GEOLOGICAL NOTE

Evidence for an Early Sagebrush Ecosystem in the Latest Eocene of Montana

Nathan D. Sheldon and Jessica M. M. Hamer¹

Department of Geological Sciences, University of Michigan, 2534 CC Little, 1100 North University Avenue, Ann Arbor, Michigan 48103, U.S.A. (e-mail: nsheldon@umich.edu)

ABSTRACT

Late Eocene strata at Little Pipestone, Montana, preserve paleosols and an undiverse but abundant trace fossil assemblage dominated by adhesive meniscate burrows placed into the ichnogenera *Taenidium*. The assemblage as a whole is most consistent with the *Scoyenia* ichnofacies. The reconstructed paleohydrological and paleoenvironmental setting that results from the combination of sedimentological, paleopedological, and ichnological data is of a seasonally desiccated, well-aerated floodplain characterized by low flood frequency and intensity, slow sediment accumulation rates, and an overall subhumid/semiarid climate very similar to a modern sagebrush steppe. This would represent the oldest documented sagebrush steppe ecosystem in Montana.

Online enhancements: appendixes.

Introduction

The increasing recognition of paleosols in nonmarine strata has greatly expanded the scope of paleoclimatic and paleoenvironmental reconstructions, as proxies now exist for past precipitation regimes (Stiles et al. 2001; Sheldon et al. 2002; Retallack 2005), past temperatures (Dworkin et al. 2005; Sheldon 2006), and past atmospheric composition (various; e.g., Tabor et al. 2004). Other features commonly described from paleosols that contribute to paleoenvironmental reconstructions include root traces/rhizoliths (Kraus and Hasiotis 2006) and trace fossils (Hasiotis 2004; Hamer et al. 2007b), and these can be used in concert with paleopedological data (e.g., Cleveland et al. 2007; Smith et al. 2008b). In particular, rhizoliths and trace fossils contribute to our understanding of paleohydrological conditions because, for example, the depth of rooting is in part due to the position of the paleowater table (Sheldon 2005). Similarly,

Manuscript received September 11, 2009; accepted February 24, 2010.

¹ Department of Earth Sciences, Royal Holloway, University of London, Egham, Surrey TW20 0EX, United Kingdom.

nonmarine organisms will not have burrowed any deeper than the level of the paleowater table with the exception of a few organisms such as crayfish. Neoichnological studies also are useful for informing our interpretations of the trace fossils because the formation of the trace can be observed directly and can be associated with a particular environment (e.g., Hembree and Hasiotis 2006; Smith and Hasiotis 2008). Late Eocene strata exposed at Little Pipestone in Montana present an ideal opportunity to explore the application of ichnological data in concert with measurable properties of the paleosols there to make a robust paleohydrological and paleoenvironmental reconstruction.

Little Pipestone

Little Pipestone is a well-known and oft-studied vertebrate locality that was first examined in detail by Earl Douglass in the early part of the twentieth century (Douglass 1901, 1903, 1905). Many of his basic taxonomic assignments are still in use (Ta-

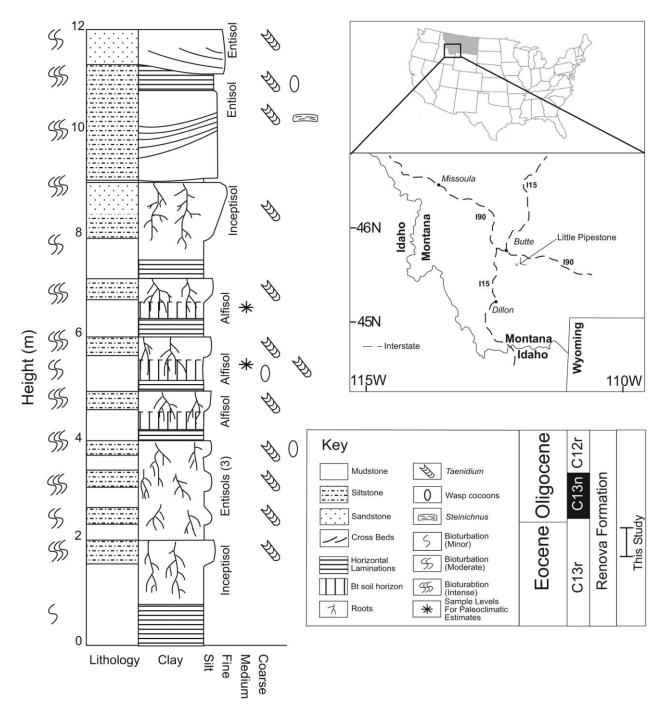


Figure 1. Representative stratigraphic section and location map.

brum and Nichols 2001), though subsequent work has greatly expanded the understanding of the assemblage there, which includes Squamata, Lepticida, Lagomorpha, Rodentia, Creodonta, Perissodactyla, and Artiodactyla (Tabrum and Nichols 2001). The sediments at Little Pipestone are part of the Climbing Arrow Member of the Renova For-

mation (latest Eocene–earliest Oligocene locally) and were deposited on the floodplain as channel and overbank deposits (Prothero 1984; Tabrum et al. 1996; Retallack 2007). They consist of buff-colored claystones, siltstones, and fine sandstones (figs. 1, 2) with some original sedimentary structures, including evidence for fluvial channels (fig.

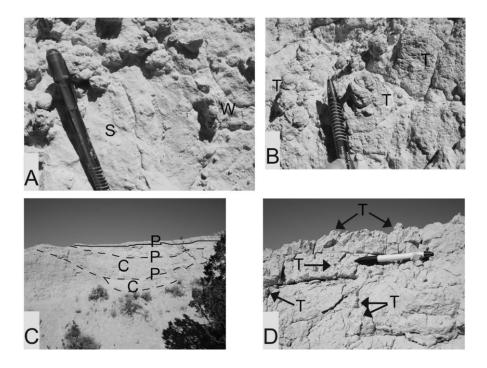


Figure 2. Representative exemplars of ichnofossils. *A, Steinichnus* (S) and wasp cocoons (W). *B, Taenidium* (T), showing vertical structure. Sediments have weathered out around the backfilled burrow, leaving a constructive ichnofossil. C, Cryptic fluvial channels (C) capped by well-bioturbated, poorly developed paleosols (P). D, Close-up of the paleosols in D with cross-sectional views of vertically oriented T

2*D*). Superimposed on these sediments are rare, poorly to moderately developed, buff-colored paleosols (fig. 2*D*, 2*E*).

Methods

The Little Pipestone locality is just east of the junction between Montana Highway 2 and Montana Highway 41 (N45°50′33.6″, W112°15′40.8″) at an elevation of 1471 m as measured by GPS (lateral accuracy of 5 m). J. M. M. Hamer measured and described a representative ~12-m stratigraphic section (fig. 1). In addition to field observations of burrows, N. D. Sheldon collected 100 burrows and measured their dimensions using calipers. That suite of samples is catalogued at the University of Michigan. Thin sections were made of six vertical burrow traces to examine internal structure. Bk depths were measured by G. Retallack during fieldwork in 2001-2002 using a tape measure and were decompacted (Sheldon and Retallack 2001) to account for postburial compaction (Sheldon and Retallack 2004); results are archived elsewhere (Retallack 2007). Paleoclimatic data reconstructed using whole-rock geochemistry are from Retallack

(2007) and Hamer (2009) and are compiled in table A1 in appendix A, which is available in the online edition or from the *Journal of Geology* office. A small number (n = 6) of bulk-rock carbon-isotopic analyses of paleosol A horizons were made using continuous-flow EA-IRMS (elemental analyzer isotope ratio mass spectroscopy), but the analyses indicated that any carbon present was at or below the detection limit (>0.01 wt%), so the site is effectively free of organic carbon. Chronostratigraphic control comes from a combination of magnetostratigraphy (Prothero 1984), biostratigraphy (Tabrum et al. 1996), and sequence stratigraphy (Hanneman et al. 2003), and specific sample age estimates are compiled in Retallack (2007) and in table A1.

Results

Paleosol Types. As part of a long-term record of paleosols in Montana, Retallack (2007) identified and named four different pedotypes (types of paleosols) at Little Pipestone at two sublocalities on either side of Montana Highway 41, two of which were exposed at the site that we are evaluating herein. The Yantun (Shoshoni "large winnowing

basket") pedotype has a semigranular structured brown (7.5YR-2.5Y) A and moderately developed Bw horizon clayey siltstone over a deep (>50 cm) Bk horizon. The Kanah (Shoshoni "thin") pedotype has a light brown (2.5Y-10YR) A and weakly developed Bw horizon clayey siltstone over shallow (<50 cm) calcareous nodules (Bk). Both pedotypes would represent Inceptisols in the USDA soil classification scheme (Soil Survey Staff 1999) and Protosols in the paleosol-specific taxonomic scheme of Mack et al. (1993; G. Retallack, pers. comm.). During our fieldwork, we have reassessed slightly the previous soil taxonomic classification because the Bk horizons identified by Retallack (2007) are noncalcareous to extremely weakly calcareous and do not fit the Soil Survey Staff (1999) definition of a Bk horizon. Based on this observation and the presence of additional weakly developed paleosols that were not previously documented, we instead identify three types of paleosols: (1) weakly developed Alfisols (A-Bt(Bw)-C profiles; Soil Survey Staff 1999) with a granular structured Bt/Bw horizon and very weak drab mottling around moderately to sparsely populous root traces (Argillisols in the Mack et al. [1993] scheme) equivalent to the Yantun pedotype; (2) moderately developed Inceptisols (A-Bw-C profiles; Soil Survey Staff 1999) with a mildly granular Bw horizon, some relict structure, and very weak drab mottling around moderately to sparsely populous root traces (Protosols in the Mack et al. [1993] scheme) equivalent to the Kanah pedotype; and (3) Entisols (A-AC-C or A-C profiles; Soil Survey Staff 1999) with relict bedding throughout and very weak drab mottling around sparse root traces (also Protosols in the Mack et al. [1993] scheme).

A final taxonomic consideration is that the paleosols all contain a significant amount of reworked rhyolite tuff (25%). However, based on Soil Survey Staff (1999) criteria, they cannot be classified as andic because nonvolcanically derived sediment also forms a considerable component of the parent material (Hamer 2009).

Trace Fossil Identification and Classification. Four distinctive types of trace fossils (fig. 2) have been identified at Little Pipestone: root traces (type 1, rhizoliths and drab-haloed branching traces), ovoid structures (type 2), Steinichnus (type 3), and an exceptionally common (fig. 3) adhesive meniscate burrow trace given a field identification of Taenidium (type 4 [fig. 2B, 2E], discussed further below). There are also some rare burrows that are walled, unlined, centimeter/decimeter in length, centimeter-width subhorizontal, relatively friable burrows with little internal structure that might be



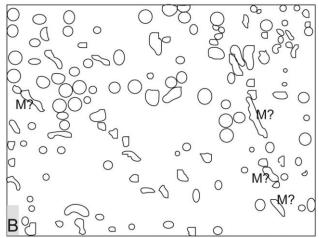


Figure 3. Arthropod burrow photos. A, Plan view photo of *Taenidium* burrow tops. B, Sketch of all of the ichnofossils present in A; subhorizontal micromammal(?) burrow (M).

attributable to micromammal burrowing (figs. 2*C*, 3*B*) but that are too poorly preserved to be formally classified as ichnotaxa. Key features are described here, and complete, formal ichnological descriptions are in appendix B, which is available in the online edition or from the *Journal of Geology* office.

The root traces (type 1) are weakly redoximorphic (i.e., drab haloed), millimeter scale (1–8-mm diameter), and drab gray in color. They typically are most abundant near the tops of the paleosols, with declining abundance with depth, and without sufficient textural difference as compared to the sedimentary matrix to classify them as rhizoliths. Though they are not taxonomically distinctive, the root trace sizes are consistent with low-stature vegetation (Retallack 2007). The ovoid structures (type 2) are millimeter/centimeter-scale, egg-shaped

casts (fig. 2A) that often are preserved with the mold intact as well. Steinichnus (type 3) have been identified from subhorizontal, decimeter-length, weakly lined, nonmeniscate burrows (fig. 2A). The Steinichnus identified here are similar to previously identified Steinichnus of Hasiotis (2004), also from a paleosol-floodplain setting. The field identification Taenidium (type 4) for the dominant trace at Pipestone was based on the fact that the burrows in question are vertical to subvertical, unlined and unwalled, and with meniscate backfill (D'Alessandro and Bromley 1987). Taenidium traces (fig. 4) at Pipestone bear a strong resemblance to other nonmarine traces identified by O'Geen and Busacca (2001) and O'Geen et al. (2002) that were designated Taenidium (Retallack 2007), though other possible interpretations will be discussed below. In the field, all of the burrowing traces are the same color as their surrounding sediments and have been filled with the same material as the surrounding sediments; thin sections of the *Taenidium* burrows suggest some minor iron oxide staining of the burrow margins (fig. 4C), but similar features are not present in any of the other ichnofossils that were identified.

Taenidium Size Distribution. The mean burrow width is 15.03 mm, with a range of 8–24 mm and a mode of 14 mm (fig. 5). The size distribution of the burrows is nearly normal (the mean and mode are nearly equal), with only a slight skew toward larger burrows resulting in a standard deviation of <3.3 mm, suggesting that the trace makers were also nearly uniform in size and therefore are likely to have been made by the same organism.

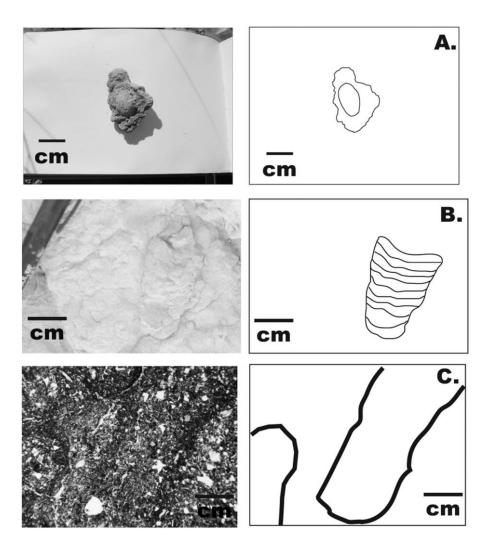


Figure 4. Trace fossil close-ups. *A*, Wasp cocoon photo and interpretive sketch. *B*, *Taenidium* burrow in profile and interpretive sketch. *C*, Thin section of a *Taenidium* burrow and interpretive sketch of slightly oxidized burrow margin. Scales are the same for the photos and the interpretive sketches.

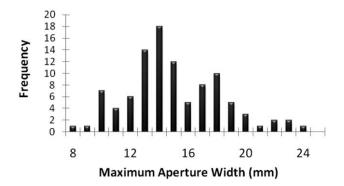


Figure 5. Burrow size distribution.

Discussion

Taenidium Identification. The ichnogenus Taenidium is broadly similar to the ichnogenera Ancorichnus, Beaconites, and Muensteria, and separation between the four was often confused in the past with different authors attributing the same ichnofossils to two or more different genera. Resolution of the problem came from work by D'Alessandro and Bromley (1987), who proposed revised guidelines for separating Taenidium from Muensteria, and from Keighley and Pickerill (1994), who proposed revised guidelines for separating Beaconites from Taenidium and Ancorichnus. Thus, by using a combination of criteria from both works, it was possible to identify the abundant ichnofossils at Little Pipestone as Taenidium on the basis of all of the burrows being vertical to subvertical, unbranched (eliminating Muensteria), unwalled and unlined (eliminating *Beaconites*), and with meniscate backfill that lacks a mantle (eliminating Ancorichnus; figs. 2-4). Furthermore, Taenidium has been previously identified in a similar fluvial setting (D'Alessandro et al. 1987; Gillette et al. 2003), while the other alternative ichnogenera are more typically used for marine or lacustrine settings.

Two other similar, recently named trace fossils that must be considered are *Feoichnus challa* igen. isp. (Krause et al. 2008) and *Naktodemasis bowni* (Smith et al. 2008a). Complicating matters is that both have been identified as traces of cicada nymphs, but they have very few characters in common beyond meniscate backfill. *Feoichnus challa* is a walled, passively filled, hemispherical, upwardly concave pan- or dish-shaped trace (Krause et al. 2008), while *N. bowni* is a compound trace that is sinuous, unbranched, and unlined and is composed of a nested series of distinct ellipsoidal packets (Smith et al. 2008a). Of these two traces,

F. challa is most similar to the adhesive meniscate burrows at Little Pipestone, though we still favor the more general Taenidium diagnosis for the following reasons: (1) N. bowni is defined by Smith et al. (2008a) as compound trace composed of individual sediment packets, but the burrows at Little Pipestone are not; (2) N. bowni identified in their type section in the Bighorn Basin are significantly smaller (modes of 2 and 8 mm, respectively, for fine- and coarse-grained sediments), with a maximum burrow diameter less than the mean burrow diameter at Little Pipestone (fig. 5); (3) though some of the F. challa ichnofossils are superficially similar to the burrows at Little Pipestone, they are significantly larger on average (by >50%; Krause et al. 2008) and have a much shallower cup shape, with relatively few elongated samples, whereas all of the burrows at Little Pipestone are elongate; (4) F. challa has been documented primarily in B horizons of paleosols, whereas the vast majority of the burrows at Little Pipestone occur instead in A horizons; and (5) F. challa paratypes often preserve a hole and groove produced by a feeding root that is not present in the Little Pipestone burrows. Though subsequent fieldwork could identify either a different size range for the Little Pipestone traces or some of the additional features required of either ichonospecies F. challa or N. bowni, at this time we feel that it is most appropriate to use the more general ichnogeneric term Taenidium to describe adhesive meniscate burrows.

Modern Burrow Analogues. While some groups of arthropods and their burrowing habits have been relatively much studied, such as crayfish (e.g., Hasiotis and Mitchell 1993), others have been subject to considerably less neoichnological study. Krause et al. (2008) and Smith and Hasiotis (2008) both studied cicada behavior and the building of their trace fossils, but as discussed in "Taenidium Identification," the traces they identified are of different sizes and of different morphologies than the traces we identified at Little Pipestone, with only a few characters in common. Furthermore, the two putative cicada traces F. challa (Krause et al. 2008) and N. bowni (Smith et al. 2008a) also have few features in common with one another. O'Geen et al. (2002) and O'Geen and Busacca (2001) examined numerous Taenidium-like traces in near-modern and modern Palouse loess sequences in Washington and were also able to identify cicadas as the trace maker. They found that cicada burrows comprise 19% of the total rooting zone in the sagebrush steppe setting there, an amount that exceeds the burrowing density described for both F. challa (Krause et al. 2008) and N. bowni (Smith et al.





Figure 6. Modern beetle burrows. *A*, Photo showing burrowing frequency by beetles. *B*, Close-up photo of a single beetle burrow.

2008a) but is much lower than the burrow density at Little Pipestone (e.g., fig. 3). Thus, among trace fossils with known trace makers, there can be a wide range of morphological features and distribution patterns, perhaps resulting from species-level differences among different types of cicadas.

At Little Pipestone, Retallack (2007) used the paleosols to reconstruct an open habitat at the time of the formation of these ichnofossils. Though we have reevaluated his pedotypes slightly on the basis of the lack of well-defined Bk horizons and have also attempted to identify the less-developed paleosols that Retallack (2007) excluded, our environmental reconstruction is the same. Root traces are present through the Little Pipestone site (and in our representative section; fig. 1), typically as small (≫1 cm) branching traces without any apparent taproots or large-diameter roots indicative of high-stature plants. This suggests an open-canopied, low-stature vegetative covering as in a sagebrush steppe ecosystem; paleoclimatic estimates (see "Paleoclimatic Reconstruction") are also consistent with this diagnosis. Looking at the modern expression of this ecosystem elsewhere in Montana yields a similar neoichnological assemblage that includes abundant traces but not a diverse assemblage (fig. 6). The 1-2-cm-diameter traces in the modern sagebrush steppe are similarly dominated by shallow subvertical to vertical burrows made by burrowing beetles. Thus, while the Taenidium trace maker at Little Pipestone may or may not have been cicada-like, it is clear that the traces were made by an arthropod of broadly similar size. Unfortunately, relatively little study has been devoted to working out burrow diameter/body size relationships among arthropods (e.g., Carrel 2003), though one recent study of prairie cicada nymphs (Cicadetta calliope) found that burrow diameters

typically were similar (typically 2–3 mm wider than carapace width) to the insect carapace diameter (Smith and Hasiotis 2008). If this relationship holds for other similar burrowing arthropods, then the mean trace maker at Little Pipestone probably had a carapace diameter of ~18 mm (mean value from fig. 5), or about three times the diameter of modern prairie cicada nymphs (Smith and Hasiotis 2008) but significantly smaller (by 40%–50%) than the modern South American cicadas and burrows described by Krause et al. (2008).

Little Pipestone Ichnofacies. Though not diverse, the trace fossil assemblage at Little Pipestone is exceptionally abundant and widely distributed, with evidence of bioturbation throughout the sediments preserved there. The depositional system was previously identified as a floodplain on the basis of channel and overbank deposits (Retallack 2007). However, neither the sediments nor the superimposed paleosols show any evidence of redoximorphic features (figs. 1, 2) other than the very weakly drab-haloed root traces and instead are nearly uniformly drab in color, suggesting that the depositional system was well drained and that the water table was typically well below the surface (Sheldon 2005). Among nonmarine ichnofacies, there are four possibilities for Little Pipestone: (1) Termitichnus, (2) Scoyenia, (3) Mermia, and (4) Coprinisphaera. Termitichnus is characterized by numerous dwelling traces, evidence of termites and bees, and moderate to high ichnodiversity; Scoyenia by backfilled feeding traces, evidence of arthropods, and low ichnodiversity; Mermia by grazing traces, evidence of water-living trace makers, and low ichnodiversity (Buatois et al. 1998 and other criteria therein); and Coprinisphaera by moderate to high ichnodiversity of insect traces, high abundance of traces, and relatively complex tiering patterns (Genise et al. 2000). On the basis of a dearth of mammalian and dwelling traces, an undiverse assemblage, and no evidence of termite nests, a strict Termitichnus definition can be eliminated. Similarly, the lack of trace made by waterliving organisms or of evidence for waterlogged sediments eliminates Mermia. The large number of arthropod traces and the presence of ovoid structures that can be attributed to a bee or wasp are consistent with the Coprinisphaera ichnofacies; however, the assemblage at Little Pipestone is not diverse and shows no evidence of tiering patterns. Thus, the ichnofossil assemblage at Little Pipestone most closely matches the Scoyenia ichnofacies, which has previously been associated with intermittently desiccated floodplain environments (Buatois and Mángano 2002). However, it may be considered as intermediate between or slightly overprinted by the Coprinisphaera ichnofacies given that the Scovenia ichnofacies is most commonly associated with relatively sparsely rooted sediments and the Alfisols are fairly densely rooted.

Paleoclimatic Reconstruction. Multiple proxies exist for reconstructing the paleoclimatic conditions under which paleosols formed, based on measurable physical and chemical properties of the paleosols themselves. For example, Retallack (2005) has recently revised a long-recognized relationship between mean annual precipitation (MAP) and the depth to a Bk horizon. An even stronger relationship exists between MAP and the chemical composition of paleosols Bt and Bw horizons, if other conditions such as minimal paleorelief and a noncarbonate parent material can be satisfied (Sheldon et al. 2002), and where there is no evidence for postburial metasomatism (Sheldon 2003; Sheldon and Tabor 2009). Both proxies for MAP have been applied to the paleosols at Little Pipestone; Bk horizon data are compiled in Retallack (2007) and estimates from Bw/Bt horizons in table A1. MAP estimates from two of the three (fig. 1) Bt horizons at Little Pipestone yield an average value of 848 mm yr⁻¹ (± 182 mm SE; Hamer 2009) for the section described herein, whereas four estimates from higher in the stratigraphic sequence from Retallack (2007) average 891 mm yr⁻¹ (± 182 mm), so the estimates are consistent and statistically indistinguishable. Retallack (2007) also made 15 Bk depth measurements of his Kanah and Yantun pedotypes within and stratigraphically below our Little Pipestone section. The Kanah pedotype paleosols (n = 10) gave a mean of 495 mm yr⁻¹, and the Yantun pedotype paleosols (n = 5) gave an average of 709 mm yr⁻¹ (overall range 448–757 mm; \pm 163 mm SE). However, few of the Bk horizons identified by

Retallack (2007) in the Little Pipestone section fulfill all of the conditions outlined by the Soil Survey Staff (1999), and most of the relatively sparse carbonate is not preserved as well-formed nodules, instead corresponding to stage 1 of development (Machette 1985). For this reason, the results from the geochemical proxy are considered more reliable. Nonetheless, the error envelopes for most of the MAP values obtained by both proxies overlap, suggesting broad correspondence, and strongly indicating semiarid to subhumid paleoclimatic conditions, which agrees with the previous regionwide reconstruction by Sheldon and Retallack (2004). Mean annual temperature (MAT) may be estimated using the chemical composition of Bt and Bw horizons (Sheldon et al. 2002; Sheldon and Tabor 2009). Two MAT estimates based on Little Pipestone Bt horizons (fig. 1) both gave 11° C ($\pm 4^{\circ}$ C), and four previous (Retallack 2007) estimates from higher within the stratigraphic section give a narrow range of 11°-14°C (±4°C; table A1). This paleoclimatic reconstruction is in good accordance with diagnosis of the trace fossil assemblage as being representative of the Scovenia ichnofacies, which characteristically occurs in low-energy, episodically wet floodplain environments (Buatois et al. 1998; Buatois and Mángano 2002; Hamer et al. 2007a).

Paleohydrological Implications. Meniscate burrows are common in nonmarine ichnofossil assemblages (Pemberton et al. 1992; Hasiotis 2002; Gillette et al. 2003; Krause et al. 2008; Smith et al. 2008a, 2008b) and are made by air-breathing organisms that do not ingest the sediment (e.g., Smith and Hasiotis 2008). Almost all burrowing organisms (cf. crayfish; Hasiotis and Mitchell 1993) will not burrow beneath the level of the water table because to do so would risk drowning. Thus, changes in the depth of burrowing are a good indicator of the relative position of the water table with respect to the surface. Frequent surface-down bioturbation would aerate the floodplain, ensuring similar redox conditions at least to the depth of the burrow and probably somewhat deeper. This regular aeration and similar redox environment would result in more uniformly colored floodplain sediments and paleosols as at Little Pipestone. Uniform, nongleyed sediment and paleosol colors are indicative of well-drained conditions (Sheldon 2003, 2005).

Given that the *Taenidium* traces are found almost exclusively in paleosol A horizons at Little Pipestone, rarely deeper in profiles, and never in the unpedogenically modified sediment between the paleosols (i.e., overbank flood deposits), the

trace maker was active only between flooding events during times of relative depositional quiescence. This is further supported by the morphology of the burrows themselves. Maitland and Maitland (1994) examined burrow diameter in intertidal zones and found that arthropods there typically made burrows with narrower openings than their subsurface width and made theoretical calculations showing how even open burrows of this type would minimize flooding of the burrow. In contrast, the *Taenidium* burrows at Little Pipestone are of uniform width or narrow with depth (fig. 4), which suggests that the trace maker was not in an environment where the flood frequency or intensity was very high, an observation consistent with the presence of Alfisols. Individual *Tae*nidium ichnofossils appear to have been penetrative into the sediments below but also slightly constructional above the top of the soil surface, with some limited on-lapping of the surrounding sediments prior to burial. Again, this is consistent with low-intensity floods (Hamer et al. 2007a). The weakly to moderately developed paleosols at Little Pipestone are also consistent with occasional but low-intensity floodplain inundation that only rarely resulted in the total burial of the soil. The semiregular addition of a small amount of new sediment would prevent the soils from ever becoming well developed or mature.

Conclusions

The late Eocene Little Pipestone locality in Montana preserves an abundant but undiverse (fig. 2)

ichnofossil assemblage composed primarily of traces from the ichnogenera Taenidium. On the basis of comparison with modern traces (fig. 6) and with previous work on sagebrush steppe settings, the trace maker is identified as an arthropod, probably a beetle or a cicada-like insect. The trace fossil assemblage as a whole can be placed in the Scoy*enia* ichnofacies, which is consistent with previous work that suggests the Scoyenia ichnofacies is common in intermittently desiccated floodplain settings. This diagnosis is in accordance with previous paleosol work (Retallack 2007) and with previous and new paleoclimatic reconstructions (Sheldon and Retallack 2004; Retallack 2007; Sheldon 2009). The reconstructed paleohydrological setting that results from the combination of sedimentological, paleopedological, and ichnological data is of a seasonally desiccated, well-aerated floodplain characterized by low flood frequency and intensity, slow sediment accumulation rates, and an overall subhumid/semiarid climate very similar to a modern sagebrush steppe, and it represents the oldest example of this ecosystem type known from Montana.

ACKNOWLEDGMENTS

N. D. Sheldon would like to acknowledge research support from Natural Environment Research Council (NERC; grant NE/D000521/1), and J. M. M. Hamer would like to acknowledge an NERC studentship. We would also like to acknowledge the many useful suggestions in Steve Driese's review and from Editor David Rowley.

REFERENCES CITED

- Buatois, L. A., and Mángano, M. G. 2002. Trace fossils from Carboniferous floodplain deposits in western Argentina: implications for ichnofacies models of continental environments. Palaeogeogr. Palaeoclimatol. Palaeoecol. 183:71–86.
- Buatois, L. A.; Mángano, M.G.; Genise, J. F.; and Taylor, T. N. 1998. The ichnologic record of the continental invertebrate invasion: evolutionary trends in environmental expansion, ecospace utilization, and behavioral complexity. Palaios 13:217–240.
- Carrel, J. E. 2003. Ecology of two burrowing wolf spiders (Areneae: Lycosidae) syntopic in Florida scrub: burrow/body size relationships and habitat preferences. J. Kans. Entomol. Soc. 76:16–30.
- Cleveland, D. M.; Nordt, L. C.; and Atchley, S. C. 2007. Paleosols, trace fossils and precipitation estimates of the uppermost Triassic strata in northern New Mexico. Palaeogeogr. Palaeoclimatol. Palaeoecol. 257:421–444.

- D'Alessandro, A., and Bromley, R. G. 1987. Meniscate trace fossils and the *Muensteria-Taenidium* problem. Palaeontology 30:743–761.
- D'Alessandro, A.; Ekdale, A. A.; and Picard, M. D. 1987. Trace fossils in fluvial deposits of the Duchesne River Formation (Eocene), Uinta Basin, Utah. Palaeogeogr. Palaeoclimatol. Palaeoecol. 61:285–301.
- Douglass, E. 1901. Fossil mammalian of the White River beds of Montana. Trans. Am. Phil. Soc. 20:237–279.
- ——. 1903. New vertebrates from the Montana Tertiary. Ann. Carnegie Mus. 2:145–149.
- ——. 1905. The Tertiary of Montana. Mem. Carnegie Mus. 2:203–224.
- Dworkin, S. I.; Nordt, L. C.; and Atchley, S. C. 2005. Determining terrestrial paleotemperatures using the oxygen isotopic composition of pedogenic carbonates. Earth Planet. Sci. Lett. 237:56–68.
- Genise, J. F.; Mángano, M. G.; Buatois, L. A.; Laza, J. H.; and Verde, M. 2000. Insect trace fossil associations in

- paleosols: the *Coprinisphaera* ichnofacies. Palaios 15: 49–64.
- Gillette, L.; Pemberton, S. G.; and Sarjeant, W. A. S. 2003. A Late Triassic invertebrate ichnofauna from Ghost Ranch, New Mexico. Ichnos 10:141–151.
- Hamer, J. M. M. 2009. Interpreting Cenozoic floodplains: a palaeopedological and ichnological perspective. PhD dissertation, Royal Holloway, University of London.
- Hamer, J. M. M.; Sheldon, N. D.; and Nichols, G. J. 2007a. Global aridity during the Early Miocene? a terrestrial paleoclimate record from the Ebro Basin, Spain. J. Geol. 115:601–608.
- Hamer, J. M. M.; Sheldon, N. D.; Nichols, G. J.; and Collinson, M. E. 2007b. Late Oligocene–Early Miocene palaeosols of distal fluvial systems, Ebro Basin, Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 247:220–235.
- Hanneman, D. L.; Cheney, E. S.; and Wideman, C. J. 2003. Cenozoic sequence stratigraphy of northwestern USA. *In* Raynolds, R. G., and Flores, R. M., eds. Cenozoic systems of the Rocky Mountain region. Denver, SEPM, p. 135–155.
- Hasiotis, S. T. 2002. Continental trace fossil atlas (Short Course Notes no. 51). Tulsa, OK, SEPM, 132 p.
- . 2004. Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses. Sediment. Geol. 167:177–268.
- Hasiotis, S. T., and Mitchell, C. E. 1993. A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo- and neoichnological evidence, and the identification of their burrowing signatures. Ichnos 2:291–314.
- Hembree, D. I., and Hasiotis, S. T. 2006. The identification and interpretation of reptile ichnofossils in paleosols through modern studies. J. Sediment. Res. 76: 575–588.
- Keighley, D. G., and Pickerill, R. K. 1994. The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*. Palaeontology 37:305–337.
- Krause, J. M.; Bown, T. M.; Bellosi, E. S.; and Genise, J. F. 2008. Trace fossils of cicadas in the Cenozoic of central Patagonia, Argentina. Palaeontology 51:405–418
- Kraus, M. J., and Hasiotis, S. T. 2006. Significance of different modes of rhizolith preservation to interpreting paleoenvironmental and paleohydrologic settings: examples from Paleogene paleosols, Bighorn Basin, Wyoming, U.S.A. J. Sediment. Res. 76:633–646.
- Machette, M. N. 1985. Calcic soils of the southwestern United States. *In* Weide, D. L., ed. Soils and Quaternary geology of the southwestern United States. Geol. Soc. Am. Spec. Pap. 203:10–21.
- Mack, G. H.; James, W. C.; and Monger, H. C. 1993. Classification of paleosols. Geol. Soc. Am. Bull. 105: 129–136.
- Maitland, D. P., and Maitland, A. 1994. Significance of burrow-opening diameter as a flood-prevention mechanism for air-filled burrows of small intertidal arthropods. Mar. Biol. 119:221–225.

- O'Geen, A. T., and Busacca, A. J. 2001. Faunal burrows as indicators of paleo-vegetation in eastern Washington, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 169:23–37.
- O'Geen, A. T.; McDaniel, P. A.; and Busacca, A. J. 2002. Cicada burrows as paleosol indicators in the inland Pacific Northwest. Soil Sci. Soc. Am. J. 66:1584–1586.
- Pemberton, S. G.; MacEachern, J. A.; and Frey, R. W. 1992. Trace fossil facies models: environmental and allostratigraphic significance. *In* Walker, R. G., and James, N. P., eds. Facies models: response to sea level change. St. John's, Newfoundland, Geol. Assoc. Can. p. 47–72.
- Prothero, D. R. 1984. Magnetostratigraphy of the early Oligocene Pipestone Springs locality, Jefferson County, Montana. Contrib. Geol. (U. Wyo.) 23:33–36.
- Retallack, G. J. 2005. Pedogenic carbonate proxies for amount and seasonality of precipitation in paleosols. Geology 33:333–336.
- ——. 2007. Cenozoic paleoclimate on land in North America. J. Geol. 115:271–294.
- Sheldon, N. D. 2003. Pedogenesis and geochemical alteration of the Picture Gorge Subgroup, Columbia River basalt, Oregon. Geol. Soc. Am. Bull. 115:1377– 1387.
- 2005. Do red beds indicate paleoclimatic conditions? a Permian case study. Palaeogeogr. Palaeoclimatol. Palaeoecol. 228:305–319.
- ——. 2006. Quaternary glacial-interglacial climate cycles in Hawaii. J. Geol. 114:367–376.
- 2009. Non-marine records of climatic change across the Eocene-Oligocene transition. *In* Koeberl, C., and Montanari, S., eds. The Late Eocene Earth: hothouse, icehouse, and impacts. Denver, Geol. Soc. Am. Spec. Pap. 452, p. 249–260.
- Sheldon, N. D., and Retallack, G. J. 2001. Equation for compaction of paleosols due to burial. Geology 21: 247–250.
- ——. 2004. Regional paleoprecipitation records from the Late Eocene and Oligocene of North America. J. Geol. 112:487–494.
- Sheldon, N. D.; Retallack, G. J.; and Tanaka, S. 2002. Geochemical climofunctions from North American soils and applications to paleosols across the Eocene-Oligocene boundary in Oregon. J. Geol. 100:687–696.
- Sheldon, N. D., and Tabor, N. J. 2009. Quantitative paleoenvironmental and paleoclimatic reconstruction using paleosols. Earth-Sci. Rev. 95:1–52.
- Smith, J. J., and Hasiotis, S. T. 2008. Traces and burrowing behaviors of the cicada nymph *Cicadetta Calliope*: neoichnology and paleoecological significance of extant soil-dwelling insects. Palaios 23:503–513.
- Smith, J. J.; Hasiotis, S. T.; Kraus, M. J.; and Woody, D. T. 2008a. Naktodemasis bowni: new ichnogenus and ichnospecies for adhesive meniscate burrows (AMB), and paleoenvironmental implications, Paleogene Willwood Formation, Bighorn Basin, Wyoming. J. Paleontol. 82:267–278.
- ——. 2008b. Relationships of floodplain ichnocoenoses to paleopedology, paleohydrology, and paleoclimate in

- the Willwood Formation, Wyoming, during the Paleocene-Eocene thermal maximum. Palaios 23:683–699. Soil Survey Staff. 1999. Keys to soil taxonomy. Blacksburg, VA, Pocahontas.
- Stiles, C. A.; Mora, C. I.; and Driese, S. G. 2001. Pedogenic iron-manganese nodules in Vertisols: a new proxy for paleo-precipitation? Geology 29:943–946.
- Tabor, N. J.; Montañez, I. P.; Zierenberg, R.; and Currie, B. S. 2004. Mineralogical and geochemical evolution of a basalt-hosted fossil soil (Late Triassic, Ischigualasto Formation, northwest Argentina): potential for paleoenvironmental reconstruction. Geol. Soc. Am. Bull. 116:1280–1293.
- Tabrum, A. R., and Nichols, R. 2001. Species named by Earl Douglass from the Tertiary intermontane basins of southwestern Montana. *In* Nichols, R., ed. Cenozoic vertebrate paleontology and geology of southwestern Montana and adjacent areas. Society of Vertebrate Paleontology Annual Meeting, 61st (Bozeman, MT, 2001), Guidebook.
- Tabrum, A. R.; Prothero, D. R.; and Garcia, D. 1996. Magnetostratigraphy and biostratigraphy of the Eocene-Oligocene transition, southwestern Montana. *In* Prothero, D. R., and Emry, R. J., eds. The terrestrial Eocene-Oligocene transition in North America. Cambridge, Cambridge University Press, p. 278–311.