Chapter 14
Biogenic Structures of Burrowing Skinks: Neoichnology of *Mabuya multifaciata* (Squamata: Scincidae)

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Contents

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Abstract Neoichnological experiments involving a species of tropical, ground-dwelling skink, *Mabuya multifasciata,* demonstrate the diversity of biogenic structures produced by medium-sized lizards. Although the majority of skinks are ground dwellers or burrowers, little is known about the biogenic structures produced by this most diverse group of lizards. The documentation of biogenic structures produced by *M. multifasciata* will aid in the identification of trace fossils produced by skinks, help to improve the fossil record of these difficult-to-preserve animals, and allow for more complete paleoecological and paleoenvironmental reconstructions. Skinks were placed in terrariums filled with sediment of varying compositions and moisture content and were allowed to burrow. Open burrows were cast with plaster, photographed, measured, and statistically analyzed. The skinks produced seven distinct burrow morphologies including various ramps, U-, and J-shaped burrows. While there was no direct correlation between burrow properties and sediment properties, the burrows showed some variations due to the changes in sediment density and moisture content. The burrows had greater average complexities and tunnel heights when the sediment moisture was increased, whereas they had lower average widths and circumferences when the sediment density was increased. The data collected in this study can be directly applied to terrestrial trace fossil assemblages in tropical paleosols to better interpret their paleoecology and assess paleoenvironmental conditions.

Keywords Trace fossil · Bioturbation · Vertebrate · Reptile · Continental · Paleoecology · Paleopedology

14.1 Introduction

The purpose of this chapter is to document the morphology of biogenic structures produced by a species of tropical, burrowing skink, *Mabuya multifasciata* (Squamata: Scincidae), in order to improve the interpretation of continental vertebrate trace fossils. This study includes the description of the basic architecture and surficial morphologies of the burrows produced by *M. multifasciata* under both constant and varied environmental conditions. Environmental conditions, including sediment moisture, composition, and density, were altered in order to evaluate how the properties of vertebrate biogenic structures changed in response to these commonly variable factors.

Due to their *in situ* preservation, trace fossils are invaluable in paleoecological and paleoenvironmental reconstructions. Historically, marine trace fossils are well studied and have been used to interpret such paleoenvironmental conditions as turbidity, salinity, sedimentation rate, and nutrient input (e.g., Frey 1970; Rhoads 1975; Bromley 1996; Uchman and Pervesler 2006; Gingras et al. 2007). Although continental ichnology is a comparatively new field, recent ichnological studies of extinct continental organisms, along with studies of modern analogs, have shown that information pertaining to paleoenvironment and even paleoclimate can also be acquired from continental trace fossils (Retallack et al. 1984; Hasiotis 2002, 2003;

Hembree et al. 2004, 2012; Hembree and Hasiotis 2007, 2008; Smith and Hasiotis 2008; Smith et al. 2008; Melchor et al. 2010). Modern continental burrowers such as moles (Gobetz and Martin 2006), snakes (Young and Morain 2003; Hembree and Hasiotis 2007), amphisbaenians (Hembree and Hasiotis 2006), cicadas (Smith and Hasiotis 2008), chafer beetles (Counts and Hasiotis 2009), ants (Halfen and Hasiotis 2010), scorpions (Hembree et al. 2012), whip scorpions (Hembree 2013), and millipedes (Hembree 2009) have been used as analogs to help interpret trace fossils and produce more robust paleoecological reconstructions. Such modern continental trace makers are sensitive to environmental changes; accordingly, trace fossils produced by their ancient equivalents can also be used to interpret environmental factors such as soil nutrient content, sediment density, sedimentation rates, fluctuations in the water table, as well as changes in mean annual precipitation and temperature (Hasiotis 2006). For example, variations in the diversity and abundance of continental trace fossils within ichnocoenoses (i.e., faunal communities) have been used to determine the response of ecosystems to changes in soil moisture regimes, nutrient content, and soil bulk density through time (Kraus and Riggins 2007).

Although vertebrate ichnology has traditionally been limited to the study of tracks and trails (e.g., Peabody 1954; Sarjeant 1975; Currie 1983; Lockley et al. 1994; Irby and Albright 2002; Kubo and Benton 2009), vertebrate trace fossils also include complex and varied burrow structures (e.g., Martin and Bennett 1977; Smith 1987; Groenewald et al. 2001; Hembree et al. 2004; Gobetz and Martin 2006; Hembree and Hasiotis 2008) . Burrowing behavior has evolved independently in several vertebrate clades, and vertebrate burrows are well represented in the geologic record with the earliest recognized burrows dating to the Early Devonian (e.g., Romer and Olson 1954; Damiani et al. 2003; Hasiotis 2003; Hasiotis 2004; Martin 2009). Despite the early appearance and persistence of vertebrate burrows in the geologic record, few researchers have studied the biogenic structures and sediment interactions of extant continental vertebrates (Voorhies 1975; Hasiotis et al. 2007). The lack of understanding of continental vertebrate trace makers has likely led to inaccurate interpretations regarding paleoenvironment and paleoclimate as discussed by Hembree and Hasiotis (2006; 2007). Experimental studies concerning modern continental vertebrates are necessary for the accurate interpretation of trace fossils and their paleoenvironmental significance. These interpretations result directly from observations of the interactions of trace makers in response to their environment (Hembree 2009, 2013; Hembree and Hasiotis 2006, 2007; Hembree et al. 2012).

Although lizards have a large geographic range and an evolutionary history that begins in the Middle to Late Triassic (Datta and Ray 2006), their ichnology has been poorly studied. Few continental trace fossils have been attributed to lizards and only a few neoichnological experiments have involved modern traces produced by lizards (e.g., Traeholt 1995; Gupta and Sinha 2001; Young and Morain 2003; Hasiotis and Bourke 2006; Hembree and Hasiotis 2006, 2007). With over 1,200 extant species, skinks are the most diverse group of lizards and members of the second largest lizard family (Zug et al. 2001). Skinks are characterized by cylindrical bodies, shortened legs, cone-shaped heads, and tapering tails, which makes
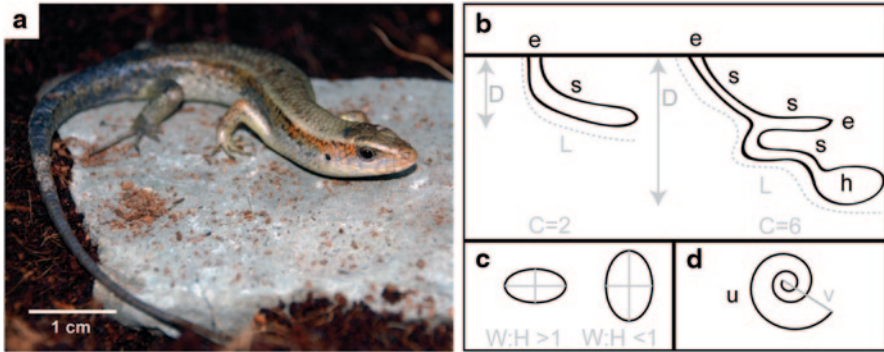
Fig. 14.1 a The many-lined sun skink *Mabuya multifasciata*. **b** Quantitative models used to describe burrows. Burrows were described in part by their maximum depth (*D*) and total length (*L*). Burrow tunnels were divided into segments (*s*) with entrances or blind endpoints (*e*), and expanded chambers (*h*). Burrow complexity (*C*) is a measure of the total number of segments, endpoints, and chambers within a single burrow: $C=s+h+e$. **c** The width-to-height ratio of two burrow tunnels. **d** The tortuosity (*T*) of a segment is calculated by dividing the total length (*u*) by the straight line distance (*v*). (Modified from Hembree and Hasiotis (2006))

them easily distinguishable from other lizards (Zug et al. 2001). Most skink species are either ground dwellers or burrowers, and are most abundant in the tropics (Zug et al. 2001). Although they have a low preservation potential due to their size and habitats, skinks are present in the fossil record as early as the Cretaceous (Estes 1969) and have been found in Paleocene, Oligocene, and Miocene sediments in North America and Australia (Estes 1969; Wellstead 1982; Martin et al. 2004). Due to their abundance, widespread habitats, and burrowing habits, skinks are excellent candidates for neoichnological investigation.

14.2   Skink Ecology and Behavior

Mabuya multifasciata, or the many-lined sun skink (Fig. 14.1a), is an exclusively tropical, medium-sized, insectivorous skink whose range extends through China, India, Malaysia, the Philippines, and New Guinea (Ji et al. 2006; Sun et al. 2009). *Mabuya multifasciata* has well developed limbs, olive gray coloration with a yellow throat, two dark brown dorsolateral lines, and numerous brown to green dorsolateral ocelli (Taylor 1963; Ji et al. 2006). Adult *Mabuya multifasciata* are known to reach a snout-to-vent (SVL) length of 117 mm (Ji et al 2006). *Mabuya multifasciata* can be distinguished from other skinks in the *Mabuya* genus by the 30–34 scale rows around the middle of the skink's body and the three to five keels on the dorsal scales (Taylor 1963). *Mabuya multifasciata* shows a preference for open, sunny spaces such as riverbeds and forest edges (Ji et al. 2006).

14.3   Materials and Methods

The burrowing behaviors of six individuals of *M. multifasciata* were observed in this study. Multiple individuals were used in order to delineate variations in biogenic structures due to differences in individual behavior. The skinks had an SVL of 9.0–9.7 cm and weighed 16.0–23.0 g.

The skinks were placed in 38 L (50 × 25 × 30 cm) and 114 L (80 × 30 × 40 cm) terrariums filled with 20 and 25 cm of sediment, respectively. Terrariums of different sizes were used to evaluate the influence of available space on the morphology of the biogenic structures. The air temperature within the terrariums was regulated with infrared, ceramic heat lamps set on a 12-h timer. A rock was placed directly underneath the heat lamp to allow for basking and a water dish was placed on the opposite side of the terrarium. A pair of UVB lights also set on a 12-h timer was also used in all of the trials. Sediments were composed of varying amounts of finely shredded coconut fiber, clay-sized soil material, fine-grained sand, and water. Sediment density was determined using a soil compaction meter (Fieldscout SC 900), and soil moisture levels were measured with a soil moisture probe (Aquaterr salinity multimeter EC−300). The surface of each terrarium was regularly sprayed with water during the experiments to maintain the desired moisture level, and the soil moisture was tested daily. Due to the temporary nature of the burrows produced by *M. multifasciata,* the trials of all the experiments were run until the skinks exited their burrows.

Experiment 1 (Exp. 1) was designed to observe and record the natural burrowing behaviors of single individuals of *M. multifasciata* under their typical sediment and moisture conditions (Table 14.1a). The sediment consisted of loose coconut fiber with an average sediment density of 0.70 kg/cm^2 and a moisture content of 40%. Trials of Exp. 1 lasted between 3 and 18 days.

Experiment 2 (Exp. 2) was designed to observe the burrowing behaviors and biogenic structures of the skinks in different types of sediment within the natural ranges of the species (Table 14.1b). The sediments consisted of a loose coconut fiber mixed with either an additional 20 wt% of clay or an additional 20 wt% of fine sand. The addition of clay to the coconut fiber increased the sediment density to an average of 1.1 kg/cm^2 whereas the addition of sand decreased the sediment density to an average of 0.35 kg/cm^2. Trials of Exp. 2 lasted between 3 and 11 days.

Experiment 3 (Exp. 3) was designed to observe the effect of sediment moisture content on skink burrowing behaviors (Table 14.1c). The sediments consisted of a loose coconut fiber with moisture content either increased to 60% or lowered to 20%. Trials of Exp. 3 lasted between 4 and 7 days.

Biogenic structures produced by the skinks were photographed daily over the test periods. Videos were also made if the skinks were actively burrowing during times of observation to document burrowing techniques. Skinks were removed from terrariums and returned to their holding tanks at the end of each test period. Removal of the skinks occurred after the animals exited their burrows to engage in feeding or basking behaviors. The open burrows were cast with Drystone™ plaster

Table 14.1 Experimental parameters

Specimen	Experiment ID	Tank size	Substrate	Temperature	Percent soil moisture	Time (days)
a. Experiment 1: Basic morphology						
MM 1	TGB1	38 L	CF	30 °C	40	7
MM 2	TGB2	38 L	CF	30 °C	40	7
MM 4	RGB1	114 L	CF	30 °C	40	7
MM 2	RGB2	114 L	CF	30 °C	40	7
MM 4	TGD1	38 L	CF	30 °C	40	14
MM 6	TGD2	38 L	CF	30 °C	40	14
b. Experiment 2: Sediment composition						
MM 4	TGL1	38 L	CFC	30 °C	40	7
MM 4	TGL2	38 L	CFC	30 °C	40	7
MM 5	RGL1	114 L	CFC	30 °C	40	7
MM 4	RGL2	114 L	CFC	30 °C	40	7
MM 2	TGN1	38 L	CFS	30 °C	40	7
MM 5	TGN2	38 L	CFS	30 °C	40	7
MM 4	RGN1	114 L	CFS	30 °C	40	7
MM 2	RGN2	114 L	CFS	30 °C	40	7
c. Experiment 3: Sediment moisture						
MM 5	TGX1	38 L	CF	30 °C	60	7
MM 5	TGX2	38 L	CF	30 °C	60	7
MM 4	RGX1	114 L	CF	30 °C	60	7
MM 2	RGX2	114 L	CF	30 °C	60	7
MM 8	TGZ1	38 L	CF	30 °C	20	7
MM 5	TGZ2	38 L	CF	30 °C	20	7
MM 4	RGZ1	114 L	CF	30 °C	20	7
MM 8	RGZ2	114 L	CF	30 °C	20	7

CF coconut fiber, *CFC* coconut fiber and 20 % clay, *CFS* coconut fiber and 20 % sand, *MM Mabuya multifasciata*

immediately after the animals were removed. The resulting casts were excavated, photographed, described, and measured using a quantitative burrow description model based on Hembree and Hasiotis (2006). The measurements in the model include maximum depth, angle of orientation, branching angles, total length, tunnel width, tunnel height, and width-to-height ratio; burrow complexity and tortuosity were then calculated for each burrow (Fig. 14.1b–d).

A nonparametric analysis was performed to test the levels of similarity among the three-dimensional burrow casts. A Bray–Curtis similarity test was performed with all burrow casts using the ten quantitative properties. The analysis produces a number between 1.0 (identical) and 0 (different) quantifying the level of similarity between the two burrows. In this study, a value of 1.0 indicates that the burrows are the same, 0.9 indicates very high similarity, 0.8 indicates high similarity, and values

of 0.7 and 0.6 indicate moderate similarity. Values less than or equal to 0.5 indicate dissimilarity.

A Spearman's rank correlation was performed to examine the potential correlation between sediment density and the properties of the skink burrows. In this analysis, each quantitative burrow property (dependent variable) was compared to the sediment density (independent variable). In Spearman's rank correlation, a correlation coefficient (Rs) above 0.90 indicates a high correlation. In addition, Mann–Whitney (M–W) and Kolmogorov–Smirnov (K–S) tests were used to determine the potential equality of the median and distribution of the properties of each burrow, respectively, under the different sediment density and moisture conditions. A ρ value of <0.05 indicates a significant difference between two samples.

14.4 Results

14.4.1 General Bioturbation Patterns of M. multifasciata

Mabuya multifasciata burrowed through an intrusion technique in the three different sediments. The skinks preferentially produced burrows in preexisting mounds and cracks on the sediment surface. To locate these features, the skink skimmed its cone-shaped head against the surface of the sediment. Once a mound or crack in the sediment was found, the skink used its front legs to create an open path in the sediment wide enough to force its head into the sediment while using its hind legs to compact and stabilize the sediment around the burrow entrance. As the skink forced its body into the sediment, it used lateral undulations of the head and body to compress the surrounding sediment and widen the burrow.

Active burrowing in loose, organic-rich sediments resulted in seven distinct burrow morphologies including ramps, sinuous ramps, branched ramps, U-shaped burrows, subhorizontal U-shaped burrows, branched U-shaped burrows, and J-shaped burrows. Open burrows were produced in all experiments with the exception of those with 20% sediment moisture. Each experimental trial resulted in a single burrow except for one experiment (TGL1) where the skink produced two separate burrows. One burrow type, the simple ramp, was replicated in all of the trials despite changes in terrarium size, sediment density, and sediment moisture. The open burrows had an average slope of 27° (11–49°; $\sigma=10$), average maximum depth of 5.3 cm (2.3–13.9 cm; $\sigma=3.0$), an average width of 2.8 cm (2.0–4.3 cm; $\sigma=0.6$), average height of 2.2 cm (1.4–3.6 cm; $\sigma=0.5$), an average circumference of 8.8 cm (6.7–11.9 cm; $\sigma=1.6$), average width-to-height ratio of 1.3 (0.7–1.8; $\sigma=0.3$), average total length of 19.5 cm (6.5–40.5 cm; $\sigma=9.3$), average complexity of 2.7 (2.0–5.0; $\sigma=1.0$), and an average tortuosity of 1.27 (1.02–1.56; $\sigma=0.20$; Table 14.2).

Table 14.2 Measurements of three dimensional burrow casts produced by *M. multifasciata* and the average and standard deviation of the ten diagnostic properties

Architecture	HT1	TGD1	TGB1	RGB1	RGN2	TGX2	TGL1B	TGD2	TGN1	TGL1A	RGL1	RGN1	RGX2	TGB2	TGN2	HT2	RGX1	TGL2	TGX1	RGB2	RGL2	Avg	Std Dev
	R	R	R	R	R	R	R	R	R	SR	SR	SR	BR	BR	BR	U	U	HU	BU	J	J		
Surface openings	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	1	1	1	0.4
Maximum depth	2.3	5.4	5.3	2.8	2.8	4.8	5.0	3.8	9.4	3.3	4.2	6.2	13.9	5.4	3.2	7.2	11.5	3.1	4.3	2.3	6.1	5.3	3.0
Total length	6.5	28.7	19.6	11.0	9.5	11.0	14.5	10.8	11.6	15.7	24.3	21.5	31.0	19.0	12.0	40.5	27.5	17.7	40.0	19.0	17.7	19.5	9.3
Maximum width	2.2	5.3	5.1	3.5	2.3	2.5	2.6	4.5	4.3	3.2	3.2	4.1	5.6	5.2	2.9	4.7	3.1	3.1	5.2	2.8	2.4		
Minimum width	1.9	2.2	1.9	2.4	2.1	2.1	1.9	2.2	2.0	1.7	1.2	2.0	1.5	3.0	2.0	2.2	2.0	1.8	2.2	1.9	1.9		
Average width	2.0	4.0	3.3	2.8	2.2	2.3	2.3	3.1	2.8	2.4	2.0	3.2	3.5	4.3	2.4	3.4	2.5	2.5	3.5	2.4	2.2	2.8	0.6
Maximum height	2.0	3.0	2.6	2.7	1.6	5.6	2.4	2.9	3.4	2.7	3.0	2.3	3.5	2.7	1.6	3.6	4.4	4.1	2.6	2.9	2.7		
Minimum height	1.3	1.9	1.5	1.6	1.2	2.4	1.4	1.4	1.5	1.3	1.2	1.7	1.6	1.9	1.5	1.9	1.4	1.8	2.0	1.6	1.4		
Average height	1.6	2.5	2.1	2.0	1.4	3.6	1.8	2.4	2.2	1.9	1.8	2.0	2.6	2.4	1.5	2.4	2.4	2.7	2.2	2.0	1.9	2.2	0.5
Average W/H ratio	1.3	1.6	1.6	1.4	1.6	0.7	1.3	1.3	1.2	1.2	1.1	1.5	1.3	1.8	1.5	1.4	1.0	0.9	1.6	1.2	1.1	1.3	0.3
Maximum circumference	7.4	13.9	12.5	9.7	6.6	14.2	8.2	11.8	14.2	9.6	11.0	10.1	17.1	13.4	7.8	14.2	16.0	13.5	13.0	9.4	8.6		
Minimum circumference	6.8	7.0	6.5	7.2	7.2	8.1	6.1	5.5	6.4	6.0	4.3	7.2	5.6	8.3	6.3	7.7	6.3	7.8	7.0	5.6	5.7		
Average circumference	7.2	11.9	9.3	8.4	6.9	10.8	6.9	8.5	9.6	7.1	6.7	8.7	10.4	11.3	7.1	10.2	9.6	10.2	9.6	7.5	7.2	8.8	1.6
Maximum slope	51	32	42	55	26	30	45	48	62	38	34	50	53	57	88	54	54	20	43	20	65		
Minimum slope	4	6	5	28	13	7	10	3	35	3	2	2	10	4	3	2	7	2	0	3	10		
Average slope	28	19	24	42	20	19	28	26	49	21	18	26	32	31	46	28	31	11	22	12	38	27	10
Branching angles	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	53	N/A	N/A	N/A	N/A	N/A	68	N/A	N/A		
Complexity	2	2	3	2	2	2	2	2	2	2	2	2	5	4	4	3	3	3	5	2	2	2.7	1.0
Tortuosity	1.02	1.24	1.07	1.20	1.19	1.16	1.18	1.03	1.22	1.15	1.27	1.23	1.07	1.70	1.56	1.37	1.41	1.45	1.23	1.54	1.42	1.27	0.20
Sediment density	0.70	0.70	0.70	0.70	0.35	0.70	1.1	0.70	0.35	1.1	1.1	0.35	0.70	0.70	0.35	0.70	0.70	1.1	0.70	0.70	1.1		
Sediment moisture	40	40	40	40	40	60	40	40	40	40	40	40	60	40	40	40	60	40	60	40	40		

Sediment density is in kg/cm²; all other measurements are in cm *BR* branched ramp, *BU* branched U-shaped burrow, *HU* horizontal U-shaped burrow, *J* J-shaped burrow, *N/A* not applicable, *R* ramp, *SR* sinuous ramp, *U* U-shaped burrow
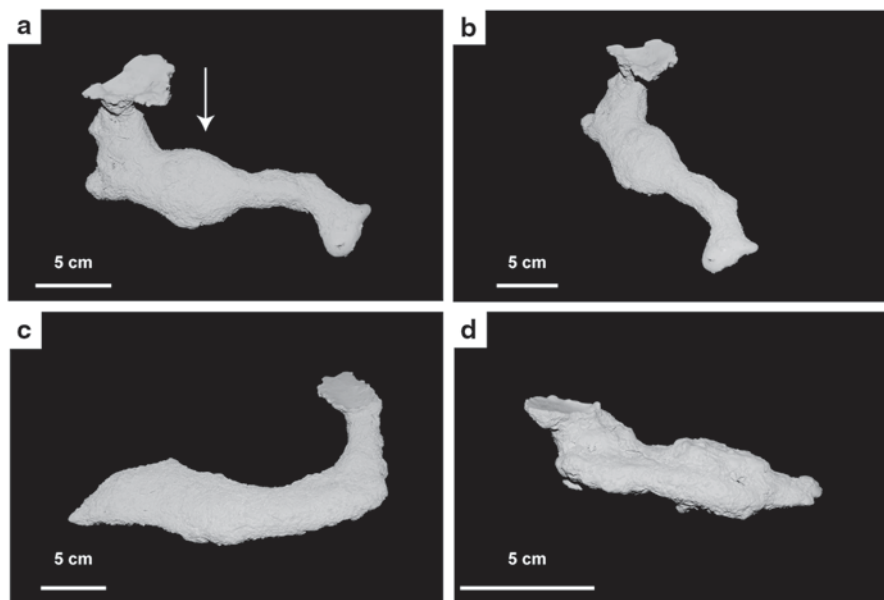
Fig. 14.2 Simple ramps. **a** Right view of a simple ramp with a laterally expanded chamber (at *arrow*; TGB1). **b** Right oblique view of a simple ramp (TGB1). **c** Left oblique view of an elongate, simple ramp (TGD1). **d** Right view of a small, simple ramp (TGD2)

14.4.2 Open Burrows and Biogenic Structures

14.4.2.1 Mounds and Depressions

These structures were simple surficial biogenic structures consisting of sediment mounds and their accompanying depressions. Mounds and depressions occurred in one experiment with 20% sediment moisture in which the skink could not produce an open burrow. The mounds and depressions had a maximum width and relief of 10.0 cm ($\bar{x}$ =7.7 cm) and 3.9 cm ($\bar{x}$ =2.7 cm), respectively. The observed mounds and depressions were isolated and were formed by sediment displacement during attempts at active burrowing.

14.4.2.2 Simple Ramps

Simple ramps (n=9) were the most common burrow morphology produced in the experiments. Simple ramps consist of a burrow with a single entrance and an elongate, sloping tunnel (Fig. 14.2). Tunnels in the simple ramp architecture have slopes of 19–49º ($\bar{x}$ =28º, σ=10). Ramps have an average maximum depth of 4.6 cm (2.3–9.4 cm; σ=2.0), an average width of 2.8 cm (2.0–4.0 cm; σ=0.6), an average height of 2.2 cm (1.4–3.6 cm; σ=0.6), an average circumference of 8.8 cm (6.9–11.9 cm;

$\sigma=1.7$), an average width-to-height ratio of 1.3 (0.7–1.6; $\sigma=0.3$), an average length of 13.7 cm (6.5–28.7 cm; $\sigma=6.7$ cm), an average complexity of 2.1 (2.0–3.0; $\sigma=0.3$), and an average tortuosity of 1.14 (1.02–1.24; $\sigma=0.08$; Table 14.2). The cross-sectional shape of the tunnels in seven of the simple ramps is flattened elliptical, although two (TGX2, TGN1) have circular cross-sections. The simple ramp architecture does not include chambers with the exception of one burrow (TGB1) with a centrally located chamber (Fig. 14.2a). Ramps occurred in all sediment types except for those with 20% sediment moisture content (Exp. 3).

14.4.2.3   Sinuous Ramps

Sinuous ramps ($n=3$) are classified as unbranched ramps that deviate laterally at least 3.0 cm from the surface opening and have a tortuosity greater than 1.1 (Fig. 14.3). Two of the sinuous ramps are flattened elliptical in cross-section, whereas the third (RGL1) is circular. The sinuous ramps have an average slope of 22° (18–26°; $\sigma=4$), an average maximum depth of 4.6 cm (3.3–6.2 cm; $\sigma=1.5$), an average width of 2.5 cm (2.0–3.2 cm; $\sigma=0.5$), an average height of 1.9 cm (1.8–2.0 cm; $\sigma=0.1$), an average circumference of 7.5 cm (7.1–8.7 cm; $\sigma=0.9$), an average width-to-height ratio of 1.3 (1.1–1.5; $\sigma=0.2$), an average length of 20.5 cm (15.7–24.3 cm; $\sigma=4.4$), an average complexity of 2.0 (2.0; $\sigma=0.0$), and an average tortuosity of 1.21 (1.15–1.27; $\sigma=0.05$; Table 14.2). Sinuous ramps occurred in experimental sediments with 20% clay and 20% sand (Exp. 2).

14.4.2.4   Branched Ramps

Branched ramps ($n=3$) consist of a burrow with a single entrance and two intersecting, sloping tunnels (Fig. 14.4). The branched ramps have an average slope of 36° (31–46°; $\sigma=8$), an average maximum depth of 7.5 cm (3.2–13.9 cm; $\sigma=5.7$), an average width of 3.4 cm (2.4–4.3 cm; $\sigma=0.8$), an average height of 2.2 cm (1.5–2.6 cm; $\sigma=0.5$), an average circumference of 9.6 cm (7.1–11.3 cm; $\sigma=1.8$), an average width-to-height ratio of 1.6 (1.3–1.8; $\sigma=0.2$), an average total length of 20.7 cm (12.0–31.0 cm; $\sigma=9.6$), an average complexity of 4.3 (4.0–5.0 cm; $\sigma=0.5$), and an average tortuosity of 1.44 (1.07–1.70; $\sigma=0.27$; Table 14.2). Two of the branched ramps have flattened elliptical cross-sectional shapes, whereas the third (TGN2) has a flat floor and roof. One branched ramp (RGX2) possesses a terminal chamber (Fig. 14.4a and b). The branched ramps were produced in experiments with 100% coconut fiber (Exp. 1), 20% sand sediment (Exp. 2), and 60% moisture content sediment (Exp. 3).

14.4.2.5   U-shaped Burrows

U-shaped burrows ($n=2$) consist of burrows with two entrances of similar dimensions that are connected by variably sloping tunnels (Fig. 14.5a and b). The tunnels

Fig. 14.3 Sinuous ramps.
a Right oblique view of an elongate, sinuous ramp with a divot (at *arrow;* RGL1).
b Overhead view of a sinuous ramp (RGN1). **c** Front oblique view of a short, sinuous ramp with three divots (at *arrows;* TGL1A)
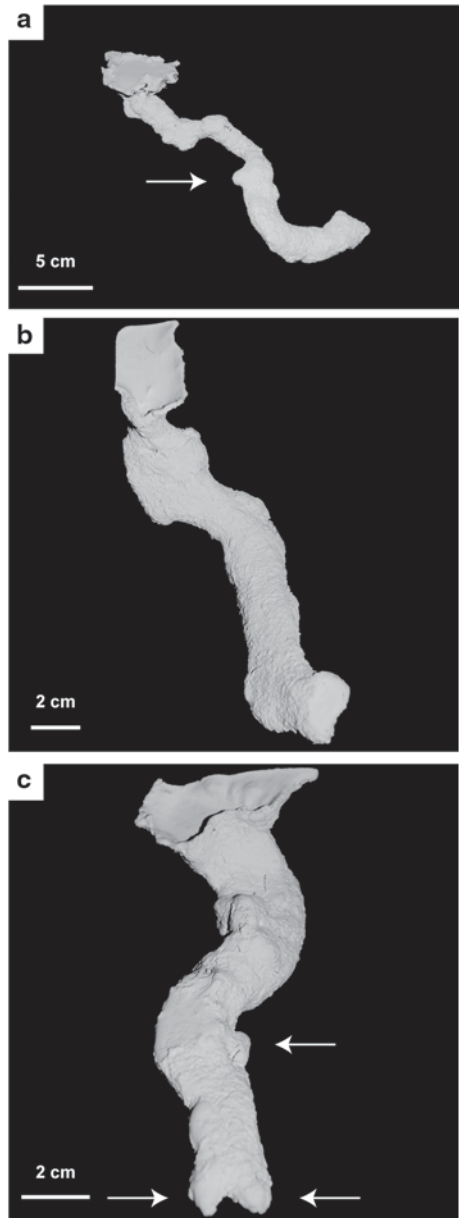
of the U-shaped burrows have an average slope of 30° (28–31°; $\sigma=2°$), an average maximum depth of 9.4 cm (7.2–11.5 cm; $\sigma=3.0$ cm), an average width of 3.0 cm (2.5–3.4 cm; $\sigma=0.5$), an average height of 2.4 cm (2.4 cm; $\sigma=0.01$), an average circumference of 9.9 cm (9.6–10.2 cm; $\sigma=0.3$), an average width-to-height ratio of 1.2 (1.0–1.4; $\sigma=0.3$), an average length of 34.0 cm (27.5–40.5 cm; $\sigma=9.2$ cm), an
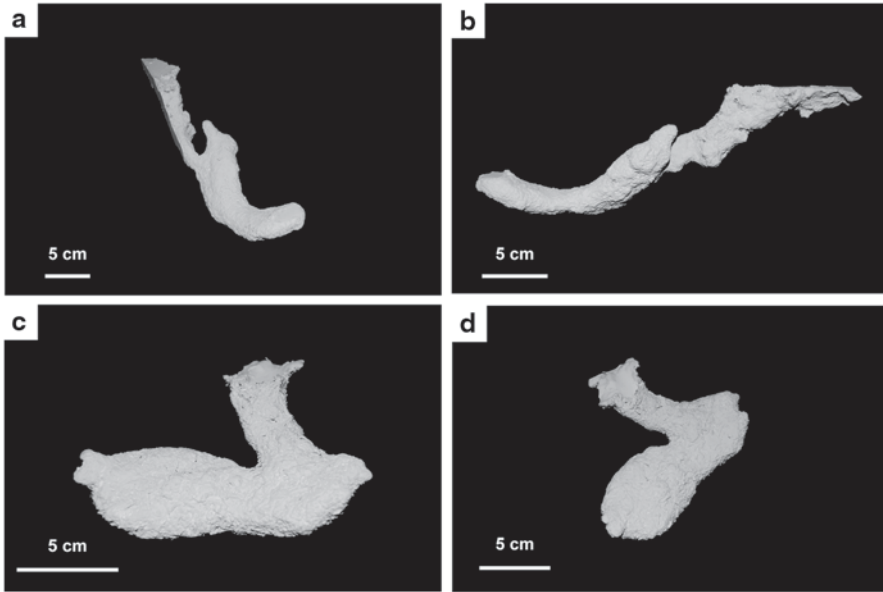
Fig. 14.4 Branched ramps. **a** Oblique view of an elongate branching ramp (RGX2). **b** Left view of an elongate branching ramp (RGX2). **c** Front view of a branched ramp with a chamber (TGB2). **d** Oblique view of a branched ramp with a chamber (TGB2)

average complexity of 3.0 (3.0; $\sigma=0.0$), and an average tortuosity of 1.39 (1.37–1.41; $\sigma=0.03$; Table 14.2). The U-shaped burrows are flattened elliptical in cross section. The paired entry tunnels either have similar slopes or slopes that may differ by up to 30°. U-shaped burrows were produced in experiments with 100 % coconut fiber with 40 % moisture content (Exp. 1) and 60 % moisture content (Exp. 3).

14.4.2.6   Subhorizontal U-shaped Burrows

A burrow ($n=1$) consisting of two entrances of similar dimensions that are connected by a tunnel with an average slope of 15° or less (Fig. 14.5c). The entrances of the single burrow have slopes of 20° and 11°. The subhorizontal, U-shaped burrow is flattened elliptical in cross-section, with an average slope of 11°, a maximum depth of 3.1 cm, a total length of 17.7 cm, an average width of 2.5 cm, an average height of 2.7 cm, an average circumference of 10.2 cm, a width-to-height ratio of 0.9, a complexity of 3, and a tortuosity of 1.45 (Table 14.2). The subhorizontal, U-shaped burrow was produced in an experiment with 20 % clay sediment (Exp. 2).

14.4.2.7   Branched U-shaped Burrows

A burrow ($n=1$) with two entrances of similar dimensions and slopes connected by a single tunnel that possesses a branch that does not connect to the surface
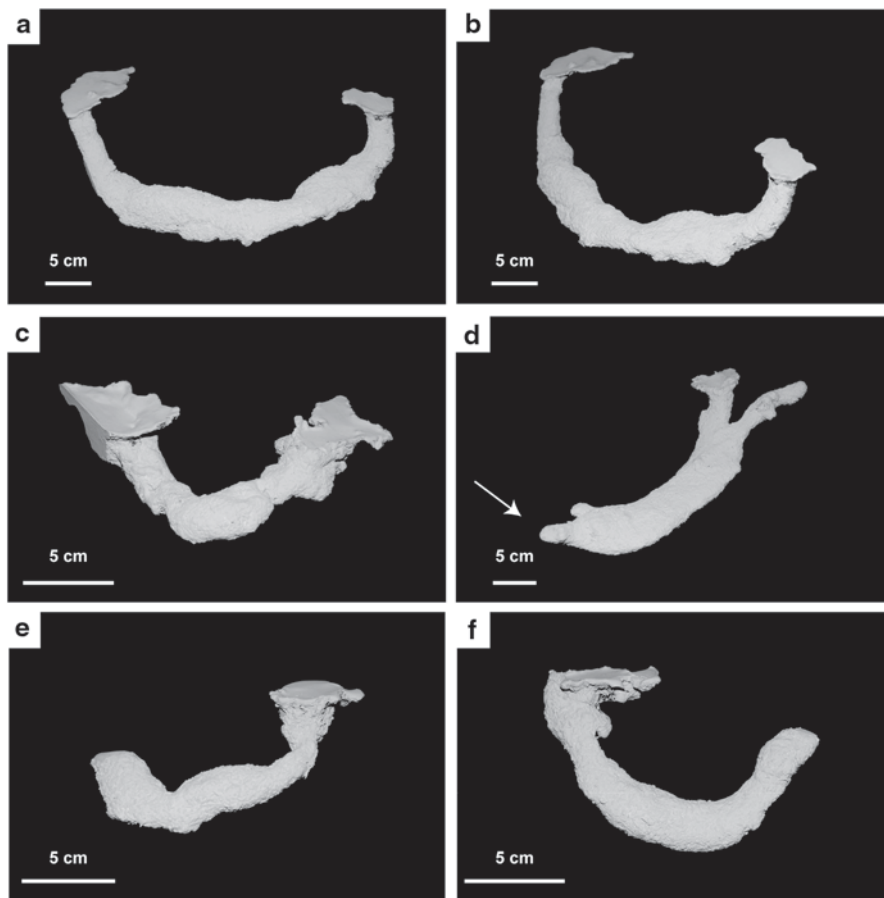
Fig. 14.5 U- and J-shaped burrows. **a** Front view of an elongate, U-shaped burrow (HT2). **b** Right oblique view of an elongate, U-shaped burrow (HT2). **c** Front view of a subhorizontal, U-shaped burrow (TGL2). **d** Left oblique view of a branched, U-shaped burrow (TGX1); second entrance not pictured (at *arrow*). **e** Left view of a J-shaped burrow (RGB2). **f** Right view of a J-shaped burrow (RGL2)

(Fig. 14.5d). The burrow has an average slope of 22°, maximum depth of 4.3 cm, an average width of 3.5 cm, an average height of 2.2 cm, an average circumference of 9.6 cm, a width-to-height ratio of 1.6, a total length of 40.0 cm, a complexity of 5, and a tortuosity of 1.23 (Table 14.2). In cross section, the branched U-shaped burrow is elliptical, but flattened on the roof and floor. The branched, U-shaped burrow was produced in an experiment with 60 % sediment moisture content (Exp. 3).

14.4.2.8   J-shaped Burrows

J-shaped burrows (*n*=2) consist of a single entrance leading to a downward-to-upward sloping tunnel that terminates within 2 cm of the sediment surface

(Fig. 14.5e and f). In cross section, the J-shaped burrows are flattened elliptical. The J-shaped burrows have an average slope of 25° (12–38°; $\sigma=25$), an average maximum depth of 4.2 cm (2.3–6.1 cm; $\sigma=2.7$), an average width of 2.3 cm (2.2–2.4 cm; $\sigma=0.1$), an average height of 2.0 cm (1.9–2.0 cm; $\sigma=0.1$), an average circumference of 7.3 cm (7.2–7.5 cm; $\sigma=0.1$), an average width-to-height ratio of 1.2 (1.1–1.2; $\sigma=0.0$), an average length of 18.4 cm (17.7–19.0 cm; $\sigma=0.9$ cm), an average complexity of 2.0 (2.0; $\sigma=0.0$), and an average tortuosity of 1.48 (1.42–1.54; $\sigma=0.01$; Table 14.2). J-shaped burrows were produced in experiments with 100 % coconut fiber sediment with 40 % moisture content (Exp. 1) and 20 % clay sediment (Exp. 2).

14.4.3   Burrow Ornamentation

With the exception of two burrow casts (HT1, RGN1), the tunnels were characterized by randomly spaced, rounded, triangular divots along the tunnel walls (Fig. 14.3a and c). A total of 75 divots were observed and measured on 19 burrow casts. The divots averaged 0.9 cm (0.4–2.6 cm; $\sigma=0.4$) in length, 1.1 cm (0.5–2.0 cm; $\sigma=0.4$) in width, and 0.8 cm (0.5–1.9 cm; $\sigma=0.3$) in height. There was no change in average divot size between experiments with different sediment properties or burrow morphology; however, the average number of divots per burrow did vary with sediment properties and with the duration of the experiments. There was an average of 3.3 divots per burrow in the 7-day experiments and 2.0 divots per burrow in 14-day experiments. The burrows produced in sediments with 20 % clay averaged 4.6 divots, whereas those produced in sediments with 20 % sand averaged 2.7 divots. Burrows produced in experiments with 100 % coconut fiber with 60 % sediment moisture content averaged 6.2 divots whereas those produced in 100 % coconut fiber with 40 % moisture content averaged 2.6 divots.

14.5   Analysis of Results

14.5.1   Comparison of Skink Burrow Architectures

The burrows produced by *M. multifasciata* were found to be highly to moderately similar to each other based on the ten quantitative properties used in the Bray–Curtis similarity test. The degrees of similarity between the burrows ranged from 0.9 to 0.6 with the majority (73 %) of the values varying between 0.9 and 0.8 (Table 14.3). No similarity values were below 0.6, and no values of 1.0 were obtained except when comparing a burrow to itself.

The average similarity values obtained when comparing burrows with the same architecture were 0.9 or 0.8 (Table 14.3). The sinuous ramps and the U-shaped burrows had the highest ($\overline{x}=0.9$) degree of similarity, whereas simple ramps, branched ramps, and J-shaped burrows had high ($\overline{x}=0.8$) degrees of similarity. There was an

Table 14.3 Bray–Curtis similarity test results for burrow casts

		HT1	TGD1	TGB1	RGB1	RGN2	TGX2	TGL1 B	TGD2	TGN1	TGL1 A	RGL1	RGN1	RGX2	TGB2	TGN2	HT2	RGX1	TGL2	TGX1	RGB2	RGL2
		R	R	R	R	R	R	R	R	R	SR	SR	SR	BR	BR	BR	U	U	HU	BU	J	J
HT1	R	1.0	0.7	0.8	0.8	0.9	0.8	0.9	0.9	0.7	0.8	0.7	0.8	0.7	0.8	0.8	0.7	0.7	0.7	0.7	0.7	0.8
TGD1	R	0.7	1.0	0.9	0.7	0.8	0.8	0.8	0.8	0.7	0.8	0.9	0.9	0.8	0.8	0.8	0.8	0.8	0.8	0.9	0.8	0.8
TGB1	R	0.8	0.9	1.0	0.8	0.8	0.8	0.9	0.9	0.8	0.9	0.9	0.9	0.8	0.9	0.8	0.8	0.8	0.8	0.8	0.8	0.9
RGB1	R	0.8	0.7	0.8	1.0	0.8	0.8	0.8	0.9	0.9	0.8	0.8	0.8	0.7	0.8	0.8	0.8	0.8	0.7	0.7	0.7	0.8
RGN2	R	0.9	0.8	0.8	0.8	1.0	0.9	0.9	0.9	0.7	0.9	0.8	0.9	0.6	0.7	0.8	0.7	0.7	0.8	0.7	0.8	0.8
TGX2	R	0.8	0.8	0.8	0.8	0.9	1.0	0.8	0.9	0.7	0.8	0.8	0.8	0.7	0.8	0.7	0.7	0.7	0.7	0.7	0.8	0.8
TGL1 B	R	0.9	0.8	0.9	0.8	0.9	0.8	1.0	0.9	0.8	0.9	0.8	0.9	0.7	0.9	0.8	0.8	0.8	0.8	0.7	0.8	0.9
TGD2	R	0.9	0.8	0.9	0.9	0.9	0.9	0.9	1.0	0.8	0.9	0.8	0.9	0.8	0.8	0.9	0.8	0.8	0.8	0.7	0.8	0.8
TGN1	R	0.7	0.7	0.8	0.9	0.7	0.7	0.8	0.8	1.0	0.7	0.7	0.8	0.8	0.8	0.9	0.7	0.8	0.6	0.6	0.6	0.9
TGL1 A	SR	0.8	0.8	0.9	0.8	0.9	0.8	0.9	0.9	0.7	1.0	0.9	0.9	0.7	0.8	0.8	0.7	0.8	0.8	0.8	0.9	0.8
RGL1	SR	0.7	0.9	0.9	0.8	0.8	0.8	0.8	0.8	0.7	0.9	1.0	0.9	0.8	0.8	0.7	0.8	0.8	0.8	0.8	0.9	0.8
RGN1	SR	0.8	0.9	0.9	0.8	0.9	0.8	0.9	0.9	0.8	0.9	0.9	1.0	0.8	0.9	0.8	0.8	0.8	0.8	0.8	0.8	0.9
RGX2	BR	0.7	0.8	0.8	0.7	0.6	0.7	0.7	0.8	0.8	0.7	0.8	0.8	1.0	0.9	0.7	0.9	0.9	0.7	0.8	0.7	0.8
TGB2	BR	0.8	0.8	0.9	0.8	0.7	0.8	0.9	0.8	0.8	0.8	0.8	0.9	0.9	1.0	0.8	0.8	0.9	0.8	0.8	0.8	0.9
TGN2	BR	0.8	0.8	0.8	0.8	0.8	0.7	0.8	0.9	0.9	0.8	0.7	0.8	0.7	0.8	1.0	0.7	0.7	0.6	0.7	0.7	0.9
HT2	U	0.7	0.8	0.8	0.8	0.7	0.7	0.8	0.8	0.7	0.7	0.8	0.8	0.9	0.8	0.7	1.0	0.9	0.7	0.9	0.7	0.8
RGX1	U	0.7	0.8	0.8	0.8	0.7	0.7	0.8	0.8	0.8	0.8	0.8	0.8	0.9	0.9	0.7	0.9	1.0	0.7	0.8	0.7	0.8
TGL2	HU	0.7	0.8	0.8	0.7	0.8	0.7	0.8	0.8	0.6	0.8	0.8	0.8	0.7	0.8	0.6	0.7	0.7	1.0	0.7	0.9	0.7
TGX1	BU	0.7	0.9	0.8	0.7	0.7	0.7	0.7	0.7	0.6	0.8	0.8	0.8	0.8	0.8	0.7	0.9	0.8	0.7	1.0	0.7	0.7
RGB2	J	0.7	0.8	0.8	0.7	0.8	0.8	0.8	0.8	0.6	0.9	0.9	0.8	0.7	0.8	0.7	0.7	0.7	0.9	0.7	1.0	0.8
RGL2	J	0.8	0.8	0.9	0.8	0.8	0.8	0.9	0.8	0.9	0.8	0.8	0.9	0.8	0.9	0.9	0.8	0.8	0.7	0.7	0.8	1.0

BR branched ramp, *BU* branched U-shaped burrow, *HU* subhorizontal U-shaped burrow, *J* J-shaped burrow, *SR* sinuous ramp, *U* U-shaped burrow

average of one instance (0–4; $\sigma=1.1$) of moderate similarity (0.7) per burrow when comparing burrows of the same architecture. No similarity values of 0.6 or lower were obtained when comparing burrows of the same architecture, and 11 of the total 19 burrows only had very high to high similarity values.

The burrows were still found to be very highly to moderately (0.9–0.7) similar on average when burrows with different architectures were compared to each other (Table 14.3). The majority ($n=12$ of 21) of interarchitecture comparisons resulted in an average similarity value of 0.8. The comparison of the sinuous ramps and the J-shaped burrows as well as the U-shaped and branched U-shaped burrows resulted in the highest average degree of similarity (0.9). Only seven comparisons between burrow architectures resulted in moderate average similarity values (0.7) and these primarily involved the U-shaped burrows. These were between U-shaped burrows and J-shaped burrows, between the subhorizontal U-shaped burrows and the simple ramps, branched ramps, U-shaped, and branched U-shaped burrows, and between the branched U-shaped burrows and the simple ramps and J-shaped burrows. When compared to each other, however, the three types of U-shaped burrows had an average similarity of 0.8. There was an average of five instances (0–11; $\sigma=3.3$) of moderate similarity (0.7–0.6) per burrow when comparing burrows of different architectures. Values of 0.6 were only obtained six times when comparing burrows of different architectures.

There were several similar individual properties across the seven different burrow architectures. The average burrow width, height, and width-to-height ratio were similar across all of the burrow morphologies with averages of 2.8 (2.0–4.3), 2.2 (1.4–3.6), and 1.3 (0.7–1.8) and standard deviations of 0.6, 0.5, and 0.3, respectively (Table 14.2). Average maximum depth, total length, circumference, and slope varied significantly with standard deviations from 1.6–10.0 (Table 14.2).

14.5.2   Morphological Variation Due to Sediment Properties

The greatest diversity of burrows was produced in trials with 100% coconut fiber with 40% moisture ($n=4$; Exp. 1) and with 100% coconut fiber with 60% moisture ($n=4$; Exp. 3). The lowest diversity of burrows was produced in trials with 20% sand ($n=2$; Exp. 2) and 100% coconut fiber with 20% moisture ($n=0$; Exp. 3).

A Spearman's rank correlation was performed with the data collected from experiments involving changes in sediment density. Correlation between the ten measured burrow properties and the three increasing sediment density values was not found to be significant (Table 14.4). The highest correlations were with width-to-height ratio and slope (Rs$=-0.48$, $\rho=0.03$; Rs$=-0.32$, $\rho=0.14$, respectively). M–W and K–S tests were used to determine if there were any statistically significant differences in the medians or distribution of burrow properties between the experiments involving changes in sediment density or moisture content

Table 14.4 Results (Rs and ρ values) of Spearman's rank correlation between sediment density and quantitative burrow properties

	Open-ings	Length	Depth	Width	Height	Circum.	W/H ratio	Slope	Com-plexity	Tortu-osity
Rs	0.15	0.15	−0.09	−0.26	0.07	−0.16	−0.48	−0.33	−0.1	0.04
P	0.53	0.51	0.69	0.25	0.77	0.49	0.03	0.14	0.66	0.88

(Table 14.5). There were only two properties that were found to be significantly different in terms of both their median and distribution ($\rho < 0.05$ for both M–W and K–S) among the burrows produced in the three sediment densities. These differences were present in burrows produced in the 20 % clay sediment (1.1 kg/cm^2), which had significantly lower average widths and average circumferences than burrows produced in the 100 % coconut fiber (0.7 kg/cm^2). There were also significantly different distributions (K–S) of average height and width-to-height ratio between these sediment densities as well; the burrows produced in 100 % coconut fiber (0.7 kg/cm^2) had a higher range of values in both properties. Comparison of burrows produced in 20 % sand (0.35 kg/cm^2) sediment with those in 100 % coconut fiber (0.7 kg/cm^2) indicated that only the median (M–W) of average height was significantly different; average burrow heights were lower in the sandy sediment. Comparison of burrows produced in 20 % sand (0.35 kg/cm^2) sediment with those in 20 % clay sediment (1.1 kg/cm^2) indicated that only the median (M–W) of width-to-height ratio were significantly different; width-to-height ratio was greater in sandy sediment.

No open burrows were produced in experiments with 20 % sediment moisture. During these experiments, the skinks were observed actively burrowing by intrusion, but the sediment was not cohesive enough to form an open burrow. These experiments only resulted in the production of mounds and depressions. The comparison of burrows produced in sediment with 40 % and 60 % moisture content indicated minimal variation in burrow properties (Table 14.5). The medians (M–W) of burrow complexity and height were significantly different as was the distribution of circumference (Table 14.5); the values of all three of these properties were higher in burrow produced in sediment with 60 % moisture content than those produced in sediment with 40 % moisture content.

Experiments involving changes in terrarium size and trial duration did not appear to produce significant differences in the burrow properties. M–W and K–S tests comparing burrows produced in 38 L and 114 L terrariums yielded no significant differences (Table 14.5). The temporary nature of the burrows produced by *M. multifasciata* led to the small sample size ($n = 2$) for the 14-day experiments preventing any statistical comparison with burrows produced in 7-day experiments ($n = 19$). The properties of these two burrows, however, were not outside the normal range of those of the burrows produced in 7 days (Table 14.2).

Table 14.5 Results (ρ values) of Mann–Whitney (M–W) and Kolmogorov–Smirnov (K–S) tests between the quantitative properties of burrows produced in sediments with different densities (kg/cm^2), sediment moisture contents (%), and tank sizes (L). *Outlined values* are considered significant at $\rho < 0.05$

		Openings	Length	Depth	Width	Height	Circum.	W/H Ratio	Slope	Complexity	Tortuosity
Density											
1.1 v 0.7	M-W	0.89	0.49	0.63	0.03	0.12	0.02	0.06	0.40	0.23	0.52
	K-S	0.32	0.32	0.84	0.05	0.03	0.03	0.05	0.68	0.32	0.92
0.7 v 0.35	M-W	0.32	0.36	0.99	0.25	0.04	0.10	0.67	0.30	0.50	0.57
	K-S	0.08	0.55	0.98	0.32	0.16	0.32	0.55	0.32	0.32	0.81
1.1 v 0.35	M-W	0.50	0.18	0.90	0.27	0.71	0.71	0.05	0.27	0.87	0.99
	K-S	0.99	0.08	0.48	0.48	0.96	0.96	0.08	0.48	0.99	0.88
Moisture											
60 v 40	M-W	0.10	0.15	0.12	0.45	0.03	0.07	0.34	0.89	0.05	0.68
	K-S	0.61	0.09	0.22	0.61	0.07	0.04	0.43	0.90	0.28	0.57
Tank Size											
38 v 114	M-W	0.59	0.56	0.83	0.29	0.31	0.20	0.44	0.86	0.43	0.49
	K-S	0.53	0.73	0.50	0.69	0.21	0.43	0.80	0.68	0.73	0.42

14.6   Discussion

14.6.1   *Burrow Morphology and Trace Maker*

Seven burrow architectures were produced by *M. multifasciata*. Several of the burrow architectures were produced by multiple individuals and were duplicated in multiple experiments. The overall forms of the seven burrow architectures were found to be similar using nonparametric statistics and the average width, height, and width-to-height ratio were found to be similar across all of the burrow morphologies. These three burrow properties resemble the dimensions of *M. multifasciata* (average trunk width: 2.7 cm, average burrow width: 2.8 cm; average trunk height: 1.8 cm, average burrow height: 2.2 cm; average trunk width-to-height ratio: 1.7, average burrow width-to-height ratio: 1.6), and are, therefore, likely directly related to the morphology of the skinks themselves. Although the dimensions of a burrow do not always correspond exactly to those of the trace maker, they can be a good indicator of the relative size (Bromley 1996; White 2005). Similar correlations have been observed between the width and height of tunnels and trace makers in recent neoichnological studies with both vertebrates and invertebrates (e.g., Smith and Hasiotis 2008; Hembree and Hasiotis 2006; Hembree 2009, 2013; Halfen and Hasiotis 2010; Hembree et al. 2012).

The burrow shape and ornamentation also reflect the morphology of *M. multifasciata*. The burrows produced by the skinks have moderately concave roofs and floors; this is similar to the trunk morphology of the skinks (Fig. 14.1). The triangular divots present along the burrow walls were likely a result of sediment probing by the skinks' triangular-shaped head. The skinks' heads averaged 1.3 cm in length and 0.9 cm in width and height, while the burrow ornamentation averaged 0.9 cm in length, 1.1 cm in width, and 0.8 cm in height. Similar triangular impressions have also been observed along the walls of extant amphisbaenian burrows (Hembree and Hasiotis 2006).

14.6.2   *Burrow Morphology and Behavior*

The three common properties of the seven burrow architectures are also a result of *M. multifasciata's* burrowing technique and three basic behaviors: dwelling, predation, and escape. Unlike burrowing by excavation which relies heavily on subsurface limb movement and may result in burrows that are larger than the trace maker (e.g., Traeholt 1995; Begall and Gallardo 2006), burrowing by intrusion tends to produce burrows with dimensions that closely match the dimensions of the trace maker. Burrows produced by intrusion may also possess compressional linings (Bromley 1996). This relationship has been observed with other soil-burrowing animals such as millipedes (Hembree 2009) and amphisbaenians (Hembree and Hasiotis 2006). All but five of the burrows have flattened elliptical cross-sections with moderately concave roofs and floors and short, arching walls. When actively burrowing, *M. multifasciata* penetrates and probes the sediment with its cone-shaped head while

it slowly undulates its body laterally to increase the width of the burrow to accommodate its trunk. These movements produce burrows with width-to-height ratios that are, on average, greater than 1.0.

The simple ramp was the most common burrow morphology produced by the skinks. This morphology provides a basic, temporary, subsurface dwelling. Simple ramps were also produced as short-lived escape structures; during daily terrarium spraying, some of the skinks rapidly burrowed into the substrate and produced ramps (RGB1). Burrow architectures with two entrances and complexities greater than or equal to 3 may be the product of predatory behavior exhibited by *M. multifasciata*. During an experiment, one individual was observed ambushing crickets from the entrance of its burrow. The dual entrances of the three types of U-shaped burrows likely increase the skinks chances of ambushing prey. Predation behavior from burrows by fossorial skinks has also been observed in the wild by Milne et al. (2002).

14.6.3 Burrow Morphology and Sediment Properties

Observations during experiments and quantitative analyses of the *M. multifasciata* burrows indicate that sediment density and moisture had some influence on the morphology of the burrows as well as whether or not open burrows could even be constructed. Increased sediment density produced burrows with lower average widths and circumferences. The increased sediment density restricted the skinks entry into and movement beneath the sediment. The skinks' difficulty in burrowing into dense sediment was indicated by the observation that the skinks spent more time at the surface before burrow construction in tanks containing these sediments. The lower widths and circumferences of the resulting burrows were likely due to the reduced ability of the skinks to perform lateral undulations which generally widened the tunnels in less dense sediment. Sediments with higher densities typically result in burrows with dimensions that are closer approximations to those of the burrower than sediments with lower densities (Bromley 1996). Burrow architecture appeared to be unaffected by increased sediment density, however. Architectures produced in the high density sediment included simple ramps, sinuous ramps, U-shaped burrows, and J-shaped burrows. Overall, Spearman's rank correlation tests did not produce coefficients that indicated a significant correlation between any of the ten burrow properties and sediment density (Table 14.4). The lack of significant correlation coefficients suggests that the morphology and behavior of the skinks have a greater influence on burrow morphology than sediment density.

Increased sediment moisture had a minimal effect on the burrow properties including higher than average burrow complexities and heights. Of the four burrows produced in experiments with increased sediment moisture, three had complexities greater than 2 (3–5). In addition, the only two burrows with complexity values of 5 were produced in sediments with increased moisture. This difference is likely due to the increased cohesion of the sediment as a result of the high moisture content which allowed for the long-term maintenance of multiple open tunnels in addi-

tion to the low density of the sediment which allowed the skinks to move easily through the subsurface. The same effect is likely responsible for the increase in tunnel height. Conversely, the inability of the skinks to produce open burrows in sediment with 20 % moisture content is the result of little-to-no sediment cohesion. The similarity of the other burrow properties despite changes in sediment moisture content again suggests that morphology and behavior of the skinks have more influence on burrow morphology than sediment properties.

14.7 Significance

14.7.1 Recognition of Skink Burrows in the Fossil Record

In order to interpret trace makers, it is essential that we are able to recognize the architecture and surficial morphology of burrows produced by modern burrowing animals. Trace fossils are classified according to a suite of ichnotaxonomic characters known as ichnotaxobases; these include aspects of ichnofossil morphology such as overall shape, orientation with respect to the sediment surface, architecture, and surficial features (Bromley 1996; Bertling et al. 2006). An understanding of the burrows produced by modern organisms is necessary to establish a set of ichnotaxobases that can be used in the identification and interpretation of trace fossils. Although only one species of burrowing skink was studied, the burrows produced by *M. multifasciata* provide a preliminary set of ichnotaxobases that will aid in the recognition and identification of skink burrows in the fossil record.

Architecture Open burrows produced by skinks include branched and unbranched subhorizontal ramps, sinuous ramps, branched and unbranched U-shaped burrows, and J-shaped burrows. These burrows include one to two surface openings, tunnels, shafts, and laterally expanded chambers.

Overall Shape The shafts and tunnels are elliptical in cross-section, with moderately flattened concave roofs and floors, and curved walls. The shafts and tunnels are approximately 1.5 times wider than high. Side branching is uncommon, but when it does occur, the branches tend to be short and do not connect to the surface.

Orientation Burrows are often subhorizontal (11–29°), occasionally oblique (30–45°), and rarely subvertical (46–74°).

Internal Structure No lining is present. The boundary between the sediment and the burrow wall is abrupt and irregular. The burrows were passively filled as a result of gravitational collapse.

Surficial Features The surfaces of the burrows are characterized by an irregular texture resulting from the surrounding sediment; however, the tops of the tunnels and chambers tend to be smoother than the floor or sides. Triangular-shaped, irregularly spaced divots are commonly preserved along the walls of the tunnels. The

width and height of the divots are approximately 37 % of the width and height of the average tunnel.

Variation from these ichnotaxobases is expected with different genera or families of skinks. For example, a burrow produced by an Australian skink (*Egernia*) is characterized by a more complex architecture consisting of multiple, interconnected, upward-branching tunnels, and a longitudinal median groove (Hasiotis and Bourke 2006). These differences in burrow morphology are likely due to the communal lifestyle and larger size of the skinks in the *Egernia* genus (Chapple 2003).

14.7.2   Paleontological and Paleoecological Significance

Burrows produced by skinks have a moderate preservation potential because they can be produced and maintained in firm and moist sediments that are resistant to collapse. The preservation of a skink burrow would require a rapid influx of sediment with a contrasting lithology. Rapid sediment influxes that could fill burrows are common along rivers and streams in Southeast Asia where storms and heavy rainfalls cause regular flooding events (Dudgeon 1999). Burrows from temperate and tropical ground-dwelling skinks such as *M. multifasciata* should, therefore, be well represented in the fossil record especially given the abundance, large geographic diversity, and long evolutionary history of skinks. The failure to recognize skink burrows has likely contributed to the scarcity of these structures in the literature. An increased awareness and recognition of skink burrows in the fossil record will allow for a more complete evolutionary and biogeographic history of this small, difficult to preserve group of animals.

Skinks are preyed upon by larger lizards, snakes, and birds (Pianka and Vitt 2006). Skinks, in turn, primarily feed on insects, but are also known to consume fruits, seeds, and vegetation (Iwamoto 1986; Grimmond et al. 1994; Attum et al. 2007; Carretero et al. 2010). Skinks are typically intermediate predators and are important components of healthy and recovering ecosystems (Iwamoto 1986; Fox 1997; Vreeland and Tietje 2000; Norbury et al. 2009). Skinks can even be the top predators in island and stressed ecosystems (Iwamoto 1986; Carretero et al. 2010) and are, therefore, vital in the maintenance of stable ecosystems as well as the further recovery of fragile ecosystems.

Due to their important roles in modern terrestrial ecosystems, the recognition of their burrows in the fossil record would allow for a better interpretation of paleoecological conditions. For example, the occurrence of skinks in a particular stratigraphic unit would suggest the presence of at least minimal vegetation for consumption, vegetative cover for thermoregulation and escape, and a stable population of arthropods. Extant lizards can typically be used to deduce the biomass of insect populations. Regressions on prey and predator weight have been used by Vezina (1985) to estimate the mean prey weight and the range of prey sizes consumed by insectivores. Sabo and Power (2002) measured the biomass of terrestrial arthropods in response to predation by the Western fence lizard (*Sceloporus occidentalis*). The

recognition of skink burrows could, therefore, be used to deduce at least the presence if not the relative abundance of other invertebrates, such as arthropods, since these food resources would be needed to support any skink population.

14.7.3 Paleopedological and Paleoenvironmental Significance

Observations made during these experiments have shown that skinks do play a role in pedogenesis. Although the burrows produced by *M. multifasciata* in the experiments did not reach a depth greater than 14.0 cm, skink burrows have been observed to reach a depth of 33.0 cm in natural settings (Hasiotis and Bourke 2006). These depths are associated with the A and B horizons of modern soils. Through the creation of burrows, mounds, and depressions, skinks mix and aerate the sediment. These processes also loosen the sediment and increase its porosity and permeability (Hole 1981; Wilkinson et al. 2009). The alteration of these sediment properties create preferred flow pathways for the migration of water and oxygen into the sediment (Schaetzl and Anderson 2005). Even when open burrows produced by *M. multifasciata* collapse, the resulting sediment is looser than the surrounding area and retains a relatively higher porosity and permeability. The creation of flow paths for water and oxygen allows for chemical processes including mineral dissolution, cementation, hydration, and oxidation to occur; these processes are essential to pedogenesis and soil maturation (Schaetzl and Anderson 2005). The skinks also directly contributed organics to the sediment in the form of fecal material and shed skin; in natural settings, these organics provide nutrients for soil microbes and plants forming the basis for soil food webs (Hole 1981; Wilkinson et al. 2009). Skinks, therefore, do affect multiple aspects of soil formation. The presence of fossil skink burrows in a paleosol would require the consideration of the influences outlined above when interpreting the soil-forming processes that produced the soil. Neoichnological work, even in laboratory settings, helps to inform on the influences of organisms on sedimentary material.

14.8 Conclusions

Neoichnological studies are necessary for the accurate interpretation of behaviors, burrowing methods, and trace makers associated with trace fossils. Because continental trace fossils are understudied with respect to their marine counterparts, traces produced in continental settings are often unrecognized, under-sampled, or excluded from study. Studies involving the neoichnology of extant continental trace makers are needed to correct this marine-based sampling bias and are crucial in the identification of continental trace makers as well as the interpretation of continental paleoenvironments and paleoecology. Since continental trace makers play a funda-

mental role in pedogenesis, continental neoichnological studies are also necessary for the interpretation of paleosols.

While engaged in dwelling, escape, and predation behaviors, the burrowing skink *M. multifasciata* produced seven distinct burrow architectures including three types of ramps (simple, sinuous, and branched), three types of U-shaped burrows (regular, subhorizontal, and branched), and J-shaped burrows. Despite the architectural differences, the burrows produced by *M. multifasciata* had similar average widths, heights, and width-to-height ratios and were found to have moderate-to-very high degrees of resemblance based on a Bray–Curtis similarity analysis (0.9–0.6). Sediment density and moisture resulted in few variations in the quantitative properties. Many of the burrows showed a conservation of form despite the changes in environmental parameters indicating that the morphology and behavior of *M. multifasciata* has a greater influence on burrow morphology than external environmental conditions.

The use of modern analogs, such as skinks, in the identification of burrows produced by reptilian continental burrowers is necessary for the accurate interpretation of the paleoecology of ancient terrestrial environments. The lack of literature concerning the burrowing behaviors and resulting structures produced by such lizards as *M. multifasciata* may result in the misidentification of lizard burrows and the exclusion of lizards from paleoecological reconstructions. Through the use of modern analogs, this study has demonstrated the range of biogenic structures produced by small, rarely preserved lizards.

This study not only allows for the potential recognition of biogenic structures produced by skinks, it also illustrates the importance of the use of modern analogs in paleontological evaluations. Biogenic structures produced by modern analogs allow for the relationships between the morphology of the trace maker, the morphology of the burrow, and environmental conditions to be directly observed. It is only through these modern observations that accurate interpretations can be made regarding trace fossils, their likely trace makers, and the surrounding environmental conditions.

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