

THE IDENTIFICATION AND INTERPRETATION OF REPTILE ICHNOFOSSILS IN PALEOSOLS THROUGH MODERN STUDIES

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ABSTRACT: The soil ecosystems of modern floodplains of North America, South America, the Caribbean, Africa, Europe, and western Asia are the habitat of a group of limbless, fossorial reptiles (Order Amphisbaenia). Although body fossils are relatively abundant in North American Paleocene and Neogene paleosols, no ichnofossils are attributed to these organisms, largely because the morphologies present in modern burrows have not been studied. Because ichnofossils tend to have a higher preservation potential than body fossils, knowledge of the architectural and surficial burrow morphologies of such burrowing vertebrates as amphisbaenians can lead to the knowledge of their true stratigraphic and geographic ranges.

The behavioral responses of a common South American amphisbaenian to variations in soil composition, moisture, and cohesion were studied in the laboratory so that the architectural and surficial morphology of their burrows could be tied to these environmental changes. Qualitative and quantitative models were designed to describe the morphology of the amphisbaenian burrows and then used to distinguish them from other floodplain burrowers, including skinks, scorpions, and crayfish. Amphisbaenians were found to produce unique two- and three-dimensional biogenic structures that could be both distinguished from those of other organisms and tied to specific environmental conditions. From these data, variations in the morphology of amphisbaenian ichnofossils can provide more accurate interpretations not only of the paleoecology, paleoenvironment, and paleoclimate of floodplain paleosols but also of rates of sedimentation.

INTRODUCTION

Trace fossils provide a critically important *in situ* record of paleoenvironmental and paleoecological change that has become an essential tool in sediment analysis. It was only through neoichnologic experiments performed with marine organisms, including annelids, arthropods, echinoderms, and bivalves (Frey 1968, 1970; Bromley and Asgaard 1975; Ekdale and Berger 1978; Frey et al. 1984; Pemberton and Frey 1985; Atkinson 1986; Kanazawa 1992; Seilacher and Seilacher 1994; Gingras et al. 2002; Gingras et al. 2004) that the environmental factors that affect trace-fossil morphology and distribution were accurately determined. These studies were designed to determine the morphological variations in biogenic structures created by specific organisms engaged in known behaviors under controlled environmental conditions, which could then be used to interpret the paleoecological and paleoenvironmental significance of many marine trace fossils. For example, studies of modern crustacean burrows revealed that *Ophiomorpha nodosa* often loses its wall lining and becomes *Thalassinoides suevicus* due to changes in substrate consistency (Bromley 1967; Bromley and Frey 1974). Similar studies of modern heart urchins (echinoids) have indicated that these organisms produce different trace morphologies depending on their behavior, *Scolicia prisca* while grazing and *Cardioichnus planus* when resting (Smith and Crimes 1983).

Despite the recent increase in studies using or reporting on the ichnology of such terrestrial environments as floodplains, similar studies of terrestrial and freshwater organisms, especially vertebrates, are

uncommon. While biologists and ichnologists have examined the life histories of fossorial and semi-fossorial terrestrial and freshwater organisms, few have been designed to evaluate organism-substrate interactions or to identify their biogenic structures in the geologic record (e.g., Chamberlain 1975; Ratcliffe and Fagerstrom 1980; Hasiotis and Mitchell 1993; Deocampo 2002; Hasiotis 2003).

Floodplains are complex depositional systems consisting of a number of different subenvironments with different sedimentologic, hydrologic, and biotic characteristics. In order to properly differentiate floodplain environments in the geologic record it is important that sedimentologists and paleontologists consider all aspects of the depositional, hydrologic, and biotic processes. Continental ichnofossils have proven to be excellent indicators of sedimentation rates, temperature, soil moisture, water-table level, and environmental stability (Retallack 1984; Genise et al. 2000; Hasiotis 2002, 2004). There are still problems, however, in recognizing and interpreting the variety of ichnofossil morphologies produced by continental organisms. Large ichnofossils of unknown affinity have been collected from Paleogene and Neogene floodplain paleosols in which body fossils of such burrowing reptiles as amphisbaenians are present, but no data from modern examples are available to differentiate the trace fossils of different types of burrowing reptiles.

Studies of the marine ichnological record show that experimental work with modern burrowing organisms is necessary to understand the paleoecology of trace fossils preserved in the continental rock record. The lack of knowledge of the types of biogenic structures produced by

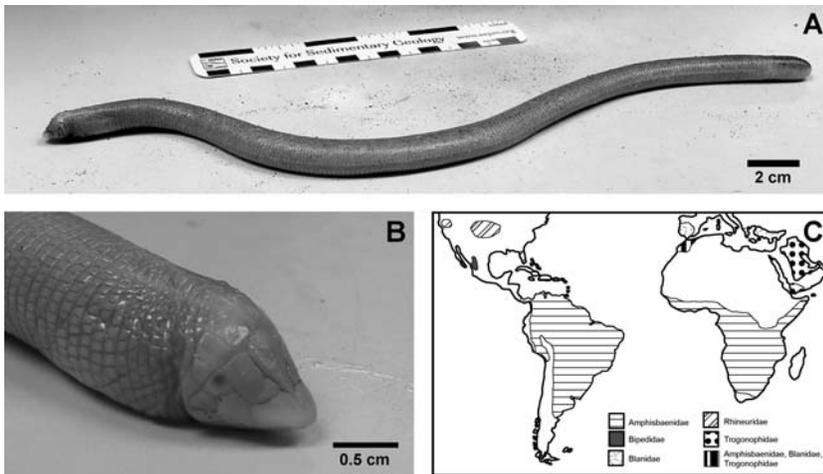


FIG. 1.—A) The amphisbaenian *Amphisbaena camurea* (Reptilia: Squamata) is adapted to a fossorial habitat and is characterized by an elongate, cylindrical body and an absence of limbs. B) The head of *A. camurea* forms a flattened, sloping snout that is used to burrow through dense soil. C) Extant amphisbaenians consist of five families present on both sides of the Atlantic in environments ranging from tropical to arid.

modern continental burrowing organisms can result in misinterpretation of continental ichnofossils, leading to inaccurate paleoecological and paleoenvironmental interpretations. Studying burrowing organisms under controlled conditions of temperature, moisture, and substrate allows morphological comparisons of modern and ancient biogenic structures for more accurate interpretations of original soil characteristics from which paleoenvironmental, paleohydrologic, and paleoclimatic conditions can be inferred.

The purpose of this paper is to document the biogenic structures that are produced by limbless burrowing reptiles of the order Amphisbaenia (Reptilia: Squamata) in a laboratory setting. The primary objective of this study is the description of variations in the morphology of amphisbaenian-produced biogenic structures and their associated behaviors due to difference in soil moisture, composition, and cohesiveness. The results of this neoichnological study, which can be applied to Mesozoic and Cenozoic floodplain deposits, allow recognition of terrestrial squamate trace fossil in paleosols, providing more accurate interpretations not only of the paleoecology, paleoenvironment, and paleoclimate of floodplain deposits but also of rates of sedimentation.

THE AMPHISBAENIA

Many extant reptile taxa spend much of their life within the substrate because the microclimate of a tunnel is buffered by the soil (Gans 1974). A number of reptile clades such as the amphisbaenians are completely fossorial and have complex adaptations that permit their entire life cycle to be spent within the substrate (Zug et al. 2001). Reptiles with burrowing adaptations are well known from the fossil record (Carroll 1988), yet their trace fossils are poorly known (Voorhies 1975).

Amphisbaenians are an important group to study because the living taxa constitute a major part of the soil ecosystem and their fossil record extends to the Paleocene (Gans 1974). Amphisbaenians create permanent, complex burrow systems in which they live, feed, and breed and are present in concentrations as high as 165/km² (Gans 1969; Papenfuss 1982). As a result, amphisbaenians are important contributors to continental bioturbation and pedogenesis. Extant amphisbaenians are grouped into the suborder Amphisbaenia, which consists of 130 species (Zug et al. 2001). Amphisbaenians are primarily limbless, burrowing lizards with a cylindrical head and trunk, 120 to 400 mm long, and are covered with rings of rectangular scales (Fig. 1A, B) (Zangerl 1944; Gans 1978; Zug et al. 2001). Recent field and laboratory studies have revealed much about their behavior and ecology (Papenfuss 1982; Abe 1984; Martin et al. 1991; Lopez et al. 1998; Webb et al. 2000; Lopez et al. 2002),

yet amphisbaenian burrow systems have never been studied or described.

The fossil record of amphisbaenians is geographically and stratigraphically widespread in the Cenozoic (Estes 1983). Fossil evidence indicates that amphisbaenians were present in Africa, North America, and Europe by at least the early Paleogene (Estes 1983; Rage 1988; Bailon 1989; Charig and Gans 1990; Murelaga et al. 2002). Fossil amphisbaenians are most abundant from Paleocene to Miocene strata of North America, including localities in Oregon, Florida, New Mexico, South Dakota, Nebraska, Colorado, and Wyoming (Estes 1983). Well preserved amphisbaenian fossils have been collected primarily from floodplain paleosols (Taylor 1951; Berman 1973, 1976, 1977). If fossil amphisbaenian taxa spent their lives producing burrow complexes, as the living representatives do, then it is likely that their burrows are preserved in the paleosols along with the body fossils, because trace fossils generally have a greater preservation potential than body fossils (Bromley 1996). Ichnofossils of subterranean tetrapods may have gone overlooked or unrecognized because little is known about the burrows of the living taxa.

Amphisbaenian Habitats

Amphisbaenians are present on both sides of the Atlantic in soil environments with climates ranging from humid tropical to xeric (Fig. 1C) (Gans 1974; Zug et al. 2001). Analysis of the distributions of amphisbaenians suggests that groundwater is one of the critical environmental factors in the geographic distribution of these reptiles (Gans 1974). When living in regions outside of the humid tropics, amphisbaenians inhabit shallow to deep soil microenvironments with high humidity (Gans 1974; Abe 1984). In arid climates, amphisbaenians live deeper within the soil near plant root systems or ephemeral stream beds, where interstitial moisture keeps the soil atmosphere saturated (Gans 1969, 1974; Papenfuss 1982). Amphisbaenians also show diurnal and seasonal shifts in burrow depth by moving closer to the sediment–air interface for warmth and downward to the phreatic zone to conserve water (Gans 1969; Martin et al. 1991; Lopez et al. 1998; Lopez et al. 2002).

Burrowing Methods and Burrow Functions

The unique morphology of amphisbaenians is a result of adaptations to a fossorial lifestyle including an elongate body, the loss of limbs, a compact skull, a modified snout, and complex musculature that allows forward and backward movement within tunnels (Gans 1974). The skulls of many species of amphisbaenians are specialized and compressed to become horizontally flattened and shovel-like or vertically flattened and

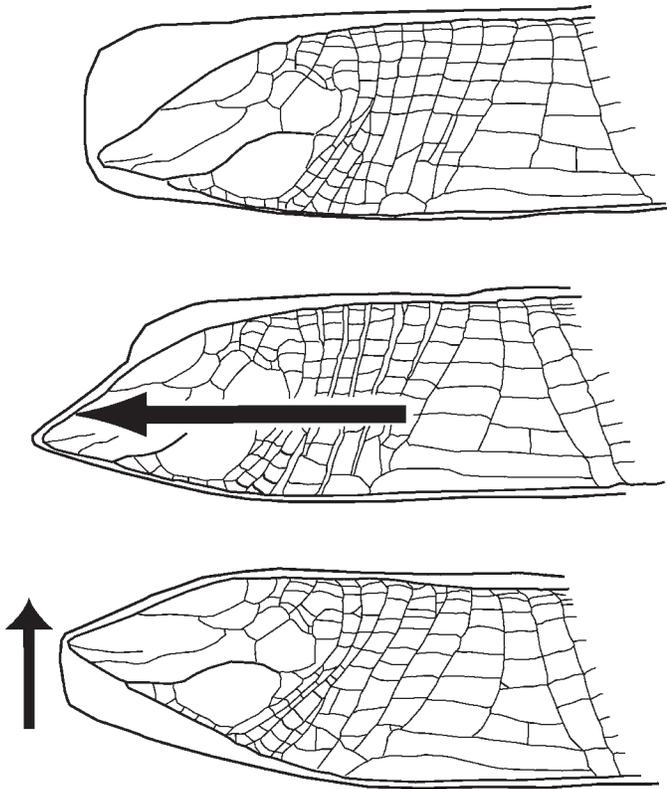


FIG. 2.—Shovel-headed amphisbaenians use forward motion to drive the horizontal edge of the snout into the soil and then widen the tunnel by raising the head to compress the soil into the roof of the tunnel (modified from Gans 1974).

keel-like (Gans 1974, 1978). Amphisbaenians burrow by a combination of excavation and compaction of the soil (Wake 1993). Shovel-headed amphisbaenians like *Amphisbaena camurea* (Fig. 1B) use the horizontal edge of the snout to first penetrate the soil and then widen the tunnel by raising the head and compressing the displaced material into the roof of the tunnel (Gans 1974) (Fig. 2). The tunnel walls are further compacted and smoothed by the amphisbaenian's body as it moves through the burrow (Gans 1974). Using this method, shovel-headed amphisbaenians are capable of digging tunnel systems in even the most compact soils (Wake 1993). Consequently, amphisbaenians have occupied soils with densities that make them unsuitable for other burrowing animals (Gans 1969).

Permanent burrows can serve a number of different and overlapping functions, including protection from the environment, defense from predators, food storage, passive predation, locomotion, and reproduction. Amphisbaenians spend most of their lives in their burrows and therefore use them for all of these functions (Gans 1978).

MATERIAL AND METHODS

This study involved two experimental designs to evaluate the morphology of amphisbaenian burrows. The first involved a standard, loose but cohesive substrate that allowed the animal to create an extensive but stable burrow system and included observing burrow morphology in two and three dimensions. Two-dimensional burrow models are necessary because these are the exposures one would expect to study in most outcrops and in cores. The second experimental design involved substrates of variable clay content to determine how the morphology of amphisbaenian burrows varies with different types of soil. Finally, these structures were described qualitatively and quantitatively using various

metrics. Quantitative models were designed so that different types of burrows created by different organisms can be distinguished in the fossil record.

The South American (Paraguay) amphisbaenian *Amphisbaena camurea* (Reptilia: Squamata: Amphisbaenidae) was used in this study. The three specimens of *A. camurea* used measured 20 cm, 25 cm, and 35 cm in length and approximately 1 cm in diameter. The laboratory was kept on a 12-hour light period and the temperature was maintained at 24–25°C. Additional heat was provided by a ceramic heat emitter positioned 20 cm above the surface of the substrate. Soil moisture was maintained at 0.2–0.1 bars with a daily water spray. Soil moisture was monitored by a Delmhorst® digital soil moisture meter attached to gypsum block sensors buried in the substrate.

Morphological Experiments

Initial experiments were designed to investigate the nature of sediment deformation and general burrow morphologies associated with the burrowing activity of the amphisbaenians. These experiments were performed in a 10-gallon aquarium measuring 50 cm L × 25 cm W × 30 cm H and a burrowing tank measuring 60 cm L × 10 cm W × 60 cm H. The long sides of the burrowing tank consisted of two glass plates, permitting the observation of the amphisbaenian while burrowing and the documentation of sediment disturbance as it occurred. Each experiment involved a single amphisbaenian. All three amphisbaenians were used in the experiments in order to determine variations in burrow morphology due to differences in size and individuals.

The aquaria and burrowing tank were filled with a moist, compressed coconut fiber substrate to simulate a loose but firm soil. This substrate was also permeable enough to allow uniform moisture throughout the soil profile. The 10-gallon aquaria were filled with 25 cm of the substrate, and the burrowing tank was filled in 10 cm layers. The lower 50 cm of the burrow tank included fine-grained calcium carbonate sand in order to allow observation of sediment mixing through the profile.

Repetitions of the burrowing experiments ran for approximately 1, 7, 14, and 21 days. The burrowing chambers were photographed prior to the onset of each experiment. Once the experiments began, the burrowing chambers were photographed daily to document sediment disturbance and bioturbation. Burrows produced in the 10-gallon aquarium were cast with dental plaster after the amphisbaenian was removed. These burrow casts were then excavated, photographed, and described. Burrows produced in the burrow tanks were photographed but were not cast.

Experiments Using Varying Substrate Composition

These experiments were designed to determine what effects substrate conditions had on the morphology of amphisbaenian burrows. As with the burrow-morphology experiments, the substrate experiments were performed in the 10-gallon aquaria. The animals used and the methods in which the burrowing chambers were filled were the same. The amphisbaenians were allowed to burrow for approximately 14 days before they were removed. Documentation of burrowing methods and casting of the burrows at the end of each experiment was the same as for the burrow-morphology experiments. Substrate consistency was varied by mixing varying amounts of clay and fine sand to form dense to loose soils. These experimental soils consisted of two profiles with uniform clay-rich (70% clay, 30% fine sand) and clay-poor (30% clay, 70% fine sand) compositions and a profile with alternating layers with clay-sand (50% clay, 50% sand) and clay-poor (30% clay, 70% sand) compositions.

Quantitative Descriptions of Burrows

For each cast burrow complex, five measurements were recorded—maximum diameter, total length, cross-sectional width : height ratio,

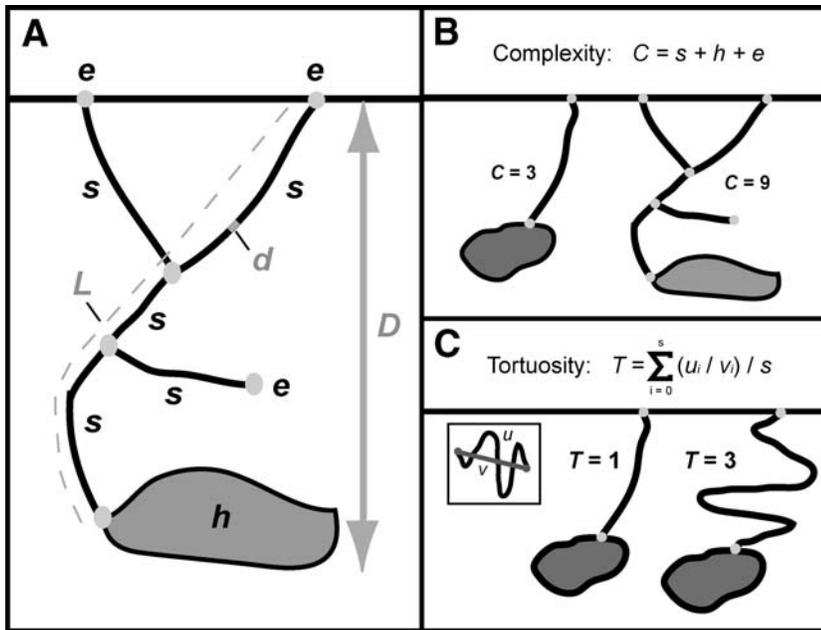


FIG. 3.—Quantitative burrow description models were used to differentiate burrow systems created by different organisms. **A**) Burrows are described by their maximum depth (D), maximum diameter (d), total length (L), and are divided into segments (s)—tunnels that start and end at an entrance, blind ending, chamber, or intersection; endpoints (e)—burrow openings to the surface or terminations within the soil; and chambers (h)—areas with a greater average diameter than the segments. **B**) Complexity is a measure of the number of segments, chambers, and endpoints within a single burrow system. **C**) Tortuosity is a measure of the average sinuosity of all of the segments of a burrow system. The tortuosity of a single segment is found by dividing the total length (u) by the straight line distance (v).

angle of branching, and maximum depth (Fig. 3A). Maximum diameter is defined as the widest tunnel. Total burrow length is the sum of the length of all of the tunnels. The cross-sectional width : height ratio was averaged from 5– to 10 tunnel cross sections. The angle of branching was measured between intersecting burrows away from the walls of the enclosures. Maximum depth to the bottom of a burrow was measured from a surface opening to the base of the deepest tunnel.

Burrow complexity and tortuosity (Fig. 3B, C) are two additional quantitative descriptions of burrow morphology. The complexity and tortuosity are independent of scale and are used to differentiate burrow systems produced by animals of different sizes (Meadows 1991). Burrow complexity (C) is a measure of the number of different tunnels, openings, and chambers that are present in a burrow system. Burrow complexity is a function of: (1) the number of segments (s)—defined as unbranched lengths of a burrow, (2) the number of openings to the soil surface or blind endings below the surface (e), and (3) the number of chambers (h)—defined as areas with a greater cross-sectional area than the segments (Fig. 3A, B). These measurements define an index of complexity (C) that is calculated by $C = s + h + e$, where $C \geq 1$. The tortuosity (T) of a burrow system is a measure of the deviation of the tunnels from a straight line (Fig. 3C). The tortuosity of an open segment is calculated by dividing the total length of the segment (u) by the straight-line distance between the ends of the segment (v). The tortuosity index of the entire burrow system is determined by calculating the average tortuosity of all of the burrow segments, or $T_s = (\sum u_i / v_i) / n$.

EXPERIMENTAL RESULTS

Burrow Morphology and Associated Behaviors

Two-dimensional exposures of amphisbaenian burrows produced near the glass walls of the burrowing tank were photographed and described (Fig. 4). These burrows are sinuous, branching, elongate tunnels, 1.5–2.5 cm in diameter depending on the cross-sectional diameter of the animal, and of variable length. The walls of the burrows are smooth, and sediment is compacted on the upper surface of the tunnel because of the excavation process. The shortest burrow segments observed are 2 cm in length, and the longest are approximately 30 cm in length. The total length of the visible burrows depended on the proximity of the amphisbaenian burrow to the glass. Final burrow length was also

shortened by burrow collapse or sediment reworking as the amphisbaenian produced new tunnels. Branches were produced at irregular intervals (Fig. 4C). The most common amphisbaenian burrow morphology is an S-shape tunnel that may be oriented horizontally to vertically (Fig. 4C, D). Secondary morphologies included short, straight tunnels and short, curved tunnels, and irregularly branched, Y-shaped tunnels (Fig. 4D).

The burrows produced in the morphological experiments were connected into a continuous burrow complex that extended throughout the available space. The development of the burrow systems by each test animal followed a similar pattern during each of the experiments. First, a burrow system of horizontal and vertical tunnels extending from the top to base of the tank was produced while the amphisbaenians determined the lateral and vertical limits of their potential range. Once this outer burrow system was completed the amphisbaenians excavated horizontal and subvertical burrows through the center of the tank connecting both sides of the larger burrow loop. Through time intersecting tunnel networks were created as the amphisbaenian burrowed through more of the substrate. These networks were produced by both the production of new branching tunnels from within preexisting tunnels as well as by the random intersection of new and old burrows during tunnel excavation. Often the amphisbaenian would move into the old burrows that were intersected in this way and the new tunnel would not be continued. Direct connections to the surface were not established after the initial penetration of the substrate.

Three-dimensional casts of amphisbaenian burrows taken from the 10-gallon aquaria consisted of individual tunnels and tunnel complexes (Fig. 5A–C). The three-dimensional amphisbaenian burrows are cylindrical in form (Fig. 5B, C). Burrow diameter is approximately the diameter of the amphisbaenian, from 1.5 to 2.5 cm with a width-to-height ratio of approximately 1.0. The three-dimensional burrow casts are part of interconnected, branching networks of tunnels (Fig. 5C). The burrow networks are composed of horizontally to vertically oriented, straight and sinuous tunnels (Fig. 5B, C).

The total length of the burrow systems from the surface to the deepest burrow was 220–472 cm (Table 1). The maximum depth of the burrow systems was 60 cm, but this was controlled by the maximum depth of the burrowing tank. Based on the results of these experiments, in nature the maximum depth of amphisbaenian burrows is likely 60 + cm. The preserved portions of the burrow complexes consisted of 15–45 segments

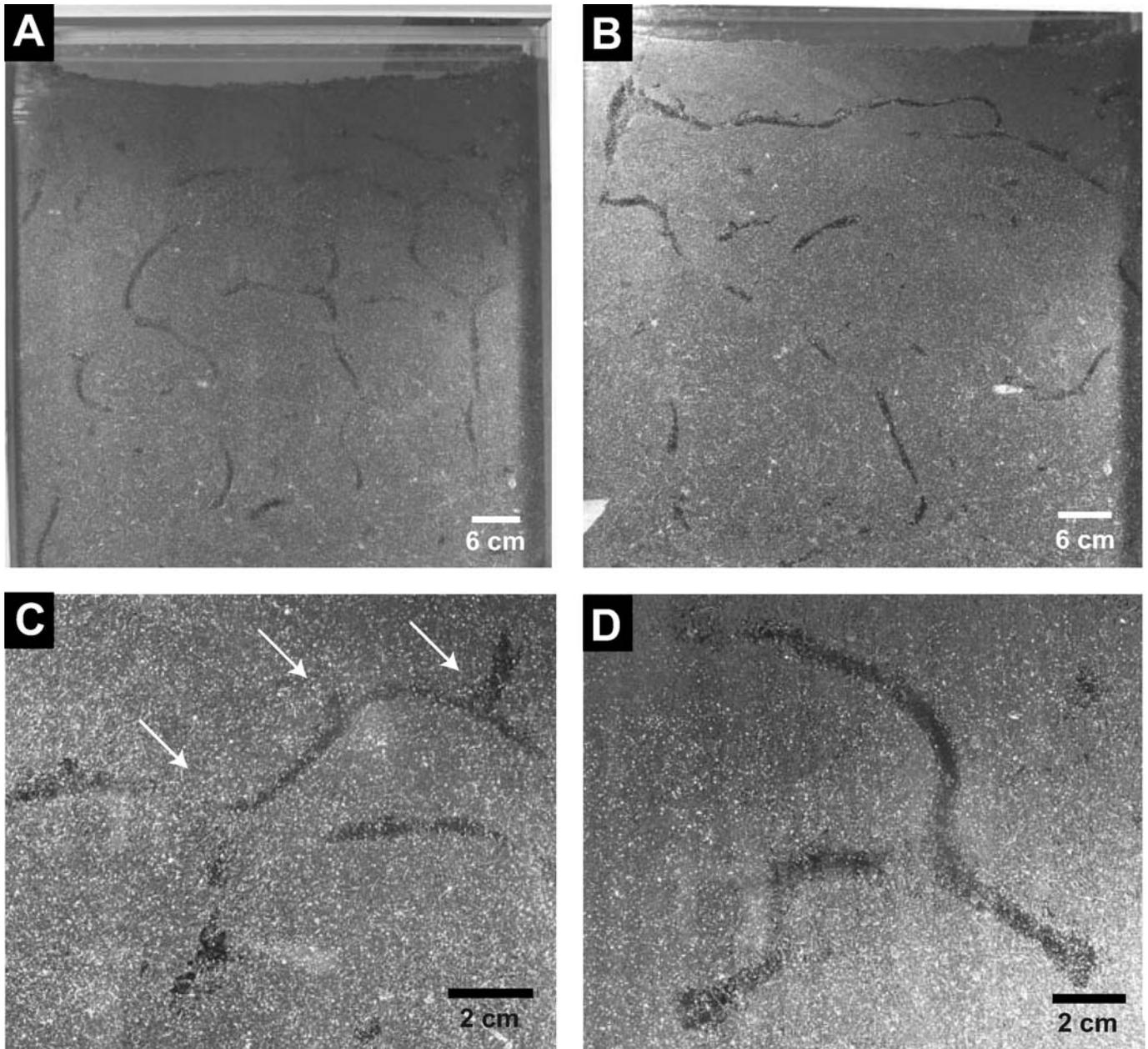


FIG. 4.—Amphisbaenian burrow morphology in two-dimensional exposures. **A, B)** The open burrow networks maintained within the 60 cm burrowing tank consisted of vertical to horizontal, branching, sinuous tunnels. The trace morphology varied from S- and J-shaped elongate burrows, short, straight and curved burrows, and Y-shaped, branching burrows. **C)** Burrow branching varied in frequency, with some tunnels branching at three or more points along a single 6 cm segment. **D)** Distinct Y-shaped, branching tunnels were produced in all of the burrowing experiments.

with no chambers (Table 1), resulting in burrow complexity indices of 15–45. The angle of branching is highly variable (Table 1) but is generally 30–90° in both the horizontal and vertical planes. Measurements of the sinuosity of individual burrow segments are given in Table 1. The variation in tunnel morphology from straight to sinuous resulted in tortuosity indices of 1.1 for the different burrow complexes (Table 1).

Morphological Variations Due to Substrate Composition

The experiments conducted using soils of different bulk densities resulted in burrow systems of varying two- and three-dimensional morphologies and complexity. In all of the substrate experiments the

amphisbaenians immediately burrowed into the substrate after being placed in the aquarium. The time spent getting completely below the surface, however, increased with increasing clay content of the soil. Burrowing time varied from approximately 30 seconds with clay-poor soil to over 4 minutes with clay-rich soil. The longer time spent on the surface of the clay-rich soil included time spent in search of a suitable entry point. The entry point remained open throughout the experiments, although the amphisbaenians never exited from the initial burrow entrance.

Biogenic structures produced in the clay-rich soil included well-defined burrows with distinct walls as part of a permanent burrow complex established in a few days and maintained over the course of the

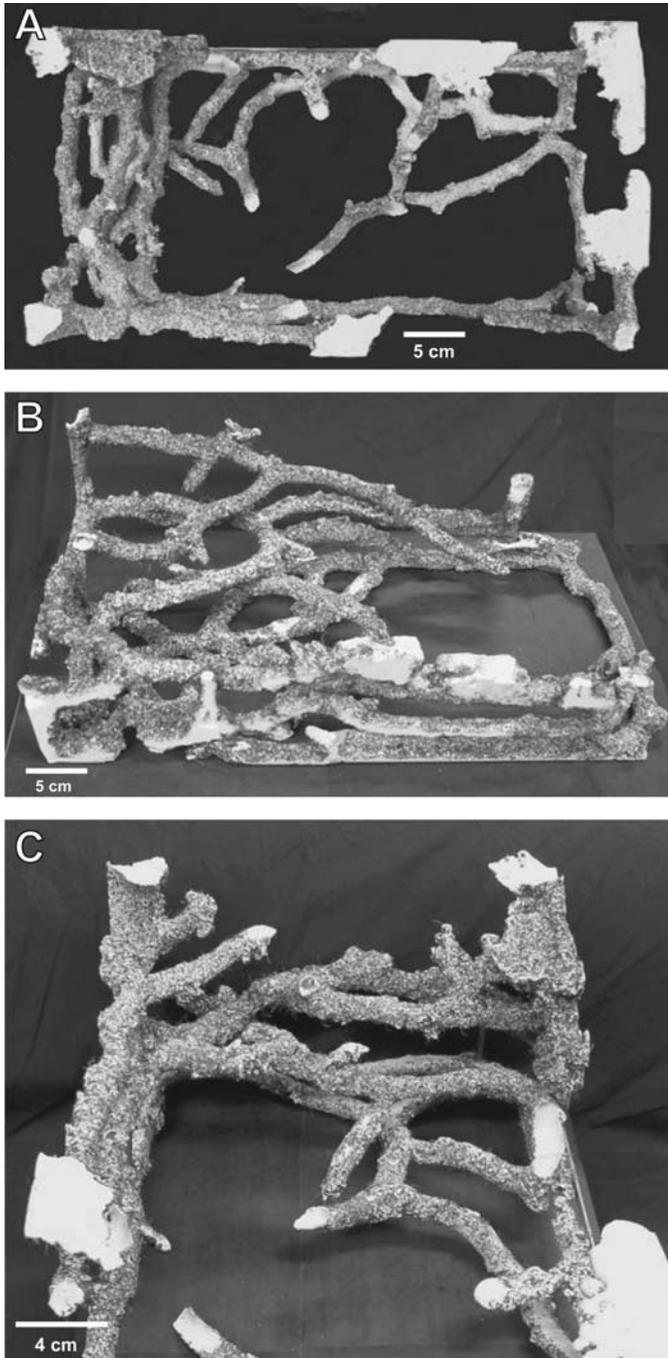


FIG. 5.—Three-dimensional amphisbaenian burrow morphology from a loose but cohesive, coconut fiber substrate. **A)** Plan view of a plaster cast of an amphisbaenian burrow system produced over 14 days. The burrow system is composed of straight and sinuous, cylindrical tunnels interconnected to form a three dimensional network. **B)** High oblique view of a plaster cast of an amphisbaenian burrow system produced over 7 days. **C)** The amphisbaenian burrow networks are composed of stacked layers of vertical burrows connected by short, horizontal burrows.

experiment. While the initial entry point was abandoned, new connections to the surface were created although the amphisbaenian never exited the burrow system. Two-dimensional exposures on the sides of the aquaria consisted of elongate, branching tunnels with a uniform 1–2 cm diameter (Fig. 6A, B). Burrow length was controlled by the size of the aquarium.

TABLE 1.—Measurements of representative three-dimensional casts of amphisbaenian burrow complexes created over different time intervals and substrate types. All measurements are in cm.

	1 day	7 days	14 days	70/30 soil
Burrow diameter	1.5–2.0	1.5–2.0	1.5–2.5	1.5–2.0
Width:height	1.0–1.1	1.0–1.1	1.0–1.1	1.0–1.5
Total length	220	448	472	435
Depth	20	20	20	20
No. segments	15	34	36	45
Branching angle	30–90	30–90	30–90	30–90
Segment tortuosity	1.0–1.1	1.0–1.1	1.0–1.1	1.0–1.1
Complexity index	15	34	36	45
Tortuosity index	1.1	1.1	1.1	1.1

The burrows consisted of predominantly elongate horizontal tunnels (Fig. 6A) with short, vertical tunnels connecting different horizontal levels (Fig. 6B).

Three-dimensional casts of the burrows in the clay-rich soil consisted of networks of straight to sinuous tunnels (Fig. 7A–D) that were cylindrical to elliptical in cross section and ranged in diameter from 1.0 to 2.0 cm (Fig. 7C, D). Some tunnels taper to a point and terminate within the substrate (Fig. 7A–C). Up to three tunnels branch from a single point accompanied by the expansion of the burrow diameter at the intersection point (Fig. 7D). The bottoms of the tunnels are smooth and flat. The roof and sides of the tunnels have triangular impressions with positive relief (Fig. 7D–G). These impressions are the marks left by the triangular snout of the amphisbaenian as it lifted and compressed the clay-rich soil into the sides of the tunnel. The apex of the triangle indicates the direction of movement of the amphisbaenian. Some tunnels have markings showing movement in two directions, demonstrating reuse and maintenance of the tunnels through time (Fig. 7F). Other triangular impressions in tunnels of larger diameter are side by side showing the expansion of the burrow width (Fig. 7G).

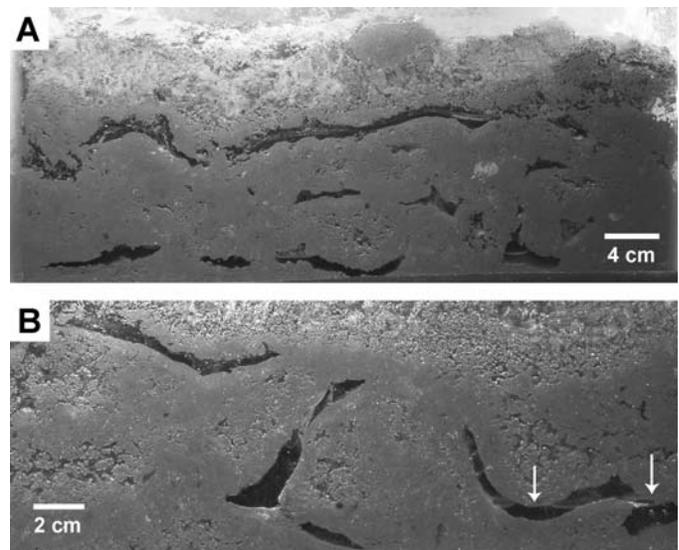


FIG. 6.—Two-dimensional exposures of amphisbaenian burrows produced in a clay-rich substrate are similar to those produced in the loose, cohesive substrate. **A)** Parallel layers of elongate, sinuous, horizontal burrows lie along the bedding plane and are connected by short vertical burrows. **B)** Distinct Y-shaped, branching tunnels in the clay-rich substrate. Standing water is present in the lower tunnels, indicated by the arrows.

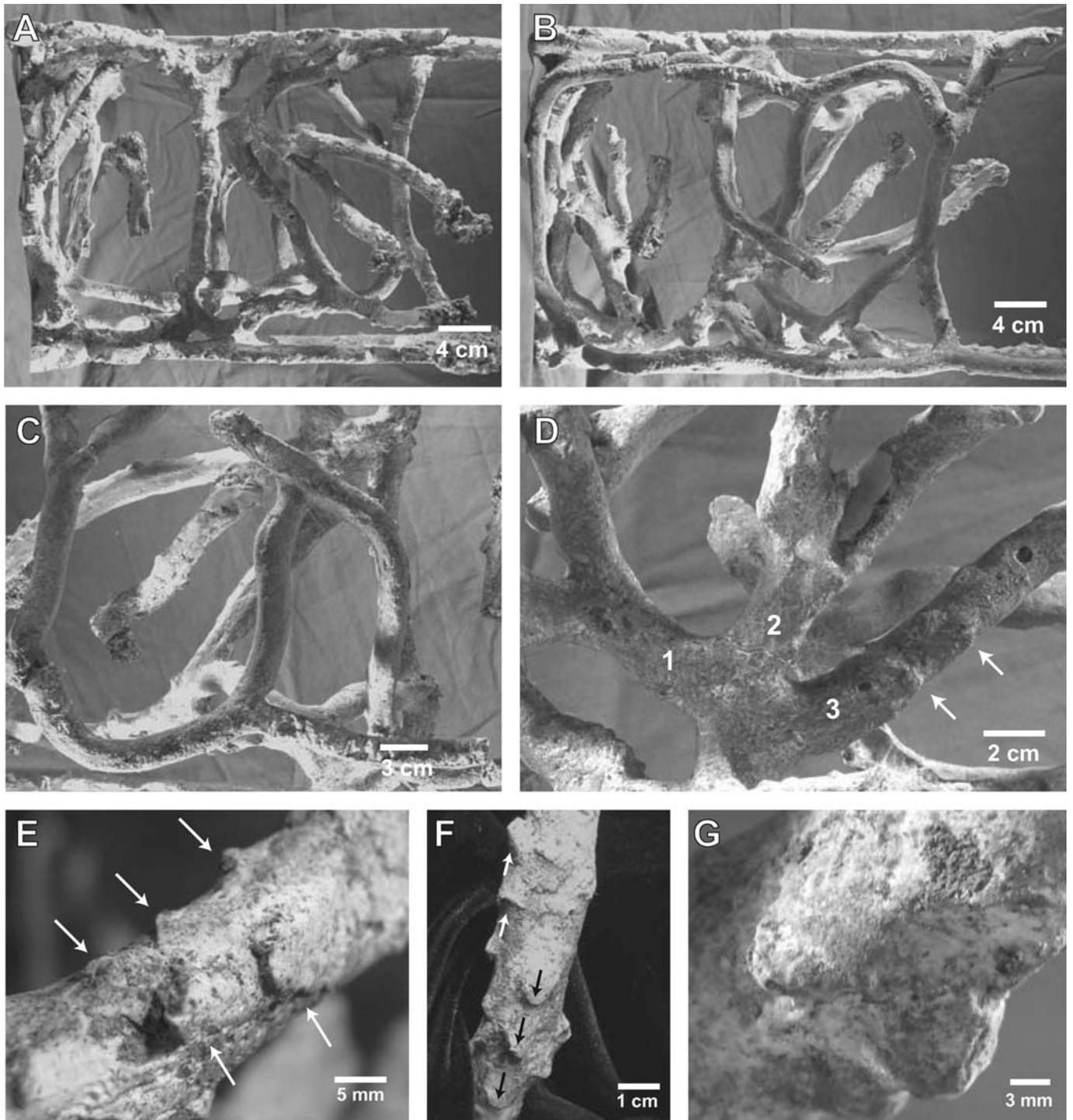


FIG. 7.—Three-dimensional amphisbaenian burrow networks produced in a clay-rich substrate. **A)** Top view of a plaster cast of an amphisbaenian burrow network. **B)** Bottom view of the burrow cast. **C)** Tunnels vary from straight to sinuous forms within the burrow system. **D)** Up to three tunnels (1–3) extend from a single junction within the burrow system. Triangular impressions are indicated by the arrows. **E)** Series of triangular impressions on roof and sides of a tunnel. **F)** Two sets of triangular impressions indicating opposite direction of movement as shown by the arrows. **G)** Paired triangular impressions on the roof of a tunnel indicating tunnel widening or repair.

The biogenic structures produced in the clay-poor soil consist of poorly defined burrows and very limited networks of interconnected burrows (Fig. 8). Burrows were produced 1–2 cm below the surface, but the amphisbaenian did not exit the substrate. The amphisbaenian produced

a constantly changing burrow system by continuing to cut new tunnels through the substrate during the experiment. Old burrows collapsed through time and were destroyed by the construction of new tunnels. Despite the lack of maintained, open burrows, a bioturbated texture was

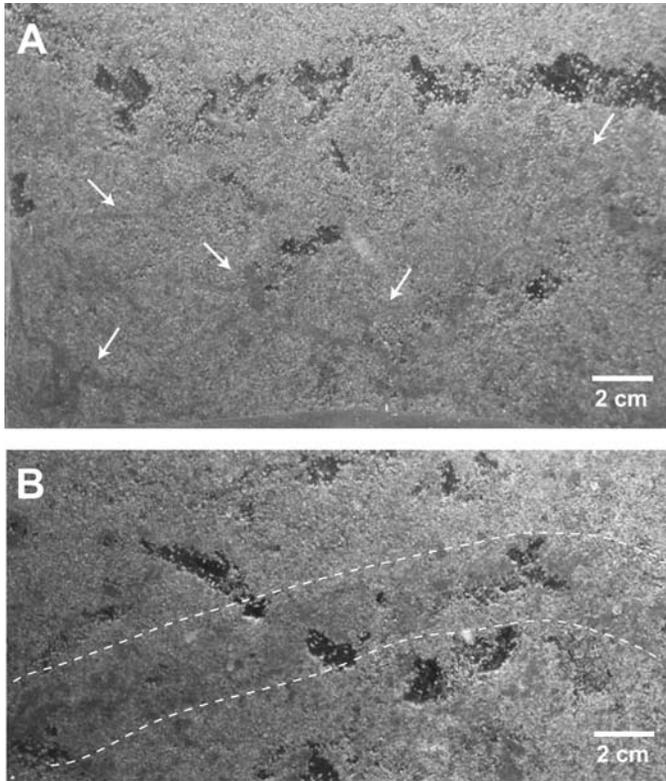


FIG. 8.— **A)** Amphisbaenian burrows were poorly preserved in the clay-poor substrate consisting of disjoined, sinuous, horizontal and vertical tunnels and soft-sediment deformation. **B)** Amphisbaenians produced a distinct ichnofabric composed of elongate, sinuous trails of dark, compacted clay indicating collapsed burrows.

produced in the two-dimensional exposures along the sides of the aquaria as elongate, sinuous trails of dark, compacted clay and sand (Fig. 8A). The compacted sediment was produced by the compression of clay and sand onto sides and tops of the tunnels by the amphisbaenian as it burrowed. After the amphisbaenian moved through the tunnel, the tops and sides gradually collapsed, leaving the trail of compacted material along the path of movement. The bioturbated texture shows multiple, horizontally oriented burrows passing through the substrate. The burrow traces have a linear, sinuous morphology and cross repeatedly through the same areas of the substrate. Additionally, 1.5–2.0 cm diameter ghost burrows composed of compacted clay and disturbed sand were produced where the amphisbaenian burrowed near the glass wall (Fig. 8B). These burrows also show repeated bioturbation of the same regions. Three-dimensional morphology was not preserved due to the disjointed nature of the burrow systems. Despite the lack of preserved open-burrow complexity, the bioturbated texture indicated that the amount of bioturbation was greater in the clay-poor soil than in the clay-rich soil. The sandy soil provided little resistance to movement; therefore the amphisbaenian was able to maintain continuous movement with minimal expenditure of energy. Particularly, open burrows tended to collapse in the loose substrate, requiring the amphisbaenian to constantly create new burrows.

The biogenic structures produced in the substrate composed of alternating layers of clay-poor and clay-sand soil (Fig. 9A) consisted of sediment mixing in addition to open burrows (Fig. 9B–E). The two-dimensional exposures of biogenic structures included open burrows that were preserved primarily in the clay-sand soil layers. These burrows consisted of short, straight to curved tunnels that were 1.0–2.5 cm in diameter, some with short branching tunnels (Fig. 9C). The open burrows

were lined by dark-colored layers of compressed clay (Fig. 9D). Collapsed burrows within the clay-poor soil were still visible due to this compressed clay lining. Other biogenic structures resulted from the sedimentologic differences of the soil layers. Where burrows crossed the layers they were deformed relative to the direction of movement (Fig. 9E). Upward-deflected bedding was the result of upward movement of the amphisbaenian, and downward-deflected bedding was the result of downward movement. Burrows that cut across the clay-sand and clay-poor layers also caused them to be offset vertically, creating structures that are morphologically similar to microfaults (Fig. 9C).

Morphological Variations Due to Soil Moisture

Variations in the amount of soil moisture also affected the morphology of the amphisbaenian burrow complexes and individual tunnels. These variations in burrow morphology were primarily the result of preservational rather than behavioral differences. The amount of soil moisture did control the maximum depth of burrowing. The majority of amphisbaenian burrows were present above the level of complete saturation. Some of the lower tunnels in the burrow complexes of the clay-rich soil, however, were partially filled with water (Fig. 6B). Experimental observations indicate that amphisbaenians do not avoid standing water in their burrows as long as air pockets are available. As a result, their burrows can be expected to be present within the vadose zone but likely not below the water table.

The morphological differences of the burrow complexes in different soil moisture levels are the result of both collapse and deformation of tunnels. In the sandy soils higher soil moisture resulted in the preservation of more open, interconnected burrows. When soil moisture was lower, the open burrows collapsed quickly after they were excavated by the amphisbaenian and the number of preserved burrows was low. The degree of sediment mixing, however, was higher in lower-moisture soils because the amphisbaenian had to constantly create new tunnels. In the clay-rich soil burrows collapsed rarely as a result of drying but morphological differences were caused by the deformation and shrinking of the wet, plastic tunnel walls. This deformation resulted in the preservation of tunnels that were narrower and flatter than those observed from drier soils (Table 1). Consequently, burrows from clay-rich soils do not always accurately indicate the true size and shape of the tracemaker.

IMPLICATIONS AND SIGNIFICANCE

Ichnological Classification

The burrows were created as a result of several interrelated behaviors. These behaviors may be classified as locomotion (*repichnia*), feeding (*fodinichnia*), and dwelling (*domichnia*). The burrows are created as a result of the amphisbaenians moving through the substrate and can therefore be classified as *repichnia*. Locomotion was also associated with burrow reuse and maintenance. Movement through the maintained tunnels was rapid, but movement accompanying burrow construction was slow, indicating that burrow systems are established and maintained for hunting efficiency as well as energy conservation associated with burrowing. The amphisbaenians were equally capable of forward and backward movement through the established tunnels. Observations during the experiments indicated that most of the burrows were maintained through the duration of the experiments. The complete burrow complexes should then be classified as *domichnia*. Tunnel extensions were also produced as means of acquiring food and can be classified as *fodinichnia*. Mealworms placed on the surface burrowed into the substrate and produced enlarged pupal chambers within a few hours. The amphisbaenians established new vertical and horizontal burrows to intersect these pupal chambers within 24 hours. Additional branches were produced from these burrows after the mealworms were eaten and are

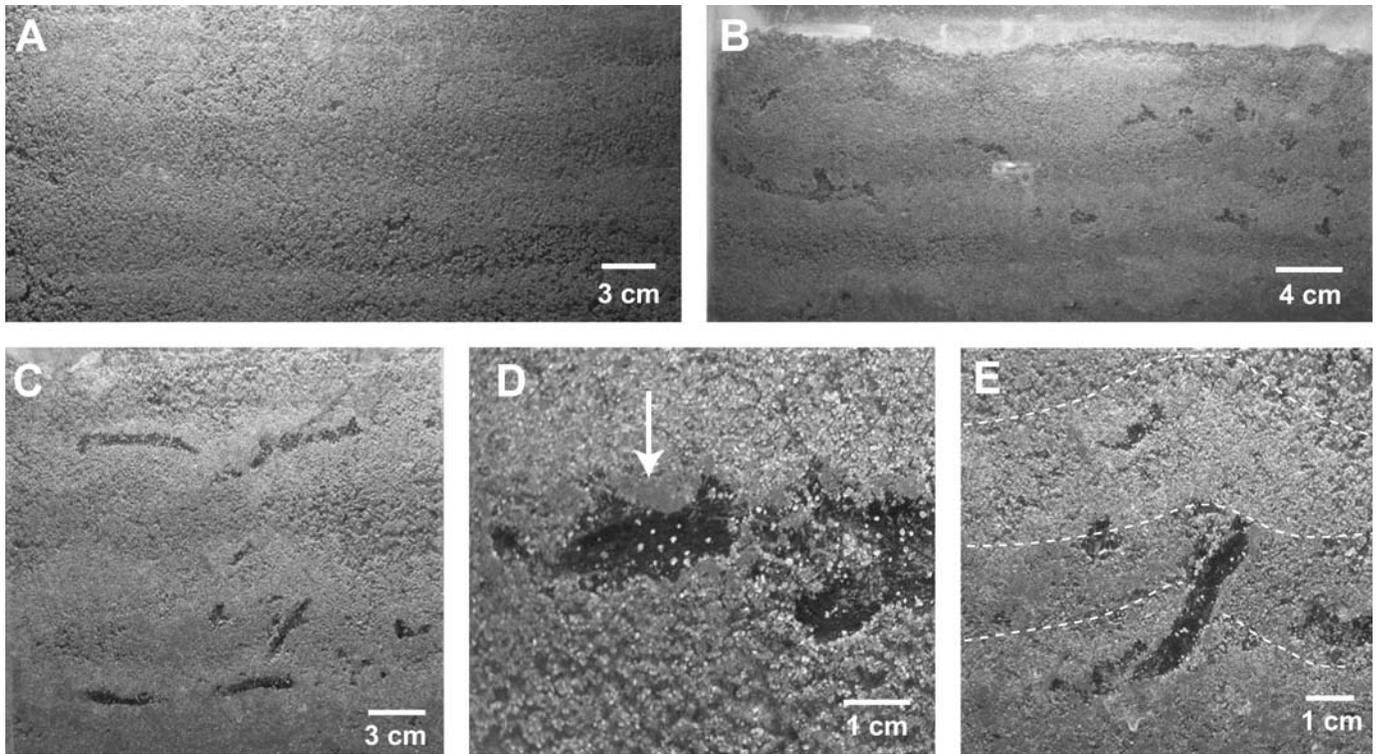


FIG. 9.—Amphisbaenian burrow produced in the alternating clay-poor and clay-sand substrate consisted of both open, interconnected burrows and deformation structures. **A)** Initial sediment layering in the experimental tank. **B)** The amphisbaenian caused sediment mixing in addition to forming open burrows within the alternating layers of sediment. **C)** Short, straight to curved burrows and Y-shaped branches were typical of two-dimensional exposures. **D)** The exposed burrows were lined by 1–2 mm thick layers of compressed clay concentrated on the tunnel roof. **E)** Deformed layers as a result of the upward or downward movement of the amphisbaenian.

possibly associated with continued hunting behavior. As a whole, the burrow systems of amphisbaenians can also be referred to as polychresichnia, or trace fossils representing many simultaneous behaviors including reproduction (e.g., Hasiotis 2003).

Infilled, two-dimensional exposures of individual amphisbaenian tunnels are similar morphologically to the ichnogenera *Palaeophycus* isp. and *Psilonichnus* isp. *Palaeophycus* consists of horizontal to oblique, cylindrical to subcylindrical, sinuous, burrows with smooth, lined walls that commonly intersect one another (Häntzschel 1975; Pemberton and Frey 1982). Importantly, the burrow fill of *Palaeophycus* consists of gravity-induced sedimentation within open burrows (Pemberton and Frey 1982). Filled amphisbaenian burrows lying along the bedding plane may, therefore, mimic the morphology of *Palaeophycus* if the compressed clay surrounding the tunnel is preserved. *Psilonichnus* is a vertically oriented burrow that typically has a J- and Y-shaped branching toward the top of the burrow (Frey et al. 1984). *Psilonichnus* is also characterized by a gravity-induced burrow fill. *Palaeophycus* isp. and *Psilonichnus* isp. are attributed to burrowing annelids and decapods, respectively, but have been described in both marine and continental deposits.

The infilled, three-dimensional burrow networks of amphisbaenians are comparable to *Thalassinoides* isp. *Thalassinoides* is diagnosed by cylindrical burrows that form three-dimensional branching systems consisting of horizontal networks connected to the surface by vertical to subvertical shafts (Häntzschel 1975; Bromley 1996). The individual tunnels are 1–20 cm in diameter and regularly branch, often as Y- or T-shaped terminations (Häntzschel 1975). Tunnels are enlarged at these intersections. *Thalassinoides* is described as the feeding and dwelling structures of decapod crustaceans, which are often preserved within the burrows (Häntzschel 1975).

Preservation Potential of Amphisbaenian Burrows

While no biogenic structure has a zero preservation potential (Bromley 1996), it has been documented that deep-tier structures do have a greater preservation potential than shallow-tier structures, which are destroyed by continual bioturbation of many types of organisms (Bromley 1996; Hasiotis and Honey 2000). The laboratory studies with amphisbaenians presented here indicate that these animals easily construct burrows up to one meter in depth. Amphisbaenian burrow networks are deep-tier structures and thus possess a high preservation potential because they are present in a variety of soil types, which are low-energy environments, and the burrow networks are maintained or reconstructed during the life of the animal. Because the same burrows are kept open for long periods of time the likelihood of the burrows being available for casting through natural processes is greater than if the animal simply burrowed through an area once and left the tunnels to collapse. Because amphisbaenians are deep-tier organisms, however, these structures are likely to be present deep within the soil profile below the homogenized upper profile (e.g., Hasiotis and Honey 2000). The lack of documented amphisbaenian burrows in the fossil record is a result of a lack of recognition rather than low preservation potential.

The lack of a constructed burrow fill is the limiting factor to the preservation potential of amphisbaenian burrows. In general, the preservation of a backfilled or provisioned burrow in a paleosol is more likely than the preservation of an open burrow. Amphisbaenian burrows produced in the laboratory also typically did not have a maintained surface connection. This limits the possibility of an amphisbaenian burrow being cast by sediment fill from the surface. The low sedimentation rates associated with most paleosols further limits the potential of passive infilling of sediment. The preservation of amphisbae-

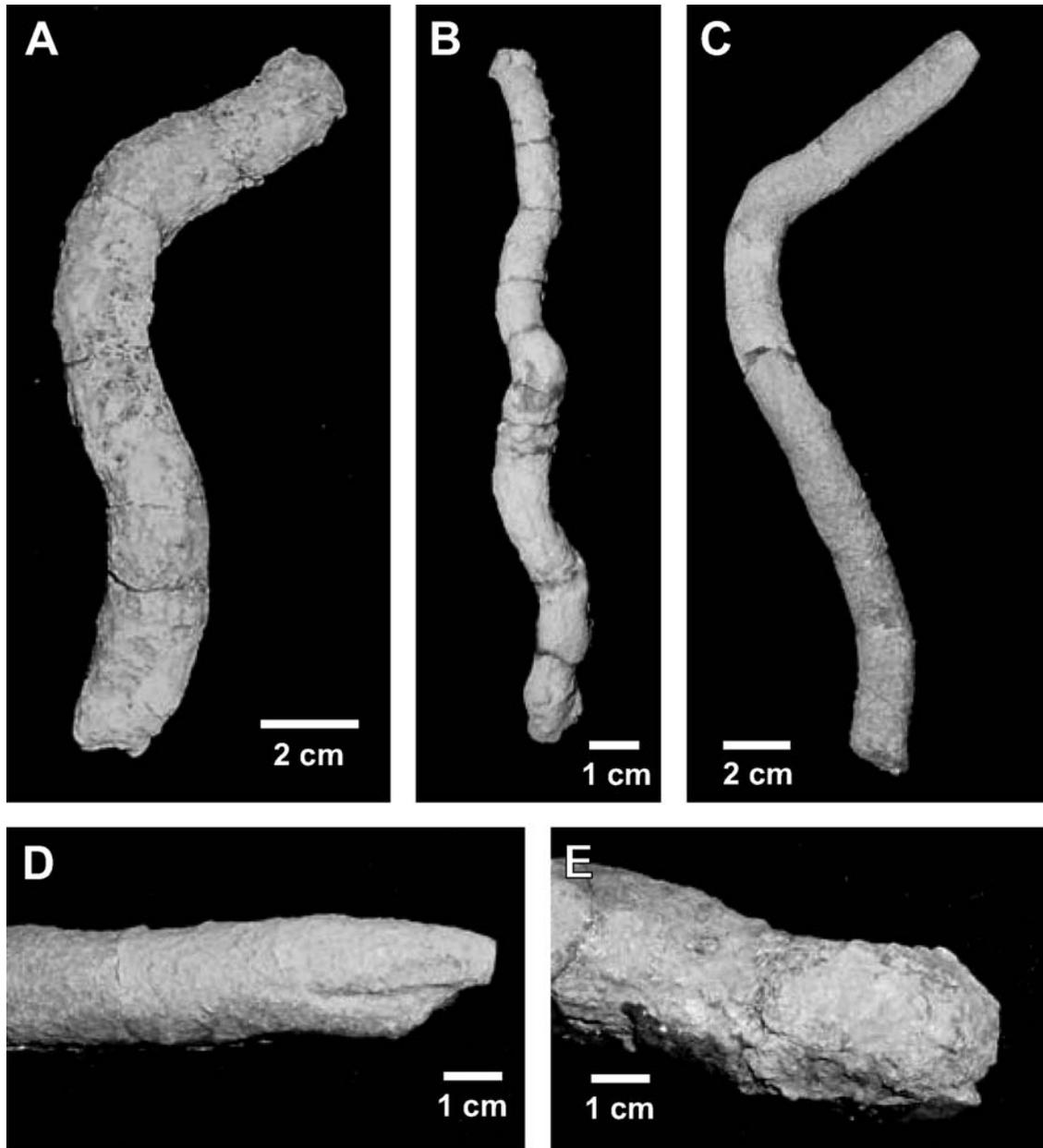


FIG. 10.—Proposed amphisbaenian burrow casts from the Eocene Willwood Formation. A–C) Isolated burrow casts are elongate, sinuous, nonbranching tunnels composed of sandstone and siltstone. D) Some of the burrow casts have asymmetrical, tapered terminations. E) Other burrow casts end in an irregular termination.

nian burrows with detrital sediment requires the rapid infilling of the burrows during a flooding or avulsion event soon after a connection with the surface has been established. Preservation of amphisbaenian burrows is more likely to be facilitated by roots following the zones of weakness and high moisture provided by the burrows. Roots tend to form dense masses around burrows, precipitating calcium carbonate as they draw in water from the soil (Martin and Bennett 1977). The calcium carbonate accumulates around the tunnel walls and eventually fills in the burrows to create casts.

In addition to three-dimensional burrow casts, the bioturbated fabric of amphisbaenians may be preserved. This type of biogenic structure has a greater preservation potential than open burrows because no casting is required (e.g., Bromley 1996). The recognition of these types of amphisbaenian ichnofabrics in outcrop, however, is more difficult. In

the laboratory experiments, amphisbaenians produced recognizable biogenic structures and bioturbated textures in both heterogeneous and homogeneous substrates. These structures included folded beds, micro-faults, ghost burrows, and trails of compacted sediment. The main barrier to the preservation of these biogenic structures and textures as an ichnofabric is the continual bioturbation of soils by other organisms.

Potential Amphisbaenian Trace Fossils

Trace fossils that are morphologically similar to those produced by amphisbaenians in the laboratory are found in paleosols of the Eocene Willwood and Miocene Pawnee Creek formations in Wyoming and Colorado, respectively. These trace fossils are preserved as isolated burrow casts and complex, three-dimensional burrow networks. No

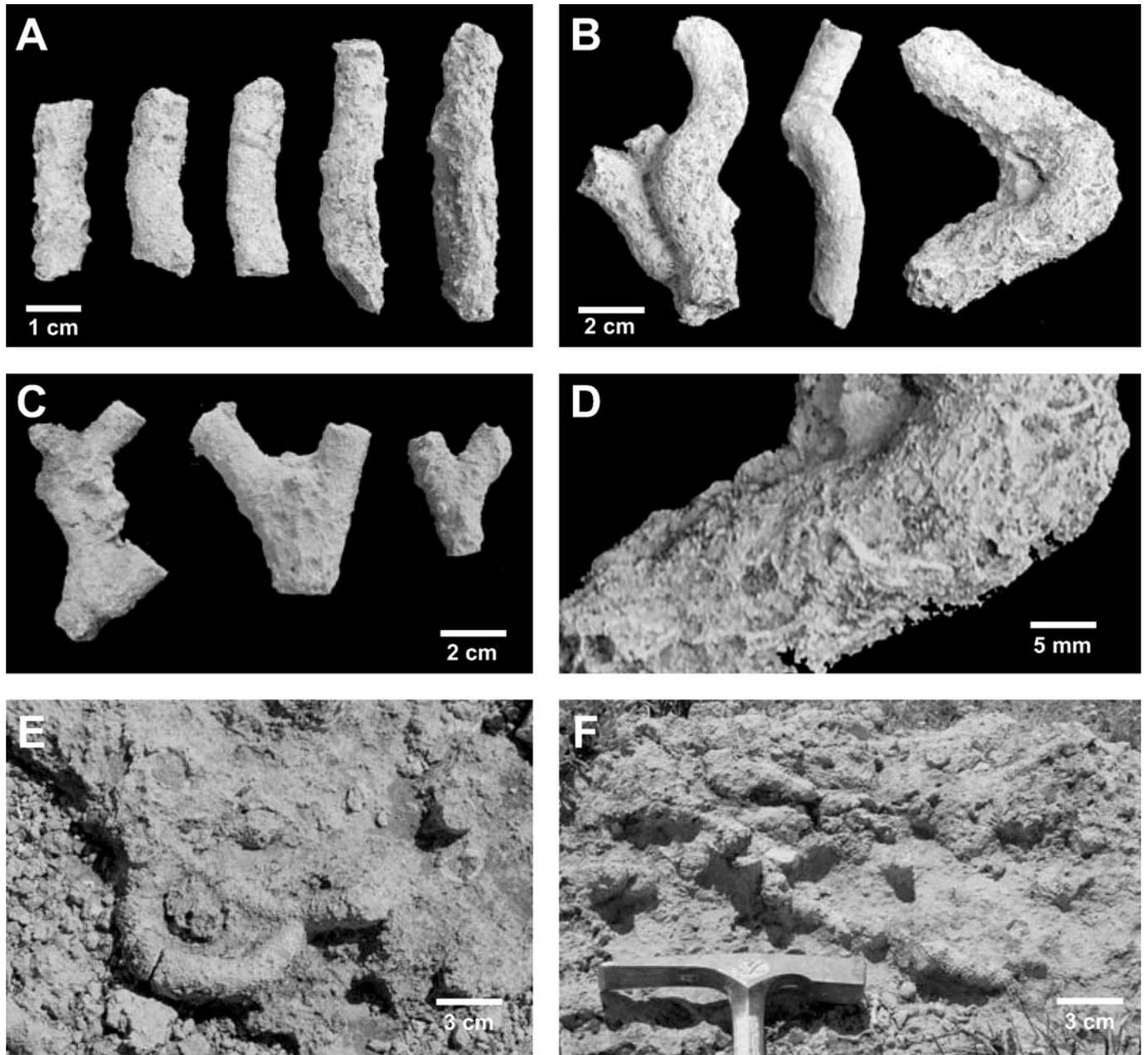


FIG. 11.—Proposed amphisbaenian trace fossils from the Miocene Pawnee Creek Formation. **A)** Cylindrical burrow casts with a circular to elliptical cross section. **B)** Sinuous, cylindrical burrow casts. **C)** Burrow casts with multiple, Y-shaped, branches. **D)** The burrow casts are preserved by the surrounding masses of calcareous rhizoliths. **E)** Burrow casts form complex, interconnected networks that extend laterally and horizontally. **F)** In outcrop the burrow casts occur in a high density.

amphisbaenian body fossils were found associated with these trace fossils. Amphisbaenian fossils are well known, however, from late Paleogene to early Neogene strata of the central United States.

Potential amphisbaenian ichnofossils from the Eocene Willwood Formation of central Wyoming consist of individual, isolated burrow casts 15–40 cm in length with a circular to ovoid cross section 1.0–1.5 cm in diameter (Fig. 10). These burrows occur in paleosols and are cast by siltstone and sandstone. The burrow casts are elongate and sinuous in form, with sinuosity indices of 1.1–1.2 (Fig. 10A–C). The burrows do not branch, and they end at either an irregular termination or taper to an asymmetrical point (Fig. 10D, E). The size and general morphology of these burrow casts is similar to that of the amphisbaenians. The siltstone

and sandstone fill suggests that these burrows were open to the surface. The absence of interconnected burrows or any evidence of branches and the irregular terminations suggests that they are only partially preserved segments of a potentially larger burrow system. While amphisbaenian fossils have not been reported from the Willwood Formation, they are well known from other Eocene paleosol-bearing formations of Wyoming, including the Wind River and Bridger formations.

Potential amphisbaenian burrow networks are found in the Miocene Pawnee Creek Formation of northeastern Colorado. These ichnofossils consist of three-dimensional, branching networks of burrow casts that occur in a calcareous paleosol. The burrow networks erode from the outcrop along bedding-plane exposures and have not been observed in

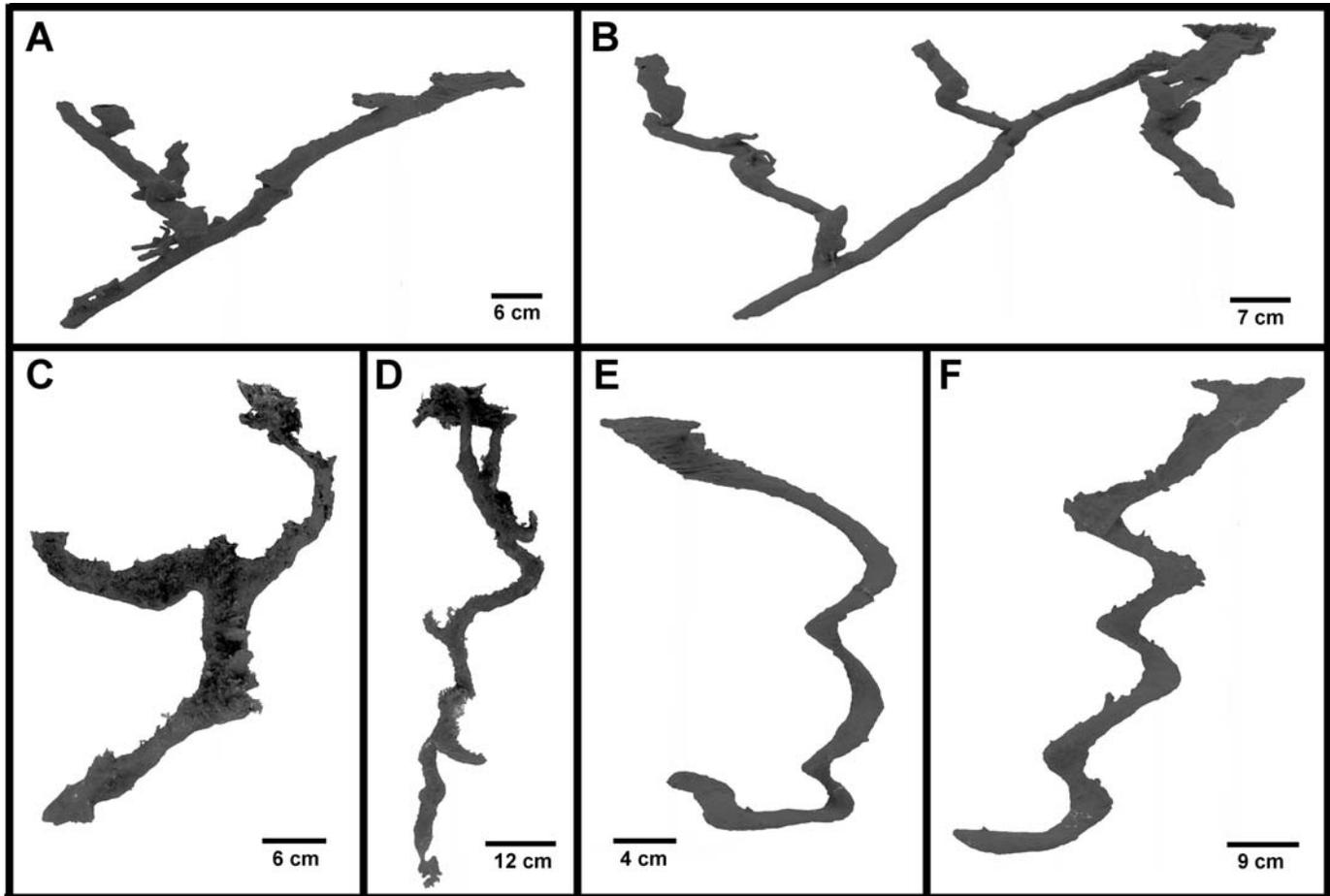


FIG. 12.—Burrow morphologies of modern continental organisms. A) Skink burrow. B) Skink burrow. C) Crayfish burrow. D) Crayfish burrow. E) Scorpion burrow. F) Scorpion burrow.

cross section. Individual burrow casts are cylindrical in form with a circular to elliptical cross section, 1.5–3.0 cm in diameter (Fig. 11A). The tunnels are straight to sinuous, with some forming U- and S-shaped patterns (Fig. 11B). The tortuosity along exposed lengths of individual burrows is 1.1–1.5. Most of the burrows branch at multiple points along their length or terminate in Y-shaped branches (Fig. 11C). In well-exposed burrows the angle of branching is 50–60°. The burrow casts are composed of carbonate mudstone and are covered by millimeter-scale rhizoliths (Fig. 11D). The rhizolith coating masks the surficial morphology of the burrows and potentially increases the diameter of the preserved cast. In outcrop the burrows form complex, branching networks that extend laterally up to 1 m and vertically into the outcrop (Fig. 11E, F). These networks are composed of elongate, sinuous, horizontal tunnels and short, curved, horizontal and subvertical tunnels.

The size and morphology of the Miocene burrow casts and burrow networks are similar to those of extant amphisbaenians. The body fossils of amphisbaenians are known from the outcrops of the underlying Oligocene White River Formation in the same locality (Estes 1983). Amphisbaenian fossils have also been reported from Miocene strata in Nebraska and South Dakota (Estes 1983).

Comparison of Amphisbaenian Burrows with Burrows of Other Organisms

The burrows of continental infaunal vertebrates and invertebrates have different morphologies as a result of differences in the morphology of the

organism, the burrowing methods, the function of the burrow, and the environments in which they occur (Hasiotis 2002). Due to their unique morphology and burrowing methods, amphisbaenian burrow networks have distinct morphological characteristics that permit their distinction from the burrows of other continental organisms. To demonstrate these differences, burrow casts of modern skinks, crayfish, and scorpions were described in the same manner as the amphisbaenian burrows and the morphologies were compared (Figure 12, Table 2).

The burrows of skinks (Reptilia: Scincidae) are composed of interconnected, inclined tunnels with multiple openings to the surface (Hasiotis and Bourke 2005) (Fig. 12A, B, Table 2). Skink burrows are composed of inclined tunnels, vertical switchbacks, and slightly enlarged terminal chambers that form a horizontally and vertically extensive system. Many freshwater crayfish (Arthropoda: Crustacea) burrows consist of a single, vertically oriented, tunnel and a variable number of short, horizontal and subvertical, side branches (Hasiotis and Mitchell 1993) (Fig. 12C, D, Table 2). The main tunnel may be straight or form a loose spiral pattern. Scorpion (Arthropoda: Arachnida) burrows are characterized by a single, horizontally flattened tunnel that is either steeply inclined or forms a subvertically oriented, spiral pattern (Hasiotis and Bourke 2005) (Fig. 12E, F, Table 2). The main tunnel terminates in a dwelling area that is wider than the tunnel.

The comparison of these biogenic structures demonstrates that based on qualitative morphology, from basic architectural and surficial morphology to such quantitative descriptions as complexity and

TABLE 2.— Characteristics of burrows made by different continental, fossorial organisms. All measurements are in cm.

	Amphisbaenian	Skink	Crayfish	Scorpion
Architectural morphology	Complex, interconnected networks; multiple branches per junction; cylindrical, sinuous to straight tunnels	Interconnected, inclined tunnels and switchbacks; elliptical, straight to curved tunnels	Simple to complex; single vertical tunnel; elliptical cylindrical, straight spiraling tunnels	Simple; single, inclined, straight to tunnel; to spiralling
Orientation	horizontal and vertical	horizontal and vertical	vertical and horizontal	vertical and horizontal
Cross section	circular to ovoid	elliptical	circular to ovoid	elliptical
Diameter	1.5–2.5	3.0–4.0	2.0–8.0	2.0–9.5
Width : height	1.0–1.5	1.8–2.3	1.0–1.6	2.2–7.2
Total length	200–400+	60–70	50–200	25–80
Depth	>100	30–35	40–200+	15–60
Terminal chamber	absent	absent	yes, expanded vertically and horizontally	yes, expanded horizontally
Branching	common 20–30 segments	common 5–10 segments	variable 1–10 segments	absent
No. surface openings	0–1	2–6	1–3	1–2
Surficial morphology	triangular impressions on top and sides of tunnels	central groove, scalloped walls	hummocky walls, appendage marks, body impressions, pleopod striae	none
Lining	compacted clay	none	discontinuous mud lining	none
Complexity index	15–40+	10–15	5–15	2–3
Tortuosity index	1.1	1.2–1.4	1.3–1.4	1.0–2.2

tortuosity, the burrows of different organisms can be easily distinguished. The morphology of these modern biogenic structures can then be applied to trace fossils in order to facilitate the identification of their tracemakers and the interpretation of their function. In addition, variations within individual trace morphologies can be used to interpret specific environmental conditions, such as depth to the water table with crayfish burrows (Hasiotis and Mitchell 1993; Hasiotis and Honey 2000; Hasiotis 2002) or soil composition and moisture with amphisbaenians.

CONCLUSIONS

Laboratory experiments with modern organisms provide burrow signatures of specific tracemakers to improve the interpretation of trace fossils and tracemakers. These experiments also help us understand the relationship between burrow morphology and organism behavior, substrate consistency, and other environmental conditions. Amphisbaenians produce three-dimensional biogenic structures with unique morphologies that can be used to distinguish their trace fossils from those of other continental organisms. In addition, the morphology of amphisbaenian burrows is also predictably variable with changes in soil composition and soil moisture.

Because complete, *in-situ* body fossils of soil organisms are not typically found within paleosols, the potential biodiversity of ancient soil communities must be determined through ichnofossils. It is important, therefore, to recognize the potential of the biogenic structures of squamates to occur as both burrow casts and sediment deformation structures. In paleosols, sediment deformation is not typically considered to be the product of fossorial vertebrates. Laboratory experiments indicate, however, that fossorial squamates are capable of folding, faulting, and mixing primary sedimentary structures. Open burrows, while not typically open to the surface, may be preserved through the activity of plants or the precipitation of carbonate and other mineral within the soil. Burrow casts from alluvial paleosols of the Eocene Willwood and Miocene Pawnee Creek formations are similar to those produced by amphisbaenians in the laboratory. The recognition of these ichnofossils also allows a better interpretation of the soil ecosystem and food web, because permanent, vertebrate soil faunas are considered rarely in paleoecological studies. Amphisbaenian ichnofossils may also be used to extend the geographic and stratigraphic range of these organisms.

Amphisbaenian ichnofossils can be useful in paleoenvironmental reconstructions of ancient floodplains. Because amphisbaenians are air breathers, they require a moderately to well-drained soil. While their burrows may extend deep into the vadose zone, they would not go typically below the permanent water table. The burrow morphology and the degree of burrow complexity can indicate the substrate consistency. Well preserved amphisbaenian burrow complexes with multiple levels of branching burrow casts suggest well-consolidated soils and low rates of aggradation permitting the establishment of permanent dwellings. The presence of surficial ornamentation on the tunnel walls indicates a moist, clay-rich soil. Ghost burrows, disrupted primary sedimentary structures, and isolated burrow casts indicate loose, sandy or silty soils. A low frequency of open burrows suggests lower levels of soil moisture.

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REFERENCES

- ABE, A.S., 1984, Experimental and field record of preferred temperature in the neotropical amphisbaenid *Amphisbaena mertensi* Stauch (Reptilia, Amphisbaenidae): Comparative Biochemistry and Physiology, v. 77, p. 251–253.
- ATKINSON, R.J.A., 1986, Mud-dwelling megafauna of the Clyde Sea area: Royal Society of Edinburgh Proceedings, v. 90B, p. 351–361.
- BAILON, S., 1989, Les amphibiens et les reptiles du Pliocene Supérieur de Balaruc II (Herault, France): Palaeovertebrata, v. 19, p. 7–28.
- BERMAN, D.S., 1973, *Spathorhynchus fossorium*, a middle Eocene amphisbaenian (Reptilia) from Wyoming: Copeia, v. 4, p. 704–721.

- BERMAN, D.S., 1976, A new amphisbaenian (Reptilia: Amphisbaenia) from the early Oligocene of Wyoming: *Journal of Paleontology*, v. 50, p. 165–174.
- BERMAN, D.S., 1977, *Spathorhynchus natronicus*, a new species of rhineurid amphisbaenian (Reptilia) from the early Oligocene of Wyoming: *Journal of Paleontology*, v. 51, p. 986–991.
- BROMLEY, R.G., 1967, Some observations on burrows of thalassinidean Crustacea in chalk hardgrounds: *Geological Society of London, Quarterly Journal*, v. 123, p. 157–182.
- BROMLEY, R.G., 1996, *Trace Fossils: Biology, Taphonomy, and Applications*: London, Chapman & Hall, 361 p.
- BROMLEY, R.G., AND ASGAARD, U., 1975, Sediment structures produced by a spatangoid echinoid: a problem of preservation: *Geological Society of Denmark, Bulletin*, v. 24, p. 261–281.
- BROMLEY, R.G., AND FREY, R.W., 1974, Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha*, and *Spongeliomorpha*: *Geological Society of Denmark, Bulletin*, v. 23, p. 311–335.
- CARROLL, R.L., 1988, *Vertebrate Paleontology and Evolution*: New York, W.H. Freeman & Company, 698 p.
- CHAMBERLAIN, C.K., 1975, Recent lebensspuren in nonmarine aquatic environments, in Frey, R.W., ed., *The Study of Trace Fossils*: New York, Springer-Verlag, p. 431–458.
- CHARIG, A.J., AND GANS, C., 1990, Two new amphisbaenians from the Lower Miocene of Kenya: *British Museum of Natural History (Geology), Bulletin*, v. 46, p. 19–36.
- DEOCAMPO, D.M., 2002, Sedimentary structures generated by *Hippopotamus amphibius* in a lake-margin wetland, Ngorongoro Crater, Tanzania: *Palaio*, v. 17, p. 212–217.
- ERDALE, A.A., AND BERGER, W.H., 1978, Deep-sea ichnofacies: modern organism traces on land and in pelagic carbonates of the western equatorial Pacific: *Palaogeography, Palaeoclimatology, Palaeoecology*, v. 23, p. 263–278.
- ESTES, R., 1983, *Sauria terrestria, Amphisbaenia*: *Handbuch der Paläoherpetologie*, Part 10a: Stuttgart, Gustav Fisher Verlag.
- FREY, R.W., 1968, The Lebensspuren of some common marine invertebrates near Beaufort, North Carolina. 1, Pelecypod burrows: *Journal of Paleontology*, v. 42, p. 570–574.
- FREY, R.W., 1970, The Lebensspuren of some common marine invertebrates near Beaufort, North Carolina. 2, Anemone burrows: *Journal of Paleontology*, v. 44, p. 308–311.
- FREY, R.W., CURRAN, H.A., AND PEMBERTON, S.G., 1984, Tracemaking activities of crabs and their environmental significance: the ichnogenus *Psilonichnus*: *Journal of Paleontology*, v. 58, p. 333–350.
- GANS, C., 1969, Amphisbaenians: reptiles specialized for a burrowing existence: *Endeavour*, v. 28, p. 146–151.
- GANS, C., 1974, *Biomechanics: An Approach to Vertebrate Biology*: Philadelphia, J.B. Lippincott Company, 261 p.
- GANS, C., 1978, The characteristics and affinities of the Amphisbaenia: *Zoological Society of London, Transactions*, v. 34, p. 347–416.
- GENISE, J.F., MANGANO, M.G., BUATOIS, L.A., LAZA, J.H., AND VERDE, M., 2000, Insect trace fossil associations in paleosols: the *Coprinsphaera* ichnofacies: *Palaio*, v. 15, p. 49–64.
- GINGRAS, M.K., PICKERILL, R., AND PEMBERTON, S.G., 2002, Resin casts of modern burrows provides analogs for composite trace fossils: *Palaio*, v. 17, p. 206–211.
- GINGRAS, M.K., MACEachern, J.A., AND PICKERILL, R., 2004, Modern perspectives on the *Teredolites* ichnofacies: observations from Willapa Bay, Washington: *Palaio*, v. 19, p. 79–88.
- HÄNTZSCHEL, W., 1975, *Treatise on Invertebrate Paleontology Part W: Miscellanea Supplement 1, Trace Fossils and Problematica*: The Geological Society of America, 269 p.
- HASIOTIS, S.T., 2002, Continental Trace Fossils: SEPM, Short Course 51, 132 p.
- HASIOTIS, S.T., 2003, Complex ichnofossils of solitary and social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems: *Palaogeography, Palaeoclimatology, Palaeoecology*, v. 192, p. 259–320.
- HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnoconosites: *Sedimentary Geology*, v. 167, p. 177–268.
- HASIOTIS, S.T., AND HONEY, J.G., 2000, Paleohydraulic and stratigraphic significance of crayfish burrows in continental deposits: examples from several Paleocene Laramide basins in the Rocky Mountains: *Journal of Sedimentary Research*, v. 70, p. 127–139.
- HASIOTIS, S.T., AND MITCHELL, C.E., 1993, A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo- and neo-ichnological evidence, and the identification of their burrowing signatures: *Ichnos*, v. 2, p. 291–314.
- HASIOTIS, S.T., AND BOURKE, M.C., 2005, Differentiating between cricket, spider, scorpion, and skink burrows in dryland environments, Simpson Desert, Northern Territory, Australia (abstract): *American Association of Petroleum Geologists, 2005 Annual Convention, Abstracts*, v. 14.
- KANAZAWA, K., 1992, Adaptation of test shape for burrowing and locomotion in spatangoid echinoids: *Palaeontology*, v. 35, p. 733–750.
- LOPEZ, P., SALVADOR, A., AND MARTIN, J., 1998, Soil temperature, rock selection, and the thermal ecology of the amphisbaenian reptile *Blanus cinereus*: *Canadian Journal of Zoology*, v. 76, p. 673–679.
- LOPEZ, P., CIVANTOS, E., AND MARTIN, J., 2002, Body temperature regulation in the amphisbaenian *Togonophis wiegmanni*: *Canadian Journal of Zoology*, v. 80, p. 42–47.
- MARTIN, J., LOPEZ, P., AND SALVADOR, A., 1991, Microhabitat selection of the amphisbaenian *Blanus cinereus*: *Copeia*, v. 1991, p. 1142–1146.
- MARTIN, L.D., AND BENNETT, D.K., 1977, The burrows of the Miocene beaver *Palaecocastor*, western Nebraska, U.S.A.: *Palaogeography, Palaeoclimatology, Palaeoecology*, v. 22, p. 173–193.
- MEADOWS, P.S., 1991, The environmental impact of burrows and burrowing animals—conclusions and a model, in Meadows, P.S., and Meadows, A., eds., *The Environmental Impact of Burrowing Animals and Animal Burrows*: The Zoological Society of London: Oxford, U.K., Clarendon Press, p. 327–338.
- MURELAGA, X., PEREDA SUBERBIOLA, X., DE BROIN, F., RAGE, J.C., DUFFAUD, S., ASTIBIA, H., AND BADIOLA, A., 2002, Amphibians and reptiles from the early Miocene of the Bardenas Reales of Navarre (Ebro Basin, Iberian Peninsula): *Geobios*, v. 35, p. 347–365.
- PAPENFUSS, T.J., 1982, The ecology and systematics of the amphisbaenian genus *Bipes*: *California Academy of Sciences, Occasional Papers*, v. 136, p. 1–42.
- PEMBERTON, S.G., AND FREY, R.W., 1982, Trace fossil nomenclature and the *Planolites*–*Palaephychus* dilemma: *Journal of Paleontology*, v. 56, p. 843–881.
- PEMBERTON, S.G., AND FREY, R.W., 1985, The *Glossifungites* ichnofacies: modern examples from the Georgia coast, U.S.A. in Curran, H.A., ed., *Biogenic Structures: Their Use in Interpreting Depositional Environments*: SEPM, Special Publication 35, p. 273–259.
- RAGE, J.C., 1988, The Le Bretou locality (Quercy Phosphorites, Tarn-et-Garonne, France) and its late Eocene vertebrate fauna: *Palaeontographica*, v. 205, p. 3–27.
- RATCLIFFE, B.C., AND FAGERSTROM, J.A., 1980, Invertebrate lebensspuren of Holocene floodplains: their morphology, origin, and paleoecological significance: *Journal of Paleontology*, v. 54, p. 614–630.
- RETALLACK, G.J., 1984, Trace fossils of burrowing beetles and bees in an Oligocene paleosol, Badlands National Park, South Dakota: *Journal of Paleontology*, v. 58, p. 571–592.
- SEILACHER, A., AND SEILACHER, E., 1994, Bivalvian trace fossils: a lesson from actual paleontology: *Courier Forschungsinstitut Senckenberg*, v. 169, p. 5–15.
- SMITH, A.B., AND CRIMES, T.P., 1983, Trace fossils formed by heart urchins—a study of *Scolicia* and related traces: *Lethaia*, v. 16, p. 79–92.
- TAYLOR, E.H., 1951, Concerning Oligocene amphisbaenid reptiles: *University of Kansas, Science Bulletin*, v. 34, p. 521–558.
- VOORHIES, M.R., 1975, *Vertebrate burrows*, in Frey, R.W., ed., *The Study of Trace Fossils: A Synthesis of Principles, Problems, and Procedures in Ichnology*: New York, Springer-Verlag, p. 325–350.
- WAKE, M.H., 1993, The skull as a locomotor organ, in Hanken, J., and Hall, B.K., eds., *The Skull. Volume 3: Functional and Evolutionary Mechanisms*: Chicago, The University of Chicago Press, p. 197–240.
- WEBB, J.K., SHINE, R., BRANCH, W.R., AND HARLOW, P.S., 2000, Life underground: food habits and reproductive biology of two amphisbaenian species from Southern Africa: *Journal of Herpetology*, v. 34, p. 510–516.
- ZÄNGERL, R., 1944, Contributions to the osteology of the skull of the Amphisbaenidae: *The American Naturalist*, v. 31, p. 417–454.
- ZUG, G.R., VITT, L.J., AND CALDWELL, J.P., 2001, *Herpetology: An Introductory Biology of Amphibians and Reptiles*: San Diego, Academic Press, 630 p.

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