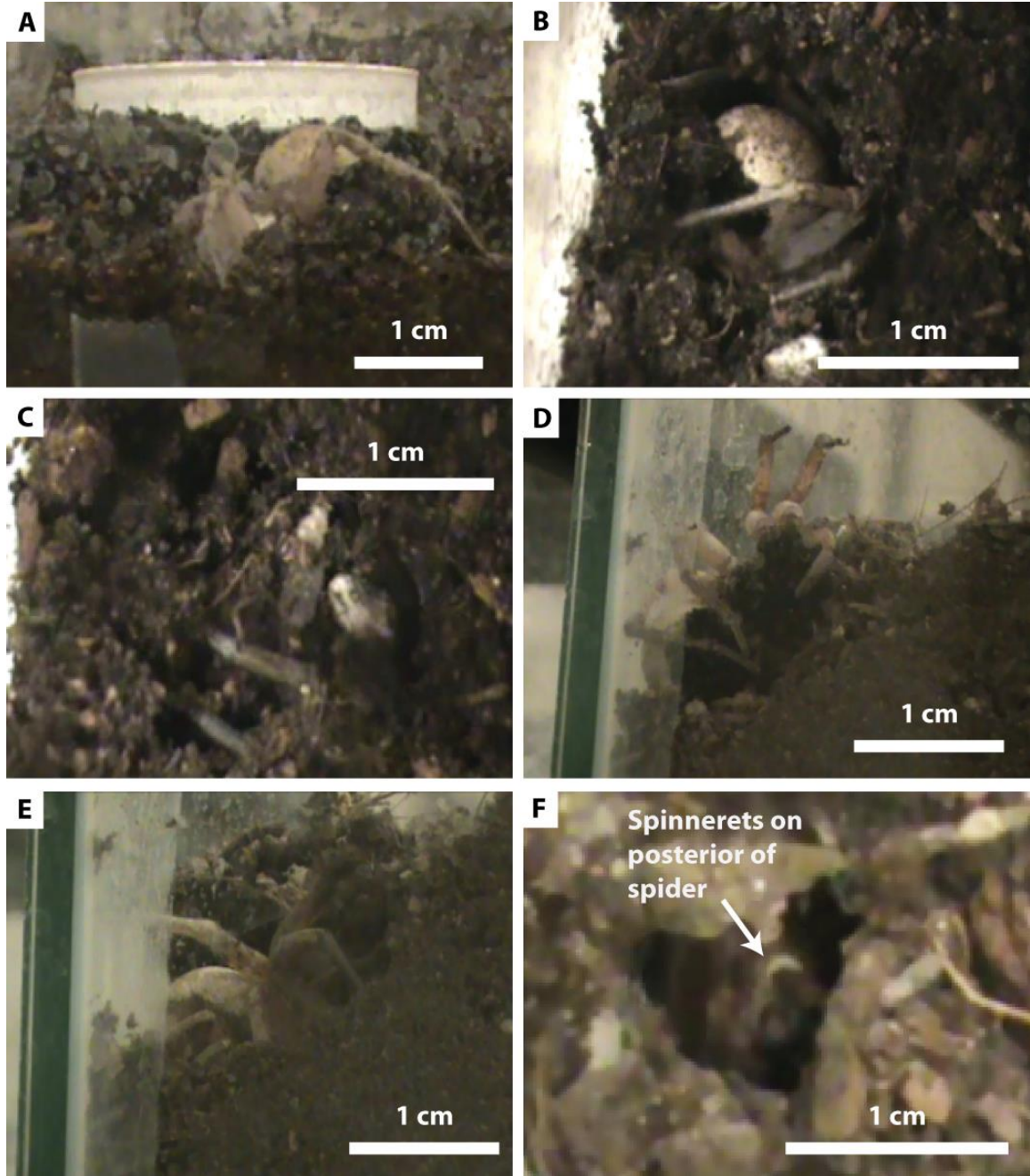


Figure 9: Burrow production by *H. lenta*. A–B) Spider pushes headfirst into the sediment until it is nearly covered. C) Spider turns around inside of the chamber to face outward, D) Spider applies silk to the sediment and moves it around, E) Spider covers itself in silk-lined sediment, F) Spinnerets tying sediment together to form a trapdoor. The sediment surrounding the spider and its burrow has been lightened.

not observed. A thin layer of silk was deposited on the sides of the burrow as the spider moved into the sediment. *Hogna lenta* covered their burrow openings with a thin layer of sediment stuck together using silk (Figure 9F).

Gorgyrella inermis produced burrows in two ways (Figure 10). Smaller individuals compacted sediment in the sides of burrows with no excavation. Larger individuals wrapped sediment at the base of the burrow in silk and threw these packets from the burrow (Figure 10D). These packets could land up to 27 cm from the burrow opening (Figure 13B). The spiders deposited a thick layer of silk along the sides of the burrow. *Gorgyrella inermis* made thick burrow trapdoors constructed of organic matter and silk attached to one side of the burrow opening with a hinge (Figure 13A). Individuals of *G. inermis* were observed searching for and reattaching trapdoors when these were removed.

The burrows were used for multiple purposes. The burrows of *G. inermis* were used for both dwelling and ambush hunting. These spiders did not leave their burrows once they were constructed. To obtain prey, *G. inermis* waited near the top of its burrow and grabbed prey that moved near the entrance with pedipalps and front legs. The prey was pulled down into the burrow for consumption. *Gorgyrella inermis* excreted waste by climbing to the top of the burrow and forcefully expelling waste away from the burrow. The burrows of *H. lenta* were used for dwelling, hunting, and nesting. These spiders were often observed at the surface, but typically retreated into their burrows in response to bright lights and disturbances in their enclosures. Although *H. lenta* is an active surface hunter, some individuals were observed ambushing prey from their burrow entrances.

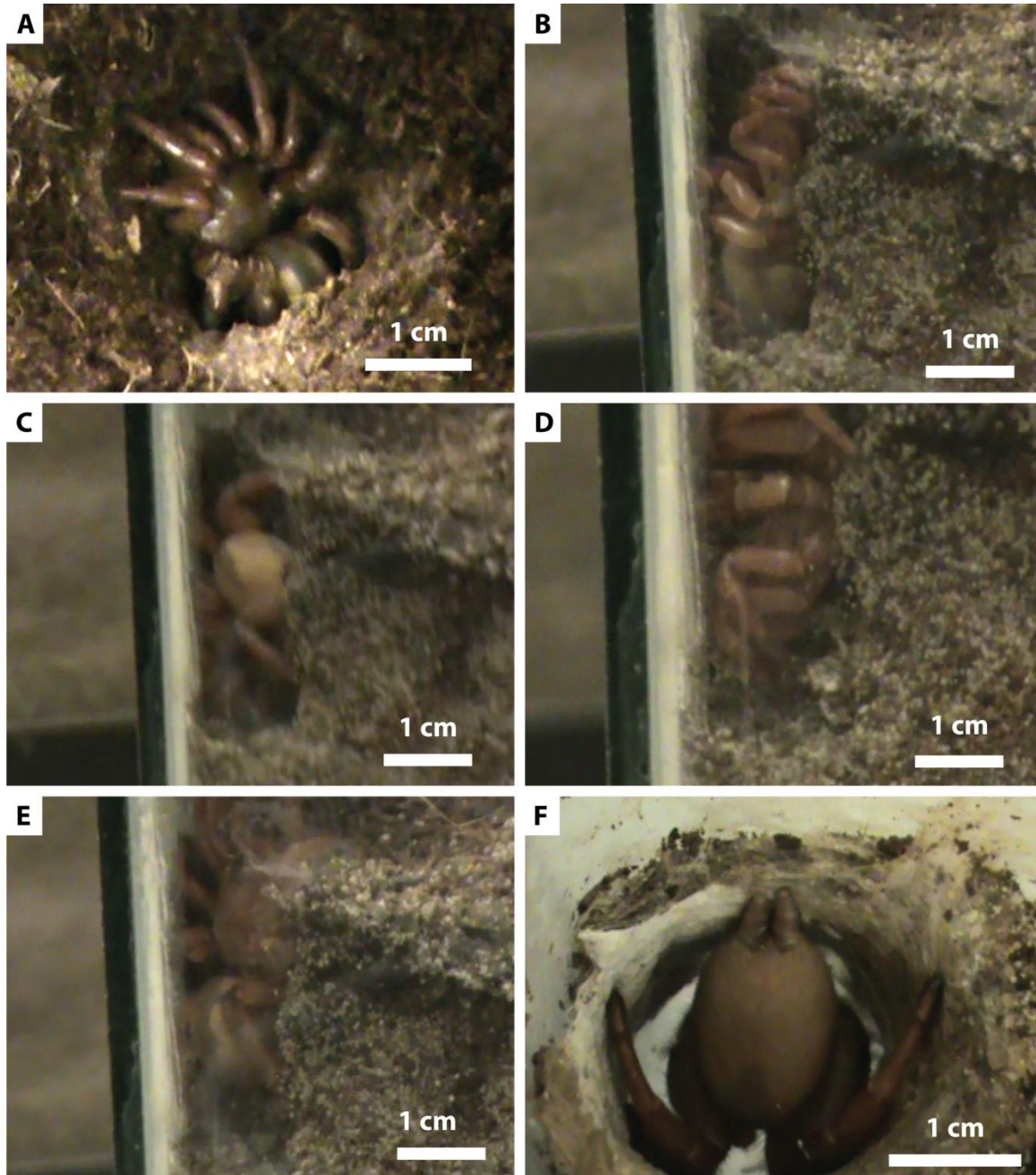


Figure 10: Burrow production by *G. inermis*. A) Spider excavates a small depression in the sediment, B) Spider deposits silk in sediment at the base of the burrow, C–D) Spider turns around inside of burrow and picks up bundles of sediment, E) The spider throws the sediment from the burrow, F) Spider deposits silk along the burrow wall.

Two individuals produced eggs during the course of the experiments, which were collected into sacs made of silk (Figure 11C). The newly hatched spiders stayed with their mother until they were large enough to strike out on their own (Figure 11B). These burrows were large enough to house the spider with its eggs (Figure 11A). *Hogna lenta* individuals with eggs rarely left their burrows to hunt.

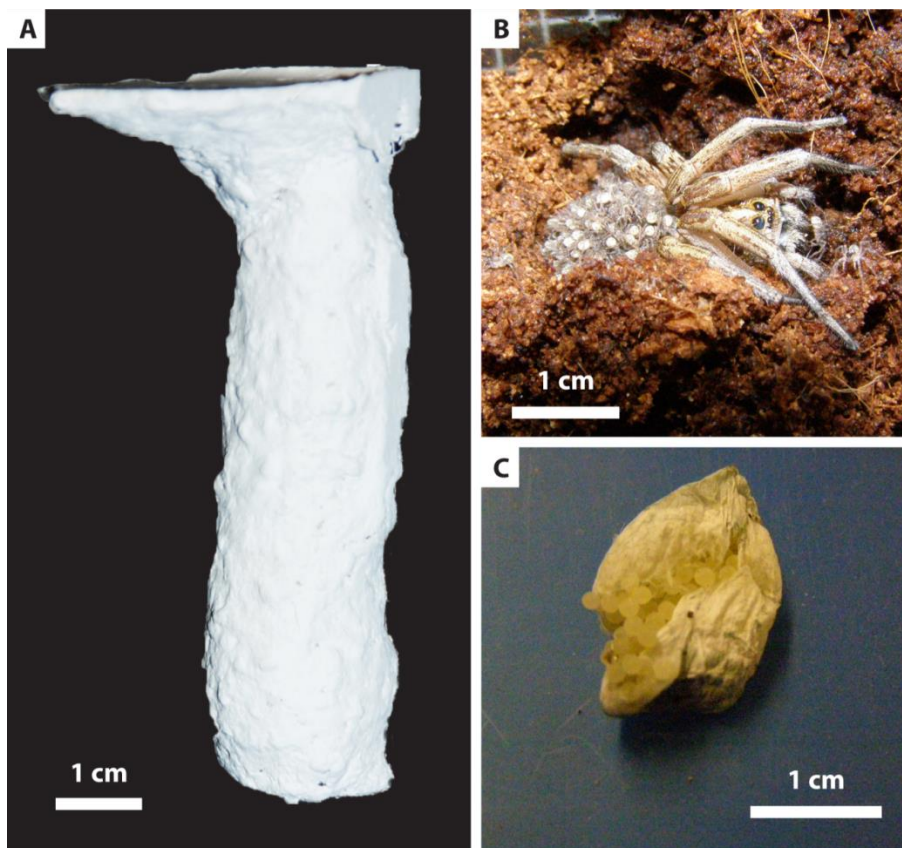


Figure 11: Brooding behavior of *H. lenta*. A) A vertical shaft that served as a brood burrow (H5), B) The spider that constructed the brood burrow and its offspring. C) An egg sac produced by another spider.

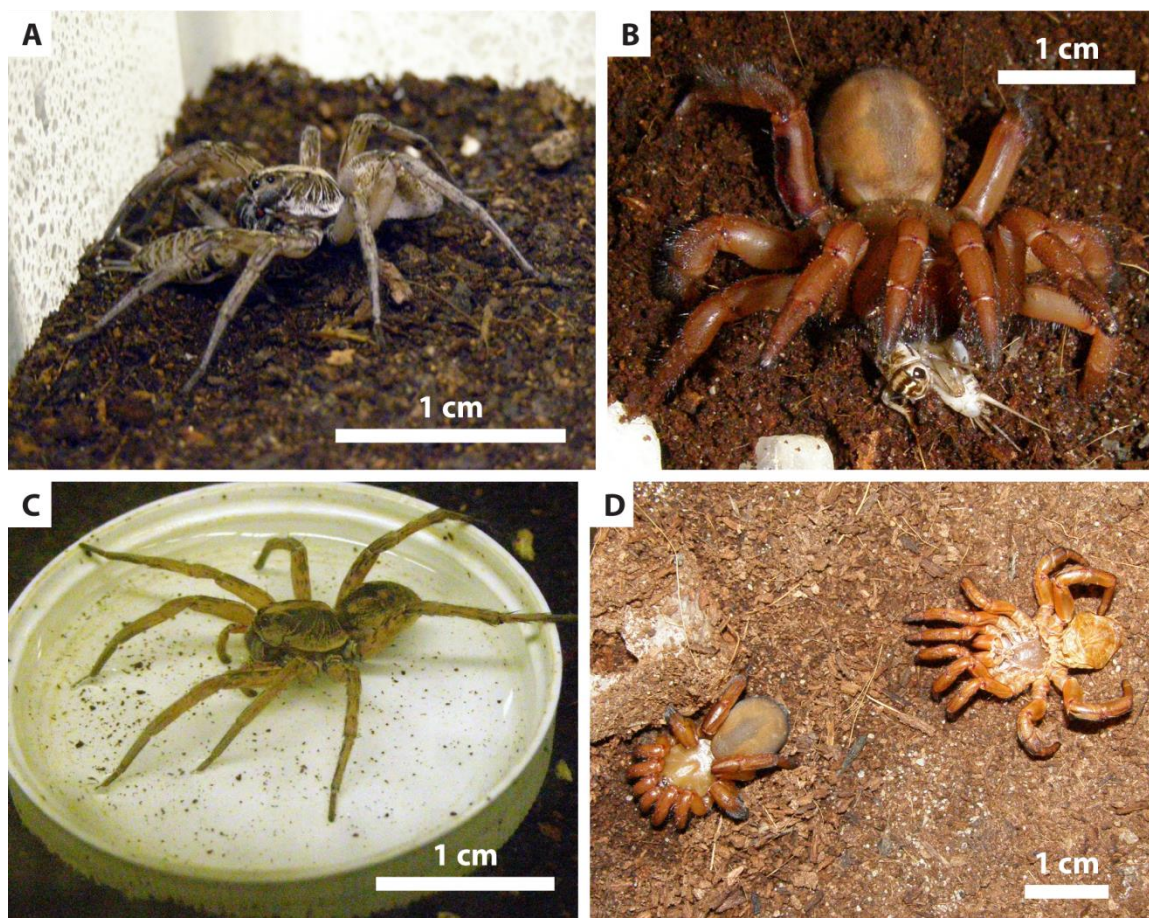


Figure 12: Behaviors observed during experiments unrelated to burrow production. A) *H. lenta* consuming prey, B) Adult *G. inermis* consuming prey, C) *H. lenta* drinking, D) Adult *G. inermis* molting. This behavior was only observed when the spiders did not construct a burrow.

Other observed behaviors include catching prey, drinking water, and molting (Figure 12).

4.2 Surface Morphology

The surface of the sediment was smoothed prior to the introduction of a spider. *Gorgyrella inermis* produced obvious trapdoors at the entrances of their burrows. The trapdoors were flush with the sediment surface except when the burrow was built against glass (Figure 13A). In these cases, the burrows protruded ~1 cm above the sediment

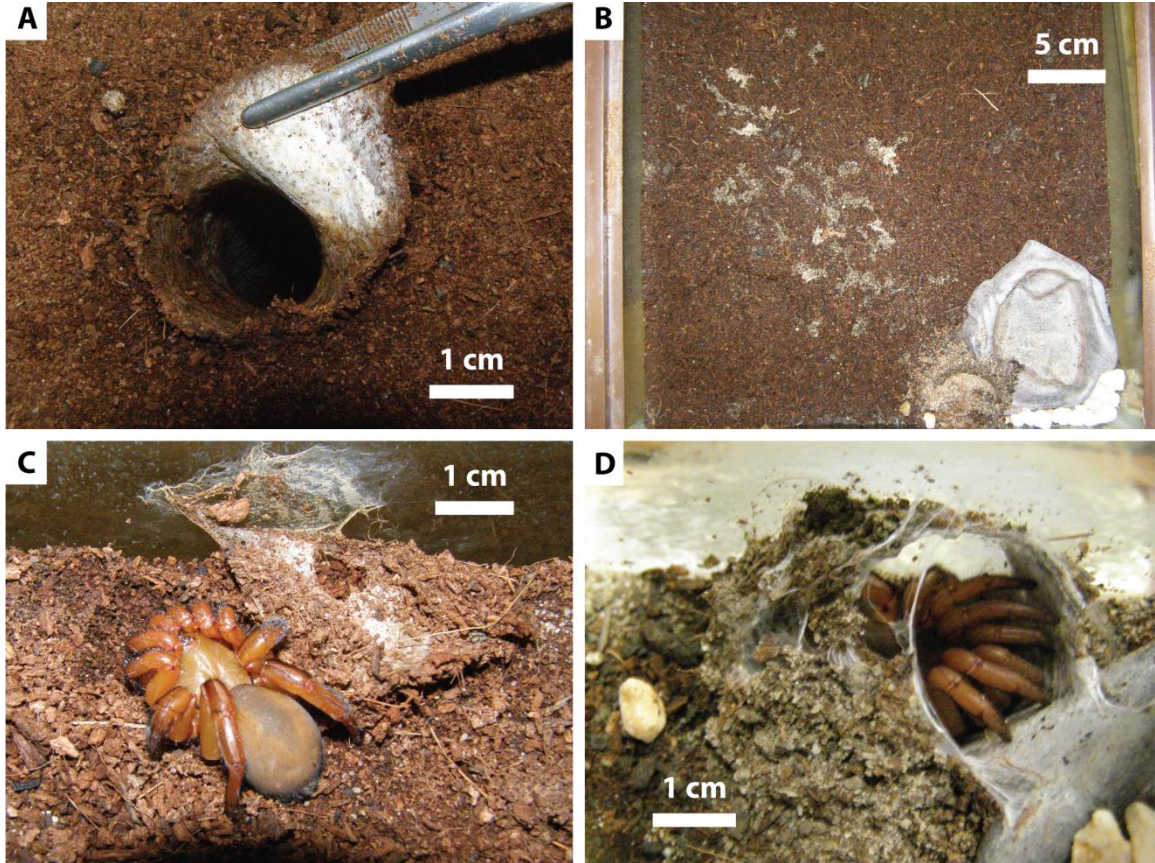


Figure 13: Surface features produced by *G. inermis*. A) Trapdoor held open at a burrow entrance, B) Sediment forcefully removed from the burrow by the spider throwing packets with its chelicerae, C) A silk mat produced by a spider that did not construct a burrow, D) A cocoon built by a spider that did not burrow. The cocoon did not extend into the sediment.

Surface features produced by *H. lenta*. A) Open trapdoor at the burrow entrance, B) Turret produced by building a burrow entrance against the sides of the terrarium, C) Silk strands deposited along the sides of the terrarium. not construct a burrow. One structure was a “mat” made of silk and sediment that was laid on the sediment surface (Figure 13C). The silk linings of these mats were as thick as the lining around a burrow and were always built against the glass walls of the terraria. The second structure was similar to a cocoon (Figure 13D). The spider constructed a mat and then enclosed itself in a covering

of silk. The spiders that built these never closed off the cocoon with a trapdoor. The cocoons were also built against the glass walls.

The burrows of *H. lenta* were usually flush with the sediment surface. In some experiments, the spiders completely closed off their burrows and did not leave during the trial. When this occurred, the sediment bulged slightly above the surrounding sediment surface, indicating the presence of a burrow (Figure 14A). *Hogna lenta* also produced turrets that could be up to 2 cm above the sediment (Figure 14B). These structures only occurred in the corners of the terraria. In addition to burrow construction, some *H. lenta* deposited lines of silk along the edges of their terraria when they did not produce a burrow (Figure 14C). These lines appeared to be constructed of a few strands of a silk and ran parallel to each other. The lines were not associated with a burrow and sometimes disappeared after the spider made its burrow.

4.3 Silk Lining of Burrow Walls

The burrows of both *G. inermis* and *H. lenta* were lined with differing amounts of silk. Both species deposited silk during burrow construction. *Gorgyrella inermis* was observed depositing a fine layer of silk while removing sediment from the bottom of the shaft. *Gorgyrella inermis* produced a much thicker layer of silk than did *H. lenta*. The silk lining of *G. inermis* burrows was thickest near the trapdoor and absent at the base of the burrow. Scratches in the silk resulted in striations present on the surface of the burrow casts (Figure 15 A, B). These were produced by spiders bracing their legs into the silk in order to climb along the burrow's length. The lining of *H. lenta* burrows had a uniform thickness along the length of the burrow, but was absent at the base. Striations were also

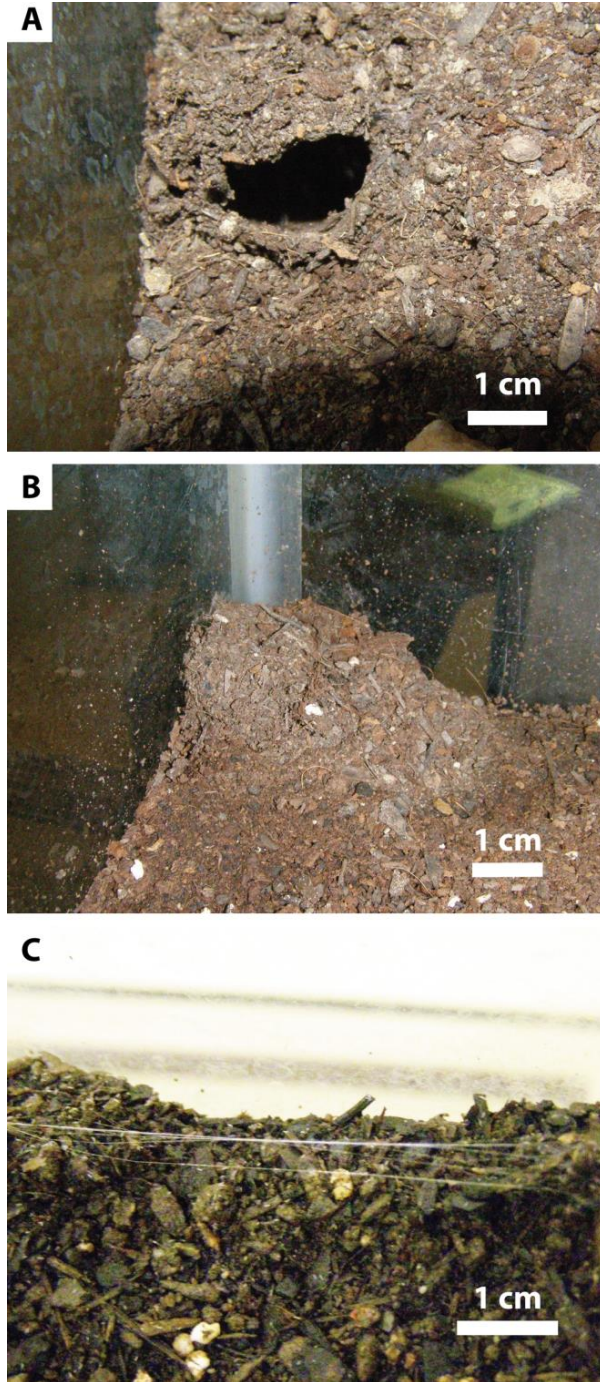


Figure 14: Surface features produced by *H. lenta*. A) Open trapdoor at the burrow entrance, B) Turret produced by building a burrow entrance against the sides of the terrarium, C) Silk strands deposited along the sides of the terrarium.

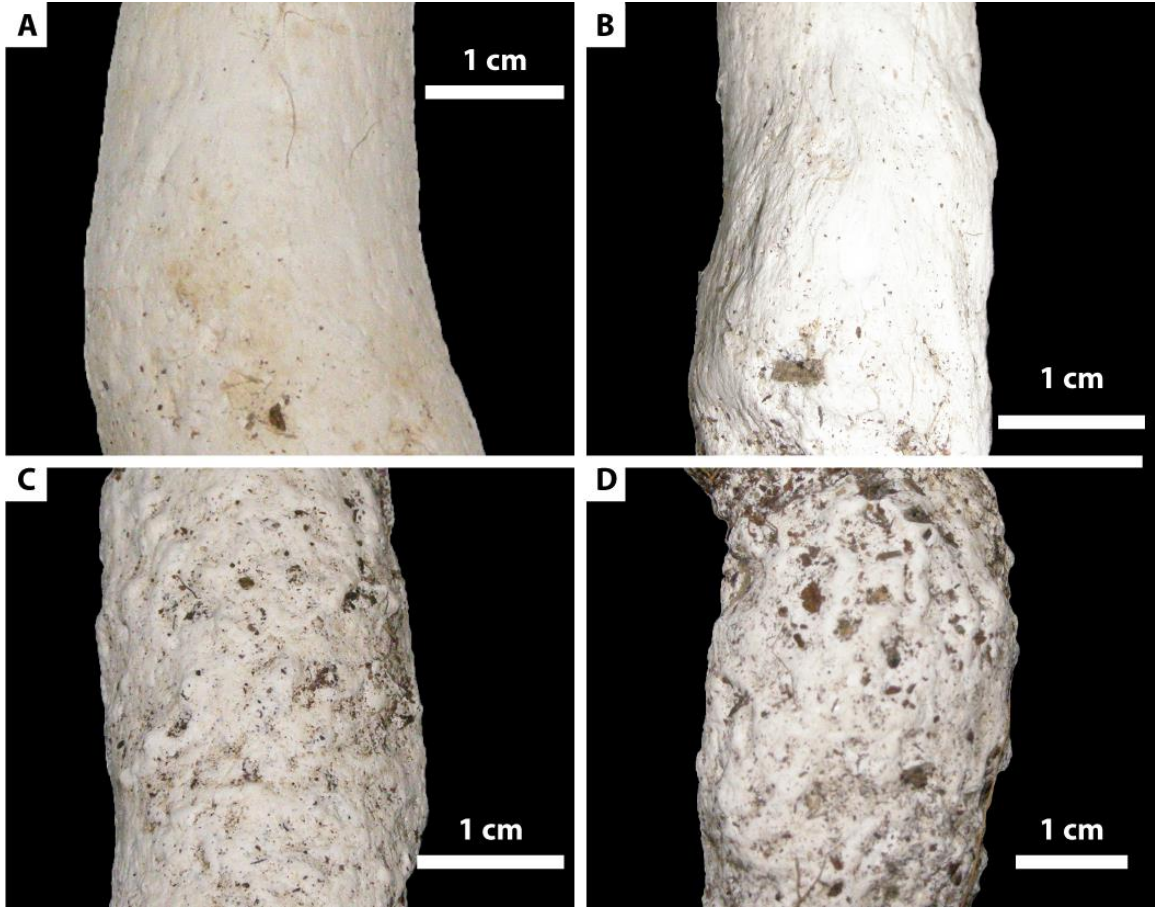


Figure 15: Striations on sides of burrow casts resulting from scratch marks preserved in the silk linings of spider burrows. The burrows were cleaned of silk and sediment but were not painted or otherwise altered. A) Burrow produced by juvenile *G. inermis*, B) Burrow produced by adult *G. inermis*, C–D) Burrows produced by *H. lenta*. The surfaces of *H. lenta* burrow casts include sediment, resulting from the thin layer of silk that lined these burrows.

present on *H. lenta* burrow casts (Figure 15 C, D); however, the striations were less well defined than those on *G. inermis* burrows.

Both species altered the thickness and extent of the silk lining when environmental conditions changed. In general, sediments that were stable, either because of increased clay or moisture content, resulted in burrows with less silk than those produced in less stable sediment. Many *H. lenta* burrows produced in more cohesive

Table 2: Number of burrow architectures produced by each species of spider. VS = vertical shaft, VC = vertical shaft with terminal chamber, SS = subvertical shaft, SC = subvertical shaft with terminal chamber, JS = J-shaped burrow, YS = Y-shaped burrow, IC = isolated chamber

Species	VS	VC	SS	SC	JS	YS	IC
<i>G. inermis</i>	13	5	5	1	1	0	1
<i>H. lenta</i>	10	1	7	0	0	1	0
Total	23	6	12	1	1	1	1
Total Sum							45

sediment did not have any detectable silk lining and those casts have a much more irregular burrow wall than those with silk linings. *Gorgyrella inermis* burrows produced in these sediments had a thinner silk lining and the linings did not extend as far into the shaft. Chambers had little to no silk. No differences in the nature of the silk lining were observed between burrows produced in 14 or 30 day trials.

4.4 Burrow Morphology

In this study, twenty-seven burrows produced by *G. inermis* and nineteen burrows produced by *H. lenta* were successfully cast. Both species produced burrows that were qualitatively very similar. Most were simple, vertical shafts with one surface opening. Seven burrow architectures were produced during these experiments: 1) vertical shafts (VS), 2) vertical shafts with terminal chambers (VC), 3) subvertical shaft (SS), 4) subvertical shafts with terminal chambers (SC), 5) J-shaped burrows (JS), 6) Y-shaped burrows (YS), and 7) isolated chambers (IC) (Table 2).

Vertical Shaft: This burrow architecture ($n = 23$) (Figure 16) (Table 3) includes vertically oriented ($75^\circ\text{--}90^\circ$, $\bar{x} = 85.9^\circ$, $SD = 4.11^\circ$), nonbranching shafts with a single surface opening that extend 3.4–16.6 cm ($\bar{x} = 7.7$, $SD = 3.57$) below the sediment surface. The

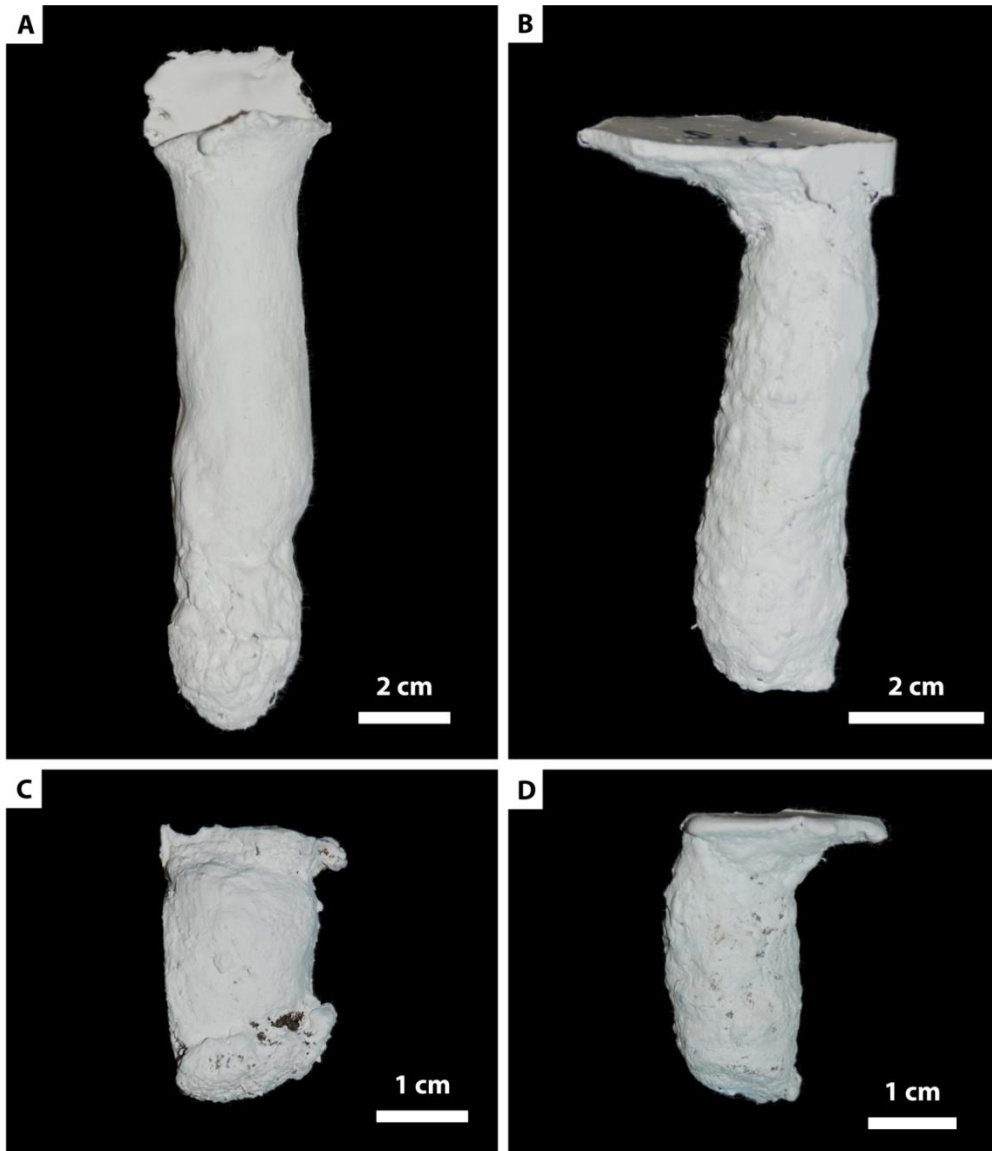


Figure 16: Vertical shafts. A) Burrow produced by an adult *G. inermis* (G9), B) Burrow produced by *H. lenta*. This burrow served as a brood burrow in addition to a dwelling structure (H5), C) Burrow produced by juvenile *G. inermis* (G15), D) Burrow produced by *H. lenta* (H7).

shafts have an elliptical cross section with a width-to-height ratio of 0.87-1.25 ($\bar{x} = 1.03$, $SD = 0.086$). The shafts are 1.36–3.92 cm ($\bar{x} = 2.45$, $SD = 0.46$) wide and 1.28–3.54 cm ($\bar{x} = 2.36$, $SD = 0.44$) high with a circumference of 3.7–10.5 cm ($\bar{x} = 7.61$, $SD = 1.37$) and total length of 3.4–17.4 cm ($\bar{x} = 7.85$, $SD = 3.70$). This architecture does not include a chamber. Vertical shafts have a complexity of 2 and tortuosity of 0.52–1.12 ($\bar{x} = 1.0$, $SD = 0.11$). This architecture was the most commonly produced and occurred in all experimental conditions. Vertical shafts were produced most often by *G. inermis* ($n = 13$).

Vertical Shaft with Terminal Chamber: This architecture ($n = 6$) (Figure 17) (Table 5) is a vertical shaft ending at a chamber. This architecture includes vertically oriented (83° – 90° , $\bar{x} = 87.0^\circ$, $SD = 3.35$), nonbranching shafts with a single surface opening that extend 3.2–16.3 cm ($\bar{x} = 9.63$, $SD = 5.05$) below the sediment surface. The shafts have an elliptical cross section with a width-to-height ratio of 0.91–1.57 ($\bar{x} = 1.16$, $SD = 0.17$). The shafts are 1.74–5.06 cm ($\bar{x} = 2.46$, $SD = 0.70$) wide and 1.43–3.40 cm ($\bar{x} = 2.12$, $SD = 0.43$) high with a circumference of 5.2–22.3 cm ($\bar{x} = 8.03$, $SD = 3.75$). The chambers have an elliptical cross section with a width-to-height ratio of 0.82–1.93 ($\bar{x} = 1.34$, $SD = 0.26$). The chambers are 1.77–5.98 cm ($\bar{x} = 3.38$, $SD = 1.26$) wide and are 1.43–3.67 cm ($\bar{x} = 2.54$, $SD = 0.56$) high with a circumference of 3.1–23.6 cm ($\bar{x} = 11.03$, $SD = 5.03$). Five of the six chambers were constructed against the glass of the terrarium and are therefore not completely round as would be expected. The total length of these burrows is 3.2–13.0 cm ($\bar{x} = 8.60$, $SD = 4.96$) of which 2.0–7.0 cm is the chamber. This architecture has a complexity of 3 and tortuosity of 1.0–1.4 ($\bar{x} = 1.11$, $SD = 0.17$).

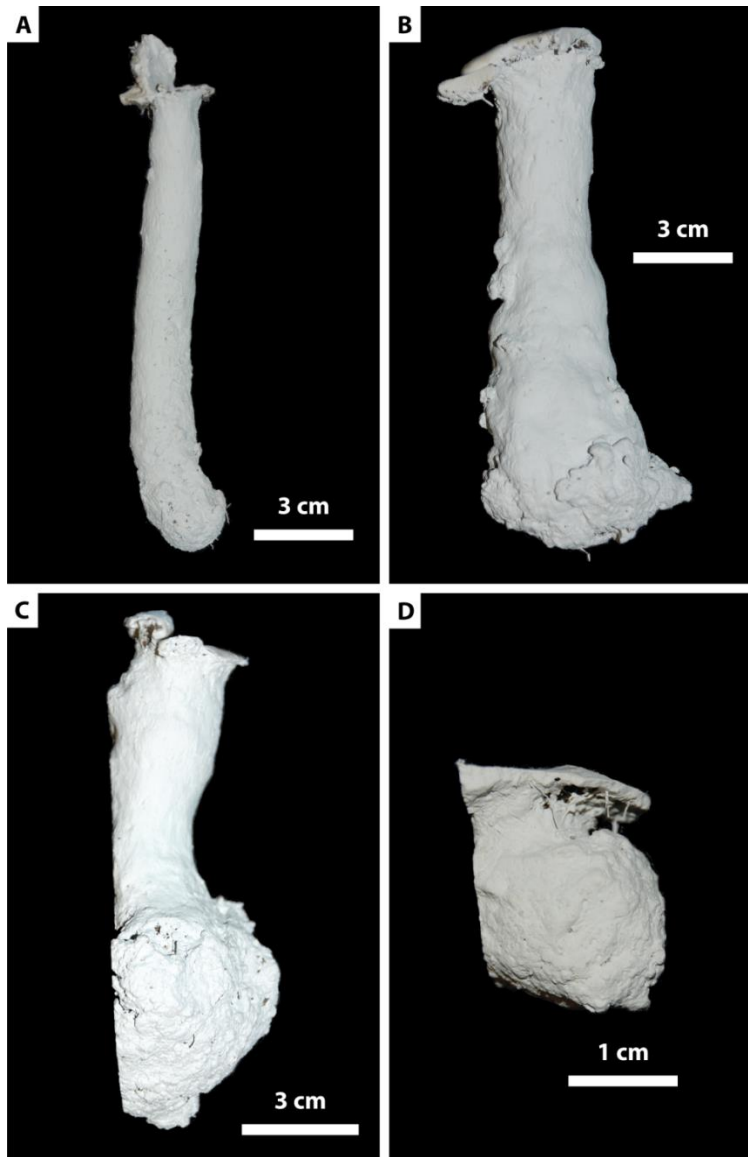


Figure 17: Vertical shafts with terminal chambers. A) Burrow produced by juvenile *G. inermis* (G2), B) Burrow produced by adult *G. inermis* (G17), C) Burrow produced by adult *G. inermis* (G16), D) Burrow produced by *H. lenta* (H4).

Subvertical Shaft: This burrow architecture ($n = 12$) (Figure 18) (Table 4) includes subvertically oriented (60° – 75° , $\bar{x} = 68.38^{\circ}$, $SD = 0.077^{\circ}$), nonbranching shafts with a single surface opening that extend 4.4–13.9 cm ($\bar{x} = 7.04$, $SD = 2.83$) below the sediment surface. The shafts have an elliptical cross section with a width-to-height ratio of 0.94–

1.15 ($\bar{x} = 1.03$, $SD = 0.077$). The shafts are 1.15–3.31 cm ($\bar{x} = 2.38$, $SD = 0.46$) wide and 1.16–3.60 cm ($\bar{x} = 2.33$, $SD = 0.43$) high with a circumference of 3.0–11.1 cm ($\bar{x} = 7.52$, $SD = 1.40$) and a total length of 4.6–14.4 cm ($\bar{x} = 7.60$, $SD = 3.11$). This architecture does not include a chamber. Subvertical shafts have a complexity of 2 and tortuosity of 1.0–1.12 ($\bar{x} = 1.06$, $SD = 0.045$). This architecture differs from the vertical shaft in that the angle from the horizontal is less than at least 80° . Subvertical shafts occurred in all experiments and were most commonly produced by *H. lenta* ($n = 7$).

Subvertical Shaft with Terminal Chamber: This architecture ($n = 1$) (Figure 19C) (Table 5) is a subvertical shaft ending in a chamber. This architecture includes a subvertically oriented (75°), nonbranching shaft with a single surface opening that extends 9.3 cm below the sediment surface. The shaft has an elliptical cross section with a width-to-height ratio of 0.82–1.01 cm ($\bar{x} = 0.98$, $SD = 0.069$). The shaft is 2.38–3.44 cm ($\bar{x} = 2.88$, $SD = 0.42$) wide and 2.41–3.59 cm ($\bar{x} = 3.01$, $SD = 0.45$) high with a circumference of 4.3–7.2 cm ($\bar{x} = 9.58$, $SD = 1.58$). The chamber has an elliptical cross section with a width-to-height ratio of 1.21–1.56 ($\bar{x} = 1.42$, $SD = 0.19$). The chamber is 2.78–5.79 cm ($\bar{x} = 4.62$, $SD = 1.61$) wide and 2.30–3.89 cm ($\bar{x} = 3.20$, $SD = 0.81$) high with a circumference of 11.1–15.3 cm ($\bar{x} = 13.33$, $SD = 2.11$). The total length of this burrow is 9.5 cm of which 3.5 cm is the chamber. The subvertical shaft with chamber has a complexity of 3 and a tortuosity of 1.0. This architecture was produced by an adult *G. inermis*.

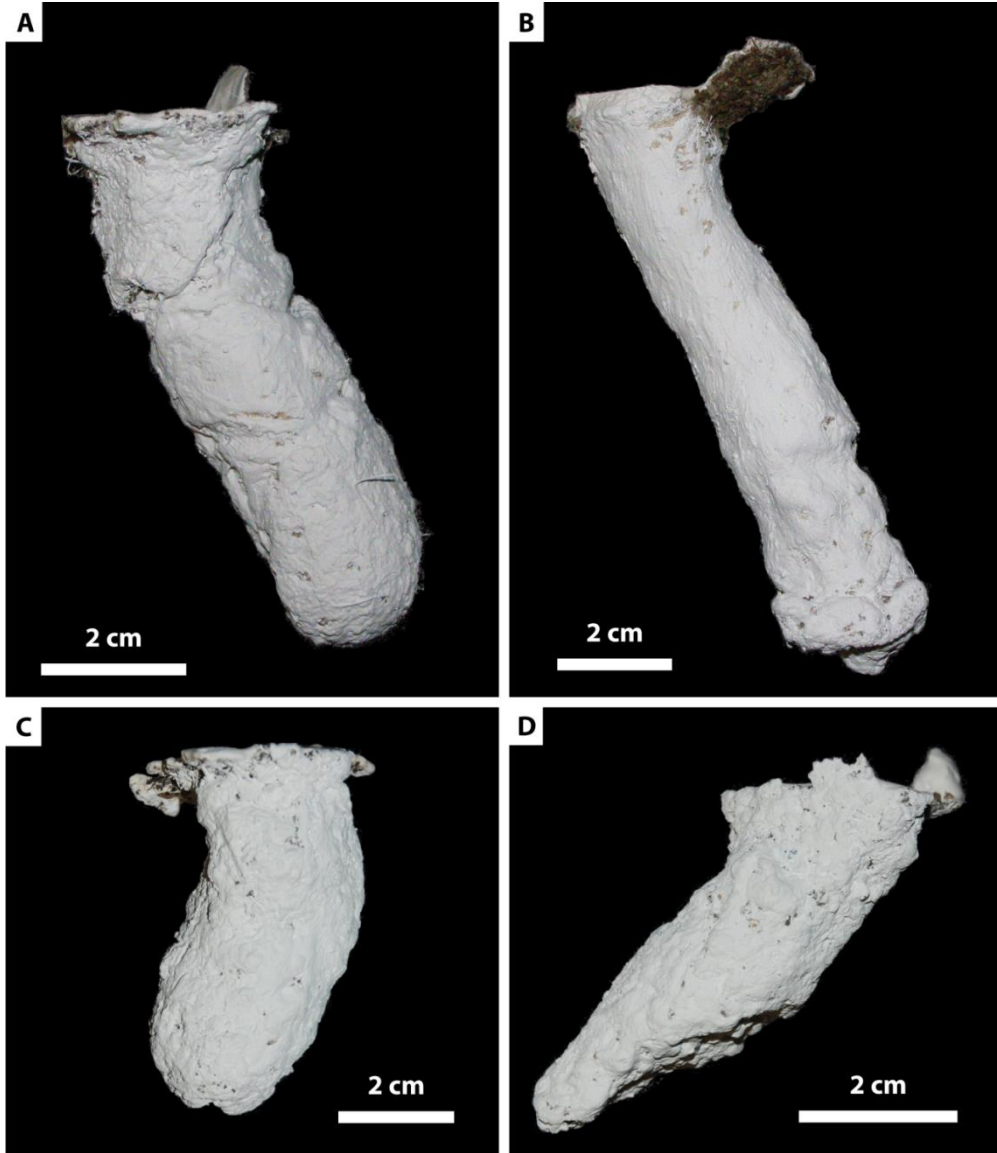


Figure 18: Subvertical shafts. A) Burrow produced by adult *G. inermis* (G24), B) Burrow produced by adult *G. inermis* (G5), C) Burrow produced by *H. lenta* (H14), D) Burrow produced by *H. lenta* (H16).

Table 4: Quantitative measurements of subvertical shafts produced by *G. inermis* and *H. lenta*.

	G5	G10	G12	G20	G24	H2	H11	H12	H13	H14	H16	H20
Surface Openings	1	1	1	1	1	1	1	1	1	1	1	1
Maximum depth	11.2	13.9	6.6	4.4	8.3	5.5	5.5	6.1	4.4	5.7	6.3	6.6
Total Length	13.2	14.4	7.8	4.6	8.4	5.7	5.6	6.2	5.2	5.8	6.9	7.4
Maximum width	3.1	2.4	3.3	2.9	3.4	2.8	2.9	2.7	2.5	3.1	2.6	3.1
Minimum width	2.3	1.5	2.1	1.8	1.6	2.1	1.8	1.6	1.2	2.3	1.7	1.7
Average width	2.6	2	2.9	2.3	2.6	2.3	2.4	2.3	2.2	2.7	2.3	2.5
Maximum height	3	2.4	3	3	2.7	2.8	2.6	2.8	2.5	2.7	2.6	3.6
Minimum height	2.1	1.8	1.9	1.5	1.8	1.9	1.6	1.6	1.4	2.3	1.2	1.9
Average height	2.3	2.1	2.5	2.4	2.4	2.2	2.2	2.4	2.2	2.5	2.3	2.8
Average W/H ratio	1.1	1	1.1	1	1.1	1	0.9	1	1	0.9	1	1.1
Maximum circumference	8.9	7.6	9.5	8.4	9.4	8.9	9	8.8	7.9	9.1	8.3	11.1
Minimum circumference	7.4	5.7	4.5	5.6	5.4	6.1	4.5	5.1	3	7.1	4.8	6
Average circumference	7.9	6.7	8.4	7.3	7.8	7.3	7.5	7.4	6.5	8.3	7.2	8.7
Maximum slope	75°	75°	70°	70°	70°	75°	60°	65°	70°	60°	60°	76°
Minimum slope	75°	75°	70°	70°	70°	75°	60°	65°	70°	60°	60°	65°
Average slope	75°	75°	70°	70°	70°	75°	60°	65°	70°	60°	60°	70.5°
Branching angles	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Complexity	2	2	2	2	2	2	2	2	2	2	2	2
Tortuosity	1.1	1	1.1	1	1	1	1.1	1.1	1.1	1	1	1.1

J-Shaped Burrow: This architecture ($n = 1$) (Figure 19D) (Table 5) includes a vertically oriented (90°), nonbranching shaft and tunnel with a single surface opening that extends 8.6 cm below the sediment surface. Near its base, the slope of the shaft turns from nearly vertical to a much smaller angle (39°). The shaft has an elliptical cross section with a width-to-height ratio of 0.92–1.53 ($\bar{x} = 1.11$, $SD = 0.19$). The shaft and tunnel are 1.72–2.03 cm ($\bar{x} = 1.87$, $SD = 0.093$) wide and 1.18–2.02 cm ($\bar{x} = 1.72$, $SD = 0.25$) high with a circumference of 5.1–6.4 cm ($\bar{x} = 5.7$, $SD = 0.46$) and a total length of 8.9 cm. The J-shaped burrow has a complexity of 2 and a tortuosity of 0.57. This architecture was produced by a juvenile *G. inermis* when the sediment moisture was lower than normal natural conditions.

Y-Shaped Burrow: This architecture ($n = 1$) (Figure 19A) (Table 5) includes a subvertically oriented (75°) shaft with a second shaft branching from the main burrow. The angle between the shafts is 90° and each shaft leads to a surface opening. The branch is oriented 35° from the horizontal. The burrow extends 4.1 cm below the sediment surface. The main shaft has an elliptical cross section with a width-to-height ratio of 0.91–1.12 ($\bar{x} = 1.02$, $SD = 0.11$). This shaft is 1.7–2.1 cm ($\bar{x} = 1.90$, $SD = 0.19$) wide and 1.7–2.3 cm ($\bar{x} = 1.93$, $SD = 0.23$) high with a circumference of 5.1–6.8 ($\bar{x} = 6.15$, $SD = 0.82$) and a total length of 4.4 cm. The branch has an elliptical cross section with a width-to-height ratio of 1.42–1.91 ($\bar{x} = 0.86$, $SD = 0.11$). The branch is 1.8–2.0 cm ($\bar{x} = 1.93$, $SD = 0.15$) wide and 1.42–1.91 cm ($\bar{x} = 1.67$, $SD = 0.34$) high with a circumference of 4.9–6.7 ($\bar{x} = 5.8$, $SD = 1.27$) and a total length of 2.3 cm. The total length of the burrow is

6.7 cm. This architecture has a complexity of 4 and an average tortuosity of 1.0. The single Y-shaped burrow was produced by *H. lenta*.

Isolated Chamber: This architecture ($n = 1$) (Figure 19B) (Table 5) includes a subvertically oriented (45°) chamber with one surface opening that extends 2.1 cm below the sediment surface. The chamber has an elliptical cross section with a width-to-height ratio of 1.13–1.41 ($\bar{x} = 1.29$, $SD = 0.15$). The chamber is 2.1–2.6 cm ($\bar{x} = 2.47$, $SD = 0.28$) wide and 1.6–2.3 cm ($\bar{x} = 1.93$, $SD = 0.34$) high with a circumference of 7.0–7.9 cm ($\bar{x} = 7.43$, $SD = 0.45$) and a total length of 3.7 cm. This architecture has a complexity of 2 and a tortuosity of 1.1. The isolated chamber was produced by an adult *G. inermis*.

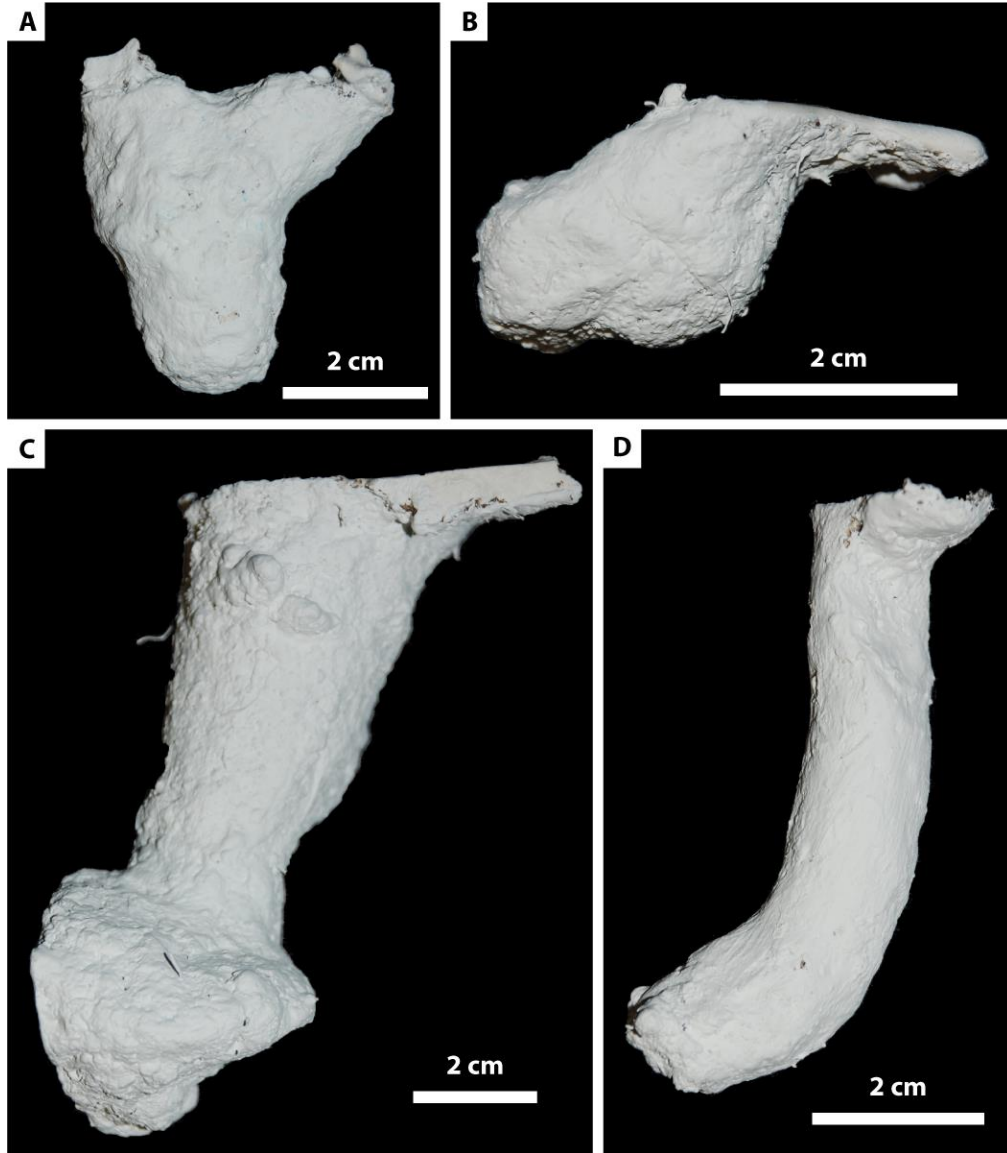


Figure 19: Other burrow architectures. A) Y-shaped burrow produced by *H. lenta* (H4), B) Isolated chamber produced by adult *G. inermis* (G6), C) Subvertical shaft with terminal chamber produced by adult *G. inermis* (G27), D) J-shaped burrow produced by juvenile *G. inermis* (G23).

Table 5: Quantitative measurements of the unique burrows casts produced by *G. inermis* and *H. lenta*: vertical shaft with terminal chamber (VC), subvertical shaft with terminal chamber (SC), the isolated chamber (IC), the J-shaped burrow (JS), and the Y-shaped burrow (YS).

Architecture	G2	G4	G16	G17	G26	H6	G27	G6	G23	H4
	VC	VC	VC	VC	VC	VC	SC	IC	JS	YS
Surface Openings	1	1	1	1	1	1	1	1	1	2
Maximum depth	16.3	7.08	13	12.5	5.7	3.2	9.3	2.1	8.6	4.1
Total Length	18.4	7.7	13.2	12.5	5.7	3.2	9.5	3.7	8.9	6.7
Maximum width	2.4	2.2	6	4.4	5.7	2.6	5.8	2.7	2	2.1
Minimum width	1.9	1.7	1.8	2.3	2.9	2.4	2.4	2.1	1.7	1.7
Average width	2.1	1.9	3.6	3	4.3	2.5	3.5	2.5	1.9	1.9
Maximum height	2.7	1.7	3.7	2.7	3.4	2.8	3.9	2.3	2	1.9
Minimum height	1.7	1.4	2.2	1.8	2.1	2.8	2.3	1.6	1.2	1.4
Average height	2.1	1.6	2.7	2.2	2.9	2.8	3.1	1.9	1.7	1.8
Average W/H ratio	1	1.2	1.3	1.3	1.5	1.1	1.1	1.3	1.1	1
Maximum circumference	7.9	6.3	15.6	12.2	23.6	7.8	15.3	7.9	6.4	6.8
Minimum circumference	5.4	5.2	3.1	6.9	17	5.1	7.2	7	5.1	4.9
Average circumference	6.6	5.6	10.7	8.4	20.8	6.8	10.8	7.4	5.7	6.0
Maximum slope	90°	90°	90°	90°	90°	85°	75°	45°	90°	75°
Minimum slope	78°	76°	90°	90°	90°	85°	75°	45°	39°	35°
Average slope	84°	83°	90°	90°	90°	85°	75°	45°	64.5°	55°
Branching angles	NA	NA	NA	NA	NA	NA	NA	NA	NA	90°
Complexity	3	3	3	3	3	3	3	2	2	4
Tortuosity	1.4	1.2	1	1	1	1	1	1.1	0.6	1

4.5 Variation in Burrow Architecture

4.5.1 Tracemaker and Architecture

Gorgyrella inermis individuals were responsible for six of the seven described architectures produced during the experiments. Individual produced 2–4 ($\bar{x} = 2.43$) different burrow architectures. The burrows produced by adult *G. inermis* were more diverse in architecture than those of the juvenile *G. inermis*, which only produced vertical shafts and the J-shaped burrow. *Hogna lenta* were responsible for four of the seven architectures produced during the experiments. Most individuals produced only one burrow architecture, however, and no individual produced more than two.

4.5.2 Environment and Architecture

Gorgyrella inermis produced five burrow architectures (vertical shaft, vertical shaft with terminal chamber, subvertical shaft, subvertical shaft with terminal chamber, and isolated chamber) in sediment modeled on the species' natural habitat. Increasing sediment density resulted in only two burrow architectures (vertical shaft and vertical shaft with terminal chamber) as well as surface mats and cocoons. Decreasing sediment moisture resulted in three burrow architectures (vertical shaft, subvertical shaft, and J-shaped burrow), whereas increasing sediment moisture resulted in only one burrow architecture (vertical shaft) and a surface mat.

Hogna lenta produced three burrow architectures (vertical shaft, vertical shaft with terminal chamber, and Y-shaped burrow) in sediment modeled on the species' natural habitat, but three individuals did not produce burrows during one trial. Increasing sediment density resulted in two burrow architectures (vertical shaft and subvertical

shaft). Increasing sediment moisture resulted in two burrow architectures (vertical shaft and subvertical shaft) and two individuals that did not burrow, whereas decreasing sediment moisture resulted in only one burrow architecture (vertical shaft) and two individuals that did not burrow.

CHAPTER 5: BURROW ANALYSES

5.1 Burrows Produced by *Gorgyrella inermis*

Twenty-eight burrows produced by *G. inermis* were compared with one another to determine similarity within the species. One vertical shaft made by *G. inermis*, G29, is represented by the silk lining of the burrow which was removed by the spider during extraction. Although used for these analyses, it was not used to describe the morphology of vertical shafts. All burrows produced by this species have a similarity of 1.0–0.7 with an average similarity of 0.90. A cluster analysis of these burrows separates the burrows into two main clusters (Figure 20). Cluster A includes all but two burrows that possess a vertical shaft and has a similarity of 0.90. Cluster B includes all burrows that possess a subvertical shaft and two vertical shafts G19 and G25 and has a similarity of 0.91. Together, these two clusters have a similarity of 0.89. The J-shaped burrow (G23) was not grouped with either cluster, and it shares a similarity of 0.84 with Clusters A and B. The isolated chamber (G6) was also not included in a cluster, and has a similarity of 0.72 with all other burrows.

5.2 Burrows Produced by *Hogna lenta*

Nineteen burrows produced by *H. lenta* were compared with one another to determine similarity within the species. All burrows produced by this species have a similarity of 1.0–0.8 with an average similarity of 0.91. A cluster analysis separates these burrows into the same types of clusters as were observed in the cluster analysis of *G. inermis* (Figure 21). Cluster A includes all burrows with a vertical shaft and has a similarity of 0.96. Cluster B includes all burrows that with a subvertical shaft and has a

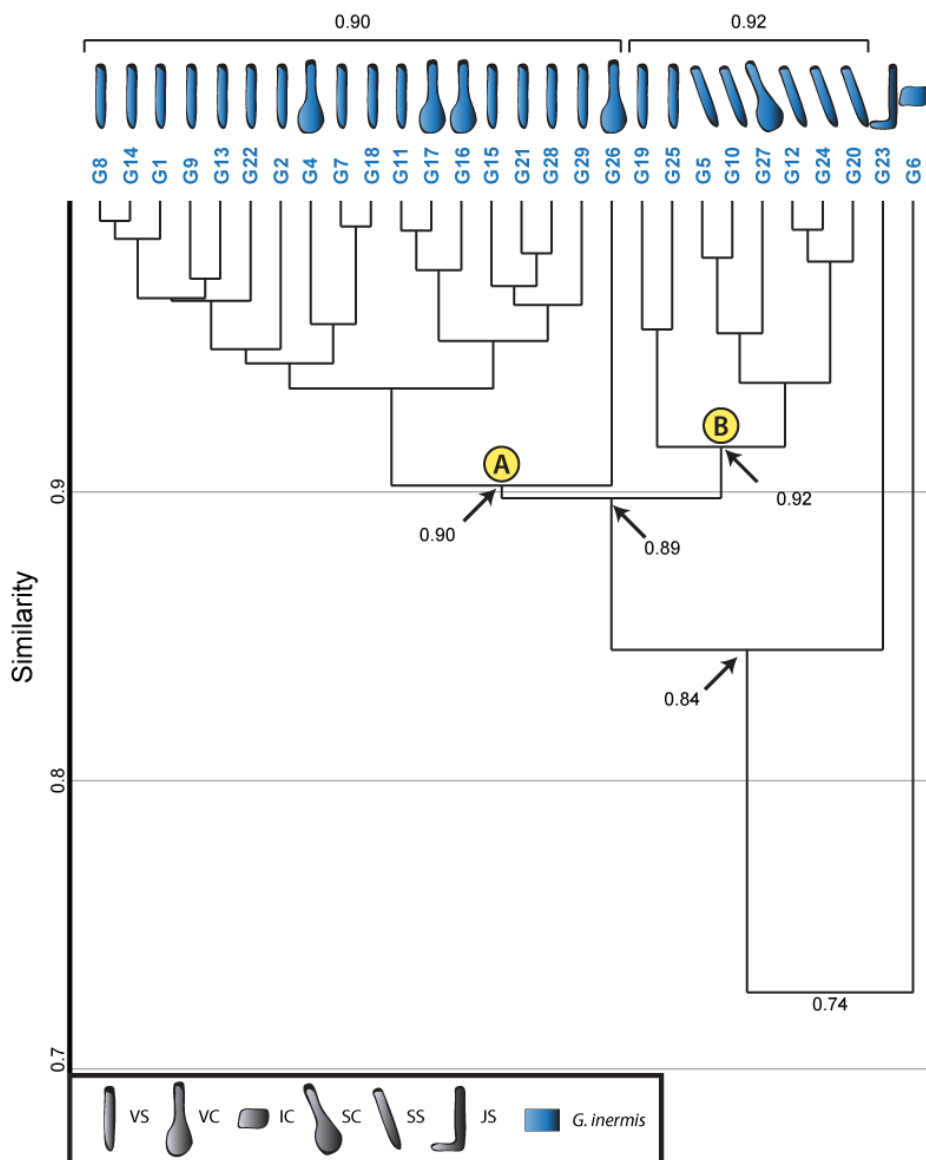


Figure 20: Cluster analysis of all burrows produced by *G. inermis* in the study. Cluster A contains burrows with a vertical component. Cluster B contains burrows with a subvertical component and two burrows with vertical components. Values located at the nodes of the dendrogram are the average Bray-Curtis similarity score of all burrows emanating from that node cluster. Brackets above the dendrogram group together main clusters and provide the average Bray-Curtis similarity score of the burrows in that cluster. Clusters indicated by letters in yellow circles are clusters of spider burrows that form in all analyses. Burrow architecture is indicated in the key at the bottom of the figure: VS = vertical shaft, VC = vertical shaft with terminal chamber, IC = isolated chamber, SC = subvertical shaft with terminal chamber, SS = subvertical shaft, JS = J-shaped burrow. Tracemaker is indicated by the color of the box with the associated name.

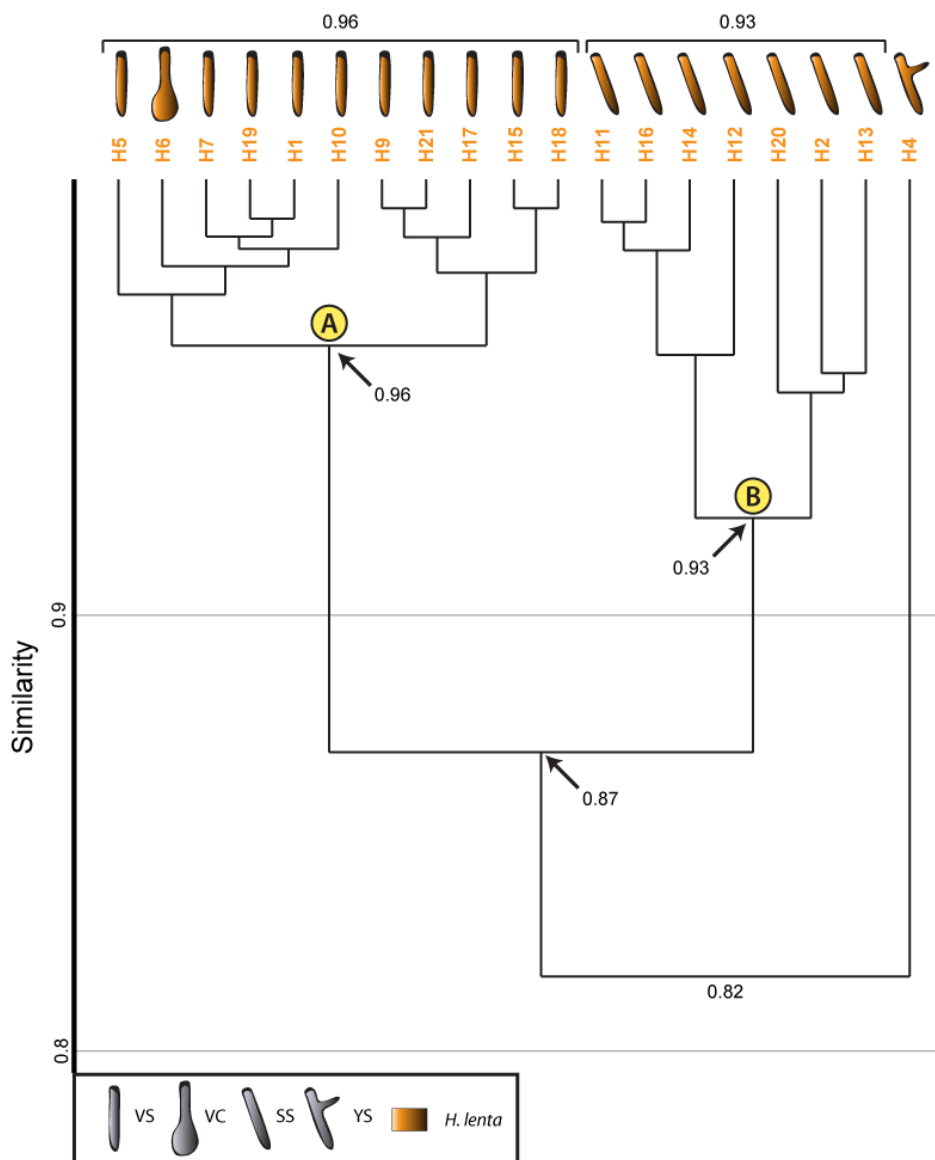


Figure 21: Cluster analysis of all burrows produced by *H. lenta* in the study. Cluster A consists mainly of burrows with a vertical component. Cluster B consists of burrows with a subvertical component. Values located at the nodes of the dendrogram are the average Bray-Curtis similarity score of all burrows emanating from that node cluster. Brackets above the dendrogram group together main clusters and provide the average Bray-Curtis similarity score of the burrows in that cluster. Clusters indicated by letters in yellow circles are clusters of spider burrows that form in all analyses. Burrow architecture is indicated in the key at the bottom of the figure: VS = vertical shaft, VC = vertical shaft with terminal chamber, SS = subvertical shaft, YS = Y-shaped burrow. Tracemaker is indicated by the color of the box with the associated name.

similarity of 0.93. Together, these two clusters have a similarity of 0.87. The Y-shaped burrow (H4) was not grouped into a cluster, and it shares a similarity of 0.82 with Cluster A and Cluster B.

5.3 Comparison Between *Gorgyrella inermis* and *Hogna lenta*

All burrows produced by *G. inermis* and *H. lenta* were used for comparison. The burrows differ in depth, total length, and width-to-height ratio (Table 6A). Bray-Curtis results show that the burrows of *G. inermis* and *H. lenta* have a similarity of 1.0–0.7 with an average similarity of 0.91 (Figure 22). A cluster analysis of the spider burrow casts does not separate the burrows of the two species (Figure 23). Cluster A (vertical burrows) and Cluster B (subvertical burrows) from the previous analyses were produced with the addition of a third cluster, Cluster C, which includes the Y- and the J-shaped burrows. Cluster A has a similarity 0.90 whereas Cluster B has a similarity of 0.92. The similarity of both clusters is 0.87. Cluster C has a similarity 0.92, and the similarity of all three clusters is 0.83. The isolated chamber does not fit into any of the three clusters. The overall similarity with all *G. inermis* and *H. lenta* burrows is 0.74. The burrows in Cluster A and B differ only in average slope and complexity (Table 8A). A comparison of these two clusters with Cluster C results in significant differences in average width, average height, average circumference, and average slope (Table 8A). Removing the isolated chamber from the cluster analysis does not alter the composition and overall similarity of each cluster. Rearranging the Bray-Curtis test matrix to reflect the cluster analysis reveals that each cluster includes Bray-Curtis scores of 1.0–0.9 (Figure 24).

Table 6: Mann-Whitney and Kolmogorov-Smirnov test results (p values) between the burrows produced by arthropods considered in this study. Boxed values indicate statistical difference ($p < 0.05$). The resulting differences are explained by providing the median, the median, the standard deviation, and the range of the properties. All measurements are in cm and all angles are in degrees. This table continues on the next page.

A. Comparison between *G. inermis* and *H. lenta*

Organism	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
Spiders	MW	0.006505	0.007414	0.4677	0.4947	0.002494	0.6257	0.5671	0.3968	0.3662
	KS	0.005944	0.0005882	0.08522	0.325	0.02798	0.317	0.6544	0.2579	0.4907

Analysis of Differences	<i>G. inermis</i>					<i>H. lenta</i>				
	Property	Mean	Median	SD	Range	Mean	Median	SD	Range	
Depth	8.9	8.45	4.22	16.6–2.1	5.78	5.7	1.47	8.7–3.2		
Total Length	9.36	8.5	4.38	18.4–2.5	6.07	6.2	1.42	8.7–3.2		
W/H Ratio	1.10	1.1	0.124	1.5–1	1.01	1.0	0.0809	1.2–0.90		

B. Comparison between other arthropods and combined burrows of *G. inermis* and *H. lenta*

Organism	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
<i>A. chalcodes</i>	MW	0.6675	0.4484	0.2795	0.7426	0.01879	0.03599	0.01724	0.2757	0.02417
	KS	0.6696	0.6128	0.02454	0.5568	0.01319	0.02991	0.01319	0.6128	0.20454

Analysis of Differences	<i>A. chalcodes</i>					<i>G. inermis</i> and <i>H. lenta</i>				
	Property	Mean	Median	SD	Range	Mean	Median	SD	Range	
W/H Ratio	0.659	0.92	0.156	1.3–0.5	1.06	1.0	0.117	1.5–0.9		
Avg Circ	14.3	8.43	6.85	9.46–7.4	7.86	7.4	2.31	20.8–5.3		
Avg Slope	26.3	35	1.77	45–25	79.56	85	11.27	90–45		
Tortuosity	0.754	1.04	0.326	1.1–0.98	1.02	1.0	0.124	1.4–0.50		

Organism	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
<i>H. arizonensis</i>	MW	0.07281	4.14E-07	5.03E-09	9.35E-05	1.32E-09	1.43E-08	1.10E-09	2.04E-09	3.38E-08
	KS	0.09865	1.04E-05	2.70E-10	0.0005116	3.23E-12	2.70E-10	1.01E-11	1.52E-08	2.13E-09

Analysis of Differences	<i>H. arizonensis</i>					<i>G. inermis</i> and <i>H. lenta</i>				
	Property	Mean	Median	SD	Range	Mean	Median	SD	Range	
Total Length	26.9	23	18.5	76–7	8.03	6.9	3.84	18.4–2.5		
Avg Width	4.34	4.4	0.553	5.2–3.1	2.48	2.3	0.515	4.3–1.7		
Avg Height	1.86	1.9	0.347	2.4–1.0	2.33	2.3	0.391	3.2–1.6		
W/H Ratio	2.41	2.4	0.434	3.1–1.7	1.06	1.0	0.117	1.5–0.9		
Avg Circ	12.3	12.3	1.96	17.3–9	7.86	7.4	2.31	20.8–53		
Avg Slope	17.2	15	11.7	45–5	79.6	85	11.3	90–45		
Complexity	4.00	3	2.12	9–3	2.21	2	0.463	4–2		
Tortuosity	1.96	1.3	1.94	9.0–1.1	1.02	1.0	0.124	1.4–0.50		

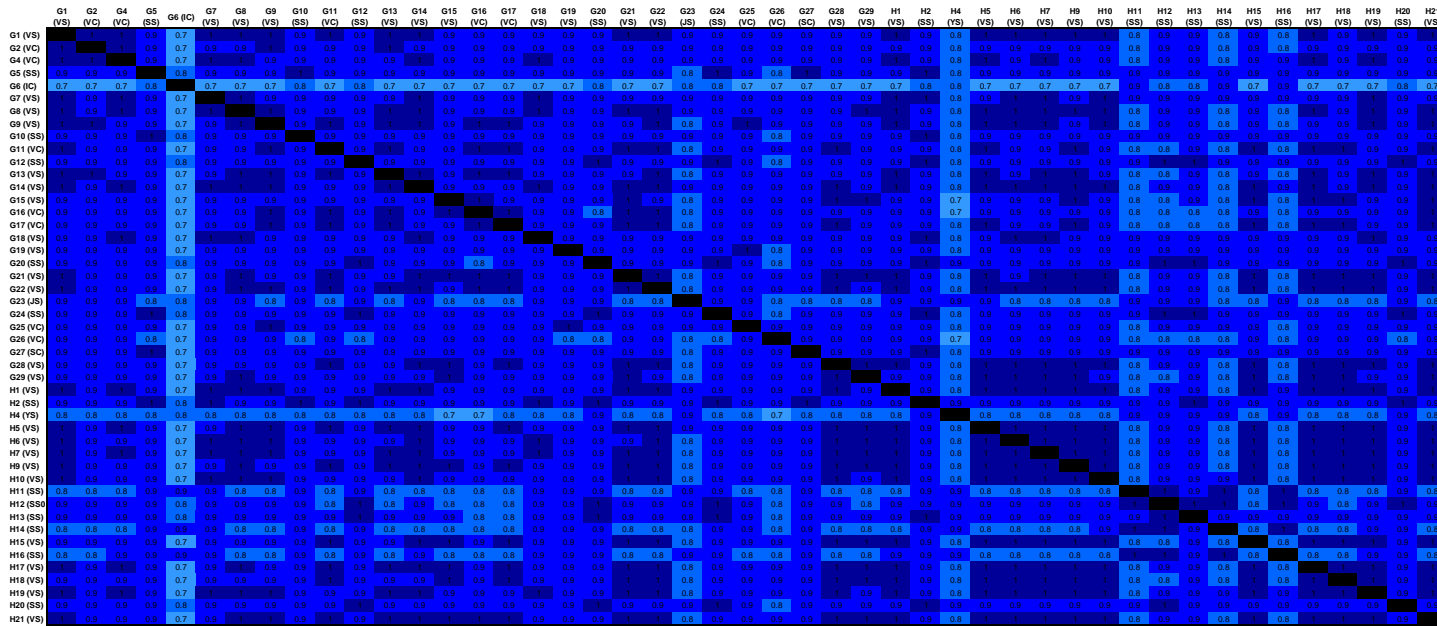
Organism	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
<i>M. giganteus</i>	MW	0.9532	0.001977	4.45E-05	0.01405	1.47E-09	1.58E-05	9.70E-06	0.01234	0.002202
	KS	0.8078	0.005419	4.45E-05	0.01874	6.13E-10	2.10E-05	2.10E-05	0.07236	0.002164

Analysis of Differences	<i>M. giganteus</i>					<i>G. inermis</i> and <i>H. lenta</i>				
	Property	Mean	Median	SD	Range	Mean	Median	SD	Range	
Total Length	17.7	14.25	15.4	66–3.8	8.03	6.9	3.84	18.4–2.5		
Avg Width	3.367	3.4	1.13	5.8–2.1	2.48	2.3	0.515	4.3–1.7		
Avg Height	2	1.9	0.512	2.9–1.0	2.33	2.3	0.391	3.2–1.6		
W/H Ratio	1.82	1.9	0.342	2.4–1.2	1.06	1.0	0.117	1.5–0.9		
Avg Circ	11.0	10.65	2.30	17–7.3	7.86	7.4	2.31	20.8–53		
Avg Slope	55.4	50	21.1	90–20	79.6	85	11.3	90–45		
Complexity	3.17	2	2.12	10–2	2.21	2	0.463	4–2		
Tortuosity	1.31	1.25	0.363	2.4–1.0	1.02	1.0	0.124	1.4–0.50		

Table 6 continued.

Organism	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
<i>N. americanus</i>	MW	1.01E-05	0.1036	6.60E-09	6.80E-09	0.2743	7.09E-09	0.007136	0.444	0.0006592
	KS	1.17E-05	0.05088	3.24E-11	1.00E-04	0.05088	3.24E-11	0.04083	0.004083	0.005033

Analysis of Differences	Property	<i>N. americanus</i>				<i>G. inermis</i> and <i>H. lenta</i>			
		Mean	Median	SD	Range	Mean	Median	SD	Range
	Depth	3.43	3	1.52	6.9–1.9	7.58	6.6	2.96	16.6–2.1
	Avg Width	0.106	0.105	0.0157	0.14–0.082	2.48	2.3	0.515	4.3–1.7
	Avg Height	0.0961	0.0923	0.0165	0.13–.078	2.33	2.3	0.391	3.2–1.6
	Avg Circ	3.3	3.11	0.486	4.4–2.6	7.86	7.4	2.31	20.8–5.3
	Avg Slope	62.4	70	22.6	90–25	79.6	85	11.3	90–45
	Complexity	2.4	2	0.737	4–2	2.21	2	0.463	4–2
	Tortuosity	6.56	1.23	14.0	43.0–1.0	1.02	1.0	0.124	1.4–0.5



Bray-Curtis Result	Interpretation
1	Comparison of Same Burrow
0.9	Identical
0.8	High Degree of Similarity
0.7-0.6	Modrate Degree of Similarity
0.5-0.0	Dissimilar to Complete Difference

Figure 22: Matrix of Bray-Curtis test results for the comparison of *G. inermis* and *H. lenta*. Similarity values range from 1.0 to 0.7. A majority (45 of 47) of the burrows are highly similar (0.9–0.8) or identical (1.0) to the other spider burrows. Burrow G7, the isolated chamber, is the least similar to the other burrows. Legend: Interpretation of matrix of Bray-Curtis scores. When burrows are compared to themselves in the matrix, the cell is black, although the score is 1.0. Cells with scores of similarity (1.0–0.6) are blue with increasing lightness. The scores of 0.9 and 0.8 were given separate colors to aid in determining finer differences when similarity scores are very high in a matrix. Cells with scores that are dissimilar to completely different are red.

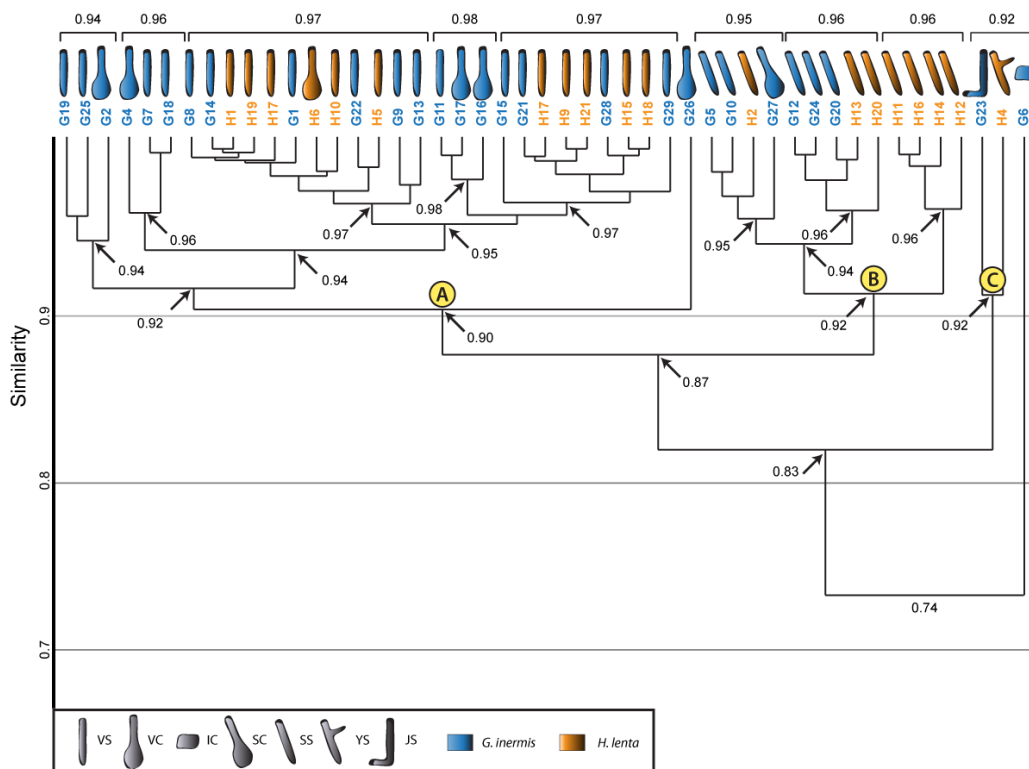


Figure 23: Cluster analysis of all burrows produced by *G. inermis* and *H. lenta*. Clusters A (vertical) and B (subvertical) are maintained, but an addition cluster, C, forms. Cluster C contains the J- and Y-shape dburrows. The isolated chamber is not included in any cluster. Values located at the nodes of the dendrogram are the average Bray-Curtis similarity score of all burrows emanating from that node cluster. Brackets above the dendrogram group together main clusters and provide the average Bray-Curtis similarity score of the burrows in that cluster. Clusters indicated by letters in yellow circles are clusters of spider burrows that form in all analyses. Burrow architecture is indicated in the key at the bottom of the figure: VS = vertical shaft, VC = vertical shaft with terminal chamber, IC = isolated chamber, SC = subvertical shaft with terminal chamber, SS = subvertical shaft, YS = Y-shaped burrow, JS = J-shaped burrow. Tracemaker is indicated by the color of the box with the associated name.

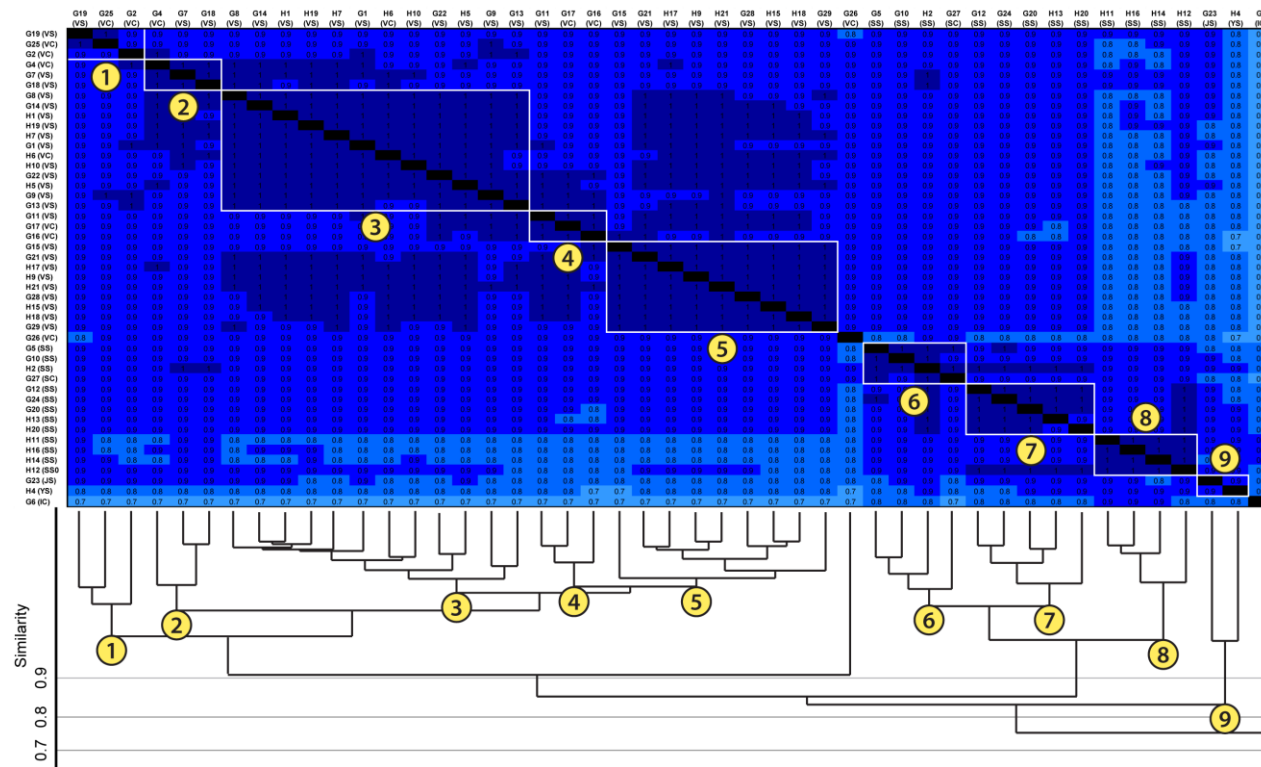


Figure 24: Combination of Bray-Curtis matrix and cluster analysis to explain how the cluster analysis groups burrows into the dendrogram. The cluster analysis groups together burrows that have the closest similarity values. The burrows in the matrix were rearranged into the order (from left to right) produced by the dendrogram. Clusters, numbered 1–9, were matched with groupings in the matrix. The groupings in the matrix are highlighted with a white box. This box contains all of the similarity values contained within that cluster. All similarity values within a grouping are either 1.0 (identical) or 0.9 (highly similar). The separation between Clusters A and B is seen between grouping 5 and grouping 6. The cells above and the cells to the left of grouping 5 (similarity scores contained in Cluster A) have similarity values of 1.0 and 0.9, whereas cells below and cells to the right of grouping 5 (similarity scores contained in Cluster B) have similarity values of 0.9 and 0.8. The small range of similarity scores (1.0–0.8) when comparing both clusters explains why the node containing both clusters has a similarity score of 0.87.

5.4 Comparisons with Other Arthropod Species

Burrow casts produced in this experiment were then compared to burrows produced by Mexican blond tarantula (*Aphonopelma chalcodes*), the Arizona desert hairy scorpion (*Hadrurus arizonensis*), the whip scorpion (*Mastigoproctus giganteus*), and the giant American millipede (*Narceus americanus*). All four species produce architectures that were similar to those made by *G. inermis* and *H. lenta*. Burrow architectures not made by the *G. inermis* and *H. lenta*, such as mazes, were included to determine to what extent the Bray-Curtis test would group burrows casts by similar architectures or by tracemakers.

Table 7: Mann-Whitney and Kolmogorov-Smirnov test results (p values) between clusters when comparing arthropods. Boxed values indicate statistical difference ($p < 0.05$). The resulting differences are explained by providing the median, the median, the standard deviation, and the range of the properties. All measurements are in cm and all angles are in degrees. This table continues on the next three pages.

A. <i>G. inermis</i> and <i>H. lenta</i>										
Clusters	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
A and B	MW	0.5284	0.8672	0.6977	0.5268	0.2726	0.7476	1.83E-07	0.2561	0.136
	KS	0.4373	0.8424	0.5739	0.4144	0.1505	0.4729	1.15E-08	0.005935	0.4033
C and (A+B)	MW	0.6862	0.7465	0.05439	0.03994	0.9541	0.04611	2.66E-02	0.1712	0.08435
	KS	0.895	0.7386	0.03906	0.02582	0.7959	0.03184	2.58E-02	0.5583	0.02083

Analysis of Differences										
Property	Mean	Median	SD	Range	Mean	Median	SD	Range		
A and B										
<i>Cluster A</i>					<i>Cluster B</i>					
Avg Slope	86.4	87	3.92	90–75	68.9	70	5.84	75–60		
Complexity	2.23	2	0.425	3–2	2.08	2	0.277	3–2		
C and (A+B)										
<i>Cluster C</i>					<i>Cluster (A+B)</i>					
Avg Width	1.9	1.9	0	1.9–1.9	2.48	2.3	0.515	4.3–1.7		
Avg Height	1.75	1.75	0.0707	1.9–1.9	2.37	2.35	0.517	3.2–1.6		
Avg Circ	5.85	5.85	0.212	6.0–5.7	7.6	7.5	2.35	20.8–5.3		
Avg Slope	59.75	59.75	6.72	64.5–55	81.3	85	9.26	90–60		
Tortuosity	0.8	0.8	0.283	1.0–0.6	1.02	1	0.124	1.4–05		

B. Spiders to <i>A. chalcodes</i>										
Clusters	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
A and B	MW	0.8119	0.874	0.6901	0.6409	0.47	0.8031	5.25E-05	0.3396	0.3312
	KS	0.9316	0.9316	0.7889	0.6404	0.1809	0.7559	2.30E-06	0.001312	0.2426
C and (A+B)	MW	0.7523	0.6274	0.04811	0.03615	0.8564	0.04138	3.67E-02	0.1424	0.07881
	KS	0.8661	0.6369	0.0347	0.0238	0.8441	0.0288	4.16E-02	0.5559	0.01959
D and (A+B+C)	MW	0.0208	0.1911	0.2138	0.07124	0.941	0.3748	1.71E-02	0.5426	0.7274
	KS	0.01583	0.2749	0.3897	0.04716	0.5551	0.737	1.30E-02	0.01918	0.6591

Table 7 continued.

Analysis of Differences	Property	Mean	Median	SD	Range	Mean	Median	SD	Range
A and B		Cluster A				Cluster B			
	Avg Slope	86.4	87	3.92	90–75	68.9	70	5.84	75–60
	Complexity	2.226	2	0.425	3–2	2.08	2	0.277	3–2
C and (A+B)		Cluster C				Cluster (A+B)			
	Avg Width	1.90	1.9	0	1.9–1.9	2.50	2.35	0.518	4.3–1.7
	Avg Height	1.75	1.75	0.0707	1.8–1.7	2.37	2.32	0.377	3.2–1.6
	Avg Circ	5.85	5.85	0.212	6–5.7	7.96	7.5	2.35	20.8–5.3
	Avg Slope	59.8	59.8	6.71	64.5–55	81.3	85	9.260	90–60
	Tortuosity	0.8	0.8	0.283	2.0–1.6	1.02	1	0.124	1.4–0.05
D and (A+B+C)		Cluster D				Cluster (A+B+C)			
	Depth	2.6	2.6	0.707	3.1–2.1	7.76	6.65	3.65	16.6–2.5
	Avg Height	1.75	1.75	0.0707	1.8–1.7	2.34	2.3	0.390	3.2–1.6
	Avg Slope	35	35	14.1	45–25	80.3	85	10.1	90–55
	Complexity	2	2	0	2–2	2.22	2	0.767	4–2

C. Spiders to *H. arizonensis*

Clusters	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
A and B	MW	0.5284	0.8672	0.6977	0.5268	0.2726	0.7476	1.83E-07	0.2561	0.136
	KS	0.4373	0.8424	0.5739	0.4144	0.1505	0.4729	1.15E-08	0.005935	0.4033
C and (A+B)	MW	0.6862	0.7465	0.05439	0.03994	0.9541	0.04611	2.66E-02	0.1712	0.08435
	KS	0.895	0.7386	0.03906	0.02582	0.7959	0.03184	2.58E-02	0.5583	0.02083
D and (A+B+C+G6)	MW	0.0779	4.14E-07	3.54E-09	1.15E-04	5.29E-10	1.48E-08	1.10E-09	5.46E-09	8.05E-09
	KS	0.09865	1.03E-05	2.70E-07	0.0009562	3.23E-12	7.68E-10	1.04EE-11	3.92E-08	1.35E-06

Analysis of Differences	Property	Mean	Median	SD	Range	Mean	Median	SD	Range
A and B		Cluster A				Cluster B			
	Avg Slope	86.4	87	3.92	90–75	68.9	70	5.84	75–60
	Complexity	2.26	2	0.425	3–2	2.08	2	0.277	3–2
C and (A+B)		Cluster C				Cluster (A+B)			
	Avg Width	1.9	1.9	0	1.9–1.9	2.5	2.35	0.377	3.2–1.6
	Avg Height	1.75	1.75	0.0707	1.9–1.9	2.37	2.3	0.517	3.2–1.6
	Avg Circ	5.85	5.85	0.212	6.0–5.7	7.6	7.5	2.35	20.8–5.3
	Avg Slope	59.75	59.75	6.72	64.5–55	81.3	85	9.26	90–60
	Tortuosity	0.8	0.8	0.283	1.0–0.6	1.03	1.0	0.110	1.4–0.5
D and (A+B+C+G6)		Cluster D				Cluster (A+B+C+G6)			
	Length	26.9	23	18.5	76–7.0	8.03	6.9	3.83	18.4–2.5
	Avg Width	4.34	4.4	0.553	5.2–3.1	2.48	2.3	0.515	4.3–1.7
	Avg Height	1.86	1.9	0.347	2.4–1.0	2.33	2.3	0.391	3.2–1.6
	W/H Ratio	2.41	2.4	0.434	3.1–1.3	1.06	1.0	0.117	1.5–0.9
	Avg Circ	12.3	12.3	1.957	17.3–9.0	7.86	7.4	2.31	20.8–5.3
	Avg Slope	17.2	15	11.7	45–5	79.6	85	11.3	90–45
	Complexity	4	3	2.12	9–3	2.21	2	0.463	4–2
	Tortuosity	1.96	1.3	1.94	9.0–1.1	1.02	1.0	0.124	1.4–0.5

D. Spiders to *M. giganteus*

Clusters	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
A and B	MW	0.5695	0.8012	0.883	0.6538	0.311	0.9417	4.21E-05	0.4108	0.3301
	KS	0.6414	0.973	0.8003	0.8466	0.07347	0.9289	8.11E-06	4.49E-05	0.05098
C and (A+B)	MW	0.4613	0.07504	0.9264	0.09654	0.1914	0.9877	5.76E-03	0.1023	0.5669
	KS	0.4241	0.2973	0.4528	0.1178	0.5131	0.4528	3.19E-03	0.2973	0.3445
D and (A+B+C)	MW	0.2556	7.86E-01	1.84E-01	5.40E-01	6.17E-02	1.69E-01	5.83E-03	5.12E-01	4.53E-01
	KS	0.2853	8.30E-01	3.65E-01	0.4104	6.31E-02	3.65E-01	3.67E-03	4.63E-03	7.81E-01

Table 7 continued.

Analysis of Differences	Property	Mean	Median	SD	Range	Mean	Median	SD	Range	
E and (A+B+C+D)	MW	0.5828	4.62E-05	4.25E-04	3.03E-01	5.02E-05	6.58E-04	5.70E-06	6.66E-06	1.57E-06
	KS	0.8059	7.21E-05	3.97E-04	0.2461	1.71E-05	8.79E-04	4.79E-07	8.79E-04	1.40E-06
A and B			Cluster A				Cluster B			
	Avg Slope	81.1	85	9.30	90–60	68.3	70	60.9	75–60	
	Complexity	2.16	2	0.370	3–2	2.07	2	0.267	3–2	
	Tortuosity	1.03	1.0	0.107	1.4–0.5	1.04	1.0	0.0514	1.1–1.0	
C and (A+B)			Cluster C				Cluster (A+B)			
	Avg Height	61.1	62.3	4.66	65–55	79.6	84.5	10.4	90–55	
D and (A+B+C)			Cluster D				Cluster (A+B+C)			
	Length	6.73	8	2.64	8.5–3.7	8.39	7.4	4.58	26.5–2.5	
	Avg Width	2.87	3	0.321	3.1–2.5	2.62	2.5	0.707	5.8–1.7	
	Avg Height	2.13	1.9	0.404	2.6–1.9	2.26	2.3	0.447	3.2–1.0	
	W/H Ratio	1.37	1.3	0.208	106–1.2	1.18	1.1	0.312	2.2–0.9	
	Avg Circ	9.73	10	2.21	11.8–7.	8.26	7.5	2.52	20.8–5.3	
	Avg Slope	48.3	50	2.89	50–45	77.9	83	12.4	90–45	
	Complexity	2	2	0	2–2	2.19	2	0.441	4–2	
	Tortuosity	1.05	1.06	0.0502	1.1–1.0	1.03	1	0.123	1.4–0.5	
E and (A+B+C+D)			Cluster E				Cluster (A+B+C+D)			
	Length	22.2	19.25	18.0	66–12.5	8.40	7.4	4.58	26.5–2.5	
	Avg Width	4.16	4.15	1	5.7–2.4	2.62	2.5	0.707	5.8–1.7	
	Avg Height	2.13	1.95	0.12	2.9–1.6	2.26	2.3	0.447	3.2–1.0	
	W/H Ratio	1.94	1.95	0.267	2.4–1.5	1.18	1.1	0.312	2.2–0.9	
	Avg Circ	12.2	10.9	3.09	17.0–8.3	8.26	7.5	2.52	20.8–5.3	
	Avg Slope	36.9	37.5	9.22	47–20	77.9	83	12.4	90–45	
	Complexity	4.5	3.5	2.67	10–2	2.19	2	0.441	4–2	
	Tortuosity	1.6	1.5	0.363	2.4–13	1.03	1.0	0.124	1.4–0.5	

E. Spiders to *N. americanus*

Clusters	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
A and B	MW	0.775	0.9409	0.8151	0.6481	0.2242	0.8738	2.08E-08	0.2501	0.1065
	KS	0.3038	0.3038	0.7461	0.5839	0.2052	0.6381	7.20E-10	2.85E-03	0.3431
C and (A+B)	MW	0.5194	0.7809	0.0084	0.006638	0.8771	0.0132	1.83E-03	0.5232	0.5072
	KS	0.8792	0.726	0.009266	0.005264	0.6869	0.007009	1.13E-03	0.02982	0.3073
D and (A+B+C+G6)	MW	0.006464	6.31E-01	2.23E-02	4.36E-03	1.90E-02	8.97E-03	9.25E-05	4.53E-02	3.03E-03
	KS	0.005894	2.10E-01	5.89E-03	0.002205	5.89E-03	5.89E-03	3.11E-05	1.72E-01	2.56E-02

Analysis of Differences	Property	Mean	Median	SD	Range	Mean	Median	SD	Range	
A and B			Cluster A				Cluster B			
	Avg Slope	86.3	87	4.09	90–75	69.1	70	5.45	75–60	
	Complexity	2.2	2	0.406	1.4–0.5	2.07	2	0.258	3–2	
C and (A+B)			Cluster C				Cluster (A+B)			
	Avg Width	0.955	0.955	1.09	1.9–0.0096	2.22	2.3	0.925	4.3–0.815	
	Avg Height	0.880	0.855	1.01	1.8–0.0083	2.10	2.3	0.825	3.2–0.0825	
	Avg Circ	4.47	4.41	1.59	6.1–3.1	7.40	7.35	2.69	20.8–2.6	
	Avg Slope	55.7	59.8	12.4	65–38.3	81.1	85	9.11	90–60	
	Complexity	2.5	2	1.00	4–2	2.16	2	0.370	3–2	
D and (A+B+C)			Cluster D				Cluster (A+B+C)			
	Depth	3.67	2.95	1.82	6.9–1.9	7.12	6.55	3.74	16.6–1.9	
	Total Length	8.09	9.7	4.09	12.5–2.34	7.54	6.75	3.88	18.4–1.9	
	Avg Width	1.01	1.09	0.883	2.5–0.105	2.12	2.3	0.985	4.3–0.0096	
	Avg Height	0.841	0.878	0.695	1.9–0.0824	2.01	2.25	0.888	3.2–0.0083	
	W/H Ratio	1.21	1.25	0.132	1.31–0.964	1.06	1.0	0.117	1.5–0.89	
	Avg Circ	4.04	3.4	1.67	7.4–3.1	7.18	7.3	2.73	20.8–2.6	
	Avg Slope	39.3	36.3	12.1	60–25	79.2	84.5	11.4	90–38.3	

Table 7 continued.

Complexity	2.67	2.5	0.816	4-2	2.19	2	0.436	4-2
Tortuosity	14.5	1.46	20.6	43-1.0	1.04	1.0	0.212	2.3-0.5

F. All Arthropods

Clusters	Test	Depth	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
A and B	MW	0.6142	0.811	0.6131	0.9046	0.1495	0.6567	2.10E-09	0.6933	0.1103
	KS	0.3741	0.212	0.6751	0.8472	0.1127	0.8173	3.00E-11	0.001851	0.2362
C and (A+B)	MW	0.6934	0.05814	0.8784	0.1142	0.4974	0.8288	8.54E-04	0.1377	0.1976
	KS	0.559	0.1132	0.4343	0.1048	0.5988	0.3781	2.56E-04	0.07935	0.1176
D and (A+B+C)	MW	0.0873	0.5791	0.1606	0.008276	0.03095	0.164	5.36E-06	0.6551	0.005936
	KS	0.1617	0.1538	0.02949	0.01397	0.004231	0.03811	1.00E-04	0.002128	0.1008
E and F	MW	0.004284	0.05873	0.6612	0.3658	0.022	0.8178	8.22E-06	0.0001995	0.3299
	KS	0.002861	0.1523	0.3668	0.7977	0.08807	0.952	2.32E-06	0.0003	0.4693
(A+B+C+D) and (E+F)	MW	0.9072	3.51E-10	7.40E-11	0.2881	9.28E-10	4.38E-10	4.77E-14	3.44E-12	1.79E-07
	KS	0.972	7.20E-09	2.25E-12	0.06005	2.41E-12	1.50E-11	1.74E-16	9.39E-11	1.07E-06

Analysis of Differences	Property	Mean	Median	SD	Range	Mean	Median	SD	Range
A and B		Cluster A				Cluster B			
	Avg Slope	85.9	85	4.09	90-75	68.9	70	5.77	75-60
	Complexity	2.17	2	0.381	3-2	2.17	2	0.529	4-2
C and (A+B)		Cluster C				Cluster (A+B)			
	Avg Slope	61.9	64.5	4.39	65-55	80.9	85	9.05	90-60
D and (A+B+C)		Cluster D				Cluster (A+B+C)			
	Avg Width	1.75	1.13	0.943	3.1-1.02	2.25	2.3	1.11	5.8-0.082
	Avg Height	1.37	1.07	0.678	2.6-0.79	1.95	2.2	0.870	3.2-0.078
	W/H Ratio	1.26	1.28	0.177	1.6-0.965	1.16	1.10	1.10	2.2-0.89
	Avg Circ	5.72	3.62	3.54	11.8-3.1	7.48	7.30	2.91	20.8-2.6
	Avg Slope	43.6	41.7	9.29	60-33	79.4	83	10.2	90-55
	Complexity	2.25	2	0.469	3-2	2.21	2	0.481	4-2
Tortuosity	11.1	1.16	18.5	43-1.0	1.06	1.0	0.209	2.3-0.5	
E and F		Cluster E				Cluster F			
	Depth	5.22	4.2	3.25	16-2.8	7.85	7.7	2.57	12.4-2.9
	W/H Ratio	2.33	2.4	0.650	3.1-0.55	1.84	2	0.476	2.5-0.77
	Avg Slope	13.3	13	6.58	25-5	35.9	35	7.84	47-25
(A+B+C+D) and (E+F)		Cluster (A+B+C+D)				Cluster (E+F)			
	Total Length	7.90	6.8	4.51	26.5-1.9	25.3	19	17.7	76-6.1
	Avg Width	2.19	2.3	1.09	5.8-0.082	4.18	4.35	1.17	6.6-0.12
	W/H Ratio	1.17	1.1	0.287	2.2-0.89	2.10	2.05	0.617	3.1-0.55
	Avg Circ	7.28	7.3	3.01	20.8-2.6	12.1	12.05	3.10	19.1-3.4
	Avg Slope	75.4	80	15.2	90-33	23.8	22.5	13.5	47-5
	Complexity	2.21	2	0.476	4-2	4.04	3	2.19	10-2
	Tortuosity	2.10	1.0	6.67	43-0.5	1.75	1.3	1.55	9.0-0.52

5.4.1 Comparison with *Aphonopelma chalcodes*

Two burrow casts (A1–A2) from a single individual were available for comparison (Appendix A). The burrows of *A. chalcodes* and the other two spiders differ in width-to-height ratio, average circumference, average slope, and tortuosity (Table 6B). Although the burrows are both subvertical ramps, one (A1) is much larger than the other. As a result, the two *A. chalcodes* burrows have a similarity of only 0.6. The similarity of burrows made by *A. chalcodes* and *G. inermis* ranges from 0.8–0.5 with an average similarity of 0.56; the similarity of *A. chalcodes* and *H. lenta* ranges from 0.7–0.5 with an average similarity of 0.56 (Appendix B). The average similarity of *A. chalcodes* compared to both *G. inermis* and *H. lenta* is 0.56. A cluster analysis of the three species reproduces Clusters A, B, and C (Figure 25). The isolated chamber (G6) is most similar to the smaller *A. chalcodes* burrow A2, and together they form Cluster D with a similarity of 0.77. Cluster D has a similarity of 0.67 with Clusters A, B, and C. Clusters A and B differ in average slope and complexity, whereas Clusters A, B, and C differ average width, average height, average circumference, average slope, and tortuosity (Table 7B). Cluster D differs from A, B, and C in depth, average height, average slope, and complexity (Table 7B). The larger *A. chalcodes* burrow A1 does not fit into any cluster, and its overall similarity with all other spider burrows is 0.56.

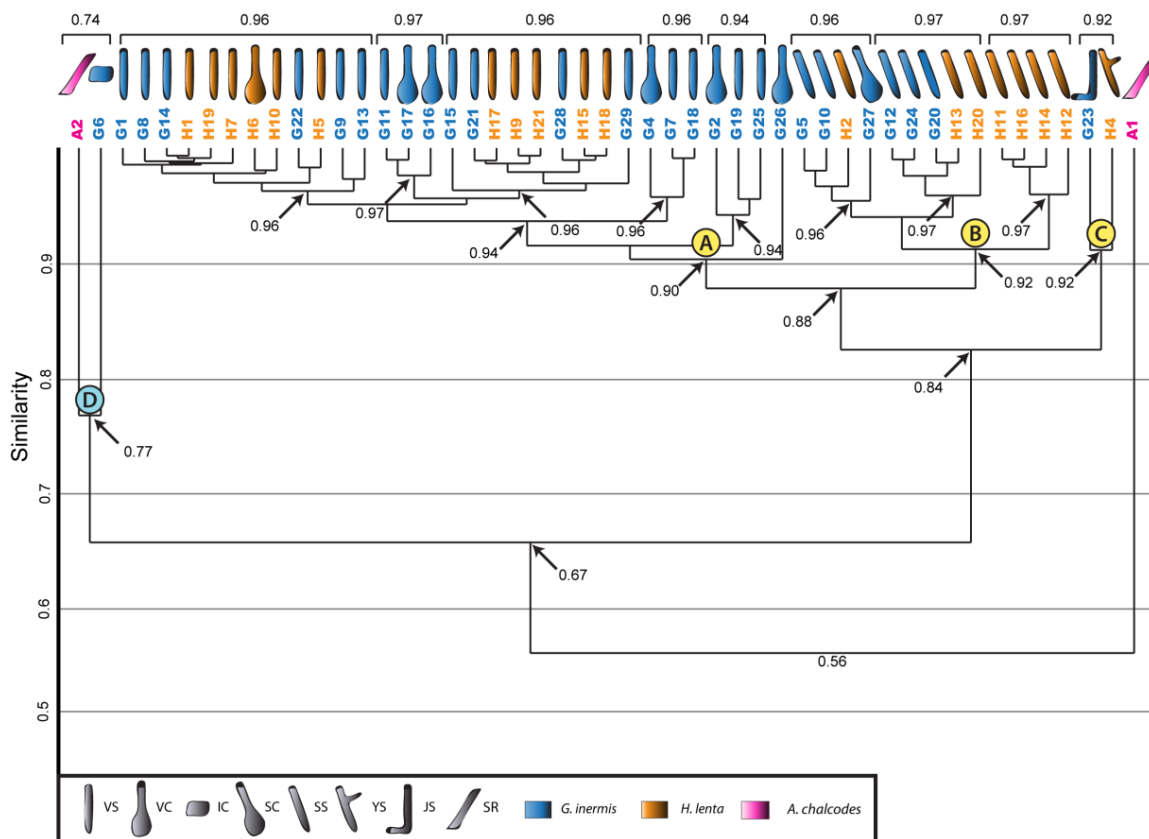


Figure 25: Cluster analysis of burrows produced by *G. inermis*, *H. lenta*, and *A. chalcodes*. Clusters A, B, and C are maintained, and the burrows G6 and A2 form a new cluster. The larger *A. chalcodes* burrow, A1, does not fall into a cluster. Values located at the nodes of the dendrogram are the average Bray-Curtis similarity score of all burrows emanating from that node cluster. Brackets above the dendrogram group together main clusters and provide the average Bray-Curtis similarity score of the burrows in that cluster. Clusters indicated by letters in yellow circles are clusters of spider burrows that form in all analyses whereas letters in blue circles are clusters that form only in this analysis. Burrow architecture is indicated in the key at the bottom of the figure: VS = vertical shaft, VC = vertical shaft with terminal chamber, IC = isolated chamber, SC = subvertical shaft with terminal chamber, SS = subvertical shaft, YS = Y-shaped burrow, JS = J-shaped burrow, SR = subvertical ramp. Tracemaker is indicated by the color of the box with the associated name.

5.4.2 Comparison with *Hadrurus arizonensis*

Seventeen burrow casts (DHS1–DHS17), comprising four different architectures, were used for comparison (Hembree et al., 2012) (Appendix C). The burrows of *H. arizonensis* differ from the spider burrows in total length, average width, average height, average width-to-height ratio, average circumference, average slope, complexity, and tortuosity (Table 6B). The similarity of the seventeen *H. arizonensis* burrows ranges from 1.0–0.5 with an average similarity of 0.75 (Appendix D). The similarity of the burrows produced by *H. arizonensis* and *G. inermis* ranges from 0.8–0.3 with an average of 0.46; the similarity of the burrows produced by *H. arizonensis* and *H. lenta* ranges from 0.8–0.3 with an average of 0.46. The comparison of *H. arizonensis* burrows with those of both *G. inermis* and *H. lenta* results in an average similarity of 0.46. A cluster analysis results in a complete separation of the spider burrows and the scorpion burrows (Figure 26). All spider burrows fall into Clusters A, B, and C, although the isolated chamber is again alone. This grouping of the spider burrows has a similarity of 0.75. All *H. arizonensis* burrows form Cluster D, with a similarity of 0.68. Clusters A and B differ in average slope and complexity, whereas Cluster A, B, and C differ in average width, average height, average circumference, average slope, and tortuosity (Table 7C). Cluster D differs from Clusters A, B, and C in all properties but maximum depth (Table 7C). The similarity of all burrows produced by the three species is 0.46. Of particular note, no subvertical ramps produced by *H. arizonensis* were similar to the subvertical shafts produced by either species of spider.

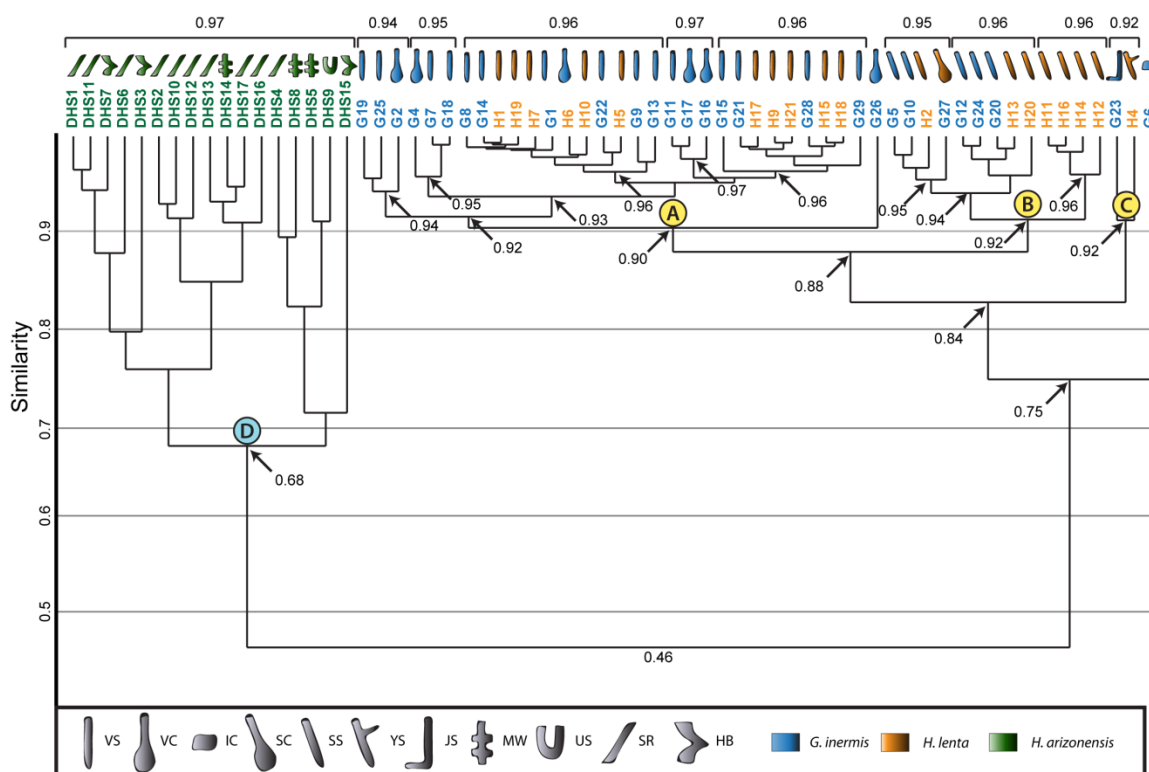


Figure 26: Cluster analysis of burrows produced by *G. inermis*, *H. lenta*, and *H. arizonensis*. Spider Clusters A, B, and C are maintained, and a separate scorpion cluster is produced. Values located at the nodes of the dendrogram are the average Bray-Curtis similarity score of all burrows emanating from that node cluster. Brackets above the dendrogram group together main clusters and provide the average Bray-Curtis similarity score of the burrows in that cluster. Clusters indicated by letters in yellow circles are clusters of spider burrows that form in all analyses whereas letters in blue circles are clusters that form only in this analysis. Burrow architecture is indicated in the key at the bottom of the figure: VS = vertical shaft, VC = vertical shaft with terminal chamber, IC = isolated chamber, SC = subvertical shaft with terminal chamber, YS = Y-shaped burrow, JS = J-shaped burrow, MW = mazework, US = U-shape burrow, SR = subvertical ramp, HB = helical burrow. Tracemaker is indicated by the color of the box with the associated name.

5.4.3 Comparison with *Mastigoproctus giganteus*

Eighteen burrow casts (WS1–15, WS27–28, WS32), comprising five different architectures, were used for comparison (Hembree, 2013) (Appendix E). The burrows of *M. giganteus* differ from the spider burrows in total length, average width, average height, average width-to-height ratio, average circumference, average slope, complexity, and tortuosity (Table 6B). The similarity of the eighteen *M. giganteus* burrows ranges from 1.0–0.5 with an average similarity of 0.75. The similarity of the burrows produced by *M. giganteus* and *G. inermis* ranges from 1.0–0.4 with an average similarity of 0.75; the similarity of the burrows produced by *M. giganteus* and *H. lenta* ranges from 1.0–0.5 with an average similarity of 0.75. The comparison *M. giganteus* with both *G. inermis* and *H. lenta* has an average similarity of 0.75 (Appendix F). A cluster analysis results in two separate groups (Figure 27). One group consists entirely of burrows produced by *M. giganteus* whereas the other group is composed of burrows produced by all three species. Five *M. giganteus* burrows are included in Cluster A with a similarity of 0.90, whereas one *M. giganteus* burrow is included in Cluster B with a similarity of 0.90. Two J-shaped burrows produced by *M. giganteus* are included in Cluster C with a similarity of 0.87. Clusters A and B differ in average slope, and complexity, whereas Cluster C differs from A and B in only average slope (Table 7D). Cluster D, a new cluster, contains the isolated chamber (G6) and two subvertical shafts produced by *M. giganteus* with a similarity of 0.90. This new cluster differs from Clusters A, B, and C in all aspects but depth (Table 7D). The three clusters have a similarity of 0.76. The similarity of all burrows produced by the three species is 0.64. Cluster E consists entirely of burrows produced by *M.*

giganteus and includes burrow architectures such as mazes, U-shaped burrows, J-shaped burrows, and one subvertical shaft. The similarity of this cluster is 0.74. Cluster E shares only depth in common with the other clusters (Table 7D). The similarity of all burrows produced by all three species is 0.64.

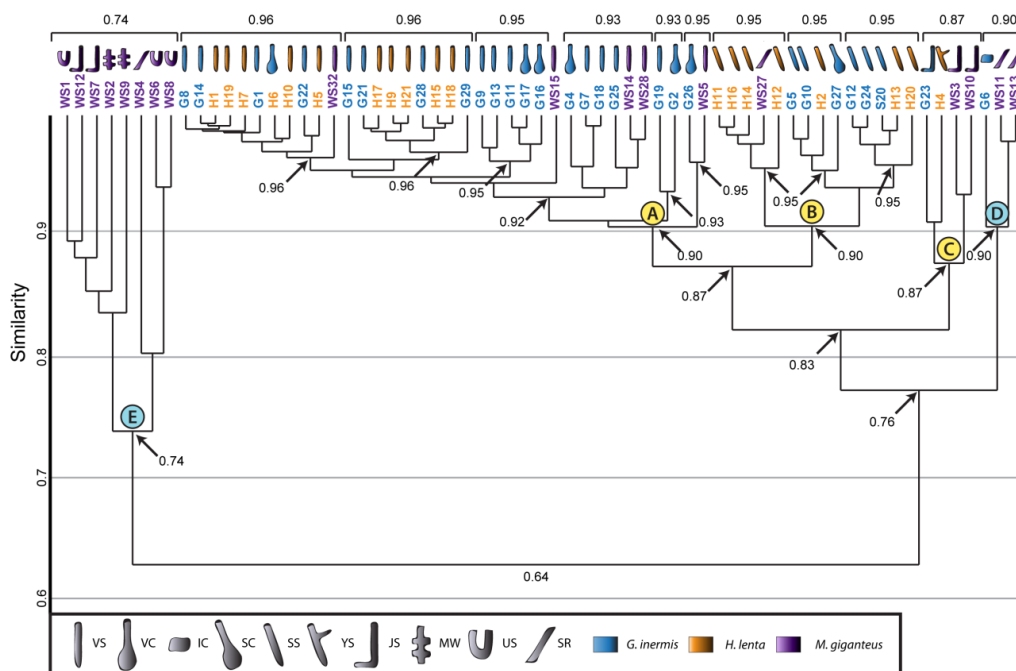


Figure 27: Cluster analysis of burrows produced by *G. inermis*, *H. lenta*, and *M. giganteus*. Spider Clusters A, B, and C are maintained with the addition of morphologically similar whip scorpion burrows, and G6 forms a new cluster. Unique burrow architectures produced by *M. giganteus* form a separate cluster. Values located at the nodes of the dendrogram are the average Bray-Curtis similarity score of all burrows emanating from that node cluster. Brackets above the dendrogram group together main clusters and provide the average Bray-Curtis similarity score of the burrows in that cluster. Clusters indicated by letters in yellow circles are clusters of spider burrows that form in all analyses whereas letters in blue circles are clusters that form only in this analysis. Burrow architecture is indicated in the key at the bottom of the figure: VS = vertical shaft, VC = vertical shaft with terminal chamber, IC = isolated chamber, SC = subvertical shaft with terminal chamber, SS = subvertical shaft, YS = Y-shaped burrow, JS = J-shaped burrow, MW = mazework, US = U-shaped burrow, SR = subvertical ramp. Tracemaker is indicated by the color of the box with the associated name.

5.4.4 Comparison with *Narceus americanus*

Fifteen burrow casts (NA21A–21F, NA23, NA25A–26B, NA28–NA29C, NA30A–NA33C), comprising six different architectures, were used for comparison (Bowen and Hembree, 2014) (Appendix G). The burrows of *N. americanus* differ from the spider burrows in depth, average width, average height, average circumference, average slope, complexity, and tortuosity (Table 6 B). The similarity of the seventeen *N. americanus* burrows ranges from 1.0–0.5 with an average similarity of 0.76 (Appendix H). The similarity of the burrows produced by *N. americanus* and *G. inermis* ranges from 1.0–0.5 with average similarity of 0.78; the similarity of the burrows produced by *N. americanus* and *H. lenta* ranges from 1.0–0.5 with an average similarity of 0.78. A cluster analysis results in two separate groups (Figure 28), both of which contain burrows produced by all three species. Five *N. americanus* burrows are included in Cluster A with a similarity of 0.89, whereas three burrows are included in Cluster B with a similarity of 0.88. Cluster A and B differ in average slope and complexity (Table 7E). Cluster C includes two *N. americanus* burrows with a similarity of 0.85. This cluster differs from Clusters A and B in average width, average height, average circumference, average slope, complexity, and tortuosity (Table 7E). The similarity of these three clusters is 0.82. Cluster D, a new cluster, is composed of five burrows produced by *N. americanus* and one burrow (G6) produced by *G. inermis*. Burrow architectures included in Cluster D are subvertical shafts, O-shaped burrows, a helical burrow, and the isolated chamber produced by *G. inermis*. This group has a similarity of 0.69 and is statistically different

from the other clusters in all aspects of burrow morphology (Table 7E). The similarity of all burrows produced by the three species is 0.65.

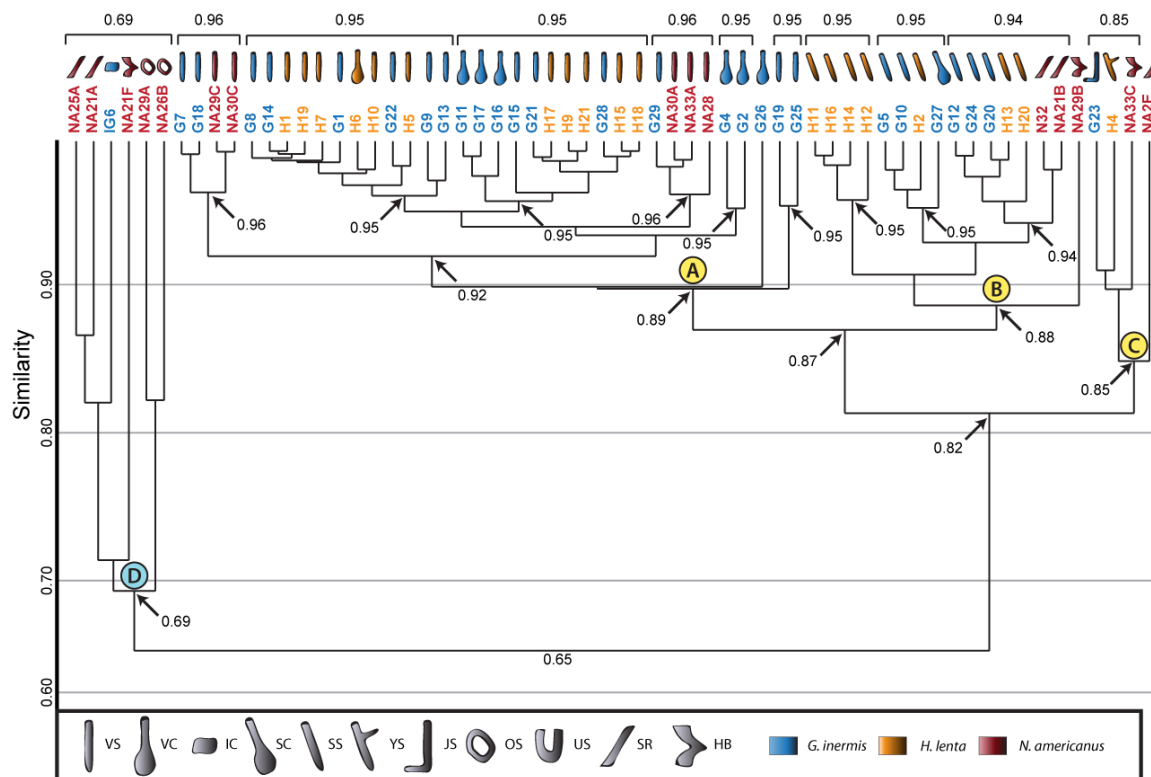


Figure 28: Cluster analysis of burrows produced by *G. inermis*, *H. lenta*, and *N. americanus*. Spider Clusters A, B, and C are maintained and include burrows produced by all three species. G6 forms a new cluster with the most dissimilar burrows produced by *N. americanus*. Values located at the nodes of the dendrogram are the average Bray-Curtis similarity score of all burrows emanating from that node cluster. Brackets above the dendrogram group together main clusters and provide the average Bray-Curtis similarity score of the burrows in that cluster. Clusters indicated by letters in yellow circles are clusters of spider burrows that form in all analyses whereas letters in blue circles are clusters that form only in this analysis. Burrow architecture is indicated in the key at the bottom of the figure: VS = vertical shaft, VC = vertical shaft with terminal chamber, IC = isolated chamber, SC = subvertical shaft with terminal chamber, SS = subvertical shaft, YS = Y-shaped burrow, JS = J-shaped burrow, OS = O-shaped burrow, US = U-shaped burrow, SR = subvertical ramp, HB = helical burrow. Tracemaker is indicated by the color of the box with the associated name.

5.4.5 Comparison of All Arthropod Burrows

A cluster analysis of the six arthropod species results in two separate groups (Figure 29). The first group consists of the four distinct clusters formed by the burrows of *G. inermis* and *H. lenta*. Clusters A, B, and C all include burrows produced by *G. inermis*, *H. lenta*, *M. giganteus*, and *N. americanus*. Cluster A has a similarity of 0.90, Cluster B has a similarity of 0.88, and Cluster C has a similarity of 0.86. The similarity of all three clusters is 0.83. Cluster A and Cluster B differ in average slope and complexity, whereas Cluster A, B, and C differ in average slope (Table 7F). Cluster D includes the burrows produced by *G. inermis*, *H. lenta*, and *N. americanus* and has a similarity of 0.73. This cluster is composed subvertical shafts, O-shaped burrows, and the isolated chamber. Cluster D differs from Clusters A, B, and C in average width, average height, width-to-height ratio, average circumference, average slope, complexity, and tortuosity (Table 7F). These four clusters have a similarity of 0.71. The second group consists of two distinct clusters, Cluster E and Cluster F, and is composed of all *A. chalcodes*, all *H. arizonensis*, eight *M. giganteus*, and one *N. americanus* burrows. Cluster E includes subvertical ramps and helical burrows and has a similarity of 0.78. Cluster F includes mazes, U-shaped burrows, J-shaped burrows, helical burrows, and subvertical ramps and has a similarity of 0.79. Clusters E and F differ in depth, width-to-height ratio, average slope, complexity, and tortuosity (Table 7F). Clusters A, B, C, and D differ from Clusters E and F in total length, average width, width-to-height ratio, average circumference, average slope, complexity, and tortuosity (Table 7F). The similarity of all burrows produced by the arthropods is 0.53.

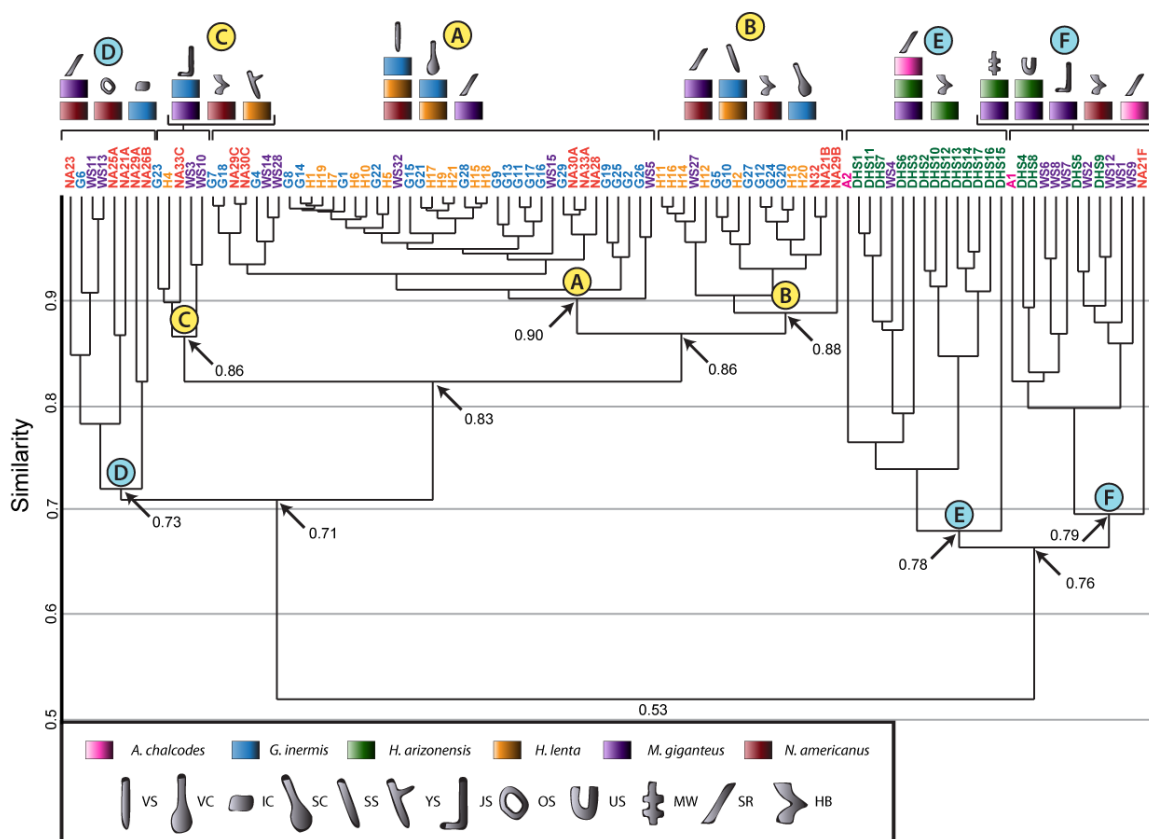


Figure 29: Combined cluster analysis of burrows produced by all arthropods considered in this study. Two large groups occur. Clusters A, B, C, and D consist of burrow produced small arachnids and millipedes. Clusters E and F consist of burrows produced by large arachnids and millipedes. The burrow architectures placed into each cluster and the tracemaker are indicated by symbols above each cluster. Multiple species boxes placed below a burrow symbol mean each species produced that burrow architecture and that it is placed into that cluster. Tracemaker is indicated by the color of the box with the associated name. Values located at the nodes of the dendrogram are the average Bray-Curtis similarity score of all burrows emanating from that node cluster. Brackets above the dendrogram group together main clusters and provide the average Bray-Curtis similarity score of the burrows in that cluster. Clusters indicated by letters in yellow circles are clusters of spider burrows that form in all analyses whereas letters in blue circles are clusters that form only in this analysis. Burrow architecture is indicated in the key at the bottom of the figure: VS = vertical shaft, VC = vertical shaft with terminal chamber, IC = isolated chamber, SC = subvertical shaft with terminal chamber, SS = subvertical shaft, YS = Y-shaped burrow, JS = J-shaped burrow, OS = O-shaped burrow, US = U-shaped burrow, MW = mazework, SR = subvertical ramp, HB = helical burrow.

5.5 Comparisons with Similar Ichnogenera

5.5.1 Comparison with *Skolithos*

Six specimens of *Skolithos* were measured for this study (Appendix I). The *Skolithos* specimens differ from the spider burrows in average width, average height, width-to-height ratio, average circumference, average slope, and complexity (Table 8). The similarity of the six specimens ranges from 1.0–0.9 with an average similarity of 0.97 (Appendix J). The similarity of *Skolithos* specimens and the burrows produced by *G. inermis* ranges from 1.0–0.7 with an average similarity of 0.87. The similarity of *Skolithos* and the burrows produced by *H. lenta* ranges from 1.0–0.7 with an average similarity of 0.86. The comparison of *Skolithos* to both *G. inermis* and *H. lenta* results in a similarity of 0.87. A cluster analysis places all six *Skolithos* specimens into Cluster A (Figure 30). The similarity of this cluster is 0.90. Within this cluster, five of the *Skolithos* specimens cluster separately from the spider burrows with a similarity of 0.96; the sixth specimen is clustered with two *G. inermis* burrows that have a similarity of 0.95. The addition of the *Skolithos* specimens moved two *G. inermis* burrows from Cluster A into Cluster B. Cluster A and Cluster B differ in average height, average circumference, average slope, and complexity (Table 9A). Cluster C, which contains no *Skolithos* specimens, differs from Cluster A and B in average slope and tortuosity (Table 9A). The similarity of all spider burrows and *Skolithos* specimens is 0.73.

Table 8: Mann-Whitney and Kolmogorov-Smirnov test results (p values) between the burrows produced by *G. inermis* and *H. lenta* and the trace fossils *Skolithos* and *Macanopsis*. Boxed values indicate statistical difference ($p < 0.05$). The resulting differences are explained by providing the median, the median, the standard deviation, and the range of the properties. All measurements are in cm and all angles are in degrees.

Comparison between Trace Fossils and combined burrows of *G. inermis* and *H. lenta*

Trace Fossil	Test	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
<i>Skolithos</i>	MW	0.5094	7.50E-05	7.96E-05	0.1031	7.94E-05	0.02786	0.2536	0.496
	KS	0.7794	9.62E-06	9.62E-06	0.001012	9.62E-06	0.1021	0.0001796	0.4499

Analysis of Differences	Property	<i>Skolithos</i>				<i>G. inermis</i> and <i>H. lenta</i>			
		Mean	Median	SD	Range	Mean	Median	SD	Range
	Avg Width	0.384	0.388	0.127	0.58–0.21	2.48	2.3	0.515	4.3–1.7
	Avg Height	0.384	0.388	0.127	0.58–0.21	2.33	2.3	0.391	3.2–1.6
	W/H Ratio	1	1	0	1–1	1.06	1.0	0.117	1.5–0.9
	Avg Circ	1.21	1.22	0.398	1.81–0.67	7.86	7.4	2.31	20.8–53
	Avg Slope	88.2	90	4.31	92–80	79.6	85	11.3	90–45
	Complexity	2	2	0	2–2	2.21	2	0.463	4–2

Trace Fossil	Test	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
<i>Macanopsis</i>	MW	0.5265	0.02398	0.04051	0.2449	0.02457	0.3952	0.002462	0.1886
	KS	0.3581	0.07959	0.0909	0.01298	0.07959	0.3581	0.02121	0.6653

Analysis of Differences	Property	<i>Macanopsis</i>				<i>G. inermis</i> and <i>H. lenta</i>			
		Mean	Median	SD	Range	Mean	Median	SD	Range
	Avg Width	1.30	1.05	0.857	2.25–0.591	2.48	2.3	0.515	4.3–1.7
	Avg Height	1.30	1.05	0.857	2.25–0.591	2.33	2.3	0.391	3.2–1.6
	W/H Ratio	1	1	0	1–1	1.06	1.0	0.117	1.5–0.9
	Avg Circ	4.07	3.30	0	7.07–1.86	7.86	7.4	2.31	20.8–53
	Complexity	3	3	0	3–3	2.21	2	0.463	4–2

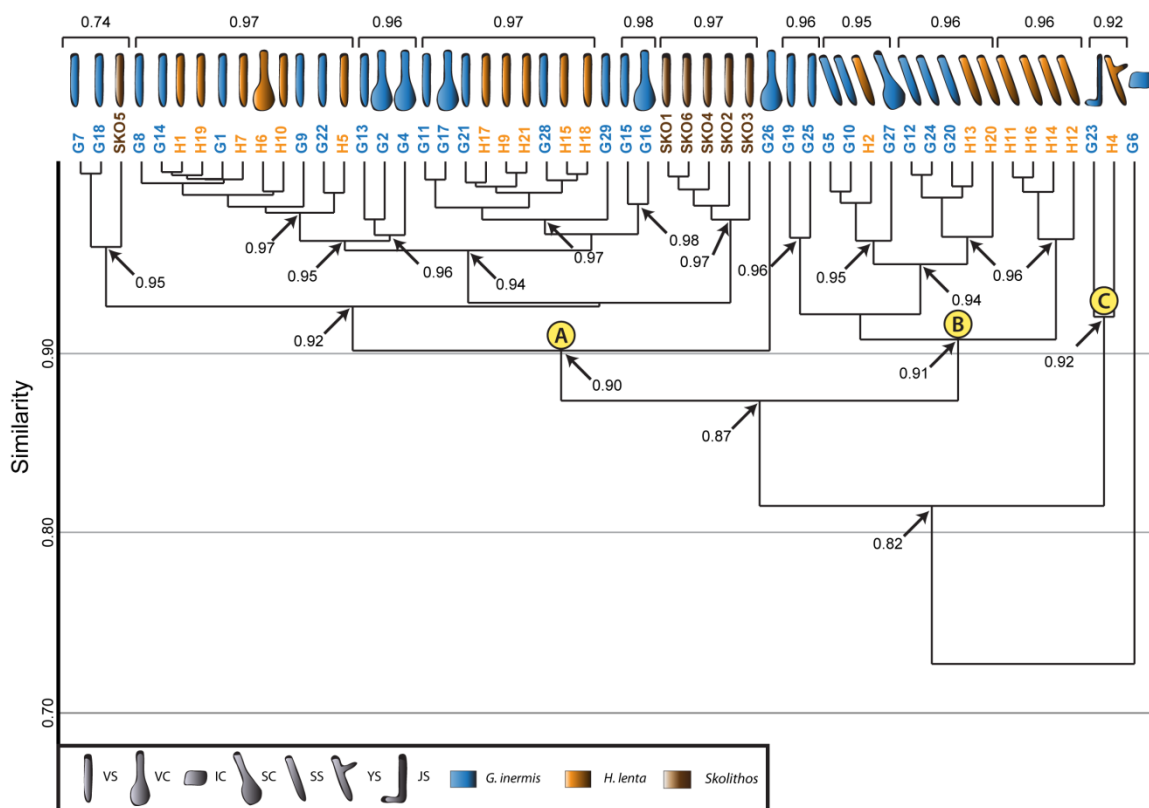


Figure 30: Cluster analysis of burrows produced by *G. inermis* and *H. lenta* and specimens of *Skolithos*. All *Skolithos* are contained within Cluster A. Within Cluster A, all five *Skolithos* are more similar to each other than they are to the spider burrows with similar shapes. Values located at the nodes of the dendrogram are the average Bray-Curtis similarity score of all burrows emanating from that node cluster. Brackets above the dendrogram group together main clusters and provide the average Bray-Curtis similarity score of the burrows in that cluster. Clusters indicated by letters in yellow circles are clusters of spider burrows that form in all analyses. Burrow architecture is indicated in the key at the bottom of the figure: VS = vertical shaft, VC = vertical shaft with terminal chamber, SS = subvertical shaft, YS = Y-shaped burrow. Tracemaker or ichnogenus is indicated by the color of the box with the associated name.

5.5.2 Comparison with *Macanopsis*

Three specimens of *Macanopsis* were used for comparison (Appendix K). *Macanopsis* specimens differ from spider burrows in average width, average height, width-to-height ratio, average circumference and complexity (Table 8). The similarity of the three specimens ranges from 1.0–0.6 with an average similarity of 0.7 (Appendix L). These three specimens are visibly different. *Macanopsis* specimen MAC2 is a vertical shaft with terminal chamber and MAC1 is a subvertical shaft with terminal chamber. Specimen MAC3 includes a vertical shaft terminating in a long chamber that resembles a tunnel. The similarity of *Macanopsis* specimens and the burrows produced by *G. inermis* ranges from 1.0–0.7 with an average similarity of 0.81; the similarity of *Macanopsis* specimens and the burrows produced by *H. lenta* ranges from 1.0–0.7 with an average similarity of 0.819. The comparison of *Macanopsis* with both *G. inermis* and *H. lenta* has an average similarity of 0.82. A cluster analysis places MAC2 into Cluster A whereas MAC1 is placed into Cluster B (Figure 31). Cluster A has a similarity of 0.91 and Cluster B has a similarity of 0.89. Clusters A and B differ in average slope and complexity (Table 9B). These two clusters have a similarity of 0.88. Cluster C contains no *Macanopsis* specimens and has a similarity of 0.92. It differs from Clusters A and B in average height, average circumference, average slope, and tortuosity (Table 9B). These three clusters have a similarity of 0.84. The isolated chamber fits into no cluster and has a similarity with Clusters A, B, and C of 0.75. The third specimen of *Macanopsis*, MAC3, does not fit into any cluster. The overall similarity of all spider burrows and *Macanopsis* specimens is 0.69.

Table 9: Mann-Whitney and Kolmogorov-Smirnov test results (p values) between the burrows within each cluster produced in the comparison of *G. inermis*, *H. lenta*, *Skolithos*, and *Macanopsis*. Boxed values indicate statistical difference ($p < 0.05$). The resulting differences are explained by providing the median, the median, the standard deviation, and the range of the properties. All measurements are in cm and all angles are in degrees.

A. Spiders to *Skolithos*

Clusters	Test	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
A and B	MW	0.397	0.05841	0.03201	0.5408	0.06692	1.80E-08	0.2501	0.4154
	KS	0.7461	0.05959	0.03497	0.1332	0.04195	7.20E-10	0.002848	0.08325
C and (A+B)	MW	0.7034	0.1587	0.1269	0.8355	0.14	0.02379	0.1374	0.07919
	KS	0.7148	0.09367	0.06789	0.8157	0.0799	0.02346	0.5555	0.01938

Analysis of Differences	Property	Mean	Median	SD	Range	Mean	Median	SD	Range
A and B	<i>Cluster A</i>					<i>Cluster B</i>			
	Avg Height	1.98	2.2	0.826	3.2–0.21	1.98	2.2	0.826	3.2–.21
	Avg Circ	6.81	7.1	3.63	20.8–0.67	6.81	7.1	3.63	20.8–0.67
	Avg Slope	87.2	88	3.26	90–80	70.0	70	1.07	80–60
	Complexity	2.2	2	0.406	3–2	2.2	2	0.405	3–2
C and (A+B)	<i>Cluster C</i>					<i>Cluster (A+B)</i>			
	Avg Slope	59.8	59.8	6.72	64.5–55	82.0	85	9.04	90–60
	Tortuosity	0.8	0.2	0.283	1.0–0.6	1.0	1	0.104	1.4–0.5

B. Spiders to *Macanopsis*

Clusters	Test	Total Length	Avg Width	Avg Height	W/H Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
A and B	MW	0.6696	0.3972	0.2616	0.2926	0.4326	2.03E-08	0.2796	0.395
	KS	0.9756	0.5153	0.3518	0.2841	0.3339	1.01E-09	0.04388	0.2687
C and (A+B)	MW	0.6797	0.08229	0.06241	0.9116	0.07078	0.0257	0.2163	0.0831
	KS	0.6725	0.05429	0.03715	0.8371	0.04501	0.02494	0.6702	0.02029

Analysis of Differences	Property	Mean	Median	SD	Range	Mean	Median	SD	Range
A and B	<i>Cluster A</i>					<i>Cluster B</i>			
	Avg Slope	87.2	87.8	3.14	90–80	70.0	70	6.06	80–60
	Complexity	2.27	2	0.450	3–2	2.1	2	0.342	3–2
C and (A+B)	<i>Cluster C</i>					<i>Cluster (A+B)</i>			
	Avg Height	1.75	1.75	0.0707	1.8–1.7	2.43	2.3	0.490	3.2–0.59
	Avg Circ	5.85	5.85	0.212	6–5.7	7.73	7.45	2.55	20.8–1.9
	Avg Slope	59.8	59.8	6.72	64.5–55	81.2	85	9.30	90–60
	Tortuosity	0.8	0.8	0.283	1.0–0.6	1.03	1.0	1.0	1.4–0.5

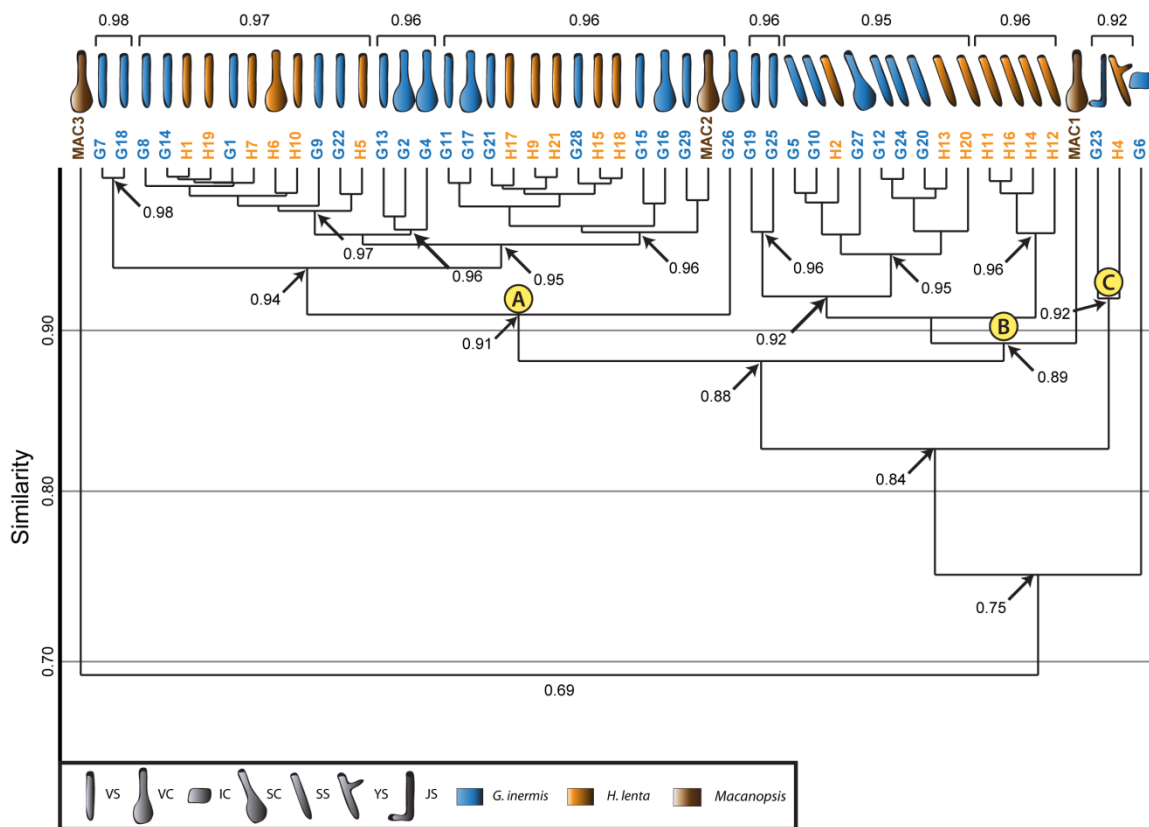


Figure 31: Cluster analysis of burrows produced by *G. inermis* and *H. lenta* and specimens of *Macanopsis*. One specimen of *Macanopsis* is included in both Clusters A and B. The third specimen, MAC3, does not fit into any cluster. Values located at the nodes of the dendrogram are the average Bray-Curtis similarity score of all burrows emanating from that node cluster. Brackets above the dendrogram group together main clusters and provide the average Bray-Curtis similarity score of the burrows in that cluster. Clusters indicated by letters in yellow circles are clusters of spider burrows that form in all analyses. Burrow architecture is indicated in the key at the bottom of the figure: VS = vertical shaft, VC = vertical shaft with terminal chamber, SS = subvertical shaft, YS = Y-shaped burrow. Tracemaker or ichnogenus is indicated by the color of the box with the associated name.

5.6 Environmental Controls on Burrow Morphology

The Mann-Whitney and Kolmogorov-Smirnov tests were used to determine if there were any statistically significant changes in burrow properties with changes in environmental conditions. Eight different analyses were run for both species, but no characteristics were found to be significantly different when conditions changed (Table 11).

Table 10: Mann-Whitney and Kolmogorov-Smirnov test results (p values) between sediment conditions. No results indicated significant differences ($p < 0.05$).

Comparisons of burrows produced in different sediment compositions and conditions										
<i>G. inermis</i>	Size: Sm to Lg Terrarium		Density: Mod to Denser		Density: Mod to Densest		Moisture: Mod to Dry		Moisture: Mod to Wet	
	MW	KS	MW	KS	MW	KS	MW	KS	MW	KS
Depth	0.06619	0.05292	0.8852	0.5344	0.3123	0.5344	0.1939	0.1075	0.4875	0.7361
Total Length	0.1761	0.3572	0.665	0.5344	0.3123	0.5344	0.1939	0.1075	0.4875	0.7361
Average Width	0.7133	0.2587	0.8852	0.9969	0.3123	0.2195	0.3123	0.1075	0.8170	0.9355
Average Height	0.9025	0.8757	0.6650	0.9969	0.3123	0.5344	0.3123	0.5344	0.8170	0.9356
Average Circ	0.7133	0.8778	0.1939	0.1075	0.3094	0.1075	0.4075	0.5344	0.8170	0.7361
Average Slope	0.8510	0.05292	0.1479	0.9969	0.5385	0.5344	0.7715	0.5344	1	0.7361
Complexity	0.1282	0.4772	0.1814	0.5344	0.8687	1	0.1814	0.5344	0.4017	0.7361
Tortuosity	0.2330	0.2235	0.6650	0.5344	0.1913	0.5344	0.1124	0.1075	0.1052	0.1376

<i>H. lenta</i>	Size: Sm to Lg Terrarium		Density: Mod to Denser		Density: Mod to Densest		Moisture: Mod to Dry		Moisture: Mod to Wet	
	MW	KS	MW	KS	MW	KS	MW	KS	MW	KS
Depth	0.6625	0.9762	0.6625	0.3197	0.8597	0.9610	0.7728	0.9906	0.77828	0.4249
Total Length	0.3827	0.3197	0.6579	0.3197	0.8597	0.9610	0.7728	0.9906	0.3865	0.4249
Average Width	0.6625	0.9762	0.6625	0.9762	0.8597	0.8214	0.7728	0.8979	0.3865	0.6001
Average Height	0.3827	0.3955	1	0.9762	0.8597	0.9610	0.7728	0.9906	0.7728	0.7796
Average Circ	1	0.9762	0.07652	0.03626	0.5926	0.6160	0.7671	0.7796	0.3743	0.4249
Average Slope	0.1642	0.3197	0.1642	0.3197	0.2756	0.1520	0.3173	0.4249	0.3329	0.4249
Complexity	1	0.9762	0.5050	0.9762	0.3865	0.9610	0.6831	0.9906	0.6831	0.9906
Tortuosity	0.6428	0.9762	0.3537	0.3197	0.8454	0.9988	0.6831	0.9906	0.7469	0.7796

CHAPTER 6: DISCUSSION

6.1 Burrow Morphology and Tracemaker

Two species of burrowing spiders produced seven different types of burrow architecture. *Gorgyrella inermis* produced six of these architectures, whereas *H. lenta* produced four. Although *G. inermis* and *H. lenta* are distantly related, both species produced four of the same burrow architectures. Individuals of both species produced multiple burrow architectures in different experiments. Nearly all burrow architectures produced by *G. inermis* and *H. lenta*, however, share common features: a single burrow opening, a nonbranching vertical to subvertical shaft with a circular-to-elliptical cross-section, a width-to-height ratio of approximately one, and surficial features related to silk-lining. These features are reflective of the general spider body form. The bodies of *G. inermis* and *H. lenta* consist of a cephalothorax and an abdomen. The eight legs radiate from the cephalothorax, forming a vaguely circular shape. This allows the spiders to move up and down the length of the shafts using a chimney climbing technique (i.e. Schäfer, 1972). The burrows do not include ramps or obvious floors as the spiders can move in any direction through the shafts. Individuals of both species were observed moving along all sides of the burrows; however, all individuals did use a preferred side to enter and exit burrows.

Surficial features resulting from a silk lining are the best indicator of a spider tracemaker. Silk linings isolate the burrow void space from the surrounding sediment and provide a foothold for the spiders to climb in the burrow. These features form smooth-walled burrow casts with scratch marks running vertically along the shaft. Although silk

production occurs in other arthropod classes (e.g. Insecta and Myriapoda), only spiders use silk to stabilize excavated burrows (Craig, 1997).

Comparisons of burrows produced by other arachnids, including other burrowing spiders, indicate other diagnostic characteristics of spider burrows. Although the spiders *A. chalcodes*, *G. inermis*, and *H. lenta* share the same spider body plan, the tarantula *A. chalcodes* is two to three times larger than *G. inermis* and *H. lenta*. *Aphonopelma chalcodes* constructed burrows by excavation of material using their pedipalps. They were not observed bundling the sediment with silk before removal. This species produced subvertical ramps with an ovoid cross section. This morphology does not allow the tarantulas to enter or exit their burrows with the chimney climbing technique used by the other two spider species. Burrow properties related to the subvertical ramp morphology and the tarantula's locomotion technique produced statistically significant differences when compared to the other spiders (Table 6B). Surficial features of tarantula burrows included protrusions on the burrow walls resulting from the excavation of sediment and the absence of a silk lining. The dissimilarity in burrow morphology between the tarantulas and other spiders would make linking the tarantula burrow to a large spider difficult.

The scorpion *H. arizonensis* and the whip scorpion *M. giganteus* are superficially very similar in morphology. Both species have large pedipalps modified into pincers, an elongate, low body, and a long tail. These arachnids, therefore, have a much different body plan than do the spiders. *Hadrurus arizonensis* excavated its burrows by kicking loose sediment behind it or by picking up sediment with its walking legs (Hembree et al.,

2012). *Mastigoproctus giganteus* gathered together sediment using its pedipalps and deposited the material outside of the burrow (Hembree, 2013). The scorpions and whip scorpions produced simple vertical shafts and subvertical ramps as well as a more diverse set of burrow architectures that included more complex burrow architectures not produced by either *G. inermis* or *H. lenta*, including U-shaped burrows, helical burrows, and mazes (Hembree et al., 2012; Hembree, 2013). The burrows of *H. arizonensis* and *M. giganteus* vary from the spider burrows in all burrow properties but depth (Table 6B). The scorpions and whip scorpions produced surficial features that differ greatly from those produced by the spiders. The burrows of *H. arizonensis* include no bioglyphs or surface sculpture marks and the texture of the walls is controlled by the surrounding sediment (Hembree et al., 2012). The upper surface of *M. giganteus* burrows is irregular and the floors are smooth whereas the walls feature paired protrusions, resulting from the excavation of material by the animal's pedipalps (Hembree, 2013).

The millipede *N. americanus* has an elongate, low body with multiple pairs of walking legs. While this species does not have any appendages specifically modified for grasping, it has been observed using its mandibles to pick up sediment grains (Bowen and Hembree, 2014). *Narceus americanus* produces simple vertical shafts and subvertical shafts as well as helical burrows, O-shaped burrows, and U-shaped burrows, architectures not produced by the spiders (Bowen and Hembree, 2014). The burrows of *N. americanus* vary from the spider burrows in all burrow properties but burrow length and width-to-height ratio (Table 6B). The similar width-to-height ratio may result from the millipede's anatomy. These animals are vaguely circular in cross section and they construct their

burrows by compression of the sediment with their bodies (Bowen and Hembree, 2014). The burrow walls and ceilings are typically smooth as a result of this burrowing technique, but because of absence of a silk lining the wall texture is controlled by the sediment.

6.2 Burrow Morphology and Behavior

The morphology of the burrows produced by *G. inermis* and *H. lenta* is related to the behaviors exhibited by these species. Most importantly, the locomotion styles employed by the spiders controlled how the spiders constructed their burrows and how they behaved inside of the finished burrows.

The average time to beginning burrow construction was five days. All burrows began as either a vertical shaft or subvertical shaft with one surface opening. Subsequent modifications to these architectures, such as second surface opening or a chamber, occurred only in experiments lasting 30 days. Both species climbed vertically inside of their burrows by bracing their legs against the sides. This behavior produces scratch marks in the silk linings and in finer-grained sediment. The spiders also walked along the bottoms of burrows with a subvertical shaft; however, a few legs were still braced against the burrow walls.

All seven burrow architectures were used for dwelling. During the experiments, *G. inermis* never left their burrows. *Gorgyrella inermis* individuals spent a majority of their time at the base of their burrows facing outward. *Gorgyrella* did have to turn around, however, because *G. inermis* eliminates waste outside of its burrow by positioning its abdomen outside of and away from the burrow entrance. The burrow

shafts produced by *G. inermis* were not wide enough to allow individuals to turn around inside of the burrows. Most individuals were, therefore, forced to climb to the top of the burrow and maneuver their bodies while straddling the burrow entrance directly underneath the trapdoor. Those that constructed chambers utilized them to turn around in and spent less time exposed at the burrow entrance. *Hogna lenta* individuals left their burrows to hunt and obtain water. These excursions occurred mainly during dark hours, and the spiders utilized the entire surface area inside of the terrarium. The burrow shafts produced by *H. lenta* were larger than their bodies and enabled individuals to turn around inside of their burrows. *Hogna lenta* individuals with egg sacs were as mobile as those without.

The morphology of *G. inermis* burrows enables this species to ambush prey from the entrance of its burrow. Spiders waited near the top of the burrow, hidden underneath the trapdoor, and used the posterior four legs to brace against the shaft walls. Two legs held onto the rim of the burrow and the two anterior legs and pedipalps were used to grab prey that came near the burrow entrance. The spider grabbed the prey and quickly pulled it into the burrow. The spider then moved to the base of the burrow to consume its prey. Individuals that did not produce burrows were still able to catch prey, but they were not as successful as evidenced by abdomens that were smaller and more desiccated compared to those living in burrows. Prey was observed escaping these individuals, whereas no prey was ever seen escaping from a burrow. The burrow architectures produced by *H. lenta* did not assist in obtaining prey. *Hogna lenta* is an active hunter that searches for prey animals near its burrow; however, one individual was observed ambushing its prey

from its burrow entrance. Most spiders consumed their prey outside of their burrows, but some *H. lenta* individuals brought their prey into the burrows.

In addition to dwelling, two *H. lenta* individuals (FWS2 and FWS5) used their burrow for brooding. These individuals laid eggs multiple times during this study. It is assumed the individuals were impregnated before arrival as the spiders were packaged separately for delivery and were kept isolated during the entire experiment. This species is not known to reproduce parthenogenetically, although some spiders do employ this reproductive strategy (e.g., Edwards et al., 2003; Korenko et al. 2009). Both spiders produced vertical shafts in less dense sediment and subvertical shafts in the densest sediment. The quantitative properties of these burrows were statistically similar those produced by the other *H. lenta* individuals that did not lay eggs (Table 12). One individual was allowed to keep its egg sac until the young hatched (60 days). This brood burrow had no unique qualitative features and its measurements were statistically similar to other *H. lenta* vertical shafts.

Table 11: Mann-Whitney and Kolmogorov-Smirnov test results (p values) between burrows produced by *H. lenta* individuals with a brood and those without a brood. No results indicated significant differences ($p < 0.05$).

Comparison between brood burrows and broodless burrows produce by <i>H. lenta</i>										
Architecture	Test	Depth	Total Length	Avg Width	Avg Height	WH Ratio	Avg Circ	Avg Slope	Complexity	Tortuosity
Vertical Shaft	MW	0.0519	0.05019	0.8961	0.3608	0.8961	0.8961	0.3865	1	0.8724
	KS	0.02626	0.02626	0.9208	0.1747	0.6509	0.9208	0.3658	0.3197	0.6509
Subvertical Shaft	MW	0.3286	0.3329	0.8465	0.8465	0.8465	0.8465	0.8407	1	0.8465
	KS	0.4739	0.4739	0.7052	0.7052	0.9093	0.7052	0.9093	0.3197	0.7052

6.3 Burrow Morphology and Sediment Conditions

Observations of the burrows produced by *G. inermis* and *H. lenta* at the conclusion of each experiment indicate that differences in sediment conditions, both sediment density and moisture, influenced the diversity of architectures produced and the possibility of burrow construction. Each species of spider was allowed to burrow in sediment of moderate density and moderate moisture. Experiments in these sediments produced the most diverse set of architectures (Table 1). Three architectures, subvertical shafts with terminal chambers, isolated chambers, and Y-shaped burrows, were only produced in this sediment type.

Increased sediment density led to fewer burrow architectures. When this occurred, both *G. inermis* and *H. lenta* produced only two burrow architecture (Table 1). Only adult *G. inermis* individuals produced chambers under these conditions; juvenile *G. inermis* individuals and *H. lenta* individuals produced only vertical and subvertical shafts. Denser sediments limited the ability of the spiders to manipulate the sediment and construct complex burrow architectures. Comparison of adult *G. inermis* burrows to those of juvenile *G. inermis* and *H. lenta* suggests that smaller spiders were not physically capable of constructing more than simple burrows. One adult *G. inermis* individual did not construct a burrow in this sediment and instead produced a silk mat. The stability of this sediment was also shown by the lack of silk lining applied to the burrow walls.

Burrowing animals may apply linings to the sides of the burrows to increase structural integrity (Bromley, 1996). The spiders did not expend energy shoring-up burrows that did not need the addition of a silk lining. Although architectural diversity was decreased,

quantitative features of these burrows were not statistically different than those produced in more ideal sediments.

Decreasing sediment moisture limited the burrow architectures produced and prevented the production of open burrows. Both *G. inermis* and *H. lenta* produced simple burrows, although one *G. inermis* individual did produce a J-shaped burrow, the only experiment in which this architecture was produced. Three individuals, one *G. inermis* and two *H. lenta*, did not produce open burrows at all. Neither the thickness of the silk linings nor the surface area of the burrow chamber covered in silk increased when compared to the burrows produced in sediments with moderate moisture.

Increasing sediment moisture also limited the number of burrow architectures produced and prevented the production of open burrows. Two of the four individuals of *G. inermis* and two of the four individuals of *H. lenta* did not construct burrows in these conditions. Those burrows that were produced were only simple vertical shafts. As observed before, the stability of the sediment was shown by the lack of silk lining applied to the burrow walls. Again, although architectural diversity was decreased, quantitative features of these burrows were not statistically different than those produced in more ideal sediments (Table 1).

These observations may be useful for interpreting soil conditions in the fossil record. Spiders had difficulty burrowing in sediments that were too dense, too dry, or too moist. These conditions can be interpreted by a decrease in burrow complexity and diversity. The identification of a silk lining may be the best indicator of environmental conditions. The production of silk has physiological cost (Breed et al., 1964; Prestwich,

1976) and spiders do not use silk when it is unnecessary. Gauging the amount of silk present when a spider burrow is identified is a reliable indicator of sediment stability, although it would be difficult to distinguish if the stability is controlled by composition or moisture content by burrow analysis alone.

CHAPTER 7: SIGNIFICANCE

7.1 Identification of Spider Burrows in the Fossil Record

Trace fossils occur in many kinds of environments, but the tracemakers may be difficult to identify. Interpretations of tracemakers may be hampered by preconceived notions or lack of information of the structures possible for a particular group of animals. Studies of live animals in controlled settings provide a framework for interpretation and identification of tracemaker. Spiders have a fossil record that extends to the Carboniferous, but body fossils are scarce until the late Mesozoic (Penney et al., 2012). Early spiders are assumed to have lived in burrows because the basal extant spiders live in burrows. Identification of spider burrows is accomplished through the recognition of unique characteristics, or ichnotaxobases, present in those burrows made by living spiders. Experimental design can aid in interpreting behaviors associated with structures and how these behaviors change in different environmental conditions. Ichnotaxobases for the burrows produced by burrowing spiders include:

Architecture: Spider burrows can include vertical shafts, vertical shafts with terminal chambers, subvertical shafts, subvertical shafts with terminal chambers, J-shaped burrows, Y-shaped burrows, and isolated chambers. These burrows include one to two surface openings, shafts, tunnels, and chambers.

Overall shape: Shafts and tunnels are elliptical in cross section. There is no clear floor or roof to these burrows. Shaft and tunnel width is nearly the same as shaft and tunnel height. Shafts and tunnels tend to be straight with tortuosity values nearly equal to 1.0. Chambers may occur at the base of a shaft or off to the side along the horizontal.

Chambers have the same cross-sectional shape and may be up to two times the size of shafts and tunnels. Branching occurs rarely. When present each branch has a single surface opening and leads to a primary shaft.

Orientation: Nearly all spider burrows are vertical (80° – 90°) or subvertical (60° – 75°) just below the burrow entrance.

Internal Structure: Burrows made by spiders possess no distinguishable lining made by manipulation of sediment. A lining of silk may be present. Fill may be passive or active, but spiders seal their burrows with trapdoors made of silk and sediment to prevent passive fill. Burrows lacking a thick silk lining were more likely to be filled passively by gravitational collapse of the sediment.

Surficial Features: Burrowing spiders line their burrows with silk. The silk is a boundary between the spider and the sediment. The amount of silk deposited differs between species and between environmental conditions. Burrows produced in sediment that is unstable have thick silk linings whereas those produced in stable sediment have thin silk linings or no silk linings. Scratch marks are preserved in silk linings running parallel to the burrow and occur along the entire length of the burrow that was encased in silk. Those burrows with little to no silk linings have irregular burrow walls heavily influenced by the sediment composition and no surficial features.

Differences were observed in these features between the two genera. The burrows of *H. lenta* tended to include subvertical shafts with little silk lining. Their burrows also included small turrets, a feature never produced by *G. inermis*. The burrows of *G. inermis* tended to include vertical shafts with thick silk linings. This spider produced more

chambers than did *H. lenta*. Despite these differences, these ichnotaxobases are the same for both spiders.

7.2 Paleontological and Paleoecological Significance

In some circumstances, trace fossils may be more beneficial to paleoenvironmental interpretation than body fossils. Trace fossils provide information about the sediment in which they are produced. They are often preserved in the sediment in which they were formed and so are able to provide reliable indicators of the paleoenvironmental conditions. This differs from body fossils, which may be carried away from the environment in which the organism lived. This transport may also disarticulate the organism's body, limiting the details obtainable about the organism's behaviors. Trace fossils also provide records of organisms with low preservation potential, namely those organisms lacking hard body parts. This is important for paleoecological interpretations as soft-bodied organisms comprise most of the biomass in any ecosystem. In addition, the diversity of trace fossils may be used as a proxy for biological diversity.

With a fossil record extending back to the Carboniferous, spider trace fossils should be commonly identified in the fossil record. Indeed, some terrestrial specimens of *Skolithos* and *Macanopsis* have been attributed to spiders (Ratcliff and Fagerstrom, 1980; Brown and Kraus, 1983; Hasiotis, 2002; and Retallack et al., 2003). A wide variety of tracemakers, however, mostly arthropods, could make burrows with similar architectures, and until this study, specific characteristics for a spider tracemaker had not yet been identified. The identification of spider burrows would allow for better

interpretation of this group's evolution as well as provide a better understanding of soil ecosystems through time. Body fossils of spiders are rare in the Paleozoic, and younger fossils are often preserved in amber (Shear, 1994). Identification of the habitats of these spiders and their role in ecosystems are difficult to assess as the body fossils are not preserved in environments in which the individuals lived.

The identification of spider burrows may help reveal when spiders began to build webs. Although fossil species interpreted to be web builders appear during the Jurassic (Penney and Selden, 2007), the earliest spider webs are found in amber from the Early Cretaceous (Brasier et al., 2009). It would be expected that as spiders begin to build webs, the number of spider burrows should decrease in the fossil record. A decrease in the number of fossil spider burrows coupled with the presence of web-building species would help narrow down when spiders began constructing webs.

Spiders are major predators of invertebrates and this order consists entirely of carnivores. The density and diversity of spiders would indicate the health of an ecosystem as they require enough animals to prey upon. Spiders are also prey items for other animals, so the presence of larger predators may be inferred as well. The number of spider individuals could be assessed by counting the number of spider burrows present in modern habitats. The density of spider abundance varies depends on species and habitat. Bradley (1996) found that the density of Australian trapdoor spiders is on average 391/ha, whereas Coyle and Incenogle (1994) found that density of a trapdoor spider in California could be up to 300 individuals per 3 m². Species of both mygalomorphs and aranemomorphs remain faithful to their burrows for long periods of time (e.g. Suttle,

2003; Hamilton et al., 2012). Burrow fidelity was also observed in this study. Individuals of *G. inermis* constructed only one burrow, whereas some individuals of *H. lenta* abandoned a burrow to construct a new one. The new burrow became the primary dwelling and the abandoned burrow became filled with sediment or collapsed. The number of spider burrows in an area can, therefore, be used to approximate the number of individuals.

7.3 Importance of Spiders in Soil Formation

The burrowing activity of spiders contributes to soil formation. In this study, burrow depth for *G. inermis* was restricted to 2.1–16.6 cm, whereas the burrows for *H. lenta* were restricted to 3.2–8.7 cm below the sediment surface. These depths are associated with the A and upper B soil horizons (0–20 cm). In nature, the burrows of *H. lenta* have been reported to be 2 m deep during the winter (Eisman et al., 2010). A major contributor to soil formation is the mixing of sediment by transporting material from the subsurface to the surface (Lavelle et al., 2006). Animals do this when excavating burrows, but this technique is not the only way in which a burrow can be produced (Bromley, 1996). Animals can also compact sediment along the sides of a burrow as they push their way into the substrate. In this study, both species of spiders mainly constructed burrows in this way. Only adult *G. inermis* individuals were observed moving sediment to the surface, but not all adults engaged in this behavior. The compaction of soil, however, changes the porosity and permeability of the sediment along the burrow walls and disrupts or destroys primary sediment structures.

Open burrows provide a direct conduit for water to penetrate deeper into sediment. The presence of silken trapdoors makes this contribution unlikely while a spider inhabits a burrow. The spiders maintain burrow integrity and repair trapdoors when these are torn or removed; however, a vacated burrow will no longer be maintained, and will then become open to the elements. Open burrows that are not sealed by a trapdoor also provide a conduit for gas exchange, which occurs continuously. Even burrows that have been filled with sediment will allow water and gases to move through the infill since the material will be less dense than the burrows walls and the surrounding matrix.

The spiders in this study were found to not contribute greatly to the introduction of organic matter into the sediment. Leftover material from prey animals was ejected from or carried out of the burrows by the spiders. Spiders that molted inside of a burrow removed the molt in a similar manner. As described earlier, *G. inermis* excretes waste outside of its burrow, and it is assumed that *H. lenta* excretes while moving outside of the burrow. The silk linings are the greatest contribution of organic matter. Spider silk is composed of mainly of proteins called spidroin (van Beek et al., 2002). Burrows produced in holding tanks prior to the beginning of the experiments had very thick silk linings. These burrows had been occupied for months to years. When a burrow is left vacant, the silk will begin to decompose providing nutrients for microbes and fungi.

Although quantitative properties did not significantly change with changes in sediment properties, the diversity of burrow architectures would enable for better interpretations of original soil composition and moisture content. The relationship

between the amount of silk used to line a burrow and the cohesiveness of the sediment is an effective means of interpreting these sediment conditions. Modern burrowing spiders live in a variety of habitats except for the most extreme polar regions. Fossil spider burrows could be present in any soil type from Entisols to Oxisols, but it is unlikely that these burrows would be found in Gelisols or sediments in cold regions. Fossil spider burrows would be associated with a number of ichnofossils including those produced by other arachnids (scorpions, whip scorpions), other soil-dwelling arthropods (millipedes, centipedes, insects), and possibly vertebrates (amphibians, reptiles, mammals), but root traces would be most common. The ability of burrowing spiders to live in many environments, including deserts with minimal vegetation, however, means that the presence of these any of these other traces fossils are not necessary to identify a spider burrow.

7.4 Use of Cluster Analyses

Cluster analyses may be used to predict the identity of a tracemaker when quantitative data are collected. A cluster analysis of six arthropod species reveals two large clusters: one composed of small arachnids and millipedes, the other composed of large arachnids and some millipedes. This division was because of multiple differences in burrow properties (Table 6F). In addition, burrows produced by the same species cluster together. In this way, the Bray-Curtis analysis isolated species by the morphology of their burrows. Therefore, if burrows produced by an unknown tracemaker are highly similar to burrows within a specific cluster, then the tracemaker is likely to either be related to those species or to engage in very similar behaviors (Table 6F). Qualitative

characteristics such as internal or surficial features may then be used to further distinguish the phylogenetic affinity of the tracemaker.

Cluster analyses may also be used to assess the quantitative similarity of an ichnogenus. When compared to the burrows of *G. inermis* and *H. lenta*, *Skolithos* specimens grouped within Cluster A, but five specimens were more similar to each other than the burrows produced by *G. inermis* and *H. lenta*. Thus, even though the basic architectures are the same, *Skolithos* are unique enough to be sorted by the Bray-Curtis analysis. This high degree of similarity between the specimens supports the placement of the specimens in the same ichnogenus. When *Macanopsis* specimens were compared to the spiders, however, the cluster analysis placed MAC2 within Cluster A, and MAC1 within Cluster B, while MAC3 was not similar to either of the other *Macanopsis* specimens or any of the spider burrows. Qualitatively, MAC1 and MAC2 are very different than MAC3 (Figure 5), and the cluster analysis confirms that they are also quantitatively different. This suggests that MAC3 may belong to a different ichnogenus than MAC1 and MAC2. This also suggests that the ichnotaxobases for *Macanopsis* are not defined in a way that separate fossil burrows that are qualitatively or quantitatively different.

CHAPTER 8: CONCLUSIONS

Although the exact identity of a tracemaker typically cannot be known, potential tracemakers may be predicted because of burrow morphology and knowledge of the fauna extant at the time the trace was produced. Neoichological studies provide a way to predict tracemakers by connecting burrow morphology to tracemaker. Studies on the neoichnology of continental species are sparse, and more work is needed to better interpret traces found in those strata interpreted as terrestrial environments. Trace fossils may also be used to aid environmental interpretations. The morphology of biogenic structures is often controlled by the sediment conditions in which the structure was produced. The relationship between burrow morphology and environmental conditions, however, can be better understood in controlled settings with live animals.

Specimens of two burrowing spiders, *G. inermis* and *H. lenta*, produced seven different burrow architectures including vertical shafts, vertical shafts with terminal chambers, subvertical shafts, subvertical shafts with terminal chambers, J-shaped burrows, Y-shaped burrows, and isolated chambers. The production of these architectures was dependent on size of the individual and the sediment conditions in which the burrow was produced. Adult individuals of *G. inermis* produced the greatest diversity of burrow architectures whereas juvenile individuals of *G. inermis* and adult individuals of *H. lenta* produced the lowest diversity. Despite the diversity of architectures, all burrows produced by the spiders include one to two surface openings, a nearly circular cross section, and surficial features influenced by a silk lining. The presence of a silk lining is a definitive characteristic of a spider tracemaker. Increasing sediment density did not

produce statistical differences in burrow measurements, but the diversity of burrow architecture was decreased and some individuals were unable to construct burrows. Sediment with low and high moisture also limited the architectural diversity and prevented some individuals from constructing burrows.

The burrows of *G. inermis* and *H. lenta* are highly similar. Although these species are not closely related, their similar life habits and body morphology control the function and morphology of their burrows. This contrasts to the burrows produced by the larger spider, *A. chalcodes*, which are dissimilar to those produced by *G. inermis* and *H. lenta*. The burrows of other arachnids, the scorpion *H. arizonensis* and the whip scorpion *M. giganteus*, are dissimilar when the burrow architecture is different from those produced by *G. inermis* and *H. lenta*, but the same architectures are highly similar. This result also occurs when the burrows of the millipede *N. americanus* are compared to the burrows produced by *G. inermis* and *H. lenta*. Qualitative data, however, can be used to differentiate those similar burrows produced by different tracemakers. The result of this study is a means to better identify tracemakers when only a burrow is found. The animals used for these comparisons represent taxa that are common and occur in a variety of habitats. By identifying possible burrow architectures and characteristics unique to the burrows of each species, the interpretations supporting the identification of a tracemaker are improved.

The comparison of the spider burrows to specimens of *Skolithos* and *Macanopsis* may be important for the identification of a tracemaker and the associated behaviors of these trace fossils. The spiders produced *Skolithos*-like burrows and *Macanopsis*-like

burrows that are statistically similar to respective specimens of the ichnogenera *Skolithos* and *Macanopsis*. Although the specimens of *Skolithos* used in this study occur in marine strata, the high similarity of *Skolithos* to the spider burrows should also apply to specimens found in continental settings. Specimens of *Skolithos* and *Macanopsis* found in continental strata could be further analyzed for bioglyphs associated with spiders, such as scratch marks and silk linings.

The proper identification of burrows produced in terrestrial settings requires a more complete understanding of the organisms that live in soil environments. Fossil burrows with the size and complexity of the burrows produced by the burrowing spiders could be interpreted as being produced by several soil organisms. The morphology and surficial features of burrows produced by spiders are directly related to the morphology of the organisms themselves. Recognition of these features will enable better interpretations of a tracemaker when simple burrows are found in paleosols and other terrestrial settings. Accurately identifying spider burrows and burrows produced by other arthropods such as scorpions, whip scorpions, and millipedes will aid in revealing the biodiversity of terrestrial ecosystems in the fossil record.

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APPENDICES

Appendix A: Quantitative data for the burrows produced by *Aphonopelma chalcodes*.

All measurements in cm. SR = subvertical ramp.

Architecture	A1	A2
	SR	SR
Surface Openings	1	1
Maximum depth	9.5	3.1
Total Length	17.9	6.1
Maximum width	7.6	3.7
Minimum width	3.6	2.9
Average width	6.6	3.4
Maximum height	6.7	2.4
Minimum height	2.5	1.2
Average height	5.1	1.9
Average W/H ratio	0.77	0.55
Maximum circumference	22.2	10.9
Minimum circumference	11.1	7.1
Average circumference	19.14	9.46
Maximum slope	55°	25°
Minimum slope	0°	25°
Average slope	27.5°	25°
Branching angles	NA	NA
Complexity	3	2
Tortuosity	0.52	0.98

Appendix C: Quantitative data for the burrows produced by *Hadrurus arizonensis*

All measurements in cm. SR = subvertical ramp, HB = helical burrow, MW = mazework, UB = U-shaped burrow.

	DHS1	DHS2	DHS3	DHS4	DHS5	DHS6	DHS7	DHS8	DHS9	DHS10	DHS11	DHS12	DHS13	DHS14	DHS15	DHS16	DHS17
Architecture	SR	SR	HB	MW	MW	SR	HB	MW	UB	SR	SR	SR	SR	SR	HB	SR	SR
Surface Openings	1	1	1	5	4	1	1	3	2	1	1	1	1	1	1	1	1
Maximum depth	3.9	2.8	7.2	7.4	6.7	4.3	4.6	8.4	8	3	4.2	3.4	4	4.2	16	5.3	6.8
Total Length	11	9	27	57	46	7	13	31	30	16	11	19	19	23	76	37	26
Maximum width	4.3	6	7.7	4.6	6.4	5.9	3.3	7.2	4.2	5.2	4.4	6.5	4.9	6.7	5.3	6.2	5.4
Minimum width	3.2	3	2.8	1.9	2.6	2.9	2.7	2.9	3	3.8	4.1	4.2	3.1	4.1	3.7	3.1	4
Average width	3.9	4.8	4.5	3.6	4.2	4.2	3.1	4.7	3.6	4.4	4.3	5.2	4.1	4.9	4.5	4.8	4.9
Maximum height	2.8	1.9	3.2	2.3	3.1	1.6	1.4	2.6	2.5	2.1	2	3.3	2.6	2.3	3.3	2.8	2.2
Minimum height	1	1.1	0.8	0.8	1.4	1	0.6	1.4	1.5	1.3	0.9	1.9	1.8	1.4	1.6	1.7	1.5
Average height	1.9	1.6	2	1.8	1.9	1.4	1	1.9	2.1	1.8	1.6	2.2	2.2	1.7	2.3	2.4	1.8
Average W/H ratio	2.1	3	2.3	2	2.2	3	3.1	2.5	1.7	2.4	2.7	2.4	1.9	2.9	2	2	2.7
Maximum circumference	12.1	14	18	14.5	17	11.5	10.5	16	11.5	13.6	11.2	16.5	13	15.5	14	15	13
Minimum circumference	10	11.2	6.5	9.5	10.5	6	8.5	9.5	10.5	9.7	6.8	11.5	9.9	10.5	10	11	11.5
Average circumference	11.2	12.7	14.5	13.1	12.2	9.4	9	12.3	11.3	11.9	10	13.9	11.5	12.5	17.3	12.9	12.6
Maximum slope	40°	10°	30°	50°	90°	30°	40°	50°	90°	10°	40°	10°	20°	20°	30°	20°	20°
Minimum slope	0°	0°	0°	0°	0°	0°	0°	0°	0°	0°	0°	0°	0°	0°	0°	0°	0°
Average slope	20°	5°	15°	27°	37°	15°	20°	30°	45°	5°	20°	5°	10°	10°	13°	8°	8°
Branching angles	NA	NA	NA	75°	75°	NA	NA	70°	NA	NA	NA	NA	NA	NA	NA	65°	NA
Complexity	3	3	3	9	9	3	3	7	4	3	3	3	3	3	3	3	3
Tortuosity	1.1	1.1	9	1.4	1.8	1.1	3.3	1.1	1.3	1.3	1.5	1.1	1.2	1.4	3.3	1.2	1.2

Appendix E: Quantitative data for the burrows produced by *Mastigoproctus giganteus*

All measurements in cm. SR = subvertical ramp, MW = mazework, UB = U-shaped burrow, VS = vertical shaft.

	WS1	WS2	WS3	WS4	WS5	WS6	WS7	WS8	WS9	WS10	WS11	WS12	WS13	WS14	WS15	WS27	WS28	WS32
Architecture	UB	MW	JS	SR	VS	UB	JS	UB	MW	JS	SR	JS	SR	VS	VS	SR	VS	VS
Surface Openings	2	2	1	1	1	2	1	2	4	1	1	1	1	1	1	1	1	1
Maximum depth	7.1	10.6	11	5.6	10.1	4.9	10.7	5.7	12.4	12.5	6.6	7.7	6.1	3.4	8.1	3.3	4.9	5.8
Total Length	29	39.5	18.5	12.5	10.1	16	16	21	66	26.5	8	17.5	8.5	3.8	10.2	4	5.7	6
Maximum width	7.6	8.1	4.3	3.9	6.3	3	5	4	6.2	6.6	3.1	6.4	3.2	2.2	4.2	2.6	3.3	3.1
Minimum width	4.5	3.4	2.6	3.4	5.3	2.2	2.4	2.9	3.7	2.6	2.8	2.7	2.8	1.9	2.7	1.6	2.2	2.5
Average width	5.7	5.4	3.6	3.7	5.8	2.4	3.4	3.4	4.6	4.1	3	4.7	3.1	2.1	3.4	2.1	2.7	2.8
Maximum height	3.2	4.3	2.8	2.1	2.9	1.7	2.3	2	2	2.4	2.9	2.5	2.1	1.1	4.4	1.9	1.9	1.3
Minimum height	2.5	1.5	2	1.7	1.9	1.3	1.7	1.5	1.7	1.2	2.2	1.9	1.8	0.9	1.5	1.1	1.6	1.2
Average height	2.8	2.9	2.3	1.9	2.2	1.6	2	1.7	1.9	1.9	2.6	2.2	1.9	1	2.6	1.5	1.7	1.3
Average W/H ratio	2	1.9	1.6	1.9	2	1.5	1.7	2	2.4	2.2	1.2	2.1	1.6	2.1	1.3	1.4	1.6	2.2
Maximum circumference	19	26.5	12	11	17	9.5	12.5	11	14.5	16	12	17	10.5	7.5	14.5	8	9.5	8
Minimum circumference	13.5	10	9.5	10	15.5	7.5	8	9.5	9	7.5	11.5	10.5	9	7	8	6.6	7.5	7.5
Average circumference	15.9	17	10.9	10.5	16.3	8.3	9.9	10.5	11.3	10.8	11.8	13.9	10	7.3	11	7.3	8.3	7.7
Maximum slope	70°	90°	80°	30°	90°	50°	70	50°	80°	90°	50°	90°	50°	90°	90°	60°	90°	85°
Minimum slope	0°	0°	40°	10°	90°	0°	0°	0°	0°	40°	50°	0°	50°	70	80°	60°	70°	80°
Average slope	47°	35°	60°	20°	90°	33°	40°	30°	45°	65°	50°	45	50°	80	85°	60°	80°	83°
Branching angles	NA	90°	NA	NA	NA	NA	NA	NA	80°	NA	NA	90°	NA	NA	NA	NA	NA	NA
Complexity	4	7	2	2	2	3	3	3	10	3	2	4	2	2	2	2	2	2
Tortuosity	2.4	1.7	1.2	1.3	1	1.6	1.3	1.4	1.4	1.3	1.1	1.7	1	1	1.2	1	1	1

Appendix F: Bray-Curtis result matrix for *M. giganteus*

This matrix displays the comparison of burrows produced by *G. inermis*, *H. lenta*, and *M. giganteus*.

Appendix G: Quantitative data for the burrows produced by *Narceus americanus*

All measurements in cm unless otherwise noted. SV = subvertical burrow, VS = vertical shaft, HB = helical burrow, OS = O-shaped burrow.

	NA32	NA23	NA25A	NA21A	NA21B	NA28	NA29C	NA30A	NA30C	NA33A	NA33C	NA29B	NA21F	NA29A	NA26B
Architecture	SV	SV	SV	SV	SV	VS	VS	VS	VS	VS	HB	HB	HB	OS	OS
Surface Openings	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Maximum depth	4.1	6.7	3	1.9	4	2.4	1.9	2.5	2.3	3.1	2.95	3.4	2.9	3.4	6.9
Total Length	4.3	8.2	9.4	2.34	4.3	3	1.9	2.5	2.6	3.1	6.8	10.7	10	10.6	12.5
Maximum width (mm)	0.93	1.69	1.17	1.30	1.45	1.40	1.17	0.93	1.04	1.20	1.18	1.06	1.65	1.29	1.80
Minimum width (mm)	0.85	0.8	0.78	1.05	1.1	1.4	1.17	0.7	0.93	1.04	0.7	0.74	0.68	0.83	0.74
Average width (mm)	0.88	1.04	1.02	1.18	1.24	1.40	1.17	0.82	0.99	1.12	0.96	0.84	1.16	1.05	1.09
Maximum height (mm)	0.98	0.95	1.01	1.25	1.23	1.38	0.9	0.88	0.93	1.47	1.17	0.92	1.15	0.96	1.13
Minimum height (mm)	0.86	0.73	0.57	1.18	1.05	0.95	0.9	0.77	0.8	1.11	0.85	0.61	0.8	0.6	0.67
Average height (mm)	0.92	0.83	0.79	1.22	1.14	1.17	0.90	0.83	0.87	1.29	0.98	0.78	0.97	0.82	0.93
Average W/H ratio	0.96	1.26	1.31	0.96	1.08	1.24	1.30	0.98	1.14	0.89	0.98	1.10	1.21	1.29	1.17
Maximum circumference	3	4.1	3.7	4.2	4.3	5	3.5	2.8	3.1	4.3	4.3	3	4.3	3.5	4.8
Minimum circumference	2.7	2.7	2.5	3.5	3.3	3.7	3.5	2.4	2.8	3.5	2.3	2.5	2.3	2.7	2.3
Average circumference	2.8	3.1	3.1	3.9	3.7	4.4	3.5	2.6	3.0	3.9	3.1	2.7	3.4	3.1	3.4
Maximum slope	70°	65°	45°	33°	73°	85°	80°	90°	80°	90°	80°	60°	55°	60°	60°
Minimum slope	70°	50°	25°	33°	70°	85°	80°	90°	80°	90°	50°	60°	0°	15°	60°
Average slope	70°	38.3°	35°	33°	71.5°	85°	80°	90°	80°	90°	65°	75°	25°	37.5°	60°
Branching angles	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	90°	NA	NA	NA
Complexity	2	2	2	2	2	2	2	2	2	2	2	4	4	3	3
Tortuosity	1	1.2	1.7	1	1.1	1.3	1	1	1.1	1	2.3	1.5	1.2	43	39

Appendix I: Quantitative data for specimens of *Skolithos*

All measurements in cm. All specimens are vertical shafts.

	SKO1	SKO2	SKO3	SKO4	SKO5	SKO6
Architecture	VS	VS	VS	VS	VS	VS
Surface Openings	1	1	1	1	1	1
Total Length	5.3	5.1	3.4	12.2	7.7	8.4
Maximum width	0.5	0.2	0.3	0.8	0.5	0.3
Minimum width	0.4	0.2	0.3	0.4	0.3	0.3
Average width	0.4	0.2	0.3	0.6	0.4	0.3
Maximum height	0.5	0.2	0.3	0.8	0.5	0.3
Minimum height	0.4	0.2	0.3	0.4	0.3	0.3
Average height	0.4	0.2	0.3	0.6	0.4	0.3
Average W/H ratio	1	1	1	1	1	1
Maximum circumference	1.4	0.7	0.9	2.4	1.6	1.1
Minimum circumference	1.3	0.7	0.9	1.4	1.1	1.1
Average circumference	1.4	0.7	0.9	1.8	1.3	1.1
Maximum slope	90°	90°	87°	90°	80°	90°
Minimum slope	90°	90°	87°	90°	80°	90°
Average slope	90°	90°	87°	90°	80°	90°
Branching angles	NA	NA	NA	NA	NA	NA
Complexity	2	2	2	2	2	2
Tortuosity	1	1	1	1	1	1

Appendix K: Quantitative data for specimens of *Macanopsis*

All measurements in cm. All specimens are vertical shafts with terminal chambers.

Architecture	MAC1	MAC2	MAC3
	VC	VC	VC
Surface Openings	1	1	1
Total Length	1.7	4.6	21
Maximum width	0.8	1.2	3.5
Minimum width	0.3	1.0	0.8
Average width	0.6	1.1	2.3
Maximum height	0.8	1.2	3.5
Minimum height	0.3	1.0	0.8
Average height	0.6	1.1	2.3
Average W/H ratio	1	1	1
Maximum circumference	2.6	3.8	11.0
Minimum circumference	1.1	3.1	2.5
Average circumference	1.9	3.3	7.1
Maximum slope	70°	90°	85°
Minimum slope	70°	90°	0°
Average slope	70°	90°	42.5
Branching angles	NA	NA	NA
Complexity	3	3	3
Tortuosity	1.1	1	1.8



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