

NAKTODEMASIS BOWNI: NEW ICHNOGENUS AND ICHNOSPECIES FOR ADHESIVE MENISCATE BURROWS (AMB), AND PALEOENVIRONMENTAL IMPLICATIONS, PALEOGENE WILLWOOD FORMATION, BIGHORN BASIN, WYOMING

JON J. SMITH,¹ STEPHEN T. HASIOTIS,^{1,2} MARY J. KRAUS,³ AND DANIEL T. WOODY³

¹The University of Kansas, Department of Geology, Lawrence, 66045-7613, (jjsmith@ku.edu), (hasiotis@ku.edu), ²Natural History Museum and Biodiversity Research Center, Lawrence, KS 66045-7613, and ³University of Colorado, Department of Geological Sciences, Boulder, 80309, (Mary.Kraus@colorado.edu), (Daniel.Woody@colorado.edu)

ABSTRACT—Adhesive meniscate burrows (AMB) are common in alluvial paleosols of the Paleogene Willwood Formation, Bighorn Basin, Wyoming. AMB are sinuous, variably oriented burrows composed of a nested series of distinct, ellipsoidal packets containing thin, tightly spaced menisci subparallel to the bounding packet. Menisci are non-pelleted and texturally homogeneous with each other and the surrounding matrix. AMB were constructed most likely by burrower bugs (Hemiptera: Cydnidae), cicada nymphs (Hemiptera: Cicadae), and less likely by scarabaeid (Coleoptera: Scarabaeidae) or carabid beetles (Coleoptera: Carabidae), based on burrow morphology and comparison to similar structures produced by these organisms in modern soils. Extant burrowing insects excavate backfilled burrows in well-rooted A and upper B horizons of soils generally below field capacity depending on soil type. This study demonstrates that AMB are distinct morphologically from such previously described ichnofossils as Beaconites, Laminites, Scoyenia, Taenidium, and Ancorichnus. *Naktodemasis bowni*, a new ichnogenus and ichnospecies, represents burrows composed of nested ellipsoidal packets backfilled with thin, tightly spaced, menisci subparallel to the bounding packet. The presence of *N. bowni* indicate periods of subaerial exposure associated with pedogenic modification under moderately to well-drained soil conditions, or during periods of better drainage in imperfectly drained soils. *N. bowni*, therefore, can differentiate alluvial paleoenvironments from marine and lacustrine paleoenvironments, as well as periods of subaerial exposure of sediments deposited in aquatic settings.

INTRODUCTION

THIS PAPER describes the morphology and paleoenvironmental implications of adhesive meniscate burrows (AMB) and discusses their potential tracemakers, inferred behaviors, and paleoecological significance. Bown and Kraus (1983) first described these burrows from floodplain paleosols of the Paleogene Willwood Formation in the Bighorn Basin, Wyoming. Meniscate burrows of this type were termed AMB (Hasiotis and Dubiel, 1994) to differentiate them (see Bown and Kraus, 1983, for description) from other burrows with superficially similar morphologies. AMB have been reported from paleosols in the Shinarump and Owl Rock members of the Upper Triassic Chinle Formation (Hasiotis and Dubiel, 1994), the Tidwell, Salt Wash, and Brushy Basin members of the Upper Jurassic Morrison Formation (Hasiotis and Demko, 1996; Hasiotis, 2004), the Upper Cretaceous North Horn and Tuscaloosa formations (Bracken and Picard, 1984; Savrda et al., 2000), and Miocene alluvial deposits in Montserrat, Spain (Hasiotis, 2002). Recent fieldwork in the Willwood Formation has produced additional observations and specimens for this study.

Backfilled burrows are interpreted generally as fodinichnia produced by deposit-feeding organisms (e.g., Toots, 1967; Stanley and Fagerstrom, 1974; Bromley and Asgaard, 1979; Bown, 1982; Frey et al., 1984; D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994). Some workers propose that backfilled burrows in continental deposits were produced by sediment-ingesting animals in subaqueous or saturated soil conditions (Buatois and Mángano, 2004; Genise et al., 2004). Our results, however, suggest that AMB were produced by burrowing insects that inhabited rooted and moderately well-drained A and upper B horizons of floodplain soils.

The architectural and surficial morphology and internal fill of AMB are compared with similar ichnogenera of backfilled burrows, including Beaconites Bradshaw, 1981; Laminates Ghent and Henderson, 1966; Scoyenia White, 1929; Taenidium Heer, 1877; and Ancorichnus Heinberg, 1974. Although these previously described ichnotaxa are superficially similar to AMB, its morphology, interpreted behaviors, probable tracemakers, and paleoenvironmental significance are distinctly different. AMB, thus, are herein assigned to a new ichnotaxon, *Naktodemasis bowni*, which represents burrows composed of distinct, ellipsoid packets that contain indistinct, meniscate backfill.

GEOLOGIC SETTING

The Willwood Formation is a 780-m-thick fluvial succession deposited during the latest Paleocene and early Eocene throughout the Bighorn Basin of northwest Wyoming (Fig. 1; Neasham and Vondra, 1972). The formation is composed primarily of red, yellow-brown, and purple mudrocks interpreted as moderately to well-developed paleosols formed on overbank deposits (Kraus, 1997; Kraus and Gwinn, 1997). Paleosols alternate vertically with heterolithic units consisting of ribbon sandstones and drab mudrocks that show weak pedogenic modification. The heterolithic intervals are interpreted as avulsion deposits produced when the main channel relocated onto the floodplain (Kraus and Aslan, 1993a; Kraus, 1996). Laterally extensive (1.5 km perpendicular to paleoflow), thick (10 m) sheet-sandstones are interpreted as the channel deposits of meandering rivers (Kraus, 1980).

An extensive record of early Eocene mammals and well-preserved floral assemblages are present throughout the Willwood Formation (e.g., Wing et al., 1995; Gingerich and Clyde, 2001). Temperature estimates derived from leaf-margin analysis of well-preserved latest Paleocene and earliest Eocene floral assemblages suggest a warm temperate to subtropical paleoclimate (Wing et al., 1991). Willwood paleosols also contain an abundant and diverse assemblage of plant, invertebrate, and vertebrate ichnofossils (Bown and Kraus, 1983; Hasiotis et al., 1993b; Kraus and Hasiotis, 2006).

AMB are present as tens to thousands of individuals in weakly, moderately, and well-developed Willwood Formation paleosols (Fig. 2). Burrows are abundant especially in strongly developed paleosols with rhizoliths, commonly to the exclusion of other trace fossils. Well-developed paleosols are characterized by red, yellow-brown, purple, and gray mottles, abundant carbonate rhizoliths and pedogenic nodules, abundant burrows, Fe-oxide nodules, and clay slickensides (Bown and Kraus, 1983; Kraus and Aslan, 1993b; Kraus, 1997). Mottles and Fe-oxide nodules are redoximorphic features formed by the reduction, mobilization, and oxidation of Fe and Mn (Vepraskas, 1999). Modern soils with these features experience saturated conditions for several months of the year followed by periods of better drainage and deeper water tables (Bigham et al., 1978; Torrent et al., 1980). The activity of the AMB tracemaker and other soil organisms produced

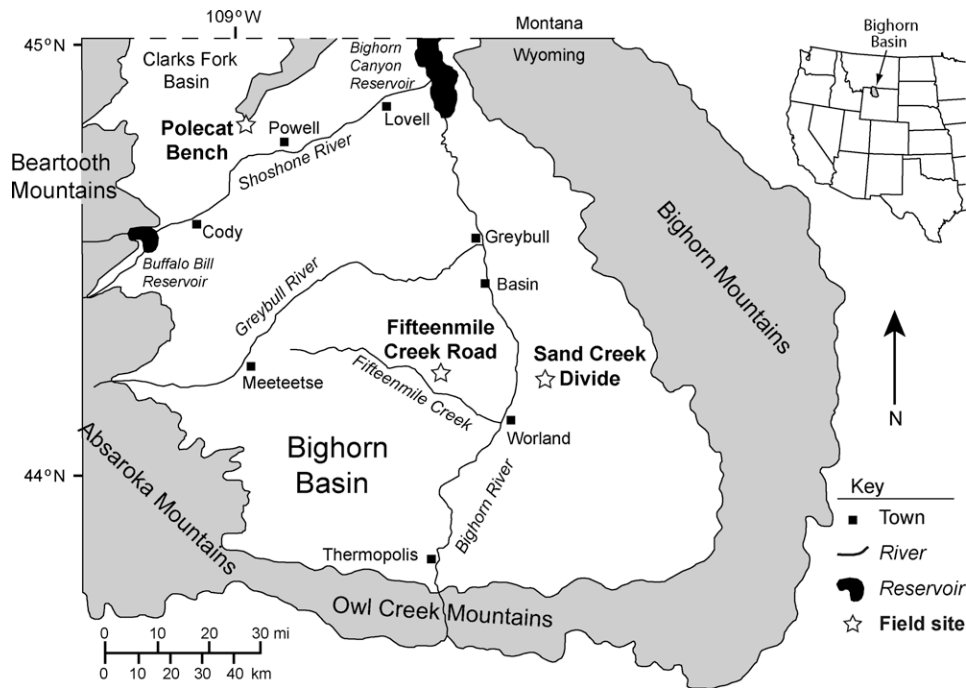


FIGURE 1—Map of the Bighorn Basin, Wyoming, showing mountain ranges surrounding the basin and the Sand Creek Divide, Polecat Bench, and Fifteenmile Creek study areas. Modified from Bown and Kraus (1981).

and enhanced much of the mottling in Willwood Formation paleosols (Neasham and Vondra, 1972; Bown and Kraus, 1983; Kraus and Hasiotis, 2006).

AMB are less common in weakly developed paleosols formed on avulsion-belt deposits. These paleosols are characterized by gray to green-gray matrix colors, and diffuse yellow-brown and purple mottles (Kraus, 1996). Weakly developed paleosols contain fewer rhizoliths, burrows, and nodules than well-developed paleosols. These features suggest poor drainage conditions and high sedimentation rates.

METHODS AND TERMINOLOGY

AMB and well-exposed Willwood Formation paleosols were examined in three areas of the Bighorn Basin: Sand Creek Divide, Polecat Bench, and Fifteenmile Creek (Fig. 1). Morphologic features of paleosols, including unit thickness, colors, nodule types, sedimentary structures, and grain size, were recorded in the field. Colors were described from fresh, dry samples. Thin sections were examined using a transmitted light microscope.

Trace fossils are described by their architectural and surficial burrow morphology and burrow fill (e.g., Hasiotis and Mitchell, 1993; Hasiotis et al., 1993a; Hasiotis et al., 2004). Architectural morphology refers to the general shape and dimensions, cross-sectional shape, and orientation of the burrows in outcrop. Surficial morphology (also known as bioglyph) includes marks of different size, shape, and orientation on the burrow walls. Burrow fill pertains to the composition, grain size, degree of compartmentalization, and arrangement of the fill.

A cell, herein, is defined as a matrix-enclosed, air-filled space produced by backfilling, periodic to permanent, fossorial organisms while dwelling, nesting, resting, or burrowing in sediments (Ratcliffe and Fagerstrom, 1980). The organism moves through the sediment by excavating sediment from one wall of the cell and depositing it on the opposite cell wall; thus the cell moves with the burrowing organism (Willis and Roth, 1962; Froeschner and Chapman, 1963). This behavior results in a burrow composed of cell-wall remnants and backfilled sediment (Fig. 3).

TRACE FOSSIL MORPHOLOGY

Architectural morphology.—Straight to sinuous, variably oriented, unbranched, and unlined burrows composed of a series of ellipsoid-shaped packets filled with menisci (Fig. 4). Packets usually crosscut adjacent packets, forming a nested appearance along the burrow length. Packets typically are asymmetrically oriented around the axis of the burrow and offset from one another (Fig. 4.3, 4.4). The length-to-width ratio of each packet depends on the spacing between individual packets; some packets have a ratio much greater than 1; others have a ratio much less than 1.

Burrows range in observed length from 1 to more than 15 cm, although highly variable orientations obscure true burrow lengths. Transverse cross sections from 0.7 to 14.0 mm are circular to elliptical in diameter. Trace-fossil size clearly relates to host-rock grain size (Fig. 5). Burrows in claystone, siltstone, or mudstone deposits are almost exclusively 1.0 to 3.0 mm in diameter. Those in sandy mudstone to fine-grained sandstone exhibit a broad range in sizes, averaging 7.1 mm in diameter. The two populations of AMB, as suggested by differences in diameter sizes, are otherwise morphologically identical.

Surficial morphology.—AMB are predominantly adhesive, meaning they cannot be easily removed as individual three-dimensional specimens and do not weather differentially from the surrounding matrix (Bown and Kraus, 1983). While not a valid ichnotaxonomic criterion, adhesion is a nearly universal characteristic regardless of such variables as burrow size, orientation, grain size of the surrounding strata, degree of pedogenic modification, and geologic age (Bown and Kraus, 1983; Hasiotis and Dubiel, 1994; Hasiotis and Demko, 1996; Hasiotis, 2002; Hasiotis, 2004). As a result, exposed burrow surfaces are rare and nearly all specimens are natural longitudinal or transverse cross sections. Burrow surfaces, when present, are mostly smooth and unornamented. Some surfaces, however, have slight annulae that correspond with the ellipsoidal packets.

Internal morphology.—The distinct packets contain thin, typically discontinuous, and tightly spaced meniscate fill less than 1 mm thick (Fig. 4). Menisci are subparallel to the individual

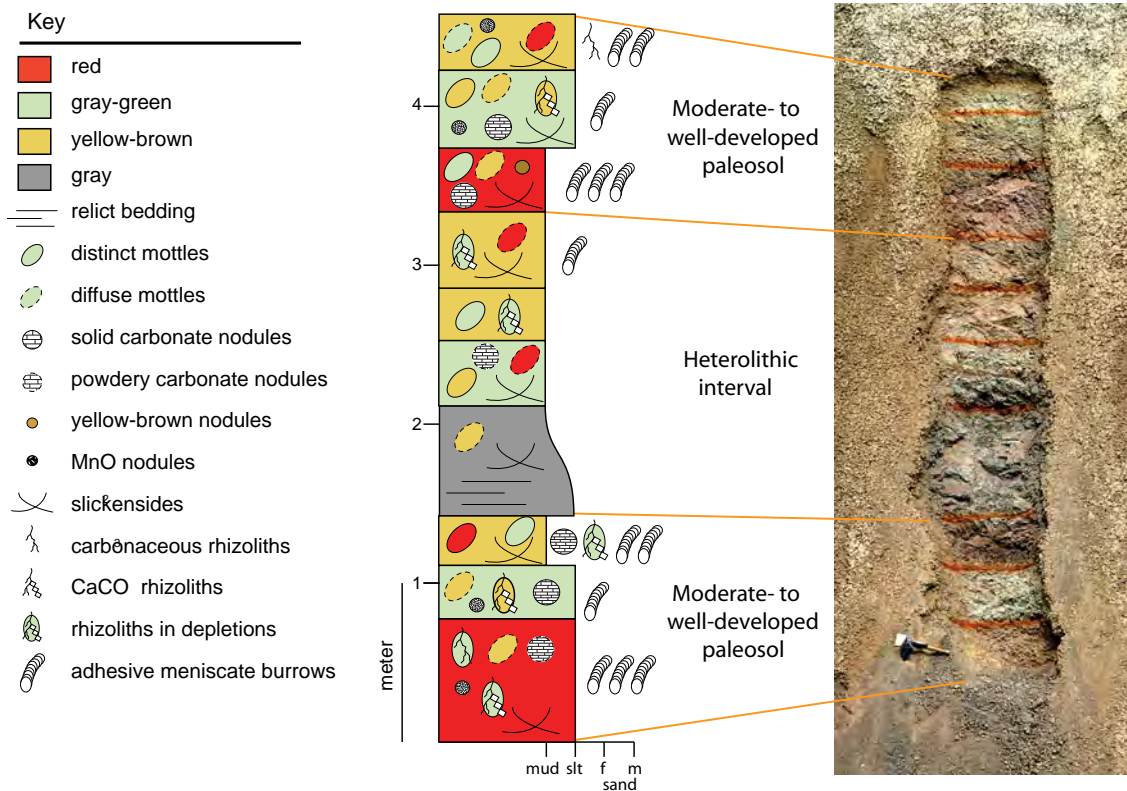


FIGURE 2—Measured section through several paleosols in the Sand Creek Divide field site showing textural features of the paleosols and the occurrence of AMB.

bounding packet and difficult to trace. Short burrow sections may be composed only of unbound menisci (Fig. 4.1, 4.2). In thin section, menisci are unpeletted and texturally homogeneous with each other and the surrounding strata (Fig. 6.1).

Red, purple, yellow-brown, or gray colors highlight commonly the packets and menisci (Fig. 4). Packet walls range in color from slightly darker than the paleosol matrix to completely gray. In most specimens, menisci alternate between those the same color as the paleosol matrix and those having colors of mottles found in the matrix. For example, a red paleosol with yellow-brown and gray mottles contains AMB with red menisci alternating with yellow-brown or gray menisci.

INTERPRETATION

AMB are compound trace fossils formed by two distinct behaviors of the tracemaking organism based on architectural and surficial morphologies and fill (Fig. 7). Packets are remnants of cells excavated and inhabited by the tracemaker for a short time period; these represent temporary dwelling structures (domichnion). Meniscate backfill within and between packets are sediment deposited during forward movement and excavation; these represent a locomotion structure (repichnion). Short burrow sections containing menisci unbound by packets represent locomotion as the primary behavior.

Cell walls are distinct because they are an excavated surface and likely compacted during occupation by the tracemaker (e.g., Villani et al., 1999). The tracemaker excavated new cells mostly adjacent to previous ones, resulting in a nested appearance. Menisci within the packets are less distinct and discontinuous; however, the concentric pattern of menisci suggests that backfilling was methodical and completed in layers.

Paleoenvironmental significance.? AMB in the Willwood Formation are most abundant in paleosols with red, yellow-brown,

and purple matrix colors; high concentrations of rhizoliths; carbonate nodules; and such redoximorphic features as mottles and Fe-oxide nodules. Many of the mottles are rhizoliths and burrows that underwent preferential gleying—the local reduction and mobilization of Fe and Mn (Kraus and Hasiotis, 2006). Such mottling is due to the presence of organic matter in these structures (Schwertmann, 1993) and occurs within the vadose zone (Vepřaskas, 1999). Likewise, alternating cell wall and menisci colors in AMB suggest differences in the incorporation of organic matter, and possibly sediment compaction, between the two burrow elements.

The association of AMB with rhizoliths suggests that the trace-makers were most abundant and active in rooted A horizons and upper B horizons. AMB commonly crosscut rhizoliths, mottles, and gleyed zones around rhizoliths (Kraus and Hasiotis, 2006), indicating they formed contemporaneously or after the onset of rooting in these paleosols. Complete bioturbation of some well-developed paleosols by AMB in the Willwood Formation is evident as a crescentic fabric in thin section (Kraus, 2002) composed of the remnants of cell walls and menisci (Fig. 6.2). AMB tracemakers were one of the primary agents of pedoturbation in moderately to well-developed paleosols (e.g., Bown and Kraus, 1983).

Paleoecology.—The AMB tracemaker was most likely an active geophile (Hasiotis, 2000) based on comparisons with modern burrowing organisms and ongoing laboratory experiments using active geophiles (Fig. 3, Smith and Hasiotis, in preparation; Counts and Hasiotis, in preparation). Many active geophiles are holometabolous insects that live in soil during the egg, larval, nymph, or adult stages of their lifecycle. Active geophiles may be temporary, periodic, or permanent residents of soils. Temporary and periodic geophiles have one or more active stages in the soil and another outside the soil, whereas permanent geophiles

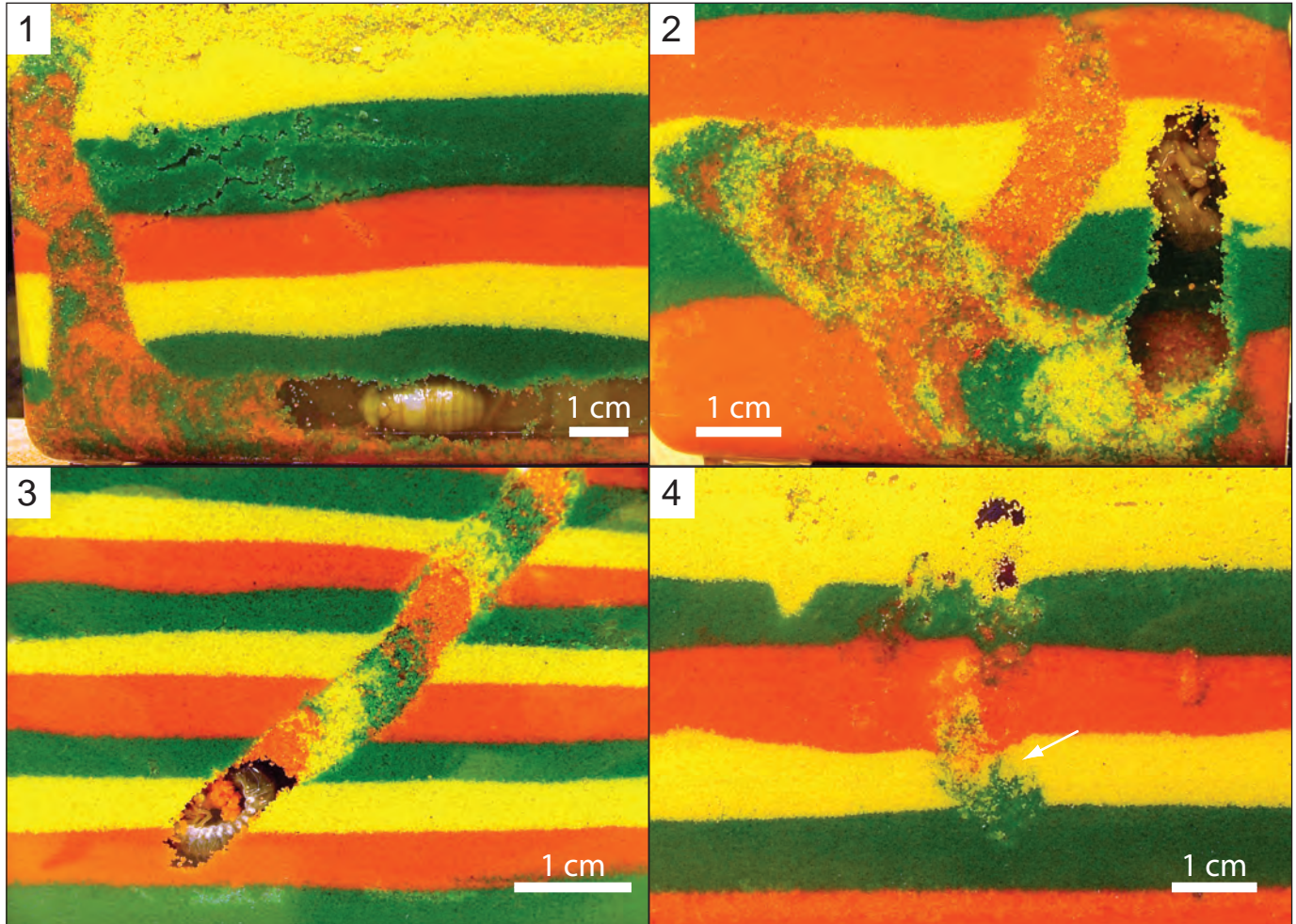


FIGURE 3—Photographs of biogenic sedimentary structures produced by modern soil-dwelling insects in laboratory experiments: 1. Enclosure with colored fine-grained sand in which a cicada burrowed and backfilled from the surface (uppermost yellow layer) to this position after 18 hours. 2. Cicada burrowed to the far left of the enclosure and then back to the right over 4 days. Note the backfill composed of menisci and crosscutting of previous burrow paths. 3. Scarab beetle larva completely enclosed in a cell after burrowing and backfilling approximately 10 cm in 4 hours. 4. Weakly developed meniscate backfilling (arrows) produced by a June beetle in colored fine sand as it burrowed from lowest green to highest yellow sand layer in center of photo.

rarely exit the soil (Wallwork, 1970). To survive the soil environment, geophilic organisms must be specifically adapted to low light levels, elevated CO_2 (hypercarbic), low O_2 levels (hypoxic), and extremes in water availability and soil moisture (Little, 1990; Villani et al., 1999).

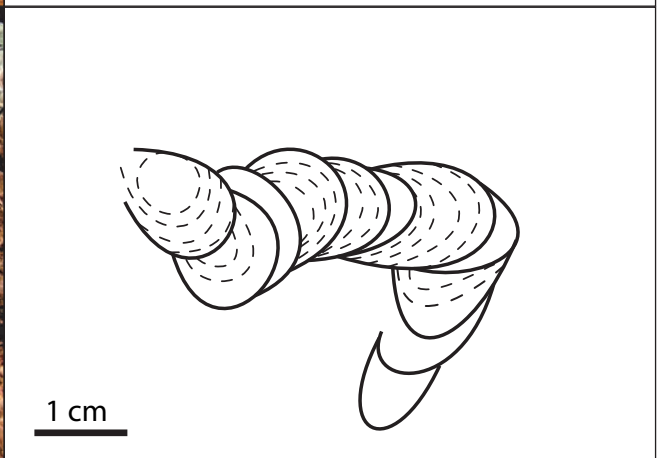
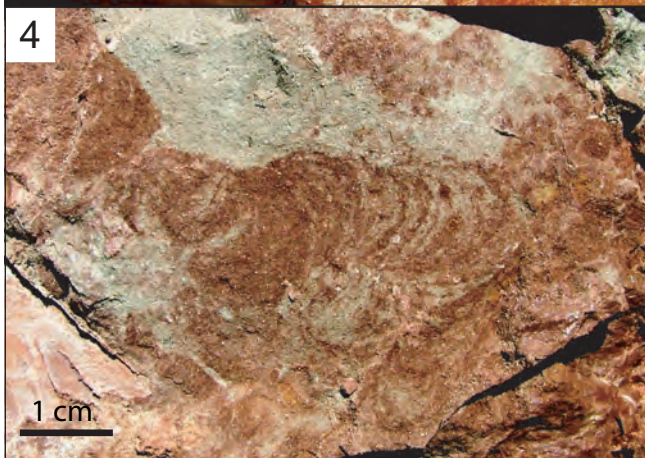
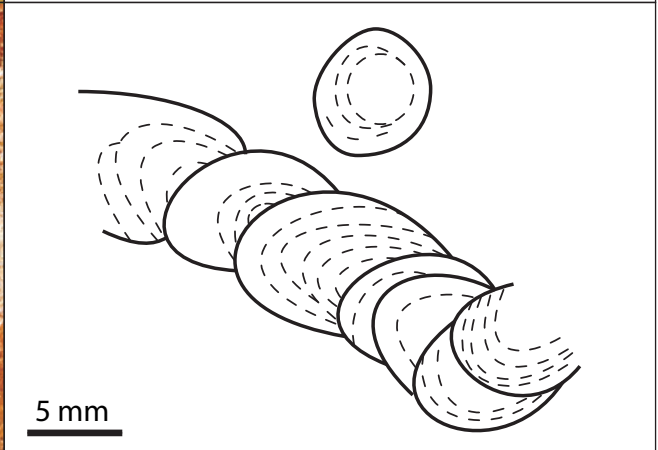
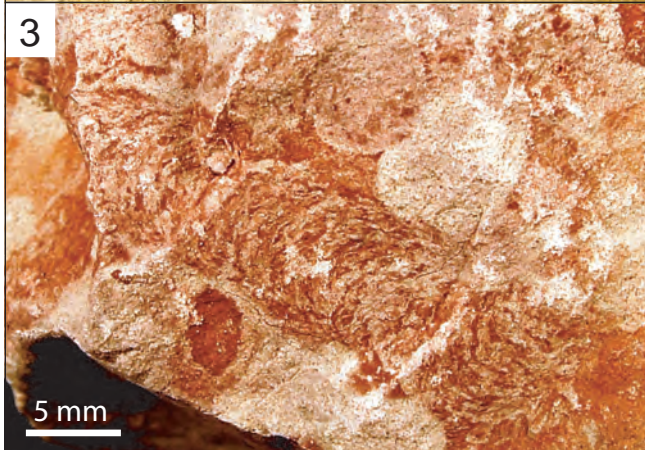
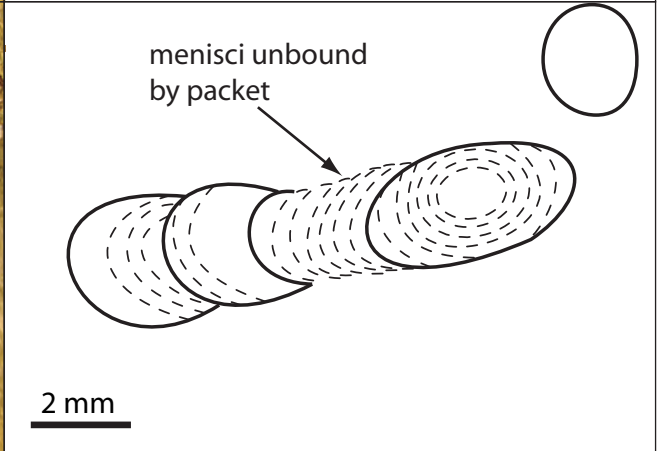
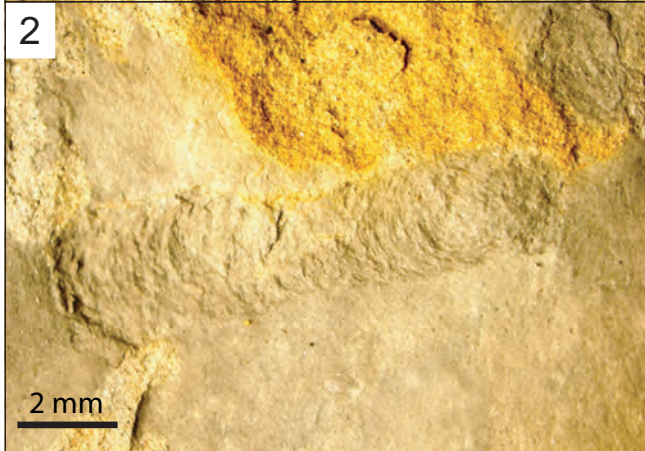
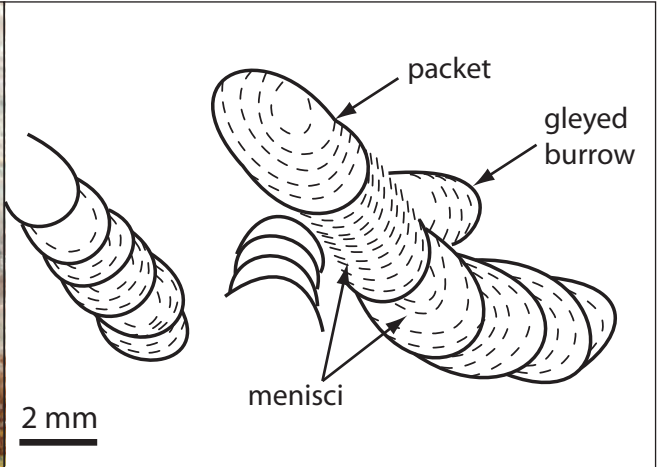
The distribution of burrow diameters based on host-deposit grain size suggests there were at least two populations of AMB-tracemaking organisms in the Willwood Formation (Fig. 5). The distribution may indicate habitat tracking by two different-sized species of tracemakers, with the smaller preferring primarily fine-grained sediments. Alternately, it could be due to varying habitat preferences during different ontogenetic stages of a single tracemaking organism (e.g., nymph and adult or larva and adult). Further study of modern backfilling soil organisms and their burrows is necessary to determine which are most likely to produce AMB-like structures.

POSSIBLE TRACEMAKERS

One or more soil-dwelling insect taxa likely constructed AMB, based on burrow morphology, burrow genesis, depositional environment, and comparisons with modern continental burrowers and ongoing laboratory experiments (Fig. 3). These include burrower bugs (Hemiptera: Cydnidae) and cicada nymphs (Hemiptera: Cicadidae), and less likely adults and larvae of burrowing ground beetles (Coleoptera: Carabidae) and scarab beetles (Coleoptera: Scarabaeidae). These insects excavate and occupy a moving cell that is backfilled as they burrow through the soil.

Burrower bugs.—The earliest body fossils of Cydnidae are from Lower Cretaceous rocks in northern Brazil (Popov and Pinto, 2000), though the oldest hemipteran fossils date from the Permian (Rasnitsyn and Quicke, 2002). Cydnids are oval, brown or black bugs 2 to 10 mm long (Daly et al., 1998). There are more than 750 recognized species with a worldwide distribution,

FIGURE 4—Photographs and line drawings of AMB from paleosols and alluvial deposits in the Willwood Formation. 1. AMB crosscutting a purple-gray depletion zone in a well-developed paleosol. Note the completely gray AMB in the center of the photo indicating multiple generations of burrowing activity, both before and after gleying of depletion zone; Holotype specimen KUMIP 313962. 2. AMB from a claystone unit showing only weak pedogenesis; note the short burrow section of menisci unbound by a packet wall. 3. Large AMB from a fine-grained sandstone. 4. A large AMB specimen from a sandy mudstone.



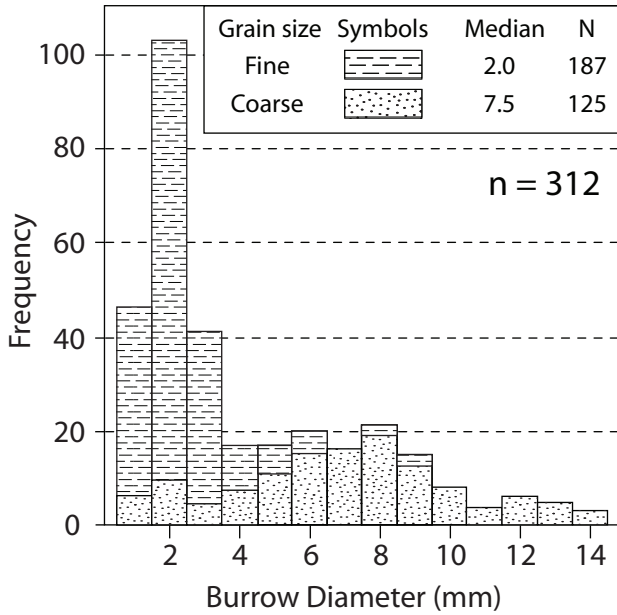


FIGURE 5—Distribution of AMB diameters from paleosols and alluvial deposits of the Willwood Formation. Burrow diameters range from 0.7 to 14 mm with modes at 2.0 and 8.0 mm. Fine-grained paleosols consist of claystone, siltstone, or mudstone whereas coarser grained paleosols are composed of sandy mudstone to fine-grained sandstone.

but burrower bugs are most diverse in the tropics and subtropics (Schuh and Slater, 1995). Extant cydnids are phytophagous, feeding on either roots or foliage, though little is known about their biology (Froeschner and Chapman, 1963; Chapin and Thomas, 2003). Most are fossorial, with both adults and nymphs having several morphological adaptations for burrowing. These include flat and smooth bodies, wedge-shaped heads, scythe-shaped tibiae for digging, and robust hind legs for pushing through the soil (Schuh and Slater, 1995).

While burrowing through sediments, cydnids occupy a moving cell slightly larger than the insect itself (Willis and Roth, 1962, see fig. 4). Cydnids burrow by scraping the sediment loose with the forelegs and pushing it aside with the head. The burrower pushes the loose soil to the rear and fills the cell behind the body. The bug turns over repeatedly in the new cell, packing the loose sediment and forming a smooth interior surface when excavation is complete (Froeschner and Chapman, 1963).

Riis and Esbjerg (1998) examined population variations of a Colombian cydnid with respect to soil depth and seasonal precipitation extremes. Cydnids were most prevalent 10 and 20 cm below the surface in soil A horizons during both the dry and rainy seasons. Optimum moisture conditions for population growth in this cydnid species was between 25% (wilting point) and 45% (field capacity) in a loamy clay (Riis et al., 2005). Willis and Roth (1962) determined the burrowing response of a different cydnid species to various types of soil and moisture levels in laboratory experiments. Burrower bugs did not burrow into a sandy loam with moisture below 7% and drowned when moisture content was above 37%.

Traces produced by extant burrower bugs are good analogs for

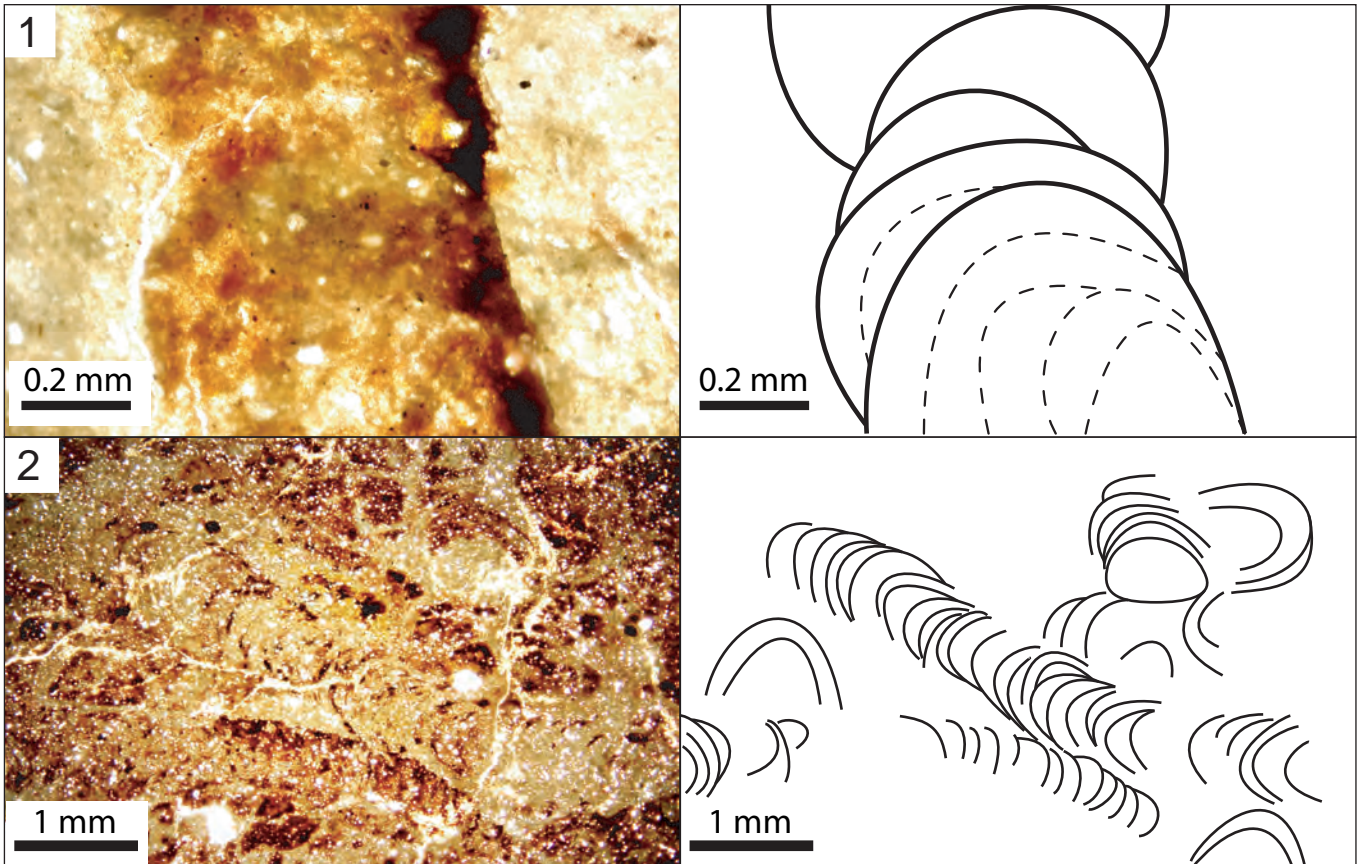
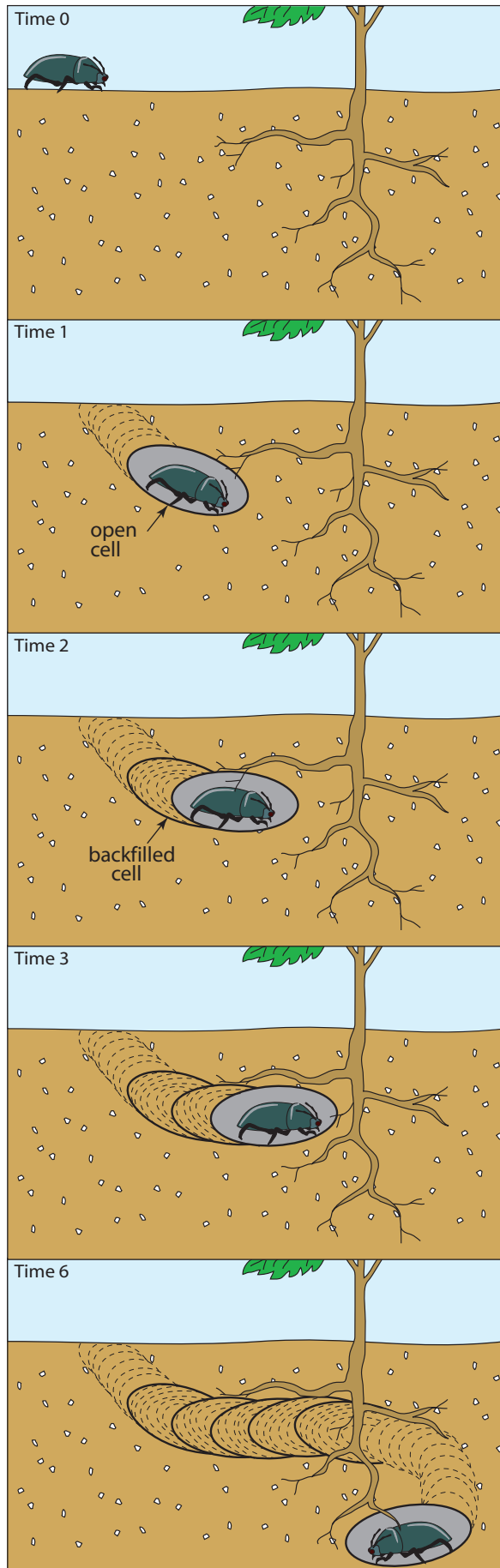


FIGURE 6—Photomicrographs in plane-polarized light with associated line drawings of AMB from well-developed paleosols. 1. Menisci are texturally homogeneous with the surrounding matrix with no evidence of pelleted sediment. 2. Well-developed paleosols commonly show a concentric fabric composed of burrow wall remnants indicating a high degree of bioturbation.



AMB. The burrowing behavior and ecological role of burrower bugs is very similar to that interpreted for the AMB tracemaker.

Cicada nymphs.—The first cicada-like insects are from the Lower Permian (Shcherbakov, 1984). The earliest fossils of true cicadas are from Triassic strata of Russia, France, and Australia; they are also known from Lower Cretaceous strata of Brazil (Lefebvre et al., 1998; Rasnitsyn and Quicke, 2002). The Cicadidae family has approximately 1500 species worldwide, though they are especially abundant and diverse in the tropics and subtropics (Daly et al., 1998). The adult cicada body is 25 to 50 mm long, whereas burrowing nymphs are stouter and wingless. Cicada nymphs lead exclusively subterranean lives from the first to fifth instars, burrowing through soil and feeding on the xylem sap of plant roots (Beamer, 1928). Several years are necessary for maturation, after which the fifth instars emerge from the soil; simultaneously and in a single generation in some species (Williams and Simon, 1995).

Depth of burrowing by cicada nymphs is likely to vary depending on stage of instar development and species. The few studies reporting cicada nymph burrow depths range from 10 to up to 100 cm below the soil surface, though nymphs are most abundant at depths between 20 and 50 cm (e.g., Hugie and Passey, 1963; O'Geen et al., 2002). Soil moisture preferences for cicada nymphs are unknown. Strandine (1940) found that soil moisture, however, was the most significant factor determining the size of adult cicada populations in three northern Illinois forests. The forest soil with the lowest average moisture content (13.5%) had nearly four times the adult cicada population of the forest with the wettest soil conditions (26%), suggesting that the cicada nymphs preferred better drained soils. Passively filled vertical burrows in some paleosols may be emergence shafts constructed by adult cicadas (Retallack, 1997). Backfilled burrows from Pleistocene and Holocene paleosols have been attributed to the subterranean movement of cicada nymphs (O'Geen and Busacca, 2001; Gregory et al., 2004; Jacobs and Mason, 2004); however, few other backfilled burrows have been recognized as such.

Ongoing experiments by Smith and Hasiotis (in preparation) demonstrate that cicada nymphs produce distinctly meniscate burrows very similar to AMB (Fig. 3.1, 3.2). In addition, the behaviors and ecological role of cicadas is similar to that interpreted for the AMB tracemaker.

Beetles.—The oldest coleopterans are from Early Permian deposits in central Europe (Ponomarenko, 1995). Carabidae and Scarabaeidae appear first in Middle Triassic Eurasian, African, and North American strata (Rasnitsyn and Quicke, 2002). The Coleoptera constitute the largest insect order with over 300,000 extant species on every continent but Antarctica (Daly et al., 1998). Though their ecologic and taxonomic diversity is enormous, all beetles undergo holometabolous (complete) metamorphosis through larval, pupal, and mature adult stages. Larval and adult beetles may have different habitat preferences and behaviors during different life stages and, therefore, different trace fossils.

Ground and scarab beetles construct open shelter burrows, brood chambers and nests, and dwellings (e.g., Chamberlain, 1975; Ratcliffe and Fagerstrom, 1980; Evans, 1991). Some ground beetles construct burrows for concealment up to 70 cm below the soil surface; burrows are less than 30 cm deep for most species (Evans, 1991). Some scarab beetles burrow to depths in

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FIGURE 7—Hypothetical construction of AMB by an insect tracemaker. Time 1. Tracemaker produces meniscate backfill as it moves through the soil. At depth, the tracemaker stops forward movement and constructs a cell that it inhabits for a time. Time 2. Tracemaker constructs an adjacent cell and backfills the older cell. Time 3–6. Tracemaker constructs a series of closely spaced cells, but also burrows for short distances between cells, creating burrow lengths composed of only meniscate backfill.

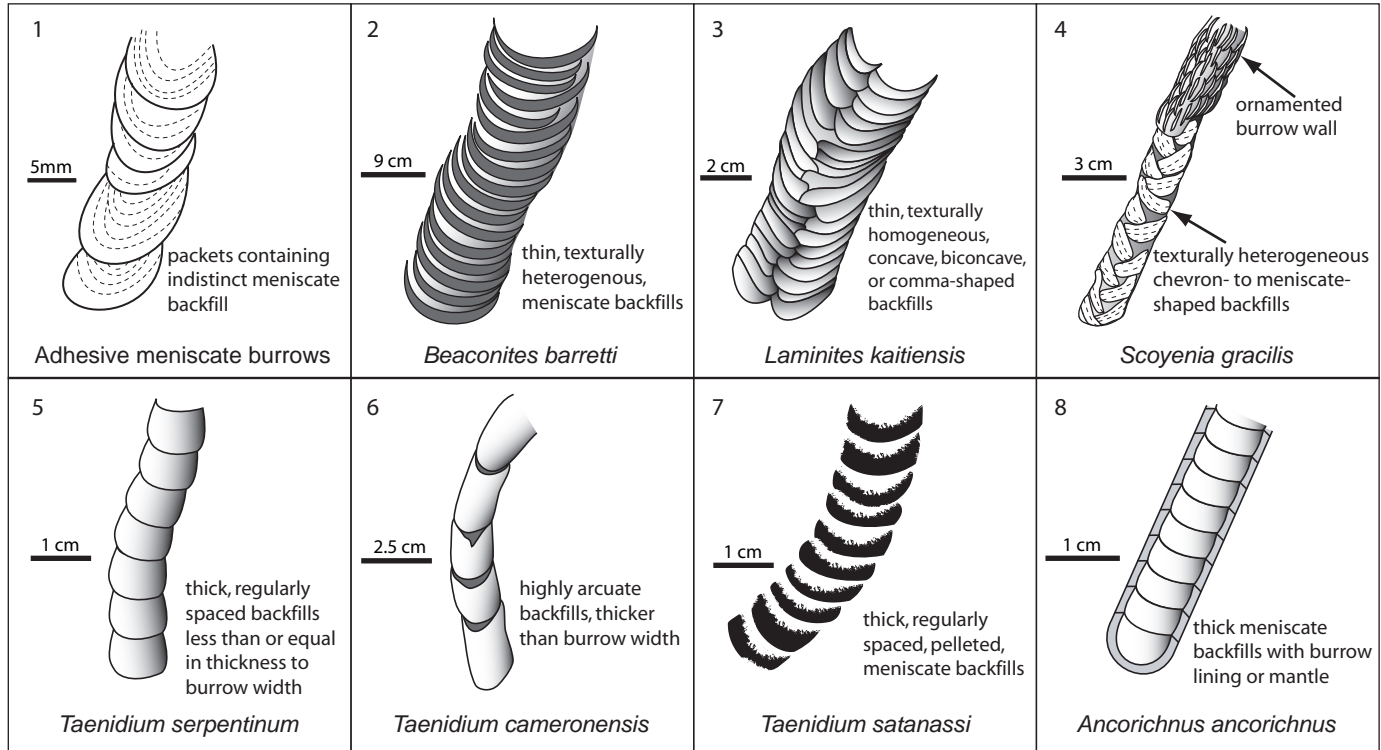


FIGURE 8—Comparison of AMB to similar backfilled ichnofossils. 1. AMB traced from Willwood Formation specimen. 2. *Beaconites barretti* traced from Gevers et al., 1971 (plate 18, fig. 2). 3. *Laminites kaitiensis* traced from Ghent and Henderson, 1966 (plate 1). 4. *Scoyenia gracilis* traced from Frey et al., 1984 (fig. 4a). 5. *Taenidium serpentinum* traced from D'Alessandro and Bromley, 1987 (fig. 7). 6. *T. cameronensis* traced from Brady, 1947 (plate 69, fig. 1). 7. *T. satanassi* traced from D'Alessandro and Bromley, 1987 (fig. 8b). 8. *Ancorichnus ancorichnus* traced from Bromley, 1996 (fig. 8.3).

excess of 1 m and may backfill portions of their burrows that lead to brood chambers (Brussaard and Runia, 1984; Hasiotis et al., 1993b).

Soil-moisture conditions influence strongly the survival of coleopteran larvae and their development to adulthood, though moisture tolerances between individual species, and between juveniles and adults, are likely highly variable. Larvae of five species of dung beetles, for example, reached adulthood in sandy loams with 4 to 12% moisture, while survivorship decreased dramatically in sediments with moisture levels over 16% (Brussaard and Slager, 1986; Osberg et al., 1994; Sowig, 1995). Japanese beetles and some chaffer beetles oviposit in moist to wet soils (~12–25.5% in silty loam) to prevent desiccation (Cherry et al., 1990; Allsopp et al., 1992), however, adult beetles tolerate moisture levels as low as 4% (Potter, 1983).

Some backfilled ichnofossils have been attributed to beetles and their larvae (Bown and Kraus, 1983; Hasiotis et al., 1993b; Hasiotis and Demko, 1996; Hasiotis, 2004). Ongoing experiments demonstrate that scarab beetle larvae can produce meniscate burrows (Fig. 3.3 and 3.4; Counts and Hasiotis, in preparation). The burrows are similar to those produced by cicadas in the laboratory (Smith and Hasiotis, in preparation), however, there are subtle differences in the packing and alignment of packets that distinctly distinguish beetle larvae backfilled burrows from those produced by cicadas.

Environmental and hydrologic implications.—If AMB were produced by burrowing insects, they indicate periods of subaerial exposure and can be used to approximate the position of the ancient ground surface in some depositional settings. Burrower bugs, cicada nymphs, and beetle larvae are most abundant 10 to 50 cm below the soil surface. The uniformity of depth ranges of these potential tracemakers makes sense given that most feed on organic matter or roots within A and upper B soil horizons. In addition, if AMB tracemakers had soil moisture tolerances similar

to those of the modern burrowing insects, their presence suggest ancient-soil moisture conditions at or below field capacity depending on soil type—generally between 5% and 45% soil moisture for the extant insects reviewed here. Soil-moisture levels reported in the previous sections under which burrowing takes place, however, were not measured with the same technique or under similar conditions. The range of soil-moisture levels demonstrate that this type of burrowing behavior takes place in soils with moisture levels above the wilting point (dry) and at or below field capacity (wet to saturated). Sediments with soil-moisture levels sustained above or below these levels do not support these types of burrowing organisms.

COMPARISON WITH OTHER BACKFILLED BURROWS

The principal diagnostic criteria for most backfilled ichnogenera are the shape of the backfill, the burrow margin, and presence or absence of branching (e.g., D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994; Bromley, 1996). Ichnofossils in this comparison include unbranched, distinctly backfilled cylindrical burrows that generally lack an obvious lining. Ichnogenera meeting these criteria include *Beaconites*, *Laminites*, *Scoyenia*, *Taenidium*, and *Ancorichnus*. AMB are distinguished primarily from similar backfilled trace fossils by having backfills organized in a nested series of discrete packets containing thin, subparallel menisci.

Beaconites barretti Bradshaw, 1981.—Highly sinuous, predominantly horizontal to subvertical burrows, 5 to 450 mm in diameter, with thin, hemispherical to highly arcuate backfills (Fig. 8.2). The tightly spaced backfills are typically composed of alternating fine- and coarse-grained sediment (Bradshaw, 1981). Backfills may be slightly offset from one another (shuffled) and merge laterally to form a crenulate burrow wall. Nearly all examples are reported from continental deposits (Keighley and Pickerill, 1994). Of the backfilled burrows analyzed in our study, the morphology

and depositional setting of Beaconites are most similar to those of AMB; however, backfills in Beaconites are thick, distinctive, and not overtly organized into discrete packets.

Laminites kaitiensis Ghent and Henderson, 1966.—Unlined, unbranched, gently meandering burrows composed of thin, 1.5 to 3 mm thick, texturally homogeneous backfills that are successively light and dark in color (Ghent and Henderson, 1966). Backfills may be concave, biconcave (bow-shaped), or comma-shaped, with the thicker part of the backfills touching or overlapping along the medial axis of the burrow (Fig. 8.3). All specimens are from marine depositional environments. *L. kaitiensis* is distinct from AMB by having relatively thick backfills that bow or meet in the medial axis of the burrow and that are not organized into packets.

Scoyenia gracilis White, 1929.—Straight to curved, unbranched, horizontal to variably oriented burrows with chevron-shaped to arcuate backfill of homogeneous or heterogeneous lithologies (Fig. 8.4; White, 1929; Bromley and Asgaard, 1979; Frey et al., 1984). Burrows may be unlined or with thin clay linings, and burrow surfaces are ornamented with a convex, mostly parallel, longitudinal striae (Frey et al., 1984; Retallack, 2001). AMB does not contain any of the features characteristic of *S. gracilis*.

Taenidium Heer, 1877.—Unlined, unbranched, straight to sinuous burrows composed of thick backfills symmetrical about the axis of the burrow (D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994). Backfill texture may be heterogeneous, homogeneous, or pelleted, depending on the *Taenidium* ichnospecies. D'Alessandro and Bromley (1987) consider valid three ichnospecies based on differences in backfill morphology. *T. serpentinum* Heer, 1877 have regularly spaced, texturally homogeneous, meniscate backfills with thicknesses that approach the diameter of the burrow (Fig. 8.5). Backfill in *T. cameronensis* (Brady, 1947) are deeply arcuate and much thicker than burrow width, but are otherwise similar to *T. serpentinum* (Fig. 8.6). *T. satanassi* D'Alessandro and Bromley, 1987 have backfills that are thinner than the burrow diameter and composed of alternating coarse-grained and pelleted fine-grained sediments (Fig. 8.7). These three ichnospecies have only been described from marine deposits (Decourten, 1978; Keighley and Pickerill, 1994). Thick, regularly spaced backfills organized symmetrically about the axis of the burrow, and heterogeneous or pelleted fill in some *Taenidium* ichnospecies, distinguish *Taenidium* from AMB.

Ancorichnus ancorichnus Heinberg, 1974.—Straight to curved, predominantly horizontal burrows containing thick backfill and surrounded by a mantle (Heinberg, 1974; Frey et al., 1984; Heinberg and Birkelund, 1984). The mantle does not represent a constructed lining but was instead produced by the reorientation of surrounding mica grains at an angle to the burrow wall (Frey et al., 1984). AMB differs from *A. ancorichnus* (Fig. 8.8) by lacking thick backfills and a distinct mantle composed of oriented sediments along the burrow wall.

DISCUSSION

Bown and Kraus (1983) postulated originally that AMB were produced by such deposit-ingesting organisms as oligochaete worms; a concept reiterated recently by Genise et al. (2004). The burrowing activities of extant oligochaetes are well studied for the important role earthworms play in soil churning and stable soil aggregate development (e.g., Darwin, 1881; Marinissen and Dexter, 1990; Blanchart et al., 1993; Graham et al., 1995). Earthworms ingest soil to feed on seeds, decaying plant material, the eggs or larvae of other organisms, and living or dead microorganisms. Undigested soil and fecal matter are deposited as a cast or pellet, either on the ground surface around the mouth of the burrow, as thin burrow linings, or loosely deposited in the open burrow and burrow chambers (Lee and Foster, 1991). It is likely that any structure produced by an oligochaete worm has casts or pellets in some portion of the burrow. In addition, most extant

earthworm burrows contain 1- to 3-mm-thick linings composed of oriented clay particles, humic material, calcium carbonate or iron oxides, depending on the food available (Lee and Foster, 1991). A trace fossil composed of pellets, *Edaphichnium*, is attributed to oligochaete worms and occurs commonly with AMB in Willwood Formation paleosols (Bown and Kraus, 1983). Burrow linings and pelleted backfill are not found in any AMB specimens; thus, earthworms and other deposit-feeding organisms are unlikely candidate tracemakers.

Meniscate burrows in paleosols have been interpreted as pedogenically overprinted, pre-existing trace fossils produced during earlier, subaqueous phases of floodplain deposition or lacustrine conditions (Buatois and Mángano, 2004; Genise et al., 2004). AMB, however, are most common in strongly developed paleosols and in close association with rhizoliths, which are commonly crosscut by AMB. Intense burrowing by soil fauna and plant rooting in these soils likely obliterated pre-existing traces constructed before the onset of pedogenesis. AMB observed in Willwood Formation paleosols, therefore, formed during, and were a primary agent of, the paleopedogenesis of these deposits. In addition, ongoing laboratory and field experiments indicate that burrowing insects (see Fig. 3) produce meniscate burrows during subaerial conditions (Counts and Hasiotis, in preparation; Smith and Hasiotis, in preparation). No one has demonstrated that larvae, nymphs, or adults of insects and other arthropods produce backfilled burrows in freshwater, subaqueous settings in the continental realm. The presence of AMB, therefore, does not suggest subaqueous settings in light of clear evidence for subaerial conditions in the Willwood Formation. Previous interpretations that AMB and other meniscate burrows indicate subaqueous conditions in lacustrine and floodplain settings must be reassessed.

AMB in outcrop and core suggest periods of subaerial exposure followed by pedogenic modification under moderately to well-drained soil conditions, or during periods of better drainage in imperfectly drained soils. AMB appear exclusively in paleosols (Hasiotis et al., 1993b; Hasiotis and Dubiel, 1994; Hasiotis and Demko, 1996; Hasiotis, 2002; Hasiotis, 2004), whereas *Laminates*, *Taenidium*, and *Ancorichnus* are reported mostly from marine strata. AMB, thus, can be used to differentiate marine and lacustrine settings from floodplain settings, as well as deposits modified by pedogenesis.

SYSTEMATIC ICNOLOGY

NAKTODEMASIS ichnogenus nov.

Diagnosis.—Sinuous, variably oriented, unbranched, and unlined burrows composed of a nested series of distinct, ellipsoid-shaped, asymmetrical packets. Packets typically are asymmetrically oriented around the axis of the burrow and offset from one another. The length-to-width ratio of each packet depends on the spacing between individual packets; some packets have a ratio much greater than 1; others have a ratio much less than 1. Packets contain thin, indistinct, and tightly spaced meniscate fill. Menisci are subparallel to the bounding packet, typically discontinuous, and difficult to trace. Short burrow sections may be composed only of unbound menisci. Menisci in thin section are unpelleted and texturally homogeneous with each other and the surrounding strata. Burrow walls exposed in the matrix are extremely rare and are mostly smooth or with slight annulae when present that correspond with the ellipsoidal packets.

Etymology.—Greek, *naktos* pressed; *dema*, bundles; *asis*, alluvium.

Type species.—*Naktodemasis bowni* isp. nov., type and only known ichnospecies.

Description.—The principal diagnostic criteria for most backfilled ichnogenes are the shape of the backfill material, the burrow margin, and the presence or absence of branching (e.g., D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994; Bromley, 1996). *Naktodemasis* is distinguished from similar backfilled trace fossils by having backfilled material organized in a nested series of discrete packets—the primary morphological characteristic of the ichnogenus. The thin, tightly spaced and distinct hemispherical

backfill of Beaconites (Fig. 8.2) superficially resemble those of Naktodemasis. Backfills in Beaconites, however, are not organized into packets and are composed commonly of alternating fine- and coarse-grained material (Bradshaw, 1981). Laminites (Fig. 8.3) differs from Naktodemasis by having relatively thick, biconcave to comma-shaped backfills that bow or meet at the medial axis of the burrow (Ghent and Henderson, 1966). Scoyenia (Fig. 8.4) contain chevron-shaped to arcuate backfill of alternating lithologies, thin to thick clay linings, and burrow surfaces ornamented by convex, mostly parallel, longitudinal striae (White, 1929; Frey et al., 1984); features that are absent in Naktodemasis. Taenidium (Fig. 8.5–8.7) is distinguished from Naktodemasis by thick backfill segments that tend to be symmetrical about the axis of the burrow and the presence of heterogeneous or pelleted fill in some Taenidium ichnospecies (D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994). Naktodemasis differs from Ancorichnus (Fig. 8.8) by lacking thick backfill segments and a distinct mantle composed of oriented sediments along the burrow wall (Heinberg, 1974; Frey et al., 1984; Heinberg and Birkelund, 1984).

Remarks.—Naktodemasis bowni is the only recognized ichnospecies at present, though morphological variants of the type are conceivable. Naktodemasis with packets containing thicker and more distinct menisci, or packets with a lining or mantle, could be assigned as additional ichnospecies.

NAKTODEMESIS BOWNI ichnospecies nov.

Figures 4, 6

Ichnofossil Type 7, BOWN AND KRAUS, 1983, p. 112, fig. 7e, 7f, p. 116, fig. 8a, 8b.

Adhesive meniscate burrows (AMB), HASIOTIS AND DUBIEL, 1994, p. 314, fig. 2c, p. 315, fig. 3a; HASIOTIS AND DEMKO, 1996, p. 362, fig. 6a; HASIOTIS, 2002, p. 60, figs. a–e; HASIOTIS, 2004, p. 192, fig. 3a, 3b.

non Muensteria isp., BRACKEN AND PICARD, 1984, p. 482, fig. 9.

non Taenidium serpentinum, SAVRDA et al., 2000, p. 230, fig. 2.

Crescentic burrows, KRAUS, 2002, p. 504, fig. 6d.

Diagnosis.—Only known ichnospecies; same as for genotype.

Etymology.—For Dr. Tom Bown, who, along with Dr. Mary Kraus, described the first specimens of the new ichnogenus and for his outstanding contributions to the science of continental ichnology.

Types.—Holotype, KUIMP 313962 (Fig. 4.1)

Type stratum.—Lower Paleogene Willwood Formation.

Type locality.—U. S. Geological Survey (Denver) fossil locality D-1204 (44°14'N, 108°10'W), southwest of Greybull, Bighorn Basin, Wyoming. Nearly ubiquitous in red, purple, and yellow-brown paleosols throughout the Willwood Formation.

Repository.—Division of Invertebrate Paleontology, Museum of Natural History and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, United States of America.

Description.—Naktodemasis bowni are present in groups of tens to thousands of individuals in weakly, moderately, and well-developed Willwood Formation paleosols. Burrows are from 1 to more than 15 cm long, although highly variable orientations obscure true burrow lengths. Transverse cross sections are circular to elliptical and range from 0.7 to 14.0 mm in diameter. Red, yellow-brown, purple, or gray commonly highlight packets and menisci.

Remarks.—N. bowni are interpreted as compound trace fossils formed by two distinct behaviors: packets representing the remnants of cells excavated and inhabited by the tracemaker for a short period of time and meniscate backfill interpreted as sediment deposited during forward movement and excavation of adjacent cells. Association of N. bowni with rhizoliths suggests the tracemakers were most abundant and active in rooted A horizons and upper B horizons of the soil profile. N. bowni were constructed most likely by such active geophilic organisms as burrower bugs (Hemiptera: Cydnidae), cicada nymphs (Hemiptera: Cicadae), and less likely by scarabaeid (Coleoptera: Scarabaeidae) or carabid beetles (Coleoptera: Carabidae).

CONCLUSION

Naktodemasis bowni are one of the most widely distributed trace fossils in Mesozoic and Cenozoic continental deposits and are nearly ubiquitous in Paleogene paleosols throughout the Rocky Mountain region (Zonneveld, personal commun.). N. bowni is distinguished from similar backfilled trace fossils by having indistinct, meniscate backfills organized in a nested series of

discrete packets. We interpret N. bowni as the intermittent locomotion and dwelling traces of burrowing insects based on the detailed study of the architectural and surficial burrow morphology and burrow fill. Burrower bugs (Hemiptera: Cydnidae) and cicada nymphs (Hemiptera: Cicadae) are the most probable trace-makers of N. bowni in the Willwood Formation. These extant insects typically burrow in A and upper B horizons of soils with moisture contents that range from above the wilting point at or below field capacity. The presence of N. bowni, thus, can help produce a clearer, more thorough interpretation of ancient drainage conditions. Information about the degree of ancient soil wetness or moisture is important for understanding past climate conditions and for reconstructing terrestrial paleolandscapes.

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