Chapter 13
The Neoichnology of Two Terrestrial Ambystomatid Salamanders: Quantifying Amphibian Burrows Using Modern Analogs

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Contents

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Abstract This experiment involved the study of two species of ambystomatid salamanders, *Ambystoma tigrinum* and *Ambystoma opacum* (Amphibia: Caudata). Individual salamanders were placed in sediment-filled terrariums and allowed to burrow for 7 to 14 days under natural environmental conditions. Salamanders were then removed and their burrows cast, excavated, and described both qualitatively and quantitatively. Quantitative measurements included the number of surface openings, width, height, width-to-height ratio, total length, maximum depth, slope, branching angle, complexity, and tortuosity. Additional experiments involved variations in soil composition and soil moisture. *Ambystoma tigrinum* burrowed through excavation and compaction techniques whereas *A. opacum* only used compaction. Burrows produced by *A. tigrinum* consisted of ramps, branched ramps, U-, W-, Y-, and J-shaped burrows. Small-scale surface mounds were also created by *A. tigrinum*. Burrows produced by *A. opacum* consisted of ramps and branched ramps. Sinuous to straight surface trails were also produced by *A. opacum*. There was no recognized change in behavior or burrow properties in response to changes in the environmental parameters.

Keywords Trace fossil · Vertebrate · Bioturbation · Continental · Paleoecology

13.1 Introduction

The purpose of this chapter is to document the burrow morphology of two species of fossorial salamanders, *Ambystoma opacum* and *Ambystoma tigrinum,* through simple experiments in a controlled, laboratory setting. The morphology of the burrows was analyzed to determine the architectural features unique to each species and to burrowing salamanders in general, as well as how the burrows' properties varied due to changes in sediment composition and soil moisture. These observations provide for a better understanding of the paleoecological, paleoenvironmental, and paleoclimatic significance of continental vertebrate trace fossils by aiding in the recognition of the behaviors represented, potential trace makers, and the associated environmental conditions.

Fossil burrows and the organisms responsible for them are rarely found together, making the interpretation of trace makers and behaviors difficult. Study of modern analogs is necessary to accurately interpret trace makers, behaviors, and environmental conditions responsible for burrows within the fossil record (Bromley 1996). Neoichnological studies have generally been restricted to organisms found in the marine realm (Frey 1968, 1970; Frey et al. 1984; Gaillard 1991; Gingras et al. 2002, 2004; Martin 2006; Hertweck et al. 2007; Pearson et al. 2007; Seike and Nara 2007) with few studies of terrestrial invertebrates (Hasiotis and Mitchell 1993; Davis et al. 2007; Smith and Hasiotis 2008; Counts and Hasiotis 2009; Hembree 2009, 2013; Halfen and Hasiotis 2010; Hembree et al. 2012) and even fewer of terrestrial vertebrates (Brand 1996; Deocampo 2002; Hembree and Hasiotis 2006, 2007; Genise et al. 2009; Melchor et al. 2012). Marine trace fossils are well documented and, through neoichnological studies, behaviors and environmental factors controlling their morphology have been accurately determined (Bromley 1996). While the study of continental ichnology is relatively new, the same methods used in the marine realm have been applied for understanding the behaviors and environmental factors involved in the occurrence and morphology of continental trace fossils, especially those of terrestrial arthropods (Hasiotis 2002, 2007). The majority of knowledge of terrestrial vertebrate ichnology is focused on fossilized tracks and trackways (e.g., Brand and Tang 1991; Lockley et al. 1994; Brand 1996; Genise et al. 2009). Increasingly, however, vertebrate burrows are being documented in the fossil record and correlations have been made between burrowing behaviors in vertebrates and climatic and environmental conditions (Romer and Olson 1954; Voorhies 1975; Groenewald et al. 2001; Miller et al. 2001; Hasiotis et al. 2004, 2007; Hembree and Hasiotis 2008).

No detailed accounts of fossil burrows definitively attributed to salamanders or salamander-like amphibians have been described in the literature. A potential reason for this is that relatively few studies of the burrowing behaviors exhibited by modern salamanders have been conducted (e.g., Semlitsch 1983) and none have described the morphology of the burrows produced. In particular, no previous studies have presented three-dimensional models of modern salamander burrows. Amphibians with body types similar to modern salamanders have a fossil record extending to the Devonian and there is a strong likelihood that some of these species were fossorial (Gardner 2001; Anderson et al. 2008; Maddin et al. 2011). True salamanders (Amphibia: Caudata) appeared in the Jurassic and fossils of salamander-like amphibians (Amphibia: Caudata: Karauridae) with morphologies indicative of burrowing behaviors appear as early as the Early Permian (Amphibia: Lepospondyli) (Holman 2006; Maddin et al. 2011). These morphological characteristics are similar to those of extant burrowing amphibians, implying that burrowing organisms with body plans similar to *A. tigrinum* and *A. opacum* extend at least as far as the Early Permian (Maddin et al. 2011). The lack of knowledge and understanding about the burrowing behaviors and burrows produced by salamanders and their ancestors could, therefore, have potentially led to the misinterpretation of these structures in the fossil record.

13.2 Salamander Ecology and Behavior

Salamanders are a diverse group of amphibians consisting of approximately 500 extant species (Vitt and Caldwell 2008). Most salamanders have well-developed tails, cylindrical and often elongate bodies, distinct heads with reduced and frequently cartilaginous skulls, and short, well-developed limbs (Vitt and Caldwell 2008). Salamanders inhabit every continent except Antarctica and Australia and are adapted to both aquatic and terrestrial habitats. The Ambystomatidae are a group of heavy bodied and tailed, mostly fossorial, salamanders ranging in length from 8–34 cm. To avoid desiccation, most species within the Ambystomatidae spend a

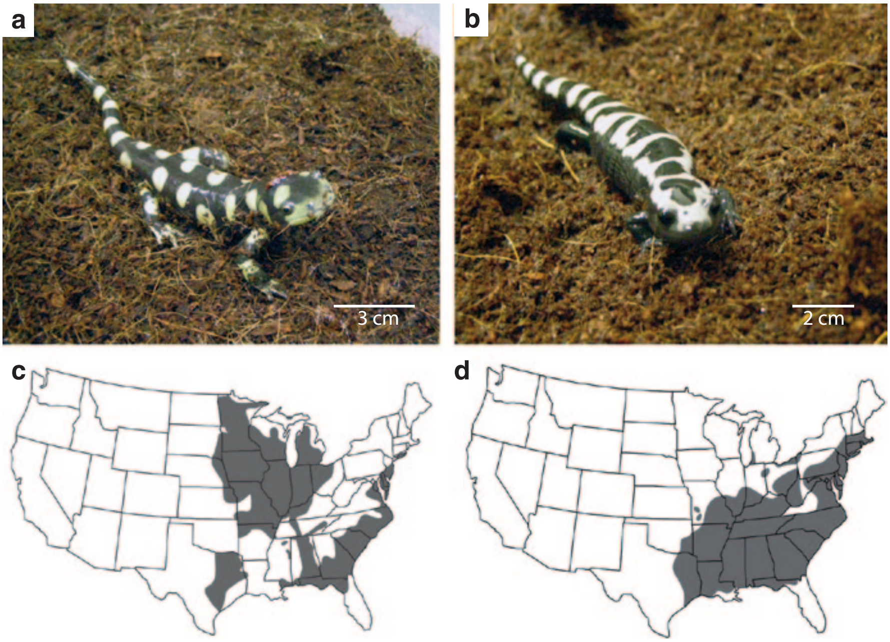


Fig. 13.1 The fossorial salamanders used in this experiment and their known geographic ranges. **a** *Ambystoma tigrinum*. **b** *Ambystoma opacum*. **c** Range of *A. tigrinum*. **d** Range of *A.opacum*

majority of their time within leaf litter or burrowed below the sediment surface (Semlitsch 1983).

Two species of salamanders from the Ambystomatidae were chosen for these experiments, *A. opacum* and *A. tigrinum* (Fig. 13.1a and b). Both species are fossorial and inhabit similar deciduous forest environments with temperatures averaging 18–20 °C within sandy loam to loamy soils with moisture levels of approximately 74 %. These are heavy bodied salamanders with short, well-developed legs and broad heads with rounded snouts. *Ambystoma tigrinum* generally has a more robust body type and adults are 5–14 cm longer than adult *A. opacum*. Both types of salamander are nocturnal, emerging from their burrow at night to hunt (Vitt and Caldwell 2008).

Ambystoma opacum (marbled salamander) has a geographic range extending from New England to Florida and as far west as eastern Texas (Anderson and Graham 1967; Fig. 13.1c). This species is the smallest of the ambystomatids, typically reaching adult sizes up to 11 cm in length. The life span of *A. opacum* is around 4 years, most of which is spent underground in burrows. Individuals mate in the fall, emerging from their burrow after a heavy rain to mate and deposit eggs. *Ambystoma opacum* burrow passively through compression by the expansion of preexisting cracks, holes, or other burrows in the sediment surface (Semlitsch 1983).

Ambystoma tigrinum (eastern tiger salamander) has a wide geographic range in eastern North America that extends from the Gulf Coastal Plains to the plains of

Table 13.1 Environmental parameters for each experiment. **a** Experiment 1. **b** Experiment 2. **c** Experiment 3

a. Basic morphology experiments			
Sediment composition	Moisture content	Enclosure size	Time
75O/25C	74 %	38, 114, and 246 L	7 days
75O/25C	74 %	38, 114, and 246 L	14 days
b. Variation in sediment composition			
Sediment composition	Moisture content	Enclosure size	Time
50O/50C	74 %	38, 114, and 246 L	14 days
50O/25C/25S	74 %	38, 114, and 246 L	14 days
c. Variation in moisture content			
Sediment composition	Moisture content	Enclosure size	Time
75O/25C	54 %	38, 114, and 246 L	14 days
75O/25C	94 %	38, 114, and 246 L	14 days

the Midwest, but it is mostly absent east of the Appalachians (Church et al. 2003; Fig. 13.1d). It is one of the largest salamander species within the ambystomatids, reaching total adult lengths of 15–25 cm. The life span of *A. tigrinum* is 12–15 years. Individuals mate in the spring, leaving their burrows to mate and deposit eggs within small ponds or streams. *Ambystoma tigrinum* actively excavate their burrows through the use of their snout and forelimbs using their hind limbs to move loose sediment backwards into soil piles (Semlitsch 1983; Kley and Kearney 2007).

13.3 Materials and Methods

The burrowing behavior and burrow morphology of wild-caught individuals of *A. opacum* and *A. tigrinum* ($n = 6$ each) were studied over the course of these experiments. Individuals of *A. opacum* were 6.0–6.2 cm long snout to vent (SVL), 1.5–1.9 cm wide, and weighed 8–13 g. Individuals of *A. tigrinum* were 7.5–9.0 cm long SVL, 1.5–2.2 cm wide, and weighed 14–30 g. The laboratory was kept on a 12-hour light cycle and temperatures were maintained at 18–23 °C throughout the study. Prey animals (crickets) were placed in the terrarium twice per week during and in-between experiments. Three different terrarium sizes, 38 L (50 × 25 × 30 cm), 114 L (60 × 45 × 40 cm), and 246 L (91 × 45 × 61 cm), were used to account for possible variations in burrow morphology due to space constraints. The sediment depth for each terrarium remained constant: 20 cm for the 38 L, 25 cm for the 114 L, and 55 cm for the 246 L. The sediment surface was sprayed with water daily to maintain moisture levels. Sediment moisture was monitored using an Aquateer EC300 moisture meter.

Experiment 1 involved the observation of the behaviors and burrow morphologies of each salamander under ideal conditions (Table 13.1a). The composition and moisture content of the sediment used in these experiments were chosen to closely mimic the physical properties of the soils occupied by *A. tigrinum* and *A. opacum* in the wild. Sediment compaction was kept at levels conducive to burrowing. The six individuals of both *A. tigrinum* and *A. opacum* were placed into separate terrariums containing a mixture of 75 % finely-shredded coconut fiber and 25 % clay loam soil (75O/25C; organic clay loam). Sediment moisture levels were kept at approximately 74 %. The experiments were conducted over 7 and 14 days to determine if the final burrow morphologies were changed over time. Experiments 2 and 3 involved variations in either sediment composition or moisture content (Table 13.1b and c). For both species, the sediment density was either increased with the addition of 25 % more clay loam (50O/50C; clay loam) or decreased with the addition of 25 % fine-grained sand (50O/25C/25S; sandy clay loam). In experiment 3, the sediment moisture content was either increased to 94 % or decreased to 54 %. The salamanders were observed under these altered conditions for 14 days. Species of *A. tigrinum* and *A. opacum* are commonly found burrowed within organic material (Semlitsch 1983). Due to this aspect of their ecology, burrows produced by *A. tigrinum* and *A. opacum* ($n = 9$ and 1, respectively) in the laboratory in 100 % organic material (i.e., coconut fiber) were also cast, excavated, and described. Terrariums filled with this sediment were primarily used as holding tanks for the salamanders between experiments. While moisture levels were not recorded with a moisture probe, they were maintained at visibly high levels (70–85 %).

During the experiments, observed burrowing activity was digitally recorded and visible changes in the sediment surface or burrow openings were recorded, measured, and photographed. At the end of each experiment, the salamanders were carefully removed from either within their burrows or from the sediment surface, as not to disturb any burrows. Open burrows were cast with quick-drying plaster, described, and measured qualitatively and quantitatively. Quantitative properties measured for each burrow cast included the number of surface openings, maximum depth, cross-sectional width, cross-sectional height, cross-sectional width-to-height ratio, total length, slope, and branching angles (Fig. 13.2a). Two additional, scale-independent, quantitative descriptions of the burrows were made: burrow complexity and tortuosity (Meadows 1991). Complexity is found by adding the total number of segments, surface openings, endpoints, and chambers of the burrow (Fig. 13.2b). Tortuosity is a measure of the deviation of a tunnel from a straight line and is found by dividing the total length of the tunnel by the straight line distance measured from end to end (Fig. 13.2c). Burrow casts were divided into different morphological types based on their qualitative and quantitative properties.

The ten quantitative measurements were then used to compare burrows of different individuals and species. The Bray–Curtis similarity test is a nonparametric statistical analysis used to determine the level of similarity between multiple samples each with multiple quantitative properties (Bray and Curtis 1957). This statistical analysis was chosen because it is capable of utilizing all ten quantitative properties together in order to quantify the similarity of each burrow cast instead of comparing each property individually. The level of similarity is ranked between 1.0–0.0, with values of 1.0 indicating burrows that are identical and 0.0 indicating burrows that are completely different (e.g., Bray and Curtis 1957). In this study, values of 0.9–0.8 indicate that the compared burrow casts have a high degree of similarity, values of

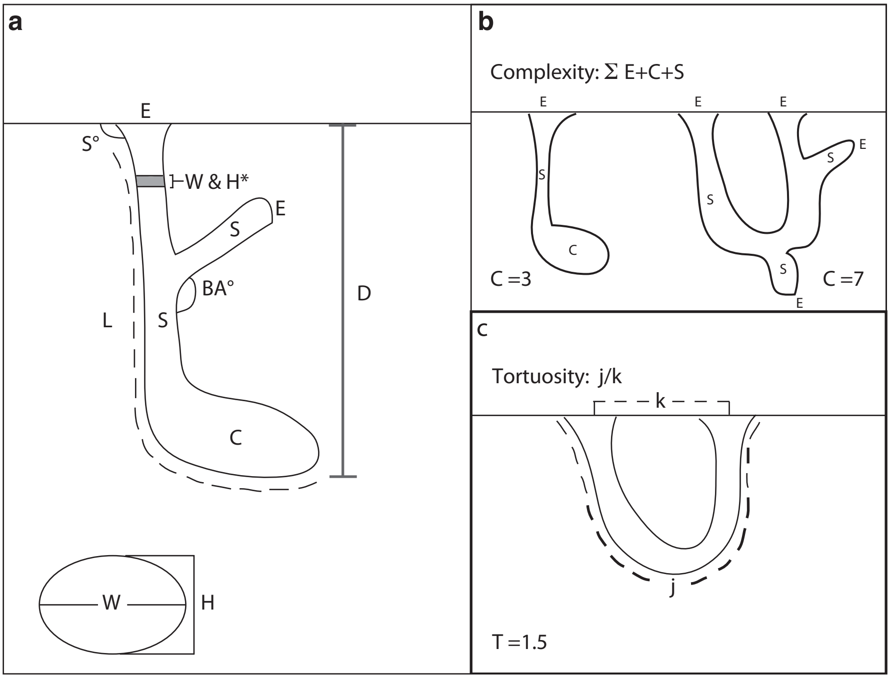


Fig. 13.2 Quantitative measurements taken for each burrow. Burrows were divided into segments (*S*), chambers (*C*), and endpoints (*E*). **a** Scale-dependent measurements include: *D* = maximum depth, *L* = total length, *W* = segment width, *H* = segment height, *S* = slope of burrow, and *BA* = branching angle. **b** Complexity. **c** Tortuosity. *j* = length of the burrow and *k* = endpoint to endpoint (*straight line*) distance. (Modified from Hembree and Hasiotis 2006)

0.7–0.6 indicate that they have a moderate level of similarity, and any values of 0.5 or less indicate that they are dissimilar following the studies of Hembree et al. (2012) and Hembree (2013).

The quantitative properties of the salamander burrows produced under different environmental conditions were analyzed using the Spearman's rank correlation test, a nonparametric statistical analysis used to determine if two variables are correlated. Sediment composition, moisture content, and enclosure size were treated as independent variables while average width, average height, average width-to-height ratio, total length, maximum depth, and slope of the burrow casts were treated as dependent variables. These analyses were performed to determine if the burrow properties were influenced by the sediment properties or habitat size. Spearman's rank correlation was also used to compare the width, height, width-to-height ratio, and length of the burrow casts to the width, height, width-to-height ratio, and length of the salamanders to determine if body size had an effect on the burrow size. Salamander body size was treated as the independent variable while burrow size was treated as the dependent variable.

Finally, two additional nonparametric analyses, the Mann–Whitney and Kolmogorov–Smirnov tests, were performed to determine if the means and distributions of the individual quantitative measurements of the burrows, excluding the number of surface openings, slope, and branching angle, produced by *A. tigrinum* and *A. opacum* were similar. All statistical analyses were conducted using PAST (Palaeontological Statistics, ver. 2.16).

13.4 Experimental Results

Both salamander species produced open burrows in all of the sediment types with little visible variation in morphology. *Ambystoma tigrinum* and *A. opacum* exhibited similar behaviors in similar sediments with occasional variation in burrowing methods unrelated to changes in the environmental parameters. Many experiments, particularly those involving *A. tigrinum,* resulted in multiple burrows being cast due to several abandoned burrows remaining open to the surface for the entire experimental period. Two experiments with *A. opacum* resulted in no burrow casts being produced. These two salamanders excavated only shallow burrows that were passively filled by gravitational collapse of the overlying sediment before the end of the experiment.

13.4.1 A. tigrinum

13.4.1.1 Behavior

Ambystoma tigrinum burrowed using both excavation and compaction techniques within 12 h of being placed in the terrarium. Excavation was used to start the burrow after which their method of burrowing would switch to compaction. Individuals excavated by bracing their bodies on the sediment surface with their hind limbs and then thrusting their forelimbs into the sediment; sediment was thrown and pulled back into small mounds (Fig. 13.3). Individuals pushed themselves farther below the surface by first forcing their snout into the sediment and then by moving their head both laterally and vertically. As the salamander burrowed deeper, this process compressed the sediment around the margins of the burrow. Depending on the individual, burrows were either inhabited for the entire experimental period ($n=36$) or were abandoned and new burrows were created ($n=18$). The salamanders spent approximately 80 % of their time below the surface, emerging from their burrows most commonly at night either through the original burrow opening or by creating a new opening.

13.4.1.2 Burrow Morphology

Ramps These commonly produced burrows ($n=41$) consist of one elliptical surface opening, one elliptical, subhorizontal-to-subvertical tunnel or shaft, and, at

Fig. 13.3 *Ambystoma tigrinum* burrowing by excavation

the end of most ($n=27$), a laterally expanded, hemispherical chamber (Fig. 13.4a and b; Table 13.2; Table A.1). Ramps were constructed by all six salamanders in all sediment compositions and moisture conditions. The total length of the ramps is 9–26 cm ($\bar{x}=15.4$ cm, SD = 3.8) and the maximum depth is 4.0–18.4 cm ($\bar{x}=9.4$ cm, SD = 3.2). The tunnels and shafts enter the sediment surface at angles of 10–90° ($\bar{x}=55°$, SD = 15) and have widths of 1.2–4.1 cm ($\bar{x}=2.9$ cm, SD = 0.5 cm), heights of 1.5–4.2 cm ($\bar{x}=2.2$ cm, SD = 0.5 cm), and width-to-height ratios of 0.6–2.1 ($\bar{x}=1.3$, SD = 0.2). The terminal chambers have widths of 2.4–5.4 cm ($\bar{x}=3.7$ cm, SD = 0.6), heights of 1.6–2.9 cm ($\bar{x}=2.2$ cm, SD = 0.3), and width-to-height ratios of 1.2–2.9 ($\bar{x}=1.7$, SD = 0.3). The heights of the chambers are, on average, the same as those of the tunnels, but the widths of the terminal chambers are typically 0.8 cm greater. Ramps have a complexity of either 2 when they consist of only one opening and a single tunnel or shaft or 3 when they also include a single chamber. The tortuosity is 1.0–1.7 ($\bar{x}=1.3$). Six ramps produced by *A. tigrinum* also possessed narrow, sinuous tunnels extending from the end of the chamber (Fig. 13.4c and d). The extensions were 1.0–2.3 cm wide, 1.2–2.6 cm high, and 2.6–5.0 cm long, dimensions which were considerably less than the rest of the burrow.

U and W-Shaped Burrows These less commonly produced burrows ($n=8$) consist of two to three, elliptical-to-circular, surface openings with two or three elliptical, subhorizontal-to-vertical tunnels or shafts connected below the surface by one or two tunnels all with similar widths and heights (Fig. 13.5; Table 13.2; Table A.1). U-shaped burrows consist of a single, continuous tunnel (Fig. 13.5a and b) whereas W-shaped burrows are composed of two intersecting U-shaped burrows (Fig. 13.5c and d). These burrows were produced in the organic clay loam and sandy clay loam sediment compositions and in soil moisture percentages of 74 and 94 %. The burrows are 12.2–34.0 cm ($\bar{x}=22.3$ cm, SD = 7.7) long and extend 3.5–7.9 cm

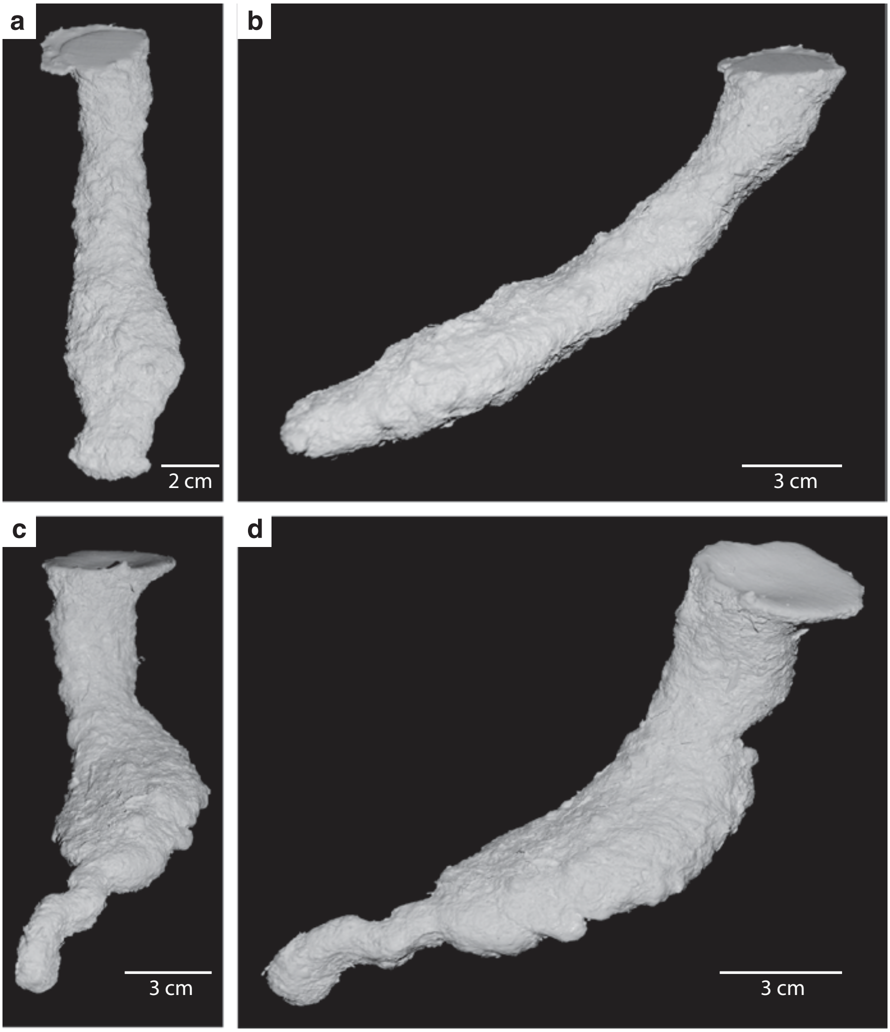


Fig. 13.4 Ramp morphologies produced by *A. tigrinum*. **a** Overhead view of a common ramp with a terminal chamber (TS2-3-1). **b** Side view of TS2-3-1. **c** Overhead view of a ramp with a narrow tunnel extending from the terminal chamber (TS6-2-2(T)). **d** Side view of TS6-2-2(T)

($\bar{x}$ = 5.7 cm, SD = 1.6) into the sediment at angles of 15–90° ($\bar{x}$ = 53°, SD = 16). The shafts and tunnels have widths of 1.5–4.8 cm ($\bar{x}$ = 3.2 cm, SD = 0.5), heights of 1.2–4.0 cm ($\bar{x}$ = 2.3 cm, SD = 0.3), and width-to-height ratios of 1.1–1.8 ($\bar{x}$ = 1.4, SD = 0.3). The complexity of the U-shaped burrows is 3 including two surface openings and a single continuous U-shaped tunnel. The W-shaped burrows have complexities of either 5, including three surface openings and two continuous U-shaped shafts or tunnels, or 6, including three surface openings and three curved shafts or tunnels that intersect beneath the surface. The tortuosities of the burrows are 1.1–2.8 ($\bar{x}$ = 1.8, SD = 0.5).

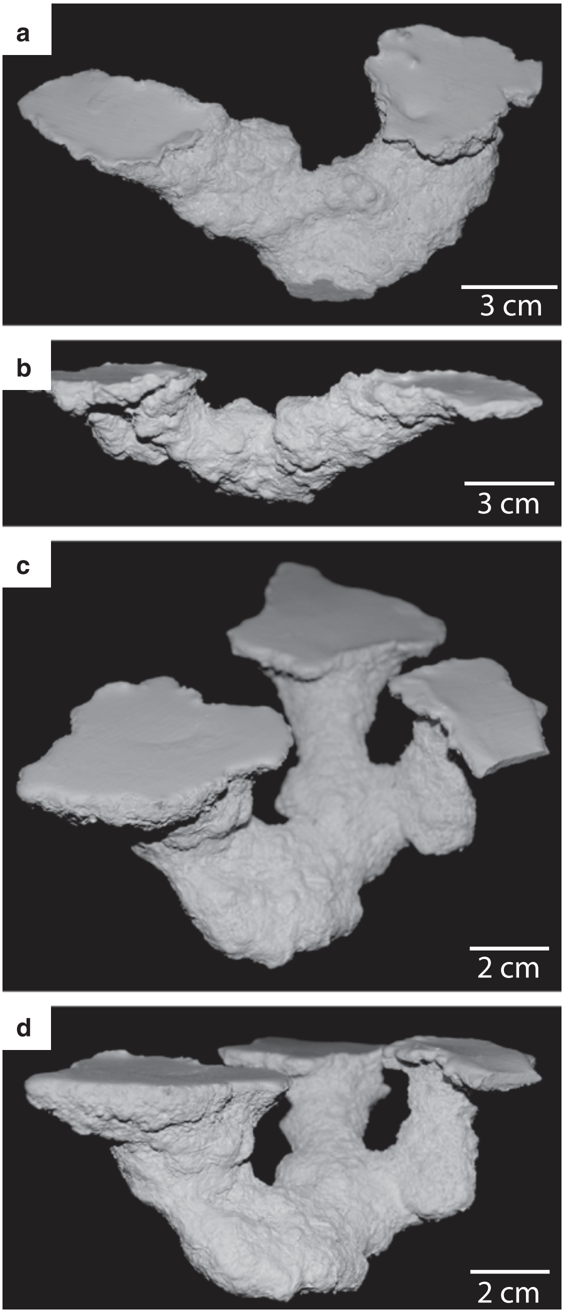


Fig. 13.5 U- and W-shaped morphologies produced by *A. tigrinum*. **a** Overhead view of a U-shaped burrow (TS3-1-1). **b** Side view of TS3-1-1. **c** Overhead view of a W-shaped burrow (TS3-1-2A). **d** Side view of TS3-1-2A

Table 13.2 Average quantitative properties of burrows produced by *A. tigrinum* and *A. opacum*

A. tigrinum

	Ramp	Branched ramp	U- and W-shaped	J-shaped	Y-shaped	Combined
Surface openings	1	1	2	1	2	1
Depth	9.4	10.1	5.7	16.7	10.7	9.0
Length	15.4	19.4	22.3	27.0	23.9	17.2
Width	3.0	2.9	3.2	2.5	2.9	3.0
Height	2.1	1.9	2.3	1.7	1.9	2.1
W/H	1.5	1.5	1.4	1.5	1.5	1.5
Slope	55.0	68.0	52.9	62.0	55.9	55.1
Branch angle	0.0	52.0	4.4	0.0	90.0	6.6
Complexity	3	5	4	2	5	3
Tortuosity	1.3	1.8	1.8	2.5	1.7	1.4

A. opacum

	Ramp	Branched ramp	Combined
Surface openings	1	1	1
Depth	7.2	5.7	7.1
Length	12.7	14.5	12.8
Width	2.9	2.9	2.9
Height	2.0	1.9	2.0
W/H	1.4	1.5	1.5
Slope	43.6	37.0	43.0
Branch angle	0.0	90.0	7.8
Complexity	2	4	2
Tortuosity	1.3	1.7	1.3

Depth, length, width, and height in cm. Combined is the average of all burrows regardless of morphology

Branched Ramp This rare burrow morphology ($n=1$) consists of an elliptical surface opening, an elliptical, subvertical tunnel, and a laterally expanded chamber with two branches (Fig. 13.6; Table 13.2; Table A.1). The branched ramp was produced in the clay loam sediment with a moisture content of 74%. The total length of the branched ramp is 19.4 cm reaching a maximum depth of 10.1 cm. The tunnel enters the sediment at an angle of 68° and has an average width of 2.7 cm, an average height of 1.9 cm, and an average width-to-height ratio of 1.5. The chamber has an average width of 3.7 cm, an average height of 2.2 cm, and an average width-to-height ratio of 1.7. The two branches extend from the chamber at angles of 52 and 70 ° leading upward and downward, respectively. The complexity of the burrow is 5 due to the single surface opening, three tunnel segments, and a single chamber. The tortuosity is 1.8.

Y-Shaped Burrows This uncommon burrow morphology ($n=3$) consists of two or three surface openings and two or three subhorizontal-to-subvertical shafts that meet under the sediment surface and terminate in one vertical shaft (Fig. 13.7a and b; Table 13.2; Table A.1). These burrows were produced in holding tanks in organic sediment. The Y-shaped burrows are 23.0–25.2 cm ($\bar{x}=23.9$ cm, SD = 1.1) in length and reach depths of 9.6–12.4 cm ($\bar{x}=10.7$ cm, SD = 1.5). The tunnels and

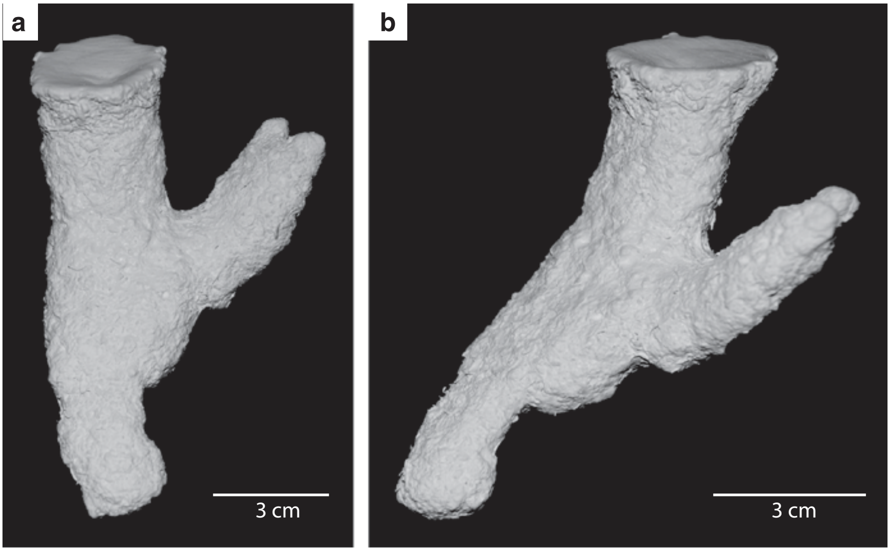


Fig. 13.6 Branched ramp morphology produced by *A. tigrinum*. **a** Overhead view of the branched ramp (TS6-2-1A). **b** Oblique view of TS6-2-1A

shafts enter the sediment at angles of 36–74° ($\bar{x}$ = 56.7° cm, SD = 12.9) and meet the single, terminal tunnel or shaft at angles of 36–74° ($\bar{x}$ = 56.7°, SD = 11.9°). The terminal tunnel or shaft begins at depths of 2.5–6.0 cm ($\bar{x}$ = 4.2 cm, SD = 1.8). The tunnels and shafts have widths of 1.8–3.8 cm ($\bar{x}$ = 2.9 cm, SD = 0.5), heights of 1.2–2.5 cm ($\bar{x}$ = 1.9 cm, SD = 0.2), and width-to-height ratios of 1.4–1.6 ($\bar{x}$ = 1.5, SD = 0.09). The complexity of the burrows is 4, 5, or 7 depending on the number of shafts (2–4) and surface openings (2–3) present. The tortuosity ranges from 1.3–2.0 ($\bar{x}$ = 1.7, SD = 0.3).

J-Shaped Burrow A rare morphology ($n = 1$) consisting of one surface opening leading to an elliptical, subvertical, J-shaped shaft (Fig. 13.7c; Table 13.2; Table A.1). This burrow was produced in a holding tank in organic sediment. The length of the burrow is 27 cm reaching a maximum depth of 16.7 cm. The shaft enters the sediment at an angle of 62° and has an average width of 2.5 cm, an average height of 1.7 cm, and an average width-to-height ratio of 1.5. The complexity of the J-shaped burrow is 2 due to its single surface opening and single shaft. The tortuosity is 2.5.

Bioglyphs Bioglyphs were commonly observed on all burrows, although they were best developed on burrows produced in clay loam sediment. Most of the bioglyphs present are rounded to elongate protrusions (Fig. 13.8a and b) as well as some bilobate or heart-shaped markings (Fig. 13.8c). The burrows possess 0–11 of these structures with a variable distribution along their length.

Surface Features Mounding was present in all sediments regardless of composition or moisture content (Fig. 13.9). The mounds were directly related to the burrow-

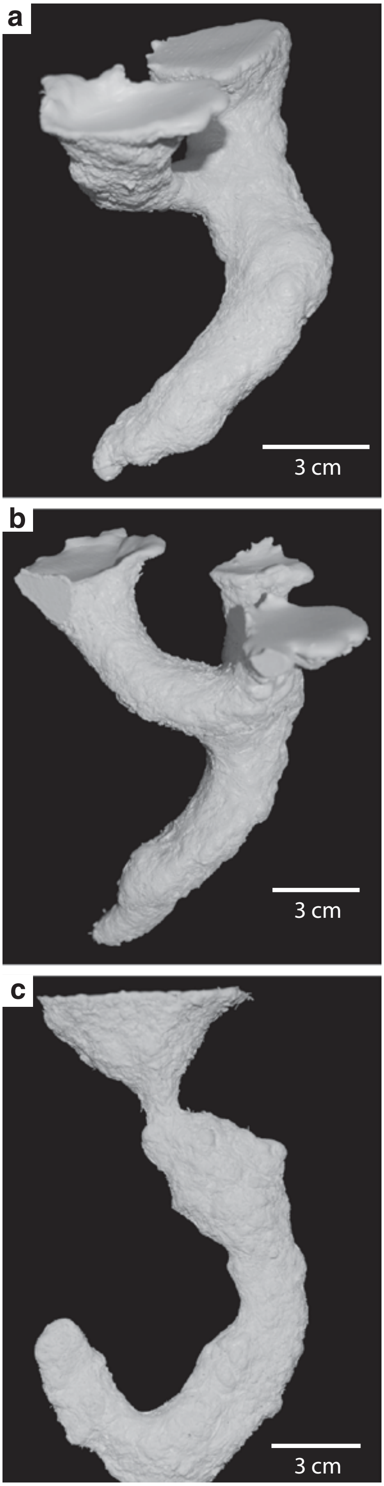
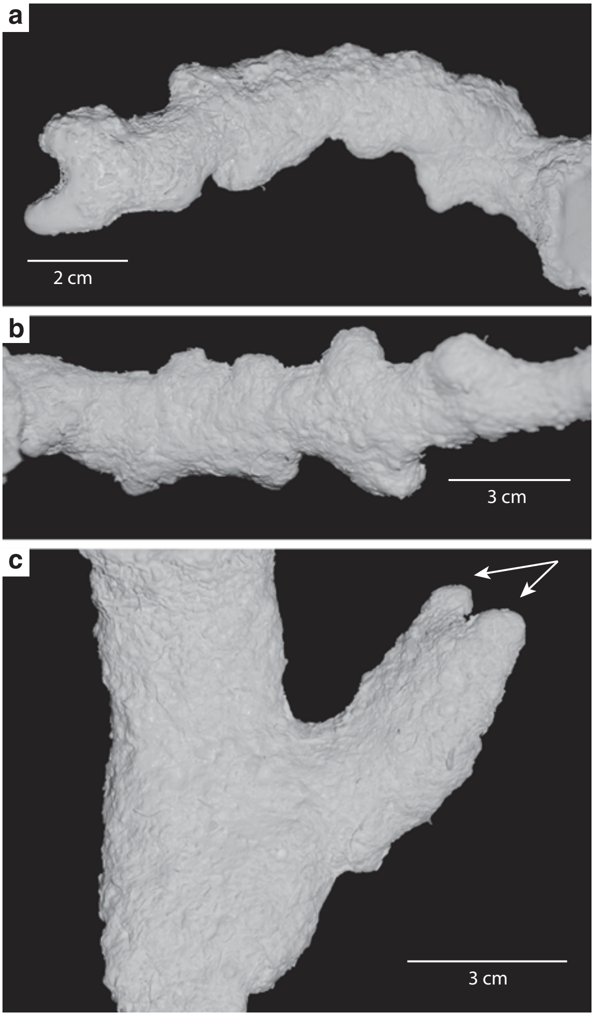


Fig. 13.7 Y- and J-shaped burrow morphologies produced by *A. tigrinum*. **a** Side view of a Y-shaped burrow with two surface openings (TSB8). **b** Side view of a Y-shaped burrow with three surface openings (TSB6). **c** Side view of a J-shaped burrow (TSB9)

Fig. 13.8 Examples of bioglyphs preserved on burrows produced by *A. tigrinum*. **a** Overhead view of a portion of a ramp (TS6-3-2) bearing elongate and rounded bioglyphs. **b** Overhead view of a portion of a ramp (TS6-3-1) bearing rounded and elongate bioglyphs. **c** Side view of a branched burrow (TS6-2-1) exhibiting a bilobate or heart-shaped bioglyph on the end of the burrow's branch



ing method employed by *A. tigrinum*. Mounds were produced as the salamanders initially excavated their burrow, using their forelimbs to pull sediment back behind them into spoil piles. Mounding was present next to the surface opening, on the side opposite the downward sloping ramp.

13.4.2 *A. opacum*

13.4.2.1 Behavior

Ambystoma opacum burrowed through compaction only, entering the sediment through cracks and holes that were already present in the surface within 24 h of

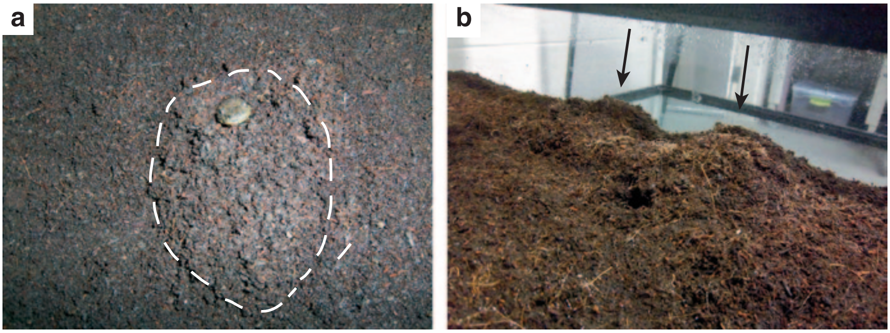


Fig. 13.9 Surface mounds produced by *A. tigrinum*. **a** Overhead view of a mound produced by an individual (TS5) in the clay loam with a moisture content of 74 %. **b** Oblique view of mounds produced by the same salamander in organic clay loam with a moisture content of 54 %

being placed in the terrariums. The salamanders first forced their snout into the sediment and then used their hind- and forelimbs to push themselves deeper. Expansion of the burrow was accomplished by moving their heads vertically and their bodies in an undulatory fashion. Once constructed, burrows commonly remained open to the surface. In 34 of the 36 experiments conducted, the burrows were inhabited for the entire length of the experiment. The salamanders spent approximately 90 % of their time in their burrow, rarely surfacing at night. When the salamanders did emerge, they did so only through their original burrow opening.

13.4.2.2 Burrow Morphology

Ramps These commonly produced burrows ($n=22$) consist of one elliptical surface opening and one elliptical-to-circular, subhorizontal-to-subvertical tunnel or shaft (Fig. 13.10a and b; Table 13.3; Table A.2). Some ramps ($n=6$) also included a laterally expanded chamber either at the end of the burrow (Fig. 13.10c and d) or just below the surface opening (Fig. 13.10e and f). Ramps were constructed in all sediment compositions and moisture conditions; those with chambers were only produced in sediments with a moisture content of 74 %. The ramps have lengths of 6.0–24.0 cm ($\bar{x}$ = 12.2 cm, SD = 4.4) and reach depths of 3.5–14.6 cm ($\bar{x}$ = 7.3 cm, SD = 3.0) at angles of 11–95° ($\bar{x}$ = 46.3°, SD = 22.8). The tunnels and shafts have widths of 1.5–4.0 cm ($\bar{x}$ = 2.9 cm, SD = 0.3), heights of 1.0–5.4 cm ($\bar{x}$ = 2.0 cm, SD = 0.3), and width-to-height ratios of 0.8–2.6 ($\bar{x}$ = 1.4, SD = 0.2). The chambers have similar dimensions to the adjacent tunnels except that their widths are, on average, 1.0 cm wider with a range in widths of 2.1–4.0 cm ($\bar{x}$ = 3.2, SD = 0.5). The complexity of the ramps is either 2, including one surface opening and single tunnel or shaft or 3 when a chamber is present. Tortuosity values are 1.0–1.9 ($\bar{x}$ = 1.3, SD = 0.3). A variation on this morphology is an L-shaped ramp which includes a subvertical to vertical shaft at the end of the burrow (Fig. 13.10g). This variation

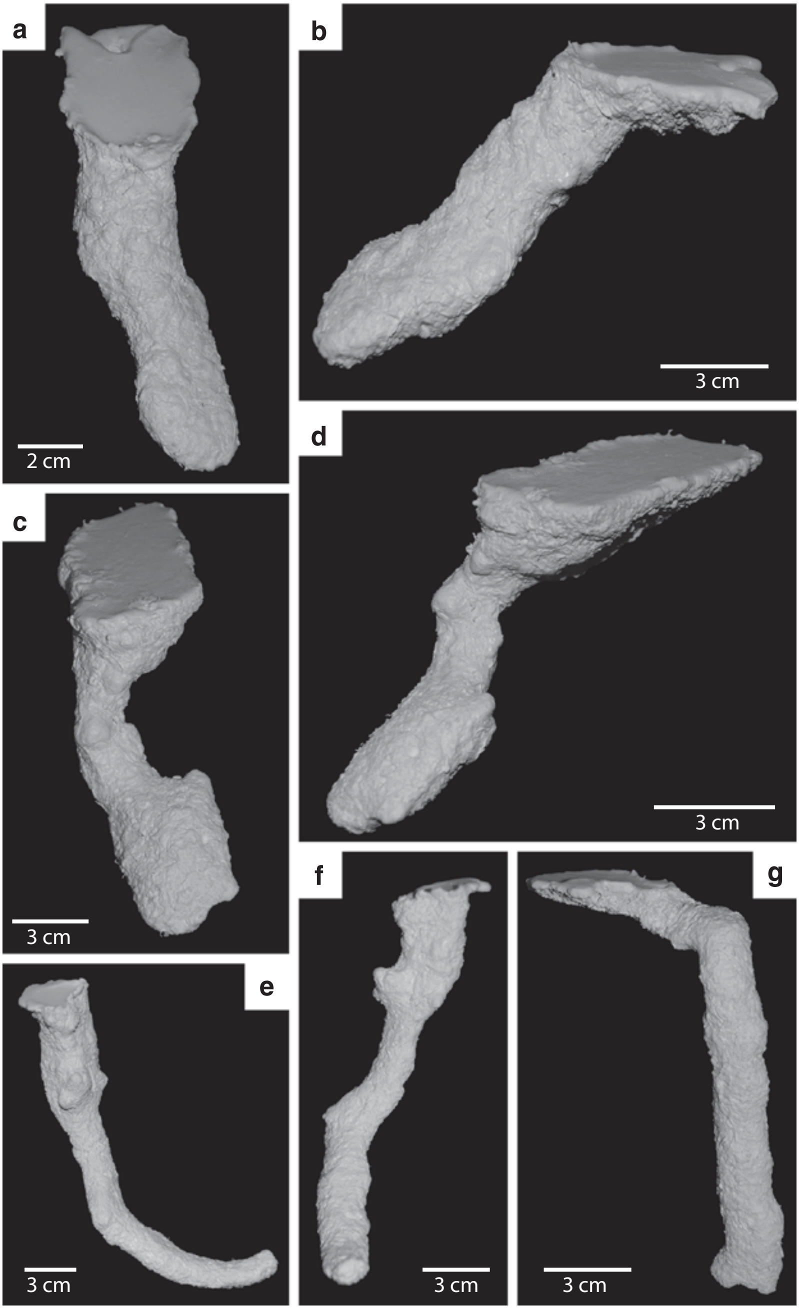


Fig. 13.10 Ramp morphologies produced by *A. opacum*. **a** Overhead view of a ramp (MS3-1-1). **b** Side view of MS3-1-1. **c** Overhead view of a ramp with a terminal chamber (MS3-2-1). **d** Side view of MS3-2-1. **e** Side view of a ramp morphology with a chamber just below the surface opening (MS4-1-1A). **f** Overhead view of MS4-1-1A. **g** Side view of an L-shaped ramp (MS4-2-2)

A. tigrinum

All	0.8
R to R	0.9
R to BR	0.7
R to UW	0.8
R to J	0.8
R to Y	0.6

UW to UW	0.8
UW to BR	0.7
UW to J	0.7
UW to Y	0.6

Y to Y	0.9
Y to BR	0.8
Y to J	0.6

A. opacum

All	0.8
R to R	0.8
R to BR	0.5

BR to BR	0.8

A. tigrinum* to *A. opacum

All	0.7
R to R	0.8
BR to R	0.6
UW to R	0.7
J to R	0.7
Y to R	0.5

R to BR	0.5
BR to BR	0.6
UW to BR	0.5
J to BR	0.7
Y to BR	0.9

Table 13.3 Average similarity values of the burrows produced by *A. tigrinum* and *A. opacum* compared within and between each species. R: ramp, BR: branched ramp, UW: U- and W-shaped burrow, J: J-shaped burrow, Y: Y-shaped burrow

was produced twice by the same salamander (MS4) in organic clay loam and sandy clay loam sediments with a moisture content of 74 %.

Branched Ramp A rare ramp morphology ($n = 2$) produced by one individual consisting of a single, elliptical opening, an elliptical, subhorizontal tunnel, and a single elliptical, subhorizontal branch (Fig. 13.11; Table 13.3; Table A.2). Branched ramps were produced in organic clay loam sediment with moisture contents of 54 and 94 %. The branched ramps have lengths of 9.0–20.0 cm ($\bar{x} = 14.5$ cm, SD = 4.4) reaching depths of 4.5–6.8 cm ($\bar{x} = 5.7$ cm, SD = 1.2) at an angle of 31–43° ($\bar{x} = 37°$, SD = 6). The branch extends off of the main burrow at an angle of 90°. The tunnels have widths of 1.5–3.8 cm ($\bar{x} = 2.9$ cm, SD = 0.5), heights of 0.9–3.1 cm ($\bar{x} = 1.9$ cm, SD = 0.2), and width-to-height ratios of 1.4–1.7 ($\bar{x} = 1.6$, SD = 0.1). The complexity is 4 including the single surface opening and three tunnel segments. The tortuosity is 1.2–2.1 ($\bar{x} = 1.7$ cm, SD = 0.5).

Bioglyphs Weakly formed bioglyphs were present on burrows of *A. opacum* from all experiments. Bioglyphs included bilobate or heart-shaped structures (Fig. 13.12a and b) as well as rare, round-to-elongate protrusions (Fig. 13.12c). The burrows possess 0–5 of these structures with a variable distribution along their length.

Surface Features Surface trails were common in the *A. opacum* terrariums in all experiments (Fig. 13.13). The trails were sinuous to straight, 2–3 cm wide and typically 1 cm deep. The production of surface trails was observed during the movement

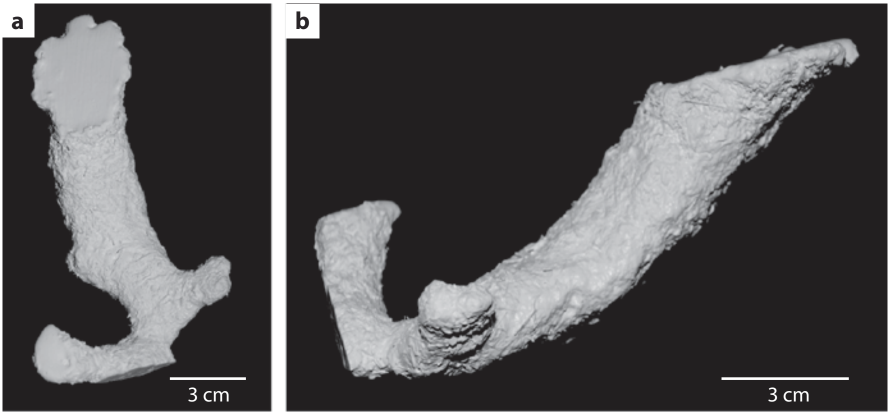


Fig. 13.11 Branched ramp produced by *A. opacum*. **a** Overhead view of branched ramp (MS2-3-1). **b** Side view of MS2-3-1

of *A. opacum* after the initiation of burrowing. Once partially burrowed, some salamanders would move laterally through the shallow sediment, pushing material aside with their snout to form the shallow trails. These trails commonly led to an open burrow.

13.5 Analysis of Burrow Morphology

13.5.1 Comparison of A. tigrinum *Burrows*

The burrows produced by *A. tigrinum* were found to be highly similar (1.0–0.8) to dissimilar (0.5–0.4) with an overall average similarity of 0.8 based upon the ten quantitative morphological characteristics used in the Bray–Curtis analysis (Table 13.3; Table A.3). The average level of similarity was highest (0.9–0.8) when burrows of the same morphology were compared with a range of 1.0–0.5 (Table 13.3). An exception to this was a single ramp (TS4-3-1) which was dissimilar (0.5) to three other ramps and only moderately similar (0.7–0.6) to all but one other ramp (Table A.3). This burrow had a nearly circular cross section (W/H = 1.0) and a low average slope (15°). When burrows of different morphologies were compared, the average level of similarity was lower (0.8–0.6) with a range of 1.0–0.4 (Table 13.3; Table A.3). In general, the level of similarity decreased with increasing complexity of the burrows; those burrows possessing branches (branched ramps, Y-shaped burrows) were found to be less similar to those without branches (ramps, U-, W-, J-shaped burrows). Y-shaped burrows in particular had relatively low levels of similarity (0.6) to the ramps, Y-, U-, and W-shaped burrows with several individual comparisons indicating dissimilarity (Table 13.3; Table A.3). Ramps, on the other hand, were highly similar (0.8) to U-, W-, and J-shaped burrows as were branched ramps and Y-shaped burrows (Table 13.3).

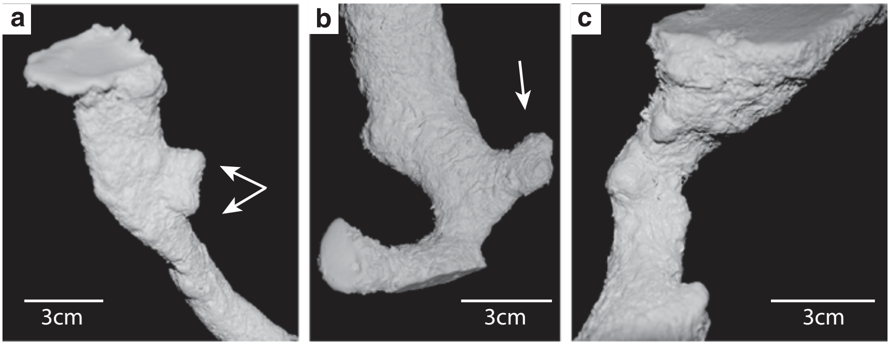


Fig. 13.12 Bioglyphs observed on burrows produced by *A. opacum*. Bilobate or heart-shaped bioglyphs exhibited on **a** the chamber of a ramp (MS4-1-1A) and **b** the shaft of the branched ramp (MS2-3-1). **c** Rounded bioglyphs on the shaft of a ramp (MS3-2-1)

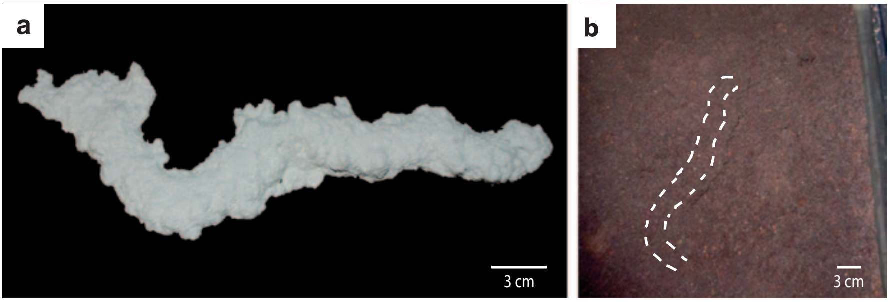


Fig. 13.13 A surface trail produced by *A. opacum.* **a** Underside of a plaster cast of a sinuous trail. **b** Trail (*outlined*) produced on the sediment surface

13.5.2 Comparison of A. opacum *Burrows*

Burrows produced by *A. opacum* were highly similar (1.0–0.8) to dissimilar (0.5–0.3) with an overall average similarity of 0.8 based upon the ten quantitative morphological characteristics used in the Bray–Curtis analysis (Table 13.3; Table A.4). The average level of similarity was highest (0.8) when burrows of the same morphology were compared with a range of 1.0–0.5 (Table 13.3). Exceptions to this included two ramps (MS4-2-2A and MS4-2-2B) which were dissimilar (0.5) to four and two other ramps, respectively (Table A.4). These two ramps had smaller average tunnel widths and heights and a lower slope than the others. Ramps and branched ramps were found to be dissimilar to each other with an average similarity of 0.5 and a range of 0.6–0.3 (Table 13.3; Table A.4). The inclusion of a branching angle and higher complexity were the primary differences.

	Width	Height	W:H Ratio	Openings	Length	Depth	Burrow Angle	Branching Angle	Tortuosity	Complexity
M-W	0.09	0.12	0.63	0.02	0.001	0.02	0.003	0.98	0.21	0.005
K-S	0.14	0.07	0.23	0.00002	0.007	0.006	0.007	0.0001	0.38	0.0001

Table 13.4 p values for the Mann–Whitney and Kolmogorov–Smirnov tests run between the quantitative burrow characteristics of *A. tigrinum* vs. *A. opacum*

13.5.3 Comparison of A. tigrinum *and* A. opacum *Burrows*

Burrows produced by *A. tigrinum* and *A. opacum* showed a wide range of similarities from high (1.0) to low (0.4) (Table A.5). On average, however, the 77 burrow casts produced by both species were found to be moderately similar (0.7) (Table 13.3). The highest levels of similarity were found between the ramp morphologies of both species (0.8) and between the Y-shaped burrows of *A. tigrinum* and the branched ramps of *A. opacum* (0.9) (Table 13.3). The ramps of *A. opacum* had the lowest levels of similarity (0.6–0.5) to the *A. tigrinum* burrows with branches (branched ramps, Y-shaped burrows). The *A. opacum* ramps were moderately similar (0.7) to the *A. tigrinum* U-, W-, and Y-shaped burrows. The branched ramps of *A. opacum* were dissimilar (0.5) to the ramps, U-, and W-shaped burrows of *A. tigrinum* and moderately similar (0.7–0.6) to the branched ramps and J-shaped burrows (Table 13.3).

While certain burrow morphologies were specific to each species, analysis of the burrow's quantitative measurements using Mann–Whitney and Kolmogorov–Smirnov tests indicated that the average width, height, width-to-height ratio, and tortuosity of all of the burrow casts of both species were similar with p values <0.05 (Table 13.4). The average values of each of these burrow properties are also similar between each species (Table 13.2). The median of the branching angles is similar between the burrows of the two species whereas the distribution is not similar (Table 13.4). Given that most (>90%) of the burrow casts of both species do not have branches, but those of *A. tigrinum* have a wider range of values, this is expected. The number of surface openings, total length, depth, average slope, and complexity of the burrow casts, however, were found to be different between the two species (Table 13.4). The average values of these burrow properties are also different between each species (Table 13.2). On average, burrows of *A. tigrinum* had more surface openings, were longer, deeper, had a greater slope, and a higher complexity than those of *A. opacum*. These differences are largely driven by the greater assortment of complex morphologies produced by *A. tigrinum*.

13.5.4 Environmental Controls on Burrow Morphology and Behavior

The quantitative properties of the burrows produced by both *A. tigrinum* and *A. opacum* were not found to have a strong correlation with variations in sediment composition, moisture content, or enclosure size (Table 13.5). The Spearman's rank

Table 13.5 Rs and associated *p* values for the Spearman's rank correlation tests run for eight of the quantitative properties of the burrows produced by *A. tigrinum* (T) and *A. opacum* (O) in comparison to: **a** Sediment composition. **b** Moisture content. **c** Enclosure size

			Width	Height	W:H ratio	Length	Depth	Burrow angle	Tortuosity	Complexity
a.	*T*	*Rs*	0.10	−0.20	0.33	0.19	0.19	0.04	0.20	0.21
		p	0.48	0.14	0.01	0.16	0.16	0.75	0.14	0.12
	O	*Rs*	0.07	−0.01	0.02	0.08	0.11	−0.16	−0.04	0.17
		p	0.73	0.96	0.92	0.70	0.63	0.47	0.85	0.44
b.	*T*	*Rs*	0.20	0.30	−0.03	0.19	0.10	0.06	−0.09	−0.08
		p	0.2	0.04	0.83	0.21	0.94	0.67	0.53	0.61
	O	*Rs*	−0.19	0.06	−0.13	−0.24	−0.37	−0.16	0.02	−0.17
		p	0.41	0.81	0.58	0.28	0.09	0.48	0.93	0.44
c.	*T*	*Rs*	−0.08	0.002	−0.19	0.09	0.10	−0.03	−0.31	−0.06
		p	0.59	0.99	0.21	0.55	0.52	0.86	0.04	0.70
	O	*Rs*	0.09	0.24	−0.05	0.01	0.05	−0.03	−0.15	−0.16
		p	0.68	0.28	0.81	0.96	0.81	0.88	0.52	0.48

Table 13.6 Rs and associated *p* values for the Spearman's rank correlation tests comparing burrow size to the body size of *A. tigrinum* (T) and *A. opacum* (O)

		L	W	H	W/H
T	*Rs*	0.33	0.29	0.21	0.07
	p	0.03	0.03	0.01	0.13
O	*Rs*	0.14	−0.28	−0.09	−0.03
	p	0.54	0.09	0.20	0.65

correlation yielded Rs values of −0.20–0.33 ($p = 0.96$–0.01) for sediment composition, −0.37–0.30 ($p = 0.94$–0.04) for sediment moisture, and −0.31–0.24 ($p = 0.99$–0.04) for enclosure size (Table 13.5). None of the Rs values were near −1.0 or 1.0 indicating that there was no strong correlation between the three environmental parameters and the quantitative burrow properties.

While none of the experimental sediments prevented burrowing by either species, there were burrow morphologies only observed in sediments with specific compositions and moisture contents. Ramps produced by both *A. tigrinum* and *A. opacum* were produced in all sediment compositions and moisture levels. The Y- and J-shaped burrows of *A. tigrinum,* however, were only produced in the organic sediment. Branched ramps of both species were not produced in the sandy clay loam. The U- and W-shaped burrows of *A. tigrinum* were observed in situ in all sediment compositions and moisture levels, but were not successfully cast in the clay loam or in tanks with soil moistures of 54 %.

13.5.5 Body Size Versus Burrow Size

The widths, heights, width-to-height ratios, and lengths of the burrow casts of *A. tigrinum* and *A. opacum* were not found to have a strong correlation with these properties of the bodies of the trace-making salamanders. The Spearman's rank correlation yielded Rs values of −0.28–0.33 ($p = 0.65$–0.01) for these four properties in both species (Table 13.6). None of the Rs values were near −1.0 or 1.0 indicating that there was no strong correlation between these dimensions of the burrows and the body of the tracemaker.

13.6 Discussion

13.6.1 Burrow Morphology and Tracemaker

The body plan of salamanders is, in general, not specialized for a fossorial lifestyle (Kley and Kearney 2007). Some members of the Amybstomatidae have modifications of the skull for burrowing, such as a flattening of the dorsal skull elements (Wake 1993), but other skeletal and muscular modifications have not been identified. This lack in specialized morphological adaptations has led to the general acceptance that, while fossorial, most ambystomatid salamanders are not active burrowers; they instead reside in leaf litter, in burrows of other organisms, or simply enlarge cracks and holes that are already present in the soil (Semlitsch 1983). While these experiments have shown that this may be true of *A. opacum,* it is not the case for *A. tigrinum* which was observed actively excavating burrows regardless of the presence or absence of cracks and holes on the sediment surface.

Regardless, both *A. tigrinum* and *A. opacum* produced permanent, open burrows with similar morphologies and quantitative properties in these experiments. The common burrow morphologies were not only produced by the same individuals, but also by different individuals and in varying experimental conditions. Differences in general burrow architecture are, therefore, attributed to variations in individual behavior. While the burrow morphologies did not greatly vary between species, the number of surface openings, lengths, depths, slopes, and complexities of the burrows were found to be dissimilar. These dissimilar quantitative properties are related to differences in the level of architectural complexity of the burrows produced by the two species. These differences are likely due to the different burrowing techniques employed by each species as well as the behaviors exhibited while occupying the burrows. The consistency in the morphology of the burrows produced by the different individuals and species of salamanders, however, suggests that salamander burrows, or those of similar animals with similar behaviors, could be distinguished from those of other tracemakers.

The results of these experiments have also reinforced that burrow size cannot be relied upon for accurately determining the size of a tracemaker. The dimensions of the burrows did not correlate to the dimensions of the individual tracemaker as observed in some other burrowing animals (e.g., White 2005). The lengths, heights, widths, and width-to-height ratios of the burrows of both species of salamanders were consistently greater than those dimensions of the salamanders. The larger cross-sectional diameters of the burrows are likely the result of the range of body motion and burrowing techniques exhibited by the salamanders. Greater burrow diameters allow for the accommodation of limb and head movements both during initial excavation and later compaction of the burrow walls. The wider tunnels and shafts also provide the salamanders the space needed to turn around inside their burrows. Similar observations have been made with the burrows of millipedes (Hembree 2009), scorpions (Hembree et al. 2012), and whip scorpions (Hembree 2013). The width of the salamander's bodies was typically greater than their height, so the elliptical cross-sectional shape, which was typical of the burrows produced, does mirror the salamanders' elliptical body plan.

Well-preserved bioglyphs closely mirror the relative shape and size of the limbs and head of the salamanders. These are best preserved in the burrows of *A. tigrinum*. The bioglyphs were produced by the animal's head, forelimbs, and hind limbs as it forced itself into the subsurface, compacting sediment around it along the way. Bioglyphs observed on burrows produced by *A. opacum* are typically poorly expressed and are not similar to the size or shape of the salamander's limbs or head. This is likely due to the weaker burrowing abilities of these salamanders. A few well-preserved bilobate structures do, however, preserve the general size and shape of the trace-making salamander's head.

13.6.2 Burrow Morphology and Behavior

The burrows produced by both *A. tigrinum* and *A. opacum* served the same behavioral purposes. Burrowing techniques did differ between species, but this had no effect on the final behavioral purpose of the burrow or on the burrow's general architecture. Burrows of both species are commonly constructed for dwelling purposes, most importantly for protection from environmental conditions and predation (Gehlbach et al. 1969; Marangio and Anderson 1977, Semlitsch 1983). Burrows produced by both species were also observed allowing for a passive means of prey capture. Prey items typically found their way down into the burrows allowing the salamander to capture and eat the prey from the protective environment of their burrow. Burrows were typically constructed within 12 h of placing a salamander in an enclosure. Once burrows were produced, salamanders were seen only on rare occasions outside of their burrows. When the salamanders did come to the surface, it occurred during the 12-h dark period.

The simplest burrows produced by the salamanders were the ramps. These burrows are representative of typical dwelling burrows and provide the minimum protection necessary from predation and adverse environmental conditions such as extreme temperatures and dryness. Chambers present in burrows serve as both dwelling areas and as turn-around points. The burrows are typically not wide enough to allow the salamander to turn around or reorient themselves, therefore, chambers or enlarged sections are created within the burrow. Overall, burrow morphologies which terminated in a chamber occurred in terrariums in which the salamanders abandoned their burrows less often. More complex burrow morphologies seen in *A. tigrinum* such as U-, W-, and Y-shaped burrows express the same behaviors as the ramps. The extra elements of these burrows were produced over time from salamanders moving upwards through the sediment creating new tunnels, shafts, and surface openings in already existing ramps. Continued burrow modification was observed only rarely in *A. opacum* with the production of two branched ramps. More typically, once specimens of *A. opacum* completed a burrow it remained largely unchanged throughout the experiment. This difference is also a result of the weaker burrowing ability of *A. opacum.*

13.6.3 Burrow Morphology, Behavior, and Sediment Properties

Sediment composition, moisture content, and enclosure size appeared to have no effect on the quantitative properties of the burrows produced by *A. tigrinum* and *A. opacum*. Both *A. tigrinum* and *A. opacum* are generalist species which are capable of producing burrows with similar morphologies in a variety of sediment types and soil environments. Burrows produced by both species in ideal conditions ranged from simple to complex and provided the individuals with the minimum cover necessary to protect themselves from external environmental conditions as well as predation. Lower moisture content as well as increased sand content decreased the cohesiveness of the sediment which, in turn, affected the behaviors of the salamanders expressed by a decrease in burrow complexity. Looser sediment would be expected to require more initial energy to compact and would also likely require the salamander to exert more energy throughout the habitation to keep the burrow open to the surface. As a result, only ramps were produced in these sediment types with the exception of one U-shaped burrow in sandy sediment and one branched ramp in the drier sediment.

13.7 Significance

13.7.1 Recognition of Salamander Burrows in the Fossil Record

The burrows created by *A. tigrinum* and *A. opacum* are representative of dwelling (domichnia) behaviors. In particular, the terminal chambers common in both species' burrows along with extended periods of inhabitance allow these burrows to be classified as domichnia. Surface trails observed in tanks of *A. opacum* are representative of locomotion (repichnia).

Architecture Burrow morphologies produced by *A. tigrinum* and *A. opacum* consist of vertical to subhorizontal ramps, with and without chambers and branches, as well as U-, W-, J-, and Y-shaped burrows. Burrows produced by both species consist of one, two, or three surface openings.

Overall Shape Burrow shafts, tunnels, and chambers are elliptical in cross section. Tunnels and shafts have widths that are commonly 1.5–2.0 times wider than they are high. Laterally expansive chambers may be present or absent. Chambers are approximately 1 cm wider than the associated tunnel or shaft.

Orientation Burrows range from rarely subhorizontal (11–15°), most commonly subvertical (20–70°), rarely near vertical (70–89°) to vertical (90°) with an average burrow orientation of 52°.

Internal Structure Burrows exhibit no visible lining and irregular burrow walls. Burrow fill is passive and often due to collapse of the burrow's opening that occurs during or after burrow abandonment.

Bioglyphs Burrows exhibit common, but scattered, rounded, elongate, or bilobate shaped protrusions of varying sizes extending off of the surface of the burrow.

13.7.2 Paleontological and Paleoecological Significance

Burrows produced by *A. tigrinum* and *A. opacum* have a moderate preservation potential. Deeper tier burrows have greater chances of preservation and the shallow nature of burrows produced by both salamander species decreases the burrows' chances of being preserved. In addition, both types of salamander produced burrows with no discernible lining. Linings are not found in all fossilized burrows and are not necessary for preservation, but they do increase the burrow's potential to be preserved and recognized. Preservation potential is increased by the fact that burrow openings were maintained by both species throughout habitation. Individuals were not observed maintaining the burrows, but the walls were continuously compacted and the burrow kept open through the animal's movements. Small-scale mounds and surface trails also have the potential to be preserved, but these would all require rapid sedimentation. Infilling of open burrows with sediment of a contrasting lithology would also aid in recognition due to the lack of a lining. This process could be common in the floodplains which salamanders typically inhabit.

Burrows of vertebrates are typically viewed as structures with large diameters (≥2 cm) and complex, branching networks (e.g., Miller et al. 2001; Hasiotis et al. 2004). While diameters of the burrows produced by *A. tigrinum* and *A. opacum* are commonly greater than 2 cm, small (1–2 cm) diameter burrows were produced. In addition, the majority (90 %) of the burrows produced by both species were simple ramps characterized by a single burrow opening, a single tunnel or shaft, and, in some, a single chamber. This study illustrates, therefore, that small diameter burrows with simple morphologies can be produced by vertebrates.

The body fossil record of salamanders is improving, but fossilized salamanders are poorly represented in the pre-Cenozoic record (Evans et al. 1988). Considering the abundance of extant, fossorial, salamander species, their widespread geographic range, and relatively long fossil record extending to the Jurassic (Holman 2006), fossilized salamander burrows should be moderately abundant. The ability to recognize salamander burrows from those of other tracemakers in the fossil record could aid in gaining a better understanding of the abundance and diversity of salamanders and their associated ecosystems, especially in the body fossil poor pre-Cenozoic. Salamanders are abundant, mid-level predators that play an important role in modern ecosystem processes (Davic and Welsh 2004). Salamander density in a variety of forested habitats ranging from New Hampshire to California has been estimated to be between 2,950 and 10,000 salamanders/ha (Burton and Likens 1975; Hairston 1987; Welsh and Lind 1992; Petranka et al. 1993; Stebbins and Cohen 1995). Salamanders play a critical role in these ecosystems and are often the dominant vertebrate predator (Hairston 1987). The absence of recorded salamander burrows is likely due to the inability to recognize such burrows or the misinterpretation of salamander burrows as those of other organisms. Salamander burrows would be representative of hidden biodiversity in areas generally devoid of body fossils. Uncovering such hidden biodiversity through trace fossils would allow for a more thorough interpretation of the ecology of the environment in question.

13.7.3 Paleopedological and Paleoenvironmental Significance

Burrows produced by the salamanders were restricted to the top 18 cm of the sediment, corresponding to the upper surface of most soils (A and upper B horizons); however, there are reports of individuals of both species being found at depths of a meter or more below the surface (Gruberg and Stirling 1972). It is possible that larger amphibians could create burrows at even greater depths. Observation of the salamanders' burrowing techniques and burrows in the laboratory has indicated that both species play a role in pedogenesis. Burrowing by both species has the potential to alter the soil through the destruction of sedimentary structures, the formation and destruction of peds, and through sediment mixing.

Small-scale mounds, which are evidence of sediment mixing, were observed on numerous occasions in terrariums occupied by *A. tigrinum* which utilized excavation as a burrowing method. Mixed soil is vital in the germination process of many plants whose seeds rely on bioturbated soils (Schaetzl and Anderson 2009). Excavation by *A. tigrinum* during initial burrow creation loosened sediment at and just below the surface. Compression of sediment, which was exhibited by both salamanders, increased the compaction and decreased the porosity and permeability of the sediment directly surrounding the burrows. Open and permanent burrows produced by the salamanders then serve as conduits which aid in the rapid downward movement of water and oxygen through the soil profile. As water moves downward, dissolution of minerals occurs, as well as the movement of dissolved ions and organics. The open burrows also allow for the upward movement of water through the soil profile through evapotranspiration, which is essential to plant growth (Schaetzl and Anderson 2009). Even when filled, sediment within the burrows continues to allow for the movement of fluids throughout the soil profile; the sediment which passively fills the burrows is typically looser than the surrounding sediment and has a greater porosity and permeability.

Along with downward movement of organics from the surface, alteration of the soil occurred through the direct addition of organics by the salamanders. Fecal material was rarely found at the surface of the enclosures, indicating defecation often took place within burrows. Individuals of *A. tigrinum* were directly observed excreting waste in their burrows. Remnants of prey animals were also observed within the burrows. The addition of organics to the soil provides nutrients for both soil microorganisms and plants.

Salamander burrows found in the fossil record would be indicative of a terrestrial, continental paleoenvironment. The hygrophilic nature of salamanders indicates that their burrows would be found in fairly moist soils within the vadose zone. Fossil salamander burrows are likely to be found in a wide array of soil types ranging from Entisols to, less likely, Aridisols. These burrows would be found in conjunction with traces produced by various soil invertebrates, plants, and possibly other vertebrates. Fossil root traces would likely be the most common trace found in conjunction with fossil salamander burrows.

13.8 Conclusions

Each species of salamander produced a morphologically consistent set of burrows which, despite architectural differences, were largely similar to each other. Burrows produced by *A. tigrinum* and *A. opacum* included two common morphologies, the ramp and branched ramp. Specimens of *A. tigrinum* also produced J-, U-, W-, and Y-shaped burrows. Differences in quantitative properties of the burrows produced by the two species were largely a result of the greater complexity and size of the *A. tigrinum* burrows. These dissimilarities were related to differences in burrowing techniques and behaviors associated with the burrows. The ramp morphologies of both species, however, were considered highly similar. The consistency in the morphology of the burrows produced by the two salamander species suggests that these burrow casts may be used as analogs for assessing potential tracemakers of fossil burrows.

Overall, sediment composition, moisture content, and enclosure size were found to have little effect on the properties of the burrows produced by either species. The lack of correlation between the quantifiable burrow properties and the environmental controls suggests that these properties are primarily controlled by the tracemakers morphology and behavior. This indicates that these burrow morphologies can be attributed to salamanders in a variety of environments.

The use of modern analogs is necessary in ichnology order to understand the potential burrow morphologies that different animals can produce and how that morphology can be affected by variations in environmental conditions. Having a defined set of burrow morphologies that can be attributed to specific groups of animals makes more accurate interpretations of burrowing methods, behaviors, and potential tracemakers possible. The results of this laboratory study of the burrowing behavior of *A. tigrinum* and *A. opacum* will aid in the identification of fossil burrows produced by ancient salamanders or amphibians with similar body types.

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Appendix

Table A.1 Detailed measurements of burrows produced by *A. tigrinum*

ID	M	SO	MD	TL	Max W	Min W	Avg W	Max H	Min H	Avg H	W/H	Max S	Min S	Avg S	BA	C	T	TS	SC	SM	SP
TS3-2-1B	R	1	5.8	9.8	3.3	1.2	2.1	2.2	1.1	1.5	1.4	35.0	35.0	35.0	0	2	1.5	38	50O/50C	74	TS3
TS3-3-1(T)	R	1	9.3	19.5	5.0	1.6	3.5	3.1	1.6	2.4	1.5	67.0	67.0	67.0	0	2	1.3	38	75O/25C	54	TS3
TS3-3-2B	R	1	4.0	11.3	4.1	1.9	3.2	2.8	1.6	2.1	1.5	31.0	31.0	31.0	0	2	1.3	38	75O/25C	94	TS3
TS4-1-1A	R	1	7.5	9.0	2.1	0.9	1.7	1.7	1.1	1.5	1.1	64.0	64.0	64.0	0	2	1.2	38	75O/25C	74	TS4
TS4-3-1	R	1	9.7	12.0	3.3	2.3	2.7	3.3	1.9	2.6	1.0	15.0	15.0	15.0	0	2	1.3	38	75O/25C	54	TS4
TS5-1-1A	R	1	9.8	13.0	4.5	2.9	3.8	3.4	2.6	2.8	1.4	53.0	53.0	53.0	0	2	1.1	246	75O/25C	74	TS5
TS5-1-1B	R	1	12.4	15.5	3.5	2.4	2.9	2.5	1.3	1.9	1.5	65.0	65.0	65.0	0	2	1	246	75O/25C	74	TS5
TS5-2-2D	R	1	8.7	12.5	3.6	2.3	3.0	3.2	1.5	2.2	1.4	62.0	62.0	62.0	0	2	1.3	246	50O/25C/25S	74	TS5
TS6-1-1G	R	1	5.2	10.0	3.0	2.1	2.7	2.0	1.5	1.8	1.5	40.0	40.0	40.0	0	2	1.6	246	75O/25C	74	TS6
TS6-1-1H	R	1	4.2	11.3	2.5	2.0	2.2	2.6	1.6	2.0	1.1	40.0	40.0	40.0	0	2	1.3	246	75O/25C	74	TS6
TS6-3-1(T)	R	1	4.7	20.9	3.5	1.1	2.2	2.6	1.2	1.8	1.2	52.0	52.0	52.0	0	2	1.1	246	75O/25C	54	TS6
TS6-3-2	R	1	4.6	17.0	3.2	1.8	2.4	2.1	1.5	1.6	1.5	34.0	34.0	34.0	0	2	1.5	246	75O/25C	94	TS6
TS7-2-1	R	1	8.5	11.0	3.6	2.3	2.9	2.5	1.6	2.0	1.5	75.0	75.0	75.0	0	2	1.3	114	50O/50C	74	TS7
TS7-2-2	R	1	8.5	11.7	3.3	2.5	3.0	2.7	1.4	1.8	1.7	64.0	64.0	64.0	0	2	1.2	114	50O/25C/25S	74	TS7
TSB1	R	1	9.6	16.1	4.2	2.1	3.1	3.1	1.6	2.2	1.4	57.0	57.0	57.0	0	3	1.1	38	100O	80	TS1
TS2-1-2	R	1	14.0	17.5	3.9	1.6	3.0	2.2	1.2	2.0	1.5	52.0	52.0	52.0	0	3	1.5	114	75O/25C	74	TS2
TS2-2-1(T)	R	1	8.9	21.9	4.1	1.5	3.1	2.9	1.6	2.0	1.6	36.0	36.0	36.0	0	3	1.3	114	50O/50C	74	TS2
TS2-2-2	R	1	5.4	18.0	4.4	1.2	3.2	2.1	1.5	1.9	1.7	37.0	37.0	37.0	0	3	1.6	114	50O/25C/25S	74	TS2
TS2-3-1	R	1	9.0	26.0	5.3	3.1	3.9	2.8	1.7	2.4	1.6	51.0	51.0	51.0	0	3	1.4	114	75O/25C	54	TS2
TS2-3-2	R	1	12.0	16.5	4.3	2.6	3.3	3.1	1.8	2.2	1.5	63.0	63.0	63.0	0	3	1.2	114	75O/25C	94	TS2
TSB3	R	1	18.4	15.0	4.0	2.1	3.3	2.4	1.5	2.1	1.6	61.0	61.0	61.0	0	3	1.2	114	100O	80	TS2
TSB7	R	1	10.1	15.0	4.2	2.4	3.4	3.1	1.9	2.4	1.4	66.0	66.0	66.0	0	3	1.2	114	100O	80	TS2
TS3-1-2B	R	1	8.3	14.0	5.0	1.9	3.2	2.5	1.7	2.0	1.6	50.0	50.0	50.0	0	3	1.4	38	75O/25C	74	TS3
TS3-2-1A	R	1	5.2	16.0	4.9	1.5	3.8	2.6	1.4	2.1	1.8	35.0	35.0	35.0	0	3	1.7	38	50O/50C	74	TS3
TS3-3-2A	R	1	12.0	16.0	4.5	2.9	3.9	3.0	1.7	2.5	1.6	90.0	10.0	43.0	0	3	1.4	38	75O/25C	94	TS3
TSB2	R	1	7.1	15.7	5.1	2.4	3.7	3.1	1.8	2.4	1.5	45.0	45.0	45.0	0	3	1.1	38	100O	80	TS3
TS4-1-1C	R	1	9.8	14.0	4.0	1.7	3.0	2.4	1.1	2.0	1.5	65.0	65.0	65.0	0	3	1.4	38	75O/25C	74	TS4
TS4-1-2	R	1	11.2	18.0	3.4	2.0	2.8	2.4	1.4	1.9	1.5	89.0	89.0	89.0	0	3	1.2	38	75O/25C	74	TS4

Table A.1 (continued)

ID	M	SO	MD	TL	Max W	Min W	Avg W	Max H	Min H	Avg H	W/H	Max S	Min S	Avg S	BA	C	T	TS	SC	SM	SP
TS4-2-1	R	1	4.8	11.5	4.4	2.4	3.5	2.6	1.9	2.3	1.5	45.0	45.0	45.0	0	3	1.5	38	50O/50C	74	TS4
TS4-2-2(T)	R	1	14.0	15.0	3.7	1.2	2.9	2.4	1.6	1.9	1.5	85.0	85.0	85.0	0	3	1.2	38	50O/25C/25S	74	TS4
TS5-1-2(T)	R	1	11.7	15.0	4.1	1.5	3.0	2.7	1.9	2.3	1.3	55.0	55.0	55.0	0	3	1	246	75O/25C	74	TS5
TS5-2-1(T)	R	1	11.2	24.0	4.4	2.1	3.2	3.7	1.9	2.4	1.3	56.0	56.0	56.0	0	3	1.3	246	50O/50C	74	TS5
TS5-2-2C	R	1	6.1	12.0	4.0	1.9	3.1	2.6	1.6	2.1	1.5	52.0	52.0	52.0	0	3	1.3	246	50O/25C/25S	74	TS5
TS5-3-1	R	1	10.1	15.7	4.0	3.1	3.6	2.9	2.1	2.5	1.4	58.0	58.0	58.0	0	3	1.1	246	75O/25C	54	TS5
TS5-3-2	R	1	14.7	18.5	4.6	2.8	3.6	2.8	2.1	2.4	1.5	67.0	67.0	67.0	0	3	1.1	246	75O/25C	94	TS5
TS6-1-1C	R	1	10.0	13.5	3.5	2.4	3.0	2.3	1.6	2.0	1.5	66.0	66.0	66.0	0	3	1.2	246	75O/25C	74	TS6
TS6-2-1B	R	1	11.2	20.0	3.7	1.4	2.7	2.4	1.4	1.9	1.4	53.0	53.0	53.0	0	3	1.2	246	50O/50C	74	TS6
TS6-2-2	R	1	11.7	18.8	4.4	1.0	3.0	2.2	1.2	1.8	1.7	82.0	82.0	82.0	0	3	1.3	246	50O/25C/25S	74	TS6
TS7-1-1	R	1	12.4	16.1	4.2	1.0	2.7	3.4	1.1	1.9	1.4	64.0	64.0	64.0	0	3	1.1	114	75O/25C	74	TS7
TS7-1-2	R	1	10.0	12.1	3.0	2.2	2.5	2.4	1.8	2.1	1.2	65.0	65.0	65.0	0	3	1.2	114	75O/25C	74	TS7
TS7-3-1	R	1	11.9	16.5	3.8	2.3	3.0	2.9	1.5	2.1	1.4	60.0	60.0	60.0	0	3	1.2	114	75O/25C	54	TS7
TS6-2-1A	BR	1	10.1	19.4	4.0	2.2	2.9	2.7	1.3	1.9	1.5	68.0	68.0	68.0	52	5	1.8	246	50O/50C	74	TS6
TS3-1-1	U	2	6.3	19.0	4.7	3.2	4.2	2.5	1.9	2.3	1.8	35.0	30.0	32.5	0	3	1.5	38	75O/25C	74	TS3
TS3-2-2	U	2	4.1	14.2	4.1	2.6	3.5	2.1	1.2	2.0	1.8	43.0	20.0	31.5	0	3	2.8	38	50O/25C/25S	74	TS3
TS6-1-1E	U	2	4.0	16.0	4.2	2.4	3.3	3.8	2.0	3.1	1.1	60.0	15.0	37.5	0	3	1.1	246	75O/25C	74	TS6
TS6-1-2	U	2	4.9	12.2	3.4	1.8	2.9	3.3	1.7	2.2	1.3	80.0	67.0	73.5	0	3	1.7	246	75O/25C	74	TS6
TS2-1-1	W	3	7.1	30.5	3.3	1.5	2.4	3.9	1.3	2.1	1.1	90.0	45.0	65.0	0	5	1.6	114	75O/25C	74	TS2
TS4-3-2	W	3	3.5	23.0	3.9	1.7	2.6	2.7	1.5	1.9	1.4	86.0	41.0	58.0	0	5	1.7	38	75O/25C	94	TS4
TSB4	W	2	7.9	34.0	4.8	2.0	3.5	3.7	1.7	2.5	1.4	87.0	50.0	68.5	35	5	1.7	38	100O	80	TS3
TS3-1-2A	W	3	7.5	29.5	4.0	1.6	2.9	4.0	1.9	2.3	1.3	80.0	33.0	56.5	0	6	2.5	38	75O/25C	74	TS3
TSB9	J	1	16.7	27.0	3.7	1.7	2.5	2.3	1.3	1.7	1.5	62.0	62.0	62.0	0	2	2.5	114	100O	80	TS2
TSB5	Y	2	9.6	23.6	3.8	2.4	3.1	2.5	1.5	1.9	1.6	48.0	36.0	42.0	90	4	1.3	114	100O	80	TS2
TSB6	Y	3	12.4	25.2	3.4	1.8	2.6	2.1	1.2	1.8	1.4	74.0	50.0	64.7	90	7	2	114	100O	80	TS2
TSB8	Y	2	10.2	23.0	3.7	1.8	3.0	2.4	1.4	1.9	1.6	63.0	59.0	61.0	90	5	1.9	114	100O	80	TS2

BA branching angle, *C* complexity, *H* height (maximum, minimum, average), *ID* burrow cast number, *M* burrow morphology, *MD* maximum depth, *S* slope (maximum, minimum, average), *SC* sediment composition, *SM* sediment moisture, *SO* number of surface openings, *SP* salamander specimen number, *T* tortuosity, *TL* total length, *TS* tank size, *W* width (maximum, minimum, average), *W/H* width-to-height ratio

Table A.2 Detailed measurements of burrows produced by *A. opacum*

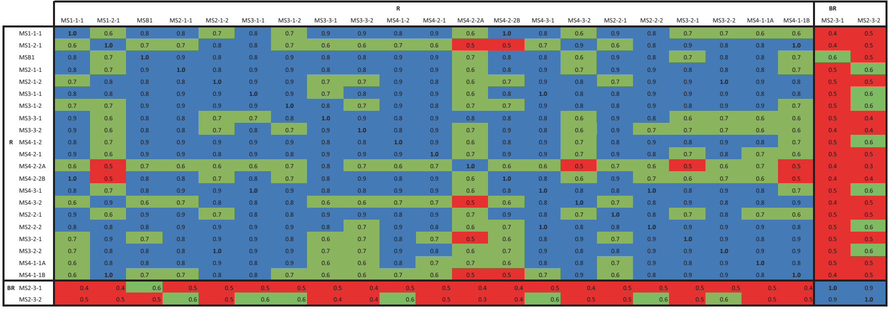
ID	M	SO	MD	TL	Max W	Min W	Avg W	Max H	Min H	Avg H	W/H	Max S	Min S	Avg S	BA	C	T	TS	SC	SM	SP
MS1-1-1	R	1	5.0	6.0	3.8	2.4	3.4	3.2	2	2.4	1.4	26	26	26	0	2	1.1	246	75O/25C	74	MS1
MS1-2-1	R	1	9.1	14.0	3.8	1.8	3.0	4.5	1.0	2.6	1.2	83	83	83	0	2	1.5	246	500/50C	74	MS1
MSB1	R	1	5.5	18.8	3.3	2.4	3.3	5.4	1.4	2.7	1.2	30	30	30	0	2	1.3	38	100O	80	MS1
MS2-1-1	R	1	7.1	10.0	3.7	2.9	3.5	2.6	2.1	2.4	1.5	37	37	37	0	2	1.3	38	75O/25C	74	MS2
MS2-1-2	R	1	5.8	16.5	3.4	2.6	3.0	2.0	1.2	1.6	1.9	55	55	55	0	2	1.5	38	75O/25C	74	MS2
MS3-1-1	R	1	7.1	10.4	3.1	2.8	3.0	2.5	1.3	1.9	1.6	45	45	45	0	2	1.1	114	75O/25C	74	MS3
MS3-1-2	R	1	10.2	16.5	3.4	2.3	2.7	2.0	1.2	1.7	1.6	40	40	40	0	2	1.1	114	75O/25C	74	MS3
MS3-3-1	R	1	5.0	13.0	3.2	2.1	2.7	2.1	1.8	1.9	1.4	20	20	20	0	2	1.4	114	75O/25C	54	MS3
MS3-3-2	R	1	3.5	10.0	2.8	2.3	2.5	2.2	1.5	1.9	1.3	22	22	22	0	2	1.3	114	75O/25C	94	MS3
MS4-1-2	R	1	4.6	13.0	2.9	1.5	2.5	2.3	1.4	1.9	1.3	41	41	41	0	2	1.9	38	75O/25C	74	MS4
MS4-2-1	R	1	5.5	10.0	3.4	2.4	3.1	1.9	1.3	1.7	1.8	30	30	30	0	2	1.0	38	50O/50C	74	MS4
MS4-2-2A	R	1	14.3	17.0	2.5	1.8	2.1	1.6	1.3	1.5	1.4	11	11	11	0	2	1.1	38	50O/25C/25S	74	MS4
MS4-2-2B	R	1	4.5	5.5	3.1	2.4	2.7	2.2	1.3	1.6	1.7	25	25	25	0	2	0.9	38	50O/25C/25S	74	MS4
MS4-3-1	R	1	4.4	10.0	3.1	2.4	2.9	2.8	2.0	2.3	1.3	45	45	45	0	2	1.4	38	75O/25C	54	MS4
MS4-3-2	R	1	9.8	9.7	3.3	1.9	2.7	2.4	1.5	1.9	1.4	78	78	78	0	2	1.0	38	75O/25C	94	MS4
MS2-2-1	R	1	7.5	9.5	3.4	2.6	2.9	2.6	1.1	1.9	1.5	27	27	27	0	3	1.2	38	50O/50C	74	MS2
MS2-2-2	R	1	5.2	12.0	4.0	2.6	3.2	2.6	1.8	2.3	1.4	48	48	48	0	3	1.3	38	50O/25C/25S	74	MS2
MS3-2-1	R	1	7.7	11.0	3.5	1.8	2.5	2.2	1.5	1.7	1.5	63	63	63	0	3	1.1	114	50O/50C	74	MS3
MS3-2-2	R	1	7.6	15.0	3.8	1.9	3.0	3.0	1.4	2.0	1.5	55	55	55	0	3	1.4	114	50O/25C/25S	74	MS3
MS4-1-1A	R	1	14.6	24.0	3.4	1.5	2.5	3.6	1.2	1.9	1.3	90	5	51	0	3	1.3	38	75O/25C	74	MS4
MS4-1-1B	R	1	8.1	14.0	3.9	1.7	2.8	3.6	1.2	2.3	1.2	83	83	83	0	3	1.4	38	75O/25C	74	MS4
MS2-3-1	BR	1	4.5	20.0	3.4	1.5	2.4	2.7	0.9	1.7	1.4	31	31	31	90	4	2.1	38	75O/25C	54	MS2
MS2-3-2	BR	1	6.8	9.0	3.8	2.6	3.3	3.1	1.4	2.0	1.7	43	43	43	90	4	1.2	38	75O/25C	94	MS2

BA branching angle, *C* complexity, *H* height (maximum, minimum, average), *ID* burrow cast number, *M* burrow morphology, *MD* maximum depth, *S* slope (maximum, minimum, average), *SC* sediment composition, *SM* sediment moisture, *SO* number of surface openings, *SP* salamander specimen number, *T* tortuosity, *TL* total length, *TS* tank size, *W* width (maximum, minimum, average), *W/H* width-to-height ratio

Table A.3 Bray–Curtis similarity index tables showing relative levels of similarity of burrows of *A. tigrinum*

A. tigrinum		R																																									BR	UW								J	Y		
		TS3-2-1B	TS3-3-1(T)	TS3-3-2B	TS4-1-1A	TS4-3-1	TS5-1-1A	TS5-1-1B	TS5-2-2D	TS6-1-1G	TS6-1-1H	TS6-3-1(T)	TS6-3-2	TS7-2-1	TS7-2-2	TSB1	TS2-1-2	TS2-2-1(T)	TS2-2-2	TS2-3-1	TS2-3-2	TSB3	TSB7	TS3-1-2B	TS3-2-1A	TS3-3-2A	TSB2	TS4-1-1C	TS4-1-2	TS4-2-1	TS4-2-2(T)	TS5-1-2(T)	TS5-2-1(T)	TS5-2-2C	TS5-3-1	TS5-3-2	TS6-1-1C	TS6-2-1B	TS6-2-2	TS7-1-1	TS7-1-2	TS7-3-1	TS6-2-1A	TS3-1-1	TS3-2-2	TS6-1-1E	TS6-1-2	TS2-1-1	TS4-3-2	TSB4	TS3-1-2A	TSB9	TSB5	TSB6	TSB8
R	TS3-2-1B	1.0	0.7	0.9	0.8	0.7	0.8	0.7	0.8	0.9	0.9	0.8	0.9	0.7	0.8	0.8	0.8	0.9	0.9	0.8	0.7	0.7	0.7	0.8	0.9	0.8	0.8	0.7	0.6	0.9	0.6	0.8	0.7	0.8	0.8	0.7	0.7	0.8	0.6	0.7	0.8	0.7	0.5	0.9	0.9	0.9	0.7	0.7	0.7	0.5	0.7	0.7	0.5	0.4	0.5
	TS3-3-1(T)	0.7	1.0	0.7	0.9	0.6	0.9	1.0	0.9	0.8	0.8	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.9	0.9	1.0	0.9	0.8	0.8	0.8	1.0	0.9	0.8	0.9	0.9	0.9	0.9	0.9	1.0	1.0	0.9	0.9	0.9	0.9	0.9	0.8	0.8	0.7	0.8	0.9	0.9	0.9	0.8	0.9	0.9	0.6	0.7	0.7
	TS3-3-2B	0.9	0.7	1.0	0.7	0.8	0.8	0.7	0.8	0.9	0.9	0.8	0.9	0.7	0.7	0.8	0.7	0.8	0.9	0.7	0.7	0.7	0.7	0.8	0.9	0.8	0.8	0.7	0.6	0.9	0.6	0.8	0.7	0.8	0.7	0.7	0.7	0.7	0.6	0.7	0.7	0.7	0.5	0.9	0.9	0.9	0.7	0.6	0.7	0.5	0.7	0.6	0.5	0.4	0.4
	TS4-1-1A	0.8	0.9	0.7	1.0	0.6	0.9	0.9	1.0	0.8	0.8	0.8	0.7	0.9	1.0	0.9	0.8	0.7	0.7	0.8	0.9	0.9	0.9	0.9	0.7	0.8	0.8	0.9	0.8	0.8	0.8	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.8	0.9	1.0	0.9	0.7	0.7	0.7	0.7	0.9	0.9	0.8	0.7	0.8	0.8	0.5	0.6	0.6
	TS4-3-1	0.7	0.6	0.8	0.6	1.0	0.7	0.6	0.6	0.7	0.7	0.6	0.7	0.6	0.6	0.7	0.7	0.7	0.7	0.6	0.6	0.6	0.6	0.7	0.7	0.7	0.7	0.6	0.5	0.7	0.5	0.7	0.6	0.7	0.7	0.6	0.6	0.7	0.5	0.6	0.6	0.6	0.4	0.7	0.7	0.7	0.6	0.5	0.5	0.4	0.6	0.6	0.4	0.4	0.4
	TS5-1-1A	0.8	0.9	0.8	0.9	0.7	1.0	0.9	0.9	0.8	0.8	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.9	0.9	0.9	1.0	0.8	0.9	0.9	0.9	0.8	0.9	0.8	1.0	0.9	1.0	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.7	0.8	0.8	0.8	0.8	0.8	0.8	0.7	0.8	0.8	0.6	0.6	0.6
	TS5-1-1B	0.7	1.0	0.7	0.9	0.6	0.9	1.0	0.9	0.8	0.8	0.9	0.8	0.9	1.0	0.9	0.9	0.8	0.8	0.8	1.0	0.9	1.0	0.9	0.8	0.9	0.8	1.0	0.9	0.8	0.9	0.9	0.9	0.9	0.9	1.0	1.0	0.9	0.9	1.0	1.0	1.0	0.8	0.7	0.7	0.8	0.9	0.9	0.9	0.7	0.8	0.9	0.5	0.7	0.6
	TS5-2-2D	0.8	0.9	0.8	1.0	0.6	0.9	0.9	1.0	0.8	0.8	0.9	0.8	0.9	1.0	0.9	0.9	0.8	0.8	0.9	1.0	0.9	1.0	0.9	0.8	0.8	0.9	1.0	0.8	0.9	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.9	0.9	0.9	1.0	0.9	0.7	0.7	0.7	0.8	0.9	0.9	0.9	0.7	0.8	0.9	0.5	0.6	0.6
	TS6-1-1G	0.9	0.8	0.9	0.8	0.7	0.8	0.8	0.8	1.0	1.0	0.8	0.9	0.8	0.8	0.8	0.8	0.9	0.9	0.8	0.8	0.8	0.8	0.9	0.9	0.9	0.9	0.8	0.7	0.9	0.7	0.8	0.8	0.9	0.8	0.7	0.8	0.8	0.7	0.8	0.8	0.8	0.6	0.8	0.9	0.9	0.8	0.7	0.8	0.6	0.7	0.7	0.5	0.5	0.5
	TS6-1-1H	0.9	0.8	0.9	0.8	0.7	0.8	0.8	0.8	1.0	1.0	0.9	0.9	0.8	0.8	0.8	0.8	0.8	0.9	0.8	0.8	0.8	0.8	0.9	0.9	0.9	0.9	0.8	0.7	0.9	0.7	0.8	0.8	0.9	0.8	0.7	0.8	0.8	0.7	0.8	0.8	0.8	0.6	0.8	0.9	0.9	0.8	0.7	0.8	0.6	0.7	0.7	0.5	0.5	0.5
	TS6-3-1(T)	0.8	0.9	0.8	0.8	0.6	0.9	0.9	0.9	0.8	0.9	1.0	0.8	0.8	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.8	0.9	0.9	0.9	0.8	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.8	0.9	0.8	0.9	0.7	0.8	0.8	0.8	0.8	0.8	0.9	0.7	0.9	0.9	0.6	0.6	0.6
	TS6-3-2	0.9	0.8	0.9	0.7	0.7	0.8	0.8	0.8	0.9	0.9	0.8	1.0	0.7	0.7	0.8	0.8	0.9	0.9	0.8	0.8	0.7	0.7	0.8	1.0	0.9	0.9	0.8	0.7	0.9	0.7	0.8	0.8	0.8	0.8	0.7	0.7	0.8	0.7	0.8	0.7	0.8	0.6	0.9	0.9	0.9	0.7	0.7	0.8	0.6	0.7	0.7	0.5	0.5	0.5
	TS7-2-1	0.7	0.9	0.7	0.9	0.6	0.9	0.9	0.9	0.8	0.8	0.8	0.7	1.0	0.9	0.9	0.8	0.7	0.7	0.8	0.9	0.9	0.9	0.8	0.7	0.8	0.8	0.9	0.9	0.8	0.9	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.9	0.7	0.7	0.7	0.7	1.0	0.8	0.8	0.7	0.8	0.8	0.5	0.6	0.6
	TS7-2-2	0.8	0.9	0.7	1.0	0.6	0.9	1.0	1.0	0.8	0.8	0.9	0.7	0.9	1.0	0.9	0.9	0.8	0.8	0.8	0.9	0.9	1.0	0.9	0.8	0.8	0.8	1.0	0.8	0.8	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.9	0.9	0.9	1.0	0.9	0.7	0.7	0.7	0.8	0.9	0.9	0.9	0.7	0.8	0.9	0.5	0.6	0.6
	TSB1	0.8	0.9	0.8	0.9	0.7	0.9	0.9	0.9	0.8	0.8	0.9	0.8	0.9	0.9	1.0	0.9	0.8	0.8	0.9	1.0	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.8	0.9	0.8	1.0	0.9	0.9	1.0	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.7	0.8	0.8	0.8	0.9	0.9	0.9	0.7	0.9	0.9	0.6	0.6	0.6
	TS2-1-2	0.8	0.9	0.7	0.8	0.7	0.9	0.9	0.9	0.8	0.8	0.9	0.8	0.8	0.9	0.9	1.0	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.8	0.9	0.8	1.0	0.9	0.9	0.9	0.9	0.9	1.0	0.8	0.9	0.9	0.9	0.7	0.8	0.8	0.8	0.8	0.8	0.9	0.7	0.9	0.9	0.6	0.6	0.6
	TS2-2-1(T)	0.9	0.8	0.8	0.7	0.7	0.8	0.8	0.8	0.9	0.8	0.9	0.9	0.7	0.8	0.8	0.9	1.0	0.9	0.9	0.8	0.8	0.8	0.9	0.9	0.9	0.9	0.8	0.7	0.8	0.7	0.8	0.9	0.8	0.8	0.8	0.8	0.9	0.7	0.8	0.8	0.8	0.6	0.9	0.9	0.9	0.7	0.8	0.8	0.6	0.8	0.8	0.6	0.5	0.6
	TS2-2-2	0.9	0.8	0.9	0.7	0.7	0.8	0.8	0.8	0.9	0.9	0.9	0.9	0.7	0.8	0.8	0.9	0.9	1.0	0.8	0.8	0.8	0.8	0.9	1.0	0.9	0.9	0.8	0.7	0.9	0.7	0.8	0.8	0.9	0.8	0.8	0.8	0.9	0.7	0.8	0.8	0.8	0.6	0.9	0.9	0.9	0.7	0.7	0.8	0.6	0.8	0.7	0.6	0.5	0.5
	TS2-3-1	0.8	0.9	0.7	0.8	0.6	0.9	0.8	0.9	0.8	0.8	0.9	0.8	0.8	0.8	0.9	0.9	0.9	0.8	1.0	0.9	0.8	0.9	0.9	0.8	0.9	0.9	0.9	0.8	0.9	0.8	0.9	0.9	0.9	0.9	0.9	0.8	0.9	0.8	0.9	0.8	0.9	0.7	0.8	0.8	0.8	0.8	0.9	0.9	0.7	0.9	0.9	0.6	0.6	0.6
	TS2-3-2	0.7	0.9	0.7	0.9	0.6	0.9	1.0	1.0	0.8	0.8	0.9	0.8	0.9	0.9	1.0	0.9	0.8	0.8	0.9	1.0	1.0	1.0	0.9	0.8	0.9	0.9	1.0	0.9	0.8	0.9	0.9	0.9	0.9	1.0	1.0	1.0	0.9	0.9	1.0	1.0	1.0	0.8	0.8	0.7	0.8	0.9	0.9	0.9	0.8	0.9	0.9	0.6	0.7	0.7
	TSB3	0.7	0.9	0.7	0.9	0.6	0.9	0.9	0.9	0.8	0.8	0.8	0.7	0.9	0.9	0.9	0.9	0.8	0.8	0.8	1.0	1.0	0.9	0.9	0.8	0.9	0.8	0.9	0.8	0.8	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.7	0.7	0.7	0.8	0.9	0.8	0.8	0.7	0.8	0.9	0.5	0.6	0.6
	TSB7	0.7	1.0	0.7	0.9	0.6	0.9	1.0	1.0	0.8	0.8	0.9	0.7	0.9	1.0	0.9	0.9	0.8	0.8	0.9	1.0	0.9	1.0	0.9	0.8	0.9	0.9	1.0	0.9	0.8	0.9	0.9	0.9	0.9	1.0	1.0	1.0	0.9	0.9	1.0	1.0	1.0	0.8	0.8	0.7	0.8	0.9	0.9	0.9	0.8	0.8	0.9	0.6	0.6	0.6
	TS3-1-2B	0.8	0.9	0.8	0.9	0.7	1.0	0.9	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.9	0.9	0.9	0.9	0.8	0.9	0.8	0.9	0.9	1.0	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.7	0.8	0.8	0.9	0.8	0.8	0.9	0.7	0.8	0.8	0.6	0.6	0.6
	TS3-2-1A	0.9	0.8	0.9	0.7	0.7	0.8	0.8	0.8	0.9	0.9	0.8	1.0	0.7	0.8	0.8	0.8	0.9	1.0	0.8	0.8	0.8	0.8	0.9	1.0	0.9	0.9	0.8	0.7	0.9	0.7	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.7	0.8	0.8	0.8	0.6	0.9	0.9	0.9	0.7	0.7	0.8	0.6	0.8	0.7	0.5	0.5	0.5
	TS3-3-2A	0.8	0.8	0.8	0.8	0.7	0.9	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	1.0	1.0	0.9	0.8	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.8	0.9	0.8	0.9	0.7	0.9	0.8	0.9	0.8	0.8	0.8	0.6	0.8	0.8	0.6	0.6	0.6
	TSB2	0.8	0.8	0.8	0.8	0.7	0.9	0.8	0.9	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.9	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	1.0	1.0	0.9	0.8	1.0	0.8	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.8	0.9	0.8	0.9	0.6	0.9	0.9	0.9	0.8	0.8	0.8	0.7	0.8	0.8	0.6	0.5	0.6
	TS4-1-1C	0.7	1.0	0.7	0.9	0.6	0.9	1.0	1.0	0.8	0.8	0.9	0.8	0.9	1.0	0.9	0.9	0.8	0.8	0.9	1.0	0.9	1.0	0.9	0.8	0.9	0.9	1.0	0.9	0.8	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.9	0.9	1.0	1.0	1.0	0.8	0.7	0.7	0.8	0.9	0.9	0.9	0.8	0.8	0.9	0.6	0.6	0.6
	TS4-1-2	0.6	0.9	0.6	0.8	0.5	0.8	0.9	0.8	0.7	0.7	0.8	0.7	0.9	0.8	0.8	0.8	0.7	0.7	0.8	0.9	0.8	0.9	0.8	0.7	0.8	0.8	0.9	1.0	0.7	1.0	0.8	0.8	0.8	0.8	0.9	0.9	0.8	1.0	0.9	0.9	0.9	0.7	0.7	0.6	0.7	0.9	0.8	0.8	0.7	0.8	0.8	0.5	0.6	0.6
	TS4-2-1	0.9	0.8	0.9	0.8	0.7	0.9	0.8	0.9	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.9	0.8	0.9	0.9	0.8	0.8	0.8	0.9	0.9	0.9	1.0	0.8	0.7	1.0	0.7	0.9	0.8	0.9	0.9	0.8	0.8	0.9	0.7	0.8	0.8	0.8	0.6	0.8	0.9	0.9	0.8	0.8	0.8	0.6	0.8	0.7	0.6	0.5	0.5
	TS4-2-2(T)	0.6	0.9	0.6	0.8	0.5	0.8	0.9	0.9	0.7	0.7	0.8	0.7	0.9	0.9	0.8	0.8	0.7	0.7	0.8	0.9	0.9	0.9	0.8	0.7	0.8	0.8	0.9	1.0	0.7	1.0	0.8	0.8	0.8	0.9	0.9	0.9	0.8	1.0	0.9	0.9	0.9	0.7	0.7	0.6	0.7	0.9	0.8	0.8	0.7	0.8	0.8	0.5	0.6	0.6
	TS5-1-2(T)	0.8	0.9	0.8	0.9	0.7	1.0	0.9	0.9	0.8	0.8	0.9	0.8	0.9	0.9	1.0	1.0	0.8	0.8	0.9	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.8	0.9	0.8	1.0	0.9	0.9	1.0	0.9	0.9	1.0	0.9	0.9	0.9	1.0	0.7	0.8	0.8	0.8	0.8	0.8	0.9	0.7	0.9	0.9	0.6	0.6	0.6
	TS5-2-1(T)	0.7	0.9	0.7	0.8	0.6	0.9	0.9	0.9	0.8	0.8	0.9	0.8	0.8	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.8	0.8	0.8	0.9	1.0	0.9	0.9	0.9	0.9	1.0	0.9	0.9	0.9	0.9	0.7	0.8	0.7	0.8	0.8	0.9	0.9	0.8	0.9	0.9	0.6	0.7	0.7
	TS5-2-2C	0.8	0.9	0.8	0.9	0.7	1.0	0.9	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.9	0.9	1.0	0.8	0.9	0.9	0.9	0.8	0.9	0.8	0.9	0.9	1.0	0.9	0.8	0.9	0.9	0.8	0.9	0.9	0.9	0.7	0.8	0.8	0.8	0.9	0.8	0.9	0.7	0.8	0.8	0.6	0.6	0.6
	TS5-3-1	0.8	0.9	0.7	0.9	0.7	0.9	0.9	0.9	0.8	0.8	0.9	0.8	0.9	0.9	1.0	0.9	0.8	0.8	0.9	1.0	0.9	1.0	0.9	0.8	0.9	0.9	0.9	0.8	0.9	0.9	1.0	0.9	0.9	1.0	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.7	0.8	0.8	0.8	0.9	0.9	0.9	0.7	0.9	0.9	0.6	0.6	0.6
	TS5-3-2	0.7	1.0	0.7	0.9	0.6	0.9	1.0	0.9	0.7	0.7	0.8	0.7	0.9	0.9	0.9	0.9	0.8	0.8	0.9	1.0	0.9	1.0	0.9	0.8	0.8	0.8	0.9	0.9	0.8	0.9	0.9	0.9	0.8	0.9	1.0	0.9	0.9	0.9	1.0	0.9	0.9	0.8	0.8	0.7	0.8	0.9	0.9	0.9	0.8	0.8	0.9	0.6	0.7	0.6
	TS6-1-1C	0.7	1.0	0.7	0.9	0.6	0.9	1.0	1.0	0.8	0.8	0.8	0.7	0.9	1.0	0.9	0.9	0.8	0.8	0.8	1.0	0.9	1.0	0.9	0.8	0.8	0.8	1.0	0.9	0.8	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.9	0.9	1.0	1.0	0.9	0.8	0.7	0.7	0.8	0.9	0.9	0.9	0.8	0.8	0.9	0.5	0.6	0.6
	TS6-2-1B	0.8	0.9	0.7	0.8	0.7	0.9	0.9	0.9	0.8	0.8	0.9	0.8	0.8	0.9	0.9	1.0	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.8	0.9	0.8	1.0	1.0	0.9	0.9	0.9	0.9	1.0	0.9	0.9	0.9	0.9	0.7	0.8	0.8	0.8	0.8	0.9	0.9	0.7	0.9	0.9	0.6	0.6	0.6
	TS6-2-2	0.6	0.9	0.6	0.8	0.5	0.8	0.9	0.9	0.7	0.7	0.8	0.7	0.9	0.9	0.9	0.8	0.7	0.7	0.8	0.9	0.9	0.9	0.8	0.7	0.8	0.8	0.9	1.0	0.7	1.0	0.9	0.9	0.8	0.9	0.9	0.9	0.9	1.0	0.9	0.9	0.9	0.8	0.7	0.7	0.7	0.9	0.8	0.8	0.7	0.8	0.8	0.5	0.6	0.6
	TS7-1-1	0.7	0.9	0.7	0.9	0.6	0.9	1.0	0.9	0.8	0.8	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.8	0.9	1.0	0.9	1.0	0.9	0.8	0.9	0.9	1.0	0.9	0.8	0.9	0.9	0.9	0.9	0.9	1.0	1.0	0.9	0.9	1.0	1.0	1.0	0.8	0.7	0.7	0.8	0.9	0.9	0.9	0.7	0.8	0.9	0.6	0.7	0.6
	TS7-1-2	0.8	0.9	0.7	1.0	0.6	0.9	1.0	1.0	0.8	0.8	0.8	0.7	0.9	1.0	0.9	0.9	0.8	0.8	0.8	1.0	0.9	1.0	0.9	0.8	0.8	0.8	1.0	0.9	0.8	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.9	0.9	1.0	1.0	0.9	0.7	0.7	0.7	0.8	0.9	0.9	0.9	0.7	0.8	0.9	0.5	0.6	0.6
	TS7-3-1	0.7	0.9	0.7	0.9	0.6	0.9	1.0	0.9	0.8	0.8	0.9	0.8	0.9	0.9	1.0	0.9	0.8	0.8	0.9	1.0	1.0	1.0	0.9	0.8	0.9	0.9	1.0	0.9	0.8	0.9	1.0	0.9	0.9	1.0	0.9	0.9	0.9	0.9	1.0	0.9	1.0	0.7	0.8	0.7	0.8	0.9	0.9	0.9	0.7	0.9	0.9	0.6	0.6	0.7
BR	TS6-2-1A	0.5	0.8	0.5	0.7	0.4	0.7	0.8	0.7	0.6	0.6	0.7	0.6	0.7	0.7	0.7	0.7	0.6	0.6	0.7	0.8	0.7	0.8	0.7	0.6	0.7	0.6	0.8	0.7	0.6	0.7	0.7	0.7	0.7	0.7	0.8	0.8	0.7	0.8	0.8	0.7	0.7	1.0	0.6	0.5	0.6	0.7	0.7	0.7	0.9	0.7	0.7	0.8	0.9	0.9
UW	TS3-1-1	0.9	0.8	0.9	0.7	0.7	0.8	0.7	0.7	0.8	0.8	0.8	0.9	0.7	0.7	0.8	0.8	0.9	0.9	0.8	0.8	0.7	0.8	0.8	0.9	0.9	0.9	0.7	0.7	0.8	0.7	0.8	0.8	0.8	0.8	0.8	0.7	0.8	0.7	0.7	0.7	0.8	0.6	1.0	0.9	0.9	0.7	0.7	0.8	0.6	0.8	0.7	0.6	0.5	0.5
	TS3-2-2	0.9	0.7	0.9	0.7	0.7	0.8	0.7	0.7	0.9	0.9	0.8	0.9	0.7	0.7	0.8	0.8	0.9	0.9	0.8	0.7	0.7	0.7	0.8	0.9	0.8	0.9	0.7	0.6	0.9	0.6	0.8	0.7	0.8	0.8	0.7	0.7	0.8	0.7	0.7	0.7	0.7	0.5	0.9	1.0	0.9	0.7	0.7	0.7	0.6	0.7	0.7	0.5	0.5	0.5
	TS6-1-1E	0.9	0.8	0.9	0.7	0.7	0.8	0.8	0.8	0.9	0.9	0.8	0.9	0.7	0.8	0.8	0.8	0.9	0.9	0.8	0.8	0.8	0.8	0.9	0.9	0.9	0.9	0.8	0.7	0.9	0.7	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.7	0.8	0.8	0.8	0.6	0.9	0.9	1.0	0.8	0.7	0.8	0.6	0.8	0.7	0.6	0.5	0.5
	TS6-1-2	0.7	0.9	0.7	0.9	0.6	0.8	0.9	0.9	0.8	0.8	0.8	0.7	1.0	0.9	0.9	0.8	0.7	0.7	0.8	0.9	0.9	0.9	0.8	0.7	0.8	0.8	0.9	0.9	0.8	0.9	0.8	0.8	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.9	0.7	0.7	0.7	0.8	1.0	0.9	0.8	0.7	0.8	0.8	0.5	0.6	0.6
	TS2-1-1	0.7	0.9	0.6	0.9	0.5	0.8	0.9	0.9	0.7	0.7	0.8	0.7	0.8	0.9	0.9	0.8	0.8	0.7	0.9	0.9	0.8	0.9	0.8	0.7	0.8	0.8	0.9	0.8	0.8	0.8	0.8	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.7	0.7	0.7	0.7	0.9	1.0	0.9	0.8	0.9	0.9	0.6	0.7	0.7
	TS4-3-2	0.7	0.9	0.7	0.8	0.5	0.8	0.9	0.9	0.8	0.8	0.9	0.8	0.8	0.9	0.9	0.9	0.8	0.8	0.9	0.9	0.8	0.9	0.9	0.8	0.8	0.8	0.9	0.8	0.8	0.8	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.7	0.8	0.7	0.8	0.8	0.9	1.0	0.8	0.9	0.9	0.6	0.6	0.7
	TSB4	0.5	0.8	0.5	0.7	0.4	0.7	0.7	0.7	0.6	0.6	0.7	0.6	0.7	0.7	0.7	0.7	0.6	0.6	0.7	0.8	0.7	0.8	0.7	0.6	0.6	0.7	0.8	0.7	0.6	0.7	0.7	0.8	0.7	0.7	0.8	0.8	0.7	0.7	0.7	0.7	0.7	0.9	0.6	0.6	0.6	0.7	0.8	0.8	1.0	0.8	0.8	0.7	0.8	0.8
	TS3-1-2A	0.7	0.9	0.7	0.8	0.6	0.8	0.8	0.8	0.7	0.7	0.9	0.7	0.8	0.8	0.9	0.9	0.8	0.8	0.9	0.9	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.9	0.9	0.8	0.9	0.8	0.8	0.9	0.8	0.8	0.8	0.9	0.7	0.8	0.7	0.8	0.8	0.9	0.9	0.8	1.0	0.9	0.6	0.7	0.7
J	TSB9	0.7	0.9	0.6	0.8	0.6	0.8	0.9	0.9	0.7	0.7	0.9	0.7	0.8	0.9	0.9	0.9	0.8	0.7	0.9	0.9	0.9	0.9	0.8	0.7	0.8	0.8	0.9	0.8	0.7	0.8	0.9	0.9	0.8	0.9	0.9	0.9	0.9	0.8	0.9	0.9	0.9	0.7	0.7	0.7	0.7	0.8	0.9	0.9	0.8	0.9	1.0	0.6	0.7	0.7
Y	TSB5	0.5	0.6	0.5	0.5	0.4	0.6	0.5	0.5	0.5	0.5	0.6	0.5	0.5	0.5	0.6	0.6	0.6	0.6	0.6	0.6	0.5	0.6	0.6	0.5	0.6	0.6	0.6	0.5	0.6	0.5	0.6	0.6	0.6	0.6	0.6	0.5	0.6	0.5	0.6	0.5	0.6	0.8	0.6	0.5	0.6	0.5	0.6	0.6	0.7	0.6	0.6	1.0	0.9	0.9
	TSB6	0.4	0.7	0.4	0.6	0.4	0.6	0.7	0.6	0.5	0.5	0.6	0.5	0.6	0.6	0.6	0.6	0.5	0.5	0.6	0.7	0.6	0.6	0.6	0.5	0.6	0.5	0.6	0.6	0.5	0.6	0.6	0.7	0.6	0.6	0.7	0.6	0.6	0.6	0.7	0.6	0.6	0.9	0.5	0.5	0.5	0.6	0.7	0.6	0.8	0.7	0.7	0.9	1.0	1.0
	TSB8	0.5	0.7	0.4	0.6	0.4	0.6	0.6	0.6	0.5	0.5	0.6	0.5	0.6	0.6	0.6	0.6	0.6	0.5	0.6	0.7	0.6	0.6	0.6	0.5	0.6	0.6	0.6	0.6	0.5	0.6	0.6	0.7	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.7	0.9	0.5	0.5	0.5	0.6	0.7	0.7	0.8	0.7	0.7	0.9	1.0	1.0

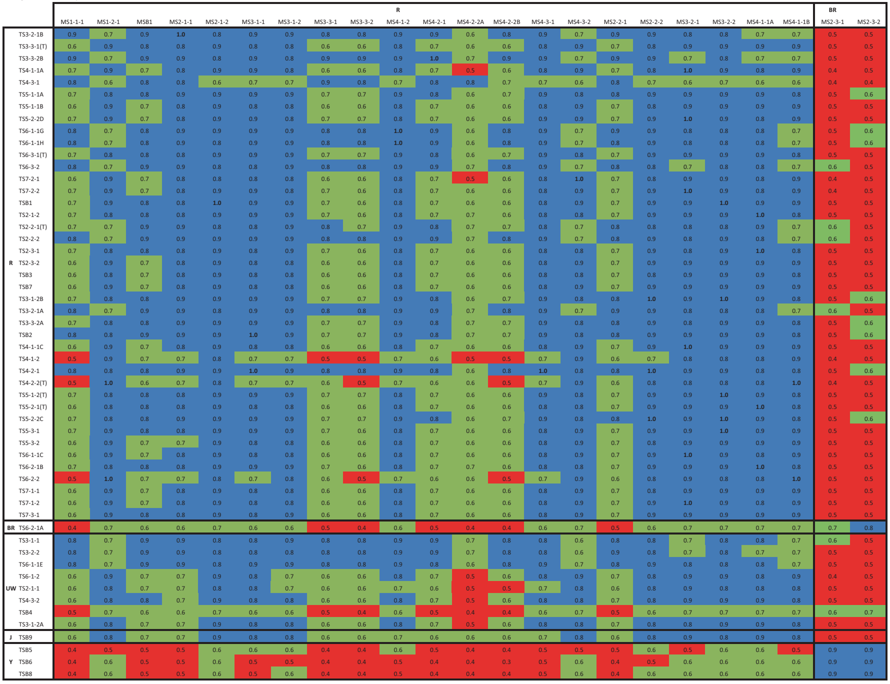
Table A.4 Bray–Curtis similarity index tables showing relative levels of similarity of burrows of *A. opacum*



A. opacum

		R																					BR	
		MS1-1-1	MS1-2-1	MSB1	MS2-1-1	MS2-1-2	MS3-1-1	MS3-1-2	MS3-3-1	MS3-3-2	MS4-1-2	MS4-2-1	MS4-2-2A	MS4-2-2B	MS4-3-1	MS4-3-2	MS2-2-1	MS2-2-2	MS3-2-1	MS3-2-2	MS4-1-1A	MS4-1-1B	MS2-3-1	MS2-3-2
R	MS1-1-1	**1.0**	0.6	0.8	0.8	0.7	0.8	0.7	0.9	0.9	0.8	0.9	0.6	**1.0**	0.8	0.6	0.9	0.8	0.7	0.7	0.6	0.6	0.4	0.5
	MS1-2-1	0.6	**1.0**	0.7	0.7	0.8	0.8	0.7	0.6	0.6	0.7	0.6	0.5	0.5	0.7	0.9	0.6	0.8	0.9	0.8	0.8	**1.0**	0.4	0.5
	MSB1	0.8	0.7	**1.0**	0.9	0.8	0.8	0.9	0.8	0.8	0.9	0.9	0.7	0.8	0.8	0.6	0.9	0.8	0.7	0.8	0.8	0.7	0.6	0.5
	MS2-1-1	0.8	0.7	0.9	**1.0**	0.8	0.9	0.9	0.8	0.8	0.9	0.9	0.6	0.8	0.9	0.7	0.9	0.9	0.8	0.8	0.8	0.7	0.5	0.6
	MS2-1-2	0.7	0.8	0.8	0.8	**1.0**	0.9	0.9	0.7	0.7	0.9	0.8	0.6	0.7	0.9	0.8	0.7	0.9	0.9	**1.0**	0.9	0.8	0.5	0.5
	MS3-1-1	0.8	0.8	0.8	0.9	0.9	**1.0**	0.9	0.7	0.8	0.9	0.9	0.6	0.8	**1.0**	0.8	0.8	0.9	0.9	0.9	0.8	0.8	0.5	0.6
	MS3-1-2	0.7	0.7	0.9	0.9	0.9	0.9	**1.0**	0.8	0.7	0.9	0.8	0.7	0.7	0.9	0.8	0.8	0.9	0.8	0.9	0.9	0.7	0.5	0.6
	MS3-3-1	0.9	0.6	0.8	0.8	0.7	0.7	0.8	**1.0**	0.9	0.8	0.9	0.8	0.8	0.8	0.6	0.9	0.8	0.6	0.7	0.6	0.6	0.5	0.4
	MS3-3-2	0.9	0.6	0.8	0.8	0.7	0.8	0.7	0.9	**1.0**	0.8	0.9	0.7	0.9	0.8	0.6	0.9	0.7	0.7	0.7	0.6	0.6	0.4	0.4
	MS4-1-2	0.8	0.7	0.9	0.9	0.9	0.9	0.9	0.8	0.8	**1.0**	0.9	0.6	0.8	0.9	0.7	0.8	0.9	0.8	0.9	0.8	0.7	0.5	0.6
	MS4-2-1	0.9	0.6	0.9	0.9	0.8	0.9	0.8	0.9	0.9	0.9	**1.0**	0.7	0.9	0.9	0.7	0.9	0.8	0.7	0.8	0.7	0.6	0.5	0.5
	MS4-2-2A	0.6	0.5	0.7	0.6	0.6	0.6	0.7	0.8	0.7	0.6	0.7	**1.0**	0.6	0.6	0.5	0.7	0.6	0.5	0.6	0.7	0.5	0.4	0.3
	MS4-2-2B	**1.0**	0.5	0.8	0.8	0.7	0.8	0.7	0.8	0.9	0.8	0.9	0.6	**1.0**	0.8	0.6	0.9	0.7	0.6	0.7	0.6	0.5	0.4	0.4
	MS4-3-1	0.8	0.7	0.8	0.9	0.9	**1.0**	0.9	0.8	0.8	0.9	0.9	0.6	0.8	**1.0**	0.8	0.8	**1.0**	0.8	0.9	0.8	0.7	0.5	0.6
	MS4-3-2	0.6	0.9	0.6	0.7	0.8	0.8	0.8	0.6	0.6	0.7	0.7	0.5	0.6	0.8	**1.0**	0.7	0.8	0.9	0.8	0.8	0.9	0.4	0.5
	MS2-2-1	0.9	0.6	0.9	0.9	0.7	0.8	0.8	0.9	0.9	0.8	0.9	0.7	0.9	0.8	0.7	**1.0**	0.8	0.7	0.8	0.7	0.6	0.5	0.5
	MS2-2-2	0.8	0.8	0.8	0.9	0.9	0.9	0.9	0.8	0.7	0.9	0.8	0.6	0.7	**1.0**	0.8	0.8	**1.0**	0.9	0.9	0.9	0.8	0.5	0.6
	MS3-2-1	0.7	0.9	0.7	0.8	0.9	0.9	0.8	0.6	0.7	0.8	0.7	0.5	0.6	0.8	0.9	0.7	0.9	**1.0**	0.9	0.8	0.9	0.5	0.5
	MS3-2-2	0.7	0.8	0.8	0.8	**1.0**	0.9	0.9	0.7	0.7	0.9	0.8	0.6	0.7	0.9	0.8	0.8	0.9	0.9	**1.0**	0.9	0.9	0.5	0.6
	MS4-1-1A	0.6	0.8	0.8	0.8	0.9	0.8	0.9	0.6	0.6	0.8	0.7	0.7	0.6	0.8	0.8	0.7	0.9	0.8	0.9	**1.0**	0.8	0.5	0.5
	MS4-1-1B	0.6	**1.0**	0.7	0.7	0.8	0.8	0.7	0.6	0.6	0.7	0.6	0.5	0.5	0.7	0.9	0.6	0.8	0.9	0.9	0.8	**1.0**	0.4	0.5
BR	MS2-3-1	0.4	0.4	0.6	0.5	0.5	0.5	0.5	0.5	0.4	0.5	0.5	0.4	0.4	0.5	0.4	0.5	0.5	0.5	0.5	0.5	0.4	**1.0**	0.9
	MS2-3-2	0.5	0.5	0.5	0.6	0.5	0.6	0.6	0.4	0.4	0.6	0.5	0.3	0.4	0.6	0.5	0.5	0.6	0.5	0.6	0.5	0.5	0.9	**1.0**

Table A.5 Bray–Curtis similarity index tables showing relative levels of similarity between burrows of *A. tigrinum* and *A. opacum*



A. tigrinum* vs *A. opacum

		R																					BR	
		MS1-1-1	MS1-2-1	MSB1	MS2-1-1	MS2-1-2	MS3-1-1	MS3-1-2	MS3-3-1	MS3-3-2	MS4-1-2	MS4-2-1	MS4-2-2A	MS4-2-2B	MS4-3-1	MS4-3-2	MS2-2-1	MS2-2-2	MS3-2-1	MS3-2-2	MS4-1-1A	MS4-1-1B	MS2-3-1	MS2-3-2
R	TS3-2-1B	0.9	0.7	0.9	**1.0**	0.8	0.9	0.9	0.8	0.8	0.9	0.9	0.6	0.8	0.9	0.7	0.9	0.9	0.8	0.8	0.7	0.7	0.5	0.5
	TS3-3-1(T)	0.6	0.9	0.8	0.8	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.8	0.9	0.9	0.9	0.9	0.5	0.5
	TS3-3-2B	0.9	0.7	0.9	0.9	0.8	0.9	0.8	0.9	0.9	0.9	**1.0**	0.7	0.9	0.9	0.7	0.9	0.9	0.7	0.8	0.7	0.7	0.5	0.5
	TS4-1-1A	0.7	0.9	0.7	0.8	0.9	0.9	0.8	0.6	0.6	0.8	0.7	0.5	0.6	0.8	0.9	0.7	0.8	**1.0**	0.9	0.8	0.9	0.4	0.5
	TS4-3-1	0.8	0.6	0.8	0.8	0.6	0.7	0.7	0.9	0.8	0.7	0.8	0.8	0.7	0.7	0.6	0.8	0.7	0.6	0.7	0.6	0.6	0.4	0.4
	TS5-1-1A	0.7	0.8	0.8	0.9	0.9	0.9	0.9	0.7	0.7	0.9	0.8	0.6	0.7	0.9	0.8	0.8	0.9	0.9	0.9	0.9	0.8	0.5	0.6
	TS5-1-1B	0.6	0.9	0.7	0.8	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.8	0.9	0.9	0.9	0.9	0.5	0.5
	TS5-2-2D	0.7	0.9	0.7	0.8	0.9	0.9	0.8	0.7	0.7	0.8	0.7	0.6	0.6	0.9	0.9	0.7	0.9	**1.0**	0.9	0.8	0.9	0.5	0.5
	TS6-1-1G	0.8	0.7	0.8	0.9	0.9	0.9	0.9	0.8	0.8	**1.0**	0.9	0.6	0.8	0.9	0.7	0.9	0.9	0.8	0.8	0.8	0.7	0.5	0.6
	TS6-1-1H	0.8	0.7	0.8	0.9	0.8	0.9	0.9	0.8	0.8	**1.0**	0.9	0.6	0.8	0.9	0.7	0.8	0.9	0.8	0.8	0.8	0.7	0.5	0.6
	TS6-3-1(T)	0.7	0.8	0.8	0.8	0.9	0.9	0.9	0.7	0.7	0.9	0.8	0.6	0.7	0.9	0.8	0.7	0.9	0.9	0.9	0.9	0.8	0.5	0.5
	TS6-3-2	0.8	0.7	0.9	0.9	0.8	0.8	0.9	0.8	0.8	0.9	0.9	0.7	0.8	0.9	0.7	0.8	0.8	0.7	0.8	0.8	0.7	0.6	0.5
	TS7-2-1	0.6	0.9	0.7	0.8	0.8	0.8	0.8	0.6	0.6	0.8	0.7	0.5	0.6	0.8	**1.0**	0.7	0.8	0.9	0.9	0.8	0.9	0.4	0.5
	TS7-2-2	0.7	0.9	0.7	0.8	0.9	0.9	0.8	0.7	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.9	**1.0**	0.9	0.8	0.9	0.4	0.5
	TSB1	0.7	0.9	0.8	0.8	**1.0**	0.9	0.9	0.7	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.9	0.9	**1.0**	0.9	0.9	0.5	0.5
	TS2-1-2	0.7	0.8	0.8	0.8	0.9	0.9	0.9	0.7	0.6	0.8	0.7	0.7	0.6	0.8	0.8	0.7	0.9	0.9	0.9	**1.0**	0.8	0.5	0.5
	TS2-2-1(T)	0.7	0.7	0.9	0.9	0.8	0.8	0.9	0.8	0.7	0.9	0.8	0.7	0.7	0.8	0.7	0.8	0.8	0.8	0.8	0.9	0.7	0.6	0.5
	TS2-2-2	0.8	0.7	0.9	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.9	0.7	0.8	0.9	0.7	0.8	0.9	0.8	0.9	0.8	0.7	0.6	0.5
	TS2-3-1	0.7	0.8	0.8	0.8	0.9	0.8	0.9	0.7	0.6	0.8	0.7	0.6	0.6	0.8	0.8	0.7	0.9	0.8	0.9	**1.0**	0.8	0.5	0.5
	TS2-3-2	0.6	0.9	0.7	0.8	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.9	0.9	0.9	0.9	0.9	0.5	0.5
	TSB3	0.6	0.8	0.7	0.8	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.8	0.7	0.8	0.9	0.9	0.9	0.8	0.5	0.5
	TSB7	0.6	0.9	0.7	0.8	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.9	0.9	0.9	0.9	0.9	0.5	0.5
	TS3-1-2B	0.7	0.8	0.8	0.9	0.9	0.9	0.9	0.7	0.7	0.9	0.8	0.6	0.7	0.9	0.8	0.8	**1.0**	0.9	**1.0**	0.9	0.8	0.5	0.6
	TS3-2-1A	0.8	0.7	0.9	0.9	0.8	0.9	0.9	0.8	0.8	0.9	0.9	0.7	0.8	0.9	0.7	0.9	0.9	0.8	0.8	0.8	0.7	0.6	0.5
	TS3-3-2A	0.7	0.8	0.8	0.9	0.9	0.9	0.9	0.7	0.7	0.9	0.8	0.7	0.7	0.9	0.8	0.8	0.9	0.8	0.9	0.9	0.8	0.5	0.6
	TSB2	0.8	0.8	0.9	0.9	0.9	**1.0**	0.9	0.7	0.7	0.9	0.8	0.7	0.7	0.9	0.8	0.8	0.9	0.9	0.9	0.9	0.8	0.5	0.6
	TS4-1-1C	0.6	0.9	0.7	0.8	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.9	**1.0**	0.9	0.9	0.9	0.5	0.5
	TS4-1-2	0.5	0.9	0.7	0.7	0.8	0.7	0.7	0.5	0.5	0.7	0.6	0.5	0.5	0.7	0.9	0.6	0.7	0.8	0.8	0.8	0.9	0.4	0.5
	TS4-2-1	0.8	0.8	0.8	0.9	0.9	**1.0**	0.9	0.8	0.8	0.9	0.8	0.6	0.8	**1.0**	0.8	0.8	**1.0**	0.9	0.9	0.8	0.8	0.5	0.6
	TS4-2-2(T)	0.5	**1.0**	0.6	0.7	0.8	0.7	0.7	0.6	0.5	0.7	0.6	0.6	0.5	0.7	0.9	0.6	0.8	0.8	0.8	0.8	**1.0**	0.4	0.5
	TS5-1-2(T)	0.7	0.8	0.8	0.8	0.9	0.9	0.9	0.7	0.7	0.8	0.7	0.6	0.6	0.9	0.8	0.7	0.9	0.9	**1.0**	0.9	0.8	0.5	0.5
	TS5-2-1(T)	0.6	0.8	0.8	0.8	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.8	0.7	0.9	0.9	0.9	**1.0**	0.8	0.5	0.5
	TS5-2-2C	0.7	0.8	0.8	0.9	0.9	0.9	0.9	0.7	0.7	0.9	0.8	0.6	0.7	0.9	0.8	0.8	**1.0**	0.9	**1.0**	0.9	0.8	0.5	0.6
	TS5-3-1	0.7	0.9	0.8	0.8	0.9	0.9	0.9	0.7	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.9	0.9	**1.0**	0.9	0.9	0.5	0.5
	TS5-3-2	0.6	0.9	0.7	0.7	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.8	0.9	0.9	0.9	0.9	0.5	0.5
	TS6-1-1C	0.6	0.9	0.7	0.8	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.9	**1.0**	0.9	0.8	0.9	0.5	0.5
	TS6-2-1B	0.7	0.8	0.8	0.8	0.9	0.9	0.9	0.7	0.6	0.8	0.7	0.7	0.6	0.8	0.8	0.7	0.9	0.9	0.9	**1.0**	0.8	0.5	0.5
	TS6-2-2	0.5	**1.0**	0.7	0.7	0.8	0.7	0.8	0.6	0.5	0.7	0.6	0.6	0.5	0.7	0.9	0.6	0.8	0.9	0.8	0.8	**1.0**	0.5	0.5
	TS7-1-1	0.6	0.9	0.7	0.8	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.8	0.9	0.9	0.9	0.9	0.5	0.5
	TS7-1-2	0.6	0.9	0.7	0.8	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.9	**1.0**	0.9	0.8	0.9	0.5	0.5
	TS7-3-1	0.6	0.9	0.8	0.8	0.9	0.8	0.9	0.6	0.6	0.8	0.7	0.6	0.6	0.8	0.9	0.7	0.9	0.9	0.9	0.9	0.9	0.5	0.5
BR	TS6-2-1A	0.4	0.7	0.6	0.6	0.7	0.6	0.6	0.5	0.4	0.6	0.5	0.4	0.4	0.6	0.7	0.5	0.6	0.7	0.7	0.7	0.7	0.7	0.8
UW	TS3-1-1	0.8	0.7	0.9	0.9	0.8	0.8	0.9	0.8	0.8	0.9	0.9	0.7	0.8	0.8	0.6	0.8	0.8	0.7	0.8	0.8	0.7	0.6	0.5
	TS3-2-2	0.8	0.7	0.9	0.9	0.8	0.8	0.8	0.8	0.8	0.9	0.9	0.7	0.8	0.8	0.6	0.9	0.8	0.7	0.8	0.7	0.7	0.5	0.5
	TS6-1-1E	0.8	0.7	0.9	0.9	0.8	0.9	0.9	0.8	0.8	0.9	0.8	0.6	0.8	0.9	0.7	0.8	0.9	0.8	0.8	0.8	0.7	0.5	0.5
	TS6-1-2	0.6	0.9	0.7	0.7	0.9	0.8	0.7	0.6	0.6	0.8	0.7	0.5	0.6	0.8	0.9	0.7	0.8	0.9	0.9	0.8	0.9	0.4	0.5
	TS2-1-1	0.6	0.8	0.7	0.7	0.8	0.8	0.7	0.6	0.6	0.7	0.6	0.5	0.5	0.7	0.8	0.6	0.8	0.9	0.8	0.8	0.8	0.5	0.5
	TS4-3-2	0.6	0.8	0.8	0.7	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.5	0.6	0.8	0.8	0.7	0.8	0.9	0.9	0.9	0.8	0.5	0.5
	TSB4	0.5	0.7	0.6	0.6	0.7	0.6	0.6	0.5	0.4	0.6	0.5	0.4	0.4	0.6	0.7	0.5	0.6	0.7	0.7	0.7	0.7	0.6	0.7
	TS3-1-2A	0.6	0.8	0.7	0.7	0.9	0.8	0.8	0.6	0.6	0.8	0.7	0.5	0.6	0.8	0.8	0.7	0.8	0.8	0.9	0.9	0.8	0.5	0.5
J	TSB9	0.6	0.8	0.7	0.7	0.9	0.8	0.8	0.6	0.6	0.7	0.6	0.6	0.6	0.7	0.8	0.6	0.8	0.9	0.8	0.9	0.8	0.5	0.5
Y	TSB5	0.4	0.5	0.5	0.5	0.6	0.6	0.6	0.4	0.4	0.6	0.5	0.4	0.4	0.5	0.5	0.5	0.6	0.5	0.6	0.6	0.5	0.9	0.9
	TSB6	0.4	0.6	0.5	0.5	0.6	0.5	0.5	0.4	0.4	0.5	0.4	0.4	0.3	0.5	0.6	0.4	0.5	0.6	0.6	0.6	0.6	0.9	0.9
	TSB8	0.4	0.6	0.5	0.5	0.6	0.5	0.6	0.4	0.4	0.5	0.4	0.4	0.4	0.5	0.6	0.4	0.6	0.6	0.6	0.6	0.6	0.9	0.9

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