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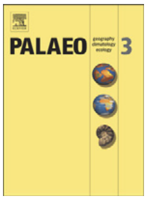

Ant-nest ichnofossils in honeycomb calcretes, Neogene Ogallala Formation, High Plains region of western Kansas, U.S.A.

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ABSTRACT

Two new ant-nest trace fossils are described from calcic sandy paleosols of the Neogene Ogallala Formation in western Kansas. The ichnofossils are preserved within and below calcrete beds weathering in positive relief as carbonate-filled casts or as cavities in negative relief. *Daimoniobarax* ichnogenus nov. is established for burrow systems composed of vertically tiered, horizontally oriented pancake-shaped chambers connected by predominantly vertical and cylindrical shafts ~0.8 cm in diameter. Ichnospecies of *Daimoniobarax* are differentiated based on differences in the plan view outline of chambers, shaft orientation, and junctions between chambers and shafts.

Daimoniobarax nephroides ichnospecies nov. is composed of an ~24–76 cm long vertical sequence of distinctly lobed chambers (~2–20 cm wide and ~1 cm high) arranged along sinuous to helical shafts. Chamber shape in plan view ranges from small teardrops to larger kidney- and U-shaped forms. Shafts intersect at chamber edges such that chambers appear to bud from the central shafts. *Daimoniobarax nephroides* is most similar to the nests of extant seed-harvester ants of the New World genus *Pogonomyrmex*. Such ants are specialized granivores and prefer sandy soils in arid to semi-arid grassland and desert regions.

Daimoniobarax tschinkeli ichnospecies nov. is ~30–80 cm in vertical extent. Chambers (~2–30 cm wide and ~1 cm high) are circular to elongate or pseudopodial in plan view. Vertical shafts are straight to slightly sinuous and intersect most often toward the center of the chambers. The generalized architecture of *D. tschinkeli* is similar to that of the nests or nest portions of several extant ant genera, though it does not closely resemble any known modern nest.

Ant ichnofossils provide valuable information on hidden biodiversity, paleohydrologic regimes, paleopedogenic processes, and paleoclimate during the time of nest occupation. Depth-related changes in chamber size and vertical spacing may also help interpret paleosurfaces and paleodepths, and serve as geopetal features.

1. Introduction

The Neogene Ogallala Formation underlies much of the North American High Plains region and is composed chiefly of fluvial and eolian sediments consisting of interbedded conglomerate, sandstone, mudrock, loess and their uncemented equivalents (Gustavson and Winkler, 1988, 1990). In the uppermost Ogallala Formation, pedocomplexes composed of multiple calcic paleosols with honeycombed to massive calcretes can be over 10 m thick (Gardner et al., 1992). Honeycomb calcretes (Stage III of Machette, 1985) were until recently thought to develop in calcified soils by the partial coalescence of carbonate nodules and pipy concretions to form a solid lattice-like framework surrounding less-indurated interstitial soil-material (Wright, 2007). Recent fieldwork in west-central and southern Kansas shows, however, that the sizes, basic structural elements, and architectural morphologies of many of the honeycomb structures in the Ogallala Formation are nearly identical to the nests of extant burrowing ants (Insecta: Hymenoptera: Formicidae).

This paper describes the morphology and paleoecological and paleoenvironmental significance of these newly recognized multi-chambered trace fossils and their interpreted tracemaking organisms. Interest in nests of subterranean social insects, particularly those of hymenopterans and isopterans, has focused largely on how nest architecture relates to such biological, behavioral, and ecological research topics as inter- and intraspecific interactions (e.g., Boulton et al., 2003), social structure and group-level behaviors (e.g., Langridge et al., 2008), and biogenic modification of soil properties (e.g., Cammeraat and Risch, 2008). Detailed information on the three-dimensional architecture of insect nests and their distinctly identifiable characteristics, however, is often lacking in these studies (Tschinkel, 2004). Our recognition of fossil ant nests in the Ogallala paleosols is due in large part to recent efforts to document the nest

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architectures of modern ants by casting them in plaster, metal, and concrete (e.g., Williams and Logfren, 1988; Tschinkel, 2003; Moreira et al., 2004; Tschinkel, 2004, 2005; Forti et al., 2007; Verza et al., 2007; Cerquera and Tschinkel, 2010; Halfen and Hasiotis, 2010; Tschinkel, 2010). Such comparisons are possible because the trace fossils of many soil-dwelling biota do not often differ significantly from the burrows and nests of extant species (e.g., Genise et al., 2000; Hasiotis, 2003; Duringer et al., 2007; Verde et al., 2007; Smith et al., 2008a; Hembree, 2009). Ichnofossils provide valuable information on hidden biodiversity in the absence of body fossils, paleopedogenic modification and processes, paleohydrologic regimes, and paleoclimatic conditions (e.g., Hasiotis, 2007; Smith et al., 2008b).

2. Geologic setting and background

The main study area is located in west-central Kansas where up to 53 m of the Neogene Ogallala Formation is exposed along the bluffs of Ladder Creek Canyon and in tributary draws in the northwestern portion of Scott County (Fig. 1). Additional Ogallala localities were examined in Ellis and Morton counties, Kansas. The formation consists mostly of gravel, sand, silt and clay of fluvial–alluvial origin, calcareous paleosols, and eolian silt and clay; local lenses of volcanic ash and lacustrine limestones are also present (Frye et al., 1956). Individual beds often grade laterally from one lithology to another and dramatic changes in thickness and bed continuity over relatively short distances are not uncommon (Waite, 1947). Calcareous paleosols occur with high stratigraphic frequency throughout the formation and are characterized by abundant carbonate nodules, pipy concretions, root traces, and irregular lenses and beds of ledge-forming calcrete (Fig. 2; Gutentag, 1988). Fossil mammal and floral assemblages (Thomasson, 1979, 1990; Zakrzewski, 1990; Martin et al., 2008) and tephrochronologic analyses of unaltered volcanic ash beds (Perkins, 1998) suggest that Ogallala deposits in Kansas range in age from middle Miocene to earliest Pliocene (Ludvigson et al., 2009). The Ogallala Formation is up to several hundred meters thick in western Kansas, but regional thickness varies greatly because of the uneven surface upon which sediments were deposited and post-Ogallala uplift and erosion (Leonard, 2002).

2.1. Devil's Backbone locality

The best-preserved and exposed ichnofossils are located approximately 1.6 km south of Lake Scott State Park in a road cut through an east–west trending ridge of Ogallala strata called the Devil's Backbone (Fig. 1). The road cut exposes ~23 vertical meters of rock composed chiefly of tan- to reddish brown-colored, moderately sorted, silty, fine- to very coarse-grained beds of arkosic sandstone (Fig. 3). Calcium carbonate pervades the section, mostly as fine-grained cement, but also

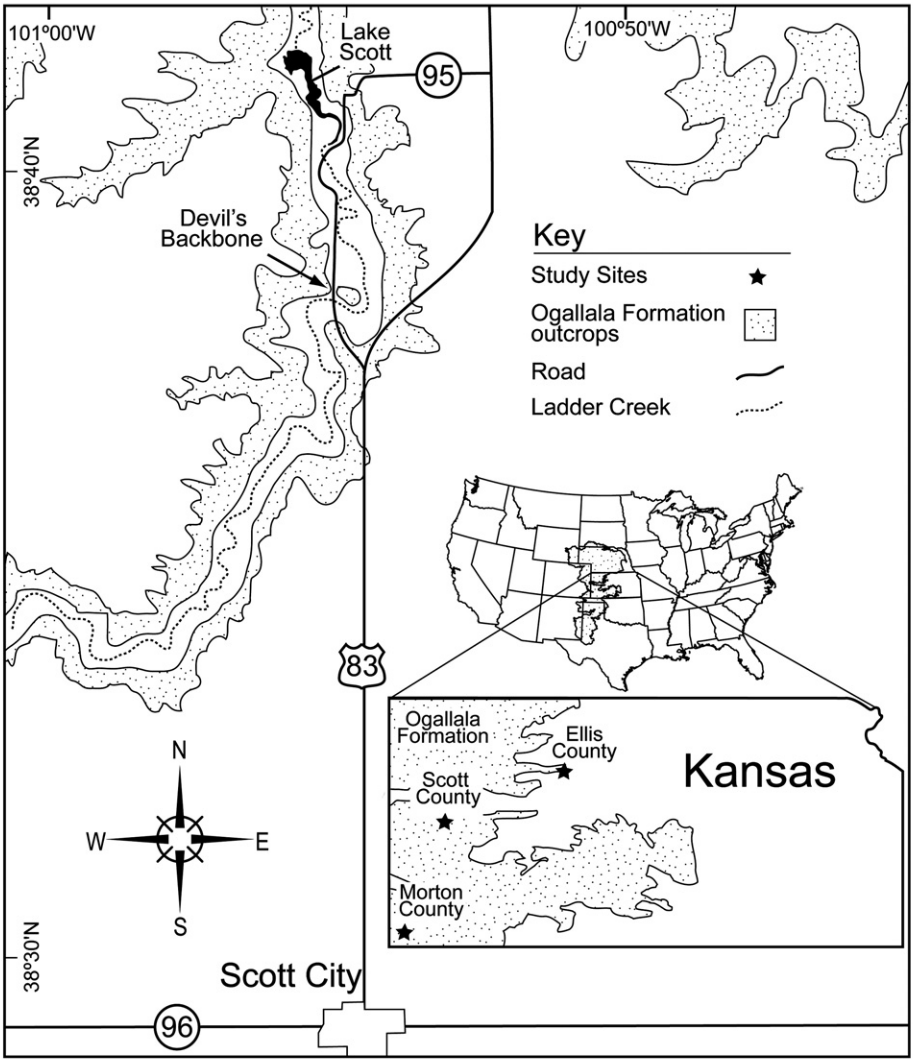

Fig. 1. Map of study area showing location of Ogallala Formation exposures and Devil's Backbone road cut in Ladder Creek Canyon, Scott County, Kansas. Inset map of Kansas shows the additional localities in Ellis and Morton Counties.

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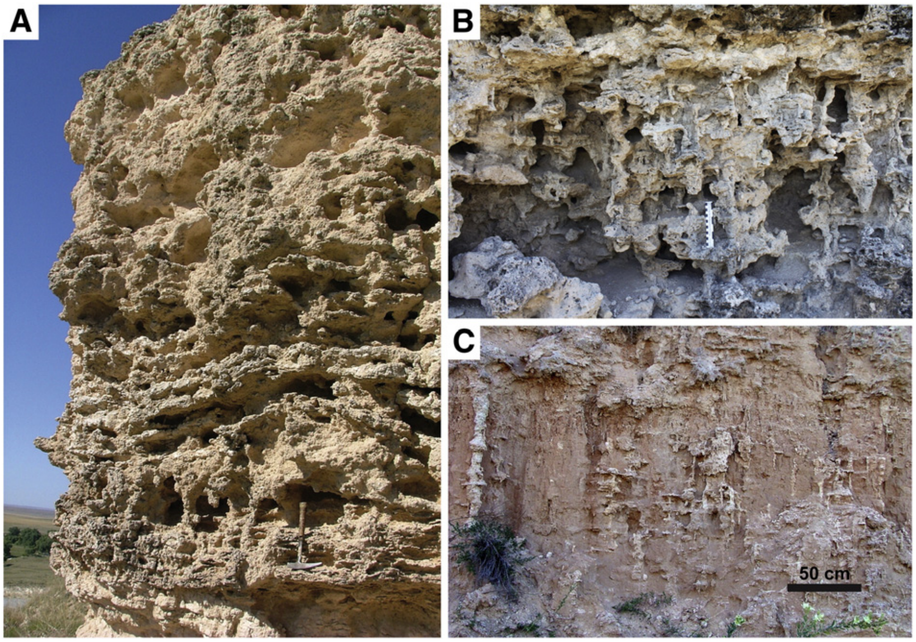

Fig. 2. Calcretes and calcareous paleosols in the Ogallala Formation along the rim of Ladder Creek Canyon: A) ledge-forming beds of massive to laminar calcrete not interpreted as trace fossils; and B) irregular beds of honeycomb calcrete showing carbonate-filled casts of multi-chambered trace fossils. C) Ichnofossils are most obvious weathering from sandstones below interbedded calcretes. Rock hammer in A is 33 cm; scale in B is 16 cm.

as powdery stringers along cracks; rounded cobble-sized and smaller nodules; pipy concretions; rhizoliths and burrow casts; and lenses and discontinuous beds of massive, nodular, and honeycomb calcrete.

These deposits are interpreted as fluvial and floodplain sediments on which composite soils with thick pedogenic and phreatic calcrete horizons developed (Gardner et al., 1992). The paleosols probably formed in overbank deposits during relatively long periods of landscape stability and low sedimentation rates between major inundations of the Ogallala floodplain (Gustavson and Winkler, 1988). In general, calcretes and macro-scale carbonate features develop in modern soils where

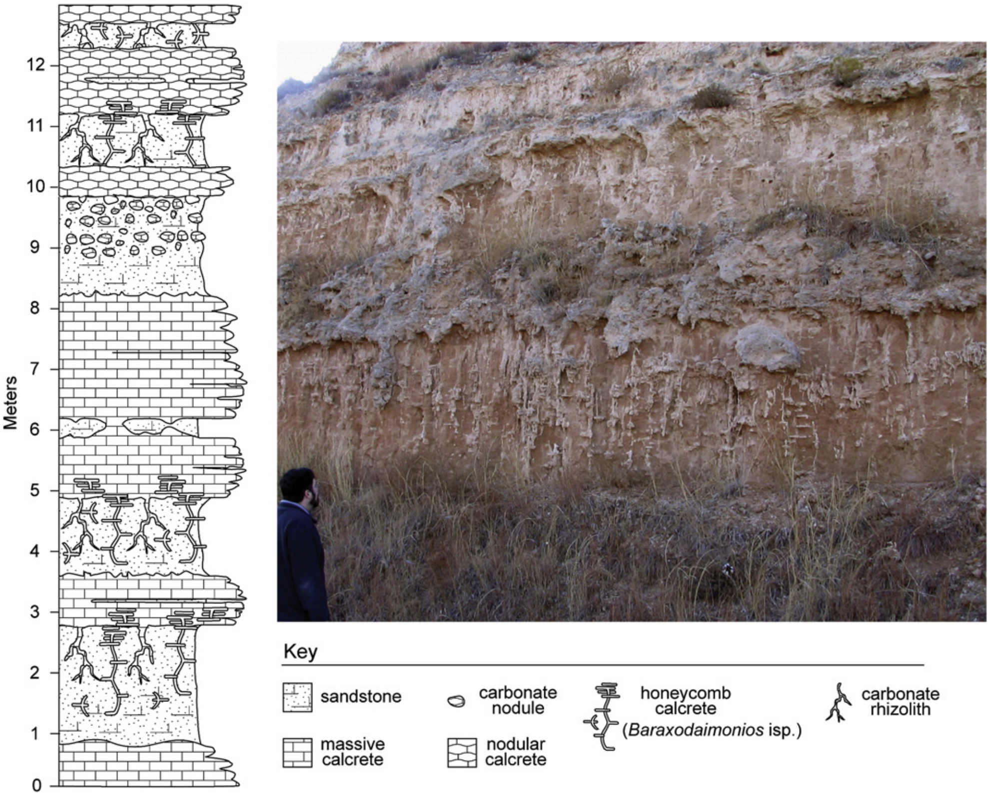

Fig. 3. Measured stratigraphic section and photograph of the lower 13 m of Ogallala Formation exposed on the west side of the Devil's Backbone road cut (N38°38′26″, W100°54′49″).

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there is a net moisture deficit, such that carbonate precipitated in a drier season is not leached from the soil profile during a wetter season (Wright, 2007). The thick calcrete horizons imply possibly arid to subhumid paleoclimatic conditions with low, seasonal rainfall and high evapotranspiration rates within a few meters of the soil surface.

We examined the structures described as honeycomb calcrete from the Devil's Backbone locality and other outcrops along the rim of Ladder Creek Canyon (Figs. 2B–C; 3). After careful inspection, we interpret many, though not all, of the nodular honeycomb structures as multi-chambered ichnofossils. The trace fossils are preserved within and below calcrete beds as carbonate-filled exichnia and endichnia weathering in positive relief, depending on the hardness of the burrow fill (Fig. 4A–D). Most burrow systems consist of a mix of hard and soft carbonate, making collection from the outcrop of more than a small section of the burrow nearly impossible. Concretionary carbonate growth on or near some of the trace fossils obscures their true architectural morphologies (Fig. 2B), though specimens without such growths are also prevalent. In some cases, the traces are present as cavities in the outcrop face due to nearly complete weathering of the burrow fill (Fig. 4D).

One of the co-authors of this paper (Thomasson, 2009) often targets weathered chamber structures in the Ladder Creek Canyon study area because they contain mass accumulations of the fossilized reproductive structures (e.g., seeds and fruits) and vegetative structures (e.g., leaves, stems, and roots) of various angiosperms. Fossil plant taxa commonly recovered include grasses (Poaceae), borages (Boraginaceae), sedges (Cyperaceae), and hackberries (Ulmaceae) (Thomasson, 2003, 2005). Paleoclimatic conditions inferred from paleobotanical assemblages suggest subhumid to subtropical savanna conditions with no extended periods of freezing weather, and higher annual rainfall than experienced currently in this region (Thomasson, 1990). Thomasson (1982) was the first to suggest that mass accumulations of well-preserved plant fossils in sediments of the Miocene Sheep Creek Formation in western Nebraska were the food caches of ancient burrowing arthropods.

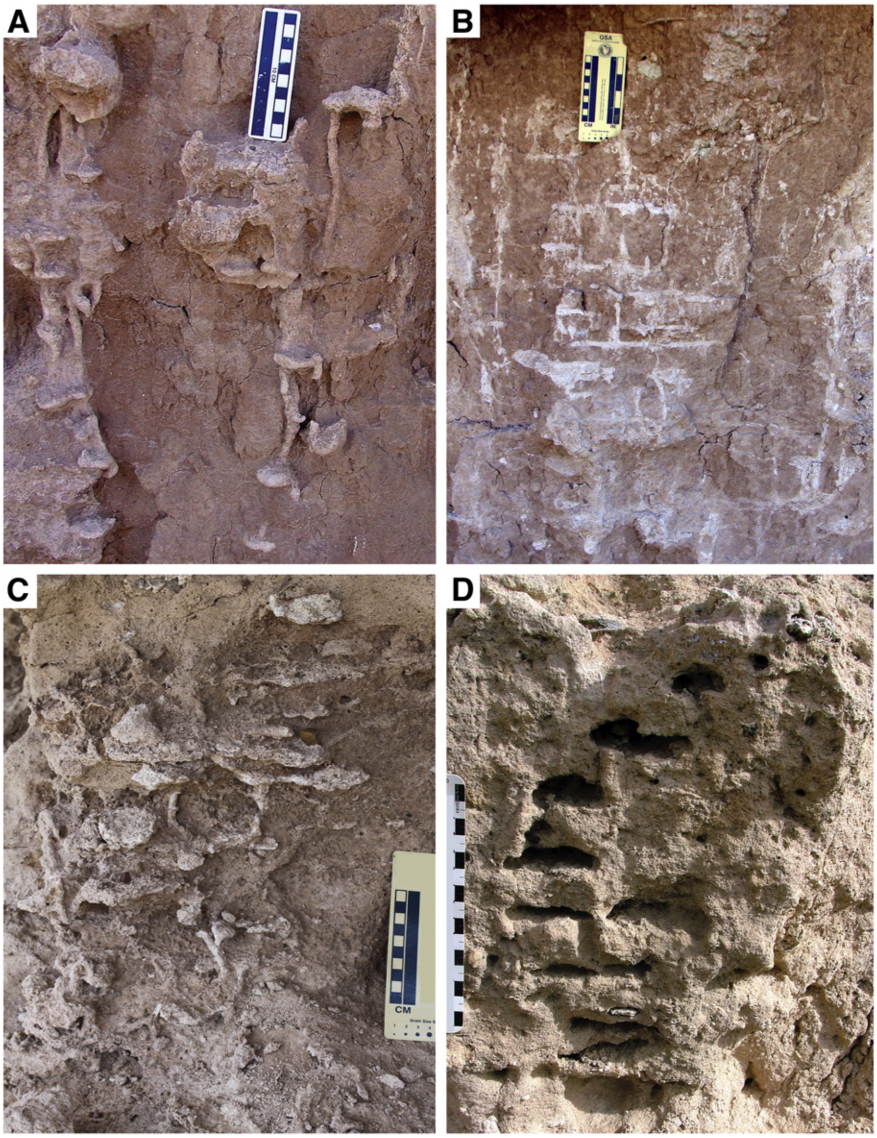

Fig. 4. Different preservational styles of in-situ, multi-chambered ichnofossils in the Ogallala Formation: fossil burrows at Devil's Backbone locality preserved in A) mostly solid carbonate and weathering in positive relief, and B) in soft carbonate and weathering in mostly negative relief. C) Silica-filled burrows weathering in positive relief in Elis County (N39°02′31″, W99°32′09″); and D) burrows in Morton County (N37°06′13″, W101°56′19″) preserved as cavities due to nearly complete weathering of the fill material. All rulers are in cm increments.

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2.2. Other localities

Ogallala localities in Ellis County (Fig. 1) correspond to sites 2, 8, 9a, 9b, and 33 of Thomasson (1979). These localities are characterized by a general coarsening upward sequence of massive ash-dominated beds of siltstone and claystone overlain by conglomeratic sandstone or lenticular beds of calcrete and volcanic ash. The chambered trace fossils are present at the bases of calcretes and ash beds and the underlying mudrock facies in the lower half of the sequence (Fig. 4C). The ichnofossils are morphologically identical to those at Devil's Backbone, but are preserved often in fibrous silica instead of carbonate.

Multi-chambered trace fossils were also examined in Ogallala Formation calcretes at the Point of Rocks landmark in the Cimarron National Grassland, Morton County, Kansas (Fig. 1). The ichnofossils at this locality are preserved most commonly as cavities in massive beds of calcareous, very well-cemented, sandy siltstone, but otherwise are morphologically identical to casts at Devil's Backbone (Fig. 4D).

3. Systematic ichnology

Figured and cited specimens, except for those represented by field photographs only, are housed in the Invertebrate Paleontology (IP) collection at the Sternberg Museum of Natural History, Fort Hays State University (FHSM), Hays, Kansas. Additional specimens are housed at the Kansas Geological Survey, Lawrence, Kansas, United States of America.

3.1. *Daimoniobarax* ichnogen. nov.

Synonymy:

1896 *Daemonelix* cakes, Barbour, p. 25, fig. 2
1897a *Daemonelix* cakes, Barbour, pl. 2, figs. 1–5, 7–9, 11
1897b *Daemonelix* cakes, Barbour, pl. 32, figs. 5–8
1982 arthropod burrows, Thomasson, p. 1013, fig. 1A–D
?1987 elliptical chambers, Sands, p. 411, pl. II.I: 6
1990 dung cake, Retallack, p. 12, fig. 207F
2002 ant nests, Hasiotis, p. 65, figs. B and C
2007 ant nests, Hamer et al., p. 228, fig. 6F
2010 ant nests, Cuevas Martínez et al., p. 170, fig. 9A–C

Etymology: From the Greek; *daimonios*, meaning 'of a spirit', and *barax*, a type of flat cake. The name refers to the type locality, Barbour's colloquial name for the trace fossil (Barbour, 1896), and the flat, pancake-like appearance of the chambers.

Type ichnospecies: *Daimoniobarax nephroides* isp. nov.

Diagnosis: Burrow system composed of a vertically tiered succession of horizontally oriented, pancake-shaped chambers connected most commonly by a single vertical to sub-vertical, cylindrical, narrow shaft (Fig. 4). Chambers are circular or reniform, to multi-lobate and elongate in plan view (Fig. 5). Chambers and shafts are unlined and form a ladder-like structure taller than it is wide.

Remarks: Daimoniobarax is distinguished from other trace fossils composed of multiple chambers by differences in overall orientation, chamber shape and abundance, and orientation and density of associated burrows. *Parowanichnus formicoides* Bown et al., 1997 is a wider than tall, grid-like lattice of densely spaced oblate to spherical chambers, shafts, and tunnels that radiate from the central part of the structure. *Parowanichnus perirhizaterion* Hembree and Hasiotis, 2008 is similar to *P. formicoides*, but chambers, shafts, and tunnels are clustered along a central rhizolith. *Socialites tumulus* Roberts and Tapanila, 2006 has a complex network of unlined and branching tunnels and shafts that connect to larger, ovate J-shaped chambers, all concentrated within and around conical structures along bedding planes. *Daimoniobarax* differs from *Attaichnus* Laza, 1982, *Termitichnus* Bown, 1982, and *Vondrichnus* Genise and Bown, 1994, in that the latter are composed of spherical to subspherical chambers. *Krausichnus* Genise and Bown, 1994, *Archeoentomichnus* Hasiotis and Dubiel, 1995, and *Fleaglellius* Genise and Bown, 1994, are characterized by tabular, distinctly lined chambers tiered such that the floor of the upper chamber is the roof of the one below and the chambers are supported by pillars and ramps. *Daimoniobarax* chambers are distinctly separate and vertically spaced from one another and show no internal supporting structures. The elongate chambers and burrows assigned to *Syntermesichnus* Bown and Laza, 1990 show conspicuous linings, unlike *Daimoniobarax*.

Trace fossils nearly identical to *Daimoniobarax* were first described by Barbour (1896, 1897a) in association with the helical ichnofossil *Daimonelix circumaxilis* from the early Miocene Harrison Formation in the High Plains of northwestern Nebraska. Barbour called the traces "*Daemonelix* [sic] cakes" because they were preserved in the same white, fibrous, silicified material as the much larger *D. circumaxilis* and because they were similar in size and thickness to a "camp griddle cake". The "cakes" were horizontally-oriented, roughly circular in plan view, though often lobed, and seldom more than 10 cm wide and ~1 cm thick; they occurred as single specimens or as pairs or in stacked clusters

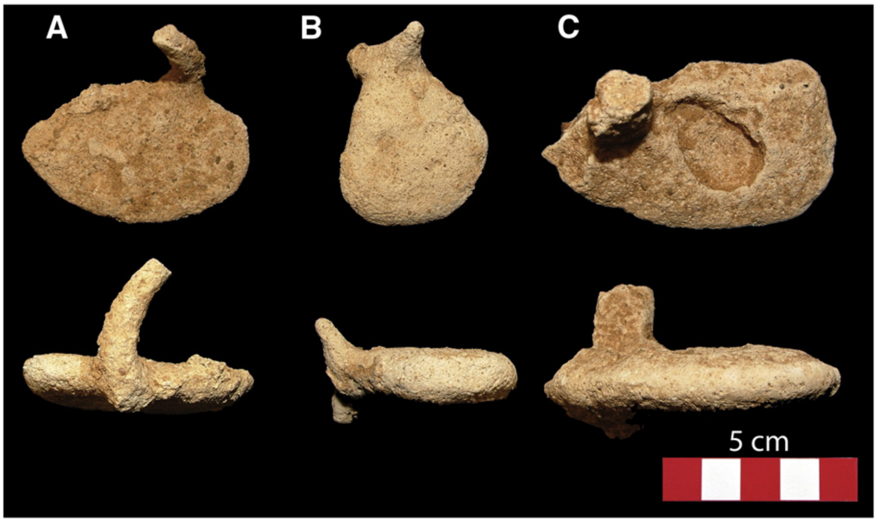

Fig. 5. Plan (top row) and side views (bottom row) of *Daimoniobarax* isp. chambers and shafts removed from outcrop; note the flat, pancake-like shape of the chambers and the helical shafts in specimens A and B.

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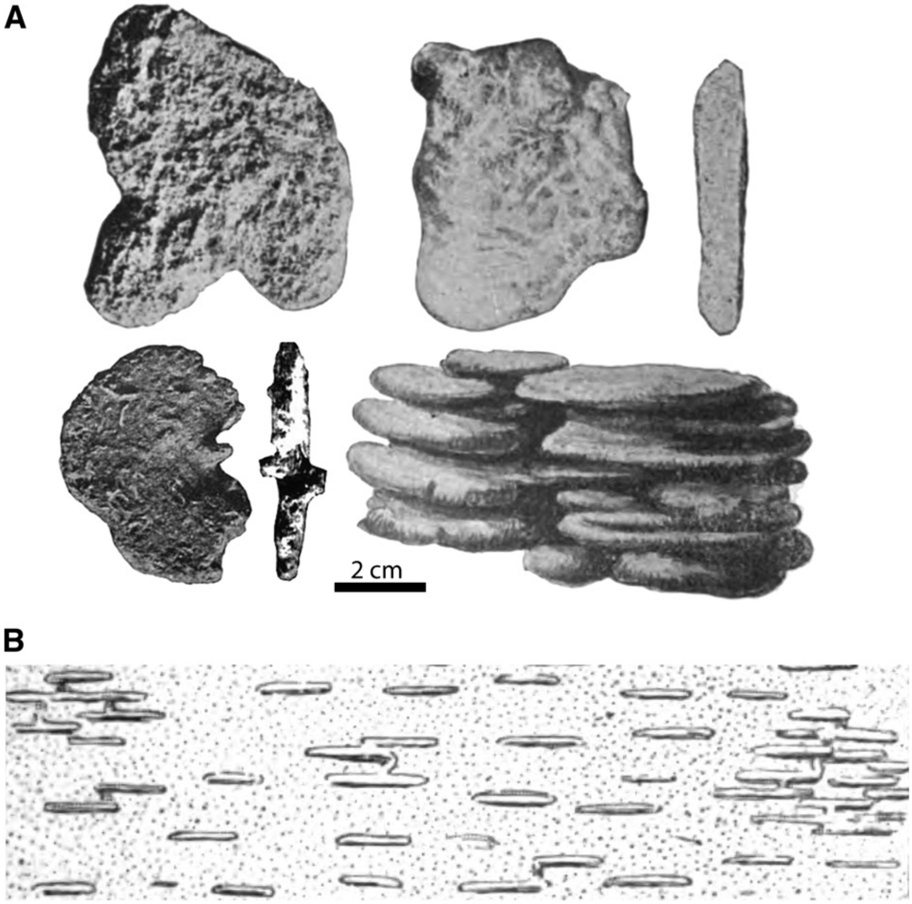

Fig. 6. Specimen photographs and illustrations of "*Daemonelix* cakes" collected by Barbour from the early Miocene Harrison Formation, northwestern Nebraska. A) Photographs of individual and stacked "cakes" in plan and lateral view, modified from Barbour (1897a); B) illustration showing the architectural arrangement in outcrop of the "cakes" and associated vertical "fibers", scale unknown; modified from Barbour (1896).

(Fig. 6A). A periphery of white tubules, or "*Daemonelix* fibers", was described in association with and connecting some of the cakes vertically (Fig. 6B). Barbour interpreted the cakes, along with *Daimonelix circumaxilis,* to be members of a phylogenetic continuum showing the evolution of giant, spiraling aquatic plants from simple root-like fibers and algal mats (Barbour, 1897b). While *D. circumaxilis* was eventually recognized as the fossilized burrow of the Miocene terrestrial beaver *Palaeocastor* sp. (Fuchs, 1893; Schultz, 1942; Martin and Bennett, 1977); the less celebrated "cakes" and smaller traces were still considered likely to be algal mats, concretions, or the coprolites of large mammals (e.g., Kindle, 1923; Lugn, 1941; Schultz, 1942; Retallack, 1990). It is clear, however, from Barbour's descriptions, illustrations, and photographic plates that the "*Daemonelix* cakes" and associated "fibers" are pieces of a multi-chambered trace fossil identical to *Daimoniobarax* (Fig. 6).

3.1.1. *Daimoniobarax nephroides* isp. nov. (Figs. 4A, C, D; 5A–B; 7A–D; 9A)

Etymology: From the Greek; *nephros*, meaning 'kidney', and *oides* meaning 'similar to'.

Holotype: Natural cross section of burrow system in outcrop (Fig. 7A).

Hypodigm: Twelve isolated chambers collected as paratypes: FHSM IP-1489 and FHSM IP-1490 (Fig. 5A–B; plan and side view respectively); and all ten specimens (FHSM IP-1491, FHSM IP-1490, FHSM IP-1492, FHSM IP-1493, FHSM IP-1494, FHSM IP-1495, FHSM IP-1496, FHSM IP-1497, FHSM IP-1498, and FHSM IP-1499) depicted in Fig. 7D.

Type locality: Lowest red sandstone interval on the west side of Devil's Backbone road cut (N38°38′26″, W100°54′49″) on Kansas Highway 95 in Ladder Creek Canyon, approximately 1.6 km south of Lake Scott State Park, Scott County, Kansas, U.S.A.

Examined material: Nine partial burrow systems were examined and measured in situ at Devil's Backbone and other Ladder Creek Canyon localities. Forty-one complete and partial chambers with or without attached shafts were measured and collected from the outcrop face and in float. Numerous additional specimens were examined at the Ellis County and Morton County locations.

Distribution: Neogene deposits of western Kansas and Nebraska. Numerous specimens were examined in strata of the Ogallala Formation along the walls of Ladder Creek Canyon and within Ogallala calcretes and volcanic-ash dominated siltstones approximately 11 km north of the City of Ellis in Sections 2 and 3, T. 12. S., R. 20 W., Ellis County, Kansas. Trace fossils were also observed in Ogallala Formation calcretes cropping out at the Point of Rocks landmark in the Cimarron National Grassland; NE¼ SE¼ section 12, T. 34 S., R. 43 W., Morton County, Kansas. Nearly identical trace fossils are reported from Neogene deposits of the Harrison and Sheep Rock Formations in western Nebraska (Barbour, 1897a; Thomasson, 1982).

Diagnosis: Chambers are distinctly lobed and range in plan view from small teardrop-shaped chambers to larger kidney-shaped and still larger U-shaped chambers. Shafts are sinuous to helical with a wide ramp angle (sensu Smith, 1987) and intersect chambers at chamber edges such that chambers appear to bud outward from shaft wall, with larger U-shaped chambers appearing to wrap back around the shaft to which they are attached.

Description: *Daimoniobarax nephroides* is composed of a 24 to 76 cm long sequence of tiered chambers with flat floors and ceilings (Fig. 7A). Chambers average 1.2 cm in height and have widths ranging from 2.0 to 19.7 cm with an average of 6.0 cm. Chambers intersect shafts at chamber edge and chambers appear to bud outward from the

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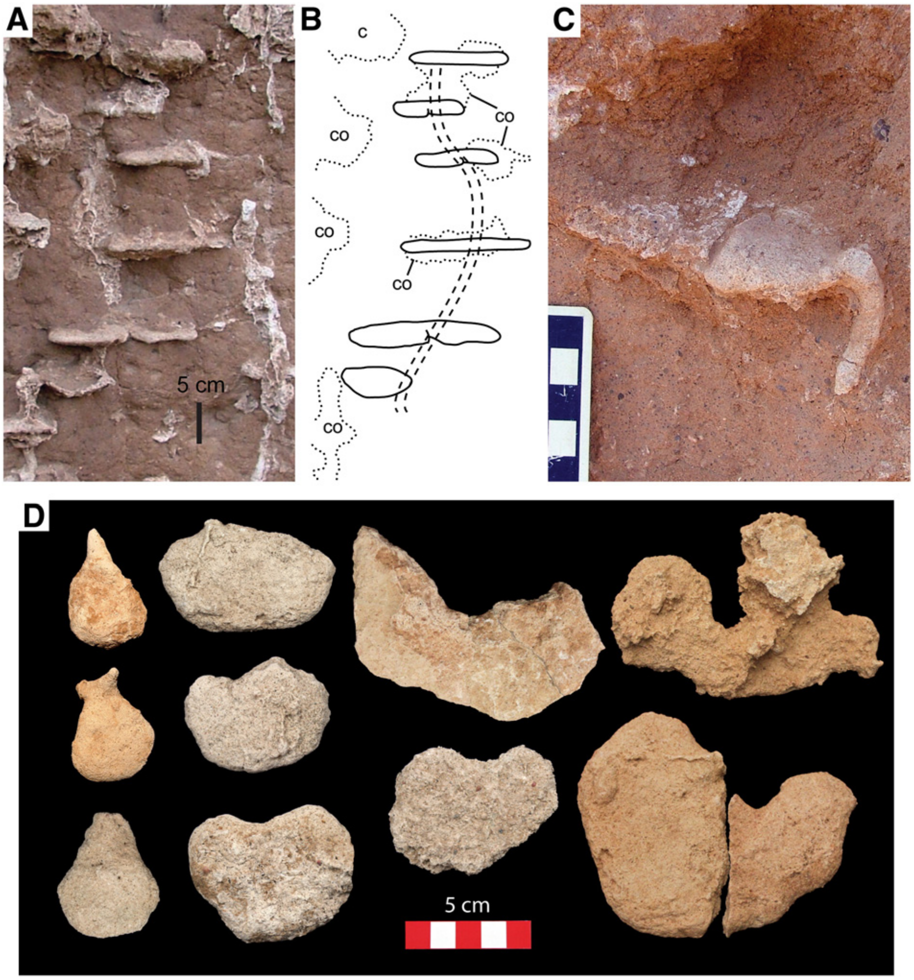

Fig. 7. Architectural morphology and chambers of *Daimoniobarax nephroides*: A) in-situ holotype at the Devil's Backbone locality; and B) line drawing interpreting architecture of the holotype (solid and dashed lines), concretions (c) and concretionary outgrowths on the ichnofossils (co) and nearby fossil chambers. C) Chamber diagnostic of *D. nephroides* showing helical shaft and intersection between the two at the chamber edge. D) Collected *D. nephroides* chambers showing a range of sizes and shapes in plan view from small teardrop-shaped chambers to larger reniform and U-shaped chambers (cf. Tschinkel, 2003, Fig. 10; 2004, Fig. 4). All rulers are in cm increments.

shaft. The point of intersection between the chambers and the shaft rotates with depth around the central shaft forming a vertical sequence of somewhat offset chambers (Figs. 4D, 7A). Smaller chambers are teardrop-shaped in plan view and intersect shafts at the narrow, pointed end of the teardrop (Fig. 7D). Larger chambers show reniform to U-shaped outlines in plan view that turn back toward and wrap around the point of intersection with the shaft (Fig. 7D). Shafts are cylindrical in cross-section with average diameters of 0.78 cm. Shafts are sinuous to loosely helical with an average deviation from the vertical of ~20–30° (Fig. 5A), though shafts between closely spaced chambers can be fairly straight. In better exposed burrow systems, the average vertical distance between the chambers is ~7 cm and this distance increases with depth. A one-way analysis of variance (ANOVA) shows that the vertical distance between *D. nephroides* chambers measured within calcrete beds is significantly shorter, $F(3, 144) = 6.19$, $p < 0.001$, such that chambers are stacked nearly on top of each other (Fig. 4C). The better exposed specimens in outcrop likely represent only a portion of the full burrow system architecture based on observations of multiple in situ specimens with partial three-dimensional exposures.

3.1.2. *Daimoniobarax tschinkeli* isp. nov. (Figs. 8A–E; 9B)

Etymology: For Dr. Walter R. Tschinkel, Florida State University formicologist, and his work inventorying the diversity and development of modern social insect nest architectures. Field recognition of *Daimoniobarax* as a trace fossil was due in no small part to Dr. Tschinkel's casts and photographs of extant ant nests.

Holotype: Natural cross section of burrow system in outcrop (Fig. 8A).

Hypodigm: Six isolated chambers collected as paratypes (FHSM IP-1500, FHSM IP-1501, FHSM IP-1502, FHSM IP-1503, FHSM IP-1504, and FHSM IP-1505), and depicted in Fig. 8E.

Type locality: Lowest red sandstone interval on the west side of Devil's Backbone road cut (N38°38′26″, W100°54′49″) on Kansas Highway 95 in Ladder Creek Canyon, approximately 1.6 km south of Lake Scott State Park, Scott County, Kansas, U.S.A.

Examined material: Eight partial burrow systems were examined and measured in situ at the Devil's Backbone and other Ladder Creek Canyon localities. Twenty-eight complete and partial chambers with and without attached shafts were collected from the outcrop face and in float.

Distribution: *Daimoniobarax tschinkeli* occurs in deposits of the Neogene Ogallala Formation in western Kansas. Numerous specimens were examined in the Ogallala Formation cropping out along the walls of Ladder Creek Canyon.

Diagnosis: Differs from *Daimoniobarax nephroides*, its closest morphological counterpart, in that (1) chamber shapes in plan view range from circular to elongate and pseudopodial; (2) shafts are predominantly straight to slightly sinuous; and (3) shafts intersect chambers toward the center of the chambers; sometimes running

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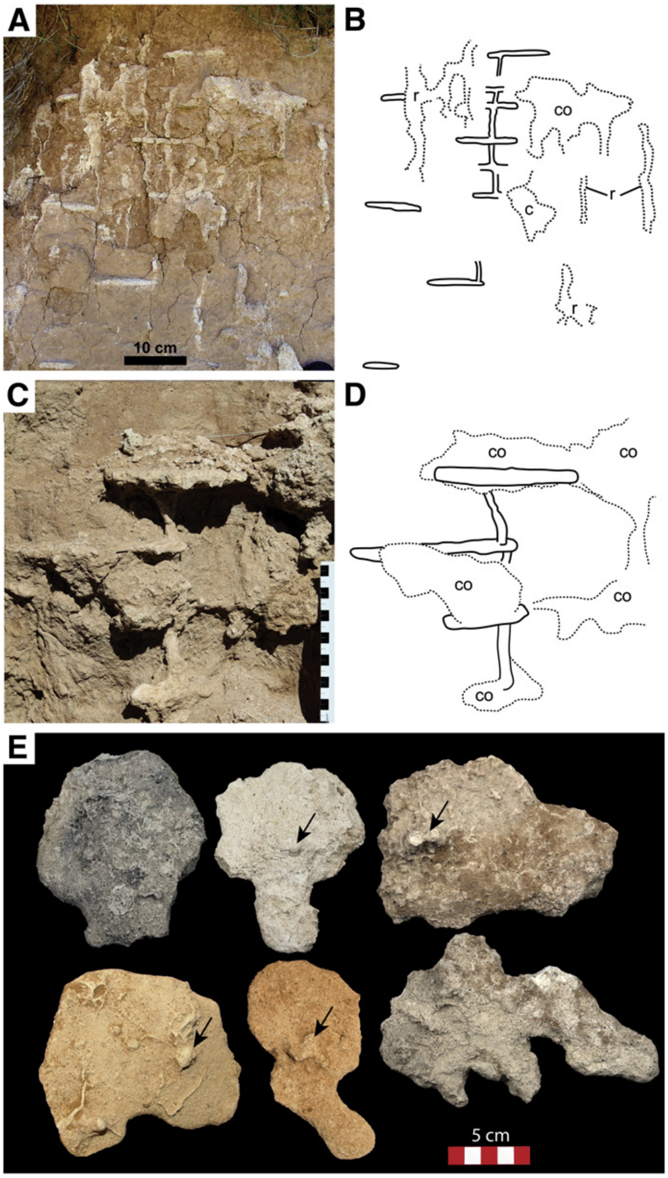

Fig. 8. Architectural morphology and chambers of *Daimoniobarax tschinkeli;* A) in-situ holotype at the Devil's Backbone locality; and B) line drawing interpretation showing architecture of the holotype (solid lines), concretions (c), concretionary outgrowths on the ichnofossils (co), and rhizoliths (r). C) *Daimoniobarax tschinkeli* specimen showing elongate chambers and relatively vertical shafts; and D) line drawing interpretation showing ichnofossil and concretionary outgrowths (co). D) Collected *D. tschinkeli* chambers displaying generally circular to elongate and pseudopodial shapes in plan view; arrows indicate point of intersection between chambers and shafts where discernible. All rulers are in cm increments.

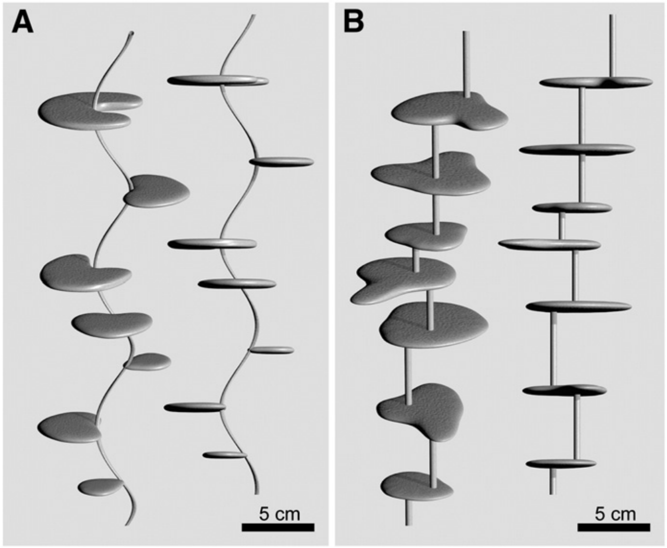

Fig. 9. Computer generated models showing the idealized architecture of *Daimoniobarax nephroides* (A; side and oblique view), and *D. tschinkeli* (B; side and oblique view). Models were produced using Blender v. 2.54 (Blender Foundation Software, 2010).

straight through the chamber and sometime entering from above and exiting from below at different locations relative to each other.

Description: *Daimoniobarax tschinkeli* burrow systems exposed in outcrop range from ~30 to 80 cm in vertical length (Fig. 8A–D). Chambers average 1.3 cm in height and have widths ranging from ~2.0–30.0 cm with an average width of 9.7 cm. Smaller chambers are circular in plan view but larger chambers show elongate to irregularly lobed outlines (Fig. 8E). Unlike *D. nephroides*, chambers do not appear to protrude in preferred direction from the shaft. Shafts are cylindrical in cross-section with an average diameter of 0.85 cm. Shafts are straight to slightly sinuous and usually intersect with chambers toward the center of each chamber or at some distance from the chamber edge. Some shafts descend directly through chambers, that is, they intersect the chamber from above and below in the same place on opposite sides. In other specimens, shafts enter and exit chambers at different locations relative to each other. Both architectures can be present in the same burrow system (Fig. 8A). Average vertical distance between the chambers is ~6 cm in articulated burrow systems showing a series of multiple chambers. As with *D. nephroides*, vertical distances between chambers increase with depth.

4. Discussion and interpretation

The sizes, basic structural elements, and architectural morphologies of *Daimoniobarax nephroides* and *D. tschinkeli* most resemble the nests of extant soil-excavating ants. Ants have a rich fossil record represented by more than 60 extant and 100 extinct fossil genera (Hölldobler and Wilson, 1990). The oldest reliably dated ant body fossils are from Early Cretaceous (Albian–Cenomanian) amber in France and Myanmar: already with indicators of eusociality, specialized caste members, and arachnid predators specialized to feed on them (Perrichot et al., 2008). Recent phylogenetic and molecular clock analyses of ant DNA suggest that the Formicidae last shared a common ancestor sometime in the mid-Jurassic to earliest Cretaceous (Moreau et al., 2006; see Brady et al., 2006 for an alternative analysis). Though fossil ants from Late Cretaceous deposits are relatively rare, they began at that time an explosive taxonomic radiation that appears to have closely tracked the proliferation of angiosperm-dominated forests and culminated in their ecological dominance of most terrestrial ecosystems by the end of the Paleogene (Wilson and Hölldobler, 2005).

Modern ants constitute the largest eusocial insect group, and, with only half of the estimated 22,000 extant species described, are often the largest insect components in modern terrestrial environments by biomass (Ward, 2007). Ants are found in virtually all terrestrial habitats, though their diversity is highest in the soil and ground litter of tropical forests where they are the dominant insect predators, scavengers, and indirect herbivores (Wilson and Hölldobler, 2005). Ant bioturbation strongly influences soil turnover rates, local porosity, and infiltration rates by aggregating, moving, or destroying ped structures and lowering soil bulk density (e.g., Cammeraat and Risch, 2008; Wilkinson et al., 2009). Ant activity and occupation of the soil may regulate local soil nutrient cycles, the concentration and decomposition of soil organic material, and the composition of local soil microbial communities (e.g., Lobry de Bruyn and Conacher, 1990; Nkem et al., 2000), especially in cold or arid environments where

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earthworms are rare (Folgarait, 1998). Ants live in colonies composed typically of one or more queens and a caste of 10 to 10^6 wingless, sterile female workers that excavate the nest, tend broods of eggs and pupae, forage for food, or act as soldiers in defense of the colony (Wilson and Hölldobler, 2005).

With the exception of a few nomadic species (army or driver ants), ants live in nests excavated in soil or constructed aboveground for shelter against temperature and moisture extremes, and for food storage, reproduction, and fungus cultivation in some species (Sudd, 1967). Nest architecture in some species also seems to organize and maintain divisions of labor and worker ages within the colony (e.g., Sendova-Franks and Franks, 1995; Tschinkel, 1999). Most ants construct nests in soil by the mechanical removal of sediment to the surface or to unused portions of the nest. The typical subterranean ant nest is composed of two basic elements: 1) more or less horizontal chambers numbering from <10 to 10^3, and 2) narrow galleries (tunnels and shafts) that connect chambers to each other and to the surface (Tschinkel, 2003). The few well-studied modern ant nests are complex structures that show species-typical differences in their overall size and orientation, number of chambers and galleries, and spatial density of individual elements (Tschinkel, 2003).

4.1. Fossil ant nests

Despite the seemingly ubiquitous presence of ants in modern terrestrial habitats and their extensive body fossil record, surprisingly few trace fossils have been attributed to ants and these are known from only a handful of localities (Hasiotis, 2003). Two ichnogenera have been interpreted confidently as the work of burrowing ants, *Attaichnus* and *Parowanichnus*.

Attaichnus kuenzelii Laza, 1982 was described from the Miocene Epecuén Formation, Argentina, and consists of large, 140–170 mm diameter, spherical to globular chambers and smaller diameter tunnels and shafts within a structure up to 3 m in height and 7 m in diameter. The chambers are invariably joined from below by shafts, 15–27 mm in diameter, that extend some distance into the chamber in some specimens. Shafts and tunnels with smaller diameters (5–9 mm) intersect the tops of chambers and the larger diameter shafts. Laza (1982) interpreted these and additional chambered ichnofossils from Pliocene and Pleistocene deposits in Argentina (Laza, 1997) to be the nests of fungus gardening (attine) ants based on their overall morphology, the size and shape of the chambers and burrow system, and the conical rim within the chambers.

Parowanichnus formicoides was first described from the late Paleocene–Eocene Claron Formation in southwestern Utah (Bown et al., 1997). It consists of more than 100 oblate to hemispherical, 10–50 mm diameter chambers surrounded by a dense network of primarily horizontal, <12 mm wide tunnels and short shafts. Tunnels, shafts, and chambers decline in number as they radiate away from the nest center forming a structure measuring ~1.0 m in height and ~3.3 m wide. *Parowanichnus formicoides* does not closely resemble any of the handful of well known nests of modern subterranean ants, though Bown et al. (1997) noted that similar modern nests with numerous horizontal tunnels are typical of humid soils. Chambered trace fossils similar to *P. formicoides* have been described from the Upper Jurassic Morrison Formation in southeastern Utah (Hasiotis and Demko, 1996). A second ichnospecies of *Parowanichnus*, *P. perirhizaterion* Hembree and Hasiotis, 2008, is very similar to *P. formicoides,* in that it is composed of a boxwork of interconnected tunnels, shafts, and chambers that radiate from the nest center, except that nest architecture follows and is confined to the immediate area around a central rhizolith.

A third possible ant nest ichnogenus is *Socialites* Roberts and Tapanila, 2006. The type and only ichnospecies, *S. tumulus,* was described from Upper Cretaceous deposits in southern Utah and is composed of a complex network of unlined and branching tunnels and shafts that connect larger ovate chambers within and around cone-shaped sedimentary structures along bedding planes. While the conical structures are very well defined, the burrow architecture within is far more cryptic and defined mainly by differently colored mottling in the sandstone below the cones. Given the lack of discernible architectural morphologies with distinguishing characteristics, an isopteran or other social insect tracemaker for *Socialites* cannot be ruled out. Other ichnofossils attributed to ants have been mentioned (e.g., Tandon and Naug, 1984; Laza, 1995; Hamer et al., 2007; Buck et al., 2010), however, the fossils themselves were either not the focus of the study or were not described in enough detail for ichnotaxonomic evaluation.

4.2. Tracemakers

4.2.1. Daimoniobarax nephroides

Daimoniobarax nephroides is most similar to the nests of modern seed-harvester ants (Formicidae: Myrmicinae), specifically of the New World genus *Pogonomyrmex* (MacKay, 1981; Tschinkel, 2004). The oldest known representative of *Pogonomyrmex* is the fossil species *P. fossilis* Carpenter from the lacustrine shale of the Eocene Florissant Formation in Colorado (Carpenter, 1930; Wilson, 1978). Given their similar nest morphologies, modern harvester ants provide a useful analog for the *D. nephroides* tracemaker. Harvester ants are so named because they collect and store seeds, grains, and other plant materials in their nests for later consumption by the colony members. *Pogonomyrmex* (or "bearded ant") is represented by more than 70 extant North and South American species (Crist, 2008). The beard is a tuft of hairs called psammophores that extend from below the heads of workers and are used in conjunction with the mandibles to carry fine sediments, small seeds, and eggs. Most harvester ants are highly specialized granivores, though some will prey on other insects when such food is readily available (Whitford and Jackson, 2007).

Seed-harvester ants are most abundant in the sandy soils of arid to semi-arid deserts and grasslands of the North American Southwest; only the Florida harvester ant, *Pogonomyrmex badius*, occurs east of the Mississippi River (Smith, 1979). Some harvester ant nests are characterized on the ground surface by a barren patch of soil that surrounds the nest entrance and has a radius of up to several meters (MacKay, 1981). Entrances in some species are capped by a broad mound of sediment that may contain internal chambers and can be up to 20 cm high and over a meter wide (Cole, 1994). A mature *Pogonomyrmex* nest may contain 150 chambers clustered directly below the surface and distributed vertically up to 4 m deep along a series of 4 to 5 helical shafts (Tschinkel, 2003, 2004). Chambers near the surface are consistently larger, more complex, and more closely spaced than those at depth, regardless of colony age and size (Tschinkel, 2004). In general, colony members are stratified within the nest by age; more mature workers are near the top of the nest and callow (immature) ants and the brood reside at depth, possibly due to a preference by younger workers for higher CO_2 concentrations (MacKay, 1981; Tschinkel, 1999).

Nest construction and chamber enlargement by the *Baraxodaimines nephroides* tracemakers were likely analogous to the excavation methods of harvester ants based on the strong morphological similarities between *D. nephroides* and modern harvester nests (Tschinkel, 2004). The teardrop shaped chambers of *D. nephroides* likely represent the nascent phase of chamber excavation (Fig. 7D). Chamber enlargement proceeded primarily by the removal of soil material from the lateral walls of the chamber and back towards and around the shafts creating horizontally oriented and bilobed, reniform chambers. Further chamber expansion in this manner resulted in large, U-shaped chambers that nearly surround central shafts.

4.2.2. Daimoniobarax tschinkeli

The chamber and shaft morphologies of *Daimoniobarax tschinkeli* and their relatively simple architectural arrangement appear more

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generalized when compared with *D. nephroides*. It should be noted that differentiation between the two *Daimoniobarax* ichnospecies is difficult without burrow systems preserved at least partially in positive relief. Though not diagnostic enough to infer a particular taxon of ant tracemaker, nest morphologies similar to *D. tschinkeli* are known from the subterranean nests or nest portions of such diverse genera as *Myrmecocystus* (Conway, 1983), *Prenolepis* (Tschinkel, 1987), *Ectatomma* (Antonialli and Giannotti, 2001), *Aphaenogaster* (Tschinkel, 2003), and *Pheidole* (Forti et al., 2007). A better understanding of the range of modern ant-nest morphologies is needed to make a more specific interpretation of the tracemaker.

4.3. Paleoenvironmental and paleoecological significance

Although modern ants live in a wide range of terrestrial habitats and climates, fossil nests can provide some specific information about paleoecological and paleoenvironmental conditions during nest construction and occupation. Recognizable ant nests in the fossil record are important because ant body fossils are relatively rare and are often preserved in amber or in lacustrine deposits (e.g., Wilson, 1978) and out of their original ecological context (Hasiotis, 2003). Fossil nests, however, are direct evidence for the presence of ants within an ancient ecosystem and such ichnofossils are more likely to be present in depositional and paleopedogenic settings where insect body fossils are rarely preserved. Although the earliest body fossil of a given taxon is more commonly used to infer its phylogenetic origin, diagnostic trace fossils can be used as proxies for the presence of an organism or group or organisms with similar behavior and anatomies (e.g., Hasiotis and Mitchell, 1993). Of equal importance is the use of ant nest ichnofossils for interpreting the evolutionary history of novel behaviors and the paleoenvironmental conditions under which these behaviors developed.

An abundance of ant nests suggests relatively low aggradational rates or a depositional hiatus during which host sediments were subaerially exposed and pedogenically modified (Hasiotis, 2007; Smith et al., 2008b). As with most modern ants, fossil tracemakers likely constructed subterranean nests in the vadose (unsaturated) zone of generally well-drained or quickly draining soils. The higher porosity and lower bulk density of the nests themselves create soil microhabitats that promote rapid drainage after precipitation (e.g., Green et al., 1999). In addition, the open burrows extend the subsurface effects of subaerial exposure and pedogenesis beyond their normal range (Hole, 1981).

The morphology of fossil ant nests may provide information on paleosurface position because the size, shape, and vertical spacing of chambers, and the number and orientation of shafts in the nests of many extant ant species change with depth (e.g., Tschinkel, 2003). For example, *Pogonomyrmex badius* chambers within 15 cm of the soil surface are consistently larger, more complex, and more closely spaced than those at depth (Tschinkel, 2004). The vertical distance between chambers along a descending shaft increases with nest depth while the size and complexity of the chambers decrease. In some mature *P. badius* nests, descending shafts branch at depth, but this always occurs within 40 cm of the ground surface. Such depth-related morphological changes could be used as paleosurface and paleodepth indicators or as geopetal features. If the paleosurface could be inferred, nest depths as suggested by the vertical height of their ichnofossils in outcrop may correspond with the depth of the local water table during the time of construction. Though such morphological features are suggested or can be quantified in some well-preserved fossil nests, e.g., the significant decreases in vertical spacing toward the tops of nests, vagaries in outcrop exposure and specimen preservation may make it difficult to interpret confidently whether seemingly connected chambers are portions of the same nest.

Fossil nests, if distinctive enough, may also suggest specific paleoclimatic interpretations. The architectural morphology of *Daimoniobarax nephroides* is very similar to the nests of modern seed-harvester ants in the genus *Pogonomyrmex*. If the *D. nephroides* tracemaker had climate and habitat preferences similar to those of modern harvester ant species, this would imply arid to semi-arid grassland or desert conditions in the High Plains region during the time of trace formation. While this interpretation is not inconsistent with the climate conditions associated with modern settings where thick petrocalcic horizons are forming (Wright, 2007), an arid to semi-arid paleoclimate is not necessarily suggested from ongoing paleobotanical studies from these same localities (Thomasson, 1979, 1990, 2003, 2009).

Although it is beyond the scope of this paper, there is increasing interest in the role that micro- and macroorganisms play in the formation and placement of calcic horizons in soils and sediments (e.g., Wright et al., 1995; Singh et al., 2007; Zhou and Chafetz, 2009). Fossil ant-nest chambers in the type locality are preserved more abundantly and stacked more closely together in calcrete beds, and possibly nearer the paleosurface, compared with less calcified underlying strata. Modern ant bioturbation lowers soil bulk densities, enhances infiltration and aeration, enriches organic matter in the nest, and redistributes soil nutrients and minerals relative to surrounding soils (e.g., Wagner et al., 1997). Likewise, the *Daimoniobarax* tracemaker may have altered physical and chemical soil properties in ways that promoted the precipitation of thick petrocalcic horizons in the Ogallala soils after burial. Research on how ancient soil biota influenced the formation of pedogenic calcretes at Ladder Creek Canyon and other Ogallala Formation localities is ongoing.

5. Conclusions

Many, though not all, of the honeycomb calcrete structures at the Devil's Backbone and other localities in the Ogallala Formation are the fossil casts of ant nests. *Daimoniobarax* is established to represent multichambered ichnofossils of this type composed of vertically tiered, horizontally oriented, pancake-shaped chambers connected by subvertical to vertical, small-diameter shafts. Two ichnospecies, *D. nephroides* and *D. tschinkeli*, can be discerned based on differences in the plan view outline of their chambers, shaft orientations, and points of intersection between chambers and shafts. In comparison with the known nest architectures of modern subterranean ant species, *D. nephroides* is most similar to the nests of New World seed-harvester ants of the genus *Pogonomyrmex*, while *D. tschinkeli* is more general in form and doesn't closely resemble any particular known modern ant or insect nest. Given that there are likely as many different ant-nest morphotypes as there are ant species, there are may be a diverse array of unrecognized or undiscovered *Daimoniobarax* ichnospecies in the geologic record. Such recognition will provide a more comprehensive understanding of the ecological diversity of ancient terrestrial environments.

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