

# Chapter 11

## Large Complex Burrows of Terrestrial Invertebrates: Neoichnology of *Pandinus imperator* (Scorpiones: Scorpionidae)

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**Abstract** Scorpions have comprised a significant portion of the diversity of predatory arthropods since the Late Paleozoic. Many of these animals are active burrowers today and likely have a substantial, if yet unrecognized, trace fossil record. This project involved the study of the burrowing behavior and biogenic structures of the scorpion *Pandinus imperator* (Scorpiones: Scorpionidae). Individuals and groups

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of five animals were placed into sediment-filled terrariums for 30–50 days after which the open burrows were cast and described. Additional experiments were conducted in sediments with two different moisture contents to evaluate the response to this altered environmental condition. Specimens of *Pandinus imperator* excavated their burrows using the first three pairs of walking legs. The burrow morphologies produced consisted of subvertical ramps, helical burrows, and branching burrows. The burrow elements were elliptical in cross section (12 cm wide × 4 cm high) with concave floors and ceilings. Decreased sediment moisture reduced the complexity of the subsurface structures and reduced the likelihood of their preservation due to gravitational collapse. Burrows of *Pandinus imperator* were compared to those of the desert scorpion, *Hadrurus arizonensis*, using nonparametric statistics and found to be distinct. Data collected from these and similar neofossil studies can be applied directly to interpret trace fossil assemblages found in continental paleoenvironments.

**Keywords** Ichnofossils · Trace fossils · Bioturbation · Continental · Behavior · Paleocology

## 11.1 Introduction

The purpose of this chapter is to describe the burrowing behaviors and resulting biogenic structures of the scorpion *Pandinus imperator* (Arthropoda: Scorpiones), using basic experimental methods in a controlled laboratory setting. This chapter describes the architectural and surficial morphologies of 3D burrows produced by *Pandinus imperator* as well as surface features produced by their burrowing activity. The burrow morphologies are linked to scorpion morphology and behavior as well as environmental conditions such as sediment moisture content. The burrows of *Pandinus imperator* are then compared to burrows produced by another species of scorpion to determine if the different species produce significantly different burrows. The goal of this research is to aid in the recognition and interpretation of scorpion burrows in the fossil record for the purpose of improving our understanding of ancient terrestrial ecosystems as well as determining if specific aspects of paleoenvironments such as sediment moisture content can be evaluated using variations in burrow morphology. Finally, direct observations of the interaction of the scorpions with the sediment allow an understanding of the role of large predatory arthropods such as scorpions in the soil-forming process.

Scorpions are arthropod predators that inhabit an array of environments from rainforests to deserts around the world (Polis 1990). Scorpions (Order: Scorpiones) represent one of the oldest groups of fully terrestrial animals with a fossil record extending to the Silurian (444–416 Ma) (Petrunkevitch 1955; Kjellesvig-Waering 1986; Sissom 1990). There are currently 116 recognized fossil species of scorpions, with the majority from the Paleozoic (84), and lesser amounts from the Mesozoic (16) and Cenozoic (16) (Dunlop et al. 2013). Scorpions with morphological traits consistent

with inhabiting terrestrial environments are present by the early Devonian (410 Ma) (Kühl et al. 2012). By at least the Mississippian, scorpions were relatively common in terrestrial environments and known Carboniferous (~340 Ma) body fossils of terrestrial scorpions are morphologically similar to the extant superfamily Scorpionoidea (Petrunkevitch 1955; Kjellesvig-Waering 1986; Sissom 1990; Jeram 2001).

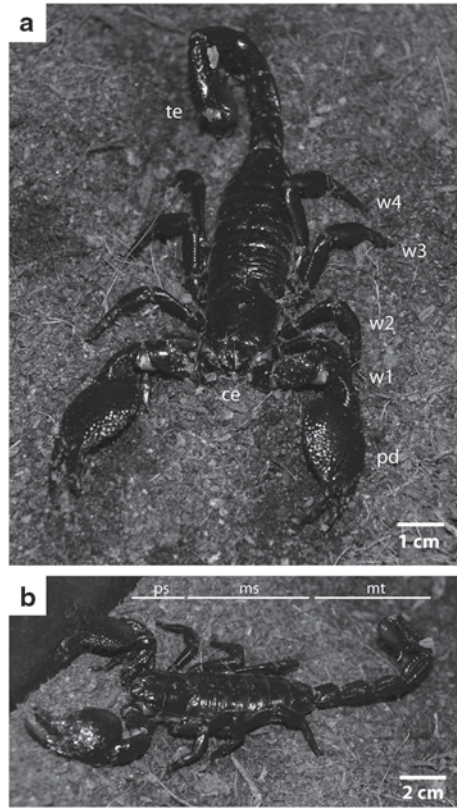
Trace fossils are easily preserved in many environments where body fossils are rare; therefore, the combination of both the body and trace fossil records are required to provide the best assessment of the evolutionary and biogeographic history of many taxonomic groups (Häntzschel 1975; Osgood 1975; Bromley 1996; Pemberton et al. 2001; Hasiotis 2003). Unfortunately, previously described trace fossils definitively attributed to scorpions have been limited to tracks and trails (Brady 1947; Picard 1977). This paucity of trace fossil data may simply be due to a failure of recognition, as a result of the lack of well-documented studies of the burrows produced by extant burrowing scorpions. Most descriptions of modern scorpion burrows provide only idealized diagrams or illustrations of burrow architectures (Williams 1966; Harrington 1978; Shorthouse and Marples 1980; Polis et al. 1986). Only recently have studies of scorpion burrows presented 3D burrow casts, documented the diversity of burrow morphologies produced by scorpions, described scorpion burrowing techniques, and investigated the impact of environmental conditions on burrow architecture (Hembree and Hasiotis 2006; Hembree et al. 2012).

While trace fossils are easily preserved, the interpretation of their tracemakers, the behaviors involved in their production, and the environments that influenced their production can be difficult. The study of the biogenic structures produced by modern burrowing organisms provides the data that make these interpretations possible. While experimental work with trace-making organisms has primarily involved nearshore, marine invertebrates; recently the volume of work on continental organisms has increased, especially studies involving soil invertebrates (Ahlbrandt et al. 1978; Ratcliffe and Fagerstrom 1980; Hasiotis and Mitchell 1993; O'Geen and Busacca 2001; Deocampo 2002; Tschinkel 2003; Gobetz 2005; Hembree and Hasiotis 2006, 2007; Lawfield and Pickerill 2006; Davis et al. 2007; Gingras et al. 2007; Rodríguez-Tovar 2007; Scott et al. 2007; Smith and Hasiotis 2008; Counts and Hasiotis 2009; Hembree 2009; Halfen and Hasiotis 2010; Hembree et al. 2012). In this research, the trace-making behaviors and the morphology of the resulting biogenic structures of modern continental burrowing organisms are studied in order to link specific morphologies to gross morphology, taxa, behaviors, and environmental conditions. These data are used to improve the interpretation of the paleobiological, paleoecological, and paleoenvironmental significance of continental trace fossils.

## 11.2 Ecology and Behavior of Burrowing Scorpions

Scorpions (Class: Arachnida) consist of almost 2,000 described extant species (Prendini 2011). Scorpions are terrestrial arthropods that have four pairs of walking legs, a pair of grasping claws or pedipalps, and a segmented tail ending in a

**Fig. 11.1** *Pandinus imperator*. **a** Adult specimen Pedipalp (*pd*), Chelicerae (*ce*), Telson (*te*), Walking legs (*w1–4*). **b** Side view Prosona (*ps*), Mesosoma (*ms*), Metasoma (*mt*)



venomous telson (Fig. 11.1a) (Hjelle 1990). The body of a scorpion is divided into three parts: (1) the prosoma consisting of the carapace, eyes, chelicerae, pedipalps, and four pairs of walking legs; (2) the mesosoma consisting of seven segments each covered by a sclerotized plate; and (3) the metasoma consisting of five segments and a sixth that bears the telson (Fig. 11.1b) (Hjelle 1990). Modern scorpions have similar body plans to Paleozoic and Mesozoic scorpions and there is little difference in external morphology among modern and fossil scorpions that live in different habitats (Hjelle 1990; Sissom 1990). Scorpions inhabit a wide range of environments and climates from arid deserts to tropical rainforests on all continents except for Antarctica (Sissom 1990). Most scorpions are nocturnal and at least opportunistically fossorial (Polis 1990). While most scorpions are solitary, some are communal and live in large groups, especially females engaged in the active care of their young (Polis and Sissom 1990). Scorpions are opportunistic predators of insects and other small arthropods as well as small reptiles and even mammals (McCormick and Polis 1990). In terms of density, diversity, and biomass, scorpions are one of the most important and successful predators in many modern habitats (Polis 1990; McCormick and Polis 1990).

Different scorpion species use a combination of chelae, chelicerae, legs, and even the tail in burrow construction (Williams 1966; Eastwood 1978; Harrington 1978; Koch 1978; Shorthouse and Marples 1980; Polis et al. 1986; Polis 1990; Rutin 1996; White 2001; Hembree et al. 2012). Burrows provide scorpions a refuge from predators and harmful environmental conditions such as extremes in temperature or humidity (Newlands 1969; Polis 1990). The burrow is an important part of almost all of the scorpion's life activities including birth, maternal care, molting, feeding, and in some species mating (Polis 1990). Burrowing scorpions spend the majority of their lives in their burrows, some only leaving for courtship, mating, and the dispersal of newborn (Williams 1966; Hadley and Williams 1968; Tourtlotte 1974; Koch 1978; Polis 1980; Bradley 1982; Shachak and Brand 1983; Warburg and Polis 1990). Burrowing scorpions that actively hunt on the surface still spend most of their time below the surface (Hadley and Williams 1968; Tourtlotte 1974; Polis 1980; Bradley 1982; Polis 1990). While on the surface, the majority of burrowing scorpions stay within 1 m of their burrow entrance (Polis 1990). These aspects of scorpion behavior highlight the importance of burrows to their ecology and evolutionary history.

*Pandinus imperator*, Koch 1842 (Scorpionidae), commonly referred to as the emperor scorpion, is among the largest extant species of scorpion reaching up to 20 cm in length and 65 g in mass (Sissom 1990). They are communal animals and can live in groups of up to 15–20 individuals (Mahsberg 1990, 2001). *Pandinus imperator* is a nocturnal hunter characterized by a pair of large pedipalps used in prey capture and defense (Casper 1985). Their large size allows them to feed on a variety of invertebrates including other scorpions as well as small vertebrates such as reptiles and rodents (McCormick and Polis 1990). *Pandinus imperator* inhabits forests and savannahs of West Africa with warm humid to subhumid climates and is known to be an obligate burrower (Polis 1990; Sissom 1990; Mahsberg 2001). Despite this knowledge, there has been very limited research on how these burrows are constructed or the details of their morphology.

### 11.3 Materials and Methods

Fifteen individuals of *Pandinus imperator* were acquired from a commercial source for use in this study. The scorpions were all mature adults (male and female) that averaged 140 mm in length (110–160 mm, SD = 14.1) from prosoma to metasoma and 25 mm in maximum width (30–40 mm, SD = 6.2) excluding the walking legs. The scorpions were allowed to acclimate in the laboratory for 1 month prior to the start of the experiments. During the acclimation period, specimens of *Pandinus imperator* were housed in groups of five individuals within 212-l terrariums filled with 20 cm of organic-rich soil and were handled as little as possible. A temperature range of 25–30 °C and humidity of 60–70% was maintained for the enclosures and a 12-h light–dark cycle was kept in the laboratory. The scorpions were fed live crickets placed in the tank once per week; the crickets were consumed gradually over the course of the week. The environmental parameters and feeding routine were maintained during the experiments as well.

**Table 11.1** Experimental parameters and resulting burrow morphologies. Sediments include organic (O), clay (C), and sand (S) components

Tank size	Specimens	Sediment composition	Sediment depth	Sediment density	Sediment moisture (%)	Burrow architecture
212	1	50-25-25% O-C-S	55	1.1–1.4	20	None
212	1	50-25-25% O-C-S	55	1.1–1.4	50	SR
212	1	50-25-25% O-C-S	55	1.1–1.4	50	SR, HB
212	5	50-25-25% O-C-S	55	1.1–1.4	20	None
212	5	50-25-25% O-C-S	55	1.1–1.4	50	SR
212	5	50-25-25% O-C-S	55	1.1–1.4	70	SR, HB, BB

Sediment density values are in  $\text{kgf/cm}^2$ , sediment depths are in cm, sediment moisture values are in percent total volume

SR subvertical ramp, HB helical burrow, BB branched burrow

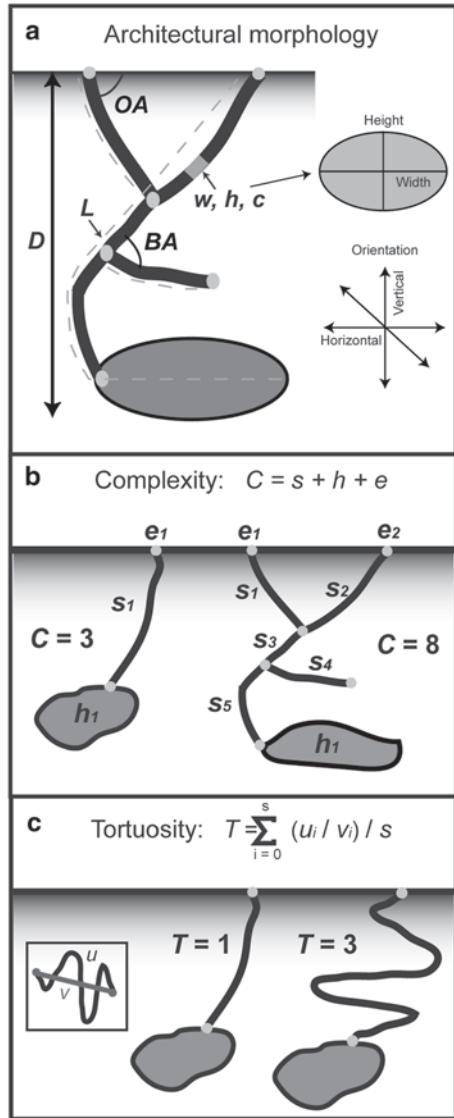
Six different experimental set ups (Table 11.1) were designed in order to: (1) observe the burrowing methods of *Pandinus imperator* individually and in groups, (2) document the surface features produced during the occupation of the test enclosures, (3) observe the behaviors associated with the burrows, and (4) document the basic burrow morphologies by producing 3D casts once the scorpions had been removed.

Single specimens and groups of five specimens were placed in sediment-filled 212 L (76 L  $\times$  46 W  $\times$  64 H cm) terrariums. Two sets of trials were run with different numbers of scorpions to determine the effects of group behavior and solitary behavior on burrow morphology. The terrariums were filled with 55 cm of sediment. The sediment thickness provided a deep substrate for burrowing but also enough open space beneath the terrarium cover ( $\sim$ 10 cm) to allow the placement of a water dish, rock, and other surface shelter as well as to prevent escape from the enclosure. The sediment used to fill the experimental enclosures had a moderate bulk density (1.1–1.4  $\text{kgf/cm}^2$ ) and was composed of 25% sand, 25% clay, and 50% organic matter. The density of the sediment was quantified using a Field Scout SC900 Soil Compaction Meter (Spectrum Technologies Inc.). The sediment composition was selected as the closest to the natural soil conditions inhabited by *Pandinus imperator*. The sediment components were thoroughly mixed to produce a homogenous composition and water was added to the mixture prior to adding it to the experimental enclosures. The sediment was mixed and compressed as it was added to the terrarium in order to improve homogeneity and increase density when needed. While sediment composition and density were maintained throughout the trials, the scorpions were exposed to variations in sediment moisture content. Soil moisture content was set to 20, 50, and 70%. These moisture values were obtained by adding predetermined quantities of water to the sediment mixture when the terrariums were filled. Sediment moisture was maintained during the trials by spraying the surface of the tank daily with 100, 200, and 300 mL of water to make up for evaporative water loss. The moisture content of the sediment was quantified using an Aquaterr EC-300 Multimeter. Measurements were taken vertically every 15 cm to ensure that the moisture content was homogenous.

Each experiment commenced with the placement of the scorpions into an enclosure. The scorpions were left in the enclosures for a period of 30–50 days before removing the specimens, when they were on or near the sediment surface. The final duration of any experiment depended upon the timing of the removal of the scorpions; first attempts to remove the scorpions began after 30 days. The scorpions were observed and digitally recorded as they burrowed. Observations made during initial burrowing included the time that elapsed before the scorpion began burrowing, the burrowing techniques used, and the time required for the animal to completely burrow into the sediment. Once the burrow was completed, daily observations were conducted to document the excavation of new burrows, destruction of old burrows, and the behaviors directly associated with the burrows. If no burrows were constructed by the end of an experimental period noted, the animal was removed, and any surface features were documented. After removing the scorpions, open burrows were filled with Drystone<sup>®</sup> plaster, excavated, and described.

The description of the 3D burrow casts included qualitative and quantitative aspects of their architectural and surficial morphology (Fig. 11.2). Architectural morphology consists of the burrow's general appearance, dimensions, cross-sectional shape of shafts and tunnels, orientation in the sediment, type and amount of branching, and degree of interconnectedness of different burrow elements. The surficial morphology includes structures (scratches, bumps, and linings) on or around the burrow walls produced during excavation and occupation of the burrow. For each burrow cast produced in these experiments, ten quantitative measurements of burrow morphology were recorded: (1) maximum depth ( $D$ ), (2) total length ( $L$ ), (3) tunnel or shaft width ( $w$ ), (4) tunnel or shaft height ( $h$ ), (5) ratio of cross-sectional width to height, (6) tunnel or shaft circumference ( $c$ ), (7) angle of shafts or tunnel with respect to the horizontal ( $OA$ ), (8) angle of branching ( $BA$ ) if present, (9) complexity, and (10) tortuosity (Fig. 11.2). Maximum depth of a burrow was measured from the highest surface opening to the base of the deepest tunnel. The total length of the burrow is the sum of the length of all of the shafts, tunnels, and chambers. The width, height, and circumference of the tunnels and shafts were measured every 5 cm along the length of the burrow. The cross-sectional width-to-height ratio was determined from the average widths and heights of the burrow's tunnels and shafts. The angle of branching was the acute angle between intersecting burrows produced away from the walls of the enclosures. Burrow complexity and tortuosity are independent of scale and are used to compare burrow systems produced by animals of different sizes (Meadows 1991). Burrow complexity ( $C$ ) is a function of: (1) the number of segments ( $s$ )—defined as non-branching lengths of a burrow, (2) the number of openings to the soil surface ( $e$ ), and (3) the number of chambers ( $h$ )—defined as areas with a greater cross-sectional area than the adjacent segments (Fig. 11.2b). These measurements define an index of complexity ( $C$ ) that is calculated by  $C = s + h + e$ , where  $C \geq 1$ . The tortuosity ( $T$ ) of a burrow system is a measure of the deviation of the tunnels from a straight line (Fig. 11.2c). The tortuosity of an open segment is calculated by dividing the total length of the segment ( $u$ ) by the straight-line distance between the ends of the segment ( $v$ ). The tortuosity index of a burrow system is determined by calculating the average tortuosity of all the burrow segments.

**Fig. 11.2** Burrow description models. **a** Architectural morphology was described by the angle of orientation ( $OA$ ), maximum depth ( $D$ ), tunnel, shaft, and chamber 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 ( $s$ ), chambers ( $h$ ), and surface openings ( $e$ ) within a single burrow system. **c** Tortuosity is the average sinuosity of all of the segments within 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))



These quantitative aspects of burrow morphology were used to determine the level of similarity between the different burrows produced by specimens of *Pandinus imperator*; their level of similarity to burrows produced by another species of scorpion (*Hadrurus arizonensis*) in separate laboratory experiments (Hembree et al. 2012), and the effect of sediment moisture on burrow morphology. To determine the relative level of similarity between burrows, ten quantitative aspects of burrow morphology were used to compare the different burrow casts using a Bray–Curtis similarity test, a nonparametric statistical analysis used to determine the level of



similarity between multiple samples with multiple quantitative properties (Hammer and Harper 2006). The Bray–Curtis similarity test was ideal for this study because it analyzes all aspects of the burrow’s morphology together, rather than simply comparing one feature such as diameter, length, or volume against another. This is important because the architecture of a burrow is a sum of many parts that should not be separated; while it is possible that the burrows of several different animals may have the same diameter, length, or volume, it is much less likely that all three are the same. The Bray–Curtis similarity test ranks the level of similarity from 0 to 1, 0 indicating completely different samples and 1 indicating identical samples. In this analysis, finer divisions were defined; values from 0.9–0.8 were considered to indicate a high degree of similarity, 0.7–0.6 a moderate degree of similarity, and values  $\leq 0.5$  dissimilarity. Mann–Whitney and Kolmogorov–Smirnov tests were used to determine the potential equality of the median and distribution of the individual properties of each burrow, respectively. These two tests were also used to compare the individual properties of the burrows of *Pandinus imperator* and *Hadrurus arizonensis*. A *p* value of  $< 0.05$  indicates a significant difference between two populations (Hammer and Harper 2006).

The properties of the burrows produced by *Pandinus imperator* in sediments with different moisture contents (20, 50, 70%) were compared using Spearman’s rank correlation, a nonparametric technique used to determine if two variables vary together (Hammer and Harper 2006). A correlation coefficient (*R*<sub>s</sub>) of 0.90 or higher suggests a high correlation (Hammer and Harper 2006). Mann–Whitney and Kolmogorov–Smirnov tests were then used to determine the potential equality of each of the properties of the burrows produced under the different sediment moisture conditions. All statistical analyses were performed with Palaeontological Statistics (PAST ver 2.16).

## 11.4 Results

Specimens of *Pandinus imperator* produced temporary to permanent open burrows with three different architectural morphologies in sediment with moderate to high sediment moisture content (Table 11.1). A total of 15 complete and well-preserved burrow casts were produced from the experimental trials (Table 11.2). Some experiments resulted in incomplete burrow casts as a result of subsurface gravitational collapse or burrows that were destroyed or filled in by the scorpions before they could be preserved. In all experiments, however, the architectural morphology of the burrows *in situ* was observed and recorded.

### 11.4.1 Behavior

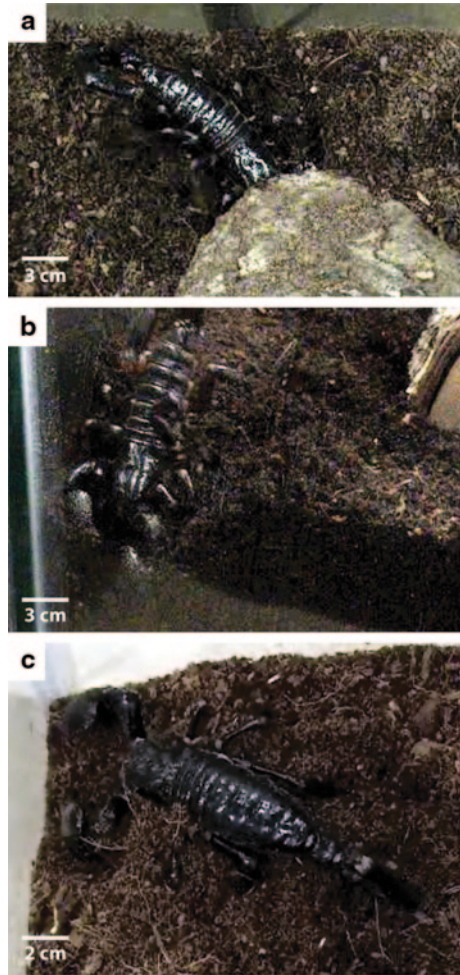
Specimens of *Pandinus imperator* started to burrow within 1–24 h of placement into the experimental enclosures. *Pandinus imperator* burrowed, by direct excavation,

**Table 11.2** Architectures, measurements, and experimental parameters of 15 representative, 3D burrow casts produced by *Pandinus imperator* (ES)

	ES1	ES4	ES6	ES7	ES9	ES11	ES13	ES14	ES15	ES2	ES3	ES5	ES12	ES8	ES10
Architecture	SR	SR	SR	SR	SR	SR	SR	SR	SR	HB	HB	HB	HB	BB	BB
Surface openings	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Maximum depth	6.5	7.5	13.0	5.0	13.0	6.0	7.0	13.0	11.0	12.5	16.0	14.0	15.0	30.0	13.0
Total length	28	12	27	18	34	29	19.5	25	14.5	34	34	29	32	80	28
Maximum width	7.6	6.8	6.2	6.3	11.6	7.1	6.3	7.1	6.4	12.0	11.3	6.4	8.3	10.6	9.9
Minimum width	6.0	4.4	4.1	3.6	3.9	3.8	4.8	5.3	4.5	7.4	5.5	4.3	4.2	4.3	3.9
Average width	6.7	6.0	4.9	5.6	8.2	6.3	5.8	6.9	5.3	9.6	8.7	5.5	6.5	6.8	6.8
Maximum height	4.4	2.9	4.8	3.6	4.2	3.8	2.7	5.8	5.4	7.1	5.4	3.4	5.9	4.4	4.9
Minimum height	2.9	1.9	2.3	2.2	1.9	1.7	1.8	4.0	1.9	3.0	3.9	2.1	2.0	2.6	2.4
Average height	3.7	2.5	3.0	2.8	2.9	2.9	2.5	5.0	3.5	3.9	4.5	2.7	4.5	3.3	3.6
Average W/H ratio	1.8	2.4	1.6	2.0	2.8	2.2	2.3	1.4	1.5	2.5	1.9	2.0	1.4	2.1	1.9
Maximum circumference	23.5	16.1	15.5	18.0	28.0	19.5	16.0	20.0	19.5	28.5	27.1	16.0	22.5	23.0	27.0
Minimum circumference	17.5	8.4	11.0	12.0	10.0	12.0	13.0	16.0	13.0	20.5	12.2	11.0	12.5	12.0	12.0
Average circumference	19.3	13.8	13.0	15.1	19.7	17.0	15.2	18.8	15.6	24.8	21.5	14.1	19.0	17.1	18.8
Maximum slope	20	40	50	20	50	20	20	35	25	30	30	50	30	40	50
Minimum slope	15	40	20	0	0	0	0	20	25	0	0	0	0	0	40
Average slope	17	40	40	13	19.3	6.7	13	27.5	25	14	24	21	18	19	47
Branching angles	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	90	90
Complexity	3	2	3	3	3	3	2	2	2	3	3	3	3	4	4
Tortuosity	1.0	1.0	1.0	1.1	1.1	1.0	1.0	1.1	1.0	1.7	1.1	1.1	1.5	1.0	1.0
Sediment Moisture	70	50	70	50	70	70	50	50	50	70	70	70	70	70	70
Specimens	5	1	1	1	5	5	1	1	1	5	5	1	1	5	1

All measurements are in cm  
 NA not applicable

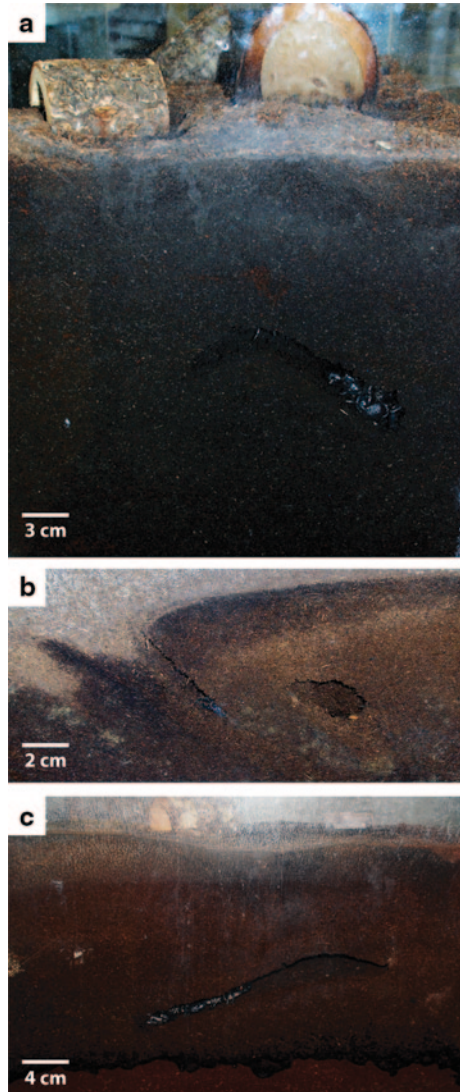
**Fig. 11.3** Burrowing techniques used by *Pandinus imperator*. **a** Excavation of sediment using the first two to three pairs of walking legs. **b** Excavation can be accomplished even in a vertical orientation. **c** Excavated sediment is gathered and held with the first three pairs of walking legs and dragged away from the burrow opening



using the first two to three pairs of walking legs (Fig. 11.3). The walking legs were used to dig sediments from the sediment surface and the burrow walls. The sediment was gathered into a loose mass, held with the first two to three pairs of walking legs, and then dragged back out of the burrow and away from the burrow opening (Fig. 11.3c). The excavated sediment was deposited in a broadly distributed pile located next to and up to 20 cm away from the burrow opening that was used consistently during excavation. During some intervals of burrow expansion, sediment was deposited along the floor of preexisting tunnels. Only very rarely were entire tunnels backfilled and this occurred only before the abandonment of burrows.

Generally, at least one or two burrows were started and abandoned before construction of the final, permanent, burrow began. These temporary burrows were either never occupied or occupied for less than 24 h. These burrows tended to be very shallow, no longer than the length of the scorpion, and went underneath objects such

**Fig. 11.4** *In situ* burrows. **a** Terminal chamber in a helical burrow. **b** A subvertical ramp. **c** The subhorizontal tunnel in a branched burrow



as logs, stones, or water dishes. In experiments with five individuals, each scorpion may have produced its own temporary burrow or up to three scorpions may have occupied the same shallow burrow. This involved one individual digging the burrow followed by one or two other scorpions entering the finished shelter. Construction of the final, permanent burrow occurred within 3–4 days after the scorpions were placed into the tanks. In experiments with five individuals, this burrow was typically constructed by only one or two of the scorpions. The rest simply entered the burrow after it was completed. Construction of the final burrow did not stop, however, as the structures were repaired as needed or modified to make the burrow deeper, lengthen the tunnels, widen the chambers, or construct new branches.

Some of the permanent burrows were constructed against the wall of the enclosure allowing the observation of the scorpion behavior within the burrows (Fig. 11.4). Once the permanent burrows were constructed, the scorpions moved very little within the burrow. When five individuals occupied a single burrow, the scorpions normally had little interaction with one another. There were, however, isolated occurrences of aggression between individuals and even cannibalism in these groups. The scorpions stayed within their burrows approximately 90% of the time during the experiments coming to the surface only during active excavation or active hunting. Coming to the surface to acquire food was not necessary, however, since the prey animals (crickets) sought out and freely entered the maintained openings of the scorpion burrows. The scorpions were often positioned just inside the burrow opening and would capture and consume crickets within the burrow. This further reduced the need for the scorpions to leave their burrows.

### 11.4.2 Surface Morphology

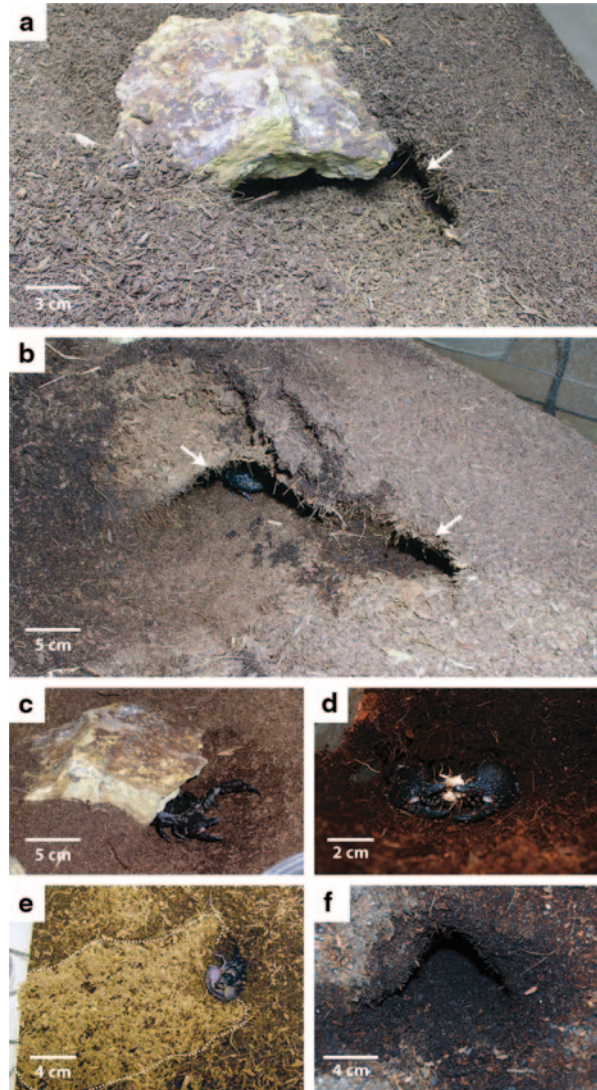
The experimental tanks were set up with flat surfaces prior to the introduction of the specimens of *Pandinus imperator*. The scorpions produced an uneven surface topography as a result of their burrowing activity. The uneven surface occurred around burrow entrances and was the result of the mounding of sediment from subsurface excavation and surface collapse around unstable openings (Fig. 11.5a, b). This uneven topography was most pronounced in experiments with moderate (50%) to low (20%) sediment moisture. Relief of up to 6 cm was produced between the depressions and mounds.

Open burrows constructed by *Pandinus imperator* had distinct surface openings. Burrow openings occurred individually (Fig. 11.5a) or paired (Fig. 11.5b) in tanks with multiple individuals; these consisted of one main burrow and a second smaller burrow which, while in close proximity, did not intersect below the surface. Burrow entrances were typically positioned beneath a stone, log, or other flat object that concealed the opening from above (Fig. 11.5c). Scorpions positioned themselves near the burrow entrance which aided in ambush prey capture (Fig. 11.5d). Sediment piles extended away from the burrow entrance which grew as the burrow was expanded and maintained over the experimental period (Fig. 11.5e). The openings were triangular in shape and on average 5 cm wide and 4 cm high at the center of the entrance (Fig. 11.5f).

### 11.4.3 Burrow Morphology

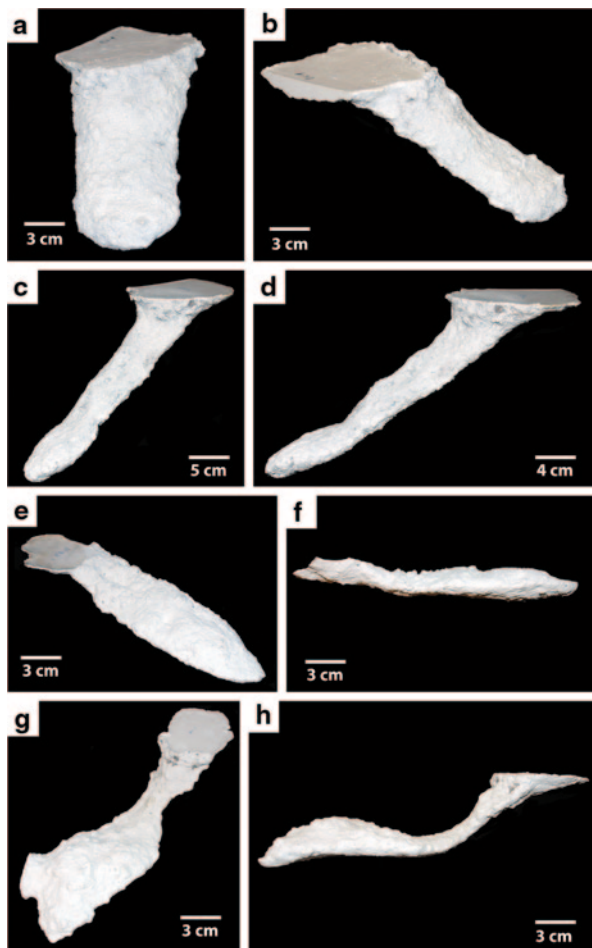
Burrows constructed by *Pandinus imperator* were kept open to the surface throughout the course of the experiments. All of the burrows had a single surface opening. The burrows had sharp, irregular walls with no evidence of a constructed lining. There were three basic types of burrows produced by single and multiple

**Fig. 11.5** Surface features and behaviors associated with *Pandinus imperator* burrows. **a** Burrow openings (at *arrow*) are often present beneath flat objects such as rocks or wood. **b** Multiple burrow openings (at *arrows*) may be close together. **c** Specimens of *Pandinus imperator* are typically near the burrow opening. **d** Burrow openings are used as a site of ambush predation. **e** Large piles of excavated sediment extend outward from the burrow opening. **f** Burrow openings of *Pandinus imperator* have a distinctive triangular morphology



individuals of *Pandinus imperator* including subvertical ramps, helical burrows, and branched burrows (Figs. 11.6–11.8). These burrow architectures were produced regardless of the number of individuals present, but they were controlled by sediment moisture content (Table 11.1). Despite these different architectures, however, they did share several similar morphological elements and quantitative properties (Tables 11.2, 11.3). The burrows consisted of shallowly sloping ( $0\text{--}40^\circ$ ,  $\bar{x}=23^\circ$ ,  $SD=11^\circ$ ) tunnels leading to laterally expanded chambers. The tunnels and chambers were elliptical in cross section with width-to-height ratios from 1.4–2.8

**Fig. 11.6** Subvertical ramps. **a** Front view of a typical subvertical ramp (ES4). **b** Side view of ES4. **c** Right oblique view of a subvertical ramp with a laterally widened terminal chamber (ES6). **d** Side view of ES6 demonstrating the difference between the top and bottom surfaces of the tunnel. **e** Top view of a gently sloping ramp with a large chamber (ES11). **f** Side view of ES11. **g** Top view of a ramp with a large laterally expanded terminal chamber (ES9). **h** Side view of ES9 showing vertical expansion of the chamber



( $\bar{x}$ =2.0, SD=0.4). The average width of tunnels, shafts, and chambers varied only from 4.9–9.6 cm ( $\bar{x}$ =6.6 cm, SD=1.3 cm), the average height from 2.5–5.0 cm ( $\bar{x}$ =3.4 cm, SD=0.8 cm), and the average circumference from 13.0–24.8 cm ( $\bar{x}$ =17.5 cm, SD=3.1 cm). Each burrow was also characterized by tunnels and chambers with inconsistent widths, heights, and circumferences along their lengths as indicated by the range between the minimum and maximum values of these properties (Table 11.2) (Fig. 11.7).

The surficial features of the *Pandinus imperator* burrows were the same across the three architectures. The upper surfaces of the tunnels and chambers were arched and marked by elongate grooves and nodes (Fig. 11.9a, b). These features were irregularly placed and did not show any preferred alignment. The lower surfaces of the tunnels and chambers were consistently smooth and flat without irregular features (Fig. 11.9c).

**Fig. 11.7** Helical burrow casts. **a** Oblique view of a large helical burrow with high tortuosity and a large terminal chamber (ES2). **b** Front oblique view of ES2. **c** Side oblique view of a helical burrow with low tortuosity and a small terminal chamber (ES3). **d** Front top view of ES3



#### 11.4.3.1 Subvertical Ramps

This burrow architecture ( $n=9$ ) includes a single surface opening leading to a shallowly sloping ( $0-50^\circ$ ,  $\bar{x}=22^\circ$ ,  $SD=11^\circ$ ), non-branching ramp that extends 5–13 cm ( $\bar{x}=9$  cm,  $SD=3$  cm) below the sediment surface (Figs. 11.4b and 11.6). The inclination of the ramp either remains constant or may vary up to  $50^\circ$  along the length of the burrow. The ramps have an elliptical cross section with a width-to-height ratio of 1.4–2.8 ( $\bar{x}=2.0$ ,  $SD=0.4$ ). The ramps are 3.6–11.6 cm ( $\bar{x}=6.2$  cm,  $SD=0.9$  cm) wide and 1.7–5.8 cm ( $\bar{x}=3.2$  cm,  $SD=0.7$  cm) high with a circumference of 8.4–28.0 cm ( $\bar{x}=16.4$  cm,  $SD=2.3$  cm) and a total length of 12.0–34.0 cm ( $\bar{x}=23.0$  cm,  $SD=6.9$  cm; Tables 11.2, 11.3). Laterally expanded chambers are present in five of the subvertical ramps and are located at the end of each burrow (Fig. 11.6e, g). The subvertical ramps possess a complexity value of 2 or 3 which includes the single surface opening, a single tunnel, and a chamber if present. The tortuosity of the ramps varies from 1.0–1.1 ( $\bar{x}=1.0$ ,  $SD=0.05$ , Table 11.2). Subvertical ramps were produced in the sediments with moderate to high moisture content (50–70%) (Table 11.1).

#### 11.4.3.2 Helical Burrows

This burrow architecture ( $n=4$ ) includes a single surface opening leading to a shallowly sloping ( $0-50^\circ$ ,  $\bar{x}=19.3^\circ$ ,  $SD=4^\circ$ ), non-branching ramp that curves from  $30-90^\circ$  as it descends 12.5–16.0 cm ( $\bar{x}=14.4$  cm,  $SD=1.3$  cm) into the sediment (Figs. 11.4a and 11.7). The inclination of the tunnel varies up to  $50^\circ$  along the length



**Fig. 11.8** Branched burrows.

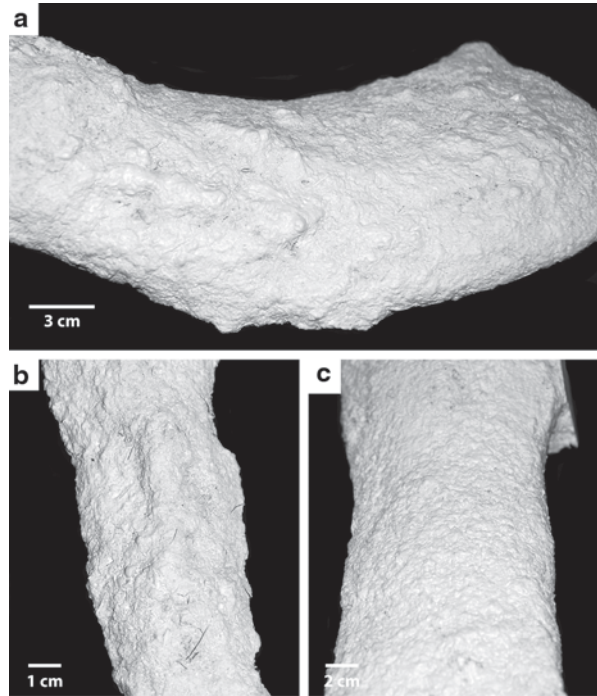
- a** Side view of a large branched burrow (ES8).
- b** Top view of ES8 showing the expansion of the two tunnels at their intersection.
- c** Side oblique view of ES8



**Table 11.3** Average properties of the three different burrow architectures of *Pandinus imperator* (SR, HB, BB), all burrows of *Pandinus imperator* (ES), and all burrows of *Hadrurus arizonensis* (DHS)

	SR	HB	BB	ES	DHS
Surface openings	1	1	1	1	2
Maximum depth	9.1	14.4	21.5	12.2	6.6
Total length	23.0	32.3	54.0	29.6	29.5
Average width	6.2	7.6	6.8	6.6	4.6
Average height	3.2	3.9	3.5	3.4	2.0
Average W/H ratio	2.0	2.0	2.0	2.0	2.4
Average circumference	16.4	19.9	18.0	17.5	12.8
Average slope	22.4	19.3	33.0	23.0	18.9
Branching angles	NA	NA	90.0	90.0	73.0
Complexity	2.6	3.0	4.0	2.9	4.3
Tortuosity	1.0	1.4	1.0	1.1	1.9

**Fig. 11.9** Surficial morphology. **a** Arched upper surface bearing elongate grooves and nodes. **b** Large central groove or ridge along the center of the arched tunnel roof. **c** Smooth and flat tunnel floor



of the burrow and in all ( $n=4$ ) examples, the tunnel terminates with a horizontally oriented, laterally expanded chamber. The helical burrows have elliptical cross sections with width-to-height ratios of 1.4–2.5 ( $\bar{x}=2.0$ ,  $SD=0.4$ ). The helical burrows are 4.2–12.0 cm ( $\bar{x}=7.6$  cm,  $SD=1.6$  cm) wide and 2.0–7.1 cm ( $\bar{x}=3.9$  cm,  $SD=0.7$  cm) high with circumferences of 11.0–28.5 cm ( $\bar{x}=19.9$  cm,  $SD=3.9$  cm) and total lengths of 29.0–34.0 cm ( $\bar{x}=32.3$  cm,  $SD=2.0$  cm; Table 11.2). The helical burrows possess a complexity value of three which includes the single surface opening, a single tunnel, and a chamber. The tortuosity of the helical burrows varies from 1.1–1.7 ( $\bar{x}=1.4$ ,  $SD=0.3$ ; Table 11.2). Helical burrows were produced only in sediments with high moisture content (70%; Table 11.1).

#### 11.4.3.3 Branched Burrows

This burrow architecture ( $n=2$ ) includes a single surface opening leading to a shallowly sloping ( $0\text{--}50^\circ$ ,  $\bar{x}=33^\circ$ ,  $SD=14^\circ$ ) ramp that intersects a horizontally oriented tunnel at  $90^\circ$  (Fig. 11.8). The burrow complex extends 13–30 cm ( $\bar{x}=21.5$  cm,  $SD=8.5$  cm) below the sediment surface (Fig. 11.4c). The inclinations of the tunnels vary up to  $40^\circ$  along the length of the burrow. The branched burrows have elliptical cross sections with width-to-height ratios of 1.9–2.1 ( $\bar{x}=2.0$ ,  $SD=0.1$ ). The ramps are 3.9–10.6 cm ( $\bar{x}=6.8$  cm,  $SD=0.0$  cm) wide and 2.4–4.9 cm ( $\bar{x}=3.5$  cm,  $SD=0.2$  cm) high with circumferences of 12.0–27.0 cm

( $\bar{x}$  = 18.0 cm, SD = 0.9 cm) and total lengths of 28.0–80.0 cm ( $\bar{x}$  = 54.0 cm, SD = 26.0 cm, Table 11.2). Laterally expanded chambers are present in each of the branched burrows ( $n$  = 2) and are located at the intersection of the two tunnels (Fig. 11.8b). The branched burrows possess a tortuosity value of 1.0 and a complexity value of 4.0 which includes the single surface opening, two tunnels, and a chamber (Table 11.2). Branched burrows were produced only in sediments with high moisture content (70%; Table 11.1).

#### 11.4.4 *Environmental Effects on Burrow Morphology*

Specimens of *Pandinus imperator* constructed burrows in all of the experiments, despite changes in the sediment moisture content or the number of individuals in the enclosure. The sediment moisture did significantly reduce the preservation potential of the burrows and influenced the complexity of the final architecture (Table 11.1). No burrows were able to be cast from sediments with 20% moisture due to the collapse of these structures soon after completion. Burrows that were produced in these low moisture enclosures were very shallow (2–4 cm) subvertical ramps or simple depressions excavated beneath rocks, wood, or other flat objects. Overall, the greatest diversity of burrows was produced in sediment with 70% moisture, including all three architectures. Only subvertical ramps were produced in sediment with 50% moisture. The amount of time that the scorpions were within the enclosure also had some effect on the final burrow architecture. The burrows were expanded and elaborated over time, increasing their complexity and tortuosity. All burrows began as shallow subvertical ramps (10–20 days) but then were made longer and deeper as the experiments progressed (40–50 days). These ramps then began to curve as they descended into the substrate (> 12 cm) to produce helical architectures or new tunnels were constructed to produce branching architectures.

Other factors had a minimal impact on the burrow morphology of *Pandinus imperator*. There was no increase in burrow complexity with more individuals. Experiments involving a single individual and multiple individuals both resulted in helical and branched burrows, although those burrows occupied by multiple individuals tended to be larger (Tables 11.1, 11.2). The enclosures themselves did not appear to restrain the morphology of the burrows. Although some burrows did intersect the enclosure walls, both helical and branched burrows were produced without such contact. In addition, the base of the deepest of the burrows (ES8, 30 cm) was far above the maximum depth of the sediment (55 cm).

#### 11.4.5 *Analysis of Burrow Morphology*

The burrows of *Pandinus imperator* were analyzed statistically to determine the similarity of the burrows to each other, the similarity of the burrows to those of another species of scorpion, and to determine the effects of sediment moisture on the burrow properties.

#### 11.4.5.1 Comparison of Burrows of *Pandinus imperator*

The burrows of *Pandinus imperator* were found to be highly (1.0–0.8) to moderately (0.7–0.6) similar, based on 10 quantitative morphological properties used in the Bray–Curtis analysis (Table 11.4a). When compared to each other, all of the burrows, regardless of architecture, had a high average similarity ( $\bar{x}=0.8$ ,  $SD=0.09$ ) with a range of 1.0–0.5. A single branching burrow (ES8) was found to be dissimilar (0.5) to one subvertical ramp (ES4), but this was the only instance of dissimilarity found. The similarity was highest when comparing burrows of the same architectural morphology (Table 11.4a). These comparisons yielded mostly high similarity values (0.9–0.8) and one pair of subvertical ramps (ES7 and ES13) that were considered identical (1.0). Instances of moderate similarity (0.7) among burrows of the same architecture were the product of only one to three specimens; for example, three subvertical ramps (ES4, ES6, ES11) out of the total nine (33%) account for all of the similarity indices  $<0.8$  within that architecture. These differences occur among the only two or three of the other subvertical ramps. Despite these minor differences, the average similarities remained high within the subvertical ramp ( $\bar{x}=0.8$ ,  $SD=0.07$ ) and helical burrow ( $\bar{x}=0.9$ ,  $SD=0.03$ ) architectures. The average similarity was only moderate ( $\bar{x}=0.7$ ,  $SD=0.00$ ) between the two branching burrow casts.

When comparing the different burrow architectures of *Pandinus imperator* together, there was little to no decrease in similarity as the complexity of the architecture increased (Table 11.4a). For example, comparing subvertical ramps to helical burrows resulted in the same overall similarity ( $\bar{x}=0.8$ ,  $SD=0.07$ ) as when comparing them to subvertical ramps. Likewise, comparing helical burrows to branching burrows resulted in a high level of similarity ( $\bar{x}=0.8$ ,  $SD=0.05$ ). Comparing subvertical ramps to branching burrows, however, resulted in a moderate level of similarity ( $\bar{x}=0.7$ ,  $SD=0.11$ ).

Using Mann–Whitney and Kolmogorov–Smirnov tests, it was found that the total length, depth, complexity, and tortuosity of the burrows were not consistent across the three architectures in terms of equality of their medians, distributions, or both (Table 11.5). The number of openings, width, height, circumference, width-to-height ratio, and slope, however, were all similar in both respects.

#### 11.4.5.2 Comparison with Burrows of *Hadrurus arizonensis*

When compared to each other, the burrows of *Hadrurus arizonensis* had a high average similarity ( $\bar{x}=0.8$ ,  $SD=0.10$ ) regardless of the architecture with a range of 0.9–0.4 (Hembree et al. 2012). The two species of burrowing scorpions were found to have three common burrow architectures including subvertical ramps, helical burrows, and branched burrows or mazes (Fig. 11.10, Table 11.3). Burrows with these three architectures were compared using the Bray–Curtis similarity test to determine if there were easily recognized differences resulting from different tracemakers. The burrows of *Pandinus imperator* were, on average, found to be moderately similar ( $\bar{x}=0.7$ ,  $SD=0.10$ ) to burrows produced by *Hadrurus*

**a**

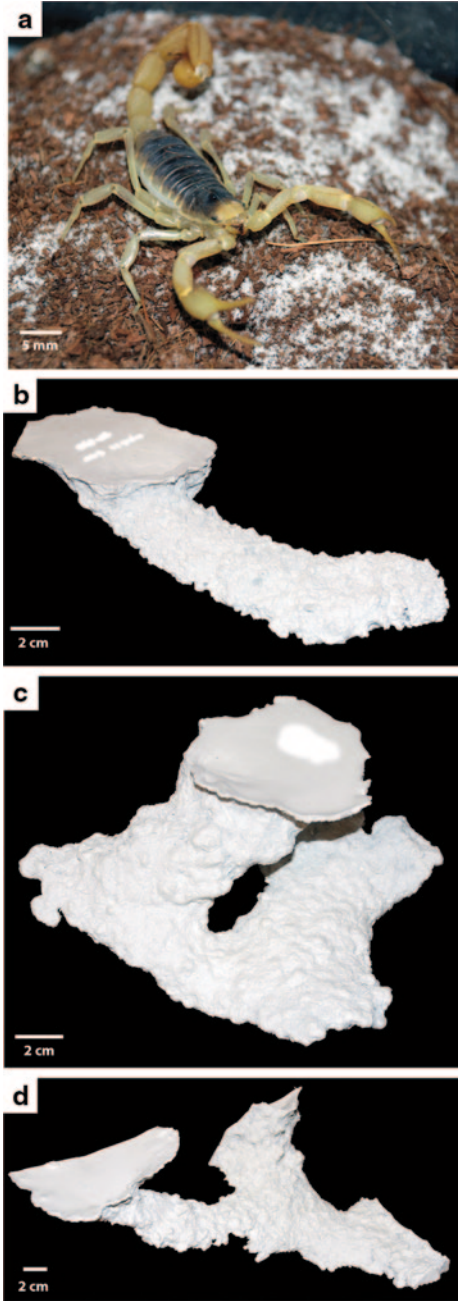
	ES1 (SR)	ES4 (SR)	ES6 (SR)	ES7 (SR)	ES9 (SR)	ES11 (SR)	ES13 (SR)	ES14 (SR)	ES15 (SR)	ES2 (HB)	ES3 (HB)	ES5 (HB)	ES12 (HB)	ES8 (BB)	ES10 (BB)
ES1 (SR)	1.0	0.8	0.8	0.9	0.9	0.8	0.9	0.8	0.9	0.8	0.8	0.8	0.9	0.6	0.8
ES4 (SR)	0.8	1.0	0.9	0.7	0.7	0.7	0.8	0.8	0.8	0.6	0.7	0.8	0.7	0.5	0.8
ES6 (SR)	0.8	0.9	1.0	0.7	0.8	0.7	0.7	0.9	0.8	0.8	0.8	0.9	0.8	0.6	0.9
ES7 (SR)	0.9	0.7	0.7	1.0	0.8	0.8	1.0	0.8	0.8	0.8	0.7	0.8	0.8	0.6	0.7
ES9 (SR)	0.9	0.7	0.8	0.8	1.0	0.8	0.8	0.9	0.8	0.9	0.9	0.9	0.9	0.7	0.8
ES11 (SR)	0.8	0.7	0.7	0.8	0.8	1.0	0.9	0.8	0.7	0.8	0.8	0.8	0.8	0.6	0.7
ES13 (SR)	0.9	0.8	0.7	1.0	0.8	0.9	1.0	0.8	0.8	0.8	0.7	0.8	0.8	0.6	0.7
ES14 (SR)	0.8	0.8	0.9	0.8	0.9	0.8	0.8	1.0	0.9	0.8	0.9	0.9	0.9	0.7	0.9
ES15 (SR)	0.9	0.8	0.8	0.8	0.8	0.7	0.8	0.9	1.0	0.7	0.8	0.9	0.8	0.6	0.8
ES2 (HB)	0.8	0.6	0.8	0.8	0.9	0.8	0.8	0.8	0.7	1.0	0.9	0.8	0.9	0.7	0.8
ES3 (HB)	0.8	0.7	0.8	0.7	0.9	0.8	0.7	0.9	0.8	0.9	1.0	0.9	0.9	0.7	0.8
ES5 (HB)	0.8	0.8	0.9	0.8	0.9	0.8	0.8	0.9	0.9	0.8	0.9	1.0	0.9	0.7	0.8
ES12 (HB)	0.9	0.7	0.8	0.8	0.9	0.8	0.8	0.9	0.8	0.9	0.9	0.9	1.0	0.7	0.8
ES8 (BB)	0.6	0.5	0.6	0.6	0.7	0.6	0.6	0.7	0.6	0.7	0.7	0.7	0.7	1.0	0.7
ES10 (BB)	0.8	0.8	0.9	0.7	0.8	0.7	0.7	0.9	0.8	0.8	0.8	0.8	0.8	0.7	1.0

**b**

	DHS1 (SR)	DHS2 (SR)	DHS6 (SR)	DHS10 (SR)	DHS11 (SR)	DHS12 (SR)	DHS13 (SR)	DHS14 (SR)	DHS16 (SR)	DHS17 (SR)	DHS3 (HB)	DHS7 (HB)	DHS15 (HB)	DHS4 (MW)	DHS5 (MW)	DHS8 (MW)
DHS1 (SR)	0.8	0.8	0.7	0.8	0.7	0.8	0.8	0.7	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8
DHS2 (SR)	0.7	0.6	0.6	0.8	0.7	0.7	0.7	0.6	0.7	0.8	0.8	0.8	0.7	0.8	0.8	0.8
DHS6 (SR)	0.8	0.7	0.6	0.8	0.6	0.6	0.8	0.6	0.7	0.7	0.6	0.6	0.7	0.7	0.7	0.6
DHS10 (SR)	0.8	0.6	0.6	0.8	0.6	0.8	0.8	0.6	0.7	0.8	0.8	0.8	0.8	0.8	0.8	0.8
DHS11 (SR)	0.8	0.8	0.7	0.8	0.7	0.7	0.8	0.7	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8
DHS12 (SR)	0.8	0.7	0.7	0.8	0.9	0.7	0.9	0.7	0.7	0.7	0.7	0.8	0.7	0.8	0.7	0.7
DHS13 (SR)	0.8	0.7	0.7	0.9	0.9	0.7	0.8	0.7	0.7	0.7	0.7	0.8	0.8	0.8	0.8	0.8
DHS14 (SR)	0.8	0.7	0.7	0.9	0.8	0.9	0.9	0.7	0.7	0.7	0.7	0.8	0.8	0.8	0.8	0.8
DHS16 (SR)	0.8	0.6	0.7	0.8	0.8	0.9	0.8	0.7	0.7	0.8	0.8	0.8	0.8	0.8	0.7	0.7
DHS17 (SR)	0.8	0.7	0.8	0.9	0.8	0.9	0.9	0.8	0.7	0.8	0.7	0.8	0.8	0.6	0.6	0.7
DHS3 (HB)	0.8	0.7	0.8	0.8	0.8	0.8	0.9	0.8	0.8	0.8	0.8	0.9	0.8	0.6	0.6	0.7
DHS7 (HB)	0.8	0.8	0.7	0.8	0.7	0.7	0.8	0.7	0.8	0.6	0.7	0.7	0.7	0.5	0.6	0.6
DHS15 (HB)	0.7	0.5	0.6	0.6	0.7	0.7	0.6	0.7	0.6	0.7	0.7	0.7	0.8	0.9	0.6	0.6
DHS4 (MW)	0.7	0.7	0.7	0.6	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.8	0.7	0.8	0.7	0.7
DHS5 (MW)	0.7	0.8	0.8	0.6	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.8	0.7	0.8	0.7	0.8
DHS8 (MW)	0.8	0.8	0.9	0.7	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.9	0.8	0.6	0.6	0.8

**Table 11.4** Bray-Curtis distance measure results based on ten quantitative burrow properties (a) Comparison matrix of all *Pandinus imperator* (ES) burrow casts. (b) Comparison matrix of *Pandinus imperator* and *Hadruus arizonensis* (DHS) burrow casts. SR subvertical ramp, HB helical burrow, BB branched burrow, MW mazework, blue high similarity, green moderate similarity, red dissimilar

**Fig. 11.10** Burrow architectures produced by *Hadrurus arizonensis*. **a** Specimen of *Hadrurus arizonensis*. **b** Subvertical ramp. **c** Helical burrow. **d** Mazework. (Modified from Hembree et al. (2012))



*arizonensis* with a range of similarity from 0.9–0.4 (Table 11.4b). The degree of similarity was found to vary little by architectural morphology. The subvertical ramps had similarity values ranging from 0.9–0.6 ( $\bar{x}=0.7$ ,  $SD=0.08$ ), the helical burrows had similarity values ranging from 0.9–0.6 ( $\bar{x}=0.7$ ,  $SD=0.06$ ), and the branching burrows had similarity values ranging from 0.8–0.7 ( $\bar{x}=0.7$ ,  $SD=0.06$ ). Similar values were obtained even when different architectures were compared (SR/HB:  $\bar{x}=0.7$ ,  $SD=0.08$ ; SR/MW:  $\bar{x}=0.7$ ,  $SD=0.06$ ; HB/MW:  $\bar{x}=0.8$ ,  $SD=0.05$ ).

Despite their different trace makers, the burrow casts of *Pandinus imperator* ( $n=15$ ) did have a few similar quantitative properties to those of *Hadrurus arizonensis* ( $n=19$ ) (Table 11.3). Using Mann–Whitney and Kolmogorov–Smirnov tests, it was found that the total length, average slope, and complexity of the burrows of the two species were similar (Table 11.5). The median and distribution of the depth, width, height, circumference, and tortuosity of the burrow casts were found to be different (Table 11.5). The median of the number of openings and width-to-height ratio were found to be different. On an average, the burrows of *Pandinus imperator* had fewer surface openings, were deeper, had tunnels with a greater width, height, and circumference, lower width-to-height ratio, and lower tortuosity than those of *Hadrurus arizonensis*.

#### 11.4.5.3 Sediment Moisture and Burrow Morphology

While the architectural morphology of the burrows produced by *Pandinus imperator* was controlled by the total sediment moisture (Table 11.1), most of the quantitative aspects of burrow morphology were not significantly altered as this variable changed. Using Spearman's rank correlation, it was found that only two (length and complexity) of the nine metrics tested (depth, length, width, height, w/h ratio, circumference, slope, complexity, and tortuosity) were significantly correlated to either sediment density or moisture content (Table 11.6). The Spearman's rank correlation yielded  $R_s$  values of 0.05–0.48 ( $p=0.86$ –0.07) for seven of the properties, whereas length and complexity yielded  $R_s$  values of 0.82 ( $p=0.0002$ ) and 0.79 ( $p=0.0005$ ), respectively (Table 11.6). Mann–Whitney and Kolmogorov–Smirnov tests supported this result, indicating the median and distribution of the lengths and complexities of burrows produced in sediments with 50 and 70% moisture content were significantly different (Table 11.5). No other property was significantly different.

## 11.5 Discussion

Specimens of *Pandinus imperator* produced three different burrow architectures over the course of the experimental trials. These different architectures were not only the product of a single species, but also of individual specimens. It has been previously recognized through neoichnological research that individual species in both marine and continental settings can produce different types of biogenic

	Openings	Length	Depth	Width	Height	Circum.	W/H Ratio	Slope	Complexity	Tortuosity
<b>Scorpion</b>	M-W	1.00	0.03	0.02	0.25	0.19	0.94	0.94	0.15	0.02
	K-S	1.00	0.03	0.04	0.36	0.30	0.99	0.51	0.51	0.10
<b>SR v BB</b>	M-W	1.00	0.16	0.09	0.29	0.48	0.91	0.41	0.03	0.45
	K-S	1.00	0.38	0.28	0.14	0.28	0.78	0.64	0.02	0.14
<b>HB v BB</b>	M-W	1.00	0.81	0.82	0.81	0.49	1.00	0.49	0.05	0.10
	K-S	1.00	0.74	0.74	0.74	0.24	0.99	0.74	0.05	0.05
<b>ES v DHS</b>	M-W	0.04	0.61	0.001	0.00001	0.00002	0.02	0.25	0.20	0.0003
	K-S	0.54	0.61	0.02	0.000001	0.000006	0.19	0.36	0.11	0.002
<b>Moisture</b>	M-W	1.00	0.003	0.08	0.20	0.11	0.85	0.90	0.004	0.59
	K-S	1.00	0.0006	0.11	0.11	0.11	0.86	0.54	0.003	0.86

**Table 11.5** Results (*p* values) of Mann–Whitney (M–W) and Kolmogorov–Smirnov (K–S) tests between the quantitative properties of three burrows architectures of *Pandinus imperator* (SR subvertical ramp, HB helical burrow, BB branched burrow), the burrows of *Pandinus imperator* (ES) and *Hadrurus arizonensis* (DHS), and of *Pandinus imperator* burrows produced in sediment with 50 and 70% moisture content



**Table 11.6** Results ( $R_s$  and  $p$  values) of Spearman's rank correlation between sediment moisture content and quantitative burrow properties. The number of burrow openings did not vary between burrow casts and was excluded from the analysis

	Openings	Length	Depth	Width	Height	Circum	W/H Ratio	Slope	Complexity	Tortuosity
$R_s$	NA	0.82	0.48	0.36	0.30	0.44	0.07	-0.05	0.79	0.16
$p$	NA	0.0002	0.07	0.19	0.29	0.10	0.82	0.86	0.0005	0.56

structures depending on the behavior exhibited and the environmental conditions (Bromley 1996; Pemberton et al. 2001; Hasiotis 2007).

### 11.5.1 Burrow Morphology and Tracemaker

Despite the different architectures of the burrows produced by *Pandinus imperator*, there was still a high level of similarity between the different burrows. The quantitative properties found to be the most similar among the three different architectures (SR, HB, BB) were the number of surface openings, average tunnel width, average tunnel height, average width-to-height ratio, average circumference, and average slope (Tables 11.3, 11.5). These properties, with the exception of the number of surface openings and slope, are directly related to the morphology of the emperor scorpions; they are an expression of the cross-sectional shape and dimensions of the animal. The tunnels are only 5–10% larger than the largest scorpion occupying the burrow. There was a much greater deviation between the size of the scorpions and the size of the chambers. Chambers were 1–7 cm wider and 1–3 cm higher than the intersecting tunnels. The size of the chambers was a function of other variables such as the number of individuals present (1 or 5), the time of occupation, sediment moisture content, and differences in individual behavior. The surficial features preserved on the upper burrow walls (Fig. 11.9), specifically the elongate grooves, record additional evidence of organism morphology—in this case the presence of appendages on the tracemaker.

The moderate level of similarity between *Pandinus imperator* burrows and those produced by *Hadrurus arizonensis* indicates that animals with similar morphologies can produce similar burrows despite taxonomic differences. Like all scorpions, both *Pandinus imperator* and *Hadrurus arizonensis* have relatively wide, but low bodies with elliptical cross sections that are carried close to the ground (Hjelle 1990). As a result, the tunnels excavated by these animals also have elliptical cross sections and the average width-to-height ratio of the burrows was similar (Tables 11.3, 11.5). The average width, height, and circumference of the *Pandinus imperator* burrows were larger than the *Hadrurus arizonensis* burrows, but this is consistent with the larger average body size of *Pandinus imperator* (Table 11.3). Similarities and differences in other aspects of burrow morphology are likely due to differences in solitary (*Hadrurus arizonensis*) versus communal (*Pandinus imperator*) behavior, burrowing techniques, and sediment properties.

### 11.5.2 *Burrow Morphology and Behavior*

Burrow morphology is a direct product of behavior and the organism's interaction with the sediment (Bromley 1996). The three different architectures of *Pandinus imperator* were used for dwelling and feeding behaviors. The morphological similarities of the different architectures were most likely partially related to these simple types of behavior, despite differences in general form. The consistent burrowing technique also caused common architectural properties between the three burrow types.

Subvertical ramps were produced quickly by the emperor scorpions soon after their introduction to the experimental tanks. Later, burrows were simply modifications of this initial design. The subvertical ramps displayed a wide range of lengths (12–34 cm) and depths (5–13 cm), but all consisted of a single surface opening, a single subvertical tunnel, and, in more than half of the burrows, a laterally expanded chamber. This basic architecture was sufficient to isolate a single or even multiple individuals from the surface environment. In a natural setting, the burrow would serve to protect the scorpions from adverse environmental conditions, such as extremes in temperature or humidity and predators (Polis 1990). During the experiments, specimens of *Pandinus imperator* spent little of their time (10–15%) outside of their burrows. This was primarily during the dark intervals when the scorpions were engaged in active hunting. Much of this time was spent within 10 cm of the burrow entrance. The laterally expanded chambers were constructed over time and were used as dwelling structures and as turn-around points for the scorpions in the subsurface, allowing the animals to reposition themselves so that they could face outward. This was particularly useful in prey ambush behaviors (Fig. 11.5d).

Some aspects of burrow morphology were affected by the communal and solitary behaviors of *Pandinus imperator*. All three architectures were produced by both solitary individuals and groups of individuals. This was likely due to the fact that final burrow construction was typically conducted by only one or two individuals; the rest simply moved into the burrow once it was complete. Differences in burrow morphology related to the number of individuals largely involved scale. While tunnels were typically the same size, chambers were larger in those burrows with multiple individuals as shown by their larger maximum values for width and circumference (Table 11.2).

The surficial structures preserved on the top of the tunnels and chambers are indicative of active excavation by *Pandinus imperator*. The elongate grooves and nodes preserved on the burrow casts record the scraping of sediment from the tunnel walls by the walking legs. The cross-sectional form of the burrows with their arched tops and flat bottoms also reflects this process. The flattened bases of the burrows are likely the result of both the compaction of the floor, by the continuous movement of the scorpions in and out of the burrow during excavation, as well as the infill of excavated sediment from deeper in the burrow along the floor.

### 11.5.3 *Burrow Morphology and Sediment Properties*

High-moisture (70%) sediments are ideal for burrow construction by *Pandinus imperator*. This is likely due to the ability of the high moisture sediment to withstand gravitational collapse due to higher levels of sediment cohesion. The emperor scorpions produced no burrow linings to provide additional support regardless of the sediment properties as seen in other types of arthropods (Bromley 1996). There may have also been a physiological component of the preference for higher moisture sediment in these experiments since *Pandinus imperator* inhabits humid environments (Sissom 1990).

Sediment moisture showed no impact on burrow depth, width, height, width-to-height ratio, circumference, slope, or tortuosity (Tables 11.5, 11.6). Results from the Spearman's rank correlation analysis resulted in an average  $R_s$  value of 0.25 for these properties. Burrow length ( $R_s=0.82$ ,  $p=0.0002$ ) and complexity ( $R_s=0.79$ ,  $p=0.0005$ ), however, did show a significant correlation with sediment moisture. As sediment moisture increased, burrows became longer and more complex. These two properties are primarily tied to burrow architecture. Helical burrows and branched burrows were only produced in the high moisture sediment and these two burrow architectures have consistently higher lengths and complexities than the subvertical ramps. In addition, four of the five subvertical ramps with chambers were produced in high moisture sediment giving them higher complexities. Subvertical ramps produced in high moisture sediment also had the highest total lengths (Table 11.2).

The minimal correlation between the quantitative aspects of burrow morphology and environment is important because it suggests that the burrow morphology is primarily controlled by the organism's morphology and behavior. The burrow morphology may therefore be useful as a proxy for scorpions and the behaviors associated with terrestrial predatory arthropods.

## 11.6 Significance

### 11.6.1 *Recognition in the Fossil Record*

Recognizing the different architectures and surficial morphologies of burrows produced by modern animals is critical for the accurate interpretation of trace fossils. Scorpion burrows lack a significant fossil record. This is surprising, given the prevalence of burrowing behavior in modern scorpions and the long evolutionary history of the group. The absence is most likely due to a failure to recognize known fossil burrows as being the result of scorpion activity. In order to properly identify scorpion burrows in the fossil record, a set of ichnotaxobases is needed. Ichnotaxobases include the architecture of a burrow, overall shape, orientation with respect to the substrate, surficial features or bioglyphs, and internal structure such as constructed linings and active fill (Bertling et al. 2006). Detailed study of the burrows of

modern animals allows for the establishment of ichnotaxobases for different groups of animals. These groups may have similar evolutionary histories, morphologies, behaviors, or all three. While some variation in the ichnotaxobases is expected from the burrows of different families, genera, or even species of scorpions, this study of *Pandinus imperator* and others like it (Hembree et al. 2012) provide a starting set of ichnotaxobases that can be used to aid in the recognition and interpretation of scorpion burrows in the fossil record.

*Architecture* Scorpion burrows include subvertical ramps, helical burrows, and branched burrows. These consist of a single surface opening, subvertical to subhorizontal tunnels, and laterally expanded chambers. Branching is uncommon. Chambers occur at the base of the burrow or at branch points.

*Overall Shape* Tunnels are elliptical in cross section with a width-to-height ratio of approximately 2.0. The tunnel roof is curved while the floor is flattened. Chambers have the same cross-sectional characteristics as tunnels but are wider. Tunnels and chambers have variable widths and heights along their length. Tunnels may be straight or sinuous curving up to 30° along a horizontal plane.

*Orientation* Burrow elements vary in orientation from horizontal (0–5°) to oblique (15–50°). The orientation changes along the length of tunnels while chambers tend to be horizontal. Most burrows contain elements with both of these orientations.

*Internal Structure* Scorpion burrows possess no distinguishable lining. The boundary between the open burrow and the surrounding sediment is abrupt and irregular. The burrow fill may be active or passive. Active fill is generally massive in appearance and accumulates from the burrow floor upward during burrow expansion. Passive fill occurs typically as a result of gravitational collapse of upper elements of the burrow.

*Surficial Features* The roofs of the tunnels and chambers are irregular and possess elongate grooves and nodes. The floors are flat and featureless.

## ***11.6.2 Paleontological and Paleoecological Significance***

Continental trace fossils have a wide range of potential uses, but they are still poorly understood (Hasiotis 2007). Additionally, while modern soils are known to contain a diverse and abundant biota, most of these organisms are poorly understood both taxonomically and ecologically (Bardgett 2005). Even worse is the lack of knowledge of the burrow morphologies produced by modern burrowing animals as well as the ways in which the soil environment (soil type, temperature, soil moisture, precipitation, etc.) affects burrowing behaviors. For many taxa this information is entirely unknown. Given this lack of knowledge of modern soil ecosystems, the ability of paleontologists and sedimentary geologists to use fossil burrows to make interpretations about ancient soil ecosystems is limited. This is the knowledge that can be obtained through neoichnology.

Burrows produced by *Pandinus imperator* displayed three different types of basic architecture. These variations were largely a product of changes in burrow morphology over time as a result of burrow modification and maintenance. The potential effect of this architectural diversity is the likelihood for an overestimation of biodiversity. Trace fossil classification and interpretation relies entirely on morphology, therefore, it is possible for each burrow form to be considered indicative of a different tracemaker. There have been several studies showing that a single tracemaker can produce multiple burrow morphologies depending on the behaviors involved and the sediment properties (Bromley 1996; Pemberton et al. 2001; Hasiotis 2007). The possible diversity of forms that can be produced by a single species or even a single individual, however, is rarely fully understood. There is a similar problem with using absolute burrow size to make interpretations about potential tracemakers. Many fossil continental burrows with large (>2 cm) cross-sectional diameters are interpreted as vertebrate burrows primarily on the basis of their size (Miller et al. 2001; Hasiotis et al. 2004; Loope 2008; Storm et al. 2010; Talanda et al. 2011). Complex branching patterns have also been considered diagnostic of vertebrate tracemakers (Miller et al. 2001; Hasiotis et al. 2004; Talanda et al. 2011). The experiments described here and in Hembree et al. (2012) have shown that scorpions are capable of producing burrows with both large diameter tunnels and chambers, in addition to branching burrow networks.

Arthropod predators are a commonly underrepresented component of reconstructions of fossil terrestrial ecosystems (DiMichele and Hook 1992; Wing and Sues 1992). Their importance in and often dominance of ecosystems, however, is clearly demonstrated by modern studies (Dindal 1990; Polis 1990; Cloudsley-Thompson 1991; Punzo 2000a, b; Bardgett 2005; Lavelle and Spain 2005; Punzo 2007). Scorpions fill a fundamental role as the intermediate predators in many modern ecosystems feeding on a variety of prey, particularly other arthropods, and serving as prey for other large predators (McCormick and Polis 1990; Polis 1990). In semi-arid and arid environments, scorpions typically represent the dominant insectivorous predators (Marples and Shorthouse 1982; McCormick and Polis 1990). Given the obvious importance of scorpions in modern ecosystems, the recognition of fossil scorpion burrows would provide for a more complete interpretation of ancient ecosystems.

The recognition of scorpion burrows in the fossil record would also improve our understanding of the evolutionary and biogeographic history of this group of common and ecologically important animals. Scorpion body fossils are relatively common in Paleozoic strata but are rarer in Mesozoic and even Cenozoic rocks (Sissom 1990; Jeram 2001). By at least the Mesozoic if not the late Paleozoic, fossil scorpions display very modern morphologies and sizes and many have been interpreted to have used burrows as permanent shelters (Sissom 1990; Jeram 2001). Given the relative rarity of body fossils, therefore, the recognition of scorpion burrows from late Paleozoic to Cenozoic deposits may be the best way to assess the true abundance and distribution of scorpion taxa.

### 11.6.3 *Paleopedologic and Paleoenvironmental Significance*

Due to the terraphilic nature of terrestrial scorpions, the burrow architectures produced in this study would be suggestive of the upper soil profile (A/B horizon) within the vadose zone (Hasiotis 2007). The temperature, average precipitation, vegetation, and soil type could vary widely given the range of environments that modern and fossil scorpions inhabit (Polis 1990; Sissom 1990). Fossil scorpion burrows could, therefore, occur in soil types from Entisols to Oxisols. Fossil scorpion burrows would likely be found in association with trace fossils produced by other soil arthropods (arachnids, myriapods, and insects), annelids, and possibly vertebrates as well as various types of fossil root traces.

As discussed in Hembree et al. (2012), the burrowing activity of scorpions plays at least a minor role in pedogenesis. The activity of *Pandinus imperator* in the laboratory enclosures extended 30 cm into the sediment which is associated with the A and upper B horizons of soils in tropical regions. Burrows of this depth would impact soil-forming processes. Laboratory studies of other tropical genera such as *Heterometrus* have resulted in burrows up to 50 cm deep (Hembree personal observation).

Specimens of *Pandinus imperator* moved sediment from the subsurface to the surface through the excavation of their burrows. This process resulted in an undulating surface topography of loose, porous sediment distinct from the compacted surface of the original material. This modified surface facilitated the downward movement of water through the enclosure. The burrowing activity also resulted in an overall mixing of the sediment as excavated material from deeper tunnels was deposited into shallower tunnel walls during burrow expansion. The active excavation of sediment in the subsurface increased the overall porosity and permeability of the sediment along the walls of the burrow, providing additional conduits for fluid flow and gas exchange.

The permanent, open burrows of *Pandinus imperator* allowed the migration of water and oxygen through the sediment profile. Such conduits are critical in pedogenesis as they allow the dissolution of minerals, the downward transportation of water, ions, and organics, and even the upward movement of water through evapotranspiration (Schaetzl and Anderson 2009). The continual maintenance of the surface openings during the occupation of the burrows allows the constant infiltration of water, sediment, organics, and other organisms into the subsurface. Even when passively filled after being abandoned, the overall porosity and permeability of the fill is higher than the original sediment due to the disruption by the scorpion. Filled burrows, therefore, continue to serve as conduits for the downward and upward migration fluids through the soil profile. Appendages of crickets and other organic debris were found within the burrow chambers of *Pandinus imperator*. The incorporation of this organic material provides a source of nutrients for soil microbes, plants, and other soil animals (Bardgett 2005; Lavelle and Spain 2005). The potential impact of burrowing scorpions on soil formation, therefore, must be considered if fossil scorpion burrows are found within paleosols.

## 11.7 Conclusions

The interpretation of trace fossils is impossible without a detailed knowledge of the diversity of biogenic structures produced by modern burrowing organisms. Neobiological studies are, therefore, critical to the interpretation of the behaviors, burrowing methods, and tracemakers represented by trace fossils as well as their paleoenvironmental significance. The architectural and surficial morphologies of the burrows of scorpions are largely unknown despite their abundance and importance in both modern and ancient ecosystems. This absence of knowledge makes the recognition of burrows, produced by scorpions and other terrestrial predatory arthropods in the fossil record, unlikely which leads to incomplete or incorrect paleoecological reconstructions.

Specimens of the burrowing scorpion *Pandinus imperator* produced burrows with three different architectures under similar environmental conditions, including subvertical ramps, helical burrows, and branched burrows. Despite their differences in architecture, there were consistent quantitative morphological properties that made the burrows similar. These properties included the number of surface openings as well as the width, height, width-to-height ratio, circumference, and slope of the tunnels and chambers. These shared properties allowed the recognition of similarity between the burrows despite the different architectures when compared using a Bray–Curtis similarity test. When compared to the burrows of another scorpion, *Hadrurus arizonensis*, the burrows of *Pandinus imperator* were found to be different from those of the other species. The burrows of *Pandinus imperator* were found to have fewer surface openings, were deeper, had tunnels with a greater width, height, and circumference, lower width-to-height ratio, and lower complexity than those of *Hadrurus arizonensis*. This suggests that even burrows produced by similar tracemakers can be distinguished when properly analyzed. These experiments effectively demonstrate that multiple burrow architectures may be produced by a single species. Individual animals produced all three of the burrow architectures observed. It is critical, to paleoecological interpretations, that each type of trace fossil does not necessarily represent a different organism. The analysis of the results of these experiments have shown that thorough descriptions of trace fossil morphology, including multiple quantitative properties, can be used to discern if distinct architectures were produced by the same or different tracemakers.

Sediment properties are considered to have an important effect, on the types of biogenic structures that can be produced and upon their final morphology, in all environmental settings (Bromley 1996; Pemberton et al 2001; Hasiotis 2007). Sediment moisture was found to affect which architectures could be produced by *Pandinus imperator*. Burrows with greater overall complexity such as helical burrows and branched burrows were only produced in sediment with high (70%) moisture content. Specimens of *Pandinus imperator* only produced simple subvertical ramps or shallow pits in sediment with lower (50%) moisture content. When sediment moisture was too low (20%), open burrows could not be maintained and collapsed. The total length and complexity of the burrows were found to be positively correlated with increasing sediment moisture.

The proper identification of large and complex burrows, produced in terrestrial ecosystems, requires knowledge of all the possible organisms that can occupy soil environments. While predatory arthropods are capable of producing large diameter, complex, branching burrow systems, fossil burrows with the size and complexity produced by the scorpions in these experiments would likely be interpreted as vertebrate burrows. A thorough understanding of these burrows and those of similar organisms such as scorpions, spiders, and centipedes will aid in revealing the hidden biodiversity of terrestrial predatory arthropods in the fossil record.

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