

NEOICHTHOLOGICAL EXPERIMENTS WITH MASKED CHAFER BEETLES (COLEOPTERA: SCARABAEIDAE): IMPLICATIONS FOR BACKFILLED CONTINENTAL TRACE FOSSILS

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ABSTRACT

Laboratory experiments conducted with larvae and adults of the northern or southern masked chafer beetle (Scarabaeidae: *Cyclocephala lurida* or *C. borealis*) tested hypotheses that beetle larvae construct meniscate, backfilled burrows and that they are distinct from backfilled burrows constructed by marine organisms. Beetle larvae were placed in narrow enclosures with laminated moist, fine-to-medium-grained sand and allowed to burrow for several weeks. Beetle larvae did not create open burrow systems but instead excavated single open cells approximately twice their body width and roughly equal to their body length. Burrowing was accomplished by scraping sediment with the head and mandibles, consolidating excavated sediment into a ball, rotating 180° with the ball to the back of the cell, and packing the ball onto the posterior end of the cell. The beetle larvae produced vertical-to-horizontal traces that were straight to tortuous and composed of discrete packets of meniscate backfill. Adult chafer beetles moved through the media using a sand-swimming motion, that is, by passing sand around their bodies with the legs. Traces produced by adults are characterized by straighter axes and mixed passive and active fill resulting from sediment collapse and sediment transported backward. When vertical, adult burrows contain chevron-shaped fill. Traces produced by these beetles are similar to adhesive meniscate burrows found in many ancient continental deposits as old as the Permian and can be assigned to *Naktodemasis* isp. We propose that *Naktodemasis* with this kind of burrow morphology were soil-dwelling insect larvae that used burrowing mechanisms similar to chafer beetle larvae. These experiments demonstrate that this kind of burrow morphology is terrestrial in origin, suggesting that previous interpretations that the burrows are subaqueous in origin need to be reevaluated.

INTRODUCTION

The ability of insect larvae, nymphs, and adults to construct meniscate, backfilled burrows in terrestrial settings is currently a subject of controversy. Backfilled burrows are thought traditionally to have been produced primarily through deposit feeding, in which organisms ingest sediment and pass it through their bodies, filling the burrow at the posterior end (e.g., Ekdale et al., 1984; Frey et al., 1984; Bromley, 1996). Many backfilled burrows in continental strata, dating back to the late Paleozoic, are thought to have been produced in lacustrine and fluvial deposits by worms or aquatic arthropods (e.g., Frey et al., 1984; Squires and Advocate, 1984; Savrda et al., 2000; Genise et al., 2004; Buatois and Mángano, 2004, 2007; Bromley et al., 2007). Other research, however, demonstrates that these types of burrows were made in subaerial terrestrial environments (e.g., Willis and Roth, 1962; O'Geen and Busacca, 2001; Smith and Hasiotis, 2008) and were frequent components of ancient paleosols (e.g., Bown and Kraus, 1983; Hasiotis and Dubiel, 1994; Retallack, 2001a,

2001b; Genise et al., 2004; Smith et al., 2008). The earliest meniscate, backfilled burrows have been reported from the Ordovician (Retallack, 2001a).

Studies concentrating on understanding the traces and trace-making behavior of modern burrowing beetles are rare. Modern burrows of other species of scarab beetles have been described by McColloch et al. (1928), Lengerken (1954), Halfpeter and Edmonds (1982), Brussaard (1983), Brussaard and Runia (1984), and Hanski and Cambefort (1991), among others.

This paper documents the burrows and burrowing mechanism of modern masked chafer-beetle larvae and adults (Coleoptera: Scarabaeidae: Dynastinae: *Cyclocephala lurida* or *C. borealis*; see Fig. 1). Neither the method by which grubs excavate sediment and fill their burrows nor burrow morphology of the larva or adult beetles has been described previously. We show that meniscate backfilled burrows are produced by modern masked chafer-beetle larvae in subaerial settings and that the morphology of these modern burrows is comparable to fossil backfilled burrows found in paleosols. Thus, the similar morphology of extant and fossil burrows indicates that ancient backfilled burrows were constructed by organisms with body plans and behaviors similar to modern insect larvae. Traces produced by beetle larvae and adults are compared to examples of morphologically similar trace fossils in ancient paleosols. These findings will aid in the interpretation of ancient environments, hydrologic conditions, and climatic settings of continental deposits, as well as marine deposits modified by pedogenic processes.

BACKGROUND

The earliest known beetle-like fossils are Early Permian (Kukalová-Peck and Willmann, 1990), and beetles (Insecta: Coleoptera) were well established by the Middle Triassic (Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005). The oldest body fossils attributed to Scarabaeoidea are from the Late Jurassic, the oldest Scarabaeidae are Early Cretaceous, and the earliest fossils from the subfamily Dynastinae are found in the Eocene (Krell, 2000, 2006).

True scarab beetles belong to the family Scarabaeidae and the order Coleoptera. Over 30,000 species are known within this family and are found on every continent except Antarctica. The Scarabaeidae include some of the largest known insects—the rhinoceros and Goliath beetles—and also include the more familiar scarab, dung, and June beetles. The biology and ecology of scarabs vary considerably among genera (Crowson, 1981).

There are at least five species of *Cyclocephala* in Kansas (Bauernfeind, 2001), all of which have similar life cycles and environmental tolerances. These beetles have a 1-year life cycle, divided into adult and larval stages. Eggs are laid within the soil in early summer to midsummer and hatch into larvae soon after. The larvae, which are soft-bodied, white grubs (Fig. 1A), go through three growth stages (instars). Each stage is successively larger than the previous, although there is little change in body morphology between these initial stages (Richter, 1966). Larvae remain in the soil the rest of the year, burrowing deeper during winter months to avoid freezing. As temperatures rise in the spring, larvae return closer

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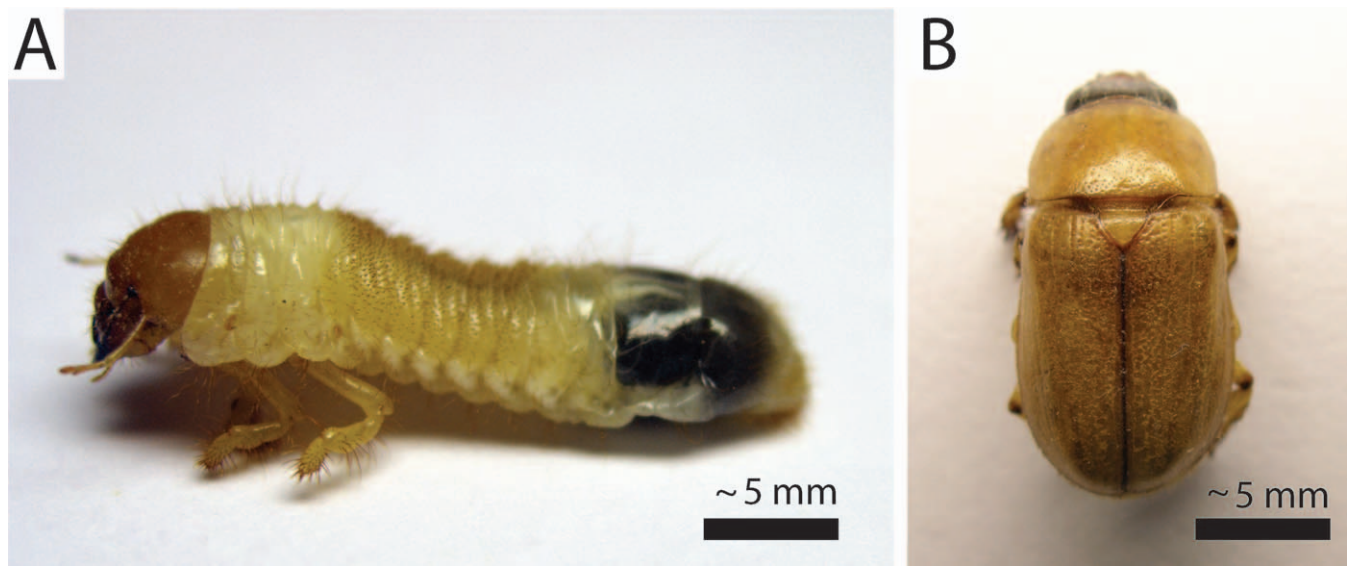


FIGURE 1—Insects used in the study. A) Masked chafer larvae. B) Masked chafer adult.

to the surface to feed, then pupate in May or June to become adult beetles (Fig. 1B; see Potter, 1998; Vittum et al., 1999; Rogers and Potter, 2002).

Potter and Gordon (1984) conducted field experiments to test the susceptibility of masked chafer grubs to heat and drought in turfgrass. In nonirrigated plots with 8%–15% soil moisture, only 1.7% of grubs survived, whereas irrigated plots, with soil moisture of 18%–27%, resulted in a 56.7% grub survival rate. Masked chafer eggs also showed decreased survival with hotter temperatures and drier conditions. These results are similar to those obtained for moisture experiments with soil bugs (Hemiptera: Cydnidae), which showed survival of nymphs in 7%–37% soil moisture with the greatest survivability under moisture levels of 14%–37% (Willis and Roth, 1962).

Larvae of the northern and southern masked chafer, *Cyclocephala lurida* and *C. borealis*, have been the subject of much research, owing to their prevalence in cultivated lawns and agricultural areas (see references in Vittum et al., 1999). Grubs are considered pests and have considerable economic impact because they feed on the roots of herbaceous plants. Most research has focused on habitat preference, distribution, and means of control (Potter, 1998; Vittum et al., 1999; Bauernfeind, 2001; Merchant et al., 2004). Burrowing mechanism and burrow characteristics are of little interest to agronomists and thus remain relatively unknown.

Masked chafers prefer vegetated habitats, including open lawns, gardens, and cultivated areas as well as grasslands and forest floors with underbrush growth. Larvae feed on living plant roots, especially grasses, and disseminated soil organic matter, making them facultative deposit feeders. Chafers are prey species for many types of animals; their eggs are frequently eaten by ants and other beetles, and the grubs are preyed on by vertebrates like armadillos and birds and parasitized by tiphiid wasps (Vittum et al., 1999; Zenger and Gibb, 2001).

MATERIALS AND METHODS

Chafer larvae were collected from two locations—an open, mulch-covered area in a suburban lawn, and a proximal floodplain characterized by mixed grasses and forbs between the Kansas River and an artificial levee. Soil trenches were hand dug by members of the University of Kansas IchnoBioGeoScience research group. Larvae were found predominantly in humic A horizons that are high in organic matter with dense roots. All larvae found in both field sites were in their third instar when collected. They were transported to the laboratory and kept alive in terraria containing the moist soil from which they were collected. Although soil moisture was not directly measured in the field, periodic rewetting kept moisture levels in terraria at approximately the same level as field moisture (see below). Grubs (Fig. 1) were identified as either northern or southern masked chafer beetles by rastral hair patterns (Vittum et al., 1999).

Three experimental containers were constructed in the laboratory to observe beetle burrowing behavior (Table 1). The thickness of sediment laminae was varied between experiments in order to determine how burrow morphology is expressed in different lamina thicknesses (thick, thin, or no laminae). Sediment composition was also altered in each experiment to test whether the amount of organic matter (none, discrete layers of organic-rich sediment, or uniformly distributed organic-rich sediment) in the sediment had an effect on burrow morphology.

The first enclosure consisted of a rectangular aquarium 16 cm high, 25 cm long, and 15 cm wide (Fig. 2). Corrugated cardboard was placed upright inside the aquarium, parallel to the aquarium walls and at distances of 7 and 15 mm from the glass sides. The interior of the aquarium not used for burrowing was filled with a mixture of sand and silt, and

TABLE 1—Enclosure parameters used in experiments 1–3.

Experiment	Enclosure length	Enclosure height	Width of burrowing space	Sediment type	Lamina thickness
1	15 cm and 25 cm	16 cm	7 mm and 15 mm (two sides of aquarium used)	Medium- to fine-grained, artificially colored, yellow, orange, and green sand, no organic matter	Mostly 5 mm; widest 10 mm
2	38.5 cm	34 cm	6 mm	Medium- to fine-grained, artificially colored, yellow, orange, and green sand, with discrete layers of natural, poorly sorted, organic-rich sediment	1–10 mm, most laminae 2–3 mm thick
3	38.5 cm	34 cm	6 mm	Natural, poorly sorted, organic-rich sand from Kansas River sandbars	No laminae

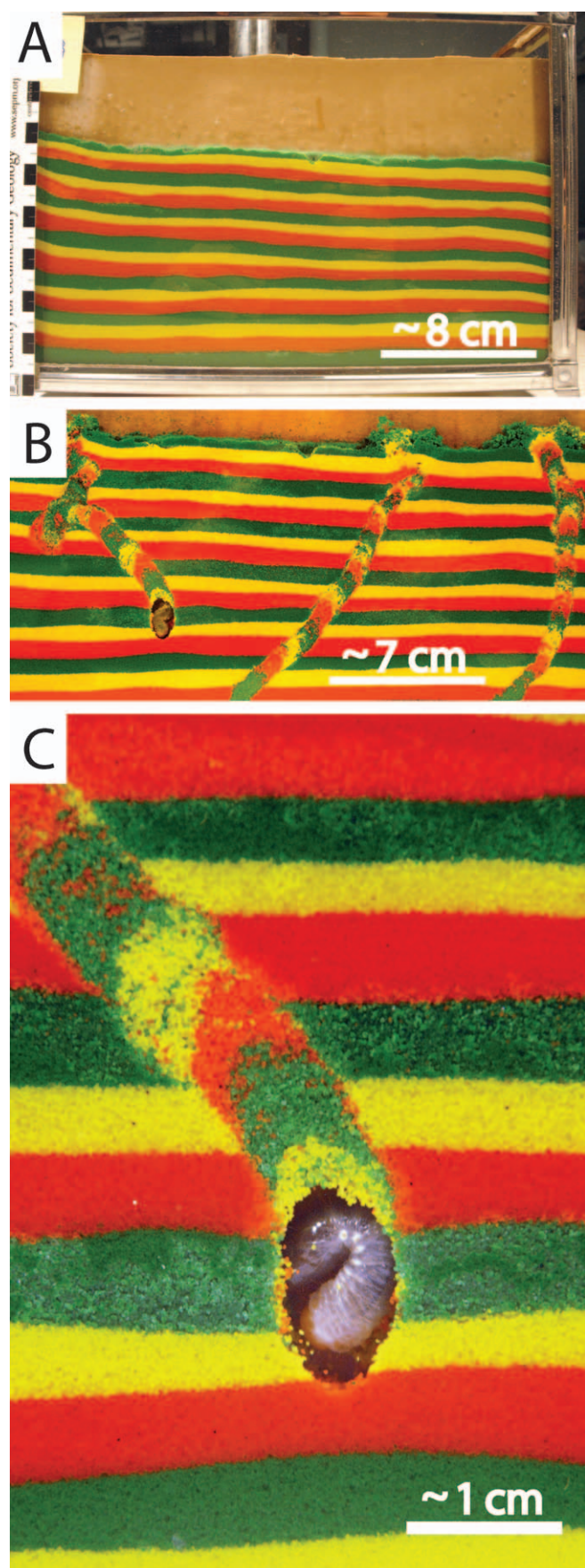


FIGURE 2—Traces produced in Experiment 1. A) Initial setup before introduction of grubs. B) Bioturbation after ~2 hours. C) Close-up of larval burrow.

the space between the cardboard and the glass used for burrowing was filled with colored sand. At the start of the experiment, beetle larvae were placed atop the colored sand, where they were forced to burrow in the narrow space between the cardboard and the glass.

Two additional enclosures were created for experiments 2 and 3 (Table 1)—these were constructed using a three-sided wood frame with inset slots cut into the wood to hold two panes of glass (Figs. 3–6). Glass panes 34 cm high, 38.5 cm long, and 0.3 cm thick were placed in the slots, separated by a space of 0.6 cm. This space had to be narrow enough to force the grubs to burrow adjacent to the glass pane in order to observe the burrowing process and resulting burrows (Fig. 7). The glass-wood contact was sealed on the outside using weather-stripping putty, although the seal was left incomplete at the bottom to allow water drainage. Prior to the start of this set of experiments, adult beetles were placed in similar enclosures and media to test whether the insects would burrow in a laboratory setting (Fig. 8). The methods and materials described here were used in the test experiments, allowing the observation and description of the beetle-burrowing activity.

In experiment 1, the burrowing medium consisted of medium (0.25–0.5 mm) to fine grained (0.125–0.25 mm), artificially colored yellow, orange, and green sand. Each sand layer was individually poured into the enclosure, producing planar laminae with sharp horizontal boundaries between layers. Colored sand laminae in experiment 1 were ~0.5 cm thick. Three grubs were placed between the cardboard partition and the glass on each side of the enclosure. No organic matter existed within the sand.

The enclosure for experiment 2 was primarily also filled with artificially colored sand, although in this experiment, 24 discrete layers of natural sediment with a higher organic matter content collected from sandbars along the Kansas River were interspersed between the colored layers (Figs. 3–5). Laminae ranged from 0.1–1.0 cm thick. Five grubs were placed in the enclosure, although only two survived for a significant time. The cause of death of these grubs is unknown, and no evidence of parasitism or infection was observed.

The enclosure for experiment 3 (Fig. 6) was filled only with organic-rich, natural sand from the Kansas River in order to create a more natural habitat and observe the effect of increased organic matter on burrowing behavior. This sand was poorly sorted and contained a higher percentage of clay and organic matter. The filling process produced faint, irregular layers created by settling of finer grained material while pouring. Three grubs were used in experiment 3, but one died shortly after the experiment began.

Sediments in all experiments were poured dry into each enclosure. The sediments were then wetted thoroughly until the entire enclosure was saturated. Water movement consolidated the sediment. Moisture content was determined by wetting a sand sample using the same method as that used to moisten the enclosures. The sample was weighed both dry and wet, and water content was then calculated as a weight percentage. The initial saturated moisture content for each experiment was ~15% water weight.

Beetle larvae were placed into the enclosures on the sediment surface immediately after the sediments were saturated. To prevent desiccation of the grubs, the sediment during each experimental run was remoistened periodically by spraying the upper surface until a wetting front developed and began to move downward through the sediment. At no time was the sediment completely resaturated. Once enclosures were set up, burrowing activity was photographed and videotaped every few minutes within the first 4 hours, decreasing in frequency throughout the duration of each experiment.

In order to test the similarity between modern beetle traces produced in experiments 1–3 and ancient backfilled trace fossils, trace fossils found in core taken in the Hugoton-Panoma gas field in southwestern Kansas were examined. Trace fossils used for comparison were found in the Speiser, Blue Rapids, and Easley Creek Shales, which form the continental portions of three asymmetric cyclothems in the upper portion of the Lower Permian Council Grove Group. Cores used for comparison, including

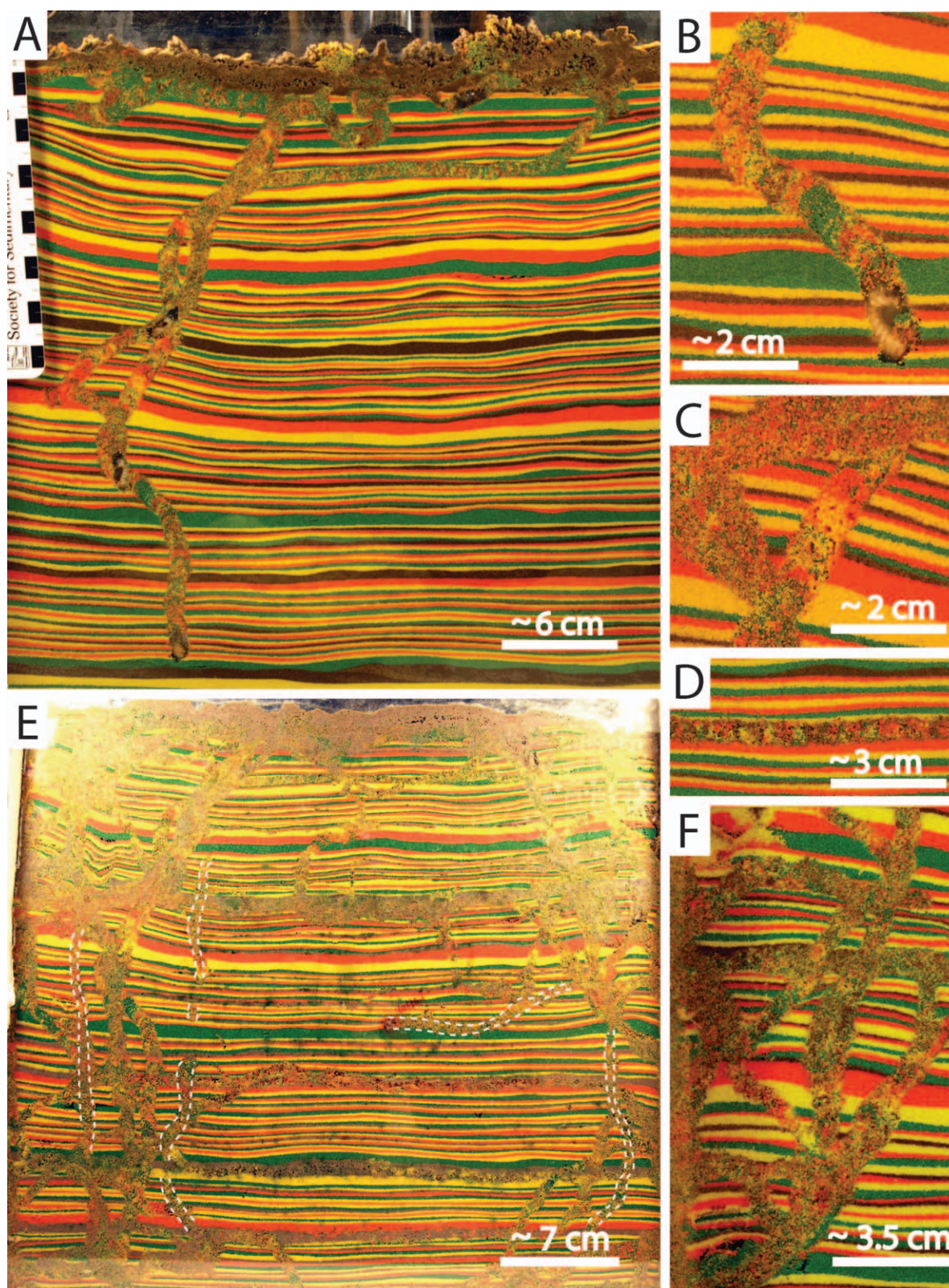


FIGURE 3—Larval traces produced in Experiment 2. A) Experiment 2 shortly after introduction of grubs. B) Close-up of larval burrow showing meniscate backfill and thin lining. C) Close-up of larval burrow showing higher porosity within burrow fill. D) Close-up of horizontal larval burrow showing exploitation of organic-rich layer. E) Photograph of entire enclosure at the end of the experiment. Adult beetle burrows traced in white. F) Larval burrow complex showing extensive reburrowing and interconnected traces.

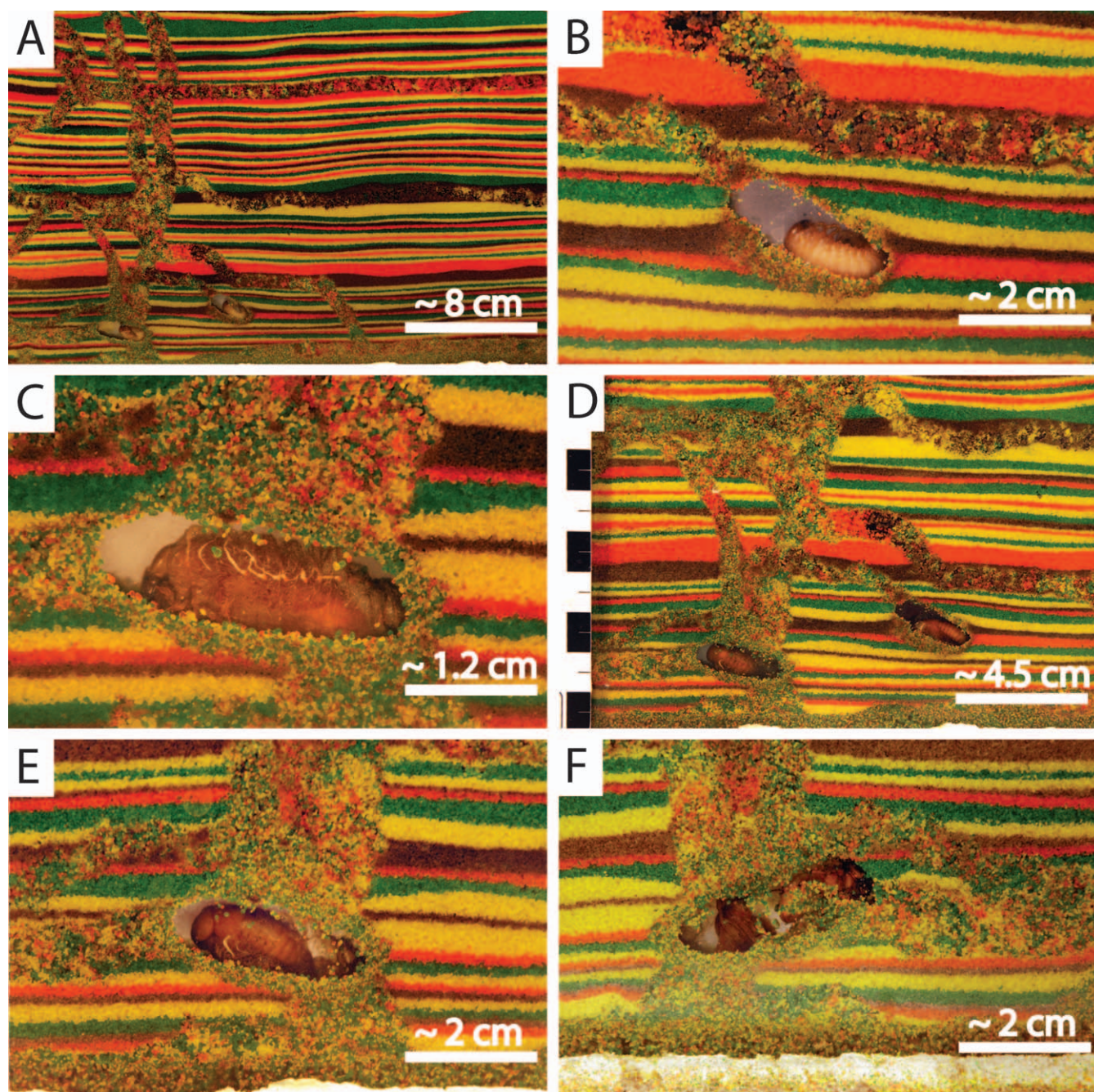


FIGURE 4—Pupaion chambers produced in Experiment 2. A) Overview of experiment 2 showing position of pupaion chambers near bottom of enclosure. B) Close-up of masked chafer larva during construction of pupaion chamber. C) Close-up of pupae approximately 2 weeks after onset of pupation. D–E) Pupae in chambers, showing thick lining surrounding chamber. F) Pupaion chamber, showing initial excavation by adult beetle a few days after hatching.

Cross H Cattle, May Beaty E 2, D Alexander, Stuart 3-34, and Prater, are stored at the Kansas Geological Survey in Lawrence, Kansas, and associated data can be accessed online (Kansas Geological Survey, 2008).

RESULTS

Burrowing Mechanism of Larvae

In all experiments, the larvae began to burrow as the moisture content lessened and the sediment became drier. Initial penetration into the media created loose, granular piles of sediment on the surface (Fig. 7). Masked chafer grubs created an elliptical, open cell and actively moved it forward by excavating sediment from the front end of the cell and depositing it at the back. This process can be divided into five steps: (1) excavation,

(2) consolidation, (3) rotation, (4) transport of sediment, and (5) packing (Fig. 7; see video in Supplementary Data¹).

1. Excavation.—Sediment is excavated through a scraping motion of the larva's mandibles and head at the anterior end of the burrow. Rather than holding sediment in the mouth, the open mandibles and head are used as a scraper and shovel, respectively, moving them toward the center of the body and immediately passing sediment to the first pair of limbs (Fig. 7A).

2. Consolidation.—As each successive measure of excavated sediment is passed to the limbs, the grub uses its legs and body to consolidate the

¹ www.paleo.ku.edu/palaios

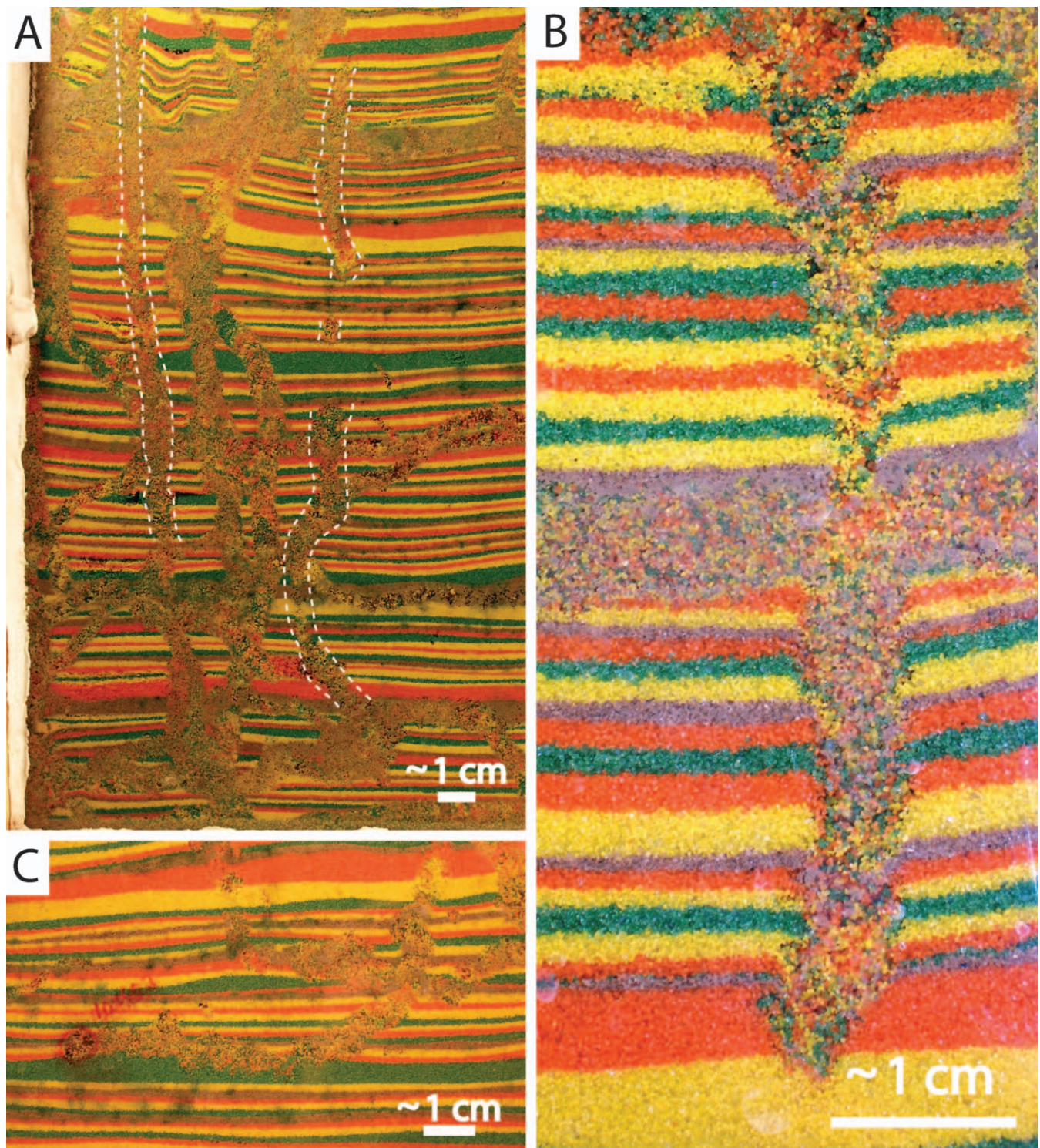


FIGURE 5—Adult beetle traces produced in Experiment 2. A) Burrow complex showing adult beetle trace (dashed lines). B) Close-up of adult beetle trace, showing downward-pointing V-shaped fill. C) Irregular horizontal burrow of adult beetle.

sediment into a ball. As the sediment package grows larger, the grub's body forms a C shape around the package. Sediment is compressed until it is large enough to fill the space between the anterior and posterior ends of the abdomen and the cell wall (Fig. 7B).

3–4. Rotation and Transport of Sediment.—Using contractions of the body, the grub braces itself against the cell wall and rotates toward the ventral side of the abdomen until the head is at the posterior end of the chamber. Concurrently, the grub pushes the sediment ball to the back of

the chamber with the head, limbs, and the front portion of the body (Figs. 7C–D). The first two pairs of legs are also used to push the sediment ball to the rear of the cell where it is compacted into the cell wall with the head and third pair of legs. The posterior of the abdomen is used to brace the grub during sediment packing. The dorsal side of the grub's abdomen is in continuous contact with the wall of the cell during the entire rotation process, often disturbing sediment along the cell wall.

5. Packing.—Once the sediment ball is at the back of the chamber, it

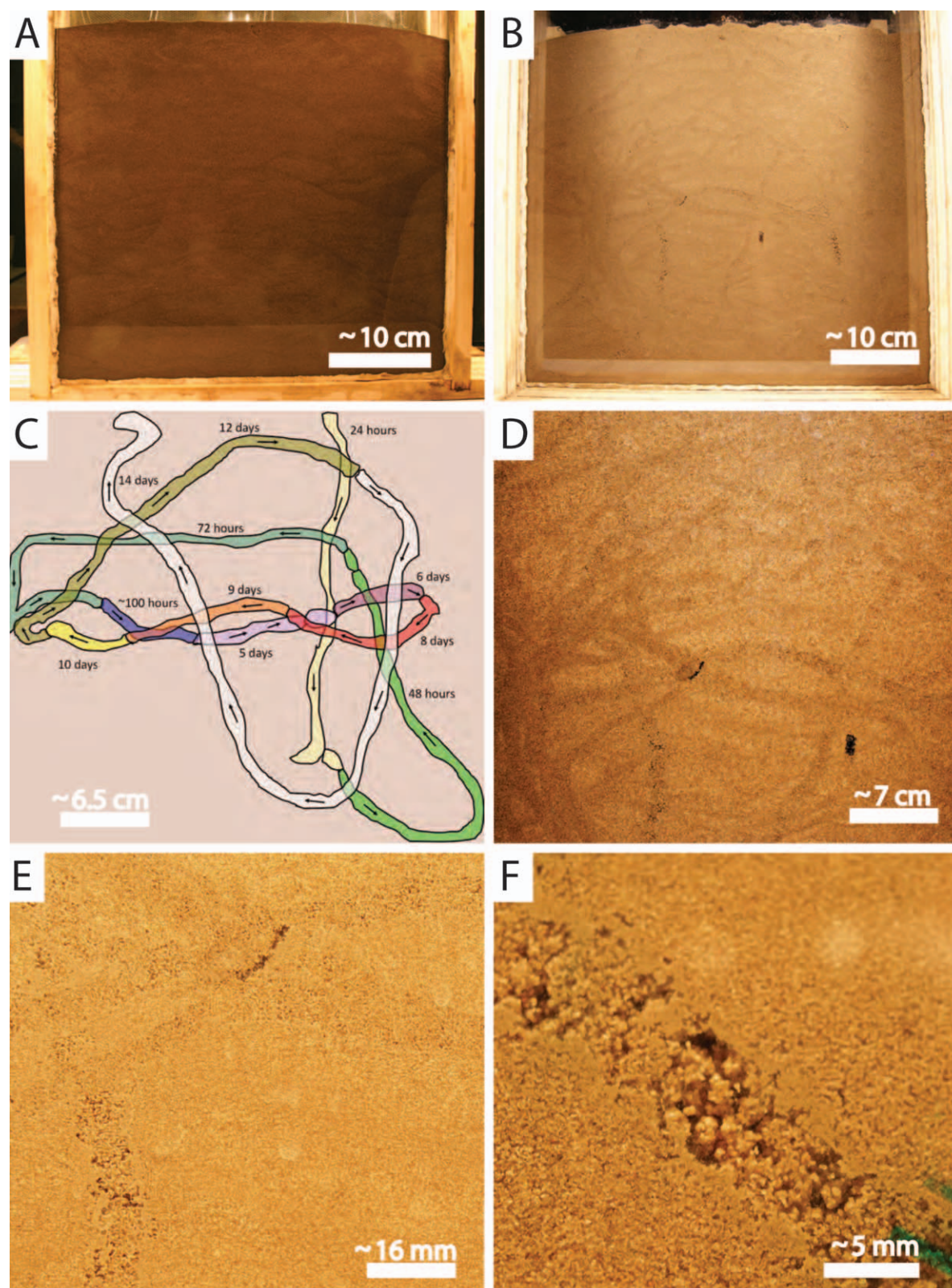


FIGURE 6—Traces produced in Experiment 3. A) Initial setup before introduction of grubs. B) Photograph of entire enclosure at end of experiment. C) Outline of burrows and burrow timing for first 2 weeks of experiment. D) Contrast-enhanced close up of burrow network. E–F) Close-up of larval burrows showing increased porosity within burrow fill.

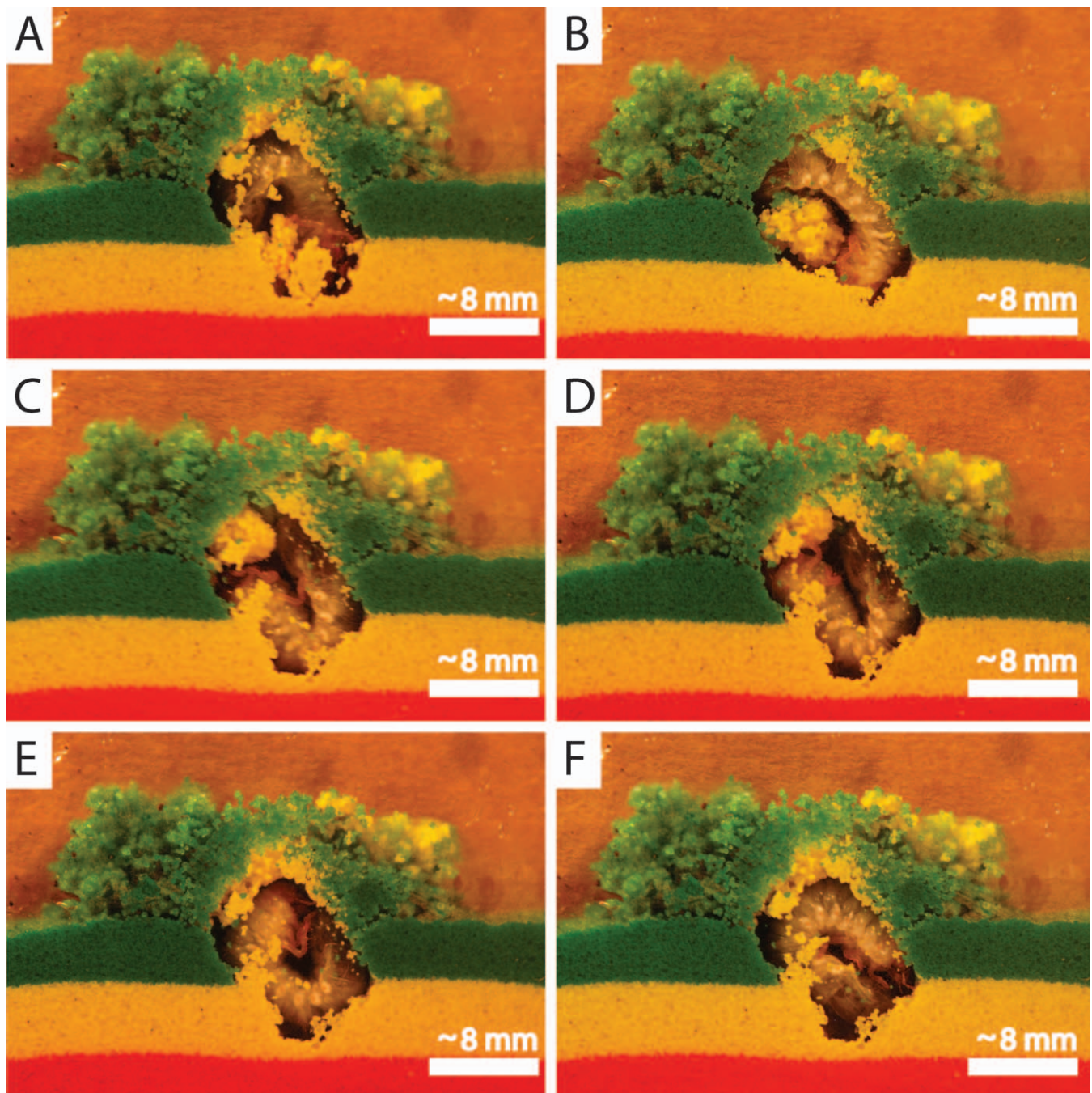


FIGURE 7—Steps in burrowing mechanism used by masked chafer larvae. A) Excavation of sediment at anterior end of cell. B) Consolidation of sediment into a ball held close to abdomen. C) Transport of sediment to posterior end of cell. D) Continued transport and compaction of sediment ball with legs. E) Compression of sediment with head and formation of meniscate backfill. F) Continued rotation and restart of burrowing process.

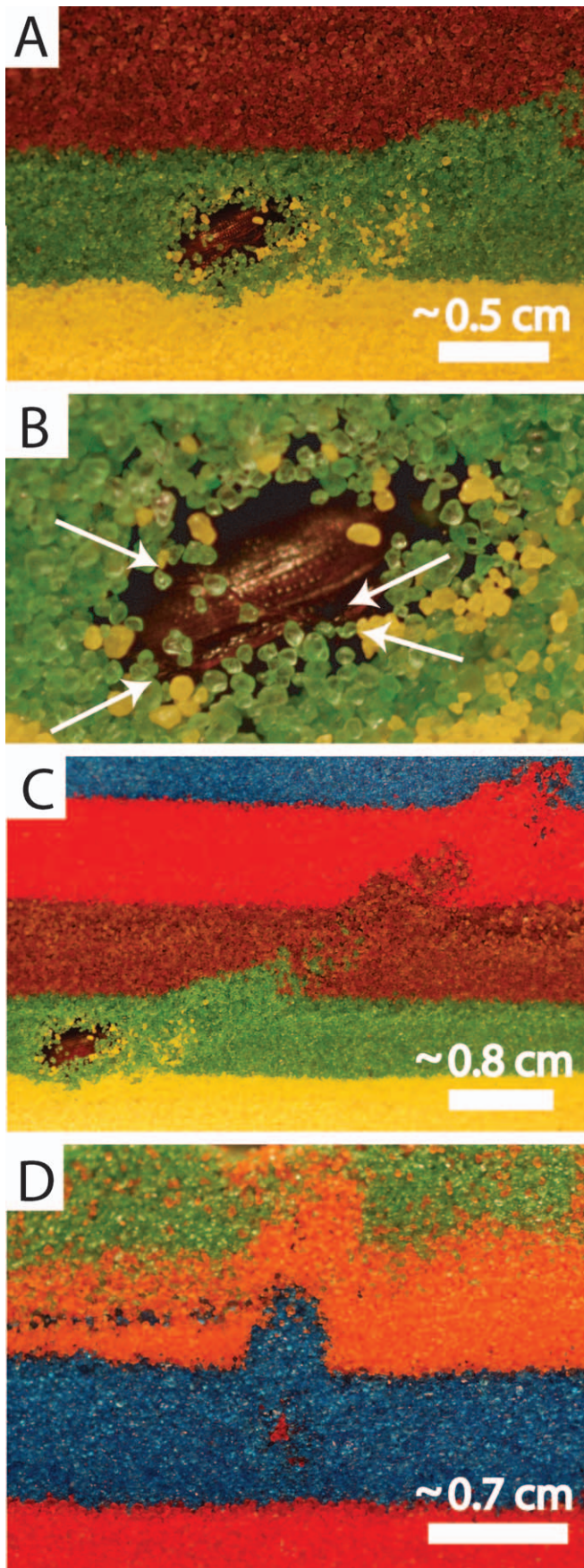
is compacted against the wall with the legs and sclerotized head, the only hard parts of the grub's body. The ball of sediment is pushed against the back wall several times in all directions to fully compact it (Fig. 7E). This also has the effect of disrupting and compacting previously back-filled sediment and sediment grains immediately outside of the cell margin. The process is then repeated as the grub rotates to the front of the cell (Fig. 7F) and continues to excavate sediment, repeating steps 1–5.

Biogenic Structures of Larvae

Burrowing in experiment 1 resulted in well-developed traces. Traces were generally vertical to subvertical and relatively straight, although abrupt changes in burrowing direction occasionally produced tortuous

burrow axes. The smaller size of enclosures used in the initial experiment prevented the development of spatially extensive burrow networks (Figs. 2B–C). Since sediment laminae in this experimental setup were much thicker than the amount of sediment transported in a single excavation session, individual meniscate backfill patterns were more difficult to observe. They were mostly visible near boundaries between layers of colored sand.

Grubs produced more extensive traces in experiment 2 owing to the larger size of the enclosure (Figs. 3A–F). Meniscate backfill was also more visible in this experiment because of the thinner sediment laminae; these were narrower than the amount of sediment excavated by the grub in each burrowing session, resulting in a mixture of colors within each



backfill packet. Some of the natural sand layers used in experiment 2 were preferentially burrowed, resulting in horizontal traces extending across the length of the enclosure (Fig. 3D). These layers were preferentially burrowed, presumably because of their higher organic matter content, which was exploited as a food source. The majority of bioturbation was around the edges of the enclosure, reflecting the movement of the organism laterally until it reached the enclosure wall (Figs. 3E–F).

In experiment 3, the lack of contrast within the sediment prevented most backfill from being visible, even though the same burrowing process was used by the grubs (Figs. 6B–E). Burrows are traceable, however, owing to their granular nature and higher porosity relative to the surrounding sediment (Figs. 6E–F). Although sediment is packed into the back of the burrow by the organism, void spaces are created between individual sediment packets. By the end of this experiment, most of the sediment in the enclosure had been reworked by the grubs, creating burrows totaling several meters in length.

Burrow Size and Shape.—Burrow width was ~ 0.75 cm and remained consistent throughout the length of the burrow. Some burrows reached nearly 2 m in length (Figs. 6B–D), as the larvae continued to burrow, feeding on organic matter and likely searching for areas with higher organic matter. The length-width relationship leads to very high length-to-width ratio— $>267:1$. Burrow width is ~ 2 times the width of the grub's body. The burrow must be wide enough for the grub to curl into a C shape and hold sediment between the anterior and posterior parts of the abdomen, as well as to rotate 360° in the cell. Burrow diameters were likely circular; however, because of the nature of enclosures we were unable to determine whether burrows were precisely circular or slightly elliptical in cross section. Burrow length was controlled mostly by the size of the enclosure and the duration of burrowing experiment. In two cases, the grubs lived long enough to pupate and emerge as adults (see section on adult beetles). True branching was not observed in any of the experiments. Numerous false branches were produced as burrows intersected previously constructed burrows, or when a grub partially reburrowed a preexisting backfilled burrow and deviated from the original course.

Orientation.—All burrows observed in these experiments had highly variable orientations, ranging from completely vertical to completely horizontal. Axes ranged from straight to highly tortuous. In some places, burrows were characterized by abrupt, angular changes in direction.

Fill.—Arcuate, densely packed meniscate backfill was created by the compaction of individual sediment balls, which were usually compacted to a thickness of 0.5–1 mm. Graded menisci were not observed. Each ball of sediment was not always placed at the center of the posterior end of the cell, nor was it evenly packed against the back wall. This created shuffled or slightly asymmetric menisci in some areas. Pellets were not observed in any of the burrows, although cohesion of soil particles in experiment 3 led to a granular texture in some burrow fills.

Linings.—A thin (<1 mm), discontinuous zone of disturbed sediment was visible along the exterior burrow margin. This was produced by the animal bracing itself against the chamber wall during excavation of sediment, rotating to the back of the cell, and packing the sediment onto the cell wall. This activity resulted in a passive, discontinuous sediment lining along the margins of the cell, which was visible in the resulting backfilled burrow.

Pupation Chambers.—Several weeks into the experiment, each surviving grub created a chamber (Fig. 4A) near the bottom of the enclosure in which to pupate. The larvae rotated and wiggled in all directions to

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FIGURE 8—Adult masked chafer beetle burrows produced in preliminary experiments to test the viability of enclosures. A) Adult beetle during locomotion. B) Close-up of adult beetle in motion; position of legs indicated by arrows. C) Adult beetle and trace produced during locomotion; direction of movement is toward the lower left corner. D) Adult beetle trace showing backfill morphology; direction of movement is toward the bottom.

emulate an ellipsoid to enlarge the locomotion cell. This behavior also caused the cell to be elongated. The larva primarily used its head and secondarily used its appendages to rework the sediment, and it used the head and the tip of the abdomen to compact the sediment to form a lining of variable thickness. The pupation chambers were ~ 3.4 cm long and ~ 1.7 cm wide. The open pupation chamber was ~ 3 cm long and ~ 1 cm wide. A lining ~ 0.2 – 0.4 cm thick surrounded the open chamber (Figs. 4B–E). Vittum et al. (1999) report that pupation chamber linings are cemented by a secretion from the grub. Sediment composing the lining is also compacted owing to grubs moving within their cell for an extended period of time. Adult beetles emerged from one of the terminal ends of the long dimension of the cocoons two weeks later and stayed within their subterranean chambers for several days (Fig. 4F). Exit burrows produced by the adults differed significantly from the burrowing traces made by the larvae (see section on adult burrows).

Burrowing Mechanism—Adults

Two adult masked chafer beetles emerged from pupae in experiment 2. Rather than using the excavation techniques exhibited by the larvae, the adults used a swimminglike behavior, pushing sediment around their bodies with their limbs as they moved through the sediment. It was more difficult to observe the burrowing mechanism used by the adults because they did not create a large, open cell. It appears that the adult beetles used their mandibles and head to chew into and loosen the sediment in front of them, while using a subtle side-to-side motion with their appendages. Excavated sediment was removed with the first pair of legs and passed backward to the second and third pair of legs—essentially moving material backward while the beetle moved forward. The second and third set of legs could be seen bracing against and moving along the margins of the burrow, particularly when the adult was against the glass. As the adult beetle moved forward, sediment also passively filled the previous occupied space by collapsing behind the beetle; thus, the fill is both passive and actively produced but does not closely resemble the backfill pattern of the larvae. An identical burrowing mechanism by adult beetles was observed in preliminary burrowing experiments using the same types of colored sediment to test the viability of the enclosures (Fig. 8).

After the adult beetles exited the chambers, they did not immediately go to the surface in the enclosure. Instead they burrowed in multiple directions within the media. Adult beetles, however, spent much less time within the sediment compared to the larvae. After initially burrowing upward, the adults changed directions and burrowed downward and horizontally. This type of burrowing mechanism resulted in less disruption of sediment and a smaller-diameter, less conspicuous trace.

Biogenic Structures—Adults

Overall burrow morphology of adult beetle traces was significantly different than the larval traces owing to the substantially different burrowing mechanism, body plan, and behavior of adult beetles (Fig. 5). Adult beetles used in preliminary burrowing trials also produced burrows similar to those observed here (Fig. 8).

Size and Shape.—Burrow diameter ranged from ~ 0.3 cm to 0.5 cm and was generally narrower than those produced by larvae, even though adult body size was equal to or wider than the body size of the grubs. Smaller diameters were primarily the result of the different burrowing mechanism of the adults. Burrow axes of adult beetle traces moved away from the glass so that only partial diameters were visible, which resulted in discontinuous traces. Burrow diameters were likely circular; however, because of the nature of enclosures we were unable to determine whether burrows were precisely circular or slightly elliptical in cross section. Length of adult traces was also much less than that of larvae.

Orientation.—Adult burrows are vertically oriented more often than larval burrows; however, adults were observed to burrow horizontally and laterally in all directions. For example, the first-emerged adult produced

a burrow consisting of a single loop from the pupation chamber to just below the surface, followed by downward movement toward the center of the enclosure. This beetle then moved laterally for several centimeters, then died. The second-emerged beetle slowly burrowed upward and exited the sediment after a few days, producing a subvertical, slightly sinuous burrow.

Fill.—Vertical-to-subvertical burrows produced by upward-moving adult beetles contained downward-pointing, chevron-shaped fill (Figs. 5A–B), which was the result of sediment collapse rather than active backfilling. Horizontal burrows contained indistinct, poorly organized fill structures (Fig. 5C), resulting in a higher porosity zone of sediment disruption compared to surrounding media.

Linings.—No linings were observed in any of the adult burrows during these and preliminary experiments with adult chafer beetles. Instead, the burrow margins appear to be more irregular compared to the larval traces (Figs. 2–4, 6).

Trace Fossils in Core

Cores from western Kansas were examined for trace fossils analogous to the burrow morphology produced by masked chafer beetles. The core was found to contain a low-diversity, high-abundance assemblage of meniscate backfilled traces. These trace fossils (Fig. 9) are associated with intervals that commonly contain rhizoliths, redoximorphic features, and zones of gleying—all characteristics of paleosols. Features of these burrows include packeted meniscate backfill, thin discontinuous linings, and unbranched, highly sinuous axes. Burrow diameters are variable and range from 0.09 cm to 1.06 cm. Meniscate backfill and packeting of menisci are visible in many burrows. Visibility of backfill is largely dependent on redoximorphic coloration and the proximity to zones of gleying; burrows near or within light-colored areas stand out in contrast to the surrounding matrix.

DISCUSSION

Masked chafer beetles produce different types of traces as larvae and adults. Backfilled meniscate burrows and walled ellipsoidal chambers are produced by the larvae, while adults produce poorly organized backfilled burrows. Trace morphology is controlled by the burrowing mechanism and behavior of the particular stage in the life history of the beetle. The behaviors of larvae and adults are an indication of their respective body morphologies.

Our results show that masked chafer larval burrows display highly organized, tightly spaced, shuffled meniscate backfill that form as the grub actively packs sediment into the rear of its locomotion cell. The larvae have several morphologic adaptations that make its unique burrowing mechanism possible. The sclerotized head and mandibles (Fig. 1; Supplementary Data¹) serve as a shoveling apparatus with which the grub excavates sediment. The long, C-shaped, soft abdomen of the grub allows it to change its shape readily during excavation, rotation, and transport of the sediment package. The grub uses the posterior of the abdomen to maintain its position in the cell while excavating with its head and mandibles. The position of the legs near the front of the body allows the grub to consolidate sediment into a ball between the anterior and posterior of the abdomen, which is held by the third pair of legs. The continuous contact of the grub's body with the cell wall during the entire burrowing process can be referred to as a form of thigmotactic behavior—that is, an organism's response to continuous contact with a solid surface (e.g., Hasiotis, 2003). The larval body plan is thus ideally suited for a fossorial lifestyle.

Masked chafer adult beetle traces did not form the distinct arcuate backfill seen in larval traces, owing to their swimming type of locomotion behavior. Poorly organized backfill and irregular burrow margins are formed because the adult does not create a large enough cell in which to physically carry excavated material from the front and pack it into the rear of the cell. Swimminglike locomotion allows the sediment to collapse

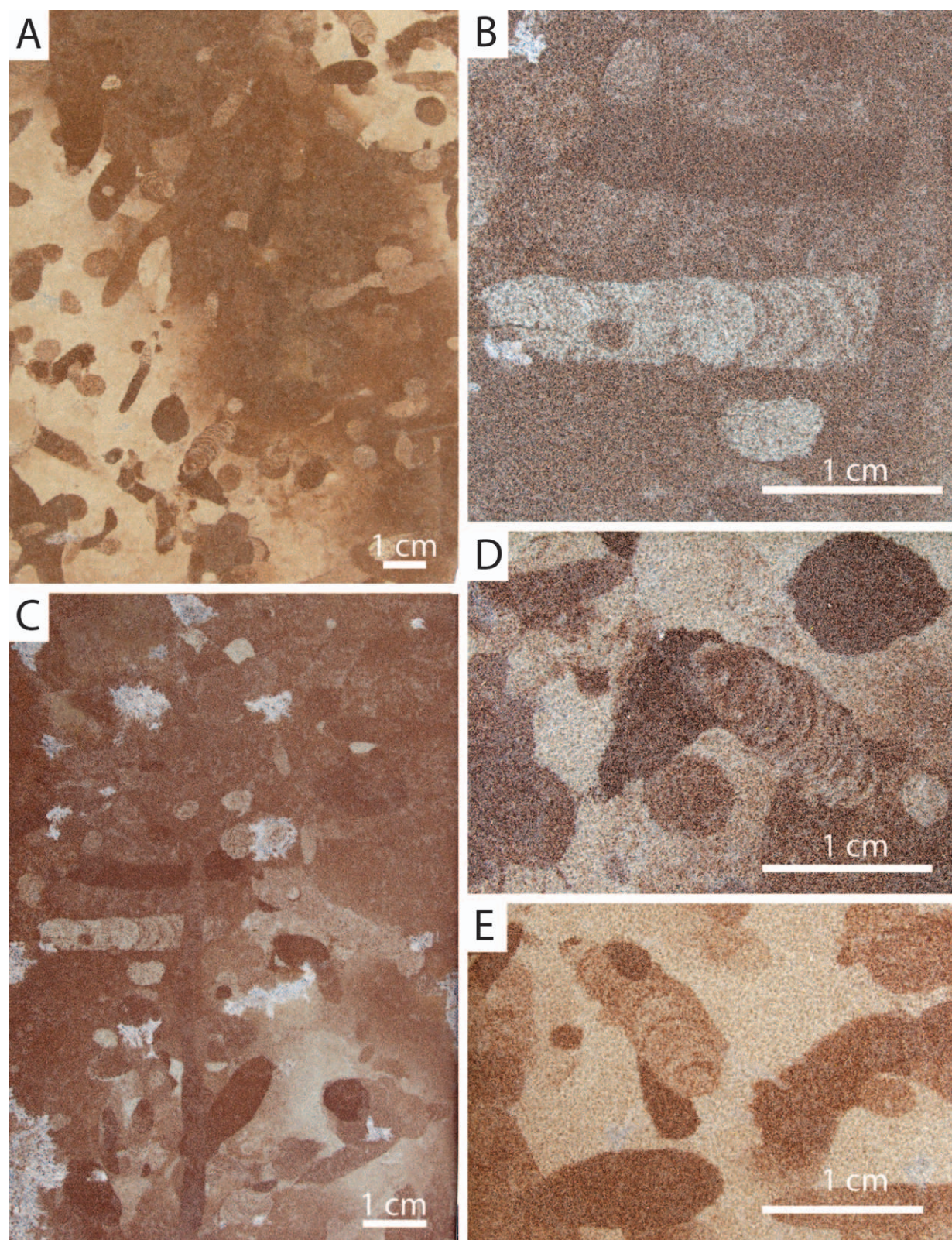


FIGURE 9—Trace fossils from Lower Permian Council Grove Group seen in core. A) Core surface showing high density of burrows in silt matrix. B) Close-up of individual burrows showing meniscate backfill. C) Core surface showing high-density of burrows, composite burrows, and cross-cutting relationships. D–E) Close-ups of individual burrows.

behind the beetle as it moves forward. Since sediment grains were simply transported around the beetle's body by the legs, the resulting burrows may lack a high degree of organization (Fig. 8).

In more compact sediment, adult beetles would likely form an irregularly shaped, elongate cell that is slightly longer than its body. The backfill would be poorly organized because the body plan of an adult beetle prevents it from using an excavation-forward, rotation-packing method similar to that of the larvae. Excavated sediment would still be transported around the body of beetle by the legs and would likely produce a granular or vuggy fill. The resultant burrow would not have been open to the soil or sediment surface. This kind of burrow morphology would be recognized as having sharp, irregular walls with or without scratch marks, depending on media firmness and grain size, and granular to vuggy fill.

Masked chafer larvae contribute to bioturbation and soil formation much more than adults. Throughout the larval stage, grubs are continually moving through the sediment. Adult beetles, however, spend most of their life above ground, and female adults usually burrow only 2–4 cm below the soil surface to deposit eggs (Potter, 1983). Adult beetle traces, therefore, are much less extensive than those of larvae. The burrowing mechanism of larvae also physically disturbs the soil more than that of adults—the swimminglike mechanism of adults results in little net movement of soil particles, while larvae actively transport sediment within their burrow.

The three experiments demonstrated that the introduction of larvae at the surface of the experiments had no adverse effect or bias on the burrow morphology or burrowing behavior of the larvae. In natural settings adults lay eggs belowground where the larvae hatch and begin to burrow. Placement of the larvae at the surface did not introduce any bias with respect to the depth of burial and amount of sediment compaction, which would have been introduced if the larvae had been artificially buried. All three experiments also showed that the larvae used the same burrowing mechanism and produced the same burrow morphologies regardless of the laminae thickness, sediment composition, or organic content.

Other Modern Meniscate Burrows and Burrowing Mechanisms

Studies describing modern terrestrial meniscate burrows are relatively uncommon (e.g., Willis and Roth, 1962; Ratcliffe and Fagerstrom, 1980; Brussaard, 1983; Brussaard and Runia, 1984; Brussaard, 1985; O'Geen and Busacca, 2001; Smith and Hasiotis, 2008). Ratcliffe and Fagerstrom (1980) illustrated many modern terrestrial traces and their trace makers but did not describe meniscate burrow patterns or burrowing mechanisms. O'Geen and Busacca (2001) described crescentic filled burrows interpreted to have been produced by cicadas, but they did not observe or describe their burrowing methods. Modern masked chafer pupation chambers have been well illustrated and summarized by Vittum et al (1999). Brussaard and Runia (1984) and Brussaard (1985) briefly described the morphology of dung beetle burrows. Studies documenting the burrowing mechanisms that produce backfilled meniscate burrows are nearly nonexistent with the exception of Brussaard (1983) and Smith and Hasiotis (2008).

Dung Beetles (Typhaeus typhoeus).—Brussaard (1983), using actively reproducing dung beetles (*Typhaeus typhoeus*), conducted experiments similar to those used in our study and described burrowing mechanism as well as burrow morphology. Together, adult male and female beetles of *T. typhoeus* excavate burrows for reproduction; these are composed of a vertical shaft with several horizontal chambers constructed and filled at different times and depths during excavation. The female lays an egg at the end of the horizontal chamber after copulation and then backfills the end part of the chamber with soil to form a separate egg chamber; no menisci are produced. The remaining portion of the horizontal chamber is backfilled with dung to form a dung sausage. Dung is compacted into the chamber by the female with her head and thorax, intermittently turning around her body length axis to apply equal force to different points

of the dung to produce a meniscate backfilled pattern. We interpret the wording in Brussaard (1983) to mean that the female remains oriented in the same direction and rotates about the long axis of the body. The dung sausage is then sealed with sand scraped from the walls from the open shaft several centimeters above the end of the dung sausage. The larva, after hatching, burrows into the dung using a somersaulting motion, which was not described in detail. Through three instars of growth, the larva eats its way through the dung sausage multiple times, backfilling the space behind it with its own excrement; the exact behavior and burrowing mechanism during this stage was not detailed. The pupation chamber is constructed in the original position of the egg chamber, where a void is created and the chamber wall is plastered with the larva's excrement. The newly hatched adult remains in the chamber for a few days to a few weeks, after which time the adult usually exits to the surface by excavating its own exit burrow. The adult excavates upward, scraping sand from above, turning around, and packing it the pupation chamber or dung sausage, although the turning process was not elucidated. This produces an 8-cm-long corridor (i.e., elongate cell or chamber) that moves upward with the adult beetle until it reaches the ground surface; it emerges to begin the life cycle again. No cell length-to-body length ratios for the dung beetle larvae or adults were reported by Brussaard (1983).

The burrowing process of adult dung beetles is distinctly different from that exhibited by adult masked chafer beetles. Dung beetles used combined male-female excavation to construct their reproductive burrow system, whereas the newly hatched adult dung beetle uses some form of excavation, turning, and packing to produce a vertical exit burrow. The final exit burrow morphology is analogous to the trace fossil *Skolithos*, which is an open vertical tube. Adult masked chafer beetles burrow into and out of the soil using only a swimming motion and do not produce an open cell (i.e., void space) that moves in unison with the individual. No open cell or vertical burrow was been observed with the adult masked chafer beetles.

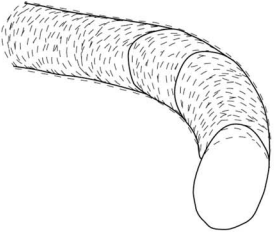
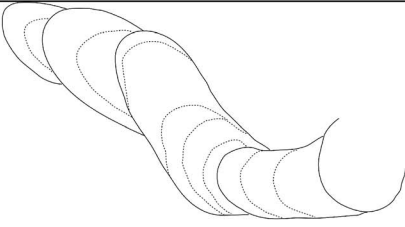
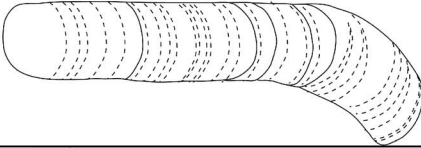
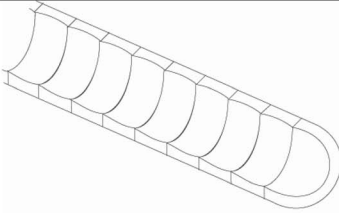
Dung beetle larvae use a somersaulting behavior to produce a back-filled burrow similar to the masked chafer beetle larvae; however, a dung beetle larva produces a backfilled burrow only within its dung sausage. The extent of this burrowing behavior differs greatly from that of masked chafer beetle larvae, which can produce meniscate backfilled burrows that are several meters long. The burrows of masked chafer beetle larvae, therefore, have a greater chance of preservation and a greater effect on pedoturbation and the rhizosphere compared to the burrows of dung beetle larvae.

The morphology of pupation chambers of dung beetle and masked chafer beetle larvae appears to be similar in size and shape, although the construction methods of the pupation chambers appear to differ. Dung beetle larvae have a chamber lining of excrement, whereas masked chafer beetle larvae have a thickened chamber wall of sand and body secretions produced by the larvae. Adult dung beetles actively backfill their pupation chambers with sediment removed during construction of a vertical exit corridor that eventually becomes an open vertical burrow at the surface. Pupation chambers of masked chafer beetle larvae are not actively filled.

Prairie Cicada (Cicadetta calliope).—Meniscate burrows and burrowing mechanisms of prairie cicada nymphs of *Cicadetta calliope* Walker 1850 (Hemiptera: Cicadidae) were observed by Smith and Hasiotis (2008) in unsaturated sediments in laboratory experiments. The experimental design was similar to that described here.

The burrowing mechanism of cicada nymphs consists of an excavation-rotation-packing process similar to that of masked chafer larvae. Like the masked chafer larvae, a nymph maintains an open cell as it moves through the sediment, excavating material from the front, forward rolling to reverse direction, and then packing the sediment ball onto the rear of the cell. The cicada nymph appears to always use a forward roll to change direction in the cell, even when excavating upside down. Rather than using the head and mandibles, the cicada nymph almost exclusively uses its large forelimbs to penetrate sediment, pull it toward the head, and

TABLE 2—Diagnostic criteria of meniscate backfilled burrows. Illustrations modified from Smith et al. (2008) and Smith and Hasiotis (2008).

Burrow or Ichnotaxon	Illustration	Diagnosis
Masked Chafer larvae burrows (modern)		Cylindrical, straight to highly tortuous, variably oriented unbranched burrows with meniscate backfill and thin, discontinuous linings. Backfill sometimes contained within larger packets, but packeted backfill are often separated by long segments of continuous, unpacketed menisci. Menisci are not always symmetrical about the central axis of the burrow. Packets of menisci are slightly offset from adjacent packets, though not to the extent of <i>N. bowni</i> .
Cicada nymph burrows (modern)		Similar diagnostic criteria to <i>N. bowni</i> ; burrows composed of a nested series of distinct, ellipsoid-shaped, asymmetrical packets which contain menisci of varying curvature. Burrow margins have a tapered and widened appearance where cicadas rotate and change directions within their burrow (Smith et al., 2008).
Adult dung beetle (<i>Typhaeus typhoeus</i>) burrows (Holocene and modern)		Mostly straight, vertical to horizontal burrows with diameter of roughly 14 mm, a series of menisci which are mostly symmetrical about the central burrow axis (Brussaard and Runia, 1984).
<i>Ancorichnus ancorichnus</i> Heinburg 1974		Cylindrical, weakly sinuous subhorizontal to horizontal burrow containing a central meniscate fill and a visibly structured mantle (Frey et al., 1984).

consolidate it into a ball held against the ventroanterior portion of the thorax just below the head. Simultaneously, hindlimbs are used to brace the nymph against the cell wall. Alternating thrusts of the left and right forelegs are used to pack the sediment ball at the rear of the burrow.

The morphology of the cicada nymph burrows also shares many similarities with burrows constructed by masked chafer larvae. Packeting of menisci is more evident in cicada burrows, reflecting periods of inactivity followed by a return to burrowing with a slight change in direction. Cicada nymph burrows are larger in diameter and more irregular as a result of the larger body size and the particular style of forward rotation of the trace maker. The cell length-to-body length ratio for cicada nymphs is larger than that for the masked chafer larvae.

Overall burrow length in the cicada experiments was shorter owing to the smaller size of the enclosures, which led to lower length-to-width ratios. Fifth-instar cicadas constructed open emergence burrows, which were not constructed by masked chafer larvae or adults (see Smith and Hasiotis, 2008, for a full description). These burrows are also analogous to *Skolithos*, and may be similar in morphology to the vertical exit burrows of adult dung beetles.

Preservation Potential

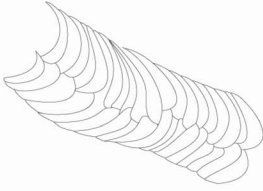
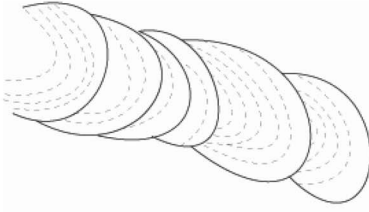

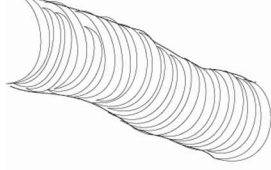
Burrows of masked chafer beetles have an excellent chance of being preserved in the fossil record, despite potential overprinting by pedogenesis. Masked chafers as well as other types of scarabaeid beetles are extremely common in certain habitats, reaching densities as high as 40 grubs per 0.1 m² in turfgrass (Potter and Gordon, 1984; Dalthrop et al., 2000). As important components of soil biota and pedogenesis (Hole,

1981; Hasiotis, 2007; Hasiotis et al., 2007), masked chafer larvae and adults have the ability to significantly bioturbate upper soil horizons in all stages of their life cycle. Most grub activity takes place within the soil root zones (e.g., Potter, 1983; Potter and Gordon, 1984; Potter et al., 1996; Vittum et al., 1999), which include the A and upper B horizons. Deeper burrows produced by grubs during overwintering or during the dry season are less susceptible to reworking by soil biota and other pedogenic processes, including future generations of masked chafers.

Larval burrows far outnumber burrows made by adults or pupae. At least 80% of the chafer beetle life cycle is spent beneath the sediment surface as a larva (Vittum et al., 1999). Winter mortality rates of larvae may be as high as 50% (Vittum et al., 1999), and mortality rates of both eggs and larvae dramatically increase during times of drought (Potter, 1983; Potter and Gordon, 1984). Fewer grubs thus survive to adulthood, and larval populations are likely to exceed adult populations. The behavior of larvae also produces more extensive burrows compared to adults because larvae feed underground and continually move in search of new food sources. Higher adult-to-larvae burrow ratios in a given area would, therefore, indicate favorable moisture and temperature conditions for masked chafer survival and, theoretically, could be used as climate, rainfall, or soil-moisture proxies.

In general, backfilled burrows rarely are observed in modern soils. Burrow-fill material like that observed in these experiments is unaltered during the burrowing process and is compositionally and texturally identical to the surrounding soil matrix, with the exception of masticated plant material and feces included in the backfill. The burrowing mechanism of larvae disturbs the soil to a greater extent when compared to adults. Adult

TABLE 2—Continued.

<i>Laminites kaitiensis</i> Ghent and Henderson, 1966		Unlined, unbranched, gently meandering burrows composed of thin, 1.5–3 mm thick, texturally homogeneous backfills successively light and dark in color. Backfills concave, biconcave (bow-shaped), or comma-shaped with the thicker part touching or overlapping along the medial axis of the burrow.
<i>Naktodemasis bowni</i> Smith et al., 2008		Sinuous, variably oriented, unbranched, unlined burrows composed of a nested series of distinct, ellipsoid-shaped, asymmetrical packets. Packets asymmetrically oriented around the burrow axis and offset from one another. Packets contain thin, indistinct, and tightly spaced meniscate fill. Menisci are subparallel to the bounding packet, unpelleted and texturally homogeneous with each other, discontinuous, and difficult to trace. Short burrow sections may be composed only of unbound menisci. Burrow wall is mostly smooth or with slight annulae and correspond with ellipsoidal packets.
<i>Scoyenia gracilis</i> White 1929		Straight to curved, unbranched, horizontal to variably oriented burrows with chevron-shaped to arcuate backfill of homogeneous or heterogeneous lithologies. Burrows may be unlined or with thin clay linings and burrow surfaces are ornamented with convex, mostly parallel, short longitudinal striae (Frey et al., 1984).
<i>Beaconites barretti</i> Bradshaw, 1981		Straight to variably meandering, unbranched, unwalled, meniscate backfilled burrow. Menisci are commonly hemispherical or deeply arcuate, tightly packed or stacked, forming noncompartmentalized backfill or thin meniscate segments.

beetle traces may be less conspicuous in the field owing to their lower abundance, smaller size, and lack of significant sediment disruption. In some cases in the laboratory experiments, porosity and permeability were variable in the burrow fill, which may have enhanced burrow preservation and visibility. Since larval burrows are constructed in three dimensions, it is unlikely that the entire length of a single burrow would be visible in a given exposure. Length-to-width ratios, therefore, could not be accurately determined.

Meniscate backfill burrows are visible in many continental trace fossils owing to redoximorphic coloration produced by differences in organic matter content between individual menisci (Hasiotis and Bown, 1992; Hasiotis et al., 1993; Retallack, 2001b). Larval and adult burrows may be highlighted by preferential gleying—the redistribution of Fe and Mn in the soil profile in the presence of organic matter due to water-table fluctuations (e.g., Schwertmann, 1993; Vepraskas, 1999)—to produce mottles of various colors. These mottles would highlight individual backfill and overall backfill patterns similar to the production of mottles in association with rhizoliths (Kraus and Hasiotis, 2006). In natural settings, masked chafer larvae would leave fecal pellets in their burrow as they ingested disseminated organic matter and fed on plant roots. This would lead to organic-rich and organic-poor parts of the burrow fill and would increase the visibility of menisci and menisci packets through redoximorphic coloration. Such patterns in meniscate backfilled burrows have been observed in the Upper Triassic Chinle Formation, Upper Jurassic Morrison Formation, Paleogene Willwood Formation, and Miocene alluvial deposits in Spain (e.g., Hasiotis et al., 1993; Hasiotis and Dubiel, 1994; Hasiotis, 2002, 2004). If chafer burrows are preserved in the geologic record, the thin linings along the exterior burrow margins may or



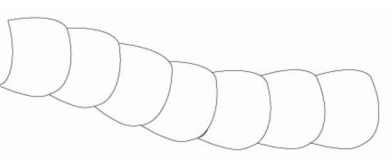
may not be visible because they are extremely thin and discontinuous, usually only a few sediment grains wide. Visibility of linings would be dependent on diagenetic enhancement.

Pupation chambers may have a high preservation potential; however, a beetle larva can only pupate once, which results in a single chamber per grub. This activity pales in comparison to the amount of bioturbation produced during the adult stage and, particularly, during the larval stage. Cell linings of pupation chambers are relatively thick and are reported to be reinforced by the larvae through some type of secretion (Vittum et al., 1999). The cell is more likely to remain open for an extended period of time, which increases its chance of being preserved as an open void. Pupation cells may also be filled with sediment washed down through the higher-porosity exit burrow left by the adult, producing passively filled, ellipsoidal molds and casts, which are common trace fossils (see the section on Ellipsoidal Trace Fossils below). The larval exuvia, shed within the cell, further increase the concentration of organic matter and may contribute to increased preservation during diagenesis.

Fossil Record of Meniscate Backfilled Burrows

Several features of chafer larval burrows distinguish them from previously described meniscate traces (Table 2). Chafer larval burrows do not show the high density, short, longitudinal striations of *Scoyenia* or the distinct thick continuous walls of *Ancorichnus* (Frey et al. 1984; Keighley and Pickerill, 1994). *Laminites* (Ghent and Henderson, 1966) can also be excluded as an analog for chafer larval burrows because individual menisci are not continuous across the entire burrow. *Beaconites* has shuffled menisci, often composed of alternating coarse- and fine-grained sediment, which are not contained within packets (Gevers et al.,

TABLE 2—Continued.

<i>Taenidium cameronensis</i> (Brady, 1947)		Unwalled meniscate burrows, secondary successive branching and intersection may be present. Meniscate packets usually longer than wide, with the deeply concave meniscate interfaces resulting in a nested appearance (D'Alessandro and Bromley, 1987).
<i>Taenidium satanassi</i> D'Alessandro and Bromley, 1987		Weakly arcuate menisci in sinuous to nearly straight burrows, the fill consisting of meniscate backfill, each containing two types of sediment of more or less equal thickness; backfill considerably shorter than wide. Darker parts of each backfill segment are composed of fecal pellets.
<i>Taenidium serpentinum</i> Heer, 1877		Well-spaced menisci about equal to or slightly less than burrow width. External molds may show slight annulation corresponding to menisci, or fine transverse wrinkling. Secondary successive branching and intersections occur. Boundary sharp and lacks lining (Keighley and Pickerill, 1994).

1971; Bradshaw, 1981). Backfill in chafer larval burrows does not show size sorting or textural differences and thus is not analogous to *Beaconites*. Ichnospecies of *Taenidium* as recognized by D'Alessandro and Bromley (1987) are morphologically inappropriate as analogs for the morphology exhibited by chafer burrows. The thick, size-sorted backfill of *T. satanassi* and the thick, symmetrical, regularly spaced backfill of *T. cameronensis* and *T. serpentinum* (D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994) are inconsistent with the thin, homogeneous, slightly asymmetric backfill and packeted menisci observed in chafer beetle larvae burrows.

Adhesive meniscate burrows, however, cannot be ruled out as analogues for chafer beetle larval burrows, based on the morphological features observed in these experiments. Adhesive meniscate burrows were first described in Eocene deposits by Bown and Kraus (1981, 1983) and occur in paleosols as old as the Permian (Counts and Hasiotis, 2006, 2007). Smith et al. (2008) erected the ichnotaxon *Naktodemasis bowni* for burrows exhibiting the morphology diagnostic of adhesive meniscate burrows, which have been likened to the burrows of cicadas, other hemipterans, and beetle larvae (Smith and Hasiotis, 2008). These traces are common in paleosols, are often found in association with rhizoliths, and have previously been attributed to insect larvae (Hasiotis and Bown, 1992; Hasiotis and Dubiel, 1994; Hasiotis, 2002, 2004, 2007; Smith et al., 2008). *Naktodemasis bowni* burrows are characterized by a series of offset ellipsoid-shaped packets composed of thin menisci—a feature present but not as pronounced in the experimentally produced traces. These burrows are straight to sinuous, variably oriented, unbranched, and unlined and are described as having short sections composed of unbound menisci. Packets of menisci are visible in some, though not all, sections of chafer larvae burrows (Fig. 4); where visible, packets are longer and better organized than those described in *N. bowni*. Packeting in *N. bowni* is hypothesized to be the result of periods of resting or changes in direction between intervals of continuous movement (e.g., Hasiotis and Dubiel, 1994; Hasiotis 2002, Smith et al., 2008). Chafer larvae burrows are similar, but not identical, to *N. bowni*, and trace fossils with morphologies similar to larval burrows may be classified as a new ichnospecies of *Naktodemasis*. The current study presents another burrowing mechanism that produces burrow morphologies similar to *Naktodemasis*.

Masked chafer beetle larvae burrows are also similar in morphology to meniscate backfilled burrows observed in continental deposits within the Lower Permian Council Grove Group in the subsurface of western Kansas (Dubois and Goldstein, 2005; Counts and Hasiotis, 2006); see

Fig. 9). Both masked chafer burrows and Permian burrows are characterized by packeted meniscate backfill, highly sinuous unbranched axes, and thin discontinuous linings. The burrow morphologies illustrated here from western Kansas core are the oldest documented morphology that may represent a burrowing behavior similar to that observed in extant masked chafer beetle larvae.

Adult beetle traces are not easily comparable to known trace fossils. The morphology of adult beetle egg-laying and emergence burrows may change considerably depending on the burrowing media. Their traces, therefore, may not have morphological features that are diagnostic.

Ellipsoidal Trace Fossils

Ellipsoidal cells constructed by the masked chafer larvae as pupation chambers superficially resemble passively filled ellipsoidal cells in paleosols found as early as the Triassic (e.g., Hasiotis, 2002, 2003). *Celliforma* is a slightly ellipsoidal to flask-shaped trace fossil with a spiral terminus and constriction at one end of the cell that indicates the trace is most likely produced by bees (e.g., Brown, 1934; Genise and Bown, 1994; Hasiotis, 2002, 2003). *Fictovichnus* (Johnston et al., 1996) is a small, ellipsoidal trace surrounded by a clay-rich zone and occasional passive infilling. Johnston et al. (1996) attribute *Fictovichnus* to the pupation chambers of beetles by comparing fossil specimens with specimens of modern pupation chambers (with a length-to-width ratio of 1.64:1). Masked chafer pupation chambers are much more elongate (with a length-to-width ratio for the interior cell of ~3:1; including a lining, ~2:1) than the type specimens of *Fictovichnus* (length to width ratio of 1.5:1 to 1.7:1). Considering all the morphological features, masked chafer pupation chambers do not conform to either *Celliforma* or *Fictovichnus*.

Rebuffoichnus and *Teisseirei* are similar to *Fictovichnus* in that they are ellipsoidal and may be surrounded by an actively constructed lining with a terminal emergence hole. Both are tentatively attributed to pupation chambers of Coleoptera. Genise (2004) distinguishes these ichnotaxa in that *Teisseirei* is characterized by an internal bioglyph and a depressed (i.e., ovate) cross section, whereas *Rebuffoichnus* differs by lacking an active fill and the presence of a rounded hole. These characters are not necessarily mutually exclusive, however. For example, photographs of *T. barattinia* in Genise (2004, fig. 3b) show a terminal emergence hole, although this character has been used to distinguish *Rebuffoichnus* from other ellipsoidal traces. Regardless of the taxonomic uncertainty, the size and preservation of *Rebuffoichnus* and *Teisseirei* preclude masked chafer

larvae as the potential trace makers of these ichnotaxa. The abundance of ellipsoidal cells in the fossil record, however, does demonstrate that pupation chambers like those produced by masked chafer beetles are often preserved in the geologic record.

IMPLICATIONS AND SIGNIFICANCE

Paleontological Significance

Although body fossils are often used to note the first appearance of a particular taxon, the presence of diagnostic trace fossils may serve as an alternative way to identify past occurrences of an organism. The presence of traces similar to those produced by extant masked chafer larvae in Permian paleosols, for example, implies the early evolution of a comparable larval body plan and burrowing, feeding, and reproductive behaviors in certain insects at that time. The trace fossils in paleosols from the Early Permian suggest that the trace maker had well-developed burrowing adaptations with a C-shaped, grublike larva that bore a large sclerotized head, strong biting mandibles, and well-developed legs. These features are also characteristic of the Superfamily Scarabaeoidea (Grimaldi and Engel, 2005). Though it may not be possible to determine the morphology of the adult from the Permian trace fossils, it could be possible that the adult form of the trace maker was similar in body plan to the adult masked chafer beetle. Such striking similarities in burrow morphologies, therefore, may indicate an earlier origination for the Scarabaeoidea. This possibility is supported by the fact that the earliest beetlelike fossils are Early Permian (Kukalová-Peck and Willmann, 1990), and additional evidence indicates that beetles had diversified by the Triassic (e.g., Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005; Hunt et al., 2007).

Paleoecological Implications

Previous studies have hypothesized that backfilled burrows are made exclusively in subaqueous settings by deposit-feeding invertebrates, which ingest sediments at one end and excrete sediments and waste products at the other, producing a meniscate backfill; these studies also suggest that it is unlikely insects could produce such burrows (e.g., Frey et al., 1984; Squires and Advocate, 1984; Genise, 2004; Genise et al., 2004; Buatois and Mángano, 2004, 2007; Bromley et al., 2007). Our study demonstrates conclusively that insects such as masked chafer beetle larvae produce actively backfilled burrows in terrestrial, subaerial well-drained settings without ingesting sediment or wholesale deposit feeding. Meniscate burrows may occur in a much wider range of environments than previously thought, and thus meniscate burrows cannot be considered diagnostic of any specific depositional environment. Environments previously thought to be subaqueous fluvial, lacustrine, or marine in origin, based only on the presence of meniscate backfilled burrows, need to be reevaluated in light of the data presented here and similar neotechnological research (e.g., Smith and Hasiotis, 2008).

Similarities in burrow morphology between masked chafer larvae traces, cicada nymphs (Smith and Hasiotis, 2008), and *Naktodemasis* (Smith et al., 2008) demonstrate that forms of *Naktodemasis* are likely produced by soil-dwelling insect larvae. *Naktodemasis* burrows have been found only in paleosols; therefore, they are likely to be diagnostic of subaerial exposure and soil formation. Beetle larvae, such as masked chafers, have specific moisture tolerances ranging from 18% to 27% (Potter, 1983; Potter and Gordon, 1984). If the trace maker of *Naktodemasis* is an insect larva similar to that of masked chafers, the presence of *Naktodemasis* likely indicates that burrowing occurred within a limited range of soil moisture content within the vadose zone. In this environment, moisture content on average would be below saturation but above the wilting point for a particular soil, that is, the minimum soil moisture at which a plant wilts and cannot recover (e.g., Brady and Weil, 2002). The presence of *Naktodemasis* would also indicate, therefore, the presence of adequate vegetation (i.e., rhizoliths) or organic matter within the soil,

because larvae need a consistent food source to survive. Since the presence of the masked chafer-like trace fossil *Naktodemasis* is indicative of soil formation, these traces may prove to be useful in recognizing paleosols as sequence boundaries and as sea-level lowstand deposits when found in combination with other pedogenic features that overprint marine deposits.

CONCLUSIONS

Masked chafer larvae burrow by creating an elliptical, open cell that is actively moved forward. The larvae excavate sediment from the front of the cell and deposit it at the back in a five-step process that includes excavation, consolidation, forward rotation, transport of sediment, and packing. Sediment is excavated through a scraping motion of the larva's mandibles and head and is moved toward the center of the body with the first pair of limbs. The legs and body consolidate the sediment into a ball, forming a C shape around the package. The grub rotates forward until the head is at the posterior end of the chamber where the sediment ball is pushed to the back of the chamber with the head, limbs, and the front portion of the body. The legs and the head simultaneously compact the sediment ball into the cell wall in all directions. The result of this burrowing mechanism is a series thin menisci. Packets are formed when the larvae excavate, stop to rest or feed, and restart the burrowing process again.

High length-to-width ratios and thin, slightly offset menisci characterize masked chafer larvae burrows. Meniscate backfill are mostly contained within packets that result from periods of inactivity followed by a change in burrowing direction. Larval burrows are also characterized by thin, discontinuous linings and a lack of true branching. Orientation and tortuosity are highly variable.

Masked chafer pupation chambers are elongate, ellipsoidal cells with a variably thick lining. Pupation chambers are larger and more elongate than locomotion cells and may have emergence holes. Pupation chambers are left open by the exiting adult beetle and subsequently may be infilled passively through time. Traces produced by masked chafer adults do not have a clear morphological signature and may not be identifiable if taphonomically or pedogenically modified by other biotic (including larval bioturbation) and abiotic processes.

Overall morphology of masked chafer larvae burrows is similar to *Naktodemasis* (adhesive meniscate burrows; Smith et al., 2008), which are interpreted to have been produced by C-shaped insect larvae and represent locomotion and dwelling behaviors. Our results add further evidence to the hypothesis that *Naktodemasis* is exclusively formed in subaerial environments and is associated with pedogenesis (e.g., Bown and Kraus, 1983; Hasiotis and Bown, 1992; Hasiotis, 2002, 2004, 2007; Hasiotis et al., 2007; Smith et al., 2008). Given the environmental tolerances of masked chafer beetle larvae, traces similar to masked chafer burrows may also be useful for reconstructing soil-moisture levels of ancient deposits, which in turn can be used for paleoenvironmental and paleoclimatic reconstruction. The presence of such burrows also implies the presence of vegetation or another source of soil organic matter. Trace fossils with morphologies similar to those traces produced by masked chafer beetle larvae may be used to extend the geographic and stratigraphic range in the geologic record of beetle taxa with similar larval body plans. Our research suggests that this may be possible for members of the Scarabaeoidea with C-shaped larvae, well-developed appendages, and a large sclerotized head, which may have evolved as early as the Permian.

This research serves as a springboard for more experiments with masked chafer-beetle larvae as well as with other trace-making continental organisms, so as to more fully investigate the influences that local media composition, soil moisture, and climate have on the viability and distribution of populations and the nature of their burrows with respect to those influences. The relationship between burrow morphology and organism behavior in both modern and ancient continental deposits can be better understood through the detailed study of extant trace-making

organisms. The present study highlights the need for additional neoichnologic research with burrowing organisms that live in various terrestrial as well as aquatic settings. Detailed knowledge of extant traces and their trace makers in the continental realm can be used to recognize the presence of related taxa or behaviors in deposits where body fossils are not preserved, as well as to aid in the reconstruction of evolutionary histories. Continental trace fossils can be calibrated against similar trace morphologies produced in neoichnological studies where the physicochemical conditions of the media and the physiology of the organism are known. This will lead to more accurate paleoenvironmental, paleohydrologic, and paleoclimatic interpretations using continental trace fossils.

ACKNOWLEDGMENTS

This research was funded by National Science Foundation, Division of Earth Sciences grant EAR-0229300 to STH. JWC acknowledges the Geological Society of America, American Association of Petroleum Geologists R.C. Moore Memorial Grant, and University of Kansas Department of Geology Joseph M. Patterson Scholarship and Summer Field Research Award for financial and research support. We thank Ian Rowell, Jon Smith, the University of Kansas IchnoBioGeoScience research group, and University of Kansas Paleosols and Ichnology classes for assistance with fieldwork, insect collection, and experimental setup and design. Frank Krell, an anonymous reviewer, and Associate Editor and Coeditor Edith L. Taylor provided thoughtful and constructive editorial comments that greatly improved the clarity of the manuscript.

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ACCEPTED AUGUST 5, 2008