ICHNOFOSSILS OF THE PALEOGENE WILLWOOD FORMATION AND THE PALEOCENE-EOCENE THERMAL MAXIMUM (PETM): RESPONSE OF AN ANCIENT SOIL ECOSYSTEM TO TRANSIENT GLOBAL WARMING

by

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Submitted to the Department of Geology and the Faculty of the Graduate School of the University of Kansas In partial fulfillment of the requirements for the degree of Doctor of Philosophy

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ABSTRACT

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This research combines paleopedological, paleontological, neoichnological, and ichnological methods to understand better the paleoenvironmental, paleoecological, and paleoclimatic significance of the trace fossils of soil-dwelling organisms preserved in paleosols. Such ichnofossils are well-preserved and abundant in the continental deposits and are important *in situ* indicators of paleohydrologic regime, degree of pedogenesis, paleoecology, and paleoclimatic setting during the time of their formation.

Naktodemasis bowni, a new ichnogenus and ichnospecies erected for adhesive meniscate burrows common in paleosols, were likely produced by burrowing insects based on their morphology and ichnopedologic associations. These burrows do not represent subaqueous, sediment-ingesting organisms as has been previously suggested.

Neoichnologic experiments examining the traces and burrowing behaviors of cicada nymphs (Hemiptera: Cicadidae) demonstrate that some burrowing hemipterans produce distinct backfilled burrows in modern soils identical to *N. bowni*. Such backfilled burrows indicate periods of subaerial exposure associated with pedogenic modification and can be used to differentiate alluvial paleoenvironments from marine and lacustrine paleoenvironments.

Freshwater crayfish burrows in paleosols of the Willwood Formation, Bighorn Basin, Wyoming, illustrate the important role that burrowing organisms played in initiating and promoting pedogenic development. Crayfish burrows and other ichnofossils in the Willwood Formation show changes in their distribution, increased abundance and diversity, and reduced size through a transient period of global warming known as the Paleocene-Eocene Thermal

Maximum (PETM). Significant changes in the distribution and abundance likely indicate that soil biotic communities responded to improvements in drainage conditions coincident with the global warming.

Burrow diameters of the most abundant ichnofossils are 30–46% smaller within the PETM interval, suggesting that the tracemakers were smaller bodied. Smaller tracemaker body sizes may have been an adaptive response to higher temperatures, lower soil moisture, or reduced nutritional values in high CO_2 vegetation. Similar body size changes in extant insect populations may be used as a new biomonitoring tool to gauge the impact of modern anthropogenic-increases in greenhouse gases and surface temperatures. This research demonstrates for the first time that ancient burrowing organisms in the continental realm were not buffered by soil environments and responded to climate perturbations in ways that are detectable in their ichnofossil record.

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Tiger got to hunt, bird got to fly;

Man got to sit and wonder, 'Why, why, why?'

Tiger got to sleep, bird got to land;

Man got to tell himself he understand.

~Kurt Vonnegut, *Cat's Cradle*, 1963

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CHAPTER 1. INTRODUCTION

This dissertation comprises five separate papers concerning the use of continental ichnofossils to interpret paleoenvironments and paleoclimatic conditions, as well as the response of continental tracemaking organisms to a well-documented climate change in the early Eocene. Abundant and well-preserved trace fossils of terrestrial and freshwater organisms are remarkably common in continental deposits (e.g., Chamberlain, 1974; Ratcliffe and Fagerstrom, 1980; Hasiotis and Bown, 1992; Hasiotis and Demko, 1996; Buatois et al., 1998; Hasiotis, 2002; 2003; 2004; Hembree and Hasiotis, 2007). Continental ichnofossils are increasingly used as surrogates for body fossils because, in many cases, they do not differ significantly from the burrows and nests of extant species (e.g., Bown and Kraus, 1983; Hasiotis et al., 1993; Hasiotis and Mitchell, 1993; Genise and Bown, 1994; Thackray, 1994; Hasiotis, 2002; 2003). Such ichnofossils record the approximate body size, habitat preference, and behavioral responses of tracemaking organisms to physical, chemical, and biological conditions in the ancient environment (e.g., Voorhies, 1975; Ekdale et al., 1984; Bromley, 1996; Hasiotis, 2002).

Trace fossils from marine deposits show significant decreases in ichnodiversity, burrowing density, burrow sizes, ichnofossil tiering, and depth of bioturbation during episodes of inferred environmental stress and subsequent mass extinction events (e.g., Pruss and Bottjer, 2004; Barras and Twitchett, 2007; Morrow and Hasiotis, 2007). Few studies have examined the response of continental ichnofossils to paleoclimatic change or mass extinction events (Wilf and Labandeira, 1999; Olsen et al., 2002). Terrestrial and freshwater invertebrates, in particular, are sensitive to changes in soil moisture and temperature because they must avoid desiccation and overheating, extreme highs and lows in soil moisture levels, and excess carbon dioxide and hypoxic soil conditions (Wallwork, 1970). Ichnofossils of soil-dwelling invertebrates are, therefore, important *in situ* indicators of the paleohydrologic regime, degree of pedogenesis, paleoecology, and paleoclimatic setting during the time of their formation (Hasiotis, 2007).

Chapter two and three illustrate how detailed ichnotaxonomy of continental ichnofossils and neoichnological experiments of extant tracemakers are critical to understanding the paleoenvironmental and paleoclimatic implications of continental trace fossils. Chapters four, five, and six describe stratigraphic changes in the distribution, abundance, and diversity of ichnofossils as proxies for soil-dwelling biota in strata of the Willwood Formation, Bighorn Basin, Wyoming, deposited before, during, and after a transient, though severe, global-warming event known as the Paleocene-Eocene Thermal Maximum (PETM).

Chapter two establishes a new ichnogenus and ichnospecies for adhesive meniscate burrows commonly reported from paleosols and alluvial strata of the Willwood Formation and other continental deposits. The detailed morphology, inferred behaviors and paleoenvironments, and possible tracemakers of these ichnofossils are discussed to demonstrate their distinctness from other backfilled ichnotaxa.

Chapter three describes the traces and burrowing behaviors of nymphs of the prairie cicada *Melampsalta calliope* (Hemiptera; Homoptera; Cicadidae) produced in neoichnological experiments under controlled laboratory conditions. The paper discusses the preservation potential of cicada nymph and adult traces, and their uses as indicators of paleoenvironment, paleohydrologic regime, and biodiversity in ancient soils that rarely preserve the body fossils of insects and other soil arthropods.

Chapter four describes ancient freshwater crayfish burrows and their role as agents of soil formation in the Willwood Formation at Polecat Bench, Bighorn Basin, Wyoming. The relationship of crayfish burrows to surrounding paleosols is discussed, as well as how changes in the vertical distribution and abundance of the burrows can be used to interpret changing paleohydrologic and paleoclimatic conditions on the Willwood floodplain during the PETM.

Chapter five describes how ichnocoenoses in alluvial deposits of the Willwood Formation at Polecat Bench show vertical changes in their distribution, abundance, and ichnodiversity during the PETM. The paper discusses how these changes likely indicate that soil biotic communities responded to significant improvements in drainage conditions coincident with global warming. These conclusions support other studies that indicate that the Bighorn Basin underwent transient drying during the PETM.

Chapter six describes how individual Willwood trace fossils at Polecat Bench show changes in their distribution, increased abundance, and significant size reductions during the PETM. The paper discusses how such inferred paleoenvironmental conditions as high temperatures, lower soil moisture, or reduced nutritional values in high CO_2 vegetation may have induced the changes observed in above- and below-ground soil biota.

The combined results of the included papers demonstrate that trace fossils preserved in continental deposits are valuable tools for the interpretation of paleoenvironments and paleoclimate change in the distant past. These papers demonstrate for the first time that ancient burrowing organisms in the continental realm were not buffered by their soil environments and responded to climate perturbations in ways that are detectable in their ichnofossil record.

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CHAPTER 2. NAKTODEMASIS BOWNI: NEW ICHNOGENUS AND ICHNOSPECIES FOR ADHESIVE MENISCATE BURROWS (AMB), AND PALEOENVIRONMENTAL IMPLICATIONS, PALEOGENE WILLWOOD FORMATION, BIGHORN BASIN, WYOMING

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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, 1993;

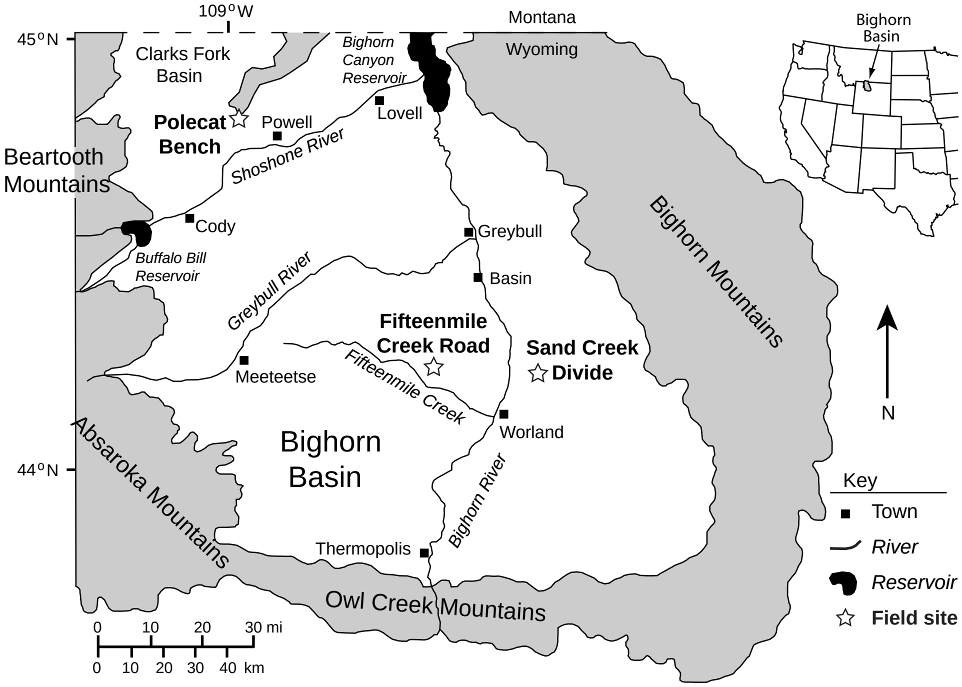

Figure 1. Map of the Bighorn Basin, Wyoming, showing mountain ranges surrounding the basin and the Sand Creek Divide, Polecat Bench, and Fifteenmile Creek study areas. Modified from Bown and Kraus (1981).

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, 1993; 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 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

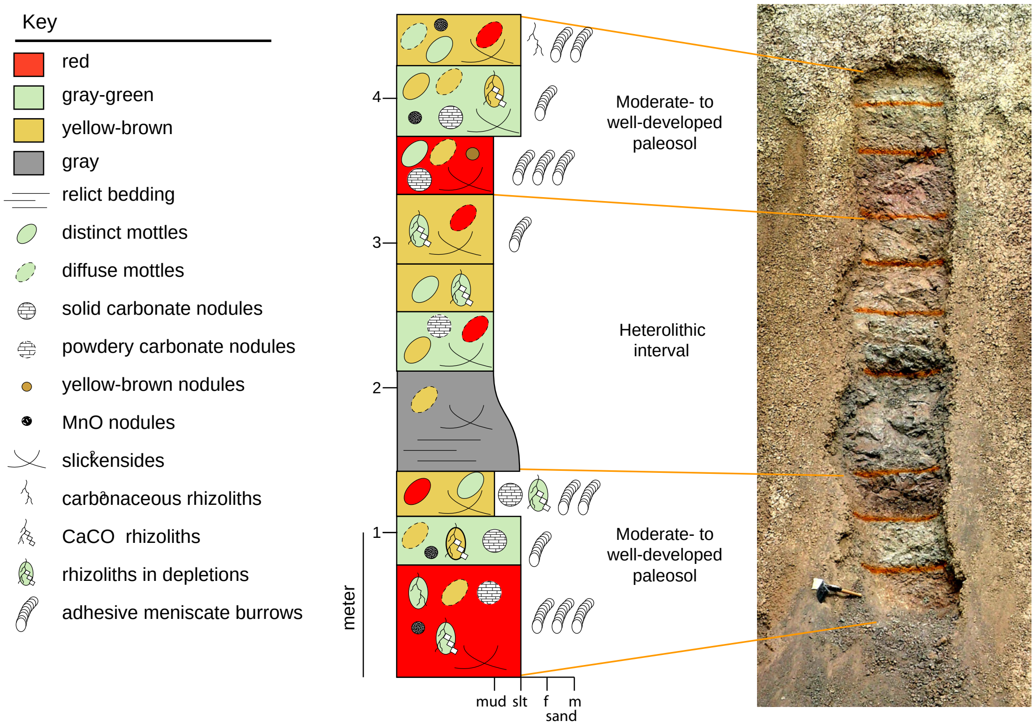

Figure 2. Measured section through several paleosols in the Sand Creek Divide field site showing textural features of the paleosols and the occurrence of AMB.

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).

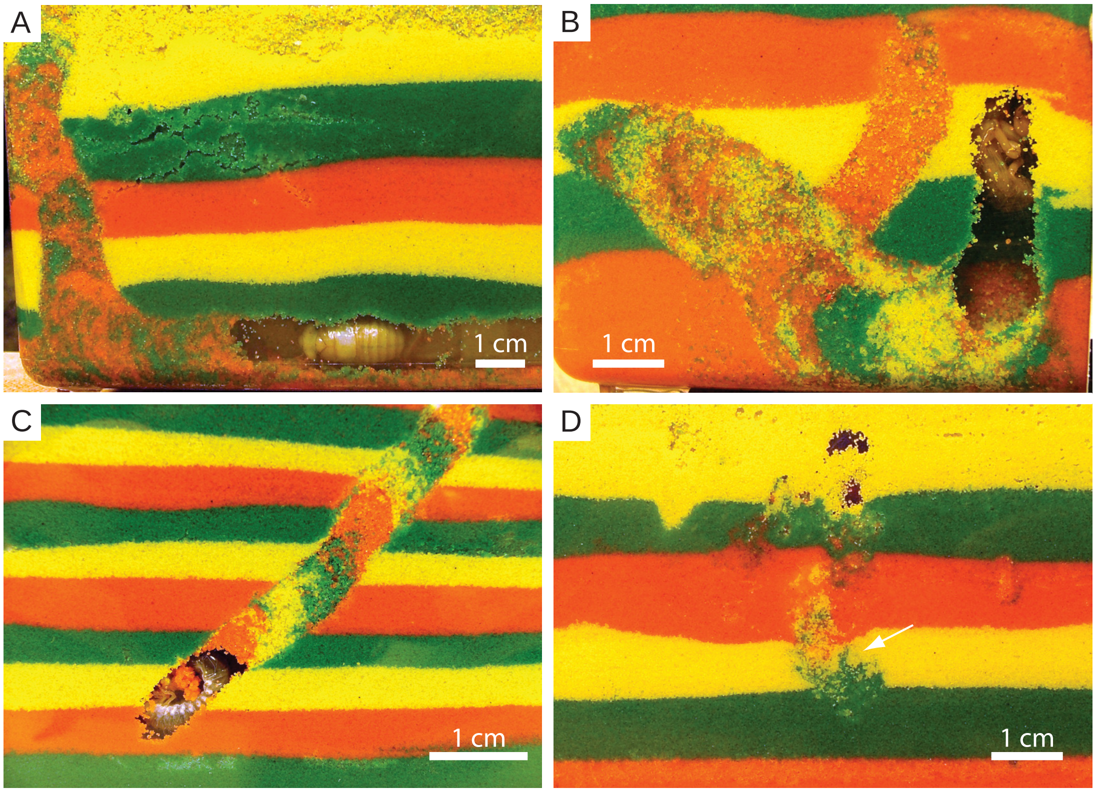

Figure 3. Photographs of biogenic sedimentary structures produced by modern soil-dwelling insects in laboratory experiments: **A)** Enclosure with colored fine-grained sand in which a cicada burrowed and backfilled from the surface (uppermost yellow layer) to this position after 18 hours. **B)** Cicada 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. **C)** Scarab beetle larva completely enclosed in a cell after burrowing and backfilling approximately 10 cm in 4 hours. **D)** 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.

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 typically 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. 4C-D). 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. Burrows are 0.7 to 14.0 mm in diameter and have circular to elliptical cross sections. 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

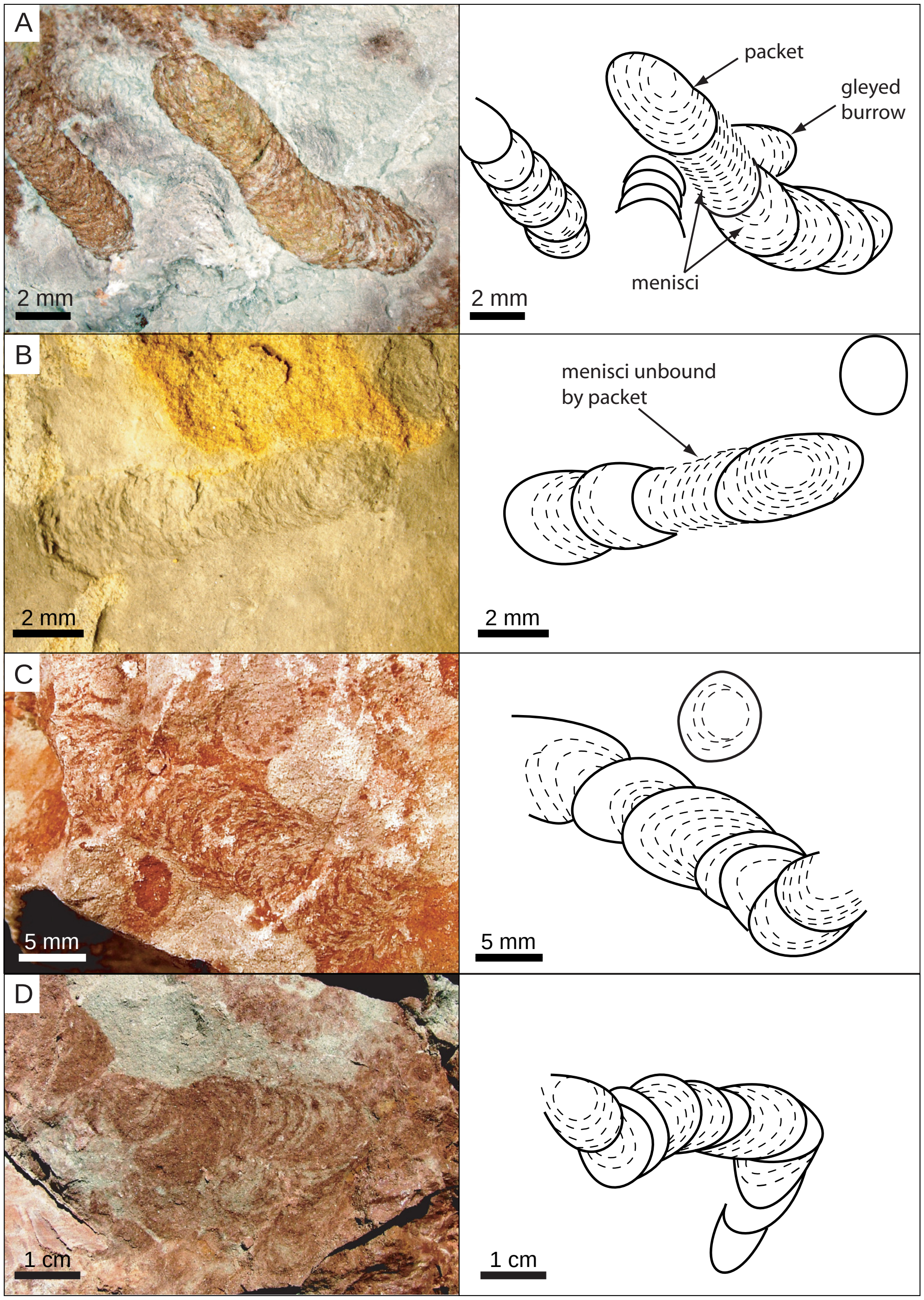

Figure 4. Photographs and line drawings of AMB from paleosols and alluvial deposits in the Willwood Formation. **A)** AMB crosscutting a purple-gray depletion zone in a well-developed paleosol. Note the completely gray AMB in the center of the photo indicating multiple generations of burrowing activity,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

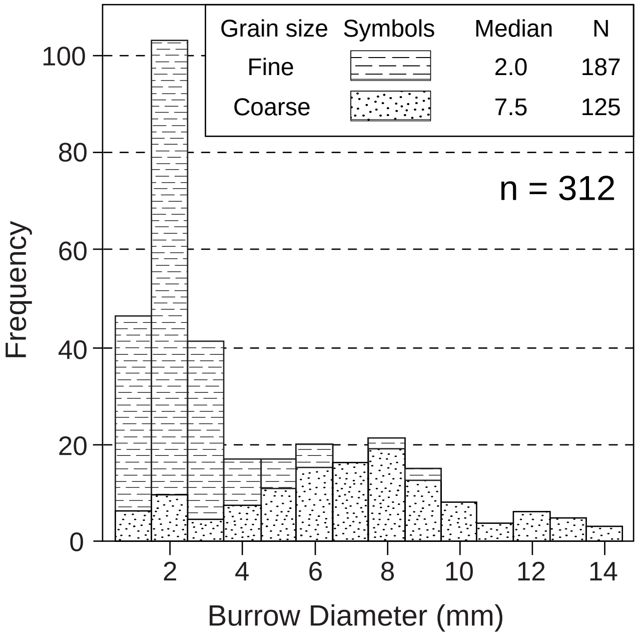

Figure 5. Distribution of AMB diameters from paleosols and alluvial deposits of the Willwood Formation. Burrow diameters range from 0.7 to 14 mm with modes at 2.0 and 8.0 mm. Fine-grained paleosols consist of claystone, siltstone, or mudstone whereas coarser grained paleosols are composed of sandy mudstone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

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 bounding packet and difficult to trace. Short burrow sections may be composed only of unbound menisci (Fig. 4A–B). In thin section, menisci are non-pelleted and texturally homogeneous with each other and the surrounding strata (Fig. 6A).

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

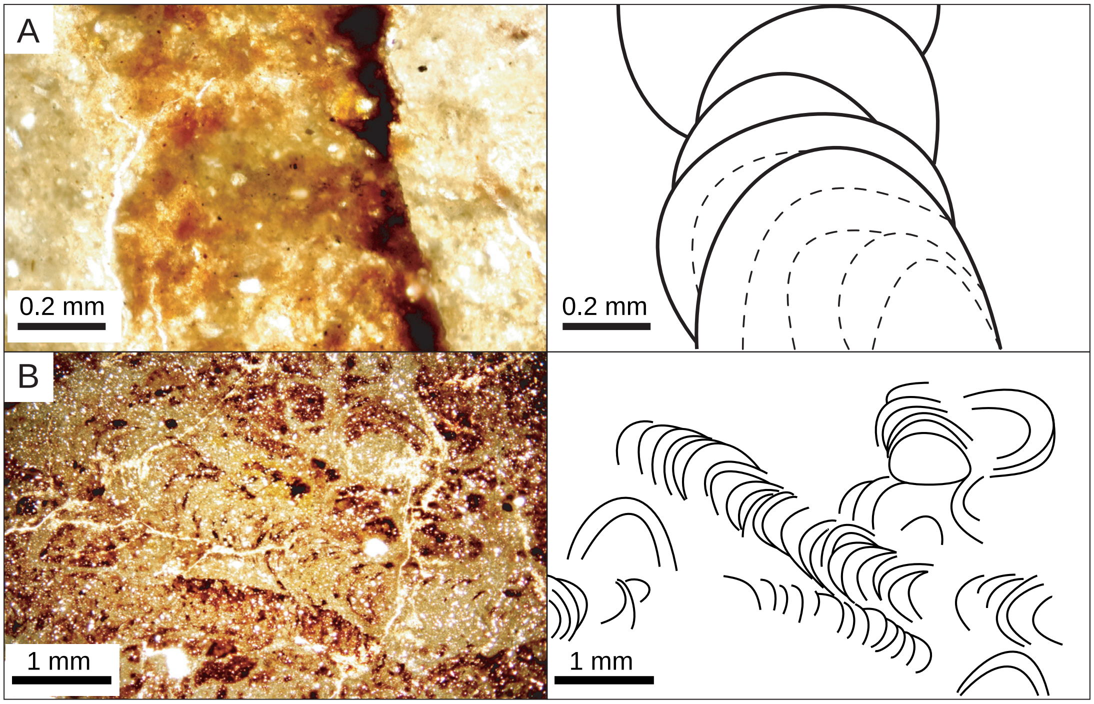

Figure 6. Photomicrographs in plane-polarized light with associated line drawings of AMB from well-developed paleosols. **A)** Menisci are texturally homogeneous with the surrounding matrix with no evidence of pelleted sediment. **B)** Well-developed paleosols commonly show a crescentic fabric composed of burrow wall remnants indicating a high degree of bioturbation.

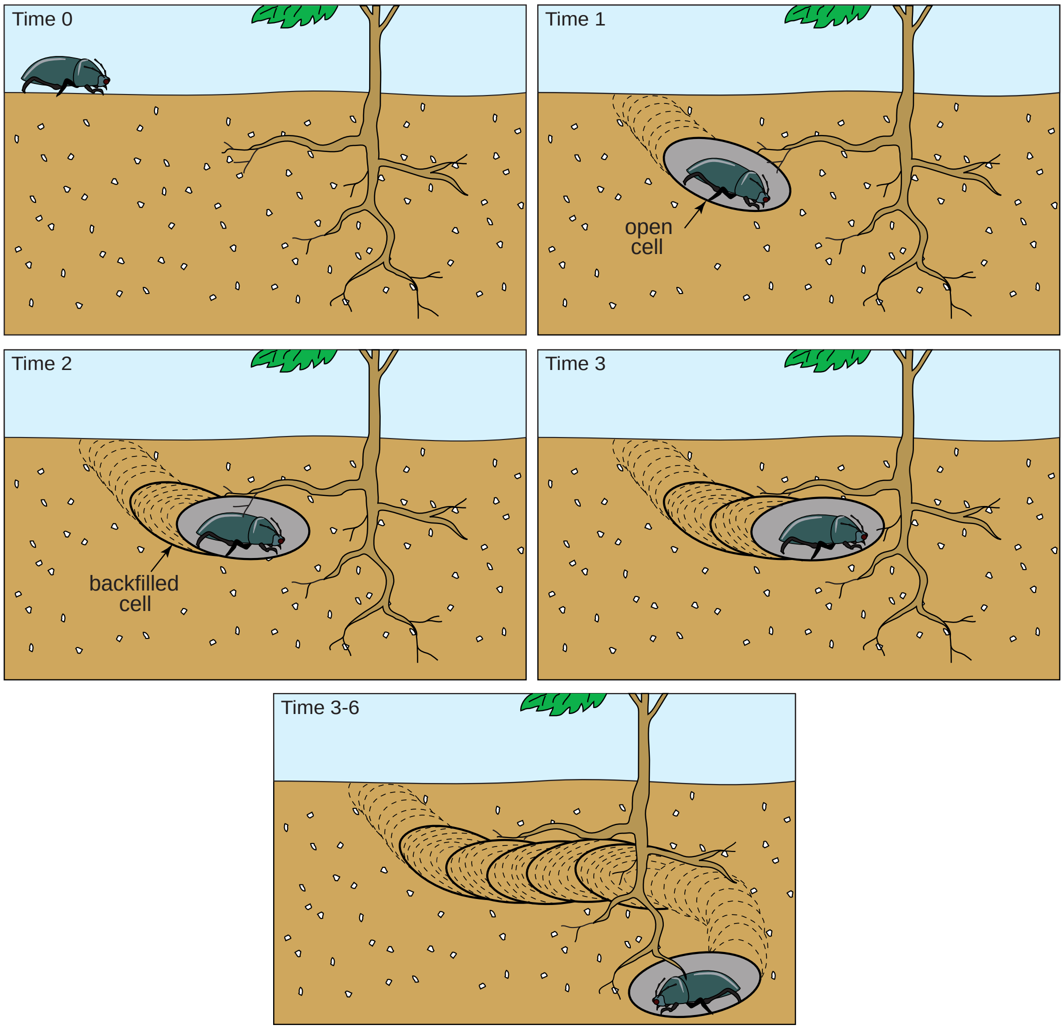

Figure 7. Hypothetical construction of AMB by an insect tracemaker. Time 1) Tracemaker produces meniscate backfill as it moves through the soil. At depth, the tracemaker stops forward movement and constructs a cell that it inhabits for a time. Time 2) Tracemaker constructs an adjacent cell and backfills 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.

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 (Vepraskas, 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 tracemakers 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. 6B). AMB tracemakers were one of the primary agents of pedoturbation in moderately to well-developed Willwood 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 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, 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 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. 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. 3A–B). 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 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. 3C–D; 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. 8B). 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

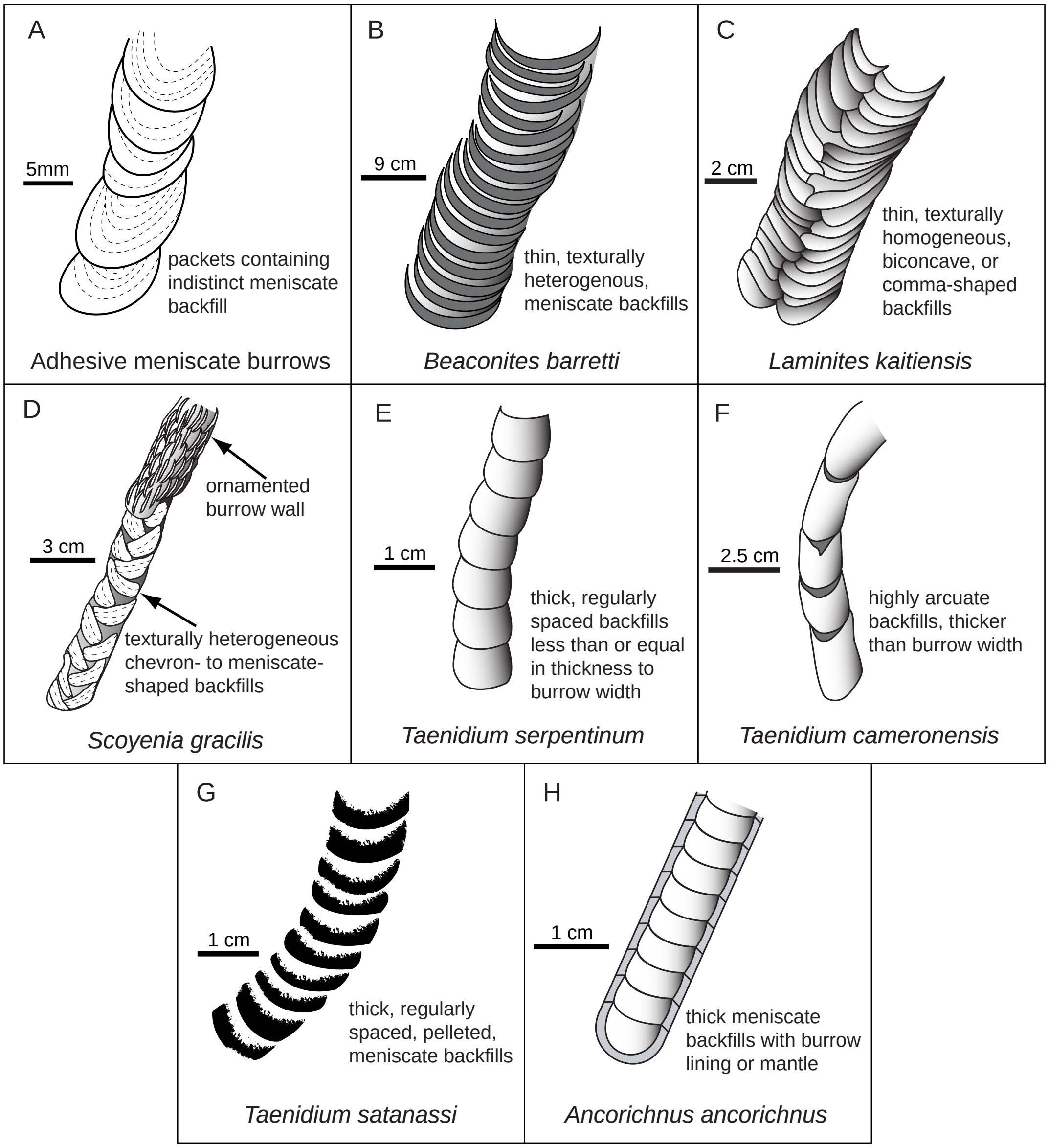

Figure 8. Comparison of AMB to similar backfilled ichnofossils. **A)** AMB traced from Willwood Formation specimen. **B)** *Beaconites barretti* traced from Gevers et al., 1971 (plate 18, fig. 2). **C)** *Laminites kaitiensis* traced from Ghent and Henderson, 1966 (plate 1). **D)** *Scoyenia gracilis*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

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. 8C). 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. 8D; 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. 8E). Backfill in *T. cameronensis* (Brady, 1947) are deeply arcuate and much thicker than burrow width, but are otherwise similar to *T. serpentinum* (Fig. 8F). *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. 8G). 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. 8H) 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 a deposit-feeding organisms such 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 ICHNOLOGY

Ichnogenus NAKTODEMASIS new ichnogenus

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 non-pelleted 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 ichnogenera 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 discreet packets—the primary morphological characteristic of the ichnogenus. The thin, tightly spaced and distinct hemispherical backfill of *Beaconites* (Fig. 8B) 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. 8C) 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. 8D) 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. 8E–G) 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. 8H) 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.

NAKTODEMASIS BOWNI new ichnospecies

Figures 4, 6

Ichnofossil Type 7, BOWN AND KRAUS, 1983, p. 112, figs. 7e, 7f, p. 116, figs. 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* sp., 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; as for the ichnogenus.

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. 4A)

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 communication). *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 tracemakers 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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CHAPTER 3. TRACES AND BURROWING BEHAVIORS OF THE CICADA NYMPH MELAMPSALTA CALLIOPE: NEOICHNOLOGY AND PALEOECOLOGICAL SIGNIFICANCE OF EXTANT SOIL-DWELLING INSECTS

Currently in review as:

Smith, J.J., and Hasiotis, S.T. Traces and burrowing behaviors of the cicada nymph *Melampsalta calliope*: neoichnology and paleoecological significance of extant soil-dwelling insects. *PALAIOS*.

ABSTRACT

This study documents the traces and burrowing behaviors of nymphs of the prairie cicada *Melampsalta calliope* (Hemiptera; Homoptera; Cicadidae) produced in neoichnological experiments. Few neoichnological studies have examined experimentally the traces of temporary and permanent soil-dwelling insects despite their role as primary agents of pedoturbation and great abundance in modern soils. *M. calliope* nymphs were collected from the C horizons of sandy fluvents along the Kansas River east of Lawrence, Kansas. The nymphs appeared to be fifth instars; 13–17 mm long and 6–7 mm wide. Nymphs were placed in plastic enclosures containing layers of colored, moist, very fine-grained sand. They burrowed immediately, excavating air-filled, sediment-enclosed cells between 20–40 mm long, averaging 9 mm wide. Burrowing was completed in three stages: 1) sediment in the forward portion of the cell was excavated and rolled into a ball with the forelimbs; 2) the nymph turned 180° using a forward roll, and moved to the cell aft; and 3) the sediment ball was pushed up against the aft cell wall and kneaded with the forelimbs into a thin layer. Resulting burrow traces are sinuous and distinctly meniscate, and demonstrate

that insect larvae construct meniscate-backfilled burrows in well-drained terrestrial settings. *M. calliope* nymphs and their traces are excellent analogs for meniscate trace fossils commonly in late Paleozoic to Cenozoic alluvial deposits and paleosols, and thus, are useful for interpreting the paleohydrogeology of the units in which they are found. Such backfilled meniscate burrows as those produced by *M. calliope* nymphs are useful in supplementing the fossil record of cicada-like hemipterans, known from the latest Permian to Early Triassic.

INTRODUCTION

This paper documents the burrowing behaviors and traces generated by the prairie cicada nymph *Melampsalta calliope* Walker 1850 (Hemiptera; Homoptera; Cicadidae) under controlled experimental conditions. Ichnofossils attributed to insects and other soil-dwelling arthropods are extremely common in continental deposits (e.g., Ratcliffe and Fagerstrom, 1980; Donovan, 1994; Buatois et al., 1998; Hasiotis, 2002; 2004; 2007). Continental neoichnology, however, has not kept pace with similar investigations of extant marine organisms. Neoichnologic studies using marine arthropods, bivalves, and echinoderms examine the range of organism behaviors and traces produced under different depositional conditions (Frey, 1968; 1970; Bromley and Asgaard, 1975; Ekdale and Berger, 1978; e.g., Frey et al., 1984; Pemberton and Frey, 1985; Atkinson and Taylor, 1991; Kanazawa, 1992; Gingras et al., 2002; Gingras et al., 2004). The experimental results of these investigations have been used to interpret the ecological, biological, and environmental significance of marine trace fossils (e.g., Frey et al., 1978; Seilacher, 1978; Frey and Pemberton, 1984; Savrda, 1995; Bromley, 1996). Few neoichnological studies have documented the traces of temporary and permanent soil-dwelling arthropods (e.g., Clark and Ratcliffe, 1989; Hasiotis and Mitchell, 1993; Tschinkel, 2003), despite their role as primary agents of pedoturbation and great abundances in modern soils (Wallwork, 1970; Hole, 1981; Hasiotis, 2002). Such studies using modern burrowing organisms as analogs for ancient continental tracemakers are critical for the accurate interpretation of the ichnologic record and paleoenvironmental, paleohydrologic, and paleoecologic information that trace fossils provide.

BACKGROUND

The approximately 1500 species of the homopteran insect family Cicadidae have a worldwide distribution, but are abundant and diverse especially in the tropics and subtropics (Daly et al., 1998). The behaviors and ecology of such periodical cicada as *Magicicada* spp. have been studied extensively because of their unique 13- and 17-year lifecycles and their synchronized, high-density emergence over large geographical areas (e.g., Simon et al., 1981; Cox and Carlton, 1988; Williams and Simon, 1995; Whiles et al., 2001). Most cicadas, however, have annually maturing generations that spend 4–7 years underground as nymphal instars, depending on the species (Lloyd and Dybas, 1966). Nevertheless, the burrowing behavior of cicada nymphs has rarely been the focus of study (e.g., Beamer, 1928).

All cicada nymphs lead exclusively subterranean lives from the first to fifth instars, burrowing through soil and feeding on the xylem sap of plant roots. Nymphs are found in a wide range of soil types, though they appear to be limited primarily to well-drained soils and by the vegetation supported by the soil (e.g., Beamer, 1928; Strandine, 1940; Hugie and Passey, 1963; Humphreys, 1989; Whiles et al., 2001; O'Geen et al., 2002). Cicada nymphs have been reported up to 1200 mm below the surface (Hugie and Passey, 1963), though nymphs are most abundant within well-rooted soil A and B horizons, typically between 100 and 300 mm from the surface (Luken and Kalisz, 1989; O'Geen and Busacca, 2001). Burrowing depth varies depending on the cicada species, developmental stage of the nymph, depth of root systems fed upon, and such soil characteristics as moisture content, texture, frost depth, and pH levels (Hugie and Passey, 1963; Luken and Kalisz, 1989). Cicada nymph soil-moisture preferences are unknown, though soil moisture was the most significant factor limiting adult cicada population size in three Illinois forests—the forest with the lowest average soil moisture content (13.5%) had nearly four times the population of the forest with the wettest (26%) soil conditions (Strandine, 1940), suggesting that the cicada nymphs preferred better drained soils.

Nymphs construct an open, vertical emergence burrow just below the soil surface toward the end of the fifth instar developmental stage (e.g., Dybas and Davis, 1962). Emergence burrows range from 70 to 400 mm long and commonly terminate in a bulbous chamber slightly larger in diameter than the burrow shaft known as a feeding cell (White et al., 1979; Humphreys, 1989; Luken and Kalisz, 1989). Cicada nymphs occupy the feeding cell prior to final emergence (Beamer, 1928). Burrow walls are solidly compacted and lined with mud pellets by some species (Dybas and Davis, 1962; Humphreys, 1989; Luken and Kalisz, 1989). Emergence burrows are long-lived structures, lasting as open shafts for up to 1 year after construction (Dybas and Davis, 1962). Some cicada nymph species use excavated sediment to construct up to 200 mm high turrets or chimneys (Humphreys, 1989; Luken and Kalisz, 1989). Turrets may assist in maintaining emergence burrow humidity by reducing exposure of the burrow interior to sunlight (Heath, 1968). Turret building varies between and within cicada species, though the conditions that initiate turret construction are unknown.

Fifth instars may occupy the feeding cell at the base of the emergence burrows for up to several weeks before an unknown stimulus triggers their final exit from the soil (Beamer, 1928). Emergent nymphs then climb any vertical surface to which they can attach themselves in preparation for their final molt (ecdysis) into a winged and sexually mature adult which lives for 2–6 weeks (Beamer, 1928). Females typically mate within a few days after ecdysis and immediately oviposit into soft or woody plant tissue. First instars hatch after 1–10 months depending on the species, fall to the ground, and begin burrowing immediately to begin the lifecycle anew.

MATERIALS AND METHODS

Cicada nymphs were collected from pits excavated in soils classified as fluvents, developed on overbank splays north of the Kansas River and east of Lawrence, Kansas. The study area is located in an open area (38° 50' N, 95° 10') vegetated with grass and small shrubs between an artificial levee and the river (Fig. 1). The soil in the study area is characterized by a 150–200 mm thick, organic-rich A horizon with dense rooting, a ~1200-mm-thick, clay-rich Bw horizon with fewer roots, a 50–200-mm-thick sand-rich BC horizon, and a sandy C horizon with a few widely spaced roots and distinct mud-draped cross-beds (Fig. 2A). The base of the BC horizon is highly undulatory, though sharp, and appears to mark the depth of significant bioturbation of the C horizon. Live cicada nymphs (Fig. 2B) were only found in the lower BC and upper C horizons (~300–500 mm deep) along with cicada molts and a few subvertical, cylindrical, sand-filled burrows likely produced by the nymphs (Fig. 2C).

The nymphs were identified as fifth instars of the prairie cicada *Melampsalta calliope* based on comparisons with photographs and anatomical illustrations in Beamer (1928). *M. calliope* is one of the most abundant annual-cicada species in Kansas and is common in North American prairie habitats from the Atlantic coast through the southern United States, to northern Mexico and northwestward to Nebraska and Colorado (Davis, 1920; Salsbury and

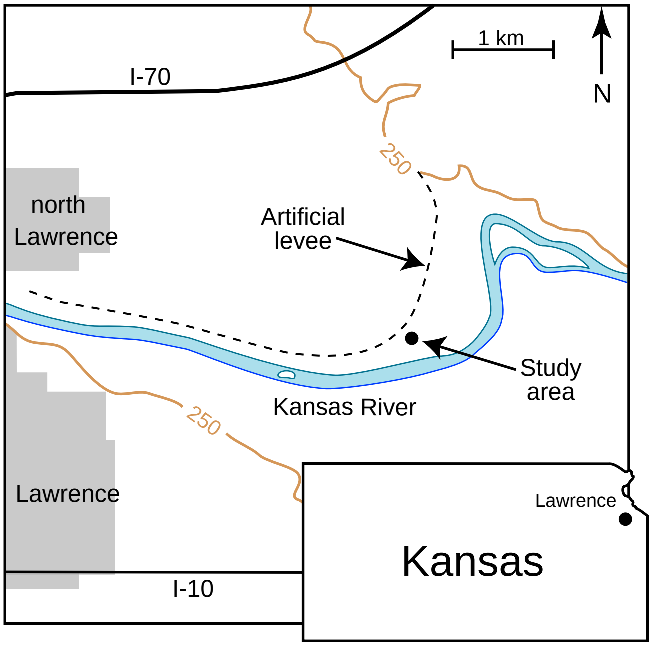

Figure 1. Location where cicada nymphs were collected on the Kansas River floodplain, west of Lawrence, Kansas.

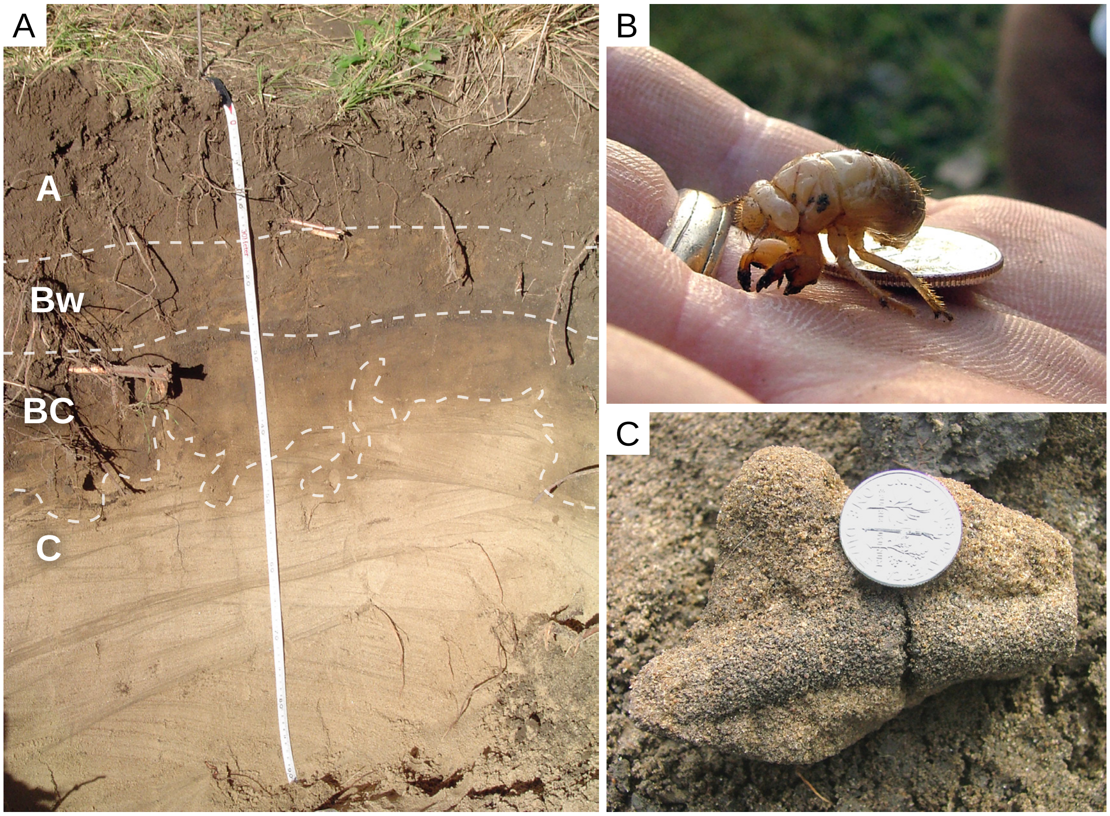

Figure 2. Soil excavation in study area. **A)** Soil horizons of fluvents developed on overbank deposits along the Kansas River; tape is 900 mm long. **B)** *Melampsalta calliope* nymphs from the BC and C horizons in association with **(C)** subvertical, sand-filled, cylindrical burrows; dimes are 17.91 mm in diameter.

White, 2000). In Kansas, female *M. calliope* oviposit in June and first instars hatch and enter the soil in August (Fig. 3). Nymphs spend approximately four years below the soil surface, feeding on xylem sap from the roots of grasses or woody plants. Fifth instars emerge from the soil between late May and early June surviving for as little as two weeks as adults (Beamer, 1928). The five nymphs collected ranged from 13–17 mm long and 6–7 mm wide across the thorax.

Burrowing experiments were conducted in a plastic-walled enclosure partitioned into three sections, one measuring 90 mm long x 25 mm wide x 100 mm high and the other two measuring 130 mm long x 25 mm wide x 100 mm high (Fig. 4A–B). The enclosures were filled with alternating 10–30-mm-thick layers of colored very fine-grained sand to highlight sediment disturbance and backfill patterns created by the cicadas. The sand was moistened prior to placing the cicadas in the enclosures to mimic the natural C horizon conditions in which they were collected, and to ensure that the sand would not collapse on the nymphs. The sand was moistened periodically during the experiments to prevent desiccation of the cicada nymphs. Undisturbed sand layers were photographed prior to the beginning of the experiments. Once the experiments began, the cicadas were video recorded while burrowing, and resulting biogenic sedimentary structures were photographed every few hours. Enclosures were covered with black construction paper when not observed to simulate a dark subterranean environment. Each experiment was allowed to run until the cicadas had thoroughly bioturbated the sand layers. After the burrowing experiments were completed, the nymphs were transferred to enclosures containing soil and vegetation collected from the A horizon of the study area.

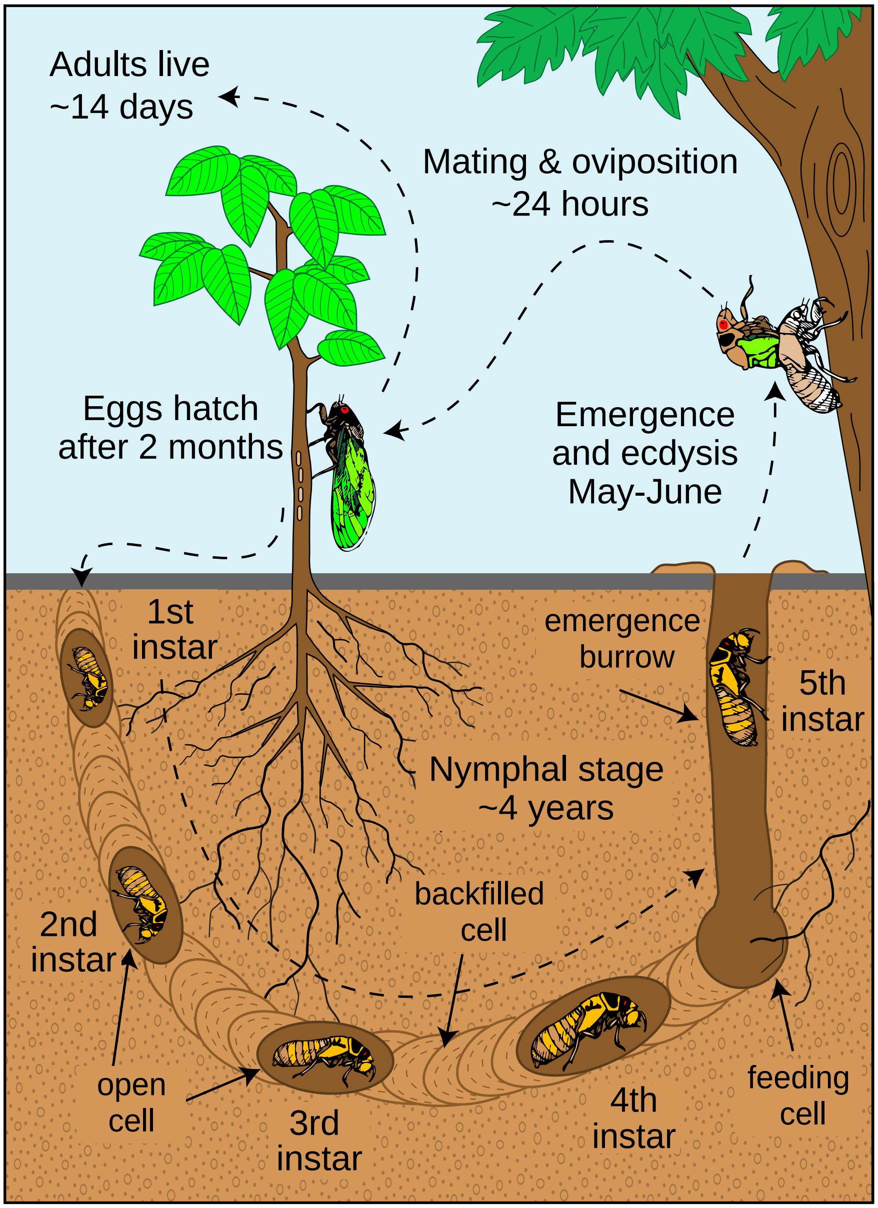

Figure 3. Above- and below-ground lifecycle of *Melampsalta calliope*.

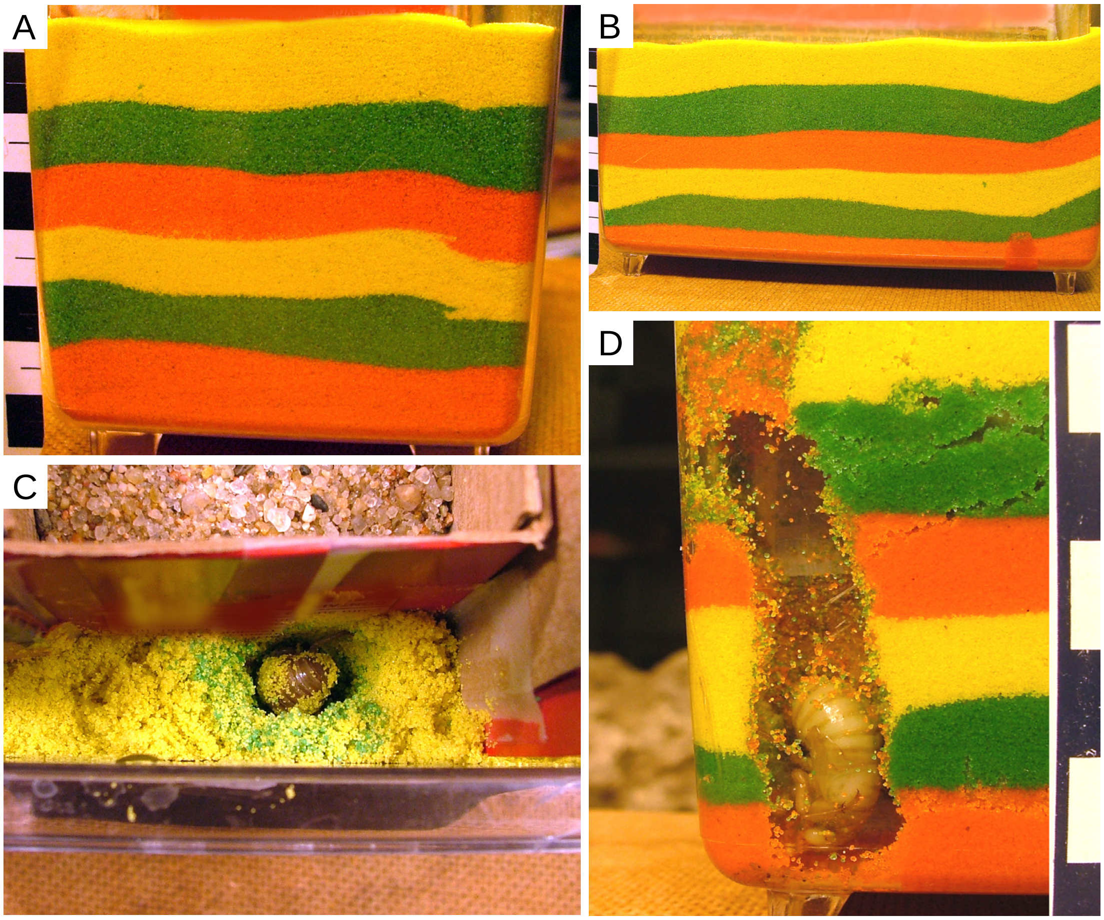

Figure 4. Sand-filled enclosures before and during cicada burrowing experiments. **A)** Initial layering of enclosure 90 mm long x 25 mm wide x 100 mm high, and the other enclosure **(B)** is 130 mm long x 25 mm wide x 100 mm high. **C)** Cicada nymph burrowing after being placed into the enclosure; note the circular cross-section of the burrow. **D)** Nymph inside a sediment-enclosed, air-filled cell.

EXPERIMENTAL RESULTS

Burrowing Behaviors

Nymphs of *Melampsalta calliope* burrowed immediately after placement in the experimental enclosures. The nymphs produced a burrow with a circular to elliptical cross section and deposited the excavated sediment on the surface around the burrow entrance (Fig. 4C). After burrowing 10–20 mm, the cicada ceased moving sediment to the surface and instead backfilled the burrow entrance. While below the surface, nymphs occupied and maintained an elongate or ovoid, air-filled cell completely enclosed by sediment. Cell dimensions were variable and ranged 20–40 mm long and 8–10 mm wide (Fig. 4D). Cicada nymphs moved through the sediment by excavating sediment from one side or wall of the cell and depositing it on the opposite cell wall.

Cicada nymphs excavated and manipulated sediment almost exclusively with their large sickle-shaped forelimbs (Fig. 5). The mid- and hind limbs did not come into contact with excavated sediment, but instead held the nymph firmly in place while burrowing. The forelimb consists of an elongate coxa and trochanter that ends in a massive, triangular femur and a bladed tibia and tarsus. The fingerlike tibia is movable against the palm of the femur, thus, together they form a prehensile digging and grasping hand. The nymphs burrowed with alternating forward thrusts of the entire foreleg into the sediment with the tibia opened (Fig. 6A). The forelimbs angled slightly inward as they thrust forward (Fig. 6B). As the forelimb retracted, the sediment was scooped by the femur toward the nymph’s head and compacted into a ball-shaped clump (Fig. 6C). After excavation of the sediment ball, nymphs rotated 180° using a forward roll while holding the sediment ball between the head and the forelegs (Fig. 6C–F). If the area of excavation was not wide enough for the forward roll, the cicadas would walk backwards to a wider portion of the cell. This maneuver resulted often in the

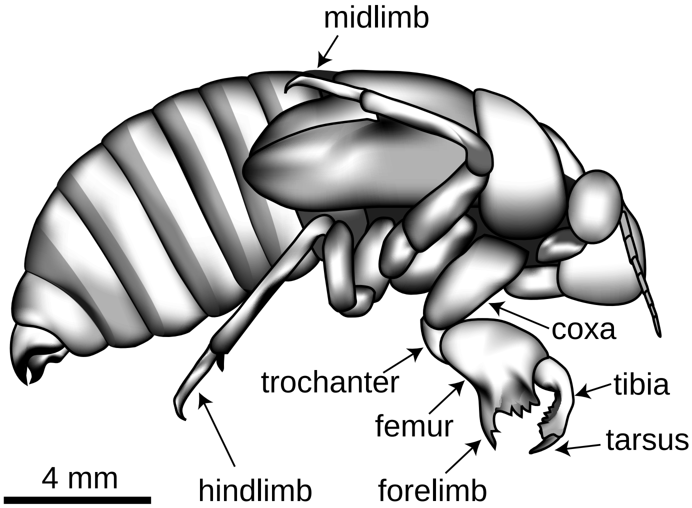

Figure 5. Anatomy of the fifth instar of *Melampsalta calliope*. Modified from Beamer (1928).

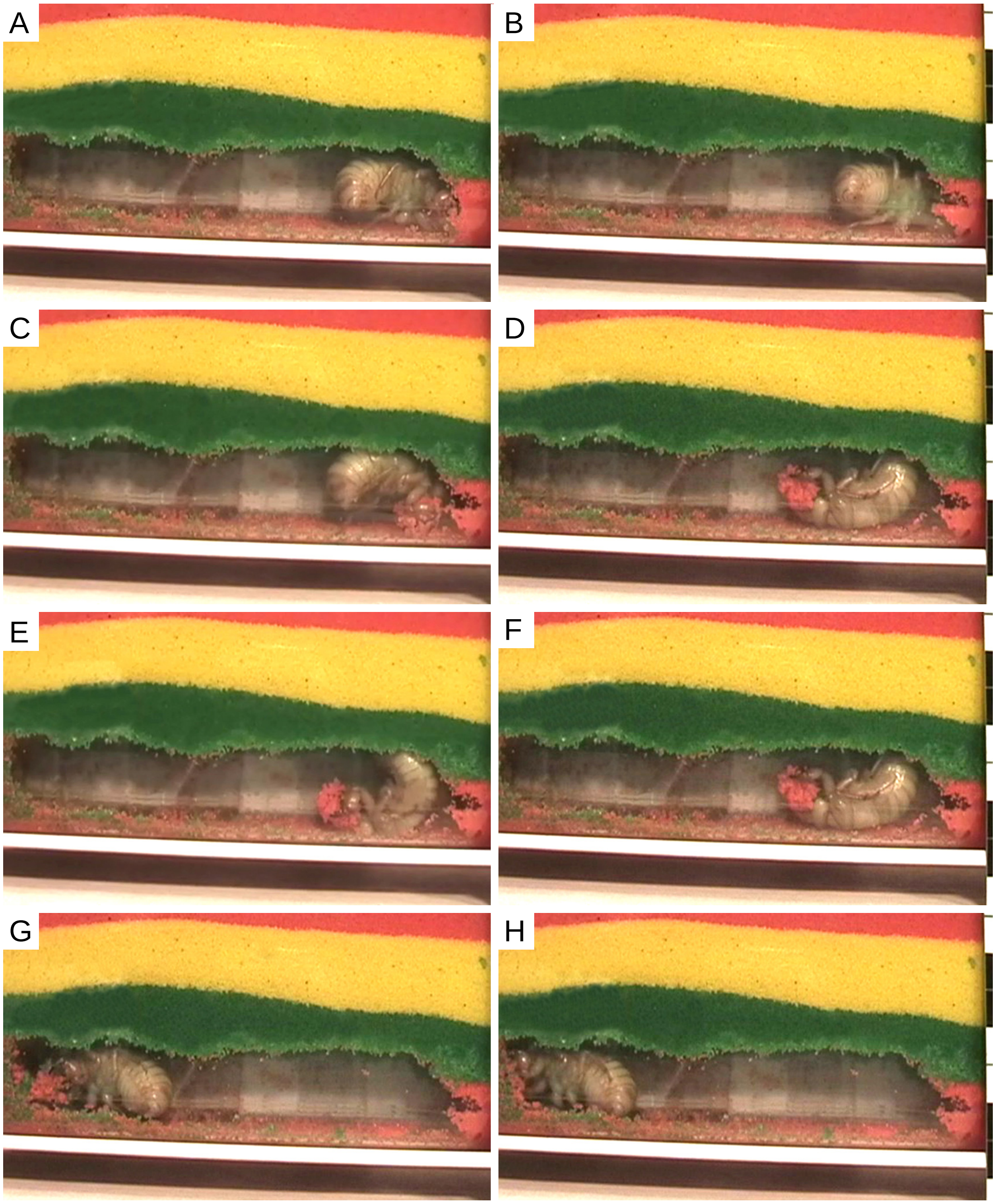

Figure 6. Screen captures of video showing *Melampsalta calliope* nymph burrowing behaviors: **A)** Nymph thrusts forelimbs into sediment, drawing back clumps with each thrust. **B)** Forelimbs scoop sediment toward body. **C)** Sediment ball is compacted and held against the head by the forelimbs. **D–F)** Nymph rotates 180° forward while holding the sediment ball. **G)** The sediment ball is pushed against the cell wall with forelimbs. **H)** The sediment is kneaded into a thin layer against the aft cell wall, thus, backfilling the cell.

cicada facing the opposite cell wall but upside down, which it sometimes corrected. The nymphs then carried the sediment ball to the aft side of the cell and pushed the sediment against the cell wall with both forelimbs (Fig. 6G). The nymphs kneaded and pressed the sediment ball into a thin layer using alternating thrusts of the forelegs (Fig. 6H). After material was kneaded into the cell wall, the nymphs once again made a 180° forward role and returned to the front of the cell to excavate more material. The cell and cicada, therefore, moved forward through the sediment by backfilling the cell aft.

Melampsalta calliope nymphs burrowed actively for several hours at a time, followed by longer periods of inactivity (Fig. 7A–F). Their initial behavior was to burrow 70–90 mm straight to the bottom of the enclosure (Fig. 7A). The nymphs burrowed in fairly random directions at depth presumably searching for food, including a few brief returns to the sediment surface (Fig. 7E).

Only one cicada nymph transferred to the vegetated and soil-filled enclosures survived long enough (~2 months) to produce an emergence burrow. This nymph constructed a short emergence burrow, exited the soil, and expired on the surface shortly after molting. Construction of the emergence burrow by fifth instar nymphs is a behavior distinctly different from the burrowing and feeding behaviors of preceding instars. Sediment was excavated in the manner previously described and transported to the surface to produce a vertical, open burrow. The balls of sediment were deposited randomly around the burrow entrance and were not used in the construction of a turret or burrow lining. Beamer (1928) reports that *Melampsalta calliope* nymphs may occupy the emergence burrow for an extended period of time—26 days in one specimen—before emerging, though the nymph in our study exited the soil and molted immediately after completing the emergence burrow.

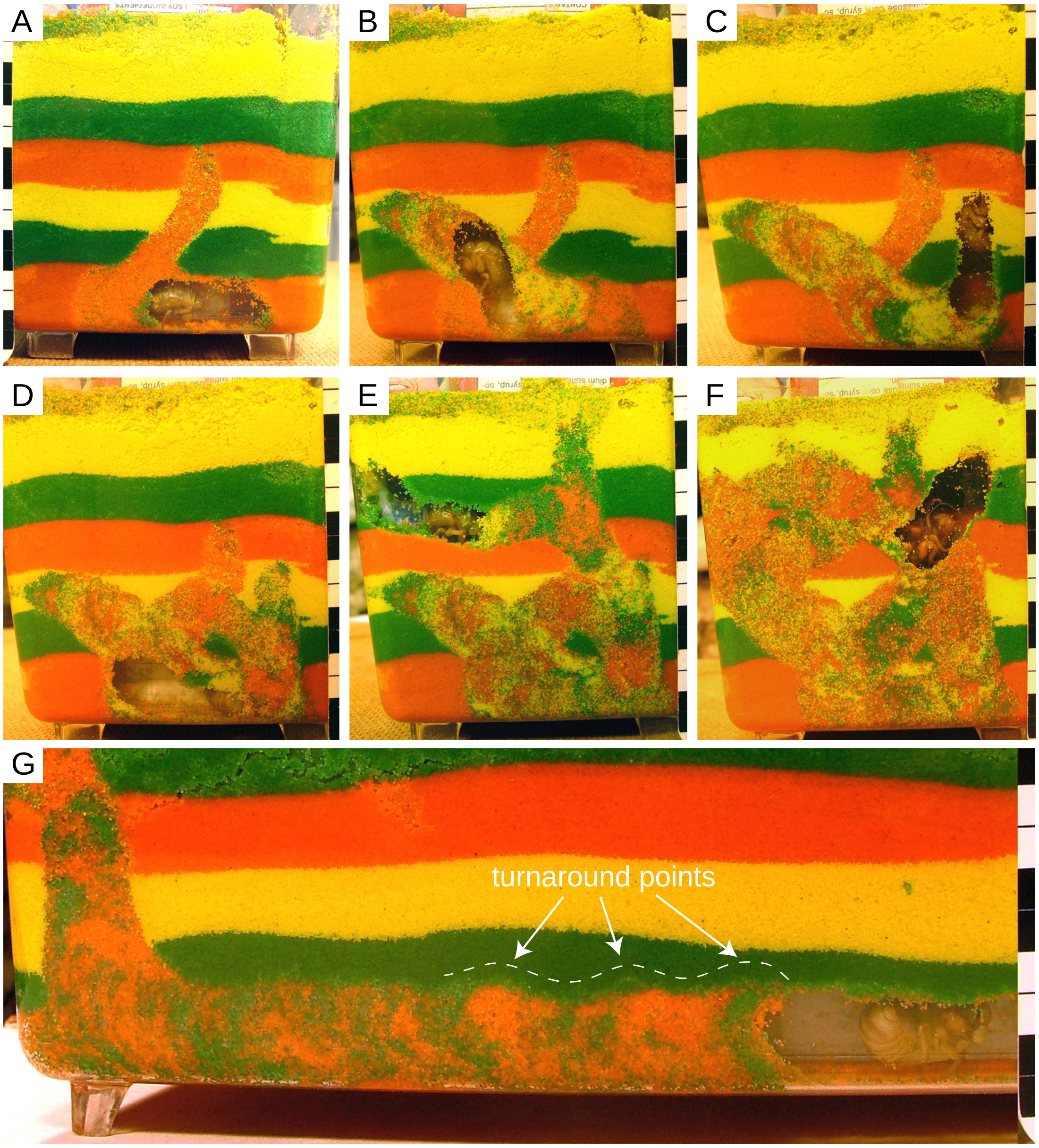

Figure 7. Experimental enclosure over fifteen days of burrowing by *Melampsalta calliope* nymph **(A–F)**. Enlargements along the length of the burrow correspond to turnaround points for the backfilling cicada **(G)**.

Trace Morphologies

For most of their lifecycle, cicada nymphs burrow below the soil surface producing straight to sinuous, unlined, burrows filled with thin, slightly to strongly curved meniscate backfills (Fig. 7A–F). Burrow widths average 8–10 mm; only 1–2 mm wider than the nymph's bodies. Unevenly spaced and 10–20 mm long sections of backfilled burrow are 13–16 mm wide, creating a tapered-and-widened appearance along the length of the burrow (Fig. 7G). Thicker burrow sections were used by the nymphs as turnaround points for backfilling purposes. The cross-sectional shape of the burrows is unknown due to the design of the enclosures. The nymphs produced burrows with circular cross sections as they entered the sediment in each experimental run, so subterranean burrows would likely be circular to elliptical in cross section as well.

The meniscate backfills are composed of cell wall remnants made conspicuous in these experiments when sediment from different colored sand-layers was incorporated into the burrow fill. The menisci vary in their curvature and distinctness along the length of the burrows. Menisci similar in appearance were typically grouped into short burrow sections or packets (Fig. 8A–B). Packets reflect separate episodes of burrowing activity based on direct observations of the cicadas during burrow excavation. Cicada burrows are, thus, composed of a series of packets containing meniscate backfill, rather than one burrow filled with a continuous series of backfills.

On its way to emergence, the nymph produced an open, cylindrical burrow ~80 mm long and ~10 mm in diameter. The burrow is very short compared with reported emergence burrow lengths 70 to 400 mm long (White et al., 1979; Humphreys, 1989; Luken and Kalisz, 1989), though this is likely due to the small size of the enclosure.

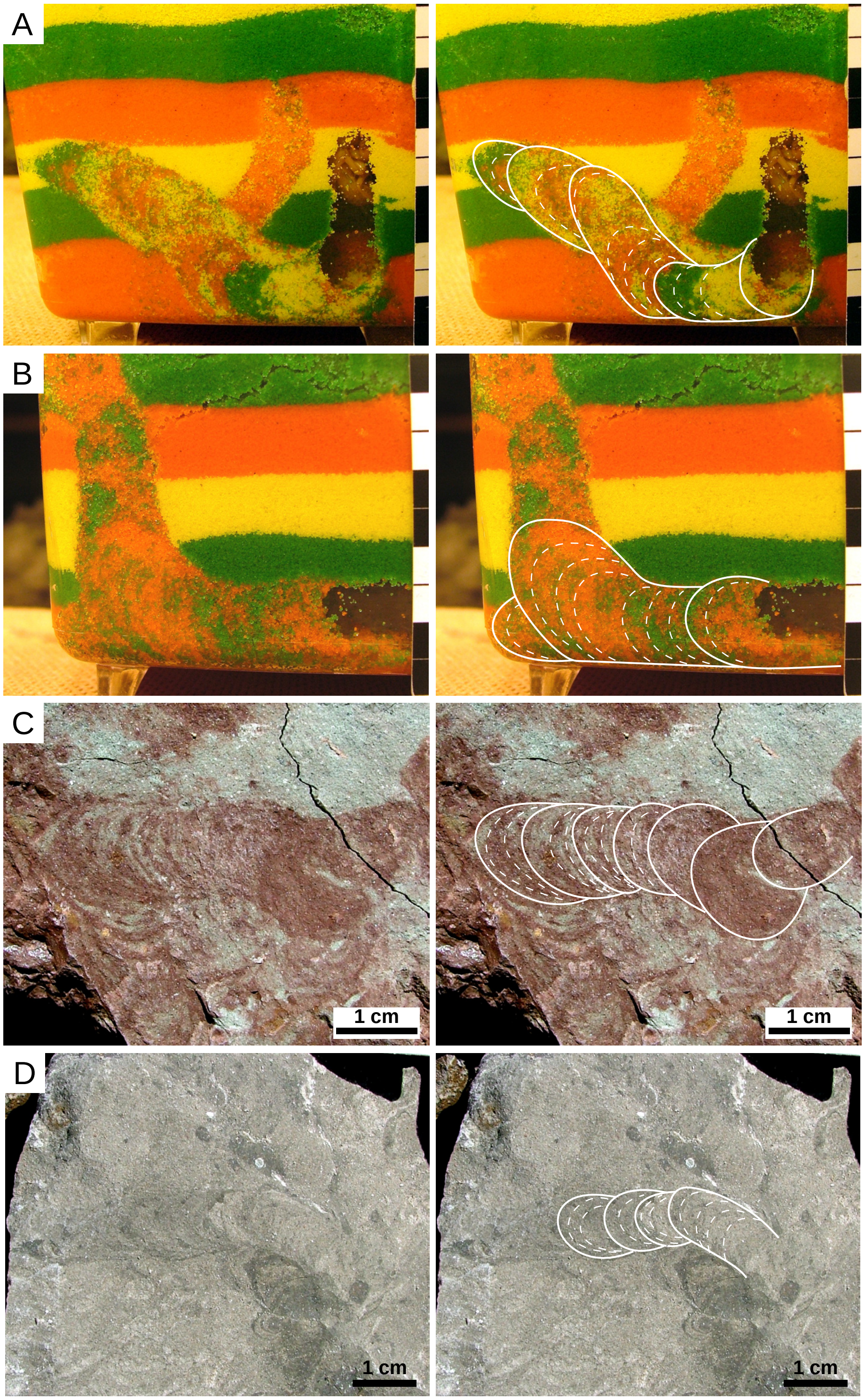

Figure 8. Comparison of *Melampsalta calliope* nymph backfilled burrows **(A–B)** with the trace fossil *Naktodemasis bowni* **(C–D)**. *N. bowni* specimens from a well-developed, well-drained paleosol **(C)** and a clay-rich sandstone deposited during an avulsion **(D)** in the Paleogene Willwood Formation, Bighorn Basin, Wyoming.

DISCUSSION

Preservation Potential

Melampsalta calliope nymphs produce at least two distinct types of traces in soils during different parts of their lifecycle: backfilled burrows during the first through fifth instars and emergence burrows by older fifth instars before exiting the soil. Modern cicada nymphs are highly abundant in a variety of soil types, thus increasing the preservation potential of their traces. Backfilled burrows are rarely observed in modern soils, however, because the fill material is unaltered during the burrowing process and texturally identical to the surrounding soil matrix—unless the burrowing organism incorporates sediments of different grain sizes and colors into the backfill (e.g., Hugie and Passey, 1963). Nymph burrows in soils with fluctuating water tables may be highlighted by mottles produced by preferential gleying—the redistribution of Fe and Mn in the soil profile in the presence of organic matter (e.g., Schwertmann, 1993; Vepraskas, 1999). Long-term burrowing by cicadas in clay-rich soils may promote the formation of distinct columnar soil-aggregates and nodular accumulations of calcium carbonate (Hugie and Passey, 1963).

Natural soil-forming processes can also destroy cicada nymph traces, especially in the soil A and upper B horizons. The impact of pedogenesis decreases with depth in the soil profile (Brady and Weil, 2002); therefore, traces produced below the most pedogenically active horizons are more likely to be preserved. Grain size of the host media will strongly influence preservation potential—burrows produced in clay-rich B soil horizons, for example, are more likely to be preserved because these are denser and harder to rework than coarser grained horizons (Brady and Weil, 2002). Nymph traces produced in highly aggradational depositional settings have the highest preservational potential because active soil-forming processes are likely to cease and move higher in the profile following major depositional events. Preservation of cicada traces, thus, is controlled by the intensity and duration of post-burrowing pedogenic modification and the position of the traces within the soil profile in relationship to active zones of pedogenesis.

Emergence burrows are left open following exit of the cicada nymph from the soil and, thus, would have to be passively infilled with sediment to be preserved. Although sedimentation rates associated with most soil environments are relatively low, emergence burrows may remain intact and open for as long as 1 year after construction (Luken and Kalisz, 1989). Mud linings constructed by some cicada species may further enhance their preservation potential (Humphreys, 1989). Most emergence burrows, however, are concentrated within the soil A horizon and are likely to be obliterated by later bioturbation and pedogenesis unless quickly buried. The mud turrets occasionally constructed above emergence burrows are unlikely to be preserved because they quickly desiccate and weather on the soil surface (Humphreys, 1989).

Paleoecological Implications

Backfilled and vertical burrows in continental strata similar to those produced by *Melampsalta calliope* suggest subaerial exposure and paleopedogenic development of the host sediment. The tracemakers were likely living within the vadose (unsaturated) zone of well-drained soils at the time of trace formation. Backfilled burrows represent foraging behavior by the nymphs and are indicative of ancient soils with root systems sufficient to support a community of xylem feeding macrofauna—whether these roots are still visible as rhizoliths or were destroyed before fossilization. The presence of such burrows indicates periods of subaerial exposure and pedogenesis in terrestrial depositional environments and can be used to differentiate these settings from freshwater aquatic or marine paleoenvironments.

Fossil backfilled burrows in continental deposits have been interpreted generally as fodinichnia produced by deposit-feeding organisms living in subaqueous or saturated soil conditions (e.g., Toots, 1967; D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994; Buatois and Mángano, 2004; Genise et al., 2004). This interpretation is partially the result of attributing the behaviors and physiochemical requirements of backfilling marine organisms to trace fossils of continental origin and their tracemakers. Meniscate burrows in continental deposits are superficially similar to such commonly occurring marine backfilled ichnofossils as *Taenidium*, though the differences in their detailed internal and external morphologies, genesis, and tracemaking organisms make them significantly distinct (e.g., Smith et al., in press). The interpretation of all backfilled ichnofossils as sediment-ingesting, aquatic organisms would imply that their host deposits were subaqueous when the traces were made (e.g., Bromley, 1996; Buatois and Mángano, 2004; Genise et al., 2004). Our research demonstrates, however, that backfilling tracemakers do not require water-saturated conditions and that meniscate ichnofossils in paleosols and other continental deposits likely do not represent the work of sediment-ingesting organisms. The construction of backfilled burrows in freshwater subaqueous settings in the continental realm has not been demonstrated, therefore, previous interpretations that meniscate burrows indicate water-saturated conditions should be revisited.

Paleontological Significance

The first cicada-like insect body fossils are from the Early 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). Cicada nymph trace fossils should be common in the fossil record given their wide geographic distribution, great abundance in modern soils, relatively high preservation potential under the right conditions, and ancient evolutionary history. Although the earliest body fossil occurrence is used to delineate the origin of a given taxon, their ichnofossils—when diagnostic—can be used as proxies for the occurrence of an organism, or group of organisms with similar bauplans or behaviors, in the fossil record (e.g., Hasiotis and Mitchell, 1993; Hasiotis and Honey, 2000; Hasiotis, 2007). Of equal importance, trace fossils and their host strata preserve the evolutionary history of acquired behaviors and the paleoecological conditions under which these behaviors were employed (Hasiotis, 2003). Traces produced by *Melampsalta calliope* in this study meet these criteria in that they are morphologically distinct and likely only to be produced by tracemakers with similar anatomies and behaviors.

Backfilled burrows with morphologies very similar to modern cicada nymph traces are commonly reported from paleosols and alluvial deposits in continental strata (e.g., Bown and Kraus, 1983; Hasiotis and Dubiel, 1994; Hasiotis and Demko, 1996; Savrda et al., 2000; Hasiotis, 2002; Counts and Hasiotis, 2006; Smith et al., in press). Backfilled burrows from Pleistocene and Holocene paleosols are the only trace fossils that have been specifically attributed to the burrowing of cicada nymphs (O'Geen et al., 2002; Gregory et al., 2004; Jacobs and Mason, 2004). *Naktodemasis bowni* is most similar in its morphology, inferred ethology, and depositional and paleoecological setting to traces produced by cicada nymphs in this study (Smith et al., in press). First described from floodplain paleosols of the Paleogene Willwood Formation in the Bighorn Basin, Wyoming (Bown and Kraus, 1983), *N. bowni* has since been reported from continental deposits dating back to the Late Paleozoic

(Counts and Hasiotis, 2006). Meniscate burrows assigned to *N. bowni* are composed of a series of distinct packets, commonly crosscutting one another, that contain thin, discontinuous meniscate fill (Fig. 8C-D). These meniscate burrows, thus, can be used as proxies in the fossil record for the likely presence of cicada nymphs and other such backfilling hemipterans as burrower bugs (Hemiptera: Cydnidae) with similar burrowing behaviors (Smith et al., in press). In addition, such meniscate trace fossils in paleosols and alluvial deposits indicate that burrowing behaviors and terrestrial, subterranean lifestyles date to the earliest body fossil occurrences of hemipterans in the Permian.

Fossil emergence burrows would be most similar to *Macanopsis astreptum* or *Cylindricum* isp., depending on whether an enlarged feeding cell is preserved at the burrow terminus. Both ichnofossils are predominately vertical, smooth-walled burrows with cylindrical cross sections, however, *Macanopsis* terminates in a roughly spherical chamber larger in diameter than the burrow shaft (Bown and Kraus, 1983) and *Cylindricum* are test-tube shaped with gently rounded burrow terminations (Linck, 1949). Such vertical burrows are common in continental deposits and in association with backfilled burrows. In addition, emergence burrows could potentially be preserved in high densities similar to *Cylindricum*, particularly in the case of periodical cicada broods which exit the soil simultaneously by the millions (e.g., Williams and Simon, 1995). Passively filled vertical burrows in some paleosols may have been constructed by emerging fifth instars (Retallack, 1997), though diagnostic characteristics of such traces are not well established and similar burrows are produced by a wide variety of organisms in continental deposits (e.g., Ratcliffe and Fagerstrom, 1980; Bown and Kraus, 1983; Hasiotis, 2002).

The emergence burrows of 13- and 17-year periodical cicadas, if recognized as such in the geologic record, could be used potentially as *in situ* geochronometers under the right depositional conditions. Alluvial floodplain and loess environments in which sedimentation rates are steady but of low volume are most likely to preserve individual cicada emergence events. Vertical aggradation rates vary widely on modern floodplains and range from 0–760 mm a^{-1} (e.g., Rumsby, 2000), but is most commonly < 10 mm a^{-1}. To observe individual emergence events in the alluvial record, sediment aggradation between emergences would have to be of such thickness that succeeding generations of emergence burrows didn’t overlap, but not so thick and rapid that burrowing cicadas were permanently buried. For example, given the 70 to 360 mm range of 17-year cicada emergence burrow lengths reported by Luken and Kalisz (1989), vertical aggradation would have to exceed ~21 mm a^{-1} between emergences to preserve distinct and non-overlapping emergence events.

CONCLUSION

Invertebrate trace fossils from continental deposits, especially paleosols, are often interpreted as the burrows, tracks, and trails of insects, though clear affinities with specific taxa in many instances are doubtful. Neoichnological experiments with extant continental organisms, thus, are paramount because the resulting traces or elements of the traces can be attributed directly to specific tracemakers, anatomical features, behaviors, and environmental conditions (e.g., Hasiotis et al., 1993; Hembree and Hasiotis, 2006; 2007). Understanding the burrowing behaviors responsible for trace formation is important because these tend to be shared by different tracemaking organisms with similar bauplans, lifecycles, and environmental requirements. The interpretive power of continental ichnology is, thus, greatly increased even when the exact tracemaker is unknown.

This research has also shown that backfilled burrows are not all produced by sediment ingestion and excretion. The morphology of meniscate traces produced by cicada nymphs, and likely other similarly adapted burrowing hemipterans, are distinct and attributable to specific behaviors and different portions of the lifecycle of an organism. Such traces are indirect evidence of biodiversity in ancient soils because the body fossils of insects and other soil arthropods are rarely preserved *in situ* within paleosols.

The presence of meniscate trace fossils attributable to insect larvae are themselves indicators of ancient pedogenesis as burrowing insects are a major faunal component in modern soils and primary agents of pedoturbation (Thorp, 1949; Hole, 1981; Hasiotis, 2007). Trace fossils similar to those produced by *Melampsalta calliope* can be used as indicators of subaerial exposure and improved drainage conditions in continental deposits as modern cicadas are limited to well-drained soils. Information about the degree of ancient soil moisture regimes is important for understanding past climate conditions and for reconstructing continental paleolandscapes. Nymph burrows suggest also the presence of plant roots and, thus, soil formation. Such meniscate trace fossils as *Naktodemasis bowni* are very similar morphologically to the burrows of modern cicada nymphs. This strong resemblance suggests that *N. bowni* tracemakers had similar body plans, burrowing methods, and habitat requirements as extant cicada nymphs. Trace fossils with similar morphologies as modern cicada nymph traces may be used to extend the geographic and stratigraphic range of these organisms in the fossil record.

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CHAPTER 4. PALEOCLIMATIC IMPLICATIONS OF CRAYFISH-MEDIATED PRISMATIC SOIL STRUCTURES IN PALEOSOLS OF THE PALEOGENE WILLWOOD FORMATION, BIGHORN BASIN, WYOMING

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ABSTRACT

Paleosols at Polecat Bench, northern Bighorn Basin, Wyoming, show prismatic structures not previously described in the Paleogene Willwood Formation. Prisms are densely spaced, 15–50 mm diameter cylinders with vertical to slightly sinuous paths up to 400 mm long, subangular to rounded vertical faces, and slightly concave to convex tops. Prism exteriors are coated commonly by <1-mm-thick clay films; exteriors also commonly show knobby and striated surficial morphologies. Prismatic structures are nearly exclusive to thinly bedded (<1 m thick) compound paleosols composed of red to red-purple sandy mudrock overlying gray to green-gray heterolithic units composed chiefly of fine-grained sandstone. In addition to prismatic structures, these paleosols are characterized by large gray mottles, slickensides, and calcareous rhizocretions which crosscut or more typically follow prism exteriors. The architectural and surficial morphology of the soil prisms suggest strongly that these are pedogenically modified freshwater crayfish burrows of the ichnospecies *Camborygma litonomos*.

At Polecat Bench, an ~40-m interval of the Willwood Formation records a transient episode of global warming known as the Paleocene-Eocene Thermal Maximum (PETM). The PETM interval is characterized by a series of predominantly red, cumulative paleosol profiles and increased soil carbonates. Prismatic soil structures and crayfish burrows are rare or absent in cumulic paleosols typical of the PETM, whereas they are locally abundant in red compound paleosols outside the PETM interval. The changes in paleosol morphology and a sharp decrease in crayfish burrows within the PETM interval suggest significantly improved soil-drainage conditions and lower water tables on the Willwood floodplain during the global warming event.

INTRODUCTION

This paper presents evidence that prismatic soil structures in a series of paleosols at Polecat Bench, northern Bighorn Basin, Wyoming, originated as freshwater crayfish burrows that mediated the pedogenic development of some alluvial deposits in the Paleogene Willwood Formation. In addition, the depth and stratigraphic distribution of burrow-mediated soil prisms provide details about hydrologic and climatic changes through a short-term, global-warming episode known as the Paleocene-Eocene Thermal Maximum (PETM). Multiple lines of evidence suggest that temperatures increased in the Bighorn Basin during the PETM (e.g., Fricke et al., 1998a; Bao et al., 1999; Koch et al., 2003), however, interpretations differ as to the effects on the regional precipitation patterns and paleohydrologic regime (e.g., Shellito et al., 2003; Bowen et al., 2004; Wing et al., 2005; Kraus and Riggins, 2007).

Burrows reported here represent the first clear fossil evidence of freshwater crayfish from the Willwood Formation. In addition, this study shows that such soil biota as crayfish initiated and enhanced the pedogenic development of some Willwood soils. The occurrence and abundances of crayfish burrows in paleosols forming before, during, and after the PETM reflect changes in hydrology in the Bighorn Basin and climate during the early Eocene and may also help to resolve conflicting paleoprecipitation interpretations for the Bighorn Basin during the PETM global warming event.

GEOLOGIC SETTING

Polecat Bench in the northern Bighorn Basin is a Pleistocene river terrace overlying an older, southwesterly dipping sedimentary rock succession spanning the uppermost Cretaceous through the lower Eocene (Bowen et al., 2001; Gingerich, 2001). The basal ~100 m of the Paleogene Willwood Formation crops out at the southern end of Polecat Bench to the north, and west of the town of Powell, Wyoming (Fig. 1). The 780-m-thick Willwood Formation is composed of alluvial mudstones, siltstones, and sandstones deposited throughout the Bighorn Basin of northwest Wyoming during the latest Paleocene and earliest Eocene (Neasham and Vondra, 1972). The Willwood contains an extensive and important biostratigraphic record of Paleocene to early Eocene mammals (e.g., Gingerich, 1989; 2001). In addition, a diverse assemblage of plant, invertebrate, and vertebrate trace fossils are abundant in Willwood paleosols and alluvial deposits (Bown and Kraus, 1983; Hasiotis et al., 1993a; Kraus and Hasiotis, 2006).

Paleocene-Eocene Thermal Maximum (PETM)

An ~40-m section of the Willwood Formation at Polecat Bench records the Paleocene-Eocene Thermal Maximum (PETM), a transient, though dramatic, global-warming event that began ~55 Ma and lasted ~100,000 years (Bowen et al., 2001; Gingerich, 2001).

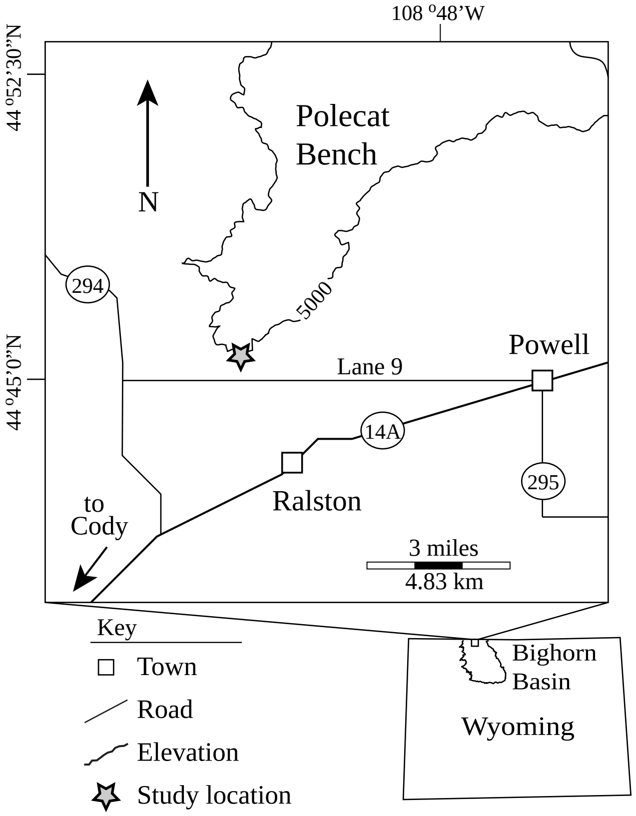

Figure 1. Study area at the southern end of Polecat Bench in the northern Bighorn Basin, Wyoming.

The PETM is recognized worldwide by strongly negative carbon isotopic values in marine carbonates and pedogenic carbonate from continental deposits (e.g., Koch et al., 1992; Zachos et al., 1993; Bowen et al., 2001; Bains et al., 2003; Koch et al., 2003). Oxygen isotope compositions of carbonate nodules (Koch et al., 2003), tooth enamel, gar scales, and Fe oxides (Fricke et al., 1998b; Bao et al., 1999), and independent data from leaf margin analysis (Wing et al., 2000) suggest that mean annual temperatures increased by 3–7°C from late Paleocene estimates to ~26°C in the Bighorn Basin during the PETM. Leaf area analyses (Wing et al., 2005) and mineral weathering indices (Kraus and Riggins, 2007) suggest a nearly 40% decline in mean annual precipitation, contrary to previous studies indicating increased precipitation during the PETM (e.g., Bowen et al., 2004). The PETM interval at Polecat Bench coincides with the Wasatchian-*Meniscotherium* (Wa-M) and Wasatchian-0 (Wa-0) faunal biozones, which mark the extinction of many Paleocene mammal species and the first appearance of artiodactyls, perissodactyls, and primates in North America (Gingerich, 2003; Magioncalda et al., 2004).

METHODS

Fifty four measured sections were excavated from 20 m below to ~20 m above the ~40-m PETM interval at Polecat Bench (Fig. 2). The stratigraphic position of the PETM interval is based on previous stable isotope studies (Bowen et al., 2001; Gingerich, 2001; Bains et al., 2003). Lithologic units within each measured section were distinguished based on grain size, matrix color, and the presence and abundance of such pedogenic features as mottles, slickensides, nodules, rhizocretions, and other trace fossils (e.g., Kraus and Gwinn, 1997). Multiple trenches were excavated through key marker beds given provincial names by Gingerich (2001) to document lateral variability of paleosols and trace fossil distributions.

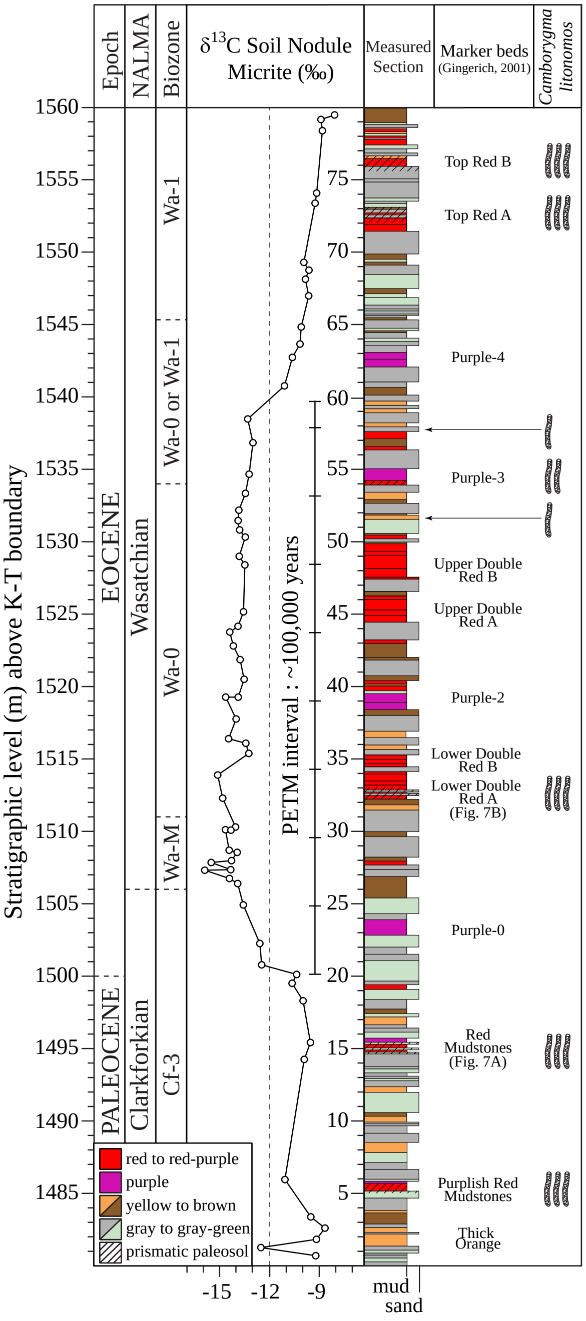

Figure 2. Composite measured section of the Willwood Formation at Polecat Bench. Stripe patterns indicate stratigraphic position of paleosols showing prismatic soil structures. Burrow symbols indicates relative abundances of *Camborygma litonomos*; three burrows indicate distinct prismatic structures with abundant well-preserved burrows, two burrows indicate few prismatic structures and well-preserved burrows, and one burrow indicates a single *C. litonomos* specimen. North American Land Mammal Age (NALMA), biochron, and marker bed information modified from Gingerich (2001); δ^{13}C isotope stratigraphy modified from Bowen et al. (2001) and Bains et al. (2003).

The stratigraphic position, abundance, physical dimensions, lateral occurrences, and vertical tiering of trace fossils were recorded for each lithologic unit. Ichnofossils are described according to their architectural and surficial burrow morphology and burrow fill from outcrop and laboratory specimens (e.g., Hasiotis and Mitchell, 1993; Hasiotis et al., 1993b; Hasiotis et al., 2004). Architectural morphology pertains to the burrow's general shape, physical dimensions, cross-sectional shape, and orientation in outcrop. Surficial morphology includes marks on the burrow walls of different sizes, shapes, and orientation. The burrow fill refers to the grain size, composition, degree of compartmentalization, and arrangement of infilling sediment (Bromley, 1996).

PALEOPEDOLOGY AND ALLUVIAL STRATIGRAPHY

Two primary lithologies are present in the Willwood Formation at Polecat Bench: varicolored mudrocks showing differing degrees of paleopedogenic development and heterolithic intervals composed of drab-colored sandstone and mudrock. Varicolored mudrock intervals are characterized by red, yellow-brown, brown, and purple matrix and mottle colors; carbonate or Fe-oxide nodules; various types and abundances of rhizocretions and other trace fossils; and slickensides. Mudrock intervals are interpreted as moderately to well-developed paleosols that developed on fine-grained overbank deposits (Kraus and Aslan, 1993; Kraus, 1996; 2002).

Matrix and mottle colors are due to differing concentrations of hematite (Fe_2O_3) and goethite ($FeO(OH)$) (e.g., Bigham et al., 1978; Schwertmann and Taylor, 1989; Schwertmann, 1993). Red paleosol colors are produced by hematite, whereas yellow-brown colors are dominated by goethite (Kraus, 2001). The redder the color, the greater the percentage of hematite and the better drained the original soil feature. Purple colors are produced by widely distributed grains of hematite in the absence of goethite (e.g., Wright et al., 2000; Kraus, 2001), and gray paleosol colors are nearly devoid of both hematite and goethite (e.g., PiPujol and Buurman, 1994). Purple and gray colors imply imperfectly drained soil conditions and likely resulted from gleying—the reduction and mobilization of Fe oxides—under prolonged saturated conditions in the presence of organic matter (e.g., Torrent et al., 1980; Wright et al., 2000). Calcium carbonate as nodules or in association with rhizocretions and burrows indicate at least moderately to well-drained soil conditions during the time of their precipitation (PiPujol and Buurman, 1997). Fe-oxide nodules, on the other hand, form in response to prolonged soil saturation and indicate imperfectly to poorly drained soil conditions (Vepraskas, 1999).

Heterolithic intervals are composed of medium gray to green-gray, fine-grained sandstone and mudrocks. These show diffuse red, yellow-brown, and purple mottles and contain fewer rhizocretions, burrows, and nodules than varicolored mudrock intervals. Heterolithic intervals are interpreted as avulsion belt deposits that were only weakly modified by paleopedogenesis (Kraus and Aslan, 1993; Kraus, 1996). Weak paleopedogenic development in these deposits suggests that sediment accumulation rates concurrent with avulsive deposition exceeded rates of pedogenesis.

Paleosol and avulsion deposit thicknesses, carbonate contents, and degrees of paleopedogenic development vary stratigraphically at Polecat Bench relative to the PETM interval (Woody, 2007).

Pre- and post-PETM deposits

Moderately to well-developed paleosols comprise ~35% of the measured section below and above the PETM interval (Fig. 2). These are less than 1 m thick typically and consist of 1–2 red, yellow-brown, brown, or purple soil B horizons interbedded with 1–4 m of avulsion belt deposits (Fig. 3A). Paleosols are interbedded with 1–4 m of avulsion belt deposits that commonly show relict bedding, dispersed organic matter, and molluscan body fossils; though most are pedogenically modified to some degree. Carbonate nodules and rhizocretions, and carbonate-filled burrows are common in paleosols and some sandstone beds, though far less abundant than in PETM interval strata.

The predominance of avulsion deposits and thin paleosol profiles outside the PETM interval suggest rapid and nonsteady rates of sedimentation. The thin paleosols are typical of compound soil profiles. Compound soils form in settings where punctuated episodes of overbank sedimentation are frequent and of such volume that pre-existing floodplain soils are buried and isolated from pedogenic processes (Marriott and Wright, 1993; Kraus, 1999).

PETM interval deposits

Paleosols comprise 55% of the PETM interval at Polecat Bench (Fig. 2). Paleosols are 1–3 m thick and composed of 2–9 separate, less than 1-m-thick beds of red, brown, yellow-brown, or purple mudrock (Fig. 3B). PETM interval paleosols show pervasive gray, yellow-brown and purple mottles; blocky soil structure; abundant carbonate nodules and calcareous rhizocretions; well-developed slickensides; and more abundant trace fossils. The tops of paleosols typically are either overprinted by overlying paleosols or truncated by erosional events. Paleosols are interbedded with 1–5 m thick intervals of avulsion belt deposits. Soil carbonate, in the form of pedogenic nodules, rhizocretions, and carbonate-filled burrows, increases significantly within the PETM interval (Woody, 2007).

Thicker and better developed soils and less frequent and thinner avulsion deposits suggests longer periods of subaerial exposure and a decrease in the frequency of avulsion

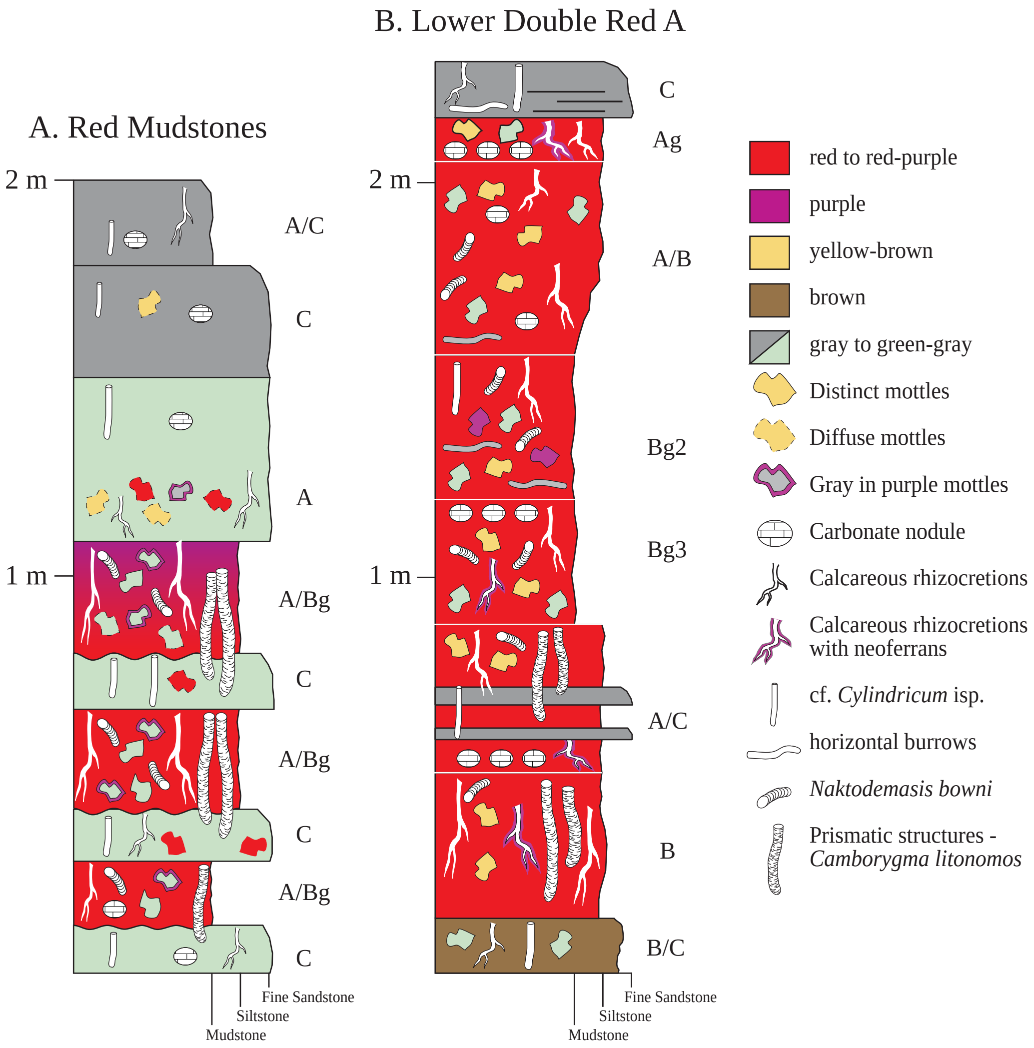

Figure 3. Representative measured sections of paleosol profiles containing prismatic soil structures. **A)** Red Mudstones paleosols are typical of compound paleosols from above and below the PETM interval. **B)** Lower Double Red A reflects a shift to thicker, cumulic paleosol profiles within the PETM interval and is the only paleosol of this type that contains prismatic soil structures. *A*, A horizon; *B*, B horizon; *C*, C horizon; *Ag* and *Bg*, gleyed A and B horizons, *B2* and *B3* indicate subdivisions of the B horizon based on different morphological properties.

deposition on the Willwood floodplain during the PETM. The thicker paleosols within the PETM interval are characteristic of cumulative soils. Cumulative soil profiles form in settings where the rate of overbank deposition is of low enough volume that sediments are incorporated into previously existing floodplain soils, rather than burying the soils and isolating them from further pedogenesis as in compound soil profiles (Marriott and Wright, 1993). The multiple beds of varicolored mudrock comprising these paleosols are interpreted as separate soil B horizons and likely indicate varying moisture conditions at depth and during different stages of paleopedogenic development. The thick accumulations of well-oxidized sediments and greater abundance of calcium carbonate as pedogenic nodules, rhizocretions, and carbonate-filled burrows suggest improved soil-drainage conditions on the Willwood floodplain during much of the PETM (Kraus and Riggins, 2007).

The cooccurrence of the PETM and thick cumulative paleosols in the Willwood Formation is not exclusive to Polecat Bench—such paleosols characterize the onset of PETM throughout the Bighorn and Powder River Basins (e.g., Wing et al., 2003; Kraus and Riggins, 2007). The wide geographic distribution of such distinctive paleosols in strata deposited during the PETM makes it highly unlikely these are due to changes in local floodplain conditions and, instead, represent an at least basin-wide if not regional change in fluvial conditions.

PRISMATIC PALEOSOLS

Prismatic soil structures at Polecat Bench are found almost exclusively in compound paleosols composed of thinly bedded (<0.5 m thick) red to red-purple (5R to 5RP) sandy mudstones overlying up to 1-m-thick beds of green-gray (5GY), fine-grained sandstone (Fig. 3A). Red to red-purple mudrock portions of these paleosols, in addition to distinct prismatic soil structures, show abundant gray mottles, moderately-developed slickensides, calcareous rhizocretions, and such invertebrate trace fossils as *Naktodemasis bowni*. Sandstone units are massive and without prismatic structures or large calcareous rhizocretions generally, though individual prisms and networks of thin calcareous rhizocretions may be present. Lithologic contacts between sandstone units and red mudstones commonly are sharp, though color contacts may be gradational to irregular due to mottling.

Prismatic Soil Structures

Description.—These are present in densities up to several hundred per m^3 in host paleosols (Fig. 4A-B). The prisms are predominantly vertical, straight to sinuous, roughly cylindrical shafts with rounded to subangular vertical faces and slightly concave to convex tops (Fig. 5A-C). Prisms are 15–50 mm in diameter and may narrow or widen slightly along their length. Prismatic structures are up to 400 mm long, however, true lengths are obscured because they disappear into or out of the outcrop face and are segmented commonly into <200 mm sections by slickensides (Fig. 4A). Prisms commonly terminate at depth in rounded to bulbous enlargements up to twice the diameter of the preceding length (Fig. 5C-D). Prism exteriors commonly show mm-scale knobby and transversely striated (cm-scale in length) surficial morphologies (Fig. 5A, E), though most are coated with <1 mm thick clay films (Fig. 5B-D). Mottles and rhizocretions crosscut or, more typically, follow prism exteriors and extend away from prismatic structures into the surrounding matrix (Fig. 4A-B, 5B). The prisms are most commonly composed of the surrounding paleosol matrix, or are composed less commonly of sediment from overlying units. In sandstone units, prisms appear to extend downwards from overlying red to red-purple mudstones—mottling along the prism exteriors commonly produce undulatory to irregular color contacts (Fig. 6A).

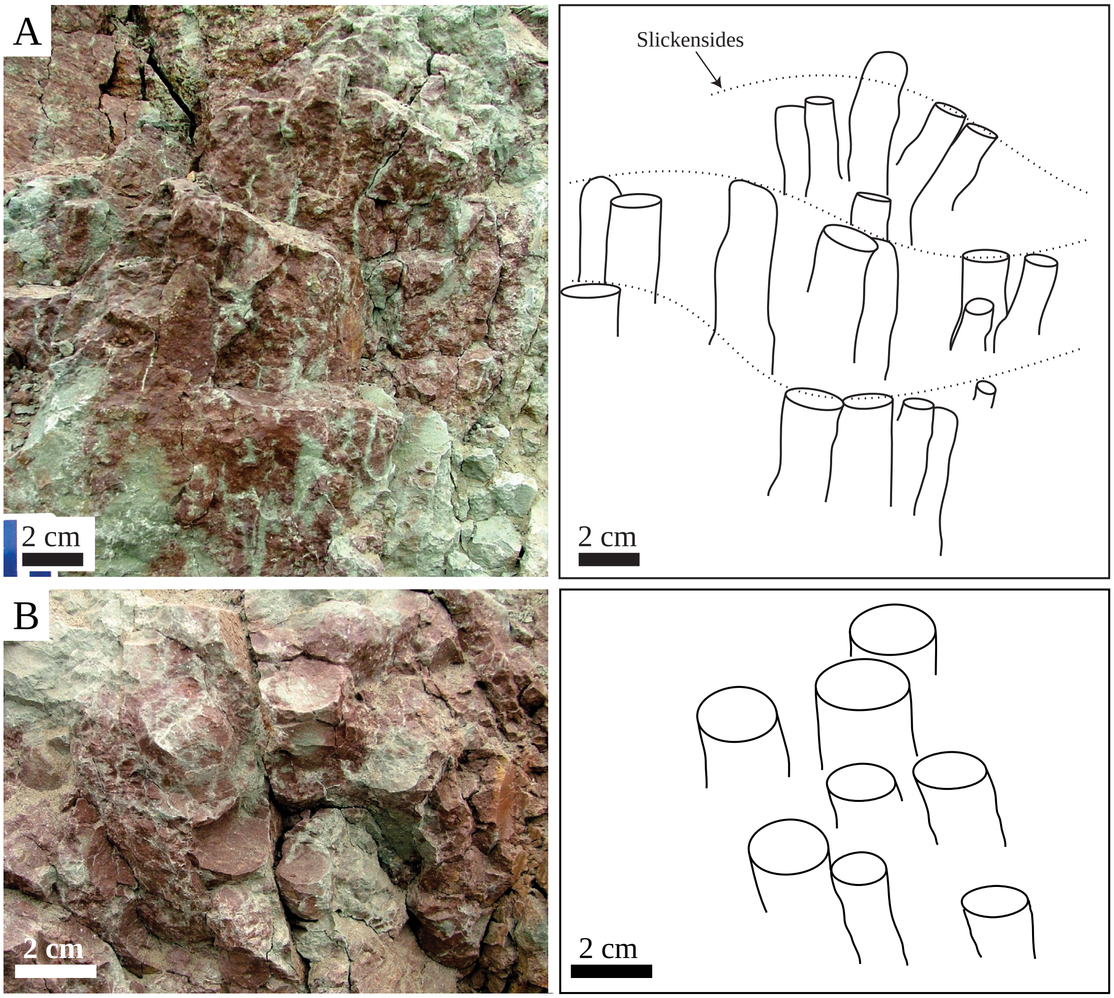

Figure 4. Outcrop view of prismatic soil structures with line drawings. **A)** Densely spaced prisms with prominent vertical gray mottles along prism exteriors in a red to red-purple compound paleosol crosscut by large planar slickensides; solid lines trace individual prisms; dotted lines trace where subhorizontal slickensides intersect with outcrop face. **B)** Closer view from above of prismatic structures showing circular cross sections and concave to convex tops.

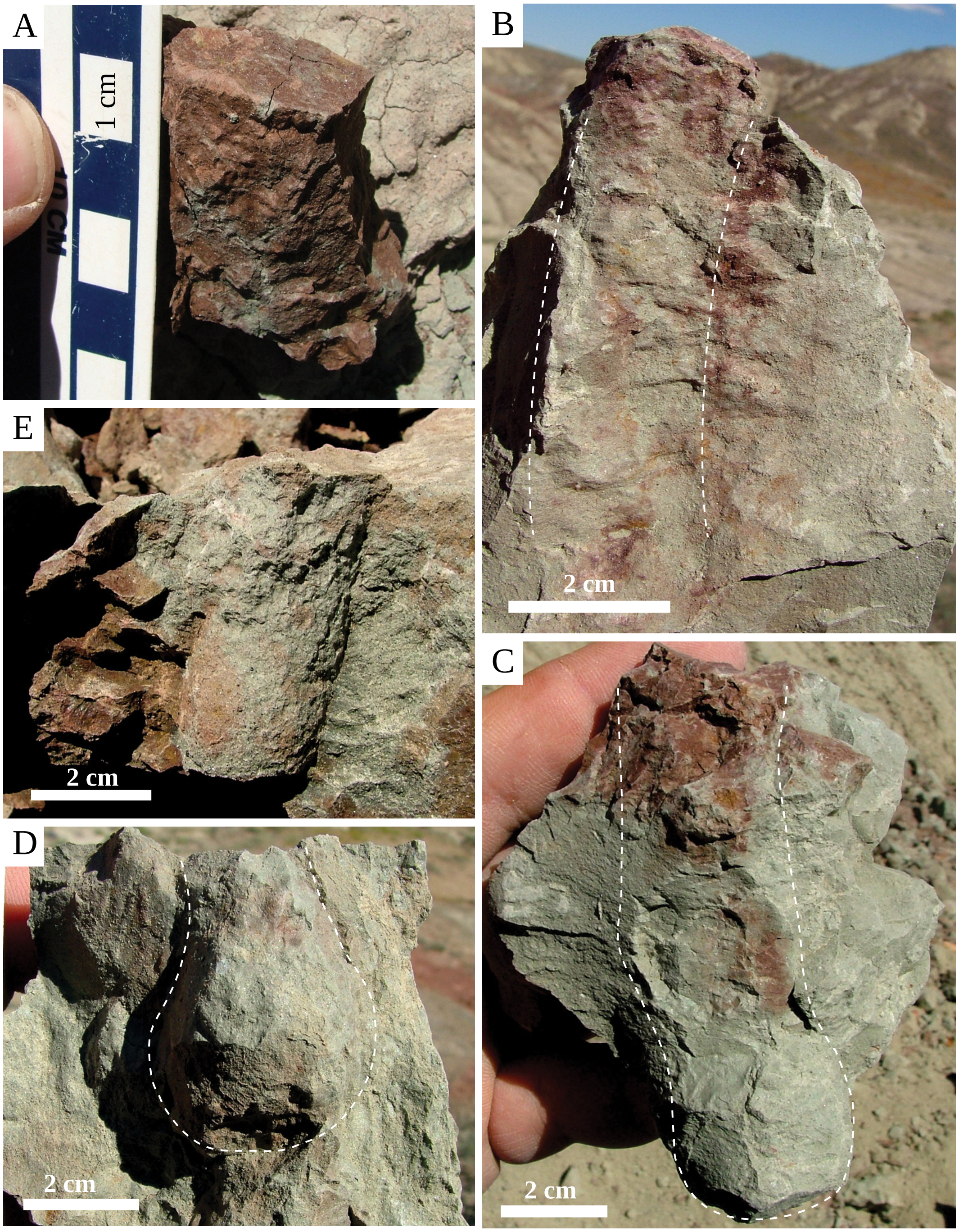

Figure 5. Individual soil prisms at Polecat Bench. **A)** Prismatic ped, note the squared-off top and slightly angular, clay-coated exterior. **B)** Section of soil prism (outlined by dashed line) from heterolithic interval showing clay slicked surface and red-purple mottling extending from prism into surrounding matrix. **C)** Soil prism outlined by dashed line terminating in a slightly larger chamber. **D)** Base of prism from heterolithic interval showing bulbous termination outlined by dashed line. **E)** Close-up of prism showing knobby surface morphology.

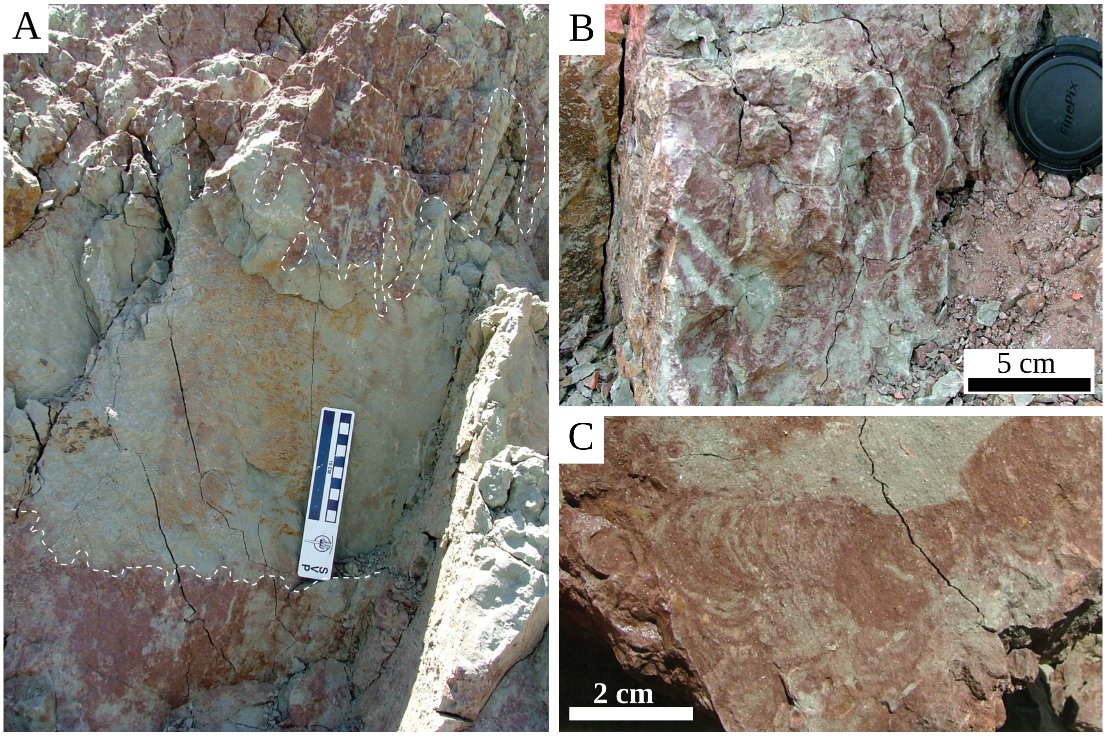

Figure 6. Field photos of features and other trace fossils associated with prismatic paleosols. **A)** Heterolithic interval interbedded with red to red-purple prismatic paleosols; upper contact is irregular and corresponds to mottling along soil prisms, lower contact is relatively sharp. **B)** Predominantly vertical, coarse calcareous rhizocretions and network of finer rhizocretions commonly associated with prismatic structures. **C)** Backfilled burrows assigned to *Naktodemasis bowni*, likely produced by burrowing insects, are also common traces in prismatic paleosols.

Interpretation.—In modern soils, prismatic peds develop commonly in smectitic sub-surface horizons under arid to semiarid conditions or in poorly drained soils and fragipans in humid regions (Brady and Weil, 2002). The architectural and surficial morphology of the prismatic soil structures at Polecat Bench, however, suggest that these are prism structures are actually the casts of freshwater crayfish burrows (Decapoda: Cambaridae). Paleosols intensely burrowed by freshwater crayfish have not previously been reported from the Willwood Formation, though they common in the Upper Triassic Chinle (Hasiotis and Dubiel, 1994), Upper Jurassic Morrison (Hasiotis et al., 1998), and Paleocene Fort Union formations (Hasiotis and Honey, 2000). The walls of extant crayfish burrows typically preserve the impressions of crayfish body parts and burrowing behaviors as scratch marks, scrape marks, striations, and knobby textures (Hasiotis and Mitchell, 1993). Fossil burrows with such surficial markings are assigned to the ichnogenus *Camborygma* and differentiated into ichnospecies based on burrow architecture (Hasiotis and Mitchell, 1993). Differences in burrow architectures (Fig. 7) preserve the tracemakers response to local and regional paleoenvironmental conditions during burrow excavation (Hasiotis and Mitchell, 1993).

Crayfish burrows at Polecat Bench are most similar to the ichnospecies *Camborygma litonomos* based on their simple architecture and relatively shallow depths. *C. litonomos* are associated commonly with pedogenically modified deposits suggesting relatively low rates of sedimentation and subaerial exposure for at least part of the year (Hasiotis and Honey, 2000). Modern crayfish that construct similar burrows spend most of their lives in open water, but burrow to reproduce or escape desiccation in areas with fluctuating water tables (Hobbs, 1942; 1981). Crayfish body fossils have not been reported from the Willwood Formation, though they are described from the early Eocene Fossil Butte Member of the Green River

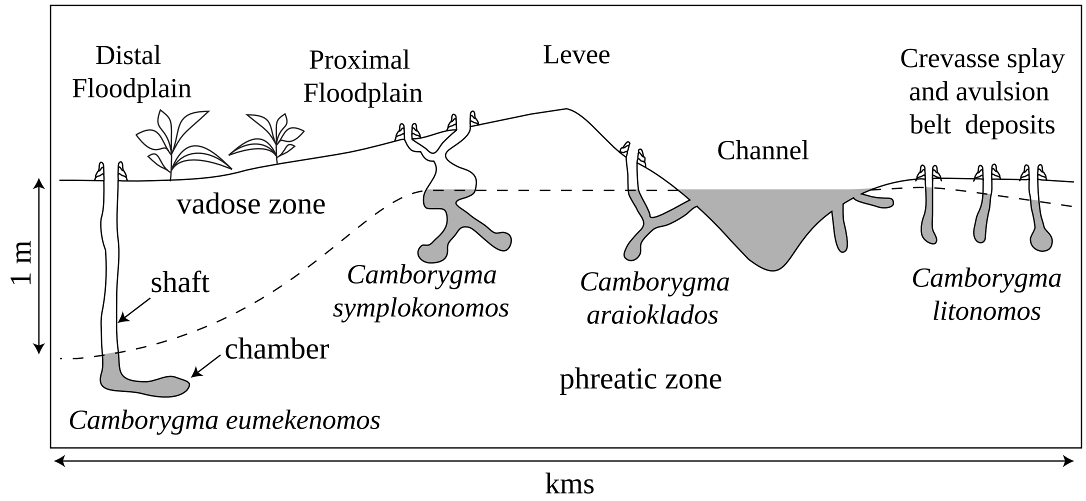

Figure 7. Architectural morphologies of the different ichnospecies of *Camborygma* with respect to position on the floodplain and depth to the water table. *Camborygma litonomos* composed of simple shafts with little branching and few chambers imply high water tables, periodic connectivity to open water sources, and shorter-term burrow occupation. Complex burrows with multiple shafts and chambers or long burrows that branch at depth indicate low water tables, decreasing access to surface waters, and long-term burrow occupation. Modified from Hasiotis and Honey (2000).

Formation in close association with the fossils of such aquatic fauna as ostracodes, shrimp, and fish (Feldmann et al., 1981). No crayfish burrows have been reported from lacustrine deposits of the Green River Formation likely because crayfish in such fully aquatic environments as rivers and lakes do not typically excavate burrows (Hobbs, 1981; Hasiotis and Mitchell, 1993).

Spiders, cicadas, lungfish, amphibians, bees and wasps, tiger beetles, and dung beetles also are known to construct vertical burrows with some form of a terminal chamber (e.g., Evans, 1963; Michener, 1974; Stanley and Fagerstrom, 1974; Ratcliffe and Fagerstrom, 1980; Doube, 1991; Hasiotis et al., 1993b; Hasiotis, 2002; Hembree et al., 2005; Hasiotis and Bourke, 2006). Their burrow morphologies and pedogenic associations, however, discount these soil organisms as the tracemakers of the Willwood Formation prismatic structures. For example, cicada nymphs (Hemiptera: Homoptera: Cicadidae) also excavate predominantly vertical shafts with bulbous terminations prior to emergence en masse from the soil during their fifth instar developmental stage (e.g., White et al., 1979; Luken and Kalisz, 1989). Prism diameters in the Willwood Formation, however, are highly variable (15–50 mm), are greater than reported diameters for cicada emergence burrows, and have a slightly right-skewed distribution (Fig. 8). All of these suggest that the prismatic structures were not constructed by cicadas but rather by populations of crayfish in different stages of development with many young adults compared to older, larger individuals.

Mottles

Description.—Vertical to subvertical, commonly downward tapering and branching, red, red-purple, and gray mottles with up to 50 mm circular to irregular-shaped cross sections and subvertical lengths up to 500 mm, commonly with red or purple rims (Fig. 4, 5B, 6A).

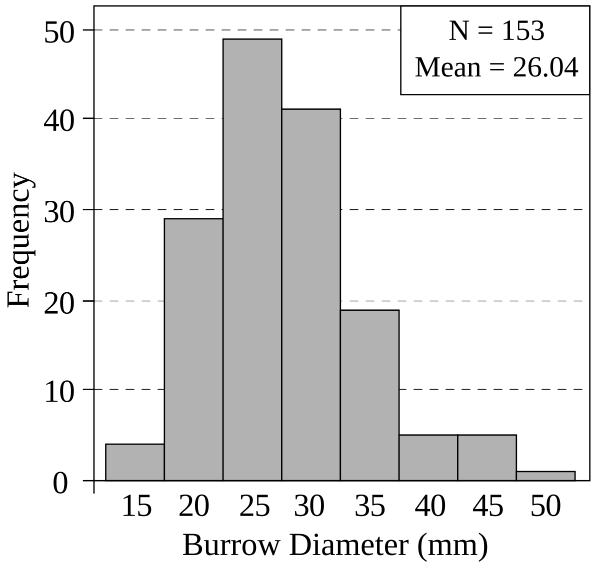

Figure 8. Histogram of *Camborygma litonomos* burrow diameters at Polecat Bench.

Interpretation.—Branching patterns and circular cross sections suggest that mottles are redoximorphic Fe depletions and concentrations within and adjacent to ancient root- and burrow-generated soil channels. Such soil channels are susceptible to gleying because of the likely presence of organic matter (e.g., Schwertmann, 1993). As waters move away from the channel to better oxygenated parts of the soil, the mobilized Fe is oxidized and precipitated as neoferrans—red and purple rims associated with mottles and traces (PiPujol and Buurman, 1994). Such redoximorphic features are common in modern soils that experience saturated soil conditions for part of the year, followed by periods of better drainage and lower water tables (Bigham et al., 1978; Torrent et al., 1980).

Slickensides

Description.—Subvertical to subhorizontal cm- to m-scale planar fractures with polished to striated, clay-lined surfaces. Entire paleosol profiles are crosscut by large slickensides that segment prismatic soil structures, rhizocretions, and other soil features (Fig. 4A). Slickensides also form along the exteriors of prisms and nodules (Fig. 5B, D).

Interpretation.—Pedogenic slickensides form around planes of weakness when smectite-rich sediment shrink and swell in response to seasonal wetting and drying (e.g., Yaalon and Kalmar, 1978; Aslan and Autin, 1998).

Calcareous Rhizocretions

Description.—Subvertical, downward tapering and branching, 10–50 mm diameter tubular structures up to 400 mm long containing solid to powdery calcite (Fig. 6B). These are also present as networks of 1–5 mm diameter structures showing a high degree of branching and containing powdery calcium carbonate, typically within gray mottles.

Interpretation.—Coarse (>10 mm) calcareous rhizocretions are interpreted as the primary roots or taproots of shrubs and other small plants based on their predominantly subvertical orientation and relatively large diameters. Networks of fine (<5 mm) rhizocretions are interpreted as the shallow root systems of smaller vegetation or the smaller diameter lateral root systems of primary roots. Calcareous rhizocretions indicate episodic saturation conditions in ancient soils—as soil drainage improves, calcite was precipitated within and around the previously saturated root channels (PiPujol and Buurman, 1997; Kraus and Hasiotis, 2006).

Naktodemasis bowni

Description.—Sinuous, variably oriented, and unlined burrows composed of a nested series of ellipsoid-shaped packets containing thin, meniscate backfills (Fig. 6C; Smith et al., in review). Burrows have <1–14 mm, circular to elliptical cross sections, are 10 to more than 150 mm long, and are present in groups of tens to thousands of individual specimens. Meniscate laminae typically are accentuated by alternating colors that correspond to matrix and mottle colors of the host rock. *Naktodemasis* are most abundant in red to red-purple mudstones, including those with prismatic soil structures.

Interpretation.—*Naktodemasis bowni* are interpreted as the locomotion and dwelling traces of burrowing insects—most likely 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 traces produced by these organisms in modern soils (Smith et al., 2008). Extant cydnids excavate backfilled burrows in well-rooted A horizons and upper B horizons of modern soils with 7–37% moisture content (Willis and Roth, 1962). Cicada nymphs and adult and larval scarabaeid beetles also excavate backfilled burrows with elliptical chambers, likely with similar soil moisture constraints (Counts and Hasiotis, 2006; Smith and Hasiotis, in review).

Cf. Cylindricum *isp.*

Description.—Predominantly vertical, straight to sinuous, unbranched, unlined, and smooth walled shafts with circular cross sections and gently rounded, unenlarged terminations. Burrow diameters range from 1–41 mm with an average diameter of 9.7 mm. Fill material typically is structureless sandstone, though burrows may also be filled with mudstone or carbonate. *Cylindricum* are uncommon in red to red-purple mudstones with prismatic soil structures, though they are the most abundant trace fossils in underlying sandstone beds.

Interpretation.—The lack of diagnostic morphologies complicates the assignment of these burrows to any specific group of tracemakers, though their orientation and preservation suggest formation in the upper vadose zone (e.g., Hasiotis, 2002). *Cylindricum* are similar to transient to temporary domichnia on modern floodplains produced by such burrowing organisms as beetles (Coleoptera), bees and wasps (Insecta: Hymenoptera), emerging cicada nymphs (Insecta: Hemiptera), spiders (Arachnida: Araneae), and mollusks (Bown and Kraus, 1983; Hasiotis, 2002).

STRATIGRAPHIC DISTRIBUTION OF CRAYFISH BURROWS

The presence and abundance of *Camborygma litonomos* as prismatic structures in paleosols vary depending on stratigraphic position relative to the PETM interval (Fig. 2). Crayfish burrows are abundant locally in red compound paleosols below and above the PETM interval, especially in the Red Mudstones and Purplish Red Mudstone (pre-PETM;

Fig. 3A) and the Top Red A and B (post-PETM) beds of Gingerich (2001). The association of red to red-purple matrix colors, prismatic soil structures, and predominantly vertical rhizocretions in these paleosols typically indicate the presence of at least a few well-preserved, if initially difficult at first to discern, *C. litonomos* specimens. Such features were not observed in some of the measured sections through Purplish Red Mudstone and Top Red A paleosols, indicating lateral variability in crayfish burrowing on the ancient floodplain. Well-preserved *C. litonomos* specimens are relatively common in prismatic paleosols below the PETM interval and sparse in such paleosols above the PETM interval.

Within the PETM interval, crayfish burrows as prismatic soil structures are present in only two paleosols: the base of Lower Double Red A (Fig. 3B) and Purple-3. Lower Double Red A is typical of the cumulative paleosols that developed during the PETM (Fig. 2). Crayfish burrows occur near the base of the profile in a series of red to red-purple mudstones and thin silty sandstone lenses atypical for the PETM interval and more characteristic of compound paleosols outside the PETM interval. Prismatic paleosols and *Camborygma litonomos* are completely absent from the predominantly red, cumulative paleosols that characterize the main body of the PETM interval between ~1512 and ~1531 m levels at Polecat Bench (Fig. 2). Purple-3 is an ~1 m thick, red-purple paleosol that more closely resembles non-PETM compound paleosols and shows weak prismatic structure in its basal ~20 cm. Other crayfish burrows observed within the PETM interval were as single *C. litonomos* specimens and from paleosols that did not show prismatic soil structures or predominantly vertical carbonate rhizocretions.

DISCUSSION

Crayfish Burrows and Pedogenic Processes

Soil biota, including freshwater crayfish, is one of the five soil-forming factors that contribute to the formation of soils in subaerially exposed continental and marine deposits (Jenny, 1941; Thorp, 1949; Hole, 1981; Retallack, 2001). Both pedoturbation (shrinking and swelling of clays, illuviation, and eluviation) and bioturbation act to destroy primary sedimentary structures and produce soil structures in the resulting soil profiles. Modern burrowing crayfish can initiate this process by homogenizing and redistributing sediments and organic matter to and from the ground surface and along the length of their burrows (Thorp, 1949; Hole, 1981; Hobbs and Whiteman, 1991). Crayfish burrows extend the effective depth of subaerial exposure and pedogenesis beyond their normal range by increasing soil aeration, improving drainage conditions, and transporting surface microorganisms deeper into the soil profile (Richardson, 1983; Stone, 1993). Richardson (1983) found that soil respiration rates near burrow walls were approximately double that only 50 mm deeper into the soil matrix. Reduced CO_2 concentrations and increased availability of O_2 in the surrounding soil stimulate the growth of microbial films, fine root networks, and fungal hyphae close to burrow walls. Improvements in gas exchange and drainage also can promote the oxidation of Fe-minerals and precipitation of calcium carbonate in the soil matrix (PiPujol and Buurman, 1997). Such organisms as burrowing crayfish that significantly modify or maintain their physical environments and regulate the availability of resources for other species are referred to often as ecosystem engineers (Jones et al., 1994; Jouquet et al., 2006).

Burrowing Eocene crayfish also likely initiated and mediated the pedogenic development of some overbank deposits on the Willwood floodplain (Fig. 9). The uppermost part of crayfish-burrowed intervals defines a relatively stable paleo-surface under which pedogenic modification of the sediment occurred (Hasiotis and Honey, 2000). As with modern crayfish, open burrows likely initiated the oxidation of Fe-bearing minerals and stimulated the growth of roots, microbial films, and fungal hyphae along the burrow walls by improving soil gas exchange and drainage. These crayfish-mediated processes probably continued along burrow walls after the burrows were abandoned and filled with sediment and likely contributed to burrow preservation by maintaining a plane of weakness between the filled burrow and the surrounding soil.

Well-preserved specimens of *Camborygma litonomos*, are uncommon in most prismatic paleosols despite the high volume of burrowing activity implied by dense collections of soil prisms. The rarity of well-preserved burrows suggests that bioturbation by crayfish in host soils had decreased or ceased altogether for some time prior to final burial of the soil. Distinct surficial morphologies on most burrows appear obscured by illuviated clay coatings, slickensides, bioturbation by other soil fauna, and plant rooting during this later, post-crayfish period of pedogenic modification. Such associated ichnofossils as *Naktodemasis bowni* and thick, predominantly vertical calcareous rhizocretions likely represent a later occupation of the soil media by tracemakers preferring lower water tables or more stable soil moisture conditions. This later period of paleopedogenesis acted to obscure or overprint pre-existing burrow fabrics, but was not vigorous enough to obliterate it completely and resulted in a prismatic soil structure and remnant *C. litonomos* burrows throughout.

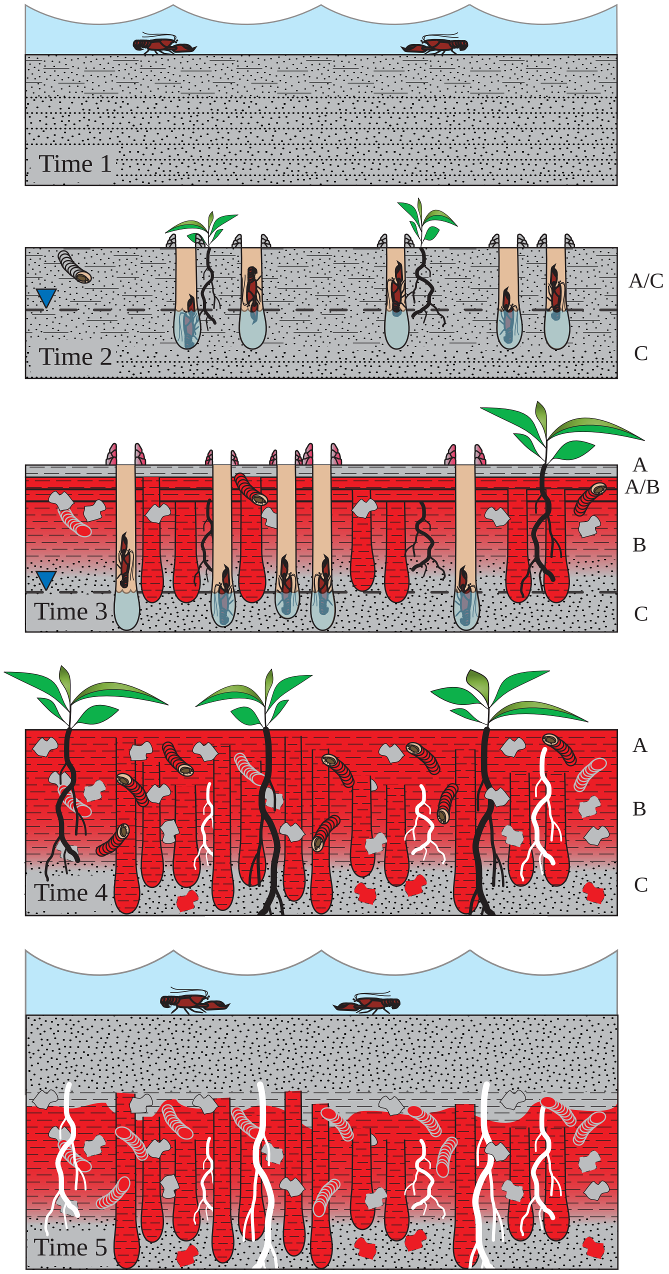

Figure 9. Interpreted formation of features associated with crayfish burrowed deposits. **Time 1)** River avulses and deposits fine-grained sand and mud onto the floodplain. **Time 2)** Flooding subsides, crayfish burrow to escape desiccation as water table (triangle) falls below the ground surface. Crayfish, plants, and other soil biota colonize the drained sediments and initiate pedogenesis. **Time 3)** Annual flooding deposits thin layers of sediment which are homogenized into the soil profile. Crayfish burrow deeper as water tables continue to fall; burrows promote oxidation and pedogenesis by improving aeration and drainage. **Time 4)** Crayfish abandon floodplain as water table deepens below levels they can reach; further pedogenesis modifies pre-existing crayfish burrows creating a prismatic soil structure. **Time 5)** Next avulsion buries and preserves the underlying soil.

Paleohydrology and Paleoclimate Implications

Modern freshwater crayfish burrow to escape extreme surface conditions or to create a source of standing water and humid air (Payette and McGaw, 2003). The depths and architectures of crayfish burrows reflect the amount of time the burrow was occupied, connectivity to surface waters, and local water-table position (Hobbs, 1942; 1981). Crayfish construct burrows that range from simple subvertical to subhorizontal shafts a few centimeters deep, to complex burrow systems as much as 5 m in depth and composed of branching corridors and chambers of various size, shape and location. Burrow depths, chamber positions, or horizontal branching often define the lower limit of the local water table. Studies of freshwater crayfish burrows in Permian to Holocene continental deposits demonstrate that their distribution, depth, and burrow architecture reflect local and regional paleohydrologic conditions (Hasiotis and Mitchell, 1993).

The most prevalent crayfish species on the Willwood floodplain were probably tertiary burrowers based on the architecturally simple and relatively shallow (< 400 mm) *Camborygma litonomos* burrows at Polecat Bench. Such species live typically in open waters and take refuge in simple, shallow burrows during the dry season in areas with relatively high or fluctuating water tables, or during the mating season (Hobbs, 1981). Prolonged episodes of low seasonal water tables and well-drained soil moisture conditions would likely preclude shallow-burrowing crayfish species from living out on the floodplain (e.g., Taylor, 1983). Tertiary burrowing species under these conditions would likely be relegated to such aquatic environments as stream channels, wetlands, and lakes (Acosta and Perry, 2001).

Decreases in the stratigraphic presence of prismatic paleosols and *Camborygma litonomos* specimens in much of the ~40-m PETM interval suggests that intense and prolonged burrowing by crayfish was less common on the Willwood floodplain during the global warming event, particularly between the ~1512 and ~1531 m levels. Less abundant crayfish burrowed soils during the PETM likely signals a significant and prolonged shift toward improved soil drainage and an overall increase in water table depths on the Willwood floodplain. Manganiferous rhizocretions, interpreted as indicating poorly drained soil conditions, follow much the same pattern—these are abundant in avulsion deposits outside the PETM interval, become increasingly rare above the ~1500 m level, and are absent between ~1512 and ~1531 m (Woody, 2007). The appearance of crayfish burrows and burrowed horizons toward the top of the PETM interval, specifically in the Purple-3 paleosol, likely signals a return to wetter conditions on the Eocene floodplain.

The formation of thick cumulative-soils, and the presence of pervasive pedogenic carbonate nodules and calcareous rhizocretions within the PETM interval also suggest that the Willwood floodplain experienced improved soil drainage conditions, along with less frequent flooding events. This interpretation agrees with previous studies that suggest the PETM coincided with sharp decreases in mean annual precipitation and drier conditions on the Willwood floodplain (Wing et al., 2005; Kraus and Riggins, 2007). Pervasive mottling, well-developed slickensides, and Fe-oxide nodules in some paleosols within the PETM interval argue against arid or ever-dry conditions; rather, these redoximorphic features suggest an overall increase in seasonality with shorter inundated periods on the floodplain and longer dry seasons resulting in lowered water tables and increased subaerial exposure (e.g., Kraus, 2001).

CONCLUSION

Paleosols and continental trace fossils must be studied with an interdisciplinary approach that evaluates the physical, biological, and chemical components of paleosols to interpret more accurately their paleopedogenic and climatic history (e.g., Hasiotis et al., 2007). Crayfish mediated soil structures in paleosols of the Willwood Formation provide valuable information with respect to hidden biodiversity in the absence of body fossils, paleopedogenic processes, paleohydrologic regime, and paleoclimatic conditions during the early Paleogene in the Bighorn Basin, Wyoming. Such trace fossils as *Camborygma*, *Naktodemasis*, *Cylindricum*, and the various types of rhizoliths, however, are not isolated components of paleosols in the Willwood Formation; they were intimately linked to soil-forming processes at work on the Willwood floodplain. Crayfish burrowing, in particular, likely initiated and mediated pedogenic development of prismatic soils by homogenizing burrowed horizons, improving soil aeration and drainage, and stimulating rooting. Together, these processes produced peds in red and red-purple Willwood soils that originated as crayfish burrows and later developed into prismatic structures. Decreases in the stratigraphic presence and abundance of crayfish burrows from most of the PETM interval suggest a decrease in sedimentation rates and long-term drop in the paleo-water table levels. These were likely due to more pronounced seasonality and a major episode of drying on the Willwood floodplain during the transient, though severe, global warming during the PETM (Kraus and Riggins, 2007).

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CHAPTER 5. RELATIONSHIP OF FLOODPLAIN ICHNOCOENOSES TO PALEOPEDOLOGY, PALEOHYDROLOGY, AND PALEOCLIMATE IN THE WILLWOOD FORMATION, BIGHORN BASIN, WYOMING, DURING THE PALEOCENE-EOCENE THERMAL MAXIMUM (PETM)

Currently in review as:

Smith, J.J., Hasiotis, S.T., Kraus, M.J., and Woody, D.T. Relationship of floodplain ichnocoenoses to paleopedology, paleohydrology, and paleoclimate in the Willwood Formation, Bighorn Basin, Wyoming, during the Paleocene-Eocene Thermal Maximum (PETM). *PALAIOS*.

ABSTRACT

Vertical changes in distribution, abundance, and ichnodiversity of ichnocoenoses—as proxies for soil biotic communities—in alluvial deposits of the Willwood Formation suggest significantly drier moisture regimes in the Bighorn Basin, Wyoming, during a transient period of global warming known as the Paleocene-Eocene Thermal Maximum (PETM). The Willwood Formation at Polecat Bench is composed of a massive mudstone lithofacies interpreted as moderately to well-developed paleosols and a heterolithic lithofacies interpreted as avulsion belt deposits. These contain an abundant assemblage of ichnofossils, including various types of rhizoliths and such invertebrate trace fossils as *Naktodemasis bowni*, *Camborygma litonomos, Edaphichnium lumbricatum*, cf. *Cylindricum* isp., cf. *Planolites* isp., cf. *Steinichnus,* and cocoon-traces, that comprise five distinct ichnocoenoses. Ichnocoenoses are categorized as dominantly terraphilic, hygrophilic, or hydrophilic based on the inferred moisture regimes of their most abundant ichnofossil morphotypes and associated pedogenic features, including the other trace fossils and rhizoliths. The interpreted moisture regimes correlate well to the paleoenvironments inferred from sedimentology and paleopedology of their host lithofacies.

Outside the PETM interval, abundant avulsion deposits and thin compound paleosols containing hygrophilic and hydrophilic ichnocoenoses suggest frequent depositional events and predominantly poor to imperfect soil-drainage conditions. Thick cumulative paleosol profiles with abundant terraphilic to hygrophilic ichnocoenoses within the PETM interval suggest dramatically improved drainage on the Willwood floodplain. Lithofacies and ichnocoenoses above the PETM interval are not significantly different from those below the PETM, indicating a return to pre-PETM moisture regimes. These conclusions support previous studies that suggest the Bighorn Basin experienced transient drying during the PETM. This study demonstrates how ichnocoenoses and their ichnopedologic associations can be used to refine paleohydrologic and paleoclimatic generalizations inferred from paleoclimate models.

INTRODUCTION

This paper describes ichnocoenoses—proxies for above- and below-ground soil biotic communities—in alluvial deposits of the Willwood Formation, Bighorn Basin, Wyoming, from before, during, and after a transient episode of global warming known as the Paleocene-Eocene Thermal Maximum (PETM). Willwood alluvial deposits and paleosols contain a diverse and abundant assemblage of plant, invertebrate, and vertebrate trace fossils (Bown and Kraus, 1983; Hasiotis et al., 1993; Smith et al., 2008). These trace fossils likely represent soil biota with specific paleoenvironmental, paleohydrologic, and paleoecologic habitat preferences (e.g., Wallwork, 1970; Hasiotis et al., 2007). The primary limiting factor on the distribution and diversity of continental organisms is the availability of freshwater (Hasiotis et al., 2007). Terrestrial and freshwater invertebrates, in particular, are sensitive to moisture and temperature conditions because they must avoid desiccation and overheating, extreme highs and lows in soil-moisture levels, and excess carbon dioxide and hypoxic soil conditions (e.g., Hasiotis, 2007, and references therein). The trace fossils of soil-dwelling organisms that shared similar sediment moisture requirements and tolerances should occur together stratigraphically as distinct assemblages or ichnocoenoses. Willwood ichnocoenoses, thus, are important *in situ* indicators of the paleoenvironment, paleohydrologic regime, degree of pedogenesis, and paleoclimatic setting during the time of their formation.

Multiple lines of evidence suggest that temperatures increased dramatically in the Bighorn Basin during the PETM. The PETM is recorded worldwide in ~55 Ma continental and marine deposits by a negative 2–6‰ carbon isotope excursion (CIE) in carbonate and dispersed organic carbon sources (e.g., Koch et al., 1992; Bowen et al., 2001; Bains et al., 2003; Magioncalda et al., 2004). Mean annual temperature (MAT) in the basin may have increased by 3–7°C from late Paleocene estimates to ~26°C based on oxygen-isotope compositions of carbonate nodules (Koch et al., 2003), tooth enamel and gar scales (Fricke et al., 1998), and Fe oxides (Bao et al., 1999). These estimates are in general agreement with those derived from leaf-margin analysis of floral assemblages in the Willwood Formation (Wing et al., 2005). The PETM was coincident with significant changes in both marine and continental biotic communities, including a mass extinction in benthic foraminifera (Thomas, 1998) and a dramatic turnover in fossil mammal faunas in North America (Gingerich and Clyde, 2001). The CIE and global warming resulted likely from a large release of ^{13}C-depleted carbon to the atmosphere (Zachos et al., 2005). Proposed carbon sources include destabilized methane clathrates from continental shelf deposits (e.g., Dickens et al., 1995), combustion of shallowly buried coal or peat (Kurtz et al., 2003), or thermogenic methane from volcanic and hydrothermal vent complexes (e.g., Svensen et al., 2004; Storey et al., 2007).

While there is little doubt that temperatures and atmospheric CO_2 levels increased substantially during the early Eocene, interpretations differ as to the effects on the regional precipitation patterns and paleohydrologic regime. Global climate modeling studies have interpreted increased precipitation in the Bighorn Basin during the PETM interval (Koch et al., 2003; Shellito et al., 2003; Bowen et al., 2004). Recent studies of fossil flora through the PETM (Wing et al., 2005) and of changes in the sedimentology, morphology and geochemistry of paleosols (Kraus and Riggins, 2007) suggest sharp declines in precipitation through this time.

Changing paleoclimatic and paleohydrologic conditions during the PETM likely influenced the diversity, distribution, and abundance of soil-dwelling organisms based on their requirements for or tolerances of different soil moisture regimes. The well-studied sedimentology and paleopedology of the Willwood Formation, abundant ichnofossils, and known stratigraphic position of the CIE at Polecat Bench offer an opportunity to test if soil communities responded to changing paleohydrologic and paleoclimatic conditions through the PETM. Changes in the distribution, ichnodiversity, and abundance of ichnocoenoses may also help to resolve conflicting paleoprecipitation and paleohydrologic interpretations for the Bighorn Basin during the PETM global warming event.

GEOLOGIC SETTING

The basal ~100 m of the Paleogene Willwood Formation crop out at the southern end of Polecat Bench—a 120-km-long Pleistocene river terrace extending south-southwest from Montana into northern Wyoming (Fig. 1). The Willwood Formation is a 780-m-thick alluvial succession deposited during the latest Paleocene and early Eocene coeval with Laramide structural development of the Bighorn Basin in northern Wyoming (Neasham and Vondra, 1972). The Willwood Formation is composed of three primary lithofacies. The first is fine-grained massive mudrock interpreted as overbank deposits on which moderately to well-developed soils formed (Kraus and Aslan, 1993). These are interbedded with the second lithofacies—heterolithic units composed of thin ribbon sandstone and mudrocks interpreted as the crevasse-splay deposits generated by channel avulsion. They show weak soil development (Kraus, 1996). The third lithofacies is composed of thick, multistoried sheet-sandstone bodies interpreted as the channel deposits of meandering rivers (Kraus and Middleton, 1987; Kraus, 2001). Thick channel sandstone bodies are present in the study area at Polecat Bench, though these are outside the measured section containing the PETM interval (Gingerich, 2001).

Polecat Bench is the most studied location for the PETM in continental deposits because the isotope chemostratigraphy and biostratigraphy associated with the CIE is highly resolved. Isotopic analyses of pedogenic carbonates (Koch et al., 1992; Bowen et al., 2001) and dispersed organic carbon from bulk rock samples (Magioncalda et al., 2004) indicate that an ~40 m interval of the Willwood Formation at Polecat Bench was deposited during the PETM. The PETM interval is also distinguished by two distinct mammalian faunas: the Wasatchian-*Meniscotherium* (Wa-M) and the Wasatchain-0 (Wa-0) biozones (e.g., Gingerich, 2001; 2003; Magioncalda et al., 2004). The Wa-M biozone represents the first

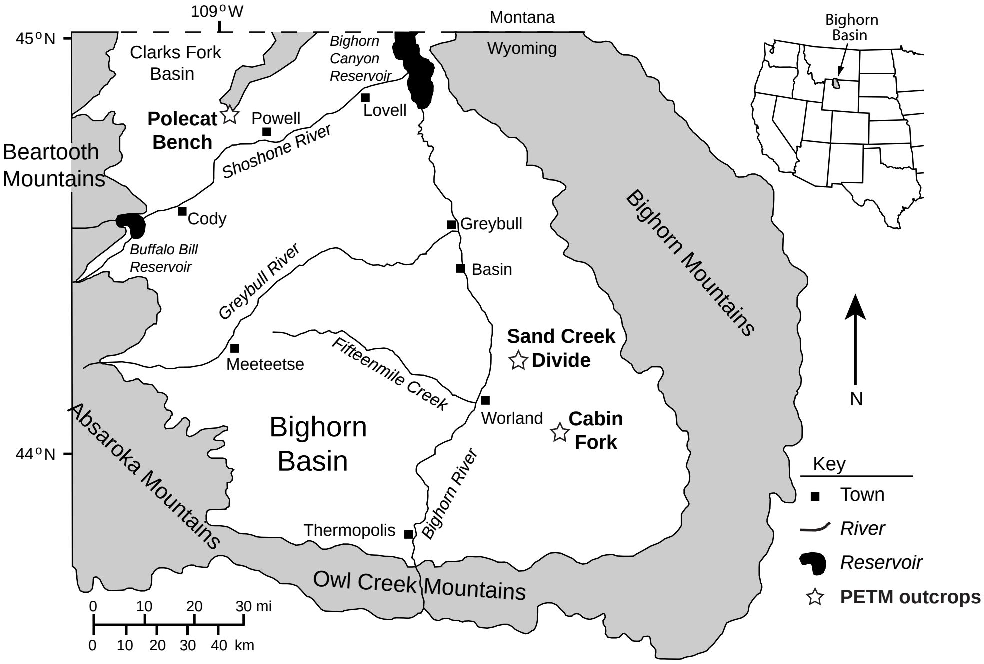

Figure 1. Locations of the Polecat Bench study area and other Willwood Formation exposures of strata deposited during the PETM (stars). Modified from Bown and Kraus (1981).

appearance of *Meniscotherium* and starts several meters above the onset of the PETM (Fig. 2). The Wa-M fauna is replaced by the Wa-0 fauna composed of the first artiodactyls, perissodactyls, hyaenodontids, and true primates in North America. The two faunas roughly correspond with the main body of the PETM interval and represent an abrupt and permanent turnover in North American fossil mammal assemblages.

METHODS

We excavated an ~80 m section in the Willwood Formation from ~20 m below to ~20 m above the ~40 m PETM interval at Polecat Bench (Fig. 2). Stratigraphic position of the PETM interval was based on previous stable isotope studies (Koch et al., 1992; Bowen et al., 2001). All units were measured with a Jacob staff and sighting level. Lithologic units were characterized in the field by color, grain size, sedimentary structures, mottle colors, nodule types and abundance, and slickensides.

The stratigraphic position and relative abundance of trace fossils were recorded for each lithologic unit. Burrows were described according to their architectural and surficial burrow morphology and burrow fill (e.g., Hasiotis and Mitchell 1993; Hasiotis et al. 1993b; Hasiotis et al. 2004). Ichnocoenoses were designated independent of the sedimentological, depositional, or paleopedologic characteristics of the surrounding strata to increase their interpretive power and to provide information about within-facies variations in ichnodiversity and paleohydrology (Hasiotis 2002, 2004). Ichnocoenoses were named based on the predominance of a particular ichnotaxon and associated ichnotaxa. The presence of rare trace fossils or uncommon associations was not used as a basis for identifying specific ichnocoenoses. Three iterations of ichnocoenoses construction were performed to test and refine paleoenvironmental and paleohydrologic interpretations by comparing the ichna

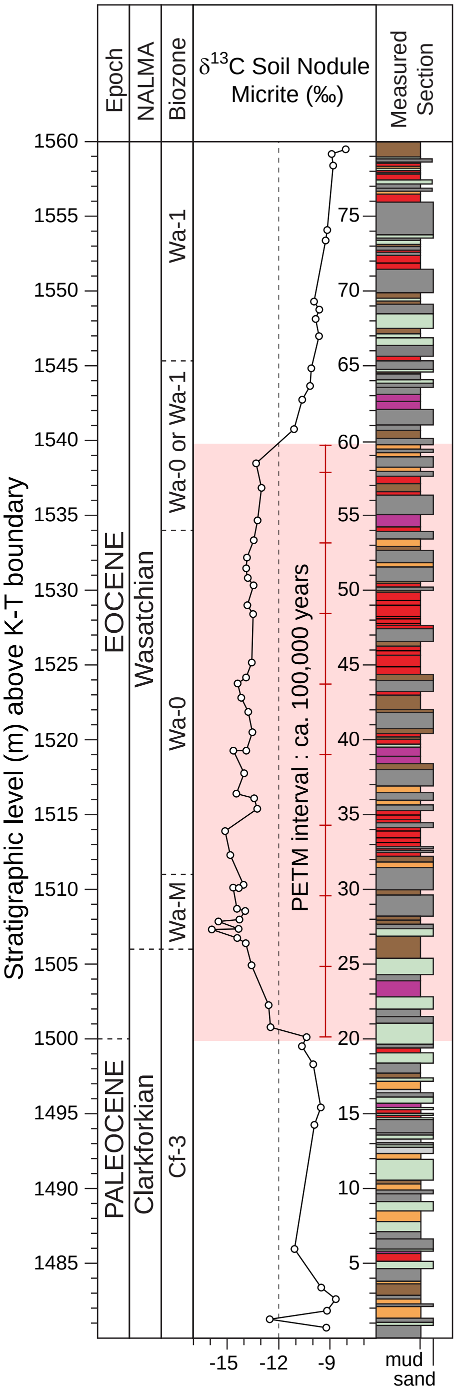

Figure 2. Composite measured section at Polecat Bench. Shaded area highlights the PETM interval. Modified from Bowen et al. (2001), Gingerich (2001), and Bains et al. (2003).

against the pedogenic characteristics and pre- and post-depositional sedimentologic context of the host strata. Chi-square tests of independence (χ^2) were preformed to evaluate relationships between the distribution of ichnocoenoses and the PETM interval. Both lithofacies and ichnocoenoses were ranked independently on a scale from 1 to 4 based on their interpreted paleohydrologic conditions—poorly, imperfectly, moderately, or well-drained regimes assigned a ranking of 1, 2, 3, or 4, respectively. Initial lithofacies drainage rankings were assigned based on the dominant matrix color and grain size of the lithofacies and then adjusted for the presence and abundance of carbonate nodules, iron-oxide nodules, or clay slickensides. Initial ichnocoenoses drainage rankings were assigned based on most common trace fossils associations and then adjusted by a half or full rank based on the abundances of calcareous rhizocretions suggesting better drained conditions, or carbonaceous roots or manganiferous rhizocretions suggesting imperfect drainage. Both sets of drainage rankings were averaged vertically at 0.5 m intervals of the measured section because the lithologic units on which they are based range from 0.04 to 1.25 m in thickness. We used nonparametric Kruskal-Wallis tests (H) to evaluate differences in estimated drainage conditions from below, within, and above the PETM interval. All statistical tests were preformed using Minitab (Release 14, Minitab Inc., State College, Penn.).

LITHOFACIES

Willwood Formation deposits at Polecat Bench are composed of two primary lithofacies: varicolored massive mudrocks and heterolithic units composed of sandstone and drab-colored mudrocks. The distinction between the two lithofacies is based largely on grain-size differences and the presence or absence of such features as mottles, nodules, clay slickensides, rhizoliths, and other trace fossils (e.g., Kraus and Aslan, 1993; Kraus, 1996; Kraus and Gwinn, 1997).

Massive-Mudrock Lithofacies

Description.—Red, yellow-brown, brown, and purple, 0.3–3.0 m thick beds of claystone, mudstone, and siltstone, all pedogenically modified to varying degrees. Primary sedimentary structures are absent, and nearly all beds contain distinct mottles, carbonate or Fe-oxide nodules, rhizoliths and other trace fossils of various types and abundances, and clay slickensides.

Interpretation.—The massive-mudrock lithofacies is interpreted as fine-grained overbank deposits on which moderately to well-developed paleosols formed (e.g., Kraus and Aslan, 1993; Kraus, 1996; 2002). Most of the paleosols are composed of several horizons distinguished primarily by vertical changes in grain size, color patterns, and such features as mottle color and intensity, carbonate nodules, Fe-oxide nodules, rhizoliths and other trace fossils, and clay slickensides. Typical paleosol profiles consists of one or more beds of red, yellow-brown, brown, or purple mudrocks containing distinct pedogenic features and interpreted as soil B horizons. These may be overlain by gray to green-gray mudstones to sandy mudstones interpreted as soil A horizons. Soil A horizons, however, are absent in many profiles likely due to truncation or to incorporation into the aggrading profiles as B horizons. B horizons generally grade downward into coarser grained units forming the base of the profiles and interpreted as C horizons.

Matrix colors and pedogenic features preserved in the B horizons are used to interpret the hydrologic regime and redox conditions of the original soils. Red, brown, and yellow-brown matrix and mottle colors are due to a mix of hematite (Fe_2O_3) and goethite ($FeO(OH)$), each of which precipitates under different hydrologic regimes (e.g., Bigham et al., 1978; Schwertmann and Taylor, 1989; Schwertmann, 1993). In general, the greater the percentage of hematite, the redder the color and better drained the original soil or soil feature. Purple colors are produced by sparse and widely distributed hematite grains in the absence of goethite (e.g., Wright et al., 2000; Kraus, 2001), whereas gray paleosol features are nearly devoid of both hematite and goethite (e.g., PiPujol and Buurman, 1994). Purple and gray colors imply imperfectly drained soil conditions and likely resulted from gleying—the reduction and mobilization of Fe oxides—under prolonged saturated conditions and in the presence of organic matter (Bigham et al., 1978; Torrent et al., 1980). Calcium carbonate is present in many paleosols, particularly within the PETM interval, as nodules or in association with rhizoliths and burrows. These types of carbonate accumulations indicate at least moderately to well-drained soil conditions during the time of their precipitation (PiPujol and Buurman, 1997). Fe-oxide nodules, on the other hand, form in response to prolonged soil saturation and indicate imperfectly to poorly drained soil conditions (Vepraskas, 1999). Pedogenic slickensides are common in Willwood paleosols and are formed by the shrinking and expansion of smectitic clays due to seasonal wetting and drying (e.g., Yaalon and Kalmar, 1978).

The degree of paleopedogenic modification was controlled primarily by variations in the rate and volume of sediment accumulation and drainage conditions during pedogenesis (e.g., Bown and Kraus, 1987; Kraus and Aslan, 1993; Kraus, 1996; 2002). The paleosol lithofacies is further divided into separate pedofacies according to the dominant matrix colors for the purpose of description and paleohydrologic interpretation.

Red Paleosols.—Red (5R to 10R) mudstone to sandy mudstone beds (<1 m thick) containing abundant to common gray, yellow-brown, and purple mottles, as well as abundant

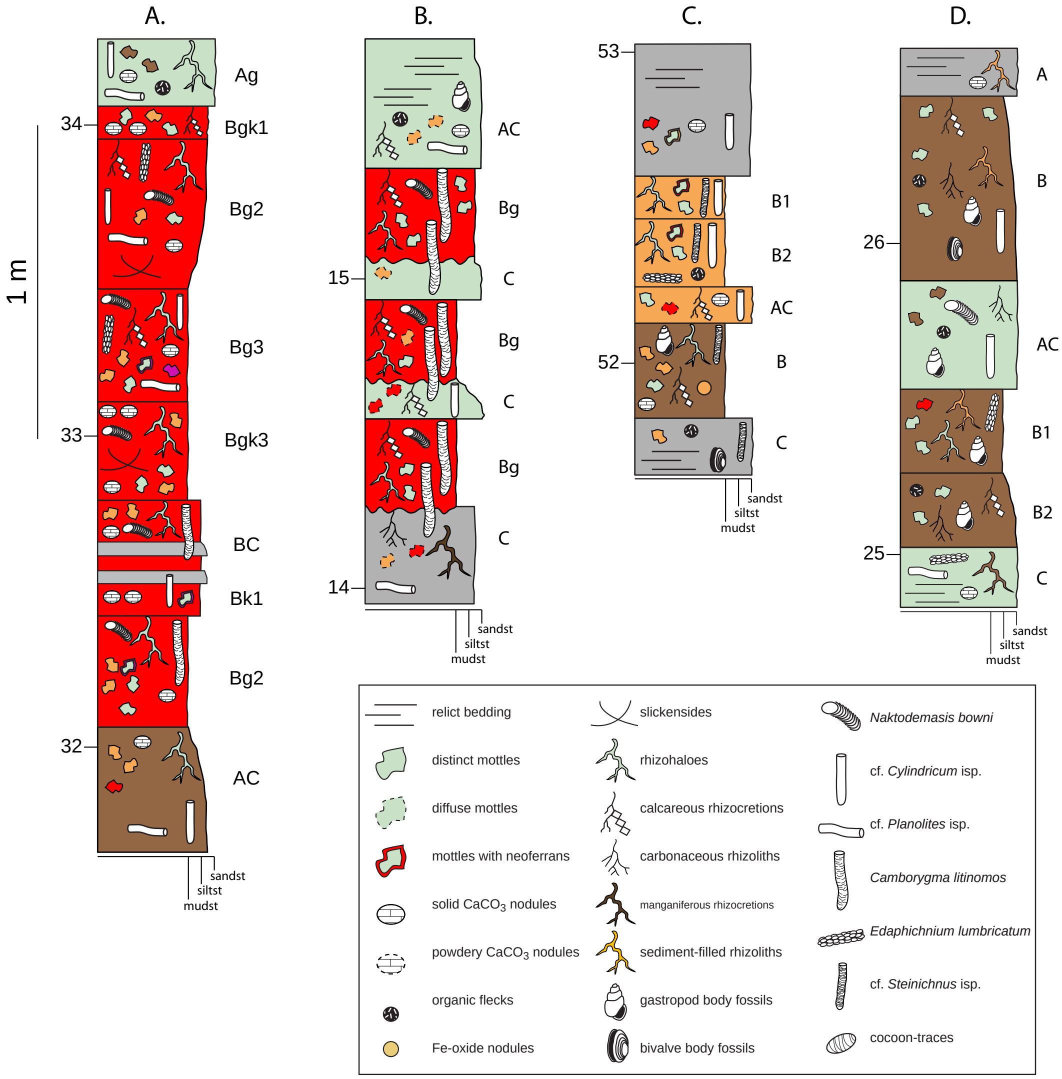

Figure 3. Measured sections through the different pedofacies at Polecat Bench. **A)** Red paleosol with multiple B horizons. **B)** Vertically stacked red paleosols. **C)** Vertically stacked yellow-brown and brown paleosol profiles. **D)** Vertically stacked brown paleosol profiles. *A*, A horizon; *B*, B horizon; *C*, C horizon; *BC*, transitional between B and C horizon; *g*, gleyed horizons; *k*, carbonate accumulations; numbers following horizon types indicate subdivisions based on different morphological properties.

carbonate nodules, moderately developed slickensides, and abundant rhizoliths of various types (Figs. 3A–B). Red matrix colors (hematite) and abundant carbonate nodules and rhizoliths indicate that red paleosols were oxidized and at least moderately drained most of the time (e.g., Schwertmann, 1993). Pervasive gray and yellow-brown mottles and clay slickensides suggest these paleosols experienced seasonal wetting and drying (e.g., Aslan and Autin, 1998).

Yellow-brown Paleosols.—Thin (<1 m thick) beds of yellow-brown (10YR) mudstone to sandy siltstone are commonly interbedded with gray to green-gray fine-grained sandstone (Fig. 3C). Gray to diffuse red mottles, yellow-brown nodules, and rhizoliths are common, whereas carbonate nodules and slickensides are rare. Rhizoliths and mottles in bounding gray sandstones are sparse when present. Yellow-brown matrix colors are due to goethite, which forms under wetter moisture conditions than hematite in modern soils (Schwertmann and Taylor, 1989). The presence of goethite, in addition to the sparse carbonate nodules and weakly developed slickensides, suggest that yellow-brown paleosols were less well drained than red paleosols (Kraus and Riggins, 2007).

Brown Paleosols.—Brown (5YR) mudstone to sandy siltstone beds (<1.5 m thick) are characterized by red and yellow-brown mottles, abundant organic flecks, and locally common rhizoliths (Fig. 3D). Carbonate nodules and weakly developed slickensides are sparse, when present. A single brown paleosol horizon is commonly interbedded within profiles otherwise dominated by red or yellow-brown horizons. Brown matrix colors, abundant organic matter, and sparse carbonate nodules suggest soil moisture conditions wetter than red paleosols (Kraus and Riggins, 2007).

Purple Paleosols.—Purple (5P to 5RP) claystone to siltstone beds up to 1 m thick characterized by common gray and yellow-brown mottles—commonly surrounding yellow-brown nodules and rhizoliths—and large, well developed slickensides (Figs. 4A). Purple mudrocks are sometimes interbedded as single horizons within red or brown paleosols. Purple matrix colors, pervasive gray mottling and yellow-brown nodules, and the near absence of carbonate suggest poor drainage and strongly reducing conditions in these soils.

Heterolithic Lithofacies

Description.—These are laterally extensive, 0.5–3.0-m-thick deposits composed of medium gray (N5) to green-gray (5GY), fine-grained sandstone interbedded with or fining upward to mudstone (Fig. 4B). Sandstones are mostly massive, though thin relict beds of wavy to cross-bedded laminae are present in some units. Sandstones commonly show faint mottles, sparse calcite nodules, rhizoliths, and other trace fossils, especially when overlain by paleosols. Incipient pedogenic development is more common in the mudrocks of this lithofacies and is characterized by faint yellow-brown or purple mottles, common black organic flecks, poorly to moderately developed slickensides, and sparse carbonate nodules and rhizoliths. The body fossils of bivalves and gastropods are common locally in heterolithic lithofacies sandstones and mudstones.

Interpretation.—The heterolithic lithofacies is interpreted as the crevasse splays and distributary channels of avulsion belt deposits (Kraus, 1996; Kraus and Wells, 1999). Avulsion deposits are volumetrically important in the Willwood Formation and typically comprise 50–80% of fine-grained intervals (Kraus, 2001; Clyde and Christensen, 2003). Weak paleopedogenic development of these deposits suggests that sediment accumulation

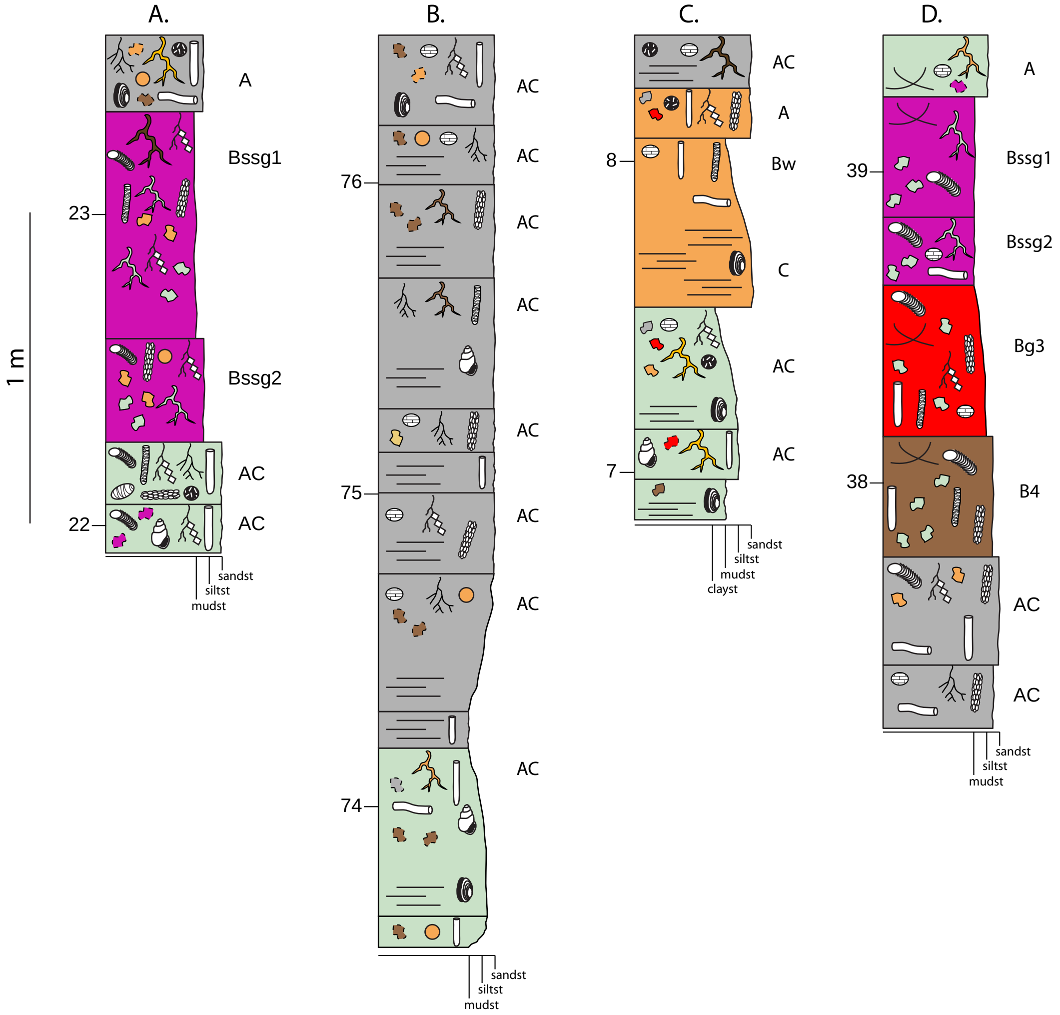

Figure 4. Measured sections through different lithofacies and pedofacies at Polecat Bench (refer to key in Fig. 3). **A)** Purple paleosol profile. **B)** Thick heterolithic interval with multiple insipient paleosol profiles suggested by rhizolith and burrow concentrations. **C)** Somewhat better developed insipient paleosol in a dominantly heterolithic measured section; *Bw* indicates development of color or structure. **D)** Thick cumulative paleosol profile with multiple B horizons suggests different paleohydrologic conditions and a complex, polygenetic development. *A*, A horizon; *B*, B horizon; *C*, C horizon; *g*, gleyed horizons; *k*, carbonate accumulations; *ss*, slickensides; numbers flowing horizon types indicate subdivisions based on different morphological properties.

rates for the avulsion deposits exceeded rates of pedogenesis. This is consistent with the rapid floodplain aggradation observed in some modern avulsion-dominated fluvial systems where up to 3 m of avulsion belt sediments were deposited in 100 years (e.g., Smith et al., 1989). The sparse carbonate and relatively high organic content of most avulsion deposits indicate that they were generally imperfectly drained and exposed for only brief periods of time (Kraus and Hasiotis, 2006).

Lithofacies Above and Below the PETM Interval

Approximately 35% of the measured section below and above the PETM interval is composed of moderately to well-developed paleosols. These are typically less than 1 m thick and consist of 1–2 red, yellow-brown, brown, or purple soil B horizons (Fig. 3B, 4C). Rhizoliths and other trace fossils tend to increase in abundance towards the tops of these soil profiles. Paleosols are interbedded with 1–4 m of avulsion belt deposits. Relict bedding, dispersed organic matter, and molluscan body fossils are common features of avulsion deposits outside the PETM interval, though most show some degree of paleopedogenic modification (Figs. 4B). Calcite, as pedogenic nodules, rhizocretions, and carbonate-filled burrows, is common in red paleosols and some sandstone beds, though far less abundant than in PETM interval strata.

The predominance of avulsion deposits (~65% of the strata) and thin, simple paleosol profiles outside the PETM interval suggests that sedimentation was fairly rapid and nonsteady. Paleosols are characteristic of compound soils that form in highly aggradational settings (e.g., Marriott and Wright, 1993; Kraus, 1999). These simple soil profiles developed on overbank sediments that accumulated gradually—perhaps annually—on the Willwood floodplain. Relatively frequent avulsion of trunk rivers, however, quickly buried the soils; effectively isolating them from further pedogenesis.

Lithofacies Within the PETM Interval

Paleosols comprise ~55% of the strata within the PETM interval at Polecat Bench. These paleosols range from 1–3 m thick and show at least 2, and up to 9, red, yellow-brown, brown, or purple horizons (Fig. 3A, 3C, 4A, 4D). The paleosols are generally finer grained than those outside the PETM interval. Rhizoliths and other trace fossils are more abundant and vertically distributed throughout the thicker paleosol profiles. Soil carbonate is prevalent throughout, but is particularly abundant in red paleosol profiles. Avulsion deposits are more widely spaced vertically than those outside the PETM interval. These deposits also show increased bioturbation, paleopedogenic modification, and far fewer molluscan body fossils.

Thicker paleosol profiles, widely-spaced avulsion deposits, and overall increases in pedogenically modified deposits within the PETM interval suggest a decrease in the rate of sediment accumulation and longer periods of subaerial exposure on the Willwood floodplain during the PETM at Polecat Bench (Woody, 2007). Most paleosols within the PETM interval are characteristic of cumulative soils that form when sedimentation rates are steady but of low volume relative to the rate of pedogenesis (Marriott and Wright, 1993; Kraus, 1999). Cumulative paleosols typically contain multiple B horizons that indicate varying moisture conditions based on different matrix colors, pedogenic features, and trace-fossil assemblages (e.g., 3A, 4D).

ICHNOLOGY

Traces with similar morphologies are assigned to discrete numbered trace-fossil types. Ichnofossils are described in the order of their relative abundance at Polecat Bench (Fig. 2)—first rhizoliths (Types 1–5), and then invertebrate trace fossils (Types 6–12). The predominant moisture regime represented by each trace fossil is interpreted as being: 1) terraphilic—organisms living within the vadose zone for which high soil moisture is a limiting factor, 2) hygrophilic—organisms living within the vadose zone for which low soil moisture is a limiting factor, or 3) hydrophilic—organisms living below the water table within a soil, or living on or below the sediment surface in open bodies of water (e.g., Hasiotis, 2002; 2004; 2007). Rhizoliths (Types 1–5) are interpreted as fossil root traces, and, as such, are all considered hygrophilic traces (Hasiotis, 2004), though the various preservational styles of rhizoliths clearly suggest the presence of some phreatophytes and different paleohydrologic regimes (Kraus and Hasiotis, 2006).

Type 1—Rhizohaloes (Fig. 5A)

Description.—Vertical to subvertical; downward tapering and commonly branching; yellow-brown, purple, or gray mottles with up to 300 mm circular cross sections and subvertical lengths up to 1000 mm, commonly with red or purple rims.

Associations.—Rhizohaloes are nearly ubiquitous in red, yellow-brown, brown, and purple paleosols, commonly as the only visible biogenic structure. The largest and most distinct examples are present in red paleosols. Rhizohaloes are associated with calcareous rhizocretions (Type 2), sediment-filled rhizoliths (Type 5), *Naktodemasis bowni* (Type 6), *Camborygma litonomos* (Type 9), cf. *Steinichnus* isp. (Type 11), *Edaphichnium lumbricatum* (Type 10), and cf.. *Cylindricum* isp. (Type 7).

Interpretation.—The branching patterns and circular cross sections suggest that the mottles are depletion zones resulting from surface-water gleying within and adjacent to

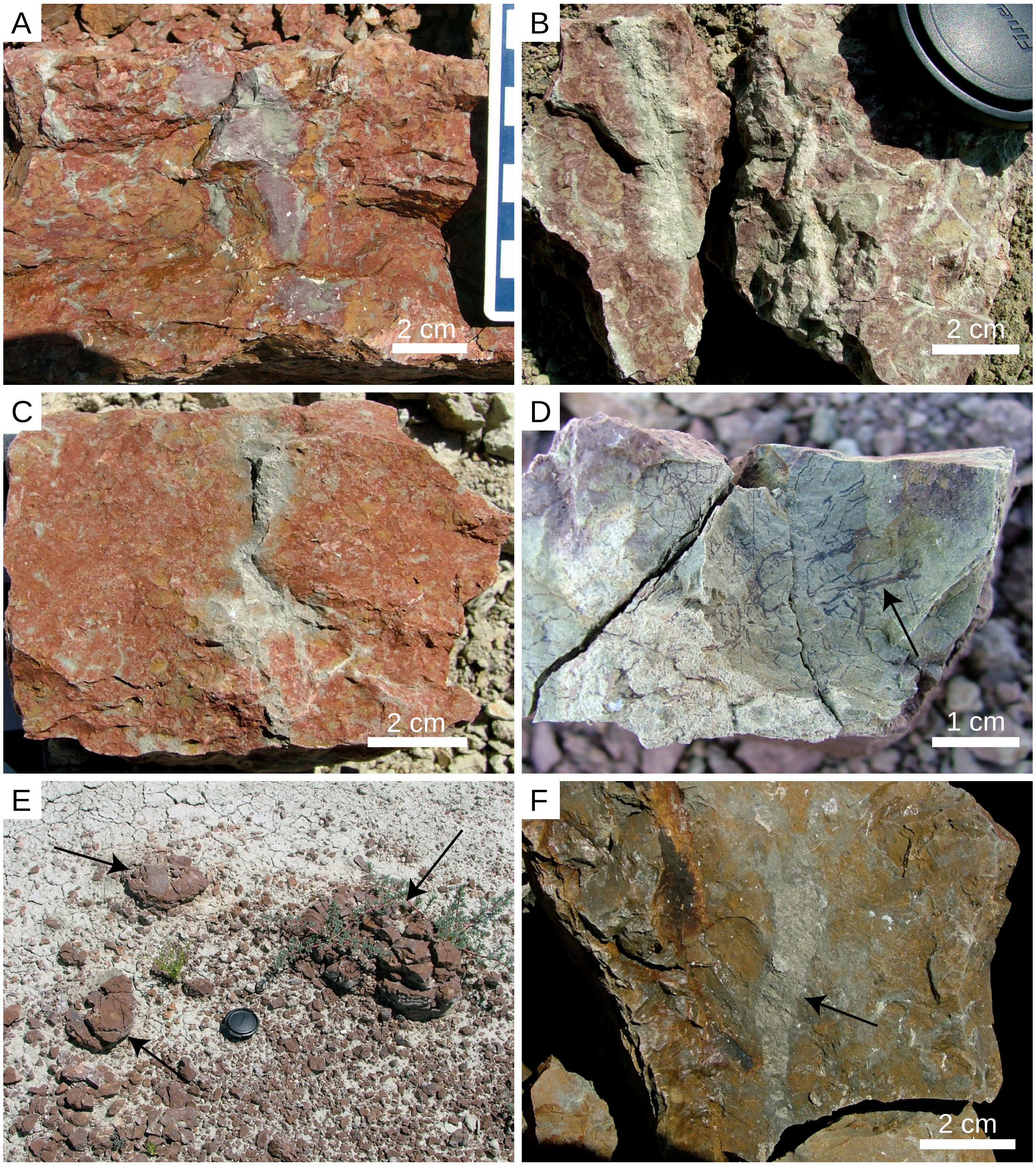

Figure 5. Rhizoliths commonly observed at Polecat Bench. **A)** Rhizohaloes in a red paleosol horizon. Note the transition from gray in the center (Fe depletions) to purple surrounded by thin, bright red neoferrans (Fe concentrations). **B)** Type 2a calcareous rhizocretion surrounded by powdery- carbonate-filled Type 2b rhizocretions. **C)** Type 2a calcareous rhizocretions tapering to branched Type 2b rhizocretions. **D)** Carbonaceous roots (arrow) preserved in a purple paleosol. **E)** Manganiferous rhizocretions (arrows) weathering out of a heterolithic interval, note shape and spacing suggestive of large root systems or casts of small trees. **F)** Sandstone-filled rhizolith (arrow) in a brown paleosol horizon.

ancient roots (Kraus and Hasiotis, 2006). Root channels are particularly susceptible to gleying because of the presence of organic matter (e.g., Schwertmann, 1993). As waters move away from the root channel to better oxygenated parts of the soil, the mobilized iron is oxidized and precipitated as neoferrans—red and purple rims associated with mottles and traces. Such redoximorphic features are common in modern soils that experience saturated soil conditions for part of the year, followed by periods of better drainage and lower water tables (Bigham et al., 1978; Torrent et al., 1980).

Type 2a-b—Calcareous rhizocretions (Fig 5B–C)

Description.—These represent two Types: 1) Type 2a—subvertical, downward tapering and branching, 10–50 mm diameter tubular structures up to 400 mm long containing solid to powdery calcite, commonly surrounded by calcareous networks or rhizohaloes (Fig. 5B); and 2) Type 2b—downward tapering, 1–5 mm diameter structures showing a high degree of branching, up to 200 mm long and containing powdery calcium carbonate, typically within rhizohaloes (Fig. 5C).

Associations.—Both types of calcareous rhizocretions are abundant in red, yellow-brown, and brown paleosols, and in gray and green-gray sandstones that underlie these paleosols. Type 2a rhizocretions are most prevalent in red paleosols and purple paleosols—commonly to the exclusion of other forms of pedogenic calcite—and in close association with rhizohaloes (Type 1), *Camborygma litonomos* (Type 9), *Naktodemasis bowni* (Type 6), and cf. *Cylindricum* isp.(Type 7).

Interpretations.—Type 2a rhizocretions are interpreted as the primary roots or taproots of shrubs and other small plants based on their predominantly subvertical orientation and relatively large diameters. Modern plants develop taproots to extend into the upper vadose zone of well-drained soils where soil moisture is high but not saturated (Aber and Melillo, 2001). Type 2b rhizocretions are interpreted as the shallow root systems of smaller vegetation or the smaller diameter lateral roots of primary roots. Calcareous rhizocretions indicate episodic saturation of the ancient soils—as soil drainage improved, calcite was precipitated within and around the previously saturated root channels (PiPujol and Buurman, 1997; Kraus and Hasiotis, 2006).

Type 3—Carbonaceous root fossils and trace fossils (Fig.5D)

Description.—Vertical to subvertical, filamentous, laterally and downward tapering, branching black structures, 0.5–2.0 mm in diameter.

Associations.—Root fossils are sparse in brown and purple paleosols, but are more common in the mudrocks of heterolithic deposits in association with sediment-filled rhizoliths (Type 5). Carbonaceous rhizoliths are rare in red paleosols, but are sometimes found in the center of Type 2a calcareous rhizocretions in these units.

Interpretation.—These are interpreted as the original organic remains of ancient roots within the traces of the root channels (Kraus and Hasiotis, 2006); in essence, these are body fossils found within their trace fossils. The preservation of organic matter suggests rapid burial or anoxic soil conditions resulting from high water tables (McCabe and Parrish, 1992).

Type 4—Manganiferous rhizocretions (Fig.5E)

Description.—Vertical to subvertical, downward tapering, rarely branching, roughly cylindrical structures 20–500 mm in diameter and up to 750 mm long. Type 4 rhizocretions are composed of black micronodules (<1 mm in diameter) of manganese oxides and goethite (Kraus and Hasiotis, 2006).

Associations.—The largest and best preserved manganiferous rhizocretions are found in heterolithic deposits. Much smaller (~40 mm long and 10–30 mm in diameter) examples of these traces are sometimes preserved in yellow-brown and brown sandy mudstones. Associated ichnofossils include sediment-filled rhizoliths (Type 5), cf. *Cylindricum* isp. (Type 7), cf. *Planolites* isp. (Type 8), and, rarely, *Camborygma litonomos* (Type 9).

Interpretation.—These are interpreted as *in situ* stump casts of trees or root systems of larger plants living on poorly drained soils (Kraus, 1988; Kraus and Hasiotis, 2006). Manganese accumulations are common in poorly drained, though not saturated, modern soils (e.g., Schwertmann and Fanning, 1976) and their precipitation is likely promoted by manganese oxidizing microorganisms (e.g., Konhauser, 1998).

Type 5—Sediment-filled rhizoliths (Fig. 5F)

Description.—Subvertical, downward tapering and branching, 2–20 mm diameter, cylindrical structures composed of sandstone or, less commonly, mudstone.

Associations.—Sediment-filled rhizoliths are found at the top of brown, yellow-brown and gray mudstone units overlain by sandstone. Associated trace fossils include Type 3 and Type 4 rhizoliths, cf. *Cylindricum* isp. (Type 7), and cf. *Planolites* isp. (Type 8).

Interpretation.—These are interpreted as root pathways infilled with sediments, left open by decay of the original root based on their dendritic morphology and comparison to modern root morphologies (Glinski and Lipiec, 1990).

Type 6—Naktodemasis bowni *(Fig. 6A–B)*

Description.—Sinuous, variably oriented, unbranched, and unlined burrows composed of a nested series of ellipsoid-shaped, menisci-backfilled packets. Burrows are from 1 to more than 150 mm long and have circular to elliptical cross sections 0.7–14 mm in diameter. Packets are backfilled with thin, discontinuous, and texturally homogeneous meniscate laminae. The meniscate backfill is typically accentuated by alternating colors that correspond to matrix and mottle colors of the host rock. Burrow walls exposed in the matrix are rare, and nearly all specimens are natural cross sections.

Associations.—*Naktodemasis bowni* are present in groups of tens to thousands of individuals in nearly all deposits at Polecat Bench but are most abundant in red, yellow-brown, brown, and purple paleosols in close association with Type 1 and Type 2a–b rhizoliths. Associated ichnofossils include *Camborygma litonomos* (Type 9), cf. *Cylindricum* isp. (Type 7), cf. *Steinichnus* isp. (Type 11), *Edaphichnium lumbricatum* (Type 10), cf. *Planolites* isp. (Type 8), and cocoon traces (Type 12).

Interpretation.—*Naktodemasis bowni* are interpreted as the intermittent locomotion and dwelling traces of burrowing insects—most likely burrower bugs (Hemiptera: Cydnidae), cicada nymphs (Hemiptera: Cicadae), and, less likely, scarabaeid (Coleoptera: Scarabaeidae) or carabid beetles (Coleoptera: Carabidae) based on burrow morphology and comparison to traces produced by these organisms in modern soils (Smith et al., 2008). Extant cydnids excavate backfilled burrows in well-rooted soils with 7–37% moisture content (Willis and Roth, 1962). Cicada nymphs and adult and larval scarabaeid beetles also excavate backfilled burrows with elliptical chambers, likely with similar soil moisture constraints (Counts and Hasiotis, 2006; Smith and Hasiotis, in review). The association of *N. bowni* with rhizoliths in moderately to well-drained paleosols suggests that the tracemakers were most abundant and

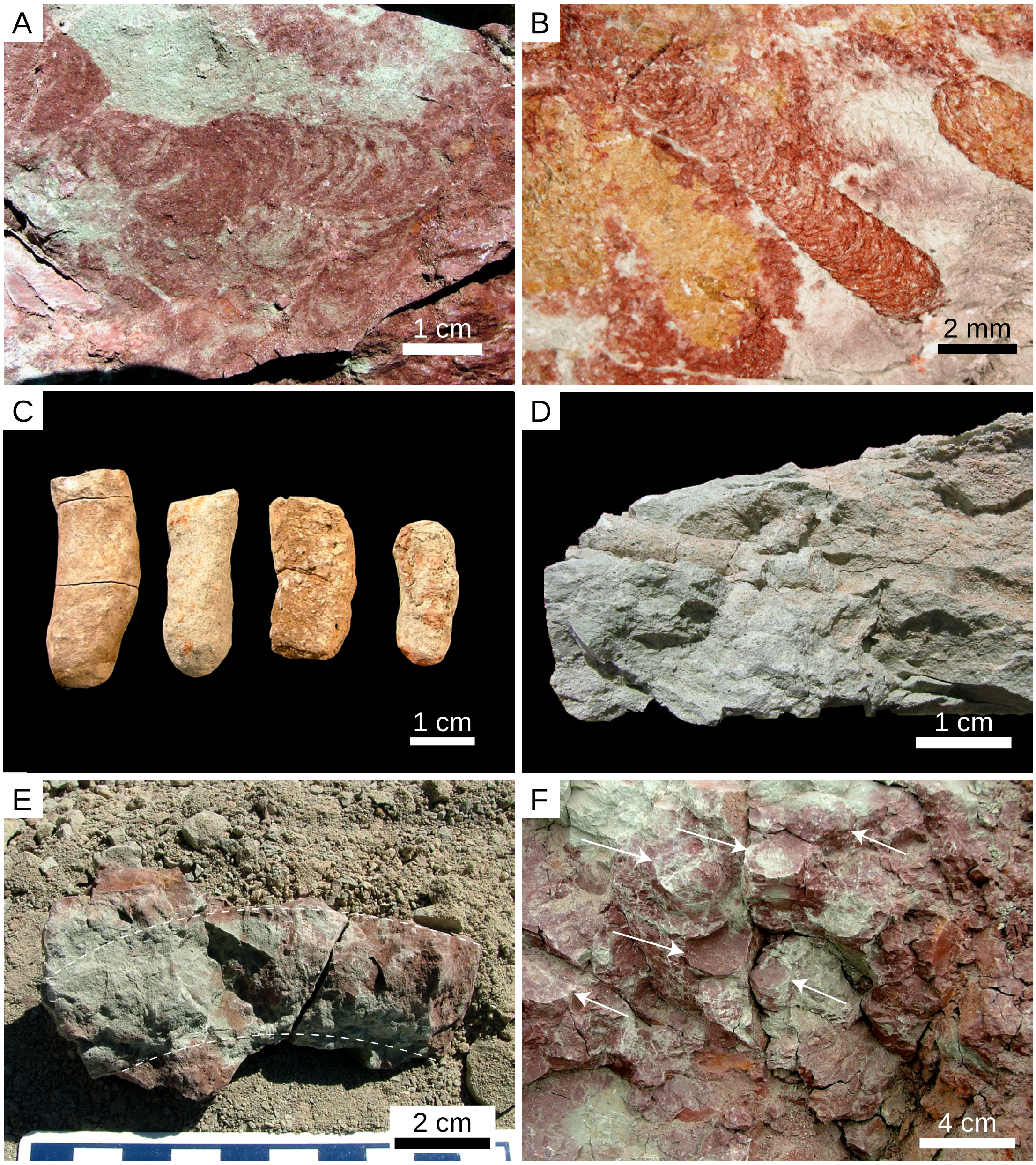

Figure 6. Burrows from the Willwood Formation at Polecat Bench. **A)** Large *Naktodemasis bowni* in a red compound paleosol. **B)** Smaller N. bowni in a yellow-brown paleosol. **C)** Burrow sections assigned to cf. *Cylindricum* isp., burrow terminations are present in the first, second, an fifth specimens from the right. **D)** Cf. *Planolites* isp. collected from a heterolithic deposit. **E)** Large *Camborygma litonomos* from red compound paleosol, burrow margin outlined by dashed white line. **F)** Prismatic soil structure produced by multiple *C. litonomos* (arrows).

active in rooted A horizons and upper B horizons of the soil profile and, thus, are terraphilic to hygrophilic in moisture preference (Smith et al., 2008).

Type 7—cf. Cylindricum *isp. (Fig. 6C)*

Description.—Vertical to subvertical, straight to sinuous, unbranched, and unlined burrows with circular to elliptical cross sections (Fig. 6C). Burrow diameters range from 1–41 mm with an average diameter of 9.7 mm. Burrow terminations are rounded when preserved. Fill material is mostly structureless sandstone, though burrows may also be filled with mudstone or carbonate.

Associations.—Cf. *Cylindricum* isp. are distributed throughout the study area at Polecat Bench, but are most commonly preserved and abundant in gray to green-gray mudstones and sandstones as the single ichnotaxon present or in association with Type 2a, 4, or 5 rhizoliths, or cf. *Planolites* isp. (Type 8). When present in red, yellow-brown, and brown paleosols, cf. *Cylindricum* isp. is associated with Type 1 and Type 2b rhizoliths, *Naktodemasis bowni* (Type 6), cf. *Steinichnus* isp. (Type 11), *Edaphichnium* isp. (Type 10), and cocoon traces (Type 12).

Interpretation.—These burrows are similar to *Cylindricum*, in that they are short, smooth walled, and predominantly vertical shafts with gently rounded terminations (Linck, 1949). The lack of diagnostic morphologies complicates the assignment of these burrows to any specific group of tracemakers. The orientation and preservation of these traces suggest they were created in the upper vadose zone and, thus, represent terraphilic to hygrophilic moisture regimes (e.g., Hasiotis, 2002). Type 7 trace fossils are similar to transient to temporary domichnia on modern floodplains produced by such burrowing organisms as beetles (Coleoptera), bees and wasps (Insecta: Hymenoptera), emerging cicada nymphs

(Insecta: Hemiptera), spiders (Arachnida: Araneae), and mollusks (Bown and Kraus, 1983; Hasiotis, 2002).

Type 8—Cf. Planolites *isp. (Fig. 6D)*

Description.—Horizontal to subhorizontal, straight to slightly sinuous, unlined, unbranched, circular to elliptical burrows with unornamented surfaces. Burrow diameters range from 1–40 mm, but most are between 5–9 mm; they do not taper or branch. Burrow terminations are gently rounded when preserved. Burrow fill is mostly structureless mudstone; though sandstone-filled burrows are also present.

Associations.—These traces are most common in gray to green-gray sandstone and mudstone, usually as the single ichnotaxon present or in association with cf. *Cylindricum* isp. (Type 7). Cf. *Planolites* isp. are less commonly associated with Types 4 and 5 rhizoliths, cf. *Cylindricum* isp. (Type 7) and *Edaphichnium lumbricatum* (Type 10) in gray to green-gray mudstones; and Type 2b rhizocretions and *Naktodemasis bowni* (Type 6) in red or brown paleosols.

Interpretation.—The distinct wall and structureless fill suggest that these represent open burrow systems that were later filled, as opposed to the infill passing through the alimentary gut of the tracemaking organisms. The tracemaking organisms in poorly drained to imperfectly drained gray mudstone and sandstone were either burrowing in the vadose zone (hygrophilic) or near the sediment-water interface under bodies of standing water (hydrophilic) given the poor drainage conditions suggested by these deposits. Cf. *Planolites* isp. in better drained paleosols may have been produced by such organisms as bees and wasps (Hymenoptera: Apocrita), beetles (Coleoptera), crickets (Orthoptera: Gryllidae), and ants (Hymenoptera: Formicidae) (Bown and Kraus, 1983; Hasiotis, 2002). Hembree and Hasiotis

(2006) compared the burrow casts of extant amphisbaenians (Reptilia: Squamata: Amphisbaenidae) with cylindrical fossil burrows collected from the Willwood Formation (Bown and Kraus, 1983). Amphisbaenians prefer moist soil habitats and the size and morphology of the modern burrow casts, with the exception of their common branching, were similar to some Type 7 and Type 8 trace fossils at Polecat Bench, suggesting that amphisbaenians are potential tracemakers.

Type 9—Camborygma litonomos *(Fig. 6E–F)*

Description.—Vertical to subvertical, straight to slightly sinuous, unlined and unbranched, cylindrical burrows with knobby and striated surficial morphology. Burrows are 10–50 mm in diameter and up to 400 mm long. Burrow terminations are bulbous and up to twice the diameter of the burrow shaft. Most burrow fill is identical to the surrounding matrix or resemble sediments of overlying units. Burrows are commonly accentuated by red, purple, or gray mottling, and many show thick clay coatings that obscure surficial morphologies.

Associations.—Camborygma litonomos are found almost exclusively in the red mudstones and gray sandstones of red paleosols outside the PETM interval at Polecat Bench. These red mudstone intervals commonly show prismatic soil structures produced by great abundances of *C. litonomos* (Smith et al., in review). Associated ichnofossils include Type 1 and 2a–b rhizoliths, *Naktodemasis bowni* (Type 6), cf. *Cylindricum* isp. (Type 7), and, rarely, cf. *Planolites* isp. (Type 8). The association of prismatic peds and Type 2a rhizocretions invariably indicates the presence of at least a few well-preserved, if initially difficult to discern, *C. litonomos*.

Interpretation.—C. litonomos are interpreted as the burrow molds and casts of freshwater crayfish (Decapoda: Cambaridae) based on their surficial morphology, simple burrow architecture, and relatively short lengths (Hasiotis and Mitchell, 1993). Modern crayfish that construct burrows similar to *C. litonomos* spend most of their lives in open water, but burrow in areas with shallow and fluctuating water tables. Crayfish are hydrophilic organisms that burrow to the local water table for the purposes of respiration, hydration, reproduction, and other biological functions (Hobbs, 1942; 1981). Burrowing by crayfish likely extended the effects of subaerial exposure deeper into the soil profile—thus improving drainage and gas exchange, stimulating the growth of microbes and plant roots, and promoting the occupation of associated terraphilic and hygrophilic tracemakers (e.g., Richardson, 1983; Hobbs and Whiteman, 1991).

Type 10—Edaphichnium lumbricatum *(Fig. 7A–B)*

Description.—Horizontal to vertical, straight to slightly sinuous, unbranched, cylindrical burrows composed of ovoid to capsule-shaped pellets. The linearly arranged pellets weather in full relief with no discernable burrow walls or extra-pelletal fill and are composed of clastic grains and micritic calcium carbonate (Bown and Kraus, 1983). Two general morphologies are present: 1) horizontal burrows composed of large, distantly spaced pellets 2–10 mm long and 0.5–5.0 mm wide (Fig. 7A); and 2) horizontal to vertical burrows filled with smaller, tightly packed pellets 1–4 mm long and 0.5–2.0 mm in diameter (Fig. 7B). Loose aggregates of pellet-shaped nodules are also observed weathering on the surface of some units.

Associations.—Pelleted burrows, though rare, are most consistently found in red, purple, and yellow-brown paleosols and less commonly in brown and gray mudrocks—

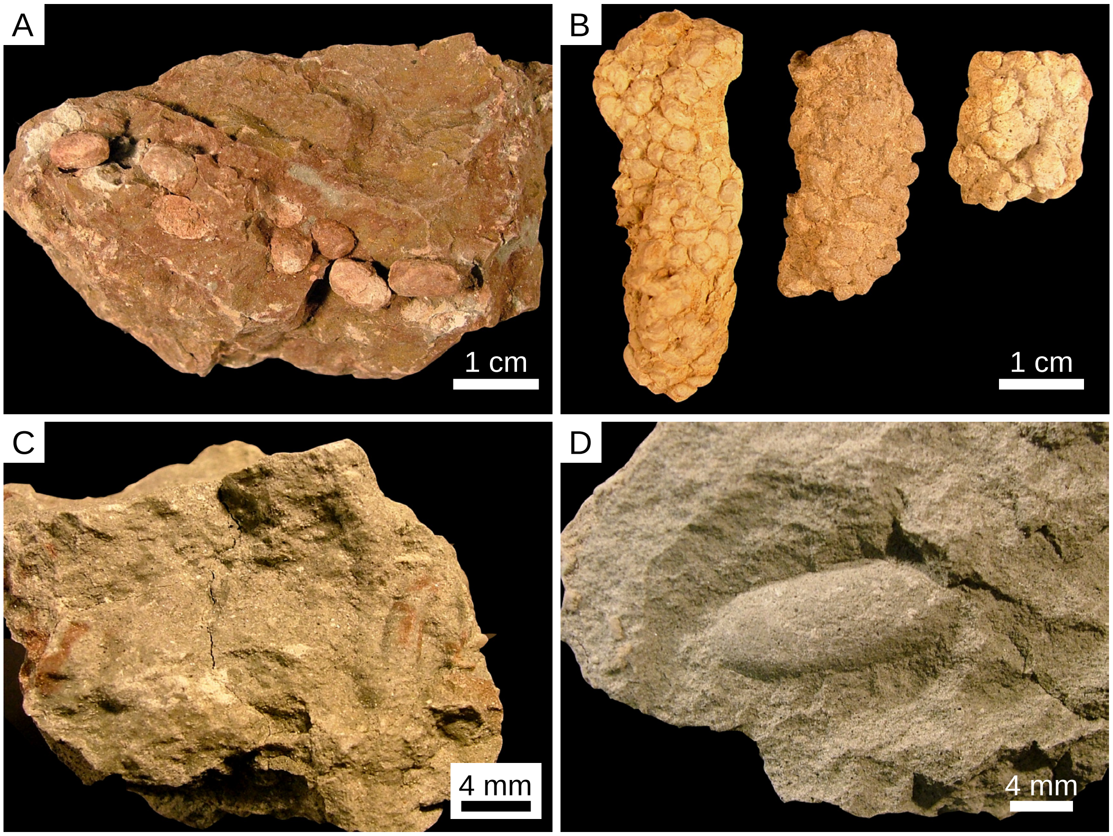

Figure 7. Burrows from the Willwood Formation at Polecat Bench. **A)** Horizontally oriented *Edaphichnium lumbricatum* showing large, distantly spaced pellets. **B)** Smaller diameter E. lumbricatum composed of tightly packed pellets. **C)** Cf. *Steinichnus* isp. with transverse ridges on burrow surface. **D)** Cocoon-shaped trace fossil from a heterolithic interval.

usually in the upper gleyed portions of paleosol horizons. Associated ichnofossils include Types 1 and 2b rhizoliths, *Naktodemasis bowni* (Type 6), cf. *Cylindricum* isp. (Type 7), cf. *Steinichnus* isp. (Type 11), and cf. *Planolites* isp. (Type 8), and cocoon traces (Type 12).

Interpretation.—Edaphichnium lumbricatum are interpreted as the burrows and fecal pellets of sediment-ingesting oligochaete worms (Bown and Kraus, 1983; Hasiotis, 2002). Extant oligochaetes ingest soil to feed on seeds, decaying plant mater, the eggs or larvae of other organisms, and microorganisms. Undigested soil and fecal matter are deposited as a cast or pellet, either on the ground surface around the burrow entrance, as thin burrow linings, or loosely deposited in the open burrow and burrow chambers (Lee and Foster, 1991). Modern earthworms feeding in calcium-rich soil environments excrete excess calcium with the feces as calcium carbonate (Lunt and Jacobson, 1944). *E. lumbricatum* represent hygrophilic behavior because air breathing earthworms must live above the phreatic zone and require soils sufficiently moist to keep from dehydrating and soft enough to burrow in (Hasiotis, 2002).

Type 11—cf. Steinichnus *isp (Fig. 7C)*

Description.—Straight to sinuous, unbranched, subvertical burrows with circular cross sections and knobby, predominantly transverse ridges. Burrow diameters are 1–9 mm with a mean diameter of 2.85 mm. The longest burrow measured ~50 mm, though most specimens are natural cross sections and true lengths are unknown. Burrow terminations are rarely observed, but gently rounded when present. Burrow fill is structureless and similar to the surrounding matrix. Burrow surfaces are ornamented with thin, tightly spaced ridges oriented transverse to the axis of the burrow. Surficial morphology is most distinct on burrows from clay-rich or slightly weathered rock.

Associations.—These traces are most common and best preserved in yellow-brown, red, and purple mudrocks and less common in gray mudstones and sandstones. Associated ichnofossils include Type 1 and 2b rhizoliths, *Edaphichnium lumbricatum* (Type 10), cf. *Cylindricum* isp. (Type 7), and *Naktodemasis bowni* (Type 6).

Interpretation.—These Willwood Formation burrows resemble *Steinichnus carlsbergi* Bromley and Asgaard 1979, in that both have surfaces ornamented with transverse ridges and both contain structureless fill. Polecat Bench specimens, however, are predominantly oriented vertically and have much smaller diameters and less distinct surficial morphology. The burrows also resemble *Scoyenia gracilis* White 1929, but the surficial morphology of *S. gracilis* is composed of longitudinally oriented, closely spaced, paired striations and the backfill is composed of distinct menisci of contrasting lithologies (Frey et al., 1984). The lack of pelleted fill and other backfill structures argue against sediment-ingesting or active backfilling by the cf. *Steinichnus* tracemaker. The burrows, instead, are interpreted as the casts of open burrows produced by compaction tunneling in which small blocks of sediment are pushed to the side and compacted as the tracemaker tunnels forward, creating a ridged and knobby inner burrow surface (Clark and Ratcliffe, 1989, see fig. 2.1 and 2.2). This tunneling method suggests a hygrophilic tracemaker limited to moist fine-grained deposits because the sediment must be cohesive and compressible. Previously described *Steinichnus* have been attributed to such terrestrial arthropods as mud-loving beetles (Coleoptera: Heteroceridae) and mole crickets (Orthoptera: Gryllotalpidae). These produce generally horizontal burrows just below the sediment surface, whereas these *Steinichnus* are predominantly subvertical and likely produced by hygrophilic insects that burrowed well below the surface.

Type 12—Cocoon traces (Fig. 7D)

Description.—Ovoid-shaped, mudstone casts 5–18 mm long and 2–9 mm wide (Fig. 7D). The casts are solitary trace fossils and have not been found in association with burrows.

Associations.—Cocoon traces are the most rare trace fossil at Polecat Bench and are preserved primarily in gray to green-gray mudstones and sandstones. Associated trace fossils include cf. *Cylindricum* isp. (Type 7), *Naktodemasis bowni* (Type 6), and *Edaphichnium lumbricatum* (Type 10).

Interpretation.—These ichnofossils are interpreted as the casts of insect cocoons, most likely those produced by digger wasps (Hymenoptera: Sphecidae) based on the cast morphology (Evans, 1963). Sphecid wasps construct nests within the A and upper B horizons of soils for food hoarding and to provide shelter for hatched larvae which spin their own cocoons from silk (Evans and Eberhard, 1970; Hasiotis, 2002).

ICHNOCOENOSES

Trace-fossil assemblages in the study area comprise five ichnocoenoses (Table. 1; Fig. 8). Each ichnocoenosis is interpreted as representing well-drained, moderately drained, imperfectly drained, or poorly drained sediments and soils based on the paleohydrologic conditions inferred from the dominant ichnofossil and other associated burrows or rhizoliths when present.

I. Naktodemasis *Ichnocoenosis*

Description.—This ichnocoenosis consists of abundant *Naktodemasis bowni* in association with Type 1 and 2a–b rhizoliths. This ichnocoenosis commonly is preserved in

Ichnocoenoses	Associated Trace Fossils	Lithofacies Associations	Paleohydrologic Interpretation	Drainage Interpretation
I. *Naktodemasis* ichnocoenosis	*Naktodemasis bowni* and Type 1, 2a-b rhizoliths	Red and brown paleosols; less common in yellow-brown and purple paleosols; incipient paleosols in avulsion deposits	Terraphilic	Well to Moderate
II. *Naktodemasis-Edaphichnium* ichnocoenosis	*Naktodemasis bowni*, *Edaphichnium lumbricatum*, cf. *Cylindricum* isp., Type 1, 2a-b rhizoliths; less commonly cf. *Steinichnus* isp., cf. *Planolites,* or cocoon traces	Red, yellow-brown, brown, and purple paleosols; incipient paleosols in avulsioion deposits	Terraphilic-Hygrophilic	Moderate
III. *Camborygma* ichnocoenosis	*Camborygma litonomos* Type 1, 2a-b rhizoliths; *Naktodemasis bowni*; rarely cf. *Cylindricum* isp. or cf. *Planolites* isp.	Red paleosols; rarely in purple paleosols and avulsion deposits	Hydrophilic-Terraphilic	Imperfect
IV. *Steinichnus* ichnocoenosis	cf. Steinichnus isp., *Edaphichnium lumbricatum*, Type 1, 2b, 3, 4, 5 rhizoliths; cf. *Cylindricum* isp., cf. *Planolites* isp.	Brown and yellow-brown paleosols; rarely in red paleosols avulsion deposits and incipient paleosols in avulsion deposits	Hygrophilic	Moderate to Imperfect
V. *Cylindricum-Planolites* ichnocoenosis	cf. *Cylindricum* isp., cf. *Planolites* isp., Type 1, 2b, 3, 4, 5 rhizoliths;	Avulsion deposits; yellow-brown and brown paleosols	Hygrophilic-Hydrophilic	Imperfect to Poor

Table 1. Summary table showing the key features of the five distinct ichnocoenoses in the Willwood Formation at Polecat Bench, Bighorn Basin, Wyoming.

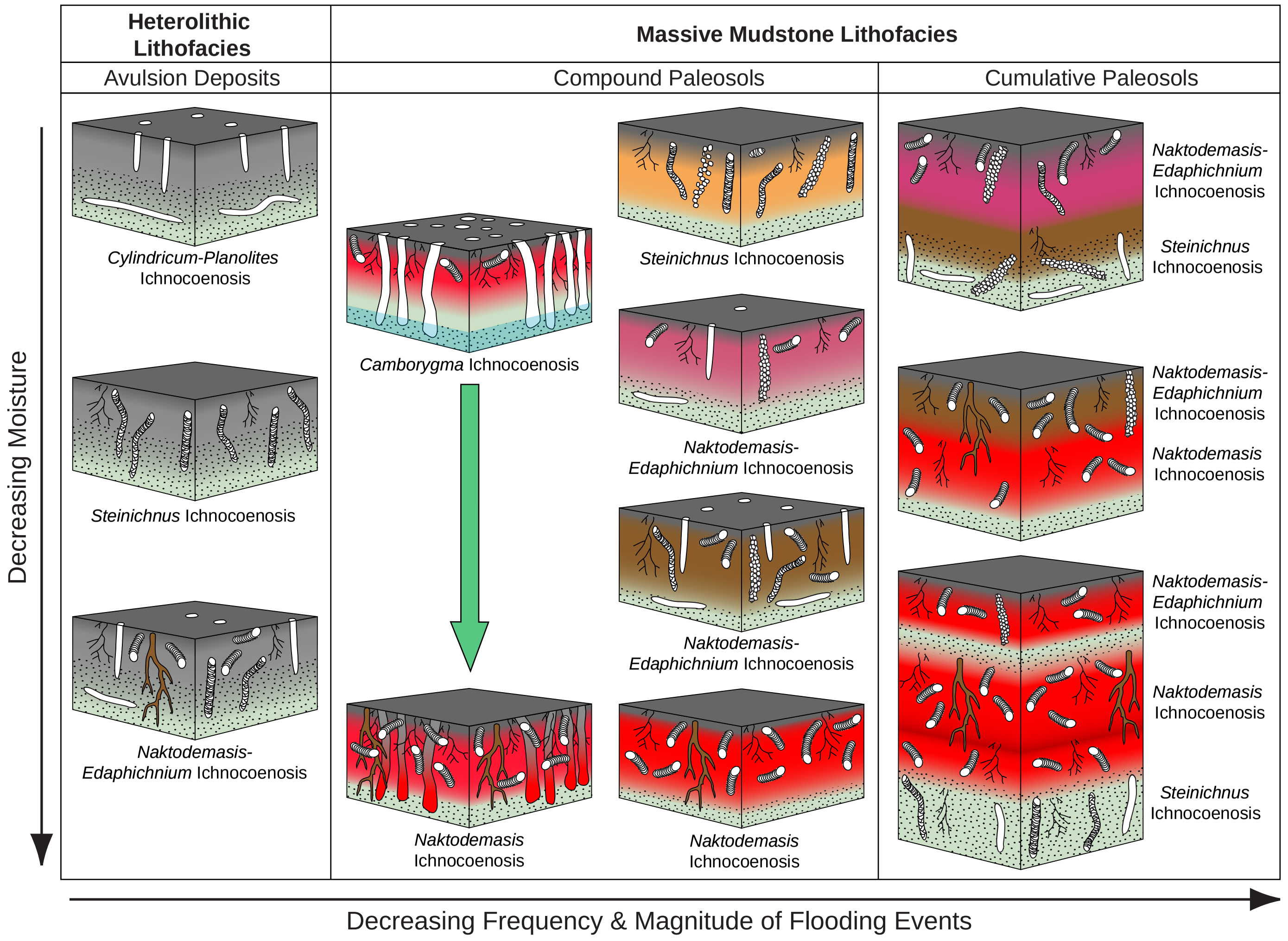

Figure 8. Ichnopedologic associations and inferred drainage conditions of ichnocoenoses in the Willwood Formation at Polecat Bench.

red and brown paleosols, and less commonly in yellow-brown paleosols, purple paleosols, and incipient paleosols in avulsion belt deposits.

Interpretation.—The great abundance of *Naktodemasis bowni* in associated deposits, to the exclusion of other ichnofossils, may be due to the obliteration of all other traces by the prolific burrowing of the *N. bowni* tracemaker. The *Naktodemasis* ichnocoenosis consists primarily of terraphilic invertebrate trace fossils and, as such, was likely formed under predominantly well-drained soil conditions. The common ichnopedologic association of the *Naktodemasis* ichnocoenosis with carbonate nodules, calcareous rhizocretions, and well-developed slickensides supports this interpretation.

II. Naktodemasis–Edaphichnium *Ichnocoenosis*

Description.—This ichnocoenosis is composed of *Naktodemasis bowni* in association with Type 1 and 2a-b rhizoliths, and *Edaphichnium lumbricatum* or cf. *Cylindricum* isp.; cf. *Steinichnus* isp., cf. *Planolites* isp., and cocoon traces are less common constituents. The *Naktodemasis–Edaphichnium* ichnocoenosis is present in red, yellow-brown, brown, and purple paleosols and some incipient paleosols in avulsion deposits.

Interpretation.—This ichnocoenosis is dominated by both *Naktodemasis* and *Edaphichnium*, and, thus, is composed of trace fossils indicating both terraphilic and hygrophilic behaviors. The ichnodiversity of this ichnocoenosis suggests variable soil moisture conditions and the occupation of the soil profile by two or more groups of tracemakers that preferred different moisture conditions—possibly entering the soil or moving vertically within the soil profile when their preferred hydrologic conditions were present. The frequent association of calcareous rhizocretions, carbonate nodules, and well-developed slickensides with this ichnocoenosis suggests the tracemakers preferred at least moderately drained soils.

III. Camborygma *Ichnocoenosis*

Description.—This ichnocoenosis is dominated by *Camborygma litonomos* and Type 2a rhizocretions. Associated trace fossils include Type 1 and 2b rhizoliths, *Naktodemasis bowni*, and, rarely, cf. *Cylindricum* isp. or cf. *Planolites* isp. The *Camborygma* ichnocoenosis is almost exclusive to red compound paleosol profiles and rare in purple paleosols. *C. litonomos* is present throughout the red paleosol profile, though associated ichnofossils and rhizoliths are typically relegated to the upper red portions of the profile.

Interpretation.—The morphology and relatively short *Camborygma litonomos* at Polecat Bench suggest relatively shallow and fluctuating water tables and, thus, imperfect soil drainage conditions (Hasiotis and Mitchell, 1993). Most *C. litonomos* burrows at Polecat Bench appear overprinted by subsequent pedogenic modification, suggesting that burrowing by crayfish in these deposits decreased or ceased for some time before burial. Associated terraphilic and hygrophilic trace fossils often cross-cut *C. litonomos* burrows and may represent bioturbation in better drained upper portions of the soil profile concurrent with crayfish burrowing or a later occupation of the soil by tracemakers of the *Naktodemasis* ichnocoenosis.

IV. Steinichnus *Ichnocoenosis*

Description.—This ichnocoenosis is composed of cf. *Steinichnus* isp. typically in association with *Edaphichnium lumbricatum*, though cf. *Cylindricum* isp., or cf. *Planolites* isp. may also be present. Ichnodiversity and ichnofossil abundance are high in brown and yellow-brown paleosols in association with Type 1, 2b, and 3 rhizoliths. This ichnocoenosis is also commonly preserved in avulsion deposits with cf. *Steinichnus* isp. as the single invertebrate ichnotaxon present and sparse Type 2b, 3, 4, or 5 rhizoliths. The *Steinichnus* ichnocoenoses is less common in red paleosols.

Interpretation.—The *Steinichnus* ichnocoenosis is interpreted as a dominantly hygrophilic assemblage of trace fossils, suggesting moderately to imperfectly drained soil regimes. Paleosols containing more abundant and diverse assemblage of trace fossils from this ichnocoenosis, along with rhizolith types that indicate predominantly unsaturated sediments, suggest overall better drainage conditions than deposits with fewer *Steinichnus* ichnocoenosis constituents.

V. Cylindricum–Planolites *Ichnocoenosis*

Description.—This ichnocoenosis is composed of cf. *Cylindricum* isp. and cf. *Planolites* isp., or, more typically, of either of these trace fossils as the single ichnotaxon present. This ichnocoenoses is preserved typically in mudrocks and sandstone of avulsion belt deposits and sometimes in association with Type 3, 4, and 5 rhizoliths. The ichnocoenosis is less common in brown and yellow-brown paleosols with sparse Type 1 and 2b rhizoliths.

Interpretation.—Predominantly subvertical to subhorizontal burrows with simple morphologies are abundantly produced in continental deposits by epiterraphilic, terraphilic, hygrophilic and hydrophilic tracemakers, though most are produced likely in the upper vadose and vadose zones (Hasiotis, 2002). Such ichnofossils as cf. *Cylindricum* isp. and cf. *Planolites* isp., thus, are not diagnostic of specific paleohydrologic regimes, beyond indicating that host sediments were sufficiently drained to allow bioturbation by some continental organisms. The low overall ichnodiversity of this ichnocoenosis, its common association with avulsion deposits showing only incipient soil formation, and its co-occurrence with Type 3, 4, and 5 rhizoliths suggest that this ichnocoenosis formed under imperfectly to poorly drained soil conditions.

Ichnocoenoses Summary

Most of the ichnocoenoses are not facies specific—individual ichnofossils are present in multiple ichnocoenoses and lithofacies (Fig. 8). The occurrence of morphologically identical trace fossils in multiple lithofacies suggests that the different ichnocoenoses associations represent different paleoenvironments and paleohydrologic conditions rather than the preservational bias of certain ichnofossils. Ichnodiversity within the individual ichnocoenoses increases as the paleopedologic and sedimentologic features of the host rocks indicate wetter or better drained soil moisture conditions. The *Naktodemasis* and *Cylindricum–Planolites* ichnocoenoses, for example, likely represent two extremes in soil moisture regimes based on their ichnopedologic associations—well-drained and poorly drained respectively—and both are commonly represented by a single ichnofossil morphotype. The *Naktodemasis–Edaphichnium*, *Steinichnus*, and *Camborygma* ichnocoenoses, on the other hand, generally show diverse assemblages of both terraphilic and hygrophilic to hydrophilic ichnofossils that suggest variable soil moisture conditions ranging from moderately to poorly drained sediments.

Distribution of Ichnocoenoses Through the PETM

The five ichnocoenoses are preserved in strata below, within, and above the PETM interval at Polecat Bench (Fig. 9). In addition, the total number of ichnocoenoses within the

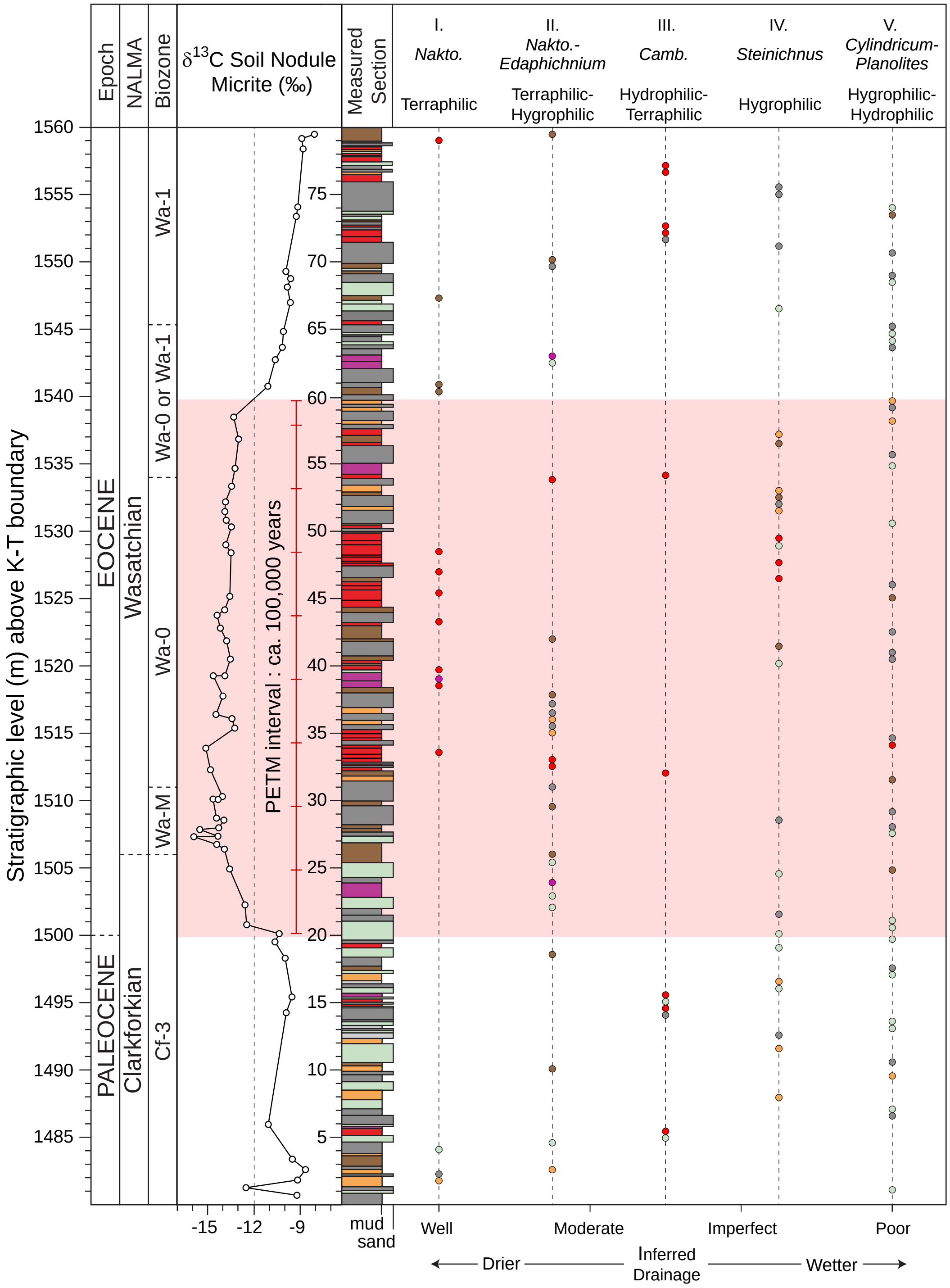

Figure 9. Stratigraphic distribution of ichnocoenoses throughout the composite measured section at Polecat Bench. Shaded area highlights the PETM interval. Modified from Bowen et al. (2001), Gingerich (2001), and Bains et al. (2003).

PETM interval is not dramatically different from the number of ichnocoenoses below and above the PETM. There is no significant difference in the distribution of the five ichnocoenoses from strata below and above the PETM interval ($\chi^2 = 0.984$, df = 4, $p < .912$). Proportions of the ichnocoenoses from within the PETM interval, however, are significantly different from those outside the PETM interval ($\chi^2 = 9.868$, df = 4, $p < 0.043$). This is due primarily to the sharp decline in the number of *Camborygma* ichnocoenoses within the PETM interval, followed by *Naktodemasis–Edaphichnium* and *Steinichnus* ichnocoenoses (Fig. 10). When this ichnocoenosis is not included in the chi-square analysis, the distribution of ichnocoenoses between non-PETM and PETM strata is no longer statistically significant ($\chi^2 = 1.846$, df = 3, $p < 0.605$). Though the proportions of the remaining ichnocoenoses are not significantly different throughout the measured section, they are greater in number within the PETM interval (Fig. 10). The *Naktodemasis*, *Naktodemasis–Edaphichnium*, and *Steinichnus* ichnocoenoses are more abundant within the PETM interval and show marked increases in the abundance and ichnodiversity of their constituent trace fossils. The *Cylindricum–Planolites* ichnocoenosis is evenly distributed, mostly in avulsion deposits throughout the measured section, though cf. *Planolites* isp. are less abundant and often absent from this ichnocoenosis within the PETM interval.

ESTIMATED DRAINAGE CONDITIONS THROUGH THE PETM

Drainage conditions estimated from the paleopedologic and sedimentologic features of the different lithofacies (Fig. 11A) indicate significantly better drainage conditions on the Willwood floodplain during the PETM (H = 7.84, $N = 160$, $p < 0.005$). Lithofacies below and above the PETM interval do not differ significantly in their interpreted paleohydrology (H = 0.32, $N = 80$, $p < 0.572$). Drainage conditions estimated from ichnocoenoses (Fig. 11B)

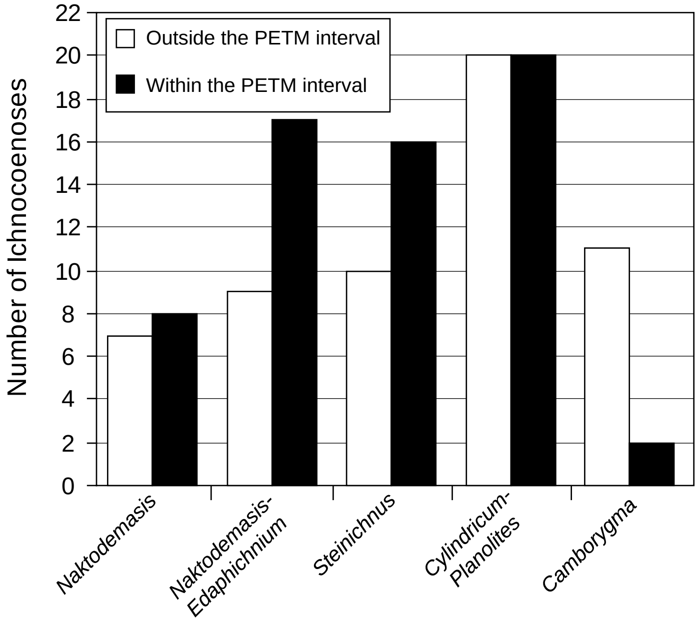

Figure 10. Histogram showing distribution of ichnocoenoses outside and within the PETM interval at Polecat Bench.

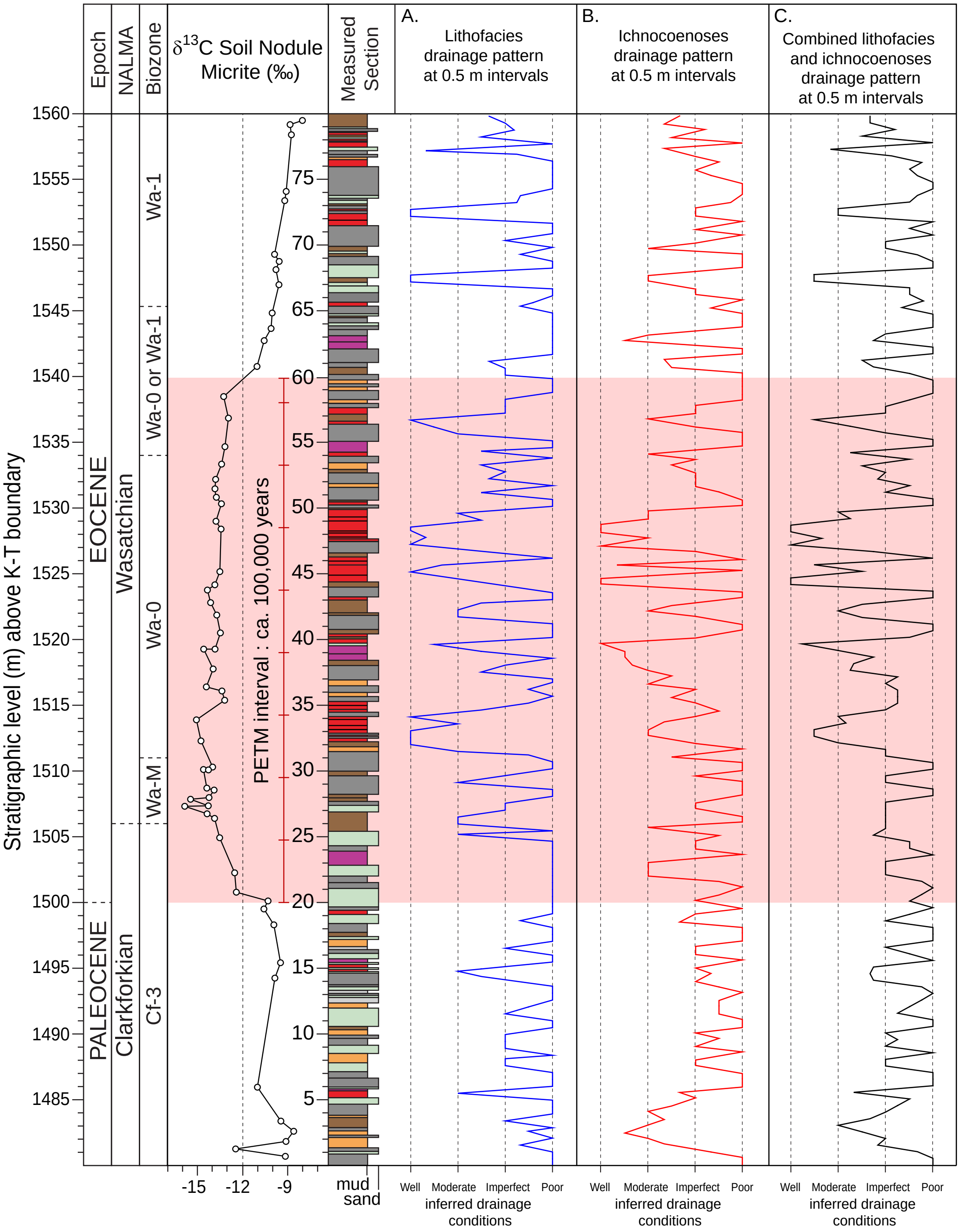

Figure 11. Estimated drainage conditions based on **A)** the dominant matrix colors and grain sizes of the lithofacies, and **B)** the paleohydrologic conditions implied by the ichnocoenoses. **C)** Drainage conditions based on the lithofacies and ichnocoenoses estimates averaged together at 0.5 meter intervals. Modified from Bowen et al. (2001), Gingerich (2001), and Bains et al. (2003).

suggest significantly better drainage conditions during the PETM ($H = 4.45$, $N = 160$, $p < 0.035$). Willwood ichnocoenoses below and above the PETM interval do not vary significantly in their estimated paleohydrologic regime ($H = 0.00$, $N = 80$, $p < 0.960$). The drainage condition from both the lithofacies and ichnocoenoses interpretations were averaged together to produce a consensus estimate that reflects both data sets (Fig. 11C, 12). In this integrated dataset, stratigraphic intervals showing distinctly different lithofacies and ichnocoenoses drainage conditions average out to reflect the implied variable moisture conditions by the conflicting patterns. In lithologic units that did not preserve ichnofossils, the lithofacies drainage condition was used as the default condition.

The integrated drainage estimates from strata below and above the PETM interval do not vary significantly ($H = 0.18$, $N = 80$, $p < 0.669$). Estimated drainage conditions within the PETM interval suggest a significant improvement in soil-drainage conditions ($H = 8.46$, $\mathrm{N} = 160$, $p < 0.004$). The integrated drainage estimates from strata within the PETM interval, however, are not uniform and do not indicate significant improvements in soil drainage until the ~1512 m level, ~12 m above the onset of the PETM. Likewise, drainage estimates derived from strata above the ~1531 m mark—9 m below the return to non-PETM isotopic values—are not significantly different those outside the PETM (Fig. 12). The most significant drainage estimate values are within a ~19 m interval within the PETM as indicated by the lithofacies and ichnocoenoses paleohydrologic interpretations. If this ~19 m section is removed from the statistical analysis, the inferred drainage conditions for the remaining ~21 m of the PETM interval are not significantly different from drainage inferred from below and above the entire PETM interval ($H = 0.38$, $N = 120$, $p < 0.539$).

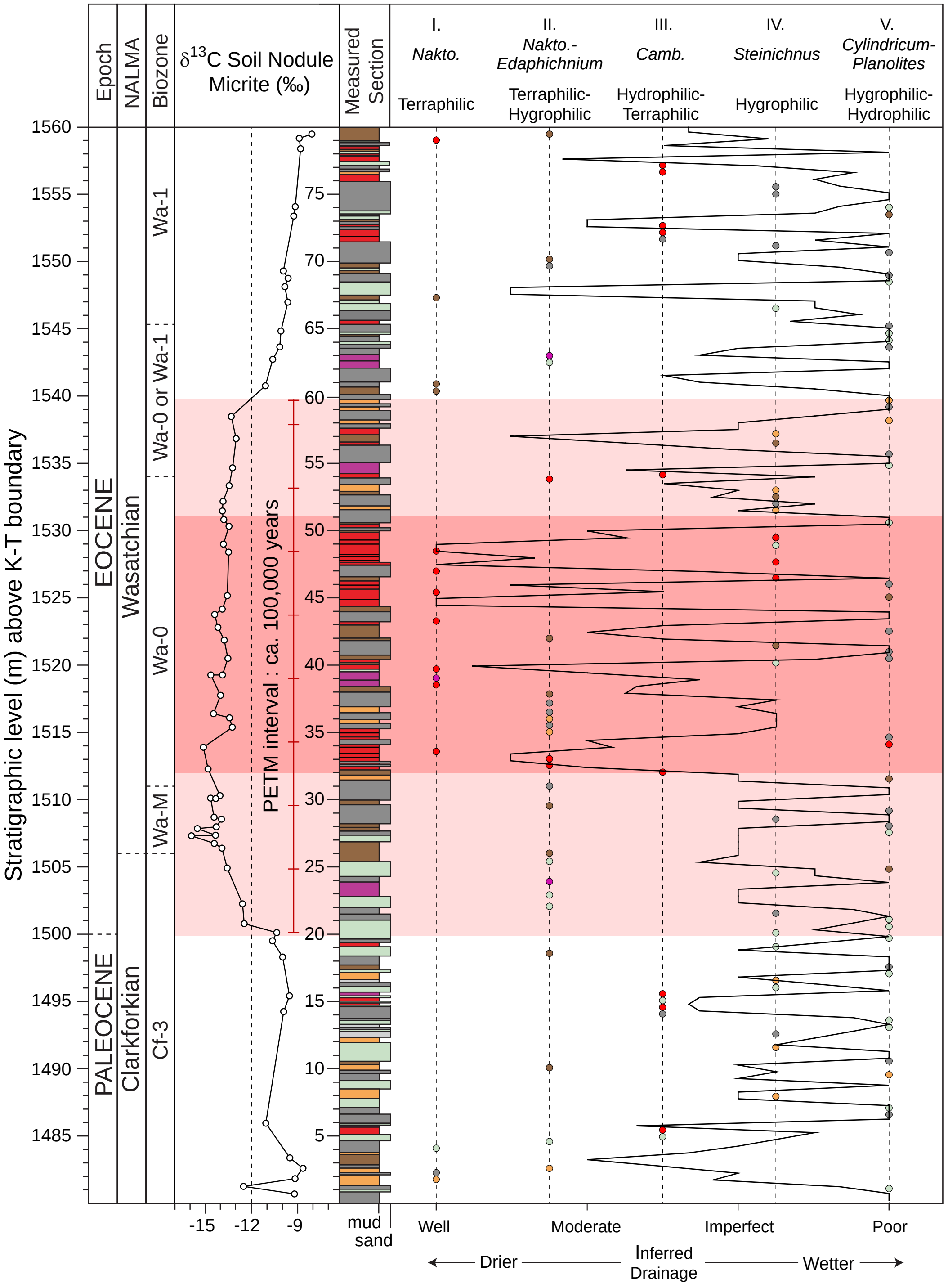

Figure 12. Summary figure showing the composite measured section, the distribution of ichnocoenoses, and estimated drainage conditions based on the combined lithofacies and ichnocoenoses estimated drainage patterns. Modified from Bowen et al. (2001), Gingerich (2001), and Bains et al. (2003).

DISCUSSION

Synthesis of Lithofacies and Ichnocoenoses

Lithofacies and ichnocoenoses of the Willwood Formation show significant differences in their interpreted moisture regimes through the PETM interval at Polecat Bench (Fig. 12). The Willwood floodplain was predominantly imperfectly to poorly drained before and after the PETM. Avulsion deposits show only incipient paleopedogenic development and commonly contain relict bedding and locally abundant molluscan body fossils. Ichnocoenoses likely implying imperfect to poor drainage conditions— in particular the *Cylindricum–Planolites* ichnocoenosis—are common and mostly in association with avulsion deposits. The development of thin red, yellow-brown, and brown compound paleosols indicates the floodplain experienced more rapid sediment accumulation and, thus, shorter periods of soil development. The paleosols contain terraphilic to hygrophilic ichnocoenoses that imply imperfect to at least moderate drainage, which is generally consistent with moisture conditions inferred from lithofacies characteristics.

Paleosols between the ~1500 and ~1512 m levels show only modest improvements in drainage compared with strata below the PETM interval suggesting that climates were transitional from wetter to drier. This lower part of the PETM interval is also the sandiest part of the study interval (Woody, 2007). Periods of climate change, especially from wet to dry, have the potential for creating large sediment fluxes due to changes in vegetation cover (e.g., Ethridge et al., 1998; Blum and Tornqvist, 2000). Greater sediment supply may have led to increased avulsion frequency and more abundant sandy deposits at the onset of the PETM (e.g., Slingerland and Smith, 1998; Murray and Paola, 2003).

Densely spaced paleosols indicate that the rate of sediment accumulation decreased during the ~1512 to ~1531 m interval (Fig. 12). Within the ~1512 and ~1531 m levels, significantly improved drainage and low water tables are implied by thick cumulative paleosols with dominantly red matrix colors and abundant pedogenic carbonate nodules, rhizohaloes, and calcareous rhizocretions. *Naktodemasis* and *Naktodemasis–Edaphichnium* ichnocoenoses are prevalent and suggest major improvements in soil drainage within this ~19 m section. The absence of the *Camborygma litonomos* ichnocoenosis in red paleosols within the ~1512 and ~1531 m levels—a pedofacies in which crayfish burrows are otherwise prevalent—suggests that water tables within this interval were at depths beyond the burrowing ability of local crayfish. Floodplain colonization by crayfish was also likely impacted negatively by less frequent and lower magnitude flooding events interpreted for the PETM interval. Manganiferous rhizocretions, interpreted as indicating poorly drained conditions, follow much the same pattern—they are abundant in avulsion deposits outside the PETM interval, become increasingly rare above the ~1500 m level, and are absent between ~1512 and ~1531 m (Woody, 2007).

A decrease in the thickness and maturity of paleosols begins ~9 m below the top of the PETM interval. The paleosols are also more widely spaced stratigraphically, suggesting that sediment accumulation rates increased. Ichnocoenoses within these deposits track the subsequent decline in drainage conditions inferred from the lithofacies and are increasingly composed of dominantly hygrophilic and hydrophilic ichnofossils. Abundant *Steinichnus* and *Cylindricum–Planolites* ichnocoenoses of low ichnodiversity suggest predominantly imperfect drainage conditions from the ~1531 m level to the top of the PETM interval. Lithofacies and ichnocoenoses above the PETM interval suggest a return to mostly pre-PETM floodplain drainage conditions, though the maturity and thickness of post-PETM paleosols are somewhat increased in comparison with paleosols below the PETM interval.

Paleoclimate Implications

The PETM interval at Polecat Bench is characterized by thick and well-developed red-cumulative-paleosols, a decrease in rates of sediment accumulation, and ichnocoenoses that suggest lower water tables and better drainage conditions than outside the PETM interval—all of which imply a significant decrease in the frequency and magnitude of flooding events during the PETM. The co-occurrence of the PETM and cumulic paleosols is not exclusive to Polecat Bench—such paleosols characterize the onset of PETM throughout the Bighorn and Powder River basins (e.g., Wing et al., 2003; Wing et al., 2005; Kraus and Riggins, 2007).

The changes in paleosol morphology and vertical trends that characterize the PETM interval were originally described by Kraus and Middleton (1987), who also observed changes in channel sandstone body size. Those changes were ascribed to a decline in the rate of sediment accumulation; however, without knowledge of the PETM, Kraus and Middleton (1987) attributed decreasing sedimentation to reduced rates of basin subsidence. Recognition of the PETM in the Bighorn Basin now allows us to attribute the sedimentologic changes at the PETM interval to climatic controls rather than tectonic activity—drier climates negatively affected precipitation and sediment flux resulting in less frequent sedimentation and drier soil moisture regimes. Considering that fluvial models and field studies commonly invoke basin subsidence as the major control of alluvial architecture (e.g., Heller and Paola, 1996; Kraus, 2002; Hickson et al., 2005), our study cautions that climate should not be ignored when analyzing alluvial stratigraphy.

The results of the ichnocoenoses analysis support other studies that indicate drying conditions on the Willwood floodplain in association with onset of the PETM in the Bighorn Basin and a return to wetter conditions toward the end of the PETM. Recently discovered fossil plant localities near the Cabin Fork area of the basin (see Fig. 1) show a rapid northward range expansion of subtropical flora within the PETM interval (Wing et al., 2005). Floral composition and leaf area analyses of these fossil plants suggest a mean annual precipitation (MAP) of ~800 mm at the onset of the global warming event—a nearly 40% decline from MAP estimates of ~1380 mm for southern Wyoming during the latest Paleocene.

Kraus and Riggins (2007) examined two Willwood sections containing paleosols formed during the PETM—at Sand Creek Divide in the center of the basin and at Polecat Bench (see Fig. 1). They interpreted significant improvements in drainage conditions based on changes in sedimentology, morphology, and geochemistry of paleosols at these locations. They interpreted a late Paleocene MAP of ~1300 mm, followed by ~900 mm MAP value at the base of the PETM and a gradual return to ~1300 mm MAP based on mineral weathering indices (Kraus and Riggins, 2007). In addition, they interpreted at least 4 wet-dry cycles, starting at nearly the base of the PETM interval (~1509 m level) at Polecat Bench, and possibly 3 similar episodes at Sand Creek Divide. Paleosols investigated by Kraus and Riggins (2007) at Polecat Bench were some of the same Willwood deposits examined in this study; thus, there is much congruence between their results and the interpretations presented in this study. Our research, based on a combination of the lithofacies and ichnocoenoses, however, suggests that soil drainage didn’t significantly improve until at least the ~1512 m level. A major difference between the two studies is that the present research includes avulsion deposits and their ichnocoenoses to interpret changes in floodplain drainage conditions. Paleosols are the most useful lithologic paleoclimate indicators at Polecat Bench because they are products of long-term exposure and weathering processes that were dictated in large part to climate (e.g., Kraus, 1999). Nevertheless, avulsion deposits included in this study also suggest improved drainage conditions through the PETM by differences in their ichnocoenoses associations and carbonate content.

CONCLUSION

Five distinct ichnocoenoses, as proxies for soil-paleocommunities, were established in paleosols and alluvial deposits at Polecat Bench based on stratigraphically reoccurring ichnofossil associations. Ichnocoenoses were designated independent of sedimentological, depositional, or paleopedologic characteristics of the surrounding strata to increase their interpretive power and to provide information about within-facies variations in ichnodiversity and paleohydrology (Hasiotis 2002, 2004). We interpret the ichnocoenoses to reflect differences in soil moisture conditions based on the inferred moisture regimes of their most abundant ichnofossil morphotypes and associated pedogenic features, including the other trace fossils and rhizoliths. This degree of resolution would not be possible using previously established ichnofacies for continental deposits because one ichnofacies can contain multiple ichnocoenoses, moisture regimes, depositional environments, and ecosystems. Proposed continental ichnofacies are too broadly defined and poorly constrained to provide reliable paleohydrologic or paleoenvironmental interpretations (Hasiotis et al., 2007).

Ichnocoenoses show changes in their inferred moisture conditions through the PETM based on the vertical changes in distribution, abundance, and ichnodiversity. Poor to imperfect drainage conditions outside the PETM interval are suggested by ichnocoenoses of low ichnodiversity and dominated by hygrophilic and hydrophilic trace fossils. Significant decreases in these same ichnocoenoses within the PETM interval, in addition to more abundant ichnocoenoses with terraphilic and hygrophilic trace fossils, suggest improved drainage on the Willwood floodplain. Improved drainage is transient though, and ichnocoenoses above the PETM interval are not significantly different from those below the PETM. The drainage patterns suggested by the ichnocoenoses are in general agreement with studies that have concluded precipitation in the Bighorn Basin decreased sharply during the PETM followed by a gradual return to pre-PETM levels.

Information about the degree of ancient soil wetness or moisture is important for understanding past climate conditions and for reconstructing continental paleolandscapes. This study demonstrates how stratigraphically controlled ichnocoenoses and their ichnopedologic associations can be used to interpret soil drainage conditions. Direct examination of the geologic record is important for testing local and regional generalizations produced by paleoclimate models, in addition to providing such models with climate information difficult to assess in other ways.

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CHAPTER 6. ANCIENT SOIL BIOTA RESPONDED TO RAPID GLOBAL WARMING DURING THE PALEOCENE-EOCENE THERMAL MAXIMUM

Currently in preparation as:

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ABSTRACT

The Paleocene-Eocene Thermal Maximum (PETM), a transient though severe global warming event, coincides with a foraminiferal mass extinction and an abrupt turnover of North American mammal faunas. Soil organisms, as recorded by their ichnofossils in the Paleogene Willwood Formation, Bighorn Basin, Wyoming, show changes in their stratigraphic distributions and abundances, and by significant reductions in body size during the PETM; perhaps as an adaptive response to high temperatures, lower soil moisture, or reduced nutritional values in high-CO_2 vegetation. We predict that extant insects may have responded or will respond to modern global warming similarly to Willwood soil fauna because anthropogenic increases in greenhouse gases and surface temperatures are similar in magnitude to climate change experienced during the PETM. Our research points toward a new and potentially powerful biomonitoring system using body size changes in living and historic collections of insects to gauge climate change.

INTRODUCTION

The Paleocene-Eocene Thermal Maximum (PETM) is recorded worldwide in ~55.8 Ma continental and marine deposits by a negative 2–6‰ carbon isotope excursion (CIE) in carbonate and dispersed organic carbon sources (Koch et al., 1992; Bains et al., 2003; Magioncalda et al., 2004). Leaf margin analyses (Wing et al., 2005) and oxygen isotope studies (Koch et al., 2003) analyses in the Paleogene Willwood Formation, Bighorn Basin, Wyoming suggest mean annual temperatures approaching 26°C during the PETM—a 3–7°C increase from latest Paleocene estimates. A nearly 40% decline in mean annual precipitation is suggested by leaf area analyses (Wing et al., 2005) and mineral weathering indices (Kraus and Riggins, 2007), contrary to previous studies indicating increased precipitation during the PETM (Bowen et al., 2004). The PETM interval coincides with an abrupt turnover in North American fossil mammal assemblages marking the transition from the Paleocene Clarkforkian (Cf) to the Eocene Wasatchian (Wa) mammal faunas (Fig. 1). The Wa-0 fauna is coincident with the main body of the PETM interval and is characterized by species 50-60% smaller than preceding Clarkforkian or later Wasatchian congenera (Gingerich, 2003).

Abundant ichnofossils in the Willwood Formation and the well-documented stratigraphic position of the CIE provide an opportunity to test if and how soil organisms respond to global warming at the Paleocene-Eocene boundary and use these findings to predict the affects of modern climate change on extant soil biota. Trace fossils during episodes of environmental stress and mass extinction events in marine deposits show significant decreases in ichnodiversity, burrowing density, burrow sizes, ichnofossil tiering, and depth of bioturbation (Barras and Twitchett, 2007). Willwood deposits contain a diverse and abundant assemblage of trace fossils likely representing invertebrate soil-dwelling biota (Bown and Kraus, 1983). Terrestrial invertebrates in particular are sensitive to changes in soil moisture and temperature because they must avoid desiccation and overheating, extreme moisture highs and lows, excess carbon dioxide, and hypoxia (Wallwork, 1970).

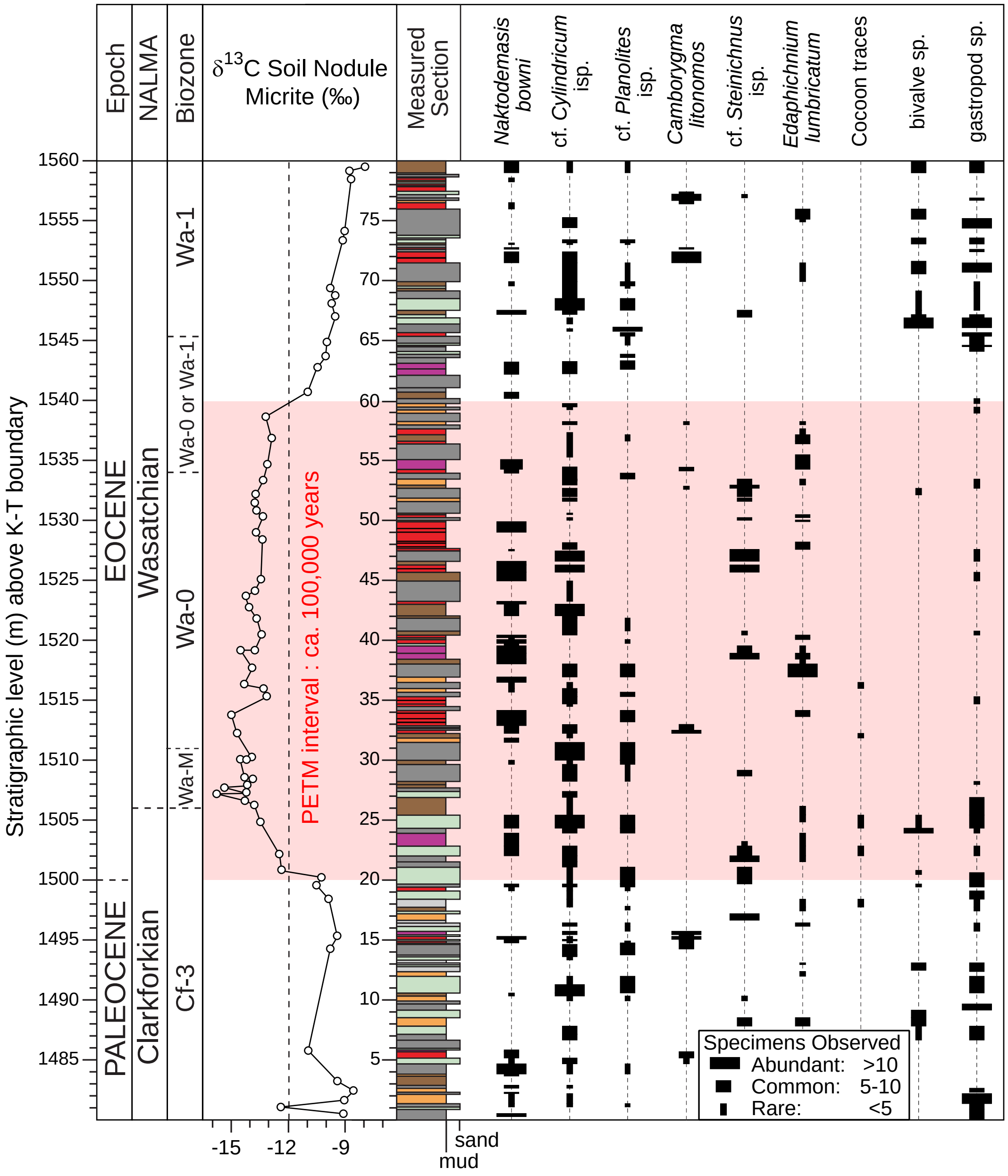

Figure 1. Composite measured section at Polecat Bench showing δ^{13}C (Bains et al., 2003), North American Land Mammal Age (NALMA) faunal zones (Magioncalda et al., 2004), meter levels, and relative abundances of ichnofossils.

GEOLOGIC FRAMEWORK

The Willwood Formation is a 780-m-thick succession of mudstone and sandstone interpreted as distal- and proximal-overbank deposits; avulsion deposits, which are complexes of crevasse-splay deposits; and trunk-channel deposits, all modified by varying degrees of pedogenesis (Kraus, 2001). An ~40 m stratigraphic interval of the Willwood Formation at Polecat Bench, northwest of Powell, Wyoming, was deposited during the PETM (Gingerich, 2001). We excavated 54 measured sections from ~20 m below to ~20 m above the PETM interval as established by previous isotopic analyses of carbonate nodules (Bowen et al., 2001) and mammalian biostratigraphic studies (Gingerich, 2001). Changes in the sedimentology, paleosol morphology, and geochemistry within this interval suggest that the Willwood floodplain experienced significantly improved drainage during the PETM (Kraus and Riggins, 2007). This interval is characterized by a series of thick, predominantly red cumulic paleosols, pervasive mottles, and abundant rhizoliths. Pedogenic carbonate nodules, and carbonate-filled rhizoliths and burrows increase dramatically within the PETM interval, particularly in red paleosols.

METHODS AND MATERIALS

We excavated 54 measured sections from ~20 m below to ~20 m above the 40-m PETM interval on Polecat Bench. The position of the PETM was established on the basis of previous isotopic analyses of carbonate nodules and mammalian biostratigraphic studies (Gingerich, 2001). We recorded the stratigraphic position, relative abundance, and diameters of trace fossils. Relative abundances through the PETM interval and with respect to similar lithologies were evaluated using the nonparametric Kruskal-Wallis test (H). Burrow widths and lengths were measured in the field with a standard metric ruler. Burrow-diameter sizes were tested using one-way analysis of variance (ANOVA, $\alpha = 0.05$) with Bonferroni adjustments to critical values ($\alpha = 0.0167$) for multiple comparisons within like-ichnofossil datasets to control for Type I error.

DISTRIBUTION OF ICHNA THROUGH THE PETM

Seven morphotypes; *Naktodemasis bowni*, *Camborygma litonomos*, *Edaphichnium lumbricatum*, cf. *Cylindricum* isp., cf. *Planolites* isp., cf. *Steinichnus* isp., and cocoon traces (Table 1) are present throughout the measured section (Fig. 1). Relative abundances of *N. bowni*, cf. *Cylindricum* isp., *E. lumbricatum*, and cf. *Steinichnus* isp. increase within the PETM interval, especially in red, yellow-brown, and purple paleosols. *N. bowni* assemblages in paleosols show significant increases in relative abundance within the PETM interval (Kruskal-Wallis test, $H = 5.76$, df = 1, $n = 35$, $P = 0.016$). *C. litonomos* and cf. *Planolites* isp. are less abundant within the PETM interval, though only *C. litonomos* in paleosols are significantly less abundant (Kruskal-Wallis test, $H = 6.32$, df = 1, $n = 11$, $P = 0.012$). The decreased abundance of *C. litonomos* from red paleosols within the PETM interval is particularly striking because their prevalence in similar deposits outside the PETM produces a distinctly prismatic structure in the paleosols. Cocoon traces are rare both before and after the PETM interval. Molluscan body fossils are common to abundant in avulsion deposits and weakly developed paleosols outside the PETM interval, but are rare or absent through much of the PETM interval.

Naktodemasis bowni, cf. *Cylindricum* isp., and cf. *Planolites* isp. are abundant enough throughout the measured section to test for changes in burrow sizes from before, during, and after the PETM interval (Figs. 2). Mean burrow diameters of *N. bowni* decrease by ~47% within the PETM interval (n=233) and are significantly smaller (ANOVA, $F = 68.8$,

Ichnofossils	Sample Size	Mean Diameter (mm)	Ichnofossil Description	Potential Tracemakers[8, 14-15]
Naktodemasis bowni	111 (233)	7.48 (3.90)	Sinuous burrows of distinct ellipsoidal packets with thin meniscate backfill	burrower bugs, cicada nymphs, beetle larvae
cf. *Cylindricum* isp.	116 (182)	12.08 (8.11)	Predominantly vertical, smooth-walled shafts commonly infilled with sand	beetles, bees, siders, mollusks
cf. *Planolites* isp.	58 (49)	8.60 (6.22)	Horizontal, smooth-walled tunnels most commonly infilled with mud	wasps, beetles, ants, crickets
cf. *Steinichnus* isp.	9 (45)	3.71 (2.70)	Predominantly vertical shafts with transverse striations	burrower bugs, beetles
Edaphichnium lumbricatum	12 (39)	7.25 (5.10)	Variably oriented burrows composed $CaCO_3$ or sediment-filled pellets	oligochaete worms
Camborygma litonomos	118 (29)	25.40 (24.51)	Vertical shafts with distinctly striated and knobby surface morphology	freshwater crayfish
cocoon traces	3 (4)	11.67 (4.00)	Ovoid cells of $CaCO_3$ or sediment, few with fine hatch pattern on surface	oligochaete worms

Table 1. Ichnofossil descriptions. Numbers within parentheses denote specimens measured from within the PETM interval.

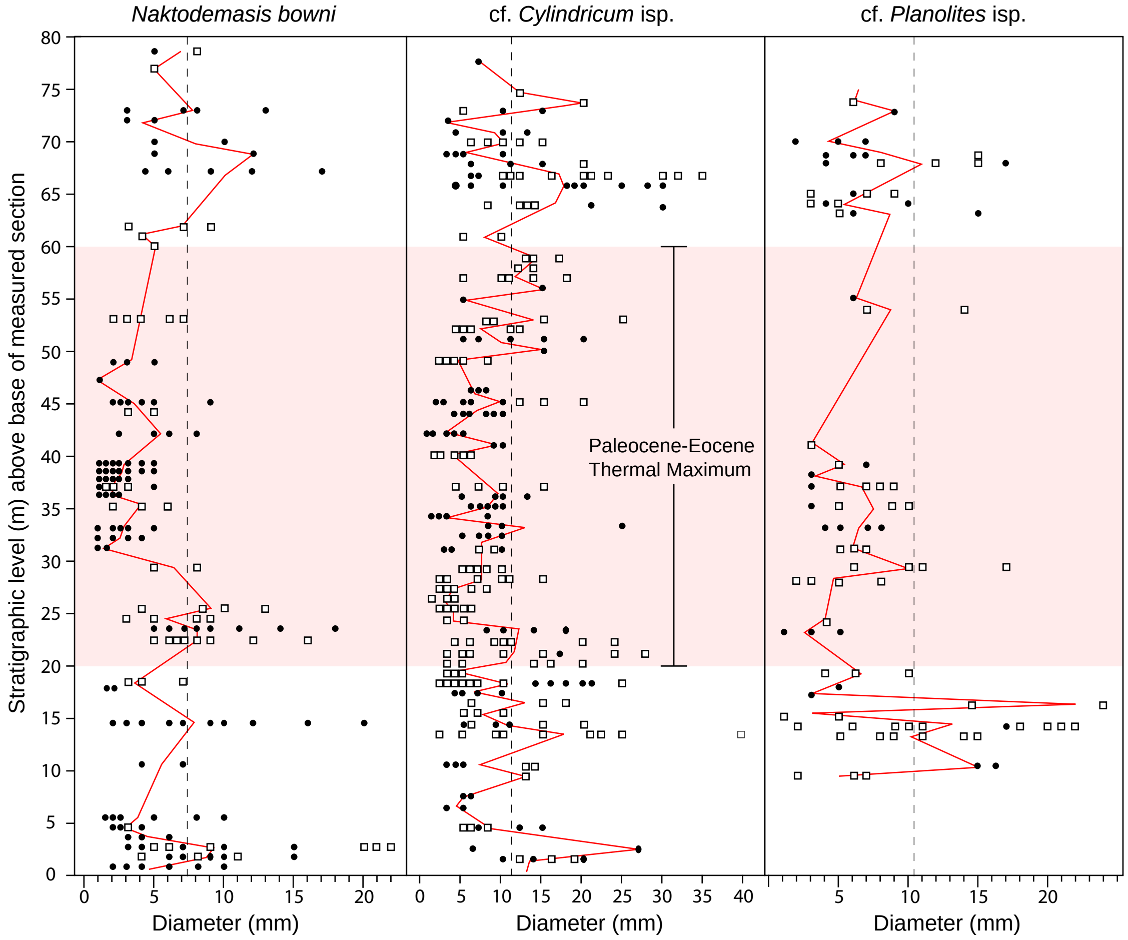

Figure 2. Size changes of ichnofossil burrow diameters through the PETM. Black circles represent mean burrow diameters from fine-grained lithologies, mostly paleosols; open squares represent mean burrow diameters from coarse-grained lithologies, mostly avulsion deposits. Trend lines indicate running average of all burrow diameters. Dashed vertical lines mark mean diameter of burrows below and above the PETM interval for each morphotype.

$P < 0.0001$) compared with those measured outside the PETM (n=111; Fig. 3). Cf. *Cylindricum* isp. in PETM strata (n=182) decrease in diameter by ~33% and are significantly smaller (ANOVA, $F = 21.20$, $P < 0.0001$) than those outside the PETM (n=116). Cf. *Planolites* isp. decrease in diameter by ~39% within the PETM interval (n=45) and are significantly smaller (ANOVA, $F = 6.23$, $P < 0.008$) than burrows outside the PETM interval (n=59). *Camborygma litonomos* within the PETM interval are not significantly different in size from those outside the PETM. Likewise, *Edaphichnium lumbricatum* and cf. *Steinichnus* isp. show no significant size changes, though they generally are smaller and more abundant within the PETM interval.

N. bowni, cf. *Cylindricum* isp., and cf. *Planolites* isp. are significantly smaller during the PETM interval regardless of host-rock grain size, suggesting that smaller burrow diameters are not due to changes in the ratio of fine- to coarse-grained deposits (Fig. 3). Applying a Bonferroni adjustment to the critical value ($\alpha = 0.0167$) to account for multiple comparisons, however, produces both significant and nonsignificant results with regard to grain size of the host rock. These results suggest that shifting lithologies within the PETM interval may account for some variance in burrow diameters, though with the following caveats: 1) all comparisons indicate a trend toward smaller burrow diameters within the PETM interval regardless of ichnofossil morphotype or lithology, 2) *Cylindricum* and *Planolites* are widely recognized as facies-independent trace fossils (Pemberton, 1982; Bromley, 1996), and 3) the necessity of applying a Bonferroni correction to independent statistical comparisons is not uniformly agreed upon (Moran, 2003).

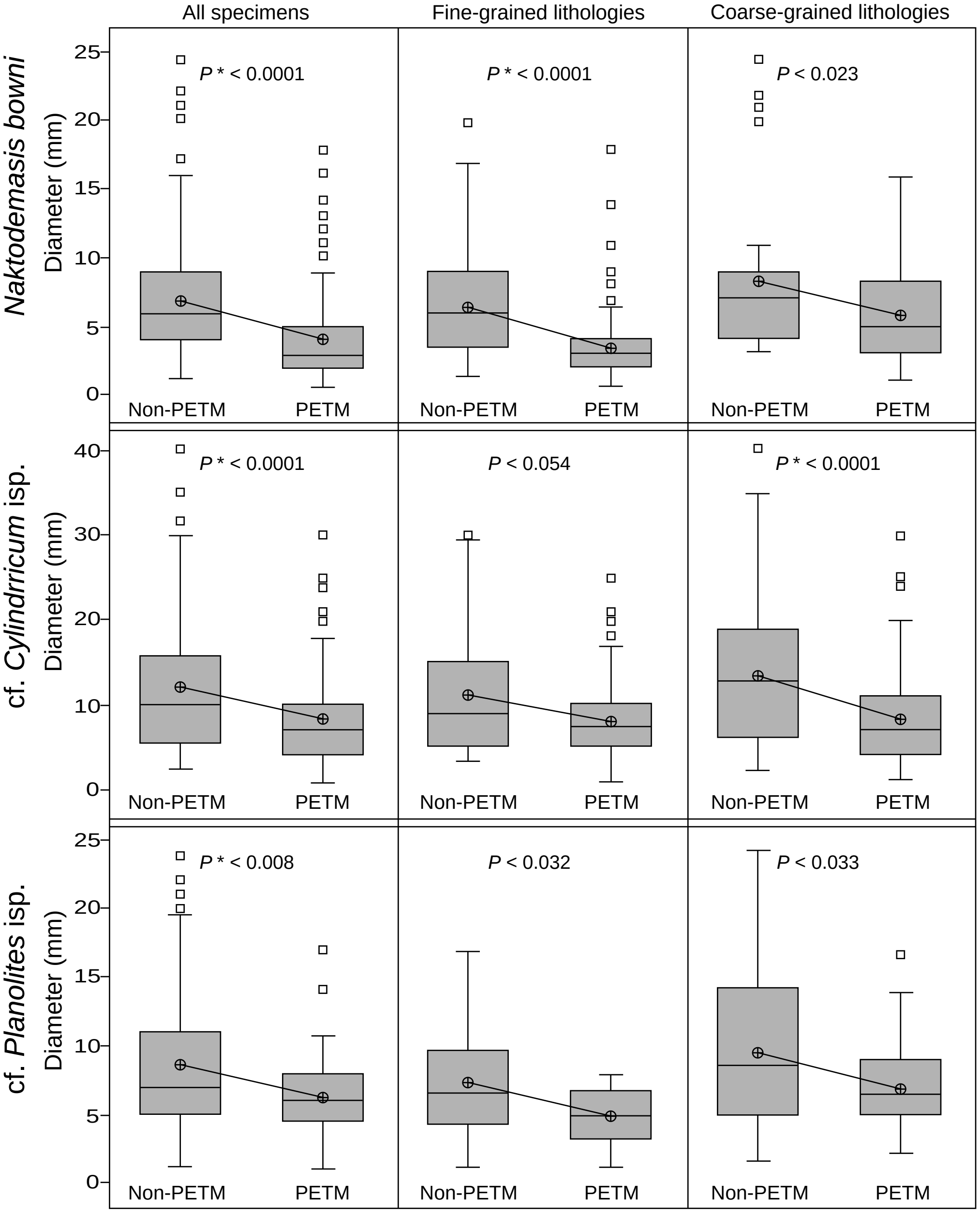

Figure 3. Box plot showing the effect of the PETM interval and grain size of host-rock lithologies on ichnofossil burrow diameters. *P*-values (ANOVA, $\alpha = 0.05$) indicate statistical significance between burrow diameters within the PETM interval (PETM) and those below and above PETM interval (Non-PETM). *P**-values indicate statistically significant results after a Bonferroni correction of the critical value ($\alpha = 0.0167$) for multiple comparisons. Box plots encompass the 25th and 75th percentile, error bars encompass the 10th and 90th percentile, open squares represent outlying values, horizontal lines represent the median, and crosshair symbols represent the mean.

RESPONSE OF SOIL BIOTA TO THE PETM

The Willwood ichnofossil record suggests that soil biota did respond to changing paleohydrologic and paleoclimatic conditions in the Bighorn Basin, and supports recent studies indicating drier conditions during the PETM (Kraus and Riggins, 2007). The greater abundance of probable insect and oligochaete ichnofossils (Hasiotis, 2002) suggests that these organisms responded positively to the better-drainage conditions and longer periods of landscape stability implied by abundant pedogenic carbonate and the development of thick, well-vegetated soils during the PETM. The majority of soil biota live within the vadose zone, and increased soil drainage or lower water tables promote pedogenesis and bioturbation by these organisms (Wallwork, 1970; Hasiotis, 2002). Likewise, the near absence of *Camborygma litonomos* throughout much of the PETM interval is also likely due to low water tables. Extant freshwater crayfish that construct burrows identical to *C. litonomos* live mostly in open waters, but burrow to reproduce or escape desiccation in areas with fluctuating water tables (Hobbs, 1981). Crayfish require standing water for respiration and were probably relegated to stream channels and other such aquatic habitats when drainage improved during the PETM. *C. litonomos* toward the top of the PETM interval likely signal a return to wetter floodplain conditions. Molluscan body fossils follow much the same pattern, especially bivalves, which are fully aquatic organisms.

Burrow size is correlated generally with tracemaker body size (Savrda and Bottjer, 1986), therefore, significant reductions in burrow diameters (33–47%) during the PETM suggest that their tracemakers were smaller bodied as well. Reduced burrow diameters within the PETM interval parallel previously documented reduction in size of Wa-0 mammal fauna (Gingerich, 2003), suggesting a common forcing mechanism or combination of causes that promoted dwarfism in both above- and below-ground biotic communities. These changes may represent the replacement of larger, pre-PETM soil biota with smaller, immigrant taxa better adapted to warmer or drier soil conditions. Alternatively, burrow-size differences may represent the environmental selection and inherited adaptation of smaller bodied soil fauna during the warming event. Climate induced intraspecific changes in body size or increased sexual dimorphism has been reported in some extant species (Parmesan, 2006).

Higher temperatures, drier climate conditions, and elevated atmospheric CO_2 levels inferred for the PETM (Zachos et al., 2001; Kraus and Riggins, 2007) may have impacted soil biota growth rates, development times, or the nutritional value of their food sources—all of which govern adult body size within a given species (Davidowitz et al., 2004). Most (80–90%) bacterium, protists, plants, insects, and other ectotherms reared under controlled conditions exhibit significantly increased growth rates, shorter development times, and smaller adult body sizes at higher temperatures (Atkinson, 1994; 1995). Higher temperatures may also suppress adult body size by increasing juvenile mortality and decreasing maximum life spans (Shaw and Bercaw, 1962; Sohal, 1986; Sibly and Atkinson, 1994). Little is known about how soil-moisture conditions influence invertebrate size, though smaller body size does correlate with drier soils in some species of dung beetles (Vessby, 2001). The direct effects of elevated atmospheric CO_2 on soil invertebrates are likely to be negligible because CO_2 concentrations are typically 10–50 times higher in soils than in the atmosphere (Kandeler et al., 1998). High CO_2 effects on vegetation, however, must indirectly affect soil biota because plant tissues and photosynthates form the base of the soil food web (Young et al., 1998). Elevated CO_2 partial pressures (twice current levels ~350 ppmv) increase photosynthesis, reduce nitrogen and rubisco concentrations—enzymes regulating carbon fixation, and substantially decrease the nutritional value of plant tissue, resulting in slower growth rates and increased mortality in some herbivorous insects (Fajer et al., 1989). Smaller adult body size might be expected under these conditions, however, size differences are often less dramatic than those associated with temperature effects (Brooks and Whittaker, 1999).

CONCLUSION

We demonstrate for the first time that soil biota respond to climate changes in ways that are detectable in the fossil record. We predict that extant insect species have responded or will respond in a similar fashion to modern global warming because anthropogenic increases in greenhouse gases and surface temperatures—initiated in the late 18th century with the onset of the industrial revolution (IPCC, 2007)—are similar in magnitude to climate changes experienced during the PETM (Zachos et al., 2005). Our research suggests that changes in adult insect size may be a potentially powerful biomonitoring tool to gauge the past and future impacts of global warming on modern ecosystems. Well-documented and extensive museum insect collections—numbering in the tens of millions worldwide and some dating back to pre-industrial times—and specimens recovered from archeological sites should be reexamined and compared with living specimens. Looking forward, ongoing and future insect monitoring programs collecting morphometric data may be able to detect body size changes over the coming decades and quantify potential climate warming effects in living populations.

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CHAPTER 7. CONCLUSION

This research demonstrates that combining paleopedological, paleontological, neoichnological, and ichnological methods can provide a broader understanding of the paleoenvironmental, paleoecological, and paleoclimatic significance of continental organisms and their trace fossils. Ichnofossils of soil-dwelling invertebrates are important *in situ* indicators of the paleohydrologic regime, degree of pedogenesis, paleoecology, and paleoclimatic setting during the time of their formation.

The morphology, interpreted behaviors, probable tracemakers, and paleoenvironmental significance of adhesive meniscate burrows (AMB) are distinctly different from such previously described backfilled ichnotaxa as *Beaconites*, *Laminites*, *Scoyenia*, *Taenidium*, and *Ancorichnus*. *Naktodemasis bowni*, a new ichnogenus and ichnospecies, thus, is erected to represent burrows composed of distinct, ellipsoid packets that contain indistinct, meniscate backfill. *N. bowni* is interpreted as the locomotion and dwelling trace of a burrowing insect—most likely burrower bugs (Hemiptera: Cydnidae) or cicada nymphs (Hemiptera: Cicadae), and less likely scarabaeid (Coleoptera: Scarabaeidae) or carabid beetles (Coleoptera: Carabidae). *N. bowni* had previously been interpreted as the fodinichnia of subaqueous, deposit-feeding organisms based on the behaviors and physiochemical requirements of organisms that create backfilled burrows in the marine realm. This research, however, suggests that *N. bowni* indicates periods of subaerial exposure and improved drainage conditions in continental deposits, and it can be used to differentiate alluvial paleoenvironments from marine and lacustrine paleoenvironments as well as periods of subaerial exposure of sediments deposited in aquatic settings.

The traces of temporary and permanent soil-dwelling insects have rarely been examined experimentally despite their role as primary agents of pedoturbation and great abundance in modern soils. Traces and burrowing behaviors of nymphs of the prairie cicada *Melampsalta calliope* (Hemiptera; Homoptera; Cicadidae) produced in neoichnological experiments demonstrate that backfilled burrows are not all produced in the same way—forward motion accomplished by sediment ingestion and excretion—and that the morphologically of meniscate traces produced by cicada nymphs and likely other similarly adapted burrowing hemipterans are distinct and attributable to specific behaviors and different portions of their lifecycle. *M. calliope* nymphs and their traces are excellent analogs for such meniscate trace fossils as *Naktodemasis bowni* commonly reported in late Paleozoic to Cenozoic alluvial deposits and paleosols, and thus, can be used to interpret the paleohydrology and paleoecology of the units in which they are found. Trace fossils with similar morphologies as modern cicada-nymph traces extend the geographic and stratigraphic range of these organisms in the fossil record.

Freshwater crayfish burrows in paleosols of the Willwood Formation provide valuable information with respect to hidden biodiversity, paleopedogenic processes, paleohydrologic regime, and changing paleoclimatic conditions during the early Paleogene in the Bighorn Basin, Wyoming. These burrows illustrate the important role that soil-dwelling biota played in initiating and enhancing pedogenic development of Willwood floodplain soils. Freshwater crayfish promoted soil development through homogenization of burrow horizon sediments, improving aeration and drainage, promoting root and fungal hyphae growth, and mediating prismatic soil structure. Crayfish are excellent indicators of environmental and paleoclimatic conditions because the architecture and depth of their burrows are dictated primarily by ambient surface conditions and local hydrologic regimes.

Research conducted in alluvial deposits of the Willwood Formation deposited during before, during, and after the Paleocene-Eocene Thermal Maximum (PETM) demonstrate that soil biota are not buffered by the soil media from severe episodes of climate change. Five distinct ichnocoenoses interpreted as representing either poorly, imperfectly, moderately, or well-drained moisture regimes show vertical changes in their distribution, abundance, and ichnodiversity through the PETM. Ichnocoenoses likely indicating dominantly poor to imperfect drainage conditions on the Willwood floodplain are common below and above the PETM interval, but decrease significantly within the interval deposited during the PETM. Improved drainage conditions during the PETM are also suggested by increases in the abundance of ichnocoenoses likely indicating moderately to well-drained soil conditions. The drainage patterns suggested by the ichnocoenoses are in general agreement with studies that have concluded precipitation in the Bighorn Basin decreased sharply during the PETM followed by a gradual return to pre-PETM levels. This study demonstrates how ichnocoenoses and their ichnopedologic associations can be used to test and refine paleohydrologic and paleoclimatic generalizations inferred from paleoclimate models.

Individual trace fossils, as proxies for soil organisms, in Willwood paleosols and alluvial deposits show changes in their distribution, increased abundance, and significant size reductions during the PETM. Changes in occurrence and abundance were likely due to better-drained soil conditions and lower water tables during the PETM, though these effects were transient. Burrow diameters of the most abundant ichnofossils are 30–46% smaller within the PETM interval, suggesting that the tracemakers were smaller bodied. Reduced burrow diameters within the PETM interval parallel previously documented Wa-0 mammal species 50–60% the size of their Clarkforkian congeners, suggesting a common forcing mechanism, or combination of causes, promoted dwarfism in both above- and below-ground biotic communities. Reduced size may have been an adaptive response to higher temperatures, lower soil moisture, or reduced nutritional values in high CO_2 vegetation. This research is the first to demonstrate that ancient soil biota respond to climate change in ways that are detectable in the fossil record. This study also proposes that similar changes in extant insect populations may be used as a new biomonitoring tool to gauge the impact of modern anthropogenic-increases in greenhouse gases and surface temperatures.

The integrated results of these studies indicate that well-preserved and abundant trace fossils of soil biota, particularly arthropods, in continental deposits are important indicators of subaerial exposure, paleopedogenesis, and landscape stability. Such traces are indirect evidence of biodiversity in ancient soils because the body fossils of soil biota are rarely preserved *in situ* within paleosols. Detailed morphologic analysis of continental trace fossils, in combination with their ichnopedologic associations, and neoichnologic studies of modern burrowing organisms are critical for improving the interpretive power of these ichnofossils, instead of relying on interpretations of similar traces produced by marine organisms. Finally, continental ichnofossils can be used to examine the paleoenvironmental, paleoecological, and paleohydrological impact on terrestrial ecosystems during periods of known climate change in the geologic past.