TWO NOVEL ICHNOSPECIES:
LARGE-DIAMETER VERTEBRATE BURROWS IN THE UPPER JURASSIC MORRISON FORMATION, SOUTHEASTERN UTAH

BY

Derek Charles William Raisanen

Submitted to the graduate degree program in the Department of Geology and the Graduate
Faculty of the University of Kansas in partial fulfillment of the requirements
for the degree of Master of Science.

Stephen T. Hasiotis, Chairperson

K. Christopher Beard

Jennifer A. Roberts

Date Defended: July 11, 2018

The Thesis Committee for Derek C.W. Raisanen
certifies that this is the approved version of the following thesis:

TWO NOVEL ICHNOSPECIES:
LARGE-DIAMETER VERTEBRATE BURROWS IN THE UPPER JURASSIC
MORRISON FORMATION, SOUTHEASTERN UTAH

____
Stephen T. Hasiotis, Chairperson

Date approved: July 11, 2018

ABSTRACT

Derek C.W. Raisanen
Department of Geology, 11 July 2018
University of Kansas

Large-diameter structures in pedogenically modified floodplain deposits in the Salt Wash Member, Upper Jurassic Morrison Formation, in southeastern Utah, are interpreted as vertebrate burrows. Two morphotypes were identified. Morphotype 1 exhibits a vertical to subvertical helical shaft leading to a subhorizontal tunnel. This morphotype is named *Daemonelix martini* (n. isp.). The helical shaft has a mean depth of 71.4 cm from the interpreted paleosurface. The mean path length of the shaft is 99.4 cm; mean dip of the whorls in the helices is 39°. The mean tunnel length is 42.3 cm. Shafts and tunnels are ovoid in cross section with the horizontal diameter slightly larger than the vertical; shaft averages 9.2 cm wide and 7.3 cm tall, tunnel averages 10.7 cm wide and 10.7 cm tall. The tracemaker was likely a fossorial mammal that used the burrows as a shelter when not foraging above ground; burrows are assigned to domichnia. Morphotype 2 structures are networks of interconnected shafts and tunnels. This morphotype is named *Fractussemita henrii* (n. igen. and n. isp.). Shaft and tunnel segments are straight, curved, or helical. The segments are at different angles 0–89º; mean length of a section is 30.7 cm. The cross sections of all elements are ovoid; mean width is 6.3 cm and the mean height is 4.9 cm. The burrows are interpreted as the work of a social mammal and represent multiple tracemaker behaviors—protection, denning, foraging. Burrows are assigned to polychresichnia. Both morphotypes have ridges and knobs preserved on burrow walls. Some surficial morphology is interpreted as scratch marks from the claws and/or teeth of the tracemakers. All burrow types are found in pedogenically-modified mudstone overlain by sandstone channel deposits. The environment of deposition is interpreted as river channel and floodplain. Primitive mammals are the most likely tracemakers for both morphotypes based on comparison to the architectural and surficial morphologies of fossil and extant vertebrate burrows and other structures. The burrows reveal the actions of small vertebrates not recorded by body fossils revealing evidence for denning and parental care in Jurassic age mammals. The burrows can also be used to help study local soil development and paleohydrologic conditions in the Salt Wash Member by showing stability of the floodplain and depth of the vadose zone.

ACKNOWLEDGMENTS

I thank everyone who made the completion of this thesis possible. First my wife Keris for getting me back to school and kicking by butt to work when required. My son and daughter for being a distraction at all the right times. My parents, Susan and Chuck, and sister Jessica for supporting my love of science. My advisor Steve Hasiotis for all the advising. Everyone in IBGS, especially Adam Jackson, Matt Jones, Andy Connolly, James Golab, Amanda Falk, Sarah Wildermuth, Josh Schmerge, and Brian Platt. Everyone at Capitol Reef National Park, especially Cindy Michelli, Lori Rome, Dave Worthington, Dava McGahee, Laura Beck, Laura Sechrist, Jason Kudulis, Kelly Karl, and Caitlin Olejniczak. Will Turner and Matt Jones for assistance in the field. Jennifer Roberts, Chris Beard, and Larry Martin for being on my committee. The other KU students that kept me going Molly Long, Brian Gibson, Angela Eichler, Wes Gapp, Cori Myers, James Lamsdell, and the undergrads I got to teach.

TABLE OF CONTENTS

PAGE LEFT BLANK INTENTIONALLY

CHAPTER ONE. INTRODUCTION

This thesis presents evidence for large-diameter structures (LS) in the Salt Wash Member of the Upper Jurassic Morrison Formation interpreted as mammal burrows. This thesis will: (1) interpret the origin of the LS using morphologic criteria and comparative morphology to falsify as many hypothesized tracemakers as possible; (2) place the LS in a paleoenvironmental and paleohydrological context; and (3) name the structures using systematic ichnotaxonomy.

This thesis is divided into two manuscripts. The first manuscript (Chapter 2) describes the architectural and surficial morphologies of the structures and how they allow for their interpretation as mammal burrows. The second manuscript (Chapter 3) describes the structures, interpreted as burrows, and places them into new ichnotaxa using the International Commission for Zoological Nomenclature, making comparisons to similar trace fossils. Both manuscripts address potential behavioral and paleoenvironmental significance of the burrows.

The Morrison Formation has yielded an abundance of body and trace fossils since the late 1800s, from giant sauropods to small invertebrates (e.g., Ostrom and McIntosh, 1966; Turner and Peterson, 1992; Gates, 2005; Foster, 2009). The mammal assemblage of the Morrison Formation is the most diverse in the world for the Late Jurassic but is geographically limited with the majority of species coming from Como Bluff, Wyoming (e.g., Prothero, 1981; Kielan-Jaworowska et al., 2004; Carrano and Velez-Juarbe, 2006). The Morrison Formation has a variety of trace fossils, with those made by invertebrates most abundant (e.g., Hasiotis and Demko, 1996; Good, 2004; Hasiotis, 2004, 2008; Britt et al., 2008). Known trace fossils from the Salt Wash Member include rhizoliths, dinosaur tracks, and numerous types invertebrate nests and burrows (e.g., Lockley et al., 1992; Robinson and McCabe, 1998; Hasiotis 2004, 2008). Plant macrofossils from the Morrison Formation are limited with a noticeable paucity of wood and mostly record herbaceous vegetation (Parrish et al., 2004; Turner and Peterson, 2004; Foster, 2009). Conifers dominate palynomorph specimens (Hotton and Baghai-Riding, 2010).

Extant vertebrate burrows occur worldwide, except in mainland Antarctica, in most continental environments (e.g., Reichman and Smith, 1990; Abba et al., 2005; Knight, 2009; le Roux et al., 2011). All major vertebrate groups have species that produce burrows (e.g., Greenwood, 1986; Reichman and Smith, 1990; Bancroft et al., 2005; Tracy et al., 2007; McAlpin et al., 2011). Fossilized vertebrate burrows are most often found in floodplain, lacustrine, or palustrine deposits (e.g., Smith, 1987; Hasiotis, 2004; Voigt et al., 2011), and less often in eolian settings (e.g., Loope et al., 1998; Riese et al., 2011). Fossil burrows occur on all continents (e.g., Martin and Bennett, 1977; Krapovickas et al., 2012; Talanda et al., 2011; Liu and Li, 2013; Voigt et al., 2011; Martin, 2009; Hasiotis et al., 2004) and are dated from the Devonian (Hasiotis, 2002; Friedman and Daeschler, 2006) to the present. Vertebrate burrows are far less common than invertebrate burrows in continental deposits (e.g., Voorhies, 1975a; Hasiotis et al., 2007). The burrow tracemaker may be identified by the occurrence of body fossils inside the burrow with features that match excavation marks (e.g., Martin and Bennett, 1977; Smith, 1987) or by comparison of architectural and surficial morphologies to known traces (e.g., Carroll, 1965; Hasiotis et al., 1993, 2004; Gobetz, 2006). Discovered and interpreted ancient vertebrate burrowers include lungfish (Berman, 1976; Hasiotis et al., 1993), amphibians (Hembree et al., 2004, 2005), therapsids (Smith, 1987: Groenwald et al., 2001), bear dogs (Hunt et al., 1983), beavers (Martin and Bennett, 1977), and kangaroo rats (Voorhies, 1975b).

There is a tendency to place vertebrate burrows in an open nomenclature. Compared with the diversity of invertebrate burrows, vertebrate burrows may appear superficially similar due a shared body plan, (Häntzschel, 1975), but detailed study of architecture and surficial morphology reveal many identifying distinctions between types. Giving a taxonomic name and description to two new vertebrate trace fossils makes these structures more useful as paleoenvironmental indicators and enhance scientific communication by increasing specificity and increasing the potential for recognition of these and similar structures in the field.

REFERENCES

ABBA, A.M., UDRIZAR SAUTHIER, D.E., and VIZCAINO, S.F., 2005, Distribution and use of burrows and tunnels of *Chaetophractus villosus* (Mammalia, Xenarthra) in the eastern Argentinean pampas: Acta Theriologica, v. 50, p. 115–124.

BANCROFT, W.J., GARKAKLIS, M.J., and ROBERTS, J.D., 2005, Burrow building in seabird colonies: a soil-forming process in island ecosystems: Pedobiologia, v. 49, p. 149–165.

BERMAN, D.S., 1976, Occurrence of *Gnathorhiza* (Osteichthyes: Dipnoi) in aestivation burrows in the Lower Permian of New Mexico with description of a new species: Journal of Paleontology, v. 50, p. 1034–1039.

BRITT, B.B., SCHEETZ, R.D., and DANGERFIELD, A., 2008, A suite of dermestid beetle traces on dinosaur bone from the Upper Jurassic Morrison Formation, Wyoming, USA: Ichnos, v. 15, p. 59–71.

CARRANO, M.T., and VELEZ-JUARBE, J., 2006, Paleoecology of the Quarry 9 vertebrate Assemblage from Como Bluff, Wyoming (Morrison Formation, Late Jurassic): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 147–159.

CARROLL, R.L., 1965, Lungfish burrows from the Michigan Coal Basin: Science, v. 148, p. 963–964.

FOSTER, J.R., 2007, Jurassic West: The Dinosaurs of the Morrison Formation and Their World:

Indiana University Press, Bloomington, 389 p.

FRIEDMAN, M., and DAESCHLER, E.B., 2006, Late Devonian (Famennian) lungfishes from the Catskill Formation of Pennsylvania, USA: Paleontology, v. 49, p. 1167–1183.

GATES, T.A., 2005, The Late Jurassic Cleveland-Lloyd Dinosaur Quarry as a drought-induced assemblage: PALAIOS, v. 20, p. 363–375.

GOBETZ, K.E., 2006, Possible burrows of mylagaulids (Rodentia: Aplodontoidea: Mylagaulidae) from the late Miocene (Barstovian) Pawnee Creek Formation, northeastern Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 119–136.

GOOD, S.C., 2004, Paleoenvironmental and paleoclimatic significance of freshwater bivalves in the Upper Jurassic Morrison Formation, Western Interior, USA. Sedimentary Geology, v. 167, p. 163–176.

GREENWOOD, P.H., 1986, The natural history of African lungfishes: Journal of Morphology, v. 190, p. 163–179.

GROENWALD, G.H., WELMAN, J., and MACEACHERN, J.A., 2001, Vertebrate burrow complexes from the early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa: PALAIOS, v. 16, p. 148–160.

HÄNTZSCHEL, W., 1975, Trace fossils and problematica (2nd edition), *in* Teichert, C. (ed.), Treatise on Invertebrate Paleontology, part W. Miscellanea, suppl. 1: Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, p. 269.

HASIOTIS, S.T., 2002, Continental trace fossils: SEPM Short Course Notes, v. 51, p. 1–132.

HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177–268.

HASIOTIS, S.T., 2008, Reply to the Comments by Bromley et al. of the paper "Reconnaissance of the Upper Jurassic Morrison Formation ichnofossils, Rocky Mountian Region. USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses" by Stephen T. Hasiotis: Sedimentary Geology, v. 208, p. 61–68.

HASIOTIS, S.T. and MITCHELL, C.E., 1993, A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo- and neo-ichnological evidence, and the identification of their burrowing signatures: Ichnos, v. 2, p. 291–314.

HASIOTIS, S. T., and DEMKO, T. M., 1996, Terrestrial and freshwater trace fossils, Upper Jurassic Morrison Formation, Colorado Plateau. The Continental Jurassic: Museum of Northern Arizona Bulletin, v. 60, p. 355–370.

HASIOTIS, S.T., WELLNER, R.W., MARTIN, A.J., and DEMKO, T.M., 2004, Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance: Ichnos, v. 11, p. 103–124.

HASIOTIS, S.T., PLATT, B.F., HEMBREE, D.I., and EVERHEART, M.J., 2007, The trace-fossil record of vertebrates, in Miller, W.III., ed., Trace Fossils—Concepts, Problems, Prospects: Elsevier, Amsterdam, p. 196–218.

HEMBREE, D.I., HASIOTIS, S.T., and MARTIN, L.D., 2004, Amphibian burrows and ephemeral ponds of the Lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 203, p. 127–152.

HEMBREE, D.I., MARTIN, L.D., and HASIOTIS, S.T., 2005, *Torridorefugium eskridgensis* (new ichnogenus and ichnospecies): Amphibian aestivation burrows from the Lower Permian Speiser Shale of Kansas: Journal of Paleontology, v. 79, p. 583–593.

HOTTON, C.L., and BAGHAI-RIDING, N.L., 2010, Palynological evidence for conifer dominance within a heterogeneous landscape in the Late Jurassic Morrison Formation, USA, *in* Gee, C.T., ed., Plants in Mesozoic Time: Morphological Innovations, Phylogeny, Ecosystems: Indiana University Press, Bloomington, p. 295–328.

HUNT, R.M., XIANG-XUE, X., and KAUFMAN, J., 1983, Miocene burrows of extinct bear dogs: indication of early denning behavior of large mammalian carnivores: Science, v. 221, p. 364–366.

KIELAN-JAWOROWSKA, Z., CIFELLI, R.L., and LUO, Z., 2004, Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure: Columbia University Press, New York, 630 p.

KNIGHT, J., 2009, Infilled pocket gopher tunnels: seasonal features of high alpine plateaux: Earth Surface Processes and Landforms, v. 34, p. 590–595.

KRAPOVICKAS, V., MANCUSO, A.C., MARSICANO, C.A., DOMNANOVICH, N.S., and SCHULTZ, C.L., 2012, Large tetrapod burrows from the Middle Triassic of Argentina: a behavioural adaptation to seasonal semi-arid climate?: Lethaia, v. 46, p. 154–169.

LE ROUX, P.C., BOELHOUWERS, J., DAVIS, J.K., HAUSSMANN, N.S., JANTZE, E.J., and MEIKLEJOHN, K.I., 2011, Spatial association of lemming burrows with landforms in the Swedish subarctic mountains: implications for periglacial feature stability: Arctic, Antarctic, and Alpine Research, v. 43, p. 223–228.

LIU, J. and LI, L., 2013, Large tetrapod burrows from the Permian Naobaogou Formation of the Daqingshan Area, Nei Mongol, China: Acta Geologica Sinica, v. 87, p. 1501–1507.

LOCKLEY, M., HUNT, A., CONRAD, K., and ROBINSON, J., 1992, Tracking dinosaurs and other extinct animals at Lake Powell: Park Science, v. 12, p. 16–17.

LOOPE, D.B., DINGUS, L., SWISHER III, C.C., and MINJIN, C., 1998, Life and death in a Late Cretaceous dune field, Nemegt basin, Mongolia: Geology, v. 26, p. 27–30.

MARTIN, A.J., 2009, Dinosaur burrows in the Otway Group (Albian) of Victoria, Austalia, and their relation to Cretaceous polar environments: Cretaceous Research, v. 30, p. 1223–1237.

MARTIN, L.D., and BENNETT, D.K., 1977, The Burrows of the Miocene Beaver *Palaeocastor*, Western Nebraska, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173–193.

MCALPIN, S., DUCKETT, P., and STOW, A., 2011, Lizards cooperatively tunnel to construct a long-term home for family members: PLoS ONE, v. 6, e19041.

OSTROM, J.H., and MCINTOSH, J.S., 1966, Marsh's Dinosaurs: The Collections from Como Bluff: Yale University Press, New Haven, 416 p.

PARRISH, J.T., PETERSON, F., and TURNER, C.E., 2004, Jurassic "savannah" –plant taphonomy and climate of the Morrison Formation (Upper Jurassic, Western USA): Sedimentary Geology, v. 167, p. 137–162.

PROTHERO, D.R., 1981, New Jurassic Mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic Theria: Bulletin of the American Museum of Natural History, v. 167, p. 281–325.

REICHMAN, O.J., and SMITH, S.C., 1990, Burrows and burrowing behavior by mammals, *in* Genoways, H.H., ed., Current Mammalogy: Plenum Press, New York, p. 197–244.

RIESE, D.J., HASIOTIS, S.T., and ODIER, G.P., 2011, Synapsid burrows and associated trace fossils in the Lower Jurassic Navajo Sandstone, southeastern Utah, U.S.A., indicates a diverse community living in a wet desert ecosystem: Journal of Sedimentary Research, v. 81, p. 299–325.

ROBINSON, J.W., and MCCABE, P.J., 1998, Evolution of a braided river system: the Salt Wash Member of the Morrison Formation (Jurassic) in southern Utah, *in* Relative Role of Eustasy, Climate, and Tectonism in Continental Rocks, SEPM Special Publications No. 59, Society for Sedimentary Geology (SEPM), p. 93–107.

SMITH, R.M.H., 1987, Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 155–169.

TALANDA, M., DZIECIOL, S., SULEJ, T., and NIEDZWIEDZKI, G., 2011, Vertebrate burrow system from the Upper Triassic of Poland: PALAIOS, v. 26, p. 99–105.

TRACY, C.R., REYNOLDS, S.J., MCARTHUR, L., TRACY, C.R., and CHRISTIAN, K.A., 2007, Ecology of aestivation in a cocoon-forming frog, *Cyclorana australis* (Hylidae): Copeia, v. 4, p. 901–912.

TURNER, C.E., and PETERSON, F., 1992, Sedimentology and stratigraphy of the Morrison Formation in Dinosaur National Monument: University of Wyoming National Park Service Research Center Annual Report, v. 16, p. 86–91.

TURNER, C.E., and PETERSON, F., 2004, Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem—a synthesis: Sedimentary Geology, v. 167, p. 309–355.

VOIGT, S., SCHNEIDER, J.W., SABER, H., HMINNA, A. LAGNAOUI, A., KLEIN, H., BROSIG, A., and FISCHER, J., 2011, Complex tetrapod burrows from Middle Triassic red beds of the Argana Basin (Western High Atlas, Morocco): PALAIOS, v. 26, p. 555–566.

VOORHIES, M.R., 1975a, Vertebrate burrows, *in* Frey, R.W., ed., The Study of Trace Fossils: Spring-Verlag, New York, p. 325–350.

VOORHIES, M.R., 1975b, A new genus and speices of fossil kangaroo rat and its burrow: Journal of Mammalogy, v. 56, p. 160–176.

CHAPTER TWO:

NEW VERTEBRATE BURROW MORPHOLOGIES IN THE SALT WASH MEMBER, UPPER JURASSIC MORRISON FORMATION, SOUTHEASTERN UTAH, USA: INTERPRETING BEHAVIOR AND ENVIRONMENT WITHOUT BODY FOSSILS

Submitted to PALAIOS as:

RAISANEN, D.C.W. and HASIOTIS, S.T., in review, **New Vertebrate Burrow Morphologies in the Salt Wash Member, Upper Jurassic Morrison Formation, Southeastern Utah, USA: Interpreting Behavior and Environment Without Body Fossils**.

ABSTRACT

Large-diameter structures in the Salt Wash Member, Upper Jurassic Morrison Formation, in southeastern Utah, are interpreted as vertebrate burrows. Two types of burrows, found at two localities, reveal the hidden biodiversity of small vertebrates in an area with a paucity of such body fossils. Morphotype 1 exhibits a vertical to subvertical helical shaft leading to a subhorizontal tunnel. The mean helical shaft depth is 71.4 cm, and mean tunnel length is 42.3 cm. Morphotype 2 burrows are networks of interconnected shafts and tunnels at angles 0–89º. Segments of the network shafts and tunnels are straight, curved, or helical. The mean length of a section is 30.7 cm. Both morphotypes have ridges and knobs preserved on burrow walls. Some surficial morphology is interpreted as scratch marks from the claws and/or teeth of the tracemakers. All burrow types are found in pedogenically-modified mudstone overlain by sandstone channel deposits. The environment of deposition is interpreted as river channel and floodplain. Primitive mammals are the most likely tracemakers for both morphotypes based on

comparison to the architectural and surficial morphologies of fossil and extant vertebrate burrows and other structures. These burrows reveal evidence for denning and parental care in Jurassic age mammals, and classified as polychresichnia. The burrows can also be used to help study local soil development and paleohydrologic conditions in the Salt Wash Member by showing stability of the floodplain and depth of the vadose zone. What is learned on the local level can be expanded to other localities where mammal burrows are identified. This paper presents two new morphologies to look for and will hopefully lead to the discovery of more.

INTRODUCTION

Modern vertebrate burrows are found nearly worldwide in most continental environments (e.g., Reichman and Smith, 1990; Abba et al., 2005; Knight, 2009; le Roux et al., 2011), and are produced by all major classes (e.g., Greenwood, 1986; Reichman and Smith, 1990; Bancroft et al., 2005; Tracy et al., 2007; McAlpin et al., 2011). Trace fossils representing vertebrate burrows are most often found in floodplain, lacustrine, or palustrine deposits (e.g., Smith, 1987; Hasiotis, 2004, 2008; Hasiotis et al., 2004; Voigt et al., 2011), as well as in eolian settings (e.g., Loope et al., 1998; Riese et al., 2011). They are preserved on all continents (e.g., Martin and Bennett, 1977; Krapovickas et al., 2012; Talanda et al., 2011; Liu and Li, 2013; Voigt et al., 2011; Martin, 2009; Hasiotis et al., 2004) and date from the Devonian (Hasiotis, 2002; Friedman and Daeschler, 2006) to the present. Vertebrate burrows are far less common than invertebrate burrows in continental deposits (e.g., Voorhies, 1975a; Hasiotis et al., 2007). Tracemakers can be identified by the occurrence of body fossils preserved inside the burrow (e.g., Martin and Bennett, 1977; Smith, 1987), or by comparison of architectural and surficial morphologies to known traces (e.g. Carroll, 1965; Hasiotis et al., 1993, 2004; Gobetz, 2006). Discovered and interpreted ancient vertebrate tracemakers are varied and include lungfish (Berman, 1976; Hasiotis et al., 1993), amphibians (Hembree et al., 2004, 2005), therapsids (Smith, 1987: Groenwald et al., 2001), bear dogs (Hunt et al., 1983), beavers (Martin and Bennett, 1977), and kangaroo rats (Voorhies, 1975b).

This paper describes two morphotypes of large-diameter structures (LS) in the Salt Wash Member of the Upper Jurassic Morrison Formation in southeastern Utah, U.S.A. (Fig. 1), interpreted as vertebrate burrows. They record a part of the paleobiodiversity mostly not represented by body fossils. Some of these LS have previously been described generally as mammal burrows (e.g., Hasiotis, 2002, 2004; Hasiotis et al., 2004), but detailed analysis has not been undertaken until now. Different sized mammals are interpreted as potential tracemakers based on the architectural and surficial morphologies of the LS. The various morphologies described here can be used to identify other vertebrate burrows in continental deposits. There has been good research done identifying the range of therapsid and cynodont burrows in the Permian and Triassic (e.g., Smith, 1987: Groenwald et al., 2001; Hasiotis et al., 2004; Talanda et al., 2011). Description of these new Jurassic structures will help in the recognition of previously unidentified mammal burrows in the Mesozoic and Cenozoic.

This study increases understanding of alluvial ecosystems preserved in the Morrison Formation by revealing new information about the nondinosaurian inhabitants and expands on the range of identified trace fossils of primitive mammals. Although the Morrison Formation has produced a diverse assemblage of small vertebrates (e.g. Prothero, 1981; Evans and Milner 1993; Carrano and Velez-Juarbe, 2006), the majority of these fossils are found well away from the study area, such as in Fruita, Colorado (e.g. Luo and Wible, 2005), and at Como Bluff quarries in Wyoming (e.g. Prothero, 1981). How cosmopolitan species from these locations may have been is not known. Being able to identify burrows in the Morrison or any formation is an aid in reconstructing the environment. Burrows and their method of preservation offer clues about the soil development and the groundwater profile.

GEOLOGIC SETTING

The Upper Jurassic Morrison Formation extends across more than $1\text{x}10^6$ km^2 of the western United States from New Mexico to Montana, and into southwest Canada (Turner and Peterson, 2004). The varied lithologies of the Morrison Formation represent mostly continental deposition after the Late Jurassic Western Interior seaway retreated northward out of the interior of North America (Turner and Peterson, 2004). Deposition of continental sediments followed the regressing shoreline as seen where the Sundance Formation grades into and intertongues with the base of the Morrison Formation in northern Utah and Colorado, and into southern Wyoming (Imlay, 1980; Turner and Peterson, 2004). The Morrison Formation is subdivided into 10 members, some of which interfinger (Turner and Peterson, 2004). They do not all occur at any one location. These members pinch out northward and eastward away from the Colorado Plateau, where the Morrison Formation remains undivided at the perimeter as it pinches out (Imlay, 1980; Turner and Peterson, 2004).

In the southern part of the basin, the base of the Morrison Formation is delineated by the J-5 unconformity (Piperingos and O’Sullivan, 1978; Turner and Peterson, 2004). Morrison Formation deposition began in the very latest Oxfordian based on palynomorphs from the Windy Hill Member and calcareous microfossils (Turner and Peterson, 2004). Deposition continued through the Kimmeridgian to the early Tithonian (Peterson, 1994). Radiometric age dates from ash beds in the Tidwell Member at the base of the formation and the Brushy Basin Member at the top indicate deposition occurred between 155–148 Ma (Kowallis et al., 1998, 2007).

Paleoenvironmental reconstructions of the Morrison Formation include depositional environments from the nearshore marine in the Windy Hill Member, fluvial in the Salt Wash Member to eolian in the Bluff Sandstone Member. The Morrison Formation is interpreted as a tropical wet-dry, savannahlike climate with periods of wetter conditions (e.g., Engelmann et al., 2004; Demko et al., 2004; Hasiotis, 2004, 2008; Parrish et al., 2004; Platt, 2012).

The Morrison Formation has abundant body fossils of dinosaurs and smaller vertebrates that have been described since the late 1800s (e.g., Ostrom and McIntosh, 1966; Turner and Peterson, 1992; Gates, 2005). The mammal assemblage of the Morrison Formation is the most diverse in the world for the Late Jurassic, but the majority of species come from Como Bluff, Wyoming (e.g., Prothero, 1981; Kielan-Jaworowska et al., 2004; Carrano and Velez-Juarbe, 2006). Numerous trace fossils are also known from the Morrison Formation, most interpreted as invertebrate in origin (e.g., Hasiotis and Demko, 1996; Good, 2004; Hasiotis, 2004, 2008; Britt et al., 2008). Known trace fossils from the Salt Wash Member include rhizoliths, dinosaur tracks, and numerous types invertebrate nests and burrows (e.g., Lockley et al., 1992; Robinson and McCabe, 1998; Hasiotis 2004, 2008).

Study Area

The LS were investigated at two localities: Locality 1 in Shootaring Canyon ~9 km north of Ticaboo, Utah, and a second, smaller locality ~11 km east of Fruita, Utah (Fig. 1). Members of the Morrison Formation exposed at the field localities include the Tidwell, Salt Wash, and Brushy Basin. Both LS localities were near the top of the Salt Wash Member.

The Salt Wash Member is a laterally discontinuous unit that, where present, lies between the Tidwell and Brushy Basin members (Peterson, 1994). At various locations the Salt Wash Member interfingers with the lacustrine Tidwell Member, fluvial Westwater Canyon Member, and eolian Bluff Sandstone and Junction Creek Members (Peterson, 1994; Turner and Peterson, 2004). The Salt Wash Member is up to 160-m thick in the Henry Mountains area (Robinson and McCabe, 1998). The Salt Wash Member is interpreted as a fluvial complex composed of channel deposits interbedded with floodplain and crevasse-splay deposits that prograded eastward with maximum extent in the middle Kimmeridgian (Peterson, 1994; Turner and Peterson, 2004; Kjemperud et al., 2008). Low-sinuosity braided streams flowing east, northeast, and southeast predominated with channels becoming straight and isolated downstream (Demko et al., 2004; Turner and Peterson, 2004). Wetland and lacustrine environments developed downstream and prograded eastward during Salt Wash Member deposition (Turner and Peterson, 2004). Streamflow was variable, indicated by interfingering between the Salt Wash Member and erg deposits of the Bluff Sandstone and Junction Creek Members to the east (Turner and Peterson, 2004) and trace-fossil occurrences within coarse-grained- and fine-grained-dominated intervals (e.g., Hasiotis 2004, 2008).

Outcrops of the Salt Wash Member at both localities are characterized by alternating layers of sandstone and mudstone interbedded with thin, discontinuous carbonate layers (Fig. 2–4). Sandstones are interpreted as fluvial deposits. The interbedded mudstone-carbonates are interpreted as paleosols. Sandstones are buff colored at both outcrops. Grain size is medium sand with pebble lags at the bottom contacts. All sandstones have ~0.3-m thick tabular crossbedding and are interpreted as bars. At both localities the sandstone units were thicker than the mudstone-carbonate units. Individual sandstone accumulated to ~ 4–12-m thick. The channels that deposited the sandstones scoured the underlying paleosols. In many places the paleosol was completely eroded and the scour surface cuts through the paleosol to underlying sandstone. At both localities three mudstone-dominated beds contain LS. The mudstone is carbonate-cemented, clay rich, and red–brown or grey–green, interpreted as a record of dry, oxidizing and wet, reducing paleohydrologic conditions. Slickensides and pseudoanticlines were observed in all mudstone beds at both localities. The carbonate is beige and mostly massive. There are some small, recrystallized areas that appear without any pattern. The mudstone-carbonate units all have sharp upper contacts and gradual bottom contacts with the over- and underlying sandstones. Two LS-bearing mudstone-carbonate units at Locality 1 vary from ~1.5–3.5-m thick. Two LS-bearing units at Locality 2 vary from 2.4–4.0-m thick.

Other body and trace fossils were found during the course of this investigation. Discrete soft-sediment deformation patterns in mudstone-carbonate units at both localities are interpreted as dinosaur tracks (Fig. 5). Rhizoliths and rhizohaloes were observed in multiple mudstone-carbonate units at Locality 1. The largest were nearly 1-m long and ~5-cm wide. Three vertebrae at Locality 2 and numerous bone fragments at both sites attributable to dinosaurs were found in sandstone beds. Locality 1 contains two enigmatic structures (Fig. 6) that may represent additional shallow tunnel burrows averaging 2.0 m long, but are too poorly preserved to provide identifying characteristics.

MATERIALS AND METHODS

Stratigraphic columns for both localities were constructed and described the lithofacies (see Fig. 2). The section at Locality 1 was measured from several meters below the lowest horizon of the structures to the top of the outcrop. The section at Locality 2 was measured from the river at the base of the outcrop to the top. LS-bearing units at both sites were followed laterally to determine the full areal extent of the layers and their relation to overlying and underlying sandstone units.

The LS were photographed in detail and their architectural and surficial morphology and sediment fill were described following the methods of Hasiotis and Mitchell (1993), Hasiotis et al. (1993), and Hembree and Hasiotis (2006). The length of segments was measured with measuring tape or calipers along the top of the LS following the midline. Penetration depth was measured vertically with tape from the highest point of the LS to the lowest. Diameters (widest and narrowest dimensions) were measured where a segment had broken exposing a cross section or around an intact segment with these dimensions exposed. The dip angle of shafts and helical elements was measured using a level (Fig. 7). Surficial morphology was described for such features as longitudinal and transverse ridges and knobby or hummocky textures from the burrow walls. The fill lithology was compared with the lithology of the matrix, over and underlying beds, and thin interbedded carbonates to identify the source of the material. We calculated LS density (#/m^2) of the most common morphotype in each layer where they were present. The LS-bearing layer and broken LS in float were examined for associated trace fossils and body fossils.

Vertebrate tracemakers for the LS are hypothesized to have been mammals. To test this hypothesis and rule out other potential tracemakers a database of LS features was constructed and compared with descriptions of identified trace fossils and abiotic constructions (Table 1; Riese et al., 2011). We compared the LS to fossil and modern burrows from different terrestrial vertebrates, rhizoliths, fluid-escape structures, and weathered rock remnants.

DESCRIPTION

Two distinct architectural morphologies of LS were identified. The most prevalent is designated Morphotype 1. The less common is Morphotype 2. All structures are preserved by muddy carbonate fill and many contain veins of recrystallized calcite. This fill weathered to a beige color that contrasted against the matrix mudstone and aided structure identification. Excavation of the structures beyond what was already exposed was not possible. The color contrast that made them stand out from the matrix had not occurred and the LS were indistinguishable from the matrix. How long the weathering contrast takes is not known at this time. No body fossils were found within the LS.

Morphotype 1

Architectural Morphology.—Morphotype 1 (M1) structures are composed of two architectural elements: a vertical to subvertical helical shaft connecting at an L-shaped junction to a horizontal tunnel (Fig. 8) (Appendix A). The cross section of both the shaft and the tunnel elements is ovoid. Where present, a marked widening at the top of the shaft has a mean diameter of 24.2 cm; range 15.2–36 cm. The mean shaft depth is 71.4 cm; range 33.7–155.6 cm. Mean shaft length is 99.4 cm; range 55.6–143.5 cm. The majority of shafts are vertical. Of those that are subvertical the mean dip angle is 48.1° from horizontal; range 35–57°. Shaft cross sections have a mean vertical diameter of 8.5 cm; range 3–10.9 cm, and a horizontal diameter of 9.2 cm; range 2.3–14 cm. The mean dip of the helical whorls is 37° from the horizontal; range 26–67°. The mean tunnel length is 42.3 cm; range 24.1–86.6 cm. Tunnel cross sections have a mean vertical diameter of 10.5 cm; range 4.27–26.7 cm, and horizontal diameter of 10.7 cm; range 4.9–20.2 cm. The majority of specimens are incomplete to some degree, lacking some or all of one or both elements. At both localities, when the tops of structures can be identified, the burrows appear to originate from the same paleosurface, 10–15 cm below the top of the layer. The M1 structures occur in the lowermost paleosol at Locality 1 and the uppermost paleosol at Locality 2 (see Fig. 2). At Locality 1 the average density is 9 LS/10 m^2. The smaller exposure at Locality 2 has a density of 10 LS/10 m^2.

Surficial Morphology.—The surficial morphology of M1 exhibits four surface textures—two types of ridges and two types of knobs. These surface morphologies appear evenly across both outcrops. On individual burrows the tops and sides of the helix and tunnel elements tend to preserve ridges, whereas knobs dominate the undersides of a burrow (Fig. 9). The larger ridge type runs longitudinally on the surface of the shaft and tunnel elements. The large ridges have rounded tops (Fig. 9A). Width is < 1 cm and length is 1 cm to 10 cm; height is < 0.5 cm. The small ridge type is made up of short segments < 1 cm long that join together at a variety of angles to create a jagged surface texture (Fig. 9B). The height is < 1 cm with steep sides. The large knobs are < 1cm tall and circle the circumference of the burrow surface, predominantly the shafts (Fig. 9C). Size of the knobs varies with the size of the shaft. Individual large knobs press against each other and are separated by thin cracks up to 1.5 cm deep. The small knob texture has individual knobs <1 cm tall and ~1 cm across, appearing together (Fig. 9D). Sometimes these would be present on the larger knobs.

Morphotype 2

Architectural Morphology—Morphotype 2 (M2) structures are composed of an interconnected network of shafts and tunnels at various angles (Fig. 10, 11) (Appendix A). Individual elements are straight (the most common), curved, or helical. The mean length of a section is 30 cm; range <1–93.3 cm. The cross sections of all elements are ovoid. The mean vertical diameter is 4.9 cm; range 2.8–14 cm. The mean horizontal diameter is 6.3 cm; range 4.5–8.7 cm. The segments vary from 0º to 89º from the horizontal and mean angle of inclination is 31º. The interconnected segments are joined randomly in a maze pattern. These LS are found at Locality 1 in the middle and lowest paleosols, at Locality 2 in the highest paleosol. Preservation is varied within the group with some specimens having segments fused together to the extent that the individual segments are not definitively discernible.

Surficial Morphology.—The surficial morphology of M2 is varied (Fig. 12). There is one ridge and one knob texture similar to those on M1 and a second ridge and second knob texture unique to this morphotype. The shared ridge texture is formed by short, thin ridges <1 cm long and <1 cm high that join together at irregular angles to create a jagged, serrated appearance (Fig. 12A). This texture is most common on the ceiling of burrows. Unique to M2 there is a set of straight, parallel ridges 1.4 cm long within the jagged texture (Fig. 12B). Concentrated on the sides and bottom of M2 specimens are small knobby texture similar to that seen on M1 (Fig. 12C). These knobs are up to 2-cm long and < 1-cm high. Arrangement of these knobs is random. A second knob texture seen on a single specimen is a series of vertically oriented knobs of roughly equal shape (Fig. 12D). They are < 1-cm tall, ~2-cm long, and ~1-cm wide.

INTERPRETATIONS OF MORPHOTYPES

Morphotype 1

The helical architecture of M1 burrows resembles corkscrew burrows produced by synapsids and mammals from the Permian to the recent (e.g., Martin and Bennett, 1977; Bown and Kraus, 1983; Smith, 1987; Butler, 1995) (Table 2). M1 is most similar to *Daemonelix*, helical burrows produced by the Miocene beaver *Palaeocastor* (Martin and Bennett, 1977). The best-preserved specimens of M1 show a widening at the top of the helix, interpreted as a turnaround where the tracemaker might change position and scan the environment. This feature is also noted in *Daemonelix* and extant prairie dog burrows (e.g., King, 1955; Martin and Bennett, 1977). In cross section, M1 is most similar to burrows attributed to mammal excavators ancient and modern (e.g., Martin and Bennett, 1977; Bown and Kraus, 1983; Laundré, 1989). The ovoid, almost circular cross section with horizontal burrow diameters of the M1 burrows slightly larger than the vertical diameters contrasts with therapsid burrows, which are characterized typically by a W- or upside-down, U-shaped (bean- or kidney-shaped) cross section (e.g., Smith, 1987; Damiani et al., 2003; Riese, 2011). The helix of M1 maintains a uniform width until it reaches the tunnel as in *Daemonelix* (Martin and Bennet, 1977). Permian dicynodont burrows in South Africa also exhibit widening helical shafts and tunnels that gently grade into a terminal chamber (Smith, 1987).

The transverse and longitudinal, small ridges along the surface of M1 burrows are most similar to the surficial morphology of *Daemonelix.* These features on *Daemonelix* are interpreted as the tooth and claw marks produced by the excavator and can be seen as the distinct product of incisors on the top of the burrow or claws on the bottom (Martin and Bennett, 1977). Diagenesis and weathering have distorted the ridges on the M1 burrows. The carbonate that preserves the architecture has also covered some original surfaces. Both large and small knobby textures are interpreted as products of preservation and these pseudosurficial morphologies are not useful for diagnosing potential tracemakers or methods of excavation. While no surficial morphologic features can be identified as the work of teeth or claws with certainty, based on the interpretation for *Daemonelix*, the small ridges on the top of the M1 burrow are more likely to be the marks produced by the teeth of the tracemaker.

A single individual or pair of tracemakers likely constructed and maintained M1 burrows, based on comparisons to extant mammalian burrowers. Permanent burrows are more complex than temporary shelters and require more effort to construct (e.g., Vleck, 1981, Reichman and Smith, 1990; Meyer, 1999). The helix and tunnel architecture has the complexity of a permanent structure, but is less complex than the elaborate networks that can be created by social or eusocial mammals (e.g., Lynch, 1980; Jarvis et al., 1994; Mankin and Getz, 1994; Skinner, 2005). The more elaborate burrows of social and eusocial mammals are multiuse with chambers for resting, waste disposal, food storage, and foraging tunnels (e.g., Bennett and Faulkes, 2000; Scharff et al., 2001). The lower complexity indicates M1 burrows were primarily used for shelter and that the tracemakers went above ground to forage. Resting underground would protect the tracemakers from temperature changes (e.g., Reichman and Smith, 1990; Meyer, 1999). The tracemakers likely did not use M1 burrows for dry season estivation as hypothesized for therapsid helical burrows, based on lack of body fossils (Smith, 1987). The M1 burrows are categorized as polychresichnia as the architecture represents a burrow for the tracemaker that may have been used for multiple purposes, such as dwelling, reproduction, and sheltering from weather extremes.

Worldwide there are eight (McKenna and Bell, 1997) to 13 (Kielan-Jaworowska et al., 2004) mammal lineages at the ordinal or family level by the Late Jurassic. The major groups identified from the Morrison Formation are docodonts, multituberculates, eutriconodonts, “symmetrodonts,” paurodontids, and dryolestids (Kielan-Jaworowska et al., 2004). There is at least one species of eutriconodont, *Fruitafossor windscheffeli*, from western Colorado that is interpreted as adapted for a fossorial lifestyle and scratch digging based on forelimbs and vertebrae, as well as peglike teeth—convergent with modern burrowing armadillos and aardvarks—for eating insects (Luo and Wible, 2005; Luo, 2007). This creature appears to be too small to have occupied M1 burrows (Foster, 2009), but supports the notion of a mammal tracemaker by showing that necessary burrowing adaptations were present at this time. A fossorial-adapted docodont, *Docofossor brachydactylus*, from the Late Jurassic in China further indicates that digging abilities were distributed across multiple mammal groups (Luo et al., 2015). No therapsids have been recovered from the Morrison Formation; thus, the lack of burrow morphologic and body-fossil evidence suggests that they are unlikely candidates for the tracemaker.

Morphotype 2

The networks preserved in M2 are interpreted as likely burrow systems for social mammals. 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; Voigt et al., 2011). M2 burrows are 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). As with M1, the ovoid cross section with a horizontal diameter slightly wider than the vertical diameter matches best with mammal burrows (e.g., Martin and Bennett, 1977; Bown and Kraus, 1983; Laundré, 1989).

The surficial morphology of M2 is more enigmatic than the architectural morphology. The short ridges are most likely to have been produced by the tracemaker. The parallel ridges on the roof of the burrow also appear to have been produced by tracemaker. Both of these morphologies are seen more prevalently in better-preserved trace fossils and modern burrows (e.g., Martin and Bennett, 1977; Burns et al., 1989; Gobetz and Martin, 2006). The random knobby texture is a pseudosurficial morphology that formed during preservation and is not useful for determining the tracemaker or mode of excavation. The repeating, parallel knob texture is similar to the scalloped walls preserved in other fossil burrows (Gobetz and Martin, 2006; Riese et al., 2011) and is interpreted as the scratch marks of a manus or pes excavating the burrow. Very similar features are seen in modern mole burrows (Gobetz, 2005) indicating the M2 excavator may have used a similar lateral-thrust or humeral-rotation digging method (Turnbull and Reed, 1967; Hildebrand, 1985).

Multiple individuals of a social group likely constructed M2 burrows. Such burrow systems require a great deal of work to construct and maintain (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). Network burrows can be 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. Skinner, 2005; Smith and Reichman, 1984); foraging tunnels closer to the surface to feed on plant roots and soil biota (e.g. Duncan and Wrangham, 1971; Lovegrove and Jarvis, 1986); reproduction (e.g. Hall and Meyers, 1978; Hickman, 1983); and waste (Reichman and Smith, 1990). Some of these uses are interpreted for fossil burrows as well (e.g., Meyer, 1999; Hasiotis et al., 2004, 2007; Riese et al., 2011). Network burrows produced by extant mammals vary greatly in size based on the size of the excavators and the degree to which the live underground. The largest burrow systems are made by species that spend the majority of their lives underground, such as moles and mole rats (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 persist for over 1000 m (e.g., Šumbera et al., 2011; Lövy, 2015). M2 burrows do not reach this size. The excavators are interpreted to come above ground to forage and interact with conspecifics. M2 burrows are categorized as polychresichnia (Hasiotis, 2003) because the architecture represents multiple behaviors and uses from the tracemaker.

The majority of mammals found in 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 for M2 burrows based on size. *Fruitafossor windscheffeli* is the smallest mammal found in the Morrison Formation and a likely tracemaker with many adaptations for scratch digging (Luo and Wible, 2005; Foster, 2009). Scratch digging is supported as a means for excavating M2 burrows based upon the repeating, parallel knob texture.

Alternative Origins

There is no evidence to falsify the hypothesis that a mammal was the excavator of both the M1 and M2 burrows. The cross sections of both burrows are ovoid unlike a therapsid or reptile burrow giving no evidence for a tracemaker with splayed legs (e.g., Smith, 1987; Groenwald et al., 2001; Hasiotis et al., 2004; Hasiotis and Burke, 2006). The architecture is more complicated than any recorded amphibian burrow, which is simple shafts or tunnels used for aestivation or hibernation (Hembree et al., 2004, 2005). Rhizoliths display a branching pattern not seen in the M1 and M2 burrows (e.g., Klappa, 1980; Loope, 1988; Hasiotis, 2002). Both M1 and M2 burrows are more well planned that any abiotic structures. Fluid escape pipes are typically found in sandstone as straight pillars with concentric rings in the fill (e.g., Netoff, 2002; Huuse et al., 2002; Hasiotis et al., 2007). Eroded rock remnants have highly variable architecture and occur in flat area exposed to a lot of wind that produces a polished surficial morphology (Lancaster, 1984). None of these are features of the M1 or M2 burrows.

Paleoenvironmental Implications

These burrows further support the interpretation of the Morrison Formation as a tropical wet-dry, savannah climate (Engelmann et al., 2004; Hasiotis, 2004, 2008; Parrish et al., 2004; Platt, 2012) and the Salt Wash Member being a fluvial-floodplain system within that environment (Peterson, 1994; Turner and Peterson, 2004; Kjemperud et al., 2008). That both burrow types are interpreted as living spaces is the first indicator of a stable floodplain environment with either gradual buildup of sediment or long periods between large depositional events. The depth of the M1 burrow type indicates a vadose zone >1-m deep. Root traces to a similar depth support this interpretation. The mode of preservation is indicative of a wet-dry climate. The accumulation of illuviated carbonate in burrows and in thin beds took place after the burrows were abandoned and filled with sediment. Through time, seasonal rain moved the minerals down through the soil for a period and deposited it during the dry season (e.g., Schaetzl and Anderson, 2009). This explains the lack of body fossils associated with the burrows, unlike burrows in other geologic deposits that were preserved by sudden filling during a flood (e.g., Martin and Bennett, 1977; Smith, 1987; Groenwald et al., 2001). The change from a dry to wet subsurface environment interpreted from the color change in the mudstone likely occurred after the burrows were preserved and was part of slow shifts in channel placement. The tracemakers of M1 and M2 burrows may have selected their burrow sites on the distal floodplain because it was such a stable environment. Correctly identifying burrows and their method of preservation in other formations will aid in paleoenvironmental interpretations of those rocks as these burrows have for the Salt Wash Member. The M1 and M2 burrows represent two potential search images for others to seek in the field to identify more morphotypes at different localities from different times.

A number of traits in early mammals can be inferred from the burrows. If both burrow types could be used to shelter young, this would be an indication for the presence of parental care in Jurassic-age mammals, something already attributed to cynodonts and seen in extant mammals (e.g., Groenwald et al., 2001; Reynolds et al., 2002). The potential for communities and communal living is another trait interpreted for mammal ancestors (e.g., Groenwald et al., 2001) and remained a useful form of organization during the Mesozoic. Burrowing allows for an excavator to create a hospitable mircoclimate when the larger environment is unfavorable for some portion of the year (e.g., Reichman and Smith, 1990). This can take the extreme of hibernation or aestivation, but extends to organisms just keeping warm at night and cool in the day (e.g., Meyer, 1999; Voigt et al., 2011). The lack of evidence for interpreting either burrow as an aestivation shelter helps limit the extremes possible in this environment.

CONCLUSIONS

Carbonate-preserved, large-diameter helical structures found in the Salt Wash Member of the Morrison Formation are interpreted as vertebrate burrows. The burrows occur in mudstone paleosols between fluvial sandstones. The M1 burrows, the most common, are composed of a helical shaft and horizontal tunnel both with ovoid cross sections. They are very similar to the Cenozoic trace fossil *Daemonelix*. These burrows are interpreted as being made by a mammal, either a single tracemaker or a pair. The M2 burrows are complex networks of shafts and tunnels with ovoid cross sections. They are similar to the burrows of small, social extant rodents. Both burrow types are classified as polychresichnia as they represent multiple uses and behaviors. No body fossils were discovered during this study. These structures highlight a hidden biodiversity not visible in the body fossil record and indicate denning and parental care in Late Jurassic mammals. The presence of fossorial mammals enhances previous environmental interpretations for the Salt Wash Member and also provides details on the local paleoenvironment. These burrows allowed the excavators a suitable mircoclimate during the more inhospitable portions of the tropical wet-dry climate during Morrison Formation deposition

ACKNOWLEDGMENTS

Thanks to R. William Turner and Matt F. Jones for assistance in the field. Thanks to reviewers for helpful comments.

REFERENCES

ABBA, A.M., UDRIZAR SAUTHIER, D.E., and VIZCAINO, S.F., 2005, Distribution and use of burrows and tunnels of *Chaetophractus villosus* (Mammalia, Xenarthra) in the eastern Argentinean pampas: Acta Theriologica, v. 50, p. 115–124.

ANDERSON, A.O., and ALLRED, D.M., 1964, Kangaroo rat burrows at the Nevada Test Site: The Great Basin Naturalist, v. 24, p. 93–101.

BANCROFT, W.J., GARKAKLIS, M.J., and ROBERTS, J.D., 2005, Burrow building in seabird colonies: a soil-forming process in island ecosystems: Pedobiologia, v. 49, p. 149–165.

BENNETT, N.C., and FAULKES, C.G., 2000, African mole-rats: ecology and eusociality: Cambridge University Press, Cambridge, 273 p.

BERMAN, D.S., 1976, Occurrence of *Gnathorhiza* (Osteichthyes: Dipnoi) in aestivation burrows in the Lower Permian of New Mexico with description of a new species: Journal of Paleontology, v. 50, p. 1034–1039.

BOWN, T.M., and KRAUS, M.J., 1983, Ichnofossils of the Alluvial Willwood Formation (Lower Eocene), Bighorn Basin, Northwest Wyoming, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 43, p. 95–128.

BRITT, B.B., SCHEETZ, R.D., and DANGERFIELD, A., 2008, A suite of dermestid beetle traces on dinosaur bone from the Upper Jurassic Morrison Formation, Wyoming, USA: Ichnos, v. 15, p. 59–71.

BURNS, J.A., FLATH, D.L., and CLARK, T.W., 1989, On the structure and function of white-tailed prairie dog burrows: The Great Basin Naturalist, v. 49, p. 517–524.

BUTLER, D.R., 1995, Zoogeomorphology: animals as geomorphic agents: Cambridge University Press, Cambridge, 231 p.

CARRANO, M.T., and VELEZ-JUARBE, J., 2006, Paleoecology of the Quarry 9 vertebrate Assemblage from Como Bluff, Wyoming (Morrison Formation, Late Jurassic): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 147–159.

CARROLL, R.L., 1965, Lungfish burrows from the Michigan Coal Basin: Science, v. 148, p. 963–964.

DAMIANI, R., MODESTO, S., ADAM, Y., and NEVELING, J., 2003, Earliest evidence of cynodont burrowing: Proceedings of the Royal Society B, v. 270, p. 1747–1751.

DAVIES, K.C., and JARVIS, J.U.M., 1986, The burrow systems and burrowing dynamics of the mole-rats *Bathyergus suillus* and *Cryptomys hottentotus* in the fynbos of south-western Cape, South Africa: Journal of Zoology, v. 209, p. 125–147.

DEMKO, T.M., CURRIE, B.S., and NICOLL, K.A., 2004, Regional paleoclimatic and stratigraphic implications of paleosols and fluvial/overbank architecture in the Morrison Formation (Upper Jurassic), Western Interior, USA: Sedimentary Geology, v. 167, p. 115–135.

DUNCAN, P., and WRANGHAM, R.W., 1971, On the ecology and distribution of subterranean insectivores in Kenya: Journal of Zoology, v. 164, p. 149–163.

ENGELMANN, G.F., CHURE, D.J., and FIORILLO, A.R., 2004, The implications of a dry climate for the paleoecology of the fauna of the Upper Jurassic Morrison Formation: Sedimentary Geology, v. 167, p. 297–308.

EVANS, S.E., and MILNER, A.R., 1993, Frogs and Salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America: Journal of Vertebrate Paleontology, v. 13, p. 24–30.

FOSTER, J.R., 2009, Preliminary body mass estimates for mammalian genera of the Morrison Formation (Upper Jurassic, North America): PaleoBios, v. 28, p. 114–122.

FRIEDMAN, M., and DAESCHLER, E.B., 2006, Late Devonian (Famennian) lungfishes from the Catskill Formation of Pennsylvania, USA: Paleontology, v. 49, p. 1167–1183.

GATES, T.A., 2005, The Late Jurassic Cleveland-Lloyd Dinosaur Quarry as a drought-induced assemblage: PALAIOS, v. 20, p. 363–375.

GOBETZ, K.E., 2005, Claw impressions in the walls of modern mole (*Scalopus aquaticus*) tunnels as a means to identify fossil burrows and interpret digging movements: Ichnos, v. 12, p. 227–231.

GOBETZ, K.E., 2006, Possible burrows of mylagaulids (Rodentia: Aplodontoidea: Mylagaulidae) from the late Miocene (Barstovian) Pawnee Creek Formation, northeastern Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 119–136.

GOBETZ, K.E., and MARTIN, L.D., 2006, Burrows of a gopher-like rodent, possibly *Gregorymys* (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 305–314.

GOOD, S.C., 2004, Paleoenvironmental and paleoclimatic significance of freshwater bivalves in the Upper Jurassic Morrison Formation, Western Interior, USA. Sedimentary Geology, v. 167, p. 163–176.

GREENWOOD, P.H., 1986, The natural history of African lungfishes: Journal of Morphology, v. 190, p. 163–179.

GROENWALD, G.H., WELMAN, J., and MACEACHERN, J.A., 2001, Vertebrate burrow complexes from the early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa: PALAIOS, v. 16, p. 148–160.

HALL, L.S., and MEYERS, K., 1978, Variations in the microclimate in rabbit warrens in semi arid New South Wales: Australian Journal of Ecology, v. 3, p. 187–194.

HASIOTIS, S.T., 2002, Continental trace fossils: SEPM Short Course Notes, v. 51, p. 1–132.

HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177–268.

HASIOTIS, S.T., 2008, Reply to the Comments by Bromley et al. of the paper “Reconnaissance of the Upper Jurassic Morrison Formation ichnofossils, Rocky Mountian Region. USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses” by Stephen T. Hasiotis: Sedimentary Geology, v. 208, p. 61–68.

HASIOTIS, S.T. and MITCHELL, C.E., 1993, A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo- and neo-ichnological evidence, and the identification of their burrowing signatures: Ichnos, v. 2, p. 291–314.

HASIOTIS, S. T., and DEMKO, T. M., 1996, Terrestrial and freshwater trace fossils, Upper Jurassic Morrison Formation, Colorado Plateau. The Continental Jurassic: Museum of Northern Arizona Bulletin, v. 60, p. 355–370.

HASIOTIS, S.T., MITCHELL, C.E., and DUBIEL, R.F., 1993, Application of morphologic burrow interpretations to discern continental burrow architects: lungfish or crayfish?: Ichnos, v. 2, p. 315–333.

HASIOTIS, S.T., KIRKLAND, J.I., and CALLISON, G., 1998, Crayfish fossils and burrows from the Upper Jurassic Morrison Formation of western Colorado: Modern Geology, v. 22, p. 481–491.

HASIOTIS, S.T., WELLNER, R.W., MARTIN, A.J., and DEMKO, T.M., 2004, Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance: Ichnos, v. 11, p. 103–124.

HASIOTIS, S.T., PLATT, B.F., HEMBREE, D.I., and EVERHEART, M.J., 2007, The trace-fossil record of vertebrates, in Miller, W.III., ed., Trace Fossils—Concepts, Problems, Prospects: Elsevier, Amsterdam, p. 196–218.

HEMBREE, D.I. and HASIOTIS, S.T., 2006, The identification and interpretation of reptile ichnofossils in paleosols through modern studies: Journal of Sedimentary Research, v. 76, p. 575–588.

HEMBREE, D.I., HASIOTIS, S.T., and MARTIN, L.D., 2004, Amphibian burrows and ephemeral ponds of the Lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 203, p. 127–152.

HEMBREE, D.I., MARTIN, L.D., and HASIOTIS, S.T., 2005, *Torridorefugium eskridgensis* (new ichnogenus and ichnospecies): Amphibian aestivation burrows from the Lower Permian Speiser Shale of Kansas: Journal of Paleontology, v. 79, p. 583–593.

HICKMAN, G.C., 1983, Influence of the semi-aquatic habit in determining burrow structure of the star-nosed mole (*Condylura cristata*): Canadian Journal of Zoology, v. 61, p. 1688–1692.

HILDEBRAND, M., 1985, Digging in quadrupeds. In Hildebrand, M., Bramble, D. M., Liem, K. L., and Wake, D. B., eds., Functional Vertebrate Morphology: The Belknap Press of Harvard University Press, Cambridge, p. 89–109.

HUNT, R.M., XIANG-XUE, X., and KAUFMAN, J., 1983, Miocene burrows of extinct bear dogs: indication of early denning behavior of large mammalian carnivores: Science, v. 221, p. 364–366.

IMLAY, R.W., 1980, Jurassic paleobiogeography of the conterminous United States on its continental setting: United States Geological Survey Professional Paper 1062. United States Government Printing Office, Washington, D.C.

JARVIS, J.U.M., O'RAIN, M.J., BENNETT, N.C., and SHERMAN, P.W., 1994, Mammalian eusociality: a family affair: Trends in Ecology and Evolution, v. 9, p. 47–51.

KAY, F.R., and WHITFORD, W.G., 1978, The burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, in southcentral New Mexico: The American Midland Naturalist, v. 99, p. 270–279.

KENAGY, G.J., 1973, Daily and seasonal pattern of activity and energetics in a heteromyid rodent community: Ecology, v. 54, p. 1201–1219.

KIELAN-JAWOROWSKA, Z., CIFELLI, R.L., and LUO, Z., 2004, Mammals from the Age of

Dinosaurs: Origins, Evolution, and Structure: Columbia University Press, New York, 630 p.

KING, J.A., 1955, Social behavior, social organization, and population dynamics in a black tailed prairie dog town in the Black Hills of South Dakota: Contribution from the Laboratory of Vertebrate Biology, no. 67, p. 1–123.

KJEMPERUD, A.V., SCHOMACKER, E.R., and CROSS, T.A., 2008, Architecture and stratigraphy of alluvial deposits, Morrison Formation (Upper Jurassic), Utah: AAPG Bulletin, v. 92, p. 1055–1076.

KNIGHT, J., 2009, Infilled pocket gopher tunnels: seasonal features of high alpine plateaux: Earth Surface Processes and Landforms, v. 34, p. 590–595.

KOWALLIS, B.J., CHRISTIANSEN, E.H., DEINO, A.L., PETERSON, F., TURNER, C.E., KUNK, M.J., and OBRADOVICH, 1998, The age of the Morrison Formation: Modern Geology, v. 22, p. 235–260.

KOWALLIS, B.J., BRITT, B.B., GREENHALGH, B.W., and SPRINKEL, D.A., 2007, New U-Pb zircon ages from an ash bed in the Brush Basin Member of the Morrison Formation near Hanksville, Utah, *in* Willis G.C., Hylland, M.D., Clark, D.L., and Chidsey, T.C., Jr., eds., Central Utah: Geology of a Dynamic Landscape: Utah Geological Association, Salt Lake City, p. 75–80.

KRAPOVICKAS, V., MANCUSO, A.C., MARSICANO, C.A., DOMNANOVICH, N.S., and SCHULTZ, C.L., 2012, Large tetrapod burrows from the Middle Triassic of Argentina: a behavioural adaptation to seasonal semi-arid climate?: Lethaia, v. 46, p. 154–169.

LAUNDRÉ, J.W., 1989, Horizontal and vertical diameter of five small mammal species in southeastern Idaho: Great Basin Naturalist, v. 49, p. 646–649.

LE ROUX, P.C., BOELHOUWERS, J., DAVIS, J.K., HAUSSMANN, N.S., JANTZE, E.J., and MEIKLEJOHN, K.I., 2011, Spatial association of lemming burrows with landforms in the Swedish subarctic mountains: implications for periglacial feature stability: Arctic, Antarctic, and Alpine Research, v. 43, p. 223–228.

LIU, J. and LI, L., 2013, Large tetrapod burrows from the Permian Naobaogou Formation of the Daqingshan Area, Nei Mongol, China: Acta Geologica Sinica, v. 87, p. 1501–1507.

LOCKLEY, M., HUNT, A., CONRAD, K., and ROBINSON, J., 1992, Tracking dinosaurs and other extinct animals at Lake Powell: Park Science, v. 12, p. 16–17.

LOOPE, D.B., DINGUS, L., SWISHER III, C.C., and MINJIN, C., 1998, Life and death in a Late Cretaceous dune field, Nemegt basin, Mongolia: Geology, v. 26, p. 27–30.

LOVEGROVE, B.G., and JARVIS, J.U.M., 1986, Coevolution between mole-rats (Bathyergidaae) and a geophyte, *Micranthus* (Iridaceae): Cimbebasia, v. 8, p. 79–85.

LÖVY, M., ŠKLÍBA, J., HROUZKOVÁ, E., DVOŘÁKOVÁ, V., NEVO, E., AND ŠUMBERA, R., 2015, Habitat and burrow system characteristics of the blind mole rat *Spalax galili* in an area of supposed systematic speciation: PLoS ONE, v. 10, e0133157.

LUO, Z., 2007, Transformation and diversification in early mammal evolution: Nature, v. 450, p. 1011–1019.

LUO, Z., and WIBLE, J.R., 2005, A late Jurassic digging mammal and early mammalian diversification: Science, v. 308, p. 103–107.

LUO, Z., MENG, Q., JI, Q., LIU, D., ZHANG, Y., and NEANDER, A.I., 2015, Evolutionary development in basal mammaliaforms as revealed by a docodontan: Science, v. 347, p. 760–764.

LYNCH, C.D., 1980, Ecology of the suricate, *Suricata suricatta* and yellow mongoose, *Cynictis* *penicillata* with special reference to their reproduction: Memoirs of the National Museum 14, Bloemfontein, 145 p.

MANKIN, P.C., and GETZ, L.L., 1994, Burrow morphology as related to social organization of *Microtus ochrogaster*: Journal of Mammalogy, v. 75, p. 492–499.

MARTIN, A.J., 2009, Dinosaur burrows in the Otway Group (Albian) of Victoria, Austalia, and their relation to Cretaceous polar environments: Cretaceous Research, v. 30, p. 1223–1237.

MARTIN, L.D., and BENNETT, D.K., 1977, The Burrows of the Miocene Beaver *Palaeocastor*, Western Nebraska, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173–193.

MCALPIN, S., DUCKETT, P., and STOW, A., 2011, Lizards cooperatively tunnel to construct a long-term home for family members: PLoS ONE, v. 6, e19041.

MCKENNA, M.C., and BELL, S.K., 1997, Classification of mammals above the species level: Columbia University Press, New York City, 631 p.

MEYER, R.C., 1999, Helical burrows as a palaeoclimate response: *Daimonelix* by *Palaeocastor*: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 147, p. 291–298.

OGG, J.G., 2004, The Jurassic Period, *in* Gradstein, F.M., Ogg, J.G., and Smith, A.G., eds., A Geologic Time Scale: Cambridge University Press, Cambridge, p. 307–343.

OGNEV, S.I., 1947, Mammals of the U.S.S.R. and adjacent countries: Israel Program for Scientific Translation, Jerusalem.

OSTROM, J.H., and MCINTOSH, J.S., 1966, Marsh's Dinosaurs: The Collections from Como Bluff: Yale University Press, New Haven, 416 p.

PARRISH, J.T., PETERSON, F., and TURNER, C.E., 2004, Jurassic "savannah" –plant taphonomy and climate of the Morrison Formation (Upper Jurassic, Western USA): Sedimentary Geology, v. 167, p. 137–162.

PETERSON. F., 1994, Sand dunes, sabkhas, streams, and shallow seas: Jurassic paleo geography in the southern part of the Western Interior Basin, *in* Caputo, M.V., Peterson, J.A., Franczyk, K.J., eds., Mesozoic Systems of the Rocky Mountain Region, USA: Rocky Mountain Section, Society for Sedimentary Geology (SEPM), Denver, p. 233–272.

PIPERINGOS, G.N. AND O'SULLIVAN, R.B., 1978, Principal unconformities in Triassic and Jurassic rocks, Western Interior United States—a preliminary survey: United States Geological Survey Professional Paper,

PLATT, B.F., 2012, Quantification of ichnological, paleoecological, paleohydrological, and paleoclimatological information from the Upper Jurassic Morrison Formation: Unpublished Ph.D. dissertation, The University of Kansas, Lawrence, 513 p.

PROTHERO, D.R., 1981, New Jurassic Mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic Theria: Bulletin of the American Museum of Natural History, v. 167, p. 281–325.

REICHMAN, O.J., and SMITH, S.C., 1990, Burrows and burrowing behavior by mammals, *in* Genoways, H.H., ed., Current Mammalogy: Plenum Press, New York, p. 197–244.

REYNOLDS, J.D., GOODWIN, N.B., and FRECKLETON, R.P., 2002, Evolutionary transitions in parental care and live bearing in vertebrates: Philosophical Transactions of the Royal Society B: Biological Sciences, v. 357, p. 269–281.

RIESE, D.J., HASIOTIS, S.T., and ODIER, G.P., 2011, Synapsid burrows and associated trace fossils in the Lower Jurassic Navajo Sandstone, southeastern Utah, U.S.A., indicates a diverse community living in a wet desert ecosystem: Journal of Sedimentary Research, v. 81, p. 299–325.

ROBINSON, J.W., and MCCABE, P.J., 1998, Evolution of a braided river system: the Salt Wash Member of the Morrison Formation (Jurassic) in southern Utah, *in* Relative Role of Eustasy, Climate, and Tectonism in Continental Rocks, SEPM Special Publications No. 59, Society for Sedimentary Geology (SEPM), p. 93–107.

SCHAETZL, R., and ANDERSON, S., 2009, Soils: Genesis and Geomorphology: Cambridge University Press, Cambridge, 817 p.

SCHARFF, A., LOCKER-GRUTJEN, O., KAWAKLIKA, M., and BURDA, H., 2001, Natural history of the giant mole-rat, *Cryptomys mechowi* (Rodentia: Bathyergidae), from Zambia: Journal of Mammalogy, v. 82, p. 1003–1015.

SHEETS, R.G., LINDER, R., and DAHLGREN, R.B., 1971, Burrow systems of prairie dogs in South Dakota, Journal of Mammalogy, v. 52, p. 451–453.

SIDOR, C.A., MILLER, M.F., and ISBELL, J.L., 2008, Tetrapod burrows the Triassic of Antarctica: Journal of Vertebrate Paleontology, v. 28, p. 277–284.

SKINNER, J.D., 2005, The Mammals of the Southern African Sub-region: Cambridge University Press, Cambridge, 814 p.

SMITH, C.C., and REICHMAN, O.J., 1984, The evolution of food caching by birds and mammals: Annual Review of Ecology and Systematics, v. 15, p. 329–351.

SMITH, R.M.H., 1987, Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 155–169.

SMITH, R.M.H., 1993, Vertebrate taphonomy of the Late Permian floodplain deposits in the southwestern Karoo Basin of South Africa: PALAIOS, v. 8, p. 45–67.

STEINER, M.B., LUCAS, S.G., and SHOEMAKER, E.M., 1994, Correlation and age of the Upper Jurassic Morrison Formation from magnetostratigraphic analysis. In: Caputo, M.V., Peterson, J.A., Franczyk, K.J. (Eds.), Mesozoic Systems of the Rocky Mountain Region, USA. Rocky Mountain Section, Society for Sedimentary Geology (SEPM), Denver, CO, p. 233–272.

SUBALUSKY, A.L., FITZGERALD, L.A., and SMITH, L.L., 2009, Ontogenetic niche shifts in the American Alligator establish functional connectivity between aquatic systems: Biological Conservation, v. 142, p. 1507–1514.

SUMBERA, R., BURDA, H., CHITAUKALI, W.N., and KUBOVA, J., 2003, Silvery mole-rats (*Heliophobius argenteocinereus*, Bathyerigidae) change their burrow architecture seasonally: Naturwissenschaften, v. 90, p. 370–373.

ŠUMBERA, R., MAZOCH, V., PATZENHAUEROVÁ, H., LÖVY, M., ŠKLÍBA, J., BRYJA, J., AND BURDA, H., 2012, Burrow architecture, family composition and habitat characteristics of the largest social African mole-rat: the giant mole-rat constructs really giant burrow systems: Acta Theriologica, v. 57, p. 121–130.

TALANDA, M., DZIECIOL, S., SULEJ, T., and NIEDZWIEDZKI, G., 2011, Vertebrate burrow system from the Upper Triassic of Poland: PALAIOS, v. 26, p. 99–105.

TRACY, C.R., REYNOLDS, S.J., MCARTHUR, L., TRACY, C.R., and CHRISTIAN, K.A., 2007, Ecology of aestivation in a cocoon-forming frog, *Cyclorana australis* (Hylidae): Copeia, v. 4, p. 901–912.

TURNER, C.E., and PETERSON, F., 1992, Sedimentology and stratigraphy of the Morrison Formation in Dinosaur National Monument: University of Wyoming National Park

Service Research Center Annual Report, v. 16, p. 86–91.

TURNER, C.E., and PETERSON, F., 2004, Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem—a synthesis: Sedimentary Geology, v. 167, p. 309–355.

TURNBULL, W. D., and REED, C. A., 1967, *Pseudochrysochloris*, a specialized burrowing mammal from the early Oligocene of Wyoming: Journal of Paleontology, v. 41, p. 623–631.

VLECK, D., 1981, Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*: Oecologia, v. 49, p. 391–396.

VOIGT, S., SCHNEIDER, J.W., SABER, H., HMINNA, A. LAGNAOUI, A., KLEIN, H., BROSIG, A., and FISCHER, J., 2011, Complex tetrapod burrows from Middle Triassic red beds of the Argana Basin (Western High Atlas, Morocco): PALAIOS, v. 26, p. 555–566.

VOORHIES, M.R., 1975a, Vertebrate burrows, *in* Frey, R.W., ed., The Study of Trace Fossils: Spring-Verlag, New York, p. 325–350.

VOORHIES, M.R., 1975b, A new genus and speices of fossil kangaroo rat and its burrow: Journal of Mammalogy, v. 56, p. 160–176.

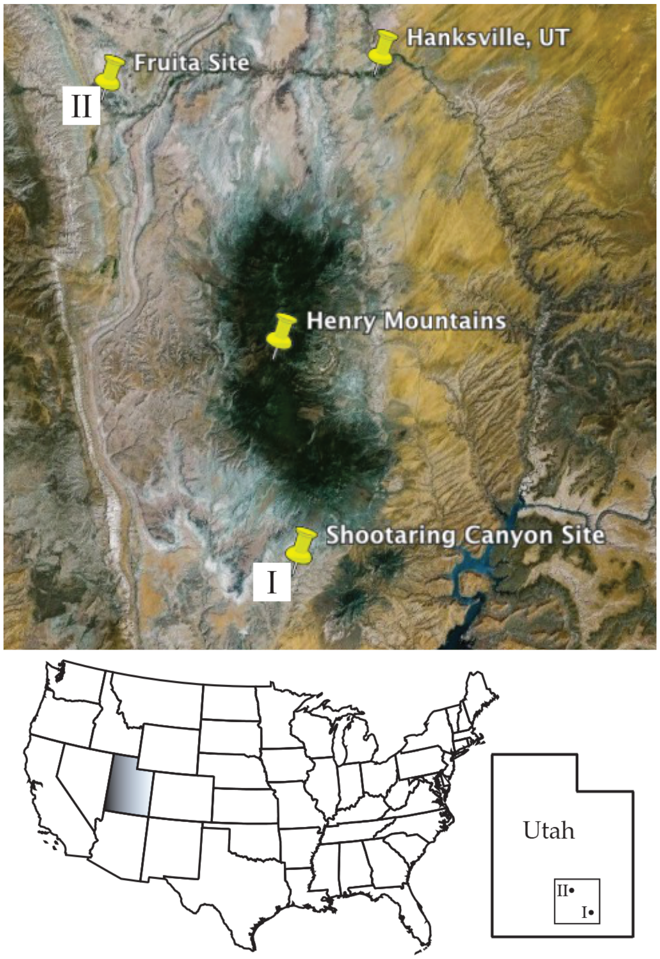

Figure 1—Location of study areas. Locality 1 in Shootaring Canyon (I) near Ticaboo, Utah and Locality 2 (II) near Fruita, Utah. Map image from Google Earth.

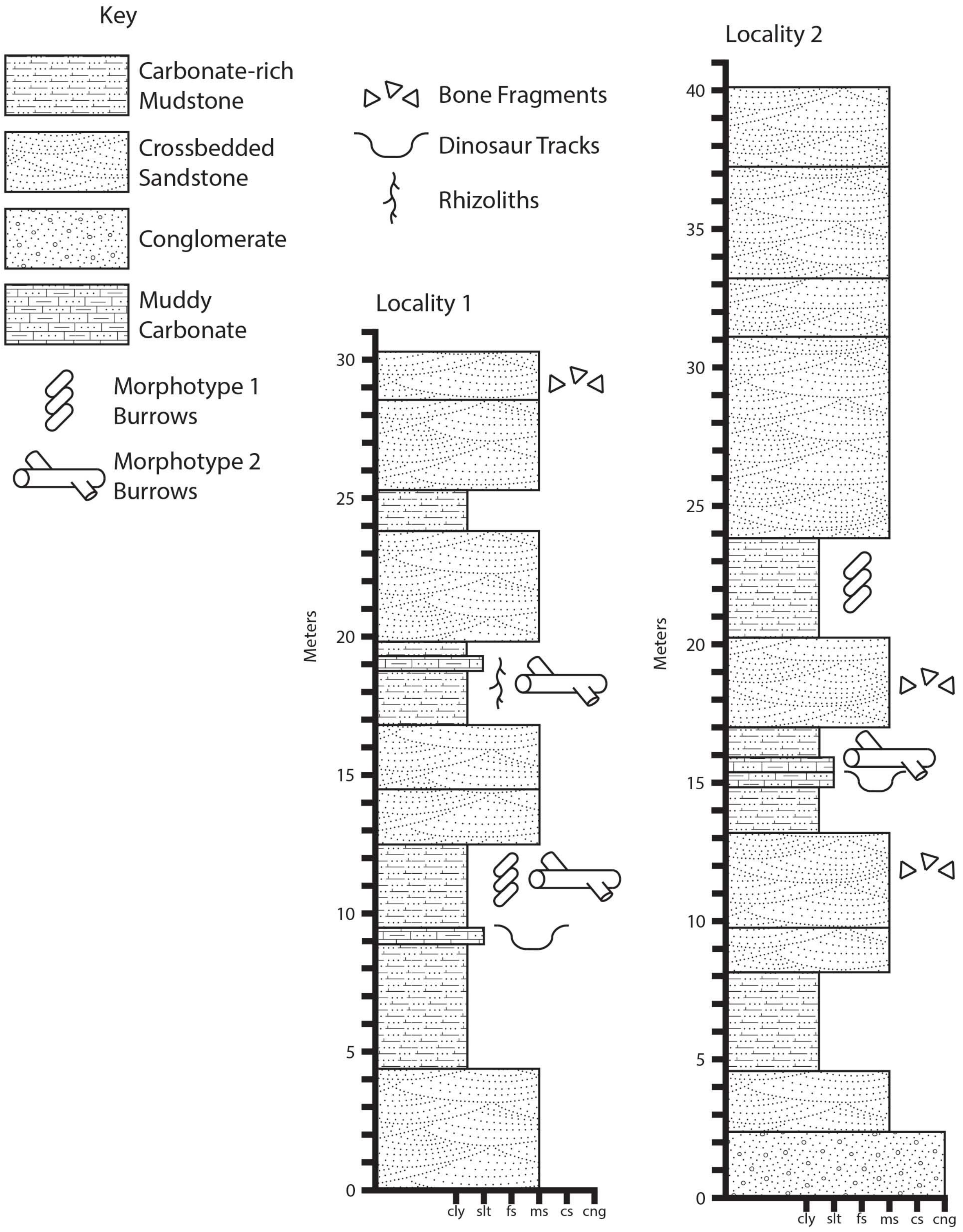
Key
Carbonate-rich Mudstone
Crossbedded Sandstone
Conglomerate
Muddy Carbonate
Morphotype 1 Burrows
Morphotype 2 Burrows
Bone Fragments
Dinosaur Tracks
Rhizoliths
Locality 1
Meters
0
5
10
15
20
25
30
cly
slt
fs
ms
cs
cng
Locality 2
Meters
0
5
10
15
20
25
30
35
40
cly
slt
fs
ms
cs
cng

Figure 2—Stratigraphic sections through the upper part of the Salt Wash Member in the study areas. Grain size: cly = clay; slt = silt; fs = fine sand; ms = medium sand; cs = coarse sand; cng = conglomerate.

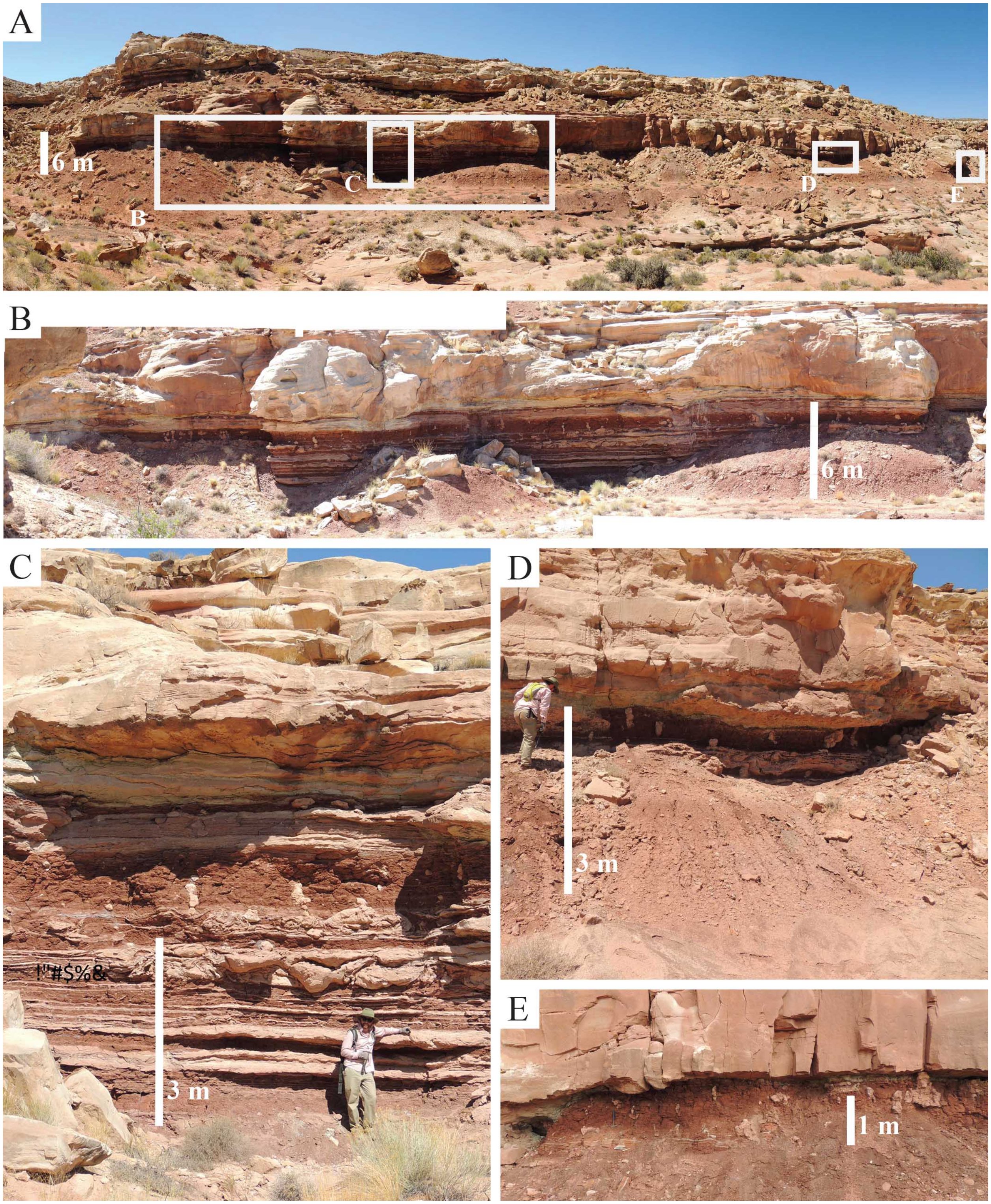
A
6 m
B
C
D
E
B
6 m
C
!"#$%&
3 m
D
3 m
E
1 m

Figure 3—Locality 1. A) Outcrop of south-facing slope. B) Closer view of thickest LS-bearing mudstone. C) Thickest mudstone and overlying sandstone. D, E) Top of LS-bearing mudstone with debris beneath.

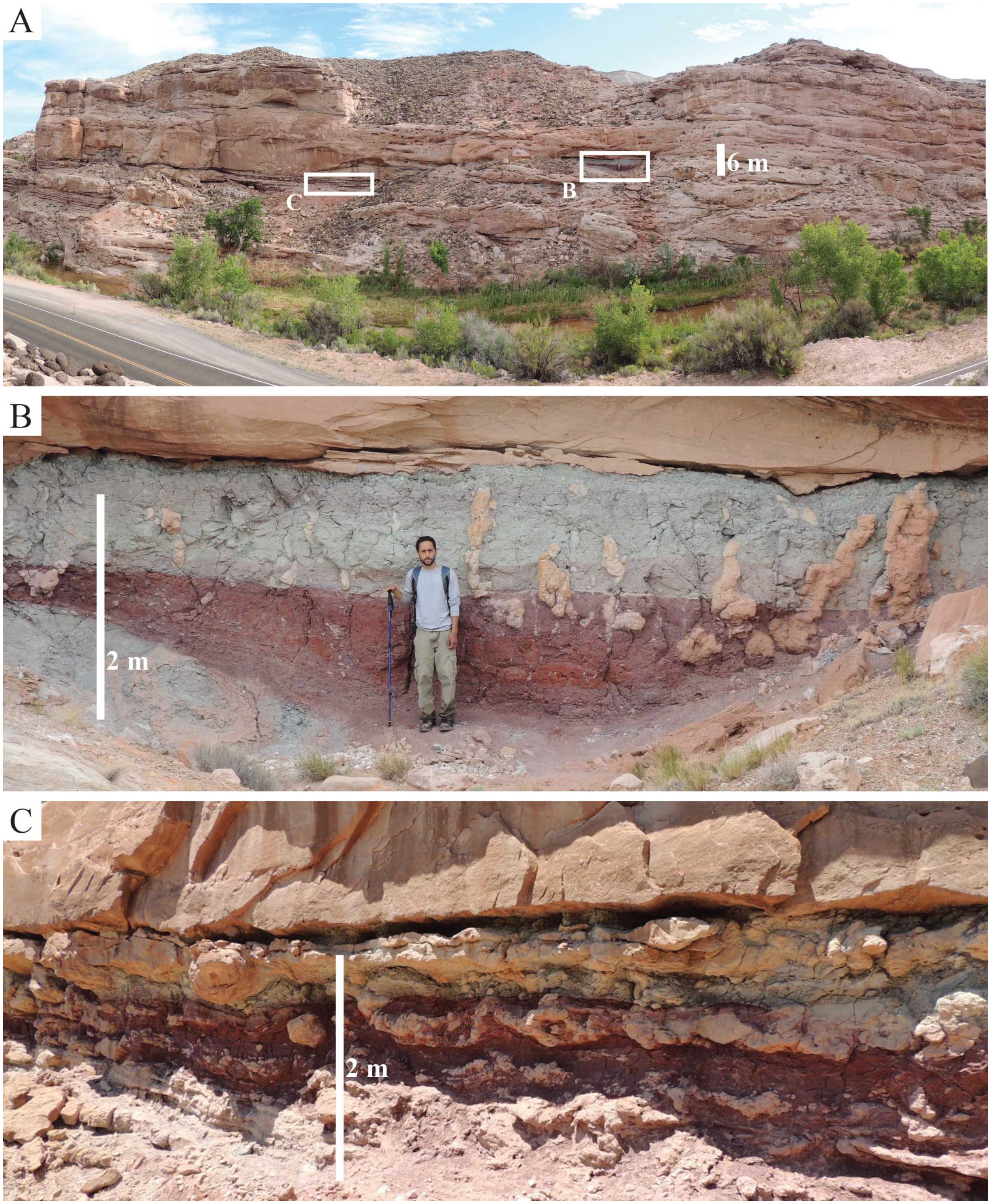

Figure 4—Locality 2. A) View of whole outcrop. B) Highest LS-bearing mudstone. C) Lowest LS-bearing mudstone with interbedded carbonate beds.

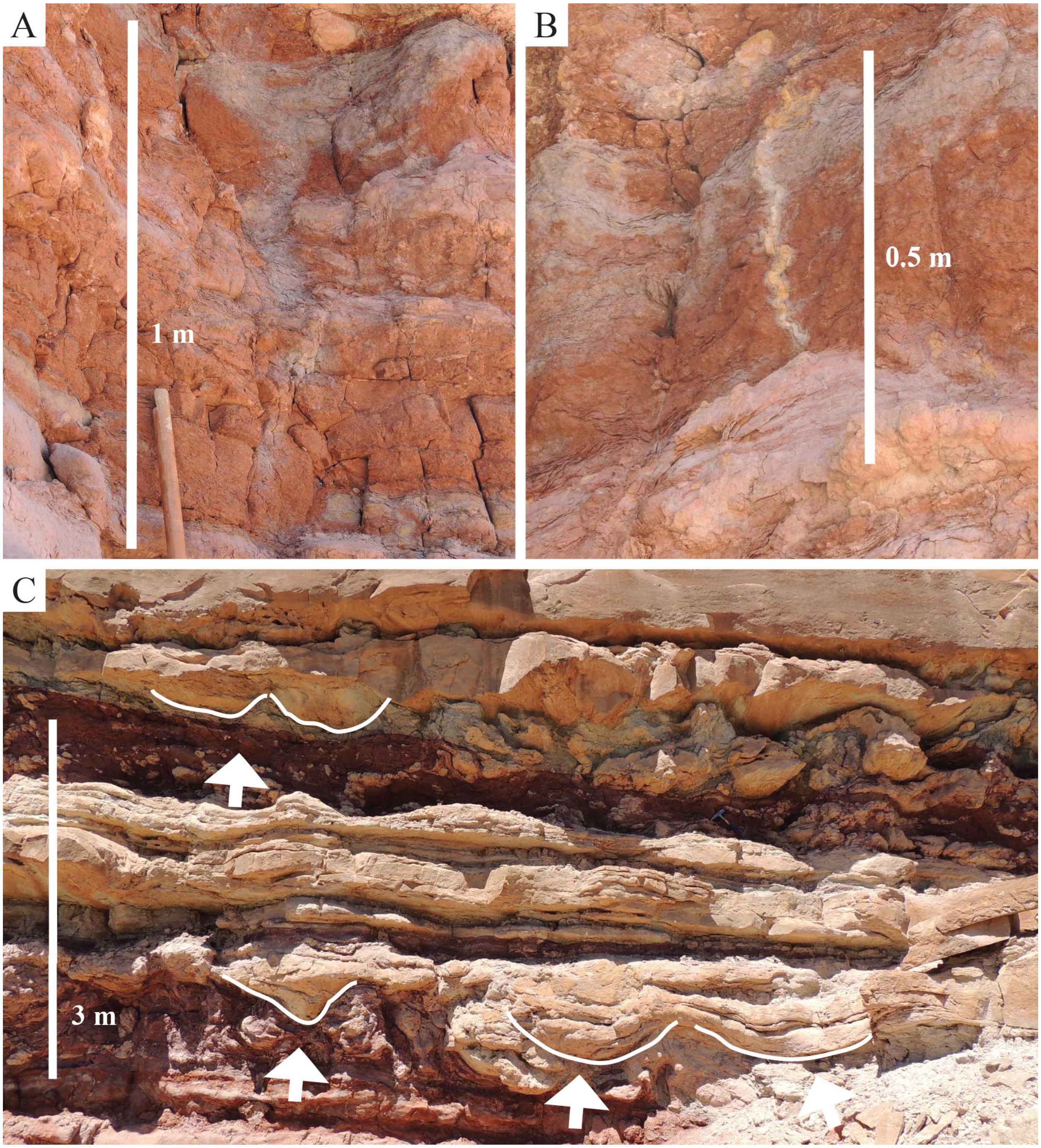

Figure 5—Associated trace fossils in outcrop. A) Rhizohalo at Locality 1. B) Rhizolith at Locality 1. C) Dinosaur tracks at Locality 2.

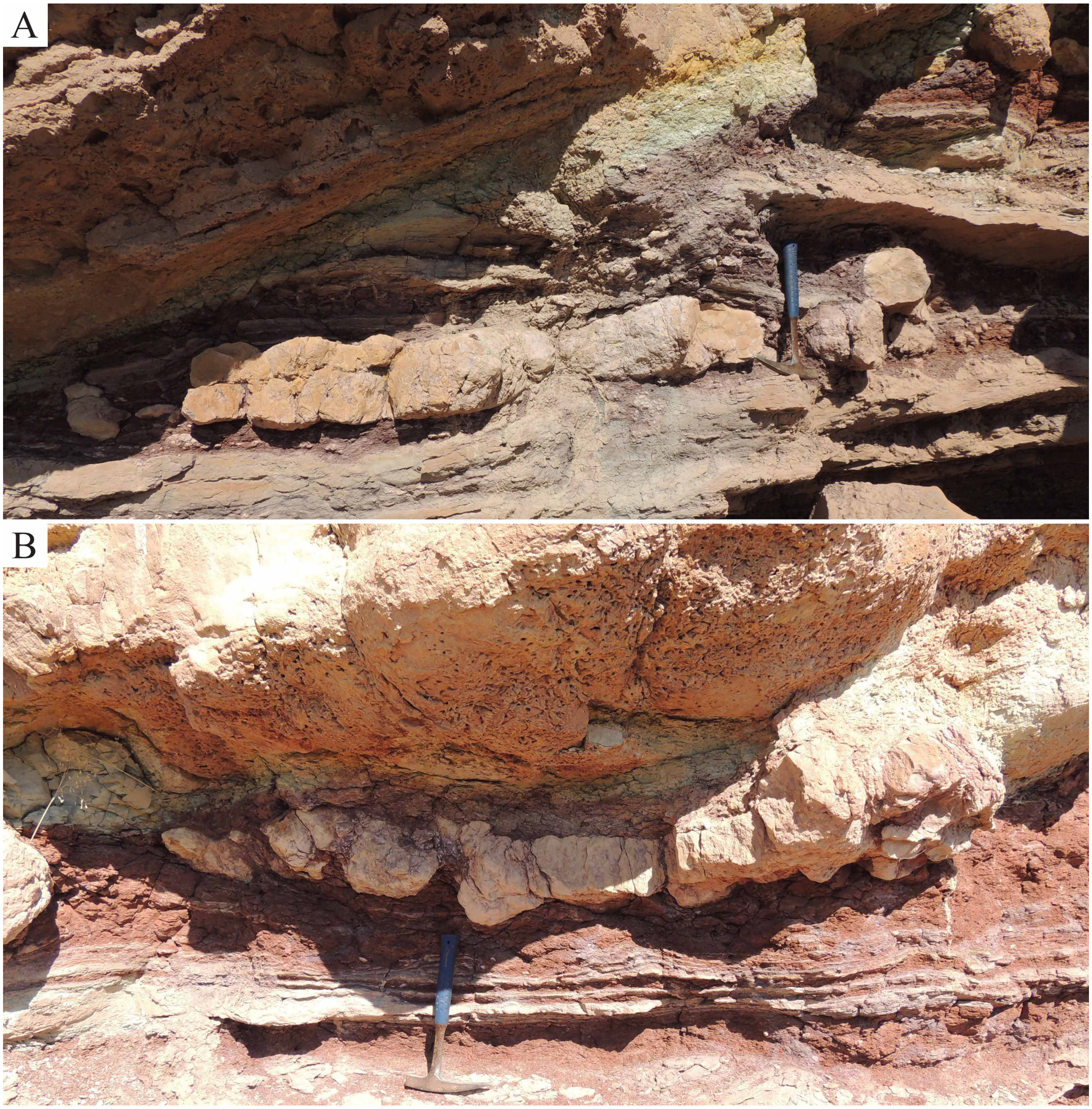

Figure 6—Examples of enigmatic structures that may be burrows. A) The majority of the surface has broken off the specimen. B) This specimen is also broken, but preserves more surface texture. Rock hammer 33 cm long.

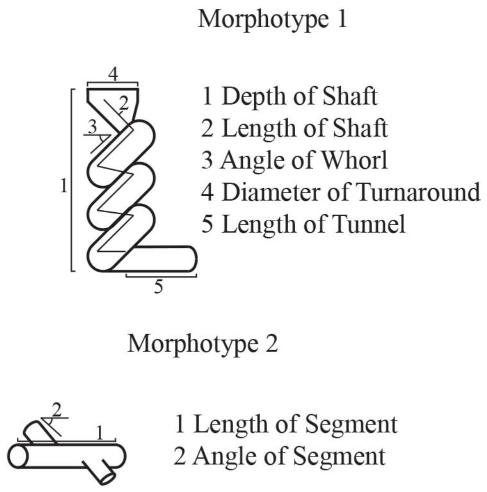

Figure 7—Schematic of burrow measurements. Show that total helix length wasn't measured.

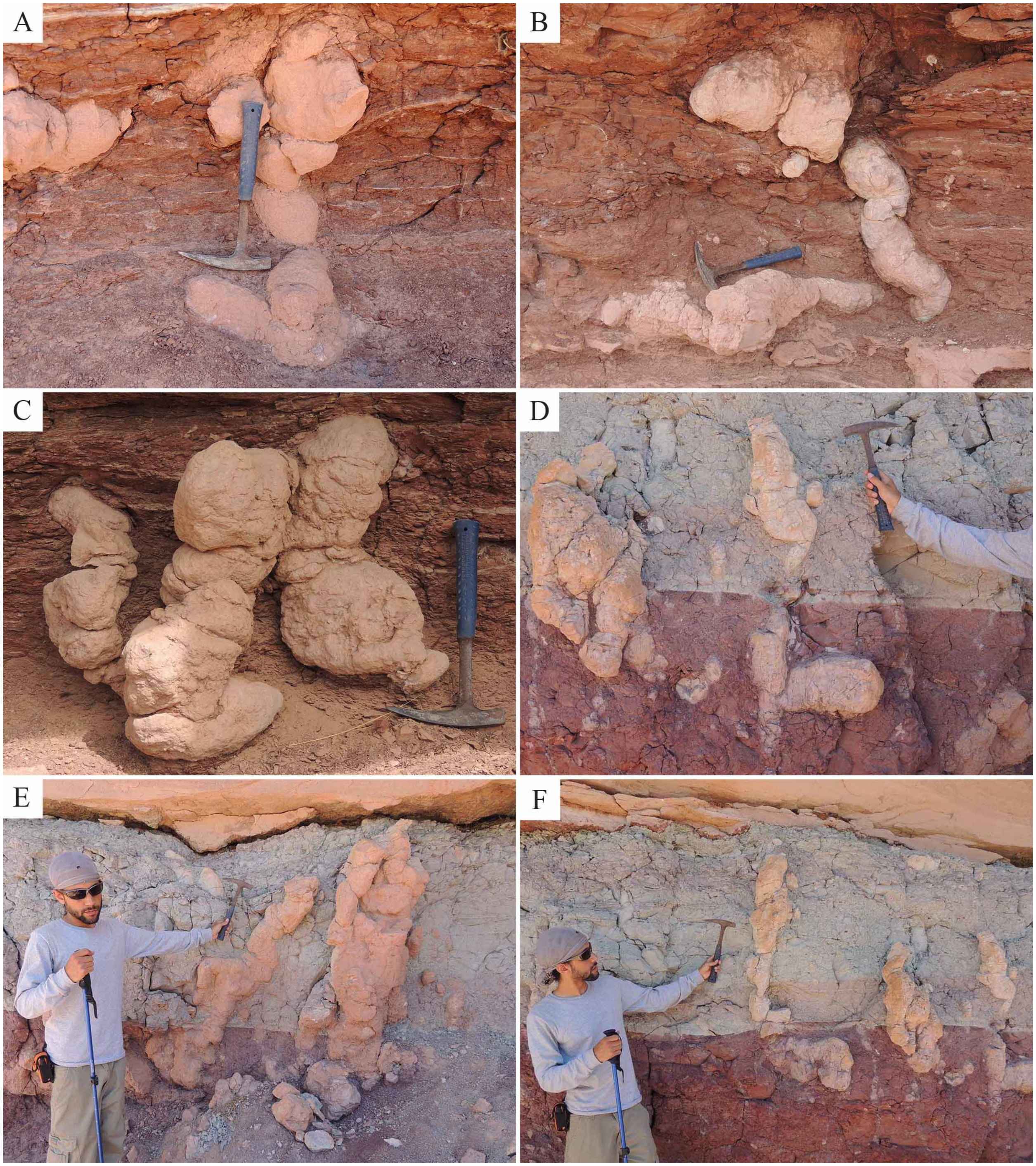

Figure 8—Examples of Morphotype 1 burrows. A, B) Individual specimens from Locality 1 showing helix and tunnel. C) Cluster of specimens from Locality 1 also showing heavy accumulation of carbonate. D, E, F) Specimens from Locality 2 showing helix and tunnel. Rock hammer for scale 33 cm long.

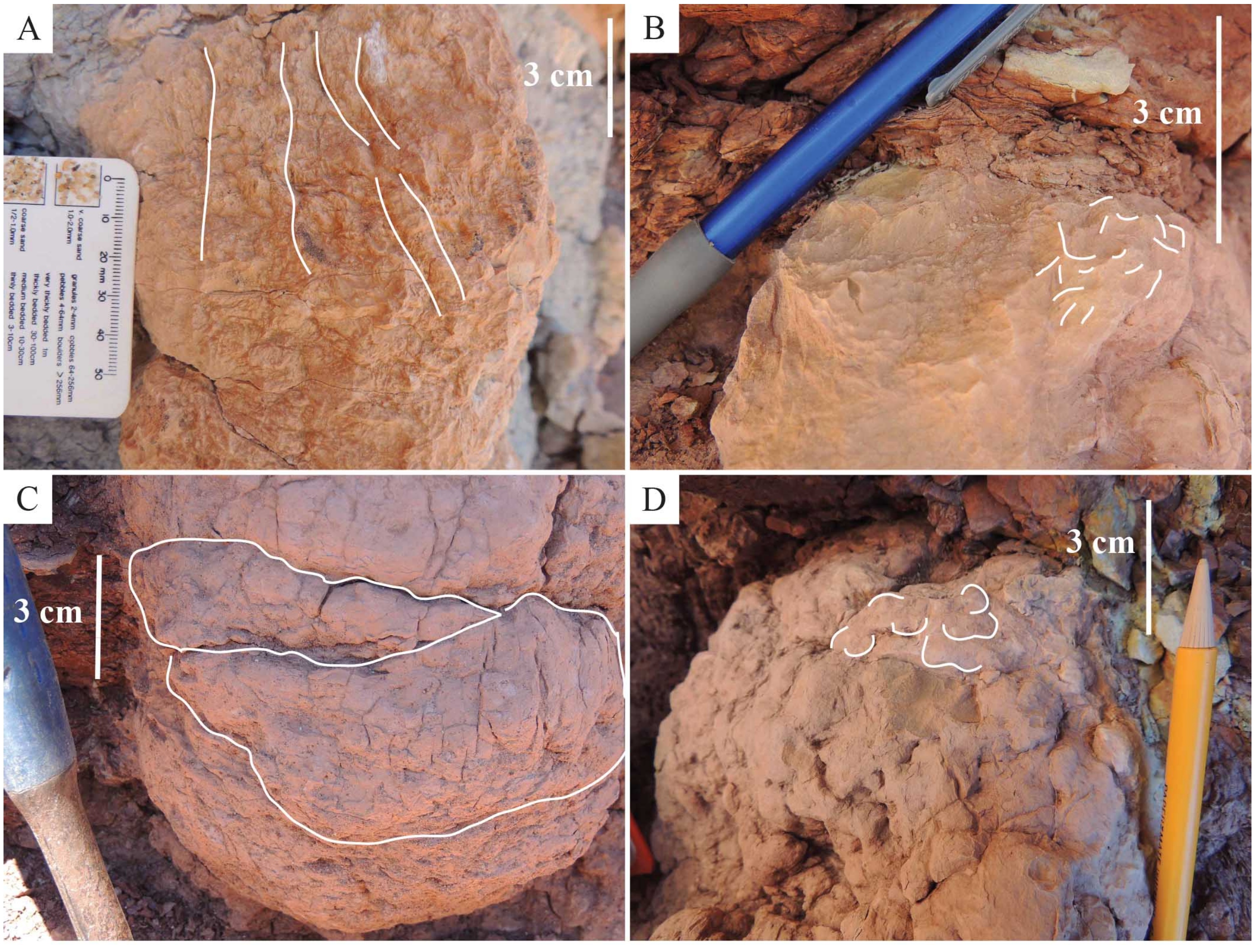

Figure 9—Examples of surficial morphology of Morphotype 1 burrows. A) Large ridges. B) Small ridges. C) Large knobs. D) Small knobs.

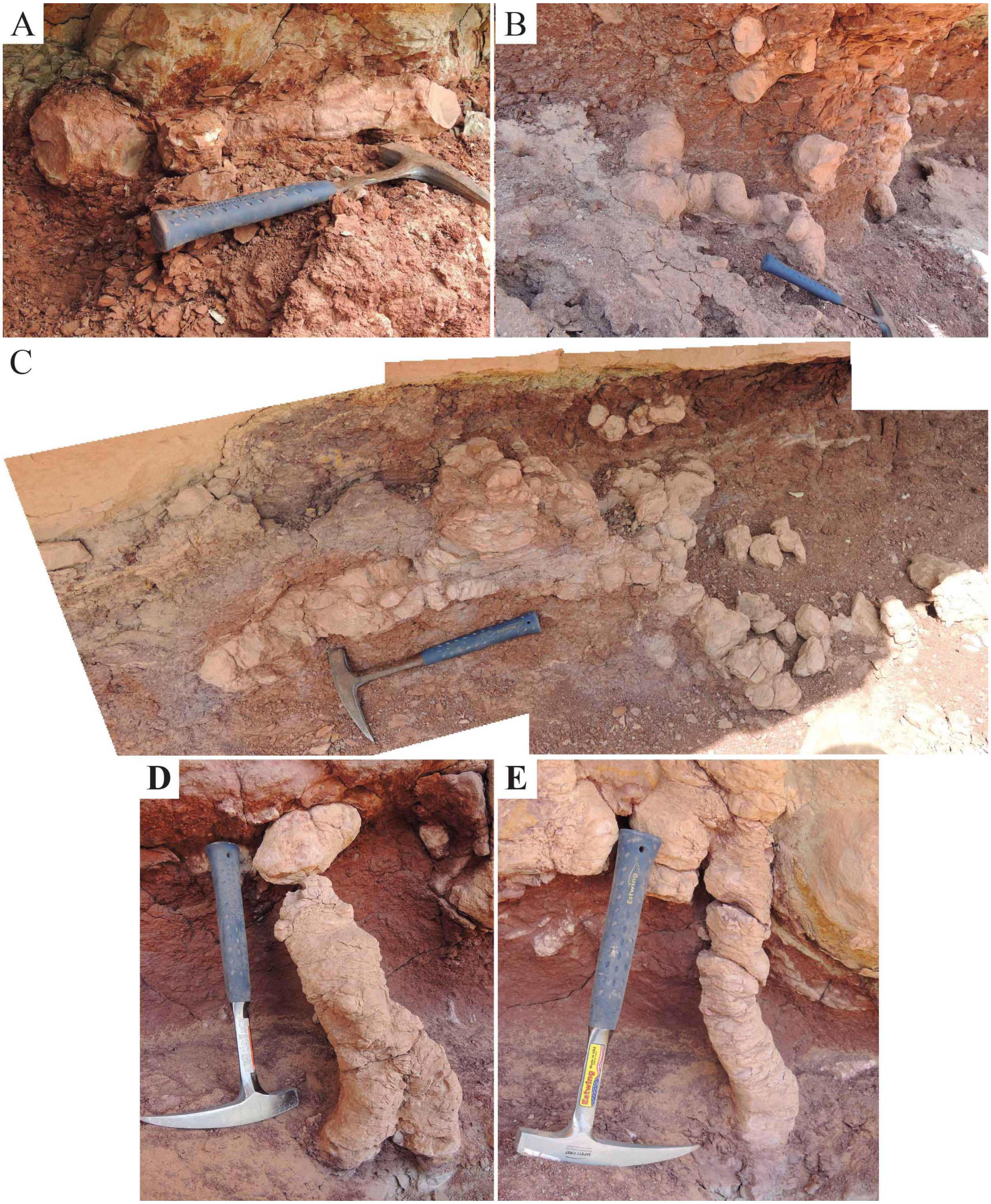

Figure 10—Examples of Morphotype 2 burrows with distinct segments. A) Smaller, fragmented specimen of horizontal tunnel. B) Smaller, fragmented specimen of helical tunnel. C) Large,

complete specimen with multiple segments. D) Smaller, fragmented vertical forking tunnel. E) Smaller, fragmented vertical tunnel. Rock hammer 33 cm long.

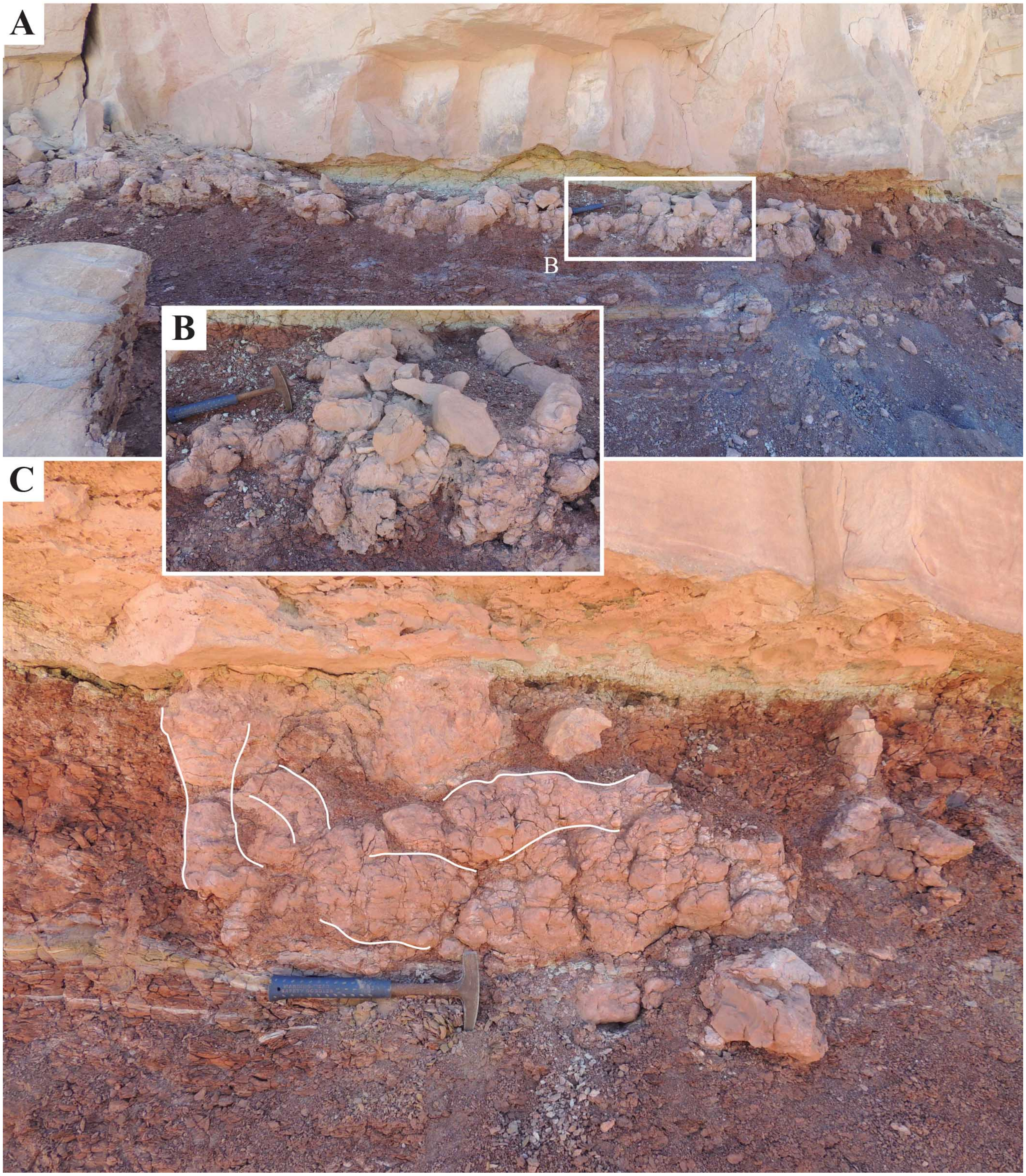

Figure 11—Examples of Morphotype 2 burrows with fused segments. A) Longer specimen with collapsed features. B) Close up showing separated burrow elements. C) Fused specimen with highlighting on potential shaft and tunnel. Rock hammer 33 cm long.

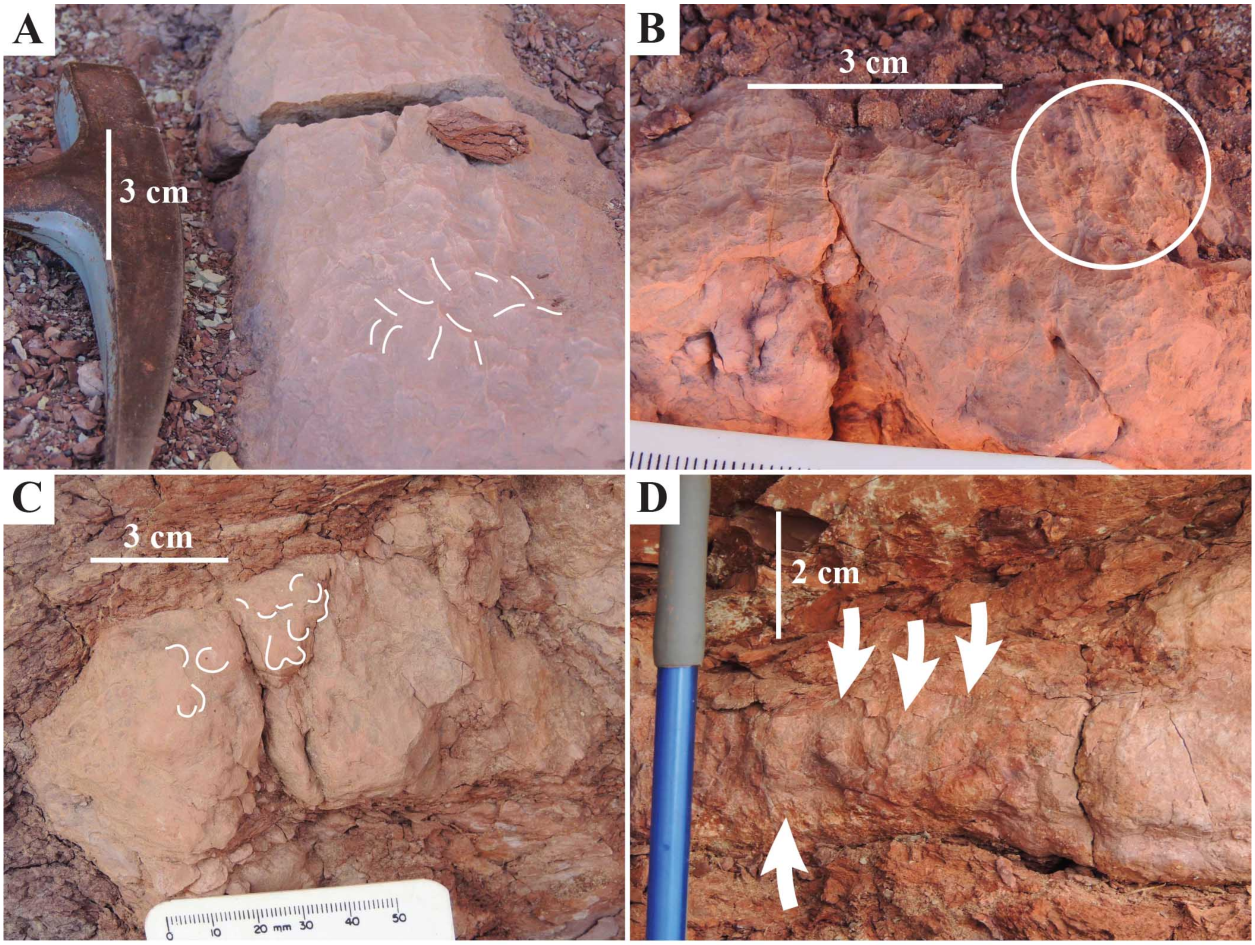

Figure 12—Examples of surficial morphology of Morphotype 2 burrows. A) Small ridges, some highlighted. B) Small ridges and parallel ridges, circled. C) Random knobs, some highlighted. D) Parallel knobs.

	Architectural Morphology	Orientation	Cross Section	Branching	Surfical Morphology	Other	References
Mammal Burrows	Long branching tunnels composed of primary shafts and laterals; helical elements	Random	Elliptical to nearly cylindrical	Simple to complex pattern	Incisor or claw marks on walls reflecting the digging apparatus	Bilobate terminus	Hasiotis et al. 2004; Gobetz 2006; Gobetz and Martin 2006
Therapsid Burrows	Inclined entry and terminal chambers connected by helix	Shallowly inclined	Flattened biconvex; elliptical	Simple	Chevrons of narrow ridges on tops and sides interpreted as scratch marks	Diameter 6–25 cm	Smith 1987; Groenwald et al. 2001; Miller et al. 2001; Hasiotis et al. 2004
Reptiles							
Skink Burrows	Interconnected, inclined tunnels and switc backs; elliptical, straight to curved tunnels	Horizontal and vertical	Elliptical	5–10 segments	Longitudinal median groove, scalloped walls	Terminal chamber absent	Hasiotis et al. 2004; Hasiotis and Bourke 2006; Hembree and Hasiotis 2006
Amphisbaena Burrows	Complex, interconnected networks; multiple branches per junction; cylindrical, sinuous straight tunnels	Horizontal and vertical	Circular to ovoid	20–30 segments	Triangular impressions on tops and sides of tunnels	Terminal chamber absent	
Amphibian Burrows	Long and short elliptical tubes	Predominantly vertical	Elliptical	None	Irregularly spaced nodes	Irregular downward tapering	Hembree et al. 2004, 2005
Rhizoliths	Downward bifurcations with decreasing diameter of branches from main system; similar diameters; dendritic pattern; rectilinear	Varied with horizontal and vertical most common; parallel to laminations or to dip direction	Circular	Branching tubes filled by materials (sand, clay) or with root	Distictive fabric from surrounding matrix	Distictive geochemical compositions and petrographic characteristics from surrounding matrix	Klappa 1980; Loope 1988; Hasiotis 2002; Kraus and Hasiotis 2006
Fluid Escape Pipes	Nearly vertical pillar-like structures cutting across host rock; distinct boudaries with respect to undisturbed wind-deposited sand	Lateral contact of massive or slumped sandstone, nearly vertical, though some display tongue-like bodies	Internal structure: Pipes can be massive, but typically cone-shaped, concentric sediment layers	None	Pipes may contain breccia blocks; external features show flow structures	Relatively homogeneous; smallest pipes 4 mm in diameter, largest pipes > 4 m	Netoff 2002; Huuse et al. 2005; Hasiotis et al. 2007
Eroded-Rock Remnants	No preferred morphology	Toward or parallel to strong winds	No preferred shape	No preffered pattern	Polishing of rock surfaces; etching; flutes and grooves	Primary sedimentary structures preserved	Lancaster 1984

Table 1—Features of biotic and abiotic structures used to identify LS tracemaker. Modified from Riese et al. (2011).

Name	Tracemaker	Architecture	Age	Formation	Environment	Reference
Daemonelix	*Palaeocastor*	Loosely coiled helical shaft with constant diameter, 6–12 whorls leading to horizontal or upward-inclined tunnel ending in terminal chamber.	Early Miocene	Harrison	Alluvial floodplain	Martin and Bennett, 1977
daimonelix (informal)	*Diictodon*	Loosely coiled helical shaft with downward-increasing diameter, 2–3 whorls exapnding into terminal chamber.	Late Permian	Teekloof	Proximal floodbasin	Smith, 1987
Ichnogyrus nididens	small mammal	Tightly coiled helical shaft with increasing diameter along length. Incomplete - both ends broken off.	Early Eocene	Willwood	Floodplain	Bown and Kraus, 1983

Table 2—Other fossilized vertebrate burrows with a helical shaft similar to Morphotype 1.

CHAPTER THREE: *DAEMONELIX MARTINI* AND *FRACTUSSEMITA HENRII* - NEW ICHNOTAXA OF VERTEBRATE BURROWS FROM THE SALT WASH MEMBER, UPPER JURASSIC MORRISON FORMATION, USA

Submitted to Journal of Paleontology as:

RAISANEN, D.C.W. and HASIOTIS, S.T., in review, ***Daemonelix martini*** **and *Fractussemita henrii*—new ichnotaxa of vertebrate burrows from the Salt Wash Member, Upper Jurassic Morrison Formation, USA.**

ABSTRACT

Large-diameter burrows in pedogenically modified floodplain deposits in the Salt Wash Member, Upper Jurassic Morrison Formation in southeast Utah, U.S.A., are interpreted as mammal burrows. *Daemonelix martini* (n. isp.) exhibits a helical shaft down to a horizontal tunnel with mean depth of 71.4 cm from the interpreted paleosurface. The mean path length of the shaft is 99.4 cm; mean dip of the whorls in the helices is 39°. The mean tunnel length is 42.3 cm. Shafts and tunnels are ovoid in cross section with the horizontal diameter slightly larger than the vertical; shaft averages 9.2 cm wide and 7.3 cm tall, tunnel averages 10.7 cm wide and 10.7 cm tall. The tracemaker was likely a fossorial mammal that used the burrows as a shelter when not foraging above ground; burrows are assigned to domichnia. *Fractussemita henrii* (n. igen. and n. isp.) is a network of interconnected shafts and tunnels; shaft and tunnel segments are straight, curved, or helical. The segments are at different angles 0–89º; mean length of a section is 30.7 cm. The cross sections of all elements are ovoid; mean width is 6.3 cm and the mean height is 4.9 cm. The burrows are interpreted as the work of a social mammal and represent multiple tracemaker behaviors—protection, denning, foraging. Burrows are assigned to

polychresichnia. Surficial morphologic features on both types preserved on the burrow walls are interpreted as scratch marks from tracemaker claws 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.

INTRODUCTION

This paper presents the new ichnotaxa, *Daemonelix martini* n. isp. and *Fractussemita henrii* n. igen. and n. isp. for vertebrate burrows in the Salt Wash Member of the Upper Jurassic Morrison Formation in southeast Utah, USA. These structures have previously been interpreted as vertebrate burrows (Hasiotis, 2002, 2004, 2008; Hasiotis et al., 2004), but have not been ichnotaxonomically treated. We present possible behaviors and tracemakers represented by *D. martini* and *F. henrii*, and comparisons are made with other burrows attributed to synapsids.

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, eolian, 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; McCahon and Miller, 2015; Bordy and Krummeck, 2016; Bordy et al., 2017). Vertebrate burrow diversity may seem limited when compared with invertebrate burrow diversity (Häntzschel, 1975), but closer analysis of architectural and surficial burrow morphology reveal significant identifying characteristics of ichnospecies. Providing an ichnotaxonomic assessment of *Daemonelix martini*, *Fractussemita henrii*, and other vertebrate trace fossils formalizes unique morphologies with a specific ichnotaxonomic designation. This specificity will enhance communication and understanding among researchers studying vertebrate burrows in deep time.

Daemonelix martini occurs in terrestrial environments in the vadose zone. They are compared with other helical burrows interpreted as therapsid and mammal in origin (Martin and Bennett, 1977; Bown and Kraus, 1983; Smith, 1987; Krapovickas et al., 2012). *Fractussemita henrii* also occur in the vadose zone and are compared with network burrows interpreted as therapsid and mammal in origin (Groenwald et al., 2001; Hasiotis et al., 2004; Gobetz, 2006; Gobetz and Martin, 2006; Riese et al., 2011; Colombi et al., 2012; Bordy and Krummeck, 2016, 2017).

GEOLOGICAL SETTING

The Morrison Formation extends over 1×10^6 km^2 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 floodplain and crevasse-splay deposits and is interpreted as a braided river system (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).

Daemonelix martini n. isp. and *Fractussemita henrii* n. igen. and n. isp. are found at two localities. 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. Both localities are composed of alternating beds of sandstone and mudstone interbedded with carbonate. The sandstones are buff colored and medium grained with coarser pebble lag deposits at the bottom contacts. All sandstones have

~0.3-m long crossbeds and are interpreted as channel deposits. The mudstones are carbonate cemented, clay rich, and exhibit slickensides and pseudoanticlines. Mudstone is red–brown or gray–green with differences occurring within a single bed. The red–brown is interpreted as well drained, oxidative conditions and the gray–green represents poorly drained, reducing conditions. The carbonate beds are beige. The interbedded mudstone-carbonate intervals are interpreted as floodplain paleosols. The lower contacts of the mudstones are gradational and the upper contacts are sharp scour surfaces. There are three mudstone layers at each site. The burrows are present in the lowest and middle paleosol at Locality 1 and the uppermost and middle paleosol at Locality 2 (Fig. 2). The two localities represent different locations in the same environment, but beds cannot be positively correlated due to local variation in scouring and deposition.

The Morrison Formation has produced a wealth of trace and body fossils from a variety of sites (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 types of invertebrate nests and burrows (Stokes, 1957; Lockley, 1992; Robinson and McCabe, 1998; Hasiotis 2004, 2008). Besides burrows of *D. martini* n. isp. and *Fractussemita henrii* n. igen. and n. isp., we identified bone fragments, dinosaur tracks, and rhizoliths at both localities.

METHODS

Over 150 structures were examined and 85 were interpreted as burrows. Potential burrows were measured with vinyl measuring tape and mechanical calipers (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 A). 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.

SYSTEMATIC ICHNOLOGY

DAEMONELIX ichnogenus, Barbour, 1896

Diagnosis.—Terrestrial unlined helical shaft with basal expansion.

Description.—A helical shaft down from a surface that exhibits an expansion at the base that may be a small chamber, tunnel, or both (Barbour, 1896; Martin and Bennett, 1977; Smith, 1987). There is space between the whorls of the helix. The cross section of the structures may be ovoid to bean shaped. The structures are unlined. Surface features may record marks from excavators.

Etymology.—Latin daemon=demon, helix=corkscrew.

DAEMONELIX MARTINI new ichnospecies

Fig. 4 for major architecture, Fig. 5–7 for *in situ* examples, Fig. 8 for surficial morphology

Diagnosis.—Unlined vertical to slightly subvertical, ovoid, helical shaft with basal horizontal, ovoid tunnel; wide flare at top of helix narrows to smaller constant diameter through rest of helix and tunnel.

Description.—Full relief casts *in situ* and in float preserved by carbonate, sometimes recrystallized, without a lining or internal structures. Composed of a vertical to subvertical helical shaft extending down from the paleosurface that joins a horizontal tunnel at an L-shaped junction. The majority of shafts were vertical. Of those that were subvertical, the dip angle was 35–57° from the horizontal surface. A widening at the top of some shafts is present. Where present, this expansion has a diameter of 15.2 cm to 36 cm. Helices penetrated 33.7 cm to 155.6 cm below the paleosurface and have a path length of 54.6 cm to 143.5 cm. The dip of the helical whorls is 26–67° from the horizontal. The cross section of both the shaft and the tunnel is ovoid. Shaft cross sections have 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 have a vertical diameter of 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 outcrop surface. 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 in outcrop.

Four surface textures—two types of ridges and two types of knobs—comprise 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 more 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 < 1 cm long that join at a variety of angles to create a jagged surface texture; their height is < 1 cm, 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. Size varies with the size of the shaft. They have expanded into each other and these large knobs are separated by thin cracks up to 1.5 cm deep. The small knob texture has individual knobs occurring together and ~1 cm in diameter. Sometimes these are present on the larger knobs.

Etymology.—Named after the late paleontologist Dr. Larry Martin, for his contribution to the study of *Daemonelix* and its tracemakers.

Types.—Holotype is represented in Fig. 4 and may be viewed in the field. Paratypes are represented in Fig. 6 and 7.

Occurrence.—Upper Jurassic Morrison Formation, Salt Wash Member, Locality 1 37°45'N and 110°42'W, Locality 2 38°17'N and 111°7'W. More detailed coordinates and meter levels are available upon request to protect the site.

Similar ancient vertebrate burrows

Multiple types of fossil burrows exhibit a similar helical architecture. Two of these burrows are already included in *Daemonelix*.

Martin and Bennett (1978).—Structures found in early Miocene deposits of western Nebraska and eastern Wyoming are interpreted as the burrows of three beaver taxa (Martin and Bennett, 1977; Martin 1987). These burrows were the first to be called *Daemonelix* (Barbour, 1892, 1895). Body fossils of the excavators are found preserved in the terminal chambers of some burrows (Peterson, 1905). Surficial features left by the incisors and claws of the tracemaker during excavation are used to identify other burrows. Fossils of carnivores (e.g., *Zodiolestes*) have also been found in some daemonelices (Riggs, 1945) and are, therefore, interpreted as predators searching the burrow system for prey.

Burrows produced by *Palaeocastor* sp. are composed of a helical shaft down from the paleosurface to a horizontal or upward inclined living chamber. They are found in groups interpreted as colonies, with one containing 186 burrows. Helixes have six to 12 coils at an angle of 25–30°. Helixes are 210–275 cm long. Depth of the helix is consistent across a locality. Helix cross sections vary from 5–21 cm, with small, medium, and large groupings for each of the three taxa of burrowing beavers, and are nearly circular with a widening diameter at the living chamber. The living chamber is 14–22 cm in diameter. The upward incline of the living chambers is 2–37°. There is no relationship between diameter and inclination. The living chambers are randomly oriented within a group, but never intersect. The features on the upper half of the burrow surface are interpreted mostly as incisor marks from excavation and the features on the bottom half are interpreted mostly as claw marks from moving out soil and general use.

Daemonelix martini is most similar to this original *Daemonelix* burrow type, but *martini* is smaller on average. The most important difference is the nature of the tunnel. Burrows of *Daemonelix* typically have a tunnel at the bottom of the helix angled above the horizontal and a distinct terminal chamber, whereas *D. martini* have a subhorizontal tunnel and no defined chamber. The tunnel itself in *D. martini* may be viewed as a chamber.

Smith (1987).—Structures found in Teekloof Formation of the Permian Beaufort Group in the Karoo Basin of South Africa are interpreted as the burrows of the dicynodont *Diictodon* (Smith, 1987). These burrows are informally assigned to the ichnogenus *Daemonelix*. Body fossils of the excavators are found preserved in the terminal chamber of some burrows.

Diictodon burrows are helixes composed of three sections—an upper decline, a middle spiral of 2 to 3 whorls, and a terminal chamber. The helix widens as it descends from 6 cm at the paleosurface to 16 cm at the end of the whorls to 25 cm in the terminal chamber. The cross section at the top of the helix is planoconvex. The cross section becomes more elliptical in the spiral with a width/height ratio of 2. The living chamber cross section is flattened biconvex. Individual burrows decline at a consistent angle, but between burrows the angle varies 10–32°.

Burrows reach an average depth of 0.5 m and few go deeper than 0.75 m. The surface of the burrows preserves parallel ridges on the outer wall of the spiral. These form a chevron pattern on the sides and roof of the terminal chamber. The bottom of the terminal chamber has similar ridges along the long axis and thin casts interpreted as rootlets.

Daemonelix martini differs from *Diictodon* burrows assigned to *Daemonelix* sp.in the shape of the helix by staying a uniform diameter from top to bottom and not expanding as the helix goes deeper. *Daemonelix martini* has a distinct separate tunnel coming off the last whorl of the helix at an L-junction, not a termination that is a greatly expanded, but smooth extension of the last whorl. The cross section of *D. martini* is more uniform and round.

Bown and Kraus (1983).—A structure found in the lower Eocene Willwood Formation in Wyoming, U.S.A., is interpreted as the burrow of a small mammal and designated *Ichnogyrus nididens* based on the architecture (Bown and Kraus, 1983). No body fossils are found associated with the burrow.

Ichnogyrus nididens is composed of a tight, symmetrical helix of 5.5–6 whorls. Each whorl is in contact with the one above and below. Unfortunately, both ends have been broken off. The helix is 22.2 cm tall and 3.5–4.6 cm in diameter. The whorls increase gradually in height and width from one end to the other. The specimen was found in float. The orientation is hypothesized to be vertical based on other types of helical burrows. The helix is hypothesized to increase in size from top to bottom and enlarge further in a terminal chamber. The fill shows no internal structures. The surface is smooth and preserves no excavation marks of the tracemaker.

Daemonelix martini is considerably larger than *Ichnogyrus nididen* in all measures, and *D. martini* lacks very tight whorls. There is space between the whorls of the *D. martini* helix.

Krapovickas et al. (2013).—Structures found in the Middle Triassic Tarjados Formation in northwest Argentina are interpreted as the burrows of nonmammalian cynodonts. The burrows are composed of a surface opening, inclined tunnel, and terminal chamber. The tunnel is up to 130 cm long, 8–14 cm tall. The incline of the tunnel varies 22–30° and the tunnel goes to a depth of 49–63 cm. Some portions of the tunnel have a bilobate cross section.

Surficial morphology produced during excavation is scarce and not described in detail. Those present are interpreted as scratch marks. They are most commonly preserved on burrow base and lateral walls and align with the long axis of the burrow.

Daemonelix martini differs from these burrows by having a helical, not straight, shaft that penetrates deeper than the Argentinian burrows. *Daemonelix martini* has a distinct separate horizontal tunnel with minimal widening, nothing bulbous defined as a horizontal chamber. *Daemonelix martini* has a round and uniform cross section.

Possible behaviors and tracemakers

Daemonelix martini likely preserves dens excavated by an individual or a pair of animals based on size and complexity. 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). *Daemonelix martini* were likely used for shelter from predators and weather. Species that make helical burrows spend most their day within, but come aboveground to forage and interact with other members of the species (Reichman and Smith, 1990; Kinlaw, 1999). The similarity between *D. martini* and the daemonelices produced by the Miocene beaver *Paleocastor* suggest that the tracemaker used *D. martini* in a similar way—sheltering in the burrow when not foraging aboveground (Martin and Bennett, 1977). *Daemonelix martini* is, therefore, assigned to the behavioral category domichnia.

There are eight (McKenna and Bell, 1997) to 13 (Kielan-Jaworowska et al., 2004) mammal lineages at the ordinal or family level identified from 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*, a docodontan (mammalilaform) 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). *Daemonelix martini* was probably constructed by an as yet undiscovered tracemaker or a known species that had no fossorial adaptations of its anatomy preserved.

FRACTUSSEMITA new ichnogenus

Type Ichnospecies.—**FRACTUSSEMITA HENRII** new ichnospecies

Diagnosis.—Unlined, low density maze of Y-branched tunnels and shafts.

Etymology.—Latin, fractus = broken, semita = path.

FRACTUSSEMITA HENRII new ichnospecies

Figures 9–12

Diagnosis.—Only known ichnospecies, same for ichnogenotype.

Description.—*Fractussemita henrii* is found in full relief casts *in situ* and in float. The burrows are unlined with no internal structures. Specimens are composed of an interconnected network of shafts and tunnels oriented at various angles. Individual elements are straight, curved, or helical. Mean length of a section is 29.97 cm; range ~1.00–93.27 cm. Cross sections of all elements are ovoid. Mean vertical diameter is 4.87 cm; range 2.84–14.04 cm. Mean horizontal diameter is 6.33 cm; range 4.47–8.66 cm. Segments vary from 0º to 89º from the horizontal and mean angle of inclination is 31º. Interconnected segments are joined randomly in a maze pattern. These burrows are found at Locality 1 in the middle and lowest paleosols and in the highest paleosol at Locality 2. Preservation is varied within the group with some 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. The first ridge texture is formed by short, thin ridges < 1 cm long and < 1 cm high that join together at odd angles to create a jagged, serrated 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 are small knobby texture. These knobs are up to 2 cm long and < 1 cm high. Arrangement of these knobs is random. A second knob 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.

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

Type.— Holotype is represented by E in Fig. 9 and may be viewed in the field. Paratypes are represented A—D in Fig. 9 and Fig. 10 and 11.

Occurrence.— Upper Jurassic Morrison Formation, Salt Wash Member, Site 1 37°46’“N and 110°42’”W, Site 2 38°17’”N and 111°7’W. More detailed coordinates and meter levels are available upon request to protect the site.

Similar ancient vertebrate burrows

Gobetz and Martin (2006).—Structures found in the early Miocene upper Harrison Formation of Nebraska are interpreted as the burrows of digging rodents, potentially *Gregorymys* sp., a gopherlike rodent found in the area (Gobetz and Martin, 2006). The burrows are assigned to the ichnotaxon *Alezichnos trogodont*. They are composed of sinuous tubes with varied direction and orientation. The elements can form a complex tunnel system with multiple branches. Some tunnels are weakly helical. Burrow cross sections are 5.6–6.7 cm in diameter and varies from being wider horizontally to wider vertically.

The surface of *A. trogodont* preserves incisor and claw traces produced during excavation. The 5.4-mm-wide incisor marks are dominant on the roof and sides of the burrows. The claw marks—3.9 mm wide and spaced up to 6 mm between grooves—are dominant on the floor, some low sides, and turns of the burrow tunnels; as well as small chambers. Both incisor and claw marks tend to parallel the long axis of the burrow.

Fractussemita henrii is like *Alezichnos trogodont* in being a network of tunnels at varied orientation, but with some important differences. The tunnel segments in *F. henrii* are less sinuous than in *Alezichnos trogodont.* Only one segment in *F. henrii* is described as helical, but many segments of *A. trogodont* are described as weakly helical. The holotype of *A. trogodont* has a bilobate chamber while no chambers are identified as part of *F. henrii.*

Gobetz (2006).—*Alezichnos chelecharatos* is found in the upper Miocene Pawnee Creek Formation of northeast Colorado are interpreted as the burrows of the mylagaulid rodent *Pterogaulus* [= *Mylagaulus*] *laevis* (Gobetz, 2006). They consist of a sinuous main tunnel with occasional branching of secondary tunnels. The primary tunnel is up to 7 m long with an ovate cross section 11–18 cm in diameter.

The surface of *A. chelecharatos* preserves ridges 3.7 mm wide and up to 9.3 mm high interpreted as claw marks produced during excavation. They occur as sets of two to three parallel ridges.

Fractussemita henrii has a similar architecture, but is smaller than these burrows in every way. The tunnel system formed by these Miocene burrows is an order of magnitude larger in total length than anything recorded for *F. henrii*. The cross sections of *F. henrii* tunnels are about half. The textures interpreted as excavation marks on *F. henrii* are smaller than their equivalent on the Miocene burrows.

Hasiotis et al. (2004).—Structures found in the Owl Rock Member of the Upper Triassic Chinle Formation in southeast Utah are interpreted as vertebrate burrows (Hasiotis et al., 2004). A network of horizontal tunnels, vertical and helical shafts, and chambers characterize these burrows. Burrow diameter ranges 4–15 cm with a circular to subcircular cross section. Shorter segments 10–35 cm long with smaller cross sections connect the longer and wider segments. Chambers are two to three times wider than the tunnels or shafts. A dicynodont is the hypothesized tracemaker.

The surface of these structures is largely obscured by precipitated carbonate. Visible features include thin longitudinal ridges interpreted as claw marks and a covering of fine rhizoliths.

Fractussemita henrii is a simpler, less-varied burrow system than these Triassic burrows. The tunnels more uniform in diameter within each network of *F. henrii.* There were no chambers identified among the connected tunnels of *F. henrii.*

Colombi et al. (2012).—Three types of structures from the Upper Triassic Ischigualasto and Los Colorados formations of northwest Argentina are interpreted as the burrows of various therapsids.

Morphotype 1 burrows are composed of T-branched, horizontal and subhorizontal tunnels, chambers, and short vertical shafts. The burrow cross section is elliptical with a mean diameter of 10 cm. Some tunnel floors have a longitudinal medial groove. The chambers have a mean diameter of 25 cm. The shafts are < 20 cm long and come down at tunnel beginnings and intersections. Individual burrows cover up to 2 m^2. Some poorly preserved 2–3 cm wide ridges on the burrow surface are interpreted as scratch marks.

Morphotype 2 burrows are composed of simple networks with one or two tunnels and several vertical shafts. Tunnels are straight to slightly curved. The cross section is elliptical with a mean width of 35 cm and mean height of 20 cm. Tunnels are enlarged at intersections with shafts. The shafts are up to 1 m long. The burrows cover 4–8 m^2 and have a high density with some newer burrows cutting through old.

Morphotype 3 burrows are composed of a complex network of straight tunnels that join obliquely at ~40° and a limited number of shafts. Cross-sectional shape and diameter is highly variable within and between burrows. Mean diameter is 7 cm. Burrow tunnels are >2.5 m long. Shafts are >50 cm long and up to 10 cm wide. These burrows are interpreted as the result of animals burrowing along an already present system of plant roots.

Fractussemita henrii shares traits with all three morphotypes, but is distinct from each one. Morphotype 1 is different from *F. henrii* in having several chambers as part of the network and medial groove occurring in some of the tunnels. Morphotype 2 has much larger shafts and tunnels in both length and diameter than anything recorded for *F. henrii.* Morphotype 2 also has a higher density. *Fractussemita henrii* shows no crosscutting within or between burrows. Morphotype 3 has some similar diameters to *F. henrii*, but overall exhibits more variability in size and cross section shape. The tunnels are longer than segments than in *F. henrii*.

Riese et al. (2011).—Structures found in the Lower Jurassic Navajo Sandstone in southeast Utah are interpreted as burrows of social mammals or therapsids (Riese et al., 2011). The burrows are composed of a network of chambers and sinuous ramps and tunnels joined at Y and T branches. The burrow cross section is bean shaped with a mean width of 9.3 cm and a mean height of 4.2 cm. The ramps dip 6–60° from the horizontal.

The surface of the burrows is mostly smooth with few exhibiting scalloped walls. The scallops are 5–7 cm wide and rise 0.5–1.5 cm above the burrow surface. The scallops are interpreted as the marks from a tracemaker's manus.

Fractussemita henrii can be differentiated from these Jurassic burrows by an ovoid cross section in all its segments rather than bean shaped. The angle of the *F. henrii* tunnel segments have greater variability than what is recorded in the other Jurassic burrows.

Groenwald et al. (2001).—Structures found in the Lower Triassic Driekoppen Formation of northeast Free State, South Africa are interpreted as burrows produced by the therapsid *Trirachodon*. The burrows are a network of branching tunnels, chambers, and funnel-shaped entrance shafts. The tunnels and chambers dip 1–23°. The cross section of the burrow is bean shaped or W shaped with a bilobate floor and arched roof. Although the shape flattens out as the tunnels move away from an entrance towards chambers that are also flattened. Tunnel diameter is 5–12 cm.

The surface of the burrows preserves diagonal and transverse markings on the base and sides that are interpreted as scratch marks from the tracemaker. The scratches become more distinct moving into the burrow away from the entrance. The scratches converge towards the center of the burrow.

Fractussemita henrii is distinguished from tunnels of a similar size by having an ovoid cross section, distinct from a bean- or W-shaped cross section. The *Trirachodon* burrows exhibit significantly less variation in the dip of tunnels than *F. henrii.*

Possible behaviors and tracemakers

The networks preserved in *Fractussemita henrii* are interpreted as burrow systems for social mammals. 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). *Fractussemita henrii* burrows are 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). The ovoid cross section with a horizontal diameter slightly wider than the vertical diameter matches best with mammal burrows (Martin and Bennett, 1977; Bown and Kraus, 1983; Laundré, 1989).

The surficial morphology of *F. henrii* is more enigmatic than the architectural morphology. The short ridges are most likely to have been produced by the tracemaker. The parallel ridges on the roof of the burrow also appear to have been produced by tracemaker. Both of these morphologies are seen more prevalently in better-preserved trace fossils and modern burrows (e.g. Martin and Bennett, 1977; Burns et al., 1989; Gobetz and Martin, 2006). The random knobby texture is a pseudosurficial morphology that formed during preservation and is not useful for determining the tracemaker or mode of excavation. The repeating, parallel knob texture is similar to the scalloped walls preserved in other fossil burrows attributed to both Mesozoic therapsids and Cenozoic mammals (Gobetz and Martin, 2006; Riese et al., 2011) and is interpreted as the scratch marks of a paw excavating the burrow. Very similar features are seen in modern mole burrows (Gobetz, 2005) indicating a potential digging method for *F. henrii*.

Fractussemita henrii are likely the work of multiple individuals, all part 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 systems are modified on a continuous or seasonal basis (e.g., Lovegrove and Jarvis, 1986; Sumbera et al., 2003; Knight, 2009). Network burrows can be 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. Skinner, 2005; Smith and Reichman, 1984); 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 interpreted for fossil burrows as well (e.g. Meyer, 1999; Hasiotis et al., 2007; Riese et al., 2011, Krapovickas et al., 2012). Network burrows produced by extant mammals vary greatly in size based on the size of the excavators and the degree to which the 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). *Fractussemita henrii* burrows do not reach this size. The excavators are not interpreted as spending their lives underground and would perhaps come aboveground for some foraging and interaction with conspecifics. *Fractussemita henrii* is categorized as polychresichnia (Hasiotis, 2003) because the architecture represents multiple behaviors and uses from the tracemaker, such as protection from predators and weather, food storage, foraging tunnels, reproduction, and waste disposal.

The majority of mammals found in 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* is the smallest mammal found in the Morrison Formation and a likely tracemaker with many adaptations for scratch digging (Luo and Wible, 2005; Foster, 2009). Scratch digging is supported as a means for excavating *F. henrii* based upon the repeating, parallel knob texture.

PALEOECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

These burrows are useful in creating a more complete picture of the Salt Wash ecosystem given the paucity of mammalian and other small vertebrate body fossils from southeast Utah. Following the example of identified tracemakers, the excavators of both *Daemonelix martini* and *Fractussemita henrii* are assumed to be herbivorous or omnivorous. Complex burrows have not been attributed to carnivores. 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 *Paleocastor* or the modern pair of prairie dogs (*Cynomys ludovicianus*) and ferrets (*Mustela nigripes*) (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 have limited representation from body fossils, but invertebrates leave a robust trace fossil record in the Morrison (e.g., Hasiotis, 2004, 2008; Foster, 2007). There may have also been neutral burrow occupants who shared the burrow with the excavators or entered after the excavators had left. The commensalism may have been a normal behavior, such as burrowing owls (*Athene cunicularia*) making use of different rodent dens across the Americas (Haug et al., 1993), or a more unique occasion, such as the amphibian (*Broomistega*) found in a burrow with an estivating therapsid (*Thrinaxodon*) (Fernandez et al., 2013).

The extant comparisons for the *Daemonelix martini* and *Fractussemita henrii* tracemakers are herbivorous or omnivorous. Such diets would require 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 is interpreted as ferns, ginkgophytes, cycads, tree ferns, horsetails, and tree litter (e.g., Ash and Tidwell, 1998; Chin and Kirkland, 1998; Turner and Peterson, 2004), but only limited wood and rhizoliths were found preserved in the study area. All the softer plants could provide nourishment to trackmakers with above and below ground growth. In turn, if the tracemakers were caching seeds in their burrows, the unconsumed seeds may have helped continue the plant community. Roots are known to preferentially follow already opened paths through the soil and can have improved nutrient uptake in burrows (e.g., Pankhurst et al., 2002; Kautz et al., 2014; Kautz, 2015). The macropores created by the burrows, in association with smaller invertebrate work, would help aerate the soil, move up nutrients, and increase water infiltration all allowing plants to expand their root systems. A healthy, robust plant community would help keep the environment stable. The lithology of the study area shows that the local fluvial system could move and wipe out large area of formerly well-drained terrain, but by helping spread plants and keeping them healthy the tracemakers ensured there was a reserve of dry environment growth when the landscape changed.

The helical burrow architecture of *Daemonelix martini* and the network of *Fractussemita henrii* appear as products of cynodont and mammal excavation multiple times over millions of years. The common shapes can thus have implications for when mammalian-associated behaviors evolved and persisted in the synapsid lineage. Some burrowing behaviors appear to be genetic (Weber et al., 2013) and could be passed through a lineage over time if the burrowing behavior 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. Meyer (1999) calculates that this design is well suited for maintaining a constant temperate environment when the weather outside the burrow becomes too hot or cold. Networks offer a similar environmental constancy and multiple entrances and exits increases chances to escape predators. Networks typically have a more stifling atmosphere with higher levels of carbon dioxide and lower levels of oxygen that excavators must be physiologically able to tolerate (e.g., Lovegrove, 1989; Reichman and Smith, 1990). The different burrow types found in the Morrison Formation indicate tracemakers not only adapted for fossoriality in skeletons that may be found in further study, but also in unpreserved soft tissues. This shows a convergence in form across synapsid groups through time.

CONCLUSIONS

The new inchnospecies *Daemonelix 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 dwelling of an unknown primitive mammal that used them to shelter from the elements and predators, and raise their young. *Daemonelix martini* is assigned to the behavioral category domichnia. The new ichnogenus and ichnospecies *Fractussemita henrii* represents the burrows of a potentially social, primitive mammal. The burrows are composed of networks of tunnels and shafts without a pattern. *Fractussemita henrii* is assigned to polychresichnia as the burrows record multiple behaviors. The cross sections of both new ichnospecies are ovoid. 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 behavior for the late Jurassic illustrating how synapsid excavators continue to converge on helical and network architecture from the Permian to the present.

ACKNOWLEDGMENTS

Thanks to R. William Turner and Matt F. Jones for assistance in the field. Thanks to AAPG and the KU Geology for funding. Thanks to the reviewers for helpful comments.

REFERENCES

Ash, S.R., Tidwell, W.D., 1998. Plant megafossils from the Brushy Basin Member of the Morrison Formation near Montezuma Creek Trading Post, southeastern Utah. Modern Geology 23/1/1–4, 321–339.

Barbour, E.H., 1892, Notes on a new order of gigantic fossils: University Studies, v. 1, p. 301–313.

Barbour, E.H., 1895, Is Daemonelix a burrow? A reply to Dr. Theodor Fuchs: The American

Naturalist, v. 29, p. 5175–27.

Barbour, E.H., 1896, Nature, structure, and phylogeny of Daemonelix: Geological Society of America Bulletin, v. 8, p. 305–314.

Bordy, E.M., and Krummeck, W.D., 2016, Enigmatic continental burrows from the early Triassic transition of the Katberg and Burgersdorp Formations in the main Karoo Basin, South Africa: PALAIOS, v. 31, p.389–403.

Bordy, E.M., Sciscio, L., Abdala, F., McPhee, B.W., and Choiniere, J.N., 2017, First Lower Jurassic vertebrate burrow from southern Africa (upper Elliot Formation, Karoo Basin, South Africa): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 468, p. 362–372.

Bown, T.M., and Kraus, M.J., 1983, Ichnofossils of the alluvial Willwood Formation (Lower Eocene), Bighorn Basin, northwest Wyoming, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 43, p. 95–128.

Chin, K., Kirkland, J.I., 1998. Probable herbivore coprolites from the Upper Jurassic Mygatt–Moore Quarry, western Colorado. Modern Geology 22/2/1–4, 249–275.

Colombi, C.E., Fernandez, E., Currie, B.S., Alcober, O.A., Martinez, R., and Correa, G., 2012, Large-diameter burrows of the Triassic Ischigualasto Basin, NW Argentina: paleoecological and paleoenvironmental implications: PLoS ONE, v. 7, e50662, doi:10.1371/journal.pone.0050662.

Duncan, P., and Wrangham, R.W., 1971, On the ecology and distribution of subterranean insectivores in Kenya: Journal of Zoology, v. 164, p. 149–163.

Fernandez, V., Abdala, F., Carlson, K.J., Rubidge, B.S., Yates, A., and Tafforeau, P., 2013, Synchrotron reveals Early Triassic odd couple: injured amphibian and aestivating therapsid share burrow: *PLoS One*, v. 8, e64978, doi.org/10.1371/journal.pone.0064978.

Foster, J.R., 2007, Jurassic West: The Dinosaurs of the Morrison Formation and Their World: Bloomington, Indiana University Press, 389 p.

Foster, J.R., 2009, Preliminary body mass estimates for mammalian genera of the Morrison Formation (Upper Jurassic, North America): PaleoBios, v. 28, p. 114–122.

Friedman**,** M., and Daeschler, E.B., 2006, Late Devonian (Famennian) lungfishes from the Catskill Formation of Pennsylvania, USA: Paleontology, v. 49, p. 1167–1183.

Gates, T.A., 2005, The Late Jurassic Cleveland-Lloyd Dinosaur Quarry as a drought-induced assemblage: PALAIOS, v. 20, p. 363–375.

Gobetz, K.E., 2006, Possible burrows of mylagaulids (Rodentia: Aplodontoidea: Mylagaulidae) from the late Miocene (Barstovian) Pawnee Creek Formation of northeastern Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 119–136.

Gobetz, K.E., and Martin, L.D., 2006, Burrows of a gopher-like rodent, possibly *Gregorymys* (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 305–314.

Groenwald, G.H., Welman, J., and Maceachern, J.A., 2001, Vertebrate burrow complexes from the early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa: PALAIOS, v. 16, p. 148–160.

Hall, L.S., and Meyers, K., 1978, Variations in the microclimate in rabbit warrens in semi arid New South Wales: Australian Journal of Ecology, v. 3, p. 187–194.

Häntzschel, W., 1975, Trace fossils and problematica (2nd edition), *in* Teichert, C., ed. Treatise on Invertebrate Paleontology, part W. Miscellanea, suppl. 1. Boulder, Colorado, Geological Society of America (and University of Kansas Press), 269 p.

Hauge, E. A., Millsap, B. A., and Martell, M. S., 1993. Burrowing owls (Speotyto cunicularia).

in Poole, A., and Gill, F., eds. The birds of North America, No. 61. Philadelphia, The Academy of Natural Sciences, p. 1–20.

Hasiotis, S.T., 2002, Continental trace fossils: SEPM Short Course Notes, v. 51, 132 p.

Hasiotis, S.T., 2003, Complex ichnofossils of solitary and social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, p. 259–320.

Hasiotis, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177–268.

Hasiotis, S.T., 2008, Reply to the Comments by Bromley et al. of the paper "Reconnaissance of the Upper Jurassic Morrison Formation ichnofossils, Rocky Mountian Region. USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses" by Stephen T. Hasiotis: Sedimentary Geology, v. 208, p. 61–68.

Hasiotis, S.T. and Mitchell, C.E., 1993, A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo- and neo-ichnological evidence, and the identification of their burrowing signatures: Ichnos, v. 2, p. 291–314.

Hasiotis, S.T., Mitchell, C.E., and Dubiel**,** R.F., 1993, Application of morphologic burrow interpretations to discern continental burrow architects: lungfish or crayfish?: Ichnos, v. 2, p. 315–333.

Hasiotis, S.T., Wellner, R.W., Martin**,** A.J., and Demko, T.M., 2004, Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance: Ichnos, v. 11, p. 103–124.

Hasiotis, S.T., Platt, B.F., Hembree, D.I., and Everheart, M.J., 2007, The trace-fossil record of vertebrates, *in* Miller III, W., ed. Trace Fossils—Concepts, Problems, Prospects. Amsterdam, Elsevier Press, p. 196–218.

Hembree, D.I. and Hasiotis, S.T., 2006, The identification and interpretation of reptile ichnofossils in paleosols through modern studies: Journal of Sedimentary Research, v. 76, p. 575–588.

Hickman, G.C., 1983, Influence of the semi-aquatic habit in determining burrow structure of the star-nosed mole (*Condylura cristata*): Canadian Journal of Zoology, v. 61, p. 1688–1692.

Joeckel, R.M., and Tucker, S.T., 2013, Exceptionally well preserved latest Miocene (Hemphillian) rodent burrows from the eastern Great Plains, United States, and a review of the burrows of North American rodents: PALAIOS, v. 28, p. 793–824.

Kautz, T., 2015. Research on subsoil biopores and their functions in organically managed soils: A review. *Renewable Agriculture and Food Systems*, *30*(4), pp.318-327.

Kautz, T., Athmann, M. and Köpke, U., 2014. Growth of barley (Hordeum vulgare L.) roots in biopores with differing carbon and nitrogen contents. *Building Organic Bridges*, *2*, pp.391-394.

Kay, F.R., and Whitford, W.G., 1978, The burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, in south-central New Mexico: The American Midland Naturalist, v. 99, p. 270–279.

Kenagy, G.J., 1973, Daily and seasonal patterns of activity and energetics in a heteromyid rodent community: Ecology, v. 54, p. 1201–11219.

Kielan-Jaworowska, Z., Cifelli, R.L., and Luo, Z., 2004, Mammals from the Age of

Dinosaurs: Origins, Evolution, and Structure: New York, Columbia University Press, 630 p.

King, J.A., 1955, Social behavior, social organization, and population dynamics in a black-tailed prairie-dog town in the Black Hills of South Dakota: Contributions from the Laboratory of Vertebrate Biology, v. p. 1–123.

Kinlaw, A., 1999, A review of burrowing by semi-fossorial vertebrates in arid environments: Journal of Arid Environments, v. 41, p. 127–145.

Kjemperud, A.V., Schomacker, E.R., and Cross, T.A., 2008, Architecture and stratigraphy of alluvial deposits, Morrison Formation (Upper Jurassic), Utah: AAPG Bulletin, v. 92, p. 1055–1076.

Krapovickas, V., Mancuso, A.C., Marsicano, C.A., Domnanovich, N.S., and Schultz, C.L., 2012, Large tetrapod burrows from the Middle Triassic of Argentina: a behavioural adaptation to seasonal semi-arid climate?: Lethaia, v. 46, p. 154–169.

Lockley, M., Hunt, A., Conrad, K., and Robinson, J., 1992, Tracking dinosaurs and other extinct animals at Lake Powell: Park Science, v. 12, p. 16–17.

Lovegrove, B.G., 1989, The cost of burrowing by the social mole rats (Bathyergidae) *Cryptomys damarensis* and *Heterocephalus glaber*: the role of soil moisture: Physiological Zoology, v. 62, p. 449–469.

Lovegrove, B.G., and Jarvis, J.U.M., 1986, Coevolution between mole-rats (Bathyergidaae) and a geophyte, *Micranthus* (Iridaceae): Cimbebasia, v. 8, p. 79–85.

Luo, Z., and Wible, J.R., 2005, A late Jurassic digging mammal and early mammalian diversification. Science, v. 308, p. 103–107.

Luo, Z., Meng, Q., Ji, Q., Liu, D., Zhang, Y., and Neander, A.I., 2015, Evolutionary development in basal mammaliaforms as revealed by a docodontan: Science, v. 347, p. 760–764.

Mankin, P.C., and Getz, L.L., 1994, Burrow morphology as related to social organization of Microtus ochrogaster: Journal of Mammalology, v. 75, p. 492–499.

Martin, L.D., 1987, Beavers from the Harrison Formation (early Miocene) with a revision of Euhapsis: Dakoterra, v. 3, p. 73–91.

Martin, L.D., and Bennett, D.K., 1977, The Burrows of the Miocene Beaver *Palaeocastor*, Western Nebraska, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173–193.

McCahon, T.J., and Miller, K.B., 2015, Environmental significance of lungfish burrows (Gnathorhiza) within Lower Permian (Wolfcampian) paleosols of the US midcontinent: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 435, p. 1–12.

McKenna, M.C., and Bell, S.K., 1997, Classification of mammals above the species level: New York City, Columbia University Press, 631 p.

Meyer, R.C., 1999, Helical burrows as a palaeoclimate response: *Daimonelix* by *Palaeocastor*: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 147, p. 291–298.

Ostrom, J.H., and McIntosh, J.S., 1966, Marsh's Dinosaurs: The Collections from Como Bluff: New Haven, Yale University Press, p. 416.

Pankhurst, C.E., Pierret, A., Hawke, B.G. and Kirby, J.M., 2002. Microbiological and chemical properties of soil associated with macropores at different depths in a red-duplex soil in NSW Australia. *Plant and Soil*, *238*(1), pp.11-20.

Peterson, O.A., 1905, Description of new rodents and discussion of the origin of Daemonelix: Memoir of the Carnegie Museum, v. 2, p. 139–196.

Prothero, D.R., 1981, New Jurassic Mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic Theria: Bulletin of the American Museum of Natural History, v. 167, p. 281–325.

Reichman, O.J., and Smith, S.C., 1990, Burrows and burrowing behavior by mammals, *in* Genoways, H.H., ed. Current Mammalogy. New York, Plenum Press, p. 197–244.

Reynolds, T.D., and Wakkinen, W.L., 1987, Characteristics of the burrows of four species of rodents in undisturbed soils in southeastern Idaho: American Midland Naturalist, v. 118, p. 245–250.

Riese, D.J., Hasiotis, S.T., and Odier, G.P., 2011, Synapsid burrows and associated trace fossils in the Lower Jurassic Navajo Sandstone, southeastern Utah, U.S.A., indicates a diverse community living in a wet desert ecosystem: Journal of Sedimentary Research, v. 81, p. 299–325.

Riggs, E.S., 1945, Some early Miocene carnivores: Field Museum of Natural History Geological Series, v. 9, p. 69–114.

Robinson, J.W., and McCabe, P.J., 1998, Evolution of a braided river system: the Salt Wash Member of the Morrison Formation (Jurassic) in southern Utah, *in* Shanley, K.W., and McCabe, P.J., eds. Relative Role of Eustasy, Climate, and Tectonism in Continental Rocks. SEPM Special Publications No. 59, p. 93–107.

Skinner, J.D., 2005, The Mammals of the Southern African Sub-region: Cambridge, Cambridge University Press, 814 p.

Smith, R.M.H., 1987. Helical Burrow Casts of Therapsid Origin from the Beaufort Group (Permian) of South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 155–170.

Smith, C.C., and Reichman, O.J., 1984, The evolution of food caching by birds and mammals: Annual Review of Ecology and Systematics, v. 15, p. 329–351.

Stokes, W.L., 1957, Pterodactyl tracks from the Morrison Formation: Journal of Paleontology, v. 31, p. 952–954.

Turner**,** C.E., and Peterson**,** F., 1992, Sedimentology and stratigraphy of the Morrison Formation in Dinosaur National Monument: University of Wyoming National Park Service Research Center Annual Report, v. 16, p. 86–91.

Turner**,** C.E., and Peterson**,** F., 2004, Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem—a synthesis: Sedimentary Geology, v. 167, p. 309–355.

Weber, J.N., Peterson**,** B.K., and Hoekstra, H.E. 2013, Discrete genetic modules are responsible for complex burrow evolution in *Peromyscus* mice: Nature, v. 493, p. 402–405.

Woodrow, D.L., and Fletcher, F.W., 1969, Devonian dipnoan aestivation cylinders: Geological Society of America, Special Paper, v. 121, p. 383–384.

Zimmerman, J.W., 1990, Burrow characteristics of the nine-banded armadillo, *Dasypus novemcinctus*: The Southwestern Naturalist, v. 35, p. 226–227.

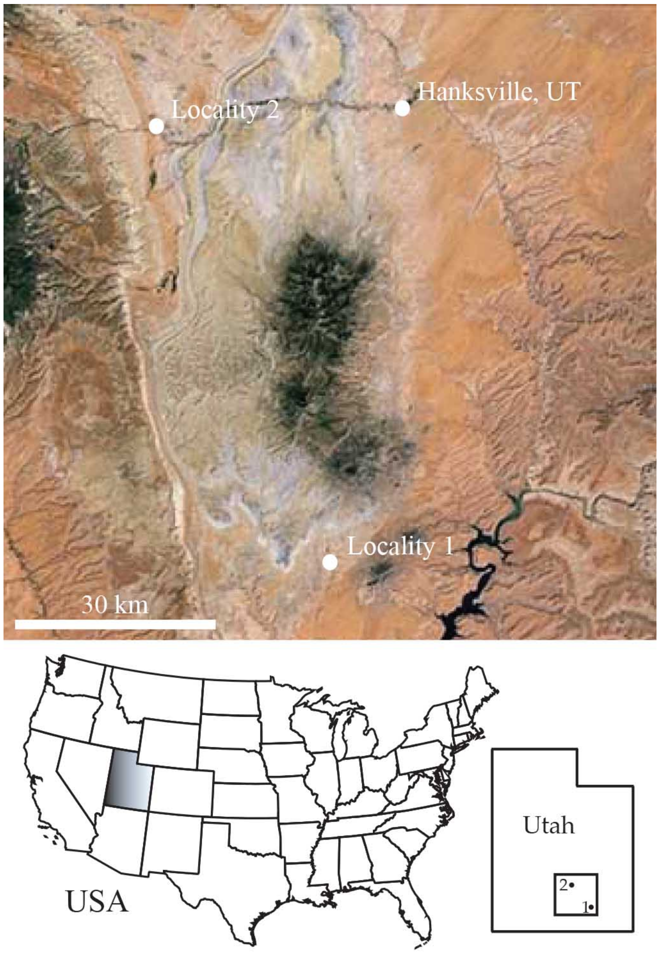

Figure 1—Location of study areas. Locality 1, Shootaring Canyon near Ticaboo, Utah; Locality 2, near Fruita, Utah. Satellite image courtesy of Google Earth.

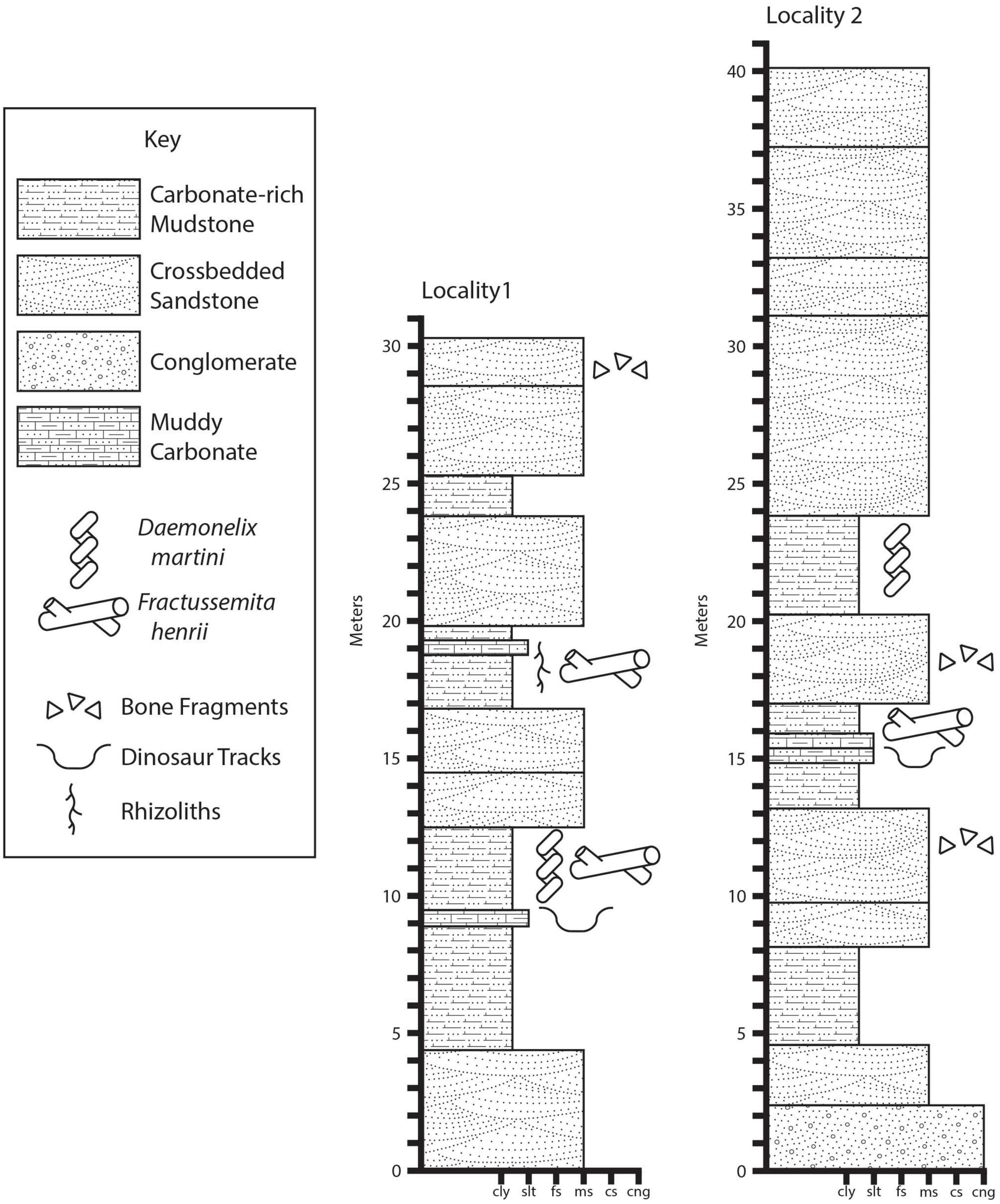

Figure 2—Stratigraphic sections through upper part of Salt Wash Member in study areas.

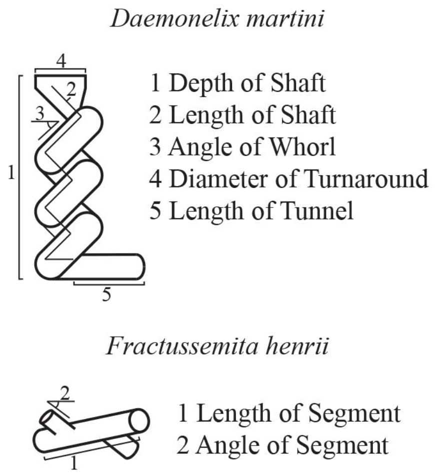

Figure 3—Schematic of burrow measurements.

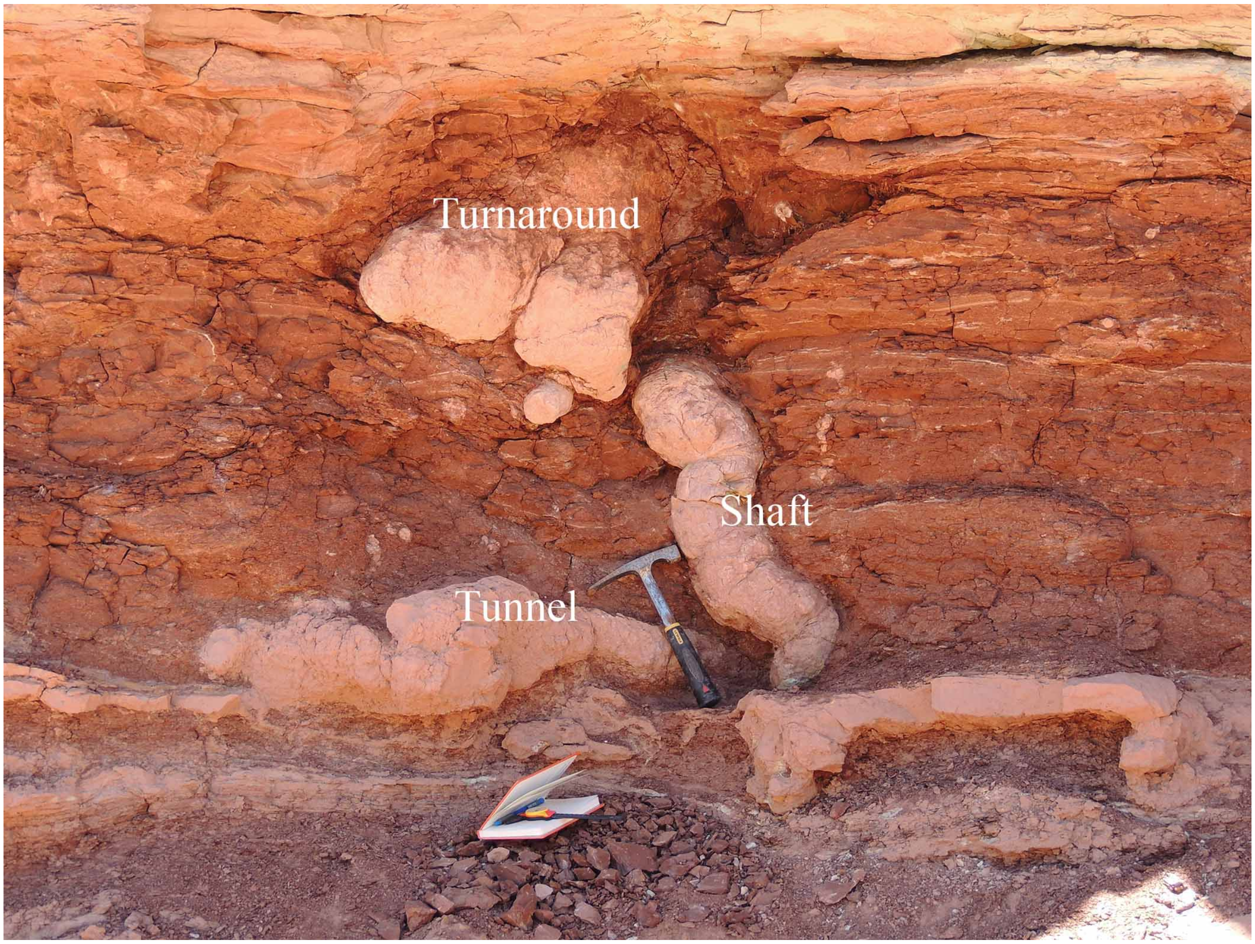

Figure 4—Example of *Daemonelix martini* with major architectural elements labeled. Rock hammer 28 cm long.

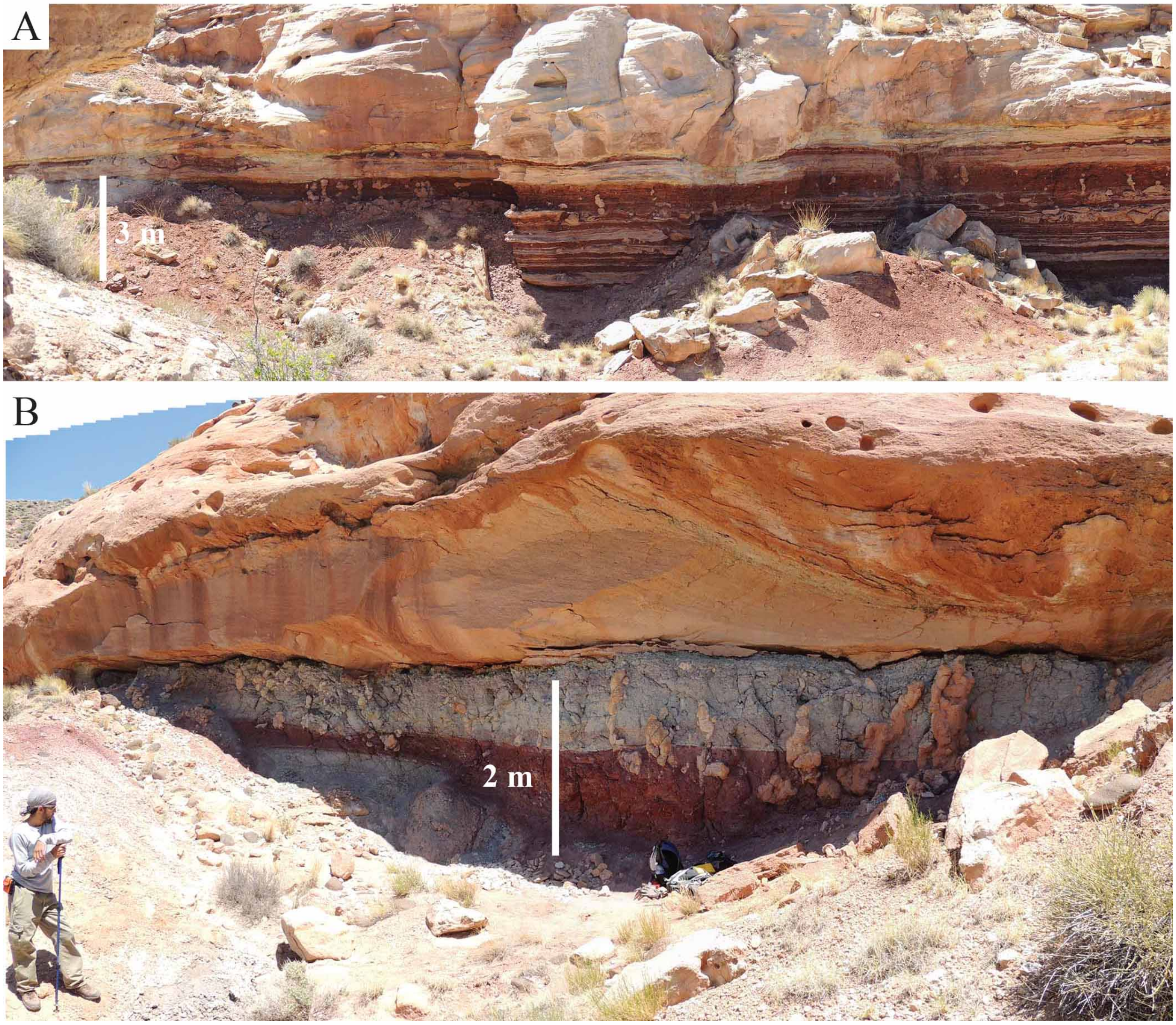

Figure 5—*Daemonelix martini* in outcrop. A) Burrows seen at a distance in lower paleosol at Locality 1. B) Burrows in upper paleosol at Locality 2.

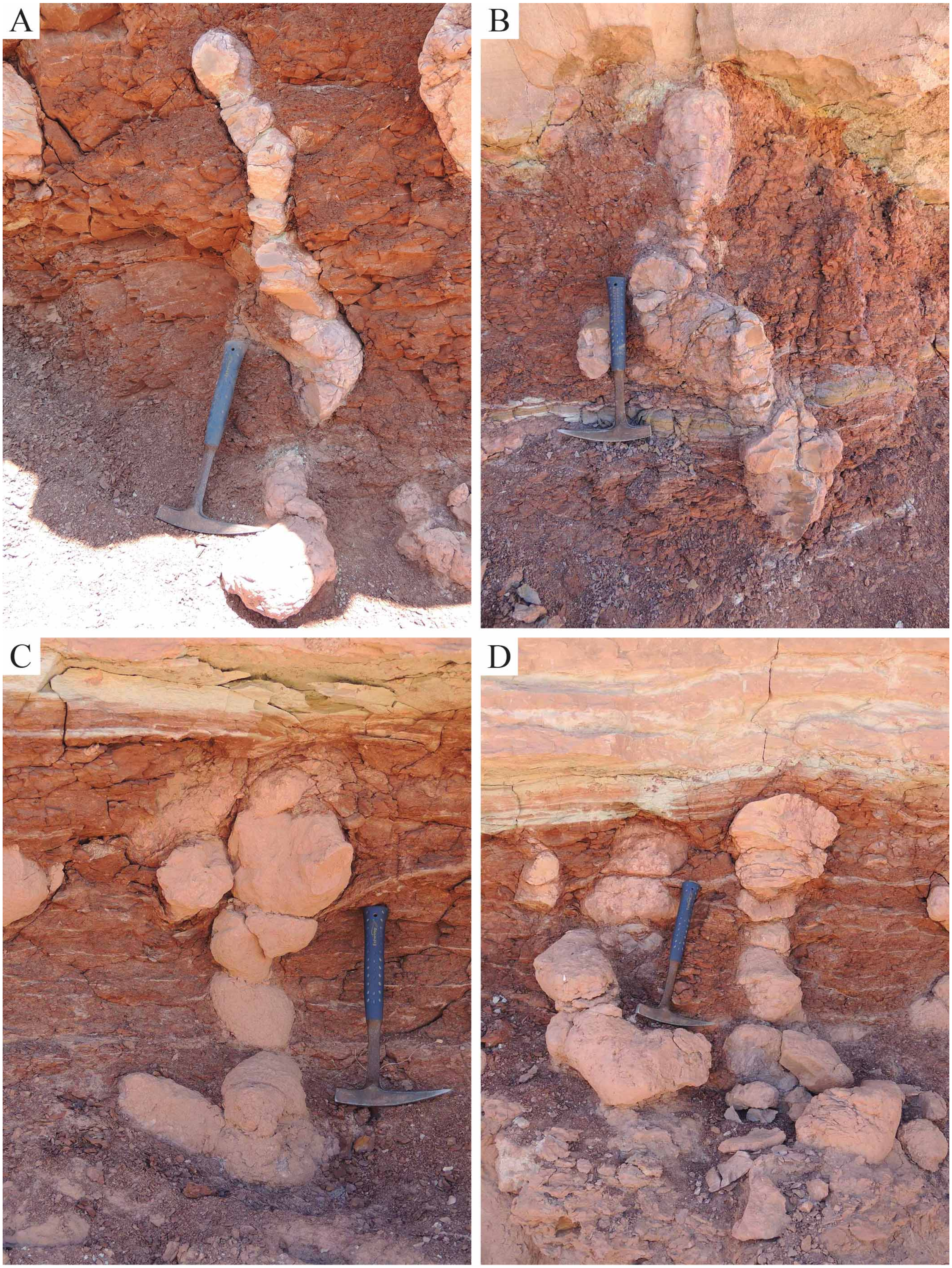
A
B
C
D

Figure 6—Examples of *Daemonelix martini* at Locality 1 near Ticaboo, Utah. Hammer 32 cm long.

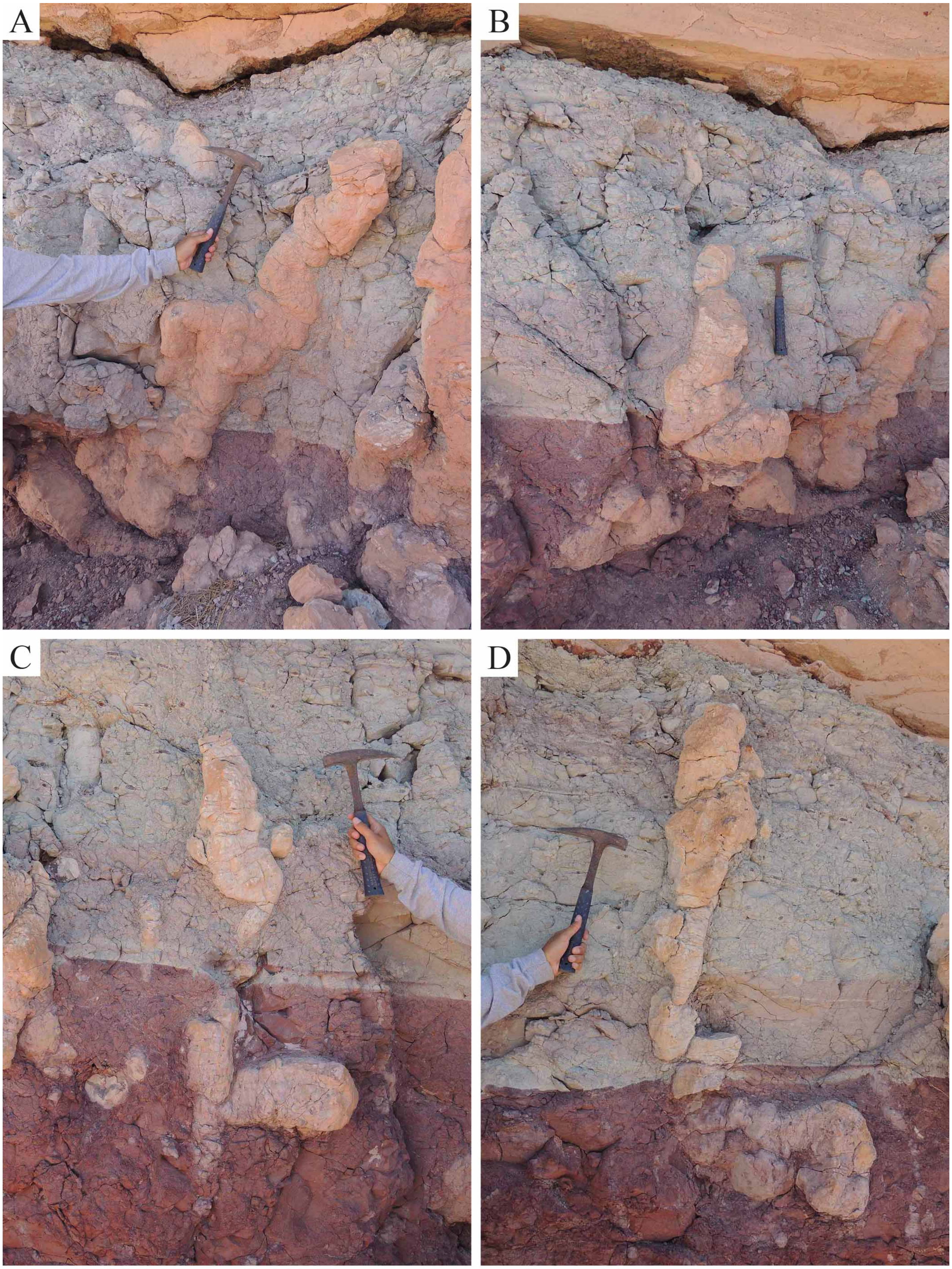
A
B
C
D

Figure 7—Examples of *Daemonelix martini* at Locality 2 near Fruita, Utah. Hammer 32 cm long.

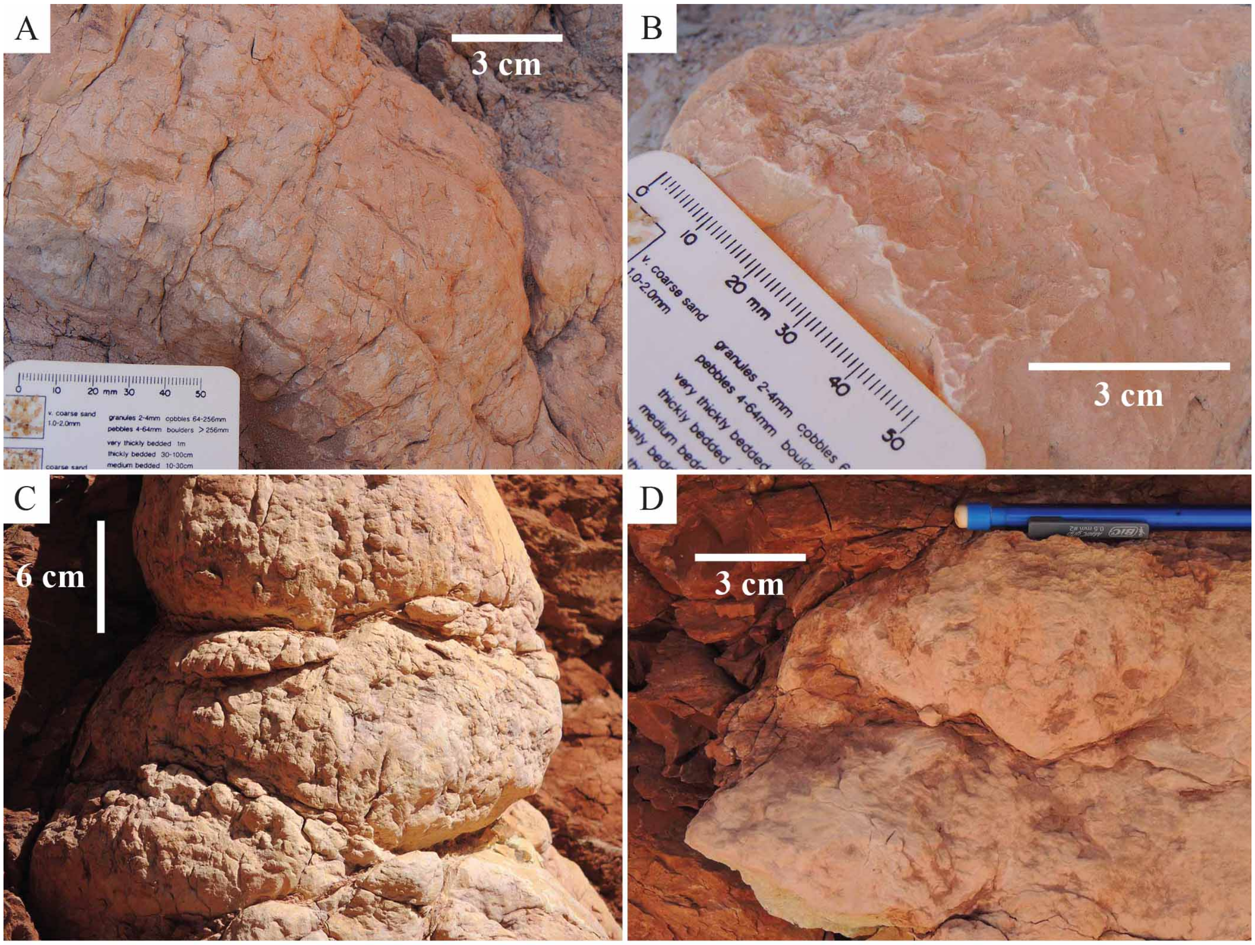

Figure 8—Surficial morphologies of *Daemonelix martini*. A) Large ridges. B) Small ridges. C) Large knobs. D) Small knobs.

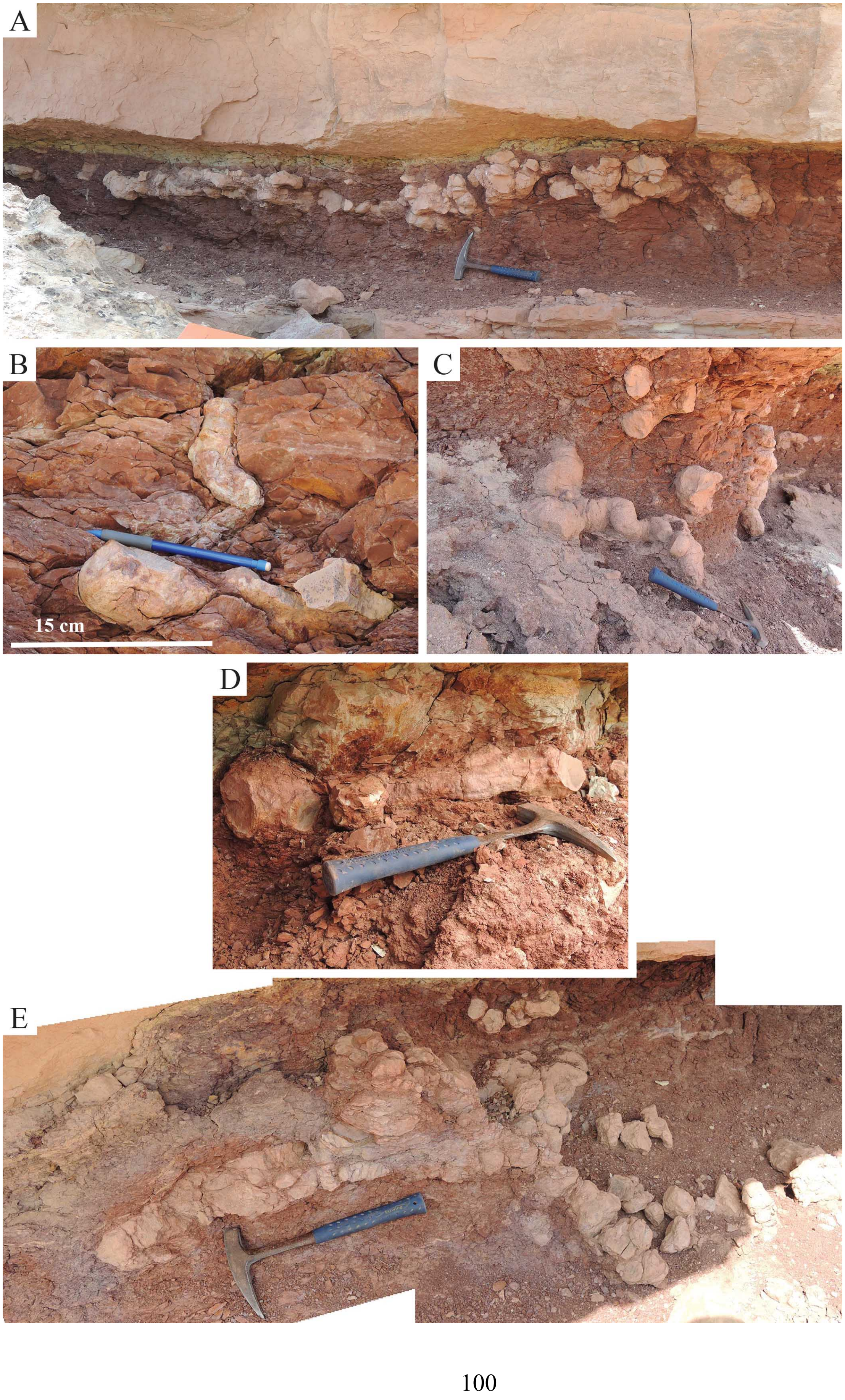
A
B
15 cm
C
D
E

Figure 9—Examples of *Fractussemita henrii* with distinct segments at Locality 1 near Ticaboo, Utah. Hammer 32 cm long.

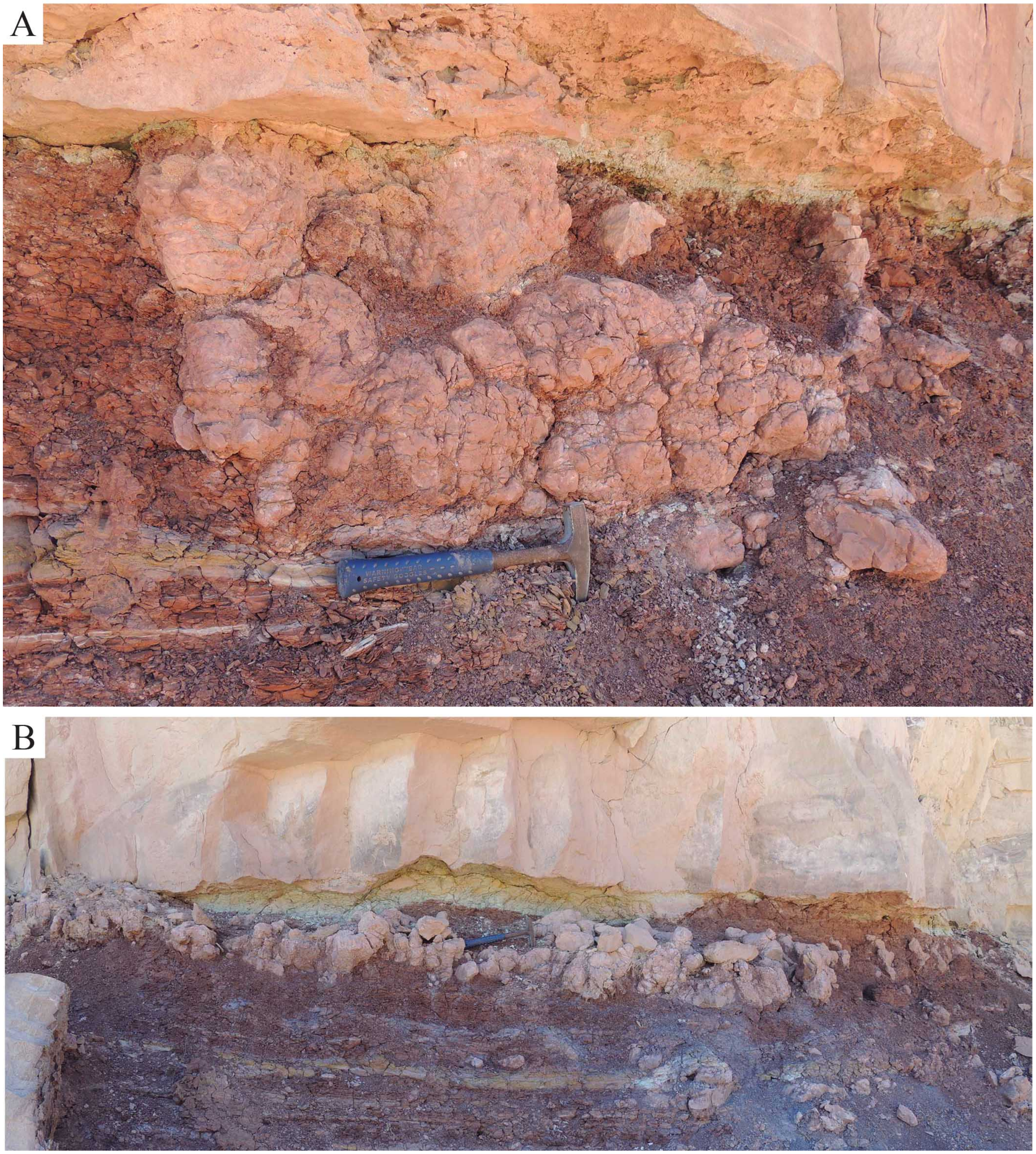

Figure 10—Examples of *Fractussemita henrii* with merged segments at Locality 1 near Ticaboo, Utah. Hammer 32 cm long.

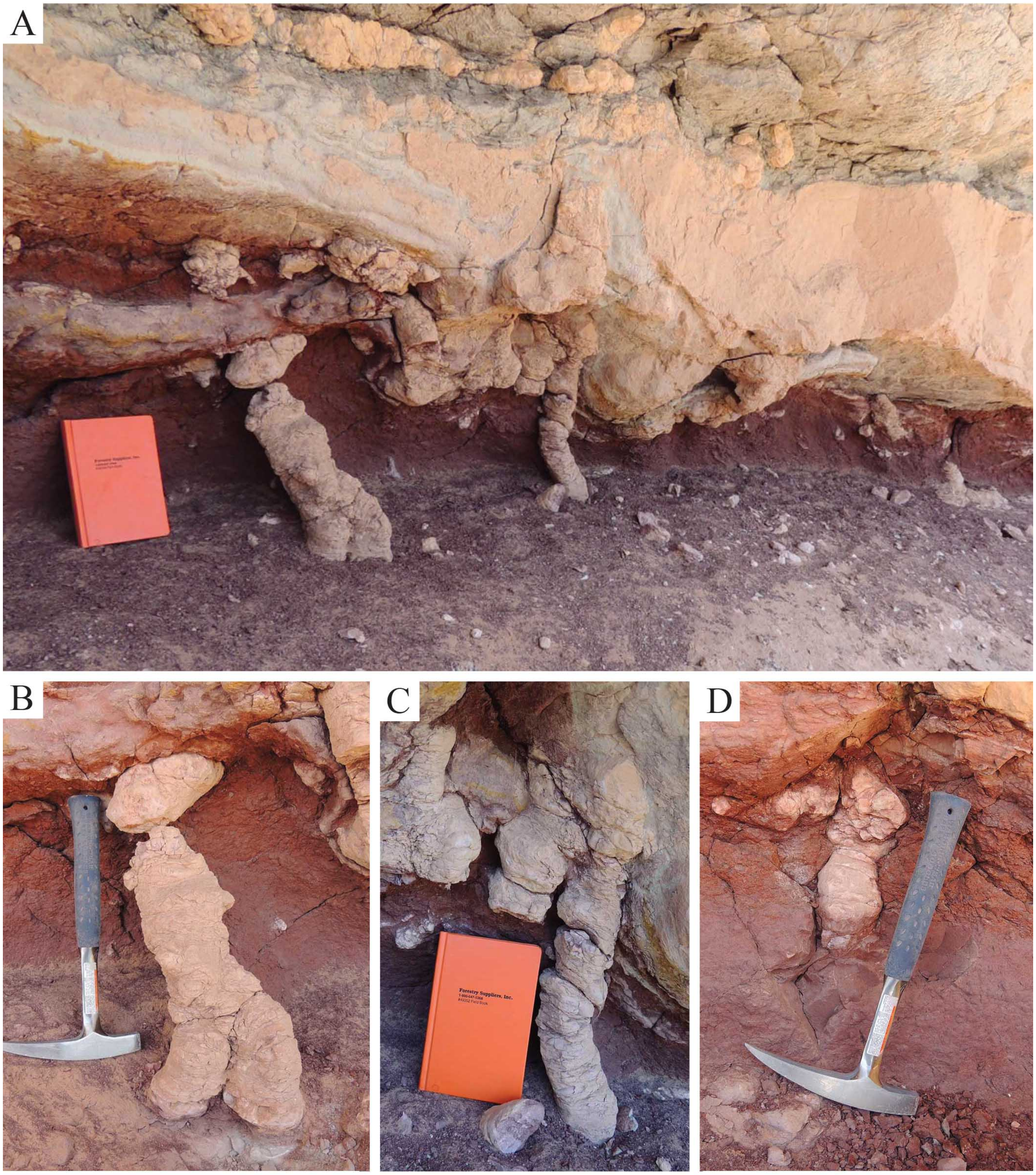

Figure 11—Examples of *Fractussemita henrii* at Locality 2 near Fruita, Utah. A) All specimens in outcrop. B, C, D) Closer view of specimens. Hammer 32 cm long. Notebook 19 cm tall.

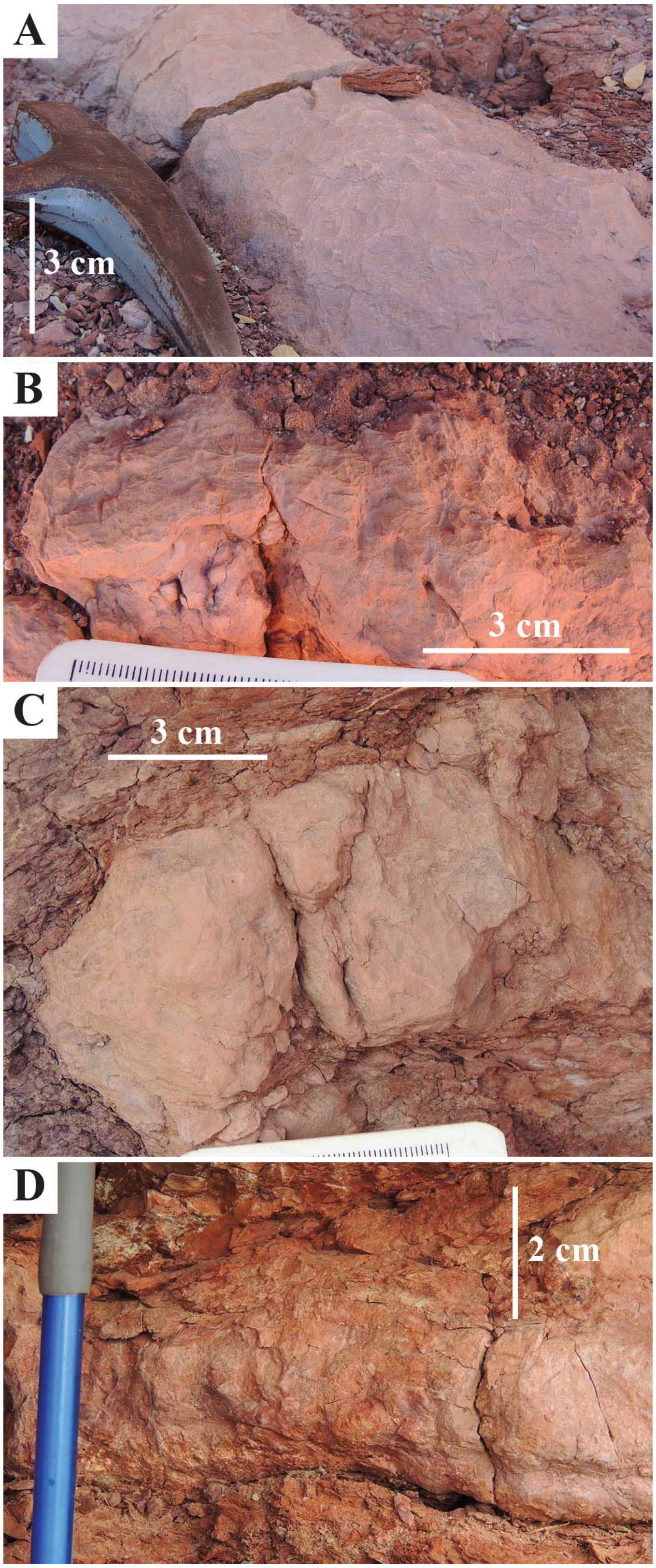
A
3 cm
B
3 cm
C
3 cm
D
2 cm

Figure 12—Surficial morphologies of *Fractussemita henrii*. A) Small ridges. B) Parallel ridges with small ridges. C) Small knobs. D) Parallel knobs.

CHAPTER FOUR. CONCLUSIONS

This thesis refined identification of structures previously identified as vertebrate burrows using criteria based on architectural and surficial morphology. The burrows are from two localities in southeast Utah, USA, in the Salt Wash Member of the Upper Jurassic Morrison Formation. The burrows were preserved by illuviated carbonate in multiple mudstone layers interpreted as paleosols. Thicker sandstone layers interpreted as channel deposits separate individual paleosols. Two types of major burrow types were identified and each named a new ichnospeices—*Daemonelix matini* and *Fractussemita henrii*.

Daemonelix matini is constructed of two architectural elements: a vertical to subvertical helical shaft that connects at an L-shaped junction to a horizontal tunnel. The cross section of the shaft and the tunnel elements is ovoid with the width being slightly larger than the height. The top of the shaft flares wider than the rest of the helix. The majority of shafts are vertical with some being subvertical. A minority of specimens preserve all parts of the burrow due to both the scour of overlying sandstones and the erosion of preserved trace fossils. When the tops of structures can be identified, the burrows appear to originate from the same paleosurface. The surface morphology of *D. martini* records features interpreted as scratch and/or tooth marks from excavation as well as accumulations of precipitated carbonate.

Daemonelix martini likely preserves dens excavated by an individual or pair based on size and complexity. Extant and ancient burrows with limited branching are typically produced for use by only a few individuals (e.g., Martin and Bennett, 1977; Smith, 1987; Reynolds and Wakkinen, 1987; Zimmerman, 1990; Kinlaw, 1999). The similarity between *D. martini* and the daemonelices produced by the Miocene beaver *Paleocastor* suggest that *D. martini* was utilized by its tracemaker in a similar way—foraging above ground and using the burrow to rest and shelter from the elements and predators (Martin and Bennett, 1977). *Daemonelix martini* is assigned to the behavioral category domichnia.

There were no body fossils found associated with *Daemonelix martini.* Although numerous mammal species are found in the Morrison Formation, none have been uncovered near the field area (e.g., Prothero, 1981; Kielan-Jaworowska et al., 2004; Foster, 2007). Jurassic mammals were a diverse assemblage with members of different groups exhibiting adaptations for a fossorial lifestyle (e.g., Luo and Wible, 2005; Luo, 2007; Luo et al., 2015). *Daemonelix martini* was probably constructed by a yet undiscovered tracemaker.

Fractussemita henrii is constructed of an interconnected network of shafts and tunnels at various angles. Individual burrow elements may be straight, curved, or helical. The cross sections of all elements are ovoid with the width being slightly larger than the height. The interconnected segments are joined randomly in a maze pattern. Some specimens are preserved by such massive accumulations of carbonate that individual segments are difficult to impossible to identify with certainty. The surficial morphology of *F. henrii* preserves the abiotic accumulation of carbonate as well as textures that are interpreted as the marks of teeth and claws used for excavation.

Fractussemita henrii is interpreted as a burrow system for social mammals. Synapsids from the Permian to the recent construct complex networks (e.g., Mankin and Getz, 1994; Groenewald et al., 2001; Gobetz and Martin, 2006; Riese et al., 2011). Maze burrows can be used for multiple purposes: protection (e.g., Kenagy, 1973, Kay and Whitford, 1978; Reichman and Smith, 1990); food storage (e.g. Skinner, 2005; Smith and Reichman, 1984); foraging (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 interpreted for fossil burrows (e.g., Meyer, 1999; Hasiotis et al., 2007; Riese et al., 2011, Krapovickas et al., 2012). The excavators are not interpreted as spending their lives totally underground and would perhaps come above ground for foraging. *Fractussemita henrii* is categorized as polychresichnia (Hasiotis, 2003).

The majority of mammals found in the Morrison Formation are small (e.g., Kielan-Jaworowska et al., 2004; Foster, 2009), so there are multiple potential tracemakers based on size. *Fruitafossor windscheffeli* is the smallest mammal found in the Morrison Formation and a likely tracemaker with many adaptations for scratch digging (Luo and Wible, 2005; Foster, 2009).

Without any body fossils in the area, *Daemonelix matini* and *Fractussemita henrii* extend knowledge of the Morrison Formation biota to reveal hidden biodiversity. They expand the image of the floodplain beyond the dinosaurs to the small vertebrate and invertebrates. Both ichnospecies contribute to interpretations of the Salt Wash Member recording a wet-dry savannah climate (e.g. Engelmann et al., 2004; Hasiotis, 2004, 2008; Parrish et al., 2004; Platt, 2012) and indicate local paleohydrologic conditions.

REFERENCES

DUNCAN, P., and WRANGHAM**,** R.W., 1971, On the ecology and distribution of subterranean insectivores in Kenya: Journal of Zoology, v. 164, p. 149–163.

ENGELMANN, G.F., CHURE, D.J., and FIORILLO, A.R., 2004, The implications of a dry climate for the paleoecology of the fauna of the Upper Jurassic Morrison Formation: Sedimentary Geology, v. 167, p. 297–308.

FOSTER, J.R., 2007, Jurassic West: The Dinosaurs of the Morrison Formation and Their World: Indiana University Press, Bloomington, 389 p.

FOSTER, J.R., 2009, Preliminary body mass estimates for mammalian genera of the Morrison Formation (Upper Jurassic, North America): PaleoBios, v. 28, p. 114–122.

GOBETZ, K.E., and MARTIN, L.D., 2006, Burrows of a gopher-like rodent, possibly *Gregorymys* (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 305–314.

GROENWALD, G.H., WELMAN, J., and MACEACHERN, J.A., 2001, Vertebrate burrow complexes from the early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa: PALAIOS, v. 16, p. 148–160.

HALL, L.S., and MEYERS, K., 1978, Variations in the microclimate in rabbit warrens in semi arid New South Wales: Australian Journal of Ecology, v. 3, p. 187–194.

HASIOTIS, S.T., 2003, Complex ichnofossils of solitary and social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, p. 259–320.

HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177–268.

HASIOTIS, S.T., 2008, Reply to the Comments by Bromley et al. of the paper “Reconnaissance of the Upper Jurassic Morrison Formation ichnofossils, Rocky Mountian Region. USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses” by Stephen T. Hasiotis: Sedimentary Geology, v. 208, p. 61–68.

HASIOTIS, S.T., PLATT, B.F., HEMBREE, D.I., and EVERHEART, M.J., 2007, The trace-fossil record of vertebrates, *in* Miller III, W. (ed.), Trace Fossils —Concepts, Problems, Prospects: Elsevier Press, Amsterdam, p. 196–218.

HICKMAN, G.C., 1983, Influence of the semi-aquatic habit in determining burrow structure of the star-nosed mole (*Condylura cristata*): Canadian Journal of Zoology, v. 61, p. 1688–1692.

KAY, F.R., and WHITFORD, W.G., 1978, The burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, in south-central New Mexico: The American Midland Naturalist, v. 99, p. 270–279.

KENAGY, G.J., Daily and seasonal patterns of activity and energetics in a heteromyid rodent community: Ecology, v. 54, p. 1201–11219.

KIELAN-JAWOROWSKA**,** Z., CIFELLI, R.L., and LUO**,** Z., 2004, Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure: Columbia University Press, New York, 630 p.

KINLAW, A., 1999, A review of burrowing by semi-fossorial vertebrates in arid environments: Journal of Arid Environments, v. 41, p. 127–145.

KRAPOVICKAS, V., MANCUSO, A.C., MARSICANO, C.A., DOMNANOVICH, N.S., and SCHULTZ, C.L., 2012, Large tetrapod burrows from the Middle Triassic of Argentina: a behavioural adaptation to seasonal semi-arid climate?: Lethaia, v. 46, p. 154–169.

LOVEGROVE, B.G., and JARVIS, J.U.M., 1986, Coevolution between mole-rats (Bathyergidaae) and a geophyte, *Micranthus* (Iridaceae): Cimbebasia, v. 8, p. 79–85.

LUO, Z., 2007, Transformation and diversification in early mammal evolution: Nature, v. 450, p. 1011–1019.

LUO, Z., and WIBLE, J.R., 2005, A late Jurassic digging mammal and early mammalian diversification. Science, v. 308, p. 103–107.

LUO, Z., MENG, Q., JI, Q., LIU, D., ZHANG, Y., and NEANDER, A.I., 2015, Evolutionary development in basal mammaliaforms as revealed by a docodontan: Science, v. 347, p. 760–764.

MANKIN, P.C., and GETZ, L.L., 1994, Burrow morphology as related to social organization of Microtus ochrogaster: Journal of Mammalology, v. 75, p. 492–499.

MARTIN, L.D., and BENNETT, D.K., 1977, The Burrows of the Miocene Beaver *Palaeocastor*, Western Nebraska, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173–193.

MEYER, R.C., 1999, Helical burrows as a palaeoclimate response: *Daimonelix* by *Palaeocastor*: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 147, p. 291–298.

PARRISH, J.T., PETERSON, F., and TURNER, C.E., 2004, Jurassic "savannah" –plant taphonomy and climate of the Morrison Formation (Upper Jurassic, Western USA): Sedimentary Geology, v. 167, p. 137–162.

PLATT, B.F., 2012, Quantification of ichnological, paleoecological, paleohydrological, and paleoclimatological information from the Upper Jurassic Morrison Formation: Unpublished Ph.D. dissertation, The University of Kansas, Lawrence, 513 p.

PROTHERO, D.R., 1981, New Jurassic Mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic Theria: Bulletin of the American Museum of Natural History, v. 167, p. 281–325.

REICHMAN, O.J., and SMITH, S.C., 1990, Burrows and burrowing behavior by mammals, *in* Genoways, H.H., ed., Current Mammalogy: Plenum Press, New York, p. 197–244.

REYNOLDS, T.D., and WAKKINEN, W.L., 1987, Characteristics of the burrows of four species of rodents in undisturbed soils in southeastern Idaho: American Midland Naturalist, v. 118,

p. 245–250.

RIESE, D.J., HASIOTIS, S.T., and ODIER, G.P., 2011, Synapsid burrows and associated trace fossils in the Lower Jurassic Navajo Sandstone, southeastern Utah, U.S.A., indicates a diverse community living in a wet desert ecosystem: Journal of Sedimentary Research, v. 81, p. 299–325.

SKINNER, J.D., 2005, The Mammals of the Southern African Sub-region: Cambridge University Press, Cambridge, 814 p.

SMITH, R.M.H., 1987. Helical Burrow Casts of Therapsid Origin from the Beaufort Group (Permian) of South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 155–170.

SMITH, C.C., and REICHMAN, O.J., 1984, The evolution of food caching by birds and mammals: Annual Review of Ecology and Systematics, v. 15, p. 329–351.

ZIMMERMAN, J.W., 1990, Burrow characteristics of the nine-banded armadillo, *Dasypus novemcinctus*: The Southwestern Naturalist, v. 35, p. 226–227.

REFERENCES

ABBA, A.M., UDRIZAR SAUTHIER, D.E., and VIZCAINO, S.F., 2005, Distribution and use of burrows and tunnels of *Chaetophractus villosus* (Mammalia, Xenarthra) in the eastern Argentinean pampas: Acta Theriologica, v. 50, p. 115–124.

ANDERSON, A.O., and ALLRED, D.M., 1964, Kangaroo rat burrows at the Nevada Test Site: The Great Basin Naturalist, v. 24, p. 93–101.

ASH, S.R., and TIDWELL, W.D., 1998. Plant megafossils from the Brushy Basin Member of the Morrison Formation near Montezuma Creek Trading Post, southeastern Utah. Modern Geology 23/1/1–4, 321–339.

BANCROFT, W.J., GARKAKLIS, M.J., and ROBERTS, J.D., 2005, Burrow building in seabird colonies: a soil-forming process in island ecosystems: Pedobiologia, v. 49, p. 149–165.

BARBOUR, E.H., 1892, Notes on a new order of gigantic fossils: University Studies, v. 1, p. 301–313.

BARBOUR, E.H., 1895, Is Daemonelix a burrow? A reply to Dr. Theodor Fuchs: The American Naturalist, v. 29, p. 5175–27.

BARBOUR, E.H., 1896, Nature, structure, and phylogeny of Daemonelix: Geological Society of America Bulletin, v. 8, p. 305–314.

BENNETT, N.C., and FAULKES, C.G., 2000, African mole-rats: ecology and eusociality: Cambridge University Press, Cambridge, 273 p.

BERMAN, D.S., 1976, Occurrence of *Gnathorhiza* (Osteichthyes: Dipnoi) in aestivation burrows in the Lower Permian of New Mexico with description of a new species: Journal of Paleontology, v. 50, p. 1034–1039.

BORDY, E.M., and KRUMMECK, W.D., 2016, Enigmatic continental burrows from the early

Triassic transition of the Katberg and Burgersdorp Formations in the main Karoo Basin, South Africa: PALAIOS, v. 31, p.389–403.

BORDY, E.M., SCISCIO, L., ABDALA, F., MCPHEE, B.W., and CHOINIERE, J.N., 2017, First Lower Jurassic vertebrate burrow from southern Africa (upper Elliot Formation, Karoo Basin, South Africa): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 468, p. 362–372.

BOWN, T.M., and KRAUS, M.J., 1983, Ichnofossils of the Alluvial Willwood Formation (Lower Eocene), Bighorn Basin, Northwest Wyoming, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 43, p. 95–128.

BRITT, B.B., SCHEETZ, R.D., and DANGERFIELD, A., 2008, A suite of dermestid beetle traces on dinosaur bone from the Upper Jurassic Morrison Formation, Wyoming, USA: Ichnos, v. 15, p. 59–71.

BURNS, J.A., FLATH, D.L., and CLARK, T.W., 1989, On the structure and function of white-tailed prairie dog burrows: The Great Basin Naturalist, v. 49, p. 517–524**.**

BUTLER, D.R., 1995, Zoogeomorphology: animals as geomorphic agents: Cambridge University Press, Cambridge, 231 p.

CARRANO, M.T., and VELEZ-JUARBE, J., 2006, Paleoecology of the Quarry 9 vertebrate Assemblage from Como Bluff, Wyoming (Morrison Formation, Late Jurassic): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 147–159.

CARROLL, R.L., 1965, Lungfish burrows from the Michigan Coal Basin: Science, v. 148, p. 963–964.

CHIN, K., and KIRKLAND, J.I., 1998. Probable herbivore coprolites from the Upper Jurassic Mygatt–Moore Quarry, western Colorado. Modern Geology, v. 23, 249–275.

COLOMBI, C.E., FERNANDEZ, E., CURRIE, B.S., ALCOBER, O.A., MARTINEZ, R., and CORREA, G., 2012, Large-diameter burrows of the Triassic Ischigualasto Basin, NW Argentina: paleoecological and paleoenvironmental implications: PLoS ONE, v. 7, e50662, doi:10.1371/journal.pone.0050662.

DAMIANI, R., MODESTO, S., ADAM, Y., and NEVELING, J., 2003, Earliest evidence of cynodont burrowing: Proceedings of the Royal Society B, v. 270, p. 1747–1751.

DAVIES, K.C., and JARVIS, J.U.M., 1986, The burrow systems and burrowing dynamics of the mole-rats *Bathyergus suillus* and *Cryptomys hottentotus* in the fynbos of south-western Cape, South Africa: Journal of Zoology, v. 209, p. 125–147.

DEMKO, T.M., CURRIE, B.S., and NICOLL, K.A., 2004, Regional paleoclimatic and stratigraphic implications of paleosols and fluvial/overbank architecture in the Morrison Formation (Upper Jurassic), Western Interior, USA: Sedimentary Geology, v. 167, p. 115–135.

DUNCAN, P., and WRANGHAM, R.W., 1971, On the ecology and distribution of subterranean insectivores in Kenya: Journal of Zoology, v. 164, p. 149–163.

ENGELMANN, G.F., CHURE, D.J., and FIORILLO, A.R., 2004, The implications of a dry climate for the paleoecology of the fauna of the Upper Jurassic Morrison Formation: Sedimentary Geology, v. 167, p. 297–308.

EVANS, S.E., and MILNER, A.R., 1993, Frogs and Salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America: Journal of Vertebrate Paleontology, v. 13, p. 24–30.

FERNANDEZ, V., ABDALA, F., CARLSON, K.J., RUBIDGE, B.S., YATES, A., and TAFFOREAU, P., 2013, Synchrotron reveals Early Triassic odd couple: injured amphibian and aestivating therapsid share burrow: *PLoS One*, v. 8, e64978, doi.org/10.1371/journal.pone.0064978.

FOSTER, J.R., 2007, Jurassic West: The Dinosaurs of the Morrison Formation and Their World: Indiana University Press, Bloomington, 389 p.

FOSTER, J.R., 2009, Preliminary body mass estimates for mammalian genera of the Morrison Formation (Upper Jurassic, North America): PaleoBios, v. 28, p. 114–122.

FRIEDMAN, M., and DAESCHLER, E.B., 2006, Late Devonian (Famennian) lungfishes from the Catskill Formation of Pennsylvania, USA: Paleontology, v. 49, p. 1167–1183.

GATES, T.A., 2005, The Late Jurassic Cleveland-Lloyd Dinosaur Quarry as a drought-induced assemblage: PALAIOS, v. 20, p. 363–375.

GOBETZ, K.E., 2005, Claw impressions in the walls of modern mole (*Scalopus aquaticus*) tunnels as a means to identify fossil burrows and interpret digging movements: Ichnos, v. 12, p. 227–231.

GOBETZ, K.E., 2006, Possible burrows of mylagaulids (Rodentia: Aplodontoidea: Mylagaulidae) from the late Miocene (Barstovian) Pawnee Creek Formation, northeastern Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 119–136.

GOBETZ, K.E., and MARTIN, L.D., 2006, Burrows of a gopher-like rodent, possibly *Gregorymys* (Geomyoidea: Geomyidae: Entoptychtinae), from the early Miocene Harrison Formation, Nebraska: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 237, p. 305–314.

G**OOD**, S.C., 2004, Paleoenvironmental and paleoclimatic significance of freshwater bivalves in the Upper Jurassic Morrison Formation, Western Interior, USA. Sedimentary Geology, v. 167, p. 163–176.

GREENWOOD, P.H., 1986, The natural history of African lungfishes: Journal of Morphology, v. 190, p. 163–179.

GROENWALD, G.H., WELMAN, J., and MACEACHERN, J.A., 2001, Vertebrate burrow complexes from the early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa: PALAIOS, v. 16, p. 148–160.

HALL, L.S., and MEYERS, K., 1978, Variations in the microclimate in rabbit warrens in semi arid New South Wales: Australian Journal of Ecology, v. 3, p. 187–194.

HÄNTZSCHEL, W., 1975, Trace fossils and problematica (2nd edition), *in* Teichert, C. (ed.), Treatise on Invertebrate Paleontology, part W. Miscellanea, suppl. 1: Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, p. 269.

HASIOTIS, S.T., 2002, Continental trace fossils: SEPM Short Course Notes, v. 51, p. 1–132.

HASIOTIS, S.T., 2003, Complex ichnofossils of solitary and social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, p. 259–320.

HASIOTIS, S.T., 2004, Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses: Sedimentary Geology, v. 167, p. 177–268.

HASIOTIS, S.T., 2008, Reply to the Comments by Bromley et al. of the paper "Reconnaissance of the Upper Jurassic Morrison Formation ichnofossils, Rocky Mountian Region. USA: Paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses" by Stephen T. Hasiotis: Sedimentary Geology, v. 208, p. 61–68.

HASIOTIS, S.T. and MITCHELL, C.E., 1993, A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo- and neo-ichnological evidence, and the identification of their burrowing signatures: Ichnos, v. 2, p. 291–314.

HASIOTIS, S. T., and DEMKO, T. M., 1996, Terrestrial and freshwater trace fossils, Upper Jurassic Morrison Formation, Colorado Plateau. The Continental Jurassic: Museum of Northern Arizona Bulletin, v. 60, p. 355–370.

HASIOTIS, S.T., MITCHELL, C.E., and DUBIEL, R.F., 1993, Application of morphologic burrow interpretations to discern continental burrow architects: lungfish or crayfish?: Ichnos, v. 2, p. 315–333.

HASIOTIS, S.T., KIRKLAND, J.I., and CALLISON, G., 1998, Crayfish fossils and burrows from the Upper Jurassic Morrison Formation of western Colorado: Modern Geology, v. 22, p. 481–491.

HASIOTIS, S.T., WELLNER, R.W., MARTIN, A.J., and DEMKO, T.M., 2004, Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance: Ichnos, v. 11, p. 103–124.

HASIOTIS, S.T., PLATT, B.F., HEMBREE, D.I., and EVERHEART, M.J., 2007, The trace-fossil record of vertebrates, in Miller, W.III., ed., Trace Fossils—Concepts, Problems, Prospects: Elsevier, Amsterdam, p. 196–218.

HAUGE, E. A., MILLSAP, B. A., and MARTELL, M. S., 1993. Burrowing owls (Speotyto cunicularia). *in* Poole, A., and Gill, F., eds. The birds of North America, No. 61. Philadelphia, The Academy of Natural Sciences, p. 1–20.

HEMBREE, D.I. and HASIOTIS, S.T., 2006, The identification and interpretation of reptile ichnofossils in paleosols through modern studies: Journal of Sedimentary Research, v. 76, p. 575–588.

HEMBREE, D.I., HASIOTIS, S.T., and MARTIN, L.D., 2004, Amphibian burrows and ephemeral ponds of the Lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 203, p. 127–152.

HEMBREE, D.I., MARTIN, L.D., and HASIOTIS, S.T., 2005, *Torridorefugium eskridgensis* (new ichnogenus and ichnospecies): Amphibian aestivation burrows from the Lower Permian Speiser Shale of Kansas: Journal of Paleontology, v. 79, p. 583–593.

HICKMAN, G.C., 1983, Influence of the semi-aquatic habit in determining burrow structure of the star-nosed mole (*Condylura cristata*): Canadian Journal of Zoology, v. 61, p. 1688–1692.

HILDEBRAND, M., 1985, Digging in quadrupeds. In Hildebrand, M., Bramble, D. M., Liem, K. L., and Wake, D. B., eds., Functional Vertebrate Morphology: The Belknap Press of Harvard University Press, Cambridge, p. 89–109.

HOTTON, C.L., and BAGHAI-RIDING, N.L., 2010, Palynological evidence for conifer dominance within a heterogeneous landscape in the Late Jurassic Morrison Formation, USA, *in* Gee, C.T., ed., Plants in Mesozoic Time: Morphological Innovations, Phylogeny, Ecosystems: Indiana University Press, Bloomington, p. 295–328.

HUNT, R.M., XIANG-XUE, X., and KAUFMAN, J., 1983, Miocene burrows of extinct bear dogs: indication of early denning behavior of large mammalian carnivores: Science, v. 221, p. 364–366.

IMLAY, R.W., 1980, Jurassic paleobiogeography of the conterminous United States on its continental setting: United States Geological Survey Professional Paper 1062. United States Government Printing Office, Washington, D.C.

JARVIS, J.U.M., O'RAIN, M.J., BENNETT, N.C., and SHERMAN, P.W., 1994, Mammalian eusociality: a family affair: Trends in Ecology and Evolution, v. 9, p. 47–51.

JOECKEL, R.M., and TUCKER, S.T., 2013, Exceptionally well preserved latest Miocene

(Hemphillian) rodent burrows from the eastern Great Plains, United States, and a review of the burrows of North American rodents: PALAIOS, v. 28, p. 793–824.

KAUTZ, T., 2015. Research on subsoil biopores and their functions in organically managed soils: A review. *Renewable Agriculture and Food Systems*, *30*(4), pp.318-327.

KAUTZ, T., ATHMANN, M. and KÖPKE, U., 2014. Growth of barley (Hordeum vulgare L.) roots in biopores with differing carbon and nitrogen contents. *Building Organic Bridges*, *2*, pp.391-394.

KAY, F.R., and WHITFORD, W.G., 1978, The burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, in southcentral New Mexico: The American Midland Naturalist, v. 99, p. 270–279.

KENAGY, G.J., 1973, Daily and seasonal pattern of activity and energetics in a heteromyid rodent community: Ecology, v. 54, p. 1201–1219.

KIELAN-JAWOROWSKA**, Z.,** CIFELLI, R.L., and LUO, Z., 2004, Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure: Columbia University Press, New York, 630 p.

KING, J.A., 1955, Social behavior, social organization, and population dynamics in a black tailed prairie dog town in the Black Hills of South Dakota: Contribution from the Laboratory of Vertebrate Biology, no. 67, p. 1–123.

KINLAW, A., 1999, A review of burrowing by semi-fossorial vertebrates in arid environments: Journal of Arid Environments, v. 41, p. 127–145.

KJEMPERUD, A.V., SCHOMACKER, E.R., and CROSS, T.A., 2008, Architecture and stratigraphy of alluvial deposits, Morrison Formation (Upper Jurassic), Utah: AAPG Bulletin, v. 92, p. 1055–1076.

KNIGHT, J., 2009, Infilled pocket gopher tunnels: seasonal features of high alpine plateaux: Earth Surface Processes and Landforms, v. 34, p. 590–595.

KOWALLIS, B.J., CHRISTIANSEN, E.H., DEINO, A.L., PETERSON, F., TURNER, C.E., KUNK, M.J., and OBRADOVICH, 1998, The age of the Morrison Formation: Modern Geology, v. 22, p. 235–260.

KOWALLIS, B.J., BRITT, B.B., GREENHALGH, B.W., and SPRINKEL, D.A., 2007, New U-Pb zircon ages from an ash bed in the Brush Basin Member of the Morrison Formation near Hanksville, Utah, *in* Willis G.C., Hylland, M.D., Clark, D.L., and Chidsey, T.C., Jr., eds., Central Utah: Geology of a Dynamic Landscape: Utah Geological Association, Salt Lake City, p. 75–80.

KRAPOVICKAS, V., MANCUSO, A.C., MARSICANO, C.A., DOMNANOVICH, N.S**., and** SCHULTZ, C.L., 2012, Large tetrapod burrows from the Middle Triassic of Argentina: a behavioural adaptation to seasonal semi-arid climate?: Lethaia, v. 46, p. 154–169.

LAUNDRÉ, J.W., 1989, Horizontal and vertical diameter of five small mammal species in southeastern Idaho: Great Basin Naturalist, v. 49, p. 646–649.

LE ROUX, P.C., BOELHOUWERS, J., DAVIS, J.K., HAUSSMANN, N.S., JANTZE, E.**J., and** MEIKLEJOHN, K.I., 2011, Spatial association of lemming burrows with landforms in the Swedish subarctic mountains: implications for periglacial feature stability: Arctic, Antarctic, and Alpine Research, v. 43, p. 223–228.

LIU, J. and LI, L., 2013, Large tetrapod burrows from the Permian Naobaogou Formation of the Daqingshan Area, Nei Mongol, China: Acta Geologica Sinica, v. 87, p. 1501–1507.

LOCKLEY, M., HUNT, A., CONRAD, K., and ROBINSON, J., 1992, Tracking dinosaurs and other extinct animals at Lake Powell: Park Science, v. 12, p. 16–17.

LOOPE, D.B., DINGUS, L., SWISHER III, C.C., and MINJIN, C., 1998, Life and death in a Late Cretaceous dune field, Nemegt basin, Mongolia: Geology, v. 26, p. 27–30.

LOVEGROVE, B.G., 1989, The cost of burrowing by the social mole rats (Bathyergidae) *Cryptomys damarensis* and *Heterocephalus glaber*: the role of soil moisture: Physiological Zoology, v. 62, p. 449–469.

LOVEGROVE, B.G., and JARVIS, J.U.M., 1986, Coevolution between mole-rats (Bathyergidaae) and a geophyte, *Micranthus* (Iridaceae): Cimbebasia, v. 8, p. 79–85.

LÖVY, M., ŠKLÍBA, J., HROUZKOVÁ, E., DVOŘÁKOVÁ, V., NEVO, E., AND ŠUMBERA, R., 2015, Habitat and burrow system characteristics of the blind mole rat *Spalax galili* in an area of supposed systematic speciation: PLoS ONE, v. 10, e0133157.

LUO, Z., 2007, Transformation and diversification in early mammal evolution: Nature, v. 450, p. 1011–1019.

LUO, Z., and WIBLE, J.R., 2005, A late Jurassic digging mammal and early mammalian diversification: Science, v. 308, p. 103–107.

LUO, Z., MENG, Q., JI, Q., LIU, D., ZHANG, Y., and NEANDER, A.I., 2015, Evolutionary development in basal mammaliaforms as revealed by a docodontan: Science, v. 347, p. 760–764.

LYNCH, C.D., 1980, Ecology of the suricate, *Suricata suricatta* and yellow mongoose, *Cynictis penicillata* with special reference to their reproduction: Memoirs of the National Museum 14, Bloemfontein, 145 p.

MANKIN, P.C., and GETZ, L.L., 1994, Burrow morphology as related to social organization of *Microtus ochrogaster*: Journal of Mammalogy, v. 75, p. 492–499.

MARTIN, A.J., 2009, Dinosaur burrows in the Otway Group (Albian) of Victoria, Austalia, and their relation to Cretaceous polar environments: Cretaceous Research, v. 30, p. 1223–1237.

MARTIN, L.D., 1987, Beavers from the Harrison Formation (early Miocene) with a revision of Euhapsis: Dakoterra, v. 3, p. 73–91.

MARTIN, L.D., and BENNETT, D.K., 1977, The Burrows of the Miocene Beaver *Palaeocastor*, Western Nebraska, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 173–193.

MCALPIN, S., DUCKETT, P., and STOW, A., 2011, Lizards cooperatively tunnel to construct a long-term home for family members: PLoS ONE, v. 6, e19041.

MCCAHON, T.J., and MILLER, K.B., 2015, Environmental significance of lungfish burrows (Gnathorhiza) within Lower Permian (Wolfcampian) paleosols of the US midcontinent: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 435, p. 1–12.

MCKENNA, M.C., and BELL, S.K., 1997, Classification of mammals above the species level: Columbia University Press, New York City, 631 p.

MEYER, R.C., 1999, Helical burrows as a palaeoclimate response: *Daimonelix* by *Palaeocastor*: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 147, p. 291–298.

OGG, J.G., 2004, The Jurassic Period, *in* Gradstein, F.M., Ogg, J.G., and Smith, A.G., eds., A Geologic Time Scale: Cambridge University Press, Cambridge, p. 307–343.

OGNEV, S.I., 1947, Mammals of the U.S.S.R. and adjacent countries: Israel Program for Scientific Translation, Jerusalem.

OSTROM, J.H., and MCINTOSH, J.S., 1966, Marsh's Dinosaurs: The Collections from Como Bluff: Yale University Press, New Haven, 416 p.

PANKHURST, C.E., PIERRET, A., HAWKE, B.G. and KIRBY, J.M., 2002. Microbiological and chemical properties of soil associated with macropores at different depths in a red-duplex soil in NSW Australia. *Plant and Soil*, *238*(1), pp.11-20.

PARRISH, J.T., PETERSON, F., and TURNER, C.E., 2004, Jurassic "savannah" –plant taphonomy and climate of the Morrison Formation (Upper Jurassic, Western USA): Sedimentary Geology, v. 167, p. 137–162.

PETERSON. F., 1994, Sand dunes, sabkhas, streams, and shallow seas: Jurassic paleo geography in the southern part of the Western Interior Basin, *in* Caputo, M.V., Peterson, J.A., Franczyk, K.J., eds., Mesozoic Systems of the Rocky Mountain Region, USA: Rocky Mountain Section, Society for Sedimentary Geology (SEPM), Denver, p. 233–272.

PETERSON, O.A., 1905, Description of new rodents and discussion of the origin of Daemonelix: Memoir of the Carnegie Museum, v. 2, p. 139–196.

PIPERINGOS, G.N. and O'SULLIVAN, R.B., 1978, Principal unconformities in Triassic and Jurassic rocks, Western Interior United States—a preliminary survey: United States Geological Survey Professional Paper,

PLATT, B.F., 2012, Quantification of ichnological, paleoecological, paleohydrological, and paleoclimatological information from the Upper Jurassic Morrison Formation: Unpublished Ph.D. dissertation, The University of Kansas, Lawrence, 513 p.

PROTHERO, D.R., 1981, New Jurassic Mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic Theria: Bulletin of the American Museum of Natural History, v. 167, p. 281–325.

REICHMAN, O.J., and SMITH, S.C., 1990, Burrows and burrowing behavior by mammals, *in* Genoways, H.H., ed., Current Mammalogy: Plenum Press, New York, p. 197–244.

REYNOLDS, T.D., and WAKKINEN, W.L., 1987, Characteristics of the burrows of four species of rodents in undisturbed soils in southeastern Idaho: American Midland Naturalist, v. 118, p. 245–250.

REYNOLDS, J.D., GOODWIN, N.B., and FRECKLETON, R.P., 2002, Evolutionary transitions in parental care and live bearing in vertebrates: Philosophical Transactions of the Royal Society B: Biological Sciences, v. 357, p. 269–281.

RIESE, D.J., HASIOTIS, S.T., and ODIER, G.P., 2011, Synapsid burrows and associated trace fossils in the Lower Jurassic Navajo Sandstone, southeastern Utah, U.S.A., indicates a diverse community living in a wet desert ecosystem: Journal of Sedimentary Research, v. 81, p. 299–325.

RIGGS, E.S., 1945, Some early Miocene carnivores: Field Museum of Natural History Geological Series, v. 9, p. 69–114.

ROBINSON, J.W., and MCCABE, P.J., 1998, Evolution of a braided river system: the Salt Wash Member of the Morrison Formation (Jurassic) in southern Utah, *in* Relative Role of Eustasy, Climate, and Tectonism in Continental Rocks, SEPM Special Publications No. 59, Society for Sedimentary Geology (SEPM), p. 93–107.

SCHAETZL, R., and ANDERSON, S., 2009, Soils: Genesis and Geomorphology: Cambridge University Press, Cambridge, 817 p.

SCHARFF, A., LOCKER-GRUTJEN, O., KAWAKLIKA, M., and BURDA, H., 2001, Natural history of the giant mole-rat, *Cryptomys mechowi* (Rodentia: Bathyergidae), from Zambia: Journal of Mammalogy, v. 82, p. 1003–1015.

SHEETS, R.G., LINDER, R., and DAHLGREN, R.B., 1971, Burrow systems of prairie dogs in South Dakota, Journal of Mammalogy, v. 52, p. 451–453.

SIDOR, C.A., MILLER, M.F., and ISBELL, J.L., 2008, Tetrapod burrows the Triassic of Antarctica: Journal of Vertebrate Paleontology, v. 28, p. 277–284.

SKINNER, J.D., 2005, The Mammals of the Southern African Sub-region: Cambridge University Press, Cambridge, 814 p.

SMITH, C.C., and REICHMAN, O.J., 1984, The evolution of food caching by birds and mammals: Annual Review of Ecology and Systematics, v. 15, p. 329–351.

SMITH, R.M.H., 1987, Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 155–169.

SMITH, R.M.H., 1993, Vertebrate taphonomy of the Late Permian floodplain deposits in the southwestern Karoo Basin of South Africa: PALAIOS, v. 8, p. 45–67.

STEINER, M.B., LUCAS, S.G., and SHOEMAKER, E.M., 1994, Correlation and age of the Upper Jurassic Morrison Formation from magnetostratigraphic analysis. In: Caputo, M.V., Peterson, J.A., Franczyk, K.J. (Eds.), Mesozoic Systems of the Rocky Mountain Region, USA. Rocky Mountain Section, Society for Sedimentary Geology (SEPM), Denver, CO, p. 233–272.

STOKES, W.L., 1957, Pterodactyl tracks from the Morrison Formation: Journal of Paleontology, v. 31, p. 952–954.

SUBALUSKY, A.L., FITZGERALD, L.A., and SMITH, L.L., 2009, Ontogenetic niche shifts in the American Alligator establish functional connectivity between aquatic systems: Biological Conservation, v. 142, p. 1507–1514.

SUMBERA, R., BURDA, H., CHITAUKALI, W.N., and KUBOVA, J., 2003, Silvery mole-rats (*Heliophobius argenteocinereus*, Bathyerigidae) change their burrow architecture seasonally: Naturwissenschaften, v. 90, p. 370–373.

ŠUMBERA, R., MAZOCH, V., PATZENHAUEROVÁ, H., LÖVY, M., ŠKLÍBA, J., BRYJA, J., and BURDA, H., 2012, Burrow architecture, family composition and habitat characteristics of the largest social African mole-rat: the giant mole-rat constructs really giant burrow systems: Acta Theriologica, v. 57, p. 121–130.

TALANDA, M., DZIECIOL, S., SULEJ, T**.**, and NIEDZWIEDZKI, G., 2011, Vertebrate burrow system from the Upper Triassic of Poland: PALAIOS, v. 26, p. 99–105.

TRACY, C.R., REYNOLDS, S.J., MCARTHUR, L., TRACY, C.R., and CHRISTIAN, K.A., 2007, Ecology of aestivation in a cocoon-forming frog, *Cyclorana australis* (Hylidae): Copeia, v. 4, p. 901–912.

TURNER, C.E., and PETERSON, F., 1992, Sedimentology and stratigraphy of the Morrison Formation in Dinosaur National Monument: University of Wyoming National Park Service Research Center Annual Report, v. 16, p. 86–91.

TURNER, C.E., and PETERSON, F., 2004, Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem—a synthesis: Sedimentary Geology, v. 167, p. 309–355.

TURNBULL**,** W. D., and REED, C. A., 1967, *Pseudochrysochloris*, a specialized burrowing mammal from the early Oligocene of Wyoming: Journal of Paleontology, v. 41, p. 623–631.

VLECK, D., 1981, Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*: Oecologia, v. 49, p. 391–396.

VOIGT, S., SCHNEIDER, J.W., SABER, H., HMINNA, A. LAGNAOUI, A., KLEIN, H., BROSIG, A., and FISCHER, J., 2011, Complex tetrapod burrows from Middle Triassic red beds of the Argana Basin (Western High Atlas, Morocco): PALAIOS, v. 26, p. 555–566.

VOORHIES, M.R., 1975a, Vertebrate burrows, *in* Frey, R.W., ed., The Study of Trace Fossils: Spring-Verlag, New York, p. 325–350.

VOORHIES, M.R., 1975b, A new genus and speices of fossil kangaroo rat and its burrow: Journal of Mammalogy, v. 56, p. 160–176.

WEBER, J.N., PETERSON, B.K., and HOEKSTRA, H.E. 2013, Discrete genetic modules are responsible for complex burrow evolution in *Peromyscus* mice: Nature, v. 493, p. 402–405.

WOODROW, D.L., and FLETCHER, F.W., 1969, Devonian dipnoan aestivation cylinders: Geological Society of America, Special Paper, v. 121, p. 383–384.

ZIMMERMAN, J.W., 1990, Burrow characteristics of the nine-banded armadillo, *Dasypus novemcinctus*: The Southwestern Naturalist, v. 35, p. 226–227.

APPENDIX A

Daemonelix martini Architectural Morphologies

Site 1 Locality

Structure ID	Shaft Depth (cm)	Length of Shaft (cm)	Incline of Shaft (degrees from horizontal)	Incline of Whorls (degrees from horizontal)	Turnaround Diameter (cm)	Shaft, Vertical Diameter (cm)	Shaft, Horizontal Diameter (cm)	Tunnel Length (cm)	Tunnel, Vertical Diameter (cm)	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	-	-	-
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+8 e	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	-	-	-	-	-	-	-

Site 2 Locality

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

Fractussemita henrii Architectural Morphologies

Site 1 Locality
Distinct Segments

Structure ID	Segment	Length (cm)	Width (cm)	Height (cm)	Incline of Segment (degrees from horizontal)	Path (straight, curved, helical)
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

Site 2 Locality

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	

Merged Segments

Structure ID	Length Along Outcrop (cm)	Depth (cm)
1i	280.50	-
2i	134.72	46.33

* Potentially two merged shafts.