

BIOGENIC STRUCTURES PRODUCED BY SAND-SWIMMING SNAKES: A MODERN ANALOG FOR INTERPRETING CONTINENTAL ICHNOFOSSILS

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ABSTRACT: A neoichnological experiment using the Kenyan sand boa, *Eryx colubrinus*, reveals the diversity of biogenic structures produced by sand-swimming vertebrates in unconsolidated sand. Documentation of these biogenic structures will aid in the identification and interpretation of similar ichnofossils in the geologic record and help improve paleoenvironmental and paleoecological reconstructions. Two sand boas and three sand-filled chambers containing 1–3 cm thick layers of fine- to medium-grained sand were used in this burrowing experiment. The burrowing activities of the snakes were observed over a 14-day period and the chambers were photographed regularly to record sediment disturbance.

Eryx colubrinus produced a number of biogenic structures including (1) cone-shaped, downward-tapering features; (2) straight, vertical tubes; (3) elongate, sinuous tunnels; (4) semicircular, concave divots; (5) downward- and upward-deflected laminae; and (6) offset laminae. These different trace morphologies are present together, forming a large compound ichnofossil resulting from locomotion, resting, and dwelling behaviors. Absent from the sand-swimming biogenic structures were active backfill features, open tunnels, and burrow linings.

The recognition and interpretation of ichnofossils in the rock record of sand-swimming vertebrates requires their association with assemblages of known terrestrial body and trace fossils, rhizoliths, and pedogenic fabrics. Given the ecology of extant sand-swimming vertebrates, their biogenic structures characterize loose sediments with low interstitial moisture and environments with arid to semiarid climates. The biogenic structures produced in this experiment represent a new type of previously unrecognized biodiversity—that of sand-swimming vertebrates. In order to understand the evolution of fossorial behavior in continental vertebrates, recognition of the morphology of all types of interactions between vertebrates and the sediment must be considered.

INTRODUCTION

The purpose of this paper is to show the diversity of traces generated by a single species of burrowing reptile, the Kenyan sand boa *Eryx colubrinus* (Reptilia: Ophidia: Boidae), through basic experimental procedures in controlled environmental conditions. The results of this neoichnologic study provide for the development of more accurate interpretations of the biological, environmental, and ecological significance of continental, vertebrate ichnofossils.

Neoichnologic studies with terrestrial and freshwater organisms, especially sand-swimming vertebrates, have rarely been performed. While some studies have examined the life histories of terrestrial and freshwater organisms and their resulting traces (e.g., Heatwole 1960; Gans 1974; Halffter 1977; Reynolds and Wakkinen 1987; Heth 1991; Laundre and Reynolds 1993; Doonan and Stout 1994; Traeholt 1995), relatively few have studied these organisms for the purpose of understanding their sediment interactions or for identifying these biogenic structures in the geologic record (e.g., Chamberlain 1975; Ratcliffe and Fagerstrom 1980; Hasiotis and Mitchell 1993; Deocampo 2002; Hasiotis 2003; Hembree and Hasiotis 2006). Experimental work with modern burrowing organisms is necessary to interpret properly ichnofossils preserved in the continental rock record. The paucity of knowledge of the trace-making

ability of modern continental burrowing organisms results in the misinterpretation of continental ichnofossils, which leads to inaccurate paleoecological and paleoenvironmental interpretations.

Vertebrate ichnofossils in continental environments are thought typically of as casts and molds of burrows, nests, tracks, or other biologically generated void or void-fill structures (Hasiotis 2002). Continental vertebrates that do not create permanent voids in sediment may produce other types of traces in sediment. Vertebrates that force their way through loose sediments without producing open burrows are referred to as sand swimmers (Gans 1974; Zug et al. 2001). The morphology of biogenic structures produced by sand swimmers is dependent primarily upon the morphology of the organism and the sediment consistency (e.g., Bromley 1996; Hasiotis 2002). The degree of bioturbation by sand-swimming vertebrates ranges from minor disruption of stratification to the complete homogenization of the sediment, depending on the size of the animal, their abundance, territorial range, and the amount of time spent in a given area (e.g., Gans 1974; Bromley 1996; Hasiotis 2002). Environmental variables that may also affect biogenic structures produced by sand swimmers include changes in precipitation, soil moisture, air temperature, solar insolation, and landscape stability (e.g., Gans 1974; Kinlaw 1999; Villiani et al. 1999;

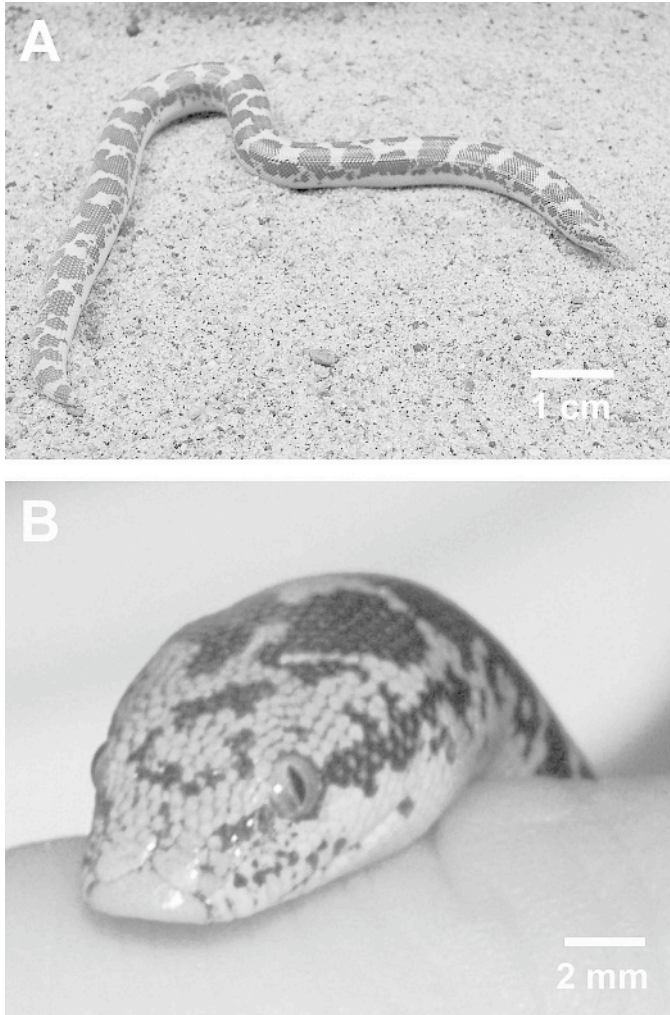


FIG. 1.— **A)** The Kenyan sand boa *Eryx colubrinus* is a semi-fossorial sand swimmer that inhabits sandy soils of Africa in environments with arid to semiarid climates. **B)** The spade-shaped head of *E. colubrinus* is characterized by a hardened, bony process at the distal tip of the snout that is used to penetrate sandy sediments.

Hasiotis 2000, 2002). The laboratory and field study of sand-swimming vertebrates and their traces is essential to accurately identify ichnofossils of these organisms and to interpret the paleoenvironmental conditions in which they were formed.

MATERIAL AND METHODS

Sand-swimming snakes were selected for study because of the extensive stratigraphic and geographic range, yet patchy and incomplete fossil record of the Serpentes. The earliest snakes are known from the Early Cretaceous (Rage 1984; Holman 2000). They radiated rapidly during the Paleogene, inhabiting all continents to become the second most speciose group of living reptiles (Zug et al. 2001). Fossil boids are present, although rare, in Upper Cretaceous strata of Argentina, Wyoming, and Montana, as well as throughout the Paleogene and Neogene of North and South America, Europe, and Africa (Rage 1984; Holman 2000). The morphology of Cretaceous and Paleogene boids has led to their interpretation as burrowers (Gilmore 1938; Holman 2000). Since the body fossils of burrowing snakes are not commonly preserved, their ichnofossils may provide additional evidence to help fill the gaps in their evolutionary history.

TABLE 1.—*Design and setup of the experimental chambers and sand layers used in the sand-swimming experiment.*

Experimental Chamber	Chamber Dimensions (L × W × H)	No. and Thickness of Layers	Sand Composition and Grain Size
A (1 sand boa)	30 × 4 × 22 cm	10 layers 2 cm thick	CaCO ₃ fine-grained
B (1 sand boa)	44 × 4 × 32 cm	8 layers 3 cm thick 8 layers 1 cm thick	SiO ₂ medium-grained CaCO ₃ fine-grained
C (2 sand boas)	30 × 6 × 22 cm	10 layers 2 cm thick	CaCO ₃ fine-grained

The Kenyan sand boa, *Eryx colubrinus* (Fig. 1), is a moderate-sized snake, typically less than 70 cm long, with a robust cylindrical body, short tail, blunt head, and small eyes (Zug et al. 2001). Kenyan sand boas are fossorial sand swimmers that inhabit loose, sandy soils in semiarid to arid climates of Africa (Zug et al. 2001). Sand boas remain below the sediment surface most of their lives and are part of the soil ecosystem (Zug et al. 2001). The function of the burrowing behavior of *E. colubrinus* is to escape such environmental stresses of these regions as temperature extremes, desiccation, and predation (Kinlaw 1999).

Two specimens of *E. colubrinus* were used in the experiment, one male and one female, measuring 25 and 30 cm long and 1 cm in diameter. The head of the Kenyan sand boa is spade shaped, with a steep slope anterior to the eyes and terminating in a hardened rostral process (Fig. 1B). The laboratory was kept on a 12-hour light period and the temperature was maintained at 22–24°C throughout the experiment. The burrowing experiment was performed in three separate chambers (experimental chambers A–C) filled with dry, loose, fine- to medium-grained, calcium carbonate and quartz sand (Table 1). Table 1 summarizes the design and setup of each of the three chambers used in the experiment. The long sides of the chambers consisted of glass plates permitting the observation and documentation of the animal's behavior. The chamber size was kept small so that the animals and their traces could be observed more easily. The glass walls of the chambers provided a cross-sectional view of the traces produced without disturbing the dry, loose sand by removing the glass walls. While the experimental design may limit the lateral movement of the animals and restrict many of the traces produced to those associated with downward and upward movement, these limitations do not reduce the usefulness of this type of experiment. The glass walls provide two-dimensional displays of three-dimensional structures within the chamber and can be likened to cross-sectional views in outcrop and core.

Alternating layers of different-colored sand were used to assist the observation of sediment disturbance. As the sand was poured directly into the chambers, the surfaces of the individual layers were smoothed but not compacted prior to the addition of the subsequent layers. A temperature gradient of 35–25°C was maintained within the burrowing chambers with a ceramic heat emitter positioned near the left side of the chambers. A water dish 0.5 cm deep was placed on the right side of the chamber. This setup was arranged to ensure the safety of the animals. The sand was kept dry except for the area in immediate contact with the water dish at the cooler end of the experimental chambers. The experiment consisted of three phases. In the first phase, a single sand boa was placed in experimental chamber A. In the second phase, the same sand boa was placed in experimental chamber B. In the third phase, two sand boas were placed in experimental chamber C. Each phase of the experiment lasted 14 days. A minimum of 7 days passed between each phase of the experiment. The undisturbed sand layers were photographed prior to the onset of each phase of the experiment. During the experiment the

chambers were photographed every 12 hours to document sediment disturbance and bioturbation.

EXPERIMENTAL RESULTS

Sand-Swimming Behavior

The spade-shaped head of the Kenyan sand boa was used as a digging tool for both the initial entrance into the sediment and subsequent movement through the sediment. Sand boas burrow into the sediment by sand swimming, pushing sediment aside with the head and temporarily displacing the sand with their bodies. Sand boas move through the sand primarily by lateral undulation (Gans 1974), resulting in minimal compaction of sediment on the tunnel roof. When a sand boa moves through dry sand, the overburden collapses behind the snake as it moves. The sides of the tunnel are, therefore, defined entirely by the sides of the animal. When a sand boa moves through moist sand the burrow remains open until the sediment dries out, after which time the burrow might be destroyed as the snake moves back through the area, or by collapse due to gravitational influence on the open space, or by filling by overlying sediment. While within the sediment, the sand boas commonly stop moving and remain below the surface for several hours. During this time they intermittently shift their bodies, resulting in additional disruption of the sediment.

General Bioturbation Patterns

Sediment disturbance reached a maximum depth of 20–22 cm in experimental chambers A and B (Fig. 2A–D). Activity near the heat lamp included shallow disruption of the upper 2–4 cm in association with basking behavior (Fig. 2B). In general, the amount of bioturbation decreased with depth. The upper 4–6 cm of the sand layers in each experimental chamber was homogenized, leaving little or no trace of the original layers. The greatest homogenization was present in experimental chambers B and C (Fig. 2C–F). In experimental chamber B, layers 1 and 2 became juxtaposed so that the coarser remnants of layer 2 were overlying the finer gray sand of layer 1 (Fig. 3A). In experimental chamber C, layers 1–3 were thoroughly mixed, but enough relict stratification remained to discern original order (Fig. 3B). The sand boas also transported sand vertically and laterally from both the surface and subsurface. Lateral transportation of sand occurred when the sand boas repeatedly entered and exited the sediment from the same area, resulting in a mound of sand at the burrow entrance (Fig. 3C, D). Sand from as much as 10 cm below the surface was added to and mixed with this mound. Preferential vertical transportation and surface accumulation of coarse-sand grains was observed also in experimental chamber B.

At depths greater than 6 cm, the degree of homogenization decreased and individual biogenic structures could be observed (Fig. 2). These structures resulted typically from the disruption of layers and the transportation of sand downward or upward through the sediment layers, depending on the animal's direction of movement. The greatest diversity of biogenic structures was present in experimental chamber A while the lowest was in experimental chamber B, which also had the lowest degree of overall bioturbation. The lower amount of bioturbation and diversity of trace morphologies was attributed to the increase in average grain size.

Sand-Swimming Biogenic Structures

Sand-swimming behavior in loose sediment resulted in a number of biogenic structures related both directly and indirectly to the activity of the snakes (Figs. 4–6). The majority of these biogenic structures were replicated in all of the experimental chambers despite changes in the size of the chambers, average grain size, and the number of sand boas involved.

Cone-Shaped Features.—The largest biogenic structures produced were conical, subcylindrical features oriented perpendicular to bedding, 4 cm in diameter and up to 6 cm deep, and terminating in a rounded base (Figs. 4A, 5C, 6A). Internally, these structures possess concave laminae that may be present on only one side of the structure (Fig. 4A). The conical structures were produced by the sand boa as it moved downward into the sediment and then curved back upward towards the surface.

U- to V-Shaped Features.—Smaller, less common biogenic structures produced by the sand boa were vertically oriented, U- to V-shaped features with smooth exterior walls (Fig. 4B). These structures were also generated as the sand boa moved down into the sediment, while pulling down sand from the overlying layers. As the boa moved back upward, sand was pulled with it, completing the U- or V-shaped trace.

Vertical Shafts.—Simple biogenic structures consisted of vertical to subvertical, cylindrical features with a straight to curved, unbranched shaft and an unstructured infill (Figs. 4C, 5D, 6B). These structures were produced as the snake burrowed deep into the sediment but without an immediate return to the surface.

Internally Laminated Features.—More complex biogenic structures consisted of elliptical, concentric laminae of sand encircling an elliptical mass (Fig. 4D). These structures were produced as the sand boa changed downward to upward movement by bending its body back on itself and exiting along the same path that it entered the sediment. Another internally complex biogenic structure was composed of a vertically or horizontally aligned series of tightly packed, concave or convex, crescent-shaped laminae (Fig. 4E, F). These structures were produced by repeated movement of the boa through a small area. Fan-shaped series of laminae were also produced, consisting of multiple layers of vertically or horizontally aligned, laminated sand radiating from a single point (Fig. 4G). The origin of these structures was not as clear but appeared to be directly related to vertical and horizontal probing of the area immediately in front of the sand boa.

Semicircular Divots.—Semicircular, concave features with unstructured fill and rounded bases were cut into the surfaces of sand layers (Figs. 4H, 5B, 6C). These structures were produced as the sand boas moved parallel to the sediment layering with a sinuous up-and-down motion. The sinuous motion created divots in the underlying layers, which were then filled with sand from above.

Straight to Sinuous, Subhorizontal Features.—Within individual sand layers were unlined, straight to tortuous, smooth-walled features with circular to elliptical cross sections (Fig. 4I, J). These biogenic structures were produced as the animal moved from one layer to another and then parallel to the sediment layering within an individual layer. The animal's movement pulled sand of differing composition from above or below its path. Another biogenic structure with a similar morphology was produced when the sand boas moved through damp sand below the cooler section of the chamber (Fig. 5A). These burrows remained open for a short period and then were filled by sediment from the surface of the burrowing tank. In the case of experimental chamber B, the fill consisted of coarser sand that had accumulated at the top of the upper sand layers.

Deformed and Offset Layers.—Additional biogenic structures created by the sand boa resembled abiotically generated, soft-sediment-deformation features. The most common of these features resembled flame structures (Fig. 4K), undulatory beds, and steep antiform and synform structures (Figs. 5E, 6D). These structures occur with diffusion of sand from underlying and overlying layers into adjacent layers. Deformed beds

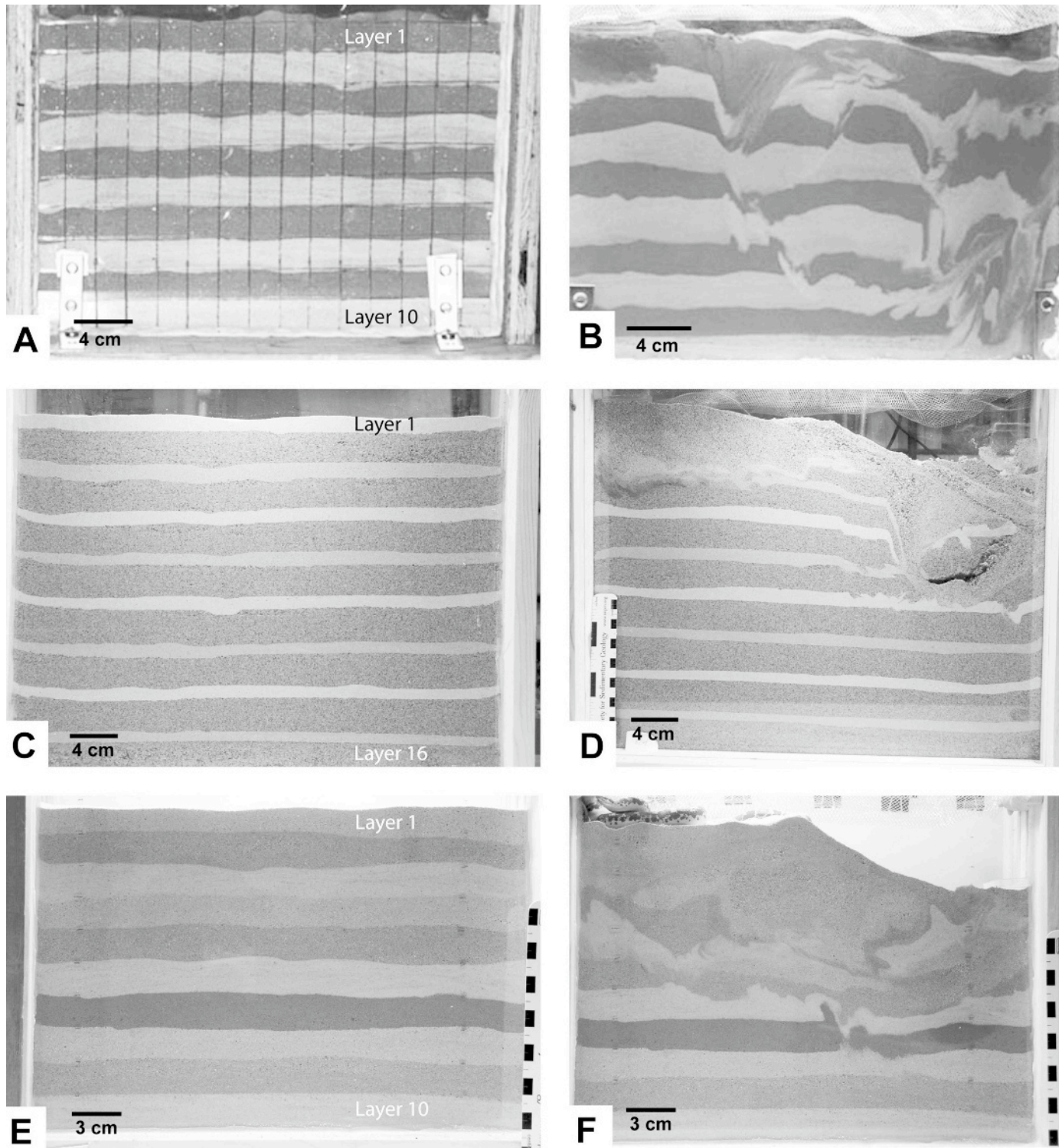


FIG. 2.— A) Initial stratification of experimental chamber A consisting of 10 2-cm-thick layers of fine-grained sand. B) Experimental chamber A after 14 days of bioturbation by a single sand boa. C) Initial stratification of experimental chamber B consisting of 3-cm-thick layers of medium-grained sand alternating with 1-cm-thick layers of fine-grained sand. D) Experimental chamber B after 14 days of bioturbation by a single sand boa. E) Initial stratification of experimental chamber C consisting of 10 2-cm-thick layers of fine-grained sand. F) Experimental chamber C after 14 days of bioturbation by two sand boas.

at the base of antiforms and synforms are either truncated sharply or grade into the surrounding lithology. The sand boas also caused layers to become offset as they crossed several sets, creating structures that resembled microfaults (Fig. 4L). The offset layers were produced as

a result of the displacement of sand by the animal as it burrowed downward. As the sand boa moved through a section of the sediment it left a void space along its path into which the overlying sand beds dropped. Where the snake crossed several beds in one episode of

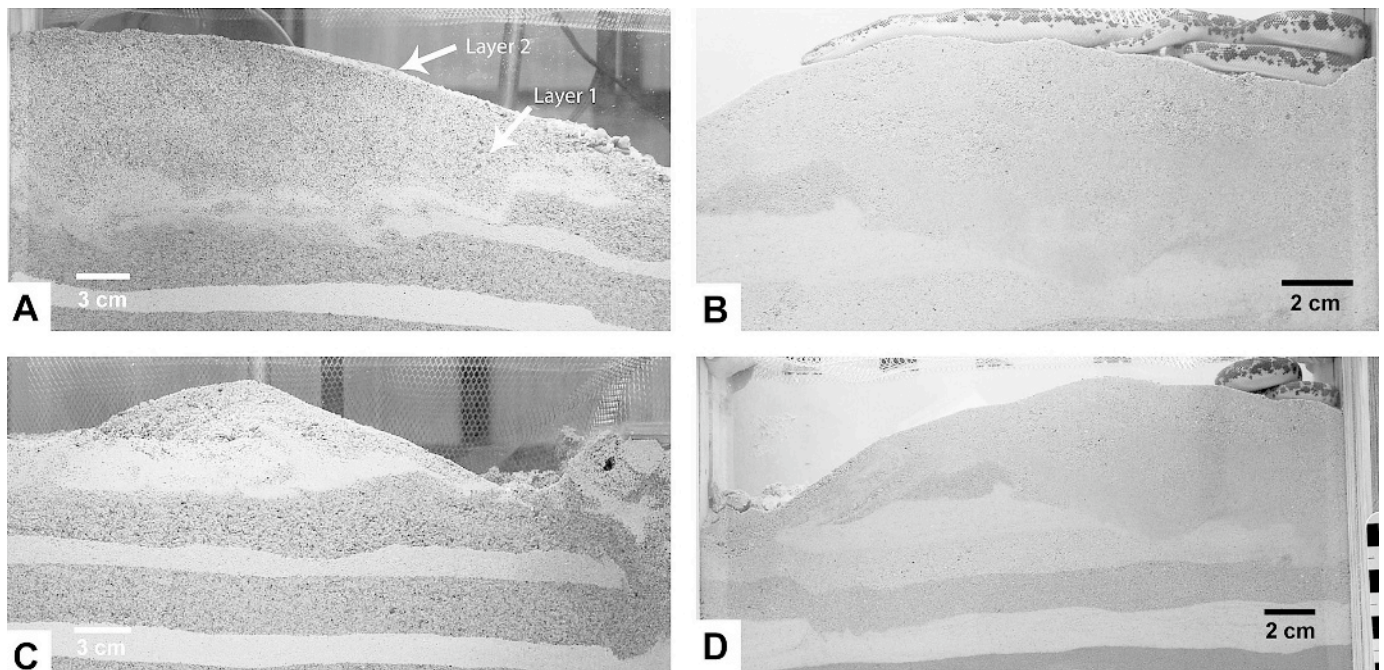


FIG. 3.—A) Sand-swimming within experimental chamber B resulted in the homogenization of the upper 5 cm of sand and the burial of the fine-grained sand of layer 1 below the medium-grained sand of layer 2. B) Homogenization of the upper 6 cm of sand in experimental chamber C. C) Mixed sand mound at the entrance of the sand boa burrow in experimental chamber B. D) Mixed sand mound in experimental chamber C.

movement, these beds were offset uniformly. Several layers were offset up to 2 cm with little other disruption to the primary sedimentary structures.

IMPLICATIONS AND SIGNIFICANCE

The experiment on sand-boa burrowing demonstrates that a wide range of biogenic structures are produced by continental organisms that do not create permanent, open structures within a well-drained, terrestrial sediment. This study also demonstrates that terrestrial, sand-swimming vertebrates are as capable as invertebrates of both altering original sedimentary fabric and generating distinct biogenic structures. The likelihood of preserving soil organisms along with their ichnofossils is low (Hasiotis 2002). Fossorial snakes are particularly rare in the fossil record (Holman 2000). The preserved evidence of sediment disturbance and biogenic structures may then be the only record of the vertebrate soil fauna (Hasiotis 2002). Preservation and recognition of the biogenic structures produced by sandswimmers requires the differentiation of stratification either by distinct bedding planes, grain-size changes, or lithologic variation. In this study, layers were distinguished by differences in color, grain size, and composition. In field studies, color differences in the sediment are possible but not as likely as changes in grain size or mineral content. As illustrated by traces preserved in experimental chamber B (Fig. 5), sand-swimming biogenic structures can be preserved as recognizable features by variations in grain size alone and can be distinguished from the surrounding sedimentary fabric. The preservation potential of these traces should therefore be significant.

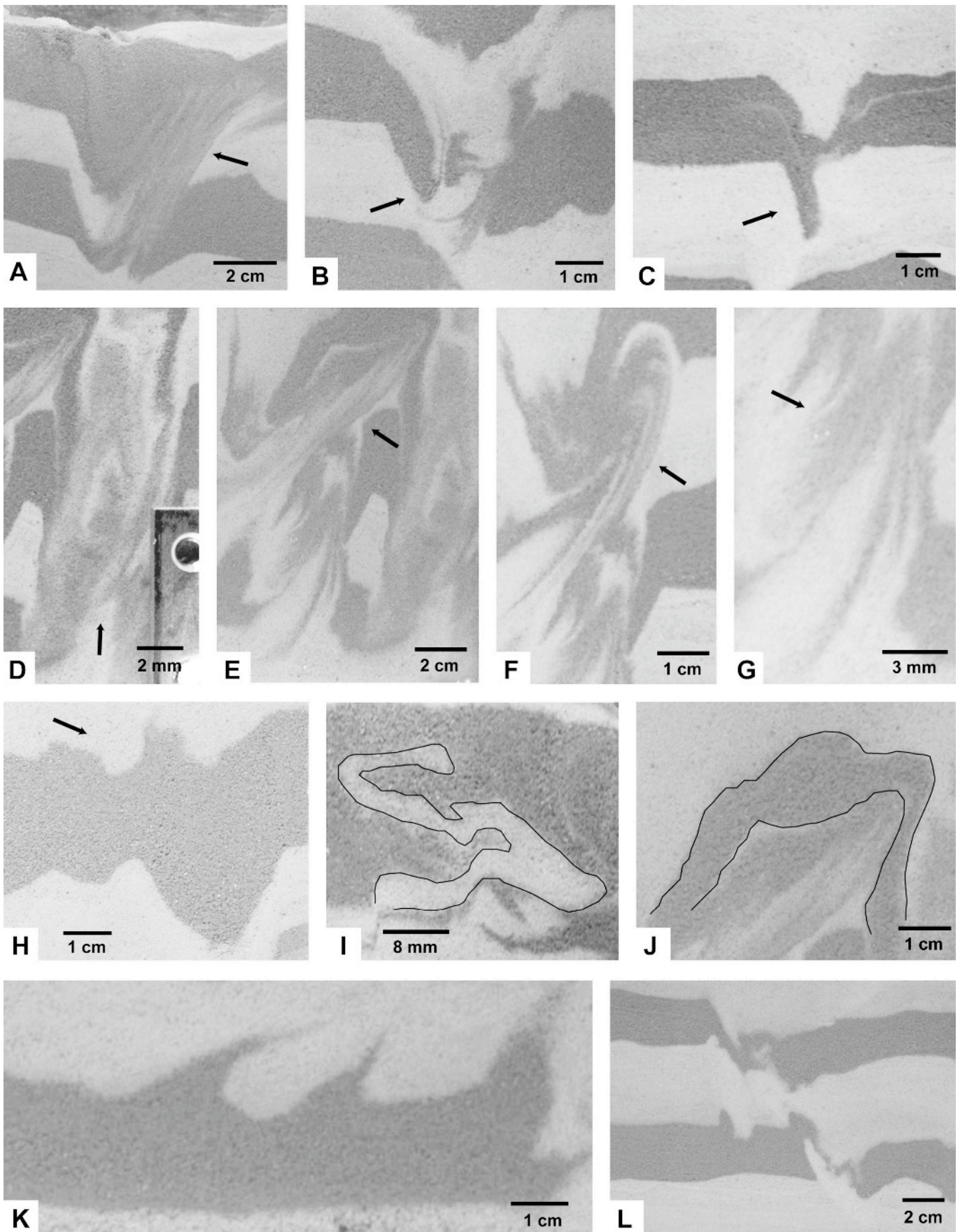
Biogenic structures documented in this study represent a new type of biodiversity not yet recognized by paleontologists, ichnologists, or sedimentologists—that of sand-swimming vertebrates. The trace-fossil record of sand-swimming behavior as well as the evolutionary history of burrowing in squamates is not well known (Voorhies 1975; Loope 2005). This is in contrast to the diversity of extant squamates that utilize the soil as a source of temporary or permanent shelter (Zug et al. 2001). The fossil record of burrowing boids, while incomplete, does include such

well-preserved, complete specimens as those from the Oligocene paleosols of the White River Formation in Wyoming (Breithaupt and Duvall 1986). The absence of associated ichnofossils attributed to sand-swimming vertebrates may be because they have not been recognized as such.

The results of this and other neoichnological studies provide a set of diagnostic criteria for identifying unknown ichnofossils in the field. Several common, repeated biogenic structures were documented in this study and are considered diagnostic of sand-swimming behavior. These include: (1) cone-shaped, downward-tapering features with some internal lamination parallel to the burrow walls; (2) straight to curved, vertical to subvertical, unlined tubes terminating in a rounded base; (3) elongate, sinuous, unlined tunnels aligned parallel or oblique to bedding; (4) semicircular, concave divots; (5) downward- and upward-deflected laminae; and (6) offset laminae. Due to the method of production, sand-swimming biogenic structures should not have internal menisci resulting from active backfilling or constructed burrow linings.

In addition to providing evidence of organism behavior, ichnofossils attributed to sand-swimming vertebrates can be useful in interpreting sediment conditions. Sand-swimming locomotion is most common in loose, sandy sediments with little to no interstitial moisture (Gans 1974). The majority of extant sand-swimming vertebrates are present in regions with an arid to semiarid climate (Zug et al. 2001). When recognized in the sedimentary record, therefore, the suite of biogenic structures represented in this experiment can be used to interpret paleoenvironmental conditions that include an arid to semiarid climate and unconsolidated, subaerial sediment with low interstitial moisture.

The sand boas produced a number of different biogenic structures while engaged in sand-swimming behavior. Upon preservation in the rock record these structures would constitute a large, compound ichnofossil. This may result in problems with the ichnotaxonomic designation of ichnofossils attributed to sand-swimming vertebrates. The potential of a single organism to create multiple ichnofossils is a well-known concept in ichnology (Pickerill 1994; Pickerill and Narbonne 1995; Bromley 1996;



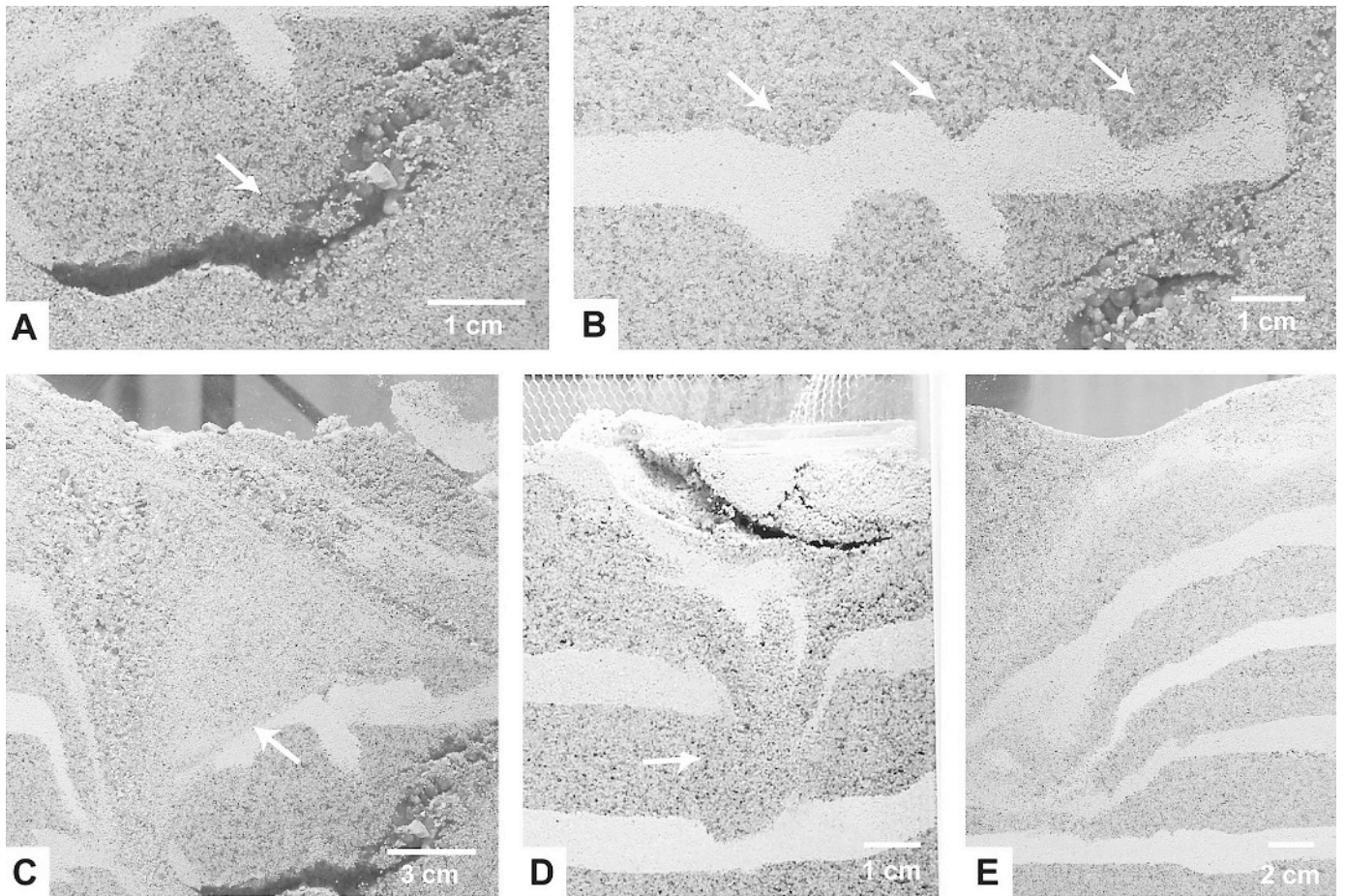


FIG. 5.—Biogenic structures produced in experimental chamber B. **A)** An open, sinuous, subhorizontal burrow produced in damp sand. **B)** Semicircular, concave divots. **C)** Large, conical, subcylindrical structure. **D)** Vertical to subvertical, cylindrical tunnel. **E)** Downward movement of the sand boa resulted in downward-deflected sand layers.

Miller 2001). As a result, ichnofossils are not named generally for their tracemakers but on the basis of their morphology (Pickerill 1994; Bromley 1996). When preserved as ichnofossils, the biogenic structures of sand-swimming snakes should be classified as a combination of morphologies rather than as a series of component morphologies. For example, a number of the individual structures resemble established ichnotaxa in two-dimensional exposures including such marine ichnogenera as *Conichmus* (Figs. 4A, 5C, 6A), *Skolithos* (Figs. 4C, 5D, 6B), *Arenicolites* (Fig. 4B), *Bergaueria* (Figs. 4H, 5B, 6C), and *Phycodes* (Fig. 4G). With three-dimensional exposures, however, these established ichnogenera may have distinct differences from those of the sand-swimming snakes. The resemblance, however, suggests that these morphologies may be fundamentally biotic in nature. This recognition can be useful in differentiating ichnofossils from abiotic sedimentary structures.

The diversity of trace morphologies produced by the sand boas provides further evidence that the interpretation of biogenic structures may be problematic in the analysis of such limited exposures as core (e.g., Chamberlain 1978; Pemberton et al. 2001). Core provides very limited lateral views of sedimentary structures and ichnofossils. Each taxonomically distinct trace left by an organism may not be considered to be the result of the behavior of a single organism when they are examined isolated from one another. The traces of the sand boa present this problem when viewed individually. If a core were taken of an individual segment, the interrelatedness of the biogenic structures would not be evident. Only when the entire bioturbated fabric is visible do the traces and soft-sediment deformation appear related and interconnected. Therefore, care must be taken when using biogenic structures to interpret trace-making organisms, behaviors, and paleoenvironments from limited core samples and outcrops.

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FIG. 4.—Biogenic structures produced in experimental chamber A. **A)** Large, conical, subcylindrical structures. **B)** Simple, vertical U- to V-shaped structure. **C)** Vertical to subvertical, cylindrical tunnel. **D)** Complex biogenic structure composed of multiple, elliptical, concentric laminae encircling a single elliptical mass. **E, F)** Complex structure composed of a series of closely spaced, vertical to subvertical, concave-up and concave-down, crescentic laminae. **G)** Fan-shaped biogenic structures composed of laminae radiating from a single point in one direction. **H)** Semicircular, concave, divot cut into the upper surface of the sand layers. **I, J)** Sinuous, unlined tunnel with a circular to elliptical cross section. **K)** Biogenic structures resembling flame structures. **L)** Offset sand layers resulting from the downward movement of the sand boa.

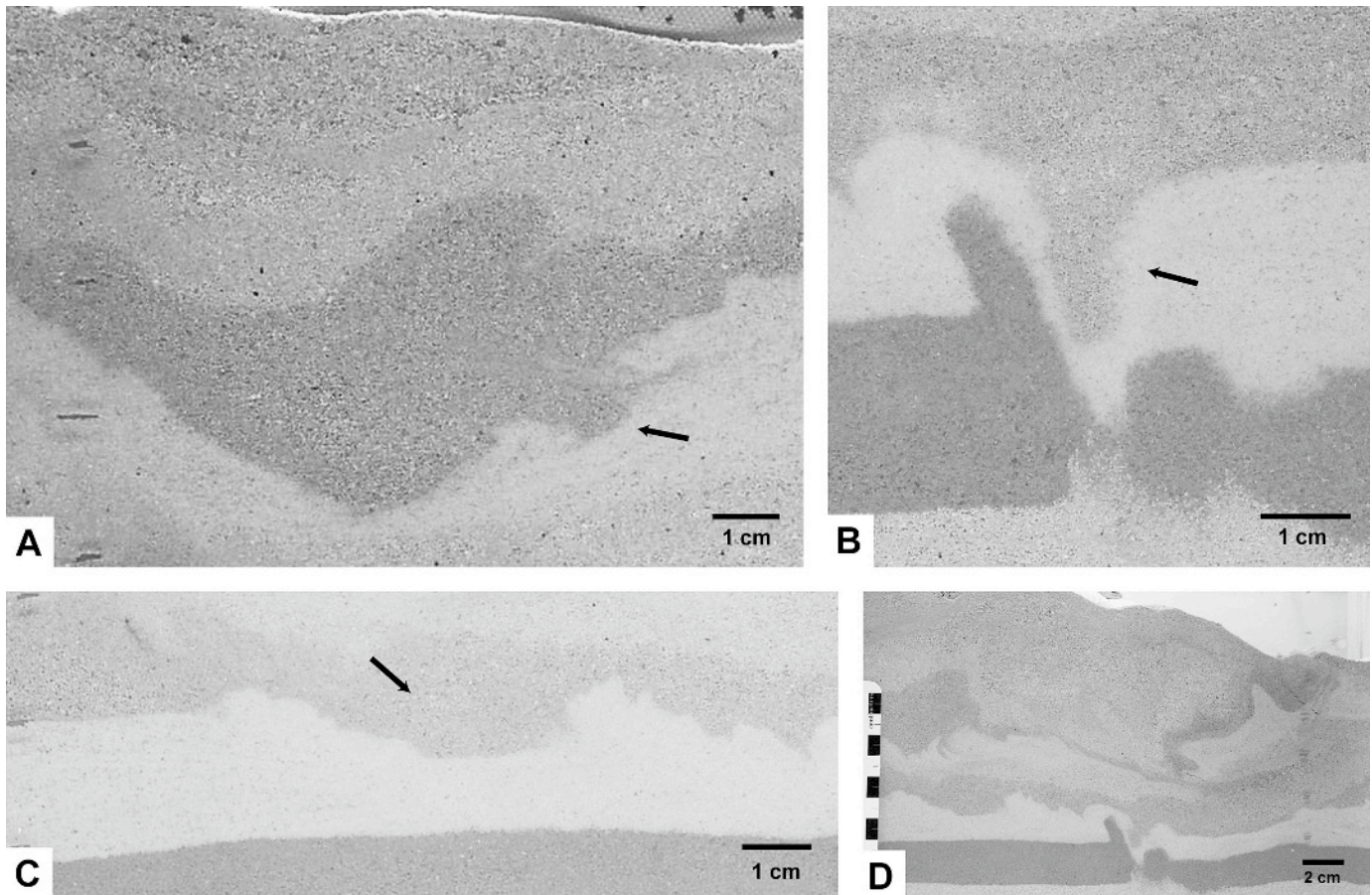


FIG. 6.— Biogenic structures generated in experimental chamber C. **A)** Large, conical, subcylindrical structure. **B)** Vertical to subvertical, cylindrical tunnel. **C)** Semicircular, concave divots. **D)** Complex array of biogenically deformed features in the upper 10 cm resulting from burrowing of two sand boas.

CONCLUSIONS

Sand-swimming vertebrates are capable of disrupting primary sedimentary structures as well as producing a diverse suite of biogenic structures. The sand boa *Eryx colubrinus* produced traces that included cone-shaped, downward-tapering structures; straight, vertical tubes; elongate, sinuous tunnels; semicircular, concave divots; downward- and upward-deflected laminae; and offset laminae. Absent from the sand-swimming, biogenic structures were active back-fill features, burrow linings, and permanent open burrow systems. The majority of these structures were recognizable only at a depth greater than 6–8 cm. Above this depth, the sand boas homogenized the sediment, altering or destroying the original sedimentary fabric. Sand-swimming biogenic fabrics, therefore, show a pattern similar to those produced by other soil-dwelling fauna in which the shallow portion of the sediment is thoroughly churned while deeper portions tend to preserve distinct bioturbation features (e.g., Hasiotis 2000, 2003). Sand-swimming biogenic structures are present up to 22 cm below the surface, which places them in the transition or even deep tier, greatly increasing their likelihood of preservation.

The diversity of biogenic structures produced in this experiment poses an interesting problem for the ichnotaxonomy of sand-swimming trace fossils. The sand-swimming traces represent compound ichnofossils (Pickerill 1994). Current explanations for this phenomenon include responses to changes in sediment consistency, such as with gradations between *Ophiomorpha nodosa* and *Thalassinoides suevicus*, and variations in organism behavior, such as with interconnected echinoid grazing traces

Cardioichnus planus and resting traces *Ancorichnus ancorichnus* (Bromley 1996). Since the sediment consistency did not vary during the experiment, behavioral changes are considered the primary cause of variation in sand-swimming biogenic structures. The morphologies represent locomotion, resting, and dwelling behaviors. Changes in trace morphology also changed, however, depending on the direction of locomotion. This situation indicates the potential for overclassification of ichnofossils attributed to sandswimming within the current system of ichnotaxonomy, where a single ichnofossil may be assigned multiple names based on morphology. Given the number of different morphologies produced by the sand-swimming boas, it is suggested here that in classification of similar trace fossils the different structures be considered part of a single, complex ichnofossil.

The ichnofossils of sand-swimming vertebrates have major importance in paleoenvironmental and paleoecological reconstructions. The recognition and interpretation of ichnofossils attributed to sand-swimming vertebrates in the rock record would require their association with such paleontologic and sedimentologic features of continental environments as assemblages of known terrestrial body and trace fossils, rhizoliths, and pedogenic fabrics. When preserved in the sedimentary record, sand-swimming biogenic structures characterize loose sediment with low interstitial moisture. Given that the majority of modern sand-swimming vertebrates occur in regions with arid to semiarid climates, their biogenic structures may also be suggestive of paleoenvironments formed under similar climatic settings. The biogenic structures produced in this experiment represent a new type of previously unrecognized biodiversity—that of sand-swimming vertebrates. The presence of such ichnofossils

would indicate that vertebrates were utilizing the sediment for protection from the environment, concealment, or prey capture.

Ichnofossils attributed to sand-swimming vertebrates can also provide evidence for the evolution of burrowing in vertebrates. Given that ichnofossils are more readily preserved than body fossils, the earliest record of vertebrate utilization of the continental sediment will be ichnofossils. Therefore, recognition of the morphology of all types of interactions between vertebrates and the sediment must be considered.

The sand-swimming experiment in glass observation chambers provides a glimpse into vertebrate–sediment interactions with minimal human disturbance. The design of the burrowing chamber, though limiting the lateral movement of the snakes, provides a beneficial means of studying vertebrate–sediment interactions, the degree of sediment mixing, and the possible structures produced. The glass walls of the burrowing chambers allow direct observation of sand-swimming phenomena that otherwise are hidden because it occurs underground and out of the realm of direct observation. This study is meant as a starting point from which future studies involving other sand-swimming and burrowing vertebrates can be designed to understand the different types of behavior that produce a variety of biogenic structures.

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