

NEW ICHNOTAXA OF VERTEBRATE BURROWS FROM THE SALT WASH MEMBER, UPPER JURASSIC MORRISON FORMATION, SOUTH-EASTERN UTAH (USA)

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Raisanen, D. C. W. & Hasiotis, S. T., 2018. New ichnotaxa of vertebrate burrows from the Salt Wash Member, Upper Jurassic Morrison Formation, south-eastern Utah (USA). *Annales Societatis Geologorum Poloniae*, 88: 181–202.

Abstract: Large-diameter burrows in pedogenically modified floodplain deposits in the Salt Wash Member, Upper Jurassic Morrison Formation, southeast Utah, U.S.A., are interpreted to have been constructed by mammals. They are distinguished as *Daimonelix martini* isp. nov., which exhibits a helical shaft down to a horizontal tunnel with a mean depth of 71.4 cm from the inferred palaeosurface. The mean path length of the shaft is 99.4 cm; mean dip of the whorls is 39°. The mean tunnel length is 42.3 cm. Shafts and tunnels are oval or elliptical in cross section with the horizontal diameter slightly larger than the vertical (ratio of ~1.26:1); the shaft averages 9.2 cm wide and 7.3 cm tall; the tunnel averages 10.7 cm wide and 10.7 cm tall. The tracemaker was likely a fossorial mammal that used the burrow as a den to shelter when not foraging above ground; the burrows are domichnia. The other from the same member is *Fractisemita henrii* igen. nov. et isp. nov., a network of interconnected shafts and tunnels; shaft and tunnel segments are straight, curved, or helical. The segments are at angles of 0–89°; mean length of a section is 30.7 cm. The cross sections of all elements are oval or elliptical; the mean width is 6.3 cm and the mean height is 4.9 cm (ratio of ~1.29:1). The burrows are interpreted as the work of a social mammal and represent multiple tracemaker behaviours: protection, denning, foraging, and possibly food storage. The burrows are polychresichnia. Surficial morphologic features preserved on the burrow walls of both types are interpreted as scratches made by the tracemaker claws and/or teeth. The burrows reveal the actions of small vertebrates not recorded by body fossils showing potential partitioning of the environment and availability of resources for small vertebrates.

Key words: Ichnofossils, continental, palaeosols, fossorial, trace fossils, domichnia, polychresichnia.

Manuscript received 24 September 2018, accepted 7 December 2018

INTRODUCTION

This paper presents two new ichnotaxa, *Daimonelix martini* isp. nov. and *Fractisemita henrii* igen. nov. et isp. nov., of vertebrate burrows in the Salt Wash Member of the Upper Jurassic Morrison Formation in southeast Utah, U.S.A. These structures have previously been interpreted as vertebrate burrows (Hasiotis, 2002, 2004, 2008; Hasiotis *et al.*, 2004; Platt, 2012), but have not been ichnotaxonomically treated. We present possible behaviours and tracemakers represented by *D. martini* and *F. henrii*, compare them to morphologically similar burrows produced by invertebrates and vertebrates, and suggest that they were most likely constructed by mammals.

Vertebrate burrows are tentatively identified in the fossil record as far back as the Devonian (Woodrow and Fletcher, 1969; Hasiotis, 2002; Friedman and Daeschler, 2006) and occur in a variety of environments – floodplain, aeolian,

lacustrine, and palustrine (e.g., Smith, 1987; Groenwald *et al.*, 2001; Hasiotis, 2002; Hasiotis *et al.*, 2007; Riese *et al.*, 2011; Krapovickas *et al.*, 2012; Joeckel and Hunter, 2013; McCahon and Miller, 2015; Bordy and Krummeck, 2016; Bordy *et al.*, 2017). Vertebrate burrow diversity may seem limited when compared with invertebrate burrow diversity (e.g., Häntzschel, 1975), but closer analysis of architectural and surficial burrow morphologies reveals significant identifying morphologic characteristics diagnostic of ichnogenera and ichnospecies. Providing an ichnotaxonomic assessment of *Daimonelix martini*, *Fractisemita henrii*, and other vertebrate trace fossils formalizes unique morphologies with specific ichnotaxonomic designations. This specificity will enhance communication and understanding among researchers studying vertebrate burrows through time.

Daimonelix martini occurs in terrestrial environments in the vadose zone. It is compared with other helical burrows interpreted as invertebrate, reptilian, therapsid, and mammalian in origin (e.g., Martin and Bennett, 1977; Bown and Kraus, 1983; Smith, 1987; Krapovickas *et al.*, 2013; Dooty *et al.*, 2014, 2015). *Fractisemita henrii* also occurs in the vadose zone and is compared with networks or mazes of burrow elements interpreted as mammal in origin (e.g., Groenwald *et al.*, 2001; Hasiotis *et al.*, 2004; Gobetz, 2006; Gobetz and Martin, 2006; Riese *et al.*, 2011; Colombi *et al.*, 2012; Joeckel and Tucker, 2013; Bordy and Krummeck, 2016, 2017).

GEOLOGICAL SETTING

The Morrison Formation extends over 1×10^6 km² in the western United States and records mostly continental environments (Turner and Peterson, 2004). The Salt Wash Member is composed of channel deposits interbedded with various degrees of pedogenically modified floodplain and crevasse-splay deposits and has been interpreted as a mixed meandering and braided river system (Hasiotis, 2004, 2008; Turner and Peterson, 2004; Kjemperud *et al.*, 2008). Channel deposits of sandstones and floodplain deposits of mudstone, siltstone, and sandstone occur in approximately equal amounts (Kjemperud *et al.*, 2008).

The Morrison Formation has produced a wealth of trace and body fossils from a variety of localities (e.g., Ostrom and McIntosh, 1966; Turner and Peterson, 1992; Hasiotis, 2004, 2008; Gates, 2005). Trace fossils already identified in the Salt Wash Member include rhizoliths, dinosaur tracks, pterosaur tracks, and numerous kinds of invertebrate nests and burrows (Stokes, 1957; Lockley, 1992; Robinson and McCabe, 1998; Hasiotis 2004, 2008). Besides the burrows *D. martini* and *F. henrii* we identified bone fragments, dinosaur tracks, and rhizoliths at both localities.

Daimonelix martini and *Fractisemita henrii* are found at two localities in southeastern Utah. Locality 1 is ~9 km north of Ticaboo, Utah, and locality 2 is ~11 km east of Fruita, Utah (Fig. 1). The Ticaboo locality is more laterally extensive than the Fruita locality and yielded over 80% of the described burrows (*Daimonelix*, 63 from locality 1 and 13 from locality 2; *Fractisemita*, 4 systems and 2 overprinted systems from locality 1 and 3 from locality 2). Both localities have alternating beds of sandstone and mudstone interbedded with pedogenic carbonate. The sandstones are pale orange brown, cross-bedded and medium-grained with coarser pebble lag deposits at the bottom contacts. All sandstones are interpreted as fluvial channel deposits. The mudstones are carbonate cemented and clay rich, and exhibit slickensides and pseudoanticlines. The lower contacts of the mudstones are gradational and the upper contacts are sharp scour surfaces. There are three mudstone layers at each locality. Mudstone is red brown or grey green with differences occurring within a single bed. The red-brown coloration is interpreted as well-drained, oxidative conditions and the grey-green coloration represents poorly drained, reducing conditions (e.g., Bown and Kraus, 1987; Smith *et al.*, 2008). The carbonate beds are yellow brown. The interbedded mudstone-carbonate intervals are interpreted as floodplain pal-

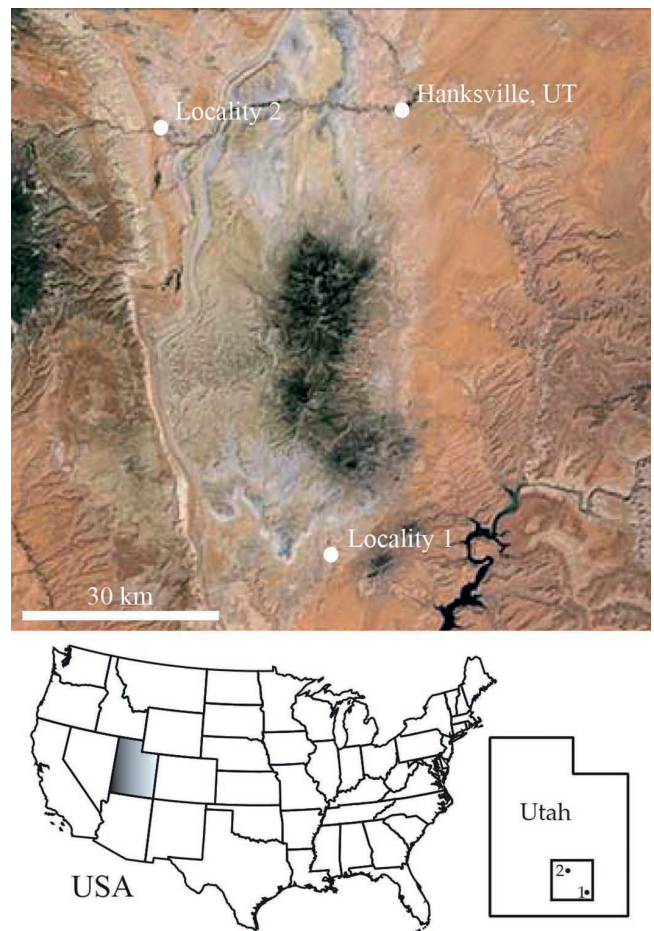


Fig. 1. Location of study areas. Locality 1 is in Shooting Canyon near Ticaboo, Utah; Locality 2 is near Fruita, Utah. Satellite image courtesy of Google Earth.

aeosols. Each succession of units is interpreted as a vertisol based on its vertic morphologic features with weakly developed Bk horizons (e.g., Retallack, 2001). The burrows are present in the lowest and middle palaeosol at locality 1 and the uppermost and middle palaeosol at locality 2 (Fig. 2). The two study sites represent different locations in the same fluvial palaeoenvironment, but beds cannot be correlated with certainty due to lack of local stratigraphic marker beds.

METHODS

Over 150 structures were examined and 85 were interpreted as burrows. Potential burrows were measured with a vinyl measuring tape to more accurately measure tortuous burrow elements and mechanical callipers (Fig. 3), photographed, and described to produce a database of qualitative descriptions and quantitative measurements to account for a full range of architectural and surficial morphologies following the methods of Hasiotis and Mitchell (1993), Hasiotis *et al.* (1993), and Hembree and Hasiotis (2006) (Appendix). Only morphologies that could clearly be determined to be burrows where included in the database. Those morphologies determined to represent dinosaur tracks, phreatic carbonate nodules, or rhizoliths were not included in the table.

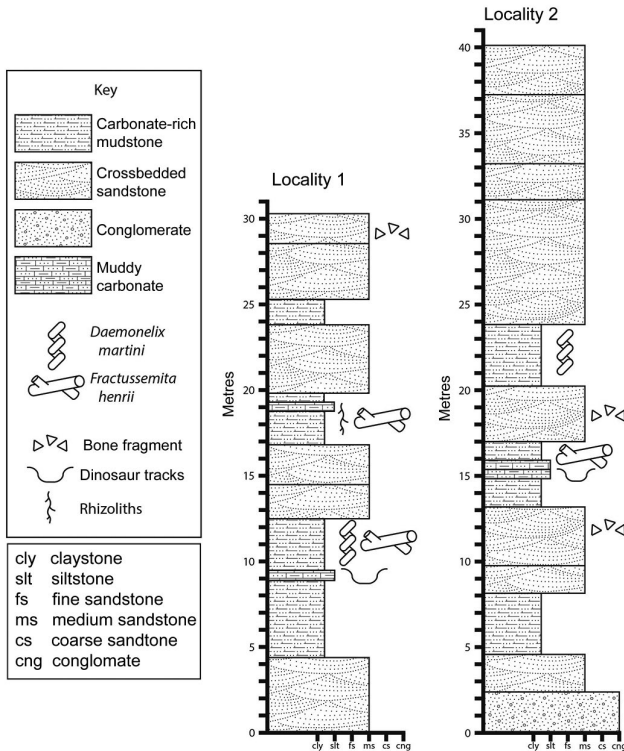


Fig. 2. Stratigraphic sections through upper part of Salt Wash Member at the study localities.

Stratigraphic columns were constructed for both localities (Fig. 2). The column for locality 1 was measured from below the lowest burrow-bearing layer to the top of the outcrop. The column for locality 2 was measured from the base to the top of the outcrop. Exact locality information cannot be published by request of the Bureau of Land Management (BLM), however, it can be obtained from the BLM in Moab, Utah, and from the University of Kansas (KU) Ichnology Collection upon request.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Daimonelix* Barbour, 1892

- 1895 *Daemonelix* – Barbour, p. 517.
- 1896 *Daemonelix* – Barbour, pp. 26–27
- 1897 *Daemonelix* – Barbour, pp. 310–311
- 1933 *Daemonhelix* – Wood and Wood, p. 824
- 1941 *Daemonelix* – Lugn, pp. 673–674
- 1942 *Daemonelix* – Schultz, p. 1
- 2013 *Daemonelix* – Joeckel and Tucker, pp. 7, 14, 27–28

Type ichnospecies: *Daimonelix circumaxilis* Barbour, 1892, by subsequent designation of Häntzschel (1975, p. W58).

Etymology: Greek *daimon* – demon, helix – spiral.

Emended diagnosis: Large, vertical, open cylindrical helical structure, regular in form, with a low- to high-angle,

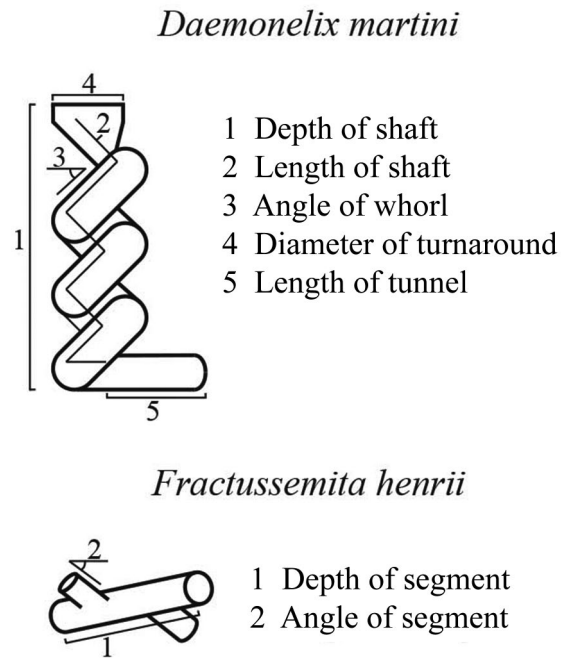


Fig. 3. Schematic of burrow measurements.

lateral protrusion at or near the base, all with or without tunnels, chambers, or helices branching from main structure (modified from Häntzschel, 1975, p. W58).

Emended description: A large, dextral or sinistral helical, unlined shaft down from a surface, with a lateral expansion as a chamber, tunnel, or both, at or near its base. Each whorl of the helix is separate from the next, though the spacing varies within and between specimens. Helix diameter tends to decrease slightly towards the base; burrow diameter tends to decrease downward and then increase toward the base; chamber height-width dimensions two to four times greater than shaft, and chamber length from one quarter to equal in length to the depth of the helix. Overall length-to-depth ratio (LDR) for preserved structures from $\sim 1.25:1$ to $\geq 4:1$; tortuosity falls within same range; morphologic complexity from 2 to 10 or more. Shafts and tunnels with oval-shaped to reniform cross section; with or without smaller diameter tunnels or helices branching at Y or T intersections from helix and/or lateral protrusion. Surficial morphology may include longitudinal to transverse ridges or striations with or without a medial groove (Barbour, 1892, 1894, 1895, 1896, 1897; Martin and Bennett, 1977; Smith, 1987; Meyer, 1999; Hasiotis *et al.*, 2004).

Remarks: Several issues exist with this ichnotaxon, which have been mostly summarized by Martin and Bennett (1977). First, Barbour (1892) never designated a type ichnospecies nor a type specimen for the gigantic, corkscrew-shaped structures he named *Daimonelix* – the devil’s corkscrew. In 1986, and again in 1897, he delineated two types of macromorphologies as “*Daemonelix irregular*” and “*Daemonelix regular*” (Barbour, 1896, pp. 26–27; Barbour, 1897, pp. 310–311), however, he did not use these designations with correct italicization or with correct capitalization consistently. Second, several variations of the spelling

have been in use since early in the existence of this ichnotaxon. Barbour (1892) originally named these structures as *Daimonelix* and proposed a taxonomic scheme from the ordinal to species level. In subsequent publications, however, he used the spelling *Daemonelix* (Barbour, 1895, 1896, 1897) – substituting *ae* for the *ai* – for these same burrow morphologies, while never using his taxonomic scheme for species. He apparently was inconsistent in the spelling of this ichnotaxon and used *Daimonelix* in his 1903 paper (Barbour, 1903). Third, since no formal ichnospecies was given for the taxon erected by Barbour (1892, 1895, 1896, 1897, 1903), Häntzschel (1975, p. W58) designated the type ichnospecies as *Daimonelix circumaxilis* Barbour, 1892. Häntzschel (1975, p. W58) used the first species designation of *circumaxilis* by Barbour (1892, p. 313) as the source of the ichnospecies, as well as using the photograph labelled figure 18 on plate III, p. 329, as the photograph published in the *Treatise* (Häntzschel, 1975, p. W57). We note that the citation for the photograph in Part W of the *Treatise of Invertebrate Paleontology* refers to Barbour (1895); however, that photograph does not come from that publication but rather from Barbour (1892, p. 329, plate III, fig. 18).

Therefore, we follow the designation of *Daimonelix circumaxilis* by Häntzschel (1975, p. W58) for gigantic, corkscrew-shaped structures. We, however, emend the diagnosis and description to encompass the range of morphologies exhibited at the ichnogenus level based on descriptions of *Daimonelix* from the literature. The description includes several quantitative measures of morphologies for a more comprehensive analysis (Fig. 3; Meyer, 1999; Hasiotis *et al.*, 2004; Hembree, 2016), which can be expanded upon in future studies of *Daimonelix* and other vertebrate burrows. The overall LDR of a burrow is the total preserved length divided by the depth of the burrow. LDR for *Daimonelix* ranges from approximately 1.25:1 to ≥ 4 :1. Tortuosity is the average sinuosity of a preserved burrow segment determined by dividing the total length by the straight-line distance, which is less than but falls within the lower range of LDR for *Daimonelix*. Complexity (morphologic complexity) of the preserved burrow is determined by the sum of the number of segments, chambers (including widened areas with a burrow segment; i.e., turnarounds), and entrances. Complexity ranges from 2 to 10, with higher values reflecting a greater number of branches, chambers, and turnarounds preserved within *Daimonelix*. Surficial morphologic features, when preserved, can be measured for their length, width, height, and related metrics based on the morphology of the ridges. The angle of divarication (AoD) of these features, measured by the angle of the feature(s) vs. the burrow segment orientation, also provides quantitative metrics for burrowing method(s) used by the tracemaker.

Daimonelix is distinguished from such helical burrows as *Gyrolithes*, *Lapispira*, and *Ichnogyrus* in several significant ways that define the geometry of each burrow type. *Gyrolithes* may be part of a larger burrow systems as multiple helices interconnected to and/or originating from one or more horizontal tunnels (e.g., Mayoral and Muñiz, 1995, 1998; Dworschak and Rordrigues, 1997; Laing *et al.*, 2018). *Gyrolithes* can be attached to *Thalassinoides* in some cases (e.g., Dworschak and Rordrigues, 1997, and referenc-

es therein). *Gyrolithes*, *Lapispira*, and *Ichnogyrus* do not have additional branches of helices or tunnels extending from the helix or basal chamber and/or tunnel (Häntzschel, 1975; Uchman and Hanken, 2013). The chamber, including its dimensions and orientation, is a significant morphologic element in any burrow, and should be included as morphologic criterion when erecting ichnotaxa (Hasiotis and Mitchell, 1993; Hasiotis *et al.*, 1993; Meyer, 1999), even if that feature in other ichnotaxa is poorly represented or variably preserved (e.g., Uchman and Hanken, 2013). In *Daimonelix*, the basal chamber can be as long as the helix is deep, while ranging from 2° to 43° (e.g., Martin and Bennett, 1977; Meyer, 1999) or more (up to ~80°; see Barbour, 1892, 1894, 1895, 1897) in angle up from a horizontal plane (i.e., rake); horizontally oriented chambers may have one or more downward conical projections near the junction of the helix and chamber. Chambers, where present or preserved in *Gyrolithes*, have the same diameter as the helix and are horizontal, low rake ($\leq 10^\circ$), or dip downward from horizontal (≤ -5 – 60°) as well as inclined in the same angle as the last whorl (Häntzschel, 1975; Mayoral and Muñiz, 1995, 1998; Mayoral 1986; Uchman and Hanken, 2013; Laing *et al.*, 2018). Only one incomplete specimen of *Ichnogyrus* is known (Bown and Kraus, 1983; Hasiotis *et al.*, 2004), but it exhibits helices in contact with one another without lateral branching originating from them. *Lapispira* exhibits double helical turns and lacks a chamber (Häntzschel, 1975; Lanés *et al.*, 2007; Uchman and Hanken, 2013). Size is not a morphologic criterion on which to base an ichnotaxon (i.e., ichnotaxobase; Bertling *et al.*, 2006), however, the scale and size range of burrow diameters, helix diameters, and whorl spacing does not overlap in range between *Daimonelix* and any of these other ichnotaxa. Size with respect to proportions of burrow diameter, whorl radius, number of whorls per unit of measure, and change in helix diameter, as well as the number of burrow elements, are viable morphologic criteria. The overall size of *Daimonelix* is two to three orders of magnitude greater than those of *Gyrolithes* and *Lapispira*, and one to two orders of magnitude greater than for *Ichnogyrus*. Most complete specimens of *Gyrolithes* or *Lapispira* could be contained within the diameter of one portion of a whorl in *Daimonelix*. Regardless of mathematical scale equations and theoretical modelling (Uchman and Hanken, 2013; Laing *et al.*, 2018), the scale and geometries of *Daimonelix* uniquely distinguish this ichnotaxon from other helical burrows.

The medium and palaeoenvironment in which helical burrows occur are noteworthy and significant to those researchers who reconstruct the depositional history and palaeoenvironmental, palaeohydrological, palaeoecological, and palaeoclimatic settings of sedimentary successions (e.g., Martin and Bennett, 1977; Meyer, 1999; Pemberton *et al.*, 2001; Hasiotis *et al.*, 2004; Hubbard *et al.*, 2004; Hasiotis 2007; Wetzel *et al.*, 2010; Hasiotis and Platt, 2012; Joeckel and Tucker, 2013). The deep, penetrative nature of *Daimonelix* (2–4 m) in alluvial and fluvial floodplain deposits modified by pedogenesis reflects groundwater profiles with a thick, well-drained vadose zone and deep phreatic zone (e.g., Martin and Bennett, 1977; Hasiotis *et al.*, 2004; Hasiotis 2007). The sediments were firm when dry, with grass

and shrub roots, pedogenic clay and carbonate from translocation, and pedogenic structure. Pore spaces contained mostly air with some water and were gravitationally drained and compacted. Nearly horizontal chambers and/or tunnels at or near the base of the helices contained sinks (conical structures) to capture any water that may have made its way down the burrow; others were constructed at higher angles as a means to drain water that filled the burrow and to trap air in case of major periods of overland flooding (e.g., Martin and Bennett, 1977). The helices also regulated airflow into and out of the burrow, as well to protect the inhabitants from potential predators (e.g., Meyer, 1999). *Daimonelix* was not constructed in subaqueous environments. Helices of *Gyrolithes* and *Lapispira* are much smaller and represent marine organisms inhabiting incised valleys and shallow coastal (including tidal-influenced bays) to shelfal marine environments (e.g., Dworschak and Rordrigues, 1997; Pemberton *et al.*, 2001; Wetzel *et al.*, 2010). Sediments within which these burrows were constructed were mostly softgrounds, whereas a few were firmgrounds or transitioned to firmgrounds deeper in the sediment profile (e.g., Hubbard *et al.*, 2004; Wetzel *et al.*, 2010). The salinity of the water above and below the sediment surface has been interpreted to range from marine brackish to fully marine (Pemberton *et al.*, 2001; Wetzel *et al.*, 2010). These burrows were never constructed within environments that experienced long-term desiccation, subaerial exposure, and pedogenesis.

Daimonelix martini ichnosp. nov.

Figs 4–8

Etymology: Named after the late University of Kansas palaeontologist Dr. Larry D. Martin for his contributions to the study of *Daimonelix* and its tracemakers.

Types: Holotype is in the field and shown in Figure 4; paratypes are in the field and shown in Figures 6–7.

Material: Sixty-three specimens in outcrop at locality 1; 13 specimens in outcrop at locality 2.

Diagnosis: Large, vertical to inclined, helical structure with narrow axis of coiling and steep angle of descent, with a horizontal to low-angle, lateral protrusion at or near the base, all without tunnels, chambers, or helices branching from the main structure or lateral protrusion.

Description: Full-relief casts *in situ* and in float without a lining or internal structure, preserved with carbonate fill, sometimes recrystallized and/or altered by microkarst. The burrow is composed of a vertical to subvertical (35–57° from the horizontal surface), helical shaft extending down from the palaeosurface that joins a horizontal tunnel as an L-shaped junction; tunnel oriented horizontally at an angle $\leq 10^\circ$ upward with no increase in diameter. An aperture at the top of some shafts is present, from 15.2 cm to 36 cm in diameter. Helices penetrate 33.7 cm to 155.6 cm below the palaeosurface and have a path length of 54.6 cm to 143.5 cm. The dip of the helical whorls is 26–67°. The cross section of both the shaft and the tunnel is oval. The shaft has a cross section with a vertical diameter of 3–11 cm and a horizontal diameter of 2.3–14 cm. Tunnels range from 24.1–86.6 cm long. Tunnel cross sections with a vertical diameter of

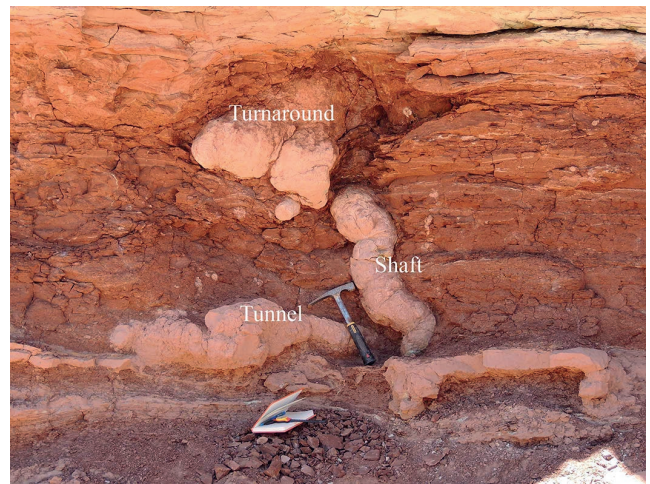


Fig. 4. Major architectural elements in *Daimonelix martini*. Hammer is 28 cm long.

4.3–26.7 cm and horizontal diameter of 4.9–20.2 cm. At locality 1, mean burrow density is 9 burrows per 10 m of laterally exposed vertical outcrop face. Locality 2 has a density of 10 burrows per 10 m. The majority of specimens are incomplete, lacking some of one or both elements, due to expression and preservation in outcrop.

Four surface textures – two types of ridges and two types of knobs – constitute the surficial morphology that appear on burrows in both outcrops. The tops and sides of helix and tunnel elements in individual burrows tend to preserve ridges, whereas the burrow undersides are dominated by knobs (Fig. 8). The larger ridge type (<1 cm wide, 1–10-cm long, <0.5-cm high) runs longitudinally on the surface of the shaft and tunnel elements. These ridges have rounded tops. Smaller ridges are composed of short segments less than 1-cm long that join at a variety of angles to create a jagged surface texture; less than 1-cm tall, but has a steeper slope from the surface compared with the larger, smoother ridges. The larger knobs circle the circumference of the burrow surface, predominantly on the shafts; their size varies with the size of the shaft. The knobs have expanded into each other and these large knobs are separated by thin cracks up to 1.5-cm deep. Some smaller knobs, ~1 cm in diameter, are present on larger knobs (Appendix).

Occurrence: Upper Jurassic Morrison Formation, Salt Wash Member; locality 1 (coordinates 37°45'N, 110°42'W), locality 2 (coordinates 38°17'N, 111°9'W). More detailed coordinates and meter levels are available upon request to protect the locality.

Remarks: The most distinguishing morphologic characteristics of *D. martini* are: 1) the narrower axis of coiling of the whorls, accompanied by steeper angles of descent, smaller diameter tunnels on average (see measurements in the Appendix), and fewer whorls; and 2) the tunnel at the base is oriented horizontally at an angle $\leq 10^\circ$ upward without an increase in diameter. Burrows of *Daimonelix* typically have a tunnel at the bottom of the helix angled above the horizontal and a distinct terminal chamber, whereas *D. martini* has a subhorizontal tunnel and no defined chamber. The tunnel itself in *D. martini* may be considered as a chamber.

Daimonelix martini is distinguished from *D. circumaxilis*, *Daimonelix* isp. (Smith 1987), and *D. petalichnus* (Hembree and Hasiotis, 2008) based on the relationship between the helix axis, steeper angles of descent, and morphology of the terminal chamber and/or tunnel. *Daimonelix circumaxilis*, designated from material in Neogene deposits of Nebraska (e.g., Barbour 1892; Häntzschel, 1975; Martin and Bennett, 1977) has a wider coiling axis, diameter to helice ratio, greater number of whorls and penetration depth (six to 12 or more coils), shallower angle of descent of the whorls (25–30°), and a moderately to well-defined terminal chamber at greater angles. *Daimonelix* isp. from the Teekloof Formation of the Middle Permian Beaufort Group (Karoo Basin, South Africa) is composed of 2 to 3 whorls that widen as it descends into a terminal chamber from 6 to 25 cm in diameter. The cross section at the top of the helix is planoconvex, becoming more elliptical as it descends with a width/height ratio of 2. The chamber cross section is a flattened biconvex. Individual burrows decline at a consistent angle, but between burrows the angle varies from 10 to 32°.

Burrows reach an average depth of 0.5 m and few go deeper than 0.75 m. Surficial morphology includes parallel ridges on the outer wall of the helix and bottom of the terminal chamber, which form a chevron pattern on the sides and roof (Smith, 1987). *Daimonelix petalichnus* in the Miocene Pawnee Creek Formation (Colorado, USA) is a helix 2.0–3.0-m deep with three to five coils, each 1.0–1.5 m wide, 0.75–1.5 m long, and 300–500 mm in diameter, forming a very wide axis of coiling of the whorls, accompanied by 5–30° angles of descent, decreasing downward with each coil. The helix has a single terminal chamber below the axis of the helical tunnel at the same angle as the final coil but not extending beyond (Hembree and Hasiotis, 2008).

Possible tracemakers: Several groups of ancient and extant vertebrates and invertebrates construct helical structures. Morphological comparisons of these structures to *D. martini* lead us to interpret that they were most likely constructed by mammals (see earlier discussions and references), a group that also constructs a variety of burrow architectures that include a combination of short helices, short to long cy-

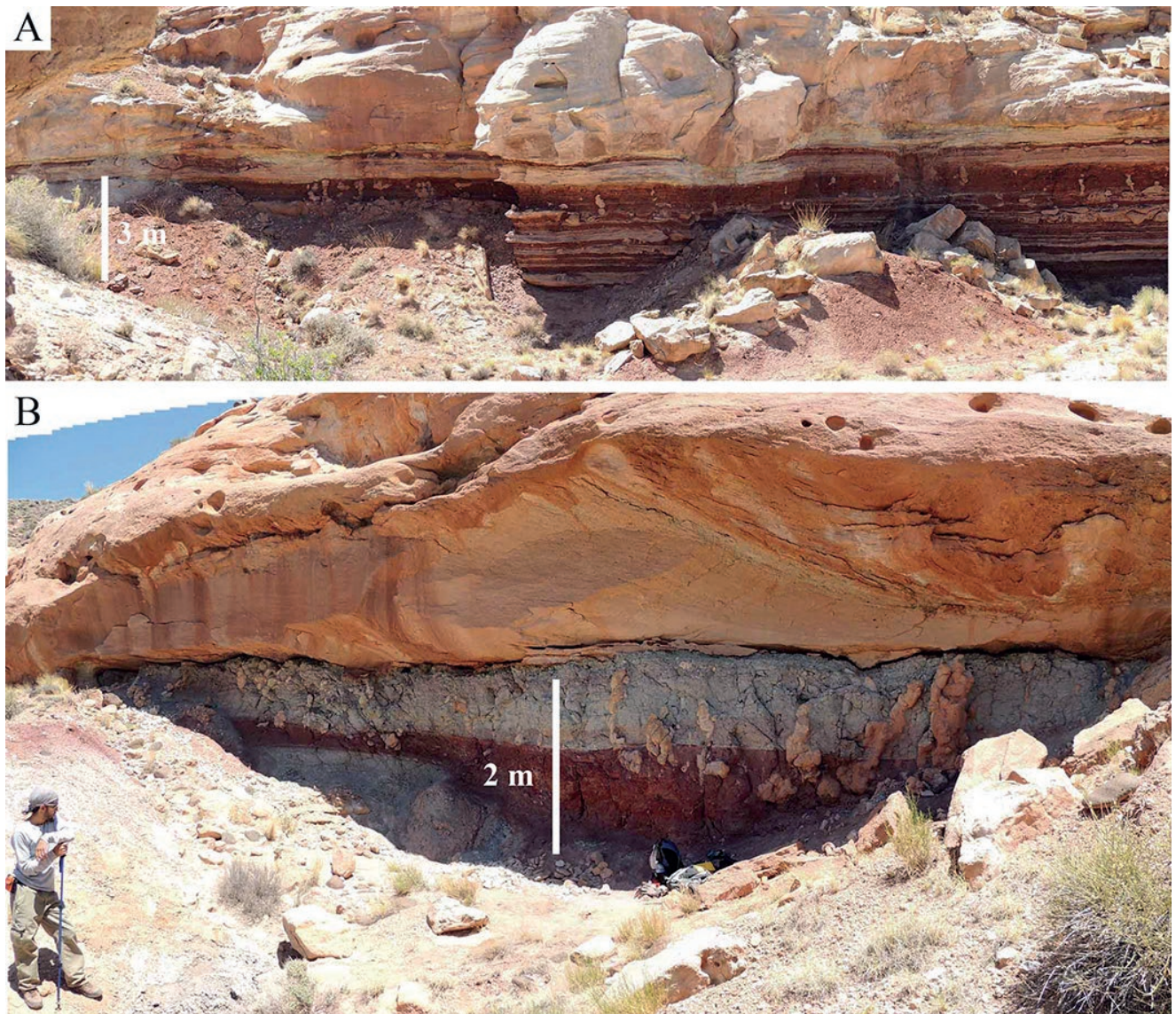


Fig. 5. *Daimonelix martini* in outcrop. **A.** Burrows seen at a distance in lower palaeosol at locality 1. **B.** Burrows in upper palaeosol at locality 2.

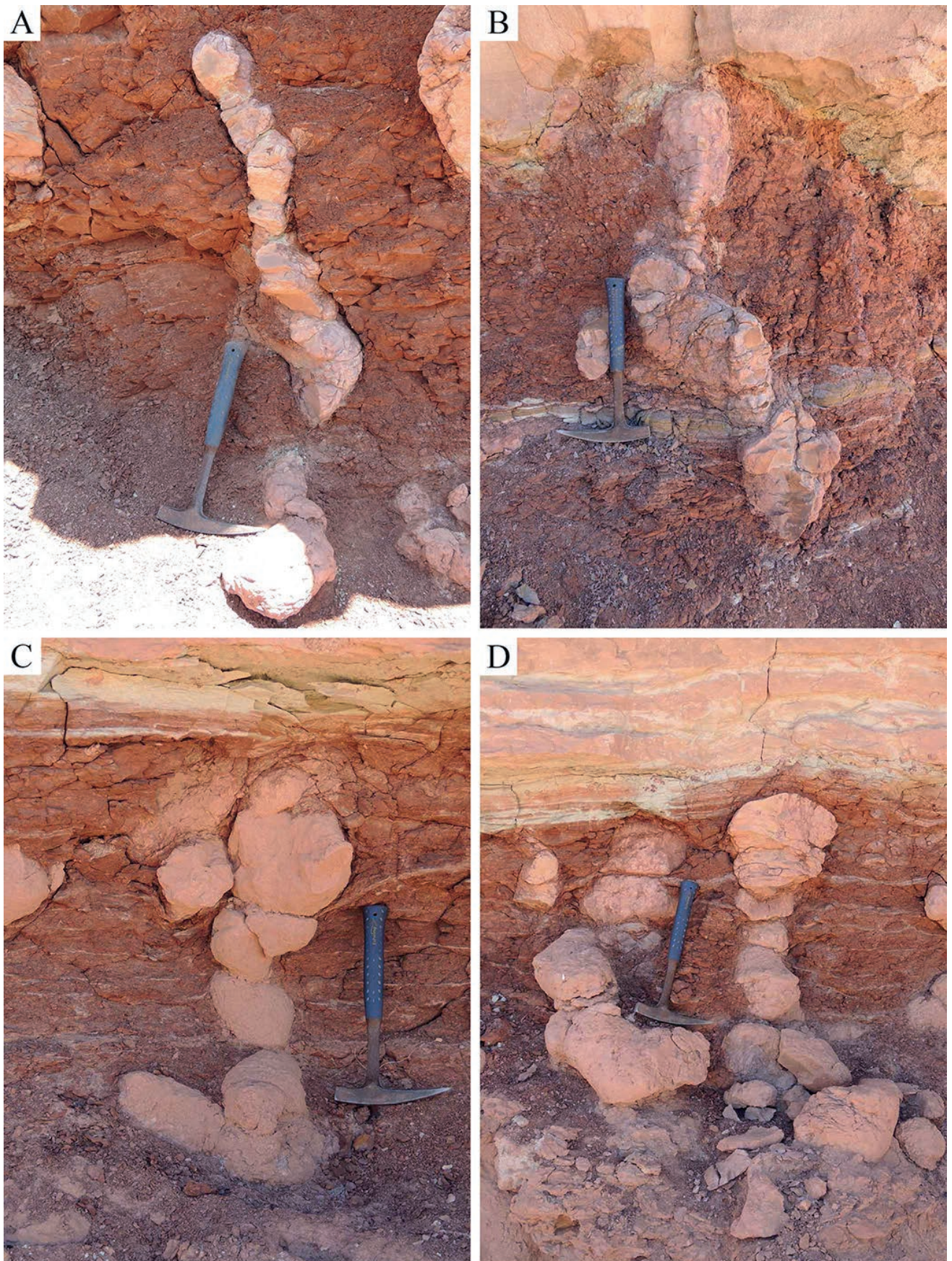


Fig. 6. Variations in morphology of paratypes of *Daimonelix martini* at locality 1 near Ticaboo, Utah, where burrows are filled with pedogenic carbonate. **A.** Shaft with a narrow axis of helix and weakly helical, with horizontal tunnel at base. **B.** Inclined, narrow axis of helix, weakly helical, to base from which horizontal tunnel once extended. **C.** Turnaround at top shaft, shaft with a narrow axis of helix but strongly helical, with inclined upward, short tunnel at base. **D.** Two closely spaced burrows with narrow axis of helix, strongly helical, with curved, horizontal tunnel at base visible in burrow on the left. Hammer is 32 cm long.

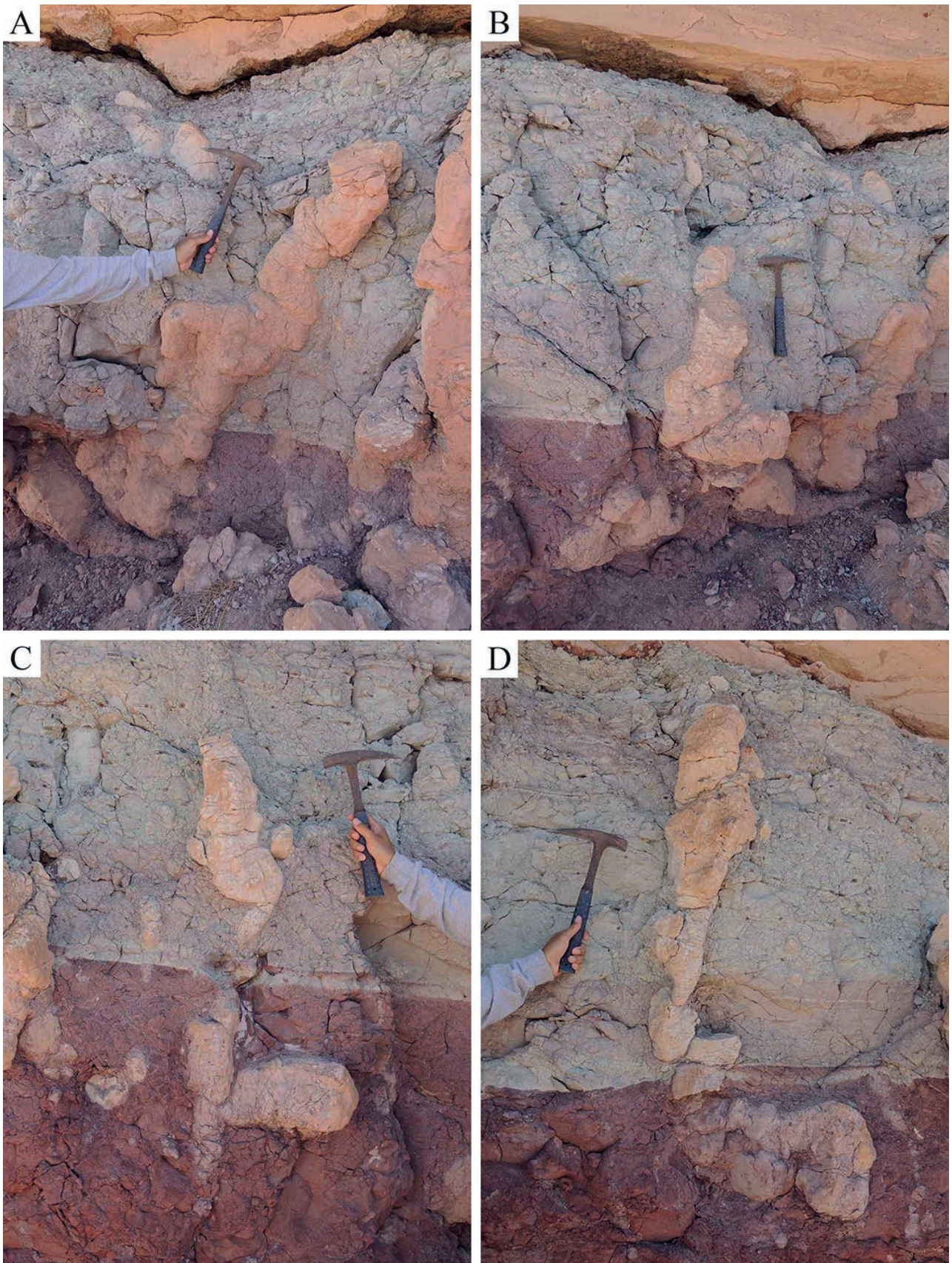


Fig. 7. Variations in morphology of paratypes of *Daimonelix martini* at locality 2 near Fruita, Utah, where most burrows are filled with and overprinted by pedogenic carbonate. **A.** Inclined, narrow axis of helix, weakly helical, to base from which horizontal tunnel once extend. **B.** Two closely spaced burrows with narrow axis of helix that widen downward, weakly helical, with curved, horizontal tunnel the base; *D. martini* on the left with straight axis of helix, while burrow on right with included axis. **C.** Shaft exhibits a narrow axis of helix and weakly helical, with horizontal tunnel near base; short portion below tunnel intersection interpreted as sink for water drainage. **D.** Shaft with a narrow axis of helix and weakly helical, with horizontal tunnel at base. Hammer is 32 cm long.

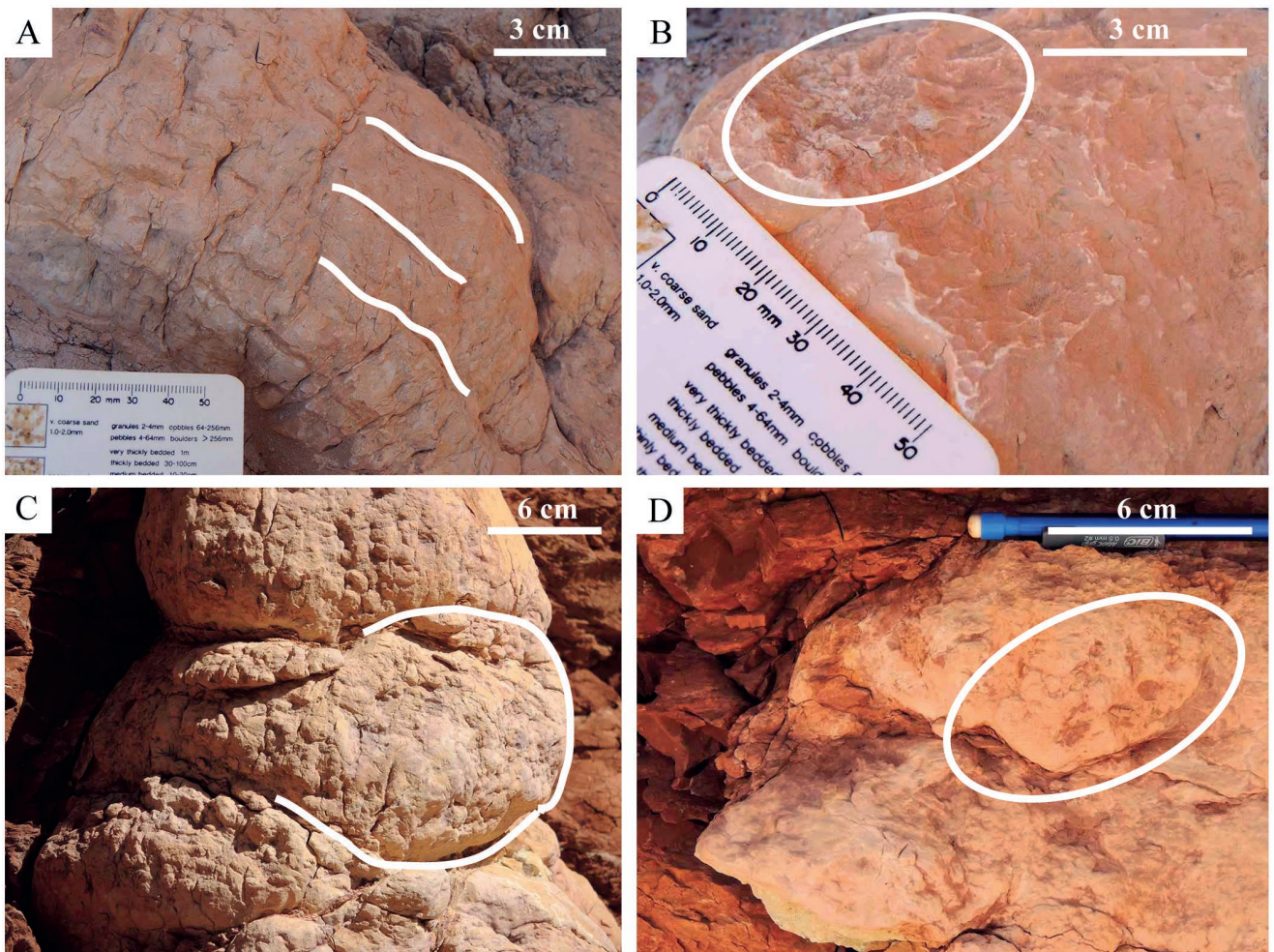


Fig. 8. Surfacial morphologies of *Daimonelix martini*. **A.** Large ridges. **B.** Small ridges. **C.** Large knobs. **D.** Small knobs. Note that preservation of features distorted by microkarstification.

lindrical and flattened shafts and tunnels that form Y- and T-shaped junctions with or without any widening in diameter where they intersect (e.g., Hasiotis *et al.*, 2004, 2007; Hembree and Hasiotis, 2007; Riese *et al.*, 2011; Joeckel and Tucker, 2013 and references therein). The surficial ridges and knobs on the walls of *D. martini* were likely produced during the maintenance and occupation of the burrows, but vertic pedoturbation of the matrix and karstification of the carbonate fill distorted many of these features.

Eight (McKenna and Bell, 1997) to 13 (Kielan-Jaworowska *et al.*, 2004) mammal lineages of order or family rank have been identified in the Late Jurassic. Many of these mammals are known from the Morrison Formation (Prothero, 1981; Foster, 2007), but none were discovered close to the field area. *Fruitafossor windscheffeli*, discovered in Fruita, Colorado, U.S.A., is interpreted as having many adaptations for a fossorial lifestyle (Luo and Wible, 2005). This is to date, however, the smallest mammal from the Morrison Formation (Foster, 2009) and was likely too small to have constructed *D. martini*. *Docofossor brachydactylus* Luo *et al.*, 2015, a docodontan (mammaliaform) from Late Jurassic China with fossorial adaptations, indicates that these features were dispersed across lineages by the time the Morrison Formation was deposited (Luo *et al.*,

2015). *Daimonelix martini* was probably constructed by an as yet undiscovered tracemaker or a known species whose anatomical fossorial adaptations were not preserved.

Helical burrows constructed by other vertebrates and invertebrates are generally similar to *D. martini* but contain distinct morphological features that eliminate or diminish them as possible tracemakers. Tracemakers discussed include ancient and extant examples of helical burrow construction.

Therapsids that construct helical burrows produce whorls whose flattened-elliptical diameter increases and widens downward and terminates in a biconvex chamber (e.g., Smith, 1987), which results in a generally conical shape apex up, base down. Other burrows constructed by therapsids were likely simple, inclined cylinders that terminated in a short, simple chamber of the same diameter or slightly larger than the burrow (e.g., Hasiotis *et al.*, 2007; Krapovickas *et al.*, 2013; Bordy and Krummeck, 2016; Bordy *et al.*, 2017). Still others are interpreted to be more complex with interconnected shafts and tunnels (Colombi *et al.*, 2012).

Reptiles, such as extant monitor lizards (e.g., Doody *et al.*, 2014, 2015), construct shallow to deep helical burrows with a long, inclined, straight entrance with or without a sharp turn within it, leading to an irregular helix, terminating in a small, widened chamber in line with the last whorl. Such

reptiles as the agamid lizards in the Arabian Peninsula (Hasiotis, unpublished data) also construct more complex burrows analogous to those of complex therapsid burrows from Triassic and Jurassic deposits (e.g., Groenewald *et al.*, 2001; Colombi *et al.*, 2012).

Terrestrial scorpions construct helical burrows similar to those of mammals, therapsids, and reptiles but differ significantly in having a strongly flattened cross section and chamber diameters (e.g., Hasiotis and Bourke, 2006; Hembree and Hasiotis, 2006; Adams *et al.*, 2016). Helices are vertical to inclined, weakly to strongly helical, with the entrance tunnel at a higher angle and the chamber at a lower angle than the adjoining whorls.

Decapod crustaceans also construct burrows with a range of helical patterns in different physicochemical conditions that result in unique morphologies. Freshwater crayfish (Decapoda: Cambaridae) burrowing in floodplains, construct vertical cylindrical burrows that are straight and/or very weakly helical about the burrow axis that penetrate the vadose zone and into the phreatic zone (e.g., Hasiotis and Mitchell, 1993; Hasiotis *et al.*, 1993). They can also be weakly and irregularly helical (e.g., Hasiotis and Bourke, 2006; Hembree and Hasiotis, 2006), which is the result most likely of stiffer soil consistency, forcing the crayfish to burrow in a spiral pattern. The thalassinidean shrimp *Axiannassa australis* Rodrigues and Shimizu, in marine intertidal to subtidal bay environments, constructs burrow networks with spiral shafts leading down to horizontal tunnels from which several more spiral shafts continue downward. These burrows are fully enclosed in fully marine salinity water even at low tide (Dworschak and Rordrigues, 1997). These shrimp burrows are considered as modern analogues of *Gyrolithes* (Dworschak and Rordrigues, 1997).

Possible behaviours: *Daimonelix martini* likely represents dens (i.e., nesting and/or habitation) excavated by an individual or a pair of animals based on the size and complexity of burrows. Architecture with limited branching is exhibited in extant and fossil synapsid burrows typically produced for use by only a few individuals (e.g., Martin and Bennett, 1977; Reynolds and Wakkinen, 1987; Smith, 1987; Zimmerman, 1990; Kinlaw, 1999). *Daimonelix martini* was also likely used for shelter from predators and weather. Mammals and other vertebrates that make helical burrows spend most their day within, but come aboveground to forage and to interact with other members of the species (e.g., Reichman and Smith, 1990; Kinlaw, 1999). The similarity between *D. martini* and the helices produced by the Miocene beaver *Palaeocastor* suggests that the tracemaker used *D. martini* in a similar way, that is, was sheltering in the burrow when not foraging aboveground (Martin and Bennett, 1977). *Daimonelix martini* is, therefore, assigned to the behavioural category domichnia.

Ichnogenus *Fractisemita* ichnogen. nov.

Type ichnospecies: *Fractisemita henrii*.

Etymology: Latin, *fractus* – broken, *semita* – path.

Diagnosis: Unlined, sparse maze of Y-branched tunnels and shafts of varying diameter, angle from the horizontal, and length, with no distinguishable chambers.

Fractisemita henrii ichnosp. nov.

Figs 9–12

Etymology: Named for the Henry Mountains area in which the fossils were discovered.

Type: Holotype is represented by Fig. 9E and may be viewed in the field. Paratypes are represented by Figure 9A–D, and Figures 10–11.

Material: 6 specimens in outcrop at locality 1; 3 specimens in outcrop at locality 2.

Diagnosis: As for ichnogenus.

Description: *Fractisemita henrii* is found in full-relief casts *in situ* and in float. Burrows are unlined with no internal structures and composed of an interconnected network of cylindrical shafts and tunnels oriented at various angles to form a maze pattern. Individual elements are straight, curved, or helical. Mean length of a section is 29.97 cm; range ~10.00–93.27 cm. Cross sections are oval with mean vertical diameter of 4.87 cm (range 2.84–14.04 cm) and mean horizontal diameter of 6.33 cm (range 4.47–8.66 cm), with a width-to-height ratio of 1.30:1. Segments have a mean angle of inclination of 31° from the horizontal (ranging from 0° to 89°). Preservation is diverse, with two specimens having segments fused together to the extent that the individual segments are not clearly discernible.

The surficial morphology exhibits two ridge textures and two knob textures (Fig. 12). The first ridge texture is formed by short, thin ridges that join together at odd angle to create a jagged appearance. In one instance there are short, thin ridges < 1 cm long and < 1 cm high that join together at odd angles to create a jagged, serrate appearance. This texture is most common on the ceiling of burrows. The second, larger ridge texture is a set of straight, parallel ridges 1.4 cm long within the jagged texture. Concentrated on the sides and bottom is a small knobby texture, with knobs up to 2 cm long and < 1 cm high; their arrangement is apparently random. A second knobby texture seen on a single specimen is a series of vertically oriented knobs of roughly equal shape. They are < 1 cm tall, ~2 cm long, and ~1 cm wide.

Occurrence: Upper Jurassic Morrison Formation, Salt Wash Member; locality 1, in the middle and lowest palaeosols (coordinates 37°46'N, 110°42'W), locality 2, in the highest palaeosol (coordinates 38°17'N, 111°7'W). More detailed coordinates and meter levels are available upon request to protect the locality.

Remarks: Most examples of *Fractisemita henrii* in outcrop are distorted by vertic pedoturbation of the mudstone matrix, as well as overprinting by pedogenic carbonate and subsequent karstification of the carbonate fills. Despite this preservation, *F. henrii* has an architectural morphology – an interconnected network of cylindrical straight, curved, or helical shafts and tunnels oriented at various angles – that is unique to burrows described from Mesozoic terrestrial continental deposits, but bears some similarity to other complex burrows interpreted as tetrapod in origin (e.g., Groenewald *et al.*, 2001; Hasiotis *et al.*, 2004; Riese *et al.*, 2011; Voigt *et al.*, 2011; Krapovickas *et al.*, 2013). The tunnel segments in *F. henrii* are weakly sinuous, shafts are inclined with very few weakly helical, and no chambers with larger dimensions than tunnels or shafts are ob-

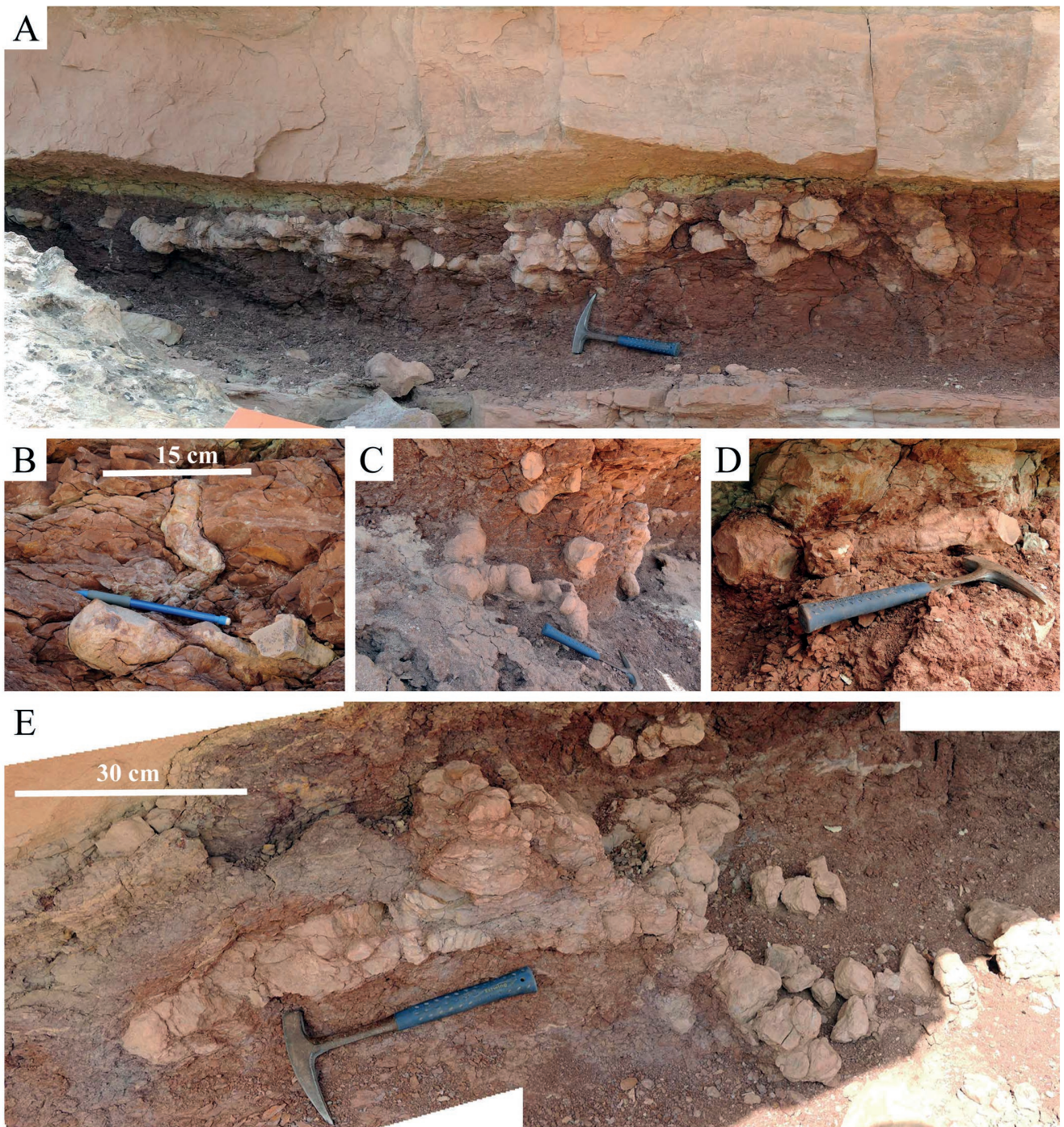


Fig. 9. Variations in morphology of *Fractisemita henrii* with distinct segments at locality 1 near Ticaboo, Utah. Paratypes A–D; Holotype E. **A.** View of tunnel networks of *F. henrii* distorted by vertic soil processes. **B.** Vertic soil processes thin and juxtapose tunnel segments. **C.** Horizontal, helical tunnel segment extending from another tunnel segment. **D.** Horizontal tunnel segment isolated by vertical processes. **E.** Plan view of horizontal, Y-shaped interconnecting tunnels that partly forms the network pattern. Hammer is 32 cm long.

served. The surficial morphology of short ridges and parallel ridges on the roof of the burrow were likely produced by the tracemaker. Both of these morphologies are more prevalent in better-preserved trace fossils and modern burrows (e.g., Martin and Bennett, 1977; Burns *et al.*, 1989; Gobetz and Martin, 2006). The repeating, parallel knob texture is similar to that of the scalloped walls preserved in other fossil burrows attributed to Mesozoic therapsids and Cenozoic mammals (e.g., Gobetz and Martin, 2006; Riese

et al., 2011) and is interpreted as the scratches produced by the manus and/or pes during excavation and maintenance of the burrow. Very similar features are seen in modern mole burrows, which Gobetz (2005) described as due to lateral-thrust digging. This may potentially be inferred in *F. henrii* as well.

Fractisemita henrii is distinguished from *Alezichnos trogodont* (Gobetz and Martin, 2006), *A. chelecharatos* (Gobetz, 2006), and complex burrow systems described

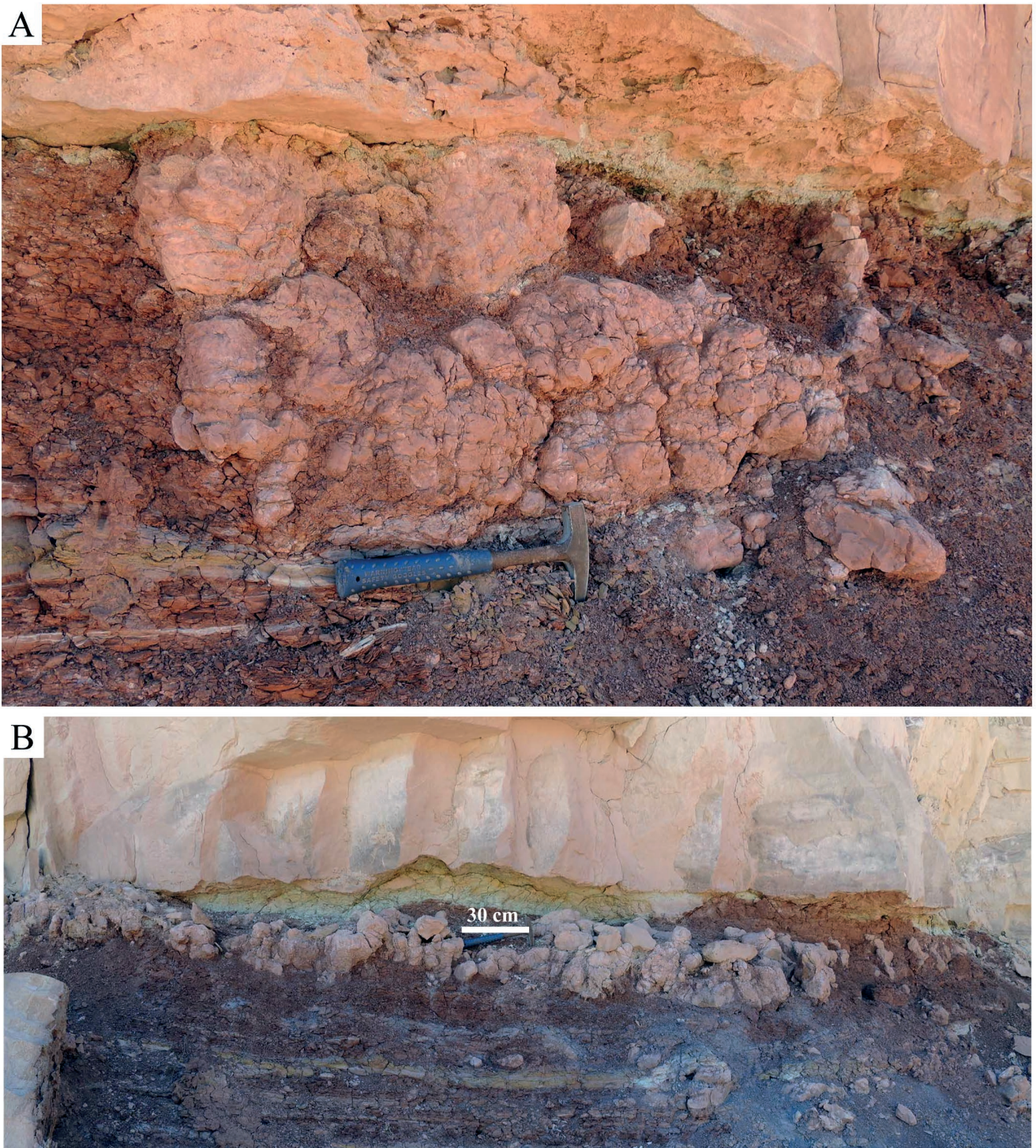


Fig. 10. Variations in morphology of the paratypes of *Fractisemita henrii* with overprinted with pedogenic carbonate to give appearance of merged segments at locality 1 near Ticaboo, Utah, all of which are distorted by vertic soil processes. **A.** Overprinted vertical shaft with network of interconnected short tunnels and shafts. **B.** Larger outcrop example of overprinted, merged shaft and tunnel networks. Hammer is 32 cm long.

from Triassic and Jurassic continental deposits from North America (Hasiotis *et al.*, 2004; Riese *et al.*, 2011), South America (Colombi *et al.*, 2007), and Africa (Groenewald *et al.*, 2001) based on the relationship between the interconnectedness of burrow elements, scratch patterns, presence of main tunnel, angles of descent, and presence and morphology of chambers.

Alezichnos trogodont has multiple branches of sinuous tunnels with varied direction and orientation, some of which are weakly helical, and with multiple chambers, some of which are bilobate. Burrow cross sections range from being wider horizontally to wider vertically within a single specimen. Burrow surfaces preserve incisor and claw traces produced during excavation that tend to parallel the long axis

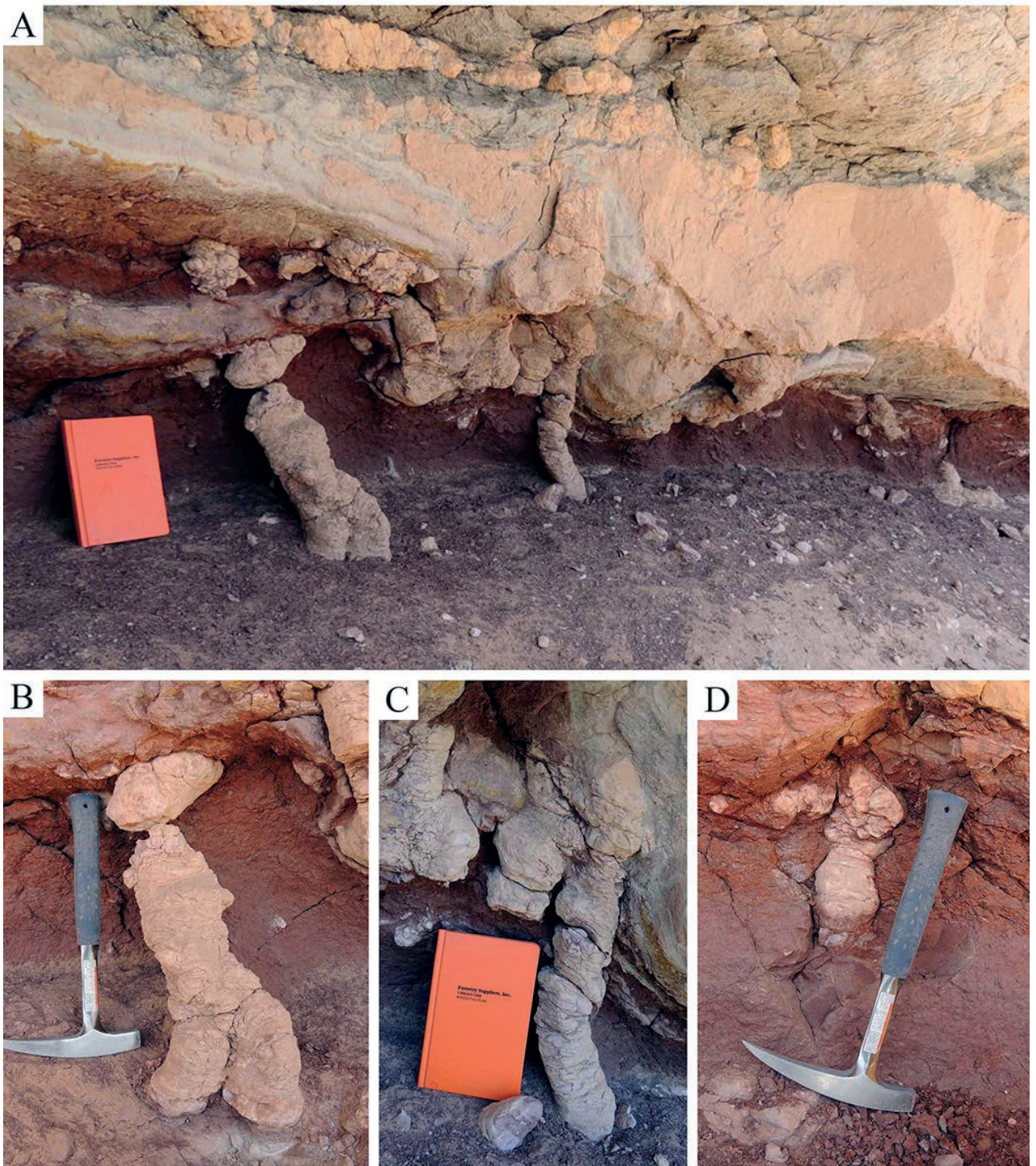


Fig. 11. Vertical shafts leading to network tunnel system of the paratypes of *Fractisemita henrii* at locality 2 near Fruita, Utah. **A.** Example of density in outcrop. **B.** Vertical shaft bifurcates downward into two slightly narrower shafts. **C.** Slightly inclined vertical shaft. **D.** Weakly helical shaft. Hammer is 32 cm long. Notebook is 19 cm long.

of the burrow. The 5.4-mm-wide incisor traces are dominant on the roof and sides of the burrows. The claw traces – 3.9 mm wide with up to 6 mm between grooves – are dominant on the floor, some low sides, and turns of the tunnels, as well as in small chambers.

Alezichnos chelecharatos consists of a sinuous main tunnel, oval in cross section and 11–18 cm in diameter, and up to 7 m long with occasional branching of secondary tunnels.

The surface contains sets of two to three parallel ridges, each 3.7 mm wide and up to 9.3 mm high interpreted as claw traces produced during excavation.

Tetrapod burrows in the Owl Rock Member, Upper Triassic Chinle Formation (southeast Utah, USA) consist of a network of horizontal tunnels, vertical and helical shafts, and chambers, with burrow diameters of 4–15 cm with a circular to subcircular cross section. Some tunnels, 10–35 cm

long with smaller cross sections, connect with longer and wider tunnel segments. Chambers are two to three times wider than the tunnels or shafts (Hasiotis *et al.*, 2004).

Three morphotypes of tetrapod burrows from the Upper Triassic Ischigualasto and Los Colorados formations of north-west Argentina (Colombi *et al.*, 2012) exhibit variably complex architecture. Morphotype 1 has several cham-

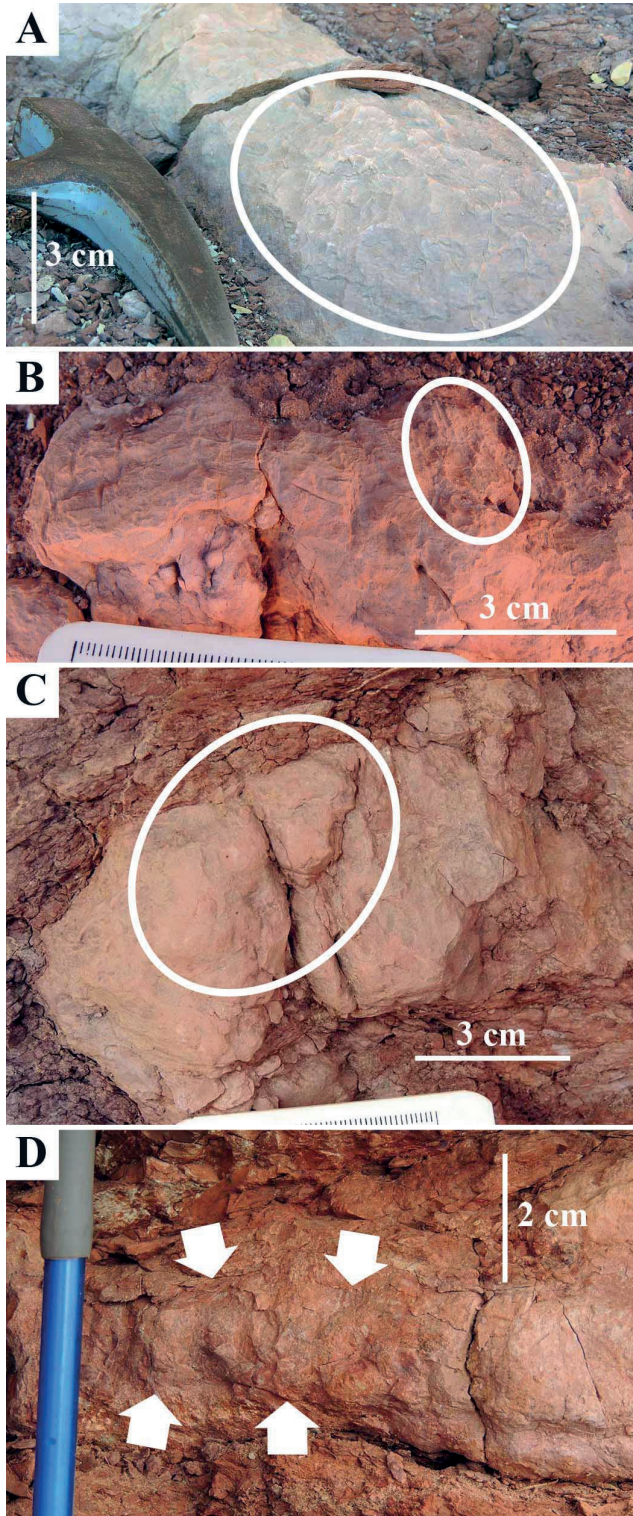


Fig. 12. Surfacial morphologies of *Fractisemita henrii*. **A.** Small ridges. **B.** Parallel ridges with small ridges. **C.** Small knobs. **D.** Parallel knobs. Note that preservation of features is distorted by microkarstification.

bers as part of the network and medial groove in some of the tunnels. Morphotype 2 has a high density of large-diameter shafts and tunnels that exhibit great lengths and appear to crosscut one another. Morphotype 3 exhibits greater variability in size and cross-section shape than morphotypes 1 and 2 for similar burrow segment lengths.

Tetrapod burrows in the Lower Jurassic Navajo Sandstone, south-east Utah, USA (Riese *et al.*, 2011), are composed of a network of chambers and sinuous ramps and tunnels joined at intersections that form Y and T branches. Burrow cross section is reniform with a mean width of 9.3 cm and a mean height of 4.2 cm (ratio of 2.21). Ramps dip 6–60°. Burrow surfaces are mostly smooth; few exhibit scalloped walls, with scallops 5–7 cm wide and rise 0.5–1.5 cm above the burrow surface.

Tetrapod burrows in the Lower Triassic Driekoppen Formation of northeastern Free State, South Africa (Groenewald *et al.*, 2001), are a network of branching tunnels, chambers, and funnel-shaped entrance shafts. Tunnel and chambers dip 1–23°. Burrow cross section is reniform or W shaped with a bilobate floor and arched roof; the burrow floor flattens out as tunnels move away from an entrance towards the chambers; tunnel diameter is 5–12 cm. Burrow surfaces contain diagonal and transverse scratches on the base and sides that converge towards the centre of the burrow and become more distinct away from the entrance.

Possible tracemakers: The networks preserved as *Fractisemita henrii* are interpreted as burrow systems produced by mammals in which vertical to inclined shafts (Fig. 11) lead to a maze pattern of tunnels and shafts (Figs 10–11). Therapsids from the Permian to the Jurassic and mammals from the Triassic to the recent construct such complex networks (e.g., Mankin and Getz, 1994; Groenewald *et al.*, 2001; Gobetz and Martin, 2006; Riese *et al.*, 2011; Joeckel and Tucker, 2013). *Fractisemita henrii* is best compared to the extant mammal burrows from such small rodents as ground squirrels or kangaroo rats (e.g., Ognev, 1947; Anderson and Allred, 1964; Reichman and Smith 1990; Joeckel and Tucker, 2013). For example, burrow networks illustrated in Joeckel and Tucker (2013) show the range of interconnectedness between weakly to strongly vertical elements of short and long extent with those more horizontal of short and long segments. Examples of modern mammal burrow networks also illustrated in Riese *et al.* (2011) demonstrate a similar range in tunnel and shaft associations. The oval or elliptical cross section of *F. henrii* shafts and tunnels, with a horizontal diameter slightly wider than the vertical diameter, also matches best with mammal burrows (e.g., Martin and Bennett, 1977; Bown and Kraus, 1983; Laundré, 1989).

Comparisons of *Fractisemita henrii* to other vertebrate and invertebrate burrows have not yielded similar morphologic features to indicate construction by other tracemakers. Freshwater crayfish construct much simpler vertical burrows and burrow systems, which extend to the depth of the water table and would not accumulate carbonate fill (e.g., Hobbs, 1981; Hasiotis and Mitchell, 1993; Hasiotis *et al.*, 1993). Such terrestrial arthropod burrows as those produced by scorpions (e.g., Hembree and Hasiotis, 2006; Adams *et al.*, 2016) do not generate comparable variability

and complexity in size-interconnectedness-depth relationships. Amphisbaenid reptiles, which are completely subterranean, construct elaborately complex burrow systems with mostly smooth walls that contain triangular markings of variable abundance (Hembree and Hasiotis, 2006). The ratio of tunnel diameters in relationship to the size of the burrow network, as well as the size of the organism, would be too small to produce *F. henrii*. Burrows produced by skinks (Reptilia: Scincidae) exhibit strongly inclined tunnels that are highly flattened and have a medial ridge (Hembree and Hasiotis, 2006). The main tunnel exhibits branches of similar diameter with sharp angle changes that form a crude helix, similar to switchback curves on steep roads, rather than true helices. Other reptiles, such as the agamid lizards in the Arabian Peninsula, construct interconnected a simpler burrow network compared to *F. henrii*, but burrow elements are extremely flattened and have a medial ridge, longitudinal scratches along the walls, and chevron-shaped scratches that converge toward the ridge (Hasiotis, unpublished data).

The majority of mammals known from the Morrison Formation are small, with an average mass of 48.5 g (Kielan-Jaworowska *et al.*, 2004; Foster, 2009). This leaves many potential tracemakers based on size. *Fruitafossor windscheffeli* Luo and Wible is the smallest mammal in the Morrison, and a likely tracemaker with many adaptations for scratch digging (Luo and Wible, 2005; Foster, 2009).

Possible behaviours: *Fractisemita henrii* is likely the work of multiple individuals of a social group. Such burrow systems require a great deal of work to construct (e.g., Vleck, 1981; Reichman and Smith, 1990). Upkeep is constant as the burrow systems are modified on a continuous or seasonal basis (e.g., Lovegrove and Jarvis, 1986; Sumbera *et al.*, 2003; Knight, 2009). Burrow networks are used for multiple purposes: protection from both predators and weather (e.g., Kenagy, 1973; Kay and Whitford, 1978; Reichman and Smith, 1990); food storage (e.g., Smith and Reichman, 1984; Skinner, 2005); foraging tunnels closer to the surface to feed on plant roots and soil biota (e.g., Duncan and Wrangham, 1971; Lovegrove and Jarvis, 1986); denning (e.g., Hall and Meyers, 1978; Hickman, 1983); and waste (Reichman and Smith, 1990). Some of these uses are inferred for fossil burrows as well (e.g., Meyer, 1999; Hasiotis *et al.*, 2004, 2007; Riese *et al.*, 2011; Krapovickas *et al.*, 2013). Burrow networks produced by extant mammals vary greatly in size based on the size of the excavators and the degree to which they live underground. The largest burrow systems are made by species that spend most of their lives underground, such as moles (Talpidae) and mole rats (Bathyergidae) (e.g., Hickman, 1983; Davies and Jarvis, 1986; Reichman and Smith, 1990). Mole rat burrows have segments tens of meters long and whole systems that can reach over 1 km (Šumbera *et al.*, 2011; Lövy, 2015). *Fractisemita henrii* does not reach this size. The excavators evidently spent their lives underground and likely came aboveground only to forage and interact with conspecifics. *Fractisemita henrii* is categorized as polychresichnia (Hasiotis, 2003).

PALAEOECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

These burrows are useful in creating a more complete picture of the Morrison ecosystem during Salt Wash Member deposition given the paucity of mammalian and other small vertebrate body fossils from southeast Utah. By analogy to known tracemakers, the excavators of both *Daimonelix martini* and *Fractisemita henrii* are thought to be herbivorous or omnivorous. Complex burrows have not been attributed to carnivores in the rock record, although they have been identified in extant terrestrial settings and constructed by lizards (e.g., Doody *et al.*, 2014, 2015). There is, though, the strong likelihood that predators, also yet unknown, were adapted to entering the burrows and preying on the excavators. There is the ancient predator-prey example of *Zodiolestes* and *Palaeocastor* or the modern pair of prairie dogs (*Cynomys ludovicianus* Elliot) and ferrets (*Mustela nigripes* Audubon and Bachman) (Riggs, 1945; King, 1955). The Morrison Formation predators may have included other synapsids or reptiles. If tracemakers were omnivorous, there would be a community of invertebrates and smaller vertebrates to consume. Both groups only have limited representation as body fossils, but invertebrates left a robust trace fossil record in the Morrison (e.g., Hasiotis, 2004, 2008; Foster, 2007). For example, Platt (2014) identified possible foraging pits of large vertebrates in palaeosols associated with the *Daimonelix martini* and *Fractisemita henrii* at locality 1. These pits were likely excavated by insectivores based on analogy with modern armadillo foraging pits.

Though there is no direct body fossil or trace-fossil evidence in the Salt Wash Member, neutral burrow occupants may have shared the burrow spaces with the excavators of *Daimonelix martini* and *Fractisemita henrii*, or entered them after the excavators had left. Commensalism may have been normal behaviour, such as the amphibian (*Broomistega*) found in a burrow with an estivating therapsid (*Thrinaxodon*) (Fernandez *et al.*, 2013), or similar to today, for example, with the burrowing owl (*Athene cunicularia* Molina) making use of different rodent dens across the Americas (Haug *et al.*, 1993).

The tracemakers of *Daimonelix martini* and *Fractisemita henrii* would have required a diverse plant community near the burrows able to sustain the different feeding habits in a time before flowering plants. Ground cover at the time of the Morrison Formation included ferns, ginkgophytes, cycads, tree ferns, horsetails, and tree litter (e.g., Ash and Tidwell, 1998; Chin and Kirkland, 1998; Turner and Peterson, 2004), their presence recorded by wood and rhizoliths preserved in the study area. Softer plants could provide nourishment to tracemakers with above- and belowground growth. If omnivorous, the tracemakers would have also fed on a large variety of invertebrates – annelids, insects, crustaceans, and other arthropods (e.g., Hasiotis, 2004, 2008) – that are represented by trace fossils in the lower part of the Morrison Formation (i.e., Tidwell and Salt Wash members) in the study areas.

The large burrows produced by tetrapods would have also influenced the development of Morrison soils and the growth of plants. Macropores and macrochannels created

by these burrows, in association with smaller invertebrate bioturbation, probably helped to aerate the soil, translocate sediment and nutrients, and increase water infiltration (e.g., Jones *et al.*, 1994; Pankhurst *et al.*, 2002; Halfen and Hasiotis, 2010a, b; Platt *et al.*, 2016). All of this activity would have encouraged expansion of plant root systems, as they are known to preferentially follow already opened and filled paths through the soil, which can improve nutrient uptake in burrows (e.g., Pankhurst *et al.*, 2002; Kautz *et al.*, 2014; Kautz, 2015). If the tracemakers were caching seeds in their burrows, the uneaten seeds may have helped continue the plant community by germinating in the subterranean environment (e.g., Vander Wall, 1990; Butler, 1995). A healthy, robust plant community would help keep the environment stable. For example, the lithofacies in the study area shows that the local fluvial channels migrated laterally (e.g., Kjemperud *et al.*, 2008), and thus possibly eroding the landscape and flooding low-lying areas. The vegetation cover and production of deeper, well-established root network had the potential to stabilize river banks and landscape, as well as to slow and even control the rate of lateral channel migration (e.g., Shankman, 1993; Gurnell, 2014; Allen *et al.*, 2018).

The helical burrow architecture and burrow maze network, as represented in the Morrison Formation by *Daimonelix martini* and *Fractisemita henrii*, respectively, appear as products of convergent and ecophenotypic evolution in cynodonts and mammals, as well as in several reptile groups, multiple times over ~260 Myr, based on the recurrence of these types of burrow architectures since the Middle Permian (e.g., Martin and Bennett, 1977; Smith, 1987; Meyer, 1999; Hasiotis *et al.*, 2004, 2007; Hembree and Hasiotis, 2008; Colombi *et al.*, 2012; Weber *et al.*, 2013; Doody *et al.*, 2015). These common architectures can, thus, have implications for when mammalian behaviours evolved and persisted in the synapsid lineage. Some burrowing behaviours appear to be genetic (Weber *et al.*, 2013) and could be passed through a lineage over time if the burrowing behaviour confers reproductive success. Architectural similarities may also be the result of a common solution to recurring environmental problems. Convergent burrow morphologies dictated by environmental conditions may explain the recurrence of helical architecture for animals burrowing in the vadose zone of terrestrial settings, such that similar or analogous morphologies also occur in the burrows of some scorpions, crustaceans, and reptiles (e.g., Hasiotis and Bourke, 2006; Hembree and Hasiotis, 2006; Doody *et al.*, 2015; Adams *et al.*, 2016). For helical burrow architecture, Meyer (1999) calculated that this design is well suited for maintaining a constant temperate environment when the weather outside the burrow becomes too hot or cold (e.g., Kenagy, 1973; Bennett *et al.*, 1988). Burrow networks (i.e., mazes) offer a similar environmental constancy and multiple entrances and exits increases chances to escape predators.

Burrow networks typically have a stifling atmosphere with high levels of carbon dioxide and low levels of oxygen that excavators must be physiologically able to tolerate (e.g., Lovegrove, 1989; Reichman and Smith, 1990). The helical and maze network burrow types found in the Morrison Formation indicate that the tracemakers were adapted for fossoriality through skeletal (which may be discovered in

future studies) and physiological (unpreserved soft tissues) modifications. This shows a convergence in form across synapsid groups through time.

CONCLUSIONS

The new ichnospecies *Daimonelix martini* from the Salt Wash Member in the Morrison Formation represents vertebrate burrows in a distal floodplain environment. They are composed of a helical shaft and horizontal tunnel, both with an ovoid cross section. The burrows are interpreted as the permanent dwellings of an unknown primitive mammal that used them to shelter from the elements and predators, and raise their young. *Daimonelix martini* is assigned to the behavioural category domichnia. The new ichnogenus and ichnospecies *Fractisemita henrii* represents the burrows of a potentially social, primitive mammal. The burrows are composed of networks of tunnels and shafts in a maze network. *Fractisemita henrii* is assigned to polychresichnia as the burrows record multiple behaviours. As no body fossils of the tracemakers are preserved, both new ichnospecies represent hidden biodiversity in the Salt Wash Member landscape. This extends beyond the tracemakers to their potential predators and prey, and the plant community of the floodplain environment. The burrows also fill in some mammalian fossorial behaviour for the Late Jurassic illustrating how synapsid excavators continue to converge on helical and network architecture from the Permian to the present.

Acknowledgements

Thanks to R. William Turer and Matt F. Jones for assistance in the field. Thanks to AAPG and the KU Geology for funding awarded to DCWR. Thanks to Brian F. Platt, an anonymous reviewer, Andrew K. Rindsberg, and guest editor Emese M. Bordy for comments and suggestions, which improved the manuscript.

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Daimonelix martini architectural morphologies

Locality 1

Structure ID	Shaft depth	Length of shaft	Incline of shaft (degrees from horizontal)	Incline of whorls (degrees from horizontal)	Turn-around diameter	Shaft, vertical diameter	Shaft, horizontal diameter	Tunnel length	Tunnel, vertical diameter	Tunnel, horizontal diameter
	(cm)									
3a	76.20	94.49	none	–	–	–	–	–	–	–
5a	66.04	–	none	–	–	–	–	–	–	–
7a	109.73	–	none	50	–	7.40	–	–	–	–
8a	–	115.82	none	–	–	–	–	67.06	–	4.85
9a	67.06	124.97	none	–	–	–	–	42.67	10.40	–
10a	67.06	–	none	–	36.03	–	–	–	–	–
12a	64.01	–	none	–	–	–	–	27.00	–	11.40
16a	59.44	–	none	–	–	–	–	–	–	–
1b	62.99	–	none	–	–	–	–	–	15.33	20.17
4b	73.15	–	none	–	–	–	–	–	8.60	–
6b	33.71	–	none	37	–	5.90	–	–	–	–
7b	45.18	–	none	–	–	8.10	–	–	–	–
8b	49.00	–	46	–	17.90	7.50	–	–	–	–
9b	52.71	–	none	–	–	7.40	–	–	–	–
10b	40.84	–	none	–	–	–	–	–	–	–
16b	68.28	75.30	50	26	–	9.42	9.27	–	–	–
17b	62.18	–	none	–	–	–	–	–	–	–
18b	–	–	none	44	–	10.02	–	–	–	–
19b	–	–	none	33	–	10.10	–	–	–	–
21b	57.30	123.15	none	–	–	5.35	6.45	–	–	–
23b	–	–	45	–	–	5.78	7.20	–	–	–
1c	45.11	–	none	–	–	–	–	–	–	–
2c	–	–	35	–	–	3.00	4.60	–	–	–
3c	57.00	–	none	–	–	–	–	–	–	–
5c	–	–	51	30	–	7.55	7.65	–	–	–
6c	48.16	–	none	–	–	7.28	–	24.08	5.90	–
7c	43.89	–	none	–	–	–	–	–	–	–
8c	–	–	none	–	–	–	–	45.72	7.00	14.70
10c	–	–	none	–	–	7.80	–	–	–	–
12c	34.75	–	none	–	–	–	–	–	–	–
15c	70.10	–	none	–	–	–	–	32.00	–	10.50
17c	66.25	–	54	–	–	–	–	–	–	–
19c	62.48	–	none	–	–	–	–	32.00	–	–
20c	–	–	none	–	–	6.20	8.00	–	–	–
21c	112.78	–	56	36	22.86	10.90	14.00	86.56	6.00	7.50
23c	87.78	–	none	–	–	–	–	–	–	–
24c	85.65	–	none	27	–	8.20	11.20	–	8.00	8.15
17d	–	–	none	–	21.34	–	–	–	–	–
18d	–	–	none	–	–	3.14	2.25	–	–	–

Structure ID	Shaft depth	Length of shaft	Incline of shaft (degrees from horizontal)	Incline of whorls (degrees from horizontal)	Turn-around diameter	Shaft, vertical diameter	Shaft, horizontal diameter	Tunnel length	Tunnel, vertical diameter	Tunnel, horizontal diameter
	(cm)									
20d	–	–	none	–	–	–	–	49.70	7.81	9.06
21d	65.23	–	none	–	–	–	–	62.48	–	–
24d	72.54	89.00	none	67	–	–	–	33.53	–	–
26d	63.40	–	none	–	–	–	–	–	–	–
2e	57.00	72.85	none	–	–	–	11.06	–	–	–
3e	56.69	–	none	–	–	–	–	–	–	–
5e	–	–	none	–	–	7.96	–	–	–	–
6e	76.81	–	none	–	–	–	–	–	–	–
7+8e	73.76	–	none	–	–	–	–	–	–	–
9e	93.88	–	none	–	–	–	–	–	–	–
15e	68.88	–	none	–	–	–	–	33.22	6.96	8.16
21e	38.40	–	none	28	–	–	–	–	–	–
25e	53.04	75.59	none	35	–	–	–	–	–	–
28e	53.04	–	none	–	–	–	–	–	–	–
32e	95.02	112.78	37	29	–	–	–	–	–	–
6f	36.88	–	none	45	30.48	–	10.50	–	–	–
7f	77.42	–	none	39	–	–	–	38.71	8.58	–
14f	–	–	none	–	–	–	–	26.21	4.27	6.20
18f	84.12	110.95	57	45	–	–	–	–	–	–
19f	82.91	–	none	–	–	–	–	–	–	–
20f	63.70	–	none	–	–	4.86	6.32	–	–	–
21f	–	–	none	–	–	–	–	39.01	–	17.37
4i	48.16	–	none	–	–	–	–	–	–	–
5i	71.63	–	none	–	–	–	–	–	–	–

Locality 2

2a	119.38	–	none	–	15.20	3.20	8.70	–	–	–
2b	106.68	–	none	–	–	–	–	–	–	–
2c	102.87	–	none	–	–	–	–	–	–	–
2d	155.58	–	none	–	–	–	–	–	–	–
2e	134.62	–	none	52	–	–	12.47	–	–	–
2f	120.02	143.51	50	49	–	9.40	10.84	–	–	–
2g	74.93	–	none	–	–	–	13.50	40.01	20.32	–
2h	83.82	–	none	–	–	8.54	9.27	33.02	14.04	–
2i	116.84	–	none	–	–	8.22	8.65	–	–	–
2j	63.50	–	none	–	–	–	9.26	–	–	–
2k	116.84	–	none	33	–	–	10.04	48.26	26.67	–
2l	60.33	–	none	–	–	10.28	12.11	–	–	–
2n	43.18	54.61	none	–	–	–	–	–	–	–

Overall mean	72.13	99.42	48.10	39.17	23.97	7.34	9.21	42.29	10.71	10.73
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Fractussemita henrii architectural morphologies

distinct segments

Locality 1

Structure ID	Segment	Length	Width	Height	Incline of Segment (degrees from horizontal)	Path (straight, curved, helical)
		(cm)				
16d	i	13.03	–	2.84	85	helical
	ii	25.06	8.06	3.90	0	curved
14f	i	<1.00	4.47	3.98	–	straight
	ii	<1.00	8.66	5.31	–	straight
	iii	47.13	6.15	5.13	0	curved
1g	i	93.27	6.26	4.10	23	helical
	ii	17.65	5.52	5.45	25	curved
	iii	<1.00	5.74	6.52	–	straight
3i	i	73.91	–	6.65	0	straight
	ii	14.39	–	14.04*	89	straight
	iii	21.31	5.22	–	43	straight
	iv	30.52	4.92	4.80	38	straight
	v	13.47	7.38	–	31	straight
	vi	5.01	6.24	–	14	straight
	vii	4.92	7.34	–	21	straight

Locality 2

2I	i	49.53	6.73	–	80	curved
2II	i	–	7.47	–	–	straight
2III	i	20.32	7.08	–	89	curved

Mean		30.68	6.48	4.87	38	
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Merged segments

Structure ID	Length along outcrop	Depth
	(cm)	
1i	280.50	–
2i	134.72	46.33